New insights into acremonium-like fungi in *Hypocreales*: A taxonomic and phylogenetic perspective

L. Zhao[1,2], J.Z. Groenewald[1], L.W. Hou[1], M. Starink-Willemse[1], B. Beek[1], O.A. Grum-Grzhimaylo[3], R.C. Summerbell[4,5], P.W. Crous[1,2*]

[1]*Westerdijk Fungal Biodiversity Institute, Uppsalalaan 8, Utrecht, 3584 CT, The Netherlands;* [2]*Microbiology, Department of Biology, Utrecht University, Padualaan 8, Utrecht, 3584 CH, The Netherlands;* [3]*Laboratory of Genetics, Plant Sciences Group, Wageningen University, Droevendaalsesteeg 1, 6708PB, Wageningen, the Netherlands;* [4]*Sporometrics, Toronto, ON, Canada;* [5]*Dalla Lana School of Public Health, University of Toronto, Toronto, ON, Canada*
Current address of LZ: State Key Laboratory of Agricultural and Forestry Biosecurity, College of Life Sciences, Fujian Agriculture and Forestry University, Fuzhou 350002, China
Current address of OAG-G: White Sea Biological Station, Faculty of Biology, Lomonosov Moscow State University, 1–12 Leninskie Gory, 119234, Moscow, Russia

[*]*Corresponding author*: Pedro W. Crous, p.crous@wi.knaw.nl

Abstract: Acremonium-like fungi represent a morphologically reduced and polyphyletic group with ecological roles ranging from saprophytes and endophytes to opportunistic pathogens, and with demonstrated potential for producing bioactive secondary metabolites. Convergent morphologies and incomplete molecular data have long hampered their taxonomic resolution. Recent studies, combining morphological features, phylogenetic analyses, and ecological and host associations have classified acremonium-like species within the orders *Cephalothecales*, *Coniochaetales*, *Glomerellales*, and *Hypocreales*. Furthermore, *Acremonium* s. str. is restricted to the family *Bionectriaceae*. However, many acremonium-like species remain to be discovered, and there are still gaps in our understanding of their ecological functions and potential applications in biotechnology. In this study, we evaluated 402 isolates of acremonium-like fungi from the CBS culture collection, including isolates that had not yet undergone molecular analysis. Isolates were analysed based on morphological characters and molecular phylogeny, for which DNA sequence data were obtained from the internal transcribed spacer regions 1 and 2 and 5.8S nuclear ribosomal RNA gene (ITS), partial 28S large subunit (LSU) nrDNA, and the protein-coding genes RNA polymerase II second largest subunit (*RPB2*) and translation elongation factor 1-alpha (*TEF1*). Our results place those isolates into the orders *Hypocreales* and *Trichosphaeriales*, distributed in 18 families and 149 species. The most represented family is *Bionectriaceae*, followed by *Sarocladiaceae* and *Trichosphaeriaceae*. We introduce two new families, seven new genera, and 33 novel species, along with four new combinations. This study provides a robust phylogenetic framework for the order *Hypocreales*, resolving 29 families, thereby stablishing a strong foundation for future ecological, medical, and biotechnological studies on this taxonomically complex group.

Key words: acremonium-like, *Bionectriaceae*, *Hypocreales*, multi-locus, new taxa, phylogeny, taxonomy.

Taxonomic novelties: New families: *Aurantidochiaceae* Lin Zhao & Crous, *Neochrysonectriaceae* Lin Zhao & Crous. **New genera:** ***Aurantidochiaceae*:** *Aurantidochium* Lin Zhao & Crous, *Lagenariomyces* Lin Zhao & Crous; ***Bionectriaceae*:** *Cannomyces* Lin Zhao & Crous, *Pilgeriellomyces* Lin Zhao & Crous; ***Neochrysonectriaceae*:** *Neochrysonectria* Lin Zhao & Crous; ***Stachybotryaceae*:** *Sporodochius* Lin Zhao & Crous; ***Trichosphaeriaceae*:** *Titanomyces* Lin Zhao & Crous. **New species:** ***Aurantidochiaceae*:** *Lagenariomyces collarulis* Lin Zhao & Crous, *Lagenariomyces varioconidialis* Lin Zhao & Crous; ***Bionectriaceae*:** *Acremonium ecuadorense* Lin Zhao & Crous, *Acremonium proliferatum* Lin Zhao & Crous, *Acremonium soli* Lin Zhao & Crous, *Acremonium tapetis* Lin Zhao & Crous, *Cannomyces spinulosus* Lin Zhao & Crous, *Clavatomyces pycnidialis* Lin Zhao & Crous, *Lasionectria eichhorniae* Lin Zhao & Crous, *Pilgeriellomyces brasiliensis* Lin Zhao & Crous, *Protocreopsis ellipsoidea* Lin Zhao & Crous, *Protocreopsis helvetica* Lin Zhao & Crous, *Protocreopsis polyphialidica* Lin Zhao & Crous, *Protocreopsis spinulosa* Lin Zhao & Crous, *Ramosiphorum sporodochiale* Lin Zhao & Crous, *Verruciconidia maritima* Lin Zhao & Crous, *Verruciconidia indonesiana* Lin Zhao & Crous, *Verruciconidia terricola* Lin Zhao & Crous, *Verruciconidia thailandica* Lin Zhao & Crous; ***Neochrysonectriaceae*:** *Neochrysonectria humicola* Lin Zhao & Crous; ***Sarocladiaceae*:** *Chlamydocillium theobromae* Lin Zhao & Crous, *Chlamydocillium viridicolor* Lin Zhao & Crous, *Parasarocladium kislosladkoense* Lin Zhao, O.A. Grum-Grzhim & Crous, *Sarocladium alniphilum* Lin Zhao & Crous, *Sarocladium catenulatum* Lin Zhao & Crous, *Sarocladium hirsutum* Lin Zhao & Crous, *Sarocladium humicola* Lin Zhao & Crous, *Sarocladium limosialveum* Lin Zhao, O.A. Grum-Grzhim & Crous, *Sarocladium nubiaquae* Lin Zhao & Crous; ***Trichosphaeriaceae*:** *Allomusicillium malicola* Lin Zhao & Crous, *Brunneomyces romanianus* Lin Zhao & Crous, *Chlamydosporiella aerina* Lin Zhao & Crous, *Titanomyces triconidiogenes* Lin Zhao & Crous. **New combinations:** ***Aurantidochiaceae*:** *Aurantidochium guadalupense* (Ramaley) Lin Zhao & Crous; ***Bionectriaceae*:** *Clavatomyces palmarum* (Zhang *et al.*) Lin Zhao & Crous; ***Sarocladiaceae*:** *Polyphialocladium margaretcollinsiae* (Y.P. Tan *et al.*) Lin Zhao & Crous; ***Stachybotryaceae*:** *Sporodochius pironii* (Alfieri & Samuels) Lin Zhao & Crous.

Citation: Zhao L, Groenewald JZ, Hou LW, Starink-Willemse M, Beek B, Grum-Grzhimaylo OA, Summerbell RC, Crous PW (2026). New insights into acremonium-like fungi in *Hypocreales*: A taxonomic and phylogenetic perspective. *Studies in Mycology* **113**: 1–71. doi: 10.3114/sim.2026.113.01
Received: 23 August 2025; **Accepted:** 3 January 2026; **Effectively published online:** 6 February 2026
Corresponding editor: Robert A. Samson

This work is dedicated to Walter Gams (9 August 1934 – 9 April 2017†), who devoted most of his career to collecting and culturing these remarkable fungi. His effort in depositing them in the CBS culture collection made this important revision possible.

Studies in Mycology

INTRODUCTION

Acremonium sensu lato (s. lat.) species represent a diverse group of fungi found in various environmental niches worldwide. These cosmopolitan species exhibit remarkable ecological versatility, driving key ecosystem processes as saprobes, pathogens, mycoparasites, and endophytes. This functional diversity underpins their dual significance in both natural ecosystems and human endeavours such as medicine, the food industry, agriculture, and biotechnology. In the medical field, acremonium-like fungi are primarily recognised as opportunistic pathogens, particularly in immunocompromised individuals, and have been linked to infections such as mycetoma, onychomycosis, keratomycosis, peritonitis, and disseminated infections (Gupta *et al.* 2000, Novicki *et al.* 2003, Perdomo *et al.* 2011, Summerbell & Scott 2015, Summerbell *et al.* 2018, de Hoog *et al.* 2000, 2020). This clinical relevance is exemplified by several species known to cause human infections, notably *A. falciforme* (current name *Neocosmospora falciformis*), *A. kiliense* (current name *Sarocladium kiliense*), and *A. recifei* (current name *Xenoacremonium recifei*), which are well-documented primary etiological agents of white-grain mycetoma, a chronic subcutaneous infection characterised by soft, white to pale grey granules (Halde *et al.* 1976, McCormack *et al.* 1987, Kwon-Chung & Bennett 1992, Lee *et al.* 1995, Agarwal *et al.* 2011, de Hoog *et al.* 2000, 2020). In the food industry, *Acremonium* s. lat. species are considered as food-spoiling microorganisms, as they have been found in cereal and grain products, leading to spoilage during storage; are associated with the deterioration of fruits and vegetables; and have also been reported to contaminate various food categories, including nuts and seeds, dairy products, bottled mineral water, and processed foods like salami, and biltong (Gams 1971, Fernández-Trujillo 1997, Fujikawa *et al.* 1997, Pitt *et al.* 1993, Pitt & Hocking 1997, 2009, 2022, Castillo *et al.* 2004, Samson *et al.* 2004, Summerbell & Scott 2015, Summerbell *et al.* 2018). In agriculture, *Acremonium* s. lat. species exhibit dual roles, some species act as plant pathogens; for example, Acremonium brown spot of bagged apples in China, a plant disease caused by *Acremonium sclerotigenum* (currently named *Acremonium egyptiacum*), causing 1–30 % annual yield losses (Li *et al.* 2014). Others function as beneficial endophytes, enhancing plant resilience to environmental stresses, such as drought, salinity, and pathogen infections, or act as mycoparasites, serving as biological control agents against plant diseases (Bettiol 1996, Choi *et al.* 2009, Doan *et al.* 2010, Jäschke *et al.* 2010, Auer & Ludwig-Müller 2014, 2015, Bobeck & Pearce 2017). Furthermore, *Acremonium* s. lat. species show significant promise in biotechnology, as they are known to produce a variety of bioactive metabolites. For example, the well-known β-lactam antibiotic cephalosporin, originally derived from *Acremonium chrysogenum*, an important industrial microorganism that produces cephalosporin C, the primary precursor of 7-amino cephalosporanic acid (7-ACA), has been successfully commercialised and is widely used in global clinical practice for treating bacterial infections (Burton & Abraham 1951, Gams 1971, Hamilton-Miller 2000, Hu & Zhu 2016). To date, over 600 secondary metabolites have been identified from *Acremonium* s. lat. species, classified into terpenoids, peptides, polyketides, and others (steroids, amides, and alkaloids), predominantly from marine sources (Qin *et al.* 2024). This emphasizes the ongoing research into the bioactive compounds produced by *Acremonium* s. lat. species, which have primarily been evaluated for their cytotoxic, antibacterial, and anti-inflammatory properties, offering valuable insights for both scientific research and the pharmaceutical industry (Qin *et al.* 2024).

The history of *Acremonium* dates back to 1809, when Link (1809) described the genus *Acremonium* based on his observation that a particular species produced solitary spores at the ends of its fertile cells. Subsequently, Gams (1968) re-examined Link's fungarium specimen and discovered that, not consistent with the original description, the type species *A. alternatum* produced its conidia in chains from thin, tapering phialides rather than as single spores. Later, the morpho-taxonomic groundwork for *Acremonium* was laid by Gams (1971), who examined 82 species and classified them into three sections (sect. *Simplex*, sect. *Gliomastix*, and sect. *Nectrioidea*) based on detailed morphological observations. Building on this framework, Morgan-Jones & Gams (1982) established sect. *Albolanosa* for grass endophytes, and sect. *Chaetomioidea* for asexual morphs of ascomycetes in the *Chaetomiaceae*. Subsequently, Lowen (1995) extended the classification to include lichenicolous species in the newly established sect. *Lichenoidea*. Glenn *et al.* (1996) conducted the first comprehensive molecular phylogenetic analysis by using partial sequences of the nuclear small subunit ribosomal DNA (18S rDNA), selecting asexual morphs from sect. *Acremonium* (*Simplex*), *Albolanosa*, *Chaetomioidea*, *Gliomastix*, and *Nectrioidea*. Their findings revealed that *Acremonium* is polyphyletic, with species associated with at least three distinct *Ascomycota* orders: *Hypocreales*, *Microascales*, and *Sordariales*. Many *Acremonium* species, typified by *A. alternatum*, were found to affiliate with the *Hypocreales*. Species of *Acremonium* sect. *Albolanosa* were reassigned to the newly established genus *Neotyphodium*, accommodating asexual morphs of *Epichloë* and related grass endophytes. In addition, phylogenetic analysis indicated that *A. furcatum* (sect. *Nectrioidea*) is potentially associated with *Ceratocystis* and *Microascus*, both of which belong to the order *Microascales*, and *A. alabamense* (sect. *Chaetomioides*) belongs to the *Sordariales* (Glenn *et al.* 1996). Summerbell *et al.* (2011) provided a DNA-based phylogenetic overview of more than 100 *Acremonium* species and related or similar taxa available in pure culture. Their analyses revealed that these species clustered into four groups: *Cephalothecaceae*, *Hypocreales*, *Plectosphaerellaceae*, and *Sordariales*. The study also designated CBS 407.66 as the epitype of the type species, *A. alternatum*. Additionally, the genus *Sarocladium* was expanded to encompass all species from the "strictum-clade," including *A. bactrocephalum*, *A. kiliense*, *A. strictum*, and *A. zeae*, and "bacillisporum-clade," including *A. bacillisporum* and *A. glaucum*. The genus *Gliomastix* was reinstated from *Acremonium* sect. *Gliomastix* with five species, and *Trichothecium* was revised under a unitary nomenclature (Summerbell *et al.* 2011). Furthermore, Summerbell *et al.* (2011) initially placed *A. atrogriseum* in *Cephalothecaceae*, a placement later confirmed by Perdomo *et al.* (2013) who transferred it to *Phialemonium* as *P. atrogriseum*. Similarly, based on multi-locus phylogenetic and morphological analyses, Giraldo & Crous (2019) subsequently revised the placement of numerous *Acremonium* species in *Plectosphaerellaceae*.

To better clarify the phylogenetic relationships and classification of acremonium-like taxa, Hou *et al.* (2023) conducted a comprehensive analysis of 633 isolates with acremonium-like morphology, including 261 ex-type isolates from 89 countries and diverse substrates, most of which were identified as belonging to species in the genus *Acremonium* or related genera based on the morphological studies of Gams (1971) and Summerbell *et al.* (2011). Phylogenetic trees based on multiple loci (ITS, LSU, *RPB2*, and *TEF1*) were used to classify species at genus and family levels, identifying 63 genera and 14 families within four orders. Species with acremonium-like asexual morphs were shown to belong to

Cephalothecales (family: *Cephalothecaceae*), *Coniochaetales* (family: *Coniochaetaceae*), *Hypocreales* (families: *Bionectriaceae*, *Clavicipitaceae*, *Cordycipitaceae*, *Myrotheciomycetaceae*, *Nectriaceae*, *Niessliaceae*, and *Sarocladiaceae*, as well as five newly established hypocrealean families), and *Trichosphaeriales* (family: *Plectosphaerellaceae*, currently referred to as *Trichosphaeriaceae*). It is worth noting that *Acremonium* sensu stricto (s. str.) was restricted to the family *Bionectriaceae*, and most fungi with acremonium-like morphologies were classified within the *Hypocreales* (Glenn *et al.* 1996, Summerbell *et al.* 2011, Hou *et al.* 2023). The latter study provided the most comprehensive and up-to-date molecular phylogenetic framework and detailed morphological data for *Acremonium* species derived from cultures, refined their circumscription, and elucidated the phylogenetic relationships of species recognised within *Acremonium*.

The *Hypocreales* is an order of fungi within the class *Sordariomycetes*, notable for its diverse ecological roles and widespread distribution. It was typified by the genus *Hypocrea*, which has a complex evolutionary history. *Hypocrea* was first described by Fries (1825) and classified within the order *Sphaeriacei*, under the suborder *Sphaerini*. Fries (1849) later refined the concept of *Hypocrea*, adopting a more restricted definition. Subsequently, Lindau (1897) established the family *Hypocreaceae*, basing it on *Hypocrea*, and introduced the order *Hypocreales* to include *Hypocreaceae* as its sole family. Rossman *et al.* (1999) revised the taxonomy of *Hypocreales*, identifying five families: *Clavicipitaceae*, *Hypocreaceae*, *Nectriaceae*, *Niessliaceae*, and the newly established *Bionectriaceae*. This classification was later reinforced by LSU sequence-based phylogenetic analysis conducted by Rossman *et al.* (2001). The sexual morph for *Hypocreales* is characterised by ascomata that are transparent, white, pale, or brightly to darkly coloured in shades of yellow, orange, red, brown, green, blue, purple, or black, with textures ranging from soft and fleshy to tough, occurring superficially on the substratum, embedded in it, or seated in a weakly to well-developed stroma, and containing unitunicate asci with 2–8 spores and ascospores that are 0–multi-septate, sometimes muriform, and either disarticulating or not; the asexual morphs are typically hyphomycetous and less frequently coelomycetous, often featuring phialidic conidiogenous cells (Rossman *et al.* 1999, Maharachchikumbura *et al.* 2015, 2016, Hyde *et al.* 2020, Perera *et al.* 2023). The recent systematic studies of *Hypocreales* were conducted by Wijayawardene *et al.* (2022), Perera *et al.* (2023), and Hou *et al.* (2023). The outline by Wijayawardene *et al.* (2022) recognised 15 families and 320 genera within *Hypocreales*. Perera *et al.* (2023) conducted a comprehensive revision of *Bionectriaceae*, *Calcarisporiaceae*, *Hypocreaceae*, *Nectriaceae*, and *Tilachlidiaceae* using both morphological data and combined gene analyses of the ITS, LSU, *RPB2*, *TEF1*, and *TUB2* regions, recognising 17 families within *Hypocreales*, including the newly established families *Ijuhyaceae*, *Stromatonectriaceae*, and *Xanthonectriaceae*, while excluding *Cylindriaceae* from *Hypocreales*. Hou *et al.* (2023) conducted the most extensive sampling of acremonium-like fungi to date, using multi-locus DNA sequencing analyses, resulting in the establishment of five new families within *Hypocreales*: *Chrysonectriaceae*, *Neoacremoniaceae*, *Nothoacremoniaceae*, *Pseudoniessliaceae*, and *Valsonectriaceae*. Additionally, the family *Pseudodiploosporaceae*, introduced by Sun *et al.* (2023) to accommodate two novel genera, *Pseudodiploospora* and *Zelopaecilomyces*, was revisited by Yu *et al.* (2024), who determined that it contains only a single genus, *Pseudodiploospora*. Yu *et al.* (2024) also proposed a new family, *Albomorchellophilaceae*, with isolates derived from infected sporocarps of cultivated morels. Furthermore, *Acremoniopsiaceae* comprises isolates mainly derived from mangrove sediments and includes *Acremoniopsis* (previously placed in *Hypocreales* incertae sedis), *Collarina* (previously in *Clavicipitaceae*), and two newly established genera, *Nothoacremoniopsis* and *Phaeocollarina* (Li *et al.* 2023). The newly proposed family *Sedecimiellaceae* includes *Sedecimiella* and *Heteroacremonium* (Li *et al.* 2023: supplementary file 1). Xiao *et al.* (2023) recently segregated the genera *Perennicordyceps*, *Pleurocordyceps*, and *Polycephalomyces* from the family *Ophiocordycipitaceae* based on morphological and phylogenetic analyses, and established a new family, *Polycephalomycetaceae*. Currently, *Hypocreales* comprises 27 families: *Acremoniopsiaceae*, *Albomorchellophilaceae*, *Bionectriaceae*, *Calcarisporiaceae, Chrysonectriaceae*, *Clavicipitaceae, Cocoonihabitaceae, Cordycipitaceae, Flammocladiellaceae, Hypocreaceae, Ijuhyaceae, Myrotheciomycetaceae, Nectriaceae, Neoacremoniaceae*, *Niessliaceae, Nothoacremoniaceae*, *Ophiocordycipitaceae, Polycephalomycetaceae, Pseudoniessliaceae*, *Pseudodiploosporeaceae*, *Sarocladiaceae, Sedecimiellaceae*, *Stachybotryaceae, Stromatonectriaceae, Tilachlidiaceae*, *Valsonectriaceae* and *Xanthonectriaceae*.

Bionectriaceae was once considered the largest family within *Hypocreales*, comprising 26 genera with perithecial and cleistothecial sexual morphs (Rossman *et al.* 1999). The ascomata are superficial or immersed, globose to pyriform, with or without a stroma, and their colours range from white, yellow, or orange to brown, reddish brown, or purple, and remain unchanged in KOH or lactic acid. The asci are unitunicate, 8-spored, clavate, or globose, with or without an apical ring. Ascospores show variations in shape, septation, and surface ornamentation, with walls that range from hyaline to brown (Rossman *et al.* 1999). The asexual morphologies include acremonium-like, penicillium-like, gliocladium-like, and verticillium-like morphs (Rossman *et al.* 1999, Summerbell *et al.* 2011). According to the phylogenetic analyses conducted by Hou *et al.* (2023), more than half of the *Acremonium* species, as recognised by Gams (1971), were classified within *Bionectriaceae*. Within *Bionectriaceae*, the 39 genera accepted in Hou *et al.* (2023) were found to include both sexual and asexual taxa. Nevertheless, most bionectriaceous genera are only known from their asexual morphs, which are mainly acremonium-like and include the following genera: *Acremonium* s. str., *Alloacremonium*, *Fusariella*, *Gliomastix*, *Gossypinidium*, *Monohydropisphaera*, *Musananaesporium*, *Ovicillium*, *Paragliomastix*, *Proliferophialis*, *Proxiovicillium* (current name: *Mastigocladium*), *Pseudoacremonium*, *Ramosiphorum*, *Septofusidium*, *Stanjemonium*, *Verruciconidia*, and *Waltergamsia* (Hou *et al.* 2023). Genera with ascomata, along with acremonium-like asexual morphs are: *Bulbithecium*, *Emericellopsis*, *Geonectria*, *Hapsidospora*, *Hydropisphaera*, *Lasionectria*, *Lasionectriella*, *Lasionectriopsis*, *Nectriopsis*, *Ochronectria*, *Paracylindrocarpon*, *Protocreopsis*, *Roumegueriella*, *Stilbocrea*, and *Verrucostoma* (Hou *et al.* 2023).

The objectives of the present study were as follows: 1) to conduct a comprehensive investigation of acremonium-like species using both morphological characteristics and molecular data, including unidentified isolates from the CBS collection and those not previously examined in Gams' monograph; 2) to reassess and refine the classification of *Acremonium* spp. and related taxa within the context of the current phylogenetic framework, clarifying their placement within *Hypocreales* and related orders; and 3) to provide detailed analyses and descriptions for those undescribed taxa, and to assign correct names to acremonium-like fungi that have been poorly understood due to their reduced morphological features.

MATERIALS AND METHODS

Isolates

A total of 402 isolates of acremonium-like fungi obtained from the CBS culture collection of the Westerdijk Fungal Biodiversity Institute (WI; Utrecht, the Netherlands) were included in this study. Most of these isolates were identified as species in the genus *Acremonium* or associated genera based on morphological characteristics or initial DNA sequence data from the CBS collection, as well as the isolates being listed in Gams' (1971) monograph *Cephalosporium-artige Schimmelpilze (Hyphomycetes)* that had not yet been subjected to molecular analysis (Supplementary Table S1).

DNA extraction, PCR amplification and sequencing

To extract genomic DNA, fungal colonies were cultured on oatmeal agar (Crous *et al.* 2019a) at room temperature for 2 wk. Genomic DNA was then isolated using the Wizard® Genomic DNA Purification Kit (Promega Corporation, Madison, WI, USA), following the manufacturer's protocol. Four gene regions (ITS, LSU, *RPB2*, and *TEF1*) were amplified using the methods outlined in Zhao *et al.* (2025). The ITS region was amplified with the primer pair ITS5/ITS4 (White *et al.* 1990), the LSU region with LR0R/LR5 primers (Vilgalys & Hester 1990, Rehner & Samuels 1994), and the *RPB2* and *TEF1* genes using the primer sets RPB2-5F2/RPB2-7CR (Liu *et al.* 1999, Sung *et al.* 2007b) and EF1-983F/EF1-2218R (Rehner & Buckley 2005), respectively. The consensus sequences for each isolate were generated by assembling the forward and reverse reads using Geneious Prime v. 2022 (Biomatters Inc., New Zealand). The corresponding GenBank accession numbers for the newly generated sequences are listed in Table S1.

Phylogenetic analyses

Alignments for four individual loci (ITS, LSU, *RPB2*, *TEF1*) were generated using MAFFT v. 7 with default settings on the online server (https://mafft.cbrc.jp/alignment/server/index.html) (Kuraku *et al.* 2013, Katoh *et al.* 2019). When necessary, manual editing of the alignments was performed using MEGA v. 7.0.21 (Kumar *et al.* 2016). Phylogenetic inferences of the concatenated alignments (ITS, LSU, *RPB2*, and *TEF1*) were performed using two Maximum Likelihood (ML) methods: RAxML and IQ-TREE. Phylogenetic analyses were performed using RAxML (Maximum Likelihood) on the CIPRES Science Gateway portal v. 3.3 (https://www.phylo.org/; Miller *et al.* 2012) and RAxML-HPC2 on ACCESS v. 8.2.12 (Stamatakis 2014), employing the default GTR substitution model and 1000 rapid bootstrap replicates. Additional maximum likelihood analyses were carried out with IQ-TREE v. 2.1.3 (Nguyen *et al.* 2015, Minh *et al.* 2020), utilising UFBoot2 bootstrapping (ultra-fast bootstrapping, with ≥ 95 % considered significant) for branch support estimation (Hoang *et al.* 2018). The optimal evolutionary model for each partition was determined using ModelFinder (Kalyaanamoorthy *et al.* 2017, Minh *et al.* 2020), as implemented in IQ-TREE. The resulting trees were visualized using FigTree v. 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree), and the concatenated data of the four loci (ITS, LSU, *RPB2*, and *TEF1*) and the phylogenetic trees were uploaded to figshare (doi: 10.6084/m9.figshare.28705967).

Morphology

Macroscopic characteristics of colonies were assessed on oatmeal agar (OA), malt extract agar (MEA), potato dextrose agar (PDA), and synthetic nutrient-poor agar (SNA) following incubation in darkness at 25 °C for 14 d. The upper and reverse surface colours of the colonies were determined using Rayner's (1970) colour charts for standardized evaluation. Microscopic structures were examined from 14-d-old colonies grown on OA or SNA under near-UV light at room temperature. Clear lactic acid was used as the mounting medium for observing the microstructures. Micro-morphological characteristics were examined using a Nikon Eclipse 80i compound microscope equipped with differential interference contrast (DIC) optics and a Nikon AZ100 dissecting microscope. Photomicrographs and measurements were captured with a Nikon DS-Ri2 high-definition colour digital camera, utilising NIS-Elements D software v. 4.50 (Nikon, Tokyo, Japan). Descriptive data, illustrations, and nomenclatural information were submitted to MycoBank (www.MycoBank.org; Crous *et al.* 2004), and corresponding specimens were preserved in the CBS Fungarium. Abbreviations used for genera in the text are as follows: *A.* = *Acremonium*, *Allo.* = *Allomusicillium*, *Aur.* = *Aurantidochium*, *B.* = *Brunneomyces*, *Ca.* = *Cannomyces*, *Chl.* = *Chlamydocillium*, *Chlam.* = *Chlamydosporiella*, *Cl.* = *Clavatomyces*, *Lag.* = *Lagenariomyces*, *L.* = *Lasionectria*, *N.* = *Neochrysonectria*, *Para.* = *Parasarocladium*, *Pil.* = *Pilgeriellomyces*, *Poly.* = *Polyphialocladium*, *Pt.* = *Protocreopsis*, *R.* = *Ramosiphorum*, *S.* = *Sarocladium*, *Spor.* = *Sporodochius*, *T.* = *Titanomyces*, *Tr.* = *Trichosphaeria*, *V.* = *Verruciconidia*.

RESULTS

Phylogenetic analyses

In this study, we investigated acremonium-like fungi taxa, analysing a total of 402 isolates. To understand the phylogenetic relationships within *Hypocreales* and related orders, an overview phylogenetic tree was constructed using ITS, LSU, *RPB2*, and *TEF1* sequences, which positioned the different families within the orders (Dataset 1). This was followed by more detailed phylogenetic analyses focusing on specific families, including *Bionectriaceae*, *Sarocladiaceae*, and *Trichosphaeriaceae*, incorporating all available isolates from these families (Datasets 2–4). The same phylogenetic methods used for Dataset 1 were also used for Datasets 2–4, ensuring consistent and comparable results across all analyses.

Dataset 1: The concatenated and aligned ITS, LSU, *RPB2*, and *TEF1* sequences from four genes and 638 taxa, belonging to the order *Hypocreales* and *Trichosphaeriales*, and its related orders, were utilised to define the boundaries at the family and order levels and to optimize the clarity and structure of the phylogenetic tree, with *Saccharata proteae* (CBS 115206) serving as the outgroup (*Dothideomycetes*, *Botryosphaeriales*, *Saccharataceae*). The alignment contained a total of 3869 characters (including gaps), with the following partitions: ITS: 1–1142, 1142 bp; LSU: 1143–1968, 826 bp; *RPB2*: 1969–2918, 950 bp; *TEF1*: 2919–3869, 951 bp. Of these, 1256 characters were conserved (ITS: 228, LSU: 400, *RPB2*: 165, *TEF1*: 463), 2402 were variable (ITS: 816, LSU: 415, *RPB2*: 702, *TEF1*: 469), and 2031 were parsimony-informative characters (ITS:

Fig. 1. The phylogenetic tree was constructed using Maximum Likelihood (RAxML) analysis, based on aligned and concatenated ITS, LSU, *RPB2*, and *TEF1* sequences from 638 isolates representing the orders *Trichosphaeriales* (Clade I) and *Hypocreales* (Clades II–XXXI), along with related orders and the outgroup. Numbers on the nodes represent Maximum Likelihood bootstrap support values: RAxML-BS (≥ 50 %) listed first, followed by IQ-TREE ultrafast bootstrap support values (IQ-TREE-BS ≥ 90 %). Newly described species are labeled in red, and new combinations are shown in blue. The isolates analysed in this study are highlighted in bold. Colored boxes indicate families, while Roman numerals correspond to families as indicated in the legend. "T" denotes ex-type isolates. The tree is rooted with *Saccharata proteae* (CBS 115206) (*Dothideomycetes*, *Botryosphaeriales*, *Saccharataceae*). The scale bar represents the expected number of substitutions per site.

699, LSU: 331, *RPB2*: 592, *TEF1*: 409). The phylogeny presented in Fig. 1 was the RAxML tree based on the combined dataset, with bootstrap support values from both RAxML (RAxML-BS > 50 %) and IQ-TREE (IQ-TREE-BS > 90 %) analyses plotted on the branches.

The phylogenetic tree (Fig. 1) mainly contains Clades I–XXXI, which show the well-supported family *Trichosphaeriaceae* within *Trichosphaeriales*, along with 27 known families, the positionally ambiguous clade *Trichonectria-Cylindromonium*, and two new families with well- or moderately supported clades within the order *Hypocreales*. The topologies observed in both the RAxML and IQ-TREE analyses were largely consistent within each generic clade of the families, except for a few family clades that shifted to different positions between two analyses, which were instances of low support between different family clades within the order *Hypocreales*. The following clades include taxonomic novelties and isolates of known species that were examined in this study. Clade I (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) encompasses species belonging to *Trichosphaeriaceae*, *Trichosphaeriales*. An individual phylogenetic tree that provides further insights into the phylogeny of *Trichosphaeriaceae* is presented in Fig. 2. Clades II–XXXI represent families within *Hypocreales*. Clade II represents the new family *Aurantidochiaceae* (RAxML-BS = 94 %, IQ-TREE-BS = 100 %) that comprises two new genera: *Aurantidochium* with its type *Aur. guadalupense,* and *Lagenariomyces*, with two new species, *Lag. collarulis* and *Lag. varioconidialis*. Clade III (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) corresponds to the family *Sarocladiaceae*. Additional details on the phylogeny of *Sarocladiaceae* are illustrated in a separate phylogenetic tree provided in Fig. 3. Clade V (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) includes species from the genera *Trichonectria* and *Cylindromonium*, which belong, respectively, to the *Hypocreales* genera incertae sedis and *Nectriaceae* (Perera *et al.* 2023, Crous *et al.* 2019b). The status of Clade V remains to be determined. Clade VII, representing the family *Niessliaceae* (RAxML-BS = 89 %, IQ-TREE-BS = 99 %), includes species of *Niesslia*, which are polyphyletic and intermixed with other species from the genera *Eucasphaeria*, *Myrtacremonium*, *Neoeucasphaeria*, and *Rosasphaeria*. Clade VIII is recognised as a new monophyletic family, *Neochrysonectriaceae*, containing the new genus *Neochrysonectria*, with type species *Neochrysonectria humicola*. Clades XXIII and XXXI exhibit a low support value in the RAxML analysis (RAxML-BS = 60 %, IQ-TREE-BS = 95 % and RAxML-BS = 53 %, IQ-TREE-BS = 96 %, respectively). The former corresponds to the family *Stachybotryaceae* and contains 37 known genera and one new genus, *Sporodochius*, which is based on the new combination *Spor. pironii*. All isolates of this species were previously recognised as *Nectriella pironii*. Clade XXXI represents the family *Bionectriaceae*, which is divided in two well-supported subclades (RAxML-BS = 89 %, IQ-TREE-BS = 100 %) and (RAxML-BS = 98 %, IQ-TREE-BS = 100 %). *Bionectriaceae* is also presented in a separate phylogenetic tree (Fig. 4). The remaining clades with isolates analysed in this study are: Clade IX (*Chrysonectriaceae*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XI (*Sedecimiellaceae*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XII (*Nectriaceae*; RAxML-BS = 98 %, IQ-TREE-BS = 100 %), Clade XIV (*Ophiocordycipitaceae*: RAxML-BS = 79 %, IQ-TREE-BS = 99 %), Clade XVII (*Clavicipitaceae*: RAxML-BS = 90 %, IQ-TREE-BS = 100 %), Clade XXI (*Cordycipitaceae*: RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXII (*Pseudoniessliaceae*: RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXIV (*Valsonectriaceae*: RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXV (*Myrotheciomycetaceae*: RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXVII (*Xanthonectriaceae*: RAxML-BS = 91 %, IQ-TREE-BS = 100 %), and Clade XXVIII (*Ijuhyaceae*: RAxML-BS = 100 %, IQ-TREE-BS = 100 %).

Dataset 2: The concatenated and aligned ITS, LSU, *RPB2*, and *TEF1* sequences from four genes and 122 taxa of the *Trichosphaeriaceae* were included, with *Monilochaetes infuscans* (CBS 379.77 and CBS 869.96), serving as outgroups (*Chaetosphaeriales*, *Australiascaceae*; Fig. 2). The alignment contained a total of 2987 characters (including gaps), with the following partitions: ITS: 1–606, 606 bp; LSU: 607–1396, 790 bp; *RPB2*: 1397–2173, 777 bp; *TEF1*: 2174–2987, 814 bp. Of these, 1803 characters were conserved (ITS: 299, LSU: 584, *RPB2*: 376, *TEF1*: 544), 1168 were variable (ITS: 293, LSU: 206, *RPB2*: 399, *TEF1*: 270), and 1052 were parsimony informative (ITS: 263, LSU: 192, *RPB2*: 353, *TEF1*: 244). The phylogeny presented in Fig. 2 was the RAxML tree based on the combined dataset, with bootstrap support values from both RAxML (RAxML-BS > 50 %) and IQ-TREE (IQ-TREE-BS > 90 %) analyses shown on the branches. The topologies observed in both the RAxML and IQ-TREE analyses were largely consistent.

The *Trichosphaeriaceae* phylogenetic tree (Fig. 2) contains Clades I-1–I-27, representing the 26 well-supported known genera and one new genus of *Trichosphaeriaceae*, *Trichosphaeriales*. The following clades include taxonomic novelties and isolates of known species that were examined in this study. Clade I-3 (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) comprised a new species *Titanomyces triconidiogenes*, classified in the new genus *Titanomyces*. Clade I-5 (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) accommodated the genus *Brunneomyces*, representing five previously described species, namely *B. brunnescens*, *B. europaeus*, *B. hominis*, *B. polyphialidens*, and *B. pseudozeylanicum*, and one new species, *B. romanianus*. Clade I-6 (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) accommodated the genus *Allomusicillium* with one known species, *Allo. domschii*, and one new species, *Allo. malicola*. The genus *Chlamydosporiella* (Clade I-12; RAxML-BS = 100 %, IQ-TREE-BS = 100 %) is represented by one known species *Chlam. restricta*, and one new species, *Chlam. aerina*. The remaining clades with isolates analysed in this study are: Clade I-4 (*Verticillium*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade I-14 (*Gibellulopsis*; RAxML-BS = 57 %, node absent in IQ-TREE phylogeny), Clade I-15 (*Chordomyces*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade I-16 (*Furcasterigmium*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade I-18 (*Musidium*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade I-20 (*Summerbellia*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade I-26 (*Brunneochlamydosporium*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade I-27 (*Plectosphaerella*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %).

Dataset 3: The concatenated and aligned ITS, LSU, *RPB2*, and *TEF1* sequences from four genes and 162 taxa represent the taxa belonging to the *Sarocladiaceae*, with *Gibellulopsis nigrescens* (CBS 120949) and *Plectosphaerella cucumerina* (CBS 101014 and CBS 131739) serving as outgroups (*Trichosphaeriales*, *Trichosphaeriaceae*; Fig. 3). The alignment contained a total of 3161 characters (including gaps), with the following partitions: ITS: 1–626, 626 bp; LSU: 627–1418, 792 bp; *RPB2*: 1419–2184, 766 bp; *TEF1*: 2185–3161, 977 bp. Of these, 1818 characters were conserved (ITS: 273, LSU: 591, *RPB2*: 296, *TEF1*: 658), 1276 were variable (ITS: 332, LSU: 198, *RPB2*: 469, *TEF1*: 277), and 1180 were parsimony informative (ITS: 314, LSU: 189, *RPB2*: 440, *TEF1*: 237). The phylogeny presented in Fig. 3 was the RAxML tree based on the combined dataset, with bootstrap support values from both

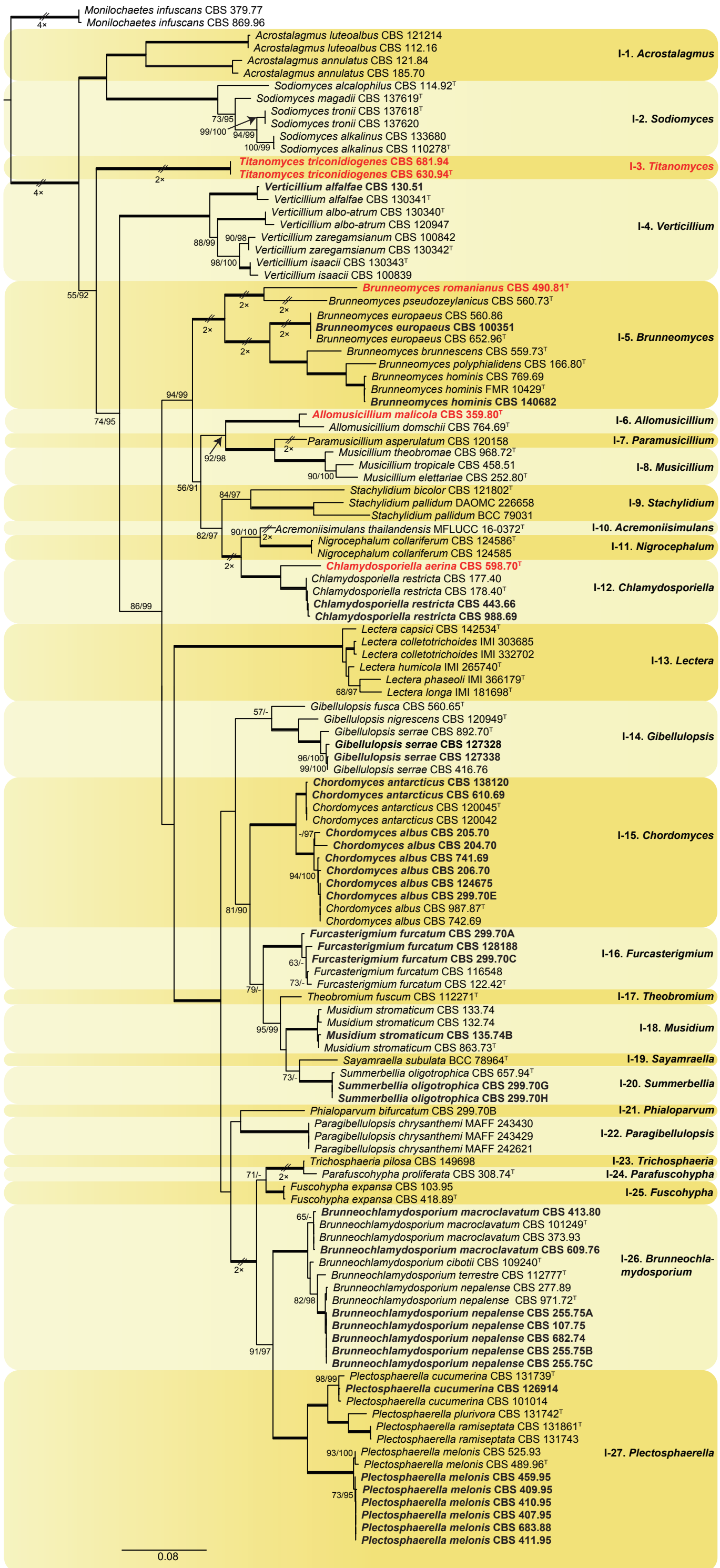

Fig. 2. The phylogenetic tree was constructed using Maximum Likelihood (RAxML) analysis, based on aligned and concatenated ITS, LSU, *RPB2*, and *TEF1* sequences from 122 isolates representing the *Trichosphaeriaceae* (Clade I in Fig. 1) within the *Trichosphaeriales*, along with the outgroup. Numbers on the nodes represent Maximum Likelihood bootstrap support values: RAxML-BS (≥ 50 %) listed first, followed by IQ-TREE ultrafast bootstrap support values (IQ-TREE-BS ≥ 90 %). Newly described species are labeled in red, and new combinations are shown in blue. The isolates analysed in this study are highlighted in bold. Colored boxes indicate genera, while Roman numerals combined with Arabic numerals indicate genera nested within families, as shown in the legend. "T" denotes ex-type isolates. The tree is rooted with *Monilochaetes infuscans* (CBS 379.77 and CBS 869.96) (*Chaetosphaeriales*, *Australiascaceae*). The scale bar represents the expected number of substitutions per site.

RAxML (RAxML-BS > 50 %) and IQ-TREE (IQ-TREE-BS > 90 %) analyses shown on the branches. The topologies observed in both the RAxML and IQ-TREE analyses were largely consistent.

The *Sarocladiaceae* phylogenetic tree (Fig. 3) contains Clades III-1–III-4, representing the four well-supported known genera of *Sarocladiaceae*. The following clades include taxonomic novelties and isolates of known species that were examined in this study. Clade III-1 (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) accommodated the genus *Polyphialocladium* containing one known species *Poly. fusisporum*, and one new combination *Poly. margaretcollinsiae* (basionym: *Chlamydocillium margaretcollinsiae*). Clade III-2 (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) comprised the type, *Chlamydocillium cyanophilum*, and additional eight known species, *Chl. acacia*, *Chl. antarcticum*, *Chl. curvulum*, *Chl. guttulatum*, *Chl. lolii*, *Chl. simulans*, *Chl. soli*, *Chl. terrestris*, and two new species, *Chl. theobromae* and *Chl. viridicolor.* Clade III-3 (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) was represented by 15 accepted species of *Parasarocladium*, including the type species *Para. radiatum*, and one new species, *Para. kislosladkoense*. Clade III-4 (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) comprises 32 previously known species of the genus *Sarocladium*, along with six newly proposed species: *S. alniphilum*, *S. catenulatum*, *S. hirsutum*, *S. humicola*, *S. limosialveum*, and *S. nubiaquae*.

Dataset 4: The concatenated and aligned ITS, LSU, *RPB2*, and *TEF1* sequences from four genes and 540 taxa belong to the *Bionectriaceae*, with *Tilachlidium brachiatum* (CBS 363.97, CBS 505.67), *Flammocladiella anomiae* (CBS 142775), *F. aceris* (CBS 138906) and *F. decora* (CBS 142776) serving as outgroups (*Hypocreales*, *Tilachlidiaceae* and *Flammocladiellaceae*; Fig. 4). The final alignment consisted of 3277 characters (including gaps), with the following partitions: ITS: 1–871, 871 bp; LSU: 872–1663, 792 bp; *RPB2*: 1664–2459, 796 bp; *TEF1*: 2460–3277, 818 bp. Of these, 1528 characters were conserved (ITS: 270, LSU: 556, *RPB2*: 263, *TEF1*: 439), 1670 were variable (ITS: 534, LSU: 228, *RPB2*: 530, *TEF1*: 378), and 1475 were parsimony informative (ITS: 458, LSU: 193, *RPB2*: 488, *TEF1*: 336). The phylogeny presented in Fig. 4 was the RAxML tree based on the combined dataset, with bootstrap support values from both RAxML (RAxML-BS > 50 %) and IQ-TREE (IQ-TREE-BS > 90 %) analyses shown on the branches. The topologies observed in both the RAxML and IQ-TREE analyses were largely consistent.

The *Bionectriaceae* phylogenetic tree (Fig. 4) contains Clades XXXI-1–XXXI-53, which represent the 51 well-supported, previously accepted genera of *Bionectriaceae*, along with two new genera proposed in this study. The following clades include taxonomic novelties and isolates of known species that were examined in this study. Clade XXXI-7 (RAxML-BS = 90 %, IQ-TREE-BS = 99 %) comprises 13 well-established species of the genus *Protocreopsis*, which have been previously documented, as well as four new species identified in this study, *Pt. ellipsoidea*, *Pt. helvetica*, *Pt. polyphialidica*, and *Pt. spinulosa*. Clade XXXI-8 (RAxML-BS = 75 %, IQ-TREE-BS = 100 %) represents the recently introduced genus *Clavatomyces*, which includes two known species, *Cl. prestoeae* and *Cl. korfii*, one new species, *Cl. pycnidialis* (characterised by pycnidial conidiomata, a relatively rare feature within the *Bionectriaceae*), and one new combination, *Cl. palmarum* (basionym: *Protocreopsis palmarum*). Clade XXXI-11 (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) includes three previously described species of *Ramosiphorum*: *R. echinophoriae*, *R. polyporicola*, and *R. thailandicum*, along with one new species, *R. sporodochiale*. The proposed new monotypic genus *Cannomyces* (Clade XXXI-13) is introduced to accommodate only one new species, *Ca. spinulosus*. The clade of *Lasionectria* (Clade XXXI-14; RAxML-BS = 86 %, IQ-TREE-BS = 100 %) comprises 14 known species, along with one new species: *L. eichhorniae*. Clade XXXI-15 (RAxML-BS = 89 %, IQ-TREE-BS = 100 %) includes nine recognised species of *Verruciconidia* and five isolates previously identified as *Acremonium* spp., which were placed into four distinct and well-supported subclades, each representing a novel species. Those species are designated *V. maritima*, *V. indonesiana*, *V. terricola*, and *V. thailandica.* Clade XXXI-40 (RAxML-BS = 100 %, IQ-TREE-BS = 100 %) includes two *Acremonium* sp. isolates, representing the novel genus *Pilgeriellomyces*, with one new species, *Pil. brasiliensis*, which forms a distinct lineage separate from other genera. The genus *Acremonium* s. str. (Clade XXXI-53; RAxML-BS = 100 %, IQ-TREE-BS = 100 %) is represented by 22 previously described species (including the type species *A. alternatum* CBS 407.66), as well as the new species *A. ecuadorense*, *A. proliferatum*, *A. soli*, and *A. tapetis*, along with several isolates previously named *A. sclerotigenum* or misidentified as *A. strictum* (now *Sarocladium strictum*), all now reclassified as *A. egyptiacum*. Other isolates analysed in our study comprise Clade XXXI-1 (*Nectriopsis*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-4 (*Mycocitrus*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-6 (*Clonostachys*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-12 (*Lasionectriopsis*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-24 (*Caespitomonium*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-31 (*Gliomastix*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-43 (*Hapsidospora*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-44 (*Bulbithecium*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-45 (*Mastigocladium*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-46 (*Ovicillium*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-49 (*Waltergamsia*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), Clade XXXI-50 (*Proliferophialis*; RAxML-BS = 100 %, IQ-TREE-BS = 100 %), and Clade XXXI-52 (*Emericellopsis*; RAxML-BS = 75 %, IQ-TREE-BS = 99 %).

Taxonomy

Phylogenetic analyses based on multi-locus sequence alignments were conducted on 402 isolates of acremonium-like fungi. These isolates represent 149 species, belonging to 17 families within *Hypocreales*, and one family, *Trichosphaeriaceae*, within *Trichosphaeriales*. This study proposes two new families and seven new genera, along with the description of 33 new species and four new combinations. One new sterile species is described based on DNA sequence data, following the methodology of Hou *et al.* (2023). Taxonomic arrangement follows phylogenetic positions, with families and genera arranged according to the clade numbering system (Figs 1–4). In Fig. 1, families are numbered with Roman numerals. In Figs 2–4, genera within *Trichosphaeriaceae* (Fig. 2), *Sarocladiaceae* (Fig. 3), and *Bionectriaceae* (Fig. 4) are arranged using a combination of Roman and Arabic numerals to indicate genera nested within families. Species within each genus are listed alphabetically.

Clade I. *Trichosphaeriaceae* G. Winter [as '*Trichosphaerieae*'], *Rabenh. Krypt.-Fl.,* Edn **2** (Leipzig): 191. 1885.
Synonym: *Plectosphaerellaceae* W. Gams *et al.*, *Nova Hedwigia* **85**: 476. 2007.

Classification: *Trichosphaeriales*, *Sordariomycetes.*

Type genus: *Trichosphaeria* Fuckel

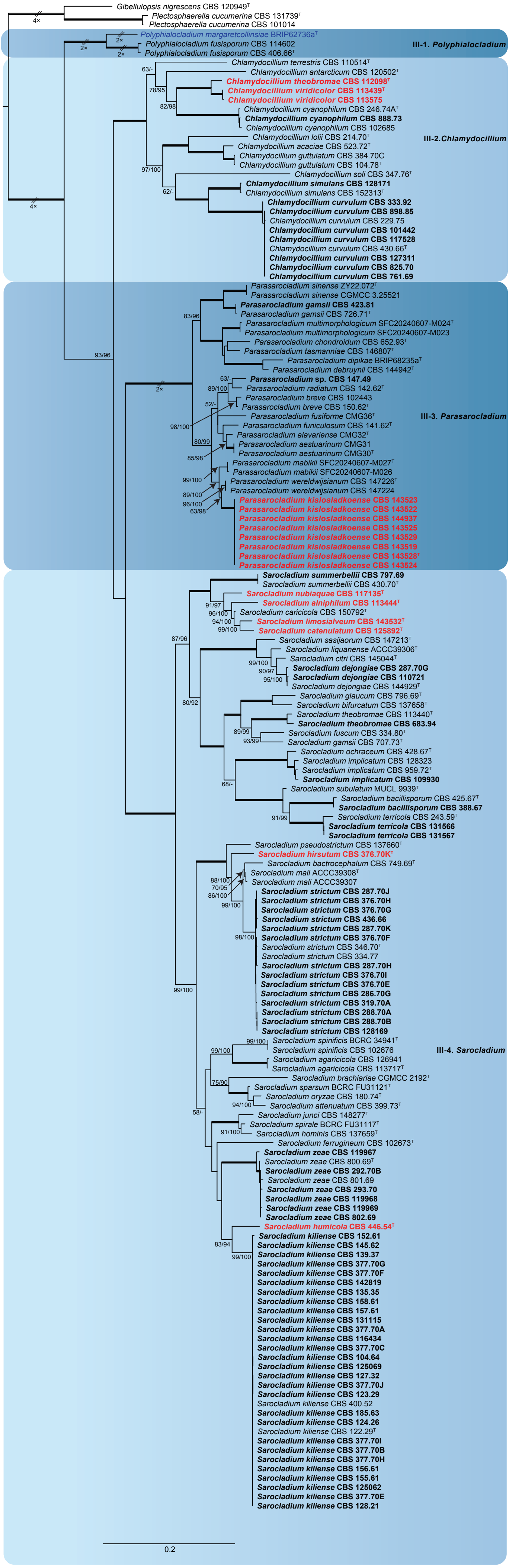

Fig. 3. The phylogenetic tree was constructed using Maximum Likelihood (RAxML) analysis, based on aligned and concatenated ITS, LSU, *RPB2*, and *TEF1* sequences from 162 isolates representing *Sarocladiaceae* (Clade III in Fig. 1) within *Hypocreales*, along with the outgroups. Numbers on the nodes represent Maximum Likelihood bootstrap support values: RAxML-BS (≥ 50 %) listed first, followed by IQ-TREE ultrafast bootstrap support values (IQ-TREE-BS ≥ 90 %). Newly described species are labeled in red, and new combinations are shown in blue. The isolates analysed in this study are highlighted in bold. Colored boxes indicate genera, while Roman numerals combined with Arabic numerals indicate genera nested within families, as shown in the legend. "T" denotes ex-type isolates. The tree is rooted with *Gibellulopsis nigrescens* (CBS 120949), *Plectosphaerella cucumerina* (CBS 101014 and CBS 131739) (*Trichosphaeriales*, *Trichosphaeriaceae*). The scale bar represents the expected number of substitutions per site.

Fig. 4. The phylogenetic tree was constructed using Maximum Likelihood (RAxML) analysis, based on aligned and concatenated ITS, LSU, *RPB2*, and *TEF1* sequences from 540 isolates representing *Bionectriaceae* (Clade XXXI in Fig. 1) within *Hypocreales*, along with the outgroups. Numbers on the nodes represent Maximum Likelihood bootstrap support values: RAxML-BS (≥ 50 %) listed first, followed by IQ-TREE ultrafast bootstrap support values (IQ-TREE-BS ≥ 90 %). Newly described species are labeled in red, and new combinations are shown in blue. The isolates analysed in this study are highlighted in bold. Colored boxes indicate genera, while Roman numerals combined with Arabic numerals indicate genera nested within families, as shown in the legend. "T" denotes ex-type isolates. The tree is rooted with *Tilachlidium brachiatum* (CBS 363.97, CBS 505.67), *Flammocladiella anomiae* (CBS 142775), *F. aceris* (CBS 138906), and *F. decora* (CBS 142776) (*Hypocreales*, *Tilachlidiaceae* & *Flammocladiellaceae*). The scale bar represents the expected number of substitutions per site.

Clade I-3. *Titanomyces* Lin Zhao & Crous, ***gen. nov.*** MycoBank MB 858416.

Etymology: Referring to the ancient Greek word τίτανος (títanos), meaning "lime" or "alkaline earth" materials such as gypsum and white clay, it references the alkaline nature of the substrate from which isolates of this genus were collected.

Mycelium consisting of branched, septate, hyaline, smooth or rough, thin-walled hyphae. Sporulation abundant, phalacrogenous, nematogenous. *Conidiophores* arising from the agar surface and aerial hyphae, solitary or aggregated, (sub-)erect, unbranched or basitonously branched, commonly with repeated percurrent or sympodial proliferation, showing conidiogenous cells as short lateral and cylindrical asymmetrical projections, hyaline, smooth-walled. *Conidiogenous cells* enteroblastic, mono- or polyphialidic, lateral or terminal, cylindrical, or subulate, straight or curved, hyaline, thick- and smooth-walled, with conspicuous collarette and periclinal thickening at conidiogenous locus, with percurrent or subterminal proliferation; polyphialides with two or three conidiogenous loci commonly present. *Conidia* globose, subglobose or ellipsoid, with both ends rounded, or with rounded apices and slightly apiculate hilum at bases, aseptate, hyaline, with thin and smooth walls, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Type: *Titanomyces triconidiogenes* Lin Zhao & Crous

Notes: The monotypic genus *Titanomyces* is introduced here for a fungal species isolated from alkaline soil in Indonesia. Phylogenetic analyses reveal that this genus forms a well-supported clade that remains distinctly separate from other genera in the family *Trichosphaeriaceae* (Fig. 2).

Titanomyces triconidiogenes Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858417. Fig. 5.

Etymology: Referring to the production of three commonly present conidiogenous loci.

Typus: **Indonesia**, from alkaline soil, collection date unknown, *K. Nagai*, Drug Serendipity Research Laboratories, Yamanouchi Pharmaceutical Co., Tokyo, Japan (**holotype** designated here CBS H-25609, ex-type living isolate CBS 630.94).

Mycelium consisting of branched, septate, hyaline, smooth or rough, thin-walled hyphae, 1.2–2.4 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous. *Conidiophores* arising from the agar surface and aerial hyphae, solitary or aggregated, (sub-)erect, unbranched or basitonously branched, bearing up to 1–3 levels with 1–2 phialides per node, up to ca 80 µm long, 1.5–3.2 µm wide at base, 1–4-septate, with repeated percurrent or sympodial proliferation, showing conidiogenous cells as short lateral and cylindrical asymmetrical projections, hyaline, smooth-walled. *Conidiogenous cells* monophialidic or polyphialidic, lateral or terminal, cylindrical or subulate, straight or curved, hyaline, thick- and smooth-walled, (8.8–)15.3–36.3(–44.7) µm long, (1.0–)1.1–2.3(–2.7) µm wide at base, 0.7–1.0 µm wide near aperture, with conspicuous collarettes and periclinal thickening at conidiogenous loci, with percurrent or subterminal proliferation; polyphialides with two or three conidiogenous loci commonly present. *Conidia* globose, subglobose or ellipsoid, with both ends rounded, or with rounded apices and slightly apiculate hilum at bases, aseptate, hyaline, thin- and smooth-walled, (1.9–)2.0–3.0(–3.5) × (1.5–)1.7–2.1(–2.4) µm (av. 2.4 × 1.9 µm, n = 100), arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 17–19 mm diam. after 14 d in darkness at 25 °C, flat, membranous, with sparse aerial mycelium, dirty white, margin entire, reverse concolourous. On MEA reaching 20–23 mm diam., flat, felty, dusty, with moderate aerial mycelium, white at centre, rosy buff at periphery, margin entire, reverse apricot at centre, luteous at periphery. On PDA reaching 13–15 mm diam., flat, slightly folded at centre, felty, with sparse aerial mycelium, creamy white, margin lobate, reverse whitish. On SNA reaching 15–18 mm diam., flat, felty, granulose, with sparse aerial mycelium, white, margin fimbriate, reverse concolourous.

Additional material examined: **Indonesia**, from alkaline soil, collection date unknown, *K. Nagai*, Drug Serendipity Research Laboratories, Yamanouchi Pharmaceutical Co., Tokyo, Japan, isolate CBS 681.94.

Notes: *Titanomyces triconidiogenes* consists of two isolates, both from alkaline soil, which were previously referred to as "*Acremonium* sp." and are commonly characterised by repeatedly percurrent and sympodial proliferation.

Based on a BLASTn search of NCBI GenBank nucleotide database, the closest hits using the ITS sequence are as follows: uncultured fungus clone RFLP41, isolated from soil in Australia [GenBank GU187862; Identity = 431/492 (88 %), 11 gaps (2 %)], and *Gibellulopsis* sp., isolated from the surface of *Atractylodes lancea* on host leaves in China [isolate 2109-2; GenBank OQ398021; Identity = 422/483 (87 %), 18 gaps (3 %)]; the closest hit using the LSU sequence is *Chlamydosporiella* sp. isolated from China [KLBMPIO127; GenBank OQ946626; Identity = 769/788 (98 %), one gap (0 %)]; the closest hit using the *RPB2* sequence is *Gibellulopsis nigrescens* isolated from potato in Israel [CBS 100829; GenBank LR026144; Identity = 494/608 (81 %), 12 gaps (1 %)]; no *TEF1* sequence was available to include in a BLASTn search.

Clade I-5. *Brunneomyces* A. Giraldo *et al.*, *Mycol. Progr.* **16**: 357. 2017.

Mycelium consisting of branched, septate, hyaline, smooth, thin-walled hyphae, becoming dark brown, verrucose, thick-walled with age. *Conidiophores* erect, unbranched or sparsely branched, septate, with short sterile basal outgrowths, commonly with sympodial proliferation, hyaline, smooth-walled. *Conidiogenous cells* enteroblastic, mono- and polyphialidic, lateral or terminal, subulate, cylindrical, or lageniform, hyaline to subhyaline or pale brown, with short cylindrical collarettes and a distinct periclinal thickening at the conidiogenous locus; commonly with repeatedly percurrent or subterminal proliferation; polyphialides with up to five conidiogenous loci present in some species. *Conidia* obovoid, fusoid, cylindrical to ellipsoidal, aseptate, hyaline or brown, smooth-walled, arranged in chains or collapsing as conidial heads in some species. *Sexual morph* not observed (adapted from Giraldo *et al.* 2017, Hou *et al.* 2023).

Type: *Brunneomyces brunnescens* (W. Gams) A. Giraldo *et al.*

Notes: *Brunneomyces* was proposed by Giraldo *et al.* (2017) to accommodate *B. brunnescens* as the type species, characterised

by sympodial conidiophores, dark brown, verrucose, thick-walled hyphae, along with two additional species, *B. hominis* and *B. europaeus*. Hou *et al.* (2023) accepted two more species, *B. polyphialidus* and *B. pseudozeylanicus*, based on available DNA data. In our study, we propose one novel species described below.

Brunneomyces romanianus Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858418. Fig. 6.

Etymology: Referring to the country, Romania, from which the holotype isolate was collected.

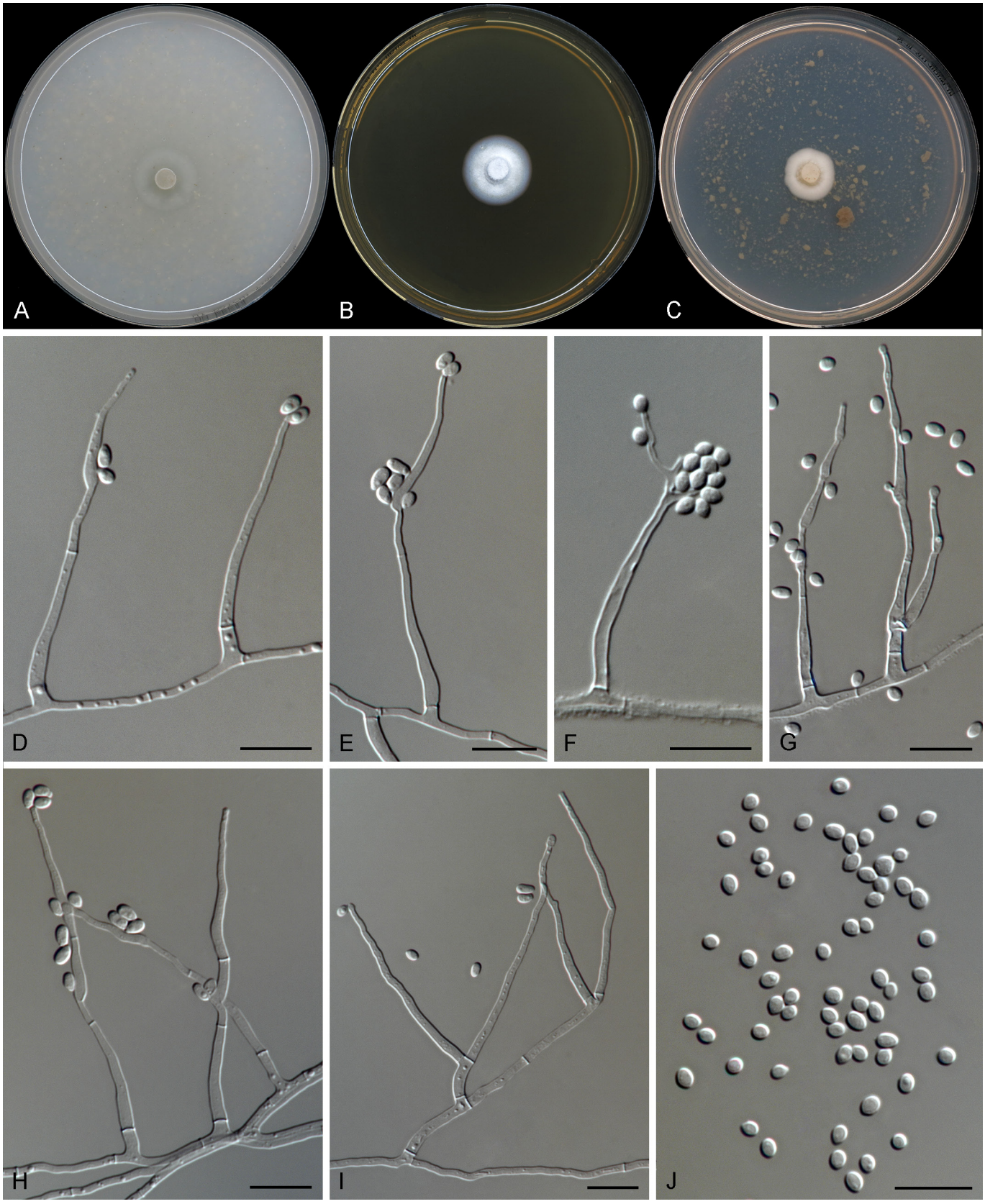

Fig. 5. *Titanomyces triconidiogenes* (ex-type CBS 630.94). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J.** Conidia. Scale bars = 10 µm.

Typus: **Romania**, mouldy soap, unknown collection date and *collector*, isol. Dec. 1980, *O. Constantinescu*, No. 1300 (**holotype** designated here CBS H-25605, ex-type living isolate CBS 490.81).

Mycelium consisting of branched, septate, hyaline, smooth, thin-walled hyphae, 1.2–2.9 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface and aerial hyphae, or from ropes formed by the mycelium, solitary or aggregated, (sub-)erect, unbranched or sparsely branched, up to ca 95 µm long, 1.2–2.7 µm wide at base, 1–3(–5)-septate, with short sterile basal outgrowths, hyaline, smooth-walled, with short sterile basal outgrowths. *Conidiogenous cells* monophialidic, lateral or terminal, (sub)cylindrical, straight or slightly curved, hyaline, smooth, thin- or

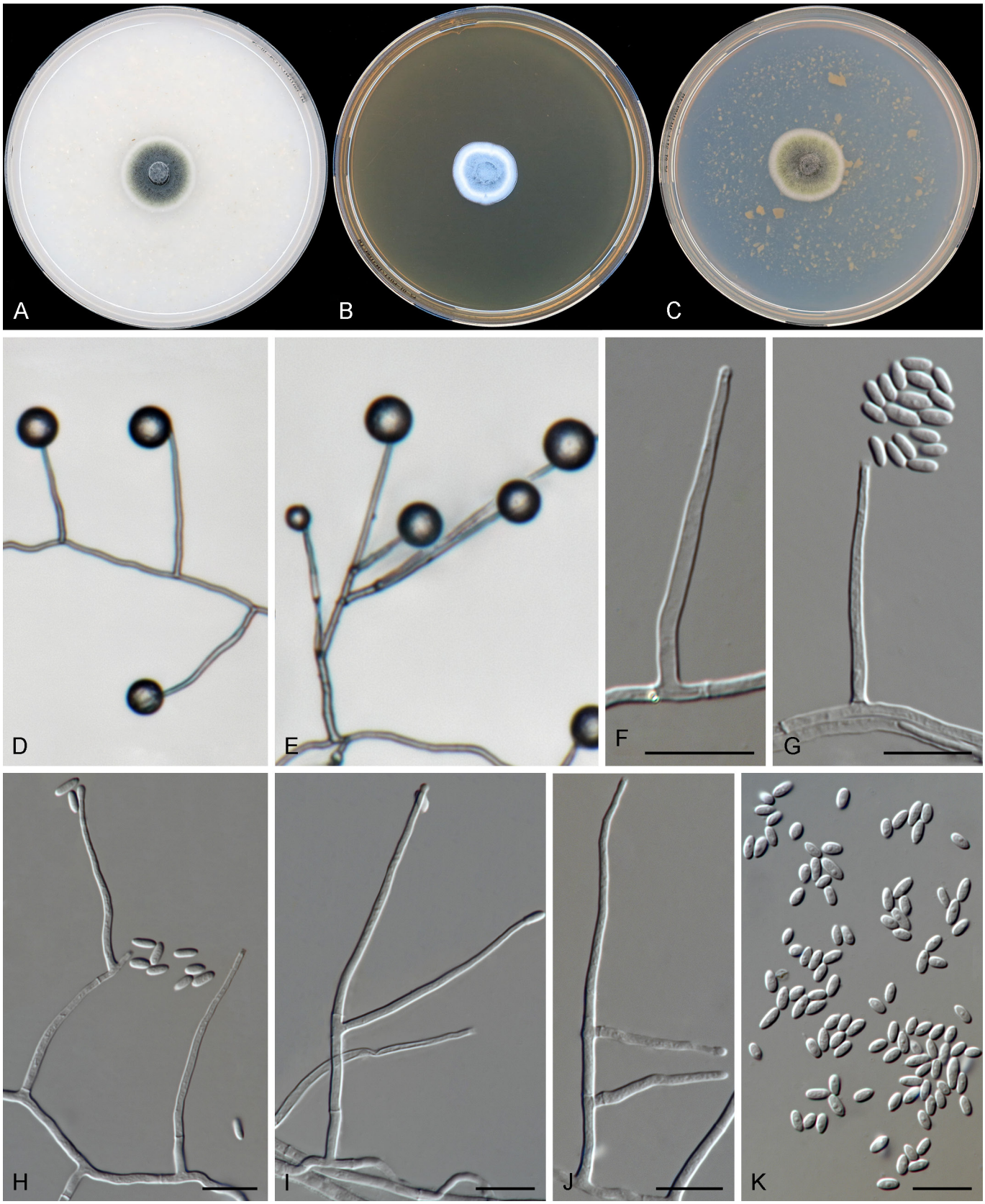

Fig. 6. *Brunneomyces romanianus* (ex-type CBS 490.81). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K.** Conidia. Scale bars = 10 µm.

thick-walled, (16.5–)26.2–44.2(–47.0) µm long, (1.2–)1.4–2.0(–2.1) µm wide at base, 0.8–1.0(–1.1) µm wide near aperture, with short collarettes and periclinal thickening at conidiogenous loci. *Conidia* cylindrical or ellipsoid, with rounded apices and slightly apiculate bases, aseptate, hyaline, with thin and smooth walls, (2.4–)3.2–4.7(–5.7) × (1.5–)1.6–2.1(–2.6) µm (av. 3.8 × 1.9 µm, n = 100), guttules, arranged in heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 23–25 mm diam. after 14 d in darkness at 25 °C, flat, felty, dusty, with sparse aerial mycelium, dark olivaceous at centre, white at periphery, margin entire, reverse pale dark green. On MEA reaching 18–20 mm diam., raised, radially folded, felty, with moderate aerial mycelium, bluish green at centre, white at periphery, margin entire, reverse pale saffron. On PDA reaching 19–22 mm diam., flat, felty, with moderate, greenish olivaceous to olivaceous buff at centre, dirty white at periphery, margin entire, reverse olivaceous buff at centre, dirty white at periphery. On SNA reaching 22–24 mm diam., flat, granulose, with sparse aerial mycelium, olivaceous buff to white, margin entire, reverse concolourous.

Notes: Based on multi-locus phylogenetic analyses, *B. romanianus* is closely related to *B. pseudozeylanicus*. However, *B. romanianus* (CBS 490.81) differs from *B. pseudozeylanicus* (CBS 560.73) in ITS (90.9 % identity, with 39 bp differences), LSU (97.6 %, 19 bp), *RPB2* (82.2 %, 136 bp), and *TEF1* (91.7 %, 56 bp) sequences. Morphologically, *B. romanianus* can be distinguished from *B. pseudozeylanicus* by its sparsely branched conidiophores, which are up to ca 95 µm long, compared to the mostly repeatedly basitonously branched conidiophores of *B. pseudozeylanicus*, reaching a maximum length of ca 318 µm. Additionally, the conidia of *B. romanianus* are ellipsoid with rounded or slightly apiculate basal ends and form conidial heads, whereas those of *B. pseudozeylanicus* are fusoid with truncate ends and form long chains (Hou *et al.* 2023).

Clade I-6. *Allomusicillium* L.W. Hou *et al.*, *Stud. Mycol.* **105**: 193. 2023.

Mycelium consisting of branched, septate, hyaline, smooth, thin- or thick-walled hyphae. *Conidiophores* arising from the agar surface or aerial hyphae, unbranched or branched, erect or curved, septate, hyaline, smooth-walled, with percurrent proliferation or sympodial proliferation. *Conidiogenous cells* enteroblastic, monophialidic or polyphialidic, lateral or terminal, subulate or subcylindrical to cylindrical, straight or slightly curved, hyaline, thick- and smooth-walled, with conspicuous or inconspicuous collarettes and periclinal thickening at conidiogenous loci; polyphialides present. *Conidia* ellipsoidal or cylindrical to short cylindrical, with slightly apiculate or truncate hilum at bases and obtuse apices, straight, aseptate, hyaline, with thin- and smooth-walled, eguttulate or guttulate, arranged in long chains or slimy heads. *Chlamydospores* and *sexual morph* not observed (adapted from Hou *et al.* 2023).

Type: *Allomusicillium domschii* (W. Gams) L.W. Hou *et al.*

Notes: *Allomusicillium*, recently introduced by Hou *et al.* (2023), is phylogenetically basal to *Musicillium* and *Paramusicillium*. It is characterised by basitonously branched conidiophores, which commonly proliferate sympodially multiple times. This distinguishes it from *Musicillium* and *Paramusicillium*, which typically have conidiophores that are either unbranched or repeatedly verticillate towards the apex (Giraldo & Crous 2019, Hou *et al.* 2023).

Allomusicillium malicola Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858419. Fig. 7.

Etymology: Referring to the host, the genus *Malus*, from which the holotype was collected.

Typus: **New Zealand**, Distr. Nelson, Moutere Hills orchard of R. Maisey, Vic. Appleby, isolated from *Malus sylvestris*, 15 Jul. 1975, *G.J. Samuels* (**holotype** designated here CBS H-25598, ex-type living isolate CBS 359.80).

Mycelium consisting of branched, septate, hyaline, smooth, thin- or thick-walled hyphae, 1.0–2.3 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous. *Conidiophores* arising from the agar surface and aerial hyphae, solitary or aggregated, (sub-)erect, unbranched or sparsely branched, up to ca 120 µm long, 1.3–3.3 µm wide at base, 1–5-septate, commonly with percurrent proliferation, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, cylindrical or subulate, straight or slightly curved, hyaline, smooth-walled, (18.5–)20.3–42.8(–46.8) µm long, (1.4–)1.5–2.2(–2.4) µm wide at base, 0.8–1.0(–1.1) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* ellipsoid or cylindrical, with rounded apices and slightly truncate at bases, aseptate, hyaline, thin- and smooth-walled, (2.6–)2.8–5.8(–6.8) × (1.4–)1.6–2.3(–2.6) µm (av. 4.3 × 1.8 µm, n = 100), eguttulate or guttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 13–15 mm diam. after 14 d in darkness at 25 °C, flat, thinly felty, dusty, with sparse aerial mycelium, white, margin entire, reverse concolourous. On MEA reaching 13–15 mm diam., raised, radially folded, felty, with moderate aerial mycelium, rosy buff at centre, white at periphery, margin undulate, reverse orange at centre, saffron at periphery. On PDA reaching 13 mm diam., raised, radially folded, thinly felty with buff radial lines, sparse aerial mycelium, creamy white, margin lobate, reverse concolourous. On SNA reaching 14 mm diam., flat, membranous, with sparse aerial mycelium, white, margin entire, reverse concolourous.

Notes: *Allomusicillium malicola* is phylogenetically closely related to *Allo. domschii* (Fig. 2, clade I-6). Morphologically, *Allo. malicola* differs from *Allo. domschii* by producing sparsely branched conidiophores with phialides up to 46.8 µm long, whereas *Allo. domschii* typically has predominantly basitonously branched conidiophores with phialides up to 70 µm long. Additionally, *Allo. malicola* lacks polyphialides, while *Allo. domschii* produces polyphialides with up to two conidiogenous loci (Hou *et al.* 2023). Furthermore, *Allo. malicola* (CBS 359.80) and *Allo. domschii* (CBS 764.69) are clearly different based on ITS (98.9 % identity, with five bp differences) and LSU (99.0 %, eight bp), no *RPB2* and *TEF1* sequences were available to compare the two isolates in a BLASTn search.

Clade I-12. *Chlamydosporiella* Giraldo López & Crous, *Stud. Mycol.* **92**: 270. 2018.

Mycelium consisting of branched, septate, hyaline, smooth and thin-walled hyphae. *Conidiophores* (sub-)erect or bent, unbranched or

basitonously branched, aseptate or septate, hyaline, smooth-walled. *Conidiogenous cells* enteroblastic, monophialidic, lateral or terminal, cylindrical or subulate, straight or slightly curved, hyaline, smooth, thin- or thick-walled, with short collarettes and inconspicuous periclinal thickening at conidiogenous loci; adelophialides present or absent. *Conidia* ellipsoid, obovoid or subglobose, aseptate, hyaline, thick- and smooth-walled, eguttulate, arranged in slimy heads. *Chlamydospores* present or absent. *Sexual morph* not observed (adapted from Giraldo & Crous 2019).

Type: *Chlamydosporiella restricta* (J.F.H. Beyma) Giraldo López & Crous

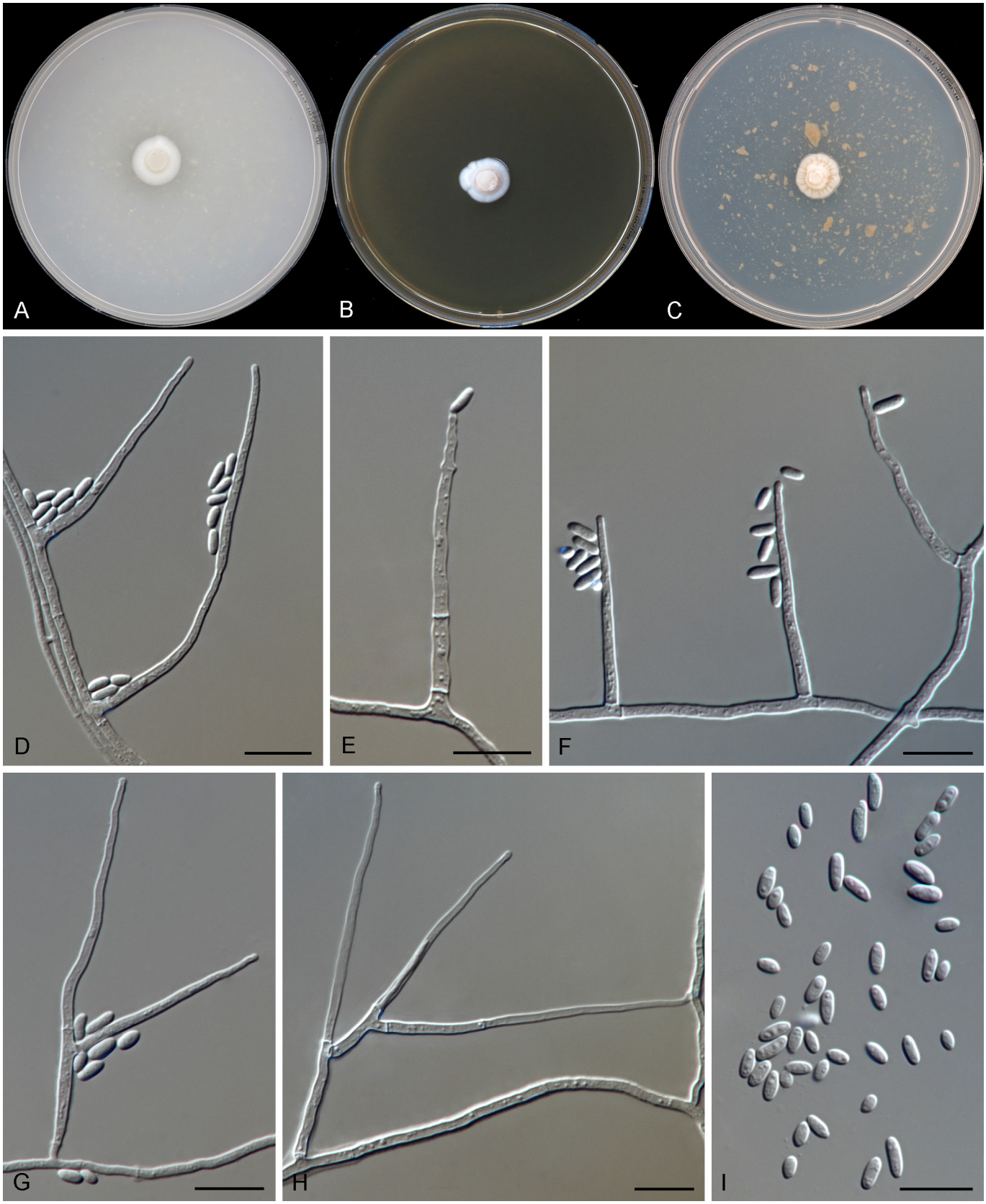

Fig. 7. *Allomusicillium malicola* (ex-type CBS 359.80). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–H.** Conidiophores. **I.** Conidia. Scale bars = 10 µm.

Notes: The genus *Chlamydosporiella* was proposed to accommodate the type species *Chlamydosporiella restricta*, which was previously classified as *Verticillium dahliae f. restrictum* by van Beyma (1940). It is characterised by obovoid to widely ellipsoidal conidia and dark olive green chlamydospores. In this study, we propose a new species, which is also characterised by obovoid to widely ellipsoidal conidia, as described below.

Chlamydosporiella aerina Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858420. Fig. 8.

Etymology: Referring to the substrate, air, from which the holotype was collected.

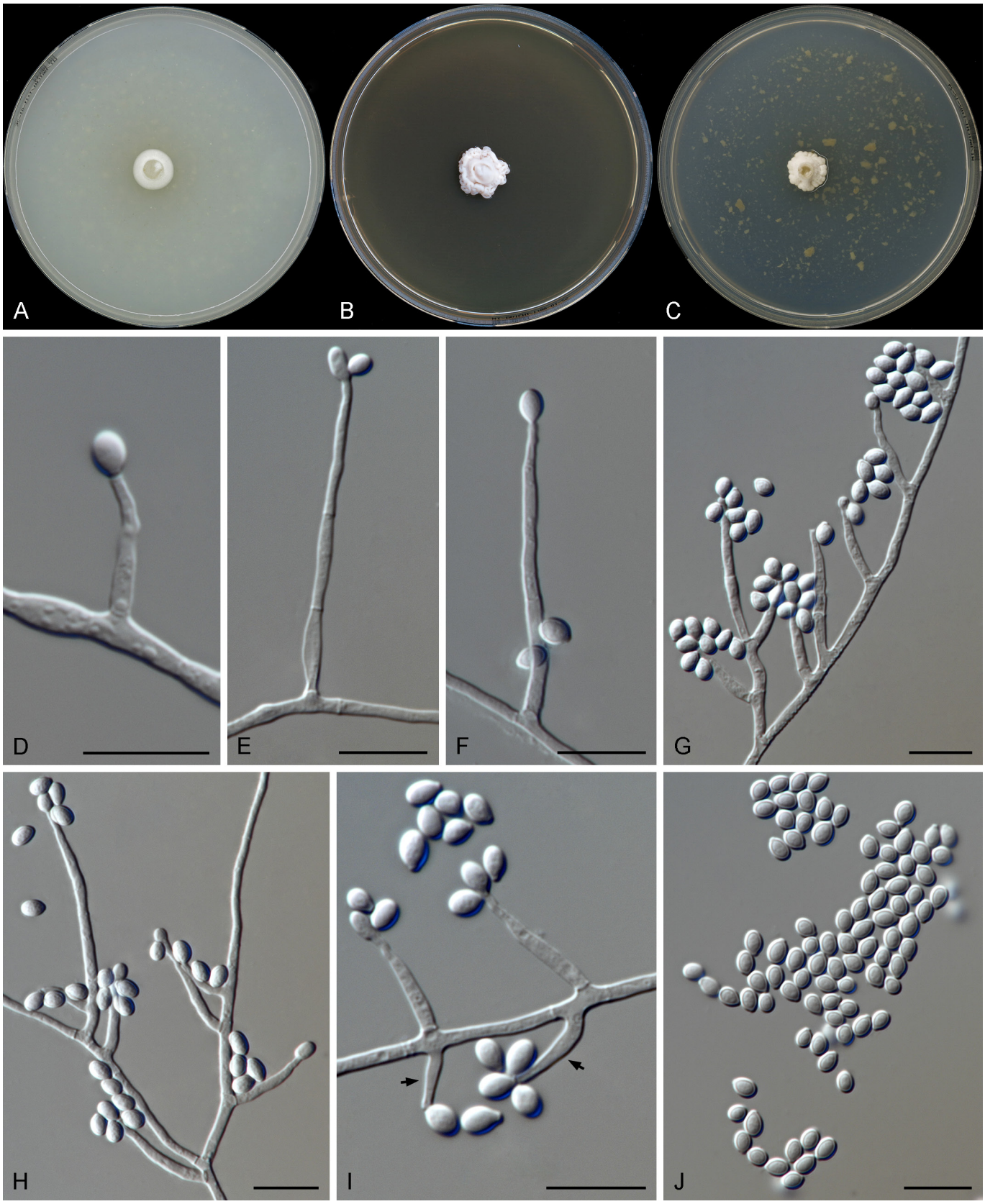

Fig. 8. *Chlamydosporiella aerina* (ex-type CBS 598.70). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores (adelophialides pointed out with arrows). **J.** Conidia. Scale bars = 10 µm.

Typus: **Finland**, Turku, isolated from air, unknown collection date and *collector*, isol. *C.E. Sonck*, No. AC2 (**holotype** designated here CBS H-25608, ex-type living isolate CBS 598.70).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.5 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface and aerial hyphae, solitary or aggregated, (sub-)erect, unbranched or basitonously branched, bearing up to 1–3 levels with 1–2 phialides per node, up to ca 45 µm long, 1.6–3.2 µm wide at base, with (0–)1–3-septate at base, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, cylindrical, subulate, slightly swollen at lower part, straight or slightly curved, hyaline, smooth-walled, (5.8–)8.8–21.4(–26.8) µm long, (1.4–)1.5–2.2(–2.6) µm wide at base, 0.8–1.0(–1.2) µm wide near aperture, with short collarettes and periclinal thickening at conidiogenous loci; adelophialides present, subulate or acicular, 4.9–17.7 × 1.4–3.2 µm. *Conidia* widely ellipsoid, obovoid or subglobose, apiculate at base, rounded at apex, aseptate, hyaline, with thick and smooth walls, (2.6–)3.0–3.9(–4.0) × (2.0–)2.2–2.8(–3.2) µm (av. 3.4 × 2.5 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 12–13 mm diam. after 14 d in darkness at 25 °C, flat, felty, dusty, with moderate aerial mycelium, white, margin entire, reverse buff. On MEA reaching 14–16 mm diam., raised, radially folded, membranous without aerial mycelium, pale rosy buff, rugose at periphery, margin irregular, reverse saffron. On PDA reaching 12 mm diam., raised, radially folded, felty, with moderate aerial mycelium, white, margin crenate, reverse rosy buff. On SNA reaching 10 mm diam., flat, felty, with sparse aerial mycelium, white, margin entire, reverse concolourous.

Notes: According to our phylogenetic analyses (Fig. 2, clade I-12), only two species, *Chlamydosporiella aerina* and *Chlam. restricta*, are placed within the *Chlamydosporiella* clade. *Chlamydosporiella aerina* (CBS 598.70) shows a close phylogenetic affinity to *Chlam. restricta* (CBS 178.40), but the two species are distinct based on molecular data, with ITS (95.1 % identity, with 25 bp differences), LSU (99.2 %, 6 bp), *RPB2* (93.7 %, 47 bp), and *TEF1* (96.0 %, 30 bp) sequences. Morphologically, *Chlam. aerina* differs from *Chlam. restricta* in producing shorter phialides (5.8–26.8 µm long in *Chlam. aerina* vs 22.7–45 µm long in *Chlam. restricta*); and narrower and wider conidia (2.6–4.0 × 2.0–3.2 in *Chlam. aerina* vs 2.2–4.7 × 1.5–2.3 µm in *Chlam. restricta*; Giraldo & Crous 2019).

Clade II. *Aurantidochiaceae* Lin Zhao & Crous, ***fam. nov.*** MycoBank MB 858421.

Etymology: Name refers to the type genus *Aurantidochium*.

Classification: *Hypocreales*, *Sordariomycetes*.

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae. *Sporulation* abundant. *Conidiophores* in orange sporodochia mostly branched, or arising from the agar surface, aerial hyphae or ropes and coils formed by mycelium, aggregated, (sub-)erect, unbranched, or basitonously branched. *Sporodochial phialides* aculeate or subulate, tapering at top, hyaline, thick- and smooth-walled. *Conidiogenous cells* enteroblastic, monophialidic, lateral or terminal, subcylindrical to cylindrical, straight or slightly curved, hyaline, thick- and smooth-walled, occasionally with percurrent proliferation. *Conidia* cylindrical or ellipsoid, straight or curved, with both ends rounded, or with a slightly apiculate or truncate base, aseptate, hyaline, with smooth, thin- or thick-walled, eguttulate, variable in size, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Type genus: *Aurantidochium* Lin Zhao & Crous

Notes: The family *Aurantidochiaceae* currently accommodates two newly described genera, *Aurantidochium* and *Lagenariomyces*, derived from four isolates labelled as "*Nectriella nolinae*" and "*Hydropisphaera suffulta*". Based on multi-locus analyses, we propose that these two genera be placed in a new family, forming a fully supported clade basal to the *Sarocladiaceae*, separated from all known families in the *Hypocreales* (Fig. 1).

Aurantidochium Lin Zhao & Crous, ***gen. nov.*** MycoBank MB 858422.

Etymology: In Latin, "*aurantido*" means "orange" and "*dochium*" refers to "sporodochium", referring to the production of orange sporodochia by the type species.

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae. *Sporulation* abundant, forming orange sporodochial conidiomata. *Conidiophores* sporodochial, mostly branched, smooth-walled. *Sporodochial phialides* terminal or lateral, aculeate or subulate, tapering at top, hyaline to pale ochreous, thick- and smooth-walled, with minute conspicuous collarette and periclinal thickening at conidiogenous loci. *Conidia* cylindrical, straight or curved, with both ends rounded, or with a slighty apiculate base, aseptate, hyaline, thin- and smooth-walled, eguttulate. *Chlamydospores* and *sexual morph* not observed.

Type: *Aurantidochium guadalupense* (Ramaley) Lin Zhao & Crous

Notes: Based on our phylogenetic analyses, the ex-type isolate of *Aurantidochium guadalupense* (CBS 110134) clustered in a separate clade, distant from the newly described genus *Lagenariomyces*. Morphologically, species in *Aurantidochium* differ in having sporodochial conidiomata, whereas species in *Lagenariomyces* produce unbranched or basitonously branched conidiophores.

Aurantidochium guadalupense (Ramaley) Lin Zhao & Crous, ***comb. nov.*** MycoBank MB 861609. Fig. 9.
Basionym: *Nectriella guadalupensis* Ramaley, *Mycotaxon* 90: 182. 2004

Typus: **USA**, Texas, Culberson County, Guadalupe Mountains National Park, 4.6 miles from the highway gate on Williams Ranch Road, from dead leaves of *Nolina micrantha*, 20 Oct. 1999, *A.W. Ramaley* (**holotype** designated here CBS H-25575, ex-type living isolate CBS 110134).

Mycelium consisting of branched, hyaline, septate, smooth- and thin-walled hyphae, 1.0–1.7 µm wide. *Sporulation* is abundant from orange sporodochial conidiomata. *Conidiophores* in orange sporodochia mostly branched, bearing multiple levels with 1–4 phialides per node, smooth-walled. *Sporodochial phialides* terminal or lateral, aculeate or subulate, tapering at top, hyaline to pale ochreous, smooth- and thick-walled, (4.8–)5.8–10.7(–11.9) µm long, 1.2–1.8(–2.0) µm wide at base, (0.7–)0.8–1.1(–1.2) µm wide

near aperture, with minute conspicuous collarette and periclinal thickening at conidiogenous loci. *Conidia* cylindrical, straight or curved, with both ends rounded, or with a slightly apiculate base, aseptate, hyaline, thin- and smooth-walled, (3.3–)3.7–5.1(–5.8) × (1.1–)1.2–1.5(–1.7) µm (av. 4.3 × 1.3 µm, n = 100), eguttulate. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 17–18 mm diam. after 14 d in darkness at 25 °C, flat, membranous with sparse aerial mycelium, buff at centre, white at periphery, margin entire, reverse dirty white. On MEA reaching 15–16 mm diam., flat, radially folded, felty, with moderate aerial mycelium, rosy buff, margin entire, reverse saffron, with radial lines. On PDA reaching 14 mm diam., flat, felty,

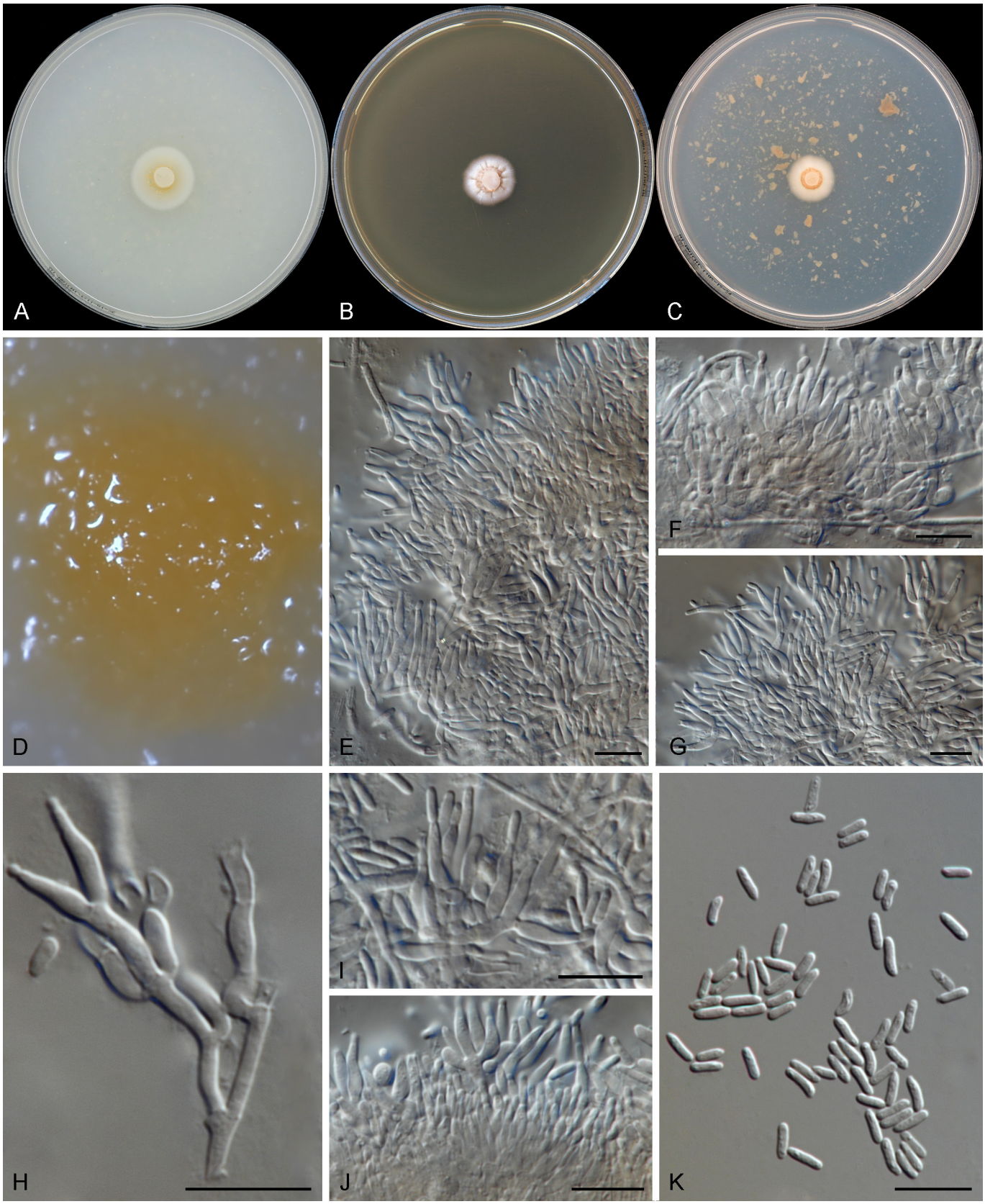

Fig. 9. *Aurantidochium guadalupense (*ex-type CBS 110134). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–G, J.** Sporodochia. **H, I**. Sporodochial phialides. **K**. Conidia. Scale bars = 10 µm.

with sparse aerial mycelium, white, with a saffron concentric ring in middle, margin entire, reverse rosy buff at centre, white at periphery. On SNA reaching 12–15 mm diam., flat, felty, with sparse aerial mycelium, white, margin fimbriate, reverse concolourous.

Notes: Isolate CBS 110134 was recorded as the ex-type isolate of "*Nectriella nolinae*" in the CBS culture collection database but was designated as the holotype of *N. guadalupensis* by Ramaley (2004). This isolate was isolated from dead leaves of *Nolina micrantha* in the USA, where it co-occurred with other fungi in its natural habitat. According to the phylogenetic inference in our study, CBS 110134 forms an independent lineage that is distant from the species in *Lagenariomyces* (Fig. 1), and it represents a new combination proposed in this study.

Lagenariomyces Lin Zhao & Crous, ***gen. nov.*** MycoBank MB 858424.

Etymology: Referring to the host, *Lagenaria siceraria*, from which the type species was isolated.

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae. Sporulation abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface and aerial hyphae, or ropes and coils formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or basitonously branched, bearing up to 1–2 levels with 1–2 phialides per node, septate, hyaline, smooth-walled, occasionally with a percurrent proliferation. *Conidiogenous cells* enteroblastic, monophialidic, lateral or terminal, cylindrical or subcylindrical, straight or slightly curved, hyaline, thick- and smooth-walled, with conspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* cylindrical or ellipsoid, straight or curved, with both ends rounded, or with a slightly truncate bases, aseptate, hyaline, with thick and smooth walls, variable in size, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Type: *Lagenariomyces varioconidialis* Lin Zhao & Crous

Notes: The genus *Lagenariomyces* is proposed here to accommodate the type species *Lag. varioconidialis*, and another species *Lag. collarulis*, characterised by producing acremonium-like conidiophores, either unbranched or basitonously branched.

Lagenariomyces collarulis Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858425. Fig. 10.

Etymology: Referring to the production of conspicuous collarettes by this species.

Typus: **USA**, Puerto Rico, unknown substrate, unknown collection date, coll. and isol. *G.J. Samuels* (**holotype** designated here CBS H-25585, ex-type living isolate CBS 122985).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.0 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or basitonously branched, bearing up to 1–2 levels with 1–2 phialides per node, up to ca 93 µm long, 1.9–3.1 µm wide at base, occasionally with a percurrent proliferation, with 1–3(–5)-septate, hyaline, smooth-walled, with cell walls usually thicker than those of vegetative hyphae. *Conidiogenous cells* monophialidic, lateral or terminal, (sub)cylindrical, or subulate, straight or slightly curved, hyaline, thick- and smooth-walled, (13.5–)14.3–42.0(–46.3) µm long, (1.5–)1.6–2.5(–2.8) µm wide at base, 0.9–1.2(–1.3) µm wide near aperture, with conspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* cylindrical or ellipsoid, with a rounded apices and slightly truncate basal ends, aseptate, hyaline, thin- and smooth-walled, (3.3–)4.0–9.6(–11.0) × (1.3–)1.4–2.2 µm (av. 6.7 × 1.8 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 37–39 mm diam. after 14 d in darkness at 25 °C, flat, membranous with sparse aerial mycelium, buff at centre, dirty white at periphery, margin entire, reverse rosy buff at centre, dirty white at periphery. On MEA reaching 35–38 mm diam., flat, felty, with moderate aerial mycelium, whitish, margin entire, reverse saffron. On PDA reaching 33–36 mm diam., flat, felty, with moderate aerial mycelium, salmon at centre, dirty white at periphery, margin fimbriate, reverse concolourous. On SNA reaching 27–30 mm diam., flat, felty, dusty, with sparse aerial mycelium, white, margin entire, reverse concolourous.

Additional material examined: **USA**, Puerto Rico, Luquillo Mts., Bisley Experimental Watershed, unknown substrate, unknown collection date, coll. and isol. *G.J. Samuels*, isolate CBS 122558 = GJS 96-25).

Notes: Based on the phylogenetic analyses (Fig. 1, clade II), *Lag. collarulis* (CBS 122985) has a close phylogenetic affinity to *Lag. varioconidialis* (CBS 122798), but with clearly different ITS (87.7 % identity, with 63 bp differences), and *TEF1* (96.2 %, 31 bp) sequences. No LSU and *RPB2* sequences were available to compare these two isolates in a BLASTn search. For a morphological comparison with *Lag. varioconidialis*, see notes below.

Lagenariomyces varioconidialis Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858426. Fig. 11.

Etymology: Referring to the production of conidia that are variable in size.

Typus: **France**, Martinique, Prêcheur, Anse Couleuvre, from meso-hygrophile forest on dead *Calabash* (*Lagenaria siceraria*), 13 Aug. 2007, unknown *collector* (**holotype** designated here CBS H-25584, ex-type living isolate CBS 122798).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.4 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes and coils formed by mycelium, solitary or aggregated, (sub-) erect, commonly unbranched, occasionally basitonously branched, bearing up to 1–2 levels with 1–2 phialides per node, up to ca 120 µm long, 1.5–3.0 µm wide at base, 1–5-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, cylindrical or subcylindrical, straight or slightly curved, hyaline, smooth-, thin- or thick-walled, (21.1–)35.4–52.8(–69.2) µm long, (1.5–)1.6–2.3 µm wide at base, 0.9–1.1(–1.2) µm wide near aperture, with conspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* cylindrical or ellipsoid, straight or curved, with both ends rounded, or with a slightly truncate bases, aseptate, hyaline, smooth- and thick-

walled, variable in size (3.2–)3.9–9.0(–11.8) × (1.4–)1.5–2.1(–2.2) µm (av. 6.2 × 1.8 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 33–35 mm diam. after 14 d in darkness at 25 °C, flat, felty, dusty, with moderate aerial mycelium, white to primrose, with concentric rings, margin undulate, reverse whitish. On MEA reaching 28–30 mm diam., raised, radially folded, thinly felty, membranous with sparse aerial mycelium, buff at centre, white at periphery, margin radially striate with lobate edge, reverse saffron with radially white lines. On PDA reaching 27–31 mm diam., felty, radially folded at centre, flat at periphery, greyish, margin

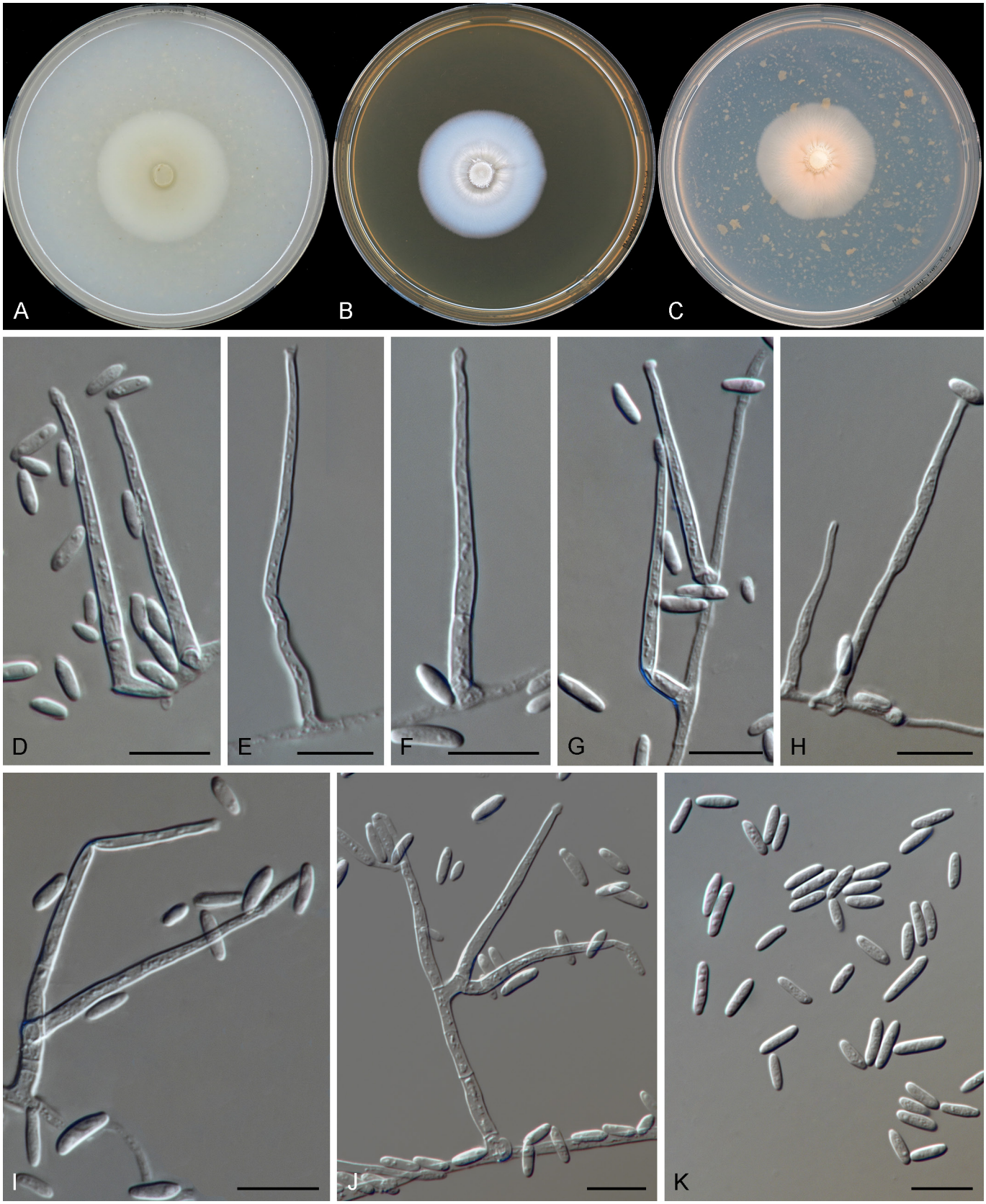

Fig. 10. *Lagenariomyces collarulis* (ex-type CBS 122985). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K.** Conidia. Scale bars = 10 µm.

fimbriate, reverse concolourous with radially white lines at centre. On SNA reaching 20–24 mm diam., flat, granulose, dusty, with moderate aerial mycelium, white, margin fimbriate, reverse concolourous.

Notes: Phylogenetically, *Lag. varioconidialis* is closely related to *Lag. collarulis*. Morphologically, *Lag. varioconidialis* differs in producing longer conidiophores, which are up to 120 µm long in *Lag. varioconidialis* vs up to 93 µm long in *Lag. collarulis*, and longer phialides, which are (21.1–)35.4–52.8(–69.2) µm long in *Lag. varioconidialis*, vs (13.5–)14.3–42.0(–46.3) µm long in *Lag. collarulis*.

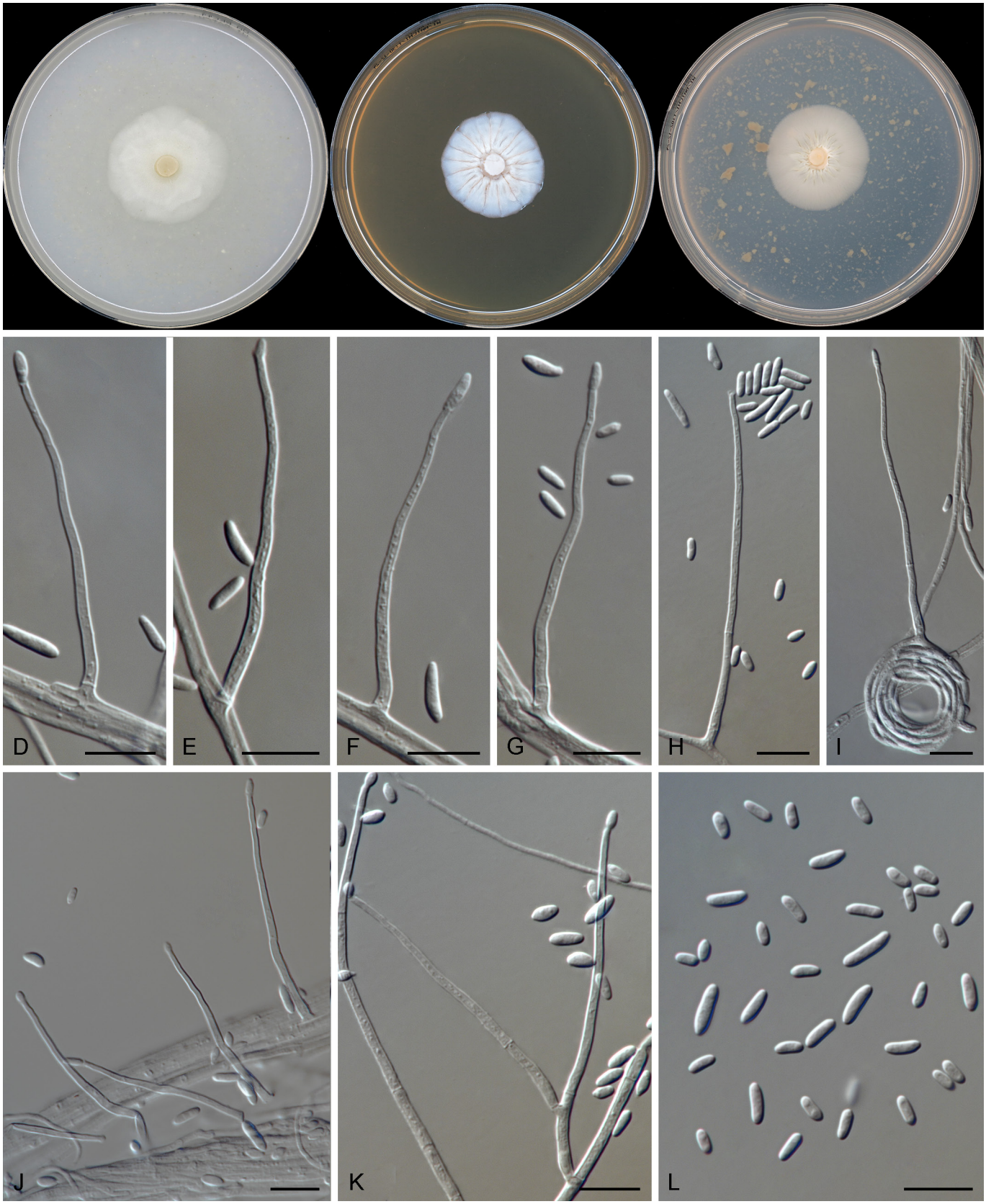

Fig. 11. *Lagenariomyces varioconidialis* (ex-type CBS 122798). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–K.** Conidiophores. **L.** Conidia. Scale bars = 10 µm.

Clade III. *Sarocladiaceae* L. Lombard, *Persoonia* **41**: 343. 2018.

Classification: *Hypocreales*, *Sordariomycetes*.

Type genus: *Sarocladium* W. Gams & D. Hawksw.

Clade III-1. *Polyphialocladium* L.W. Hou *et al.*, *Stud. Mycol*. **105**: 186. 2023.

Mycelium consisting of branched, septate, hyaline, smooth hyphae with thin walls. *Conidiophores* arising directly from aerial or substratal mycelium, unbranched or basitonously branched, solitary or aggregated, straight or curved, often with repeatedly sympodial proliferations. *Conidiogenous cells* enteroblastic, mono- or polyphialidic, lateral, subulate or subcylindrical, hyaline, with thick and smooth walls, commonly with percurrent, terminal, or subterminal proliferation, with conspicuous periclinal thickening and cylindrical collarettes at conidiogenous loci. *Conidia* ovoid to broadly fusoid, straight, with both ends acutely pointed, aseptate, hyaline, smooth- and thin-walled, eguttulate, typically arranged in chains (adapted from Hou *et al.* 2023).

Type: *Polyphialocladium fusisporum* L.W. Hou *et al.*

Notes: *Polyphialocladium* was introduced by Hou *et al.* (2023), with only one species, *Poly. fusisporum*, and can be morphologically distinguished from other genera in *Sarocladiaceae* by its basitonously branched conidiophores, which undergo repeated sympodial proliferation.

Polyphialocladium margaretcollinsiae (Y.P. Tan *et al.*) Lin Zhao & Crous, ***comb. nov.*** MycoBank MB 858429.
Basionym: *Chlamydocillium margaretcollinsiae* Y.P. Tan *et al.*, *Index Austral. Fungi* **29**: 3. 2024.

Description and illustration: Tan & Shivas (2024a).

Typus: **Australia**, Queensland, Mission Beach, isolated from an ant (*Polyrhachis brevinoda*) infected with *Ophiocordyceps* sp., 7 Jun. 2015, *T.S. Marney, M.D.E. Shivas & R.G. Shivas* [**holotype** BRIP 62736a (metabolically inactive culture)].

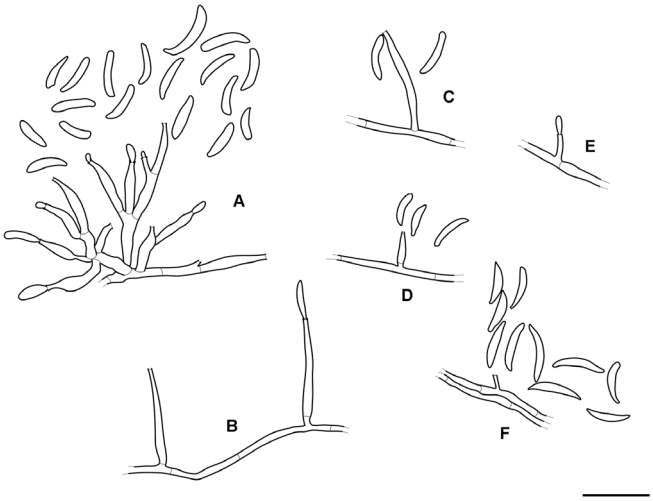

Fig. 12. *Chlamydocillium antarcticum* (ex-type CBS 120502). **A–D.** Conidiophores and conidia. **E, F.** Adelophialides and conidia. Scale bars = 10 µm.

Notes: *Chlamydocillium margaretcollinsiae* was isolated from an ant (*Polyrhachis brevinoda*), infected by *Ophiocordyceps* sp., and described based on DNA only (Tan & Shivas 2024a). In the present study, phylogenetic analyses showed that the ex-type isolate of *Chl. margaretcollinsiae* clusters within the genus *Polyphialocladium* (Fig. 3, clade III-1), and therefore a new combination *Poly. margaretcollinsiae* of this species is proposed here.

Clade III-2. *Chlamydocillium* Zare & W. Gams, *Mycol. Progr*. **15**: 1018. 2016.
Synonym: *Kiflimonium* Summerb. *et al.*, *Microorganisms* **6**: 17. 2018.

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae. *Conidiophores* arising directly from aerial or substratal mycelium, or from ropes of hyphae, solitary or aggregated, erect or slightly curved, unbranched or basitonously branched, producing solitary and/or verticillate phialides up to three per node, septate. *Conidiogenous cells* enteroblastic, mono- and polyphialidic, lateral or terminal, (sub-)cylindrical, subulate or acicular, hyaline, with smooth, thin or thick walls, and inconspicuous or conspicuous periclinal thickening and collarette at conidiogenous loci; adelophialides present or absent. *Conidia* cylindrical, ellipsoid, bacilliform, short reniform or allantoid, curved or straight, with obtuse apices and bases, or slightly apiculate at bases, aseptate, hyaline, with smooth, thin or thick walls, eguttulate or guttulate, arranged in slimy heads. *Chlamydospores* (sub-)globose, ellipsoid, ampulliform, doliiform, oblong, ovoid, limoniform, lateral or intercalary, mostly single or in chains (adapted from Zare & Gams 2016, Hou *et al.* 2023).

Type: *Chlamydocillium cyanophilum* Zare &W. Gams

Notes: The genus *Chlamydocillium* was introduced by Zare & Gams (2016), with *Chl. cyanophilum* as type and only species. It is characterised by its solitary and/or verticillate phialides (with up to three per node conidiophores) and abundant oblong to ellipsoidal chlamydospores. Hou *et al.* (2023) proposed six new species and one new combination within *Chlamydocillium*. In this study, we propose two new species below.

Chlamydocillium antarcticum L.W. Hou, *et al.*, *Stud. Mycol.* **105**: 181. 2023. Fig. 12.

Typus: **Antarctica**, Victoria Land, Dry Valleys, Don Juan Pond, unknown substrate, unknown collection date, *L. Connell*, No. 03-143 (**holotype** CBS H-24710, ex-type isolate CBS 120502).

Description based on drawing from the ex-type CBS 120502: *Mycelium* consisting of branched, septate hyphae, 1.0–1.5 µm wide. *Conidiophores* solitary or aggregated, erect, unbranched or basitonously branched, with 1–2 phialides per node, 5.0–26.0 µm long, 1.0–2.0 µm wide at base. *Conidiogenous cells* monophialidic, lateral or terminal, subulate or subcylindrical, 4.0–15.5 µm long, 1.0–1.5 µm wide at base, 0.6–1.0 µm wide near aperture, sometimes with intercalary phialides; adelophialides present. *Conidia* cylindrical or allantoid, curved, with apiculate or rounded ends and slightly truncate bases, aseptate, 5.0–9.0 × 1.0–1.5 µm. *Sexual morph*: not present.

Culture characteristics: Hou *et al.* (2023).

Notes: *Chlamydocillium antarcticum* collected from Antarctica was introduced by Hou *et al.* (2023) based on DNA description with the ITS, LSU, *RPB2*, and *TEF1* genetic markers. Hou *et al.* (2023) did not observe the morphology of this isolate. However, R.C. Summerbell made the drawing while he was at the Westerdijk Institute, and we have included it here, depicting the species with subulate or subcylindrical phialides and curved conidia.

Chlamydocillium theobromae Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858431. Fig. 13.

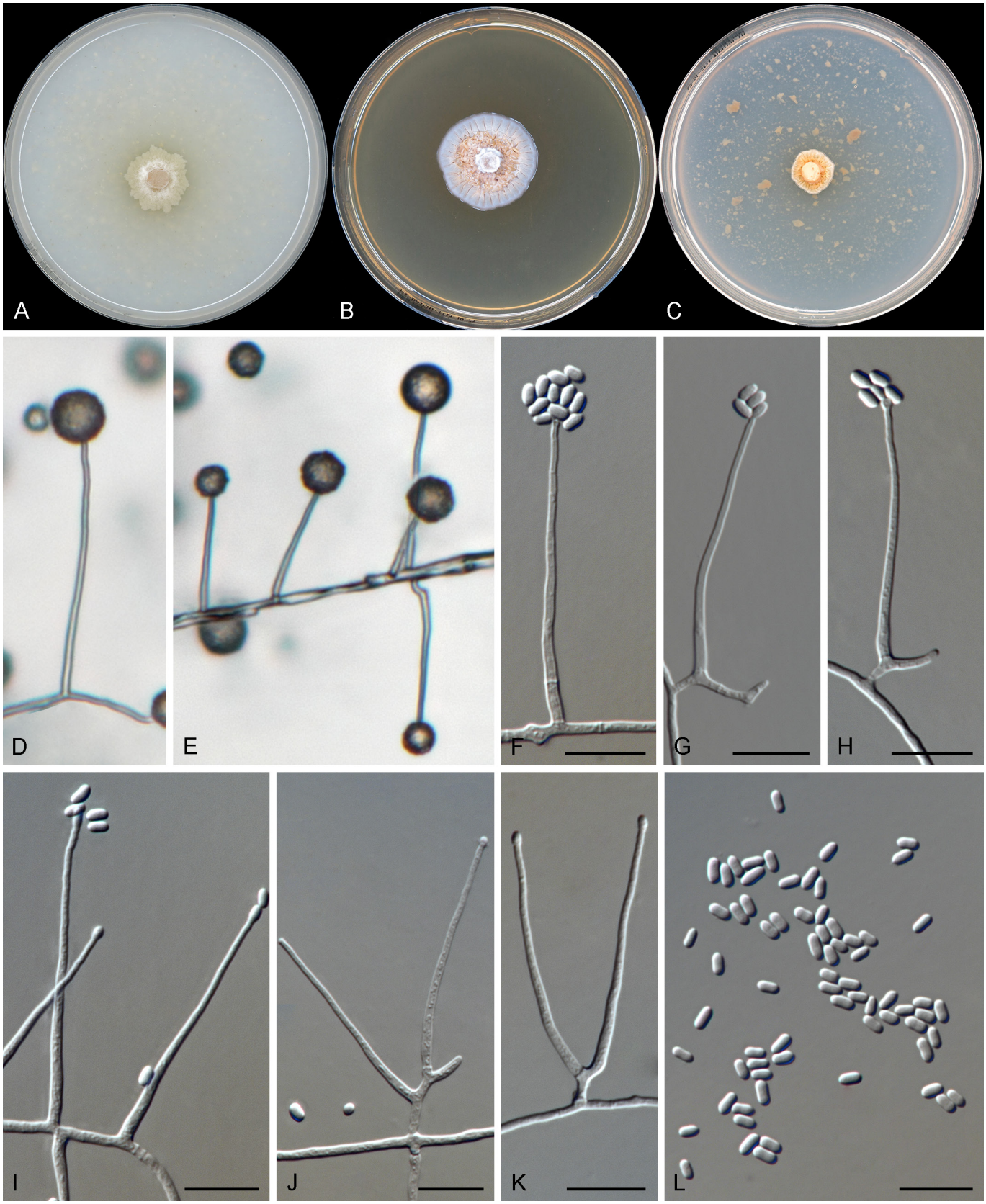

Fig. 13. *Chlamydocillium theobromae* (ex-type CBS 112098). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–K.** Conidiophores. **L.** Conidia. Scale bars = 10 µm.

Etymology: Referring to the host, *Theobroma gileri*, from which the holotype was collected.

Typus: **Ecuador**, Pichincha Prov., Vincente Maldonado, Km 120 to Quito, Rio Caoni, Arasha Resort, from *Theobroma gileri*, stem tissue, unknown collection date and *collector*, isol. 8 May 2000, *H.C. Evans* & *K.A. Holmes* (**holotype** designated here CBS H-25577, ex-type living isolate CBS 112098).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.3 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous. *Conidiophores* arising from the agar surface and aerial hyphae, solitary, erect, unbranched or sparsely branched, up to ca 66 µm long, 1.2–2.4 µm wide at base, 1–3-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, subulate, or subcylindrical, straight or slightly curved, hyaline, with smooth, thin or thick walls, (20.0–)24.0–42.5(–56.8) µm long, (1.1–)1.4–1.9 µm wide at base, 0.7–0.9(–1.0) µm wide near aperture, with conspicuous collarettes and periclinal thickening at conidiogenous loci; adelophialides absent. *Conidia* short cylindrical, with both ends rounded, aseptate, hyaline, smooth- and thin-walled, (2.2–)2.5–3.0(–3.3) × (1.2–)1.4–1.8(–1.9) µm (av. 2.8 × 1.6 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 19–21 mm diam. after 14 d in darkness at 25 °C, flat, felty, with sparse aerial mycelium, whitish to buff, margin fimbriate, reverse saffron at centre, buff at periphery. On MEA reaching 25–28 mm diam., raised, radially folded, rugose, felty, with sparse aerial mycelium, rosy buff, margin crenate, reverse orange to saffron. On PDA reaching 12–17 mm diam., raised, radially folded, membranous, with sparse aerial mycelium, saffron at centre, buff at periphery, margin crenate, reverse saffron. On SNA reaching 8–13 mm diam., flat, felty, with sparse aerial mycelium, white, margin fimbriate, reverse concolourous.

Notes: According to the phylogenetic inferences in the present study (Fig. 3, III-2), *Chl. theobromae* is closely related to *Chl. viridicolor* (described below). Morphologically, *Chl. theobromae* can be distinguished from *Chl. viridicolor* by its colony colour and growth rate on OA media. *Chlamydocillium theobromae* forms colonies that are white to buff, reaching a diameter of 19–21 mm within 14 d, while *Chl. viridicolor* forms colonies that are dark bluish green to greyish yellow green, with a diameter of 37–41 mm within the same period. Additionally, *Chl. theobromae* produces sparsely branched conidiophores, in contrast to the regularly branched conidiophores of *Chl. viridicolor*. Furthermore, CBS 112098 (*Chl. theobromae*) and CBS 113439 (*Chl. viridicolor*) have clearly different ITS (96.4 % identity, with 18 bp differences), LSU (99.2 %, 6 bp), *RPB2* (95.9 %, 31 bp), and *TEF1* (98.5 %, 12 bp) sequences.

Chlamydocillium viridicolor Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858432. Fig. 14.

Etymology: Referring to the greenish colony colour in culture.

Typus: **Ecuador**, from *Theobroma* sp., unknown collection date, *H.C. Evans* & *K.A. Holmes*, CABI (**holotype** designated here CBS H-25578, ex-type living isolate CBS 113439).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.1 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes and coil formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or basitonously branched, bearing up to 1–3 levels with 1–4 phialides per node, slightly swollen, flat at lower part, up to ca 60 µm long, 1.2–2.6 µm wide at base, 1–3-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, subulate or cylindrical, straight or slightly curved, hyaline, smooth- and thick-walled, (10.8–)13.4–44.7(–47.7) µm long, (1.1–)1.3–1.8(–1.9) µm wide at base, 0.7–0.9(–1.0) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci; adelophialides absent. *Conidia* short cylindrical or ellipsoid, with both ends rounded, aseptate, hyaline, smooth- and thin-walled, (2.1–)2.3–4.1(–4.6) × 1.4–1.8(–1.9) µm (av. 2.9 × 1.6 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 37–41 mm diam. after 14 d in darkness at 25 °C, flat, powdery, dusty, with sparse aerial mycelium, dark bluish green with whitish at centre, greyish yellow green at periphery, margin entire, reverse bluish green to greyish yellow-green centre, straw at periphery. On MEA reaching 33–39 mm diam., raised, radially folded, rugose, membranous with sparse aerial mycelium, dark green with yellow green at centre, vinaceous buff at periphery, margin crenate, reverse dark bluish green at centre, luteous at periphery. On PDA reaching 29–36 mm diam., flat, hairy at centre, felty at periphery, with moderate aerial mycelium, yellowish green to white at centre, pale vinaceous in middle, vinaceous buff at periphery, margin entire, reverse dark green at centre, pale luteous at periphery. On SNA reaching 36–40 mm diam., flat, membranous, pale green at centre, dirty white at periphery, margin entire, reverse concolourous.

Additional material examined: **Ecuador**, from *Theobroma* sp., unknown collection date and *collector*, isolate CBS 113575.

Notes: Our phylogenetic analyses reveal that *Chl. viridicolor* is closely related to *Chl. theobromae*. For a comprehensive morphological and phylogenetic comparison with *Chl. viridicolor*, please refer to the notes under *Chl. theobromae*.

Clade III-3. *Parasarocladium* Summerb. *et al.*, *Microorganisms* **6**: 17. 2018.

Mycelium consisting of branched, septate, hyaline hyphae, occasionally inflated with brown guttules. *Conidiophores* arising laterally from vegetative hyphae, erect, solitary or aggregated, unbranched or basitonously branched, aseptate or septate, smooth, hyaline. *Conidiogenous cells* enteroblastic, monophialidic or polyphialidic, elongate-ampulliform to subcylindrical, subulate, acicular, arising laterally from hyphae or in terminal pairs, verticils of three, or small monopodially branched tufts of up to four from conidiophores, hyaline, smooth-walled, with inconspicuous or conspicuous periclinal thickening and collarettes. *Conidia* cylindrical, ellipsoid, oblong, ovoid, bacilliform or fusoid, with both ends rounded, or with slightly apiculate bases, aseptate, smooth-walled, straight or slightly curved, eguttulate or guttulate, arranged in slimy or dry heads. *Chlamydospores* and *sexual morph* not observed (adapted from Summerbell *et al.* 2018, Hou *et al.* 2023).

Type: *Parasarocladium radiatum* (Sukapure & Thirum.) Summerb. *et al.*

Notes: Summerbell *et al.* (2018) introduced the genus *Parasarocladium* to accommodate three soil-inhabiting, acremonium-like species: *Para. breve*, *Para. gamsii*, and *Para. radiatum* (type species). Subsequently, Crous *et al.* (2018b, 2020, 2021) proposed the following species that have associations with soil and plant host: *Para. debruynii*, *Para. tasmanniae*, and *Para. wereldwijsianum*. Additionally, Gonçalves *et al.* (2020) introduced three species of *Parasarocladium* found on macroalgae: *Para. aestuarinum*, *Para. alavariense*, and *Para. fusiforme*. In recent years, more species have been published, including *Para. chondroidum*, *Para. dipikae*,

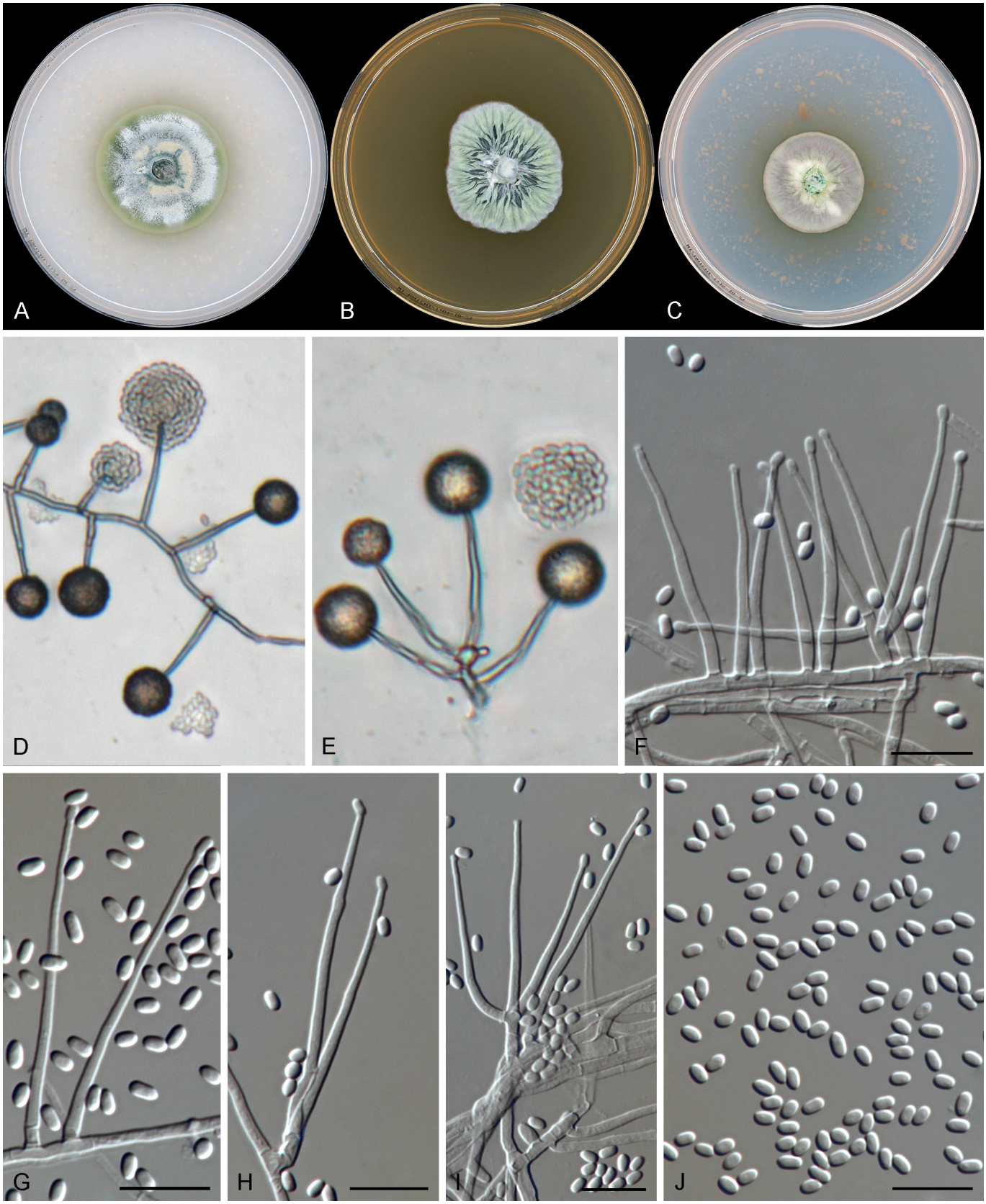

Fig. 14. *Chlamydocillium viridicolor* (ex-type CBS 113439). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J.** Conidia. Scale bars = 10 µm.

Para. funiculosum, *Para. mabikii*, *Para. multimorphologicum*, and *Para. sinense* (Hou *et al.* 2023, Tan & Steinrucken 2024b, Zhang *et al.* 2024b, Lee *et al.* 2025). To date, there are 13 known species of *Parasarocladium* with available DNA data.

Parasarocladium kislosladkoense Lin Zhao, O.A. Grum-Grzhim. & Crous, ***sp. nov.*** MycoBank MB 858433. Fig. 15.

Etymology: Referring to the location, the Kislo-Sladkoe Lake, from which the majority of the isolates in this species were collected.

Typus: **Russia**, Murmansk region, Kislo-Sladkoe Lake detaching from the White Sea, from oozy littoral, semi-fresh lake, 0.1 m a.s.l., 2010, *O.A. Grum-Grzhimaylo* (**holotype** designated here CBS H-25590, ex-type living isolate CBS 143528).

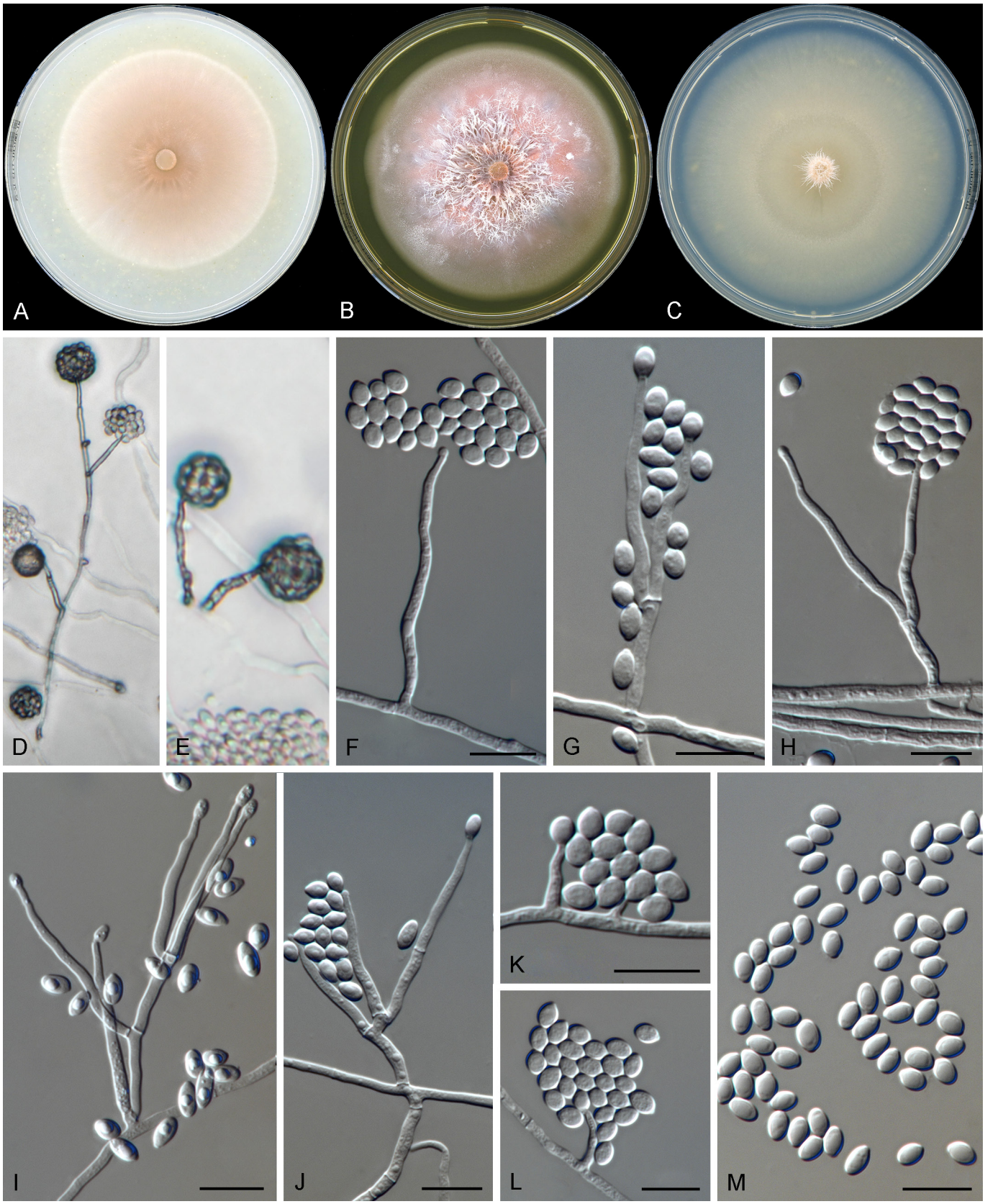

Fig. 15. *Parasarocladium kislosladkoense* (ex-type CBS 143528). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K, L.** Adelophialides. **M.** Conidia. Scale bars = 10 µm.

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.2–3.3 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or basitonously branched, bearing up to 1–3 levels with 1–4 phialides per node, up to ca 126 µm long, 1.2–2.8 µm wide at base, (0–)1–5-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, subcylindrical or subulate, straight or slightly curved, hyaline, with smooth, thin or thick walls, (14.2–)18.3–32.4(–36.5) µm long, (1.2–)1.4–2.2(–2.4) µm wide at base, 0.8–1.2 µm wide near aperture, with minute collarettes and periclinal thickening at conidiogenous loci; adelophialides subulate or acicular, 2.5–17.0 × 1.0–2.2 µm. *Conidia* ellipsoid, commonly with a round apex and a median truncate hilum at base, aseptate, hyaline, smooth- and thick-walled, (2.8–)3.5–5.1(–5.3) × 2.3–3.1(–3.2) µm (av. 4.3 × 2.7 µm, n = 100), guttulate, arranged in dry heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 63–64 mm diam. after 14 d in darkness at 25 °C, flat, dusty, with sparse aerial mycelium, saffron to dirty white, margin entire, reverse rosy buff to buff. On MEA reaching 75–78 mm diam., flat, felty, hairy, with abundant aerial mycelium, peach with white mycelium at centre, buff at periphery, margin entire, reverse apricot, with short radial lines. On PDA reaching 77–78 mm diam., flat, felty, dusty, with sparse aerial mycelium, buff, margin entire, reverse rosy buff. On SNA reaching 40–44 mm diam., flat, felty, with sparse aerial mycelium, white, margin irregularly, reverse concolourous.

Additional materials examined: **Netherlands**, Gelderland Province, Ermelo, from soil, 2017, *M.& M. Elmers*, isol. 2018, *L. Lombart & A. Giraldo Lopez*, isolate CBS 144937. **Russia**, Murmansk region, Kislo-Sladkoe Lake detaching from the White Sea, from oozy littoral, semi-fresh lake, 0.1 m a.s.l., 2010, *O.A. Grum-Grzhimaylo*, isolates CBS 143519, CBS 143522 and CBS 143529; Murmansk region, Kislo-Sladkoe Lake detaching from the White Sea, from oozy littoral, semi-fresh lake, surface, 2010, *O.A. Grum-Grzhimaylo*, isolates CBS 143523, CBS 143524 and CBS 143525.

Notes: Seven isolates from oozy littoral sediments in Russia were described as "*Acremonium* sp." by Grum-Grzhimaylo *et al.* (2018). In addition, one isolate isolated from soil in the Netherlands was included in our study. All eight isolates were examined and identified as representing a novel species within the genus *Parasarocladium*. In our phylogenetic tree, *Para. kislosladkoense* is most closely related to *Para. wereldwijsianum* (RAxML-BS = 89 %, IQ-TREE-BS = 97 %; Fig. 3, clade III-3), but it shows clear differences in *RPB2* (96.8 %, 24 bp) and *TEF1* (98.8 %, 9 bp) sequences, with ITS (99.6 % identity, with 2 bp differences) and LSU (100 %, 0 bp) being highly similar. Morphologically, *Para. kislosladkoense* can be distinguished from *Para. wereldwijsianum* by producing shorter conidia that are (2.8–)3.5–5.1(–5.3) µm in *Para. kislosladkoense*, and 4–10 µm in *Para. wereldwijsianum* (Crous *et al.* 2021).

Clade III-4. *Sarocladium* W. Gams & D. Hawksw., *Kavaka* **3**: 57. 1976 (1975).

Mycelium septate, hyaline, becoming pale brown with age, with smooth and thin walls. *Conidiogenous apparatus* ranging from adelophialides, solitary, orthotropic phialides to conidiophore structures with one or a few branches, or with cymose branching or occasionally with one or two ranks of loosely structured verticils. *Conidiogenous cells* enteroblastic, mono- or polyphialidic, lateral, terminal or intercalary, subcylindrical, subulate, acicular, aculeate to acerose, straight or slightly curved, or undulate, hyaline, with thin or thick, smooth walls, with distinct or inconspicuous collarettes and periclinal thickening, proliferating percurrently in some species. *Conidia* cylindrical to fusoid to bacilliform, oblong, ellipsoidal, ovoid, spindle-shaped, limoniform to subglobose or irregular, with rounded or tapered-truncate ends, aseptate, hyaline or subhyaline, thin- and smooth-walled, borne in mucoid heads or dry chains. *Chlamydospores* present or absent (adapted from Summerbell *et al.* 2011, Giraldo *et al.* 2015, Hou *et al.* 2023).

Type: *Sarocladium oryzae* (Sawada) W. Gams & D. Hawksw.

Notes: The genus *Sarocladium* was initially described by Gams & Hawksworth (1976), accommodating the type species *S. oryzae* and another species, *S. attenuatum*, both of which are fungal pathogens associated with sheath blast of rice. Later, the circumscription of *Sarocladium* has been revised and redefined through several studies (Summerbell *et al.* 2011, Yeh & Kirschner 2014, Giraldo *et al.* 2015, Liu *et al.* 2017, Hou *et al.* 2023, Crous *et al.* 2024b). In this study, we propose six new species below.

Sarocladium alniphilum Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858434. Fig. 16.

Etymology: Referring to the host, *Alnus rubra*, from which the holotype isolate was collected.

Typus: **Canada**, British Columbia, Queen Charlotte Islands, Graham Island, Naikoon Provincial Park, trail from Hiellen River to Tow Hill, 54°2'25.7"N, 131°55'9.2"W, 0–10 m a.s.l., from lenticels in bark of *Alnus rubra*, 19 Oct. 1998, *K.A. Seifert*, specimen DAOM 867476 (**holotype** designated here CBS H-25579, ex-type living isolate CBS 113444 = CCFC 226667 = KAS 679).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.2–2.4 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or poor branched, bearing up to 1–2 levels with 1–3 phialides per node, up to ca 107 µm long, 1.7–3.6 µm wide at base, 1–4-septate, occasionally with a percurrent proliferation, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, terminal or lateral, subcylindrical or subulate, straight, hyaline, thick- and smooth-walled, (25.3–)27.3–50.8(–57.3) µm long, (1.4–)1.8–2.6(–2.9) µm wide at base, 0.9–1.1(–1.2) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci; polyphialides and adelophialides not observed. *Conidia* cylindrical, straight or slightly curved, with rounded apices and slightly truncate bases, aseptate, hyaline, with thin and smooth walls, (2.8–)3.2–6.3(–7.0) × (1.6–)1.7–2.5(–2.8) µm (av. 4.5 × 2.0 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 51–53 mm diam. after 14 d in darkness at 25 °C, flat, felty, with sparse aerial mycelium, dirty white at centre, white at periphery, margin entire, reverse dirty white. On MEA reaching 47–50 mm diam., flat, hairy, with abundant aerial mycelium, rosy buff to dirty white, margin entire,

reverse saffron. On PDA reaching 46–48 mm diam., flat, hairy at centre, thinly felty at periphery, with moderate aerial mycelium, white to dirty white, margin entire, reverse dirty white. On SNA reaching 48–52 mm diam., flat, membranous, with sparse aerial mycelium at centre, white, margin undulate, reverse concolourous.

Notes: Based on our phylogenetic analyses (Fig. 3, clade III-4), *S. alniphilum* has a close phylogenetic affinity to *S. caricicola*, *S. catenulatum*, *S. limosialveum*, and *S. nubiaquae*. Morphologically, *S. alniphilum* differs from *S. caricicola*, *S. catenulatum* and *S. nubiaquae* in producing longer conidiophores, which are up to 107

Fig. 16. *Sarocladium alniphilum* (ex-type CBS 113444). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K.** Conidia. Scale bars = 10 µm.

µm long in *S. alniphilum* vs up to 50 µm long in *S. caricicola*, up to 38 µm long in *S. catenulatum*, and up to 85 µm long in *S. nubiaquae*, and longer phialides, which are (25.3–)27.3–50.8(–57.3) µm long in *S. alniphilum*, vs 15–40 µm long in *S. caricicola*, (9.4–)12.6–24.7(–27.7) µm long in *S. catenulatum*, and (8.6–)13.2–37.9(–44.2) µm long in *S. nubiaquae* (Crous *et al.* 2024b). Furthermore, *S. alniphilum* (CBS 113444) and *S. limosialveum* (CBS 143532) are clearly different based on ITS (95.6 % identity, with 23 bp differences), LSU (98.9 %, 9 bp), *RPB2* (93.4 %, 50 bp), and *TEF1* (96.2 %, 30 bp) sequences.

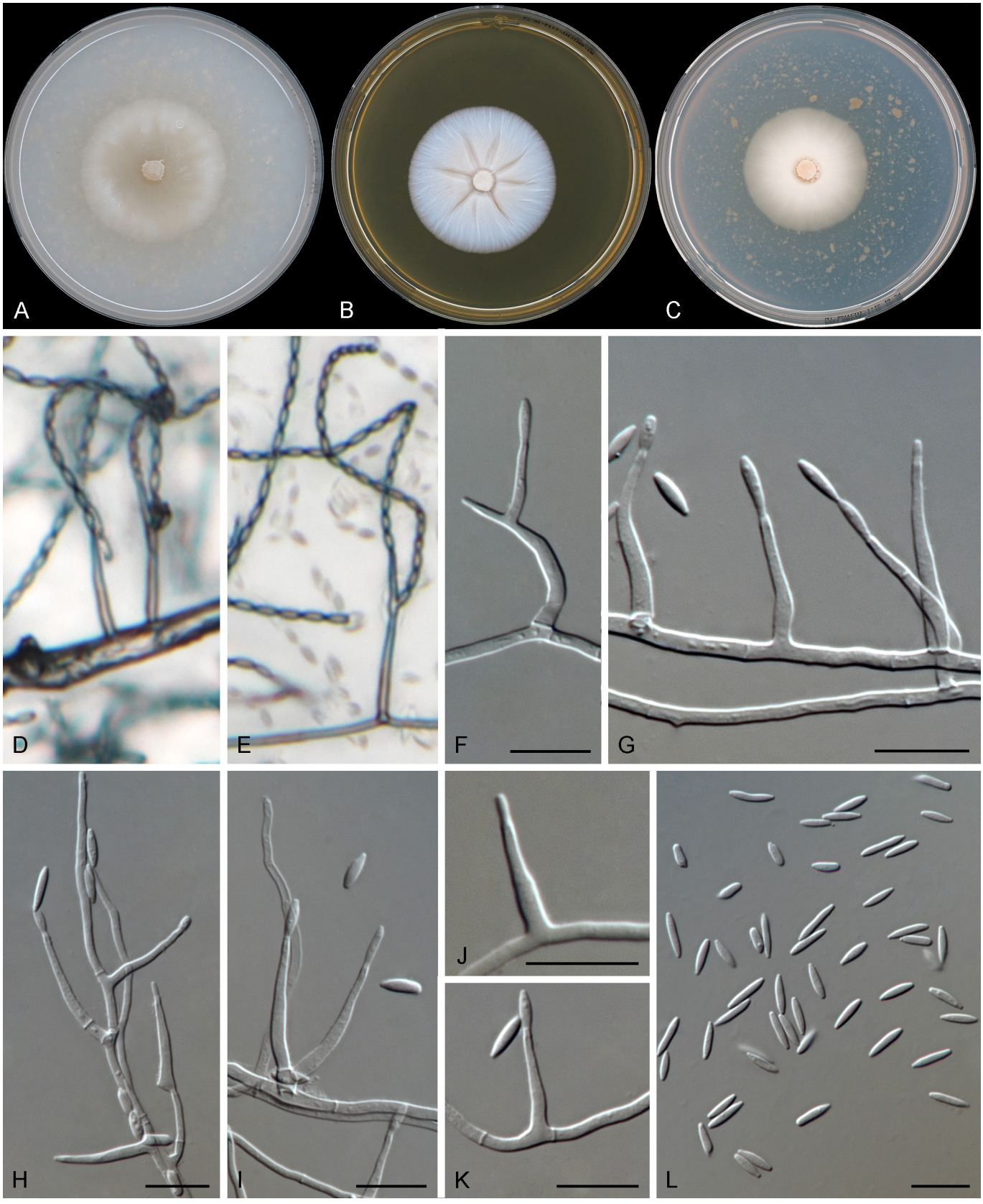

Fig. 17. *Sarocladium catenulatum* (ex-type CBS 125892). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J, K.** Adelophialides. **L.** Conidia. Scale bars = 10 µm.

Sarocladium catenulatum Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858435. Fig. 17.

Etymology: Derived from the Latin word "*catena*," meaning chain, referring to the production of conidia arranged in chains.

Typus: **USA**, Wyoming, Rock Springs (DOE site; 11km west of Rock Springs), from soil, A1 horizon soil from bunchgrass rhizosphere, 1978, unknown *collector* (**holotype** designated here CBS H-25586, ex-type living isolate CBS 125892).

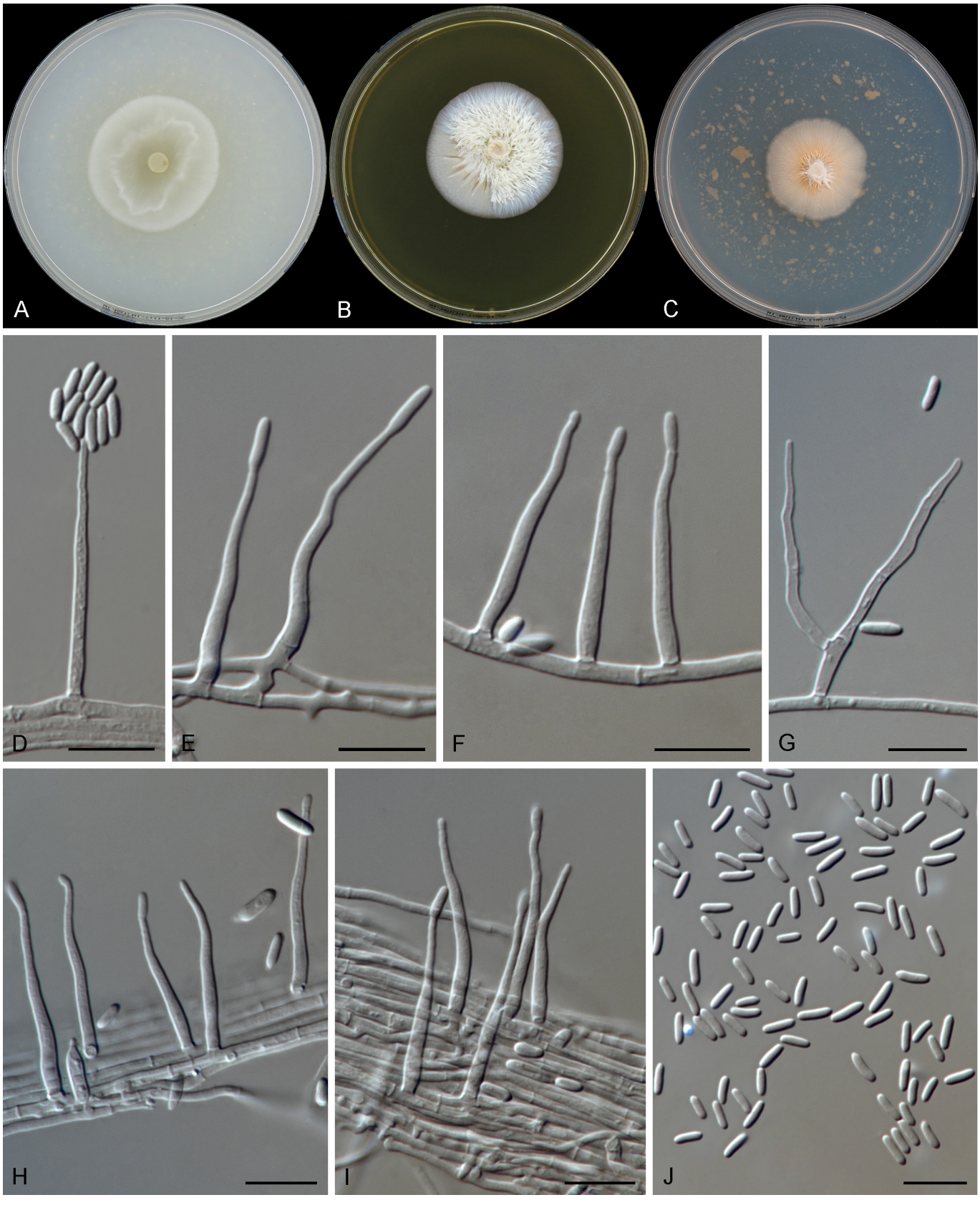

Fig. 18. *Sarocladium hirsutum* (ex-type CBS 376.70K). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J.** Conidia. Scale bars = 10 µm.

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.3 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or sparsely branched, up to ca 38 µm long, 1.5–3.1 µm wide at base, aseptate or 1–4-septate, commonly with percurrent proliferation, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, subulate, straight or slightly curved, hyaline, smooth- and thick-walled, (9.4–)12.6–24.7(–27.7) µm long, (1.5–)1.7–2.3(–2.6) µm wide at base, (0.7–)0.8–1.0 µm wide near aperture, with inconspicuous collarette periclinal thickening at conidiogenous locus; adelophialides present, subulate, or acicular, 3.1–17.2 × 1.1–3.0 µm. *Conidia* long fusoid, or clavate, with apiculate ends at both ends, or with rounded apices and apiculate bases, aseptate, hyaline, thin- and smooth-walled, (3.8–)4.0–7.0(–8.3) × (1.1–)1.3–2.0(–2.3) µm (av. 5.6 × 1.6 µm, n = 100), eguttulate, arranged in chains. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 40–42 mm diam. after 14 d in darkness at 25 °C, flat, finely felty, with sparse aerial mycelium, buff at centre, dirty white at periphery, margin lobate, reverse buff. On MEA reaching 41 mm diam., flat, radially folded, felty, with moderate aerial mycelium, rosy buff, margin entire, reverse luteous. On PDA reaching 34–35 mm diam., flat, felty, with moderate aerial mycelium, dirty white at centre, buff at periphery, margin entire, pale luteous to buff. On SNA reaching 32–33 mm diam., flat, membranous without aerial mycelium, white, margin entire, reverse concolourous.

Notes: Phylogenetically (Fig. 3, clade III-4), *S. catenulatum* is most closely related to *S. limosialveum*, but with clearly different ITS (98.7 % identity, with 7 bp differences), LSU (99.9 %, 1 bp), *RPB2* (93.8 %, 47 bp), and *TEF1* (97.8 %, 18 bp) sequences. Morphologically, *S. catenulatum* differs from *S. limosialveum* in its shorter phialides, which are (9.4–)12.6–24.7(–27.7) µm in *S. catenulatum*, vs (29.5–)30.8–48.6(–54.4) µm in *S. limosialveum*, and larger conidia, which are (3.8–)4.0–7.0(–8.3) × (1.1–)1.3–2.0(–2.3) µm (av. 5.6 × 1.6 µm) in *S. catenulatum*, vs (2.9–)3.2–6.5(–7.4) × 1.2–1.7(–1.8) µm (av. 4.5 × 1.4 µm) in *S. limosialveum*. Additionally, the conidia in *S. catenulatum* are arranged in chains, while those in *S. limosialveum* are arranged in slimy heads.

Sarocladium hirsutum Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858436. Fig. 18.

Etymology: Referring to the "hairy" colonies on MEA.

Typus: **Zaire**, now the Democratic Republic of the Congo, Lovanium, from leaf of *Digitaria polybotrya*, unknown collection date and *collector*, isol. *G.L. Hennebert* (**holotype** designated here CBS H-25600, ex-type living isolate CBS 376.70K).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.0 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched, or sparsely unbranched, up to ca 45 µm long, 1.6–2.6 µm wide at base, 1–3-septate, occasionally with a sympodial proliferation, 1–2-septate at base, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, terminal or lateral, subulate or subcylindrical, straight or slightly curved, hyaline, with thick and smooth walls, (18.6–)19.5–32.8(–37.2) µm long, (1.5–)1.7–2.2(–2.7) µm wide at base, (0.7–)0.8–1.0(–1.1) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci; polyphialides and adelophialides not observed. *Conidia* cylindrical, with both ends rounded, aseptate, hyaline, with thin and smooth walls, (3.7–)4.2–6.5(–7.1) × (1.2–)1.3–1.7 µm (av. 5.3 × 1.5 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 36–39 mm diam. after 14 d in darkness at 25 °C, flat, felty, dusty, with sparse aerial mycelium, buff at centre, white at periphery, with irregular ring, margin undulate, reverse concolourous. On MEA reaching 39–42 mm diam., raised, radially folded, with abundant aerial mycelium, hairy and creamy white at centre, felty, white at periphery, margin entire, reverse luteous. On PDA reaching 30 mm diam., membranous and radially folded at centre, flat and felty at periphery, with moderate aerial mycelium, salmon at centre, rosy buff at periphery, margin filiform, reverse rosy buff. On SNA reaching 31–32 mm diam., flat, membranous with sparse aerial mycelium, white, margin undulate, reverse concolourous.

Notes: The ex-type isolate CBS 376.70K was isolated from the leaf of *Digitaria polybotrya* in Zaire, now the Democratic Republic of the Congo, and was originally labelled as "*Acremonium strictum*" by Gams (1971). According to our phylogenetic analyses, it forms a separate lineage in the genus *Sarocladium*, closely related to *S. pseudostrictum* (Fig. 3). Morphologically, *S. hirsutum* differs from *S. pseudostrictum* by producing shorter phialides that measure (18.6–)19.5–32.8(–37.2) µm long in *S. hirsutum* vs 20–47 µm long in *S. pseudostrictum*, and longer conidia measuring (3.7–)4.2–6.5(–7.1) µm long in *S. hirsutum* vs 3–5 µm long in *S. pseudostrictum* (Giraldo *et al.* 2015).

Sarocladium humicola Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858437. Fig. 19.

Etymology: Referring to soil, the substrate from which the holotype isolate was collected.

Typus: **Zaire**, now Democratic Republic of the Congo, Yangambi, from soil, unknown collection date and *collector*, isol. *J.A. Meyer* (**holotype** designated here CBS H-25603, ex-type living isolate CBS 446.54).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.1–2.2 µm wide. *Sporulation* abundant, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or branched, bearing up to 1–3 levels with 1–4 phialides per node, up to ca 136 µm long, 1.8–3.4 µm wide at base, 1–4(–6)-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, terminal or lateral, (sub) cylindrical, or subulate, straight or slightly curved, hyaline, smooth- and thin-walled, (3.9–)21.9–39.2(–44.2) µm long, 1.0–1.8(–2.0) µm wide at base, 0.7–1.0(–1.1) µm wide near aperture, occasionally with percurrent proliferation, with inconspicuous collarettes and periclinal thickening at conidiogenous loci; polyphialides and adelophialides not observed. *Conidia* cylindrical or slightly clavate, with rounded ends and truncate bases, aseptate, hyaline, smooth- and thin-walled, (2.8–)3.4–6.3(–7.6) × (1.3–)1.4–1.8(–2.0) µm (av. 4.5 × 1.6

µm, n = 100), guttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 77–80 mm diam. after 14 d in darkness at 25 °C, flat, felty, granulose, with abundant aerial mycelium, dirty white to buff, margin entire, reverse honey. On MEA reaching 85 mm diam., flat, cotton, abundant aerial mycelium, white, margin entire, reverse orange to pale luteous with radial lines. On PDA reaching 85 mm diam., flat, cotton to felty, with abundant aerial mycelium, white to buff, margin fimbriate, reverse apricot at centre, buff at periphery. On SNA reaching 85 mm diam., flat, felty, with sparse aerial mycelium, dusty, white, margin entire, reverse concolourous.

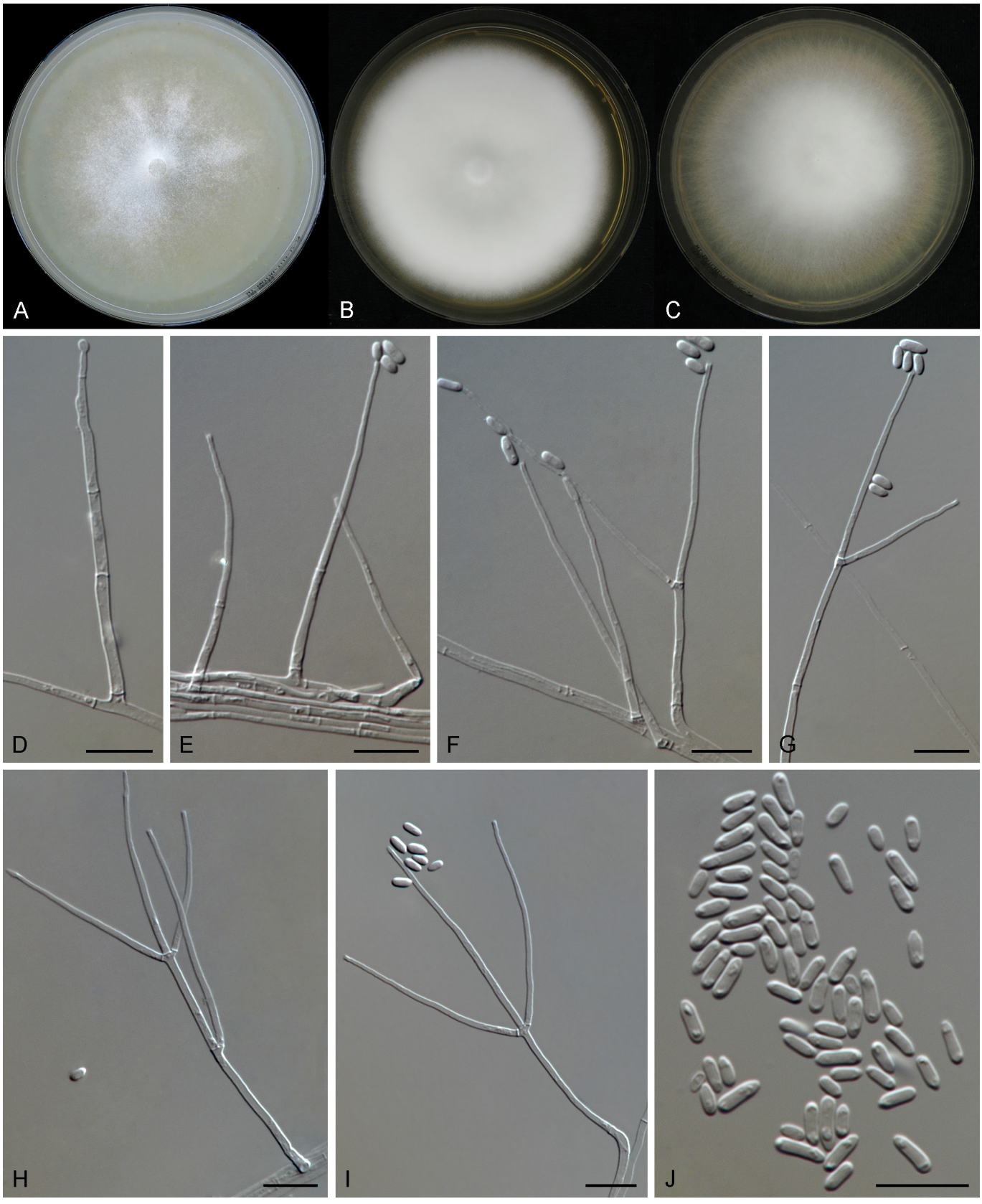

Fig. 19. *Sarocladium humicola* (ex-type CBS 446.54). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J.** Conidia. Scale bars = 10 µm.

Notes: Based on our phylogenetic analyses, *S. humicola* has a close phylogenetic affinity to *S. kiliense*, but *S. humicola* (CBS 446.54) differs from *S. kiliense* (CBS 122.29) in ITS (96.7 % identity, with 17 bp differences), LSU (99.4 %, 5 bp), *RPB2* (91.1 %, 59 bp), and *TEF1* (96.2 %, 30 bp) sequences. Furthermore, *S. humicola* can be distinguished from *S. kiliense* by its shorter phialides, which are (3.9–)21.9–39.2(–44.2) µm long in *S. humicola*, vs 25–45(–70) µm long in *S. kiliense* (Gams 1971). Additionally, chlamydospores are observed in *S. kiliense* but are absent in *S. humicola* (Gams 1971).

Sarocladium limosialveum Lin Zhao, O.A. Grum-Grzhim. & Crous, ***sp. nov.*** MycoBank MB 858438. Fig. 20.

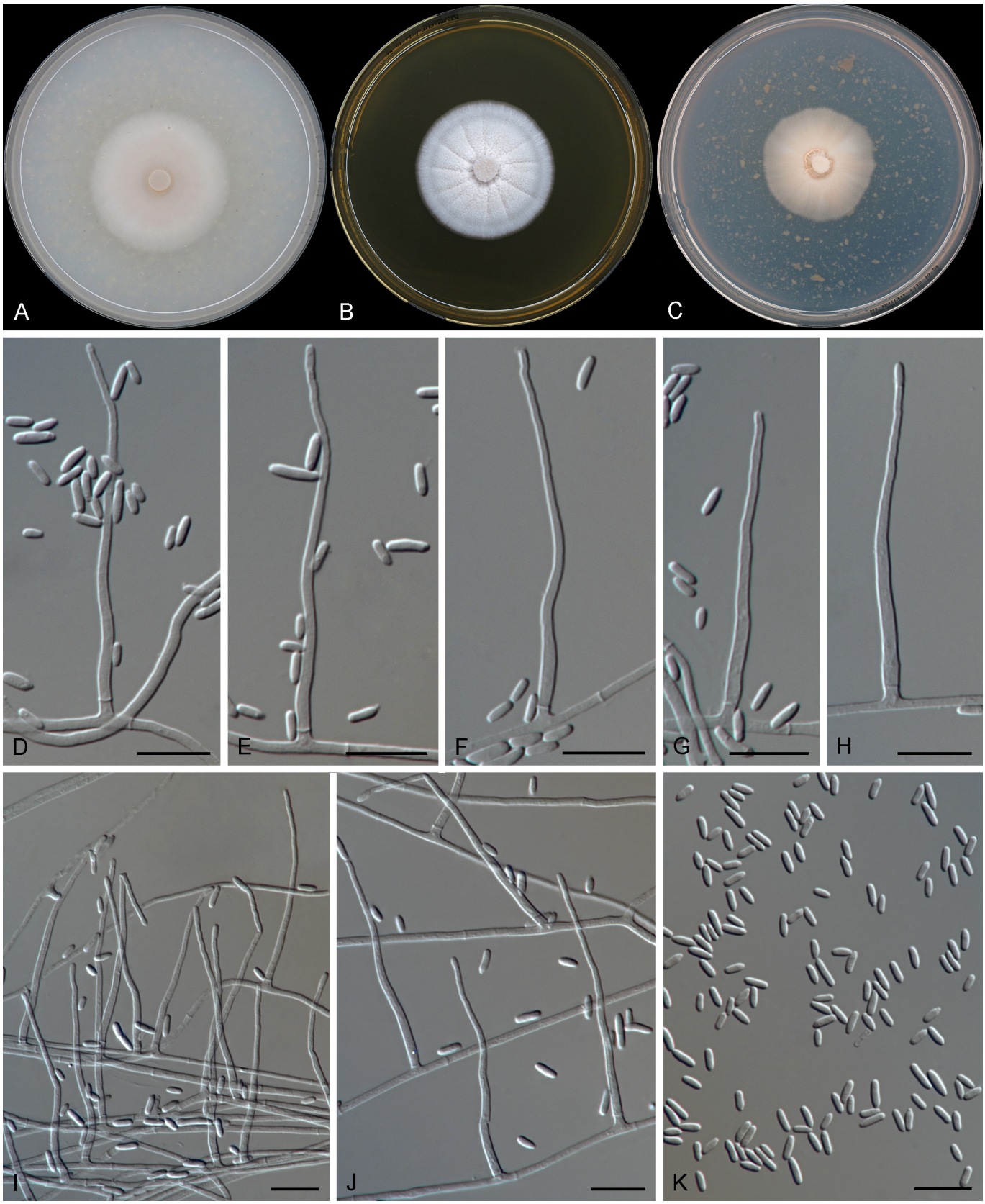

Fig. 20. *Sarocladium limosialveum* (ex-type CBS 143532). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K.** Conidia. Scale bars = 10 µm.

Etymology: Referring to the substrate, oozy lake bottom, from which the holotype isolate was collected.

Typus: **Russia**, Murmansk region, Ershovskoye Lake detaching from the White Sea, from oozy bottom, semi-fresh lake, 1.6 m below the surface, 2010, *O.A. Grum-Grzhimaylo* (**holotype** designated here CBS H-25591, ex-type living isolate CBS 143532).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.1–1.7 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched, up to ca 66 µm long, 1.4–2.4 µm wide at base, 1–2(–3)-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, subcylindrical or subulate, straight or slightly curved, hyaline, thick- and smooth-walled, (29.5–)30.8–48.6(–54.4) µm long, (1.4–)1.5–2.0 µm wide at base, 0.8–1.0 µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci; polyphialides and adelophialides not observed. *Conidia* cylindrical, straight or slightly curved, with both ends rounded, or with truncate bases, aseptate, hyaline, thin- and smooth-walled, (2.9–)3.2–6.5(–7.4) × 1.2–1.7(–1.8) µm (av. 4.5 × 1.4 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 40–41 mm diam. after 14 d in darkness at 25 °C, flat, membranous, with sparse aerial mycelium, rosy buff at centre, buff at periphery, margin entire, reverse concolourous. On MEA reaching 39–40 mm diam., woolly, with abundant aerial mycelium, raised at centre, radially folded toward periphery, creamy white, margin flat and entire, reverse saffron, with buff radial lines. On PDA reaching 28–33 mm diam., flat, felty, with moderate aerial mycelium, rosy buff, margin dentate, reverse buff. On SNA reaching 31–33 mm diam., flat, felty, with sparse aerial mycelium, white, margin filiform, reverse concolourous.

Notes: The ex-type isolate CBS 143532 was previously identified as "*Acremonium* sp." by Grum-Grzhimaylo *et al.* (2016). However, based on our phylogenetic analysis, it falls within the *Sarocladium* clade. Phylogenetically, *S. limosialveum* is most closely related to *S. catenulatum*. For morphological and phylogenetic comparison see notes under *S. catenulatum*.

Sarocladium nubiaquae Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858439. Fig. 21.

Etymology: Referring to the substrate, cloud water, from which the holotype isolate was collected.

Typus: **China**, from cloud water, unknown collection date, coll. and isol. *M. Sancelme*, Univ. Blaise Pascal, Aubierre Cedex, France (**holotype** designated here CBS H-25583, ex-type living isolate CBS 117135).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.5 µm wide. *Sporulation* moderate, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes and coils formed by mycelium, solitary, (sub-)erect, unbranched or sparsely branched, occasionally with sympodial proliferation, up to ca 85 µm long, 1.4–2.6 µm wide at base, aseptate or 1–4-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, terminal or lateral, subcylindrical or subulate, straight or slightly curved, hyaline, smooth-and thick-walled, (8.6–)13.2–37.9(–44.2) µm long, (1.2–)1.6–2.0(–2.3) µm wide at base, 0.7–1.1 µm wide near aperture, with inconspicuous or conspicuous collarettes and periclinal thickening at conidiogenous loci; polyphialides with two conidiogenous loci occasionally present; adelophialides present, subulate or acicular, 3.5–15.0 × 1.3–3.0 µm. *Conidia* bacilliform or cylindrical, straight or curved, with both ends rounded, or with slightly truncate bases, aseptate, hyaline, smooth- and thin-walled, (3.0–)3.6–6.7(–8.2) × (1.1–)1.2–1.7(–2.0) µm (av. 4.9 × 1.4 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 39–40 mm diam. after 14 d in darkness at 25 °C, flat, with membranous with sparse aerial mycelium, dirty white to buff, margin entire, reverse concolourous. On MEA reaching 35–37 mm diam., flat, radially folded, felty, with moderate aerial mycelium, rosy buff at centre, white at periphery, margin entire, reverse saffron with white radial lines. On PDA reaching 30–32 mm diam., flat, rugose at centre, felty at periphery, with moderate aerial mycelium, dirty white, margin entire, reverse concolourous. On SNA reaching 22–29 mm diam., flat, felty, with sparse aerial mycelium, white, margin rhizoids, reverse concolourous.

Notes: According to the phylogenetic analyses, *S. nubiaquae* is closely related to *S. alniphilum*, *S. caricicola*, *S. catenulatum*, and *S. limosialveum* (Fig. 3, clade III-4). Morphologically, *S. nubiaquae* differs from *S. alniphilum* and *S. limosialveum* by producing shorter phialides, which are (8.6–)13.2–37.9(–44.2) µm long in *S. nubiaquae*, vs (25.3–)27.3–50.8(–57.3) µm long in *S. alniphilum*, and (29.5–)30.8–48.6(–54.4) µm long in *S. limosialveum*; it differs from *S. caricicola* and *S. catenulatum* by its longer conidiophores, which are up to 85 µm long in *S. nubiaquae*, vs up to 50 µm long in *S. caricicola*, and up to 38 µm long in *S. catenulatum*, and slightly smaller conidia, which are (3.0–)3.6–6.7(–8.2) × (1.1–)1.2–1.7(–2.0) µm (av. 4.9 × 1.4 µm) in *S. nubiaquae*, vs (4–)5–7 × (1.5–)2 µm in *S. caricicola*, and (3.8–)4.0–7.0(–8.3) × (1.1–)1.3–2.0(–2.3) µm (av. 5.6 × 1.6 µm) in *S. catenulatum* (Crous *et al.* 2024b).

Clade VIII. *Neochrysonectriaceae* Lin Zhao & Crous, ***fam. nov.*** MycoBank MB 858440.

Etymology: Referring to the type genus *Neochrysonectria*.

Classification: *Hypocreales*, *Sordariomycetes.*

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae. *Conidiophores* solitary or aggregated, (sub-) erect, unbranched or basitonously branched, septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, terminal or lateral, cylindrical or subulate, straight or slightly curved, hyaline, thick- and smooth-walled. *Conidia* clavate, obovoid or pyriform, with rounded apices and apiculate bases, aseptate, hyaline, with thin- and smooth-walled, eguttulate, arranged in chains. *Chlamydospores* and *sexual morph* not observed.

Type genus: *Neochrysonectria* Lin Zhao & Crous

Notes: The family *Neochrysonectriaceae*, represented by only one culture, CBS 820.70, was previously identified as "*Acremonium*

alternatum" by Gams (1971). However, according to our phylogenetic analyses, this isolate formed an independent lineage and is distinct from all known families within *Hypocreales* (Fig. 1).

Neochrysonectria Lin Zhao & Crous, ***gen. nov.*** MycoBank MB 858441.

Etymology: Referring to its phylogenetically similarity with *Chrysonectria.*

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae. *Sporulation* moderate, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from

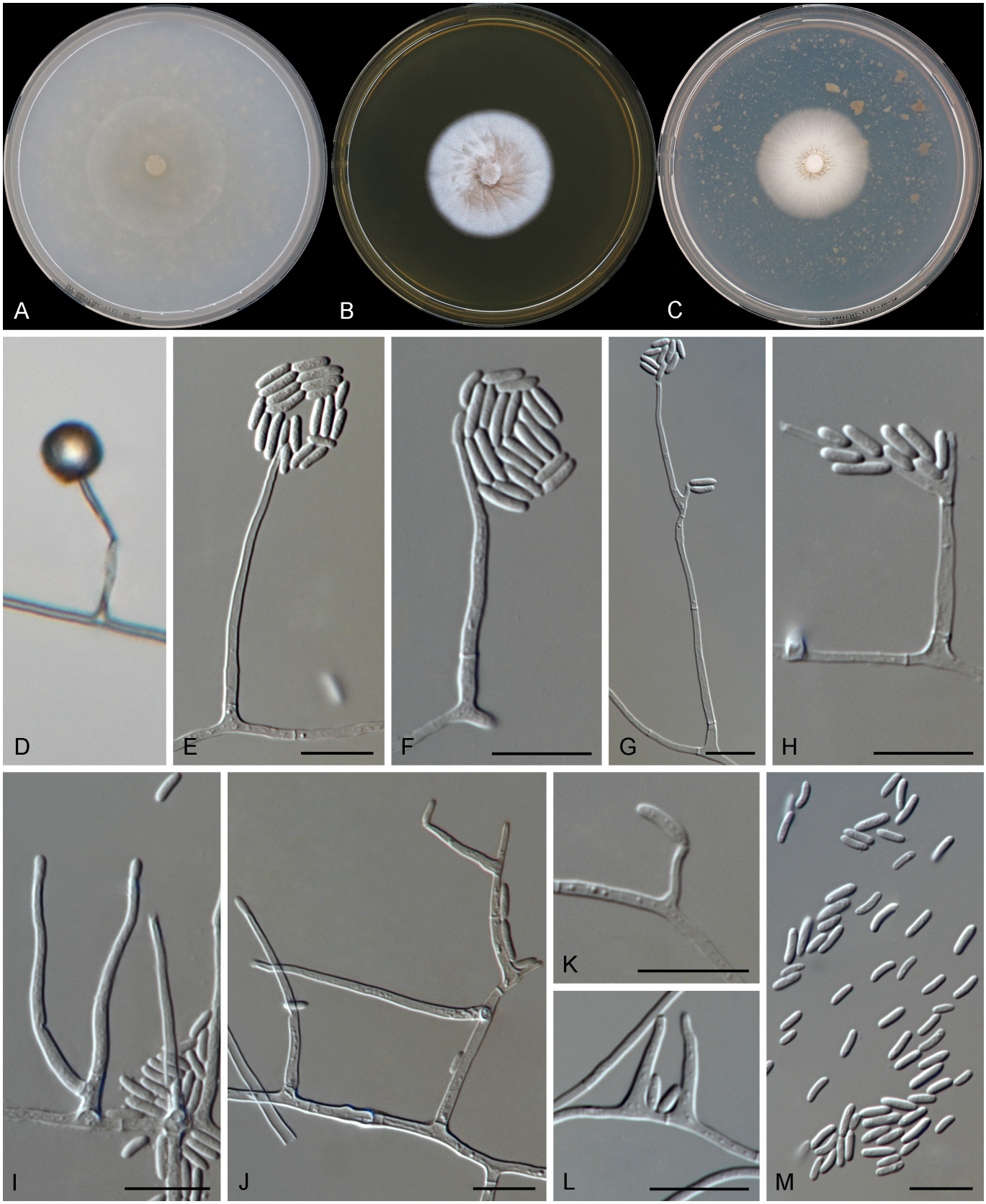

Fig. 21. *Sarocladium nubiaquae* (ex-type CBS 117135). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K, L.** Adelophialides. **M.** Conidia. Scale bars = 10 µm.

the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or basitonously branched, bearing 1–3 phialides per node, septate, hyaline, smooth-walled. *Conidiogenous cells* enteroblastic, monophialidic, terminal or lateral, cylindrical or subulate, straight or slightly curved, hyaline, smooth-walled, with inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* clavate, obovoid, or pyriform, with rounded apices and apiculate bases, aseptate, hyaline, with thin and smooth walls, eguttulate, arranged in chains. *Chlamydospores* and *sexual morph* not observed.

Type: *Neochrysonectria humicola* Lin Zhao & Crous

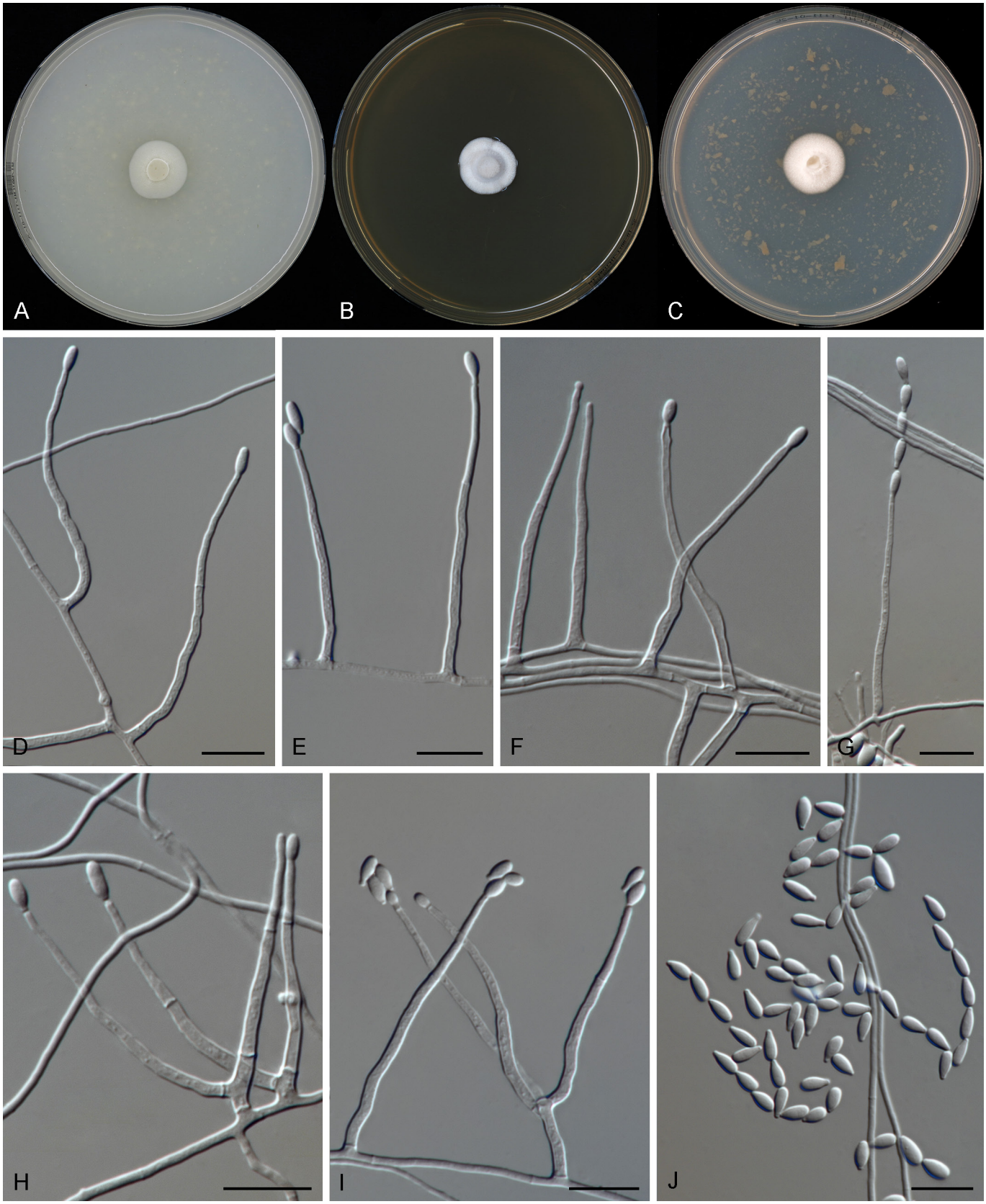

Fig. 22. *Neochrysonectria humicola* (ex-type CBS 820.70). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J.** Conidia. Scale bars = 10 µm.

Notes: The monotypic genus *Neochrysonectria* is proposed here to accommodate its sole species, *N. humicola*, which is also the type species. In our study, *N. humicola* is closely related to species in *Chrysonectriaceae* (Fig. 1, clade IX). Morphologically, *Neochrysonectria* differs from *Chrysonectria* in the shape of its conidia, which in *Neochrysonectria* are clavate, obovoid, or pyriform with conspicuous apiculate bases and arranged in chains, whereas in *Chrysonectria* the conidia are subglobose or broadly ellipsoidal, and they are arranged in slimy heads. Additionally, polyphialides and crystals are absent in *Neochrysonectria* but present in *Chrysonectria.*

Neochrysonectria humicola Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858442. Fig. 22.

Etymology: Referring to soil, from which this fungus was isolated.

Typus: **Netherlands**, Gelderland Province, Wageningen, from field soil, unknown collection date and *collector*, isol. *J.W. Veenbaas-Rijks* (**holotype** designated here CBS H-25612, ex-type living isolate CBS 820.70)

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 0.9–1.6 µm wide. *Sporulation* moderate, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or basitonously branched, bearing 1–3 phialides per node, up to ca 60 µm long, 1.5–2.7 µm wide at base, each with 1–3-septae, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, cylindrical, or subulate, straight or slightly curved, hyaline, thick- and smooth-walled, (7.0–)11.8–39.7(–45.2) µm long, (1.2–)1.4–2.0 µm wide at base, 0.7–1.0(–1.1) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* clavate, obovoid, or pyriform, with rounded apices and distinctly apiculate bases, aseptate, hyaline, with thin- and smooth-walled, (3.3–)4.1–5.7(–7.4) × (1.7–)1.8–2.5(–2.9) µm (av. 4.9 × 2.2 µm, n = 100), eguttulate, arranged in chains. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 15–17 mm diam. after 14 d at room temperature, flat, felty, dusty, with moderate aerial mycelium, white, margin entire, reverse buff. On MEA reaching 17 mm diam., raised, felty, with abundant aerial mycelium, white, margin lobate, reverse saffron. On PDA reaching 18 mm diam., flat, felty, with abundant aerial mycelium, white, margin entire, reverse concolourous. On SNA reaching 11 mm diam., flat, felty, with moderate aerial mycelium, white, margin dentate, reverse concolourous.

Notes: The multi-locus phylogenetic analyses show that isolate CBS 820.70 represents a new family, introduced here as *Neochrysonectriaceae*.

Based on a BLASTn search of NCBI GenBank nucleotide database, the closest hits of CBS 820.70 with the ITS sequence is listed as *Hypocreales* sp., isolated from macroalgae *Palmaria palmata* in France [mms1845; GenBank OR584250; Identity = 480/514 (93 %), seven gaps (1 %)]; the closest hit using the LSU sequence is *Myrtacremonium eucalypti*, isolated from *Eucalyptus globulus* in Australia [CBS 142161; GenBank OQ055621; Identity = 754/777 (97 %), two gaps (0 %)]; the closest hit using the *RPB2* sequence is *Tolypocladium reniformisporum*, isolated from *Ophiocordyceps sinensis* in China [YFCC 1805002; GenBank MK984574; Identity = 617/760 (81 %), eight gaps (1 %)]; the closest hit using the *TEF1* sequence is *Thyridium curvatum*, isolated from diesel fuel in USA [D216; GenBank XM_031139949; Identity = 732/798 (92 %), eight gaps (1 %)].

Clade XXIII. *Stachybotryaceae* L. Lombard & Crous, *Persoonia* **32**: 283. 2014.

Classification: *Hypocreales*, *Sordariomycetes*.

Type genus: *Stachybotrys* Corda

Sporodochius Lin Zhao & Crous, ***gen. nov.*** MycoBank MB 858443.

Etymology: Named after the sporodochia produced by the type species.

Mycelium consisting of branched, septate, hyaline, smooth or slightly warted, thin- or thick-walled hyphae. *Conidiophores* solitary or forming pale orange to luteous sporodochial conidiomata. *Solitary conidiophores* (sub-)erect, unbranched or sparsely branched, occasionally with a percurrent proliferation, hyaline, smooth-walled. *Conidiogenous cells* enteroblastic monophialidic, lateral or terminal, subcylindrical to cylindrical, straight or slightly curved, hyaline, thick- and smooth-walled, with minute collarettes and conspicuous periclinal thickening at conidiogenous loci. *Sporodochial conidiophores* mostly branched, bearing multiple levels, smooth-walled. *Sporodochial phialides* mostly lateral, subulate, tapering at top, smooth-walled, with minute collarettes and periclinal thickening at conidiogenous loci. *Setae* present, spinulose, septate. *Conidia* ellipsoid, aseptate, hyaline, thin- and smooth-walled, eguttulate, arranged in slimy heads.

Type: *Sporodochius pironii* (Alfieri & Samuels) Lin Zhao & Crous

Notes: All isolates from the genus *Sporodochius* were previously identified as *Nectriella pironii* based on morphological characters. *Nectriella* was recognised in *Bionectriaceae*, but no DNA data are available for the type species of *Nectriella*, *Nectriella fuckelii*. Our phylogenetic analyses indicate that these isolates form a fully supported and independent clade, distinct from other genera within *Stachybotryaceae* (Fig. 1). Therefore, based on the phylogenetic analyses, we propose the establishment of the genus *Sporodochius*. Morphologically, it is characterised by asexual morphs ranging from mononematous to sporodochial conidiomata that align well with those typical of *Stachybotryaceae* (Alfieri & Samuels 1979, Lombard *et al.* 2016).

Sporodochius pironii (Alfieri & Samuels) Lin Zhao & Crous, ***comb. nov.*** MycoBank MB 858444. Fig. 23.
Basionym: *Nectriella pironii* Alfieri & Samuels, *Mycologia* **71**: 1181. 1980.

Typus: **USA**, Florida, Gainesville, from *Aphelandra squarrosa*, Mar. 1978, coll. and isol. *S.A. Alfieri* (**holotype** GJS 78-24 in NY, ex-type living isolate CBS 264.80, specimen CBS H-25596).

Mycelium consisting of branched, septate, hyaline, smooth or slightly warted, thin- or thick-walled hyphae, 1.5–3.5 µm wide. *Sporulation* abundant from conidiophores arising from the agar surface, aerial mycelium, ropes formed by mycelium, or from the production of pale

orange to luteous sporodochia. *Solitary conidiophores* solitary or aggregated, (sub-)erect, unbranched or sparsely branched, bearing up to 1–2 levels with 1–2 phialides per node, up to ca 111 µm long, 2–5 µm wide at base, 2–7-septate, occasionally with a percurrent proliferation, hyaline, smooth-walled, with relatively thick walls at lower or middle part. *Conidiogenous cells* monophialidic, lateral or terminal, subcylindrical to cylindrical, straight or slightly curved, hyaline, thick- and smooth-walled, (15.7–)18.9–30.6(–31.6) µm long, (2.0–)2.1–3.0(–3.3) µm wide at base, (1.1–)1.2–1.7(–1.8) µm wide near aperture, with minute collarettes and conspicuous periclinal thickening at conidiogenous loci. *Sporodochial conidiophores* mostly branched, bearing multiple levels with 1–3 phialides per node, smooth-walled. *Sporodochial phialides* mostly lateral, subulate, tapering at top, smooth-walled, (10.0–)10.3–21.4(–23.4)

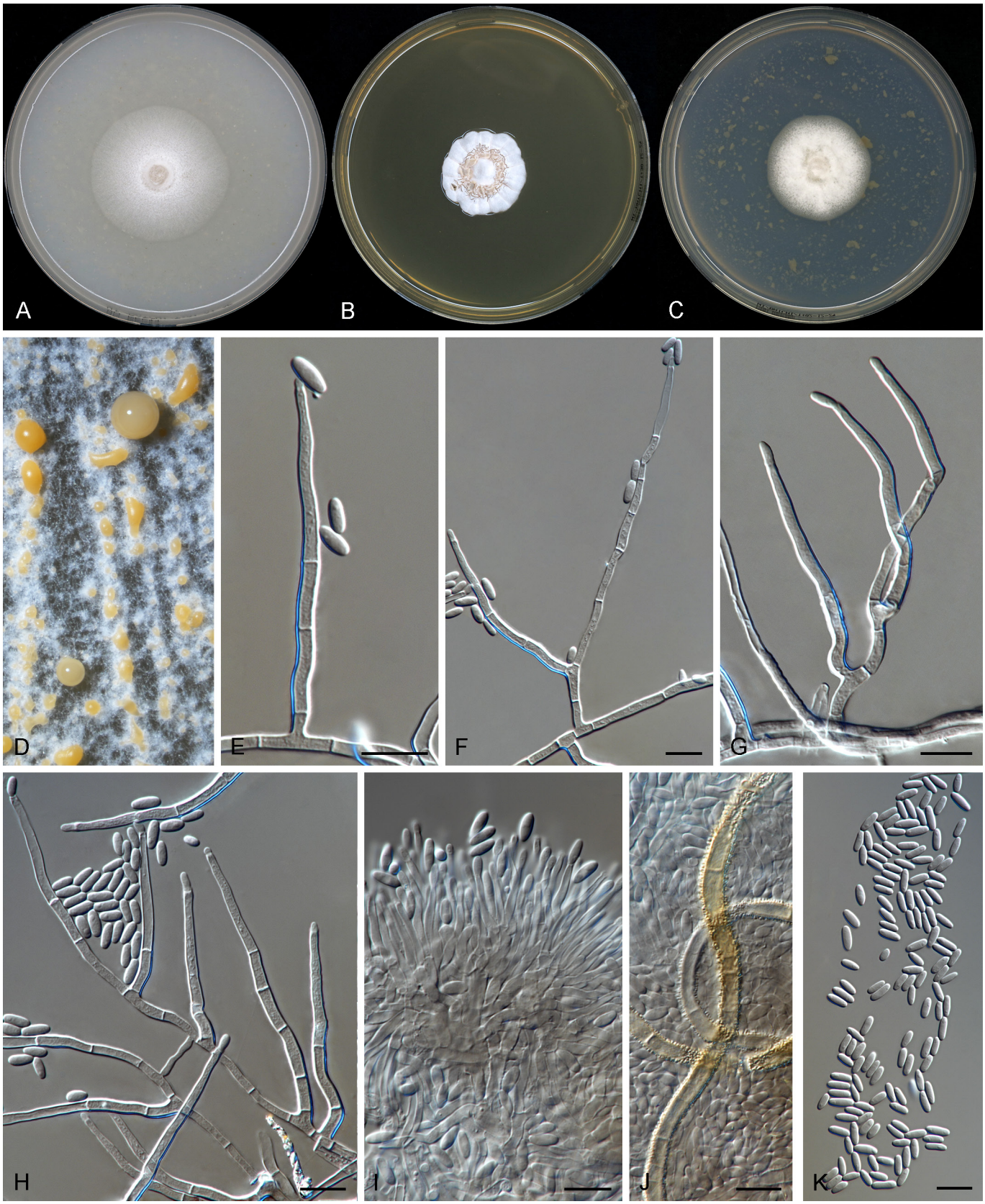

Fig. 23. *Sporodochius pironii* (ex-type CBS 264.80). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D.** Sporodochial conidiomata. **E–H.** Conidiophores. **I.** Sporodochia. **J.** Setae. **K.** Conidia. Scale bars = 10 µm.

µm long, (1.4–)1.5–2.6(–2.8) µm wide at base, 1.0–1.3(–1.6) µm wide near aperture, with minute collarettes and periclinal thickening at conidiogenous loci. *Setae* present, spinulose, septate, yellow to yellow-brown, 3.0–5.6 µm. *Conidia* from solitary conidiophores and sporodochial conidiophores not significantly different, aseptate, ellipsoid, both rounded ends, hyaline, with thin and smooth walls, (3.4–)4.3–7.2(–7.8) × (1.8–)2.0–2.7(–2.9) µm (av. 5.9 × 2.3 µm, n = 200), eguttulate, arranged in slimy heads. *Sexual morph* from natural substrate is described and illustrated in Alfieri & Samuels (1979).

Culture characteristics: Colonies on OA reaching 38–40 mm diam. after 14 d in darkness at 25 °C, flat, floccose at centre, thinly felty and granulose at periphery, with moderate aerial mycelium, white, margin entire, reverse buff. On MEA reaching 25–27 mm diam., raised, rugose, radially folded, felty, with moderate aerial mycelium, white at centre, rosy buff in middle, white at periphery, margin lobate, reverse saffron with white radial lines. On PDA reaching 29–31 mm diam., flat, floccose, cotton, with abundant aerial mycelium, white at centre, buff at periphery, margin entire, reverse whitish. On SNA reaching 25–27 mm diam., flat, granulose, dusty, with moderate aerial mycelium, white, margin crenate, reverse concolourous.

Additional materials examined: **USA**, Florida, from *Euphorbia pulcherrima*, unknown collection date and *collector*, isol. *S.A. Alfieri*, No. 068-1858, isolate CBS 170.75; Florida, from *Cuphea* sp., unknown collection date, coll. and isol. *S.A. Alfieri*, isolate CBS 177.75A = CCT 5381; Florida, from *Psychotria undata*, unknown collection date, coll. and isol. *S.A. Alfieri*, isolate CBS 177.75B; Florida, from *Jussiaea peruviana,* unknown collection date, coll. and isol. *S.A. Alfieri*, isolate CBS 177.75C; Florida, from *Hydrangea macrophylla*, unknown collection date, coll. and isol. *S.A. Alfieri*, isolate CBS 177.75D = CCT 5382; Florida, from *Codiaeum variegatum*, unknown collection date, coll. and isol. *S.A. Alfieri*, isolate CBS 231.80A = G.J.S. 78-27; Florida, from *Leucophyllum frutescens*, stem, unknown collection date and *collector*, isolate CBS 231.80B = G.J.S. 78-32; Florida, Apoka, from *Aphelandra squarrosa*, 29 Jun. 1978, *J.F. Knauss*, isolate CBS 231.80C = G.J.S. 78-40; Florida, from *Pittosporum tobira*, unknown collection date, coll. and isol. *S.A. Alfieri*, isolate CBS 573.74A; Florida, from *Codiaeum variegatum*, Feb. 1971, coll. and isol. *S.A. Alfieri*, isolate CBS 573.74B; Florida, from *Hedera helix*, unknown collection date, coll. and isol. *S.A. Alfieri*, isolate CBS 573.74C; Florida, from *Ligustrum sinense*, unknown collection date, coll. and isol. *S.A. Alfieri*, isolate CBS 573.74D.

Notes: In this study, we examined 13 isolates deposited in the CBS collection as *Nectriella pironii*, including the ex-type isolate of *Nectriella pironii*, CBS 264.80. Based on phylogenetic analyses, these 13 isolates formed a fully supported lineage representing the new genus *Sporodochius* within the family *Stachybotryaceae*, with *Spor. pironii* as the type species. The morphology of *Spor. pironii* closely matches the features described in the original record, including a kutilakesa-like asexual morph, which produces an acremonium-like synasexual morph and sporodochial conidiomata, with bright orange conidial mass, and yellow to yellow-brown setae, except for the production of shorter conidia (3.4–)4.3–7.2(–7.8) µm vs 6–8(–9) µm, and longer sporodochial phialides, which are (10.0–)10.3–21.4(–23.4) µm long vs 7–14 µm (Alfieri & Samuels 1979). These might result from the different media used for morphological observations.

Clade XXXI. *Bionectriaceae* Samuels & Rossman, *Stud. Mycol.* **42**: 15. 1999.

Classification: *Hypocreales*, *Sordariomycetes*.

Type genus: *Bionectria* Speg.

Clade XXXI-7. *Protocreopsis* Yoshim. Doi, *Kew Bull.* **31**: 551. 1977.

Ascomata perithecial, globose or subglobose, superficial on substrata, densely gregarious, or solitary, hyaline to orange, KOH-, papillate or apapillate, ostiolate, completely enclosed in long, white, or tan, or green, flexuous hyphae. *Peridium* comprising a single region of small, brick-like cells. *Asci* clavate to fusoid, arranged in bi- to pluriseriate, with a simple apex or an indistinct apical ring, 8-spored. *Ascospores* ellipsoid or fusoid, 1-septate, hyaline, typically striate. *Asexual morph*: acremonium-like. Saprobic on decaying of monocotyledonous plants, with a preference for lichens, wood, and foliage (adapted from Doi 1977, Rossman *et al.* 1999, Lechat *et al.* 2016b).

Type: *Protocreopsis fusigera* (Berk. & Broome) Yoshim. Doi

Notes: Doi (1977) established the genus *Protocreopsis* for nectria-like fungi with pallid ascomata surrounded by white to tan hyphae and striate ascospores, including the type species *Pt. zingibericola* (currently treated under *Pt. fusigera*) and *Pt. palmicola*. Hou *et al.* (2023) accepted seven species with available DNA data. Later, Visagie *et al.* (2024) and Crous *et al.* (2024b) described two new species, *Pt. physciae* and *Pt. globulosa*, which were isolated from the lichens *Physcia caesia* (*Physciaceae*) and *Lecania cyrtella* (*Ramalinaceae*), respectively. Subsequently, Zhao *et al.* (2025) proposed two new species and two new combinations in *Protocreopsis*. To date the genus *Protocreopsis* includes 13 known species based on molecular data. In the present study, four new species are introduced below.

Protocreopsis ellipsoidea Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858445. Fig. 24.

Etymology: Referring to the ellipsoid conidia produced by this species.

Typus: **Netherlands**, North Holland Province, Alkmaar, unknown substrate, unknown collection date and *collector*, isol. Jul 1963, *Van Bakel* (**holotype** designated here CBS H-25576, ex-type living isolate CBS 112.70).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.5 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial mycelium, or ropes formed by mycelium, solitary, (sub-)erect, unbranched or sparsely branched, up to ca 65 µm long, 2.0–3.2 µm wide at base, with 1–2-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, subcylindrical to cylindrical, straight or slightly curved, hyaline, thick- and smooth-walled, (14.0–)38.5–53.0(–61.1) µm long, (1.4–)1.8–2.5(–2.9) µm wide at base, (0.8–)0.9–1.1(–1.2) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia*

ellipsoid, ovoid or cylindrical, with rounded ends and truncate bases, aseptate, hyaline, thick- and smooth-walled, (4.1–)4.8–6.6(–6.8) × (2.1–)2.2–2.9(–3.2) µm (av. 5.6 × 2.5 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 44–46 mm diam. after 14 d in darkness at 25 °C, flat, granulose, dusty, with sparse aerial mycelium, buff at centre, dirty white at periphery, margin entire, reverse buff. On MEA reaching 34–36 mm diam., raised, radially folded, felty, floccose, with moderate aerial mycelium, pale luteous at centre, white in middle, buff at periphery, margin crenate, reverse apricot to orange, with buff radial lines. On PDA reaching 26–27 mm diam., raised, radially folded, thinly felty, with sparse aerial mycelium, dirty white, margin crenate, reverse salmon, with rosy buff radial lines. On SNA reaching 32 mm diam., flat, granulose, dusty, with sparse aerial mycelium, white, margin crenate, reverse concolourous.

Notes: The isolate CBS 112.70 was previously identified as "*Acremonium rutilum*" by Gams (1971), which is now the basionym of *Protocreopsis rutila*. Based on our molecular phylogeny, this isolate forms an independent lineage, which is distinct from all known species within *Protocreopsis* and separate from *Pt. rutila* (Fig. 4, clade XXXI-7).

Based on a BLASTn search of NCBI GenBank nucleotide database, the closest hits of CBS 112.70 with the ITS sequences are listed as *Bionectriaceae* sp. [CA01; GenBank PQ298325; Identity = 492/493 (99 %), one gap (0 %)]; *Hypocreales* sp., isolated from cultivated soil in Japan [MAFF307192; GenBank LC43384; Identity = 485/494 (98 %), one gap (0 %)]; *Hypocreales* sp., isolated from *Allophylus punctatus* in Ecuador [E14023c, GenBank KF466233; Identity = 479/489 (98 %), two gaps (0 %)]; the closest hit using the LSU sequence are *Pt. rutila* isolated from humus rich soil in Netherlands [CBS 394.70; GenBank OQ430070; Identity = 776/776 (100 %), no gaps (0 %)]; *Verruciconidia persicina*, isolated from soil in Belgium [CBS 378.70C; GenBank HQ232080; Identity = 776/777 (99 %), one gap (0 %)]; *Pt. rutila*, isolated from moist wall in greenhouse in Germany [CBS 229.70; GenBank OQ430076; Identity = 775/776 (99 %), no gaps (0 %)]; the closest hit using the *RPB2* sequence is *Geosmithia* sp., isolated from Poland [CCF 3703; GenBank LR535689; Identity = 193/232 (83 %), two gaps (0 %)]; *Hydropisphaera fungicola*, isolated from *Ulocladium atrum* in USA [CBS 122304; GenBank OQ454063; Identity = 529/669 (79 %), five gaps (0 %)]; *Hydropisphaera peziza* [CBS 102038 GenBank DQ522444; Identity = 529/669 (79 %), five gaps (0 %)]; the closest hit using the *TEF1* sequence is *Pt. rutila*, isolated from a moist greenhouse wall in Germany [CBS 396.66; GenBank OQ471142; Identity = 667/717 (93 %), no gaps (0 %)]; *Pt. rutila*, isolated from a moist greenhouse wall in Germany [CBS 229.70; GenBank

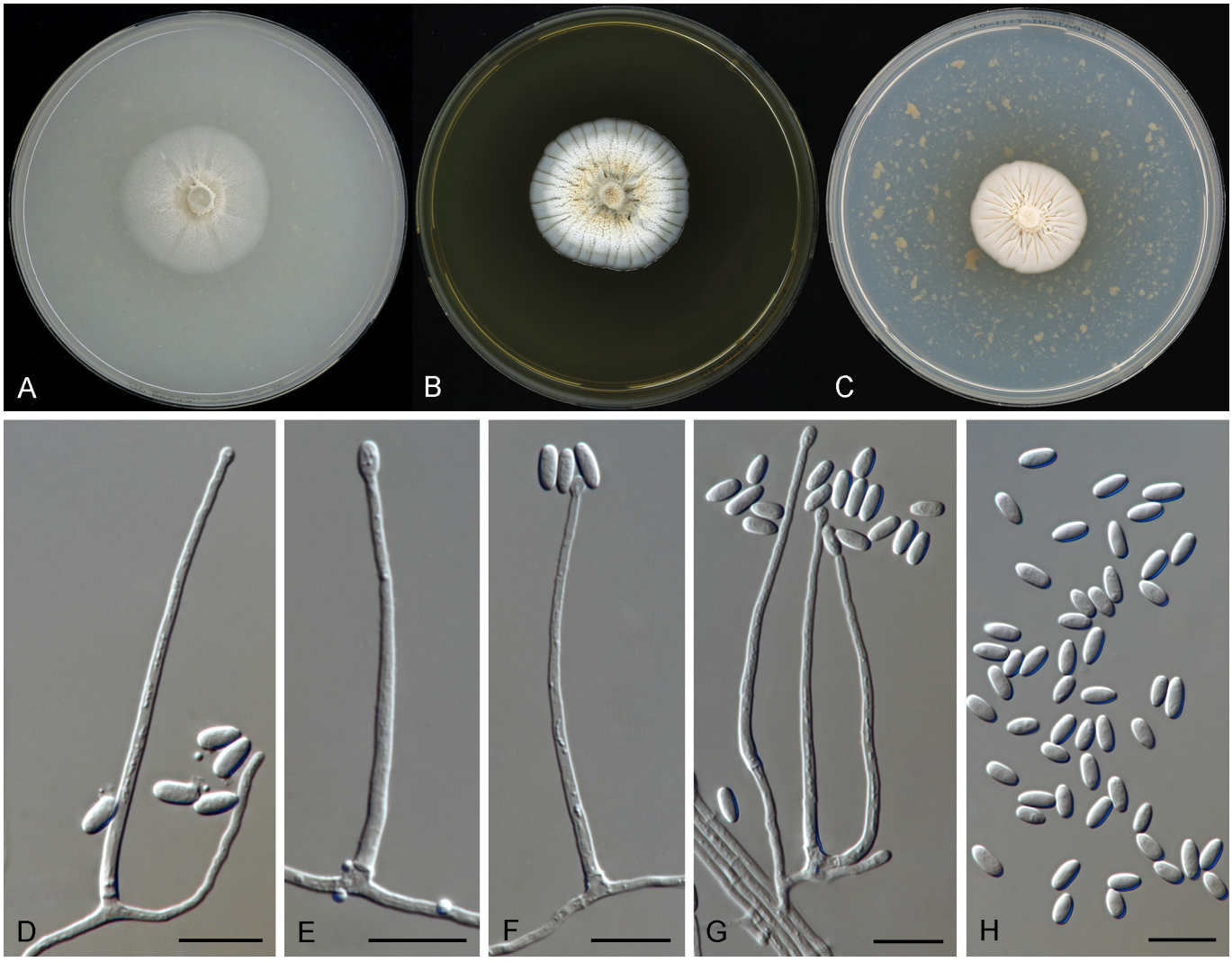

Fig. 24. *Protocreopsis ellipsoidea* (ex-type CBS 112.70). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness**. D–G.** Conidiophores. **H.** Conidia. Scale bars = 10 µm.

OQ471141; Identity = 667/717 (93 %), no gaps (0 %)]; *Pt. rutila,* isolated from humus rich soil in Netherlands[CBS 394.70; GenBank OQ471135; Identity = 666/718 (93 %), two gaps (0 %)].

Protocreopsis helvetica Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858446. Fig. 25.

Etymology: From Latin *Helvetia*, name for Switzerland, referring to the country where this fungus was collected.

Typus: **Switzerland**, near Zurich, SWI, from A1 horizon soil, Swiss beech-cherry forest, deciduous forest, isolated from soil, 1961, unknown *collector* (**holotype** designated here CBS H-25587, ex-type living isolate CBS 127989).

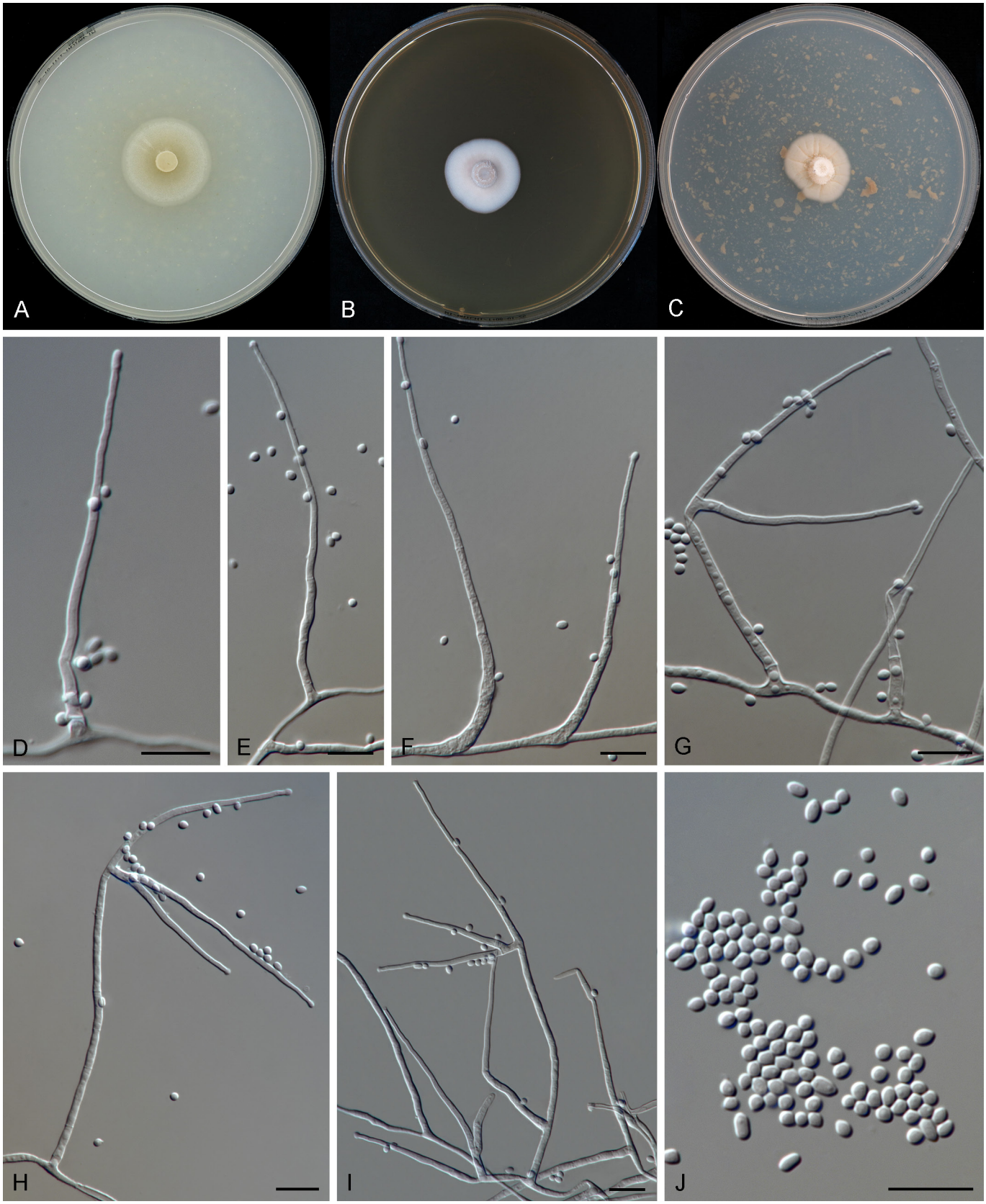

Fig. 25. *Protocreopsis helvetica* (ex-type CBS 127989). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J.** Conidia. Scale bars = 10 µm.

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.1–2.3 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous. *Conidiophores* arising from the agar surface and aerial mycelium, solitary or aggregated, (sub-) erect, unbranched or branched, bearing up to 1–3 levels with 1–3 phialides per node, up to ca 125 µm long, 1.7–4.0 µm wide at base, 1–7-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, terminal or lateral, subcylindrical or subulate, straight or slightly curved, hyaline, smooth- and thick-walled, (12.8–)16.8–46.7(–47.7) µm long, (1.2–)1.6–2.3(–2.5) µm wide at base, (0.7–)0.8–1.1(–1.2) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* globose, subglobose, or ellipsoid, with both ends rounded, or with slightly apiculate bases, aseptate, hyaline, thin- and smooth-walled, (1.5–)1.7–3.0(–3.3) × (1.2–)1.3–1.9(–2.1) µm (av. 2.3 × 1.6 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 25–28 mm diam. after 14 d in darkness at 25 °C, flat, thinly felty, dusty, with moderate aerial mycelium, buff at centre, white at periphery, margin entire, reverse pale luteous at centre, buff at periphery. On MEA reaching 21–22 mm diam., flat, felty, with sparse aerial mycelium, rosy buff at centre, white at periphery, margin entire, reverse orange at centre, saffron at periphery. On PDA reaching 18–20 mm diam., flat, radially folded, felty, with sparse aerial mycelium, rosy buff, margin slightly lobate, reverse salmon. On SNA reaching 15 mm diam., flat, felty, with sparse aerial mycelium, white, margin irregular, reverse concolourous.

Notes: According to the phylogenetic analyses in the current study, *Pt. helvetica* groups with *Pt. chlamydospora* and *Pt. gallica* (Fig. 4, clade XXXI-7). However, *Pt. helvetica* can be distinguished from *Pt. chlamydospora* and *Pt. gallica* by it smaller conidia, which are (1.5–)1.7–3.0(–3.3) × (1.2–)1.3–1.9(–2.1) µm (av. 2.3 × 1.6 µm, n = 100) in *Pt. helvetica*, vs (5.3–)6.1–10.3(–11.4) × (3.0–)3.3–4.5 µm (av. 8.2 × 3.9 µm, n = 100) in *Pt. chlamydospora*, and (4.4–)4.7–7.2(–11.4) × (2.4–)2.7–3.3(–3.4) µm (av. 5.9 × 3.0 µm, n = 100) in *Pt. gallica* (Zhao *et al.* 2025). Additionally, *Pt. helvetica* differs by producing smooth-walled conidiophores, whereas the other two species produce rough-walled conidiophores (Zhao *et al.* 2025).

Protocreopsis polyphialidica Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858447. Fig. 26.

Etymology: Referring to the polyphialides commonly produced by the ex-type isolate.

Typus: **Canada**, Ontario, human, left hip, 18-yr-old female, unknown collection date and *collector* (**holotype** designated here CBS H-25582, ex-type living isolate CBS 116130).

Mycelium consisting of branched, septate, hyaline, smooth-, thin- or thick-walled hyphae, 1.1–2.1 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, *Conidiophores* arising from the agar surface and aerial mycelium, solitary or aggregated, (sub-)erect, unbranched or basitonously branched, bearing up to 1–2 levels with 1–2 phialides per node, up to ca 50 µm long, 1.6–3.3 µm wide at base, with short sterile basal outgrowths, aseptate or 1–3-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic or polyphialidic, lateral or terminal, subulate or ampulliform, straight or slightly curved, hyaline, with smooth, thin or thick walls, (6.9–)8.1–18.8(–21.0) µm long, (1.6–)1.7–2.5(–2.9) µm wide at base, 0.8–1.0(–1.1) µm wide near aperture, with minute collarettes and periclinal thickening at conidiogenous loci; polyphialides with two conidiogenous loci commonly present; adelophialides present, subulate or ampulliform, 6.2–8.2 × 1.5–1.9 µm. *Conidia* fusoid, or ellipsoid, with apiculate hila at both ends or with rounded apices and apiculate bases, aseptate, hyaline, thick- and smooth-walled, (2.7–)3.0–3.9(–4.4) × (1.6–)1.8–2.4(–2.8) µm (av. 3.4 × 1.2 µm, n = 100), guttulate, arranged in chains. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 22–24 mm diam. after 14 d in darkness at 25 °C, flat, felty, dusty, with sparse aerial mycelium, pure yellow to sulphur yellow, margin entire, reverse yellowish. On MEA reaching 25–26 mm diam., flat, floccose, with abundant aerial mycelium, buff to rosy buff, margin entire, reverse saffron. On PDA reaching 20–21 mm diam., flat, felty, with moderate aerial mycelium, white to buff, margin entire, reverse saffron at centre, buff at periphery. On SNA reaching 21 mm diam., flat, felty, dusty, with sparse aerial mycelium, white, margin entire, reverse concolourous.

Notes: *Protocreopsis polyphialidica* is most closely related to *Pt. vulpina*; however, it is distinguished by producing shorter phialides, which are (6.9–)8.1–18.8(–21.0) µm long in *Pt. polyphialidica*, vs (9.1–)17.9–51.5(–66.5) µm in *Pt. vulpina*, and smaller conidia, which are (2.7–)3.0–3.9(–4.4) × (1.6–)1.8–2.4(–2.8) µm (av. 3.4 × 1.2 µm, n = 100) in *Pt. polyphialidica*, vs (4.0–)4.4–5.9(–7.0) × (1.5–)1.6–2.1(–2.2) µm (av. 5.1 × 1.9 µm, n = 100) in *Pt. vulpina* (Zhao *et al.* 2025). Additionally, polyphialides and adelophialides are present in *Pt. polyphialidica*, but absent in *Pt. vulpina* (Zhao *et al.* 2025). Furthermore, *Pt. polyphialidica* (CBS 116130) differs from *Pt. vulpina* (CBS 565.76) in ITS (97.4 % identity, with 15 bp differences), and *TEF1* (98.5 %, 12 bp) sequences, no LSU and *RPB2* sequence were available to compare these two isolates in a BLASTn search.

Protocreopsis spinulosa Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858448. Fig. 27.

Etymology: Referring to the production of spinulose conidiophores.

Typus: **Brazil**, State of Ceará, Pacajus county, associated with *Pilgeriella anacardii*, on leaf of *Anacardium occidentale*, unknown collection date, *F.C.O. Freire*, isol. *W. Gams* (**holotype** designated here CBS H-25607, ex-type living isolate CBS 591.97).

Mycelium consisting of branched, septate, hyaline, smooth-, thin- or thick-walled hyphae, 1.4–3.2 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial mycelium, or from ropes formed by mycelium, solitary or aggregated, (sub-) erect, unbranched or basitonously branched, bearing up to 1–3 levels with 1–2 phialides per node, up to ca 102 µm long, 2.2–3.9 µm wide at base, 2–4(–7)-septate, smooth at lower part, finely to coarsely spinulose at middle and upper part, *Conidiogenous cells* monophialidic, mostly lateral, or terminal, subcylindrical to cylindrical, straight or slightly curved, thick- and rough-walled, spinulose, (6.6–)9.9–36.0(–40.1) µm long, (2.4–)2.7–3.3(–3.5) µm wide at base, 1.3–2.0(–2.3) µm wide near aperture, with conspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* clavate, obovoid, or ellipsoid, mostly with rounded apices and distinctly truncate bases, hyaline at first, becoming pale brown with age,

thick- and smooth-walled, (3.8–)4.5–8.0(–9.2) × (2.7–)3.1–4.0(–4.1) µm (av. 6.7 × 3.5 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 22–23 mm diam. after 14 d in darkness at 25 °C, flat, felty, floccose, granulose, dusty, with moderate aerial mycelium, white to yellowish, with concentric rings, margin lobate, reverse straw. On MEA reaching 26–28 mm diam., flat, radially folded, cotton, with abundant aerial mycelium, white, margin slightly lobate, reverse saffron with white radial lines. On PDA reaching 30–31 mm diam., flat, felty, with abundant aerial mycelium, white at centre, dirty white at periphery, margin lobate,

Fig. 26. *Protocreopsis polyphialidica* (ex-type CBS 116130). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–H.** Conidiophores. **I, J.** Adelophialides. **K.** Conidia. Scale bars = 10 µm.

reverse salmon. On SNA reaching 36–39 mm diam., flat, floccose, with moderate aerial mycelium, white, margin undulate, reverse concolourous.

Notes: The multi-locus phylogenetic analyses show that *Pt. spinulosa* and *Pt. freycinetiae* cluster together, forming a distinct basal branch within *Protocreopsis*, but *Pt. spinulosa* (CBS 591.97) shows clear differences from *Pt. freycinetiae* (CBS 573.76) in ITS (97.3 % identity, with 14 differences), LSU (99.2 %, 6 bp), *RPB2* (96.8 %, 24 bp), and *TEF1* (97.5 %, 20 bp) sequences. Morphologically, both *Pt. spinulosa* and *Pt. freycinetiae* have coarsely spinulose conidiophores, but they differ in producing shorter phialides (6.6–)9.9–36.0(–40.1) µm long

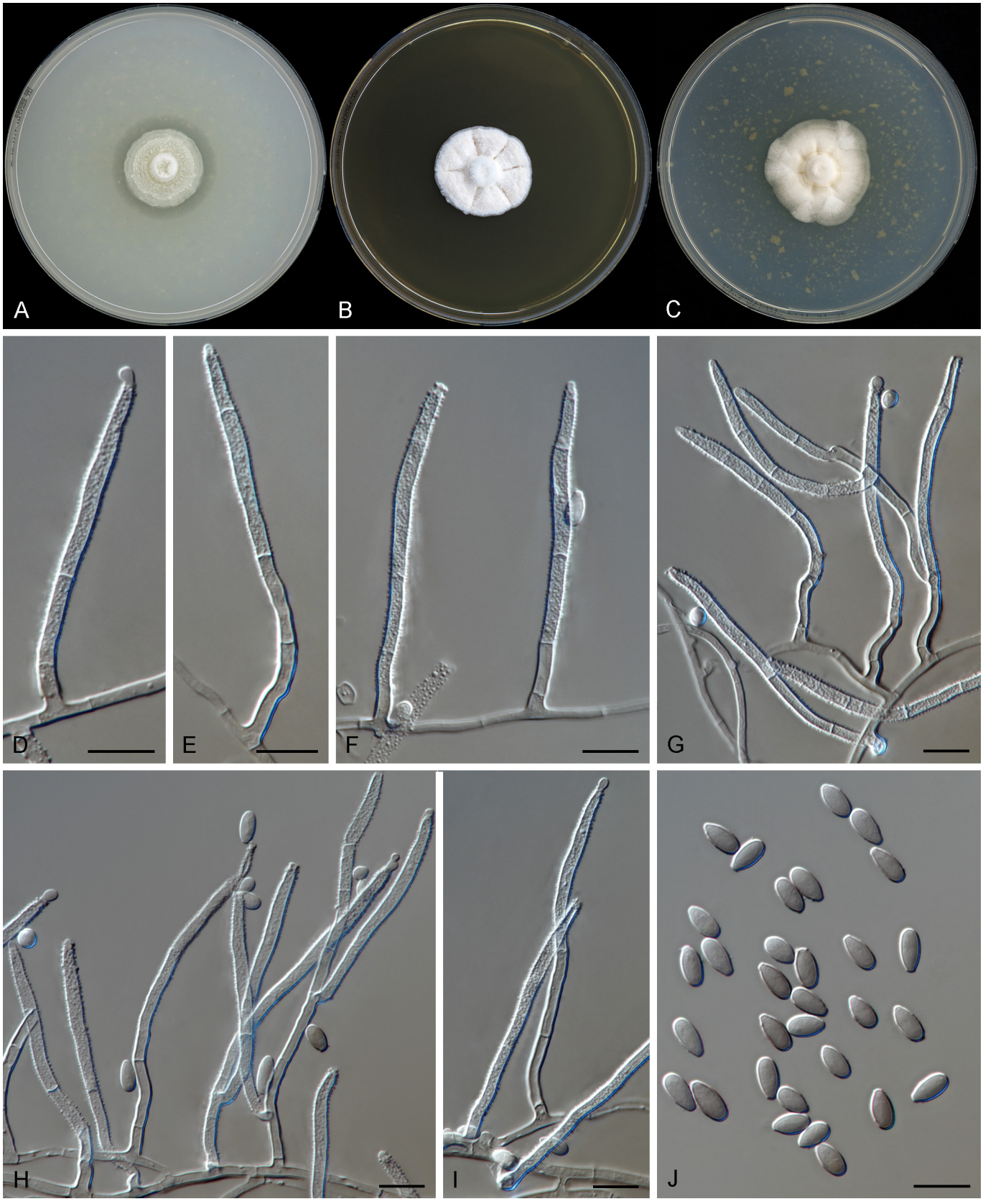

Fig. 27. *Protocreopsis spinulosa* (ex-type CBS 591.97). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J.** Conidia. Scale bars = 10 µm.

in *Pt. spinulosa* vs (23–)35–40(–50) µm long in *Pt. freycinetiae*, and narrower conidia (3.8–)4.5–8.0(–9.2) µm in *Pt. spinulosa* vs 6.5–9.5(–11) µm in *Pt. freycinetiae* (Samuels 1976).

Clade XXXI-8. *Clavatomyces* Lin Zhao & Crous, *Stud. Mycol.* **111**: 161. 2025.

Ascomata perithecial, globose to sub-globose, orange-brown, solitary, gregarious or scattered, uniloculate, non-stromatic, immersed in mycelium, enclosed in white hyphae. *Peridium* composed of two regions: outer region with subglobose to angular cells, inner region with elongate, flattened cells. *Asci* clavate or cylindric-clavate, unitunicate, apex round, without an apical ring, 8-spored. *Ascospores* fusoid, slightly curved, 1-septate, constricted or not at septum, hyaline, thick-walled, with verrucose surface and striations. *Asexual morph*: hyphomycetous or coelomycetous. *Hyphomycetous asexual morph*: stilbella-like or acremonium-like. *Conidiophores* unbranched, or once or twice branched, rarely three times monochasial. *Conidiogenous cells* enteroblastic, monophialidic or polyphialidic, terminal or lateral, cylindrical, subulate, or ampulliform, straight or slightly curved, hyaline; adelophialides present or absent. *Coelomycetous synasexual morph*: *Conidiomata* pycnidial, scattered or aggregated, globose to sub-globose, semi-immersed or immersed in the agar, ostiolate. *Pycnidial wall* pseudoparenchymatous. *Conidiogenous cells* enteroblastic, monophialidic, terminal or lateral, subulate, or acicular, straight or slightly curved, hyaline, smooth-and thick-walled. *Conidia* formed on hyphomycetous or coelomycetous morph, clavate, cylindrical, ellipsoid or obovoid, straight or slightly curved, with both ends rounded, or with apiculate or truncate bases, or with median or laterally displaced hilum bases, aseptate, hyaline, smooth, thin- or thick-walled (adapted from Zhang *et al.* 2024a, Zhao *et al.* 2025).

Type: *Clavatomyces prestoeae* Lin Zhao & Crous

Notes: The genus *Clavatomyces* was proposed for two species: *Cl. prestoeae*, characterised by its asexual morph with a stilbella-like form, and *Cl. korfii*, defined by its sexual morph, with perithecia immersed in mycelium and finely striate and verrucose ascospores (Zhao *et al.* 2025). In this study, we introduced one new species, *Cl. pycnidialis*, which presents both hyphomycetous and coelomycetous morphologies, as well as one new combination, *Cl. palmarum*, characterised by a perithecial sexual morph.

Clavatomyces palmarum (Zhang *et al.*) Lin Zhao & Crous, ***comb. nov.*** MycoBank MB 858450.
Basionym: *Protocreopsis palmarum* S.N. Zhang *et al.*, *Fungal Diversity* **127**: 157. 2024.

Typus: **China**, Guangdong Province, Guangzhou City, Tianhe District, 1190 Tianyuan Rd, South China Botanical Garden, on decaying petioles of *Licuala* sp., 3 Sep. 2019, *Y. Feng*, SNC155 (**holotype** HKAS 115709, ex-type living isolate GZCC21-0256).

Description and illustration: Zhang *et al.* (2024a).

Notes: Phylogenetic analyses of the combined ITS, LSU, *RPB2*, and *TEF1* dataset indicate that *Protocreopsis palmarum* belongs to the genus *Clavatomyces* (Fig. 4, clade XXXI-8). Accordingly, we propose the new taxonomic combination *Clavatomyces palmarum*.

Clavatomyces pycnidialis Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858451. Fig. 28.

Etymology: Referring to the production of pycnidia.

Typus: **Netherlands**, from tap water, unknown collection date, *K. Breuker*, Solvay Pharmaceuticals b.v. Olst (**holotype** designated here CBS H-25574, ex-type living isolate CBS 102156).

Mycelium consisting of branched, septate, hyaline, smooth, thin- or thick-walled hyphae, 1.0–2.5 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial mycelium, or ropes or coils formed by mycelium, solitary or aggregated, (sub-) erect, unbranched or sparsely branched, up to ca 47 µm long, 1.0–2.3 µm wide at base, aseptate or 1–2-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, terminal or lateral, subulate or ampulliform, straight or slightly curved, hyaline, with smooth, thin- or thick-walled, (7.4–)10.1–22.8(–29.0) µm long, (1.0–)1.1–1.8(–2.0) µm wide at base, 0.7–1.0(–1.1) µm wide near aperture, with conspicuous collarettes and periclinal thickening at conidiogenous loci; polyphialides with two or three conidiogenous loci present; adelophialides subulate, or acicular, (3.9–)4.9–14.0(–14.3) × (0.8–)1.1–1.8(–2.0). *Conidia* cylindrical, ellipsoid, or obovoid, straight or curved, with both ends rounded, or with slightly apiculate bases, aseptate, hyaline, smooth- and thin-walled, (2.2–)2.8–4.2(–4.6) × 1.1–1.6(–1.8) µm (av. 3.5 × 1.4 µm, n = 100), eguttulate, arranged in slimy heads. *Coelomycetous synasexual morph* present. *Conidiomata* pycnidial, scattered or aggregated, globose to sub-globose, semi-immersed or immersed in agar, ostiolate. *Pycnidial wall* pseudoparenchymatous. *Conidiogenous cells* monophialidic, terminal or lateral, subulate, or acicular, straight or slightly curved, hyaline, smooth- and thick-walled, (6.7–)7.8–12.8(–15.8) µm long, (1.1–)1.2–1.8(–2.0) µm wide at base, 0.8–1.0 µm wide near aperture, with conspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* ellipsoid, obovoid or short cylindrical, with rounded distal ends and median or laterally displaced hilum bases, aseptate, hyaline, smooth- and thick-walled, (1.8–)2.3–3.1(–3.9) × (1.2–)1.4–1.9(–2.1) µm, (av. 2.7 × 1.6 µm, n = 100), eguttulate. *Conidial matrix* yellowish. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 72–75 mm diam. after 14 d in darkness at 25 °C, flat, granulose, dusty, with moderate aerial mycelium, buff at centre, with vinaceous buff concentric rings in middle, dirty white at periphery, margin entire, reverse white to vinaceous buff. On MEA reaching 73–74 mm diam., flat, radially folded, floccose, or cotton, with abundant aerial mycelium, white with ochraceous edge, margin entire, reverse umber, with white radial lines. On PDA reaching 69–70 mm diam., flat, felty, dusty, hairy, with moderate aerial mycelium, dirty white with vinaceous buff at centre, buff at periphery, margin entire, reverse rosy buff at centre, dirty white at periphery. On SNA reaching 70–72 mm diam., flat, felty, with sparse aerial mycelium, dusty, white, margin entire, reverse concolourous.

Notes: *Clavatomyces pycnidialis* is represented by the isolate CBS 102156, which was isolated from tap water in the Netherlands and was previously identified as "*Acremonium* sp." in the CBS collection. This species produces acremonium-like conidiophores, with polyphialides and adelophialides present. More notably, it can produce pycnidia after the formation of acremonium-like conidiophores, which we verified through single spore isolations.

According to our phylogenetic analyses, *Cl. prestoeae*, together with *Cl. korfii* and the new combination *Cl. palmarum*, forms a poorly supported clade (Fig. 4, RAxML-BS = 67 %, IQ-TREE-BS = 100 %). The new species *Cl. pycnidialis* is closely related to this moderately supported clade (Fig. 4, RAxML-BS = 75 %, IQ-TREE-BS = 100 %). Although the morphology of *Cl. pycnidialis* differs from other species within the genus *Clavatomyces*, separating it into a new genus would require reconsidering the status of *Cl. korfii*, and *Cl. palmarum*, and *Cl. prestoeae*, which may belong to new genera as well. Therefore, in the present study, we choose to retain *Cl. pycnidialis* within *Clavatomyces*.

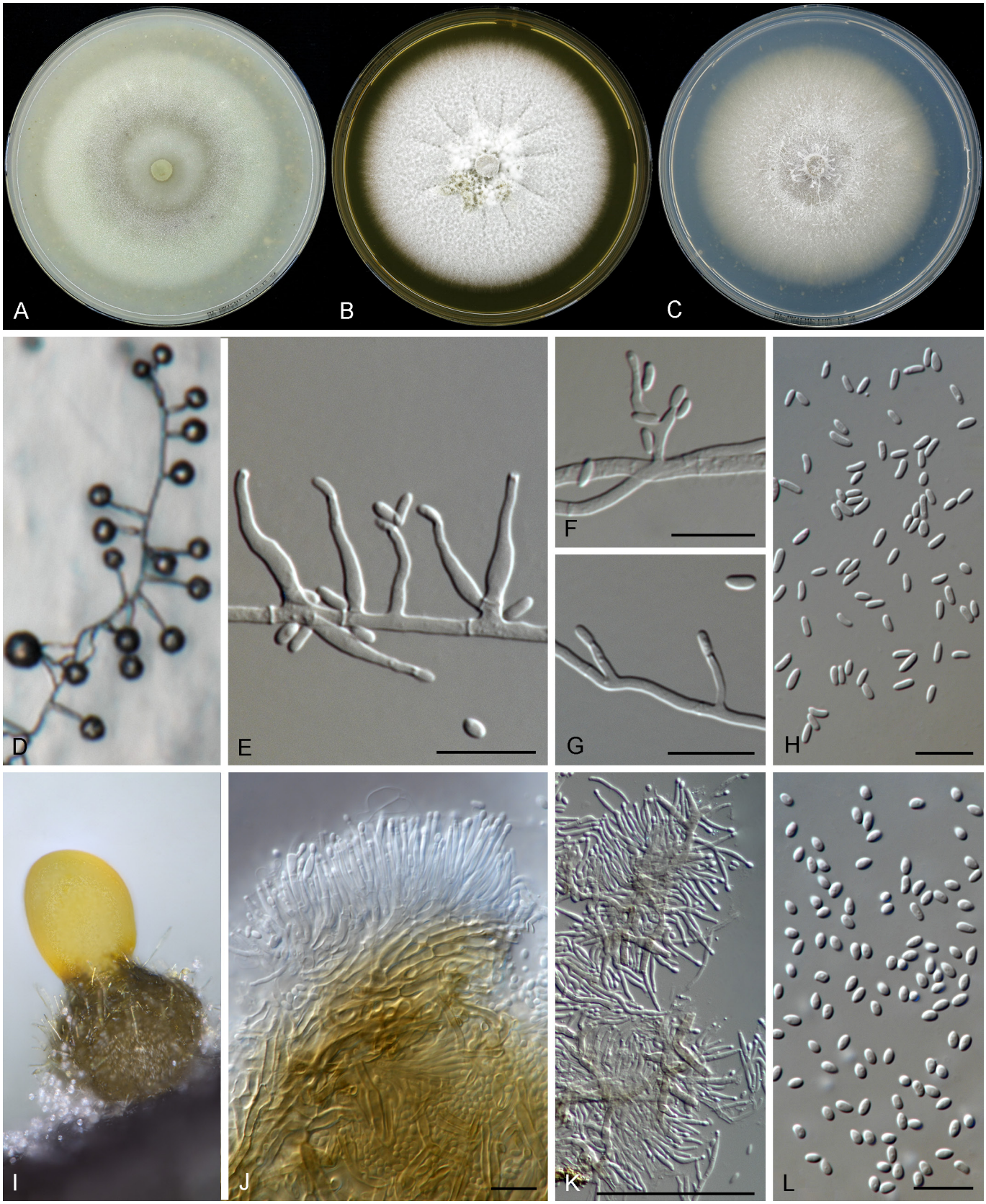

Fig. 28. *Clavatomyces pycnidialis* (ex-type CBS 102156). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–H.** Hyphomycetous asexual morph. **D, E.** Conidiophores. **F.** Polyphialides. **G.** Adelophialides. **H.** Conidia. **I–L.** Coelomycetous synasexual morph. **I.** Pycnidia. **J, K.** Conidiophores. **L.** Conidia from pycnidia. Scale bars: D–H, J, L = 10 µm; K = 50 µm.

Clade XXXI-11. *Ramosiphorum* L.W. Hou *et al.*, *Stud. Mycol.* **105**: 100. 2023.

Mycelium consisting of branched, septate, hyaline, smooth or rough, thin- or thick-walled hyphae. *Conidiophores* (sub-)erect or curved, unbranched, basitonously, or verticillately branched, aggregated in sporodochial-like structures, septate, hyaline, smooth-walled, occasionally coarse at lower part, with cell walls normally thicker than those of vegetative hyphae. *Conidiogenous cells* enteroblastic, monophialidic, terminal or lateral, (sub)cylindrical or subulate, hyaline, with thick, smooth or rough walls, with conspicuous cylindrical collarette and periclinal thickening at conidiogenous loci. *Conidia* globose, subglobose, ellipsoid or obovoid, with both ends rounded, or with slightly apiculate basal ends, aseptate, hyaline, with smooth or rough, thin or thick walls, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed (adapted from Hou *et al.* 2023).

Type: *Ramosiphorum polyporicola* L.W. Hou *et al.*

Notes: The genus *Ramosiphorum* was proposed by Hou *et al.* (2023) to accommodate the type species *R. polyporicola* and two other species, *R. echinoporiae* and *R. thailandicum*. It is characterised by the production of repeatedly branched conidiophores and sporodochial-like conidiomata. Based on our multi-locus phylogenetic analyses, we propose one new species within the genus, which produces sporodochium-like structures and profusely branched conidiophores, agreeing with the generic characterisation of *Ramosiphorum*.

Ramosiphorum sporodochiale Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858452. Fig. 29.

Etymology: Referring to the production of sporodochium-like structures.

Typus: **Germany**, Eifel, Auberg near Gerolstein, from dung of sheep, 26 Sep. 1980, coll. *H.A. van der Aa*, isol. *W. Gams* (**holotype** designated here CBS H-25606, ex-type living isolate CBS 554.80).

Mycelium consisting of branched, septate, hyaline, smooth, thin- or thick-walled hyphae, 1.3–4.1 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-) erect, unbranched or basitonously branched, aggregated as sporodochium-like structures, bearing up to 1–3 levels with 1–4 phialides per node, up to ca 80 µm long, 1.9–3.6 µm wide at base, 1–4-septate, hyaline, with smooth or rough walls. *Conidiogenous cells* monophialidic, terminal or lateral, subulate or subcylindrical, occasionally slightly swollen at lower part, straight or slightly curved, hyaline, with thick, smooth or rough walls, (7.9–)15.2–33.5(–45.2) µm long, (1.3–)1.7–2.5(–2.7) µm wide at base, (0.7–)0.8–1.1 µm wide near aperture, with conspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* subglobose, broadly ellipsoid or obovoid, with both ends rounded, with rounded distal ends and apiculate basal ends, aseptate, hyaline, with thick and smooth walls, (2.0–)2.1–3.1(–3.5) × 1.8–2.2(–2.4) µm (av. 2.6 × 2.0 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 26 mm diam. after 14 d at room temperature, flat, floccose at centre, felty at periphery, granulose, with moderate aerial mycelium, white to yellowish, margin undulate, reverse sulphur yellow. On MEA reaching 18 mm diam., raised, radially folded, felty, with moderate aerial mycelium, white, margin crenate, reverse apricot to salmon. On PDA reaching 25–27 mm diam., flat, floccose, short hairy, with abundant aerial mycelium, white to yellowish, margin fimbriate, reverse orange at centre, pale salmon at periphery. On SNA reaching 28–31 mm diam., flat, felty, granulose, dusty, with moderate aerial mycelium, white, margin fimbriate, reverse concolourous.

Notes: *Ramosiphorum sporodochiale* is phylogenetically (Fig. 4, clade XXXI-11) closely related to *R. polyporicola*, but *R. sporodochiale* (CBS 554.80) differs from *R. polyporicola* (CBS 123779) in ITS (97.9 % identity, with 11 bp differences), LSU (99.6 %, 3 bp), and *TEF1* (97.2 %, 22 bp) sequences, while no *RPB2* sequence was available to compare the two isolates in a BLASTn search. Morphologically, *R. sporodochiale* differs from *R. polyporicola* in producing shorter conidiophores, up to ca 80 µm long in *R. sporodochiale* vs ca 105.5 µm long in *R. polyporicola* (Hou *et al.* 2023).

Clade XXXI-13. *Cannomyces* Lin Zhao & Crous, ***gen. nov.*** MycoBank MB 858453.

Etymology: Derived from the host genus *Canna*, combined with the Greek word *myces* (fungus), referring to the isolation of the type species from the leaf of *Canna coccinea*.

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, or aerial mycelium, solitary or aggregated, (sub-) erect, unbranched or sparsely branched, 1–2-septate, hyaline, thick-walled, roughened or finely to coarsely spinulose, with cell walls usually thicker than those of vegetative hyphae. *Conidiogenous cells* enteroblastic, monophialidic, mostly lateral, subulate or lageniform, straight or slightly curved, hyaline, spinulose, with thick, roughened walls, with inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* fusoid, straight, with symmetrically thick and truncate ends, aseptate, hyaline, thick- and smooth-walled, eguttulate, arranged in long chains. *Chlamydospores* and *sexual morph* not observed.

Type: *Cannomyces spinulosus* Lin Zhao & Crous

Notes: CBS 726.87 represents a new genus, *Cannomyces*, which is phylogenetically closely related to *Lasionectria* (Fig. 1, clade XXXI; Fig. 4, clades XXXI-13 & XXXI-14), but differs by producing roughened or finely to coarsely spinulose conidiophores in *Cannomyces*, whereas *Lasionectria* has smooth-walled conidiophores. The genera also differ in the size of conidia: those in *Cannomyces* are fusoid with truncate bases and apices, while, in *Lasionectria*, conidia are ellipsoid, cylindrical, drop-shaped, obovoid, or obpyriform, with rounded apices and apiculate bases (Hou *et al.* 2023). Therefore, we introduce a new genus here, with *Cannomyces spinulosus* as its type species.

Cannomyces spinulosus Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858454. Fig. 30.

Etymology: Referring to the production of spinulose conidiophores.

Typus: **Cuba**, Matanzas Province, Amarillas, from leaf of *Canna coccinea*, unknown collection date and *collector*, isol. 24 Jan. 1987, *R.F. Castañeda*, No. C97/30 (**holotype** designated here CBS H-25610, ex-type living isolate CBS 726.87).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.7 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface or aerial mycelium, solitary or aggregated, (sub-)erect, unbranched or sparsely branched, up to ca 45 µm long, 2.2–4.2 µm wide at base,

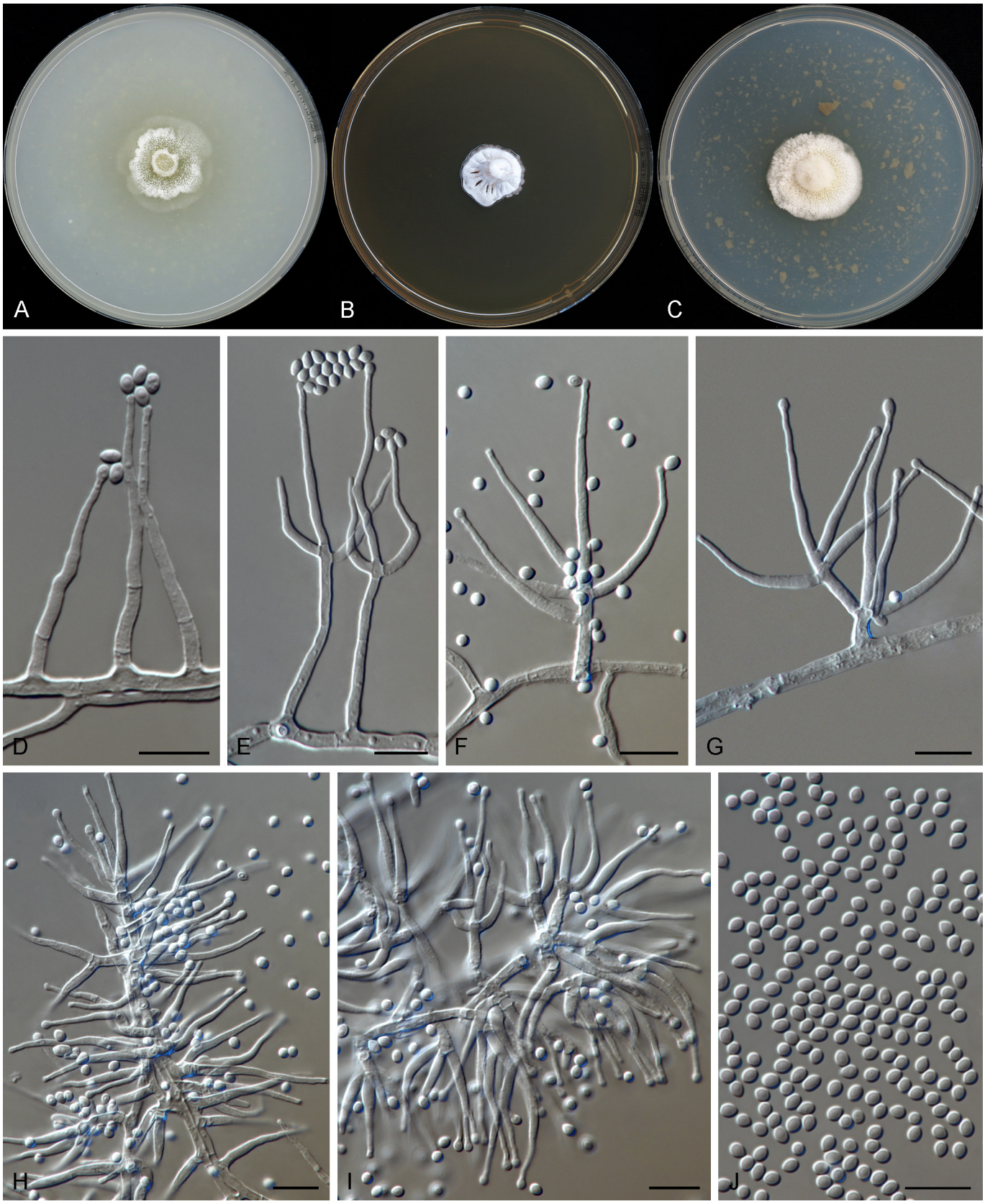

Fig. 29. *Ramosiphorum sporodochiale* (ex-type CBS 554.80). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J.** Conidia. Scale bars = 10 µm.

1–2-septate, hyaline, thick-walled, roughened or finely to coarsely spinulose, with cell walls usually thicker than those of vegetative hyphae. *Conidiogenous cells* monophialidic, mostly lateral, subulate or lageniform, straight or slightly curved, hyaline, with thick and roughened walls, spinulose, (13.7–)15.3–26.6(–33.0) µm long, (2.2–)2.4–3.6(–4.2) µm wide at base, 0.9–1.2 µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* fusoid, straight, with symmetrically thickened, truncate bases and apices, hyaline, aseptate, thick- and smooth-walled, (4.7–)5.3–7.8(–8.0) × (1.7–)1.8–2.5(–2.7) µm (av. 6.7 × 2.1 µm, n = 100), eguttulate, arranged in long chains. *Chlamydospores* and *sexual morph* not observed.

Fig. 30. *Cannomyces spinulosus* (ex-type CBS 726.87). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K.** Conidia. Scale bars = 10 µm.

Culture characteristics: Colonies on OA reaching 15–19 mm diam. after 14 d in darkness at 25 °C, flat, felty, floccose, with moderate aerial mycelium, rosy buff to buff, margin dentate, reverse rosy buff, with honey soluble pigment around margin of colony. On MEA reaching 19–20 mm diam., raised, radially folded, felty, with sparse aerial mycelium, rosy buff at centre, pale rosy buff at periphery, margin radially striate with lobate edge, reverse saffron. On PDA reaching 13–15 mm diam., raised, radially folded, felty, rugose, with sparse aerial mycelium, salmon, margin lobate, reverse umber at centre, salmon at periphery. On SNA reaching 12–13 mm diam., flat, felty, thinly granulose, with sparse aerial mycelium, white, margin irregular, reverse concolourous.

Notes: CBS 726.87 was deposited as "*Acremonium longisporum*" in the CBS collection. *Acremonium longisporum* has phialides generally simple, evenly warty along their entire length, and conidia clearly blunt at both ends, smooth, thin-walled, arranged in long chains (Gams 1971). However, DNA sequences of type material of *A. longisporum* (basionym *Torula longispora*; Preuss 1848) are not available, and according to our phylogenetic analyses, the isolate studied here is phylogenetically distinct from species of *Acremonium* s. str, forming a separate, well-supported clade (Figs 1, 4). Additionally, the only isolate of *A. longisporum*, CBS 113.69 (Gams 1971), was examined by Hou *et al.* (2023) and renamed as *Waltergamsia fusidioides*. Further collections are needed to obtain cultures of *A. longisporum*.

Clade XXXI-14. *Lasionectria* (Sacc.) Cooke, *Grevillea* **12**(no. 64): 111. 1884.

Ascomata perithecial, subglobose to globose, non-stromatic, superficial, ranging in colour from orange to dark reddish-orange or dark brown, slightly darker in KOH but not KOH+, collapsed or slightly cupulate when desiccated, often bearing fasciculate and/or solitary hairs. *Peridium* consists of two regions: an outer region composed of thick-walled, pigmented cells, and an inner region of elongate, thin-walled, hyaline cells. *Asci* clavate, unitunicate, with a simple apex, 8-spored. *Ascospores* typically ellipsoid, 1-septate, hyaline, typically smooth-walled, but occasionally warty or with longitudinal striations. *Asexual morph*: hyphomycetous, acremonium-like (adapted from Rossman *et al.* 1999, Hou *et al.* 2023).

Type: *Lasionectria mantuana* (Sacc.) Cooke

Notes: Within the *Bionectriaceae* the genus *Lasionectria* is distinguished by its ascomatal wall structure, which consists of thick-walled cells with small lumina (Rossman *et al.* 1999). Rossman *et al.* (1999) included three species within the genus: the type, *L. mantuana*, and *L. sylvana* and *L. vulpina* (currently classified as *Protocreopsis vulpina*). Hou *et al.* (2023) accepted 10 species within *Lasionectria* based on available sequence data. More recently, Zhao *et al.* (2025) described two additional species, *L. chondroidea* and *L. phormii*. In this study, we propose one further new species within *Lasionectria*.

Lasionectria eichhorniae Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858455. Fig. 31.

Etymology: Referring to the host, *Eichhornia crassipes*, from which the ex-type isolate was collected.

Typus: **USA**, Central Louisiana or Florida, from *Eichhornia crassipes*, unknown collection date and *collector*, isol. *R.E. Rintz* (**holotype** designated here CBS H-25594, ex-type living isolate CBS 211.74).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.3–2.5 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, straight or irregularly wavy, unbranched or basitonously branched, bearing 1–3 levels and with 1–3 phialides per node, up to ca 200 µm long, 2.0–4.0 µm wide at base, (1–)2–6-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, terminal or lateral, cylindrical or subcylindrical, straight or waved, hyaline, thick- and smooth-walled, (22.5–)44.2–73.8(–88.3) µm long, (1.6–)1.9–2.5(–2.9) µm wide at base, (1.1–)1.2–1.4(–1.5) µm wide near aperture, with short collarettes and periclinal thickening at conidiogenous loci. *Conidia* ellipsoid or cylindrical, straight or curved, with rounded distal ends and truncate basal ends, sometimes with a slightly laterally displaced hilum, aseptate, hyaline, thick- and smooth-walled, (3.8–)5.3–7.6(–8.3) × (2.2–)2.4–2.8(–2.9) µm (av. 6.6 × 2.6 µm, n = 100), eguttulate, arranged in dry heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 34–36 mm diam. after 14 d in darkness at 25 °C, flat, floccose, dusty, with moderate aerial mycelium, white, with concentric rings, margin crenate, reverse buff. On MEA reaching 32–34 mm diam., raised, cotton, with abundant aerial mycelium, white with saffron liquid exudate at middle, with concentric rings, margin fimbriate, reverse rust to orange. On PDA reaching 32–36 mm diam., flat, concentric rings, cotton, with abundant aerial mycelium, white, margin fimbriate, reverse apricot at centre, salmon at periphery. On SNA reaching 28–30 mm diam., flat, felty, with sparse aerial mycelium, dusty, white, margin entire, reverse concolourous.

Notes: The isolate CBS 211.74 was previously identified as "*Acremonium zonatum*" in the CBS collection, a species currently considered a synonym of *Mycocitrus zonatus*. However, in our molecular phylogeny it forms an independent lineage within *Lasionectria*, clearly distinct from all currently known species of this genus (Fig. 4, clade XXXI-14).

Based on a BLASTn search of the NCBI GenBank nucleotide database the closest hits of CBS 211.74 using the ITS sequence are listed as *Septofusidium stevensiae* isolated from Australia [BRIP 72951a; GenBank NR_182628; Identity = 482/529 (91 %), 18 gaps (3 %)]; *Lasionectria sansevieriae*, isolated from *Sansevieria hyacinthoides* leaves in South Africa [CBS 146973; GenBank NR_173049; Identity = 531/588 (90 %), 21 gaps (3 %)]; the closest hit using the LSU sequence is *Acremonium biseptum* (current name *Lasionectria bisepta*), isolated from wheat field soil in Netherlands [CBS 753.69; GenBank MH871184; Identity = 757/774 (98 %), no gaps (0 %)]; the closest hit using the *RPB2* sequence is *Lasionectria cerealis*, isolated from sand dune soil A1 horizon in United Kingdom [CBS 207.65; GenBank OQ454080; Identity = 641/756 (85 %), no gaps (0 %)]; the closest hit using the *TEF1* sequence is *Lasionectria antillana*, isolated from dead inflorescence of *Heliconia* in Martinique [CBS 122797; GenBank OQ470981; Identity = 669/706 (95 %), no gaps (0 %)].

Clade XXXI-15. *Verruciconidia* L.W. Hou *et al.*, *Stud. Mycol.* **105**: 87. 2023.

Mycelium consisting of branched, septate, hyaline or pale brown, thin or thick-walled, rough- or smooth-walled hyphae. *Conidiophores* arise from vegetative hyphae or from ropes formed by the mycelium, (sub-)erect, straight or curved, unbranched or sparsely branched, hyaline, septate, with smooth or rough walls. *Conidiogenous cells* enteroblastic, monophialidic, terminal or lateral, (sub)cylindrical or subulate, hyaline, with thick, rough or smooth walls, and conspicuous or inconspicuous collarette and periclinal thickening at conidiogenous loci; adelophialides may be present or absent; polyphialides with two conidiogenous loci occasionally present. *Conidia* cylindrical, (broadly) ellipsoid, ovoid, subglobose, clavate, oval or oblong, rounded at both ends or with slightly apiculate or truncate bases, straight, aseptate, hyaline, thin- or thick- walled, smooth- or rough- walled, eguttulate or guttulate, arranged in slimy/

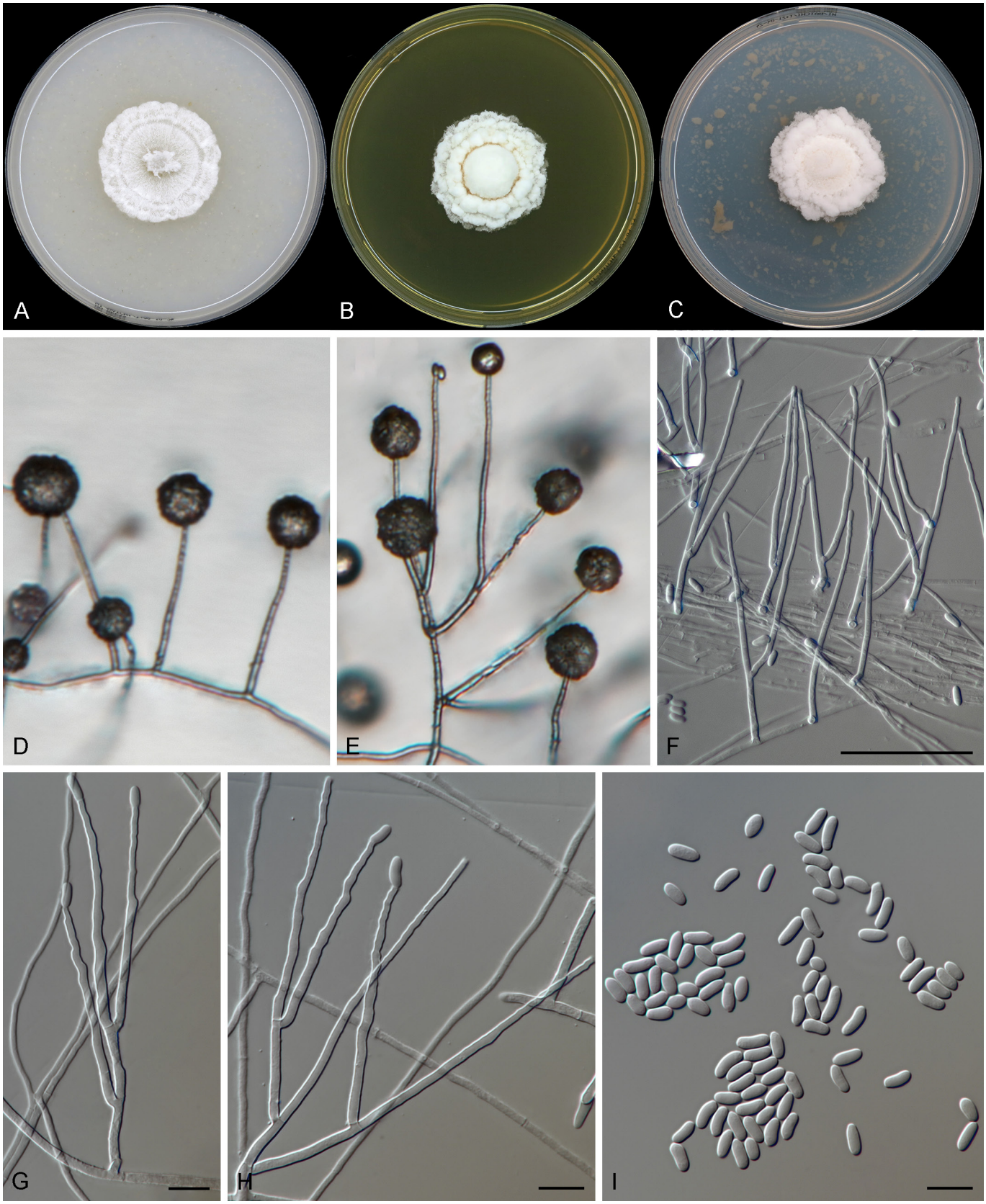

Fig. 31. *Lasionectria eichhorniae* (ex-type CBS 211.74). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–H.** Conidiophores. **I.** Conidia. Scale bars: G–I = 10 µm; F = 50 µm.

dry heads or long chains. *Chlamydospores* and *sexual morph* not observed (adapted from Hou *et al.* 2023).

Type: *Verruciconidia verruculosa* (Nicot) L.W. Hou *et al.*

Notes: *Verruciconidia* was introduced by Hou *et al.* (2023) to accommodate species characterised by the production of verrucose (warty) conidia. Hou *et al.* (2023) accepted seven species within *Verruciconidia* based on available sequence data. Here, we propose an additional four new species, supported by phylogenetic analyses and morphological characteristics.

Verruciconidia maritima Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858457. Fig. 32.

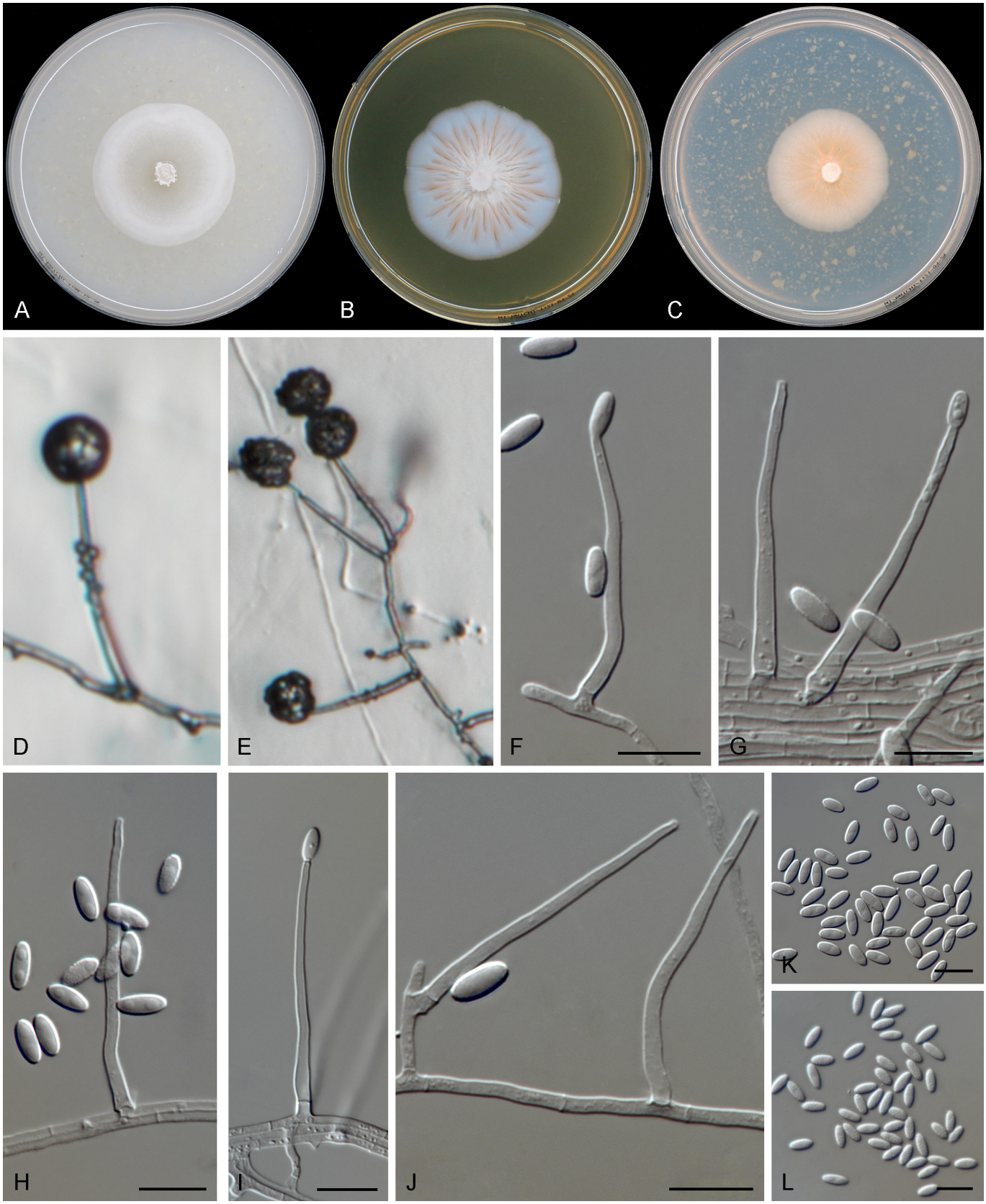

Fig. 32. *Verruciconidia maritima* (ex-type CBS 385.96). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K, L.** Conidia. Scale bars = 10 µm.

Etymology: Referring to the location along the coast from which the holotype isolate was collected.

Typus: **Papua New Guinea**, Madang, Jais Aben, from stony soil along the coast, Nov. 1995, *A. Aptroot*, isol. Nov. 1995, *A. van Iperen*, No. A 193 (**holotype** designated here CBS H-25601, ex-type living isolate CBS 385.96).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.2–2.4 µm wide, forming bundles. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from vegetative hyphae or from ropes and coils formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or sparsely branched, up to ca 75 µm long, 1.8–3.2 µm wide at base, 1–2(–3)-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, subulate or (sub)cylindrical, slightly swollen at lower part, straight or slightly curved, hyaline, thick and smooth-walled, (5.3–)7.8–40.2(–43.3) µm long, (1.3–)1.5–2.5 µm wide at base, 0.8–1.1(–1.3) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* cylindrical or ellipsoid, with rounded distal ends and truncate basal ends, aseptate, hyaline, thick- and rough-walled, (5.2–)5.7–7.3(–7.6) × (2.1–)2.4–3.1(–3.4) µm (av. 6.5 × 2.8 µm, n = 100), guttulate, arranged in dry heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 40–43 mm diam. after 14 d in darkness at 25 °C, flat, felty, dusty, with sparse aerial mycelium, buff at centre, white at periphery, margin entire, reverse dirty white. On MEA reaching 42–45 mm diam., raised, radially folded, felty, with sparse aerial mycelium, salmon at centre, dirty white at periphery, margin lobate, reverse saffron with white radial lines. On PDA reaching 34–41 mm diam., flat, radially folded, felty, with sparse aerial mycelium, saffron at centre, dirty white at periphery, margin entire, reverse salmon with radial lines. On SNA reaching 25–29 mm diam., flat, membranous without aerial mycelium, white, margin rhizoids, reverse concolourous.

Notes: *Verruciconidia maritima* is closely related to *V. terricola* and *V. verruculosa* (Fig. 4, clade XXXI-15). Morphologically, *V. maritima* differs from *V. terricola* in producing larger conidia, which are (5.2–)5.7–7.3(–7.6) × (2.1–)2.4–3.1(–3.4) µm (av. 6.5 × 2.8 µm) in *V. maritima*, vs (3.9–)4.6–5.8(–6.5) × (2.1–)2.2–3.0(–3.1) µm (av. 5.2 × 2.6 µm) in *V. terricola*. It also differs from *V. verruculosa* in producing longer conidiophores (up to 75 µm long in *V. maritima* vs 46.5 µm in *V. verruculosa*; Hou *et al.* 2023).

Verruciconidia indonesiana Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858458. Fig. 33.

Etymology: Referring to the country, Indonesia, from which the holotype isolate was collected.

Typus: **Indonesia**, from alkaline soil, unknown collection date and *collector*, isol. *K. Nagai*, Drug Serendipity Research Laboratories, Yamanouche Pharmaceutical Co., Tokyo, Japan (**holotype** designated here CBS H-25611, ex-type living isolate CBS 737.94).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.2–2.8 µm wide. *Sporulation* phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or sparsely branched, up to ca 87 µm long, 1.6–3.8 µm wide at base, 1–3-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, terminal or lateral, cylindrical or subulate, straight, hyaline, with smooth and thick walls, (13.1–)16.1–48.5(–50.5) µm long, (1.6–)1.7–2.8(–3.1) µm wide at base, 1.0–1.3(–1.4) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* cylindrical or clavate, with rounded distal ends and truncate basal ends, aseptate, hyaline, thin- and smooth-walled, (4.1–)4.7–8.0(–9.6) × (1.9–)2.0–2.7(–2.9) µm (av. 6.1 × 2.3 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 66–70 mm diam. after 14 d in darkness at 25 °C, flat, felty, with sparse aerial mycelium or membranous without aerial mycelium, dirty white, margin entire, reverse concolourous. On MEA reaching 60–67 mm diam., flat, floccose, hairy, with abundant aerial mycelium, white at centre, dirty white at periphery, margin entire, reverse saffron with radial lines. On PDA reaching 71–80 mm diam., flat, aerial mycelium arranged radially, floccose, mycelial ropes abundant, dirty white, margin filiform, reverse concolourous. On SNA reaching 62–64 mm diam., flat, felty, with sparse aerial mycelium, dusty, white, margin entire, reverse concolourous.

Notes: The isolate CBS 737.94 was isolated from alkaline soil in Indonesia and tentatively identified as "*Acremonium* sp.". According to our phylogenetic analyses, *V. indonesiana* is represented by a single isolate, which forms a basal branch and is distantly related to other species within *Verruciconidia* (Fig. 4, clade XXXI-15). The morphology of this species fits well with that of *Verruciconidia*, being acremonium-like, with unbranched or sparsely branched conidiophores and cylindrical or ellipsoid conidia.

Based on a BLASTn search of NCBI GenBank nucleotide database, the closest hit using the ITS sequence of *V. indonesiana* (CBS 737.94) is *V. persicina*, isolated from a water sample in Mexico (Cuatro Cienegas) [isolate DD; GenBank KU933732; Identity = 475/541 (88 %), 24 gaps (4 %)]. The closest hit using the LSU sequence is *Paracylindrocarpon foliicola*, isolated from *Puteria pallida* leaf in France [CBS 140758; GenBank KX986914; Identity = 769/777 (99 %), two gaps (0 %)].

Verruciconidia terricola Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858459. Fig. 34.

Etymology: Referring to the substrate, soil, from which this species was isolated.

Typus: **Germany**, Kiel-Kitzeberg, from wheat field soil, isol. 1962, by *W. Gams*, No. C 176 (**holotype** designated here CBS H-25602, ex-type living isolate CBS 431.66).

Mycelium consisting of branched, septate, hyaline, smooth, thin- or thick-walled hyphae, 1.3–3.2 µm wide, forming bundles. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes formed by mycelium, solitary or aggregated, (sub-)erect, unbranched or sparsely branched, up to ca 65 µm long, 2.3–3.9 µm wide at base, 1–3-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, terminal or lateral, subulate, hyaline, with thick, smooth or rough walls, (30.0–)32.6–43.0(–49.0) µm long, (1.9–)2.1–2.6(–2.8) µm wide at base, 0.9–1.1 µm wide near aperture, with short

collarettes and inconspicuous periclinal thickening at conidiogenous loci. *Conidia* ellipsoid or oval, with both ends rounded, or with truncate bases, aseptate, hyaline, thick- and rough-walled, warty, (3.9–)4.6–5.8(–6.5) × (2.1–)2.2–3.0(–3.1) µm (av. 5.2 × 2.6 µm, n = 100), guttulate, arranged in dry conidial heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 46–49 mm diam. after 14 d in darkness at 25 °C, flat, felty, dusty, with abundant aerial mycelium, dirty white, with concentric rings, margin entire, reverse whitish. On MEA reaching 43–45 mm diam., flat, radially folded, felty, with moderate aerial mycelium, dirty white to buff, margin entire, reverse saffron with white radial lines. On PDA reaching 50–

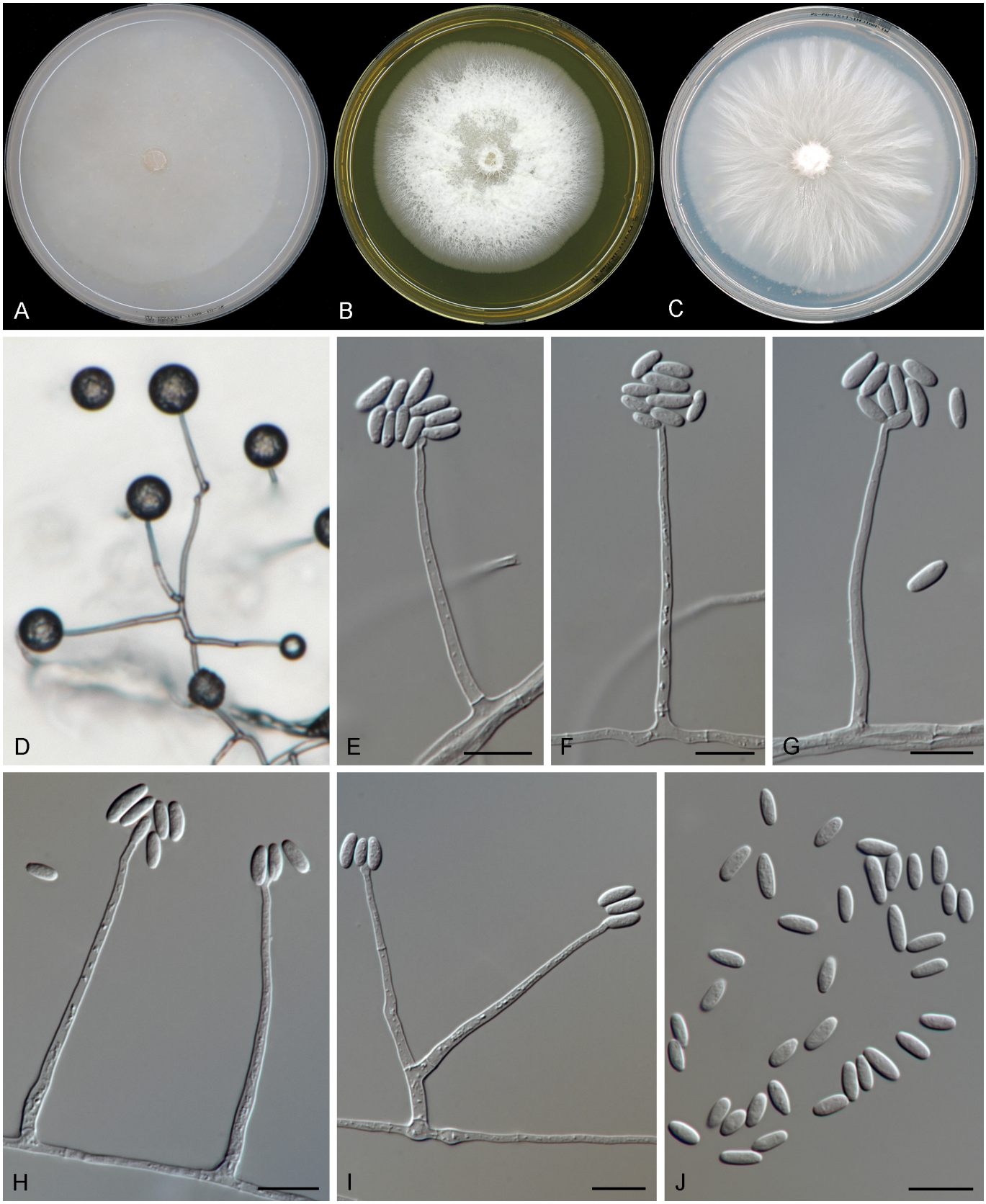

Fig. 33. *Verruciconidia indonesiana* (ex-type CBS 737.94). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J.** Conidia. Scale bars = 10 µm.

52 mm diam., flat, felty, granulose, with abundant aerial mycelium, dirty white, margin entire, reverse pale buff with radial lines. On SNA reaching 48–50 mm diam., flat, dusty, with sparse aerial mycelium, white, margin entire, reverse whitish.

Additional material examined: **Chile**, from soil, unknown collection date and *collector*, isol. *J. Grinbergs*, No. 115.73, isolate CBS 568.74.

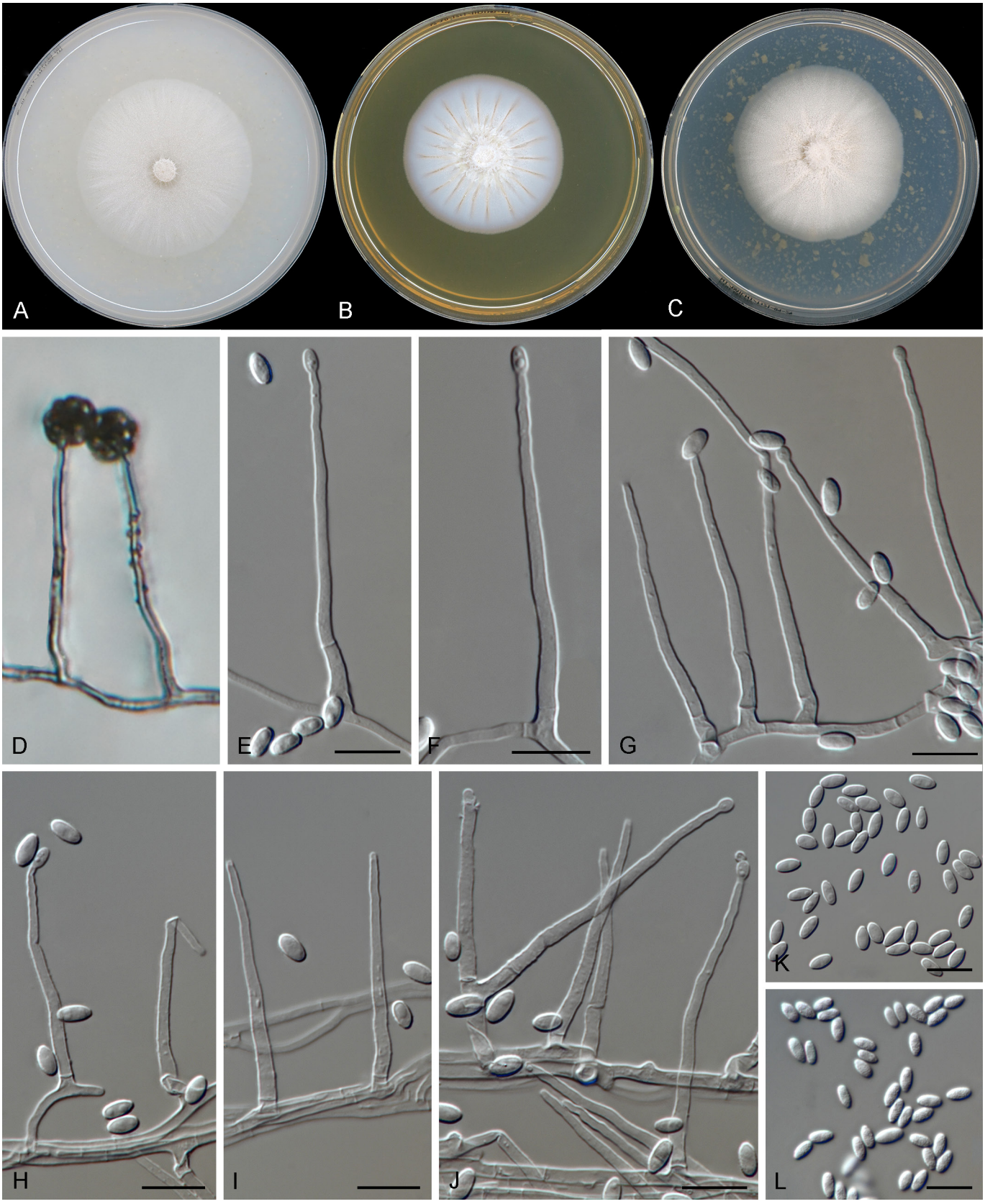

Fig. 34. *Verruciconidia terricola* (ex-type CBS 431.66). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K, L.** Conidia. Scale bars = 10 µm.

Notes: Based on the phylogenetic analyses, *Verruciconidia terricola* has a close phylogenetic affinity to *V. maritima* and *V. verruculosa*. However, *V. terricola* (CBS 431.66) differs clearly from *V. maritima* (CBS 385.96) in the ITS (99.1 % identity, with 5 bp differences), LSU (99.9 %, 1 bp), *RPB2* (94.3 %, 43 bp), and *TEF1* (96.6 %, 26 bp) sequences. Similarly, *V. terricola* differs clearly from *V. verruculosa* (CBS 989.69) in the ITS (98.3 % identity, with 9 bp differences), LSU (99.9 %, 1 bp), *RPB2* (95.6 %, 33 bp), and *TEF1* (97.7 %, 17 bp) sequences. Morphologically, *V. terricola* can be distinguished from *V. maritima* by its smaller conidia, (3.9–)4.6–5.8(–6.5) × (2.1–)2.2–3.0(–3.1) µm (av. 5.2 × 2.6 µm, n = 100) in *V. terricola*, vs (5.2–)5.7–7.3(–7.6) × (2.1–)2.4–3.1(–3.4) µm (av. 6.5 × 2.8 µm, n = 100) in *V. maritima*, and from *V. verruculosa* by its shorter conidiophores, up to ca 65 µm long in *V. terricola* vs up to ca 46.5 µm long in *V. verruculosa* (Hou *et al.* 2023).

Verruciconidia thailandica Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858460. Fig. 35.

Etymology: Referring to the country, Thailand, from which the holotype isolate was collected.

Typus: **Thailand**, Chiang Mai Province, Mae Taeng Distr., Ban Pha Deng village, 900 m.a.s.l., from decaying wood, 9 Aug. 2014, *W. Gams* (**holotype** designated here CBS H-25589, ex-type living isolate CBS 139715).

Mycelium consisting of branched, septate, hyaline, smooth, thin- or thick-walled hyphae, 1.3–2.6 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* arising from the agar surface, aerial hyphae, or ropes and coils formed by mycelium, solitary or aggregated, (sub-) erect, unbranched, or branched, bearing up to 1–2 levels with 1–2 phialides per node, up to ca 82 µm long, 1.9–3.3 µm wide, 1–3(–4)-septate, hyaline, smooth- or rough-walled. *Conidiogenous cells* monophialidic, terminal or lateral, cylindrical or subulate, straight or slightly curved, hyaline, thick and rough-walled, (12.8–)20.4–42.3(–45.0) µm long, (1.5–)2.0–2.8(–3.1) µm wide at base, (0.9–)1.0–1.4 µm wide near aperture, with minute inconspicuous collarettes and periclinal thickening at conidiogenous loci; polyphialides with two conidiogenous loci occasionally present. *Conidia* cylindrical or oblong, with both ends rounded, or with slightly truncate bases, aseptate, hyaline, thick- and smooth-walled, (4.8–)5.1–6.4(–6.9) × (1.9–)2.1–2.4(–2.5) µm (av. 5.8 × 2.3 µm, n = 100), guttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 44–45 mm diam. after 14 d in darkness at 25 °C, flat, felty, with sparse aerial mycelium, rosy buff at centre, dirty white at periphery, with inconspicuous white radial lines, margin lobate, reverse buff. On MEA reaching 43–44 mm diam., flat, radially folded, felty, with abundant aerial mycelium, rosy buff to dirty white, with concentric rings, margin crenate, reverse saffron. On PDA reaching 45–46 mm diam., flat, felty, with moderate aerial mycelium, rosy buff to dirty white, with concentric rings, margin crenate, reverse buff. On SNA reaching 32–36 mm diam., flat, felty, with moderate aerial mycelium, dusty, white, margin entire, reverse concolourous.

Notes: Phylogenetically, *Verruciconidia thailandica* is closely related to *V. guizhouensis*, but it differs by producing longer, narrower conidia, (4.8–)5.1–6.4(–6.9) × (1.9–)2.1–2.4(–2.5) µm (av. 5.8 × 2.3 µm) in *V. thailandica* compared to 3.5–5.0 × 2.5–3.0 µm in *V. guizhouensis*. Additionally, *V. thailandica* produces longer phialides, (12.8–)20.4–42.3(–45.0) µm, while in *V. guizhouensis* phialides are 15.5–33.5 µm long. Furthermore, the molecular sequences distinguish *V. thailandica* (CBS 139715) and *V. guizhouensis* (SQT04): ITS (94.0 % identity, with 30 bp differences), *RPB2* (89.9 %, with 76 bp differences), and *TEF1* (96.2 %, with 28 bp differences) (Tong *et al.* 2023).

Clade XXXI-40. *Pilgeriellomyces* Lin Zhao & Crous, ***gen. nov.*** MycoBank MB 858461.

Etymology: Referring to the host, *Pilgeriella anacardii*, from which the type species was collected.

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae. *Conidiophores* solitary or aggregated, (sub-) erect, straight or slightly curved, arising directly from the agar surface, superficial hyphae, or ropes of hyphae, unbranched or sparsely branched, hyaline, smooth-walled. *Conidiogenous cells* enteroblastic, monophialidic, mostly lateral, subcylindrical or acicular, hyaline, with thick, smooth walls, and inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* cylindrical or ellipsoidal, with both sides rounded, aseptate, hyaline, eguttulate, and arranged in slimy heads.

Type: *Pilgeriellomyces brasiliensis* Lin Zhao & Crous

Notes: *Pilgeriellomyces* represents a distinct lineage and is phylogenetically segregated from other genera within *Bionectriaceae* (Figs 1, 4). Morphologically, *Pilgeriellomyces* is characterised by acremonium-like fungi, with simple conidiophores and aseptate, ellipsoidal conidia.

Pilgeriellomyces brasiliensis Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858462. Fig. 36.

Etymology: Referring to the country, Brazil, where all isolates of this species were collected.

Typus: **Brazil**, State Ceará, Pacajus county, *Pilgeriella anacardii*, on leaf of *Anacardium occidentale*, unknown collection date, *F.C.O. Freire*, isol. 1997, *W. Gams*, No. 3 (**holotype** designated here CBS H-25573, ex-type living isolate CBS 100346).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.2 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* solitary or aggregated, (sub-)erect, straight or slightly curved, arising directly from the agar surface or superficial hyphae, or from ropes of hypha, unbranched or sparsely branched, up to ca 75 µm long, (1.4–)1.5–2.4(–2.8) µm wide at base, 1–3-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, mostly lateral, subcylindrical or acicular, hyaline, thick- and smooth-walled, (35.0–)37.3–60.4(–68.1) µm long, 1.4–2.0(–2.1) µm wide at base, 0.7–0.9 µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci. *Conidia* cylindrical or ellipsoidal, both sides rounded, aseptate, hyaline, thin- and smooth-walled, (3.1–)3.2–4.7(–5.0) × (1.1–)1.2–1.6(–1.7) µm (av. 3.8 × 1.4 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 33–35 mm diam. after 14 d in darkness at 25 °C, flat, membranous, with sparse aerial mycelium, white, margin entire, reverse primrose. On MEA reaching 31–34 mm diam., raised, radially folded, rugose, floccose, with moderate aerial mycelium, white to buff, margin lobate, reverse saffron with white radial lines. On PDA reaching 33–35 mm diam., raised, radially folded, floccose, with moderate aerial mycelium, rosy buff, margin entire, reverse buff to rosy buff, with radial lines. On SNA reaching 27–31 mm diam., flat, dusty, with sparse aerial mycelium, white, margin crenate, reverse concolourous.

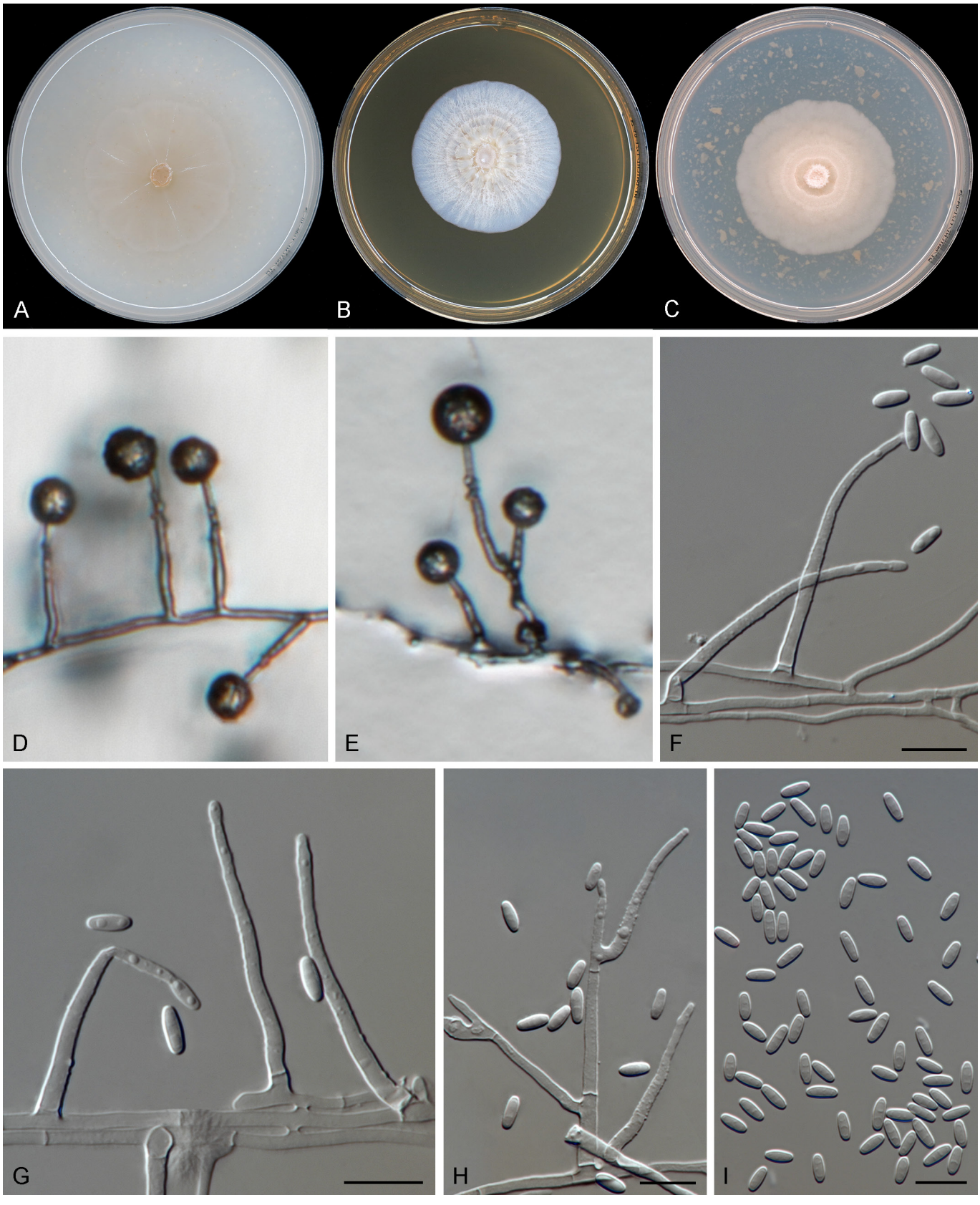

Fig. 35. *Verruciconidia thailandica* (ex-type CBS 139715). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–H.** Conidiophores. **I.** Conidia. Scale bars = 10 µm.

Additional material examined: **Brazil**, State Ceará, Pacajus county, *Pilgeriella anacardii*, on leaf of *Anacardium occidentale*, unknown collection date, *F.C.O. Freire*, isol. 1997, *W. Gams*, No. 3, isolate CBS 100345.

Notes: The CBS 100345 and CBS 100346 were isolated from *Pilgeriella anacardii* on a leaf of *Anacardium occidentale* in Brazil, and deposited as "*Acremonium* sp." in the CBS collection, representing the new species *Pilgeriellomyces brasiliensis*.

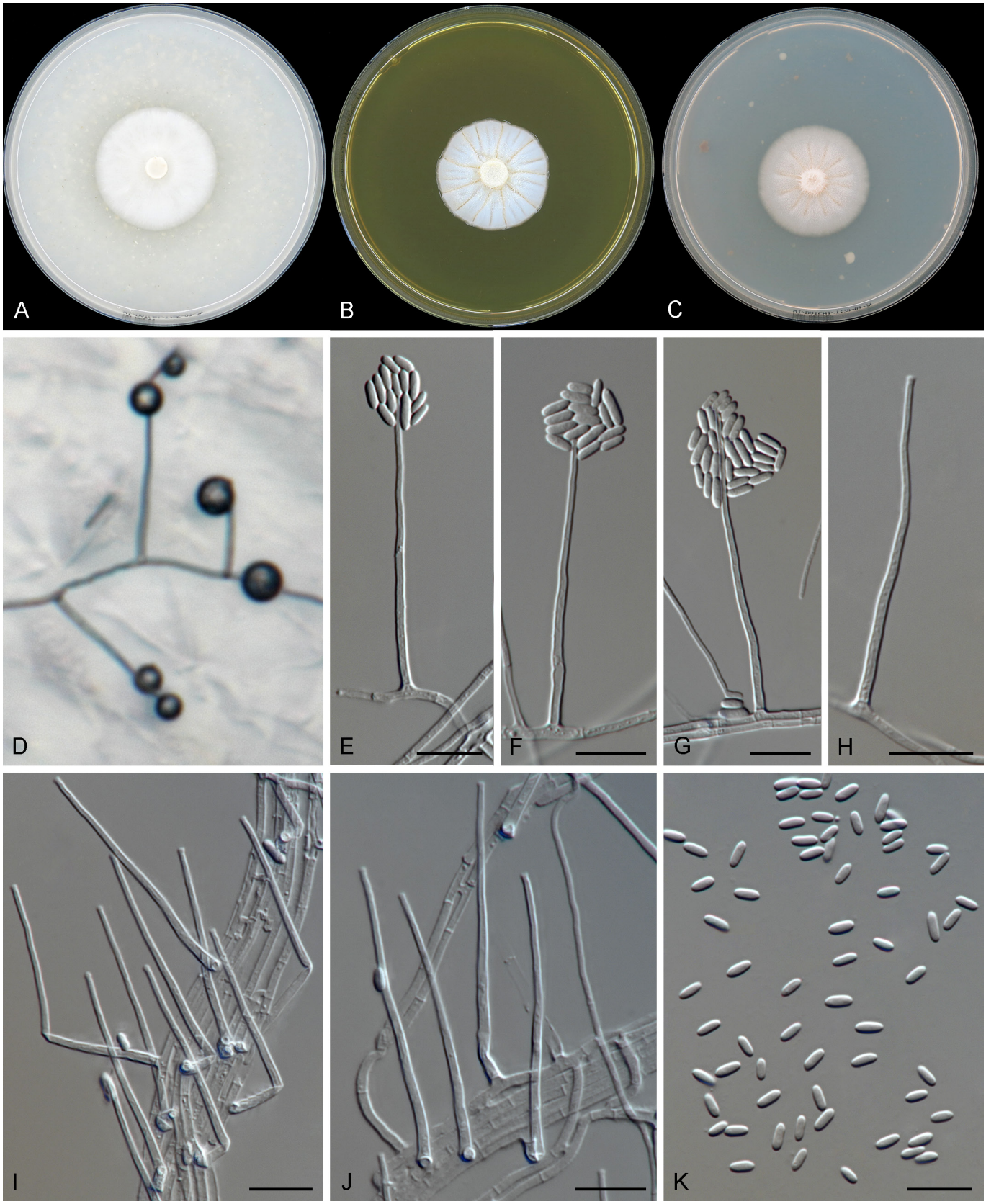

Fig. 36. *Pilgeriellomyces brasiliensis* (ex-type CBS 100346). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K.** Conidia. Scale bars = 10 µm.

Based on a BLASTn search of NCBI GenBank nucleotide database, the closest hit for the ITS sequence is *Geosmithia* sp., isolated from mangrove rhizosphere sediments in Kenya [RMM15F1, GenBank MT543122; Identity = 402/436 (92 %), nine gaps (2 %)]. The closest hit for the LSU sequence is *Geosmithia microcorthyli*, isolated from the ambrosial layer on the gallery wall of *Microcorthylus* sp. in Costa Rica [CCF 3861, ex-type isolate of *Geosmithia microcorthyli*; GenBank NG_067560; Identity = 762/777 (98 %), one gap (0 %)]. The closest hit for the *RPB2* sequence is *Geosmithia capensis*, isolated from *Widdringtonia cedarbergensis* in South Africa, Cederberg [CMW59310, GenBank PQ045586; Identity = 348/453 (77 %), 11 gaps (2 %)]. The closest hit for the *TEF1* sequence is *Bulbithecium borodinense*, isolated from soil in a sugarcane field in Japan [CBS 101148, GenBank OQ470795; Identity = 753/795 (95 %), no gaps].

Clade XXXI-53. *Acremonium* Link, *Mag. Gesell. Naturf. Freunde*, Berlin **3**(1–2): 15. 1809.

Mycelium consisting of branched, septate, hyaline, smooth hyphae, with thin or thick walls. *Conidiophores* arise directly from aerial or substratal mycelium, from ropes or coils formed by mycelium, solitary, erect, straight or irregularly curved, unbranched or repeatedly basitonously, verticillately, or asymmetrically branched, 1–3(–10)-septate, hyaline, smooth-walled, proliferating sympodially or percurrently. *Conidiogenous cells* enteroblastic, mono- or polyphialidic, lateral or terminal, awl-shaped, subulate, (sub-) cylindrical, or acicular, hyaline, smooth, with thin or thick walls, with a distinct or inconspicuous collarette and periclinal thickening at the conidiogenous loci, with percurrent or subterminal proliferations in some species and chromophilic staining on basal septum in others; polyphialides present or absent. *Conidia* with a variable shape, ranging from bacilliform, cylindrical, ellipsoidal, fusoid to short fusoid, (sub-)globose, ovoid, obovoid, pyriform to tear-shaped, with both ends rounded, or truncate or apiculate at apices or bases, with or without a hilum, aseptate, hyaline or slightly pigmented, with smooth, thin or thick walls, eguttulate or guttulate, arranged in slimy heads or in chains. *Chlamydospores* present or absent. *Sexual morph* not observed (adapted from Hou *et al.* 2023).

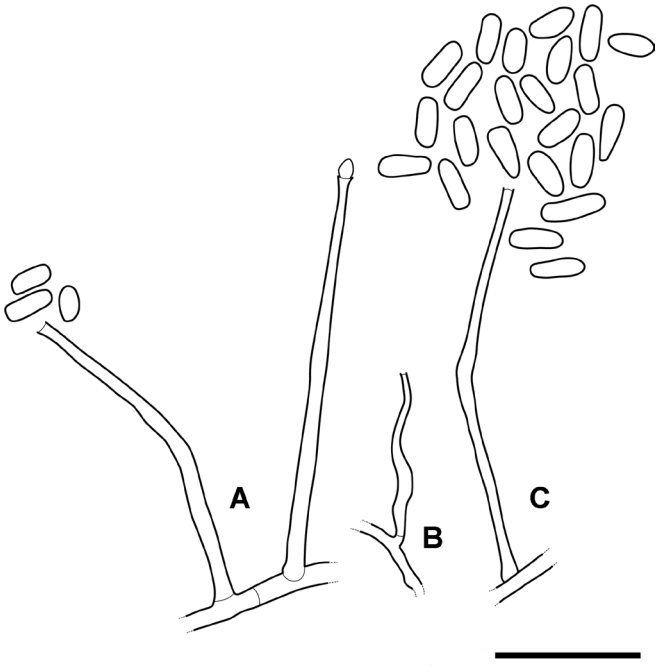

Fig. 37. *Acremonium ecuadorense* (ex-type CBS 113632). **A, C.** Conidiophores and conidia. **B.** Conidiophore. Scale bars = 10 µm.

Type: *Acremonium alternatum* Link

Notes: Multi-locus phylogenetic analyses conducted by Hou *et al.* (2023) demonstrated that *Acremonium* s. str., which includes the generic type species *A. alternatum* (ex-type isolate CBS 407.66), is confined to the *Bionectriaceae*. Zhao *et al.* (2025) agreed with the findings of Hou *et al.* (2023), who recognized 19 species within the genus *Acremonium*. In addition, Zhao *et al.* (2025) incorporated an additional known species, *A. agapanthi* (Crous *et al.* 2024a), proposed a new species, and established a robust phylogenetic framework, bringing the total number of recognized species to 21. Therefore, to date, *Acremonium* s. str. comprises 22 species with available DNA data, including *A. behniae* (Crous *et al.* 2020), which was not included in the previous treatments. Below, we add four new species to this genus.

Acremonium ecuadorense Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858463. Fig. 37.

Etymology: Named after the country where the fungus was collected, Ecuador.

Typus: **Ecuador**, *Theobroma*, unknown collection date, *H.C. Evans & K.A. Holmes*, CABI (**holotype** designated here CBS H-25580, ex-type living isolate CBS 113632).

Culture sterile. *Acremonium ecuadorense* differs from its close phylogenetic neighbours *A. behniae* (CBS 146824) (Fig. 4) by unique nucleotide substitutions and indels in the four investigated loci (see direct sequence comparisons deposited at figshare.com; doi: 10.6084/m9.figshare.28705967): *A. ecuadorense* (CBS 113632) and *A. behniae* (CBS 146824): ITS position 24 (A), 30 (C), 39 (C), 46 (gap), 62 (T), 65 (T), 68 (A), 85 (T), 102 (T), 103 (gap), 106 (gap), 115 (gap), 124 (gap), 163 (G), 188 (G), 203 (G), 204 (C), 206 (T), 221 (G), 230 (T), 250 (T), 251 (C), 259 (T), 275 (C), 276 (T), 283 (T), 288 (G), 324 (A), 539 (G), 546 (C), 556 (T), 586 (G), 599 (C), 600 (T), 602 (T), 610 (C), 612 (G), 616 (C), 617 (A), 652 (gap), 657 (C), 669 (C), 683 (gap), 684 (T), 685 (C), 686 (T), 691 (T), 700 (T), 716 (gap), 717 (gap), 723 (A), 738 (A), 765 (A), 760 (C), 763 (C), 768 (T), 779 (gap), 782 (G), 783 (A), 791 (C), 795 (C), 798 (C). LSU position: 946 (C), 949 (T), 1015 (C), 1031 (A), 1034 (G), 1072 (A), 1223 (C), 1225 (A), 1267 (T), 1268 (G), 1269 (T), 1300 (C), 1306 (C), 1325 (T), 1326 (C), 1351 (T); *RPB2* position 1666 (T), 1672 (G), 1681 (T), 1684 (C), 1690 (T), 1693 (C), 1696 (T), 1699 (C) 1708 (G), 1711 (C), 1714 (A), 1723 (G), 1734 (C), 1736 (T), 1745 (C), 1746 (T) 1751 (T), 1752 (T), 1760 (C), 1766 (C), 1769 (G), 1772 (A), 1775 (T), 1793 (A), 1799 (T), 1812 (A), 1817 (T), 1826 (A), 1829 (G), 1832 (A), 1835 (A), 1844 (T), 1848 (A), 1850 (G), 1859 (C), 1862 (A), 1865 (C), 1880 (C), 1884 (A), 1885 (G) 1886 (T), 1898 (T), 1904 (T), 1910 (A), 1911 (C), 1912 (G), 1913 (C), 1916 (T) 1931 (C), 1952 (A), 1956 (T), 1967 (A), 1970 (G), 1988 (C), 1998 (T), 2001 (A), 2010 (C), 2013 (C), 2016 (T), 2019 (C), 2025 (C), 2031 (C), 2040 (G), 2046 (T), 2052 (T), 2058 (A), 2061 (A), 2070 (T), 2076 (T), 2079 (A), 2085 (C), 2091 (A), 2097 (G), 2098 (C), 2118 (C), 2121 (T), 2123 (G), 2133 (C), 2136 (G), 2143 (G), 2145 (T), 2148 (C), 2157 (A), 2166 (G), 2169 (A), 2205 (G), 2208 (T), 2211 (C), 2223 (T), 2226 (C), 2236 (T), 2238 (G), 2241 (C), 2244 (T), 2247 (A), 2250 (A), 2253 (G), 2256 (A), 2268 (T), 2278 (T), 2281 (C), 2284 (A), 2288 (C), 2299 (T), 2308 (A), 2317 (G), 2320 (C), 2326

(A), 2329 (C), 2332 (G), 2338 (T), 2347 (T), 2348 (A), 2349 (C), 2368 (A), 2378 (A), 2387 (A), 2399 (A), 2402 (T), 2411 (A), 2414 (T), 2423 (T), 2429 (T), 2432 (C), 2441 (C), 2444 (T), 2450 (C); *TEF1* position 2492 (C), 2513 (G), 2516 (C), 2522 (C), 2579 (A), 2654 (T), 2657 (T), 2661 (C), 2666 (C), 2676 (C), 2678 (T), 2685 (C), 2697 (G), 2698 (C), 2702 (T), 2714 (C), 2727 (G), 2728 (G), 2738 (G), 2742 (C, insertion), 2743 (T, insertion), 2744 (C, insertion), 2749 (G), 2750 (T), 2766 (G), 2769 (C), 2785 (G), 2802 (T), 2805 (T), 2808 (T), 2893 (G), 2928 (C), 2955 (G), 2979 (C), 2980 (G), 2983 (C), 2989 (G), 2990 (A), 2991 (G), 3027 (C), 3030 (G), 3039 (T), 3045 (C), 3085 (C), 3086 (A), 3087 (A), 3093 (C), 3132 (C), 3147 (C), 3150 (C), 3156 (C), 3162 (T), 3168 (C), 3210 (T), 3248 (G).

Description based on drawing from CBS 113632: *Mycelium* consisting of branched, septate hyphae, 1.0–1.5 µm wide. *Conidiophores* solitary, erect, unbranched, 1-septate at base, 25.0–29.0 µm long, 1.4–2.0 µm wide at base. *Conidiogenous cells* monophialidic, lateral, acicular or subcylindrical, 23.0–28.0 µm long, 1.4–2.0 µm wide at base, 0.6–1.0 µm wide near aperture. *Conidia* cylindrical or clavate, with rounded ends, aseptate, 2.0–4.5 × 1.1–1.8 µm.

Culture characteristics: Colonies on OA reaching 19–23 mm diam. after 14 d in darkness at 25 °C, flat, felty, with abundant aerial mycelium, white, with concentric rings, margin entire, reverse dirty white. On MEA reaching 24–26 mm diam., flat, felty, with abundant aerial mycelium, white, with concentric rings, margin entire, reverse saffron at centre, pale luteous at periphery. On PDA reaching 11–12 mm diam., flat, felty, with moderate aerial mycelium, white to buff, with concentric rings, margin dentate, reverse rosy buff. On SNA reaching 17–19 mm diam., flat, felty, granulose, with moderate aerial mycelium, white, margin entire, reverse concolourous.

Notes: The isolate CBS 113632, collected from *Theobroma* sp. in Ecuador, did not sporulate in culture during our observations; therefore, this species is described based on DNA sequence data. Fortunately, R.C. Summerbell made a drawing while he was at the Westerdijk Institute, and we have included it as a morphological illustration to complement the sequence-based description (Fig. 37). Phylogenetically, it is distinct from other sequenced *Acremonium* species (Fig. 4, clade XXXI-53). Therefore, *A. ecuadorense* is introduced here as a new species.

Based on a BLASTn search of NCBI GenBank nucleotide database, the closest hit for the ITS sequence is *A. charticola*, isolated from nails in Greece [UOA/HCPF 14413, GenBank KC253940; Identity = 507/555 (91 %), nine gaps (1 %)]. The closest hit for the LSU sequence is *A. acutatum*, isolated from nails in China [isolate 03914, GenBank KT878339; Identity = 767/778 (99 %), two gaps (0 %)]. The closest hit for the *RPB2* sequence is *A. acutatum*, isolated from skin scraping of a patient with clinical eczema in the Netherlands [CBS 829.73, GenBank OQ453834; Identity = 625/758 (82 %), four gaps (0 %)]. The closest hit for the *TEF1* sequence is *A. egyptiacum*, isolated from Iran [CBS 113719, GenBank OQ470758; Identity = 733/779 (94 %), four gaps (0 %)].

Acremonium proliferatum Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858464. Fig. 38.

Etymology: Referring to conidiophores with percurrent proliferation.

Typus: **Unknown**, human fingernail, together with *Candida parapsilosis* and *Trichophyton rubrum*, unknown collection date and *collector*, isol. *G.G. & G.D. Haarlem*, No. C 86-248 (**holotype** designated here CBS H-25604, ex-type living isolate CBS 486.86).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–2.3 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous. *Conidiophores* solitary or aggregated, (sub-)erect, straight or slightly curved, arising directly from the agar surface or superficial hyphae, unbranched or basitonously branched, usually proliferating percurrently, up to ca 121 µm long, (1.2–)1.5–2.3(–2.4) wide at base, 1–3(–4)-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, (sub-)cylindrical, hyaline, thick- and smooth-walled, (13.4–)21.0–43.4(–47.7) µm long, (1.0–)1.4–2.1(–2.2) µm wide at base, 0.7–1.0(–1.1) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci, with percurrent proliferation. *Conidia* aseptate, ellipsoidal, ovoid, or short cylindrical, with round distal ends and indistinctly apiculate basal ends, aseptate, hyaline, thin- and smooth-walled, (2.8–)3.2–4.6(–5.3) × (1.3–)1.5–2.2(–2.5) µm (av. 3.9 × 1.8 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 25–27 mm diam. after 14 d in darkness at 25 °C, flat, felty, with sparse aerial mycelium, white, margin undulate, reverse concolourous. On MEA reaching 20–21 mm diam., raised, radially folded, felty, with abundant aerial mycelium, salmon at centre, white at periphery, margin crenate, reverse saffron. On PDA reaching 27–30 mm diam., flat, hairy at centre, felty to membranous at periphery, with abundant aerial mycelium, white, margin entire, reverse buff. On SNA reaching 28–29 mm diam., flat, membranous without aerial mycelium, white, margin entire, reverse concolourous.

Additional materials examined: **Germany**, Kiel-Kitzeberg, mouldy cellar wall, unknown collection date and *collector*, isol. Feb 1966, *W. Gams*, isolate CBS 221.70. **Italy**, Padova, soil, unknown collection date and *collector*, isol. Aug. 1960, *C.A. Ghillini*, isolate CBS 160.61.

Notes: According to the phylogenetic analyses in the present study (Fig. 4, clade XXXI-53), *Acremonium proliferatum* is closely related to *A. brunneisporum*, *A. gamsianum*, and *A. stroudii*. Morphologically, *A. proliferatum* differs from *A. brunneisporum* and *A. gamsianum* by producing longer conidiophores, which are up to 121 µm long in *A. proliferatum*, compared to those up to 61.5 µm long in *A. brunneisporum*, and up to 56 µm long in *A. gamsianum* (Hou *et al.* 2023). Phylogenetically, *A. proliferatum* (CBS 486.86) and *A. stroudii* (CBS 138820) are clearly different based on ITS (90.4 % identity, with 50 bp differences), LSU (99.7 %, 2 bp), *RPB2* (93.6 %, 48 bp), and *TEF1* (96.6 %, 24 bp) sequences.

Acremonium soli Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858465. Fig. 39.

Etymology: Referring to the substrate from which this fungus was isolated, soil.

Typus: **Netherlands**, Gelderland Province, Ermelo, soil, Mar. 2017, *M.& M. Elmers*, isol. Apr. 2017, *L. Lombard & A. Giraldo Lopez* (**holotype** designated here CBS H-25592, ex-type living isolate CBS 144381= JW 259001).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.1–2.1 µm wide. *Sporulation* abundant, phalacrogenous, nematogenous and plectonematogenous.

Conidiophores solitary or aggregated, (sub-)erect, straight or slightly curved, arising directly from the agar surface or superficial hyphae, sometimes radiating out from coils or ropes formed by mycelium, unbranched or repeatedly basitonously branched, with percurrent proliferation, bearing 1–3 levels with 1–3 phialides per node, up to ca 97 µm long, 1.5–2.9 µm wide at base, 1–5-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, lateral or terminal, subcylindrical or subulate, straight or wavy at top part, hyaline, thick- and smooth-walled, (12.2–)25.2–47.7(–55.5) µm long, (1.2–)1.3–2.1(–2.4) µm wide at base, (0.6–)0.7–0.9(–1.0) µm wide near aperture, with inconspicuous collarettes and periclinal thickening at conidiogenous loci, usually with percurrent proliferation. *Conidia* cylindrical or ellipsoidal, with rounded apical ends and apiculate bases, aseptate, hyaline, thin- and smooth-walled, (2.2–)3.5–5.9(–

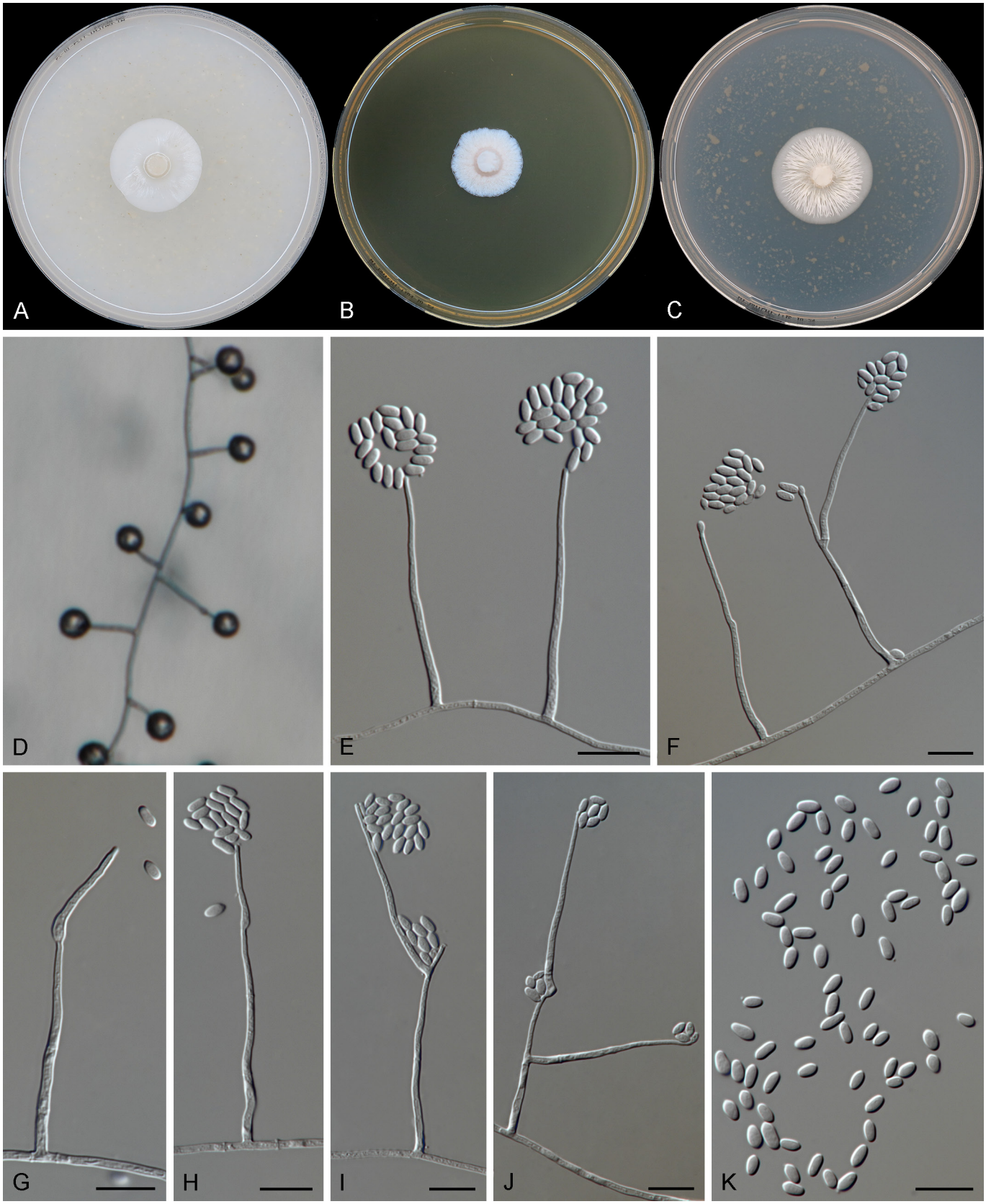

Fig. 38. *Acremonium proliferatum* (ex-type CBS 486.86). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–J.** Conidiophores. **K.** Conidia. Scale bars = 10 µm.

6.6) × (1.4–)1.5–2.0(–2.2) µm (av. 4.5 × 1.7 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* present, terminal, lateral or intercalary, single, sub-globose or obovoid, hyaline, smooth- and thick-walled, (3.6–)4.0–5.8(–6.5) × (3.0–)3.1–4.1(–5.0). *Sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 24–35 mm diam. after 14 d in darkness at 25 °C, flat, membranous, with sparse aerial mycelium, white, margin entire, reverse concolourous. On MEA reaching 22–29 mm diam., raised, radially folded, hairy, rugose, with moderate aerial mycelium, salmon, margin lobate, reverse saffron.

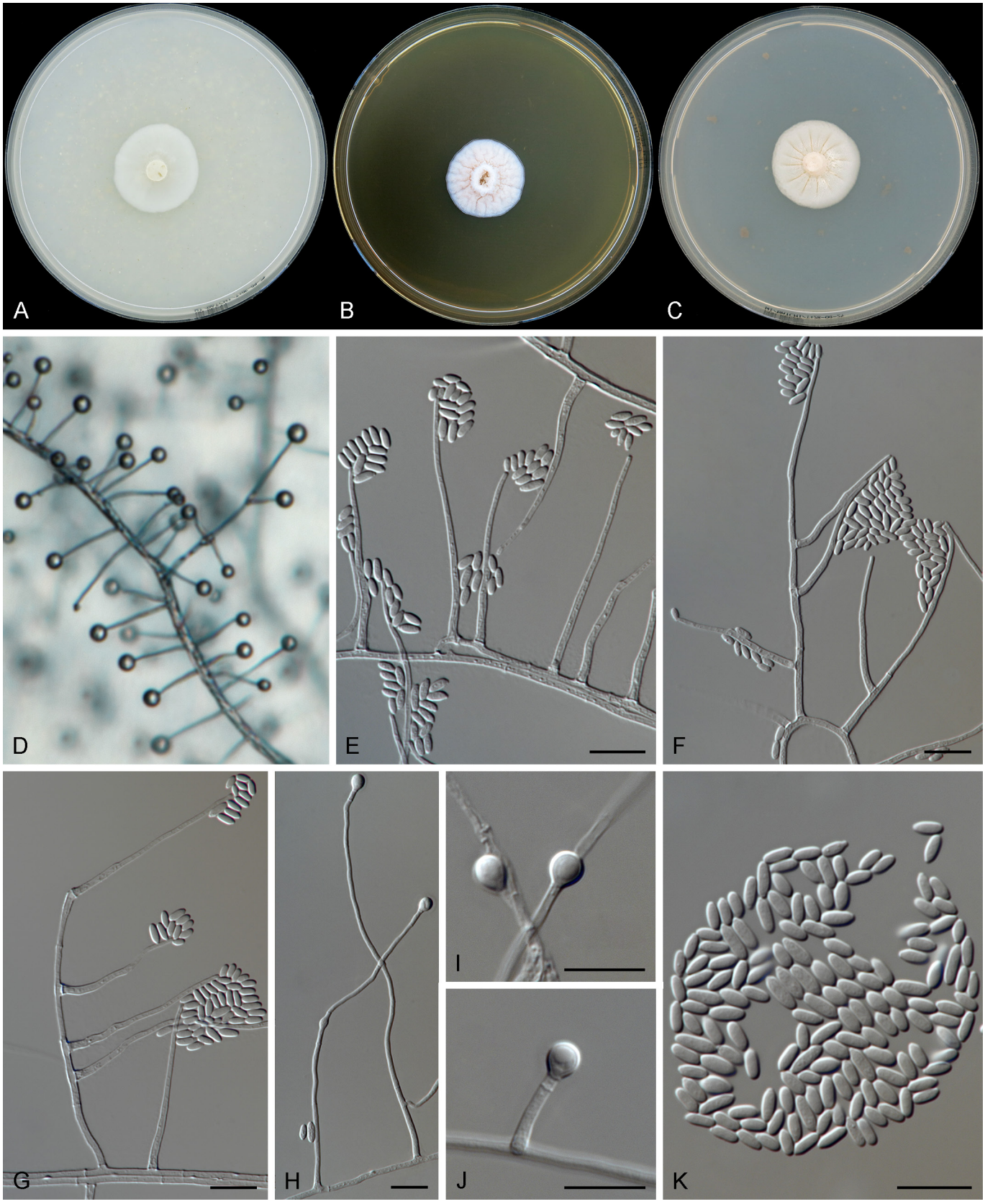

Fig. 39. *Acremonium soli* (ex-type CBS 144381). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–G.** Conidiophores. **H–J.** Chlamydospores. **K.** Conidia. Scale bars = 10 µm.

On PDA reaching 25–29 mm diam., raised, radially folded, felty or hairy, with sparse aerial mycelium, dirty white, margin entire, reverse rosy buff, with radial lines. On SNA reaching 27–28 mm diam., flat, membranous without aerial mycelium, white, margin entire, reverse concolourous.

Notes: Phylogenetically, *Acremonium soli* is closely related to *A. charticola*, but it shows clear differences in ITS (97.7 % identity, with 12 bp differences), LSU (100 %, 0 bp), *RPB2* (94.5 %, 41 bp), with no *TEF1* comparison available. Morphologically, *A. soli* can be distinguished from *A. charticola* by producing larger conidia,

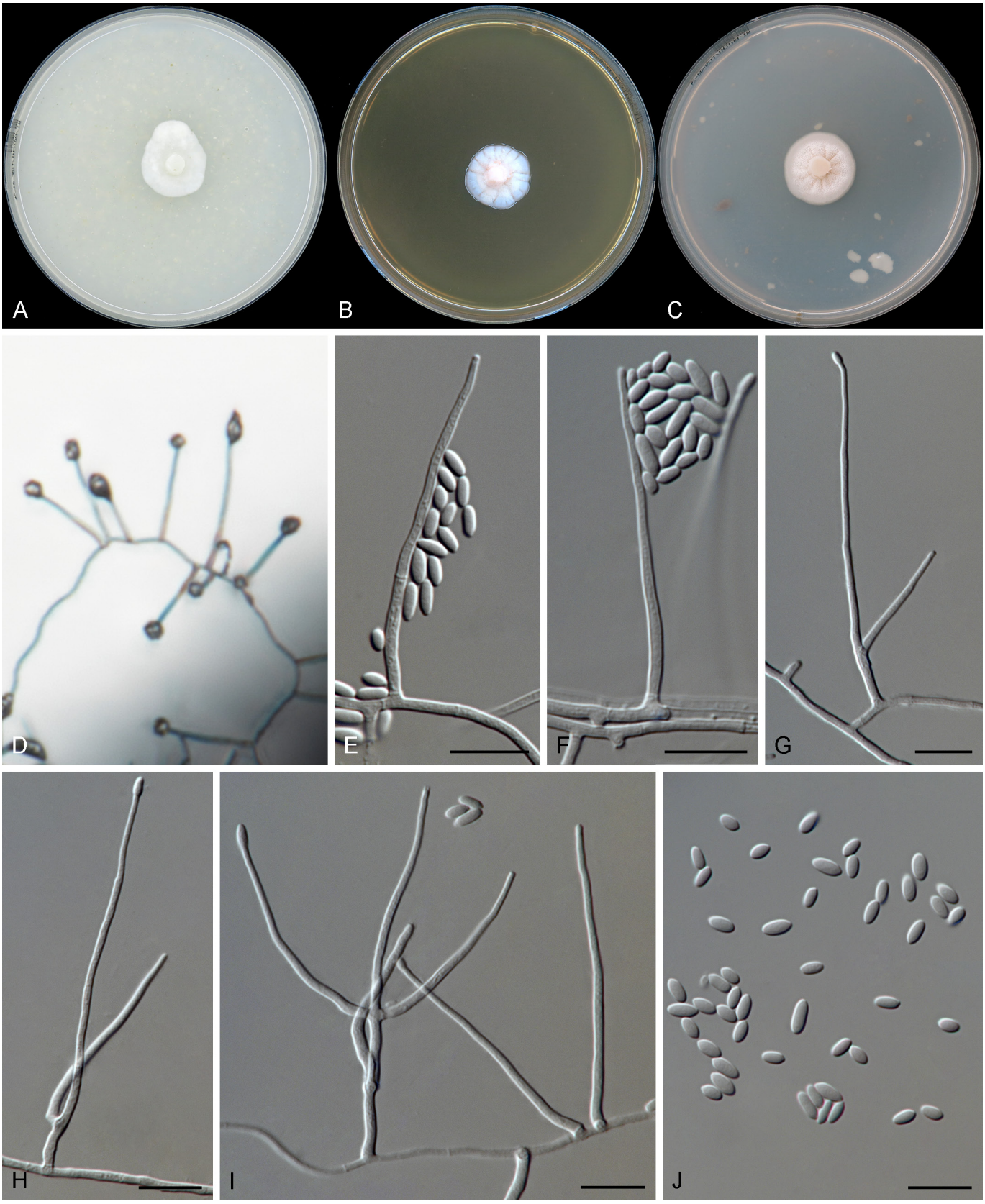

Fig. 40. *Acremonium tapetis* (ex-type CBS 220.70). **A–C.** Colonies on OA, MEA and PDA after 14 d at 25 °C in darkness. **D–I.** Conidiophores. **J.** Conidia. Scale bars = 10 µm.

measuring (2.2–)3.5–5.9(–6.6) × (1.4–)1.5–2.0(–2.2) µm in *A. soli* vs 3.2–4.5 × 1.4–2.0 µm in *A. charticola*, and by the presence of chlamydospores in *A. soli*, which are absent in *A. charticola*. *Acremonium soli* lacks crystals, they are abundant and elongated in *A. charticola* (Gams 1971).

Acremonium tapetis Lin Zhao & Crous, ***sp. nov.*** MycoBank MB 858466. Fig. 40.

Etymology: From Latin "*tapetum*", meaning wallpaper. Referring to the substrate, mouldy wallpaper, from which the holotype isolate was collected.

Typus: **Germany**, Kiel-Kitzeberg, mouldy wallpaper, unknown collection date and *collector*, isol. Feb. 1966, *W. Gams* (**holotype** designated here CBS H-25595, ex-type living isolate CBS 220.70).

Mycelium consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.0–1.8 µm wide, forming bundles. *Sporulation* abundant, phalacrogenous, nematogenous, plectonematogenous. *Conidiophores* solitary or aggregated, (sub-)erect, straight or slightly curved, arising directly from the agar surface or superficial hyphae, sometimes radiating from coils or ropes formed by mycelium, unbranched, or basitonously branched, bearing 1–2 levels with 1–3 phialides per node, up to ca 110 µm long, 1.4–2.3 µm wide at base, 1–3-septate, hyaline, smooth-walled. *Conidiogenous cells* monophialidic, mostly lateral or terminal, (sub)cylindrical, straight or slightly curved, hyaline, thick- and smooth-walled, (20.7–)29.2–51.9(–58.8) µm long, (1.2–)1.3–1.8(–2.3) µm wide at base, 0.7–1.0 µm wide near aperture, with short collarettes and inconspicuous periclinal thickening at conidiogenous loci. *Conidia* ellipsoidal or cylindrical, both rounded terminaly, or with median or laterally displaced hilar bases, aseptate, hyaline, thin- and smooth-walled, (2.5–)2.8–5.0(–5.8) × (1.5–)1.6–2.1(–2.3) µm (av. 3.8 × 1.8 µm, n = 100), eguttulate, arranged in slimy heads. *Chlamydospores* and *sexual morph* not observed.

Culture characteristics: Colonies on OA reaching 18–23 mm diam. after 14 d in darkness at 25 °C, flat, membranous, with sparse aerial mycelium, white, margin lobate, reverse dirty white. On MEA reaching 18–20 mm diam., raised, radially folded, felty to hairy, with sparse aerial mycelium, salmon at centre, whitish at periphery, margin lobate, reverse pale saffron, with slight radial lines. On PDA reaching 21–22 mm diam., flat, radially folded, floccose, with moderate aerial mycelium, dirty white at centre, buff at periphery, margin undulate, reverse rosy buff. On SNA reaching 19–21 mm diam., flat, membranous, with sparse aerial mycelium, slightly dusty, white, margin entire, reverse concolourous.

Additional material examined: **Austria**, Innsbruck, Rauschbrunnen, decaying bark of *Fagus sylvatica*, unknown collection date and *collector*, isol. *W. Gams*, No. 588, CBS H-8364 and CBS H-8365, isolate CBS 228.70.

Notes: Based on the phylogenetic analyses, *A. tapetis* is closely related to *A. brunneisporum*, *A. gamsianum*, *A. proliferatum*, and *A. stroudii*, but *A. tapetis* (CBS 220.70) differs from *A. brunneisporum* (CBS 413.76) in ITS (91.8 %, with 42 bp differences), LSU (98.8 % 9 bp), *RPB2* (87.9 %, 85 bp), and *TEF1* (93.7 %, 51 bp); from *A. gamsianum* (CBS 881.73) in ITS (92.4 %, with 39 bp differences), LSU (98.6 %, 11 bp), RPB2 (91.0 %, 63 bp), and *TEF1* (95.2 %, 39 bp); from *A. proliferatum* (CBS 486. 86) in ITS (90.8 %, with 51 bp differences), LSU (98.6 %, 11 bp), *RPB2* (91.6 %, 59 bp), and *TEF1* (94.2 %, 41 bp); from *A. stroudii* (CBS 138820) in ITS (91.3 %, with 45 bp differences), LSU (98.6 % 11 bp), *RPB2* (91.3 %, 61 bp), and *TEF1* (93.9 %, 49 bp).

DISCUSSION

Species of *Acremonium* s. lat. are globally widespread and found in various environmental niches, characterised by simple, slender conidiophores, and small, single-celled, often hyaline conidia. The most recent study on acremonium-like fungi was conducted by Hou *et al.* (2023), who provided a comprehensive phylogenetic and morphological framework, analysing isolates from a variety of substrates such as soil, plant material, fungal hosts, insects, airborne particles, aquatic environments, and human substrata. Building on this comprehensive analysis, the present study further investigates the diversity and classification of acremonium-like fungi. Although Hou *et al.* (2023) provided critical insights into this group, many species remained unresolved, leaving gaps in our understanding of their taxonomy, ecological roles, and biotechnological potential. To address these gaps, we aimed to expand upon their findings by utilising both morphological and molecular data to reassess the classification of acremonium-like species within the current phylogenetic framework.

In this study we analysed 402 isolates of acremonium-like fungi and related taxa using phylogenetic analyses based on multi-locus sequencing (ITS, LSU, *RPB2*, and *TEF1*) and morphological characterisation. These isolates represent 149 species, including 18 families within the orders *Hypocreales* and *Trichosphaeriales*. This study identified new taxa across a range of known and new families and genera: within *Hypocreales*, two new genera (*Aurantidochium*, and *Lagenariomyces*) were proposed in the newly described family *Aurantidochiaceae*. Within *Bionectriaceae*, new species were confirmed in the genera *Acremonium*, *Clavatomyces*, *Lasionectria*, *Protocreopsis*, *Ramosiphorum*, and *Verruciconidia*, and two new genera *Cannomyces* and *Pilgeriellomyces* were introduced. Additionally, a new genus, *Neochrysonectria*, was described in the newly established family *Neochrysonectriaceae*. In *Sarocladiaceae*, several new species were confirmed in the known genera *Chlamydocillium*, *Parasarocladium*, *Polyphialocladium*, and *Sarocladium*, while a new genus, *Sporodochius*, was proposed within *Stachybotryaceae*. Furthermore, within *Trichosphaeriales*, a new genus *Titanomyces* was identified in *Trichosphaeriaceae*, along with new species described in the genera *Allomusicillium*, *Brunneomyces*, and *Chlamydosporiella*. Specifically, this study proposes two new families, seven new genera, four new combinations, and 33 new species.

Insights on *Trichosphaeriaceae*

Members of *Trichosphaeriaceae* (*Trichosphaeriales*) play a crucial role in nutrient cycling as saprobes, decomposing organic matter like plant debris, wood, and litter (Maharachchikumbura *et al.* 2016, Hyde *et al.* 2020). Some species interact with plants and other organisms as endophytes in mutualistic relationships or as pathogens impacting plant health and biodiversity (Aguirre-Hudson 1991, Pinnoi *et al.* 2003, Maharachchikumbura *et al.* 2016, Hyde *et al.* 2020). Historically, the genus *Trichosphaeria* was established by Fuckel (1870), followed by the establishment of the family *Trichosphaeriaceae* by Winter (1885, as *Trichosphaerieae*) to accommodate eight genera, with *Trichosphaeria* as the type genus.

The family is characterised by superficial, stroma-less perithecia that are membranous to leathery, often hairy or bristly, and surrounded by tangled hyphae (Winter 1885). Barr (1983) introduced the order *Trichosphaeriales* to include the sole family *Trichosphaeriaceae*. However, in a later study, Barr (1990) re-evaluated character states and concluded that the superficial position of ascomata is insufficient to justify separation at the ordinal level, subsequently accepting *Trichosphaeriaceae* as part of the *Xylariales*. In that treatment, Barr (1990) accepted four genera in the family: *Acanthostigma*, *Eriosphaeria*, *Rhamphoria*, and *Trichosphaeria*, although the family was later recognized as heterogeneous (Barr & Cannon 1994). Some taxa were reclassified into other families, and due to unresolved phylogenetic relationships, Réblová & Winka (2001) recommended not adding any new genera until the phylogeny of the type species *Trichosphaeria pilosa* was clarified. Subsequently, Réblová & Gams (2016) designated a neotype for *Tr. pilosa* after examining various collections and suggested limiting *Trichosphaeria* to the sole member of *Trichosphaeriaceae* until further collections of *Tr. pilosa* could offer more clarity. In a recent study, Crous *et al.* (2023) resolved the phylogenetic position of *Tr. pilosa* and designated an epitype for the species. Their results showed that the epitype of *Tr. pilosa* falls within the clade formerly recognised as *Plectosphaerellaceae*, which is nested within the earlier-named *Trichosphaeriaceae* (Winter 1885), subsuming the more recently established *Plectosphaerellaceae* (Zare *et al.* 2007) as a synonym and, based on the phylogeny of *Tr. pilosa*, currently contains 25 genera (Crous *et al.* 2023). Our study aligns well with the previous studies of Crous *et al.* (2023), confirming that *Trichosphaeriaceae* contains 28 genera (Fig. 2; one genus, *Longitudinalis*, is not shown in Fig. 2), including the 25 known genera outlined by Crous *et al.* (2023) and two new genera (*Parafuscohypha* and *Allomusicillium*) proposed by Hou *et al.* (2023). In addition, our study proposes one additional new genus, *Titanomyces*, along with its type species, *T. triconidiogenes*, and three novel species within known genera, i.e., *Allo. malicola*, *B. romanianus*, and *Chlam. aerina* (Fig. 2).

Further insights on *Hypocreales*

The *Hypocreales* encompasses fungi with lifestyles ranging from saprophytic to parasitic and mutualistic (Rossman *et al.* 1999), exhibiting remarkable ecological diversity, from associations with plants, fungi, algae, bryophytes, lichens, insects, humans and animals to occurrences in coprophilous substrates and in leaf litter, soil, water and air across terrestrial, freshwater and marine habitats (Perera *et al.* 2023). Recently, Hou *et al.* (2023) demonstrated that most acremonium-like fungi are phylogenetically placed within the *Hypocreales*, with *Acremonium* s. str. being restricted to the *Bionectriaceae*. In our study, most isolates were confirmed to belong to the *Bionectriaceae*, while others fall into the *Chrysonectriaceae*, *Clavicipitaceae*, *Cordycipitaceae*, *Ijuhyaceae*, *Myrotheciomycetaceae*, *Nectriaceae*, *Niessliaceae*, *Ophiocordycipitaceae*, *Pseudoniessliaceae*, *Sarocladiaceae*, *Sedecimiellaceae*, *Stachybotryaceae*, *Valsonectriaceae*, and *Xanthonectriaceae*. This phylogenetic analysis underscores the taxonomic diversity within these families and further confirms the complexity of the phylogenetic relationships among acremonium-like fungi.

Members of the *Bionectriaceae* mainly inhabit terrestrial and freshwater ecosystems, with occasional occurrences in marine habitats. They play significant roles in pharmaceutical, commercial, and biotechnological industries by serving as biodegraders and biocontrol agents, and some taxa also act as valuable sources of bioactive secondary metabolites (Goswami *et al.* 2008, Choi *et al.* 2009, Wicklow & Poling 2009, Urbanek *et al.* 2017, Hyde *et al.* 2020, Sun *et al.* 2020, Hou *et al.* 2023, Perera *et al.* 2023, Zhao *et al.* 2023, Qin *et al.* 2024). Recent research by Zhao *et al.* (2025) accepted 50 genera with available sequence data, most of which have known asexual morphs with acremonium-, gliocladium-, penicillium-, stilbella-, or verticillium-like characteristics, while sexual morphs, documented for 25 genera, are characterised by perithecial or cleistothecial ascomata (Rossman *et al.* 1999, Hou *et al.* 2023, Perera *et al.* 2023). Expanding on these findings, our phylogenetic analyses, consistent with these results, also revealed that the *Bionectriaceae* comprises 53 genera with available DNA data, including two newly proposed genera, *Cannomyces* and *Pilgeriellomyces*, which we introduce here (Fig. 3), and additionally, the genus *Linodochium*, previously lacking molecular data, was first included in the family by Crous *et al.* (2024b). Based on our phylogenetic analyses of a combined ITS, LSU, *RPB2*, and *TEF1* dataset, we have described 18 new taxa within the *Bionectriaceae*, including *A. ecuadorense*, *A. proliferatum*, *A. soli*, *A. tapetis*, *Ca. spinulosus*, *Cl. palmarum*, *Cl. pycnidialis*, *L. eichhorniae*, *Pil. brasiliensis*, *Pt. ellipsoidea*, *Pt. helvetica*, *Pt. polyphialidica*, *Pt. spinulosa*, *R. sporodochiale*, *V. maritima*, *V. indonesiana*, *V. terricola*, and *V. thailandica*. Furthermore, our *Hypocreales* phylogeny revealed that the *Bionectriaceae* clade, which was moderately supported (Fig. 1; clade XXXI), was related to the families *Stromatonectriaceae* and *Tilachlidiaceae* (Fig. 1 clade XXIX, XXX). However, within this clade, the *Bionectriaceae* was divided into two highly supported subclades, raising the intriguing question of whether the *Bionectriaceae* could be paraphyletic.

Other acremonium-like fungi identified in this study belong to the families *Chrysonectriaceae*, *Pseudoniessliaceae*, and *Valsonectriaceae*. The *Chrysonectriaceae* was introduced to accommodate the known genus *Chrysonectria*, which was described to accommodate *Chrysonectria finisterrensis* by Lechat *et al.* (2018), and was considered closely related to *Nectriaceae*, *Neoacremoniaceae*, and *Pseudoniessliaceae* (Hou *et al.* 2023). Our results confirm that *Chrysonectriaceae* is more closely related to *Nectriaceae*, *Neoacremoniaceae*, and *Sedecimiellaceae*. *Pseudoniessliaceae* was established to accommodate the genus *Pseudoniesslia*, including its type species, *Pseudoniesslia minutispora*, which was initially described as *Niesslia minutispora* and characterised by sporodochial conidiomata and conidiophores bearing terminal whorls of relatively long phialides (Gams *et al.* 2019, Hou *et al.* 2023). *Valsonectriaceae* was introduced for *Valsonectria* (type species: *Valsonectria pulchella*), a species originally reported from decaying branches of *Melia azedarach* in Argentina, characterised by ascomata immersed in the stromal periphery, globose and yellow in colour, ascospores that are ellipsoid to fusoid, evenly 2-celled, yellow-brown, smooth, and coarsely striate, and acremonium-like asexual morphs (Spegazzini 1881, Rossman *et al.* 1999).

The *Clavicipitaceae* is a cosmopolitan family found in various terrestrial ecosystems, with the highest species diversity in subtropical and tropical regions, and a broad host range spanning arthropods, the hypogeous genus *Elaphomyces*, and endophytes and epiphytes of *Poaceae*, although most species are host-specific or parasitise closely related species (Kobayasi 1941, 1982, Diehl 1950, Rogerson 1970, Samson *et al.* 1988, Sung *et al.* 2007a). Sung *et al.* (2007a) conducted multi-locus phylogenetic analyses and, along with examining the texture, pigmentation, and morphology of stromata, established a framework for classifying *Cordyceps* and clavicipitaceous fungi. Based on their findings, they proposed

dividing clavicipitaceous fungi into three families: *Clavicipitaceae* characterised by stromata or subiculum that are either darkly or brightly coloured, fleshy or tough; *Cordycipitaceae*, based on the type species *Cordyceps militaris*, characterised by brightly coloured, fleshy stromata; and *Ophiocordycipitaceae*, characterised by darkly pigmented, rarely brightly coloured, tough, fibrous to pliant stromata, rarely fleshy (Sung *et al.* 2007a). In this study, our results are consistent with those of Sung *et al.* (2007a) and clearly demonstrate that the three families *Clavicipitaceae*, *Cordycipitaceae*, and *Ophiocordycipitaceae* are distinct (Fig. 1; clades XIV, XVII, XXI).

Rossman *et al.* (1999) accepted *Ijuhya* within *Bionectriaceae* and designated *Ijuhya peristomialis* as the type species, which is characterised by hyphomycetous, acremonium-like features. Perera *et al.* (2023) conducted phylogenetic inference and excluded *Ijuhya* from *Bionectriaceae*, establishing a new family to accommodate *Ijuhya* and *Kallichroma*, the latter of which was also previously placed in *Bionectriaceae*. In addition, Perera *et al.* (2023) excluded the monotypic genera *Bullanockia* and *Xanthonectria* from *Bionectriaceae* and established a new family, *Xanthonectriaceae*, to accommodate these unique genera. Both *Bullanockia* and *Xanthonectria* are notable for producing acremonium-like asexual morphs, with *Xanthonectria* characterized by pale yellow to orange ascomata, an ascomatal wall with three regions up to 80 µm thick and ascospores with (3–)5–7(–9) septa, while *Bullanockia* lacks a recorded sexual morph (Crous *et al.* 2016, Lechat *et al.* 2016a). In accordance with our current experimental results, we agree with the findings of Perera *et al.* (2023) that the clade of *Ijuhya* and *Kallichroma*, as well as the clade of *Xanthonectria* and *Bullanockia* form a distinct clade separate from *Bionectriaceae*. Our results also show that *Flammocladiellaceae*, *Xanthonectriaceae*, and *Ijhyaceae* cluster together in a well-supported clade (Fig. 1; clades XXVI–XXVIII).

Myrotheciomycetaceae was originally introduced by Crous *et al.* (2018a), with conidiophores that are hyaline, smooth to warty, unbranched to branched, subcylindrical, and with terminal and lateral conidiogenous cells. In recent studies on *Hypocreales*, it has been demonstrated that *Myrotheciomycetaceae* is most closely related to the clade which includes five families: *Flammocladiellaceae*, *Ijuhyaceae*, *Stromatonectriaceae*, *Tilachlidiaceae*, and *Xanthonectriaceae* (Perera *et al.* 2023, Hou *et al.* 2023). Our study also confirmed that the phylogenetic relationship of *Myrotheciomycetaceae* is consistent with their findings, but with moderate support (Fig. 1; clade XXV).

Lombard *et al.* (2015) conducted a multi-locus phylogenetic analysis and morphological observations to resolve 47 genera in the *Nectriaceae*, which showed that *Nectriaceae* is closely related to the *Tilachlidiaceae*. Recent studies have shown that *Nectriaceae* is either the sister group to *Niessliaceae* (Perera *et al.* 2023) or closely related to *Chrysonectriaceae* and *Neoacremoniaceae* (Hou *et al.* 2023). Our phylogenetic analyses indicate that *Nectriaceae* is monophyletic with strong support (Fig. 1; clade XII), consistent with the findings of Hou *et al.* (2023). It is closely related to *Chrysonectriaceae* and *Neoacremoniaceae*, as well as closely related to *Sedecimiellaceae* and the newly described family *Neochrysonectriaceae*, as described in our study (Fig. 1; clades VIII–XI). *Sedecimiellaceae* was established by Li *et al.* (2023) to accommodate the known genus *Sedecimiella* and the newly described genus *Heteroacremonium*. *Sedecimiella* was originally introduced by Pang *et al.* (2010), along with its type species, *Sedecimiella taiwanensis*. Hou *et al.* (2023) transferred *Sedecimiella* to the newly established family *Neoacremoniaceae*, while in the same year, Li *et al.* (2023) established the new family *Sedecimiellaceae* to accommodate *Sedecimiella*. Our results support the classification proposed by Li *et al.* (2023), and we further suggest that *Parapyrenis maritima* should also be placed in *Sedecimiellaceae* (Fig. 1; clade XI).

Within *Niessliaceae*, Hou *et al.* (2023) indicated in their study that there were unresolved genera, including *Acremoniopsis*, *Collarina*, *Cylindromonium*, *Niesslia*, and *Trichonectria*. Recent research showed two genera, *Acremoniopsis* and *Collarina*, along with two new genera *Nothoacremoniopsis* and *Phaeocollarina*, belong to a new family, *Acremoniopsidaceae* (Li *et al.* 2023). Additionally, based on our multi-locus sequences, the *Cylindromonium-Trichonectria* taxa form a fully supported clade (Fig. 1; clade V), encompassing the asexual *Cylindromonium* and sexual *Trichonectria*, which could be regarded as a potential new family. *Cylindromonium* was erected as a genus within the *Nectriaceae* to circumscribe acremonium-like taxa, characterised by unbranched, hyaline, phialidic conidiophores, as well as cylindrical conidia, which are either 1-septate or multi-septate (Crous *et al.* 2019b, Crous *et al.* 2024b). The lichenicolous genus *Trichonectria* was previously accepted in *Bionectriaceae* by several authors (Rossman *et al.* 1999, Maharachchikumbura *et al.* 2015, 2016, Wijayawardene *et al.* 2020, 2022), although it was regarded as *Hypocreales* incertae sedis (Perera *et al.* 2023). The *Cylindromonium-Trichonectria* clade remains unresolved within *Hypocreales* because of the missing sequence data from the type, *Trichonectria hirta*. The *Niessliaceae*, however, is in need of urgent revision, as Hou *et al.* (2023) placed isolates such as CBS 766.69 (ex-type of *A. guillematii*), CBS 101149 (ex-type of *A. cavaraeanum*), CBS 159.70 (ex-type of *A. incrustatum*), CBS 154.72 (ex-type of *A. nigrosclerotium*) and CBS 134.33 (ex-type of *Cephalosporium ballagii*) in this family. However, our study (data not shown here) reveals different results. The ex-type isolates of *A. cavaraeanum* and *A. incrustatum* group outside the *Niessliaceae*, displaying a closer relationship with *Calcarisporiaceae*, whereas the ex-type isolate of *A. guillematii* is positioned within the newly proposed family *Acremoniopsidaceae*. Further studies are needed to clarify the classification of these taxa. Furthermore, the *Niessliaceae* (Fig. 1, clade VII) is polyphyletic, and includes species of *Niesslia* which are intermixed with other species from the genera *Eucasphaeria*, *Myrtacremonium*, *Neoeucasphaeria*, and *Rosasphaeria*.

The family *Sarocladiaceae* was introduced by Crous *et al.* (2018b) to include two genera, *Parasarocladium* and *Sarocladium*, characterised by monophialidic conidiogenous cells and unicellular conidia, which are ellipsoidal, bacilliform to fusoid, forming slimy heads or chains, and placed within the *Hypocreales* (Crous *et al.* 2018b, Hyde *et al.* 2020). Zare & Gams (2016) established a new genus, *Chlamydocillium*, with uncertain family affiliation. Later, based on phylogenetic analysis, *Chlamydocillium* was transferred to the family *Sarocladiaceae* by Hou *et al.* (2023), who also proposed a new genus, *Polyphialocladium*, within *Sarocladiaceae*. These findings align with our results, confirming four known genera within *Sarocladiaceae*: *Chlamydocillium*, *Parasarocladium*, *Polyphialocladium*, and *Sarocladium*. In our study, we have also identified and described nine new species within this family: two new species in the genus *Chlamydocillium*: *Chl. theobromae* and *Chl. viridicolor*; one new species in *Parasarocladium*: *Para. kislosladkoense*; and six new species in *Sarocladium*: *S. alniphilum*, *S. catenulatum*, *S. hirsutum*, *S. humicola*, *S. limosialveum*, and *S. nubiaquae*. Whereas Crous *et al.* (2018b) reported *Sarocladiaceae* as sister to *Bionectriaceae*, Hyde *et al.* (2020) found the family to be closely associated with *Flammocladiellaceae*. In our phylogenetic analyses, *Sarocladiaceae* was found to be a sister clade to the newly described family *Aurantidochiaceae*, which we introduce in

this study. These findings underscore the ongoing refinement of the phylogenetic framework for *Sarocladiaceae*.

Stachybotryaceae was introduced by Crous *et al.* (2014) to include the genera *Myrothecium*, *Peethambara*, and *Stachybotrys*. These fungi are mainly saprobic or pathogenic to plants and animals, including important plant and human pathogens, as well as species used in industry and commerce for biodegradation and biocontrol (Lombard *et al.* 2016, Hyde *et al.* 2020). They have asexual morphs featuring mononematous, sporodochial, or synnematous conidiomata, producing conidia in dark green to black masses, and some also show sexual morphs with perithecial ascomata that remain unchanged in KOH (Crous *et al.* 2014). In a subsequent study, Lombard *et al.* (2016) identified 33 genera within *Stachybotryaceae* through multi-locus phylogenetic analysis and morphological data. Wijayawardene *et al.* (2018) recognised 36 genera, while Hyde *et al.* (2020) accepted 39 genera. Our findings are consistent with those of previous studies (Lombard *et al.* 2016, Wijayawardene *et al.* 2018, Hyde *et al.* 2020). In our multi-locus phylogenetic analyses, 38 genera are recognised within *Stachybotryaceae* (excluding one genus due to lacking molecular data), including the new genus, *Sporodochius*. However, the bootstrap support for *Stachybotryaceae* clade was low/moderate (Fig. 1; clade XXIII), which may be attributed to the limited availability of molecular data for some species, with only ITS sequences being available.

Concluding remarks

In the present study, we advanced the phylogeny-based classification of hypocrealean fungi by integrating multi-locus phylogenetic analyses with morphological and cultural characteristics. Through this approach, we proposed new fungal names that more precisely delineate taxa and establish a stable framework for scientific communication. These names enable the accurate definition and effective communication of organisms. Furthermore, they facilitate reliable predictions about fungal biology and ecological functions based on the knowledge associated with these names (Rossman & Palm-Hernández 2008). Moreover, we systematically addressed and resolved several long-standing taxonomic ambiguities within acremonium-like fungi, taxa that have remained poorly understood due to their morphologically reduced and simplified structures, which have historically hindered accurate identification. Accurate and stable scientific nomenclature is fundamental not only for specialist taxonomists, but also for a broad range of end-users in fields such as plant pathology, clinical diagnostics, biosafety, food security, quarantine regulations, and industrial applications. Given the immense diversity of fungi in ecology, lifestyle, and methods of study, nomenclatural systems must remain both stable and traceable to ensure consistency over time. Scientific names should convey as much reliable information as possible, including classification and phylogeny, the latter reflecting evolutionary history. This is particularly important because, when nomenclature aligns with phylogenetic relationships, it enables informed predictions about fungi of agricultural, clinical, industrial, and environmental relevance, including their potential pathogenicity, appropriate control measures, and potential commercial applications, thereby linking taxonomic precision directly to practical decision-making (Rossman & Palm-Hernández 2008, Lücking *et al.* 2020, 2021, Yurkov *et al.* 2021, Zhao 2025). The integration of molecular data with morphological and ecological information has been essential for resolving taxonomic ambiguities and advancing our understanding of these fungi. The revised taxonomic framework developed in this study not only enables more accurate species identification but also provides deeper insights into their ecological roles and potential commercial applications, particularly for taxa with reduced or simplified morphological traits. By reclassifying non-monophyletic genera into monophyletic lineages, researchers in other disciplines can more reliably compare genuinely related species, rather than relying on superficially applied names that may refer to distantly related taxa. These findings highlight the critical need for ongoing taxonomic revision, which will facilitate more precise and efficient species identification in the future.

Furthermore, understanding the ecological roles and biotechnological potential of acremonium-like fungi is important. Most acremonium-like species are saprobic, although some can form endophytic relationships with plants or function as opportunistic pathogens in humans and animals, and they are commonly found in soil, plant debris, and aquatic environments (Gams 1971, 1975, Summerbell & Scott 2015, Summerbell *et al.* 2018, de Hoog *et al.* 2020, Hou *et al.* 2023). In recent years these fungi have attracted attention due to their biotechnological potential, as certain species can produce valuable bioactive metabolites (Qin *et al.* 2024). Although interest in acremonium-like fungi has increased and some taxonomic issues have already been resolved, several challenges still remain. Taxonomic ambiguities persist due to morphological similarities and limited molecular data for many species, highlighting the need for further phylogenetic and genomic studies. Additionally, the ecological roles of these fungi, particularly their interactions with host plants and other microorganisms, are not yet well understood. More research is required to explore their potential as plant symbionts or pathogens. Moreover, although some species show promise for biotechnological applications, the metabolic pathways responsible for producing bioactive compounds remain inadequately explored. Future research should integrate multi-omics approaches to unlock the full potential of these fungi and address ongoing taxonomic and functional challenges.

ACKNOWLEDGEMENTS

We would like to thank the China Scholarship Council (CSC) for financial support to LZ (CSC student number: 202006510014). PWC is grateful to the European Union's Horizon 2020 research and innovation program (RISE) under the Marie Skłodowska-Curie grant agreement No. 101008129, project acronym 'Mycobiomics', and the Dutch NWO Roadmap grant agreement No. 2020/ENW/00901156, project 'Netherlands Infrastructure for Ecosystem and Biodiversity Analysis – Authoritative and Rapid Identification System for Essential biodiversity information' (acronym NIEBA-ARISE) for funding. We thank M. Sandoval-Denis for helping redraw Figures 12 and 37 in Adobe Illustrator, updating the previous hand-drawn versions.

DECLARATION ON CONFLICT OF INTEREST

The authors include members of the Editorial Board of Studies in Mycology. They were not involved in the journal's review of, or decisions related to, this manuscript.

REFERENCES

Agarwal S, Capoor MR, Ramesh V, *et al.* (2011). First case of *Acremonium kiliense* mycetoma in a New Delhi resident: A brief review. *Journal de mycologie médicale* **21**: 130–133. https://doi.org/10.1016/j.

mycmed.2011.01.005
Aguirre-Hudson B (1991). A taxonomic study of the species referred to the ascomycete genus *Leptorhaphis*. *Bulletin of the British Museum (Natural History) Botany* **21**: 85–192.
Alfieri SA, Samuels GJ (1979). *Nectriella pironii* and its Kutilakesa-like anamorph, a parasite of ornamental shrubs. *Mycologia* **71**: 1178–1185. https://doi.org/10.1080/00275514.1979.12021129
Auer S, Ludwig-Müller J (2014). Effects of the endophyte *Acremonium alternatum* on oilseed rape (*Brassica napus*) development and clubroot progression. *Albanian Journal of Agricultural Sciences* **13**: 15–20.
Auer S, Ludwig-Müller J (2015). Biological control of clubroot (*Plasmodiophora brassicae*) by the endophytic fungus *Acremonium alternatum*. *Journal of Endocytobiosis and Cell Research* **26**: 43–49.
Barr ME (1983) The ascomycete connection. *Mycologia* **75**:1–13. https://doi.org/10.1080/00275514.1983.12021631
Barr ME (1990). Prodromus to nonlichenized, pyrenomycetous members of class Hymenoascomycetes. *Mycotaxon* **39**: 43–184.
Barr ME, Cannon P (1994). Discussion 3: *Calosphaeriales*, *Clavicipitales*, *Coryneliales*, *Diaporthales*, *Diatrypales*, *Halosphaeriales*, *Hypocreales*, *Meliolales*, *Ophiostomatales*, *Phyllachorales*, *Sordariales*, *Trichosphaeriales*, and *Xylariales*. In: *Ascomycete Systematics: Problems and Perspectives in the Nineties* (Hawksworth DL, ed.) New York & London: Plenum Press: 371–378. https://doi.org/10.1007/978-1-4757-9290-4_35
Bettiol W (1996). Biological control of plant pathogens in Brazil: application and current research. *World Journal of Microbiology and Biotechnology* **12**: 505–510. https://doi.org/10.1007/BF00419464
Bobeck DR, Pearce CJ (2017). Agricultural microbial inoculant compositions and uses thereof. *United States patent application* US 15/702, 417. Washington, DC: U.S. Patent and Trademark Office.
Burton HS, Abraham EP (1951). Isolation of antibiotics from a species of Cephalosporium. Cephalosporins P1, P2, P3, P4 and P5. *Biochemical Journal* **50**: 168–174. https://doi.org/10.1042/bj0500168
Castillo MD, González HHL, Martinez EJ, *et al.* (2004). Mycoflora and potential for mycotoxin production of freshly harvested black bean from the Argentinean main production area. *Mycopathologia* **158**: 107–112. https://doi.org/10.1023/B:MYCO.0000038426.05215.89
Choi GJ, Kim JC, Jang KS, *et al.* (2009). Biocontrol activity of *Acremonium strictum* BCP against *Botrytis* diseases. *Plant Pathology Journal* **25**: 165–171. https://doi.org/10.5423/PPJ.2009.25.2.165
Crous PW, Akulov A, Balashov S, *et al.* (2023). New and interesting fungi. 6. *Fungal Systematics and Evolution* **11**: 109–156. https://doi.org/10.3114/fuse.2023.11.09
Crous PW, Cowan DA, Maggs-Kölling G, *et al.* (2020). Fungal Planet description sheets: 1112–1181. *Persoonia* **45**: 251–409. https://doi.org/10.3767/persoonia.2020.45.10
Crous PW, Gams W, Stalpers JA, *et al.* (2004). MycoBank: an online initiative to launch mycology into the 21st century. *Studies in Mycology* **50**: 19–22.
Crous PW, Hernández-Restrepo M, Schumacher RK, *et al.* (2021). New and interesting fungi. 4. *Fungal Systematics and Evolution* **7**: 255–343. https://doi.org/10.3114/fuse.2021.07.13
Crous PW, Jurjević Z, Balashov S, *et al.* (2024a). Fungal Planet description sheets: 1614–1696. *Fungal Systematics and Evolution* **13**: 183–440. https://doi.org/10.3114/fuse.2024.13.11
Crous PW, Luangsa-ard JJ, Wingfield MJ, *et al.* (2018b). Fungal Planet description sheets: 785–867. *Persoonia* **41**: 238–417. https://doi.org/10.3767/persoonia.2018.41.12
Crous PW, Shivas RG, Quaedvlieg W, *et al.* (2014). Fungal Planet description sheets: 214–280. *Persoonia* **32**: 184–306. https://doi.org/10.3767/003158514X682395
Crous PW, Verkley GJM, Groenewald JZ, *et al.* (2019a). *Fungal Biodiversity*. Westerdijk Laboratory Manual Series 1. Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands.
Crous PW, Wingfield MJ, Burgess TI, *et al.* (2016). Fungal Planet description sheets: 469–557. *Persoonia* **37**: 218–403. https://doi.org/10.3767/003158516X694499
Crous PW, Wingfield MJ, Burgess TI, *et al.* (2018a). Fungal Planet description sheets: 716–784. *Persoonia* **40**: 240–393. https://doi.org/10.3767/persoonia.2018.40.10
Crous PW, Wingfield MJ, Jurjević Ž, *et al.* (2024b). Fungal Planet description sheets: 1697–1780. *Fungal Systematics and Evolution* **14**: 325–577. https://doi.org/10.3114/fuse.2024.14.19
Crous PW, Wingfield MJ, Lombard L, *et al.* (2019b). Fungal Planet description sheets: 951–1041. *Persoonia* **43**: 223–425. https://doi.org/10.3767/persoonia.2019.43.06
de Hoog GS, Guarro J, Gené J, *et al.* (2000). *Atlas of Clinical Fungi*, 2nd edition. Centraalbureau voor Schimmelcultures, Utrecht.
de Hoog GS, Guarro J, Gené J, *et al.* (2020). *Atlas of Clinical Fungi*, 4th e-edition. Utrecht/Reus.
Diehl WW (1950). *Balansia and the Balansiae in America*. Agriculture Monograph No. 4, USDA, Washington, D.C.
Doan TT, Jäschke D, Ludwig-Müller J (2010). An endophytic fungus induces tolerance against the clubroot pathogen *Plasmodiophora brassicae* in *Arabidopsis thaliana* and *Brassica rapa* roots. *Acta Horticulturae* **867**: 173–180. https://doi.org/10.17660/ActaHortic.2010.867.22
Doi Y (1977). *Protocreopsis*, a new genus of the *Hypocreales*. *Kew Bulletin* **31**: 511–555. https://doi.org/10.2307/4119401
Fernández-Trujillo JP, Martínez JA, Salmerón MC, *et al.* (1997). Isolation of *Acremonium* species causing postharvest decay of peaches in Spain. *Plant Disease* **81**: 958–958. https://doi.org/10.1094/PDIS.1997.81.8.958A
Fries E (1825). *Systema orbis vegetabilis: Primas lineas novae constructionis periclitatur Elias Fries*. e Typographia Academica.
Fries EM (1849). *Summa Vegetabilium Scandinaviae* **2**: 259–572.
Fuckel L (1870). Symbolae mycologicae. Beiträge zur Kenntniss der Rheinischen Pilze. *Jahrbücher des Nassauischen Vereins für Naturkunde* **23–24**: 1–459. https://doi.org/10.5962/bhl.title.47117
Fujikawa H, Wauke T, Kusunoki J, *et al.* (1997). Contamination of microbial foreign bodies in bottled mineral water in Tokyo, Japan. *Journal of Applied Microbiology* **82**: 287–291. https://doi.org/10.1046/j.1365-2672.1997.00353.x
Gams W (1968). Typisierung der Gattung *Acremonium*. *Nova Hedwigia* **16**: 141–145.
Gams W (1971). *Cephalosporium-artige Schimmelpilze (Hyphomycetes)*. Gustav Fischer Verlag, Stuttgart, Germany.
Gams W (1975). Cephalosporium-like hyphomycetes: some tropical species. *Transactions of the British Mycological Society* **64**: 389–404. https://doi.org/10.1016/S0007-1536(75)80138-0
Gams W, Hawksworth DL (1976) ['1975']. The identity of *Acrocylindrium oryzae* Sawada and a similar fungus causing sheath rot of rice. *Kavaka* **3**: 57–61.
Gams W, Stielow B, Gräfenhan T, *et al.* (2019). The ascomycete genus *Niesslia* and associated monocillium-like anamorphs. *Mycological Progress* **18**: 5–76. https://doi.org/10.1007/s11557-018-1459-5
Giraldo A, Gené J, Sutton DA, *et al.* (2015). Phylogeny of *Sarocladium* (*Hypocreales*). *Persoonia* **34**: 10–24. https://doi.org/10.3767/003158515X685364
Giraldo A, Gené J, Sutton DA, *et al.* (2017). New acremonium-like species in the *Bionectriaceae* and *Plectosphaerellaceae*. *Mycological Progress* **16**: 349–368. https://doi.org/10.1007/s11557-017-1271-7
Giraldo A, Crous PW (2019). Inside *Plectosphaerellaceae*. *Studies in Mycology* **92**: 227–286. https://doi.org/10.1016/j.simyco.2018.10.005
Glenn AE, Bacon CW, Price R, *et al.* (1996). Molecular phylogeny of

Acremonium and its taxonomic implications. *Mycologia* **88**: 369–383. https://doi.org/10.1080/00275514.1996.12026664

Gonçalves MFM, Vicente TFL, Esteves AC, *et al.* (2020). Novel halotolerant species of *Emericellopsis* and *Parasarocladium* associated with macroalgae in an estuarine environment. *Mycologia* **112**: 154–171. https://doi.org/10.1080/00275514.2019.1677448

Goswami J, Pandey RK, Tewari JP, *et al.* (2008). Management of root knot nematode on tomato through application of fungal antagonists, *Acremonium strictum* and *Trichoderma harzianum*. *Journal of Environmental Science and Health Part B* **43**: 237–240. https://doi.org/10.1080/03601230701771164

Grum-Grzhimaylo OA, Debets AJ, Bilanenko EN (2016). The diversity of microfungi in peatlands originated from the White Sea. *Mycologia* **108**: 233–254. https://doi.org/10.3852/14-346

Grum-Grzhimaylo OA, Debets AJ, Bilanenko EN (2018). Mosaic structure of the fungal community in the Kislo-Sladkoe Lake that is detaching from the White Sea. *Polar Biology* **41**: 2075–2089. https://doi.org/10.1007/s00300-018-2347-9

Gupta A, Jain H, Lynde C, *et al.* (2000). Prevalence and epidemiology of onychomycosis in patients visiting physicians' offices: a multicenter Canadian survey of 15,000 patients. *Journal of the American Academy of Dermatology* **43**: 244–248.

Halde C, Padhye AA, Haley LD, *et al.* (1976). *Acremonium falciforme* as a cause of mycetoma in California. *Sabouraudia* **14**: 319–326. https://doi.org/10.1080/00362177685190461

Hamilton-Miller JMT (2000). Sir Edward Abraham's contribution to the development of the cephalosporins: a reassessment. *International Journal of Antimicrobial Agents* **15**: 179–184. https://doi.org/10.1016/S0924-8579(00)00179-5

Hoang DT, Chernomor O, von Haeseler A, *et al.* (2018). UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* **35**: 518–522. https://doi.org/10.1093/molbev/msx281

Hou LW, Giraldo A, Groenewald JZ, *et al.* (2023). Redisposition of acremonium-like fungi in *Hypocreales*. *Studies in Mycology* **105**: 23–203. https://doi.org/10.3114/sim.2023.105.02

Hu Y, Zhu B (2016). Study on genetic engineering of *Acremonium chrysogenum,* the cephalosporin C producer. *Synthetic and Systems Biotechnology* **1**: 143–149. https://doi.org/10.1016/j.synbio.2016.09.002

Hyde KD, Norphanphoun C, Maharachchikumbura SSN, *et al.* (2020). Refined families of *Sordariomycetes*. *Mycosphere* **11**: 305–1059. https://doi.org/10.5943/mycosphere/11/1/7

Jäschke D, Dugassa-Gobena D, Karlovsky P, *et al.* (2010). Suppression of clubroot (*Plasmodiophora brassicae*) development in *Arabidopsis thaliana* by the endophytic fungus *Acremonium alternatum*. *Plant Pathology* **59**: 100–111. https://doi.org/10.1111/j.1365-3059.2009.02199.x

Kalyaanamoorthy S, Minh BQ, Wong TKF, *et al.* (2017). ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* **14**: 587–589. https://doi.org/10.1038/nmeth.4285

Katoh K, Rozewicki J, Yamada KD (2019). MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* **20**: 1160–1166. https://doi.org/10.1093/bib/bbx108

Kobayasi Y (1941). The genus *Cordyceps* and its allies. *Science Reports of the Tokyo Bunrika Daigaku* (Section B, no. 84) **5**: 3–20.

Kobayasi Y (1982). Keys to the taxa of the genera *Cordyceps* and *Torrubiella*. *Transactions of the Mycological Society of Japan* **23**: 329–364.

Kumar S, Stecher G, Tamura K (2016). MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* **33**: 1870–1874. https://doi.org/10.1093/molbev/msw054

Kuraku S, Zmasek CM, Nishimura O, *et al.* (2013). aLeaves facilitates on-demand exploration of metazoan gene family trees on MAFFT sequence alignment server with enhanced interactivity. *Nucleic Acids Research* **41**: W22–W28. https://doi.org/10.1093/nar/gkt389

Kwon-Chung KJ, Bennett JW (1992). *Medical Mycology*. Lea & Febiger, Philadelphia.

Lechat C, Fournier J, Moreau PA (2016a). *Xanthonectria*, a new genus for the nectrioid fungus *Nectria pseudopeziza*. *Ascomycete.org* **8**: 172–178. https://doi.org/10.25664/art-0185

Lechat C, Fournier J, Priou JP (2018). *Chrysonectria*, a new genus in the *Nectriaceae* with the new species *C. finisterrensis* from France. *Ascomycete.org* **10**: 121–125. https://doi.org/10.25664/art-0237

Lechat C, Fournier J, Richter T (2016b). *Protocreopsis caricicola* (*Hypocreales*, *Bionectriaceae*), the first species of *Protocreopsis* reported from a temperate area of the northern hemisphere. *Ascomycete.org* **8**: 30–32. https://doi.org/10.25664/art-0168

Lee MW, Kim JC, Choi JS, *et al.* (1995). Mycetoma caused by *Acremonium falciforme*: successful treatment with itraconazole. *Journal of the American Academy of Dermatology* **32**: 897–900. https://doi.org/10.1016/0190-9622(95)91557-5

Lee WJ, Kim JS, Jo SM, *et al.* (2025). Taxonomic study of sixteen unrecorded and five new species of *Hypocreales* from the Korean marine environment. *Mycobiology* **53**: 144–167. https://doi.org/10.1080/12298093.2024.2418664

Li BH, Wang CC, Dong XL, *et al.* (2014). *Acremonium* brown spot, a new disease caused by *Acremonium sclerotigenum* on bagged apple fruit in China. *Plant Disease* **98**: 1012. https://doi.org/10.1094/PDIS-02-14-0113-PDN

Li M, Raza M, Song S, *et al.* (2023). Application of culturomics in fungal isolation from mangrove sediments. *Microbiome* **11**: 272. https://doi.org/10.1186/s40168-023-01708-6

Lindau G (1897). *Hypocreales*. In: *Die natürlichen Pflanzenfamilien*, vol 1. (Engler HA, Prantl KAE, eds). Verlag W. Engelman, Leipzig: 343–372.

Link HF (1809). Observationes in ordines plantarum naturales. Dissertatio I. *Magazin der Gesellschaft Naturforschenden Freunde Berlin* **3**: 3–42.

Liu XB, Guo ZK, Huang GX (2017). *Sarocladium brachiariae sp. nov*., an endophytic fungus isolated from *Brachiaria brizantha*. *Mycosphere* **8**: 827–834. https://doi.org/10.5943/mycosphere/8/7/2

Liu YJ, Whelen S, Hall BD (1999). Phylogenetic relationships among ascomycetes: evidence from an RNA polymerse II subunit. *Molecular Biology and Evolution* **16**: 1799–1808. https://doi.org/10.1093/oxfordjournals.molbev.a026092

Lombard L, Houbraken J, Decock C, *et al.* (2016). Generic hyper-diversity in *Stachybotriaceae*. *Persoonia* **36**: 156–246. https://doi.org/10.3767/003158516X691582

Lombard L, van der Merwe NA, Groenewald JZ, *et al.* (2015). Generic concepts in *Nectriaceae*. *Studies in Mycology* **80**: 189–245. https://doi.org/10.1016/j.simyco.2014.12.002

Lowen R (1995). *Acremonium* section *Lichenoidea* section nov. and *Pronectria oligospora* species nov. *Mycotaxon* **53**: 81–95.

Lücking R, Aime MC, Robbertse B, *et al.* (2020). Unambiguous identification of fungi: where do we stand and how accurate and precise is fungal DNA barcoding? *IMA Fungus* **11**: 14.

Lücking R, Aime MC, Robbertse B, *et al.* (2021). Fungal taxonomy and sequence-based nomenclature. *Nature microbiology* **6**: 540–548.

Maharachchikumbura SS, Hyde KD, Jones EG, *et al.* (2015). Towards a natural classification and backbone tree for *Sordariomycetes*. *Fungal Diversity* **72**: 199–301. https://doi.org/10.1007/s13225-015-0331-z

Maharachchikumbura SS, Hyde KD, Jones EG, *et al.* (2016). Families of *Sordariomycetes*. *Fungal Diversity* **79**: 1–317. https://doi.org/10.1007/s13225-016-0369-6

McCormack JC, McIntyre PB, Tilse MH, *et al.* (1987). Mycetoma associated

with *Acremonium falciforme* infection. *Medical Journal of Australia* **147**: 187–188. https://doi.org/10.5694/j.1326-5377.1987.tb133355.x

Miller MA, Pfeiffer W, Schwartz T (2012). The CIPRES science gateway: enabling high-impact science for phylogenetics researchers with limited resources. In: *Proceedings of the 1st conference of the extreme science and engineering discovery environment: Bridging from the extreme to the campus and beyond*. Association for Computing Machinery, USA: 1–8. https://doi.org/10.1145/2335755.2335836

Minh BQ, Schmidt HA, Chernomor O, *et al.* (2020). IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* **37**: 1530–1534. https://doi.org/10.1093/molbev/msaa015

Morgan-Jones G, Gams W (1982). Notes on *Hyphomycetes*. XLI. An endophyte of *Festuca arundinacea* and the anamorph of *Epichloe typhina*, new taxa in one of two new sections of *Acremonium*. *Mycotaxon* **15**: 311–318.

Nguyen LT, Schmidt HA, Von Haeseler A, *et al.* (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* **32**: 268–274. https://doi.org/10.1093/molbev/msu300

Novicki TJ, LaFe K, Bui L, *et al.* (2003). Genetic diversity among clinical isolates of *Acremonium strictum* determined during an investigation of a fatal mycosis. *Journal of Clinical Microbiology* **41**: 2623–2628. https://doi.org/10.1128/jcm.41.6.2623-2628.2003

Pang KL, Alias SA, Chiang MWL, *et al.* (2010). *Sedecimiella taiwanensis gen. et sp. nov*., a marine mangrove fungus in the *Hypocreales* (*Hypocreomycetidae*, *Ascomycota*). *Botanica Marina* **53**: 493–498. https://doi.org/10.1515/bot.2010.061

Perdomo H, García D, Gené J, *et al.* (2013). *Phialemoniopsis*, a new genus of *Sordariomycetes*, and new species of *Phialemonium* and *Lecythophora*. *Mycologia* **105**: 398–421. https://doi.org/10.3852/12-137

Perdomo H, Sutton DA, García D, *et al.* (2011). Spectrum of clinically relevant *Acremonium* species in the United States. *Journal of Clinical Microbiology* **49**: 243–256. https://doi.org/10.1128/jcm.00793-10

Perera RH, Hyde KD, Jones EBG, *et al.* (2023). Profile of *Bionectriaceae*, *Calcarisporiaceae*, *Hypocreaceae*, *Nectriaceae*, *Tilachlidiaceae*, *Ijuhyaceae fam. nov.*, *Stromatonectriaceae fam. nov*. and *Xanthonectriaceae fam. nov*. *Fungal Diversity* **118**: 95–271. https://doi.org/10.1007/s13225-022-00512-1

Pinnoi A, Jones EBG, McKenzie EHC, *et al.* (2003). Aquatic fungi from peat swamp palms: *Unisetosphaeria penguinoides gen. et sp. nov*., and three new *Dactylaria* species. *Mycoscience* **44**: 377–382. https://doi.org/10.1007/S10267-003-0124-1

Pitt JI, Hocking AD (2022). Ecology of fungal food spoilage. In: *Fungi and Food Spoilage*. Springer International Publishing: 3–12. https://doi.org/10.1007/978-3-030-85640-3_2

Pitt JI, Hocking AD (1997). *Fungi and Food Spoilage*. 2nd edn. Blackie Academic and Professional, London.

Pitt JI, Hocking AD (2009). *Fungi and Food Spoilage*. 3rd edn. New York: Springer. https://doi.org/10.1007/978-0-387-92207-2

Pitt JI, Hocking AD, Bhudhasamai K, *et al.* (1993). The normal mycoflora of commodities from Thailand. 1. Nuts and oilseeds. *International Journal of Food Microbiology* **20**: 211–226. https://doi.org/10.1016/0168-1605(93)90166-E

Preuss CGT (1848). Deutschlands Flora, Abt. III. *Die Pilze Deutschlands* **6**(25–26): 1–48.

Qin Y, Lu H, Qi X, *et al.* (2024). Recent advances in chemistry and bioactivities of secondary metabolites from the genus *Acremonium*. *Journal of Fungi* **10**: 37. https://doi.org/10.3390/jof10010037

Ramaley AW (2004). *Nectriella guadalupensis* and its Dendrodochium-like anamorph (*Bionectriaceae*, *Hypocreales*): a new species on *Agavaceae*. *Mycotaxon* **90**: 181–186.

Rayner RW (1970). *A Mycological Colour Chart*. CMI and British Mycological Society. Kew, Surrey, England.

Réblová M, Gams W (2016). A revision of *Sphaeria pilosa* Pers. and re-evaluation of the *Trichosphaeriales*. *Mycological Progress* **15**: 52. https://doi.org/10.1007/s11557-016-1195-7

Réblová M, Winka K (2001). Generic concepts and correlations in ascomycetes based on morphological and molecular data: *Lecythothecium duriligni gen. et sp. nov*. with *Sporidesmium* anamorph and *Ascolacicola aquatica sp. nov*. *Mycologia* **93**: 478–493. https://doi.org/10.1080/00275514.2001.12063181

Rehner SA, Buckley E (2005). A *Beauveria* phylogeny inferred from nuclear ITS and EF1-alpha sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* **97**: 84–98. https://doi.org/10.1080/15572536.2006.11832842

Rehner SA, Samuels GJ (1994). Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. *Mycological Research* **98**: 625–634.

Rogerson CT (1970). The hypocrealean fungi (*Ascomycetes*, *Hypocreales*). *Mycologia* **62**: 865–910. https://doi.org/10.1080/00275514.1970.12019033

Rossman AY, Palm-Hernández ME (2008). Systematics of plant pathogenic fungi: why it matters. *Plant Disease* **92**: 1376–1386. https://doi.org/10.1094/PDIS-92-10-1376

Rossman AY, McKemy JM, Pardo-Schultheiss RA, *et al.* (2001). Molecular studies of the *Bionectriaceae* using large subunit rDNA sequences. *Mycologia* **93**: 100–110. https://doi.org/10.1080/00275514.2001.12061283

Rossman AY, Samuels GJ, Rogerson CT, *et al.* (1999). Genera of *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* (*Hypocreales*, *Ascomycetes*). *Studies in Mycology* **42**: 1–248.

Samson RA, Evans HC, Latgé J-P (1988). *Atlas of Entomopathogenic Fungi*. Springer-Verlag, Berlin, Heidelberg, New York. https://doi.org/10.1007/978-3-662-05890-9

Samson RA, Hoekstra ES, Frisvad JC (2004). *Introduction to Food-Borne Fungi*, 7th edn. Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands.

Samuels GJ (1976). Perfect states of *Acremonium*: The genera *Nectria*, *Actiniopsis*, *Ijuhya*, *Neohenningsia*, *Ophiodictyon*, and *Peristomialis*. *New Zealand Journal of Botany* **14**: 231–260. https://doi.org/10.1080/0028825X.1976.10428664

Spegazzini C (1881). Fungi argentini additis nonnullis brasiliensibus montevideensibusque. Pugillus quartus (Continuación). *Anales de la Sociedad Científica Argentina* **12**: 193–227.

Stamatakis A (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Summerbell RC, Gueidan C, Guarro J, *et al.* (2018). The Protean *Acremonium*. *A. sclerotigenum*/*egyptiacum*: Revision, Food Contaminant, and Human Disease. *Microorganisms* **6**: 88. https://doi.org/10.3390/microorganisms6030088

Summerbell RC, Gueidan C, Schroers HJ, *et al.* (2011). *Acremonium* phylogenetic overview and revision of *Gliomastix*, *Sarocladium*, and *Trichothecium*. *Studies in Mycology* **68**: 139–162. https://doi.org/10.3114/sim.2011.68.06

Summerbell RC, Scott JA (2015). *Acremonium*. In: *Molecular Biology of Food and Water Borne Mycotoxigenic and Mycotic Fungi* (Paterson RRM, Lima N, eds). CRC Press, Boca Raton, USA: 115–128. https://doi.org/10.1201/b18645

Sun ZB, Li SD, Ren Q, *et al.* (2020). Biology and applications of *Clonostachys rosea*. *Journal of Applied Microbiology* **129**: 486–495. https://doi.org/10.1111/jam.14625

Sun J, Yu S, Lu Y, *et al.* (2023). Proposal of a new family *Pseudodiploösporeaceae fam. nov.* (*Hypocreales*) based on phylogeny of *Diploöspora longispora* and *Paecilomyces penicillatus*. *Mycology* **14**: 60–73.

Sung GH, Hywel-Jones NL, Sung JM, *et al.* (2007a). Phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi. *Studies in Mycology* **57**: 5–9. https://doi.org/10.3114/sim.2007.57.01

Sung GH, Sung JM, Hywel-Jones NL, *et al.* (2007b). A multi-gene phylogeny of *Clavicipitaceae* (*Ascomycota*, *Fungi*): identification of localized incongruence using a combinational bootstrap approach. *Molecular Phylogenetics and Evolution* **44**: 1204–1223. https://doi.org/10.1016/j.ympev.2007.03.011

Tan YP, Shivas RG (2024a). Nomenclatural novelties. *Index of Australian Fungi* **29**: 1–10. https://doi.org/10.5281/zenodo.10602835

Tan YP, Steinrucken TV (2024b). Nomenclatural novelties. *Index of Australian Fungi* **36**: 1–21. https://doi.org/10.5281/zenodo.11137737

Tong SQ, Peng L, Wu YJ (2023). *Acremonium capsici* and *A. guizhouense*, two new members of *Acremonium* (*Hypocreales*, *Sordariomycetes*) isolated from the rhizosphere soil of *Capsicum annuum*. *MycoKeys* **95**: 1–13. https://doi.org/10.3897/mycokeys.95.97062

Urbanek AK, Rymowicz W, Strzelecki MC, *et al.* (2017). Isolation and characterization of Arctic microorganisms decomposing bioplastics. *AMB Express* **7**: 1–10. https://doi.org/10.1186/s13568-017-0448-4

van Beyma FH (1940). Beschreibung einiger neuer Pilzarten aus dem Centraalbureau voor Schimmelcultures, Baarn (Nederland), VI. Mitteilung. *Antonie van Leeuwenhoek* **6**: 263–290. https://doi.org/10.1007/BF02146191

Vilgalys R, Hester M (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

Visagie CM, Yilmaz N, Allison JD, *et al.* (2024). New and interesting fungi. 7. *Fungal Systematics and Evolution* **13**: 441–494. https://doi.org/10.3114/fuse.2024.13.12

White TJ, Bruns T, Lee S, *et al.* (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: a guide to methods and applications* (Innis MA, Gelfand DH, Sninsky JJ, *et al.*, eds). Academic Press, New York, USA: 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wicklow DT, Poling SM (2009). Antimicrobial activity of pyrrocidines from *Acremonium zeae* against endophytes and pathogens of maize. *Phytopathology* **99**: 109–115. https://doi.org/10.1094/PHYTO-99-1-0109

Wijayawardene NN, Hyde KD, Al-Ani LK, *et al.* (2020). Outline of *Fungi* and fungus-like taxa. *Mycosphere* **11**: 1060–1456. https://doi.org/10.5943/mycosphere/11/1/8

Wijayawardene NN, Hyde KD, Dai DQ, *et al.* (2022). Outline of *Fungi* and fungus-like taxa – 2021. *Mycosphere* **13**: 53–453. https://doi.org/10.5943/mycosphere/13/1/2

Wijayawardene NN, Hyde KD, Lumbsch HT, *et al.* (2018). Outline of *Ascomycota*: 2017. *Fungal Diversity* **88**: 167–263. https://doi.org/10.1007/s13225-018-0394-8

Winter G (1885). *Rabenhorst's Kryptogamen-Flora, Pilze - Ascomyceten,* Ed. 2, **1**(2): 193–528.

Xiao YP, Wang YB, Hyde KD, *et al.* (2023). *Polycephalomycetaceae*, a new family of clavicipitoid fungi segregates from *Ophiocordycipitaceae*. *Fungal Diversity* **120**: 1–76. https://doi.org/10.1007/s13225-023-00517-4

Yeh YH, Kirschner R (2014). *Sarocladium spinificis*, a new endophytic species from the coastal grass *Spinifex littoreus* in Taiwan. *Botanical Studies* **55**: 1–6. https://doi.org/10.1186/1999-3110-55-25

Yu FM, Jayawardena RS, Luangharn T, *et al.* (2024). Species diversity of fungal pathogens on cultivated mushrooms: A case study on morels (*Morchella*, *Pezizales*). *Fungal Diversity* **125**: 157–220. https://doi.org/10.1007/s13225-023-00531-6

Yurkov A, Alves A, Bai FY, *et al.* (2021). Nomenclatural issues concerning cultured yeasts and other fungi: why it is important to avoid unneeded name changes. *IMA Fungus* **12**: 18.

Zare R, Gams W, Starink-Willemse M, *et al.* (2007). *Gibellulopsis*, a suitable genus for *Verticillium nigrescens*, and *Musicillium*, a new genus for *V. theobromae*. *Nova Hedwigia* **85**: 463–489. https://doi.org/10.1127/0029-5035/2007/0085-0463

Zare R, Gams W (2016). More white verticillium-like anamorphs with erect conidiophores. *Mycological Progress* **15**: 993–1030. https://doi.org/10.1007/s11557-016-1214-8

Zhang SN, Hyde KD, Jones EBG, *et al.* (2024a). Current insights into palm fungi with emphasis on taxonomy and phylogeny. *Fungal Diversity* **127**: 55–301. https://doi.org/10.1007/s13225-024-00536-9

Zhang ZY, Pan H, Tao G, *et al.* (2024b). Culturable mycobiota from Guizhou Wildlife Park in China. *Mycosphere* **15**: 654–763. https://doi.org/10.5943/mycosphere/15/1/5

Zhao L, Groenewald JZ, Hernández-Restrepo M, *et al.* (2023). Revising *Clonostachys* and allied genera in *Bionectriaceae*. *Studies in Mycology* **105**: 204–265. https://doi.org/10.3114/sim.2023.105.03

Zhao L, Groenewald JZ, Hou LW, *et al.* (2025). *Bionectriaceae*: a poorly-known family of hypocrealean fungi with major commercial potential. *Studies in Mycology* **111**: 115–198. https://doi.org/10.3114/sim.2025.111.04

Zhao L (2025). *Revision of Bionectriaceae and acremonium-like fungi in Hypocreales.* Ph.D. dissertation, Utrecht University, Netherlands. https://doi.org/10.33540/3082

Supplementary Material: https://studiesinmycology.org/

Table S1. Isolates used in this study with details of their host, location, and GenBank accessions numbers.