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CHECKLIST

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A first checklist of macrofungi for South Africa

Tonjock Rosemary Kinge[1,2], Gary Goldman[3], Adriaana Jacobs[4],
George Gatere Ndiritu[5], Marieka Gryzenhout[1]

1 *Department of Genetics, University of the Free State, Bloemfontein, PO Box 339, Bloemfontein 9300, Republic of South Africa* **2** *Department of Biological Sciences, Faculty of Science, University of Bamenda, P.O. Box 39, Bambili, North West Region, Cameroon* **3** *MushroomFundi, Cape Town, South Africa* **4** *National Collection of Fungi, Mycology Unit, Plant Health and Protection, Agricultural Research Council, Pretoria, South Africa* **5** *School of Natural Resources and Environmental Studies, Karatina University, P.O. Box 1957, Karatina 10101, Kenya*

Corresponding author: *Marieka Gryzenhout* (gryzenhoutm@ufs.ac.za)

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Abstract

Macrofungi are considered as organisms that form large fruiting bodies above or below the ground that are visible without the aid of a microscope. These fungi include most basidiomycetes and a small number of ascomycetes. Macrofungi have different ecological roles and uses, where some are edible, medicinal, poisonous, decomposers, saprotrophs, predators and pathogens, and they are often used for innovative biotechnological, medicinal and ecological applications. However, comprehensive checklists, and compilations on the diversity and distribution of mushrooms are lacking for South Africa, which makes regulation, conservation and inclusion in national biodiversity initiatives difficult. In this review, we compiled a checklist of macrofungi for the first time (excluding lichens). Data were compiled based on available literature in journals, books and fungorium records from the National Collection of Fungi. Even if the list is not complete due to numerous unreported species present in South Africa, it still represents an overview of the current knowledge of the macromycetes of South Africa. The list of names enables the assessment of gaps in collections and knowledge on the fungal biodiversity of South Africa, and downstream applications such as defining residency status of species. It provides a foundation for new names to be added in future towards developing a list that will be as complete as possible, and that can be used by a wide audience including scientists, authorities and the public.

Keywords

biodiversity, conservation, macrofungi, Myxomycetes, slimemolds, South Africa, species lists

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Introduction

Macrofungi are fungi that form large fructifications visible without the aid of the microscope and include representatives from the *Basidiomycota* and *Ascomycota* (Roda 2010; Servi et al. 2010). Common names used to refer to these fungi include mushrooms, toadstools, cup fungi, gilled fungi, jelly fungi, coral fungi, stink fungi, bracket fungi, polypores, puffballs, earth starts, truffles, and birds nest fungi (Egbe et al. 2013) and illustrates the visibility of these fungi to the public. Ecologically, macrofungi can be grouped as saprobes, parasites and symbiotic species (for instance mycorrhiza). Most terrestrial macrofungi are saprobes or mycorrhizal symbionts, but some are pathogens of plants or fungi, while those fruiting on woody substrates are usually either saprobes or plant pathogens (Mueller et al. 2007; Maria and Tzenka 2014).

Many macrofungi are edible and rich sources of carbohydrates, proteins, vitamins, and minerals for humans (Ananbeh 2003; Gençcelep et al. 2009). They can be naturally harvested or cultivated commercially. For rural communities they serve as a source of protein and income, especially for women. Macrofungi have great bio-exploitation potential in medicine or industry such as in the production of penicillin, lovastatin, and other globally significant medicines, and they remain an untapped resource with enormous industrial potential (Hyde et al. 2019). Mushrooms and other types of macrofungi can grow on decayed organic matters rich in lignin, cellulose, and other complicated carbohydrates, breaking them down for other uses or for bioremediation purposes (Kulshrestha et al. 2014). Modern pharmacological research confirms that large parts of traditional knowledge regarding the medicinal effects of macrofungi are due to proven antifungal, antibacterial, antioxidant, antiviral or other medicinal properties, besides being used as functional foods (Wani et al. 2010). For instance, some of the best known substances present in fungi showing pharmacological properties (especially anticancer and immunological) are polysaccharides (Wasser 2002; Mordali et al. 2007; Zhang et al. 2007; Hyde et al. 2019). Polysaccharides or polysaccharide-protein complexes present in fungi have gained the attention of researchers because it is believed that they can inhibit tumor growth and boost the immune system of the organism. They can enhance host defensive potential or represent biological response modifiers (Leung et al. 2006; Mordali et al. 2007). However, regulation of fungal bio-exploration and research in South Africa is hampered by the absence of biodiversity knowledge.

The fruiting bodies of slime molds or myxomycetes are occasionally observed together with those of macrofungi. The first species was described in 1654 by naturalist Thomas Panckow, who thought it was a species of fungi because of its resemblance to puffballs (Martin and Alexopoulos 1969). Slime molds have two major stages in their lifecycles: a mobile trophic (feeding) and a static fruiting body (reproductive) stage. Modern classifications place them in the Mycetozoan group of Amoebozoa (Baudalf 2008; Fiore-Donno et al. 2010). As bacterivores, slime molds are major components of decomposition and nutrient cycles where they enhance release of nutrients tied up in the microbial biomass (Stephenson and Feest 2015). It is estimated that myxomycete amoebas alone represent more than 50% of the total amoebae for some agricultural soils (Feest and Campbell 1986). Recent studies suggest that more attention should be placed on the use of slime molds as indicators of soil quality.

A small percentage of the 2.2 to 3.8 million species of fungi estimated in the world are currently described and these are mostly in temperate regions (Hawksworth and Lücking 2017). The tropical regions with the highest fungal diversity have not been fully explored (Hawksworth 2001). The reasons for this disparity, even in First World countries, are taxonomic obstacles that are worsened by a paucity of trained mycologists and especially systematists. The low number of published, rigorous, long-term studies on fungal biodiversity also prevents conclusive answers (Mueller et al. 2007). Not even basic questions, such as those related to the number of macrofungal or slime mold species at a specific location, or whether such diversity is greater in one type of forest than in another, can often be answered.

Despite the importance of macrofungi, information on their diversity is scanty, especially in Africa (Osarenkhoe et al. 2014). Thus, due to the lack of human capacities, national monographs of biodiversity in many African countries rarely encompass fungi. This leads to an unfortunate bias in the complete assessment of biodiversity, the unawareness by the public and decision makers of fungi as important components of ecosystem functioning, and frustration from end users at the lack of information (Gryzenhout et al. 2012). Regulation of fungal natural resources and quarantine is thus severely impeded by the lack of lists and information readily available. Not surprisingly, the fungal biodiversity in southern Africa has been relatively poorly studied to date, and no host has been thoroughly treated (Crous et al. 2006; Gryzenhout et al. 2010, 2012). A working checklist will be greatly beneficial to illustrate strengths and gaps in our fungal biodiversity knowledge in South Africa, and will be useful for regulatory authorities.

To address the lack of basic information for macrofungi in South Africa, the aim of this review was to compile a macrofungal and slime mold names list based on current knowledge and resources. We defined macrofungi as having spore-bearing structures visible to the naked eye (mushrooms, brackets, puffballs, false-truffles, cup fungi, etc.). Since slime molds are also readily observed by the public and perceived as fungi (although they do not reside in the kingdom of Fungi), known slime molds from South Africa were also included. Lichens (structures formed by fungi living in close association with algae and cyanobacteria) were excluded from this review because they represent another ill-studied group without solid supportive capacity, but lichen species should be added in future.

Materials and methods

The species list was compiled from journal and book publications, and national fungorium records. It is not based on field observations. It is hosted on the website www.themycologyblog.com, which is live and can continuously be refined, expanded and updated. The species list is incorporated by the online resource Cybertruffle's Robigalia (http://www.cybertruffle.org.uk/) and the database of the National Collection of Fungi of South Africa (http://www.arc.agric.za/arc-ppri/Pages/Biosystematics/Mycology%20Unit%20(Fungi)/Mycology-National-Collection-of-Fungi.aspx).

Results

The macrofungal checklist compiled in this review (Table 1) presents the first national list for macrofungi and slime molds in South Africa. It includes macrofungal and slime mold species names from previous field guides, other publications, as well as names obtained from the National Collection of Fungi's PREM fungorium (based on 3597 records), hosted by the Plant Health and Protection (http://www.arc.agric.za/arc-ppri/Pages/ARC-PPRI-Homepage), Agricultural Research Council, South Africa (Table 1). Myxomycete records include 107 species. In total, the South African checklist presented here includes 1160 species, 307 genera and 95 families.

The Basidiomycota consisted of 1008 species, 251 genera and 72 families. At the class level, the Agaricomycetes had the highest number (Fig. 1) of species (992), genera (242), and families (68) hosting 86% of the total number of species of macrofungi. The largest order was represented by the Agaricales (504 species) followed by the Polyporales (251 species), Boletales (50 species), Russulales (49 species) and Geastrales (33 species). The smallest orders were the Gloeophyllales and Gomphales with only two species. The largest family was the Agaricaceae (180 species) followed by the Polyporaceae (172 species). Orders with only two species were the Gloeophyllale and Gomphales, while the Thelephorales had four, and the Tremmelales 6 species.

The Ascomycota was represented by 44 species distributed among 20 genera and 10 families. The Pezizomycetes had 34 species, Sordariomycetes 9 species and the Leotiomycetes one species (Table 1). However, the total number of species in these groups are biased in this study to include only those that can be considered as a macrofungus. One member of the Mucorales (*Pilobolus crystallinus*, Mucoromycota) was also included (Table 1).

More than hundred slime molds have been recorded from South Africa based on the list (Table 1, Fig. 1), with the Physarales (Myxomycota) having the most species (57 species). The 107 names of slime molds contributed originated from published and unpublished sources (Duthie 1917a, b; Doidge 1950; Ndiritu et. al. 2009; Ndiritu and De Haan 2017; Winset KE unpubl. data). Only accepted taxonomic names following the nomenclatural criteria proposed by Lado (2005–2018), which is recognized by the Encyclopedia of Life under Species 2000 and ITIS Catalogue of Life (http://eol.org/), were used. All of the five orders of myxomycetes are present in South Africa, and include the Echinosteliales (represented by one family and one genus), Liceales (four families and six genera), Physarales (two families and three genera), Stemonitales (one family and seven genera) and Trichiales (two families and seven genera). The Protosteliales (Protostelids), a sixth order though not generally regarded

Table 1. Checklist of macrofungi and myxomycetes from South Africa.

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fungarium	Field guides	Previous publications (if not in field guides)
Fungi	Ascomycota	Leotiomycetes	Helotiales	Chlorociboriaceae	*Chlorociboria*	*aeruginosa*	(Nyl.) Kanouse ex C.S. Ramamurthi, Korf & L.R. Batra		Yes	
		Pezizomycetes	Pezizales	Helvellaceae	*Paxina*	*leucomelas*	(Pers.) Kuntze		Yes	
					Helvella	*crispa*	(Scop.) Fr.		Yes	
						lacunosa	Afzel.		Yes	
				Morchellaceae	*Morchella*	*conica*	Krombh.	PREM	Yes	
						elata	Fr.		Yes	
						hybrida	Pers.	PREM		
				Pezizaceae	*Kalaharituber*	*pfeilii*	(Henn.) Trappe & Kagan-Zur		Yes	
					Peziza	*ammophila*	Saut.		Yes	
						dehnii	Rabenh.	PREM		
						hortensis	P. Crouan & H. Crouan	PREM		
						macropus	Schumach.	PREM		
						nilgherrensis	Cooke	PREM		
						ostracoderma	Korf	PREM		
						repanda	Pers.	PREM		
						silvestris	(Boud.) Sacc. & Traverso	PREM		
						spissa	Berk.	PREM		
						subrepanda	Cooke & W. Phillips	PREM		
						vesiculosa	Bull.	PREM		
					Pseudohelotium	*pineti*	(Batsch) Fuckel	PREM		
					Terfezia	*austroafricana*	Marasas & Trappe			Marasas and Trappe 1973
						bourdieri	Chatin		Yes	
						claveryi	Chatin		Yes	
				Pyrenomataceae	*Anthracobia*	*melaloma*	(Alb. & Schwein.) Arnould		Yes	
					Isaria	*psychidae*	Pole-Evans	PREM		
						sinclairii	(Berk.) Lloyd		Yes	
					Scutellinia	*badio-berbis*	(Berk. ex Cooke) Kuntze.	PREM		
						margaritacea	(Berk. ex Cooke) Kuntze.	PREM		
						phlyctispora	(Lepr. and Mont.)	PREM		
						scutellata	(L.) Lamb.	PREM	Yes	
				Rhizinaceae	*Rhizina*	*undulata*	Fr.		Yes	
				Sarcoscyphaceae	*Phillipsia*	*kermesina*	Kalchbr. & Cooke			Kalchbrenner and Cooke 1880
				Tuberaceae	*Tuber*	*aestivum*	(Wulfen) Spreng	PREM		
						melanosporum	Vittad.		Yes	
					Choiromyces	*echinulatus*	Trappe & Marasas			Trappe and Marasas 1973
		Sordariomycetes	Hypocreales	Cordycipitaceae	*Cordyceps*	*velutipes*	Massee			Massee 1895

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Ascomycota	Sordariomycetes	Xylariales	Xylariaceae	*Daldinia*	*concentrica*	(Bolton) Ces. & De Not.		Yes	
					Poronia	*oedipus*	(Mont.) Mont.		Yes	
					Xylaria	*longipes*	Nitschke		Yes	
						hypoxylon	L. (Grev.)		Yes	
						polymorpha	(Pers.) Grev.		Yes	
						schreuderiana	Van der Byl			Van der Byl 1932
						stilboidea	Kalchbr. & Cooke			Kalchbrenner and Cooke 1880
					Penzigia	*verrucosa*	Mill			Miller 1942
	Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	*Agaricus*	*actiniceps*	Kalchbr. & Cooke			Kalchbrenner and Cooke 1881
						abruptibulbus	Peck	PREM		Van der Westhuizen and Eicker 1988
						alboargillascens	(A. Pearson) Bon			
						alveolatus	Kalchbr.			Kalchbrenner 1881
						arvensis	Schaeff.	PREM	Yes	
						augustus	Fr.	PREM	Yes	
						aures	(Massee) F.M. Bailey	PREM		
						bisporus	(J.E. Lange) Imbach	PREM	Yes	
						bitorquis	(Quél.) Sacc.	PREM	Yes	
						caliginosus	Jungh.	PREM		
						campestris	L.	PREM	Yes	
						chortophilus	Berk.			Berkeley 1843
						comtulus	Ces. ex Mussat	PREM	Yes	
						crocopeplus	Berk. & Broome		Yes	
						diminutivus	Peck		Yes	
						episphaeria	Berk.			Berkeley 1846
						griseovinaceus	A. Pearson ex Pegler			Pearson 1996
						inandae	Cooke			Cooke 1890
						montagnei	Kalchbr.	PREM	Yes	
						nobilis	(A. Pearson) Heinem.	PREM	Yes	
						papilionaceus	Bull.	PREM		
						paurophyllus	Berk.			Berkeley 1876
						peroxydatus	Berk.			Berkeley 1843
						placomyces	Peck	PREM	Yes	
						pleropus	Kalchbr. & MacOwan	PREM		
						pogonatus	Kalchbr.			Kalchbrenner 1881
						purpurellus	(F.H. Møller) F.H. Møller	PREM		Van der Westhuizen and Eicker 1988
						sagittiformis	Kalchbr. & Cooke			Kalchbrenner and Cooke 1881
						semotus	Fr.	PREM	Yes	
						separatus	L.	PREM		
						silvaticus	Schaeff.	PREM	Yes	

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fungarium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	*Agaricus*	*silvicola*	(Vittad.) Peck		Yes	
						sulphurellus	Kalchbr. & Cooke	PREM		
						trisulphuratus	Berk.	PREM	Yes	
						umbellifer var. *cinnabarinus*	Berk.			Berkeley 1843
						xanthodermus	Genev.	PREM	Yes	
						xanthodermus var. *griseus*	(A. Pearson) Bon & Cappelli	PREM		
						xanthodermus var. *lepiotoides*	Maire		Yes	
						xanthodermus var. *meleagrioides*	(A. Pearson) Bon & Cappelli		Yes	
					Arachnion	*alborosella*	Verwoerd	PREM		
						album	Schwein.	PREM		
						firmoderma	Verwoerd	PREM		
						scleroderma	C.G. Loyd	PREM		
					Battarrea	*levispora*	Massee	PREM		
						lycoperdon	(Dicks.) Pers.	PREM		
						phalloides	(Dicks.) Pers.	PREM	Yes	As Battarrea stevenii
						tepperiana	F. Ludw.	PREM		
					Battarreoides	*diguetii*	(Pat. & Har.) R. Heim & T. Herrera	PREM		
					Bovista	*acocksii*	De Villiers, Eicker & Van der Westh.			De Villiers et al. 1989
						capensis	(Fr.) J.C. Coetzee & A.E. van Wyk			Coetzee & Van Wyk 2005
						juglandiformis	Berk. ex Massee			Massee 1888
						lilacina	Mont. & Berk.	PREM		
						promontorii	Kreisel			Kreisel 1967
						umbrina	Bottomley			Bottomley 1948
					Calvatia	*caelata*	(Bull.) Morgan	PREM		
						candida	(Rostk.) Hollós	PREM		
						capensis	(Lloyd) J.C. Coetzee, Eicker & A.E. van Wyk	PREM		
						cyathiformis	(Bosc) Morgan	PREM		
						flava	(Massee) Kreisel	PREM		
						gigantea	(Batsch) Lloyd	PREM		
						incerta	Bottomley			Bottomley 1948
						lepidophora	(Ellis & Everh.) Coker & Couch	PREM		
						lilacina	(Mont. & Berk.) Henn.	PREM	Yes	
						rubroflava	(Cragin) Lloyd	PREM		
					Chlamydopus	*meyenianus*	(Klotzsch) Lloyd	PREM		
					Chlorophyllum	*molybdites*	(G. Mey.) Massee	PREM	Yes	

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	*Chlorophyllum*	*africanum*	Z.W. Ge & A. Jacobs	PREM		Ge et al. 2018
						palaeotropicum	Z.W. Ge & A. Jacobs	PREM		Ge et al. 2018
					Coniolepiota	*spongodes*	(Berk. & Broome) Vellinga		Yes	
					Coprinellus	*curtus*	(Kalchbr.) Vilgalys, Hopple & Jacq. Johnson	PREM		
						disseminatus	(Pers.) J.E. Lange		Yes	
						domesticus	(Bolton) Vilgalys, Hopple & Jacq. Johnson		Yes	
						ephemerus	(Bull.) Redhead, Vilgalys & Moncalvo	PREM		
						heptemerus	(M. Lange & A.H. Sm.) Vilgalys, Hopple & Jacq. Johnson		Yes	
						micaceus	(Bull.) Vilgalys, Hopple & Jacq. Johnson	PREM	Yes	
						truncorum	(Scop.) Redhead, Vilgalys & Moncalvo	PREM		
					Coprinopsis	*atramentaria*	(Bull.) Redhead, Vilgalys & Moncalvo	PREM	Yes	
						cinerea	(Schaeff.) Redhead, Vilgalys & Moncalvo	PREM		
						lagopus	(Fr.) Redhead, Vilgalys & Moncalvo		Yes	
						nivea	(Pers.) Redhead, Vilgalys & Moncalvo	PREM	Yes	
						picacea	(Bull.) Redhead, Vilgalys & Moncalvo	PREM		Wood 2017
						stercorea	(Fr.) Redhead, Vilgalys & Moncalvo	PREM		
					Coprinus	*agricola*	A. Pearson			Pearson 1950
						comatus	(O.F. Müll.) Pers.	PREM	Yes	
						digitalis	(Batsch) Fr.	PREM		
						papillatus	(Batsch) Fr.	PREM		
						punctatus	Kalchbr.	PREM		
					Crucibulum	*vulgare*	Tul. & C. Tul.	PREM		
					Disciseda	*candida*	(Schwein.) Lloyd	PREM		
						castanea	(Lév.) Bottomley	PREM		
						cervina	(Berk.) G.H. Cunningham	PREM		
						hypogaea	(Cooke & Massee) G. Cunn.	PREM		
						verrucosa	G. Cunn.	PREM		
					Gyrophragmium	*delilei*	Mont	PREM		
					Langermannia	*wahlbergii*	(Fr.) Dring	PREM		
					Lepiota	*acutesquamosa*	(Weinm.) P. Kumm.	PREM		Van der Westhuizen and Eicker 1988
						canescens	A. Pearson	PREM		
						citrinella	Beeli	PREM		
					Lepiota	*cristata*	(Bolton) P. Kumm.	PREM	Yes	
						cristatocystidiata	A. Pearson	PREM		

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	*Lepiota*	*cutifracta*	A. Pearson	PREM		
						flava	Beeli	PREM		Van der Westhuizen and Eicker 1988
						fustiformis	A. Pearson	PREM		
						goossensiae	Beeli	PREM		Van der Westhuizen and Eicker 1988
						helveola	Bres.		Yes	
						hispida	Gillet	PREM		Van der Westhuizen and Eicker 1988
						ianthina	Sacc.	PREM		Van der Westhuizen and Eicker 1988
						lutea	Matt.	PREM		
						morganii	(Peck) Sacc.	PREM		
						naucina var. *leucothites*	(Vittad.) Sacc.	PREM		
						nympharum	(Kalchbr.) Kalchbr.	PREM		Van der Westhuizen and Eicker 1988
						praeclara	A. Pearson			Pearson 1950
						parvannulata	(Lasch) Gillet	PREM		Van der Westhuizen and Eicker 1988
						rhizobola	(Berk.) Sacc.	PREM		
						roseolescens	A. Pearson	PREM		
						roseosquamosa	Beeli	PREM		Van der Westhuizen and Eicker 1988
						truncata	A. Pearson	PREM		
						umbrinozonata	A. Pearson	PREM		
						varians	(Kalchbr. & MacOwan) Sacc.	PREM		
						virescens	Pat.	PREM		
					Leucoagaricus	*bisporus*	Heinem.	PREM	Yes	
						leucothites	(Vittad.) Wasser		Yes	
						naucina	(Vittad.) Wasser	PREM		Van der Westhuizen and Eicker 1988
						rubrotinctus	(Peck) Singer		Yes	
						birnbaumii	(Corda) Singer	PREM	Yes	
						brebissonii	(Godey) Locq.		Yes	
						cepistipes	(Sowerby) Pat.	PREM		
						fragilissimus	(Ravenel ex Berk. & M.A. Curtis) Pat.		Yes	
						zeyheri	(Berk.) Singer	PREM		
					Lycoperdon	*asperum*	(Lév.) Speg.	PREM		
						caespitosum	Welw. & Curr.	PREM		
						caffrorum	Kalchbr. & Cooke	PREM		
						djurense	Henn.	PREM		
						duthiei	Bottomley	PREM		
						flavum	Massee	PREM		
						gunnii	Berk.	PREM		
						hiemale	Vent.	PREM		
						perlatum	Pers.	PREM	Yes	

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fungarium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	*Lycoperdon*	*polymorphum*	Vittad.	PREM		
						pratense	Pers.		Yes	As Vascellum pratense
						pusillum	Batsch	PREM		
						qudenii	Bottomley	PREM		
						radicatum	Durieu & Mont.	PREM		
						subincarnatum	Peck	PREM		
						umbrinum	Hornem.	PREM		
					Macrolepiota	*excoriatus*	(Schaeff.) Wasser	PREM		Van der Westhuizen and Eicker 1988
						procera	(Scop.) Singer	PREM	Yes	
						prominens	(Sacc.) M.M. Moser		Yes	
						rhacodes	(Vittad.) Singer		Yes	
						zeyheri	(Berk. & Singer) Heinem.	PREM	Yes	
					Montagnea	*aurenaria*	(DC.) Zeller			Reid and Eicker 1991
						haussknechtii	Rabenh.			Reid and Eicker 1991
					Montagnites	*candollei*	Speg.	PREM		
					Mycenastrum	*corium*	(Guers.) Desv.	PREM		
					Parasola	*hemerobia*	(Fr.) Redhead, Vilgalys & Hopple	PREM		
						plicatilis	(Curtis) Redhead, Vilgalys & Hopple	PREM	Yes	
					Polyplocium	*inquinans*	Berk.	PREM		
					Psalliota	*campestris*	(L.) Quél.	PREM		
						alboargillascens	A. Pearson	PREM		
						arvensis	Schaeff.	PREM		
						arvensis var. *hortensis*	W.G. Sm.	PREM		
						comtula	(Fr.) Quél.	PREM		
						duriuscula	Velen.	PREM		
						mixta	A. Pearson	PREM		
						nobilis	A. Pearson			Pearson 1950
						placomyces	Peck	PREM		
						pratensis	(Schaeff.) Gillet	PREM		
						rodmanni	(Peck) Kauffman	PREM		
						volvata	A. Pearson			Pearson 1950
						xanthoderma var. *meleagrioides*	A. Pearson	PREM		
					Secotium	*gueinzii*	Kunze			Kunze 1840
						obtusum	C.G. Loyd	PREM		
					Tulostoma	*albicans*	V.S. White		Yes	
						bonianum	Pat.		Yes	
						cyclophorum	Lloyd		Yes	
						exasperatosporum	J.E. Wright	PREM		

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fungarium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	*Tulostoma*	*gracilipes*	J.E. Wright	PREM		
						lesliei	Van der Byl	PREM		
						purpusii	Henn.		Yes	
						transvaalii	C.G. Loyd	PREM		
					Xanthagaricus	*luteolosporus*	(Heinem. & Little Flower) Little Flower, Hosag. & T.K. Abraham	PREM	Yes	
				Amanitaceae	*Amanita*	*aureofloccosa*	Bas		Yes	
						capensis	Walleyn & Rammeloo		Yes	
						excelsa	(Fr.) Bertill.	PREM	Yes	
						foetidissima	D.A. Reid & Eicker	PREM	Yes	
						mappa	(Batsch) Bertill.		Yes	
						muscaria	(L.) Lam.	PREM	Yes	
						pantherina	(DC.) Krombh.	PREM	Yes	
						phalloides	(Vaill. ex Fr.) Link	PREM	Yes	
						phalloides var. *alba*	Costantin & L.M. Dufour		Yes	
						phalloides var. *umbrina*	(Ferry) Maire		Yes	
						reidii	Eicker & Greuning		Yes	
						pleropus	(Kalchbr. & MacOwan) D.A. Reid	PREM	Yes	
						rubescens	Pers.	PREM	Yes	
						solitaria	(Bull.) Fr.	PREM		
						strobiliformis	(Paulet ex Vittad.) Bertill.	PREM	Yes	
						vaginata	(Bull.) Lam.	PREM		
						veldiei	D.A. Reid & Eicker		Yes	
					Limacella	*guttata*	(Pers.) Konrad & Maubl.		Yes	
					Saproamanita	*praeclara*	(A. Pearson) Redhead, Vizzini, Drehmel & Contu	PREM	Yes	
				Bolbitiaceae	*Bolbitius*	*titubans*	(Bull.) Fr.	PREM	Yes	
						vitellinus	(Pers.) Fr.	PREM	Yes	
						liberatus	(Berk.) R. Heim	PREM		
					Conocybe	*apala*	(Fr.) Arnolds		Yes	
						tenera	(Schaeff.) Fayod	PREM	Yes	
					Galeropsis	*mitriformis*	(Berk.) R. Heim	PREM		
					Pluteolus	*reticulatus*	(Pers.) Gillet	PREM		Van der Westhuizen and Eicker 1988
				Broomeiaceae	*Broomeia*	*congregata*	Berk.	PREM	Yes	
						ellipsospora	Höhn.	PREM	Yes	
				Clavariaceae	*Clavaria*	*abietina*	Schumach.	PREM		
						capensis	Thunb.			Thunberg 1800
						cinerea	Bull.	PREM		

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Fungi	Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	*Clavaria*	*cladoniae*	Kalchbr.	PREM		
						contorta	Holmsk.	PREM		
						corniculata	Schaeff.	PREM		
						cristata	(Holmsk.) Pers.	PREM		
						flaccida	Fr.	PREM		
						helicoides	Pat. & Demange	PREM		
						kunzei	Fr.	PREM		
						laeticolor	Berk. & M.A. Curtis	PREM		
						ligula	Schaeff.	PREM		
						persimilis	Cotton	PREM		
						pulchra	Peck	PREM		
						stricta	Schumach.	PREM		
					Clavulinopsis	*luteoalba*	(Rea) Corner		Yes	
						ochracea	Corner	PREM		
					Mucronella	*aggregata*	(Fr.) Fr.	PREM		
				Cortinariaceae	*Cortinarius*	*argutus*	Fr.	PREM		
						brunneolimosus	A. Pearson	PREM		
						camurus	Fr.	PREM		Van der Westhuizen and Eicker 1988
						castaneus	(Bull.) Fr.	PREM		
						fuscotinctus	Rea	PREM		Van der Westbuizen and Eicker 1988
						lepidopus	Cooke	PREM		Van der Westbuizen and Eicker 1988
						multiformis	(Fr.) Fr.	PREM		
						radiofibrillosus	A. Pearson	PREM		
					Locellina	*acetabulosa*	(Sowerby) Sacc.	PREM		
				Cyphellaceae	*Chondrostereum*	*purpureum*	(Pers.) Pouzar	PREM	Yes	
					Cyphella	*tabacina*	Cooke & W. Phillips	PREM		
						applanata	P.H.B. Talbot	PREM		
						farinacea	Kalchbr. & Cooke	PREM		
				Entolomataceae	*Claudopus*	*variabilis*	(Pers.) Fr.	PREM		
					Clitopilus	*prunulus*	(Scop.) P. Kumm.	PREM	Yes	
					Entoloma	*lividum*	(Bull.) Quél.	PREM		
						olivipes	A. Pearson ex Pegler			Pearson 1996
						sagittiforme	(Kalchbr. & Cooke) Sacc.	PREM		
				Fistulinaceae	*Fistulina*	*africana*	Van der Byl	PREM	Yes	
				Hydnangiaceae	*Laccaria*	*amethystea*	(Bull.) Murrill	PREM	Yes	
						laccata	(Scop.) Cooke	PREM	Yes	
						tortilis	(Bolton) Cooke		Yes	
				Hygrophoraceae	*Hygrocybe*	*aurantiorufa*	A. Pearson ex Pegler			Pearson 1996
						chlorophana	(Fr.) Wünsche		Yes	

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Fungi	Basidiomycota	Agaricomycetes	Agaricales	Hygrophoraceae	*Hygrocybe*	*conica*	Velen.	PREM	Yes	
						nigrescens	(Quél.) Kühner	PREM	Yes	
						zuluensis	Boertm.			Boertman 1998
					Hygrophorus	*coccineus*	(Schaeff.) Fr.	PREM		
						conicus	(Schaeff.) Fr.	PREM		
						conicus var. *nigrescens*	(Quél.) Konrad & Maubl.	PREM		
							(Quél.) Konrad & Maubl.	PREM		
						discolor	(Feltgen) Sacc. & Trotter	PREM		
				Incertae sedis	*Anellaria*	*separata*	(L.) P. Karst.	PREM		
					Panaeolina	*foenisecii*	(Pers.) Maire	PREM	Yes	
					Panaeolus	*caliginosus*	(Jungh.) Gillet	PREM		
						campanulatus	(L.) Quél.	PREM		Van der Westhuizen and Eicker 1988
						fimicola	(Pers.) Gillet	PREM		
						fimicoloides	A. Pearson	PREM		
						papilionaceus	(Bull.) Quél.	PREM	Yes	
						retirugus	(Fr.) Gillet	PREM		
						semiovatus	(Sowerby) S. Lundell & Nannf.		Yes	
						semiovatus f. *exannulatus*	A. Pearson			Pearson 1950
						solidipes	(Peck) Sacc.	PREM		
						sphinctrinus	(Fr.) Quél.	PREM		
						subbalteatus	(Berk. & Broome) Sacc.		Yes	
				Inocybaceae	*Astrosporina*	*maritima*	(P. Karst.) Rea	PREM		Van der Westhuizen and Eicker 1988
					Crepidotus	*austroafricanus*	Pilát			Pilát 1950
						haustellaris	(Fr.) P. Kumm.	PREM		
						inandae	Cooke	PREM		
						mollis	(Schaeff.) Staude	PREM	Yes	
						pogonatus	Kalchbr.	PREM		
						variabillis	(Pers.) P. Kumm.	PREM	Yes	
					Inocybe	*cinnamomea*	A. Pearson ex Pegler			Pearson 1996
						congregata	A. Pearson			Pearson 1950
						curvipes	P. Karst.			Vellinga et al. 2009
				Inocybaceae	*Inocybe*	*eutheles*	Sacc.	PREM	Yes	
						hirtella	Bres.		Yes	
						lanuginella	(J. Schröt.) Konrad & Maubl		Yes	
						microspora	J.E. Lange	PREM		Van der Westhuizen and Eicker 1988
						mixtilis	(Britzelm.) Sacc.	PREM		Van der Westhuizen and Eicker 1988
						*	Gillet		Yes	
						patouillardii	Bres.		Yes	

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Fungi	Basidiomycota	Agaricomycetes	Agaricales	Inocybaceae	*Inocybe*	*pullata*	A. Pearson ex Pegler			Pearson and Pegler 1996
					Phaeoglabrotricha	*farinacea*	(Kalchbr. & Cooke) W.B. Cooke	PREM		
					Phaeosolenia	*densa*	(Berk.) W.B. Cooke	PREM		
				Lyophyllaceae	*Lyophyllum*	*decastes*	(Fr.) Singer		Yes	
					Podabrella	*microcarpa*	(Berk. & Broome) Singer	PREM		
					Termitomyces	*clypeatus*	R. Heim		Yes	
						microcarpus	(Berk. & Broome) R. Heim		Yes	
						reticulatus	Van der Westh. & Eicker		Yes	
						sagittiformis	(Kalchbr. & Cooke) D.A. Reid		Yes	
						schimperi	(Pat.) R. Heim		Yes	
						umkowaan	(Cooke & Massee) D.A. Reid		Yes	
				Marasmiaceae	*Calyptella*	*capensis*	W.B. Cooke & P.H.B. Talbot	PREM		
						capensis	(Berk.) D.A. Reid		Yes	
					Marasmius	*bekolacongoli*	Beeli		Yes	
						calopus	(Pers.) Fr.	PREM		
						candidus	(Bolton) Fr.	PREM		
						delectans	Morgan	PREM		Van der Westhuizen and Eicker 1988
						epiphyllus	(Pers.) Fr.	PREM		Van der Westhuizen and Eicker 1988
						filaris	Kalchbr. & MacOwan	PREM		
						haematocephalus	(Mont.) Fr.		Yes	
						helvolus	Berk.	PREM		
						oreades	(Bolton) Fr.		Yes	
						oreadoides	Pass.	PREM		
						petalinus	Berk. & M.A. Curtis	PREM		
						rotula	(Scop.) Fr.	PREM		Van der Westhuizen and Eicker 1988
						scorodonius	(Fr.) Fr.	PREM		Van der Westhuizen and Eicker 1988
						siccus	(Schwein.) Fr.	PREM		Van der Westhuizen and Eicker 1988
						tener	Berk. & M.A. Curtis	PREM		
						thwaitesii	Berk. & Broome	PREM		
						titanosporus	D.A. Reid & Jacot Guill.			Reid and Guillarmod 1988
				Marasmiaceae	*Marasmius*	*zenkeri*	Henn.	PREM		
					Solenia	*minima*	Cooke & W. Phillips	PREM		
						natalensis	W.B. Cooke	PREM		
						rhoina	W.B. Cooke	PREM		
				Mycenaceae	*Cruentomycena*	*viscidocruenta*	(Cleland) R.H. Petersen & Kovalenko		Yes	
					Favolaschia	*thwaitesii*	(Berk. & Broome) Kuntze	PREM	Yes	
					Mycena	*acicula*	(Schaeff.) P. Kumm.	PREM		Van der Westhuizen and Eicker 1988
						aetites	(Fr.) Quél.		Yes	

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Fungi	Basidiomycota	Agaricomycetes	Agaricales	Mycenaceae	*Mycena*	*alcalina*	(Fr.) P. Kumm.	PREM		
						alcalinoides	A. Pearson	PREM		
						clavicularis	(Fr.) Gillet	PREM		
						corticola	(Schumach.) Quél.	PREM		Van der Westhuizen and Eicker 1988
						hiemalis	(Osbeck) Quél.	PREM		
						hyalina	A. Pearson	PREM		
						pura	(Pers.) P. Kumm.		Yes	
						rhodiophylla	(Kalchbr.) Sacc.	PREM		
						rubromarginata	(Fr.) P. Kumm.	PREM		
						sciola	(Kalchbr.) Sacc.	PREM		
						vibecina	A. Pearson	PREM	Yes	
				Niaceae	*Flagelloscypha*	*applanata*	(P.H.B. Talbot) W.B. Cooke	PREM		
					Lachnella	*alboviolascens*	(Alb. & Schwein.) Fr.	PREM		
				Nidulariaceae	*Cyathus*	*berkeleyanus*	(Tul. & C. Tul.) Lloyd	PREM		
						dasypus	Nees	PREM		
						hookeri	Berk.	PREM		
						microsporus	Tul. & C. Tul.	PREM		
						minutosporus	Lloyd	PREM		
						montagnei	Tul. & C. Tul.	PREM		
						olla	(Batsch) Pers.	PREM	Yes	
						pallidus	Berk. & M.A. Curtis	PREM		
						poeppigii	Tul. & C. Tul.	PREM		
						stercoreus	(Schwein.) De Toni	PREM		
						striatus	(Huds.) Willd.		Yes	
						vernicosus	(Bull.) DC.	PREM		
				Omphalotaceae	*Anthracophyllum*	*nigritum*	(Lév.) Kalchbr.	PREM		
						archeri	(Berk.) Pegler		Yes	
					Gymnopus	*androsaceus*	(L.) Della Magg. & Trassin.	PREM	Yes	
					Marasmiellus	*candidus*	(Fr.) Singer		Yes	
					Omphalotus	*olearius*	(DC.) Singer		Yes	
				Phelloriniaceae	*Phellorinia*	*inquinans*	Berk.	PREM		
						squamosa	Kalchbr. & MacOwan	PREM		
						strobilina	(Kalchbr.) Kalchbr.	PREM		
				Physalacriaceae	*Armillaria*	*fuscipes*	Petch.		Yes	Coetzee et al. 2000
						gallica	Marxm.			Coetzee et al. 2003
						mellea	(Vahl) P. Kumm.	PREM	Yes	Coetzee et al. 2000
						ramentacea	(Bull.) Gillet	PREM		
					Armillariella	*polymyces*	(Pers.) Singer & Clémençon		Yes	
					Cyptotrama	*asprata*	(Berk.) Redhead & Ginns	PREM	Yes	

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Fungi	Basidiomycota	Agaricomycetes	Agaricales	Physalacriaceae	*Oudemansiella*	*canarii*	(Jungh.) Höhn.	PREM		
					Hymenopellis	*radicata*	(Relhan) Singer	PREM		Van der Westhuizen and Eicker 1988
					Physalacria	*decaryi*	Pat.	PREM		
					Xerula	*atrocaerulea*	R.H. Petersen & Bougher			Petersen and Bougher 2008
				Pleurotaceae	*Pleurotus*	*applicatus*	(Batsch) P. Kumm.	PREM		
						geesterani	Singer			Singer 1962
						gilvescens	(Kalchbr.) Sacc.	PREM		
						lenticula	(Kalchbr.) Sacc.	PREM		
						limpidus	(Fr.) Sacc.	PREM		
						ostreatus	(Jacq.) P. Kumm.	PREM	Yes	
						perpusillus	(Lumn.) Gillet	PREM		
						pulmonarius	(Fr.) Quél.		Yes	
						sajor-caju	(Fr.) Singer	PREM		
						sciadium	(Kalchbr. & MacOwan) Sacc.	PREM		
						septicus	(Fr.) P. Kumm.	PREM		
				Pluteaceae	*Pluteus*	*atromarginatus*	(Konrad) Kühner	PREM		
						pellitus	(Pers.) P. Kumm.	PREM		
						romelli	(Britzelm.) Sacc.		Yes	
						salicinus	(Pers.) P. Kumm.		Yes	
						semibulbosus	(Lasch) Gillet		Yes	
						thomsonii	(Berk. & Broome) Dennis	PREM		
					Volvariella	*speciosa*	(Fr.) Singer		Yes	
				Podaxaceae	*Podaxis*	*africana*	De Villiers, Eicker & Van der Westh.	PREM		
						pistillaris	(L.) Fr.	PREM	Yes	
						rugospora	De Villiers, Eicker & Van der Westh.	PREM		
				Psathyrellaceae	*Ozonium*	*omnivorum*	Shear	PREM		
					Psathyrella	*griseola*	A. Pearson	PREM		
						condolleana	(Fr.) Maire		Yes	
						lionella	A. Pearson ex Pegler			Pearson 1996
				Psathyrellaceae	*Psathyrella*	*praelonga*	A. Pearson			Pearson 1950
						varicosa	A. Pearson			Pearson 1950
				Pterullaceae	*Pterula*	*subulata*	Fr.		Yes	
				Schizophillaceae	*Schizophyllum*	*commune*	Fr.		Yes	
				Sebacinaceae	*Sebacina*	*schweinitzii*	(Peck) Oberw.		Yes	
				Strophariaceae	*Agrocybe*	*praecox*	(Pers.) Fayod	PREM	Yes	
						pediades	(Fr.) Fayod		Yes	
					Deconica	*atrorufa*	(Schaeff.) P. Karst.	PREM		
						coprophila	(Bull.) Fr.	PREM		

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Fungi	Basidiomycota	Agaricomycetes	Agaricales	Strophariaceae	*Deconica*	*protea*	(Kalchbr.) Desjardin & B.A. Perry			Kalchbrenner 1876 (as *Agaricus proteus*)
					Flammula	*alnicola*	(Fr.) P. Kumm.	PREM		
						harmoge	(Fr.) Sacc.	PREM		
						hybrida	(Bull.) Gillet	PREM		
						laetilamellata	A. Pearson	PREM		
						luxurians	A. Pearson	PREM		
						papillata	A. Pearson	PREM		
						penetrans	(Fr.) Quél.	PREM		
						sapinea	(Fr.) Pat.	PREM		
					Galera	*hypnorum*	(Batsch) Quél.	PREM		
						lateritia	(Fr.) P. Kumm.	PREM		
						pygmaeoaffinis	(Fr.) Quél.	PREM		Van der Westhuizen and Eicker 1988
						spartea	Velen.	PREM		Van der Westhuizen and Eicker 1988
						tenera	(Schaeff.) P. Kumm.	PREM		
						tenera var. *siliginea*	(Fr.) P. Kumm.	PREM		
					Gymnopilus	*hybridus*	(Bull.) Maire		Yes	
						junonius	(Fr.) P.D. Orton	PREM	Yes	
						penetrans	(Fr.) Murrill	PREM	Yes	
						sapineus	(Fr.) Murrill		Yes	
					Hebeloma	*angustispermum*	A. Pearson	PREM		
						anthracophilum	Maire	PREM		
						crustuliniforme	(Bull.) Quél.		Yes	
						cylindrosporum	Romagn.	PREM	Yes	
						nudipes	(Fr.) Kalchbr.	PREM		
						sinapizans	(Paulet) Gillet		Yes	
						spoliatum	(Fr.) Gillet	PREM		
					Hymenogaster	*albellus*	Massee & Rodway	PREM		
						reticulatus	Zeller & C.W.	PREM		
					Hypholoma	*candolleanum*	(Fr.) Quél.	PREM		
						fasciculare	(Huds.) P. Kumm.	PREM	Yes	
						lateritium	(Schaeff.) P. Kumm.	PREM		
					Kuehneromyces	*mutabilis*	(Schaeff.) Singer & A.H. Sm.	PREM		
					Leratiomyces	*ceres*	(Cooke & Massee) Spooner & Bridge 2008		Yes	
					Naucoria	*pediades*	(Fr.) P. Kumm.	PREM		
						russa	(Cooke & Massee) Sacc.	PREM		
						scolecina	(Fr.) Quél.	PREM		
						semiorbicularis	(Bull.) Quél.	PREM		

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Fungi	Basidiomycota	Agaricomycetes	Agaricales	Strophariaceae	*Naucoria*	*undulosa*	(Fr.) Sacc.	PREM		
					Pholiota	*aurivella*	(Batsch) P. Kumm.	PREM		
						caperata	(Pers.) Gillet	PREM		
						cylindracea	(DC.) Gillet	PREM		
						flammans	(Batsch) P. Kumm.	PREM		
						mutabilis	(Schaeff.) P. Kumm.	PREM		
						parva	A. Pearson	PREM		
						pseudoerebia	A. Pearson	PREM		
						squarrosa	(Oeder) P. Kumm.		Yes	
						spectabilis	(Fr.) P. Kumm.	PREM		
						togularis	(Bull.) P. Kumm.	PREM		
						unicolor	(Vahl) Gillet	PREM		
					Psilocybe	*coprophila*	(Bull.) P. Kumm.		Yes	
						cylindrispora	A. Pearson			Pearson 1950
						natalensis	Gartz, D.A. Reid, M.T. Sm. & Eicker	PREM		
					Stropharia	*coccinea*	A. Pearson ex Pegler			Pearson 1996
						semiglobata	(Batsch) Quél.		Yes	
					Tubaria	*furfuracea*	(Pers.) Gillet		Yes	
				Tricholomataceae	*Amparoina*	*spinosissima*	(Singer) Singer		Yes	
					Cellypha	*rhoina*	(W.B. Cooke) W.B. Cooke	PREM		
					Clitocybe	*expallens*	(Pers.) P. Kumm.	PREM		
						fragrans	(With.) P. Kumm.	PREM		
						gentianea	Quél.	PREM		
						nuda	(Bull.) H.E. Bigelow & A.H. Sm.	PREM		Van der Westhuizen and Eicker 1988 (as *Lepista nuda*)
						rivulosa	(Pers.) P. Kumm.	PREM		
						splendens	(Pers.) Gillet	PREM		
						toxica	Stephens			Stephens 1966
					Collybia	*acervata*	(Fr.) P. Kumm.	PREM		
						albuminosa	(Berk.) Petch	PREM		Van der Westhuizen and Eicker 1988
						butyracea	(Bull.) P. Kumm.	PREM		Van der Westhuizen and Eicker 1988
						chrysopepla	(Berk. & M.A. Curtis) A. Pearson	PREM		
						distorta	(Fr.) Quél.	PREM	Yes	
						dryophila	(Bull.) P. Kumm.	PREM	Yes	
						extuberans	(Fr.) Quél.	PREM		
						extuberans	(Fr.) Quél.	PREM		
						fragrantissima	A. Pearson	PREM		
						fusipes	(Bull.) Quél.	PREM	Yes	
						macilenta	(Fr.) Gillet	PREM		

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Fungi	Basidiomycota	Agaricomycetes	Agaricales	Tricholomataceae	*Collybia*	*maculatoides*	A. Pearson	PREM		
						ocellata	(Fr.) P. Kumm.	PREM		
						radicata	(Relhan) Quél.	PREM		
						stridula	(Fr.) Sacc.	PREM		
						velutipes	(Curtis) P. Kumm.	PREM		
					Lepista	*caffrorum*	(Kalchbr. & MacOwan) Singer	PREM	Yes	
						sordida	(Schumach.) Singer	PREM	Yes	
					Macrocybe	*lobayensis*	(R. Heim) Pegler & Lodge	PREM	Yes	
						titans	(H.E. Bigelow & Kimbr.) Pegler, Lodge & Nakasone	PREM		
					Melanoleuca	*brevipes*	(Bull.) Pat.	PREM		
						melaleuca	(Pers.) Murrill	PREM		
					Omphalia	*glaucophylla*	(Lasch) Sacc.	PREM		Van der Westhuizen and Eicker 1988
						micromeles	(Berk. & Broome) Sacc.	PREM		
						oniscus	(Fr.) Gillet	PREM		
						pyxidatoides	A. Pearson	PREM		
						rustica	(Fr.) Quél.	PREM		
					Tricholoma	*albobrunneum*	(Pers.) P. Kumm.		Yes	
						eucalypticum	A. Pearson			Pearson 1950
						melaleucum f. *acystidiatum*	A. Pearson	PREM		
						meridianum	A. Pearson			Pearson 1950
						saponaceum	(Fr.) P. Kumm.		Yes	
						ustale	(Fr.) P. Kumm.		Yes	
					Tricholomopsis	*rutilans*	(Schaeff.) Singer		Yes	
					Tricholosporum	*laeteviolaceum*	D.A. Reid, Eicker, Clémençon & Cec. Roux	PREM		
					Trogia	*cantharelloides*	(Mont.) Pat.		Yes	
			Auriculariales	Auriculariaceae	*Auricularia*	*auricula-judae*	(Bull.) Quél.	PREM	Yes	
						delicata	(Mont.) Henn.	PREM		
						emini	Henn.	PREM		
						fuscosuccinea	(Mont.) Henn.	PREM		
						mesenterica	(Dicks.) Pers.	PREM		
						polytricha	(Mont.) Sacc.	PREM		
						sambucina	Mart.	PREM		
					Eichleriella	*macrospora*	(Ellis & Everh.) G.W. Martin	PREM		
					Exidia	*glandulosa*	(Bull.) Fr.	PREM	Yes	
						purpureocinerea	MacOwan & Kalchbr.	PREM		
					Heterochaete	*byliana*	Talbot	PREM		

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Auriculariales	Auriculariaceae	*Heterochaete*	*grandispora*	P.H.B. Talbot	PREM		
				Incertae sedis	*Aporpium*	*caryae*	(Schwein.) Teixeira & D.P. Rogers	PREM		
			Boletales	Boletaceae	*Aureoboletus*	*gentilis*	(Earle) Klofac		Yes	
					Boletus	*aureus*	Schaeff.		Yes	
						aestivalis	(Paulet) Fr.	PREM	Yes	
						bovinus	Rostk.	PREM		
						bovinus var. *virido-caerulescens*	A. Pearson	PREM		
						collinitus	Fr.	PREM		
						edulis	Rostk.	PREM	Yes	
						flavus	Pollini	PREM		
						grevillei	Klotzsch	PREM		
						curtipes	Massee			Massee 1908
						pinicola	Sw.		Yes	
						reticulatus	Schaeff.		Yes	
						stellenbossiensis	Van der Byl			Van der Byl 1925
						subflammeus	Berk.			Berkeley 1876
					Buchwaldoboletus	*hemichrysus*	(Berk. & M.A. Curtis) Singer		Yes	
					Chalciporus	*piperatus*	(Bull.) Bataille	PREM	Yes	
					Imleria	*badia*	(Fr.) Vizzini	PREM	Yes	
					Leccinum	*duriusculum*	(Schulzer ex Kalchbr.) Singer	PREM	Yes	
					Octaviania	*africana*	Lloyd	PREM		
						flava	(Rodway) G. Cunn.	PREM		
					Xerocomellus	*chrysenteron*	(Bull.) Šutara		Yes	
				Boletinellaceae	*Phlebopus*	*sudanicus*	(Har. & Pat.) Heinem.	PREM	Yes	
				Boletinellaceae	*Phlebopus*	*colossus*	(R. Heim) Singer		Yes	
				Coniophoraceae	*Coniophora*	*arida*	(Fr.) P. Karst.	PREM		
						cerebella	(Pers.) Pers.	PREM		
						fodinarum	P.H.B. Talbot	PREM		
						incrustata	P.H.B. Talbot	PREM		
						mollis	Ginns			Ginns 1982
						olivacea	Massee	PREM		
						papillosa	P.H.B. Talbot	PREM		
					Gyrodontium	*capense*	D.A. Reid			Reid 1963
				Gyroporaceae	*Gyroporus*	*castaneus*	(Bull.) Quél.	PREM	Yes	
				Paxillaceae	*Melanogaster*	*ambiguus*	(Vittad.) Tul. & C. Tul.	PREM		
					Paxillus	*extenuatus*	Fr.	PREM		
						involutus	(Batsch) Fr.	PREM	Yes	

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Boletales	Paxillaceae	*Paxillus*	*panuoides*	(Fr.) Fr.	PREM	Yes	
				Rhizopogonaceae	*Rhizopogon*	*capensis*	C.G. Loyd	PREM		
						luteolus	Fr. & Nordholm		Yes	
				Sclerodermataceae	*Pisolithus*	*tinctorius*	(Mont.) E. Fisch.	PREM	Yes	
					Scleroderma	*capense*	C.G. Loyd	PREM		
						cepa	Pers.		Yes	
						citrinum	Pers.		Yes	
						flavidum	Ellis & Everh.		Yes	
						verrucosum	(Bull.) Pers.		Yes	
						stellenbosiensis	Verwoerd	PREM		
				Serpulaceae	*Serpula*	*himantioides*	(Fr.) P. Karst.		Yes	
				Suillaceae	*Suillus*	*bellinii*	(Inzenga) Watling		Yes	
						bovinus	(L.) Roussel		Yes	
						granulatus	(L.) Roussel		Yes	
						luteus	(L.) Roussel		Yes	
			Cantharellales	Cantharellaceae	*Cantharellus*	*cibarius*	Fr.	PREM		
						longisporus	Heinem.		Yes	
				Ceratobasidiaceae	*Pellicularia*	*asperula*	D.P. Rogers	PREM		
						filamentosa	(Pat.) D.P. Rogers	PREM		
						fodinarum	P.H.B. Talbot & V.C. Green	PREM		
						vaga	(Berk. & M.A. Curtis) D.P. Rogers ex Linder	PREM		
				Clavulinaceae	*Clavulina*	*cinerea*	(Bull.) J. Schröt.	PREM		
						cristata	(Holmsk.) J. Schröt.	PREM	Yes	
			Corticiales	Corticiaceae	*Corticium*	*argillaceum*	Bres.	PREM		
					Corticium	*armeniacum*	Sacc.	PREM		
						coeruleum	(Lam.) Fr.	PREM		
						confluens	(Fr.) Fr.	PREM		
						gloeosporum	P.H.B. Talbot	PREM		
						laetum	(P. Karst.) Bres.	PREM		
						luteocystidiatum	P.H.B. Talbot	PREM		
						moniliforme	P.H.B. Talbot	PREM		
						portentosum	Berk. & M.A. Curtis	PREM		
						punctulatum	Cooke	PREM		
						salmonicolor	Berk. & Broome	PREM		
						scutellare	Berk. & M.A. Curtis	PREM		
						tumulosum	P.H.B. Talbot	PREM		
						vagum	Berk. & M.A. Curtis	PREM		
					Cytidia	*flocculenta*	(Fr.) Höhn. & Litsch.	PREM		

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fungarium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Corticiales	Corticiaceae	*Dendrothele*	*duthiei*	P.H.B. Talbot	PREM		
					Laetiporus	*baudonii*	(Pat.) Ryvarden		Yes	
						sulphureus	(Bull.) Murrill	PREM	Yes	
					Tretopileus	*sphaerophorus*	(Berk. & M.A. Curtis) S. Hughes & Deighton	PREM		
			Geastrales	Geastraceae	*Geasteropsis*	*conrathi*	Hollós	PREM		
					Geastrum	*ambiguum*	Mont.	PREM		
						arenarium	Lloyd	PREM		
						bryantii	Berk.	PREM		
						campestre	Morgan	PREM		
						coronatum	Pers.	PREM		
						dissimile	Bottomley	PREM		
						fimbriatum	Tul. & C. Tul.	PREM		
						floriforme	Vittad.	PREM		
						fornicatum	(Huds.) Hook.	PREM		
						hieronymi	Henn.	PREM		
						hygrometricum	Pers.	PREM		
						kotlabae	V.J. Staněk		Yes	
						lageniforme	Cooke	PREM		
						limbatum	Fr.	PREM	Yes	
						mammosum	De Toni	PREM		
						minimum	Chevall.	PREM		
						mirabile	Mont.	PREM		
						nanum	Pers.	PREM		
						pectinatum	Pers.	PREM	Yes	
						pouzarii	V.J. Staněk	PREM		
						quadrifidum	DC. ex Pers.	PREM		
						rabenhorstii	Kunze	PREM		
						saccatum	Speg.	PREM	Yes	
						schmidelii	Vittad.	PREM		
						schweinitzii	(Berk. & M.A. Curtis) Zeller		Yes	
						sessile	(Sowerby) Pouzar		Yes	
						smardae	V.J. Staněk	PREM		
						striatum	Quél.	PREM		
						triplex	Jungh.	PREM	Yes	
						velutinum	Morgan	PREM		
					Myriostoma	*coliforme*	(Dicks.) Corda	PREM	Yes	
						coliforme var. *capillisporum*	V.J. Staněk			Staněk 1958

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Incertae sedis	Incertae sedis	*Riessia*	*semiophora*	Fresen.	PREM		
			Phallales	Phallaceae	*Anthurus*	*archeri*	(Berk.) E. Fisch.	PREM		
					Aseroë	*rubra*	Labill.	PREM	Yes	
					Blumenavia	*angolensis*	(Welw. & Curr.) Dring		Yes	
					Clathrella	*roseolescens*	E. Fisch.	PREM		
					Clathrus	*affinis*	Lloyd	PREM		
						archeri	(Berk.) Dring	PREM	Yes	
						gracilis	(Berk.) Schltdl.	PREM		
						pseudocancellatus	(E. Fisch.) Lloyd	PREM		
						transvaalensis	Eicker & D.A. Reid		Yes	
					Ileodictyon	*gracile*	Berk.			Bottomley 1948; Coetzee 2010
					Itajahya	*galericulata*	Möller	PREM	Yes	
						rosea	(Delile) E. Fisch.		Yes	
					Jaczewskia	*phalloides*	Mattir.	PREM		
					Kalchbrennera	*corallocephala*	(Welw. & Curr.) Kalchbr.	PREM	Yes	
					Lysurus	*cruciatus*	(Lepr. & Mont.) Henn.			Bottomley 1948; Coetzee 2010
						gardneri	Berk.	PREM		
					Mutinus	*bambusinus*	(Zoll.) E. Fisch.	PREM		
						caninus	(Huds.) Fr.	PREM		
						simplex	Lloyd.	PREM		
					Phallus	*duplicatus*	Bosc		Yes	
						impudicus	L.	PREM	Yes	
						indusiatus	Vent.	PREM	Yes	
					Phallus	*rubicundus*	(Bosc) Fr.	PREM	Yes	
			Polyporales	Fomitopsidaceae	*Daedalea*	*biennis*	(Bull.) Fr.	PREM		
						hobbsii	Van der Byl	PREM		
						quercina	(L.) Pers.	PREM	Yes	
					Fomitopsis	*ochroleuca*	(Berk.) G. Cunn.	PREM		
					Gloeocystidium	*tenue*	(Pat.) Höhn. & Litsch.	PREM		
					Phaeolus	*schweinitzii*	(Fr.) Pat.	PREM	Yes	
					Rhodofomitopsis	*lilacinogilva*	(Berk.) B.K. Cui, M.L. Han & Y.C. Dai	PREM	Yes	
				Ganodermataceae	*Amauroderma*	*leptopus*	(Pers.) J.S. Furtado	PREM		
						fuscoporia	Wakef.			Wakefield 1948
						rude	(Berk.) Torrend	PREM	Yes	
						schomburgkii	(Mont. & Berk.) Torrend	PREM		
						sprucei	(Pat.) Torrend		Yes	
						zuluense	Talbot	PREM		
					Ganoderma	*alluaudi*	Pat. & Har.	PREM		
						annulare	(Fr.) Gilb.	PREM		

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Fungi	Basidiomycota	Agaricomycetes	Gloeophyllales	Gloeophyllaceae	*Gloeophyllum*	*sepiarium*	(Wulfen) P. Karst.	PREM	Yes	
						trabeum	(Pers.) Murrill	PREM	Yes	
			Gomphales	Gomphaceae	*Ramaria*	*formosa*	(Pers.) Quél.		Yes	
				Clavariadelphaceae	*Clavariadelphus*	*clavulinoides*	R.H. Petersen			Petersen 1967
			Hymenochae-tales	Hymenochae-taceae	*Coltricia*	*perennis*	(L.) Murrill	PREM	Yes	
					Fomitoparia	*capensis*	M. Fisch., Cloete, L. Mostert & Halleen			Cloete et al. 2014
					Fomitoparia	*punctata*	(P. Karst.) Murrill		Yes	
					Fuscoporia	*gilva*	(Schwein.) T. Wagner & M. Fisch.		Yes	
					Hydnum	*auriscalpium*	Lour.	PREM		
						longospinosum	Lloyd	PREM		
						mucidum	Pers.	PREM		
						sclerodontium	Mont. & Berk.	PREM		
						setosum	Pers.	PREM		
					Hymenochaete	*cinnamomea*	(Pers.) Bres.	PREM		
						contiformis	G. Cunn.	PREM		
						fasciculata	P.H.B. Talbot	PREM		
						fulva	Burt	PREM		
						luteobadia	(Fr.) Höhn. & Litsch.	PREM		
						ochromarginata	P.H.B. Talbot	PREM	Yes	
						pinnatifida	Burt	PREM		
						rubiginosa	(Dicks.) Lév.	PREM	Yes	
						semistupposa	Petch	PREM		
						tabacina	(Sowerby) Lév.	PREM		
			Hymenochae-tales	Hymenochae-taceae	*Hymenochaete*	*tristicula*	(Berk. & Broome) Massee	PREM		
					Phellinus	*gilvus*	(Schwein.) Pat.	PREM	Yes	
						igniarius	(L.) Quél.		Yes	
						resupinatus	M. Fisch., Cloete, L. Mostert & Halleen			Cloete et al. 2016
						rimosus	(Berk.) Pilát	PREM	Yes	
					Polystictus	*albobadius*	C.G. Loyd	PREM		
						doidgei	C.G. Loyd	PREM		
						subiculoides	C.G. Loyd	PREM		
					Trichaptum	*byssogenum*	(Jungh.) Ryvarden		Yes	
			Incertae sedis	Incertae sedis	*Cotylidia*	*aurantiaca* f. *infundibuliformis*	D.A. Reid	PREM		
					Grandinia	*bicolor*	P.H.B. Talbot	PREM		
					Heterochaete	*byliana*	P.H.B. Talbot	PREM		
					Heterochaete	*grandispora*	P.H.B. Talbot	PREM		
					Oxyporus	*populinus*	(Schumach.) Donk	PREM		

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Fungi	Basidiomycota	Agaricomycetes	Polyporales	Ganodermataceae	*Ganoderma*	*applanatum*	(Pers.) Pat.	PREM	Yes	
						aridicola	J.H. Xing & B.K. Cui			Xing et al. 2016
						austroafricanum	Coetzee, M.J. Wingf., Marinc., Blanchette			Crous et al. 2014
						chilense	(Fr.) Pat.	PREM		
						colossus	Fr.) C.F. Baker	PREM		
						cf. cupreum	(Sacc.) Bres.			Tchotet et al. 2019
						curtisii	(Berk.) Murrill	PREM		
						destructans	M.P.A. Coetzee, Marinc., M.J. Wingf.			Coetzee et al. 2015
						dunense	Tchotet, Rajchenb. & Jol. Roux			Tchotet et al. 2018
						eickeri	Tchotet, M.P.A. Coetzee, Rachjenb. & Jol. Roux			Tchotet et al. 2019
						eminii	Henn.	PREM		
						cf. cupreum	(Sacc.) Bres			Tchotet et al. 2019
						enigmaticum	M.P.A. Coetzee, Marinc., M.J. Wingf.			Coetzee et al. 2015
						fulvellum	Bres.	PREM		
						hildebrandii	Henn.	PREM		
						knysnamense	Tchotet, M.P.A. Coetzee, Rachjenb. & Jol. Roux			Tchotet et al. 2019
						lucidum	(Curtis) P. Karst.	PREM	Yes	
						mastoporum	(Lév.) Pat.	PREM		
						mollicarnosum	(Lloyd) Sacc. & Trotter	PREM		
						nigrolucidum	(Lloyd) D.A. Reid	PREM		
						oerstedii	(Fr.) Torrend	PREM		
						oregonense	Murrill	PREM		
						oroflavum	(Lloyd) C.J. Humphrey	PREM		
						resinaceum	Boud.	PREM	Yes	Tchotet et al. 2019
						tornatum	(Pers.) Bres.	PREM		
						zonatum	Murrill	PREM		
				Incertae sedis	*Crustodontia*	*chrysocreas*	(Berk. & M.A. Curtis) Hjortstam & Ryvarden		Yes	
				Meruliaceae	*Acia*	*conferta*	P.H.B. Talbot	PREM		
						stenodon	(Pers.) Bourdot & Galzin	PREM		
						uda	(Fr.) P. Karst.	PREM		
					Aegerita	*webberi*	H.S. Fawc	PREM		
					Bjerkandera	*adusta*	(Willd.) P. Karst.	PREM	Yes	
					Cymatoderma	*elegans*	Jungh.	PREM	Yes	
					Gloeoporus	*conchoides*	Mont.	PREM		
						dichrous	(Fr.) Bres.	PREM		
					Irpex	*dregeanus*	(Berk.) P.H.B. Talbot	PREM		

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Fungi	Basidiomycota	Agaricomycetes	Polyporales	Meruliaceae	*Irpex*	*flavus*	(Jungh.) Kalchbr.	PREM		
						grossus	Kalchbr.	PREM		
						modestus	Berk. ex Cooke	PREM		
						obliquus	(Schrad.) Fr.	PREM		
						villereus	Berk. & Broome	PREM		
					Laschia	*frieseana*	(Henn.) Sacc.	PREM		
						pustulata	Berk. & Broome	PREM		
						volkensii	Bres.	PREM		
					Merulius	*corium*	(Pers.) Fr.	PREM		
						gelatinosus	Petch	PREM		
						himantioides	Fr.	PREM		
						lacrymans	(Wulfen) Schumach.	PREM		
						molluscus	Fr.	PREM		
						pinastri	(Fr.) Burt	PREM		
						rufus	Pers.	PREM		
						squalidus	Fr.	PREM		
						tremellosus	Schrad.	PREM		
					Mycoleptodon	*ochraceus*	(Pers.) Bourdot & Galzin	PREM		
					Odontia	*arguta*	(Fr.) Quél.	PREM		
						bicolor	(Alb. & Schwein.) Quél.	PREM		
						mellea	(Berk. & Broome) Rea	PREM		
					Phlebia	*strigosozonata*	(Schwein.) Lloyd	PREM		
					Podoscypha	*affinis*	(Berk. & M.A. Curtis) Pat.	PREM		
						involuta	(Klotzsch) Imazeki	PREM		
						parvula	(Lloyd) D.A. Reid	PREM	Yes	
				Phanerochaetaceae	*Pseudolagarobasidium*	*acaciicola*	Ginns			Wood and Ginns 2006
				Podoscyphaceae	*Abortiporus*	*biennis*	(Bull.) Singer		Yes	
				Polyporaceae	*Coriolopsis*	*lata*	(Berk.) Ryvarden	PREM		
						polyzona	(Pers.) Ryvarden	PREM	Yes	
						strumosa	(Fr.) Ryvarden	PREM		
					Coriolus	*azureus*	(Fr.) G. Cunn.	PREM		
						obducens	(Pers.) Bourdot & Galzin	PREM		
						pubescens	(Schumach.) Quél.	PREM		
						unicolor	(Bull.) Pat.	PREM		
						zonatus	(Nees) Quél.	PREM		
					Daedaleopsis	*confragosa*	(Bolton) J. Schröt.	PREM	Yes	
					Favolus	*brasiliensis*	(Fr.) Fr.	PREM		
						europaeus	Fr.	PREM		

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Fungi	Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae	*Favolus*	*friesii*	Berk. & M.A. Curtis	PREM		
						hispidulus	Berk. & M.A. Curtis	PREM		
						spathulatus	(Jungh.) Lév.	PREM	Yes	
					Fomes	*annosus*	(Fr.) Cooke	PREM		
						caliginosus	(Berk.) Cooke	PREM		
						caryophylli	(Racib.) Bres.	PREM		
						conchatus	(Pers.) Gillet	PREM		
						connatus	(Weinm.) Gillet	PREM		
						fraxineus	(Bull.) Cooke	PREM		
						fulvus	(Scop.) Gillet	PREM		
						geotropus	(Cooke) Cooke	PREM		
						gibbosus	(Blume & T. Nees) Sacc.	PREM		
						gilvus	(Schwein.) Lloyd	PREM		
						glaucoporus	Lloyd	PREM		
						hornodermus	(Mont.) Cooke	PREM		
						kamphoeveneri	(Fr.) Sacc.	PREM		
						langloisii	Murrill) Sacc. & D. Sacc.	PREM		
						laricis	(F. Rubel) Murrill	PREM		
						leucophaeus	(Mont.) Cooke	PREM		
						lignosus	(Klotzsch) Bres.	PREM		
						lividus	(Kalchbr. ex Cooke) Sacc.	PREM		
						macgregorii	Bres.	PREM		
						marginatus	(Pers.) Fr.	PREM		
						marmoratus	(Berk. & M.A. Curtis) Cooke	PREM		
						melanoporus	(Mont.) Sacc.	PREM		
						minutulus	Henn.	PREM		
						pachyphloeus	Corner	PREM		
						pectinatus	Lloyd	PREM		
						pinicola	(Sw.) Cooke	PREM		
						putearius	Weir	PREM		
						ribis	(Schumach.) Gillet	PREM		
						rimosus	(Berk.) Cooke	PREM		
						robinsoniae	(Murrill) Sacc. & Trotter	PREM		
						roburneus	Lázaro Ibiza	PREM		
						roseus	(Alb. & Schwein.) Fr.	PREM		
						scalaris	(Berk.) Sacc.	PREM		
						senex	(Nees & Mont.) Cooke	PREM		
						sessilis	(Murrill) Sacc. & D. Sacc.	PREM		
						ulmarius	(Sowerby) Gillet	PREM		

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Fungi	Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae	*Fomes*	*ungulatus*	Lázaro Ibiza	PREM		
						velutinus	Bres.	PREM		
						yucatanensis	(Murrill) Sacc. & D. Sacc.	PREM		
						zambesianus	(Lloyd) Sacc.	PREM		
						zuluensis	Wakef.	PREM		
					Funalia	*gallica*	(Fr.) Bondartsev & Singer		Yes	
						leonina	(Klotzsch) Pat.	PREM		
						protea	(Berk.) D.A. Reid		Yes	
						trogii	(Berk.) Bondartsev & Singer		Yes	
					Grammothele	*pseudomappa*	P.H.B. Talbot	PREM		
					Heliocybe	*sulcata*	(Berk.) Redhead & Ginns		Yes	
					Hexagonia	*albida*	Lloyd	PREM		
						crinigera	Fr.	PREM		
						discopoda	Pat. & Har.	PREM		
						dregeana	Lév.	PREM		
						friesiana	Speg.	PREM		
						glabra	(P. Beauv.) Ryvarden	PREM		
						hirta f. *hystrix*	(Cooke) O. Fidalgo	PREM		
						pobeguinii	Har.	PREM		
						polygramma	(Mont.) Fr.	PREM		
						rigida	Berk.	PREM		
						speciosa	Fr.	PREM		
						tenuis	(Hook.) Fr.	PREM	Yes	
						tricolor	Fr.	PREM		
						zambesiana	Torrend	PREM		
					Lentinus	*arcularius*	(Batsch) Zmitr	PREM	Yes	
						bissus	Quél.	PREM		
						fastuosus	Kalchbr. & MacOwan	PREM		
						flabelliformis	(Bolton) Fr.	PREM		
						lecomtei	Fr.	PREM		
						murrayi	Kalchbr. & MacOwan	PREM		
						nigripes	Fr.	PREM		
						omphalodes var. *africanus*	A. Pearson			Pearson 1950
						sajor-caju	(Fr.) Fr.	PREM	Yes	
						strigosus	Fr.	PREM	Yes	
						stuppeus	Klotzsch	PREM	Yes	
						tigrinus	(Bull.) Fr.	PREM		
						tuber-regium	(Fr.) Fr.	PREM		

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae	*Lentinus*	*velutinus*	Fr.	PREM	Yes	
						villosus	Klotzsch	PREM	Yes	
						zeyheri	Berk.	PREM		
					Lenzites	*abietina*	(Bull.) Fr.	PREM		
						aspera	(Klotzsch) Fr.	PREM		
						betulina	(L.) Fr.	PREM	Yes	
						guineensis	(Afzel. ex Fr.) Fr.	PREM		
						junghuhnii	Lév.	PREM		
						palisoti	(Fr.) Fr.	PREM		
						quercina	(L.) P. Karst.	PREM		
						repanda	(Mont.) Fr.	PREM		
						tricolor	(Bull.) Fr.	PREM		
					Lopharia	*lirellosa*	Kalchbr. & MacOwan			Kalchbrenner & MacOwan 1881
						mirabilis	(Berk. & Broome) Pat.	PREM		
					Lignosus	*sacer*	(Afzel. ex Fr.) Ryvarden	PREM	Yes	
					Microporus	*xanthopus*	(Fr.) Kuntze	PREM	Yes	
					Nigroporus	*vinosus*	(Berk.) Murrill	PREM		
					Neolentinus	*lepideus*	(Fr.) Redhead & Ginns	PREM	Yes	
					Panus	*stipticus*	(Bull.) Fr.	PREM		
						stipticus var. *farinaceus*	(Schumach.) Rea	PREM		
						stuppeus	(Klotzsch) Pegler & R.W. Rayner	PREM		
					Perenniporia	*ochroleuca*	(Berk.) Ryvarden	PREM		
					Picipes	*badius*	(Pers.) Zmitr. & Kovalenko		Yes	
					Phellinus	*badius*	(Cooke) G. Cunn.	PREM	Yes	
						robustus	(P. Karst.) Bourdot & Galzin	PREM	Yes	
					Polyporus	*adustus*	(Willd.) Fr.	PREM		
						affinis	Blume & T. Nees	PREM		
						anebus	Berk.	PREM		
						arenosobasus	Lloyd	PREM		
						australiensis	Wakef.	PREM		
						baurii	Kalchbr.	PREM		
						berkeleyi	Fr.	PREM		
						biformis	Fr.	PREM		
						chilensis	Speg.	PREM		
						cichoriaceus	Berk.	PREM		
						conchatus	C.G. Loyd	PREM		
						cotoneus	Pat. & Har.	PREM		
						cuticularis	(Bull.) Fr.	PREM		

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae	*Polyporus*	*dictyopus*	Mont.	PREM	Yes	
						doidgeae	Wakef.	PREM		
						durbanensis	Van der Byl	PREM		
						durus	(Timm) Kreisel	PREM		
						favoloides	Henn.	PREM		
						flabelliformis	Klotzsch	PREM		
						flexilis	Van der Byl	PREM		
						fruticum	Berk. & M.A. Curtis	PREM		
						gilvus	(Schwein.) Fr.	PREM		
						grammocephalus	Berk.	PREM		
						heteroclitus	(Bolton) Fr.	PREM		
						immaculatus	Berk. ex Lloyd	PREM		
						isidioides	Berk,			Berkeley 1843
						mastoporus	Lév.	PREM		
						ochrolaccatus	Mont.	PREM		
						ochroleucus	Berk.	PREM		
						ochroporus	Van der Byl	PREM		
						patouillardi	Lloyd	PREM		
						picipes	Rostk.	PREM		
						pocula	(Fr.) Berk. & M.A. Curtis	PREM		
						radiatus	(Sowerby) Fr.	PREM		
						rhipidium	Berk.	PREM		
						rubidus	Berk.	PREM		
						rugulosus	Lasch	PREM		
						rusticus	C.G. Loyd	PREM		
						schweinitzii	Fr.	PREM		
						semipileatus	Peck	PREM		
						setiporus	Berk.	PREM		
						squamosus	(Huds.) Fr.	PREM		
						subradiatus	Bres.	PREM		
						telfairii	Klotzsch	PREM		
						trichiliae	Van der Byl	PREM		
						undatus	Pers.	PREM		
						varius	(Pers.) Fr.	PREM		
						vibecinus var. *antilopum*	Kalchbr.	PREM		
					Pycnoporus	*sanguineus*	(L.) Murrill	PREM	Yes	
					Trametes	*albotexta*	C.G. Loyd	PREM		
						capensis	Lloyd			Doidge 1950

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Polyporales	Polyporaceae	*Trametes*	*cingulata*	Berk.		Yes	
						elegans	(Spreng.) Fr.	PREM	Yes	
						gibbosa	(Pers.) Fr.		Yes	
						griseolilacina	Van der Byl	PREM		
						hirsuta	(Wulfen) Loyd	PREM	Yes	
						keetii	Van der Byl	PREM		
						meyenii	(Klotzsch) Lloyd		Yes	
						subflava	C.G. Loyd	PREM		
						versicolor	(L.) Loyd	PREM	Yes	
			Russulales	Auriscalpiaceae	*Lentinellus*	*omphalodes* var. *africanus*	A. Pearson		Yes	
				Hericiaceae	*Dentipellicula*	*austroafricana*	Jia J. Chen, L.L. Shen & Y.C. Dai			Chen et al. 2015
					Laxitextum	*bicolor*	(Pers.) Lentz	PREM	Yes	
				Lachnocladiaceae	*Asterostroma*	*cervicolor*	(Berk. & M.A. Curtis) Massee	PREM		
					Dichostereum	*rhodosporum*	(Wakef.) Boidin & Lanq.	PREM		
					Lachnocladium	*cristatum*	Lloyd	PREM		
						zenkeri	Henn.	PREM		
				Peniophoraceae	*Peniophora*	*arenata*	P.H.B. Talbot	PREM		
						aspera	(Pers.) Sacc.	PREM		
						carnea	(Willd.) P. Karst.	PREM		
						cinerea	(Pers.) Cooke	PREM		
						filamentosa	(Berk. & M.A. Curtis) Moffatt	PREM		
						gigantea	(Fr.) Massee	PREM		
						heterocystidia	Burt	PREM		
						longispora var. *brachyspora*	P.H.B. Talbot & V.C. Green	PREM		
						lycii	Höhn. & Litsch.	PREM		
						pelliculosa	P.H.B. Talbot	PREM		
						quercina	(Pers.) Cooke	PREM		
						rimicola	(P. Karst.) Höhn. & Litsch.	PREM		
						roumeguerei	(Bres.) Bres.	PREM		
						tenuis	(Pat.) Massee	PREM		
						tristicula	(Berk. & Broome) Boidin & Lanq.	PREM		
						velutina	(DC.) Cooke	PREM		
				Russulaceae	*Lactarius*	*deliciosus*	(L.) Gray	PREM	Yes	
						hepaticus	Plowr.	PREM	Yes	
					Lactifluus	*piperatus*	(L.) Pers.	PREM		Van der Westhuizen and Eicker 1988
					Russula	*agaricina*	(Kalchbr. ex Berk.) Trappe & T.F. Elliott			Berkeley 1876
						caerulea	Fr.		Yes	

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Agaricomycetes	Russulales	Russulaceae	*Russula*	*capensis*	A. Pearson		Yes	
						fallax	(Fr.) Fr.		Yes	
						sardonia	Fr.	PREM	Yes	
						sororia	(Fr.) Romell		Yes	
						xerampelina	(Schaeff.) Fr.		Yes	
				Stereaceae	*Aleurodiscus*	*acerinus* var. *longispora*	Höhn. & Litsch.,	PREM		
						disciformis	(DC.) Pat.	PREM		
						limonisporus	D.A. Reid	PREM		
						mirabilis	(Berk. & M.A. Curtis) Höhn.	PREM		
						polygonioides	(P. Karst.) Pilát	PREM		
						roseus	(Pers.) Höhn. & Litsch.	PREM		
					Stereum	*adnatum*	C.G. Loyd	PREM		
						australe	Lloyd		Yes	
						erumpens	Burt			Burt 1920
						hirsutum	(Wild.) Pers.	PREM	Yes	
						laxum	C.G. Loyd	PREM		
						ostrea	(Blume & T. Nees) Fr.		Yes	
						rimosum var. *africanum*	P.H.B. Talbot	PREM		
						subpiliatum	Berk. & M.A. Curtis	PREM		
						tomentosum	Van der Byl	PREM		
						turgidum	C.G. Loyd	PREM		
			Thelephorales	Thelephoraceae	*Hypochnus*	*eylesii*	Van der Byl	PREM		
						michelianus	Caldesi	PREM		
					Thelephora	*penicillata*	C.G. Loyd	PREM		
						terrestris	Ehrh.		Yes	
		Dacrymycetes	Dacrymycetales	Dacrymycetaceae	*Arrhytidia*	*involuta*	(Schwein.) Coker	PREM		
					Calocera	*cornea*	(Batsch) Fr.	PREM	Yes	
						viscosa	(Pers.) Fr.	PREM		
					Dacrymyces	*deliquescens*	(Bull.) Duby	PREM		
						palmatus	(Schwein.) Burt	PREM		
					Dacryopinax	*elegans*	(Berk. & M.A. Curtis) G.W. Martin	PREM		
						spathularia	(Schwein.) G.W. Martin	PREM	Yes	
					Femsjonia	*natalensis*	Cooke	PREM		
		Incertae sedis	Incertae sedis	Incertae sedis	*Naematoloma*	*capnoides*	(Fr.) P. Karst.	PREM		
						fasciculare	(Huds.) P. Karst.	PREM		
		Tremellomycetes	Tremellales	Tremellaceae	*Tremella*	*fuciformis*	Berk.		Yes	
						mesenterica	(Schaeff.) Retz.		Yes	

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Fungi	Basidiomycota	Tremellomycetes	Tremellales	Tremellaceae	*Tremella*	*micropera*	Kalchbr. & Cooke			Kalchbrenner and Cooke 1880
						microspora	Lloyd			Lloyd 1920
					Phaeotremella	*foliaceae*	(Pers.) Wedin, J.C. Zamora & Millanes		Yes	
				Sirobasidiaceae	*Sirobasidium*	*magnum*	Boedijn 1934		Yes	
	Mucoromycota	Mucoromycetes	Mucorales	Pilobolacecae	*Pilobolus*	*crystallinus*	(F.H. Wigg.) Tode		Yes	
Amoebozoa	Mycetozoa	Myxomycetes	Echinosteliales	Echinosteliaceae	*Echinostelium*	*coelocephalum*	T.E.Brooks & H.W.Keller			See text
			Liceales	Cribrariaceae	*Cribraria*	*argillacea*	(Pers. ex J.F.Gmel.) Pers.			See text
						cancellata	(Batsch) Nann.-Bremek.			See text
						intricata	Schrad.			See text
						tenella	Schrad.			See text
				Dictydiaethaliaceae	*Dictydiaethalium*	*plumbeum*	(Schumach.) Rostaf.			See text
				Liceaceae	*Licea*	*biforis*	Morgan			See text
						kleistobolus	G.W.Martin			See text
						pedicellata	(H.C.Gilbert) H.C.Gilbert			See text
				Tubiferaceae	*Lycogala*	*epidendrum*	(L.) Fr.			See text
						flavofuscum	(Ehrenb.) Rostaf.			See text
					Reticularia	*lycoperdon*	Bull.			See text
					Tubifera	*ferruginosa*	(Batsch) J.F. Gmel.			See text
			Physarales	Didymiaceae	*Diachea*	*leucopodia*	(Bull.) Rostaf.			See text
					Diderma	*subdictyospermum*	(Rostaf.) G.Lister			See text
						effusum	(Schwein.) Morgan			See text
						hemisphaericum	(Bull.) Hornem.			See text
						saundersii	(Berk. & Broome ex Massee) Lado			See text
					Didymium	*melanospermum*	(Pers.) T.Macbr.			See text
						difforme	(Pers.) Gray			See text
						eximium	Peck			See text
						iridis	(Ditmar) Fr.			See text
						nigripes	(Link) Fr.			See text
						squamulosum	(Alb. & Schwein.) Fr. & Palmquist			See text
					Mucilago	*crustacea*	F.H.Wigg.			See text
				Physaraceae	*Badhamia*	*foliicola*	Lister			See text
						macrocarpa	(Ces.) Rostaf.			See text
						affinis	Rostaf.			See text
						nitens	Berk.			See text
						spinispora	(Eliasson & N.Lundq.) H.W.Keller & Schokn.			See text
						utricularis	(Bull.) Berk.			See text
					Badhamiopsis	*ainoae*	(Yamash.) T.E.Brooks & H.W.Keller			See text

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Amoebozoa	Mycetozoa	Myxomycetes	Physarales	Physaraceae	*Craterium*	*leucocephalum*	(Pers. ex J.F.Gmel.) Ditmar			See text
						aureum	(Schumach.) Rostaf.			See text
						dictyosporum	(Rostaf.) H.Neubert, Nowotny & K.Baumann			See text
						minutum	(Leers) Fr.			See text
					Fuligo	*cinerea*	(Schwein.) Morgan			See text
						muscorum	Alb & Schwein			See text
						septica	(L.) F.H.Wigg.			See text
					Leocarpus	*fragilis*	(Dicks.) Rostaf.			See text
					Physarella	*oblonga*	(Berk. & M.A.Curtis) Morgan			See text
					Physarum	*cinereum*	(Batsch) Pers.			See text
						melleum	(Berk. & Broome) Massee			See text
						pezizoideum	(Jungh.) Pavill. & Lagarde			See text
						album	(Bull.) Chevall.		Yes	See text
						auriscalpium	Cooke			See text
						bitectum	G.Lister			See text
						bivalve	Pers.			See text
						bogoriense	Racib.			See text
						citrinum	Schumach.			See text
						compressum	Alb. & Schwein.			See text
						confertum	T.Macbr.			See text
						didermoides	(Pers.) Rostaf.			See text
						digitatum	G.Lister & Farquharson		Yes	See text
						flavicomum	Berk.			See text
						gyrosum	Rostaf.			See text
						javanicum	Racib.			See text
						leucophaeum	Fr.			See text
						leucopus	Link			See text
						mutabile	(Rostaf.) G.Lister			See text
						notabile	T.Macbr.			See text
						nucleatum	Rex			See text
						penetrale	Rex			See text
						pusillum	(Berk. & M.A.Curtis) G.Lister			See text
						roseum	Berk. & Broome			See text
						stellatum	(Massee) G.W.Martin			See text
						tenerum	Rex			See text
						vernum	Sommerf.			See text
						viride	(Bull.) Pers.			See text
					Willkommlangea	*reticulata*	(Alb. & Schwein.) Kuntze			See text

Kingdom	Phylum	Class	Order	Family	Genus	Species	Authority	Fun-garium	Field guides	Previous publications (if not in field guides)
Amoebozoa	Mycetozoa	Myxomycetes	Stemonitales	Stemonitidaceae	*Amaurochaete*	*atra*	(Alb. & Schwein.) Rostaf.			See text
					Comatricha	*alta*	Preuss			See text
						nigra	(Pers. ex J.F.Gmel.) J.Schröt.			See text
					Enerthenema	*papillatum*	(Pers.) Rostaf.			See text
					Lamproderma	*arcyrioides*	(Sommerf.) Rostaf.			See text
						scintillans	(Berk. & Broome) Morgan			See text
					Stemonaria	*irregularis*	(Rex) Nann.-Bremek., R.Sharma & Y.Yamam.			See text
						longa	(Peck) Nann.-Bremek.			See text
					Stemonitis	*splendens*	Rostaf.			See text
						axifera	(Bull.) T.Macbr.			See text
						fusca	Roth			See text
						herbatica	Peck			See text
						pallida	Wingate			See text
					Stemonitopsis	*typhina*	(F.H.Wigg.) Nann.-Bremek.			See text
			Trichiales	Dianemaceae	*Calomyxa*	*metallica*	(Berk.) Nieuwl.			See text
				Trichiaceae	*Arcyria*	*cinerea*	(Bull.) Pers.			See text
						denudata	(L.) Wettst.			See text
						incarnata	(Pers. ex J.F.Gmel.) Pers.			See text
						insignis	Kalchbr. & Cooke			See text
						minuta	Buchet			See text
						obvelata	(Oeder) Onsberg			See text
						oerstedii	Rostaf.			See text
						pomiformis	(Leers) Rostaf.			See text
					Hemitrichia	*clavata*	(Pers.) Rostaf.			See text
						serpula	(Scop.) Rostaf. ex Lister			See text
					Metatrichia	*vesparia*	(Batsch) Nann.-Bremek. ex G.W.Martin & Alexop.			See text
					Oligonema	*schweinitzii*	(Berk.) G.W.Martin			See text
					Perichaena	*depressa*	Lib.			See text
						corticalis	(Batsch) Rostaf.			See text
					Trichia	*persimilis*	P.Karst.			See text
						affinis	de Bary			See text
						botrytis	(J.F.Gmel.) Pers.			See text
						favoginea	(Batsch) Pers.			See text
						scabra	Rostaf.			See text
						varia	(Pers. ex J.F.Gmel.) Pers.			See text
		Protostelids	Protosteliales	Ceratiomyxaceae	*Ceratiomyxa*	*fruticulosa*	(O.F.Müll.) T.Macbr.			See text
					Ceratium	*sphaeroideum*	Kalchbr. & Cooke			Kalchbrenner and Cooke 1880

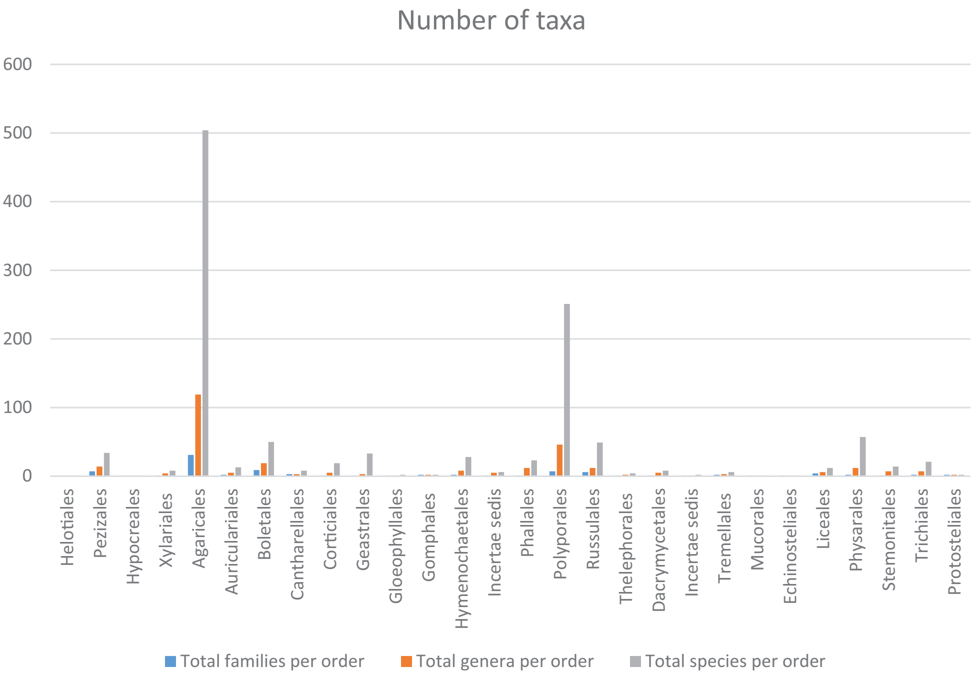

Figure 1. Bargraph indicating proportions of families, genera and species per order.

as myxomycetes, is represented by only two species, *Ceratiomyxa fruticulosa* (O.F. Müll.) T. Macbr and *Ceratium sphaeroideum* Kalchbr. & Cooke (Kalchbrenner and Cooke 1880; Spiegel et al. 2017).

As expected, cosmopolitan and widespread species in Africa have been reported from South Africa, such as *Arcyria cinerea* (Bull.) Pers., *Arcyria denudata* (L.) Wettst., *Stemonitis fusca* Roth, *Physarum pusillum* (Berk. & M.A. Curtis) G. Lister, *P. compressum* Alb. & Schwein., *Lycogala epidendrum* (L.) Fr., *Diderma hemisphaericum* (Bull.) Hornem., *Stemonitis splendens* Rostaf., *Didymium squamulosum* (Alb. & Schwein.) Fr. & Palmquist, *Fuligo septic* (L.) F.H. Wigg., *Hemitrichia serpula* (Scop.) Rostaf. ex Lister, *Metatrichia vesparia* (Batsch) Nann.-Bremek. ex G.W. Martin & Alexop. and *Pericheana depressa* Lib (http://www.discoverlife.org/). The number of species reported from South Africa also compares favorably with the approximately 375 myxomycete species reported from the African continent and its territories (Ndiritu and de Haan 2017). However, this is fewer than the 431 species reported from 30 countries in the Neotropics and 880 species from across the world (Lado 2005–2018).

Myxomycetes are not represented in PREM. This large deficit is most likely because slime molds have a different biology from fungi. This also reflects the limited focus that the broad fungal diversity has received in South Africa, with a much larger focus on disease causing fungi of plants, animals and humans. Even within mycological circles, slime molds have received very limited attention and there has been no expertise in studying them.

Discussion

The checklist gives an overview of the visible mycobiota of South Africa from different sources of data. The checklist presented in this publication is the first for South African macrofungi and is as comprehensive as can be of currently collected and published macrofungi. The list will serve as a foundation to add names to a future real-time, developing, online list that should eventually become as complete as possible, similar to what is available for other organisms in South Africa such as plants and animals. Information on South African macrofungi is still scanty and a great degree of inventorying is needed to document existing species, as well as new species, in order to produce more detailed checklists of macrofungi of South Africa. It will also need future refinement and additions are already forthcoming, including ecological and distribution information.

South Africa has a long history of mycology. Based on what was published in the available field guides on macrofungi for South Africa (Stephens and Kidd 1953a, b; Levin et al. 1985; Van der Westhuizen and Eicker 1994; Branch 2001; Gryzenhout 2010; Goldman and Gryzenhout 2019), the most common macrofungal species reported across all the years belonged to several genera, including *Agaricus* L., *Amanita* Pers., *Boletus* L., *Coprinus* Pers., *Lactarius* Pers., *Laetiporus* Murr., *Macrolepiota* Singer, *Russula* Pers., and *Suillus* Gray. There exists a level of overlap of species mentioned in the different field guides, but each field guide also included unique species while not one of them is complete or comprehensive due to publishing constraints. However, even the guides combined do not yet encompass the diversity of known and unknown species present in South Africa.

A number of scientific publications exist that listed macrofungi for South Africa in general. Doidge (1950) summarized the content of her book in tabular form, listing 835 Ascomycete species, 1704 Basidiomycetes species (36%) and several species of myxomycetes. The phytopathogenic component of these species, and species discovered since then, were summarized by Crous et al. (2000). Van der Westhuizen and Eicker (1988) listed the various fungi known at that stage in the Pretoria area (Gauteng Province), while Gorter and Eicker (1988) provided Afrikaans names for a list of fungi. Vellinga et al. (2009) and Wood (2017) listed a number of fungi, including macrofungi that they considered to be introduced into South Africa.

Eicker and Baxter (1999) presented a good overview of research done on basidiomycetes from 1977 to 1999. Their publication provides references to studies on the genera and species of *Phaeolus* (Pat.) Pat., *Pisolithus* Alb. & Schwein., *Termitomyces* R. Heim, *Amanita* Pers., *Chlorophyllum* Massee, *Clathrus* P. Micheli ex L., *Hymenagaricus* Heinem., *Lepiota* (Pers.) Gray, *Macrolepiota* Singer, *Leucoagaricus* Locq. ex Singer, *Leucocoprinus* Pat., *Montagnea* Fr. and *Hymenochaete* Lév. A monograph on resupinate and stereoid *Hymenomycetes*, a revision of *Hymenochaete* Lév. (*Hymenochaetaceae*) (Job, 1987) and a series of papers dealing with *Stereum* Pers., *Lopharia* Kalchbr. & MacOwan, *Cymatoderma* Jungh. and the *Thelephoraceae* (Gorter, 1979). Paul A. van der Byl was known for his pioneering work on polypores or bracket fungi while Averil M. Bottomley documented South African Gasteromycetes (Bottomley, 1948). New species of Gasteromycetes were described, such as *Bovista acocksii* De Villiers, Eicker & Van der Westhuizen (De Villiers et al. 1989), but limited information is still available for the Geasteraceae of South Africa (Coetzee and Van Wyk 2003). A new basidiomycetous species, namely *Pseudolagarobasidium acaciicola* Ginns, was considered to be a potential biocontrol against the invasive weed *Acacia cyclops* (Wood and Ginns 2006; Kotzé et al. 2015).

A number of recent studies on macrofungi included DNA phylogenetic data. For example, studies during the early part of the last century reported *Armillaria mellea* (Vahl: Fr.) P. Kumm. in South Africa (Pole 1933; Kotzé 1935; Bottomley 1937), that was largely associated with an expanding plantation forestry industry and the pathogenic nature of the fungus. However, recent morphologic and DNA-based studies showed that the fungus killing pine trees in South Africa is *A. fuscipes* Petch (Coetzee et al. 2000), while the Northern Hemisphere species *A. mellea* and *A. gallica* Marxm. & Romagn. are restricted to the Western Cape on non-native trees and dying *Protea* plants in the Kirstenbosch Botanical Gardens, respectively (Coetzee et al. 2000, 2003). However, recent studies alarmingly showed that *A. mellea* is spreading to native fynbos areas and is able to infect a number of native plants in natural ecosystems of the Western Cape (Coetzee et al. 2018).

A number of new *Ganoderma* species were discovered through the use of DNA sequences. These include *Ganoderma austroafricanum* Coetzee, M.J. Wingf., Marinc., Blanchette on *Jacaranda mimosifolia*, which was assumed to be the main causal agent of root rot on these trees (Crous et al. 2014), *G. enigmaticum* M.P.A. Coetzee, Marinc., M.J. Wingf. and *G. destructans* M.P.A. Coetzee, Marinc., M.J. Wingf. (Coetzee et al. 2015). *Ganoderma destructans*, another novel species *G. dunense* Tchotet, Rachjenb. & Jol. Roux, an undescribed novel species of *Ganoderma*, and *Pseudolagaricobasidion acaciicola* were also found associated with dying plants of the invasive weed *Acacia cyclops* in the Eastern and Western Cape Province (Tchoumi et al. 2018). A survey (Tchotet et al. 2017) on wood-rotting basidiomycetes from various declining native tree species in the Garden Route National Park (Western Cape) also showed *Ganoderma* to be the most prominent associated group, together with *Innonotus*, *Fomitoparia* and *Wrightoporia* to a lesser degree. The study also defined other operational taxonomic units (OTUs) with sequence data from such symptoms, and assigned tentative identities based on closest sequence hits on the UNITE database. In Tchotet et al. (2019) the OTU's belonging to *Ganoderma* was further characterized based on multigene phylogenies and brought up the number of *Ganoderma* species present in South Africa to 13. From the study another two new species, namely *G. eickeri* Tchotet, M.P.A. Coetzee, Rachjenb. & Jol. Roux and *G. knysnamense* Tchotet, M.P.A. Coetzee, Rachjenb. & Jol. Roux, were described, and the two phylogenetetic groups named as *G.* cf. *resinaceum* Boud. and *G.* cf. *cupreum* (Sacc.) Bres. could indicate the first reports of these species in South Africa. *Ganoderma* cf. *cupreum* has not been previously collected or observed (Table 1), while specimens of *G. resinaceum* are present in PREM and the species has been recorded previously (Table 1).

A new *Fomitiporia* species, *F. capensis* M. Fisch., M. Cloete, L. Mostert, F. Halleen, was described from South Africa based on fruit body morphology and combined internal transcribed spacer (ITS) and large-subunit ribosomal RNA gene (LSU) sequence comparisons (Cloete et al. 2014). The new species *Phellinus resupinatus* M. Fisch., M.

Cloete, L. Mostert, F. Halleen, was found to be associated with the disease esca and white rot on grape vines (Cloete et al. 2016). Two new *Chlorophyllum* species, namely *C. palaeotropicum* Z.W. Ge & A. Jacobs and *C. africanum* Z.W. Ge & A. Jacobs, were described based on morphology and DNA sequences of the ITS, partial LSU, the second largest subunit of RNA polymerase II (*rpb*2) and translation elongation factor 1-α (*tef*1) sequences (Ge et al. 2018). The jacaranda stinkhorn (*Itajahya galericulata* Möller) in Pretoria was also typed phylogenetically (Marincowitz et al. 2015).

Fungi associated with termite mounds formed the focus of a number of studies. *Termitomyces* spp. associated with some termite species are arguably some of the best known fungi among non-specialists in South Africa, as they are rather obvious, numerous, interesting and a well-loved delicacy. A number of species have been described from South Africa (Botha and Eicker 1991a, b; Eicker and Baxter 1999; Fine Licht et al. 2005), but not all species of *Termitomyces* associated with the 42 South African fungus growing termite species have been characterized. Neither have the *Xylaria* Hill ex Schrank species (Ascomycetes, Xylariaceae) associated with termite nests been fully characterized. However, *X. fioriana* Sacc. was identified and described in South Africa (Saccardo 1891). Another well-known associate with termite mounds, *Podaxis pistillaris* (L.) Fr., was also found to consist of more than one phylogenetic lineage, including several collections from Africa, that could be supported morphologically and ecologically (Conlon et al. 2016, 2019).

A total of 105 myxomycete species (Table 1) are known from South Africa (Ndiritu and De Haan 2017). The first record of myxomycetes of South African myxomycetes was published in 1917 (Duthie 1917a). Additional published surveys included Duthie (1917b) and Doidge (1950). One would expect more species in South Africa especially when considering the presence of diverse habitats across such a large surface area. Clearly, this is a vastly understudied and underexploited group in South Africa supported by no local expertise.

A number of species presented in past field guides (Table 1), which should present studied fungi, do not have specimens lodged in PREM (15%, excluding slime molds) and are thus not present in our National Collection. For instance, none of the important termite-cultivated *Termitomyces* species, including the iconic *Termitomyces umkowaan* (Cooke & Massee) D.A. Reid that is readily consumed by many, has fungorium specimens in PREM. These even include commonly occurring species such as *Schizophyllum commune* Fr. that are widespread throughout South Africa and that can even be observed in dry conditions. Only 14% of fungi (excluding slime molds) published in previous field guides are also lodged in PREM (Table 1).

Conversely, a very large proportion of species in PREM (77% excluding slime molds) have not been included in popular field guides and are thus largely unknown to citizens interested in these fungi, and even professional mycologists. These pieces of forgotten knowledge are crucial to complete the current and future status of our fungal biodiversity, and represent a glimpse of the diversity in earlier times. For instance, 11 species of *Pholiota* (Fr.) P. Kumm. are lodged in PREM but did not feature in previous field guides. A twelfth species, *P. squarrosa* (Oeder) P. Kumm., is the only species currently listed in field guides but specimens for this species are not lodged in PREM

(Table 1). Many of these collections representing genera or closely related groups, however, represent invaluable research opportunities to update the status of species in South Africa in the form of monographs and contemporary phylogenetic studies, to add new samples and possibly describe novel species.

Although great care was taken to eliminate possible synonyms present in the list, and to provide the most recent names for species listed under previous names (Index Fungorum 2019; Crous et al. 2004), a number of synonyms and previous names most likely are still present. It is impossible to continuously crosscheck the list, but errors can be rectified with future revisions for certain groups in the list that aim to eliminate these problems. It is also important to remember when using the list for research, that previous synonyms (including original published or collected names as listed in the contemporary taxonomic databases Index Fungorum and Mycobank) must also be searched.

A number of names listed in Doidge (1950) are not yet present in the list. Since a large proportion of these listed names have new combinations, it was uncertain whether the original author/-s observed them in the sense of what they are called today, or to what genus or species they were attributed to in the past. Some of these names also proved to be non-existent. Due to the importance of Doidge (1950) and the large number of names it contains, it was thus decided to rather treat the names included in Doidge (1950) separately where they can be more carefully linked to existing names and collections and their validity verified, before inclusion in the current checklist published here.

We emphasize that data obtained from publications and books were based on names only at this stage, because although published, some names were not supported by voucher collections that can be used to validate the accuracy of the included names. Even lists obtained from the fungorium, although tied to specimens, may represent misidentifications, previous synonyms or specimens not yet updated to recent systematic schemes for the particular taxon. Furthermore, a large number of macrofungi are still unnamed in South Africa, remain undiscovered, or new reports continue to be generated where discovered fungi could be identified. However, the working list presented here should form a solid foundation to revise names and add more names in future, especially if tied to certain targets or priorities matched to existing expertise and collaborations.

Having a fungal name list is invaluable. It is the first step towards compiling an atlas for macrofungi, similar to what exists for other organisms in South Africa (for example, Harrison et al. 1997). Such an atlas can also include distribution, ecological and biological data useful for diverse end users in governmental institutions, and those linked to conservation, ecology, academia and citizen science (Gryzenhout 2015). Additional products would be used to compile, for the first time, a red-list of macrofungi based on International Union for the Conservation of Nature (IUCN) criteria, and guidelines to protect them based on their biology. It will aid to identify indicator species to monitor ecological integrity and change. The residency status of macrofungi can be defined better, and species that are truly endemic, naturalized, introduced or invasive can be defined properly within each group. The need for this is already evident where fungi have been previously listed (Vellinga et al. 2009; Wood 2017) but there was no national list for comparison. In fact, one species listed in Vellinga et al. (2009), *Inocybe curvipes* P. Karst., is not present in previous publications or in PREM (Table 1). The checklist information can be used in education for the sustainable and safe use of fungal natural resources, to produce conservation awareness and regulation to protect naturally harvested species and habitats from over-harvesting (Gryzenhout et al. 2010, 2012). Lastly, the lists will be instrumental to do gap assessments from the compiled data to help identify research needs in future, for example where to focus surveys and collections, revisions, and where the greatest gaps for species descriptions exist. A list will also enable citizen scientist collaboration and participation and make the study of fungi more transparent (Gryzenhout 2015).

Human capacity should be developed in the area of mycology and biodiversity conservation. The species found in each region of South Africa is still unknown and there have not been any recent monographic works. Furthermore, a great need exists to continue revising the list, to ensure that more representatives of species are added and taxonomic revisions are undertaken and included in the list. The list should also be enabled to continue and long-term plans should be developed to ensure its sustainability.

The list presented is only based on species and specimens that could be named. A great deal of unknown taxa of macrofungi still exist. In fact, approximately 200 "unknown" macrofungal species of the fungorium records were left out from the list. Furthermore, approximately half of the records lodged in MushroomMap (http://adu.org.za/) represent fungi that could not be identified, whereas a great number of equally unknown fungi is posted on the Mushrooms for South Africa Facebook page (https://www.facebook.com/groups/MushroomsSouthernAfrica/), or communicated by citizen scientists (Gryzenhout 2015). This great deficit or inability to name numerous South African macrofungi is indicative of the great diversity that we have, the large proportion that are still undiscovered, unstudied, and hence under-utilized, and the paucity of human capacity to do this (South African Fungal Diversity Network 2013). Without active description and characterization, these fungi will remain in obscurity.

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RESEARCH ARTICLE

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Diseases of *Cymbopogon citratus* (Poaceae) in China: *Curvularia nanningensis* sp. nov.

Qian Zhang[1], Zai-Fu Yang[1], Wei Cheng[2], Nalin N. Wijayawardene[3],
Kevin D. Hyde[4], Zhuo Chen[5], Yong Wang[1]

1 *Department of Plant Pathology, Agriculture College, Guizhou University, Guiyang, Guizhou Province, 550025, China* **2** *Department of Practaculture Science, Animal Science College, Guizhou University, Guiyang, Guizhou 550025, China* **3** *Center for Yunnan Plateau Biological Resources Protection and Utilization, College of Biological Resource and Food Engineering, Qujing Normal University, Qujing, Yunnan 655011, China* **4** *Center of Excellence in Fungal Research and School of Science, Mae Fah Luang University, Chiang Rai, 57100, Thailand* **5** *Key Laboratory of Green Pesticide and Agricultural Bioengineering, Ministry of Education, Guizhou University, Guiyang 550025, China*

Corresponding author: *Zhuo Chen* (gychenzhuo@aliyun.com), *Yong Wang* (yongwangbis@aliyun.com)

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Abstract

Five *Curvularia* strains isolated from diseased leaves of lemongrass (*Cymbopogon citratus*) in Guangxi Province, China, were examined. NCBI-Blast searches of ITS sequences suggested a high degree of similarity (99–100%) to *Curvularia akaii*, *C. akaiiensis*, *C. bothriochloae*, *C. heteropogonis* and *C. sichuanensis*. To accurately identify these strains, we further analysed their morphology and phylogenetic relationships based on combinations of ITS, GAPDH, and *tef*1 gene sequences. Morphological observations indicated that the key character differing from similar species was conidial size, whereas phylogenetic analyses indicated that the five strains represent one species that is also distinct from *C. akaii*, *C. akaiiensis* and *C. bothriochloae* by conidial size and conidiophore length. Thus, the strains examined are found to represent a new species described herein as *Curvularia nanningensis*. The pathogenicity test on the host and detached leaves confirmed the new species to be pathogenic on *Cymbopogon citratus* leaves. Standardised requirements for reliable identification of *Curvularia* pathogens are also proposed.

Keywords

Cymbopogon, phylogeny, plant disease, Pleosporaceae, taxonomy

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Introduction

Cymbopogon citratus Stapf (lemongrass), believed to be a native of Malaysia, is now widely distributed in all continents and particularly in America, China, Guatemala and Southeast Asia. Essential oil from lemongrass is often used in aromatherapy (Williamson et al. 1996; Noel et al. 2002; Yang and Lei 2005; Shah et al. 2011). As a traditional Chinese medicine, lemongrass is known to provide relief from a variety of ailments including eczema, cold, headache and stomach-ache (Zhou et al. 2011). Guatemala is known to be the main exporter of lemongrass with about 250 tons per year. China produces 80 to 100 tons of lemongrass annually and the USA and Russia each imports about 70 tons per year (DAFF 2012). Depending on climatic conditions, lemongrass can be severely infected with a rust disease caused by *Puccinia nakanishikii* Dietel in Hawaii and California (Gardner 1985; Koike and Molinar 1999). In Brazil, a rust on lemongrass caused by another *Puccinia* species named *P. cymbopogonis* Massee has been reported (Vida et al. 2006). Joy et al. (2006) summarised the various disease symptoms and their causal agents of lemongrass.

Curvularia spp. infect many herbaceous plants including *Cymbopogon* Spreng. (Smith et al. 1989). *Helminthosporium cymbopogi* C.W. Dodge (≡ *Curvularia cymbopogonis* (C.W. Dodge) J.W.Groves & Skolko) is responsible for a severe disease of lemongrass in the lowlands of Guatemala (Dodge 1942). Barua and Bordoloi (1983) discovered *C. verruciformis* causing disease on *Cymbopogon flexuosus* Stapf. *Curvularia andropogonis* (Zimm.) Boedijn led to foliage blight of *Cymbopogon nardus* (L.) Rendle in the Philippines (Sato and Ohkubo 1990). Thakur (1994) reported *C. lunata* (Wakker) Boedijn as the causal agent of a new blight disease of *Cymbopogon martini* (Roxb.) Wats. var. *motia* Burk. Chutia et al. (2006) discovered that a leaf blight of *Cymbopogon winterianus* Jowitt is caused by *Curvularia* spp., resulting in a dramatic change in oil yield and its constituents. Recently, Santos et al. (2018) characterised the morphological and molecular diversity of the isolates of *C. lunata*, associated with *Andropogon* Linn. seeds.

Starting in 2010, there have been outbreak reports of pathogenic *Curvularia* in Asian countries, especially India and Pakistan (Pandey et al. 2014; Avasthi et al. 2015; Majeed et al. 2015). As China is a neighbouring country, we felt obligated to evaluate the potential threat of *Curvularia* to our crops. A severe *Curvularia* leaf blight disease was observed in three farms of *Curcuma aromatica* Salisb. in Hainan Province during 2010 (Chen et al. 2013). Gao et al. (2012) reported a new rice black sheath spot disease caused by *C. fallax* Boedijn in Hunan Province. Our research group is also conducting a disease survey on the occurrence of *Curvularia* diseases in Southwest China since 2017. Two new pathogens (*C. asianensis* Manamgoda, L. Cai & K.D. Hyde and *C. microspora* Y. Liang, K.D. Hyde, J. Bhat & Yong Wang bis), which affected *Epipremnum pinnatum* (L.) Engl. and *Hippeastrum rutilum* Herb. (Liang et al. 2018; Wang et al. 2018), respectively, were found.

Meanwhile, a severe leaf blast disease on lemongrass was found in Guangxi Province, China, that first appeared on the tips of leaves. As the infection progressed, more than 30% of leaves showed different degrees of abnormalities, while in the later stages more than 50% of the upper leaves appeared diseased and disease incidence reached 80% or above in the lower leaf blades. We provide a detailed morphological description and phylogenetic analyses of the pathogen confirming it as a new *Curvularia* species. Koch's postulates (see later text) have been carried out to confirm its pathogenicity. Our study provides a further understanding of *Curvularia* disease on lemongrass in China.

Materials and methods

Isolation

Leaves of *Cymbopogon citratus* showing leaf blast symptoms were collected from Guangxi Medicinal Botanical Garden in Nanning, China, during 2017. Diseased leaf pieces were surface disinfected with 70% ethanol for 30 s, 1% NaClO for 1 min and repeatedly rinsed in sterile distilled water for 30 s. For isolation of *Curvularia*, conidia were removed from the diseased tissue surface using a sterilised needle and placed in a drop of sterilised water followed by microscopic examination. The spore suspension was drawn with a Pasteur pipette and transferred to a Petri dish with 2% water agar (WA) or 2% malt extract agar (MEA) and 100 mg/l streptomycin to inhibit the growth of bacteria. The plates were incubated for 24 h in an incubator (25°C) and examined for single spore germination under a dissecting microscope. Germinating conidia were transferred separately to new 2% MEA plates (Chomnunti et al. 2014).

Morphological studies

Single germinated spores were transferred to PDA or MEA and incubated at 28°C in a light incubator with 12 h light/12 h darkness. Ten days later, the colony and morphological characters were recorded according to Manamgoda et al. (2011, 2012). Colony diameters on PDA and MEA were measured at 1, 3, 5 and 7 days post-inoculation and average growth rates were calculated. Conidia and conidiophores were examined using a compound microscope fitted with a digital camera (Olympus BX53). The holotype specimen is deposited in the Herbarium of the Department of Plant Pathology, Agricultural College, Guizhou University (HGUP). An ex-type culture is deposited in the Culture Collection of the Department of Plant Pathology, Agriculture College, Guizhou University, China (GUCC) and Mae Fah Luang University Culture Collection (MFLUCC) in Thailand (Table 1).

DNA Extraction and Sequencing

Fungal cultures were grown on PDA at 28°C until the entire Petri dish (90 mm) was colonised. Fresh fungal mycelia were scraped off the surface of the PDA using a sterilised scalpel. A BIOMIGA Fungus Genomic DNA Extraction Kit (GD2416,

Table 1. Sequences used for phylogenetic analysis.

Species name	Strain number	GenBank Accession numbers		
		ITS	GAPDH	tef1
Curvularia aeria	CBS 294.61^T	HE861850	HF565450	–
C. affinis	CBS 154.34^T	KJ909780	KM230401	KM196566
C. ahvazensis	CBS 144673^T	KX139029	MG428693	MG428686
C. akaii	CBS 317.86	KJ909782	KM230402	KM196569
C. akaiiensis	BRIP 16080^T	KJ415539	KJ415407	KJ415453
C. alcornii	MFLUCC 10-0703^T	JX256420	JX276433	JX266589
C. americana	UTHSC 08-3414^T	HE861833	HF565488	–
C. asiatica	MFLUCC 10-0711^T	JX256424	JX276436	JX266593
C. australiensis	BRIP 12044^T	KJ415540	KJ415406	KJ415452
C. australis	BRIP 12521^T	KJ415541	KJ415405	KJ415451
C. bannonii	BRIP 16732^T	KJ415542	KJ415404	KJ415450
C. beasleyi	BRIP 10972^T	MH414892	MH433638	MH433654
C. beerburrumensis	BRIP 12942^T	MH414894	MH433634	MH433657
C. boeremae	IMI 164633^T	MH414911	MH433641	–
C. borreriae	CBS 859.73	HE861848	HF565455	–
	MFLUCC 11-0422	KP400638	KP419987	KM196571
C. bothriochloae	BRIP 12522^T	KJ415543	KJ415403	KJ415449
C. brachyspora	CBS 186.50	KJ922372	KM061784	KM230405
C. buchloes	CBS 246.49^T	KJ909765	KM061789	KM196588
C. carica-papayae	CBS 135941^T	HG778984	HG779146	–
C. chiangmaiensis	CPC 28829^T	MF490814	MF490836	MF490857
C. chlamydospora	UTHSC 07-2764^T	HG779021	HG779151	–
C. clavata	BRIP 61680b	KU552205	KU552167	KU552159
C. coatesiae	BRIP 24261^T	MH414897	MH433636	MH433659
C. coicis	CBS 192.29^T	JN192373	JN600962	JN601006
C. colbranii	BRIP 13066^T	MH414898	MH433642	MH433660
C. crustacea	BRIP 13524^T	KJ415544	KJ415402	KJ415448
C. cymbopogonis	CBS 419.78	HG778985	HG779129	–
C. dactyloctenicola	CPC 28810^T	MF490815	MF490837	MF490858
C. dactyloctenii	BRIP 12846^T	KJ415545	KJ415401	KJ415447
C. deightonii	CBS 537.70	LT631356	LT715839	–
C. ellisii	CBS 193.62^T	JN192375	JN600963	JN601007
C. eragrosticola	BRIP 12538^T	MH414899	MH433643	MH433661
C. eragrostidis	CBS 189.48	HG778986	HG779154	–
C. geniculata	CBS 187.50^T	KJ909781	KM083609	KM230410
C. gladioli	CBS 210.79	HG778987	HG779123	
C. graminicola	BRIP 23186^T	JN192376	JN600964	JN601008
C. gudauskasii	DAOM 165085	AF071338	–	–
C. harveyi	BRIP 57412^T	KJ415546	KJ415400	KJ415446
C. hawaiiensis	BRIP 11987^T	KJ415547	KJ415399	KJ415445
C. heteropogonicola	BRIP 14579^T	KJ415548	KJ415398	KJ415444
C. heteropogonis	CBS 284.91^T	JN192379	JN600969	JN601013
C. hominis	CBS 136985^T	HG779011	HG779106	–
C. homomorpha	CBS 156.60^T	JN192380	JN600970	JN601014
C. inaequalis	CBS 102.42^T	KJ922375	KM061787	KM196574
C. intermedia	CBS 334.64	HG778991	HG779155	–
C. ischaemi	CBS 630.82^T	JX256428	JX276440	–
C. kenpeggii	BRIP 14530^T	MH414900	MH433644	MH433662
C. kusanoi	CBS 137.29^T	JN192381	–	JN601016
C. lamingtonensis	BRIP 12259^T	MH414901	MH433645	MH433663
C. lunata	CBS 730.96^T	JX256429	JX276441	JX266596
C. malina	CBS 131274^T	JF812154	KP153179	KR493095
C. mebaldsii	BRIP 12900^T	MH414902	MH433647	MH433664
C. micropus	CBS 127235^T	HE792934	LT715859	–
C. microspora	GUCC 6272^T	MF139088	MF139106	MF139115
C. miyakei	CBS 197.29^T	KJ909770	KM083611	KM196568
C. mosaddeghii	IRAN 3131C^T	MG846737	MH392155	MH392152
C. muehlenbeckiae	CBS 144.63^T	HG779002	HG779108	–

Species name	**Strain number**	**GenBank Accession numbers**		
		ITS	**GAPDH**	**tef1**
C. neergaardii	BRIP 12919^{T}	KJ415550	KJ415397	KJ415443
C. nanningensis sp. nov.	GUCC 11000	MH885316	MH980000	MH980006
	GUCC 11001	MH885317	MH980001	MH980007
	GUCC 11002	MH885318	MH980002	MH980008
	GUCC 11003	MH885319	MH980003	MH980009
	GUCC 11005^{T}	MH885321	MH980005	MH980011
C. neoindica	BRIP 17439	AF081449	AF081406	–
C. nicotiae	CBS 655.74^{T} = BRIP 11983	KJ415551	KJ415396	KJ415442
C. nodosa	CPC 28800^{T}	MF490816	MF490838	MF490859
	CPC 28801	MF490817	MF490839	MF490860
	CPC 28812	MF490818	MF490840	MF490861
C. nodulosa	CBS 160.58	JN601033	JN600975	JN601019
C. oryzae	CBS 169.53^{T}	KP400650	KP645344	KM196590
C. ovariicola	CBS 470.90^{T}	JN192384	JN600976	JN601020
C. pallescens	CBS 156.35^{T}	KJ922380	KM083606	KM196570
C. palmicola	MFLUCC 14-0404	MF621582	–	–
C. papendorfii	CBS 308.67^{T}	KJ909774	KM083617	KM196594
C. perotidis	CBS 350.90^{T}	JN192385	KJ415394	JN601021
C. petersonii	BRIP 14642^{T}	MH414905	MH433650	MH433668
C. pisi	CBS 190.48^{T}	KY905678	KY905690	KY905697
C. platzii	BRIP 27703b^{T}	MH414906	MH433651	MH433669
C. portulacae	CBS 239.48^{T} = BRIP 14541	KJ415553	KJ415393	KJ415440
C. prasadii	CBS 143.64^{T}	KJ922373	KM061785	KM230408
C. protuberata	CBS 376.65^{T}	KJ922376	KM083605	KM196576
C. pseudobrachyspora	CPC 28808^{T}	MF490819	MF490841	MF490862
C. pseudolunata	UTHSC 09-2092^{T}	HE861842	HF565459	–
C. pseudorobusta	UTHSC 08-3458	HE861838	HF565476	–
C. ravenelii	BRIP 13165^{T}	JN192386	JN600978	JN601024
C. reesii	BRIP 4358^{T}	MH414907	MH433637	MH433670
C. richardiae	BRIP 4371^{T}	KJ415555	KJ415391	KJ415438
C. robusta	CBS 624.68^{T}	KJ909783	KM083613	KM196577
C. rouhanii	CBS 144674^{T}	KX139030	MG428694	MG428687
C. ryleyi	BRIP 12554^{T}	KJ415556	KJ415390	KJ415437
C. senegalensis	CBS 149.71	HG779001	HG779128	–
C. sesuvii	Bp-Zj 01^{T}	EF175940	–	–
C. shahidchamranensis	IRAN 3133C^{T}	MH550084	MH550083	–
C. soli	CBS 222.96^{T}	KY905679	KY905691	KY905698
C. sorghina	BRIP 15900^{T}	KJ415558	KJ415388	KJ415435
C. spicifera	CBS 274.52	JN192387	JN600979	JN601023
C. sporobolicola	BRIP 23040b^{T}	MH414908	MH433652	MH433671
C. subpapendorfii	CBS 656.74^{T}	KJ909777	KM061791	KM196585
C. trifolii	CBS 173.55	HG779023	HG779124	–
C. tripogonis	BRIP 12375^{T}	JN192388	JN600980	JN601025
C. tropicalis	BRIP 14834^{T}	KJ415559	KJ415387	KJ415434
C. tsudae	ATCC 44764^{T}	KC424596	KC747745	KC503940
C. tuberculata	CBS 146.63^{T}	JX256433	JX276445	JX266599
C. uncinata	CBS 221.52^{T}	HG779024	HG779134	–
C. variabilis	CPC 28813	MF490820	MF490842	MF490863
	CPC 28814	MF490821	MF490843	MF490864
	CPC 28815^{T}	MF490822	MF490844	MF490865
	CPC 28816	MF490823	MF490845	MF490866
C. verruciformis	CBS 537.75	HG779026	HG779133	–
C. verruculosa	CBS 150.63	KP400652	KP645346	KP735695
	CPC 28792	MF490825	MF490847	MF490868
	CPC 28809	MF490824	MF490846	MF490867
C. warraberensis	BRIP 14817^{T}	MH414909	MH433653	MH433672
Bipolaris drechsleri	MUS0028	KF500532	KF500535	KM093761
B. maydis	CBS 136.29^{T}	AF071325	KM034846	KM093794

Ex-type isolates were labeled with “^{T}”.

BIOMIGA, Inc., San Diego, California, USA) was used to extract the genomic DNA. DNA amplification was performed in a 25 µl reaction volume which contained 2.5 µl 10 × PCR buffer, 1 µl of each primer (10 µM), 1 µl template DNA, 0.25 µl Taq DNA polymerase (Promega, Madison, WI, USA) and 18.5 µl ddH_2O. Primers used and thermal cycling programme for PCR amplification of the ITS (ITS4/ITS5), GAPDH (gpd1/gpd2) and *tef*1 (EF-526F/1567R) genes were followed as described previously (White et al. 1990; Berbee et al. 1999; Schoch et al. 2009; Liang et al. 2018).

Phylogenetic analyses

DNA sequences originated from five strains (GUCC 11000, GUCC 11001, GUCC 11002, GUCC 11003 and GUCC 11005) and reference sequences of ex-type or representative sequences of *Curvularia* species were downloaded from GenBank database (Table 1) with strains of *Bipolaris maydis* (Y. Nisik. & C. Miyake) Shoemaker (CBS 136.29) and *B. drechsleri* Manamgoda & Minnis (MUS0028) as outgroup taxa. Alignments for each locus were performed in MAFFT v7.307 online version (Katoh and Standley 2016) and manually verified in MEGA 6.06 (Tamura et al. 2013). Phylogenetic analyses were performed by Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian methods. Sequences were optimised manually to allow maximum alignment and maximum sequence similarity as detailed in Manamgoda et al. (2012). MP analyses were performed in PAUP v. 4.0b10 (Swofford 2003) using the heuristic search option with 1,000 random taxa additions and tree bisection and reconnection (TBR) as the branch-swapping algorithm. Five thousand maxtrees were set to build up the phylogenetic tree. The characters in the alignment matrix were ordered according to ITS+GAPDH+*tef*1 with equal weight, and gaps were treated as missing data. The MP phylogenetic analysis of *Curvularia* ITS sequences included pathogens from China, India and Pakistan and the wrong sequence (KN879930), actually belonging to *Alternaria alternata* (taxon:5599), was selected as the outgroup. The Tree Length (TL), Consistency Indices (CI), Retention Indices (RI), Rescaled Consistency Indices (RC) and Homoplasy Index (HI) were calculated for each tree generated. The resulting PHYLIP file was used to generate the ML tree on the CIPRES Science Gateway (https://www.phylo.org/portal2/login.action) using the RAxML-HPC2 black box with 1000 bootstrap replicates and GTRGAMMA as the nucleotide substitution model. For Bayesian inference analysis, the best model of evolution (GTR+I+G) was determined using MrModeltest v2 (Nylander 2004). Bayesian inference analysis was done using MrBayes v 3.2.6 (Ronquist et al. 2012). Bayesian analyses were launched with random starting trees for 2 000 000 generations and Markov chains were sampled every 1000 generations. The first 25% resulting trees were discarded as burn-in. Alignment matrices are available in TreeBASE under the study ID 25080.

Koch's Postulate test

To confirm the pathogenicity of the fungus, five healthy plants of *Cymbopogon citratus* were inoculated with 5 mm diameter mycelial plugs of the five isolates (GUCC 11000, GUCC 11001, GUCC 11002, GUCC 11003 and GUCC 11005) cut from the margins of 10-day-old actively growing cultures; the control was treated with sterile agar plugs. The plants were kept for two days in an illuminating incubator at 28° ± 3°C. Additionally, two plants were sprayed with distilled water and kept as control under the same conditions. Both inoculated (host and detached leaves) and control plants were kept for two days in an illuminating incubator at 28 ± 3°C. After four days of incubation, the inoculated plants and leaves were observed for the development of symptoms (Zhang et al. 2018). Infected leaves were collected and the fungus was re-isolated using PDA medium and the ITS sequence was compared with original strains.

Results

Phylogenetic analyses

First, we compared the DNA sequence identity of ITS, GAPDH and *tef*1 gene regions (Table 2). Among our five strains, there was only one base difference. In the ITS gene region, for *C. akaiiensis*, the base sequence was identical to our strains; only 1 difference for *C. bothriochloae*; base differences were 8 for *C. akaii*, 9 for *C. deightonii* and 5 for *C. sichuanensis*. Only *C. heteropogonis* had noticeable (25) base differences with our strains. In the GAPDH and *tef*1 gene regions, the mutation rate of DNA bases was apparently faster than the ITS region. There were between 9 to 19 base differences in GAPDH and 3 to 8 in *tef*1. This means that in *Curvularia*, GAPDH has a faster

Table 2. DNA sequence differences between *Curvularia nanningensis* and related species in three gene regions.

Species	Strain number	ITS (1–547 bp)	GAPDH (550–1031bp)	tef1 (1034–1899 bp)
C. nanningensis	GUCC11000	0	1	0
	GUCC11001	0	0	0
	GUCC11002	0	1	0
	GUCC11003	0	1	0
	GUCC11005^{T}	0	0	0
C. akaii	CBS 317.86	8	9	4
C. akaiiensis	BRIP 16080^{T}	0	10	5
C. bothriochloae	BRIP 12522^{T}	1	19	8
C. deightonii	CBS 537.70	9	13	–
C. heteropogonis	CBS 284.91^{T}	25	12	3
C. sichuanensis	HSAUP II.2650-1^{T}	5	–	–

^{T} = ex-type

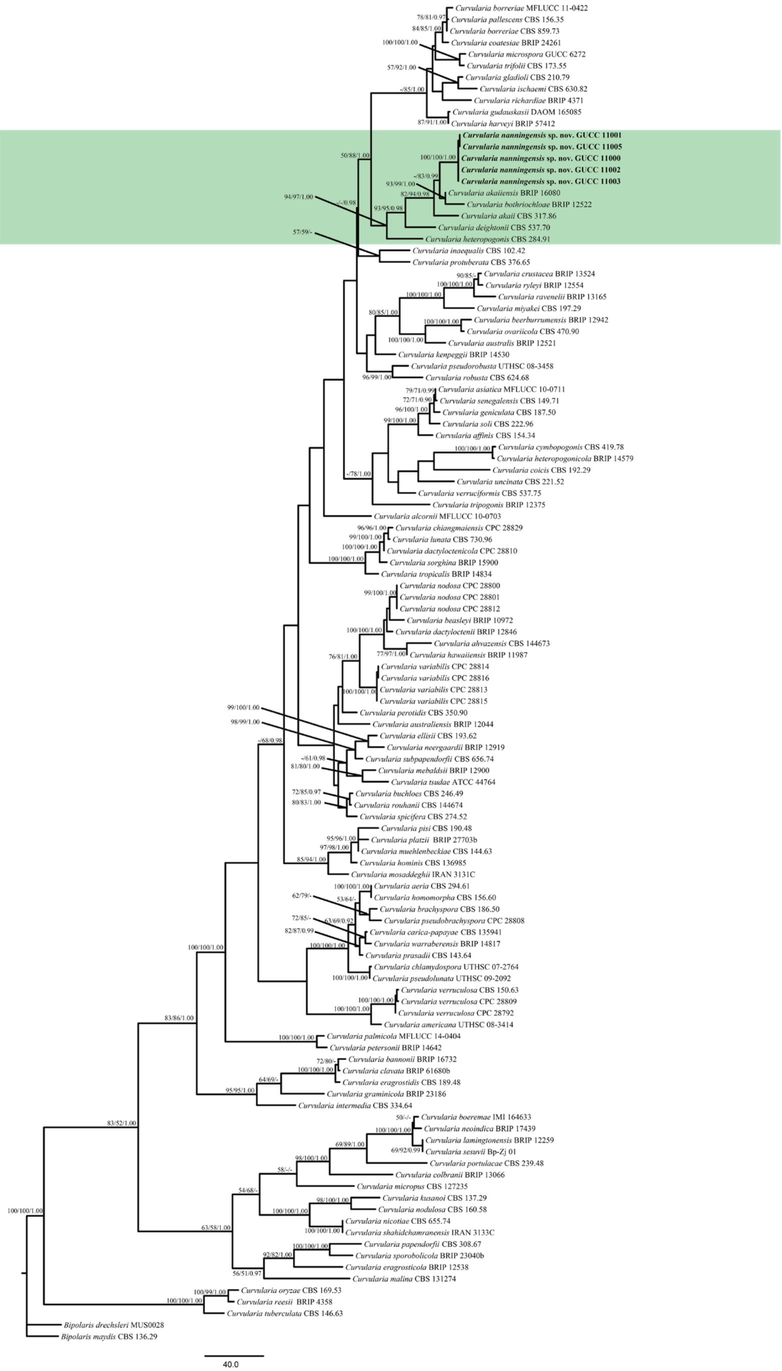

Figure 1. Maximum Parsimony (MP) topology of *Curvularia* generated from a combination of ITS, GAPDH and *tef*1 sequences. *Bipolaris maydis* (CBS 136.29) and *B. drechsleri* (MUS0028) were used as outgroup taxa. MP and ML above 50% and BPP values above 0.90 were placed close to topological nodes and separated by "/". The bootstrap values below 50% and BPP values below 0.90 were labelled with "-". Our main research clade was labelled with green colour.

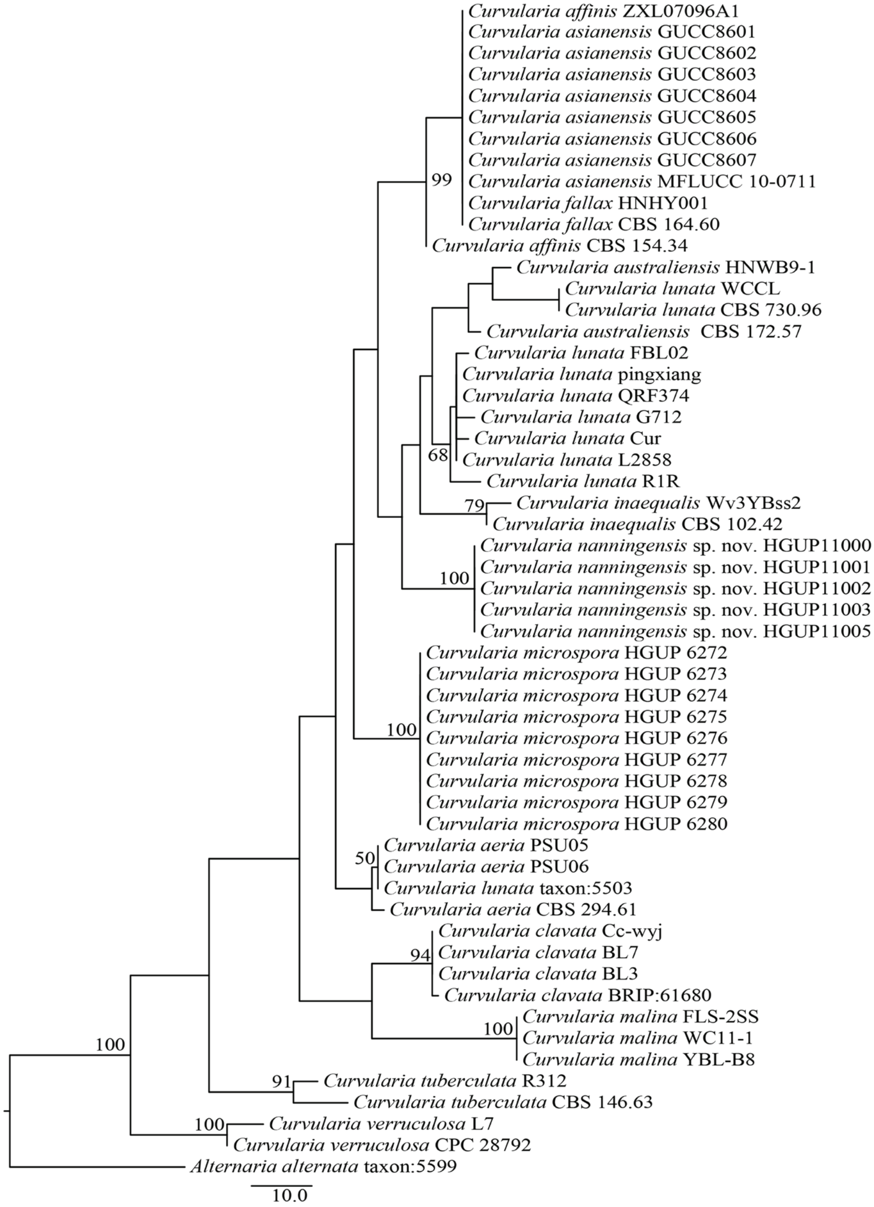

Figure 2. Maximum Parsimony (MP) analysis of *Curvularia* pathogens in China, India and Pakistan based on ITS sequences. *Alternaria alternata* (taxon:5599) was used as outgroup taxon. Bootstrap values (≥ 50%) of the MP method are shown near the nodes.

evolutionary rate than ITS and *tef*1 and therefore some mycologists have suggested the use of ITS+GAPDH for phylogenetic analysis and GAPDH as a secondary barcode marker for accurate identification.

The alignment of *Curvularia* combining three gene fragments (ITS, GAPDH and *tef*1) comprised 116 strains belonging to 104 taxa. In order to accurately identify our strains, phylogenetic analysis included all ex-type and published strains of all *Curvularia* spp. described recently (Hyde et al. 2017; Marin-Felix et al. 2017; Dehdari et al. 2018; Heidari et al. 2018; Hernández-Restrepo et al. 2018; Mehrabi-Koushki et al. 2018; Tan et al. 2018; Jayawardena et al. 2019) which are listed in Table 1. The final alignment comprised 2032 characters (each gene fragment was separated with 2 "N") including gaps (ITS: 1–600, GAPDH: 603–1162 and tef1: 1165–2032). Among these characters, 2032 are constant, 125 variable characters are parsimony-uninformative and 503 are parsimony-informative. The parameters of the phylogenetic trees are TL = 2590, CI = 0.38, RI = 0.72 and HI = 0.62. In the *Curvularia* phylogenetic tree (Figure 1), all isolates grouped together with 100% (MP and ML) bootstrap support. Our strains (GUCC 11000, 11001, 11002, 11003 and 11005) formed a strongly supported group (MP: 100%; ML: 100%; BPP: 1.00) with a close relationship to *C. akaii*, *C. akaiiensis*, *C. bothriochloae*, *C. deightonii* and *C. heteropogonis* with high bootstrap support (MP: 94%; ML: 97%; BPP: 1.00). In this group, the five examined strains were closer to *C. akaii*, *C. akaiiensis* and *C. bothriochloae* and also showed high bootstrap support (MP: 82% and ML: 94%; BPP: 0.98).

The phylogenetic analysis of the ITS gene region evaluated all new *Curvularia* pathogens recently described from China, India and Pakistan. The aligned matrix consisted of fifty-four ITS sequences and included ex-type sequences of 13 *Curvularia* species (Supplementary Table 1). The phylogenetic tree (Figure 2) indicated that ITS BLAST searches only provided limited value for pathogenic identification. In *Curvularia lunata*, only one sequence WCCL (MG063428) showed a very close relationship with the ex-type strain sequence of *C. lunata* CBS 730.96 (MG722981). The other eight sequences were grouped into two branches, e.g. taxon:5503 (LN879926) which might belong to *C. aeria,* while the other seven formed an independent lineage. ITS sequences did not separate *Curvularia affinis*, *C. asianensis* and *C. fallax* and some of their sequences even clustered with *C. australiensis* HNWB9-1 (KT719300). After multi-gene analysis, the phylogenetic distance was shown to be unreliable and may suggest whether they belong perhaps to different species.

Taxonomy

Curvularia nanningensis **Qian Zhang, K.D. Hyde & Yong Wang bis, sp. nov.**

MycoBank No: 829056
Facesoffungi number: FoF 05596
Figure 3A–I

Diagnosis. Characterised by the size of conidia.

Type. China, Guangxi Province, Nanning City, Guangxi Medicinal Botanical Garden, 22°51'N, 108°19'E, on blighted leaves of *Cymbopogon citratus*, 30 Septem-

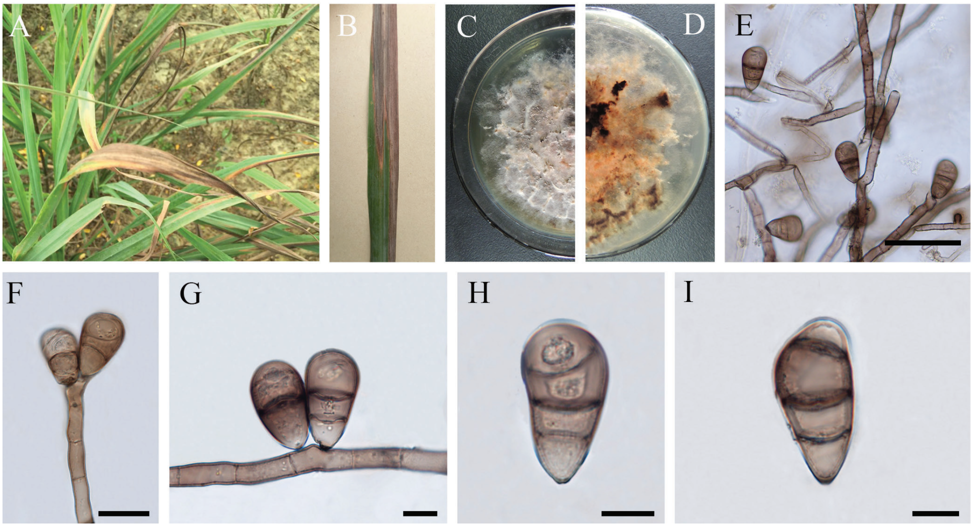

Figure 3. *Curvularia nanningensis* (GUCC11005, holotype) **A**, **B** diseased symptom **C** colony on PDA from above **D** colony on PDA from below **E**–**G** conidia and conidiophores **H**–**I** conidia. Scale bars: 50 µm (**E**), 20 µm (**F**), 10 µm (**G**–**I**).

ber 2017, Q. Zhang, ZQ0091 (HGUP 11005, holotype, MFLU19-1227, isotype), GUCC 11005 and MFLUCC 19-0092, ex-type.

Description. Pathogenic on *Cymbopogon citratus*. Fungus initially producing white to grey lesions with dark borders on all parts of the shoot, later enlarging and coalescing over entire leaf.

Colonies on PDA irregularly circular, with mycelial growth rate = 1.0 cm/day, vegetative hyphae septate, branched, subhyaline to brown, smooth to verruculose, 2–3 µm, anastomosing. *Aerial mycelium* dense, felted, initially pale grey, becoming darkened and greyish-green at maturity, producing black extracellular pigments. On MEA, the colony morphology similar to PDA, with growth rate = 1.35 cm/day. **Sexual morph**: Undetermined. **Asexual morph**: Hyphomycetous. *Conidiophores* macronematous, arising singly, simple or branched, flexuous, 8–10 septate, geniculate, pale brown to dark brown, paler towards apex, 120–200 × 2–3 µm (av. = 170 × 2.5 µm, n = 30). *Conidiogenous cells* polytretic, sympodial, terminal, sometimes intercalary, cicatrised, with thickened and darkened conidiogenous loci up to 1.0–1.2 µm diam., smooth. *Mature conidia* 3 to rarely 4 septa, acropleurogenous, obovoid, usually straight to curved at the slightly wider, smooth-walled, larger third cell from the base, 24.5–36.0 × 14.0–20.5 µm (av. = 29.5 × 17.5 µm, n = 50), sub-hyaline to pale brown end cells, pale brown to dark brown at intermediate cells, with conspicuous or sometimes slightly protuberant hilum. Germination of conidia bipolar.

Distribution. China, Guangxi Province, Nanning City.

Other material examined. China, Guangxi Province, Nanning city, Guangxi Medicinal Botanical Garden, on blight leaves of *C. citratus*, 30 September 2017,

Q. Zhang, ZQ0087 (HGUP 11000); ZQ0088 (HGUP 11001); ZQ0089 (HGUP 11002); ZQ0090, (HGUP 11003).

Etymology. With reference to the location, Nanning City where the fungus was isolated.

Pathogenicity test

Four days after inoculation, blast symptoms appeared on all inoculated plants, which were similar to symptoms of plants in the field (Figures 3A, B, 4A, B). Non-treated control plants remained healthy without any symptoms (Figure 4C). *Curvularia nanningensis* was re-isolated from the lesions of inoculated plants and the identity of the fungus was confirmed by sequencing the ITS region. Meanwhile, a detached leaf-experiment was also conducted in an illuminated incubator at 28 ± 3°C, where similar symptoms appeared on healthy inoculated leaves of *Cymbopogon citratus* after four days (Figure 4 D right), while the control leaf (Figure 4 D left) did not show symptoms.

Discussion

Phylogenetic analysis based on combined DNA sequences of ITS, GAPDH and *tef*1 showed that our strains were related to three *Curvularia* species named *C. akaii* (Tsuda & Ueyama) Sivan., *C. akaiiensis* Sivan. and *C. bothriochloae* Sivan., Alcorn & R.G. Shivas. The main morphological characters that discriminate our strains from related species are the size-range of conidia and length of conidiophores. *Curvularia bothriochloae* produced conidia measuring 30–47 × 15–25 µm (Sivanesan et al. 2003) while *C. akaiiensis* produced the smallest conidia (22.5–27.5 × 7.5–15.5 µm). Conidial length of *C. nanningensis* was very close to *C. akaii* (24–34 µm) (Tsuda and Ueyama 1985) but the conidia of our species were broader than those of *C. akaii* (8.7–13.8 µm). Conidiophores of *C. nanningensis* were shorter than those of *C. bothriochloae* (360–425 µm) (Alcorn 1990). In the case of *C. sichuanensis* Meng Zhang & T.Y. Zhang, only one ITS sequence AB453881 was available in GenBank for analysis. While examining our sequences, only 4–5 bp differences were revealed in 499 bp characters between *C. nanningensis* and *C. sichuanensis,* thus indicating a close relationship between the two strains based on ITS sequence data and likely between the two species. However, according to Zhang et al. (2007), the conidial width of *C. sichuanensis* (10–15 µm) is smaller than *C. nanningensis* (14–20.5 µm) on PDA. For *C. sichuanensis*, the conidial wall of the median cell is deepened and thickened while *C. nanningensis* obviously does not have these characters. Meanwhile, the hilum of conidia in *C. sichuanensis* is obviously protuberant while *C. nanningensis* lacked this character.

The pathogenicity test based on natural inoculation and detached leaves (Figure 3) confirmed that *Curvularia nanningensis* is a pathogen of *Cymbopogon citratus* blast disease. We previously named our strains as *C. cymbopogonis* following a previous report of the species by Groves and Skolko (1945) as a seed-borne pathogen of *Cymbopogon*

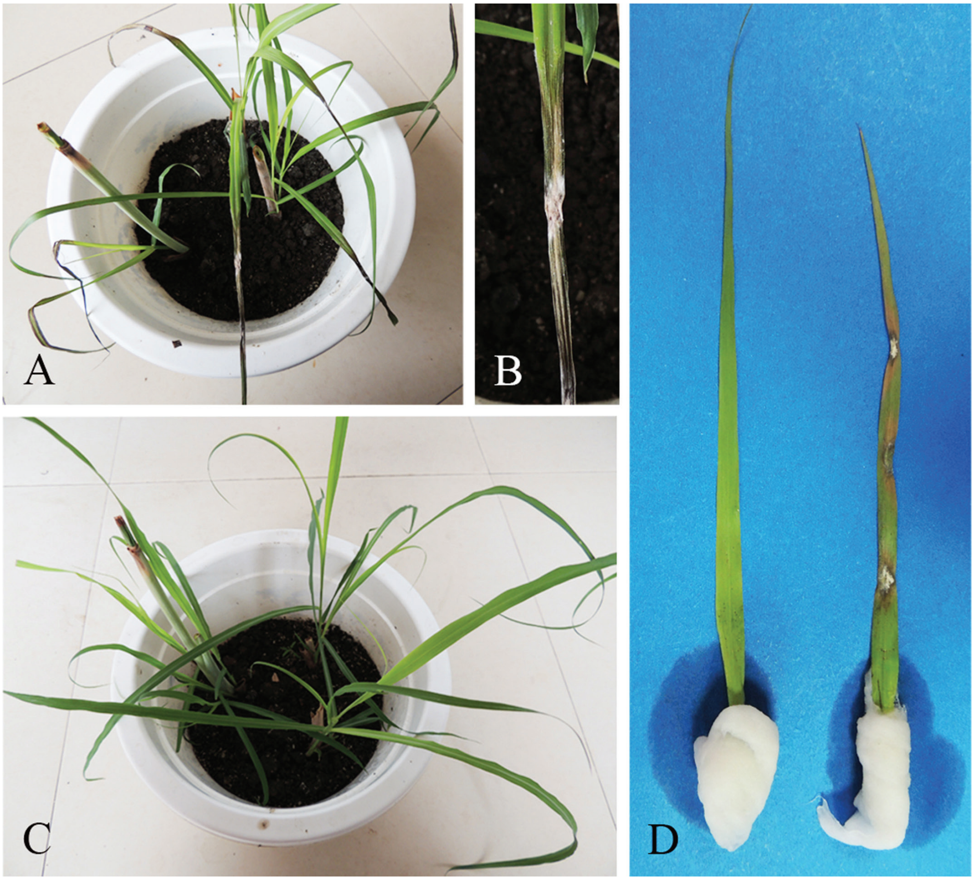

Figure 4. Pathogen inoculation and symptom (4 days). **A** *Cymbopogon citratus* inoculated and disease symptom **B** inoculation point and disease symptom **C** control **D** detached experiment. Left. Control. Right. Inoculation point and disease symptoms.

nardus. *Curvularia cymbopogonis* is a common pathogen which also causes diseases of sugar-cane, rice, seedlings of itchgrass, *Agrostis palustris* Huds. and *Dactylis glomerata* L. (Santamaria et al. 1971; Walker and White 1979; Olufolaji 1996; Yi et al. 2002). A single strain named *C. cymbopogonis* (CBS 419.78) included in our analyses grouped distant from *C. nanningensis* but its reliability seems questionable and apparently belongs to a different species (Fig. 1). We further checked the original description of this species (Groves and Skolko 1945) and found that differences in conidial shape mainly resulted from conidial width (*C. cymbopogonis*: 11–13 µm vs *C. nanningensis*: 14–20.5 µm). Additionally, Groves and Skolko (1945), Hall and Sivanesan (1972) and Yi et al. (2002) reported that *C. cymbopogonis* produced 4 to 5-septate conidia, whereas conidia of *C. nanningensis* only had 3-septa. *Curvularia* spp. are important pathogens of lemongrass. Morphological studies together with phylogenetic analyses provided evidence that *C. nanningensis* is a new pathogen distinct from all hitherto reported diseases on lemongrass. Our findings expanded the documented diversity of *Cymbopogon* pathogens within the genus *Curvularia* and further clarified the taxonomy of this novel pathogen, *Curvularia nanningensis*.

Moreover, 29 first reports of *Curvularia* diseases on different plants in China, India and Pakistan were found in the literature from 2010 to the present. It is evident that in this vast geographical area, *Curvularia* spp. have maintained a close association with plant diversity and thereby possess a rich fungal diversity that is affected by crops distribution. Among them, six reports only provided morphological data and more than half (16) only referred to ITS sequence data and morphological description (Suppl. Table 1). For unknown reasons, Iftikhar et al. (2016) misidentified the *Curvularia* pathogen with an *Alternaria* sequence (LN879930.1). Our phylogenetic tree, based on 54 reported ITS sequence data of *Curvularia* diseases in these countries (Figure 2), also indicated that this approach is not effective for identifying these pathogens, especially in the case of *C. lunata* as a prevalent species. However, identification of *Curvularia* isolates by multi-gene phylogenetic analyses has withstood scrutiny (Liang et al. 2018; Wang et al. 2018; Zhang et al. 2018). Additionally, nearly all reports, even for severe diseases, are based on a single isolate, which preclude an objective evaluation. We, therefore, propose the following standardised steps as required for the reliable identification of *Curvularia* diseases: 1) collect several isolates from diseased samples, 2) obtain sequences of the ITS, GAPDH and *tef*1 or at least ITS+GAPDH for phylogenetic analysis, 3) perform BLAST searches with sequences originated from ex-type or representative strains in GenBank, and 4) combine morphological comparison and phylogenetic analysis for accurate identification.

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Supplementary material 1

Table S1. Disease occurrence caused by *Curvularia* spp. in China, India and Pakistan

Authors: Qian Zhang, Zai-Fu Yang, Wei Cheng, Nalin N. Wijayawardene, Kevin D. Hyde, Zhuo Chen, Yong Wang

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The genus *Melanconis* (Diaporthales)

Walter M. Jaklitsch[1,2], Hermann Voglmayr[1,2]

1 *Institute of Forest Entomology, Forest Pathology and Forest Protection, Department of Forest and Soil Sciences, BOKU-University of Natural Resources and Life Sciences, Franz Schwackhöfer Haus, Peter-Jordan-Straße 82/I, 1190 Vienna, Austria* **2** *Division of Systematic and Evolutionary Botany, Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Wien, Austria*

Corresponding author: *Walter M. Jaklitsch* (walter.jaklitsch@univie.ac.at)

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Abstract

The genus *Melanconis* (Melanconidaceae, Diaporthales) in the strict sense is here re-evaluated regarding phylogenetic structure, taxonomy, distribution and ecology. Using a matrix of sequences from ITS, LSU, *ms204*, *rpb2*, *tef1* and *tub2*, eight species are recognised and their phylogenetic positions are determined. Based on phylogenetic, morphological and geographical differentiation, *Melanconis marginalis* is subdivided into four subspecies. *Melanconis italica* is reduced to a subspecies of *Melanconis marginalis*. The two species *Melanconis larissae* from *Betula* sp. and *M. pacifica* from *Alnus rubra* are described as new. *Melanconis alni* and *M. stilbostoma* are lectotypified and *M. alni*, *M. marginalis* and *M. stilbostoma* are epitypified. All GenBank sequences deposited as *Melanconis alni* are shown to actually represent *M. marginalis* and those as *M. marginalis* belong to the newly described *M. pacifica*. Currently, *Alnus* and *Betula* are the sole host genera of *Melanconis*. All species and subspecies are (re-)described and illustrated. In addition, the neotypification of *Melanconium pterocaryae* is here validated.

Keywords

Juglanconis, *Melanconiella*, *Melanconium*, multigene phylogeny, pyrenomycetes, systematics, 1 new combination, 2 new species

Introduction

Melanconis, the type genus of the family Melanconidaceae (Diaporthales), was originally described by Tulasne (1856) with *M. stilbostoma* as its generic type, but without a generic diagnosis. His inclusion of species like *M. spodiaea* made the genus heterogeneous from the beginning. Since then, many species names have been erected in the genus. In his generic revision, Wehmeyer (1941) treated the genus in a very wide sense, organising the species in subgenera and sections, which themselves were heterogeneous, containing species of genera like *Chapeckia*, *Coryneum* (*Pseudovalsa*), *Macrodiaporthe*, *Massariovalsa*, *Melanconiella* or *Pseudovalsella*. Barr (1978) accepted *Melanconis* roughly in the sense of Wehmeyer´s subgenus *Eumelanconis*, which included *Melanconiella*. In this sense, the genus *Melanconis* was one of many genera of the large family Melanconidaceae and was defined by a distinct ectostromatic disc, a more or less well-developed entostroma, two-celled hyaline or brown ascospores with or without appendages, in combination with melanconium- or discosporium-like asexual morphs (Barr 1978). The first phylogenetic analyses of the Diaporthales (Castlebury et al. 2002; see also Jaklitsch et al. 2016, Senanayake et al. 2018), however, suggested that Melanconidaceae should be confined to its type genus *Melanconis* with a restricted number of species. This phylogenetic generic concept corresponds, apart from a few exceptions, with Wehmeyer's (1941) section Stilbostomae of his subgenus *Eumelanconis*. Subsequently, many names have been combined in other genera in various families following morphological and/or phylogenetic analyses (Barr 1978; Jaklitsch and Voglmayr 2004; Voglmayr and Jaklitsch 2008; De Silva et al. 2009). *Melanconiella* was extensively studied by Voglmayr et al. (2012), who determined that species of *Melanconis* cause more conspicuous bumps in the host bark than those of *Melanconiella* and form light-coloured, white or yellowish ectostromatic discs. Wehmeyer (1941) had used this trait to distinguish his section Stilbostomae from his Chrysostromae, which are characterised by dark coloured discs. Although light coloured discs are not uncommon in *Melanconiella*, Wehmeyer's (1941) section Chrysostromae of his subgenus *Eumelanconis* basically matches the phylogenetically conceived genus *Melanconiella*, except for a few species, which belong elsewhere. For some of these species, the new genus *Juglanconis* was established in the new family Juglanconidaceae (Voglmayr et al. 2017, 2019). Two other species were segregated from *Melanconis* to *Alnecium* and *Phaeodiaporthe* by Voglmayr and Jaklitsch (2014). Voglmayr et al. (2012) found an unexpectedly high species diversity in *Melanconiella*, particularly on *Carpinus* spp. and showed that its species either have a melanconium- or a discosporina-like asexual morph, but never both morph types. They gave also information of taxonomic placement of other *Melanconis* spp. Here we treat the residual species of *Melanconis* in the strict sense.

Materials and methods

Sample sources

All isolates included in this study originated from ascospores or conidia of freshly collected specimens derived from recently dead branches or twigs. Details of the strains including NCBI GenBank accession numbers of gene sequences used to compute the phylogenetic trees are listed in Table 1. Strain acronyms, other than those of official culture collections, are used here primarily as strain identifiers throughout the work. Representative isolates have been deposited at the Westerdijk Fungal Biodiversity Centre (CBS-KNAW), Utrecht, The Netherlands. Details of the specimens, used for morphological investigations, are listed in the Taxonomy section under the respective descriptions. Herbarium acronyms are according to Thiers (2019). Freshly collected specimens have been deposited in the Fungarium of the Department of Botany and Biodiversity Research, University of Vienna (WU) and in the Fungarium of the Natural History Museum of Vienna (W).

Morphology

Microscopic observations were made in tap water, except where noted. Morphological analyses of microscopic characters were carried out as described by Jaklitsch (2009). Methods of microscopy included stereomicroscopy using a Nikon SMZ 1500 and Nomarski differential interference contrast (DIC), using the compound microscopes Nikon Eclipse E600 or Zeiss Axio Imager.A1 equipped with a Zeiss Axiocam 506 colour digital camera. Images and data were gathered using a Nikon Coolpix 4500 or a Nikon DS-U2 digital camera and measured by using the NIS-Elements D v. 3.0 or 3.22.15 or Zeiss ZEN Blue Edition software packages. For certain images of ascomata, the stacking software Zerene Stacker v. 1.04 (Zerene Systems LLC, Richland, WA, USA) was used. Measurements are reported as maxima and minima in parentheses and the range representing the mean plus and minus the standard deviation of the number of measurements given in parentheses.

Culture preparation, DNA extraction, PCR and sequencing

Ascospore isolates were prepared and grown on 2% corn meal dextrose agar (CMD; CMA: Sigma, St Louis, Missouri; supplemented with 2% (w/v) D(+)-glucosemonohydrate) or 2% malt extract agar (MEA; 2% w/v malt extract, 2% w/v agar-agar; Merck, Darmstadt, Germany). Growth of liquid cultures and extraction of genomic DNA was performed as reported previously (Voglmayr and Jaklitsch 2011; Jaklitsch et al. 2012) using the DNeasy Plant Mini Kit (QIAgen GmbH, Hilden, Germany). The following loci were amplified and sequenced: a ca. 1.6 kb fragment containing the terminal part of the small subunit nuclear ribosomal DNA (nSSU rDNA), the complete internal transcribed spacer region (ITS1-5.8S-ITS2) and a ca. 900 bp fragment of the large subunit nuclear ribosomal DNA (nLSU rDNA), amplified and sequenced as a single fragment with primers V9G (De Hoog and Gerrits van den Ende 1998) and LR5 (Vilgalys and Hester 1990); a ca. 1 kb fragment of the guanine nucleotide-binding protein subunit beta (*ms204*) gene with primers MS-E1F1 and MS-E5R1 (Walker et al. 2012); a ca. 1.2 kb fragment of the RNA polymerase II subunit 2 (*rpb2*) gene with primers fRPB2-5F and fRPB2-7cR (Liu et al. 1999) or dRPB2-5f and dRPB2-7r (Voglmayr et al. 2016); and a ca. 1.3–1.5 kb fragment of the translation elongation factor 1-alpha (*tef1*) gene with primers EF1-728F (Carbone and Kohn 1999) and TEF1LLErev (Jaklitsch et al. 2005). For the β-tubulin (*tub2*) gene, either a ca. 0.45 kb fragment was amplified with primers T1 (O'Donnell and Cigelnik 1997) and BtHV2r (Voglmayr et al. 2016) or a ca. 1.6 kb fragment with primer pairs T1 and T22 (O'Donnell and Cigelnik 1997) or T1D and T22D (Voglmayr et al. 2019).

Table 1. Isolates and accession numbers of sequences used in the phylogenetic analyses.

Taxon	Strain[1]	Origin	Host	GenBank accession no.[2]					
				ITS	LSU	*ms204*	*rpb2*	*tef1*	*tub2*
Juglanconis appendiculata	MC	Greece	*Juglans regia*	KY427141	KY427141	KY427159	KY427191	KY427210	KY427227
Juglanconis japonica	MAFF 410079 = ME20*	Japan	*Pterocarya rhoifolia*	KY427155	KY427155	KY427172	KY427205	KY427224	KY427240
Juglanconis juglandina	CBS 133343 = ME22	Austria	*Juglans regia*	KY427149	KY427149	KY427166	KY427199	KY427218	KY427234
Juglanconis oblonga	CBS 133344 = ME14	USA	*Juglans cinerea*	KY427151	KY427151	KY427168	KY427201	KY427220	KY427236
Juglanconis pterocaryae	CBS 144326 = D272*	Austria	*Pterocarya fraxinifolia*	MK229175	MK229175	MK238314	MK238324	MK238332	MK238338
Melanconis alni	CBS 131693 = MAMI	Austria	*Alnus glutinosa*	**MN784962**	**MN784962**	**MN780721**	**MN780745**	**MN780774**	**MN780803**
	CBS 131695 = MAW* (from ascospores)	Austria	*Alnus glutinosa*	**MN784963**	**MN784963**	**MN780722**	**MN780746**	**MN780775**	**MN780804**
	MEW*(from conidia)	Austria	*Alnus glutinosa*	**MN784964**	**MN784964**	**MN780723**	**MN780747**	**MN780776**	**MN780805**
	MAIV	France	*Alnus incana*	**MN784965**	**MN784965**	**MN780724**	**MN780748**	**MN780777**	**MN780806**
	D156	Poland	*Alnus glutinosa*	**MN784966**	**MN784966**	**MN780725**	**MN780749**	**MN780778**	**MN780807**
Melanconis betulae	CFCC 50471*	China	*Betula albosinensis*	KT732952	KT732971	–	KT732984	KT733001	KT733022
	CFCC 50472	China	*Betula albosinensis*	KT732953	KT732972	–	KT732985	KT733002	KT733023
	CFCC 50473	China	*Betula albosinensis*	KT732954	KT732973	–	KT732986	KT733003	KT733024
Melanconis groenlandica	CBS 116450 = UPSC 3407*	Denmark (Greenland)	*Betula nana*	KU878552	KU878553	–	–	KU878554	KU878555
	MAFF 410219 = M4-2 = ME1	Japan	*Betula maximowicziana*	**MN784967**	**MN784967**	**MN780726**	**MN780750**	**MN780779**	**MN780808**
	CBS 133341 = LCM191.01 = ME10	USA	*Betula papyrifera*	**MN784968**	**MN784968**	**MN780727**	**MN780751**	**MN780780**	**MN780809**
	CBS 133339 = LCM 02.02 = ME13	USA	*Betula* sp.	**MN784969**	**MN784969**	**MN780728**	**MN780752**	**MN780781**	**MN780810**
	CBS 133340 = LCM 185.01	USA	*Betula papyrifera*	**MN784970**	**MN784970**	**MN780729**	**MN780753**	**MN780782**	**MN780811**
Melanconis itoana	MAFF 410080 = LFP-M4-9 = ME8	Japan	*Betula ermanii*	**MN784971**	**MN784971**	**MN780730**	**MN780754**	**MN780783**	**MN780812**
	CFCC 50474	China	*Betula albosinensis*	KT732955	KT732974	–	KT732987	KT733004	KT733025
	CFCC 52876	China	*Betula albosinensis*	MK096324	MK096364	–	MK096409	MK096284	–
	CFCC 52877	China	*Betula albosinensis*	MK096326	MK096366	–	MK096411	MK096286	–
	CFCC 52878	China	*Betula albosinensis*	MK096327	MK096367	–	MK096412	MK096287	–
Melanconis larissae	CBS 123196 = AR 3886 = ME7*	USA	*Betula* sp.	**MN784972**	**MN784972**	**MN780731**	**MN780755**	**MN780784**	**MN780813**
Melanconis marginalis subsp. *europaea*	D157	Austria	*Alnus alnobetula*	**MN784973**	**MN784973**	–	**MN780756**	**MN780785**	–
	D158	Austria	*Alnus alnobetula*	**MN784974**	**MN784974**	**MN780732**	**MN780757**	**MN780786**	**MN780814**
	D257	Austria	*Alnus incana*	**MN784975**	**MN784975**	–	**MN780758**	**MN780787**	**MN780815**
	CBS 131692 = MAI*	Austria	*Alnus incana*	**MN784976**	**MN784976**	**MN780733**	**MN780759**	**MN780788**	**MN780816**
	CBS 131694 = MAV	Austria	*Alnus alnobetula*	**MN784977**	**MN784977**	**MN780734**	**MN780760**	**MN780789**	**MN780817**
	MAV1	Austria	*Alnus alnobetula*	**MN784978**	**MN784978**	**MN780735**	**MN780761**	**MN780790**	**MN780818**
Melanconis marginalis subsp. *italica*	MFLUCC 16-1199*	Italy	*Alnus cordata*	MF190151	MF190096	–	–	–	–
	MFLUCC 17-1659*	Italy	*Alnus cordata*	MF190152	MF190097	–	MF377602	–	–

Taxon	Strain[1]	Origin	Host	GenBank accession no.[2]					
				ITS	LSU	*ms204*	*rpb2*	*tef1*	*tub2*
Melanconis marginalis subsp. *marginalis*	D321 (from ascospores)*	Canada	*Alnus alnobetula* subsp. *crispa*	**MN784979**	**MN784979**	–	**MN780762**	**MN780791**	**MN780819**
	D321a (from α-conidia)*	Canada	*Alnus alnobetula* subsp. *crispa*	**MN784980**	**MN784980**	–	**MN780763**	**MN780792**	**MN780820**
	D321b (from β-conidia)*	Canada	*Alnus alnobetula* subsp. *crispa*	**MN784981**	**MN784981**	–	**MN780764**	**MN780793**	**MN780821**
	CBS 109496 = AR 3529 = ME2	Russia	*Alnus alnobetula* subsp. *maximowiczii*	**MN784982**	**MN784982**	**MN780736**	**MN780765**	**MN780794**	**MN780822**
	AR 4864 = ME5	USA	*Alnus alnobetula*	**MN784983**	**MN784983**	**MN780737**	**MN780766**	**MN780795**	**MN780823**
	CBS 133346 = AR 4865 = ME6	USA	*Alnus alnobetula*	**MN784984**	**MN784984**	**MN780738**	**MN780767**	**MN780796**	**MN780824**
	MAFF 410218 = M4-6 = ME9	Japan	*Alnus alnobetula* subsp. *maximowiczii*	**MN784985**	**MN784985**	**MN780739**	**MN780768**	**MN780797**	**MN780825**
Melanconis marginalis subsp. *tirolensis*	CBS 122310 = AR 3748 = ME4*	Austria	*Alnus alnobetula*	**MN784986**	**MN784986**	**MN780740**	**MN780769**	**MN780798**	**MN780826**
	D322a	Austria	*Alnus alnobetula*	**MN959458**	**MN959458**	–	**MN989415**	**MN989416**	**MN989417**
Melanconis pacifica	CBS 109744 = AR 3442 = AFTOL-ID 2128	Canada	*Alnus rubra*	EU199197	AF408373	–	DQ862022	DQ862038	EU219103, DQ862038
Melanconis stilbostoma	D143	Poland	*Betula pendula*	KY427156	KY427156	KY427173	KY427206	KY427225	KY427241
	D258	Italy	*Betula aetnensis*	**MN784987**	**MN784987**	–	**MN780770**	**MN780799**	**MN780827**
	CBS 109778 = AR 3501 = AFTOL-ID 936 = ME11*	Austria	*Betula pendula*	**MN784988**	**MN784988**	**MN780741**	**MN780771**	**MN780800**	**MN780828**
	MAFF 410225 = M3-9 = ME12	Japan	*Betula platyphylla* var. *japonica*	**MN784989**	**MN784989**	**MN780742**	**MN780772**	**MN780801**	**MN780829**
	CBS 121894 = MS	Austria	*Betula pendula*	KY427156	KY427156	**MN780743**	JQ926302	JQ926368	**MN780830**
	CBS 133338 = DMW 514.3	USA	*Betula papyrifera*	**MN784990**	**MN784990**	**MN780744**	**MN780773**	**MN780802**	**MN780831**
	CFCC 50475	China	*Betula platyphylla*	KT732956	KT732975	–	KT732988	KT733005	KT733026
	CFCC 50476	China	*Betula platyphylla*	KT732957	KT732976	–	KT732989	KT733006	KT733027
	CFCC 50477	China	*Betula platyphylla*	KT732958	KT732977	–	KT732990	KT733007	KT733028
	CFCC 50478	China	*Betula platyphylla*	KT732959	KT732978	–	KT732991	KT733008	KT733029
	CFCC 50479	China	*Betula platyphylla*	KT732960	KT732979	–	KT732992	KT733009	KT733030
	CFCC 50480	China	*Betula platyphylla*	KT732961	KT732980	–	KT732993	KT733010	KT733031
	CFCC 50481	China	*Betula platyphylla*	KT732962	KT732981	–	KT732994	KT733011	KT733032
	CFCC 50482	China	*Betula platyphylla*	KT732963	KT732982	–	KT732995	KT733012	KT733033
	CFCC 50483	China	*Betula platyphylla*	KT732964	KT732983	–	KT732996	KT733013	KT733034
	CFCC 52843	China	*Betula platyphylla*	MK096338	MK096378	–	MK096423	MK096298	–
	CFCC 52844	China	*Betula platyphylla*	MK096341	MK096381	–	MK096426	MK096301	–
	CFCC 52845	China	*Betula platyphylla*	MK096343	MK096383	–	MK096428	MK096303	–

Taxon	Strain[1]	Origin	Host	GenBank accession no.[2]					
				ITS	LSU	***ms204***	***rpb2***	***tef1***	***tub2***
Melanconis stilbostoma	CFCC 52846	China	*Betula platyphylla*	MK096347	MK096387	–	MK096432	MK096307	–
	CFCC 52847	China	*Betula platyphylla*	MK096348	MK096388	–	MK096433	MK096308	–
	CFCC 52848	China	*Betula platyphylla*	MK096349	MK096389	–	MK096434	MK096309	–
	CFCC 52849	China	*Betula platyphylla*	MK096328	MK096368	–	MK096413	MK096288	–
	CFCC 52850	China	*Betula platyphylla*	MK096329	MK096369	–	MK096414	MK096289	–
	CFCC 52851	China	*Betula platyphylla*	MK096330	MK096370	–	MK096415	MK096290	–
	CFCC 52852	China	*Betula platyphylla*	MK096331	MK096371	–	MK096416	MK096291	–
	CFCC 52853	China	*Betula platyphylla*	MK096332	MK096372	–	MK096417	MK096292	–
	CFCC 52854	China	*Betula platyphylla*	MK096333	MK096373	–	MK096418	MK096293	–
	CFCC 52855	China	*Betula platyphylla*	MK096334	MK096374	–	MK096419	MK096294	–
	CFCC 52856	China	*Betula platyphylla*	MK096335	MK096375	–	MK096420	MK096295	–
	CFCC 52857	China	*Betula platyphylla*	MK096336	MK096376	–	MK096421	MK096296	–
	CFCC 52858	China	*Betula platyphylla*	MK096337	MK096377	–	MK096422	MK096297	–
	CFCC 52859	China	*Betula platyphylla*	MK096339	MK096379	–	MK096424	MK096299	–
	CFCC 52860	China	*Betula platyphylla*	MK096340	MK096380	–	MK096425	MK096300	–
	CFCC 52861	China	*Betula platyphylla*	MK096342	MK096382	–	MK096427	MK096302	–
	CFCC 52862	China	*Betula platyphylla*	MK096344	MK096384	–	MK096429	MK096304	–
	CFCC 52863	China	*Betula platyphylla*	MK096345	MK096385	–	MK096430	MK096305	–
	CFCC 52864	China	*Betula platyphylla*	MK096346	MK096386	–	MK096431	MK096306	–
	CFCC 52865	China	*Betula platyphylla*	MK096316	MK096356	–	MK096401	MK096276	–
	CFCC 52866	China	*Betula platyphylla*	MK096317	MK096357	–	MK096402	MK096277	–
	CFCC 52867	China	*Betula platyphylla*	MK096318	MK096358	–	MK096403	MK096278	–
	CFCC 52868	China	*Betula platyphylla*	MK096319	MK096359	–	MK096404	MK096279	–
	CFCC 52869	China	*Betula platyphylla*	MK096320	MK096360	–	MK096405	MK096280	–
	CFCC 52870	China	*Betula platyphylla*	MK096321	MK096361	–	MK096406	MK096281	–
	CFCC 52871	China	*Betula platyphylla*	MK096322	MK096362	–	MK096407	MK096282	–
	CFCC 52872	China	*Betula platyphylla*	MK096323	MK096363	–	MK096408	MK096283	–
	CFCC 52873	China	*Betula platyphylla*	MK096350	MK096390	–	MK096435	MK096310	–
	CFCC 52874	China	*Betula platyphylla*	MK096351	MK096391	–	MK096436	MK096311	–
	CFCC 52875	China	*Betula platyphylla*	MK096325	MK096365	–	MK096410	MK096285	–

[1] Ex-type strains marked by an asterisk; [2] Sequences in bold were generated in the present study

PCR products were purified using an enzymatic PCR cleanup (Werle et al. 1994), as described in Voglmayr and Jaklitsch (2008). DNA was cycle-sequenced using the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit v. 3.1 (Applied Biosystems, Warrington, UK) and the PCR primers; in addition, primers ITS4 (White et al. 1990), LR2R-A (Voglmayr et al. 2012) and LR3 (Vilgalys and Hester 1990) were used for the SSU-ITS-LSU region, TEF1_INTF (forward, Jaklitsch 2009) and TEFD_iR1 (reverse, Jaklitsch and Voglmayr 2019) or TEF1_INT2 (reverse, Voglmayr and Jaklitsch 2017) for *tef1* and BtHVf (Voglmayr and Mehrabi 2018) and BtHV2r for the long fragment of *tub2*. Sequencing was performed on an automated DNA sequencer (3730xl Genetic Analyzer, Applied Biosystems).

Phylogenetic analyses

The newly generated sequences were aligned with the *Melanconis* sequences of Fan et al. (2016, 2018) and a few additional GenBank sequences. Species of *Juglanconis* were selected as outgroup (Voglmayr et al. 2017, 2019); the GenBank accession numbers of the sequences, used in the phylogenetic analyses, are given in Table 1. All alignments were produced with the server version of MAFFT (www.ebi.ac.uk/Tools/mafft), checked and refined using BioEdit v. 7.2.6 (Hall 1999). For phylogenetic analyses, all sequence alignments (ITS, LSU, *ms204*, *rpb2*, *tef1* and *tub2*) were combined.

Maximum Likelihood (ML) analyses were performed with RAxML (Stamatakis 2006) as implemented in raxmlGUI 1.3 (Silvestro and Michalak 2012), using the ML + rapid bootstrap setting and the GTRGAMMA substitution model with 1000 bootstrap replicates. The matrix was partitioned for the different gene regions and substitution model parameters were calculated separately for them.

Maximum Parsimony (MP) analyses were performed with PAUP v. 4.0a166 (Swofford 2002). All molecular characters were unordered and given equal weight; analyses were performed with gaps treated as missing data; the COLLAPSE command was set to MINBRLEN. MP analysis of the combined multilocus matrix was done, using a parsimony ratchet approach. For this, a nexus file was prepared using PRAP v. 2.0b3 (Müller 2004), implementing 10000 ratchet replicates with 25% of randomly chosen positions upweighted to 2, which were then run with PAUP. MP bootstrap analyses were performed with 1000 replicates, using 5 rounds of random sequence addition and subsequent TBR branch swapping (MULTREES option in effect, steepest descent option not in effect) during each bootstrap replicate, with each replicate limited to 100000 rearrangements.

In the Results and Discussion sections, bootstrap values (BS) below 70% are considered low, between 70–90% medium and above 90% high.

Results

Revision of *Melanconis* sequences deposited in GenBank

Comparison of our sequences with GenBank sequences revealed that all accessions of *Melanconis alni* and *M. marginalis*, deposited in GenBank, were misidentified. All GenBank accessions of *M. alni* were shown to actually represent *M. marginalis*, while the single isolate of *M. marginalis* turned out to be a new species, described as *M. pacifica* below. These misidentifications were also confirmed by morphological re-investigation of specimens from which these sequences were generated.

Phylogenetic analyses

Of the 6052 characters included in the combined multilocus analyses, 925 were parsimony informative (133 from ITS-LSU, 142 from *ms204*, 214 from *rpb2*, 245 from *tef1* and 191 from *tub2*). The best ML tree (lnL = −18240.558) revealed by RAxML is shown as Fig. 1. The MP analysis revealed 3394 MP trees 1647 steps long, which were identical except for some differences within species and a polytomy at the *M. groenlandica-M. larissae-M.stilbostoma* node (not shown). Tree topology of the MP strict consensus tree was compatible with the ML tree, except for a sister group relationship of *M. marginalis* subsp. *europaea* and *M. marginalis* subsp. *marginalis* and some minor topological differences within species and subspecies (not shown).

All species of *Melanconis* received high (*M. itoana*, *M. groenlandica*) to maximum (*M. alni*, *M. betulae*, *M. marginalis*, *M. stilbostoma*) support in both analyses (Fig. 1). Sister group relationship of *M. alni* and *M. pacifica* and monophyly of the three betulicolous species *M. groenlandica*, *M. larissae* and *M. stilbostoma* received maximum support as well. Within *Melanconis marginalis*, two main subclades were evident with ML and MP BS above 85%, one containing accessions from eastern Canada, Alaska, Japan and the Russian Far East and another with accessions from Central Europe; in addition to these two main subclades, the *Melanconis marginalis* clade contained two deviating lineages, an Italian collection from ?*Alnus cordata* described as *M. italica* by Senanayake et al. (2017) and two accessions from eastern Tyrol from *Alnus alnobetula*. In light of this geographical differentiation, a substantial genetic variability within these clades (Fig. 1) and minor morphological differences, these four lineages are formally recognised on the subspecies level.

Culture characteristics

Culture images of seven studied *Melanconis* species, grown on MEA and CMD, are illustrated in Figure 2. Culture descriptions are given under the respective species.

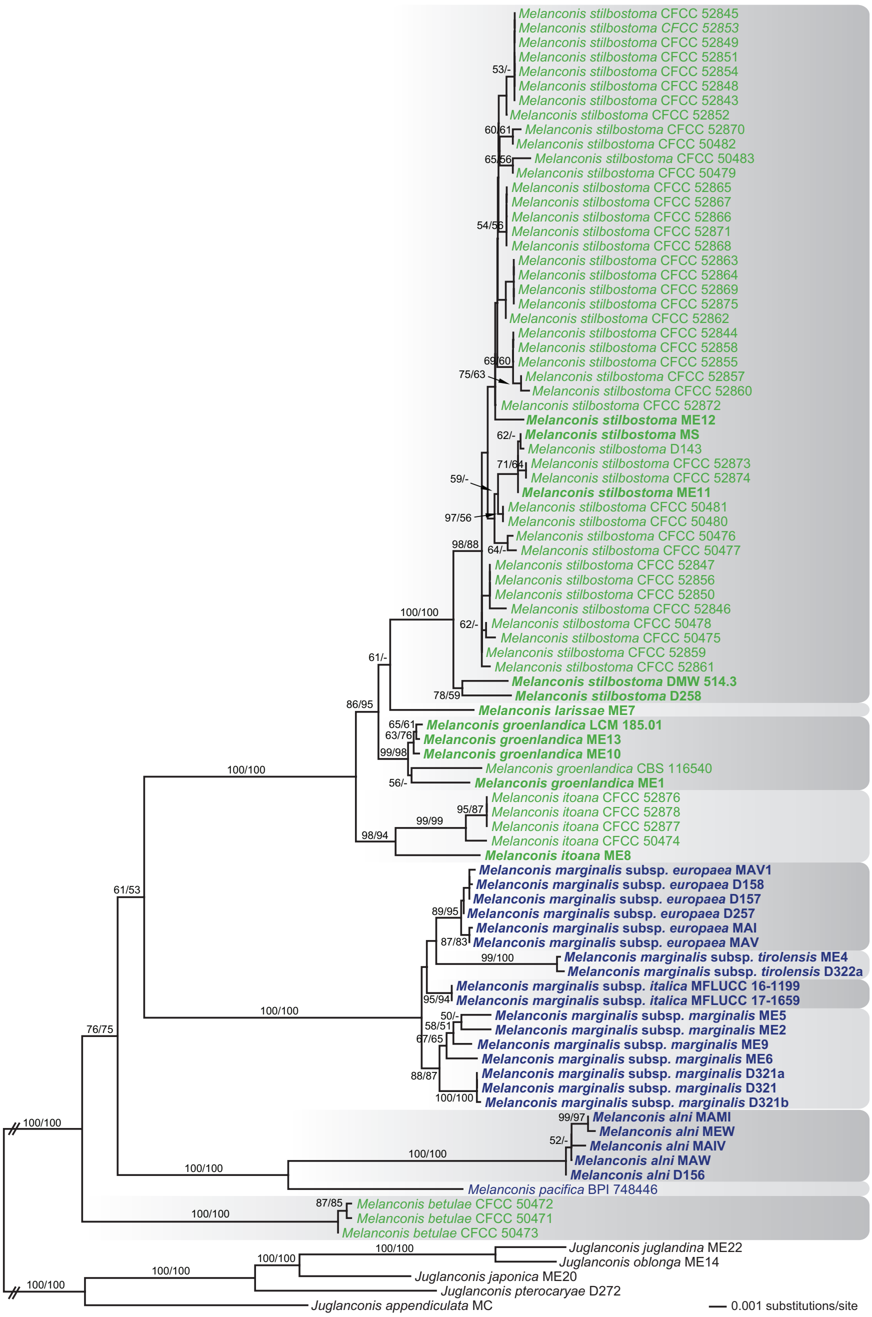

Figure 1. Phylogram of the best ML tree (lnL = –18240.558) revealed by RAxML from an analysis of the ITS-LSU-*ms204*-*rpb2*-*tef1*-*tub2* matrix of *Melanconis*, with 5 species of *Juglanconis* (Juglanconidaceae) selected as outgroup. ML and MP bootstrap support above 50% are given at the first and second position, respectively, above or below the branches. Strain numbers are given following the taxon names; strains formatted in bold were sequenced in the current study. *Melanconis* taxa occurring on *Alnus* are marked blue, those on *Betula* in green. The broken branches to the outgroup were scaled to 10%.

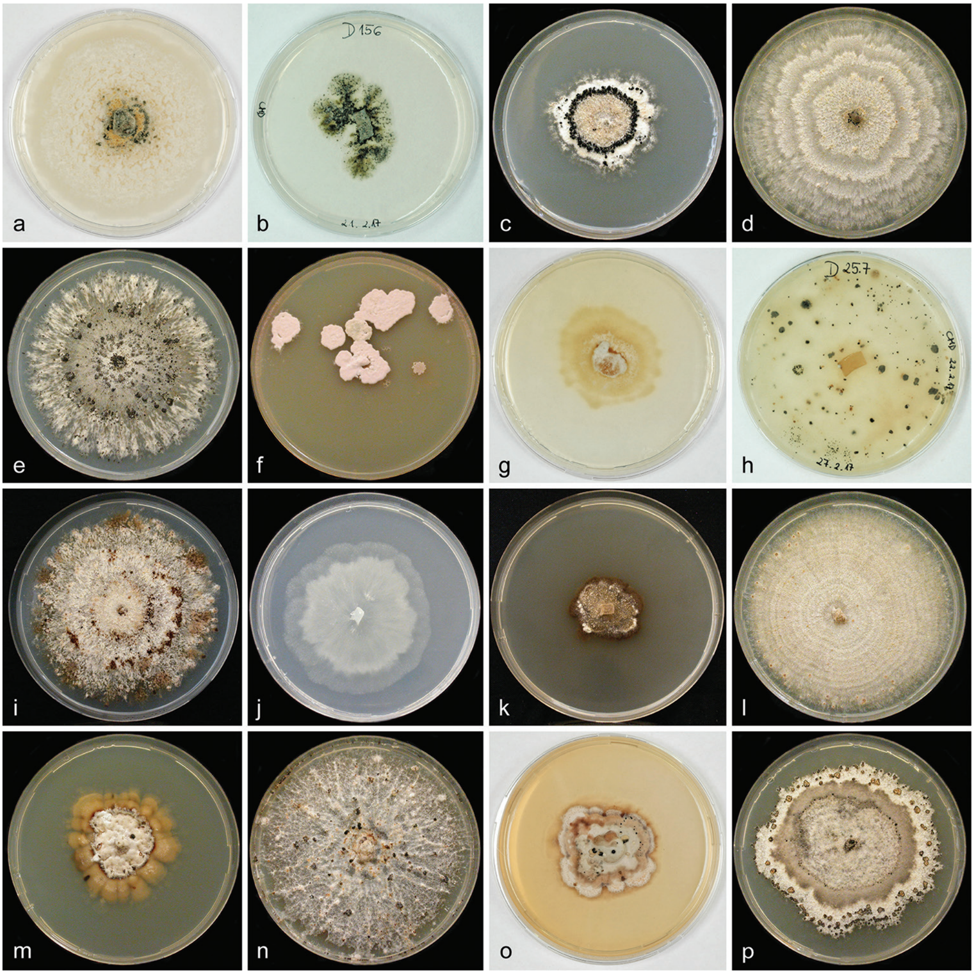

Figure 2. *Melanconis* cultures. **a–c** *M. alni* (**a, b** D156, **c** MAW) **d** *M. groenlandica* ME13 **e** *M. itoana* ME8 **f** *M. larissae* ME7 (after irregular rehydration) **g–i** *M. marginalis* subsp. *europaea* (**g, h** D257, **i** MAI) **j–l** *M. marginalis* subsp. *marginalis* (**j, k** D321, **l** ME5) **m** *M. marginalis* subsp. *tirolensis* ME4 **n** *M. pacifica* ME3 **o, p** *M. stilbostoma* (**o** D143, **p** ME11) **a, b, g, h, j, o** on CMD **c–f, i, k, l–n, p** on MEA **a, b, g, h, j** at 16 °C, **j, k** at 22 °C **c–f, i, k, l–n, p** at room temperature **a, g, j, k** after 3 weeks **b, h** after 3 **c, i** 5 **d–f, l–n, p** 3.7 **o** 2 months.

Taxonomy

Melanconis Tul. & C. Tul., Select. fung. carpol. (Paris) 2: 115 (1863).

?= *Melanconium* Link : Fr., Mag. Gesell. naturf. Freunde, Berlin 3(1–2): 9 (1809).

Type species. *Melanconis stilbostoma* (Fr. : Fr.) Tul. & C. Tul., Select. fung. carpol. (Paris) 2: 115 (1863).

Notes. Tulasne (1856) had already mentioned *Melanconis*, but did not give a generic diagnosis. Hence, the species he newly described were invalid, but became validated by reference in Tulasne and Tulasne (1863) (Paul Kirk, pers. comm.).

In contrast to *Diaporthe*, species of *Melanconis* always develop in bark, never in wood and lack stromatic zones. Pseudostromata are pulvinate to conical, circular to elliptic in outline and usually slightly project beyond the bark surface with perithecial contours remaining indistinct. Ectostromatic discs usually project distinctly from the surface of the pseudostromata and are bright, white to yellowish, to brown when old.

Nomenclaturally, the older genus *Melanconium* potentially competes with the younger genus *Melanconis*. However, as outlined in Rossman et al. (2015), the generic concept of *Melanconium* and the true identity of its generic type, *M. atrum*, are obscure and they therefore recommended to protect the well-defined *Melanconis* over *Melanconium*, which was formally adopted in the last ICN (Turland et al. 2018, Appendix III).

Melanconis alni **Tul. & C. Tul., Select. fung. carpol. (Paris) 2: 122 (1863).**
Figures 3, 4

≡ *Melanconis alni* Tul., Annls Sci. Nat., Bot., sér. 4, 5: 109 (1856). (Nom. inval., Art. 35.1).
= *M. alniella* Rehm, Ascom. exs. 148 (1872).
?= *Melanconium apiocarpum* Link, in Willdenow, Sp. pl., Edn 4 6(2): 90 (1825).
?= *M. sphaeroideum* Link, in Willdenow, Sp. pl., Edn 4 6(2): 92 (1825).
?= *Stilbospora microsperma* Pers., Observ. mycol. (Lipsiae) 1: 31 (1796).

Diagnosis. *Melanconis alni* is recognised by ascospores having filiform, tapering appendages and dark brown α-conidia with a pale to subhyaline median area.

Type material. ***Lectotype,*** here designated: FRANCE, Hauts-de-Seine, Chaville, on *Alnus glutinosa*, 1 Feb 1856, Tulasne (PC 0723592; MBT390380). ***Epitype,*** here designated: AUSTRIA, Oberösterreich, Raab, Wetzlbach, grid square 7648/1, on *Alnus glutinosa*, 4 Jun 2011, H. Voglmayr (WU 31883; ex-epitype cultures CBS 131695 = MAW (from ascospores), MEW (from α-conidia); MBT390381).

Description. ***Sexual morph:*** *Pseudostromata* developing in bark after the asexual morph and sometimes with acervuli of the asexual morph still present within their sides, 0.9–2.7 mm diam., scattered, pulvinate, more or less circular in outline, slightly projecting from the bark surface and then causing a greyish bark surface; consisting of an ectostromatic disc and perithecia embedded in an entostroma. *Ectostromatic discs* 0.3–1.4 mm diam., white to yellowish, brownish when old, flat to convex, circular, fusoid, angular or elongate in section, projecting up to 0.6 mm. *Ostiolar necks* cylindrical, laterally attached on perithecia and convergent in the disc, centrally only on centrally arranged perithecia, 1–15(–20) per disc, in the disc plane, convex to papillate and slightly projecting, with dark rounded tips; first pale brownish to greyish-brown, turning black, (70–)93–162(–210) μm (n = 33) diam. apically, mostly present at the margins but often also randomly within the disc. *Entostroma* bark-coloured, not or

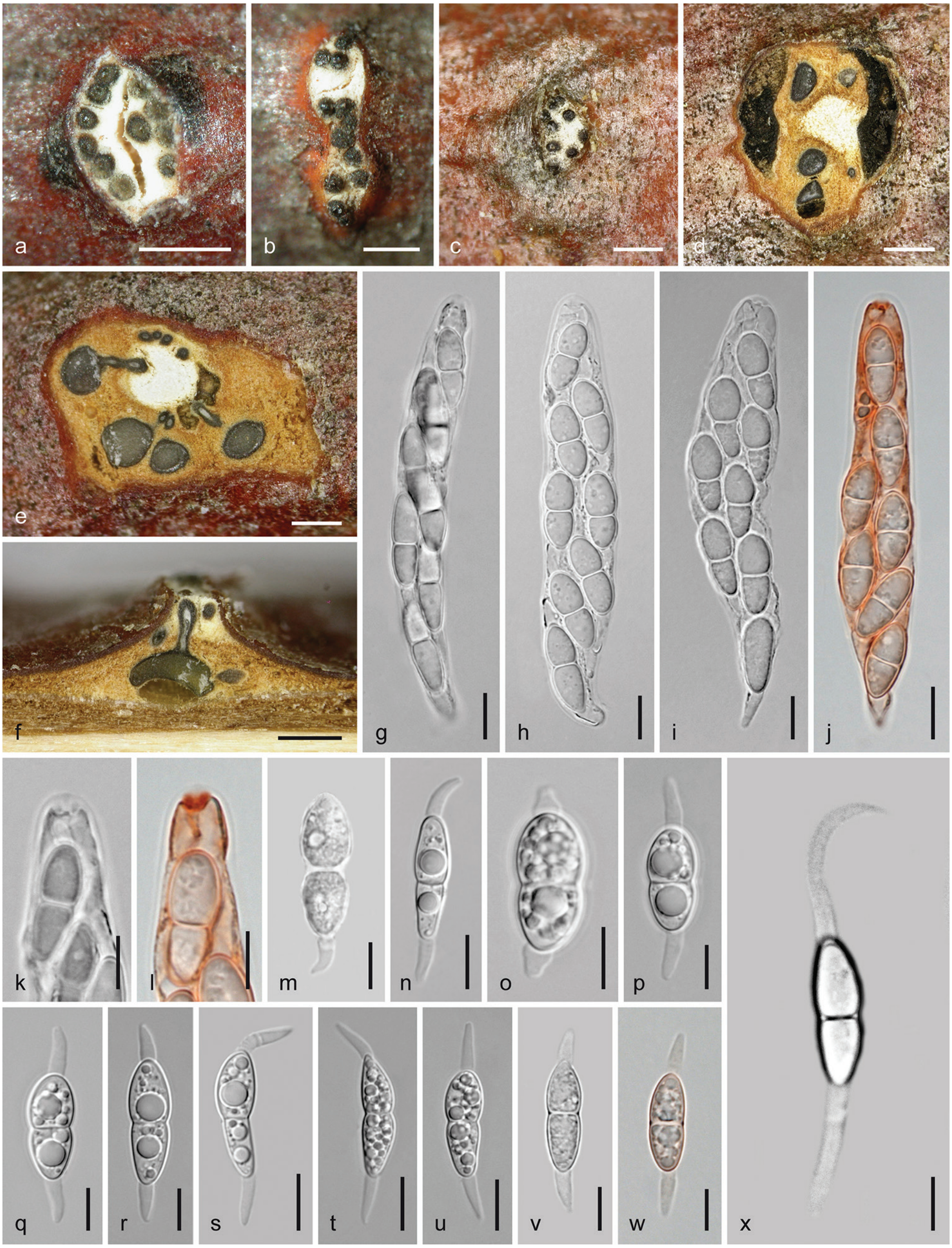

Figure 3. *Melanconis alni*. Sexual morph **a, b** ectostromatic discs **c** pseudostroma with ectostromatic disc in face view **d** cross section showing remnants of asexual morph at the sides of the sexual pseudostroma **e** cross section showing perithecia with lateral ostiolar necks and central column **f** vertical section showing perithecium with central ostiolar neck **g–j** asci **k, l** ascus apices showing apical ring **m–x** ascospores **j, l, w** in aqueous Congo Red **a, b, i** WU 31885 = W.J. 148 **c–f, j, o–q** epitype WU 31884 = MAIV **g, h, k, l, x** WU 37043 = J.F. 10104 **m** lectotype PC 0723592 **n** WU 37042 = D156 **r, s** WU 31882 = MAMI **t, u** WU 31883 = MAW **v** WU 31887 = W.J. 1194 **w** WU 31886 = W.J. 178. Scale bars: 400 µm (**a, b, d–f**), 500 µm (**c**), 10 µm (**g–j, n, s–u**), 7 µm (**k–m, o–r, v–x**).

only slightly paler than the surrounding bark, consisting of bark cells and some light-coloured hyphae. *Perithecia* (390–)450–645(–765) µm (n = 24) diam., formed below overmature conidiomata in valsoid configuration, globose to subglobose, collapsing up- or laterally inwards upon drying. *Hamathecium* of wide multiguttulate paraphyses, collapsing, dissolving and usually absent amongst mature asci. *Asci* floating free at maturity, (68–)79–97(–110) × (10.5–)12.5–16.5(–21) µm (n = 114), narrowly clavate, fusoid, oblong to nearly ellipsoid, with an apical ring staining in Congo Red but invisible or indistinct in the strongly thickened apex in 3% potassium hydroxide (KOH), containing 8 biseriate ascospores. *Ascospores* (14.5–)16–21(–25.3) × (4.7–)6–7.8(–9) µm, l/w (1.9–)2.3–3.2(–4.8) (n = 198), hyaline, ellipsoid, clavate or inequilaterally fusoid, bicellular with upper cell usually slightly wider, slightly or strongly constricted at the median septum, thick-walled, multiguttulate or with one large and several small guttules when fresh, with a filiform, tapering and acute, less commonly short and stout rounded, triangular or truncate appendage (2.5–)4.7–10(–24.3) × (1.7–)2.3–3(– 4) µm, l/w (1–)1.8–3.8(–8.4) (n = 224) at one or both ends; in 3% KOH, appendages invisible and cells tending to be more equal.

Asexual morph acervular, often conspicuous due to thick black conidial masses, first subperidermal, after ejection forming deposits 0.5–3.6 mm diam., sometimes confluent from 2–3 conidiomata and then up to 5 mm long, projecting to 0.5 mm. *Conidiomata* scattered, gregarious, sometimes confluent, pulvinate to conical, (0.6–)0.8–2.5 mm diam., consisting of a superficial, ca. 0.2–1.3 mm wide, flat, white to yellowish, slightly projecting disc becoming concealed by dark brown to black conidial deposits, a whitish to yellowish, when old orange-brown, compact, more or less pseudoparenchymatous base, in the centre arising as central column with circular to longish outline and sometimes wavy margin, surrounded by conidiophores and black conidial chambers. *Conidiophores* emerging radially from the pseudoparenchymatous base and column surface, filiform, to ca. 50 × 4 µm, branching 1–3 times from their bases producing whorls of conidiogenous cells. *Conidiogenous cells* (10–)12–43 × 2–4 µm, annellidic, more or less cylindrical, hyaline, turning brown with age, forming more or less simultaneously two types of conidia on top. *Conidia* dimorphic, *α-conidia* (9–)10.5–12.2(–14) × (4.8–)6.8–8(–9) µm, l/w (1.2–)1.4–1.7(–2.4) (n = 301), dark brown, more or less cuboid or subglobose and often with pinched sides or oval, oblong to broadly ellipsoid, with a diffuse or more or less well-defined, paler to subhyaline median area or stripe; β-conidia produced in small numbers, (5.3–)7.3–10.3(–11.5) × (2–)2.5–3.2(–3.7) µm, l/w (2–)2.6–3.9(–4.7) (n = 38), oblong, mostly straight, hyaline to subhyaline, turning dilute brownish with age, containing few minute guttules, with a distinct basal abscission scar.

Culture: Colony on CMD at 16 °C first hyaline, turning yellowish-brown from the centre, becoming covered by flocks of white aerial hyphae and conidiomata forming around the centre or colony irregular, with limited growth, turning green to black due to conidiomata; on MEA first hyaline, circular, with short aerial hyphae, forming concentric zones, the outer white, the inner turning brown, black conidiomata forming between the zones, margin becoming diffuse and the entire colony turning brown. Odour indistinct.

Distribution and ecology. *Melanconis alni* occurs in Europe on dead twigs and branches of *Alnus glutinosa* and *A. incana*, mainly at lower elevations.

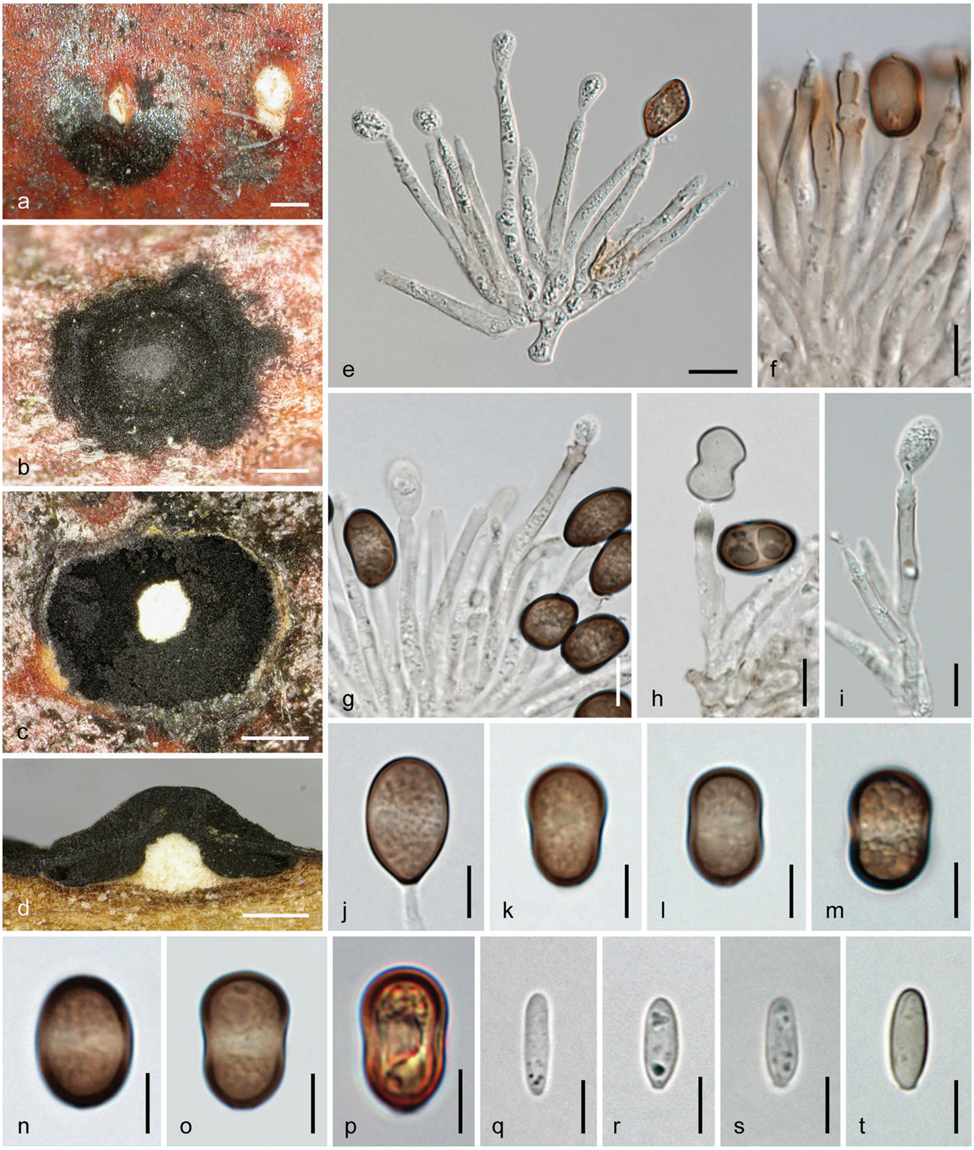

Figure 4. *Melanconis alni*. Asexual morph **a, b** conidiomata in face view **c** conidioma in cross section **d** conidioma in vertical section **e–i** conidiophores and conidiogenous cells **j–p** α-conidia **q–t** β-conidia **a, f** WU 31885 = W.J. 148 **b–d, h, m, q, s** epitype WU 31884 = MAIV **e, i** PC0723596 **g, j, k** lectotype PC0723592 **l, r** WU 37043 = J.F. 10104 **n, t** PC0723595 **o** WU 31886 = W.J. 178 **p** *M. atrum* isotype K(M) 171588 **e–o, q–t** in 3% KOH. Scale bars: 300 µm (**a–d**), 10 µm (**e**), 7 µm (**f–i**), 5 µm (**j–t**).

Additional material examined. Austria, Kärnten, Eisenkappel, Bad Vellach, Vellacher Kotschna, grid square 9653/1, on *Alnus incana*, 7 Sep 1998, W. Jaklitsch W.J. 1194 (WU 31887); St. Margareten im Rosental, village area, at the brook Tumpfi, grid square 9452/4, on *Alnus glutinosa*, 18 Jul 1994, W. Jaklitsch W.J. 148 (WU 31885);

Trieblach, Drau-Auen, near Kucher, grid square 9452/2, on *Alnus incana*, 7 Aug 1994, W. Jaklitsch W.J. 178 (WU 31886); Niederösterreich, Michelbach, Mayerhöfen, on *Alnus glutinosa*, 18 Jun 2011, H. Voglmayr (WU 31882, culture CBS 131693 = MAMI). FRANCE, Alpes-de-Haute-Provence, Trigance SE Castellane, at the river Jabron ca. 500 m elev. before entering the Verdon river, on *Alnus incana*, 4 Aug 2011, H. Voglmayr (WU 31884; culture MAIV); Ariége-Rimont, Peyrau, on *Alnus glutinosa*, soc. *Diplodia* sp., 26 Jul 2010, J. Fournier J.F. 10104 (WU 37043); Hauts-de-Seine, Chaville, on *Alnus glutinosa*, 11 Oct 1852, Tulasne (PC 0723589, PC 0723596); Meudon, on *Alnus glutinosa*, 13 May 1856, Tulasne (PC 0723593); Oise, Pierrefonds, on *Alnus glutinosa*, 30 Jul 1857, Tulasne (PC 0723590, PC 0723591); Yvelines, Viroflay, on *Alnus glutinosa*, July 1860, Tulasne (PC 0723594, PC 0723595); no collection data, Tulasne (PC 0723588). POLAND, S Kuligi, Biebrzański Park Narodowy, on *Alnus glutinosa*, 28 Jul 2015, H. Voglmayr (WU 37042, culture D156).

Notes. *Melanconis alni* was described by Tulasne from *Alnus glutinosa* in 1856 after a presentation of the topic in April 1856. Tulasne and Tulasne (1863) validated the name in *Melanconis*, illustrated ascospores with typical long acute appendages and mentioned material from Meudon and Chaville. In PC, nine specimens of Tulasne are extant in the *Melanconis alni* folder; three of them were collected after its description in 1856 and, for one, no collection data are available. PC 0723590, PC 0723591, PC 0723593, PC 0723594 and PC 0723595 were collected after the publication date. PC 0723588 (no data) and PC 0723589, PC 0723596 from 1852 only contain asexual morph, but in the protologue, the sexual morph is also described. Therefore, we select PC 0723592, which also contains few pseudostromata of the sexual morph, as the lectotype. In PC 0723592 and PC 0723595, both α- and β-conidia are present. Generally, β-conidia are inconspicuous and produced in small numbers, i.e. they are easily overlooked. Asci in old herbarium material are shrunk and difficult to rehydrate, therefore significantly smaller than those of fresh material. In KOH, the ascus apex becomes very thick and the ring disappears; also ascospore appendages disappear in KOH.

Tulasne and Tulasne (1863) and Wehmeyer (1941) listed the following asexual morph names, amongst others, as linked to *M. alni*: *Stilbospora microsperma* Pers. Material with this name is not accessible in L; *Melanconium sphaeroideum* Link (1825) is more generally given as the name of the asexual morph. Sieber et al. (1991) used another name described by Link (1825), *Melanconium apiocarpum*, for the asexual morph of *Melanconis alni*. As Link´s type material of these taxa is not extant in B, we are unable to draw a conclusion about their identity; in addition, the descriptions in Link (1825) are vague and he gave no hosts. Therefore, we continue to use the name *M. alni*, which is generally well-known. Type material of *Melanconium atrum* Link, the generic type of *Melanconium*, described from Germany (K(M) 171588, slide from *Melanconium atrum* type material from Persoon´s herbarium) has conidia of the same shape, size and lighter median band (Fig. 4p) and may thus be conspecific with *M. alni*, but it was described from *Fagus sylvatica*. According to Sutton (1964), Link had sent his material to Persoon, because in the herbarium of the latter 3 specimens labelled *M. atrum* were extant. The host of one of these materials was identified as *Fagus*, based on bark structure. This specimen was selected as lectotype. The slide K(M) 171588 (= IMI 102914) was prepared from the lectotype and is thus an isotype. Accordingly, *Melanconium atrum* is a different species, despite its morphological similarity with *M. alni*, because the latter only occurs on *Alnus* spp. We have not seen any *Melanconium* on *Fagus*, but Petrini and Fisher (1988), Sieber et al. (1991) and Kowalski and Kehr (1992) reported and isolated *M. atrum* as an endophyte of *Fagus*. For α-conidia of isolates from *Fagus sylvatica* and *Quercus robur*, Sieber et al. (1991) reported mean sizes of 11.7–12 × 8.5–8.9 μm, which were similar to those from *Alnus glutinosa* (on average, 10.1–12.3 × 5.9–7.4 μm). However, the protein profiles revealed by isozyme electrophoresis differed markedly between the isolates from *Alnus glutinosa* and those from *Fagus*/*Quercus*, confirming them to represent distinct species that may not even be congeneric. Another fact may support the presence of morphologically similar but rare taxa on Fagaceae, as, for example, *Melanconium gourdaeforme* with similar conidia was described by Kobayashi (1968) from *Castanea*. A narrow light band is also characteristic for conidia of *Melanconiella ostryae* (Voglmayr et al. 2012).

Ascospore appendages of *Melanconis alni* may sometimes be similar to those of *M. marginalis*, at least in fractions, although truncate appendages in *M. alni* are rather a consequence of microscopic mount preparation. On *Alnus incana* both species occur, therefore the asexual morph should be sought for to reliably identify the species.

Melanconis betulae **C.M. Tian & X.L. Fan, in Fan, Du, Liang & Tian, Mycol. Progr. 15(4/40): 4 (2016).**

Note. According to Fan et al. (2016), who described this species as an asexual morph from Gansu Province in China on *Betula albosinensis*, *Melanconis betulae* can be distinguished from *M. stilbostoma* by the smaller average length of its alpha conidia (10 vs. 12 μm). Phylogenetically, *M. betulae* is remote from the other betulicolous *Melanconis* species (Fig. 1).

Melanconis groenlandica **(M. Bohn) L. Lombard & Crous, in Lombard et al. Persoonia 36: 234 (2016).**

≡ *Myrothecium groenlandicum* M. Bohn, Mycotaxon 46: 336 (1993) (Basionym).

Type material. *Holotype* (not examined): Greenland, Qaqortoq, (isolated from) twigs of *Betula nana*, July 1991, M. Bohn (C; dried culture UPSC 3416; isotype in UPS; living cultures CBS 116450 = UPSC 3407, UPSC 3416).

Description (after Bohn 1993): Colonies on PDA and MEA 30–33 mm after 10 d (52–62 mm after 20 d), appearing leathery, at first whitish to greyish, later becoming greyish-orange, particularly on MEA; margin superficial, entire on MEA but fimbriate to lobate on PDA; exudate and diffusible pigment absent; reverse greyish-orange, especially at the margin; brownish, thick-walled, chlamydospore-like swollen portions 6–18 µm diam. present. *Conidiomata* appearing after ca. 14 d as dark green pustules of various sizes, irregularly scattered over the colony surface, but sometimes arranged in concentric rings, particularly in old cultures, initially covered by mycelium but becoming almost black and shiny at later stages due to the mass of conidia; conidiomata sporodochial (acervular?), irregular, dark green, up to 2 mm diam., scattered, gregarious or coalescent, composed of a 50–70 µm high stroma of *textura intricata* and conidiophores. Marginal hyphae and setae absent. *Conidiophores* arising from the stroma, branched, septate, yellowish to brownish, ca. 40–75 µm × 2–4 µm. *Conidiogenous cells* cylindrical to subulate, 15–25 × 2–3 µm, arranged in verticils of 2–4 at the top of the conidiophore, sometimes also intercalary, provided with conspicuous, pigmented collarettes and producing conidia by percurrent growth. *Conidia* black and shiny in mass, olivaceous to brownish under the microscope, straight, cylindrical with rounded ends, sometimes slightly narrowing towards the base or apiculate, (9–)10–12(–15) × (5–)6(–7) µm, with smooth wall. Teleomorph not formed after 3 months incubation.

Culture (own observations): Colony on MEA circular, first hyaline, turning and long remaining whitish, with age forming narrow concentric zones with tooth-like margins and turning pale brownish. Odour indistinct to unpleasant.

Distribution and ecology. *Melanconis groenlandica* is known from North America (Greenland, USA) and Japan from *Betula maximowicziana*, *B. nana* and *B. papyrifera*.

Additional collections sequenced. Japan, Hokkaido, Sorachi, Furano, Hokkaido Experimental Forest of Univ. Tokyo, on *B. maximowicziana*, 25 Sep 1964, T. Kobayashi (TFM FPH2478, culture MAFF 410219 = M4-2, ME1). USA: New Hampshire, close to the top of Mount Washington, on *Betula* sp., 28 Jul 2006, L. Mejia (BPI 879597; culture CBS 133339 = LCM 02.02 = ME13); New York, Adirondack High Peaks Region, Marcy Dam, on *Betula papyrifera*, 2 Jun 2007, L. Mejia (BPI 881485; culture CBS 133341 = LCM191.01 = ME10); ibidem, same host, 9 Jun 2007, L. Mejia (BPI 881515; culture CBS 133340 = LCM 185.01).

Note. This species was isolated as a putative endophyte from *Betula nana* and described from MEA and potato dextrose agar as a species of *Myrothecium*. In our phylogenetic analyses, three isolates from North America and one from Japan grouped with the ex-type isolate of *M. groenlandica* with high support.

Melanconis itoana Tak. Kobay., Bull. Govt Forest Exp. Stn Meguro 226: 19 (1970).

Type material. *Holotype:* Japan, Shizuoka, Fujinomiya, Mt. Fuji, on *Betula ermanii*, 6 Aug 1968, T. Kobayashi (TFM FPH3375; ex-type culture MAFF 410080 = LFP-M4-9 = ME8).

Description. See Kobayashi (1970) and Fan et al. (2016).

Culture: Colony on MEA circular, first hyaline, forming a white outer and brown inner zone, with radial stripes; conidiomata forming mostly in the inner zone. Odour indistinct.

Note. This species occurs on *Betula ermanii* in Japan and *Betula albosinensis* in China and is particularly well characterised by its long narrow fusoid conidia, which are more or less pointed at each end. It was originally described by Kobayashi (1970) in detail and the asexual morph was redescribed by Fan et al. (2016), who gave slightly shorter measurements of conidia (12–13.5(–14) × 3.5–4(–4.5) µm). Our measurements of conidia are (13–)14.7–17.5(–20) × (3–)3.5–4.3(–4.7) µm, l/w (3–)3.6–4.7(– 5.4) (n = 100), upon examination of the holotype, which corresponds with Kobayashi (1970). The Chinese accessions genetically differ significantly from the ex-type culture from Japan (Fig. 1) and may therefore merit separation.

Melanconis larissae Jaklitsch & Voglmayr, sp. nov.

MycoBank No: 834108
Figure 5

Diagnosis. *Melanconis larissae* differs from *M. stilbostoma* by α-conidia having a broad diffuse light-coloured zone.

Type material. ***Holotype.*** USA, New York, Adirondack Mts., Cranberry Lake, on *Betula* sp., 13 Jun 2002, L. Vasilyeva (BPI 870998; ex-type culture CBS 123196 = A.R. 3886, ME7).

Etymology. Named after the collector Larissa Vasilyeva.

Description. ***Sexual morph:*** *Pseudostromata* 1.8–2.7 mm diam., scattered to aggregated, not or only scarcely projecting from the bark surface, pulvinate, circular to elliptical in outline; consisting of an ectostromatic disc and perithecia embedded in an entostroma around a central column and sometimes conidial locules present on the ostiolar level. *Ectostromatic discs* 0.5–1.4 mm diam. or long, slightly projecting, fusoid to circular, flat or concave, white to yellow, often concealed by ostioles; central column beneath disc brightly white at upper levels, yellow amongst ostiolar necks at lower levels, consisting of hyaline hyphae and colourless crystals. *Ostiolar necks* cylindrical, laterally or centrally attached on perithecia, convergent and irregularly inserted in the disc; visible part (88–)130–204(–230) µm (n = 32) diam., 1–12 per disc, black, subglobose to subconical with flat or pointed tips, projecting to 200 µm. *Entostroma* consisting of hyaline hyphae and bark cells. *Perithecia* (420–)490–650(–690) µm (n = 14) diam., arranged in valsoid configuration around and below central column, globose to subglobose, collapsing up- or laterally inwards upon drying. *Peridium* pseudoparenchymatous, consisting of a dark brown small-celled outer and a hyaline to brownish, large-celled inner layer. *Hamathecium* absent at maturity. *Asci* floating free at maturity, (69–)84–106(–117) × (11–)13–17.5(–19.7) µm (n = 22), fusoid to oblong, with an apical ring distinct in water and staining in Congo Red, but invisible or indistinct in 3% KOH, containing (2–)4–8 ascospores in biseriate or obliquely uniseriate arrangement. *Ascospores* (14.8–)17–21.5(–25) × (5.8–)6.5–8.3(–9.7) µm, l/w (1.9–)2.3–3(–3.7) (n = 93), ellipsoid to subfusoid, symmetric or inequilateral, bicellular, hyaline, dilute brownish when old, slightly constricted at the central to slightly eccentric septum, thick-walled, becoming verruculose with age, devoid of appendages.

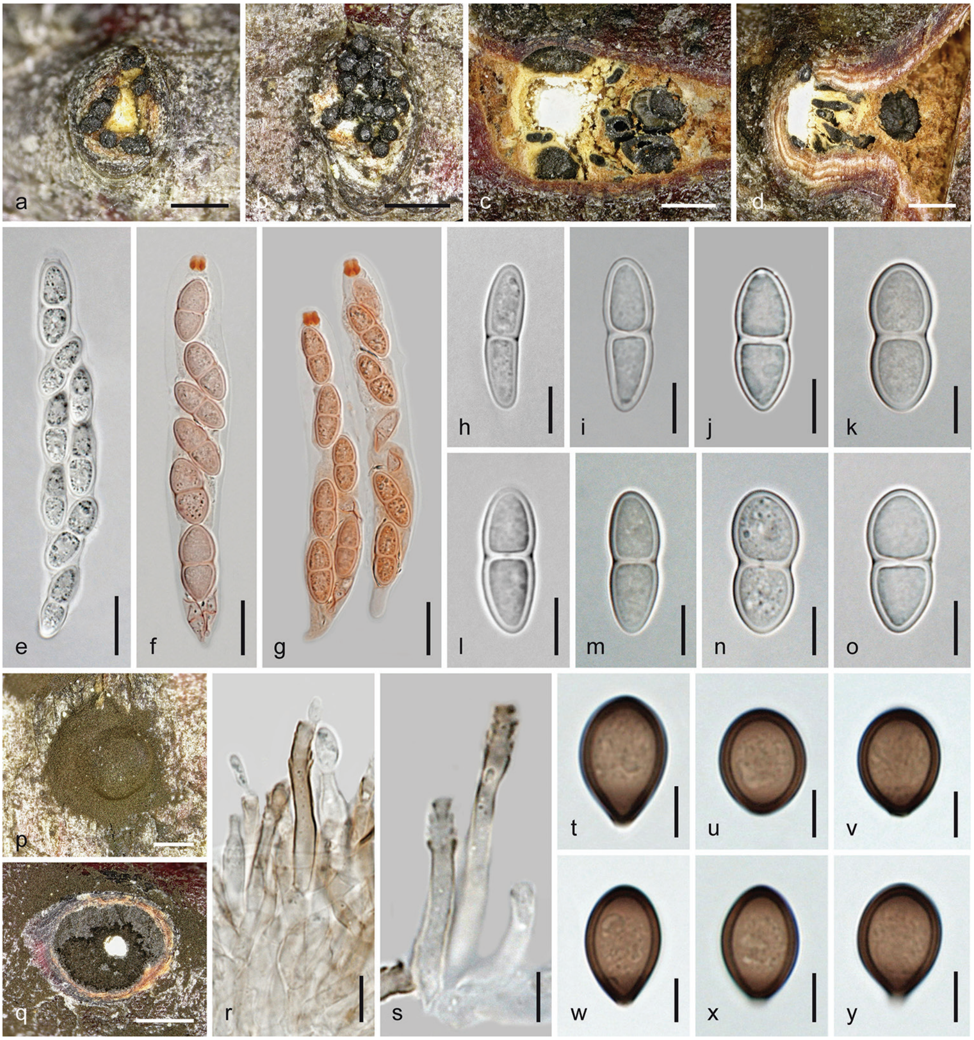

Figure 5. *Melanconis larissae* holotype (BPI 870998) **a–o** sexual morph **a, b** ectostromatic discs **c, d** cross sections showing white upper and yellow lower parts of central columns, ostiolar necks and perithecia **e–g** asci **h–o** ascospores **f, g** in aqueous Congo Red **p–y** asexual morph **p** conidial deposit **q** conidioma in cross section **r, s** conidiophores and conidiogenous cells (showing annellations in **s**) **t–y** α-conidia **r–y** in 3% KOH. Scale bars: 500 µm (**a–d, p, q**), 15 µm (**e–g**), 7 µm (**h–o, r**), 5 µm (**s–y**).

Asexual morph acervular, intermingled with pseudostromata of the sexual morph or developing separately, conspicuous. First white tissue (central column) forming within the bark, becoming surrounded by a yellow margin and narrow whitish to yellowish discs emerging through bark cracks, followed by the production of conidia in olivaceous to dark brown chambers. *Conidiomata* 1.3–2.7 mm diam., pulvinate, more or less circular in outline, scattered or crowded. *Covering discs* 0.25–1.2 mm long, narrowly fusoid or longish to circular, flat to convex, whitish to yellowish, becoming obscured by large, coppery to olivaceous brown conidial deposits 1–4 mm diam., projecting to 1.2 mm, also confluent from two or several conidiomata; discs and pulvinate or conical columns beneath consisting of *textura intricata* of hyaline hyphae and numerous colourless crystals, becoming brittle with age. *Conidiophores* emerging around the central column from a pseudoparenchymatous base, ca. 40–70 µm long, filiform, branched near the base and usually 1–3 fold asymmetrically at higher levels, first hyaline, turning brown from their tips; terminal *conidiogenous cells* (10.5–)14.5–28(–36.5) × (1.7–)2.5–3.5(–4.2) µm (n = 70), cylindrical and often widened towards base, with funnel-shaped collarette and up to 5 or 6 annellations, densely arranged, repetitive, producing α-conidia. *Conidia* (9.7–)11–13(–14.5) × (6.5–)7.7–9(–9.5) µm, l/w (1.1–)1.3–1.6(–2.2) (n = 66), oval, subglobose to drop-like, unicellular, dark brown, thick-walled, with a broad lighter coloured median zone and a small scar, smooth. No β-conidia detected.

Culture: Colony on MEA at room temperature circular, dense, first hyaline, turning rosy. Odour indistinct to musty.

Distribution and ecology. *Melanconis larissae* is known from a single specimen collected in New York State from an unidentified species of *Betula*.

Notes. The description of this taxon is based on a single specimen with overmature sexual morph and well-developed asexual morph with thick masses of conidia. *Melanconis larissae* differs from *M. stilbostoma* by the broad light-coloured zone of its conidia. No β-conidia have been detected in this specimen, but oblong to ellipsoid, hyaline to dilute brownish conidia 5–9 × 1.7–5 µm, which we interpret as immature α-conidia.

Melanconis marginalis **(Peck) Wehm., Pap. Michigan Acad. I. 6: 382 (1926).**

Notes. This species is here subdivided into four subspecies below. See under subsp. *marginalis* for the original species.

Although Wehmeyer (1926a) combined *Diaporthe marginalis* in *Melanconis*, he later (Wehmeyer 1941) argued that the conidia only differ from those of *M. alni* in depth of pigmentation and, therefore, reduced *M. marginalis* to a subspecies of the latter. In Europe, where, owing to Wehmeyer (1941), *Melanconis* on *Alnus* was always identified as *M. alni*, Petrak (1941) reported *Melanconium dimorphum* for the first time, described both conidial types, but still found it probable that *Melanconium dimorphum* was an abnormal form of *M. sphaeroideum*, the putative name of the asexual morph of *M. alni*. Kobayashi (1970) and Jensen (1984), however, were convinced that *Melanconis marginalis* should be treated as a species separate from *M. alni*, which is here confirmed phylogenetically. In addition, ascospores of *M. marginalis* are narrower, usually more oblong and symmetric than those of *M. alni* and appendages shorter, stouter and rounded or truncate at the ends, which swell and become diffuse in mounts.

Melanconis marginalis **subsp.** ***europaea*** **Jaklitsch & Voglmayr, subsp. nov.**

MycoBank No: 834109
Figures 6, 7

Diagnosis. This subspecies of *Melanconis marginalis* occurs in Europe and differs from the American subsp. *marginalis* phylogenetically and by slightly larger asci, ascospores and ascospore appendages.

Type material. ***Holotype.*** Austria, Steiermark, Judenburg, Pusterwald, Hinterwinkel, grid square 8651/4, on *Alnus incana*, 11 Jun 2011, H. Voglmayr (WU 31888, culture CBS 131692 = MAI).

Etymology. For its occurrence in Europe.

Description. ***Sexual morph:*** *Pseudostromata* 1.5–3.6 mm diam., usually conspicuous and numerous, scattered to tightly aggregated, forming pustules, pulvinate, circular to elliptical in outline, typically elevated beyond bark surface; consisting of an ectostromatic disc and perithecia embedded in an entostroma around a central column. *Ectostromatic discs* 0.5–2.1 diam. or long, discrete, less commonly confluent, bright white to yellowish, turning brownish with age, variable, fusoid, elliptic or circular in outline, flat, convex, concave, entire or coarsely fissured and crumbly, projecting up to 1 mm including projecting part of the pseudostroma; central column beneath disc whitish to yellowish, consisting of hyaline hyphae and colourless crystals. *Ostiolar necks* cylindrical, laterally attached on perithecia, centrally attached only on centrally arranged perithecia, convergent in the disc margin or crowded at the ends of fusoid discs, 1–25(–35) per disc. Visible part of the ostiolar necks (53–)103–167(–212) µm (n = 90) diam., black or brown with black tips, usually circular in section, sometimes plane with the disc, but much more frequently papillate and projecting to 250 µm, often resembling minute perithecia with pointed tips or discoid with depressed centre to nearly ring-like, sometimes conical to bristle-like and projecting to 0.4 mm. *Entostroma* bark coloured, not or only slightly paler than the surrounding bark, consisting of bark cells and some light-coloured hyphae. *Perithecia* (450–)515–680(–810) µm (n = 58) diam., arranged in valsoid configuration around and below central column, globose to subglobose, collapsing up- or laterally inwards upon drying. Peridium pseudoparenchymatous, consisting of a dark brown small-celled outer and a hyaline to brownish, large-celled inner layer. *Hamathecium* of broad multiguttulate paraphyses, collapsing, dissolving and usually absent amongst mature asci. *Asci* floating free at maturity, (52–)68–85(–98) × (8.7–)10.5–15.5(–18.7) µm (n = 126), narrowly fusoid to oblong or narrowly ellipsoid, with an apical ring distinct in water and staining in Congo Red, but invisible or indistinct in 3% KOH, containing 8 biseriate or obliquely uniseriate ascospores. *Ascospores* (13.8–)17–20(–22.8) × (3.5–)4.7–6.5(–7.7) µm, l/w (2.5–)2.9–3.8(–5.5) (n = 242), hyaline, mostly oblong or narrowly ellipsoid, sometimes broadly ellipsoid upon release, symmetric or inequilateral, bicellular with nearly equal cells, slightly or strongly constricted at the median septum, multiguttulate or with few large and several small guttules when fresh, with a short and broad, rounded,

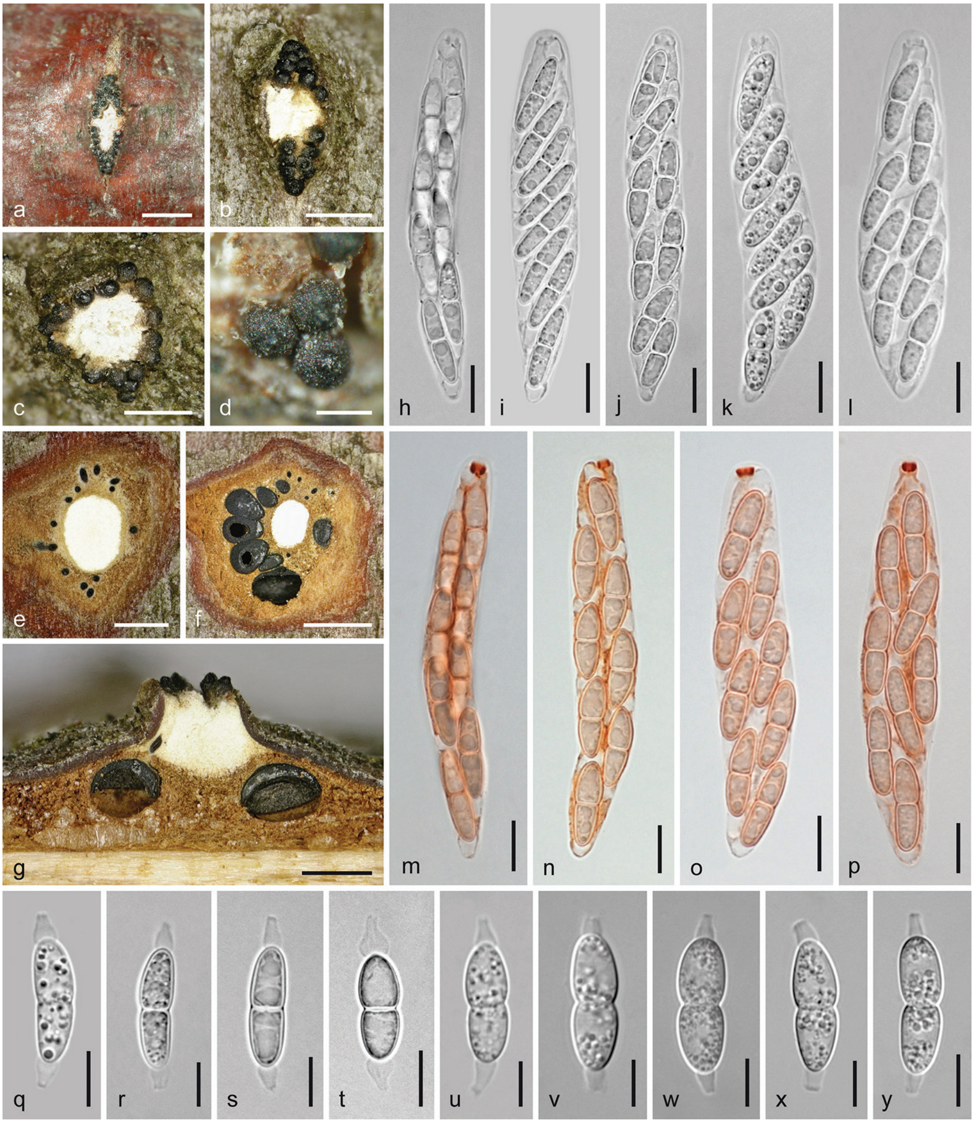

Figure 6. *Melanconis marginalis* subsp. *europaea*. Sexual morph **a** pseudostroma in face view **b, c** ectostromatic discs **d** subglobose visible part of ostiolar necks **e, f** cross sections (**e** showing central column and marginal ostioles **f** showing central column and perithecia) **g** vertical section showing central column and two perithecia **h–p** asci **q–y** ascospores **m–p** in aqueous Congo Red **a** WU 31890 = MAV1 **b–g, j, n, q, s, t, w–y** holotype WU 31888 = MAI **h, i, m** WU 37045 = D158 **k, r** WU 36699 **l, p** WU 31172 **o** WU 29888 **u** WU 31889 = MAV **v** WU 38243. Scale bars: 1 mm (**a, f**), 500 µm (**b, c, e, g**), 150 µm (**d**), 10 µm (**h–q, t**), 7 µm (**r, s, u–y**).

sometimes tapering, angular or bell-shaped and typically terminally truncate appendage (1.8–)2.7–4.7(–8.4) × (2–)2.5–4(–5.5) µm, l/w (0.4–)0.9–1.5(–2.8) (n = 318), at one or both ends becoming invisible in 3% KOH and Congo Red after release.

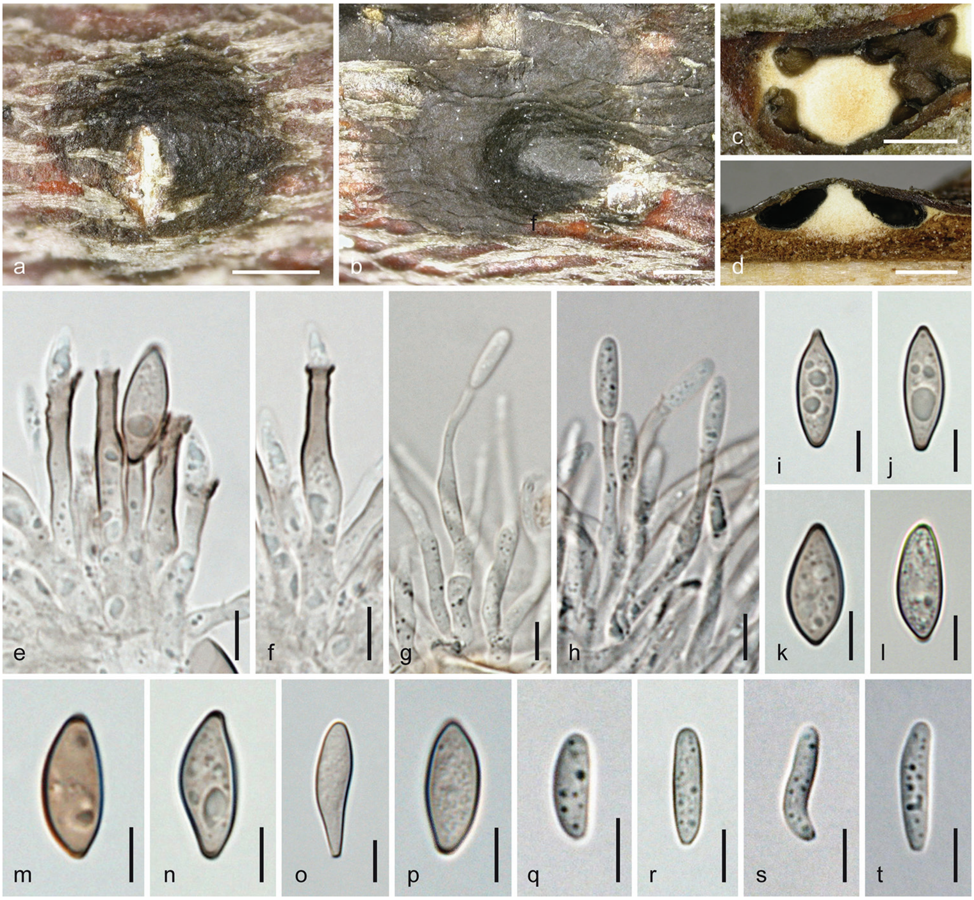

Figure 7. *Melanconis marginalis* subsp. *europaea*. Asexual morph **a, b** conidiomata and conidial deposits in face view **c** conidioma with β-conidia in cross section **d** conidioma with α-conidia in vertical section **e–h** conidiophores and conidiogenous cells (producing α-conidia in **e, f**, β-conidia in **g, h**) **i–p** α-conidia **q–t** β-conidia **e–t** in 3% KOH **a, b, d–f, i–k, q–s** WU 37044 = D157 **c, g, h, l, t** WU 31893 **m** WU 31891 = W.J. 1542 **n** WU 31888 = MAI **o, p** WU 31889 = MAV. Scale bars: 500 µm (**a–d**), 5 µm (**e–t**).

Asexual morph acervular, intermingled with pseudostromata of the sexual morph or more frequently developing separately, usually inconspicuous, but sometimes becoming conspicuous due to greyish-brown to dark brown conidial deposits 0.2–0.6 mm diam., rarely confluent from 2 conidiomata and then up to more than 1 cm long. First, white to yellow tissue (central column) forming within the bark, becoming visible by pustulate bark and narrow whitish to yellowish or brownish slit-like discs emerging through bark cracks, usually first followed by the production of β-conidia in olivaceous chambers and later α-conidia on the same or similar conidiophores turning the contents brown and oozing out from ends of the discs or perithecia of the sexual morph formed below the acervulus. *Conidiomata* 1–2 mm diam., pulvinate, more or less circular in outline, scattered or aggregated in lines. *Covering discs* 0.3–

0.9(–1.6) mm (n = 45) long, narrowly fusoid or longish to rounded, plane to convex, becoming covered and obscured by conidial deposits; discs and pulvinate or conical columns beneath, consisting of compact *textura intricata* of hyaline hyphae and numerous colourless crystals. *Conidiophores* emerging around the central column or directly on bark in dense palisades, up to ca. 50 µm long, filiform, branched near the base or sometimes 1–2 fold asymmetrically at higher levels, hyaline, turning brown from their tips; terminal conidiogenous cells (10–)14.5–23(–27) × (1.8–)2.3–3.5(–5) µm (n = 90), cylindrical and often widened in the middle or towards base and at the funnel-shaped tips beyond its width, with up to 3 annellations, producing β-conidia and/or α-conidia. *Conidia* dimorphic, α-conidia (9–)11–14(–16.3) × (3.2–)4.5–5.5(–6.2) µm, l/w (1.7–)2.2–2.9(–3.6) (n = 172), first hyaline, soon turning pale to medium brown or greyish-brown, unicellular, mostly fusoid, but also oblong, oval or ellipsoid, straight, less commonly slightly curved, upper end usually subacute and sometimes elongated, lower end narrowly truncate, containing several guttules, smooth; β-*conidia* (8–)9–11.5(–12.7) × (2–)2.5–3(–3.3) µm, l/w (2.8–)3.3–4.6(–5.8) (n = 39), hyaline to dilute brownish, unicellular, oblong to cylindrical, straight or slightly curved, thick-walled in water, with few guttules to eguttulate, smooth.

Culture: Colony on CMD at 16 °C first hyaline, partly or entirely turning brownish or ochre, either covered by a dense white mat of aerial hyphae or not, sometimes becoming indistinctly zonate, sometimes forming irregularly disposed conidiomata; on MEA at room temperature, first hyaline to whitish, soon forming a few broad zones with uneven margins forming teeth, the latter partly turning brown.

Distribution and ecology. Common on *Alnus alnobetula* (syn. *A. viridis*) and *A. incana* in mountainous areas of Central and Eastern Europe (confirmed for Austria, the Czech Republic fide Podlahová 1973, Romania fide Szász 1966 and Switzerland fide Sieber et al. 1991).

Other material examined. Austria, Burgenland, Forchtenstein, Kohlstatt, on *Alnus incana*, 24 Sep 2016, H. Voglmayr & W. Jaklitsch (WU 37046, culture D257); Kärnten, Hüttenberg, Knappenberg, grid square 9053/3, on *Alnus alnobetula*, 10 Jun 1992, W. Jaklitsch (WU 15093); Niederösterreich, Aspangberg-St. Peter, Mariensee, grid square 8461/4, on *Alnus alnobetula*, 23 Sep 2009, H. Voglmayr (WU 29888); Steiermark, Hartberg, Pinggau, Schaueregg, Alte Glashütte, on *Alnus alnobetula*, 28 Jul 2012, W. Jaklitsch & H. Voglmayr (WU 38243); Judenburg, Pusterwald, grid square 8652/3, on *Alnus alnobetula*, 11 Jun 2011, H. Voglmayr (WU 31890, culture MAV1); Liezen, Kleinsölk, walking path between Breitlahnhütte and Schwarzensee, grid square 8649/3, on *Alnus alnobetula*, 6 Aug 2003, W. Jaklitsch W.J. 2296 (BPI 843621; culture CBS 121480 = A.R. 4013); St. Nikolai im Sölktal, Sölker Paß, grid square 8750/1, on *Alnus alnobetula*, 14 Jun 2011, H. Voglmayr (WU 31889, culture CBS 131694 = MAV); Spital am Semmering, near Pfaffensattel, grid square 8460/2, on *Alnus alnobetula*, 15 Aug 2003, W. Jaklitsch W.J. 2331 (BPI 872072; culture A.R. 4032); ibidem, same host, 8 Jul 2010, I. Krisai-Greilhuber & H. Voglmayr (WU 31172); ibidem, same host, 7 Apr 2015, H. Voglmayr (WU 36699); Tirol, Kühtai, between Haggen and Kühtai, near Zirmbachalm, grid square 8732/3, on *Alnus alnobetula*, 3 Sep 2003, W Jaklitsch W.J.

2368 (W 2004-0000062); Prägraten, Bodenalm, on *Alnus alnobetula*, 18 Jun 2015, H. Voglmayr & W. Jaklitsch (WU 37044; culture D157); Umbalfälle, grid square 8939/4, on *Alnus alnobetula*, 28 Aug 2000, W. Jaklitsch W.J. 1542 (WU 31891, BPI 748444; culture CBS 109773 = A.R. 3500; AFTOL-ID 2127); same area and host, 17 Jun 2015, H. Voglmayr & W. Jaklitsch (WU 37045; culture D158); Vienna, Landstraße, Botanical garden, Alpinum, grid square 7864/1, on *Alnus alnobetula*, 21 Aug 1994, H. Voglmayr (WU 12976); same place and host, 6 Jan 2012, H. Voglmayr (WU 31893).

Notes. This subspecies differs mainly in its occurrence in (Central) Europe and by forming a clade of its own in phylogenetic analyses (Fig. 1). While the differences of the European accessions in each marker included are few, they are consistent, resulting in a well-delimited clade in the multigene analyses. As the morphological differences from *M. marginalis* subsp. *marginalis* are only small, we prefer to classify the European taxon as a subspecies rather than a separate species.

Under the name *Melanconis alni*, Podlahová (1973) described both sexual and asexual morphs of a Czech collection from *Alnus alnobetula* which clearly represents *M. marginalis*, and Szász (1966) listed and described the species (as *Melanconium dimorphum*) from Romania, again from *Alnus alnobetula*. In his isozyme studies of *Melanconium*, Sieber et al. (1991) included a Swiss isolate from *Alnus alnobetula* (as *Melanconium* sp. 1). This isolate showed a distinct but similar isozyme pattern to North American collections of *Melanconis marginalis* and had a mean conidial size of 11.7 × 4.3 μm, indicating that this isolate also represents *Melanconis marginalis* subsp. *europaea*.

Melanconis marginalis **subsp.** ***italica*** **(Senan., Camporesi & K.D. Hyde) Jaklitsch & Voglmayr, comb. et stat. nov.**

MycoBank No: 834110

≡ *Melanconis italica* Senan., Camporesi & K.D. Hyde, in Senanayake et al., Stud. Mycol. 86: 273 (2017) (Basionym).

Type material. ***Holotype.*** Italy, Province of Forlì-Cesena, Fiumicello di Premilcuore, on dead branch of *Alnus cordata*, 4 Dec 2013, E. Camporesi IT 1557 (MFLU 17–0879; ex-type cultures MFLUCC 16–1199, MFLUCC 17–1659; isotype BBH 42441).

Notes. It is presently unclear, whether this poorly described and illustrated taxon that is only known from a single collection is simply *Melanconis marginalis* subsp. *europaea* or merits a subspecies name of its own. First, the host given by the authors, *Alnus cordata*, naturally occurs in southern Italy and Corsica and, thus, may be correct only if planted in the collection area, which is not given by the authors. Secondly, the ascospores are in the range of other subspecies and appendages are neither mentioned nor illustrated, although a few are visible in their ascus images. Apparently, ascospores were mounted in KOH, where appendages are invisible. Thirdly, they describe the asexual morph from culture and include only a poor image of conidia without giving any measurements. Last but not least, only LSU, ITS and *rpb2* are available, which are insufficient to reliably resolve its true phylogenetic position. In addition, instead of comparing their taxon with *M. marginalis*, they compare it with *M. alnicola* (Jaap 1917), which is a synonym of *Alnecium auctum*.

Melanconis marginalis **subsp.** ***marginalis*** **(Peck) Wehm., Pap. Michigan Acad. I. 6: 382 (1926).**

Figures 8, 9

≡ *Diaporthe marginalis* Peck, Rep. (Annual) Trustees State Mus. Nat. Hist., New York 39: 52 (1887) [1886] (Basionym).
≡ *Melanconis alni* var. *marginalis* (Peck) Wehm., Revision of *Melanconis*, *Pseudovalsa*, *Prosthecium* & *Titania*: 27 (1941).
= *Diaporthe nivosa* Ellis & Everh., Proc. Acad. nat. Sci. Philad. 42: 222 (1890).
= *Melanconium dimorphum* Peck, Ann. Rep. New York State Mus. Nat. Hist. 40: 62 (1887).

Type material. ***Holotype*** of *Diaporthe marginalis*: USA, New York, Essex County, Elisabethtown, on *Alnus alnobetula* subsp. *crispa* (given as *Alnus viridis*), May 1885, C.H. Peck (NYSf 1859!; material separated into 2 envelopes NYSf 1859.1 and NYSf 1859.2). ***Epitype***, here designated: CANADA, New Brunswick, Charlotte Co., 1.5 km SW of Little Lepreau, on *Alnus alnobetula* subsp. *crispa* attached to the tree, soc. *Tortilispora aurantiaca*, 3 Sep 2019, D. Malloch (WU 37850; ex-epitype cultures CBS 146200 = D321 (from ascospores), D321a (from α-conidia), D321b (from β-conidia); MBT390382).

Description. ***Sexual morph:*** *Pseudostromata* immersed in bark causing pustules, scattered or aggregated, sometimes fused in pairs, 1.2–3.2 mm diam., pulvinate, circular to elliptic in outline, often elevated beyond bark surface; consisting of an ectostromatic disc and perithecia embedded in an entostroma around a central column, sometimes also acervuli containing α-conidia on the ostiolar level. *Ectostromatic discs* 0.3–1.5(–2) mm diam. or long, bright white to yellowish or cream, flat, convex or concave, sometimes fissured or with dark stellate stripes around disc on the bark surface, sometimes concealed by ostioles, circular, elliptic or fusoid in outline, typically distinctly projecting up to 1 mm including projecting part of the pseudostroma; central column beneath disc white to yellowish, consisting of hyaline hyphae and colourless crystals. *Ostiolar necks* cylindrical, laterally attached on perithecia, centrally attached only on centrally arranged perithecia, convergent in the disc margin or crowded at the ends of fusoid discs, sometimes completely filling disc, 1–15(–22) per disc. Visible part of the ostiolar necks (55–)87–153(–230) µm (n = 128) diam., shiny black or brown with black tip, flat discoid to ring-like, papillate to subglobose with pointed tip or conical, sometimes bristle-like and projecting up to 0.6 mm. *Entostroma* bark coloured, not or only slightly paler than the surrounding bark, consisting of bark cells and some light-coloured hyphae. *Perithecia* (420–)480–650(–750) µm (n = 34) diam., arranged in valsoid configuration around and below central column, depressed subglobose, collapsing up- or laterally inwards upon drying. Peridium pseudoparenchymatous, consisting of a dark brown small-celled outer and a hyaline to brownish, large-celled inner layer. *Hamathecium* of broad multiguttulate paraphyses, collapsing, dissolving and usually absent amongst mature asci. *Asci* floating free at maturity, (46–)56–69(–82) × (10–)11–14.5(–18) µm (n = 116), mostly oblong to fusoid, but also clavate or narrowly ellipsoid, with an apical ring distinct in water and staining in Congo Red but invisible or indistinct in 3% KOH, containing 8 ascospores in bi- or obliquely uniseriate arrangement. *Ascospores* (13.8–)15.5–18(–20.7) × (3.7–)4.5–5.7(–7.7) µm, l/w (2.4–)2.9–3.7(–4.4) (n = 236), hyaline to yellowish, oblong to ellipsoid, bicellular with equal or slightly unequal cells, slightly to distinctly constricted at the more or less median septum, multiguttulate or with few large and several small guttules when fresh, with a roundish to triangular or broadly oblong to beak-like and truncate appendage (1.1–)1.8–3.5(–6.1) × (2.2–)2.5–3.5(–4.2) µm, l/w (0.4–)0.6–1.2(–2.1) (n = 140) at each end; in 3% KOH, ascospores wider and more ellipsoid; appendages mostly invisible.

Asexual morph acervular, intermingled with pseudostromata of the sexual morph or more frequently developing separately, usually inconspicuous but sometimes becoming conspicuous due to greyish-brown to dark brown conidial deposits to 2.7 mm diam., sometimes confluent from 2 conidiomata and then up to 7 mm long. First white to yellow tissue (central column) forming within the bark, becoming visible by pustulate bark and narrow whitish to yellowish or brownish slit-like discs emerging through bark cracks, usually first followed by the production of β-conidia in olivaceous chambers, followed by fusion of the chambers and production of α-conidia on the same or similar conidiophores, turning the cavity brown and oozing out from ends of the discs or perithecia of the sexual morph formed beneath. *Conidiomata* ca. 0.9–3 mm long or diam., pulvinate, more or less circular in outline, scattered or aggregated in lines. *Covering discs* 0.3–0.7 mm long or diam., narrowly fusoid or longish to circular, plane to convex, white-yellowish-brownish, becoming covered and obscured by conidial deposits; discs and pulvinate or conical columns beneath consisting of compact *textura intricata* of hyaline hyphae and numerous colourless crystals. *Conidiophores* emerging around the central column from a *textura intricata*, fasciculate, filiform, branched near the base or sometimes 1–2 fold asymmetrically at higher levels, hyaline, turning brown from their tips; terminal conidiogenous cells (10–)13.5–23(–31) × (1.7–)2–3(–3.5) µm (n = 68), cylindrical and often widened in the middle or towards the base and at the funnel-shaped tips beyond its width, annellidic, producing α- and/or β-conidia. *Conidia* dimorphic, α-conidia (9–)10.5–13.3(–16.8) × (3.8–)4.5–5.3(– 6) µm, l/w (1.7–)2–2.8(–3.9) (n = 171), first hyaline, soon turning light to medium brown, unicellular, mostly fusoid, but also oblong, oval, citriform or ellipsoid, straight or slightly curved to sigmoid, upper end often subacute, lower end narrowly truncate, containing several guttules or eguttulate, smooth; β-conidia (6–)8–10.5(–12.2) × (1.7–)2.2–2.8(– 3) µm, l/w (2.4–)3–4.6(–6.4) (n = 46), hyaline to dilute brownish, unicellular, oblong to cylindrical, sometimes reniform, straight or curved, thick-walled in water, with few guttules to eguttulate, smooth.

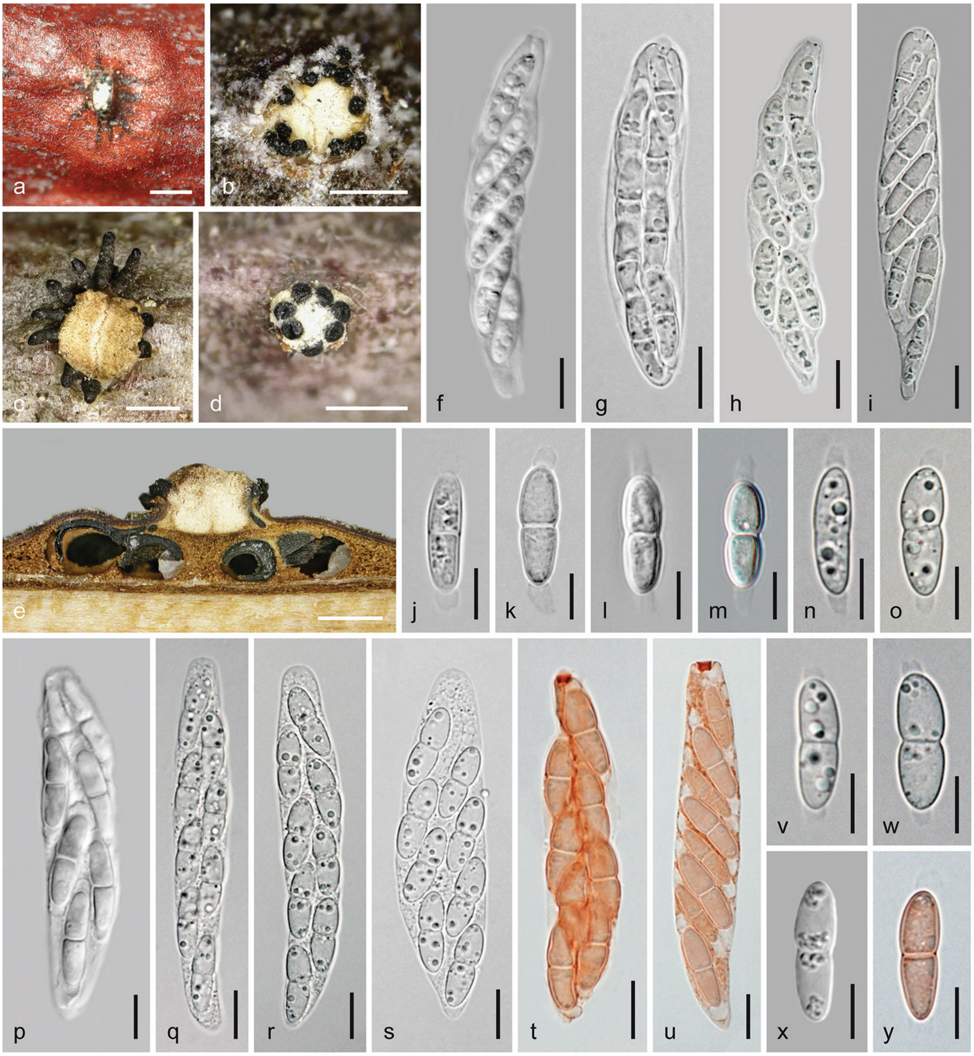

Figure 8. *Melanconis marginalis* subsp. *marginalis*. Sexual morph **a** pseudostroma in face view **b–d** ectostromatic discs (note conical to bristle-like ostiolar necks in **c** discoid in **d**; **e** vertical section showing central column and perithecia **f–i, p–u** asci **j–o, v–y** ascospores **t, u, y** in aqueous Congo Red **x** in 3% KOH **a, f** BPI 614844 **b, g, h, t** holotype NYSf 1859 **c, k, j** BPI 748233 **d, e, n, o, q–s, v, w, y** epitype WU 37850 **i, u** DAOM 227767 **l, m** DAOM 202917 **p** BPI 614977 **x** DAOM 86074. Scale bars: 500 µm (**a–e**), 10 µm (**f–i, q–u**), 7 µm (**j–p, v–y**).

Culture: Colony on CMD at 22 °C circular with slightly uneven margin, hyaline to whitish, forming a broad inner white zone with tooth-like margin and narrow hyaline outer zones; on MEA at room temperature circular, first hyaline to white, margin becoming diffuse, narrow or coarse concentric zones formed, turning brown from the margins, aerial hyphae short, dense, surface sometimes becoming imbricate, sometimes growth limited and ceasing after a few weeks.

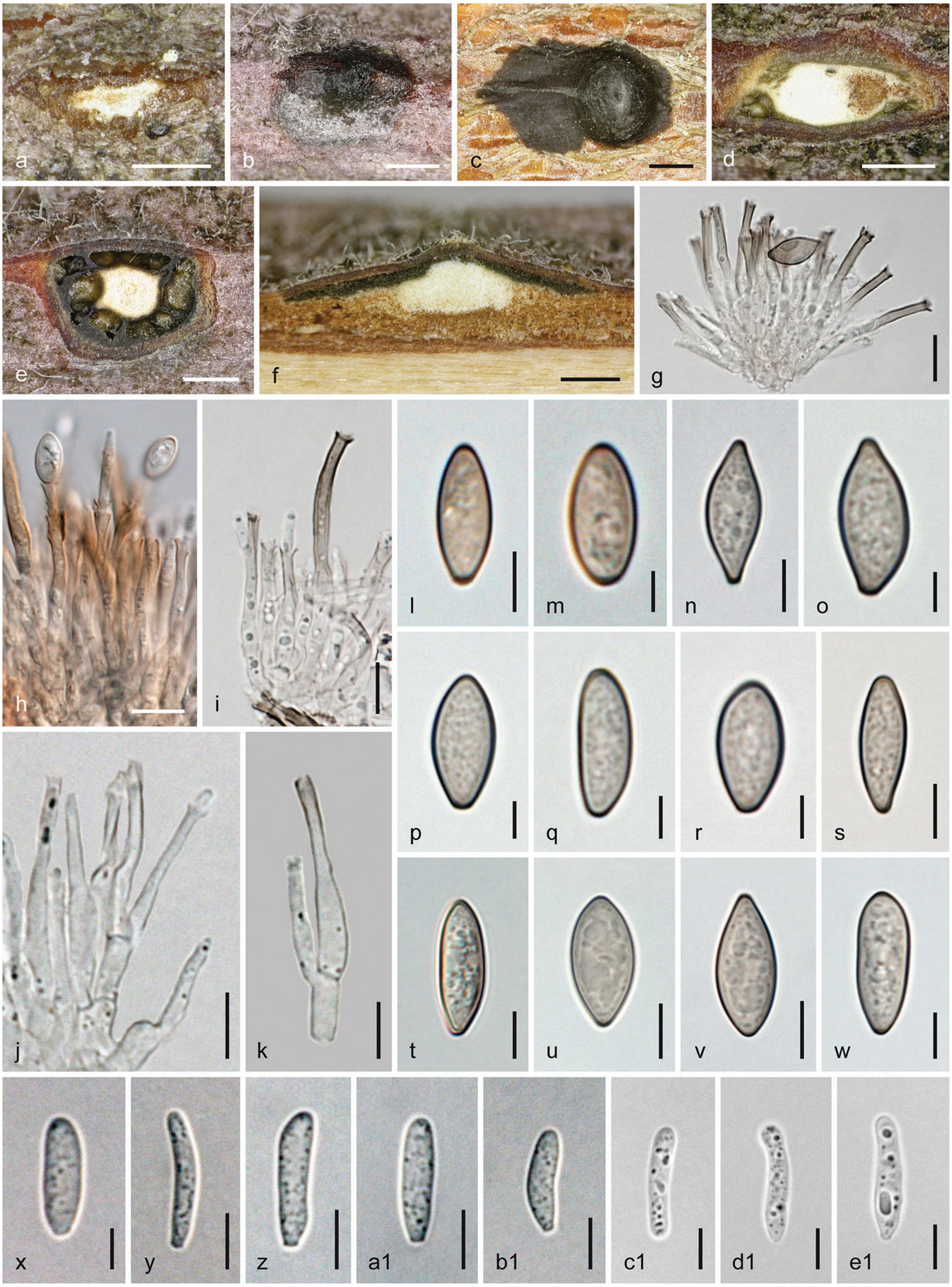

Figure 9. *Melanconis marginalis* subsp. *marginalis*. Asexual morph **a** early stage of covering disc **b, c** conidiomata and conidial deposits in face view **d, e** conidiomata in cross section (**d** with β-conidia, **e** with α-conidia) **f** conidioma with α-conidia in vertical section **g–k** conidiophores and conidiogenous cells (producing α-conidia in **g, h** β-conidia in **i–k**) **l–w** α-conidia **x–e1** β-conidia **g–e1** in 3% KOH **a, b, d–g, i–k, n–s, x–b1** epitype WU 37850 = D321 **c, t–w, c1–e1** DAOM 227767 **h, l, m** BPI 614844. Scale bars: 300 µm (**a, e, f**), 500 µm (**b, d**), 1 mm (**c**), 10 µm (**g, h**), 7 µm (**i, t–v**), 5 µm (**j–l, n, s, w, y–e1**), 3 µm (**m, o–r, x**).

Distribution and ecology. Widespread in North America and also occurring in Japan and eastern Russia on various subspecies of *Alnus alnobetula* and *A. incana*; recorded also from *A. rubra* (Sieber et al. 1991; see also material cited below).

Additional material examined. Canada, British Columbia, Kelowna, June Springs road, June Springs trail, on *Alnus incana*, 18 Jul 1999, J. Ginns 10834 (DAOM 227767; measurements separately given, see below under Notes); Nelson, on *Alnus incana* subsp. *tenuifolia*, soc. *Cryptosporella* sp., 26 Jun 1930, G.G. Hedgcock (BPI 614844, F.P. 50704); Victoria, Lake Cowichan, Mesachie Lake, 48.7942N 124.1573W, on *Alnus rubra*, 14 Sep 1988, C. Dorworth (DAVFP 24976, dried culture PFC-051 only); Victoria, Ucluelet, Kennedy Lake, 49.0416N 125.5315W, on *Alnus rubra*, 16 May 1987, C. Dorworth (DAVFP 24972, dried culture PFC-025 only); Manitoba, W Hawk Lake, on *Alnus* sp., 5 Jun 1932, G.R. Bisby 4593 (DAOM 202917); Nova Scotia, Kings Co., Glenmont, on *Alnus alnobetula* subsp. *crispa* (as *Alnus crispa* var. *mollis*), 25 Jul 1936, I.L. Conners (Ottawa 3798 (DAOM)); Kentville, on *Alnus alnobetula* subsp. *crispa*, 11 May 1953, D. Creelman (DAOM 54346); Ontario, District of Nipissing, Temagami Forest Reserve, Lake Temagami, Bear Island, on *Alnus alnobetula* subsp. *crispa* (as *Alnus viridis* var. *mollis*), 19 Jun 1933, R.F. Cain 2686 (DAOM 86075); trail at Matagama Point, on *Alnus alnobetula* subsp. *crispa* (as *Alnus crispa* var. *mollis*), 23 Jun 1933, R.F. Cain 2687 (DAOM 86074); Sharp Rock Inlet, on *Alnus alnobetula* subsp. *crispa* (as *Alnus crispa* var. *mollis*), 29 Jun 1933, R.F. Cain (BPI 614977, F.P. 69748). Japan, Hokkaido, Shirikinai, on *Alnus alnobetula* subsp. *maximowiczii*, 1 Sept 1967, T. Oguchi (TFM FPH3290; culture MAFF 410218 = M4-6, ME9). RUSSIA, Sakhalin Island, Lake Dvoynoe, on *Alnus alnobetula* subsp. *maximowiczii*, 3 Aug 2000, A. Bogachova, comm. L. Vasilyeva (BPI 748233; culture CBS 109496 = A.R. 3529, ME2). USA, Alaska, Fairbanks, Large Animal Research Station, on *Alnus alnobetula*, 5 Aug 2011, L. Mejia (BPI 884096; culture A.R. 4864, ME5); same area, on *Alnus alnobetula* (given as *Betula neoalaskana*), 5 Aug 2011, L. Mejia (BPI 884097; culture CBS 133346 = A.R. 4865, ME6); Juneau, on *Alnus alnobetula* subsp. *sinuata*, 6 Sep 1936, D.V. Baxter (BPI 615125).

Notes. The asexual morph of *Melanconis marginalis* subsp. *marginalis* is inconspicuous with usually only thin greyish patches of α-conidia. The two types of conidia may be present at the same time or only one is present; acervuli containing α-conidia are sometimes present in pseudostromata of the sexual morph. The specimen DAOM 227767 from *Alnus incana* differs from all others by very large and conspicuous conidial deposits (Fig. 9c), slightly larger α-conidia, (13–)14.5–16.5(–17.5) × (5–)5.8–7(–8) μm, l/w (1.8–)2.1–2.8(–3.4) (n = 70) and longer and more slender β-conidia, (7.5–)12.5–16(–17.3) × (1.7–)2.2–3(–3.5) μm, l/w (4–)4.6–6.7(–9) (n = 35) and also by slightly larger asci, (68–)74–88(–95.5) × (10–)12–15.5(–18.2) μm (n = 26), which approach the European subspecies. Although Jensen (1984) gave a range of 9–17 × 3–7 μm for α-conidia and 10–18 × 2–3 μm for β-conidia of *M. marginalis*, it is unclear, whether all examined specimens, including DAOM 227767, phylogenetically belong to *M. marginalis* subsp. *marginalis* or a different subspecies or even species. Jensen

(1984) reported exceptionally long ascospores (19–32 µm) for four of his collections from Idaho, which also differed in their colony characters; due to lack of DNA data, the taxonomic status of these collections is unclear. While all our North American and Eastern Asian accessions of *M. marginalis* subsp. *marginalis* sequences originated from various subspecies of *Alnus alnobetula*, the accessions investigated by Jensen (1984) originated from *Alnus incana* subsp. *tenuifolia*. Sieber et al. (1991), who investigated *M. marginalis* from British Columbia, recorded mean conidial sizes of 11.2–11.8 × 4.4–4.7 µm for two isolates from *A. rubra*, while those from three isolates of *Alnus alnobetula* were slightly larger (13.6–14 × 5.6–5.9 µm). These data demonstrate the need of additional detailed investigations of the *M. marginalis* complex in western North America. Kobayashi (1970) determined the following sizes for Japanese collections of *M. marginalis*: asci 70–93 × 10–15 µm, ascospores 15–23 × 4–6.5 µm, mostly 17–20 × 4.5–5.5 µm, α-conidia 11.5–15 × 4–6.5 µm, β-conidia 7.5–12.5 × 1.5–2.5 µm. He also mentioned that the Japanese collections usually lacked ascospore appendages, which, however, may be due to the use of a mounting medium instead of water in his microscope mounts. This is supported by the fact that he also reported a lack of appendages in his *M. pterocaryae*, which was disproved by re-investigation of the type (Voglmayr et al. 2017).

Sizes of asci depend on the age of the material. They shrink with time and in specimens, which are 20 or more years old, they are smaller and do not obtain the original size even in KOH; also, it is very difficult to release ascospores from asci. In fresher specimens, asci are easily separable and ascospores are readily released. Vital asci open readily in mounts. Nonetheless, fresh asci of the epitype of subsp. *marginalis* were distinctly smaller than fresh asci of subsp. *europaea*.

Poor representation of the asexual morph in fungarium specimens may be due to the fact that the sexual morph is usually abundant, with numerous white ectostromatic discs; thus, the asexual morph may have been neglected during collecting or even discarded. β-conidia are often absent or scant and old amongst α-conidia in dark conidial deposits, hence they are either not formed or produced before α-conidia.

Melanconis marginalis **subsp.** ***tirolensis*** **Jaklitsch & Voglmayr, subsp. nov.**

MycoBank No: 834111

Figures 10, 11

Diagnosis. This subspecies differs from *Melanconis marginalis* subsp. *europaea* and subsp. *marginalis* phylogenetically and by slightly larger α-conidia, asci, ascospores and ascospore appendages.

Type material. ***Holotype:*** Austria, Tirol, Osttirol, Prägraten am Großvenediger, Umbalfälle, grid square 8939/4, on *Alnus alnobetula*, 10 Sep 2001, W. Jaklitsch W.J. 1796 (BPI 872035; ex-type culture CBS 122310 = A.R. 3748 = ME4; part preserved as isotype WU 31892, asexual morph only present in the latter).

Etymology. Named after its occurrence in Tirol, Austria.

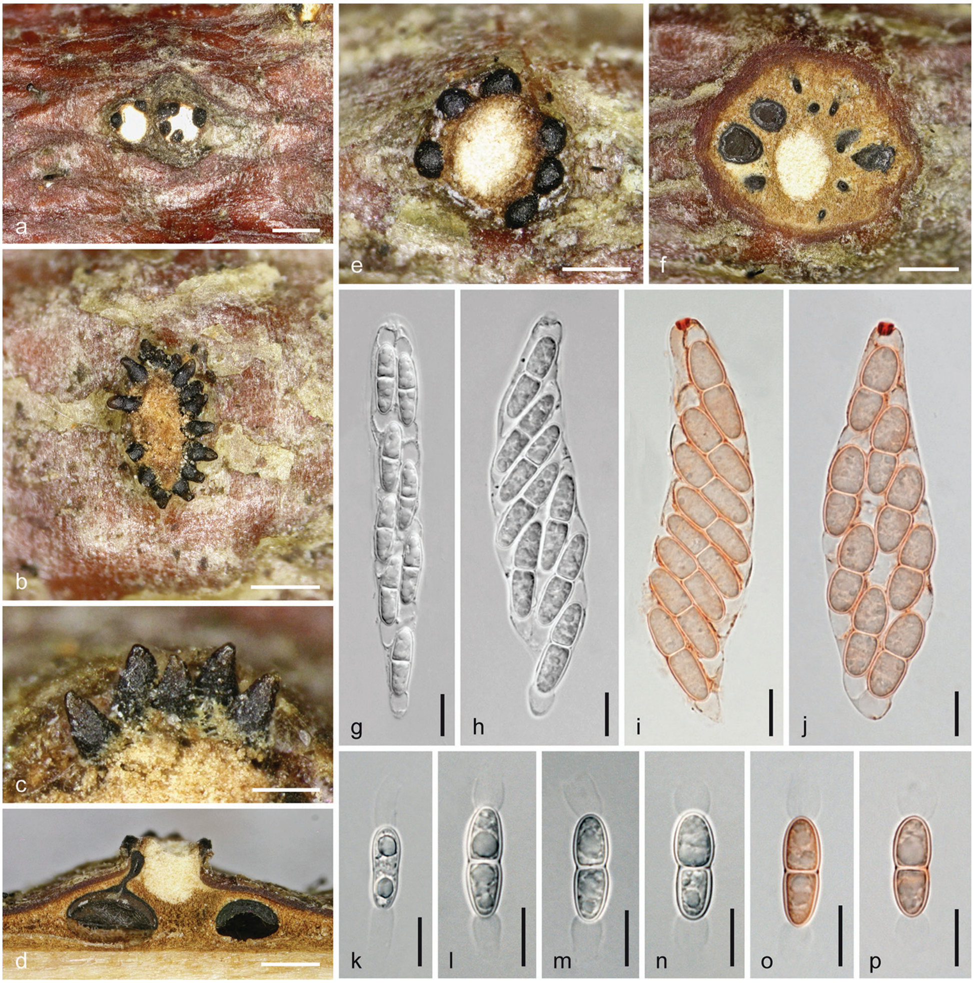

Figure 10. *Melanconis marginalis* subsp. *tirolensis*. Sexual morph **a, b** pseudostromata with ectostromatic discs **c** conical ostioles **d** vertical section showing central column and two perithecia **e** ectostromatic disc with subglobose ostiolar tips **f** cross section showing central column, marginal ostioles and upper parts of perithecia **g–j** asci (compressed in **j**) **k–p** ascospores; **i, j, o, p** in aqueous Congo Red **a, c, k–p** holotype BPI 872035 **b, d–j** isotype WU 31892. Scale bars: 500 µm (**a, b, d, f**), 150 µm (**c**), 300 µm (**e**), 10 µm (**g–p**).

Description. ***Sexual morph:*** *Pseudostromata* 1.3–5.5 mm diam., conspicuous and numerous, scattered to aggregated, pulvinate, circular to elliptical in outline, elevated beyond bark surface forming pustules; consisting of an ectostromatic disc and perithecia embedded in an entostroma around a central column. *Ectostromatic discs* 0.35–1.55 mm (n = 43) diam. or long, bright white to yellowish, turning brownish with age, mostly fusoid, also elliptic or circular in outline, mostly flat, crumbly, distinctly projecting up to 1.3 mm, including projecting part of the pseudostroma; central column beneath disc white to yellowish, consisting of hyaline hyphae and colourless crystals. *Ostiolar necks* cylindrical, laterally or centrally attached on perithecia,

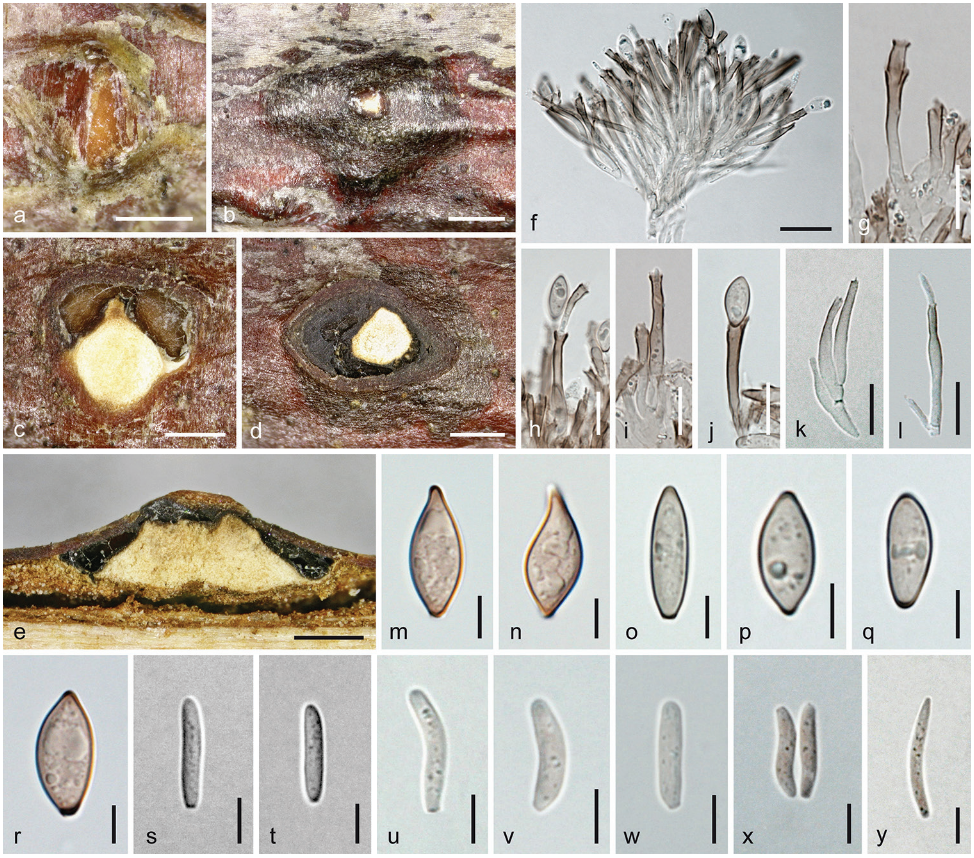

Figure 11. *Melanconis marginalis* subsp. *tirolensis* (isotype WU 31892). Asexual morph **a, b** conidiomata showing covering discs in face view **c, d** conidiomata in cross section (**c** with β-conidia **d** with α-conidia) **e** conidioma with α-conidia in vertical section **f–l** conidiophores and conidiogenous cells (**k, l** producing β-conidia) **m–r** α-conidia **s–y** β-conidia **f–y** in 3% KOH. Scale bars: 500 µm (**a–e**), 15 µm (**f**), 10 µm (**g–l**), 5 µm (**m–y**).

convergent in the disc margin or crowded at the ends of fusoid discs, 1–15 per disc. Visible part of the ostiolar necks (53–)85–180(–240) µm (n = 56) diam., black, often with olivaceous tips, frequently conical to bristle-like and projecting to 0.4 mm, but also papillate, resembling minute perithecia or discoid with depressed centre. *Entostroma* bark coloured, not or only slightly paler than the surrounding bark, consisting of bark cells and some light-coloured hyphae. *Perithecia* (510–)570–780(–900) µm (n = 36) diam., arranged in valsoid configuration around and below central column, globose to subglobose, collapsing up- or laterally inwards upon drying. Peridium pseudoparenchymatous, consisting of a dark brown small-celled outer and a hyaline to brownish, large-celled inner layer. *Hamathecium* absent at maturity. *Asci* floating free at maturity, (74–)86–102(–115) × (11.3–)13–20(–25) µm (n = 61), fusoid to oblong or clavate, short-stipitate prior to full maturation, with an apical ring distinct in water and staining in Congo Red, but invisible or indistinct in 3% KOH, containing 8 biseriate or obliquely uniseriate ascospores. *Ascospores* (15.8–)17.8–21.2(–24) × (4.5–)5.5–7(–8) µm, l/w (2.5–)2.8–3.5(–4) (n = 123), hyaline, turning pale brown with age, oblong to ellipsoid, symmetric to slightly inequilateral with nearly equal cells, slightly or strongly constricted at the median septum, multiguttulate or with 1–2 large and several small guttules when fresh, with a short and broad, rounded, parabolic or vesicular, sometimes tapering but typically terminally broadly truncate appendage (2–)3.8–6.2(–9.5) × (3–)4–5.7(–7.2) µm, l/w (0.4–)0.8–1.4(–2) (n = 104) at each end, after release becoming invisible in 3% KOH, but partly persistent in Congo Red.

Asexual morph acervular, intermingled with pseudostromata of the sexual morph or developing separately, inconspicuous. First white to yellowish tissue (central column) forming within the bark, becoming visible by slightly pustulate bark and narrow whitish to yellowish discs emerging through bark cracks, usually first followed by the production of β-conidia in olivaceous chambers and later α-conidia or both more or less simultaneously on the same or similar conidiophores, chambers fusing into a single locule, turning brown and dark conidial patches 0.5–1.5 mm diam. or perithecia of the sexual morph forming. *Conidiomata* 1.2–3.2 mm diam., pulvinate, more or less circular in outline, scattered or crowded. *Covering discs* 0.2–1.5 mm (n = 14) diam. or long, narrowly fusoid or longish to circular, flat to convex, whitish, yellowish to brownish; discs and pulvinate or conical columns beneath consisting of compact *textura intricata* of hyaline hyphae and numerous colourless crystals, becoming brittle with age. *Conidiophores* emerging around the central column in dense palisades, up to ca. 65 µm long, filiform, branched near the base and usually 1–3 fold asymmetrically at higher levels, first hyaline, turning brown from their tips; terminal conidiogenous cells (9–)15–25(–28) × (1.7–)2.3–3.2(–3.7) µm (n = 63), cylindrical and often widened towards base, even wider at the funnel-shaped tips, with up to 3 annellations, proliferating and producing α- or β-conidia. *Conidia* dimorphic, α-conidia (10–)11.5–16.3(–21.8) × (2.5–)4.5–6.3(–7.5) µm, l/w (1.8–)2.1–3.2(–5.3) (n = 70), first hyaline, soon turning light to medium brown, mostly fusoid, also oblong, oval or ellipsoid, straight or slightly curved, upper end usually subacute and sometimes elongated, lower end narrowly truncate, containing several guttules, smooth; β-conidia (7.3–)8.8–12(–16.5) × (2–)2.2–2.7(–3.4) µm, l/w (2.6–)3.3–5.3(–8.9) (n = 104), hyaline, dilute brownish with age, sometimes turning rosy in 3% KOH, oblong to cylindrical, straight or curved or sigmoid, thick-walled in water, smooth, with truncate basal scar and minute guttules to eguttulate.

Culture: Colony on MEA dense, first hyaline to white, with restricted growth, forming brown radial portions mostly submerged in the agar. Odour unpleasant.

Distribution and ecology. Co-occurring with *Melanconis marginalis* subsp. *europaea* in a subalpine area of eastern Tyrol, Austria, Europe, on *Alnus alnobetula*.

Additional material examined. Austria, Tirol, Osttirol, Virgental, Prägraten am Großvenediger, Lasörling, Zopatnitzen on path between Wetterkreuz and Berger See, 2100 m a.s.l., on *Alnus alnobetula*, 26 Oct 2019, H. Voglmayr & C.M. Botoaca (WU 37851; culture D322a (from α-conidia)).

Notes. As this subspecies differs morphologically only subtly from the other varieties of *M. marginalis*, we prefer to classify it as a subspecies rather than a separate species. While the ITS sequences of *Melanconis marginalis* subsp. *tirolensis* differs from *Melanconis marginalis* subsp. *europaea* in only a single base pair, the differences are substantial in all other markers included, particularly *tef1* and *tub2*.

Melanconis pacifica **Jaklitsch & Voglmayr, sp. nov.**

MycoBank No: 834112
Fig. 12

Diagnosis. This species is characterised by its occurrence on *Alnus rubra* and α-conidia, which are wider and darker than those of *M. marginalis* and differ by a different shape and absence of a light band from those of *M. alni*.

Type material. ***Holotype.*** Canada, British Columbia, Sidney, off Jura, on *Alnus rubra*, 26 May 2000, M.E. Barr 1021A (DAOM 230637; ex-type culture CBS 109744; isotype BPI 748446).

Etymology. For its occurrence in the Pacific region of western North America.

Description. ***Asexual morph:*** *Conidiomata* 0.7–2.1 mm diam., visible as dark brown to blackish spots, acervular, subperidermal, scattered, discrete, rarely two confluent, pulvinate to conical, consisting of an erumpent central or eccentric, circular or elliptic to fusoid, flat or convex *disc* 0.2–1.3 mm diam., whitish, yellowish to reddish-orange when young, becoming concealed by ejected conidia and internally a narrow central or eccentric, whitish to yellowish stromatic column sometimes fraying out laterally and a dark ring-like periphery containing conidia. *Conidia* becoming discharged through a mostly slit-like rupture of the disc, forming dark brown to black, up to 0.7 mm high masses or tendrils. *Conidiophores* densely aggregated forming palisades, up to ca. 50 µm long, arising from a yellowish, nearly pseudoparenchymatous tissue of compacted hyphae, either consisting solely of conidiogenous cells or of a stout main axis with few side branches and a terminal whorl of 2–4 more or less vertical conidiogenous cells, hyaline to yellowish. *Conidiogenous cells* mostly 11–32 × (2–)2.5–3.3(–3.5) µm, annellidic, more or less cylindrical, hyaline, turning brown with age, forming simultaneously two types of conidia on top. *Conidia* dimorphic, *α-conidia* (8.8–)10.5–12.5(–15.5) × (5–)6.5–7.7(–8.8) µm, l/w (1.2–)1.4–1.8(–2.7) (n = 615), oval to ellipsoid, dark brown, with a distinct basal abscission scar; *β-conidia* (6.2–)8.2–12.5(–18.5) × (2–)2.3–3(–3.6) µm, l/w (1.7–)3–4.9(–7.6) (n = 103), oblong to cylindrical, straight or curved, sometimes sigmoid or kidney-shaped to subellipsoid, hyaline, turning dilute brownish with age, typically containing two subterminal groups of minute guttules, with a distinct basal abscission scar.

Culture: Colony on MEA circular, first hyaline, turning white and later brownish in spots or patches, with stellate margin and radial stripes; black conidiomata forming along the stripes. Odour indistinct.

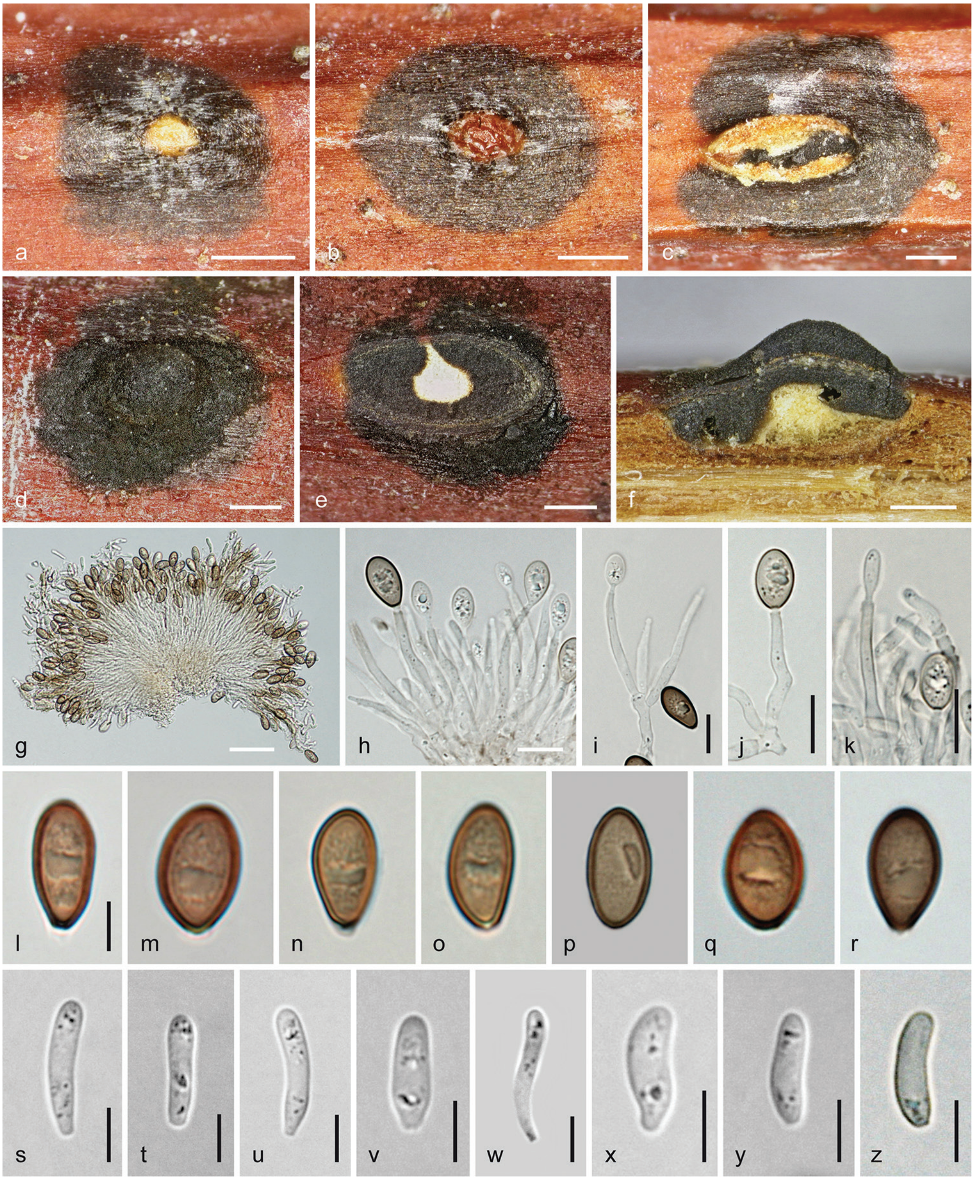

Figure 12. *Melanconis pacifica*. Asexual morph **a–d** conidiomata in face view **e** conidioma in cross section **f** conidioma in vertical section **g–k** conidiophores (**g** with both conidial types, note annellations in right conidiophore in **k**) **l–r** α-conidia **s–z** β-conidia **a–k, n–p, z** DAOM 220988 **l, m, r–y** holotype DAOM 230637 **q** isotype BPI 748446 **g–o, r–z** in 3% KOH. Scale bars: 300 μm (**a–f**), 30 μm (**g**), 10 μm (**h–k**), 5 μm (**l–z**).

Additional materials examined (all on/from *Alnus rubra*). Canada, British Columbia, Sidney, Bazan Bay, 28 May 1995, M.E. Barr (DAOM 220988); Victoria, 26 km N of Campbell River, 50.1262N, 125.3084W, 2 Jan 1989, T.N. Sieber

(DAVFP 24981, dried culture PFC-071 only); Caycuse, W shore of Cowichan Lake, 48.8810N, 124.4321W, 24 Oct 1988, T.N. Sieber (DAVFP 24980, dried culture PFC-068 only); Gordon Head, C. Dorworth's property, 48.4396N, 123.3380W, 4 Jun 1988, C. Dorworth (DAVFP 24973, dried culture PFC-043 only); East Sooke, 48.4377N, 123.7436W, 29 Jun 1948, W.G. Ziller (DAVFP 3092); Nanaimo, DeCourcy Island, 49.0641N, 123.7732W, 1 Jun 1988, C. Dorworth (DAVFP 24974, dried culture PFC-047 only); Parksville, NW Bay, 3.1 km W of M&B office, 49.3238N, 124.1479W, 13 Jul 1988, C. Dorworth (DAVFP 24975, dried culture PFC-050 only); Port Renfrew, Sombrio Beach, 48.5229N, 124.2866W, 4 Nov 1988, C. Dorworth (DAVFP 24977, dried culture PFC-053 only); Revelstoke, Jordan River, gravel pit S of the river, 48.4356N, 124.0140W, 24 Oct 1988, C. Dorworth (DAVFP 24978, dried culture PFC-055 only); ibid., 24 Oct 1988, T.N. Sieber (DAVFP 24979, dried culture PFC-067 only); Sooke, East Sooke Park, Babbington Trail, 48.3485N, 123.6073W, 9 Sep 1988, C. Dorworth (DAVFP 25029, dried culture PFC-054).

Notes. The description is largely based on DAOM 220988 due to good development of conidiomata. However, we select DAOM 230637 as the holotype, because DNA data are only available for this specimen. Microscopic data of the two specimens are identical. This species is currently only known as an asexual morph. One specimen from Victoria (DAVFP 3092) contains also an immature sexual morph, which corresponds to *Melanconis alni* superficially. Barr apparently identified her collections as *M. marginalis* because the latter was, at that time, considered to be the only alnicolous species occurring in North America (Jensen 1984), which also occurs on *A. rubra* (Sieber et al. 1991). However, the conidia of the latter species are longer, more fusoid, have a larger l/w ratio and are lighter in colour than those of *M. pacifica*. α-conidia of *M. pacifica* and *M. alni* are virtually identical in size. Those of the latter, however, have a different shape, a median light band and a more greyish-brown colour. Remarkably, Wehmeyer (1941) mentioned a collection from the American Pacific region (Oregon) which had conidia resembling *Melanconium sphaeroideum*, a synonym of *M. alni*. Sieber et al. (1991) included 10 isolates from *Alnus rubra*, sampled in British Columbia, that they identified as *Melanconium apiocarpum*, another synonym of *M. alni* (see above), based on conidial size and shape. Their measurements and, in particular, their illustration (fig. 2a) of α-conidia fully agree with *M. pacifica*. The isozyme patterns of Sieber et al. (1991) revealed high similarities, but also diagnostic differences between the isolates from European *A. glutinosa* and Canadian *A. rubra*, which is in agreement with the close phylogenetic relationship between *M. alni* and *M. pacifica*. Our morphological re-investigations of the isolates of Sieber et al. (1991), which are kept as dried cultures at DAVFP (see specimens cited above), confirmed that they represent *M. pacifica*.

In DAOM, two additional specimens, labelled *Melanconis marginalis* collected by Barr in the same area, are extant, DAOM 227727 and DAOM 227345. These specimens, however, do not contain *M. pacifica*, but the sexual morph of a *Diaporthe* sp.

Melanconis stilbostoma **(Fr. : Fr.) Tul. & C. Tul., Select. fung. carpol. (Paris) 2: 115 (1863).**

Figure 13

≡ *Sphaeria stilbostoma* Fr. : Fr., K. svenska Vetensk-Akad. Handl., ser. 3, 39: 102 (1818) (Basionym)

≡ *Melanconis stilbostoma* (Fr. : Fr.) Tul., Annls Sci. Nat., Bot., sér. 4, 5: 109 (1856). (Nom. inval., Art. 35.1).

?= *Melanconium bicolor* Nees : Fr., Syst. Pilze (Würzburg): 32 (1816) [1816–17].

= *Melanconium betulinum* J.C. Schmidt & Kunze, Deutschl. Schwämme, Neunte Lieferung: 3 (1819).

= *Melanconium elevatum* Corda, Icon. fung. (Prague) 3: 22 (1839).

Type material. ***Lectotype.*** Sweden, without data, Fries, Scleromyc. Suec. no. 145, as *Sphaeria stilbostoma* (UPS:BOT:F-117590, lectotype here designated; MBT390467)). ***Epitype,*** here designated: Austria, Tirol, Prägraten, Umbalfälle, grid square 8939/4, on *Betula pendula*, 28 Aug 2000, W. Jaklitsch W.J. 1543 (BPI 748447; ex-epitype culture CBS 109778 = A.R. 3501 = ME11; AFTOL-ID 936; MBT390383; iso-epitype WU 31897).

Description. ***Sexual morph:*** *Pseudostromata* 1.3–3.6(–4.5) mm diam., scattered to aggregated, slightly or distinctly projecting from bark surface, pulvinate with bluntly conical centre (projecting disc), circular to elliptical in outline; consisting of an ectostromatic disc and perithecia embedded in an entostroma around a central column and often chambers filled with conidia. *Ectostromatic discs* 0.4–2.4(–2.7) mm diam. or length, fusoid to circular, projecting from the bark surface to 0.5 mm, less commonly 1 mm including pseudostroma, white or yellow, brown when old, flat, concave or convex, often completely filled by tips of ostiolar necks; central column beneath disc brightly white to yellow, consisting of hyaline hyphae and colourless crystals. *Ostiolar necks* cylindrical, laterally or centrally attached on perithecia, convergent and densely and irregularly or evenly disposed in the disc or around the margin; visible part in the discs (106–)139–231(–283) μm (n = 68) diam., 1–25 per disc, shiny black, convex papillate, discoid with depressed centre or conical to cylindrical and projecting to 300 μm. *Entostroma* paler than surrounding inner bark, consisting of hyaline to white hyphae and bark cells, sometimes forming white patches. *Perithecia* (450–)540–700(–780) μm (n = 45) diam., arranged in valsoid configuration around and below central column, globose to subglobose, collapsing upon drying. *Peridium* pseudoparenchymatous, consisting of a dark brown small-celled outer and a hyaline to brownish, large-celled inner layer. *Hamathecium* absent at maturity. *Asci* floating free at maturity, (69–)80–123(–141) × (10–)13–18(–21) μm (n = 64), fusoid to oblong or narrowly clavate, with an apical ring distinct in water and staining in Congo Red but invisible or indistinct in 3% KOH, containing 4–8 biseriate or obliquely uniseriate ascospores. *Ascospores* (13.7–)16–19(–23) × (4.7–)6.5–8.5(–9.7) μm, l/w (1.9–)2.1–2.7(–3.6) (n = 186), first narrow, fusoid or oblong and with small roundish appendages (1.5–)2–5(–7.3) × (2.2–)3.3–5.5(–6.8) μm, l/w (0.3–)0.5–1.1(–1.7) (n = 60) within

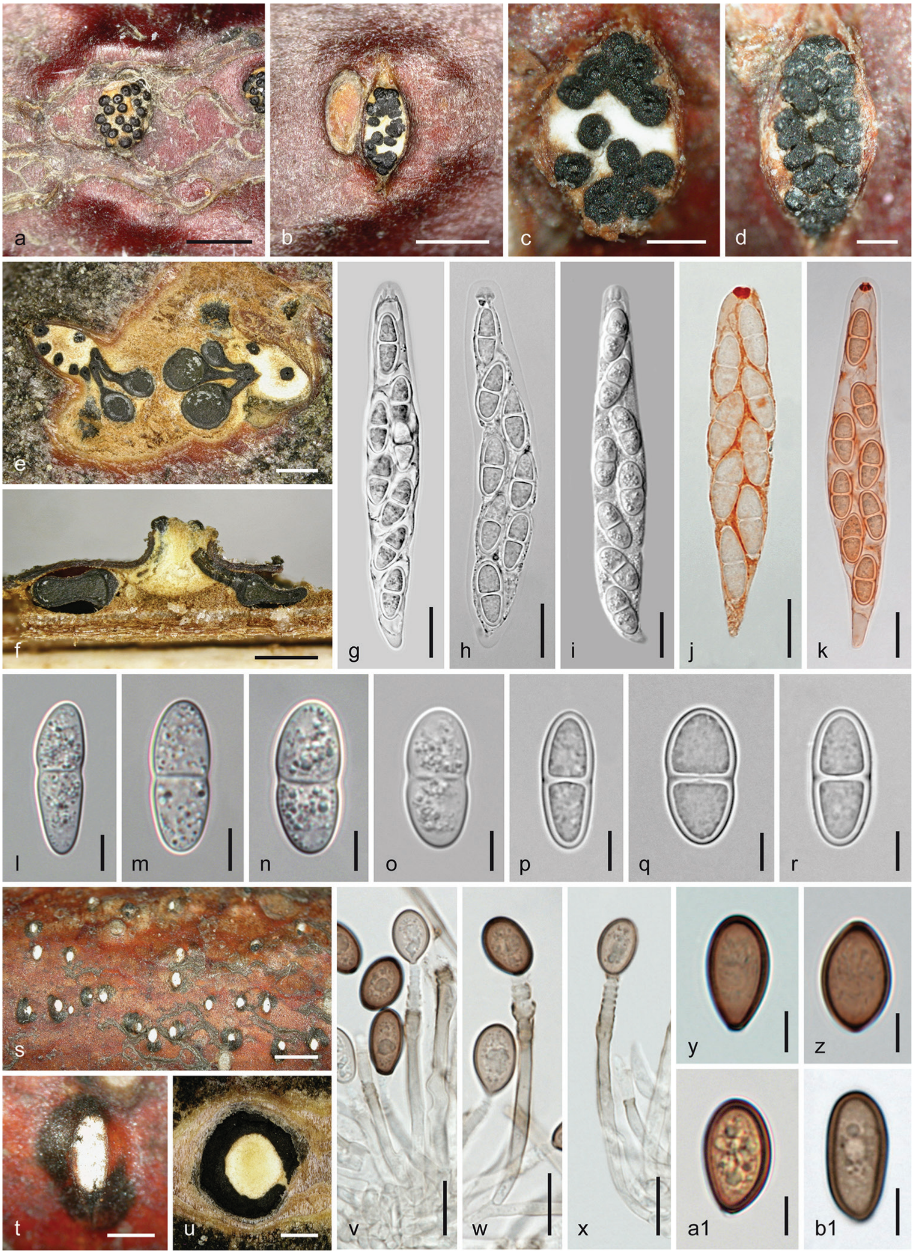

Figure 13. *Melanconis stilbostoma*. **a–r** Sexual morph **a–d** pseudostromata with ectostromatic discs in face view **e** cross section through 2 adjacent pseudostromata **f** vertical section showing 2 perithecia, ostiolar necks and central column **g–k** asci **l–r** ascospores **j, k** in aqueous Congo Red **s–b1** Asexual morph **s, t** conidiomata in face view **u** conidioma in cross section **v–x** conidiophores and conidiogenous cells **y–b1** α-conidia **v–b1** in 3% KOH **a, j, s, v–x** iso-epitype WU 31897 = W.J. 1543 **b–d** WU 31896 **e–g, i, k, o** WU 38241 **h, p, q** WU 36779 **l–n, a1** WU31899 **r** WU 37048 **t** WU 31894 **u** WU 15266 **y** *M. betulinum* B700016529 **z** *M. betulinum* B700016528 **a1** WU31899 **b1** WU 35970 = D143. Scale bars: 1 mm (**a, b**), 300 µm (**c, d**), 500 µm (**e, f, t, u**), 15 µm (**g–k**), 5 µm (**l–r, y–b1**), 2 mm (**s**), 10 µm (**v–x**).

asci, later becoming broadly ellipsoid with rounded ends, symmetric or inequilateral, slightly constricted at the central to slightly eccentric septum, hyaline, thick-walled, smooth; appendages fugaceous and absent on released ascospores.

Asexual morph acervular, intermingled with pseudostromata of the sexual morph or developing separately, conspicuous. First white tissue (central column) forming within the bark, becoming surrounded by sterile yellow margin and narrow discs rupturing bark epidermis, followed by the production of conidia in olivaceous to black chambers containing black conidial masses translucent though bark. *Conidiomata* 0.9–3.2 mm diam., subconical or pulvinate, more or less circular in outline, scattered or crowded.

Covering discs 0.3–1.2 mm long, slit-like to circular, flat to convex, shiny white to yellowish, becoming obscured by dark olivaceous brown to black conidial deposits forming patches to 2.7 mm diam., sometimes confluent to 1 cm; discs and pulvinate or conical columns beneath, consisting of dense *textura intricata* of hyaline hyphae and numerous colourless crystals, becoming brittle with age. *Conidiophores* emerging around the central column from a pseudoparenchymatous base, filiform, branched near the base and usually 1–3 fold asymmetrically at higher levels, first hyaline, turning brown from their tips; terminal *conidiogenous cells* (11.5–)18–33(–42.5) × (2–)2.5–3.5(–4.5) µm (n = 47), more or less cylindrical, with up to 5 or 6 annellations, densely arranged, repetitive, producing α-conidia. *Conidia* (10.5–)12.5–15(–17.5) × (6.2–)7.2–8.5(–9.5) µm, l/w (1.3–)1.6–2(–2.7) (n = 260), oval, ellipsoid or subglobose, 1-celled, dark brown, thick-walled, smooth, with a few drops and a small scar. No β-conidia detected.

Culture: Colony on CMD at 16 °C forming irregular white and brown to ochre zones partly covered by aerial hyphae or hyaline, undifferentiated, forming brown spots and irregularly disposed conidiomata; on MEA at room temperature first white, later with broad white and brown zones with undulating margin and conidiomata forming mostly on the outer margin. Odour indistinct to fruity.

Distribution and ecology. *Melanconis stilbostoma* occurs frequently on *Betula* spp. on the northern Hemisphere in Asia, Europe and North America (Barr 1978; Fan et al. 2016, 2018; Kobayashi 1970; Sogonov et al. 2008).

Other material examined. (all on twigs of *Betula pendula* except where noted): **Austria**, Kärnten, Gallizien, near Wildensteiner Wasserfall, grid square 9453/3, 11 Jul 2007, W. Jaklitsch (WU 31896); St. Margareten im Rosental, village area, grid square 9452/4, 27 May 1992, W. Jaklitsch (WU 15266); Trieblach, below Cihuc, grid square 9452/2, 14 Apr 2001, W. Jaklitsch W.J. 1740 (WU 31895, BPI 872036; culture A.R. 3637); Wograda, grid square 9452/3, 27 May 1997, W. Jaklitsch W.J. 1080 (WU 31894); same area and host, 31 May 2000, W. Jaklitsch W.J. 1474 (BPI 871332); Zabrde, grid square 9452/4, 7 Aug 1993, W. Jaklitsch (WU 15191); Niederösterreich, Aspangberg-St. Peter, Außerneuwald, Höllergraben, grid square 8462/1, 24 May 2015, G. Koller (WU 36779); Edlitz, Königsberg, grid square 8562/2, 14 Jul 2007, W. Jaklitsch W.J. 3125 (specimen lost; culture MS = CBS 121894); Friedersbach, S and SO from the village, grid square 7457/2, 19 Aug 2001, W. Jaklitsch W.J. 1775 (BPI 872038; culture A.R. 3725); Neunkirchen, Gloggnitz, Saloder, village area, grid square 8361/2, 10 May 2015, G. Koller (WU 36752); Grimmenstein, between Eben and the Kulmriegel, grid square 8362/4, 14 May 2015, G. Koller (WU 36812); Thaures, grid square 7156/1, 21 Sep 1997, W. Jaklitsch W.J. 1109 (WU 37048); Weidlingbach, grid square 7763/1, 27 Jun 1999, W. Jaklitsch W.J. 1329 (WU 37049); Oberösterreich, Schärding, Raab, Rothmayrberg, Rothmayr, 10 Mar 2012, H. Voglmayr (WU 38241); St. Willibald, Großer Salletwald, at the road B 129 to Peuerbach, grid square 7648/1, 31 Dec 2011, H. Voglmayr (WU 31899); Vienna, Alsergrund, at the hospital AKH, grid square 7764/3, 23 Jul 1993, W. Jaklitsch (WU 15537); Favoriten, Rothneusiedl, grid square 7864/3, 4 Sep 1993, W. Jaklitsch (WU 15758); ibidem, 22 Jan 1994, W. Jaklitsch (WU 15559). **Czech Republic**, Bohemia, Malonty, Hodonický potok, grid square 7253/3, 25 Sep 2003, W. Jaklitsch W.J. 2427 (WU 31898). **Germany**, no collection data (type material B 700016528 and B 700016529 of *Melanconium betulinum* from B). **Italy**, Sicily, Etna, SW Linguaglossa, near I Due Monti, on *Betula aetnensis*, 18 Jun 2016, H. Voglmayr & W. Jaklitsch (WU 37047; culture D258). **Japan**, Nagano, Karuizawa, Mt. Asama, on *Betula platyphylla* Sukachev var. *japonica* (Miq.) Hara, 21 Sep 1965, T. Kobayashi (TFM FPH2710; culture MAFF 410225 = M3-9 = ME12). **Poland**, Narewka, NE Nowa Lewkowo, 27 Jul 2015, H. Voglmayr (WU 35970; culture D143).

Notes. *Melanconis stilbostoma* and its basionym *Sphaeria stilbostoma* (α *papula*) were mentioned by Tulasne (1856), but the combination was invalid due to the lack of a generic diagnosis; it was, however, validated in Tulasne and Tulasne (1863). According to Ibai Olariaga, who examined the type in UPS, there are 3 scalps of *Betula* bark containing many clustered perithecia with black ostiolar necks erumpent through a white disc; neither asci nor spores were found, but brown α-conidia are present abundantly. As the type collection was distributed in Fries' Scleromyceti Sueciae no. 145, we here lectotypify the species with the copy preserved in UPS, which we epitypify with a recent well-developed collection for which a culture and sequence data are available.

Several asexual morph names have been linked with *Melanconis stilbostoma*: *Melanconium bicolor* predates *Melanconis stilbostoma*, but there is no material extant in B, thus it cannot be checked; also *Quercus* but not *Betula* was given as host in the protologue. In addition, *Melanconis stilbostoma* is a well-known and well-defined name for the generic type of *Melanconis*. The second name is *Melanconium betulinum*, which is clearly a later synonym upon our examination of type material. *Melanconium elevatum* is another synonym. We have, however, not seen type material of this taxon, but the description and illustrations in Corda (1839) are conclusive. *Melanconis stilbostoma* is a very common fungus on birch throughout the northern hemisphere and likely the most conspicuous species of *Melanconis* due to the shiny white discs of both morphs, contrasting the dark conidial deposits. In older specimens, the latter may have olivaceous tones, but much less conspicuously than with *M. larissae*. The latter species differs also in a broad light zone present on its conidia. *Melanconis stilbostoma* was already cultured by Wehmeyer (1926b) on birch twigs from material, whose ascospore measurements were (13–)15–18 × 5–8 µm, corresponding to those of Barr (1978: 12–18.5 × 6.5–8(–9) µm). Wehmeyer (1941) gave (13–)15–19(–23) × (5–)6–7.5(–9) µm for ascospores, which is in accordance with our measurements ((13.7–)16–19(–23) × (4.7–)6.5–8.5(–9.7) µm); Kobayashi (1970) measured 13–25 × 4–7.5 µm, mostly 15–20 × 5–7 µm and Fan et al. (2016) gave (19–)21.5–23.5(–25) × (6–)7–8 µm, which is slightly larger. Wehmeyer (1941) noted for α-conidia from culture and exsiccata mostly 10–16 × 5.5–7.5 µm and 6.5–12 × 2–2.5 for β-conidia in culture; Barr (1978) found only α-conidia and measured 9–16.5 × 5–7.5 µm, which is in accordance with our observations from Europe (see above). Asian authors gave 9–16.5 × 5–7.5 µm (Kobayashi 1970) and (8.5–)9–14.5(–16) × (4.5–)5–6(–6.5) µm (Fan et al. 2016) for α-conidia, but, in some collections, they also found cylindrical to allantoid, unicellular, hyaline β-conidia, 9–11.5 × 1.5–2.5 µm (Kobayashi 1970) or (9–)10–11(–12.5) × (2–)2.5–3 µm (Fan et al. 2016).

Validation of neotypification

Here we also validate the neotypification of *Melanconium pterocaryae*, the basionym of *Juglanconis pterocaryae* by Voglmayr et al. (2019), where the new requirement to explicitly state the MBT number in the typification proposal was missing:

***Juglanconis pterocaryae* (Kuschke) Voglmayr & Jaklitsch, in Voglmayr, Castlebury & Jaklitsch, Persoonia 38: 150 (2017).**

≡ *Melanconium pterocaryae* Kuschke, Trudy Tiflissk. Bot. Sada 28: 25 (1913) (Basionym).

Typification. Austria, Oberösterreich, Bad Hall, Kurpark, on corticated twigs of *Pterocarya fraxinifolia*, 20 Oct 2017, W. Jaklitsch (WU 39981, neotype of *Melanconium pterocaryae* here proposed; ex neotype culture D272 = CBS 144326; MBT 389379).

Discussion

Circumscription of the genus *Melanconis*, morphology and delimitation from morphologically similar genera

As already mentioned in the Introduction, the genus *Melanconis* historically has been considered a large, heterogeneous genus. Many species were removed to other genera in the past on morphological grounds or due to different associated asexual morphs: *Chapeckia* (Barr 1978), *Caudospora* (Starbäck 1889), *Hapalocystis* (Fuckel 1863), *Macrodiaporthe* (Petrak 1920), *Massariovalsa* (Saccardo 1882; Barr 1978), *Phaeodiaporthe* (Petrak 1920), *Pseudovalsa* (Ces and De Not 1863) and *Pseudovalsella* (Höhnel 1918). Only recently, species were relegated to other genera and families based on molecular phylogenetic analyses: *Alnecium* (Voglmayr and Jaklitsch 2014), *Caudospora* (Voglmayr and Mehrabi 2018), *Coryneum*/*Pseudovalsa* (De Silva et al. 2009), *Hapalocystis* (Jaklitsch and Voglmayr 2004), *Juglanconis* (Voglmayr et al. 2017, 2019), *Lamproconium* (Norphanphoun et al. 2016), *Melanconiella* (Voglmayr et al. 2012), *Phaeo-*

diaporthe (Voglmayr and Jaklitsch 2014), *Stilbospora*/*Prosthecium* (Voglmayr and Jaklitsch 2008, 2014).

All melanconis-like species form their fructifications in bark and lack black zones, which delimit the pseudostromata from surrounding bark tissue in genera like *Diaporthe*. The sexual morph in *Melanconis* sensu stricto is characterised by distinctly projecting white to yellowish ectostromatic discs, which continue as stromatic central columns downwards, by entostroma, which is optically scarcely different from internal bark tissue, by long cylindrical ostiolar necks, which converge in the disc, by hyaline bicellular ascospores with or without appendages, by absence of paraphyses at maturity and asci, which have an apical ring and are released from the subhymenium at maturity. Conidiomata of the asexual morph are acervular. They commonly produce two types of conidia, melanconium-like brown α-conidia and narrow hyaline to brownish β-conidia. Species of *Dendrostoma* in the Erythrogloeaceae (Jaklitsch and Voglmayr 2019; Jiang et al. 2019) also produce two types of conidia on the same conidiophores, but both are hyaline. Acervuli of *Melanconis*, however, particularly in *M. marginalis*, form chambers, in which first β-conidia are produced. Such chambers are still present when α-conidia are produced, but in the latest stages of maturation, the entire fertile region around the central column is filled with α-conidia and appears as a single locule. In species of the morphologically most similar genera *Melanconiella* (Voglmayr et al. 2012) and *Juglanconis* (Voglmayr et al. 2017, 2019), pseudostromata are less conspicuous and project to a lesser degree from the bark surface than in *Melanconis*. The central column in *Melanconiella* is usually grey, dull yellow to greenish, only rarely white and often poorly developed and ascospores may be hyaline or brown. The most striking difference between *Melanconis* and *Melanconiella* lies in the asexual morph. In *Melanconis*, each species produces α- and β-conidia in the same conidiomata, whereas each species of *Melanconiella* only produces a single type of conidia, either brown melanconium-like (corresponding to α-conidia) or hyaline discosporina-like conidia (corresponding to β-conidia). Species of *Juglanconis* only produce melanconium-like conidia, which have a gelatinous sheath (also present in a few *Melanconiella* spp.) and differ from the other genera by the presence of verrucae on the inner surface of the conidial wall.

Molecular phylogeny, species numbers, concept and delimitation

In *Melanconiella*, 15 species have been recognised (Voglmayr et al. 2012; Fan et al. 2018) and five in *Juglanconis* (Voglmayr et al. 2017, 2019). Fan et al. (2016, 2018) included five species of *Melanconis* sensu stricto in their phylogenetic trees. Here we add three species, of which two are new. While all betulicolous species, except for the basal *M. betulae*, formed a highly supported clade, those on *Alnus* were scattered in between, so no general evolutionary pattern in host association could be revealed. Remarkably, within species, a commonly high genetic divergence and variability was observed (e.g. within *M. groenlandica*, *M. itoana*, *M. marginalis* and *M. stilbostoma*; see Fig. 1), contrary to *Melanconiella* and *Juglanconis*, where the species clades were genetically rather homogeneous (Voglmayr et al. 2012, 2017, 2019; Fan et al. 2018). This may, in part, be attributed to the wider geographic distribution and host range of these *Melanconis* species, but it may also indicate that they are within the process of evolutionary radiation and speciation. Although the species concept in *Melanconis* is primarily based on phylogenetic analyses, we consider morphological and ecological evidence as important criteria for taxonomic conclusions. The taxa on *Betula* spp. may be more or less easily distinguished by differences in the morphology of α-conidia and by ecology: α-conidia of *M. larissae* have a large light-coloured zone, those of *M. itoana* have a l/w ratio of > 3 and those of *M. betulae* and *M. groenlandica*, as given by the respective authors, are shorter than those of the other species, albeit similar. However, the latter two species occur on different host species: *M. betulae* on *Betula albosinensis*, *M. groenlandica* on *Betula maximowicziana*, *B. nana* and *B. papyrifera*.

Taxa on *Alnus* spp. may pose difficulties in differentiation. Ascospores of *M. alni* and *M. marginalis* differ in shape, size and particularly in appendages from each other. Nonetheless, all features are overlapping and, for example, ascospore appendages of *M. alni* are not always long and pointed, particularly in old fungarium specimens, but show some similarities with those of *M. marginalis*. In such cases, it is important to have the asexual morph in order to study its conidia, which are strikingly different from those of *M. marginalis*. The same applies to *Melanconis* accessions from the western North American *Alnus rubra*, where the co-occurring *M. pacifica* and *M. marginalis* can be reliably distinguished by their conidia (see, for example, also fig. 2 in Sieber et al. 1991).

The situation is particularly complex within *M. marginalis*, which splits up into four subclades in our phylogenetic analyses. Morphology amongst those subclades is very similar, measurements are heavily overlapping and only subtle differences or tendencies are recognisable. In addition to the lack of distinctive morphological characters, there is also a substantial amount of genetic variation within the two of the four subclades, for which several accessions are available, particularly within *M. marginalis* sensu stricto, which will certainly increase if more accessions from additional geographic areas and *Alnus* species and subspecies are added. Only a small part of the distribution area of *M. marginalis* is yet sampled. We, therefore, do not think that these subclades should be interpreted as different species, but as a single variable species. Acknowledging the geographical and genetic differentiaton, we decided to classify them as subspecies that may be within the process of speciation. Vicariant speciation may be the reason for splitting of the *M. marginalis* clade into two main clades, but the residual two clades that are only based on a single and two specimens, were gathered within a small restricted region in Austria and northern Italy. The internal structure of the whole clade may therefore change, in particular, if isolates from additional specimens collected in western and central Russia were added to the phylogenetic analyses and if sequences of all phylogenetic markers of *Melanconis marginalis* subsp. *italica* were included.

Misidentification of *M. alni* and *M. marginalis* is also prominent in GenBank sequences that were used in all published phylogenetic analyses including these species, resulting in an interchanged application of the names. Based on, as we now know, incorrect assumptions purported in the literature (e.g. Wehmeyer 1941) that *M. marginalis* is a North American and *M. alni* a European species, Central European accessions of *M. marginalis* were misidentified as *M. alni*. Vice versa, M.E. Barr misidentified her Canadian isolate from *Alnus rubra*, that is closely related to *M. alni* and here described as *M. pacifica*, as *M. marginalis*. Therefore, all sequences currently deposited in GenBank as *M. alni* actually represent *M. marginalis*, while those of *M. marginalis* belong to *M. pacifica*.

Hosts

While *Juglanconis* is confined to the Juglandaceae, subtribus Juglandinae (Voglmayr et al. 2017, 2019), both *Melanconiella* and *Melanconis* occur on the Betulaceae. So far, species of *Melanconiella* primarily occur on the subfamily Coryloideae with the exception of *M. betulae* and *M. decorahensis*, which inhabit *Betula* (Voglmayr et al. 2012; Fan et al. 2018). In contrast, *Melanconis* is confined to *Alnus* and *Betula*, the sole genera of the subfamily Betuloideae. While all known *Melanconis* species are highly host specific on the generic level (i.e. no *Melanconis* species occurs on *Alnus* as well as *Betula* hosts), host specificity is less expressed and variable concerning their host species range. In addition, the same host species is commonly used by more than one *Melanconis* species. For instance, the widely distributed *M. stilbostoma* has been recorded from various species of *Betula*, which is likewise true for *M. groenlandica* (for confirmed hosts, see Table 1). Conversely, *M. betulae* is so far only known from a single host, *B. albosinensis*, which, however, is also host for *M. itoana* (Fan et al. 2016, 2018). For *Melanconis* species on *Alnus*, *M. alni* and *M. marginalis* show some host specificity but are not strictly host specific; while *A. glutinosa* and *A. alnobetula* are apparently only colonised by *M. alni* and *M. marginalis*, respectively, both species occur on *A. incana*. *Melanconis pacifica*, here described as a new species, seems to be host specific on *A. rubra*, which, however, also harbours *M. marginalis*. Therefore, the host species are of limited use for species identification and additional investigations are required to elucidate the host range of the various *Melanconis* species.

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Arboricolonus simplex gen. et sp. nov. and novelties in *Cadophora*, *Minutiella* and *Proliferodiscus* from *Prunus* wood in Germany

Steffen Bien[1], Ulrike Damm[1,2]

1 *Senckenberg Museum of Natural History Görlitz, PF 300 154, 02806 Görlitz, Germany* **2** *International Institute Zittau, Technische Universität Dresden, Markt 23, 02763 Zittau, Germany*

Corresponding author: *Ulrike Damm* (ulrike.damm@senckenberg.de)

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Abstract

During a survey on fungi associated with wood necroses of *Prunus* trees in Germany, strains belonging to the Leotiomycetes and Eurotiomycetes were detected by preliminary analyses of ITS sequences. Multi-locus phylogenetic analyses (LSU, ITS, *TUB*, *EF-1a*, depending on genus) of 31 of the 45 strains from *Prunus* and reference strains revealed several new taxa, including *Arboricolonus* **gen. nov.**, a new genus in the Helotiales (Leotiomycetes) with a collophorina-like asexual morph. Seven *Cadophora* species (Helotiales, Leotiomycetes) were treated. The 29 strains from *Prunus* belonged to five species, of which *C. luteo-olivacea* and *C. novi-eboraci* were dominating; *C. africana* **sp. nov.**, *C. prunicola* **sp. nov.** and *C. ramosa* **sp. nov.** were revealed as new species. The genus *Cadophora* was reported from *Prunus* for the first time. *Phialophora bubakii* was combined in *Cadophora* and differentiated from *C. obscura*, which was resurrected. Asexual morphs of two *Proliferodiscus* species (Helotiales, Leotiomycetes) were described, including one new species, *Pr. ingens* **sp. nov**. Two *Minutiella* species (Phaeomoniellales, Eurotiomycetes) were detected, including the new species *M. pruni-avium* **sp. nov**. *Prunus avium* and *P. domestica* are reported as host plants of *Minutiella*.

Keywords

Ascomycota, Eurotiomycetes, Leotiomycetes, new taxa, phylogeny, systematics

Introduction

In order to study the mycobiome of wood necroses of economically important *Prunus* species in Germany, a survey has been conducted using isolation techniques. Based on preliminary analyses of generated ITS sequences, several strains belonging to the Leotiomycetes and Eurotiomycetes were detected. Some of them were recently identified as species of *Collophorina* and related genera (Bien et al. 2020). Further strains showed morphological or genetical affiliation to the genera *Cadophora*, *Proliferodiscus* (Leotiomycetes) and *Minutiella* (Eurotiomycetes).

Leotiomycetes and Eurotiomycetes are both ecologically and morphologically highly diverse classes (Geiser et al. 2006, 2015; Wang et al. 2006b; LoBuglio and Pfister 2010; Johnston et al. 2019). Members of the Leotiomycetes have been described as plant pathogens, especially wood rot fungi, endophytes, nematode-trapping and mycorrhiza-forming fungi, as well as terrestrial and aquatic saprobes (Wang et al. 2006a; Hustad and Miller 2011). Eurotiomycetes are commonly known as saprotrophs and parasites of plants and animals; however, the number of pathogens is relatively low, compared to Sordariomycetes or Dothideomycetes (Geiser et al. 2006, 2015).

The genus *Cadophora* (Ploettnerulaceae, Helotiales, Leotiomycetes) was established in 1927 based on *C. fastigiata* (Lagerberg et al. 1927). Melin and Nannfeldt (1934) added five new species to *Cadophora*, while Davidson (1935) described two additional species that were isolated from stained wood or pulpwood products. Subsequently, Conant (1937) determined that *Phialophora* and *Cadophora* were congeneric and transferred the eight species of *Cadophora* to *Phialophora*. In the monograph of *Phialophora*, Schol-Schwarz (1970) included *C. fastigiata* and *C. malorum*, as well as *Margarinomyces bubakii* in *Phialophora*. Gams (2000) reinstated the genus *Cadophora* for phialophora-like species with more or less pigmented hyphae and pale phialides (*C. fastigiata*, *C. melinii*, *C. malorum*, *C. repens*). For some of these, a relationship with sexual morphs in some discomycete genera, such as *Mollisia* and *Pyrenopeziza*, has been demonstrated (Le Gal and Mangenot 1960, 1961). This connection was confirmed by LSU sequence analysis by Harrington and McNew (2003). However, to date, the type species of none of the genera has been epitypified. Currently, the genus *Cadophora* comprises 17 species. Species of *Cadophora* have been isolated from plants (e.g. Di Marco et al. 2004; Gramaje et al. 2011; Crous et al. 2015; Travadon et al. 2015; Walsh et al. 2018), soil (Kerry 1990; Hujslová et al. 2010; Agustí-Brisach et al. 2013) and decaying wood (Nilsson 1973; Blanchette et al. 2004, 2010).

Haines and Dumont (1983) compared specimens of *Dasyscyphus inspersus* (syn. *Peziza inspersa*) with the type species of the genera *Dasyscyphus* and *Lachnum* and revealed this species not to be congeneric with either of them. Based on spore, hair, paraphysis and subiculum morphology, they erected the new genus *Proliferodiscus* within the family Hyaloscyphaceae (Helotiales, Leotiomycetes). Today, the genus *Proliferodiscus* comprises eight species and is known from woody hosts in tropical and temperate regions worldwide (Haines and Dumont 1983; Spooner 1987; Cantrell and Hanlin 1997; McKenzie et al. 2000; Hofton et al. 2009; Han et al. 2014a; Haelewaters et al. 2018; Ekanayaka et al. 2019).

Crous and Gams (2000) described the genus *Phaeomoniella* (Celotheliaceae, Phaeomoniellales, Eurotiomycetes) based on *Pa. chlamydospora*, the causal agent of Esca disease of grapevine wood (Bertsch et al. 2013; Fontaine et al. 2016; Gramaje et al. 2018). Damm et al. (2010) discovered several new *Phaeomoniella* species from *Prunus* wood in South Africa that were combined in new genera by Crous et al. (2015). One of them, *Minutiella tardicola* (syn. *Pa. tardicola*), was characterised by the very slow growth of the cultures and minute pycnidia (Damm et al. 2010). Most members of Celotheliaceae have been found on *Prunus* (Damm et al. 2010) or other woody hosts from angiosperms and gymnosperms (Crous and Gams 2000; Nordén et al. 2005; Lee et al. 2006; Crous et al. 2008, 2009, 2015, 2016; Zhang et al. 2012; Úrbez-Torres et al. 2013; Yurkewich et al. 2017).

In this study, we aim to (1) systematically place strains isolated from necrotic wood of *Prunus* trees in Germany, as well as some additional strains tentatively identified as *Cadophora* within Leotiomycetes and Eurotiomycetes and (2) formally describe new taxa.

Methods

Sampling and fungal isolation

Branches with wood symptoms (e.g. canker, necroses, wood streaking, gummosis) were sampled from plum (*Prunus domestica*), sour cherry (*P. cerasus*) and sweet cherry (*P. avium*) orchards in Saxony, Lower Saxony and Baden-Württemberg, Germany, in 2015 and 2016. Additionally, a wood sample from a sour cherry tree located in a garden in Bavaria, as well as three strains previously isolated from wood of *P. salicina* in South Africa and two *Phialophora bubakii* strains, all tentatively identified as *Cadophora* spp. in preliminary analyses, were included. Wood pieces (5 × 5 × 5 mm) from the transition zone of symptomatic to non-symptomatic wood tissue, as well as pieces of the same size from non-symptomatic wood of the same branch, were surface sterilised (30 s in 70% ethanol, 1 min in 3.5% NaOCl, 30 s in 70% ethanol), washed for 1 min in sterilised water and placed on synthetic nutrient-poor agar medium (SNA; Nirenberg 1976), as well as oatmeal agar medium (OA; Crous et al. 2019), both supplemented with 100 mg/l penicillin, 50 mg/l streptomycin sulphate and 1 mg/l chloramphenicol. After incubation for several days at 25 °C, hyphal tips of developing fungi were transferred to SNA medium with a sterilised needle. Single-conidial isolates were obtained from the strains for further study. Sampling and isolation of the strains from South Africa was similar (Damm et al. 2007).

The strains are maintained in the culture collections of the Senckenberg Museum of Natural History Görlitz, Germany (GLMC), the Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands (CBS) and the German Collection of Microorganisms and Cell Cultures, Braunschweig, Germany (DSMZ). Specimens (dried cultures), including type specimens were deposited in the fungarium of the Senckenberg Museum of Natural History Görlitz (GLMC).

Morphological analysis

To enhance sporulation, autoclaved filter paper and double-autoclaved pine needles were placed on the surface of the SNA medium. The cultures were incubated in the dark at 25 °C. Colony growth and characters on SNA and OA, for some strains additionally on potato dextrose agar (PDA; Crous et al. 2019) and malt extract agar (MEA; Oxoid Ltd., England; 1.5% agar, Difco, USA), were noted after 2 and 4 wk. Colony colours were rated according to Rayner (1970). After 2 or 4 wk, microscopic preparations were made in clear lactic acid and observations and measurements (30 measurements per structure) were made with a Nikon SMZ18 stereomicroscope (SM) or with a Nikon Eclipse N*i*-U light microscope with differential interference contrast (LM). Photographic images were captured with Nikon Digital Sight DS-Fi2 cameras installed on the above-mentioned microscopes, making use of the Nikon NIS-Elements software (v.4.30).

DNA extraction, PCR amplification and sequencing

Of the forty-two strains isolated from *Prunus* wood in Germany, three strains from *Prunus* wood in South Africa, as well as two strains of *Phialophora bubakii* that were included in this study, 34, 4 and 8 strains had been identified as species of *Cadophora*, *Minutiella* and *Proliferodiscus*, respectively, in preliminary analyses based on ITS sequences. Twenty-two *Cadophora* strains, six *Proliferodiscus* strains, all *Minutiella* strains as well as an unidentified Leotiomycete strain were selected for phylogenetic analyses (Table 1).

Genomic DNA of the isolates was extracted using the method of Damm et al. (2008). A partial sequence of the 28S nrDNA (LSU) and the 5.8S nuclear ribosomal gene with the two flanking internal transcribed spacers ITS1 and ITS2 (ITS) were amplified and sequenced using the primer pairs LR0R (Rehner and Samuels 1994) + LR5 (Vilgalys and Hester 1990) and ITS1F (Gardens and Bruns 1993) + ITS-4 (White et al. 1990), respectively. Additionally, partial sequence of the β-tubulin gene (*TUB*) and the translation elongation factor 1α (*EF-1a*) of strains belonging to the genus *Cadophora* were generated using the primer pairs BTCadF + BTCadR (Travadon et al. 2015) and EF1-688F + EF1-1251R (Alves et al. 2008), respectively. The β-tubulin gene of the genus *Minutiella* was sequenced using the primer pair Bt2a + Bt2b (Glass and Donaldson 1995).

The PCR reaction mixture contained 1 µl of 1:10 DNA template, 2.5 µl 10X buffer (Peqlab, Erlangen, Germany), 1 µl of each primer (10mM), 2.5 µl $MgCl_2$ (25mM), 0.1 µl *Taq* polymerase (0.5 U, Peqlab, Erlangen, Germany) and 2.5 µl of 2mM dNTPs. Each reaction was made up to a final volume of 20 µl with sterile water. DNA amplifications were carried out in a Mastercycler pro S (Eppendorf, Hamburg, Germany). The amplification conditions for ITS and *EF-1a* were: initial denaturation at 95 °C for 5 min; followed by 30 cycles of denaturation at 94 °C for 30 s, annealing at 51 °C for 30 s and extension at 72 °C for 60 s; and a final extension step at 72 °C for 3 min. The amplification conditions for the primer pair Bt2a + Bt2b were: initial denaturation at

94 °C for 4 min; followed by 38 cycles of denaturation at 94 °C for 60 s, annealing at 61 °C for 60 s and extension at 72 °C for 45 s; and a final extension step of 5 min at 72 °C. For amplifications of LSU and *TUB* with the primer pair BTCadF + BTCadR, the PCR conditions were set according to Paulin and Harrington (2000) and Travadon et al. (2015), respectively.

The PCR products were visualised on a 1% agarose gel and sequenced using the same primers by the Senckenberg Biodiversity and Climate Research Centre (BiK-F) laboratory (Frankfurt, Germany). The forward and reverse sequences were assembled by using BioEdit Sequence Alignment Editor (v. 7.2.5; Hall 1999).

Phylogenetic analysis

For the phylogenetic analyses, sequences, especially those of ex-type strains, were downloaded from GenBank and added to the sequences generated in this study and those of the appropriate outgroup sequences in four datasets. In order to determine the generic placement of strain GLMC 459, sequences of close matches from blastn searches with its LSU and ITS sequences were combined with sequences of the phylogenetic reassessment of Hyaloscyphaceae by Han et al. (2014b) (dataset 1). Three datasets were generated to determine the systematic position of strains of the genera *Cadophora* (ITS, *TUB*, *EF-1a*; dataset 2), *Minutiella* (LSU, ITS, *TUB*; dataset 3) and *Proliferodiscus* (LSU, ITS; dataset 4). The datasets were aligned automatically using MAFFT v. 7.308 (Katoh et al. 2002, Katoh and Standley 2013) and manually adjusted where necessary.

The phylogenetical analyses were conducted using Bayesian Inference (BI), Maximum Likelihood (ML) and Maximum Parsimony (MP). For BI analyses, the best fit model of evolution for each partition was estimated by MEGA7 (Kumar et al. 2016). Posterior probabilities were determined by Markov Chain Monte Carlo sampling (MCMC) in MrBayes v. 3.2.6 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) as implemented in Geneious v. 10.2.2 (Kearse et al. 2012), using the estimated models of evolution. For each dataset, four simultaneous Markov chains were run for 1 million generations and trees were sampled every 100th generation. The first 2000 trees, which represent the burn-in phase of the analyses, were discarded and the remaining 8000 trees were used to calculate posterior probabilities in the majority rule consensus trees. The ML analyses were performed by RAxML v. 8.2.11 (Stamatakis 2006, 2014) as implemented in Geneious v. 10.2.2 (Kearse et al. 2012), using the GTRGAMMA model with the rapid bootstrapping and search for best scoring ML tree algorithm, including 1000 bootstrap replicates. The MP analyses were performed with MEGA7 (Kumar et al. 2016) using tree-bisection-reconnection (TBR) as the branch-swapping algorithm. The robustness of the trees was evaluated by 1000 bootstrap replicates and 10 random sequence additions. Tree length, consistency index, retention index and composite index of the resulting trees were calculated. The DNA sequences generated in this study were deposited in GenBank (Table 1), the alignments in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S24703).

Table 1. List of strains analysed in this study, with collection details and GenBank accession numbers.

Species	Accession no.[1]	Host/ substrate	Country	GenBank no.[2]			
				LSU	ITS	*TUB*	*EF1-α*
Arboricolonus simplex	GLMC 459^{T}	*Prunus domestica*	Germany	**MN232924**	**MN232935**	–	–
Cadophora africana	CBS 120890^{T}	*Prunus salicina*	South Africa	–	**MN232936**	**MN232967**	**MN232988**
Cadophora bubakii (as *Phialophora bubakii*)	CBS 198.30^{T}	margarine	Czech Republic	–	MH855111	–	**MN232989**
Cadophora luteo-olivacea	GLMC 517	*Prunus domestica*	Germany	–	**MN232937**	**MN232968**	**MN233003**
	GLMC 1264	*Prunus domestica*	Germany	–	**MN232938**	**MN232969**	**MN233004**
	GLMC 1310	*Prunus domestica*	Germany	–	**MN232939**	**MN232970**	**MN233005**
	GLMC 1517	*Prunus domestica*	Germany	–	**MN232940**	**MN232971**	**MN233006**
	GLMC 1545	*Prunus domestica*	Germany	–	**MN232941**	**MN232972**	**MN233007**
Cadophora novi-eboraci	GLMC 239	*Prunus cerasus*	Germany	–	**MN232942**	**MN232973**	**MN232990**
	GLMC 273	*Prunus cerasus*	Germany	–	**MN232943**	**MN232974**	**MN232991**
	GLMC 274	*Prunus cerasus*	Germany	–	**MN232944**	**MN232975**	**MN232992**
	GLMC 342	*Prunus cerasus*	Germany	–	**MN232945**	**MN232976**	**MN232993**
	GLMC 688	*Prunus cerasus*	Germany	–	**MN232946**	**MN232977**	**MN232994**
	GLMC 1472	*Prunus cerasus*	Germany	–	**MN232947**	**MN232978**	**MN232995**
Cadophora obscura (as *Phialophora bubakii*)	CBS 269.33	fresh water	Sweden	–	**MN232948**	–	**MN232996**
Cadophora prunicola	CBS 120891^{T}	*Prunus salicina*	South Africa	–	**MN232949**	**MN232979**	**MN232997**
	STEU 6103	*Prunus salicina*	South Africa	–	**MN232950**	–	–
	GLMC 276	*Prunus cerasus*	Germany	–	**MN232951**	**MN232980**	**MN232998**
	GLMC 362	*Prunus domestica*	Germany	–	**MN232952**	–	–
	GLMC 735	*Prunus cerasus*	Germany	–	**MN232953**	**MN232981**	**MN232999**
	GLMC 1574	*Prunus domestica*	Germany	–	**MN232954**	**MN232982**	**MN233000**
	GLMC 1633	*Prunus domestica*	Germany	–	**MN232955**	**MN232983**	**MN233001**
Cadophora ramosa	GLMC 377^{T}	*Prunus cerasus*	Germany	–	**MN232956**	**MN232984**	**MN233002**
Minutiella pruni-avium	GLMC 1624^{T}	*Prunus avium*	Germany	**MN232925**	**MN232957**	**MN232985**	–
	GLMC 1667	*Prunus avium*	Germany	**MN232926**	**MN232958**	**MN232986**	–
Minutiella sp.	GLMC 1636	*Prunus domestica*	Germany	**MN232927**	**MN232959**	–	–
	GLMC 1687	*Prunus domestica*	Germany	**MN232928**	**MN232960**	**MN232987**	–
Proliferodiscus ingens	GLMC 1751^{T}	*Prunus avium*	Germany	**MN232929**	**MN232961**	–	–
Proliferodiscus sp.	GLMC 460	*Prunus domestica*	Germany	**MN232930**	**MN232962**	–	–
	GLMC 470	*Prunus domestica*	Germany	**MN232931**	**MN232963**	–	–
	GLMC 502	*Prunus domestica*	Germany	**MN232932**	**MN232964**	–	–
	GLMC 1301	*Prunus domestica*	Germany	**MN232933**	**MN232965**	–	–
	GLMC 1761	*Prunus avium*	Germany	**MN232934**	**MN232966**	–	–

[1] CBS: Culture collection of the Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; GLMC: Culture collection of Senckenberg Museum of Natural History Görlitz, Görlitz, Germany; STEU: University of Stellenbosch, Stellenbosch, South Africa.

[2] LSU: nuclear large subunit ribosomal DNA; ITS: internal transcribed spacers and intervening 5.8S nrDNA; *TUB*: β-tubulin gene; *EF1-α*: translation elongation factor 1-α gene.

Sequences generated in this study are emphasised in bold face. ^{T}ex-type cultures.

Results

Phylogenetic analyses

The combined sequence dataset 1 consisted of 59 isolates including the outgroup *Geoglossum nigritum* strain AFTOL-ID 56 and comprised 1540 characters, of which 436 characters were parsimony-informative, 578 variable and 885 constant. The gene boundaries on the LSU-ITS multi-locus alignment were as follows: LSU: 1–890 and ITS: 891–1540. The final ML optimisation likelihood of ML analysis was: lnL = -15669.074659. One most parsimonious tree was generated by MP analysis with tree length: 693 steps, consistency index: 0.298780, retention index: 0.555126 and composite index: 0.186644 and 0.165861 for all sites and parsimony informative sites, respectively. The BI phylogeny, including BI posterior probability values as well as ML and MP bootstrap support values, is shown in Fig. 1.

The clades in Fig. 1 represent all clades of the multi-locus phylogeny of the "Hyaloscyphaceae" by Han et al. (2014b) as well as clades formed by sequences of the closest matches from blastn searches with the ITS and LSU sequences of strain GLMC 459 in GenBank. Strain GLMC 459 from *P. domestica* in Germany forms a long single-strain clade that does not belong to any of the above-mentioned clades and is located close to *Polydesmia pruinosa* TNS-F-12764, strains belonging to Clade 9 in Han et al. (2014b) and a clade formed by three strains of *Polyphilus*. The clade, formed by GLMC 459 and these taxa, is not supported.

The combined sequence dataset 2 of *Cadophora* consisted of 70 isolates including the outgroup *Hyaloscypha finlandica* CBS 444.86 and comprised 1594 characters, of which 498 characters were parsimony-informative, 692 variable and 859 constant. The gene boundaries in the multi-locus alignment were as follows: ITS: 1–575, *TUB*: 576–1133 and *EF-1α*: 1134–1594. Five most parsimonious trees were generated by MP analysis with tree length: 205 steps, consistency index: 0.536145, retention index: 0.931189 and composite index: 0.581425 and 0.499252 for all sites and parsimony informative sites, respectively. The BI phylogeny, including BI posterior probability values as well as ML (lnL = -9335.686864) and MP bootstrap support values, is shown in Fig. 2.

The phylogeny consists of two main clades belonging to 21 clades representing different *Cadophora* species. The two main clades are formed by BI and ML analyses; both are supported by BI (100%); however, only the second clade is supported by ML and MP analyses (100% and 74%, respectively). In the first main clade, six strains isolated from *P. cerasus* in Saxony and Bavaria form a well-supported clade (100/100/83% BI posterior probability, ML and MP bootstrap support values, respectively) with strains of *C. novi-eboraci* including its ex-type strain. A further five strains from *P. cerasus* and *P. domestica* in Saxony and Baden-Württemberg and two strains from *P. salicina* in South Africa form a well-supported clade (100/99/78%) that does not include any previously described species. One strain isolated from *P. salicina* in South Africa (CBS 120890) and a strain referred to as *C.* "*novi-eboraci*" (CBS 101359) form single-strain clades and belong to a well-supported clade with *C. novi-eboraci* and *C. prunicola* (100/81/99%). One strain isolated from *P. cerasus* in Saxony (GLMC 377) forms a well-supported clade (100/100/94%) with four strains referred to as *C.* "*spadicis*". Within the second main clade, five strains isolated from *P. domestica* in all three sampling areas in Germany form a well-supported clade (100/94/–%) with 16 strains of *C. luteo-olivacea* including its ex-type strain. Two strains of *Phialophora bubakii* CBS 198.30 and CBS 837.69, both originating from margarine, form a well-supported clade (100/100/99%) sister to a third strain (CBS 269.33) from fresh water in Sweden that forms a single-strain clade. The clade formed by all three strains is well-supported (100/93/–%) as well.

The combined sequence dataset 3 consisted of 29 isolates of the Celotheliaceae and the outgroup *Capronia fungicola* CBS 614.96 and comprised 1904 characters, of which 486 characters were parsimony-informative, 685 variable and 1182 constant. The gene boundaries in the multi-locus alignment were as follows: LSU: 1–840 and ITS: 841–1482, *TUB*: 1483–1904. One most parsimonious tree was generated by MP analysis with tree length: 384 steps, consistency index: 0.558989, retention in-

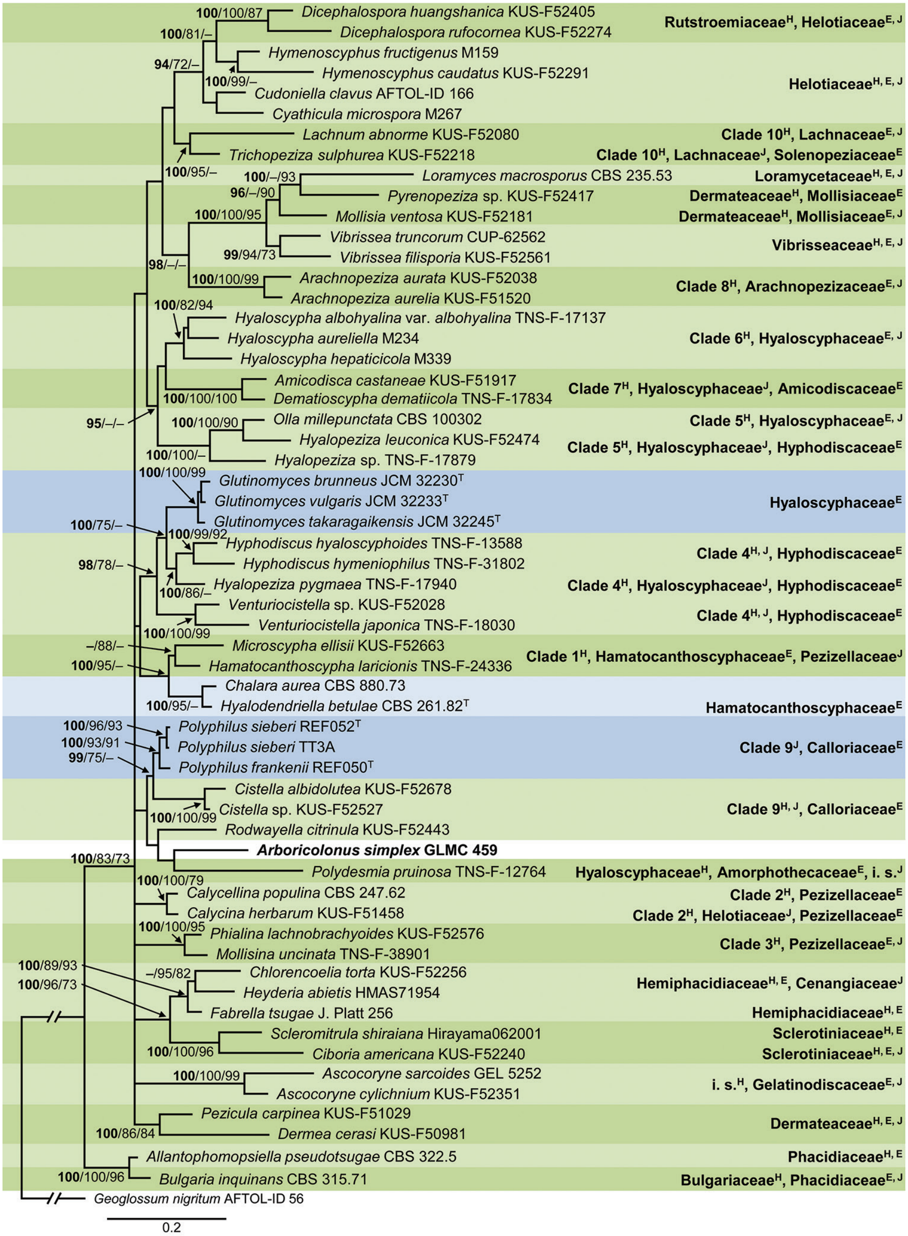

Figure 1. Phylogeny of dataset 1 obtained by Bayesian Inference analysis of the combined LSU and ITS sequence alignment for generic placement of strain GLMC 459. *Geoglossum nigritum* strain AFTOL-ID 56 is used as outgroup. BI posterior probability support values above 90% (bold) and ML and MP bootstrap support values above 70% are shown at the nodes. The strain, analysed in this study, is emphasised in bold. Green backgrounds indicate sequences included in the analyses of Han et al. (2014b). Blue backgrounds indicate close matches of GLMC 459 in blastn searches. Clades 1–10 of Hyaloscyphaceae, according to the analyses of Han et al. (2014b), are listed to the right. Family names are listed to the right, according to Han et al. (2014b, superscript H), Ekanayaka et al. (2019, superscript E) and Johnston et al. (2019, superscript J). Branches that are crossed by diagonal lines are shortened by 50%.

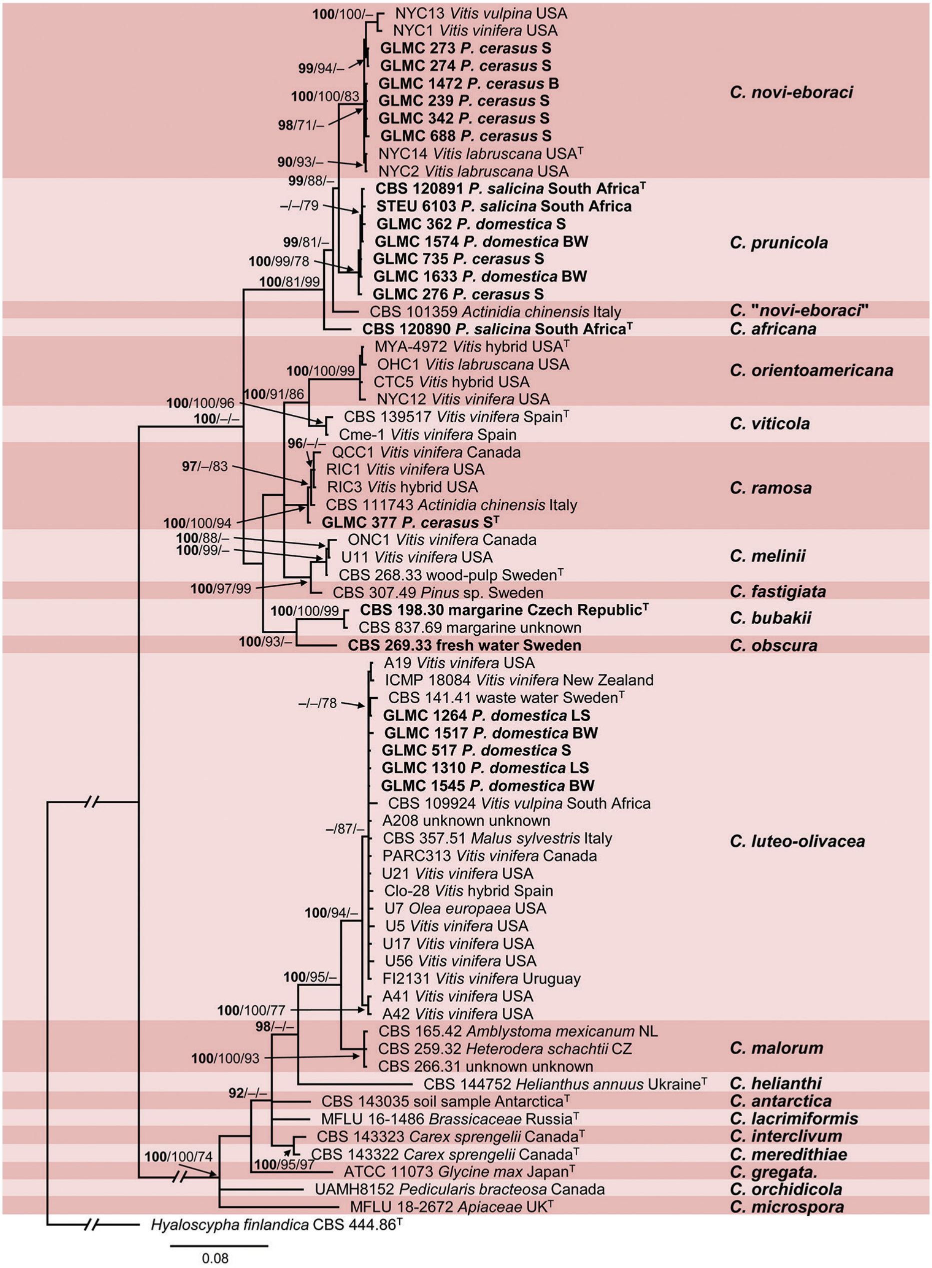

Figure 2. Phylogeny of dataset 2 obtained by Bayesian Inference analysis of the combined ITS, *TUB*, *EF-1a* sequence alignment of *Cadophora*. *Hyaloscypha finlandica* strain CBS 444.86 is used as outgroup. Host plant or substrate and country of isolation are given for every strain. For strains isolated from *Prunus* spp. in Germany, the German Federal State is given in abbreviation as location. Species names are listed to the right. BI posterior probability support values above 90% (bold), ML and MP bootstrap support values above 70% are shown at the nodes. The strains, analysed in this study, are emphasised in bold. Numbers of ex-type and ex-isotype strains are emphasised with a superscript T. Branches that are crossed by diagonal lines are shortened by 50%. B: Bavaria; BW: Baden-Württemberg; LS: Lower Saxony; S: Saxony.

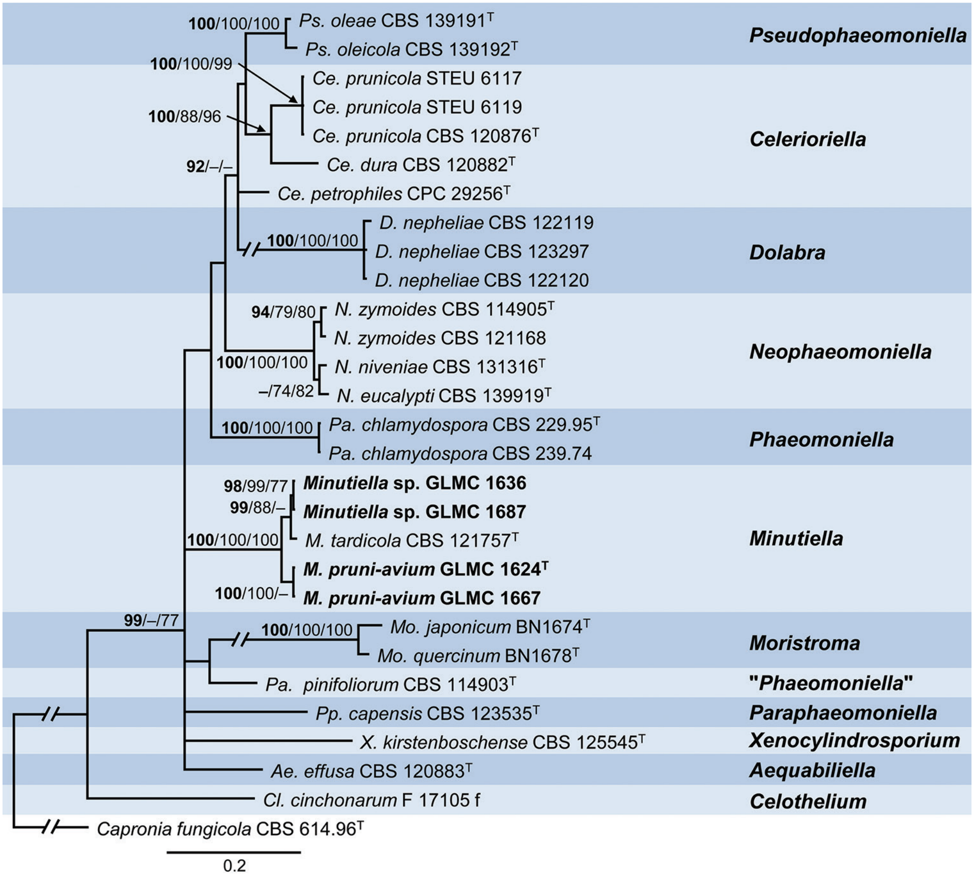

Figure 3. Phylogeny of dataset 3 obtained by Bayesian Inference analysis of the combined LSU, ITS, *TUB* sequence alignment of Phaeomoniellales, including *Minutiella*. *Capronia fungicola* strain CBS 614.96 is used as outgroup. BI posterior probability support values above 90% (bold), ML and MP bootstrap support values above 70% are shown at the nodes. The strains analysed in this study are emphasised in bold. Numbers of ex-type strains are emphasised with a superscript T. Branches that are crossed by diagonal lines are shortened by 50%.

dex: 0.779804 and composite index: 0.458467 and 0.435901 for all sites and parsimony informative sites, respectively. The BI phylogeny, including BI posterior probability values as well as ML (lnL = -9719.124620) and MP bootstrap support values, is shown in Fig. 3.

The 12 main clades of the phylogeny represent genera of the Celotheliaceae; all species for which sequences are available, are included. Four isolates from this study group in a well-supported clade (100/100/100%) with *Minutiella tardicola*. Two of the strains isolated from *P. domestica* form a well-supported sister clade (98/99/77 %) to the single-strain clade formed by the ex-type strain of *M. tardicola*. A further two strains isolated from *P. avium* form a well-supported clade (100/100/–%), sister to the clade consisting of *M. tardicola* and *Minutiella* sp.

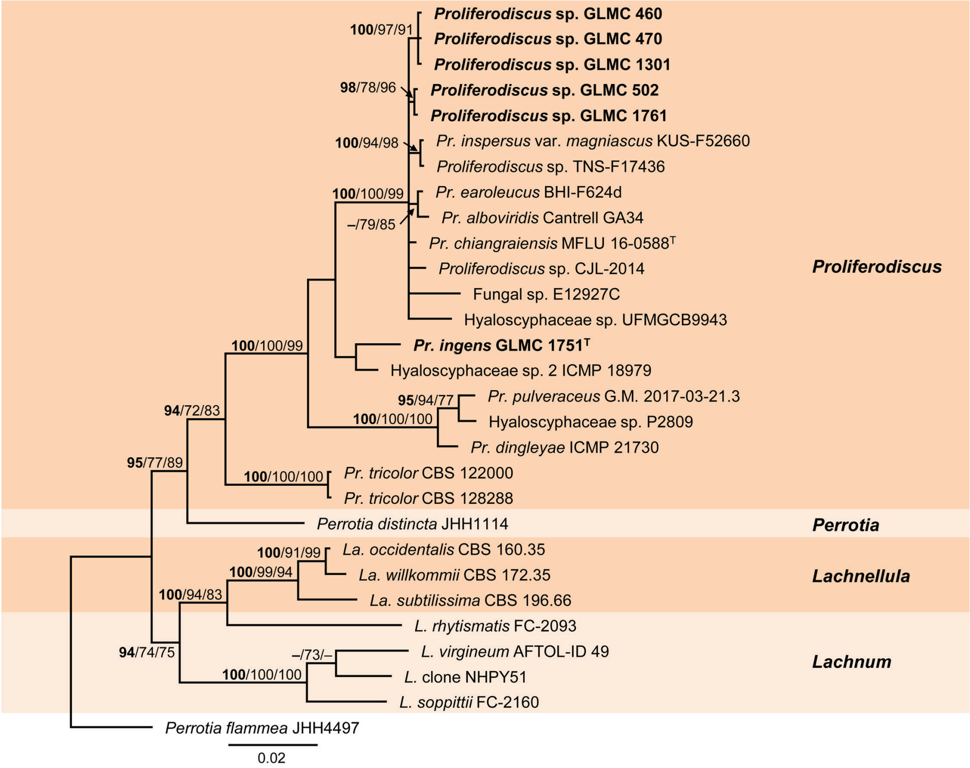

Figure 4. Phylogeny of dataset 4 obtained by Bayesian Inference analysis of the combined LSU, ITS sequence alignment of *Proliferodiscus* and close relatives. *Perrotia flammea* strain JHH4497 is used as outgroup. BI posterior probability support values above 90% (bold), ML and MP bootstrap support values above 70% are shown at the nodes. The strains, analysed in this study, are emphasised in bold. Numbers of ex-type strains are emphasised with a superscript T.

The combined sequence dataset 4 consisted of 29 isolates of *Proliferodiscus* and closely related genera including the outgroup *Perrotia flammea* JHH4497 and comprised 1385 characters, of which 152 characters were parsimony-informative, 204 variable and 1174 constant. The gene boundaries in the multi-locus alignment were as follows: LSU: 1–854 and ITS: 855–1385. Seven most parsimonious trees were generated by MP analysis with tree length: 263 steps, consistency index: 0.651341, retention index: 0.807611 and composite index: 0.526030 and 0.482422 for all sites and parsimony informative sites, respectively. The BI phylogeny obtained by Bayesian Inference, including BI posterior probability values as well as ML (lnL = -4019.800817) and MP bootstrap support values, is shown in Fig. 4.

The main clades represent closely related genera. Six strains from *Prunus* wood in Germany group in the *Proliferodiscus* clade. Five of them, from *P. avium* and *P. domestica*, cluster with seven ambiguously identified strains and the type strain of *Pr. chiangraiensis* in a well-supported clade (100/100/99%). Strain GLMC 1751 forms a single-strain clade sister to “Hyaloscyphaceae sp. 2” ICMP 18979.

Taxonomy

Based on DNA sequence data and morphology, the 33 strains studied (Table 1) are assigned to four genera, of which seven species belong to *Cadophora*, two species to *Minutiella* and two species to *Proliferodiscus*, including 5 species that proved to be new to science and are described. Two strains, referred to as *Phialophora bubakii*, proved to belong to two distinct species within *Cadophora*. Strain GLMC 459 could not be assigned to any known genus and is therefore described as new genus. All species studied in culture are characterised below.

Arboricolonus **S.Bien & Damm, gen. nov.**

MycoBank No: 832106

Type species. *Arboricolonus simplex* S.Bien & Damm.

Etymology. Referring to the life inside tree wood (*arbor* Lat. = tree + *colonus* = settler).

Description. *Colonies* slow-growing, moist, white or buff colours on oatmeal agar medium, lacking aerial mycelium. *Sporulation* conidia formed on hyphal cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, intercalary, reduced to short discrete phialides or, more often, collarettes formed directly on hyphal cells, collarettes short tubular to funnel-shaped. *Conidia* aggregated around the hyphae, small, hyaline, 1-celled, cylindrical, ovoidal to allantoid. *Vegetative hyphae and phialides* hyaline, smooth-walled, septate, branched.

Arboricolonus simplex **S.Bien & Damm, sp. nov.**

MycoBank No: 832107

Figures 5A, 6

Type. Germany, Saxony, orchard north of Wölkau, 50°58'42.3"N, 13°49'40.0"E, from brown wedge-shaped necrosis in wood of *Prunus domestica*, 16 Jan 2015, S. Bien leg., GLM-F106309 – ***holotype***; GLMC 459 = CBS 145520 = DSM 109147 – culture ex-type.

Etymology. Named after the simple, reduced conidiophores.

Description. *Sexual morph* not observed. *Asexual morph on SNA. Vegetative mycelium* hyaline, smooth-walled, septate, branched, 1–3 µm wide, sometimes hyphal cells inflated and constricted at the septa, chlamydospores absent. *Sporulation* abundant, conidia formed on hyphal cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, integrated or terminal, discrete phialides, ampulliform to navicular, 4–7 × 2–3 µm, often reduced to small necks or openings on hyphae, opening 0.5–1 µm wide, collarettes short tubular to funnel-shaped, 0.5–1 µm long, periclinal thickening sometimes visible. *Conidia* aggregated in heads or slimy masses around hyphae, hyaline, smooth-walled, aseptate, straight to ± curved, cylindrical,

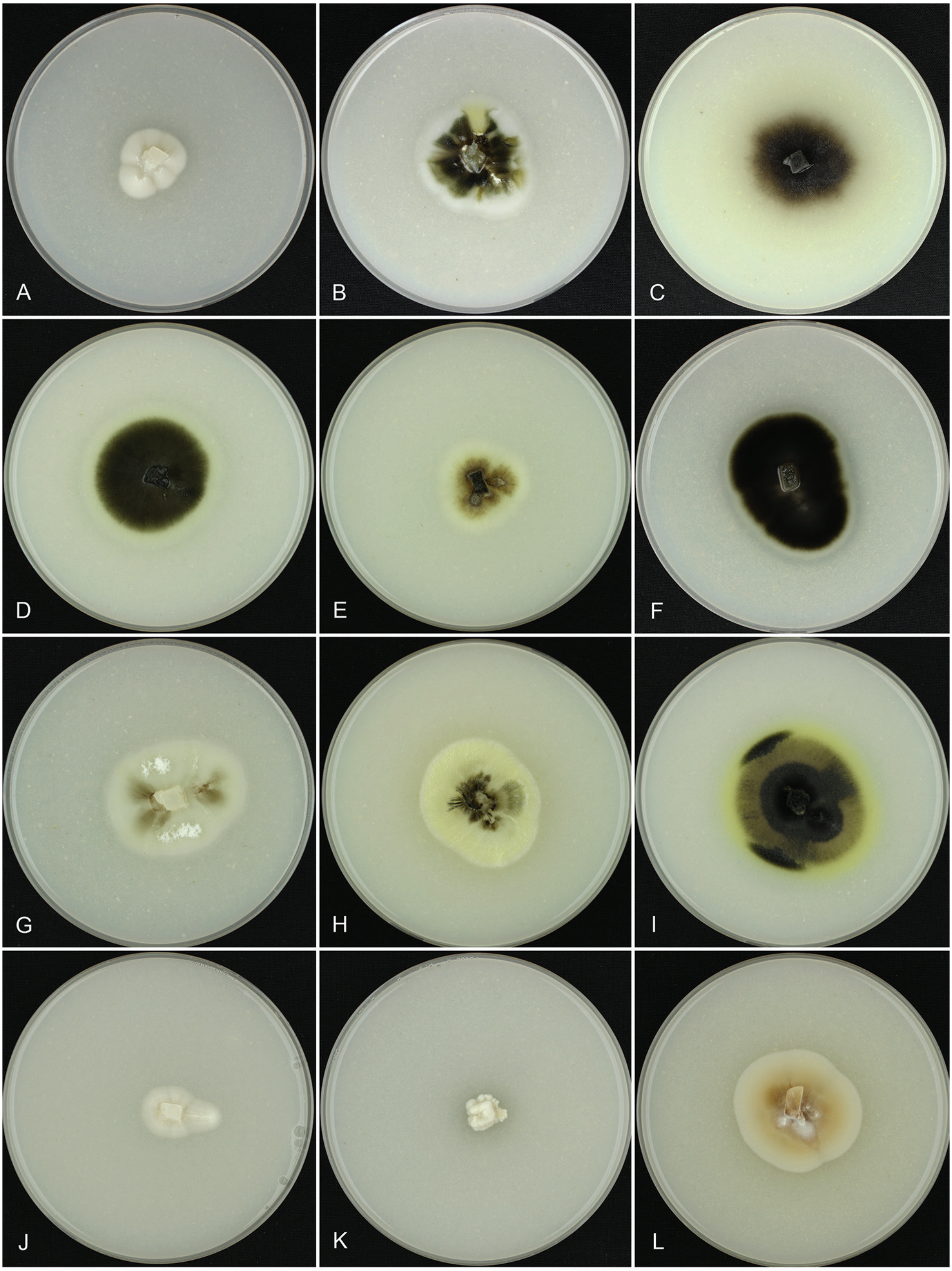

Figure 5. Colony surface of analysed strains on OA medium. **A** *Arboricolonus simplex* GLMC 459^T **B** *Cadophora africana* CBS 120890^T **C** *C. bubakii* CBS 198.30^T **D** *C. luteo-olivacea* GLMC 1264 **E** *C. novi-eboraci* GLMC 1472 **F** *C. obscura* CBS 269.33 **G** *C. prunicola* CBS 120891^T **H** *C. prunicola* GLMC 1633 **I** *C. ramosa* GLMC 377^T **J** *Minutiella pruni-avium* GLMC 1624^T **K** *Proliferodiscus ingens* GLMC 1751^T **L** *Proliferodiscus* sp. GLMC 460. Cultures **A, J–L** after 4 wk. Cultures **B–I** after 2 wk. Strains with a superscript T are ex-type cultures.

elongate ovoidal to allantoid, with one end rounded, the other end rounded to truncate, 3–4(–4.5) × 1–1.5(–2) µm, mean ± SD = 3.6 ± 0.6 × 1.3 ± 0.2 µm, L/W ratio = 2.8.

Culture characteristics. *Colonies on OA* flat to slightly raised with an entire to undulate margin, hyaline, whitish to buff, lacking aerial mycelium, reverse same colours, 2–4 mm diam. in 2 wk, 6–10 mm diam. in 4 wk; *on SNA* flat to slightly raised with an entire to undulate margin, hyaline to whitish, lacking aerial mycelium, reverse same colours, 1–2 mm diam. in 2 wk, 3–6 mm diam. in 4 wk.

Notes. The morphology of *Arboricolonus simplex* is reminiscent of collophorina-like species regarding the colonies that are slow growing, the lack of aerial mycelium and the conidiogenous cells that are mostly reduced to short necks or openings with collarettes on hyphae (Damm et al. 2010; Bien et al. 2020). In contrast to these genera, microcyclic conidiation has not been observed in *Arboricolonus.* This genus belongs to the Leotiomycetes as well; however, it is not closely related to *Collophorina* and collophorina-like genera (Phacidiales) treated by Bien et al. (2020). A class-wide phylogenetic analysis of LSU-ITS places it within the order Helotiales (data not shown).

A blastn search with the ITS sequence of *A. simplex* in GenBank resulted in uncultured and unidentified strains with ≤ 92% identity, for example, an uncultured Helotiales clone from soil in the USA (HQ021771, JH Vineis et al., unpubl. data), while the closest matches with strains, identified at least to the genus level, were strains of *Glutinomyces vulgaris* with 90% identity (e.g. LC218288; Nakamura et al. 2018). The closest matches in a blastn search with the LSU sequence were, with ≤ 97% identity, the ex-type strain of *Hyalodendriella betulae* (EU040232; Crous et al. 2007), a strain identified as *Chalara aurea* (MH872551; Vu et al. 2019) and strains belonging to *Polyphilus sieberi* (e.g. MG719708; Ashrafi et al. 2018).

Cadophora africana **Damm & S.Bien, sp. nov.**

MycoBank No: 832108
Figures 5B, 7

Type. South Africa, Western Cape Province, Franschhoek, from necrosis in wood of *Prunus salicina* close to old pruning wound, 10 June 2004, U. Damm leg., CBS H-19984 – ***holotype***; GLM-F117479 – ***isotype***; CBS 120890 = STE-U 6203 = GLMC 1892 – culture ex-type.

Etymology. Named after the continent of origin, Africa.

Description. *Sexual morph* not observed. *Asexual morph on SNA. Vegetative mycelium* hyaline, smooth-walled, septate, branched, 1–3 µm wide, hyphal cells sometimes inflated and constricted at the septa, sometimes becoming brown with age, chlamydospores absent. *Sporulation* abundant, conidia formed on hyphal cells. *Conidiophores* hyaline, smooth-walled, mesotonously branched, occasionally with acropleurogenous branching, up to 35 µm long. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, discrete conidiogenous cells cylindrical to navicular, often constricted and sometimes widened at the base, 8–18 × 1.5–3 µm, necks cylindrical, 1–2 × 1–1.5 µm, collarettes

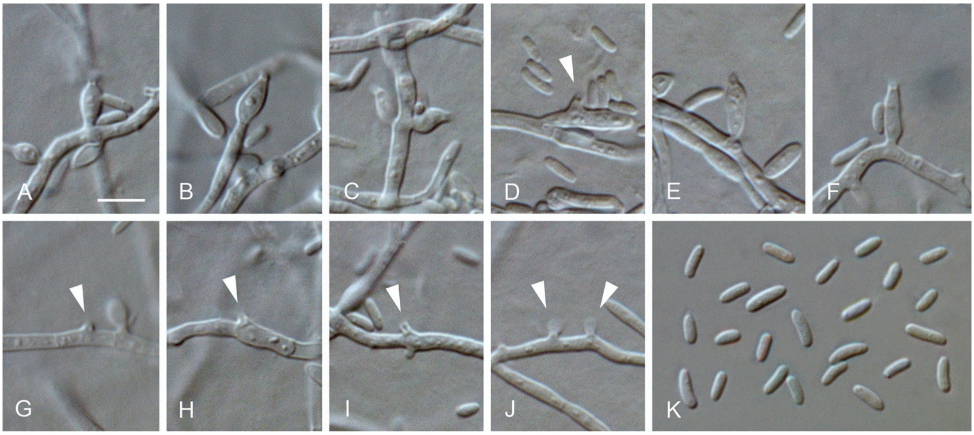

Figure 6. *Arboricolonus simplex* gen. et sp. nov. **A–J** conidiogenous cells (arrows indicate conidiogenous openings or short necks) **K** conidia **A–K** from SNA **A–K** LM. Scale bar: 5 µm (**A** applies to **B–K**).

distinct, cylindrical to narrowly funnel-shaped, 0.5–1.5 µm long, 1–1.5 µm wide at the upper edge, opening 1–1.5 µm wide, periclinal thickening observed. *Conidia* aggregated in heads, hyaline, smooth-walled, aseptate, mostly globose to subglobose or obovoid to tear-shaped, sometimes ellipsoidal, (2–)2.5–4(–4.5) × (1.5–)2–2.5(–3) µm, mean ± SD = 3 ± 0.5 × 2.1 ± 0.2 µm, L/W ratio = 1.4.

Culture characteristics. *Colonies on SNA* flat with an entire to undulate margin, white to buff, sometimes grey olivaceous to olivaceous, lacking aerial mycelium, reverse same colours, 6–14 mm diam. in 2 wk (25 °C in the dark); *Colonies on OA* flat with an entire to undulate margin, primrose to amber, grey olivaceous to olivaceous black, often with a white margin, partly covered by floccose white aerial mycelium, reverse buff to grey olivaceous, 22–30 mm diam. in 2 wk (25 °C in the dark); *Colonies on PDA* flat to raised, entire edge, short aerial mycelium, pale buff, after > 2 wk with pale olivaceous to pale olivaceous grey patches or sectors, reverse same colours, 30 mm diam. in 2 wk (20 °C). *Colonies on MEA* flat to low umbonate, with entire edge, abundant velvety aerial mycelium, mycelium and surface white to very pale smoke-grey; reverse very pale luteous, ochreous to buff, in diffuse daylight with concentric oliveceous-grey rings, 30 mm diam. in 2 wk (20 °C).

Notes. *Cadophora africana* was isolated once from *P. salicina* in South Africa. *Cadophora africana*, as well as *C. bubakii* and *C. ramosa*, form subglobose conidia. However, conidia of *C. africana* are mostly globose to subglobose, sometimes even tear-shaped, while those of *C. ramosa* are often ellipsoidal, elongate-ellipsoidal to cylindrical and the portion of subglobose conidia in *C. bubakii* is comparatively low. Therefore, conidia of both species are on average longer (4.9 µm and 3.6 µm, respectively) than those of *C. africana* (3 µm) and with a larger L/W ratio (2.2 and 2.1, respectively; *C. africana*: 1.4).

The ITS sequence of *C. africana* strain CBS 120890 differs in eleven nucleotides from the ex-type strain of *C. prunicola* and in nine nucleotides, both from the ex-type strain of *C. novi-eboraci* NYC14 and from strain CBS 101359. The differences to these

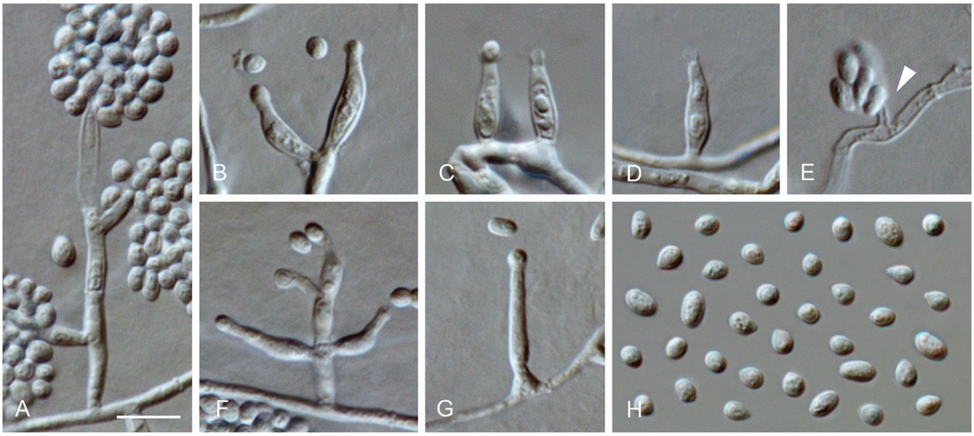

Figure 7. *Cadophora africana* sp. nov. **A–G** conidiophores and conidiogenous cells (arrow indicates a short neck) **H** conidia **A–H** from SNA **A–H** LM. Scale bar: 5 µm (**A** applies to **B–H**).

strains exceed 30 and 18 nucleotides in the *TUB* and *EF-1a* sequences, respectively. The closest match in a blastn search with the ITS sequence of *C. africana* is strain NYC13 of *C. novi-eboraci* (identity 98.48%), which is included in our phylogeny.

Cadophora bubakii (Laxa) Damm & S.Bien, comb. nov.

Figures 5C, 8

Margarinomyces bubakii Laxa, Zentbl. Bakt. ParasitKde, Abt. II 81: 392. 1930. (Basionym)
≡ *Phialophora bubakii* (Laxa) Schol-Schwarz, Persoonia 6 (1): 66. 1970.

Type. Czech Republic, Prague, from a margarine factory, margarine, O. Laxa leg., collection date unknown (isolated by O. Laxa, deposited in CBS collection by O. Laxa probably 1930), CBS H-491, CBS H-7316, GLM-F117482 – ***isotypes***; CBS 198.30 = IMI 24000 = NCTC 3273 = VKM F-162 = LM 288 = LM 793 = GLMC 1895 – culture ex-isotype.

Description. *Sexual morph* not observed. *Asexual morph on SNA. Vegetative mycelium* hyaline, smooth-walled, septate, branched, 1–3 µm wide, sometimes becoming brown with age, chlamydospores absent. *Sporulation* abundant, conidia formed on hyphal cells. *Conidiophores* hyaline, smooth-walled, occasionally with acropleurogenous branching, up to 26 µm long. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, discrete conidiogenous cells cylindrical to navicular, often slightly inflated having a flask-shaped appearance, often constricted at the base, 3–12 × 1.5–3.5 µm, necks cylindrical, 1–2.5 × 1–2 µm, collarettes distinct, cylindrical to funnel-shaped, 0.5–1 µm long, 1–1.5 µm wide at the upper edge, opening 1–1.5 µm wide, periclinal thickening observed. *Conidia* aggregated in heads, hyaline, smooth-walled, aseptate, subglobose to ellipsoidal or cylindrical with both ends rounded, straight or slightly curved, (2–)2.5–4.5(–6) × 1.5–2 µm, mean ± SD = 3.6 ± 0.9 × 1.7 ± 0.2 µm, L/W ratio = 2.1.

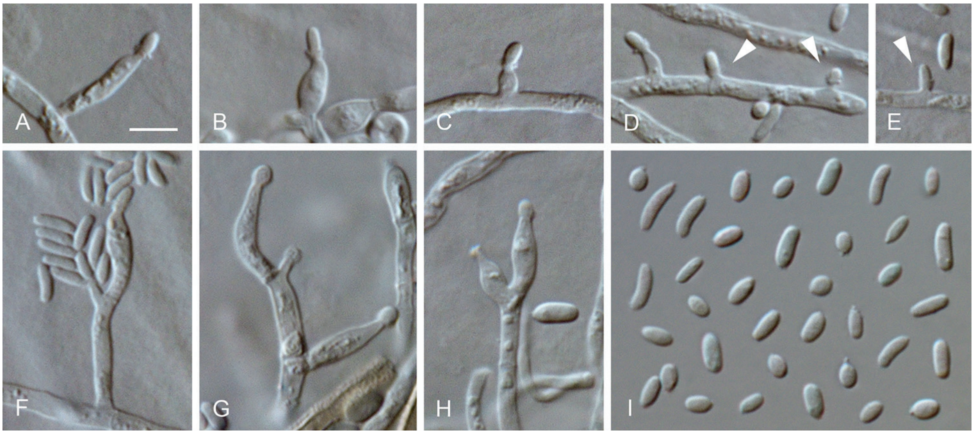

Figure 8. *Cadophora bubakii* comb. nov. **A–H** conidiophores and conidiogenous cells (arrows indicate short necks) **I** conidia **A–I** from SNA **A–I** LM. Scale bar: 5 µm (**A** applies to **H–I**).

Culture characteristics. *Colonies on SNA* flat with an entire to undulate margin, white, lacking aerial mycelium, reverse same colour, 36–56 mm diam. in 2 wk (25 °C in the dark); *Colonies on OA* flat with an entire to undulate margin, olivaceous to olivaceous black, sometimes covered by floccose aerial mycelium, olivaceous grey, reverse same colours, 24–27 mm diam. in 2 wk (25 °C in the dark).

Notes. The genus *Margarinomyces* was described 1930 with *Ma. bubakii* as type species after causing problems in a margarine factory in Czech Republic by forming greenish-black spots on and in margarine cubes that smelled like bitter-almond (benzaldehyde) (Laxa 1930). The fungus was shown to survive 20 min at 60 °C and to be resistant to organic preservatives such as sodium benzoate that was, however, only tolerated in margarine up to a concentration of 0.2% (Laxa 1930). According to the CBS website, strain CBS 198.30 is ex-isotype of *Ma. bubakii*. Schol-Schwarz (1970) included *Ma. bubakii* in *Phialophora* and considered *C. obscura* as a synonym. The genus *Margarinomyces* had been included in *Phialophora* by Gams and McGinnis (1983), though excluded by Cole and Kendrick (1973), but *Ma. bubakii* has never been considered as a species of *Cadophora* before. All nine *Margarinomyces* species had been combined in other genera, most of them in *Coniochaeta* (http://www.indexfungorum.org).

Cadophora bubakii (strain CBS 198.30) differs from *C. obscura* (strain CBS 269.33) by forming conidiogenous cells that are often slightly inflated and therefore flask-shaped, while those of CBS 269.33 are mostly narrow cylindrical. Conidia of strain CBS 198.30 are sometimes subglobose and, on average, distinctly shorter than the ellipsoidal to cylindrical conidia of CBS 269.33. Moreover, colonies of CBS 198.30 grow faster. Van Beyma (1943) compared *Ma. bubakii* and *Ph. obscura* and mentioned flask-shaped conidiogenous cells and a faster colony growth rate of *Ma. bubakii* and narrow phialides of *Ph. obscura* as well. However, the conidia shape of both species was described and illustrated as rod-shaped.

The ITS sequences of the two *C. bubakii* strains included in the phylogeny of this study, CBS 198.30 and CBS 837.69, are identical but differ both in 19 nucleotides from that of the *C. obscura* strain CBS 269.33. The *EF-1a* sequence of the two species differs in 31 nucleotides. The *TUB* sequences of CBS 198.30 and CBS 269.33 were not able to be aligned with each other and the rest of the dataset and therefore excluded from the phylogeny.

A blastn search with the ITS sequence of CBS 198.30 resulted in high similarities (99.82% and 99.64%) with "*Ph. bubakii*" strains CBS 837.69 (included in our analysis) and CBS 836.69, both isolated from margarine, as well as CBS 834.69, isolated from wood pulp of *Populus tremula* (Vu et al. 2019).

Cadophora luteo-olivacea **(J.F.H.Beyma) T.C.Harr. & McNew**

Figures 5D, 9

Description. *Sexual morph* not observed. *Asexual morph on SNA. Vegetative mycelium* hyaline, smooth-walled, septate, branched, 1–10 µm wide, hyphal cells often, sometimes very strongly inflated and constricted at the septa, chlamydospores absent. *Sporulation* abundant, conidia formed on hyphal cells. *Conidiophores* hyaline, smooth-walled, simple or septate and branched, up to 40 µm long. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, cylindrical to ± inflated, 3–14 × 1.5–4 µm, sometimes integrated, necks cylindrical, 0.5–3 µm long, collarettes funnel-shaped, 1–1.5 µm long, 1–2 µm wide at the upper edge, opening 1–1.5 µm wide, periclinal thickening not observed. *Conidia* aggregated in heads, hyaline, smooth-walled, aseptate, cylindrical, rarely ellipsoidal, straight, sometimes slightly curved, both ends rounded, conidia of strain GLMC 1310 measure (2–)4–7(–8) × 1.5–2.5 µm, mean ± SD = 5.3 ± 1.4 × 2.0 ± 0.3 µm, L/W ratio = 2.7, while those of GLMC 1264 are longer, measuring (3–)5–8(–10) × 1.5–2 µm, mean ± SD = 6.4 ± 1.6 × 1.8 ± 0.2 µm, L/W ratio = 3.5.

Culture characteristics. *Colonies on SNA* flat with an entire margin, hyaline, sometimes filter paper partly pale olivaceous to olivaceous, lacking aerial mycelium, reverse same colours, strains GLMC 1264 and GLMC 1310 5–15 mm diam., strains GLMC 517 and GLMC 1501 32–43 mm diam. in 2 wk (25 °C in the dark); *Colonies on OA* flat with an entire margin, buff, olivaceous buff, olivaceous to olivaceous black, lacking aerial mycelium or partly covered by pale grey aerial mycelium, reverse same colours, 28–44 mm diam. in 2 wk (25 °C in the dark).

Notes. In total, 12 strains of *C. luteo-olivacea* were isolated from *Prunus domestica* in Baden-Württemberg (3), Lower Saxony (8) and Saxony (1). Two strains from Baden-Württemberg, two strains from Lower Saxony and the strain from Saxony had been selected for the phylogenetic analyses. The complete sequence dataset of *C. luteo-olivacea*, including reference strains, exhibits a variation of up to five nucleotides within ITS, up to nine nucleotides within *TUB* and up to 16 nucleotides within *EF-1a* sequences. The ITS sequences of the strains from this study are identical with those of the ex-type strain, except for GLMC 1517, which differs in five nucleotides, while

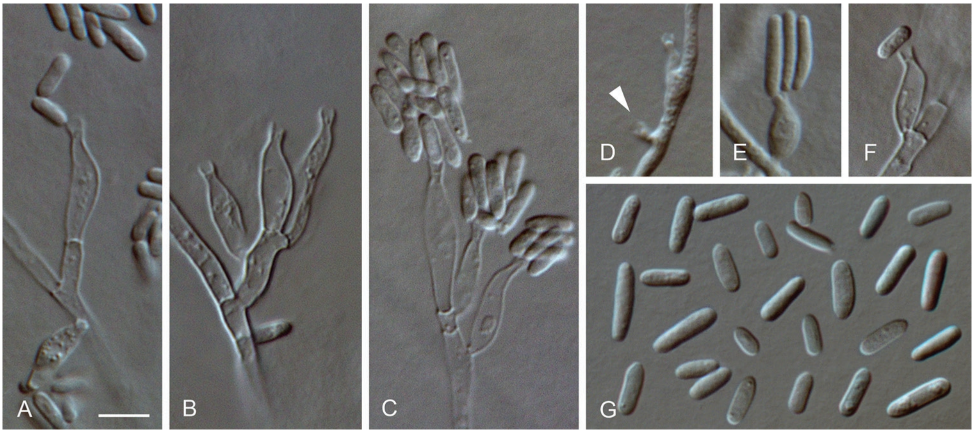

Figure 9. *Cadophora luteo-olivacea.* **A–F** conidiophores and conidiogenous cells (arrow indicates a short neck) **G** conidia **A–G** from SNA **A–G** LM. Scale bar: 5 µm (**A** applies to **B–G**).

all *TUB* sequences of our isolates differ in eight to nine nucleotides from the ex-type strain. The *EF-1a* sequence of all strains from this study differs in five nucleotides from the ex-type strain, except for GLMC 1264 with no differences.

Material examined. Germany, Lower Saxony, Hollern-Twielenfleth, orchard, 53°36'13.6"N, 9°31'50.8"E, from brown wedge-shaped necrosis in wood of *Prunus domestica*, 8 Oct. 2015, S. Bien leg., GLM-F107114, culture GLMC 1264 = CBS 145524 = DSM 109143; Lower Saxony, Hollern-Twielenfleth, orchard, 53°36'13.6"N, 9°31'50.8"E, from brown wedge-shaped necrosis in wood of *P. domestica*, 8 Oct 2015, S. Bien leg., GLM-F107160, culture GLMC 1310 = CBS 145525 = DSM 109142; Saxony, in orchard north of Wölkau, 50°58'42.3"N, 13°49'40.0"E, from brown wedge-shaped necrosis in wood of *P. domestica*, 16 Jan 2015, S. Bien leg., GLM-F106367, culture GLMC 517; Baden-Württemberg, orchard west of Nussbach, 48°31'55.8"N, 8°00'52.4"E, from brown wedge-shaped necrosis in wood of *P. domestica*, 23 Aug 2016, S. Bien leg., GLM-F110581, culture GLMC 1501; Baden-Württemberg, orchard east of Nussbach, 48°31'57.3"N, 8°01'49.6"E, from brown wedge-shaped necrosis in wood of *P. domestica*, 23 Aug 2016, S. Bien leg., GLM-F110597, culture GLMC 1517 = CBS 145526 = DSM 109141.

Cadophora novi-eboraci Travadon, D.P.Lawr., Roon.-Lath., Gubler, W.F.Wilcox, Rolsh. & K.Baumgartner

Figures 5E, 10

Description. *Sexual morph* not observed. *Asexual morph on SNA. Vegetative mycelium* hyaline, smooth-walled, septate, branched, 1–4 µm wide, sometimes hyphae inflated and constricted at the septa, chlamydospores absent. *Sporulation* abundant, conidia formed on hyphal cells. *Conidiophores* hyaline, smooth-walled, mostly simple, rarely

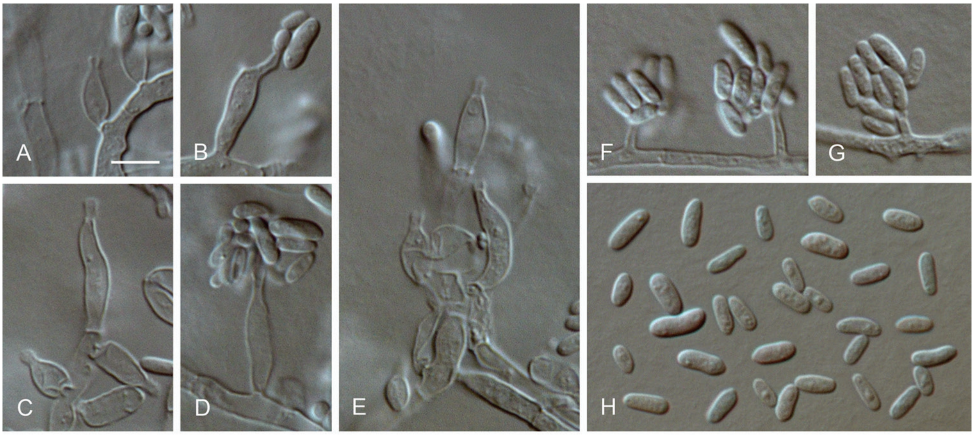

Figure 10. *Cadophora novi-eboraci* **A–G** conidiophores and conidiogenous **H** conidia **A–H** from SNA **A–H** LM. Scale bar: 5 µm (**A** applies to **B–H**).

septate and branched, up to 20 µm. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, often integrated, discrete conidiogenous cells ampulliform, ellongate-ampulliform to navicular, 7–17 × 1.5–3 µm, necks cylindrical, 1–1.5 × 1.5–5.5 µm, collarettes cylindrical to narrowly funnel-shaped, 1.5–2 µm long, 0.5–1.5 µm wide at the upper edge, opening 0.5–1 µm, periclinal thickening sometimes observed. *Conidia* aggregated in heads, hyaline, smooth-walled, aseptate, cylindrical, elongate-ellipsoidal to ellipsoidal, straight, rarely slightly curved, with both ends rounded, (3–)4.5–6.5(–8.5) × 1.5–2(–2.5) µm, mean ± SD = 5.4 ± 1.1 × 1.8 ± 0.4 µm, L/W ratio = 2.9.

Culture characteristics. *Colonies on SNA* flat with an entire to undulate margin, hyaline to pale smoke grey, filter paper partly pale luteous to very pale smoke grey, lacking aerial mycelium, reverse same colours, 5–7 mm diam. in 2 wk (25 °C in the dark); *Colonies on OA* flat with an entire to undulate margin, fawn to umber with a pale luteous to luteous margin, partly covered by floccose white aerial mycelium, reverse fawn, pale olivaceous to pale luteous, 18 mm diam. in 2 wk (25 °C in the dark).

Notes. In total, eight strains of *C. novi-eboraci* were isolated from *Prunus cerasus* in Saxony (7) and Bavaria (1). Five of the strains from Saxony and the strain from Bavaria had been selected for the phylogenetic analyses. The complete sequence dataset of *C. novi-eboraci* exhibits a certain amount of variation in the loci analysed. The ITS and *EF-1a* sequences exhibited a maximum of one and two nucleotide differences to those of the ex-type strain NYC14, respectively. The *TUB* sequences were more variable; the *TUB* sequence of strain NYC13 differs in 15 nucleotides from that of NYC14. The *TUB* sequences of the strains from this study only differ with a maximum of two nucleotides from the ex-type strain.

Material examined. Germany, Bavaria, in garden east of Wolferszell, 48°57'38.8"N, 12°38'24.9"E, from non-symptomatic wood of *Prunus cerasus*, 2 Oct 2016, J. Simmel leg., GLM-F110552, culture GLMC 1472 = CBS 145758 = DSM 109145.

Cadophora obscura **Nannf., Svenska Skogsvårdsföreningens Tidskrift 50: 418 (1934)**
Figures 5F, 11

≡ *Phialophora obscura* (Nannf.) Conant, Mycologia 29(5): 598 (1937)

Type. Sweden, Umeå, Sofiehem, Sofiehems trämassefabrik, from fresh water, E Melin leg., collection date unknown, UPS F-153532 – ***holotype*** (not seen); unknown source, E Melin, collection date unknown (isolated by E Melin and JA Nannfeldt No. 389:11, deposited in CBS collection by E Melin probably 1933), CBS H-7589, CBS H-7590, GLM-F117483 – ***isotypes***; CBS 269.33 = GLMC 1896 – culture ex-isotype.

Description. *Sexual morph* not observed. *Asexual morph on SNA. Vegetative mycelium* hyaline, smooth-walled, septate, branched, 1–3.5 µm wide, sometimes becoming brown with age, chlamydospores absent. *Sporulation* abundant, conidia formed on hyphal cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, discrete conidiogenous cells cylindrical to navicular, often bent, sometimes constricted at the base, 3–19 × 2–3 µm, necks cylindrical, 1–3.5 × 1.5–2 µm, collarettes distinct, cylindrical to funnel-shaped, 0.5–1.5 µm long, 1–1.5 µm wide at the upper edge, opening 1–1.5 µm wide, periclinal thickening observed. *Conidia* aggregated in heads, hyaline, smooth-walled, aseptate, ellipsoidal to cylindrical, mostly slightly curved, with both ends rounded, (3–)3.5–6(–7) × 1.5–2(–2.5) µm, mean ± SD = 4.8 ± 1.2 × 1.7 ± 0.3 µm, L/W ratio = 2.8.

Culture characteristics. *Colonies on SNA* flat with an entire to fimbriate margin, white to cinnamon, filter paper buff to olivaceous, lacking aerial mycelium, reverse same colours, 14–16 mm diam. in 2 wk (25 °C in the dark); *Colonies on OA* flat with an entire margin, olivaceous black to greenish-black, with honey to white margin, sometimes covered by floccose, olivaceous grey aerial mycelium, reverse same colours, 14–20 mm diam. in 2 wk (25 °C in the dark).

Notes. *Cadophora obscura* was originally described by Melin and Nannfeldt (1934) from freshwater in Sweden. According to the CBS website, strain CBS 269.33 is an "ex-isotype" culture. However, as Melin and Nannfeldt (1934) only isolated this species once and stated that they handed the strains from their study over to the Centraalbureau voor Schimmelcultures in Baarn now Westerdijk Fungal Biodiversity Institute, this can only be the ex-holotype strain. However, we were not able to allocate this strain to the holotype without doubt.

This species had previously been regarded as belonging to the genus *Phialophora* (Medlar 1915) and as a synonym of *Phialophora bubakii* (Schol-Schwarz 1970). However, based on the phylogeny of this study, both species are distinct species of the genus *Cadophora*. *Cadophora obscura* (CBS 269.33) differs from *C. bubakii* (CBS 198.30) by forming conidiogenous cells that are mostly narrow cylindrical, while those of CBS 198.30 are often flask-shaped. Conidia of *C. obscura* are distinctly longer than those of *C. bubakii*; subglobose-shaped conidia were not observed. Colony growth is slower compared to *C. bubakii*.

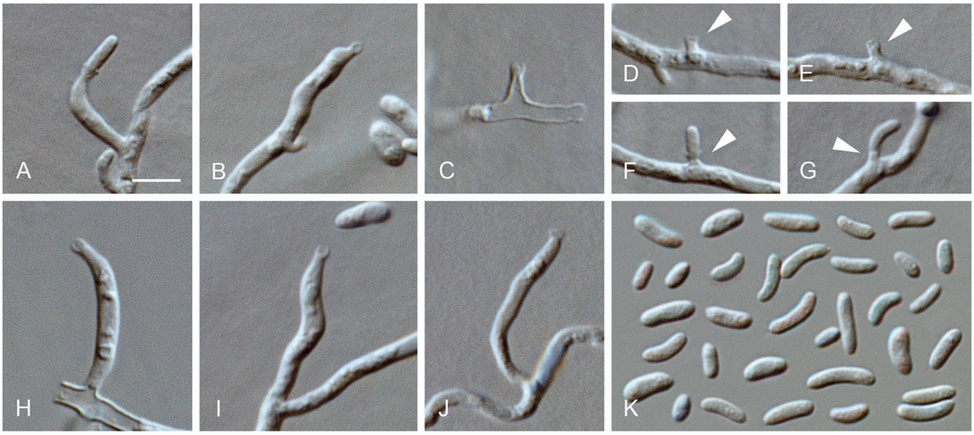

Figure 11. *Cadophora obscura* **A–J** conidiophores and conidiogenous cells (arrows indicate short necks) **K** conidia **A–K** from SNA **A–K** LM. Scale bar: 5 µm (**A** applies to **B–K**).

The ITS and *EF-1a* sequences of the ex-type strains of *C. bubakii* and *C. obscura* differ in 19 and 31 nucleotides, respectively. The *TUB* sequences of the two species were excluded from the analyses (see Notes of *C. bubakii*).

The ITS sequence of CBS 269.33 is 100% identical with three strains isolated from archaeological wood in Greenland (586-C, 592-B, 588-A, NB Pedersen et al., unpubl. data).

Cadophora prunicola Damm & S.Bien, sp. nov.

MycoBank No: 832109
Figures 5G, H, 12

Type. South Africa, Western Cape province, Franschhoek, from reddish-brown necrosis in wood of *Prunus salicina* close to an old pruning wound, 10 June 2004, U. Damm leg., CBS H-19985 – ***holotype***; GLM-F117487 – ***isotype***; CBS 120891 = STE-U 6202 = GLMC 1902 – culture ex-type.

Etymology. Named after its host genus, *Prunus* + suffix -cola (dweller).

Description. *Sexual morph* not observed. *Asexual morph on SNA. Vegetative mycelium* hyaline, septation hardly visible, branched, 1–3 µm wide, sometimes becoming brown with age, chlamydospores absent, hyphae of strain GLMC 735 in some parts inflated and restricted at the septae and up to 5 µm wide. *Sporulation* abundant, conidia formed on hyphal cells. *Conidiophores* hyaline, simple or septate and branched, up to 50 µm long. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, cylindrical, often inflated and bent in the upper part or attenuated at the base, delicate (disintegrating quickly), 4–15 × 1.5–2 µm, in strains GLMC 735 and GLMC 1574 sometimes integrated, necks cylindrical, 3–3.5 × 1 µm, collarettes distinct, funnel-shaped, cylindrical, 1–3 µm long, 1–2 µm wide at the upper edge, opening 1–1.5 µm wide, periclinal thickening sometimes observed. *Conidia* aggregated in heads, hyaline, smooth-

Figure 12. *Cadophora prunicola* sp. nov. **A–G** conidiophores and conidiogenous cells **H** conidia **A–H** from SNA **A–H** LM. Scale bar: 5 µm (**A** applies to **B–H**).

walled, aseptate, ellipsoidal, cylindrical to ovoidal, straight, rarely slightly curved, both ends rounded, (2.5–)3–6.5(–9) × 1.5–2 µm, mean ± SD = 4.9 ± 1.8 × 1.7 ± 0.3 µm, L/W ratio = 2.8, conidia of strain GLMC 1574 smaller, measuring (2.5–)3.5–5(–6.5) × 1.5–2.5(–3) µm, mean ± SD = 4.2 ± 0.7 × 1.4 ± 0.4 µm, L/W ratio = 2.1.

Culture characteristics. *Colonies on SNA* (strains GLMC 735, GLMC 1574 and GLMC 1633) flat with an entire to undulate margin, whitish, lacking aerial mycelium, reverse same colours, 18–27 mm diam. in 2 wk (25 °C in the dark). *Colonies on OA* (strains GLMC 735, GLMC 1574 and GLMC 1633) flat with an entire margin to undulate margin, buff, very pale luteus to cinnamon, lacking aerial mycelium, except for strain GLMC 1574 that was partly covered by white woolly aerial mycelium, reverse buff to fawn, 20–27 mm diam. in 2 wk (25 °C in the dark). *Colonies on PDA* (CBS 120891) flat to raised, entire margin, mycelium and surface white to very pale smoke-grey, with age turning isabelline to olivaceous in the centre, abundant velvety aerial mycelium, reverse straw to pure yellow, 18 mm diam. in 2 wk (25 °C). *Colonies on MEA* (CBS 120891) raised with entire margin, mycelium and surface white to very pale luteous, with age turning isabelline, abundant velvety aerial mycelium, reverse buff, honey to salmon, in diffuse daylight with a concentric apricot ring between centre and margin, 24 mm diam. in 2 wk (25 °C).

Notes. *Cadophora prunicola* was isolated from *Prunus salicina* (2) in the Western Cape Province of South Africa, from *P. cerasus* (3) and *P. domestica* (2) in Saxony and *P. domestica* (3) in Baden-Württemberg, Germany. The strains from South Africa, as well as three strains from both hosts from Saxony and two strains from Baden-Württemberg, were selected for the phylogenetic analyses. This species is similar to *C. novi-eboraci* and *C. africana*, but differs by forming conidiophores of up to 50 µm length and conidiogenous cells that are often inflated. Subglobose or tear-shaped conidia as in *C. africana* have not been observed. The ITS, *TUB* and *EF-1a* sequences of *C. prunicola* differ in 8, 29 and 9 nucleotides, respectively, from *C. novi-eboraci* and in 11, 30 and 20 nucleotides, respectively, from *C. africana*.

A blastn search with the ITS sequence of *C. prunicola* in GenBank showed a 100% identity with an uncultured *Cadophora* from dead wood of *Fagus sylvatica* in Germany (LC015696, Floren et al. 2015).

Additional material examined. Germany, Saxony, orchard east of Lungkwitz, 50°56'12.4"N, 13°47'36.6"E, from brown wedge-shaped necrosis in wood of *Prunus cerasus*, 11 Aug 2015, S. Bien leg., GLM-F106569, culture GLMC 735 = CBS 145521 = DSM 109135; Baden-Württemberg, orchard west of Nussbach, 48°31'55.8"N, 8°00'52.4"E, from brown necrosis in wood of *P. domestica*, 23 Aug 2016, S. Bien leg., GLM-F110714, culture GLMC 1633 = CBS 145522 = DSM 109146; Baden-Württemberg, orchard east of Nussbach, 48°31'57.3"N, 8°01'49.6"E, from brown wedge-shaped necrosis in wood of *P. domestica*, 23 Aug 2016, S. Bien leg., GLM-F110654, culture GLMC 1574; South Africa, Western Cape province, Franschhoek, from necrosis in wood of *P. salicina* close to old pruning wound, 10 June 2004, U. Damm leg., STE-U 6103.

Cadophora ramosa S.Bien & Damm, sp. nov.

MycoBank No: 832110
Figures 5I, 13

Cadophora spadicis Travadon, D.P.Lawr., Roon.-Lath., Gubler, W.F.Wilcox, Rolsh. & K.Baumgartner, *Fungal Biology* 119(1): 62 (2015). nom. inval., Art. 40.6 (Shenzhen)(Synonym).

Type. Germany, Saxony, orchard north of Kunnerwitz, 51°07'27.5"N, 14°56'36.3"E, from dark brown necrosis in wood of *Prunus cerasus*, 15 Jan 2015, S. Bien leg., GLM-F106227 – ***holotype***; GLMC 377 = CBS 145523 = DSM 109144 – culture ex-type.

Etymology. Named after the often densely branched conidiophores (*ramosus* Lat. = branching).

Description. *Sexual morph* not observed. *Asexual morph on SNA. Vegetative mycelium* hyaline, smooth-walled, septate, branched, 1–5 µm wide, chlamydospores absent. *Sporulation* abundant, conidia formed on hyphal cells. *Conidiophores* hyaline, smooth-walled, septate, often densely branched, up to 50 µm long. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, flask-shaped, 4.5–11.5 × 2.5–3.5 µm µm, collarettes narrowly funnel-shaped, 1.5–2 µm long, 1–1.5 µm wide at the upper edge, opening 0.5–1 µm, periclinal thickening sometimes observed. *Conidia* aggregated in heads, hyaline, smooth-walled, aseptate, subglobose, ovoidal, ellipsoidal to elongate-ellipsoidal, straight, with both ends rounded, different spore-shapes formed from the same conidiogenous cells, sporulation often inside the medium, (3.5–)4–6(–9) × 2–2.5(–3) µm, mean ± SD = 4.9 ± 1.2 × 2.2 ± 0.3 µm, L/W ratio = 2.2, rarely up to 15 × 2.5 µm.

Culture characteristics. *Colonies on SNA* flat with an entire margin, hyaline, filter paper partly pale olivaceous to olivaceous, lacking aerial mycelium, reverse same col-

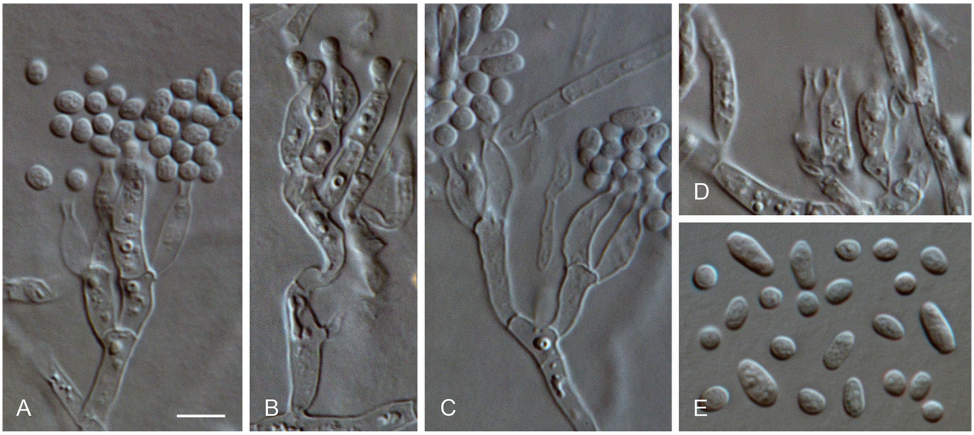

Figure 13. *Cadophora ramosa* sp. nov. **A–D** conidiophores and conidiogenous cells **E** conidia **A–E** from SNA **A–E** LM. Scale bar: 5 µm (**A** applies to **B–E**).

ours, 32–40 mm diam. in 2 wk (25 °C in the dark). *Colonies on OA* flat with an entire margin, pale cinnamon, with an umber inner and pale luteous outer margin, partly covered by woolly white to grey aerial mycelium, reverse pale cinnamon, with a citrine inner and pale luteous outer margin, 24–28 mm diam. in 2 wk (25 °C in the dark).

Notes. *Cadophora ramosa* was previously described from grapevine in North America as *C. spadicis* (Travadon et al. 2015). Although Travadon et al. (2015) indicated *C. spadicis* as a new species, they listed a basionym and added the authorities of that basionym in brackets with the new name, as if they would combine an already existing species in a new genus, which was not the case. As Travadon et al. (2015) described *C. spadicis* as a new species, they should have listed a holotype (Art. 40.6, Art. 9.1, Turland et al. 2018); however, they listed a neotype, although original material was available (Art. 9.8). Therefore, the name *C. spadicis* is invalid. Moreover, the "neotype" listed is a living strain and not a (metabolically inactive) specimen. The species listed as "basionym" of *C. spadicis* by Travadon et al. (2015), *C. melinii*, was based on a wrong identification of strain CBS 111743 by Prodi et al. (2008), the strain that was listed as "neotype" of *C. spadicis*. However, the ex-type strain of *C. melinii*, CBS 268.33, was included in the study of Travadon et al. (2015) and belonged to a different clade in the phylogeny of that publication. Moreover, the authors listed as authorities of the "basionym" are the authors of the publication in which strain CBS 111743 was wrongly identified (Prodi et al. 2008) and not the authorities of *C. melinii*. Finally, although probably not intended as the whole name, prior to the authorities and "sp. nov.", Travadon et al. (2015) listed "*Cadophora spadicis* CBS 111743", which could be interpreted as not being a binary combination consisting of the name of the genus followed by a single specific epithet (Art. 23.1).

As the name *C. spadicis* is invalid, we described the species newly as *C. ramosa* on the basis of a specimen from *Prunus cerasus* in Saxony, Germany, collected in this study. The morphology of the ex-type strain of *C. ramosa* shows a high morphological concordance with the strains described as *C. spadicis* by Travadon et al. (2015). Conidiophores, conidiogenous cells, conidia and collarettes have similar shapes and sizes. The ITS, *TUB* and *EF-1a* sequences of *C. ramosa* differ at most in two, four and two nucleotides, respectively, which is a lower genetic variation than in *C. luteo-olivacea* and *C. novi-eboraci*.

Minutiella pruni-avium **S.Bien & Damm, sp. nov.**

MycoBank No: 832111
Figures 5J, 14

Type. Germany, Baden-Württemberg, orchard west of Nussbach, 48°31'55.8"N, 8°00'52.4"E, from brown necrosis in wood of *Prunus avium*, 23 Aug 2016, S. Bien leg., GLM-F110704 – ***holotype***; GLMC 1624 = CBS 145513 = DSM 109150 – culture ex-type.

Etymology. Name refers to the host species, *Prunus avium*.

Description. *Sexual morph* not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, smooth-walled, septate, branched, 1–3 µm wide, lacking chlamydospores. *Sporulation* abundant, conidia formed directly on hyphal cells, in conidiomata and by microcyclic conidiation. *Conidiophores on hyphae* reduced to conidiogenous cells, conidiogenous loci formed terminally. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, mostly reduced to mere openings with collarettes formed directly on hyphal cells, discrete phialides rare, navicular, constricted at the base, 5.5–14.5 × 1.5–2.5 µm; collarettes rarely visible or flaring, < 0.5–3 µm long, opening 0.5–1.5 µm, periclinal thickening sometimes visible. *Conidia* aggregated in masses around the hyphae, hyaline, smooth-walled, aseptate, oblong to ellipsoidal, mostly straight, sometimes slightly curved, with both ends rounded, sometimes with a prominent scar on one end, (2.5–)3–5(–6) × 1–1.5(–2) µm, mean ± SD = 3.9 ± 0.9 × 1.4 ± 0.2 µm, L/W ratio= 2.8. *Conidiomata* produced on OA in 2–4 wk; solitary or aggregated, globose to subglobose, unilocular, immersed to superficial, 50–340 µm wide, olivaceous to black, mostly glabrous, sometimes with a few hairs, opening with an irregular rupture. *Conidiophores* reduced to conidiogenous cells. *Conidiogenus cells* enteroblastic, hyaline, smooth-walled, conidiogenous loci formed terminally, discrete phialides, globose to ampulliform or navicular, 3.5–7.5 × 2–3.5 µm, opening 0.5–1 µm, periclinal thickening sometimes visible. *Conidia* hyaline, smooth-walled, cylindrical to ellipsoidal, sometimes slightly curved, with both ends rounded, (2.5–)3–4.5(–6) × (1–)1.5–2(–3) µm, mean ± SD = 3.8 ± 0.8 × 1.7 ± 0.4 µm, L/W ratio = 2.2. *Microcyclic conidiation* occurs from minute collarettes at one or both ends of primary conidia that develop into swollen mother cells, often thick-walled, sometimes septate, > 5 µm long, 2–3.5 µm wide.

Culture characteristics. *Colonies on OA* flat with entire margin, white to saffron, with scattered umber spots due to conidiomata formation, aerial mycelium lacking, spore masses oozing from conidiomata buff, reverse white to buff, 4–8 mm diam. in 2

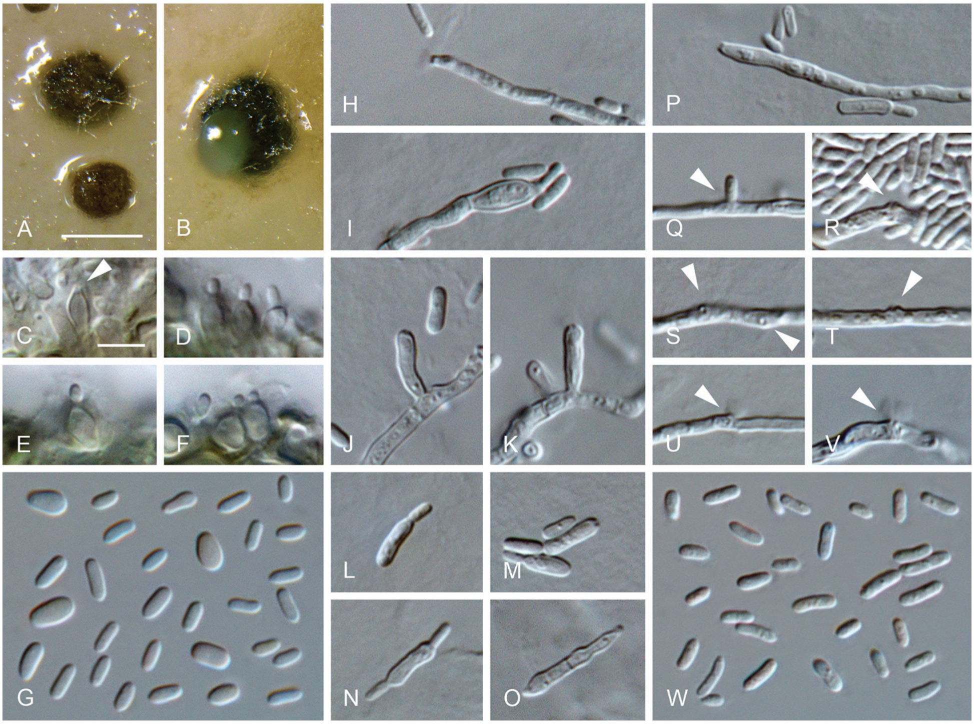

Figure 14. *Minutiella pruni-avium* sp. nov. **A, B** conidiomata **C–F** conidiogenous cells lining the inner wall of a conidioma **G** conidia formed in conidiomata **H–K, P–V** conidiogenous cells formed on hyphal cells (arrows indicate conidiogenous openings) **L–O** mother cells **W** conidia formed on hyphal cells **A–G** from OA **H–W** from SNA **A, B** SM, **C–W** LM. Scale bars: 200 µm (**A** applies to **B**), 5 µm (**C** applies to **D–W**).

wk, 6–10 mm diam. in 4 wk. *Colonies on SNA* flat with entire margin, white, lacking aerial mycelium, reverse same colour; < 1–2 mm diam. in 2 wk, 6–8 mm diam. in 4 wk.

Notes. Two strains of *Minutiella pruni-avium* were isolated from wood of *Prunus avium*. The LSU sequences of these strains differ in three and one nucleotides from those of *M. tardicola* and *Minutiella* sp., respectively. The ITS region shows 11 differences to *M. tardicola* and 9 differences to *Minutiella* sp. The *TUB* sequence of *M. tardicola* and *Minutiella* sp. differ in one nucleotide, however, in 35 and 33 nucleotides compared to *M. pruni-avium*. *Minutiella pruni-avium* differs from *Minutiella tardicola* and the strains of *Minutiella* sp. by forming larger conidiomata, longer discrete phialides and flaring collarettes of up to 3 µm.

The closest match in a blastn search with the ITS sequence of strain GLMC 1624 is the type strain of *Minutiella tardicola* CBS 121757 with 97.9% identity (NR132006, Damm et al. 2010).

Additional material examined. Germany, Baden-Württemberg, orchard west of Nussbach, 48°32'11.3"N, 8°01'01.3"E, from brown necrosis in wood of *Prunus avium*, 23 Aug 2016, S. Bien leg., GLM-F110750, culture GLMC 1667 = CBS 145514 = DSM 109149.

Proliferodiscus ingens S.Bien & Damm, sp. nov.

MycoBank No: 832112
Figures 5K, 15

Type. Germany, Baden-Württemberg, orchard south of Oppenau, on a hill, 48°27'57.6"N, 8°09'11.0"E, from necrotic wood of *Prunus avium*, 24 Aug 2016, S. Bien leg., GLM-F110834 – ***holotype***; GLMC 1751 = CBS 145519 = DSM 109148 – culture ex-type.

Etymology. Named after the comparatively huge conidiomata (*ingens* Lat. = huge).

Description. *Sexual morph* not observed. *Asexual morph on OA. Vegetative hyphae* hyaline, smooth-walled, septate, branched, 1.5–3 µm wide, lacking chlamydospores. *Sporulation* abundant, conidia formed in conidiomata. *Conidiomata* produced on OA in 2–4 wk, solitary or aggregated, subglobose, unilocular, superficial, 250–1000 µm wide, dull green to grey olivaceous, almost glabrous to completely covered with hairs, opening with an irregular rupture. *Conidiophores* hyaline, smooth-walled, septate, sometimes branched at the base and above, conidiogenous loci formed terminally. *Conidiogenus cells* enteroblastic, hyaline, smooth-walled, navicular to subulate, tapering towards apices, 8–15 × 1–2 µm; collarettes hardly visible, cylindrical, < 1 µm long, opening 0.5–1 µm, periclinal thickening sometimes visible. *Conidia* hyaline, smooth-walled, aseptate, cylindrical to ellipsoidal, straight, with both ends rounded, 2.5–3(–3.5) × 1–1.5 µm, mean ± SD = 2.9 ± 0.2 × 1.4 ± 0.1 µm, L/W ratio = 2.1.

Culture characteristics. *Colonies on OA* raised with entire to crenated margin, buff to pale olivaceous grey, white at the margin, with umber to black spots due to conidiomata, aerial mycelium sparse, white, reverse buff to cinnamon, 1–2 mm diam. in 2 wk, 2–3 mm diam. in 4 wk. *Colonies on SNA* flat to very low convex with entire to fimbriate margin, white, lacking aerial mycelium, reverse same colour; 1–2 mm diam. in 2 wk, 2–3 mm diam. in 4 wk.

Notes. Strain GLMC 1751, described here as *Proliferodiscus ingens*, was isolated from *Prunus avium* in Baden-Württemberg. Only the asexual morph of this fungus was observed. Asexual morphs have previously rarely been observed in the genus *Proliferodiscus* and no complete description is available. However, Baral and Kriegelsteiner (1985) and Dennis (1949) mention an asexual morph of *Pr. pulveraceus*. Dennis (1949) observed multilocular pycnidia with slender conidiophores (10–12 µm long) and spherical conidia (1 µm diam.), whereas Baral and Krieglsteiner (1985) described oval conidia, measuring 1.5–1.7 × 1.2–1.4 µm, produced on verticillately branched conidiophores. In contrast to the description of Dennis (1949), the strains observed here produce unilocular pycnidia. Conidia of *Pr. ingens* are larger than conidia of *Pr. pulveraceus* in both descriptions. The asexual morph of *Pr. ingens* differs from that of the other *Proliferodiscus* strains observed in this study by producing larger, darker conidiomata, a different conidial shape and a lower growth rate.

The closest match in a blastn search with the ITS sequence of strain GLMC 1751 with 97.7% identity is "Hyaloscyphaceae sp. 2" strain ICMP 18979 from symptomless leaves of *Nothofagus fusca* in New Zealand (JN225935, Johnston et al. 2012).

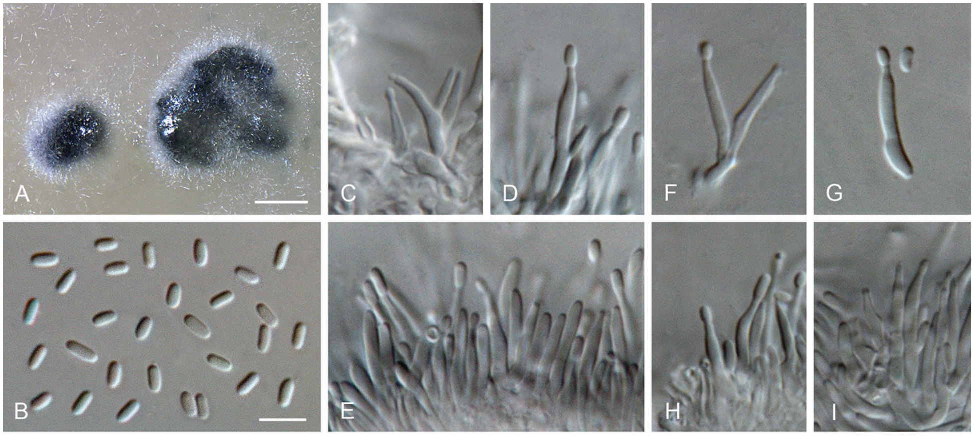

Figure 15. *Proliferodiscus ingens* sp. nov. **A** conidiomata **B** conidia formed in conidiomata **C–E, H, I** conidiogenous cells lining the inner wall of a conidioma **F, G** detached conidiogenous cells **A–I** from OA **A** SM **B–I** LM. Scale bars: 300 µm (**A**), 5 µm (**B** applies to **C–I**).

Proliferodiscus sp.

Figures 5L, 16

Description. *Sexual morph* not observed. *Asexual morph on OA. Vegetative hyphae* hyaline, smooth-walled, septate, branched, 1.5–3 µm wide, lacking chlamydospores. *Sporulation* abundant, conidia formed in conidiomata. *Conidiomata* produced on OA, SNA and pine needles in 2–4 wk, solitary or aggregated, subglobose, unilocular, superficial, 125–500 µm wide, luteous, almost glabrous to completely covered with hairs, opening with an irregular rupture. *Conidiophores* hyaline, smooth-walled, septate, simple or branched, conidiogenous loci formed terminally. *Conidiogenus cells* enteroblastic, hyaline, smooth-walled, navicular to subulate, tapering towards apices, 9–14 × 1–2 µm, collarettes cylindrical, < 1 µm long, opening 0.5–1 µm, periclinal thickening sometimes visible, conidiogenous cells often extend to form new conidiogenous openings, extensions flask-shaped to navicular. *Conidia* hyaline, smooth-walled, aseptate, mostly globose to obovoid, sometimes cylindrical to ellipsoidal, straight, with both ends rounded, 1.5–2(–3) × 1.5(–2) µm, mean ± SD = 1.9 ± 0.3 × 1.5 ± 0.1 µm, L/W ratio = 1.2.

Culture characteristics. *Colonies on OA* flat to effuse with entire to fimbriate margin, white to buff, cinnamon to sienna at the margin, aerial mycelium sparse, white, reverse buff, cinnamon to sienna; 6–14 mm diam. in 2 wk, 16–32 mm diam. in 4 wk. *Colonies on SNA* flat to effuse with entire to fimbriate margin, white, lacking aerial mycelium, reverse same colour; 6–18 mm diam. in 2 wk, 20–34 mm diam. in 4 wk.

Notes. In total, five strains of *Proliferodiscus* sp. have been isolated from wood of *Prunus domestica* in Saxony (3) and Lower Saxony (1) as well as *P. avium* in Baden-Württemberg (1). Two subclades are formed by these strains, which differ in one and four nucleotides in the LSU and ITS sequences, respectively. No morphological differences were noticed between strains of the two subclades. They form a well-supported clade (100/100/99%) with eight strains retrieved from GenBank, including the ex-type

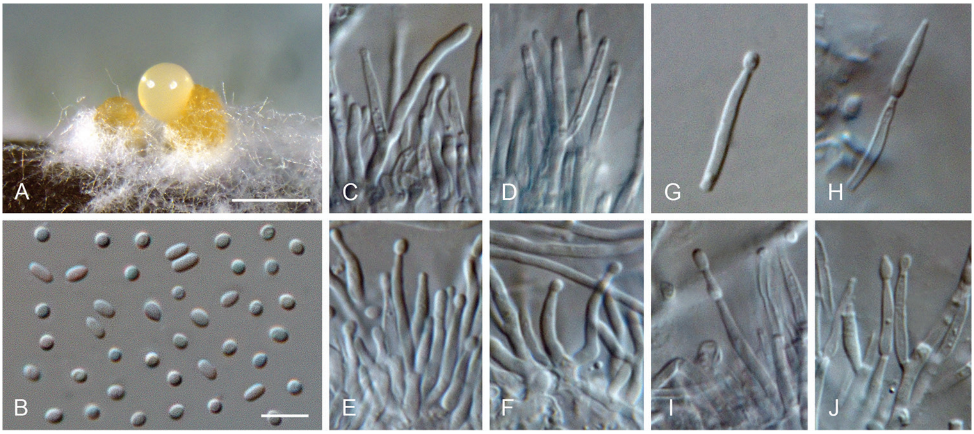

Figure 16. *Proliferodiscus* sp. **A** conidiomata **B** conidia formed in conidiomata **C–F, I–J** conidiogenous cells lining the inner wall of a conidioma **G, H** detached conidiogenous cells **H–J** extensions on conidiogenous cells **A–J** from OA **A** SM **B–J** LM. Scale bars: 300 μm (**A**), 5 μm (**B** applies to **C–J**).

strain of the recently described *Pr. chiangraiensis*. The conidial shape of these strains is similar to that of the asexual morph of *Pr. pulveraceus* observed by Baral and Krieglsteiner (1985); the conidia are slightly larger, but the measurements overlap. However, we cannot link these strains to *Pr. pulveraceus* on this basis, because the species was described based on its sexual morph and no sequences of type material are available. Moreover, a recently published sequence, designated as *Pr. pulveraceus* (MN066320, G Marson unpubl.), belongs to a different clade in our phylogeny.

One striking feature was observed in our collections: new conidiogenous cells grow out of conidiogenous openings (Fig. 16H–J). This feature has previously been observed in species of other genera, for example, *Fusarium graminearum* (Domsch et al. 2007) and several *Colletotrichum* species (Damm et al. 2012, 2019).

The anamorphic states of the observed strains of *Proliferodiscus* sp. differ from *Pr. ingens* (strain GLMC 1751, this study) by the colour and the smaller size of conidiomata, faster culture growth rate on OA and SNA and the shape of the conidia.

Material examined. Germany, Saxony, in orchard north of Wölkau, 50°58'42.3"N, 13°49'40.0"E, from brown necrosis in wood of *Prunus domestica*, 16 Jan 2015, S. Bien leg., GLM-F106310, culture GLMC 460 = CBS 145517 = DSM 109138; Baden-Württemberg, orchard west of Nussbach, 48°31'55.8"N 8°00'52.4"E, from necrotic wood of *P. avium*, 23 Aug 2016, S. Bien leg., GLM-F110844, culture GLMC 1761 = CBS 145518 = DSM 109137; Saxony, in orchard north of Wölkau, 50°58'42.3"N, 13°49'40.0"E, from brown necrosis in wood of *P. domestica*, 16 Jan 2015, S. Bien leg., GLM-F106320, culture GLMC 470; Lower Saxony, Hollern-Twielenfleth, orchard, 53°36'13.6"N, 9°31'50.8"E, from brown wedge-shaped necrosis in wood of *P. domestica*, 8 Oct 2015, S. Bien leg., GLM-F107151, culture GLMC 1301; Saxony, in orchard north of Wölkau, 50°58'42.3"N, 13°49'40.0"E, from brown necrosis in wood of *P. domestica*, 16 Jan 2015, S. Bien leg., GLM-F106352, culture GLMC 502.

Discussion

The new genus *Arboricolonus* is described, based on one strain, GLMC 459, that could not be assigned to any known genus. Closest matches of ITS (90% identity) and LSU (97% identity) sequences of this fungus with strains identified at least to the genus level were strains of *Glutinomyces vulgaris*, *Chalara aurea*, *Hyalodendriella betulae* and *Polyphilus sieberi*; (Ashrafi et al. 2018; Crous et al. 2007; Nakamura et al. 2018; Vu et al. 2019). The asexual morph of *Arboricolonus simplex* clearly differs from these genera. The monotypic genus *Hyalodendriella* forms pigmented micro- and macroconidiophores directly on hyphae as well as pigmented limoniform to ellipsoid and prominently apiculate conidia (Crous et al. 2007), while *Chalara* is characterised by forming sessile or stalked phialides with basal ventres, long collarettes and deep-seated conidiogenous loci; conidia are cylindrical and often produced in basipetal chains (Holubová-Jechová 1984; Kowalski 2006). However, *Chalara*, is highly polyphyletic; species have been placed in different classes of Ascomycota (Paulin and Harrington 2000; Koukol 2011). As the type species belongs to the Sordariomycetes (*Chalara fusidioides*), strain CBS 880.73 probably does not even belong in *Chalara* s. str. The genera *Polyphilus* and *Glutinomyces* were described, based on sequence data and colony morphology only (Ashrafi et al. 2018; Crous et al. 2017; Nakamura et al. 2018); no asexual morphs are available that could be compared to *Arboricolonus*.

For systematic placement of the genus on order level, we conducted a class-wide phylogenetic analysis of LSU-ITS with reference sequences of Leotiomycetes which clearly places it in the order Helotiales (data not shown). The closest matches from LSU and ITS blastn searches indicate the relationship of this new genus to the Hyaloscyphaceae, the largest family of the Helotiales that is mainly circumscribed by features of sexual morphs (Jaklitsch et al. 2016). Han et al. (2014b) and Johnston et al. (2019) demonstrated the polyphyly of the family. For the placement of the new genus on family level, we included LSU and ITS sequences of selected sequences from all clades of Hyaloscyphaceae and closely related families recognised by Han et al. (2014b) in their multi-locus ML analyses, as well as the closest matches from the blastn searches. The clades in our phylogeny are mostly well-supported and in agreement with the clades in Han et al. (2014b). However, most of these clades are placed on a polytomous branch. Due to the lack of a stable backbone, the exact placement of clades in relation to each other shown by the ML analyses of Han et al. (2014b) could not be confirmed and remains inconclusive. Furthermore, as shown in Fig. 1, family designation of the included strains according to Han et al. (2014b), Johnston et al. (2019) and Ekanayaka et al. (2019) is highly problematic.

The new genus *Arboricolonus* clusters in our phylogeny with sequences of *Polyphilus*, *Cistella*, *Rodwayella* and *Polydesmia*, however, on short branches, they lack posterior probability or bootstrap support. Therefore, we consider the placement of the genus as of uncertain taxonomic position on family level (Helotiales, incertae sedis). We did not find any record of asexual morphs of *Cistella* and *Rodwayella* for morphological comparison with the new genus. In contrast to *Arboricolonus simplex*, *Polydesmia pruinosa* (asexual morph: *Brefeldochium pruinosum*) produces septate falcate conidia in sporodochia (Verkley 2005).

Except for the lack of microcyclic conidiation, the genus *Arboricolonus* morphologically resembles *Collophorina* and related genera by forming slow growing cultures, conidiophores that are reduced to short phialides or openings on hyphae with minute to flaring collarettes and cylindrical to ellipsoid conidia with obtuse ends (Bien et al. 2020). A similar morphological appearance could be explained with a similar lifestyle within plant wood and is therefore regarded as a result of convergent evolution. The possibility of morphological adaptation of collophorina-like species to the habitat within the woody plant body has previously been discussed by Bien et al. (2020).

In total, 29 strains of *Cadophora* have been isolated from wood in Germany, all from *Prunus cerasus* and *P. domestica*, of which 17 were included our phylogeny. A further three strains included in the analyses originated from wood of *P. salicina* in South Africa.

The strains of *C. novi-eboraci* from this study were all isolated from wood of *P. cerasus* in Saxony and Bavaria, Germany. *Cadophora novi-eboraci* was described from decaying wood of *Vitis* spp. in the USA (Travadon et al. 2015) and recently reported from necrotic wood of *Malus domestica* in Germany (Gierl and Fischer 2017). To our knowledge, this is the first report of *C. novi-eboraci* from *Prunus* wood worldwide.

Strain CBS 101359 from stained wood of *Actinidia chinensis* in Italy had been referred to as *C. malorum* by Di Marco et al. (2004) and Prodi et al. (2008). Travadon et al. (2015) identified it as *C. novi-eboraci*. In our phylogeny, it is placed distantly from both species. We therefore regard this strain as a different taxon.

Cadophora luteo-olivacea was originally isolated from wastewater in Sweden (Van Beyma 1940). This species has been reported mostly from *Vitis vinifera* and several other woody hosts worldwide (Farr and Rossman 2019), but not from *Prunus*. Fischer et al. (2016) isolated this species from grapevine nurseries and vineyards in Germany. In this study, *C. luteo-olivacea* was isolated from *Prunus domestica* in all three sampling areas. Therefore, this is the first report of *C. luteo-olivacea* from *Prunus* wood worldwide. *Cadophora luteo-olivacea* seems to be not only widely distributed, but also very variable. Gramaje et al. (2011) observed a high variability of colony pigmentation within *C. luteo-olivacea*, which was also observed by Harrington and McNew (2003), not only in this, but also in other species of the genus. We noticed that the *TUB* and *EF-1a* sequences of the ex-type strain CBS 141.41 and strain A42, identified as *C. luteo-olivacea* by Travadon et al. (2015), differed in 8 and 16 nucleotides, respectively. Strains, isolated from *Prunus* wood in this study, show up to nine and five nucleotide differences in the *TUB* and *EF-1a* sequences, respectively. In the resulting single-locus trees (not shown), subgroups are formed that are, however, not concordant and therefore do not represent independent evolutionary lineages. This phenomenon was previously studied in the highly variable species *Colletotrichum siamense* (Liu et al. 2016), that had been regarded as species complex, based on single-locus analyses. Except for a small cluster formed by two strains from the study of Travadon et al. (2015), no subgroups are formed in the multi-locus phylogeny.

Three of the *Cadophora* species we isolated from *Prunus* wood, namely *C. luteo-olivacea*, *C. novi-eboraci* and the newly described *C. ramosa* (syn. *C. spadicis*), were previously associated with wood diseases like cankers or Petri disease of *Vitis* spp., (e.g. Casieri et al. 2009; Halleen et al. 2007; Fischer et al. 2016; Travadon et al. 2015; Pintos et al. 2018). Several other fungal species are reported both from *Vitis* and fruit trees as well, for example, several species belonging to the Botryosphaeriaceae, Diatrypaceae and the genus *Phaeoacremonium* (Damm et al. 2007, 2008; Moyo et al. 2018); fruit trees were referred to as alternative hosts of grapevine trunk disease pathogens. Similar to these fungi, *Cadophora* species could be transferred to grapevine plants from *Prunus* trees grown in close vicinity to vineyards. To our knowledge, the genus *Cadophora* has never been reported from *Prunus* before (Farr and Rossman 2019 as well as all references listed in this study). Moreover, we found new species on this host genus. One of them, *C. prunicola*, was isolated from three different *Prunus* species, *P. cerasus*, *P. domestica* and *P. salicina*, both in Germany and South Africa. A second new species, *C. africana*, is so far only known from *P. salicina* in South Africa. Based on a blastn search with its ITS sequence, *C. prunicola* was detected as an uncultured *Cadophora* in dead wood of *Fagus sylvatica* in Germany (Floren et al. 2015), but so far, there is no report of any of these two species in *Vitis* wood.

In addition to the strains isolated from *Prunus* trees in Germany and South Africa, we included strains of *Phialophora bubakii*, because we noticed a close affinity to the genus *Cadophora* by preliminary sequence comparisons (not shown). *Phialophora bubakii* that was originally described from margarine as *Margarinomyces bubakii* (Laxa 1930) and combined in *Cadophora* in this study, had previously been reported from wood of *Pinus strobus* and *Populus* sp. (Ellis 1976), where it caused blue stain on timber, from *Betula pendula* in Poland (Mulenko et al. 2008), further from subcutaneous infections (Porto 1979) and from corneal ulcers (Eiferman et al. 1983), both in humans and dogs in several countries (Hoog et al. 2000). An ITS sequence of a strain from wood pulp of *Populus tremula*, identical to that of the ex-isotype strain, is available in GenBank (Vu et al. 2019), confirming the occurrence of *Ph. bubakii* on *Populus* wood. The remaining reports lack sequence data and are therefore doubtful. Some of the reports could actually refer to other species that could have been confused due to similar morphology. None of the *C. bubakii* and *C. obscura* strains, included in this study, originated directly from wood or infections of mammals. However, the ex-isotype strain of *C. obscura* apparently originates from water in a "trämassefabrik" (trämassa = wood pulp) and therefore possibly from the processed wood itself. An identical ITS sequence from archaeological wood in Greenland (NB Pedersen et al., unpubl. data) suggests the occurrence of *C. obscura* in wood as well.

The *TUB* sequences of *C. bubakii*, *C. obscura* and *C. viticola* were excluded from the phylogenetic analyses, because all of them differed tremendously from each other and from the rest of the dataset. Furthermore, sequencing *TUB* of *C. obscura* (CBS 269.33), using either the forward or the reverse primer, generated two vastly differing sequences (data not shown). Sequencing *TUB* of *Aspergillus* spp. by Peterson (2008) and Hubka and Kolarik (2012) also resulted in different sequences from the same species, which were regarded as possible paralogous gene fragments. Based on the data in this study, we assume a similar situation in *Cadophora*.

All *Cadophora* species treated in this study can be distinguished by all single loci analysed (data not shown). Due to the high genetic variation within some of them, the use of more than one locus is recommended for further studies on this genus.

The genus *Minutiella* was isolated for the first time from wood of *Prunus armeniaca* in South Africa and described as *Phaeomoniella tardicola* (= *M. tardicola*) (Damm et al. 2010). This is the first report of the genus *Minutiella* and the Phaeomoniellales, in general, from *P. avium* and *P. domestica* worldwide. The genus *Minutiella* is, so far, only known from wood of *Prunus* trees. More specifically, *M. tardicola* is known from *P. armeniaca* in South Africa, the new species *M. pruni-avium* from *P. avium* in Germany and *Minutiella* sp. from *P. domestica* in Germany (Damm et al. 2010; this study). This genus also forms reduced conidiogenous cells; probably an adaption to the living conditions inside wood like *Collophorina* and related species and *Arboricolonus* (Bien et al. 2020; this study).

The two *Minutiella* strains GLMC 1636 and GLMC 1687 are morphologically indistinguishable from *M. tardicola*, however, differ in LSU, ITS and *TUB* sequences from this species. The description of this further new species is in preparation (C. Kraus, pers. comm.).

The LSU-ITS-*TUB* phylogeny of the Celotheliaceae shows a high similarity to the previously compiled LSU phylogeny in Chen et al. (2015). In this study, we provide the first multi-locus phylogeny of the family. For a conclusive placement of genera within this family, more data is needed, since all phylogenies lack a deep node support (Chen et al. 2015; this study). "*Phaeomoniella*" *pinifoliorum* apparently represents a separate genus. A new genus was, however, not described, as no strain and only ITS sequence data were available for characterisation of this genus.

Proliferodiscus has been reported from wood and bark of several woody hosts worldwide (Albertini and Schweinitz 1805; Dennis 1949; Baral and Krieglsteiner 1985; Spooner 1987; Weber and Bresinsky 1992; Haelewaters et al. 2018; Farr and Rossman 2019). Dennis (1949) lists *Prunus insititia* as one of the hosts of *Proliferodiscus pulveraceus.* In this study, two *Proliferodiscus* species have been collected from wood of *P. avium* and *P. domestica*.

The species delimitation in the genus *Proliferodiscus* was previously based on the morphology of the sexual morphs only (e.g. Haines and Dumont 1983; Baral and Krieglsteiner 1985; Spooner 1987; Hofton et al. 2009). Six of the species had been described even before 1900 in other genera and were transferred to this genus later. Only few morphological treatments of *Proliferodiscus* species contained information on asexual morphs (Dennis 1949; Baral and Krieglsteiner 1985). The genus has not been treated in modern terms yet.

There are sequences of ten strains/specimens identified as *Proliferodiscus* in GenBank, none of them is ex-type, except for the recently described *Pr. chiangraiensis*. The available sequences of *Proliferodiscus* belong to three main clades in our phylogeny. One well-supported clade in our phylogeny contains several apparently closely related strains/specimens, for which different names have been applied.

Most of our strains from *Prunus*, belonging to two subclades of the same main clade, did not show any morphological differences of the asexual morph and only differed in few nucleotides from each other and from the remaining specimens/sequences within this clade. Therefore, we refrained from describing two new species in this clade and refer to the strains as *Proliferodiscus* sp. In order to allow comparison with asexual morphs in this genus in the future, we provided a description of this species, as well as of the newly described species *Pr. ingens*. In order to provide a solid basis for identifications and detections of new species, *Proliferodiscus* species need to be epitypified and data of both sexual and asexual morphs, as well as sequence data, need to be provided.

Conclusion

The isolation of fungal strains from necrotic wood of *Prunus* species in Germany and South Africa revealed several unknown taxa within Leotiomycetes and Eurotiomycetes. Based on morphology and multi-locus molecular analyses, we described one new genus and six new species in four genera. Although previously unknown from wood of *Prunus* trees, the genus *Cadophora* was revealed to be a common wood inhabitant of *P. cerasus* and *P. domestica* in Germany, but apparently not of *P. avium*. The genus *Minutiella*, originally described from *P. armeniaca* in South Africa, also occurs in *Prunus* wood in Germany and, thus, belongs to the common genera in *Prunus* wood as well. Our analyses of the genus *Proliferodiscus* also contributes to the knowledge of this genus by the first detailed descriptions of asexual morphs of this genus. The results underline the sparse knowledge of several fungal genera from wood and of the wood mycobiome of the economically important host genus *Prunus*. The morphological data presented here and the up-to date molecular frameworks will provide a basis for further studies on these genera and on wood diseases of *Prunus* trees.

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Supplementary material 1

Complete list of strains included in this study, with collection details, GenBank accession numbers and references

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Xiao-Lan He[1], Egon Horak[2], Di Wang[1], Tai-Hui Li[3],
Wei-Hong Peng[1], Bing-Cheng Gan[1]

1 *Soil and Fertilizer Institute, Sichuan Academy of Agricultural Sciences, Chengdu 610066, China* **2** *Schlossfeld 17, A-6020 Innsbruck, Austria* **3** *State Key Laboratory of Applied Microbiology Southern China, Guangdong Provincial Key Laboratory of Microbial Culture Collection and Application, Guangdong Institute of Microbiology, Guangdong Academy of Sciences, Guangzhou 510070, China*

Corresponding author: *Xiao-Lan He* (xl_he@qq.com)

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We found that Table 1 “A list of taxa, specimens and GenBank accession numbers of sequences used in this study” had been omitted and figure legends 1–7 were not the final version after our manuscript was published. Table 1 and revised figure legends 1–7 are now provided below.

Table 1. A list of taxa, specimens and GenBank accession numbers of sequences used in this study.

Taxa	Collection No.	Origin	GenBank accessions			
			ITS	LSU	RPB2	mtSSU
Alboleptonia aff. *sericella*	MCA1978	—	—	GU384609	GU384632	GU384583
A. stylophora	AST84	—	—	GU384610	GU384633	GU384584
Calocybe carnea	—	—	AF357028	AF223178	DQ367432	AF357097
Claudopus minutoincanus	DLL 9871	Australia	—	HQ731514	HQ731517	HQ731511
C. viscosus	DLL 9788	Australia	—	HQ731516	HQ731518	HQ731513
Clitopilus hirneolus	MEN 199956	Italy	—	GQ289211	GQ289278	GQ289352
E. abortivum	H den Bakker 92	Canada	—	GQ289150	GQ289222	GQ289290
E. albidoquadratum	P. Manimohan 667, holotype	India: Kerala	—	GQ289150	GQ289222	GQ289290
E. albidum	YL 3218	Canada	KC710102	KC710151	—	KC710180
E. albomagnum	Gates E2030	Australia	KC710065	KC710137	—	KC710165
E. alcedicolor	E. Arnolds 02-760276, holotype	The Netherlands	KC710123	GQ289152	GQ289224	GQ289292
E. allochroum	JVG 1060902-1	Spain	KC898376	KC898522	—	KC898488
E. almeriense	LIP JVG 990105I, holotype	Spain: Almer A	KJ001428	—	—	—
E. alpinum	SAAS 774, holotype	China: Sichuan	KJ658969	KJ658972	—	—
E. asterosporum	K479	Japan: Okayama	AB691990	AB692007	AB692017	—
E. atrosericeum	K69-310 G262084, holotype	France	LN850607	—	—	—
E. azureosquamulosum	GDGM 27355	China: Guangdong	JQ410333	JQ410325	—	JQ993073
E. bisporigerum	KK 106/02	Finland	LN850534	—	LN850682	—
E. bloxamii	MEN 200442	Austria, EU	KC710087	GQ289154	GQ289226	GQ289294
E. brunneoumbonatum	CAL 317, holotype	India	KX774266	—	—	—
E. boreale	KK 106/09, holotype	Finland	LN850624	—	LN850697	—
E. byssisedum var. *microsporum*	SAAS 1160	China: Sichuan	**KU312118**	**KU534231**	**KU534476**	**KU534421**
E. byssisedum var. *microsporum*	SAAS 1828	China: Sichuan	**KU312120**	**KU534234**	**KU534477**	**KU534433**

Taxa	Collection No.	Origin	GenBank accessions			
			ITS	LSU	RPB2	mtSSU
E. caccabus	MEN 200324	Belgium	KC710063	GQ289155	GQ289227	GQ289295
E. caesiolamellatum	Wölfel, 20.2.2000, holotype	Canary Islands	KC710126	KC710157	—	KC710187
E. caespitosum	GDGM 27564	China: Hainan	JQ281477	JQ320130	JQ993078	JQ993070
E. callichroum var. *venustum*	G. Wölfel, F. Hampe (L, Wö E17/10, holotype *E. venustum*)	Germany	KC898355	KC898523	—	KC898490
E. callidermum	Stubbe 06252 (GENT)	The Netherlands	KC710115	KC710153	—	KC710183
E. cephalotrichum	C. Ulje 1997-08-01 Netherlands	The Netherlands	—	GQ289157	GQ289229	GQ289297
E. cettoi	Zuccherelli et al. 11.IX.1992, holotype	Italy	LN850560	—	LN850687	—
E. chalybeum	E. Morozova (LE254353)	Russia: Leningrad	KC898445	KC898500	—	KC898465
E. chytrophilum	R.M. Dähncke (L 855, holotype)	Spain: Canary Islands	KC898434	KC898519	—	KC898479
E. clypeatum	MEN 198302	The Netherlands	KC710059	KC710136	—	KC710164
E. cocles	J. Vauras 9770F	Finland	—	GQ289230	GQ289159	GQ289299
E. coelestinum	L. Marina (LE258103)	Russia: Sverdlovsk	KC898362	KC898524	—	KC898494
E. coeruleogracilis	MEN 2004055	Australia: Tasmania	KC710107	GQ289167	GQ289238	GQ289307
E. coeruleoviride	Stubbe 06236	Malaysia	KC710057	KC710134	—	KC710162
E. conchatum	SAAS 1117	China: Sichuan	**KU312103**	**KU534225**	**KU534463**	**KU534420**
E. conchatum	SAAS 1014	China: Sichuan	**KU312105**	**KU534224**	**KU534462**	**KU534418**
E. conchatum	SAAS 1712, holotype	China: Sichuan	**KU312111**	**KU534220**	**KU534459**	**KU534432**
E. conferendum	MEN 200330	Slovakia	KC710055	KC710133	KC710191	KC710161
E. conicosericeum	LIP JVG 1080514, holotype	—	JX454878	—	—	—
E. costatum	G. Immerzeel 2000-10-10	The Netherlands	—	GQ289161	GQ289232	GQ289301
E. crassicystidiatum	GDGM 28821, paratype	China: Guangdong	KC678997	JQ291567	JQ993085	JQ993058
E. cremeoalbum	O300037, holotype	Norway	LN850559	—	LN850686	—
E. crepidotoides	GDGM 43979, holotype	China: Hainan	KJ958982	KJ958983	KJ958984	KJ958985
E. crepidotoides	GDGM 29287	China: Hainan	—	KM581267	KM581269	KM581268
E. cretaceum	G. Gates E 1181, holotype	Australia: Tasmania	KC710064	GQ289162	GQ289233	GQ289302
E. crocotillum	SAAS 255, holotype	China: Sichuan	KC555561	KC555558	KP226185	—

Taxa	Collection No.	Origin	GenBank accessions			
			ITS	LSU	RPB2	mtSSU
E. crocotillum	SAAS 175	China: Sichuan	KC555560	KC555557	—	—
E. cyanostipitum	GDGM 31318, holotype	China: Jilin	NR154977	KY972694	—	—
E. dichroum	LE234260	Russia: Zhiguli	KC898442	KC898528	—	KC898487
E. eminens	KK 417/12, holotype	Finland	LN850584	—	—	—
E. euchroum	LE262995	Russia: Caucasus	KC898417	KC898516	—	KC898483
E. eugenei	E. Popov (LE253771 holotype)	Russia: Primorsky	KC898438	KC898529	—	—
E. excentricum	M. Meusers E 1705	Germany	—	GQ289163	GQ289234	GQ289303
E. fasciculatum	L.R. Hesler 29376, holotype	U.S.A.	LN850614	—	—	—
E. flabellatum	SAAS 1501	China: Guizhou	**KU312115**	**KU534215**	**KU534471**	—
E. flabellatum	SAAS 1080, holotype	China: Guizhou	**KU312116**	**KU534217**	**KU534470**	—
E. flavifolium	Y. Lamoureux 2846 (CMMF)	Canada, Québec	KC710097	KC710150	—	KC710179
E. flocculosum	JVG 1080920-20	Spain: Barcelona	KJ001438	KJ001463	—	—
E. fumosobrunneum	MEN2005120, holotype	Canada, Newfoundland	KC710125	KC710156	—	KC710186
E. furfuraceum	GDGM 28818, holotype	China: Jinlin	JX975293	JQ993094	JQ993084	JQ993062
E. fuscohebes	LIP JVG 960127, holotype	—	JX454908	—	—	—
E. gelatinosum	G. Gates E792	Australia: Tasmania	KC710103	GQ289165	GQ289236	GQ289305
E. gracilior	G. Gates E1220	Australia: Tasmania	KC710112	GQ289169	GQ289240	GQ289309
E. graphitipes	JVG 1071208-10	Spain: Bizkaia	KJ001449	KJ001458	—	—
E. gregarium	SAAS 1220, holotype	China: Yunnan	**KU312122**	**KU534237**	**KU534474**	**KU534423**
E. gregarium	SAAS 1493	China: Yunnan	**KU312125**	**KU534238**	**KU534475**	**KU534430**
E. griseocarpum	SAAS 1230, holotype	China: Tibet	MH020753	KU534253	KU534500	KU534438
E. griseocyaneum	O. Morozova (LE254351)	Russia: Caucasus	KC898444	KC898498	—	KC898463
E. griseolazulinum	P. Manimohan 738, holotype	India: Kerala	—	GQ289166	GQ289237	GQ289306
E. griseopruinatum	JLC030924-8, isotype	France	LN850556	—	—	—
E. haastii	ME Noordeloos 2004055	Australia: Tasmania	—	GQ289167	GQ289238	GQ289307
E. halophilum	LIP JVG 961228H, holotype	Spain: Almer A	KJ001441	KJ001461	—	—
E. hebes	E. Hartman 1992-10-28	Netherlands	—	GQ289170	GQ289241	GQ289310

Taxa	Collection No.	Origin	GenBank accessions			
			ITS	LSU	RPB2	mtSSU
E. henricii	HKAS 63414	China: Henan	—	JQ410332	JQ993076	JQ993069
E. hirtipes	JVG 990510-2	—	JX454935	—	—	—
E. hypogaeum	K382, holotype	Japan: Oita	AB692001	AB692009	AB692019	—
E. incanum	HKAS 54614	China: Yunnan	JQ281488	JQ320127	—	—
E. indigoticoumbrinum	ME Noordeloos 200406 3, holotype	Australia: Tasmania	—	GQ289242	GQ289171	GQ289311
E. indoviolaceum	P. Manimohan 700, holotype	India: Kerala	—	GQ289172	GQ289243	GQ289312
E. indutoides	O. Morozova (LE254354)	Russia: Leningrad	KC898451	KC898503	—	KC898468
E. infundibuliforme	TENN:013964, holotype	USA: Tennessee	HQ179671	HQ179671	—	—
E. juncinum	JC-19981012.5a (Ex-1004)	—	JX454902	—	—	—
E. kermandii	G. Gates E227, holotype	Australia: Tasmania	—	GQ289173	GQ289244	GQ289313
E. kerocarpus	WU18878, holotype	Austria	LN850576	—	LN850688	—
E. lampropus	UPS: BOT: F-176490, neotype	Sweden	KC898377	KC898471	—	KC898506
E. aff. *Luteum*	GDGM 28991	China	—	JQ993093	JQ993075	—
E. lepidissimum	E. Popov (LE254871)	Russia: Novgorod	KC898363	KC898531	—	KC898493
E. lupinum	KK 13/14 & J. Vauras, holotype	Finland	LN850570	—	LN850695	—
E. luteodiscum	CAL 132, holotype	India	KX774267	—	—	—
E. luridum	MEN 2005108	Italy	KC710091	KC710146	KC710192	KC710175
E. majaloides	KK 782/12	Finland	LN850478	—	LN850654	—
E. malenconii	JVG 1111118-1	—	JX454946	—	—	—
E. manganaense	G. Gates E369, isotype	Australia: Tasmania	KC710085	KC710143	—	KC710172
E. mastoideum	GDGM 26597, holotype	China: Guangdong	JQ291564	JQ320126	—	—
E. mirum	KK 99/14, holotype	Finland	LN850548	—	LN850699	—
E. mougeotii	LE254352	Russia: Caucasus	KC898446	KC898499	—	KC898464
E. murrayi	QI 1001	China: Liaoning	KJ658967	JQ993090	JQ993081	JQ993064
E. myrmecophilum	G. Tjallingii-Beukers 1981-10-30	Netherlands	KC710120	GQ289174	GQ289245	GQ289314
E. nidorosum	KK 419/12	Finland	LN850503	LN850706	LN850673	—
E. nitens	JC-19981012.5b (Ex-1004)	—	JX454901	—	—	—

Taxa	Collection No.	Origin	GenBank accessions			
			ITS	LSU	RPB2	mtSSU
E. nitidum	ME Noordeloos 200426	Slovakia	KC710122	GQ289175	GQ289246	GQ289315
E. ochreoprunuloides	E. Arnolds 01-142, holotype	Germany	KC710092	KC710147	—	KC710176
E. olivaceohebes	Dhancke 2507	—	JX454932	—	—	—
E. omiense	GDGM 27563	China:	JQ281487	JQ410330	JQ993079	JQ993067
E. pallideradicatum	A. Hausknecht, isotype ex WU 189010	Austria	—	GQ289176	GQ289247	GQ289316
E. pallidocarpum	GDGM 28828	China: Jilin	JQ320106	JQ410331	JQ993080	JQ993074
E. paludicola	KK 386/12	Finland	LN850516	—	LN850678	—
E. palustre	KK 101/14, holotype	Finland	LN850592	—	LN850692	—
E. parasiticum	ME Noordeloos 200330	Belgium	—	GQ289177	GQ289248	GQ289317
E. paragaudatum	KK 383/08, holotype	Finland	LN850530	—	LN850691	—
E. perbloxamii	MEN 2004071, holotype	Australia: Tasmania	KC710117	GQ289178	GQ289249	GQ289318
E. percoelestinum	T. Bulyonkova (LE254327)	Russia: Novosibirsk	KC898359	KC898526	—	KC898496
E. phaeocarpum	LIP JVG 1031018, holotype	Spain: La Rioja	KJ001430	KJ001462	—	—
E. phaeomarginatum	ME Noordeloos 2004127	Australia: Tasmania	—	GQ289179	GQ289250	GQ289319
E. philocistus	Hausknecht & Reinwald 9.XI.1998, paratype	Portugal	LN850600	—	—	—
E. placidum	S. Lundell (5276) & G. Haglund (UPS: BOT: F-121714, epitype)	Sweden	KC898394	KC898514	—	KC898481
E. pleurotoides	SAAS 1215	China: Yunnan	**KU312112**	**KU534229**	**KU534467**	**KU534422**
E. pleurotoides	SAAS 1252, holotype	China: Yunnan	**KU312113**	**KU534227**	**KU534468**	**KU534424**
E. pleurotoides	SAAS 1354	China: Yunnan	**KU312114**	**KU534228**	**KU534469**	**KU534425**
E. politum	KK 289/09	Finland	LN850511	—	LN850677	—
E. porphyrescens	ME Noordeloos 2004113	Australia: Tasmania	—	GQ289182	GQ289253	GQ289322
E. praegracile	GDGM 29251	China: Guangdong	JQ281482	JQ320129	JQ993077	JQ993072
E. prismaticum	K381	Japan: Tokyo	AB691998	AB692006	AB692016	—
E. procerum	ME Noordeloos 2004070	Australia: Tasmania	—	GQ289183	GQ289254	GQ289323
E. prunuloides	MEN 200340	Slovakia	KC710073	GQ289184	GQ289255	GQ289324
E. pseudofavrei	JVG 1060930-7	—	JX454886	—	—	—

Taxa	Collection No.	Origin	GenBank accessions			
			ITS	LSU	RPB2	mtSSU
E. pygmaeopapillatum	ME Noordeloos 200364	Slovakia	—	GQ289185	GQ289256	GQ289325
E. quadratum	GDGM 28953	China: Jiangxi	—	KJ648471	KP226183	—
E. radicipes	KK 42/14, holotype	Finland	LN850585	—	LN850693	—
E. readiae	ME Noordeloos 2004050	Tasmania: Australia	—	GQ289186	GQ289257	GQ289326
E. reductum	SAAS 1016	China: Sichuan	**KU312117**	**KU534236**	**KU534482**	**KU534435**
E. reductum	SAAS 1091, holotype	China: Yunnan	**KU312123**	**KU534232**	**KU534480**	**KU534419**
E. reductum	SAAS 1608	China: Yunnan	**KU312124**	**KU534233**	**KU534481**	**KU534431**
E. rhodocylix	K (M): 147598	United Kingdom: Wales	KJ001415	KJ001450	—	—
E. rhodopolium	KK 1664/12	Sweden	LN850497	LN850705	LN850705	—
E. rivulare	KK 703/12, holotype	Finland	LN850544	LN850701	LN850707	—
E. rubropilosum	SAAS 406	China: Sichuan	MH020761	KU534218	KU534488	KU534439
E. rusticoides	LIP JVG 1020416U, epitypus	Spain: Tarragona	KJ001434	KJ001478	—	—
E. sarcitum	A. Hausknecht 1994-04-20	Austria	—	GQ289188	GQ289259	GQ289328
E. saussetiense	G. Eyssartier 08-067, holotype	France	LN850594	—	—	—
E. sericatum	KK 299/08	Finland	LN850442	—	LN850630	LN850702
E. sericellum	ME Noordeloos 200315	Belgium	—	GQ289190	GQ289261	GQ289330
E. sericeonitidum	TB 7144	—	EF421108	AF261315	EF421016	EF421108
E. serpens	KK 410/09, holotype	Finland	LN850526	—	LN850694	—
E. serrulatum	ME Noordeloos 2004062	Australia: Tasmania	—	GQ289192	GQ289263	GQ289332
E. setastipes	L.R. Hesler 13853, holotype	U.S.A.	LN850619	—	—	—
E. sinuatum	J. Wisman 2003-09-19	Netherlands	KC710109	GQ289193	GQ289264	GQ289333
E. sordidulum	Co-David 2003	Belgium	KC710062	GQ289194	GQ289265	GQ289334
Entoloma sp.	K389	Japan: Oita	AB691993	AB692008	AB692018	—
Entoloma sp.1	083001	China: Yunnan	**KU312119**	**KU534230**	**KU534479**	**KU534437**
Entoloma sp.1	SAAS 1154	China: Sichuan	**KU312121**	**KU534235**	**KU534478**	**KU534434**
Entoloma sp.2	SAAS 369	China: Jilin	**KU312104**	**KU534216**	**KU534483**	**KU534416**
Entoloma sp.3	SAAS 203	China: Jilin	KJ658966	KJ658971	KU534473	KU534415
Entoloma sp.4	SAAS 712	China: Shaanxi	KJ658970	KJ658973	KU534472	KU534417

Taxa	Collection No.	Origin	GenBank accessions			
			ITS	**LSU**	**RPB2**	**mtSSU**
Entoloma sp.5	SAAS 315	China: Sichuan	—	—	—	—
E. subcaesiocinctum	SAAS 133	China: Jilin	KY711236	KY972697	—	—
E. sublaevisporum	LIP JVG 1070823T, holotype	Spain	KC898436	KC898518	—	KC898478
E. subtenuicystidiatum	GDGM 28459	China: Jiangxi	JQ320109	JQ320116	—	JQ993071
E. tectonicola	P. Manimohan (741, holotype)	India	—	GQ289196	—	GQ289336
E. tenellum	Dhancke 2820	—	JX454933	—	—	—
E. tenuissimum	GDGM 28813	China: Jilin	JX975295	JQ993097	JQ993086	JQ993059
E. terreum	Esteve-Raventós et al. 16.X.2003, holotype	Spain	LN850547	—	—	—
E. tjallingiorum	S. Ryman (6124) (UPS: BOT: F-016378, holotype)	Sweden	KC898412	KC898509	—	KC898474
E. trachyosporum	H. den Bakker 1901	Canada	KC710121	GQ289199	—	GQ289339
E. transmutans	ME Noordeloos 2004155	Australia: Tasmania	—	GQ289200	GQ289268	GQ289340
E. turbidum	MEN 200351	Slovakia	KC710060	GQ289201	GQ289269	GQ289269
E. undatum	ME Noordeloos 200327	Belgium	—	GQ289202	GQ289270	GQ289342
E. undatum	JVG 1051115-19	Spain: Girona	KJ001410	KJ001455	—	—
E. undulatosporum	SFC 11021902	Spain: Barcelona	KJ001412	KJ001454	—	—
E. valdeumbonatum	M. Meusers E4565, holotype	Germany	—	GQ289203	GQ289271	GQ289343
E. venustum	L, Wö E17/10, holotype	Germany	KC898355	KC898523	—	KC898490
E. vindobonense	Wu 20810, holotype	—	JX454802	—	—	—
E. violaceovillosum	P. Manomohan 645, holotype	India: Kerala	—	GQ289205	GQ289273	GQ289345
E. violaceozonatum	V. Liiv (L 275, holotype)	Estonia	KC898448	KC898502	—	KC898467
Inocephalus hypipamee	DLL 10071	Australia	—	JQ624609	JQ624616	JQ624604
Inocephalus plicatus	DLL 10216	Australia	—	JQ624615	JQ624623	JQ624606
Inocephalus sp. 1	MCA 2479	—	—	GU384622	GU384640	GU384593
Inocephalus sp. 2	GD-b	Argentina	DQ490636	DQ457683	DQ472728	—
Inocephalus sp. 3	MCA 1867	—	—	GU384621	GU384638	GU384591

Taxa	**Collection No.**	**Origin**	**GenBank accessions**			
			ITS	**LSU**	**RPB2**	**mtSSU**
Leptonia sp.	MCA 1486	—	—	GU384623	GU384635	GU384589
Lyophyllum leucophaeatum	—	—	AF357032	AF223202	DQ367434	AF357101
Nolanea sericea	VHAs 03/02	—	—	DQ367423	DQ367435	EF421099
N. strictior	DUKE-JM96/10	—	EF421109	—	EF421017	EF421100
Pouzarella albostrigosa	DL Largent 9641	Australia: Queensland	—	HQ876535	HQ876513	HQ876557
P. farinosa	DL Largent 9934, holotype)	Australia: Queensland	—	HQ876516	HQ876495	HQ876538
P. lasia	DL Largent 9662	Australia: Queensland	—	HQ876529	HQ876507	HQ876551
P. pilocystidiata	DL Largent 9932, holotype	Australia: Queensland	—	HQ876521	HQ876500	HQ876543

Sequences in bold are newly generated in this study.

Figure 1. Basidiomes of *Claudopus* species. **a** Basidiomes of *E. conchatum* on soil (SAAS 1712) **b** Basidiomes of *E. conchatum* on stem of live *Pinus* (SAAS 1014) **c** Pileus of *E. flabellatum* (SAAS 1501) **d** Lamellae of *E. flabellatum* (SAAS 1080). **e** Basidiomes of *C. gregarium* on bark-wood of live *Castanopsis* (SAAS 1220) **f** Red droplets on the lamellar edges of *E. gregarium* (SAAS 1493) **g** Basidiomes of *E. pleurotoides* on decaying bark-wood of *Castanopsis* (SAAS 1215) **h** Basidiomes of *E. pleurotoides* on bark-wood of live *Castanopsis* (SAAS 1252) **i** Basidiomes of *E. reductum* on decaying stump of *Castanopsis* (SAAS 1091) **j** Mature basidiomes of *E. reductum* on rock (SAAS 2068) **k** Young basidiomes of *E. reductum* on soil (SAAS 1016) **l** Lamellae of *E. byssisedum* var. *microsporum* (SAAS 1828) **m** Basidiomes of *E. byssisedum* var. *microsporum* on decaying stump of *Betula* (SAAS 1160).

Figure 2. Microscopic structures of *Entoloma conchatum* (holotype): **a** Basidiospores **b** Pileipellis.

Figure 3. Microscopic structures of *Entoloma flabellatum* (holotype). **a** Basidiospores **b** Pileipellis.

Figure 4. Microscopic structures of *Entoloma gregarium* (holotype). **a** Basidiospores **b** Pileipellis.

Figure 5. Microscopic structures of *Entoloma pleurotoides* (holotype). **a** Basidiospores **b** Pileipellis.

Figure 6. Microscopic structures of *Entoloma reductum* (holotype). **a** Basidiospores **b** Pileipellis.

Figure 7. Microscopic structures of *Entoloma byssisedum* var. *microsporum* (SAAS 1279). **a** Basidiospores **b** Pileipellis.