

Updating species diversity of *Colletotrichum*, with a phylogenomic overview

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Abstract: The genus *Colletotrichum* includes important plant pathogens, endophytes, saprobes and human pathogens. Even though the polyphasic approach has facilitated *Colletotrichum* species identification, knowledge of the overall species diversity and host distribution is largely incomplete. To address this, we examined 952 *Colletotrichum* strains isolated from plants representing 322 species from 248 genera, or air and soil samples, from 87 locations in China, as well as 56 strains from Saudi Arabia, Thailand, Turkey, and the UK. Based on morphological characteristics and multi-locus phylogenetic analyses, the strains were assigned to 107 species, including 30 new species described in this paper and 18 new records for China. The currently most comprehensive backbone tree of *Colletotrichum*, comprising 16 species complexes (including a newly introduced *C. bambusicola* species complex) and 15 singleton species, is provided. Based on these analyses, 280 species with available molecular data are accepted in this genus, of which 139 have been reported in China, accounting for 49.6 % of the species. *Colletotrichum siamense*, *C. karsti*, *C. fructicola*, *C. truncatum*, *C. fioriniae*, and *C. gloeosporioides* were the most commonly detected species in China, as well as the species with the broadest host range. By contrast, 76 species were currently found to be associated with a single plant species or genus in China. To date, 33 *Colletotrichum* species have been exclusively reported as endophytes. Furthermore, we generated and assembled whole-genome sequences of the 30 new and a further 18 known species. The most comprehensive genome tree comprising 94 *Colletotrichum* species based on 1 893 single-copy orthologous genes was hence generated, with all nodes, except four, supported by 100 % bootstrap values. Collectively, this study represents the most comprehensive investigation of *Colletotrichum* diversity and host occurrence to date, and greatly enhances our understanding of the diversity and phylogenetic relationships in this genus.

Key words: Backbone tree, Fungal systematics, Multi-locus phylogeny, New taxa, Phylogenomics, Plant pathogen, Taxonomy

Taxonomic novelties: New species: *Colletotrichum arecacearum* F. Liu, Z.Y. Ma & L. Cai, *Colletotrichum bicoloratum* F. Liu, W.P. Wu & L. Cai, *Colletotrichum bromeliacearum* F. Liu & L. Cai, *Colletotrichum buxi* F. Liu, W.P. Wu & L. Cai, *Colletotrichum chamaedoreae* F. Liu, W.P. Wu & L. Cai, *Colletotrichum crousii* F. Liu, Z.Y. Ma & L. Cai, *Colletotrichum danxiashanense* F. Liu, W.P. Wu & L. Cai, *Colletotrichum diversisporum* F. Liu, W.P. Wu & L. Cai, *Colletotrichum diversum* F. Liu & L. Cai, *Colletotrichum dolichoconidiophori* F. Liu, W.P. Wu & L. Cai, *Colletotrichum iris* F. Liu & L. Cai, *Colletotrichum monsterae* F. Liu, W.P. Wu & L. Cai, *Colletotrichum multiseptatum* F. Liu, W.P. Wu & L. Cai, *Colletotrichum nageiae* F. Liu, W.P. Wu & L. Cai, *Colletotrichum obovoides* F. Liu & L. Cai, *Colletotrichum parabambusicola* F. Liu, W.P. Wu & L. Cai, *Colletotrichum paraendophytum* F. Liu, W.P. Wu & L. Cai, *Colletotrichum reniforme* F. Liu, Z.Y. Ma & L. Cai, *Colletotrichum schimae* F. Liu, W.P. Wu & L. Cai, *Colletotrichum shivasii* F. Liu & L. Cai, *Colletotrichum sinuatum* F. Liu, W.P. Wu & L. Cai, *Colletotrichum subacidae* F. Liu, Z.Y. Ma & L. Cai, *Colletotrichum subsalicis* F. Liu & L. Cai, *Colletotrichum subvariabile* F. Liu, W.P. Wu & L. Cai, *Colletotrichum syngoniicola* F. Liu, Z.Y. Ma & L. Cai, *Colletotrichum telosmae* F. Liu, W.P. Wu & L. Cai, *Colletotrichum tibetense* F. Liu & L. Cai, *Colletotrichum variabile* F. Liu, W.P. Wu & L. Cai, *Colletotrichum zhaoqingense* F. Liu & L. Cai, *Colletotrichum zhejiangense* F. Liu, W.P. Wu & L. Cai.

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INTRODUCTION

Colletotrichum is the only genus of the *Glomerellaceae* (*Glomerellales*, *Sordariomycetes*, *Ascomycota*), and is regarded as one of the 10 most important genera of plant pathogenic fungi in the world (Dean *et al.* 2012). A few species are opportunistic human pathogens, including *C. dematum*, *C. gigasporum*, *C. gloeosporioides* and *C. truncatum* that can cause keratitis and subcutaneous infections (Guarro *et al.* 1998, Damm *et al.* 2009, Shiraishi *et al.* 2011, Shivaprakash *et al.* 2011, Liu *et al.* 2014, Buchta *et al.* 2019). In rare cases, *Colletotrichum* species have been reported to infect animals, e.g. *C. fioriniae* (as *C. acutatum* var. *fioriniae*), infecting a scale insect, and *C. acutatum* (*s. lat.*), infecting a sea turtle (Manire *et al.* 2002, Marcelino *et al.* 2008). *Colletotrichum* also includes plant endophytes, and saprobes from a wide range of substrates, such as the soil, water, and air (Liu *et al.* 2014).

Accurate species identification is important for understanding biodiversity, host-parasite interaction, and evolutionary history, and

for monitoring and controlling plant pathogens, and developing quarantine measures. Previous host- and morphology-oriented systematics of *Colletotrichum* is, however, not regarded as natural, does not reflect the phylogenetic relationships, and has largely impeded meaningful investigation of species diversity in this genus. To establish a stable and natural classification system, the use of molecular data in combination with morphological, geographical, and ecological data has increasingly been employed (Cai *et al.* 2009, Cannon *et al.* 2012, Marin-Felix *et al.* 2017, Jayawardena *et al.* 2020).

In the genus *Colletotrichum*, a species complex (also called an ‘aggregate’) is defined as a group of species that form a monophyletic clade and exhibit shared characteristics (e.g. similar conidial morphology) (Cannon *et al.* 2012). The current classification system of *Colletotrichum* comprises 15 species complexes, *i.e.* the *C. acutatum*, *C. agaves*, *C. boninense*, *C. caudatum*, *C. dematum*, *C. destructivum*, *C. dracaenophilum*, *C. gigasporum*, *C. gloeosporioides*, *C. graminicola*, *C. magnum*, *C. orbiculare*, *C.*

orchidearum, *C. spaethianum*, and *C. truncatum* species complexes, as well as a number of singletons (Marin-Felix et al. 2017, Damm et al. 2019, Jayawardena et al. 2020, Bhunjun et al. 2021). The *C. caudatum* species complex forms an inner clade of the *C. graminicola* species complex, and was annotated as *C. caudatum* sub-aggregate in the phylogenetic tree, but referred to as a species complex by Crouch (2014). Subsequently, many researchers refer to this group as a *C. caudatum* species complex (e.g. Marin-Felix et al. 2017, Jayawardena et al. 2020). Recently, Bhunjun et al. (2021) recommended treating the two species complexes as one, i.e. the *C. graminicola-caudatum* species complex.

ITS is a useful DNA barcode for assigning *Colletotrichum* species to species complexes (Cannon et al. 2012), but different loci are being employed to resolve the different species complexes. For example, six loci (*act*, *chs-1*, *gapdh*, *his3*, ITS, and *tub2*) have been used for the *C. acutatum*, *C. dematioides*, *C. destructivum*, *C. dracaenophilum*, *C. magnum*, *C. orchidearum*, *C. spaethianum* and *C. truncatum* species complexes (Damm et al. 2009, 2012a, 2014, 2019), with an additional locus each for the *C. boninense* (*cal*) and *C. orbiculare* (*gs*) species complexes (Damm et al. 2012b, 2013), and three additional loci (*ApMat*, *cal*, and *gs*) for the *C. gloeosporioides* species complex (Weir et al. 2012, Liu et al. 2015). Meanwhile, *act*, *chs-1*, *gapdh*, ITS, and *tub2* have been used for the *C. gigasporum* species complex (Liu et al. 2014), and *apn2*, ITS, *Mat1/Apn2*, and *sod2* have been used for the *C. caudatum* and *C. graminicola* species complexes (Crouch et al. 2009a, Crouch 2014). Furthermore, the combined use of *ApMat* and *gs* in phylogenetic analysis is very useful for species delimitation in the *C. gloeosporioides* species complex (Liu et al. 2015).

Based on phylogenetic analyses of multiple loci, the backbone tree of *Colletotrichum* has been constructed and is frequently updated by the addition of newly described species. The tree includes 119 species in Cannon et al. (2012); 189 species in Jayawardena et al. (2016) and Marin-Felix et al. (2017); 247 species in Jayawardena et al. (2020); and 248 species in Bhunjun et al. (2021). The continuous discovery of new species indicates very high species diversity in this genus. In China, most *Colletotrichum* taxa are reported in the form of single or few species, or species associated with a certain host (e.g. Tao et al. 2013, Liu et al. 2015, Zhang et al. 2020), and there is a lack of systematic and biodiversity investigation of these fungi.

In the current study, we aimed to: 1) resolve the systematic placement of 1 008 *Colletotrichum* strains collected, mostly in China, since 1993; 2) characterise newly discovered species based on all available data; 3) supplement missing sequences of the *act*, *chs-1*, *gapdh*, *his3*, and *tub2* genes of some known species, and build an integrated dataset for *Colletotrichum*; 4) construct a robust and reliable phylogeny of *Colletotrichum* including all species with type-derived sequences; and 5) improve knowledge on the diversity and host occurrence of *Colletotrichum* species in China. In addition, all *Colletotrichum* species with an available genome sequence were used for the construction of a whole-genome species tree to help resolve species boundaries and define species complexes.

MATERIALS AND METHODS

Isolates

In the current study, 1 008 *Colletotrichum* isolates, associated with at least 322 host plant species in 248 genera, from the LC Culture

Collection (a personal culture collection of Lei Cai, housed in the Institute of Microbiology, Chinese Academy of Sciences) and the Novozymes Culture Collection were analysed. Of these, 952 were collected at 87 locations in China and 56 at 26 locations in Saudi Arabia, Thailand, Turkey, and the UK. Representative cultures of the new species described herein were deposited in the China General Microbiological Culture Collection (CGMCC). Type specimens were deposited in the Mycological Herbarium, Institute of Microbiology, Chinese Academy of Sciences, Beijing, China (HMAS).

Morphology

The isolates were cultivated on potato dextrose agar (PDA; DifcoTM, Becton, Dickinson and Company, Sparks, MD, USA) and synthetic nutrient-poor agar (SNA; Nirenberg 1976) supplemented with double-autoclaved pine needles placed on the agar surface. The cultures were incubated at room temperature (25 °C) under a 12 h day/night regime. After 7 d, fungal growth rates were measured and the colony characteristics were noted. Colony colours were rated using the colour charts of Rayner (1970). Morphological observations of reproductive structures were performed using a Nikon AZ100 dissecting microscope (DM) and a Nikon Eclipse 80i compound microscope with differential interference contrast (DIC) illumination, both equipped with a Nikon DS-Ri2 high-definition colour digital camera. Slides were prepared using lactic acid. Measurements and descriptions of microscopic structures were preferentially made from cultures grown on SNA. If sterile on SNA, structures produced on PDA, oatmeal agar (OA), malt extract agar (MEA) (Crous et al. 2019), or pine needles were described. Hyphal appressoria were induced using a slide culture technique (Cai et al. 2009) or observed directly on the reverse side of colonies grown on SNA. At least 30 measurements were made for each structure, and the mean value, standard deviation, and minimum–maximum values are given, with the extreme measurements in parentheses. Descriptions and illustrations of taxonomic novelties were deposited in MycoBank (www.MycoBank.org; Crous et al. 2004).

Molecular analyses using barcoding sequences

Total genomic DNA was extracted from fresh mycelia of each isolate using a modified CTAB protocol (Guo et al. 2000). All primers used in the current study are listed in Table 1. PCR amplification was performed as described by Crouch et al. (2009a) and Liu et al. (2016). PCR amplicons were purified and sequenced by the SinoGenoMax Company (Beijing, China). The forward and reverse reads were paired, and consensus sequences calculated in MEGA v. 7.0.21 (Kumar et al. 2016).

Primarily, *ApMat*, *gapdh*, *gs*, ITS, or *tub2*, which are good discriminative loci in different species complexes in *Colletotrichum* (Damm et al. 2012a, b, 2013, 2014, 2019, Liu et al. 2015, Jayawardena et al. 2016), were selected for PCR amplification and sequencing. All efforts were made to assign isolates to species complexes and to identify them to species level, by BLASTn searches of the NCBI GenBank or by phylogenetic analyses using single locus sequences.

For isolates of species that could not be determined based on the above analyses, an ITS tree was first used for inferring delimitation to the species complex level, and further multi-locus phylogenetic analyses and phenotypic characterisation were then performed for species delimitation. Regarding the multi-locus analyses, a concatenated sequence dataset of *act*, *chs-1*, *gapdh*, *his3*, ITS, and *tub2*, including all *Colletotrichum* species for which molecular data

Table 1. Primers used in this study, with originating loci, sequences and references.

Locus	Product name	Primer name	Direction	Sequence (5'-3')	Reference
act	Actin	ACT-512F	Forward	ATGTGCAAGGCCGGTTTCGC	Carbone & Kohn (1999)
		ACT-783R	Reverse	TACGAGTCCTTCTGGCCCAT	Carbone & Kohn (1999)
apn2	Mat1 and the adjacent DNA lyase gene	Apn1W1F	Forward	ATGGAGCACAAAAACGAACA	Crouch <i>et al.</i> (2009b)
		Apn1W1R	Reverse	GCGGAGCAGAGGATGTAGTC	Crouch <i>et al.</i> (2009b)
cal	Calmodulin	CL1C	Forward	GAATTCAAGGAGGCCTCTC	Weir <i>et al.</i> (2012)
		CL2C	Reverse	CTTCTGCATCATGAGCTGGAC	Weir <i>et al.</i> (2012)
chs-1	Chitin synthase	CHS-79F	Forward	TGGGGCAAGGATGCTTGGAAAG	Carbone & Kohn (1999)
		CHS-345R	Reverse	TGGAAGAACCATCTGTGAGAGTTG	Carbone & Kohn (1999)
ApMat	Apn2-Mat1-2 intergenic spacer and partial mating type Mat1-2 gene	AMF1	Forward	CCAGAAATACACCGAACTTGC	Silva <i>et al.</i> (2012)
		AMR1	Reverse	TCATTCTACGTATGTGCCCG	Silva <i>et al.</i> (2012)
gapdh	Glyceraldehyde-3-phosphate dehydrogenase	GDF1	Forward	GCCGTCAACGACCCCTCATTGA	Guerber <i>et al.</i> (2003)
		GDR1	Reverse	GGGTGGAGTCGTACTTGAGCATGT	Guerber <i>et al.</i> (2003)
gs	Glutamine synthetase	GSF1	Forward	ATGGCCGAGTACATCTGG	Guerber <i>et al.</i> (2003)
		GSR1	Reverse	GAACCGTCGAAGTTCCAC	Guerber <i>et al.</i> (2003)
		GSLF2	Forward	TACACGAGSAAAAGGATACGC	Liu <i>et al.</i> (2016)
		GSLR1	Reverse	AGRCCGACATTGTCAGTATCG	Liu <i>et al.</i> (2016)
his3	Histone3	CYLH3F	Forward	AGGTCCACTGGTGGCAAG	Crous <i>et al.</i> (2004)
		CYLH3R	Reverse	AGCTGGATGTCCTTGGACTG	Crous <i>et al.</i> (2004)
ITS	Internal transcribed spacer	ITS1	Forward	TCCGTAGGTAAACCTGCGG	White <i>et al.</i> (1990)
		ITS4	Reverse	TCCTCCGCTTATTGATATGC	White <i>et al.</i> (1990)
Mat1/Apn2	The 3' end of <i>apn2</i> and the 5' end of the mating type gene <i>Mat1-2</i>	Mat1M72F	Forward	ACGGCAAACGGCTCAGGGAGTG	Crouch <i>et al.</i> (2009b)
		Mat1M72R	Reverse	AATGCCGAGTCCCACGAGGTTCG	Crouch <i>et al.</i> (2009b)
sod2	Manganese-superoxide dismutase	SOD625F	Forward	GCCCCACAGTACATATTGCCTAACG	Crouch <i>et al.</i> (2006)
		SOD625R	Reverse	TCATCCCGGGAGCCAGAAAACCT	Crouch <i>et al.</i> (2006)
tub2	β -tubulin 2	T1	Forward	AACATGCGTAGGATTGTAAGT	O'Donnell & Cigelnik (1997)
		Bt2b	Reverse	ACCCTCAGTGTAGTGACCCCTGGC	Glass & Donaldson (1995)

are available, was used to construct the overview phylogeny for the genus (Cannon *et al.* 2012, Damm *et al.* 2012a, b, 2013, 2014, 2019, Weir *et al.* 2012, Liu *et al.* 2014, Jayawardena *et al.* 2016, Marin-Felix *et al.* 2017). Two additional sequence datasets were used for the *C. caudatum* species complex (*apn2*, ITS, Mat1/Apn2, and *sod2*) and *C. graminicola* species complex (*act*, *chs-1*, ITS, *sod2*, and *tub2*) (Crouch *et al.* 2009a, Cannon *et al.* 2012, Crouch 2014). All novel sequences obtained in the current study were submitted to the NCBI GenBank (www.ncbi.nlm.nih.gov; Tables S1–S3).

Sequence alignments of the individual loci were prepared using MAFFT v. 7 (<http://mafft.cbrc.jp/alignment/server/index.html>) and manually edited in MEGA v. 7.0.21. Maximum-likelihood (ML) and Bayesian analysis (BA) were used for phylogenetic inferences of the ITS alignment and concatenated alignments. MrModelTest v. 2.2 (Nylander 2004) was used to determine the optimal nucleotide substitution model for each locus. The individual gene trees were assessed for clade conflicts between the individual phylogenies.

Maximum-likelihood and BA were implemented using the CIPRES Science Gateway portal (<https://www.phylo.org/>; Miller *et al.* 2012) using RAxML-HPC BlackBox v. 8.2.10 (Stamatakis 2014) and MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003), respectively. For ML analyses, GTR+GAMMA

substitution model with 1 000 bootstrap iterations was set. Bayesian analyses were computed with four simultaneous Markov Chain Monte Carlo chains, 200 M generations, and a sampling frequency of 1 000 generations for the first dataset and 100 generations for the other two datasets, ending the run automatically when standard deviation of split frequencies fell below 0.01. The burn-in fraction was set to 0.25, after which the 50 % majority rule consensus trees and posterior probability (PP) values were calculated. The resulting trees were plotted using FigTree v. 1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree>).

Whole-genome sequencing

Phylogenomic analysis was performed to better define the species complex boundaries for *Colletotrichum* and help to understand the fungal evolution in this genus. Whole-genome sequences were generated for ex-type strains of new species described in the current study and for 18 known species that were available. Reference genomes were retrieved from NCBI (Table S4). All isolates were purified using a single-spore isolation method (Zhang *et al.* 2013). Hyphae of 4-d-old colonies growing on PDA were transferred to 50 mL of potato dextrose broth (PDB) and cultivated

for 3–6 d at 25 °C at 150 rpm. Fresh mycelia were filtered through four layers of sterile gauze and were then stored at -80 °C. DNA libraries were prepared using DNeasy Plant Mini kit (Qiagen). The libraries were sequenced as 150 bp pair-end reads using Illumina NovaSeq 6000 platform. Genome assemblies were deposited in the National Microbiology Data Center (NMDC) under BioProject NMDC10017886.

Genome assembly and gene annotation

Read quality was assessed by using FastQC v. 0.11.8 (Andrews & Babraham 2010). Clean reads were assembled with SPAdes v. 3.12.0 (Bankevich *et al.* 2012), using the ‘careful’ mode and various kmers (21, 33, 55, 77, 99). Scaffolds shorter than 200 bp were removed from subsequent analyses. Genome assembly quality was assessed using QUAST v. 5.0.2 (Alexey *et al.* 2013). Genome completeness was assessed using genome mode in BUSCOs v. 2.0.1 (Mathieu *et al.* 2019), with Sordariomyceta_odb9 gene set.

Gene prediction for the 48 newly sequenced and 46 previously published genomes of *Colletotrichum* (Table S4) were done using the Funannotate pipeline v. 1.7.0 (Palmer 2016). Repetitive elements were initially soft-masked using default parameters. Next, the prediction step of funannotate pipeline (funannotate predict) was implemented using --busco_db Sordariomycetes, --busco_seed_species *Verticillium longpororum*1 and default parameters. Predicted proteins were firstly annotated using eggNOG-mapper v. 2 (Huerta-Cepas *et al.* 2017) and then compared via BlastP (e-value $\leq 1e-10$) against Fungal Cytochrome P450 (Moktali *et al.* 2012) and Transporters Classification Database (Saier *et al.* 2016). Carbohydrate-active enzymes annotation was predicted using dbCAN v. 2.0.6 (Yin *et al.* 2012) with DIAMOND, Hotpep and HMMER as default settings, and the genes found by at least two tools were regarded as candidates. The SignalP v. 5.5 (Armenteros *et al.* 2019), TMHMM v. 2.0 (Krogh *et al.* 2001), TargetP v. 2.0 (Emanuelsson *et al.* 2000), EffectorP v. 1.0 (Sperschneider *et al.* 2016) were incorporated to predict effectors.

Phylogenomic tree construction

The phylogenetic relationships between *Colletotrichum* members were inferred based on orthologs of all (94) assembled genomes (Table S4), using *Verticillium dahliae* as the outgroup. Predicted proteins were clustered into orthologous groups by using Orthofinder v. 2.3.3 (Emms & Kelly 2019). Amino acid sequences of 1 893 single-copy orthologs were aligned using MAFFT v. 7.407 (Katoh & Standley 2013) with default settings. Conserved sites in the alignment were extracted using Gblocks v. 0.91b (Castresana 2000) and then concatenated. A JTT substitution model of the concatenated alignment resulting from analysis in ProtTest v. 3.4.2 (Darriba *et al.* 2011) was used for phylogenomic tree construction using RAxML v. 8.2.12 (Stamatakis 2014) with 1 000 bootstrap iterations.

RESULTS

Single-locus analysis

Based on BLASTn search and single-locus phylogenetic analyses using ApMat, *gapdh*, *gs*, or *tub2*, we attempted to assign the 1 008

strains analysed (Table S5) to species level. For the undetermined strains, a single ITS phylogenetic analysis was performed to allocate them into species complexes. The ITS alignment contained 618 characters, including alignment gaps. The ML search revealed a best tree with an InL of -8314.217491. The BA was run for 20 025 000 generations, and a 50 % consensus tree and posterior probabilities were calculated from 30 040 trees from two analysis runs. The analysed strains were thus separated into 14 species complexes and six singleton clades. Four taxa (*C. bambusicola*, *C. hsienjenchang*, *C. metake*, and *C. parabambusicola* sp. nov.), characterised by straight conidia, formed a main clade, which was denoted as a new species complex (Fig. S1). The *C. graminicola* species complex was polyphyletic in the ITS tree. *Colletotrichum riograndense*, which had previously been considered as belonging to the *C. spaethianum* species complex, was however phylogenetically basal to the *C. bambusicola* and *C. spaethianum* species complexes. Furthermore, the topologies of the single ITS tree and multi-locus tree were compared to determine whether the grouping of species within species complexes was congruent.

Multi-locus phylogeny

Overview phylogeny of *Colletotrichum* based on six loci
The combined *act*, *chs-1*, *gapdh*, *his3*, ITS, and *tub2* sequence alignment that was used for overview phylogeny construction contained 250 currently accepted *Colletotrichum* species and *Monilochaetes infuscans* (CBS 869.96) as the outgroup. The final alignment contained 2 659 characters (*act*: 322; *chs-1*: 251; *gapdh*: 441; *his3*: 417; ITS: 606; *tub2*: 622) including the alignment gaps, and 1 944 characters were unique site patterns. The ML search revealed a best tree with an InL of -74738.627777. MrModelTest recommended Dirichlet base frequencies for all data partitions of the BA. The GTR+I+G model was suggested for *act*, *gapdh*, and ITS, and the HKY+I+G model for *chs-1*, *his3*, and *tub2*. The BA was run for 39 980 000 generations, and a 50 % consensus tree and posterior probabilities were calculated from 59 972 trees from two runs.

The topologies of the six-locus phylogenetic trees generated by ML and BA were congruent and consistent with the species complex delimitation reported previously (Cannon *et al.* 2012, Marin-Felix *et al.* 2017, Bhunjun *et al.* 2021), but differed from the ITS tree constructed in the current study in the grouping of *C. guangxiense* and *C. riograndense* on species complex level. In the six-locus tree, *C. guangxiense* and four additional taxa (*C. bambusicola*, *C. hsienjenchang*, *C. metake*, and *C. parabambusicola* sp. nov.) formed a new species complex (Fig. 1). By contrast, *C. guangxiense* was basal to the *C. caudatum*, *C. destructivum* and *C. graminicola* species complexes in the ITS tree (Fig. S1). *Colletotrichum riograndense*, belonging to the *C. spaethianum* species complex in the six-locus phylogeny (Fig. 1), was in the ITS tree basal to a clade formed by the *C. bambusicola*, *C. caudatum*, *C. destructivum*, *C. graminicola*, and *C. spaethianum* species complexes (Fig. S1).

The *C. caudatum* species complex formed a subclade of the *C. graminicola* complex and some taxa in the two species complexes were indistinguishable in the six-locus tree (Fig. 1), e.g. *C. caudatum* and *C. somersetense*, *C. ochraceae* and *C. zoysiae*, *C. axonopodi* and *C. hanau*.

The phylogenies of the *C. caudatum* and *C. graminicola* species complexes

As two different sets of loci were previously used for the phylogenetic analyses of *C. caudatum* and *C. graminicola* species complexes, separate analyses were performed herein.

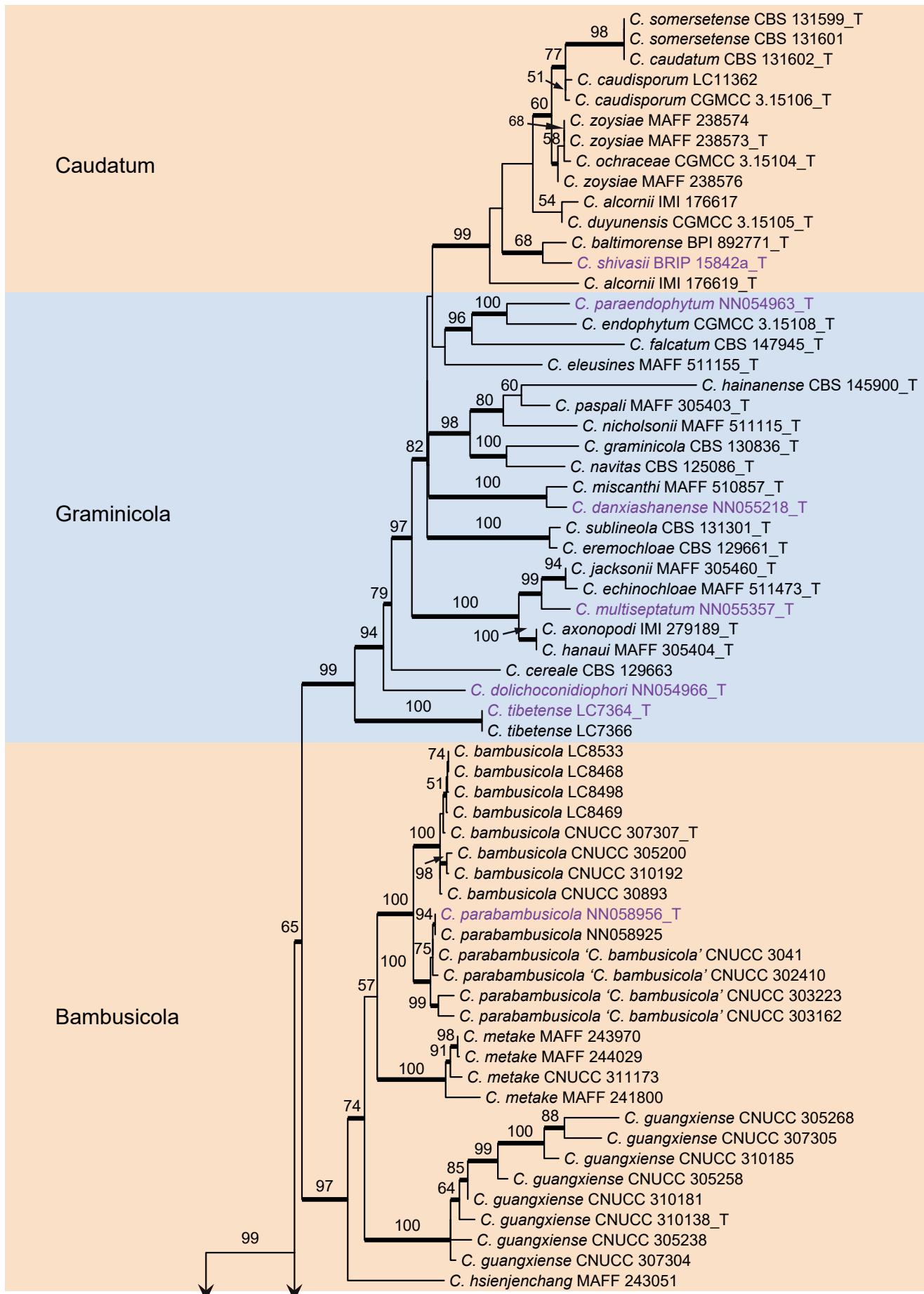


Fig. 1. Phylogenetic tree of *Colletotrichum* calculated with a maximum likelihood analysis of the combined *act*, *chs-1*, *gapdh*, *his3*, ITS, and *tub2* sequence alignment. Bayesian posterior probabilities (PP > 0.90) are emphasised by thickened branches, maximum likelihood bootstrap support values (> 50 %) are shown at the nodes. Species complexes are indicated with coloured boxes, with their names listed at the left. Ex-type strains are indicated with "T" in the end of the taxa labels. Latin names and ex-type strain numbers of the new species described in the current study are shown in purple font.

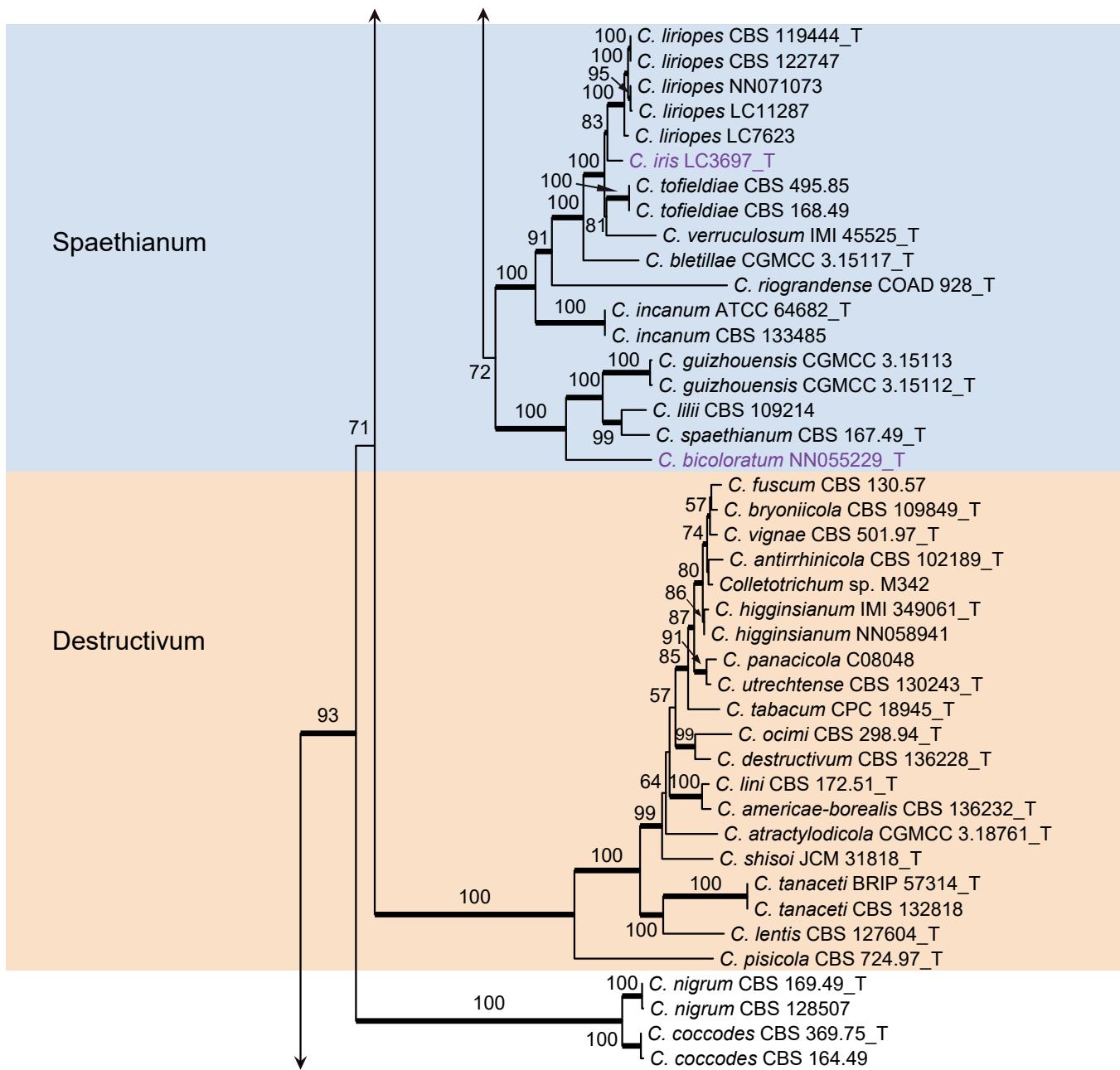


Fig. 1. (Continued).

Colletotrichum caudatum species complex (Fig. 2): The dataset consisted of 14 strains, with *C. gloeosporioides* (IMI 356878) as the outgroup. The final sequence alignment contained 2 949 characters (apn2: 805; ITS: 439; Mat1/Apn2: 1253; sod2: 452) including alignment gaps, and 301 characters were unique site patterns. The ML search revealed a best tree with an lnL of -6 746.046698. The BA was run for 260 000 generations, and a 50 % consensus tree and posterior probabilities were calculated from 5 202 trees from two runs. The topologies of phylogenetic trees generated by ML and BA were congruent. In the four-locus phylogenetic tree of *C. caudatum* species complex (Fig. 2), strain BRIP 15842a formed a sister clade to the ex-type of *C. baltimorensis* on a long branch, distinct from the other clades, representing a novel species. The two strains of *C. alcornii* (IMI 176617 and IMI 176619) were separated into two distant clades, sharing 97 % (419/431) ITS sequence similarity, and may represent different species.

Colletotrichum graminicola species complex (Fig. 3): The dataset consisted of 22 strains, with *C. gloeosporioides* (IMI 356878)

as the outgroup. The final alignment contained 2 117 characters (act: 255; chs-1: 278; ITS: 507; sod2: 564; tub2: 513) including alignment gaps, and 725 characters were unique site patterns. The ML search revealed a best tree with an lnL of -10629.345037. The BA was run for 1 000 generations, and a 50 % consensus tree and posterior probabilities were calculated from 202 trees from two runs. The topologies of the phylogenetic trees generated by ML and BA were congruent. In the five-locus phylogenetic tree of the *C. graminicola* species complex (Fig. 3), the analysed strains formed five distinct clades on long branches.

Whole-genome data and phylogenomic assessment

The *Colletotrichum* genomes varied from 35.03 Mbp to 109.66 Mbp in size and encoded from 8 424 to 14 841 protein-coding genes (Fig. 4, Table S4), and neither correlated with the phylogenetic position (Fig. 4) nor lifestyle of the species (Table S4), except for the genome sizes of the *C. orbiculare* species complex (> 82 Mbp)

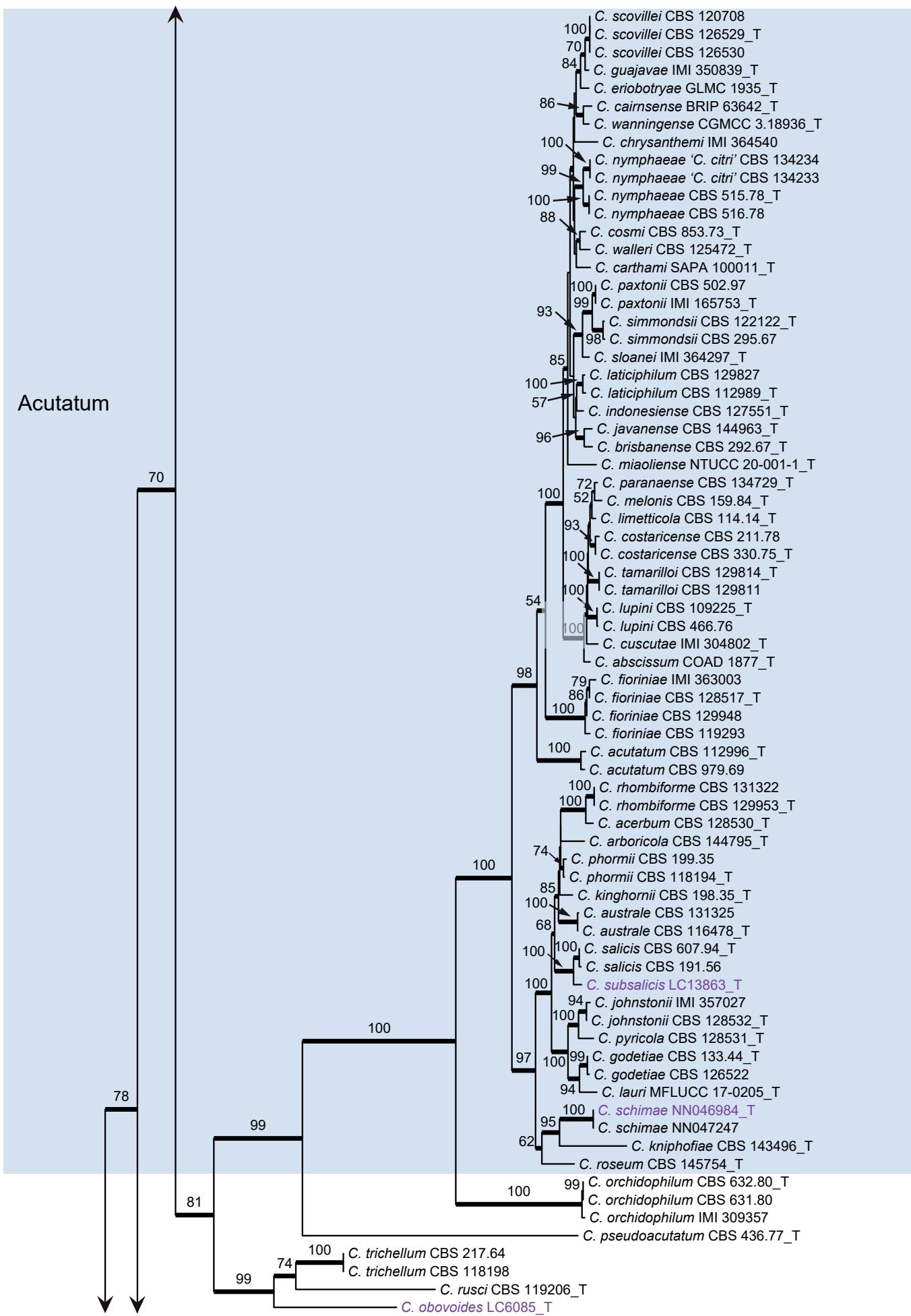
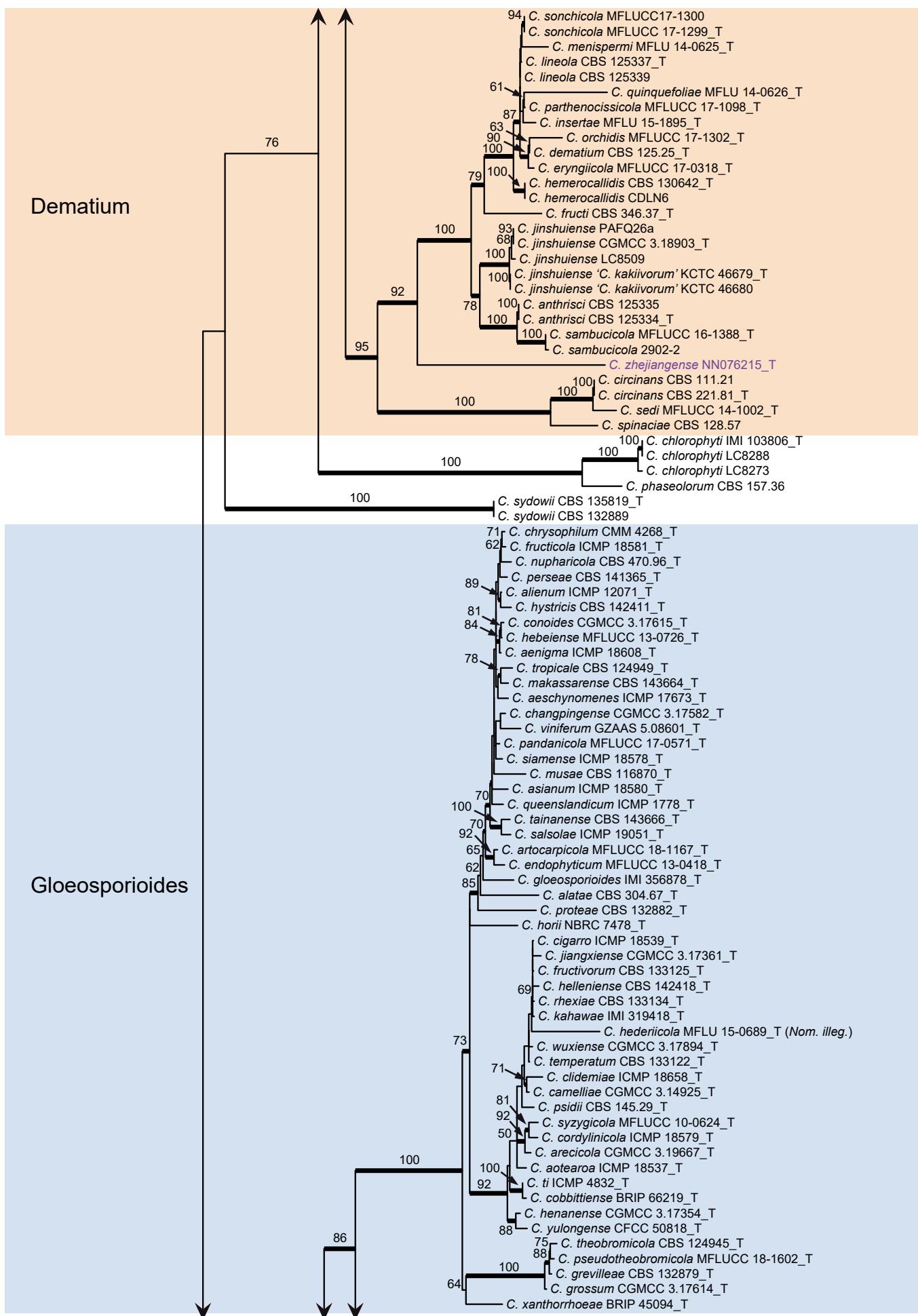


Fig. 1. (Continued).

**Fig. 1.** (Continued).

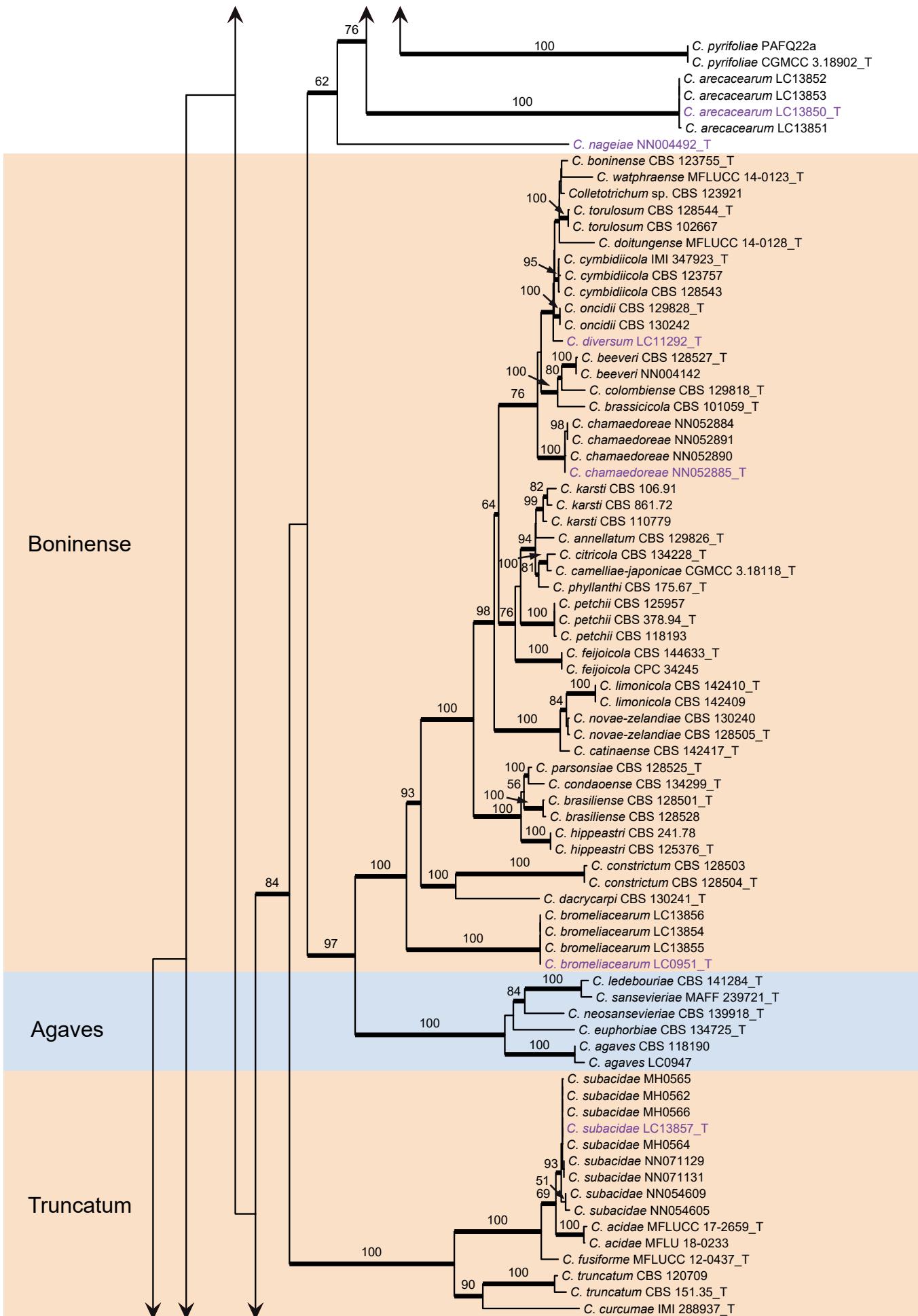


Fig. 1. (Continued).

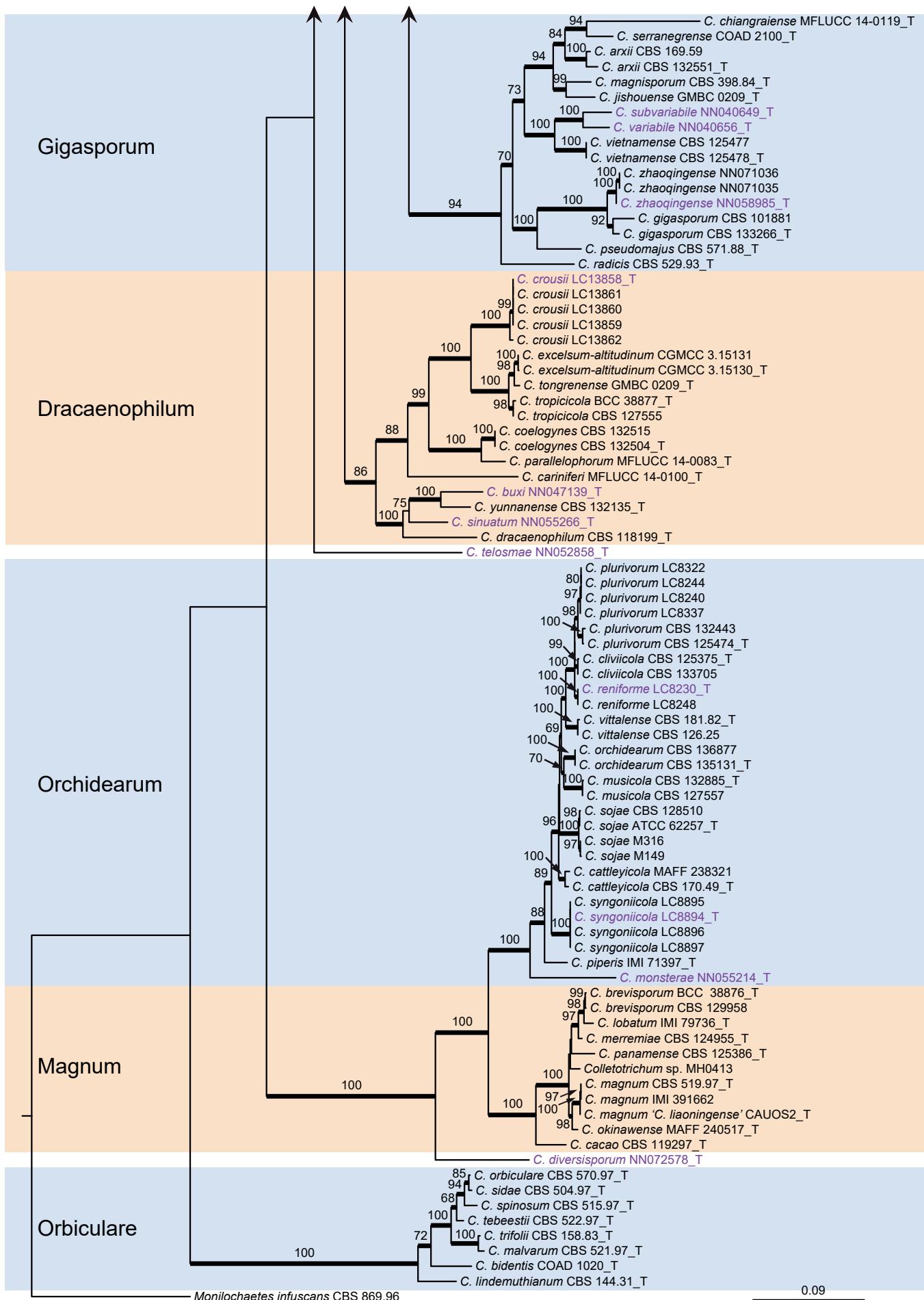


Fig. 1. (Continued).

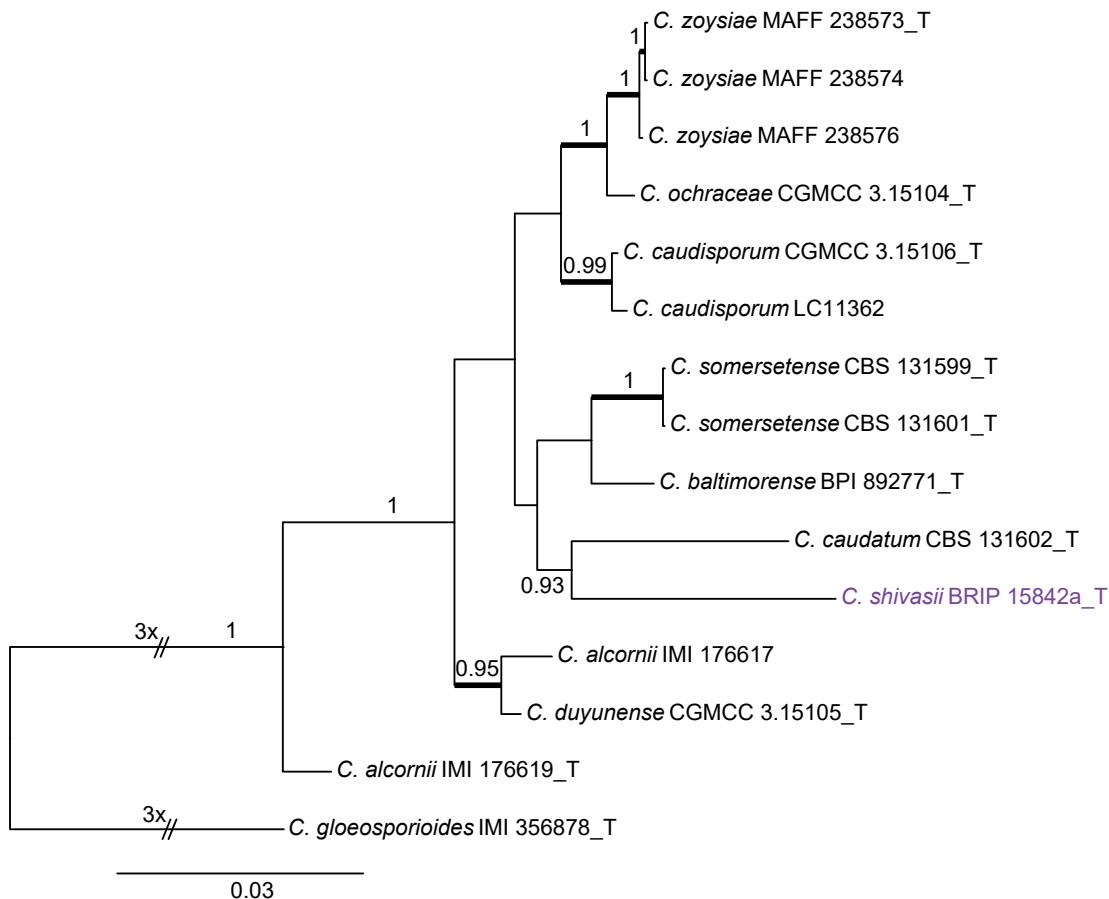


Fig. 2. Phylogenetic tree of the *C. caudatum* species complex resulting from a Bayesian analysis of the combined *apn2*, ITS, Mat1/Apn2, and *sod2* sequence alignment. Maximum likelihood bootstrap support values (> 70 %) are emphasised by thickened branches, bayesian posterior probabilities (PP > 0.90) are shown at the nodes. The scale bar represents the expected number of changes per site. Ex-type strains are indicated with "T" in the end of the taxa labels. Latin names and ex-type strain numbers of the new species described in the current study are shown in purple font.

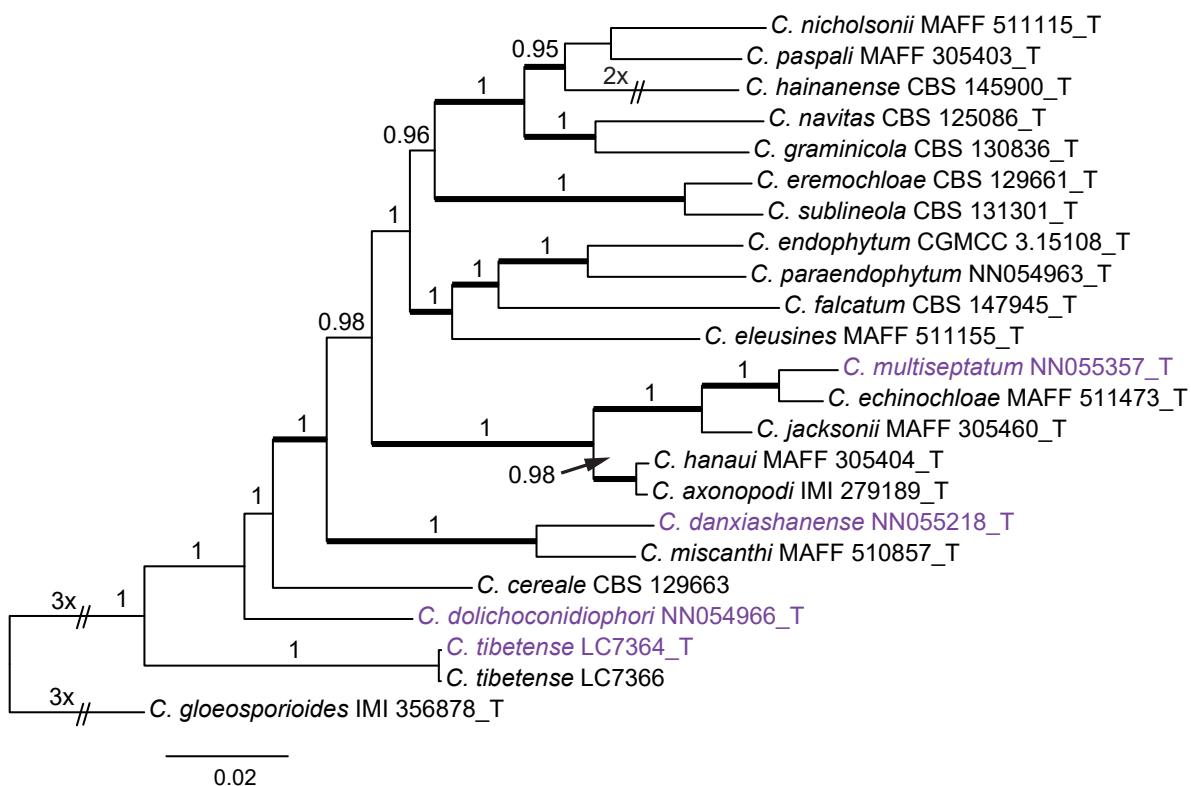


Fig. 3. Phylogenetic tree of the *C. graminicola* species complex resulting from a Bayesian analysis of the combined *act*, *chs-1*, ITS, *sod2*, and *tub2* sequence alignment. Maximum likelihood bootstrap support values (> 70 %) are emphasised by thickened branches, bayesian posterior probabilities (PP > 0.90) are shown at the nodes. The scale bar represents the expected number of changes per site. Ex-type strains are indicated with "T" in the end of the taxa labels. Latin names and ex-type strain numbers of the new species described in the current study are shown in purple font.

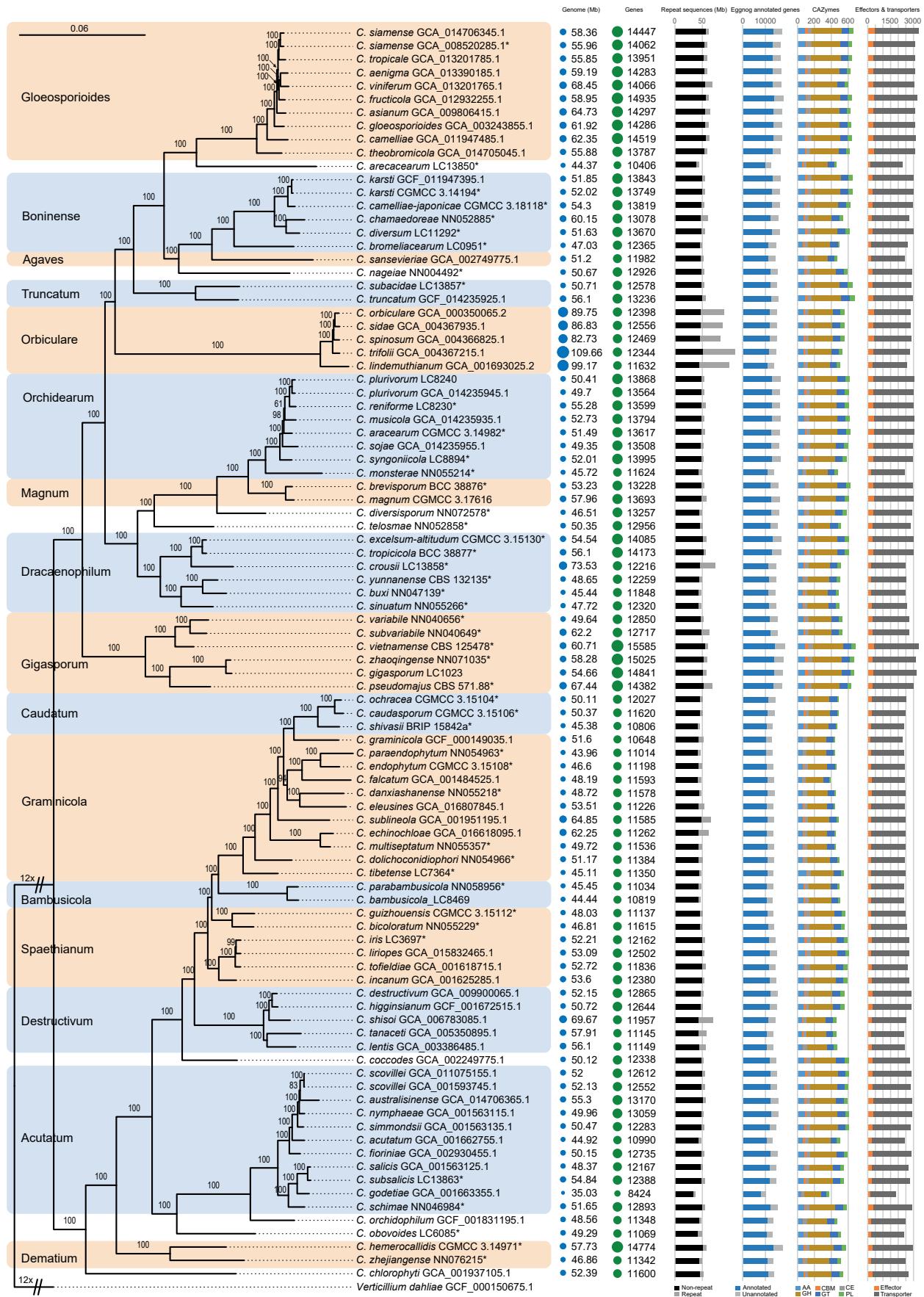


Fig. 4. Maximum likelihood phylogenomic tree generated from a concatenated alignment of sets of orthologous protein sequences. A total of 1 893 single-copy orthologs were retained. The tree was estimated based on the JTT substitution model. Ex-type strains are indicated with “*” in the end of the taxa labels. Genome and assembly features are shown at the right side of the phylogenetic tree. From left to right: Genomes (Mb): genome size in Mb; Genes: number of predicted genes; Repeat sequences (Mb): genome sizes showing proportion of repeat elements in these genomes; Eggnoog annotated genes: number of predicted protein coding genes with and without functional annotation based on eggnoog database; CAZymes: gene number with the distribution of CAZyme classes, auxiliary activities (AA), carbohydrate binding molecules (CBM), carbohydrate esterases (CE), glycoside hydrolases (GH), glycosyl transferases (GT), polysaccharide lyases (PL); Effectors & transporters: number of predicted effectors and transporters.

that were generally larger than those of other species (Fig. 4). However, disproportionate to the large genome, the *C. orbiculare* species complex encodes relatively smaller number of genes, CAZymes and transporters than a few other species complexes, e.g. *C. gigasporum*, *C. gloeosporioides*, and *C. orchidearum* species complexes. On the contrary, *C. orbiculare* species complex possesses the highest proportion of repeat content than other species in this genus (Fig. 4), which may contribute to its large genome (Haridas et al. 2020). Moreover, compared to other members in *Colletotrichum*, species associated with gramineous plants in the *C. bambusicola*, *C. caudatum*, and *C. graminicola* species complexes are characterised by small genome size and small number of genes, CAZymes and transporters.

Using 94 *Colletotrichum* species covering 16 species complexes and one outgroup, a high confidence whole-genome-based phylogenetic tree was generated (Fig. 4). The Gblocks filtered alignment of 1 893 single-copy orthologs consisted of 655 956 characters, including alignment gaps. All nodes, except for four (two in the *C. orchidearum* species complex, and the other two in the *C. graminicola* and *C. spaethianum* species complexes respectively), received 100 % bootstrap support (Fig. 4). The species tree supported the taxonomic status of all species newly described in the current study (Fig. 4). The strain with the assembly accession GCA_001593745.1 was labeled as *C. acutatum* at the time the genome was published; it was however revealed to be *C. scovillei* in the species tree (Fig. 4).

Taxonomy

Five taxa (*C. bambusicola*, *C. guangxiense*, *C. hsienjenchang*, *C. metake*, and *C. parabambusicola* sp. nov.) characterised by straight conidia formed a well-supported clade in the six-locus tree (Fig. 1), representing a new species complex, herein called the *C. bambusicola* species complex. Based on the molecular analyses, morphological examination, and habitat and geographical comparisons, 30 new species are introduced herein.

Colletotrichum arecacearum F. Liu, Z.Y. Ma & L. Cai, **sp. nov.**
MycoBank MB 841370. Fig. 5.

Etymology: Named after its host plant family, Arecaceae.

Description: Colonies on PDA 19–22 mm diam in 7 d, flat with entire edge, saffron in the centre, white at the margin, aerial mycelium sparse, reverse creamy white. Vegetative hyphae hyaline, smooth-walled, septate, branched. Sporulating on OA, conidiomata scattered or confluent, immersed, olivaceous. Conidiophores usually reduced to conidiogenous cells. Conidiogenous cells hyaline, smooth-walled, ampulliform, rarely subcylindrical, straight or curved, collarette distinct, periclinal thickening sometimes visible, $8.5\text{--}15 \times 4.5\text{--}7.5 \mu\text{m}$. Conidia hyaline, aseptate, smooth-walled, guttulate, cylindrical, occasionally slightly curved, with one end round and one end subacute, $12.5\text{--}18.5 \times 4\text{--}5.5 \mu\text{m}$ (av. \pm SD = $15.5 \pm 1.3 \times 4.7 \pm 0.3 \mu\text{m}$), L/W ratio = 3.3. Appressoria and setae not observed.

Typus: **China**, Guangxi, Guangxi Botanical Garden of Medicinal Plants, on leaves of an unidentified species in Arecaceae, Jun. 2017, Z.Y. Ma & L.W. Hou (holotype HMAS 350634, ex-type culture CGMCC 3.20509 = LC13850 = MH0003).

Additional materials examined: **China**, Guangxi, Guangxi Botanical Garden of Medicinal Plants, on leaves of an unidentified species in Arecaceae, Jun. 2017, Z.Y. Ma & L.W. Hou, living cultures LC13851 (= MH0003-1), LC13852 (= MH0003-2), LC13853 (= MH0003-3).

Notes: *Colletotrichum arecacearum*, *C. pyrifoliae*, and *C. nageiae* sp. nov. clustered basal to the broadly known *C. gloeosporioides* species complex (Fig. 1). These three species produce cylindrical conidia, similar to those produced by the *C. gloeosporioides* complex (Weir et al. 2012), but are temporarily considered as singleton species because the ingroup taxa of the *C. gloeosporioides* complex are much more tightly related to each other than to them. *Colletotrichum arecacearum* is distinct from other species in this genus at each locus sequenced in the current study, and morphologically differs from the most closely related species *C. pyrifoliae* in producing shorter and wider conidiogenous cells ($8.5\text{--}15 \times 4.5\text{--}7.5 \mu\text{m}$ vs. $15\text{--}32 \times 3\text{--}5 \mu\text{m}$), and slightly shorter and thinner conidia ($12.5\text{--}18.5 \times 4\text{--}5.5 \mu\text{m}$ vs. $14\text{--}23 \times 5.5\text{--}7 \mu\text{m}$), and differs from *C. nageiae* sp. nov. in producing wider conidiogenous cells ($8.5\text{--}15 \times 4.5\text{--}7.5 \mu\text{m}$ vs. $10\text{--}20 \times 2.5\text{--}4.5 \mu\text{m}$) and longer conidia ($12.5\text{--}18.5 \times 4\text{--}5.5 \mu\text{m}$ vs. $9\text{--}13.5 \times 4.5\text{--}6 \mu\text{m}$).

Colletotrichum bambusicola C.L. Hou & Q.T. Wang, Mycologia 113: 452. 2021. Fig. 6.

Description: Colonies on PDA 52–56 mm diam in 7 d, flat with undulate edge, white to pale grey, aerial mycelium dense, reverse pale grey with mouse grey to black halo, white at the edge. Sexual morph developed on SNA. Ascomata ovoid to obpyriform, medium to dark brown, $180\text{--}195 \times 95\text{--}110 \mu\text{m}$, glabrous, ostiolate, neck pale brown, outer layer composed of angular cells, medium brown, $8\text{--}18.5 \mu\text{m}$ diam. Ascii cylindrical to obclavate, hyaline, $58\text{--}72 \times 7\text{--}10 \mu\text{m}$, 8-spored. Ascospores uni- to bi-seriate, hyaline, smooth-walled, aseptate, allantoid with rounded ends, rarely straight or very slightly curved, $14\text{--}19 \times 4\text{--}6 \mu\text{m}$ (av. \pm SD = $16 \pm 1.1 \times 5 \pm 0.5 \mu\text{m}$), L/W ratio=3.2.

On SNA, conidiomata acervular, scattered, semi-immersed, conidiophores and setae formed on a cushion of roundish, hyaline to pale brown cells. Setae pale to dark brown, smooth-walled, straight or flexuous, 3–4-septate, $60\text{--}74 \mu\text{m}$ long, basal cell cylindrical, $4\text{--}4.5 \mu\text{m}$ diam, tip more or less acute. Conidiophores hyaline to pale brown, smooth-walled, septate, branched. Conidiogenous cells hyaline, smooth-walled, cylindrical, occasionally ampulliform, $21\text{--}33 \times 2.5\text{--}3 \mu\text{m}$. Conidia hyaline, aseptate, smooth-walled, cylindrical, straight, occasionally slightly curved, both ends rounded, or one end rounded and one end \pm acute, $12\text{--}15.5 \times 3.5\text{--}6 \mu\text{m}$ (av. \pm SD = $14.0 \pm 1.0 \times 4.3 \pm 0.7 \mu\text{m}$), L/W ratio = 3.2. Appressoria single or gregarious, olivaceous, irregular outline with crenate or lobed margin, or clavate, $8.5\text{--}17.5 \times 5\text{--}12 \mu\text{m}$ (av. \pm SD = $12.3 \pm 2.3 \times 8.2 \pm 1.7 \mu\text{m}$).

Typus: **China**, Guangxi Zhuang Autonomous region, on seeds of *Phyllostachys edulis*, Sep. 2016, C.L. Hou & Q.T. Wang (holotype CAF80001, ex-type culture CFCC 54250 = ACCC 39709 = CNUCC 307307).

Additional materials examined: **China**, Fujian, Fuzhou, Wuyi Mountain, on *Petasites hybridus*, Aug. 2016, Z.Y. Ma, WYS14, living culture LC8469 (= M0288); ibid. living cultures LC8468 (= M0287); Fujian, Fuzhou, Wuyi Mountain, on *P. hybridus*, Aug. 2016, Z.Y. Ma, WYS40, living culture LC8498 (= M0322); Fujian, Fuzhou, Wuyi Mountain, on *Patrinia villosa*, Aug. 2016, Z.Y. Ma, WYS66, living culture LC8533 (= M0362).

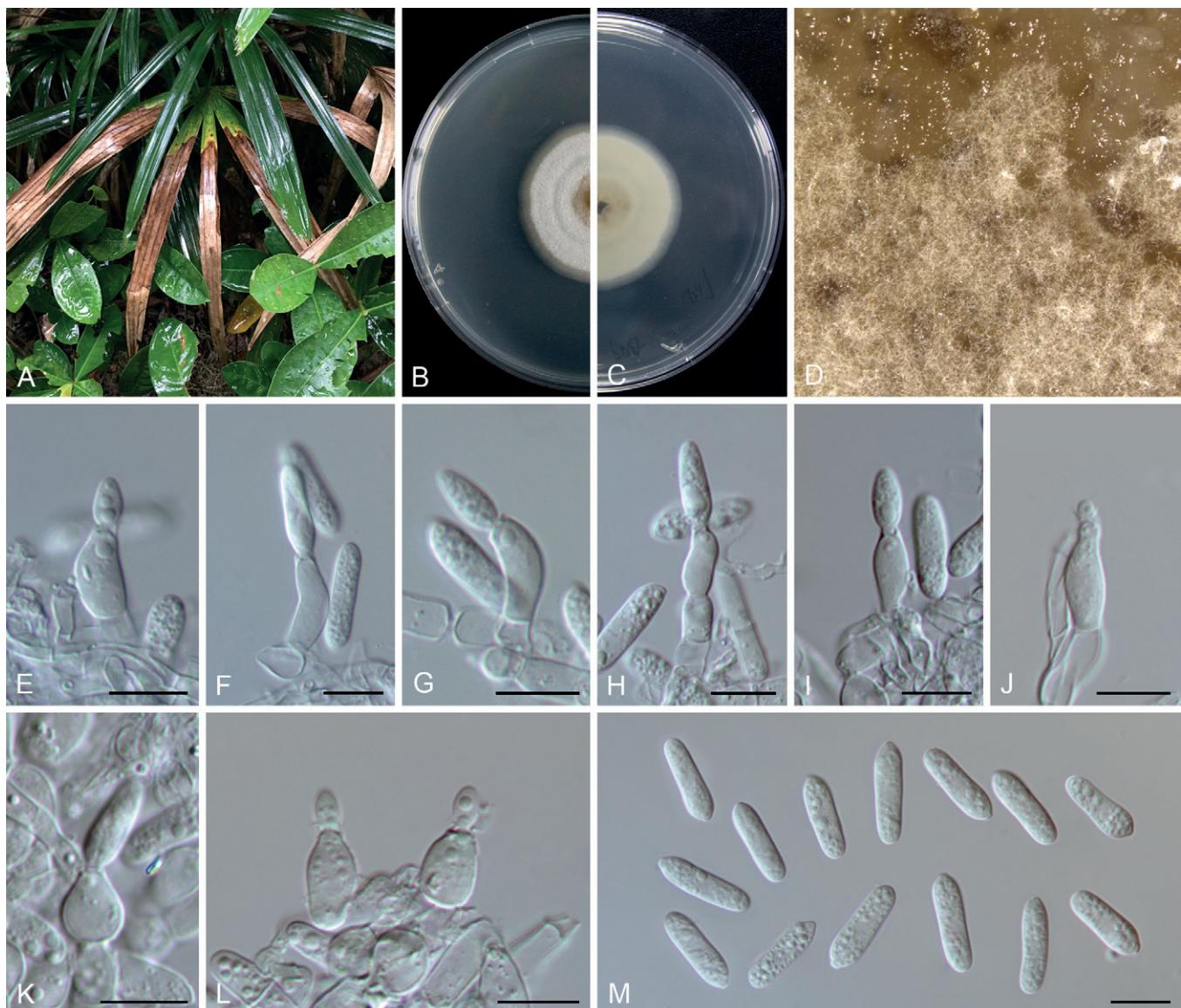


Fig. 5. *Colletotrichum arecacearum* (ex-type culture LC13850). **A.** Disease symptom on the host plant. **B, C.** Front and reverse colony on PDA (7 d). **D.** Colony surface on OA (7 d), with immersed, olivaceous conidiomata. **E–L.** Conidiogenous cells and conidia. **M.** Conidia. Scale bars = 10 µm.

Notes: Here, we describe the sexual morph of *C. bambusicola*, which was lacking in the original description based on collections from bamboo in Wang et al. (2021). This fungus was treated in a broader sense although two subclades were recognised. However, after broader sampling for the phylogenetic analysis and detailed morphological comparisons, we concluded that a new species should be proposed to distinguish the two clades (Fig. 1). *Colletotrichum bambusicola* differs in 3 bp in *act*, 2 bp in *gapdh*, 24 in *his3*, 1 bp in *ITS*, 11 bp in *tub2* from *C. parabambusicola* sp. nov. Morphologically, *C. bambusicola* differs from *C. parabambusicola* sp. nov. in that it produces longer ascospores ($58\text{--}72 \times 7\text{--}10 \mu\text{m}$ vs. $47\text{--}55 \times 6.5\text{--}7.5 \mu\text{m}$) and ascospores ($14\text{--}19 \times 4\text{--}6 \mu\text{m}$ vs. $10\text{--}14.5 \times 3\text{--}5.5 \mu\text{m}$), and a larger conidium L/W ratio (3.2 vs. 2.6).

***Colletotrichum bicoloratum* F. Liu, W.P. Wu & L. Cai, sp. nov.**
Mycobank MB 841371. Fig. 7.

Etymology: Named to reflect the bicoloured conidiogenous cells.

Description: Colonies on PDA 52 mm diam in 7 d, flat with entire edge, white, aerial mycelium dense, reverse greyish sepia to fuscous black. On MEA, setae rarely observed, dark brown, smooth-walled, straight, 3–4-septate, up to 51 µm long, basal cell

cylindrical, 3.5 µm diam, tip acute. Conidiophores formed directly on hyphae, usually reduced into conidiogenous cells. Conidiogenous cells hyaline or dark brown, smooth-walled, ampulliform, $6\text{--}10.5 \times 4\text{--}6 \mu\text{m}$ (av. \pm SD = $8.8 \pm 1.4 \times 4.8 \pm 0.6 \mu\text{m}$). Conidia hyaline, aseptate, smooth-walled, curved, tapering towards apex and base, base usually obtuse and broader than the apex, $12\text{--}16 \times 3\text{--}4 \mu\text{m}$ (av. \pm SD = $14 \pm 0.9 \times 3.6 \pm 0.3 \mu\text{m}$), L/W ratio = 3.9. Appressoria single, medium to dark brown, usually ellipsoidal to subcircular, or irregularly shaped, rarely 2-celled, $5\text{--}9 \times 4\text{--}6.5 \mu\text{m}$.

Typus: **China**, Guangdong Province, Guangzhou, Yuexiu Park, on dead leaves of *Ophiopogon japonicus*, 29 Dec. 2012, W.P. Wu (holotype HMAS 350648, ex-type culture CGMCC 3.20510 = LC13882 = NN055229).

Notes: *Colletotrichum bicoloratum* is phylogenetically closely related to *C. guizhouensis*, *C. lili* and *C. spaethianum* in the *C. spaethianum* species complex, but differs from *C. guizhouensis* and *C. lili* in producing shorter and wider conidiogenous cells ($6\text{--}10.5 \times 4\text{--}6 \mu\text{m}$ vs. $12\text{--}25 \times 2\text{--}2.5 \mu\text{m}$ in *C. guizhouensis*, $7\text{--}20 \times 2\text{--}3.5 \mu\text{m}$ in *C. lili*) and smaller appressoria ($5\text{--}9 \times 4\text{--}6.5 \mu\text{m}$ vs. $6\text{--}14.5 \times 5\text{--}11 \mu\text{m}$ in *C. guizhouensis*, $7.5\text{--}28.5 \times 4.5\text{--}14 \mu\text{m}$ in *C. lili*), and differs from *C. spaethianum* in producing wider conidiogenous cells ($6\text{--}10.5 \times 4\text{--}6 \mu\text{m}$ vs. $6\text{--}16 \times 3\text{--}4 \mu\text{m}$) and shorter conidia

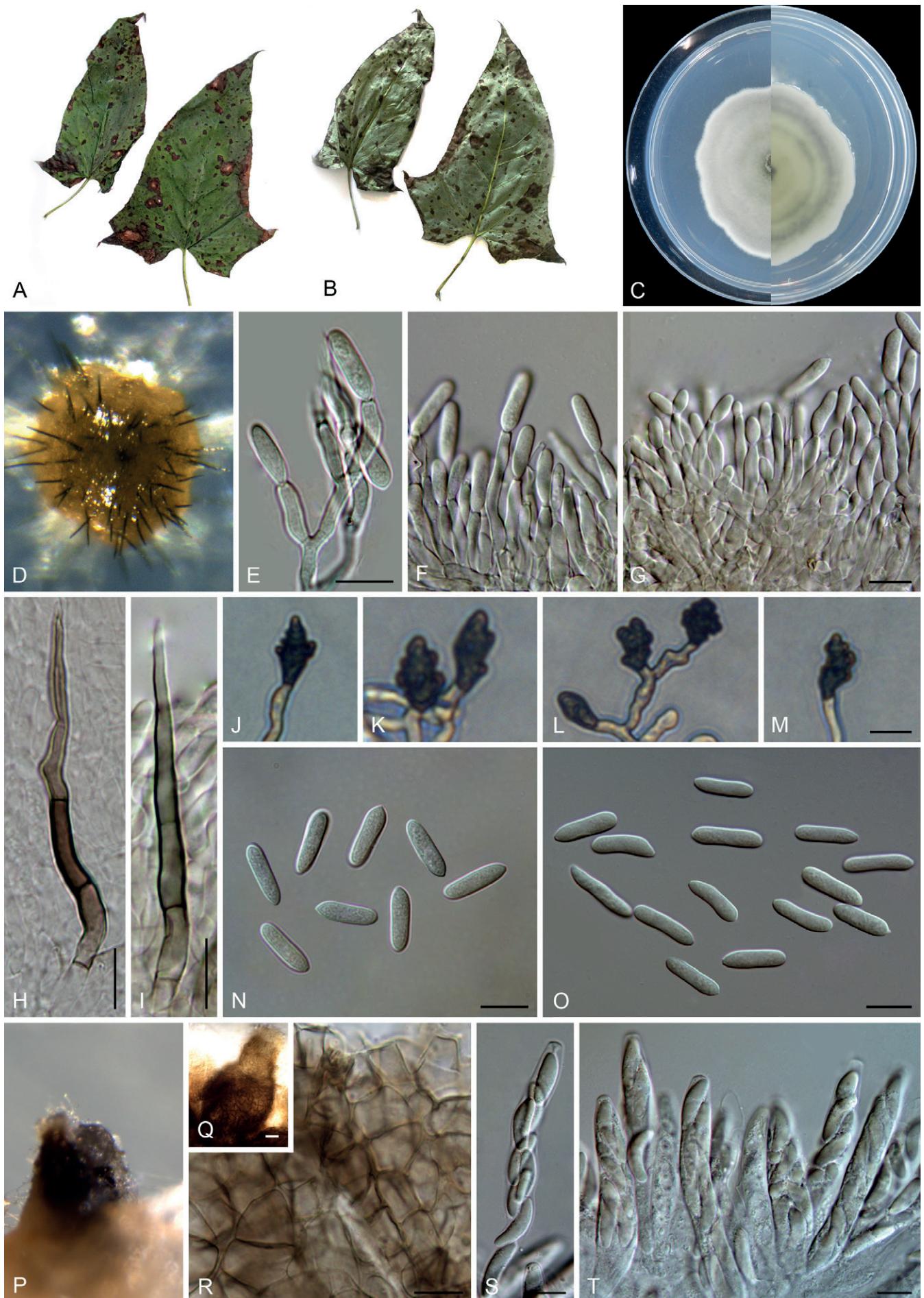


Fig. 6. *Colletotrichum bambusicola* (C–E, H, J–N from LC8469, F–G, I, O from LC8468, P–T from LC8533). **A, B.** Disease symptoms on the host plants. **C.** Front and reverse colony on PDA (7 d). **D.** Acervulus. **E–G.** Conidiophores, conidiogenous cells and conidia. **H, I.** Setae. **J–M.** Appressoria. **N, O.** Conidia. **P, Q.** Ascocarps. **R.** Ascocarp wall. **S, T.** Asci and ascospores. Scale bars =10 µm. Scale bar of M applies to J–M.

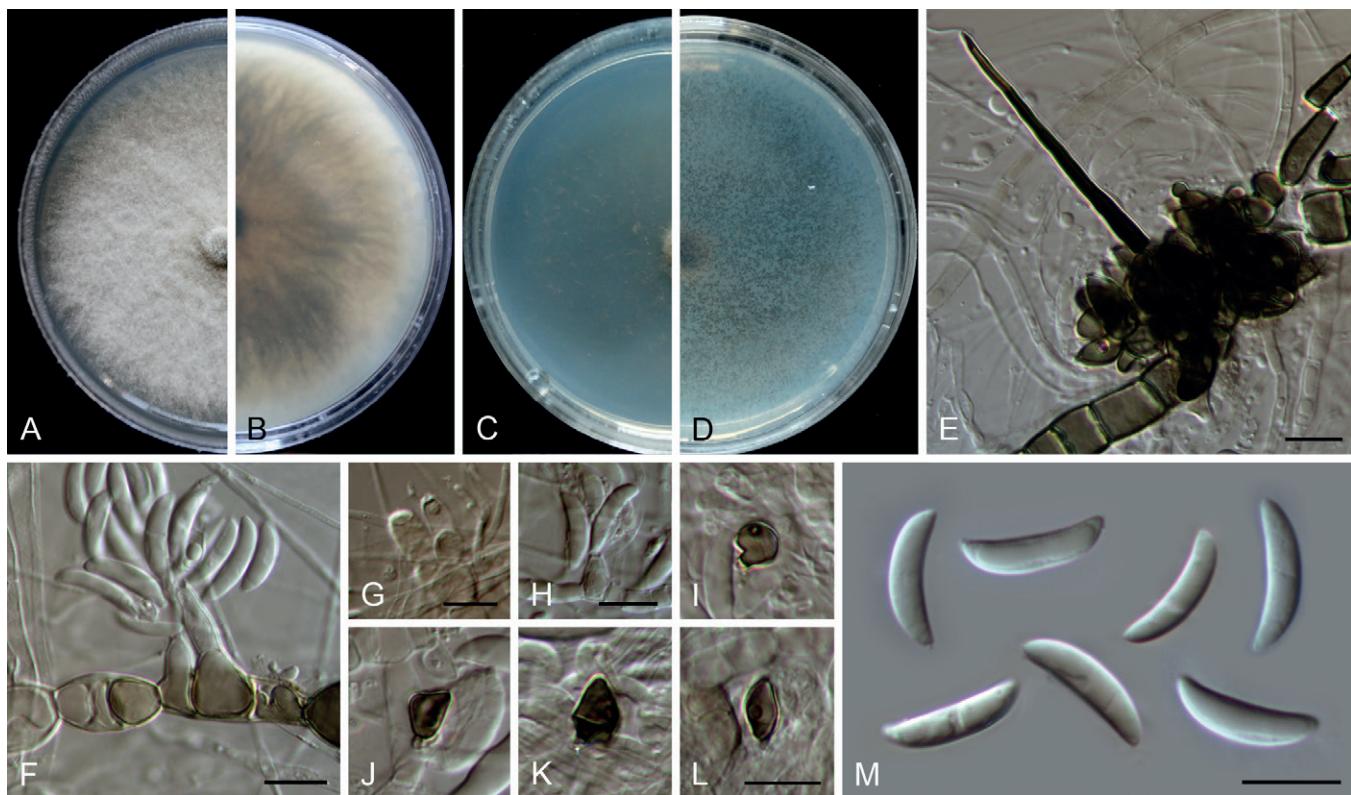


Fig. 7. *Colletotrichum bicoloratum* (ex-type culture NN055229). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Seta and conidiophores. **F–H.** Conidiogenous cells and conidia. **I–L.** Appressoria. **M.** Conidia. Scale bars = 10 µm.

($12\text{--}16 \times 3\text{--}4 \mu\text{m}$ vs. $13.5\text{--}29 \times 3\text{--}4.5 \mu\text{m}$) (Damm *et al.* 2009). *Colletotrichum bicoloratum* can be identified to species level by analysing any of the locus used in the current study.

Like most species in the *C. spaethianum* species complex, the associated host of *C. bicoloratum*, *Ophiopogon japonicus*, is also a petaloid monocotyledon plant. To the best of our knowledge, this is the first report of a *Colletotrichum* species associated with this plant host in China (Farr & Rossman 2021).

Colletotrichum bromeliacearum F. Liu & L. Cai, *sp. nov.* MycoBank MB 841372. Fig. 8.

Etymology: Named after the host plant family, *Bromeliaceae*.

Description: Colonies on PDA 40–47 mm diam in 7 d, flat with undulate edge, cinnamon in the centre, white towards the margin, aerial mycelia sparse, reverse brown vinaceous, dark brick, white towards margin. On PDA, conidiomata acervular, gregarious, pale luteous. Setae olivaceous grey to olivaceous black, smooth-walled, 2–3-septate, 21–73 µm long, basal cell cylindrical or cylindric-conical, 3–5 µm diam, tip more or less acute. Conidiophores formed from a cushion of roundish and pale brown cells, solitary or branched, septate, hyaline to pale brown. Conidiogenous cells hyaline or pale brown, smooth-walled, cylindrical, ovoid, 9–20 × 3.5–7 µm. Conidia hyaline, aseptate, smooth-walled, cylindrical with both ends round, 8.5–16 × 5–7.5 µm (av. ± SD = $12 \pm 1.8 \times 6.2 \pm 0.7 \mu\text{m}$), L/W ratio = 1.9. Appressoria single, mostly globose to subglobose, rarely subcylindrical or irregular outline, with undulate edge, 5–8(–15) × 4.5–8 µm (av. ± SD = $6.7 \pm 0.9 \times 6 \pm 0.9 \mu\text{m}$).

Typus: **China**, Yunnan, on a bromeliad plant (*Bromeliaceae*), 2010, F. Liu (holotype HMAS 350626, ex-type culture CGMCC 3.20527 = LC0951).

Additional materials examined: **China**, Yunnan, on a bromeliad plant (*Bromeliaceae*), 2010, F. Liu, living cultures LC13854, LC13855, LC13856.

Notes: Four strains of *C. bromeliacearum* formed a distinct clade in the *C. boninense* species complex (Fig. 1). This species is distinct from other species in this genus at each locus sequenced in the current study. Hitherto, five *Colletotrichum* species were known from *Bromeliaceae*, *i.e.* *C. ananas*, *C. brevisporum*, *C. truncatum*, *C. gloeosporioides*, and *C. setosum* (Farr & Rossman 2021). *Colletotrichum bromeliacearum* is easily distinguished from *C. brevisporum*, *C. truncatum*, and *C. gloeosporioides* based on molecular and morphological characters (different species complexes), and from *C. ananas* [*Nom. inval.*, Art. 39.1 (Shenzhen)] and *C. setosum* in producing different shapes of conidia (cylindrical and straight vs. curved) (Garud 1968), as well as shorter and wider conidia ($8.5\text{--}16 \times 5\text{--}7.5 \mu\text{m}$ vs. $15\text{--}17 \times 4\text{--}5 \mu\text{m}$) (Patterson 1900), respectively.

Colletotrichum buxi F. Liu, W.P. Wu & L. Cai, *sp. nov.* MycoBank MB 841373. Fig. 9.

Etymology: Named after the host plant genus, *Buxus*.

Description: Colonies on PDA growing very slowly, reaching 8–11 mm diam after 7 d, flat with undulate edge, saffron to orange, conidial masses abundant, orange, aerial mycelium sparse, reverse salmon. Conidiomata not developed, abundant conidial masses (Fig. 9 E) formed on the surface of PDA, covered by aerial mycelium, orange, confluent. Conidiophores formed directly on hyphae, hyaline, septate, branched, 32–74 µm in length. Conidiogenous cells hyaline, smooth-walled, cylindrical to subcylindrical, variable in size, 9.5–26 × 2–4.5 µm (av. ± SD = $18.6 \pm 4.1 \times 3.4 \pm 0.7 \mu\text{m}$). Conidia hyaline, mostly aseptate, sometimes

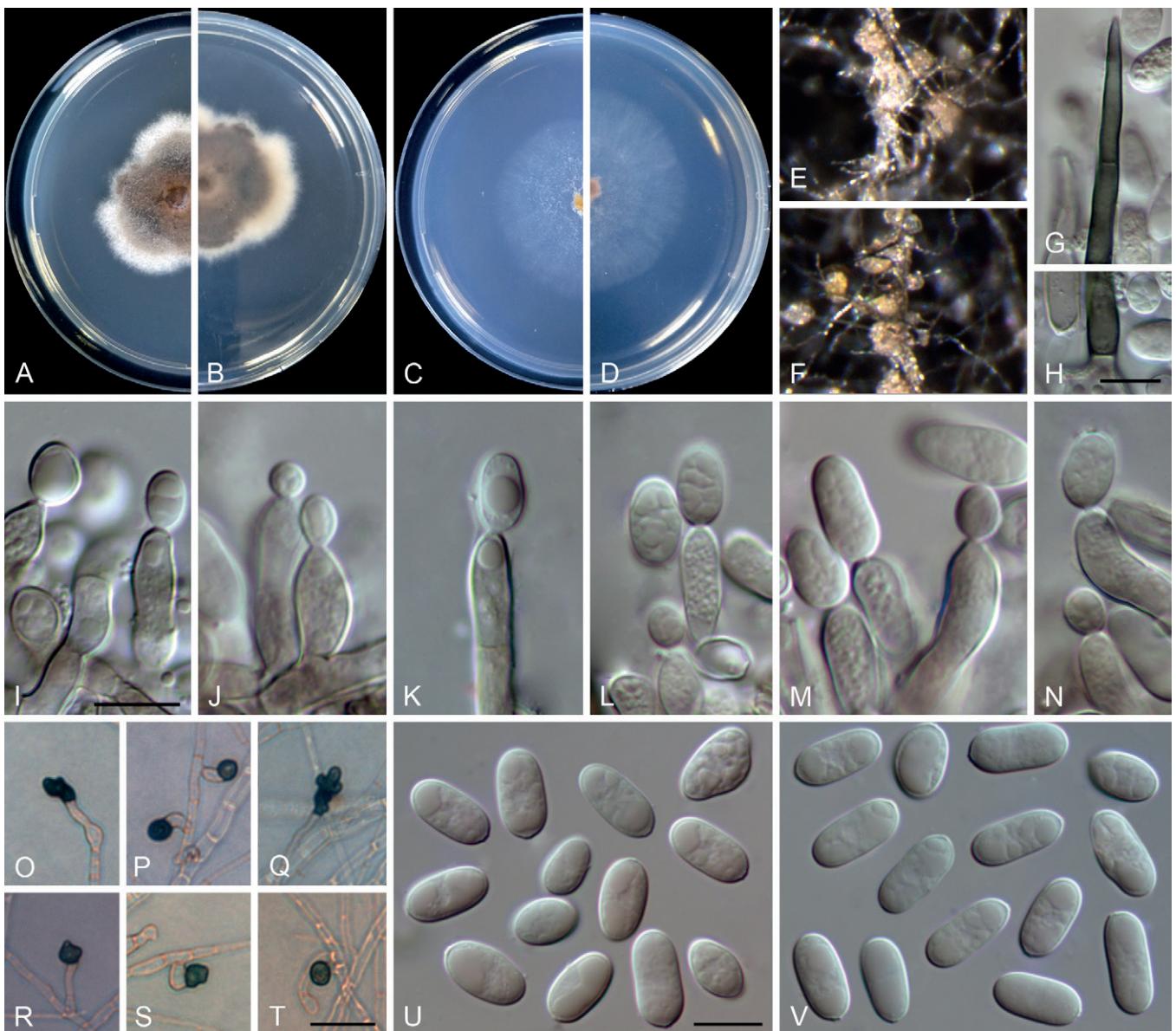


Fig. 8. *Colletotrichum bromeliacearum* (ex-type culture LC0951). **A, B.** Front and reverse colony on PDA (9 d). **C, D.** Front and reverse colony on SNA (9 d). **E, F.** Conidiomata on PDA. **G.** Tip of a seta. **H.** Base of a seta. **I–N.** Conidiogenous cells and conidia. **O–T.** Appressoria. **U, V.** Conidia. Scale bars: H, I, U = 10 µm; T = 20 µm. Scale bar of I applies to I–N; T applies to O–T; U applies to U, V.

1-septate and germinating with thin and flexuous germ tubes developing from the middle or apex of the conidia (Fig. 9 F, J), smooth-walled, cylindrical, both ends round, or one end obtuse and another end round, $9.5\text{--}14.5 \times 4\text{--}6 \mu\text{m}$ (av. \pm SD = $12.2 \pm 1.2 \times 5.1 \pm 0.4 \mu\text{m}$), L/W ratio = 2.4. Appressoria mostly clavate, sometimes subcylindrical or with an irregular outline and with a crenate or lobed margin, $5\text{--}12 \times 3.5\text{--}6 \mu\text{m}$ (av. \pm SD = $7.5 \pm 1.8 \times 4.4 \pm 0.7 \mu\text{m}$). Setae not observed.

Typus: **China**, Yunnan Province, Kunming, Kunming Botanical Garden, on healthy leaves of *Buxus* sp., 10 May 2002, W.P. Wu (**holotype** HMAS 350642, ex-type culture CGMCC 3.20511 = LC13873 = NN047139).

Additional material examined: **China**, Yunnan Province, Kunming, Kunming Botanical Garden, on *Buxus sinica* var. *parvifolia*, 20 Dec. 1993, W.P. Wu, living culture LC14551 (= NN004149).

Notes: *Colletotrichum buxi* resides within the *C. dracaenophilum* species complex in the multi-locus phylogenetic tree (Fig. 1). It shares low sequence similarity with the phylogenetically related species *C. yunnanense* at *act* (93.8 %), *chs-1* (98.8 %), *gapdh*

(89.5 %), *his3* (94.9 %), *tub2* (97.3 %), and *ITS* (97.4 %), and differs in producing longer conidiophores (32–74 µm vs. 10–30 µm) and conidiogenous cells (9.5–26 µm vs. 6–12 µm), and shorter conidia (9.5–14.5 µm vs. 14–21 µm) (Liu *et al.* 2007).

Colletotrichum chamaedoreae* F. Liu, W.P. Wu & L. Cai, *sp. nov.
MycoBank MB 841374. Fig. 10.

Etymology: Named after the host plant genus, *Chamaedorea*.

Description: Colonies on PDA 42–48 mm diam in 7 d, orange in the centre due to the formation of abundant conidial masses, white at the margin, reverse orange in the centre and white towards the margin. Vegetative hyphae hyaline, smooth-walled, septate, branched, 2.5–4.5 µm diam. On PDA, ascomata globose, subglobose or with an irregular shape, solitary or gregarious, brown to black, sub-immersed or immersed, ostiolate, outer wall composed of pale brown to dark brown angular cells, $6.5\text{--}19.5 \times 3.5\text{--}12 \mu\text{m}$ diam (av. \pm SD = $12.8 \pm 3.1 \times 7.3 \pm 2.2 \mu\text{m}$). Interascal tissue composed of hyaline, thin-walled, septate paraphyses, 2.5–5.5 µm diam. Asci obclavate

or clavate, hyaline, $41\text{--}65 \times 12\text{--}16 \mu\text{m}$, 8-spored. Ascospores uniseriately or irregularly arranged, hyaline, smooth-walled, aseptate, fusoid or subcylindrical with gently tapering rounded ends, straight or slightly curved, $14.5\text{--}21.5 \times 4.5\text{--}6.5 \mu\text{m}$ (av. \pm SD = $17.7 \pm 1.8 \times 5.3 \pm 0.5 \mu\text{m}$), L/W ratio = 3.3.

Conidial masses amber to buff, protruded from the dark brown to black conidiomata. Setae medium brown to dark brown, smooth-walled, 1–7-septate, $36\text{--}95 \mu\text{m}$ long, basal cells cylindrical, sometimes inflated in the middle, $4\text{--}8 \mu\text{m}$ diam, the tip acute or rounded. *Conidiophores* 0–1-septate, usually reduced to conidiogenous cells. *Conidiogenous cells* hyaline, cylindrical to subcylindrical, smooth-walled, straight or slight curved, sometimes extending to form new conidiogenous loci, $11\text{--}27 \times 3.5\text{--}9.5 \mu\text{m}$. *Conidia* hyaline, aseptate, smooth-walled, guttulate, often with two

big and a number of small guttules, cylindrical, the apex round, the base with a prominent truncate scar, straight, $13.5\text{--}19 \times 4.5\text{--}6.5 \mu\text{m}$ (av. \pm SD = $15.7 \pm 1.4 \times 5.6 \pm 0.3 \mu\text{m}$), L/W ratio = 2.8. *Appressoria* not observed.

Typus: **China**, Yunnan Province, Jinghong, Xishuangbanna Botanical Garden, on healthy leaves of *Chamaedorea erumpens*, 19 Mar. 2010, W.P. Wu (**holotype** HMAS 350639, ex-type culture CGMCC 3.20512 = LC13868 = NN052885).

Additional materials examined: **China**, Yunnan Province, Jinghong, Xishuangbanna Botanical Garden, on healthy leaves of *Chamaedorea erumpens*, 19 Mar. 2010, W.P. Wu, living cultures LC13867 (= NN052884), LC13869 (= NN052890), LC13870 (= NN052891).

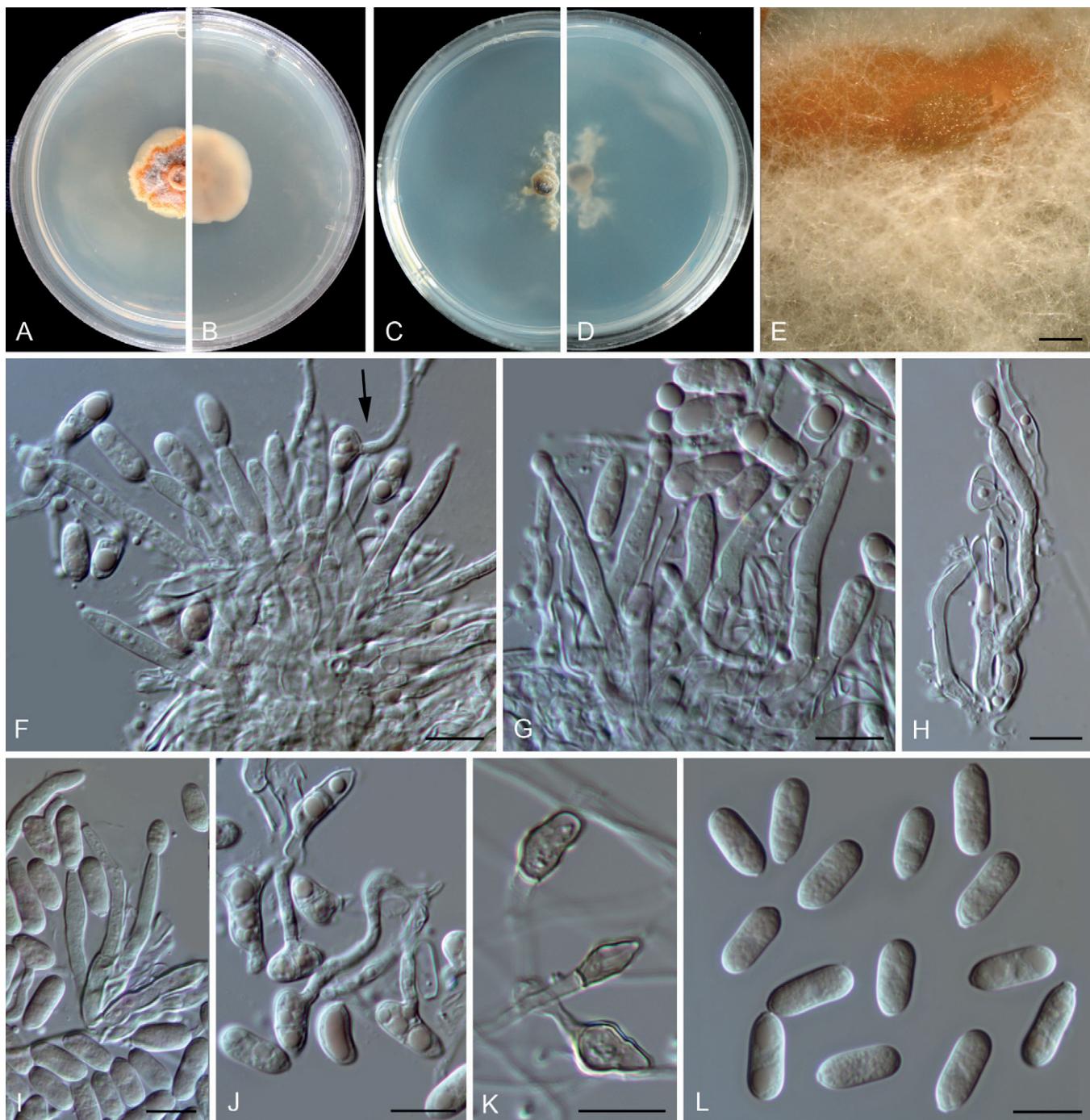


Fig. 9. *Colletotrichum buxi* (ex-type culture NN047139). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidial masses on PDA. **F–I.** Conidiophores, conidiogenous cells and conidia (arrow in F points to a germinating conidium). **J.** Germinating conidia. **K.** Appressoria. **L.** Conidia. Scale bars: E = $300 \mu\text{m}$; F–L = $10 \mu\text{m}$.

Notes: *Colletotrichum chamaedoreae* belongs to the *C. boninense* species complex (Fig. 1). Conidiogenous cells that extend to form new conidiogenous loci have previously been observed in species

of the *C. boninense* species complex, e.g. in *C. annellatum*, *C. constrictum*, *C. cymbidiicola*, *C. novae-zelandiae*, and *C. oncidii*. However, their conidia are shorter and the conidium L/W ratio

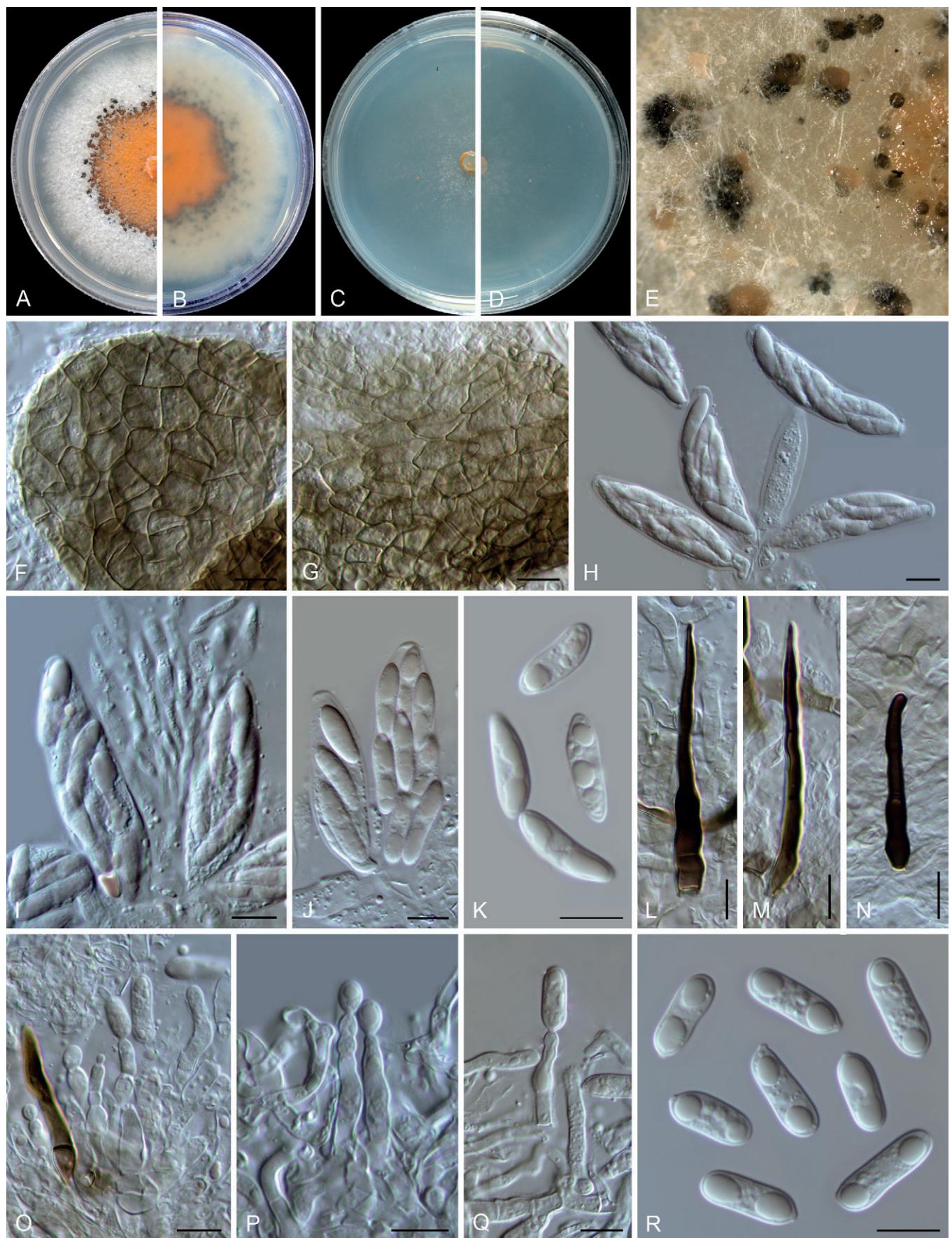


Fig. 10. *Colletotrichum chamaedoreae* (ex-type culture NN052885). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidiomata and ascomata on SNA. **F, G.** Ascomata wall. **H–J.** Ascospores and paraphyses. **K.** Ascospores. **L–N.** Seta. **O–Q.** Conidiophores, conidiogenous cells and conidia. **R.** Conidia. Scale bars = 10 µm.

is lower than those of *C. chamaedoreae* (Damm *et al.* 2012b). In addition, *C. chamaedoreae* is distinct from other species in this genus at each locus sequenced in the current study, and morphologically differs from the most closely related species *C. brassicicola* in that it produces shorter ascospores ($41\text{--}65 \times 12\text{--}16 \mu\text{m}$ vs. $65\text{--}105 \times 12\text{--}13.5 \mu\text{m}$), and longer and wider conidiogenous cells ($11\text{--}27 \times 3.5\text{--}9.5 \mu\text{m}$ vs. $7\text{--}14 \times 4\text{--}5.5 \mu\text{m}$) (Damm *et al.* 2012b).

Colletotrichum chiangraiense X.Y. Ma *et al.*, MycoKeys 43: 34. 2018.

Notes: *Colletotrichum chiangraiense* was shown to be a member of the *C. boninense* species complex in the original description (Ma *et al.* 2018), but resided within the *C. gigasporum* species complex in our multi-locus tree, forming an unusually long branch (Fig. 1). BLASTn search of the NCBI GenBank using ITS and *act* sequences of *C. chiangraiense* (ex-type MFLUCC 14-0119) yielded closest matches with species in the *C. gigasporum* species complex, while using *tub2* yielded closest matches with species in the *C. boninense* species complex. Therefore, it is very likely that the sequences provided in Ma *et al.* (2018) were misplaced or with sequencing errors. The taxonomic status of *C. chiangraiense* requires confirmation by re-examination and re-sequencing of the type.

Colletotrichum crousei F. Liu, Z.Y. Ma & L. Cai, *sp. nov.* MycoBank MB 841375. Fig. 11.

Etymology: Named in honour of the mycologist Pedro Crous, one of the major contributors to recent improvements in *Colletotrichum* systematics.

Description: Colonies on PDA 44–46 mm diam in 7 d, flat with undulate edge, rosy buff, covered by cottony and white aerial mycelium, reverse dark vinaceous buff, white towards margin. On PDA, conidiomata not observed, conidiophores formed directly from hyphae, conidial masses pale vinaceous buff, confluent. Conidiophores hyaline, solitary, sometimes branched at the base, up to 35 μm , usually reduced to conidiogenous cells. Conidiogenous cells hyaline, aseptate, smooth-walled, cylindrical to ampulliform, $9\text{--}22 \times 4.5\text{--}6 \mu\text{m}$. Conidia hyaline, aseptate, smooth-walled, cylindrical, both ends obtuse, or apex obtuse and bottom gradually narrowed with a prominent truncate scar, $12.5\text{--}18.5 \times 6.5\text{--}8 \mu\text{m}$ (av. $\pm \text{SD} = 16 \pm 1.6 \times 7 \pm 1.6 \mu\text{m}$), L/W ratio = 2.2. Appressoria and setae not observed.

Typus: China, Guangxi, Chongzuo, Guangxi Nonggang National Nature Reserve, on leaf of *Rhaphidophora* sp., Jun. 2017, Z.Y. Ma & L.W. Hou, NG56 (*holotype* HMAS 350636, ex-type culture CGMCC 3.20513 = LC13858 = MH0588).

Additional materials examined: China, Guangxi, Chongzuo, Guangxi Nonggang National Nature Reserve, on leaf of *Rhaphidophora* sp., Jun. 2017, Z.Y. Ma & L.W. Hou, NG56 (Fig. 11A, B), living cultures LC13859 (= MH0589), LC13860 (= MH0592), LC13861 (= MH0727); on leaf of *Rhaphidophora* sp., Jun. 2017, Z.Y. Ma & L.W. Hou, NG58 (Fig. 11C, D), living culture LC13862 (= MH0759).

Notes: *Colletotrichum crousei* is phylogenetically related to *C. excelsum-altitudinum*, *C. tongrenense*, and *C. tropicicola* in the *C. dracaenophilum* species complex, but differs in that it produces wider conidia ($6.5\text{--}8 \mu\text{m}$ vs. $5\text{--}7 \mu\text{m}$ in *C. excelsum-altitudinum* and *C. tongrenense*, $4.5\text{--}5.5 \mu\text{m}$ in *C. tropicicola*) with a lower L/W ratio (2.2 vs. generally 2.4–3.3) (Tao *et al.* 2013, Damm *et al.* 2019, Zhou

et al. 2019), and larger conidiogenous cells ($9\text{--}22 \times 4.5\text{--}6 \mu\text{m}$ vs. $2\text{--}11 \times 1\text{--}2 \mu\text{m}$ in *C. tongrenense*) (Zhou *et al.* 2019). Moreover, *C. crousei* is distinct from other species in this genus at each locus sequenced in the current study.

Colletotrichum danxiashanense F. Liu, W.P. Wu & L. Cai, *sp. nov.* MycoBank MB 841376. Fig. 12.

Etymology: Named after the location where the fungus was collected, Danxia Mountain.

Description: Colonies on PDA 52 mm diam in 7 d, flat with rhizoids edge, surface covered by floccose white, aerial mycelium, reverse pale luteous to brown. Vegetative hyphae hyaline or pale brown, smooth-walled, septate, branched. On SNA, conidiomata not developed, conidiophores formed directly on hyphae, terminally or laterally. Setae not observed. Conidiophores reduced to conidiogenous cells. Conidiogenous cells hyaline, rarely pale brown, smooth-walled, ampulliform to cylindrical, $6\text{--}12 \times 2.5\text{--}5.5 \mu\text{m}$, periclinal thickening not observed. Conidia hyaline, aseptate, smooth-walled, guttulate, falcate with \pm acute or obtuse ends, $18.5\text{--}29.5 \times 3\text{--}4.5$ (av. $\pm \text{SD} = 24.4 \pm 3.1 \times 3.8 \pm 0.4$), L/W ratio = 6.4. Appressoria single, medium brown to dark brown, subcircular, subcylindrical, or irregularly shaped, $6\text{--}10 \times 6\text{--}7 \mu\text{m}$ (av. $\pm \text{SD} = 8.3 \pm 1.4 \times 6.4 \pm 0.4 \mu\text{m}$).

Typus: China, Guangdong Province, Shaoguan, Danxia Mountain, on dead leaves of probable *Misanthus* sp., 25 Dec. 2012, W.P. Wu (*holotype* HMAS 350650, ex-type culture CGMCC 3.20514 = LC13885 = NN055218).

Notes: *Colletotrichum danxiashanense* belongs to the *C. graminicola* species complex and forms a sister clade to *C. miscanthi* (Fig. 3). Both species are morphologically similar and associated with the same host genus, *Misanthus*, but with clearly different *act* (98.3 % identity, with 4 bp differences), *chs-1* (99.6 % identity, with 1 bp difference), *ITS* (98.9 % identity, with 5 bp differences), *sod2* (90.5 % identity, with 35 bp differences), and *tub2* (97.9 % identity, with 10 bp differences) sequences.

Colletotrichum diversisporum F. Liu, W.P. Wu & L. Cai, *sp. nov.* MycoBank MB 841377. Fig. 13.

Etymology: Refers to the diverse shapes of conidia.

Description: Colonies on PDA 49 mm diam in 7 d, flat with entire edge, smoke to mouse grey in the centre, white towards the margin, aerial mycelium more or less sparse, reverse smoke grey. Vegetative hyphae hyaline, smooth-walled, septate, branched. On PDA, conidiomata not developed, conidiophores formed directly on hyphae. Conidiophores hyaline or very pale brown, septate, branched. Conidiogenous cells hyaline, smooth-walled, cylindrical, $14\text{--}33 \times 2.5\text{--}3.5 \mu\text{m}$. Conidia hyaline, aseptate, smooth-walled, guttulate, variable in shape and size, cylindrical, ellipsoidal or ovoid, sometimes constricted in the centre or near the base, $9.5\text{--}16.5 \times 3.5\text{--}8 \mu\text{m}$ (av. $\pm \text{SD} = 11.5 \pm 1.5 \times 5.2 \pm 1.1 \mu\text{m}$), L/W ratio = 2.2. Sometimes conidia becoming 1-septate and germinating after 10 d, germ tubes flexuous and thinner than hyphae (Fig. 13 G). Appressoria and setae not observed.

Typus: China, Guangdong Province, Guangzhou, South China Botanical Garden, on dead leaves of *Dracaena angustifolia*, 28 Feb. 2016, W.P. Wu (*holotype* HMAS 350655, ex-type culture CGMCC 3.20515 = LC13890 = NN072578).

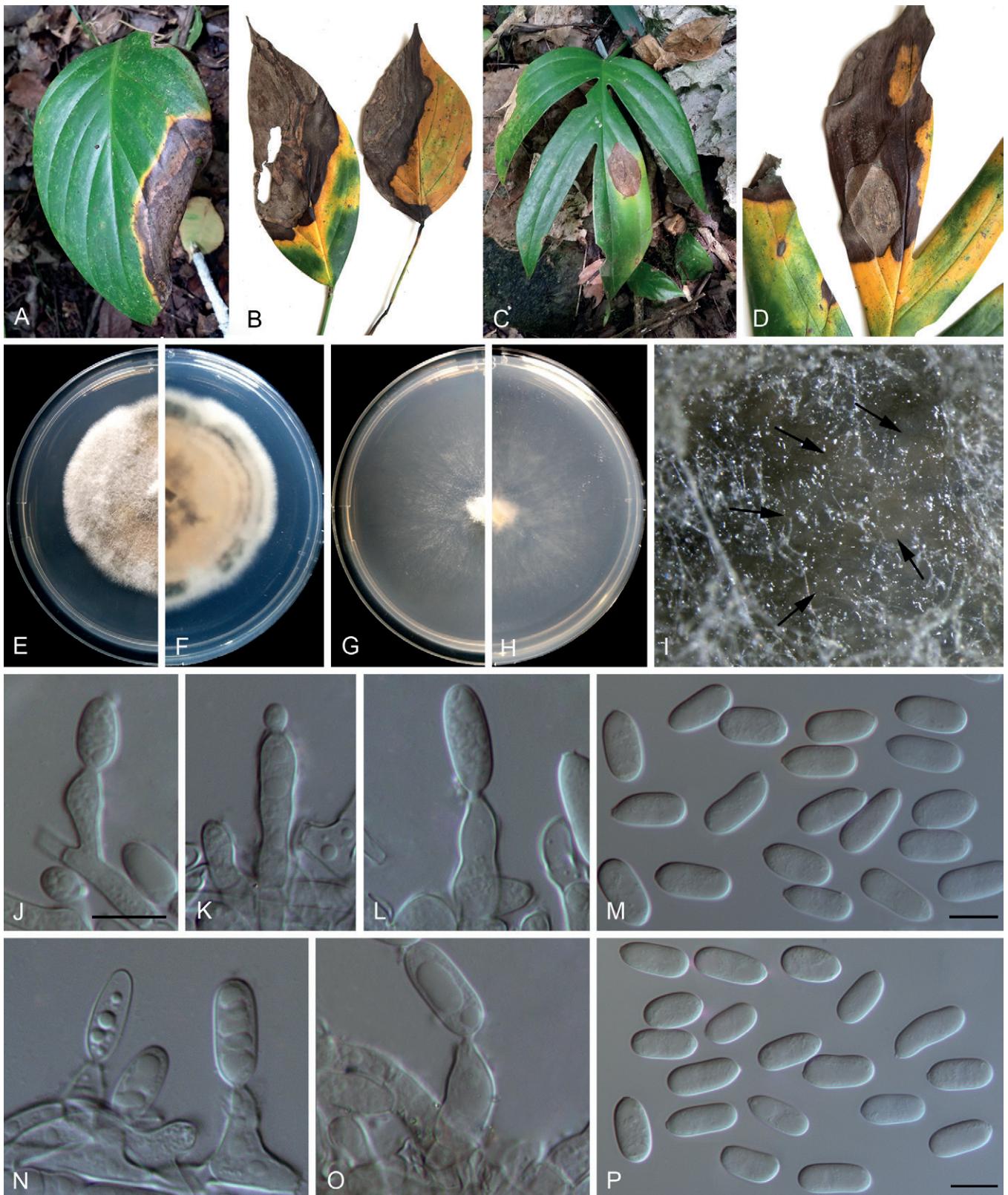


Fig. 11. *Colletotrichum crousii* (ex-type culture LC13858). **A–D.** Disease symptoms on *Rhaphidophora* spp. **E, F.** Front and reverse colony on PDA (7 d). **G, H.** Front and reverse colony on SNA (7 d). **I.** Conidioma on SNA. **J–L, N, O.** Conidiophores, conidiogenous cells and conidia. **M, P.** Conidia. Scale bars = 10 µm. Scale bar of J applies to J–L, N, O.

Notes: *Colletotrichum diversisporum* is basal to the *C. magnum* and *C. orchidearum* species complexes (Fig. 1). It is characterised by a production of conidia of variable shapes and sizes, and can be easily differentiated from other species by analysing any of the loci sequenced in the current study.

***Colletotrichum diversum* F. Liu & L. Cai, sp. nov.** MycoBank MB 841378. Fig. 14.

Etymology: Named to reflect the formation of two different types of conidiophores.

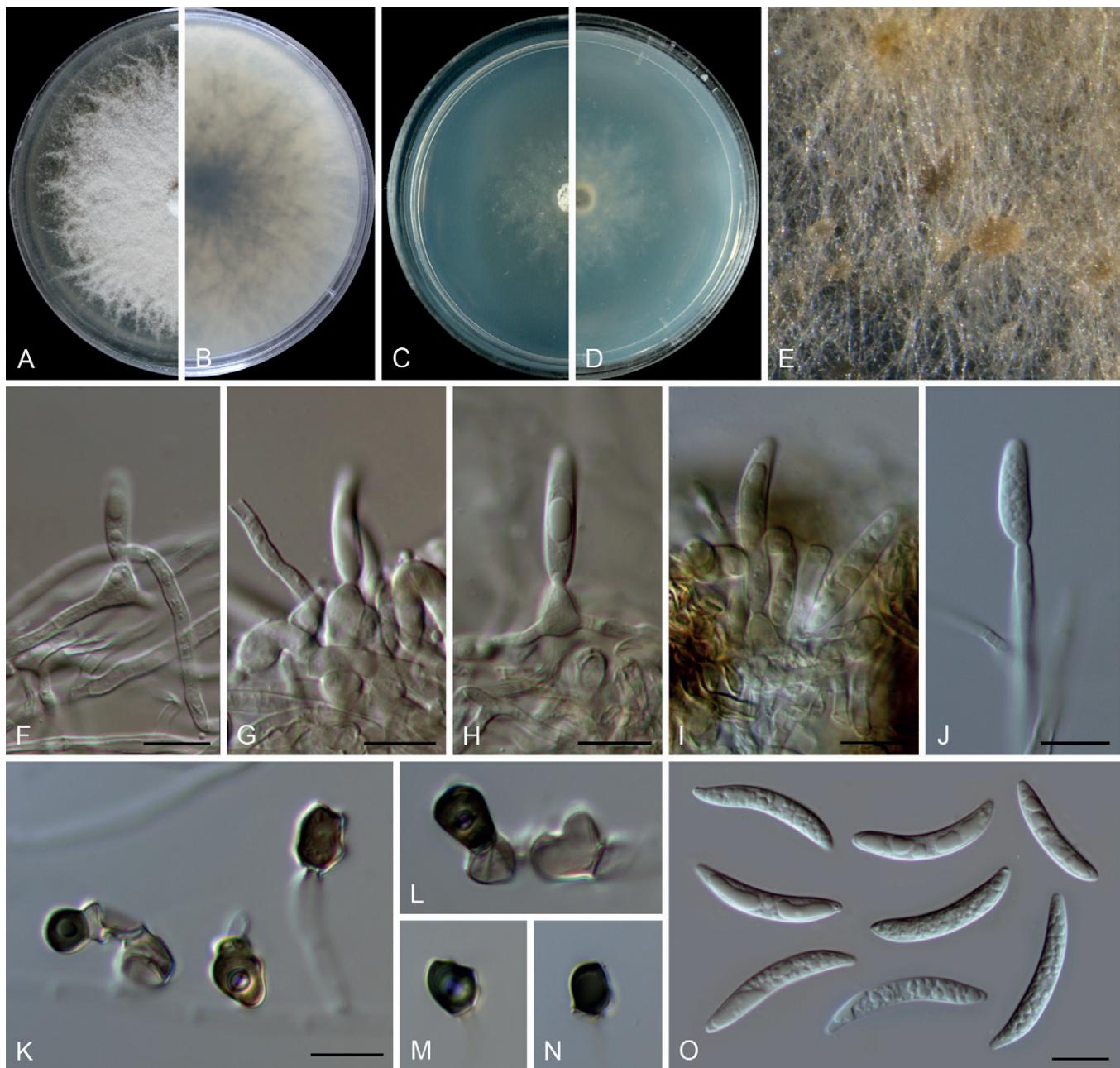


Fig. 12. *Colletotrichum danxiashanense* (ex-type culture NN055218). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidial masses on PDA. **F–J.** Conidiogenous cells and conidia. **K–N.** Appressoria. **O.** Conidia. Scale bars = 10 µm. Scale bar of K applies to K–N.

Description: Colonies on PDA 36–39 mm diam in 7 d, flat with undulate edge, pale glaucous grey, aerial mycelium sparse, surface partly covered with orange conidial masses, reverse white. Vegetative hyphae hyaline, smooth-walled, septate, branched. On SNA, conidiomata acervular, scattered or gregarious, conidiophores formed on a cushion of subglobose pale brown cells (type I, Fig. 14 D–F) or directly from vegetative hyphae (type II, Fig. 14 H–L). The first type of conidiophores hyaline, branched, up to 45 µm, sometimes reduced to conidiogenous cells; conidiogenous cells hyaline, ampulliform to obclavate, sometimes cylindrical, often extending to form new conidiogenous loci, 11.5–17.5(–22.5) × 3–5.5 µm (av. ± SD = 14.6 ± 2.4 × 4.3 ± 0.6 µm), periclinal thickening distinct. The second type of conidiophores hyaline, septate, branched, up to 80 µm; conidiogenous cells hyaline, smooth-walled, cylindrical or subcylindrical, sometimes irregularly inflated, variable in length, (7–)12–32 × 3–4.5 µm (av. ± SD = 20.9 ± 6.2 × 3.7 ± 0.6 µm), usually extending to form new conidiogenous loci, periclinal thickening distinct. Conidia hyaline, aseptate, smooth-

walled, guttulate, straight, cylindrical with one end round and one end slightly acute, 12–15.5 × 4.5–5.5 µm (av. ± SD = 14.1 ± 0.8 × 5.2 ± 0.3), L/W ratio = 2.7. Appressoria and setae not observed.

Typus: China, Yunnan Province, Honghe Hani and Yi Autonomous Prefecture, Mengzi county, Nanhu park, on *Pholidendron selloum*, 12 May 2016, Q. Chen (**holotype** HMAS 350633, ex-type culture CGMCC 3.20516 = LC11292 = CQ775).

Notes: *Colletotrichum diversum* is basal to the phylogenetic clade that comprises *C. boninense*, *C. cymbidiicola*, *C. doitungense*, *C. oncidii*, *C. torulosum* and *C. watphraense* in the *C. boninense* species complex (Fig. 1), and shares low sequence similarity with the most closely related species *C. oncidii* at *act* (97.9 %) and *gapdh* (96.9 %) and 99 % similarities at *his3*, *ITS* and *tub2*. Morphologically, the two species differ with respect to the formation of conidiophores and conidiogenous cells. On SNA, *C. diversum* forms conidiophores either on a cushion of subglobose pale

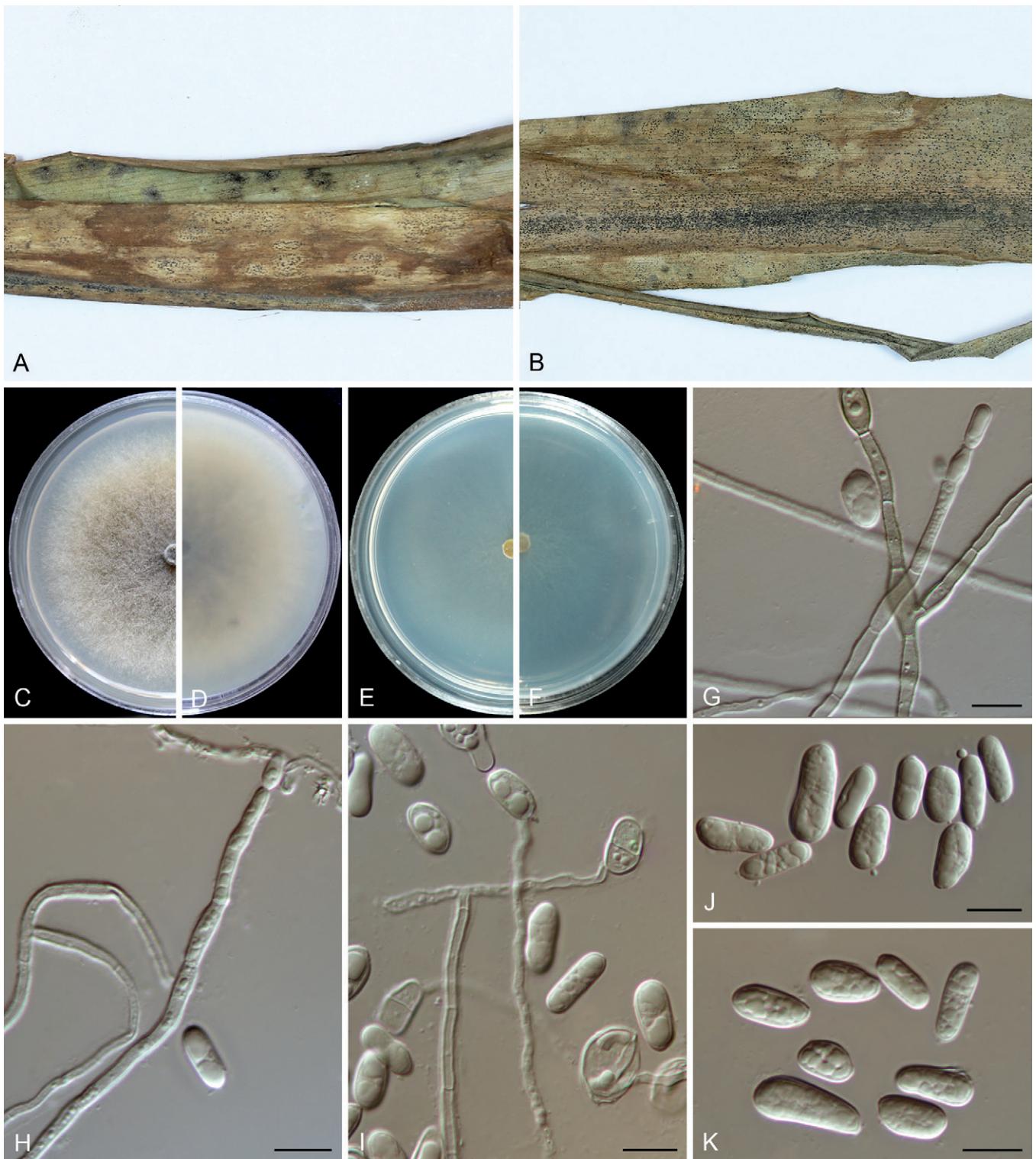


Fig. 13. *Colletotrichum diversisporum* (ex-type culture NN072578). **A, B.** Disease symptoms on host plant. **C, D.** Front and reverse colony on PDA (7 d). **E, F.** Front and reverse colony on SNA (7 d). **G, H.** Conidiophores, conidiogenous cells and conidia. **I.** Germinating conidium. **J, K.** Conidia. Scale bars = 10 µm.

brown cells or directly from vegetative hyphae, while *C. oncidi* only forms conidiophores directly from hyphae. In addition, *C. diversum* produces ampulliform to obclavate or (sub)-cylindrical conidiogenous cells, while only cylindrical cells have been observed for *C. oncidi* (Damm *et al.* 2012b).

To date, *Colletotrichum* species known to be associated with *Philodendron selloum* are *C. orchidearum* (Hou *et al.* 2016, Damm *et al.* 2019), and *C. philodendri* which lacks type-derived sequence data (Alfieri *et al.* 1984). Furthermore, *C. diversum* morphologically differs from *C. philodendri* with respect to the shape (cylindrical with obtuse ends vs. round at one end and acute at the other end) and width (4.5–

5.5 µm vs. 3.5–4 µm) of the conidia. Geographically, *C. philodendri* was reported in the Americas (Brazil and the US) (Hennings 1905, Alfieri *et al.* 1984), while, to date, *C. diversum* is only known in China.

Colletotrichum dolichoconidiophori* F. Liu, W.P. Wu & L. Cai, *sp. nov. MycoBank MB 841379. Fig. 15.

Etymology: Named to reflect the formation of long conidiophores. **Description:** Colonies on PDA 40–41 mm diam in 7 d, flat with fimbriate edge, pale grey in the centre, white toward the margin, aerial mycelium floccose, reverse fuscous black, white at margin.

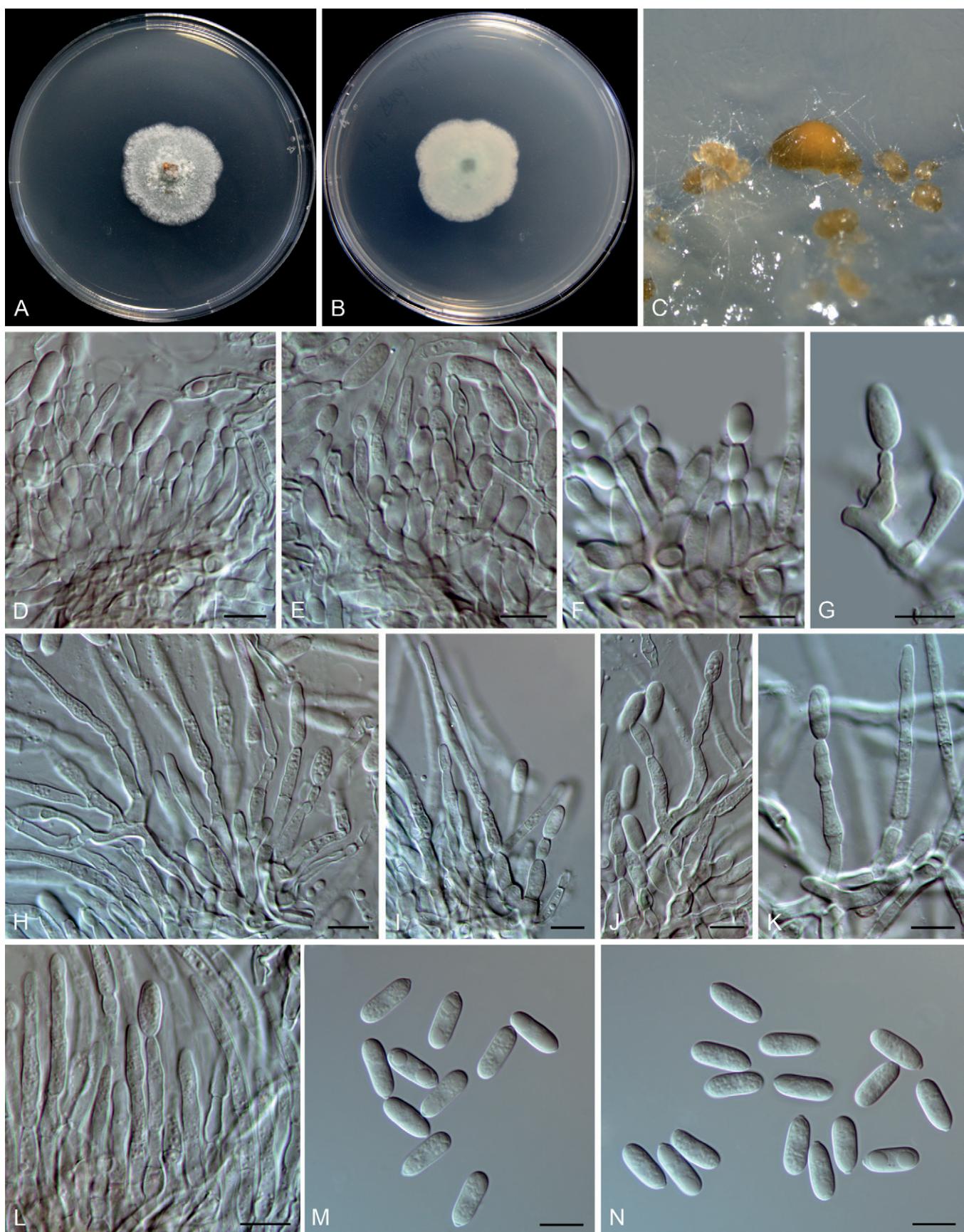


Fig. 14. *Colletotrichum diversum* (ex-type culture LC11292). **A, B.** Front and reverse colony on PDA (6 d). **C.** Conidiomata and conidial masses. **D–G.** Type I of conidiophores and conidia. **H–L.** Type II of conidiophores and conidia. **M, N.** Conidia. Scale bars = 10 μ m.

Vegetative hyphae hyaline to pale brown, smooth-walled, septate, branched. Conidiomata not developed. On PDA, conidiophores formed directly on hyphae, hyaline to very pale brown, smooth-walled, cylindrical, up to 250 μ m. Conidiogenous cells cylindrical to

subcylindrical, rarely ampulliform, hyaline, 6–23 \times 2–4 μ m. Setae abundant, brown, smooth- and thick-walled, 0–3-septate, 41–110 μ m long, basal cell cylindrical, inflated, flask shaped or globose, 3.5–8 μ m diam, tip \pm acute. Conidia hyaline, aseptate, smooth-

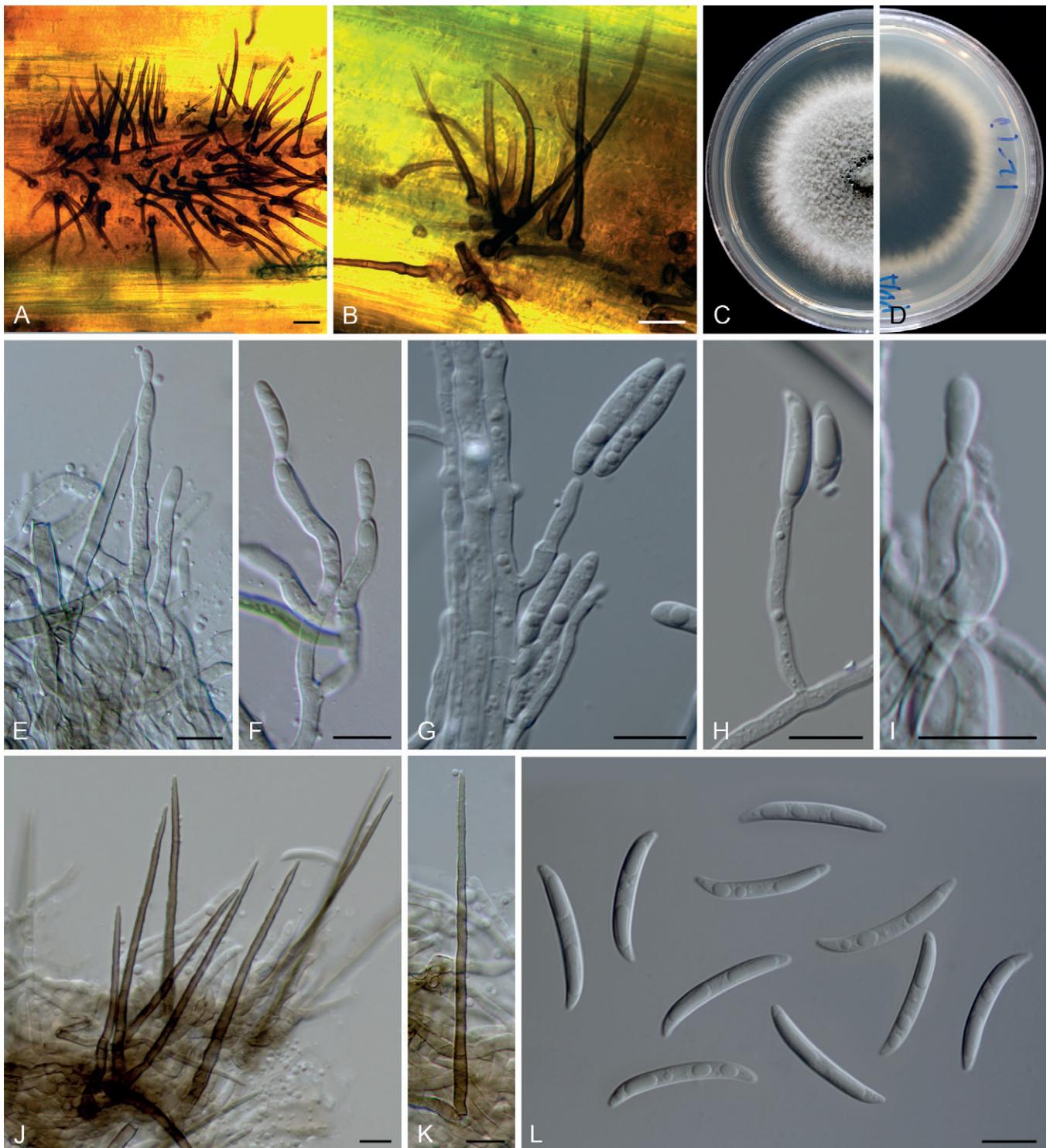


Fig. 15. *Colletotrichum dolichoconidiophori* (ex-type culture NN054966). **A, B.** Conidiomata with setae on the host plant. **C, D.** Front and reverse colony on PDA (7 d). **E–I.** Conidiophores, conidiogenous cells and conidia. **J, K.** Setae. **L.** Conidia. Scale bars: A, B = 20 µm; E–L = 10 µm.

walled, falcate, central part of the conidium almost straight with parallel walls, gradually tapering towards a slightly rounded to ± acute apex and a truncate base, with a similar radian, 19–27.5 × 2.5–3.5 µm (av. \pm SD \pm 24.9 \pm 1.92 \times 3.1 \pm 0.29 µm), L/W ratio = 8. *Appressoria* not observed.

Typus: **China**, Beijing, Huairou, Beigoucun, on an unidentified grass, 10 Sep. 2012, W.P. Wu (**holotype** HMAS 350654, ex-type culture CGMCC 3.20517 = LC13889 = NN054966).

Notes: *Colletotrichum dolichoconidiophori* belongs to the *C. graminicola* species complex (Fig. 1). It shares very low sequence similarity with all

currently accepted species in the genus, even with the most closely related species *C. cereale* CBS 129663 (Figs 1, 3, *act*: 90.7 %; *chs-1*: 96 %; *ITS*: 96.7 %; *sod2*: 91.8 %; *tub2*: 92.2 %). Morphologically, *C. dolichoconidiophori* differs from *C. cereale* in that it produces longer conidiogenous cells (6–23 × 2–4 µm vs. 2–6 × 1–2 µm).

Colletotrichum guangxiense C.L. Hou & Q.T. Wang, Mycologia 113: 454. 2021.

Notes: Intraspecific branches in the *C. guangxiense* clade suggest a high degree of genetic variation in this species, mainly within the *act* and *tub2* sequences examined in the current study.

Colletotrichum iris F. Liu & L. Cai, *sp. nov.* MycoBank MB 841383. Fig. 16.

Etymology: Named after the host plant genus, *Iris*.

Description: Colonies on PDA 33–34 mm diam in 7 d, flat, aerial mycelium dense, white, reverse pale luteous, centre part fuscous black, and with a fuscous black halo towards margin. On PDA, conidiomata scattered or confluent, dark brown to black, immersed. Setae not observed. Conidiophores hyaline to pale brown, branched, septate, up to 65 µm. Conidiogenous cells hyaline or pale brown, smooth-walled, cylindrical, occasionally ampulliform, straight or flexuous, 12.5–22.5 × 3–4.5 µm. Conidia hyaline, aseptate, smooth-walled, curved, apex ± acute, base usually broader and truncate, 18–28 × 2–4 µm (av. ± SD = 22 ± 2.6 × 3.4 ± 0.5 µm), L/W ratio = 6.5. Appressoria single or in small groups, medium brown, mostly irregular shaped, occasionally

ellipsoidal to subcircular, 5–16 × 3–10 µm (av. ± SD = 9.6 ± 2.6 × 6.7 ± 1.8 µm).

Typus: China, Jiangxi, Lushan Botanical Garden, on *Iris japonica*, 4 Sep. 2013, N. Zhou (**holotype** HMAS 350628, ex-type culture CGMCC 3.20518 = LC3697).

Notes: *Colletotrichum iris* is closely related to *C. liriopes* in the *C. spaethianum* species complex (Fig. 1), but differs genetically in 2 bp of the act nucleotide sequence, 1 bp of *chs-1*, 13 bp of *gapdh*, 12 bp of *his3*, 1 bp of ITS and 3 bp of *tub2*. Morphologically, *C. iris* differs from *C. liriopes* in that it produces thick-walled, pale brown conidiogenous cells and a higher conidium L/W ratio (6.5 vs. 5.0) (Damm *et al.* 2009). Like most other species in the *C. spaethianum* complex (Damm *et al.* 2009), *C. iris* was isolated from the petaloid monocotyledon plant, *Iris japonica*. Six other *Iris*-associated species in the genus are *C. circinans*, *C.*

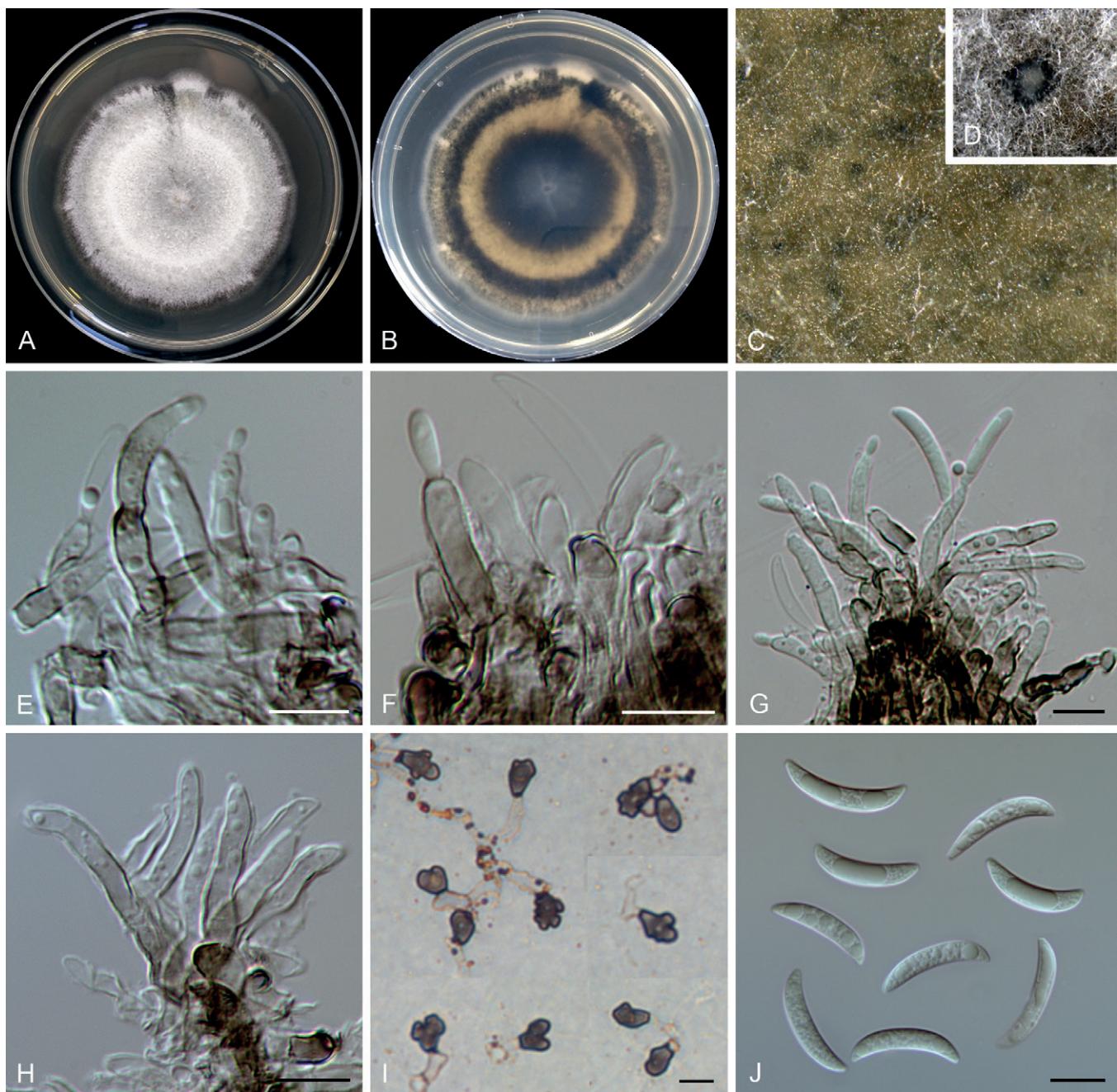


Fig. 16. *Colletotrichum iris* (ex-type culture LC3697). A, B. Front and reverse colony on PDA (7 d). C, D. Immersed conidiomata. E–H. Conidiophores, conidiogenous cells and conidia. I. Appressoria. J. Conidia. Scale bars = 10 µm.

coccodes, *C. dematum*, *C. gloeosporioides*, *C. siamense*, and *C. tofieldiae* (Farr & Rossman 2021), which are phylogenetically distinct from *C. iris*. Moreover, *C. iris* morphologically differs from another *Iris*-associated species *C. liliacearum* (DNA sequences are unavailable) in producing longer conidia ($18\text{--}28 \times 2\text{--}4 \mu\text{m}$ vs. $12\text{--}17 \times 2.5\text{--}3.5$) (Ferraris 1902).

Colletotrichum jasminigenum Wikee et al., Fungal Diversity 46: 174. 2011.

Notes: *Colletotrichum jasminigenum* was shown to be a member of the *C. truncatum* species complex (Hyde et al. 2014). However, BLASTn search of the NCBI GenBank using *gapdh* and *act* sequences of *C. jasminigenum* (ex-holotype MFLUCC 10-0273) yielded the closest matches with species of the *C. gloeosporioides* species complex, while using ITS and *tub2* sequences indicated that it belongs to the *C. truncatum* species complex. Therefore, it is likely that the sequences of MFLUCC 10-0273 provided in Wikee et al. (2011) were mixed up with those of other species or contained major sequencing errors. To clarify the taxonomic status of *C. jasminigenum*, type specimen and culture inquiries were submitted to the culture collections (CGMCC and MFLUCC) mentioned in the original publication (Wikee et al. 2011). Unfortunately, the ex-type could not be located in CGMCC. We suspected that it might not have been preserved in the culture collection, as the strain number was not mentioned in Wikee et al. (2011). Furthermore, specimen delivery from MFLUCC was not allowed because of the current quarantine measures for international mail. Therefore, the taxonomic status of *C. jasminigenum* requires further examination and re-sequencing of the type.

Colletotrichum jinshuiense M. Fu & G.P. Wang, Persoonia 42: 21. 2018.

Synonym: *Colletotrichum kakiivorum* H.Y. Jung & S.Y. Lee [as '*kakiivorum*'], Mycol. Prog. 17: 1118. 2018.

Typus: China, Hubei Province, Wuhan, on leaves of *Pyrus pyrifolia* cv. Jinshui, 1 Aug. 2016, M. Fu (holotype HMAS 247824, ex-type culture CGMCC 3.18903).

Additional material examined: China, Fujian Province, Fuzhou, Wuyi Mountain, on *Dioscorea zingiberensis*, Aug. 2016, L. Cai & Z.Y. Ma, living culture LC8509 (= M0333).

Notes: The ex-type strains of *C. jinshuiense* (Fu et al. 2019, published online 24 Jul. 2018) and *C. kakiivorum* (Lee & Jung 2018, published online: 30 Jul. 2018) cluster together in a well-supported clade within the *C. dematum* species complex (Fig. 1), and their *act*, *chs-1*, *gapdh*, *his3*, ITS, and *tub2* sequences share high similarity (99.8 %), with only two base-pair differences. Morphologically, *C. jinshuiense* and *C. kakiivorum* produce conidiogenous cells, conidia, and appressoria with essentially similar shapes and dimensions. Hence, *C. kakiivorum* is synonymised with the previously published *C. jinshuiense*.

Colletotrichum liriopes Damm et al., Fungal Diversity 39: 71. 2009. Fig. 17.

Typus: Mexico, APHIS interception Houston 057263, on *Liriope muscari*, 29 Nov. 2000, M.J. Segall (holotype CBS H-20364, ex-type culture CBS 119444).

Additional materials examined: China, Shan'xi, Xi An, Huqing Hot Spring, on dead leaves of *Osmanthus fragrans*, 1 Jul. 2015, W.P. Wu, living culture NN071073; Tibet, Bomi county, Suotong village, on Poaceae, 13 Jun. 2015, F. Liu, living culture LC7623; Yunnan Province, Honghe Hani and Yi Autonomous Prefecture, Mengzi county, DaTun Sea, on *Liriope spicata*, 12 May 2016, Q. Chen, living culture LC11287.

Notes: *Colletotrichum liriopes* is phylogenetically related to *C. iris* in the *C. spaethianum* species complex. This species is pathogenic to *Eria coronaria* (Yang et al. 2011), *Liriope muscari* (Damm et al. 2009), *L. spicata* (this study), and *Rohdea japonica* (Kwon & Kim 2013), endophytic in *Bletilla ochracea* and *Peione bulbocodioides* (Yang et al. 2011), and saprophytic on dead stalk of *Hemerocallis fulva* (Yang et al. 2011) and dead leaves of *Osmanthus fragrans* (this study).

Colletotrichum magnum (Jenkins & Winstead) Rossman & W.C. Allen, IMA Fungus 7: 4. 2016.

Basionym: *Glomerella magna* Jenkins & Winstead, Phytopathology 54: 453. 1964.

Synonym: *Colletotrichum liaoningense* Y.Z. Diao, et al., Persoonia 38: 34. 2017.

Typus: USA, on *Citrullus lanatus*, unknown collection date, R. Rodriguez, ex-epitype culture CBS 519.97.

Additional material examined: China, Liaoning Province, Xingcheng city, on chili fruits (*Capsicum annuum* var. *conoides*), Oct. 2012, Y.Z. Diao, ex-type culture of *C. liaoningense* CGMCC 3.17616 (= CAUOS2 = LC6228).

Notes: Since the sequence data and phylogenetic assessment of *C. liaoningense* are questionable (Damm et al. 2019), we re-sequenced six loci of its ex-type culture CAUOS2, twice, in the present study. Comparison with sequences deposited in the NCBI GenBank by Diao et al. (2017) revealed that the sequences of four loci were consistent except for 1–3 base-pair differences [99 % sequence similarity shared at *cal* (433/435), *chs-1* (294/297), *gapdh* (257/258), and *tub2* (679/680)]; however, the sequences of ITS and *act* differed at many positions [96 % similarity on ITS (478/500) and *act* (252/263)]. Therefore, the original sequences of CAUOS2 are incorrect, and the sequences newly generated in the current study have been deposited in GenBank (Table S1) and used for six-locus phylogenetic analyses (Fig. 1).

Colletotrichum liaoningense is phylogenetically indistinguishable from *C. magnum* (Fig. 1), and their *act*, *chs-1*, *his3*, ITS, and *tub2* sequences are 100 % identical, while the *gapdh* sequences are 96 % (250/260) identical. Consequently, *C. liaoningense* is synonymised with the older name *C. magnum*.

Colletotrichum metake Sacc., Annls Mycol. 6: 557. 1908.

Notes: *Colletotrichum metake* was originally described on a dead culm of bamboo (*Arundinaria japonica*) in Italy (Costa, Vittorio, Treviso) and characterised by oblong conidia ($22 \times 5.5\text{--}6 \mu\text{m}$) (Saccardo 1908), but without type designation. In the current study, four bamboo-associated strains of *C. metake* (Sato et al. 2012, Wang et al. 2021) clustered in a well-supported clade (Fig. 1). Three of these strains were from *Pleioblastus simonii* in Japan and one from *Chimonobambusa quadrangularis* in China. However, none of these strains is suitable for type designation because of the inconsistency with the original collection site and host of the species (Hyde & Zhang 2008).

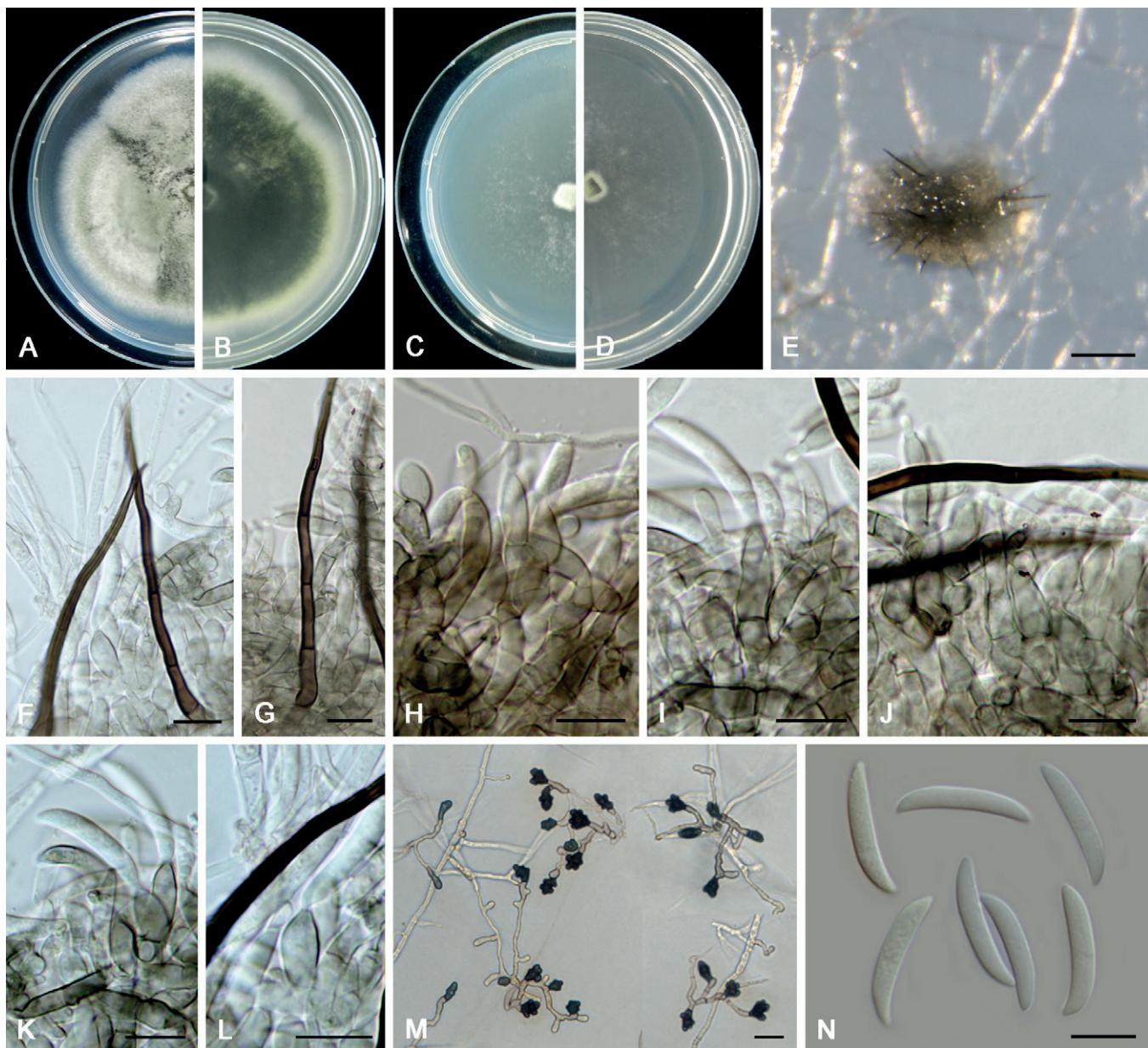


Fig. 17. *Colletotrichum liriores* (LC11287). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidioma. **F, G.** Setae. **H–L.** Conidiophores, conidiogenous cells and conidia. **M.** Appressoria. **N.** Conidia. Scale bars: E = 80 µm; F–N = 10 µm.

***Colletotrichum monsterae* F. Liu, W.P. Wu & L. Cai, sp. nov.**
Mycobank MB 841384. Fig. 18.

Etymology: Named after the host plant genus, *Monstera*.

Description: Colonies on PDA 52 mm diam in 7 d, flat with entire edge, aerial mycelium white and floccose, reverse saffron. Vegetative hyphae hyaline to pale brown, smooth-walled, septate, branched. Conidiomata black, submerged, conidial masses buff, abundantly formed on the surface of the agar medium or directly on hyphae. Setae not observed. Conidiophores brown, base dark brown, mostly gradually becoming paler towards the tip, 1–3-septate, solitary or branched at the bottom, 46–102 µm long. Conidiogenous cells pale to medium brown, smooth-walled, cylindrical, 15–51.5 × 3.5–6 µm (av. ± SD ± 33 ± 11.1 × 4.7 ± 0.8). Conidia hyaline, aseptate, smooth-walled, guttulate, cylindrical to subcylindrical, rarely ovoid, straight, sometimes slightly curved, with obtuse ends or gradually tapering towards the base, on SNA 13–22.5 × 4.5–6 µm (av. ± SD ± 18.2 ± 2.1 × 5 ± 0.4), L/W ratio

= 3.6, on PDA 16.5–24.5 × 3.5–5 (av. ± SD ± 20.6 ± 1.9 × 4.4 ± 0.3), L/W ratio = 4.7. Appressoria single, medium to dark brown, mostly irregularly shaped, rarely cylindrical, with undulate to lobate margins, 8.5–19 × 4.5–11.5 µm.

Typus: China, Guangdong Province, Guangzhou, Zhaoqing, Seven Star Cave (Qixingyan), on diseased leaf of *Monstera deliciosa*, 24 Dec. 2012, W.P. Wu (**holotype** HMAS 350640, ex-type culture CGMCC 3.20519 = LC13871 = NN055214).

Notes: Although represented by a single strain, *C. monsterae* is phylogenetically distinct from all currently accepted species of *Colletotrichum* at each locus sequenced in the current study and is basal to other species in the *C. orchidearum* species complex (Fig. 1). Morphologically it is different from most species in the genus, including the closest related species, *C. piperis*, and the two other *Monstera deliciosa*-associated species, *C. gloeosporioides* (French 1989) and *C. orchidearum* (Damm et al. 2019), by producing long brown conidiophores reminiscent of setae.

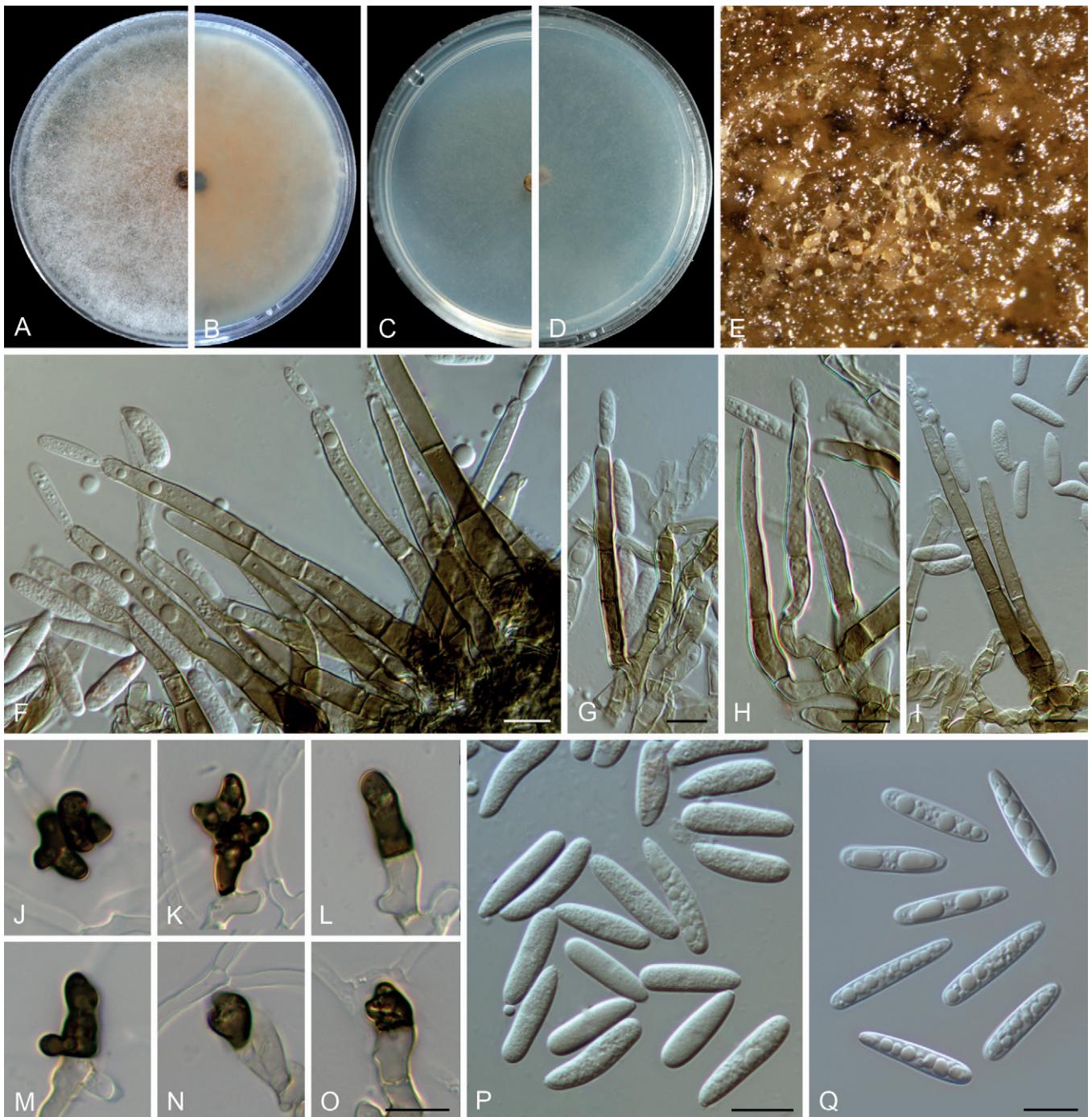


Fig. 18. *Colletotrichum monsterae* (ex-type culture NN055214). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidiomata (black, submerged) and conidial masses (buff, superficial). **F–I.** Conidiophores bearing conidia. **J–O.** Appressoria. **P.** Conidia formed on SNA. **Q.** Conidia formed on PDA. Scale bars = 10 µm.

Colletotrichum multisepatum* F. Liu, W.P. Wu & L. Cai, *sp. nov.
Mycobank MB 841385. Fig. 19.

Etymology: Named to reflect the multiple septa of its seta.

Description: Colonies on PDA 49 mm diam in 7 d, flat with entire edge, saffron to peach, aerial mycelium unconsolidated, reverse peach to umber. Vegetative hyphae hyaline to pale brown, smooth-walled, septate, branched. Conidiomata not developed, abundant conidial masses formed on the surface of medium, salmon, brown to black, solitary or gregarious. Setae medium brown to dark brown, smooth-walled, 50–62 µm long, 2–4-septate, base cylindrical, sometimes slightly inflated, 4.5–6 µm diam, tip ± acute or rounded. Conidiophores formed

directly from hyphae, hyaline to pale brown, 1–3-septate, usually branched at the bottom and reduced to conidiogenous cells. Conidiogenous cells hyaline or pale brown, smooth-walled, ampulliform, bullet-shaped, or subcylindrical, variable in length, 8.5–21.5 × 3–5.5 µm (av. ± SD = 13.1 ± 3 × 4 ± 0.5 µm), collarette observed. Conidia hyaline, aseptate, smooth-walled, guttulate, curved, or slightly curved, gradually tapering towards the round apex and truncate base, sometimes less curved towards the base, on PDA 16.5–26 × 3–4.5 µm (av. ± SD = 19.8 ± 2.3 × 3.7 ± 0.3 µm), L/W ratio = 5.4, on SNA 20–25.5 × 3.5–4.5 µm (av. ± SD = 21.8 ± 1.5 × 3.9 ± 0.2 µm), L/W ratio = 5.6. Only one appressorium observed, irregular shaped, dark brown, 10 × 5.5 µm.

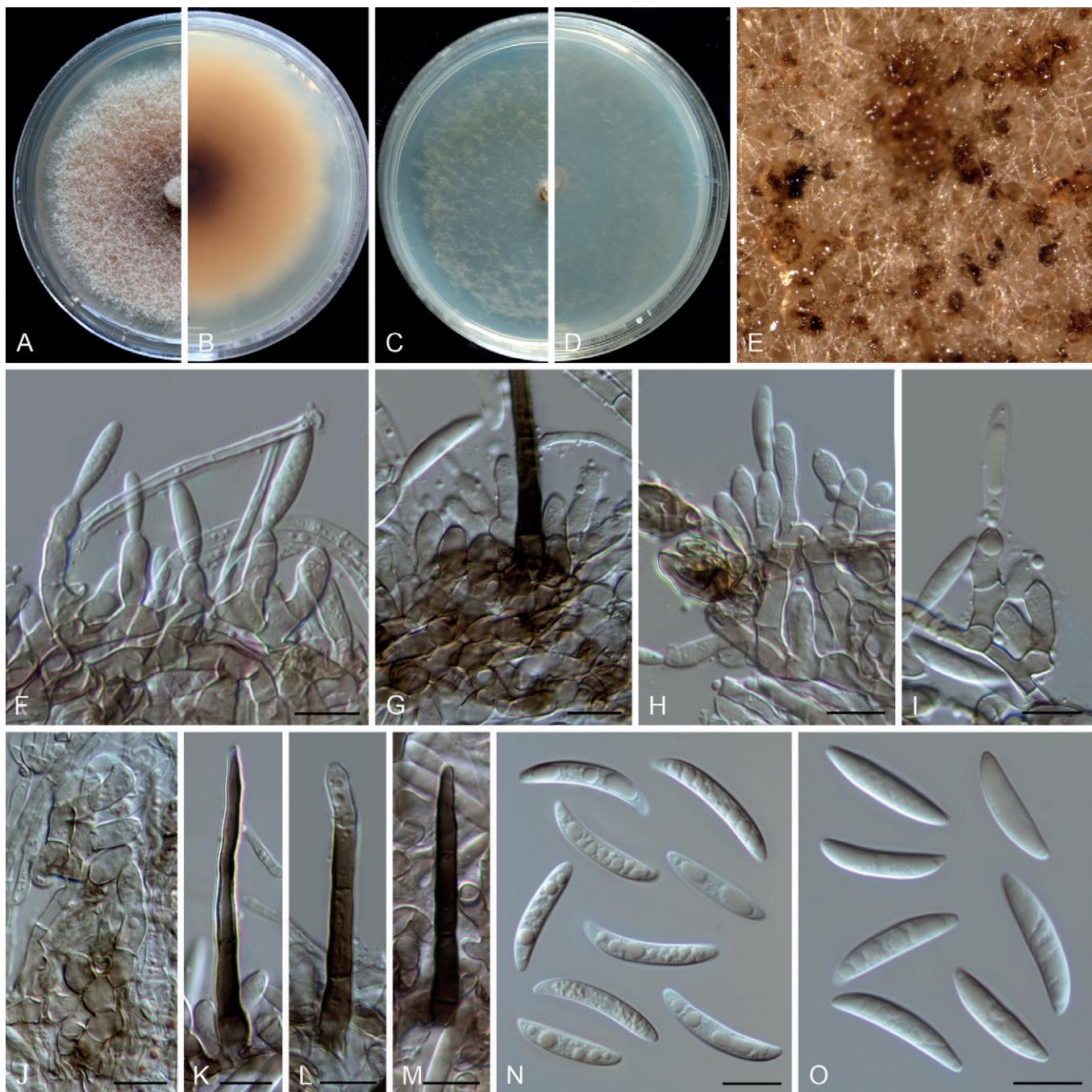


Fig. 19. *Colletotrichum multiseptatum* (ex-type culture NN055357). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidial masses on PDA. **F–I.** Conidiophores, conidiogenous cells and conidia on PDA. **J.** Conidiogenous cells on SNA. **K–M.** Setae on PDA. **N.** Conidia on SNA. **O.** Conidia on PDA. Scale bars = 10 µm.

Typus: China, Guangdong Province, Shaoguan, Danxia Mountain, on dead culm of an unidentified grass, 25 Dec. 2012, W.P. Wu (**holotype** HMAS 350651, ex-type culture CGMCC 3.20520 = LC13886 = NN055357).

Notes: *Colletotrichum multiseptatum*, belonging to the *C. graminicola* species complex, is phylogenetically related to *C. echinochloae* (Fig. 3), but shares low sequence similarity at *sod2* (97 %) and even lower whole-genome sequence similarity (95 %) with that species. Morphologically, *C. multiseptatum* differs from *C. echinochloae* in that it produces shorter setae [50–62 µm vs. 79.8–145.5(–186.3) µm] and exhibits a higher L/W ratio of the conidia (5.4–5.6 vs. 3.5–5) (Moriwaki & Tsukiboshi 2009). Furthermore, the conidia of *C. echinochloae* are more curved and both ends are more acute than those of *C. multiseptatum*.

***Colletotrichum nageiae* F. Liu, W.P. Wu & L. Cai, sp. nov.**
MycoBank MB 841386. Fig. 20.

Etymology: Named after the host plant genus, *Nageia*.

Description: Colonies on PDA growing slowly, reaching 32 mm diam after 7 d, flat with entire edge, white, aerial mycelium sparse, reverse pale buff. On SNA, vegetative hyphae hyaline to brown, smooth-walled, septate, branched, 1.5–2 µm diam. Conidiomata dark brown to black, beneath the media. Setae pale brown to brown, straight to flexuous, smooth-walled, 2–3-septate, 57–62 µm long, basal cells cylindrical, 3.5–4.5 µm diam, the tip rounded. Conidiophores septate, branched, conidiogenous cells hyaline to pale brown, cylindrical, smooth-walled, straight, 10–20 × 2.5–4.5 µm. Conidia hyaline, aseptate, smooth-walled, cylindrical, straight,

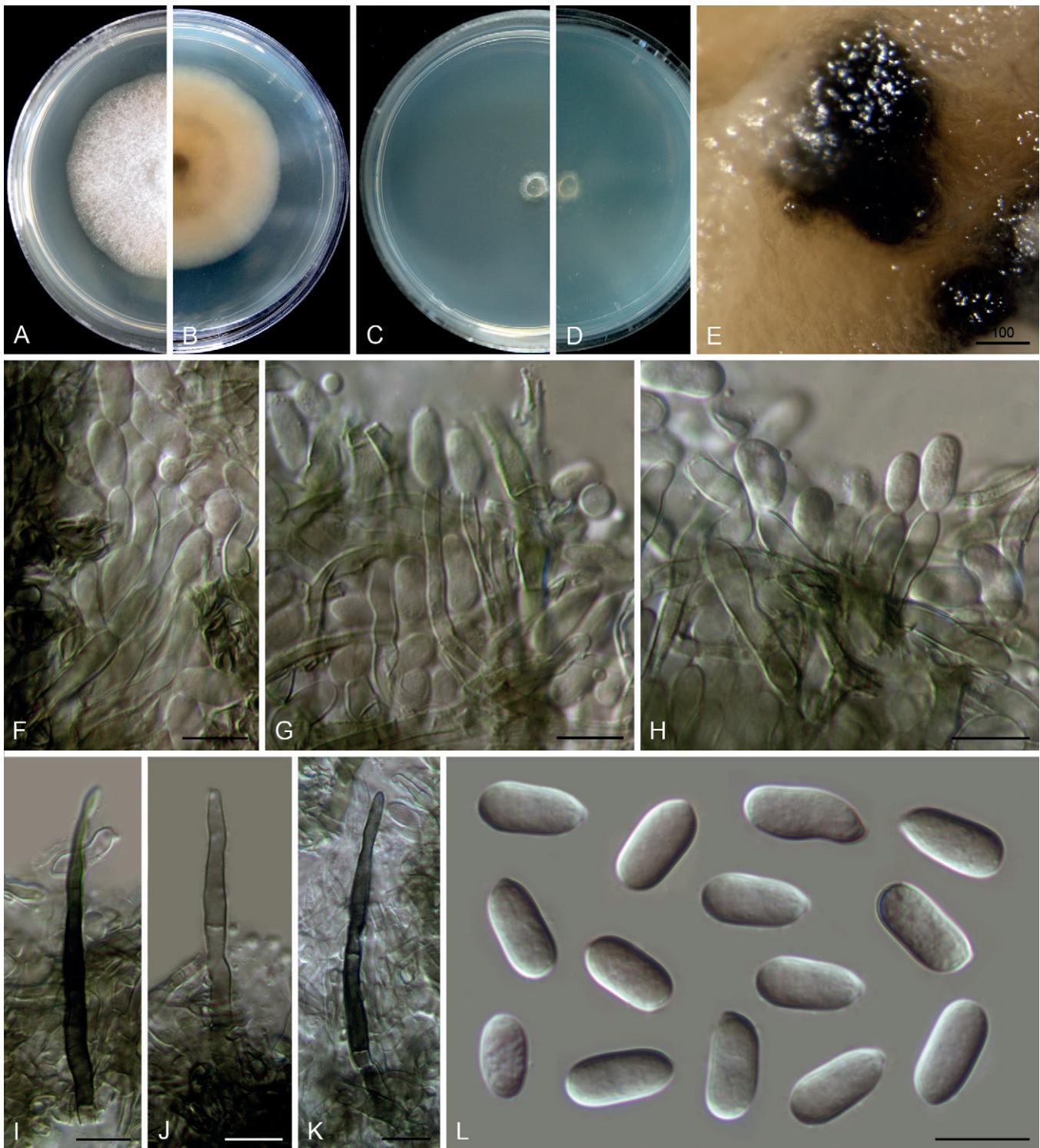


Fig. 20. *Colletotrichum nageiae* (ex-type culture NN004492). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidioma. **F–H.** Conidiogenous cells and conidia. **I–K.** Setae. **L.** Conidia. Scale bars: E = 100 µm; F–L = 10 µm.

9–13.5 × 4.5–6 µm (av. \pm SD = 11.5 \pm 0.9 × 5.3 \pm 0.4 µm), L/W ratio = 2.2, the apex obtuse, the bottom gradually narrowed with a prominent truncate scar. Appressoria not observed.

Typus: China, Yunnan Province, Kunming, Kunming Botanical Garden, on healthy leaves of *Nageia nagi*, 20 Dec. 1993, W.P. Wu (**holotype** HMAS 350638, ex-type culture CGMCC 3.20521 = LC13866 = NN004492).

Notes: Although the conidial morphology of *C. nageiae* resembles that of species in the *C. boninense* species complex, it is a singleton species that clusters basal to *C. gloeosporioides* species complex and

is phylogenetically distinct from all currently accepted *Colletotrichum* species (Fig. 1). Furthermore, BLASTn search revealed very low sequence similarity with the sequences of other species deposited in the NCBI GenBank, based on the comparisons of *act* (up to 86 % identity shared with species in the *C. gloeosporioides* and *C. gigasporum* species complexes), *cal* (up to 80 % identity shared with species in the *C. gloeosporioides* and *C. gigasporum* species complexes), *chs-1* (up to 93 % identity shared with species in the *C. boninense* species complex), *gapdh* (up to 87 % identity shared with species in the *C. boninense* species complex), *gs* (up to 78 % identity shared with species in the *C. boninense* species complex), *his3* (up

to 91 % identity shared with species in the *C. gloeosporioides* and *C. gigasporum* species complexes), and *tub2* (up to 83 % identity shared with species in the *C. boninense* species complex).

Colletotrichum obovooides F. Liu & L. Cai, **sp. nov.** MycoBank MB 841387. Fig. 21.

Etymology: Named to reflect the obovoid shape of conidia.

Description: Colonies on PDA 28–33 mm diam in 7 d, flat with fimbriate edge, white, abundant pale luteous and confluent conidial masses formed on the surface of medium, reverse white, or buff because of the production of conidial masses. Vegetative hyphae hyaline, smooth-walled, septate, branched. On SNA, conidiomata acervular, superficial or semi-immersed, black, protruding with white or buff conidial masses. Setae not observed. Conidiophores hyaline, septate, branched, formed directly from hyphae or on a cushion of pale brown cells, up to 70 µm. Conidiogenous cells hyaline, smooth-walled, cylindrical, rarely ampulliform, 5–24 × 2.5–4 µm. Conidia hyaline, aseptate, smooth-walled, obovoid, sometimes clavate, 10.5–15.5 × 5.5–7.5 µm (av. ± SD ± 12.7 ± 1.1 × 6.5 ± 0.4), L/W ratio = 1.9. Appressoria solitary, brown to dark brown, aseptate, smooth-walled, subglobose, bullet-shaped, clavate, or navicular, 7.5–13 × 4.5–9.5 µm (av. ± SD = 10.2 ± 1.7 × 6.2 ± 1.2 µm).

Typus: **China**, Tibet, Bomi county, Suotong village, on leaf of an unidentified plant, 13 Jun. 2015, Q. Chen, ST10 (**holotype** HMAS 350629, ex-type culture CGMCC 3.20522 = LC6085 = JJR053).

Notes: *Colletotrichum obovooides* is a singleton species, not belonging to any species complex (Fig. 1), and differs genetically from the most closely related species *C. rusci* in 24 bp of the *act* nucleotide sequence, 18 bp of *chs-1*, 41 bp of *his3*, 40 bp of ITS, and 53 bp of *tub2*. Morphologically, *C. obovooides* distinctly differs from the two phylogenetically related species, *C. trichellum* (conidia fusoid, straight or slightly curved, 15–28 × 3–5 µm, Duke 1928) and *C. rusci* (conidia subfusoid or cymbiform, curved, 16–23 × 4–5 µm, Damm *et al.* 2009), in that it produces obovoid or clavate, and smaller conidia (10.5–15.5 × 5.5–7.5 µm).

Colletotrichum orchidis Jayaward. *et al.*, Mycosphere 11: 595. 2020.

Notes: Phylogenetically, *C. orchidis* belongs to the *C. dematium* species complex (Fig. 1). However, BLASTn search of the NCBI GenBank using sequences of different loci of *C. orchidis* yielded controversial results. The closest matches identified by BLASTn search using *gapdh*, *chs-1*, *act*, and *tub2* sequences of the ex-type MFLUCC 17-1302 (Jayawardena *et al.* 2020) are species that belong to the *C. dematium* species complex. However, based on the ITS sequence similarity, the closest matches are *C. panacicola*, *C. destructivum*, and *C. utrechtense*, which belong to the *C. destructivum* species complex, and *C. trifolii*, which belongs to the *C. orbiculare* species complex. This inconsistency might explain the unusually long branch of *C. orchidis* in the six-locus tree (Fig. 1), and requires re-examination of the ex-type.

Colletotrichum parabambusicola F. Liu, W.P. Wu & L. Cai, **sp. nov.** MycoBank MB 841388. Fig. 22.

Etymology: Named after its close phylogenetic relationship with *C. bambusicola*.

Description: Colonies on PDA 48–52 mm diam in 7 d, flat with crenate edge, pale grey to mouse grey, aerial mycelium dense and floccose, reverse saffron. Sexual morph formed on PDA. Ascomata medium to dark brown, outer wall composed of dark brown angular or rarely subglobose cells. Interascal tissue composed of paraphyses, thin-walled, hyaline, septate, 1–3 µm diam. Ascii cylindrical, hyaline, 47–55 × 6.5–7.5 µm, 8-spored. Ascospores arranged uniserately or irregularly, hyaline, smooth-walled, aseptate, allantoid or cylindrical to ellipsoidal, 10–14.5 × 3–5.5 µm, (av. ± SD = 12 ± 1.1 × 4 ± 0.6 µm), L/W ratio = 3. Conidiomata subimmersed, globose, black, solitary or gregarious, conidial masses buff. Setae not observed. Conidiophores formed directly on hyphae, hyaline, septate, branched, 21–48 µm long. Conidiogenous cells hyaline, smooth-walled, ampulliform, subcylindrical, 8–21.5 × 3–5 µm (av. ± SD = 12.9 ± 3.5 × 3.8 ± 0.5 µm). Conidia hyaline, aseptate, smooth-walled, guttulate, variable in shape, ellipsoidal, cylindrical, ovoid, ossiform, obclavate, with obtuse ends, 9.5–20.5 × 4–8 (av. ± SD ± 13.9 ± 2.7 × 5.3 ± 1), L/W ratio = 2.6. Appressoria single, brown, subcircular, globose to subglobose, clavate, pyriform, 6.5–15 × 4.5–6.5 µm.

Typus: **China**, Shanghai Botanical Garden, on dead culm of bamboo, 22 May 2015, W.P. Wu (**holotype** HMAS 350649, ex-type culture CGMCC 3.20523 = NN058956 = LC13884).

Additional material examined: **China**, Shanghai Botanical Garden, on dead culm of bamboo, 22 May 2015, W.P. Wu, living culture LC13883 (= NN058925).

Notes: *Colletotrichum parabambusicola* shares low sequence similarity with the phylogenetically related species *C. bambusicola* at *act* (97.7 %), *gapdh* (92.1 %), *his3* (94.2 %), ITS (99.8 %), and *tub2* (97.3 %). Morphologically, it differs from *C. bambusicola* in producing smaller ascii (47–55 × 6.5–7.5 µm vs. 58–72 × 7–10 µm) and ascospores (10–14.5 × 3–5.5 µm vs. 14–19 × 4–6 µm) and exhibiting a lower conidium L/W ratio (2.6 vs. 3.2).

Colletotrichum paraendophytum F. Liu, W.P. Wu & L. Cai, **sp. nov.** MycoBank MB 841389. Fig. 23.

Etymology: Named to reflect its close phylogenetic relationship with *C. endophytum*.

Description: Colonies on PDA 52 mm diam in 7 d, flat with entire edge, mouse grey, aerial mycelium fluffy, reverse fuscous black with a white margin. Vegetative hyphae hyaline to pale brown, smooth-walled, septate, branched. On SNA, conidiomata scattered, semi-immersed. Setae dark brown, smooth-walled, 1–2-septate, 38–160 µm long, basal cell cylindrical, sometimes paler than the other cells, 3–6 µm diam, tip acute or round. Conidiophores either septate, branched, formed from a cushion of roundish brown cells, or reduced to conidiogenous cells. Conidiogenous cells hyaline to pale brown, smooth-walled, cylindrical to ampulliform, straight, 9.5–15 × 3–5 µm, periclinal thickening distinct, sometimes extending to form a new conidiogenous locus. Conidia hyaline, aseptate, guttulate, smooth-walled, slightly curved, gradually tapering towards a rounded apex and a usually truncate base, with a similar radian, 18.5–23 × 3–4.5 (av. ± SD = 21 ± 0.9 × 3.8 ± 0.3 µm), L/W ratio = 5.5. Appressoria not observed.

Typus: **China**, Beijing, Huairou, Beigoucun, on an unidentified grass, 10 Sep. 2012, W.P. Wu (**holotype** HMAS 350653, ex-type culture CGMCC 3.20524 = LC13888 = NN054963).

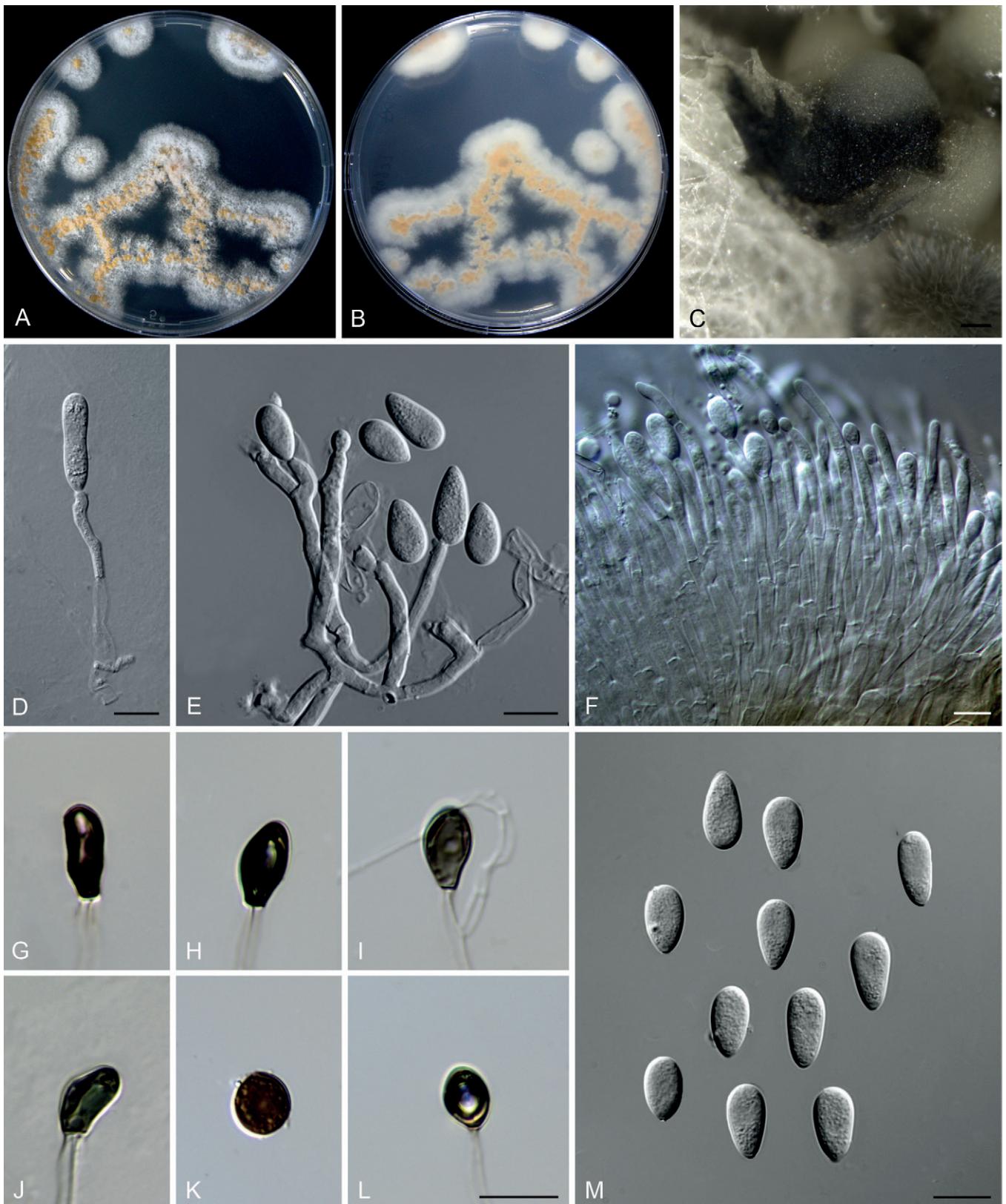


Fig. 21. *Colletotrichum obovoides* (ex-type culture LC6085). **A, B.** Front and reverse colony on PDA (6 d). **C.** Conidioma. **D–F.** Conidiophores, conidiogenous cells and conidia. **G–L.** Appressoria. **M.** Conidia. Scale bars: C = 100 µm; D, E, L, M = 10 µm; F = 20 µm. Scale bar of L applies to G–L.

Notes: *Colletotrichum paraendophytum* is phylogenetically closely related to *C. endophytum* in the *C. graminicola* species complex (Figs 1, 3), but differs in that it produces differently shaped conidia (slightly curved vs. pronouncedly curved) and with a different conidium L/W ratio (5.5 vs. 4.8). In addition, *C. paraendophytum* produces semi-immersed brown conidiomata, which are absent

in *C. endophytum* (Tao et al. 2013). Furthermore, the two species share low sequence similarity at *act* (95.2 %), *chs-1* (98.2 %), *ITS* (97.9 %), *sod2* (92.8 %), and *tub2* (92.1 %).

Colletotrichum plurivorum Damm et al., Stud. Mycol. 92: 31. 2018. Fig. 24.

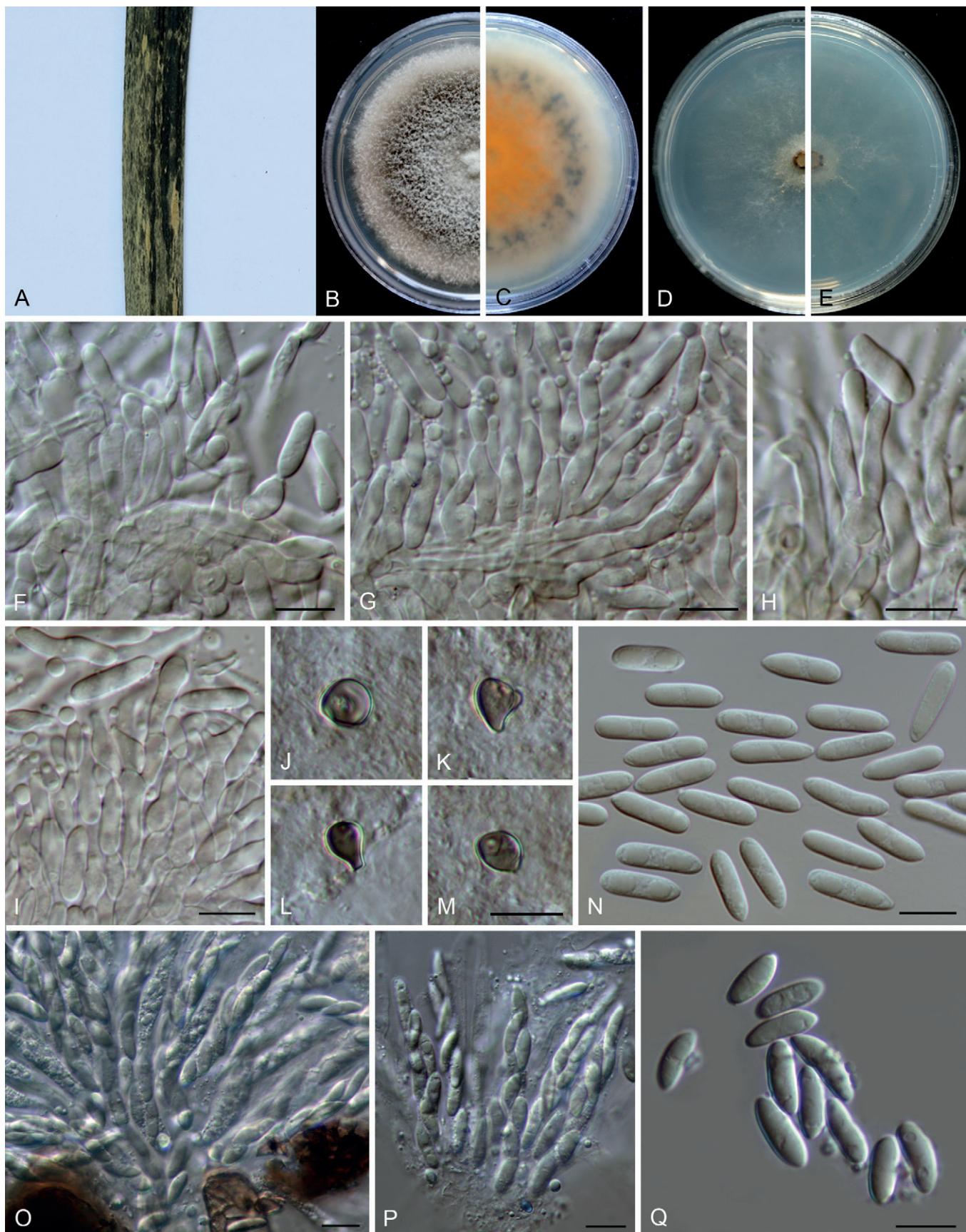


Fig. 22. *Colletotrichum parabambusicola* (ex-type culture NN058956). **A.** Disease symptom on host plant. **B, C.** Front and reverse colony on PDA (7 d). **D, E.** Front and reverse colony on SNA (7 d). **F–I.** Conidiophores, conidiogenous cells and conidia. **J–M.** Appressoria. **N.** Conidia. **O, P.** Asci. **Q.** Ascospores. Scale bars: F–I, M–Q = 10 µm. Scale bar of M applies to J–M.

Description: Colonies on PDA 35–51 mm diam in 7 d, flat with undulate edge. Vegetative hyphae hyaline to medium brown, smooth-walled, septate, branched. On PDA, ascomata globose, subglobose or with an irregular shape, solitary or gregarious, black, 130–300 µm diam,

formed on the surface of the medium and usually covered by aerial mycelium, ostiolate, outer wall composed of greenish grey angular cells, 2–6 µm diam. Interascal tissue composed of thin-walled, hyaline, septate paraphyses. Asci cylindrical, obclavate to clavate,

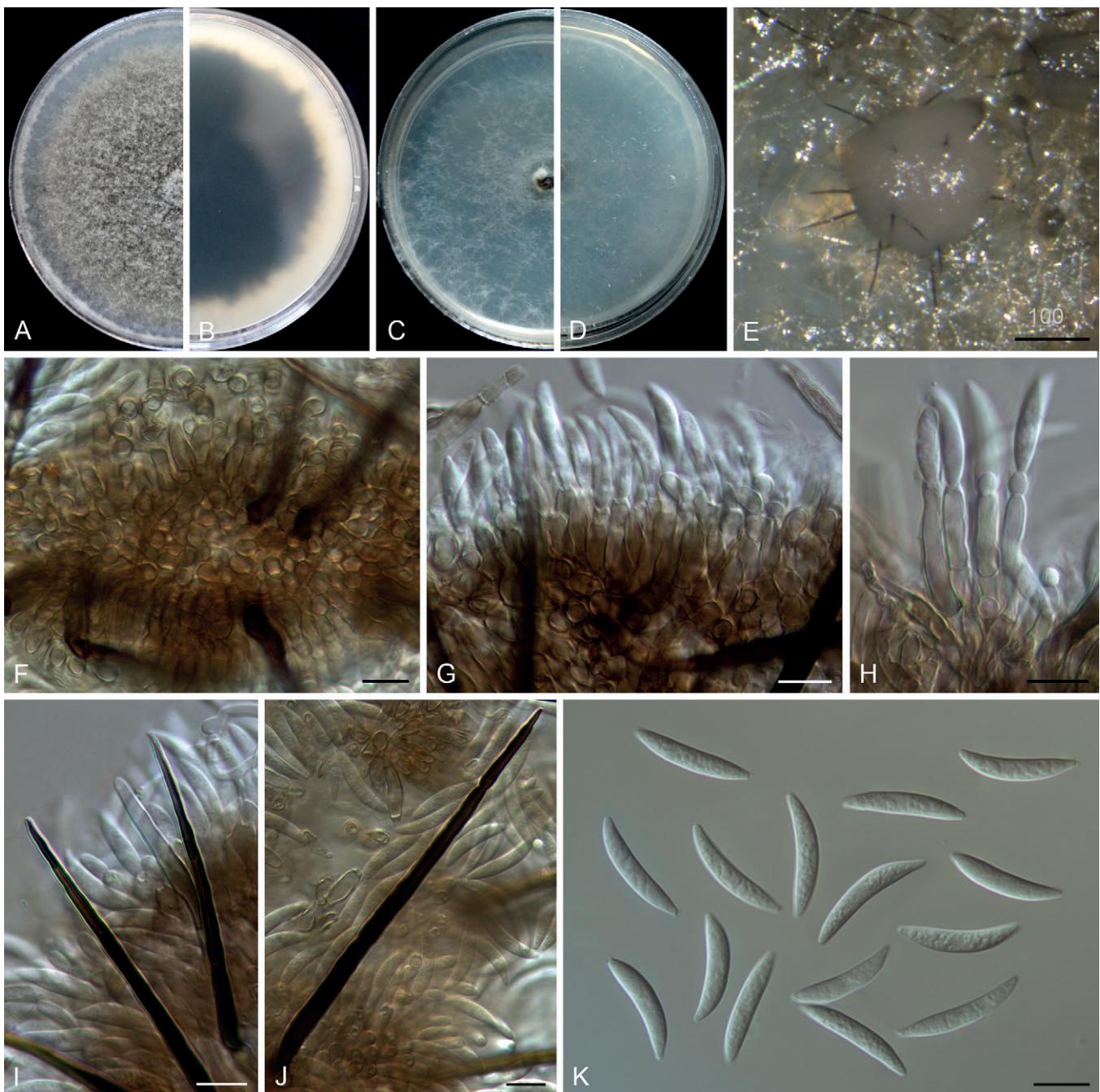


Fig. 23. *Colletotrichum paraendophytum* (ex-type culture NN054963). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidial mass with setae. **F–H.** Conidiophores, conidiogenous cells and conidia. **I, J.** Setae. **K.** Conidia. Scale bars: F–K = 10 µm.

33–54.5 × 7.5–13 µm, 8-spored. Ascospores hyaline, smooth-walled, aseptate, fusoid, clavate, with rounded ends, straight or slightly curved, 15–22.5(–25.5) × 4.5–6 µm, (av. ± SD = 18.5 ± 2.7 × 5.3 ± 0.5 µm), L/W ratio = 3.5. Conidiomata acervular, solitary or confluent, superficial or semi-immersed, protruding pale luteous conidial masses. Setae pale brown to dark brown, usually smooth-walled at the base and verruculose at the top, 1–3-septate, 54–82 µm long, basal cells cylindrical, 3.5–6 µm diam, the tip ± acute. Conidiophores solitary or branched, septate, usually reduced to conidiogenous cells. Conidiogenous cells hyaline, cylindrical, ovoid to obclavate, smooth-walled, 11–31 × 2.5–5 µm. Conidia hyaline, aseptate, smooth-walled, guttulate, cylindrical with obtuse ends, straight, 9–13.5 × 4.5–5.5 µm (av. ± SD = 11.3 ± 1.1 × 5 ± 0.3 µm), L/W ratio = 2.3. Appressoria not observed.

Typus: Vietnam, Da Lat-Lam Dong, from anthracnose on leaf of *Coffea*

sp., collection date unknown, P. Nguyen & E. Liljeroth (**holotype** CBS H-21496, ex-type culture CBS 125474).

Additional materials examined: China, Fujian, Fuzhou, Wuyi Mountain, on *Paederia foetida*, Aug. 2016, Z.Y. Ma & L. Cai, WYS8, living cultures LC8240 (= M51), LC8244 (= M55), LC8322 (= M136); on *Vigna unguiculata*, Aug. 2016, Z.Y. Ma & L. Cai, FJWYS01, living culture LC8337 (= M151).

Notes: *Colletotrichum plurivorum* exhibits a large host range and high degree of genetic variation (Damm *et al.* 2019). This is the first report of *C. plurivorum* on *Paederia foetida* and *Vigna unguiculata*.

Colletotrichum quinquefoliae Jayaward. *et al.*, Fungal Diversity 78: 83. 2016.

Notes: *Colletotrichum quinquefoliae* was described as a distinct species in the *C. dematium* species complex (Li *et al.* 2016) and

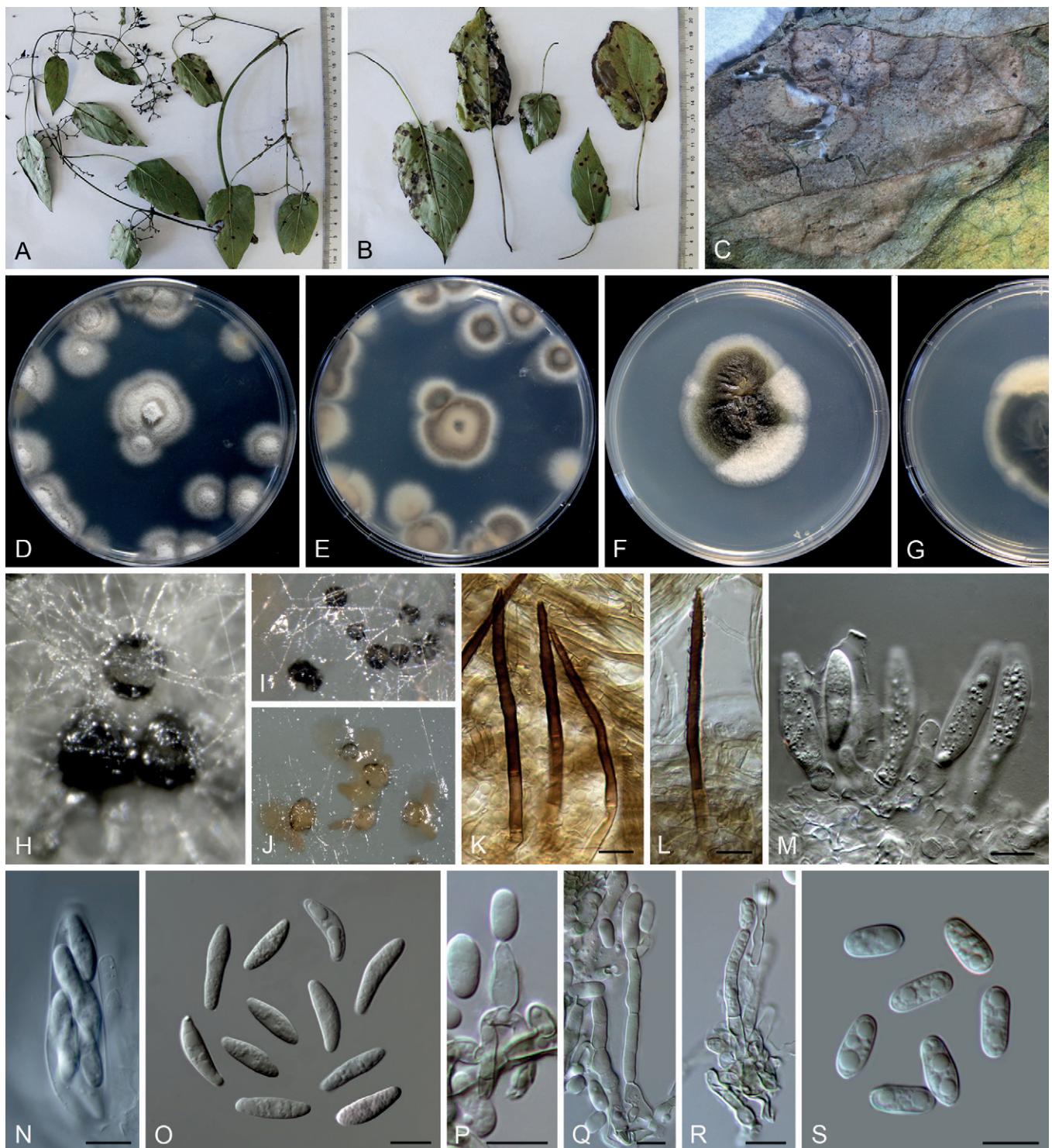


Fig. 24. *Colletotrichum plurivorum* (D–E, H–J. LC8337; F–G, K–S. LC8240). **A, B.** Disease symptoms on *Paederia foetida*. **C.** Disease symptom on *Vigna unguiculata*. **D–G.** Front and reverse colonies on PDA (6 d). **H, I.** Ascomata. **J.** Conidiomata and conidial mass. **K, L.** Setae. **M, N.** Ascii. **O.** Ascospores. **P–R.** Conidiophores, conidiogenous cells and conidia. **S.** Conidia. Scale bar = 10 µm.

forms an unusually long branch in the multi-locus phylogenetic tree (Fig. 1). Based on the BLASTn searches, ITS, *gapdh*, and *tub2* sequences of its type MFLU 14-0626 (Li et al. 2016) share high similarity with those of species in the *C. dematium* species complex. However, the closest matches using the *act* sequence (KU236389.1) is *C. siamense* (> 99 % identity), belonging to the *C. gloeosporioides* species complex, which very likely reflects a confusion with another specimen and may explain the strangely long branch of *C. quinquefoliae*. The type of *C. quinquefoliae* and its derived sequences are thus in need of reexamination.

Colletotrichum reniforme F. Liu, Z.Y. Ma & L. Cai, *sp. nov.* MycoBank MB 841390. Fig. 25.

Etymology: Named to reflect the reniform shape of ascospores.

Description: Colonies on PDA 60–64 mm diam in 7 d, flat with entire edge, pale grey with white edge, floccose aerial mycelium, reverse olivaceous grey to iron grey with off-white edge. Vegetative hyphae hyaline, smooth-walled, septate, branched. Sexual morph formed on SNA. Ascomata solitary or gregarious, superficial to semi-immersed, globose or irregular, black, outer wall composed of angular cells,



Fig. 25. *Colletotrichum reniforme* (ex-type culture LC8230). **A.** Disease symptom on *Smilax cocculoides*. **B.** Front and reverse colony on PDA (6 d). **C, D.** Conidiomata and conidial masses on pine needle and SNA, respectively. **E–H.** Appressoria. **I.** Conidiophores. **J.** Conidia. **K–O.** Setae. **P, Q.** Ascomata on SNA and pine needle, respectively. **R, S.** Ascospores. **T.** Ascospores. Scale bars: P, Q = 200 µm; R = 20 µm; H–K, M, O, S, T = 10 µm. Scale bar of H applied to E–H.

medium brown. *Interascal tissue* composed of paraphyses, thin-walled, hyaline, septate. Asci cymbiform to subcylindrical, hyaline, 33.5–49.5 × 6.5–11.5 µm, 8-spored. Ascospores uniseriately arranged, hyaline, smooth-walled, aseptate, allantoid to reniform

with rounded ends, 13.5–16 × 4–5 µm (av. ± SD = 14.8 ± 0.7 × 4.5 ± 0.3 µm), L/W ratio = 3.2. On SNA amended with pine needle, conidiomata acervular, scattered or gregarious, semi-immersed. Setae straight or flexuous, smooth-walled, sometimes verrucous

in the upper half, basal cell medium brown, gradually becoming dark brown towards the tip, 1–2-septate, 65–89 µm long, basal cell cylindrical, 3.5–4.5 µm diam, the tip ± acute. *Conidiophores* hyaline to pale brown, septate, branched, 25–35 µm, usually reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth-walled, cylindrical, subcylindrical to ampulliform, 5.5–11.5(–14) × 2.5–5 µm. *Conidia* hyaline, aseptate, smooth-walled, guttulate, straight, cylindrical, both ends obtuse, 11.5–16 × 4–5.5 µm (av. ± SD = 13.6 ± 0.9 × 4.7 ± 0.3), L/W ratio = 2.9. *Appressoria* single, medium to dark brown, various in shape, subcircular, ovoid, navicular, ellipsoidal or irregular in outline, 9–14.5 × 4.5–7.5 µm (av. ± SD = 11.6 ± 1.4 × 5.5 ± 0.7 µm).

Typus: China, Fujian, Fuzhou, Wuyi Mountain, on *Smilax cocculoides*, Aug. 2016, Z.Y. Ma & L. Cai, WYS3 (**holotype** HMAS 350631, ex-type culture CGMCC 3.20525 = LC8230 = M41).

Additional material examined: China, Fujian, Fuzhou, Wuyi Mountain, on *Paederia foetida*, Aug. 2016, Z.Y. Ma & L. Cai, WYS8, living culture LC8248 (= M59).

Notes: *Colletotrichum reniforme* is closely related to *C. cliviicola* in the *C. orchidearum* species complex (Fig. 1), but these two species are easily differentiated on the basis of morphological characteristics. The conidiophores of *C. reniforme* are inconspicuous on SNA and pine needles, and difficult to distinguish from the pale brown acervulus cells, while those of *C. cliviicola* are easily recognised and usually elongating up to 70 or 80 µm in 3 wk (Damm *et al.* 2019). The conidiogenous cells of *C. reniforme* are shorter and thinner than those of *C. cliviicola* [5.5–11.5(–14) × 2.5–5 µm vs. 7.5–23 × 4.5–7.5 µm]. Furthermore, microcyclic conidiation is observed in *C. cliviicola*, but not in *C. reniforme*. According to Damm *et al.* (2019) and Yang *et al.* (2009), the appressoria of *C. cliviicola* usually have undulate to lobate margins, while those of *C. reniforme* are flat.

Colletotrichum schimae F. Liu, W.P. Wu & L. Cai, **sp. nov.** MycoBank MB 841391. Fig. 26.

Etymology: Named after the host plant genus, *Schima*.

Description: Colonies on PDA 33–38 mm diam in 7 d, flat with entire or undulate edge, white, aerial mycelium dense, reverse umber in the centre, pale luteous towards the margin. *Conidiomata* and *setae* not observed. On SNA, *conidiophores* formed directly from aerial mycelium, hyaline, aseptate or septate. *Conidiogenous cells* hyaline, cylindrical, formed terminally or laterally on hyphae, variable in size, up to 45 µm long. *Conidia* hyaline, smooth-walled, guttulate, cylindrical to fusoid, with ± acute ends, 8.5–14 × 2.5–4 µm (av. ± SD = 11.6 ± 1.1 × 3.5 ± 0.3 µm), L/W ratio = 3.3. *Appressoria* pale brown, solitary, ellipsoidal, subglobose, bullet or irregular shape, 5–12.5 × 3.5–7 µm.

Typus: China, Hunan Province, Chenzhou, Yizhang County, Mangshan, on healthy leaves of *Schima* sp., 12 Apr. 2002, W.P. Wu (**holotype** HMAS 350647, ex-type culture CGMCC 3.20526 = LC13880 = NN046984).

Additional material examined: China, Hunan Province, Chenzhou, Yizhang County, Mangshan, on healthy leaves of *Schima* sp., 12 Apr. 2002, W.P. Wu, living culture LC13881 (= NN047247).

Notes: *Colletotrichum schimae* is phylogenetically related to *C. kniphofiae* in the *C. acutatum* species complex, and shares low sequence similarity at *act* (92 %), *chs-1* (96.2 %), *gapdh* (89.8 %),

ITS (98.4 %), and *tub2* (94.9 %). Moreover, *C. schimae* is distinct from all other species in this genus at each locus sequenced in the current study. Morphologically, *C. schimae* differs from *C. kniphofiae* in that it produces smaller-sized conidia (8.5–14 × 2.5–4 µm vs. 17–37 × 5–7 µm) (Crous *et al.* 2018).

Colletotrichum shivasii F. Liu & L. Cai, **sp. nov.** MycoBank MB 841392. Fig. 27.

Etymology: Named in honour of the mycologist Roger Shivas, who provided the ex-type culture of this species for the study.

Description: Colonies on PDA 75–80 mm diam in 7 d, flat with fimbriate edge, aerial mycelium white, reverse white at first, becoming orange to black at the centre with time. On PDA, *conidiomata* not observed. *Conidiophores* formed directly from aerial mycelium, hyaline to very pale grey, septate, up to 37 µm. *Setae* not observed. *Conidiogenous cells* cylindrical, smooth-walled, 12–16 µm in length. *Conidia* hyaline, smooth-walled, apex reduced into a filiform appendage (10)–12.5–23 µm, conidia body slightly curved or straight, 27.5–47.5 µm long (including appendages), 2.5–4 µm wide (av. ± SD = 39.4 ± 5.2 × 3.6 ± 0.5 µm), L/W ratio = 10.9. *Appressoria* pale to medium brown, pyriform to subcircular, 6–11.5 × 4.5–7.5 µm (av. ± SD = 7.8 ± 1.5 × 6 ± 1.1 µm).

Typus: Australia, Queensland, Tablelands, Wongabel Road, Atherton, on leaf of *Themeda triandra*, Feb. 2004, probably J.L. Alcorn (**holotype** HMAS 350627, ex-type culture LC1400 = BRIP 15842a).

Notes: *Colletotrichum shivasii* belongs to the *C. caudatum* species complex. Species in this complex comprise widespread fungal pathogens of warm-season grasses, and are easily differentiated from other species in the genus by producing caudate conidia (Crouch 2014). *Colletotrichum shivasii*, associated with the perennial tussock-forming grass *Themeda triandra* in Australia, is morphologically similar to the closely related species *C. caudatum*, but harbours nucleotide polymorphisms at ITS (96.9 % similarity), *sod2* (92.9 % similarity), and *Mat/Apn2* (82.1 % similarity).

Colletotrichum sinuatum F. Liu, W.P. Wu & L. Cai, **sp. nov.** MycoBank MB 841393. Fig. 28.

Etymology: Named to reflect the sinuate setae and conidiophores.

Description: Colonies on PDA 42 mm diam in 7 d, flat with entire edge, white to pale saffron, aerial mycelium sparse, reverse pale saffron with a black centre. *Conidiomata* not formed, conidial masses and *setae* abundantly formed on the surface of medium. *Setae* medium to dark brown, smooth-walled or verruculose, mostly sinuate, 2–5-septate, 67–175 µm long, basal cells cylindrical, sometimes inflated, 4–9.5 µm diam, the tip acute or rounded. *Conidiophores* formed directly from hyphae, hyaline to brown, branched, 1–4-septate, 32–122 µm in length. *Conidiogenous cells* hyaline to pale brown, smooth-walled, cylindrical, rarely subulate, variable in length, on SNA 11.5–34 × 2.5–5 µm (av. ± SD = 21.9 ± 5.4 × 3.8 ± 0.6 µm), on PDA 15–37 × 3–5 µm (av. ± SD = 24.8 ± 6.5 × 4 ± 0.5 µm). *Conidia* hyaline, aseptate, smooth-walled, cylindrical, apex obtuse, tapering at base to a truncate hilum, mostly straight, rarely slightly curved, on SNA 14.5–19 × 3.5–5 µm (av. ± SD = 16.9 ± 1.2 × 4.4 ± 0.4 µm), L/W ratio = 3.8, on PDA 14.5–21 × 4.5–5.5 µm (av. ± SD = 17.8 ± 1.5 × 4.8 ± 0.3 µm), L/W ratio = 3.7. *Appressoria* not observed.

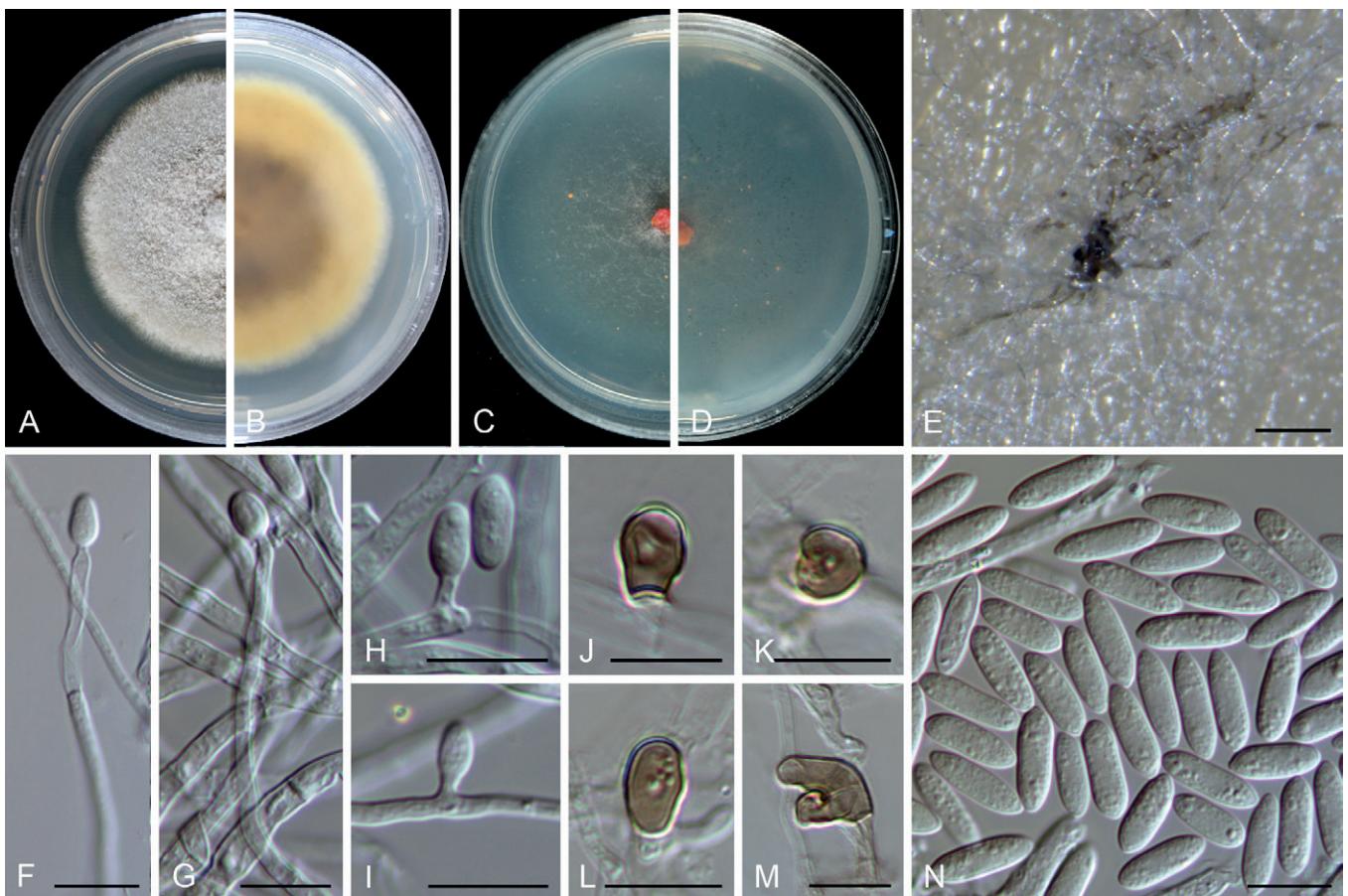


Fig. 26. *Colletotrichum schimae* (ex-type culture NN046984). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidial mass on SNA. **F–I.** Conidiophores, conidiogenous cells and conidia. **J–M.** Appressoria. **N.** Conidia. Scale bars = 10 µm.

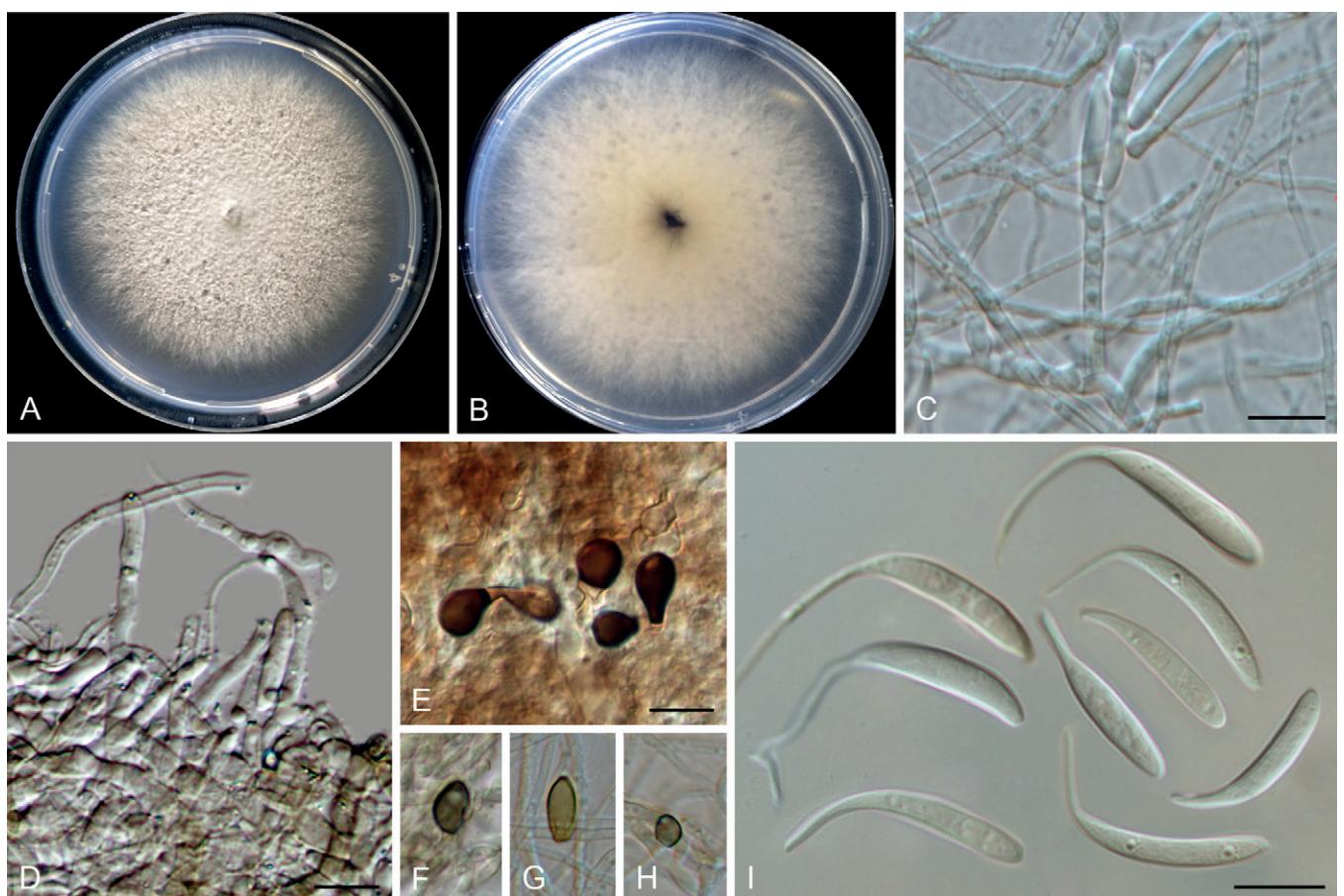


Fig. 27. *Colletotrichum shivasii* (ex-type culture BRIP 15842a). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Conidiophores and conidiogenous cells. **E–H.** Appressoria. **I.** Conidia. Scale bars = 10 µm.

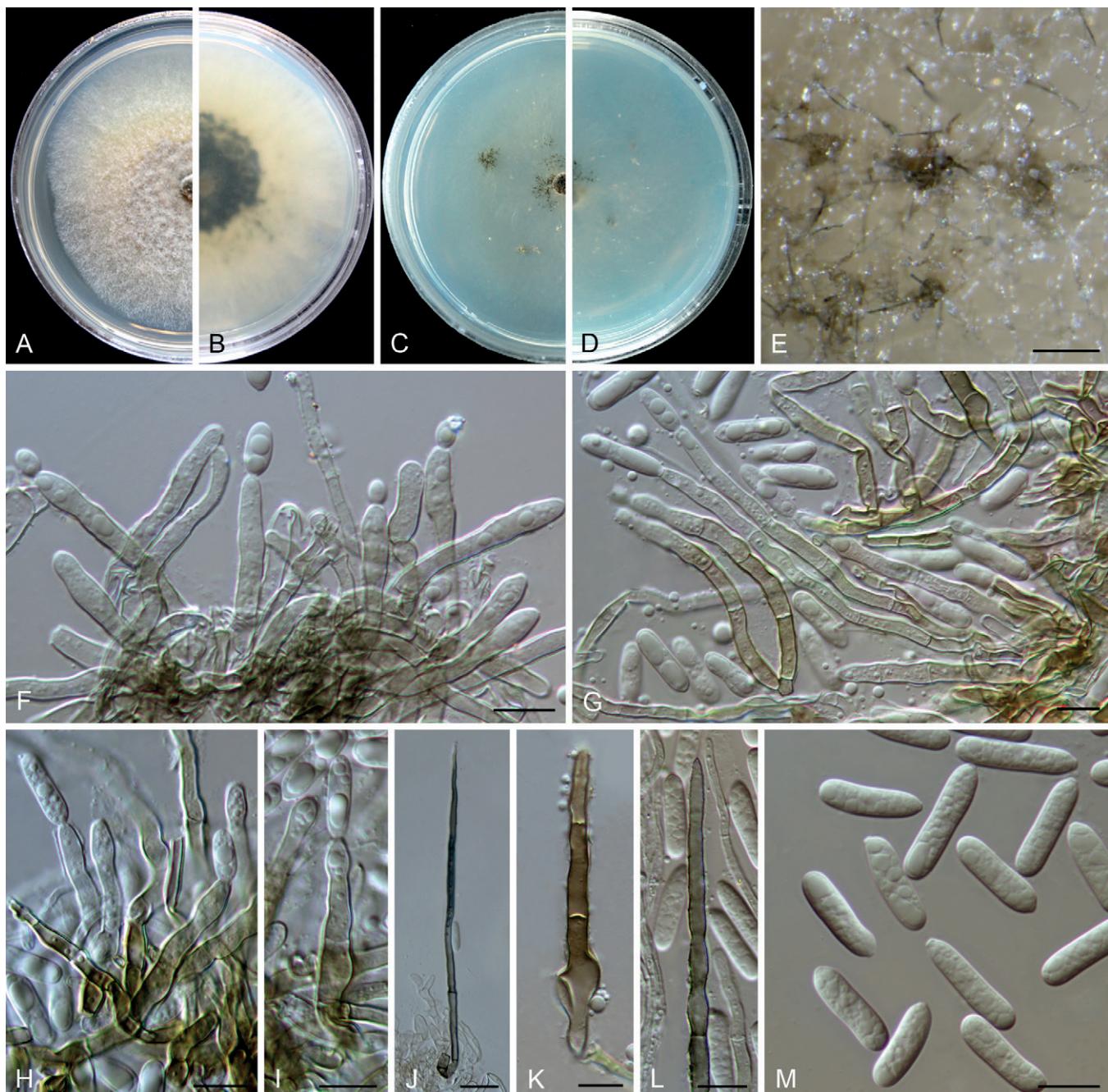


Fig. 28. *Colletotrichum sinuatum* (ex-type culture NN055266). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidial masses and setae on SNA. **F–I.** Conidiophores, conidiogenous cells and conidia. **J–L.** Setae. **M.** Conidia. Scale bars: E = 100 µm; J = 20 µm; F–I, K–M = 10 µm.

Typus: China, Guangdong Province, Guangzhou, Yuexiu Park, on dead leaves of *Ophiopogon japonicus*, 29 Dec. 2012, W.P. Wu (**holotype** HMAS 350643, ex-type culture CGMCC 3.20528 = LC13874 = NN055266).

Notes: *Colletotrichum sinuatum* belongs to the *C. dracaenophilum* species complex. It shares low sequence similarity with the most closely related species *C. yunnanense* at act (91.6 %), chs-1 (97.6 %), gapdh (87.4 %), his3 (92.4 %), ITS (96.5 %), and tub2 (96.3 %). Moreover, *C. schimae* is distinct from all other species in this genus at each locus sequenced in the current study. This species morphologically differs from the phylogenetically related species *C. buxi* sp. nov., *C. dracaenophilum*, and *C. yunnanense* in that it produces distinctly longer conidiophores and conidiogenous cells. Two other *O. japonicus*-associated species, *C. truncatum* and *C. falcatum* (Raabe et al. 1981, Miller 1992), are easily distinguished from *C. sinuatum* in that they produce curved conidia.

Colletotrichum subacidae F. Liu, Z.Y. Ma & L. Cai, **sp. nov.** MycoBank MB 841394. Fig. 29.

Etymology: Named to reflect its close phylogenetic relationship with *C. acidae*.

Description: Colonies on PDA 43–51 mm diam in 7 d, flat with undulate edge, glaucous grey to smoke grey in the centre, white at the margin, aerial mycelium sparse, reverse greenish grey in the centre, white at the margin. On PDA, conidiomata acervular, gregarious, semi-immersed. Setae dark brown, 1–3-septate, 80–165 µm long, base cylindrical, smooth-walled, 5–9 µm diam, tip acute to obtuse. Conidiophores hyaline to pale brown, smooth-walled, septate, solitary or branched, formed from a cushion of roundish brown cells. Conidiogenous cells hyaline, smooth-walled, cylindrical, 9–20 × 2–4.5 µm. Conidia hyaline, aseptate, smooth-

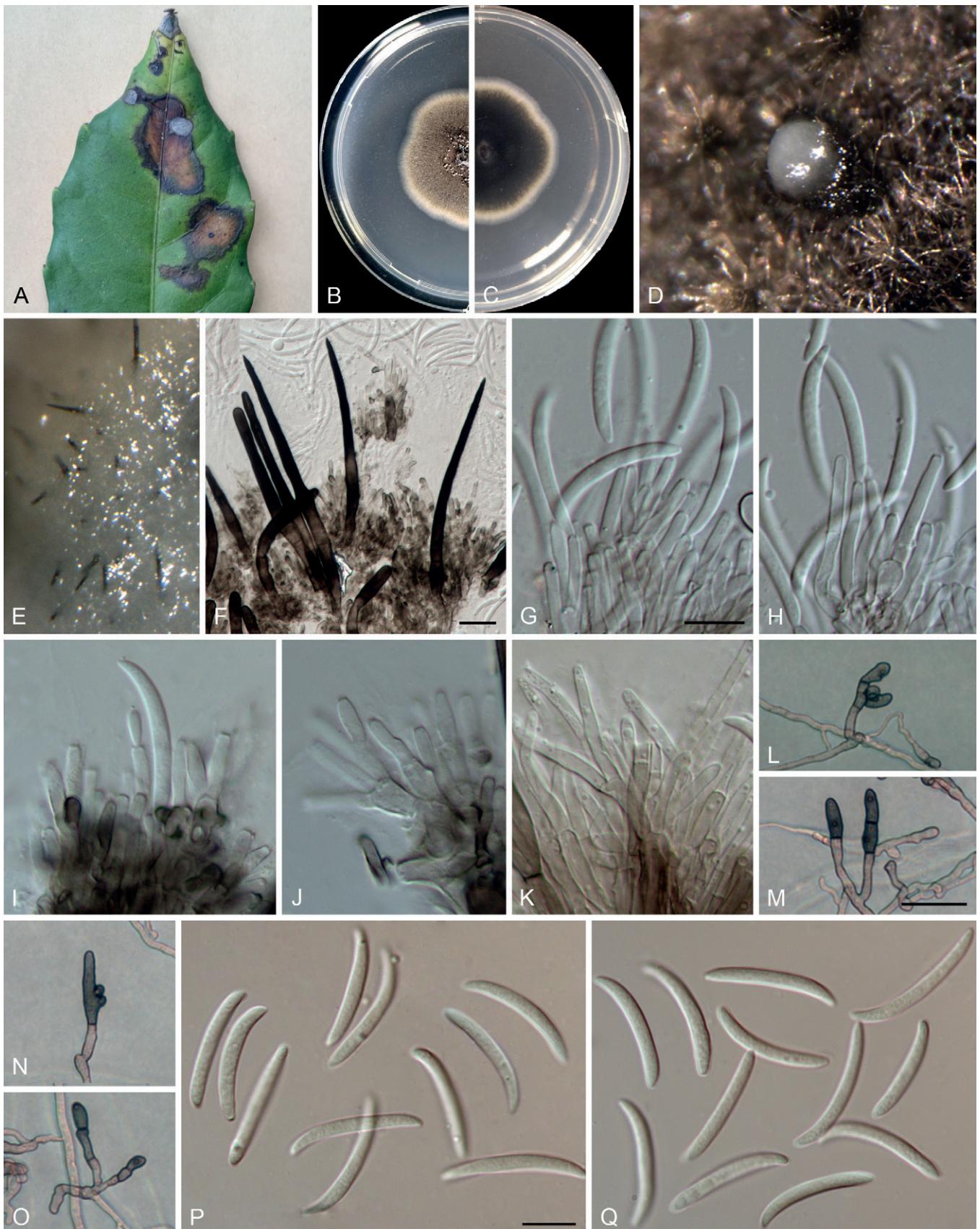


Fig. 29. *Colletotrichum subacidae* (ex-type culture LC13857). **A.** Disease symptom on host plant. **B, C.** Front and reverse colony on PDA (6 d). **D.** Conidioma on PDA. **E, F.** Setae. **G–K.** Conidiophores, conidiogenous cells and conidia. **L–O.** Appressoria. **P, Q.** Conidia. Scale bars: F, M = 20 µm; G, P = 10 µm. Scale bar of G applies to G–K; M applies to L–O; P applies to P–Q.

walled, slightly curved, central part of conidium almost straight with parallel walls, apex more or less acute, base usually truncate, $21\text{--}30 \times 2.5\text{--}4 \mu\text{m}$ (av. \pm SD = $26 \pm 2.3 \times 3 \pm 0.3 \mu\text{m}$), L/W ratio

= 8.5. Appressoria brown, usually in groups, mostly oblong to subcylindrical, rarely irregular in outline, $8\text{--}25 \times 5\text{--}8 \mu\text{m}$ (av. \pm SD = $15.5 \pm 4.4 \times 6.5 \pm 1.0 \mu\text{m}$), L/W ratio = 2.3.

Typus: China, Guangxi, Chongzuo, Guangxi Nonggang National Nature Reserve, on *Tetrastigma obovatum*, Jun. 2017, Z.Y. Ma & L.W. Hou (**holotype** HMAS 350635, ex-type culture CGMCC 3.20529 = LC13857 = LH01).

Additional materials examined: China, Beijing, Xibeiwang, Beijing Medical Botanical Garden, on a diseased stem of *Asparagus officinalis*, 9 Sep. 2012, W.P. Wu, living culture NN054605; on a diseased leaf of *Hosta* sp., 9 Sep. 2012, W.P. Wu, living culture NN054609; Guangxi, Chongzuo, Guangxi Nonggang National Nature Reserve, on *Tetrastigma obovatum*, Jun. 2017, Z.Y. Ma & L.W. Hou, living cultures LC15821, LC15822, LC15823; Hubei Province, Wuhan Botanical Garden, on a dead leaf petiole of *Ailanthus altissima*, 2 Aug. 2015, W.P. Wu, living cultures NN071129, NN071131.

Notes: *Colletotrichum subacidae* is phylogenetically allied with *C. acidae* (Fig. 1), but these two species share low sequence similarity at *gapdh* (93.8 %), *act* (94.3 %), and *tub2* (97.6 %). Morphologically, *C. subacidae* differs from *C. acidae* with respect to the shape and size of appressoria (oblong to subcylindrical, 8–25 × 5–8 µm vs. round, oval or irregular, 11–23 × 9–18 µm) and the size of conidiogenous cells (9–20 × 2–4.5 µm vs. 1–2 × 2–3.5 µm) (Samarakoon et al. 2018). Moreover, the conidia of *C. acidae* are more strongly curved than those of *C. subacidae*.

***Colletotrichum subsalicis* F. Liu & L. Cai, sp. nov.** MycoBank MB 841395. Fig. 30.

Etymology: Named to reflect its close phylogenetic relationship with *C. salicis*.

Description: Colonies on PDA 39–40 mm diam in 7 d, flat with entire edge, pale mouse grey in the centre, white at the margin, aerial mycelium sparse, reverse brown vinaceous, mouse grey and white towards the margin. On PDA, conidiomata acervular, scattered, semi-immersed, protruding saffron conidial masses. Setae not observed. Conidiophores formed from a cushion of pale brown angular cells, septate, branched, 17–41 µm. Conidiogenous cells hyaline to pale brown, smooth-walled, mostly cylindrical to ampulliform, rarely ovoid, 11–20 × 2–5 µm, periclinal thickening visible. Conidia hyaline, aseptate, smooth-walled, fusoid, 13–16 × 3.5–5 µm (av. ± SD = 14 ± 0.9 × 4.5 ± 0.9 µm), L/W ratio = 3.2. Appressoria single, olivaceous, smooth-walled, mostly clavate with a truncate base, sometimes irregular, 6–13 × 2–6 µm (av. ± SD = 8.5 ± 1.7 × 4 ± 1.7 µm), L/W ratio = 2.1.

Typus: China, Beijing, Baihuashan National Nature Reserve Forest Station, *Populus alba*, 19 Sep. 2018, Q. Chen (**holotype** HMAS 350637, ex-type culture CGMCC 3.20530 = LC13863 = CQ1168).

Notes: *Colletotrichum subsalicis* forms a sister clade to *C. salicis* in the *C. acutatum* species complex (Fig. 1), but morphologically differs from the latter in conidium shape (fusoid vs. cylindrical to clavate) and appressorium size (6–13 × 2–6 µm, av. ± SD = 8.5 × 4 µm, L/W ratio = 2.1 vs. 6–19.5 × 5–9.5 µm, av. ± SD = 11.5 × 7.6 µm, L/W ratio = 1.5) (Damm et al. 2012a). Furthermore, the sexual morph of *C. salicis* is more commonly observed in culture than the asexual morph (Damm et al. 2012a), but is absent in *C. subsalicis*. *Colletotrichum subsalicis* and *C. salicis* share 98.8 % genomic similarity.

***Colletotrichum subvariabile* F. Liu, W.P. Wu & L. Cai, sp. nov.** MycoBank MB 841396. Fig. 31.

Etymology: Named to reflect its close phylogenetic relationship with *C. variabile*.

Description: Colonies on PDA 48–49 mm diam in 7 d, flat with entire edge, pale salmon, covered by white and pale greenish grey aerial mycelium, reverse pale salmon, variegated with pale greenish grey spots. On PDA, conidiomata submersed, globose, black, solitary or gregarious, in which conidiophores hardly observed. Conidiophores, formed directly on hyphae, usually reduced to conidiogenous cells, terminally or laterally. Conidiogenous cells rarely observed, hyaline to pale brown, cylindrical, or ampulliform, 2–12 µm in length. Conidia hyaline with salmon guttules, smooth-walled, cylindrical with obtuse apex and truncate base, 18–27 × 5.5–8 µm, av. ± SD = 22.1 ± 2.5 × 6.7 ± 0.8 µm, L/W ratio = 3.3. Setae and appressoria not observed.

Typus: China, Yunnan Province, Kunming, Kunming Botanical Garden, on healthy leaves of an unknown plant (endophyte), 20 Dec. 1993, W.P. Wu (**holotype** HMAS 350645, ex-type culture CGMCC 3.20531 = LC13876 = NN040649).

Notes: *Colletotrichum subvariabile*, belonging to the *C. gigasporum* species complex (Fig. 1), shares low sequence similarity with the phylogenetically related species *C. variabile* sp. nov. at *act* (95.2 %), *chs-1* (97.2 %), *gapdh* (94.2 %), *his3* (95 %), *tub2* (97.9 %), and *ITS* (97.8 %). Morphologically, *C. subvariabile* differs from *C. variabile* in that it produces shorter conidiogenous cells (2–12 µm vs. 9–34 µm) and has a lower conidium L/W ratio (3.3 vs. 3.8).

***Colletotrichum syngoniicola* F. Liu, Z.Y. Ma & L. Cai, sp. nov.** MycoBank MB 841397. Fig. 32.

Etymology: Named after the host plant genus, *Syngonium*.

Description: Colonies on PDA 56–58 mm diam in 7 d, flat with entire edge, smoke grey to greenish grey with white edge, aerial mycelium sparse and short, reverse greenish grey to olivaceous black, off-white at the margin. On SNA, vegetative hyphae hyaline or brown, smooth-walled, septate, branched. Conidiomata not developed. Conidiophores formed directly from hyphae, conidial masses buff to honey. Setae not observed. Conidiophores hyaline to brown, septate, branched, up to 130 µm long, basal cells more or less thick-walled. Conidiogenous cells hyaline, rarely pale brown, smooth-walled, cylindrical or slightly tapering towards the apex, 8–19(–24) × 3.5–5.5 µm. Conidia hyaline, aseptate, smooth-walled, guttulate, cylindrical with obtuse ends, sometimes the base tapering to a truncate hilum, (9–)11–18.5(–23.5) × 3.5–5.5 (av. ± SD = 14.9 ± 1.2 × 4.1 ± 0.4), L/W ratio = 3.6. Appressoria single or gregarious, medium to dark brown, terminally at the tip of the hyphae, mostly irregularly shaped, with undulate to lobate margins, sometimes elliptical with an entire margin, 7.5–18 × 3.5–9 µm (av. ± SD = 10.1 ± 2.7 × 5.8 ± 1.7 µm).

Typus: China, Guangdong, Shenzhen, from a leaf spot of *Syngonium* sp., Nov. 2016, Y.Z. Diao, SZ36 (**holotype** HMAS 350632, ex-type culture CGMCC 3.20532 = LC8894 = M0745).

Additional materials examined: China, Guangdong, Shenzhen, from leaf spots of *Syngonium* sp., Nov. 2016, Y.Z. Diao, SZ36, living cultures LC8895 (= M0746), LC8896 (= M0747), LC8897 (= M0748).

Notes: *Colletotrichum syngoniicola* belongs to the *C. orchidearum* species complex (Fig. 1), and shares low sequence similarity with

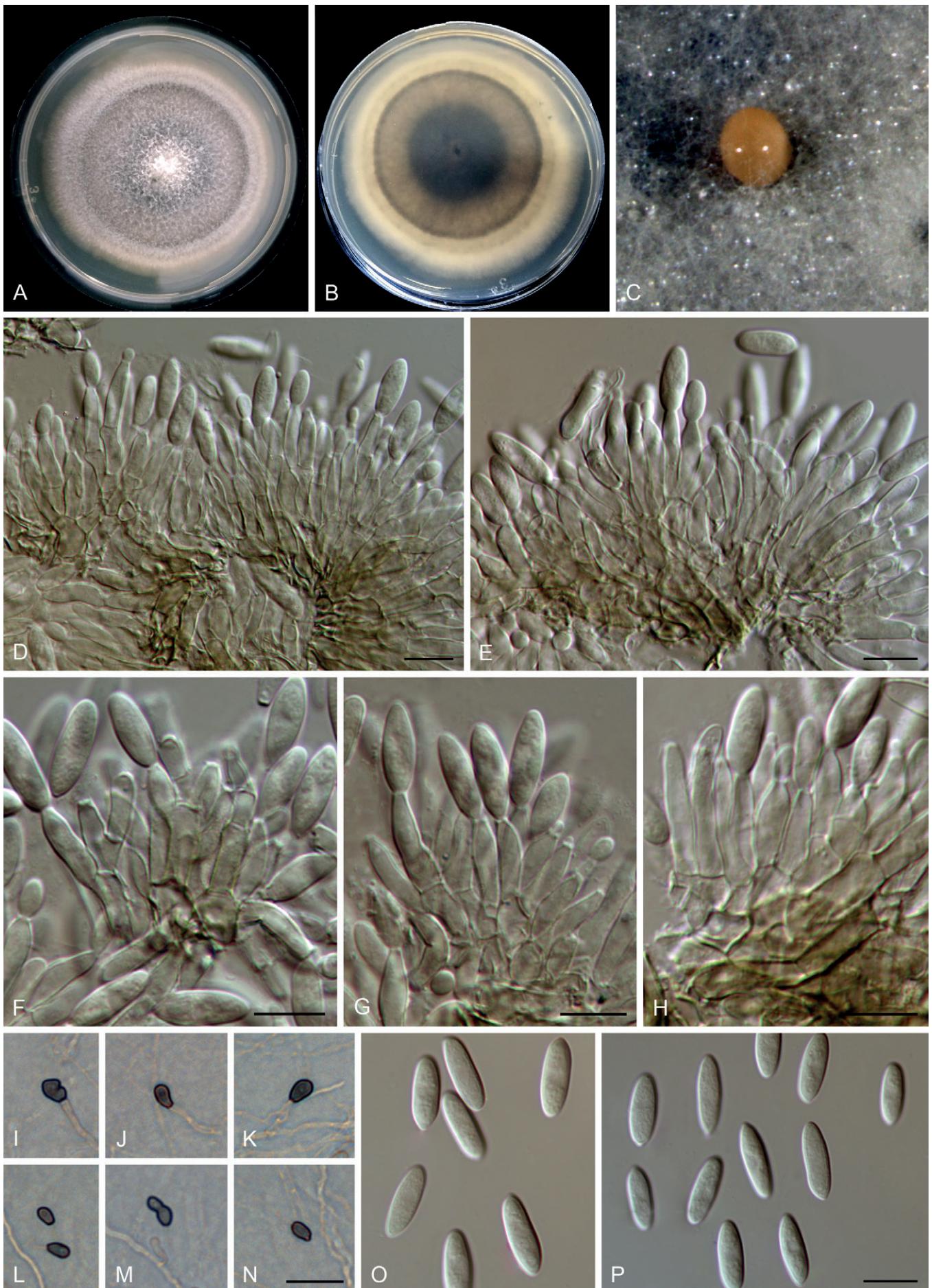


Fig. 30. *Colletotrichum subsalicis* (ex-type culture LC13863). **A, B.** Front and reverse colony on PDA (13 d). **C.** Conidioma on PDA. **D–H.** Conidiophores, conidiogenous cells and conidia. **I–N.** Appressoria. **O, P.** Conidia. Scale bars: D–H, P = 10 µm; N = 20 µm. Scale bar of N applies to I–N; P applies to O, P.

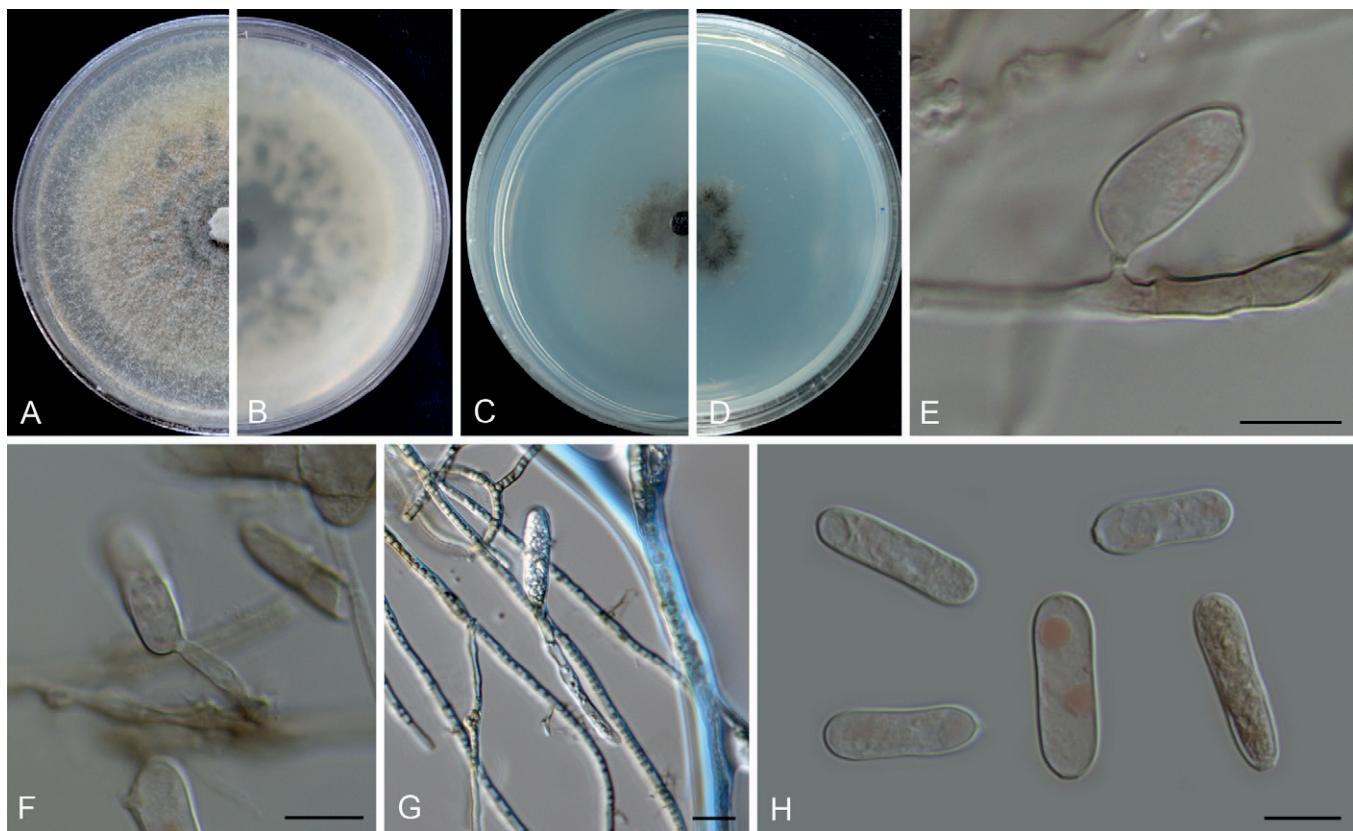


Fig. 31. *Colletotrichum subvariable* (ex-type culture NN040649). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E–G.** Conidiophores, conidiogenous cells and conidia. **H.** Conidia. Scale bars = 10 µm.

the phylogenetically related species *C. piperis* at *act* (95.3 %), *chs-1* (98.4 %), *gapdh* (93.2 %), *his3* (96.5 %), *tub2* (97.5 %), and ITS (99 %). Morphologically, *C. syngoniicola* differs from *C. piperis* in that it produces relatively darker conidiophores (Damm et al. 2019). Moreover, although *C. syngoniicola* is characterised by the unusual conidiophores that are long-branched and brown, resembling those of *C. monsterae* sp. nov., the two species share low sequence similarity at *act* (89.3 %), *chs-1* (92.8 %), *gapdh* (87.7 %), *his3* (91.9 %), ITS (97.6 %), and *tub2* (93.5 %).

***Colletotrichum telosmae* F. Liu, W.P. Wu & L. Cai, sp. nov.** MycoBank MB 841398. Fig. 33.

Etymology: Named after the host plant genus, *Telosma*.

Description: Colonies on PDA growing slowly, 28–29 mm diam in 7 d, raised with concave edge, grey, reverse iron grey with pale amber margin, a pale amber ring more towards the centre of the colony corresponds to the production of conidial masses on the surface. Vegetative hyphae hyaline to pale brown, smooth-walled, septate, branched. On SNA, conidiomata not developed, conidiophores formed directly on hyphae, conidial masses buff to brown. Setae not observed. Conidiophores hyaline to pale brown, 1–4-septate, branched, up to 80 µm long. Conidiogenous cells hyaline, smooth-walled, cylindrical, 8–24 × 2–4 µm (av. ± SD ± 18.3 ± 3.5 × 3 ± 0.3 µm), collarette visible. Conidia hyaline, aseptate, smooth-walled, guttulate, cylindrical with obtuse ends, 10.5–11.5 × 3.5–5 µm (av. ± SD ± 11 ± 0.4 × 4 ± 0.2 µm), L/W ratio = 2.8. Appressoria ellipsoidal, subcircular, medium brown to dark brown, 5.5–11.5 × 3.5–7 µm (av. ± SD ± 7.2 ± 1.6 × 5 ± 1 µm), with conidia-like cells formed from the appressoria, 6.5–7.5 × 5–5.5 µm.

Typus: China, on healthy leaves of *Telosma cordarum*, 24 Mar. 2010, W.P. Wu (holotype HMAS 350641, ex-type culture CGMCC 3.20533 = LC13872 = NN052858).

Notes: The endophytic *C. telosmae*, phylogenetically related to the *C. dracaenophilum* species complex (Fig. 1), is a singleton species and can be distinguished from all currently accepted species of *Colletotrichum* at each locus sequenced in the current study. Its cylindrical conidia resemble species in many complexes, especially the *C. gloeosporioides* and *C. dracaenophilum* complexes. However, the conidia-like cells that form on the *C. telosmae* appressoria (Fig. 33L–M) have not been previously observed in this genus. This is the first report of a *Colletotrichum* species on *Telosma cordarum*.

***Colletotrichum tibetense* F. Liu & L. Cai, sp. nov.** MycoBank MB 841399. Fig. 34.

Etymology: Named after the location where the fungus was collected, Tibet.

Description: Colonies on PDA growing slowly, 21–24 mm diam in 7 d, flat with fimbriate edge, straw, aerial mycelium sparse, reverse straw. Vegetative hyphae hyaline, smooth-walled, septate, branched. Sporulating on SNA and pine needle, conidiomata not developed, conidiophores formed directly from hyphae and hardly observed, conidial masses abundant, pale luteous to buff, scattered or confluent. Setae not observed. Conidiophores hyaline, aseptate, unbranched, reduced to conidiogenous cells. Conidiogenous cells hyaline, smooth-walled, cylindrical, straight or flexuous, 19.5–32.5 × 2 µm. Conidia hyaline, aseptate, guttulate, smooth-walled, curved, central part of conidium almost straight with parallel walls, gradually

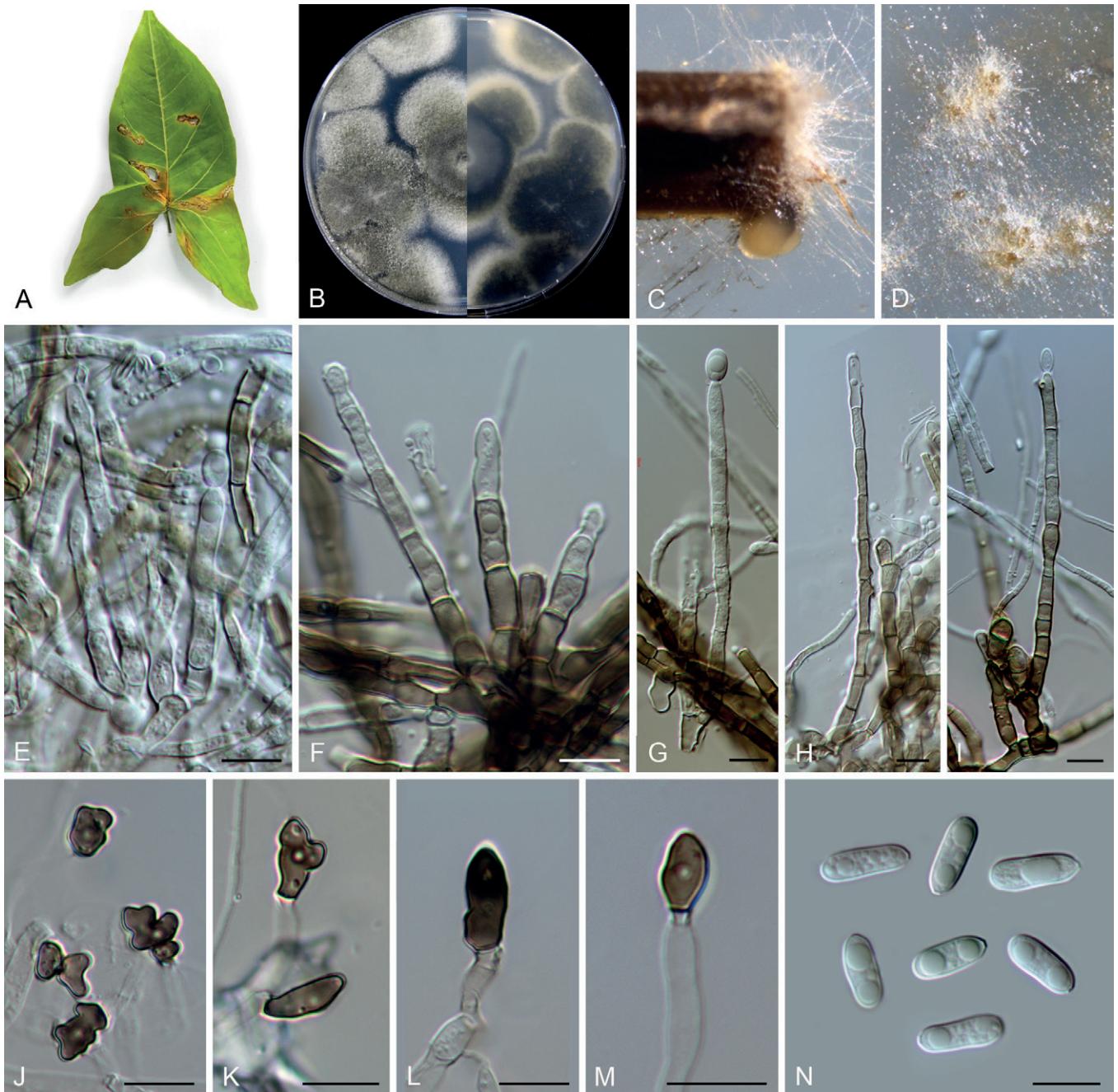


Fig. 32. *Colletotrichum syngoniicola* (ex-type culture LC8894). **A.** Disease symptom on *Syngonium* sp. **B.** Front and reverse colony on PDA (6 d). **C.** **D.** Conidiomata and conidial masses on pine needle and SNA, respectively. **E–I.** Conidiophores, conidiogenous cells and conidia. **J–M.** Appressoria. **N.** Conidia. Scale bars = 10 µm.

tapering towards a ± acute or slightly rounded apex and a usually truncate base, with a similar radian, $11.5\text{--}18.5 \times 2.5\text{--}4 \mu\text{m}$ (av. \pm SD = $16.4 \pm 1.7 \times 3.1 \pm 0.3 \mu\text{m}$), L/W ratio = 5.3. Appressoria discrete or gregarious, brown, smooth-walled, subglobose, obovoid, clavate with truncate base, or sometimes irregularly shaped, lobed, $6\text{--}9.5 \times 3.5\text{--}7 \mu\text{m}$ (av. \pm SD = $8.1 \pm 0.9 \times 5.3 \pm 0.8 \mu\text{m}$).

Typus: **China**, Tibet, Bomi county, Suotong village, on an unidentified species of Poaceae, 13 Jun. 2015, F. Liu, BM12 (**holotype** HMAS 350630, ex-type culture CGMCC 3.20534 = LC7364 = LJM48).

Additional material examined: **China**, Tibet, Bomi county, Suotong village, on Poaceae, 13 Jun. 2015, F. Liu, BM12, living culture LC7366.

Notes: *Colletotrichum tibetense* belongs to the *C. graminicola* species complex (Fig. 1) and is characterised by slow growth

rate on PDA (21–24 mm diam in 7 d) and abundant sporulation. It morphologically differs from the closely related species *C. dolichoconidiophori* (Figs 1, 3) in producing longer conidiogenous cells ($19.5\text{--}32.5 \times 2 \mu\text{m}$ vs. $6\text{--}23 \times 2\text{--}4 \mu\text{m}$), shorter conidia ($11.5\text{--}18.5 \times 2.5\text{--}4 \mu\text{m}$ vs. $19\text{--}27.5 \times 2.5\text{--}3.5 \mu\text{m}$), and with a lower conidium L/W ratio (5.3 vs. 8). The closest matches revealed by BLASTn search using the *act*, *chs-1*, *sod2*, *tub2*, and ITS sequences of the ex-type strain LC7364 were *C. cereale* (92.7 %), *C. hanaui* (95 %), *C. sublineola* (86.3 %), *C. navitas* (89.3 %), and *C. tofieldiae* (99.8 %), respectively.

Colletotrichum variabile F. Liu, W.P. Wu & L. Cai, **sp. nov.** MycoBank MB 841400. Fig. 35.

Etymology: Named to reflect the variable length of conidiogenous cells.

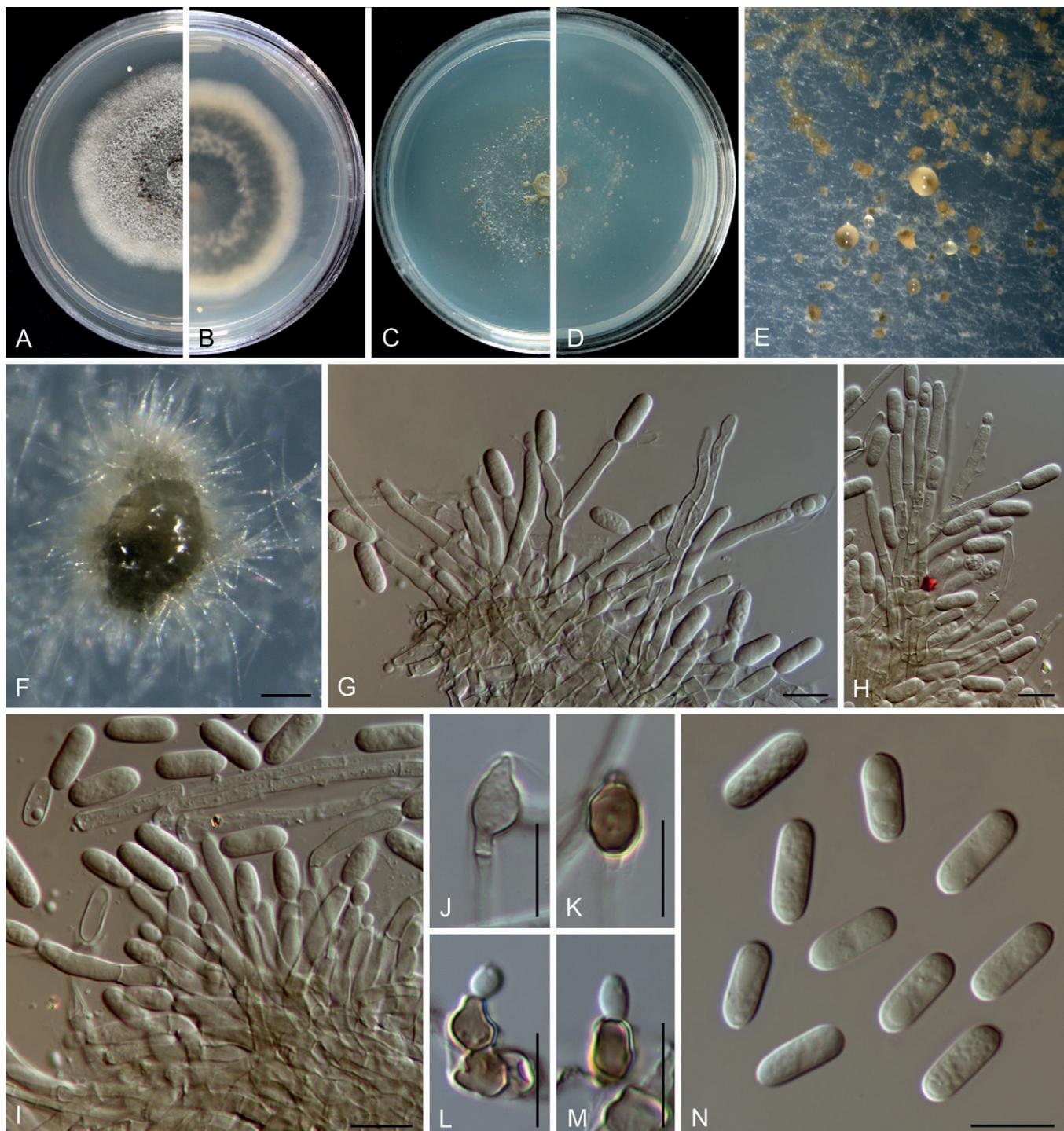


Fig. 33. *Colletotrichum telosmae* (ex-type culture NN052858). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E, F.** Conidial masses on SNA. **G–I.** Conidiophores, conidiogenous cells and conidia. **J–M.** Appressoria. **N.** Conidia. Scale bars: F = 100 µm; G–N = 10 µm.

Description: Colonies on PDA 42 mm diam in 7 d, flat with entire edge, white to pale saffron, aerial mycelium sparse, reverse pale saffron with a black region in the centre. On PDA, conidiomata and setae not observed. Conidial masses salmon, formed among the aerial mycelium. Conidiophores formed directly from the aerial mycelium, hyaline, branched, 1–5-septate. Conidiogenous cells cylindrical to subcylindrical, rarely ovoid, hyaline, 9–34 × 4–5.5 µm. Conidia hyaline, smooth-walled, guttulate, cylindrical with obtuse ends, sometimes slightly narrowed at the centre, becoming 1–3-septate with age, (16–)19–27.5 × 4.5–7 µm, av. ± SD = 22.5 ± 2.2 × 6.0 ± 0.6 µm, L/W ratio = 3.8. Appressoria irregular outline with crenate or lobed margin, clavate, brown, 7.5–9 × 4.5–5.5 µm.

Typus: China, Yunnan Province, Kunming, Kunming Botanical Garden, from healthy leaves of an unknown plant, 20 Dec. 1993, W.P. Wu (**holotype** HMAS 350644, ex-type culture CGMCC 3.20535 = LC13875 = NN040656).

Notes: *Colletotrichum variabile* belongs to the *C. gigasporum* species complex. It shares low sequence similarity with the phylogenetically related species *C. subvariabile* sp. nov. at act (95.2 %), chs-1 (97.2 %), gapdh (94.2 %), his3 (95 %), tub2 (97.9 %), and ITS (97.8 %), and differs from that species in that it produces longer conidiogenous cells (9–34 µm vs. 2–12 µm). In addition, *C. variabile* differs from other species in the *C. gigasporum* species complex in the mode of conidiophore and conidium formation (directly on the aerial mycelia vs. on a cushion of cells).

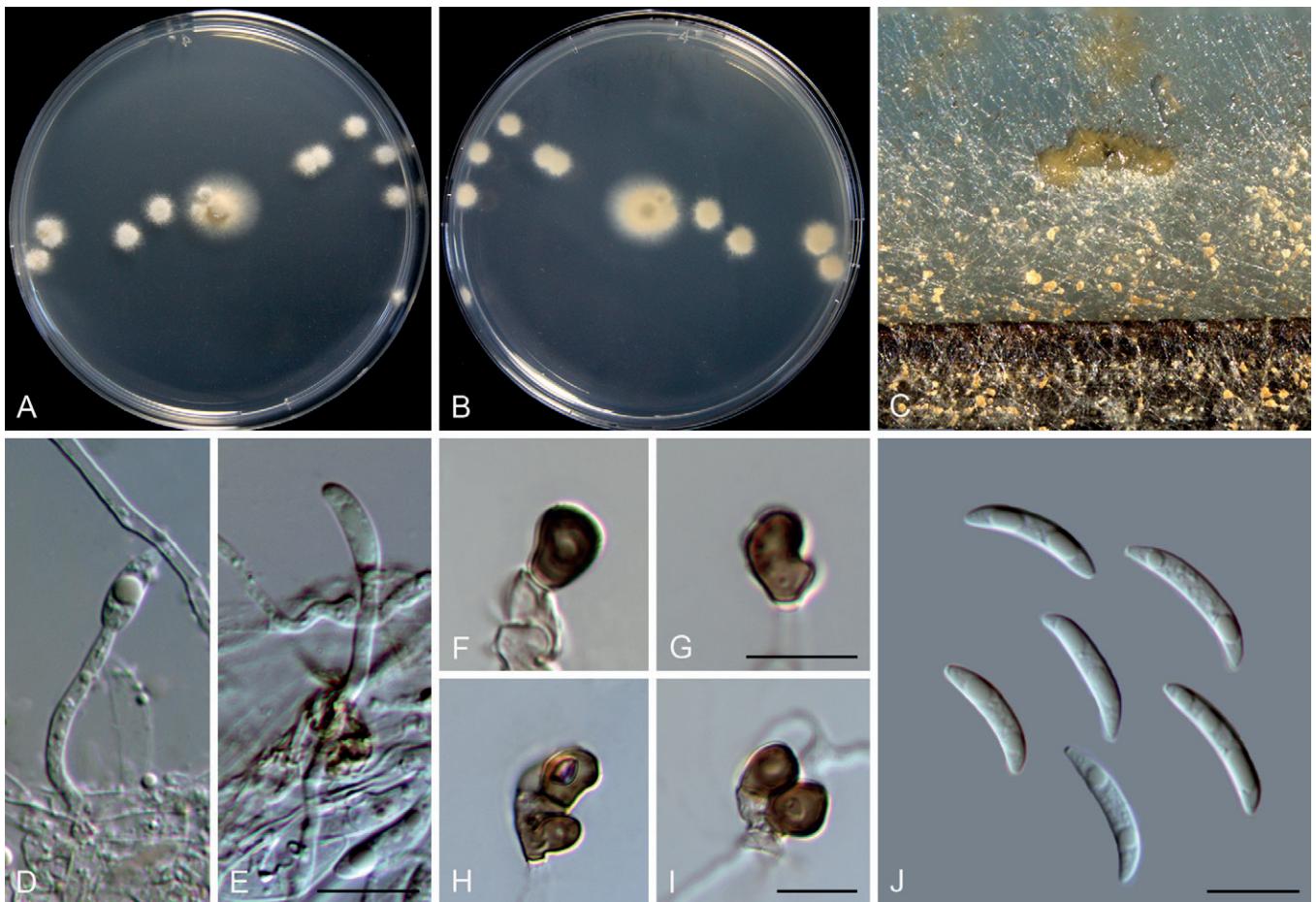


Fig. 34. *Colletotrichum tibetense* (ex-type culture LC7364). **A, B.** Front and reverse colony on PDA (6 d). **C.** Conidial masses on pine needle and SNA. **D, E.** Conidiogenous cells and conidia. **F–I.** Appressoria. **J.** Conidia. Scale bars = 10 µm. Scale bar of E applies to D, E; G applies to F, G; I applies to H, I.

Colletotrichum zhaoqingense* F. Liu & L. Cai, *sp. nov. MycoBank MB 841401. Fig. 36.

Etymology: Named after the location at which the fungus was collected, Zhaoqing.

Description: Colonies on PDA 52 mm diam in 7 d, flat with entire edge, medium to dark mouse grey, aerial mycelium floccose, reverse dark mouse grey. On SNA, conidiomata acervular, scattered, semi-immersed to immersed, protruding hyaline or salmon conidial masses, surrounded by dark brown setae. Setae 1–4-septate, 66–112 µm long, basal cells cylindrical, sometimes conical, smooth-walled, 5–6.5 µm diam, tip acute. Conidiophores formed from a cushion of roundish to angular pale brown cells, or formed directly on aerial mycelium, solitary or branched, septate, hyaline to pale brown, 0–4-septate. Conidiogenous cells cylindrical, rarely ovoid, hyaline to pale brown, 10–22 × 4.5–8 µm. Conidia hyaline, smooth-walled, guttulate, cylindrical with obtuse ends, 20–24 × 5.5–7 µm, av. ± SD = 21.3 ± 0.9 × 6.3 ± 0.6 µm, L/W ratio = 3.4. Appressoria variable in shape, globose, subglobose, ovoid, or irregular outline with a crenate or lobed margin, pale brown, 5.5–18 × 3.5–6.5 µm.

Typus: **China**, Zhejiang Province, Hangzhou Botanical Garden, on dead petiole of an unidentified palm (Arecaceae), 12 Jun. 2015, W.P. Wu (**holotype** HMAS 350646, ex-type culture CGMCC 3.20536 = LC13878 = NN071035).

Additional materials examined: **China**, Guangdong Province, Zhaoqing, Seven Star Cave (Qixingyan), on *Musa* sp., 24 Dec. 2012, W.P. Wu, living culture NN055284; Guangzhou, on *Carica papaya*, 10 Dec. 2013, W.P.

Wu, living culture NN057644; Zhejiang Province, Hangzhou Botanical Garden, on dead petiole of palm (Arecaceae), 12 Jun. 2015, W.P. Wu, living cultures LC13877 (= NN058985), LC13879 (= NN071036).

Notes: *Colletotrichum zhaoqingense* forms a sister clade to *C. gigasporum* (Fig. 1), but differs morphologically from the latter in producing smaller conidia (20–24 × 5.5–7 µm vs. 22–32 × 6–9 µm) (Liu et al. 2014). Furthermore, on the molecular level, these two species share low sequence similarity at *chs-1* (98 %), *gapdh* (97.3 %), and *ITS* (93.2 %).

Colletotrichum zhejiangense* F. Liu, W.P. Wu & L. Cai, *sp. nov. MycoBank MB 841402. Fig. 37.

Etymology: Named after the location at which the fungus was collected, Zhejiang Province.

Description: Colonies on PDA 34–35 mm diam in 7 d, flat with crenate edge, grey to purple slate, aerial mycelium dense, reverse violet slate with grey margin. Conidiomata black, columnar, straight, conidial masses hyaline. Conidiophores formed from a cushion of elliptical or angular and medium brown cells, branched, septate, hyaline to pale brown. Setae brown to olivaceous black, smooth-walled, 1–3-septate, 45–139 µm long, basal cells cylindrical to slightly conical, 4–8 µm diam, tip acute or round. Conidiogenous cells smooth-walled, cylindrical, 5.5–11.5 × 2.5–4.5 µm (av. ± SD = 8.8 ± 1.9 × 3.5 ± 0.5 µm). Conidia hyaline, aseptate, smooth-walled, curved, central part almost straight with parallel walls, gradually tapering towards the ends with a similar radius, 20.5–

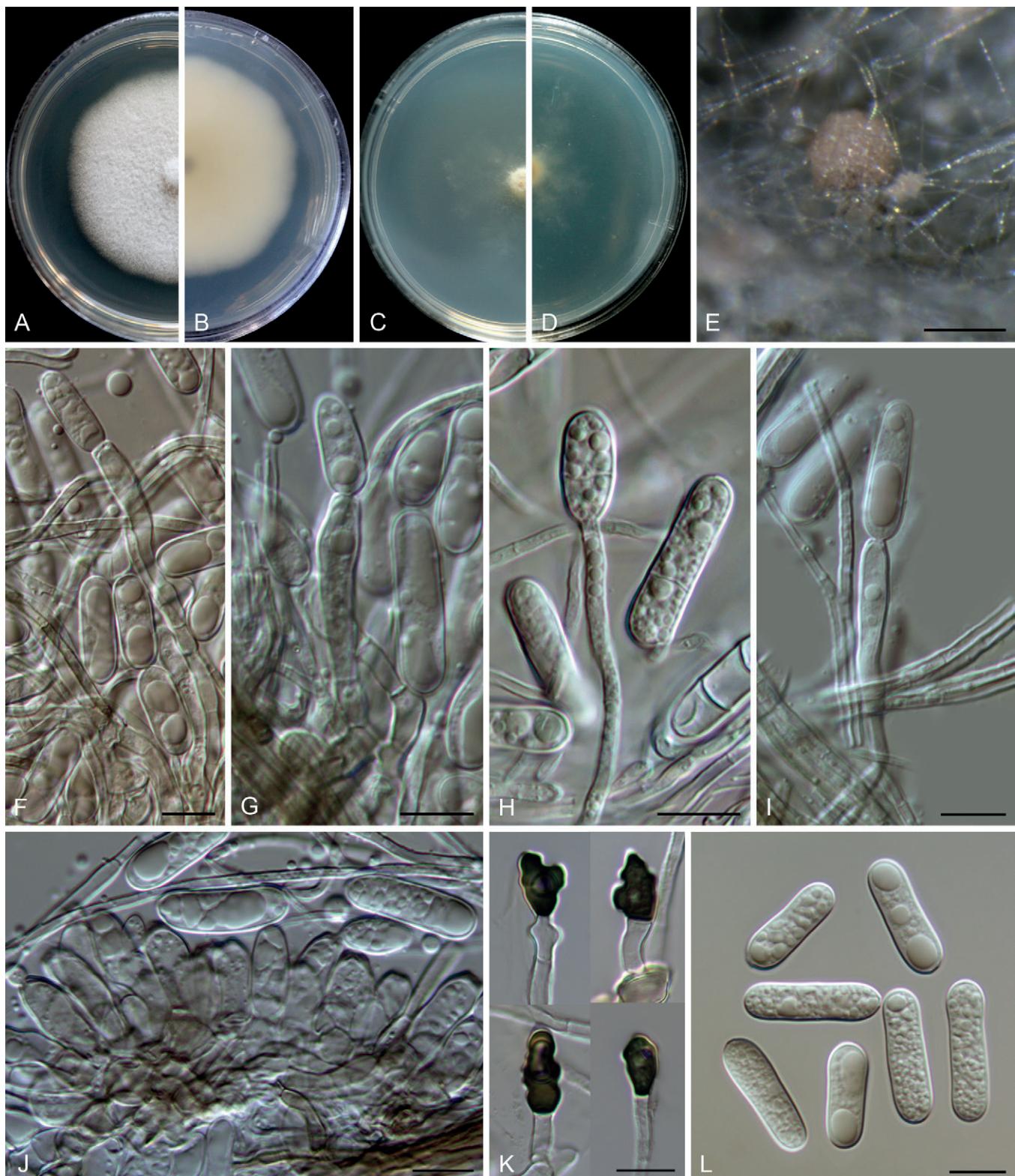


Fig. 35. *Colletotrichum variabile* (ex-type culture NN040656). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidial mass. **F–J.** Conidiophores, conidiogenous cells and conidia. **K.** Appressoria. **L.** Conidia. Scale bars = 10 µm.

$24.5 \times 3\text{--}4 \mu\text{m}$ (av. \pm SD = $22 \pm 0.9 \times 3.3 \pm 0.2 \mu\text{m}$), L/W ratio = 6.7. Appressoria not observed.

Typus: China, Zhejiang Province, Chun'an County, Qiandao Lake, on dead leaves of an unidentified tree, 18 Oct. 2018, W.P. Wu (**holotype** HMAS 350652, ex-type culture CGMCC 3.20537 = LC13887 = NN076215).

Notes: *Colletotrichum zhejiangense* belongs to the *C. dematium* species complex (Figs 1, S1), and is characterised by typical

curved conidia with parallel walls in the middle, as is also observed for other species in this group. BLASTn search of *C. zhejiangense* sequences in the NCBI GenBank revealed very low sequence similarity with other species; the closest matches of the *act*, *chs-1*, *gapdh*, ITS and *tub2* sequences were *C. fructi* (89.1 % identity), *C. insertae* (94.4 %), *C. lineola* (68.9 %), *C. fructi* (98.6 %) and *C. dematium* (89.2 %), respectively.

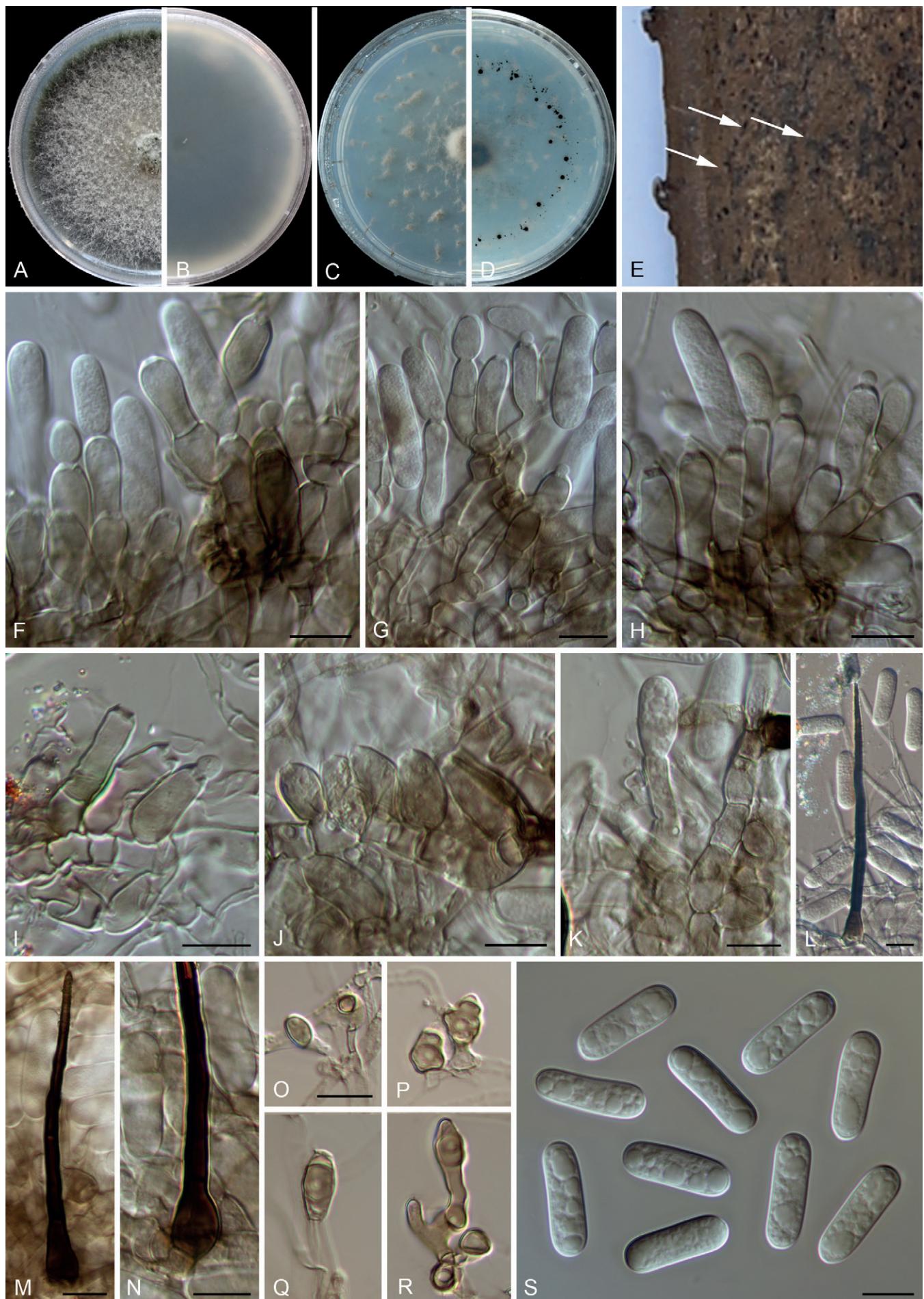


Fig. 36. *Colletotrichum zhaoqingense* (A–D, I–L, N–S: ex-type culture NN058985, E–H, M: NN071035). **A, B.** Front and reverse colony on PDA (7 d). **C, D.** Front and reverse colony on SNA (7 d). **E.** Conidiomata (black) on dead petiole of palm. **F–K.** Conidiophores, conidiogenous cells and conidia. **L–N.** Setae. **O–R.** Appressoria. **S.** Conidia. Scale bars: F–O, S = 10 µm. Scale bar of O applies to O–R.

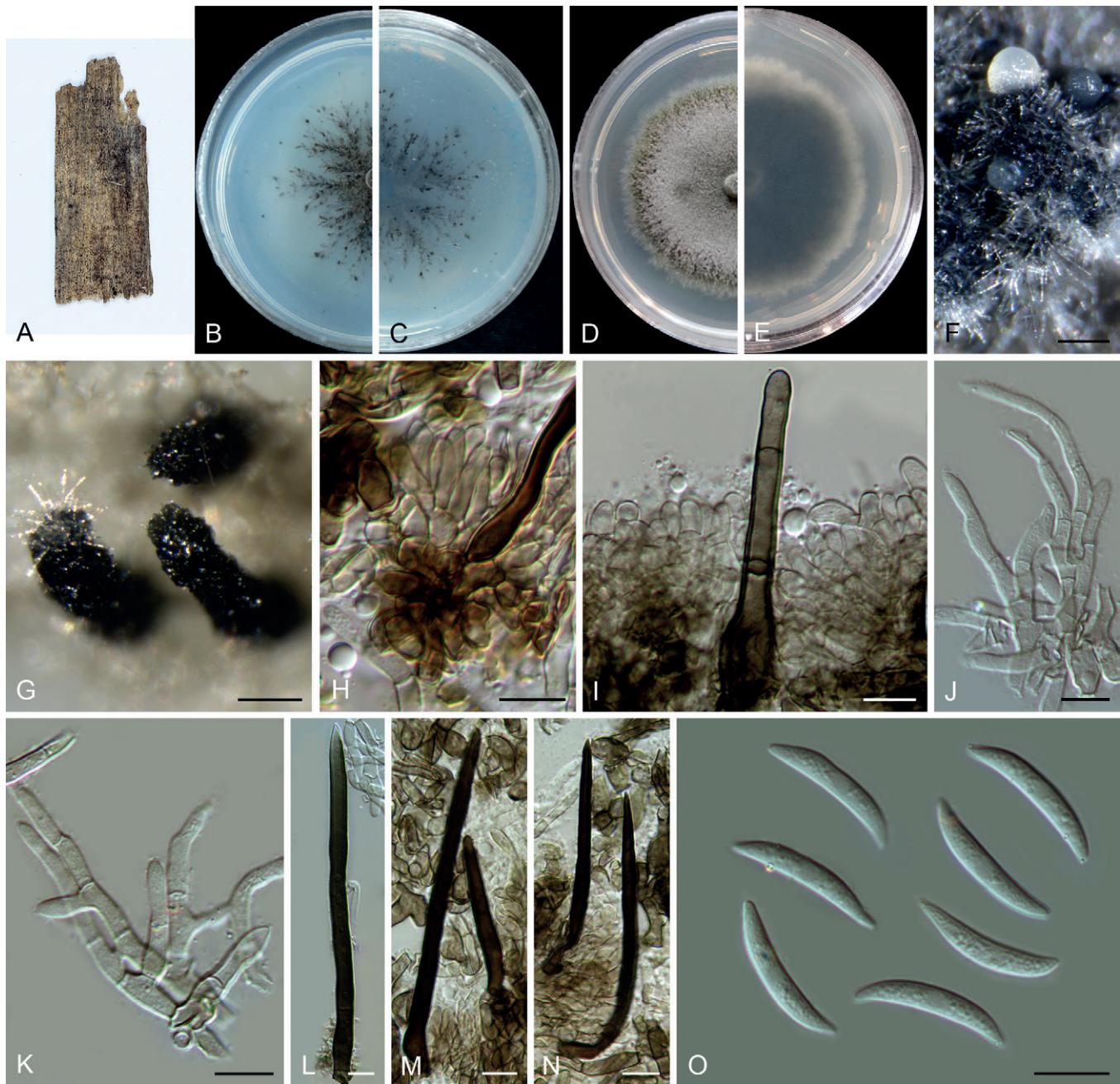


Fig. 37. *Colletotrichum zhejiangense* (ex-type culture NN076215). A. Symptom on the dead leaf of an unidentified tree. B, C. Front and reverse colony on SNA (7 d). D, E. Front and reverse colony on PDA (7 d). F, G. Conidiomata. H, I. Conidiophores, conidiogenous cells and setae. J, K. Conidiophore-like hyphae. L–N. Setae. O. Conidia. Scale bars: F, G = 100 µm; H–O = 10 µm.

Species diversity of *Colletotrichum* in China

In the current study, based on BLASTn searches and phylogenetic analyses of single-, multi-locus and whole-genome sequences, 1 008 strains were assigned to 107 species, belonging to 16 species complexes and 10 singletons (Fig. 38), of which 97 were isolated in China (Tables S5, S6). The majority of analysed strains belong to the *C. gloeosporioides* species complex (Fig. 38). However, because of the unavailability of ApMat and gs sequences for some taxa in the *C. gloeosporioides* species complex, species identification in this group was difficult or unfeasible. Hence, only tentative identification was provided for 183 strains in the current study. Among all the identified species, *C. siamense* was the most common taxon, followed by *C. karsti*, *C. fructicola*, *C. truncatum*, *C. fioriniae*, and *C. gloeosporioides* (Fig. 39).

Furthermore, we summarised the host-association data for *Colletotrichum* species from China, that were retrieved from 224

peer-reviewed papers published in 2009 or later (Table S6), and in which the species had been identified employing a modern classification approach. As of 1 Apr. 2021, 139 species belonging to 15 species complexes and 10 singleton species have been reported in China, including the 30 new species and 18 new records reported in the current study (Table S6, Fig. 38). The top six most common species listed in the preceding paragraph are also the species with the widest host range in China (Fig. 39). On the other hand, 76 species have to date been reported from a single plant species or genus (Table S6).

DISCUSSION

In the current study, we generated 67 type-derived sequences for known *Colletotrichum* species that were omitted or have been erroneously sequenced in various previous publications. This helped

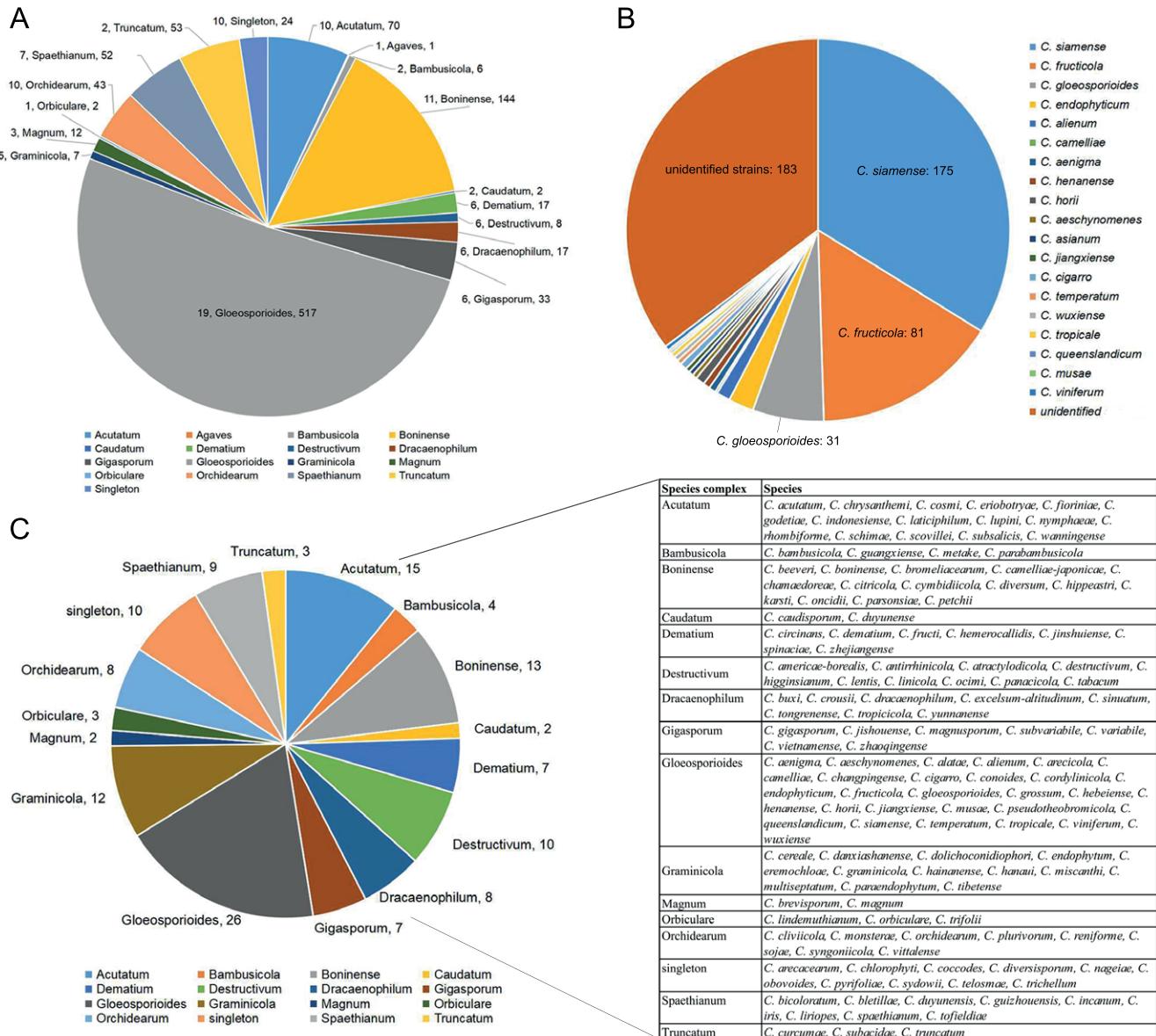


Fig. 38. Statistics of *Colletotrichum* strains and species in this study. **A.** Proportion of all 1 008 strains analysed in this study (left: number of species, right: number of strains). **B.** Proportion of the 517 strains (right: number of strains) of species in the *C. gloeosporioides* species complex analysed in this study. **C.** Proportion and summary of species within each species complex distributed in China based on this and previous studies (right: number of species).

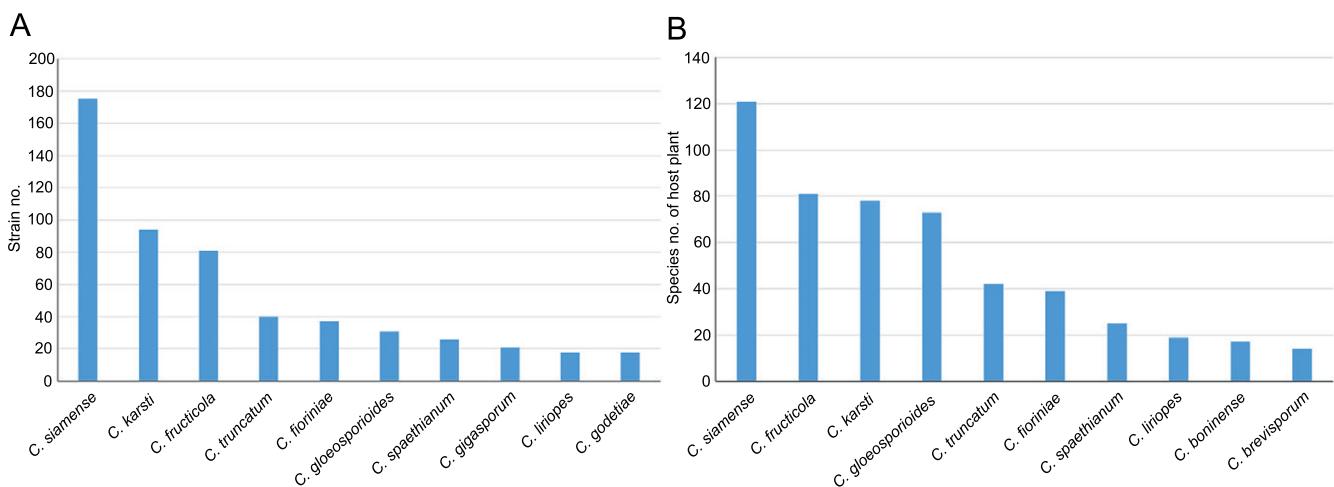


Fig. 39. Statistics of *Colletotrichum* species in this study. **A.** The most common ten species identified in this study. **B.** The ten species with the widest host range in China based on this study.

to clarify the existing taxonomic confusion (e.g. *C. liaoningense* and *C. ochraceae*), and also greatly contributed to the reconstruction of a robust backbone tree for *Colletotrichum*. Nevertheless, the identity of a few ambiguous species is still pending clarification, as we were unable to obtain their type or type-derived DNA, e.g. in the case of *C. chiangraicense*, *C. jasminigenum*, and *C. quinquefoliae*. Several strains that had been isolated from different bamboo hosts form a distinct clade in the multi-locus phylogeny (Fig. 1), which we refer to as the *C. bambusicola* species complex. The strains previously identified as *C. metake* and *C. hsienjenchang* (Sato *et al.* 2012) do not include type material, and hence their identity has not yet been clarified. Furthermore, the *C. metake* strains neither originate from the type location (Italy) nor from the host that *C. metake* was originally described on (*Arundinaria japonica*, Saccardo 1908), and might even represent more than one species. The two species will be examined in detail in a subsequent study (U. Damm, unpub. data). Overall, together with the 30 species newly described in the current study, 265 of the 280 *Colletotrichum* species were herein assigned to 16 species complexes, with the remaining 15 species regarded as singletons (Fig. 1, Tables S1–S3).

Among the 16 species complexes, the *C. acutatum*, *C. boninense*, and *C. gloeosporioides* species complexes contain more species than the other species complexes. Coincidentally, most strains analysed in the current study belong to these three species complexes (Fig. 38), with more than half (518/1 008) belonging to the *C. gloeosporioides* species complex. Although the combined use of ApMat and gs is very effective in resolving species in the *C. gloeosporioides* species complex (Liu *et al.* 2015), we did not employ the two loci in the multi-locus analyses herein, as they had been only rarely sequenced from species in other species complexes. To date, 51 species for which DNA sequence data are available have been accepted in the *C. gloeosporioides* species complex (Fig. 1); however, the species boundaries are still not well defined for several species. For example, the sequences of the six loci analysed and even whole-genome sequences of *C. kahawae* s. str. and its closest relatives (*C. cigarro*, *C. fructivorum*, *C. hedericola*, *C. hellenense*, *C. kahawae*, *C. rhexiae* and *C. jiangxiense*), *C. conoides* and *C. hebeiense*, *C. wuxiense* and *C. temperatum*, and *C. cibitiiense* and *C. ti* exhibit very few nucleotide differences (Liu *et al.*, unpub. data). Hence, resolution of the taxonomy of the *C. gloeosporioides* species complex requires a further in-depth study, preferably involving whole-genome data.

Based on the findings of the current study, data retrieved from the USDA fungal database (Farr & Rossman 2021), and data from previous studies (Table S6), we observed that *Colletotrichum* species vary widely with respect to host specificity and host range, although determination of the host range is somewhat biased as pathogenic fungi have received much more attention to date than endophytes and saprobes. Species with both broad and narrow host range are found in most species complexes (Crouch *et al.* 2014, Table S6), especially in the *C. acutatum*, *C. boninense* and *C. gloeosporioides* species complexes. In contrast, species in the *C. caudatum* and *C. graminicola* species complexes are exclusively associated with monocots, and mostly restricted to single species or members of the Poaceae (Crouch *et al.* 2009a, 2014). Comparative genomic analyses indicate that host specificity may be related to gene family contractions (Baroncelli *et al.* 2016), loss of functional genes (Gan *et al.* 2016, Stajich 2017), and maintenance of a targeted arsenal of virulence factors (O'Connell *et al.* 2012). In-depth comparative genomic and transcriptomic analyses, as well as verification experiments of functional genes, are required to elucidate the molecular mechanisms of host specialisation and expansion.

Many *Colletotrichum* species have been isolated from healthy plant tissue and are referred to as endophytes, of which some are also known to be plant pathogenic. However, this does not necessarily imply that all endophytes can switch to a necrotrophic lifestyle (Cannon *et al.* 2012), and distinguishing between the two life strategies is difficult. According to Bhunjun *et al.* (2021), 16 out of the 40 endophytic *Colletotrichum* species can cause disease symptoms in host plants. Our large-scale survey revealed only three additional necrotrophs among the previously known endophytic species (*C. caudisporum*, *C. duyunensis*, and *C. metake*) (Table S7). By contrast, six newly described species (*C. buxi*, *C. chamaedoreae*, *C. nageiae*, *C. schimae*, *C. telosmae*, and *C. variable*) have been isolated exclusively as endophytes to date. This largely implies that some of the 33 *Colletotrichum* species that are currently reported as endophytes only (Table S7) might live as beneficial organisms in the host plant and may not cause plant disease.

Although morphological characters are insufficient to distinguish *Colletotrichum* species, they are considered as important taxonomic characters for the identification of species to species complexes (Cannon *et al.* 2012). For example, conidia of most species in the *C. acutatum* species complex have acute ends or at least one acute end (Damm *et al.* 2012a); conidia of most species in the *C. gigasporum* species complex are notably larger than those formed by other species complexes (Liu *et al.* 2014); and typical conidia of *C. boninense* species complex are cylindrical with a prominent basal scar (Damm *et al.* 2012b). However, many species in various species complexes (e.g. the *C. dracaenophilum*, *C. magnum*, and *C. orchidearum* species complexes), as well as singleton species, form cylindrical conidia with round ends, which is regarded as a typical feature of the *C. gloeosporioides* complex (Damm *et al.* 2019). A schematic overview of the typical conidium and ascospore features of each *Colletotrichum* species complex is provided in Fig. 40. In general, species of the *C. acutatum*, *C. bambusicola*, *C. boninense*, *C. dracaenophilum*, *C. gigasporum*, *C. gloeosporioides*, *C. magnum*, *C. orbiculare*, and *C. orchidearum* species complexes produce straight conidia, while species in the *C. caudatum*, *C. dematium*, *C. graminicola*, *C. spaethianum*, and *C. truncatum* species complexes produce curved conidia (Damm *et al.* 2012a, b, 2013, 2014, 2019, 2020, Weir *et al.* 2012, Yang *et al.* 2012, Crouch 2014, Liu *et al.* 2014, 2015, Jayawardena *et al.* 2016, Liu 2016, Fu *et al.* 2019, Zhang *et al.* 2020). Of note, species complexes with curved conidia are scattered throughout the phylogenetic tree, which indicates that curved spores may have evolved more than once within the genus.

The ITS and multi-locus trees constructed in the current study are consistent with previous reports that the species complexes in *Colletotrichum* are monophyletic except for the *C. graminicola* species complex (Cannon *et al.* 2012, Marin-Felix *et al.* 2017, Bhunjun *et al.* 2021). In the multi-locus phylogenetic tree of the current study (Fig. 1), the *C. graminicola* species complex is inclusive of the *C. caudatum* species complex residing at the top of the clade. However, morphologically, the *C. caudatum* species complex is easily differentiated from the *C. graminicola* species complex by the formation of a filiform appendage at the apex of the curved conidia (Crouch 2014, Fig. 40). Initially, we suspected that this incongruence might be a consequence of the largely incomplete sequence dataset for this group. Specifically, the *his3/gapdh* sequences of most species in the *C. graminicola* species complex, and those of *gapdh/chs-1/his3/act/tub2* of most species in the *C. caudatum* species complex are unavailable, and treated as missing data in the alignments (e.g. Marin-Felix *et al.* 2017, Bhunjun *et al.* 2021, and the current study). However, the subsequent species tree based on 1 893 single-copy orthologous



Fig. 40. An illustration of the diversity of conidia and ascospores in different species complexes of *Colletotrichum*. **A, B.** *Acutatum* (**A.** Conidia of *C. schimae*, NN046984; **B.** Ascospores of *C. salicis*, CBS 607.94). **C.** *Agaves* (Conidia of *C. agaves*, CBS 118190). **D, E.** *Bambusicola* (**D.** Conidia of *C. bambusicola*, LC8468; **E.** Ascus and ascospores of *C. bambusicola*, LC8533). **F, G.** *Boninense* (**F.** Conidia of *C. chamaedoreae*, NN052885; **G.** Ascus and ascospores of *C. chamaedoreae*, NN052885). **H.** *Caudatum* (Conidia of *C. shivasii*, BRIP 15842a). **I.** *Dematium* (Conidia of *C. zhejiangense*, NN076215). **J.** *Destructivum* (Conidia of *Colletotrichum* sp., LC8517). **K.** *Dracaenophilum* (Conidia of *C. buxi*, NN047139). **L, M.** *Gigasporum* (**L.** Conidia of *C. magnisporum*, CBS 398.84; **M.** Ascospores of *C. pseudomajus*, CBS 571.88). **N, O.** *Gloeosporioides* (**N.** Conidia of *C. gloeosporioides*, CGMCC 3.17360; **O.** Ascospores of *C. alienum*, CBS 115183). **P.** *Graminicola* (Conidia of *C. multisepatum*, NN055357). **Q.** *Magnum* (Conidia of *C. magnum*, CGMCC 3.17616). **R.** *Orbiculare* (Conidia of *C. orbiculare*, CBS 570.97). **S, T.** *Orchidearum* (**S.** Conidia of *C. orchidearum*, CBS 135131; **T.** Ascospores of *C. reniforme*, LC8230). **U.** *Spaethianum* (Conidia of *C. iris*, LC3697). **V.** *Truncatum* (Conidia of *C. subacidae*, LC13857). Scale bars = 10 µm.

genes (Fig. 4) revealed the same topology of this group as that in the multi-locus tree (Fig. 1). It is therefore most likely that species in the *C. caudatum* species complex are descendants of a common ancestor of the *C. graminicola* species complex, from which evolved a filiform appendage at the conidial apex. The two species complexes probably should be regarded as one species complex (the *C. graminicola-caudatum* species complex) as proposed by Bhunjun et al. (2021), or as *C. caudatum* sub-aggregate in the *C. graminicola* species complex, as proposed by Crouch (2014).

Although ITS is generally useful for assigning *Colletotrichum* species to species complexes, the allocation of a few individual species within the *C. bambusicola*, *C. caudatum*, *C. destructivum*, *C. graminicola*, and *C. spaethianum* species complexes somewhat contradicts that achieved by using multiple loci. For example, *C. riograndense*, a member of the *C. spaethianum* species complex according to the six-locus phylogeny (Fig. 1), is basal to the *C. bambusicola* and *C. spaethianum* species complexes in the ITS tree (Fig. S1). By contrast, the affiliation of species to species complexes is much more congruent between the six-locus tree and the whole-genome tree (Fig. 4), except for the *C. spaethianum* species complex, which is divided into two subclades in the genome tree. These contradictions among the single- and six-locus gene trees, and the genome tree might result from incomplete lineage sorting, horizontal gene transfer, and hybridisation or recombination through speciation events (Degnan & Rosenberg 2009).

By 3 June 2021, 207 whole genomes of 69 *Colletotrichum* species (Table S4) have been deposited in the NCBI and JGI databases, representing 24.6 % of the currently accepted *Colletotrichum* species. Whole-genome sequences of additional 48 species, including 30 new and 18 known species, were generated and assembled in the current study, increasing the number of genome-sequenced species to 116 (41.4 % of the species, Table S4). To better define the species complex boundaries and reveal the evolutionary relationship of *Colletotrichum*, we generated a whole-genome-based phylogenetic tree in this study. In accordance with the six-locus tree (Fig. 1), most species complexes formed well-supported clades in the species tree, except for the *C. spaethianum* species complex, which did not form a monophyletic clade. As expected, the *C. boninense* and *C. gloeosporioides* species complexes with a large number of species and a wide range of hosts had generally larger number of genes and CAZymes (Fig. 4). This is consistent with the conclusion of Baroncelli et al. (2016) that host range is associated with gene family expansion and contraction in *Colletotrichum*. However, the numbers of genes and CAZymes greatly varied among species in the *C. acutatum* species complex, another species rich group with broad host range. For example, *C. godetiae*, associated with at least 18 genera of host plants (Farr & Rossman 2021), possesses the smallest genome size and number of genes, CAZymes and transporters of this genus (Fig. 4). Considering the importance of the genus *Colletotrichum*, we recommend genome sequencing of all species, especially those plant and human pathogens. This effort will not only pave the way toward a fully resolved *Colletotrichum* tree of life, but also provide essential data revealing their evolution and adaptation mechanisms, and improve the understanding of the genetic basis of various biological features and metabolic potential of these fungi.

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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Fig. S1. Phylogenetic tree of *Colletotrichum* resulting from the RAxML analysis of the ITS sequence alignment. Bootstrap support values (1 000 replicates, GTR-GAMMA model) > 50 % are shown at the nodes. The scale bar represents the expected number of changes per site. Species complexes are indicated with coloured boxes, their names are listed at the left. Ex-type strains are indicated with “T” in the end of the taxa labels.

Table S1. DNA barcodes of all accepted *Colletotrichum* spp. except for the ones in the *C. graminicola* and *C. caudatum* species complexes.

Table S2. DNA barcodes of the accepted *Colletotrichum* spp. in the *C. caudatum* species complex.

Table S3. DNA barcodes of the accepted *Colletotrichum* spp. in the *C. graminicola* species complex.

Table S4. *Colletotrichum* species for which whole-genome sequences are available, retrieved from NCBI and JGI, or generated in the current study.

Table S5. All strains identified in the current study.

Table S6. The substrate/host information for *Colletotrichum* species analysed in the current study, and host information of species reported in China retrieved from literature.

Table S7. *Colletotrichum* species reported as endophytes in previous publications and in the current study.

FIG. S1

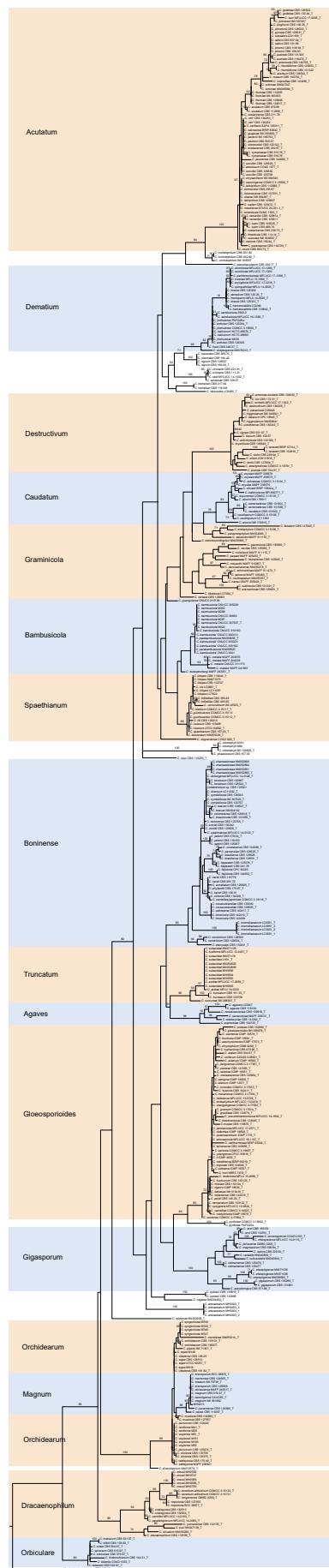


Fig. S1. Phylogenetic tree of *Colletotrichum* resulting from the RAxML analysis of the ITS sequence alignment. Bootstrap support values (1 000 replicates, GTR-GAMMA model) > 50 % are shown at the nodes. The scale bar represents the expected number of changes per site. Species complexes are indicated with coloured boxes, their names are listed at the left. Ex-type strains are indicated with "T" in the end of the taxa labels.

Table S2. DNA barcodes of the accepted *Collectorichum* spp. in the *C. caudatum* species complex.

Species	Culture ^a	Type	Species complex	Host	Country	ITS	GenBank numbers ^b							
							Mat1/APN2	apn2	sod2	gapdh	chs-1	his3	act	tub2
<i>C. alcornii</i>	IMI 176619*	Holotype	Caudatum	<i>Imperata cylindrica</i> var. <i>major</i>	Australia	JX076858	—	—	—	—	—	—	—	—
<i>C. alcornii</i>	IMI 176617	Holotype	Caudatum	<i>Bothriochloa bladhii</i>	Australia	JX076857	—	—	—	—	—	—	—	—
<i>C. baltimorens</i>	BPI 892771, SD-11*	Holotype	Caudatum	<i>Sorghastrum nutans</i>	USA	JX076866	JX076905	JX076927	JX076886	—	—	—	—	—
<i>C. caudatum</i>	CBS 131602, BPI 892767, NY07-CC04*	Epi-type	Caudatum	<i>Sorghastrum nutans</i> cv. Rumsey	USA	JX076860	JX076893	JX076932	JX076878	—	—	—	—	—
<i>C. caudisporum</i>	CGMCC 3.15106*, LC2311	Holotype	Caudatum	<i>Betilla ochracea</i>	China	JX625162	OK225173	MZ674035	KC843512	MZ799318	MZ673852	KC843526	JX625190	MZ799232
<i>C. caudisporum</i>	LC11362	Holotype	Caudatum	<i>Poaceae</i>	China	MZ598485	—	—	MZ674039	MZ664089	MZ799319	MZ673865	MZ664143	MZ673966
<i>C. dipynense</i>	CGMCC 3.15105*, LC2307	Holotype	Caudatum	<i>Betilla ochracea</i>	China	JX625160	—	—	MZ674034	KC843515	MZ799320	MZ673851	KC843530	JX625187
<i>C. gloeosporioides</i>	IMI 356878*, ICMP 17821, CBS 112999	Epi-type	Gloeosporioides	<i>Citrus sinensis</i>	Italy	JX010152	—	—	MZ799225	JX010365	JX010056	JX009818	JQ005413	JX010445
<i>C. ochraceum</i>	CGMCC 3.15104*, LC2303	Holotype	Caudatum	<i>Betilla ochracea</i>	China	JX625156	OK225172	MZ799226	MZ674033	KC843513	MZ799317	MZ673849	KC843527	JX625183
<i>C. shivasii</i> sp. nov.	LC1400, BRIP15842a*	Holotype	Caudatum	<i>Themeda thriandra</i>	Australia	MZ598384	OK225171	—	MZ674032	MZ664088	MZ799316	MZ673848	MZ664134	MZ673957
<i>C. somersetense</i>	CBS 131599, JAC 11-11*	Holotype	Caudatum	<i>Sorghastrum nutans</i>	USA	JX076862	JX076895	JX076918	JX076880	—	—	—	—	—
<i>C. somersetense</i>	CBS 131601, JAC 11-13	Holotype	Caudatum	<i>Sorghastrum nutans</i>	USA	JX076863	JX076894	JX076919	JX076881	—	—	—	—	—
<i>C. zoysiae</i>	MAFF 238573*	Holotype	Caudatum	<i>Zoysia tenuifolia</i>	Japan	JX076871	JX076899	JX076922	—	—	—	—	—	—
<i>C. zoysiae</i>	MAFF 238576	Holotype	Caudatum	<i>Zoysia tenuifolia</i>	Japan	JX076874	JX076902	JX076924	JX076884	—	—	—	—	—
<i>C. zoysiae</i>	MAFF 238574	Holotype	Caudatum	<i>Zoysia tenuifolia</i>	Japan	JX076872	JX076900	JX076923	JX076882	—	—	—	—	—

^aAsterisk (*) refers to ex-type strains.^bBold (highlighted in blue) indicated the sequences generated in this study.

Table S3. DNA barcodes of the accepted *Colletotrichum* spp. in the *C. graminicola* species complex.

Species	Culture ^a	Type	Species complex	Host	Country	ITS	GenBank numbers ^b								
							chs-1	act	tub2	sod2	matr-2	apn2	MAT1/APN2	h3	gapdh
<i>C. axonopodi</i>	IMI 279189*	Holotype	Graminicola	<i>Axonopus affinis</i>	Australia	MJ521697							EU364993	FJ377907	—
<i>C. cereale</i>	CBS 1296/63, K520BHG		Graminicola	<i>Bromus inermis</i>	USA	JQ005774	JQ005795	JQ005837	JQ005858	DQ132277	DQ131946	—	—	—	J0005816
<i>C. dantisaharense</i> sp. nov.	LC13885, NN055218*	Holotype	Graminicola	Probably dead leaves of <i>Miscanthus</i> sp.	China	MZ98898	MZ799330	MZ664196	MZ674016	MZ674022	—	—	—	—	MZ673918 MZ664101
<i>C. dolichocladophori</i> sp. nov.	LC13889, NN054966*	Holotype	Graminicola	Grass	China	MZ98896	MZ799329	MZ664194	MZ674014	MZ674041	—	—	—	—	MZ673916 MZ664094
<i>C. echinochloae</i>	MAFF 511473*	Holotype	Graminicola	<i>Echinochloa esculenta</i>	Japan	AB439811	TX519218	JX519226	JX519234	JX519243	AB440153	AB439820	—	—	—
<i>C. elaeisinae</i>	MAFF 511155*	Epitype	Graminicola	<i>Elaeis indica</i>	Japan	JX519218	JX519226	JX519234	JX519243	EU54234	—	EU365038	—	—	—
<i>C. endophytum</i>	CGMCC 3.15108*, LC2338	Holotype	Graminicola	<i>Blennia ochracea</i>	China	JX625177	MZ799327	KC43353	JX625206	MZ674036	—	—	—	—	MZ673853 KC843521
<i>C. eremicola</i>	CBS 129661*	Holotype	Graminicola	<i>Eremochloa ophiuroides</i> , diseased leaf tissue	USA	JX519220	JX519228	JX519236	JX519245	JQ478449	—	JQ478476	JQ478462	—	—
<i>C. falcatum</i>	CGMCC 3.14187, CBS 147945*	Neotype	Graminicola	<i>Saccharum officinarum</i>	Indonesia	HM171677	JQ005793	JQ005835	JQ005856	—	—	HM569770	HM569769	JQ005814	—
<i>C. glocosporioides</i>	IMI 356878*, ICMP 17821, CBS 112999	Epitype	Glocosporioides	<i>Citrus sinensis</i>	Italy	JX010152	JX009818	JX009531	JX010445	JX010365	—	—	—	JQ005413	JX010056
<i>C. graminicola</i>	CBS 130836*, M 1.001	Epitype	Graminicola	<i>Zea mays</i>	USA	JQ005767	JQ005788	JQ005830	JQ005851	MZ674031	EU365081	—	FJ377994	HQ005809	—
<i>C. hananense</i>	CBS 145900*	Holotype	Graminicola	<i>Axonopus compressus</i>	China	KY242705	—	—	KY242711	—	KY242714	KY242708	—	—	—
<i>C. hanau</i>	MAFF 305404*	Holotype	Graminicola	<i>Digitaria ciliaris</i>	Japan	JX519217	JX519225	—	JX519242	EU54205	—	EU365008	FJ377922	—	—
<i>C. jacksonii</i>	MAFF 305460*	Holotype	Graminicola	<i>Echinochloa esculenta</i>	Japan	JX519216	JX519224	JX519233	JX519241	EU54212	—	—	—	—	—
<i>C. miscanthi</i>	MAFF 510857*	Holotype	Graminicola	<i>Miscanthus sinensis</i>	Japan	JX519221	JX519229	JX519237	JX519246	EU54224	—	EU365028	—	—	—
<i>C. multisepiatum</i> sp. nov.	LC13886, NN055357*	Holotype	Graminicola	Dead culm of grass	China	MZ98901	MZ799331	MZ664199	MZ674019	MZ674043	—	—	—	—	MZ673921 MZ664099
<i>C. nardum</i>	CBS 130837*	Holotype	Graminicola	<i>Panicum virgatum</i>	USA	JQ005770	JQ005793	JQ005835	JQ005875	—	GQ91969	GQ919071	JQ005812	—	—
<i>C. nubiosum</i>	MAFF 511155*	Holotype	Graminicola	<i>Polygonum dilatatum</i>	Japan	JQ005770	JQ005791	JQ005833	JQ005854	EU54229	—	EU365033	FJ377946	—	—
<i>C. paroedephylum</i> sp. nov.	LC13888, NN054963*		Graminicola	Grass	China	MZ98895	MZ799328	MZ664193	MZ674013	MZ674040	—	—	—	—	MZ673915 MZ664057
<i>C. paspali</i>	MAFF 305403*	Holotype	Graminicola	<i>Paspalum notatum</i>	Japan	JX519219	JX519227	JX519235	JX519244	EU54204	—	EU365007	FJ377921	—	—
<i>C. sublineolea</i>	CBS 131301*, S3.001	Epitype	Graminicola	<i>Sorghum vulgare</i>	Burkina Faso	JQ005771	JQ005792	JQ005834	JQ005855	DQ132051	EU365121	FJ378029	JQ005813	—	—
<i>C. tibetense</i> sp. nov.	LC7364*	Holotype	Graminicola	<i>Poaceae</i>	China	MZ98840	MZ799339	MZ664138	MZ673961	MZ674037	—	—	—	MZ673860 MZ772866	—
<i>C. tibetense</i> sp. nov.	LC7366		Graminicola	<i>Poaceae</i>	China	MZ98841	MZ799340	MZ664139	MZ673962	MZ674038	—	—	—	MZ673861 MZ772867	—

^aAsterisk (*) refers to ex-type strains.^bBold (highlighted in blue) indicated the sequences generated in this study.

Table S7. *Colletotrichum* species reported as endophytes in previous publications and in the current study.

Species	Endophyte	Pathogen	Saprobe	Species complex	Reference
<i>C. aotearoa</i>	Yes	Yes		Gloeosporioides	Bhunjun <i>et al.</i> (2021)
<i>C. arxii</i>	Yes			Gigasporum	Bhunjun <i>et al.</i> (2021)
<i>C. bambusicola</i>	Yes			Bambusicola	Wang <i>et al.</i> (2021)
<i>C. bambusicola</i>		Yes		Bambusicola	This study
<i>C. beeveri</i>	Yes			Boninense	This study
<i>C. bleiillae</i>	Yes			Spaethianum	Bhunjun <i>et al.</i> (2021)
<i>C. boninense</i>	Yes	Yes		Boninense	Bhunjun <i>et al.</i> (2021)
<i>C. brevisporum</i>	Yes	Yes		Magnum	Bhunjun <i>et al.</i> (2021)
<i>C. brevisporum</i>	Yes	Yes		Magnum	This study
<i>C. buxi sp. nov.</i>	Yes			Dracaenophilum	This study
<i>C. cacao</i>	Yes			Magnum	Bhunjun <i>et al.</i> (2021)
<i>C. cariniferi</i>	Yes			Dracaenophilum	Bhunjun <i>et al.</i> (2021)
<i>C. caudisporum</i>	Yes			Caudatum	Bhunjun <i>et al.</i> (2021)
<i>C. caudisporum</i>		Yes		Caudatum	This study
<i>C. cereale</i>	Yes	Yes		Graminicola/caudatum	Bhunjun <i>et al.</i> (2021)
<i>C. chamaedoreae sp. nov.</i>	Yes			Boninense	This study
<i>C. chiangraiense</i>	Yes			Boninense	Bhunjun <i>et al.</i> (2021)
<i>C. cigarro</i>	Yes	Yes		Gloeosporioides	This study
<i>C. circinans</i>	Yes	Yes		Dematium	This study
<i>C. clivicola</i>	Yes	Yes		Orchidearum	This study
<i>C. cordylinicola</i>	Yes	Yes		Gloeosporioides	Bhunjun <i>et al.</i> (2021)
<i>C. cosmi</i>	Yes			Acutatum	This study
<i>C. cymbidiicola</i>	Yes	Yes		Boninense	This study
<i>C. dacrycarpi</i>	Yes			Boninense	Bhunjun <i>et al.</i> (2021)
<i>C. dematium</i>	Yes	Yes	Yes	Dematium	Bhunjun <i>et al.</i> (2021)
<i>C. destructivum</i>	Yes			Destructivum	This study
<i>C. doitungense</i>	Yes			Boninense	Bhunjun <i>et al.</i> (2021)
<i>C. duyunensis</i>	Yes			Graminicola/caudatum	Bhunjun <i>et al.</i> (2021)
<i>C. duyunensis</i>		Yes		Graminicola/caudatum	This study
<i>C. endophytum</i>	Yes		Yes	Graminicola/caudatum	Bhunjun <i>et al.</i> (2021)
<i>C. excelsum-altitudinum</i>	Yes			Dracaenophilum	Bhunjun <i>et al.</i> (2021)
<i>C. fioriniae</i>	Yes	Yes		Acutatum	Bhunjun <i>et al.</i> (2021)
<i>C. fioriniae</i>	Yes	Yes		Acutatum	This study
<i>C. fructicola</i>	Yes	Yes	Yes	Gloeosporioides	Bhunjun <i>et al.</i> (2021)
<i>C. fructivorum</i>	Yes	Yes		Gloeosporioides	Bhunjun <i>et al.</i> (2021)
<i>C. gigasporum</i>	Yes	Yes		Gigasporum	This study
<i>C. godetiae</i>	Yes	Yes		Acutatum	This study
<i>C. guangxiense</i>	Yes			Bambusicola	Wang <i>et al.</i> (2021)
<i>C. guizhouensis</i>	Yes			Spaethianum	Bhunjun <i>et al.</i> (2021)
<i>C. horii</i>	Yes	Yes		Gloeosporioides	This study
<i>C. indonesiense</i>	Yes			Acutatum	This study
<i>C. jiangxiense</i>	Yes	Yes		Gloeosporioides	Bhunjun <i>et al.</i> (2021)
<i>C. jishouense</i>	Yes			Gigasporum	Bhunjun <i>et al.</i> (2021)
<i>C. karstii</i>	Yes	Yes		Boninense	This study
<i>C. liriopes</i>	Yes	Yes		Spaethianum	Bhunjun <i>et al.</i> (2021)
<i>C. liriopes</i>	Yes	Yes		Spaethianum	This study
<i>C. magnusporum</i>	Yes			Gigasporum	This study
<i>C. metake</i>	Yes	Yes		Bambusicola	Sato <i>et al.</i> (2012), Wang <i>et al.</i> (2021)
<i>C. merremiae</i>	Yes			Magnum	Bhunjun <i>et al.</i> (2021)
<i>C. miscanthi</i>	Yes			Graminicola/caudatum	Bhunjun <i>et al.</i> (2021)
<i>C. musae</i>	Yes	Yes		Gloeosporioides	Bhunjun <i>et al.</i> (2021)
<i>C. nageiae sp. nov.</i>	Yes			singleton	This study
<i>C. oncidii</i>	Yes	Yes		Boninense	This study
<i>C. panamense</i>	Yes			Magnum	Bhunjun <i>et al.</i> (2021)
<i>C. pandanicola</i>	Yes			Gloeosporioides	Bhunjun <i>et al.</i> (2021)
<i>C. parallellophorum</i>	Yes			Dracaenophilum	Bhunjun <i>et al.</i> (2021)
<i>C. parsoniae</i>	Yes			Boninense	Bhunjun <i>et al.</i> (2021)
<i>C. phyllanthi</i>	Yes	Yes		Boninense	Bhunjun <i>et al.</i> (2021)
<i>C. rhexiae</i>	Yes	Yes		Gloeosporioides	Bhunjun <i>et al.</i> (2021)

Table S7. *Colletotrichum* species reported as endophytes in previous publications and in the current study.

Species	Endophyte	Pathogen	Saprobe	Species complex	Reference
<i>C. rhombiforme</i>	Yes			Acutatum	This study
<i>C. schimae sp. nov.</i>	Yes			Acutatum	This study
<i>C. serratogrense</i>	Yes			Gigasporum	Bhunjun <i>et al.</i> (2021)
<i>C. sydowii</i>	Yes	Yes		singleton	This study
<i>C. telosmae sp. nov.</i>	Yes			singleton	This study
<i>C. temperatum</i>	Yes	Yes		Gloeosporioides	Bhunjun <i>et al.</i> (2021)
<i>C. theobromicola</i>	Yes	Yes		Gloeosporioides	Bhunjun <i>et al.</i> (2021)
<i>C. tofieldiae</i>	Yes			Spaethianum	Bhunjun <i>et al.</i> (2021)
<i>C. tofieldiae</i>	Yes	Yes		Spaethianum	This study
<i>C. tongrenense</i>	Yes			Dracaenophilum	Bhunjun <i>et al.</i> (2021)
<i>C. tropicicola</i>	Yes	Yes		Dracaenophilum	This study
<i>C. variabile sp. nov.</i>	Yes			Gigasporum	This study
<i>C. watphraense</i>	Yes			Boninense	Bhunjun <i>et al.</i> (2021)
<i>C. yunnanense</i>	Yes			Dracaenophilum	Bhunjun <i>et al.</i> (2021)
<i>C. yunnanense</i>	Yes			Dracaenophilum	This study