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Phylogeny and genetic diversity of the banana Fusarium wilt pathogen *Fusarium oxysporum* f. sp. *cubense* in the Indonesian centre of origin

N. Maryani[1,2,3*], L. Lombard[4], Y.S. Poerba[5], S. Subandiyah[6], P.W. Crous[2,4], and G.H.J. Kema[1,2*]

[1]*Wageningen University and Research, Wageningen Plant Research, The Netherlands;* [2]*Wageningen University and Research, Laboratory of Phytopathology, Wageningen, The Netherlands;* [3]*Biology Education, Universitas Sultan Ageng Tirtayasa (UNTIRTA), Banten, Indonesia;* [4]*Westerdijk Fungal Biodiversity Institute, Uppsalalaan 8, 3584CT, Utrecht, The Netherlands;* [5]*Research Centre for Biology, Indonesian Institute of Sciences (LIPI), Cibinong, Indonesia;* [6]*Entomology and Phytopathology Department, Gajah Mada University, Yogyakarta, Indonesia*

*Correspondence: N. Maryani, nani.maryanimartawi@wur.nl; G.H.J. Kema, gert.kema@wur.nl

Abstract: *Fusarium oxysporum* f. sp. *cubense* (Foc), the causal agent of Fusarium wilt or Panama disease on banana, is one of the major constraints in banana production worldwide. Indonesia is the centre of origin for wild and cultivated bananas, which likely co-evolved with Foc. This study explored the widest possible genetic diversity of Foc by sampling across Indonesia at 34 geographically and environmentally different locations in 15 provinces at six islands. This resulted in a comprehensive collection of ~200 isolates from 40 different local banana varieties. Isolates were identified and assessed using sequence analysis of the translation elongation factor-1alpha (*tef1*), the RNA polymerase II largest subunit (*rpb1*), and the RNA polymerase II second largest subunit (*rpb2*). Phylogenetic analyses of these genes allowed the identification of 180 isolates of *Fusarium oxysporum* f. sp. *cubense* (Foc), and 20 isolates of the *Fusarium fujikuroi* species complex (FFSC), the *Fusarium incarnatum-equiseti* species complex (FIESC), and the *Fusarium sambucinum* species complex (FSSC). Further analyses, incorporating a worldwide collection of Foc strains, revealed nine independent genetic lineages for Foc, and one novel clade in the *Fusarium oxysporum* species complex (FOSC). Selected isolates from each lineage were tested on the banana varieties Gros Michel and Cavendish to characterise their pathogenicity profiles. More than 65 % of the isolates were diagnosed as Tropical Race 4 (Foc-TR4) due to their pathogenicity to Cavendish banana, which supports the hypothesis that Foc-TR4 is of Indonesian origin. Nine independent genetic lineages for Foc are formally described in this study. This biodiversity has not been studied since the initial description of Foc in 1919. This study provides a detailed overview of the complexity of Fusarium wilt on banana and its diversity and distribution across Indonesia.

Key words: Morphology, New species, Panama disease, Pathogenicity, Tropical Race 4, 11 New taxa.

Taxonomic novelties: New species: *Fusarium cugenangense* N. Maryani, L. Lombard, Kema & Crous, *F. duoseptatum* N. Maryani, L. Lombard, Kema & Crous, *F. grosmichelii* N. Maryani, L. Lombard, Kema & Crous, *F. hexaseptatum* N. Maryani, L. Lombard, Kema & Crous, *F. kalimantanense* N. Maryani, L. Lombard, Kema & Crous, *F. odoratissimum* N. Maryani, L. Lombard, Kema & Crous, *F. phialophorum* N. Maryani, L. Lombard, Kema & Crous, *F. purpurascens* N. Maryani, L. Lombard, Kema & Crous, *F. sangayamense* N. Maryani, L. Lombard, Kema & Crous, *F. tardichlamydosporum* N. Maryani, L. Lombard, Kema & Crous, *F. tardicrescens* N. Maryani, L. Lombard, Kema & Crous.

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INTRODUCTION

Indonesia is one of the main centres of origin for banana in South-East Asia (Valmayor *et al.* 1999). Edible banana cultivars are descendants from two ancestral wild *Musa* species, *Musa acuminata* Colla (AA, 2n = 22) and *Musa balbisiana* Colla (BB, 2n = 22) (Simmonds 1962). These diversified into various edible varieties comprising diploids (AA, BB), triploids (AAA, AAB, ABB) and tetraploids (ABBB). Indonesia is the main contact area between species and subspecies of wild banana in sub-centres of diversity (Perrier *et al.* 2011) and, therefore, represents the primary gene centre for banana, resulting in a huge phenotypic and genotypic diversity. Indonesia is among the top 10 banana producing countries (FAOSTAT 2017) with over 200 varieties that are presently grown in almost every region of the Indonesian archipelago (Nasution 1993). The actual number of identified cultivated banana varieties could easily surpass 500. Banana is one of Indonesia's primary fruit commodities (BPS 2017), with most production supplying the domestic market.

Despite this great diversity and high popularity of bananas, there are some constraints on production. The most important of these is fungal diseases, including Fusarium wilt, also known as Panama disease (Stover 1962a). Fusarium wilt is caused by the soil-borne fungus *Fusarium oxysporum* f. sp. *cubense* (Foc), which first appeared in the 1900s in a banana plantation on Java (Stover 1962a) and thereafter disseminated to other banana production areas in Indonesia and beyond. This devastating agent of wilt on banana was first reported in the literature from samples collected in a Cuban banana plantation, and it subsequently gained notoriety as *Fusarium cubense* (Smith 1910).

The history of Fusarium wilt on banana goes back to the 20th century when this disease eliminated thousands of hectares of the favoured Gros Michel banana in Central America. The outbreak evolved into one of the worst plant epidemics of all times. The discovery of resistant Cavendish bananas eventually quenched the epidemic and the variety was so successful that it was disseminated around the world until it attained its current predominance in the global banana trade. The resistance of Cavendish bananas to the so-called Foc-Race1 strains, which caused the epidemic in Gros Michel is unique and durable. The risk of global monocultures is evident and problems surfaced again once other pathogenic *Fusarium oxysporum* strains

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appeared that were able to cause Fusarium wilt in Cavendish plantations. A harmful strain was initially reported from Taiwan, from whence it spread further into South-East Asia, and recently to the Indian subcontinent, the Middle East and Africa (Ordonez *et al.* 2015). The ongoing epidemic in Cavendish bananas is caused by a unique genotype, Vegetative Compatibility Group (VCG) 01213, of Foc and is called Tropical Race 4 (TR4). It has caused significant losses in commercial and subsistence production areas of Taiwan, Malaysia, and the northern territories of Australia (Su *et al.* 1986, Gerlach *et al.* 2000, Hermanto *et al.* 2009). In Indonesia, Nasir *et al.* (1999) reported that Fusarium wilt occurred from the Aceh province of Sumatra in the far west, to the far eastern Papua province. Losses in export Cavendish plantations in southern Sumatra have exceeded 70 %. In Northern Sumatra over 1 000 ha of plantations were destroyed within 3 yr after the appearance of the disease in this area (Nasir *et al.* 1999). Not only was Cavendish affected, but also many local popular varieties named in Bahasa Indonesia with 'Pisang' (='banana') variety names, such as Pisang Raja Bulu, P. Raja Sereh, P. Ambon, P. Mas and P. Barangan, were damaged. The affected varieties are very important for the local markets (Hermanto *et al.* 2009).

To date, no control method has yet been identified or successfully implemented to effectively manage TR4. This is further complicated by the soil-borne nature of Foc and its ability to produce persistent chlamydospores that contaminate soils for decades (Booth 1971). Essentially, there are presently no control methods, except prevention by using pathogen-free tissue culture plants planted in non-infested soil (Ploetz 1994), and the adoption of quarantine strategies. However, these practices are mostly applied in large commercial plantations, but not in smallholder settings. Evidently, the development of new resistant banana cultivars would be the most effective control strategy to follow, and therefore research on the diversity of this pathogen is essential, particularly since it has been shown to be polyphyletic (O'Donnell *et al.* 1998, 2009). It is therefore essential to acquire a better understanding of the differences between the genetic lineages for developing control strategies, and for effective resistance breeding.

In *Fusarium* systematics, Foc belongs to the *Fusarium oxysporum* species complex (FOSC). Four clades of FOSC have been identified using translation elongation factor 1-alpha (*tef1)* and mitochondrial subunit rDNA (*mtssu*), with Foc isolates clustering as basal lineage (O'Donnell *et al.* 2004). The incorporation of Foc isolates from native host populations, especially those from indigenous ecosystems, will be of great importance for diversity studies of this complex species.

Diversity studies on Foc isolates were conducted by using various physiological and molecular methods, which included VCGs (Moore *et al.* 1993), random amplified polymorphic DNA markers (RAPDs; Bentley *et al.* 1995), restriction fragment length polymorphisms (RFLPs; Koenig *et al.* 1997), amplified fragment length polymorphism (AFLP; Groenewald *et al.* 2006) and DNA sequence analyses (O'Donnell *et al.* 1998). These studies showed that the South-East Asian population of this fungus exhibits a high degree of variation, suggesting that Foc lineages co-evolved with their hosts in South-East Asia (Ploetz & Pegg 1997). However, these studies used Foc isolates from various disconnected geographical areas and lacked evidence on genetic diversity from the genetic centre of banana diversity, which is likely also the origin of the co-evolving Foc (Buddenhagen 2007). It has alternatively been suggested that Foc has multiple independent evolutionary origins, both within and outside the *Musa* genetic centre (Bentley *et al.* 1998). Using the phylogenetic genealogical approach, O'Donnell *et al.* (1998) identified five independent genetic lineages of Foc in a global population. Using a similar approach and additional data, Fourie *et al.* (2009) found three additional lineages. However, neither of these studies included Indonesian populations, and hence only limited information is available on the diversity of Foc at the centre of origin of banana.

Here, we explore the genetic diversity among Indonesian Foc strains that were isolated from local banana varieties in various different ecosystems across the country. This overview of the complexity of Fusarium wilt of banana enables us to greatly improve our knowledge of the taxonomic and phylogenetic position of Foc in the FOSC.

MATERIALS AND METHODS

Isolates

A comprehensive survey of Fusarium wilt of banana was undertaken in Indonesia. In total, 34 locations in 15 provinces were visited, representing the main banana-producing regions in Java, Sumatra, Kalimantan, Sulawesi, Papua, and Nusa Tenggara (Table 1, Fig. 1). Sampling expeditions to the former three islands were undertaken in 2014, whereas the other islands were sampled in 2015. Sampling locations were identified in two to three different regions in each province. Diagnostic specimen were collected from diseased banana plants displaying typical Fusarium wilt symptoms: yellowing of older leaf margins, collapsed leaves at the petioles, and pseudostem discolouration and splitting. The pseudostems of the diseased plants were cut and discoloured vascular strands were sampled and placed on sterile filter paper to dry, and were eventually packed in a paper envelope. Global positioning coordinates were recorded and ecological parameters, including soil pH, light intensity and vegetation of the sampling area were collected at each site. For each banana plant sampled, the youngest (cigar) leaf was taken for ploidy identification of the germplasm by flow-cytometry analyses and morphological characterisation following Valmayor *et al.* (1999) and Simmonds & Shepherd (1955), as well as *in-situ* comparisons with local banana varieties in the *Musa* collection at the Indonesian Institute of Sciences (LIPI) Cibinong, Bogor, Indonesia.

Isolation

The dried pseudostem samples were cut into pieces of 2 × 3 cm and plated on Komada medium (Komada 1975). After approximately 2 d, fungal colonies resembling *Fusarium* were transferred to potato dextrose agar (PDA) plates (Leslie & Summerell 2006). Axenic cultures were derived by streaking a small amount of conidia, collected with the tip of an inoculation needle, on water agar (WA) plates, which allowed conidia to separate. After 24 h of incubation, plates were observed under a dissection microscope at 50× magnification and single germinating conidia were collected and transferred to PDA. Monospore isolates were either maintained on PDA or in 20 % (v/v) glycerol at −80 °C. All isolates were deposited in the Indonesian Culture Collection (InaCC) Cibinong, Indonesia. Twenty-four Foc isolates,

Table 1. Names and geographical details of 34 sampling locations in Indonesia for establishing the Indonesian *Fusarium oxysporum* f. sp. *cubense* collection.

Province	District	GPS		
		Long.	Lat.	Alt. (m)
East Kalimantan	Kutai Timur	117.62	0.68	57
	Benajam	116.77	−1.62	21
Central Kalimantan	Kapuas Timur	114.48	−3.10	16
	Katingan	113.42	−1.71	35
	Palangkaraya	114.02	−2.43	18
South Kalimantan	Kota Baru	116.22	−2.58	118
	Tanah Bumbu	115.74	−3.63	13
	Banjar	115.03	−3.41	34
West Borneo	Kubu Raya	109.29	−0.06	8
	Pontianak	109.34	−0.04	17
West Java	Bogor	107.10	−6.68	657
	Cianjur	107.10	−7.02	875
	Sukabumi	106.79	−7.01	263
Central Java	Kendal	110.35	−7.20	794
	Semarang	110.59	−7.00	9
	Demak	110.74	−7.06	21
East Java	Lumajang	113.11	−8.08	637
	Bondowoso	113.94	−8.09	379
	Purwodadi	112.75	−7.82	491
	Jember	113.68	−8.24	39
Aceh	Jantho Aceh Besar	95.63	5.35	133
North Sumatra	Karo	98.25	3	NA
	Brastagi	98.51	3.19	NA
West Sumatra	Bukittinggi	100.38	−0.29	NA
	Padang	100.35	−0.94	NA
South Sumatra	Ogan Ilir	104.70	−3.29	27
	Palembang	104.75	−2.99	NA
Lampung	Way Jepara	105.54	−5.56	NA
Papua	Sentani Jayapura	140.83	−2.65	NA
South Sulawesi	Barru	119.62	−4.08	8
	Bone	120.02	−4.62	101
	Maros	119.63	−5.10	48
	Sidreng Rappang	119.69	−3.93	165
East Nusa Tenggara	Sikka Flores	122.37	−8.61	20

representing the known VCG's (Ordonez *et al.* 2015) in the global Foc collection were included for phylogenetic analyses.

DNA isolation, amplification and analyses

Total genomic DNA was extracted from axenic isolates grown for 7 d on PDA, using the DNA Wizard Magnetic DNA Purification System for Food kit (Promega, USA) following the protocols provided by the manufacturer. Partial gene sequences were determined for the RNA polymerase largest subunit gene (*rpb1*) using primers RPB1-Fa & RPB1-G2R (O'Donnell *et al.* 2010), the RNA polymerase second largest subunit gene (*rpb2*) using primers RPB2-5f2 & RPB2-7cr (O'Donnell *et al.* 2010), and the translation elongation factor 1-alpha gene (*tef1*) using primers EF1 & EF2 (O'Donnell *et al.* 1998). Amplicons were sequenced in both directions using the same primer pairs as were used for amplification to ensure integrity of the sequences.

Consensus sequences were determined and assembled using MEGA v. 6 (Tamura *et al.* 2013) and compared to representative sequences from previous studies (O'Donnell *et al.* 1998, Fourie *et al.* 2009, Ordonez *et al.* 2015). Subsequent alignments for each individual locus were generated using MAFFT v. 7.110 (Katoh & Standley 2013) and manually corrected if necessary. The individual sequences generated in this study were compared with those maintained in the *Fusarium* MLST database (http://www.westerdijkinstitute.nl/fusarium/) and the NCBI's GenBank, and relevant sequences were included in the subsequent phylogenetic inference. Phylogenetic congruencies of the three loci were tested using a 70 % reciprocal bootstrap criterion (Mason-Gamer & Kellogg 1996).

Phylogenetic inference in this study was based on Maximum Likelihood (ML) and Bayesian Inference (BI). The ML analysis was performed using RAxML v. 8. (randomised accelerated (sic) maximum likelihood for high performance computing) (Stamatakis 2014) through RAxML BlackBox (http://embnet.vital-it.ch/raxml-bb/index.php). Bootstrap support (BS) was determined automatically by the software to assess the robustness of the analyses. The BI analysis was performed using MrBayes v. 3.2 (Ronquist *et al.* 2012). A Markov Chain Monte Carlo (MCMC) algorithm of four chains was initiated in parallel from a random tree topology with a heating parameter set at 0.3. The MCMC analyses lasted until the average standard deviations of split frequencies were below 0.01 with phylogenies saved every 1 000 generations. The first 25 % of saved phylogenies were discarded as the "burn-in" phase and posterior probabilities (PP) were determined from the remaining phylogenies. All the sequences generated in this study were deposited in the European Nucleotide Archive (ENA) and the alignments in TreeBASE.

Morphology

All Foc isolates were grown on carnation leaf agar (CLA; Fisher *et al.* 1982), synthetic low-nutrient agar (SNA; Nirenberg 1981) and PDA to induce sporulation under continuous light (Osram L18W/840 Cool White) for 7 d at 25 °C. Growth rates of all isolates were determined after 7 d incubation at 25 °C in the dark on PDA. Colony colours were determined using the mycological colour charts of Rayner (1970). Gross morphological characters, including microconidia, macroconidia, chlamydospores and conidiophores, were examined (50×) after mounting fungal structures in sterile water and observed using light microscopy at 1 000× magnification. For each taxonomically informative structure, the extremes are provided, but for conidia we calculated the 95 % confidence intervals and provide extremes in parentheses. All descriptions, illustrations and nomenclatural data were deposited in MycoBank (Crous *et al.* 2004).

Pathogenicity assays

Isolates of Foc clustering in different clades based on the MLST analyses were selected for pathogenicity assays. The Foc-TR4 reference strain FocII5-NRRL 54006 (Ordonez *et al.* 2015) was included as a positive control, and negative controls were treated with water. For all assays, we followed the inoculum production, inoculation and diseases assessment protocols developed by Garcia-Bastidas *et al.* (2018, in submission) using 2–3-mo-old Cavendish and Gros Michel plants. Prior and post-inoculation greenhouse conditions were adjusted to a constant day temperature of 25 °C (ambient light until max. 16 h), a night temperature of 23 °C, and a relative humidity of $\geq$ 75 %. After 7 wk, disease severities were

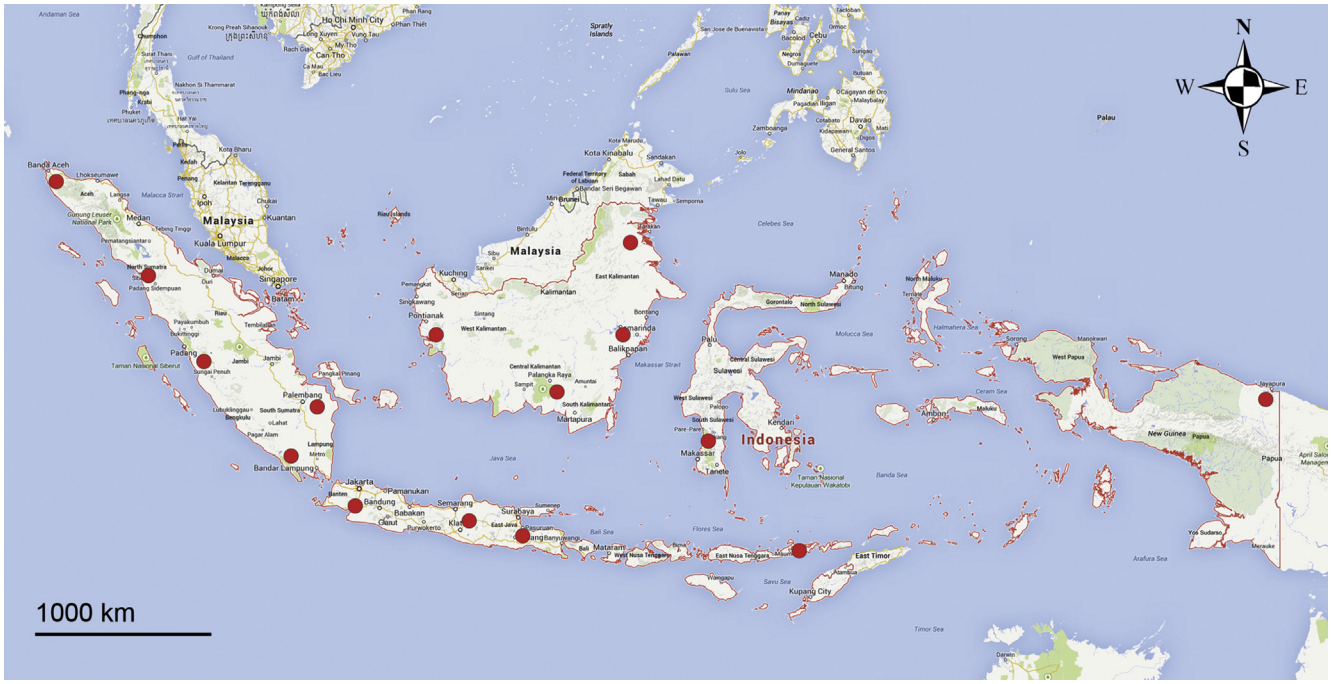

Fig. 1. Map of sampling collection in 2014–2015 in the island of Java, Sumatra, Kalimantan, Sulawesi, Papua, and Flores.

evaluated by scoring external foliage and internal corm symptoms.

RESULTS

Isolates

Symptoms characteristic of Fusarium wilt were observed in most of the sampling locations on a diverse suite of banana varieties in typical backyards and in a Cavendish industrial plantation (Fig. 2). In total, 40 local banana varieties showed Fusarium wilt symptoms and were sampled (Table 2, Fig. 3). However, wild banana species, including *Musa acuminata* var. *bantamensis* in West Java, *M. acuminata* var. *rutilifes* in the forest of East Java, and *M. acuminata* var. *microcarpa* and *M. bornensis* in Kalimantan, and the *Musa*-related species, *Ensete glaucum* in Flores, were consistently free of external Fusarium wilt symptoms. In total, 203 isolates were obtained from the symptomatic banana plants (Table 3).

Phylogenetic analyses

Approximately 632 bp were determined for *tef1*, 864 bp for *rpb2* and 1 444 bp for the *rpb1* gene regions. The congruency analyses revealed no conflicts in tree topologies, with only minor differences in branch support. Therefore, the sequences of the three loci were combined in a single dataset for subsequent analyses. For the BI and ML analyses, a GTR+I+G model was selected for all three gene regions and incorporated into the analyses. The ML tree topology confirmed the tree topologies obtained from the BI analyses, and therefore, only the ML tree is presented.

The combined *tef1, rpb1* and *rpb2* sequences dataset included 244 ingroup taxa and *F. dimerum* (NRRL 36140) as outgroup taxon. This dataset consisted of 2 909 characters, which yielded a single best ML tree with −lnL = -9286.260647 (Fig. 4). The BI lasted for 11 M generations, and the consensus tree, with posterior probabilities, was calculated from 8 251 trees left after 2 750 trees were discarded as the "burn-in" phase.

Phylogenetic inference of the three gene regions placed all isolates recovered from the symptomatic samples in the genus *Fusarium* (Fig. 4). Of these, 180 isolates clustered in the FOSC clade, one isolate clustered in the *Fusarium sambucinum* species complex (FSSC) closely related to *F. longipes*, 11 isolates clustered in the *Fusarium incarnatum-equiseti* species complex (FIESC), and eight isolates clustered in the *Fusarium fujikuroi* species complex (FFSC). The highest phylogenetic support was obtained using the *tef1* and *rpb1* gene regions. The *rpb2* gene region displayed less resolution of the isolates, between the various *Fusarium* species complexes and within each complex. The clades representing FIESC and FSSC resolved in this study were highly supported (BS = 100 %; PP = 1). The FFSC resolved FOSC and other members of the FFSC into two highly supported clades (BP = 100 %; PP = 1 & BP = 97 %; PP = 1, respectively).

In the FOSC, using the single gene analyses of *tef1*, and after incorporation of the dataset of O'Donnell *et al.* (2004) and Fourie *et al.* (2009), two clades were resolved as in the previous study (O'Donnell *et al.* 2004; Fig. 5). None of the Indonesian isolates resided in Clade 3. A single isolate, representing FocCNPMF.R1 (Dita *et al.* 2010), clustered in the FOSC Clade 4. The phylogeny, however, revealed one new clade in the FOSC (BP = 100 %, PP = 1.0), assigned to FOSC Clade 5, comprising five isolates that were isolated from Pisang Kepok (ABB, 2n = 33) and Pisang Ambon (AAA, 2n = 33) in Central and South Kalimantan.

Further analyses of the Foc phylogeny using the combined *tef1, rpb1* and *rpb2* dataset included 216 ingroup taxa and *F. fujikuroi* (CBS 221.76.) as an outgroup taxon (Fig. 6). The majority of Indonesian isolates clustered in Clade 1, including eight previously established Foc lineages (Fig. 6; O'Donnell *et al.* 1998, Fourie *et al.* 2009), and the overall phylogeny revealed nine independent clonal lineages (Fig. 6). The Indonesian Foc isolates were equally distributed across the nine lineages except for L9 that did not include any Indonesian isolate. We did not

Fig. 2. Symptoms of Fusarium wilt on banana. **A**. External wilting symptom on leaves in a monoculture plantation in Lampung, Sumatra. **B**. External wilting symptom in a backyard home plantation in Cianjur, West Java. **C**. Splitting of the pseudostem. **D**. Internal symptoms, discoloration of the pseudostem. **E**. Discoloration of the corm.

identify significant correlation between the origin of the isolates and host genotypes.

Taxonomy

Based on phylogenetic inference and morphological observations, several novel *Fusarium* taxa could be identified in this study, and these are described below.

Foc Lineage L1

Fusarium odoratissimum N. Maryani, L. Lombard, Kema & Crous, **sp. nov.** MycoBank MB826800. Figs 7, 8.

Etymology: Name refers to the strong odour associated with older cultures.

Macroconidia abundant on CLA, less abundant on PDA and SNA, formed on sporodochia on CLA and on aerial conidiophores on SNA and PDA, falcate, (44–)59–75(–79) × 6–8 µm (av. 67 × 7 µm), 0–6-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* mono- or polyphialidic on sporodochia, or formed directly on hyphae (lateral phialides), 12–28 × 4–8 µm. *Microconidia* abundant on PDA and SNA, less frequent on CLA, oval to ellipsoid, (6–)8–16(–23) × (4–)6(–8) µm (av. 12 × 5 µm), 0–3-septate, arranged in false heads on branched conidiophores carried on hyphae. Aerial conidiophores rare on CLA and SNA but formed abundantly on PDA, branched sparsely or formed laterally. *Chlamydospores* globose to subglobose, formed intercalarily or terminally, single or in pairs, (7–)9–13(–14) × (7–)8–11(–12) µm, rarely produced on SNA after 7 d, rough-walled.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C with an average growth rate of 4.5–5.0 mm/d. Colony reverse, uniformly white and unpigmented. Colony surface dry, cottony, white, with filamentous margin. No exudates observed. Aerial mycelium abundant, cottony, with abundant sporulation. Sporodochia formed abundantly on CLA after 7 d, pale orange.

Table 2. List of 40 susceptible local banana varieties at six Indonesian islands from which samples were taken to isolate *Fusarium oxysporum* f. sp. *cubense* strains.

Islands	Banana varieties			Scientific name[1]	Genome[1]
	Local name	Popular name	International name		
Sumatra	Pisang Ayam	Pisang Barangan	Lakatan	*Musa acuminata*	AAA
	P. Wak	P. Awak	Awak	*Musa* sp.	ABB
	P. Abe	P. Kepok	Saba	*Musa* sp.	ABB
	P. Talon	P. Raja	Raja	*Musa* sp.	AAB
	P. Barangan	P. Barangan	Lakatan	*Musa acuminata*	AAA
	P. Tanduk Bawen	P. Tanduk	Horn	*Musa* sp.	AAB
	P. Mas	P. Mas	Sucrier	*Musa acuminata*	AA
Kalimantan	P. Sanggar/Manurun/Nipah	P. Kepok	Saba	*Musa* sp.	ABB
	P. Awak/Pulau Pinang	P. Awak	Awak	*Musa* sp.	ABB
	P. Ambon	P. Ambon Hijau	Cavendish	*Musa acuminata*	AAA
	P. Susu	P. Raja Sereh	Silk	*Musa* sp.	AAB
	P. Hawa	P. Awak	Awak	*Musa* sp.	ABB
	P. Gelobok	P. Awak	Awak	*Musa* sp.	ABB
	P. Talas	P. Talas	NA	*Musa acuminata*	AA
	P. Selendang	NA	NA	*Musa acuminata*	AAA
	Dwarf Cavendish	P. Kapal	Dwarf Cavendish	*Musa acuminata*	AAA
	P. Raja	P. Raja Bulu	Raja	*Musa* sp.	AAB
	P. Kepok	P. Kepok	Saba	*Musa* sp.	ABB
Java	P. Mas Kirana	P. Mas Kirana	Sucrier	*Musa acuminata*	AA
	P. Embuk	NA	NA	*Musa* sp.	AAB
	P. Kongkong	NA	NA	*Musa acuminata*	AAA
	P. Susu	P. Raja Sereh	Silk	*Musa* sp.	AAB
	P. Glintung	NA	NA	–	NA
	P. Ambon	P. Ambon Kuning	Gros Michel	*Musa acuminata*	AAA
	P. Ambon Lumut	P. Ambon Hijau	Cavendish	*Musa acuminata*	AAA
	Cau Langadai	P. Siem	NA	*Musa* sp.	ABB
	Cau Apu	P. Siem	NA	*Musa* sp.	ABBB
	P. Jimbluk	P. Siem Jumbo	NA	*Musa* sp.	ABBB
	P. Uli	P. Uli	NA	*Musa acuminata*	AA
	P. Raja Nangka	P. Nangka	Laknau	*Musa acuminata*	AAA
	P. Cavendish	P. Ambon Hijau	Cavendish	*Musa acuminata*	AAA
	P. Kepok Pipik	P. Kepok Putih	NA	*Musa* sp.	ABB
	P. Raja	P. Raja Bulu	Raja	*Musa* sp.	AAB
Papua	P. Tanduk	P. Tanduk	Horn	*Musa* sp.	AAB
	P. Raja	P. Raja Bulu	Raja	*Musa* sp.	AAB
Sulawesi	P. Kepok	P. Kepok	Saba	*Musa* sp.	ABB
	P. Ambon	P. Ambon Hijau	Cavendish	*Musa acuminata*	AAA
	P. Cere	NA	NA	*Musa acuminata*	AAA
East Nusa Tenggara	P. Kepok	P. Kepok	Saba	*Musa* sp.	ABB
	P. Barangan	P. Barangan	Lakatan	*Musa acuminata*	AAA

[1] https://www.crop-diversity.org/mgis/taxonomy.

Geography and host: Kutai Timur, East Kalimantan, *Musa* sp. var. Pisang Kepok (ABB).

Pathogenicity: Pathogen on Gros Michel (AAA) and Cavendish (AAA).

Material examined: **Indonesia**, Kampung Salak Martadinata, Kutai Timur, East Kalimantan (117°26′850″E and 0°11′590″N), on infected pseudostem of *Musa* sp. var. Pisang Kepok (ABB), 16 Jun. 2014, N. Maryani (**holotype** preserved as metabolically inactive culture, InaCC F822).

Notes: Fusarium odoratissimum formed a small cryptic clade within the L1 cluster (Fig. 6), and can be distinguished by the septation of its macroconidia (0–6-septate) and microconidia (0–3-septate), characteristics not common for *F. oxysporum* (Leslie & Summerell 2006). This species also produces chlamydospores relatively more rapidly than was observed for other *Fusarium* isolates examined in this study. *F. odoratissimum* and all isolates in L1 produce a strong peculiarly stale odour in mature cultures, of which the causal volatiles remain to be characterised. Pathogenicity tests showed that *F. odoratissimum* and all isolates in L1 were able to infect Cavendish and Gros Michel bananas. Isolates in this lineage were thus classified as Foc-TR4.

Foc Lineage L2

Fusarium purpurascens N. Maryani, L. Lombard, Kema & Crous, **sp. nov.** MycoBank MB826801. Fig. 9.

Etymology: Name reflects the purple pigmentation which was observed when cultivated on potato dextrose agar.

Macroconidia abundant on CLA, less abundant on PDA and SNA, formed on sporodochia on CLA and on aerial conidiophores on SNA and PDA, falcate (50–)55–63(–67) × (4–)6–7(–9) µm (av. 59 × 7 µm), 3–5-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* mono- or polyphialidic on sporodochia, or formed directly from hyphae (lateral phialides), 5–45 × 3–8 µm. *Microconidia* abundant on

Fig. 3. Local Indonesian banana varieties. **A.** Pisang Raja Bulu (AAB). **B.** Pisang Awak (ABB). **C.** Pisang Ambon Hijau (AAA). **D.** Pisang Udang (ABB). **E.** Left, Pisang Raja Manten (AAB), right, Pisang Barangan (AAA). **F.** Pisang Mas Lampung (AA). **G.** Pisang Tanduk (AAB). **H.** Pisang Susu (AAB). **I.** Pisang Kepok (ABB). **J.** Pisang Jarum (AA).

PDA and SNA, less frequent on CLA, ovoid to ellipsoid, (8–) 18(–37) × (3–)5(–6) µm (av. 12 × 4 µm), 0–1-septate, arranged in false heads on branched conidiophores carried on hyphae. Aerial conidiophores rare on CLA and SNA, and formed abundantly on PDA, branched sparsely or formed laterally. *Chlamydospores* not observed.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C with an average growth rate of 4.4–4.8 mm/d. Colony reverse, livid purple. Colony surface dry, cottony, white, filamentous in the centre and livid purple towards the margin, forming exudate droplets. Aerial mycelium abundant, cottony, with moderate sporulation. Sporodochia formed abundantly on CLA after 7 d, pale orange.

Geography and host: Kutai Timur, East Kalimantan, *Musa* sp. var. Pisang Kepok (ABB).

Table 3. Details of strains included in the phylogenetic analyses.

Species name	Accession number[1]	Identification[2]	f. sp	Country	Host	GenBank/ENA accession[3]		
						rpb1	*rpb2*	*tef1*
Fusarium cugenangense	[9]InaCC F983	7	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479559	LS479307	LS479756
	InaCC F984	7	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479560	LS479308	LS479757
	NRLL 36118	7	*cubense*	Thailand	*Musa* sp. var. Pisang Kepok	LS479477	LS479221	LS479669
	NRRL 25433	7	*vasinvectum*		*Gossypium* sp.	LS479462	LS479202	LS479648
F. dimerum	NRRL 36140				*Citrus* sp.	HM347203	HM347218	HM347133
F. duoseptatum	[4,5]FocMal43	5	*cubense*	Malaysia	*Musa* sp. var. Pisang Rastali	–	LS479207	LS479653
	InaCC F828	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Rastali	LS479520	LS479266	LS479715
	InaCC F829	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Rastali	LS479528	LS479274	LS479723
	InaCC F831	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Rastali	LS479538	LS479285	LS479734
	InaCC F835	5	*cubense*	Indonesia	*M. acuminata* var. Dwarf Cavendish	LS479567	LS479315	LS479764
	InaCC F911	5	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	–	LS479234	LS479683
	InaCC F915	5	*cubense*	Indonesia	*Musa* sp. Pisang Raja	LS479494	LS479238	LS479687
	[8]InaCC F916	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479495	LS479239	LS479688
	InaCC F920	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Hawa	LS479499	LS479244	LS479693
	InaCC F921	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Hawa	LS479500	LS479245	LS479694
	InaCC F975	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Awak	LS479549	LS479296	LS479745
	InaCC F976	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Awak	LS479550	LS479297	LS479746
	InaCC F977	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479551	LS479298	LS479747
	InaCC F978	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479552	LS479299	LS479748
	[8]InaCC F979	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479553	LS479300	LS479749
	InaCC F980	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479554	LS479301	LS479750
	Indo80	5	*cubense*	Indonesia	*Musa* sp. var. Pisang Hawa	LS479619	LS479387	LS479829
	NRRL 36115	5	*cubense*	Malaysia	*M. acuminata* var. Pisang Ambon	LS479475	LS479218	LS479666
	NRRL 36116	5	*cubense*	Malaysia	*Musa* sp. var. Pisang Keling	–	LS479219	LS479667
F. grosmichelii	[8]InaCC F820	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	–	LS479364	LS479810
	InaCC F832	4	*cubense*	Indonesia	*Musa* sp. var. Pisang Awak	LS479542	LS479289	LS479738
	[8]InaCC F833	4	*cubense*	Indonesia	*Musa* sp. var. Pisang Awak	LS479548	LS479295	LS479744
	[8]InaCC F848	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479588	LS479338	LS479786
	InaCC F849	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479589	LS479339	LS479787
	InaCC F850	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	–	LS479340	LS479788
	[8]InaCC F851	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	–	LS479341	LS479789
	[8]InaCC F852	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon Lumut	–	LS479342	LS479790
	InaCC F853	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon Lumut	–	LS479343	LS479791
	InaCC F854	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon Lumut	LS479591	LS479345	LS479793
	InaCC F855	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon Lumut	LS479592	LS479346	LS479794
	InaCC F859	4	*cubense*	Indonesia	*M. acuminata* var. Cavendish	LS479596	LS479350	LS479796
	InaCC F861	4	*cubense*	Indonesia	*M. acuminata* var. Cavendish	LS479597	LS479351	LS479797
	InaCC F862	4	*cubense*	Indonesia	*M. acuminata* var. Cavendish	LS479598	LS479352	LS479798
	InaCC F863	4	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem Jumbo	LS479599	LS479353	LS479799
	InaCC F867	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon Kuning	–	LS479360	LS479806
	InaCC F868	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon Kuning	–	LS479361	LS479807
	InaCC F884	4	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479616	LS479382	LS479824

Table 3. (Continued).

Species name	Accession number[1]	Identification[2]	f. sp	Country	Host	GenBank/ENA accession[3]		
						rpb1	*rpb2*	*tef1*
	InaCC F887	4	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem Jumbo	LS479620	LS479388	LS479830
	InaCC F888	4	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem Jumbo	LS479621	LS479389	LS479831
	Indo83	4	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	–	LS479390	–
	NRRL 36120	4	*cubense*	Thailand		LS479478	LS479222	LS479670
F. fujikuroi	CBS 221.76	FFSC			*Oryza sativa*	–	–	JN695747
F. hexaseptatum	[8]InaCC F866	8	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon Kuning	–	LS479359	LS479805
F. incarnatum-equiseti	NRRL 45997	FIESC			Poaceae	–	GQ505850	GQ505672
F. kalimantanense	[9]InaCC F917	FOSC Clade 5 Nov.	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479497	LS479241	LS479690
	InaCC F918	FOSC Clade 5 Nov.	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	–	LS479242	LS479691
	InaCC F922	FOSC Clade 5 Nov.	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	–	LS479246	LS479695
F. longipes	NRRL 20695	FSSC				–	GQ915493	GQ915509
F. mangiferae	UMA F0924	FFSC			*Mangifera indica*	KP753435	KP753442	KP753402
F. odoratissimum	[7]FocII5-NRRL 54006	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Manurung	LS479459	LS479198	LS479644
	InaCC F816	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479485	LS479228	LS479677
	[7]InaCC F817	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479556	LS479304	LS479753
	InaCC F818	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479584	LS479333	LS479782
	InaCC F819	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479600	LS479354	LS479800
	InaCC F821	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Raja	LS479609	LS479374	LS479818
	[7]InaCC F822	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Raja	LS479618	LS479386	LS479828
	[7]InaCC F824	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479486	LS479229	LS479678
	InaCC F825	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Raja	LS479496	LS479240	LS479689
	[7]InaCC F836	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Mas Kirana	LS479577	LS479325	LS479774
	InaCC F837	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Mas Kirana	LS479578	LS479326	LS479775
	InaCC F838	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Mas Kirana	LS479579	LS479327	LS479776
	InaCC F839	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Mas Kirana	LS479580	LS479328	LS479777
	InaCC F840	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Embuk	–	LS479329	LS479778
	InaCC F841	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Embuk	LS479581	LS479330	LS479779
	[7]InaCC F846	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	–	LS479336	LS479785
	InaCC F847	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479587	LS479337	–
	[7]InaCC F856	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem	LS479593	LS479347	–
	InaCC F857	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem	LS479594	LS479348	LS479795
	InaCC F858	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem	LS479595	LS479349	–
	InaCC F864	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem	–	LS479356	LS479802
	InaCC F865	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem	–	LS479358	LS479804
	InaCC F870	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479602	LS479363	LS479809
	InaCC F871	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	–	LS479365	LS479811
	InaCC F873	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479604	LS479369	LS479814
	InaCC F874	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479606	LS479371	–
	InaCC F875	1	*cubense*	Indonesia	*M. acuminata* var. Cavendish	LS479607	LS479372	LS479816
	InaCC F876	1	*cubense*	Indonesia	*M. acuminata* var. Cavendish	LS479608	LS479373	LS479817

(*continued on next page*)

Table 3. (Continued).

Species name	Accession number[1]	Identification[2]	f. sp	Country	Host	GenBank/ENA accession[3]		
						rpb1	*rpb2*	*tef1*
	InaCC F877	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479610	LS479375	LS479819
	InaCC F878	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479611	LS479376	–
	InaCC F879	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479612	LS479377	LS479820
	InaCC F880	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	–	LS479378	LS479821
	InaCC F881	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479613	LS479379	–
	InaCC F882	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479614	LS479380	LS479822
	InaCC F883	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479615	LS479381	LS479823
	InaCC F885	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Raja	–	LS479384	LS479826
	InaCC F890	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479623	LS479392	–
	[7]InaCC F891	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Glitung	–	LS479393	LS479833
	InaCC F892	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479624	LS479394	LS479834
	InaCC F893	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479625	LS479395	LS479835
	InaCC F894	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479626	LS479396	LS479836
	InaCC F896	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Wak	LS479629	LS479399	LS479839
	InaCC F897	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479630	LS479400	LS479840
	InaCC F898	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479631	LS479401	LS479841
	[7]InaCC F899	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479632	LS479402	LS479842
	InaCC F900	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479633	LS479403	LS479843
	InaCC F901	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479634	LS479404	LS479844
	InaCC F902	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Talon	LS479635	LS479405	LS479845
	InaCC F903	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479636	LS479406	LS479846
	InaCC F904	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479637	LS479407	LS479847
	InaCC F905	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479638	LS479408	LS479848
	InaCC F906	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479639	LS479409	LS479849
	InaCC F907	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Tanduk	LS479487	LS479230	LS479679
	[7]InaCC F908	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Tanduk	LS479488	LS479231	LS479680
	[7]InaCC F909	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Mas	LS479489	LS479232	LS479681
	InaCC F910	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Mas	LS479490	LS479233	LS479682
	InaCC F912	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479491	LS479235	LS479684
	InaCC F919	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Awak	LS479498	LS479243	LS479692
	InaCC F923	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Raja	LS479501	LS479247	LS479696
	InaCC F924	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Raja	LS479502	LS479248	LS479697
	InaCC F925	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Raja	LS479503	LS479249	LS479698
	InaCC F926	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Raja	LS479504	LS479250	LS479699
	[7]InaCC F927	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Raja	LS479506	LS479252	LS479701
	InaCC F928	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Raja	LS479507	LS479253	LS479702
	InaCC F929	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Tanduk	LS479508	LS479254	LS479703
	InaCC F930	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Tanduk	LS479509	LS479255	LS479704
	[7]InaCC F931	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Tanduk	LS479510	LS479256	LS479705
	InaCC F932	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Tanduk	LS479511	LS479257	LS479706
	InaCC F933	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479512	LS479258	LS479707
	InaCC F934	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479514	LS479260	LS479709
	InaCC F935	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479515	LS479261	LS479710
	[7]InaCC F936	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479516	LS479262	LS479711

Table 3. (Continued).

Species name	Accession number[1]	Identification[2]	f. sp	Country	Host	GenBank/ENA accession[3]		
						rpb1	*rpb2*	*tef1*
	InaCC F937	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479517	LS479263	LS479712
	InaCC F938	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479518	LS479264	LS479713
	InaCC F939	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479519	LS479265	LS479714
	InaCC F942	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479521	LS479267	LS479716
	InaCC F943	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479522	LS479268	LS479717
	InaCC F944	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479523	LS479269	LS479718
	InaCC F945	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479524	LS479270	LS479719
	InaCC F946	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479525	LS479271	LS479720
	InaCC F947	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479526	LS479272	LS479721
	InaCC F948	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479527	LS479273	LS479722
	InaCC F953	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479529	LS479275	LS479724
	InaCC F954	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479530	LS479276	LS479725
	InaCC F955	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479531	LS479277	LS479726
	InaCC F973	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479547	LS479294	LS479743
	InaCC F985	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479562	LS479310	LS479759
	InaCC F986	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479563	LS479311	LS479760
	[7]InaCC F988	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479565	LS479313	LS479762
	InaCC F989	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479566	LS479314	LS479763
	InaCC F990	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok Pipik	LS479568	LS479316	LS479765
	InaCC F994	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Mas Kirana	LS479569	LS479317	LS479766
	[7]InaCC F997	1	*cubense*	Indonesia	*M. acuminata* var. Cavendish	LS479572	LS479320	LS479769
	[7]InaCC F998	1	*cubense*	Indonesia	*M. acuminata* var. Cavendish	LS479573	LS479321	LS479770
	InaCC F999	1	*cubense*	Indonesia	*M. acuminata* var. Cavendish	LS479574	LS479322	LS479771
	InaCC F1000	1	*cubense*	Indonesia	*M. acuminata* var. Cavendish	LS479575	LS479323	LS479772
	Indo4	1	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479590	LS479344	LS479792
	Indo51	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem	LS479601	LS479355	LS479801
	Indo53	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem	–	LS479357	LS479803
	Indo61	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	–	LS479366	LS479812
	Indo62	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	–	LS479367	–
	Indo66	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479605	LS479370	LS479815
	Indo77	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok Pipik	LS479617	LS479383	LS479825
	Indo89	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Wak	LS479627	LS479397	LS479837
	Indo204	1	*cubense*	Indonesia	*Musa* sp. var. Pisang Uli	LS479561	LS479309	LS479758
	Indo222	1	*cubense*	Indonesia	*M. acuminata* var. Cavendish	LS479576	LS479324	LS479773
	[4]JV11	1	*cubense*	Jordan	*M. acuminata* var. Cavendish	LS479465	LS479205	LS479651
	[4]Leb1.2C	1	*cubense*	Lebanon	*M. acuminata* var. Cavendish	LS479466	LS479206	LS479652
	NRRL 36102	1	*cubense*	China	*M. acuminata* var. Cavendish	LS479468	LS479209	LS479655
	[4]Pak1.1A	1	*cubense*	Pakistan	*M. acuminata* var. Cavendish	LS479479	LS479223	LS479671
	[4]Phi2.6C	1	*cubense*	Philippines	*M. acuminata* var. GCTCV218	LS479480	LS479224	LS479672
F. oxysporum	CAV794	FOSC Clade 1	*cubense*	Indonesia	*Musa* sp. var. Pisang Rubus	–	–	FJ664922
	CAV300	FOSC Clade 1	*cubense*	Indonesia	*M. acuminata* var. Valery	–	–	FJ664932
	CAV1107	FOSC Clade 1	*cubense*	Vietnam	*Musa* sp. var. Cuoi Xiem	–	–	FJ664950

(*continued on next page*)

Table 3. (Continued).

Species name	Accession number[1]	Identification[2]	f. sp	Country	Host	GenBank/ENA accession[3]		
						rpb1	*rpb2*	*tef1*
	CAV299	FOSC Clade 1	*cubense*	Nigeria	*M. acuminata* var. Gros Michel	–	–	FJ664946
	CAV602	FOSC Clade 2	*cubense*	Australia	*M. acuminata* var. Lady Finger	–	–	FJ664957
	CAV189	FOSC Clade 2	*cubense*	Malawi	*Musa* sp. var. Harare	–	–	FJ664956
	CAV194	FOSC Clade 2	*cubense*	Indonesia	*Musa* sp. var. Pisang Siem	–	–	FJ664955
	[4,6,8]FocCNPMF-R1	FOSC Clade 4	*cubense*	Brazil	*Musa* sp. var. Silk	LS479457	LS479196	LS479642
	NRRL 34936	FOSC Clade 3	*lycopersici*		*Solanum lycopersicum*	LS479460	LS479200	LS479646
	NRRL 26406	FOSC Clade 3	*melonis*		*Cucumis melo*	LS479461	LS479201	LS479647
	NRRL 54002	FOSC Clade 3			Soil	LS479455	LS479194	LS479640
	NRRL 26381	FOSC Clade 3	*lycopersici*		*S. lycopersicum*	LS479456	LS479195	LS479641
	NRRL 25603	FOSC Clade 1	*cubense*		*M. acuminata*	–	–	AF008487
	NRRL 22550	FOSC Clade 1	*pernicosum*		*Albizia julibrissin*	–	–	AF008506
	NRRL 25357	FOSC Clade 1			Soil	–	–	AF008481
	NRRL 26035	FOSC Clade 1	*canariensis*		*Phoenix canariensis*	–	–	AF008485
	NRRL 20433	FOSC Clade 2	*inflexum*		*Viciba faba*	–	–	AF008479
	NRRL 25607	FOSC Clade 2	*cubense*		*M. acuminata* x *M. balbisiana*	–	–	AF008489
	NRRL 25609	FOSC Clade 2	*cubense*		*M. acuminata* x *M. balbisiana*	–	–	AF008490
	NRRL 26022	FOSC Clade 2	*cubense*		*M. acuminata* x *M. balbisiana*	–	–	AF008491
	NRRL 25598	FOSC Clade 2	*glycines*		*Glycine* sp.	–	–	AF008496
	NRRL 26178	FOSC Clade 2	*melonis*		*Cucumis melo*	–	–	AF008503
	NRRL 25420	FOSC Clade 2	*vasinvectum*		*Gossypium hirsutum*	–	–	AF008512
	NRRL 25369	FOSC Clade 2			*Terminalia ivorensis*	–	–	AF008482
	NRRL 26406	FOSC Clade 3	*melonis*		*C. melo*	–	–	AF008504
	NRRL 26379	FOSC Clade 3	*radicis-lycopersici*		*S. esculentum*	–	–	AF008508
	NRRL 22549	FOSC Clade 3	*passiflorae*		*Passiflora edulis*	–	–	AF008505
	NRRL 26033	FOSC Clade 3	*radicis-lycopersici*		*S. esculentum*	–	–	AF008507
	NRRL 26574	FOSC Clade 3	*erythroxily*		*Erythroxylum coca*	–	–	AF008495
	NRRL 26383	FOSC Clade 3	*lycopersici*		*S. esculentum*	–	–	AF008502
	NRRL 26380	FOSC Clade 3	*lycopersici*		*S. esculentum*	–	–	AF008509
	NRRL 26029	FOSC Clade 3	*cubense*		*M. acuminata X M. balbisiana*	–	–	AF008493
	NRRL 22555	FOSC Clade 3	*tuberosi*		*S. tuberosum*	–	–	AF008511
	NRRL 26203	FOSC Clade 3	*lycopersici*		*S. esculentum*	–	–	AF008501
	NRRL 26374	FOSC Clade 3			*Homo sapiens*	–	–	AF008483
	NRRL 25594	FOSC Clade 4	*batatas*		*Ipomoea batatas*	–	–	AY337717
	NRRL 26360	FOSC Clade 4				–	–	AY527522
F. phialophorum	[4,5]FocIndo25	3	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon	LS479464	LS479204	LS479650
	[4,5]FocST4.98	3	*cubense*	Spain	*M. acuminata* var. Dwarf Cavendish	LS479484	LS479227	LS479676
	InaCC F826	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Wak	LS479505	LS479251	LS479700
	InaCC F827	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Wak	LS479513	LS479259	LS479708
	InaCC F830	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479536	LS479282	LS479731
	InaCC F834	3	*cubense*	Indonesia	*M. acuminata* var. Pisang Selendang	LS479557	LS479305	LS479754
	InaCC F842	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Embuk	LS479582	LS479331	LS479780
	InaCC F843	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Embuk	LS479583	LS479332	LS479781
	[8]InaCC F844	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479585	LS479334	LS479783

Table 3. (Continued).

Species name	Accession number[1]	Identification[2]	f. sp	Country	Host	GenBank/ENA accession[3]		
						rpb1	*rpb2*	*tef1*
	InaCC F845	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479586	LS479335	LS479784
	InaCC F869	3	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon Kuning	–	LS479362	LS479808
	InaCC F889	3	*cubense*	Indonesia	*M. acuminata* var. Pisang Ambon Kuning	LS479622	LS479391	LS479832
	InaCC F969	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Wak	LS479543	LS479290	LS479739
	InaCC F970	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Wak	LS479544	LS479291	LS479740
	[8]InaCC F971	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Wak	LS479545	LS479292	LS479741
	InaCC F972	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Wak	LS479546	LS479293	LS479742
	InaCC F980	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479555	LS479302	LS479751
	InaCC F981	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	–	LS479303	LS479752
	InaCC F982	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479558	LS479306	LS479755
	InaCC F987	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479564	LS479312	LS479761
	InaCC F995	3	*cubense*	Indonesia	*M. acuminata* var. Pisang Kongkong	LS479570	LS479318	LS479767
	[8]InaCC F996	3	*cubense*	Indonesia	*M. acuminata* var. Pisang Kongkong	LS479571	LS479319	LS479768
	Indo64	3	*cubense*	Indonesia	*Musa* sp. var. Pisang Susu	LS479603	LS479368	LS479813
	NRRL 36101	3	*cubense*	Australia	*Musa* sp. var. Mons Mari	LS479467	LS479208	LS479654
	NRRL 36103	3	*cubense*	Philippines	*M. acuminata* var. Cavendish	LS479469	LS479210	LS479656
	NRRL 36109	3	*cubense*	Australia	*Musa* sp. var. SH 3142	LS479471	LS479214	LS479661
	NRRL 36110	3	*cubense*	Australia	*Musa* sp. var. Mons	–	–	LS479662
	NRRL 36112	3	*cubense*	South Africa	*M. acuminata* var. Cavendish	LS479473	LS479216	LS479664
	[4,6]Race1.0124	3	*cubense*	Cuba		LS479483	–	LS479675
F. proliferatum	NRRL 62905	FFSC				KU171687	KU171707	KU171727
F. purpurascens	ATCC76244	2	*cubense*	USA	*M. acuminata* var. Apple	–	LS479199	LS479645
	InaCC F823	2	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479628	LS479398	LS479838
	[8]InaCC F886	2	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	–	LS479385	LS479827
	InaCC F913	2	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479492	LS479236	LS479685
	InaCC F914	2	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479493	LS479237	LS479686
	[8]InaCC F966	2	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479539	LS479286	LS479735
	InaCC F967	2	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479540	LS479287	LS479736
	InaCC F968	2	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479541	LS479288	LS479737
	NRRL36107	2	*cubense*	Honduras	*Musa* sp. var. Maqueno	–	LS479213	LS479659
F. sacchari	NRRL 13999	FFSC				–	–	AF160278
F. sangayamense	[9]InaCC F960	FOSC Clade 5 Nov.	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	LS479537	LS479283	LS479732
	InaCC F961	FOSC Clade 5 Nov.	*cubense*	Indonesia	*Musa* sp. var. Pisang Kepok	–	LS479284	LS479733
F. tardichlamydosporum	[4,6]FocCNPMF-R2	6	*cubense*	Brazil	*Musa* sp. var. Monthan	LS479458	LS479197	LS479643
	InaCC F956	6	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479532	LS479278	LS479727
	InaCC F957	6	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479533	LS479279	LS479728
	[8]InaCC F958	6	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479534	LS479280	LS479729
	InaCC F959	6	*cubense*	Indonesia	*M. acuminata* var. Pisang Barangan	LS479535	LS479281	LS479730
	NRRL 36105	6	*cubense*	Honduras	*Musa* sp. var. Bluggoe	LS479470	LS479211	LS479657
	NRRL 36106	6	*cubense*	Australia	*M. acuminata* var. Lady finger	–	LS479212	LS479658

(*continued on next page*)

Table 3. (Continued).

Species name	Accession number[1]	Identification[2]	f. sp	Country	Host	GenBank/ENA accession[3]		
						rpb1	***rpb2***	***tef1***
	NRRL 36108	6	*cubense*	Tanzania	*Musa* sp. var. Ney Poovan	–	–	LS479660
	NRRL 36111	6	*cubense*	Australia	*Musa* sp. var. Bluggoe	LS479472	LS479215	LS479663
	NRRL 36117	6	*cubense*	Malaysia	*Musa* sp. var. Pisang awak legor	LS479476	LS479220	LS479668
F. tardicrescens	NRRL 36113	9	*cubense*	Malawi	*Musa* sp. var. Harare	LS479474	LS479217	LS479665
	NRRL 37622	9	*pisi*		*Cicer* sp.	LS479463	LS479203	LS479649
	NRRL 54005	9	*raphani*		*Raphanus* sp.	LS479482	LS479226	LS479674
	NRRL 54008	9	*conglutinans*		*Raphanus* sp.	LS479481	LS479225	LS479673
F. verticilloides	NRRL 20956	FFSC			*Zea mays*	–	–	FN552074
Fusarium sp.	InaCC F872	FFSC		Indonesia	*Musa* sp. var. Pisang Raja Nangka	–	LS479850	LS479441
	InaCC F940	FIESC		Indonesia	*M. acuminata* var. Pisang Cere	–	LS479855	LS479443
	InaCC F941	FIESC		Indonesia	*M. acuminata* var. Pisang Cere	–	LS479856	LS479444
	[9]InaCC F950	FFSC		Indonesia	*Musa* sp. var. Pisang Kepok	LS479870	LS479852	–
	InaCC F951	FFSC		Indonesia	*Musa* sp. var. Pisang Kepok	LS479871	LS479853	–
	InaCC F952	FFSC		Indonesia	*Musa* sp. var. Pisang Kepok	LS479872	LS479854	–
	InaCC F962	FFSC		Indonesia	*M. acuminata* var. Pisang Talas	–	LS479868	LS479453
	InaCC F963	FIESC		Indonesia	*Musa* sp. var. Pisang Awak	LS479875	LS479859	LS479445
	InaCC F964	FIESC		Indonesia	*Musa* sp. var. Pisang Awak	LS479876	LS479860	LS479446
	InaCC F965	FIESC		Indonesia	*M. acuminata* var. Pisang Talas	LS479877	LS479863	LS479448
	[9]InaCC F974	FSSC		Indonesia	*Musa* sp. var. Pisang Awak	LS479880	LS479866	LS479451
	InaCC F991	FFSC		Indonesia	*Musa* sp. var. Pisang Kepok	LS479881	LS479867	LS479452
	[9]InaCC F992	FFSC		Indonesia	*M. acuminata* var. Pisang Mas Kirana	LS479882	LS479869	LS479454
	InaCC F993	FFSC		Indonesia	*M. acuminata* var. Pisang Mas Kirana	–	LS479851	LS479442
	Indo161	FIESC		Indonesia	*M. acuminata* var. Pisang Talas	LS479873	LS479857	–
	Indo167	FIESC		Indonesia	*Musa* sp. var. Pisang Kepok	LS479874	LS479858	–
	Indo 174	FIESC		Indonesia	*Musa* sp. var. Pisang Awak	–	LS479861	–
	Indo175	FIESC		Indonesia	*M. acuminata* var. Pisang Talas	–	LS479862	LS479447
	Indo186	FIESC		Indonesia	*Musa* sp. var. Pisang Kepok	LS479878	LS479864	LS479449
	Indo188	FIESC		Indonesia	*Musa* sp. var. Pisang Awak	LS479879	LS479865	LS479450

[1] InaCC: Indonesian Culture Collection, Research Center for Biology, Indonesian Institute of Sciences (LIPI) Cibinong, Indonesia; ATCC: American Type Culture Collection, U.S.A.; CAV: Forestry Agricultural Biotechnology Institutre (FABI), University of Pretoria South Africa; CBS: The Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; Indo: Collection of N. Maryani at Wageningen Plant Research, Wageningen University, The Netherlands; NRRL: Agricultural Research Service Culture Collection, USA; UMAF: Microbiology and Plant Pathology Laboratory Collection, University of Malaga, Spain.

[2] Foc lineage/FOSC clade/*Fusarium* species complex.

[3] *rbp1*: RNA polymerase II largest subunit; *rpb2*: RNA polymerase II second largest subunit; *tef1*: translation elongation factor-1alpha.

[4] Collection of Wageningen Plant Research, Wageningen University, The Netherlands.

[5] Ecosciences Precinct, Brisbane Australia.

[6] Embrapa Cassava & Tropical Fruits, Brazil.

[7] Pathogenic on Cavendish and Gros Michel (Tropical Race 4).

[8] Pathogenic on Gros Michel (Race 1).

[9] Non-pathogenic on Cavendish and Gros Michel.

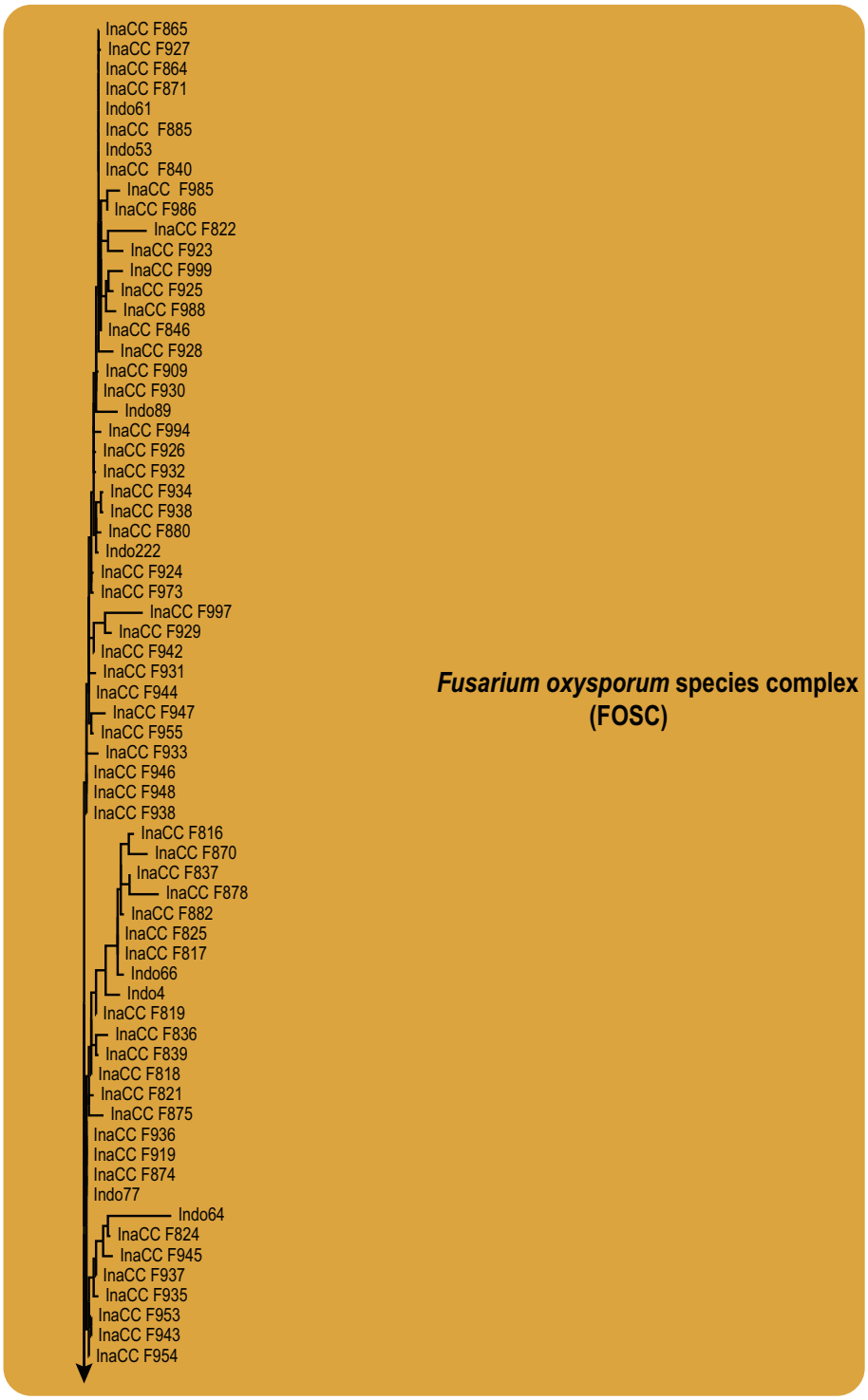

Fig. 4. Maximum likelihood tree inferred from the combined *rpb1, rpb2* and *tef1* genes sequence data set of 244 isolates. The bootstrap support values (BP) and Bayesian posterior probabilities (PP) are given at nodes. Coloured blocks indicate the various *Fusarium* species complexes included. The tree is rooted to *Fusarium dimerum* (NRRL 36140).

Pathogenicity: Pathogen on Gros Michel (AAA).

Material examined: **Indonesia**, Kampung Salak Martadinata, Kutai Timur, East Kalimantan (117°26′684″E, 0°26′684″N), on infected pseudostem of *Musa* sp. var. Pisang Kepok (ABB), 17 Jun. 2014, N. Maryani (**holotype** preserved as metabolically inactive culture, InaCC F886).

Notes: *Fusarium pupurascens* exhibits the strongest purple colony colour on PDA of all the isolates with purple colonies. It is relatively slow-growing compared to other isolates clustered in lineage L1. No chlamydospores were observed for this species, in contrast to other L1 members, which readily produce chlamydospores in culture. Furthermore, *F. purpurascens* produces exudate droplets, something not observed among other L1 isolates. Older cultures become pigmented, a distinctive phenomenon rarely seen in L1. *F. purpurascens* and other isolates in this lineage were able to infect Gros Michel, and were therefore classified as Foc-Race1.

Foc Lineage L3

Fusarium phialophorum N. Maryani, L. Lombard, Kema & Crous, **sp. nov.** MycoBank MB826802. Fig. 10.

Etymology: Name refers to its elongated phialidic collarettes observed in culture.

Macroconidia abundant on CLA, less abundant on PDA and SNA, formed on sporodochia on CLA and on aerial conidiophores on

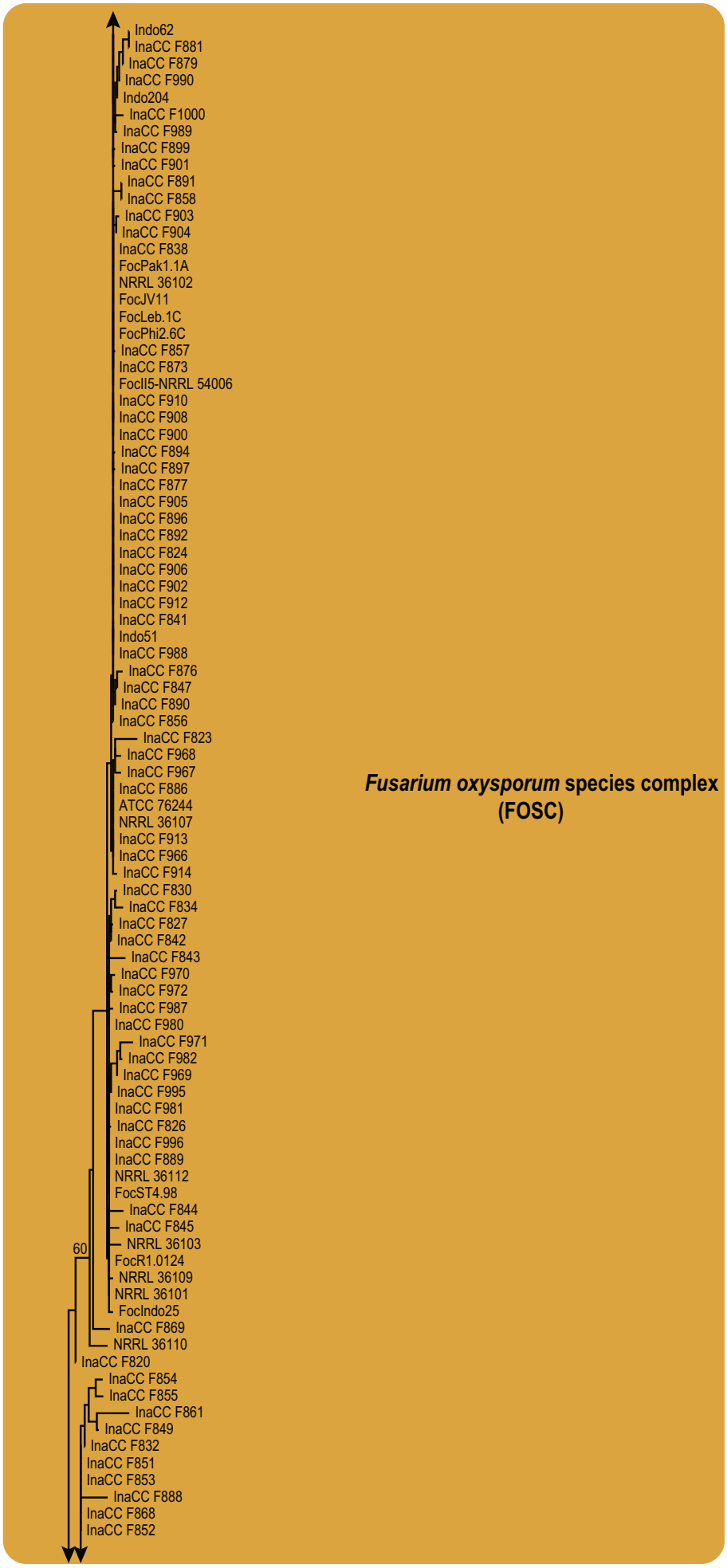

Fig. 4. (Continued).

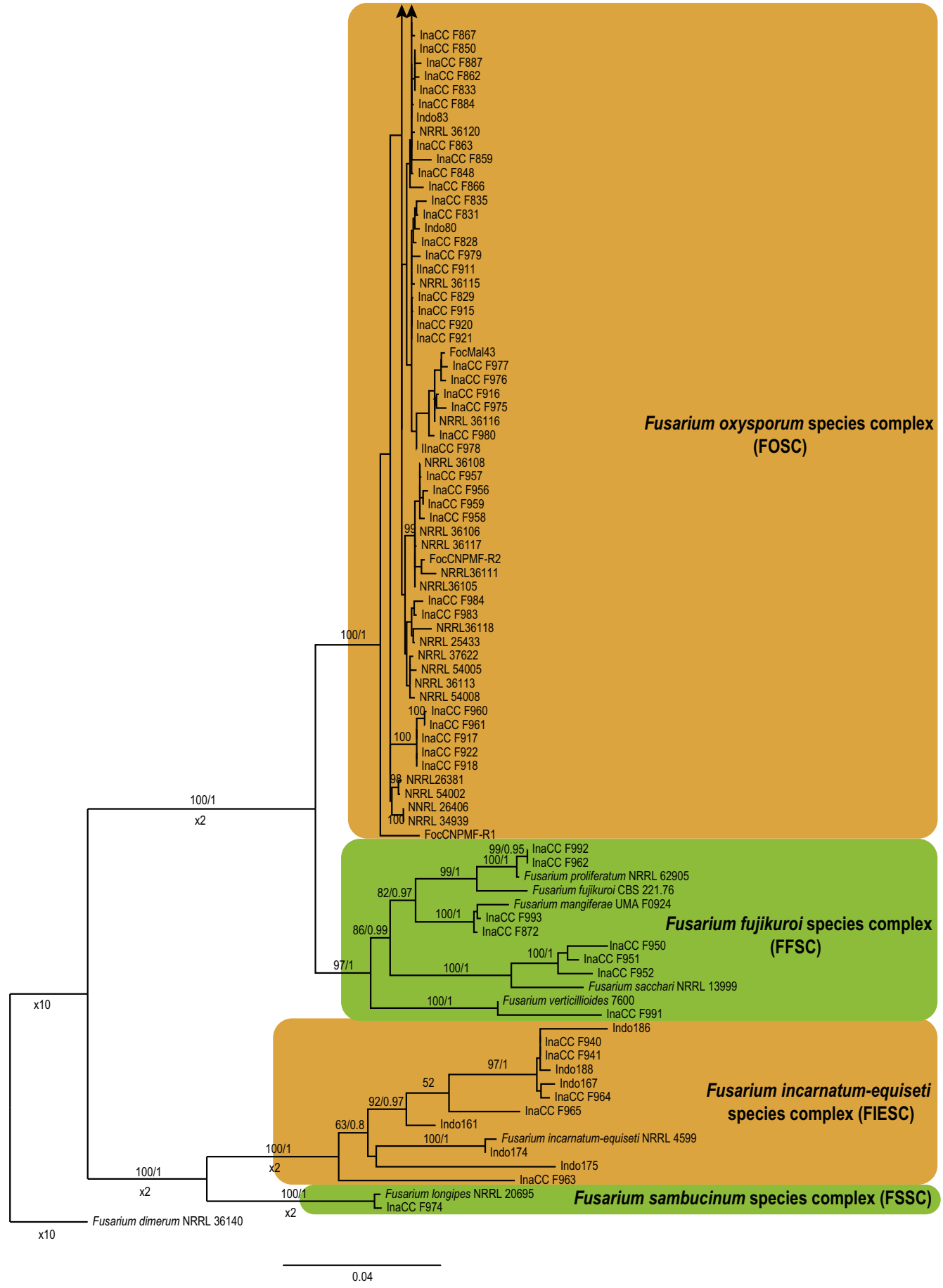

Fig. 4. (Continued).

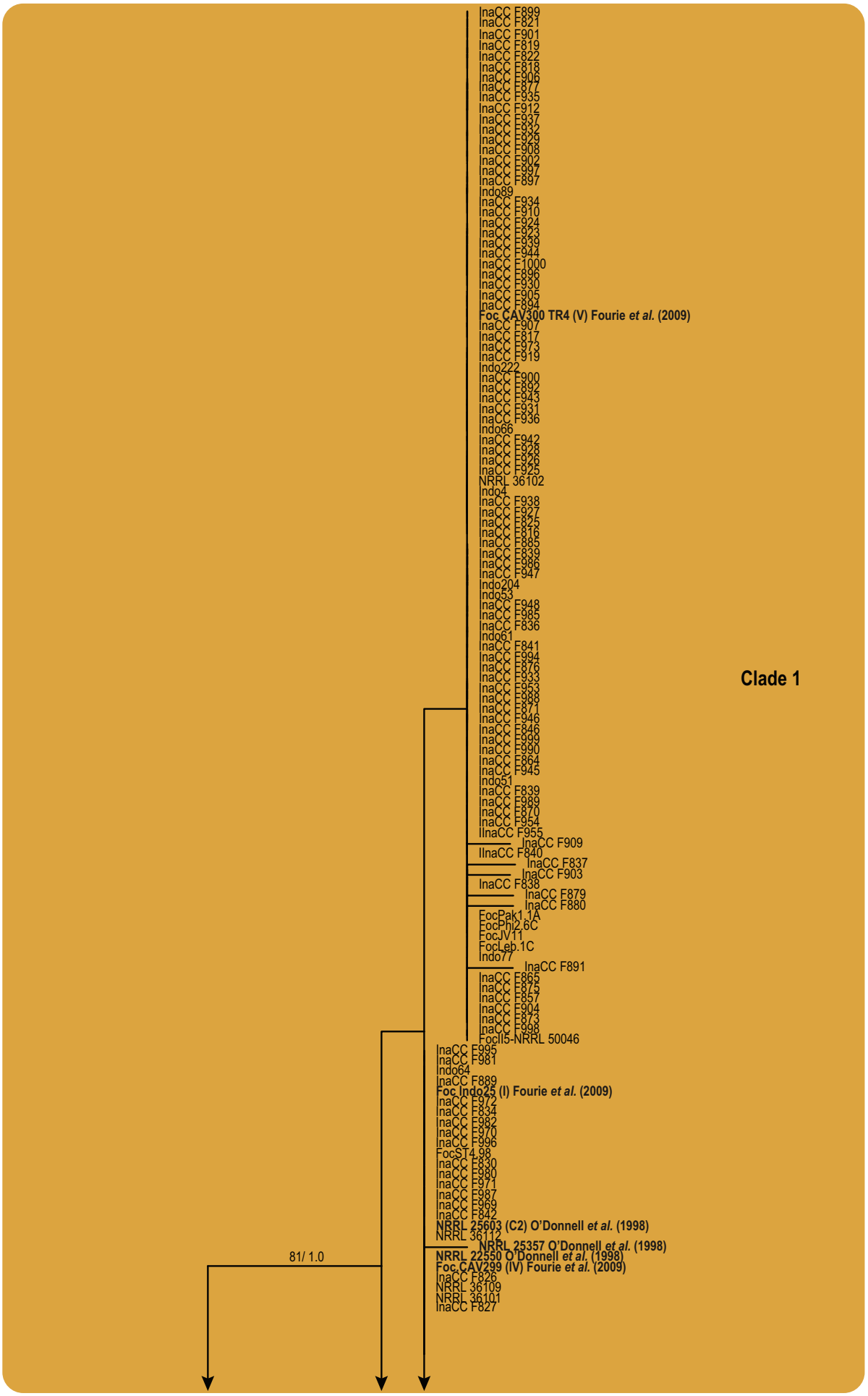

Fig. 5. Maximum likelihood tree inferred from the *tef1* gene sequence data set of 183 Indonesian isolates in the FOSC clade. Included are representatives of the studies by O'Donnell *et al.* (1998, 2004) and Fourie *et al.* (2009), indicated in **bold**. The bootstrap support values >70 % (BS) and Bayesian posterior probabilities >0.95 (PP) are given at nodes. The tree is rooted to *Fusarium fujikuroi* (CBS 221.76).

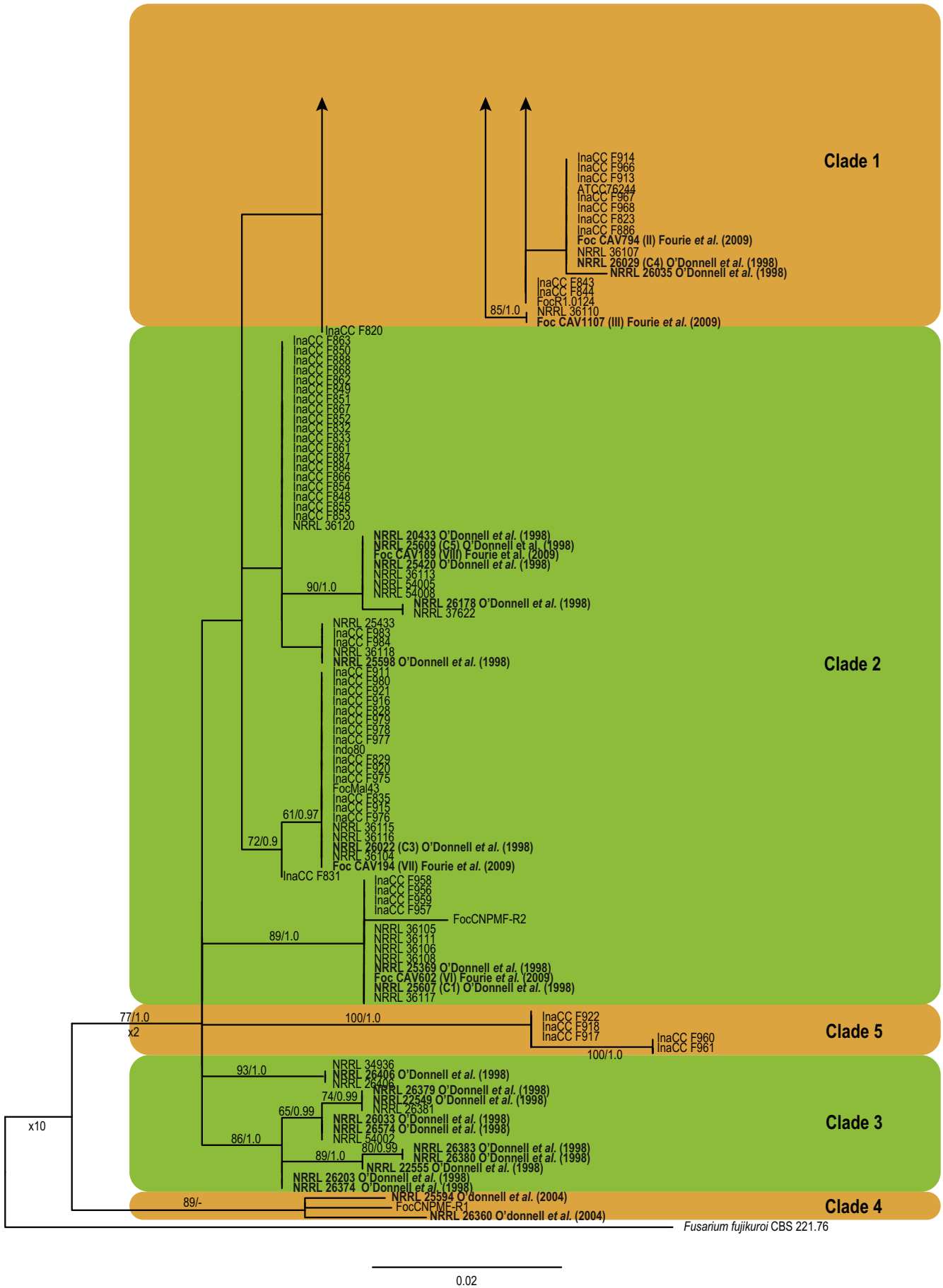

Fig. 5. (Continued).

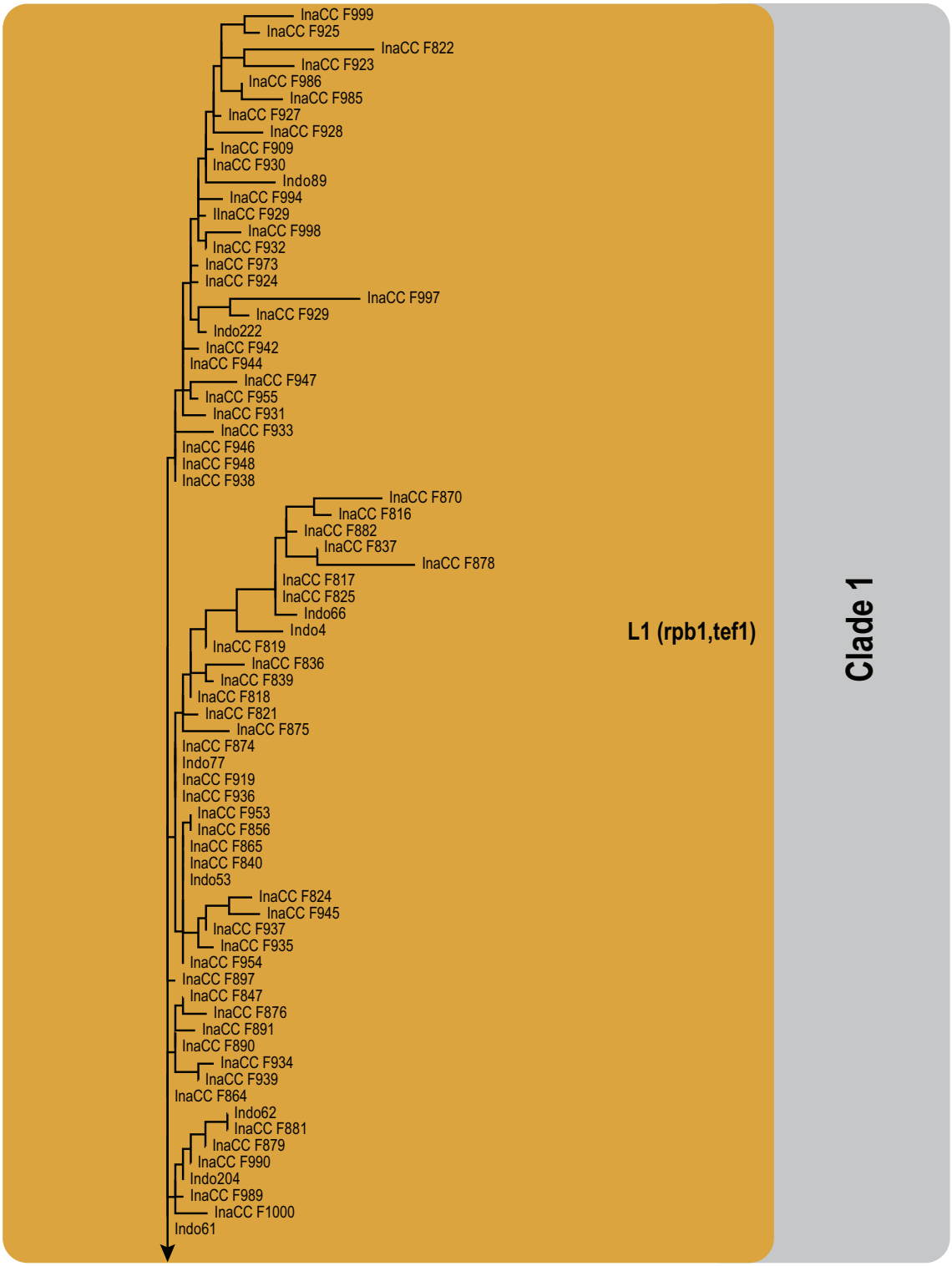

Fig. 6. Maximum likelihood tree inferred from the combined *rpb1*, *rpb2* and *tef1* genes sequence data sets. The bootstrap support values >70 % (BS) and Bayesian posterior probabilities >0.95 (PP) are given at nodes. Foc lineages are numbered based on the consensus from single and combine gene data sets represented by the coloured blocks. The tree is rooted to *Fusarium fujikuroi* (CBS 221.76).

SNA and PDA, falcate, (50–)54–60(–62) × (3–)4–5(–7) µm (av. 57 × 7 µm), 2–5-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* monophialidic on sporodochia, or formed directly from hyphae (lateral phialides) with elongated collarettes, 7–41 × 3–7 µm. *Microconidia* abundant on PDA, less frequent on CLA, ovoid to ellipsoid, (6–)7–16(–24) × (3–)4(–6) µm (av. 12 × 5 µm), 0–1-septate, arranged in false heads on branched or lateral conidiophores carried on hyphae. Aerial conidiophores rare on CLA and SNA and formed abundantly on PDA, branched sparsely or forming short lateral conidiophores. *Chlamydospores* globose to subglobose, formed terminally, single or in pairs, (8–)9–12(–13) × (9–)10(–11) µm, rarely produced on SNA after 7 d, rough-walled.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C with an average growth rate of 4.9–5.2 mm/d. Colony reverse, uniformly white and unpigmented. Colony surface dry, cottony, white, filamentous margin. No exudates observed. Aerial mycelium abundant, cottony, with high sporulation.

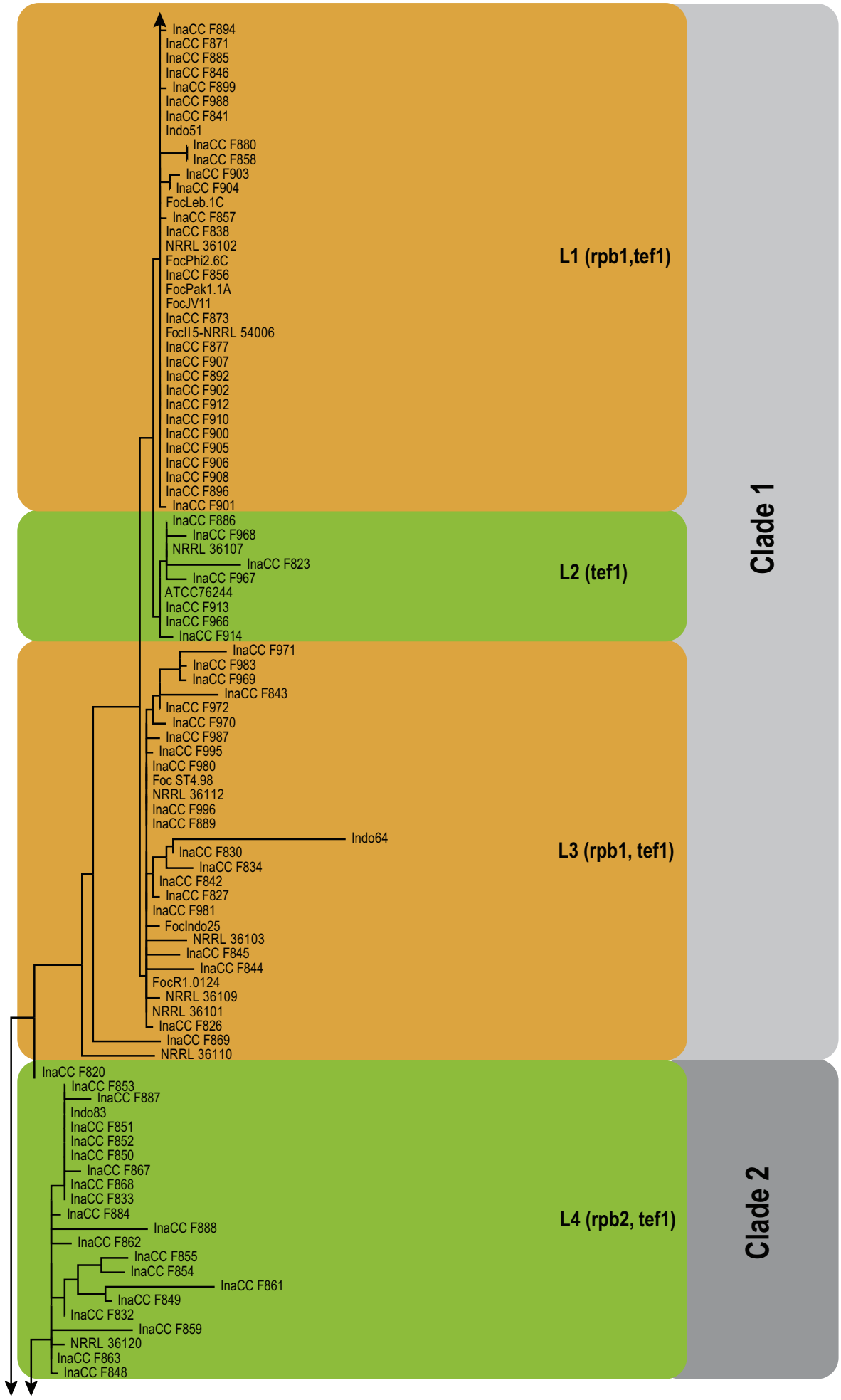

Fig. 6. (Continued).

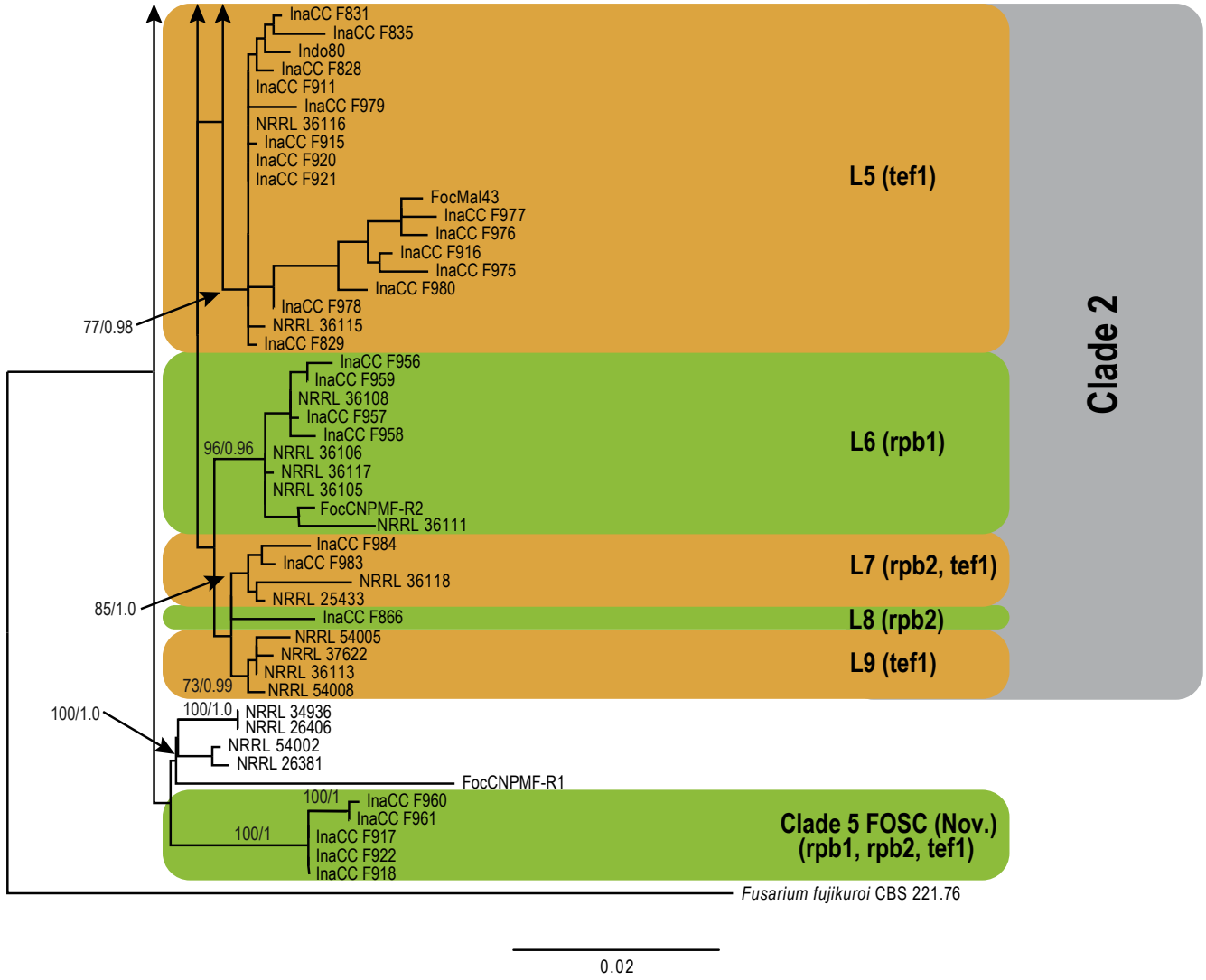

Fig. 6. (Continued).

Sporodochia formed abundantly on CLA after 7 d, pale orange to orange.

Geography and host: Tanah Bumbu, South Kalimantan, *Musa* sp. var. Pisang Awak (ABB).

Pathogenicity: Pathogen on Gros Michel (AAA).

Materials examined: **Indonesia,** Kampung Betung, Tanah Bumbu, South Kalimantan (115°37′477″E, 3°37′45″S), on infected pseudostem of *Musa* sp. var. Pisang Awak (ABB), 20 Jun. 2014, N. Maryani (**holotype** preserved as metabolically inactive culture, InaCC F971).

Notes: *Fusarium phialophorum* has elongated phialidic collarettes, which are rarely found in other lineages. Polyphialidic conidiophores were not found, and chlamydospores were formed, but were rare. Isolates in this lineage were able to infect Gros Michel but not Cavendish, and were therefore classified as Foc-Race1.

Foc Lineage L4

Fusarium grosmichelii N. Maryani, L. Lombard**,** Kema & Crous, **sp. nov.** MycoBank MB826803. Fig. 11.

Etymology: Name reflects its association with the banana variety Gros Michel.

Macroconidia abundant on CLA, less abundant on PDA and SNA, formed on sporodochia on CLA and on aerial conidiophores on SNA and PDA, falcate, (47–)51–59(–64) × (5–)6–8(–9) µm (av. 55 × 7 µm), 3–5-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* mono- or polyphialidic on sporodochia, on branched conidiophores, or formed directly from hyphae (lateral phialides), (8–)16–28(–36) × (3–)4–6(–7) µm. *Microconidia* abundant on PDA and SNA, less frequent on CLA, ovoid to ellipsoid, (4–)9–17(–21) × (3–)4–6(–7) µm (av. 12 × 5 µm), 0–1-septate, arranged in false heads on branched or lateral conidiophores carried on hyphae. *Chlamydospores* globose to subglobose, formed terminally or intercalarily, single or in clumps, rarely produced on SNA after 7 d, rough-walled.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C with an average growth rate of 4.7–5.0 mm/d. Colony reverse in the dark uniformly white and unpigmented. Colony surface dry, cottony white with filamentous margin. No exudates observed. Aerial mycelium abundant, cottony, with abundant sporulation. Sporodochia formed abundantly on CLA after 7 d, pale orange to orange.

Geography and host: Bogor, West Java, *Musa acuminata* var. Pisang Ambon Lumut (AAA).

Pathogenicity: Pathogen on Gros Michel (AAA).

Materials examined: **Indonesia**, Suakarya Megamendung, Bogor, West Java (106°54′214″E, 6°41′185″N), on infected pseudostem *Musa acuminata* var.

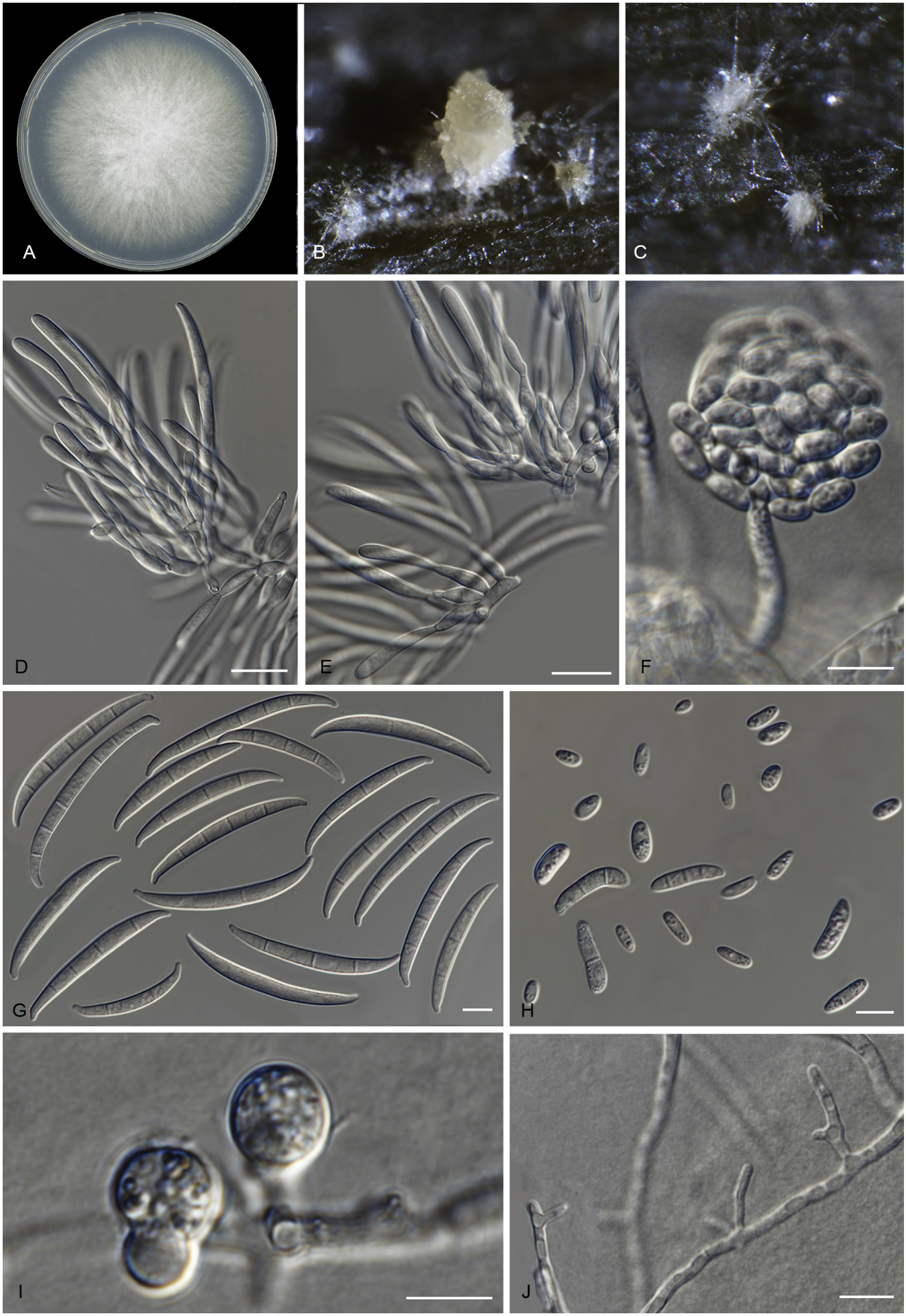

Fig. 7. *Fusarium odoratissimum* (InaCC F817). **A.** Culture grown on PDA. **B–C.** Sporodochia on carnation leaves. **D–E.** Sporodochial branched conidiophores with monophialides. **F.** False head. **G.** Falcate-shaped macroconidia. **H.** Microconidia. **I.** Chlamydospores. **J.** Polyphialides. Scale bars D–J = 10 μm.

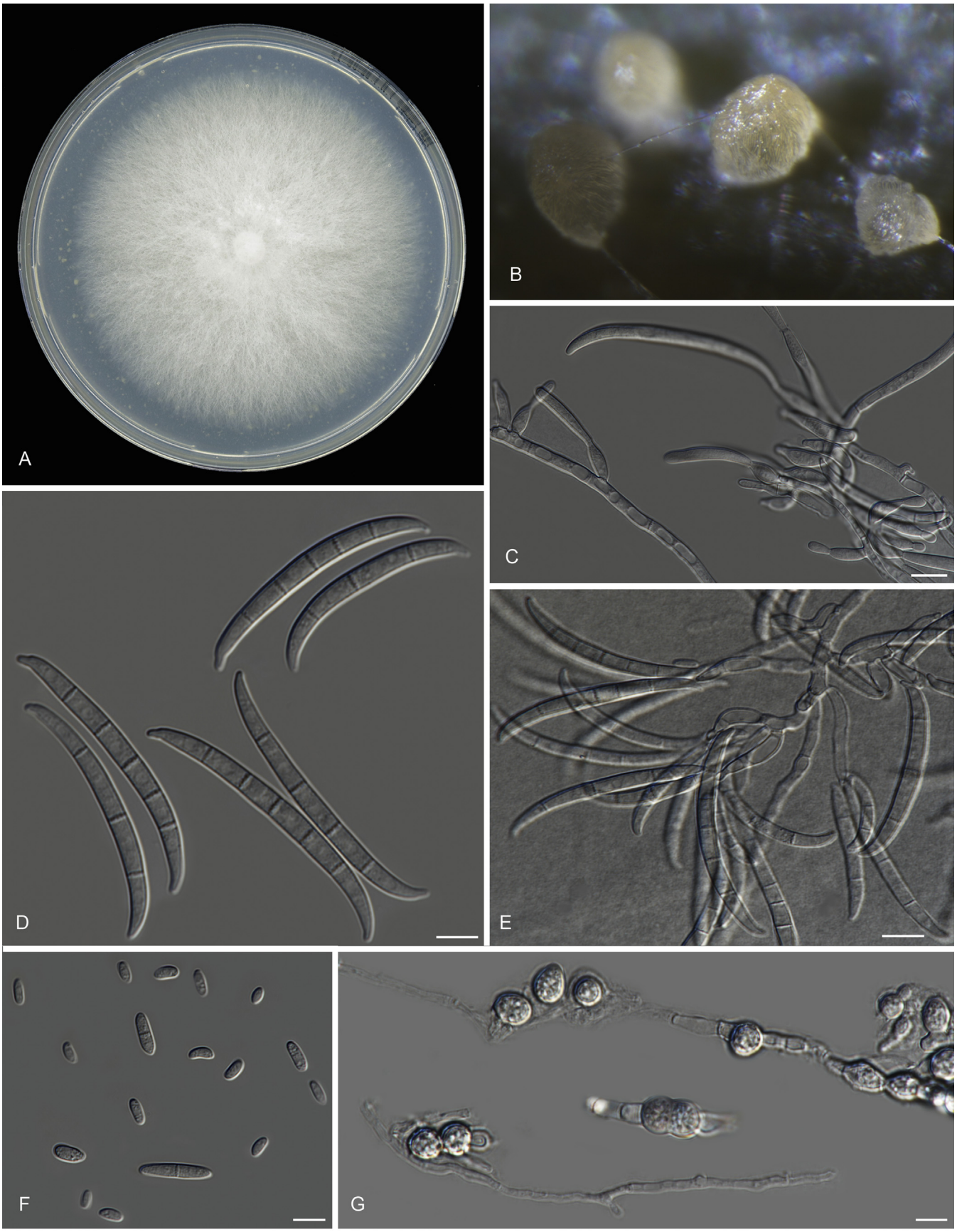

Fig. 8. *Fusarium odoratissimum* (ex-type InaCC F822). **A.** Culture grown on PDA. **B.** Sporodochia on carnation leaves. **C.** Monophialides with initial conidia being formed. **D.** Falcate-shaped macroconida. **E.** Branched conidophores. **F.** Elliptical microconidia. **G.** Thick-walled chlamydospores. Scale bars C–G = 10 μm.

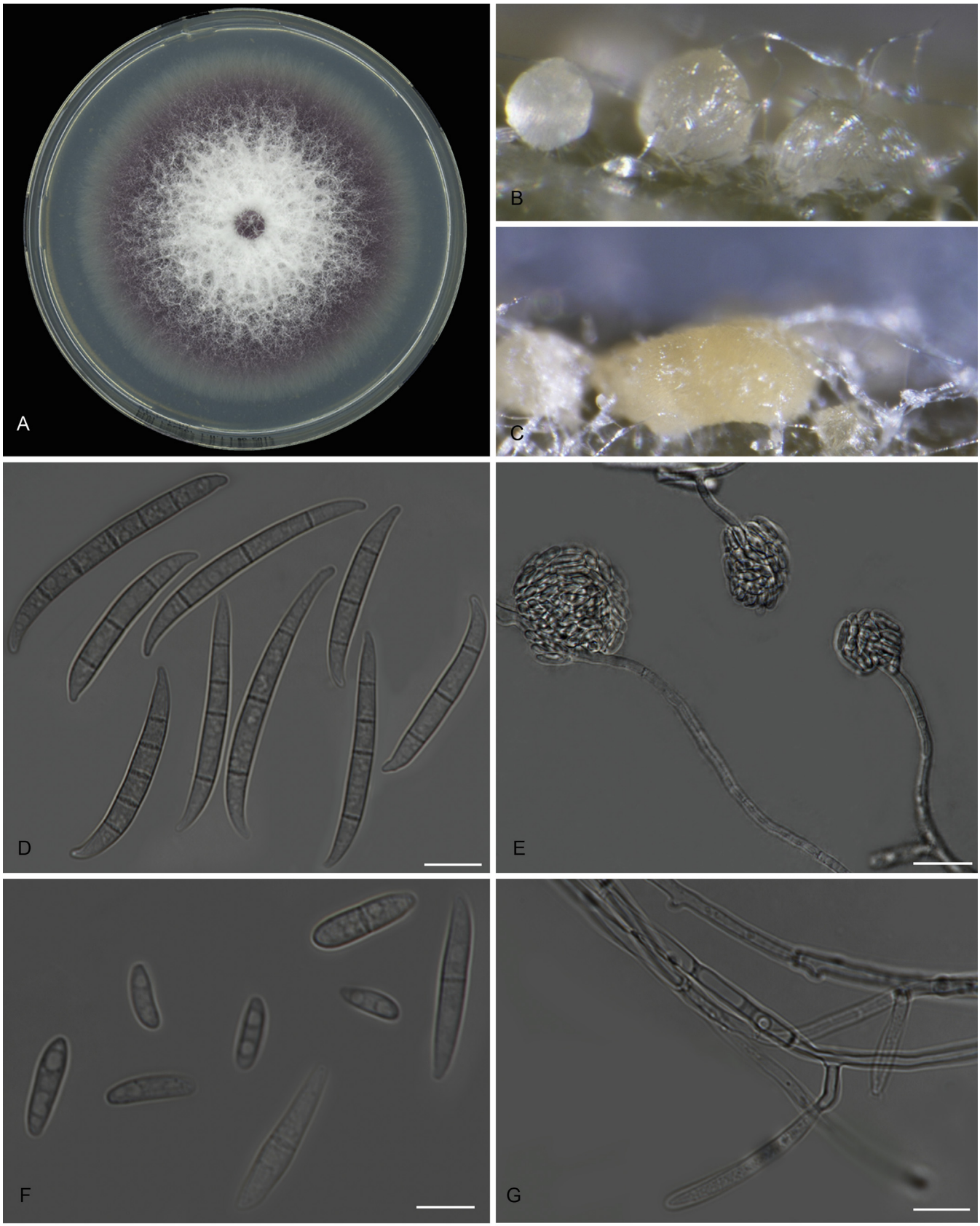

Fig. 9. *Fusarium purpurascens* (ex-type InaCC F886). **A.** Culture grown on PDA. **B–C.** Sporodochia grown on carnation leaves. **D.** Falcate-shaped macroconidia. **E.** False heads. **F.** Microconidia. **G.** Monophialides. Scale bars D–G = 10 μm.

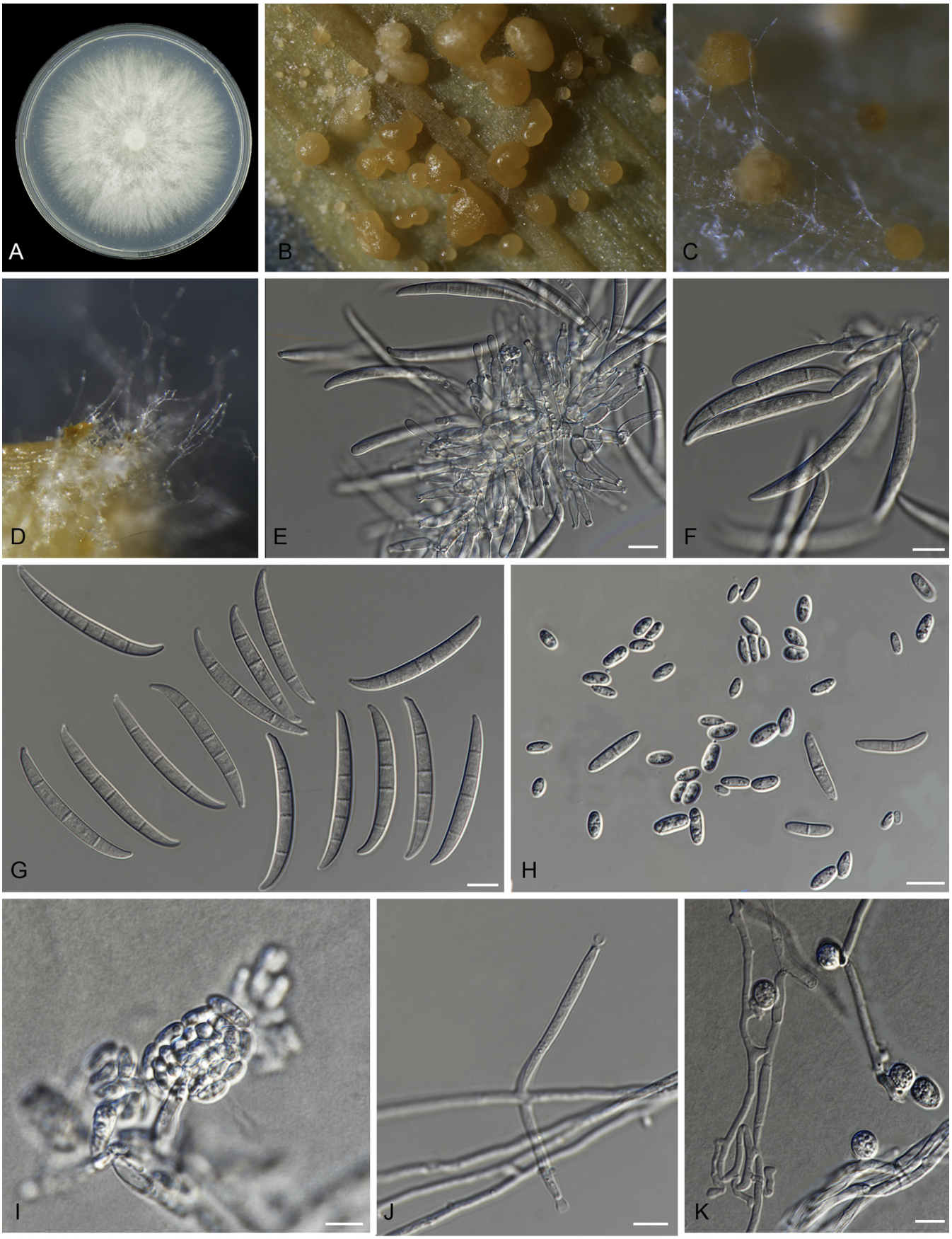

Fig. 10. *Fusarium phialophorum* (ex-type InaCC F971) **A.** Culture grown on PDA. **B–C.** Sporodochia on carnation leaves. **D.** Aerial conidiophore on carnation leaves. **E–F.** Sporodochial phialides. **G.** Falcate-shaped macroconidia. **H.** Microconidia. **I.** False head. **J.** Lateral monophialides with long collaretes. **K.** Thick-walled chlamydospores. Scale bars E–K = 10 μm.

Pisang Ambon Lumut (AAA), 10 Jul. 2014, N. Maryani, (**holotype** preserved as metabolically inactive culture InaCC F833).

Notes: *Fusarium grosmichelii* is morphologically very similar to *F. phialophorum*, but differs in having a higher number of septa in its macroconidia (3–5-septate). *F. grosmichelii* and others in this lineage are morphologically similar to *F. odoratissimum*, but *F. grosmichelii* was not able to infect Cavendish. Most of the isolates in L4 were tested on Gros Michel, and were able to cause disease, and were thus classified as Foc-Race1.

Foc Lineage L5

Fusarium duoseptatum N. Maryani, L. Lombard, Kema & Crous, **sp. nov.** MycoBank MB826804. Fig. 12.

Etymology: Name reflects the fact that its microconidia are frequently 2-septate.

Macroconidia abundant on CLA, less abundant on PDA and SNA, formed on sporodochia on CLA and on aerial conidiophores on SNA and PDA, falcate, (50–)53–63(–68) × (5–)6–8(–9) µm (av. 58 × 7 µm), 3–5-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* mono- or polyphialidic on sporodochia, or on aerial hyphae, or formed directly from hyphae as lateral phialides, (5–)9–25(–38) × (3–)4–7(–9) µm. *Microconidia* abundant on PDA and SNA, less frequent on CLA, ovoid to ellipsoid, (9–)21(–33) × (2–)3(–6) µm (av. 15 × 5 µm), 0–2-septate, arranged in false heads on branched conidiophores carried on hyphae. Aerial conidiophores rare on CLA and SNA, formed abundantly on PDA, branched sparsely or formed laterally. *Chlamydospores* globose to subglobose, formed laterally, intercalary or terminally, single or in pairs, (6–)8–10(–11) × (6–)7–9(–11) µm, abundantly produced on SNA after 7 d, rough-walled.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C with an average growth rate of 3.8–4.1 mm/d. Colony reverse violet, mycelium becoming purple, and pigmented with age. Colony surface dry, cottony violet in the centre, and white towards the margin. No exudates observed. Aerial mycelium abundant, cottony, with moderate sporulation. Sporodochia formed abundantly on CLA after 7 d, pale orange to orange.
Geographic and host: Kapuas, Central Kalimantan, *Musa* sp. var. Pisang Kepok (ABB).

Pathogenicity: Pathogen on Gros Michel (AAA).

Material examined: **Indonesia**, Serapat tengah, Kapuas Timur, Central Kalimantan (114°28′65″E, 3°6′9″S), on infected pseudostem of *Musa* sp. var. Pisang Kepok (ABB), 22 Jun. 2014, N. Maryani, (**holotype** preserved as metabolically inactive culture InaCC F916).

Notes: *Fusarium duoseptatum* has distinctive septation in its microconidia, being 0–2-septate, thus differing from *F. grosmichelii*, which is 0–1-septate. The former is relatively slow-growing compared to members of the most closely related lineage, L4, and forms pigmentation in the centre of colony that is not observed in isolates of L4. *F. duoseptatum* and most of the members of L5 were able to infect Gros Michel, and were therefore classified as Foc-Race1.

Foc Lineage L6

Fusarium tardichlamydosporum N. Maryani, L. Lombard, Kema & Crous, **sp. nov.** MycoBank MB826805. Fig. 13.

Etymology: Name reflects the delayed chlamydospore production observed in this species.

Macroconidia abundant on CLA, less abundant on PDA and SNA, formed on sporodochia on CLA and on aerial conidiophores on SNA and PDA, falcate, (36–)37–43(–45) × (4–)5–6(–7) µm (av. 40 × 5 µm), 3–5-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* monophialidic on sporodochia, or on aerial hyphae, or formed directly on hyphae as lateral phialides, (3–)7–14(–19) × (2–)3–5(–8) µm. *Microconidia* abundant on PDA and SNA, ovoid to ellipsoid, (3–)5–9(–15) × (2–)5(–9) µm (av. 7 × 3 µm), 0–2-septate, arranged in false heads on branched conidiophores carried on hyphae. Aerial conidiophores rare on CLA and SNA and formed abundantly on PDA, branched sparsely or formed laterally. *Chlamydospores* abundantly produced after 4 wk, globose to subglobose, (6–)7–10(–13) × (4–)6–9(–10) µm, formed terminally or intercalarily, single or in pairs, rough-walled.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C with an average growth rate of 4.6–5.6 mm/d. Colony reverse sparsely dark purple in the centre, becoming white towards the margins, and purple slate, pigmented with age. Colony surface dry, cottony, with white filamentous margin, and lacking exudates. Aerial mycelium abundant, cottony, with abundant sporulation. Sporodochia formed abundantly on CLA after 7 d, pale orange to orange.

Geography and host: Sikka Flores, *Musa acuminata* var. Pisang Barangan (AAA).

Pathogenicity: Pathogen on Gros Michel (AAA).

Materials examined: **Indonesia**, Desa Kota Uneng Kecamatan Alok, Sikka Flores, East Nusa Tenggara (112°12′16″E, 8°37′11″S), on infected pseudostem of *Musa acuminata* var. Pisang Barangan (AAA), 21 Aug. 2015, N. Maryani, (**holotype** preserved as metabolically inactive culture, InaCC F958).

Notes: Colonies of *Fusarium tardichlamydosporum* are relatively fast growing (av. 4.6–5.6 mm/d) compared to those of *F. duoseptatum* (av. 38–41 mm/d). Polyphialidic conidiophores were not observed in this species/lineage. Chlamydospores were produced, but only after 4 wk. *F. tardichlamydosporum* was able to infect Gros Michel, and is therefore classified as Foc-Race1.

Foc Lineage L7

Fusarium cugenangense N. Maryani, L. Lombard, Kema & Crous, **sp. nov.** MycoBank MB826807. Fig. 14.

Etymology: Name reflects Cugenang, the location where this species was collected in Indonesia.

Macroconidia abundant on CLA, formed on sporodochia, on aerial conidiophores or on lateral phialides, falcate, (44–)47–54(–57) × (5–)6–7(–8) µm (av. 53 × 7 µm), 3–6-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* monophialidic on sporodochia, or on aerial hyphae, or formed directly from hyphae as lateral phialides, (5–)12–31(–45) × (3–)5–7(–8) µm. *Microconidia* abundant on PDA and SNA, less frequent on CLA, ovoid to ellipsoid, (7–)8–11(–24) × (2–)7(–12) µm (av. 12 × 5 µm), 0–3-septate, arranged in false heads on branched conidiophores carried on hyphae. Aerial conidiophores rare on CLA and SNA, and formed abundantly on PDA, branched sparsely or formed laterally. *Chlamydospores* rarely produced on SNA after 4 wk, globose to subglobose, (9–)10–14(–16) × (10–)11–14(–16) µm, formed terminally, single or in pairs, rough-walled.

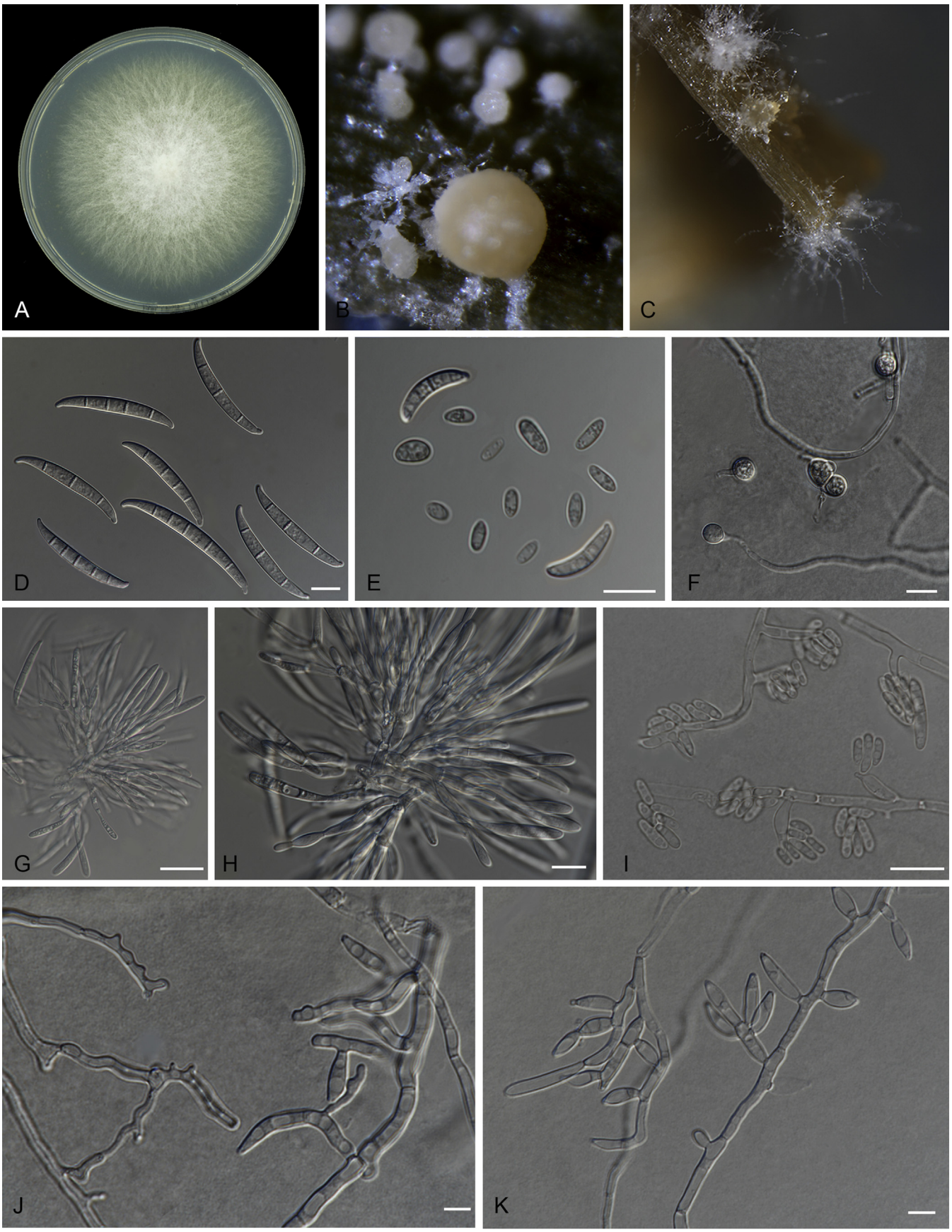

Fig. 11. *Fusarium grosmichelii* (ex-type InaCC F833). **A.** Culture grown on PDA. **B.** Sporodochia on carnation leaves. **C.** Aerial conidiophores from stereo microscope. **D.** Falcate-shaped macroconidia. **E.** Microconidia. **F.** Chlamydospores. **G–H**. Sporodochial phialides. **I**. False heads. **J.** Polyphialides. **K.** Branched conidiophore. Scale bars D–F, H–K = 10 μm, G = 20 μm.

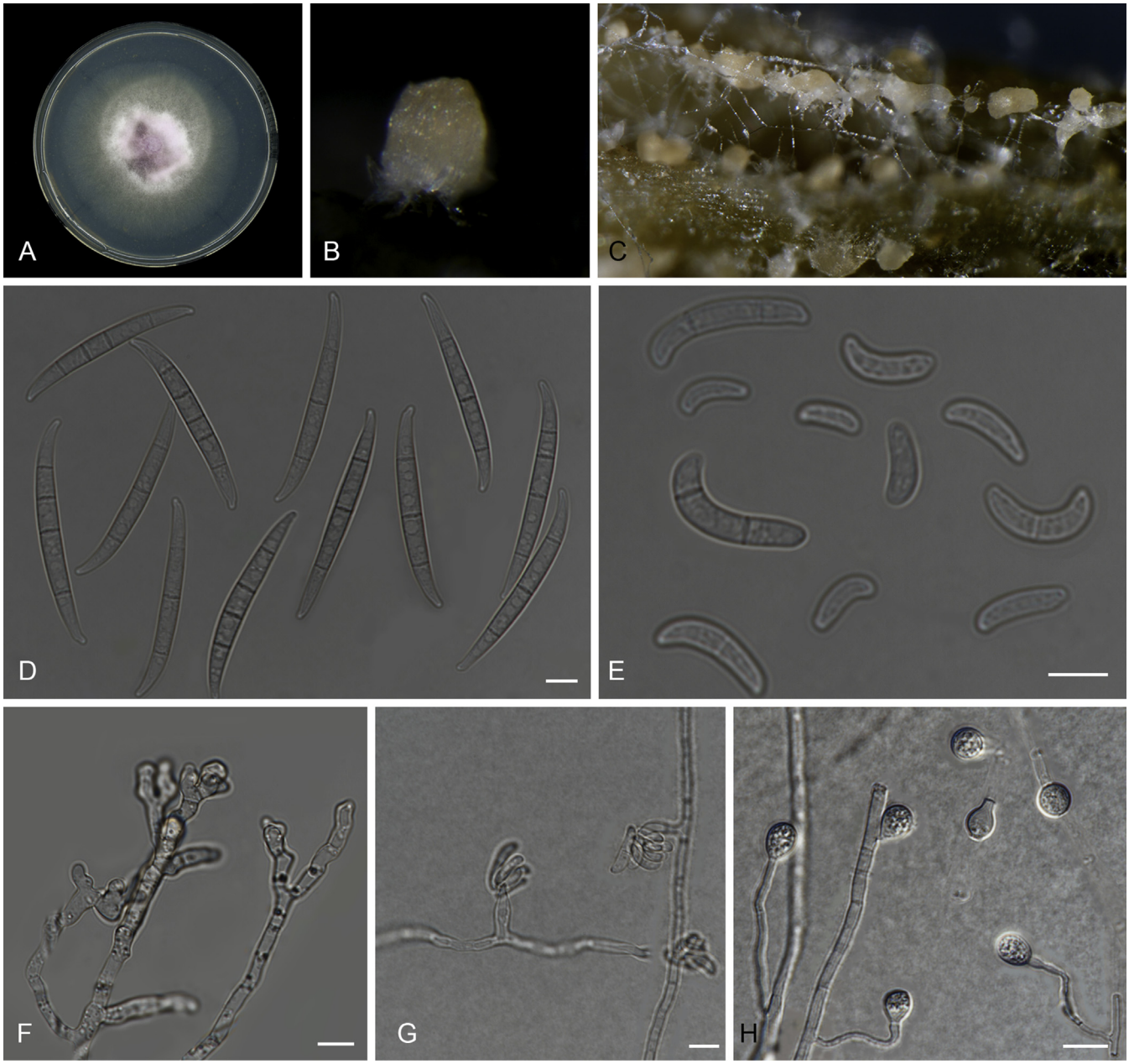

Fig. 12. *Fusarium duoseptatum* (ex-type InaCC F916). **A.** Culture grown on PDA. **B–C.** Sporodochia on carnation leaves. **D.** Falcate-shaped macroconidia. **E.** Microconidia. **F.** Polyphialidic conidiogenous cells. **G.** False heads. **H.** Chlamydospores. Scale bars D–H = 10 μm.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C with an average growth rate of 5.2–5.4 mm/d. Colony reverse purple at center to pale viscous grey, white towards the margins, becoming purple slate with age, and pigmented. Colony surface dry, cottony, dark purple to white with filamentous margin, lacking exudates. Aerial mycelium abundant, cottony, with profuse sporulation. Sporodochia formed abundantly on CLA after 7 d, pale orange to orange.

Geography and host: Cianjur, West Java, *Musa* sp. var. Pisang Kepok (ABB).

Pathogenicity: Non-pathogenic on Gros Michel (AAA) and Cavendish (AAA).

Material examined: **Indonesia,** Cugenang, Cianjur, West Java (107°4′109″E, 6°47′867″S), on infected pseudostem *Musa* sp. var. Pisang Kepok (ABB), 10 Jul. 2014, N. Maryani, (**holotype** preserved as metabolically inactive culture, InaCC F984).

Notes: L7, including *Fusarium cugenangense* and other isolates, represents an Indonesian lineage with isolates that are closely related to other formae speciales (Fig. 6; e.g. NRRL 25433 *F. oxysporum* f. sp. *vasinvectum*). Polyphialidic conidiogenous cells were not observed in this species. This species has macroconidia with unique septation (3–6-septate) and microconidia (0–3-septate), which is rather uncommon for *F. oxysporum* species. This species causes a slight infection on Cavendish and Gros Michel, and testing on other cultivars such as Bluggoe (Pisang Kepok, ABB) are needed to fully classify strains as Foc-Race2.

Foc Lineage L8

Fusarium hexaseptatum N. Maryani, L. Lombard, Kema & Crous, **sp. nov.** MycoBank MB826808. Fig. 15.

Etymology: Name reflects the six conidial septa observed in its macroconidia.

Macroconidia abundant on CLA, less so on PDA and SNA, formed on sporodochia on CLA and on aerial conidiophores on SNA and PDA, falcate, (34–)45–71(–76) × (5–)6–8(–9) μm (av.

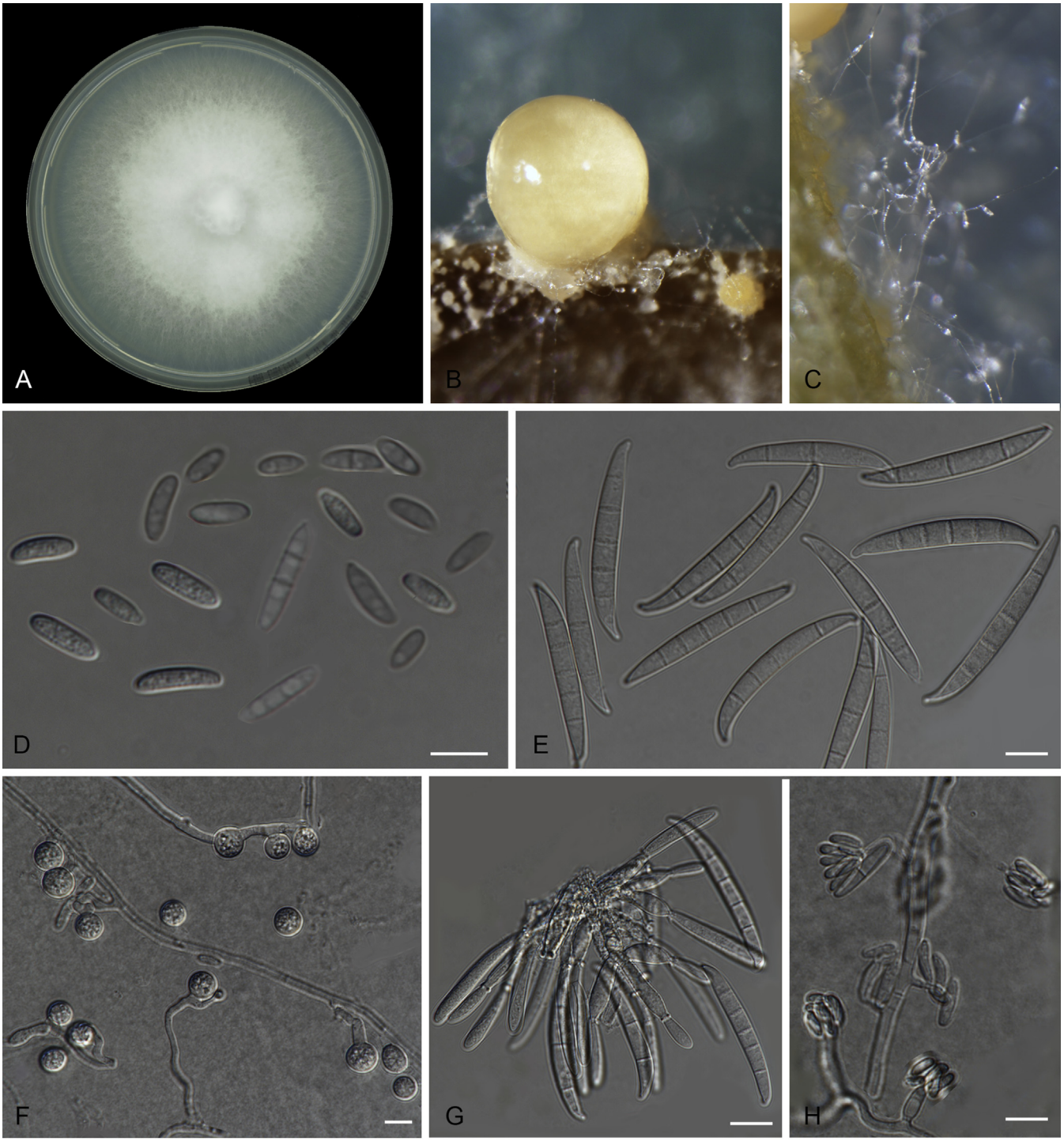

Fig. 13. *Fusarium tardichlamydosporum* (ex-type InaCC F958). **A.** Culture grown on PDA. **B.** Sporodochia on carnation leaves. **C.** Aerial conidiophore. **D.** Microconidia. **E.** Falcate-shaped macroconidia. **F.** Chlamydospores. **G.** Sporodochial phialides. **H.** False heads. Scale bars D–H = 10 μm.

58 × 7 μm), 3–6-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* mono- or polyphialidic on sporodochia, or formed directly from on hyphae (lateral phialides), 7–20 × 2–6 μm. *Microconidia* abundant on PDA and SNA, rare on CLA, ovoid to ellipsoid, (4–)8–23(–29) × (2–)7(–12) μm (av. 16 × 5 μm), 0–1-septate, arranged in false heads on branched conidiophores carried on hyphae. Aerial conidiophores rare on CLA and SNA and formed abundantly on PDA, branched sparsely or formed laterally. *Chlamydospores* abundantly formed in hyphae, globose to subglobose, (5–)14(–20) × (4–)6–12(–17) μm, formed terminally or intercalarily, single or in pairs.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C with an average growth rate of 4.9–5.9 mm/d. Colony reverse, in the dark, white and becoming livid purple in the center of the colony. Colony surface with filamentous margin, dry, cottony, white becoming livid vinaceous in age. No exudates observed. Aerial mycelium abundant, cottony, with high sporulation. Sporodochia formed abundantly on CLA after 7 d, colourless to pale orange.

Geography and host: Sukabumi, West Java, Pisang Ambon Kuning (AAA).

Pathogenicity: Pathogen on Gros Michel (AAA).

Material examined: **Indonesia,** Parakan Lima, Sukabumi, West Java (107°5′869″E, 6°50′614″S), on infected pseudostem *Musa acuminata* var. Pisang Ambon Kuning (AAA), 7 Oct. 2014, N. Maryani, (**holotype** preserved as metabolically inactive culture, InaCC F866).

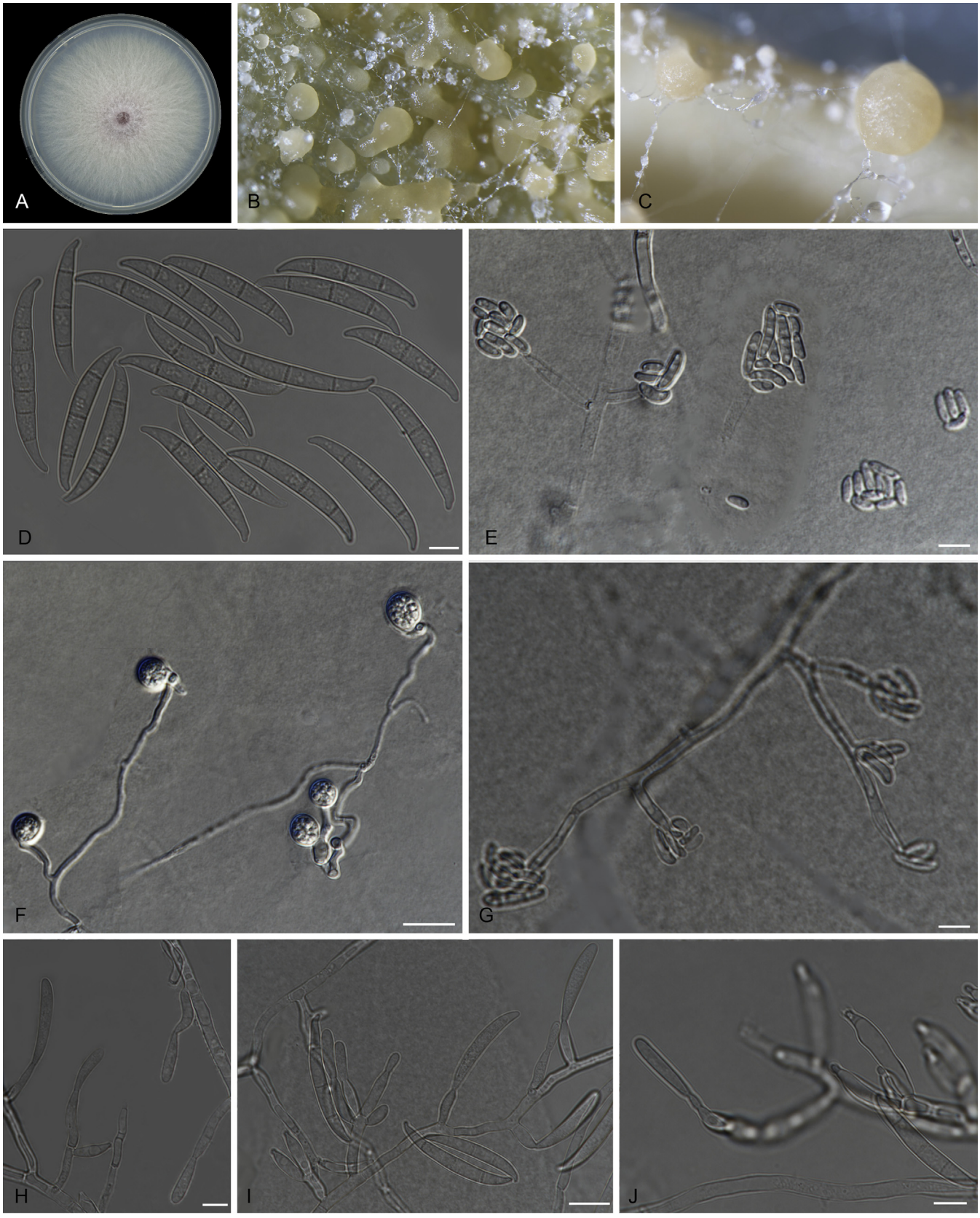

Fig. 14. *Fusarium cugenangense* (ex-type InaCC F984). **A.** Culture grown on PDA. **B–C.** Sporodochia on carnation leaves. **D.** Falcate-shaped macroconidia. **E.** Microconidia. **F.** Chlamydospores. **G.** False heads. **H.** Monophialidic conidiogenous cells. **I–J.** Branched conidiophores. Scale bars D–J = 10 μm.

Notes: Fusarium hexaseptatum is the single species in L8. Macroconidia with 6 septa are abundantly observed in this lineage, whereas in L7 and L9, they are very rare. This lineage is distinguished from L7 and L9 by its ability to cause disease on Gros Michel, and therefore it was classified as Foc-Race1. *F. hexaseptatum* has chlamydospores that are relatively large compared to those in other lineages (av. 9 × 9 μm).

Foc Lineage L9

Fusarium tardicrescens N. Maryani, L. Lombard**,** Kema & Crous, **sp. nov.** MycoBank MB826809. Fig. 16.

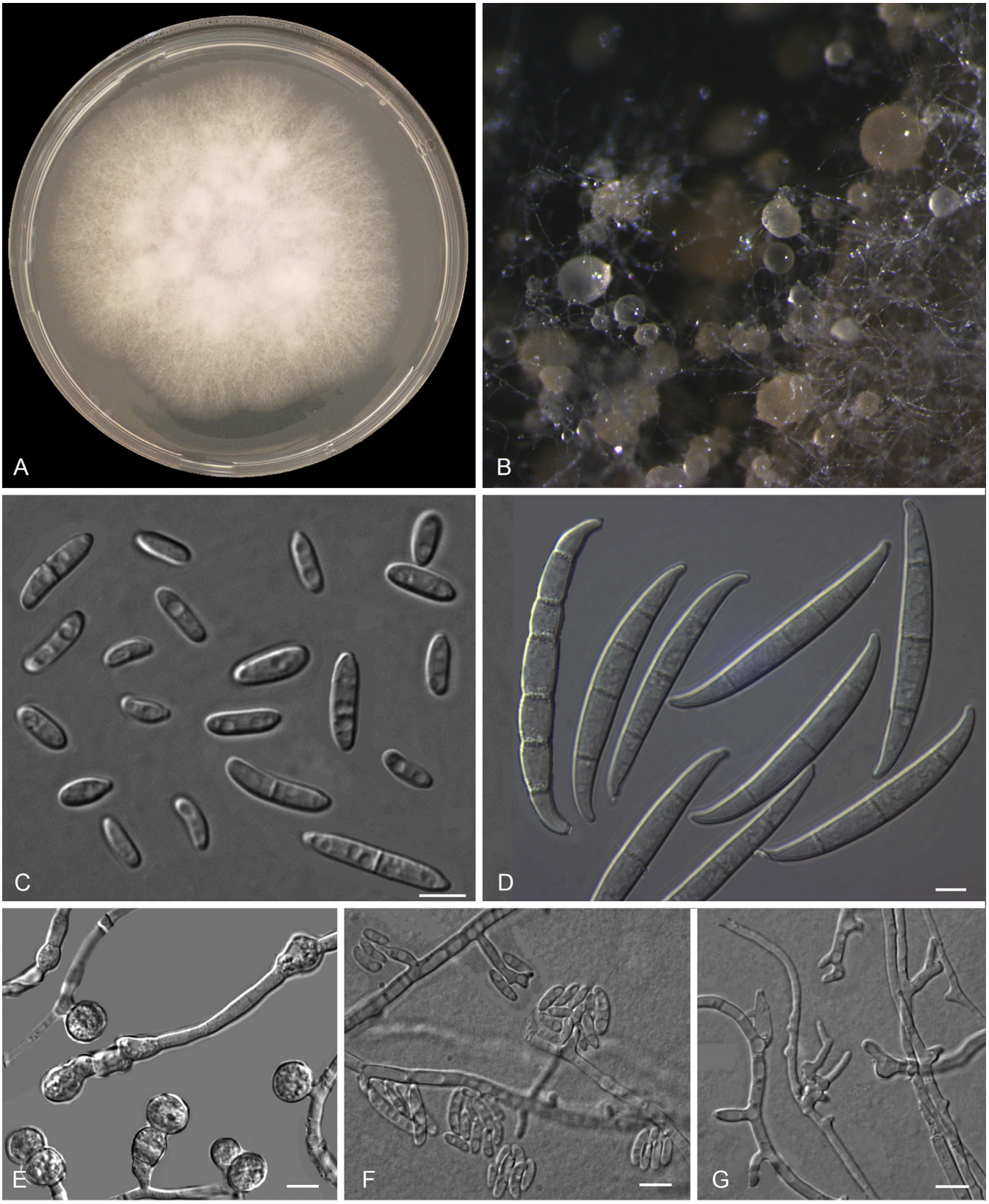

Fig. 15. *Fusarium hexaseptatum* (ex-type InaCC F866). **A.** Culture grown on PDA. **B.** Sporodochia on carnation leaves. **C.** Microconidia. **D.** Falcate-shaped macroconidia. **E.** Thick-walled chlamydospores. **F.** False heads. **G.** Monophialides and polyphialides. Scale bars C–G = 10 μm.

Etymology: Name reflects the slow growth rate in culture.

Macroconidia abundant on CLA and SNA, less abundant on PDA, formed on sporodochia on CLA and on aerial conidiophore on SNA and PDA, falcate, (52–)56–75(–89) × (5–)6–8(–9) μm (av. 66 × 7 μm), 2–6-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* mono- and polyphialidic on sporodochia formed directly from hyphae (lateral phialides), 7–32 × 2–6 μm. *Microconidia* abundant on PDA and SNA, less so on CLA, ovoid to ellipsoid, (7–)10–16(–20) × (2)–5(–7) μm (av. 13 × 4 μm), 0–1-septate, arranged in false heads on branched conidiophores carried on hyphae. *Chlamydospores*

globose to subglobose, (5–)7–9(–10) × (5–)6–8(–10) µm, formed intercalarily or terminally, singly or in pairs, produced abundantly on SNA after 7 d, brown, rough-walled.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C with an average growth rate of 2.9–3.9 mm/d. Colony reverse, in the dark, dark violet becoming dark livid and pigmented. Colony surface dry, cottony, dark purple becoming dark livid. No exudates observed. Aerial mycelium abundant, cottony, with abundant sporulation. Sporodochia formed abundantly on CLA after 7 d, pale orange to orange.

Geography and host: NA.

Pathogenicity: NA.

Material examined: **Malawi,** Karonga**,** Misuku Hills, *Musa sapientum* cv. Harare, 1989, R.C. Ploetz (**holotype** preserved as metabolically inactive culture CBS 102024 = NRRL 36113).

Notes: *Fusarium tardicrescens* in L9 represents one of two lineages which clustered with other formae speciales. This lineage does not contain any Indonesian isolates. *F. tardicrescens* is the slowest growing species (av. 2.9–3.9 mm/d). *F. tardicrescens* causes moderate infection on both Cavendish and Gros Michel (Ordonez 2018).

Novel Clade/Taxa in FOSC

Fusarium kalimantanense N. Maryani, L. Lombard, Kema & Crous, **sp. nov.** MycoBank MB826810. Fig. 17.

Etymology: Name reflects Kalimantan, the island in Indonesia from where this fungus was collected.

Macroconidia abundant on CLA, less abundant on PDA and SNA, formed on sporodochia on CLA and on aerial conidiophores on SNA and PDA, falcate, (52–)56–63(–65) × (5–)6–7(–8) µm (av. 59 × 7 µm), 3–5-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* monophialidic on sporodochia, or on aerial hyphae, or formed directly from hyphae as lateral phialides, (9–)11–15(–16) × (2–)3(–5) µm. *Microconidia* abundant on PDA and SNA, less frequent on CLA, ovoid to ellipsoid, (6–)8–15(–20) × (2–)3–4(–7) µm (av. 12 × 4 µm), aseptate, arranged in false heads on branched conidiophores borne on hyphae. Aerial conidiophore sparse on CLA and SNA and formed abundantly on PDA, branched sparsely or formed laterally. *Chlamydospores* rarely produced on SNA after 7 d, globose to subglobose, formed terminally or laterally, single or in pairs, (6–)7–10(–11) × (7–)8–9(–10) µm, rough-walled.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C with an average growth rate of 4.8–1.2 mm/d. Colony reverse rosy buff (pinkish) to white towards the margins, becoming fuscous black and pigmented with age. Colony surface dry, cottony, rosy buff (pinkish) to white, becoming purplish grey with age, filamentous margin, and lacking exudates. Aerial mycelium abundant, cottony, with moderate sporulation. Sporodochia formed abundantly on CLA after 7 d, pale orange to orange.

Geography and host: Katingan, Central Kalimantan, *Musa acuminata* var. Pisang Ambon (AAA).

Pathogenicity: Non-pathogenic on Gros Michel (AAA) and Cavendish (AAA).

Material examined: **Indonesia**, Pulau Malam, Katingan, Central Kalimantan (113°13′333″E, 1°36′374″S), on infected pseudostem *Musa acuminata* var. Pisang Ambon (AAA), 23 Jun. 2014, N. Maryani, (**holotype** preserved as metabolically inactive culture, InaCC F917).

Notes: *Fusarium kalimantanense* represents a new clade (Clade 5) in FOSC, which was previously considered to include only four clades (Fig. 5; sensu O'Donnell *et al.* 2004). This species has relatively fast-growing colonies compared to those of other members of FOSC in this study, and has a unique character in its aseptate microconidia. *F. kalimantanense* causes a slight infection on both Cavendish and Gros Michel. Further pathogenicity tests on other cultivars like Bluggoe (syn. Pisang Kepok, AAB) will be required to determine its race.

Fusarium sangayamense N. Maryani, L. Lombard, Kema & Crous, **sp. nov.** MycoBank MB826811. Fig. 18.

Etymology: Name reflects Sangayam, the location from where this species was collected in Indonesia.

Macroconidia abundant on CLA and SNA, rare on PDA, formed on sporodochia on CLA and on aerial conidiophores on SNA and PDA, falcate, (48–)52–60(–65) × (5–)6–7(–8) µm (av. 56 × 7 µm), 2–5-septate, with apical cells papillate, basal cells foot-shaped. *Conidiogenous cells* monophialidic, similar in sporodochia and on hyphae, polyphialidic, rare, (6–)11–31(–47) × (3–)4–6(–9) µm. *Microconidia* abundant on PDA and SNA, less frequent on CLA, ovoid to ellipsoid, (8–)9–17(–24) × (3–)4–6(–7) µm (av. 13 × 5 µm), 0–1-septate, arranged in false heads on branched conidiophores borne on hyphae. Aerial conidiophores rare on CLA, and formed abundantly on SNA and PDA, sparsely branched, and formed laterally. *Chlamydospores* rarely produced on SNA after 7 d, globose to subglobose, formed terminally or intercalarily, single or in pairs, (6–)7–10(–12) × (6–)7(–9) µm, rough-walled.

Culture characteristics: Colony on PDA showing optimal growth at 25 °C, with an average growth rate of 3.5–4.2 mm/d. Colony reverse uniformly white and unpigmented. Colony surface dry, cottony, white, with filamentous margin and lacking exudates. Aerial mycelium abundant, cottony, with moderate sporulation. Sporodochia formed abundantly on CLA after 7 d, pale orange.

Geography and host: Kota Baru, South Kalimantan, *Musa* sp. var. Pisang Kepok (ABB).

Pathogenicity: Non-pathogenic on Gros Michel (AAA) and Cavendish (AAA).

Material examined: **Indonesia**, Sangayam, Kota Baru, South Kalimantan (115°59′440″E, 2°20′420″S), on infected pseudostem of *Musa* sp. var. Pisang Kepok (ABB), 19 Jun. 2014, N. Maryani, (**holotype** preserved as metabolically inactive culture, InaCC F960).

Notes: Isolates of *Fusarium sangayamense* formed a subclade in the new FOSC Clade 5 (Fig. 6) with high support (BP = 100 % and PP = 1.0). *F. sangayamense* can be distinguished from *F. kalimantanense* based on the septation of its macroconidia (2–5-septate) and microconidia (0–1-septate). This species has polyphialidic conidiogenous cells, which are absent in *F. kalimantanense*. *F. sangayamense* was not able to infect Cavendish or Gros Michel.

Pathogenicity assays

The pathogenicity assay showed that all collected Foc isolates were able to cause typical Fusarium wilt symptoms on either

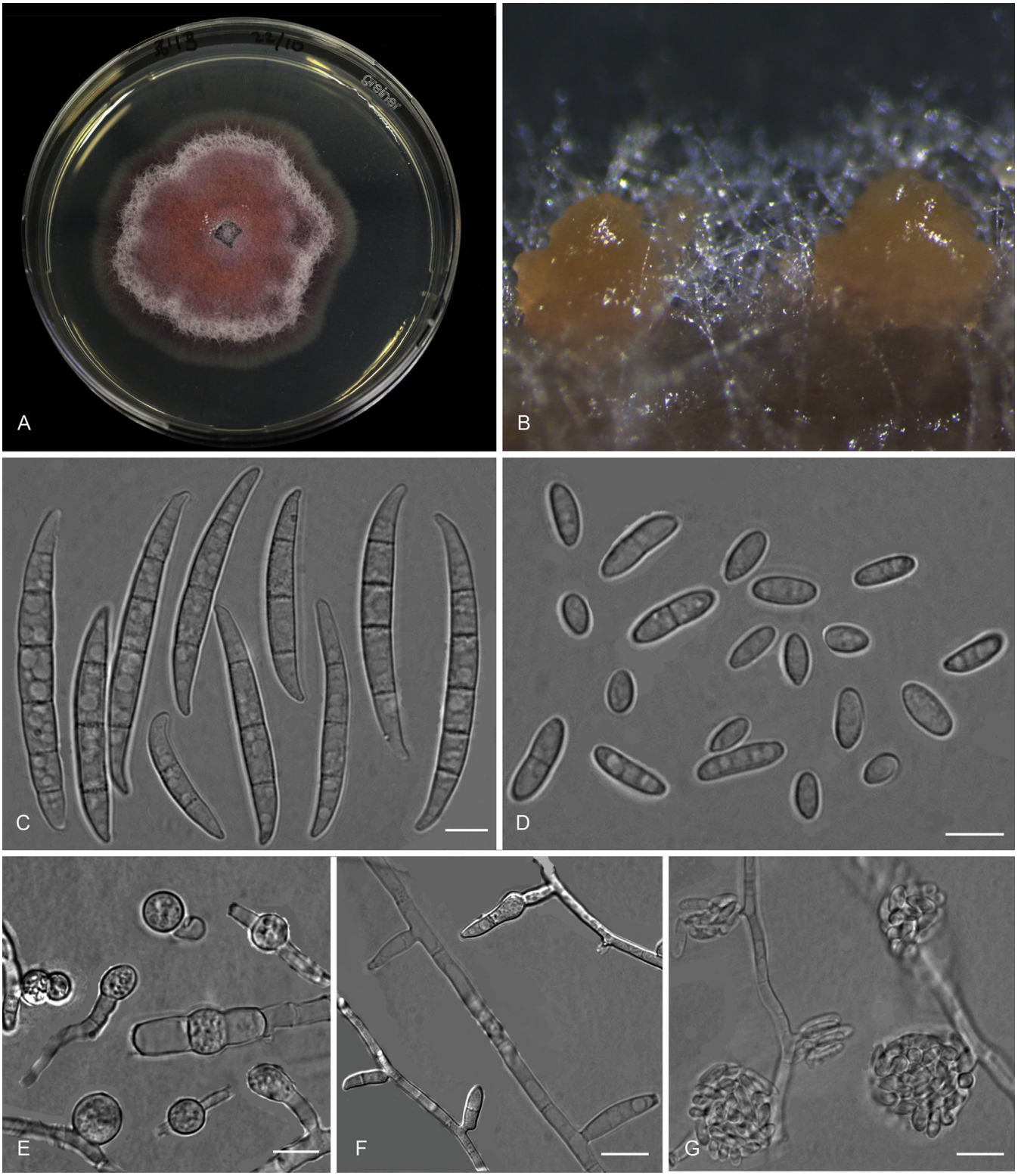

Fig. 16. *Fusarium tardicrescens* (ex-tyoe CBS 102024). **A.** Culture grown on PDA. **B.** Sporodochia on carnation leaves. **C.** Falcate-shaped macroconidia. **D.** Microconidia. **E.** Thick-walled chlamydospores. **F.** Monophialides produce microconidia and macroconidia. **G.** False head. Scale bars C–G = 10 μm.

Cavendish or Gros Michel, or in both varieties (Fig. 19). The positive control isolate FocII5-NRRL 54006 was lethal to both varieties, whereas all negative (water) controls remained free of disease. Isolates affecting Cavendish were classified as Foc-TR4 (Su *et al.* 1986), while those only infecting Gros Michel were classified as Foc-Race1 (Stover 1962a, Ploetz 1990). No fewer than 65 % of the isolates clustered in L1, which only comprised the strains that caused Fusarium wilt in Cavendish and hence, represented Foc-TR4. The rest of the isolates tested were able to infect Gros Michel and are therefore considered to be Foc-Race1 strains. Strains fitting this pathogenicity profile were equally distributed over all other lineages, except L7 and L9. L7 contains two Indonesian isolates that caused a slight discolouration of the corms of both varieties. Isolates in the new clade within FOSC were not able to cause disease in either tested banana variety. Isolates identified as other *Fusarium* species in the phylogenetic analyses were negative in all pathogenicity assays.

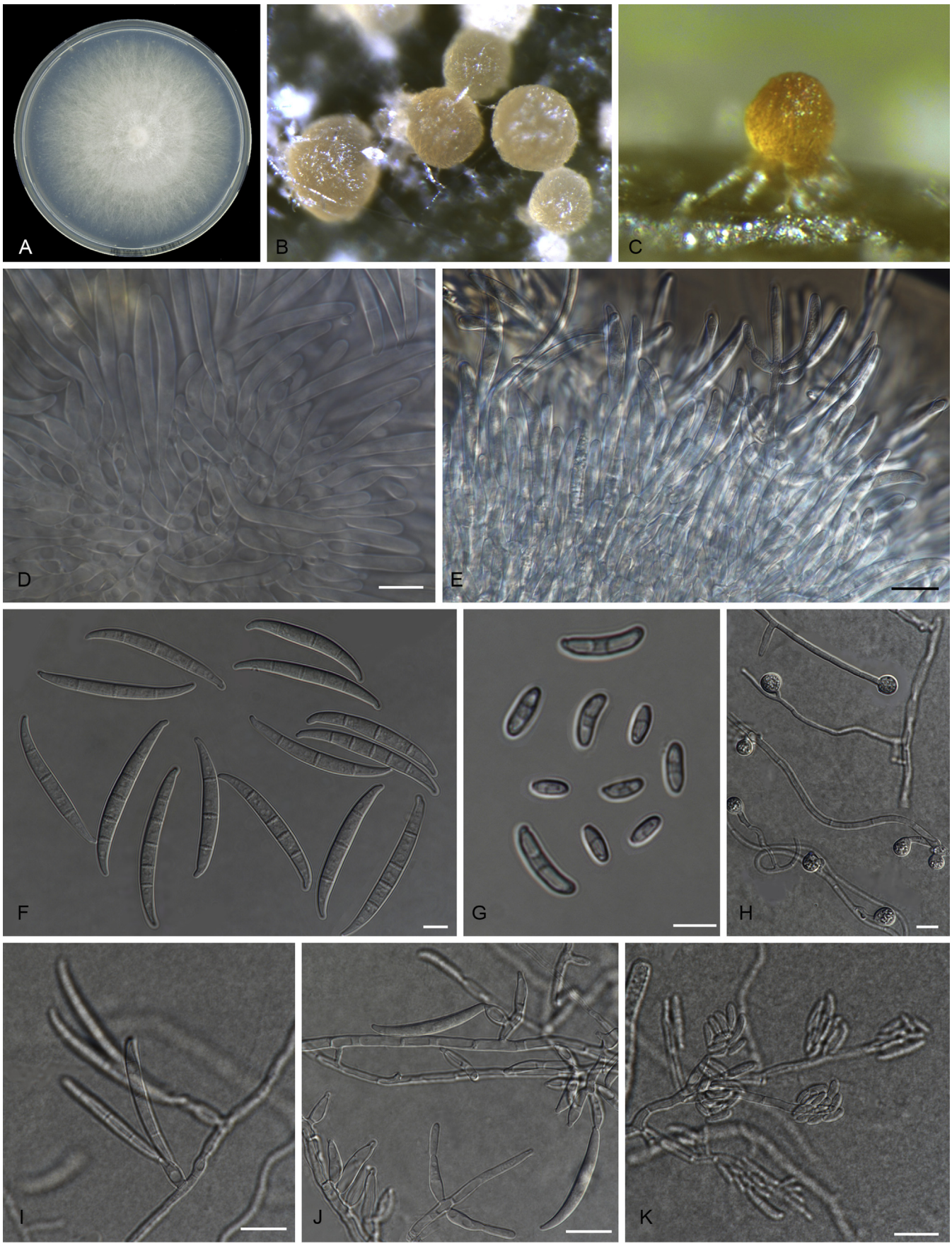

Fig. 17. *Fusarium kalimantanense* (ex-type InaCC F917). **A.** Culture grown on PDA. **B–C.** Sporodochia on carnation leaves. **D–E.** Sporodochial phialides. **F.** Falcate-shaped macroconidia. **G.** Microconidia. **H.** Thick-walled chlamydospores. **I.** Monophialides producing macroconidia. **J.** Branched conidiophores. **K.** False heads. Scale bars D–K = 10 μm.

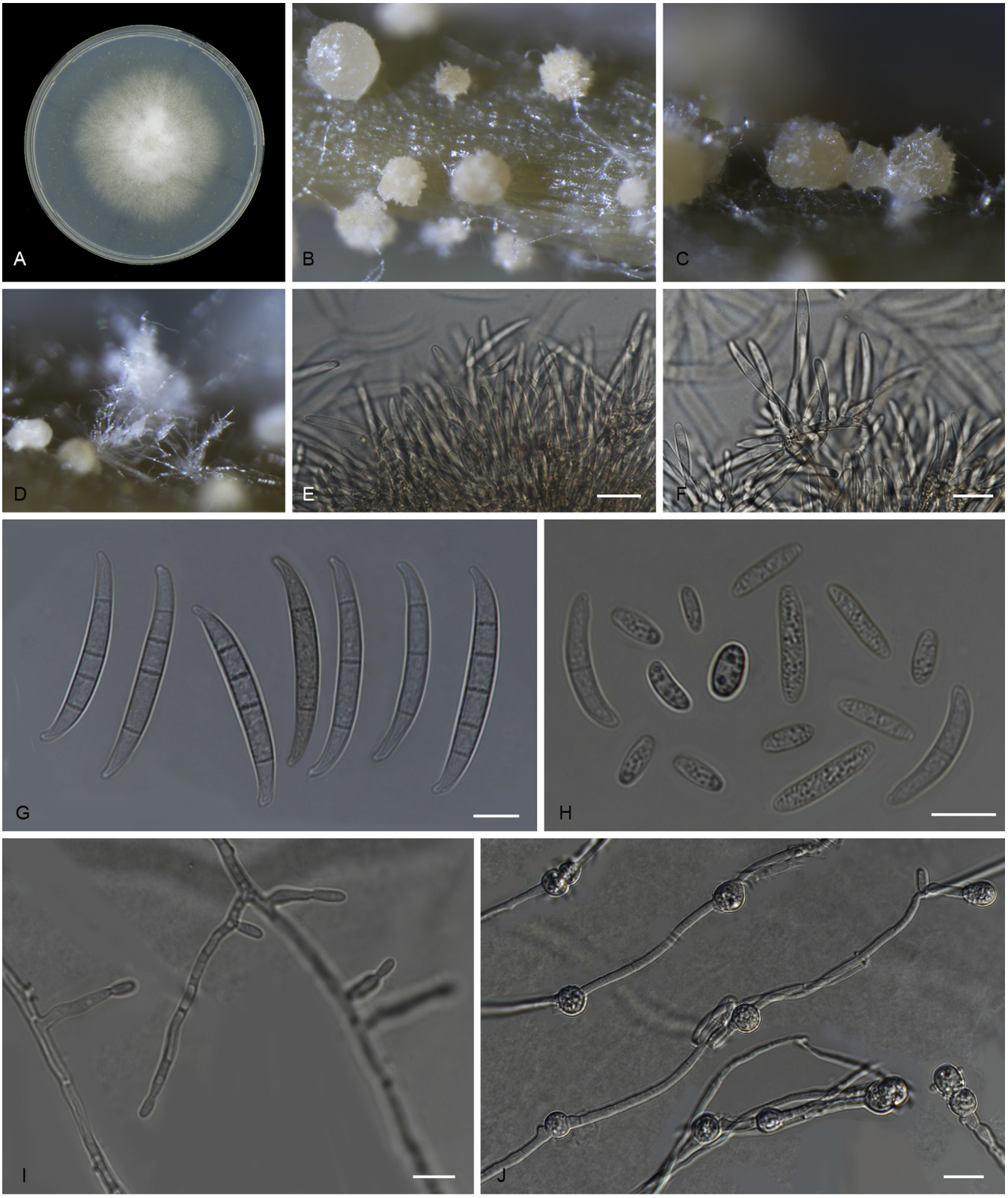

Fig. 18. *Fusarium sangayamense* (ex-type InaCC F960). **A.** Culture grown on PDA. **B–C.** Sporodochia on carnation leaves. **D.** Aerial conidiophore. **E–F.** Sporodochial phialides. **G.** Falcate-shaped macroconidia. **H.** Microconidia. **I.** Short monophialides. **J.** Thick-walled chlamydospores. Scale bars D–J = 10 μm.

DISCUSSION

The *Musa* gene centre (Perrier *et al.* 2011), as with the wheat gene centre in the Middle-East (Banke *et al.* 2004, Stukenbrock *et al.* 2007) and that of potato in Central Mexico (Grünwald & Flier 2005), contains a myriad of endemic diseases that co-evolved with the host. It is therefore considered a typical hot-spot of pathogen diversity (Stukenbrock & McDonald 2008). The gene centre of *Musa* has been studied in detail since the previous century. The wild ancestor of edible banana, *Musa acuminata,* originated in South-East Asia and Melanesia, and *Musa balbisiana* originated in South Asia (Perrier *et al.* 2011), where Indonesia is the contact area between these two wild *Musa* species. Approximately 11–13 *Musa acuminata* sub-species are of Indonesian origin, found in Sumatra, Kalimantan, Java, and the Lesser Sundas (Daniells 1995, Simmonds

Fig. 19. Pathogenicity assays. **A.** External wilting symptoms. **B–C.** Left panel Cavendish and right panel Gros Michel, corm symptom caused by Foc-Race1, *Fusarium tardichlamydosporum*. **D–E.** Left panel Cavendish and right panel Gros Michel, corm symptom caused by Foc-TR4, *Fusarium odoratissimum*.

1962). Most of the *Musa balbisiana* sub-species found in Java, Sumatra, and Sulawesi originate from India (Ochse & Bakhuizen van den Brink 1931, De Langhe 2009). However, the genetic diversity of *Musa* pathogens in the centre of origin of *Musa* has remained virtually unsampled. Although a recent overview of Foc in Asia was published (Mostert *et al.* 2017), a need remained for a thorough taxonomic analysis of Foc in its centre of origin. Our results present the most comprehensive study of Foc in the Indonesian gene centre of banana to date. Isolates of Foc were recovered from all the samples that were collected in all areas surveyed. The results demonstrated that Fusarium wilt is widely distributed in Indonesia and could be found in every banana producing area surveyed. Past reports showing compatible results have spanned an area from Aceh province in the west to Papua province in the east (Nasir *et al.* 1999, Wibowo *et al.* 2011). In 2012, 1 700 of the 21 000 acres of cultivated banana suffered from Fusarium wilt in Indonesia, including large commercial Cavendish plantations (Jumjunidang *et al*. 2012). Factors making this disease difficult to control include traditional farming practices, limited quarantine restriction on movement of planting material, and limited knowledge on the dissemination of the pathogen(s). As a result, the disease is unwittingly distributed to new areas. Moreover, the abundant diversity of banana varieties in Indonesia allows farmers to easily change the varieties they grow, resulting in epidemiological contact that allows the pathogen to infect new cultivars in different areas.

Demographic factors could have played a significant role in the dissemination of this disease in Indonesia. Java is the most populated island and, therefore, banana production and the available cultivated varieties are the most numerous on this island, as is the pathogen. Mass migration of people from this over-populated island to less populated islands such as Kalimantan, Sumatra, and Papua from 1980 to 1990 could account for the dissemination of Fusarium wilt throughout Indonesia, since infected banana planting material was taken along (Nasir *et al.* 1999).

The high number of local banana varieties from which Foc was recovered indicate that co-evolution of this pathogen is occurring along with its host in this region. Nasir *et al.* (1999) reported that 15 local varieties in Sumatra were susceptible to Fusarium wilt, including the most popular varieties, Pisang Ambon Kuning (AAA, Gros Michel synonym), Barangan (AAA) and Pisang Raja Sereh (AAA). This finding was reconfirmed in this study. An increasing number of infected varieties was also reported by Hermanto *et al.* (2009) and Jumjunidang *et al.* (2012). Of the hundreds of banana cultivars identified in Indonesia, many appear to be resistant or partially resistant to Fusarium wilt, a prior finding that was also observed during the present survey. No wild banana or close relative surveyed in this study showed any symptoms of Fusarium wilt. In Africa, *Ensete ventricosum*, a member of the *Musaceae*, is susceptible to Foc-Race2 (Ploetz 2006). By contrast, *Ensete glaucum* growing on the outskirt forest of Flores, Indonesia, was found to be healthy. None of the wild *M. acuminata* varieties found during the surveys was susceptible to Fusarium wilt. This finding is in agreement with some reports and greenhouse experiments on the infection of Foc on wild *M. acuminata*. *Musa acuminata* var. *malaccensis* from the Malaysian Peninsula was reported to be experimentally resistant (Javed *et al.* 2004), as was its sister variety *M. acuminata* var. *malaccensis* from Sumatra. This study and our observations during surveys indicate that Indonesia is the primary gene centre of Foc, and the most likely place to find a diverse palette of disease resistance markers for Fusarium wilt in banana.

The high diversity of Foc isolates found in this study is unparalleled by the findings of any previous study (O'Donnell *et al.* 1998, Fourie *et al.* 2009) where a similar approach was used. The taking of larger numbers of samples in Indonesia inclusive of more banana cultivars, could result in an even higher diversity, as well as the discovery of yet more novel taxa belonging to FOSC. This accords with the view of Leslie & Summerell (2006), who stated that the most informative studies on the systematics and evolution of *Fusarium* species from natural ecosystems, as well as different agro-ecosystems, should incorporate native host populations, in order to allow discovery of the full existing species diversity (Leslie & Summerell 2006).

Employing rotations with alternative crops, such as corn, sugar cane, peanuts and coffee, was found to decrease disease incidence in some plantations in Sumatra, Java, and Kalimantan. However, this practice probably has allowed for other *Fusarium* species, pathogenic to the rotation crops, to become established in these plantations, explaining their recovery in this study. These species include *F. mangiferae, F. proliferatum F. sacchari* and *F. verticillioides,* which are members of the *Fusarium fujikuroi* species complex (FFSC) and are associated with several tropical

crops (Marasas *et al.* 2006, Ploetz 2006) such as mango, maize, rice and sugarcane (Hsuan *et al.* 2011). These crops were commonly found in the areas surveyed for Fusarium wilt on bananas during this study. *Fusarium proliferatum* and *F. oxysporum* have been reported from the roots of the wild banana, *M. acuminata,* from Malaysia (Zakaria & Rahman 2011), which is closely related to several other *M. acuminata* varieties present in Sumatra and Java (Nasution 1990). This study represents the first report of both *F. longipes* and *F. incarnatum-equiseti* from banana varieties displaying symptoms of Fusarium wilt, although disease symptoms could not be induced in the pathogenicity assays undertaken here. However, both species are well-known as soil inhabitants and saprobes with a wide global distribution in tropical regions (Leslie & Summerell 2006). They could, therefore, be secondary colonisers of the decaying vascular tissue collected during the survey. The majority of the isolates that clustered outside the FOSC clade are well-known endophytes of various plant hosts, saprobes, and soil inhabitants, and are known to be non-pathogenic to banana (Waalwijk *et al.* 1996, O'Donnell *et al.* 1998).

In the FOSC clade, the Indonesian isolates were equally distributed throughout the two previously known clades in FOSC (*sensu* O'Donnell *et al.* 2004). Several of these *F. oxysporum* isolates are known as endophytes of banana (O'Donnell *et al.* 1998), and are unable to induce disease on Cavendish or Gros Michel. Isolates obtained in this study that were found to be non-pathogenic to both banana cultivars tested were distantly related to the pathogenic isolates, and were more closely related to other formae speciales that are pathogenic to other crops. This finding supported the observations of Gordon & Okamoto (1992), who reported that *Fusarium oxysporum* f. sp. *melonis*, pathogenic to cucurbits, is only distantly related to non-pathogenic strains. This also supports the view that Foc and other formae speciales of *F. oxysporum* have a polyphyletic origin (Baayen *et al.* 2000, O'Donnell *et al.* 2009).

Nine Foc lineages were revealed in this study, albeit with varying levels of statistical support, and described as new species. This conclusion was based on combinations of the genealogical approaches described by Dettmann *et al.* (2003) and Laurence *et al.* (2014), with supporting evidence from the inclusion of eight previously established lineages of FOC (O'Donnell *et al.* 1998; Fourie *et al.* 2009). A lineage is recognised as independent in this system if it is found to be concordantly supported by the majority of the loci, or is well supported by at least one locus but not contradicted by any other locus. Two previously known clades of Foc were resolved in this study (Boehm *et al.* 1994, Bentley *et al.* 1995, O'Donnell *et al.* 1998, Fourie *et al.* 2009), with the majority of the isolates fell into in Clade1, Lineage1. This lineage, classified as Foc-TR4, was found on every island surveyed, including Papua and Flores and those that were previously thought to be free of Foc-TR4. This is in agreement with some reports on Fusarium wilt in Indonesia, which note that the majority of Foc strains isolated appeared to be Foc-TR4 (O'Neill *et al.* 2011, Jumjunidang *et al.* 2012). In terms of phylogenetic diversity, Foc-TR4 isolates were less diverse than Foc-Race1, which occurred in almost all lineages. The number of diverse banana varieties sampled could be the reason for the tremendous diversity of Foc-Race1 isolates found in this study. Many of the banana sampled belong to varieties Gros Michel (AAA) or Silk (AAB), both known to be highly susceptible to Foc-Race1 (Waite & Stover 1960).

The partial sequences of the three coding gene regions employed in this study, *tef1, rpb1* and *rpb2*, are well-known to be robust for use in molecular-based identification of *Fusarium* species (O'Donnell *et al.* 2015), but are unable to distinguish all of the 24 VCGs (Puhalla 1985, Ordonez *et al.* 2015) that are known to represent the widest genetic diversity of Foc. Direct VCG identification is a relatively objective but time-consuming test, and the results indicate genetic similarity rather than genetic differences (Kistler 1997). Therefore, VCGs represent good phenotypic characters for assessing diversity within populations, but genetic relationships among VCGs need to be assessed by other molecular tools.

The high diversity found, based on the number of isolates recovered from different banana varieties and the high number of lineages resolved in this study, support the hypothesis that the pathogen(s) co-evolved with the host in the host's centre of origin (Ploetz & Pegg 1997). The unique agro-ecosystems and variety of ecological niches found where banana cultivation is practiced in Indonesia provide a conducive environment for the pathogen to evolve. As mentioned above, subsistence farming in Indonesia has allowed for the dissemination of banana varieties with varying degrees of tolerance and resistance to Fusarium wilt. This practice may have created a suitable environment for the incumbent pathogen to evolve and to adapt to newly introduced banana varieties. The dynamics of host diversity in these agro-ecosystems will continue to select for new pathogens (Stukenbrock & McDonald 2008), a process that, in this study, yielded a diversity of species able to infect newly introduced banana cultivars.

Another scenario that could account for the high Foc diversity in Indonesia, irrespective of a lack of sexual reproduction, is horizontal gene transfer. *Fusarium oxysporum* has the ability to transfer specific chromosomes, sometimes containing unique pathogenicity genes, among non-pathogenic and pathogenic strains, resulting in new pathogenic lineages (Rep & Kistler 2010). This phenomenon is well recorded in *Fusarium oxysporum* f. sp. *lycopersici*, a pathogen of tomato (Ma *et al.* 2010). A recent study of the effector profile of different formae speciales of *F. oxysporum*, including Foc, indicated that these fungi have specific and unique effector profiles that reflect vertical and horizontal inheritance (van Dam *et al.* 2016). The endophytic character of some *F. oxysporum* strains, some of which are weak soil-borne pathogens (Stover 1962b), allows for relatively easy assimilation of pathogenicity genes from related pathogenic *F. oxysporum* strains via horizontal gene transfer (Vlaardingerbroek *et al.* 2016).

The race concept has been used extensively in *F. oxysporum* classification system by plant pathologists. Based on the results of the present study, it can be inferred that the Foc-TR4 isolates evolved recently from predecessors in Foc-Race1. Foc-Race1 displayed a higher phylogenetic diversity in this study than Foc-TR4. Once established, both races apparently co-evolved in the same region, meaning that possible horizontal gene transfer could be involved in the high diversity level seen in Foc-Race1, as well as in the emergence of Foc-TR4.

It was initially thought that the origin of pathogenic Foc is from non-pathogenic root inhabitants or endophytes of various wild *M. acuminata* plants in Java and Sulawesi that became pathogenic after their introduction to foreign banana germplasm (Buddenhagen 2007). Alternatively, native Foc-Race1 isolates may have been exposed to selection pressure through

exposure to newly introduced banana varieties, as Foc-Race1 is known to infect diverse varieties like Silk (AAB), Pome (AAB), and Pisang Awak (ABB) (Waite & Stover 1960, Ploetz 2006). Isolates that clustered in the newly resolved subclade in the FOSC in this study were found to be non-pathogenic towards both Cavendish and Gros Michel. These isolates only caused initial discoloration in the corm, without any further disease development. They might be pathogenic on other germplasm, but until more banana varieties can be tested, this idea remains speculation.

Our study demonstrates that the Indonesian Foc population might be the most genetically diverse ever studied. Further genetic study of this population using deeper genomic coverage should now be conducted. Pathogenicity tests using more banana varieties could be used to assess the wide range of pathogenicity.

Our study gives an insight into the complexity of Fusarium wilt on banana in Indonesia. This is very important for disease management not only in Indonesia but also worldwide. As the pathogen continues to evolve, new lineages could arise and escape Indonesia. In striving to find banana resistance to Fusarium wilt, researchers should consider the high diversity of Indonesian Foc reported here as one of the main obstacles to overcome.

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