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Cover: *Entoloma indikon*, habit *in situ*.

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Melanodevriesia, a new genus of endolichenic oleaginous black yeast recovered from the Inner Mongolia Region of China

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Abstract: Black yeasts are a phylogenetically diverse group of ascomycetous fungi that may exist in both unicellular and mycelial morphs. This group of fungi contains numerous commercially significant species as well as others whose precise roles are unknown, such as endolichenic species. There is currently a paucity of data about endolichenic black yeast species. To bridge this gap, we surveyed China's Inner Mongolia Autonomous Region in July 2019. Several fungal species associated with diverse lichens were isolated during this survey. Among these were two isolates of a previously unknown species of oleaginous black yeast from *Mycosphaerellales*. Analyses of morphological and molecular data revealed that these two isolates were closely related to *Xenodevriesia strelitziicola* (*Xenodevriesiaceae*), although with significant differences. As a result, we established the genus *Melanodevriesia gen. nov.* to describe this previously unknown species, *Melanodevriesia melanelixiae sp. nov.* In addition, we used Transmission Electron Microscopy to visualise the intracellular oil bodies metabolised by this fungus in its unicellular state. The black yeast species identified in this study may have a wide range of commercial applications. More research is needed to determine the chemical composition of the microbial oil synthesized by this fungus and whether it has commercial value.

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INTRODUCTION

Fungi and algae (or cyanobacteria) form a symbiotic relationship known as lichen (Lutzoni & Miadlikowska 2009). *Ascomycota* makes up the bulk of lichenised fungi, whereas the remaining fungi are from the *Basidiomycota* (He & Zhang 2012). In addition to these symbiotic fungi, lichen thalli also house a variety of other fungi such as endolichenic fungi (Kellogg & Raja 2017). The ecological role of these non-symbiotic fungi is still largely unknown (Singh *et al.* 2017). It is estimated that more than 18 000 endolichenic fungi colonise lichen thalli (Nash 2008); this includes a group of fungi often referred to as "black yeasts" (also known as "black fungi") (Cañete-Gibas & Wiederhold 2018).

Black yeasts are melanised, non-lichenised and dematiaceous fungi that can concurrently exist in both unicellular and mycelial forms (Zalar *et al.* 1999). The group is phylogenetically diverse, although it mostly consists of fungi from *Ascomycota* (Selbmann *et al.* 2014b). Most of these black yeasts are from the classes *Dothideomycetes* and *Eurotiomycetes* (Egidi *et al.* 2014, Selbmann *et al.* 2014a). Black yeasts from *Dothideomycetes* concentrate in the order *Mycosphaerellales* (Abdollahzadeh *et al.* 2020), whereas in *Eurotiomycetes* they exclusively represent *Chaetothyriales* (Selbmann *et al.* 2005, Isola *et al.* 2016, Selbmann *et al.* 2014b, Sun *et al.* 2020). Melanisation and meristematic growth amongst these fungi evolved in response to extreme environments, in which they thrive (de Hoog 1993, Haase *et al.* 1999, Prenafeta-Boldú *et al.* 2006), such as high temperature, UV radiation, toxic chemicals, oligotrophic environments and many more (Jacobson 2000, Langfelder *et al.* 2003, Lian *et al.* 2005, Selbmann *et al.* 2005, Dadachova *et al.* 2007, Dadachova & Casadevall 2008, Zhao *et al.* 2010).

Apart from melanin, black yeasts also metabolise various other compounds that allow them to thrive in these extreme habitats such as betaine, carotenoids, mycosporines, trehalose and polyalcohols (Moreno *et al.* 2018). Furthermore, while growing on a carbohydrate-rich substrate, some black yeast species accumulate microbial oils (Lamers *et al.* 2016). Single-cell oils or microbial oils are intracellularly stored lipids produced by a variety of oleaginous microorganisms, such as fungi, bacteria, and algae (Li *et al.* 2008, Bellou *et al.* 2016). Single-cell oils are composed of triacylglycerols (TAGs), free fatty acids, polar lipids, sterols, hydrocarbons, and pigments (Ratledge 2004). Microbial oils are preferred over plant- and animal-derived oils because they can be readily scaled up through the application of biotechnology. Furthermore, seasonal fluctuations, geographic location, harvest time, and transportation, which are obstacles in the production

of plant and animal oils, do not influence on the production of single-cell oil (Ward & Singh 2005, Thiru *et al.* 2011).

Oleaginous yeasts are a favoured source of microbial oils because they may accumulate more lipids than other microorganisms. Furthermore, the oil synthesised by bacteria is stored on the external membrane, making it difficult to extract, whereas those produced intracellularly by algae and yeasts have a high concentration of unsaturated fatty acids (Vasconcelos *et al.* 2019). So far, oleaginous yeast such as *Yarrowia lipolytica*, *Rhodotorula glutinis*, *Cryptococcus curvatus*, and *Lipomyces starkeyi* have all been widely studied (Qiao *et al.* 2017).

The majority of black yeast research in China is focused on species that cause human diseases, such as *Exophiala asiatica*, *Aureobasidium* spp., and others (Li *et al.* 2009, Wang *et al.* 2019). The knowledge on endolichenic black yeast species from China and globally is currently scarce. In an attempt to overcome this gap, we surveyed China's Inner Mongolia Autonomous Region in July 2019. Several fungal species associated with diverse lichens were isolated during this survey. Among them were two isolates of a previously unknown species of black yeast from the order *Mycosphaerellales*. In this study, we described this black yeast species using both morphological and genetic data. In addition, we used transmission electron microscopy to visualize the intracellular oil bodies associated with this newly discovered species.

MATERIALS AND METHODS

Collections of lichens

Several *Melanelixia subargentifera* thalli were collected in July 2019 from Mt. Qingyangcheng, Balin Right Banner, Chifeng City, Inner Mongolia Autonomous Region (14 98.8m a.s.l., 44°13'45"N, 118°44'57"E). An individual lichen thallus was scraped off the substrate and kept separately in paper bags. Fungal isolations were made from lichen thalli in the laboratory.

Isolation of fungi from lichen thalli

An individual lichen thallus was cleaned with tap water and then repeatedly rinsed with sterile deionised water. The upper cortex of the thallus was scraped off using a Leica Zoom 2000 dissecting microscope. Pieces of medullary tissues were put on the surface of potato dextrose agar medium (PDA; 46 g PDA powder (Qingdao Hope Bio-Technology Co., Ltd., Shandong, China), and 1 L distilled water, pH 5.6 ± 0.2) amended with 0.05 % streptomycin (Cao *et al*. 2002). All Petri dishes were incubated at 25 °C for 14 d. Mycelia emerging from medullary tissues were sub-cultured onto new PDA plates.

DNA extraction, amplification and sequencing

Using the modified CTAB technique (Doyle & Doyle 1990), genomic DNA was extracted from 14-d-old fungal cultures growing on PDA. For all fungal isolates, the complete internal transcribed spacer (ITS) and partial nuclear large subunit ribosomal DNA (LSU) regions were amplified using primers ITS1/ITS4 (White *et al.* 1990) and LR0R/LR5 (Vilgalys & Hester 1990), respectively.

Each 50 µL of PCR amplification reaction included 19 µL of PCR grade water, 25 µL of 1-5™ 2× High-Fidelity Master Mix (Tsingke Biotech Co., China), 2 µL of each primer (10 µM), and 1 µL DNA template. For both gene regions, PCR amplifications were conducted with an initial denaturation at 94 °C for 3 min, followed by 30 cycles of 94 °C for 30 s, 56 °C for 1 min, 72 °C for 1 min; and final extension at 72 °C for 10 min. Positive amplifications were verified using agarose gel electrophoresis and stained using ethidium bromide. Sangon Biotech Company (Shanghai, China) cleaned and sequenced the PCR products.

The BLAST algorithm (Altschul *et al.* 1990) available through NCBI GenBank was used for the preliminary identification of the fungal DNA sequences. All DNA sequences generated in this study were deposited in NCBI GenBank's nucleotide database (Table 1).

Sequence alignment and phylogenetic analyses

During the preliminary identification of the ITS and LSU sequence data, two of our isolates appeared as a potentially new taxon, closely linked to *Xenodevriesia* and *Paradevriesia* (*Mycosphaerellales*). As a result, two separate datasets for the ITS and LSU gene regions were constructed for phylogenetic analyses. The sequences of the supposedly new taxon identified in this study were included in this data set, as well as selected taxa from the order *Mycosphaerellales* retrieved from GenBank. For phylogenetic taxon sampling, the neighbour-joining trees generated during BLAST searches and previously published phylogenetic by Crous *et al.* (2020) were used. Both datasets were aligned separately with MAFFT v. 7 (Katoh *et al.* 2019) and manually adjusted with MEGA v. 10.2.0 (Kumar *et al.* 2018).

Phylogenetic analyses of single-gene and concatenated datasets were done using maximum likelihood (ML), Bayesian inference (BI) and maximum parsimony (MP) approaches. Software required for ML and BI analyses were accessed through the CIPRES Science Gateway platform (https://www.phylo.org) (Miller *et al.* 2010). The best models of nucleotide substitution were determined by using jModelTest v. 2.1.6 (Darriba *et al.* 2012). RAxML v. 8.2.12 was used for ML analyses with GTR+GAMMA as the substitution model and 1 000 bootstrap replications (Stamatakis *et al.* 2008). For BI analyses, MrBayes v. 3.2.7 (Ronquist & Huelsenbeck 2003) with four MCMC chains were run from a random starting tree for 5 M generations with the stop value set at 0.01, the temperature set at 0.2, with trees sampled every 100 generations. We discarded 25 % of trees sampled as burn-in and the remaining trees (37 500) were used to construct majority rule consensus trees. The MP analyses were performed using MEGA v. 10.2.0 with 1 000 bootstrap replicates, gaps were treated as a fifth state character. The phylogenetic trees from the ML, MP and BI analyses were viewed using FigTree v. 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/). All the alignments and phylogenetic trees were submitted to TreeBASE under accession number 28863.

Colony morphology and light microscopy

The two isolates (CGMCC3.20308 and CGMCC3.20309) of the potentially new taxon from *Mycosphaerellales* were used for recording culture morphology and microscopic structures. For this purpose, both isolates were sub-cultured onto PDA and oatmeal agar (OA; 30 g oatmeal, 15 g agar, 1 L distilled water, pH 7.2 ± 0.2). All the Petri plates were incubated at 25 °C for 40 d. Microscopic morphological characters such as hyphae, conidia, and conidiophores were photographed and measured (n =50 /

Table 1. GenBank accession numbers of selected taxa from *Mycosphaerellales* used for phylogenetic analyses. The new species is shown in boldface.

Species	Strain/Voucher	LSU	ITS
Batcheloromyces alistairii	CPC 18251	JX556237	JX556227
Batcheloromyces leucadendri	CPC 18277	JF499852	JF499832
Batcheloromyces proteae	CBS 110696	EU019247	JF746163
Capnodium coffeae	CBS 147.52	GU214400	MH856967
Capnodium coffeicola	MFLUCC15-206	KU358920	KU358921
Cladosporium cladosporioides	CBS 129108	MH876646	MH865207
Cladosporium herbarum	CBS 129088	MH876640	MH865203
Cladosporium myrtacearum	CBS 126349	MH875385	MH863925
Cladosporium phyllactiniicola	CBS 126354	MH875390	MH863930
Cladosporium pseudocladosporioides	CBS 125993	MH875333	MH863872
Cladosporium scabrellum	CBS 126358	MH875394	MH863934
Cladosporium tenuissimum	CBS 125995	MH876286	MH864840
Cladosporium varians	CBS 126361	MH875397	MH863937
Devriesia shelburniensis	CBS 115876	KF442544	KF442505
Juncomyces californiensis	CPC 37989	MT373351	NR_170828
Lecanosticta pini	CBS 871.95	GQ852598	GU214663
Leptoxyphium madagascariense	CBS 124766	MH874923	MH863407
Melanodevriesia melanelixia sp.nov.	**CGMCC3.20308**	**MW528742**	**MW528736**
	CGMCC3.20309	**MW580586**	**MW580587**
Meristemomyces frigidus	CCFEE5457	GU250389	KF309967
Microcyclosporella mali	CBS 126135	MH875501	MH864044
Microxiphium theae	CBS 202.30	MH866561	MH855113
Montagnula cylindrospora	UTHSC-DI16-208	LN907351	LT796834
Muriphila oklahomaensis	CCF5751	LR736041	LR736040
Mycosphaerelloides madeirae	CBS 116066	KX286989	AY853188
Neocatenulostroma germanicum	CBS 539.88	EU019253	MH862143
Neocatenulostroma microsporum	CBS 110890	EU019255	AY260097
Neodevriesia cladophorae	OUCMBI110119	KU578114	KP269029
Neodevriesia grateloupiae	OUCMBI101249	KU578120	KU578118
Neodevriesia modesta	CCFEE5672	KF310026	KF309984
Neodevriesia simplex	CCFEE5681	KF310027	KF309985
Neodevriesia strelitziae	CBS 122379	GU301810	MH863206
Paramycosphaerella watsoniae	CPC 37392	MN567653	MN562146
Paradevriesia compacta	CBS 118294	NG_059089	NR_144955
Paradevriesia pseudoamericana	CPC 16174	GU570544	GU570527
Paradevriesia americana	CBS 117726	NG_059077	NR_159866
Phyllachora pomigena	CBS 195.33	MH866862	MH855411
Polychaeton citri	CBS 116435	GU214469	GU214649
Pseudotaeniolina globosa	CBS 109889	MH874434	MH862844
Ramularia acris	CBS 109794	KX287010	KX287311
Ramularia acroptili	CBS 120253	EU019257	EU019257
Ramularia helminthiae	CPC 11504	KX287183	KX287481
Ramularia lethalis	CPC 25910	KX287174	KX287472
Ramularia tovarae	CBS 113305	KJ504764	KJ504807
Stenella araguata	CBS 105.75	EU019250	MH860897
Teratosphaeria dimorpha	CPC 14132	FJ493215	FJ023537
Teratosphaeria ovata	CPC 14632	FJ493218	FJ023538
Teratosphaeria profusa	CPC 12821	FJ493220	FJ493196

Table 1. (Continued).

Species	Strain/Voucher	LSU	ITS
Xenodevriesia strelitziicola	CBS 122480	NG_059085	MH863214
	X1045	GU214635	GU214635
Xenopenidiella nigrescens	DOC356	KU216335	KT833169
Xenoramularia arxii	CBS 342.49	NG_058254	KX287552
Xenoteratosphaeria jonkershoekensis	CBS 122897	MH874777	MH863253

structure) using a Leica DFC495 camera attached to a Leica DM6 microscope. ImageJ was used for measuring the taxonomically relevant structures (Collins 2007).

The ex-holotype cultures were deposited in Beijing, China General Microbiological Culture Collection Center (CGMCC). The type specimen was deposited in the Institute of Microbiology's (HMAS) Fungarium in Beijing, China.

Electron microscopy for visualising intracellular oil bodies

For visualising intracellular oil bodies using transmission electron microscopy (TEM), isolates of the unknown fungus were sub-cultured onto PDA for 14 d. Thereafter, the yeast-like cells were fixed using 2.5 % glutaraldehyde at 4 °C for 2–3 h (Brisson *et al.* 1996). The fixed cells were rinsed repeatedly using 0.1 M phosphate buffer saline (PBS; pH 7.2). Cells were post-fixed using 1 % osmium tetroxide for 1.5 h in darkness. These post-fixed cells were rinsed twice with PBS followed by ultrapure water (three to four times). The cells were gradually dehydrated with 50, 70, 80, and 90 % ethanol, then 90 % acetone and absolute acetone. The dehydrated tissues were embedded in Epon 812 and sliced into 70 nm ultra-thin sections using a Leica UC7 ultra-microtome. Sections were stained using 2 % uranyl acetate for 15 min followed by lead citrate for 8 min (Reynolds 1963). Stained sections were dried under infrared light for 10 min. The structure of oil bodies in the cells were observed using a Hitachi HT-7800 transmission electron microscope at 80 kV.

RESULTS

Phylogenetic analyses

In the phylogeny of selected taxa from the *Mycosphaerellales*, *Cladosporiales* and *Capnodiales*, the ML tree topologies were largely consistent between the datasets (Fig. 1). However, compared to the LSU and concatenated ITS+LSU phylogeny, the placement of the novel species differed in the ITS phylogeny. In both the LSU and ITS+LSU phylogenies the new species is sister to *Xenodevriesia strelitziicola* in the *Xenodevriesiaceae*. However, posterior probability and maximum-likelihood bootstrap values supporting this clustering were highly significant for the LSU tree only (Fig. 1). In the ITS tree, the new species emerged as a basal lineage to a clade that included species of *Neodevriesia*, *Paradevriesia*, and *X. strelitziicola* with poor statistical support. The parsimony analyses did not provide any support for the associations in the ITS+LSU and ITS phylogenies, but moderate support in the LSU phylogeny (Fig. 1). The strange placement of our isolates in the ITS phylogeny could be an artefact of the divergent ITS sequences spanning different families used in the analysis.

The tree topologies from both the LSU and ITS+LSU datasets, as well as the accompanying statistical support values, revealed that our two isolates of the previously undescribed species represents a new genus. Below, we establish the new genus *Melanodevriesia* to accommodate this unknown species as *Melanodevriesia melanelixiae sp. nov*.

Taxonomy

Melanodevriesia H.L. Si, W.Q. Cao, & T. Bose, ***gen. nov.*** MycoBank MB 839404.

Etymology: The name refers to the black colony formed by the fungus when growing on PDA and OA.

Slow-growing colonies on PDA and OA are black to brownish black in colour. The fungus grows in a yeast-like unicellular state on PDA, producing pseudohyphae by continuous budding. These yeast-like cells have several conspicuous intracellular oil bodies. The thallus on OA and other oligotrophic media is made up of septate straight or corrugated branching hyphae.

Type species: *Melanodevriesia melanelixiae* H.L. Si, W.Q. Cao & T. Bose

Notes: *Melanodevriesia* is currently a monotypic genus that includes *M. melanelixiae*, which is described below. Despite being a sister genus of *Xenodevriesia* (*Xenodevriesiaceae*), *Melanodevriesia* has distinct morphological characteristics. *Melanodevriesia* has two thallus morphologies: yeast-like and mycelial, both of which are black to brownish black in colour, but *Xenodevriesia* possesses a brown mycelial thallus (Crous *et al.* 2019). *Melanodevriesia* produces chlamydospores which are lacking in *Xenodevriesia*.

Melanodevriesia melanelixiae H.L. Si, W.Q. Cao, T. Bose, *sp. nov.* MycoBank MB 840429. Figs 2, 3.

Etymology: The name is derived from the lichen *Melanelixia subargentifera*, from which both isolates of this fungus were obtained.

This fungus can exist in both a yeast-like and a mycelial state. The yeast-like thallus produces pseudohyphae through budding. These *pseudohyphae* are branched, septate, constricted at the septa, composed of oval to urceiform cells, hyaline to brown in colour, smooth-walled, guttulate, measuring 1.4–3 × 2.3–4.6 µm (Fig. 2). In the *mycelial state*, hyphae grow into the substrate. *Hyphae* branched, septate, smooth-walled, smooth or corrugated, cylindrical, hyaline to pale brown in colour, measuring 1.3–2 µm wide (Fig. 2). *Chlamydospores* spherical to ovoid in shape, solitary often monilioid forming radiating clusters, smooth-walled, pale

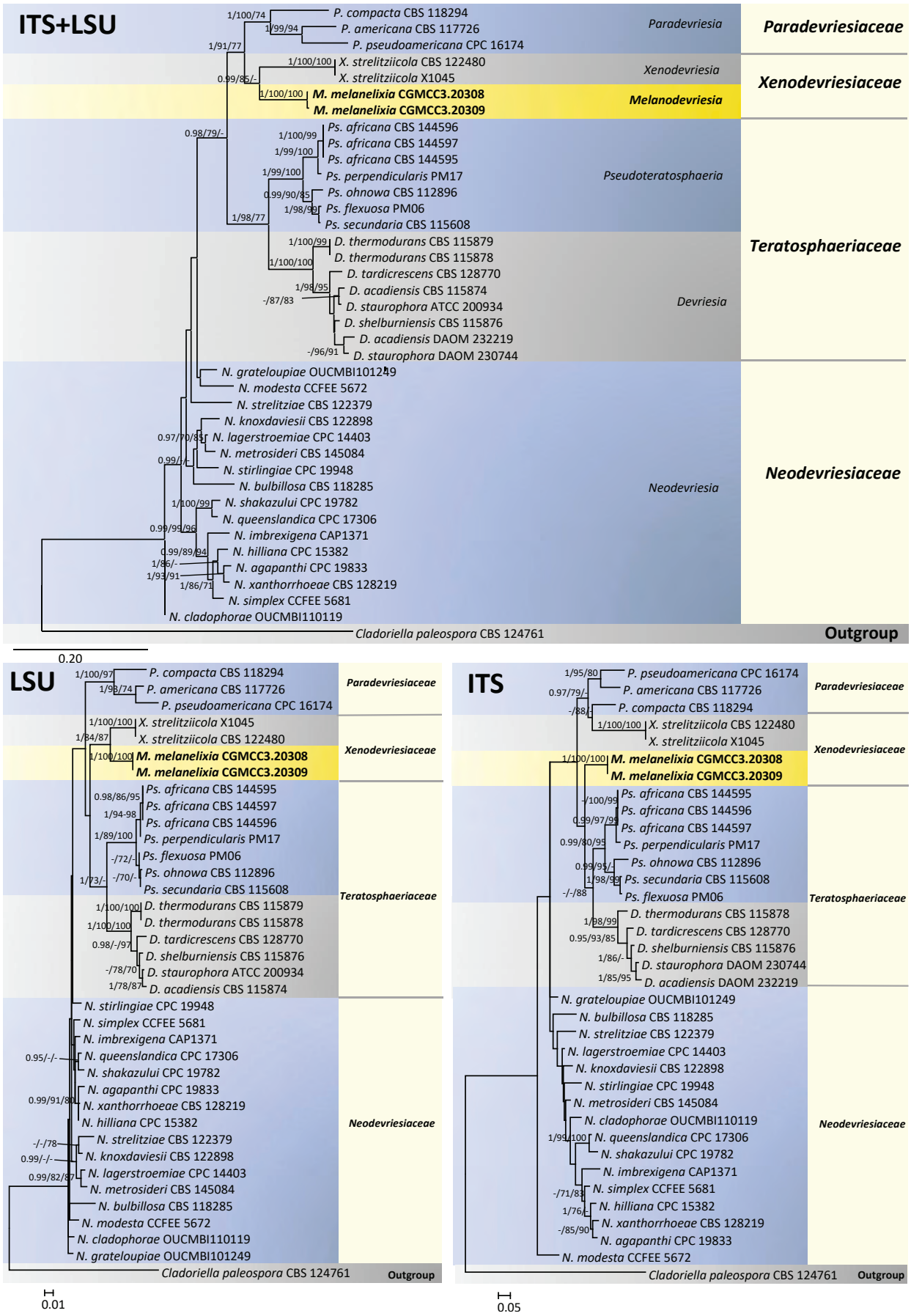

Fig. 1. Maximum likelihood trees were constructed using single gene (ITS and LSU) and concatenated (ITS+LSU) datasets. In the ITS+LSU and LSU trees, both isolates of *Melanodevriesia melanelixiae sp. nov.* formed a monophyletic clade and were sisters to *Xenodevriesia strelitziicola*. However, this clustering was highly significant for the LSU tree only. In the ITS tree, *M. melanelixia* emerged as a basal diverging taxon within a clade that includes species of *Neodevriesia, Paradevriesia, and Xenodevriesia strelitziicola,* but with poor statistical support. The numbers on the branches are statistical support values, Bootstrap values (< 75 %) from maximum likelihood and maximum parsimony analyses, respectively. Thickened branches indicate the posterior probability values ≥ 0.90.

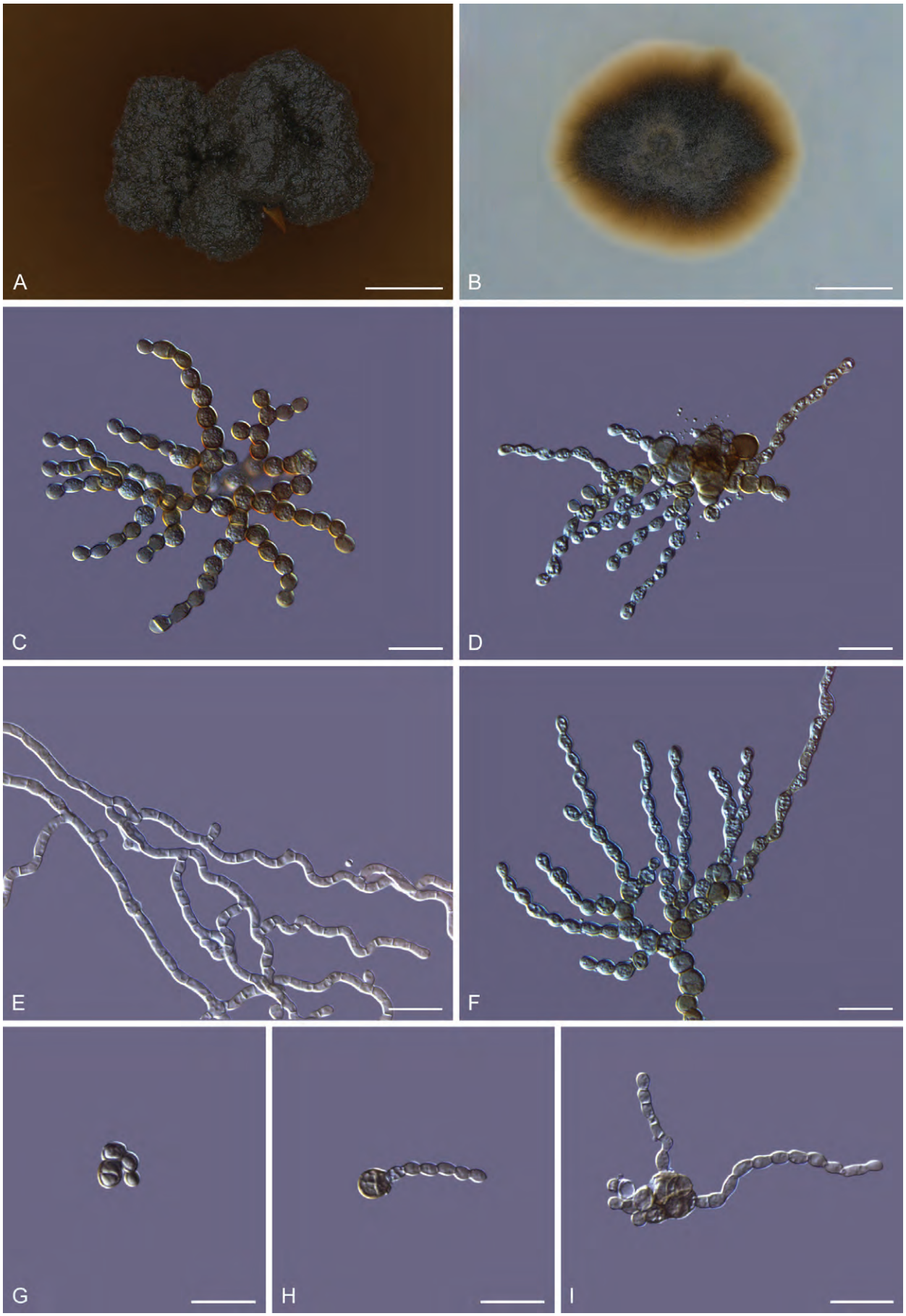

Fig. 2. Morphology of *Melanodevriesia melanelixiae sp. nov.* (ex-type CGMCC3.20309). Colony morphology on potato dextrose agar (**A**) and oatmeal agar (**B**). **C, D.** Microscopic structures of 14-d-old culture growing on PDA medium with yeast-like unicellular morph forming pseudohyphae through budding. **E.** Straight and corrugated septate hyphae produced by the mycelial state of the fungus. **F.** A cluster of monilioid chlamydospores. **G–I.** Single chlamydospores germinating into unicellular cells that multiply through budding, forming a multicellular structure from which pseudohyphae emerge. Scale bars: A, B = 2 mm; C–I = 10 µm.

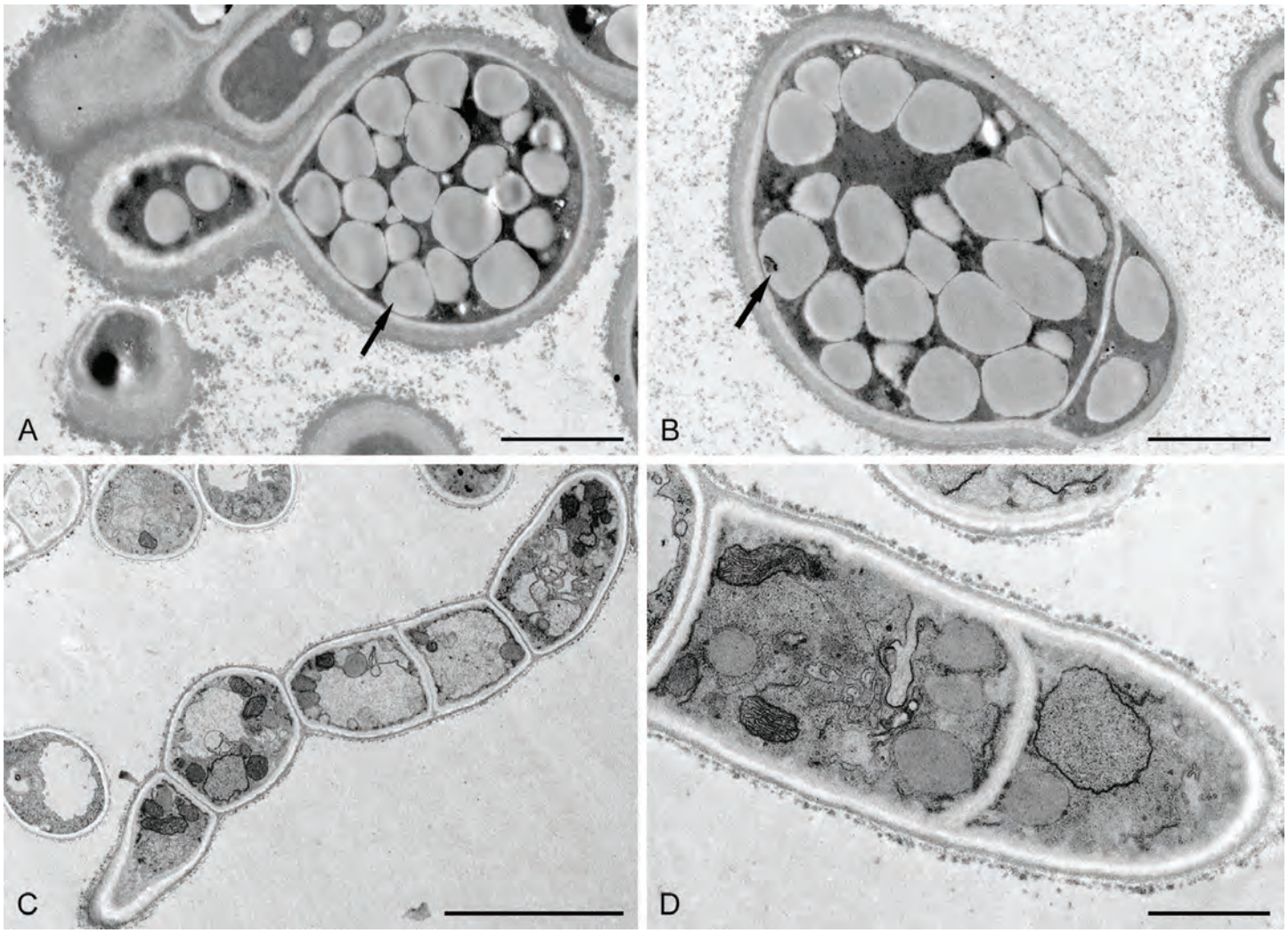

Fig. 3. Transmission electron microscopic images of pseudohyphae and mycelium of *Melanodevriesia melanelixiae sp. nov.* (ex-type CGMCC3.20309). **A, B.** Budding yeast-like unicellular cell with thick cell walls. Multiple intracellular oil bodies concealing the cell organelles (indicated with arrows). **C, D.** Septate hyphae with a thin cell wall that is devoid of intracellular oil bodies. Due to the lack of intracellular oil bodies, various cell organelles are visible. Scale bars: A, B = 2 µm; C = 10 µm; D = 1 µm.

brown to dark brown in colour, usually aseptate, rarely septate, guttulate, measuring 2.8–4.2 × 2.8–4.8 µm (Fig. 2). Chlamydospores geminate into yeast-like *unicellular conidia* that are globose to subglobose in shape, pale brown to dark brown in colour, thick-walled, measuring 4–7.3 × 3.6–6.2 µm (Fig. 2). These unicellular cells multiply through budding (Fig. 2) forming multicellular structures from which pseudohyphae emerge randomly (Fig. 2). No sexual reproductive structures were observed.

Culture characteristics: After 12 wk on PDA, the surfaces of the colonies were dark brown to black with the reverse dull brown in colour, erumpent, hollow, with irregular margins, rarely with a few aerial mycelia. After a few weeks after subculturing, the colony stains the PDA brown. Colonies slow-growing, reaching 3.1 ± 0.1mm diam after incubating at 25 °C for 12 wk (Fig. 2).

After 8 wk on OA, the colonies are round to oval in shape, with smooth margins, surface taupe brown to olive-brown with the reverse taupe brown in colour. Colonies are slow-growing on OA yet faster than on PDA, reaching 5.42 ± 0.2 mm diam after incubating at 25 °C for 8 wk (Fig. 2).

Intracellular oil bodies: The TEM of yeast-like cells grown on PDA revealed thick cell walls with many inconspicuous oil bodies concealing the other cell organelles. Hyphae grown on OA lacked thick cell walls and intracellular oil bodies (Fig. 3).

Typus: **China**, Inner Mongolia Autonomous Region, Chifeng, Balin Right Banner, Mt. Qingyangcheng, 44°13'46"N, 118°44'57"E, 1 498.8 m alt, isolated from the medullary tissue of *Melanelixia subargentifera*, 7 Jul. 2019, *H.L. Si* (**holotype** HMAS 350275; ex-type culture CGMCC3.20308).

Notes: *Melanodevriesia melanelixiae* differs from *X. strelitziicola* in that it contains at least two thallus morphologies and chlamydospores. Besides this, we did not observe any sexual reproductive structures (Crous *et al.* 2009, 2019).

DISCUSSION

In the present study, two isolates of a black yeast species were isolated from two separate thalli of *Melanelixia subargentifera* collected at the same coordinates. Analyses of morphological and molecular data revealed that these two isolates represent an undescribed genus. As a result, we established *Melanodevriesia gen. nov.* to describe this fungus as *Melanodevriesia melanelixiae*

sp. nov. The TEM images revealed that during the unicellular phase of its life cycle, this fungus accumulates multiple prominent intracellular oil bodies.

In our LSU and ITS+LSU phylogenies, *Melanodevriesia melanelixiae sp. nov.* emerged as a sister taxon of *X. strelitziicola*, a mycelial fungus isolated from a *Strelitzia* sp. in South Africa (Crous *et al.* 2009, 2019). This clustering, however, was only significant in the LSU tree. Future discoveries of new species from *Xenodevriesiaceae* and the availability of sequences from additional gene regions may aid in further delimiting this family.

Melanodevriesia melanelixiae sp. nov. was isolated from the medullary tissue of the lichen *Melanelixia subargentifera*. The slow growth and melanisation of this fungus, like that of other black yeasts, allow it to flourish in harsh conditions like the one where we collected our samples in China. We were unable to determine the particular ecological role of *M. melanelixiae*. However, we believe that this fungus increases the overall fitness of the lichen, allowing it to flourish in harsh environments. This is not an unreasonable hypothesis because *Phaeotheca*, an early-diverging capnodiaceous black yeast encapsulates the algae *Trentepohlia* when proliferating within the thallus of *Racodium rupestre* (Crous *et al.* 2009). This loose association of black yeast and algae might be the early stages of lichen development because the fungus increases the carbon supply to the algae (Gostinčar *et al.* 2012).

Transmission electron microscopy images of our newly discovered fungus, *M. melanelixiae,* revealed that in its yeast-like form, this organism accumulates a copious number of intracellular oil bodies. Similar to several other black yeast species, the microbial oil metabolised by *M. melanelixiae* might have a wide range of commercial applications. However, more research is needed to determine the chemical composition of the microbial oil metabolised by *M. melanelixiae* and if this fungus can be commercially exploited for the production of microbial oils.

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Neohygrocybe pseudoingrata, a new grassland species from Slovakia and the Czech Republic

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Abstract: *Neohygrocybe pseudoingrata*, a new waxcap species known from Slovakia and the Czech Republic, is characterised by its pale greyish coloured and often robust basidiomata (or sporocarps), nitrous smell, context without colour changes, hollow, contorted and compressed stipe and smooth or slightly fibrillose pileus surface. Based on morphology and DNA analysis of ITS and LSU sequences of the collected specimens, *N. pseudoingrata* belongs to *Neohygrocybe* sect. *Neohygrocybe* together with *N. ovina, N. nitrata* and *N. ingrata*. Collections of *N. pseudoingrata* form a well-supported clade in phylogenetic trees.

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INTRODUCTION

The genus *Hygrocybe* as delimited in Boertman (2010) has been split into a number of genera (*Chromosera*, *Cuphophyllus*, *Gliophorus*, *Gloioxanthomyces*, *Hygrocybe, Neohygrocybe* and *Porpolomopsis*) by Lodge *et al*. (2013). *Neohygrocybe* differs from most *Humidicutis*, *Porpolomopsis* and *Gliophorus* species in lacking bright pigments. Lodge *et al*. (2013) described *Neohygrocybe* as having swollen, and stuffed stipes that become hollow; pileus 2–6 cm, hemispherical, becoming umbonate, smooth to scaly, margin becoming fissured, brick colour to fuscous cinereous; lamellae few, sublunate, uncinate, broad, venose, white at first, becoming cinereous.

Members of the genus *Hygrocybe s. l.* (*Hygrocybe*, *Neohygrocybe*, *Gliophorus*, *Porpolomopsis*) and *Cuphophyllus* fall into distinct clades but they usually occur together and are often treated as one group for conservation purposes (*e.g*., Boertmann 2010). Most of these genera occur in "unimproved", mowed or grazed grasslands in Europe, where they figure as good indicators of conservation value of semi-natural and natural grasslands (Adamčík & Kautmanová 2005, Boertmann 2010, Fuljer *et al*. 2020). These grasslands are usually characterised by very low levels of dissolved nitrate and phosphate (Ejrnæs & Brunn 1995). *Hygrocybe s. l.* species, together with a *Clavariaceae*, *Entoloma* and *Geoglossaceae,* form a so called "CHEG" group, by reason of sharing ecological similarities (Rotheroe 2001). However, waxcaps can also produce basidiomata in habitats such as peat bogs, sand dunes and woodlands (Cantrell & Lodge 2000, Griffith *et al.* 2004, Boertmann 2010) and in North America and the tropics they are mainly found in forests (*e.g*. Hesler & Smith 1963, Pegler & Fiard 1978, Læssøe & Boertmann 2008).

The ecological role of waxcaps is still unclear, despite intensive research in this field. Griffith *et al.* (2004) referred to the fact that some of the waxcaps can occur in the grasslands together with mosses and this connection was also noticed by Boertmann (2010). However, their biology remains a mystery since isotopic signatures indicate that they are neither mycorrhizal nor saprotrophic (Seitzman *et al.* 2011, Halbwachs *et al*. 2013). Recent studies revealed that some of the waxcaps can be associated with plant roots and they probably have a biotrophic lifestyle with plants (Halbwachs *et al.* 2013, 2018). Tello *et al*. (2013) proved that at least one species, *Hygrocybe virginea*, is a maternally transmitted endophytic fungus associated with *Plantago lanceolata*.

In this report we describe a taxon new to science found in central European grasslands. It is also likely to have a wider distribution.

MATERIAL AND METHODS

Collections and morphological analyses

Waxcaps were collected in Slovakia and the Czech Republic during 2014–2020, from July to October, at 23 localities by F. Fuljer, M. Zajac and M. Mička. Most of the collections were from the Javorníky Mts. (northwestern part of Slovakia) and the rest were from Biele Karpaty, Jablunkovské medzihorie, Kysucká vrchovina, Turzovská vrchovina (Slovakia) and Českotřebovská

vrchovina (Czech Republic) mountains. Soil type has been determined based on the geological map of Slovakia (http://apl.geology.sk/gm50js).

Descriptions of macro-morphological features were based on fresh material. Colours were coded according to the Pantone colour chart (Pantone Colour Finder 2021). Twenty basidiomata were studied and measured from the holotype collection.

The micromorphology of the studied specimens was investigated by F. Fuljer, D. Boertmann and I. Kautmanová using a Kapa Mic D117 with integrated camera, a Leica SM-Lux, a DIC microscope Nikon Eclipse Ni-U and microphotography were captured by a Nikon DS-Ri2 camera. NIS-Elements Basic Research and MiCam v. 2.4 imaging software were used to measure and examine microscopic features. Tissues, spores and other micro-morphological structures were examined fresh or rehydrated in H_2O or in Congo Red ammonia solution. Altogether 575 spores from 14 basidiomata were studied and measured; spores were measured mainly from spore deposits in H_2O. Fifty basidia, 50 sterigmata and 50 basidioles from five basidiomata were investigated from the rehydrated material in ammonial Congo Red solution. Other microscopic structures, such as gill trama, pileipellis and stipitipellis, were observed in three basidiomata from the holotype. Q value refers to the division of length and width of microscopic structures. Qav refers the average value of Q and av. refers the average length and width of microscopic features.

Type material was deposited in the herbarium of the Slovak National Museum-Natural History Museum, Bratislava (BRA). Nomenclature follows Lodge *et al.* (2013) and Index Fungorum (indexfungorum.org).

DNA extraction, amplification, sequencing

Total genomic DNA was extracted from dried tissue using DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol, but with prolonged incubation time of up to 3 h after addition of the RNA-lytic enzyme. PCR was performed using a BioRad C1000 Touch™ Thermal Cycler. Target region of the internal transcribed spacer regions of ribosomal DNA (ITS) was amplified using primers ITS5 (5'-GGAAGTAAAAGTCGTAACAAGG-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3'; White *et al*. 1990). The large ribosomal subunit of ribosomal DNA (LSU) was amplified using primers LR0R (5'-ACCCGCTGAACTTAAGC-3') and LR5 (5'-TCCTGAGGGAAACTTCG-3'; Vilgalys & Hester 1990). The amplification reactions were conducted in 25 µL total volume using a GoTaq Flexi PCR kit (Promega), the reaction mixture containing 20–25 ng total DNA template, 1 µL of both primers (10 µM), 5 µL of Buffer (5×), 2.5 µL of dNTP (2 mM), 2 µL of $MgCl_2$ (25 mM), 0.2 µL GoTaq Flexi polymerase (5 U) and the final volume was added with ultra pure water. The amplification reaction for ITS and LSU regions was set up as follows: 3 min initial denaturation at 95 °C, 32 cycles (95 °C for 30 s, 55 °C for 30 s, and 72 °C for 1 min + increasing time 2 s per cycle), 10 min final elongation at 72 °C. The PCR products were analysed on 2 % agarose gel. PCR products were purified using a Thermosensitive Alkaline Phosphatase (FastAP) and Exonuclease 1 (Exo 1) (Thermo Fisher Scientific Inc., USA) according to manufacturer's instructions. The partial gene was sequenced in a commercial laboratory (Eurofins Genomics GmbH, Cologne, Germany). Sequences were visualised, edited and aligned in MEGA-X (Kumar *et al.* 2018). Sequence similarity searches were performed using GenBank BLASTn (http://www.ncbi.nlm.nih.gov/BLAST/) and BOLD Identification System (https://www.boldsystems.org/).

Phylogenetic analysis

DNA sequences of *Neohygrocybe* species and selected outgroup of *Cuphophyllus fornicatus* were downloaded from NCBI on 21 Jan. 2021. All sequences retrieved in this study were sent to BOLD database and transferred to GenBank and accession numbers are listed in Table 1. Evolutionary analyses were conducted in MEGA X (Kumar *et al.* 2018) by using the Maximum Likelihood method and Tamura-Nei model (Tamura & Nei 1993). The tree with the highest log likelihood (-3667.62) is shown (Fig. 1). The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Joining and BioNJ algorithms to a matrix of pair wise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. This analysis involved 26 ITS sequences. There were a total of 782 positions in the final dataset. In the tree, *Neohygrocybe* species were positioned on a separate branch close to the clade of *N. nitrata*, which is consistent with the results from macro- and microcharacters observations.

RESULTS

Taxonomy

Neohygrocybe pseudoingrata Fuljer, Zajac, Boertm. & Kautmanova, ***sp. nov.*** MycoBank MB 842316. Figs 2, 3.

Etymology: Name refers to *Neohygrocybe ingrata*, a species with similar morphology.

Typus: **Slovakia**, Javorníky Mts., Melocík, Veľké Rovné, *ca*. 300 m E from the main road, N49°20'28.14" E18°30'37.65", alt. 798 m, cow grazed and mowed grassland, 21 Jul. 2020, *F. Fuljer* (**holotype** BRA CR33023, ITS GenBank MZ479356, LSU GenBank MZ479363, ITS BOLD NEOHY001-21).

Habitat & *Distribution*: Known from Slovakia and the Czech Republic, probably more widespread but possibly misidentified as *N. ingrata* or *N. nitrata*. Growing gregarious and very often caespitose and may also sporulate in half rings, sometimes solitary or scattered. It has been recorded in different vegetation types, but always in unimproved semi-natural mesic meadows and pastures, from July to October, on acidic, neutral and calcareous soils.

Pileus 20–80 mm, at first hemispherical, later convex to applanate, irregular, often irregularly contorted, sometimes umbonate, or centrally compressed and with splitting margin; surface smooth, or radially fibrillose, dry, when old very often uneven, buff brown, pale brownish, greyish brown, dark brownish grey (Pantone 463C to Pantone 466C). *Stipe* 35–100 × 8–32 mm, fusiform, clavate; irregularly furrowed, compressed, often contorted and tawn; hollow; surface smooth, dry, white with slightly greyish or brownish tinges (Pantone 4246C to

Table 1. Collections studied and analysed in this study by molecular methods with collection numbers, country of origin, GenBank and BOLD accession numbers (some collections of *N. pseudoingrata* were not sequenced, for all collections check Additional materials examined).

Species	Herbarium number	Origin	ITS GenBank Accession No.	ITS BOLD Accession No.
N. ingrata	BRA CR34493	Slovakia	MZ479336	NEOHY 008-21
	BRA CR34490	Slovakia	MZ479339	NEOHY 019-21
	BRA CR34489	Slovakia	MZ479337	NEOHY 025-21
	BRA CR34488	Slovakia	MZ479338	NEOHY 026-21
N. nitrata	BRA CR34492	Czechia	MZ479340	NEOHY 009-21
N. ovina	BRA CR34491	Slovakia	MZ479341	NEOHY 010-21
	BRA CR34487	Slovakia	MZ479342	NEOHY 027-21
N. pseudoingrata sp. nov.	BRA CR33023 holotype	Slovakia	MZ479356	NEOHY 001-21
	BRA CR34363	Slovakia	MZ479355	NEOHY 002-21
	BRA CR34377	Slovakia	MZ479354	NEOHY 003-21
	BRA CR34369	Slovakia	MZ479353	NEOHY 004-21
	BRA CR34368	Slovakia	MZ479352	NEOHY 005-21
	BRA CR34367	Slovakia	MZ479351	NEOHY 006-21
	BRA CR34364	Slovakia	MZ479350	NEOHY 007-21
	BRA CR34374	Slovakia	MZ479349	NEOHY 011-21
	BRA CR34373	Slovakia	MZ479348	NEOHY 012-21
	BRA CR34362	Slovakia	MZ479347	NEOHY 013-21
	BRA CR34371	Slovakia	MZ479346	NEOHY 014-21
	BRA CR34511	Slovakia	MZ479345	NEOHY 015-21
	BRA CR34382	Slovakia	MZ479344	NEOHY 016-21
	BRA CR34365	Slovakia	MZ479343	NEOHY 017-21
	BRA CR34372	Slovakia	MZ479362	NEOHY 018-21
	BRA CR34502	Slovakia	MZ479361	NEOHY 020-21
	BRA CR34378	Slovakia	MZ479360	NEOHY 021-21
	BRA CR34384	Slovakia	MZ479359	NEOHY 022-21
	BRA CR34383	Slovakia	MZ479358	NEOHY 023-21
	BRA CR34370	Slovakia	MZ479357	NEOHY 024-21

Pantone 4247C). *Lamellae* adnexed, often very broad and thick, ventricose, brittle, white with brownish or greyish hue, much paler than pileus, slightly paler than stipe (Pantone P 1-9 C, Pantone 7527C) , sometimes with paler edges. *Context* not reddening (without any colour changes), white, white with brownish hue, especially in cap (in stipe Pantone 7527C, in pileus Pantone 4645C, Pantone 4655C or Pantone 4665C); rather fragile, fibrillose. *Smell* unpleasant, significantly nitrous. *Taste* neutral, sometimes farinaceous. *Spore deposit* white. *Basidiospores* broadly ellipsoid, ellipsoid to ellipsoid-oblong, thin-walled, smooth, hyaline, non-amyloid, sometimes with one big vacuole, (6.5–)7.2–10.2(–11.8) × (4.4–)4.7–6.4(–7.5) µm, av. = 8.4 × 5.5 µm, Q = (1.1–)1.3–1.8(–2.1), Qav. = 1.56 (575 spores from 14 basidiomata measured from the type collections). *Basidia* (33.5–)35–51(–55) × (5.5–)6.8–9.5(–11.3) µm, av. = 42 × 8 µm (50 basidia from five basidiomata measured from the holotype), predominantly 4-spored, narrowly clavate to clavate, sterigmata (2.5–)2.7–6.6(–6.9) µm (50 sterigmata from five basidiomata measured from the holotype), awl-shaped. *Basidioles* (30.5–)33–46(–49) × (5.4–)5.9–8.7(–10.1) µm (50 basidioles from five basidiomata measured from the holotype), clavate to broadly clavate. *Cystidia* absent. *Pileipellis* a cutis with cells 28–146 × 3.5–15 µm. *Stipitipellis* a cutis with some free hyphal ends (resembling a thrichoderm) with cells 25–160 × 3.9–17 µm, cells below pileipellis with brownish content. *Gill trama* subregular with cells 30–155 × 4–26.5 µm (some up to 400 µm), ± cylindrical, vermiform and sometimes with slightly inflated ends, long slender cells in centre and shorter cells to the sides. *Clamps* abundant in all tissues.

Additional materials examined: **Czech Republic**, Českotřebovská vrchovina Mts., Česká Třebová, alt. 475 m, mesic mowed meadow, 27 Jul. 2020, *M. Mička* (BRA CR34358). **Slovakia**, Javorníky Mts., Tomborov Salaš, Pšurnovice (Bytča), N49°14’2.85” E18°31’59.94”, alt. 384 m, cow grazed and mowed meadow, 4 Oct. 2014, *F. Fuljer* (BRA CR34502); Melocík, Veľké Rovné, N49°20’33.42” E18°30’31.18”, alt. 791 m, small overgrown meadow hidden in the forest, 29 Aug. 2019, *F. Fuljer* (BRA CR34375); Dučkov, Vysoká nad Kysucou, N49°21’38.56” E18°31’51.30”, alt. 722 m, mesic mowed meadow, 31 Aug. 2018, *F. Fuljer* (BRA CR34374); Škápová, Petrovice, N49°14’54.65” E18°31’47.48”, alt. 458 m, mesic mowed meadow, 1 September 2019, F. Fuljer (BRA CR34370); under the Holý vrch, Hvozdnica, N49°12’46.52” E18°27’0.67”, alt. 547 m, mesic mowed meadow on calcareous soils, 19 Sep. 2019, *F. Fuljer* (BRA CR34377); Škápová, Petrovice, N49°15’2.01” E18°31’52.58”, alt. 426 m, mesic mowed meadow, 2 Oct. 2019, *F. Fuljer & M. Zajac* (BRA CR34376);

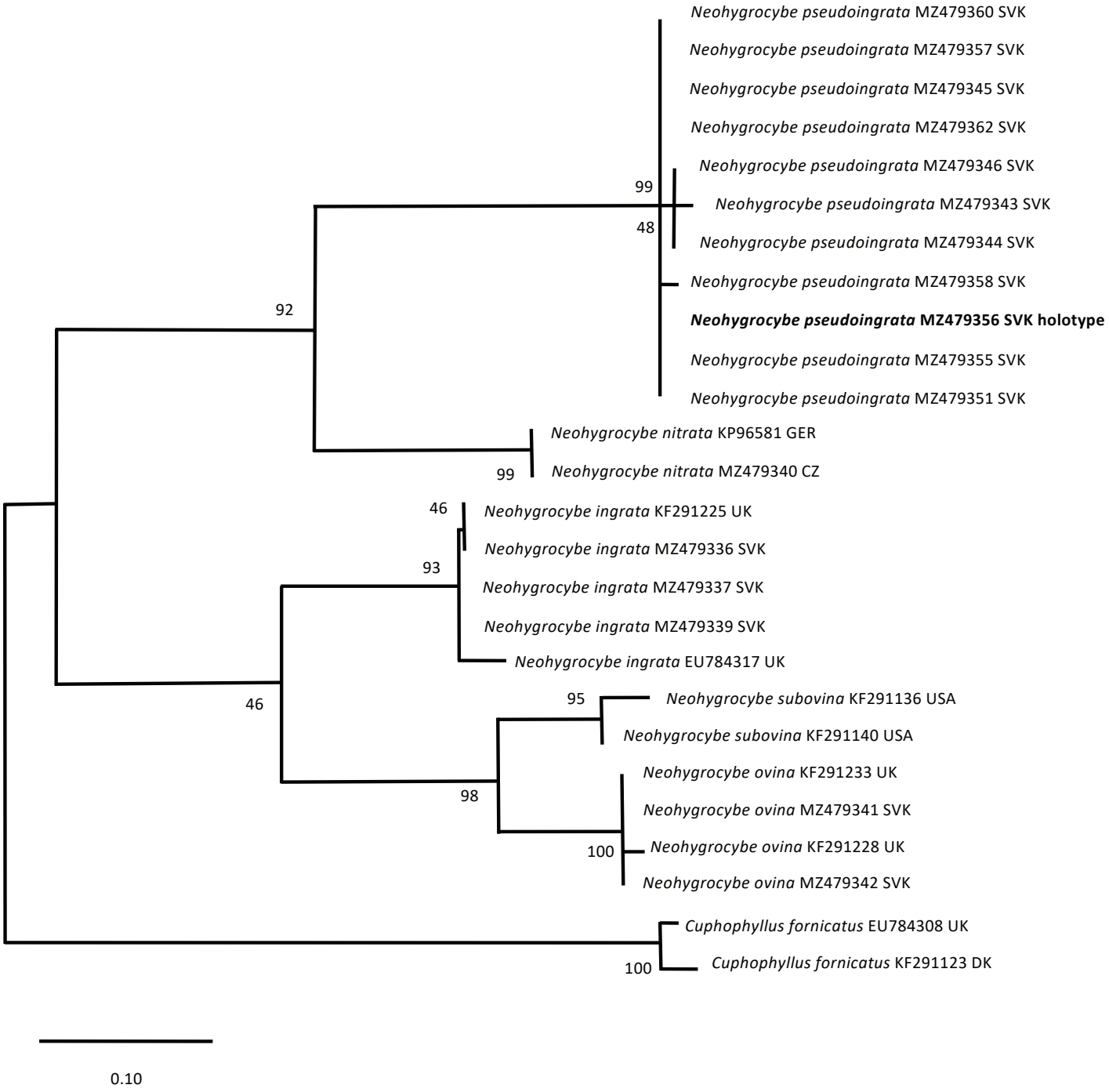

Fig. 1. Maximum likelihood tree obtained from the analysis of ITS sequences of *Neohygrocybe* and *Cuphophyllus fornicatus* as outgroup. Bootstrap support values are indicated at the nodes.

under the Medvedie hill, Petrovice, N49°15'46.82" E18°31'1.80", alt. 422 m, mesic overgrown meadow, 2 Oct. 2019, *F. Fuljer & M. Zajac* (BRA CR34372); Benková, Petrovice, N49°16'4.53" E18°30'52.90", alt. 451 m, mesic mowed meadow, 2 Oct. 2019, *F. Fuljer & M. Zajac* (BRA CR34371); Medvedie, Petrovice, N49°15'53.80" E18°30'57.08", alt. 444 m, overgrown part of mesic meadow, 27 Oct. 2019, *F. Fuljer* (BRA CR34370); Baránkovci, Štiavnik, N49°16'50.71" E18°25'12.50", alt. 692 m, cow grazed pasture, 8 Jul. 2020, *F. Fuljer* (BRA CR34363); Benková, Petrovice, N49°16'2.26" E18°30'47.03", alt. 477 m, mesic mowed meadow, 13 Jul. 2020, *F. Fuljer* (BRA CR34369); Setechov, Petrovice, N49°16'7.00" E18°29'46.72", alt. 560 m, overgrown meadow, 16 Jul. 2020, *F. Fuljer* (BRA CR34368); Vrchrieka, Vysoká nad Kysucou, N49°21'41.23" E18°33'3.74", alt. 790 m, mesic mowed meadow, 22 Jul. 2020, *F. Fuljer* (BRA CR34367); Krželʹ, Papradno, N49°17'40.49" E18°20'15.30", alt. 772 m, overgrown complex of meadows, 24 Jul. 2020, *F. Fuljer* (BRA CR34366); Čiakov, Kolárovice, N49°19'27.38" E18°31'25.04", alt. 674 m, overgrown meadow, 25 Jul. 2020, *F. Fuljer* (BRA CR34365); Tomborov Salaš, Pšurnovice (Bytča), N49°14'0.45" E18°31'57.01", alt. 373 m, cow grazed meadow, 25 Jul. 2020, *F. Fuljer* (BRA CR34364); Brezie, Petrovice, N49°15'41.07" E18°30'57.63", alt. 456 m, mowed meadow, 12 Sep. 2020, *F. Fuljer* (BRA CR34355); Zákysučie, Krásno nad Kysucou, N49°22'44.18" E18°48'59.35", alt. 559 m, overgrowing mesic heathland, 10 Oct. 2020, *F. Fuljer* (BRA CR34356); Medvedie 2, Petrovice, N49°15'46.45" E18°30'51.77", alt. 466 m, small sized overgrown meadow, 26 Oct. 2020, *F. Fuljer* (BRA CR34357); Jablunkovské medzihorie Mts., Poľana, Skalité, N49°30'16.3" E18°55'32.9"alt. 730 m, mesophilic mowed meadow, 25 Jul. 2020, *M. Zajac* (BRA CR34381); Turzovská vrchovina Mts.,

Fig. 2. Macromorphological characters of *Neohygrocybe pseudoingrata*. **A.** Basidiomata in the natural habitat, where the holotype was collected (BRA CR33023, holotype). **B.** Different shapes of basidiomata (PHFF11143, paratype). **C.** The robust stature of *N. pseudoingrata* in the natural habitat (PHFF11554, paratype). **D.** Basidiomata in the natural habitat (PHFF10723, paratype). **E.** Basidioma with brownish pileus, in the natural habitat (PMZ554, paratype). **F.** Basidioma with greyish pileus, in the natural habitat (PHFF11080, paratype). **G.** Cross-section of the well-grown basidioma, hollow stipe and adnexed lamellae visible (BRA CR33023, holotype). **H.** Closer, ventral view on the compressed stipes and lamellae (BRA CR33023, holotype). **I.** Closer view showing the colour, shape and smooth surface of the pileus (BRA CR33023, holotype). Scale bars = 20 mm.

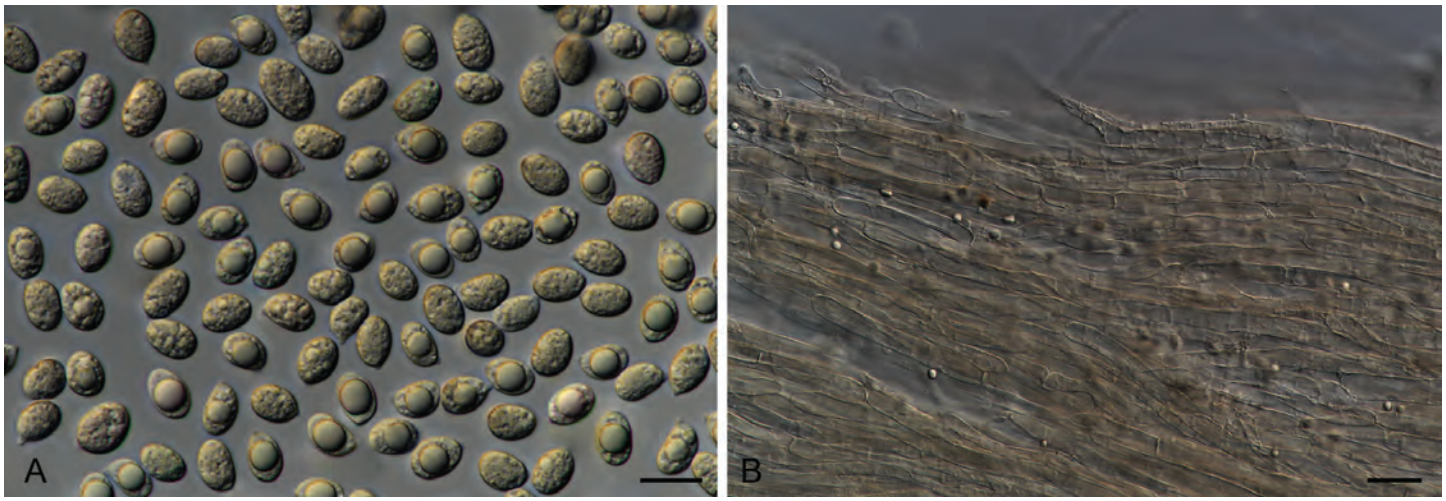

Fig. 3. *Neohygrocybe pseudoingrata* (BRA CR33023, holotype). **A.** Basidiospores. **B.** Pileipellis. Scale bars: A = 10 µm; B = 20 µm.

Boháčovci, Korňa, N49°26'33.33" E18°31'49.19", alt. 714 m, mesic mowed meadow, 8 Sep. 2019, *F. Fuljer* (BRA CR34362); Ďurajčíkovci, Korňa, N49°25'46.13" E18°31'4.40", alt. 698 m, mesic mowed meadow, 8 Sep. 2019, *F. Fuljer* (BRA CR34379); Hlavice – Flintovci, Klokočov, N49°27'52.4" E18°36'33.2", alt. 720 m, mesic mowed meadow, 10 Sep. 2019, *M. Zajac* (BRA CR34382); Kysucká vrchovina Mts., Tatarovci – Senkov, Povina, N49°18'08.7" E18°43'52.7", alt. 633 m, mesic mowed meadow, 11 Sep. 2019, *Z. Václavová* (BRA CR34384); Harvelka, Nová Bystrica, N49°21'27.10" E19°8'50.17", alt. 808 m, sheep grazed pasture, 25 Sep. 2019, *F. Fuljer & M. Zajac* (BRA CR34378); Harvelka, Nová Bystrica, N49°21'25.21" E19°8'4.39", alt. 783 m, sheep grazed pasture, 17 Sep. 2020, *F. Fuljer* (BRA CR34359); Brodenec, Snežnica, N49°15'42.87" E18°47'4.41", alt. 459 m, mesic mowed meadow, 7 Oct. 2020, *F. Fuljer* (BRA CR34360); Kysucké Beskydy Mts., Serafinov vlek, Skalité, N49°29'39.1" E18°57'48.8", alt. 725 m, mesic mowed meadow, 28 Sep. 2019, *M. Zajac* (BRA CR34383); Biele Karpaty Mts., Kopánka, Horné Orechové, N48°55'31.31" E18°1'59.62", alt. 261 m, cow grazed pasture, 20 Oct. 2020, *F. Fuljer* (BRA CR34361).

DISCUSSION

Due to the dull colouration of the basidiomata and dry surfaces of stipe and pileus, this new waxcap clearly belongs to the genus *Neohygrocybe*, as has been confirmed also by the phylogenetic analysis. It is a well recognisable species, characterised by robust dull coloured basidiomata, nitrous smell, non-reddening context, pale brownish and greyish, smooth or finely fibrillose pileus, slightly greyish or brownish, contorted, compressed and hollow stipe and broadly ellipsoid to ellipsoid spores (Figs 2, 3). Closely related species are *N. ingrata, N. nitrata* and *N. ovina*. The most similar species is *N. ingrata,* in which the context stains reddish. Young basiomata of *N. pseudoingrata* and *N. ingrata* can be very similar, distinguished only by the reddening context of *N. ingrata*. *Neohygrocybe nitrata* also has a nitrous smell and also lacks the reddish reaction of the context, but it is usually smaller (up to 60–70 mm high), with a more or less squamulose dark brown pileus and thinner stipe (up to 6 mm diam) which is also dark brown. *Neohygrocybe ovina* is much darker, with dark brown, dark grey or almost black stipe, pileus and lamellae and the context is strongly reddening, and the cap may be squamulose. Several other *Neohygrocybe*-taxa have been described from North and Central America, Australia, New Zealand and China (many not yet combined into the genus) such as *Hygrocybe lepidopellis*, *H. cinerascens*, *H. mellita*, *H. albomarginata*, *H. caespitosa*, *H. melleofusca*, *H. ovinoides*, *H. fuligineosquamosa*, *H. waolipo, Neohygrocybe griseonigra*, *N. innata, N. subovina*, and *N. squarrosa* (Hesler & Smith 1963, Pegler 1983, Horak 1990, Desjardin & Hemmes 1997, Cantrell & Lodge 2004, Young 2005, Bessette *et al*. 2012, Wang *et al.* 2018). None of these have been sequenced, but all differ from *N. pseudoingrata* in darker colouration, spore morphology, structure of pileus surface or colour changes. *Cuphophyllus* species differ by deeply decurrent lamellae; *C. fornicatus* is the single species of the genus that lacks decurrent lamellae and strongly resembles *N. pseudoingrata* but for the nitrous smell. Dull coloured *Gliophorus* species differ by lubricous cap and stipe surfaces. *Pseudotricholoma metapodium* is characterised by amyloid spores, solid, non-compressed stipe and lamellae that are not veined.

The indicator value for valuable grasslands of *N. pseudoingrata* is uncertain. Recorded collections from Slovakia and the Czech Republic are from mowed meadows or extensively grazed pastures and were accompanied by various CHEG fungi. Further research will reveal whether the species is rare or only overlooked and misinterpreted. Based on the numerous collections from NW Slovakia it can be assumed that *N. pseudoingrata* is probably common in Slovakia and should be searched for in neighbouring countries.

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Paraphoma garibaldii sp. nov. causing leaf spot disease of *Campanula rapunculoides* in Italy

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Abstract: Leaf and stem spots are among the most important diseases compromising ornamental plants worldwide. In this study, *Paraphoma garibaldii sp. nov*. is described from leaf lesions on *Campanula rapunculoides* in Piedmont, Northern Italy. The new species was characterised using a polyphasic approach including morphological characterisation and a multilocus molecular phylogenetic analysis based on partial nucleotide sequences of the translation elongation factor 1-α (*tef1*), the internal transcribed spacers (ITS) region and the β-tubulin (*tub2*) markers. Pathogenicity tests and the fulfilment of Koch's postulates confirm *P. garibaldii* as a novel foliar pathogen of *Campanula rapunculoides*. Presently, the fungal infection due to *Paraphoma garibaldii* is known from a single location in Italy, and further surveys are required to determine its distribution and relative importance.

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INTRODUCTION

The genus *Phoma* was introduced by Saccardo (1880), but the generic concept was significantly revised by Boerema & Bollen (1975). Boerema *et al.* (2004) divided this genus in nine sections based on morphological features. The section *Paraphoma* was distinguished based on the presence of setose pycnidia and muriform chlamydospores. However, this classification system revealed several difficulties in understanding species boundaries and in reflecting the evolutionary relationships among species. Furthermore, molecular analyses revealed that *Paraphoma* is polyphyletic, and related to genera affiliated with the families *Phaeosphaeriaceae* (de Gruyter *et al.* 2010), *Cucurbitariaceae* and *Coniothyriaceae* (Chen *et al.* 2015). *Paraphoma* is based on *P. radicina*, which was isolated from roots of *Prunus cerasus* in Australia and from rootstocks of *Malus sylvestris* in the Netherlands (de Gruyter *et al.* 2010). Currently, 14 species are included within the genus: *P. chlamydocopiosa*, *P. chrysantemicola*, *P. convolvuli*, *P. dioscoreae*, *P. fimeti*, *P. ledniceana*, *P. melnickii*, *P. pye*, *P. radicina*, *P. rhaphiolepidis*, *P. salicis, P. variabilis* and *P. vinacea* (Crous *et al*. 2021). Species within *Paraphoma* are generally regarded as soil-borne pathogens. They usually cause root and crown rot disease, but they have been isolated from necrotic leaf spots on *Tanacetum cinerariifolium* (Moslemi *et al.* 2016, 2018). Several *Paraphoma* spp. have been reported in association with ornamental and herbaceous plant hosts. For instance, *P. chrysanthemicola* was isolated from leaf spots on *Atractylodes japonica* in China (Ge *et al.* 2016). Three *Paraphoma* species were found in association with *T. cinerariifolium* in Australia: *P. vinacea* (Moslemi *et al.* 2016), *P. chlamydocopiosa* and *P. pye* (Moslemi *et al.* 2018), *Paraphoma radicina* was isolated from crown rot on *Medicago sativa* in China (Cao *et al.* 2020), while *P. convolvuli* and *P. melnikiae* were identified in association with leaf spots of *Convolvulus arvensis* in Russia (Gomzhina *et al.* 2020).

Ornamental plants represent an economically important sector of agriculture worldwide. Presently, Europe is leading in ornamental plant production, with The Netherlands ranking first, followed by Italy (DG-AGRI-G2 2020). In particular, bedding plants represent a major group in the ornamental sector with a continuous increasing commercial value and relevance. However, seeds, propagation materials and growing media could consistently influence bedding plants cultivation, as there are several diseases affecting them (Guarnaccia *et al.* 2021a). *Campanula* spp. are popular bedding plants, and these are planted on the borders of parks and gardens (Garibaldi *et al.* 2017a). Several fungal pathogens have been found in association with *Campanula* spp. in Italy including *Sclerotinia sclerotium* on *Ca. carpatica* (Garibaldi *et al.* 2002), *Coleosporium campanulae* on *Ca. rapunculoides* and *Ca. trachelium* (Garibaldi *et al.* 2017b, 2021), and *Golovinomyces orontii* on *Ca. glomerata* and *Ca. rapunculoides* (Garibaldi *et al.* 2012, 2018). *Campanula* spp. are also severely affected by leaf anthracnose caused by *Colletotrichum lineola* and *C. nymphaeae* (Guarnaccia *et al.* 2021b) and Alternaria leaf spot caused by *Alternaria alternata* which can cause severe defoliation (Garibaldi *et al.* 2017a). Moreover, different *Campanula* spp. were reported as susceptible to *Rhizoctonia solani* and as hosts of phoma-like taxa, such as *Stagonosporopsis trachelii* (Garibaldi *et al.* 2015, Guarnaccia *et al.* 2021a).

In this study a new *Paraphoma* sp. associated with leaf spots on *Campanula rapunculoides* was identified and characterised on the basis of morphological features and multi-locus DNA phylogeny. Pathogenicity and Koch's postulates were tested.

MATERIALS AND METHODS

Field surveys and fungal isolation

The surveys were conducted in a garden in Piedmont, Northern Italy (45°36'43.8"N 8°03'22.7"E), a site constantly monitored as a representative area exposed to the introduction of new plant pests since the historical data known for this site and its geographical isolation.

At the end of June 2020, leaf spots and stem necrosis were observed on 6-mo-old plants of *Ca. rapunculoides*. The disease index was recorded as the number of symptomatic plants. Small sections (0.2–0.5 cm long) from the margin of lesions were surface disinfected with 1 % sodium hypochlorite for 1 min, rinsed once in sterile distilled water, dried on sterile filter paper and placed on 2 % potato dextrose agar (PDA) plates amended with 25 ppm streptomycin sulphate (Sigma-Aldrich, St. Louis, MO, USA). The plates were incubated at 25 ± 1 °C under a 12 h photoperiod. After 48–72 h of incubation, mycelial plugs were taken from the margin of the resulting colonies and transferred to fresh PDA plates. After 5 d, pure cultures were established from single hyphal tip transfers. Stock cultures were maintained at -80 °C in the Agroinnova (University of Torino) culture collection, Torino, Italy. Reference strains and specimens are maintained in the CBS culture collection of the Westerdijk Fungal Biodiversity Institute (WI), Utrecht, the Netherlands.

DNA extraction, PCR amplification and sequencing

Total DNA was extracted with an E.Z.N.A.® Fungal DNA Mini Kit (Omega Bio-Tek, Darmstadt, Germany), according to the manufacturer's instructions. The nuclear ribosomal internal transcribed spacer (ITS) region was amplified using ITS1 and ITS4 primers (White *et al.* 1990). The primers TUB2Rd and TUB4Fd (Aveskamp *et al.* 2009) were used to amplify part of the β-tubulin (*tub2*) gene. The partial translation elongation factor 1-α (*tef1*) gene was amplified with EF1-728F (Carbone & Kohn 1999) and EF2 (O'Donnell *et al.* 1998) primers. The amplification mixtures and cycling conditions for all three loci were followed as described in each of the cited references. Both strands of the PCR products were sequenced by Eurofins Genomics Service (Ebersberg, Germany). The sequences generated were analysed using Geneious v. 11.1.5 (Kearse *et al*. 2012, Auckland, New Zealand) and consensus sequences were processed.

Phylogenetic analyses

The newly generated sequences were analysed using BLAST search on the NCBIs GenBank (https://blast.ncbi.nlm.nih.gov/Blast.cgi) database to achieve a taxonomic framework by determining the closest relatives. The MAFFT v. 7 online program (http://mafft.cbrc.jp/alignment/server/index.html) (Katoh & Standley 2013) was used to align each gene region of the sequences obtained from this study and sequences downloaded from GenBank. Alignments were then manually adjusted by MEGA v. 7 (Kumar *et al.* 2016). The analyses were conducted individually for each locus (data not shown) and as multi-locus analysis, with the aim of identifying the isolates at species level. Reference sequences were selected based on recent studies on *Paraphoma* species (Moslemi *et al.* 2016, Cao *et al.* 2020, Gomzhina *et al.* 2020, Magaña-Dueñas *et al*. 2021). The phylogeny was developed based on Maximum Parsimony (MP) approach for all individual loci, and on both MP and Bayesian Inference (BI) methods for the concatenated multilocus analyses. For BI, the best evolutionary model for each partition was selected with MrModeltest v. 2.3 (Nylander 2004) and incorporated into the analyses. MrBayes v. 3.2.5 (Ronquist *et al.* 2012) was used to generate phylogenetic trees under optimal criteria per partition. The Markov Chain Monte Carlo (MCMC) analysis used four chains and started from a random tree topology. The heating parameter was established at 0.2 and trees were sampled every 1 000 generations. The analyses were considered done when the average standard deviation of split frequencies was less than 0.01. The MP analyses were conducted using PAUP (Swofford 2003). Phylogenetic relationships were estimated by heuristic searches with 100 random additional sequences. Tree bisection-reconnection was adopted, with the branch swapping option set at 'best trees' only with all characters weighted equally and alignment gaps treated as fifth state. Tree length (TL), consistency index (CI), retention index (RI) and re-scaled consistency index (RC) were calculated, and the parsimony and the bootstrap analyses (Hillis & Bull 1993) were based on 1 000 replications. Sequences generated in this study were deposited in GenBank (Table 1), and the alignments in TreeBASE (www.treebase.org; study number S29045).

Morphology

Slide preparations were mounted in lactic acid from colonies sporulating on sterilised pine needles placed on 2 % tap water agar (PNA) (Smith *et al.* 1996). Observations were performed under a Nikon SMZ25 dissection-microscope, and a Zeiss Axio Imager 2 bright field microscope using differential interference contrast (DIC) illumination, and images recorded on a Nikon DS-Ri2 camera with associated software. Colony features and pigment production were described on 2 % malt extract agar (MEA), PDA and oatmeal agar (OA; Crous *et al*. 2019) after 2 wk at 25 °C. Colony colours were scored using the colour charts of Rayner (1970). The taxonomic novelty was registered in MycoBank (www.MycoBank.org; Crous *et al*. 2004).

Pathogenicity

Pathogenicity tests were performed on healthy *Ca. rapunculoides* plants grown in 2 L pots. The virulence of a representative isolate (CBS 148459) grown for 15 d on PDA at 25 °C, was tested. Leaves of three 5-mo-old plants of *Ca. rapunculoides* were sprayed with a conidial suspension (1×10^5 conidia/mL). Sterile water was sprayed on three plants used as negative control. All inoculated and non-inoculated plants were covered with a transparent plastic film to retain a high level of relative humidity (RH) and kept in a growth chamber at 23 °C with a 12 h photoperiod. The plastic film was removed after 7 d. The experiment was repeated once. All plants were irrigated 2–3 times per week and examined daily for disease symptom development. Disease incidence (DI) was recorded as described above. The inoculated fungi were re-isolated and identified by sequencing the *tub2* and *tef1* loci, thus fulfilling Koch's postulates.

Table 1. GenBank accession numbers of *Paraphoma* spp. and closely related taxa included in this study.

		GenBank accession no.[2]		
Species	**Culture No.[1]**	**ITS**	***tub2***	***tef1***
Juncaceicola alpina	CBS 456.84	KF251181	KF252285	KF253139
J. typharum	CBS 296.54	KF251192	KF252686	KF253148
Neosetophoma samarorum	CBS 138.96	KF251160	KF252655	KF253119
Neostagonospora caricis	CBS 135092	KF251163	KF252658	–
Paraphoma aquatica	FMR 16956^{T}	OU612361	OU612355	–
P. chlamydocopiosa	UMPc01	KU999072	KU999084	KU999080
P. chrysanthemicola	CBS 172.70	KF251165	KF252660	KF253123
	CBS 522.66^{T}	KF251166	KF252661	KF253124
P. convolvuli	MF 9.222	MG764055	–	–
	MF 9.265	MG764062	MG779457	–
	MF 9.301	MG764060	MG779461	–
P. dioscoreae	CBS 135100^{T}	KF251167	KF252662	KF253125
	CPC 11355	KF251168	KF252663	KF253126
	CPC 11361	KF251169	KF252664	KF253127
P. fimeti	CBS 170.70^{T}	KF251170	KF252665	KF253128
	CBS 368.91	KF251171	KF252666	KF253129
P. garibaldii	**CBS 148459**	**OL435708**	**OL449254**	**OL449256**
	CBS 148460	**OL435709**	**OL449255**	**OL449257**
P. ledniceana	CBS 146533	MT371091	MT372661	MT372654
P. melnikiae	MF 9.182	MG764058	MG779454	–
	MF 9.294^{T}	MG764059	MG779455	–
	MF 9.88	MG764063	MG779456	–
P. pye	UMPp02	KU999073	KU999087	KU999081
P. radicina	CBS 102875^{T}	KF251173	KF252668	KF253131
	CBS 111.79	KF251172	KF252667	KF253130
P. rhaphiolepidis	CBS 142524^{T}	KY979758	KY979924	KY979896
P. salicis	CBS 146797	MW883437	MW890140	–
P. vinacea	UMPV002	KU176885	KU176893	KU176897
Setophoma terrestris	CBS 335.29	KF251246	KF252729	KF253196
Xenoseptoria neosaccardoi	CBS 120.43	KF251280	KF252761	KF253227

[1] CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CPC: Culture collection of Pedro Crous housed at Westerdijk Fungal Biodiversity Institute; FMR: Faculty of Medicine and Health Sciences, Reus, Spain; MF: All-Russian Institute of Plant Protection; UMP: University of Melbourne, Ex-type and ex-epitype cultures are indicated with superscript T.

[2] ITS: internal transcribed spacers 1 and 2 together with 5.8S nrDNA; *tub2*: beta-tubulin gene; *tef1*: translation elongation factor 1-α gene. Sequences newly generated in this study are indicated in **bold**.

RESULTS

Field survey and fungal isolation

Leaf symptoms identified as those caused by *Paraphoma* spp. were found in the investigated site with a disease incidence value of 50 %, considered as the percentage of affected leaves. The symptoms were observed on 6-mo-old *Campanula rapunculoides* plants grown in open fields in a private garden. The observed symptoms consisted of grey to brown, necrotic, circular, converging lesions on leaves, chlorotic yellowing and, in some case, defoliation of the investigated host. Moreover, necrosis on stems and wilting of the apical part of the plant were observed. Several colonies resembling *Paraphoma* sp. appeared following isolation, and two monohyphal strains (CBS 148459, CBS 148460) were used for morphological and molecular characterisation.

Taxonomy

Paraphoma garibaldii Guarnaccia, M.L. Gullino & Crous, ***sp. nov.*** MycoBank MB 842029. Fig. 1.

Etymology: Named after Prof. Angelo Garibaldi, in recognition of his contribution to research on ornamental plant diseases.

Conidiomata pycnidial, erumpent to superficial on PNA, wall of 3-4 layers of brown, thin-walled *textura angularis*, globose, 200–300 µm diam, covered by brown, septate, thick-walled, subcylindrical

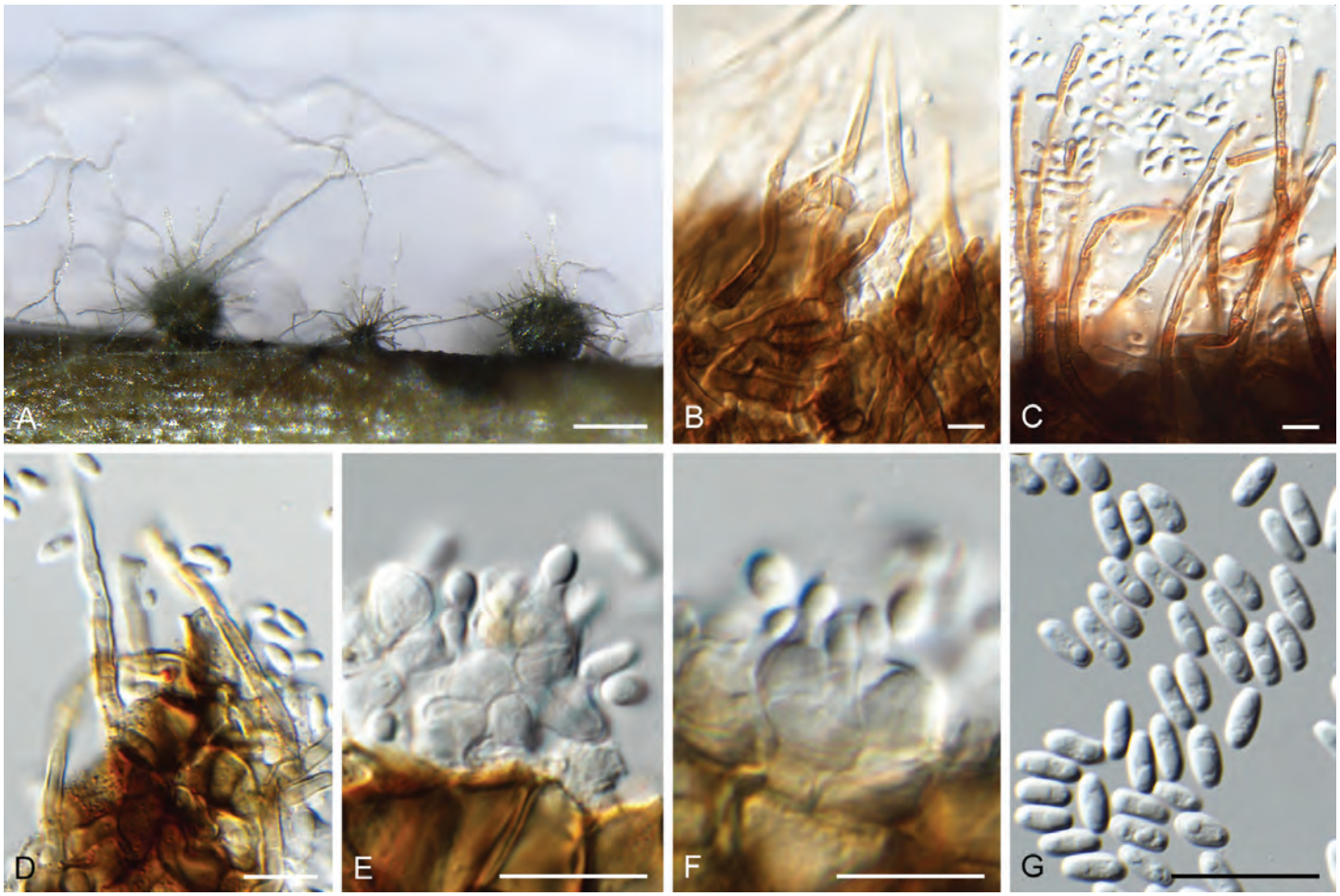

Fig. 1. *Paraphoma garibaldii* (CBS 148459). **A.** Pycnidia with setae forming on PNA. **B–D.** Brown setae arising from outer pycnidial wall. **E, F.** Conidiogenous cells giving rise to conidia. **G.** Aseptate, guttulate conidia. Scale bars: A = 300 µm; All others = 10 µm.

setae, 30–70 × 3–4 µm, with obtuse ends. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, phialidic, hyaline, smooth-walled, ampulliform to doliiform, 5–8 × 4–6 µm, with prominent periclinal thickening. *Conidia* solitary, aseptate, hyaline, smooth-walled, guttulate, subcylindrical, obtuse at the apex and truncate at the base, (4–)5–6(–7) × (2–)2.5(–3) µm.

Culture characteristics: On MEA, PDA and OA, colonies erumpent, spreading with moderate aerial mycelium and even lobate margins, up to 70 mm diam after 2 wk, surface and reverse red.

Typus: **Italy**, Piedmont, Biella, on leaf spots of *Campanula rapunculoides* (*Campanulaceae*), May 2021, *A. Garibaldi* (**holotype** CBS H-24894, culture ex-type CBS 148459).

Additional material examined: **Italy**, Piedmont, Biella, on leaf spots of *Ca. rapunculoides*, May 2021, *A. Garibaldi,* CBS 148460.

Notes: *Paraphoma garibaldii* is phylogenetically distinct from all 14 species of the genus. Morphologically, its conidia are similar to those of *P. variabilis* (4–8 × 2–3 µm, from dung, Spain; Crous *et al*. 2021), but distinct in that the latter has greyish colonies and shorter (7–25 × 2.5–3 µm), subhyaline setae.

Phylogenetic analyses

Based on the results by BLAST search, all the sequences obtained in this study showed high similarity (around 96 %) with species included in the *Paraphoma* genus, however they were identical with no particular species. Three alignments representing single locus analyses of ITS, *tub2*, *tef1* (data not shown), and a combined alignment of the three loci were analysed. The single phylogenetic analysis generated by each locus produced a similar tree topology. The strains of *Paraphoma garibaldii* formed a well-supported monophyletic clade in the ITS, *tub2* and *tef1* single-locus trees, with maximum bootstrap values, respectively. The multi-locus phylogeny consisted of 30 sequences, including *Setophoma terrestris* (CBS 335.29, Gomzhina *et al.* 2020) as outgroup. A total of 1 172 characters (ITS: 1–502, *tub2*: 509–777, *tef1*: 784–1 172) were included in the phylogenetic analysis, 456 characters were parsimony-informative, 239 were variable and parsimony-uninformative, and 464 were constant. A maximum of 1 000 equally MP trees were saved (Tree length = 1 899, CI = 0.656, RI = 0.737 and RC = 0.483). Bootstrap support values from the MP analysis are included on the Bayesian tree in Fig. 2. For the BI, MrModeltest suggested that all partitions should be analysed with dirichlet state frequency distributions. The following models were recommended by MrModeltest and used: GTR+I+G for ITS, K80+G for *tub2* and HKY+G for *tef1*. In the BI, the ITS partition had 219 unique site patterns, the *tub2* partition had 161 unique site patterns, the *tef1* partition had 245 unique site patterns and the analysis ran for 675 000 generations, resulting in 1 352 trees of which 534 trees were used to calculate the posterior probabilities.

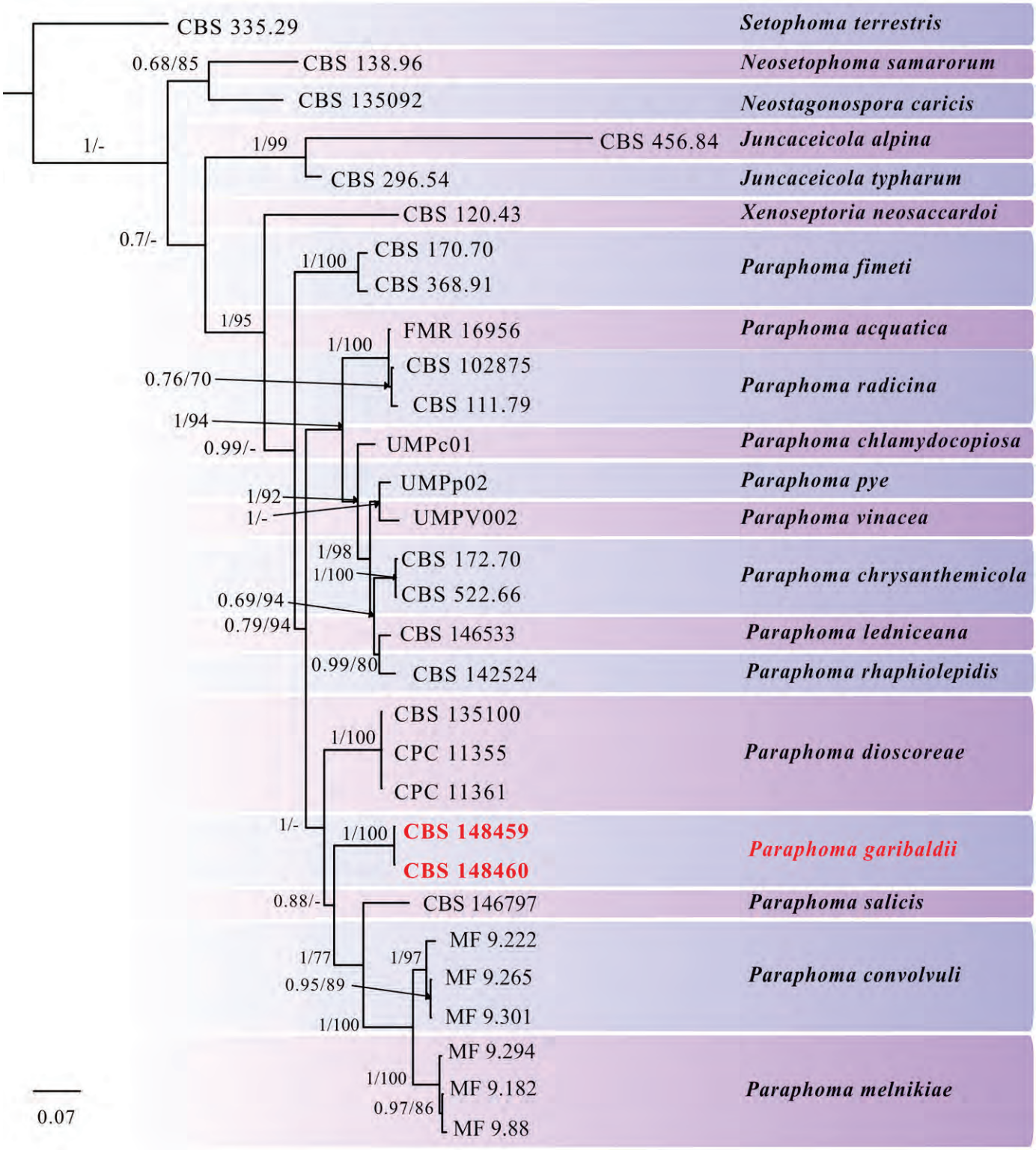

Fig. 2. Consensus phylogram of 1352 trees resulting from BI of the combined ITS, *tub2* and *tef1* datasets. Bayesian posterior probability values and bootstrap support values are indicated at the nodes. The tree was rooted with *Setophoma terestris* (CBS 335.29).

Pathogenicity

Isolate CBS 148459 was pathogenic for 100 % of the inoculated *Ca. rapunculoides* plants causing similar symptoms observed for the first time on the cultivated plants grown in the garden. Dark brown leaf spots appeared 7 d after inoculation, and leaves wilted 5 d after the appearance of large chlorotic areas and the expansion of necrotic tissues (Fig. 3). No symptoms appeared on control plants. The pathogen was consistently re-isolated from the inoculated plants and identified with molecular analysis as described above.

DISCUSSION

In this study two *Paraphoma* isolates were recovered from *Ca. rapunculoides* plants showing leaf spot symptoms in Piedmont, Northern Italy during 2021, and identified based on single and multi-locus (ITS, *tub2* and *tef1*) phylogenetic analyses, as well as morphological characters. These analyses revealed the two isolates to represent a novel species erected here as *Paraphoma garibaldii*.

The robust three-locus based analysis distinguished *P. garibaldii* from other *Paraphoma* species, and other genera

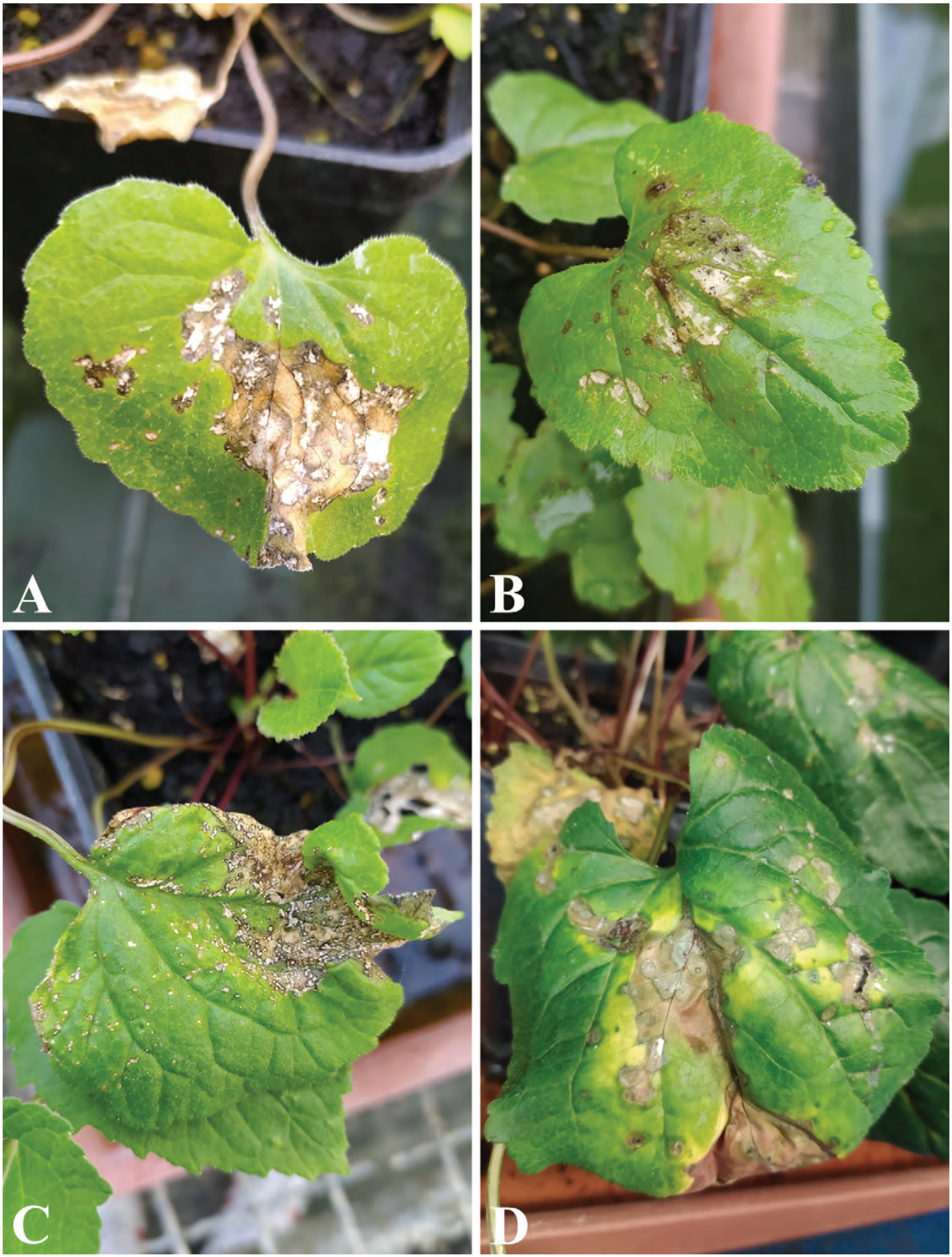

Fig. 3. Symptoms caused after artificial inoculation of *Paraphoma garibaldii* on *Campanula rapunculoides*. **A.** Necrotic leaf area. **B, C.** Leaf spots. **D.** Necrosis surrounded by a chlorotic area.

causing foliar diseases on this crop, such as *Alternaria*, *Coleosporium*, *Colletotrichum* and *Stagonosporopsis*. In spite on the recent detection of similar leaf diseases caused by other fungal species in the same geographic area (Guarnaccia *et al*. 2021b), *P. garibaldii* was the only fungus associated with leaf spot disease in this survey, demonstrating it was able to cause leaf spot disease independently. Furthermore, pathogenicity tests confirmed that *P. garibaldii* causes the disease on *Ca. rapunculoides,* thereby fulfilling Koch's postulates.

This study has revealed and characterised a novel pathogenic fungal species, *P. garibaldii,* associated with leaf spot on *Campanula rapunculoides*, which is one of the most common ornamental bedding plants in Italy. As no epidemiological data are yet available, it is not possible to suggest any control strategies to control *P. garibaldii* infections. Several previous studies in the same geographical area have revealed a wide diversity of soil- and air-borne fungal species (Garibaldi *et al*. 2017a), including more taxa pathogenic to *Campanula* spp. (Guarnaccia *et al*. 2021b). Further surveys are required to determine the distribution of *P. garibaldii*, as it might represent a limiting factor for future cultivation of *Ca. rapunculoides*.

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Conflict of interest: The authors declare that there is no conflict of interest.

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Dendrodacrys: a new genus for species with branched hyphidia in *Dacrymyces s.l.*, with the description of four new species

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species delimitation
systematics

Abstract: A new genus named *Dendrodacrys* is proposed for a monophyletic group in *Dacrymycetaceae*, containing species with pulvinate to depressed basidiocarps, distinctly branched hymenial hyphidia, and up to 3-septate mature basidiospores. Four taxa in this group, occurring in Europe, are proposed as new species, *viz*. *De. ciprense*, *De. concrescens*, *De. ellipsosporum*, and *De. oblongisporum*, based both on morphological and DNA data (nrDNA, *RPB1*, *RPB2*, *TEF-1α*, 12S). These new species are all described in detail, illustrated, and compared with other published taxa that with which they can be confounded. The new combination *De. paraphysatum* is proposed after revising the type material of *Dacrymyces paraphysatus*, but other combinations or potentially new non-European species descriptions are postponed pending further studies of additional specimens.

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INTRODUCTION

Dacrymyces s.l. is currently treated as a genus of saprotrophic jelly-fungi distributed worldwide, and comprises about half of the species of the class *Dacrymycetes* (McNabb 1973, Reid 1974, Shirouzu *et al.* 2009, 2017). The distinction between genera in *Dacrymycetes* has traditionally been based on the macro- and micromorphological characters of the basidiocarps. Within the series of monographic studies on *Dacrymycetes* carried out by R.F.R. McNabb, the genus *Dacrymyces* seemed to be particularly difficult to circumscribe (McNabb 1973), especially against the genus *Heterotextus* (McNabb 1965). In fact, *Dacrymyces* has frequently been treated as a hotchpotch to include any taxa that could not be properly placed in other, well-characterised genera in the *Dacrymycetes*. As a result, this generic name is often applied to any species producing gelatinous to cartilaginous, cushion-shaped or turbinate basidiocarps, with a rather homogeneous hyphal structure, and either with an amphigenous hymenium or a sterile cortex of cylindrical to moderately differentiated, inflated cells (less so than in *Heterotextus*).

The phylogenetic relationships in *Dacrymycetes* have been re-evaluated with molecular data, and numerous independent studies have shown *Dacrymyces* to be highly polyphyletic (*e.g.* Shirouzu *et al.* 2007, 2013a, 2017, Zamora & Ekman 2020, Savchenko *et al.* 2021). Recent taxonomic revisions have focused on *Dacryonaemataceae* and *Unilacrymaceae* (Zamora & Ekman 2020) and on *Cerinomycetaceae* (Savchenko *et al.* 2021). In these revisions, several species with dacrymyces-like basidiocarps, not closely related to the type of *Dacrymyces*, *Da. stillatus*, have already been clarified and combined into monophyletic genera. On the other hand, the generic boundaries within *Dacrymycetaceae* are far from clear, because phylogenetic relationships among several groups of *Dacrymyces s.l.* and other genera (*e.g*. *Calocera*, which is also polyphyletic) are not currently well-supported, and phenotypic characters distinguishing the different clades overlap considerably. As a result, mycologists studying this class have been very cautious not to make the taxonomy of the group more intricate, avoiding unnecessary splitting and further creation of difficult-to-diagnose genera.

In the course of several sampling campaigns in various European countries during the last 12 yr, we found some specimens of *Dacrymyces s.l.* with conspicuous and often branched hyphidia that turned out to be undescribed species. Our aim is to describe these new species, providing both morphological studies and phylogenetic analyses, as well as a comparison with other morphologically similar species.

Preliminary DNA-based phylogenetic analyses placed them in the same clade as a specimen identified as *Da. dendrocalami*, a species with conspicuously branched hyphidia (Oberwinkler & Tschen 1989). The presence of these branched hyphidia seems to be a rather uncommon character within the family

Dacrymycetaceae, according to Zamora & Ekman (2020). We will therefore evaluate whether this clade merits recognition at generic level, as a further step to solve the polyphyly of *Dacrymyces s.l*.

MATERIAL AND METHODS

Sampling

Specimens were collected in the field in both hydrated and dry states. Some fresh specimens were kept in a refrigerated humid chamber up to 2–3 d in order to study the macro- and micromorphological structures of the living basidiocarps. Otherwise, samples were dried at room temperature and kept as fungarium specimens in CWU, G, H, and UPS (Thiers 2021) for subsequent morphological study. We selected 17 of these newly collected specimens, representing five putative new species, for molecular study.

We chose a subset of representative taxa from all main clades in Zamora & Ekman (2020) to investigate the phylogenetic placement of the target group within the class *Dacrymycetes*. We selected up to two samples per species with at least two unlinked DNA regions available to minimise missing data. For the species delimitation analyses, we restricted the sampling to species in the target clade (putative new genus), and included the only other additional sample (*Da. cf. adpressus*, TNS-21069, AB472729) with DNA data available in GenBank. Nomenclature has been updated following Zamora & Ekman (2020) and Savchenko *et al.* (2021).

Morphology

The morphological methods largely follow Zamora & Ekman (2020) and are thus only briefly summarised below. Basidiocarps were photographed when fresh or after being hydrated, with either a Canon EOS 700D or an Infinity 1 macro camera coupled with a Leica MZ 75 dissecting microscope. The micromorphology was studied with a Zeiss AxioImager A1 compound microscope by mounting hand-cut sections in water and 5 % KOH, and photographs were taken in the latter medium with an AxioCamICc3 digital camera, using differential interference contrast (DIC). Microscopic structures were measured in KOH solution at 630×, either directly or with the aid of Piximètre v. 5.10 (Henriot & Cheype 2016). Hyphidium width was measured in the upper half, basidium length was considered from the apex (excluding sterigmata) to the basal septum, and basidiospore length from the most protuberant part near the hilar appendix (considered subterminal and measured separately) to the opposite pole; the largest perpendicular dimension to these lengths was treated as the width. The basidiospore length/width ratio is expressed as Q. Terminology for the basidium apex follows Van de Put (2014).

General protocols for laboratory work were explained in detail in Zamora & Ekman (2020); Ukrainian samples were processed following Savchenko *et al.* (2021). DNA extractions were always carried out from a single basidiocarp using Chelex 100, following the protocol of Ferencova *et al.* (2017). We amplified fragments of the nrDNA (18S, ITS, nrLSU), *RPB1*, *RPB2*, *TEF-1α*, and 12S (mtSSU) DNA regions using the following primer combinations: The 18S was amplified in two parts with the primer pairs NS1/NS4 (White *et al.* 1990) and NS21UBC/SR6 (Gargas & Taylor 1992, Vilgalys unpubl.). The ITS + nrLSU (D1–D3) region was amplified using ITS1F/LR5 (Gardes & Bruns 1993, Vilgalys & Hester 1990). The *RPB1* was amplified with DacryRPB1-1F/DacryRPB1-2r (Zamora & Ekman 2020). The *RPB2* was amplified either with DacryRPB2-6F/DacryRPB2-11aR, or with DacryRPB2-6.2F/DacryRPB2-11bR (Zamora & Ekman 2020), sometimes using nested PCR. The *TEF-1α* was amplified using EF1-1018F/EF1-2218R (Stielow *et al.* 2015, Rehner & Buckley 2005) and Efdf/EF1-1953R (Rehner unpubl.). Finally, for the 12S we used either the primers DacryMS1 combined with Dacry12S-2r or Dacry12S-4r (Zamora & Ekman 2020), or substituted the forward DacryMS1 with an external newly designed primer, Dacry12S-1F (5' AGGTAGTTGRTAGTGTAA 3'), combined with Dacry12S-2r. PCR programmes followed Zamora & Ekman (2020). Sequencing was done by Macrogen using the amplification primers, except for the *RPB1* for which we mostly used the internal DacryRPB1-A and DacryRPB1-C (Zamora & Ekman 2020).

Sequence alignment

Sequences were assembled and edited in Sequencher v. 4.1.4 (Gene Codes, USA), using IUPAC ambiguity codes for heteromorphic positions. Newly generated sequences are included in Table 1, while information of the remaining sequences can be found in Zamora & Ekman (2020) and in the Joint Genome Institute (Grigoriev *et al.* 2014). We built two alignments, the first one for inferring a general phylogeny to show the phylogenetic position of the new species and to identify the main clades that may deserve generic recognition, and a second alignment to perform species delimitation analyses, containing only the new species and closely related taxa. Most alignments were inferred using MAFFT v. 7 (Katoh & Standley 2013, G-INS-i option) for the ribosomal regions, or manually in the case of the protein coding genes, back-translating them into nucleotides after having excluded introns and aligned the amino acids (introns were not used in subsequent analyses). Two highly variable regions of the 12S, appearing between the conserved motifs AWTTCWTT and GAAMWATGT, and AGGGTTCGYRG and GMTWGAATCW, respectively (some base changes in certain species occur in these motifs) were excluded from the analyses. The 12S region was not used for species delimitation since it was available for only two species in the target clade (*De. concrescens* and *De. ellipsosporum*). The ITS1 and ITS2 were extremely variable across some of the target species and several trials with MAFFT resulted in substantially different alignments; thus, these regions were only included in the species delimitation analysis and after being aligned with BAli-Phy (Suchard & Redelings 2006). We prepared a backbone alignment with up to two samples per species (the ones with the most dissimilar sequences), and executed four runs with 5×10^4 iterations each. ITS1 and ITS2 were treated as two separate partitions, using the GTR + I + Γ model for nucleotide substitutions and the rs07 model for insertion/deletion events. The first 25 % of the runs were discarded as burn-in and the summarised samples showed an average standard deviation of splits frequencies < 0.005, and effective sample sizes > 7 000, verified using Tracer v. 1.7 (Rambaut *et al.* 2018). Alignments are available in TreeBASE (TB2:S29109).

Phylogenetic analyses

We tested congruence among unlinked DNA regions by performing a maximum likelihood (ML) phylogenetic analysis

Table 1. DNA sequences generated in this study, with GenBank accession numbers and voucher information.

Taxon	Country and province	Voucher	GenBank accession numbers					
			18S	ITS + nrLSU	*RPB1*	*RPB2*	*TEF-1α*	12S
Dendrodacrys ciprense	Cyprus, Lemesos	UPS F-946590 (holotype)	OM515350	OM519385	OM502304	OM502321	OM502337	—
	Cyprus, Lemesos	UPS F-946591	OM515351	OM519386	OM502305	OM502322	OM502338	—
	Cyprus, Lemesos	UPS F-946592	OM515352	OM519387	OM502306	OM502323	—	—
Dendrodacrys aff. ciprense	Cyprus, Lemesos	UPS F-946593	OM515353	OM519388	OM502307	OM502324	OM502339	—
Dendrodacrys concrescens	Sweden, Öland	UPS F-946601	OM515354	OM519389	OM502308	OM502325	OM502340	OM677448
	Sweden, Öland	UPS F-946602 (holotype)	OM515355	OM519390	OM502309	OM502326	OM502341	—
	Sweden, Uppland	UPS F-946603	OM515356	OM519391	OM502310	OM502327	OM502342	OM677449
Dendrodacrys ellipsosporum	Spain, Madrid	UPS F-946604 (holotype)	OM515357	OM519392	OM502311	OM502328	OM502343	OM677450
	Spain, Madrid	UPS F-946605	OM515358	OM519393	OM502312	OM502329	OM502344	OM677451
	Spain, Balearic Islands	UPS F-946606	OM515359	OM519394	OM502313	OM502330	OM502345	OM677452
	Spain, Madrid	UPS F-946607	OM515360	OM519395	OM502314	OM502331	OM502346	OM677453
	Spain, Madrid	UPS F-946608	OM515361	OM519396	OM502315	OM502332	OM502347	OM677454
	Ukraine, Crimea	CWU(MYC)4092	OM515362	OM519397	OM502316	—	OM502348	—
	Ukraine, Crimea	CWU(MYC)7560	OM515363	OM519398	OM502317	OM502333	OM502349	—
Dendrodacrys oblongisporum	Norway, Sogn og Fjordane	UPS F-946599	OM515364	OM519399	OM502318	OM502334	OM502350	—
	Spain, Madrid	UPS F-979568 (holotype)	OM515365	OM519400	OM502319	OM502335	OM502351	—
	Spain, Madrid	UPS F-979569	OM515366	OM519401	OM502320	OM502336	OM502352	—

of each dataset using IQ-TREE v. 1.6.12 (Nguyen *et al.* 2015), running 500 standard bootstrap (bs) replicates. We considered a conflict among topologies when a strongly supported (bs ≥ 75 %) clade from one phylogeny was contradicted by another strongly supported clade in another phylogeny (Mason-Gamer & Kellogg 1996). The partitioning scheme and model parameters were calculated based on the Bayesian information criterion with the version of ModelFinder (Kalyaanamoorthy *et al.* 2017) integrated into IQ-TREE. We used five potential subsets for the nrDNA dataset (18S, ITS1, 5.8S, ITS2, and nrLSU), three for each protein coding gene alignment (codon positions), and left the 12S dataset unpartitioned. Since no incongruence was detected, the datasets were concatenated and analysed using ML and Bayesian inference. In a previous study (Zamora & Ekman 2020) the use of the much more computationally intense coalescence analyses did not show any substantial improvements or topological changes. Therefore, the trees obtained here through the analyses of the concatenated dataset are considered representative of the species tree.

Maximum Likelihood analyses were performed as indicated above for each single-region alignment, repeating the analyses five times starting from random trees. Brach support was assessed by standard bootstrapping, performing 500 replicates in total. Bayesian analyses were done with MrBayes v. 3.2.6 (Ronquist *et al.* 2012), using the same partitioning scheme obtained in the ML analysis, with model parameters but not tree topology unlinked across subsets, and using model jumping to sample across models in each subset (Huelsenbeck *et al.* 2004). We allowed a gamma distributed rate heterogeneity across sites (approximated by four categories) and a proportion of invariant sites. We used the following priors: a (1, 1, 1, 1, 1, 1) Dirichlet prior for the substitution rates, a (1, 1, 1, 1) Dirichlet prior on the state frequencies, and a uniform (0, 1) prior for the proportion of invariable sites. Branch lengths were linked and proportional across partitions, and we used the compound Dirichlet prior Unconstrained:GammaDir (1, 0.158, 1, 1), based on the tree length estimates from the best replicate of the ML analysis. Mixing was considered adequate with the temperature parameter set to 0.2. We executed four runs starting from random trees, each with four chains, for up to 1×10^8 generations and sampling every 1 000th tree. The analyses were automatically stopped when the average standard deviation of split frequencies (ASDSF) dropped below 0.01. The first half of the analysis was discarded as burn-in, and the 50 % majority-rule tree with posterior probabilities (pp, considered significant when ≥ 0.95) and average branch lengths was calculated from the post-burn-in trees. We checked with Tracer v. 1.7 (Rambaut *et al.* 2018) that effective sample size (ESS) for each parameter was above 200. Trees were visualised in FigTree v. 1.4 (Rambaut 2016) and rooted based on the results from Zamora & Ekman (2020).

Species delimitation

Specimens were assigned to putative species using the multispecies coalescent approach implemented in STACEY v.

1.2.4 (Jones 2017) as part of the BEAST2 platform (Bouckaert *et al.* 2014). Clock and tree model parameters were estimated independently for each of the four unlinked DNA regions. An uncorrelated lognormal relaxed clock model (Drummond *et al.* 2006) was used. The dataset was divided into eight subsets (two for each non-recombining DNA region, one with lower and the other with higher substitution rates), as follows: (i) 18S + 5.8S + nrLSU, (ii) ITS1 + ITS2, (iii–v) 1st + 2nd codon positions of protein coding regions, (vi-viii) 3rd codon position of protein coding regions. Model parameters were estimated for each DNA subset with bModelTest (Bouckaert & Drummond 2017), allowing all transition/transversion split models. We ran four MCMC parallel analyses for 2×10^8 generations, sampling every $1 \times 10^{4\text{th}}$ tree. The collapse height parameter was set as $\varepsilon = 10^{-4}$, and we used the Beta (1,1) prior on the collapse weight parameter (ω). We noted some convergence problems in one of the runs for one of the partitions (1st + 2nd codon positions of *TEF-1α*) and excluded this run for subsequent analyses. The first half of the other three runs was discarded as burn-in. The most likely number of clusters (*i.e.* putative species) was calculated from the remaining sample using SpeciesDelimitationAnalyzer (Jones *et al*. 2015). The similarity matrix of pairwise posterior probabilities was visualised and plotted in R (R Core Team 2021) following Jones *et al.* (2015).

RESULTS

Phylogeny

The best partitioning scheme and models for each subset in the concatenated ML analysis were: (i) 18S, TN + F + I + Γ4, (ii) 5.8S + 12S, GTR + F + I + Γ4, (iii) nrLSU, TN + F + I + Γ4, (iv) *RPB1* 1st + *RPB2* 1st, TIM2 + F + I + Γ4, (v) *RPB1* 2nd + *RPB2* 2nd, TIM3 + F + I + Γ4, (vi) *RPB1* 3rd + *RPB2* 3rd, GTR + F + I + Γ4, (vii) *TEF-1α* 1st, F81 + F + I + Γ4, (viii) *TEF-1α* 2nd, JC + I + Γ4, and (ix) *TEF-1α* 3rd, GTR + F + Γ4. All ML tree replicates had a similar topology, and the likelihood score for the best one was lnL = -73248.971. The concatenated Bayesian analysis halted after 5×10^6 generations (ASDSF < 0.01). All parameters had an ESS exceeding 800 in the posterior sample, and all PSRF values were in the range 0.998–1.005. The topologies of the 50 % majority-rule Bayesian consensus tree and of the ML trees were similar, and thus only the best ML tree with bs and pp values is shown in Fig. 1.

The overall topology of the *Dacrymycetes* tree (Fig. 1) is highly consistent with that reported by Zamora & Ekman (2020). The four families recognized received bs = 100 % and pp = 1.00 support. Within *Dacrymycetaceae*, we have identified the same 8 main groups (D1–D8), plus *Dacrymyces fennicus* as sister to D6 (*Femsjonia*) with high support (bs = 93 %, pp = 1.00). Clades D1, D2, D4–D7 received bs = 100 % and pp = 1.00 support, clade D3 was represented by a single sample, and clade D8 was well-supported (bs = 77 %, pp = 1.00). The target group (clade D5) was sister to clade D8 (clampless species) with partial support (bs = 58 %, pp = 1.00). Within clade D5, relationships were generally highly supported. *Dacrymyces cf*. *dendrocalami* and *Da. cf*. *adpressus* were resolved as sister to each other with bs = 100 % and pp = 1.00 support. Four putative new species (see below), named *Dendrodacrys ciprense*, *De. concrescens*, *De. ellipsosporum*, and *De. oblongisporum*, also received bs = 100 % and pp = 1.00 support. In addition, *De. ciprense* and *De. oblongisporum*, together with an isolated sample (*De. aff*. *ciprense*) formed a well-circumscribed clade with bs = 100 % and pp = 1.00 support, but the relationships among these three groups only received partial support (bs = 72 %, pp = 0.97).

Species delimitation

SpeciesDelimitationAnalyzer yielded two main species delimitation schemes, one with seven putative species (45.1 % posterior probability), and the other with eight putative species (34.7 % posterior probability). All other delimitation schemes had < 5 % posterior probability. All relevant model parameters in the STACEY analysis had an ESS exceeding 500 in the posterior sample. The topology of the STACEY chronogram is almost fully supported above the species level (Fig. 2). From the root, two main clades can be distinguished; the first is fully supported and includes *Da. cf*. *dendrocalami* (one sample estimated as one species) and *Da. cf*. *adpressus* (a fully supported clade with two samples, estimated as either one or two species). The other main clade is well-supported (pp = 0.97) and includes four putative species, *i.e*. *De. concrescens* (fully supported clade with three specimens), *De. ellipsosporum* (fully supported clade with seven specimens), *De. ciprense* (fully supported clade with three specimens), *De. aff*. *ciprense* (one isolated specimen), and *De. oblongisporum* (fully supported clade with three specimens). The branches connecting these five putative species received full support except for the sister relationship between *De. aff*. *ciprense* and *De. oblongisporum*, which is unsupported (pp = 0.9).

Within each putative species (cluster) in the scheme of seven species, all included specimens had a high posterior probability (pp > 0.9) of belonging to the cluster they were assigned, except for the two specimens of *Da. cf*. *adpressus*. In this case, the probability that they belonged to the same species was pp = 0.54. The posterior probability that any specimen belonged to a different species to which it was assigned was very low (pp < 0.001).

Taxonomy

Dendrodacrys J.C. Zamora, A. Savchenko, Á. González-Cruz, Prieto-García, Olariaga & Ekman, ***gen. nov.*** MycoBank MB 842993.

Etymology: From the Greek δένδρον (*dendron*, branched like a tree) and δάκρυ (*dacry*, tear), so as to refer to a genus of *Dacrymycetaceae* with branched hyphidia.

Typus: *Dendrodacrys ellipsosporum* J.C. Zamora, A. Savchenko, Á. González-Cruz, Prieto-García, Olariaga & Ekman

Description: *Basidiocarps* firm- to soft-gelatinous when fresh, xerotolerant or not, ± sessile and with or without a rooting base, pulvinate to depressed, yellow-orange to brown. *Hymenium* amphigenous or ± confined to the upper part of the fruitbody, then with a distinct sterile cortex. *Clamp-connections* present except in one of the currently included taxa. Terminal cells of cortical/marginal hyphae ± cylindrical to narrowly clavate, thin- to thick-walled. Internal hyphae and subhymenial hyphae mostly thin-walled. *Basidia* 2-spored, often cylindrical to clavate, more rarely ± urniform; apex U- to W-shaped, rarely Y-shaped. *Hyphidia* present, distinct, simple to moderately branched, reaching or surpassing the level of the young basidia, but only sometimes forming a conspicuous layer on them. Recently

Fig. 1. Maximum likelihood phylogram of the class *Dacrymycetes*, with bootstrap (bs) and posterior probabilities (pp) values indicated at species level or above. Thickened branches are considered well-supported (bs ≥ 75 % and pp ≥ 0.95), asterisks (*) denote full support (bs = 100 %, pp = 1.00), and other values are included only when bs ≥ 60 % and pp ≥ 0.9. Notation D1–D8 in *Dacrymycetaceae* follows Zamora & Ekman (2020) for convenience, and the new genus *Dendrodacrys* is highlighted. Samples with newly generated data are indicated in bold.

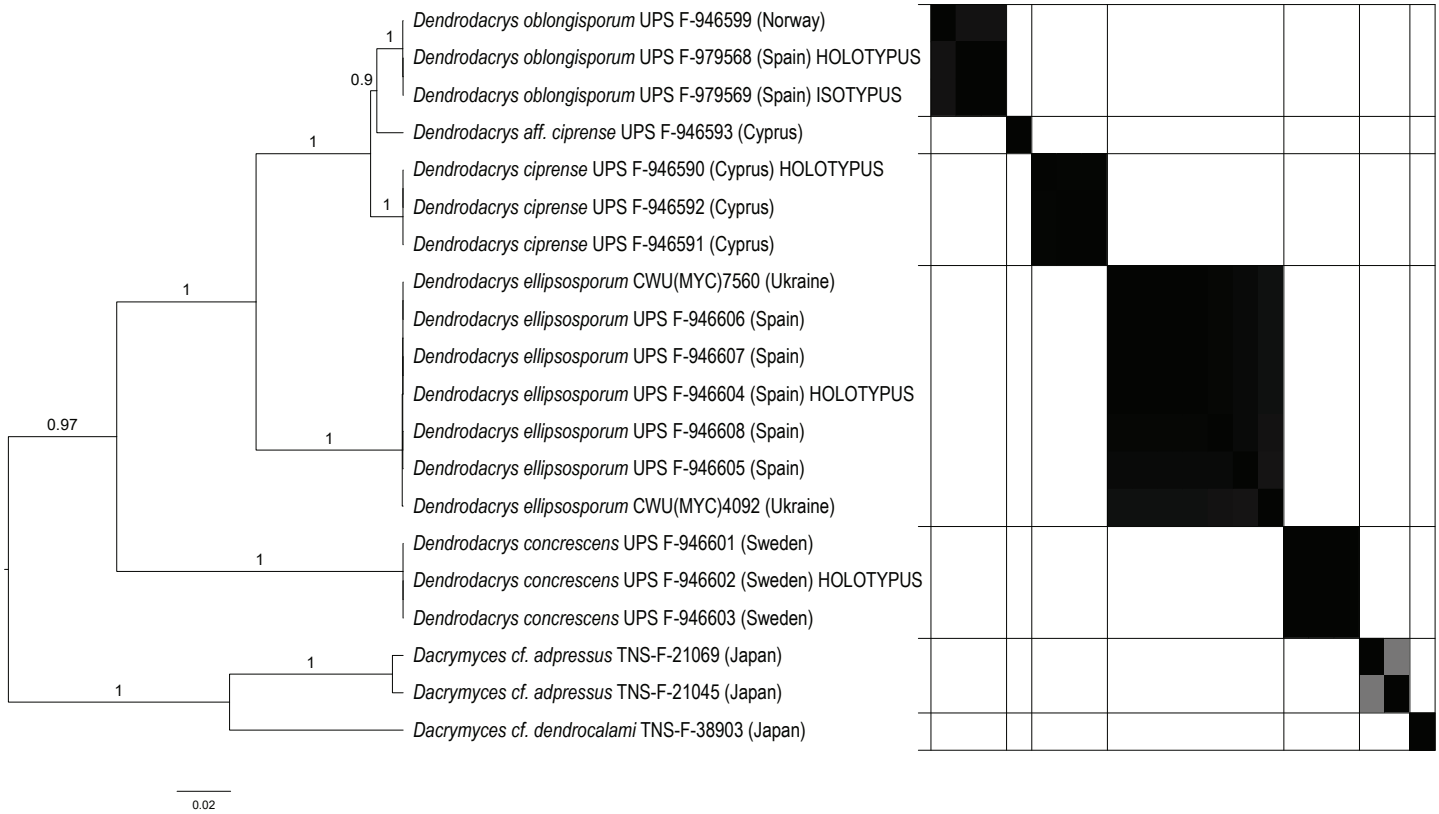

Fig. 2. STACEY species delimitation analysis. Chronogram with posterior probabilities at and above species level, and similarity matrix. Clusters separated by lines indicate the scheme of putative species with highest posterior probability.

discharged and still aseptate basidiospores uninucleate. Mature basidiospores 0–3-septate, thin- to thick-walled, hyaline, subglobose to cylindrical-allantoid. *Spore print* cream to orange, also visible from the spore pruinescence on the basidiocarps (*e.g*. Fig. 3C). *Microconidia* infrequent, ellipsoid to cylindrical. *Cell cytoplasm* with abundant lipid bodies, and with carotenoids ± visible under the light microscope, sometimes inconspicuous. Brownish diffuse parietal pigments sometimes visible in the cortical/marginal hyphae.

Included species: *Dendrodacrys ciprense*, *De. concrescens*, *De. ellipsosporum*, *De. oblongisporum*, *De. paraphysatum*. Two additional species provisionally identified as "*Da. cf. dendrocalami*" and "*Da. cf. adpressus*" are also included here.

Dendrodacrys ciprense J.C. Zamora ***sp. nov.*** MycoBank MB 842994. Fig. 3.

Etymology: The adjectival specific epithet refers to the country where the known specimens were found.

Typus: **Cyprus**, Lemesos, Mesa Potamos, picnic area, on *Pinus brutia* branches, 2 Dec. 2017, *J.C. Zamora* (**holotype** UPS F-946590).

Description: *Basidiocarps* gelatinous, (0.2–)0.4–1.5(–1.8) mm in diam, slightly erumpent and pustulate when very young, becoming pulvinate to applanate, often with an inconspicuous central root-like projection, gregarious and sometimes partially coalescing but retaining evidence of the individual origin; in hydrated state amber coloured to orangish when young, soon orangish brown to brown, ± dark brown when old; dark brown to blackish when dried. *Hymenium* ± confined to the upper part of the basidiocarps, irregularly spreading to the margins; sterile cortex often distinct, or at least with a sterile area in the lower part of the basidiocarps. Terminal cells of cortical/marginal hyphae narrowly clavate to slightly fusiform or almost cylindrical, 5.4–9.0 µm diam, ± thick-walled, with walls not clearly gelatinised but cells often embedded in a gelatinous matrix, sometimes with secondary simple septa, with a brownish, diffuse parietal pigmentation well-visible especially in the darkest basidiocarps. Internal hyphae 1.8–5.0 µm diam, thin- to slightly thick-walled, clamped, some with roughened walls. *Hyphidia* frequent, conspicuous, moderately to densely branched, rarely simple, 2.1–4.4(–5.7) µm diam (wider towards the base and becoming thinner in the upper half or third), often with 1–2 clamped septa throughout their length, reaching or surpassing the level of the young basidia but not forming a layer on them. Young basidia cylindrical to narrowly clavate; mature basidia 49.5–74.4 × 4.4–9.5 µm, with two subapical sterigmata, 16.5–34.0 × 3.9–6.0 µm; basidium apex often slightly protruding. *Basidiospores* thin-walled, (13.6–)16.4–20.1 × (5.5–)6.0–8.9 µm, 2.2 ≤ Q ≤ 3.2 (n = 20), cylindrical-allantoid to slightly arachiform, becoming 3-septate at maturity, not constricted at septa or only slightly constricted, uninucleate prior to septation; hilar appendix conspicuous, *ca*. 1 µm long. Basidiospore germination not seen. Carotenoid contents present in the cytoplasm of most cells but rather inconspicuous, not bright yellow-orange.

Ecology and distribution: Only known from *Pinus brutia* forests in Cyprus. For a more accurate knowledge of its ecological preferences, the species should be looked for in other areas where the host is present (northeastern Mediterranean basin). Probably at least partially xerotolerant.

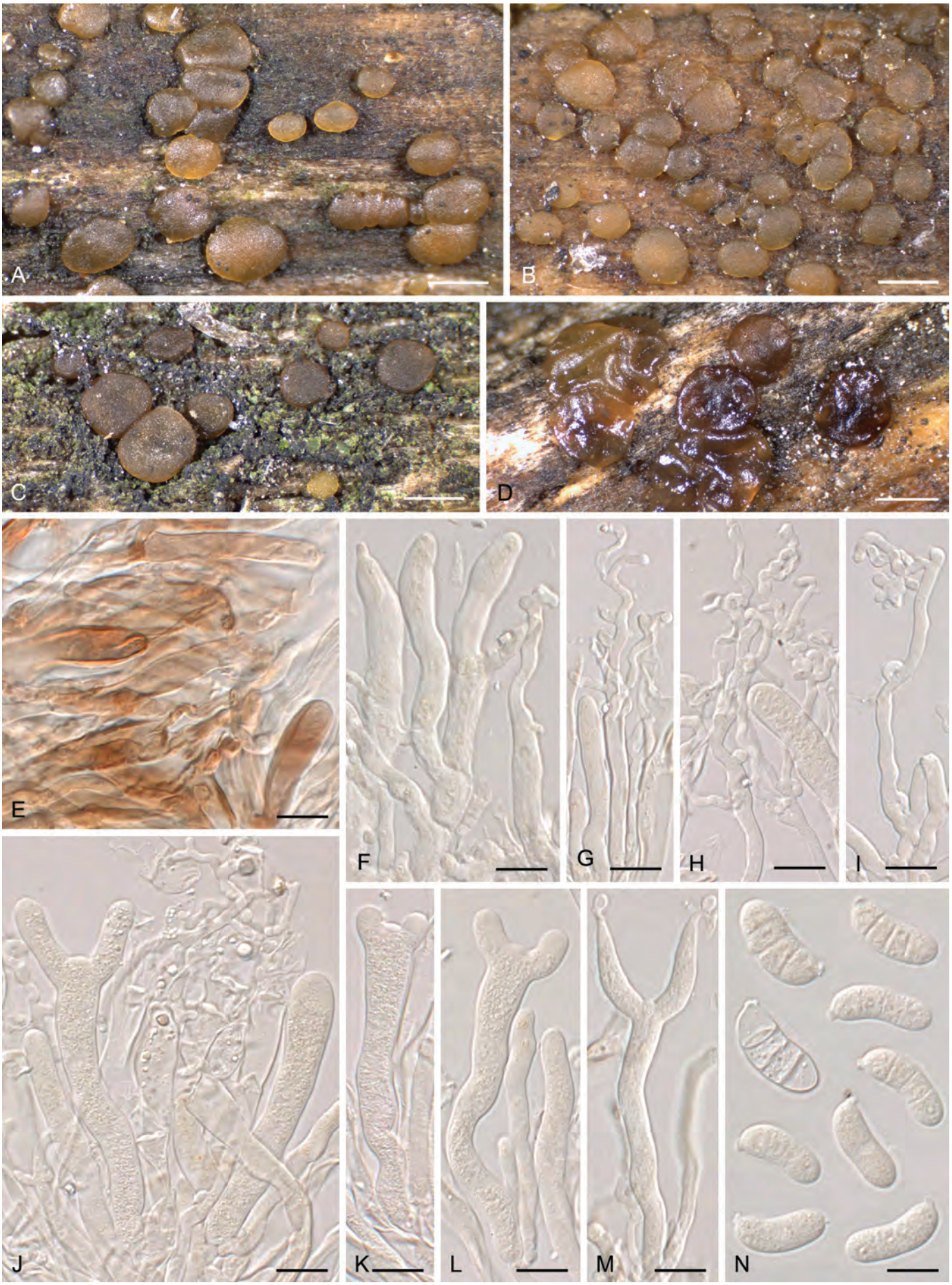

Fig. 3. *Dendrodacrys ciprense*. **A–D.** Macromorphology; basidiocarps in fresh conditions. **E–N.** Micromorphology. **E, F.** Terminal cells of cortical hyphae. **G–I.** Hyphidia. **J–M.** Basidia. **N.** Basidiospores. A–C, F–H, J–N from UPS F-946590 (holotype); D, E, I from UPS F-946592. Scale bars: A–D = 1 mm; E–N = 10 µm.

Additional specimens examined: **Cyprus**, Lemesos, Mesa Potamos, on *Pinus brutia* branches, 2 Dec. 2017, *J.C. Zamora*, UPS F-946591; Platres, on *Pinus brutia* branch, 3 Dec. 2017, *J.C. Zamora*, UPS F-946592.

Notes: This species can be easily distinguished by the combination of dark basidiocarps, often with distinct brownish parietal pigments but not very conspicuous carotenoids, distinctly branched hyphidia, and cylindrical-allantoid, thin-walled, 3-septate mature basidiospores. There are very few *Dacrymyces s.l.* described with branched hyphidia, 3-septate ± allantoid basidiospores, and non-yellow/orange basidiocarps. We studied part of the type material of *Dacrymyces paraphysatus* (the holotype, NY00738304, and one isotype, K[M] 8355) and *Da. enatus* var. *macrosporus* (the holotype, BPI725717, and four isotypes, NY03684200, LSU00135945, TAAM192134, and K[M] 95953, the last one annotated as "*Dacrymyces dendrohyphidia* P. Roberts", *nom. herb.*). These taxa clearly differ from *De. ciprense* by having distinctly thick-walled and differently sized basidiospores: in *Da. paraphysatus* 12.8–16.0 × 5.2–6.0 µm measured in cotton blue from the holotype, (13.4–)13.9–17.6(–22.1) × 5.7–7.4(–7.9) µm measured in KOH from the isotype; 13.5–17.5(–21) × 5–7 µm from McNabb (1973); in *Da. enatus* var. *macrosporus* 13.1–15.1(–15.4) × (5.3–)5.4–6.6(–6.8) µm measured in cotton blue from BPI725717, NY03684200, LSU00135945, and TAAM192134, (10.1–)12.1–16.6 × 5.4–7.2 µm measured in KOH from K(M) 95953; 11–15.5 × 4.5–5.5(–6.5) µm from McNabb (1973). In addition, in these taxa some basidiospores are constricted at septa and pigmented, the hyphidia are 1–2(–2.5) µm wide (rather constant through their length), heavily branched, forming a conspicuous layer on the hymenium, sometimes pigmented, and the basidiocarps are either individually larger or may form masses of some cm in extent (McNabb 1973, and own observations). Furthermore, *Da. paraphysatus* and *Da. enatus* var. *macrosporus* seem to be restricted to tropical areas, occurring on angiosperm wood (McNabb 1973). These two taxa clearly belong to the new genus *Dendrodacrys*, and we have combined *Da. paraphysatus* for being the one validly published at species level.

We have found one specimen (UPS F-946593), inhabiting a *Cistus* branch, that is morphologically and phylogenetically close to *De. ciprense*, but differs by having paler coloured basidiocarps, with almost indistinct brownish parietal pigments, barely inflated and ± thin-walled terminal cells of cortical hyphae, slightly narrower basidia (4.2–6.8 µm wide), slightly smaller basidiospores (14.5–17.2[–19.1] × 5.7–7.3 µm), and simple to sparingly branched hyphidia. Also, all sequenced DNA regions place it as close but substantially different from *De. ciprense*, and the STACEY analysis considered it as another putative species (Fig. 2). These results suggest that this sample probably represents a different species, but we cannot properly evaluate its intraspecific variation based on a single specimen and refrain from describing it here.

Dendrodacrys concrescens J.C. Zamora & Ekman, ***sp. nov.*** MycoBank MB 842995. Fig. 4.

Etymology: The specific epithet is an adjectival form based on the participle of the Latin verb *concresco* ("grow together"), and it refers to the habit of the basidiocarps, growing closely aggregated.

Typus: **Sweden**, Öland, Böda par., Lindreservatet, on a fallen *Pinus sylvestris* trunk, 3 Oct. 2017, *J.C. Zamora*, (**holotype** UPS F-946602; **isotypes** in G and H).

Description: *Basidiocarps* gelatinous to soft-gelatinous, 0.2–1 mm diam, erumpent when very young and later spreading on the substrate, pustulate to pulvinate, growing in densely aggregated groups and coalescing to form masses of several cm^2, partially retaining evidence of pustular origin at least when fresh; orange to yellowish orange or ochraceous orange in hydrated state, becoming orangish brown when dried and being reduced to a varnish-like layer on the substrate. *Hymenium* ± amphigenous, irregularly spreading to the margins; sterile areas around the margin often visible in young basidiocarps, becoming inconspicuous when basidiocarps coalesce. Terminal cells of marginal hyphae ± cylindrical, 3.3–6.3 µm diam, thin- to ± thick-walled, apex sometimes pointed, with hyaline walls and some cytoplasmic, yellow-orange carotenoids. Internal hyphae (1.5–)2.0–4.0 µm diam, mostly thin-walled, clamped. *Hyphidia* unevenly distributed, conspicuous only in some areas, moderately to densely branched, transitioning to simple towards the margin, 2.8–3.4 µm diam (wider towards the base and becoming thinner in the upper third); often with 1–2 clamped septa throughout their length, reaching ± the same level of young basidia, or some surpassing them. Young basidia cylindrical to narrowly clavate; mature basidia (27.3–)29.3–49.3(–52.1) × 4.5–6.2 µm, with two apical or subapical sterigmata, 16.3–36.5 × 2.7–3.9 µm, apex of the mature basidium rarely protruding. *Basidiospores* thin-walled, 12.0–16.2(–18.1) × 4.8–6.3 µm, 2.0 ≤ Q ≤ 3.3 (n = 40), cylindrical-allantoid to slightly arachiform, becoming 3-septate at maturity, not visibly constricted at septa, uninucleate prior to septation; hilar appendix conspicuous, *ca*. 1 µm long. Germinating basidiospores producing cylindrical microconidia, *ca*. 5.0–7.0 × 2.0–3.0 µm (few germinating basidiospores seen). Carotenoid contents very conspicuous in the majority of the cells of the basidiocarps, bright yellow-orange.

Ecology and distribution: All studied specimens come from the hemiboreal zone in Sweden, but one GenBank accession (LC492199, released after our datasets were compiled) corresponds to a nrLSU sequence identical to ours of *De. concrescens*, having been generated from a Japanese specimen (HNo1210, Shirouzu *et al.* 2020). Even if the species grows on a relatively common substrate, *i.e*. ± old, decorticated logs of *Pinus sylvestris*, it seems to be rare, since it was only encountered three times during intense sampling between 2017 and 2020. We have not found any additional specimens in GB, H, O, S, or UPS herbaria. It does not seem to tolerate desiccation well, as the cells of the collected specimens quickly died when the samples were dried.

Additional specimens studied: **Sweden**, Öland, Böda par., Trollskogens NR, on a fallen *Pinus sylvestris* trunk, 5 Oct. 2017, *J.C. Zamora*, UPS F-946601; Uppland, Uppsala, Norra Lunsen NR, on an old, fallen *Pinus sylvestris* log, 19 Nov. 2017, *J.C. Zamora*, UPS F-946603.

Notes: *Dendrodacrys concrescens* is easy to recognise in the field by its conspicuous and dense masses of fused small basidiocarps, on decorticated *Pinus* logs. When dried, it resembles a thin layer of varnish and the individual basidiocarps become indistinguishable. Two species share some morphological similarities with *De. concrescens* according to the literature, *viz*.

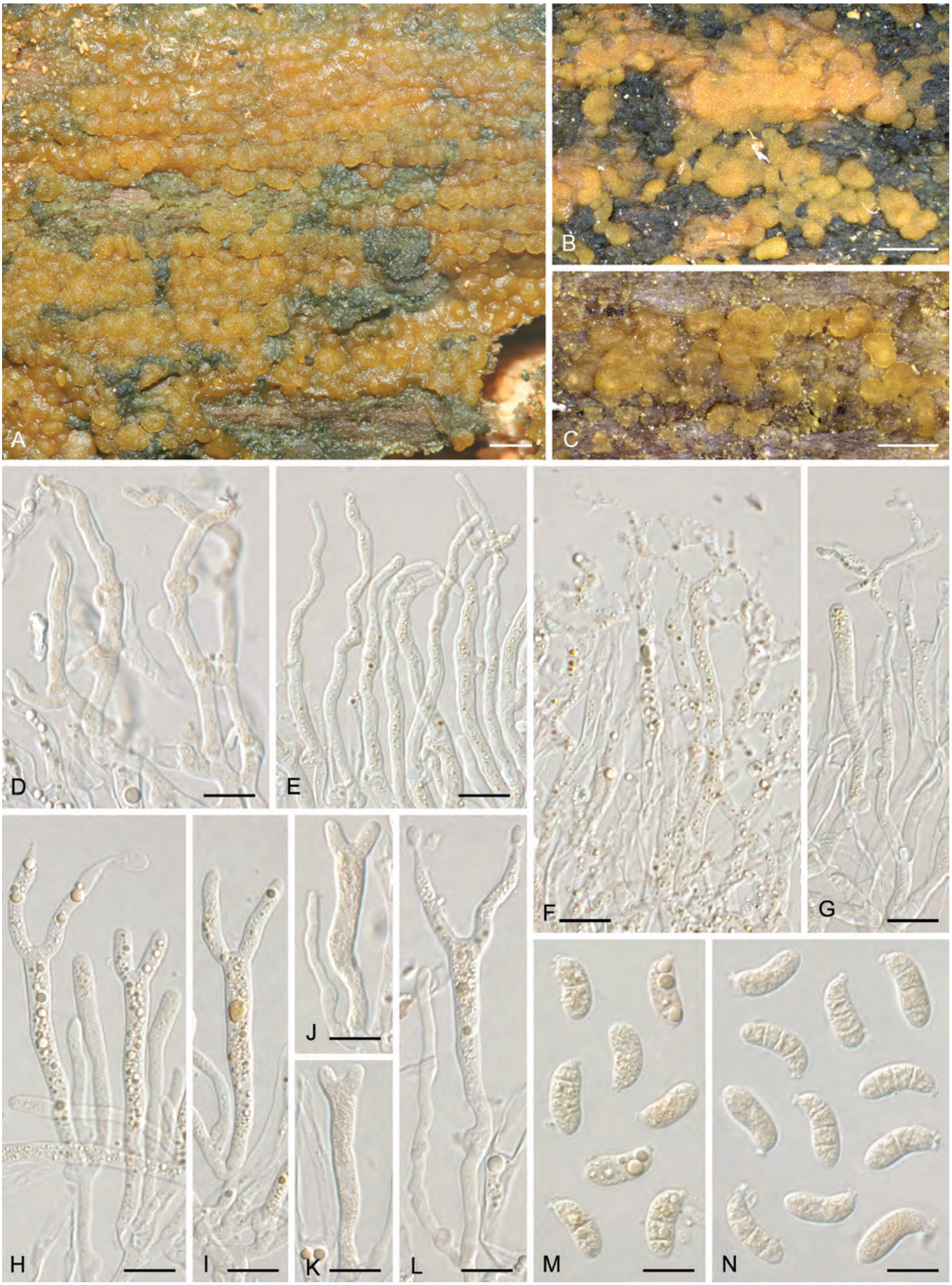

Fig. 4. *Dendrodacrys concrescens*. **A–C.** Macromorphology; basidiocarps in fresh conditions. **D–N.** Micromorphology. **D, E.** Terminal cells of marginal (D) and submarginal (E) hyphae. **F, G.** Hyphidia. **H–L.** Basidia. **M, N.** Basidiospores. A, B, E–I, M from UPS F-946602 (holotype); C, D, J–L, N from UPS F-946603. Scale bars: A–C = 1 mm; D–N = 10 µm.

Dacrymyces adpressus and *Da. fennicus*. We have studied type material of both. *Dacrymyces adpressus* has simple or indistinct hyphidia and larger individual basidiocarps, not so conspicuously fusing as they grow, and the lectotype was collected on angiosperm wood (Grognot 1863, McNabb 1973). *Dacrymyces fennicus*, considered as a synonym of *Da. adpressus* by McNabb (1973), shares the habitat with *De. concrescens*, and we have even found both species growing on a single log. However, *Da. fennicus* produces larger, well-separated basidiocarps that are normally not applanate and only sometimes coalesce. In addition, the hyphidia are often indistinct and always simple. Specimens identified as *Da. adpressus* from Japan (that likely do not represent *Da. adpressus s.str*.), and a specimen of *Da. fennicus* with a sequenced genome are well-distinguished from *De. concrescens* based on the available molecular data (Fig. 1). In particular, the ITS1 sequences of *De. concrescens* are highly deviant from those of any other species in the *Dacrymycetes*. In Shirouzu *et al.* (2020), HNo1210 (see "Ecology and distribution" above) was considered to be an unidentified clade (Clade O).

Dendrodacrys ellipsosporum J.C. Zamora, A. Savchenko, Á. González-Cruz, Prieto-García, Olariaga & Ekman, ***sp. nov.*** MycoBank MB 842996. Fig. 5.

Etymology: The specific epithet is a compound adjective referring to the shape of the basidiospores, based on the ancient Greek ελλειψοειδή (ellipsoid) and σπορά (spora).

Typus: **Spain**, Madrid, Becerril de la Sierra, on *Juniperus thurifera* exposed branches, 30 Dec. 2017, *J.C. Zamora et al.* (**holotype** UPS F-946604; **isotypes** in G and H); *idem*, on *Juniperus oxycedrus* wood, UPS F-946610 (**isotype**).

Description: *Basidiocarps* gelatinous to firm-gelatinous, (0.3–) 0.5–2.0 mm diam, at first erumpent, pustulate or pulvinate, but soon becoming applanate and slightly pezizoid when dried, often with a central root-like projection, gregarious but sometimes partially coalescing; in hydrated state orangish yellow when young, soon amber coloured to dull orange or brownish orange, chestnut brown when old; orangish brown to blackish when dried. *Hymenium* confined to the upper part of the basidiocarps or sometimes spreading to the margins, sterile cortex more or less distinct, or at least always with a sterile area in the lower part of the basidiocarps. Terminal cells of cortical/marginal hyphae ± cylindrical to irregularly dilated, (3.3–)4.1–7.6(–9.0) µm diam, thin- to more or less thick-walled, often with secondary simple septa, with a brownish, diffuse parietal pigmentation especially in the darkest basidiocarps. Internal hyphae 2.0–6.0 µm diam, thin- to slightly thick-walled, clamped, some with a roughened surface. *Hyphidia* rather common, distinct, most of them sparingly branched but varying from simple to rather densely branched, 2.1–3.6 µm diam (rather constant throughout their length or somewhat wider towards the base), often with 1–2 clamped septa throughout their length, reaching or surpassing the level of young basidia but not forming a conspicuous layer on them. Young basidia cylindrical to narrowly clavate or narrowly obpyriform; mature basidia (33.5–)40.0–73.0(–82.0) × (5.3–)6.3–12.8 µm, with two subapical sterigmata, 18.0–44.0 × 4.7–6.8 µm, apex of the mature basidium often slightly protruding. Basidium wall sometimes thickened. *Basidiospores* thin-walled, 13.9–25.7(–26.8) × (7.0–)9.7–14.2(–15.5) µm, 1.2 ≤ Q ≤ 2.2 (n = 50), commonly ellipsoid to narrowly ovoid, but rather variable from almost subglobose to lacrymiform/pyriform, 0–1(–3)-septate at maturity, not to sometimes slightly constricted at septa, uninucleate prior to septation; hilar appendix conspicuous, *ca*. 1.0–1.5 µm long. Basidiospore germination by the formation of hyphae or, more frequently, producing ellipsoid to narrowly ellipsoid conidia, *ca*. 5.0–6.0 × 2.0–2.5 µm (few germinating basidiospores observed). Carotenoid contents present in the cytoplasm of most cells, but particularly visible at basidia and basidiospores, sometimes inconspicuous and often of a dull orangish cream to moderately orange.

Ecology and distribution: Rather common in the Mediterranean forests, woodlands, and scrub biome of the Iberian Peninsula and Balearic Islands, always associated with *Juniperus spp*. Also found in the southern coast of Crimea. The species is highly xerotolerant and prefers exposed branches, undergoing repeated cycles of dryness and hydration.

Additional specimens examined: **Spain**, Balearic Islands, Ibiza, Alla dins, Pollença, on *Juniperus phoenicea* wood, 7 Dec. 2018, *I. Olariaga*, UPS F-946606; Castilla-La Mancha, Guadalajara, Tamajón, near ermita de la Virgen de los Enebrales, on *Juniperus thurifera* branches, 28 Dec. 2019, *J.C. Zamora, J. Señoret, B. Zamora, P.L. Aznar & S. Pardillo*, UPS F-979748; Guadalajara, Turmiel, entre Anquela del Ducado y Turmiel, junto a la carretera CM-2107, fallen *Juniperus thurifera* log, 24 Jan. 2016, *I. Olariaga*, UPS F-946613; Madrid, Becerril de la Sierra, on unidentified wood, 16 Jan. 2010, *J.C. Zamora, J.C. Campos, Á. González, F. Prieto & G. Sánchez*, UPS F-946609; Madrid, Colmenarejo, colada de Cabeza Aguda, on *Juniperus oxycedrus* branches, 28 Dec. 2012, *J.C. Zamora, F. Prieto & Á. González*, UPS F-946608; Madrid, Colmenarejo, Cercados del Huerto, on *Juniperus oxycedrus* dead branches, 24 Dec. 2019, *J.C. Zamora, I. Olariaga, Á. González, F. Prieto & B. Zamora*, UPS F-979765; Madrid, Colmenarejo, Presa Vieja, on *Juniperus oxycedrus* branches, 24 Dec. 2019, *J.C. Zamora, I. Olariaga & B. Zamora*, UPS F-979756; Madrid, Hoyo de Manzanares, Finca La Ladera, on *Juniperus oxycedrus* exposed branches, 11 Jan. 2018, *I. Olariaga, J.C. Zamora, F. Pancorbo & L.A. Parra*, UPS F-946605; *ibid.*, on *Juniperus oxycedrus* branch, still attached to the tree, 4 Jan. 2018, *I. Olariaga*, UPS F-946611; Madrid, Hoyo de Manzanares, Finca Las Viñas, on *Juniperus oxycedrus* branch, still attached to the tree, 19 Dec. 2017, *M. Prieto & I. Olariaga*, UPS F-946612; Madrid, Lozoya, on *Juniperus thurifera* wood, 13 Dec. 2009, *Á. González, F. Prieto, B. Zamora & J.C. Zamora*, UPS F-946607. **Ukraine**, Crimea, Greater Yalta, Mys Martyan Nature Reserve, on *Juniperus excelsa* twig, 1 Jul. 2004, *A. Bereznitskyi*, CWU(MYC)4092, LE262836; *ibid.*, 30 Jun. 2004, *S. Klimova*, CWU(MYC)4093, LE262830; *ibid.*, Mys Martyan Nature Reserve, cape Nikitin, unidentified wood, 2 Jun. 2004, *S. Klimova, A. Bereznitskyi*, CWU(MYC)7560.

Notes: This species is easily distinguished by its ovoid to cylindrical-ellipsoid, thin-walled basidiospores with 0–3 transverse septa at maturity that never become muriform, a morphology that is unique in *Dacrymyces s.l.* Besides, the combination of relatively large and dull-coloured basidiocarps, large basidia, conspicuous hyphidia, and xeric habitat on exposed *Juniperus* wood further distinguishes it from any other known species. There are, however, two other accepted species in the *Dacrymycetes* with typically ovoid to ellipsoid basidiospores. The first is *Dacrymyces ovisporus*, which has shorter, subglobose to broadly ovoid basidiospores, becoming muriform at maturity due to the formation of transverse, longitudinal and oblique septa (Brefeld 1888, McNabb 1973), simple hyphidia, and larger basidiocarps that are bright orangish

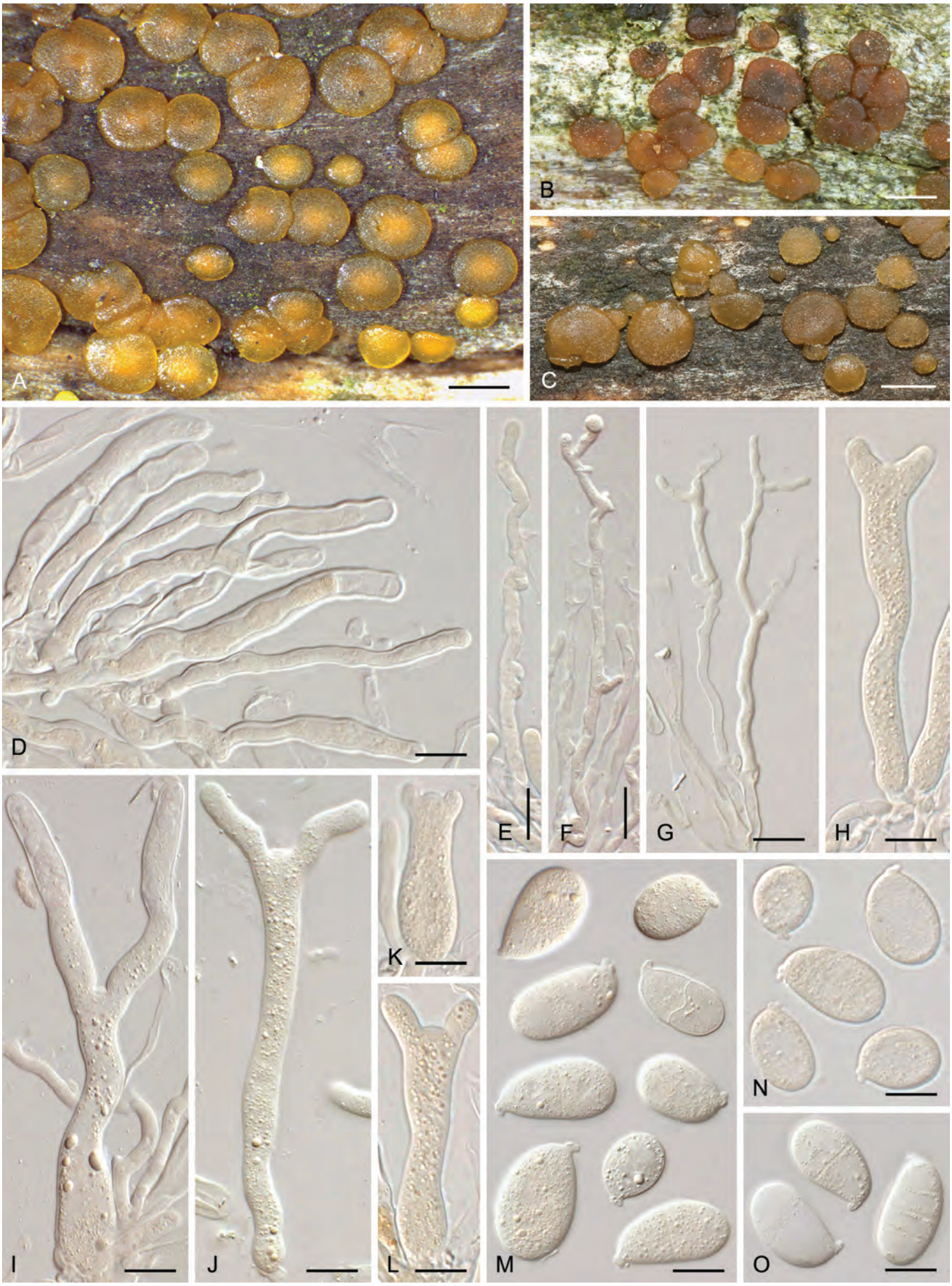

Fig. 5. *Dendrodacrys ellipsosporum*. **A–C.** Macromorphology of fresh basidiocarps. **D–O.** Micromorphology. **D.** Terminal cells of cortical hyphae. **E–G.** Hyphidia. **H–L.** Basidia. **M–O.** Basidiospores. A, B, D, F, G, I, J, M from UPS F-946604 (holotype); C, O from UPS F-946607; E, K, L, N from UPS F-946610 (isotype); H from UPS F-946605. Scale bars: A–C = 1 mm; D–O = 10 µm.

yellow. This species is typically found in *Pinus* wood and stains the substrate yellow (Torkelsen 1997). In addition, the specimens of *Da. ovisporus* included in the phylogenetic analyses show no close relationship with our samples of *De. ellipsosporum* (Fig. 1). Two of the Ukrainian studied specimens (CWU[MYC]4092 and CWU[MYC]4093) were indeed cited as *Da. ovisporus* in Malysheva & Akulov (2011). The second species with similarly shaped basidiospores is *Unilacryma bispora*. The dull colours and the presence of branched hyphidia are reminiscent of *De. ellipsosporum*, but the basidiocarps of the latter are larger, some carotenoid pigment is usually visible in the cytoplasm contents, the basidiospores never become muriform as in *U. bispora*, and septa in internal hyphae are always clamped. This species is also not closely related to *De. ellipsosporum*, belonging to a different family (Fig. 1).

Among other species names described in the literature for taxa that could be closely related to the new species, we found the old name *Da. castaneus* (Rabenhorst 1844). The data from the protologue are vague, but there are three characteristics that may agree with *De. ellipsosporum*. The first and most important one is the spore shape, which is defined as ovoid. In addition, the sporocarps are said to be brownish (hence, the epithet), and were found on a dry, dead branch. Unfortunately, no further data on the substrate or the ecology were indicated, and no iconography or specimens are cited. On the other hand, there are some characters that do not match well with *De. ellipsosporum*, and even raise doubts about the belonging of *Da. castaneus* to *Dacrymycetaceae*. The spores are said to have a dark central part and a bright edge, as if the cytoplasm was dark and the wall hyaline, something remarkably unusual for a species in *Dacrymycetaceae*. The hyphae are also said to have brown areas. The sporocarps are described as rounded, but the dimensions indicate they can be up to twice longer than wide when fresh, almost disappearing when dried, while in *De. ellipsosporum* they are almost circular and remain very conspicuous when dried, being easily visible in the field. It should be taken into account that Rabenhorst included in his concept of *Dacrymyces* (as "*Dacryomyces*") species that nowadays we know belong to other groups, *e.g*. *Da. violaceus* and *Da. fragiformis*, which are most likely members of the *Tremellomycetes*. Therefore, the name *Da. castaneus* could refer to a non-*Dacrymycetes* jelly fungus. The dark interior of the spores already caused Fries (1874) to express doubts about its classification. The name *Da. castaneus* has not been in use during the last century and was interpreted differently by other mycologists in the past. For example, Saccardo (1888) suggested that the spores mentioned in the protologue could actually be conidia, and also indicated that the species was found on lemon tree branches in Portugal and Germany, a substrate on which we would never expect *De. ellipsosporum* to occur. Neuhoff (1936) suggested that it may represent *Exidia badio-umbrina*, while Kennedy (1958) listed it as a possible, yet dubious, synonym of *Dacrymyces enatus* var. *enatus*. McNabb (1973) agreed with Kennedy (1958) while noting that original material could not be traced. Donk (1966) considered it as a *nomen dubium*, and judging by the information indicated above, we agree with this decision and do not see any advantage to rescuing this name. A possible neotypification of *Da. castaneus*, the only currently possible choice to fix the application of the name, would be difficult and subjective, since the lack of original material and the insufficient data contained in the diagnosis do not allow to make an informed and objective decision. For all these reasons, we prefer to describe *De. ellipsosporum* as a well-defined new species, and to reject *Da. castaneus* as a *nomen dubium* and *ambiguum* for the time being, at least until any original material could be found.

Dendrodacrys oblongisporum J.C. Zamora & Ekman, ***sp. nov***. MycoBank MB 842997. Fig. 6.

Etymology: The specific epithet is a Latin compound adjective of *oblongus* and *spora* (with a Greek origin but treated as Latin), and refers to the shape of the basidiospores.

Typus: **Spain**, Madrid, Bustarviejo, close to Puerto de Canencia, on *Juniperus communis subsp. alpina* dead branches, 28 Dec. 2019, *J.C. Zamora, P.L. Aznar, S. Pardillo, J. Señoret & B. Zamora* (**holotype** UPS F-979568); *idem*, UPS F-979569 (**isotype**). Note – the holotype and isotype are two different individuals, collected in well-separated bushes but treated as duplicates following Art. 8.2.

Description: *Basidiocarps* gelatinous to firm-gelatinous, (0.2–) 0.4–1.2 mm diam, barely erumpent when young, pulvinate to applanate, some becoming ± pezizoid when drying up, gregarious or in small groups, rarely coalescing; yellowish orange, ochraceous orange to amber coloured in hydrated state, becoming orange to orangish brown when dried. *Hymenium* ± confined to the upper part of the basidiocarps, irregularly spreading to the margins; sterile cortex often distinct, or at least with a sterile area in the lower part of the basidiocarps. Terminal cells of marginal hyphae narrowly clavate to cylindrical, 3.9–6.9 µm diam, ± thick-walled, with hyaline walls and some cytoplasmic, often not very conspicuous, yellow-orange carotenoids. Internal hyphae 1.5–4.0 µm diam, mostly thin-walled, clamped. *Hyphidia* present, often moderately branched but varying from simple to ± densely branched, 2.0–3.8 µm diam (width rather constant throughout their length or somewhat wider towards the base; bumps sometimes present), often with 1–2 clamped septa throughout their length, reaching the level of basidia or some surpassing them. Young basidia cylindrical to narrowly clavate; mature basidia 42.5–70.0(–92.0) × 5.0–7.8 µm, with two subapical sterigmata, 17.0–34.5 × 3.8–6.2 µm, apex of the mature basidium slightly protruding or not. *Basidiospores* thin-walled or with walls slightly thickened when old, 13.5–18.5(–19.0) × 6.3–9.4 µm, 1.6 ≤ Q ≤ 2.4 (n = 41), often oblong but varying from ellipsoid, narrowly ovoid, to ± cylindrical-allantoid, becoming 3-septate at maturity, not constricted at septa or only slightly, uninucleate prior to septation; hilar appendix conspicuous, *ca*. 1.0 µm long. Basidiospore germination not seen. Carotenoid contents visible in the majority of the cells but especially in the basidia, cream-orange to yellow-orange.

Ecology and distribution: Insufficiently known. This species has been found in only two distant localities, one in the Mediterranean forests, woodlands and scrub biome (central Iberian Peninsula, submediterranean climate due to the high elevation), and the other in the taiga biome (southwestern Scandinavia, hyperhumid southern boreal to hemiboreal coniferous forests). In both places, *De. oblongisporum* inhabited thin branches of coniferous trees and bushes, still attached to the living plants. It may be a widespread but uncommon species, or overlooked due to its small size and macroscopic similarity with many other *Dacrymyces s.l*. species. At least partly xerotolerant.

Additional specimen studied: **Norway**, Sogn og Fjordane, Førde, Viafjellet, on *Pinus sylvestris* branches, 5 Jul. 2018, *S. Ekman*, UPS F-946599.

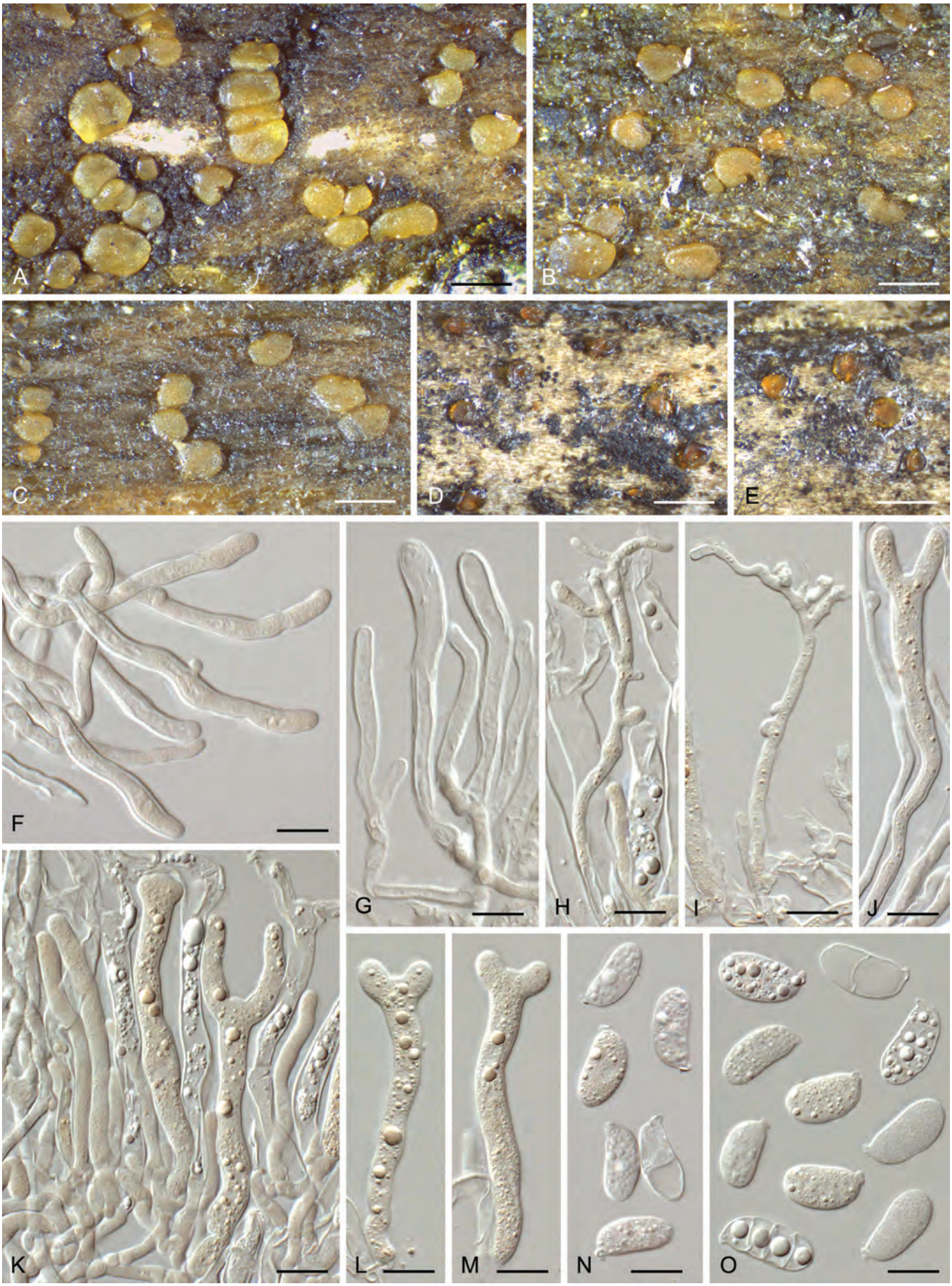

Fig. 6. *Dendrodacrys oblongisporum*. **A–E.** Macromorphology; hydrated (A–C) and dried (D, E) basidiocarps. **F–O.** Micromorphology. **F, G.** Terminal cells of cortical hyphae. **H, I.** Hyphidia. **J–M.** Basidia. **N, O.** Basidiospores. A–C, G–I, K–M, O from UPS F-979568 (holotype); D–F, J, N from UPS F-946599. Scale bars: A–E = 1 mm; F–O = 10 µm.

Notes: *Dendrodacrys oblongisporum* resembles *Dacrymyces adpressus* and *Da. fennicus* based on literature. However, both species lack branched hyphidia, *Da. adpressus* occurs on angiosperm wood (Grognot 1863), and *Da. fennicus* typically grows on thick branches or logs of *Pinus*, not on thin branches or twigs as *De. oblongisporum*. The basidiospores in both *Da. adpressus* and *Da. fennicus* are also more distinctly allantoid, and the terminal cells of the cortical/marginal hyphae thin-walled. Finally, molecular data clearly separate *Da. fennicus* and *De. oblongisporum*, and the available DNA sequences from specimens identified as *Da. adpressus* from Japan (that probably do not represent *Da. adpressus s.str.*) also distinguish these species into well-separated clades (Fig. 1). From other species of *Dendrodacrys*, the combination of the basidiospore shape, presence of clamp-connections, and isolated, small yellow-orange basidiocarps is diagnostic. Specifically, *De. ciprense* produces darker, more brownish basidiocarps, and cylindrical-allantoid basidiospores ($2.2 \leq Q \leq 3.2$). Basidiocarps of *De. concrescens* are smaller and coalesce to form extense masses, the basidiospores are smaller and especially narrower (4.8–6.3 µm wide), and the ecology is also different, growing on fallen pine logs. *Dendrodacrys ellipsosporum* has larger and especially broader basidiospores [(7.0–)9.7–14.2(–15.5) µm wide], slightly broader basidia, and often darker basidiocarps. Finally, *Da. cf. dendrocalami* lacks clamp-connections and the basidiospores are thick-walled.

DISCUSSION

Is a new genus needed in *Dacrymycetaceae*?

Zamora & Ekman (2020) and Savchenko *et al.* (2021) showed that branched hyphidia seemed to be a common feature in *Cerinomycetaceae*, *Dacryonaemataceae* and *Unilacrymaceae*, and probably plesiomorphic in the last two families. By contrast, branched hyphidia in *Dacrymycetaceae* were only found in certain groups and seemed to be a secondary acquisition of this character state or a reversion to the plesiomorphic state. Specifically, until now, branched hyphidia have been found in only two small species groups of *Dacrymycetaceae*. One is the clade containing *Dacryopinax elegans* (generic type) and *Dacrymyces san-augustinii*, which is nested in the large group of mostly clampless species (clade D8). The other clade is D5, where most species have clamp-connections. The group including *Dacryopinax elegans* and *Da. san-augustinii* is morphologically very heterogeneous and difficult to diagnose, since *Dacryopinax elegans* has brownish, long-stalked, cochleariform to auricularioid basidiocarps with unilateral hymenium, and thick-walled, 3-septate basidiospores, while *Da. san-agustinii* (and also *Da. novae-zelandiae*, which lacks conspicuously branched hyphidia) has ± yellow-orange, sessile, cushion-shaped basidiocarps with a poorly defined sterile cortex, and thin-walled, multiseptate basidiospores.

Clade D5, on the other hand, is considerably more homogeneous and easier to diagnose, comprising species with sessile, cushion-shaped to flattened basidiocarps, branched hyphidia, and mature basidiospores with up to three septa. All known species in this group have clamp-connections, with the exception of *Da. cf. dendrocalami*, which seems to have lost them. From a phylogenetic point of view, clade D5 and the group containing *Dacryopinax elegans* are not closely related, so it is not possible to delimit a single, monophyletic genus that would include all *Dacrymycetaceae* species with branched hyphidia. In addition, it would be difficult to justify the inclusion of species in clade D5 even in a very broad and extended genus *Dacrymyces*, since that would imply merging well-known genera such as *Calocera s.str*. with *Dacrymyces*. Such an assemblage would hardly be diagnosable in terms of the most used characters in *Dacrymycetes* taxonomy, like the presence or absence of clamp-connections, basidiospore morphology (including shape, wall thickness, and septation), presence or absence of distinct hyphidia, development of a sterile cortex and terminal cells of its hyphae, or the morphology of the basidiocarps. Therefore, the recognition of clade D5 as a distinct genus does not imply oversplitting *Dacrymyces*, but on the contrary, it increases the diagnosability of the genera in *Dacrymycetaceae* and partially alleviates the rampant polyphyly of *Dacrymyces s.l*. Further generic rearrangements are expected in the future, but only after phylogenies with better resolution (especially in clade D8) are obtained and monographic studies of the different clades have been performed. To emphasize the character of branched hyphidia in the species currently included in clade D5, we chose the name *Dendrodacrys*. None of the included species contain the type of any validly published generic or infrageneric names in *Dacrymycetaceae*, most of which were already treated by Zamora & Ekman (2020) and Savchenko *et al.* (2021), so there is no other nomenclatural choice than proposing a new generic name.

Species delimitation in *Dendrodacrys*

STACEY results showed a rather clear assignment of most specimens to a single cluster (putative species), except for the uncertainty whether the two specimens of *Da. cf. adpressus* should be considered as one or two putative species. The amount of data for TNS-21069 is much smaller than for the other samples in the dataset, since only nrLSU data was available and only five substitutions separate the two *Da. cf. adpressus* specimens. This is clearly insufficient to get a reliable estimate of the population structure and possible speciation events within this species or species complex. By comparison, there are seven substitutions and one indel separating the two most distant nrLSU sequences of *De. ellipsosporum* [obtained from UPS F-946606 and CWU(MYC)4092], but thanks to the information contained in the remaining DNA regions, STACEY did not have problems to suggest that both samples belong to a same cluster, with very high posterior probability. As reported elsewhere, coalescence-based species delimitation is prone to oversplitting (*e.g*. Jackson *et al.* 2017, Sukumaran & Knowles 2017, Chambers & Hillis 2020, Leaché *et al.* 2019). Putative species suggested by such methods should be critically evaluated using all available data and not directly translated to nominal species. This is especially true when the amount of data is small, *e.g.* few specimens or populations per putative species, and/or few unlinked DNA regions with enough variation. Nevertheless, these two samples were mostly assigned to the same putative species in our analyses, which agrees with a conservative approach.

From a phenotypical point of view, the basidiospore morphology is demonstrated here to be particularly useful to characterise species in *Dendrodacrys*, being almost like a "fingerprint" for species recognition. In fact, the delimitation of the new species found during our study does not really appear to represent a challenge for the morphology- and coalescence-based species delimitation analyses. Among the proposed

new species, *De. concrescens* and *De. ellipsosporum* have a particularly striking morphology and very distinct DNA sequence data, making them unlikely to be confused with any other species. *Dendrodacrys ciprense* and *De. oblongisporum* are rather closely related according to our phylogenetic reconstructions, and both species produce non-coalescing, cushion-shaped basidiocarps and somewhat curved, thin-walled basidiospores. However, they are still well-defined and readily distinguishable on account of the colour of the basidiocarps, size and shape of the basidiospores, cell pigments, ecology, and molecular data (see Fig. 2 and observations under the mentioned taxa).

Notes on extra-European taxa

Dacrymyces dendrocalami is easily distinguished from the related taxa by clampless septa, wide basidia, sterigmata exceeding basidia in length, and spore shape. If the Japanese specimens are confirmed to belong to this taxon, then the species would be known from Japan and Taiwan, occurring on angiosperm wood. The characteristic dendroid hyphidia allow identification as *Dendrodacrys* even on a purely morphological basis, but we prefer to await the revision of the type material before proposing the required combination.

The Japanese *Dacrymyces cf. adpressus* is most likely an undescribed species. This angiosperm wood-dwelling species differs from the lectotype of *Da. adpressus* by the presence of abundant dendroid hyphidia. Yet another specimen (**Japan**, Wakayama, Mt. Shirami, on dead unidentified branches, 12 Oct. 2006, *T. Shirouzu* HNo. 554, TNS-F-21069) presumably belongs to this taxon, but we did not include it in the analyses due to the lack of data.

Dacrymyces paraphysatus and *Da. enatus* var. *macrosporus* are two morphologically close species that clearly belong to *Dendrodacrys* (see observations under *De. ciprense*). *Dacrymyces enatus* var. *macrosporus* is thus not closely related to *Da. enatus* var. *enatus* (syn. *Cerinomyces enatus*; see Savchenko *et al.* 2021), but its delimitation against *Da. paraphysatus* needs to be re-evaluated with additional specimens. Therefore, we do not make the combination in *Dendrodacrys* for the time being. Concerning *Da. paraphysatus*, we accept it as an independent species after studying the type material, and since it is already published at the species level, the combination can be safely made without risking the publication of a superfluous name:

Dendrodacrys paraphysatum (L.S. Olive) J.C. Zamora & A. Savchenko, ***comb. nov***. MycoBank MB 842998.
Basionym: *Dacrymyces paraphysatus* L.S. Olive, *Bull. Torrey Bot. Club* **85**: 106. 1958.

Calocera arborea (Shirouzu *et al.* 2013b), which was considered part of clade D5 in Zamora & Ekman (2020), was not included in the present study pending a morphological revision of the available material, and the generation of additional DNA data. With only ITS and nrLSU sequences currently available, the phylogenetic position of this species varied between studies. For instance, in Shirouzu *et al.* (2013b, 2016, 2017) it did not form a clade with *Da. cf. adpressus* and *Da. cf. dendrocalami*. This species shares with *Dendrodacrys* the cushion-shaped fertile heads of the basidiocarps and the 3-septate mature basidiospores. However, it has strikingly long and branched stalks, which could be seen as an extraordinary development of the parts that are often rooting into the substrate in several other species of *Dacrymycetes*. Most importantly, branched hyphidia were not indicated in the protologue, but these structures are not always easy to find. Their absence should be confirmed before taxonomic conclusions are drawn.

Further details on the taxonomy of the cited additional non-European species, as well as an identification key for the genus *Dendrodacrys*, will be included in a forthcoming study.

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Peronosporaceae species causing downy mildew diseases of *Poaceae*, including nomenclature revisions and diagnostic resources

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Abstract: Downy mildew pathogens of graminicolous hosts (*Poaceae*) are members of eight morphologically and phylogenetically distinct genera in the *Peronosporaceae* (*Oomycota, Peronosporales*). Graminicolous downy mildews (GDMs) cause severe losses in crops such as maize, millets, sorghum, and sugarcane in many parts of the world, especially in tropical climates. In countries where the most destructive GDMs are not endemic, these organisms are often designated as high-risk foreign pathogens and subject to oversight and quarantine by regulatory officials. Thus, there is a need to reliably and accurately identify the causal organisms. This paper provides an overview of the *Peronosporaceae* species causing graminicolous downy mildew diseases, with a description of their impact on agriculture and the environment, along with brief summaries of the nomenclatural and taxonomic issues surrounding these taxa. Key diagnostic characters are summarized, including DNA sequence data for types and/or voucher specimens, morphological features, and new illustrations. New sequence data for *cox*2 and 28S rDNA markers are provided from the type specimens of three species, *Peronosclerospora philippinensis*, *Sclerospora iseilematis*, and *Sclerospora northii*. Thirty-nine species of graminicolous downy mildews are accepted, and seven previously invalidly published taxa are validated. Fifty-five specimens are formally designated as types, including lectotypification of 10 species, neotypification of three species, and holotype designation for *Sclerophthora cryophila*.

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INTRODUCTION

Graminicolous downy mildews (GDMs) are diseases caused by members of the *Peronosporaceae* (*Oomycota*, *Peronosporales*). GDM pathogens are obligate, biotrophic parasites of cultivated and wild cereals and other grasses in the *Poaceae* family (Kenneth 1981, Spencer & Dick 2002). In regions of the world where the most destructive GDM pathogens reside, these diseases can result in significant crop losses (60–100 %) of staple food and forage crops such as maize (*Zea mays*), pearl millet (*Pennisetum glaucum*), sorghum (*Sorghum* spp.), and sugarcane (*Saccharum* spp.) (Exconde & Raymundo 1974, Safeeulla 1976, Kenneth 1981, Rathore *et al.* 2002, Putnam 2007, Kumar *et al*. 2012, Li *et al.* 2020). In parts of the world where these organisms are not present, foreign GDM pathogens are often regulated as quarantine pests by governmental agencies and are subject to strict control measures to prevent their spread. For example, in the USA, the maize pathogens *Peronosclerospora philippinensis* and *Sclerophthora rayssiae* var. *zeae* pose such a significant potential threat to the country's agriculture that they are regulated as Select Agents. Designation of a plant pathogen as a Select Agent in the USA is a notable distinction, as there are only seven plant pathogenic organisms so named, and placement in this category subjects them to the same general oversight program that also deals with deadly human pathogens such as the plague bacterium *Yersinia pestis*, the smallpox virus, and the SARS-associated coronavirus (SARS-CoV).

As with all organisms capable of inciting plant diseases, reliable and accurate identification of the GDM pathogens is crucial, but identification is only possible when the characters that can be used to identify them are clearly known. Any taxonomic or nomenclatural confusion that would lead to the misidentification of species or misapplication of a name could hinder efforts to identify introduced species, detect emerging pathogen threats, and track the spread of disease (Thines & Choi 2016, Petrželová *et al*. 2017, Davis & Crouch 2022a). However, this group has never been monographed, and practical diagnosis of GDM pathogens is hindered by the absence of an updated, centralized treatment of the group. Key identification resources such as morphological descriptions, diagnostic traits, host associations, and molecular datasets for exemplary materials are currently spread across hundreds of papers spanning more than 100 years, sometimes in obscure and difficult to obtain publications. To our knowledge, one species – *Sclerospora farlowii* – has never been illustrated and several species are not formally typified. The most recent comprehensive taxonomic reviews of the *Peronosporaceae* pathogens of grasses were published more than four decades ago, harkening back to Kenneth's summary of the group in 1981 and Waterhouse's seminal review in 1964. Since Waterhouse's review, nineteen new species, one variety, and five new genera of GDM pathogens have been discovered, and molecular phylogenetic data has been used to study these organisms since 2002 (Riethmüller *et al*. 2002). Thus, the goal of this paper is to provide an annotated summary of the names applied to the *Peronosporaceae* species causing downy mildew diseases on *Poaceae*. We briefly discuss the impact of each species, and when possible, summarize resources and descriptions, provide new illustrations, address nomenclatural issues, and discuss possible research that could help clarify outstanding taxonomic issues.

MATERIALS AND METHODS

In compiling this treatment, Waterhouse (1964) and Shaw (1975, 1978) were used as starting points. A literature search was conducted online using Google Scholar, Index Fungorum, and MycoBank for publications dealing the nomenclature, taxonomy, and economic impacts of GDM pathogens. Herein, names of *Peronosporaceae* species causing downy mildew diseases of *Poaceae* are listed alphabetically by the genus they are currently assigned to. Given the similarity between host and pathogen epithets throughout this paper, all Latin binomials are given without abbreviation throughout the text to avoid confusion.

Host association

The USA National Fungus Collections (BPI) fungus/host databases were initially consulted for distribution and host information (Farr & Rossman 2021). BPI online databases are cited as Farr & Rossman (2021) to summarize reports of species listed in "checklist" type publications; relevant publications where identifications were reviewed and verified are directly cited. The Plant List (http://www.theplantlist.org), World Flora Online (http://www.worldfloraonline.org/), and the Germplasm Resources Information Network (GRIN, http://www.ars-grin.gov/) were used as sources for plant name synonymy, in that order. When there were disagreements among the three sources, preference was given to GRIN. Plant hosts from the original collection are listed as current name (synonym, subfamily, tribe) following Sorgen *et al.* (2015).

Typification and validation of names

Lectotypes or neotypes were designated for effectively published species when original materials and/or specimens consistent with the protolog were available, following the current International Code of Nomenclature for algae, fungi, and plants (ICNafp; Turland *et al.* 2018); these are summarized in Table 1. Names that were not validly described according to the rules of the ICNafp but representing distinct taxa are validated following the ICNafp (Turland *et al.* 2018). New taxa and typifications were registered with MycoBank and are cited as MB and MBT accession numbers, respectively. Fungarium abbreviations follow the New York Botanical Garden's Index Herbariorum (Verkeley *et al.* 2014).

Identification resources

Morphological features for asexual and sexual structures are summarized in Supplementary Table S1. Diagnoses are provided for some – but not all – species where sufficient traits were available to provide a reliable diagnosis, but it is important to note that morphological characteristics of *Peronosporaceae* are influenced by environment and host (Runge *et al.* 2012) and may therefore vary. Full descriptions from the species protologs and/or non-original sources are provided, with protolog descriptions taking precedence and other sources used when the protolog information was incomplete or determined by later authors as incorrect.

For *Peronosporaceae* fungarium specimens examined at BPI and the Canadian National Mycological Fungarium (DAOM) for this work, macroscopic images of the type specimens were obtained and are included in this paper as Supplementary Figs S1–S23.

Line drawings of microscopic features were prepared from published reference materials and new images of *Sclerospora farlowii* (Figs 1–11). Objects and scale bars from original sources were opened in Photoshop CS6, the contour of objects traced, then the illustrations were standardized to a uniform style, with a gray mottling representing cytoplasm and solid grays representing solid walls. Thick black lines represent significant boundries, such as the ones between cytoplasm and wall. Thin lines were used to represent delimitations of vesicles or zoospores, and dashed lines were used to delineate vacuoles. As much as possible, drawings were placed at the same scale to facilitate comparisons of the structures. New microscopic images were prepared from the type specimen of *Sclerospora farlowii*, as illustrations of this pathogen have never been published. Specimen material was rehydrated in 85 % lactic acid, stained with cotton blue, and visualized using a Zeiss Axio Imager M2 microscope (Carl Zeiss Microscopy, Thornwood, NY). Images were captured with an Axiocam 503 color digital camera using differential contrast illumination and processed with Zen 2 Pro v. 3.4 software (Carl Zeiss Microscopy).

DNA sequence data resources are summarized for types and/or voucher specimens when available. Accession numbers for nucleotide sequences of the barcode markers *cox*2 and 28S rDNA were obtained from the National Center for Biotechnology Information (NCBI) GenBank (https://www.ncbi.nlm.nih.gov/)

Table 1. Summary of type and exemplar materials for *Peronosporaceae* pathogens of *Poaceae*. Of the 66 total type specimens, 48 types are newly designated in the current paper (highlighted in bold text). Basionyms are given if different from the current name.

Current name	Basionym	Specimen	Specimen status	Year Collected	Host	Locale	*Cox*2 sequence	28S rDNA sequence	References
Baobabopsis donbarrettii R.G. Shivas *et al.*		BRIP 54675	Holotype	2011	*Perotis rara*	Australia, Western Australia	KT248948	KT248945	Thines *et al.* (2015)
Baobabopsis enneapogonis Thines *et al.*		BRIP 49822	Holotype	2007	*Enneapogon cylindricus*	Australia, Northern Territory	KT248946	—	Thines *et al.* (2015)
Baobabopsis marneyi R.G. Shivas *et al.*		BRIP 70341	**Holotype**	2019	*Enneapogon polyphyllus*	Australia, Queensland, Georgetown	OK336436	—	Ryley *et al.* (2022)
Eraphthora butleri (W. Weston) Telle & Thines	*Sclerospora butleri* W. Weston	BPI 187075	**Lectotype**	1927	*Eragrostis aspera*	Malawi (formerly Nyasaland), Bulaki	—	—	Weston (1933), this paper
		FH 965376	**Isotype**	1927	*Eragrostis aspera*	Malawi (formerly Nyasaland), Bulaki	—	—	Weston (1933), this paper
		BPI 187074	Might be isotype?	1927	Collection metadata incomplete	Collection metadata incomplete	—	—	Weston (1933), this paper
Eraphthora drenthii M. J. Ryley *et al.*		DAR 4201	Holotype	1950	*Eragrostis cilianensis*	Australia, New South Wales	HQ413338	—	Ryley *et al.* (2022)
Eraphthora occultata Y.P. Tan *et al.*		DAR 16237	Holotype	1967	*Eragrostis cilianensis*	Australia, New South Wales	OK391240	—	Ryley *et al.* (2022)
Graminivora graminicola (Naumov) Thines & Göker	*Bremia graminicola* Naumov	LEP4385	**Lectotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper
		BPI 786232	**Isotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper
		LEP4384	**Isotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper
		LEP4377	**Isotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper
		FH 01012075	**Isotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper
		E00297399	**Isotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper

Table 1. (Continued).

Current name	Basionym	Specimen	Specimen status	Year Collected	Host	Locale	*Cox*2 sequence	28S rDNA sequence	References
		HUH 738	Voucher	2001	*Arthraxon hispidus*	China, Yunnan, A Zi Ying	KP965747	KP965742	Thines & Göker (2006)
Peronosclerospora aristidae J. Kruse *et al.*		BRIP 67069	Holotype	2018	*Aristida hygrometrica*	Australia, Queensland	OK336438	—	Ryley *et al.* (2022)
Peronosclerospora boughtoniae M.J. Ryley *et al.*		BRIP 14388	Holotype	1978	*Sorghum plumosum*	Australia, Queensland, Lizard Island	OK33649	—	Ryley *et al.* (2022)
Peronosclerospora dichanthiicola (Thirum. & Naras.) C.G. Shaw	*Sclerospora dichanthiicola* Thirum. & Naras.	Illustration	**Lectotype**	1952	*Dichanthium annulatum*	India, Bihar	—	—	Thirumalachar & Narasimhan (1952), this paper
Peronosclerospora eriochloae Ryley & Langdon		BRIP 13693	Holotype	1979	*Eriochloa pseudoacrotricha*	Australia, Upper Pilton, Queensland	—	—	Ryley & Langdon (200)1
		BRIP 13691	**Isotype**	1979	*Eriochloa pseudoacrotricha*	Australia, Upper Pilton, Queensland	—	—	Ryley & Langdon (2001)
		BRIP 13692	**Isotype**	1979	*Eriochloa pseudoacrotricha*	Australia, Upper Pilton, Queensland	—	—	Ryley & Langdon (2001)
		FR-0046005	**Isotype**	1979	*Eriochloa pseudoacrotricha*	Australia, Upper Pilton, Queensland	HQ261813	HQ261786	Telle *et al.* (2011)
Peronosclerospora heteropogonis Siradhana *et al.*		HOH 898	**Holotype**	2005	*Zea mays*	India: Rajasthan, Udaipur	EU116054	—	Thines *et al.* (2008), this paper
Peronosclerospora ischaemi M.J. Ryley *et al.*		BRIP 70369	Holotype	2019	*Ischaemum fragile*	Australia, Queensland	OK336443	OK350686	Ryley *et al.* (2022)
Peronosclerospora jamesiae R.G. Shivas *et al.*		BRIP 65234	Holotype	2016	*Sorghum intrans*	Australia, Northern Territory, Wagait Beach	OK336444	—	Ryley *et al.* (2022)
Peronosclerospora mactaggartii R.G. Shivas *et al.*		BRIP 57677	Holotype	2012	*Sorghum timorense*	Austrlia, Northern Territory, Dorat Rd., Robins Falls	OK336446	OK350687	Ryley *et al.* (2022)
Peronosclerospora maydis (Racib.) C.G. Shaw	*Peronospora maydis* Racib.	KRAM O-5859(J)	Lectotype	1897?	*Zea mays*	Indonesia, Java, Jawa Tengah	MW025835	—	Suharjo *et al.* (2020)
		BPI 789413	**Isotype**	1897?	*Zea mays*	Indonesia, Java, Jawa Tengah			This paper
Peronosclerospora miscanthi (T. Miyake) C.G. Shaw	*Sclerospora miscanthi* T. Miyake	BPI 187301	**Neotype**	1915	*Miscanthus sinensis*	Taiwan: Taipei	—	—	Miyake (1912), this paper
		Stevens 811[1]	Voucher	1930	*Miscanthus japonicus*	Philippines, Luzon	HQ261811	HQ261784	Telle *et al.* (2011)

Table 1. (Continued).

Current name	Basionym	Specimen	Specimen status	Year Collected	Host	Locale	*Cox2* sequence	28S rDNA sequence	References
Peronosclerospora noblei (W. Weston) C.G. Shaw	*Sclerospora noblei* W. Weston	DAR 1075	**Lectotype**	1928	*Sorghum leiocladum*	Australia, New South Wales	—	—	Weston (1929), this paper
		DAR 1076	**Isotype**	1928	*Sorghum leiocladum*	Australia, New South Wales	—	—	Weston (1929), this paper
		BPI 187306	**Isotype**	1928	*Sorghum leiocladum*	Australia, New South Wales	OK185343	OK255496	Weston (1929), this paper
		FH 965379	**Isotype**	1928	*Sorghum leiocladum*	Australia, New South Wales	—	—	Weston (1929), this paper
Peronosclerospora panici R.G. Shivas *et al.*		DAR 35733	**Holotype**	1980	*Panicum laevinode*	Australia, New South Wales, Narromine	HQ261814	HQ261787	Telle *et al.* (2011), Ryley *et al.* (2022)
Peronosclerospora philippinensis (W. Weston) C.G. Shaw	*Sclerospora philippinensis* W. Weston	BPI 187314	**Lectotype**	1919	*Zea mays*	Philippines, Los Banos	—	—	Weston (1920), this paper
		BPI 187044	**Isotype**	1919	*Zea mays*	Philippines, Los Banos	OK185341	OK181682	Weston (1920), this paper
		BPI 187311	**Isotype**	1919	*Zea mays*	Philippines, Los Banos	—	—	Weston (1920), this paper
		BPI 187313	**Isotype**	1919	*Zea mays*	Philippines, Los Banos	—	—	Weston (1920), this paper
		FH 965382	**Isotype**	1919	*Zea mays*	Philippines, Los Banos	—	—	Weston (1920), this paper
		FH 965383	**Isotype**	1919	*Zea mays*	Philippines, Los Banos	—	—	Weston (1920), this paper
Peronosclerospora sacchari (T. Miyake) Shirai & Hara	*Sclerospora sacchari* T. Miyake	BPI 187331	**Lectotype**	1910	*Saccharum officinarium*	Taiwan	—	—	Miyake (1927), this paper
		BRIP 44241A	Voucher	2004	*Saccharum* sp.	East Timor	EU116052	HQ261764	Telle *et al.* (2011)
Peronosclerospora sargae R.G. Shivas *et al.*		BRIP 27691	Holotype	2000	*Sorghum timorense*	Australia, Northern Territory	HQ261809	HQ261782	Shivas *et al.* (2012)
Peronosclerospora schizachyrii R.G. Shivas *et al.*		BRIP 67070	Holotype	2018	*Schizachyrium fragile*	Australia, Queensland	OK336452	OK350689	Ryley *et al.* (2022)
Peronosclerospora sehimatis M.J. Ryley *et al.*		BRIP 49806	Holotype	2006	*Sehima nervosum*	Australia, Northern Territory, Arnhem Highway, Jabira	OK336453	—	Ryley *et al.* (2022)
Peronosclerospora sorghi (W. Weston & Uppal) C.G. Shaw	*Sclerospora sorghi* (Kulk.) W. Weston & Uppal	BPI 187336	**Lectotype**	1915	*Sorghum vulgare*	India, Coimbatore	—	—	Weston & Uppal (1932), this paper
		HUH 897	Voucher	2005	*Sorghum bicolor*	India, Karnataka, Dharwad	EU116055	—	Thines *et al.* (2008)

Table 1. (Continued).

Current name	Basionym	Specimen	Specimen status	Year Collected	Host	Locale	*Cox*2 sequence	28S rDNA sequence	References
Peronosclerospora spontanea (W. Weston) C.G. Shaw	*Sclerospora spontanea* W. Weston	BPI 187043	**Lectotype**	1919	*Saccharum spontaneum*	Philippines, Los Banos	—	—	Weston (1921), this paper
		BPI 187073	**Isotype**	1919	*Saccharum spontaneum*	Philippines, Los Banos	—	—	Weston (1921), this paper
Peronosclerospora westonii J.A. Crouch & Thines		Illustration	**Holotype**	1961	*Iseilema prostratum*	India, Poona	—	—	Srinivasan *et al.* (1961), this paper
Poakatesthia penniseti (R.G. Kenneth & J. Kranz) Thines & Göker	*Plasmopara penniseti* R. G. Kenneth & Kranz	IMI 137328c	Holotype	1968	*Pennisetum glaucum*	Ethiopia, Bako/Shoa	EF426475	—	Thines & Göker (2007)
Sclerophthora cryophila W. Jones		DAOM 20643	**Holotype**	1948	*Dactylis glomerata*	Canada, British Columbia	—	—	Jones (1955), this paper
Sclerophthora lolii J.A. Crouch & Thines		Illustration	**Holotype**	1964	*Lolium rigidum*	Israel, Mikve	—	—	Kenneth (1964), this paper
Sclerophthora macrospora (Sacc.) Thirum. *et al.*	*Sclerospora macrospora* Sacc.	BPI 187265	**Neotype**	1895	*Phlaris arundinaceae*	Germany, Saxony, Königstein	—	—	This paper
		BPI 187266	**Isotype**	1895	*Phlaris arundinaceae*	Germany, Saxony, Königstein	—	—	This paper
		HUH 892	Voucher		*Zea mays*	China	KP965748	EU826119	Choi *et al.* (2015)
Sclerophthora rayssiae J.A. Crouch & Thines		Illustration	**Holotype**	1964	*Hordeum vulgare*	Israel, Valley of Esdraelon	—	—	Kenneth *et al.* (1964), this paper
Sclerophthora zeae J.A. Crouch & Thines		HCIO 29038	**Holotype**	1965	*Zea mays*	India, Pantnagar	—	—	Payak & Renfro (1967), this paper
Sclerospora farlowii Griffiths		BPI 187077	**Lectotype**	1900	*Chloris virgata*	United States of America, Arizona	—	—	Griffiths (1907), this paper
		BPI 187076	**Isotype**	1900	*Chloris virgata*	United States of America, Arizona			Griffiths (1907), this paper
		BPI 187078	**Isotype**	1900	*Chloris virgata*	United States of America, Arizona			Griffiths (1907), this paper
		FH 965329	**Isotype**	1900	*Chloris virgata*	United States of America, Arizona			Griffiths (1907), this paper
		FH 1093687	**Isotype**	1900	*Chloris virgata*	United States of America, Arizona			Griffiths (1907), this paper
Sclerospora graminicola (Sacc.) J. Schröt.	*Protomyces graminicola* Sacc.	Schneider 553[2]	Holotype	1886?	*Setaria viridis*	Poland: Legnica (Liegnitz), Waldau			Schröeter (1886)
		HV532	Voucher		*Pennisetum glaucum*	India, Gulbarga, Karnataka	DQ365768	AY035514, AY273987	Nayaka *et al.* (2017)

Table 1. (Continued).

Current name	Basionym	Specimen	Specimen status	Year Collected	Host	Locale	*Cox*2 sequence	28S rDNA sequence	References
Sclerospora iseilematis Thirum. & Naras.		BPI 187262	**Lectotype**	1947	*Iseilema prostratum*	India, Mysore	OK185342	OK255493	Thirumalachar & Narasimhan (1949), this paper
		IMI 38399	**Isotype**	1947	*Iseilema prostratum*	India, Mysore	—	—	Thirumalachar & Narasimhan (1949), this paper
Sclerospora northii W. Weston		BPI 187307	**Lectotype**	1924	*Saccharum maximum*	Fiji Islands, Suva	—	—	Weston (1929), this paper
		FH 965380	**Isotype**	1924	*Saccharum maximum*	Fiji Islands, Suva	—	—	Weston (1929), this paper
Sclerospora secalina Naumov		Not designated	—	1949?	*Secale cereale*	Former U.S.S.R.	—	—	Naumov (1949)
Viennotia oplismeni J.A. Crouch & Thines		GZU 335974	**Holotype**	1963	*Oplismeni hirtellus*	Guinea, near Kindia	—	AY035527, AY273977	Göker *et al.* (2003), this paper
		IMI 103944	**Isotype**	1963	*Oplismeni hirtellus*	Guinea, near Kindia	—	—	Göker *et al.* (2003), this paper
		BPI 784624	**Isotype**	1963	*Oplismeni hirtellus*	Guinea, near Kindia	—	—	Göker *et al.* (2003), this paper

[1] Stevens Philippine Fungi, Island of Luzon, No. 811.

[2] Herbarium Schlesischer Pilze: W. G. Schneider, No. 553.

for accessions that were associated with specimens lodged in reference collections and described in peer-reviewed literature. "Unpublished" NCBI nucleotide accessions with uncertain provenance and/or lacking association with a peer-reviewed scientific publication were not included in the summary. New *cox*2 and 28S rDNA sequence data was extracted from unpublished genome assemblies of three species: *Peronosclerospora philippinensis, Sclerospora iseilematis*, and *Sclerospora northii*. Genome data was generated using Illumina sequencing technology following the general protocols described in Fletcher *et al.* (2018); a full paper describing these genomes is forthcoming.

RESULTS

Including the six species described as part of this paper for validation purposes (see Taxonomy section, below), there are 39 distinct and validly published species that cause downy mildew diseases of *Poaceae* hosts. Three subfamilies in the *Poaceae*, the warm season (C4 photosynthesis) grass subfamilies *Chlorioideae*, *Panicoideae*, and the cool-season (C3 photosynthesis) grass subfamily *Pooideae*, are parasitized by these organisms. With the notable exception of the widespread pathogen *Sclerophthora macrospora*, all the most destructive, widespread, and economically important GDM pathogens parasitize cereals and other grasses in the *Panicoideae*. In contrast with the pathogens of the *Panicoideae*, the GDM species known from *Chlorideae* hosts (*Baobabopsis donbarretti*, *Baobabopsis enneapogonis*, *Eraphthora butleri*, *Sclerophthora farlowii*) have rarely been reported or were reported just once at the time of the original descriptions.

The species *Sclerospora magnusiana* (Sorokine 1889) is an uncertain member of the genus *Sclerospora*, given that its host – the spore-forming horsetail plant [*Equisetum* sp. (*Equisetaceae, Pterdophytes*)] – is not a member of *Poaceae*. Waterhouse (1964) suggested that the species might be a chytrid rather than a member of *Sclerospora*, but Sorokine's (1889) description and depiction of the formation of oospores appear to depict an oomycete. However, unlike *Sclerospora graminicola*, which produces oospores embedded in the host tissue, the mature oospores of *Sclerospora magnusiana* form a powder-like layer on the infected plants (Sorokine 1889). Sorokine did not specify a type, but LEP contains a specimen (LEP 9584) collected by N. Sorokine on *Equisetum arvense* from Orsk, Russia in 1894 that could serve as neotype for the species and should be examined, especially using molecular data. However, as *Sclerospora magnusiana* does not infect a grass, it is not included in our summary.

Taxonomy

Baobabopsis R.G. Shivas *et al.*, *IMA Fungus* **6**: 484. 2015.

Type species: *Baobabopsis donbarrettii* R.G. Shivas *et al.*, *IMA Fungus* **6**: 485. 2015.

Description: *Sporangiophores* evanescent, hyaline, cylindrical, 75–120 µm × 20–28 µm wide, unbranched, with 5–20 ampulliform to lageniform ultimate branchlets. *Sporangia* hyaline, deciduous. *Oogonia* subglobose, golden yellow, 27–45 × 25–39 µm; wall (including warts) uneven, verrucose with rounded warts, 3–11 µm thick. *Oospores* globose to broadly ellipsoidal, pale to golden yellow, 19–29 × 18–28 µm, one per oogonium; wall even, smooth, 1–3 µm thick (Thines *et al*. 2015).

Diagnosis: *Baobabopsis* is distinguished from all other *Peronosporaceae* genera in that it produces broad club-shaped to cylindrical sporangiophores bearing a cluster of terminal ampulliform projections that give rise to sporangia. The genus is also distinguished through its position in phylogenetic trees constructed using 28S rDNA and *cox*2 sequence data.

Note: *Baobabopsis* currently contains three species and is exclusively known from Australia as a parasite of *Chloridoideae* hosts (Thines *et al*. 2015, Ryley *et al.* 2021).

Baobabopsis donbarrettii R.G. Shivas *et al.*, *IMA Fungus* **6**: 485. 2015.

Typus: **Australia**, Western Australia, Kununurra, near Lake Kununurra, *Perotis rara* (*Chloridoideae*, *Cynodonteae*), 19 Apr. 2011, *R.G. Shivas & T.Y. Chi* (**holotype** BRIP 54675).

Description: *Sporangiophores* cylindrical, evanescent, hyaline, 75–120 × 20–28 µm, with 5–20 terminal ampulliform to lageniform branches with a narrow neck 7–14 × 3–7 µm. *Sporangia* broadly ellipsoidal, hyaline, narrowed slightly approaching base, 16–20 × 11–18 µm. *Oogonia* subglobose, golden yellow, (27–)32.5–36.0–39.5(–45) × (25–)28–31.7–36(–39) µm diam; wall (including warts) uneven, densely verrucose with rounded warts, 3–9 µm thick. *Oospores* globose to broadly ellipsoidal subhyaline to golden yellow, (19–)22–24.1–27(–29) × (18–)20–22.5–25(–28) µm diam; wall smooth, even, 1–3 µm thick (Thines *et al.* 2015; Fig. 1A).

Diagnosis: Produces broad club-shaped to cylindrical sporangiophores, a unique feature among the *Peronosporaceae*. Differs from *Baobabopsis enneapogonis* because of its parasitism of *Perotis rara*, the production of densely verrucose oogonia walls and its unique *cox*2 sequence, which shares 98.2 % nucleotide identity with *Baobabopsis enneapogonis*.

Reference sequence data: Ex-holotype nucleotide sequences KT248948 (*cox*2) and KT248945 (28S rDNA).

Host range: Known only from the type specimen on *Perotis rara*.

Notes: To our knowledge, this species has not been reported since its description in 2015 (Thines *et al.* 2015). The host is native to and widely distributed across Australia, and is also known from New Guinea, the Philippines, Thailand, and Vietnam. It is unknown if the range of *Baobabopsis donbarrettii* extends beyond the type locale or whether the species has any significant impact on host populations.

Baobabopsis enneapogonis Thines *et al.*, *IMA Fungus* **6**: 486. 2015.

Typus: **Australia**, Northern Territory, East MacDonnel Ranges, near Corroboree Rock turnoff, *Enneapogon cylindricus* (*Chloridoideae, Eragrostideae*), 21 Apr. 2007, *A.R. McTaggart, J. Liberato, M.D.E. & R.G. Shivas* (**holotype** BRIP 49822).

Description: *Oogonia* subglobose, golden yellow, (30–)32.5–36.3–40(–42) × (29–)30–33.1–36(–39) µm; wall moderately verrucose with rounded warts, 3–11 µm thick (including warts), uneven, remnants of antheridium often attached. *Oospores* globose to broadly ellipsoidal, pale to golden yellow, (20–) 21.3–23.0–24.7(–26) × (19–)20.5–21.9–23.5(–24) µm diam; wall even, smooth, (1–)1.5(–2) µm thick. Asexual morph not observed (Thines *et al*. 2015; Fig. 1B).

Diagnosis: Differs from *Baobabopsis donbarrettii* based on (1) the production of slightly less prominent warts, and moderately verrucose oogonial walls; (2) its unique *cox*2 sequence, which shares 98.2 % nucleotide identity with *Baobabopsis donbarrettii*; and (3) parasitism of *Enneapogon avenaceus* and *Enneapogon cylindricus.* Differs from *Baobabopsis marneyi* based on its unique *cox*2 sequence, which shares 96 % nucleotide identity.

Reference sequence data: Ex-holotype nucleotide sequence KT248946 (*cox*2).

Host range: *Enneapogon avenaceus*, *Enneapogon cylindricus* (*Chloridoideae*, *Eragrostideae*).

Notes: Sporangiophores have not been observed from *Baobabopsis enneapogonis*, so it is unknown whether this species shares the diagnostic broad club-shaped to cylindrical sporangiophores observed from *Baobabopsis donbarrettii*.

To our knowledge, this species has not been reported since its description in 2015 when four collections in Australia were made between 2007 to 2014 (Thines *et al*. 2015). *Enneapogon avenaceus* and *Enneapogon cylindricus* are endemic to Australia but are not known elsewhere in the world. Many members of the genus *Enneapogon* are globally distributed; however, it is not

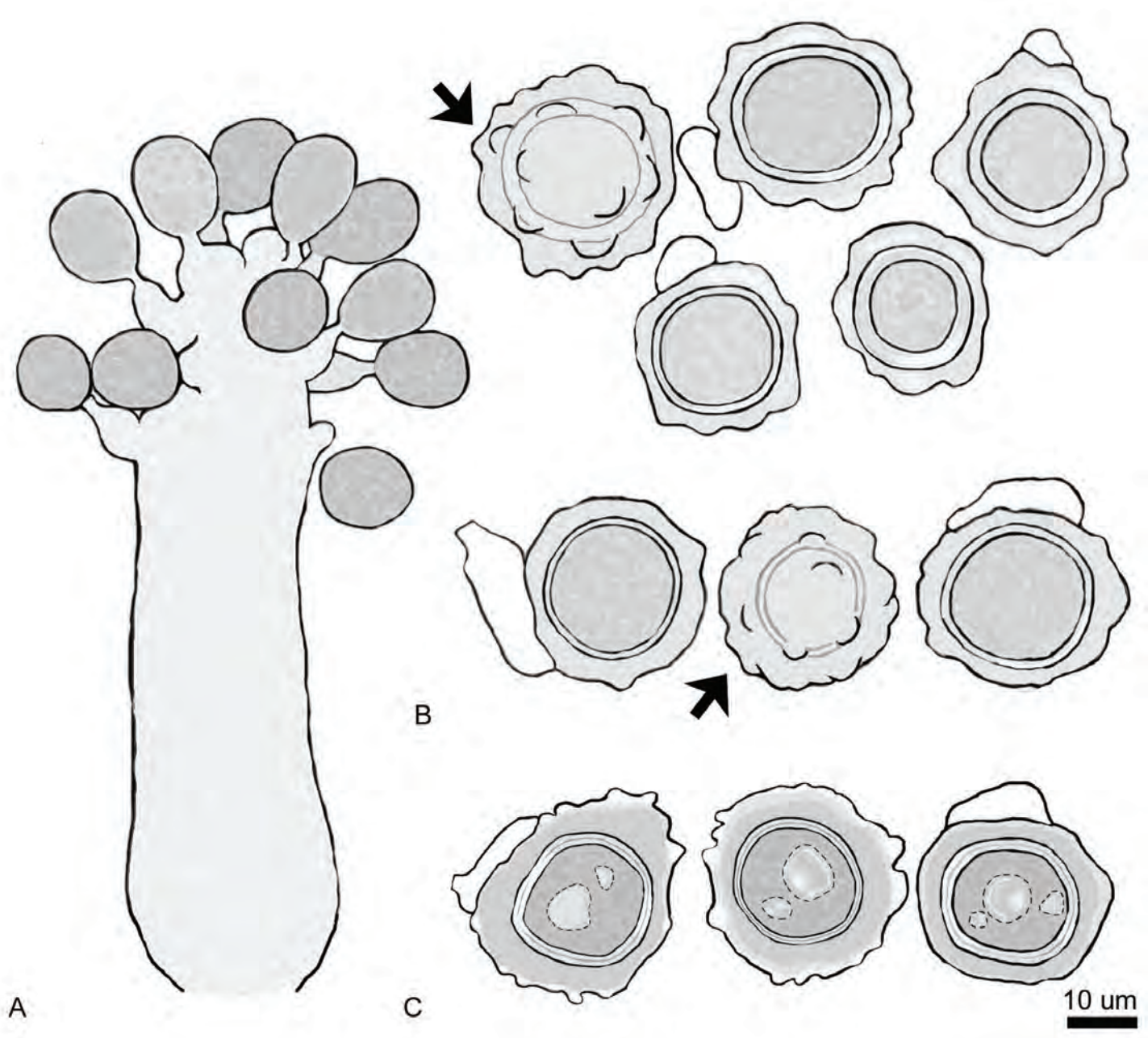

Fig. 1. A. *Baobabopsis donbarrettii*, sporangiophore (left) and oospores in cross-section, some with antheridia attached (upper right). One oospore is shown in surface view (arrow). **B.** *Baobabopsis enneapogonis*, oospores in cross-section, some with antheridia attached. One oospore is shown in surface view (arrow). **C.** *Baobabopsis marneyi*, oospores. Illustrations were prepared from published reference images found in Thines *et al.* (2015) and Ryley *et al.* (2022).

known if the host range of *Baobabopsis enneapogonis* extends beyond the two reported hosts or if the pathogen is distributed outside of Australia.

Because *Baobabopsis enneapogonis* parasitizes two of the same hosts and is similar in appearance to *Baobabopsis marneyi*, discrimination between these species should be confirmed using *cox*2 sequence data.

Baobabopsis marneyi R.G. Shivas *et al*., *Mycol. Progr*. **21**: 300. 2022.

Typus: **Australia**, Queensland, Georgetown, *Enneapogon polyphyllus* (*Chloridoideae, Eragrostideae*), 13 Apr. 2019, *J. Kruse, A.R. McTaggart, M.J. Ryley, M.D.E. & R.G. Shivas* (**holotype** BRIP 70341).

Description: *Oogonia* sub-globose to globose, golden brown, (24–)26–33(–35) µm diam; wall 3–8 µm thick (including warts), uneven, tuberculate, warts rounded 3–5 × 2–3 µm. *Oospores* globose to sub-globose, hyaline, (19–)21–24(–25) µm diam, adnate with oogonial wall; wall 1–2 µm thick, even, smooth (Ryley *et al.* 2021; Fig. 1C).

Diagnosis: *Baobabopsis marneyi* is distinguished from other species in the genus *Baobabopsis* through its unique *cox*2 sequence, which shares 92 % nucleotide identity with *Baobabopsis donbarrettii* and 96 % nucleotide identity with *Baobabopsis enneapogonis*. Differs from *Baobabopsis donbarrettii* by its parasitism of *Enneapogon* species.

Reference sequence data: Ex-holotype nucleotide sequence OK336436 (*cox*2).

Host range: *Enneapogon avenaceus*, *Enneapogon cylindricus, Enneapogon polyphyllus* (*Chloridoideae*, *Eragrostideae*).

Notes: *Baobabopsis marneyi* is recently documented from collections made on the foliage of three species of *Enneapogon* from three regions of Australia (Ryley *et al.* 2021). Infection results in the blades of grass splitting along the vascular strands, sometimes up to 20 cm in length. Given the overlapping host range and morphology of *Baobabopsis marneyi* and *Baobabopsis enneapogonis*, *cox*2 sequence data should be used to discriminate these two species.

Eraphthora Telle & Thines [as '*Erapthora*'], *Mycol. Progr*. **11**: 127. 2012.

Type species: *Eraphthora butleri* (W. Weston) Telle & Thines, *Mycol. Progr*. **11**: 127. 2012.

Diagnosis: Similar to *Basidiophora* and *Benua*, this species is unique among all other *Peronosporaceae* genera in possessing simple, club shaped sporangiophores. Differs from *Basidiophora* and *Benua* by the production of evanescent sporangiophores, oospores with thicker walls, and its parasitism of *Eragrostis* (Telle & Thines 2012).

Notes: The genus *Eraphthora* was established to accommodate the pathogen originally described as *Sclerospora butleri* based on the production of thick-walled oospores resembling those of *Sclerospora* (Weston 1921). Following the discovery that *Sclerospora butleri* produces unbranched, club-shaped sporangiophores and zoospores, these morphological characters were used to justify the transfer of the species to the genus *Basidiophora* (Thirumalachar & Whitehead 1952). However, Thirumalachar & Whitehead also noted that nocturnal sporangiospore production and host leaf shredding were not known from *Basidiophora* and suggested that the species might represent an intermediate form between *Basidiophora* and *Sclerospora* (Thirumalachar & Whitehead 1952). Subsequent authors rejected placement of *Sclerospora butleri* in *Basidiophora,* arguing that host preference, oogonial morphology, and the nocturnal production of evanescent sporangial structures were better aligned with the genus *Sclerospora* (Kenneth & Kranz 1973, Dick *et al*. 1984, Barreto & Dick 1991). In 2012, Telle & Thines erected the new genus *Erapthora* based on the unique combination of morphological characters and the *cox*2 phylogenetic distinctiveness that places it as the sister lineage of *Sclerophthora*.

The recent identification of two new species of *Eraphthora* parasitizing *Eragrostis cilianensis* (Ryley *et al*. 2021) introduces a new complication regarding members of the genus *Eraphthora*. Although the genus is typified by *Eraphthora butleri* (Telle & Thines 2012), the four specimens of this species that were examined when *Eraphthora* was erected were later identified as *Eraphthora drenthii* (Ryley *et al*. 2021). The two newly described species—*Eraphthora drenthii* and *Eraphthora occultata*—are sustantially different from generic type *Eraphthora butleri*, in that they produce substantially larger oospores, thicker oospore walls, and produce different symptoms in the host plant (Ryley *et al*. (2021). Additional molecular phylogenetic research incorporating type materials of *Eraphthora butleri* is recommended for further clarification of how these organisms are related to one another.

Eraphthora butleri (W. Weston) Telle & Thines, *Mycol. Progr*. **11**: 127. 2012.
Basionym: *Sclerospora butleri* W. Weston, *Phytopathol.* **21**: 125. 1933.
Synonyms: *Basidiophora butleri* (W. Weston) Thirum. & M. D. Whitehead *Amer. J. Bot*. **39**: 4. 1952.
'*Sclerophthora butleri*' (W. Weston) M. W. Dick, *Straminipilous Fungi* (Dordrecht): 147. 2001. [*nom. inval*., presumably *lapsus calami* (Telle & Thines 2012)].

Typus: **Malawi** (formerly Nyasaland), Bulaki, Evans tobacco estate, *Eragrostis aspera* (*Chloridoideae, Eragrostideae*), Mar. 1927, *E. J. Butler* [**lectotype** designated here, BPI 187075 (MBT 10002143); **isotype** designated here, FH 965376 (MBT 10002144)]. Supplementary Fig. S1 shows the lectotype BPI 187075.

Description: *Oogonia* spherical to irregularly subspherical, pallid golden to dark amber, 33–36.9 µm (up to 29–40.9 µm) diam, contents comprising a finely granular, hyaline or grayish matrix, with one or several oil droplets not arranged in any definite pattern; wall relatively even with numerous bluntly rounded, papillate to finger-like protrusions, 4–10 µm (excluding protrusions), protrusions hyaline, base 2–4 × 2–5 µm high. *Oospores* spherical, hyaline, 19–22.9 µm diam; wall 2–3 µm thick. Asexual morph not observed (Weston 1933; Fig. 2A).

Diagnosis: Except for *Basidiophora* and *Benua*, differs from all *Peronosporaceae* by its simple, unbranched, club-shaped sporangiophores. Differs from *Basidiophora* and *Benua* by

its parasitism of *Eragrostis* spp., thick-walled oospores and tuberculate oogonial wall, and nocturnal production of evanescent sporangiophores. *Eraphthora butleri* is distinguished from *Eraphthora drenthii* and *Eraphthora occultata* based on having smaller oospores, thinner oospore walls, and the symptoms produced in the parasitized host.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Eragrostis aspera*. Also reported from *Eragrostis amabilis* and *Eragrostis tremula* (*Chloridoideae*, *Eragrostideae*).

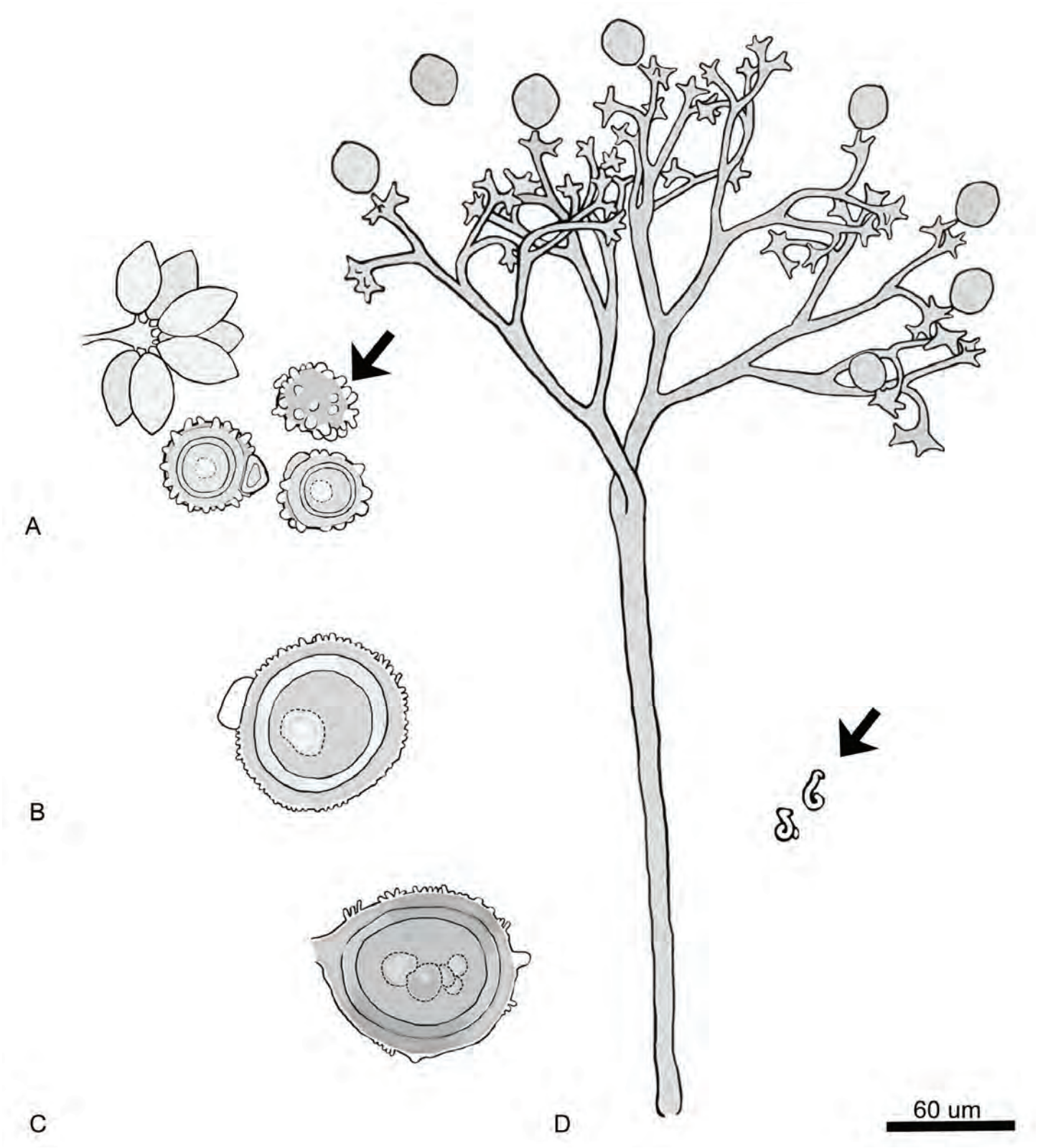

Fig. 2. A. *Eraphthora butleri*, sporangiophore and oospores in cross sections with antheridia attached. One oospore is shown in surface view (arrow). **B.** *Eraphthora drenthii*, oospores. **C.** *Eraphthora occultata*, oospores. **D.** *Graminivora graminicola*, sporangiophore and helical haustoria (arrow). Illustrations were prepared from published reference images found in Weston (1933), Thirumalchar & Whitehead (1952), Thines & Göker (2006) and Ryley *et al.* (2022).

Notes: *Eraphthora butleri* is reported on weedy species of *Eragrostis* from Africa, Australia, India, and Italy (Weston 1921, 1933, Patel 1949, Waterhouse 1964, Telle & Thines 2012, Farr & Rossman 2021). The type host, *Eragrostis aspera*, is a weedy grass distributed throughout Africa, India, and Malaysia in temperate and tropical regions. Natural infections of *Eragrostis aspera* by *Eraphthora butleri* result in disease symptoms such as chlorosis and malformed, shredded leaves (Weston 1921, 1933, Patel 1949, Telle & Thines 2012). As noted by Telle & Thines (2012) it is unknown whether *Eraphthora butleri* can infect agronomic species of *Eragrostis* such as *Eragrostis tef* (teff).

Reports prior to 2021 show *Eragrostis cilianensis* as a host of *Eraphthora butleri*, but new research shows that downy mildew on this host is attributable to at least two new species, *Eraphthora drenthii* and *Eraphthora occultata* but is not known from *Eraphthora butleri* (Ryley *et al.* 2021). To our knowledge, nucleotide sequence data from *bona fide* specimens of *Eraphthora butleri* are not currently available. Nucleotide sequences from specimens previously accepted as *Eraphthora butleri* parasitizing *Eragrotis cilianensis* are now known to be *Eraphthora drenthii* (DAR 4201: HQ413338; DAR 4200: HQ413337; DAR 4288: HQ413339; FR-0046004: HQ413336, KP965746, KT248944) (Ryley *et al.* 2021).

Weston did not designate a holotype, but specimens were accessioned at BPI and FH (BPI 187075, FH 965376). These specimens bear the published collection details and are annotated in Weston's handwriting; BPI 187075 is designated here as the lectotype for *Eraphthora butleri*.

Eraphthora drenthii M.J. Ryley *et al.*, *Mycol. Progr*. **21**: 301. 2022.

Typus: **Australia**, New South Wales, *Eragrostis cilianensis* (*Chloridoideae, Eragrostideae*), Apr. 1950, *P. Valder* (**holotype** DAR 4201).

Description: *Oogonia* globose to subglobose, light golden, (64–)68–84(–92) µm diam; wall uneven, 4–7 × 2–3 µm, with subhyaline, digitate, straight to curved projections measuring 7–8 µm thick. *Oospores* globose to sub-globose, (52–)56–67(–73) µm diam, adnate with oogonial wall, often with a single central vacuole; wall even, smooth 6–8 µm thick (Ryley *et al.* 2021; Fig. 2B).

Diagnosis: Differs from *Eraphthora butleri* on the basis of having larger oospores, thicker oospore walls, symptoms induced in the host, and parasitism of *Eragrostis cilianensis*. Differs from *Eraphthora drenthii* based on nucleotide sequence of the *Cox*2 marker. Differs from *Eraphthora occultata* based on nucleotide sequence of the *Cox*2 marker.

Reference sequence data: Ex-holotype nucleotide sequence HQ413338 (*cox*2).

Host range: Known only from the type host *Eragrostis cilianensis*.

Notes: The type host, *Eragrostis cilianensis*, is naturalized through most parts of the world, including Europe, Asia, Africa and North America. It is not yet known if *Eraphthora drenthi* is co-distributed with the host. To date, *Eraphthora cilianensis* is only known from from four specimens of *Eragrostis cilianensis* collected during the 1950s in Australia and from an unidentified species of *Eragrostis* collected in Italy. Unlike the generic type *Eraphthora butleri*, which induces leaf fraying in its hosts, *Eraphthora drenthii* parastism results in malformed inflorescences (Ryley *et al.* 2021).

Eraphthora occultata Y.P. Tan *et al.*, *Mycol. Progr*. **21**: 303. 2022.

Typus: **Australia**, New South Wales, Warren, *Eragrostis cilianensis* (*Chloridoideae, Eragrostideae*), Jan. 1967, *K. Brennan* (**holotype** DAR 16237).

Description: *Oogonia* globose to subglobose, light golden, (65–)71–90(–95) µm diam; wall uneven, 4–10 µm, with straight to curved, sub-hyaline, digitate projections measuring 4–7 × 3 µm thick. *Oospores* globose to sub-globose, (57–)60–71(–75) µm diam, adnate with oogonial wall, often with a single central vacuole; wall even, smooth, 5–6 µm thick. Asexual morph not observed (Ryley *et al.* 2021; Fig. 2C).

Diagnosis: Differs from *Eraphthora butleri* on the basis of having larger oospores, thicker oospore walls, symptoms induced in the host, and parasitism of *Eragrostis cilianensis*. Differs from *Eraphthora drenthii* based on nucleotide sequence of the *Cox*2 marker.

Reference sequence data: Ex-holotype nucleotide sequence OK392240 (*cox*2).

Host range: Known only from the type specimen on *Eragrostis cilianensis*.

Notes: *Eraphthora occultata* shares many features in common with its sister species, *Eraphthora cilianensis*, including morphology and parasitism of *Eragrostis cilianensis*. However, it has only been observed once from the type collection made in Australia in 1967.

Graminivora Thines & Göker, *Mycol. Res*. **110**: 651. 2006.

Type species: *Graminivora graminicola* (Naumov) Thines & Göker, *Mycol. Res.* **110**: 652. 2006.

Diagnosis: Differs from all other *Peronosporaceae* through differences in haustorium morphology, sporangiophore morphology and ultrastructure, and nucleotide sequences of rDNA.

Notes: The genus *Graminivora*, typified by *Graminivora graminicola*, was erected to accommodate the pathogen originally described as *Bremia graminicola*. The species was originally described as a *Bremia* based on features that were thought to be unique to the genus during the early 20th century. Specifically, *Bremia graminicola* produces lasting, dichotomously branched sporangiophores with inflated ends, multiple sterigmata and subglobose sporangia (Naumov 1913). Thines & Göker (2006) documented differences in haustorium and sporangiophore morphology and 28S rDNA sequences between the *Bremia* generic type and *Bremia graminicola*, resulting in the transfer of *Bremia graminicola* into the new genus *Graminivora*. *Graminivora* contains one species and is distributed in four Asian countries as a parasite of *Arthraxon hispidus*.

Graminivora graminicola (Naumov) Thines & Göker, *Mycol. Res*. **110**: 652. 2006.
Basionym: *Bremia graminicola* Naumov, *Bull. Soc. Mycol. France* **29**: 275. 1913.
Synonym: *Bremia graminicola* var. *indica* Patel, *Indian Phytopathol.* **1**: 106. 1949.

Typus: **Russia**, South Ussuriysk region, Siberia, *Arthraxon hispidus* (*Panicoideae, Andropogoneae*), 31 Jul. 1912, *N. Naumov* (**lectotype** designated here LEP 4385 [MBT 10002145]; **isotypes** BPI 786232, LEP 4377, LEP 4384, FH 01012075, E 00297399 [MBT 10002146]). Supplementary Fig. S2 shows the lectotype BPI 786232.

Description: *Sporangiophores* hyaline with inflated base above stomata; curved, dichotomous or irregular branching in the upper part, usually 4–6 times, after the last ramification inflated into a vesicle carrying four ultimate branchlets (sometimes two, as many as eight, typically in even numbers), up to 600 µm long × 9–10 µm wide at the base and 5–6 µm wide in the terminal ramifications. *Sporangia* globose to ovoid, hyaline, average diam 12 µm, with short basal and papilla at the slightly flattened apical end, mode of germination unknown. *Oospores* not observed (Naumov 1913, Thines *et al*. 2006; Fig. 2D).

Diagnosis: Differs from *Bremia* species in that it parasitizes *Arthraxon hispidus*, and produces hyphal haustoria that often form small spirals, with sporangiophores that usually show strong curving from the very start of ramifications, and swollen sporangiophore tips that typically carry 2–4 ultimate branchlets. Differs from other *Peronosporaceae* on the basis of lasting, dichotomously branched sporangiophores with inflated ends and its phylogenetic position based on *cox*2 and 28S rDNA sequences.

Reference sequence data: Sequence data not available from type materials. Ex-HUH 738 nucleotide sequences KP965747 (*cox*2), KP965742 (28S rDNA).

Host range: Known only from the type host *Arthraxon hispidus*.

Notes: *Graminivora graminicola* is known only from *Arthraxon hispidus* from China, India, Japan, and Russia (Togashi 1926, Ito 1936, Patel 1949, Novotel'nova & Pystina 1985, Tao 1998, Thines & Göker 2006). Parasitized leaves are discolored with variably sized yellow to reddish spots, often running parallel to the leaf veins, with leaves eventually withering and dying (Naumov 1913). The type host – a weedy grass commonly known as small carpetgrass—is native to the Asian continent where *Graminivora graminicola* has been reported. It is unknown if *Graminivora graminicola* also resides in North America, where *Arthraxon hispidus* is present as a highly invasive species thought to have been introduced to the continent in 1876. Although *Arthraxon hispidus* is widely distributed worldwide, there is no indication of any economic or ecological impact on the host when infected by this pathogen.

The Harvard Herbarium database lists the collection location of FH 01012075 as "Liberia, Africa," which appears to be a misreading of Naumov's handwriting. On the digitized version of the specimen label for FH 01012075 (http://storage.idigbio.org/fh/mycology/barcode-01012/FH01012075.jpg), one can see the ambiguity of the first letter (L/S) of the location. Naumov (1913) lists the location as "aux environs de Wladiwostok" and "Austro-Ussuriensi (Rossiae orient.)," which roughly translates to "around Wladiwostok" and "Ussurijsk region of eastern Russia." Both fall within the broad geographic area known as "Siberia"; therefore, "Liberia" is incorrect. Similarly, the online database of the Royal Botanical Garden of Edinburgh lists the location of E 00297399 as "Jaczewski, Poland," which is also an error in digitizing the specimen label. Both the FH and BPI specimens originated from "Herbario Instituti Mycol. et Phytopath. Jaczewski Petropolis," which is the former name of LEP. Assuming LEP also sent E their specimen, it seems likely "Jaczewski Petropolis" was incorrectly entered as the location of collection instead of the herbarium from which the material was sent.

Naumov did not designate a holotype, but materials from the original collection were found in BPI, E, FH, and LEP. LEP 4385 is designated here as the lectotype for *Graminivora graminicola*.

Peronosclerospora (S. Ito) Hara, in Shirai & Hara, List of Japanese Fungi hitherto unknown, 3rd Edn: 247 ['257']. 1927.
Basionym: *Sclerospora* subgen. *Peronosclerospora* S. Ito, *Bot. Mag., Tokyo* **27**: 218. 1913.
Peronosclerospora (S. Ito) C.G. Shaw, *Mycologia* **70**: 594. 1978. [*nom. illegit.*, Art. 53.1]

Type species: *Peronosclerospora sacchari* (T. Miyake) Shirai & Hara, *List of Japanese Fungi hitherto unknown*, **3rd edn**: 247 ['257'] (1927).

Description: No description was provided for the basionym *Sclerospora* subgen. *Peronosclerospora* or by Shirai & Hara when the genus *Peronosclerospora* was erected (Ito 1913; Shirai & Hara 1927). In his superfluous description of *Peronosclerospora*, Shaw (1978) provided a useful description of the genus, as follows: "*Mycelium* parasitic in higher plants, hyaline, coenocytic; imperfect state like *Sclerospora* except that conidia are always produced rather than sporangia. *Conidiophores* produced at night, erect, dichotomously branched two to five times; sterigmata conoid to subulate, usually two, but three or four in some species. *Conidia* ellipsoid, ovoid or cylindrical, wall of uniform structure, neither operculate or poroid, always germinating by a single germ tube. *Oogonia* subglobose to spherical. *Oospores* globose or subglobose, 25–55 µm in diam; oospore wall partially or completely fused to the wall of the oogonium, oospore wall of three layers: exosporium chestnut to reddish brown at maturity, irregularly ridged, 1.0–3.0 µm thick; mesosporium very thin, hyaline; endosporium hyaline, uniformly thick, 1.5–3.5 µm thick."

Notes: The distinction between what we now recognize as *Peronosclerospora* and the genus *Sclerospora* was first pointed out by Ito (1913), who split *Sclerospora* into two subgenera based on differences in asexual spore germination, which occurs directly by germ tubes in *Peronosclerospora* and indirectly by zoospores in *Sclerospora*. Ito recognized that two taxa would fall into the new subgenus *Sclerospora* subgen. *Peronosclerospora*; namely *Sclerospora sacchari* and *Sclerospora graminicola* var. *andropogonis-sorghi* (Ito 1913). *Sclerospora* subgen. *Peronosclerospora* was described as the genus *Peronosclerospora* in 1927 (Shirai & Hara 1927), with just one species (*Peronosclerospora sacchari*) transferred as the generic type (Shirai & Hara 1927). The original description of *Peronosclerospora* went unnoticed among some members of

the scientific community, resulting in the description of several non-zoosporic species in the genus *Sclerospora* rather than in *Peronosclerospora* (*Sclerospora dichanthiicola*, *Sclerospora philippinensis*, *Sclerospora sorghii*, *Sclerospora westonii*), and a second, superfluous description of the genus in 1978 (Shaw 1978, Shaw & Waterhouse 1980).

From a practical standpoint, discriminating between *Peronosclerospora* and *Sclerospora* based on differences in asexual structures is not a trivial matter. Development of asexual spores by members of both genera is nocturnal under natural conditions. In *Peronosclerospora*, structures persist for just a few hours in the early morning until they germinate under conducive environmental conditions (*e.g.*, Sriinivasan *et al*. 1961). After germination, the asexual spores and related structures rapidly collapse, leaving no trace behind. As a result, asexual structures are not well preserved on herbarium materials and other collections on non-living host material, hindering identification and taxonomic study. Structures of *Sclerospora* last longer, but within a few days can also vanish. The challenging application of asexual spore morphology for *Peronosclerospora* identification is further complicated by the impact of environmental effects, such as host species, variety, and climate, on spore size and shape (Delanie 1972, Leu 1973, Kimigafukuro 1979, Bock *et al.* 2000, Dudka *et al.* 2007, Runge & Thines 2011).

Peronosclerospora currently includes 12 species that are parasites of hosts in the subfamily *Andropogoneae*, including destructive pathogens of staple crops such as maize, sorghum, and sugarcane. The genus is widely distributed across the eastern hemisphere, including Africa, Australia, East Asia, and Oceania. Just one species of *Peronosclerospora* – *Peronosclerospora sorghi* – is well documented from the Western Hemisphere, following its introduction to Central America in the 1950s (Toler *et al.* 1959, Futtrell 1974, Frederickson & Renfro 1977). *Peronosclerospora eriochloae* (as *Peronosclerospora globosa*) was reported from Texas in a meeting abstract (Kubicek & Kenneth 1984), however those reports need further scrutiny to verify the identity of the pathogen.

Peronosclerospora aristidae J. Kruse *et al.*, *Mycol. Progr*. **21**: 303. 2022.

Typus: **Australia**, Queensland, in leaves of *Aristida hygrometrica* (*Poales*, *Poaceae*), 27 Apr. 2018, *J. Kruse, M.J. Ryley, S.M. Thompson, M.D.E. & R.G. Shivas* (**holotype** BRIP 67069).

Description: *Oogonia* globose to sub-globose, golden yellow, (30–)39–51(–53) µm diam; wall with sparse, low, irregular, truncate ridges, 6–14 µm thick. *Oospores* globose to sub-globose, golden yellow, (23–)27–31(–32) µm diam, adnate with oogonal wall, with a single vacuole; wall even, smooth, hyaline, 1–2 µm thick. Asexual morph not observed (Ryley *et al*., Fig. 3A).

Diagnosis: Differs from all other *Peronosclerospora* based on oogonial walls with irregular, low, truncate ridges, parasitisim of *Aristida hygrometrica*, and its phylogenetic position based on the *cox*2 nucleotide sequences.

Reference sequence data: Ex-holotype nucleotide sequence OK336438 (*cox*2).

Host range: Known only from the type specimen on *Aristida hygrometrica*.

Notes: The host of *Peronosclerospora aristidae*, *Aristida hygrometrica*, is an Australian native grass, and the only known member of the the subfamily *Aristidoide* associated with a downy mildew. Infection by *Peronosclerospora aristidae* results in splitting of the leaf blade into strands that can measure up to 50 cm long.

Peronosclerospora boughtoniae M.J. Ryley *et al.*, *Mycol. Progr*. **21**: 303. 2022.

Typus: **Australia**, Queensland, Lizard Island, in leaves of *Sorghum plumosum* (*Poales*, *Poaceae*), 7 May 1978, *V.H. Broughton* (**holotype** BRIP 14388).

Description: *Oogonia* globose to sub-globose, light golden brown, (25–)29–40(–50) µm in diam; wall smooth with occasional scabrid, flattened sides bordered by inconspicuous ridges, 1–12 µm thick. *Oospores* globose, hyaline, (22–)24–29(–31) µm diam; wall even, smooth, 1–2 µm thick. Asexual morph not observed (Ryley *et al*., Fig. 3B).

Diagnosis: Differs from *Peronosclerospora maydis* on the same host in that it has smaller oospores. Distinguished from *Peronosclerospora mactaggartii* on *Sorghum timorense* through its unique *cox*2 sequence (96 % nucleotide identity).

Reference sequence data: Ex-holotype nucleotide sequence OK33649 (*cox*2).

Host range: Known only from the type specimen on *Sorghum plumosum.*

Notes: Infection by *Peronosclerospora boughtoniae* results in splitting of the leaf blade into strands that can measure up to 15 cm long.

Peronosclerospora dichanthiicola (Thirum. & Naras.) C.G. Shaw, *Mycologia* **70**: 595. 1978.
Synonym: *Sclerospora dichanthiicola* Thirum. & Naras. [as '*dichanthicola*'], *Phytopathol.* **42**: 598. 1952.

Typus: Illustration in *Phytopathol.* **42**: 597, fig. 1, 1952 (**lectotype** designated here [MBT 10002147]) based on collection made in **India**, Bihar, in the culms of *Dichanthium annulatum* (*Panicoideae*, *Andropogoneae*), 18 Dec. 1951, *M. J. Thirumalachar*.

Description: *Conidiophores* evanescent, nocturnal, erect, 83–130 µm long × 13 µm wide at basal plug, 17–27 µm wide at main axis branching point; basal part isodiametric, 33 × 13 µm width with inconspicuous knob-like structure at the base; branches are dichotomous (rarely secondary and tertiary branches), 2–6 in number, 33–37 × 83–90 µm, usually with primary branches that give rise to 2–3 obconical tapering sterigmata with conidia. *Conidia* globose to obovoid, hyaline, thin-walled, 21–28 × 15–18 µm, germinating by germ tubes. *Oospores* unknown (Thirumalachar *et al*. 1952; Fig. 3D).

Reference sequence data: No sequence data available.

Host range: Known only from the type specimen on *Dichanthium annulatum*.

Notes: To our knowledge, reports of *Peronosclerospora dichanthiicola* are limited to a single observation on *Dichanthium annulatum*, an important perennial forage grass in India (Waterhouse 1964, Thirumalachar & Narasimhan 1952, Farr & Rossman 2021). *Dichanthium annulatum* infected with *Peronosclerospora dichanthiicola* exhibits leaves that are chlorotic with yellow streaks, but there is no indication as to the overall impact of the pathogen on plant health (Thirumalachar & Narasimhan 1952). Given the rarity of *Peronosclerospora dichanthiicola* and its inability to infect maize or sorghum

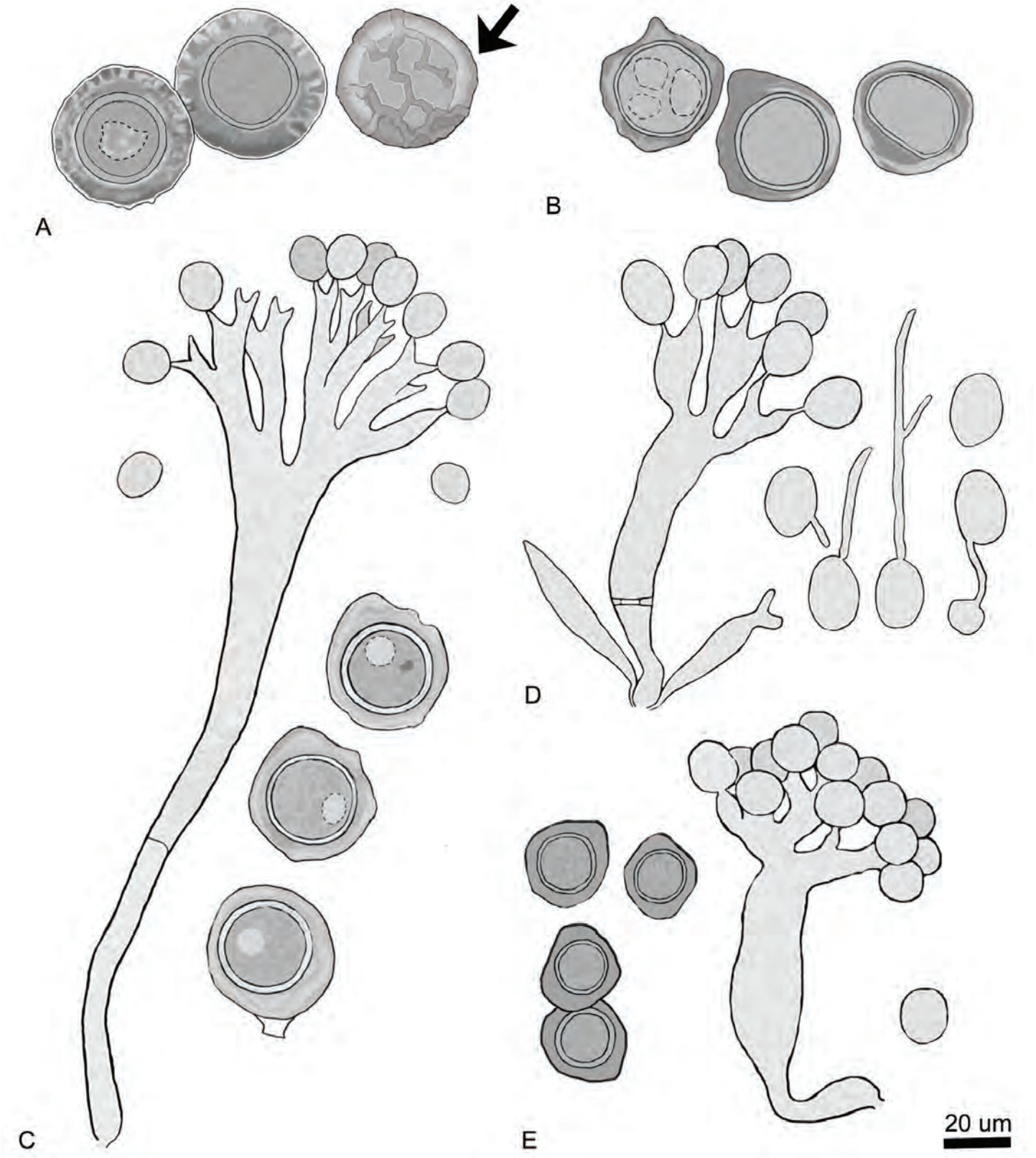

Fig. 3. A. *Peronosclerospora aristidae,* oospores in cross-section and one in surface view (arrow). **B.** *Peronosclerospora boughtoniae*, oospores. **C.** *Peronosclerospora eriochloae* sporangiophore and oospores. **D.** *Peronosclerospora dichanthicola*, mature and immature sporangiospores and germinating sporangia. **E.** *Peronosclerospora heteropogonis*, oospores and sporangiophore. Illustrations were prepared from published reference images in Thirumalachar & Narasimhan (1952), Siradhana *et al*. (1980), Ryley & Langdon (2001) and Ryley *et al.* (2022).

(Thirumalachar & Narasimhan 1952), the pathogen appears have little to no discernable impact on cultivated crops.

The species was described from material collected from India in 1951, but a type was not formally designated and it is unknown whether any materials from the study of Thirumalachar & Narasimhan (1952) were preserved in a reference collection. Although oospores were not observed, the asexual morph was well documented in the original publication, therefore an illustration from that publication is utilized as the lectotype.

Peronosclerospora eriochloae Ryley & Langdon, *Mycotaxon* **79**: 89. 2001.

Typus: **Australia**, Upper Pilton, Queensland, on tillers of *Eriochloa pseudoacrotricha* (*Panicoideae, Paniceae*), 9 Apr. 1979, *M.J. Ryley* [**holotype** BRIP 13693; **isotypes** BRIP 13691, BRIP 13692, FR-0046005 (MBT 10002148)].

Description: *Conidiophores* hyaline, 245–280 µm long with septum 90–115 µm above base; swollen base 6–13 µm wide decreasing to 6–9 µm wide at septum; above septum diam increases to 20–30 µm at the start of branching; dichotomously branched with secondary, tertiary, and quaternary branches 45–100 µm wide; sterigmata at tips of branches, conoid-subulate 4–9 µm long × 3–4 µm wide. *Conidia* globose to subglobose hyaline, (9–)13.3(–18) × (9–)12(–13.4) µm, without operculum or pore; germinating by one or two germ tubes. *Oogonium* globose to subglobose, orange to luteus, (33–)46.6(–70) µm diam; wall hyaline, confluent with oospore wall, 1.0–1.5 µm thick. *Oospores* globose, hyaline, 27–33.5(–46) µm diam, one per oogonium; wall in two layers with exosporium reddish brown, 2–15 µm thick; and endosporium hyaline, 2–3 µm thick. (Ryley & Langdon 2001; Fig. 3C).

Reference sequence data: Ex-isotype FR-0046005 nucleotide sequences HQ261813 (*cox*2), HQ261786 (28S rDNA).

Host range: *Eriochloa pseudoacrotricha*, *Eriochloa laevinode*, *Zea mays* (*Panicoideae*, *Andropogoneae*).

Notes: *Peronosclerospora eriochloae* has been identified from three hosts in Australia (Ryley & Langdon 2001, Telle *et al*. 2011), but it is unknown if the pathogen is distributed outside of that country. *Eriochloa pseudoacrotricha* is native to and widely distributed in Australia but also has been introduced across the southern USA (Texas) and South America. Based on similarities in morphological characteristics, Ryley & Langdon (2001) hypothesized that the invalidly published *Peronosclerospora globosa* described from *Eriochloa contracta* in Texas (Kubicek & Kenneth 1984) might represent the same species as *Peronosclerospora eriochloae*; see notes on *Peronosclerospora globosa* below.

The impact of *Peronosclerospora eriochloae* on host populations is not known. Infection of *Eriochloa pseudoacrotricha* results in tillers that do not produce inflorescences, and abnormally wide, chlorotic frayed leaves that eventually become necrotic (Ryley & Langdon 2001).

'***Peronosclerospora globosa***' Kubicek & R.G. Kenneth, *Phytopathol.* **74**: 792. 1984. [*nom. nud*, Art. 36.1, 39.1]

Typus: *non designates.*

Notes: Reported on *Eriochloa contracta* from the southern USA (Texas) and on *Eriochloa creba* (*Panicoideae, Paniceae*) from New South Wales, Australia (Kubicek & Kenneth 1984). Kubicek & Kenneth (1984) proposed the name *Peronosclerospora globosa* along with a short English description in a meeting abstract but never effectively published a Latin description or designated a holotype (Ryley & Langdon 2001). Based on morphology, Ryley & Langdon (2001) found their specimen of *Peronosclerospora eriochloae* on *Eriochloa pseudoacrotricha* similar to *Peronosclerospora globosa*, but deemed it sufficiently different to describe it as a new species rather than validate *Peronosclerospora globosa*. If specimens from the Texas collections referred to in Kubicek & Kenneth (1984) can be located, they should be further examined to see if they represent a distinct species. However, it is unknown if Kenneth's collections are extant, as a search of Mycoportal, BPI, and TAMU did not yield any specimens corresponding to the Texas collection.

Peronosclerospora heteropogonis J.A. Crouch ***sp. nov.*** MycoBank MB 840573.
Synonym: '*Peronosclerospora heteropogonis*' Siradhana *et al.* [as '*heteropogoni*'] *Curr. Sci*. **49**: 316. 1980. [*nom. inval*., Art. 40.1].

Typus: **India**, Rajasthan, Udaipur, Sisarma, on leaves of *Zea mays* (*Panicoideae*, *Andropogoneae*), 2005, *K. Mathur* (**holotype** designated here, HOH 898).

Description: *Conidiophores* evanescent, nocturnal, erect, with dichotomous branching and secondary and tertiary branches with a swollen base; from base to branching 81.6–142.8 × 14.3–255.5 µm with an average of 101.8 × 20.1 µm. *Conidia* globose, hyaline, thin-walled without operculum or pore, 14.3–22.4 × 14.3–20.4 (17.7 × 16.2) µm; germination by germ tubes. *Oospores* globose, tuberculate, persistent, 24.5–36.7 (29.0) µm diam, mostly fused to oogonial wall, contents granular, germination by zoospores (Siradhana *et al*. 1980; Fig. 3E).

Diagnosis: Similar morphology as *Peronosclerospora sorghi* but differs by its inability to infect sorghum and in oospore morphology, with *Peronosclerospora heteropogonis* producing tuberculate oospores and *Peronosclerospora sorghi* producing oospores that have an irregularly polygonally-angled ornamentation. Distinct on the basis of the nucleotide sequence of *cox*2.

Reference sequence data: Ex-holotype nucleotide sequence EU116054 (*cox*2).

Host range: *Heteropogon contortus*, *Zea mays* (*Panicoideae, Andropogoneae*).

Notes: *Peronosclerospora heteropogonis* causes Rajasthan downy mildew disease of *Heteropogon contortus* (spear grass) and maize on a regional basis in the Udaipur district of the state of Rajasthan in India (Siradhana *et al*. 1980, Yen *et al*. 2004). The disease can be quite destructive, leading to leaf chlorosis and shredding in both hosts, and causing as much as 60–80 % yield loss in susceptible hybrid corn lines depending on inoculum load and weather conditions (Dange *et al*. 1973, 1974, Rathore *et al.* 2002). However, research of this downy mildew is ranked as a low priority in India based on prevalence, incidence and acreage affected (Thakur & Mathur 2002).

This species was first reported as *Peronosclerospora sorghi* on *Heteropogon contortus* (Dange *et al.* 1973, Siradhana *et al.* 1980) and later described as *Peronosclerospora heteropogonis* based on morphology and the inability to infect sorghum, which distinguished the species from *Peronosclerospora sorghi* (Siradhana *et al*. 1980). However, Siradhana *et al.* (1980) did not designate a holotype, which means that *Peronosclerospora heteropogonis* Siradhana *et al.* was not validly published (Art. 40.1, Turland *et al.* 2018). In 2005, Thines *et al*. (2008) made a fresh collection of the pathogen from the Udaipur region of India from maize (HOH 898), where the original collections by Siradhana *et al*. (1980) were made. Thines *et al.* (2008) confirmed the distinctiveness of HOH 898 from *Peronosclerospora sorghi* and other members of the genus using a molecular phylogenetic analysis of *cox*2; this specimen is therefore designated the holotype for the newly validated species.

Peronosclerospora ischaemi M.J. Ryley *et al.*, *Mycol. Progr*. **21**: 304. 2022.

Typus: **Australia**, Queensland, on leaves of *Ischaemum fragile* (*Panicoideae*, *Andropogoneae*), 14 Apr. 2019, *J. Kruse, A.R. McTaggert, M.J. Ryley, M.D.E. & R.G. Shivas* (**holotype** BRIP 70369).

Description: *Oogonia* subglobose to irregular, golden brown, (55−)61−68(−70) × (49−)56−65(−68) µm diam; wall uneven, flattened, smooth, 5−20 µm thick. *Oospores* globose, hyaline, (35−)41−48(−50) diam, adnate with oogonium wall, with a single vacuole; wall µm thick, even, smooth, hyaline, 4−6 µm thick (Fig. 4A). Asexual morph not observed (Ryley *et al*. 2022).

Diagnosis: Distinct from other *Peronosporaceae* based on parasitisim of *Ischaemum fragile*. Distinguished from sister species *Peronosclerospora jamesiae* and *Peronosclerospora sehima* based on the nucleotide sequence of *cox*2 (98 % sequence similarity).

Reference sequence data: Ex-holotype nucleotide sequence OK336433 (*cox*2), OK350683 (28S rDNA).

Host range: Known only from the type specimen on *Ischaemum fragile*.

Notes: The host of *Peronosclerospora ischaemi, Ischaemum fragile*, a species distributed across parts of Australia and New Guinea, and is the only known member of the the genus *Ischaemum* associated with a downy mildew. Infection by *Peronosclerospora ischaemi* results in splitting of the leaf blade into tangled vascular strands that can measure up to 30 cm long.

Peronosclerospora jamesiae R.G. Shivas *et al.*, *Mycol. Progr*. **21**: 304. 2022.

Typus: **Australia**, Northern Territory, Wagait Beach, in leaves of *Sorghum intrans* (*Panicoideae*, *Andropogoneae*), 1 Apr. 2016, *R.S. James* (**holotype** BRIP 65234).

Description: *Oogonia* highly variable shape including sub-globose, ovoid and cuboid, dark golden brown, (40–)46–60(–80) µm in diam; wall smooth, rounded to flat, occasionally concave, 2–15 µm thick. *Oospores* sub-globose to ovoid sometimes with a flattened side, (30–)32–42(–55) µm diam, with prominent oil globule; wall hyaline, even, smooth, 1–2 µm thick (Fig. 4B). Asexual morph not observed (Ryley *et al*. 2022).

Diagnosis: Differs from other *Peronosporaceae* on *Sorghum* spp. by having larger oospores with a darker oogonial wall. Differes from sister species *Peronosclerospora ischaemi* and *Peronosclerospora sehima* based on the nucleotide sequence of *cox*2 (98 % nucleotide similarity) and parasitism of *Sorghum intrans*.

Reference sequence data: Ex-holotype nucleotide sequence OK336444 (*cox*2).

Host range: Known only from the type host *Sorghum intrans*.

Notes: The host of *Peronosclerospora jamesiae, Sorghum intrans*, is a wild annual grass species native to Northern regions of Australia. Infection by *Peronosclerospora jamesiae* results in splitting of the leaf blade into tangled vascular strands that can measure up to 30 cm long.

Peronosclerospora mactaggartii R.G. Shivas *et al.*, *Mycol. Progr*. **21**: 305. 2022.

Typus: **Australia**, Northern Territory, Dorat Rd., Robins Falls, in leaves of *Sorghum timorense* (*Panicoideae*, *Andropogoneae*), Apr. 2012, *A.R. McTaggart & R.G. Shivas* (**holotype** BRIP 57677).

Description: *Oogonia* sub-globose to globose, light golden brown, (30–)33–36(–40) µm diam; wall smooth, uneven, 1–8 µm thick. *Oospores* globose, (23–)25–27(–29) µm diam, with a single vacuole, adnate with oogonial wall; wall hyaline, even, smooth 1–2 µm thick. (Fig. 5A). Asexual morph not observed (Ryley *et al*. 2022).

Diagnosis: Distinguished from *Peronosporaceae* causing grass downy mildews based on the nucleotide sequence of *cox*2, which shares 96 % similarity with the most closely related taxon, *Peronosclerospora boughtoniae*.

Reference sequence data: Ex-holotype nucleotide sequence OK336446 (*cox*2), OK350687 (28S rDNA).

Host range: Known only from the type specimen on *Sorghum timorense*.

Notes: Infection by *Peronosclerospora mactaggartii* results in splitting of the leaf blade into tangled vascular strands that can measure up to 20 cm long.

Peronosclerospora maydis (Racib.) C.G. Shaw, *Mycologia* **70**: 595. 1978.
Basionym: *Peronospora maydis* Racib., *Ber. Deutsch. Bot. Ges.* **15**: 475. 1897.
Synonyms: *Sclerospora maydis* (Racib.) E. J. Butler, *Memoirs of the Dept. Agric. India. Bot. Ser.* **5**: 275. 1913.
Sclerospora javanica Palm, *Meded. Lab. Pl. Ziekt. Buitenz*. **32**: 18. 1918.
Peronosclerospora australiensis R.G. Shivas *et al.*, *Australas. Pl. Pathol*. **41**: 126. 2012.

Typus: **Indonesia**, Java, Jawa Tengah, Tengal, *Zea mays* (*Panicoideae, Andropogoneae*), *sine dat.* [**lectotype** KRA O-5859(J); **isotypes** BPI 789413 (MBT 10002149), in KRAM, and M. Raciborski, *Cryptogamae parasiticae* in Insula Java Lectae 7]. Supplementary Fig. S3 shows the isotype BPI 789413.

Description: *Mycelium* coenocytic, intercellular, parasitic throughout host (excluding roots), with many differentially shaped haustoria, and two kinds of hypha: straight and sparsely branched, and lobed and irregularly branched. *Conidiophores* robust, erect, 200–550 µm high × 20–25 µm wide, with septated basal cells 60–180 µm long, dichotomously branched 2–4 times, branchlets with two or more (generally 3–6) conical sterigmata (6–9 µm long) each bearing one individual sporangium. *Sporangia* hyaline, oval or spherical to subspherical, non-papillate, and 15–18 µm wide, direct germination by 1–2 germ tubes (Raciborski 1897; Fig. 4C). *Sexual structures* rare or unknown (Semangoen 1970), that have been described from the type specimen of what was originally described as *Peronosclerospora australiensis* but is now accepted as a synonym of *Peronosclerospora maydis* (Suharjo *et al*. 2020); that description is as follows: *Oogonia* golden orange to yellowish or reddish brown, globose, subglobose, broadly ellipsoidal to irregularly polyangular, 55–76 µm diam; exosporium 2–15 µm wide, uneven, smooth, convoluted. *Oospores* one per oogonium,

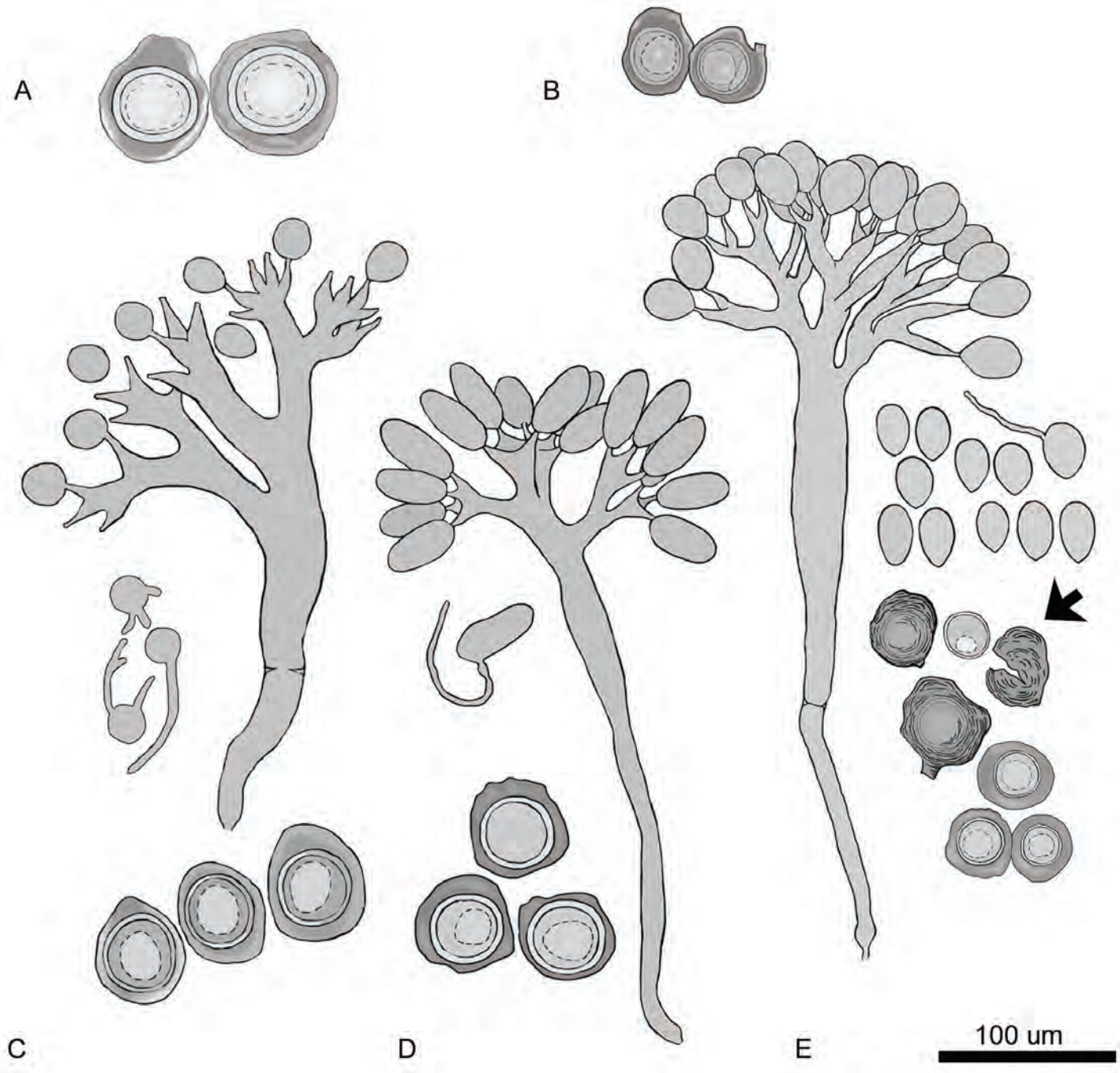

Fig. 4. A. *Peronosclerospora ischaemi*, oospores. **B.** *Peronosclerospora jamesiae*, oospores. **C.** *Peronosclerospora maydis*, sporangiophore, germinating sporangia, and oospores. **D.** *Peronosclerospora miscanthi*, sporangiophore, germinating sporangium, and oospores. **E.** *Peronosclerospora noblei*, sporangiophore, sporangia, and oospores. The top three oogonia are illustrated in surface view, including one oogonium that is one cracked open with an oospore released from oogonial wall (arrow). Illustrations were prepared from published reference images in Raciborski (1897), Weston (1929, 1942), Chu (1953), Shivas *et al.* (2012), Widiantini *et al*. (2015) and Ryley *et al.* (2022).

sub-hyaline to pale yellow, globose or broadly ellipsoidal, 39–55 µm diam, often with a large vacuole; endosporium 2.5–4.0 µm wide, even, smooth (Shivas *et al.* 2012; Fig. 4C).

Diagnosis: Sequence analysis of *cox*2 has been used to differentiate *Peronosclerospora maydis* from other *Peronosclerospora* spp. (Suharjo *et al.* 2020).

Reference sequence data: Ex-lectotype nucleotide sequence MW025835 (*cox*2).

Host range: *Saccharum spontaneum*, *Sorghum arundinaceum*, *Sorghum timorense*, *Zea mays*, *Zea mexicana*, *Zea mexicana* × *Zea mays* hybrids (*Panicoideae*, *Andropogoneae*).

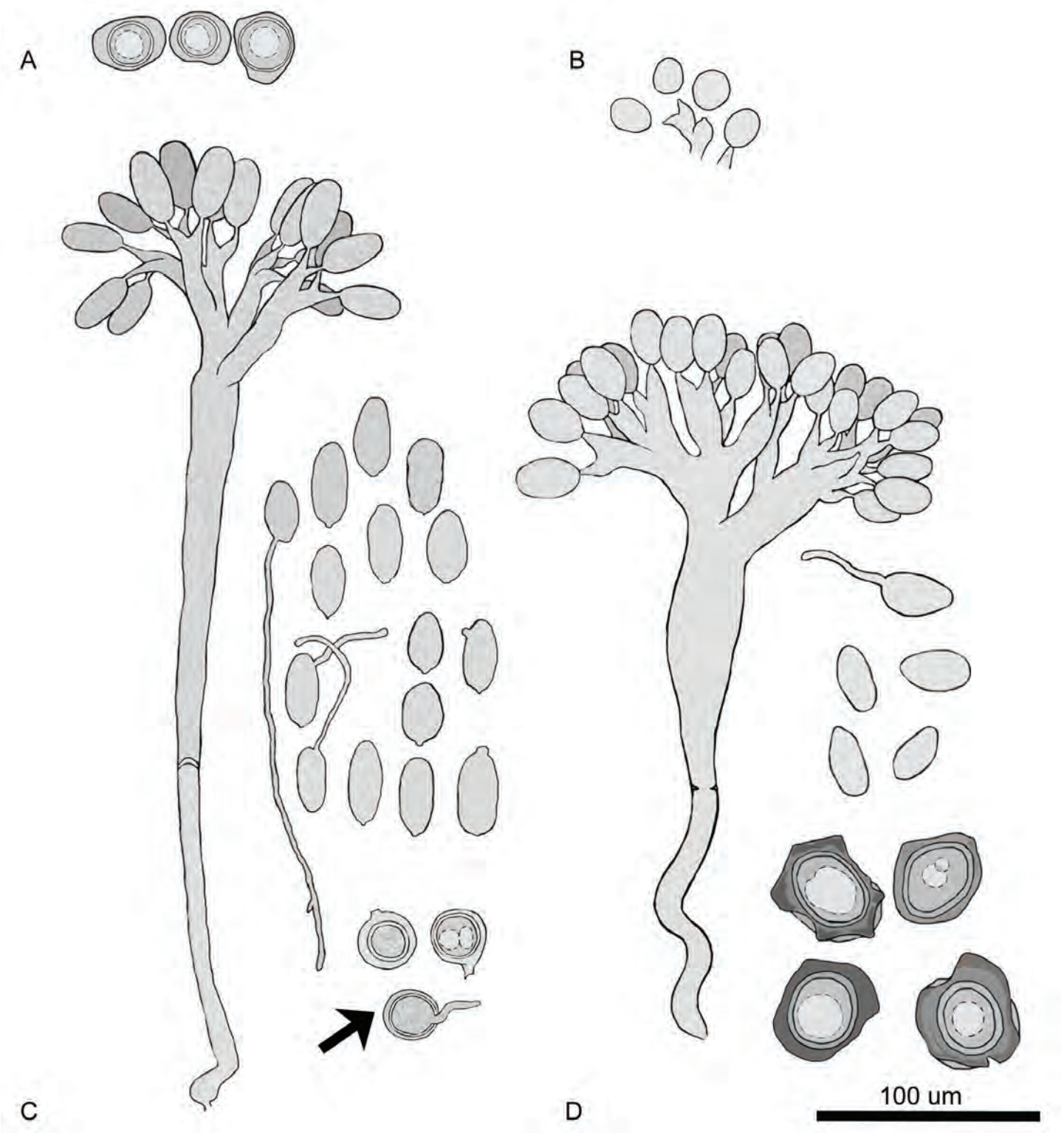

Fig. 5. A. *Peronosclerospora mactaggartii*, oospores. **B.** *Peronosclerospora panici*, sporangia and fragments of sporangiophore tips. **C.** *Peronosclerospora philippinensis*, sporangiophores, sporangia (including germinating sporangia), and oospores (including one germinating oospore, arrow). **D.** *Peronosclerospora sacchari*, sporangiophore, sporangia (including germinating sporangia), and oospores. Illustrations were prepared from published reference images in Miyake (1912), Weston (1920), Acedo & Exconde (1967), Elazegui & Exconde (1968), Singh & Chaube (1968), and photographs of *Peronosclerospora philippinensis* provided by Gary Peterson.

Notes: *Peronosclerospora maydis* is the causal agent of Java downy mildew and is one of the three most devastating downy mildew pathogens of maize (Lukman *et al.* 2016). In Indonesia, crop damages of 40–100 % have been recorded (Pudjiwati *et al.* 2013). Disease symptoms include severe chlorosis in the upper leaves, stunting, deformation, and lodging; infections by *Peronosclerospora maydis* may lead to death in susceptible maize varieties (Smith & Renfro 2016). The pathogen is widely distributed in the tropics of Australia, China, India, Indonesia, Jamaica, Taiwan, Thailand, and Venezuela. Reports of *Peronosclerospora maydis* in the Congo Democratic Republic and Argentina are considered possible misidentifications (Semangoen 1970, Kenneth 1976).

Sexual structures are rare or absent under natural or experimental conditions on the type host (Semangoen 1970, Suharjo *et al.* 2020), but were described from *Sorghum timorense* plants in Australia (Shivas *et al.* 2012). Oospores of *Peronosclerospora maydis* infecting maize originally described by Raciborski (1897) and Rutgers (1916) were later identified as *Pythium* spp. and *Paramecium* spp. (Palm 1918, Semangoen 1970).

Peronosclerospora miscanthi (T. Miyake) C.G. Shaw, Mycologia **70**: 596. 1978.
Basionym: *Sclerospora miscanthi* T. Miyake ex. Trotter [as '*mischanthi*'], in *Trotter, Syll. Fung. (Abellini)* **24**: 65. 1926.

Typus: **Taiwan**, Taipei, *Miscanthus sinensis* var. *formosanus*, 20 Jul. 1915, *K. Sawada* [**neotype** designated here BPI 187301 (MBT 10002150)]. Supplementary Fig. S4 shows the neotype BPI 187301.

Description: *Conidiophores* 97–300 (up to 438) × 12–37 µm, branched twice at the tip. *Conidia* elongately ovoid, (37.2–) 41.8(–48.6) × 14.3–22.9 µm (av. 41.8 × 18) µm diam, germinate directly by a germ tube. *Oogonia* reddish brown, mostly 58.3–63.5 × 51.5–56.9 (range 43.2–80 × 33.2–64.8) µm, walls unevenly thick from 3–8 µm to 12–24 µm thick, with small excrescences. *Oospores* 43.5–47.1 µm diam (Miyake 1912, Chu 1953; Fig. 4D).

Reference sequence data: Ex-NY: Stevens Philippine Fungi, Island of Luzon, No. 811 nucleotide sequences HQ261811 (*cox*2), HQ261784 (28S rDNA).

Host range: *Miscanthus japonicus*, *Miscanthus sinensis*, *Saccharum officinale*, *Saccharum robustum*, *Saccharum spontaneum* (*Panicoideae, Andropogoneae*).

Notes: Leaf splitting downy mildew disease caused by *Peronosclerospora miscanthi* was first identified in 1912 in Taiwan (Miyake 1912). The pathogen was subsequently reported from several species of *Miscanthus* and two species of *Saccharum* from China, Fiji, New Guinea, the Philippines, and Taiwan, with most reports of the pathogen presented in the form of checklists and surveys (Ito & Tokunaga 1935, Chu 1953, Waterhouse 1964, Telle *et al*. 2011). Inoculation experiments show that *Peronosclerospora miscanthi* has the ability to infect maize, but natural infections of this host are unknown (Shaw 1975). Infected *Miscanthus sinensis* leaves have white to yellowish white spots that eventually turn brown and are shredded (Ito & Tokunaga 1935, Waterhouse 1964). Pupipat (1975) considered the disease only a minor economic problem on sugarcane.

Miyake discovered this pathogen and made a report of it in the same publication in which *Peronosclerospora sacchari* is described (Miyake 1912). Although Miyake included a short discussion of the disease and briefly summarized the oospore morphology in that publication, he did not name the species at that time and no illustrations were included. In the 1914 English translation version of Miyake 1912, a note from Miyake was added (dated July 1913), stating that the pathogen would be described as a new species under the name of *Scelerospora* [sic] *miscanthus*, T. Miy. In 1926, Trotter validated the species, referring to Miyake 1912 for the description. Chu (1953) provided the first illustrations of the pathogen and a description of both the sexual and asexual morphology; Chu's description is consistent with the oospore morphology detailed in Miyake's text (1914). Therefore, the description provided above is primarily drawn from Chu (1953).

Further research is needed to address questions about whether or not *Peronosclerospora miscanthi* and *Peronosclerospora sacchari* are conspecific. Both species share similar oospore morphology (Chu 1935, Ito & Tokunaga 1935, Miyake 1914, Telle *et al*. 2011). Molecular phylogenetic analysis showed that a specimen of *Peronosclerospora miscanthi* and a *Peronosclerospora sacchari* voucher specimen (BRIP 44241) together a formed a distinct, highly supported clade (Telle *et al.* 2011), with the two species differing by just 0.92 % across two markers (1 426 nt).

The original description and validating publication for the species did not designate a holotype; BPI holdings include BPI 187301 dated 1915 from *Miscanthus sinensis* in Taiwan; this specimen is here designated as the species neotype.

Peronosclerospora noblei (W. Weston) C. G. Shaw, *Mycologia* **72**: 426. 1980.
Basionym: *Sclerospora noblei* W. Weston, *Phytopathol.* **19**: 1112. 1929.

Typus: **Australia**, New South Wales, Glenn Innes, *Sorghum leiocladum* (*Panicoideae, Andropogoneae*) Feb. 1928, *R. J. Noble* [**lectotype** designated here DAR 1075 (MBT 10002151); **isotypes** BPI 187306, DAR 1076, FH 965379 (MBT 10002152)]. Supplementary Fig. S5 shows the lectotype BPI 187306.

Description: *Oogonium* ovoid, ellipsoid, pyriform, or subspherical, 28–44 µm. Oogonial wall of variable thickness, typically 5–10 µm but ranging from 3–20 µm giving the appearance of bluntly rounded projections and sometimes the overall oogonia shape as gibbous and unsymmetrical; wall color dark, ranging from golden to rich brown; oogonial stalk fragments often retained. *Oospores* spherical, hyaline to pale golden, 23–28.9 (mode 25–26.9, range 20–34) µm in diam; wall 1–1.5 µm thick, contents comprising finely granular material with denser aggregations and oil drops, central to eccentric in position. Germination not observed (Weston 1929; Fig. 4E).

Diagnosis: In describing the species, Weston indicated that *Peronosclerospora noblei* is readily distinguishable from *Sclerospora graminicola* by the small size of the oospores, their thin walls, and the uniquely rounded exterior of the oogonium (versus flattened) with rounded surface prominences occurring due to the variable wall thickness and not due to out-bulgings.

Reference sequence data: Ex-isotype BPI 187306 nucleotide sequences, OK185343 (*cox*2), OK255496 (28S rDNA).

Host range: *Sorghum leiocladum*, *Sorghum plumosum* (*Panicoideae, Andropogoneae*).

Notes: *Peronosclerospora noblei* is only known from Australia (Weston 1929, 1942, Ryley & Langdon 2001, Thines *et al.* 2008, Farr & Rossman 2021). The type host, the wild sorghum *Sorghum leidocladum*, is indigenous to the northern tropical regions of Australia and not known from elsewhere in the world. *Sorghum leiocladum* infected by *Peronosclerospora noblei* show malformation, tillers mostly vegetative rather than flowering, and chlorotic, frayed leaves held in an abnormal bunch-like manner; infected leaves eventually become necrotic and die (Ryley 2001, 2002, Ryley & Langdon 2001). A second native Australian grass, *Sorghum plumosum* (as *Andropogon australis* or *Andropogon* sp.), is also listed as a host in checklists (Waterhouse 1964, Farr & Rossman 2021). However, the association of *Peronosclerospora noblei* with *Sorghum plumosum* bears further investigation, as molecular phylogenetic identity of a *Peronosclerospora* sp. specimen on *Sorghum plumosum* suggests that this organism is not conspecific with any known *Peronosclerospora* species and is not closely aligned with *Peronosclerospora noblei* (Thines *et al.* 2008).

As part of the description for *Sclerospora noblei*, Weston provided detailed collection data, but did not specify a holotype. Examination of Weston's collections at BPI, DAR, and FH identified specimens of *Sclerospora noblei* on *Sorghum leiocladum* with the outer envelopes both bearing the label of the *Herbarium of W. H. Weston* (BPI 187306, FH 965379). These specimens were annotated with the same collection data that was detailed in the protolog, written in Weston's hand. There can be no doubt that these are the original specimens described by Weston; DAR 1075 is therefore used to lectotypify the species.

Peronosclerospora panici R.G. Shivas *et al.*, *Mycol. Progr*. **21**: 306. 2022.

Typus: **Australia**, New South Wales, Narromine, on leaves of *Panicum laevinode* (as *Panicum whitei*) (*Panicoideae, Andropogoneae*), 4 Mar. 1980, *G. Stovold* (**holotype** DAR 35733).

Description: *Conidia* globose to sub-globose, rarely ovoid, hyaline, aseptate, (15–)15–17(–20) × (12–)13–16(–18) µm, thin walled without operculum or pore (Fig. 5B), germination by germ tube. Sexual morph not observed (Ryley *et al.* 2022)

Diagnosis: Differs from the sister taxon *Peronosclerospora erichloae* based on the nucleotide sequence of *cox2* (98 % sequence smiliarity with BRIP 22711).

Reference sequence data: Ex-holotype nucleotide sequence HQ261814 (*cox*2), HQ261787 (28S rDNA).

Host range: Known only from the type specimen on *Panicum laevinode*.

Notes: The host of *Peronosclerospora panici*, *Panicum laevinode*, is a forage species primarily restricted to Australia. Additional downy mildews have been reported from *Panicum* species globally (*Peronosclerospora sorghi*, *Sclerophthora macrospora, Sclerospora gramincola*).

Peronosclerospora philippinensis (W. Weston) C. G. Shaw, *Mycologia* **70**: 596. 1978.
Basionym: *Sclerospora philippinensis* W. Weston, *J. Agric. Res*., Washington **19**: 118. 1920.
Synonym: '*Sclerospora maydis*' Reinking, *Philipp. J. Sci, A* **13**: 1. 1918. [*nom. illegit*., Art. 53.1]
Possible synonym: *Sclerospora indica* E. J. Butler, *Fungi of India (Calcutta)*: 7. 1931.

Typus: **Philippines**, Laguna Province, Los Banos, *Zea mays*, 9 Feb. 1919, *W.H. Weston* [**lectotype** designated here BPI 187314 (MBT10002153); **isotypes** BPI 187044, BPI 187311, BPI 187313, FH 965382, FH 965383 (MBT10002154)]. Supplementary Fig. S6 shows the lectotype BPI 18731; Supplementary Figs S7–S9 show isotypes BPI 187044, BPI 187311, and BPI 187313, respectively.

Description: *Hyphae* intercellular throughout host (excluding root); branched, typically 8 µm diam, irregularly constricted and inflated; simple vesiculiform to subdigitate haustoria, 2 µm diam. *Conidiophores* evanescent, nocturnal, erect, 150–400 × 15–26 µm with basal cell, dichotomously branched two to four times; sterigmata conoid to subulate and slightly curved, 10 µm long. *Conidia* elongate ellipsoid, elongate ovoid, or rounded cylindrical, apex slightly rounded, hyaline, usually 17–21 × 17–39 µm with a minute apiculus at the base, episporium thin, contents minutely granular, germinating directly by a germ tube. *Oogonia* 22.9 µm diam, wall smooth, fragments of oogonial stalk or antheridia often adherent (Weston 1920). *Oospores* spherical, (15.3–)19.2(–22.6) µm diam, hyaline or straw-colored; wall smooth, 2.0–3.9 µm thick; contents finely granular with oil droplets, positioned central to eccentric; germination via single germ tube (Acedo & Exconde 1967; Fig. 5C).

Diagnosis: Efforts to discriminate *Peronosclerospora philippinensis* from related taxa with overlapping host ranges may not provide clear cut differentiation. *Peronosclerospora philippinensis* oospores are reported as smaller in size than those of *Peronosclerospora miscanthi*, *Peronosclerospora sacchari*, and *Peronosclerospora spontanea* (Sivanesan & Waller (1986). Conidial morphology distinguishes *Peronosclerospora philippinensis* from *Peronosclerospora spontanea*, which has more elongated and slender conidiophores and conidia (Waterhouse 1964), and from *Peronosclerospora sorghi*, which has conidiophores with a basal plug and smaller conidia (Weston & Uppal 1932, Janruang & Unartngam 2018), but these structures may be subject to variation depending on environmental conditions and host (Exconde *et al.* 1968, Leu 1973, Widiantini *et al.* 2015). Several authors have questioned whether or not *Peronosclerospora philippinensis* and *Peronosclerospora sacchari* are the same species based on morphological similarity, shared host range, and phenotypic profiles generated from isozyme analyses (Weston 1920, Bonde *et al.* 1984, Micales *et al.* 1988), but at present no conclusive data are available.

At the time of writing (February 2022), NCBI GenBank contained accessions for 26 sequences identified as *Peronosclerospora philippinensis*, but except for the sequences generated for this paper from the isotype BPI 187044, none of the sequences are associated with voucher specimens or type material. Twenty-four of the NCBI accessions are internal transcribed spacer (ITS) sequences. We recommend exercising caution in using these ITS accessions for identification, as the sequences are very diverse and share only 92.9–96.2 %

identity with one another, suggesting that either some are misidentified or that there are misassemblies of the sequences resulting from long stretches of repeat elements known to occur in some downy mildew genera (Thines *et al.* 2007). Readers are also cautioned that *cox*2 and rDNA 28S sequences have limited utility for identification of this species because these marker sequences share 99.2–100 % identity to sequence data from voucher materials of *Peronosclerospora miscanthi* and *Peronosclerospora sacchari*. DNA sequencing from type materials at additional loci may help resolve species boundaries and provide badly needed diagnostic resources for *Peronosclerospora philippinensis.*

Reference sequence data: Ex-isotype BPI 187044 nucleotide sequences OK185341 (*cox*2), OK181682 (28S rDNA).

Host range: *Miscanthus japonicus, Saccharum officinarum, Saccharum spontaneum, Sorghum arundinaceum, Sorghum bicolor, Sorghum halepense, Sorghum propinquum, Zea mays, Zea mexicana, Zea mexicana* × *Zea mays* hybrids (*Panicoideae*, *Andropogoneae*).

Experimental host range: *Peronosclerospora philippinensis* is capable of parasitizing several additional hosts under experimental conditions: *Andropogon* spp., *Botriochloa* spp., *Eulalia fulva, Miscanthus japonicus, Sorghum plumosum, Tripsacum* spp., *Zea diploperennis*, *Zea luxurians*, and *Zea perennis* (Bonde & Peterson 1983). Some of these plants are common perennial forage and wild prairie grasses in the USA and globally; therefore, they serve as inoculum reservoirs (Bonde & Peterson 1983).

Notes: *Peronosclerospora philippinensis*, causing Philippine downy mildew, is one of the most destructive and virulent pathogens infecting maize, with crop losses reaching as much as 80–95 % under favorable conditions (Exconde & Raymundo 1974, Exconde 1975, CABI 2021). Sugarcane crop losses are lower, ranging from 9–38 % (CABI 2021). The pathogen is recognized globally as a threat to plant health, with measures enacted in several parts of the world to restrict its movement. According to the European and Mediterranean Plant Protection Organization Global databases (EPPO 2021), *Peronosclerospora philippinensis* is a quarantine pest in Mexico and Morocco and is subjected to regulation in China and three EPPO regions due to its inclusion on the EPPO A1 invasive pest list. In the USA, *Peronosclerospora philippinensis* is included in the USDA Plant Protection and Quarantine Select Agents and Toxins list (www.selectagents.gov/sat/list.htm).

Symptoms of *Peronosclerospora philippinensis* infecting maize and sorghum are very similar to those of other downy mildews affecting *Poaceae*, including chlorotic streaks along the length of the leaf, tassel malformation, and seed sterility, which make diagnosis based on symptomology on this host difficult (Baer & Lalusin 2013, Smith & Renfro 2016). Sugarcane plants infected with *Peronosclerospora philippinensis* show discolorations at the base of the young leaves, chlorotic spots that turn brick red as leaves age, and thinner canes (Thompson *et al.* 2013). These symptoms are very similar to those caused by *Peronosclerospora sacchari* and *Peronosclerospora spontanea* infecting *Saccharum* but differ from those of *Peronosclerospora miscanthi*, which always causes leaf-splitting (Sivanesan & Waller 1986, Thompson *et al.* 2013).

The geographic distribution of *Peronosclerospora philippinensis* as reported in online resources (such as CABI, EPPO, and the BPI databases) at the time of writing were conflicted. Given the challenges associated with diagnosing the species using morphology and symptomology, readers are cautioned that in the absence of molecular data, the pathogen is easily misdiagnosed and some reports may be erroneous. Records indicate that *Peronosclerospora philippinensis* has been found in Bangladesh, the Democratic Republic of the Congo, India, Indonesia, Nepal, Pakistan, and the Philippines (Weston 1920, Doidge 1950, Gattani 1950, Ali 1959, Watson 1971, Bains & Jhooty 1982, Bonde *et al.* 1984, Farr & Rossman 2021; Faruq *et al.* 2014, Subedi 2015, Muis *et al.* 2016, Ekawati & Gusnawaty 2018, Pakki *et al.* 2019). Records of *Peronosclerospora philippinensis* in Japan and South Africa are not considered valid by CABI (CABI 2021). Janruang & Unartngam (2018) have recently suggested that *Peronosclerospora philippinensis* should be removed from the list of maize pathogens present in Thailand. Reports of the pathogen in the USA by EPPO (2021) and CABI are of uncertain origin but may be based on the existence of a specimen of *Peronosclerospora philippinensis* on maize held by herbarium WSP that is annotated as originating from Frederick, Maryland, USA (WSP60943). However, WSP60943 was taken from an experimental plant maintained within the USDA-ARS biosafety level 3 containment facilities on the Fort Detrick USA Army base. The *Peronosclerospora philippinensis* strain used to inoculate the WSP60943 specimen was originally collected by Ofelio R. Exconde from University of Philippines, Los Banos College, Laguna, Philippines in 1975 (M. Bonde, G. Peterson, pers. comm.).

Weston did not specify a holotype, but examination of his specimens at BPI and FH identified several specimens of *Sclerospora philippinensis* on *Zea mays* with the outer envelopes bearing the label of the *Herbarium of W. H. Weston* and annotated with the same collection data that was detailed in Weston's protolog. Labels for BPI 187314, BPI 187044 and FH 965383 are written in Weston's hand, and the two BPI specimens contain Weston's handwritten annotations together with his correspondence regarding the material (BPI 187314). There can be no doubt that these are the original specimens described by Weston; BPI 187306 is therefore used here to lectotypify the species.

Peronosclerospora sacchari (T. Miyake) Shirai & Hara, List of Japanese fungi hitherto unknown, **3rd edn**: 257. 1927.
Basionym: *Sclerospora sacchari* T. Miyake, *Rep. Sugar Exper. Stn, Gov. Formosa* **1**: 12. 1912.
Synonyms: *Sclerospora sorghi-vulgaris* Mundk. [as (Kulk.) Mundk.], *Indian J. Agric. Sci.* **20**: 138. [1950] 1951.
'Peronosclerospora sacchari' (T. Miyake) C.G. Shaw, *Mycologia* **70**: 595. 1978. [*nom. illegit.*, Art. 53.1]

Typus: **Taiwan**, *Saccharum officinarium* (*Panicoideae, Andropogoneae*) 8 Oct. 1910, *collector not specified* [**lectotype** designated here BPI 187331 (MBT 10002155)]. Supplementary Fig. S10 shows the lectotype BPI 187331.

Description: *Conidiophores* fugacious, erect, hyaline, 160–170 µm long; wall smooth, thin; base slightly narrower (10–15 µm broad), one or rarely two septate; middle part about two to three times broader than the base apex; two or three times branched two or three times each branch stocky and conical shaped. *Conidia* elliptical or oblong, hyaline, 25–41 × 15–23

µm, or 49–54 × 19–23 µm, apex rounded, base slightly apiculate or rounded, wall thin and smooth; direct germination by germ tubes. *Oogonium* irregularly elliptical, castanian brown, 49–58 × 55–73 µm; wall thickness unequal. *Oospores* globular, yellow, 40–50 µm diam, wall 3.8–5 µm thick; germination by germ tubes (Miyake 1912; Fig. 5D).

Diagnosis: *Peronosclerospora sacchari* shares similar morphology, host range, and induces similar symptoms in the parasitized host as *Peronosclerospora philippinensis* (Miyake 1912, Weston 1920, Ito & Tokunaga 1935, Chu 1953, Telle *et al.* 2011). Elazegui & Exconde (1968) reported size and shape differences from the conidiophores of *Peronosclerospora sacchari* and *Peronosclerospora philippinensis*, but these differences might be the result of interspecific variability and/or environmental influences (Leu 1973, Widiantini *et al.* 2015). Refer to *Diagnosis* section for *Peronosclerospora philippinensis* above for additional discussion.

Reference sequence data: Ex-BRIP 44241A nucleotide sequences EU116052 (*cox*2), HQ261764 (28S rDNA).

Host range: *Saccharum edule, Saccharum officinarum*, *Saccharum robustum*, *Saccharum spontanea*, *Tripsacum dactyloides, Sorghum vulgare* var. *technicum, Zea mays*, and *Zea mexicana* (*Panicoideae, Andropogoneae*).

Experimental host range: Bonde & Peterson (1981, 1983) showed that under experimental conditions, *Peronosclerospora sacchari* systemically infects 18 species of grasses in the genera of *Andropogon*, *Bothriochloa*, *Eulalia*, *Schizachyrium*, and *Sorghum* (Bonde & Peterson 1981), suggesting a possible role for these plants as alternate hosts.

Notes: *Peronosclerospora sacchari* causes sugarcane downy mildew on sugarcane or maize (also known as leaf stripe disease). This species is known from the Western-Pacific region of Asia and Oceania (Farr & Rossman 2021) where it has significant economic impact on the sugarcane industry (Sugarcane Research Australia 2019). The most characteristic symptoms of *Peronosclerospora sacchari* on sugarcane are chlorotic leaf stripes that turn red with age, brown lesions on external stalk surfaces, and stunting of infected stools.

The first sighting of *Peronosclerospora sacchari* causing a leaf splitting disease occurred in 1909 at the Sugar Experiment Station in Taiwan on sugarcane fields planted with canes of Australian origin (Miyake 1912). By 1912, the disease was so widespread and destructive that the Taiwanese government ordered destruction of all affected sugarcane cuttings across two cities and 18 villages (Miyake 1912). Severe epidemics on sugarcane occurred in Taiwan between 1962–1967 (Payak 1967). In India, *Peronosclerospora sacchari* was first recovered from maize from the Tarai area of Uttar Pradesh (where sugarcane was planted widely) in 1968 (Singh 1968). Since then, *Peronosclerospora sacchari* outbreaks on maize have been sporadic and natural infection of sugarcane has not been observed in India (Payak 1975a, b, Sugarcane Research Australia 2019). In the late 1950s the pathogen was introduced to Australia through infected sugarcane cuttings, producing severe economic losses (Pupipat 1975, Suma & Magarey 2000), but an aggressive eradication plan enacted by the government resulted in the eradication of *Peronosclerospora sacchari* from Australia by the mid-1960s (Suma & Magarey 2000, Shivas *et al.* 2012). Reports of *Peronosclerospora sacchari* from the Eastern hemisphere (Central America, South America and the USA) are unconfirmed as these reports are derived from checklist publications (Farr & Rossman 2021).

A holotype was not designated when the species was described, but the collection details for BPI 187331 match those described by Miyake (Miyake 1912); we therefore use this specimen to lectotypify *Peronosclerospora sacchari*.

Peronosclerospora sargae R.G. Shivas *et al.*, *Australas. Pl. Pathol.* **41**: 128. 2012.

Typus: **Australia**, Northern Territory, Florence Falls, *Sorghum timorense*, (*Panicoideae, Andropogoneae*), 13 Mar. 2000, *R.G. Shivas, I.T. Riley, C. & K. Vánky* (**holotype** BRIP 27691).

Description: *Oogonia* globose, subglobose to broadly ellipsoidal, occasionally irregularly polyangular, pale yellow to yellowish brown, (30–)37.9(–47) µm diam; wall 2–8 µm thick, smooth, uneven. *Oospores* globose, pale yellow, (24–)29.3(–34) µm diam, often containing large vacuole; wall (1.5–)2.1(–3.0) µm thick, even, smooth. Asexual morph not observed (Shivas *et al.* 2012; Fig. 6C).

Diagnosis: *Peronosclerospora sargae* shows similar morphological features to *Peronosclerospora noblei*; however, these species can by distinguished based on the thickness of the oospore wall, host range, and sequence of the *cox*2 and 28S rDNA loci (Shivas *et al.* 2012).

Reference sequence data: Ex-holotype nucleotide sequences HQ261809 (*cox*2) and HQ261782 (28S rDNA).

Notes: *Peronosclerospora sargae* has not been reported since its initial description (Farr & Rossman 2021) and is only known from the type specimen (Telle *et al.* 2011, Shivas *et al.* 2012). The host, *Sorghum timorense* (Down's sorghum), is endemic to tropical regions of Australia and several islands north of Australia; the impact of *Peronosclerospora sargae* on populations of this wild grass is unknown.

Peronosclerospora schizachyrii R.G. Shivas *et al.*, *Mycol. Progr.* **21**: 306. 2022.

Typus: **Australia**, Queensland, Mareeba Wetlands, *Schizachyrium fragile* (*Panicoideae, Andropogoneae*), 27 Apr. 2018, *J. Kruse, M.J. Ryley, S.M. Thompson, M.D.E. & R.G. Shivas* (**holotype** BRIP 67070).

Description: *Oogonia* globose to sub-globose, golden brown, (35–)41–55(–65) µm diam; wall 6–32 µm thick, uneven, polyangular, smooth. *Oospores* globose to sub-globose, hyaline, (26–)29–39(–47) µm in diam, adnate with oogonial wall, with a single vacuole; wall 1–4 µm thick, even, smooth. Asexual morph not observed. (Ryley *et al.* 2022; Fig. 6A).

Diagnosis: Differs from the sister taxon *Peronosclerospora erichloae* on the basis of the nucleotide sequence of *cox2* (98 % sequence smiliarity with BRIP 22711).

Reference sequence data: Ex-holotype nucleotide sequences OK336452 (*cox*2) and OK350689 (28S rDNA).

Host range: Known only from the type specimen on *Schizachyrium fragile*.

Notes: *Peronosclerospora schizachyrii* is the only known downy mildew from naturally infected hosts in the genus *Schizachyrium*, although experimental infection of *Schizachyrium* spp. by isolates identified as *Peronosclerospora* sacchari and *Peronosclerospora philippinensis* has been demonstrated (Bonde & Peterson 1983). Infection by *Peronosclerospora schizachyrii* results in splitting of the leaf blade into tangled vascular strands that can measure up to 10 cm long. The host, *Schizachyrium fragile*, is endemic to northern and central regions of Australia; the impact of *Peronosclerospora schizachyrii* on populations of this wild grass is unknown.

Peronosclerospora sehimatis M.J. Ryley *et al.*, *Mycol. Progr.* **21**: 307. 2022.

Typus: **Australia**, Northern Territory, Arnhem Highway, Jabiru, *Sehima nervosum*, (*Panicoideae, Andropogoneae*), 12 Apr. 2006, *M.J. Ryley & R.G. Shivas* (**holotype** BRIP 49806).

Description: *Oogonia* globose to sub-globose, light golden brown, (38–)45–58(–63) µm diam; wall 3–15 µm thick, smooth, uneven. *Oospores* one per oogonium, globose, (28–)34–42(–46) µm diam, adnate with oogonial wall, with a single vacuole; wall 2–4 µm thick, hyaline, even, smooth. Asexual morph not observed (Ryley *et al.* 2022; Fig. 6B).

Diagnosis: Differs from the related taxa *Peronosclerospora ischaemi* and *Peronosclerospora jamesiae* based on the nucleotide sequence of *cox2* (98 % sequence smiliarity); differs from other *Peronosporaceae* based on its parasitism of *Sehima nervosum*.

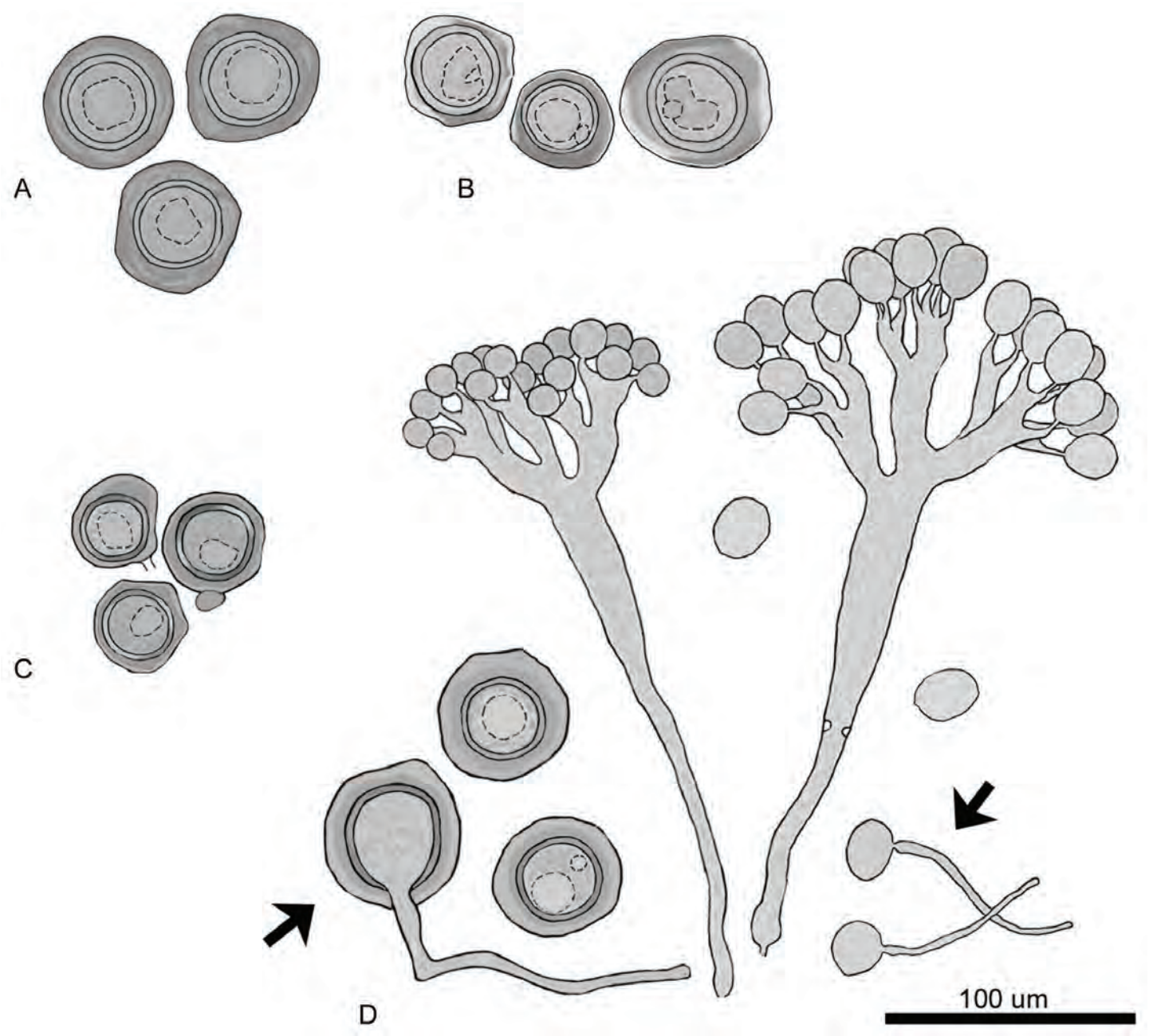

Fig. 6. A. *Peronosclerospora schizachyrii*, oospores. **B.** *Peronosclerospora sehimatis*, oospores. **C.** *Peronosclerospora sargae*, oospores. **D.** *Peronosclerospora sorghi*, sporangiophores at two stages (young and mature) and oospores. Arrows point to germinating oospores and sporangia. Illustrations were prepared from published reference images in Weston (1932), Shivas (2012), Ryley *et al.* (2021) and Ryley *et al.* (2022).

Reference sequence data: Ex-holotype nucleotide sequence OK336453 (*cox*2).

Host range: Known only from the type specimen on *Sehima nervosum*.

Notes: The host is widespread in Australia, tropical parts of Asia, and Africa, however *Peronosclerospora sehimatis* is the only known downy mildew from hosts in the genus *Sehima*. Infection by *Peronosclerospora sehimatis* results in splitting of the leaf blade into tangled vascular strands that can measure up to 10 cm long.

Peronosclerospora sorghi (W. Weston & Uppal) C.G. Shaw, *Mycologia* **70**: 596. 1978.
Basionym: *Sclerospora graminicola var*. *andropogonis-sorghi* Kulk., *Memoirs of the Dept. Agric. India, Bot. Ser*. **55**: 272. 1913.
Synonyms: *Sclerospora sorghi* (Kulk) W. Weston & Uppal, *Phytopathol.* **22**: 582. 1932.
Sclerospora sorghi W. Weston & Uppal, *Phytopathol.* **22**: 582. 1932.
Sclerospora andropogonis-sorghi (Kulk.) Mundk., *Indian J. Agric. Sci*. **20**: 138. 1951.
'Sclerospora andropogonis-sorghi' (Kulk.) Kulk. ex Safeeulla & Thirum. *Mycologia* **47**: 177. 1955. [*nom. nud.*, Art. 11.2]
Sorosporium andropogonis-sorghi S. Ito, *Trans. Sapporo Nat. Hist. Soc*. **14**: 93. 1935.

Typus: **India**, Coimbatore, *Sorghum bicolor* (*Panicoideae, Andropogoneae*), *collector not specified* [**lectotype** designated here BPI 187336 (MBT 10002156)]. Supplementary Fig. S11 shows the lectotype BPI 187336.

Description: *Conidiophores* erect, spreading, comprising basal cell, main axis more or less complex, usually dichotomously branched, expanded top; 100–150 µm length to the septum (rarely by a partial, ring-like thickening); main axis 15–25 µm diam; basal cell 7–9 µm wide, knobbed or bulbous at base. Branching comprising short, stout dichotomies usually with primary, secondary, and tertiary branches terminating in tapering sterigmata; sterigmata 13 µm long. *Conidia* suborbicular, hyaline, 21–24.9 × 19–22.9 µm (range 15–28.9 × 15–26.9 µm) diam, thin walled, germination direct by germ tubes. *Oogonia* with thick, irregularly polygonally-angled oogonial wall closely enveloping the oospore. *Oospores* spherical, hyaline, 31–36.9 µm (mode 35–36.9 µm, range 25–42.9 µm) diam; wall light Mars Yellow, 1.1–2.7 (range 0.3–4.3 µm) thick; contents finely granular with oil globules, positioned centrally or eccentric; germination direct by a branched, hyaline germ tube, 4.4 µm average width (range 2.5–8.3 µm) (Weston & Uppal 1932; Fig. 6D).

Diagnosis: Direct germination of conidia readily distinguishes *Peronosclerospora sorghi* from *Sclerospora graminicola* and other *Peronosporaceae* parasites of grasses with sporangia that germinate by means of zoospores. Distinguished from other *Peronosclerospora* species by molecular analyses including phylogenetic analysis of the *cox*2 marker, isozyme phenotypes, and SSR fragment analysis (Bonde *et al.* 1984, Micales *et al*. 1988, Thines *et al.* 2008).

Reference sequence data: Ex-HUH 897 (also referred to as "2ps001") nucleotide sequences EU116055 and HQ261790 (*cox*2), HQ261763 (28S rDNA).

Host range: *Sorghum bicolor* (*Andropogon sorghum*) *Sorghum* spp., *Zea mays*, *Zea mexicana* (*Panicoideae, Andropogoneae*). Possible reports from *Panicum maximum* and *Rottobellia exalta*.

Notes: *Peronosclerospora sorghi* is primarily associated with destructive global outbreaks of sorghum and maize downy mildew diseases. This species provides a textbook example of an invasive pathogen that moved from its endemic range in the Old World into the New World, first invading Central and South America during the 1950s and later the USA in the 1960s (Fredericksen & Renfro 1977). The pathogen quickly became widespread in the Americas after its introduction, causing heavy damages to sorghum and maize production. For example, in 1969 in the USA state of Texas, sorghum and maize losses due to *Peronosclerospora sorghi* were estimated at $2.5 million (Fredericksen *et al.*1969), the equivalent of $712.6 million in 2021 dollars.

The first known sighting of *Peronosclerospora sorghi* occurred in 1907, when Butler reported the pathogen infecting jowar (sorghum; *Sorghum bicolor*) in India (Butler 1907). Kulkarni provided the first name for the pathogen in 1913 when he described *Sclerospora graminicola* var. *andropogonis-sorghi,* primarily based on the observation that the conidia of the sorghum pathogen germinated by hyphae and not by zoospores, distinguishing it from *Sclerospora graminicola sensu stricto* (Kulkarni 1913). Weston & Uppal (1932) described *Sclerospora sorghi* in 1932 on the basis of *Sclerospora graminicola* var. *andropogonis-sorghi*. Given the parenthetical citation of Kulkarni and the fact that Weston & Uppal did not designate a type, their apparent intention was to make a new combination. But in naming the species, the replaced synonym did not supply the final epithet, and as a result some authors have treated *Sclerospora sorghi* as a replacement name (Shaw 1978) rather than a combination. However, the provisions of Art. 24.4 apply in this situation, allowing for the designation of a binary combination instead of an infraspecific epithet without change of authorship. Consequently, *Sclerospora sorghi* (Kulk.) W. Weston & Uppal was published as a new combination at a new rank (*comb. & stat. nov.*).

A holotype has not been designated for this species. BPI 187336 is part of the collection reported by Kulkarni (1913), and the specimen contains abundant, well preserved material, including both the conidial and oospore stages. We therefore designate BPI 187336 as the lectotype for *Peronosclerospora sorghi*.

Peronosclerospora spontanea (W. Weston) C.G. Shaw, *Mycologia* **70**: 597. 1978.
Basionym: *Sclerospora spontanea* W. Weston, *J. Agric. Res*, Washington **20**: 678. 1921.

Typus: **Philippines**, Laguna Province, Los Banos, Luzon, on leaves and shoots of *Saccharum spontaneum* (*Panicoideae, Andropogoneae*), 17 Aug. 1921, *W.H. Weston* [**lectotype** designated here BPI 187043 (MBT 10002157); **isotype** BPI 187073 (MBT 10002158)]. Supplementary Fig. S12 shows the lectotype BPI 187043; Supplementary Fig. S13 shows isotype BPI 187073.

Description: *Conidiophores* evanescent, nocturnal, erect, single or grouped, 350–550 µm length, basal cell 140–260 × 5–8 µm and usually exceeding or at least equaling in length the extent of the main axis from the septum to the primary branches;

more or less complex dichotomous branching system, and straight terminal sterigmata 13 µm long. *Conidia* elongately ellipsoid or cylindrical, hyaline, mostly 39–45 × 15–17 µm diam, finely granular content, thin wall, rounded apex lacking papilla, rounded base with apiculum of attachment, germination by germ tubes. *Oogonia* not observed (Weston 1921; Fig. 7A).

Diagnosis: *Sclerospora spontanea* is distinguished from *Peronosclerospora philippinensis* on maize hosts by having conidiophores that are more elongate and slenderer, with basal cells less knobbed and expanded at the base; branches longer, slenderer, less constricted at point of origin; sterigmata longer; slenderer and straighter conidia. However, cautious interpretation of asexual characters is recommended, as variation due to environmental factors may hinder accurate species discrimination.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Miscanthus japonicus, Saccharum spontaneum*, *Saccharum officinarum*, *Zea mays*, *Zea mexicana* (*Panicoideae*, *Andropogoneae*).

Experimental host range: *Peronosclerospora spontanea* can infect *Miscanthus japonicus* and *Zea mexicana* under experimental conditions (Weston 1921).

Notes: *Peronosclerospora spontanea* is known from the Philippines where it causes downy mildew disease of *Saccharum spontaneum* (bugang grass) and *Zea mays* (Weston 1921, Pupipat 1975) and has been documented once from cultivated sugarcane (*Saccharum officinarum*; Weston 1921). The pathogen may be limited to the Philippines, where Weston reported three sites with heavy natural infections of wild bugang grass and one natural infection of a single stand of sugarcane in the Visayas region (Weston 1921). However, a possible incidence of *Peronosclerospora spontanea* from Thailand during 1938 has been noted (Pupipat 1975, Shaw 1975, Farr & Rossman 2021).

The type host (*Saccharum spontaneum*) is a wild sugarcane native to India that has been introduced across tropical regions of Africa, Asia, and the Mediterranean, sometimes as an outcome of its widespread use in sugarcane breeding; it is often considered a noxious weed. *Saccharum sponteaneum* is not greatly damaged by infections of *Peronosclerospora spontanea*, exhibiting only minor chlorotic leaf striping and no deformation (Weston 1921). In contrast, *Peronosclerospora spontanea* is described as extremely debilitating to maize, with symptoms and damages to maize similar to those produced by *Peronosclerospora philippinesis* (Weston 1921).

In his description of the species, Weston did not designate a holotype. Weston's August 1921 collections of *Saccharum spontaneum* colonized by oogonia of *Sclerospora spontanea* are accessioned as BPI 187043 and BPI 187073 and match the published collection details; BPI 187043 is hereby used to lectotypify *Peronosclerospora spontanea*. One additional specimen of *Sclerospora spontanea* collected in December 1921, BPI 187342, consists of dried conidia scraped from the surface of diseased maize leaves that had been inoculated from conidia originally harvested from *Saccharum spontaneum*, and includes a typewritten note signed by Weston (Supplementary Fig. S14).

Peronosclerospora westonii J.A. Crouch & Thines ***sp. nov.*** MycoBank MB 840574.

Synonyms: '*Sclerospora westonii*' Sriniv. *et al*., *Bull. Torrey Bot. Club* **88**: 94. 1961. [*nom. inval.*, Art. 40.1]

'*Peronosclerospora westonii*' (Sriniv. *et al*.) C.G. Shaw, *Mycologia* **70**: 597. 1978. [*nom. inval.* Art. 35.1]

Typus: Illustration in *Bull. Torrey Bot. Club* **88**: 93, fig. 7, 1961 (**holotype** designated here) based on collection made in **India**, Poona, *Iseilema prostratum* (as *Iseilema laxum*; *Panicoideae, Andropogoneae*), Jul./Aug. 1960, *M.C. Srinivasan*, *M.J. Narasimhan*, *M.J. Thirumalachar*.

Description: *Conidiophores* 600–1 000 µm long, with single basal compartment; 9–11.5 µm broad at the basal compartment, 20–27 µm broad at main axis branching. Dichotomous branching, 20–25 µm high × 12–15 µm spread; typically limited to 2–4 primary branches with 2–3 obconical tapering sterigmata with conidia; rarely main axis producing secondary branches. *Conidia* globose to ovoid, hyaline 12–19 µm in diam, thin-walled, with granular contents at maturity, germinating by germ tubes. *Oogonia* spherical, subglobose, 40–50 µm diam, with granular contents. *Oospores* spherical, golden-brown, 23–29 µm diam, wall 6–9 µm thick, covered by the outer oogonial wall layer. (Srinivasan *et al.* 1961; Fig. 7B).

Diagnosis: In common with *Peronosclerospora dichanthiicola, Peronosclerospora westonii* has an aggregated, undifferentiated conidiophore branch structure, a feature that distinguishes the species from the well-developed branching structure of *Peronosclerospora noblei, Peronosclerospora philippinensis*, *Peronosclerospora sorghi,* and *Peronosclerospora spontanea*. However, conidia of *Peronosclerospora westonii* are smaller than those of *Peronosclerospora dichanthiicola*, measuring 12–19 µm diam versus 21–28 × 15–18 µm, respectively. *Peronosclerospora westonii* occurs on the same host species as *Peronosclerospora iseilematis*, but can be differentiated by differences in oospore size, with the spherical golden-brown oospores of *Peronosclerospora westonii* measuring 23–29 µm diam with thick endosporium walls of 6–9 µm thickness *vs*. the spherical, pale oospores of *Sclerospora iseilematis* measuring 38–50 µm diam with endosporium walls of 3.0–3.5 µm thickness.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Notes: To our knowledge, *Peronosclerospora westonii* has not been reported since the species was first diagnosed in 1961 (Srinivasan *et al.* 1961, Waterhouse 1964, Farr & Rossman 2021). The type host *Iseilema prostratum* (musal grass) is a common forage grass distributed in the waterlogged tropical regions of southern India and continental southeast Asia. The original report of *P. westonii* described leaves with chlorotic yellow streaking that became necrotic and eventually led to leaf shredding (Srinivasan *et al.* 1961).

Sclerospora westonii Sriniv. *et al*. is an invalid name, as Srinivasan *et al.* (1961) neglected to designate a type (Art. 40.1, Turland *et al.* 2018). The invalid status of *Sclerospora westonii* also renders *P. westonii* (Sriniv. *et al*.) C.G. Shaw invalid, as the name is based on an invalid basionym (Art. 35.1, Turland *et al.* 2018). It is unknown whether specimens utilized by Srinivasan *et al.* (1961) were formally lodged in a reference collection;

therefore, an illustration is utilized here as the holotype for the species, providing clear morphological features including conidiophores, sterigmata, conidia, oogonium, and oospores (Srinivasan *et al.* 1961).

'***Peronosclerospora zeae***' C. L. Yao, *Curr. Genet*. **22**: 415–420. 1992. [*nom. inval*., Art. 30.9, 36.1., 40.1]

Typus: *Non designatus*.

Notes: The first appearance of this name is found in Yao's (1991) dissertation; however, there was no description and a type was not designated. Yao *et al.* (1992) later applied this name and inaccurately referenced the dissertation as the effective publication. Later authors considered the strains used by Yao (1991) to be *Peronosclerospora maydis* (Perumal *et al.* 2008).

Poakatesthia Thines & Göker, *Mycol. Res.* **111**(12): 1381. 2007.

Type species: *Poakatesthia penniseti* (R.G. Kenneth & J. Kranz) Thines & Göker, *Mycol. Res.* **111**: 1381. 2007.

Notes: The genus *Poakatesthia* was designated to accommodate the pathogen originally described as *Plasmopara penniseti* based on the production of sporangiophores that are shaped similarly to those found in the genus *Plasmopara* (Kenneth & Kranz 1973). Thines & Göker (2007) designated the new genus *Poakatesthia* based on the unique morphology of the haustoria

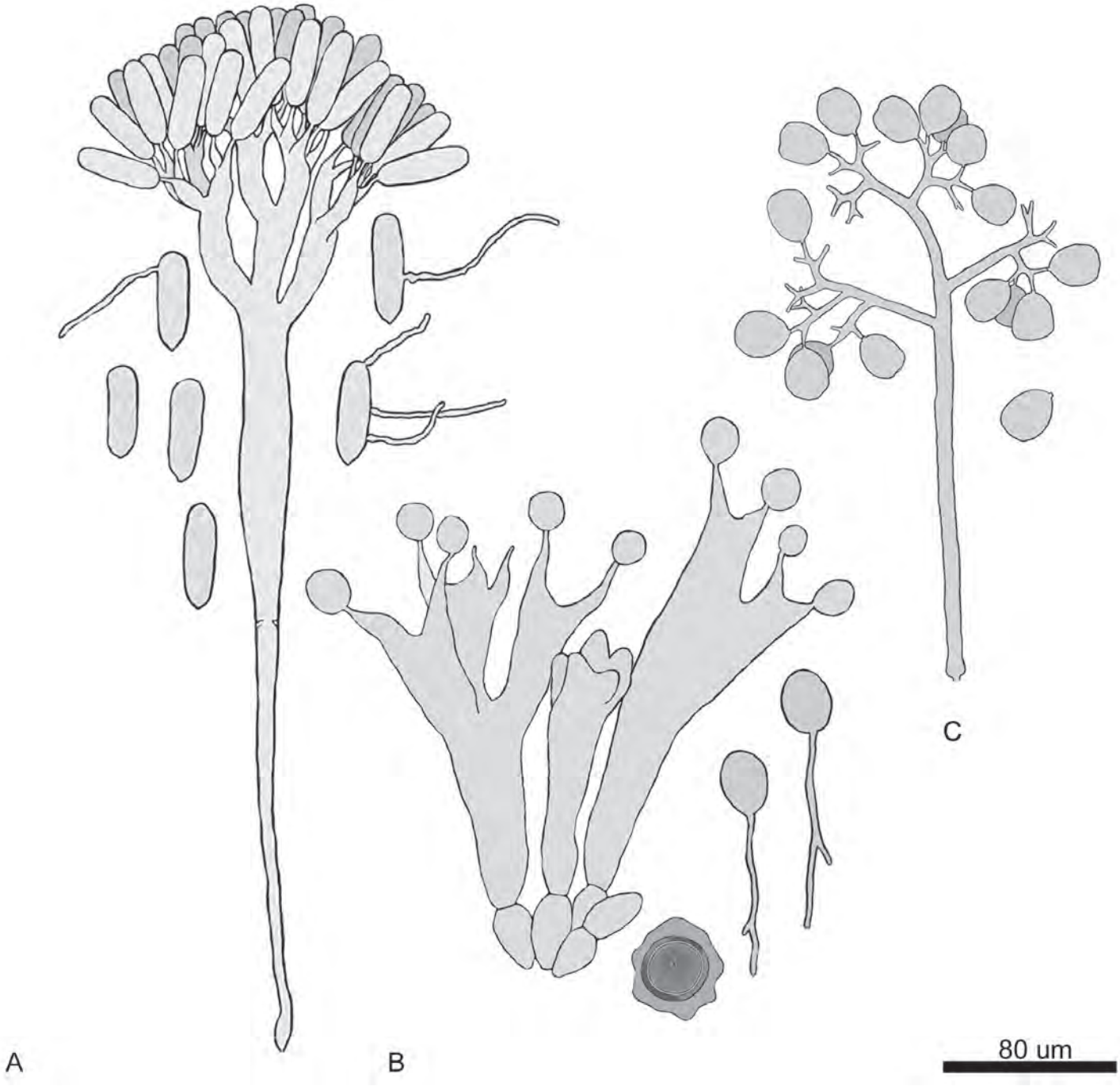

Fig. 7. A. *Peronosclerospora spontanea*, sporangiophore and sporangia (some germinating). **B.** *Peronosclerospora westonii*, sporangiophore, germinating sporangia and oospores. **C.** *Poakatesthia penniseti,* sporangiophore. Illustrations were prepared from published reference images in Weston (1921), Srinivasan *et al.* (1961), Titatarn & Syamanda (1978) and Thines *et al*. (2007).

and *cox2* sequence data that characterizes *Poakatesthia penniseti*. *Poakatesthia* contains one species and is known only from Ethiopia as a parasite of *Pennisetum glaucum*.

Poakatesthia penniseti (R.G. Kenneth & J. Kranz) Thines & Göker, *Mycol. Res.* **111**: 1381. 2007.
Synonym: *Plasmopara penniseti* R.G. Kenneth & Kranz, *Trans. Brit. Mycol. Soc*. **60**: 591. 1973.

Typus: **Ethiopia**, Bako/Shoa, *Pennisetum glaucum* (*Panicoideae, Paniceae*), Oct. 1968, *J. Kranz* (**holotype** IMI 137328c).

Description: *Sporangiophores* hyaline, amphigenous, erect, 300–580 µm high; trunk 0.55–0.77 of total height × 8–11 µm width; dichotomously branched once or twice, then branched irregularly monopodially to subdichotomously two or three times at right angles. Ultimate branchlets straight or slightly curved, usually two divaricate at apices of final branch, tapered with truncate tip, 4.7–9.5 µm long × 3.2 µm wide at base; 1–2 ultimate branchlets sometimes along sides on final branch, 4.7–12.6 µm long. *Sporangia* hyaline, wide obovoid with +/- flattened apical end and poroid papilla, base peducellate; 19–23.7 × 14.2–17 (19) µm. *Oogonia* not observed (Kenneth & Kranz 1973; Fig. 7C).

Diagnosis: Sporangiophore morphology similar to *Plasmopara* but differs based on obovoidal to egg shaped sporangia with flattened apex, intracellular mycelium and parasitism of *Pennisetum penniseti*. Uniquely diagnosed based on nucleotide sequence of *cox*2 that shares just 94.5 % identity with *Viennotia oplismeni*, its most closely related species.

Reference sequence data: Ex-holotype nucleotide sequence EF426475 (*cox*2).

Notes: *Poakatesthia penniseti* has not been reported since its initial description on pearl millet (*Pennistum glaucum*; Kenneth & Kranz 1973, Thines *et al.* 2007, 2008, Thines & Choi 2016, Farr & Rossman 2021), one of the most important staple food crops in India and several regions of Africa. Disease symptoms on infected plants were described as minor, and largely affected lower leaves of plants across an experimental plot in a remote region of the Ethiopian highlands (Kenneth & Kranz 1973). Initial symptoms are diffuse, small watersoaked spots or stripes that expand and coalesce to form irregular brown stripes between the veins leading to eventual necrosis (Kenneth & Kranz 1973). Since pearl millet was first introduced by seed to this isolated region of Ethiopia in 1966, Kenneth & Kranz speculated that the pathogen might have originated from one of several indigenous *Pennisteum* spp. growing in the area (Kenneth & Kranz 1973).

Sclerophthora Thirum., C.G. Shaw & Naras., *Bull. Torrey Bot. Club* **80**: 304. 1953.

Type species: *Sclerophthora macrospora* (Sacc.) Thirum. *et al*., *Bull. Torrey Bot. Club* **80**: 299. 1953.

Notes: *Sclerophthora* was erected by Thirumalachar *et al.* (1953) to accommodate *Sclerophthora macrospora*, a species that exhibits morphological characters typical of both *Sclerospora* (thick-walled oospores) and *Phytophthora* (hyphal sporangiophores, large, lemon-shaped phytophthora-like sporangia). The genus differs from all other *Peronosporaceae* genera, as it typically produces hardly differentiated sporangiophores, sporangia that germinate to produce biflagellate zoospores, and thick-walled oospores measuring 30–80 µm diam. It is unknown whether indirect oospore germination is a common trait for *Sclerophthora*, as oospore germination has not been described for the other five species currently assigned in the genus. It should be noted that the great variation in symptoms caused by the different species, as well as some morphological traits of the sporangia produced render it doubtful if the genus is monophyletic.

Sclerophthora cryophila W. Jones, *Canad. J. Bot*. **33**: 352. 1955.

Typus: **Canada**, British Columbia, Saanichton, *Dactylis glomerata* (*Pooideae, Poeae*), 1 Jun. 1948, *W. Jones* [**holotype** designated here DAOM 20643 (MBT 10002159)]. Supplementary Fig. S15 shows the holotype DAOM 20643.

Description: *Sporangiophores* short, sterigma-like, unbranched. *Sporangia* obpyriform, hyaline, (22.5–)30.5–38(–45.5) µm × (11.5–)15–19(–22.5) µm, apically poroid, pedicels persistent; nocturnal under natural conditions. *Oogonia* subglobose to spherical, sinuous, golden to amber-brown, (29.5–)38.5(–51.5) µm diam; wall 1.9-3.8 µm thick (average 3.7). *Antheridia* paragynous. *Oospores* spherical, (20–)31.8(–37.5) µm diam; wall (1.5–)2.6(–3.5) µm thick, confluent with oogonial wall (Jones 1955; Fig. 8A).

Diagnosis: Distinct from *Sclerophthora macrospora* in that it has smaller oospores, oogonia, and sporangia, and thinner oogonium walls.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Dactylis glomerata* (*Pooideae, Poeae*). Possible hosts: *Apluda mutica, Dichanthium annulatum, Digitaria marginata, Heteropogon contortus* (*Panicoideae*).

Notes: *Sclerophthora cryophila* was first reported on the cool-season grass *Dactylis glomerata* (orchard grass) from Canada (Jones 1955). Orchard grass infected by *Sclerophthora cryophila* in field plots produced symptoms described as similar to the effects of frost injury, with yellow/brown streaks on leaves and occasional pale brown to pale cream discoloration of inflorescence sheaths (Jones 1955). Although the type host is widely distributed across North America in stands of wild grown plants or cultivated as a high-quality forage grass, there have not been reports of *Sclerophthora cryophila* from orchard grass since the collection from the original outbreak (Jones 1955).

There have been reports of *Sclerophthora cryophila* from India affecting four hosts in the subfamily *Panicoideae* (Srinivasan & Thirumalachar 1962, Safeeulla *et al.* 1963). The morphology of the pathogen described from *Apluda mutica, Dichanthium annulatum, Digitaria marginata*, and *Heteropogon contortus* is consistent with *Sclerophthora cryophila* (Srinivasan & Thirumalachar 1962). Given the host range associated with these reports and our current understanding of downy mildew pathogens as mostly narrowly host-specific organisms (Thines & Choi 2016), the identification of *Sclerophthora cryophila* from

these warm-season grasses suggests that the species may be a complex of morphologically similar species. This is partially supported by the results of cross-inoculation experiments, where strains of *Sclerophthora cryophila* from *Digitaria marginata* and *Heteropogon contortus* were unable to infect each other's hosts (Srinivasan & Thirumalachar 1962).

Under natural conditions, *Sclerophthora cryophila* produces sporangiophores nocturnally for just a few hours in the early morning under conducive conditions, but sporangia collected from warm-season hosts exhibit no periodicity and can be readily induced by floating infected leaf sections on water (Srinivasan & Thirumalachar 1962), which is similar

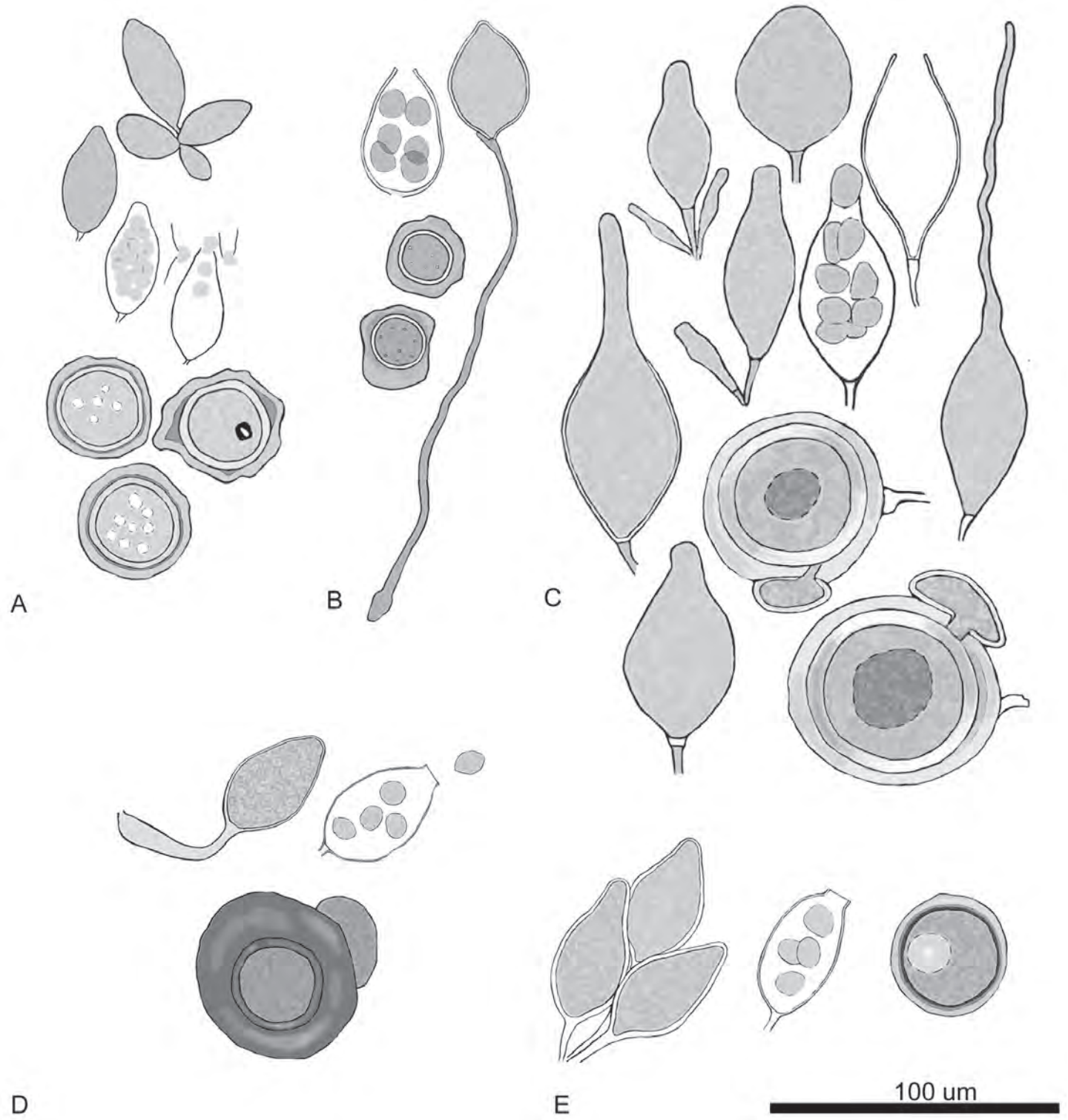

Fig. 8. A. *Sclerophthora cryophila*, sporangiophores, sporangia with zoospores, and oospores. **B.** *Sclerophthora lolii*, sporangiophores, sporangium with emerging zoospores, and oospores. **C.** *Sclerophthora macrospora*, sporangiophores (with sporangia filled with undifferentiated cytoplasm, empty, with emerging zoospores, or germinating), and oospores. **D.** *Sclerophthora rayssiae*, sporangiophore, sporangium with emerging zoospores, and oospores. **E.** *Sclerophthora zeae*, sporangiophore, sporangium with emerging zoospores, and oospore. Illustrations were prepared from published reference images in Jones (1955), Srinivasan & Thirumalachar (1962), Kenneth (1963), Waterhouse (1964), Payak & Renfro (1967) and Ryley *et al.* (2021).

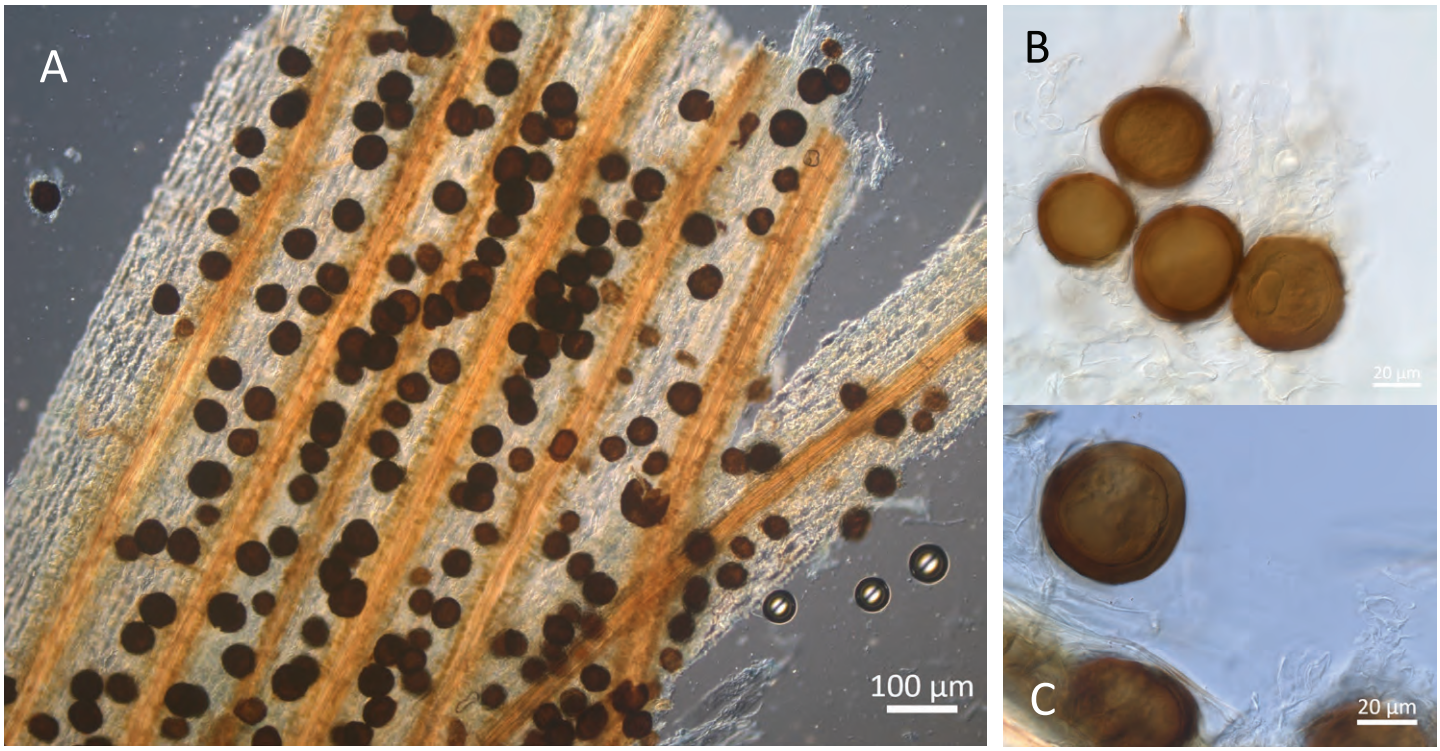

Fig. 9. *Sclerospora farlowii.* **A.** Oospores embedded in host tissue. **B, C.** Oospores.

to *Sclerophthora macrospora* (Thirumalachar *et al.* 1953), *Sclerospora graminicola*, and *Sclerospora sorghi* (Safeeulla & Thirumalachar 1956).

A holotype specimen was not formally designated for *Sclerophthora cryophila*. Jones indicated in the protolog that type materials were deposited in the herbarium of the Plant Pathology Laboratory, Saanichton, B.C.; the Saanichton collections were later transferred to DAOM. DAOM holdings of *Sclerophthora cryophila* include six specimens on *Dactylis glomerata*, but just one of these specimens (DAOM 20643) was collected on 1 Jun. 1948 by W. Jones, consistent with the species protolog. DAOM 20643 is clearly the sole specimen used to describe *Sclerophthora cryophila* and is therefore the holotype (Art. 9.1).

Sclerophthora lolii J.A. Crouch & Thines, ***sp. nov.*** MycoBank MB 840575.
Synonym: '*Sclerophthora lolii*' R.G. Kenneth, *Israel J. Bot.* **12**: 139. 1963. [*nom. inval.* Art. 40.1].

Typus: Illustration in *Israel J. Bot.* 12: 137–138, fig. 1–3, 1964 (**holotype** designated here) based on collection made in **Israel**, Mikve, *Lolium rigidum* (*Pooideae, Poeae*), Feb. 1962, *R.G. Kenneth*.

Description: *Sporangiophores* hyaline, slender, bearing sporangia. *Sporangia* lemon-shaped, 40.7–55.0(–63.7) × 25.2–35.0 µm; base with persistent peduncle, apex papillate, poroid, thin-walled; 10–15 pyriform *zoospores* produced within sporangium, 7.8–10.7 µm long, escaping through sporangial apex. *Oogonia* spherical to subspherical, sinuous, 25.2–28.8 µm diam. *Oospores* spherical, golden brown, 10.8–18.0 µm diam, smooth-walled, moderately thin-walled, centrally located within confluent thick oogonial walls (Kenneth 1963; Fig. 8B).

Diagnosis: Sporangia size and shape similar to *Sclerophthora cryophila* and *Sclerophthora raysiae*, but *Sclerophthora lolii* can be discriminated from these two species based on its smaller oogonia and oospore size. The length of the pyriform zoospores (7.8–10.7 µm), as with *Eraphthora butleri, Sclerophthora raysiae*, and *Sclerophthora zeae*, is distinctive among the *Peronosporaceae* (Kenneth 1963).

Reference sequence data: No sequence data available from type material or bona fide specimens.

Notes: Weedy, immature wild ryegrass (*Lolium rigidum*) infected with *Sclerophthora lolii* exhibit only mild disease symptoms, appearing as localized yellow patches on leaves that eventually necrotize without inducing leaf shredding (Kenneth 1964). To our knowledge, there have been no subsequent reports of this pathogen since the original 1962 discovery in Israel.

Sclerophthora lolii R.G. Kenneth was not validly published since a type specimen was not designated but was required at the time of publication (Art. 40.1; Turland *et al.* 2018). Kenneth's collection at HUJ, including his specimen of this species, appears to have been lost, but published illustrations of the original material clearly depict the diagnostic features of the organism and are therefore designated as the holotype for the newly validated species.

Sclerophthora macrospora (Sacc.) Thirum. *et al.*, *Bull. Torrey Bot. Club* **80**: 299. 1953.
Basionym: *Sclerospora macrospora* Sacc., *Hedwigia* **29**: 155. 1890.
Synonyms: *Sclerospora kriegeriana* Magnus, *Verh. Ges. Deutsch. Naturf.* **67**: 100. 1896.
Kawakamia macrospora (Sacc.) Hara, *Nôgyôkoku* [*Agriculturalist*] **9**: 24. 1915.
? *Nozemia macrospora* (Sacc.) Tasugi, 1931.
Phytophthora macrospora (Sacc.) S. Ito & Tanaka, *Ann. Phytopath. Soc. Japan* **10**: 138. 1940.

Possible synonyms: *Sclerospora oryzae* Brizi, *Natura, Milano* **10**: 168–180. 1919.
Phytophthora oryzae (Brizi) Hara, *Diseases of the rice plant* [*Ineno Byogai*], **Edn 2**: 57. 1939.

Typus: **Germany**, Saxony, Königstein, near the Königstein Fortress, *Phlaris arundinaceae (Pooideae*), 26 Aug. 1895, *P. Magnus* [**neotype** designated here BPI 187265 (MBT 10002160); **isotypes** BPI 187266 (MBT 10002161), MICH00010280]. Supplementary Fig. S16 shows the neotype BPI 187265; Supplementary Fig. S17 shows isotype BPI 187266.

Description: *Mycelium* hyaline, without septa, with haustoria, intercellular, aggregating near vascular bundles. *Sporangiophores* emerging from stomata, external hyphae (8–) 14(–28) µm long × 1–4 µm wide; undifferentiated from hyphae in the host, sympodial. *Sporangia* in clusters of 4–5, limoniform, obovate or ellipsoidal, hyaline to slightly purplish, moderately papillate; 58–98 × 30–65 µm (natural material) or (65–)87(–113) × (33–)44(–55) µm (in water). *Zoospores* at first ovate or irregularly kidney shaped, somewhat globose when motile, spherical at rest, (13–)11(–16) × (10–)13(–14) µm, may produce zoosporangia (10–)13(–16) µm diam with germ tubes 1.6–2.5 µm wide. *Oogonia* somewhat globose, light greenish to greenish brown, 50–95 × 55–100 µm (mostly 57–73 × 63–75 µm) and averaging 65 × 69 µm; wall 2.5–7.5 µm thick, commonly (3.8–)4.3(–5) µm thick. *Antheridia* laterally attached, hyaline to light yellow, obovate to ellipsoidal, wall slightly thickened, (13–)15(–23) × (23–)28(–41) µm, wall (1.8–)2.5(–3.8) µm thick. *Oospores* hyaline, somewhat globose, attached closely to the wall of the oogonium (43–)57(–70) × (43–) 60(–73) µm; wall (3.8–)6.5(–10) µm thick, germinate indirectly by germ tube (Saccardo 1890, Tanaka 1940, Waterhouse 1964, Fig. 8C).

Diagnosis: The morphology of the asexual stage (short, unbranched, and undifferentiated sporangiophores) and the indirect germination of sporangia differentiate *Sclerophthora macrospora* from *Sclerospora* and all other *Peronosporaceae* genera. *Sclerophthora macrospora* can be distinguished from *Sclerospora graminicola* by its larger zoospores, and from *Sclerospora secalina* by its hyaline, larger oospores (Waterhouse 1964).

Reference sequence data: Ex-HUH 892 nucleotide sequences KP965748 (*cox*2), EU826119 (28S rDNA).

Host range: This species is reported from approximately 141 *Poaceae* hosts globally, comprising tropical and temperate cereals, forage grasses, turf grasses, and many weedy grasses (Pupipat 1975, Safeeulla 1976, Farr & Rossman 2021). However, it is possible that *Sclerophthora macrospora* is a species complex (Telle *et al.* 2011, Telle & Thines 2012, Thines *et al*. 2015). Molecular phylogenetic analyses of multiple isolates of *Sclerophthora macrospora* from different hosts resolved several distinct clades, with isolates collected from the same host species often falling within different clades (Telle & Thines 2012). Reported hosts include *Avena sativa (Pooideae, Poeae), Eleusine coracana (Chloridoideae*, *Cynodonteae*), *Festuca* spp. (*Pooideae, Poinae*), *Hordeum vulgare* (*Pooideae, Triticeae*), *Lolium* spp. (*Pooideae, Poinae*), *Pennisetum glaucum* (*Pooideae, Poeae*), *Oryza sativa* (*Oryzoideae, Oryzeae*), *Sorghum bicolor* (*Panicoideae, Andropogoneae*), *Triticum* spp. (*Pooideae, Panicoideae), Zea mays* (*Panicoideae, Andropogoneae*), and others (see *Notes*).

Notes: *Sclerophthora macrospora* causes diseases referred to as either downy mildew, crazy top, or witches' broom; on rice the pathogen causes yellow wilt, and on turfgrass it causes yellow tuft. The pathogen has a world-wide distribution in temperate and warm climate regions of Africa, Asia, Europe, the Americas, and Oceania. In Morocco and the USA, *Sclerophthora macrospora* is a quarantine pest. It is subjected to regulations in Egypt, Paraguay, Bahrain, and two EPPO regions due to its inclusion on the EPPO A1/A2 invasive pest list (EPPO 2021). The pathogen is considered of minor importance on maize, rice, sorghum, sugarcane, turfgrass, and wheat (Smith & Renfro 2016, Lee & Groth 2018, Sugarcane Research Australia 2019, CIMMYT 2021). However, because of high levels of disease incidence (> 50 %) and yield losses as high as 100 %, *Sclerophthora macrospora* has a significant economic impact on the production of finger millet (*Eleusine coracana*), pearl millet (*Pennisetum glaucum*), and other small millets in Africa and Asia, especially in India (Nagaraja & Das 2016, Nagaraja *et al.* 2016). The most characteristic symptoms induced by *Sclerophthora macrospora* are phyllody and the development of distorted, twisted, abnormally large panicles, tassels, or heads (Holliday 1980).

A holotype was not designated for *Sclerophthora macrospora* (Saccardo 1890), and no illustrations were published with the protolog. The protolog indicates that collections were made in Australia from living leaves of an unnamed species of *Alopecurus* (*Pooideae, Poodae*), a genus that currently comprises 45 species and also previously included species that are now members of at least 14 different genera. In the absence of original materials, we selected BPI 187265 to serve as the neotype for *Sclerophthora macrospora*. BPI 187265 is one of the original collections made by Magnus in 1895 when he described *Sclerospora kriegeriana* (Magnus 1896), a later synonym of *Sclerospora macrospora* published just a few years after Saccardo's work (Thirumalachar *et al.* 1953, Waterhouse 1964, Telle & Thines 2012).

Sclerophthora rayssiae J.A. Crouch & Thines ***sp. nov.*** MycoBank MB 840576.
Synonym: '*Sclerophthora rayssiae*' R.G. Kenneth *et al.*, *Bull. Torrey Bot. Club* **91**: 189. 1964. [*nom. inval.* Art. 40.1].

Typus: illustration in *Bull. Torrey Bot. Club* 91: 186, figs 1–4, 1964 (**holotype** designated here) based on a collection made in **Israel**, Valley of Esdraelon, Mishmar Ha-Emek, *Hordeum vulgare* (*Pooideae, Triticeae*), 24 Mar. 1958, *R.G. Kenneth*, *Y. Koltin*, & *I. Wahl*.

Description: *Sporangiophores* very short, hyphoid, nocturnal under natural conditions. *Sporangia* lemon shaped or ovate, hyaline 28.8–55.0 × 19.2–27.9 µm, base with wedge-shaped pedicel, apex poroid and sometimes protruding, granular, infrequently germinating directly but primarily germinating indirectly by 6–10 reniform zoospores through the apical pore. *Zoospores* biflagellate, 7.5 × 11.0 µm long. *Oogonia* usually sinuous, unevenly thickened, 44.4–59.2(–61.4) µm diam. *Antheridia* paragynous, closely appressed to oogonium. *Oospores* abundant throughout mesophyll within lesions, solitary, or in groups or clumped, not tending to congregate in any area of the blade. *Oospores* globular, occasionally subglobular, light golden amber, 29.6–44.4 (mostly 33.3) µm diam; wall deep golden brown, smooth and thin; usually eccentrically located within oogonial wall (Kenneth *et al.* 1964; Fig. 8D).

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Hordeum vulgare* (*Pooideae, Triticeae*).

Notes: *Sclerophthora rayssiae* was first identified in Israel in 1958 causing downy mildew disease in fields of *Hordeum vulgare* (barley). The disease recurred at the same site annually from 1961–1963 and was considered widespread throughout two regions of the country (Kenneth *et al.* 1964). Infected plants show symptoms such as minor leaf lesions and did not induce host deformation (Kenneth *et al.* 1964). Subsequently there have been limited reports of the pathogen (Farr and Rossman 2021). Barley downy mildew outbreaks that occurred in 2003–2004 and 2007–2008 in India were attributed to *Sclerophthora rayssiae*, but the pathogen identity cannot be readily confirmed, as the report was limited to an abstract (Singh *et al.* 2009) and did not detail the pathogen morphology. As such, we cannot rule out the possibility that the destructive symptomology (stunting, chlorosis, deformation leading to plant death) described in the 21st century Indian outbreaks might represent an outbreak of crazy top caused by *Sclerophthora macrospora* (Miles and Epps 1942, Oswald and Houston 1951) because the symptomology differs greatly from the descriptions of *Sclerophthora rayssiae* as a weak pathogen on the same host (Kenneth *et al.* 1964).

A type specimen was not designated but was required at the time of publication; therefore, *Sclerophthora rayssiae* R.G. Kenneth was not validly published (1964). Kenneth's collection at HUJ, including his specimen of this species, is thought to be lost. However published illustrations of the original material clearly depict the diagnostic features and are used as the holotype for the newly validated species.

Sclerophthora zeae J.A. Crouch & Thines, ***sp. nov.*** MycoBank MB 840577.
Synonym: '*Sclerophthora rayssiae* var. *zeae*' Payak & Renfro, *Phytopathol.* **57**: 395. 1967. [*nom. inval*. Art. 35.1].

Typus: **India**, Pantnagar (U. P.), *Zea mays* var. *indurate* (*Panidoideae, Andropogoneae*), 12 Oct. 1965, *M.M. Payak* & *B.L. Renfro* (**holotype** designated here, HCIO 29038).

Description: *Sporangiophores* short, hyphal. *Sporangia* ovate, obclavate, elliptic, hyaline, 29.0–66.5 × 18.5–26.0 µm, smooth-walled, poroid apex truncate or rounded, with a persistent, straight or curvate peduncle, producing 4–8 zoospores. *Zoospores* spherical, hyaline, 7.5–11.0 µm diam. *Oogonia* subglobose, hyaline to light straw-colored, 33–44.5 µm diam, thin-walled, with 1–2 paragynous antheridia. *Oospores* spherical or subspherical, hyaline, 29.5–37.0 µm diam; wall smooth and glistening, 4 µm thick, wall confluent with oogonial wall; contents include prominent oil globule; centrally located in the oogonium (Payak & Renfro 1967; Fig. 8E).

Diagnosis: The large size of *Sclerophthora zeae* zoospores (7.5–11.7 µm long), as with *Eraphthora butleri, Sclerophthora lolii*, and *Sclerophthora rayssiae*, is distinctive among the *Peronosporaceae* (Kenneth *et al*. 1964, Payak & Renfro 1967). Parasitic to *Zea mays*, which differentiates it from the host range of all other *Sclerophthora* species with the exception of *Sclerophthora macrospora.* Differs from *Sclerophthora rayssiae* based on the following morphological characters: smaller oogonia (33.0–44.5 µm *vs*. 44.4–59.2 µm for *Sclerophthora rayssiae*) with thin even walls (versus the sinuous, unevenly thickened walls of *Sclerophthora rayssiae*); the absence of the golden to amber brown oogonia and oospores exhibited by *Sclerophthora rayssiae*; a sporangial shape that is obovate, obclavate, or elliptic,

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Digitaria bicornis*, *Digitaria sanguinalis (Panicoideae, Panicodae*); *Zea mays* (*Panicoideae, Andropogoneae*).

Notes: Payak & Renfro (1967) first documented the causal agent of brown stripe downy mildew of maize as *Sclerophthora rayssiae* var. *zeae*, which was collected from severe disease outbreaks that occurred throughout several regions of India in the early 1960s. The pathogen is not known from outside India. Disease symptoms are distinct from those caused by *Sclerophthora macrospora,* in that leaf shredding and deformation are not observed (Payak & Renfro 1967). Only the leaves are infected and show narrow vein-delimited chlorotic stripes parallel to the vascular tissue with well-defined margins that eventually became reddish brown to purple (Galgóczy *et al*. 2014).

Brown stripe downy mildew can result in maize yield losses between 20–100 % depending on cultivar susceptibility and weather (Putnam 2007). In present day India, the disease is of minor importance compared to other maize diseases and is generally adequately controlled using cultivar resistance and chemical applications (B.M. Prassa and Sujay Rakshit, pers. comm.; Lal *et al.* 1980, Basadrai *et al.* 2002, Singh & Singh 2012). In the USA, this pathogen is regulated under strict quarantine protocols as a USDA-APHIS Select Agent because it is considered a significant potential threat to the country's agricultural security.

Sclerophthora rayssiae var. *zeae* Payak & Renfro was not validly published, as it was based on the invalid basionym *Sclerophthora rayssiae* R.G. Kenneth (Art. 35.1, Turland *et al.* 2018). This provides us with a unique opportunity to revisit the taxonomy of the organism from a modern perspective, given the narrow species concept that we now recognize as the primary evolutionary trajectory for downy mildew pathogens (Gäumann 1918, 1923, Gustavsson 1959). In their decision to describe the organism as a variety and not assign the rank of species, Payak & Renfro adopted a broad species concept in assigning a taxonomic rank that was consistent with the accepted practice of the time and in line with the approach of most applied plant pathologists (de Bary 1863, Yerkes & Shaw 1959). Payak & Renfro (1967) were of the opinion that the host differences between the two organisms were not sufficient evidence to warrant the delimitation of a new species. However, Payak & Renfro also acknowledged several morphological features and the differing host range of *Sclerophthora rayssiae*, parasitic of the cool-season grass *Hordeum vulgare* (*Pooideae*), and *Sclerophthora zeae*, which is parasitic of warm-season *Panidoideae* grasses. Based on diagnosable morphological differences and host range, we treat this organism as a separate species rather than a varietal form of *Sclerophthora rayssiae*.

Sclerospora J. Schröt., *Hedwigia* **18**: 86. 1879.
Synonyms: *Sclerospora* subgen. *Sclerospora*, *Hedwigia* **18**: 86. 1879.

'Sclerospora subgen. *Eusclerospora'*, *Bot. Mag.*, Tokyo **27**: 218. 1913. [*nom. nud.*, Art. 21.3, 22.2]
Sclerospora subgen. *Sclerospora* J. Schröt., *Hedwigia* **18**: 86. 1879. [*nom. nud.*, Art. 22.1]

Type species: *Sclerospora graminicola* (Sacc.) J. Schröt., in Cohn, *Krypt.-Fl. Schlesien (Breslau)* **3.1**(9–16): 236. 1886 [1889].

Description: *Sporangiophores* stiffly upright with sparse straight branches. *Sporangia* ovate, with a papilla at the apex, forming zoospores. *Oospores* spherical with very thick, multi-layered, brown wall that fuses with the skin of the oogonium (Schröter 1886).

Notes: *Sclerospora* was the first *Peronosporaceae* genus specifically erected to accommodate a grass parasite, and the type species *Sclerospora graminicola* was the first graminicolous downy mildew pathogen ever described, albeit three separate times (Shaw 1975). Members of the genus are diagnosed through their asexual structures – the sporangial production of zoospores, evanescent sporangiophores with multiple branches, and a sporangial papilla – morphological traits that uniquely distinguish members of the genus from other *Peronosporaceae*.

In practice, identification of the *Sclerospora* is difficult to achieve based on morphological features alone, given the evanescent nature of the diagnostic asexual stage. *Sclerospora* sporangial structures are formed nocturnally in the presence of dew on living host material, persist only for a few hours to days, and finally collapse, desiccate, and/or gelatinize after zoospore discharge (Kenneth 1970, Jeger *et al.* 1998). This means that asexual structures are often not preserved on herbarium materials or other dried specimens, limiting their value for identification and taxonomic study. Given the destructive nature of *Sclerospora graminicola* parasitizing the staple food crops pearl millet and foxtail millet (*Pennisetum glaucum, Setaria italica*) this fundamental limitation carries important implications for detecting, preventing, and quarantining downy mildew disease on millet crops globally.

Currently, *Sclerospora* contains five validly described species and is unique among the graminicolous downy mildew genera in that three different host subfamilies are parasitized. However, our understanding of *Sclerospora* species boundaries and host association within the genus is poorly defined. The generic identity of *Sclerospora farlowii*, *Sclerospora iseilematis*, *Sclerospora northii*, and *Sclerospora secalina* is not reliable at present, as these species were all described as members of the genus *Sclerospora* based on oogonial structures, in the absence of diagnostic asexual characters. However, the oogonial morph of these species shares common features: oogonia and oospores are generally dark colored, spherical to sub-globose, with thick, multi-layered oogonial walls fused to the oogonia (Schröter 1886).

For species-level discrimination of *Sclerospora*, a combination of morphological and host range characters is the only approach currently available. However, the globally distributed, broad-host-range type species *Sclerospora graminicola* appears to be a species complex, with 198 records of the pathogen reported from 20 species of *Poaceae* (Farr & Rossman 2021). It is conceivable that many graminicolous downy mildew outbreaks were attributed to *Sclerospora graminicola* based on insufficient evidence or simply because the species was one of just a few downy mildew pathogens known from *Poaceae* hosts during the late 19th and early 20th centuries.

Until the taxonomy of this genus can be further studied and resolved, it is clear that accurate diagnosis of *Sclerospora* species is a daunting task. Molecular phylogenetic research across host populations and incorporating type materials will be required to provide a basic framework to support identification, diagnostics, and taxonomic resolution of the *Sclerospora*.

Sclerospora farlowii Griffiths, *Bull. Torrey Bot. Club* **34**: 207. 1907.
Synonyms: '*Sclerophthora farlowii*' (Griffiths) R.G. Kenneth, *Israel J. Bot.* **12**: 139. 1963 [1964]. [*nom. nud.*, Art. 36.1, 39.1]
'*Sclerophthora farlowii*' (Griffiths) R. G. Kenneth, *Phytoparasitica* **7**: 50. 1964. [*nom. nud.*, Art. 36.1, 39.1]

Typus: **USA**, Arizona, Cochise, *Chloris virgata* (as *Chloris elegans*; *Chloridoideae, Cynodonteae*), Oct. 1900, *D. Griffiths* [**lectotype** designated here, BPI 187077 (MBT 10002162); **isotypes** BPI 187076, BPI 187078, FH 965329, FH 1093687 (MBT 10002163)]. Supplementary Fig. S18 shows the lectotype BPI 1187077. Supplementary Figs S19 and S20 show isotypes BPI 187076 and BPI 187078.

Description: *Oospores* sub-globose, deep dark reddish brown and often appearing black and opaque, 28–45 µm diam. Asexual morph not observed. (Griffiths 1907; Figs 9, 10A).

Diagnosis: *Sclerospora farlowii* produces sub-globose, deep dark reddish-brown oospores that often appear black and opaque and parasitizes *Chloris virgata*, which taken together are unique features for *Peronosporaceae* parasitizing hosts in the *Poaceae* family. *Peronosclerospora miscanthi* and *Peronosclerospora noblei* also produce dark reddish to amber brown oospores of similar diam to those of *Sclerospora farlowii,* but these species differ by their globose-shaped oospores versus the sub-globose oospores of *Sclerospora farlowii* and by their host range, which is limited to *Andropogoneae* hosts.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Chloris virgata (Chloridoideae, Cynodonteae)*; possible reports on *Cynodon dactylon (Chloridoideae, Cynodonteae*); *Deyeuxia* sp. (*Poaceae, Pooideae*).

Notes: Griffiths (1907) noted that *Sclerospora farlowii* was one of the most common "fungi" encountered in southern Arizona being locally abundant but with little to no discernable impact on the health of the infected host plants. The type host, *Chloris virgata* (feather fingergrass), is native to the Americas. It is most notable as a highly adaptable, prolific weed in numerous ecosystems and an aggressive invasive plant outside its native range.

The reports of *Sclerospora farlowii* on *Cynodon dactylon* and *Deyeuxia* sp. from checklist publications (Farr & Rossman 2021) need further investigation. Given that most *Peronosporaceae* species are highly specialized and their taxonomy follows a narrow species concept (*e.g.*, García-Blázquez *et al.* 2008, Thines & Choi 2016, Petrželová *et al.* 2017), it seems unlikely that these hosts from three different plant genera with different photosynthetic pathways are parasitized by *Sclerospora farlowii*. There are also several smuts that parasitize *Deyeuxia* species that could potentially be mistaken for the resting spores of a sclerospora-like species (Vánky & Guo 2001), as was the case when *Sclerospora graminicola* was mistakenly brought into

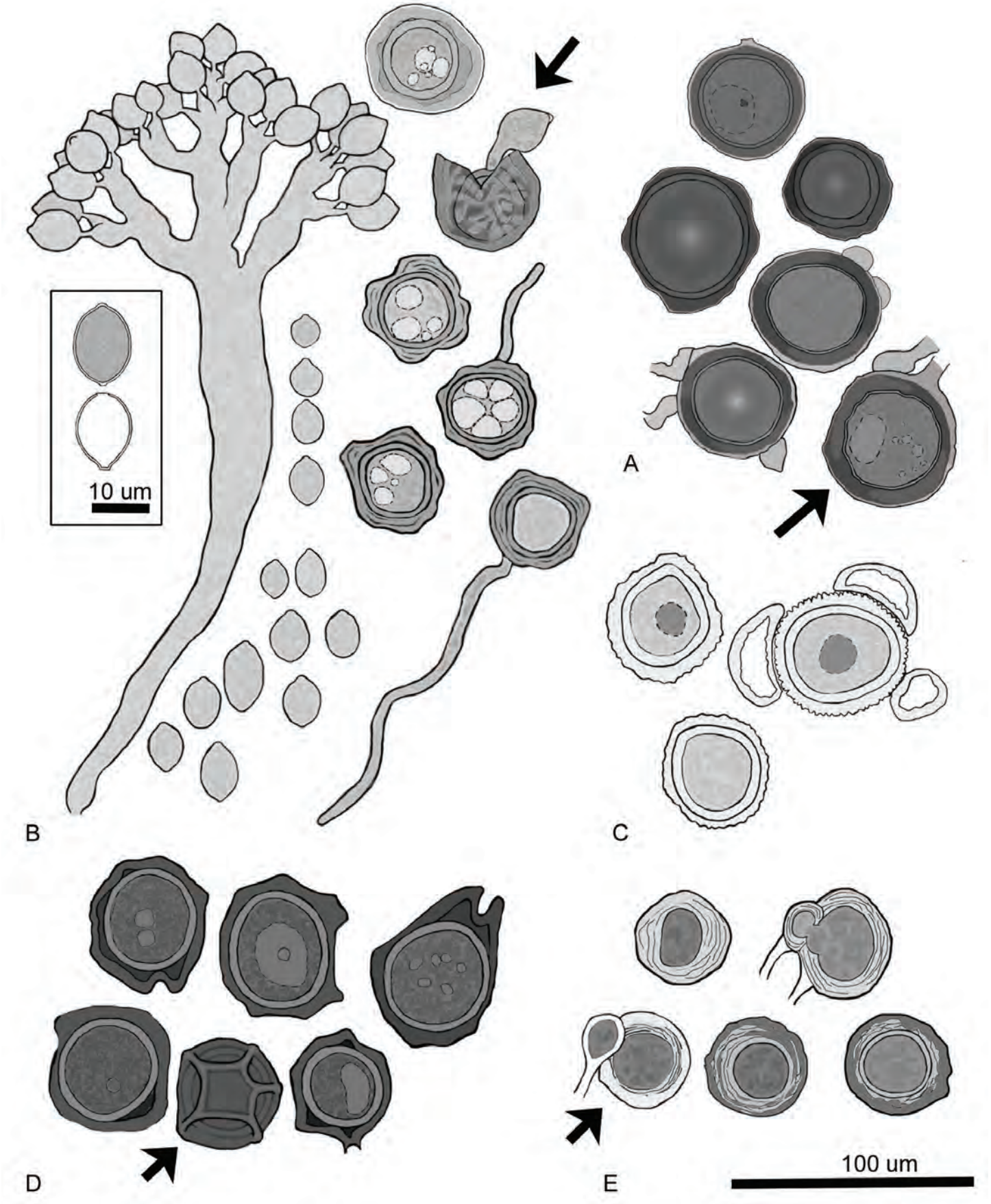

Fig. 10. A. *Sclerospora farlowii*, oogonium (arrow) and oospores **B.** *Sclerospora graminicola*, sporangiophore, sporangia, including a close-up of a cytoplasm-filled sporangium and an empty sporangium (inset); oospores, including an oospore germinating to produce a sporangium (arrow). **C.** *Sclerospora iseilematis*, oospores. **D.** *Sclerospora northii*, oospores, one in surface view (arrow). **E.** *Sclerospora secalina*, oogonium with antheridium (arrow) and oospores in various stages of maturity. Illustrations were prepared from published reference images in Weston (1924, 1929), Howe (1930), Naumov (1949), Thirumalachar & Narasimhan (1949), Pande (1972), and Thakur *et al*. (2011).

connection with the smut species *Ustilago urbani* (Waterhouse 1964, Shaw 1975).

In some publications, *Sclerospora farlowii* is listed under the name *Sclerophthora farlowii* (Griffiths) R.G. Kenneth (Kenneth 1981, Dick 2001, 2013, Spencer & Dick 2002). At the time of this writing (September 2021), MycoBank and Index Fungorum give the current name as *Sclerophthora farlowii* (Griffiths) R.G. Kenneth, *Israel J. Bot.*: 139. 1964. However, a publication by R.G. Kenneth in the *Israel Journal of Botany* from the year 1964 does not exist. A publication by R.G. Kenneth from 1963 in the *Israel Journal of Botany* does exist, and on page 139, one finds the diagnosis of *Sclerophthora lolii* R. G. Kenneth *sp. nov*., but not *Sclerophthora farlowii* (Griffiths) R. G. Kenneth *comb. nov*. The first published mention of *Sclerophthora farlowii* (Griffiths) R.G. Kenneth dates to 1979 (Kenneth 1979), in a scientific meeting abstract that states that examination of the *Sclerospora farlowii* herbarium material supports the hypothesis that the species should be transferred to *Sclerophthora*. Based on annotation labels in the Farlow Herbarium, these examinations took place in 1978. However, *Sclerophthora farlowii* (Griffiths) R. G. Kenneth is invalid under ICN Art. 36.1 and Art. 39.1 (Turland *et al.* 2018).

The original species description for *Sclerospora farlowii* is brief and limited to a description of oospore morphology. In Kenneth's 1979 meeting abstract, host range was cited as justification for transfer of *Sclerospora farlowii* to *Sclerophthora*, along with unspecified "sporangia and hyphoid sporangiophore" features, but host range is not a defining trait for the genus *Sclerophthora* and no details were provided about morphological characters. Overall, additional research is required to resolve any taxonomic uncertainty surrounding the generic identity of *Sclerospora farlowii*.

Griffiths did not designate a holotype for *Sclerospora farlowii*, although it was not required at the time of publication (Griffiths 1907). The original collections were distributed to BPI and FH, and in Griffith's personal herbarium (Griffiths 1907). Examination of the BPI collections identified specimen BPI 187077, BPI 18076, and BPI 187078 with the same collection details described by Griffith's, with notes written in W.H. Weston's handwriting that these were type material. BPI 187077 is herein used to lectotypify the species.

Sclerospora graminicola (Sacc.) J. Schröt., in Cohn, *Krypt.-Fl. Schlesien (Breslau)* **3.1**(9–16): 236. 1886.
Basionym: *Protomyces graminicola* Sacc., *Mycotheca Veneti* **5**: no. 496. 1876.
Synonyms: *Ustilago (?) urbanii* Magnus [as '*urbani*'], *Verh. Bot. Ver. Prov. Brandenb*. **20**: 52. 1878.
Sclerospora graminicola (Sacc.) J. Schröet., *Hedwigia* **18**: 86. 1879.
Peronospora setariae Pass., *Grevillea* **7**: 99. 1879.
Peronospora graminicola (Sacc.) Sacc., *Michella* **2**: 586. 1882.
Sclerospora graminicola var. *setariae-italicae* Traverso, *Boll. Soc. Bot. Ital.* **1902**: 1968. 1902.
Sclerospora graminicola var. *graminicola* Kulk*., Memoirs of the Dept. Agric. India, Bot. Ser*. **55**: 272. 1913.
'*Sclerospora graminicola*' Schröter *apud* Oudemans, *Enum. Syst. Fungi*. **1**: 719. 1919. [*nom. inval.* Art 32.1(c)]. A slip of the pen for *Peronospora graminicola* (Sacc.) Sacc.
'Sclerospora setariae-italicae' (Traverso) Cif. & Sousa da Câmara, *Quad. Ist. Bot. Uni. Pavia* **30**: 233. 1963. [*nom. inval.,* Art. 41.1]
Typus: **Poland**, Liegnitz, Waldau, Breslau, *Setaria viridis*, date unknown, *W.G. Schneider*, Herbarium Schlesischer Pilze: 553.

Description: *Sporangiophores* evanescent, nocturnal, erect, 100 × 12–15 µm; branched in the lower part but usually with a few short, thick branches that are dichotomously or trichotomously formed at the top and crowned with numerous ultimate branchlets on which sporangia are borne. *Sporangia* hyaline, subglobose to elliptical, slightly pointed at the free end, with a thin smooth wall; rapidly germinate in water, liberating zoospores in variable numbers, from three to four and up to a dozen or more zoospores per sporangium depending on size. *Zoospores* irregularly kidney shaped, unequal-sided, flattened bodies, 9–12 µm diam, forming two oppositely directed flagella on the concave side, and germinating via hyphae. *Oogonia* elliptical, angular or irregular shape due to irregularly thickened wall, tawny to brown or chestnut brown, (34–)42(–52) µm diam; wall irregular with thickened areas and conspicuous ridges, 4–11 µm, sometimes up to 17 µm thick, making the whole spore, thus, 33–45 µm (sometimes up to 50 µm) diam. *Oospores* spherical, yellow (Chromotaxia), (22.5–)32(–35) µm diam; wall evenly thickened, smooth. (Butler 1907, Schröeter 1886; Fig. 10B).

Diagnosis: Evanescent sporangiophores with multiple branches bearing sporangia uniquely distinguish *Sclerospora graminicola* from members of the *Peronosporaceae* outside of the genus *Sclerospora*. Differs from *Sclerospora iseilematis*, and *Sclerospora secalina* by having an oogonial wall with conspicuous ridges. Differs from *Sclerospora northii* by having smaller oogonia (41 µm diam versus 51–61 µm diam, respectively).

Reference sequence data: Ex-HV532 nucleotide sequences DQ365768 (*cox*2), AY035514 (28S rDNA D1/D2/D3), AY273987 (28S rDNA D7/D8).

Host range: *Setaria* spp. and *Pennisetum glaucum* (*Panicoideae, Paniceae*). Globally, the species is also reported as a parasite of 20 species of *Poaceae* in two subfamilies including 13 genera: *Beckeropsis, Digitaria, Echinochloa, Euchlaena*, *Panicum, Pennisetum*, *Setaria*, *Sorghum*, *Zea* (*Panicoideae*); *Alopecurus*, *Dactylis*, *Holcus*, and *Triticum* (*Pooideae*) (Weston & Weber 1928, Farr & Rossman 2021). As discussed in the Notes section below, the true host range and impact of this species may be limited to *Setaria* spp. or even the type host *Setaria viridis* (wild foxtail millet).

Notes: *Sclerospora graminicola* reportedly impacts production of two widely cultivated staple human food crops significantly: pearl millet (*Pennisetum glaucum*) and foxtail millet (*Setaria italica*; Safeeulla 1976, Francis & Williams 1983, Kumar *et al.* 2012). Pearl millet in Africa and Asia are the most affected by *Sclerospora graminicola*, with losses of 20–100 % reported (Kumar *et al*. 2012). Crop losses in foxtail millet can range between 20–70 % (Li *et al.* 2020). To date, pearl millet has not been reported as a host in the Americas (Francis & Williams 1983, Kumar *et al.* 2012, K.M. Devos, *pers. comm.*).

There are multiple lines of evidence that suggest *Sclerospora graminicola* is a species complex in need of careful taxonomic evaluation, particularly across host populations (M. Thines, unpubl. data). Broadly speaking, since most *Peronosporaceae* species are specialized to parasitism of a single or only a few host species, records of this species as a broad-host range pathogen of 13 different genera across two plant families are inconsistent with

expectations for the species (*e.g.*, Thines & Choi 2016, Petrželová *et al.* 2017). More specifically, most – but not all – experimental evidence from host range studies points to the distinction between *Sclerospora graminicola* strains that infect pearl millet from those that infect *Setaria* spp., including foxtail millet (Melhus *et al.* 1928, Safeeulla 1976, Francis & Williams 1983, Singh *et al*. 1993). Since *Sclerospora graminicola* isolates from pearl millet are heterothallic with two mating types (Michelmore *et al*. 1982, Idris & Ball 1984), the inability of strains from *Setaria* spp. to infect pearl millet could indicate that the lineage(s) on *Setaria* spp. are reproductively isolated from the lineages on pearl millet, which satisfies the separation of the two lineages into two species under a biological species concept. Molecular studies of *Sclerospora graminicola* are very limited, with only a few specimens from pearl millet analyzed using *cox*2 and 28S rDNA sequence data (Thines *et al.* 2008, Telle *et al.* 2011, Thines *et al.* 2015), although the availability of whole genome sequence data (Nayaka *et al*. 2017) may lead to new investigations of species diversity.

Sclerospora iseilematis Thirum. & Naras., *Indian Phytopathol*. **2**: 49. 1949.

Typus: **India**, Mysore, Nandi Hills, *Iseilema prostratum* (as *Iseilema laxum*; *Panicoideae, Andropogoneae*), 20 Jan. 1947, *M.J. Narasimhan* & *H.C. Govindu* [**lectotype** designated here BPI 187262 (MBT 10002239); **isotype** IMI 38399 (MBT 10002240)]. Supplementary Fig. S21 shows the lectotype BPI 187262.

Description: *Oogonia* sub-globose to spherical, pale golden-yellow, 43–61 µm diam; wall deeply folded, tuberculate, almost spiny, 5.5 µm thick. *Antheridia* 2–5, conoid to triangular, 27–40 × 15.5–27 µm, persistent in mature oospore. *Oospores* spherical, hyaline, 38–50 µm diam, plerotic, inner contents granular and enclosing a few droplets; wall 3–3.5 µm thick, confluent with the oogonial wall. Asexual morph not observed (Thirumalachar & Narasimhan 1949; Fig. 10C).

Diagnosis: Parasitizes the same host as *Peronosclerospora westonii*, but can be differentiated by oospore size, with the spherical, pale oospores of *Sclerospora iseilematis* measuring 38–50 µm diam with tuberculate endosporium walls 3.0–3.5 µm thick versus the spherical golden-brown oospores of *Peronosclerospora westonii* measuring 23–29 µm diam with smooth endosporium walls 6–9 µm thick. Differs from *Sclerospora graminicola, Sclerospora northii*, and *Sclerospora secalina* by having a tuberculate, almost spiny oogonial wall. Differs from *Sclerospora farlowii* by its parasitism of *Iseilema prostratum*.

Reference sequence data: Ex-lectotype nucleotide sequences OK185342 (*cox*2), OK255493 (28S rDNA).

Host range: Known only from the type host *Iseilema prostratum.*

Notes: *Sclerospora iseilematis* has not been reported since its original description in 1949, when a single field of *Iseilema prostratum* (musal grass) with downy mildew disease symptoms was documented in India (Thirumalachar & Narasimhan 1949). The type host is native to the Indian subcontinent and parts of South-East Asia, but the extent to which the pathogen is distributed with the host is unknown. *Sclerospora iseilematis* infections result in witches-broom-like inflorescences with reduced internodal elongation and excessive proliferation and branching of the spikelets. Although oogonia production is heavy within the mesophyll of infected leaves, no leaf shredding symptoms occur, and leaf symptoms are limited to chlorosis (Thirumalachar & Narasimhan 1949).

Since Thirumalachar & Narasimhan (1949) only observed the oogonial morph, it is impossible to conclude from morphological data alone that *Sclerospora iseilematis* is a member of the genus *Sclerospora*. The basic morphological features that define *Sclerospora* are only found in the sporangia: namely, through the evanescent production of sporangiophores with multiple branches, and the sporangial production of zoospores that escape through a pailla.

A holotype specimen was not designated in the protolog, although collection details were listed, followed by the word "type." BPI contains a specimen of *Sclerospora iseilematis* (BPI 187262) with collection details matching those given in the protolog and marked "type" on the outer envelope and as part of the enclosed handwritten annotations; we therefore use this specimen to lectotypify the species.

Sclerospora northii W. Weston [as '*nothi*'], *Phytopathol.* **19**: 965. 1929.
Synonym: *'Sclerophthora northii'* (W. Weston) Thirum. *et al.*, *Bull. Torrey Bot. Club* **80**: 300. 1953. [*nom. nud.*, Art. 36.1, 39.1]

Typus: **Fiji Islands**, Suva, Rarawai Estate, *Saccharum maximum* (as *Erianthus maximus* var. *seemanii*; *Panicoideae, Andropogoneae*), 23 Jun. 1924, *H.F. Clarke* [**lectotype** designated here BPI 187307 (MBT 10002241), **isotype** FH 965380 (MBT 10002242)]. Supplementary Fig. S22 shows the lectotype BPI 187307.

Description: *Oogonia* rounded polyhedral with several flattened faces bordered by ridges, occasionally irregular, elongate pyriform, or unequally rounded oblong, amber brown (sometimes raw sienna to argus brown), 40–70 µm (up to 57–60.9 µm × 51–56.9 µm) diam; wall with arched irregular, ridged prominences, 3–5 µm (occasionally to 10 µm); remains of oogonial stalk or antheridium rare. *Oogonia* spherical, hyaline to pale amber, 39–46.9 µm (mode 41–44.9 µm; up to 35–52 µm) diam, contents finely granular with denser aggregations, central area usually clear with occasionally one or more oil globules; wall dense, smooth, homogeneous to indistinctly lamellate, 2–4.5 µm thick. Asexual morph not observed. (Weston 1929b; Fig. 10D).

Diagnosis: Distinguished from *Peronosclerospora miscanthi, Peronosclerospora spontanea* and *Peronosclerospora sacchari,* which also parasitize *Saccharum* spp., due to the production of oospores each enclosed in a darkened, thickened oogonial wall with several flattened polyhedral faces. Differs from *Sclerospora iseiliematis* and *Sclerospora secalina* by having an oogonial wall with conspicuous ridges and by parasitism of *Saccharum maximum*. Differs from *Sclerospora graminicola* by having larger oogonia (51–61 µm diam *vs.* 41 µm diam, respectively). Differs from *Sclerospora farlowii* by parasitism of *Saccharum maximum*.
Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: Known only from the type host *Saccharum maximum Panicoideae*, *Andropogoneae*.

Notes: *Sclerospora northii* was reported as a pathogen of *Saccharum maximum*, a native reed-like grass common in Fiji

(Weston 1929). Infected plants were dried and brown with shredded leaves (Weston 1929). The pathogen has not been reported since the original 1924 sighting, and it is unknown what impact *Sclerospora northii* has on host populations.

At the time of writing (September 2021), Index Fungorum listed the current name for this species as *'Sclerophthora northii'* (W. Weston) Thirum. *et al*., *Bull. Torrey Bot. Club* **80**: 300. 1953. However, the correct name for this pathogen is *Sclerospora northii* W. Weston. The publication cited for *"Sclerophthora northii,"* in which the genus *Sclerophthora* was first described, did not make a new combination for *Sclerospora northii*, and the species was not mentioned at any point in the article.

As discussed by Shaw (1978), the asexual morph of this pathogen has not been observed. *Sclerospora northii* was one of five *Sclerospora* species that were not transferred to *Peronosclerospora* by Shaw (1978), as the absence of any record of asexual reproductive structures precluded assignment to either *Peronosclerospora* or *Sclerospora*.

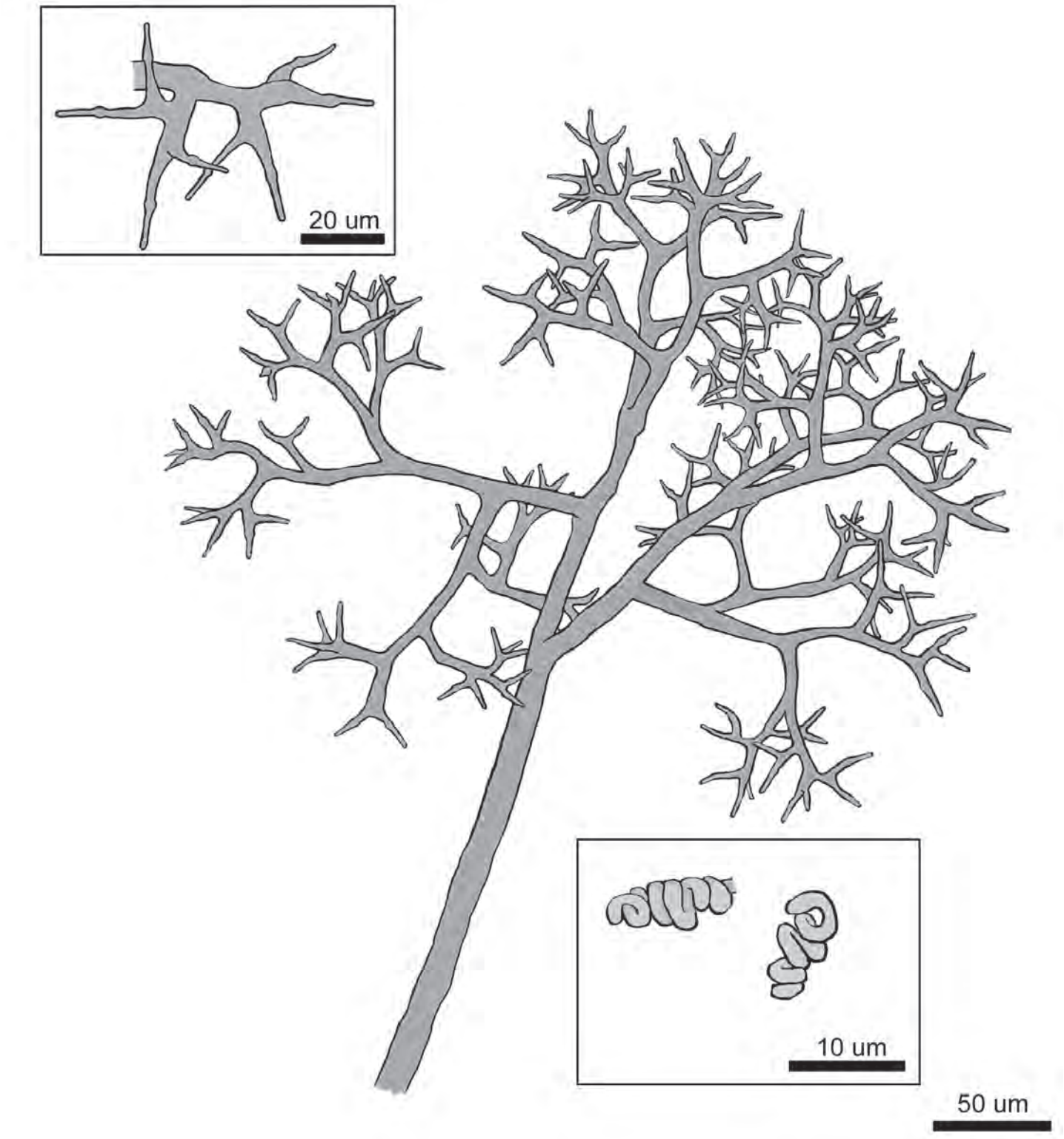

Fig. 11. *Viennotia oplismeni*, sporangiophore, with close-up of indeterminant sporangiophore tips (top inset) and helical haustoria (bottom inset). Illustrations were prepared from published reference images in Goker *et al*. (2007).

Weston did not designate a holotype for *Sclerospora northii*; however, he provided detailed collection data regarding his materials. BPI and FH holdings that originate from Weston's collections includes specimens BPI 187307 and FH 965380 with identical collection data as that which is communicated in the protolog, detailed in Weston's handwriting, and is written on a label from the *Herbarium of W. H. Weston*. These specimens are undoubtably part of Weston's original specimen collection used for describing the species; BPI 187307 is here used to lectotypify *Sclerophthora northii*.

Sclerospora secalina Naumov, *Notul. Syst. Sect. Cryptog. Inst. Acad. Sci. USSR* **6**: 79. 1949.

Typus: *Non designatus*.

Description: *Oogonia* sub-spherical, 33–38 [or 48] µm diam; wall smooth without tubercules or ridges. *Antheridia* 14.7 × 18 µm diam. *Oospores* spherical, deep ocher, then brown, 31–46 [or 36] µm diam at maturity; wall smooth. (Waterhouse 1964; Fig. 10E).

Diagnosis: Distinct from *Sclerophthora macrospora* parasitizing *Secale cereale* by oospore size and coloration, which are much smaller in *Sclerospora secalina* (versus a diam of 62.5 µm or more and hyaline oospores of *Sclerophthora macrospora*). Differs from *Sclerospora iseilematis*, *Sclerospora graminicola*, and *Sclerospora northii* by having a smooth oogonial wall without tubercules or ridges. Differs from *Sclerospora farlowii* by parasitism of *Secale cereale*.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Secale cereale* (*Pooideae*, *Triticaceae*).

Notes: According to Farr & Rossman (2021), this species has not been reported since its initial description as a parasite of *Secale cereale* (cereal rye) in the former USSR during 1942 (Waterhouse 1964). Since Naumov only observed the oogonial morph (Waterhouse 1964), the generic status of *Sclerospora secalina* is not clear. In the absence of sporangial features and/or molecular data, it is not possible to conclude with certainty that this species is a member of the genus *Sclerospora*.

Viennotia J.A. Crouch & Thines, ***gen. nov.*** MycoBank MB 840578.
Synonym: *'Viennotia*' Göker *et al.* [*nom. inval*. Art. 35.1]

Type species: *Viennotia oplismeni* J.A. Crouch & Thines

Description: *Canad. J. Bot*. **81**: 682. 2003. Haustoria hyaline, hyphoid, intracellular, long, often tightly coiled and slender. Sporangiophores hyaline, monopodially branched, with ultimate branches that are straight to slightly curved. Parasitic to members of the *Poaceae* (Göker *et al*. 2003).

Diagnosis: Differs from all other graminicolous downy mildews in sporangiophores that show recurrent outgrowth after sporangia have been shed (Thines 2009).

Notes: The genus *Viennotia* was based on an invalid basionym without type specimen (see notes on *Viennotia oplismeni*, below), rendering it invalid itself (Art. 40.1) Hence, the genus could not be described by reference to the type species (Art. 10.1), as it was not validly published, invalidating the genus description. Therefore, we validate the genus name and the type species here.

Viennotia oplismeni J.A. Crouch & Thines, ***sp. nov.*** MycoBank MB 840579.
Synonyms: *'Plasmopara oplismeni*' Vienn.-Bourg., *Bull. Soc. Mycol. France* **75**: 33. 1959. [*nom. inval*. Art. 40.1].
'*Viennotia oplismeni'* (Vienn.-Bourg.) Göker *et al.*, *Canad. J. Bot.* **81**: 682. 2003. [*nom. inval.* 35.1].

Typus: **Guinea**, near Kindia, on leaves of *Oplismeni hirtellus* (*Panicoideae, Panicodae*), 3 Nov. 1963, *J. Kranz* (**holotype** GZU 335974 designated here, **isotypes** BPI 784624, IMI 103944). Supplementary Fig. S23 shows the isotype BPI 784624.

Description: *Haustoria* intracellular, hyphoid, slender, long and often tightly coiled. *Sporangiophores* hyaline, monopodially branched, 180–230 × 6–8 µm; branching in the upper third into spreading branches; terminal branches straight to slightly curved divided at right angles into short ramifications with swellings typically carrying three sterigmata; sterigmata bloated and pinched, 14–23 µm long. *Sporangia* 14–28 × 11–17 µm. *Oogonia* not observed (Figs 11, S23).

Diagnosis: Differs from other *Peronosporaceae* by parasitizing *Oplismeni* spp. Differs from *Poakatesthia penniseti* by having globular citroform sporangia, shorter and dichotomously branched sporangiophores, and larger ultimate branchlets. Differs from *Graminivora graminicola* by 28S DNA sequences and, by successive outgrowth of the ultimate branchlets after sporangia have been shed, a feature that also distinguishes the species from all other graminicolous downy mildews.

Reference sequence data: Ex-holotype nucleotide sequences AY035527 (28S rDNA D1/D2/D3), AY273977 (28S rDNA D7/D8).

Host range: *Oplismeni hirtellus*, *Oplismeni compositus* (*Panicoideae, Panicodae*).

Notes: Reported just twice, on *Oplismeni hirtellus* (basketgrass) and *Oplismeni compositus* (running mountaingrass) from Guinea (Viennot-Bourgin 1959, Kranz 1965). The first report of the species did not list any symptoms associated with the host infection, but Kranz (1965) documented leaves that were streaked yellow and rapidly rotted. Although both hosts have a cosmopolitan distribution across most tropical and subtropical parts of the world, *Viennotia oplismeni* has not been reported since 1963 (Kranz 1965); therefore, it is unknown if the species has any impact on host populations.

Plasmopara oplismeni was not validly published, as a type was not designated as required at the time, meaning that *Viennotia oplismeni* (Vienn.-Bourg.) Göker *et al.* and the genus *Viennotia* Voglmayr *et al.* were not validly published (Art. 10.1, 40.1, Turland *et al.* 2018). It is unknown if Viennot-Bourgin's collections from 1955 are extant, and no illustrations of the species were provided (Viennot-Bourgin 1959). Duplicate collections of Kranz' materials are held at BPI, GZU, IMI (K) (det. G.M. Waterhouse, conf. H. Vogelmayr); these specimens were made from the same host in the same locale where Viennot-

Bourgin made collections. GZU 335974 was studied by Göker *et al.* (2003) when they designated the genus *Viennotia*, and it has been characterized through morphological and molecular analysis (Kenneth & Kranz 1973, Riethmüller *et al*. 2002, Göker *et al*. 2003, Thines *et al.* 2006, Thines 2009). This specimen is therefore designated as the holotype for *Viennotia oplismeni*.

DISCUSSION

Graminicolous downy mildews are predominantly tropical or subtropical, with only two of the seven genera, *Sclerophthora* and *Sclerospora*, extending into cool temperate climates (Spencer & Dick 2002, Davis & Crouch 2022a, b). As most tropical ecosystems are generally understudied, our current knowledge of the GDMs is restricted to species occurring on crops and some anecdotal reports from wild grasses (Waterhouse 1964, Shaw 1975, this paper). Interestingly, maize seems to be highly susceptible to a variety of GDM species (Kenneth 1989), and descriptions of some species, such as *Peronosclerospora maydis* and *Peronosclerospora philippinensis* are based on infections on this host. However, maize is not native to the natural range of *Peronosclerospora*, suggesting that the high susceptibility of maize is because of a naivity to downy mildew pathogens (Thines 2014), in line with the hypothesis that host susceptibility increases with increasing geographic distance from potential pathogens (Thines 2019). As maize is not native to Asia, the natural host reservoir may be in indigenous grasses. Because naturally occurring infections of wild and weedy grasses have not been systematically studied, the original source of inoculum is unknown for most species affecting maize, complicating phytosanitary measures. Only recently has a native host has been identified for *Peronosclerospora maydis* (Suharjo *et al.* 2020). Thus, studies of the GDMs in unmanaged habitats are highly warranted.

Although we treat the GDMs as a group in this review, it is unclear if the *Peronosporaceae* affecting grasses are monophyletic. So far, three potentially monophyletic groups have been identified from *Poaceae* hosts – the graminicolous downy mildews with lasting sporangiophores (*Graminivora*, *Poakatesthia*, and *Viennotia*), a group comprising *Eraphthora* and *Sclerophthora*, and the graminicolous downy mildews with evanescent sporangiophores (*Baobabopsis*, *Peronoscleropsora*, *Sclerospora*). The relationships of these groups remain unclear (Thines 2014), as well as how the other downy mildew genera are related to them. Thines (2009) hypothesized that, due to some plesiomorphic characters and a high degree of morphological variation, the evolution of downy mildews might have started out from graminicolous hosts, but as multigene phylogenetic data are lacking for most GDMs, this hypothesis has not yet been tested. In any case, the phytophthora-like species affecting sedges that are unculturable and have been placed in a genus of their own, *Kawakamia*, should be included in studies of these organisms, even though the independence of *Kawakamia* on the genus level was doubted in the most recent monograph of *Phytophthora* (Erwin and Ribeiro 1996). In addition, several sclerophthora-like species that share morphological similarities with *Kawakamia*, including *Sclerophthora zeae* and *Sclerophthora cryophila,* should be included in subsequent studies. Considering the often nonspecific and minor symptoms caused by the phytophthora/sclerophthora-like species affecting *Poales*, it seems likely that the few scattered reports of these organisms are only the tip of iceberg of their total diversity.

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Supplementary Material: http://fuse-journal.org/

Fig. S1. *Eraphthora butleri* lectotype BPI 187075.
Fig. S2. *Graminivora graminicola* lectotype BPI 786232.
Fig. S3. *Peronosclerospora maydis* isotype BPI 789413.
Fig. S4. *Peronosclerospora miscanthi* neotype BPI 187301.
Fig. S5. *Peronosclerospora noblei* lectotype BPI 187306.
Fig. S6. *Peronosclerospora philippinensis* lectotype BPI 18731.
Fig. S7. *Peronosclerospora philippinensis* isotype BPI 187044.
Fig. S8. *Peronosclerospora philippinensis* isotype BPI 187311.
Fig. S9. *Peronosclerospora philippinensis* isotype BPI 187313.
Fig. S10. *Peronosclerospora sacchari* lectotype BPI 187331.
Fig. S11. *Peronosclerospora sorghi* lectotype BPI 187336.
Fig. S12. *Peronosclerospora spontanea* lectotype BPI 187043
Fig. S13. *Peronosclerospora spontanea* isotype BPI 187073.
Fig. S14. *Peronosclerospora spontanea* BPI 187342.
Fig. S15. *Sclerophthora cryophila* holotype DAOM 20643.
Fig. S16. *Sclerophthora macrospora* neotype BPI 187265.
Fig. S17. *Sclerophthora macrospora* isotype BPI 187266.
Fig. S18. *Sclerospora farlowii* lectotype BPI 187077.
Fig. S19. *Sclerospora farlowii* isotype BPI 187076.
Fig. S20. *Sclerospora farlowii* isotype BPI 187078.
Fig. S21. *Sclerospora iseilematis* lectotype BPI 187262.
Fig. S22. *Sclerospora northii* lectotype BPI 187307.
Fig. S23. *Viennotia oplismeni* isotype BPI 784624.
Table S1. Summary of the primary features of the asexual and sexual structures produced by *Peronosporaceae* species that cause downy mildew diseases of *Poaceae* hosts.

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Contributions to the revision of the genus *Entoloma* (*Basidiomycota, Agaricales*) in Europe: six new species from subgenus *Cyanula* and typification of *E. incarnatofuscescens*

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Abstract: In anticipation of a phylogenetically revised monograph of *Entoloma* in Europe, six new species of subgenus *Cyanula* are described here. *Entoloma cistocruentatum* is associated with *Cistus* in Spain, *E. dislocatum* occurs in montane regions in Catalonia (Spain) and Tuscany (Italy), *E. indikon* is known from Denmark and three species are mainly distributed in the Nordic countries in Europe: *E. calceus*, *E. perchalybeum* and *E. praecipuum*. *Entoloma incarnatofuscescens*, from the /Rusticoides clade is neotypified. A fully amended description is given based on molecular evidence, which includes the recently described *E. violaceoparkensis* and *E. klofacianum* which became later synonyms.

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INTRODUCTION

This study is part of a large-scale molecular phylogenetic and morphological revision of the /Cyanula clade of the genus *Entoloma* in Europe to be published in due course (Dima *et al.* in prep.) and a new, completely revisited monograph of all European species of the /Cyanula clade (Noordeloos in prep.). The /Cyanula clade is here defined in a wide sense, including all clampless, often vividly coloured species, formerly included in subgen. *Leptonia* but shown to be phylogenetically quite distant from the clamped *Leptonia s. str.* taxa (Morozova *et al.* 2014). The material in the present study comes from various sources. In the Nordic countries, much work has been done on *Entoloma*, in the framework of the Norwegian *Entoloma* project and studies of the alpine mycota in Sweden resulting in a constant flow of publications in recent years (Brandrud *et al*. 2018, 2019, Crous *et al*. 2021, Dima *et al.* 2021, Haelewaters *et al*. 2021, Noordeloos *et al*. 2018, 2020). Jordi Vila and collaborators studied the mycota of Spain, Catalonia (Caballero & Vila 2013, Vila & Caballero 2007, 2009, Vila & Llimona 2010, Vila *et al.* 2013, 2014, 2021) which yielded some of the proposed new taxa.

The phylogenetic position of the new species described here will be dealt with in depth in a forthcoming study based on a world-wide sampling of the subgenus *Cyanula* (Dima *et al.* in prep.).

MATERIAL AND METHODS

Morphology

All collections studied were photographed in the field and attention was paid in observing the surrounding vegetation and putative ecology for each collection based on above-ground observations. The material was described after collecting to document the ephemeral macroscopic characters (especially colours) and dried and stored in the respective fungaria. Microscopic characters were studied with standard light microscopy methods. Spores, basidia and cystidia were observed in squash preparations of small parts of the lamellae in 5 % KOH or 1 % Congo Red in concentrated NH_4OH. The pileipellis was examined on a radial section of the pileus in water. Basidiospore

dimensions are based on observing 40 spores in side view, while cystidia and basidia dimensions are based on observing at least 10 structures per collection. Basidia were measured excluding sterigmata and the spores excluding hilum. Spore length to width ratio is reported as 'Q' and average length to width ratio is reported as 'Qav'. All studied material is stored in the herbaria of Oslo (O), Gothenburg (GB), or Leiden (L), unless otherwise indicated.

DNA extraction and sequencing

Total DNA of most of the samples was extracted from 15–30 mg of dry material, using a NucleoSpin Plant II Mini Kit (Macherey-Nagel, Düren, Germany) following the manufacturer's instructions. Final elutions were done in a total volume of 100 µL elution buffer. The internal transcribed spacer (ITS) was amplified with primers ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990). Polymerase chain reaction (PCR) protocols were following Dima *et al.* (2016) and Papp & Dima (2018). The successful PCR amplification was checked on a 1 % agarose gel stained with Ethidium bromide. Sanger sequencing was performed by LGC Genomics (Berlin, Germany) with the same primers used in the PCR amplification. Molecular study of some material was performed in the Norwegian Barcode of Life (NorBOL) or followed Alvarado *et al.* (2015). Chromatograms were checked and edited with the CodonCode Aligner package (CodonCode Corp., Centerville, Massachusetts, USA). Sequence comparison with public and own databases followed Noordeloos *et al.* (2017). Our dataset is composed of 117 nrDNA ITS sequences, carefully selected after an initial analysis using published and all our unpublished ITS sequences (data not shown). Newly generated sequences were submitted to GenBank. The dataset was aligned in MAFFT online v. 7 (http://mafft.cbrc.jp/alignment/server) choosing the E-INS-I strategy (Katoh & Standley 2013). The alignment was checked and edited in SeaView v. 5 (Gouy *et al.* 2021). Maximum Likelihood (ML) phylogenetic reconstruction was performed in PhyML v. 3.1 (Guindon *et al.* 2010) using the non-parametric, Shimodaira-Hasegawa version of the approximate likelihood-ratio test (SH-aLRT) (Anisimova *et al.* 2011) with the following settings: GTR+I+G model of evolution, gamma distribution of 10 rate categories and tree topology search as SPR. The resulting phylogenetic tree (Fig. 1) was edited in MEGA 7 (Kumar *et al.* 2016) and Adobe Illustrator CS4.

RESULTS

Phylogeny

We used a total of 115 *Entoloma* and two *Clitopilus* sequences (as outgroup) for our analysis. The ITS alignment comprises 915 characters including gaps. The resulting phylogenetic tree from the PhyML analysis is shown in Fig 1. All of the species described as new to science or typified in this study received high statistical support in our analysis. Altogether 19 ITS barcode sequences were newly generated for this study (Fig. 1).

Taxonomy

Entoloma cistocruentatum Vila, Noordel. & Dima, ***sp. nov.*** MycoBank MB 840817 Fig. 2A, D.

Etymology: The epithet refers to the morphological similarity with *Entoloma cruentatum* and the habitat under *Cistus*.

Basidiocarps collybioid. *Pileus* 15–20 mm diam, convex to plano-convex, flattened to somewhat depressed at centre, not umbonate; not hygrophanous, not translucently striate or only slightly at margin of younger specimens, very dark blue-black, barely fading when aging; entirely finely fibrillose to subsquamulose, especially with age. *Lamellae* unequal with few lamellulae, adnate, relatively distant, somewhat thick, pale greyish blue then with pink tinges; with a slightly paler, entire, or somewhat irregular, concolourous edge, particularly in immature specimens. *Stipe* 25–35 × 3–4 mm, cylindrical, often twisted, concolourous with pileus or paler, finely fibrillose to subsquamulose, especially towards the apex; with white tomentose base. *Context* pale grey blue. *Taste* and *smell* not noted. *Basidiospores* 8–9.6 × 5.9–6.9 µm, av. 9.0 × 6.4 µm; Q = 1.16–1.62, Qav = 1.4, heterodiametrical, (5–)6(–7)-angled in side view. *Basidia* 32–38 × 8.5–10 µm; 4-spored, almost cylindrical. *Lamella edge* fertile. *Cheilocystidia* absent. *Pileipellis* a cutis with transitions to a trichoderm, with elements 3.7–9 µm wide. *Subpellis* with broader cylindrical elements, up to 24 µm. *Pigment* blue, intracellular, abundant in pileipellis. *Clamp-connections* absent in all tissues.

Habitat and distribution: In Mediterranean vegetation with *Cistus salviifolius* and *C. monspeliensis*, on siliceous soils. Known only from Spain.

Typus: **Spain**, Catalonia, Selva, Tossa de Mar, Serra d'Aiguafina, alt. 80 m a.s.l., under *Cistus salviifolius* and *C. monspeliensis* on siliceous soil, 17 Dec. 2002, *X. Llimona*, *J. Vila* & *E. Ballesteros* (**holotype** L-0607521, **isotype** JVG 1021217-2) – ITS sequence, GenBank ON008482.

Notes: *Entoloma cistocruentatum* nests within the /Asprellum clade and is distinctive on account of its very dark blue-black basidiocarps, fibrillose-squamulose stipe, fertile lamella edge and relatively small spores. *Entoloma asprellum* is very different, usually with a brown, rarely blue, translucently striate pileus and much larger spores. *Entoloma chalybeum*, in the /Chalybeum clade, it can also have dark blue tones but is differentiated by its microscopy (spores, lamella edge) and habitat on grasslands and the recently described *E. caeruleopinophilum*, of the same clade, has less dark blue colours, striate pileus and larger spores. It also resembles of *E. cruentatum* and *E. pseudocruentatum* because of the blue tinged basidiocarps, small spores and fertile lamella edge. However, both these species are phylogenetically very distant and belong to different clades in subgenus *Cyanula* (Crous *et al.* 2021). *Entoloma cistocruentatum* is morphologically most easily distinguished from *E. cruentatum* and *E. pseudocruentatum* by the non-translucently striate pileus and Mediterranean habitat.

Entoloma dislocatum Vila, Dima & Noordel., ***sp. nov.*** MycoBank MB 840819 Fig. 2B, E.

Etymology: Named after its remarkable phylogenetic position in an essentially extra-European clade within *Cyanula*.

Basidiocarps collybioid. *Pileus* 10–40 mm diam, convex to conico-convex then applanate, sometimes depressed to umbilicate at the centre, not hygrophanous, not translucently striate or up

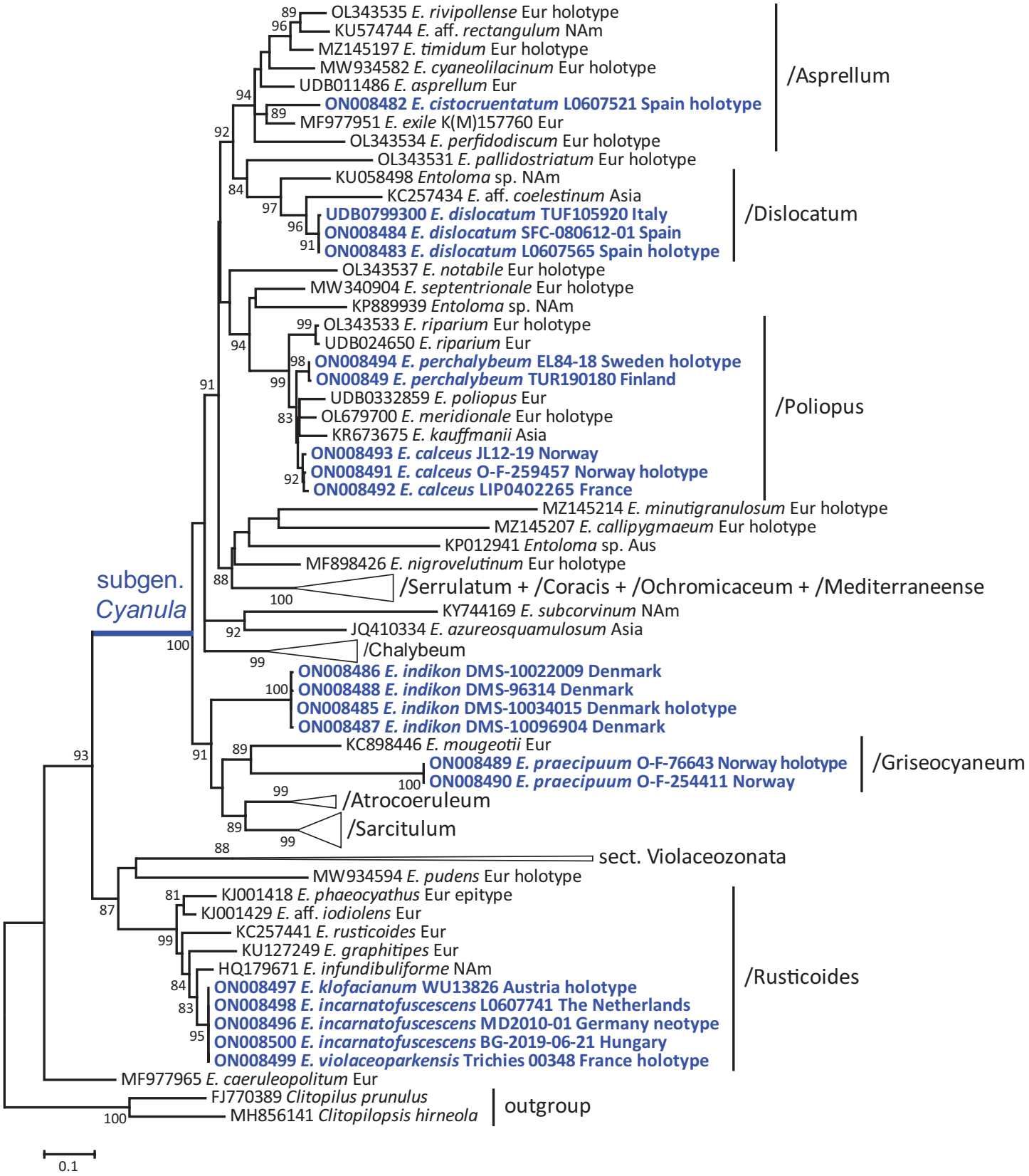

Fig. 1. Phylogenetic tree derived from Maximum Likelihood (PhyML) analysis based on nrITS1-5.8S-ITS2 data. ML bootstrap support (BS) values are shown at the nodes (BS > 80 %). Species treated in this study are marked with blue.

to half the radius in well hydrated specimens, vivid blue (Italian collection) to dark blue or blue grey, almost black at centre, paler, more grey-tinged in old specimens, especially at the margin, finely fibrillose-tomentose, more squamulose towards the centre. *Lamellae* adnate to subdecurrent, relatively distant and thick, sometimes ventricose, rarely anastomosing, white to pale grey then with pink tinges, rarely with blue tinges (Italian collection), with entire, concolourous edges, or sometimes with grey-blue tones in old specimens. *Stipe* 25–40(–60) × 3–4 mm, central, cylindrical, concolourous with pileus or paler, glabrous to slightly tomentose or with scattered fibrils, white tomentose at base. *Context* thin, pale greyish. *Taste* and *smell*

Fig. 2. A, D. *Entoloma cistocruentatum*, **A.** Habit *in situ*. **D.** Spores. **B, E.** *Entoloma dislocatum*. **B.** Habit *in situ*. **E.** Spores. **C, F, G.** *Entoloma indikon*. **C.** Habit *in situ*. **F.** Spores. **G.** Lamella edge. Scale bar = 10 µm. All figures from the respective holotypes.

indistinct. *Basidiospores* 8.2–10.7 × 5.7–7.6 µm, av. 9.5 × 6.6 µm, Q = 1.27–1.8, Qav = 1.46, heterodiametrical, 6–7(–8)-angled, rarely with a subnodulose aspect in side view. *Basidia* 27–35 × 12–14 µm, 4-spored, narrowly clavate. *Lamella edge* sterile to heterogeneous. *Cheilocystidia* 40–65 × 12–16 µm, subcylindrical to clavate, hyaline or with diffuse blue-grey intracellular pigment. *Pileipellis* a cutis of cylindrical hyphae, 10.5–16.5 µm wide, with transitions to a trichoderm at the centre and clavate terminal elements, up to 18 µm wide. *Pigment* grey to blue greyish, intracellular in pileipellis. *Clamp-connections* absent in all tissues.

Habitat and distribution: Terrestrial in deciduous mixed forest (*Fagus sylvatica*) on calcareous soil; in mixed deciduous forest

(*Castanea sativa*) on acid soil and in a forest of *Quercus ilex*, *Q. humilis* and *Pinus pinea*, under *Hedera helix* and *Rubus ulmifolius* on acid soil. Known from Spain and Italy.

Typus: **Spain**, Catalonia, Osona, Vidrà, near Collfred, alt. 1 340 m a.s.l., under *Fagus sylvatica*, on calcareous soil, 17 Sep. 2008, *J. Vila* & *X. Llimona* (**holotype** L-0607565, **isotype** JVG 1080917-4) – ITS sequence, GenBank ON008483.

Additional materials examined: **Italy**, Monti Sabatini, Bracciano-Martignano Regional Natural Park (Rome), alt. 530 m a.s.l., on the road through a *Castanea sativa* forest, 2 Nov. 2020, *A. Knijn* & *A. Ferretti*, TUF105920 – ITS sequence, UNITE UDB0799300. **Spain**, Catalonia, Vallès Oriental, Santa Maria de Martorelles Serra de Marina, alt. 360 m a.s.l., in a forest of *Quercus ilex*, *Q. humilis* and *Pinus pinea*, under *Hedera helix* and *Rubus ulmifolius* on acid soil, 12 Jun. 2008, *F. Caballero*, SFC 080612-01 – ITS sequence, GenBank ON008484.

Notes: At first sight, *Entoloma dislocatum* is similar to *E. chalybeum* with its dark blue, opaque pileus and stipe. However, the lamellae lack blue tinges, and the lamella edge is concolourous or vaguely tinged blue, whereas that of *E. chalybeum* is dark brown to bluish black. Also, the spores of *E. dislocatum* are distinctly smaller. And finally, the habitat in deciduous forest is different. Both *E. dislocatum* and the recently published *E. pallidostriatum* (Vila *et al.* 2021) do not belong to the /Chalybeum or /Poliopus clades, but take a rather isolated position in a small, but distinct clade with some poorly known extralimital species (Dima *et al.* in prep.). Knijn *et al*. (2021) described an unnamed blue *Cyanula* species from Italy, which corresponds with *E. dislocatum* after a comparison of the ITS sequences.

Entoloma indikon Kehlet, Noordel. & Dima, ***sp. nov.*** MycoBank MB 842932 Fig. 2C, F, G.

Etymology: ινδικών = dark blue, referring to the stipe colour. The name derives from the Greek word '*indikon*' which simply means 'from India' or indigo, a blue dye shipped from India to Europe.

Basidiocarps collybioid. *Pileus* 10–35 mm diam, campanulate to convex then plano-convex with acute or slightly flattened to truncate centre, with straight, later somewhat crenulate margin, medium to dark reddish brown with darker, blackish brown centre ("eye"), vaguely translucently striate when fresh, then distinctly and deeply translucently striate, minutely granulose all over at first, later covered with fine fibrillose patches, more or less glabrous towards margin. *Lamellae* L= about 36, l = 3–5, adnate-emarginate to deeply emarginate, ventricose, whitish or creamy-pink, then brownish pink, with slightly irregular, concolourous edge. *Stipe* 30–70 × 2–4 mm, cylindrical or gradually broadened towards base, rather pale blue to dark blue-violaceous all over, not glabrous but with scattered whitish longitudinal fibrils, base white tomentose. *Basidiospores* 8.5–10(–11) × 6.5–8.4 µm, av. 9.5–9.6 × 7.0–7.4 µm, Q = 1.1–1.45, Qav = 1.3–1.35, heterodiametrical to subisodiametrical, 5–6 angled in sideview with pronounced angles. *Basidia* 34–50 × 9.5–12.5 µm, 4-spored, clavate. *Lamella edge* heterogeneous to entirely sterile, made up of scattered or densely packed hyphae with tufts of subcylindrical to fusiform terminal elements, 6–15 µm wide, without or with pale blue, intracellular pigment. *Pileipellis* a cutis with transitions to a trichoderm, with clavate terminal elements, 100–140 × 20–50 µm. *Pigment* brown, intracellular. *Stipitipellis* a cutis of cylindrical hyphae, 4.5–12 µm, wide, with clusters of clavate to subcylindrical terminal elements ("caulocystidia"). *Clamp-connections* absent in all tissues.

Habitat and distribution: Terrestrial in damp humus under *Alnus* and *Frangula*. Only known from two localities in central Sjælland, Denmark, including the type locality, where it has been observed during several years.

Typus: **Denmark**, Sjælland, Lejre, Helvigstrup Skov, terrestrial in damp humus, with *Alnus glutinosa*, *Frangula alnus* and ferns in undergrowth, 14 Sep. 2019, *T. Kehlet* (**holotype** DMS-10034015, C) – ITS sequence, GenBank ON008485.

Additional materials examined: **Denmark**, Sjælland, Lejre, Helvigstrup Skov, 10 Sep. 2019, *T. Kehlet*, DMS-10022009 (C) – ITS sequence, GenBank ON008486; *ibid.*, 19 Sep. 2020, *T. Kehlet*, DMS-10096904 (C) – ITS sequence, GenBank ON008487; Sjælland, Strandskov, near Englerup, 12 Jun. 2010, *T. Læssøe*, DMS-96314 (C) – ITS sequence, GenBank ON008488.

Notes: *Entoloma indikon* is a sister species of *E. phaeodiscum* (Vila & Caballero 2007) from which it differs in colour of the pileus and stipe, the pileus often becoming deeply translucently striate, the more distinctly fibrillose stipe surface and the heterogeneous to sterile lamella edge. Both species share small, iso- to heterodimetrical spores and belong to the small /Phaeodiscum clade, sister to the /Griseocyaneum clade.

Entoloma praecipuum J.B. Jordal, Noordel. & Dima, ***sp. nov***. MycoBank: MB 842929 Fig. 3A–D.

Etymology: *praecipuus* (Lat.) = special, extraordinary.

Basidiocarps collybioid. *Pileus* 10–25 mm broad, campanulate to convex, expanding with age with umbilicate center and undulating margin, not distinctly hygrophanous, deeply translucently striate when moist, very dark sepia at centre, moderately dark brown on limb and paler brown at margin and between the striae, rather smooth when young, then innately fibrillose breaking up in scattered, irregular and relatively coarse squamules with age. *Lamellae* rather crowded, deeply emarginate, ventricose, initially pale grey then pale pink with coarsely serrate, concolourous edge. *Stipe* 50–70 × 2–5 mm, cylindrical, gradually broadened towards base, almost white, hyaline, covered in white, innate fibrils lengthwise, very brittle and easily splitting lengthwise. *Smell* and *taste* not known. *Basidiospores* 7.5–10(–10.5) × 5.0–7.0 µm, av. 8.5–10 × 5.5-6.0 µm, Q = 1.0–1.3, Qav = 1.1–1.15, subisodiamatrical to shortly heterodiametrical, mostly 5, rarely 6-angled in side-view, with fairly sharp angles. *Basidia* 20–27 × 7–10 µm, 4-spored, clampless. *Lamella edge* sterile with densely clustered, subcylindrical-flexuous cheilocystidia, septate, with terminal elements of 20–34 × 5–11 µm, without pigment. *Hymenophoral trama* regular, made up of cylindrical to inflated hyphae, 4–15 µm wide. *Pileipellis* a cutis to a trichoderm of cylindrical to inflated hyphae, 10–20 µm wide with clavate terminal elements, up to 25 µm wide. *Pigment* pale brown, intracellular in pileipellis. Brilliant granules scarce in trama of pileus and lamellae. *Stipitipellis* a cutis of narrow, cylindrical

Fig. 3. A–D. *Entoloma praecipuum*. **A.** Habit *in situ*. **B.** Spores. **C.** Lamella edge. **D.** Pileipellis (all from holotype). **E–H.** *Entoloma calceus.* **E, F.** Habit *in situ*. **G.** Spores. **H.** Lamella edge (E from PAM00092901, all other figures from holotype). Scale bar = 10 µm (spores); 20 µm (lamella edges); 40 µm (pileipellis).

hyphae, 4–11 µm wide, with a few loose terminal endings, especially at apex. *Clamp-connections* absent in all tissues.

Habitat and distribution: In semi-natural grasslands, rich in *Hygrocybe* and *Entoloma* species. So far only known from the type locality and a nearby locality, both in Norway.

Typus: **Norway**, Møre og Romsdal, Sunndal, Jordalsgrend, Jordalsøra, in semi-natural meadow, southern boreal zone, 30 Jul. 2020, *J.B. Jordal* (**holotype** O-F-76643; **isotype** L-0607467) – ITS sequence, GenBank ON008489.

Additional material examined: **Norway**, Møre og Romsdal, Sunndal, Jordalsgrend, Jordalsvøttu, in semi-natural meadow, southern boreal

zone, 28 Aug. 1994, *G. Gaarder & J.B. Jordal*, O-F-254411 – ITS sequence, GenBank ON008490.

Notes: *Entoloma precipuum* belongs to the /Griseocyaneum clade, where is takes a rather isolated position (data not shown). It differs from most species in this clade by the less distinctly squamulose, but rather innately fibrillose, translucently striate pileus, complete lack of blue tinges and the sterile lamella edge. *Entoloma kedrovense* from the Russian Far East (Noordeloos & Morozova 2008) is somewhat similar but has a squamulose pileus and larger spores.

Entoloma calceus Noordel., Bendiksen, Brandrud, P.-A. Moreau & Vila, ***sp. nov.*** MycoBank MB 842930 Fig. 3E–H.
Misapplied name: *Entoloma atromarginatum* (Romagn. & J. Favre) Zschiesch. *sensu* Moreau in Noordeloos, 2004: 1333 (photo).

Etymology: From Latin *calceus* = shoe, referring to the shape of the lake at the type-locality: "Skotjern", which means lake in shape of a shoe.

Basidiocarps collybioid. *Pileus* 10–25(–30) mm diam, conico-campanulate then hemispherical, with small but usually marked depression, sometimes truncate-conical to convex, initially not hygrophanous and hardly translucently striate, becoming translucently striate-grooved, entirely blackish-blue to deep violaceus blue at first, then fading to pale mouse-grey, sometimes however, retaining the blackish-blue colour at centre, finally discolouring whitish to pale pinkish with age. *Lamellae* about 35 reaching stipe, 1–2 series of lamellae, rather distant, ventricose almost free, remaining white for a relatively long time, then pale pink; edge serrulate, concolourous with sides or black especially towards margin of pileus. *Stipe* 60–80 × 1–2 mm, smooth, deep blue when young, later hyaline grey-blue, paler at apex, white towards base. *Context* very thin and brittle, deep bluish when young. *Smell* none. *Basidiospores* (10–)10.9–12.5(–14) × (7.5–)8–9.5 µm, av. 10.5–11.8 × 7.9–8.8 µm, Q = (1.2–)1.3–1.6, heterodiametrical, with 6–7 angles. *Basidia* 22–30 × 8.5–10.5 µm, cylindrical, mostly 4-spored (a few 2-spored, generating macrospores up to 13.8 × 9.6 µm), clampless. *Lamella edge* sterile of the serrulatum type, made of an alternance of clusters of cheilocystidia 7–15 µm broad, some septate, clavate to lageniform, some irregularly shaped almost tibiiform, issued from radially arranged hyphae, more abundant towards insertion of stipe, with or without dark brown intracellular pigment. *Hymenophoral trama* made of parallel, mostly slender hyphae 3.5–9 µm wide, cylindrical to inflate towards septa, smooth, pale, mixed with numerous vascular hyphae 5–6 µm wide, strongly branched and forming a reticulum. *Pileipellis* a cutis with transitions to a trichoderm of somewhat gelatinized cylindrical hyphae 3.5–5.5 µm wide, with clavate terminal elements, 10–25 µm wide. *Pigment* dark blue, intracellular in pileipellis. *Stipitipellis* a simple cutis without hairs or caulocystidia. *Stipititrama* with numerous lactiferous hyphae. *Clamp-connections* absent.

Habitat and distribution: Terrestrial, sphagnophilous, in mires, fens and peat-bogs in boreal-montane biomes, such as a swamp area in *Picea abies* forest, and in a few with *Carex rostrata.* Also found in pioneer vegetation in an inundated zone of hydropower plant. Known from Norway and France.

Typus: **Norway,** Oppland, Lunner, Skotjernfjellet og Snellingsrøysene Nature Reserve, in swamp *Picea abies* forest margin along small mire stripe (7 m broad, dominated by *Carex rostrata* in *Sphagnum* sp. (*cf. russowii*), 580 m a.s.l., 11 Aug. 2018, *E. Bendiksen & T.E. Brandrud*, TEB 051-18 (**holotype** O-F-259457) – ITS sequence, GenBank ON008491.

Additional material examined: **France**, Isère, Séchilienne, lac Luitel, floating peat bog, attached to *Sphagnum magellanicum*, 29 Sep. 2000, *P.-A. Moreau*, PAM00092901 (LIP 0402265) – ITS sequence, GenBank ON008492. **Norway**, Nordland, Hattfjelldal, Røsvassholmen, in *Picea abies* forest with short-grown and sparse vegetation in the water regulation zone, 22 Aug. 2019, *J. Lorås*, JL12-19 – ITS sequence, GenBank ON008493.

Notes: *Entoloma calceus* is an attractive species, with initially bright, deep violaceous blue pileus and stipe. The pileus, however, changes dramatically with age to mouse-grey and becomes slightly translucently striate. The lamella edge has a structure similar to that of *E. serrulatum* and can be pigmented or not. Our current studies in subgen. *Cyanula*, to be published in due course (Dima *et al.* in prep.) make clear, that a coloured lamella is not of great diagnostic value in *Cyanula*. The collection from France (PAM00092901) has a blackish-brown lamella edge contrasting with the pale colours of pileus and stipe and was accordingly identified as *E. atromarginatum* (Noordeloos 2004). This taxon, described from peat bogs in the French Jura (Romagnesi & Favre 1938), was described and illustrated as a pale brown species, which may resemble discoloured specimens of *E. calceus* (Fig. 3E). Our original identification of the French collections differed mainly by larger spores and persistent light blue colours; this pale colour could have escaped J. Favre's colour-blind eyes. Our observations of the lectotype (M.E. N.) confirm the spore dimensions provided by Romagnesi & Favre (12–15 × 7–9 µm); *E. calceus* has distinctly shorter spores, 10.5–11.8 × 7.9–8.8 µm. The lectotype of *R. atromarginatus* appeared unsuitable for the extraction of DNA and no modern collection strictly matching the protologue is known to us at this time.

Entoloma perchalybeum Noordel., J.B. Jordal & Dima, ***sp. nov.*** MycoBank MB 842931 Fig. 4.

Etymology: *per* (Lat.) = resembling, referring to the likeness with *E. chalybeum*.

Basidiocarps collybioid. *Pileus* 10–25 mm diam, hemispherical to convex, finally expanded, with blunt, subumbilicate centre, not hygrophanous, initially not translucently striate, but becoming deeply translucently striate to centre with age, very dark blackish blue and entirely tomentose at first, then paler between the striate and at margin, more purplish brown, with fine, dark blue, pointed squamules all over. *Lamellae* moderately distant, adnate, white with blue tinge, with entire, concolourous edge. *Stipe* 20–40 × 2–4 mm, cylindrical, dark blue like pileus, smooth, polished, base white tomentose. *Basidiospores* 9.0–12.5 × 6.4–9.2 µm; average 10.1–10.8 × 7.4–7.9 µm, Q = 1.2–1.5; Qav. = 1.20–1.37, heterodiametrical, with 6–7 rather blunt angles. *Basidia* 25–36 × 9.5–12.5 µm, subclavate, remarkably constricted, round base, 4-spored. *Lamella edge* sterile. *Cheilocystidia* 25–58 × 5.5–19 µm, cylindrical, subclavate, hyaline (type). *Hymenophoral trama* of cylindrical hyphae 3.5–15 µm wide. *Pileipellis* a cutis of cylindrical, inflated hyphae, 9–35 µm wide, terminal cells 30–50 × 12–16 µm, short clavate, brown intracellular pigment in ammonia. *Pigment*

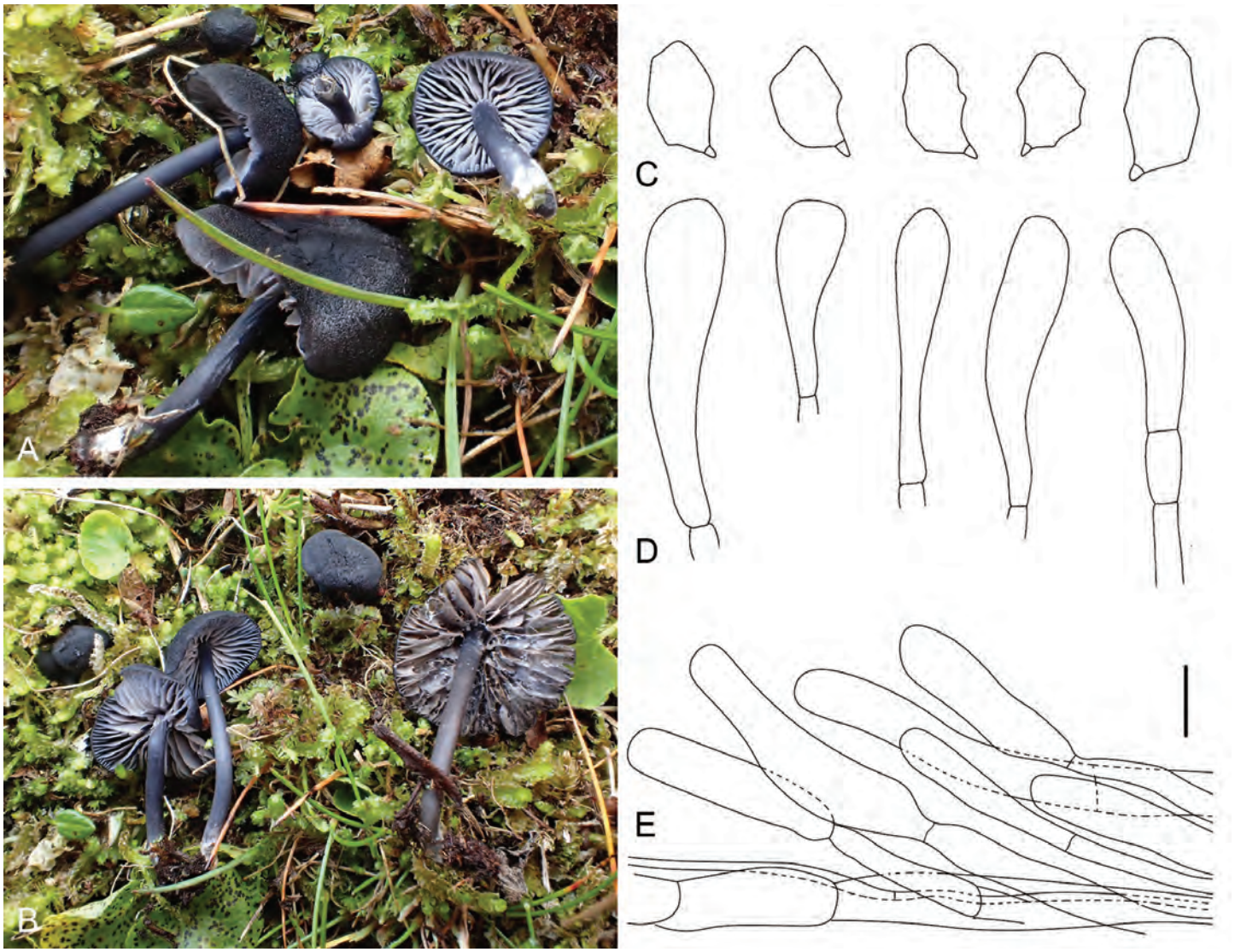

Fig. 4. *Entoloma perchalybeum*. **A, B.** Habit *in situ*. **C.** Spores. **D.** Cheilocystidia. **E.** Pileipellis (all from holotype). Scale bar = 10 µm (spores, cystidia); 20 µm (pileipellis).

brown grey, intracellular vacuolar and granular (in ammonia). *Stipitipellis* a cutis of cylindrical hyphae, 3.5–9 µm wide, pale brown intracellular pigment, hyaline, surface with some short terminal cells 25–40 × 11–17 µm. *Clamp-connections* absent in all tissues.

Habitat and distribution: Terrestrial in groups, calciphilous, in alpine heaths and boreal, damp mixed forest with *Picea abies*, *Pinus sylvestris*, *Betula* spp. and *Alnus incana*. Subarctic, found in Northern Fennoscandia only.

Typus: **Sweden**, Pite Lappmark, Arjeplog, west of Nuorta Krapesvarre, in rich alpine vegetation, low alpine zone, 12 Aug. 2018, *J.B. Jordal, E. Larsson & J. Vauras* (**holotype** GB-0209474, **isotype** L-0608235) – ITS sequence, GenBank ON008494.

Additional material examined: **Finland**, Regio kuusamoensis, Kuusamo, Valtavaara Nature Reserve, damp forest with *Picea abies*, *Pinus sylvestris*, *Betula* spp. and *Alnus incana*, 30 Aug. 2005, *J. Vauras*, TUR190180 – ITS sequence, GenBank ON008495.

Notes: *Entoloma perchalybeum* shares many characters with *E. chalybeum*, particularly when fresh on account of the very similar colour, non-translucently striate, squamulose pileus, polished stipe and blue tinge in the lamellae, but the pileus becomes quickly translucently striate when maturing (*cf. Entoloma lazulinum*). Both *E. chalybeum* and *E. lazulinum* usually have brown instead of blue lamella edges and furthermore are phylogenetically very distant (Dima *et al.* in prep.).

Neotypification and emendation of *Entoloma incarnatofuscescens*

Entoloma incarnatofuscescens (Britzelm.) Noordel., *Persoonia* **12**: 461. 1985. MB 104243 Fig. 5.
Basionym: *Agaricus incarnatofuscescens* Britzelm., *Ber. naturhist. Augsburg* **8**: 6. 1894.
Synonyms: *Leptonia incarnatofuscescens* (Britzelm.) Sacc., *Syll. Fung.* **11**: 47. 1895.
Entoloma klofacianum Noordel. *et al.*, *Öst. Z. Pilzk.* **4**: 128. 1995.
Entoloma violaceoparkensis Noordel. & Trichies, in Noordeloos, *Entoloma* s.l., Fungi Europaei vol. 5 (Saronno) 5a: 1120. 2004.
? *Rhodophyllus leptonipes* Kühner & Romagn., *Rev. Mycol.* (Paris) **19**: 6. 1954.

Emended description: *Basidiocarps* omphalioid. *Pileus* 5–25(–40) mm broad, campanulate or conical then convex or plano-

Fig. 5. *Entoloma incarnatofuscescens*. Habit, spores and pileipellis. **A, B** and **D.** Neotype. **C.** Holotype of *E. violaceoparkensis*. **E.** L-0607741. **F.** Holotype of *E. klofacianum*. Scale bars = 10 µm.

convex with involute then deflexed margin, usually with distinctly umbilicate centre to funnel-shaped, more rarely with slight depression or with small umbo, weakly to distinctly hygrophanous, when moist usually deeply translucently striate, rarely not, pinkish brown, yellowish brown to reddish brown, darker at centre and on striae, sometimes blue or violaceous-brown, slightly to distinctly pallescent on drying to greyish brown, minutely squamulose at centre, fibrillose towards margin or minutely tomentose-squamulose all over. *Lamellae* distant to moderately crowded, adnate or emarginate with decurrent tooth, then decurrent, triangular to segmentiform, sometimes veined on sides, pale grey or brown then pinkish brown, rarely with bluish tinge, with concolourous or slightly darker edge. *Stipe* 15–70 × 1–3 mm, cylindrical or compressed, often with bulbous base, dark to medium dark blue-grey, steel blue or violaceous-brown, smooth, glabrous, polished or with scattered longitudinal fibrils, white tomentose at base. *Context* brown in cortex of pileus, blue-grey in cortex of stipe, inner parts almost white. *Smell* none or

slightly farinaceous. *Basidiospores* 7.5–10.5(–11) × 6.0–8.5 µm, Q = 1.0–1.45(–1.6), Qav = 1.15–1.4, iso- to heterodiametrical, (4–) 5–7 angled in side view. *Basidia* 20–43 × 7–12 µm, clampless or rarely clamped. *Lamella edge* fertile. *Cystidia* absent. *Pileipellis* a trichoderm of strongly inflated clavate to spheropedunculate elements, up to 30 µm wide. *Pileitrama* regular, made up of strongly inflated hyphae, 4–20 µm wide. *Pigment* parietal, probably also pale intracellular in pileipellis; also rarely minutely encrusting in lower parts of pileipellis. Brilliant granules sparse. *Clamp-connections* absent or scarcely present.

Habitat and distribution: Terrestrial, saprotrophic, often on bare, preferably loamy, nutrient rich, damp soil in mixed forest, parks and gardens. Widespread and probably fairly common all over Europe.

Typus: **Germany**, Bayern, Kleinhartpenning, Hackensee, 16 Aug. 2010, *M. Dondl* (**neotype** MD 2010-01 (L), designated here) – MycoBank MBT 10005752, ITS sequence, GenBank ON008496.

Additional materials examined: **Austria**, Styria, Bad Gleichenberg, Kurpark (MTB 9161/1), 31 Aug. 1994, *W. Klofac*, WU 13826, holotype of *E. klofacianum* – ITS sequence, GenBank ON008497. **Germany**, Bayern, 86316 Friedberg, 12 Aug. 2019, *T. Laschner*, L-0607741 – ITS sequence, GenBank ON008498. **France**, Moselle, Moyeuvre-Petite, 8 Aug. 2002, *G. Trichies* 00348, holotype of *E. violaceoparkensis* (L-0607466) – ITS sequence, GenBank ON008499. **Hungary**, Mecsek Mts, Kárász, 21 Jun. 2019, *G. Benkő & K. Fábrics*, BG-2019-06-19 (ELTE) – ITS sequence, GenBank ON008500.

Notes: This tiny, omphalinoid species, which in its typical form is easy to recognise on morphological characters, is often taken for a species of *Cyanula* because of the steel-blue, polished stipe, appears to belong to the /Rusticoides clade, which is rather distantly related to *Cyanula*. It appears to be rather variable in colour. Besides the normally pinkish brown to yellow brown pileus, also variants with blue and violaceous tinges are now included in this species as became clear from the molecular genetic study of *E. violaceoparkensis* and *E. klofacianum*. The shape of the spores varies considerably from subisodiametrical to distinctly heterodiametrical, often within one basidiocarp and includes also the variant with predominantly 4–5 angled, subisodiametrical spores, described as *E. klofacianum*. Clamp-connections are usually not found but can be present in the hymenium or pileipellis. Intracellular pigment is dominant, but sometimes also slight incrustations are found in the lower part of the pileipellis and in pileitrama. *Rhodophyllus leptonipes* probably represents a later synonym, based on the morphology (Kühner & Romagnesi 1954), but the lectotype (PC) appeared unsuitable for DNA extraction to confirm it.

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Mammalian mycophagy: A global review of ecosystem interactions between mammals and fungi

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Abstract: The consumption of fungi by animals is a significant trophic interaction in most terrestrial ecosystems, yet the role mammals play in these associations has been incompletely studied. In this review, we compile 1 154 references published over the last 146 years and provide the first comprehensive global review of mammal species known to eat fungi (508 species in 15 orders). We review experimental studies that found viable fungal inoculum in the scats of at least 40 mammal species, including spores from at least 58 mycorrhizal fungal species that remained viable after ingestion by mammals. We provide a summary of mammal behaviours relating to the consumption of fungi, the nutritional importance of fungi for mammals, and the role of mammals in fungal spore dispersal. We also provide evidence to suggest that the morphological evolution of sequestrate fungal sporocarps (fruiting bodies) has likely been driven in part by the dispersal advantages provided by mammals. Finally, we demonstrate how these interconnected associations are widespread globally and have far-reaching ecological implications for mammals, fungi and associated plants in most terrestrial ecosystems.

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INTRODUCTION

Fungi have many different strategies for spore dispersal. The most widespread mechanism among macrofungi involves liberating spores into air currents via forcible discharge (ballistospory among *Basidiomycetes* and bursting of the asci among *Ascomycetes*) (Buller 1909, Money 1998, Trail 2007). Other fungi rely on mutualisms with organisms that ingest their sporocarps as a food reward for subsequent dispersal. The term "mycophagy" refers to the consumption of fungi by vertebrates and invertebrates. Animals consume many groups of fungi that form macroscopic sporocarps both above ground (epigeous, *e.g.* mushrooms, brackets or cups) and below ground (hypogeous, *e.g.* truffles). These animals often act as important vectors for the spread of fungal spores across landscapes. Mammals, reptiles and birds are significant fungal dispersers (Fogel & Trappe 1978, Claridge & May 1994, Maser *et al*. 2008, Elliott *et al.* 2019a, b, Caiafa *et al.* 2021), but specialised dispersal associations have been most thoroughly studied among invertebrates (Fogel 1975, Hammond & Lawrence 1989, Schigel 2012, Kitabayashi *et al.* 2022). For example, in one of its developmental stages, the entomopathogenic fungal genus *Massospora* alters the behaviour of male cicadas by using cathinone (an amphetamine) and psilocybin (a tryptamine) to cause males to simulate the behaviour of sexually receptive females (Boyce *et al.* 2018, Cooley *et al.* 2018). This chemical manipulation causes males to attempt copulation with the infected pseudo-female, leading to further transmission of fungal spores. There are numerous other examples of specialised invertebrate-fungal associations. The polypore *Cryptoporus volvatus* has a veil enclosing its fertile surface; a diversity of insects live between these layers and disperse spores by entering and exiting via a portal hole through the veil (Ingold 1953, Kadowaki 2010, Elliott 2020). Members of the *Phallaceae* (stinkhorns and relatives) release pungent aromas that attract spore dispersing flies (Tuno 1998), while some shelf fungi (*e.g. Cerrena unicolor*) have incredibly specialised associations with wood-boring *Hymenoptera* that disperse spores as oidial inoculum transmitted into the wood via the wasp's ovipositors (Ingold 1953, Bunyard 2015). Other fungi (*e.g. Guyanagaster necrorhizus* as well as some members of the *Leucocoprineae, Lepiotaceae*, *Mycosphaerella*, *Phaeosphaeria*, *Termitomyces* and *Tricholomataceae*) rely entirely on termites,

ants and snails for their dispersal (Chapela *et al.* 1994, Silliman & Newell 2003, Nobre *et al.* 2011, Koch & Aime 2018). In addition to the many specialised associations with invertebrates, fungi have also evolved a diversity of reproductive morphologies that are well adapted to mammalian dispersal. Although associations between fungi and vertebrates are not as specialised as those between fungi and invertebrates, many fungi consumed by mammals have evolved a sequestrate sporocarp morphology (spores are enclosed in a persistent skin called the pileus or peridium). This skin makes it difficult for the spores of sequestrate fungi to disperse without being eaten by animals. Sequestrate sporocarp morphologies include some epigeous fungi and a great diversity of hypogeous fungi (commonly referred to as truffles or truffle-like fungi) that have independently arisen in multiple fungal linages and have evolved more than 100 times (Bonito *et al.* 2013, Sheedy *et al*. 2015, Truong *et al.* 2017, Elliott & Trappe 2018, Elliott *et al.* 2020a, Palfner *et al.* 2020). While there is some debate about what evolutionary factors may have driven the rise of sequestrate morphologies (Sheedy *et al*. 2015), the high diversification of sequestrate species in many fungal groups may reflect the dispersal advantages of mycophagy and the major role that mammals played in the process (Trappe 1988, Trappe & Claridge 2005, Maser *et al.* 2008, Trappe *et al.* 2009, Beever & Lebel 2014).

Fungi with sequestrate sporocarp structures have numerous reproductive benefits, including substantial protection from extreme climatic conditions (temperature and humidity) and a reduced likelihood of being eaten by mammals before spores are mature (Maser *et al.* 2008, Beever & Lebel 2014). These factors have likely contributed to the loss of forcible discharge among sequestrate taxa and encouraged the transition away from producing a stalk (which is usually not composed of spore-bearing tissue). The loss of these traits allows sporocarps to optimise spore production in a larger percentage of reproductive tissue. On the other hand, trade-offs include susceptibility to saturated soil (*e.g.* rotting in place) and the reliance on other organisms to disperse spores. To remedy this, many sequestrate fungi have developed strategies to increase the probability of discovery by animals, such as the production of aromatic attractants (Maser *et al.* 2008). The mammals that excavate and consume hypogeous fungi will subsequently disperse spores through their faeces. Soil disturbance (bioturbation) from digging for hypogeous fungi increases fungal dispersal within the soil and improves soil aeration and organic matter decomposition (Fleming *et al.* 2014, Davies *et al.* 2018, Palmer *et al.* 2020).

Sequestrate fungi are predominantly ectomycorrhizal (ECM), so their successful dispersal is key to plant nutrition, regeneration and survival in many forest systems (Tedersoo *et al.* 2010). In exchange for a carbon source, these fungi form beneficial associations with the roots of their hosts and are vital to plant nutrient uptake and water movement (Allen 1991, 2007 Agerer 2001, Peay *et al.* 2008, Tedersoo & Smith 2013). In the rhizosphere, continuous mycelia of multiple ECM fungal species form a "mycorrhizal network" linking plants of the same or different species; within the network, fungal and plant species interact, compete and provide positive/negative feedbacks that can affect both plant and fungal communities (Gorzelak *et al.* 2015). Disruptions of mycorrhizal networks (*e.g.* through impacts on biodiversity that result in the loss of mammal dispersers) can therefore negatively affect regeneration of ECM plant species and forest resilience after disturbance (Dundas *et al.* 2018, Liang *et al.* 2020).

Previous work on animal-fungal interactions has provided in-depth study and/or reviews on the ecological impacts and importance of fungal consumption by birds (Elliott *et al.* 2019a, Caiafa *et al.* 2021), reptiles (Elliott *et al.* 2019b) and invertebrates (Fogel 1975, Hammond & Lawrence 1989, Schigel 2012). Given these previous works, we chose to focus this review on the associations between fungi and their mammal consumers and how these interactions are beneficial to fungal dispersal, mammal nutrition, host plant communities and overall ecosystem health. As highlighted below, these dispersal modes and their interconnected associations are widespread yet remain incompletely studied in comparison to other fields, such as pollination and seed dispersal ecology. Reproductive success often depends on interconnections between organisms, and these associations can range from specialist to generalist (Wheelwright & Orians 1982, Richardson *et al.* 2000, Schiestl 2004, Schupp *et al.* 2010). Ecosystem processes are complex and multifaceted, and there are inevitably multiple evolutionary factors – aridification in particular – that have contributed to the rise of sequestrate sporocarp morphologies. Considering the dispersal advantages facilitated by vertebrate vectors through the consumption of fungi, we argue that mammalian mycophagy has likely been a major contributing factor to the rise of a wide range of sequestrate sporocarp morphologies.

MATERIAL AND METHODS

This review is part of a series examining the associations between macrofungi and vertebrates; the two previous reviews examined interactions between fungi and birds (Elliott *et al.* 2019a) and between fungi and reptiles (Elliott *et al.* 2019b). In this study, we carefully reviewed references of relevant publications and conducted methodical searches in relevant journals, databases and search engines for publications detailing the behaviours and diets of hundreds of mammal species. We concentrated our search effort on dietary studies based on known behaviours of mammal species, including a focus on terrestrial rather than oceanic mammal groups. For practical reasons, we restricted our literature search to publications written in English, French, German, Portuguese and Spanish. Sources written in a few other languages were included when we were able to determine the mammal species reported to eat fungi, but we did not systematically review the literature beyond these five languages. We incorporated many of the references cited in the review of small mammal mycophagy by Fogel & Trappe (1978), but we could not locate all of the literature they cite. In total, we compiled 1 154 references published over the last 146 years (Fig. 1) reporting fungal consumption by 508 mammal species belonging to 15 orders (Fig. 2).

The number of publications on mammalian mycophagy is substantially greater than that on birds and reptiles combined. To make this review as comprehensive as possible in regard to the mammal species that eat fungi, we omitted imprecise notes (*e.g.* those that mention a "squirrel" or a "mouse" eating a mushroom) when we could not determine which mammal species was being discussed. Some publications (*e.g.* Berkeley & Broome 1887, Reess & Fisch 1887, Chatin 1892, Thaxter 1922, Zeller 1939, Dowding 1959, Hilton 1980) used general names like bandicoot, potoroo, shrew, mole, rock rabbit, dormouse, mouse, pine squirrel, jerboa, field mouse, chipmunk, wood rat,

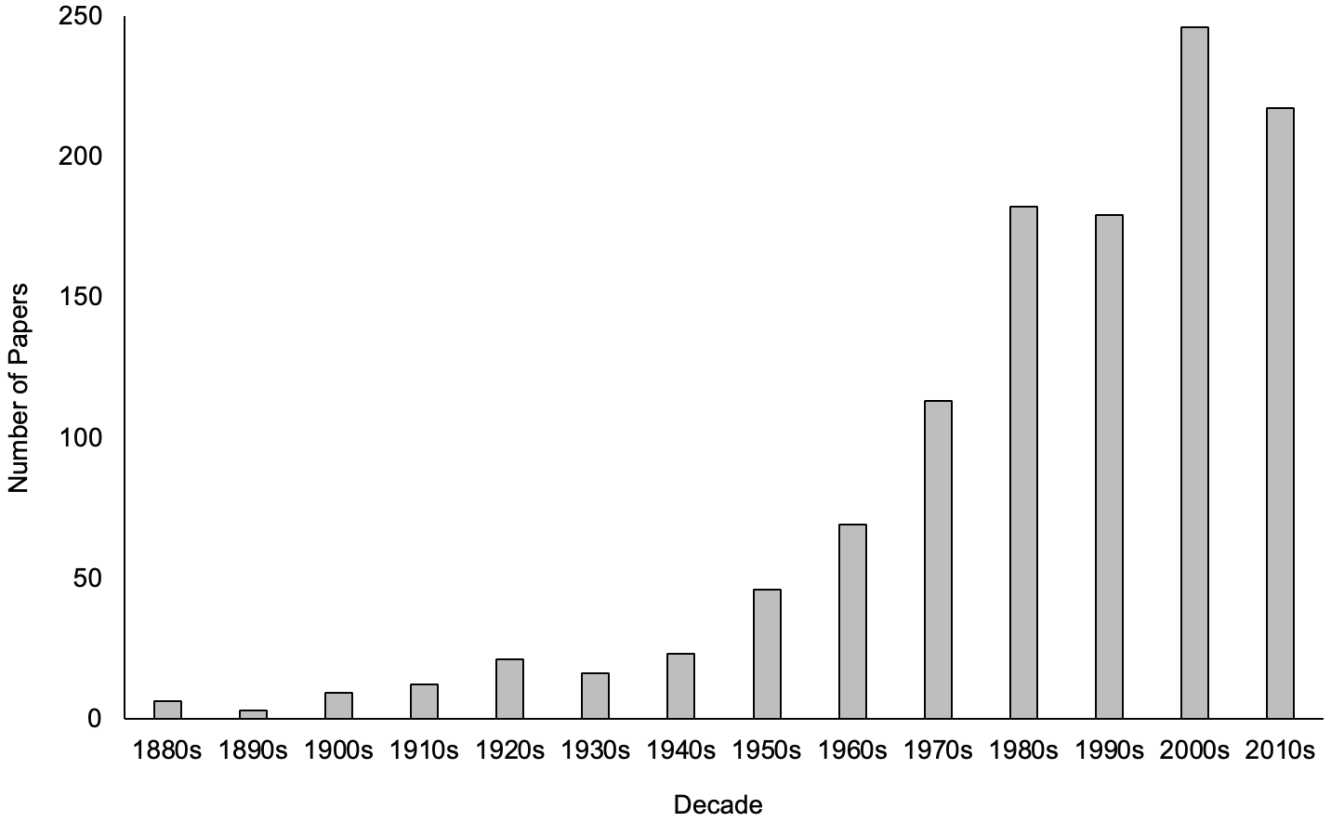

Fig. 1. Illustration of the number of publications reporting mammal mycophagy published each decade between 1880 and 2020.

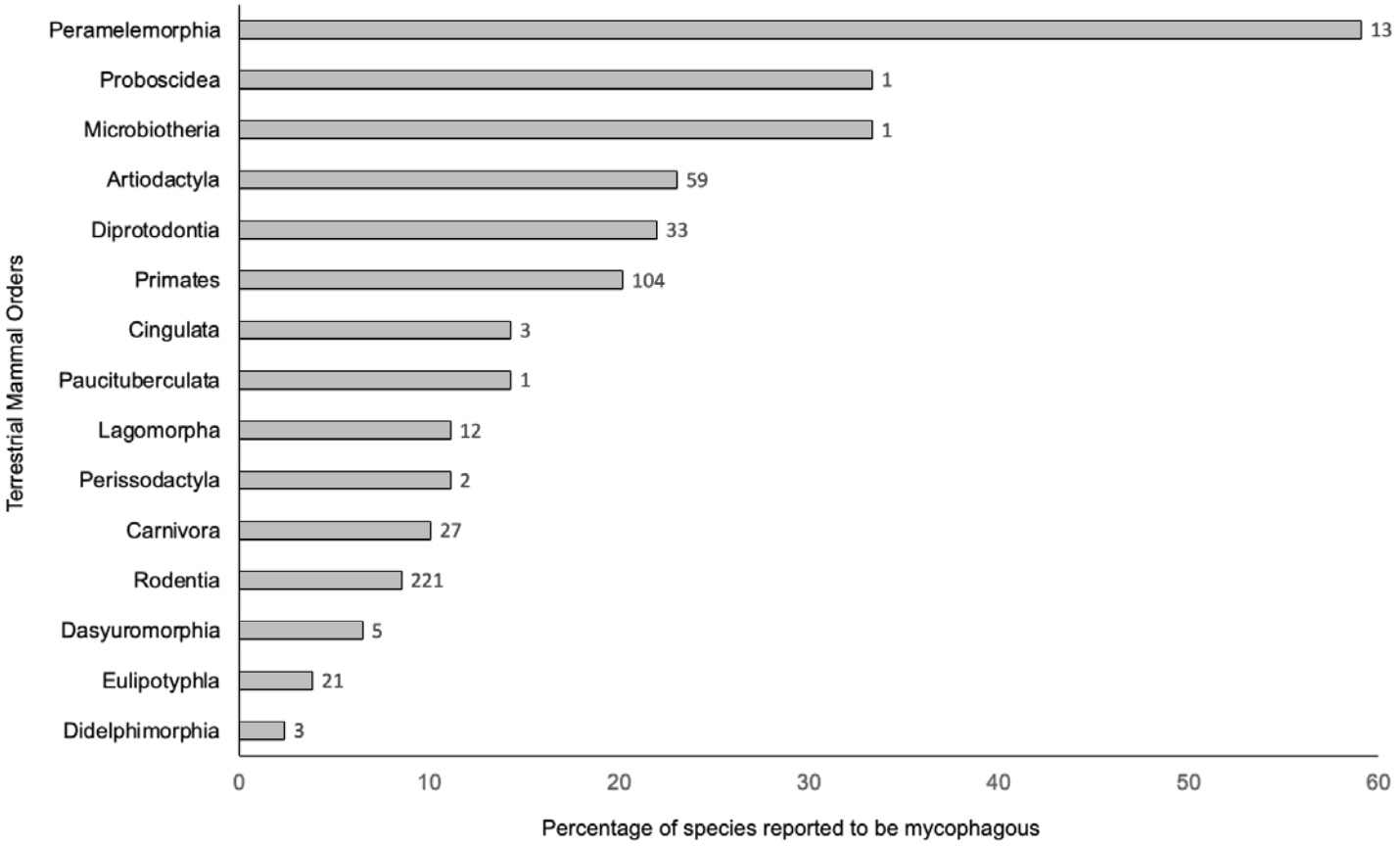

Fig. 2. Percentage of extant members of each order that has been reported to consume fungi. Numbers at end of graph bars indicate number of extant mycophagous species we found reported in the literature. Number of species in each order is based on Hamilton & Leslie (2021). Note that this figure only includes extant species. Two species that appear in the tables are not included in this graph and those are American mastodon (*Mammut americanum*) and neanderthal (*Homo neanderthalensis*).

deer and game animal. In these instances, we did our best to determine what mammal species the authors were referring to, but we sometimes disregarded reports due to lack of taxonomic clarity about the mammal species involved. Groups such as mice or squirrels are among the most thoroughly documented mycophagous mammals, so no value was lost by discarding imprecise species reports.

Where necessary, we updated names from their original citation to reflect current nomenclature. The taxonomy and common names of mammals included in this review follow the nomenclature of Wilson & Mittermeier (2009, 2011, 2014), Mittermeier *et al.* (2013), Jackson & Groves (2015), and Wilson *et al.* (2016, 2017, 2018, 2019). Total number of mammal species in each order is based on Hamilton & Leslie (2021). Rates of mycophagy may differ among subspecies, but we did not consider subspecies due to the large number of mammal species covered. In many instances, there was not enough information for us to determine which subspecies was involved and its taxonomic validity. Researchers interested in these particular issues can easily refer to the primary references provided under cited species in Supplementary Tables S1–S11.

Some mammalogists incorrectly assume that fungi are eaten mostly by rodents or other small mammals. This misconception led us to focus this review on the diversity of mammals that eat fungi rather than the diversity of fungal taxa eaten. Although some studies identify what fungi are eaten, most only mention "fungi" or "mushrooms" in the mammal diet. Terms used in cited references range from formal species names to general terms like toadstool, shelf mushroom, bracket fungus, truffle and puffball. When authors did provide identification, it was rarely possible to determine how accurately they had identified the fungal species; thus, it was not realistic for us to verify fungal identifications. We have not included lichens or myxomycetes in this review. We discarded the information from Maser *et al.* (1988) because they listed spores of three ECM truffle genera that were consumed by a range of mammals, but the habitats they sampled did not contain ECM host plants that are likely to associate with these fungi. Apart from this case, we have no reason to believe that the fungi and mammals reported were inaccurately identified. Researchers interested specifically in the diversity of fungal taxa eaten by mammals can consult the following reviews as starting points: Fogel & Trappe (1978), Claridge & May (1994), Claridge *et al.* (1996), Piattoni *et al.* (2016), and Nuske *et al.* (2017a, b). We also compiled a list of fungal species that are consumed and whose spores remain viable after passage through the gut of mammals (Table 2).

Our review does not include literature related to animal poisoning as a result of eating fungi. Although there is a substantial body of work in veterinary literature related to pet poisoning (*e.g.* Cleland 1934, Cole 1993, Naude & Berry 1997, Puschner *et al.* 2007, Beug & Shaw 2009, Bates *et al.* 2014, Möttönen *et al.* 2014, Bates 2016 and Seljetun 2017), this area of research has little relevance to mycophagy in wild animals. The behaviour and food choices of captive individuals does not necessarily represent their wild relatives, and we are unaware of any evidence of poisoning cases among wild individuals.

RESULTS

Diversity of mammal mycophagists by order

The following section provides tables listing a brief overview of the mammal groups that contain the 508 species reported to eat fungi. For anyone interested in the full lists and references for mammal mycophagy compiled by this review please also refer to the data provided in Supplementary Tables S1–11. Because we have updated the nomenclature to current taxonomy, names we list are not necessarily the same as in the cited references. This section is broken into subsections organised phylogenetically by mammalian order. Each of the 15 orders reported to eat fungi is briefly introduced. Any order containing three or more mycophagous species has a supplementary table where families, genera and species are organised alphabetically.

Mycophagy has been studied in great detail for some orders (*e.g.* rodents), whereas studies of other orders are limited. Likewise, some mammal species are included in numerous reports describing their roles as mycophagists and spore dispersal vectors, whereas other species have seldom or never been studied to determine whether or not they consume fungi. It is important to note that the number of cited references does not necessarily reflect the level of fungal consumption for a given species. There are undoubtedly many seldom studied species not on these lists that frequently eat fungi, and some of those may rely on fungi for a higher percentage of their diet than do the species for which we cite dozens of references. Some groups of terrestrial mammals with highly specialised diets, such as ant or termite feeding specialists (*e.g.* the families *Tachyglossidae*, *Myrmecobiidae*, *Manidae* and *Myrmecophagidae*), likely never deliberately consume fungi. It is also possible that some mammals – including species of cats (*Felidae*) – lack the ability to produce chitinases (Cornelius *et al.* 1975) that allow them to digest fungi, and this may lead to their avoidance of fungi as food. More studies are needed to understand the link between mammalian biosynthesis of chitinases and mycophagy.

In order to distinguish how important fungi are for mammal consumption, Claridge & Trappe (2005) proposed four categories of mammal mycophagists: obligate, preferential, casual or accidental. In the context of this review, we aimed to compile a comprehensive list of all mammal species that have ever been reported to utilise fungi as food. Unfortunately, the level of mycophagy of the vast majority of the 508 listed species has not been sufficiently studied for us to accurately classify most species we list within one of these four categories. With continued research, we hope it will become possible to classify more mammals within these categories; but in the context of this review, we use only the taxonomic categories listed below.

Marsupials

Didelphimorphia

The opossums are a relatively small order of marsupials native to the Americas. The diets of many members of the group are poorly studied, but we found reports of fungi in the diets of three species all within the family *Didelphidae* (Supplementary Table S1). Based on our review, we show that approximately 2.4 % of the extant members of this order have been shown to eat fungi (Fig 2).

Paucituberculata
The shrew-opossums of South America have been relatively poorly studied. To date, only the long-nosed shrew-opossum (*Rhyncholestes raphanurus*) has been reported to eat fungi (Meserve *et al.* 1988). Based on our review, we show that approximately 14.3 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Microbiotheria
The Monito del Monte (*Dromiciops gliroides*) is one of three species in the order *Microbiotheria*. It is found in southern South America and has been reported to eat small amounts of fungi (Meserve *et al.* 1988). Based on our review, we show that at least a third of the extant members of this order have been shown to eat fungi (Fig. 2).

Dasyuromorphia
These carnivorous marsupials are endemic to Australia, New Guinea and several neighbouring islands and include animals such as: antechinus, dunnarts, the kowari, mulgaras, quolls and the Tasmanian devil. They are primarily carnivores or insectivores, but we found reports of fungi in the diets of five species in the family *Dasyuridae* (Supplementary Table S2, Fig 3D). Based on our review, we show that approximately 6.5 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Peramelemorphia
The bandicoots and bilbies are endemic to Australia, New Guinea, and several surrounding islands. Although many of the New Guinean species remain poorly studied, most species in this order that have been studied have been shown to eat fungi. Some species that were once thought to have large geographic distributions have also been recently shown to be distinct species. We found reports of fungi in the diets of 13 species in three families (Supplementary Table S3). Based on our review, we show that approximately 59 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Diprotodontia
The diprotodont marsupials are the largest and most diverse group of marsupial mammals and include koala, wombats, possums, gliders and macropods (the latter includes all kangaroos, wallabies, potoroos, bettongs, rat-kangaroos and their relatives). They are native only to Australia, New Guinea and several surrounding islands. This group has a diversity of dietary specialisations, and some members of the order rely heavily on fungi for large portions of their diet. We found reports of fungi in the diets of 33 species in eight families (Supplementary Table S4, Fig. 3C). Based on our review, we show that approximately 22 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Placental Mammals

Cingulata
Armadillos are a relatively small order of placental mammals and are native to the Americas. There has been limited research on the overall importance of fungi in armadillo diets, but we found reports of fungi in the diets of three species in two families (Supplementary Table S5). Based on our review, we show that approximately 14.3 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Proboscidea
The elephants comprise only three extant species that are restricted to Africa and southern Asia. The members of this group are primarily herbivores, with fungi playing only a very limited role in their diets. We only found mention of trace amounts of fungi in the diets of the living African Elephant (*Loxodonta africana*) (Paugy *et al.* 2004) and the extinct American Mastodon (*Mammut americanum*) that once occurred in North America (Newsom & Mihlbachler 2006). Given the size of both animals and the fungi that were reported, it is hard to definitively know if this represents deliberate mycophagy or incidental consumption of spores. But in this instance and until further studies are conducted on elephants, we are considering mycophagy to be any evidence of fungi in the diet. Based on our review, we show that approximately a third of the extant members of this order have been shown to eat fungi (Fig. 2).

Primates
Primates are a widely distributed and diverse group of placental mammals. If humans (*Homo sapiens*) are included, they can be found in virtually every habitat on Earth and are one of the most adaptable and successful species of mammals. Over the past hundred years, waste management systems used by many modern humans have changed our role as spore dispersers, but undoubtedly hardly more than 100 years ago, almost all humans that ingested fungi were playing a role in the dispersal of fungal spores. Although it has been shown that early humans and neanderthals (*H. neanderthalensis*) consumed fungi as food, their role as spore dispersers has not been as thoroughly studied as that of some other hominids (see Supplementary Table S6). Excluding all the plant pathogens and diseases that humans have accidentally spread, modern humans deliberately transport and cultivate numerous mycorrhizal and saprotrophic fungi as well as their associated plant species (Stamets 1993, Cotter 2014, Zambonelli *et al.* 2015, Guerin-Laguette *et al.* 2020). Modern humans have been documented to harvest more than 2 100 edible mushroom species both for personal use and commercial sale (Li *et al.* 2021), which is more species than has been documented by any other mammal in this review. In the process of picking, cleaning, carrying and sometimes shipping sporocarps, spores are inevitably being dispersed. There are obviously numerous ways - both positive and negative - that humans contribute to spore dispersal, and given that there have been hundreds of papers and books published about ethnomycology, this topic warrants a review of its own and is beyond the scope of this study. In Supplementary Table S6 we only cite a selection of papers that we think are most relevant to fungi consumption by humans, but it is important to note that this is the only mammal species that we have deliberately left incomplete.

There have been two previous reviews specifically relating to primate mycophagy. We encourage readers who are particularly interested in primate mycophagy to also refer to the earlier reviews by Hanson *et al.* (2003) and Sawada (2014). For our study, we found reports of fungi in the diets of 105 primate species in 13 families (Supplementary Table S6, Fig. 3B). This is more species than has been previously compiled. Hanson *et al.* (2003) reported just over 20 species, and Sawada (2014) showed nearly 60 species. Despite the diversity of primate species that consume fungi, they are frequently overlooked in primate dietary studies or are lumped in with plants, “other” or unidentified; this is the case even in major reviews on primate

Fig. 3. A selection of mycophagous mammals with fungal fruiting bodies. **A.** Mount Graham red squirrel with a partially dried fungus in its mouth on Mount Graham in Arizona, USA. **B.** In northwestern Cambodia, a Germain's langur holds a mushroom that it is eating. **C.** A northern bettong eats an unidentified truffle in northern Queensland, Australia. **D.** A brown Antechinus pauses near the fruiting body of a sequestrate species of *Descolea* (lower right corner of image) in eastern New South Wales, Australia. Image A © Eirini Pajak. Image B © Brenda de Groot. Image C © Stephanie Todd. Image D © Stephen Mahony.

nutrition and diets (*e.g.* Lambert & Rothman 2015). Unlike the majority of references, we cite that have reported mycophagy in other orders of mammals, almost all papers cited in this section are based on observational studies. There is much merit in observational methods to improve understanding of the biology and behaviour of mammals; but as has been shown with ornithological studies (Elliott *et al.* 2019a), using these methods in isolation makes it exceedingly easy to overlook, misidentify or underestimate the importance of the fungal components of diets. We suspect that if primate researchers employed the typical scat analysis methods commonly used in groups that are harder to observe, a far greater diversity of primates would be shown to utilise fungi for food and likely at a higher rate than is currently estimated among some species. Based on our review, we show that approximately 20.2 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Lagomorpha

The hares, rabbits and pikas are a relatively small group of widely distributed placental mammals. They primarily eat plant material, but we found reports of fungi in the diets of 12 species in three families (Supplementary Table S7). Based on our review, we show that approximately 11.1 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Rodentia

The rodents are a highly diverse and widespread order of placental mammals with native members found in most regions except the coldest portions of the Arctic and Antarctic and some islands (*e.g.* New Zealand). The members of this order are arguably some of the most important dispersers of fungal spores, and for some species, fungi represent large portions of their diet. We found reports of fungi in the diets of 221 species in 14 families (Supplementary Table S8, Fig. 3A). Based on our review, we show that approximately 8.5 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Eulipotyphla

The *Eulipotyphla* are a diverse order of widely distributed placental mammals that includes hedgehogs, moonrats, shrews, moles and solenodons. They are often considered to be primarily insectivorous, but we found reports of fungi in the diets of 21 species in three families (Supplementary Table S9). Based on our review, we show that approximately 3.9 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Carnivora

The carnivores are widely distributed, and while many members of this order are primarily carnivorous, a wide diversity of species augment their diet with many other food types. We found reports of fungi in the diets of 27 species in nine families (Supplementary Table S10). Based on our review, we show that approximately 10.1 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Perissodactyla

The odd-toed ungulates of the order *Perissodactyla* are a relatively small order of placental mammals that are mostly grazers; the order includes horses, asses, zebras, rhinos and tapirs. Though they show little reliance on fungi, we found reports of fungi in the diets of the horse (*Equus caballus*) (Hastings & Mottram 1915, Cleland 1934) and the mountain tapir (*Tapirus pinchaque*) (Downer 1996, 2003). Other than these two species, we found no indication of fungi consumption by this order. Based on our review, we show that approximately 11.1 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Artiodactyla

The even-toed ungulates are a diverse and widespread group of placental mammals (*e.g.* cattle, sheep, deer, pigs, giraffes, camels and llamas). Most species in this group are relatively large-bodied, so fungi often do not comprise a bulk of their diet; however, fungi do appear to be nutritionally important to them. We found reports of fungi in the diets of 59 species in seven families (Supplementary Table S11). Based on our review, we show that approximately 23 % of the extant members of this order have been shown to eat fungi (Fig. 2).

DISCUSSION

Feeding on fungi

Feeding preferences between fungal taxa, morphologies and portions of sporocarps

Several factors likely contribute to fungal food choices and species selection. It is possible that toxicity may be a factor in species selection, but there is very limited data on fungal toxins in relation to wild mammals. Sawada *et al.* (2014) studied fungal species preference in relation to their toxicity among Japanese macaques (*Macaca fuscata*) and found that this species of primate eats a diversity of fungi. They suggested that individuals use different methods to avoid poisonous mushrooms, including previous knowledge and on-site assessment of taste (but not smell). The macaques generally ate fungi without examining them; but when they were hesitant and tasted the sporocarps before eating, Sawada *et al.* (2014) determined the fungus was more likely to be a toxic species. Since almost all knowledge of fungal toxicity is in relation to humans and a few species of mammalian pets, it is difficult to determine the toxicity of fungi for specific mammal species. For the most part, what – if any – role fungal toxins play in food selection is still unknown.

Mammals are likely to prefer nutritionally rich fungal taxa that produce easily detectable aromas or colours. In response to these selection pressures, some fungi may produce chemicals and/or compounds to make certain parts of their sporocarps desirable. Even though mycophagy may have contributed to the success of certain fungal groups and sporocarp morphologies, there has been limited research that directly investigates the selection pressure from mammal food choices on fungal reproductive patterns and morphologies. Herbivores often selectively feed on certain species or parts of plants, sometimes preferentially selecting the tender new growth (Wilsey 1996, Pérez-Harguindeguy *et al.* 2003), and we suspect that preferential feeding strategies likely occur in fungi as well. There is evidence of different nutritional value within the sporocarps of some fungi. The chemical composition and nutritional value of desert truffles in the genera *Terfezia* and *Tirmania* vary between taxa and the different layers of sporocarps, depending upon whether or not the peridium (outer skin) of these truffles was removed or left on the exterior (Hussain & Al-Ruqaie 1999). Grönwall & Pehrson (1984) also found variation in nutritional value between

the peridium and spores of the sequestrate ECM species *Elaphomyces granulatus*, while Vogt *et al.* (1981) detected differences in nutrient concentrations between mycorrhizal and decomposer fungal species.

Among the numerous members of the family *Russulaceae* that are important foods for mammals, some species/genera produce latex (including the genera *Arcangeliella*, *Lactarius*, *Lactifluus*, *Multifurca* and *Zelleromyces*), while members of the closely related genus *Russula* do not. The latex is produced in laticiferous hyphae, and in some species these hyphae also serve to store precursors of pungent dialdehydes (Camazine & Lupo 1984). The chemistry of the latex varies between species, and this may impact animal consumption. For example, the latex produced by *Lactarius volemus* contains polyisoprene, which is also found in rubber (Ohya *et al.* 1998) and appears to deter invertebrates from feeding. Therefore, invertebrates are less likely to feed on the latex-producing genus *Lactarius* than the closely related *Russula* species that do not produce latex (Taskirawati & Tuno 2016). Latex is most abundant in young sporocarps and deterred slugs in experimental feeding studies; once the sporocarp aged, latex production slowed or stopped and slugs ate *Lactarius* and *Russula* species at similar rates (Taskirawati & Tuno 2016). There may also be a finite number of latex-producing hyphae within each sporocarp, and as the sporocarp expands, it becomes more dispersed/diluted for the feeding animal. It is therefore possible that latex protects young sporocarps from being consumed by animals before spore maturation, at which point latex production is reduced and the sporocarps of lactating members of the family *Russulaceae* become more desirable to invertebrates. Latex production in fungi is restricted to a relatively small number of genera, so its impact on food preferences has limited relevance across the entire fungal kingdom. Nevertheless, we suspect a similar negative correlation between small mammal mycophagy and latex production.

Among many groups of animals, evidence suggests that the hymenium (spore-bearing surface) is preferentially selected for food instead of other portions of the sporocarp. Vogilino (1895) and Buller (1909) first suggested that gastropods preferentially eat gills/reproductive surfaces before other structures, an observation that we also made in slugs and other invertebrates (Fig. 4). Due to their large nature and faster movements (at least compared to slugs), mammals' feeding preferences are more difficult to observe. However, a few studies suggest that mammals also show a preference toward different portions of fungal sporocarps. For example, brown lemurs (*Eulemur* spp.) seem to preferentially eat the cap while discarding other parts of mushrooms (Overdorff 1993), and Humboldt's flying squirrels (*Glaucomys oregonensis*) preferentially feed on the reproductive tissues of epigeous fungi (Thysell *et al.* 1997). The volcano deermouse (*Neotomodon alstoni*) and the North American deermouse (*Peromyscus maniculatus*) are both known to eat entire fungal sporocarps but have a preference for the hymenium (Castillo-Guevara *et al.* 2012). Walton (1903) noted that North American red squirrels (*Tamiasciurus hudsonicus*) regularly ate the gills of mushrooms and rejected the rest of the sporocarp. Using camera trapping, Elliott & Vernes (2021a) showed that several species of Australian vertebrates (both mammals and birds) fed on *Amanita* mushrooms, with a preference for the caps of sporocarps. We observed that many small mammals (especially rodents) preferentially eat the hymenium before other portions of the fungal sporocarp (Fig. 5A–F), but larger mammals (*e.g.* deer) often ingest any parts they can find (Fig. 5G–H).

As outlined in the Introduction, sequestrate fungi have sporocarps with reproductive tissues enclosed within one or more layers of skin. In many cases, they are also hypogeous (*i.e.* sporulating below ground). It is not known when and where the first sequestrate fungi appeared, but estimates suggest that the first Australian sequestrate taxa emerged 34–13 million years ago during the Oligocene and Miocene, while many Australian mycophagous mammals appeared around 16 million years ago (Sheedy *et al*. 2015). In sequestrate basidiomycete species, the energy used for producing sporocarps with a stalk and cap can be relocated toward producing more sporocarps and/or spores; for cup fungi relatives (*Ascomycota*), the increased layering and folding of the hymenium increases the volume of spore-bearing tissue. Among these morphologies, spore dispersal relies heavily on animal consumption instead of air currents or water. Therefore, sequestrate sporulating morphologies likely evolved in partial response to feeding preferences toward different parts of the sporocarp. There are inevitably multiple factors that have contributed to the rise of sequestrate sporulating habits, *e.g.* as a response to major climatic changes such as aridification (Sheedy *et al*. 2016). Some groups, such as the *Mesophelliaceae*, predate the rise of mycophagy specialist mammals and may therefore have initially formed associations with early invertebrates or more generalist feeders (Sheedy *et al*. 2016).

Among sequestrate species with fleshy (non-powdery) sporocarps, the entire sporocarp is generally consumed; but in groups such as the genus *Elaphomyces* and the family *Mesophelliaceae*, powdery spores appear to be the least desirable portion (Figs 6, 7). Many small animals favour the exterior of *Elaphomyces* sporocarps by selectively eating the peridium (Fig. 6). Research on North American red squirrels by Vernes *et al.* (2014) showed that when *Elaphomyces* truffles are unearthed, the squirrel cleans the outer peridium by "shucking" adherent soil and mycelium from the truffle before it is eaten or cached (see Supplementary Video S1). Members of the family *Mesophelliaceae* differ in having a thin and non-nutritious outer layer surrounding a nutritious central core, with spores packed in between the two (Fig. 7). Animals typically peel the outer layer and focus on eating the central core; this is especially the case after fire when *Mesophelliaceae* truffles can become more fragrant and are often more easily discovered by foraging mammals (Trappe *et al.* 1996, Maser *et al*. 2008). Vernes (2000) noted that the discarded outer peridia and spore-bearing mass of *Mesophellia clelandi* littered the ground around bettong digs on burnt ground, but this was never recorded on unburnt ground. Spores of both *Elaphomyces* and *Mesophelliaceae* are common in faecal pellets of a broad range of mammals, and both groups are partly reliant on animals for their dispersal. Even though the spore-producing portions of sporocarps are not necessarily targeted, mammals inevitably ingest spores in the process and spill spores onto their fur. The leftovers of sporocarps are often left exposed on the ground or a log (Figs 6, 7), from where they can be carried away by wind or water.

Caching and hoarding of fungi

A diversity of mammal species cache and hoard foods to varying degrees (Vander Wall 1990). These behaviours have been arguably best studied among rodents, particularly in squirrels that bury nuts and/or cache cones. Fungal caching behaviours have been most frequently noted among North American red squirrels, but similar behaviours occur in rodents from other

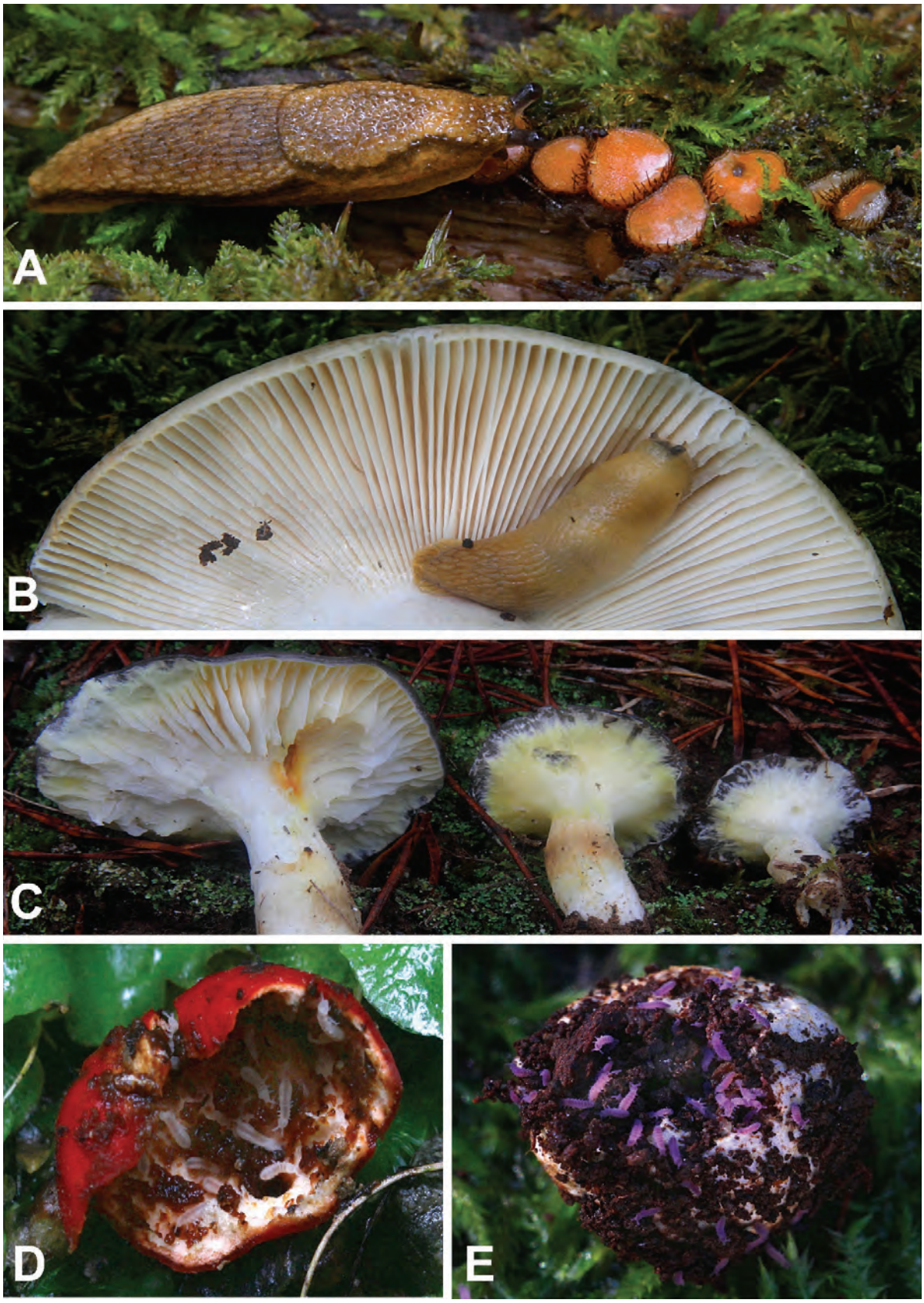

Fig. 4. Invertebrates display dietary preferences toward the reproductive portions of fungal fruiting bodies. **A.** *Arion subfuscus* feeds on the hymenium of several eyelash cups (*Scutellinia scutellata*) in Rusk County, Wisconsin, USA. Note the light-coloured sections of the fertile surface where the slug has eaten the reproductive tissues but not the rest of the fruiting body. **B.** An *Arion* sp. eats the gills on a *Russula* sp. in the Tucker County, West Virginia, USA. **C.** The gills of three *Hygrophorus hypothejus* fruiting bodies have succumbed to the feeding activities of a gastropod in Rutherford County, North Carolina, USA. The upper surfaces of the caps of these three fruiting bodies had been left untouched. **D.** Springtails hollowed out and ate the entirety of the spore-containing surfaces of the sequestrate fungus *Leratiomyces erythrocephalus* near Wellington, New Zealand. Note the visible brown line down the middle of the springtails that shows evidence of their digestive tracts filled with spores. **E.** The hollowed out skin of a sequestrate *Descolea* sp. that has had spores eaten by a lilac-coloured *Brachystomella* sp. in Barrington Tops National Park, New South Wales, Australia. Images © Todd F. Elliott.

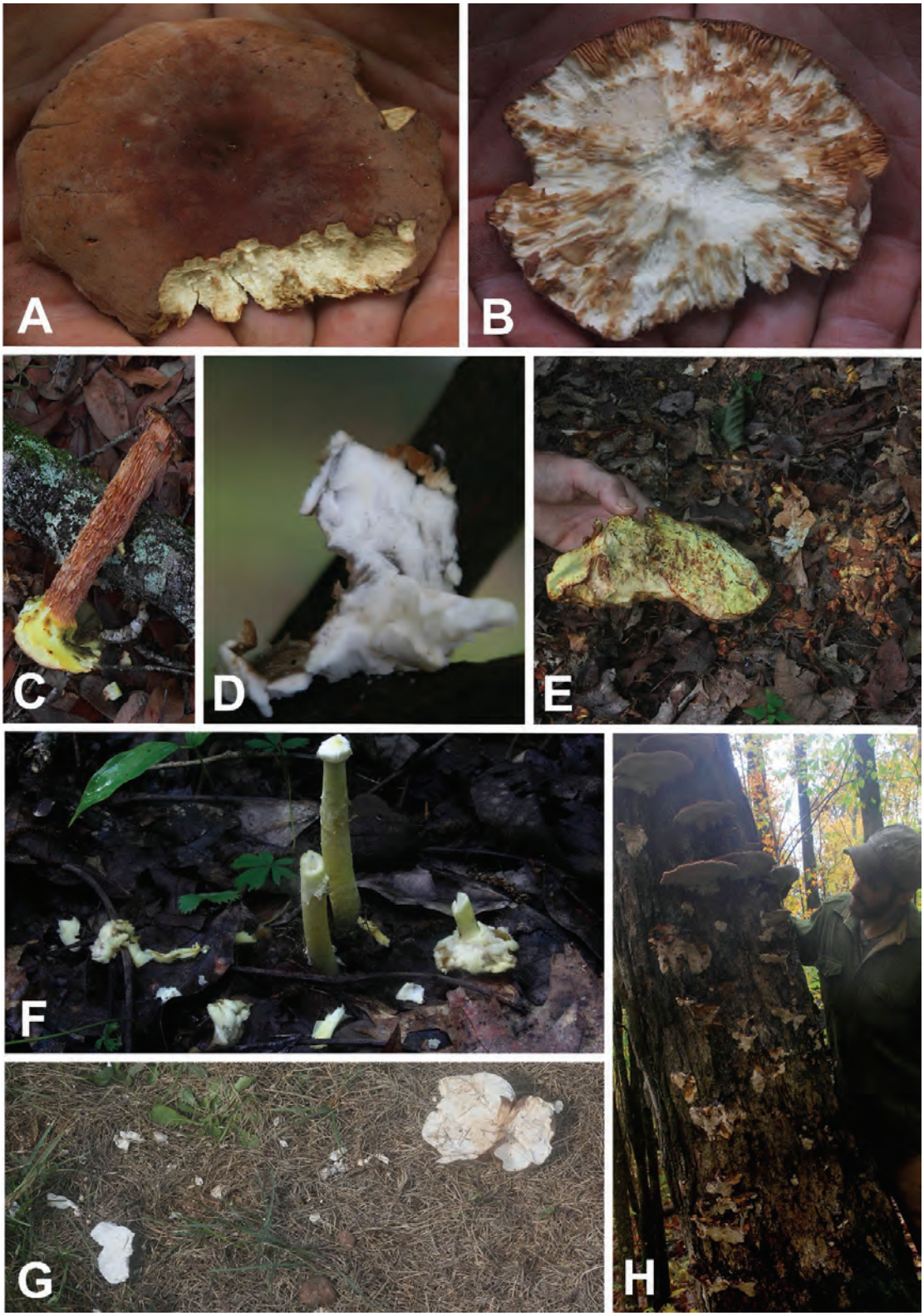

Fig. 5. Examples showing how mammalian mycophagists often selectively feed on the reproductive tissues of fruiting bodies. **A.** The upper surface of a *Lactarius corrugis* fruiting body from Buncombe County, North Carolina, USA. Note there is a little evidence of feeding on the margin of the cap. **B.** The same fruiting body as previous image but almost all of the gills have been removed by a feeding rodent. **C.** The remnants of a *Boletellus russellii* fruiting body left on a stick by a feeding rodent (likely a squirrel) Broward County, Florida, USA. The stem was virtually untouched, but all of the reproductive tissues and part of the cap were removed before the fruiting body was discarded. **D.** A *Russula* fruiting body with all of the gills removed by a feeding rodent in Randolph County, West Virginia, USA. Only part of the stem and a very thin section of the upper portion of the fruiting body remained. **E.** An unidentified bolete fruiting body ravaged by a feeding rodent in Tucker County, West Virginia. Most of the sterile portion of the cap remained, and the stem and other sterile portions were left in a chewed pile (visible in the right corner of the image). The rodent appeared to have ingested every bit of the pore surface. **F.** Stems and part of the cap surface of one fruiting body is all that remains of these two *Amanita jacksonii* fruiting bodies in Rutherford County, North Carolina. **G.** Immature *Calvatia craniiformis* fruiting bodies eaten before spore maturity by white-tailed deer in York County, Pennsylvania, USA. **H.** Entire *Ischnoderma resinosum* fruiting bodies eaten up to the maximum browse height of a white-tailed deer in Rusk County, Wisconsin, USA. Images © Todd F. Elliott.

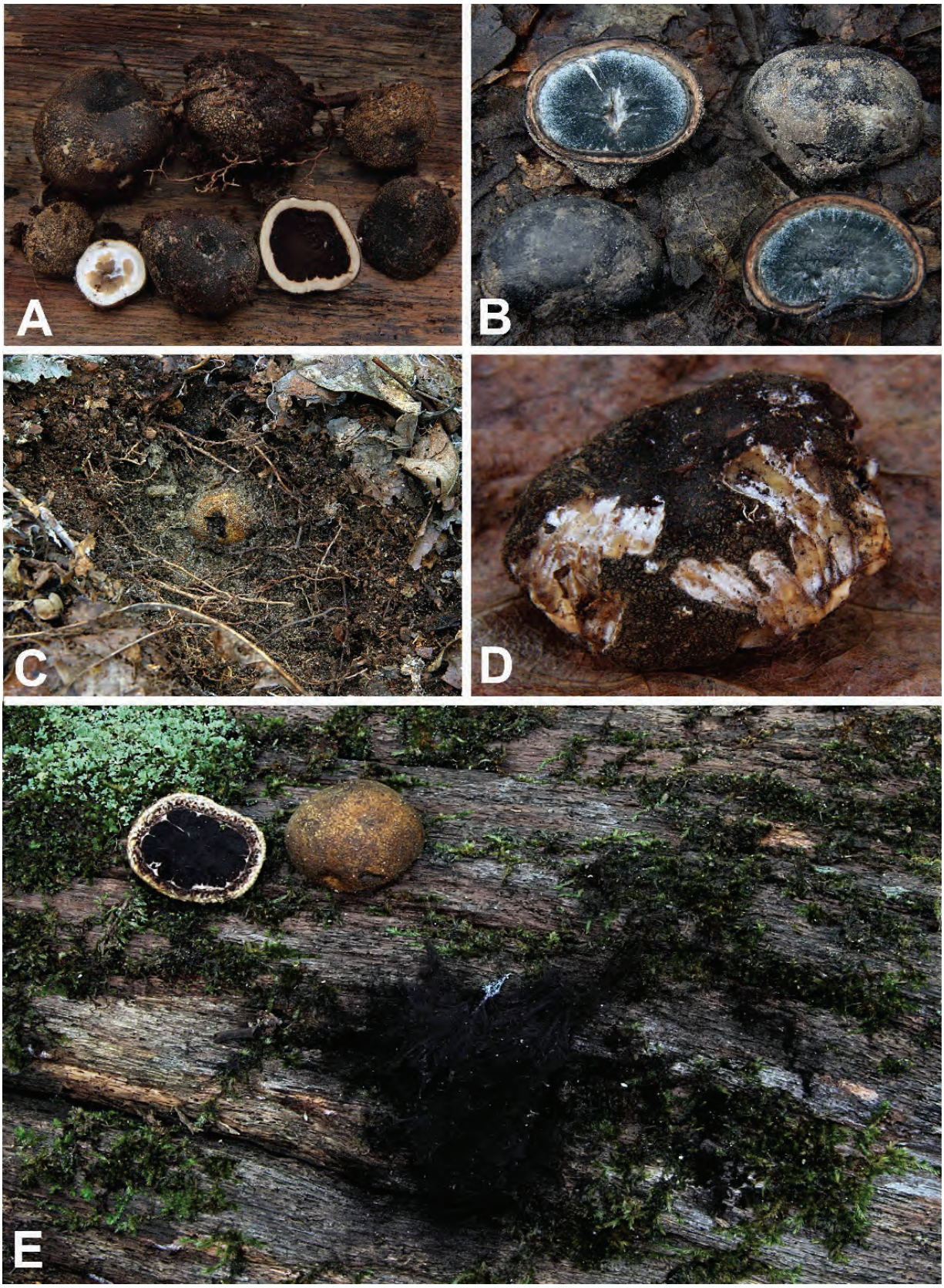

Fig. 6. The widely distributed sequestrate genus *Elaphomyces* is an important food source for mammals wherever it has been studied. **A.** The eastern North American endemic *E. macrosporus* and many other members of this genus have thick outer peridial layers that are sought out by mammals. **B.** *Elaphomyces favosus*, a tropical African species eaten by mammals that also illustrates the thick outer layers. **C.** An unidentified *Elaphomyces* sp. from Rutherford Coungy, North Carolina, USA that has been partially excavated by the foraging activities of a small mammal. Note the dark spot where several small bites have been taken. **D.** A single *Elaphomyces* fruiting body from Transylvania County, North Carolina that was excavated and partially eaten by a small rodent. Note the teeth marks on much of the peridium. **E.** While truffle hunting in Rutherford County, North Carolina, the first author encountered an area filled with extensive animal digs; a nearby log had this pile of powdery black *Elaphomyces* spores placed on top. Truffle raking near the digs uncovered this fruiting body of *E. americanum*, and microscopic examination revealed that the black spores left piled on the log matched those of the collected fruiting body. A chipmunk or squirrel was likely responsible for this tailings pile. Images © Todd F. Elliott.

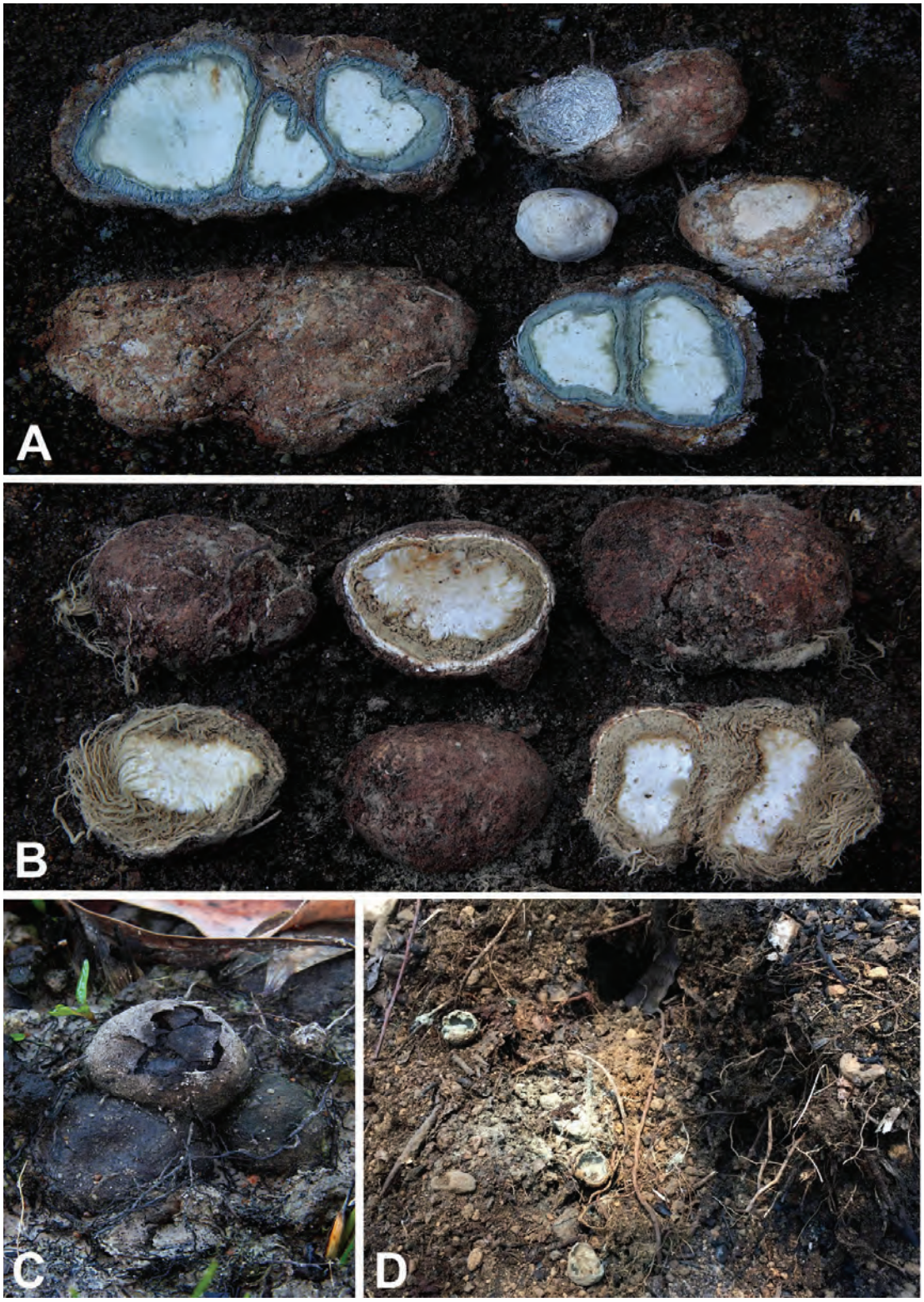

Fig. 7. Examples of members of the fire-adapted mycorrhizal family *Mesophelliaceae*. Widespread in *Eucalyptus* forests across Australia and an important food source for a diversity of mammals. **A.** *Mesophellia* (Reidsdale, New South Wales, Australia) fruiting bodies are often located deeper in the soil than other groups of sequestrate fungi and often grow in nearly confluent clusters. Note that the exterior of the fruiting body incorporates soil and mycorrhizal roots. The next layer is filled with powdery, greenish grey spores, and the central white core is the desired food of foraging mammals. **B.** *Andebbia pachythrix* (Braidwood, New South Wales), shares similar fruiting morphology and requires mammals to peel the exterior before they can eat the core. **C.** Three exposed fruiting bodies of a member of the *Mesophelliaceae* that were burned in a fire (Victoria, Australia). These fruiting bodies were close to the surface and exposed to excessive heat, which likely caused them to be overlooked by mammals foraging post fire. Fruiting bodies that are located deeper in the soil and are exposed to fire often produce a highly pungent aroma reminiscent of rotting onions. **D.** In the aftermath of the intense 2019/2020 Bee's Nest Fire near Dundurrabin, New South Wales, the first author was extinguishing a burning log and found the skins and spores of these three *Mesophellia* fruiting bodies in the tailings pile of a small mammal excavation approximately 20 m away from what was still burning. The mammal responsible for the tailings pile had successfully extracted the core and left behind the skin and spores. Due to the recent fire, there was little other food within several kilometers of this site, which highlights the importance of this family of fungi as post-fire food for Australian mammals. Images © Todd F. Elliott.

regions of the world that experience cold winters or other environmental/climatic factors that can lead to seasonal food shortages. Though their fungal caching behaviours have been far less thoroughly studied than nut/seed dispersal, rodents likely perform ecosystem functions that are of similar importance.

Early naturalists frequently wrote with amusement about the labours and physical feats of small squirrels as they built their fungal caches and struggled to haul large fungal sporocarps into the canopy to dry them for winter. Merriam (1884: 214) noted the following about a North American red squirrel:

> *"From his liking for mushrooms some would consider him an epicure, but in whatever light we regard this taste, it is a droll spectacle to see him drag a large 'toadstool' to one of his storehouses. If the 'umbrella' happens to catch on some stick or log and is broken from the stem, as is frequently the case, he is pretty sure to scold and sputter for a while, and then take the pieces separately to their destination".*

Most squirrels that have been studied were observed to dry fungal sporocarps on branches and later hide these in caches (Fig. 8). In some areas, squirrels dry so many mushrooms in tree branches that it has been described to look like a decorated Christmas tree (Odell 1925, Murie 1927). Some authors have reported only the drying behaviour, but given that squirrels are typically secretive about their caches, it is easy to overlook where they may have stored the dried mushrooms. It is also possible that in some regions or among some squirrel species, mushrooms are left in their original drying sites; however, further studies are needed to confirm this. Buller (1917, 1922) reported that North American red squirrels store dried sporocarps in hollow trees, crow nests, woodpecker nests and even boxes in old houses. Laursen *et al.* (2003) noted that in Alaska, northern flying squirrels and North American red squirrels hollowed out witches' brooms that were produced by spruce broom rust or yellow witches' broom rust (*Chrysomyxa arcotostaphyli*); the squirrels then used these cavities to raise their young and cache dried mycorrhizal fungi (both epigeous and hypogeous species). Jung *et al.* (2010) noted that North American red squirrels also used witches' brooms as nests, lining them with American bison (*Bison bison*) hair and storing dried fungi for the winter. Vernes & Poirier (2007) noted that a North American red squirrel filled a robin nest with more than 50 dried sporocarps from the hypogeous genus *Elaphomyces* (Fig. 8C). Caches made by North American red squirrels can often be quite large. Buller (1922) examined a box found in an abandoned house that was used as a North American red squirrel cache, and he reported it to weigh nearly 0.5 kg and contain 116 fungal sporocarps; another cache contained up to 300 sporocarps. Hardy (1949) studied a large North American red squirrel cache in a hollow tree containing 59 fungal specimens. He was able to identify at least 13 fungal species, most of which were ECM taxa; the most numerous species (30 specimens) was the sequestrate fungus *Hymenogaster tener*.

Kato (1985) noted that the Japanese squirrel (*Sciurus lis*) cached walnuts and pinecones in trees and underground, while fungi were only cached in trees. He also reported that underground food was eaten mainly in the spring. Foods stored below ground are naturally harder for thieves to find, but squirrels struggle to access them under deep snow. It is therefore usually important for squirrels to also cache food in elevated locations; however, Lampio (1967) reported that in Finland, Eurasian red squirrels (*Sciurus vulgaris*) dug cached fungi from under the snow. The amount of fungi and other foods cached likely correlates with climate and food availability in winter and inevitably varies between regions, habitats and species. Buller (1922) suggested that Great Britain's winters might be too wet for rodents to store fungi, and this may explain the higher frequency of reports on caching behaviours from the colder and drier parts of North America and Eurasia. In Scotland, for example, the Eurasian red squirrel was estimated to cache a minimum of 42 sporocarps across its home range (Lurz & South 1998); this is a much lower number than what has been generally reported among squirrel species in northern North America (Buller 1917, 1922, Dice 1921, Murie 1927, Hatt 1929, Hardy 1949, Smith 1965, 1968a). On the other hand, caches of Eurasian red squirrels in northern Finland have been estimated to contain approximately 440 stored fungi per hectare and possibly as many as 1 800 sporocarps per individual (Sulkava & Nyholm 1987). These studies show that caching rates vary both within the same species of squirrel from different latitudes and between squirrel species across the Northern Hemisphere, and may correlate with the length of winter, snow cover and other climatic conditions.

Fungi typically require air drying and subsequent storage in very dry caches (Fig. 8), while other foods preserve better in varying weather conditions. Despite the wide array of foods eaten by the North American red squirrel, their fungal caches typically do not contain other food items (Hardy 1949). Quality of drying and storage locations for fungi appear to be important to squirrels. Experimental studies suggest that most mushrooms stored in caches for a long period of time tend to lose nutritional value, particularly with exposure to freezing and thawing cycles (Frank 2009). This nutritional degradation may explain why squirrels are typically very diligent in making sure that stored fungi are dry, saving the driest and best insulated storage sites for fungi and/or to build their nests. Dice (1921) described a North American red squirrel nest on a shelf in an old Alaskan cabin where, by October, the squirrel had collected a large number of fungi. He reported that every open can was packed with dried mushrooms, while sporocarps that were not fully dry were spread out on the shelves. Hendricks & Hendricks (2015) observed that North American red squirrels in Montana preferred to dry/cache mushrooms on dead branches, possibly because they have better airflow.

Learning to dry a mushroom and cache it in an appropriate location for long-term storage is a relatively complex skill that squirrels progressively acquire with practice. Smith (1968a) observed that young North American red squirrels began to attempt this activity as early as three days out of the nest. He reported that in the first 10 days out of the nest, three young squirrels dropped 12 of the 32 fungi they attempted to hang on branches. They only dropped 10 out of 70 by their third week, while their mother only dropped three out of the 165 fungi that she hung to dry.

The full diversity of mammals that cache fungi is poorly known. As discussed earlier, most studies have focused on North American red squirrels, the Eurasian red squirrel and the Japanese squirrel, while there are few reports of other rodents caching fungi. Two studies reported the Siberian chipmunk (*Tamias sibiricus*) and the Uinta chipmunk (*T. umbrinus*) to cache fungi (Ognev 1966, Bergstrom 1986), but we were unable to find any additional information about other chipmunk species caching fungi. Most researchers who have studied the nests and behaviour

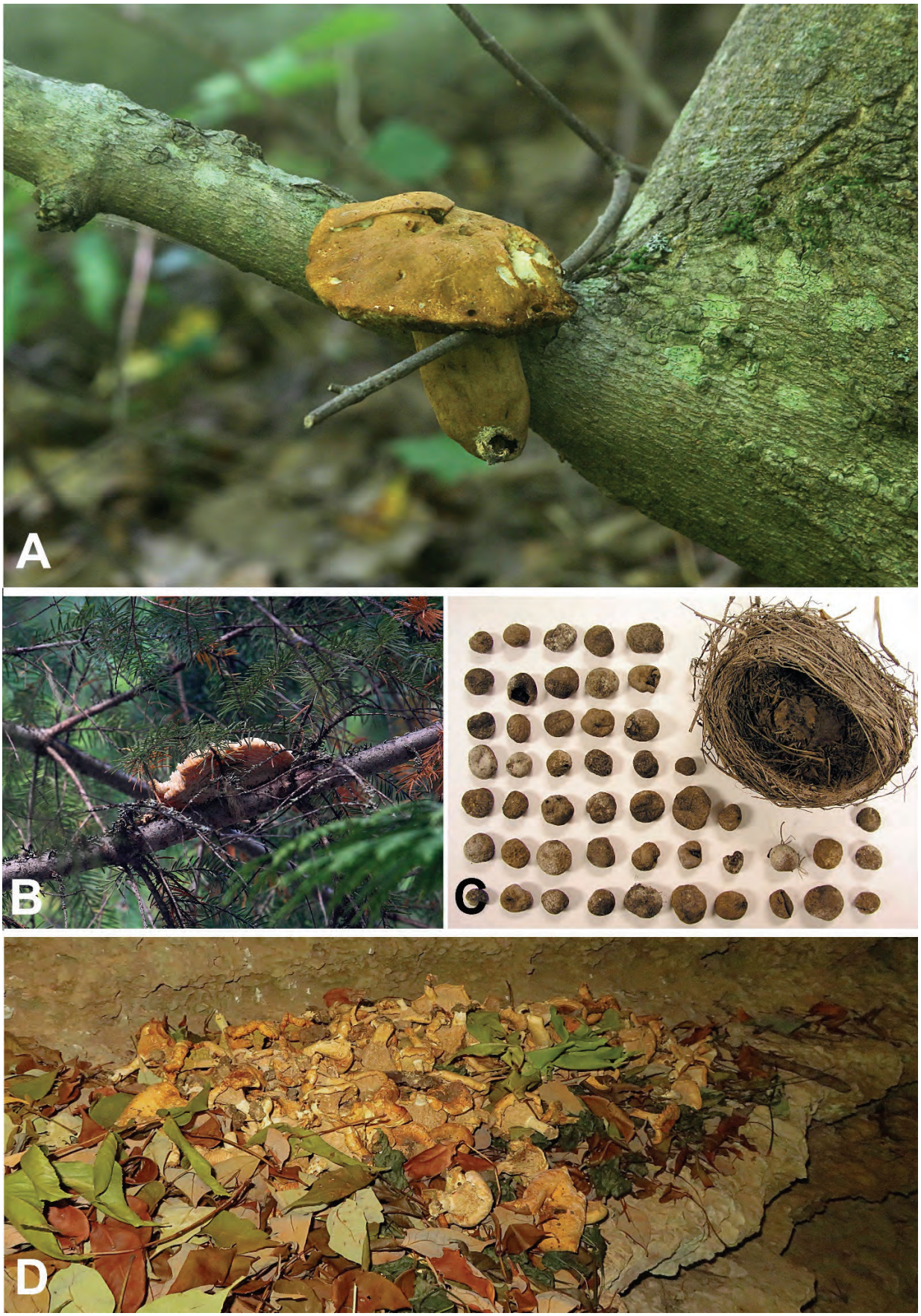

Fig. 8. Examples of fungi hung or cached by rodents. **A.** An entire bolete fruiting body carefully hung by a North American red squirrel in Tucker County, West Virginia, USA. **B.** A species of *Amanita* hung to dry by an unidentified squirrel (likely a Douglas's squirrel based on the species frequently observed in that area) in Chelan County, Washington, USA. **C.** A North American red squirrel in New Brunswick, Canada cached more than 50 *Elaphomyces* fruiting bodies inside of this abandoned robin nest (see: Vernes and Poirier 2007). **D.** A large Allegheny woodrat cache of dried fungi (likely mostly members of the *Russulaceae*) found inside of a cave in Adams County, Ohio, USA. Images A & B © Todd F. Elliott. Image C © Karl Vernes. Image D © Laura S. Hughes.

of various North American woodrats (*Neotoma* spp.) have reported that they frequently cache and collect fungi along with other seemingly random non-food objects (see papers reporting mycophagy for this genus in Supplementary Table S8 and Fig. 8D). *Neotoma* species, sometimes called pack rats, are notorious hoarders. They certainly use the stored fungi for food, but it is difficult to determine how reliant they are on the food value of cached fungi or whether this behaviour is simply an extension of their predisposition for hoarding random objects. Further study of fungal caching behaviours among various *Neotoma* species is needed to fully understand these interactions. Kangaroo rats frequently cache food, but we only found one study reporting fungi caching behaviours, and this was in the banner-tailed kangaroo rat (*Dipodomys spectabilis*) (Vorhies & Taylor 1922).

Species of the shrew family, *Soricidae*, have very fast metabolisms that require them to cache food (Moore 1943, Maser & Hooven 1974, Martin 1981, Robinson & Brodie 1982, Carraway 1985, Merritt 1986, Vander Wall 1990, Schwartz & Schwartz 2001, Rychlik & Jancewicz 2002, Urban 2016). Although this aspect of shrew biology remains relatively incompletely studied, many species are reported to eat fungi (Supplementary Table S9). Though we could not find any reports of caching fungi by shrews, further research may reveal such behaviour in some species. Some species of pocket mice (*Heteromyidae*), voles (*Cricetidae*), lemmings (*Cricetidae*) and gophers (*Geomyidae*) cache food (Vander Wall 1990, Schwartz & Schwartz 2001, Connior 2011), and members of these groups have been reported to eat fungi (Supplementary Table S8). However, we have so far been unsuccessful in locating explicit reports of these groups caching fungi, likely due to insufficient research having been undertaken on this topic.

Reports of fungal caching behaviours have focused on cold regions of the Northern Hemisphere. In regions where fungal caching does not occur, it is possible that fungi sporulate for a larger portion of the season, the climate is not conducive to fungal storage, or animals are adapted to seasonal fungal consumption and periodically rely on other food sources. It seems probable that mycophagous mammals in the Southern Hemisphere also cache fungi, though we could not find any evidence of such events even in the large volume of mycophagy literature published in Australia; we could also find no evidence in the literature for South America or Southern Africa. In Australia, some mycophagous mammals – including brush-tailed bettongs (*Bettongia penicillata*), musky rat-kangaroos (*Hypsiprymnodon moschatus*) and giant white-tailed rats (*Uromys caudimaculatus*) – have been reported to cache seeds (Forget & Vander Wall 2001, Theimer 2001, Theimer 2003, Murphy *et al.* 2005). Musky rat-kangaroos and giant white-tailed rats primarily reside in wet tropical habitats in northeastern Queensland, Australia. This type of wet tropical habitat is not conducive to storing fungi since they would quickly rot in humid warm conditions. Since brush-tailed bettongs reside in areas that would be better suited to storing fungi (compared to the tropics of northern Queensland), it is possible that they may be caching fungi on occasion or some fungi may be available throughout the season, but to our knowledge this has not been specifically studied. Further research may uncover that this behaviour is more widespread both geographically and among more mammal species.

For animals that store fungi, these caches provide an important food for seasons when the resource is less readily available. In addition to the species that make stores, other mammals and birds may depend on raiding the caches. For example, Andreev (1978) noted that Siberian jays (*Perisoreus infaustus*) survived Eurasian winters in part by feeding heavily on fungi stolen from rodent caches. Carey (1991) noted that during the night, Humboldt's flying squirrels raid caches of fungi made by diurnal squirrels. Stealing food from squirrel caches comes at a risk to the thief, since some squirrels can be violent (Seagears 1949–1950) and are usually highly defensive of their stores. Occasionally they have been reported to fight to the death over cache ownership (Smith 1968a). The diversity of mammals that cache fungi or raid these caches is still poorly understood, and more studies are needed to understand their importance as winter food.

The ecological implications of mammal caching behaviours for fungal dispersal are not fully understood. By placing fungi to dry several metres off the ground, rodents help with the release of fungal spores higher into air currents. Connor (1960) noted that North American red squirrels bury "small puffballs" in pits; he unfortunately did not identify the fungal species involved, but it is likely some type of hypogeous fungi. It is therefore possible that squirrels may dig hypogeous fungi in one location and bury them somewhere else. Regardless of whether squirrels really store fungi below ground or simply forget them, this behaviour has potentially important implications for fungal dispersal.

Nutritional advantage of fungi consumption

Since fungal cell walls are primarily composed of chitin (Cork & Kenagy 1989a, Balestrini *et al.* 2000) that is difficult for humans to digest when raw, there is a widespread myth that fungi are nutritionally insignificant; however, cooking fungi makes them highly digestible and nutritionally beneficial to humans (Wani *et al.* 2010). While cooking fungi is irrelevant in the context of wildlife nutrition, many mammals are capable of biosynthesizing chitinases and digesting raw fungal tissues to access nutrients (Cornelius *et al.* 1975, Boot *et al.* 2001, Wallis *et al.* 2012, Polatyńska 2014). The Abert's squirrel (*Sciurus aberti*) carries mushrooms to its nest as one of the first non-milk foods its young eat (Keith 1956), suggesting that fungi are highly digestible for this species. Fungi also do not require the processing often carried out on other foods (*e.g.* husking nuts, peeling fruit, extracting seeds). Young mammals such as the juvenile Tana River mangabey (*Cercocebus galeritus*) take advantage of this simple source of nutrition before they learn to process more energy intensive foods (Kivai 2018). Some arboreal mammals even risk predation by descending from the canopy to feed on highly desirable fungi. Germain's langurs (*Trachypithecus germaini*) have been found to come to the ground to pick fungal sporocarps and then immediately retreat into the trees to consume them (de Groot & Nekaris 2016; Fig 3D). Among other primates such as the grivet monkey (*Chlorocebus aethiops*), higher ranking members of troops tend to eat higher portions of fungi while lower ranking members eat more fruit (Isbell *et al.* 1999). The use of troop status to acquire fungi indicates that they are highly desirable; this is likely due to nutritional advantages, flavour or aroma. Japanese macaques (*Macaca fuscata*), which are known to eat at least 67 fungal species, can be so enthusiastic about fungi that fights frequently break out over possession and consumption of sporocarps (Sawada *et al.* 2014). Eastern gorillas (*Gorilla beringei*) apparently have similar disagreements within the troop over ownership of a highly valued species of *Ganoderma* fungus, as noted by Fossey (1983: 76) in the following:

> *"Still another special food is bracket fungus* (Ganoderma applanatum), *a parasitical tree growth resembling a large solidified mushroom. The shelflike projection is difficult to break free from a tree, so younger animals often have to wrap their arms and legs awkwardly around a trunk and content themselves by only gnawing at the delicacy. Older animals who succeed in breaking the fungus loose have been observed carrying it several hundred feet from its source, all the while guarding it possessively from more dominant individuals' attempts to take it away. Both the scarcity of the fungus and the gorillas' liking of it cause many intragroup squabbles, a number of which are settled by the silverback, who simply takes the item of contention for himself".*

Fungal biochemistry is complex and varies between taxonomic groups (Mendel 1898, Kinnear *et al.* 1979, Vogt *et al.* 1981, Blair *et al.* 1984, Grönwall & Pehrson 1984, Jabaji-Hare 1988, Hussain & Al-Ruqaie 1999, Claridge & Trappe 2005, Barros *et al.* 2007, 2008, Kalač 2009, Ouzouni *et al.* 2009, Wani *et al.* 2010, Wallis *et al.* 2012, Zambonelli *et al.* 2017, Lucchesi *et al.* 2021). The nutritional value for mammals also varies between fungal species and between different parts of the sporocarp. The nutritional role that fungi play in mammals' diets therefore varies between individuals, species, seasons, and the availability of other foods. Grönwall & Pehrson (1984) estimate that Eurasian red squirrels can reach up to half of their daily energetic requirements by eating fungi. As previous studies and reviews on mycophagy have typically shown, fungi are a significant source of nutrition and biomass for small mammals (Fogel & Trappe 1978, Claridge & May 1994, Claridge *et al.* 1996, Johnson 1996, Luoma *et al.* 2003, Polatyńska 2014, Nuske *et al.* 2017a, b, Zambonelli *et al.* 2017). Fungi are also important for some larger mammal species, including deer in the family *Cervidae* that rely heavily on fungi as a large portion of their diet (Strode 1954, Lovaas 1958, Kirkpatrick *et al.* 1969, Hungerford 1970, Launchbaugh & Urness 1992, also see Supplementary Table S11). The white-tailed deer (*Odocoileus virginianus*) has been reported to eat as many as 580 fungal species (Cadotte 2018). Ungulates generally eat larger fungal species, and since these taxa tend to sporulate most prolifically in the autumn and early winter, they are often more seasonally important. In cold regions of Eastern and Northern Europe, various ungulate species have been reported to excavate frozen mushrooms from under the snow (Blank 2003, Inga 2007).

Water constitutes up to 80–95 % of the biomass of fungal sporocarps (Claridge & Trappe 2005, Barros *et al.* 2007) and represents an important source of hydration for small mammals. In some cases, fungal sporocarps can be the major or only source of water for small mammals (Getz 1968). Using fungi as a water source therefore increase the adaptability of some mammals to marginal habitats where available surface water is scarce. This may explain the high diversity of mycophagous mammals in Australian dry woodlands and other similar environments around the world.

Fungal sporocarps generally contain more proteins and nutrients than plant material (Wallis *et al.* 2012) and can be an important source of essential amino acids (Blair *et al.* 1984). In larger mammals, fungi are not necessarily an important source of dietary biomass but can provide key nutrients that are often scarce or inaccessible in other food sources. Selenium, for example, is an important microelement in mammal diets that is found in relatively high levels in some fungi (Watkinson 1964, Quinche 1983a, b, Claridge & Trappe 2005, Falandysz 2008, Costa-Silva *et al.* 2011, Kabuyi *et al.* 2017). Selenium deficiency can lead to nutritional muscular dystrophy (white muscle disease), and many livestock feeding mixes include selenium supplements (Gupta & Gupta 2000, Claridge & Trappe 2005, Falandysz 2008). Fungi are likely one of the primary sources of selenium for wild mammals, thus making fungi an important food even if only small quantities are ingested.

In addition to selenium, fungi contain a wide array of essential amino acids, fats, fatty acids, carbohydrates, minerals, nutrients and proteins (Claridge & Trappe 2005). Some groups of fungi, including members of the families *Glomeraceae, Gigasporaceae* and *Mesophelliaceae*, also have high lipid and fatty acid content (Kinnear *et al.* 1979, Jabaji-Hare 1988). Many aspects of the chemical composition of various fungal species can boost animal health even in very small quantities. Studies on livestock and poultry feeds have experimentally shown the high value of fungi as a dietary supplement even in low dosages. When fungi were given to broiler chickens, for example, the chickens generally experienced increased weight gain and improved resistance to pathogens (Bederska-Łojewska *et al.* 2017). These benefits were detected even when fungi were added at levels of as low as 2 % in poultry diets. In addition to the use of sporocarps in the livestock feed industry, research has suggested that using mycelium as a fermenting agent can also provide antioxidants and improve the overall quality of livestock feeds (Ukpebor *et al.* 2007, Abdullah *et al.* 2016).

Most information about the nutritional composition of fungi is known from species cultivated for human or livestock feed, so there is very little information on the nutritional value of most wild fungal species. Deciphering the impacts of fungal consumption by wild animals is also more complex than in captive populations. Studies of wild populations of the heavily mycophagous eastern bettong (*Bettongia gaimardi*) suggested that an increase in fungi in the marsupial's diet correlated with an improved body condition (Johnson 1994b). Female eastern bettongs are more heavily mycophagous than males, and the growth rate of pouch young is positively correlated to the abundance of fungal sporocarps (Johnson 1994b). However, it remains difficult to measure the direct physiological impacts of fungal species in the diet of a given individual or species since there are many co-occurring variables. The idea of mammals "self-medicating" by using fungi and plants with certain pharmacological properties is still speculative, but research into some foods used by animals – including fungi – has uncovered compounds with promising pharmacological properties (Huffman 1997, 2003, Cousins & Huffman 2002). These studies compare some of the medicinal compounds found in pharmacological studies with food choice in primates; however, it is more difficult to relate medicinal compounds used for medical applications to the diets of mammals more distantly related to humans.

Fungi consumption has a variety of positive impacts for many mammals, but some fungal species are bioaccumulators that can absorb environmental toxins when they are growing in contaminated areas (Ernst 1985, Colpaert & Van Assche 1987, Gast *et al.* 1988, Brown & Hall 1989, Gadd 1994, Gonzalez-Chavez *et al.* 2004, Pokorny *et al.* 2004, Fomina *et al.* 2005, Soylak *et al.* 2005, Shavit & Shavit 2010, Dulay *et al.* 2015). Isotope studies in Europe have shown that fungi absorb radiocesium, which can be transmitted to animals that ingest contaminated sporocarps and

then move up the food chain to eventually contaminate humans and other apex predators that have eaten these mycophagous game animals (Johnson & Nayfield 1970, Hove *et al.* 1990, Karlén *et al.* 1991, Fielitz 1992, Johanson 1994, Strandberg & Knudsen 1994, Avila *et al.* 1999, Zibold *et al.* 2001, Hohmann & Huckschlag 2005, Steiner & Fielitz 2009, Dvořák *et al.* 2010, Škrkal *et al.* 2015). Environmental contaminants are often the by-products of human activities such as agriculture, mining, bombing and manufacturing. The movement of these toxins through food webs from primary to secondary consumers is undoubtedly more widespread than is currently known, and further studies are needed to thoroughly understand the role that fungi play in the bioaccumulation and magnification of toxins through the food chain.

Evolutionary significance of mammal mycophagy

The role of mycophagy in fungal spore dispersal

Fungi disperse across ecosystems either vegetatively (through mycelium growth or asexual propagules) or sexually (via spore dispersal). Mycelium is the non-reproductive part of a fungus and is composed of a network of fine root-like filaments. In habitats with similar or compatible plant communities, mycorrhizal fungi commonly colonise seedlings through mycelial spread (Jonsson *et al.* 1999). In fragmented, highly disturbed or degraded areas, mycelial spread tends to be less effective, and spores are the primary means of establishment (Trappe & Strand 1969, Bruns *et al.* 2009, Okada *et al.* 2022).

Even though spores theoretically enable fungi to disperse over greater distances than mycelial spread does, only a small percentage of spores generally disperse successfully at significant distances. Many widespread mycorrhizal fungal species successfully disperse through air currents (Warner *et al.* 1987, Allen *et al.* 1989, Geml *et al.* 2008), but a high percentage of spores land very close to their source and very few spores are able to colonise new areas. Estimates suggest that only about 2 % of spores from wind-dispersed basidiomycete species travel beyond 5.2 m of the parent sporocarps (Li 2005), while about 5 % of spores travel beyond one metre (Galante *et al.* 2011). Among ectomycorrhizal fungi, density and diversity of wind-dispersed spores decrease with distance from forest edges, with few spores detected at distances over 1 km from the forest edge (Peay *et al.* 2012). Once landed, spores must find suitable substrates (for saprophytic species) or hosts (for mycorrhizal and parasitic species) to germinate. For sexual reproduction, individuals need to meet nearby compatible genetic strains. Therefore, spores landing closer to their parent sporocarps have a greater probability of finding suitable habitat and mating types (Kytöviita 2000, Peay *et al.* 2012, Horton 2017); however, proximity to the parent may also reduce the genetic diversity (thus the adaptability and resilience) of the species in the area. For example, low genetic diversity detected in populations of the hypogeous commercial truffle *Tuber melanosporum* is likely due to difficulties in long-distance spore dispersal (Taschen *et al.* 2016). Such genetic bottlenecks could be a result of too few animal dispersers.

Fungal sporocarps are often ephemeral and delicate, but their spores are far more resilient. Spores typically survive the enzymatic tribulations of the mammalian digestive tract and regularly germinate once deposited in scats (See next section and Tables 1, 2). Since mammals can eat entire sporocarps, mycophagy would account for the dispersal of a greater percentage of spores from a single sporocarp than would wind dispersal. Some rodents also co-disperse bacteria that interact with root-associated fungi and play important roles in nitrogen fixation (Li *et al.* 1986, Li & Maser 1986). Since an individual mammal often consumes multiple sporocarps, their scats may contain spores from multiple individuals and species of fungi that are deposited within close proximity to each other. Mycophagy is therefore an effective means of long-distance dispersal of fungal spores and improving genetic diversity within fungal populations.

Fungal spore dispersal through mycophagy can greatly impact the species composition, genetic diversity and adaptability of mycorrhizal fungal communities (Gehring *et al.* 2002, Nuske 2017, Dundas *et al.* 2018, Valentine *et al.* 2018, Miranda *et al.* 2019, Nuske *et al.* 2019). Mycophagous mammals may have played a role in the movement and recolonisation of mycorrhizal fungi under major climatic changes such as glaciation, with obvious impacts on the current distribution of fungal species and associated plants (Murat *et al.* 2004, Piattoni *et al.* 2016). It is difficult to estimate the long-term biogeographic impact of mycophagy at a global scale, but several studies have addressed these questions on a smaller scale, *e.g.* in degraded, newly forming or transitional systems. For example, mammals play a vital role in the transport of mycorrhizal inoculant into newly forming soils at the forefront of receding glaciers in the alpine zone of the North Cascades Mountains, USA (Cázares & Trappe 1994). Scats of mycophagous animals enable ectomycorrhizal tree establishment in nutrient-poor sandy dune environments in Oregon, USA (Ashkannejhad 2003, Ashkannejhad & Horton 2006). After the volcanic eruption of Mount Saint Helens in Washington, USA, the spore-containing scats of mammals served as vectors of mycorrhizal spores into newly formed sterile soils within the blast zone (MacMahon & Warner 1984, Allen 1987). In newly produced coal mine spoils, mycorrhizal spores can be dispersed by grasshoppers and rabbits (Ponder 1980). Small mycophagous mammals such as voles are key to habitat succession engineered by North American beavers (*Castor canadensis*), a species that causes more ecosystem-level change than any other non-human mammal. When beaver ponds eventually silt in, they become meadows dominated by herbaceous communities that typically associate with arbuscular mycorrhizal fungi, while the surrounding forests are dominated by ECM plants. Southern red-backed voles (*Myodes gapperi*) regularly eat hypogeous ECM fungi on the forested edges of beaver meadows and inadvertently carry spores into the meadows in their scats; this behaviour builds up a spore bank that assists ECM tree species in recolonising areas affected by beavers (Terwilliger & Pastor 1999). Similar meadow colonisation by ECM spores was observed in Oregon as a result of western pocket gophers (*Thomomys mazama*) depositing ingested fungal spores in below ground faecal chambers (Maser *et al.* 1978b). In regions where non-native pines (*Pinus* spp.) are farmed in plantations, a variety of mycophagous animals spread the spores of pine-associated mycorrhizal fungi outside the bounds of pine plantations, potentially contributing to the spread of these trees (Nuñez *et al.* 2013, Wood *et al.* 2015, Policelli *et al.* 2019, 2022, Aguirre *et al.* 2021).

Spore viability

Fungal spores tend to be very robust and remain viable after passage through the digestive system of a diverse range of invertebrates (Tuno 1998, Trappe & Claridge 2005, Kitabayashi & Tuno 2018, Vašutová *et al.* 2019, Ori *et al.* 2021) and birds (Caiafa *et al.* 2021).

Table 1. Mammal species experimentally shown to disperse viable mycorrhizal fungal spores.

Genus and species of mammals	Common Name	Method*	Viable	Rate*	Citation
Aepyprymnus rufescens	Rufous Bettong	IT	Yes	?	Reddell *et al.* (1997)
Bettongia penicillata	Brush-tailed Bettong	IT	Yes	+	Lamont *et al.* (1985)
Bettongia tropica	Northern Bettong	IT	Yes	?	Reddell *et al.* (1997)
Bison bison	American Bison	IT	Yes	?	Lekberg *et al.* (2011)
Callospermophilus saturatus	Cascade Golden-mantled Ground Squirrel	M	Yes	+	Cork & Kenagy (1989a)
Cervus canadensis	Wapiti/Elk	IT	Yes	?	Allen (1987)
Cervus elaphus	Western Red Deer	IT	Yes	?	Wood *et al.* (2015)
Ctenomys knighti	Catamarca Tuco-tuco	IT	Yes	?	Fracchia *et al.* (2011)
Glaucomys oregonensis	Humboldt's Flying Squirrel	M, IT	Yes	-	Colgan & Claridge (2002)
Glaucomys sabrinus	Northern Flying squirrel	IT	Yes	+	Caldwell *et al.* (2005)
Hystrix cristata	Crested Porcupine	M	Yes	?	Ori *et al.* (2018)
Isoodon fusciventer	Dusky-bellied Bandicoot	IT	Yes	+, ?	Smith (2018), Tay *et al.* (2018)
Isoodon macrourus	Northern Brown Bandicoot	IT	Yes	?	Reddell *et al.* (1997)
Lepus europaeus	European Hare	IT	Yes	?	Aguirre *et al.* (2021)
Loxodonta africana	African Elephant	IT	Yes	?	Paugy *et al.* (2004)
Melomys cervinipes	Fawn-footed Melomys	IT	Yes	?	Reddell *et al.* (1997)
Microtus oregoni	Creeping Vole	G	Yes	?	Trappe & Maser (1976)
Mus musculus	House Mouse	IT	Yes	+	Ori *et al.* (2021)
Myodes californicus	Western Red-backed Vole	M, IT	Yes	-	Colgan & Claridge (2002)
Myodes gapperi	Southern Red-backed Vole	IT	Yes	-	Terwilliger & Pastor (1999)
Neotomodon alstoni	Mexican Volcano Mouse	M	Yes	+, =	Castillo-Guevara *et al.* (2011, 2012), Pérez *et al.* (2012)
Odocoileus hemionus	Mule Deer	IT	Yes	?	Ashkannejhad & Horton (2006)
Perameles nasuta	Long-nosed Bandicoot	IT	Yes	?	McGee & Baczocha (1994), Reddell *et al.* (1997), McGee & Trappe (2002)
Peromyscus leucopus	White-footed Deermouse	IT	Yes	?	Rothwell & Holt (1978), Miller (1985)
Peromyscus maniculatus	North American Deermouse	IT, M	Yes	?,+,=	Rothwell & Holt (1978), Castillo-Guevara *et al.* (2011, 2012), Pérez *et al.* (2012)
Potorous tridactylus	Long-nosed Potoroo	IT	Yes	+	Claridge *et al.* (1992)
Proechimys semispinosus	Tome's Spiny-rat	IT	Yes	?	Mangan & Adler (2002)
Pseudalopex gymnocercus	Pampas Fox	IT	Yes	?	Aguirre *et al.* (2021)
Rattus fuscipes	Bush Rat	IT	Yes	?	Reddell *et al.* (1997)
Rattus rattus	Black Rat	IT	Yes	?	McGee & Baczocha (1994), McGee & Trappe (2002)
Reithrodontomys humulis	Eastern Harvest Mouse	IT	Yes	?	Rothwell & Holt (1978)
Rupicapra rupicapra	Alpine Chamois	IT	Yes	?	Wiemken & Boller (2006)
Sciurus aberti	Abert's Squirrel	IT	Yes	=	Kotter & Farentinos (1984)
Sus scrofa	Eurasian Wild Pig	M, IT	Yes	+,?	Nuñez *et al.* (2013), Piattoni *et al.* (2014), Livne-Luzon *et al.* (2017), Aguirre *et al.* (2021)
Sylvilagus floridanus	Eastern Cottontail	IT	Yes	+	Ponder (1980)
Tamias townsendii	Townsend's Chipmunk	M, IT	Yes	+	Colgan & Claridge (2002)
Thomomys talpoides	Northern Pocket Gopher	IT	Yes	?	Allen & MacMahon (1988)
Trichosurus vulpecula	Common Brush-tail Possum	IT	Yes	?	Wood *et al.* (2015)
Uromys caudimaculatus	Giant White-tailed Rat	IT	Yes	?	Reddell *et al.* (1997)
Two species of deer *Cervus elaphus* (Western Red Deer) *Dama dama* (Common Fallow Deer)		IT	Yes	?	Nuñez *et al.* (2013)

Table 1. (Continued).

Genus and species of mammals	Common Name	Method*	Viable	Rate*	Citation
Mixed scats from *Rattus fuscipes*, *R. rattus*, *R. villosissimus* and *Perameles nasuta* were shown to contain viable VAM spores, but it is unclear which species were actually tested for viability		IT	Yes	?	McGee & Baczocha (1994)
Ten species of small European mammals were examined in this study but it is unclear if viability was tested in all mammals		IT	Yes	?	Schickmann (2012)

A list of at least 40 mammal species that have been experimentally shown to disperse viable fungal spores through their scats. ***Method:** M: microscopic assessment, IT: Inoculation Trials, G: germination trial in vitro. ***Rate:** +: improved viability when consumed by animals compared to control, =: equal viability from scats to control, -: reduced viability compared to control, ?: no comparative viability data.

Table 2. Species of mycorrhizal fungi whose spores have been experimentally shown to remain viable after mammal consumption.

Fungal species	Method*	Viability	Rate*	Citation
Acaulospora morrowiae	IT	Yes	?	Lekberg *et al.* (2011)
Amphinema sp.	IT	Yes	?	Nuñez *et al.* (2013)
Archaeospora trappei	IT	Yes	?	Lekberg *et al.* (2011)
Densospora tubiformis	IT	Yes	?	McGee & Baczocha (1994)
Descolea angustispora	IT	Yes	?	Tay *et al.* (2018)
Elaphomyces granulatus	M	Yes	+	Cork & Kenagy (1989a)
Endogone aggregata	IT	Yes	?	McGee & Baczocha (1994)
Glomus atrouva	IT	Yes	?	McGee & Baczocha (1994), McGee & Trappe (2002)
Glomus australe	IT	Yes	?	McGee & Baczocha (1994)
Glomus fuegianum	IT	Yes	?	McGee & Baczocha (1994)
Glomus intraradices	IT	Yes	?	Lekberg *et al.* (2011)
Glomus macrocarpum	G, IT	Yes	?	Trappe & Maser (1976), Allen & MacMahon (1988), McGee & Baczocha (1994)
Glomus pellucidum	IT	Yes	?	McGee & Baczocha (1994), McGee & Trappe (2002)
Glomus spp.	IT	Yes	?	Allen (1987), McGee & Baczocha (1994)
Hebeloma mesophaeum	IT	Yes	?	Nuñez *et al.* (2013)
Laccaria trichodermophora	M, IT	Yes	+,-	Castillo-Guevara *et al.* (2011), Pérez *et al.* (2012)
Melanogaster sp.	IT	Yes	?	Nuñez *et al.* (2013)
Pyronemataceae	IT	Yes	?	Tay *et al.* (2018)
Rhizophagus fasciculatus	IT	Yes	?	Rothwell & Holt (1978)
Rhizopogon cf. arctostaphyli	IT	Yes	?	Nuñez *et al.* (2013)
Rhizopogon evadens	IT	Yes	?	Ashkannejhad & Horton (2006)
Rhizopogon fuscorubens	IT	Yes	?	Ashkannejhad & Horton (2006)
Rhizopogon occidentalis	IT	Yes	?	Ashkannejhad & Horton (2006)
Rhizopogon pseudoroseolus	IT	Yes	?	Aguirre *et al.* (2021)
Rhizopogon cf. rogersii	IT	Yes	?	Nuñez *et al.* (2013)
Rhizopogon roseolus	IT	Yes	?	Nuñez *et al.* (2013)
Rhizopogon salebrosus (group)	IT	Yes	?	Ashkannejhad & Horton (2006)
Rhizopogon truncatus	M, IT	Yes	?	Colgan & Claridge (2002)
Rhizopogon vinicolor	M, IT	Yes	varied	Colgan & Claridge (2002)
Rhizopogon spp. (3 unidentified species)	IT	Yes	?	Wood *et al.* (2015)
Russula aff. *cuprea*	M	Yes	=	Castillo-Guevara *et al.* (2012)
Suillus brevipes	IT	Yes	?	Ashkannejhad & Horton (2006)
Suillus granulatus	IT	Yes	?	Wiemken & Boller (2006), Aguirre *et al.* (2021)
Suillus luteus	IT	Yes	?	Nuñez *et al.* (2013), Wood *et al.* (2015)
Suillus tomentosus	M, IT	Yes	+	Castillo-Guevara *et al.* (2011), Pérez *et al.* (2012)

Table 2. (Continued).

Fungal species	Method*	Viability	Rate*	Citation
Suillus umbonatus	IT	Yes	?	Ashkannejhad & Horton (2006)
Thelephora americana	IT	Yes	?	Ashkannejhad & Horton (2006)
Thelephoraceae T73.1	IT	Yes	?	Ashkannejhad & Horton (2006)
Tomentella sublilicina	IT	Yes	?	Ashkannejhad & Horton (2006)
Tuber aestivum	M, IT	Yes	+	Piattoni *et al.* (2014), Ori *et al.* (2018, 2021)
Tuber borchii	IT	Yes	?	Livne-Luzon *et al.* (2017)
Tuber canaliculatum	IT	Yes	?	Miller (1985)
Tuber oligospermum	IT	Yes	?	Livne-Luzon *et al.* (2017)
Tuber shearii	IT	Yes	?	Miller (1985)
Tuberaceae	IT	Yes	?	Tay *et al.* (2018)
Unidentified (27 ECM taxa including *Ascomycetes* and *Basidiomycetes*)	IT	Yes	+	Claridge *et al.* (1992)
Unidentified taxa (including: *Elaphomyces* spp., *Glomus* sp., *Hysterangium separabile*, *Rhizopogon* spp., *Sclerogaster xerophilum* and *Sedecula pulvinata*)	IT	Yes (unclear which taxa)	=	Kotter & Farentinos (1984)
Colonisation by one or more of the following VAM taxa: *Glomus* spp., *Scutellospora gregaria* and *S. verrucosa*	IT	Yes (unclear which taxa)	?	Paugy *et al.* (2004)
A preliminary examination of the scats indicated that at least *Hysterangium*, *Descolea* and *Reddellomyces*, but a full list was beyond the scope of the study. Based on the results both ECM and VAM taxa remained viable	IT	Yes (unclear which taxa)	+	Smith (2018)
Dark septate endophytes and VAM fungi	IT	Yes	?	Fracchia *et al.* (2011)
Unidentified (at least 7 ECM taxa)	IT	Yes	+	Lamont *et al.* (1985)
VAM fungi	IT	Yes	+	Ponder (1980)
VAM fungi including *Glomus* spp. (3 unidentified species) and *Sclerocystis coremioides* unclear if all or some were viable	IT	Yes	?	Mangan & Adler (2002)
Unidentified ECM and VAM taxa	IT	Yes	?	Reddell *et al*. (1997)
Unidentified ECM fungi	IT	Yes	-	Terwilliger & Pastor (1999)
Unidentified ECM fungi	IT	Yes	?	McGee & Baczocha (1994)
Unidentified ECM fungi	IT	Yes	+	Caldwell *et al.* (2005)
Unidentified ECM fungi	IT	Yes	?	Schickmann (2012)

A list of at least 58 taxa of mycorrhizal fungi that have been experimentally shown to remain viable after passage through the digestive systems of mammals. ***Method:** M: microscopic assessment, IT: inoculation trials, G: germination trial in vitro. ***Rate:** +: improved viability when consumed by animals compared to control, =: equal viability from scats to control, -: reduced viability compared to control, ?: no comparative viability data, varied: different rates depending on mammal species. (Note: the names of the fungi listed in this table in some cases have been updated to reflect recent taxonomic/nomenclatural changes and may differ from the name listed in the original publication.)

Reess & Fisch (1887) and Hastings & Mottram (1915) first suggested that hypogeous fungi such as *Elaphomyces* may benefit from mammal dispersal, although they were not able to demonstrate spore viability. The concept of spore dispersal through mammal mycophagy assumes that spores remain viable after passage through the mammalian digestive system. To fully understand how frequently spores remain viable and among how many different mammal species, we reviewed the literature that tested spore viability in mammal faeces. Reess & Fisch (1887) tried multiple approaches with *Elaphomyces* spores extracted from scats of the common fallow deer (*Dama dama*), but both their controls and spores extracted from scats proved unsuccessful. Considering that mycorrhizae research was in its infancy in the 1880's, they were likely facing methodological limitations. Aside from this early attempt, we found multiple studies focusing on different groups of mycorrhizal fungi and using various microscopy techniques or inoculation/germination trials. These studies detected viable spores from more than 58 mycorrhizal fungal species after their passage through the digestive system of at least 40 mammal species (Tables 1, 2). We were unable to find any studies showing that fungal spores were no longer viable after ingestion by mammals.

Spore resilience may be due in part to melanins that limit the disintegration (lysis) of spore cell walls (Bloomfield & Alexander 1967, Zambonelli *et al.* 2017). Although further studies are needed to fully understand the relationship between melanins

and mammalian digestive enzymes, the digestive enzymes of mammals appear to be no match for the melanins in fungal spores. It has been suggested that spores with ornamentation or thicker walls are more adept at surviving the digestive systems of animals (Korf 1973). Although there may be situations where this hypothesis holds true, there are fungi with smooth, thin-walled spores (*e.g.* the genera *Suillis* and *Rhizopogon*) that have been thoroughly documented to survive mammalian digestive systems (Table 2).

Although further empirical testing is needed, our review also revealed that at least 10 species of mammals may increase spore germination/viability after ingestion (Table 1). Colgan & Claridge (2002) suggested that several factors, such as body temperature, passage time and digestive anatomy, may impact spore viability. Nuñez *et al.* (2013) showed that twice as many seedlings inoculated with Eurasian wild pig (*Sus scrofa*) faeces formed mycorrhizal colonisation when compared with seedlings inoculated with western red deer (*Cervus elaphus*) and common fallow deer (*Dama dama*) faeces. The authors were unable to decipher whether these differences were due to the digestive system of deer decreasing spore viability, or if the digestive enzymes of wild pigs caused scarification that alleviates spore dormancy and increases germination. Scarification of fungal spores (*i.e.* erosion or breaking down of spore wall microstructures) after transit through mammalian digestive systems has only been studied in a few fungal taxa and is probably more common than presently known. For example, asci of *Tuber aestivum* break apart and the spore ornamentation is worn down after passage through digestive systems of Eurasian wild pigs (Piattoni *et al.* 2014, 2016). Despite this apparent damage, spores from faeces formed heavier mycorrhizal colonisation than non-ingested spores in inoculation trials. Different animals cause different amounts of spore scarification, and in general, longer passage rates among larger animals likely increase spore liberation from asci and/or scarification. For example, when comparing *Tuber* spores ingested by wild pigs with those ingested by the long-tailed field mouse (*Apodemus sylvaticus*), Zambonelli *et al.* (2017) suggested that the digestive system of the long-tailed field mice had liberated far fewer spores from their asci than did that of wild pigs.

There are likely situations where both seeds and associated fungal spores are dispersed in the same scat (Pirozynski & Malloch 1988), and it is possible that both are simultaneously being scarified, thus increasing their chance to match with suitable mycorrhizal symbionts. These studies are analogous to animal ingestion of fruits that can facilitate the disruption of seed dormancy and increases seed germination rates (Stiles 1992, Traveset *et al.* 2007). In mycology, similar studies remain scarce but are necessary to improve our understanding of these trophic interactions.

The role of aromas in mycophagy and fungal evolution

Evidence suggests that some bird species may encounter fungi simply by chance while others select them based on colour or aroma (Elliott & Marshall 2016, Elliott & Vernes 2019). Although terrestrial native mammals are absent from New Zealand, the country has a diversity of exceptionally colourful endemic truffles that may be a result of selective pressure from visually cued foraging birds (Beever & Lebel 2014, Elliott *et al.* 2019a). There are numerous reports of mammals eating epigeous fungi, but since these fungal sporocarps are easily visible above the surface of the soil, it is difficult to determine if mammals detect them by visual or olfactory cues or a combination of both. Fossey (1983: 131) provided an example of two young eastern gorillas named Pucker and Coco seeking out "bracket fungi" for food using what appears to be visual cues:

> *"One day while walking in a new area, Pucker suddenly ran toward a large cluster of* Hagenia *trees on the edge of the forest leading to the mountain. Coco leapt from my arms in rapid pursuit — which was unusual. I thought they were making a dash for the mountain and was hastily taking out the bananas when both infants halted below one of the larger trees. They peered up at the tree like children looking up a chimney on Christmas eve. I had never seen them so fascinated by a tree, nor could I determine what it was that so strongly attracted them. Suddenly the two began frenziedly climbing the huge trunk, leaving me even more puzzled. About thirty feet above the ground they stopped, pig-grunted at one another, and avidly started biting into a large bracket fungus. Previously I had noted these shelflike growths, which protrude from* Hagenia *tree trunks and rather resemble overgrown solidified mushrooms*[...] *Try as they might, neither Coco nor Pucker could pry the fungus from its anchorage on the trunk, so they had to content themselves with gnawing chunks out of it. A half-hour later only a remnant remained. Reluctantly they descended, but as we walked on they gazed longingly back at the tree with the fungus elixir".*

The role of aroma is more obvious in hypogeous fungi, where the selective advantage of mycophagy contributed to the convergent rise of sequestrate sporulating morphologies in multiple fungal lineages (Sheedy *et al*. 2016, Truong *et al.* 2017, Elliott & Trappe 2018, Elliott *et al.* 2020a). Sequestrate sporocarps can be partially emergent or hidden entirely below the soil surface, placing the reproductive success of sporocarps and the species at the whim of animal detection. Many sequestrate fungi have lost their ability for the forcible discharge of spores (Thiers 1984) and therefore rely on the production of volatile olfactory cues to attract animal dispersers (Maser *et al.* 1978a, Talou *et al.* 1987, 1990, Donaldson & Stoddart 1994, Stephens *et al.* 2020).

Due to the culinary/economic importance of many members of the sequestrate genus *Tuber*, the chemistry of sequestrate fungal aromas has been most thoroughly studied in this genus (Splivallo *et al.* 2011, Molinier *et al.* 2015, Splivallo *et al.* 2015, Vita *et al.* 2018, Mustafa *et al.* 2020). Based on experiments with domestic dogs and pigs, Talou *et al.* (1990) suggested that dimethyl sulphide was the primary aroma responsible for the detection of mature *T. melanosporum* sporocarps. Dimethyl sulphide is also the primary odour that attracts truffle specialist arthropods (Pacioni *et al.* 1991). These relationships are analogous to plants attracting pollinators with nectar and seed dispersers with sugary fruits, but animal-fungal interactions remain less thoroughly studied. We argue that similarly interdependent associations have been developed by sequestrate fungi through the production of strong aromas that entice animals to find them when spores reach maturity. The level of specialisation and specificity in these aromas is still up for debate, and it is currently unknown whether some fungi can mimic pheromones to target certain species or sexes of mammalian dispersers. Claus *et al.* (1981) suggested that the ability of pigs to detect *T. melanosporum* may be linked to a steroidal pheromone (5α-androst-16-en-3α-ol) that is similar to sex chemicals produced by the mammal. Ultimately, it is hard to

prove whether wild pigs are so passionately interested in truffles merely because they are tasty and nutritious or as a result of some sexual pheromonal trickery. Unlike analogous co-evolutionary associations involved in seed dispersal and pollination, we are unaware of any highly specialised associations that are exclusive between a mammal and a fungal species. However, it would be interesting to explore further whether the selective advantages offered by mycophagy could lead to more specialised dispersal associations.

There are many observational reports of mammals detecting hypogeous fungi by sense of smell, such as deer digging up hypogeous fungi hidden below the soil surface (Cowan 1945). Bermejo *et al.* (1994: 888) described a bonobo (*Pan paniscus*) seemingly using smell to locate an unidentified "truffle" species in the Democratic Republic of Congo:

> "*…standing quadrupedally, digs up the earth, first with one hand, then with the other, in search of subterranean truffles. She puts her face closer to the hole that she has dug and looks closely. Then she carefully puts one hand into the hole and withdraws it immediately, putting her fingers to her nose to detect the scent of truffles. She faithfully repeats this operation again and again"*.

This type of behaviour is not restricted solely to this species of primate. On multiple occasions, we have observed humans displaying nearly identical foraging behaviours while attempting to locate commercially valuable truffles in the wild and on cultivated truffle farms.

Smith (1968a) made extensive observations of the behaviour of young North American red squirrels in their first few days out of the nest as they learned what to eat. Smith (1968a: 42) described the following observation:

> *"On the third day one of the young travelled over 100 ft from the nest, at which point it sniffed along the ground and dug up a false truffle (*Hymenogastrales*). It ate all of the first false truffle, dug up another, and ate half of that before making an unsuccessful attempt to cache the rest in a tree".*

Based on this observation, squirrels appear to have an innate knowledge about using their sense of smell to detect hypogeous fungi and subsequently caching sporocarps. By making careful daylight observations from the day this squirrel was born, Smith (1968a) demonstrated that the behaviour of this young squirrel was truly innate and was not acquired from observing a parent or other individual (also see section: Caching and hoarding of fungi). He suggested that the young would gradually become more adept at this task, since it took over two minutes for this juvenile to dig up the first truffle and another nine minutes to eat it, while its mother could perform the same activity in approximately one minute.

Brown hyenas (*Hyaena brunnea*) in the southern Kalahari Desert are primarily scavengers of vertebrate remains, but they reportedly also use their acute sense of smell to detect and eat the hypogeous desert truffle *Kalaharituber pfeilii* (Mills 1978). Brown hyenas are heavily reliant on odours when foraging, and Mills (1978) reported in great detail how they utilised wind direction to detect and locate food, including desert truffles. In April of 1975, Mills reported brown hyenas picking up a scent on the breeze on 21 occasions, making upwind turns of up to 200 m and then digging for a few seconds in the sand before they uncovered specimens of *K. pfeilii*. We (TFE, JMT and KV) have observed similar behaviours among domesticated dogs trained to hunt *Tuber melanosporum, Lucangium carthusiana* and other commercially harvested truffles. On multiple occasions, we have seen highly trained truffle dogs step on partially emergent immature truffles, totally unaware of their presence, while signalling their handlers toward a ripe truffle nearby.

These examples suggest that aroma can be an important factor in controlling truffle consumption and preventing them from being discovered before spores are mature/ready to germinate. In western North America, the dusky-footed woodrat (*Neotoma fuscipes*) regularly eats hypogeous fungi of the genera *Gautieria* and *Hysterangium* (Parks 1919, 1922). Parks (1922) noted that in the process of digging up ripe sporocarps, woodrats often overlooked or even discarded unripe specimens. The more strong-smelling species were more regularly consumed, suggesting a preferential selection for mature hypogeous sporocarps likely due to the strength of the aromas. Parks (1922) also noted that when different hypogeous fungal species sporulated in close proximity to one another, dusky-footed woodrats preferentially ate more aromatic species and ignored other readily accessible taxa, even if they were significantly larger. The diversity and abundance of truffles (particularly the genus *Gautieria*) was also higher near dusky-footed woodrat nests, but without a randomised survey method it is not possible to prove if this is a meaningful correlation. Based on this early naturalist's observations, it is possible that when dusky-footed woodrats defecate in close proximity to their nests, they might inadvertently "farm" truffles close to the security and safety of their homes. More in-depth and rigorous studies are needed to follow up on Parks' observations.

These examples illustrate some of the reproductive and dispersal advantages of sequestrate fungi that produce aromatic compounds. How specialised these associations are and whether certain aromas are more appealing to different individuals, sexes or taxonomic groups of animals remains to be directly assessed. In a study investigating the interactions between sporulating depths, volatile production and rodent mycophagy of the genus *Elaphomyces*, Stephens *et al.* (2020) showed that deeper sporulating *Elaphomyces* species had distinct volatile organic compound profiles and produced significantly higher quantities of aromatic compounds compared to other members of the genus that sporulated closer to the soil surface. They also concluded that rodents were selecting for species that sporulated deeper in the soil but produced stronger volatiles. The aromas of some hypogeous fungi are potent enough to be detected with portable electronic gas detectors such as flame ionisation or explosimeters (Talou *et al.* 1988). Thus, some hypogeous species produce aromas that are so strong-smelling that they may be detected by animals that do not typically rely on olfactory abilities when foraging. Stronger aromas potentially translate into more frequent consumption and better dispersal, but more complex interactions also occur. Pacioni (1986) suggests that in Europe, domestic truffle dogs trained to detect white truffle species (*Tuber borchii* and *T. magnatum*) are less effective at finding black truffle species (*T. aestivum*, *T. brumale*, *T. macrosporum*, *T. melanosporum*, *T. mesentericum* and *T. uncinatum*), and *vice versa*. The aroma composition of these two groups differs only in the presence of one or more atoms of sulphur (Pacioni 1986), indicating that aromatic specialisation is possibly aimed at different animal dispersers. Donaldson & Stoddart (1994) showed that acetaldehyde, ethyl acetate, *n*-propyl

acetate, isobutyl acetate, ethyl isobutanoate, ethyl butanoate and ethyl propanoate were the compounds responsible for eastern bettongs' attraction to and detection of species of *Mesophellia*. Ultimately, it is still unknown whether it is the combination of different aromatic compounds or the strength of the compounds themselves that is more impactful on mammalian sporocarp detection.

Mammal movements and impacts of primary versus secondary spore dispersal

Fungal spores ingested by mammals are generally only dispersed within the home range of an individual, and for most mammals, there is a direct relationship between larger body size and larger home range (Lindstedt *et al.* 1986, Swihart *et al.* 1988). The dispersal potential of any vertebrate species depends on three factors: passage rate (*i.e.* transit time through the animal's gastrointestinal tract); movement pattern (*i.e.* how far the individual will move as well as the size of its home range); and speed (*i.e.* how fast the animal will travel within its home range). These three factors are key to estimating the dispersal potential of fungi ingested by any animal.

Due to the small size and vast numbers of spores produced by fungal sporocarps, spores can linger in the mammalian gut for longer periods than other larger dietary components (Danks 2012). The passage rate of macrofungal spores has been directly studied in five mammal species: two Murids, one Sciurid, one Macropodid and domestic pigs (*Sus scrofa*) (Danks 2012, Piattoni *et al.* 2016). This small sub-sample does not reflect the large diversity of mammal mycophagists, and there is likely variability between species and individuals of the same species depending on weight, size, intestinal morphology, sex, age, health, movement, other dietary components and season/temperature (Cork & Kenagy 1989b, Comport & Hume 1998, Danks 2012, Piattoni *et al.* 2016, Elliott *et al.* 2020b). This area of research is still in its infancy in comparison to the extensive botanical research regarding vertebrate seed dispersal. More studies on spore passage rates in many groups of mammals are needed to better understand the processes behind fungal spore dispersal in various mammal species and to develop modelling applications similar to those widely used by plant ecologists. One modelling study showed that swamp wallabies (*Wallabia bicolor*) regularly disperse fungal spores hundreds of metres (in some instances up to 1 265 m) from where the sporocarp was initially ingested (Danks *et al.* 2020). Such long-distance dispersal events have strong ecological significance for fungal taxa, particularly those with sequestrate sporocarp morphologies. To our knowledge, this is the only study of its kind, and such modelling approaches show promise in their potential to demonstrate that a diversity of animal species carry spores for similar or even greater distances than does the swamp wallaby.

Secondary dispersal (diplochory) by predators that consume primary mycophagists is another important mode of fungal spore dispersal. This concept was first investigated more than a century ago in toads that dispersed viable fungal spores by eating slugs that had eaten fungi (Vogilino 1895, Buller 1909). Since then, very little modern research has directly investigated secondary dispersal, and it is still unclear how widespread it is. Numerous animals are likely playing a role, including the white-headed woodpecker (*Picoides albolarvatus*) that feeds on insects known to disperse spores of the veiled polypore (*Cryptoporus volvatus*) (Watson & Shaw 2018). These woodpeckers – as well as numerous other insectivorous birds and mammals – can inadvertently act as secondary dispersers of fungi. In most cases, secondary dispersal of fungal spores can greatly increase their dispersal distance, as insectivorous birds and mammals typically move over much larger distances than the primary consumers they prey upon (Schickmann 2012, Schickmann *et al.* 2012). Predators such as eagles, owls and hawks frequently prey on mycophagous rodents, and their aerial journeys inevitably disperse spores far more widely than those of the small earthbound mammals (Trappe 1988, Colgan 1997, Luoma *et al.* 2003, Halbwachs & Bässler 2015). Larger mammalian carnivores such as canids regularly feed on smaller mycophagous mammals. Because predators have much larger-scale movement patterns than their prey, these carnivores have the potential to provide a vital yet overlooked ecosystem function through secondary dispersal of mycorrhizal fungi. The pampas fox (*Lycalopex gymnocercus*) has been reported to disperse mycorrhizal fungal spores, but it is currently unclear if this is an example of primary or secondary dispersal (Aguirre *et al.* 2021). Many bats are also likely acting as secondary dispersers of fungi by ingesting insects that eat fungi (O'Malley 2013). New Zealand's flightless bats (*Mystacina*) may ingest fungi (Lloyd 2001); but this group of bats are atypical, and there is still insufficient data to confirm if they are fungal dispersers. Given the resiliency of fungal spores (see Tables 1, 2), it is unlikely that secondary dispersal negatively impacts their viability, but further studies are needed to address these questions.

When a scat is deposited by a primary or secondary disperser, it is not necessarily at the end of its journey. Numerous organisms interact with scats and may further impact spore dispersal. Some mammals eat scats (coprophagy) and may therefore further disperse spores or improve spore germination rates (Zambonelli *et al.* 2017). In many terrestrial ecosystems, scarab beetles move and bury animal dung, including that from mycophagous mammal species. Scarab beetles can further disperse or bury seeds (Vander Wall & Longland 2004), but very little research has assessed dung beetles as dispersal vectors of fungal spores in mammal scats. At least three species of scarab beetles (*Onthophagus ferox*, *O. rupicra* and *Thyregis* spp.) disperse spores from the brush-tailed bettong (*Bettongia penicillata*) after feeding on the scats of this mammal (Christensen 1980). Several Australian species of *Orthophagus* have claws on their legs that are modified for grasping the fur of mammals, including mycophagous wallabies and bettongs. This adaptation allows the beetle to cling to the animal until it defecates; upon defecation, the beetle drops from the animal and immediately buries the dung to use as a brood chamber for its larvae (Matthews 1972). Although it has yet to be directly studied, this behaviour in many scarab beetles likely improves the success of mycorrhizal fungal spores by burying them in the rhizosphere and thus facilitating mycorrhizal root colonisation.

Ecosystem implications of mammal mycophagy

Bioturbation resulting from mycophagy

The digging activities of animals excavating hypogeous fungi contribute to bioturbation (soil disturbance) and provide important soil aeration for water penetration and organic matter decomposition (Lamont 1995, Garkaklis *et al.* 1998, 2000, 2003, 2004, Newell 2008, James *et al.* 2009, Valentine *et al.* 2013, 2018, 2021, Fleming *et al.* 2014, Clarke *et al.* 2015, Davies *et al.* 2018, Palmer *et al.* 2020, 2021). Various mycophagous animals

perform bioturbation to varying degrees, and the relative importance of animal-mediated soil turnover is also dependant on the region and soil type. In Australia, the role of mycophagous vertebrates in soil turnover has been relatively well studied in some regions. Many Australian forests are dominated by *Eucalyptus* species and their relatives (Holliday 1989). Leaves in these groups often contain high levels of oils that leach into the soil, creating a hydrophobic film on the soil surface that impairs water penetration (Garkaklis *et al.* 1998). The combination of soil dryness and oil concentration at the soil surface creates a layer of flammable material that increases the sensitivity of these forests to fires. In a healthy system, a multitude of vertebrates forage in the litter and dig down into the mineral soil in search of truffles and other subterranean foods. These activities contribute to the breaking up of the hydrophobic layer at the soil surface and create micro catchments, thus improving water penetration and assisting with organic matter decomposition (Lamont 1995, Garkaklis *et al.* 1998, 2000, 2003, 2004, Newell 2008, James *et al.* 2009, Valentine *et al.* 2013, 2018, Fleming *et al.* 2014, Davies *et al.* 2018, Palmer *et al.* 2020, Maisey *et al.* 2021).

The degree of bioturbation depends on the size of the animal and its foraging habits. Superb lyrebirds (*Menura novaehollandiae*) eat a diversity of hypogeous fungi (Elliott & Vernes 2019), and each individual is estimated to displace an average of 155.7 tonnes of soil per hectare per year (Maisey *et al.* 2021). Mammals typically turn over less soil than ground foraging birds, likely due to their keen olfactory abilities that allow them to pinpoint the locations of subterranean food (Elliott *et al.* 2019a). Ground foraging birds need to scratch larger areas to find food that they cannot necessarily detect by smell. Still, mammals contribute greatly to soil turnover. The brush-tailed bettong digs between 38 and 114 excavations per night, and each individual is estimated to displace an average of 4.8 tonnes of soil per year (Garkaklis *et al.* 2004). The southern brown bandicoot (*Isoodon obesulus*) has been estimated to dig about 45 foraging excavations per day and in the process displace about 10.74 kg of soil, resulting in a soil turnover of approximately 3.9 tonnes per year per individual (Valentine *et al.* 2013). Some of the larger desert species such as the greater bilby (*Macrotis lagotis*) and the burrowing bettong (*Bettongia lesueur*) are estimated to turn over approximately 30 tonnes of soil per year per individual (Newell 2008). These examples demonstrate the wide range in the rate/quantity of soil disturbance by various mammal species. Given that Australia is believed to have the greatest diversity of hypogeous fungi (Bougher & Lebel 2001, Claridge 2002) and is also home to numerous mycophagous mammal species, it is very likely that these interactions have coevolved.

In healthy systems, many individuals and species co-occur, and their combined foraging efforts are key to maintaining healthy forest soils. Due to the introduction of foxes and cats to Australia, many of these bioturbating mammals have disappeared from much of their historic ranges or became extinct (Bilney 2014, Fleming *et al.* 2014, Vernes *et al.* 2021). We suspect that the loss of mycophagous mammal species and the subsequent loss of their soil turnover capacities may be a contributing factor in the increased frequency/intensity of fires, as well as in the desertification of some regions of the continent. Though early foresters recognised the importance of well-aerated soil for the health of Australian forests and for the reduction of intense wildfires (Hutchins 1916), these aspects of forest ecology are unfortunately rarely considered in current forest management plans.

Ecosystem impact on below ground and above ground communities

The examples described in the previous section illustrate how mammal-mediated dispersal plays a major role in shaping the composition of soil-fungal communities. The mycorrhizal interactions between these fungi and plant roots can also directly impact plant community composition through plant-soil feedbacks (Liang *et al.* 2020) and have rippling impacts on overall ecosystem biodiversity. In the Mediterranean region, inoculation trials showed that the roots of *Pinus halepensis* seedlings inoculated with forest soil were dominated by the ectomycorrhizal fungus *Geopora* (Livne-Luzon *et al.* 2017); when faeces from Eurasian wild pigs were added to the inoculum, the ectomycorrhizal species composition shifted and became dominated by *Tuber* and other ECM species consumed preferentially by animals. The decline or extinction of mycophagous mammals may drastically affect mycorrhizal fungal diversity in soils and, in turn, directly impact the spore inoculum available to associated plants. In Western Australia, Dundas *et al.* (2018) showed that in conservation areas where mycophagous marsupials were protected within predator-proof fences, the mycorrhizal community was primarily composed of ectomycorrhizal hypogeous species that associated with the dominant tree *Corymbia calophylla*; in non-fenced areas where these mammals were virtually absent, arbuscular mycorrhizal fungi were four times more abundant. Since few species of arbuscular mycorrhizal fungi produce sporocarps that are large enough to be deliberately ingested by mammals, this suggests that mycophagy can generate fungal community shifts linked to selective pressure from mammal food choice toward specific fungal species or morphologies. Since different types of mycorrhizal fungi associate with different types of plant hosts (Trappe 1962, Brundrett & Tedersoo 2018), mycophagy likely affects the species composition of plant communities as well. For example, the biomass of *C. calophylla* seedlings inoculated with soil from fenced areas was significantly higher than when seedlings were inoculated with soil from non-fenced areas (Dundas *et al.* 2018). This suggests that the presence of mycophagous mammals likely affected the vegetation through plant-soil feedback, particularly in the ratio of ectomycorrhizal versus arbuscular mycorrhizal associations. The role of mammals as dispersal vectors of mycorrhizal fungi is likely of similar magnitude to the impact of mammals on seed dispersal in tropical forests, where a phenomenon described as “empty forests” occurs when mammal disappearance leads to significant plant biodiversity loss (Peres *et al.* 2016). It is therefore crucial to take these trophic interactions into account in conservation plans for mammals, fungi and plants.

Methodological considerations

This review highlights the ubiquitous nature of mycophagy, and yet the list we provide (Supplementary Tables S1–11) is undoubtedly far from complete. We have tried to be as comprehensive as possible and have considered all regions where terrestrial mammals are found, but there are undoubtedly species that we have overlooked or that remain unstudied. As with most reviews, this manuscript is biased toward regions and/or groups of mammals that have received more research attention. The highest diversity of mycophagous mammals has been documented in North America (Fig. 9), mostly due to the enormous diversity of rodent species recorded to consume fungi. Compared to North America, fewer rodents but a wider range of mammal orders have been recorded

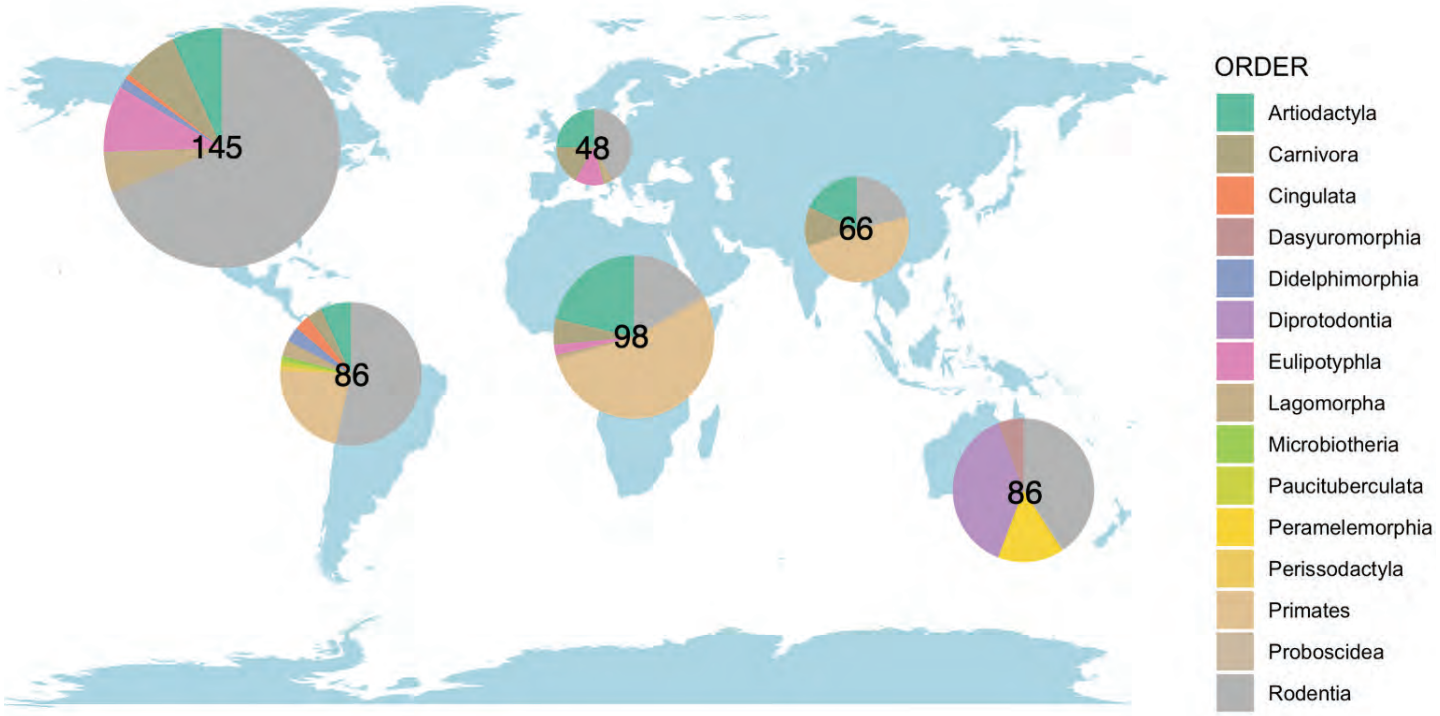

Fig. 9. Map depicting the number of mycophagous mammal species recorded per continent in North America, Central and South America, Europe, Africa, Asia (including Sulawesi) and Oceania. Colour-coded areas correspond to the number of recorded species from each mammal order. Extinct species (Neanderthals and American mastodon) have not been included. The native range of species is only considered in the context of this map. Widespread and/or exotic species (black rat, brown rat, cattle, dog, goat, grey wolf, horse, house mouse, human and sheep) have not been included given the difficulty in mapping their wild distribution and because it was not possible to determine if their mycophagous behaviour was also widespread.

to consume fungi in Central and South America, while mycophagy studies in Africa and Asia have primarily focused on primates (Fig. 9). Most studies from tropical regions, and especially Africa, are based on observational studies; very few use microscopic faecal analyses commonly applied in other regions. This likely explains why there are few reports of mycophagy among small mammals, and especially rodents, in Africa despite reports that truffles are used by traditional hunters as bait for trapping a diversity of small mammals (Kimura *et al.* 2015). It is thus highly probable that fungi are consumed as a highly desirable food by a diversity of small mammals in the region. In Oceania, endemic species of marsupials greatly contributed to the diversity of mycophagous mammals that have been documented; Europe unsurprisingly had the lowest diversity of mycophagous mammals, in correlation with the lower diversity of mammals (Fig. 9).

Language has also limited the comprehensiveness of this review. We focused on English, French, German, Portuguese and Spanish literature with a few additional works in other languages, but there are undoubtedly relevant references written in other languages that we have overlooked. This is particularly true for older references since it has only recently become more common to include English abstracts in non-English manuscripts. For example, we may have overlooked records of Asiatic mycophagous mammal species that were published in native languages; this may partially explain the lower number of mycophagous species recorded from Asia in comparison with other regions (Fig. 9).

Over the course of writing this review, we found little consistency in the way researchers refer to vertebrates eating fungi; a variety of terms were used, such as mycophagy, mycophagous, fungivory, fungivore, endozoochorous, mushroom eating or fungus eating. Some studies did not use any of these terms and only mentioned fungi in the diet list. This inconsistency in terminology hinders the development of a coherent body of knowledge about these associations. Therefore, we strongly encourage authors to use standardised terms: "mycophagy" for the action of eating fungi, with "fungus" (or "fungi") used to describe the dietary item(s). Whenever possible, we also recommend that researchers collect, voucher (deposit in a recognised herbarium) and identify (as specifically as possible) the fungi involved in the association. Adoption of these practices will allow a more comprehensive understanding of the impacts of mammals on fungal spore dispersal and the importance of different fungal species in mammal nutrition. We hope that this work will serve as a foundation for further research on mammal-fungi interactions, while also improving our understanding and awareness of these important associations.

Methods to aid fungal identification in mycophagy studies

Depending on the objectives of the study, several methods can be used to identify fungi in animal diets. Feeding behaviour has been reported through chance observations of feeding events among many animals, and systematic observational studies reporting mycophagy are particularly common in primate research. It is also possible to use camera traps to observe fungal feeding, although this can be difficult since most fungi sporulate and then decompose quite quickly. Camera trapping requires the researchers to either place fungi within the field of view of the camera or be very strategic and/or lucky with camera placement to actually capture fungal sporulation (Vernes *et al.*

2014, Vernes & Jarman 2014, Schmid *et al*. 2019, Ferkingstad 2020, Elliott & Vernes 2021a, see Supplementary Video S1).

The most common method used in the studies we reviewed is scat and/or stomach content analysis. It is rarely possible to identify fungi in the stomach of an animal using macro morphological characters, because most fungal tissues are soft and quickly become amorphous. Microscopic analysis of spores in stomach or faecal material is far more reliable. Gordon & Comport (1998) directly evaluated the effectiveness of different micro-analysis techniques, and we encourage future researchers to consider their work when selecting appropriate methods for their studies. In general, either a small subsample of stomach or faecal material is mounted on a slide, or the entire scat/stomach sample is sieved and only the fine fraction examined. The range of mounting mediums used in mycophagy studies includes KOH, water or alcohol at various percentages. Melzer's Reagent (Leonard 2006) is also used in studies focusing on fungal dietary components, since the spores of certain fungal groups produce reactions that are helpful in the taxonomic identification of spores. For best results, slide mount examination should be performed between 400 and 1 000× magnification. The accuracy of fungal species identification based on spores will vary depending on the existing background information available for fungal taxonomy in the region of interest. Ideally, fungal inventories have been performed in the area near where mammal samples were collected, allowing researchers to match spores from the mammal samples with collections of fungal sporocarps. When such information is not available, researchers depend on relevant fungal keys for the region where the study is being conducted. In this regard, Castellano *et al.* (1989) published a key that is specifically designed to identify the spores of hypogeous fungi from animal scats.

In recent years, new techniques have been developed to identify fungi in animal diets. Stable isotope signatures of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) can be used to decipher between fungi and various groups of plants in faecal samples, since ECM fungi (representing most of the fungi consumed by animals) have higher $\delta^{15}N$ values (Hobbie *et al.* 2017). Similarly, if fungal amino acids are incorporated into animal protein, the ratio of radiocarbon ($\Delta^{14}C$) in hair samples from mycophagous animals will be higher than in herbivores, since many fungi assimilate organic nitrogen from the soil with a higher $\Delta^{14}C$ than in the CO_2 incorporated by plants during photosynthesis (Hobbie *et al.* 2013). These methods are effective for deciphering fungi from plant diets but do not allow for the identification of specific fungal groups involved. There is a rise in the implementation of molecular-based approaches using DNA meta-barcoding of environmental samples (including faeces and gut contents), though they have not yet been widely employed in mycophagy studies (see: Nuske *et al.* 2019, Cloutier *et al.* 2019, Hopkins *et al.* 2021, Bradshaw *et al.* 2022). Detailed guidelines for fungal meta-barcoding are becoming abundant (see: Nguyen *et al.* 2015, Tedersoo & Lindahl 2016, Nilsson *et al.* 2019), and we strongly encourage researchers to standardise and publish detailed laboratory and bioinformatic protocols to make studies comparable between animal species and regions. Because of PCR biases toward certain fungal groups during the preparation of library amplicons, sequence abundance from next generation sequencing platforms is not directly equivalent to species, relative abundance and needs to be interpreted with caution (Pickles *et al.* 2020); this thus hinders detailed diet quantification. In addition, it is risky to base determination of mycophagy solely on these methods since the presence of fungal DNA does not necessarily indicate intentional fungal consumption nor that the fungus was "alive". We therefore encourage a rigorous and informative approach combining sequence data (with appropriate controls for DNA contamination) with microscopic examination to confirm the presence of ingested fungal material in the samples.

Finally, we wish to point out that many of the fungal groups that are frequently eaten by animals (particularly hypogeous taxa) are often inconspicuous and therefore difficult to survey. For example, States (1984) noted that the rare fungus *Sedecula pulvinata* was seldom collected during sporocarp inventories, but spores were frequently found in rodent scats in the survey area. Since *S. pulvinata* sporulates deeper underground than other hypogeous fungal species, it is frequently overlooked by humans that lack the ability of mycophagous mammals to detect its odours. Using molecular analyses of small mammal scats, Bradshaw *et al.* (2022) detected multiple species of *Rhizopogon* that were rarely collected in fungal surveys. This further highlights the potential application of animal scats as a tool in fungal surveys. Species that are rare or seldom collected may be more effectively found by foraging mammals than by scientists. This makes molecular and/or microscopic analysis of animal scats a viable surveying method to detect rare or overlooked species of fungi (Piattoni *et al.* 2016, Cloutier *et al.* 2019, Bradshaw *et al.* 2022).

CONCLUSIONS AND FUTURE DIRECTIONS OF RESEARCH

Mycophagy plays a major role in animal nutrition and fungal dispersal, with direct impacts on plant communities and overall ecosystem health. The selective pressures that mammals apply toward different fungal sporocarp morphologies, aromas, colours and habits most likely contribute to shaping fungal diversity, with critical consequences for mycorrhizal communities below and above ground. We hope that this review can serve as a foundation to inspire further research into these ecologically important yet understudied associations (Fig. 10) and their consequences for animals, fungi and plants. To expand our understanding of these associations, we highlight several key future directions of mycophagy research:

There is a need for baseline studies addressing whether fungi are a dietary component of many groups of mammals in understudied regions of the world. This is particularly true for small mammals in Africa and Asia (Fig. 9). Based on the application of inappropriate methods for determining mycophagy and the inconsistent geographic coverage of studies, it is likely that the 508 mammal species we report to consume fungi is a gross underestimation of the reality and Fig. 2 likely does not fully represent mycophagy across mammalian orders. Future studies need to take into consideration the application of appropriate methods (as outlined in the two previous sections) to determine if fungi are a component of mammal diets. The inclusion of these novel approaches would substantially improve our understanding of mammalian mycophagy globally. It would also be interesting to further investigate the diversity of mammals that practice fungal caching/hoarding behaviours and their role in fungal spore dispersal. Additionally, most research on the nutritional value of fungi has focused on cultivated mushroom species and their nutritional application for humans and/or livestock; we hope future studies will strive for a better

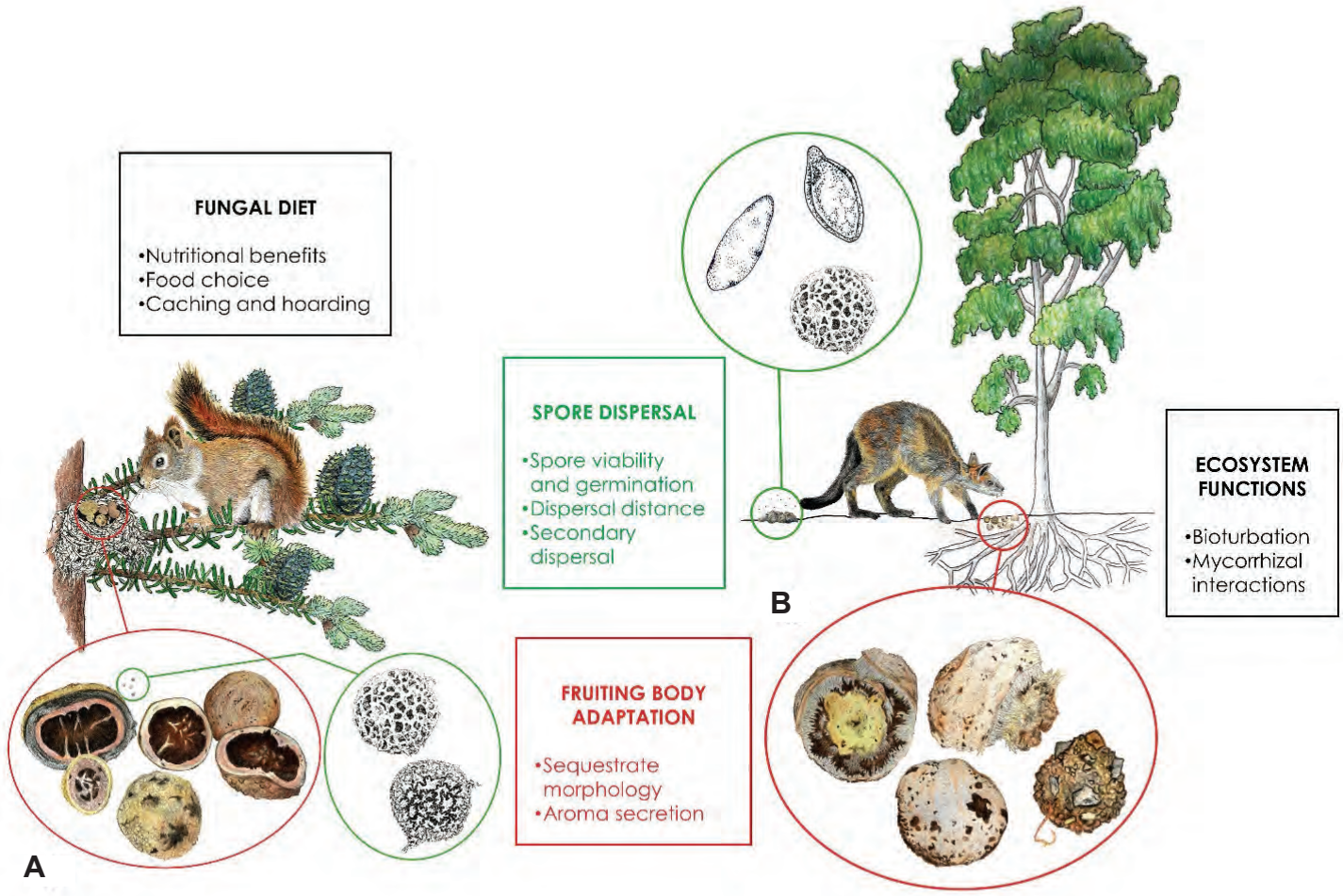

Fig. 10. Illustration representing the interactions between mammals, truffles and their ectomycorrhizal host plants. **A.** The left side of the illustration shows a North American red squirrel (*Tamiasciurus hudsonicus*) caching *Elaphomyces* truffles in an abandoned bird nest in a fir tree. **B.** In the right side of the illustration a swamp wallaby (*Wallabia bicolor*) can be seen digging for *Mesophellia* truffles at the base of an associated eucalypt tree. The wallaby also disperses fungal spores of several taxa in its scats. Illustration © PameFagus (Pamela Ciudad Martin).

understanding of the nutritional needs of wildlife consuming wild fungi, as well as preferences toward different portions of sporocarps.

To fully understand the role of mammals in spore dispersal, experimental studies on spore viability, passage rates and impacts of the presence of mycophagous mammals on soil-fungal communities need to be expanded to more mammal groups and wider geographic areas. The field of mycophagy would also benefit from a better understanding of spore enzymatic scarification in the digestive system of mammals, movement patterns combined with passage rates of different animals, and secondary dispersal by apex predators. Additionally, in order to understand the selective pressures that mammal mycophagy can apply toward the rise of certain sporocarp traits, such as sequestrate and/or hypogeous sporulating morphologies, experimental approaches are needed to determine feeding preferences toward certain traits (*e.g.* aromas, colours, shapes, nutritional components). Recent multi-gene and genome-wise molecular studies will allow researchers to determine more precisely the timing and diversification rate at which certain traits and species appeared in different groups of fungi (Varga *et al*. 2019, Sánchez-García *et al*. 2020). Coupled with predictive modelling, these studies can help to determine the role of co-occurring factors – such as past and future climate change – in the rise of certain fungal reproductive strategies.

Finally, mycophagy research needs to be considered in the wider context of the ecosystems in which these interactions occur. A handful of studies have focused on bioturbation by mammals foraging for hypogeous fungi and how mammal mycophagy contributes to the overall diversity of ectomycorrhizal fungal species, but these types of studies have so far been relatively geographically restricted. Extending these studies to other regions would significantly contribute to our understanding of the implications of mycophagy for soil aeration, water penetration, mycorrhizal plant communities and overall soil and ecosystem health.

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Supplementary Material: http://fuse-journal.org/

Table S1. The three members of the *Didelphimorphia* that have been reported to consume fungi.

Table S2. The five members of the *Dasyuromorphia* that have been reported to consume fungi.

Table S3. The 13 members of the order *Peramelemorphia* that have been reported to consume fungi.

Table S4. The 33 members of the *Diprotodontia* that have been reported to consume fungi.

Table S5. The three members of the *Cingulata* that have been reported to consume fungi.

Table S6. The 105 species in the order *Primates* that have been reported to consume fungi.

Table S7. The 12 members of the order *Lagomorpha* that have been reported to consume fungi.

Table S8. The 221 species within the order *Rodentia* that have been reported to consume fungi.

Table S9. The 21 members within the order *Eulipotyphla* that have been reported to consume fungi.

Table S10. The 27 members within the order *Carnivora* that have been reported to consume fungi.

Table S11. The 59 members within the order *Artiodactyla* that have been reported to consume fungi.

Video S1. When *Elaphomyces* truffles are unearthed, the North American red squirrel cleans the outer peridium by "shucking" adherent soil and mycelium from the truffle before it is eaten or cached (Vernes *et al.* 2014).

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Fusarium and allied fusarioid taxa (FUSA). 1

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Abstract: Seven *Fusarium* species complexes are treated, namely *F. aywerte* species complex (FASC) (two species), *F. buharicum* species complex (FBSC) (five species), *F. burgessii* species complex (FBURSC) (three species), *F. camptoceras* species complex (FCAMSC) (three species), *F. chlamydosporum* species complex (FCSC) (eight species), *F. citricola* species complex (FCCSC) (five species) and the *F. concolor* species complex (FCOSC) (four species). New species include *Fusicolla elongata* from soil (Zimbabwe), and *Neocosmospora geoasparagicola* from soil associated with *Asparagus officinalis* (Netherlands). New combinations include *Neocosmospora akasia, N. awan, N. drepaniformis, N. duplosperma, N. geoasparagicola, N. mekan, N. papillata, N. variasi* and *N. warna.* Newly validated taxa include *Longinectria gen. nov.*, *L. lagenoides*, *L. verticilliforme*, *Fusicolla gigas* and *Fusicolla guangxiensis*. Furthermore, *Fusarium rosicola* is reduced to synonymy under *N. brevis.* Finally, the genome assemblies of *Fusarium secorum* (CBS 175.32), *Microcera coccophila* (CBS 310.34), *Rectifusarium robinianum* (CBS 430.91), *Rugonectria rugulosa* (CBS 126565), and *Thelonectria blattea* (CBS 952.68) are also announced here.

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INTRODUCTION

Several initiatives in recent years have addressed problems that face contemporary fungal taxonomy. The Fungal Planet series was launched to overcome the reluctance of most mycology journals to publish single new species descriptions (Crous *et al.* 2011). The Genera of Fungi (GoF) project facilitated the application of fungal generic names through the re-collection of generic types and the designation of epitypes or neotypes (Kirk *et al.* 2013, Crous *et al*. 2014). The Fungal Systematics and Evolution (FUSE) series allowed the effective combination of molecular phylogenetic data with phenotypic data to link sexual, asexual and synasexual morphs to known or newly described taxa following the end of the dual nomenclatural system (Crous *et al.* 2015). Finally, the Genera of Phytopathogenic Fungi (GOPHY) project was introduced to stabilize the taxonomy of fungal phytopathogens at generic and species levels, coupled with biological information about host distribution, pathogenicity, disease symptomatology and DNA barcodes for accepted species (Marin-Felix *et al.* 2017). The aforementioned publication series inspired other similar initiatives worldwide, such as Fungal Biodiversity Notes (Liu *et al.* 2015), Fungal Biodiversity Profiles (Adamčík *et al.* 2015), Mycosphere Notes (Thambugala *et al*. 2017), and the more recent New and Interesting Fungi (Crous *et al.* 2018). With an average of 10 to more than 100 new taxa per issue, these publications have become valuable tools for the description of new fungal families, genera and species, as well as for the dissemination of knowledge about the world's fungal diversity.

In FUSA we introduce a new series of specialised papers focusing on the taxonomy, phylogeny, systematics, ecology and pathogenicity of known and novel *Fusarium* and allied fusarioid taxa. *Fusarium* (*F.*) and related genera are globally distributed fungi, found in diverse substrates, although most commonly in soil, living and dead plant material, air and water (Nelson *et al.* 1994, Leslie & Summerell 2006, Aoki *et al.* 2014, Leslie & Summerell 2011). Much of the historical importance of these fungi is based on the economically impactful of plant pathogenic species that infect a wide spectrum of crops inducing cankers, dieback, dry rot of roots and seeds, scab and wilt diseases (Booth 1971, Summerell *et al.* 2003); as well as numerous mycotoxigenic species endanger animal and human health (Nelson *et al.* 1994, O'Donnell *et al.* 2018). Nevertheless, in the last decade several taxa have gained importance as opportunistic human and animal pathogens, particularly members of *Neocosmospora* (formerly the *Fusarium solani* species complex), *Bisifusarium* (formerly the *Fusarium dimerum* species complex) and members of at least five species complexes of *Fusarium sensu stricto* (van Diepeningen *et al.* 2014, Lombard *et al.* 2015, Sandoval-Denis *et al*. 2018, 2019, Crous *et al.* 2021b).

The main goal of FUSA is to publish modern diagnoses of fusarioid taxa, based on multilocus phylogenies, ideally accompanied by genomic data, morphological descriptions, as well as physiological and ecological data. These data will subsequently be placed in an online database, www.fusarium.org, linked to the fusarioid-ID database, which aims to provide a stable, regularly updated, and user-friendly platform for the identification of *Fusarium* and other fusarioid genera and species through advanced BLASTn queries of well-curated DNA sequences.

Contributors are encouraged to use FUSE as an instrument for typification events to stabilise the application of names by designating accurate lectotypes, epitypes and neotypes;

proposing taxonomic novelties such as new combinations and replacement names; and publishing undescribed morphologies for known taxa (asexual/sexual-morph connections). The selection of culture media, culture conditions and the morphological treatment must be based on standardised fusarioid laboratory protocols, as outlined in Crous *et al.* (2021b); fungal descriptions must be standardised and follow given examples; description of new species should be accompanied by a brief, comprehensive taxonomic discussion; all taxonomic novelties must be registered in MycoBank and ex-type or ex-isotype strains should be deposited in the CBS collection if possible (hosted in the Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands). Mycologists and other researchers wishing to contribute to future issues of FUSA are encouraged to contact the Editor-in-Chief (p.crous@wi.knaw.nl).

MATERIALS AND METHODS

Methods, media, protocols and molecular analyses follow guidelines as outlined by Crous *et al.* (2021b). Sequences derived in this study were deposited in GenBank (Table 1), alignments and phylogenetic trees in Figshare (www.figshare.com; doi identifier 10.6084/m9.figshare.20076044), and taxonomic novelties in MycoBank (www.MycoBank.org; Crous *et al*. 2004). Alignments composition and evolutionary models are summarized in Table 2.

Genome assembly

DNA was extracted from mycelium grown on SAM (Kruse *et al*. 2017) culture plates as described earlier (Mishra *et al*. 2018). Library construction and short-read sequencing was done by a commercial sequencing provider (BGI, Hongkong, PRC). Pair-end reads (150 bp, 400 bp insert) were cleaned with *Trimmomatic* v. 0.39 (Bolger *et al.* 2014) with the following settings: remove leading and trailing low quality (< 3) or N bases; cutting when the average quality per base dropped below 15 in a 4-base sliding window; Illumina adaptor removal; removing reads shorter than 70 bp. Cleaned reads were used to assemble genomes with *velvet* v. 1.2.10 (Zerbino & Birney, 2008) using a k-mer value of 93. Assembly statistics were obtained using the stats.sh script of the BBTools package (Bushnell 2021). The assembly quality was evaluated with BUSCO v. 5.2.2 against the fungi_odb10 library (Manni *et al.* 2021). Genome annotation was done with maker v. 3.01.03 (Cantarel *et al.* 2008) for gene prediction using the protein sequences of *Fusarium oxysporum* from the UniProt database as reference. All genomes were submitted to GenBank (see Table 3 for details).

RESULTS

Phylogeny

For this study, three multilocus analyses were carried out. The datasets were analysed using IQ-TREE v. 2.1.3 (Nguyen *et al*. 2015, Minh *et al*. 2020) and MrBayes v. 3.2.7 (Ronquist & Huelsenbeck 2003) as indicated in Crous *et al.* (2021b).

An overview of currently accepted taxa in *Fusarium* species complexes treated in this study is shown in a phylogeny constructed from combined *rpb1*, *rpb2* and *tef1* data of 62 strains, encompassing eight species complexes *i.e.*, *Fusarium aywerte* (FASC), *F. buharicum* (FBSC), *F. burgessii* (FBURSC), *F. camptoceras* (FCAMSC), *F. chlamydosporum* (FCSC), *F. citricola* (FCCSC), and *F. concolor* (FCOSC), including the outgroup taxa (*F. lateritium* NRRL 13622 and *F. stilboides* NRRL 20429, both species belonging to the *F. lateritium* species complex) (Fig. 1). IQ-TREE best tree (log-likelihood -26203.881) was found after 102 iterations. Bayesian analysis lasted for 235 000 generations and recovered 472 trees from which 354 where sampled. The phylogeny resolved all the treated species complexes with high statistical support. Thirty species are recognised (two in FASC, three each in FBURSC and FCAMSC, five each in FCCSC, and FBSC; eight in FCSC, and four in FCOSC). Additionally, three phylogenetic species awaiting formal description were found, of which one resolved in FCSC (*Fusarium* sp. FCSC 9) and two in the FBSC (clades *Fusarium* sp. 1, and *Fusarium* sp. 2)

Fusicolla: A phylogeny was constructed using combined *acl1*, ITS, LSU, *rpb2* and *tub2* sequences of 23 strains representing 18 species of *Fusicolla* (*Fu.*), plus two outgroup taxa (*Macroconia leptosphaeriae* CBS 10001 and *Scolecofusarium ciliatum* CBS 148938) (Fig. 2). IQ-TREE best tree (log-likelihood -15164.779) was found after 117 iterations. Bayesian analysis lasted for 1 535 000 generations and recovered 3 072 trees from which 2 304 where sampled. Two strains obtained from soil in Zimbabwe (MUCL 58143, 58144) are formally described below as the novel species *Fusicolla elongata*. Sequence data from additional *Fusicolla* species known from culture (*Fu*. *gigas*, *Fu*. *hughesii*, *Fu*. *guangxiensis*) or sequenced from fungarium specimens (*Fu*. *reyesiana*) were initially included in the phylogenies and later removed from the final analyses due to their incomplete datasets (nrDNA or only ITS1 and ITS2 sequences available). Two species recently invalidly published *i.e*., *Fu*. *gigas* and *Fu*. *guangxiensis* are re-validated here based on the original protologue (Liu *et al*. 2022).

Neocosmospora: A combined alignment was built including ITS, *rpb1*, *rpb2*, and *tef1* sequences from 73 strains representing the known species diversity of the Ambrosia Clade (Kasson *et al.* 2013) and close relatives from Clades 1, 2 and 3 of *Neocosmospora* (O'Donnell 2000) (Fig. 3). IQ-TREE best tree (log-likelihood -20219.033) was found after 103 iterations. Bayesian analysis lasted for 480 000 generations and recovered 962 trees from which 722 where sampled. The Ambrosia Clade was found to encompass 23 phylogenetic species (AF 1-23), 15 of which have been formally described to date. *Fusarium* species are recombined in *Neocosmospora* including seven species in the Ambrosia Clade (*N. akasia*, *N. drepaniformis*, *N. duplosperma*, *N. mekan*, *N. papillata*, *N. variasi*, and *N. warna*) and the distantly related although ecologically similar *N. awan*. The ex-type of *F. rosicola* (YJ1) clustered with *N. brevis*, and the former is synonymised under the latter. A previously undescribed, phylogenetically well-differentiated clade composed of seven soil isolates obtained from different asparagus (*Asparagus officinalis*) fields, formed a basal lineage in Clade 2. This lineage is formally proposed below as the novel species *N. geoasparagicola*.

Table 1. Collection details and GenBank accession numbers of isolates treated in this study.

Species	Strain[1]	Country and substrate/ host	GenBank accession number[2]						
			acl1	ITS	LSU	*rpb1*	*rpb2*	*tef1*	*tub2*
Fusarium abutilonis	NRRL 66737[T]	Canada, *Abutilon theophrasti*				JAJJWN010000057[†]	JAJJWN010000064[†]	JAJJWN010000135[†]	
Fusarium aconidiale	CBS 147772[T]	France, *Triticum aestivum*	-	-	-	MZ078192	MZ078218	MZ078246	-
Fusarium algeriense	CBS 142638[T]	Algeria, *Triticum durum*	-	-	-	MF120488	MF120499	MF120510	-
Fusarium anguioides	LC7240	China, bamboo	-	-	-	MW024433	MW474388	MW580442	-
	NRRL 25385	China, bamboo	-	-	-	JX171511	JX171624	MH742689	-
Fusarium atrovinosum	CBS 445.67[T]	Australia, *Triticum aestivum*	-	-	-	MN120713	MW928822	MN120752	-
	CBS 130394	USA, human leg	-	-	-	MN120714	MN120734	MN120753	-
	NRRL 13444	Australia, corn soil	-	-	-	JX171454	JX171568	GQ505403	-
	NRRL 34013	USA, human toe nail	-	-	-	-	GQ505472	GQ505408	-
	NRRL 34016	USA, human leg	-	-	-	HM347170	GQ505475	GQ505411	-
Fusarium austroafricanum	NRRL 66741[T]	South Africa, *Pennisetum clandestinum*	-	-	-	MH742537	MH742616	MH742616	-
	NRRL 66742	South Africa, *Pennisetum clandestinum*	-	-	-	MH742538	MH742617	MH742688	-
Fusarium aywerte	NRRL 25410[T]	Australia, soil	-	-	-	JX171513	JX171626	JABCQV010000336[†]	-
Fusarium bambusarum	CGMCC 3.20820[T]	China, bamboo	-	-	-	MW024434	MW474389	MW580443	-
	LC7187	China, bamboo	-	-	-	MW024435	MW474390	MW580444	-
Fusarium beomiforme	CBS 100160[T]	Australia, soil	-	-	-	MF120485	MF120496	MF120507	-
Fusarium buharicum	CBS 178.35[ET]	Uzbekistan, *Gossypium herbaceum*	-	-	-	KX302920	KX302928	KX302912	-
	CBS 796.70	Iran, *Hibiscus cannabinus*	-	-	-	JX171449	JX171563	-	-
Fusarium burgessii	CBS 125537[T]	Australia, soil	-	-	-	MT409440	HQ646393	HQ667148	-
Fusarium camptoceras	CBS 193.65[ET]	Costa Rica, *Theobroma cacao*	-	-	-	MW928800	MN170383	AB820706	-
Fusarium celtidicola	MFLUCC 16-0526[T]	Italy, *Celtis australis*	-	-	-	MH576579	**ON759296**	**ON745620**	-
Fusarium chlamydosporum	CBS 145.25[NT]	Honduras, *Musa sapientum*	-	-	-	MN120715	MN120735	MN120754	-
	CBS 615.87	Cuba, *Colocasia esculenta*	-	-	-	JX171526	GQ505469	GQ505405	-
	CBS 677.77	Solomon Islands, soil	-	-	-	MN120716	GQ505486	GQ505422	-
	NRRL 34019	USA, human eye	-	-	-	-	GQ505478	GQ505414	-
	NRRL 43633	USA, human sinus	-	-	-	-	GQ505493	GQ505429	-
Fusarium citricola	CBS 142421[T]	Italy, *Citrus reticulata*	-	-	-	LT746290	LT746310	LT746197	-

Table 1. (Continued).

Species	Strain[1]	Country and substrate/ host	GenBank accession number[2]						
			acl1	ITS	LSU	*rpb1*	*rpb2*	*tef1*	*tub2*
	CPC 27067	Italy, *Citrus limon*	-	-	-	LT746287	LT746307	LT746194	-
Fusarium concolor	CBS 183.34^{T}	Uruguay, *Hordeum vulgare*	-	-	-	MH742492	MH742569	MH742650	-
	CBS 677.94	South Africa, soil	-	-	-	MH742503	MH742580	MH742660	-
Fusarium convolutans	CBS 144207^{T}	South Africa, *Kyphocarpa angustifolia* rhizosphere	-	-	-	LT996193	LT996141	LT996094	-
	CBS 144208	South Africa, *Kyphocarpa angustifolia* rhizosphere	-	-	-	LT996194	LT996142	LT996095	-
Fusarium guadeloupense	CBS 102302^{T}	Guadeloupe, soil				JAJJWL010000373[†]	JAJJWL010000322[†]	JAJJWL010000221[†]	
	NRRL 66743	USA, human blood				JAJJWM010000272[†]	JAJJWM010000096[†]	JAJJWM010000091[†]	
Fusarium humicola	CBS 124.73^{T}	Pakistan, soil	-	-	-	MN120718	MN120738	MN120757	-
Fusarium juglandicola	CBS 147773^{T}	France, *Juglans regia*	-	-	-	MZ078190	MZ078215	MZ078243	-
	CBS 147775	France, *Juniperus* sp.	-	-	-	MZ078191	MZ078217	MK034341	-
Fusarium kotabaruense	InaCC F963^{T}	Indonesia, *Musa* sp.	-	-	-	LS479875	LS479859	LS479445	-
Fusarium lateritium	NRRL 13622	USA, *Ulmus* sp.	-	-	-	JX171457	JX171571	JAAVTZ000000000[†]	-
Fusarium microconidium	CBS 119843^{T}	Unknown	-	-	-	MN120721	-	MN120759	-
Fusarium nelsonii	CBS 119876^{T}	South Africa, plant debris	-	-	-	MN120722	GQ505468	GQ505404	-
	CBS 119877	Unknown	-	-	-	MN120721	MN120741	MN120759	-
Fusarium neosemitectum	CBS 189.60^{T}	Congo, *Musa sapientum*	-	-	-	-	MN170422	MN170489	-
	CBS 190.60	Congo, *Musa sapientum*	-	-	-	-	MN170423	MN170490	-
Fusarium peruvianum	CBS 511.75^{T}	Peru, *Gossypium* sp.	-	-	-	MN120728	MN120746	MN120767	-
Fusarium salinense	CBS 142420^{T}	Italy, *Citrus sinensis*	-	-	-	LT746286	LT746306	LT746193	-
	CPC 26403	Italy, *Citrus sinensis*	-	-	-	LT746304	LT746191	LT746284	-
Fusarium sp. (FCSC9)	NRRL 13338	Australia, soil	-	-	-	JX171447	JX171561	GQ505402	-
Fusarium sp. 1	NRRL 66179	USA, *Hibiscus moscheutos*	-	-	-	KX302921	KX302929	KX302913	-
	NRRL 66180	USA, *Hibiscus moscheutos*	-	-	-	KX302922	KX302930	KX302914	-
	NRRL 66181	USA, *Hibiscus moscheutos*	-	-	-	KX302923	KX302931	KX302915	-
	NRRL 66182	USA, *Hibiscus moscheutos*	-	-	-	KX302924	KX302932	KX302916	-
	NRRL 66183	USA, *Hibiscus moscheutos*	-	-	-	KX302925	KX302933	KX302917	-

Table 1. (Continued).

Species	Strain[1]	Country and substrate/ host	GenBank accession number[2]						
			acl1	ITS	LSU	*rpb1*	*rpb2*	*tef1*	*tub2*
	NRRL 66184	USA, *Hibiscus moscheutos*	-	-	-	KX302926	KX302934	KX302918	-
Fusarium sp. 2	NRRL 66739	China, unknown				JAJJWO010000055[†]	JAJJWO010000203[†]	JAJJWO010000256[†]	
Fusarium spinosum	CBS 122438[T]	Brazil, *Cucumis melo*	-	-	-	MN120729	MN120747	MN120768	-
	NRRL 43631	USA, human leg	-	-	-	HM347187	GQ505491	GQ505427	-
Fusarium sporodochiale	CBS 220.61[T]	South Africa, soil	-	-	-	MN120731	MN120749	MN120770	-
Fusarium stilboides	NRRL 20429	Nyasaland, *Coffea* sp.	-	-	-	JX171468	JX171582	-	-
Fusarium sublunatum	CBS 189.34[T]	Costa Rica, soil	-	-	-	JX171451	JX171565	-	-
	CBS 190.34	Costa Rica, soil	-	-	-	KX302927	KX302935	KX302919	-
Fusarium tjaynera	NRRL 66246[T]	Australia, *Triodia microstachya*	-	-	-	KP083268	KP083279	EF107152	-
Fusicolla acetilerea	BBA 63789[T]	Japan, polluted soil	HQ897839	HQ897790	U88108	-	HQ897701	-	-
Fusicolla aquaeductuum	CBS 268.53	Netherlands, rubber tubing	-	MH857190	MH868728	-	-	-	-
	CBS 837.85[ET]	Germany, plug in water tap	-	KM231823	KM231699	-	-	-	KM232094
Fusicolla betae	BBA 64317[ET]	Germany, *Triticum aestivum*	HQ897917	-	-	-	HQ897781	-	-
Fusicolla bharatavarshae	NFCCI 4423[T]	India, *Avicennia marina*	-	MK152510	MK152511	-	MK157022	-	MK376462
Fusicolla cassiae-fistulae	MFLUCC 19-0318[T]	Thailand, *Cassia fistula*	-	MT215497	MT215549	-	-	-	-
Fusicolla elongata	CBS 148934[T]	Zimbabwe, soil	**ON759286**	**ON763203**	**ON763200**	-	**ON759297**	-	**ON745628**
	CBS 148935	Zimbabwe, soil	**ON759287**	**ON763204**	**ON763201**	-	**ON759298**	-	**ON745629**
Fusicolla epistroma	BBA 62201[ET]	UK, *Diatrypella* sp., on *Betula* sp.	HQ897901	-	AF228352	-	HQ897765	-	-
Fusicolla gigantispora	HKAS 101990	Thailand, *Bruguiera* sp.	-	MN047106	MN017870	-	-	-	-
	MFLU 16-1206[T]	Thailand, *Avicennia marina*	-	MN047105	MN017876	-	-	-	-
Fusicolla gigas	CGMCC 3.20680	China, soil	-	OK465362	OK465449	-	-	-	-
Fusicolla guangxiensis	CGMCC 3.20679	China, rotten twig	-	OK465363	OK465450	-	-	-	-
Fusicolla matuoi	CBS 581.78	Japan, *Albizzia julibrissin*	HQ897858	KM231822	KM231698	-	HQ897720	-	KM232093
Fusicolla melogrammae	CBS 141092[T]	UK, *Melogramma campylosporum* on *Carpinus* sp.	-	KX897140	KY092489	-	HQ897720	-	MW834305
Fusicolla meniscoidea	CBS 110189[T]	Australia, soil	MW834043	MW827613	MW827654	-	MW834010	-	MW834306
	CBS 186.34	Germany, *Acer* sp.	-	MH855482	MH866963	-	-	-	-

Table 1. (Continued).

Species	Strain[1]	Country and substrate/ host	GenBank accession number[2]						
			acl1	ITS	LSU	*rpb1*	*rpb2*	*tef1*	*tub2*
Fusicolla ossicola	CBS 140161[T]	Belgium, bone of wild boar	-	MF628022	MF628021	-	MW834011	-	MW834307
Fusicolla quarantenae	CBS 141541[T]	Brazil, *Melocactus zehntneri*	MW834044	MW553789	MW553788	-	MW556626	-	MW556624
Fusicolla septimanifiniscientiae	CBS 144935[T]	Netherlands, soil	-	MK069422	MK069418	-	-	-	MK069408
Fusicolla siamensis	MFLUCC 17-2577[T]	Thailand, *Cassia fistula*	-	MT215498	MT215550	-	-	-	-
Fusicolla sporellula	CBS 110191[T]	South Africa, soil	MW834044	MW827614	MW827655	-	MW834012	-	MW834308
Fusicolla violacea	CBS 634.76[T]	Iran, *Quadraspidiotus perniciosus*	-	KM231824	U88112	-	HQ897696	-	KM232095
Geejayessia atrofusca	NRRL 22316	USA, *Staphylea trifolia*	-	AF178423	-	JX171496	EU329502	AF178361	-
Geejayessia cicatricum	CBS 125552	Slovenia, dead twig	-	HQ728145	-	-	HQ728153	HM626644	-
Macroconia leptosphaeriae	CBS 100001	Netherlands, *Leptosphaeria* sp.	HQ897891	HQ897810	HQ897755	MW834203	HQ728164	-	KM232097
Neocosmospora acutispora	CBS 145461[T]	Guatemala, *Coffea arabica*	-	LR583700	-	MW834210	LR583814	LR583593	-
Neocosmospora akasia	CBS 146880[T]	Indonesia, *Euwallacea perbrevis*	-	MN954357	-	-	MT009931, MT010011	MT009971	-
	CMW52865	Indonesia, *Acacia crassicarpa*	-	MN954330	-	-	MT009904, MT009984	MT009943	-
Neocosmospora ambrosia	CBS 571.94[ET]	India, *Euwallacea fornicatus*	-	EU329669	-	MW834211	EU329503	FJ240350	-
	NRRL 62942	Sri Lanka, *Camellia sinensis*	-	KM406631	-	KM406638	KM406638, KM406645	KM406624	-
Neocosmospora awan	CBS 146882[T]	Indonesia, *Acacia crassicarpa*	-	MN954345	-	-	MT009919, MT009999	MT009973	-
	CBS 146884	Indonesia, *Acacia crassicarpa*	-	JQ038014	-	-	JQ038028	JQ038007	-
Neocosmospora brevis	CBS 144387[T]	Belgium, soil-water	-	LR583708	-	MW834214	LR583822	LR583601	-
	CPC 27191	Italy, *Citrus sinensis*	-	LT746248	-	-	LT746313	LT746200	-
	YJ1	China, *Rosa chinensis*	-	MW724816	-	-	MW795356	MW795357	-
	YJ2	China, *Rosa chinensis*	-	MW724817	-	-	MW795358	MW795359	-
Neocosmospora cryptoseptata	CBS 145463[T]	French Guiana, bark	-	AF178414	-	MW834215	EU329510	AF178351	-
Neocosmospora drepaniformis	NRRL 62941[T]	Singapore, unknown	-	KM406633	-	JAALXN000000000[†]	KM406640, KM406647	KM406626	-

Table 1. (Continued).

Species	Strain[1]	Country and substrate/ host	GenBank accession number[2]						
			acl1	ITS	LSU	*rpb1*	*rpb2*	*tef1*	*tub2*
Neocosmospora duplosperma	NRRL 62583[T]	USA, *Euwallacea fornicatus*	-	KC691581	-	KC691611	KC691642, KC691671	KC691553	-
	NRRL 62585	USA, *Euwallacea fornicatus*	-	KC691577	-	KC691607	KC691638, KC691667	KC691549	-
Neocosmospora euwallaceae	CBS 135854[T]	Israel, *Euwallacea* sp.	-	JQ038014	-	JQ038021	JQ038028	JQ038007	-
	NRRL 62626	USA, *Euwallacea* sp.	-	KC691560	-	KC691590	KC691621, KC691650	KC691532	-
Neocosmospora floridana	NRRL 62608	USA, Boxelder tree infested with *Euwallacea interjectus*	-	KC691562	-	KC691592	KC691623, KC691652	KC691534	-
	NRRL 62628[T]	USA, *Euwallacea interjectus*	-	KC691563	-	KC691593	KC691624, KC691653	KC691535	-
Neocosmospora geoasparagicola	CBS 148936	Netherlands, soil	-	**ON763206**	-	**ON759289**	**ON759300**	**ON745621**	-
	CBS 148937[T]	Netherlands, soil	-	**ON763207**	-	**ON759290**	**ON759301**	**ON745622**	-
	CPC 39931	Netherlands, soil	-	**ON763208**	-	**ON759291**	**ON759302**	**ON745623**	-
	CPC 39932	Netherlands, soil	-	**ON763209**	-	**ON759292**	**ON759303**	**ON745624**	-
	CPC 40571	Netherlands, soil	-	**ON763210**	-	**ON759293**	**ON759304**	**ON745625**	-
	CPC 40579	Netherlands, soil	-	**ON763211**	-	**ON759294**	**ON759305**	**ON745626**	-
	CPC 40628	Netherlands, soil	-	**ON763212**	-	**ON759295**	**ON759306**	**ON745627**	-
Neocosmospora illudens	CBS 147303	New Zealand, *Beilschmiedia tawa*	-	AF178393	-	JX171488	JX171601	AF178326	-
Neocosmospora kuroshio	CBS 142642[T]	USA, *Euwallacea* sp. gallery	-	LR583723	-	KX262236	KX262256	KX262216	-
	NRRL 62946	USA, *Platanus racemosa*	-	KM406637	-	KM406644	KM406650	KM406630	-
Neocosmospora kurunegalensis	CBS 119599[T]	Sri Lanka, recently cut tree	-	JF433036	-	MW834228	LR583838	DQ247511	-
Neocosmospora lichenicola	CBS 623.92[ET]	Germany, human	-		-	-	LR583845	LR583620	-
Neocosmospora mahasenii	CBS 119594[T]	Sri Lanka, unknown tree	-	JF433045	-	MW834231	LT960563	DQ247513	-
Neocosmospora mekan	CBS 146885[T]	Indonesia, *Euwallacea similis*	-	MN954342	-	-	MT009916, MT009996	MT009956	-
	CBS 146886	Indonesia, *Acacia crassicarpa* infested with *Euwallaceae* spp.	-	MN954335	-	-	MT009909, MT009989	MT009962	-
Neocosmospora nirenbergiana	CBS 145469[T]	French Guiana, Bark	-	AF178403	-	-	EU329505	AF178339	-
Neocosmospora obliquiseptata	NRRL 62610	Australia, *Euwallacea* sp. gallery	-	KC691575	-	KC691605	KC691636, KC691665	KC691547	-

Table 1. (Continued).

Species	Strain[1]	Country and substrate/ host	GenBank accession number[2]						
			acl1	ITS	LSU	*rpb1*	*rpb2*	*tef1*	*tub2*
	NRRL 62611[T]	Australia, *Euwallacea* sp. gallery	-	KC691576	-	KC691606	KC691637, KC691666	KC691535	-
Neocosmospora oligoseptata	CBS 143241[T]	USA, *Euwallacea validus*	-	KC691566	-	KC691596	LR583854	KC691538	-
	NRRL 62582	USA, *Ailanthus* sp.	-	KC691569	-	KC691599	KC691630, KC691659	KC691541	-
Neocosmospora papillata	NRRL 62943[T]	Sri Lanka, *Camellia sinensis*	-	KM406635	-	KM406642	S24402*	KM406628	-
	NRRL 62944	Sri Lanka, *Euwallaceae* sp. on *Camellia sinensis*	-	KM406634	-	KM406641	KM406648	KM406627	-
Neocosmospora phaseoli	CBS 265.50	USA, *Phaseolus* sp.	-	LR583750	-	-	KJ511278	FJ919464	-
Neocosmospora plagianthi	NRRL 22632	New Zealand, *Hoheria glabrata*	-	AF178417	-	JX171501	JX171614	AF178354	-
Neocosmospora rectiphora	CBS 125726	Sri Lanka, dead tree	-	JF433043	-	MW834248	MW834028	JF433026	-
	CBS 125727[T]	Sri Lanka, dead tree	-	JF433034	-	MW834249	LR583871	DQ247509	-
Neocosmospora rekana	CMW53690	Indonesia, *Euwallacea fornicatus*	-	MN249098	-	-	MN249141, MN249112	MN249155	-
	CMW52862[T]	Indonesia, *Euwallacea perbrevis*	-	MN249094	-	-	MN249137, MN249108	MN249151	-
Neocosmospora robusta	CBS 145473[T]	Venezuela, bark	-	AF178405	-	MW834251	EU329507	AF178341	-
Neocosmospora samuelsii	CBS 114067[T]	Guyana, bark	-	LR583764	-	MW834252	LR583874	LR583644	-
Neocosmospora sp. (AF-6)	NRRL 62590	USA, *Euwallacea fornicatus* gallery	-	KC691574	-	KC691604	KC691635, KC691664	KC691546	-
	NRRL 62591	USA, *Euwallacea fornicatus* gallery	-	KC691573	-	KC691603	KC691634, KC691663	KC691545	-
Neocosmospora sp. (AF-9)	NRRL 22643	Costa Rica, *Xyleborus ferrugineus*	-	KC691583	-	KC691613	KC691644, KC691673	DQ247628	-
	NRRL 66088	USA, *Delonix regia*	-	KM406632	-	KM406639	KM406646	KM406625	-
Neocosmospora sp. (AF-13)	UCR4674	Taiwan, *Euwallacea* sp.	-	KX262208	-	KX262248	KX262268	KX262228	-
	UCR4675	Taiwan, *Euwallacea* sp.	-	KX262209	-	KX262249	KX262269	KX262229	-
Neocosmospora sp. (AF-14)	UCR4672	Taiwan, *Euwallacea* sp.	-	KX262206	-	KX262246	KX262266	KX262226	-
	UCR4681	Taiwan, *Euwallacea* sp.	-	KX262215	-	KX262255	KX262275	KX262235	-
Neocosmospora sp. (AF-15)	UCR4679	Taiwan, *Euwallacea* sp.	-	KX262213	-	KX262253	KX262273	KX262233	-
Neocosmospora sp. (AF-16)	UCR4673	Taiwan, *Euwallacea* sp.	-	KX262207	-	KX262247	KX262267	KX262227	-
	UCR4678	Taiwan, *Euwallacea* sp.	-	KX262212	-	KX262252	KX262272	KX262232	-
Neocosmospora sp. (AF-17)	UCR4676	Taiwan, *Euwallacea* sp.	-	KX262210	-	KX262250	KX262270	KX262230	-
	UCR4680	Taiwan, *Euwallacea* sp.	-	KX262214	-	KX262254	KX262274	KX262234	-

Table 1. (Continued).

Species	Strain[1]	Country and substrate/ host	GenBank accession number[2]						
			acl1	ITS	LSU	*rpb1*	*rpb2*	*tef1*	*tub2*
Neocosmospora sp. (AF-18)	UCR4677	Taiwan, *Euwallacea* sp.	-	KX262211	-	KX262251	KX262271	KX262231	-
Neocosmospora tuaranensis	NRRL 22231[T]	Malaysia, *Hevea brasiliensis*	-	KC691570	-	KC691600	KC691660, KC691631	KC691542	-
	NRRL 46519	Malaysia, beetle on *Hevea brasiliensis*	-	KC691572	-	KC691602	KC691633	KC691544	-
Neocosmospora variasi	CBS 146888[T]	Indonesia, *Acacia crassicarpa* infested with *E. perbrevis*	-	MN954356	-	-	MT009913, MT009993	MT009967	-
	CBS 146889	Indonesia, *Acacia crassicarpa* infested with *E. perbrevis*	-	MN954357	-	-	MT009914, MT009994	MT009968	-
Neocosmospora vasinfecta	NRRL 22166[ET]	USA, *Gossypium* sp.	-	DQ094319	-	SSHR01002742[†]	EU329497	AF178350	-
	NRRL 43467	USA, human eye	-	EF453092	-	HM347178	EF469979	EF452940	-
Neocosmospora warna	CBS 146891[T]	Indonesia, *Euwallacea perbrevis*	-	MN954346	-	-	MT009920, MT010000	MT009955	-
	CBS 146893	Indonesia, *Euwallacea perbrevis*	-	MN954351	-	-	MT009925, MT010005	MT009958	-
Scolecofusarium ciliatum	CBS 148938	Ukraine, *Peniophora rufomarginata*	**ON759288**	**ON763205**	**ON763202**	-	**ON759299**	-	**ON745630**

[1] CBS: Westerdijk Fungal Biodiverity Institute (WI), Utrecht, The Netherlands; CGMCC: China General Microbiological Culture Collection Centre, Beijing, China. CMW: Culture collection at the FABI, University of Pretoria, South Africa; CPC: Collection of P.W. Crous, held at WI; HKAS: Herbarium of Cryptogams, Kunming Institute of Botany, Kunming, China; InaCC: Indonesian Culture Collection, Cibinong, Indonesia; LC: Collection of Lei Cai, held at the Institute of Microbiology, Chinese Academy of Sciences, Beijing, China. MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; NFCCI; National Fungal Culture Collection of India, Pune, India; NRRL: Agricultural Research Service Culture Collection, National Center for Agricultural Utilization Research, USDA, Peoria, USA; UCR: collection of the University of California, Riverside, USA; YJ: Pathology Laboratory, Nanjing Forestry University, Nanjing, China. [ET]: Ex-epitype; [NT]: Ex-neotype; [T]: Ex-type.

[2] *acl1*: partial ATP citrate lyase gene; ITS: internal transcribed spacer regions with intervening 5.8S nrRNA gene; LSU: 28S large subunit of the nrDNA; *rpb1*: partial DNA-directed RNA polymerase II largest subunit gene; *rpb2*: partial DNA-directed RNA polymerase II second largest subunit gene, two accession numbers refer to two non-contiguous fragments; *tef1*: partial translation elongation factor 1-alpha gene; *tub2*: partial beta-tubulin gene. [†]: sequences extracted from full genome sequences; *: sequence available at TreeBASE (study number); sequences generated in this study are shown in **bold**.

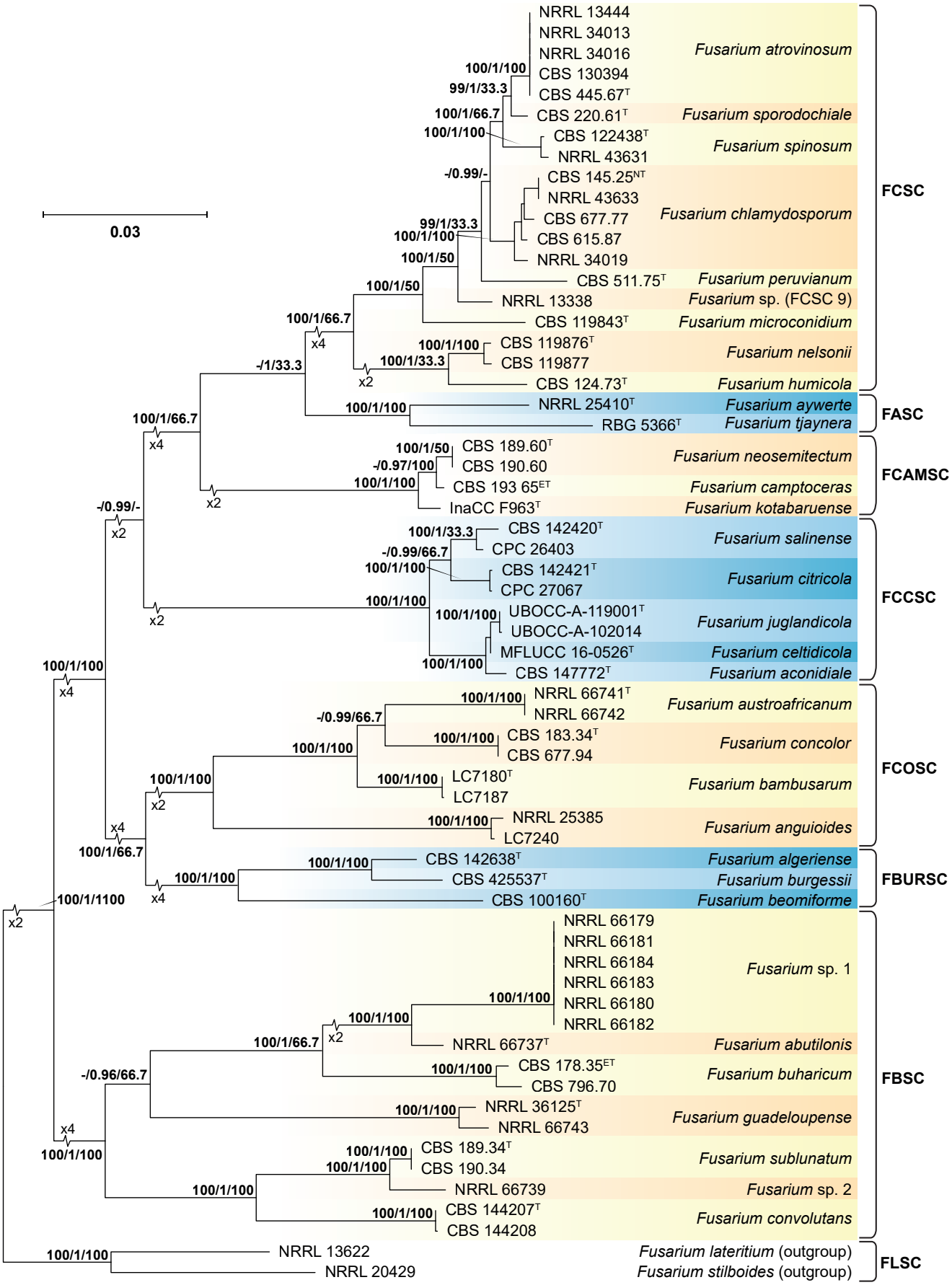

Fig. 1. IQ-TREE phylogeny inferred from the combined *rpb1*, *rpb2* and *tef1* sequences of currently accepted species belonging to seven species complexes (SC) of *Fusarium i.e.*, *F. aywerte* (FASC), *F. buharicum* (FBSC), *F. burgessii* (FBURSC), *F. camptoceras* (FCAMSC), *F. chlamydosporum* (FCSC), *F. citricola* (FCCSC), and *F. concolor* (FCOSC). Numbers at the nodes correspond to IQ-TREE bootstrap values ≥ 95 % followed by Bayesian posterior probabilities ≥ 0.95, and IQ-TREE gene concordance factors. The tree is rooted to *F. lateritium* NRRL 13622 and *F. stilboides* NRRL 20429 (FLSC). The scale bar indicates the expected number of nucleotide substitutions per site. Species complexes are indicated on the right and highlighted with coloured blocks. Ex-epitype, ex-neotype, and ex-type strains are indicated with ET, NT, and T, respectively.

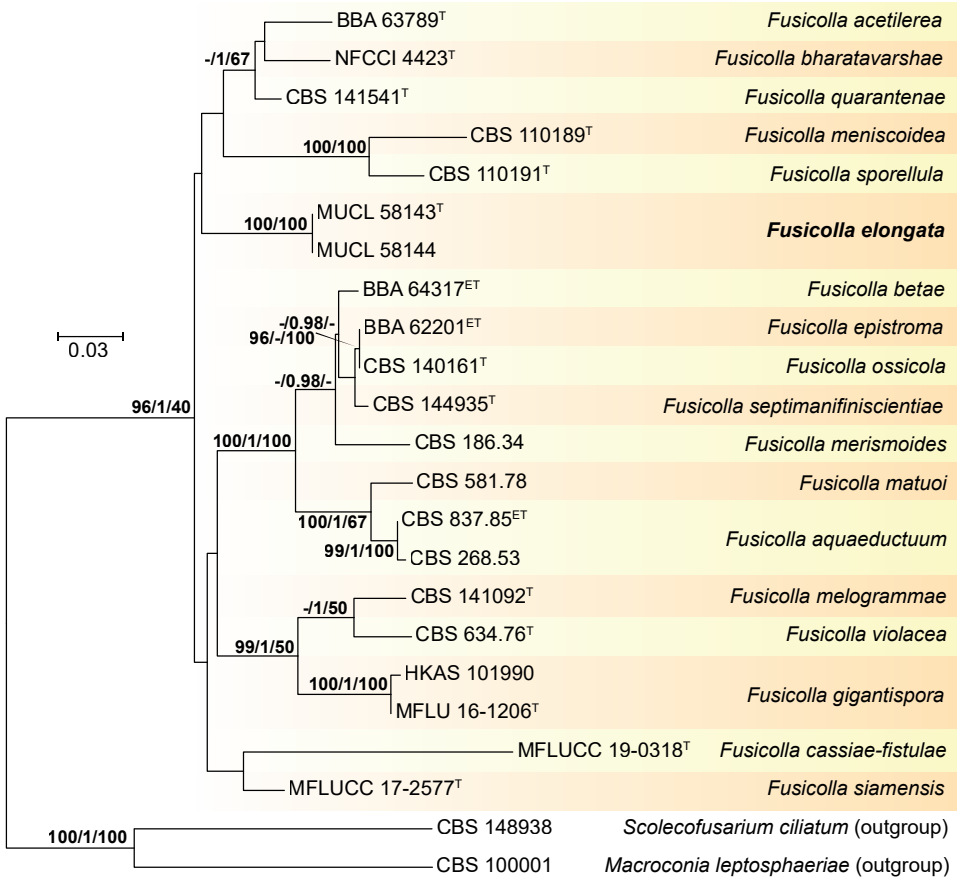

Fig. 2. IQ-TREE phylogeny inferred from the combined *acl1*, ITS, LSU, *rpb2* and *tub2* sequences of *Fusicolla* spp. Numbers at the nodes correspond to IQ-TREE bootstrap values ≥ 95 % followed by Bayesian posterior probabilities ≥ 0.95, and IQ-TREE gene concordance factors. The tree is rooted to *Macroconia leptosphaeriae* CBS 10001 and *Scolecofusarium ciliatum* CBS 148938. The scale bar indicates the expected number of nucleotide substitutions per site. Novel taxa are indicated in **bold**. Ex-epitype and ex-type strains are indicated with ET and T, respectively.

Table 2. Summary of phylogenetic information for the different analyses in this study.

Genus	Locus[1]	Number of sites (including gaps)[2]					Model selection[3]	
		Total	Conserved	Variable	Informative	BI unique site patterns	IQ-TREE (BIC)	BI (AIC)
Fusarium	*rpb1*	1 774	1 134	639	568	713	TNe+I+G4	SYM+I+G
	rpb2	1 657	1 085	572	535	592	TIM2e+I+G4	SYM+I+G
	tef1	517	217	285	245	348	TIM2e+G4	GTR+G
	Combined	3 948	2 436	1 496	1 348	1 653	-	-
Neocosmospora	ITS	464	333	128	99	180	TNe+R3	GTR+I+G
	rpb1	1 588	1 151	437	319	435	TIM3e+I+G4	GTR+I+G
	rpb2	1 465	1 057	408	336	454	TNe+I+G4	GTR+I+G
	tef1	688	394	283	200	342	TIM2+F+G4	GTR+I+G
	Combined	4 205	2 935	1 256	954	1 411	-	-
Fusicolla	*acl1*	866	454	382	201	298	TNe+G4	GTR+G
	ITS	516	391	110	56	123	TIM2e+G4	GTR+G
	LSU	474	423	50	28	56	K2P+I	GTR+G+I
	rpb2	1 702	1 220	482	290	415	TIM2e+G4	GTR+G+I
	tub2	482	299	175	109	177	K2P+G4	HKY+G
	Combined	4 040	2 787	1 199	684	1 069	-	-

[1] *acl1*: ATP citrate lyase large subunit; LSU: 28S large subunit of the nrDNA; ITS: Internal transcribed spacer region of the nrDNA; *tef1*: partial translation elongation factor 1-alpha gene; *rpb1*: partial DNA-directed RNA polymerase II largest subunit gene; *rpb2*: partial DNA-directed RNA polymerase II second largest subunit gene; *tub2*: partial beta-tubulin gene.

[2] BI: Bayesian inference.

[3] BIC: Evolutionary model selected by ModelFinder in IQ-TREE; AIC: Evolutionary model selected by MrModeltest under the Akaike Information Criterion

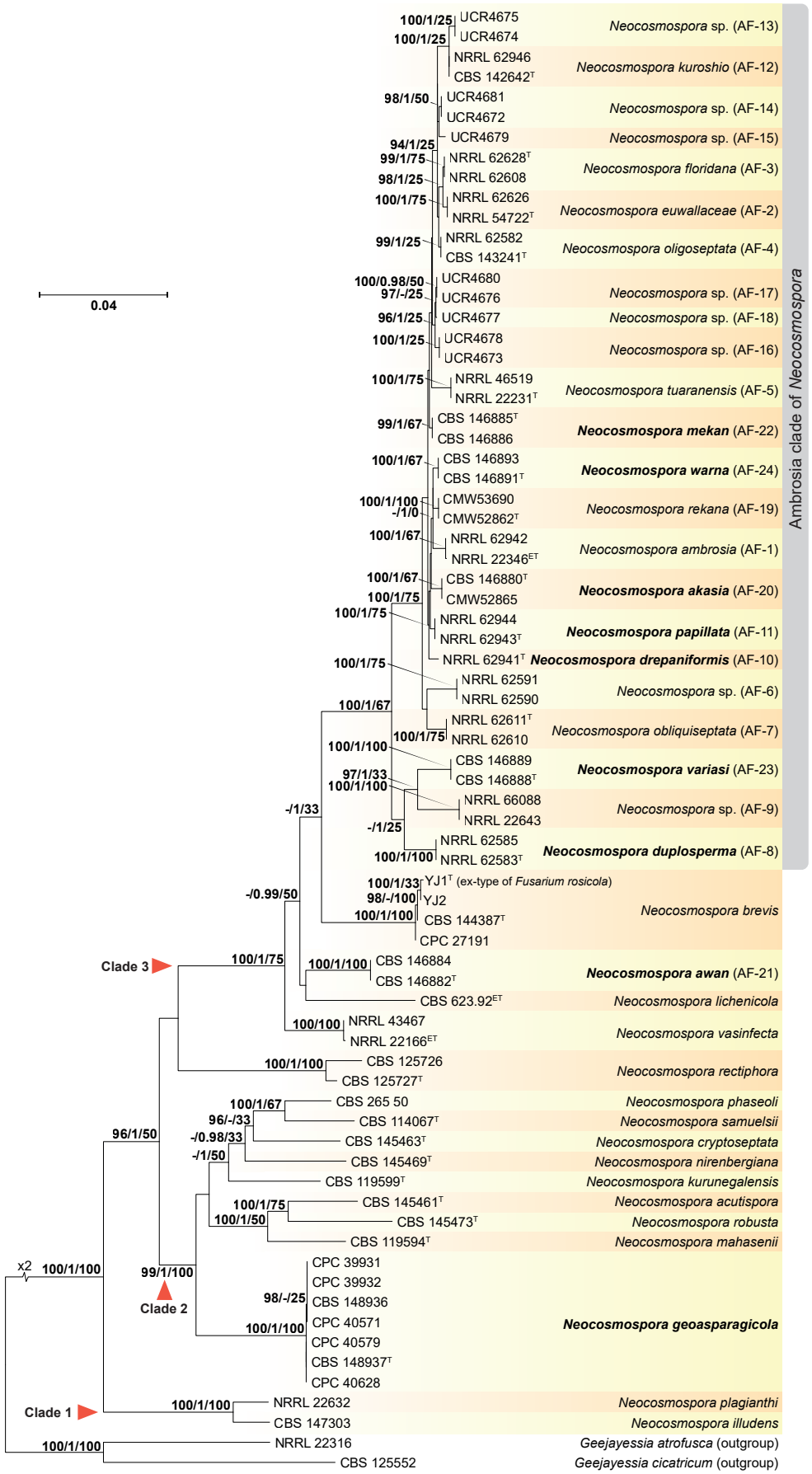

Fig. 3. IQ-TREE phylogeny inferred from the combined ITS, *rpb1*, *rpb2* and *tef1* sequences of representative *Neocosmospora* spp. Numbers at the nodes correspond to IQ-TREE bootstrap values ≥ 95 % followed by Bayesian posterior probabilities ≥ 0.95, and IQ-TREE gene concordance factors. The tree is rooted to *Geejayessia atrofusca* NRRL 22316 and *G. cicatricum* CBS 125552. The scale bar indicates the expected number of nucleotide substitutions per site. New combinations and species are indicated in **bold**. Numbers between parenthesis indicate former phylogenetic species nomenclature. The 'Ambrosia clade' of *Neocosmospora* is indicated on the right. Ex-epitype and ex-type strains are indicated with ET and T, respectively.

Table 3. Basic statistics of the assembled genomes announced in this publication.

Species	Strain[1]	BioProject ID	Complete BUSCOs [%]	Assembly size [Mbp]	No. of scaffolds	Scaff. N50 [kbp]	Longest scaff. [kbp]	Total no. of CDS
Fusarium secorum	CBS 175.32	PRJNA826072	99.1 %	50.5	15 085	17.3	156.3	46 001
Microcera coccophila	CBS 310.34	PRJNA826070	98.7 %	36.7	2 725	27.3	177.9	24 411
Rectifusarium robinianum	CBS 430.91^{T}	PRJNA826068	98.7 %	34.7	2 358	27.4	219.8	25 210
Rugonectria rugulosa	CBS 126565	PRJNA826071	98.8 %	46.9	2 884	56.0	353.8	30 877
Thelonectria blattea	CBS 952.68^{T}	PRJNA826075	98.9 %	38.9	3 001	34.8	221.9	26 348

[1] ^{T} = Ex-type.

TAXONOMY

Fusarium aywerte species complex (FASC)

Fusarium aywerte (Sangal. & L.W. Burgess) Benyon & L.W. Burgess, *Mycol. Res.* **104**: 1171. 2000. MB 466154. Fig. 4.
Basionym: *Fusarium avenaceum* subsp. *aywerte* Sangal. & L.W. Burgess, *Mycol. Res*. **99**: 287. 1995. MB 363513.

Holotypus: DAR 69501 (dried culture).

Ex-type culture: DAR 69501 = F10108 = NRRL 25410.

Type locality: **Australia**, Northern Territory, Deep Well.

Type substrate: Soil (from a depth of 5–10 cm) associated with roots of *Triodia basedowii*.

Descriptions and illustrations: See Sangalang *et al*. (1995a), Benyon *et al.* (2000) and Leslie & Summerell (2006).

Reference culture: **Australia**, Northern Territory, Little Palm Creek, soil under *Plectrachne* sp. (*Poaceae*), 1992, *D. Backhouse*, CBS 395.96 = F 10989.

Diagnostic features: *Colonies* with greyish rose mycelium and red pigment on PDA, having optimal growth at 25 °C; *microconidia* not observed; *sporodochia* with monophialides give rise to long, thin, flexuous, 6–8-septate *macroconidia* with a long tapering apical cell and a well-developed, elongated foot-shaped basal cell; *chlamydospores* absent (Sangalang *et al*. 1995a, Leslie & Summerell 2006).

Notes: *Fusarium aywerte* was initially described as a subspecies of *F. avenaceum* (Sangalang *et al.* 1995b), later to be recognised as a distinct species (Benyon *et al*. 2000). Besides the molecular differences, there are morphological, physiological and ecological differences between *F. aywerte* and *F. nurragi*. *Fusarium aywerte* has longer macroconidia and a faster growth rate than those of *F. nurragi*. Further, *F. aywerte* occurs in the rhizosphere of tussock-forming grasses (*Plectrachne*, *Triodia*) in arid tropical regions in northern Australia, while *F. nurragi* occurs in the rhizosphere of coastal heathland plants (*Kunzea ambigua*, *Banksia serrata*, *Allocasuarina paradoxa*) in temperate regions in southern Australia (Sangalang *et al*. 1995a, b).

Fusarium tjaynera J.L. Walsh *et al.*, *Fungal Diversity* **77**: 361. 2015. MB 812309. Fig. 5.

Holotypus: RBG 5367 (metabolically inactive and dried culture).

Ex-type culture: NRRL 66246 = RBG 5367.

Type locality: **Australia**, Northern Territory, Litchfield National Park.

Type substrate: *Triodia microstachya*.

Description and illustrations: See Laurence *et al.* (2016).

Diagnostic features: *Colonies* with white to greyish rose aerial mycelium and red to burgundy reverse on PDA; mono- to polyphialides give rise to oval, 0–1-septate *microconidia* in false heads (*1-septate, subcylindrical mesoconidia also present); orange *sporodochia* give rise to falcate, slender, parallel dorse-ventral sides, (4–)5(–7)-septate *macroconidia* with a tapering, curved apical cell and well-developed, foot-shaped basal cell; *chlamydospores* absent (*emended from Laurence *et al.* 2016).

Notes: *Fusarium tjaynera* has been isolated from soil as well as from *Triodia macrostachya*, *Sorghum interjectum* and *S. intrans* in northern Australia (Laurence *et al.* 2016). *Fusarium tjaynera* is considered endemic to Australia. *Fusarium tjaynera* resembles *F. aywerte*, but can be distinguished by the production of microconidia [described as oval, but illustrated as subcylindrical; figs 47, 48 in Laurence *et al.* (2016)] and red pigmentation on PDA. Compared to *F. longipes* (distinctly notched basal cell), *F. tjaynera* has an indistinctly notched basal cell, and a less prominently elongated whip-like apical cell (Burgess *et al.* 1994, Laurence *et al.* 2016).

Fusarium buharicum species complex (FBSC)

Fusarium abutilonis Gräfenhan, Nirenberg & Seifert, *Mycologia* DOI: 10.1080/00275514.2022.2071563 [7]. 2022.

Holotypus: BPI 924391, dried culture of NRRL 66737.

Ex-type culture: NRRL 66737 = DAOMC 213370.

Type locality: **Canada**, Ontario.

Type substrate: On *Abutilon theophrasti*.

Descriptions and illustrations: O'Donnell *et al*. (2022).

Diagnostic features: *Colonies* reverse orange, sometimes turning greyish brown or greyish blue in the centre; surface smooth or

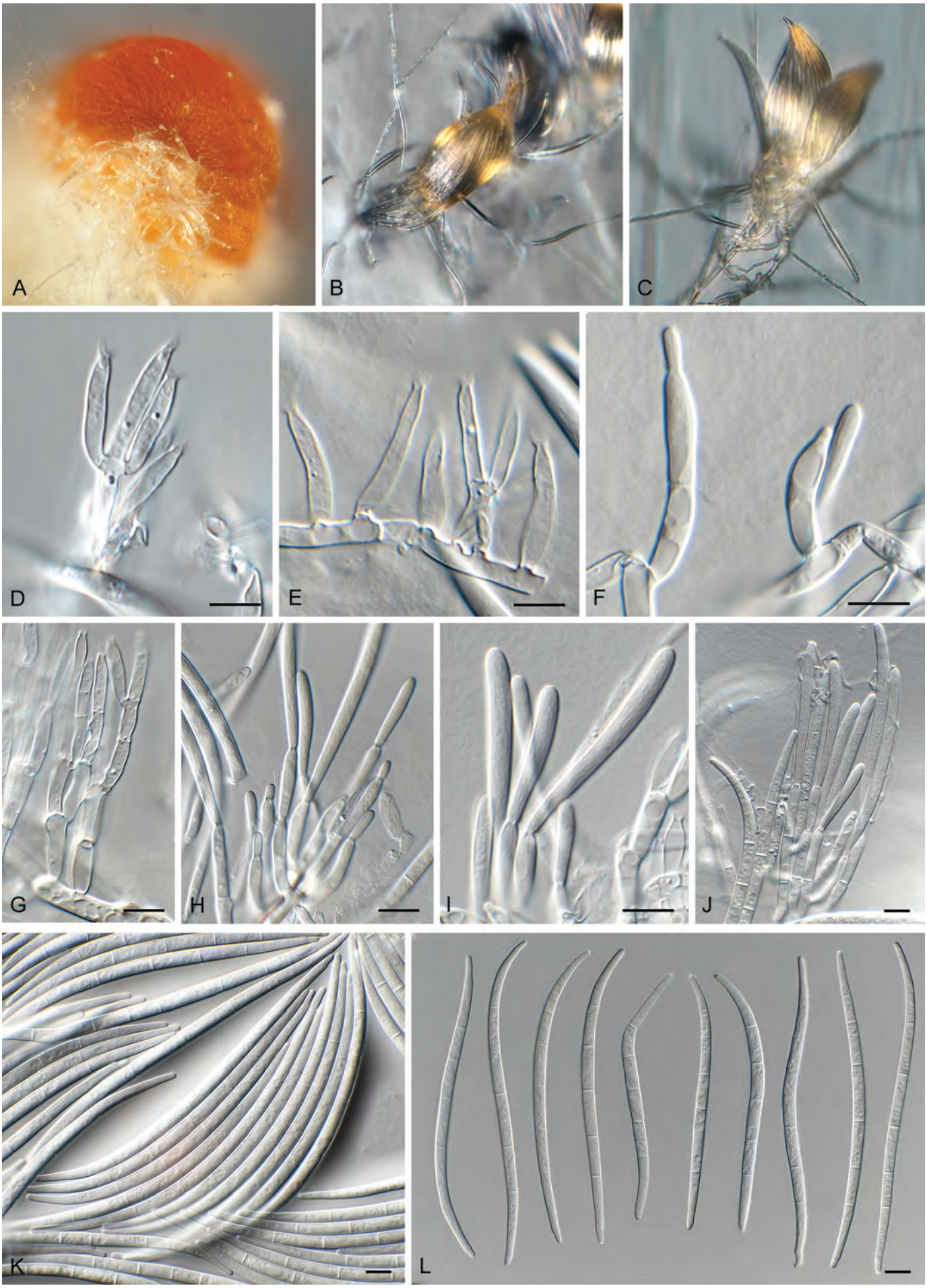

Fig. 4. *Fusarium aywerte* (CBS 395.96). **A.** Sporodochium on CLA. **B, C.** Sporodochia on SNA. **D–G, J.** Aerial conidiophores with monophialides. **H, I.** Sporodochial conidiophores. **K, L.** Macroconidia. Scale bars = 10 µm.

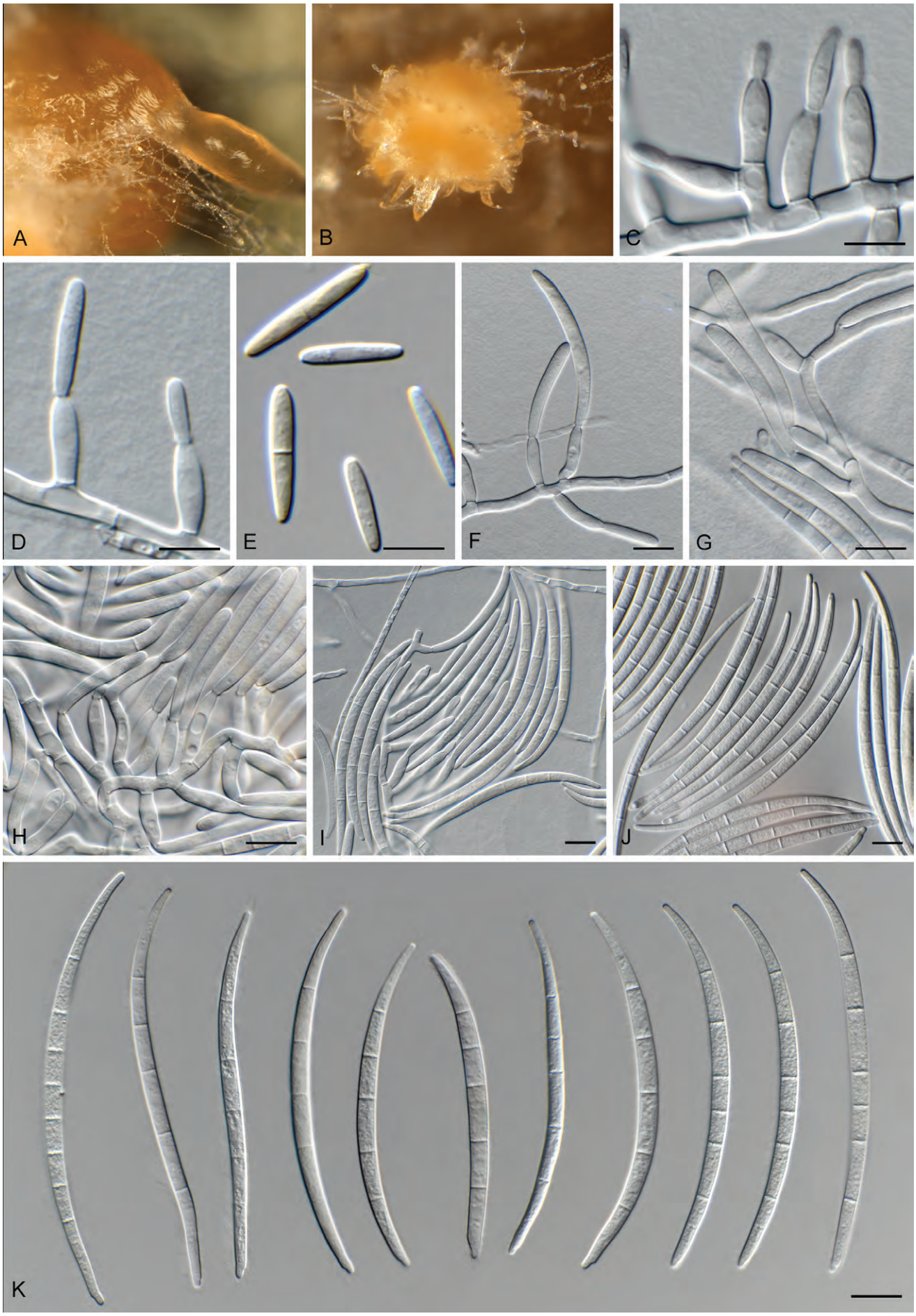

Fig. 5. *Fusarium tjaynera* (NRRL 66246). **A, B.** Sporodochia on CLA. **C, D.** Aerial conidiophores with monophialides giving rise to microconidia. **E.** Microconidia. **F, G.** Aerial conidiophores with monophialides giving rise to macroconidia. **H.** Sporodochial conidiophores. **I–K.** Macroconidia. Scale bars = 10 µm.

slightly mealy, orange, sometimes turning greyish brown in the centre, aerial mycelium white, sparse to slightly lanose to cottony, margin transparent or white on PDA, having optimal growth at 25 °C; aerial conidia 1–3-septate, sparse to absent, from monophialides; *sporodochia* pale orange, with monophialides giving rise to almost straight to curved, walls parallel in the centre, (4–)5(–6)-septate *macroconidia* with a conical and slightly hooked apical cell and well-developed foot-shaped basal cell; *chlamydospores* sparse, single or in chains of up to six, intercalary or terminal, hyaline, globose (O'Donnell *et al*. 2022).

Notes: Under some conditions sporodochial conidia of *F. abutilonis* may appear blue, as reported for *F. buharicum* (Gerlach & Nirenberg 1982). *Fusarium abutilonis* is a putative leaf, stem, and root rot pathogen of some *Malvaceae* and *Fabaceae*, and has also been isolated from soil (O'Donnell *et al*. 2022).

Fusarium buharicum Jacz. *ex* Babajan & Teterevn.-Babajan, *Mater. Mikol. Fitopat. Ross*.: 216. 1929. MB 314210.

Holotypus: LEP 127667.

Epitypus: **Uzbekistan**, Tashkent, on *Gossypium herbaceum*, 1928, *A.I. Raillo*, CBS 178.35 (preserved as metabolically inactive culture, designated by Crous *et al*. 2021b).

Ex-epitype culture: CBS 178.35 = DSM 62166 = IMB 11176 = NRRL 25488.

Descriptions and illustrations: See Gerlach & Nirenberg (1982).

Diagnostic features: *Colonies* pinkish brown, ochraceous to salmon, partly aeruginous, greyish to dark blue or nearly black on PDA, having optimal growth at 25 °C; *microconidia* not observed; sporodochia with monophialides give rise to straight, subcylindrical, (3–)5(–8)-septate *macroconidia* with a short, hooked apical cell and well-developed foot-shaped basal cell; *chlamydospores* in intercalary chains and terminal, in aerial mycelium and especially in conidia (Gerlach & Nirenberg 1982).

Notes: *Fusarium buharicum* was initially described as a pathogen of cotton (*Gossypium*) from the cotton plantations near Bukhara city in Uzbekistan (at that time – the Uzbek Soviet Socialist Republic) on which it induced collar rot symptoms, leading to plant death. With the introduction of resistant and more high yielding varieties of cotton, however, the disease lost its economic significance (Booth 1971). *Fusarium buharicum* was also found to be an important pathogen of kenaf (*Hibiscus cannabinus*) in Iran (CBS 796.70), on which it caused root, crown and stem rot (Gerlach & Sharif 1970). Sandoval-Denis *et al.* (2018b) described *F. convolutans* as a new soil-borne species occurring in South Africa, which is closely related to *F. buharicum* but distinct in that it has by its shorter, less septate and less curved macroconidia, and forms sterile hyphal coils in culture. Booth (1971) mentioned that older cultures of *F. buharicum* form intercalary globose chlamydospores in hyphae or in macroconidial cells, being pale brown, smooth-walled 10–14 µm diam at maturity. Gerlach & Nirenberg (1982) designated CBS 178.35 as neotype of *F. buharicum* as they were unable to locate the type specimen. However, A. Jaczweski did deposit a specimen in LEP, and therefore, CBS 178.35 was retained as epitype for the species (Crous *et al.* 2021b).

Fusarium convolutans Sand.-Den. *et al*., *MycoKeys* **34**: 77. 2018. MB 825102.

Holotypus: CBS H-23495 (dried OA culture).

Ex-type culture: CBS 144207 = CPC 33733.

Type locality: **South Africa**, Kruger National Park, Skukuza, Granite Supersite.

Type substrate: Rhizosphere soil under *Kyphocarpa angustifolia*.

Description and illustrations: See Sandoval-Denis *et al*. (2018b).

Diagnostic features: *Colonies* white to cream coloured on surface, reverse white, with straw to yellow diffusible pigment on PDA, having optimal growth at 30 °C; aerial monophialides giving rise *macroconidia* in false heads, lunate to falcate, curved to somewhat straight, (1–)3-septate, with a blunt to conical apical cell and papillate to distinct foot-shaped basal cell; sporodochia absent; *chlamydospores* abundant, in hyphae or conidia, intercalary or terminal, single or in clumps; sterile, coiled, sometimes branched hyphal projections abundantly formed laterally from the substrate and aerial mycelium (Sandoval-Denis *et al*. 2018b).

Notes: *Fusarium convolutans* is characterised by forming sterile, coiled hyphal projections, similar to structures observed in *F. circinatum*, *F. pseudocircinatum* and *F. sterilihyphosum*. The three latter species, however, are genetically unrelated to *F. convolutans*, being members of the FFSC. Furthermore, they are distinct in that they have microconidia, and lack chlamydospores (Leslie & Summerell 2006).

Fusarium guadeloupense Gräfenhan, Nirenberg & Seifert, *Mycologia* DOI: 10.1080/00275514.2022.2071563 [9]. 2022.

Holotypus: BPI 924391, dried culture of NRRL 36125.

Ex-type culture: NRRL 36125 = CBS 102302 = BBA 70872.

Type locality: **Guadeloupe**.

Type substrate: From soil.

Descriptions and illustrations: O'Donnell *et al*. (2022).

Diagnostic features: *Colonies* reverse orange with greyish brown; surface white to reddish grey, aerial mycelium white to reddish grey, dense, cottony on PDA, fast growing, having optimal growth at 25 °C; *microconidia* absent; *sporodochia* pale to greyish orange, with monophialides giving rise to almost straight to slightly curved, dorsal surface more curved than ventral surface, broadest at or slightly above the centre, 5(–6)-septate *macroconidia* with a conical and slightly bent apical cell and poorly developed foot-shaped basal cell; *chlamydospores* single or in chains, intercalary or terminal, hyaline, mostly globose (O'Donnell *et al*. 2022).

Notes: *Fusarium guadeloupense* is presently known from two strains, one collected from soil in Guadeloupe, and the other from human blood in Texas, USA. The latter isolate was

Fig. 6. *Fusarium sublunatum* (CBS 189.34). **A, B.** Sporodochia on CLA. **C–F.** Sporodochial conidiophores. **G.** Chlamydospores. **H.** Macroconidia. Scale bars = 10 µm.

also able to grow at 37 °C, suggesting that it might be able to infect humans and animals, although this remains to be proven (O'Donnell *et al*. 2022).

Fusarium sublunatum Reinking, *Zentralbl. Bakteriol.,* Abt. 2, **89**: 510. 1934. MB 279278. Fig. 6.
Synonyms: *Fusarium sambucinum* var. *sublunatum* (Reinking) Bilaĭ, *Mikrobiol. Zhurn. (Kiev)* **49**: 6. 1987. MB 346814.

Fusarium elongatum Reinking, *Zentralbl. Bakteriol. Parasitenk.,* Abt. 2, **89**: 511. 1934. MB 263929.
Fusarium sublunatum var. *elongatum* Reinking, *Die Fusarien, ihre Beschreibung, Schadwirkung und Bekämpfung*: 82. 1935. MB 434115.

Authentic material: B 70 0100189.

Lectotypus: **Costa Rica**, Limón, soil from *Musa sapientum* plantation, 1933, *O.A. Reinking*, CBS 189.34 (preserved as metabolically inactive culture, designated by Crous *et al.* 2021b).

Ex-type culture: BBA 62431 = CBS 189.34 = DSM 62431 = IMB 5238 = NRRL 13384 = NRRL 20840.

Descriptions and illustrations: See Reinking (1934), Gerlach & Nirenberg (1982).

Diagnostic features: *Colonies* pale beige, rose to cinnamon on PDA, having optimal growth at 25 °C; *microconidia* not observed; *sporodochia* with monophialides give rise to falcate, inequilaterally curved, (3–)5(–8)-septate *macroconidia* with a hooked apical cell and well-developed foot-shaped basal cell; *chlamydospores* abundant in aerial hyphae and conidia, in pairs, chains or clusters (Gerlach & Nirenberg 1982).

Notes: *Fusarium sublunatum* was described from soil samples collected in a *Musa* plantation in Costa Rica. No holotype specimen could be located for *F. sublunatum* and therefore the metabolically inactive culture CBS 189.34 (= IMB 5238), which represents the ex-type culture (Gerlach & Nirenberg 1982), was designated as lectotype (Crous *et al.* 2021b). *Fusarium sublunatum* var. *elongatum* (original culture CBS 190.34 = NRRL 20897), also described from soil collected in a banana plantation in Costa Rica, proved to be a synonym of *F. sublunatum* (Raillo 1950, Gerlach & Nirenberg 1982).

Fusarium burgessii species complex (FBURSC)

Fusarium algeriense Laraba & O'Donnell, *Mycologia* **109**: 944. 2017 (2018). MB 820565. Fig. 7.

Holotypus: BPI 910347 (dried culture).

Ex-type culture: CBS 142638 = IL-79 = KOD 1247 = NRRL 66647.

Type locality: **Algeria**, Guelma Province, Djeballah Khemissi.

Type substrate: *Triticum durum*.

Description and illustrations: See Laraba *et al*. (2017).

Diagnostic features: *Colonies* reddish orange, brownish grey, yellowish white to purplish grey on PDA, having optimal growth at 25 °C; **microconidia* developing in false heads, on superficial and immersed mycelium, subcylindrical, straight to curved, 0–1-septate; *sporodochia* with monophialides give rise to straight to falcate, slender, 1–3(–4)-septate *macroconidia* with a hooked apical cell and well-developed foot-shaped basal cell; **chlamydospores* intercalary, globose to subglobose, in chains, sparse, hyaline (*emended from Laraba *et al.* 2017).

Notes: *Fusarium algeriense* represents a species within the *F. burgessii* species complex causing crown rot of durum wheat in Algeria (Laraba *et al.* 2017). Following its description, crown rot symptoms of bread wheat in two provinces of Azerbaijan were also attributed to *F. algeriense* (Özer *et al.* 2020).

Morphologically, *F. algeriense* needs to be compared to *F. burgessii* and *F. beomiforme*, which have an optimal growth at 30 °C, and produce abundant chlamydospores. Isolates of *F. algeriense* had an optimal growth at 25 °C, lacked chlamydospore production in culture, and produced monophialides, with reniform or ellipsoidal, mostly aseptate microconidia. In contrast, *F. burgessii* has polyphialides, and *F. beomiforme* has monophialides, but with globose-to-napiform, 0–1-septate microconidia (Laraba *et al.* 2017).

Fusarium beomiforme P.E. Nelson *et al.*, *Mycologia* **79**: 886. 1987. MB 122057. Fig. 8.

Holotypus: DAOM 196987 (dried culture).

Ex-type culture: ATCC 64067 = CBS 100160 = DAOM 196987 = DAR 58880 = F 5759 = FRC M-1425 = IMI 316127 = MRC 4593 = NRRL 13606.

Type locality: **Australia**, Queensland, Rockhampton.

Type substrate: Plant debris in soil.

Descriptions and illustrations: See Nelson *et al.* (1987) and Leslie & Summerell (2006).

Diagnostic features: *Colonies* pale orange to white, with orange red to red-brown pigmentation on PDA; optimal growth at 30 °C; monophialides produce false heads with 0–1-septate napiform to globose *microconidia* in aerial mycelium; *sporodochia* with monophialides giving rise to long falcate, 3–4(–5)-septate *macroconidia* with a slightly curved apical cell and notched basal cell, and slow to form, abundant, intercalary, single to chains of *chlamydospores* in aerial and submerged hyphae (Nelson *et al*. 1987).

Notes: *Fusarium beomiforme* was described from soil and plant debris collected in the Markham Valley of Papua New Guinea (where sorghum had been cultivated), from grassland areas in the vicinity of Rockhampton, Emerald, Longreach, and Boulia along the Tropic of Capricorn in Queensland, Australia, and from Hluhluwe, KwaZulu-Natal, South Africa (Nelson *et al*. 1987). Since then, *F. beomiforme* has also been recovered from Thailand (from soil where previously sorghum had been cultivated; Mohamed Nor *et al*. 2019), though to date, *F. beomiforme* has not been reported to be pathogenic, and is probably a saprobe.

Fusarium burgessii M.H. Laurence *et al*., *Fungal Diversity* **49**: 109. 2011. MB 519216. Fig. 9.

Holotypus: CBS 125537 (preserved as metabolically inactive culture).

Ex-type culture: CBS 125537 = NRRL 66654 = RBG 5315.

Type locality: **Australia**, Queensland, Idalia National Park.

Type substrate: Soil.

Description and illustrations: See Laurence *et al.* (2011).

Diagnostic features: *Colonies* white to yellow with yellow pigmentation on PDA, having optimal growth at 30 °C; mono- to

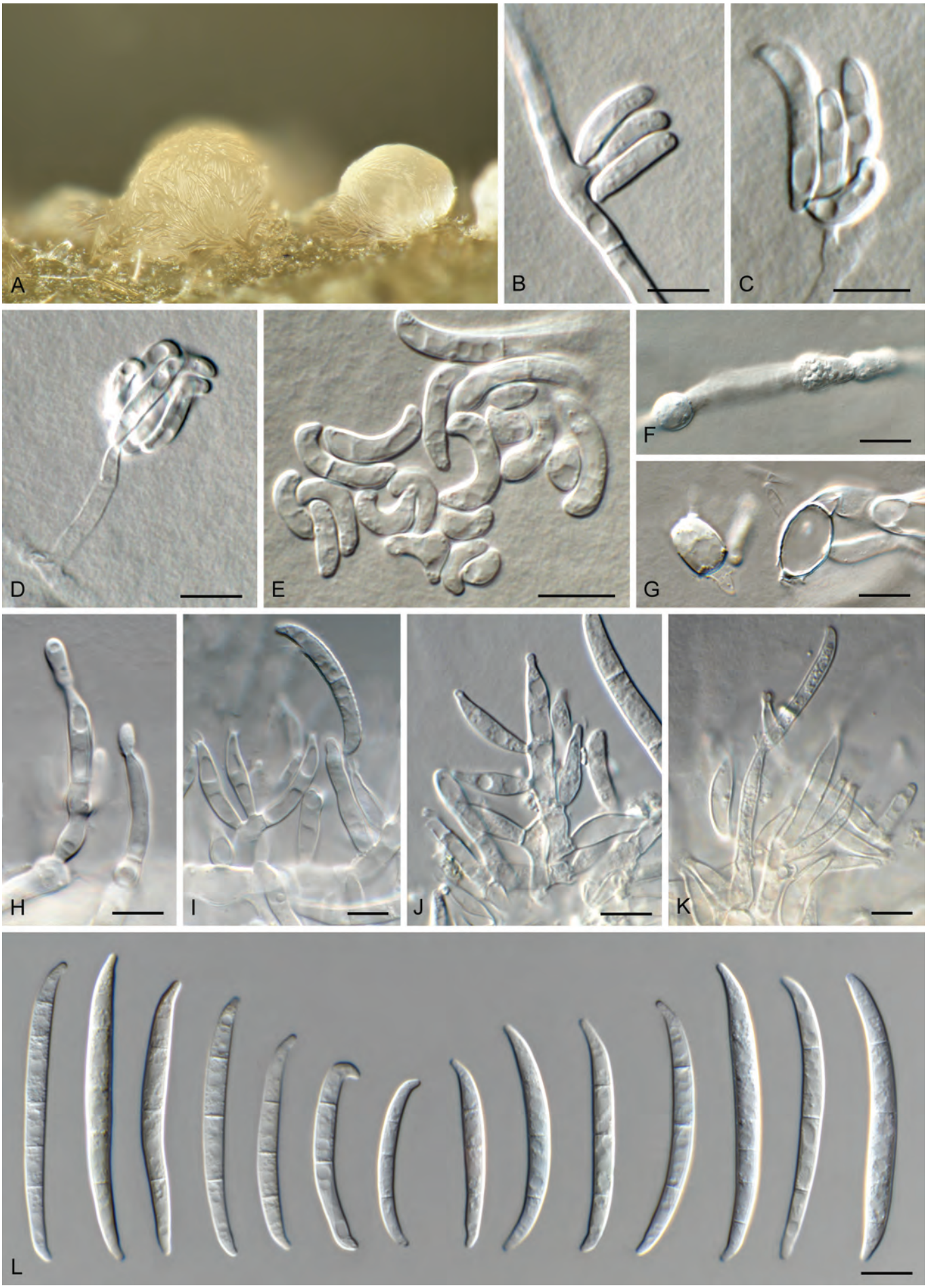

Fig. 7. *Fusarium algeriense* (CBS 142638). **A.** Sporodochium on CLA. **B–D.** Aerial conidiophores with monophialides. **E.** Microconidia. **F, G.** Chlamydospores. **H–K.** Sporodochial conidiophores. **L.** Macroconidia. Scale bars = 10 µm.

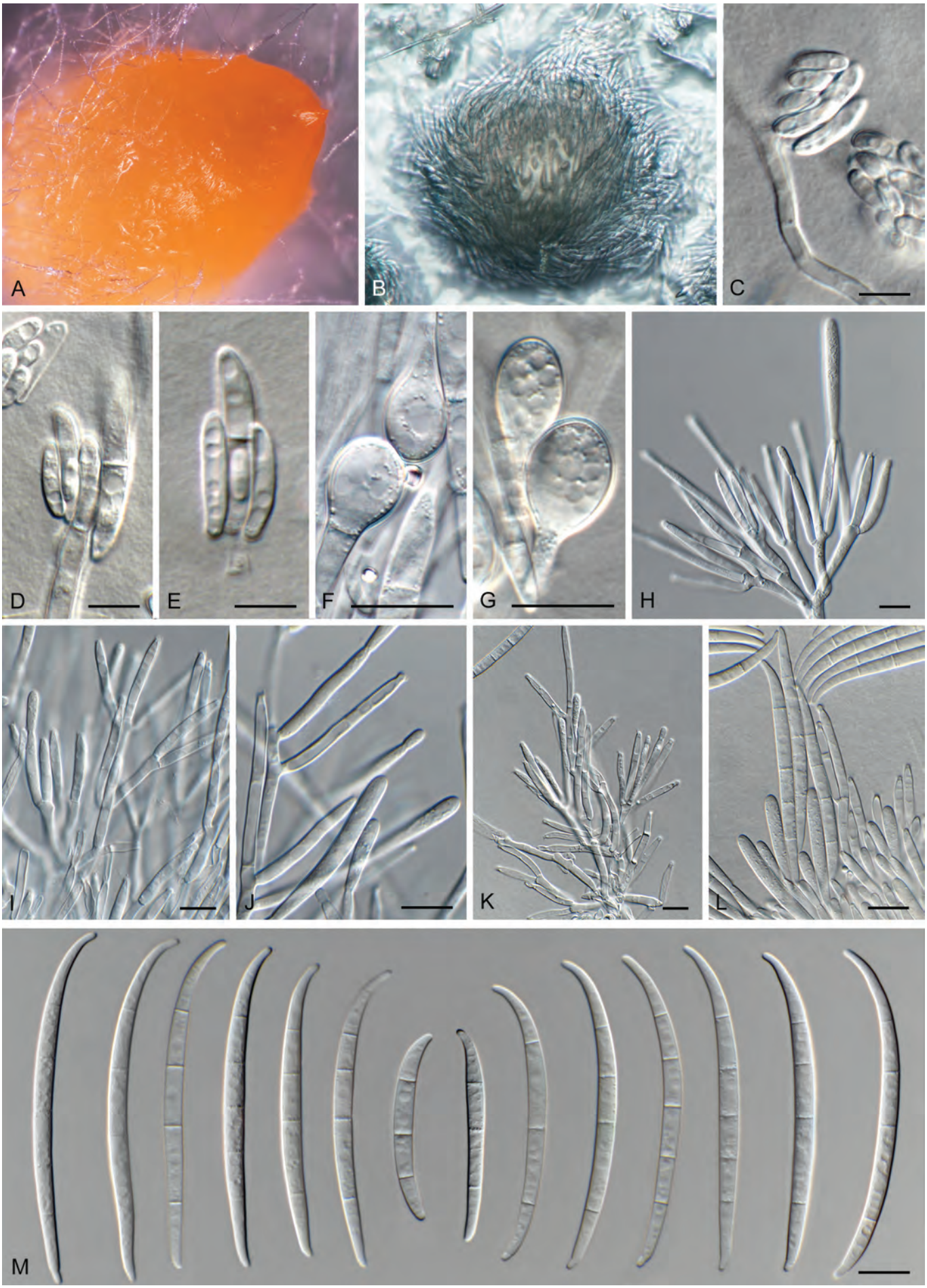

Fig. 8. *Fusarium beomiforme* (CBS 100160). **A, B.** Sporodochia on SNA. **C–E.** Microconidia. **F, G.** Chlamydospores developing in macroconidia. **H–L.** Sporodochial conidiophores. **M.** Macroconidia. Scale bars = 10 µm.

Fig. 9. *Fusarium burgessii* (CBS 125537). **A.** Sporodochium on CLA. **B.** Aerial conidiophores with monophialides giving rise to micro- and macroconidia. **C–F.** Microconidia. **G–J.** Sporodochial conidiophores. **K.** Macroconidia. Scale bars = 10 µm.

polyphialides produce false heads with 0–1-septate oval, elliptical or reinform *microconidia* in aerial mycelium; *sporodochia* with mono- to polyphialides produce short to medium length, falcate, 3-septate *macroconidia* with a slightly curved to hooked apical cell and notched to well-developed, foot-shaped basal cell; *chlamydospores* in both aerial and submerged hyphae, terminal and intercalary, solitary or in chains (Laurence *et al.* 2011).

Notes: *Fusarium burgessii* was described from Australia, and is known to occur in soils from Longreach, Queensland, to Finke Gorge National Park, Northern Territory (Laurence *et al*. 2011). Morphologically, it is allied to *F. algeriense* and *F. beomiforme* (see discussion under *F. algeriense*), and morphotype B (isolated from the rhizosphere of indigenous *Gossypium* spp.), which presently still represents an undescribed species (Laurence *et al*. 2011).

Fusarium camptoceras species complex (FCAMSC)

Fusarium camptoceras Wollenw. & Reinking, *Phytopathology* **15**: 158. 1925. MB 259537. Fig. 10.

Neotypus: CBS H-24077, designated in Xia *et al*. (2019).

Ex-neotype culture: ATCC 16065 = ATCC 24364 = BBA 9810 = CBS 193.65 = DSM 62167 = IMB 9810 = IMI 112500 = NRRL 20716 = NRRL 36344.

Neotype locality: **Costa Rica**.

Neotype substrate: Cushion gall of *Theobroma cacao*.

Descriptions and illustrations: See Wollenweber & Reinking (1935), Booth (1971), Gerlach & Nirenberg (1982), Marasas *et al*. (1998) and Leslie & Summerell (2006).

Diagnostic features: *Colonies* brown on PDA, having optimal growth at 25 °C; *microconidia* not observed; aerial polyphialides formed on loosely branched conidiophores giving rise to av. 3–4-septate mesoconidia, and macroconidia; *sporodochia* with monophialides give rise to falcate, 3–5(–7)-septate *macroconidia* with a pointed apical cell and obtuse to well-developed, foot-shaped basal cell; intercalary chains, pairs or clusters of *chlamydospores* in aerial and submerged hyphae, never in terminal pairs (Marasas *et al.* 1998, Leslie & Summerell (2006).

Notes: *Fusarium camptoceras* was described from subtropical and tropical regions (Costa Rica, Ecuador, Honduras, Angola), recovered from decaying *Coffea, Musa* and *Theobroma* spp. (Marasas *et al.* 1998). Reports prior to 1998 could represent two species separated from *F. camptoceras*, namely *F. musarum* and *F. nelsonii*, which differ regarding their red pigmentation on PDA, size and septation of their mesoconidia (*F. musarum* av. 5–6-septate; *F. nelsonii* av. 3-septate), sporodochia (absent in *F. musarum*; present in *F. nelsonii*), and the pattern in which chlamydospores are formed (in terminal pairs in *F. nelsonii*, solitary or chains in *F. camptoceras* and *F. musarum*) (Marasas *et al.* 1998). Further studies are needed to confirm the role of *F. camptoceras* as plant pathogen.

Fusarium kotabaruense Maryani *et al*., *Persoonia* **43**: 65. 2019. MB 828964.

Holotypus: InaCC F963 (preserved as metabolically inactive culture).

Ex-type culture: InaCC F963 = Indo172.

Type locality: **Indonesia**, South Kalimantan, Kota Baru, Kecamatan Pamukan Barat, Desa Sungai Birah.

Type substrate: Infected pseudostem of *Musa* var. Pisang Hawa (ABB).

Description and illustrations: See Maryani *et al*. (2019).

Diagnostic features: *Colonies* rosy buff on PDA, having optimal growth at 25 °C; aerial hyphae and orange *sporodochia* with mono- and polyphialides give rise to macroconidia, falcate, (2–)3–5(–7)-septate, with blunt apical cell and poorly-developed, foot-shaped basal cell; *chlamydospores* not observed (Maryani *et al.* 2019).

Notes: *Fusarium kotabaruense* represents a fast-growing species which clustered basal to the FIESC, and was shown to be better accommodated in the *Fusarium camptoceras* species complex (Xia *et al.* 2019, Crous *et al*. 2021b). Although assumed to lack sporodochia, isolates on CLA incubated under nuv-light did produce orange sporodochia. This species is characterised by its mono- to polyphialides, fast-growing cultures and multiseptate conidia (Maryani *et al.* 2019).

Fusarium neosemitectum L. Lombard *et al*., *Persoonia* **43**: 214. 2019. MB 831845.

Holotypus: CBS H-24067.

Ex-type culture: CBS 189.60.

Type locality: **Democratic Republic of the Congo**.

Type substrate: *Musa sapientum*.

Description and illustrations: See Xia *et al.* (2019).

Diagnostic features: *Colonies* white, felty to velvety on PDA, with abundant aerial mycelium; aerial mono- to polyphialides giving rise to *macroconidia*, ellipsoid to falcate, curved dorsiventrally, (1–)2–4(–5)-septate; blunt, conical to slightly papillate apical cell and blunt to poorly-developed, foot-shaped basal cell; *sporodochia* and *chlamydospores* not observed (Xia *et al.* 2019).

Notes: *Fusarium neosemitectum* can be distinguished from closely related species, such as *F. kotabaruense* and *F. camptoceras*, by the presence of short phialidic pegs on the aerial mycelium, not observed for the latter two species. All three species in FCAMSC appear to be tropical species due to their origins and they also share a mutual host genus, *Musa* (Marasas *et al.* 1998, Maryani *et al*. 2019).

Fusarium chlamydosporum species complex (FCSC)

Fusarium atrovinosum L. Lombard & Crous, *Fungal Syst. Evol*. **4**: 190. 2019. MB 831559.

Holotypus: CBS H-24015.

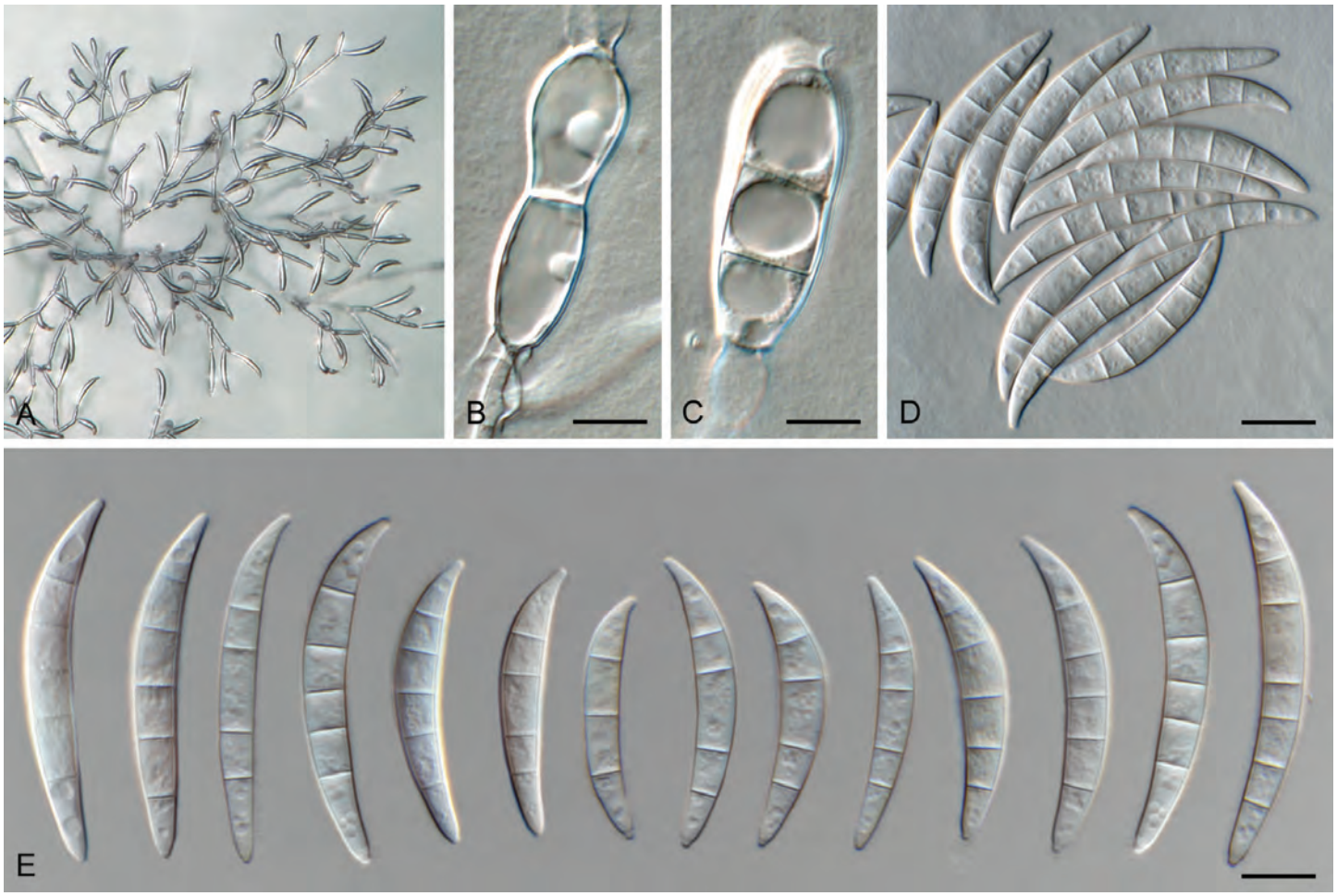

Fig. 10. *Fusarium camptoceras* (CBS 193.65). **A.** Aerial conidiophores with monophialides. **B, C.** Chlamydospores. **D, E.** Macroconidia. Scale bars = 10 µm.

Ex-type culture: BBA 10357 = CBS 445.67 = DSM 62169 = IMB 10357= IMI 096270 = NRRL 26852 = NRRL 26913.

Type locality: **Australia**.

Type substrate: *Triticum aestivum*.

Description and illustrations: See Lombard *et al*. (2019).

Diagnostic features: *Colonies* on the surface greyish rose to vinaceous to buff in the centre, with abundant aerial mycelium, and livid red to dark vinaceous in reverse on PDA; aerial polyphialides giving rise to false heads with fusiform to ellipsoidal to obovoid, 0–1(–2)-septate *microconidia*; *chlamydospores* abundant, globose to subglobose, thick-walled, smooth to slightly verrucose, formed terminally or intercalarily in chains of three or more (Lombard *et al*. 2019).

Notes: *Fusarium atrovinosum* is closely related to *F. chlamydosporum, F. spinosum* and *F. sporodochiale* and can be distinguished from these three species by the lack of monophialides on aerial mycelium, the lack of sporodochia, and abundant chlamydospores.

Fusarium chlamydosporum Wollenw. & Reinking, *Phytopathology* **15**: 156. 1925. MB 260522.
Synonyms: *Fusarium chlamydosporum* var. *chlamydosporum*, *Phytopathology* **15**: 156. 1925. MB 429587.
Fusarium sporotrichioides var. *chlamydosporum* (Wollenw. & Reinking) Joffe, *Mycopathol. Mycol. Appl*. **53**: 211. 1974. MB 348165.
Dactylium fusarioides Gonz. Frag. & Cif., *Bol. Real Soc. Esp. Hist. Nat*. **27**: 280. 1927. MB 265606.
Fusarium fusarioides (Gonz. Frag. & Cif.) C. Booth, *The genus Fusarium*: 88. 1971. MB 314214.
Pseudofusarium purpureum Matsush., *Microfungi of the Solomon Islands and Papua-New Guinea*: 47. 1971. MB 321785.

Neotypus: CBS 145.25 (preserved as metabolically inactive culture), designated in Lombard *et al.* (2019).

Ex-neotype culture: CBS 145.25 = NRRL 26851 = NRRL 26912.

Neotype locality: **Honduras**, Tela.

Neotype substrate: Pseudostem of *Musa sapientum*.

Descriptions and illustrations: See Booth (1971), Gerlach & Nirenberg (1982) and Leslie & Summerell (2006).

Diagnostic features: *Colonies* with white mycelium and greyish rose to burgundy pigment on PDA; *microconidia* abundant, straight to reniform, 0(–2)-septate, arising from aerial mono- and polyphialides; *sporodochia* rare, with monophialides give

rise to thick-walled, unequal dorsiventrally curved, 3–5-septate *macroconidia* with a short, curved, pointed apical cell and poorly to well-developed, foot-shaped basal cell; *chlamydospores* abundant, formed rapidly in aerial mycelium, submerged hyphae and on agar surface, verruculose and pale brown, in chains or clusters (Marasas *et al.* 1998, Leslie & Summerell 2006).

Notes: *Fusarium chlamydosporum* (FCSC) is common in soils and grains from arid and semi-arid regions (Burgess & Summerell 1992, Kanaan & Bahkali 1993, Sangalang *et al*. 1995a), and from plant material displaying disease symptoms that include crown rot (Du *et al*. 2017), blight (Satou *et al*. 2001), damping-off (Engelbrecht *et al*. 1983, Lazreg *et al.* 2013) and stem canker (Fugro 1999). It has also been implicated in human and animal fusarioses (O'Donnell *et al*. 2009). Records prior to Lombard *et al.* (2019) need to be interpreted with care, as this was shown to be a species complex O'Donnell *et al*. (2009, 2018). Subsequent to these studies, five of these taxa were named, with several additional species in the FCSC still awaiting formal description. Furthermore, *F. chlamydosporum* var. *fuscum* was raised to species level, as *F. coffeatum,* in the *F. incarnatum-equiseti* species complex (FIESC) (Lombard *et al.* 2019).

Fusarium humicola L. Lombard & Crous, *Fungal Syst. Evol*. **4**: 191. 2019. MB 831561.

Holotypus: CBS H-24016.

Ex-type culture: ATCC 24372 = CBS 124.73 = IMI 128101 = NRRL 25535.

Type locality: **Pakistan**.

Type substrate: Soil.

Description and illustrations: See Lombard *et al.* (2019).

Diagnostic features: *Colonies* fulvous to ochreous in the centre becoming vinaceous to livid red towards the margin, reverse dark vinaceous to vinaceous on PDA; aerial mono- to polyphialides giving rise to *microconidia* in false heads, ellipsoidal to obovoid, 0–3-septate; *sporodochia* pale luteous to pale salmon, with monophialides give rise to falcate, mostly straight with dorsiventrally curved apical and basal cells 3–5-septate *macroconidia* with a curved, blunt to papillate apical cell and well-developed, foot-shaped basal cell; *chlamydospores* not observed (Lombard *et al.* 2019).

Note: *Fusarium humicola* is closely related to *F. nelsonii*, which has smaller, more strongly curved sporodochial conidia, and abundant chlamydospores.

Fusarium microconidium L. Lombard & Crous, *Fungal Syst. Evol*. **4**: 192. 2019. MB 831562.

Holotypus: CBS H-24017.

Ex-type culture: CBS 119843 = KSU 11396 = MRC 8391.

Type locality: Unknown.

Type substrate: Unknown.

Description and illustrations: See Lombard *et al*. (2019).

Diagnostic features: *Colonies* rose to rosy vinaceous to pale luteous on surface, with abundant aerial mycelium, and livid red to dark vinaceous in reverse on PDA; aerial mono- or polyphialides giving rise to *microconidia*, fusoid to ellipsoidal to obovoid, 0–1-septate; *sporodochia* and *chlamydospores* not observed (Lombard *et al*. 2019).

Notes: *Fusarium microconidium* is distinguished from other species in the FCSC based on the production of predominantly aseptate microconidia and lack of sporodochia and chlamydospores.

Fusarium nelsonii Marasas & Logrieco, *Mycologia* **90**: 508. 1998. MB 443596.

Holotypus: BPI 802927; *isotypi* DAOM 225260 and PREM 55396.

Ex-type culture: ATCC 201410 = CBS 119876 = FRC R-8670 = ITEM 1229 = MRC 4570 = NRRL 28505 = NRRL 53945.

Type locality: **South Africa**, Western Cape Province, Malmesbury.

Type substrate: Plant debris in wheat field soil.

Descriptions and illustrations: See Marasas *et al.* (1998) and Leslie & Summerell (2006).

Diagnostic features: *Colonies* with white floccose mycelium and red pigmentation on PDA, having optimal growth at 30 °C; aerial polyphialides giving rise to *mesoconidia*, fusoid to lanceolate, straight to curved, (0–)3-septate; *sporodochia* cream coloured, with monophialides giving rise to straight or falcate, 3(–5)-septate *macroconidia* with a curved, blunt apical cell (beak-like) and poorly-developed, foot-shaped basal cell; *chlamydospores* abundant and rapidly formed in aerial and submerged hyphae, intercalary or terminal, single, in pairs, chains or clumps (Marasas *et al.* 1998, Leslie & Summerell 2006).

Notes: *Fusarium nelsonii* was described from South Africa, where it was isolated from *Triticum* soil, plant debris, *Medicago* roots, *Sorghum* malt and *Zea mays* kernels (Marasas *et al.* 1998). It has been reported from *Triticum* in Iran (Chehri *et al.* 2010), *Sorghum* in India (Lincy *et al.* 2011), fruit blight of *Cucumis sativus var*. *sativus* and stalk rot of *Zea mays* in China (Ahmad *et al.* 2020, Zhang *et al*. 2021).

Fusarium nelsonii produces macro- and mesoconidia (aerial mycelium), which distinguishes it from *F. musarum* (macroconidia absent), and has shorter meso- and macroconidia than *F. camptoceras*.

Fusarium peruvianum L. Lombard & Crous, *Fungal Syst. Evol*. **4**: 194. 2019. MB 831564.

Holotypus: CBS H-24019.

Ex-type culture: CBS 511.75.

Type locality: **Peru**.

Type substrate: Seedlings of *Gossypium* sp.

Description and illustrations: See Lombard *et al*. (2019).

Diagnostic features: *Colonies* fulvous to ochreous in the centre becoming coral to vinaceous towards the margin, with abundant aerial mycelium, and livid red to dark vinaceous in reverse on PDA; aerial phialides mostly polyphialidic, giving rise to micro- and macroconidia; *microconidia* ellipsoid to obovoid, 0–3(–4)-septate, *macroconidia* fusoid to falcate, straight or gently dorsiventrally curved, with a blunt apical cell and indistinct papillate to poorly-developed, foot-shaped basal cell; *chlamydospores* abundant, intercalary or terminal, single or in pairs; *sporodochia* not observed (Lombard *et al*. 2019).

Note: *Fusarium peruvianum* can be distinguished from other species in the FCSC by having falcate aerial macroconidia and 4-septate obovoid microconidia.

Fusarium spinosum L. Lombard *et al*., *Fungal Syst. Evol*. **4**: 195. 2019. MB 831565.

Holotypus: CBS H-24020.

Ex-type culture: CBS 122438.

Type locality: **Brazil**.

Type substrate: *Galia melon* imported into the Netherlands.

Description and illustrations: See Lombard *et al*. (2019).

Diagnostic features: *Colonies* rose to rosy vinaceous to pale luteous in the centre, with abundant aerial mycelium, reverse fulvous to ochreous with rosy vinaceous flames on PDA; aerial mono- to polyphialides giving rise to micro- and macroconidia in false heads; *microconidia* fusoid to ellipsoidal to obovoid, straight to curved, 0–3-septate; *macroconidia* falcate, slightly dorsiventrally curved, 3-septate, apex blunt, with an indistinct papillate to poorly-developed foot-shaped basal cell; *chlamydospores* abundant, intercalary or terminal, single or in chains; *sporodochia* not observed (Marasas *et al.* 1998, Leslie & Summerell 2006).

Note: *Fusarium spinosum* is distinguished from other species in the FCSC by only forming 3-septate, falcate macroconidia.

Fusarium sporodochiale L. Lombard & Crous, *Fungal Syst. Evol*. **4**: 196. 2019. MB 831566.

Holotypus: CBS H-12681.

Ex-type culture: ATCC 14167 = CBS 220.61 = MUCL 8047 = NRRL 20842.

Type locality: **South Africa**, Gauteng Province, Johannesburg.

Type substrate: Soil.

Description and illustrations: See Lombard *et al*. (2019).

Diagnostic features: *Colonies* rose to rosy vinaceous to sulphur yellow, with abundant aerial mycelium, reverse livid red to dark vinaceous on PDA; aerial phialides mostly polyphialidic, giving rise to *microconidia* in false heads, fusoid to ellipsoidal to obovoid, (0–)1-septate; *sporodochia* pale luteous to pale orange, with monophialides giving rise to falcate, slightly to strongly dorsiventrally curved *macroconidia*, tapering towards both ends, with an elongated, strongly curved apical cell and a blunt and distinct foot-shaped basal cell, (1–)5–6(–10)-septate; *chlamydospores* not observed (Lombard *et al*. 2019).

Notes: *Fusarium sporodochiale* is unique within the FCSC, producing up to 10-septate sporodochial macroconidia. Additionally, the apical cell of macroconidia is more elongated and hooked than those of other species in this complex.

Fusarium citricola species complex (FCCSC)

Fusarium aconidiale L. Lombard & Crous, *Persoonia* **46**: 523. 2021. MB 839622.

Holotypus: CBS H-24769.

Ex-type culture: CBS 147772 = CPC 37959 = UBOCC-A-109005.

Type locality: **France**.

Type substrate: *Triticum aestivum*.

Description and illustrations: See Crous *et al.* (2021a).

Diagnostic features: *Colonies* white to rosy buff, flat, woolly to cottony with radial patches of white aerial mycelium, reverse white to pale rosy buff on PDA; aerial phialides monophialidic, but *microconidia* not observed; *sporodochia* crystalline to pale cream, with monophialides giving rise to falcate, straight to moderately curved *macroconidia*, tapering towards the basal part, apical cell more or less equally sized than the adjacent cell, curved to hooked; basal cell well-developed, foot-shaped, rarely papillate, 3(–5)-septate; *chlamydospores* not observed (Crous *et al.* 2021a).

Notes: *Fusarium aconidiale* is similar to *F. juglandicola* but does not produce red pigment under continuous white light nor any chlamydospores or aerial microconidia, distinguishing it from other members of the FCCSC. Furthermore, *F. aconidiale* produces predominantly 3-septate sporodochial conidia and much less frequently 4- and 5-septate sporodochial conidia compared to *F. juglandicola*. (Crous *et al.* 2021a).

Fusarium celtidicola Q.J. Shang *et al.*, *Phytotaxa* **361**: 255. 2018. MB 553845. Figs 11, 12.

Holotypus: MFLU 15-3646; *isotypus* HKAS 95020.

Ex-type culture: KUMCC 16-0019 = MFLUCC 16-0526; ex-isotype culture KUMCC 16-0019 = MFLUCC 16-0526.

Type locality: **Italy**, Forlì-Cesena Province, Forlì, Viale dell'Appennino.

Type substrate: Dead branch of *Celtis australis*.

Description and illustrations: See Shang *et al.* (2018).

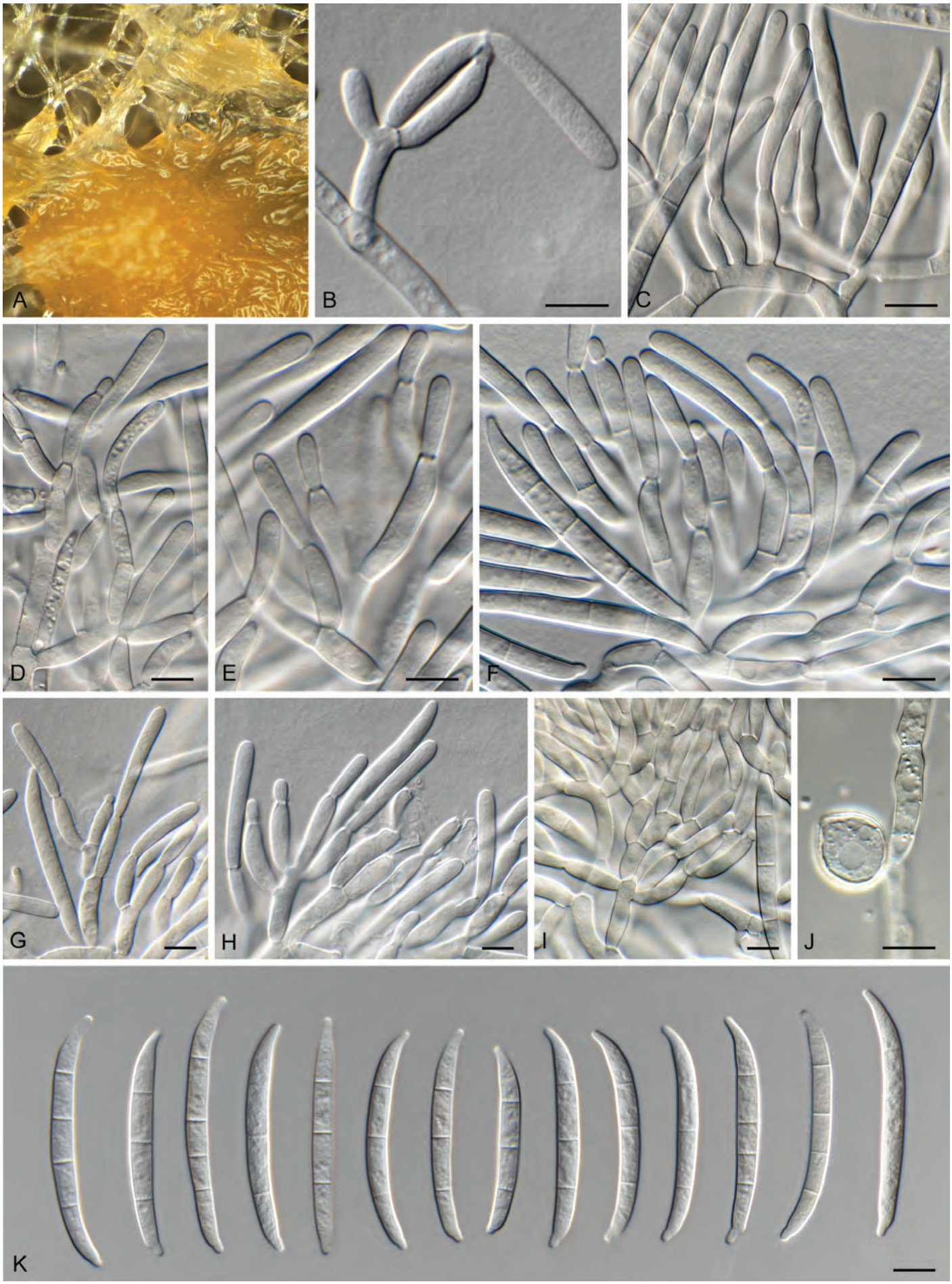

Fig. 11. *Fusarium celtidicola* (MFLUCC 16-0526). **A.** Sporodochium on CLA. **B.** Aerial conidiophore. **C–I.** Sporodochial conidiophores with monophialides. **J.** Chlamydospore. **K.** Macroconidia. Scale bars = 10 µm.

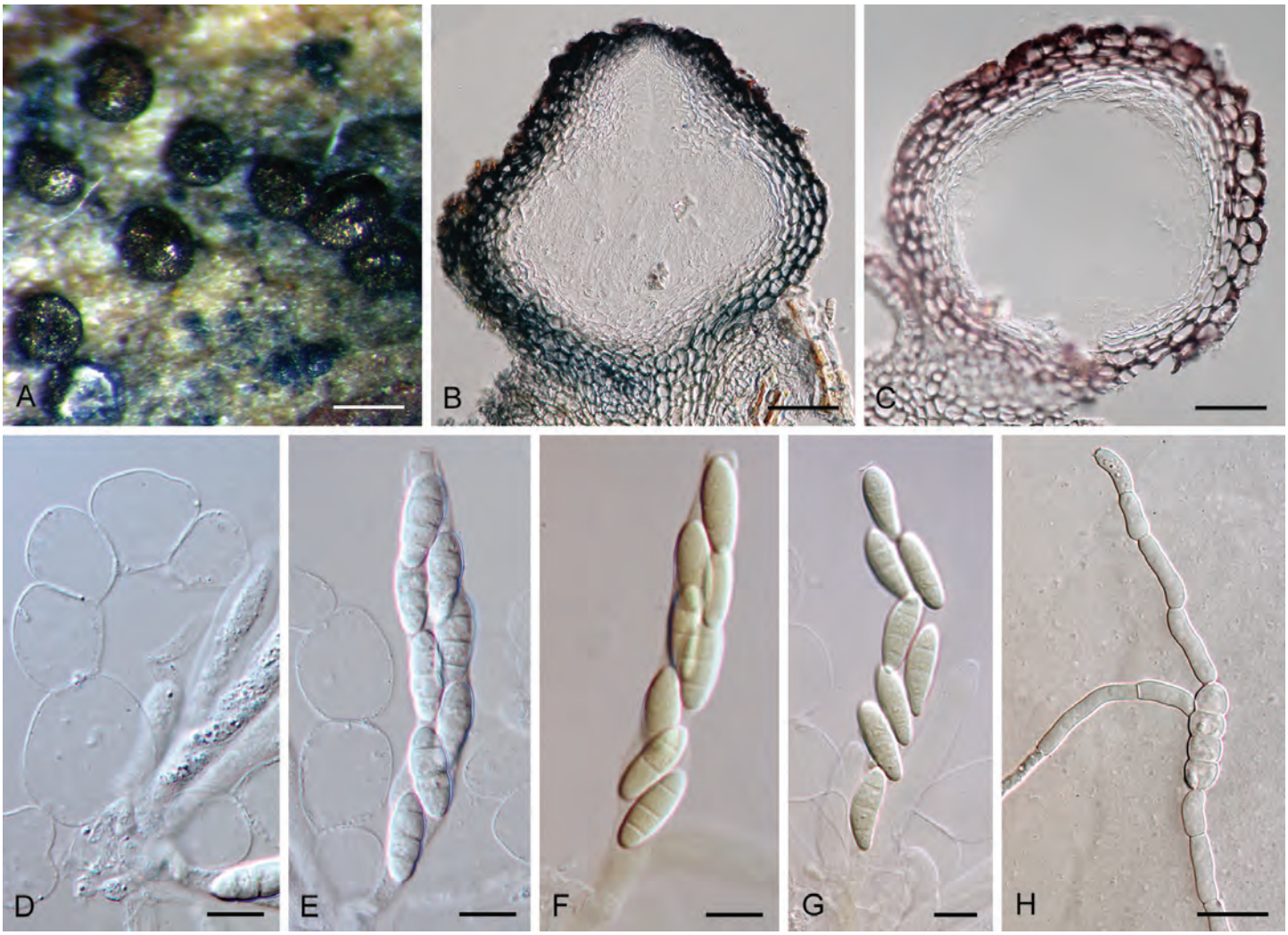

Fig. 12. *Fusarium celtidicola* (MFLUCC 16-0526). **A.** Perithecial ascomata on host surface. **B, C.** Vertical section through perithecia. **D–G.** Hamathecial catenophyses, and asci. **H.** Germinating ascospore. (F, G in Melzer's reagent). Scale bars: A = 100 µm, B, C = 30 µm, D–H = 10 µm (Photos from Shang *et al.* 2018).

Diagnostic features: *Colonies* on the surface white, reddish at the centre, and reddish white in reverse on PDA; aerial monophialides giving rise to micro- and macroconidia; *microconidia* oblong to naviculate, straight or curved, 1–3-septate; *macroconidia* naviculate to falcate, 3–5-septate with a curved, blunt apical cell and poorly-developed, foot-shaped basal cell; *chlamydospores* intercalary in aerial hyphae, in pairs or chains (Shang *et al.* 2018).

Notes: *Fusarium celtidicola* is distinct from other members of the FCCSC in that it produces chlamydospores, and has a sexual morph with blue-black to dark purple perithecia, and ellipsoid to obovoid to fusoid, 0–3-septate, smooth-walled ascospores (Shang *et al.* 2018).

Fusarium citricola Guarnaccia *et al.*, *Persoonia* **40**: 12. 2017 (2018). MB 820246.

Holotypus: CBS H-23020 (dried SNA/CL culture).

Ex-type culture: CBS 142421 = CPC 27805.

Type locality: **Italy**, Cosenza, Rocca Imperiale.

Type substrate: Crown of *Citrus reticulata* 'Caffin'.

Description and illustrations: See Sandoval-Denis *et al.* (2018a).

Diagnostic features: *Colonies* pale luteous to pale yellow on surface (orange to red when incubated in light), reverse pale luteous to straw (diffusible pigment absent in the dark, an orange to red pigment sometimes present when incubated in the light) on PDA; aerial monophialides giving rise to *microconidia*, ellipsoidal to falcate, 0–3-septate; *sporodochia* bright orange, with monophialides giving rise to falcate, dorsiventrally curved *macroconidia* with almost parallel sides, tapering slightly towards both ends, with a blunt to papillate, curved apical cell and poorly to well-developed, foot-shaped basal cell, (1–)2–4(–6)-septate; *chlamydospores* absent (Sandoval-Denis *et al.* 2018a).

Notes: *Fusarium citricola* was shown to be the cause of cankers on diverse *Citrus* spp. in Apulia and Calabria in southern Italy. *Fusarium citricola* resembles *F. salinense*, but can be distinguished in having slightly smaller sporodochial conidia, often with a gentle and symmetrical dorsiventral curvature, and 0–3-septate microconidia (*vs* the often asymmetrically curved macroconidia and 0–1(–2)-septate microconidia in *F. salinense*) (Sandoval-Denis *et al.* 2018a).

Fusarium juglandicola L. Lombard & Crous, Persoonia **46**: 521. 2021. MB 839621.

Holotypus: CBS H-24770.

Ex-type culture: CBS 147773 = CPC 37962 = UBOCC-A-119001.

Type locality: **France**, Rhone-Alps region.

Type substrate: Bud of *Juglans regia*.

Description and illustrations: See Crous *et al.* (2021a).

Diagnostic features: *Colonies* white to pale luteous on surface and reverse on PDA; aerial monophialides giving rise to macroconidia; *microconidia* absent; *sporodochia* with monophialides giving rise to falcate, moderately dorsiventrally curved *macroconidia* with almost parallel sides, tapering towards both ends, with a blunt to slightly hooked, somewhat curved apical cell and papillate to well-developed, foot-shaped basal cell, (1–)3–4(–5)-septate; *chlamydospores* absent (Crous *et al.* 2021a).

Notes: *Fusarium juglandicola* was isolated from walnut, *Juniperus* sp., and eggs from an unknown species in southeast France. *Fusarium juglandicola* is unique within the FCCSC by lacking microconidia and red pigments, even when incubated under continuous white light (Crous *et al.* 2021a).

Fusarium salinense Sand.-Den. *et al*., *Persoonia* **40**: 15. 2017 (2018). MB 820245.

Holotypus: CBS H-23019 (dried SNA/CL culture).

Ex-type culture: CBS 142420 = CPC 26973.

Type locality: **Italy**, Sicily, Messina, Leni.

Type substrate: Twigs of *Citrus sinensis*.

Description and illustrations: See Sandoval-Denis *et al.* (2018a).

Diagnostic features: *Colony* surface pale luteous to sulphur yellow with white to pale luteous margins, reverse pale luteous to orange toward the centre of the colony. Yellow diffusible pigment sometimes present, while red colonies and diffusible pigments occur when incubated in light on PDA, having optimal growth at 25 °C; aerial monophialides giving rise to *microconidia*, ovoid, ellipsoid to falcate, 0–1(–2)-septate; *sporodochia* flesh, salmon to orange coloured, with monophialides give rise to falcate, (2–)3–4(–5)-septate, slender *macroconidia*, with a gentle curvature and nearly parallel dorsiventral lines or an unequal curvature, slightly more pronounced in the upper part of the spore, tapering slightly towards the basal end, with a papillate and curved apical cell and a poorly-developed, foot-shaped basal cell; *chlamydospores* absent, but rounded, thin-walled hyphal swellings sometimes present in old cultures. (Sandoval-Denis *et al.* 2018a).

Notes: *Fusarium salinense* is known from Sicily (Italy), and Salina (Aeolian Island), and is associated with canker symptoms on three different *Citrus* species. It produces sparingly branched conidiophores in the aerial mycelium, especially in young cultures, but its growth soon becomes pionnotal. *Fusarium salinense* can be distinguished from *F. citricola* by producing shorter sporodochial phialides and slightly longer and robust macroconidia, often with an unequal dorsiventral curvature (Sandoval-Denis *et al.* 2018a).

Fusarium concolor species complex (FCOSC)

Fusarium bambusarum M.M. Wang & L. Cai, *Persoonia* **48**: 25. 2022. MB 346784.

Typus: HMAS 351575 (dried SNA/CL culture).

Type locality: **China**, Jiangxi Province.

Type substrate: From bamboo.

Descriptions and illustrations: See Wang *et al*. (2022).

Diagnostic features: *Colonies* white on PDA, with dense aerial mycelium; aerial monophialides giving rise to *microconidia* in false heads, ovoid to fusoid-ellipsoid, aseptate; *sporodochia* orange grey on carnation leaf agar, with monophialides give rise to falcate *macroconidia*, slightly bent with parallel sides, with a papillate to hooked, curved apical cell, and well-developed, foot-shaped basal cell, 3–6-septate; *chlamydospores* terminal, globose, becoming rough and thick-walled (Wang *et al.* 2022).

Notes: *Fusarium bambusarum* is distinguished from other taxa in the FCOSC based on its 3–6-septate macroconidia, and having monophalidic aerial phialides (Wang *et al.* 2022). Presently this taxon is only known from bamboo collected in Jiangxi Province, China.

Fusarium anguioides Sherb., *Mem. Cornell Univ. Agric. Exp. Sta*. **6**: 169. 1915. MB 159197.
Synonym: *Fusarium avenaceum* var. *anguioides* (Sherb.) Bilaĭ, *Mikrobiologicheskij Zhurnal* (Kiev) **49**: 6. 1987. MB 346784.

Typus: ?CUP-007479, BPI 72044 neotype (not Code compliant).

Type locality: **USA**, New York, Castile.

Type substrate: *Solanum tuberosum*.

Descriptions and illustrations: See Sherbakoff (1915), Gerlach & Nirenberg (1982) and Nelson *et al*. (1995).

Diagnostic features: *Colonies* cream, pink, rose to carmine or yellowish to ochre, becoming yellowish brown or red-brown to brown with age on PDA, having optimal growth at 25 °C; aerial mono- to polyphialides giving rise to *microconidia*, ovoid to fusoid, 0–3-septate; *sporodochia* orange to cinnamon or brick coloured, with monophialides give rise to falcate, *macroconidia*, slightly bent to anguiform, slender, tapering toward both ends, with an elongated, elegantly curved apical cell and well-developed, foot-shaped basal cell, (3–)5–7-septate; *chlamydospores* absent, but hyphal swellings do occur (Gerlach & Nirenberg 1982).

Notes: Sherbakoff (1915) provided an illustration with the original protologue of *F. anguioides* and placed material in CUP,

as CUP-007479. The neotype (BPI 72044) designated by Nelson *et al*. (1995) originated from China and was isolated from soil in a bamboo grove, and is thus unsuitable. An isolate from the original locality (USA) and host (*Solanum tuberosum*) needs to be selected.

Fusarium austroafricanum A. Jacobs *et al.*, *Mycologia* **110**: 1197. 2018. MB 823959. Fig. 13.

Holotypus: PREM 62137 (dried culture); *paratypi* PREM 62138 and PREM 62139 (dried cultures).

Ex-holotype culture: NRRL 66741 = PPRI 10408 = PPRI 23548; ex-paratype cultures: CBS 120990 = DAOM 192987 = FRC M-2406 = NRRL 53441 = PPRI 23546 and NRRL 66742 = PPRI 10412.

Type locality: **South Africa**, Eastern Cape Province, Humansdorp.

Type substrate: Endophyte of *Pennisetum clandestinum*.

Description and illustrations: See Jacobs-Venter *et al*. (2018).

Diagnostic features: *Colony* surface white to reddish white, reverse pale orange on PDA, having optimal growth at 30 °C; aerial mono- to polyphialides giving rise to *microconidia*, oval to obovoid, aseptate; *sporodochia* with monophialides give rise to falcate, (3–)5(–8)-septate *macroconidia* with a blunt apical cell and poorly-developed, foot-shaped basal cell; *chlamydospores* singly or in intercalary or terminal clusters (Jacobs-Venter *et al*. 2018).

Notes: *Fusarium austroafricanum* is similar morphologically to *F. concolor* and *F. babinda*, but forms white to reddish white colonies on PDA, whereas those of *F. concolor* are white to pale orange, and those of *F. babinda* are pale orange to violet. Morphologically, *F. austroafricanum* differs from *F. concolor* and *F. babinda* in the shape of the apical cell on the macroconidia, *i.e*. blunt (*F. austroafricanum*), papillate (*F. concolor*) or slightly curved to hooked (*F. babinda*) (Reinking 1934, Marasas *et al.* 1986, Jacobs-Venter *et al*. 2018).

Fusarium concolor Reinking, *Zentralbl. Bakteriol.,* Abt. 2, **89**: 512. 1934. MB 261626.
Synonym: *Fusarium polyphialidicum* Marasas *et al.*, *Mycologia* **78**: 678. 1986. MB 102972.

Holotypus: IMI 112502.

Ex-type culture: BBA 2607 = BBA 63601 = CBS 183.34 = DAOM 225131 = DSM 62179 = IMB 10330 = IMI 112502 = NRRL 13994.

Type locality: **Uruguay**, Montevideo.

Type substrate: *Hordeum vulgare*.

Descriptions and illustrations: See Gerlach & Nirenberg (1982) and Marasas *et al.* (1986).

Diagnostic features: *Colonies* whitish, reverse white to yellow on PDA, having optimal growth at 25 °C; aerial mono- to polyphialides giving rise to *microconidia* in false heads, obovoid, fusoid to subclavate, (0–)1(–2-)septate; *sporodochia* white to pale orange, with mono- to polyphialides give rise to straight or falcate, 3–5(–9)-septate *macroconidia* with a long and tapered to curved apical cell and well-developed, foot-shaped basal cell; *chlamydospores* abundant, intercalary and terminal in hyphae and conidia, single, in pairs, chains or clusters (Gerlach & Nirenberg 1982, Marasas *et al.* 1986).

Notes: Balmas *et al*. (2010) and Jacobs-Venter *et al*. (2018) considered that *F. polyphialidicum* was a synonym of *F. concolor*, which was originally described based on a single isolate from diseased barley in Uruguay (Reinking 1934). *Fusarium concolor* has a wide distribution and host range, occurring in Africa (South Africa, Zimbabwe), Australasia (Australia), Europe (Italy, Spain), South America (Uruguay), and North America (USA, Hawaii), and has also been associated with human infections (Jacobs-Venter *et al*. 2018).

Taxonomic novelties

Novel species are described in *Fusicolla* and *Neocosmospora*. Additionally, arguments for recognising distinct genera in the terminal fusarioid clade of the *Nectriaceae* were presented by Crous *et al*. (2021b) and Hill *et al*. (2022). In this regard, several species recently assigned to *Fusarium s. str*., are herewith allocated to *Neocosmospora*.

Fusicolla elongata Decock, Crous & Sand.-Den., ***sp. nov.*** MycoBank MB 843499. Fig. 14.

Etymology: From Latin *elongare*, meaning elongated, in reference to its long conidia.

Description: *Conidiophores* prostrate, emerging from vegetative hyphae, intermixed and confluent, commonly as single phialides borne laterally on hyphae or reduced to phialidic pegs; rarely and mostly on the colony periphery, conidiophores erect, simple or branched once or twice laterally and irregularly, terminating in a single conidiogenous cell. *Conidiogenous cells* monophialidic, subcylindrical, (3–)8–31.5(–40) × (1.5–)2–4(–4.5) µm, smooth- and thin-walled, with or without noticeable periclinal thickening, and a minute, non-flared apical collarette. *Macroconidia* slender to somewhat elongate, almost straight to gently curved, apical cell barely curved with a rounded apex, basal cell obtuse, non-foot-shaped, (3–)4–5-septate, predominantly 5-septate, hyaline, smooth- and thin-walled; 3-septate conidia: 66.5–82 × 2.5–3 µm (av. 73.6 × 2.8 µm); 4-septate, (64–)74.5–92.5(–97) × (2.5–)3–4 µm (av. 83.5 × 3.2 µm); 5-septate, (81.5–)85–96(–100.5) × 2.5–4 µm (av. 90.5 × 3.3 µm). *Microconidia*, *chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies at 25 °C after 7 d: On PDA reaching 17–22 mm diam, orange to apricot at centre, white to pale salmon at periphery, flat, slightly folded to cerebriform at centre, membranous to slimy, lacking aerial mycelium, margin entire; reverse white to pale salmon, without diffusible pigments. On SNA reaching 15–22 mm diam, buff to pale salmon, flat, membranous to slimy at centre, aerial mycelium lacking or scattered in irregular, short patches; reverse white to pale saffron without diffusible pigments. On OA reaching 22–28 mm diam, pale luteous, pale amber to ochraceous, flat, membranous, with abundant and confluent sporulation forming slimy masses and concentric rings, lacking aerial mycelium, margin entire to filamentous; reverse pale luteous without diffusible pigments.

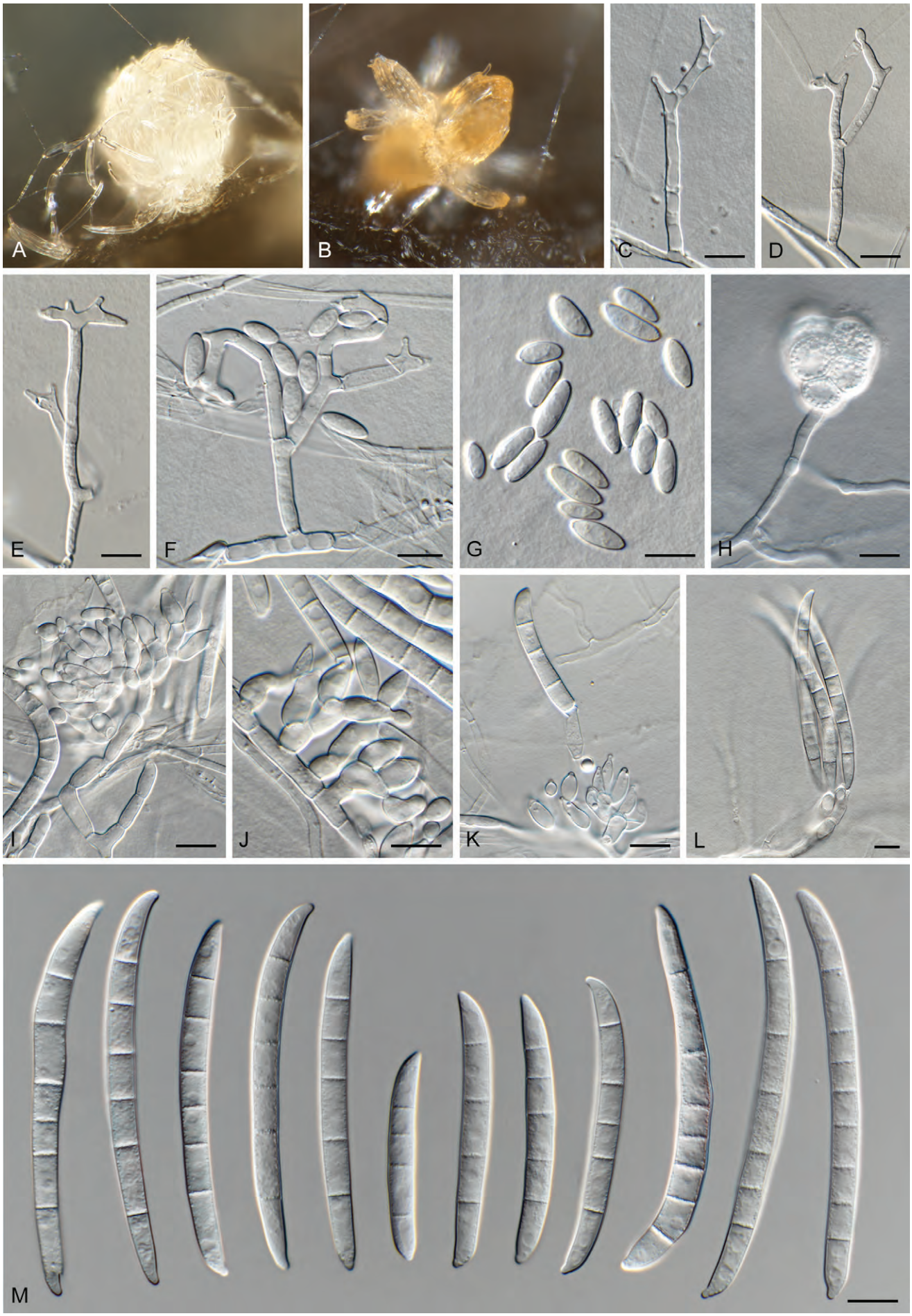

Fig. 13. *Fusarium austroafricanum* (CBS 120990). **A, B.** Sporodochia on CLA. **C–F.** Aerial conidiophores with polyphialides giving rise to microconidia. **G.** Microconidia. **H.** Chlamydospore. **I–L.** Sporodochial conidiophores giving rise to macroconidia. **M.** Macroconidia. Scale bars = 10 µm.

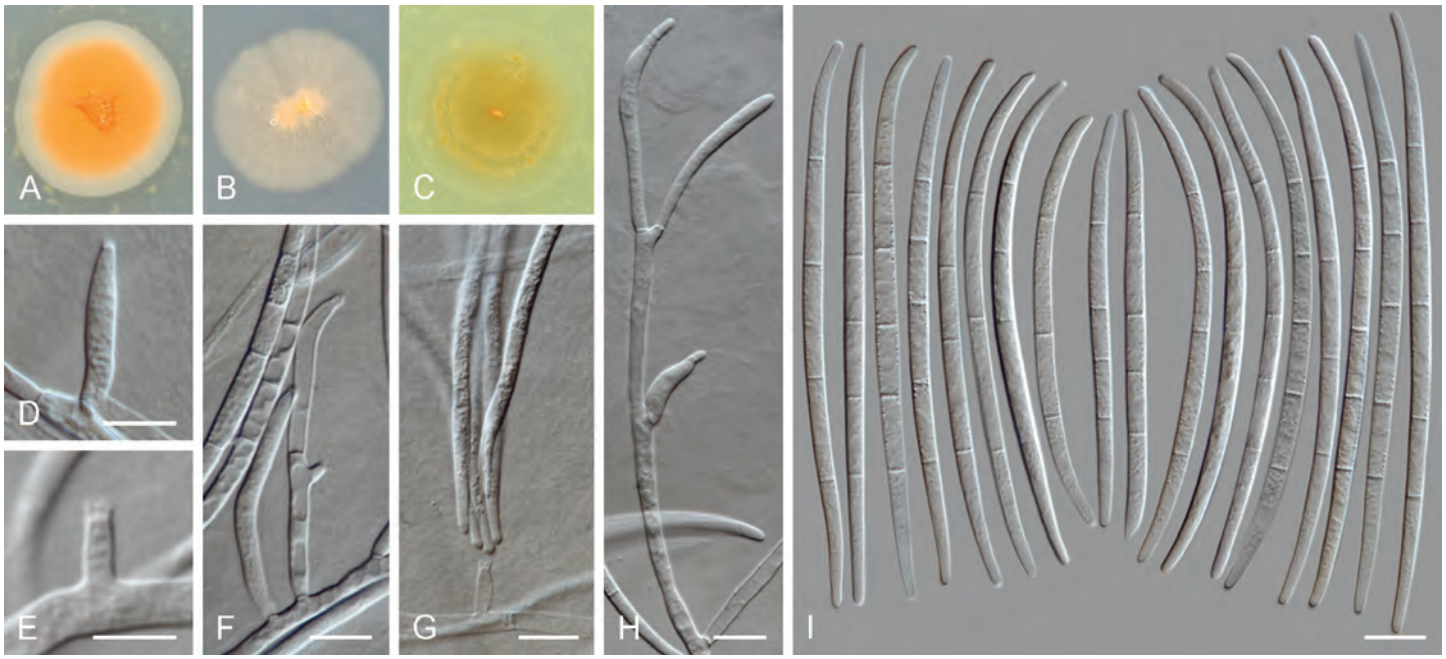

Fig. 14. *Fusicolla elongata* (MUCL 58143 ex-type). **A–C.** Colony surface on PDA, SNA and OA, respectively. **D–H.** Conidiophores and conidiogenous cells. **I.** Conidia. Scale bars: E = 5 µm; all others = 10 µm.

Typus: **Zimbabwe**, Matabeleland North, Victoria Falls area, from soil, Apr. 1996, *C. Decock*, isol. number 51V (**holotype** CBS H-24945, culture ex-type MUCL 58143 = CBS 148934).

Additional material examined: **Zimbabwe**, Matabeleland North, Victoria Falls area, from soil, Apr. 1996, *C. Decock*, isol. number 52V, culture MUCL 58144 = CBS 148935.

Notes: *Fusicolla elongata* produces characteristic long 3–5-septate conidia. Other *Fusicolla* species producing conidia with similar septation include *Fu. acetilerea*, *Fu. violacea*. However, *Fu. elongata* forms exceptionally long conidia which distinguishes this species from every other known species in the genus. *Fusicolla elongata* can be further distinguished from *Fu. acetilerea* by the lack of chlamydospores in the former species. Additionally, while both *Fu. acetilerea* and *Fu. violacea* have brownish to dark red-brown colony pigmentation, colonies of *Fu. elongata* are consistently orange to salmon coloured (Gerlach & Nirenberg 1982).

Fusicolla gigas Chang Liu, Z.Q. Zeng & W.Y. Zhuang, ***sp. nov.*** MycoBank MB 844496.

Etymology: Name refers to the large-sized macroconidia produced by this species.

Holotypus: CGMCC 3.20680 (permanently preserved in a metabolically inactive state).

Ex-type culture: CGMCC 3.20680.

Type locality: **China**, Chongqing City, Wushan County, Hongchiba National Forest Park.

Type substrate: Isolated from soil.

Description and illustration: Liu *et al*. (*Phytotaxa* **536**: 167. 2022).

Diagnostic features: *Colonies* orange to pale yellow with orange margin and slimy appearance on PDA; aerial monophialides giving rise to micro- and macroconidia; *microconidia* aseptate, slightly to markedly curved; *macroconidia* falcate to long-fusiform, (1–)3(–4)-septate, with a hooked apical cell and foot-shaped basal cell; *chlamydospores* and *sexual morph* not observed (Liu *et al*. 2022).

Fusicolla guangxiensis Z.Q. Zeng, C. Liu & W.Y. Zhuang, ***sp. nov.*** MycoBank MB 844497.

Etymology: Name refers to the type locality of the type specimen.

Holotypus: CGMCC 3.20679 (permanently preserved in a metabolically inactive state).

Ex-type culture: CGMCC 3.20679.

Type locality: **China**, Guangxi autonomous region, Fangchenggang City, Shangsi County, Shiwandashan National Forest Park.

Type substrate: Isolated from an unidentified rotten twig.

Description and illustration: Liu *et al*. (*Phytotaxa* **536**: 169. 2022).

Diagnostic features: *Colonies* orange with pale luteous margin and slimy appearance on PDA; aerial monophialides giving rise to macroconidia; *macroconidia* falcate to long-fusiform, (0–)1(–3)-septate, with an acute to hooked apical cell and an acute, non-pedicellate basal cell; *microconidia*, *chlamydospores* and *sexual morph* not observed (Liu *et al*. 2022).

Notes: *Fusicolla gigas* and *Fu. guangxiensis* were invalidly published because the protologue did not explicitly mention the

holotypes were preserved in a metabolically inactive state [Art. 40.8 (Shenzhen)]. Both species are validated here.

Longinectria O. Savary, M. Coton, E. Coton & J-L. Jany, ***gen. nov.*** MycoBank MB 844395.

Etymology: From the Latin *longus* = long, "Longi-" refers to the phialides length observed for the *Longinectria* species and "*-nectria*" refers to the *Nectriaceae* family.

Ascomatal morph unknown. *Conidiophores* with variable-length phialides, sometimes extremely long (*e.g.* 153–237 µm), lateral, sometimes verticillate, hyaline. *Macroconidia* straight to slightly curved, apical cell morphology blunt to papillate and a basal cell often notched, 0–3-septate, hyaline. *Microconidia* ovoid, ellipsoid to allantoid, 0–1 septate, hyaline. *Chlamydospores* absent to abundant, globose, single, in pairs or chains, intercalary or terminal (from Savary *et al*. 2021).

Type species: *Longinectria lagenoides* O. Savary, M. Coton, E. Coton & J-L. Jany

Notes: The genus *Longinectria*, together with its two known species, *L. lagenoides* and *L. verticilliformis*, were invalidly published as two numbers were cited as holotypes for each species [Art. 40.7, 40.8 (Shenzhen)] (Savary *et al*. 2021). The names were subsequently published in *Index Fungorum*, but as the type species of the genus was not indicated, the genus was still not validly published [Art. 40.1 (Shenzhen)], and the species also rendered invalid [Art. 35.1 (Shenzhen)]. The genus and species are thus validated here.

Longinectria lagenoides O. Savary, M. Coton, E. Coton & J-L. Jany, ***sp. nov.*** MycoBank MB 844396.

Holotypus: UBOCC-A-120039 (permanently preserved in a metabolically inactive state).

Ex-type culture: UBOCC-A-120039 = CBS 147588.

Type locality: **France**.

Type substrate: Isolated from Swiss cheese.

Description and illustration: Savary *et al*. (*Mycosphere* **12**: 1089. 2021) .

Etymology: From Latin *lagoena* = bottle, refers to the observed phialide shape.

Diagnostic features: *Colonies* brown with folded surface and brown pigmentation and powdery aerial mycelium (sporulation) on PDA, growing between 5 and 25 °C, having optimal growth at 20 °C; aerial monophialides giving rise to micro- and macroconidia; monophialides extremely long or reduced to conidiogenous pegs on hyphae; *microconidia* 0–1-septate, ovoid to allantoid; *macroconidia* straight, 0–3-septate, apical cell blunt to papillate, and poorly-developed, foot-shaped basal cell; *chlamydospores* globose, typically intercalary, or terminal, two or more. No known mycotoxins already described to be produced by *Fusarium*, *Penicillium*, *Aspergillus* or *Alternaria* spp. were detected (Savary *et al*. 2021).

Longinectria verticilliformis O. Savary, M. Coton, E. Coton & J-L. Jany, ***sp. nov.*** MycoBank MB 844397.

Etymology: Name refers to the subverticillate arrangement of phialides.

Holotypus: UBOCC-A-120043 (permanently preserved in a metabolically inactive state).

Ex-type culture: UBOCC-A-120043 = CBS 147589.

Type locality: **France**.

Type substrate: Isolated from an Italian cheese (Alpeggio).

Description and illustration: Savary *et al*. (*Mycosphere* **12**: 1091. 2021).

Diagnostic features: *Colonies* white to white grey with powdery to cottony aerial mycelium on PDA, growing between 5 and 25 °C, with optimal growth at 20 °C; aerial monophialides giving rise to micro- and macroconidia; *microconidia* 0–1-septate, straight or curved, reniform; *macroconidia* straight, ellipsoidal, 1–3-septate, with a blunt to papillate apical cell and foot-shaped basal cell; *chlamydospores* not observed. No known mycotoxins already described to be produced by *Fusarium*, *Penicillium*, *Aspergillus* or *Alternaria* spp. were detected (Savary *et al*. 2021).

Neocosmospora akasia (Lynn & I. Barnes) Crous & Sand.-Den., ***comb. nov.*** MycoBank MB 843501.
Basionym: *Fusarium akasia* Lynn & I. Barnes, *Mycologia* **113**: 544. 2021. MB 834436.

Holotypus: PREM 62607; *paratypi* PREM 62608 and PREM 62609.

Ex-type culture: CBS 146880 = CMW 54735 = PPRI 27978; ex-paratype cultures CBS 146881 = CMW 54741 = PPRI 27979 and CBS 147161 = CMW 54752 = PPRI 27980.

Type locality: **Indonesia**, Riau, Pelalawan.

Type substrate: From head (including mycangium) of *Euwallacea perbrevis* (TSHBa) in stems of *Acacia crassicarpa.*

Description and illustrations: Lynn *et al.* (2021).

Diagnostic features: *Colony* surface white, buff to saffron or fulvous in dark, buff to honey darkening to red, blood red in ambient daylight, reverse yellowish white to buff ,darkening to isabelline or cinnamon in the dark, saffron to orange, darkening to rust and blood red after 1 mo in ambient daylight on PDA, having optimal growth at 30 °C; aerial monophialides giving rise to *microconidia* in false heads, ovoid to obovoid, slightly curved, 0–1(–2)-septate; *sporodochia* buff to pale orange, with monophialides give rise to slightly curved, clavate, with ridged appearance, (0–)1–4(–5)-septate *macroconidia* with a blunt apical cell and obtuse to poorly-developed, foot-shaped basal cell; *chlamydospores* sparse, in hyphae and conidia, single or in pairs (Lynn *et al.* 2021).

Notes: *Neocosmospora akasia* is associated with the ambrosia beetles, *Euwallacea perbrevis* and *E. similis* in plantations of

Acacia crassicarpa in Indonesia. It is characterized by clavate conidia which are slightly constricted at the septa, giving it a ridged appearance, and having arched, thick aerial conidiophores that taper slightly at the base (Lynn *et al.* 2021).

Neocosmospora awan (Lynn & I. Barnes) Crous & Sand.-Den., ***comb. nov.*** MycoBank MB 843502.
Basionym: *Fusarium awan* Lynn & I. Barnes, *Mycologia* **113**: 544. 2021. MB 834437.

Holotypus: PREM 62602; *paratypi* PREM 62594 and PREM 62604.

Ex-type culture: CBS 146882 = CMW 54719 = PPRI 27973; ex-paratype cultures CBS 146883 = CMW 53705 = PPRI 27957 and CBS 146884 = CMW 54722 = PPRI 27975.

Type locality: **Indonesia**, Riau, Pelalawan.

Type substrate: From head (including mycangium) of *Euwallacea similis* in stems of *Acacia crassicarpa.*

Description and illustrations: Lynn *et al.* (2021).

Diagnostic features: *Colony* surface colour white in the dark, white darkening to honey after 1 mo in ambient daylight, in reverse yellowish white to buff in the dark, buff darkening to ochreous after 1 mo in ambient daylight on PDA, having optimal growth at 30 °C; aerial monophialides giving rise to *microconidia* in false heads, ovoid, 0–1(–2)-septate, and flute-shaped, 1–3-septate *macroconidia*; sporodochia luteous to ochreous, with monophialides giving rise to curved, cylindrical or slightly clavate or flute-shaped, (0–)2–3(–4)-septate macroconidia with a narrowly papillate to blunt apical cell and obtuse to poorly-developed, foot-shaped basal cell; *chlamydospores* abundant, intercalary and terminal in hyphae and conidia, single, in pairs or chains (Lynn *et al.* 2021).

Notes: *Neocosmospora awan* is associated with ambrosia beetles, *Euwallacea perbrevis* and *E. similis*, in plantations of *Acacia crassicarpa* in Indonesia. It is characterised by having abundant chlamydospores that form in hyphae and mature conidia, having multiseptate aerial macroconidia that are elongated-ovoid in shape, and very narrow sporodochial macroconidia. Furthermore, phylogenetically it groups separate from the Ambrosia Clade within *Neocosmospora*.

Neocosmospora brevis Sand.-Den. & Crous, *Persoonia* **43**: 119. 2019. MB 831176.
Synonym: *Fusarium breve* (Sand.-Den. & Crous) O'Donnell *et al.*, *Index Fungorum* **440**: 1. 2020. MB 557673.
New synonym: *Fusarium rosicola* Lin Huang *et al.*, *Pl. Pathol.* **70**: 2065. 2021. MB 839201.

Holotypus: CBS H-23975.

Ex-type culture: CBS 144387 = MUCL 16108.

Type locality: **Belgium**, Heverlee.

Type substrate: Soil-water polluted with diethylene glycerol and ethylene glycerol.

Description and illustrations: Sandoval-Denis *et al.* (2019), He *et al.* (2021).

Diagnostic features: *Colony* surface orange to saffron or pale yellow, reverse orange, luteous to amber to pale yellow on PDA, having optimal growth at 25 °C; aerial monophialides giving rise to *microconidia* in false heads, oval, ellipsoidal to subclavate, straight or slightly curved, 0–1(–2)-septate; *sporodochia* with monophialides give rise to falcate, slightly dorsiventrally curved, 3–5-septate *macroconidia*, apical cell blunt and rounded, basal cell without a well-developed foot-shaped basal cell; *chlamydospores* abundant, globose to subglobose, terminal or intercalary on hyphae or conidia, solitary or in chains (Sandoval-Denis *et al.* 2019).

Notes: *Fusarium rosicola* was described as a pathogen of Chinese rose (*Rosa chinensis*) (He *et al*. 2021). Apparent morphological and physiological differences with its closest relative, *N. brevis*, in their phylogenetic analysis were not supported in our analysis (Fig. 3). We attribute these differences to intraspecific variability in *N. brevis*.

Neocosmospora drepaniformis (T. Aoki *et al.*) Crous & Sand.-Den., ***comb. nov.*** MycoBank MB 843503.
Basionym: *Fusarium drepaniforme* T. Aoki *et al.*, *Mycologia* **113**: 1098. 2021. MB 558018.

Holotypus: BPI 923530 (dried culture), *isotypus* IMI 351954.

Ex-type culture: NRRL 62941 (= KOD 147) = MAFF 247230.

Type locality: **Singapore**.

Type substrate: Unknown woody host.

Description and illustrations: Aoki *et al.* (2021).

Diagnostic features: *Colony* surface white, yellowish white to pale yellow, becoming pale orange, light orange to greyish orange with age, reverse yellowish white or pale yellow to greyish yellow on PDA, having optimal growth at 25 °C; aerial monophialides giving rise to *microconidia* in false heads, ellipsoidal, oblong-ellipsoidal, fusoid-ellipsoidal to clavate, straight or sometimes curved and reniform or crescent-shaped, some obovate to comma-shaped, 0–1(–3)-septate; *sporodochia* sparse, with monophialides give rise to clavate and straight (in the dark), to falcate (under nuv-light), (0–)3–7-septate *macroconidia*, with a papillate apical cell and poorly to well-developed, foot-shaped basal cell; *chlamydospores* intercalary and terminal in hyphae and conidia, single, in chains or small clusters (Aoki *et al*. 2021).

Notes: *Neocosmospora drepaniformis* was originally deposited as "*F. bugnicourtii*" (on *Camellia sinensis*: West Bengal) based on IMI 351954. It is characterised by forming multiseptate curved conidia, especially under nuv-light. Some conidia become swollen in the apical part, appearing wedge-shaped (Aoki *et al*. 2021).

Neocosmospora duplosperma (T. Aoki *et al.*) Crous & Sand.-Den., ***comb. nov.*** MycoBank MB 843504.
Basionym: *Fusarium duplospermum* T. Aoki *et al.*, *Mycologia* **113**: 1091. 2021. MB 558017.

Holotypus: BPI 923529 (dried culture).

Ex-type culture: NRRL 62583 = MAFF 247220.

Type locality: **USA**, Florida, Miami-Dade County, Homestead.

Type substrate: From the oral mycangium of *Euwallacea perbrevis* trapped in a *Persea americana* grove.

Description and illustrations: Aoki *et al*. (2021).

Diagnostic features: *Colony* surface white, yellowish white, pale yellow, light yellow to greyish yellow, becoming pale orange to greyish orange, or reddish white to pale red, reddish grey to greyish red with age in the dark, reverse pigment absent or yellowish white, pale yellow to light yellow, some greyish orange, brownish orange to yellowish brown or brown, sometimes with yellowish pigments in the agar on PDA, having optimal growth at 25 °C; aerial monophialides giving rise to *microconidia* in false heads, ellipsoid, oblong-ellipsoid, fusoid-ellipsoid to short-clavate, straight or sometimes curved, reniform or crescent-shaped, some obovate to comma-shaped, 0–1-septate; *sporodochia* with monophialides give rise to two distinct conidial types, i) short-clavate to obovate or naviculate, straight or curved, with obtuse apex and truncate base, 0–1(–2)-septate, and ii) straight or curved, wedge-shaped, (1–)3–5(–7)-septate, swollen in the apical region, with a tapering apical cell, base with a poorly to well-developed, foot-shaped basal cell; *chlamydospores* delayed, intercalary and terminal in hyphae and conidia, single or in chains (Aoki *et al*. 2021).

Notes: *Neocosmospora duplosperma* can be distinguished by forming two morphologically distinct types of multiseptate conidia, namely (i) long, slender, and falcate, or (ii) relatively short, apically swollen, curved and wedge-shaped ("dolphin-like"). Furthermore, *N. duplosperma* is characterised by forming brownish orange colonies on PDA, which differs other species in the *Neocosmospora* Ambrosia Clade, which typically produce whitish, yellowish, or greyish coloured colonies on PDA (Aoki *et al*. 2021).

Neocosmospora geoasparagicola Sand.-Den., Crous, de Boer, Katschnig & W. Jonkers, ***sp. nov.*** MycoBank MB 843505. Fig. 15.

Etymology: Named after the substrate from which all the original specimens were collected: soil from *Asparagus officinalis* fields.

Conidiophores erect or prostrate, borne on the agar substrate and aerial mycelium, 45–190 µm tall, simple or branched laterally and sympodially, bearing terminal single phialides; aerial conidiogenous cells monophialidic, subulate to subcylindrical, smooth- and thin-walled, 21–61 × 2.5–5 µm, with short and flared apical collarettes, periclinal thickening inconspicuous or absent, rarely proliferating laterally and apically. *Aerial conidia* falcate, smooth- and thick-walled, gently dorsiventrally curved, robust, with a blunt, slightly curved apical cell, basal cell obtuse to poorly-developed, foot-shaped, undistinguishable in shape from sporodochial conidia, 3–4(–5)-septate, predominantly 3-septate, 3-septate conidia: (37–)39–50(–56.5) × (4–)5–6.5 µm (av. 44 × 5.3 µm); 4-septate conidia: (49–)51–63(–67.5) × 5.5–7 µm (av. 56.5 × 6 µm); 5-septate conidia: 54.5 × 5.5 µm (only one element observed); overall: (37–)39–54(–67.5) × 4.5–6.5 µm (av. 46.6 × 5.4 µm), borne at the tip of monophialides and accumulating forming elongated false-heads. *Sporodochia* pale luteous to pale orange, formed on aerial and substrate mycelium, and on the surface of carnation leaves. *Sporodochial conidiophores* simple or laterally and irregularly branched bearing terminal monophialides or groups of 2–4 monophialides; *sporodochial conidiogenous cells* monophialidic, doliiform, subulate to subcylindrical, (13–)14.5–22(–31) × 3.5–6 µm, smooth and thin-walled, with a vasiform apical collarette and inconspicuous to absent periclinal thickening. *Sporodochial conidia* falcate, gently dorsiventrally curved, robust, with a blunt, slightly curved apical cell, basal cell obtuse to poorly-developed, foot-shaped, 3–5-septate, predominantly 4-septate, hyaline, smooth- and thick-walled; 3-septate conidia: (43.5–)47–55(–60) × 5–7 µm (av. 51 × 6 µm); 4-septate conidia: (46–)52–60(–63) × 5–7 µm (av. 56.1 × 6 µm); 5-septate conidia: (52.5–)55–64(–68) × 5–7 µm (av. 59.2 × 6.1 µm); overall: (43.5–)52–61(–68) × 5–7 µm (av. 56.6 × 6 µm). *Chlamydospores* and *sexual form* not observed.

Culture characteristics: Colonies at 25 °C after 7 d: On PDA reaching 38–43 mm diam, white to pale buff, pale vinaceous buff at periphery, flat, dusty to felty with or without cottony patches or concentric rings of short aerial mycelium, membranous at periphery, margin entire to slightly filamentous; reverse white to pale buff, ochreous to umber at centre, without diffusible pigments. On SNA reaching 36–42 mm diam, white to pale buff, flat, membranous to dusty at centre, aerial mycelium scarce; reverse white, without diffusible pigments. On OA reaching 40–48 mm diam, white to pale buff, flat, felty, with concentric rings of short, white aerial mycelium, margin entire to slightly lobate; reverse pale buff without diffusible pigments.

Typus: **Netherlands**, Limburg, Kessel, from field soil cultured with *Asparagus officinalis* '*Guelph Millennium*' field, 19 Nov. 2020, *M. Sandoval-Denis & L. Lombard* (holotype CBS H-24947, culture ex-type CBS 148937 = CPC 40592).

Additional material examined: **Netherlands**, Limburg, Kessel, from field soil cultured with *Asparagus officinalis* field, 2019, *W. de Boer* (cultures CBS 148936 = CPC 39928, 39931, 39932); from field soil cultured with *Asparagus officinalis* '*Cygnus*' field, 13 Nov. 2020, *M. Sandoval-Denis & L. Lombard* (culture CPC 40579); from field soil cultured with *A. officinalis* '*Grolim*' field. 13 Nov. 2020, *M. Sandoval-Denis & L. Lombard* (culture CPC 40571); from field soil cultured with *A. officinalis* '*Schneekopf*' field, 13 Nov. 2020, *M. Sandoval-Denis & L. Lombard* (culture CPC 40628).

Notes: *Neocosmospora geoasparagicola* was isolated from soil from several *Asparagus officinalis* experimental fields (Bejo Zaden, Kessel, Limburg, Netherlands) where diverse *Asparagus* varieties have been cultivated. *Neocosmospora geoasparagicola* nested within Clade 2 of *Neocosmospora*, which contains mostly species from Asia and the Americas, including *N. phaseoli*, an important root pathogen of *Fabaceae* (O'Donnell 2000, Nalim *et al*. 2011, Sandoval-Denis *et al*. 2019). Subsequent pathogenicity testing, however, showed that *N. geoasparagicola* is not a pathogen of *A. officinalis* (data not shown).

Species in *Neocosmospora* Clade 2 are characterised by forming often large multiseptate macroconidia from aerial and sporodochial phialides, while generally lacking microconidia. While consistent with general morphological features of taxa in Clade 2, *N. geoasparagicola* clustered basally, and

Fig. 15. *Neocosmospora geoasparagicola* (CBS 148937 ex-type). **A–D.** Sporodochia formed on the surface of carnation leaves. **E–H.** Aerial conidiophores and conidiogenous cells. **I–K.** Sporodochial conidiophores and conidiogenous cells. **L.** Conidia. Scale bars: B–D = 20 µm; J = 5 µm; all others = 10 µm.

clearly separated phylogenetically and biogeographically from the remaining species in this group. Morphologically, *N. geoasparagicola* is most similar to *N. cryptoseptata* and *N. nirenbergiana*. *Neocosmospora geoasparagicola* can be differentiated from *N. cryptoseptata* by it slightly longer conidia and sporodochial phialides. There is considerable morphological overlap between *N. geoasparagicola* and *N. nirenbergiana*. However, sporodochial conidia of *N. geoasparagicola,* which are indistinguishable from aerial macroconidia, are shorter and tend to present longer apical cells than those of *N. nirenbergiana*. By contrast, aerial conidia of *N. nirenbergiana* are considerably different from its sporodochial counterparts, being shorter and somewhat pointy. Additionally, *N. geoasparagicola* lacks reddish pigments, a feature commonly observed in *N. nirenbergiana*.

Neocosmospora mekan (Lynn & I. Barnes) Crous & Sand.-Den., ***comb. nov.*** MycoBank MB 843506.
Basionym: *Fusarium mekan* Lynn & I. Barnes, *Mycologia* **113**: 547. 2021. MB 834438.

Holotypus: PREM 62600; *isotypi* PREM 62601 and PREM 62602.

Ex-type culture: CBS 146885 = CMW 54714 = PPRI 27971; ex-paratype cultures CBS 146886 = CMW 53696 = PPRI 27956 and CBS 146887 = CMW 54717 = PPRI 27972.

Type locality: **Indonesia**, Riau, Pelalawan.

Type substrate: From head (including mycangium) of *Euwallacea similis* in stems of *Acacia crassicarpa.*

Description and illustrations: Lynn *et al.* (2021).

Diagnostic features: *Colony* surface white, greyish flax blue to greyish violet in the dark, white to pale mouse grey darkening to purple slate and rust after 1 mo in ambient daylight, reverse yellowish white to fawn in the dark, bay darkening to chestnut and blood red after 1 mo in ambient daylight on PDA, having optimal growth at 30 °C; aerial monophialides giving rise to *microconidia* in false heads, ovoid to obovoid, rarely pyriform, 0–1(–2)-septate, aerial macroconidia long ovoid, apex blunt, basal cell obtuse, 0–3(–4)-septate; *sporodochia* luteous to ochreous, with monophialides give rise to straight or slightly curved, sub-fusoid, widest in apical third, wedge-shaped, 0–5(–6)-septate *macroconidia* with a blunt apical cell and obtuse to poorly-developed, foot-shaped basal cell; *chlamydospores* abundant, intercalary and terminal in hyphae and conidia, single, in pairs or chains, rarely in clusters (Lynn *et al.* 2021).

Notes: *Neocosmospora mekan* is associated with *Euwallacea perbrevis* and *E. similis* beetles in plantations of *Acacia crassicarpa* in Indonesia. It is distinguished by its multiseptate (evenly spaced), slightly curved, elongate, subfusoid to wedge-shaped macroconidia, and chlamydospores that tend to form at both the apex and base of mature macroconidia (Lynn *et al.* 2021).

Neocosmospora papillata (T. Aoki *et al.*) Crous & Sand.-Den., ***comb. nov.*** MycoBank MB 843507.
Basionym: *Fusarium papillatum* T. Aoki *et al.*, *Mycologia* **113**: 1097. 2021. MB 558019.

Holotypus: BPI 923531 (dried culture).

Ex-type culture: NRRL 62943 (= KOD 796) = MAFF 247228.

Type locality: **Sri Lanka**, Central Province, Kandy.

Type substrate: From the mycangium of a living female *Euwallacea perbrevis* beetle from a gallery in a branch of infested *Camellia sinensis* bush.

Description and illustrations: Aoki *et al*. (2021).

Diagnostic features: *Colony* surface white, yellow white to pale yellow, orange white initially, becoming partly pale orange to greyish orange in the dark, reverse pale yellow to light yellow, or greyish yellow on PDA, having optimal growth at 25 °C; aerial monophialides giving rise to *microconidia* in false heads, oblong-ellipsoid, fusoid-ellipsoid to clavate, straight or crescent- or comma-shaped, also sometimes forming swollen clavate to falcate, straight or curved conidia, 0–1(–3)-septate; *sporodochia* with monophialides give rise clavate to falcate, often gently curved, sometimes crescent-shaped (0–)3–7(–8)-septate *macroconidia*, often swollen in their upper parts with a papillate apical cell (protrude ventrally), with poorly to well-developed, foot-shaped basal cell; *chlamydospores* intercalary and terminal in hyphae and conidia, single or in chains (Aoki *et al*. 2021).

Notes: *Neocosmospora papillata* frequently forms multiseptate clavate conidia with papillate apical cells that protrude ventrally, especially under nuv-light, which distinguishes it from other species in the *Neocosmospora* Ambrosia Clade. Morphologically it resembles *N. drepaniformis*, but is distinct in that macroconidia often possess a papillum protruding ventrally from the apical cells, and their ultimate and penultimate apical cells are often swollen so that they are widest in the terminal half. Macroconidia of *N. drepaniformis*, however, are often widest at the second to fourth cells from the apex (Aoki *et al*. 2021).

Neocosmospora variasi (Lynn & I. Barnes) Crous & Sand.-Den., ***comb. nov.*** MycoBank MB 843508.
Basionym: *Fusarium variasi* Lynn & I. Barnes, *Mycologia* **113**: 549. 2021. MB 834439.

Holotypus: PREM 62595; *paratypi* PREM 62596 and PREM 62597.

Ex-type culture: CBS 146888 = CMW 53734 = PPRI 27958; ex-paratype cultures CBS 146889 = CMW 53735 = PPRI 27959 and CBS 146890 = CMW 54696 = PPRI 27968.

Type locality: **Indonesia**, Riau, Pelalawan.

Type substrate: From *Euwallacea perbrevis* in stems of *Acacia crassicarpa.*

Description and illustrations: Lynn *et al.* (2021).

Diagnostic features: *Colony* surface white or livid purple to fawn in the dark, with white to livid purple to bay segments, darkening to dark brick or violate slate or black after 1 mo in ambient daylight, reverse yellowish white to fawn in the dark, with white with rust to umber segments, occasionally entirely darkening to umber or black after 1 mo in ambient daylight on PDA, having optimal growth at 30 °C; aerial monophialides giving rise to *microconidia* in false heads, ovoid to obovoid, or short-clavate, curved,

0–1(–2)-septate; *sporodochia* luteous to ochreous or dull green to dark violet, with monophialides that give rise to falcate to clavate, 3–6(–7)-septate *macroconidia* with a papillate apical cell and poorly to well-developed, foot-shaped basal cell; *chlamydospores* abundant, intercalary and terminal in hyphae and conidia, single, in pairs, chains or often in clusters (Lynn *et al.* 2021).

Notes: *Neocosmospora variasi* is associated with the ambrosia beetle, *Euwallacea perbrevis*, in plantations of *Acacia crassicarpa* in Indonesia. It is characterised by having aerial micro- and macroconidia, which vary in size and shape. Furthermore, it produces abundant chlamydospores in clusters, which is unusual for species in the Ambrosia Clade of *Neocosmospora*. Lynn *et al.* (2021) were also of the opinion that as presently defined, *N. variasi* might represent two cryptic taxa.

Neocosmospora warna (Lynn & I. Barnes) Crous & Sand.-Den., ***comb. nov.*** MycoBank MB 843509.
Basionym: *Fusarium warna* Lynn & I. Barnes, *Mycologia* **113**: 551. 2021. MB 834440.

Holotypus: PREM 62603; *paratypi* PREM 62605 and PREM 62606.

Ex-type culture: CBS 146891 = CMW 54720 = PPRI 27974; ex-paratype cultures CBS 146892 = CMW 54724 = PPRI 27976 and CBS 146893 = CMW 54726 = PPRI 27977.

Type locality: **Indonesia**, Riau, Pelalawan.

Type substrate: From head (including mycangium) of *Euwallacea perbrevis* in stems of *Acacia crassicarpa.*

Description and illustrations: Lynn *et al.* (2021).

Diagnostic features: *Colony* surface white to livid purple to vinaceous purple, with white segments, to fawn at margins in the dark, lavender to violet or livid violet with white segments, darkening to livid vinaceous or dark vinaceous to dark purple with sepia margins after 1 mo in ambient daylight, reverse yellowish white to fawn in the dark, pale vinaceous grey white with rust to umber, darkening to dark brick after 1 mo in ambient daylight on PDA, having optimal growth at 25 °C; aerial monophialides giving rise to *microconidia* in false heads, obovoid to ovoid to short-clavate, rarely curved, 0–3(–4-) septate; sporodochia luteous to ochreous, or dull green to sepia, with monophialides giving rise to short-clavate, wedge-shaped (widest at apical septum), 1–4(–6)-septate *macroconidia* with a papillate apical cell and obtuse basal cell; *chlamydospores* sparse, intercalary and terminal in hyphae and conidia, single, in pairs, often clusters (Lynn *et al.* 2021).

Notes: *Neocosmospora warna* is associated with *Euwallacea perbrevis* beetles in plantations of *Acacia crassicarpa* in Indonesia. It is characterised by multi-septate, thick, short-clavate, wedge-shaped (widest at apical septum), papillate sporodochial conidia that taper toward the obtuse basal cell, and small chlamydospores (Lynn *et al.* 2021).

Genome announcements

Other than providing illustrations, diagnoses and multilocus phylogenies of fusarioid taxa, a further aim of the FUSA series is to also provide access to genome data of newly sequenced species, the first of which are published here.

The assemblies of *Fusarium secorum* (CBS 175.32), *Microcera coccophila* (CBS 310.34), *Rectifusarium robinianum* (CBS 430.91), *Rugonectria rugulosa* (CBS 126565), and *Thelonectria blattea* (CBS 952.68) are announced here. They were obtained from high coverage Illumina data (168–283×). Quality assessment done with BUSCO against 758 genes from the library for *Fungi* showed a high completeness (> 98 %) and a low duplication level (< 1 %) for the analysed genomes. The genome sizes varied from 34.7 Mbp to 50.5 Mbp. Assemblies of *R. rugulosa, M. coccophila, R. robinianum*, and *T. blattea* showed similar number of scaffolds while in the *F. secorum* genome their amount was significantly increased due to a high number (> 10 k) of scaffolds with sizes smaller than < 1 kbp. The total number of annotated gene models varied from 24 411 in *M. coccophila* to 46 001 in *F. secorum.* All assemblies were deposited in GenBank, detailed statistics and BioProject numbers are shown in Table 3.

Conflict of interest: The authors declare that there is no conflict of interest.

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