Revising *Clonostachys* and allied genera in *Bionectriaceae*

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Abstract: *Clonostachys* (*Bionectriaceae*, *Hypocreales*) species are common soil-borne fungi, endophytes, epiphytes, and saprotrophs. Sexual morphs of *Clonostachys* spp. were placed in the genus *Bionectria*, which was further segregated into the six subgenera *Astromata*, *Bionectria*, *Epiphloea*, *Myronectria*, *Uniparietina*, and *Zebrinella*. However, with the end of dual nomenclature, *Clonostachys* became the single depository for sexual and asexual morph-typified species. Species of *Clonostachys* are typically characterised by penicillate, sporodochial, and, in many cases, dimorphic conidiophores (primary and secondary conidiophores). Primary conidiophores are mononematous, either verticillium-like or narrowly penicillate. The secondary conidiophores generally form imbricate conidial chains that can collapse to slimy masses, particularly on sporodochia. In the present study, we investigated the species diversity within a collection of 420 strains of *Clonostachys* from the culture collection of, and personal collections at, the Westerdijk Fungal Biodiversity Institute in Utrecht, the Netherlands. Strains were analysed based on their morphological characters and molecular phylogeny. The latter used DNA sequence data of the nuclear ribosomal internal transcribed spacer regions and intervening 5.8S nrDNA (ITS) and partial 28S large subunit (LSU) nrDNA and partial protein encoding genes including the RNA polymerase II second largest subunit (*RPB2*), translation elongation factor 1-alpha (*TEF1*) and β-tubulin (*TUB2*). Based on these results, the subgenera *Astromata*, *Bionectria*, *Myronectria* and *Zebrinella* are supported within *Clonostachys*. Furthermore, the genus *Sesquicillium* is resurrected to accommodate the former subgenera *Epiphloea* and *Uniparietina*. The close relationship of *Clonostachys* and *Sesquicillium* is strongly supported as both are inferred phylogenetically as sister-genera. New taxa include 24 new species and 10 new combinations. Recognition of *Sesquicillium* distinguishes species typically forming a reduced perithecial stroma superficially on plant tissue from species in *Clonostachys* often forming well-developed, through bark erumpent stromata. The patterns of observed perithecial wall anatomies, perithecial wall and stroma interfaces, and asexual morph diversifications described in a previously compiled monograph are used for interpreting ancestral state reconstructions. It is inferred that the common ancestor of *Clonostachys* and *Sesquicillium* may have formed perithecia superficially on leaves, possessed a perithecial wall consisting of a single region, and formed intercalary phialides in penicilli of conidiophores. Character interpretation may also allow hypothesising that diversification of morphs occurred then in the two genera independently and that the frequently stroma-linked *Clonostachys* morphs evolved together with the occupation of woody host niches and mycoparasitism.

Key words: Biocontrol, *Bionectriaceae*, multi-locus, mycoparasitism, new taxa, phylogeny, soil-borne, taxonomy.
Taxonomic novelties: New species: *Clonostachys aurantiaca* L. Zhao & Crous, *Clonostachys australiana* L. Zhao & Crous, *Clonostachys bambusae* L. Zhao & Crous, *Clonostachys buxicola* L. Zhao & Crous, *Clonostachys cylindrica* L. Zhao & Crous, *Clonostachys ellipsoidea* L. Zhao & Crous, *Clonostachys flava* L. Zhao, Crous & Schroers, *Clonostachys fujianensis* L. Zhao & Crous, *Clonostachys fusca* L. Zhao, Crous & Schroers, *Clonostachys garysamuelsii* L. Zhao & Crous, *Clonostachys hongkongensis* L. Zhao & Crous, *Clonostachys longiphialidica* L. Zhao, Crous & Schroers, *Clonostachys obovatispora*, L. Zhao & Crous, *Clonostachys palmae* L. Zhao, Crous & Schroers, *Clonostachys parasporodochialis* L. Zhao & Crous, *Clonostachys penicillata* L. Zhao, Crous & Schroers, *Clonostachys reniformis* L. Zhao & Crous, *Clonostachys vacuolata* L. Zhao, Crous & Schroers, *Clonostachys venezuelae* L. Zhao, Crous & Schroers, *Mycocitrus synnematus* L. Zhao & Crous, *Nectriopsis didymii* L. Zhao & Crous, *Sesquicillium intermediophialidicum* L. Zhao & Crous, *Sesquicillium neerlandicum* L. Zhao & Crous, *Sesquicillium symmetricum* L. Zhao & Crous. **New combinations:** *Mycocitrus coccicola* (J.A. Stev.) L. Zhao & Crous, *Mycocitrus coxeniae* (Y.P. Tan *et al.*) L. Zhao & Crous, *Sesquicillium essexcoheniae* (Y.P. Tan *et al.*) L. Zhao & Crous, *Sesquicillium lasiacidis* (Samuels) L. Zhao, Crous & Schroers, *Sesquicillium phyllophilum* (Schroers) L. Zhao, Crous & Schroers, *Sesquicillium rossmaniae* (Schroers) L. Zhao, Crous & Schroers, *Sesquicillium saulense* (Lechat & J. Fourn.) L. Zhao & Crous, *Sesquicillium sesquicillii* (Samuels) L. Zhao, Crous & Schroers, *Sesquicillium spinulosisporum* (Lechat & J. Fourn.) L. Zhao & Crous, *Sesquicillium tornatum* (Höhn.) Schroers. **New synonyms:** *Clonostachys aranearum* W.H. Chen *et al.*, *Clonostachys chuyangsinensis* H. Yu & Y. Wang, *Clonostachys eriocamporesiana* R.H. Perera & K.D. Hyde, *Clonostachys granuligera* (Starbäck) Forin & Vizzini, *Clonostachys indica* Prasher & R. Chauhan, *Clonostachys spinulosa* R.H. Perera *et al.*, *Clonostachys squamuligera* (Sacc.) Forin & Vizzini, *Clonostachys wenpingii* (J. Luo & W.Y. Zhuang) Z.Q. Zeng & W.Y. Zhuang. **Epitypes (basionyms):** *Fusidium buxi* J.C. Schmidt ex Link, *Verticillium candelabrum* Bonord.

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INTRODUCTION

The family *Bionectriaceae* is based on the sexual morph-typified genus *Bionectria* (Spegazzini 1919). Rossman *et al.* (1999) included a total of 21 perithecial and fiv cleistothecial genera when describing the family. Classification of four of the cleistothecial genera (*Emericellopsis*, *Heleococcum*, *Mycoarachis*, and *Roumegueriella*) in the family were supported based on phylogenetic analysis of the partial 28S large subunit (LSU) nrDNA gene, which also suggested that the *Bionectriaceae*, including related asexual morphs, could be monophyletic (Rossman *et al.* 2001). Phylogenetic analyses that are based on widely available LSU rDNA sequences now suggest

that the *Bionectriaceae* includes 47 genera (Wijayawardene *et al.* 2018, Hyde *et al*. 2020b).

Members of the *Bionectriaceae* are herbicolous, corticolous, lichenicolous, fungicolous or coprophilous. They mostly occur in terrestrial or freshwater habitats and are less common in marine habitats. Ascomata occur superficially on the substratum or are formed on a poorly or well-developed erumpent stroma and are solitary or densely aggregated, crowded, perithecial, and rarely cleistothecial. Their colour is pallid and ranges from white, yellow, orange to tan or brown and does not change in KOH or lactic acid. Asexual morphs are acremonium-, gliocladium-, gyrostroma-, penicillium-, or verticillium-like. Conidiophores are mono- or dimorphic, mononematous or sporodochial or synnematous and typically hyaline and smooth, while those of a few taxa can be subhyaline to brown or blackish brown and finely echinulated. Conidia, produced typically by phialidic conidiogenous cells, are unicellular to multi-septate, ellipsoid, fusoid to subfusoid, sometimes with papillate or truncate ends, hyaline to greenish hyaline or olivaceous grey, and smooth or striated (Rossman *et al.* 1999, Hyde *et al.* 2020b).

Spegazzini (1919) proposed the genus *Bionectria* based on a single species, *B. tonduzii*. Samuels (1988a) combined *B. tonduzii* to *Nectria tonduzii* and noted its similarity to *N. ochroleuca*. *Nectria apocyni*, *N. aureofulva*, *N. byssicola*, *N. pallidula*, *N. ochroleuca*, and *N. subquaternata* were classified in the *N. ochroleuca* group (Samuels 1976). Schroers & Samuels (1997) transferred the *N. ochroleuca* group to *Bionectria* based on morphological characters.

According to dual nomenclatural concepts, the sexual morph-typified *Bionectria* was selected as the generic umbrella by Schroers (2001), while at the same time, the use of binominals in the asexual morph-typified genus *Clonostachys* were equally promoted. However, with the end of dual nomenclature, *Clonostachys* was recommended for conservation over *Bionectria* (Rossman *et al.* 2013). *Clonostachys* includes soil-borne species, mycoparasites, endophytes, epiphytes or saprotrophs (Schroers 2001, Moreira *et al.* 2016). It was first described by Corda (1839) and is based on *C. araucaria*, which now is considered a synonym of *C. rosea* (basionym *Penicillium roseum*), the asexual morph of *N. ochroleuca*.

Schroers (2001) described 44 species of *Clonostachys*/*Bionectria* based on morphology and molecular phylogenetic data [the internal transcribed spacer region and intervening 5.8S nrRNA gene (ITS) and partial β-tubulin (*TUB2*)]. Because of considerable diversity of morphological patterns seen mainly in the sexual morphs, Schroers (2001) divided the genus *Bionectria* into six newly distinguished subgenera, namely *Astromata*, *Bionectria*, *Epiphloea*, *Myronectria*, *Uniparietina*, and *Zebrinella*. For example, different kinds of ascomatal wall anatomy with either one, two or three regions, and morphologically diverse ascospores that could be smooth, spinulose, striate or warted and 0- or 1-septate were accepted to characterise *Clonostachys*/*Bionectria*. Mainly elements of the asexual morph were considered useful for linking the different subgenera into one generic concept (Schroers 2000: fig. 5). They consisted of penicillate, frequently sporodochial, in many cases dimorphic conidiophores (referred to here as the primary and secondary conidiophores), and phialidic conidiogenous cells formed either terminally or subapically by phialide supporting cells. The primary conidiophores are mononematous, either verticillium-like or narrowly penicillate, and form heads of watery conidial masses. The secondary conidiophores are loosely to adpressed penicillate, or sporodochial, forming imbricate conidial chains that can collapse to slimy masses (Schroers 2001).

Although *Clonostachys* undoubtedly belongs to *Bionectriaceae*, its taxonomic position in relation to other genera within the family remains unclear (Rossman *et al.* 1999, Hyde *et al*. 2020b). In the present study, we therefore investigated 420 additional, preliminarily identified strains of *Clonostachys* and allied genera, deposited in the CBS culture collection and the Johanna Westerdijk (JW) citizen science collection (collected from Dutch soils by school children; Groenewald *et al*. 2018, Giraldo *et al.* 2019, Hou *et al.* 2020, Crous *et al.* 2021) of the Westerdijk Fungal Biodiversity Institute. We used morphological and molecular phylogenetic analyses. The latter were based on the nuclear ribosomal internal transcribed spacer regions and intervening 5.8S nrDNA (ITS) and partial sequences for the 28S large subunit (LSU) nrDNA. These were combined with partial protein-encoding genes including the DNA-directed RNA polymerase II second largest subunit (*RPB2*), translation elongation factor 1-alpha (*TEF1*), and β-tubulin (*TUB2*) gene regions to reconstruct a phylogenetic backbone of, and define robust species boundaries within, the genus *Clonostachys*. An additional aim of this study was to re-evaluate the taxonomic circumscription of *Clonostachys* among related genera within *Bionectriaceae*.

MATERIALS AND METHODS

Isolates

Fungal strains were obtained from the CBS culture collection and Johanna Westerdijk (JW) citizen science collection of the Westerdijk Fungal Biodiversity Institute (WI; Utrecht, the Netherlands, formerly CBS-KNAW). New and interesting strains from JW were deposited in the CBS fungal collection. A total of 420 isolates including taxa preliminarily identified as *Clonostachys* and of allied genera were included in this study and their morphological traits and molecular phylogeny characterised (Supplementary Table S1).

DNA extraction, PCR amplification and sequencing

Genomic DNA was extracted from fungal colonies growing on oatmeal agar (OA; Crous *et al.* 2019) for 7–14 d at room temperature using the Wizard® Genomic DNA purification Kit (Promega Corporation, Madison, WI, USA), following the manufacturer's protocol. Five loci were amplified: the ITS region was amplified using the primer pair ITS5/ITS4 (White *et al.* 1990); the LSU region was amplified using the primer pair LR0R/LR5 (Vilgalys & Hester 1990, Rehner & Samuels 1994); *RPB2*, *TEF1* and *TUB2* genes were amplified using the primer pairs RPB2-5F2/RPB2-7CR (Liu *et al.* 1999, Sung *et al.* 2007), EF1-983F/EF1-2218R (Rehner & Buckley 2005) and T1/T22 (O'Donnell & Cigelnik 1997). For sequencing, the same primer sets were used except for the partial *TUB2* gene, where the additional primer TUB4Rd (Woudenberg *et al.* 2009) was used. The consensus sequences of each isolate were assembled from forward and reverse sequences using Geneious Prime 2022 (Biomatters Inc., New Zealand). Sequences newly generated in this study and their GenBank (http://www.ncbi.nlm.nih.gov) accession numbers are shown in Supplementary Table S1.

Phylogenetic analyses

Subsequent alignments for five individual loci (ITS, LSU, *RPB2*, *TEF1,* and *TUB2*) were generated with MAFFT v. 7 using the default settings on the web server of the European Bioinformatics Institute (EMBL-EBI) (http://www.ebi.ac.uk/Tools/msa/ mafft/) (Katoh & Standley 2013, Li *et al.* 2015). These alignments were manually edited in MEGA v. 7.0.21 when necessary (Tamura *et al.* 2013). Maximum-likelihood (ML) and Bayesian analyses (BA) were used for phylogenetic inferences of individual sequence alignments and the concatenated (ITS, LSU, *RPB2*, *TEF1,* and *TUB2*) alignments. Maximum-likelihood analyses were conducted using the CIPRES Science Gateway portal v. 3.3 (https://www.phylo.org/; Miller *et al*. 2012) and RAxML-HPC2 on XSEDE v. 8.2.12 (Stamatakis 2014) with default GTR substitution matrix and 1 000 rapid bootstrap replications. Additional ML analyses were performed using IQ-TREE v. 2.1.2 (Nguyen *et al*. 2015, Minh *et al*. 2020) with ultrafast bootstrapping (UFBoot2; Hoang *et al*. 2018) for estimation of branch support. The most suitable evolutionary model for each partition was estimated using ModelFinder (Kalyaanamoorthy *et al.* 2017; Minh *et al.* 2020) as implemented in IQ-TREE. MrModelTest v. 2.2 (Nylander 2004) was used to determine the optimal nucleotide substitution model for each locus. Bayesian analyses were performed using MrBayes v. 3.2.6 (Ronquist *et al.* 2012). Markov Chain Monte Carlo sampling (MCMC) analyses of four chains were started in parallel from a random tree topology. Four simultaneous Markov chains were run for 10 M generations and trees were sampled every 1 000 generation or until the run was stopped automatically when the average standard deviation of split frequencies fell below 0.01. The first 25 % of the trees were discarded as the burn-in phase of each analysis, and the remaining trees were used to calculate posterior probabilities (PP). The resulting trees were plotted using FigTree v. 1.4.2 (http://tree.bio.ed.ac.uk/ software/figtree). Alignments and the phylogenetic trees derived from this study were uploaded to figshare (doi: 10.6084/m9.figshare.22894592).

Morphology

Macroscopic descriptions were made from colonies on oatmeal agar (OA), potato dextrose agar (PDA), and synthetic nutrient-poor agar (SNA; Nirenberg 1976, Crous *et al.* 2019) after 7 d in the darkness at 25 °C. Colony diameters and characters were measured after 7 d. Colony colours (upper surface and reverse) were rated following the colour charts of Rayner (1970). Micro-morphological characters were recorded mostly from 5–14-d-old colonies on OA or SNA under near-UV light at room temperature, using structures from relatively young parts of the colony. Clear lactic acid was used as mounting medium for the observation of micromorphological structures of stromata, perithecia, perithecial walls, asci, ascospores, conidiophores and conidia (Schroers 2001). Observations of micro-morphological characteristics were processed with a Nikon Eclipse 80i compound microscope with differential interference contrast (DIC) optics and a Nikon AZ100 dissecting microscope. Photomicrographs and measurements were taken with a Nikon DS-Ri2 high-definition colour digital camera using the NIS-elements D software v. 4.50 (Nikon, Tokyo, Japan). All descriptions, illustrations and nomenclatural data were deposited in MycoBank (www.MycoBank.org; Crous *et al.* 2004), and specimens were deposited in the CBS Fungarium.

RESULTS

Phylogenetic analyses

For inferring the phylogeny of the genus *Clonostachys* within the *Bionectriaceae*, we analysed aligned DNA sequence data from five concatenated loci (ITS, LSU, *RPB2*, *TEF1*, and *TUB2*) in dataset 1. To obtain a more precise phylogenetic relationship of species within *Clonostachys*, more inclusive analyses based on DNA sequence data from five loci were carried out for the genus (dataset 2).

Dataset 1: Concatenated and aligned ITS, LSU, *RPB2*, *TEF1*, and *TUB2* sequences from 269 taxa represent several genera belonging to the *Bionectriaceae*, with *Tilachlidium brachiatum* (CBS 363.97, CBS 505.67), *Flammocladiella anomiae* (CLL 16017), *F. aceris* (CBS 138906) and *F. decora* (CBS 142776) serving as outgroups (*Hypocreales*, *Tilachlidiaceae* & *Flammocladiellaceae*; Fig. 1). The final alignment consisted of 4 245 characters, including alignment gaps (gene boundaries ITS: 1–691, 691 bp; LSU: 692–1 495, 804 bp; *RPB2*: 1 496–2 288, 793 bp; *TEF1*: 2 289–3 103, 815 bp, *TUB2*: 3 104–4 245, 1 142 bp). Among these, 2 315 character sites were conserved (ITS: 257, LSU: 605, *RPB2*: 297, *TEF1*: 484, *TUB2*: 672), 1 872 were variable (ITS: 407, LSU: 198, *RPB2*: 477, *TEF1*: 330, *TUB2*: 460), and 1 646 were parsimony informative characters (ITS: 338, LSU: 167, *RPB2*: 453, *TEF1*: 281, *TUB2*: 407).

The phylogenetic trees based on dataset 1 were generated with Maximum-likelihood and Bayesian analyses. According to the result of MrModelTest, the GTR+I+G model was proposed for all loci investigated. The Bayesian analysis of the concatenated five-locus alignment lasted for 10 075 000 generations and 20 152 trees were generated after the average standard deviation of split frequencies value was below 0.01 in the BI analysis. A total of 15 114 trees were used for calculating the posterior probabilities (PP) after the first 25 % of trees were discarded as the burn-in phase. The three phylogenetic analyses (RAxML, IQ-TREE, and MrBayes) overall displayed the same species clades and mainly differed with regards to the backbone relationships between species clades/lineages. The best RAxML tree based on the combined dataset is presented here with bootstrap support values of ML analyses (RAxML-BS / IQ-TREE-BS) and relevant Bayesian posterior probabilities (PP) shown at the nodes (RAxML-BS > 50 % / IQ-TREE-BS > 90 % / PP > 0.90) (Fig. 1). RAxML trees targeting each of the used partitions individually (ITS, LSU, *RPB2*, *TEF1*) are presented as Supplementary Figs S1–S4; *TUB2* is not shown as those sequences were mainly available only for *Clonostachys*.

The resulting phylogenetic tree (Fig. 1) resolved 24 well-supported clades, representing 24 genera in the *Bionectriaceae*. In our study, one clade has isolates preliminarily identified as *Sesquicillium microsporum* that are here reassigned to *Nectriopsis* (100 % /100 % / 1), with one new species, *Nectriopsis didymii*. Two clades have isolates preliminarily identified as *Clonostachys* that are here assigned to *Mycocitrus* (96 % / 98 % / 0.99) and *Stephanonectria* (100 % / 100 % / 1). The genus *Sesquicillium* (97 % / 100 % / 1) is resurrected to accommodate the subgenera *Epiphloea* (except *C. setosa*) and *Uniparietina*, with three new species and seven new combinations. The genus *Clonostachys* (99 % / 100 % / 1) includes the subgenera *Astromata*, *Bionectria*, *Myronectria* and *Zebrinella* with 49 known and 19 new species (Figs 1, 2). However, the here presented dataset also supports that *Sesquicillium* and *Clonostachys* derive from the same ancestor, as their phylogenetic sister group relatedness is highly supported (95 % / 99 % / 1).

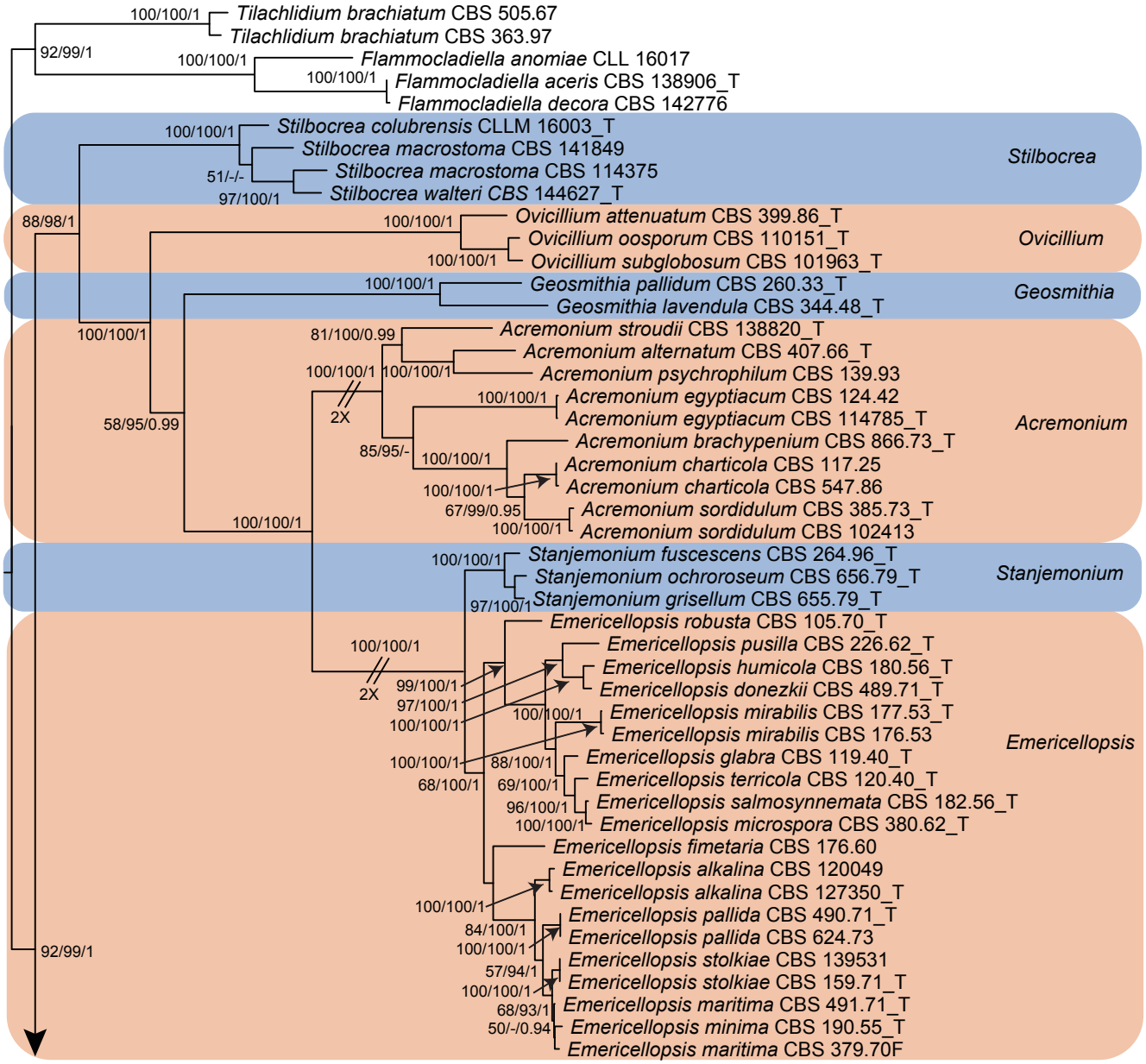

Fig. 1. Phylogenetic tree inferred from a Maximum Likelihood (RAxML) analysis based on aligned and concatenated ITS, LSU, *RPB2*, *TEF1* and *TUB2* sequences of 269 strains representing *Bionectriaceae* and outgroups. Numbers at branches indicate support values (RAxML-BS / IQ-TREE-BS / BI-PP) above 50 % / 90 % / 0.9. New species are printed in red font, new combinations in blue font and coloured boxes highlight genera. Roman numerals indicate subgenera as coded in the legend. "T" indicates ex-type strains. The tree is rooted to *Flammocladiella aceris* CBS 138906, *F. decora* CBS 142776, *F. anomiae* CLL 16017, *Tilachlidium brachiatum* CBS 363.97, and *T. brachiatum* CBS 505.67 (*Hypocreales*, *Flammocladiellaceae* & *Tilachlidiaceae*). Scale bar represents expected number of changes per site.

The individual gene trees had variable success in resolving genus clades (Supplementary Figs S1–S4). Although they generally resolved the same genus clades, the order and association between the clades were not always the same due to low support in the backbones of the trees. The ITS phylogeny (Supplementary Fig. S1) recovered all the genus clades presented in Fig. 1, with the exception that it intermixed species of *Emericellopsis* and *Stanjemonium*. The LSU phylogeny (Supplementary Fig. S2) recovered all genera presented in Fig. 1, but did not cluster species of *Lasionectria* in a monophyletic clade and intermixed several subclades of *Sesquicillium* and *Clonostachys* intermixed in a polytomy. The *RPB2* phylogeny (Supplementary Fig. S3) recovered all genera presented in Fig. 1, with the exception that it intermixed species of *Emericellopsis* and *Stanjemonium*. The *TEF1* phylogeny (Supplementary Fig. S4) recovered all genera presented in Fig. 1, but did not cluster all species of *Nectriopsis* in a monophyletic clade (*Nectriopsis lindauiana* clustered basal to *Stilbocrea* without any support) while *Clonostachys buxicola* and *Clonostachys pityrodes* formed a clade sister to the monophyletic *Stephanonectria* clade but with an unsupported connecting node.

Dataset 2: This dataset consisted of 394 ingroup isolates that formed a fully supported clade representing *Clonostachys*, with the bionectriaceous *Acremonium alternatum* (CBS 407.66) and *A. stroudii* (CBS 138820) used as outgroups (Fig. 2). The final alignment consisted of 4 055 characters, including alignment gaps (gene boundaries ITS: 1–565, 565 bp; LSU: 566–1 366, 801 bp; *RPB2*: 1 367–2 133, 767 bp; *TEF1*: 2 134–2 941, 808 bp; *TUB2*: 2 942–4 055, 1 114 bp). Among these, 2 654 character sites were

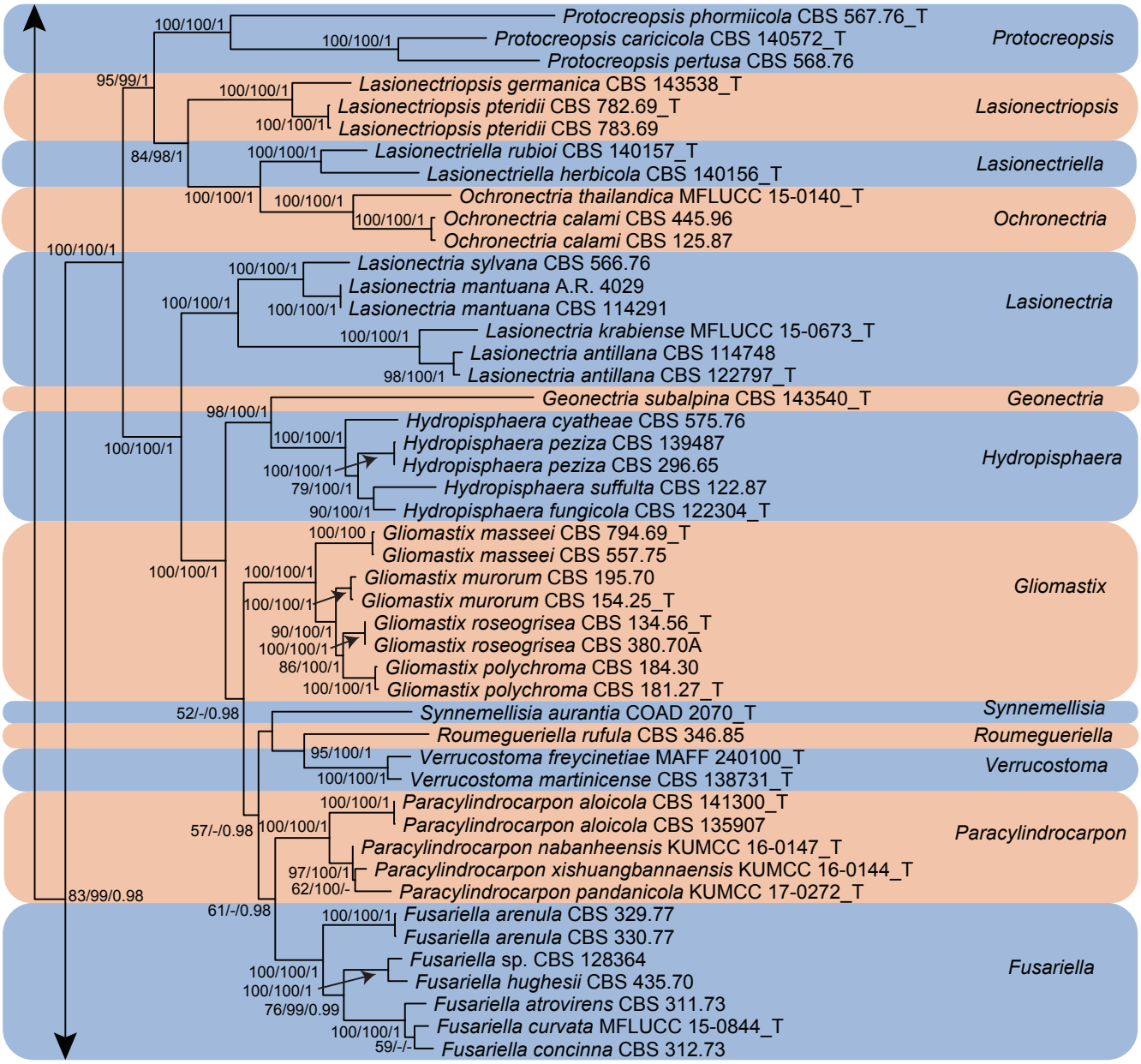

Fig. 1. (Continued).

conserved (ITS: 330, LSU: 694, *RPB2*: 378, *TEF1*: 576, *TUB2*: 676), 1 366 were variable (ITS: 220, LSU: 106, *RPB2*: 382, *TEF1*: 232, *TUB2*: 426), and 1 185 were parsimony informative (ITS: 175, LSU: 90, *RPB2*: 353, *TEF1*: 194, *TUB2*: 373).

The phylogenetic trees based on dataset 2 were generated with Maximum-likelihood analyses and Bayesian analyses. According to the result of MrModelTest, the SYM+I+G model was proposed for ITS, GTR+I+G model for LSU, *RPB2*, and *TEF1*, and HKY+I+G model for *TUB2*. The Bayesian analysis of the concatenated five-locus alignment lasted for 67 905 000 generations and 135 812 trees were generated after the average standard deviation of split frequencies value was below 0.013 in the BI analysis. A total of 101 860 trees were used for calculating the posterior probabilities (PP) after the first 25 % of trees were discarded as the burn-in phase. The three phylogenetic analyses (RAxML, IQ-TREE, and MrBayes) overall displayed the same species clades and mainly differed with regards to the backbone relationships between species clades/ lineages. The best RAxML tree based on the combined dataset is presented here with bootstrap support values of ML analyses (RAxML-BS / IQ-TREE-BS) and relevant Bayesian posterior probabilities (PP) shown at the nodes (RAxML-BS > 50 % / IQ-TREE-BS > 90 % / PP > 0.90) (Fig. 2). RAxML trees targeting each of the used partitions individually (ITS, LSU, *RPB2*, *TEF1*) are presented in Supplementary Figs S5–S8; *TUB2* is not shown as no sequences were available for the outgroup taxa. Well-supported clades in the phylogenetic tree based on dataset 2 include 49 known and 19 new species of *Clonostachys* (Fig. 2, Supplementary Fig. S9).

The individual gene trees had variable success in resolving species clades (Supplementary Figs S5–S8). Although they generally resolved the same species clades, with the exception of LSU (see below), the order and association between the clades were not always the same due to low support in the backbones of the trees. The ITS phylogeny (Supplementary Fig. S5) recovered the majority of the species clades presented in Fig. 2, with some exceptions where species were not monophyletic (*e.g.*, *C. eriocamporesii*) or

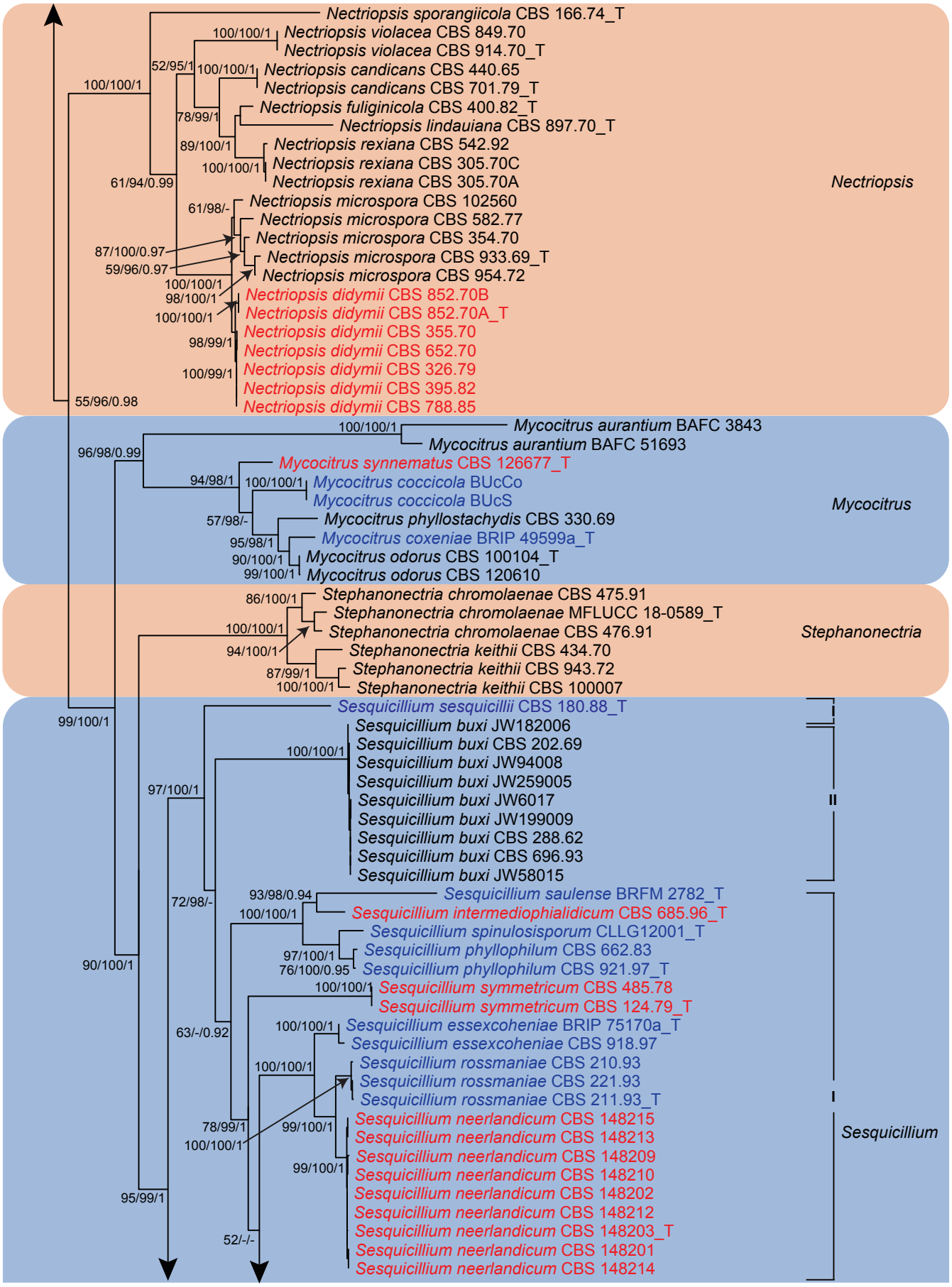

Fig. 1. (Continued).

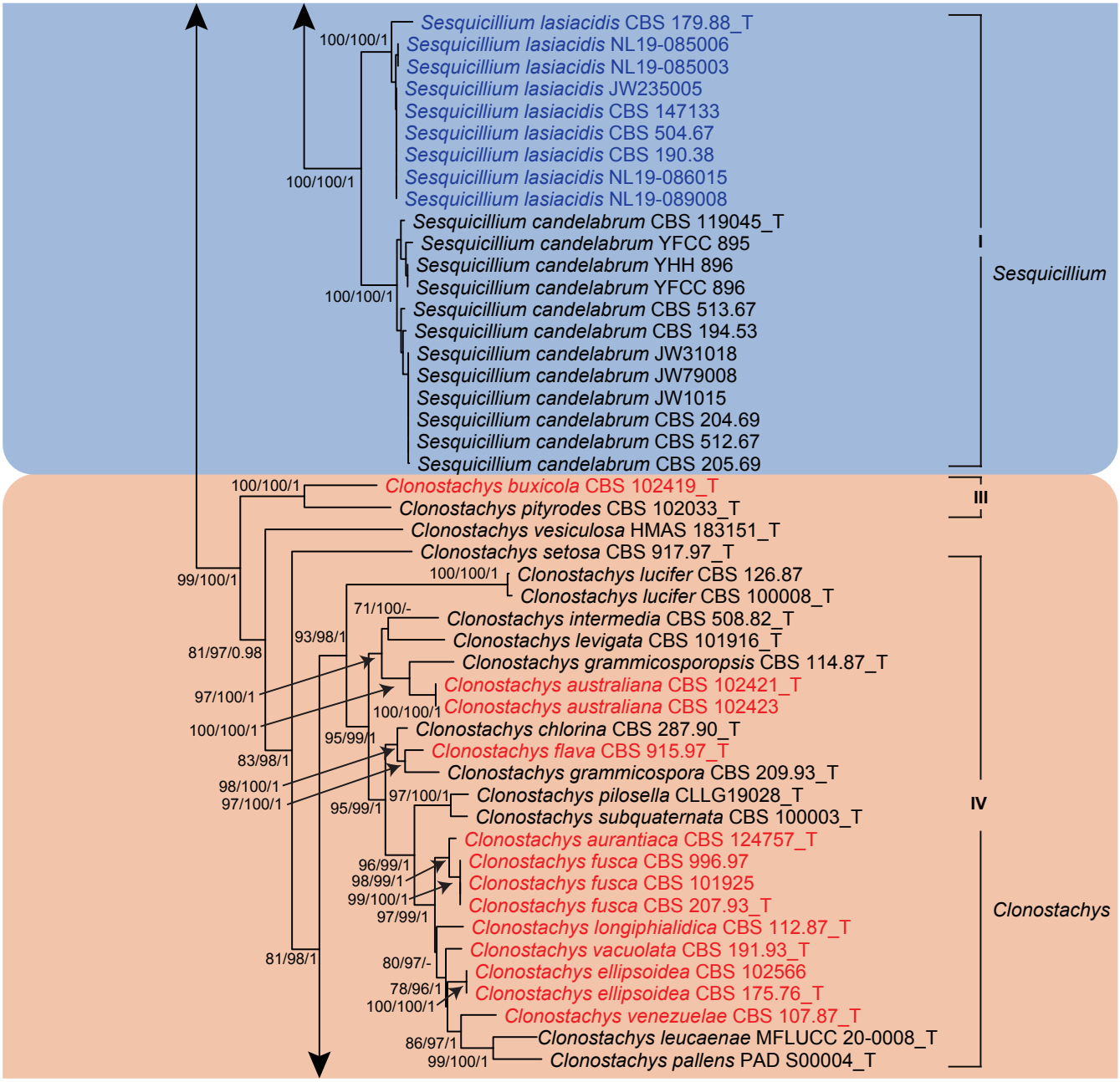

Fig. 1. (Continued).

indiscernible (*e.g. C. rogersoniana* / *C. cylindrica*, *C. reniformis* / *C. viticola*, *C. farinosa* / *C. apocyni*, and numerous species intermingled with *C. rosae* and *C. solani*). The LSU phylogeny (Supplementary Fig. S6) recovered some of the species clades presented in Fig. 2, but the majority were poorly resolved or intermixed. The *RPB2* phylogeny (Supplementary Fig. S7) recovered all species clades presented in Fig. 2, with variable branch lengths. The *TEF1* phylogeny (Supplementary Fig. S8) recovered all species clades presented in Fig. 2, with some exceptions where species were not monophyletic [*e.g. C. farinosa*, *C. sporodochialis*, *C. rosea* (one isolate not clustering with the rest)].

Taxonomy

Based on multi-locus phylogenetic inferences, supported by morphological observations, habitat information and geographical comparisons, a total of 420 isolates including taxa preliminarily identified as *Clonostachys* and of allied genera were examined in this study. Cultures were shown to represent taxa belonging to *Clonostachys*, *Mycocitrus*, *Nectriopsis, Sesquicillium* and *Stephanonectria*. Among these, 24 new species and 10 new combinations are proposed. Furthermore, one epitypification is proposed, one genus resurrected, and eight species epithets are reduced to synonymy. Two new species that proved to be sterile are described based on DNA sequence data, following the approach of Hou *et al.* (2023). Genera are arranged according to their position on the phylogenetic tree (Fig. 1), and species are arranged alphabetically (Figs 1, 2).

Nectriopsis Maire, Ann. Mycol. 9: 323. 1911.
Synonyms: *Dasyphthora* Clem., Gen. Fung. (Minneapolis): 45. 1909.
Peloronectriella Yoshim. Doi, Bull. Natl. Sci. Mus., Tokyo, N.S. 11: 179. 1968.

Type: *Nectriopsis violacea* (J.C. Schmidt ex Fr.) Maire

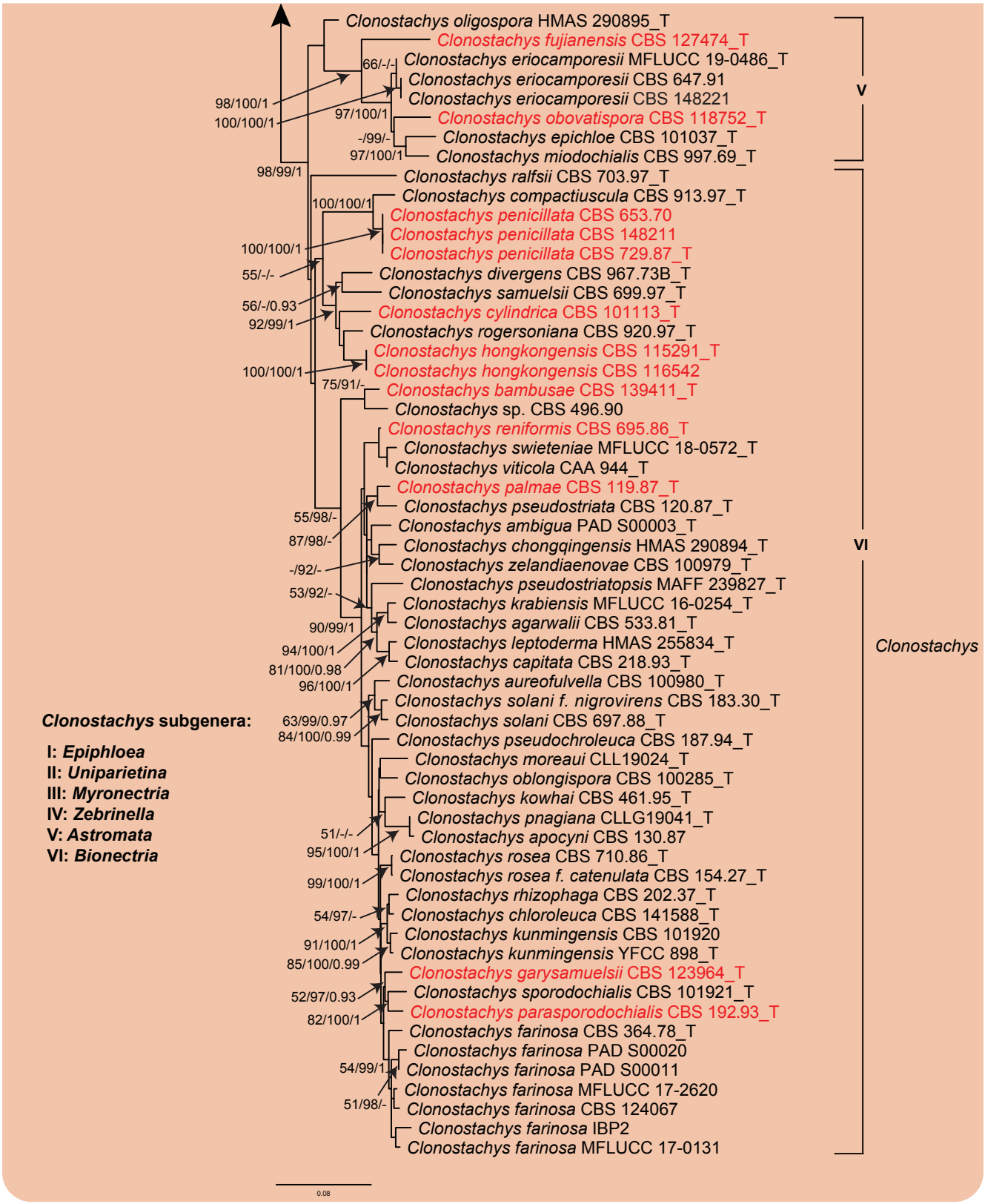

Fig. 1. (Continued).

Sexual morph on the natural substratum. *Perithecia* superficial or immersed in substratum, rarely inconspicuously stromatic, up to 200 µm diam, nearly white to pale yellow or orange, KOH-. *Perithecial wall* up to 20 µm thick, comprising a single region of small, thin-walled, non-descript cells; cells at surface of perithecia wall forming a *textura epidermoidea*. *Asci* cylindrical to clavate, apex simple or with a ring, 8-spored. *Ascospores* ellipsoidal, hyaline, (0–)1-septate. *Asexual morphs* acremonium-, gliocladium-, or verticillum-like (adapted from Rossman *et al*. 1999).

Notes: *Nectriopsis* was established with four species of hypocrealean fungi having ascomata in a byssoid stroma and considered intermediate between *Nectria* and *Hypomyces*. Clements (1909) placed *Dasyphthora* in *Hypocreaceae* with only

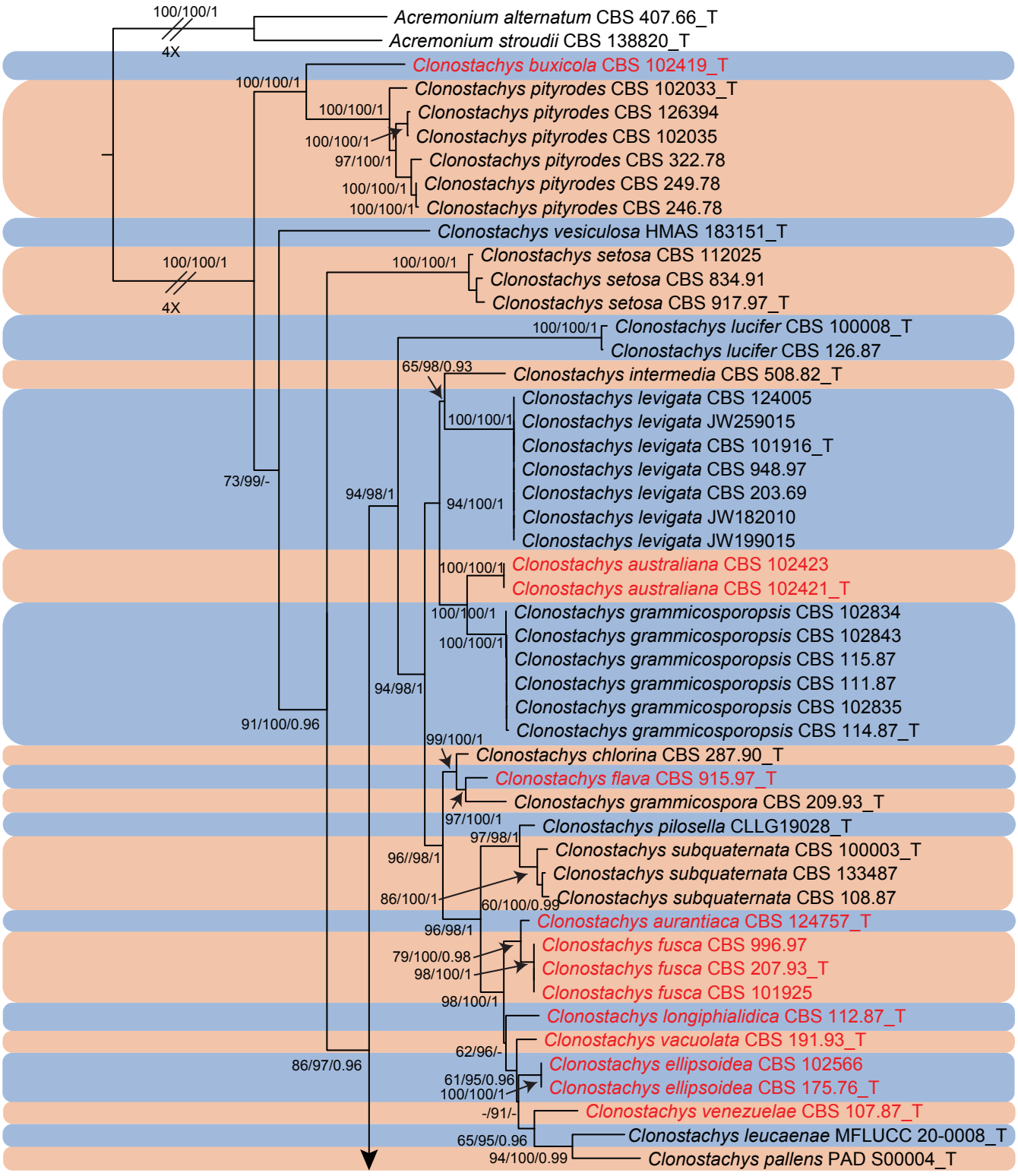

Fig. 2. Phylogenetic tree inferred from a Maximum Likelihood (RAxML-ML) analysis based on aligned and concatenated ITS, LSU, *RPB2*, *TEF1* and *TUB2* sequences of 394 strains representing *Clonostachys* and outgroups. Numbers at branches indicate support values (RAxML-BS / IQ-TREE-BS / BI-PP) above 50 % / 90 % / 0.9. New species are printed in red font and coloured boxes highlight species clades / lineages. "T" indicates ex-type strains. A detailed view of the collapsed clade at the bottom of the phylogenetic tree can be found in Fig. S9. The tree is rooted to *Acremonium alternatum* CBS 407.66 and *A. stroudii* CBS 138820 (*Hypocreales*, *Bionectriaceae*). Scale bar represents expected number of changes per site.

one species, *D. lasioderma*, that was later included in *Nectriopsis* (Samuels 1988a). Samuels (1988a) presented a thorough account of the genus, treating 43 species. The monotypic genus *Peloronectriella* was introduced for a fungus on bamboo, having elongate, tuberculate stromata with a nectria-like, but pale yellowish, KOH- ascomata, and 1-septate ascospores (Doi 1968). Rossman *et al*. (1999) regarded *Peloronectriella* as synonym of *Nectriopsis* according to its morphological characters.

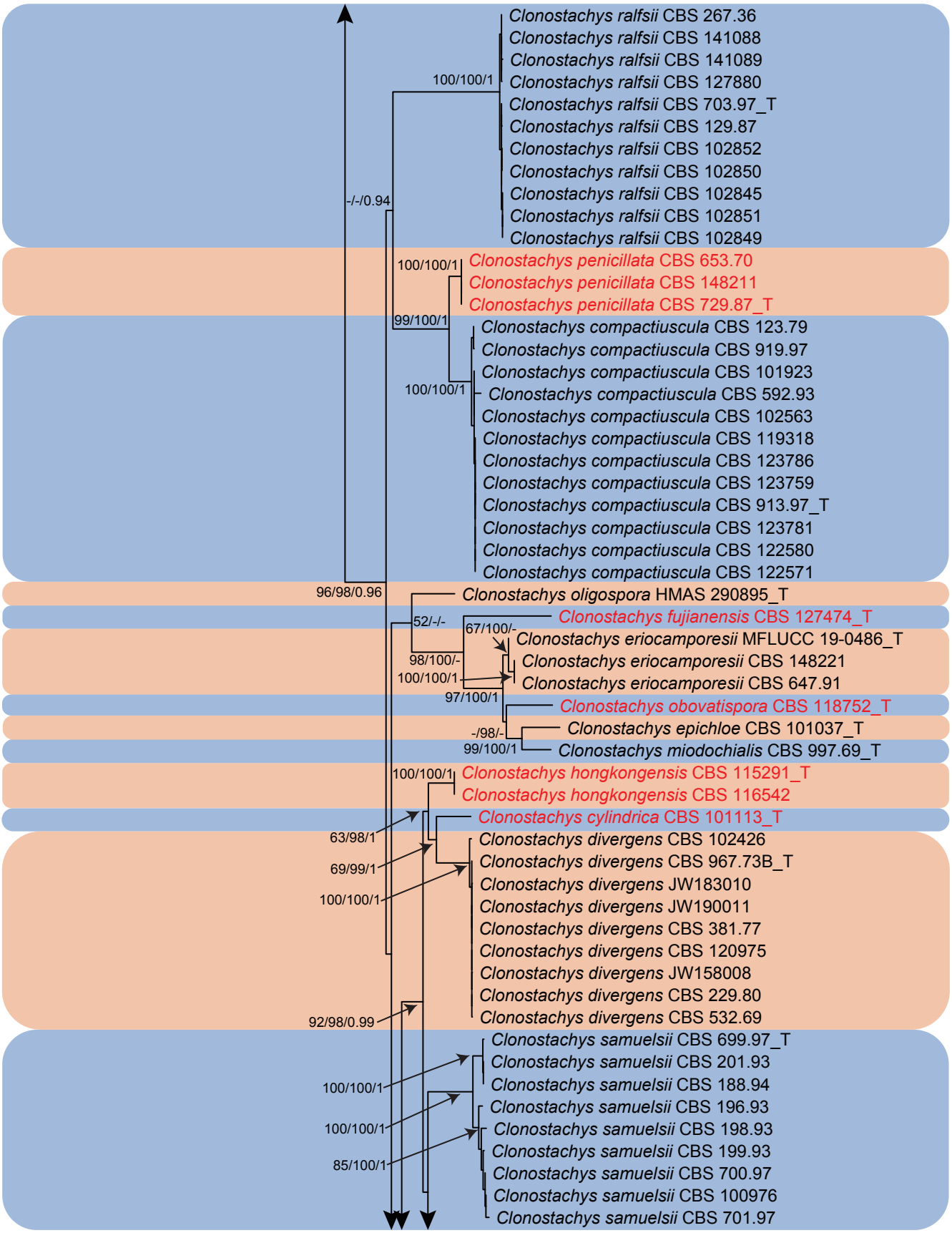

Fig. 2. (Continued).

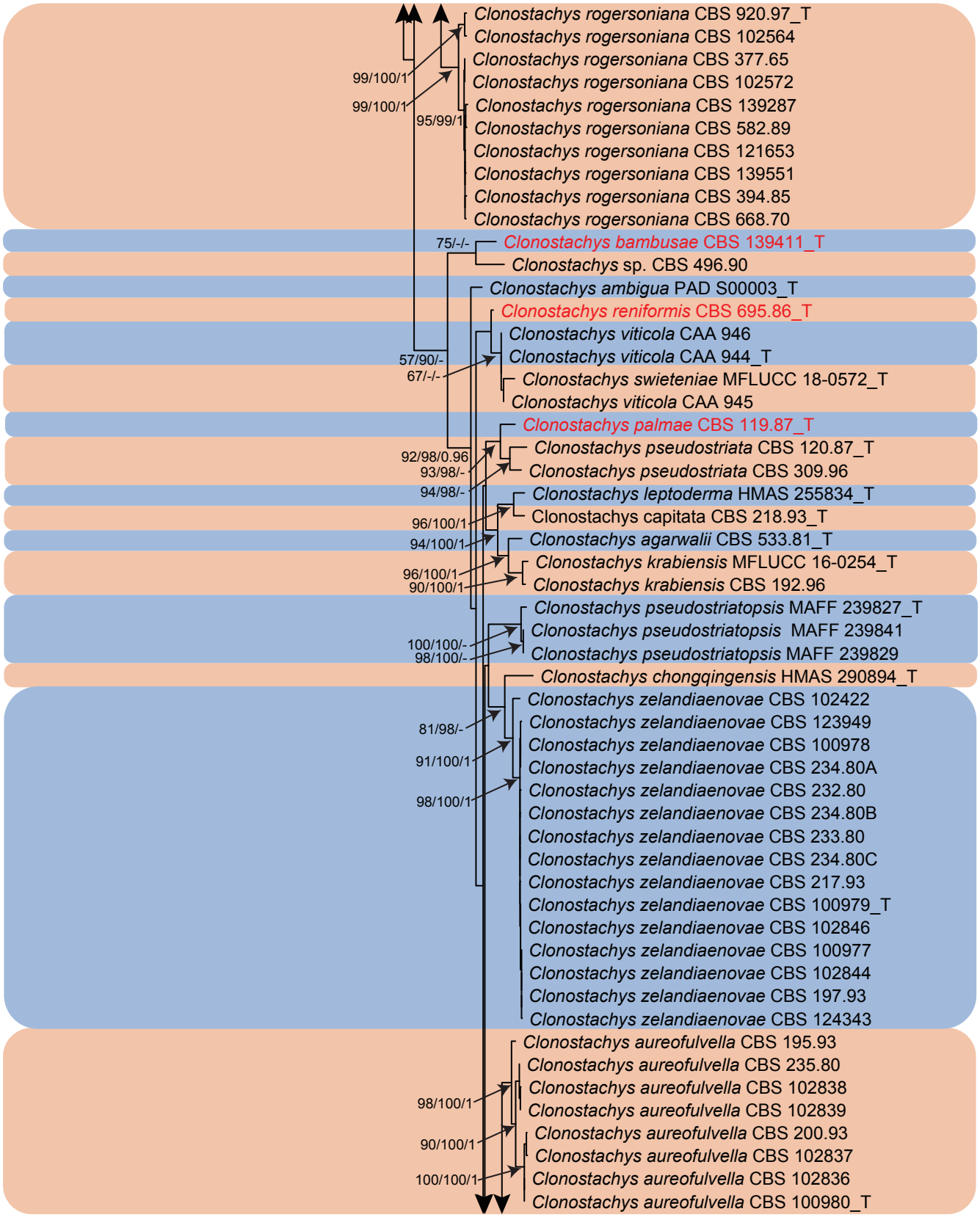

Fig. 2. (Continued).

Nectriopsis didymii L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848432. Fig. 3.

Etymology: Referring to the host, *Didymium melanospermum*, from which the holotype strain was collected.

Typus: **Germany**, Eifel, Geeser Wald near Gerolstein, on *Didymium melanospermum*, Sep. 1970, W. Gams (**holotype** designated here: CBS H-18226, ex-type living culture CBS 852.70A).

Sexual morph unknown. *Mycelia* consisting of branched, septate, hyaline, smooth- and thin-walled hyphae, 1.5–2.8 µm diam.

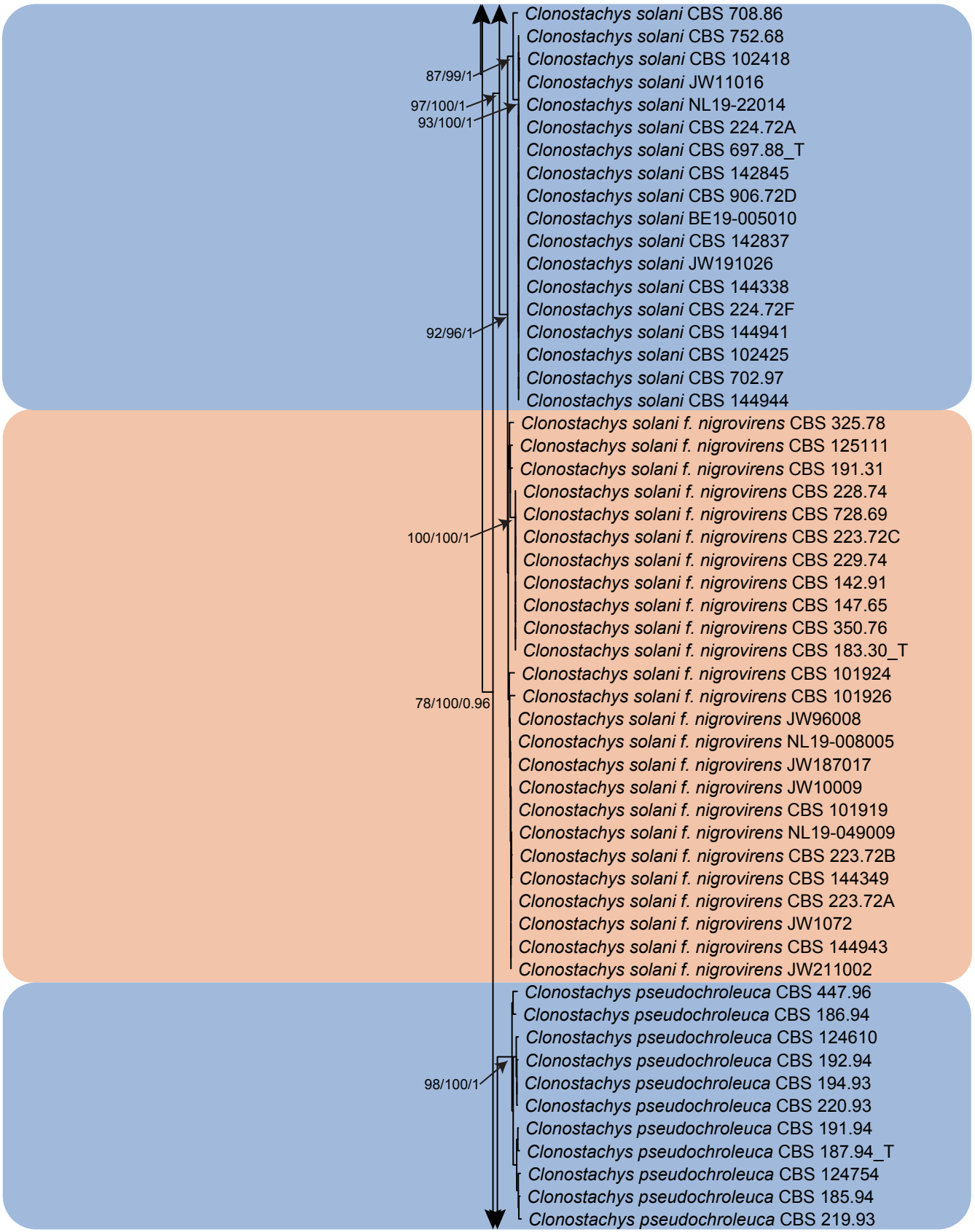

Fig. 2. (Continued).

Conidiophores hyaline, smooth, verticillately branched, lateral branches decreasing in length towards the apex of the main axis. *Conidiogenous cells* consisting of *discrete phialides*, terminal, in whorls of 2–4, flask-shaped, (4.2–)6.0–12.3(–19.8) µm long, (1.0–) 1.1–1.7(–1.9) µm wide at base, 0.6–0.9(–1.0) µm wide near apex (n = 70); *intercalary phialides* rare, below whorls of terminal phialides, with up to 3 µm long lateral pegs. *Conidia* aseptate, hyaline, smooth-walled, globose or subglobose, without laterally displaced hilum, (1.8–)2.0–2.5(–2.7) × 1.6–1.9(–2.1) µm (av. = 2.2 × 1.8 µm, n = 150).

Culture characteristics: Colonies on OA reaching 30–35 mm diam after 7 d in darkness at 25 °C, flat, with entire margin, pure white,

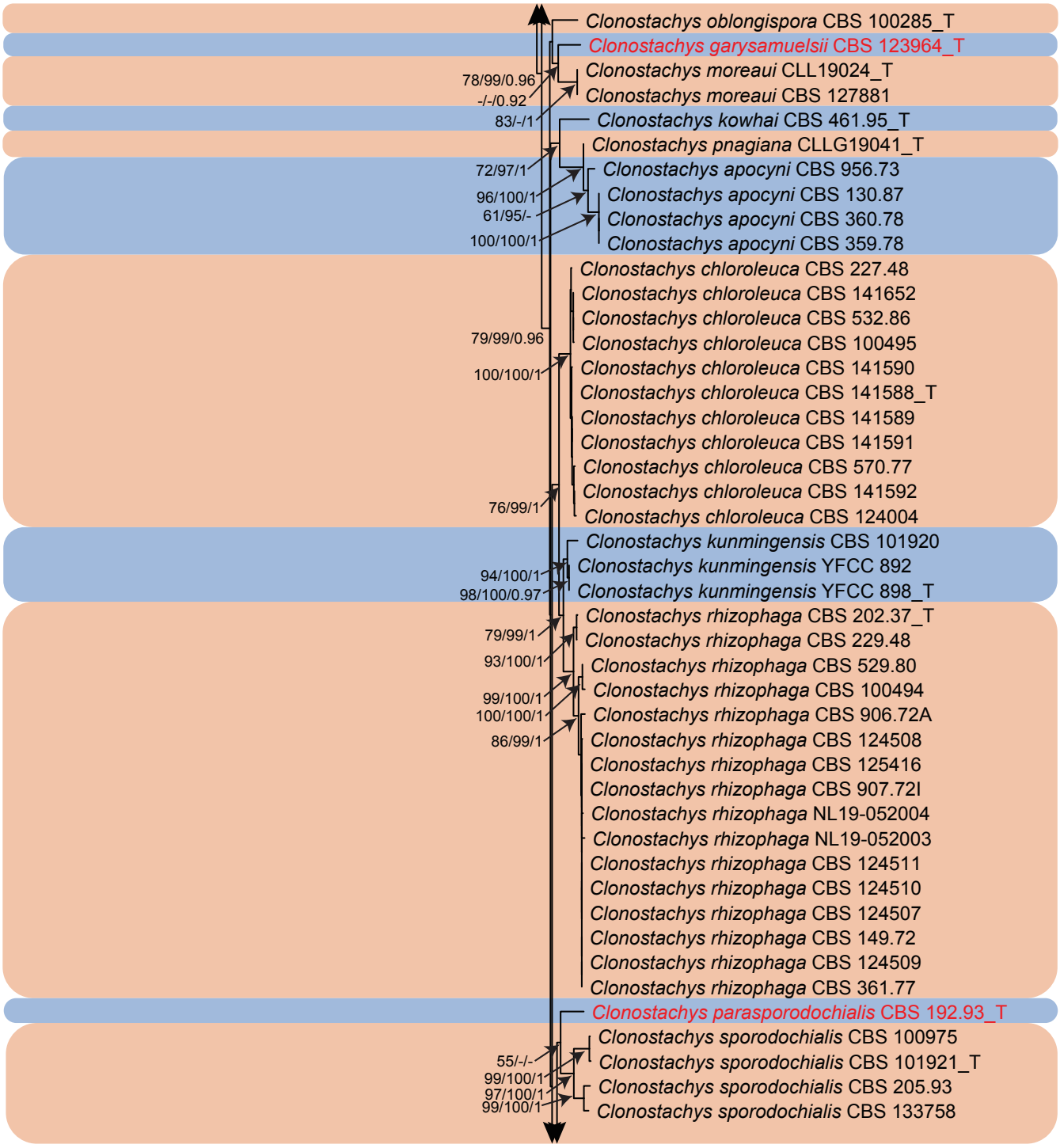

Fig. 2. (Continued).

aerial mycelium sparsely developed, mealy, with a thin layer of conidiophores, distinctly zonate, reverse whitish. Colonies on PDA reaching 27–28 mm diam, flat, with entire margin, aerial mycelium moderate, felty, pale yellow, reverse concolourous. Colonies on SNA reaching 19–22 mm diam, flat, with dendritic margin and sparsely produced aerial mycelium, whitish, sporulation absent or sparse, reverse concolourous.

Additional materials examined: **Canada**, Ontario, Petawawa, forest soil, B2 horizon, under *Populus tremuloides*, Aug. 1968, G.C. Bhatt, No. PET 114 (B), culture CBS 652.70; Ontario, Petawawa, forest soil under *Populus tremuloides*, Oct. 1968, G.C. Bhatt, No. PET 160, specimen CBS H-18229, culture CBS 355.70. **Germany**, Eifel, Pelmer Wald bei Gerolstein, on *Didymium melanospermum*, 15 Sep. 1970, W. Gams, specimen CBS H-18225, culture CBS 852.70B. **Netherlands**, Noord-Brabant, St. Anthonis, on *Pseudotsuga menziesii*, litter, Oct. 1985, W. Gams & M. Schlag, specimen CBS H-3999, culture CBS 788.85. **Sweden**, dung of isopod, date unknown, B.E. Söderström, culture CBS 326.79. **Trinidad and Tobago**, Nariva Swamp, twig, Aug. 1981, D.J. Stradling, culture CBS 395.82.

Notes: Based on our phylogenetic analysis, *N. didymii* (Fig. 1; 98 % / 99 % / 1) and *N. microspora* (Fig. 1; 61 % / 98 % / -) form a fully-supported clade (Fig. 1). Morphologically, *N. didymii* differs from *N. microspora* in shorter hyphal width (1.5–2.8 µm *vs* 2.5–4.0 µm), and longer terminal phialides [(4.2–)6.0–12.3(–19.8) µm *vs* (6–)7–10(–15) µm]. Furthermore, sequences clearly distinguish the ex-type strains CBS 852.70A (*N. didymii*) from CBS 933.69 (*N. microspora*) [ITS (99.6 % identity, with 2 bp differences), *RPB2* (96.1 %, 29 bp),

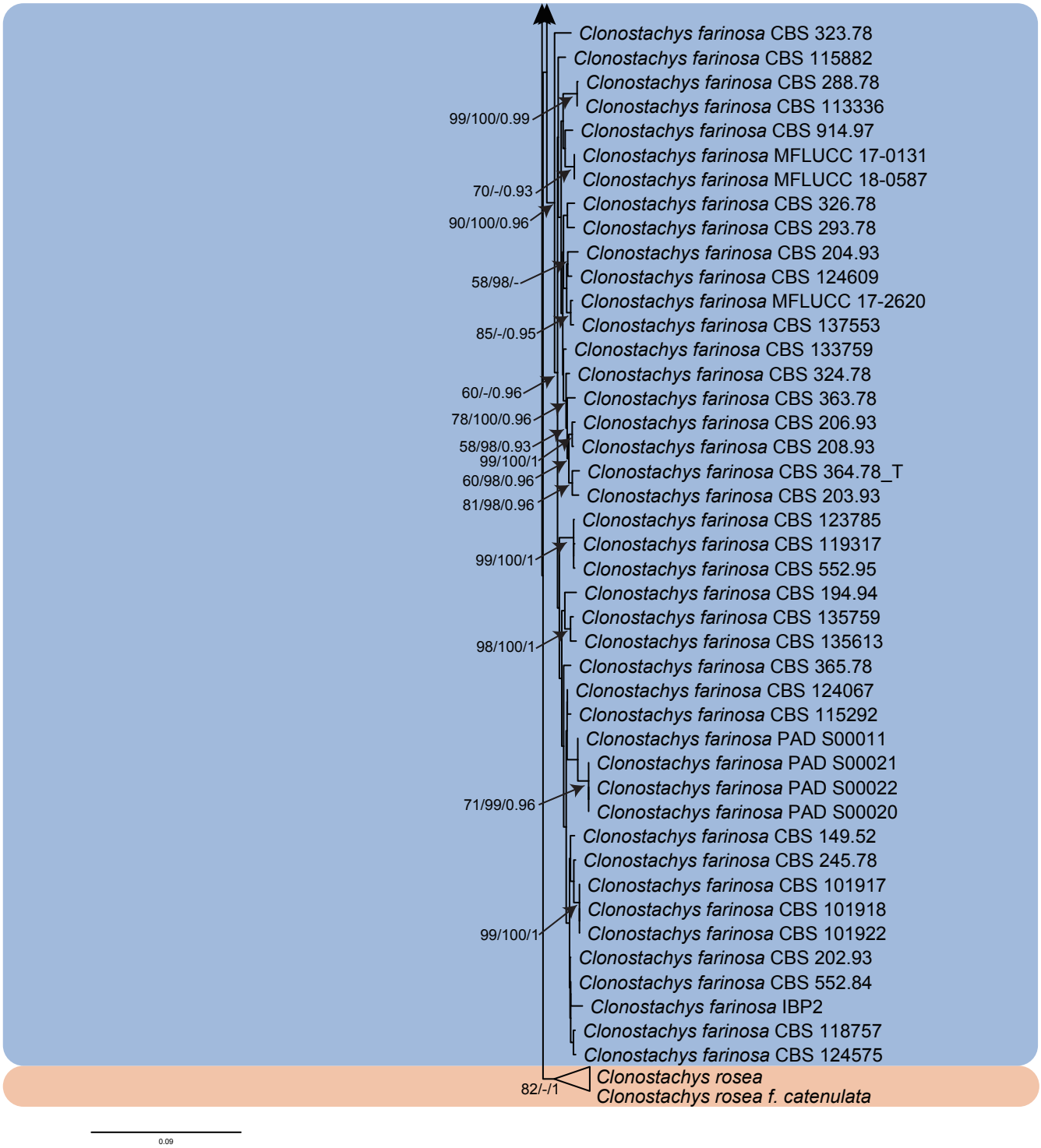

Fig. 2. (Continued).

TEF1 (98.2 %, 15 bp) and *TUB2* (99.1 %, 7 bp)]. Therefore, a new species is introduced here as *N. didymii*. Both species have an overall similar conidiophore morphology that differs clearly from the frequently irregularly branched, acremonium- or, less frequently, gliocladium-like conidiophores of other *Nectriopsis* species (Samuels 1988a). Intercalary phialides are not often seen in conidiophores in *Nectriopisis*, however, Samuels (1988a) illustrated such conidiogenous cells for *N. epimyces* and *N. microthecia.*

Nectriopsis microspora (Jaap) L.W. Hou *et al.*, Stud. Mycol. 105: 109. 2023. Fig. 4.

Basionym: *Verticillium microsporum* Jaap, Verh. Bot. Vereins Prov. Brandenburg 58: 38. 1916.

Synonyms: *Sesquicillium parvulum* Veenb.-Rijks, Acta Bot. Neerl. 19: 323. 1970.

Sesquicillium microsporum (Jaap) Veenb.-Rijks & W. Gams, in Gams, Cephalosporium-artige Schimmelpilze (Stuttgart): 226. 1971.

Tolypocladium microsporum (Jaap) Bissett, Canad. J. Bot. 61: 1318. 1983.

Gliocladium microsporum (Jaap) Arx, Mycotaxon 25: 157. 1986.

Typus: **Netherlands**, Oostelijk Flevoland, wheat field soil, date unknown, J.W. Veenbaas-Rijks (**holotype** CBS H-7751, ex-type culture CBS 933.69 = ATCC 18.932).

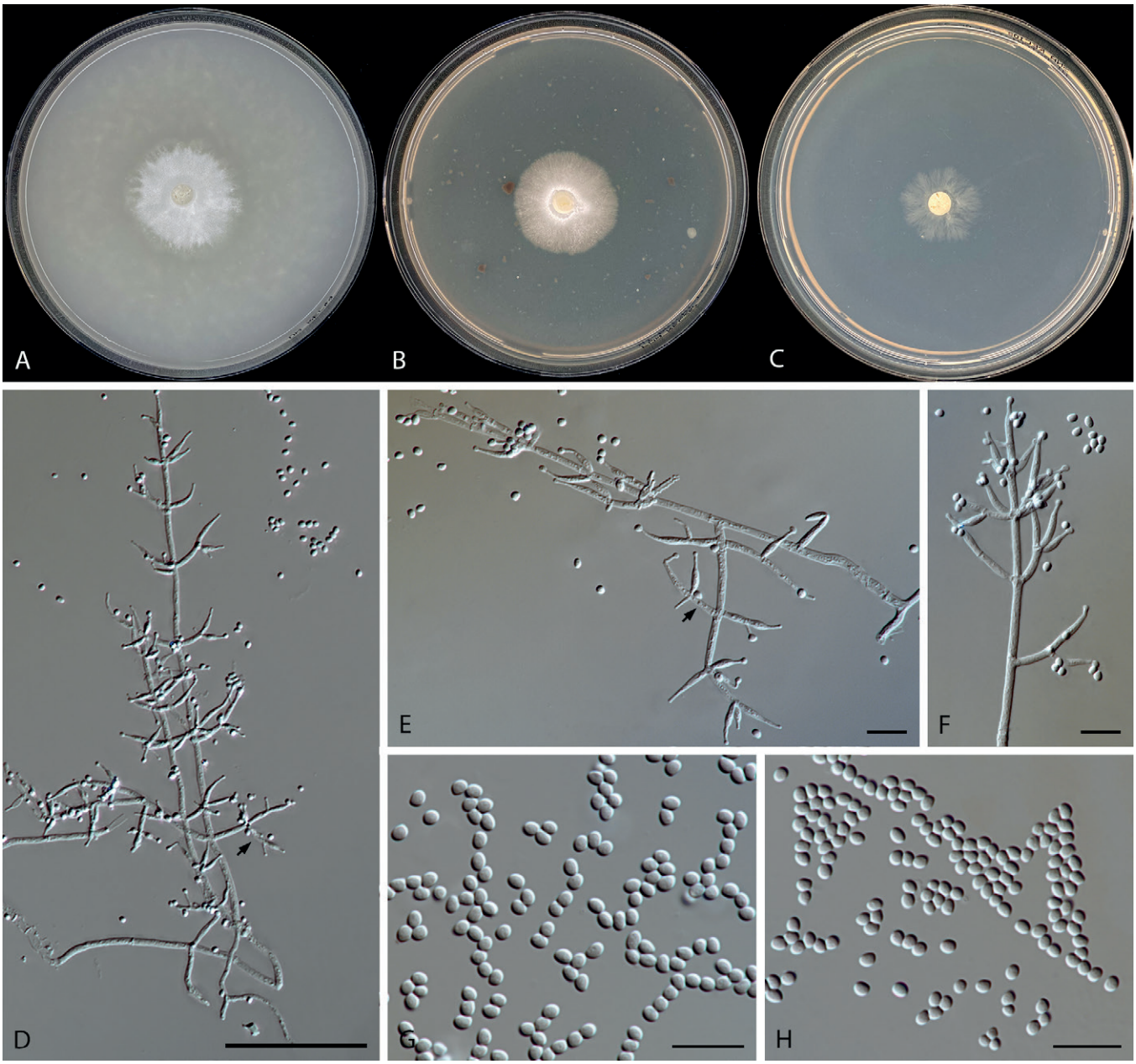

Fig. 3. *Nectriopsis didymii* (ex-type CBS 852.70A). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–F.** Conidiophores. **G, H.** Conidia. Black arrows indicate intercalary phialides. Scale bars: D = 50 µm; E–H = 10 µm.

Descriptions and illustrations: Veenbaas-Rijks (1970), Gams (1971).

Additional materials examined: **Canada**, Ontario, Aberfoyle, forest soil under *Thuja occidentalis*, Sep. 1966, G.C. Bhatt, specimen CBS H-18228, culture CBS 354.70. **Japan**, Kamogawa, Hachijo Island, living *Cycadaceae*, Mar. 1996, T. Okuda, culture CBS 102560. **Netherlands**, Utrecht, Berenkuil, soil, Sep. 1972, D. Mulder, culture CBS 954.72. **USA**, Wisconsin, Madison, leaf litter of *Acer saccharum*, unknown date and collector, culture CBS 582.77.

Notes: This species was originally introduced as *S. parvulum* (Veenbaas-Rijks 1970). Its taxonomic history is complex. Veenbaas-Rijks (1970) described *S. parvulum* as a new species of *Sesquicillium*, distinguishing it from *S. buxi* and *S. candelabrum* (Gams 1968) by the size and shape of its conidia. Gams (1971) treated *S. parvulum* as a synonym of *S. microsporum*, with *Verticillium microsporum* as basionym. Bissett (1983) transferred *S. microsporum* to *Tolypocladium* because of the rather irregular branching pattern of its conidiophores, false phialidic whorls, intercalary phialides with elongated phialidic pegs, and masses of slimy conidia. Samuels (1989) accepted classification of this species in *Sesquicillium*, while noting that *S. microsporum* differed from other *Sesquicillium* species in size ranges and shapes of its phialides and conidia, rather dry conidial chains, and more irregularly branched and poorly developed penicilli. Relatedness of *S. microsporum* and *Nectriopsis* was hypothesised earlier on the basis of the myxomyceticolous lifestyle and analyses of LSU sequences (Rogerson & Stephenson 1993, Schroers 2001). In the present study, according to our phylogenetic analyses, strains identified as *S. microsporum* clustered in a lineage (Fig. 1; 61 % / 98 % / -) of the genus *Nectriopsis* and is closely related to *N. didymii* (Fig. 1). For morphological comparison with the other species of this genus, see notes under *N. didymii*.

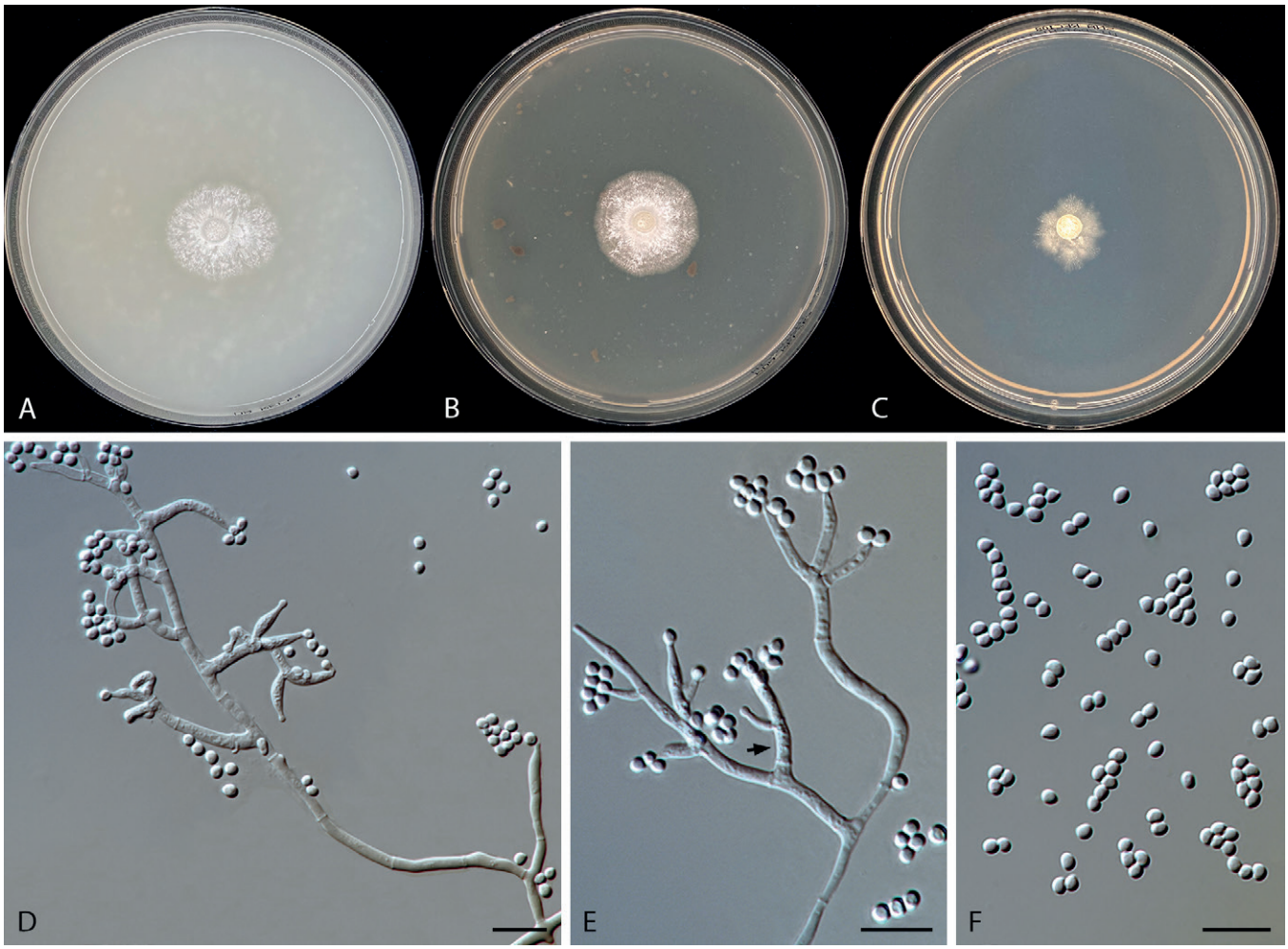

Fig. 4. *Nectriopsis microspora* (ex-type CBS 933.69). **A–C.** Colonies on OA, PDA, SNA after 7 d at 25 °C. **D, E.** Conidiophores. **F.** Conidia. Black arrows indicate intercalary phialides. Scale bars = 10 µm.

Mycocitrus Möller, Bot. Mitt. Tropen. 9: 297. 1901.
Synonym: *Shiraiella* Hara, Bot. Mag. (Tokyo) 28: 274. 1914.

Type: *Mycocitrus aurantium* Möller

Sexual morph on the natural substratum. *Stroma* well-developed, surface buff to rufous or light orange, KOH-, clasping and surrounding the substratum. *Ascomata* perithecial, surface partially to fully immersed, with apices barely visible, densely gregarious, forming a single layer. *Asci* cylindrical, ascal apex simple, 8-spored. *Ascospores* 1-septate, ellipsoid, hyaline, spinulose. *Asexual morphs* commonly acremonium-like (adapted from Rossman *et al.* 1999).

Notes: *Mycocitrus* was first described from culms of living bamboo and *Microstachys* in southern Brazil (Möller 1901). The type species, *M. aurantium*, is characterised by its large, fleshy, orange stromata that clasp and surround bamboo culms, with perithecial ascomata partially to fully immersed in the upper region of the stromata. Later, a second species, *M. phyllostachydis* (bas. *Ustilaginoidea phyllostachydis*), was collected in Japan on *Phyllostachys* and added to the genus (Doi 1967). *Mycocitrus* was originally placed in the "*Hypocreaceen*, *Didymosporae*" (Möller 1901), and later in *Hypocreaceae* (Doi 1967). The proposal by Rossman *et al*. (1999) to include *Mycocitrus* in the *Bionectriaceae* was based on morphology. Leite *et al*. (2018) obtained two bamboo-inhabiting *M. aurantium* cultures in South America. Their phylogeny was based on ITS sequences and suggested prematurely that *Mycocitrus* forms an independent lineage within *Hypocreales*, distinct from *Bionectriaceae*, *Nectriaceae*, *Cordycipitaceae*, *Clavicipitaceae*, and *Hypocreaceae*. However, Hou *et al*. (2023) revealed that *Mycocitrus* clusters within the *Bionectriaceae* based on a multi-locus phylogenetic analysis, what is supported in the present analysis (Fig. 1).

Mycocitrus coccicola (J.A. Stev.) L. Zhao & Crous, ***comb. nov.***
MycoBank MB 848434.
Basionym: *Tubercularia coccicola* J.A. Stev., Rep. (Annual) Puerto Rico Insular Exp. Sta., 1916–1917: 91. 1917.
Synonyms: *Clonostachys coccicola* (J.A. Stev.) H.T. Dao, Mycol. Prog. 15: 6. 2016.
Nectria tuberculariae Petch, Trans. Brit. Mycol. Soc. 7: 157. 1921.

Materials examined: **Australia**, New South Wales, Cornwallis, armoured scale insects, date and collector unknown, culture BucCo; New South Wales, Somersby, armoured scale insects, date and collector unknown, culture BucS.

Notes: *Mycocitrus coccicola* was originally described as *Tubercularia coccicola* (Stevenson 1917) before Dao *et al*. (2016) placed it in *Clonostachys* as *C. coccicola*. In our study, the phylogenetic analysis of the combined ITS, LSU, *TEF1*, *RPB2*, and *TUB2* dataset revealed that *C. coccicola* clusters within the genus *Mycocitrus* (Fig. 1) and a new combination is proposed here.

Mycocitrus coxeniae (Y.P. Tan *et al.*) L. Zhao & Crous, ***comb. nov.*** MycoBank MB 848911.
Basionym: *Clonostachys coxeniae* Y.P. Tan *et al.*, Index of Australian Fungi 5: 3. 2023.

Description: Tan & Shivas (2023).

Notes: Tan & Shivas (2023) recently coined *Clonostachys coxeniae*, but without any proper description, illustration or discussion of morphological characters. Their deposited sequence identifies this species as a member of genus *Mycocitrus* (Fig. 1).

Mycocitrus odorus L.W. Hou *et al.*, Stud. Mycol. 105: 111. 2023. Fig. 5.

Typus: **Netherlands**, Amsterdam, Slotervaart Hospital, onychomycosis (human), unknown date, W.C. van Dijk & W. Pauw (**holotype** specimen CBS H-24690, ex-type living culture CBS 100104).

Description and illustration: Hou et al. (2023).

Additional materials examined: **Netherlands**, human skin, unknown collection date and collector, culture CBS 120610. **Sweden**, Stockholm, human skin, unknown collection date and collector, culture CBS 232.75B.

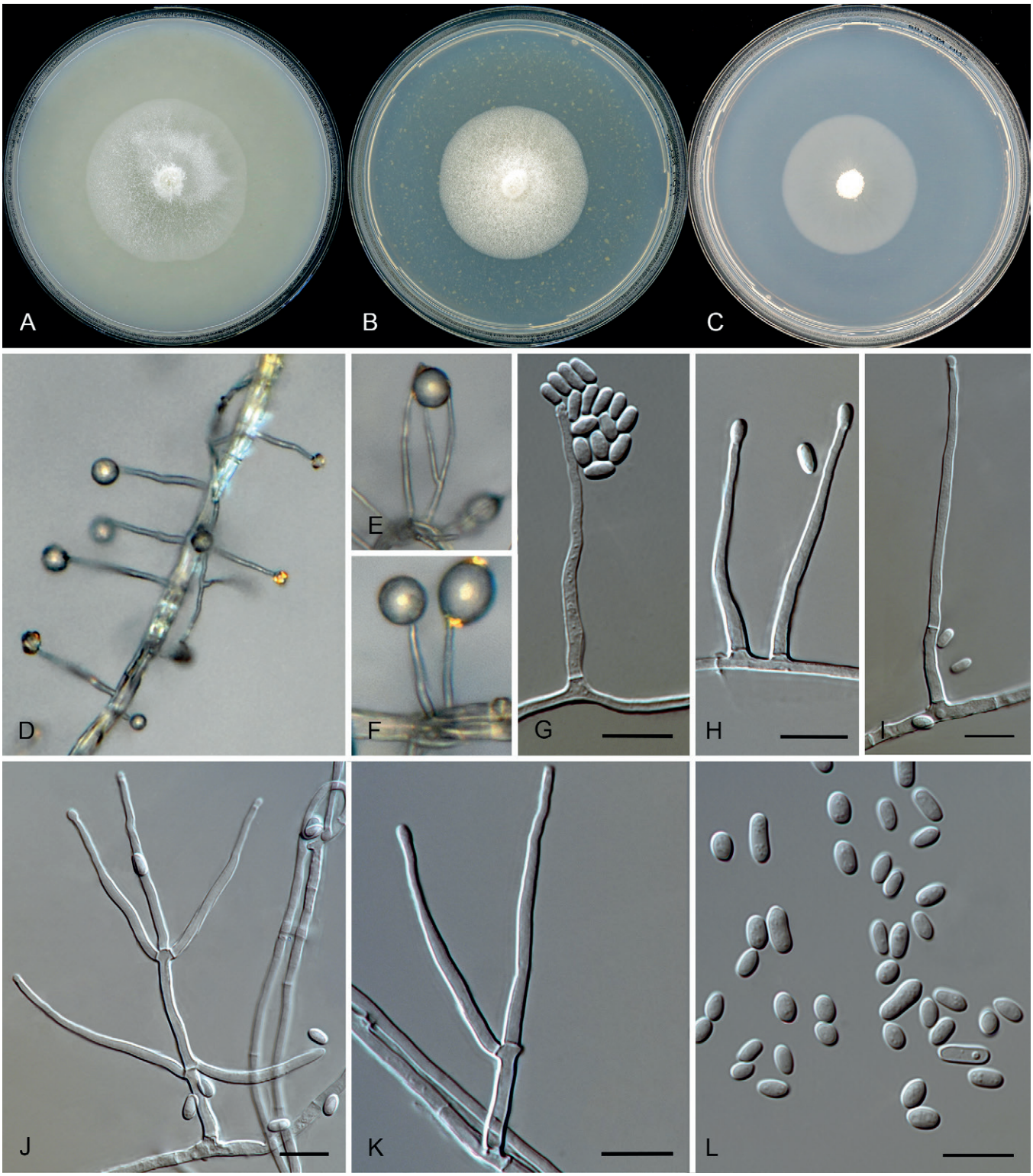

Fig. 5. *Mycocitrus odorus* (CBS 120610). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–K.** Conidiophores. **L.** Conidia. Scale bars = 10 µm.

Note: *Mycocitrus odorus* was recently described by Hou *et al.* (2023) as a novel species in *Mycocitrus* (Fig. 1).

Mycocitrus phyllostachydis (Syd. & P. Syd.) Yoshim. Doi, Bull. Natl. Sci. Mus., Tokyo, N.S. 10: 31. 1967.
Basionym: *Ustilaginoidea phyllostachydis* Syd. & P. Syd., Mém. Herb. Boissier 4: 5. 1900.
Synonyms: *Hypocreopsis phyllostachydis* (Syd. & P. Syd.) I. Miyake & Hara, Bot. Mag., Tokyo 24: 333. 1910.
Shiraiella phyllostachydis (Syd. & P. Syd.) Hara, Bot. Mag., Tokyo 28: 402. 1914.

Description and illustration: Doi (1967).

Material examined: **Japan**, on *Phyllostachys* sp. (*Poaceae*), unknown date, W. Gams, specimen CBS H-14839, culture CBS 330.69 = IFO 8912.

Notes: Gams (1971) examined the culture of *M. phyllostachydis* (CBS 330.69) isolated from *Phyllostachys* sp. in Japan. Based on the phylogenetic analyses, classification of *U. phyllostachydis* in *Mycocitrus*, as proposed by Doi (1967), is confirmed here (Fig. 1).

Fig. 6. *Mycocitrus synnematus* (ex-type CBS 126677). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–F.** Synnemata. **G.** Detail of the apical portion of a synnema. **H–K.** Conidiogenous cells. **L.** Conidia. Scale bars: F = 100 µm; G = 50 µm; H–L = 10 µm.

Mycocitrus synnematus L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848435. Fig. 6.

Etymology: Name refers to the production of synnemata.

Typus: **Sri Lanka**, from wood, date unknown, G.J. Samuels (**holotype** designated here CBS H-25131, ex-type living culture CBS 126677).

Sexual morph unknown. *Synnemata* erect, golden brown, occurring singly or in groups, abundant in culture. *Conidiophores* macronematous, branched, asymmetric-biverticillate or monoverticillate. *Conidiogenous cells* phialidic, cylindrical, straight or slightly curved, slightly tapered at the apex, in terminal whorls of 2–5, (13.2–)16.2–45.4(–59.6) × (1.2–)1.5–2.0(–2.1) µm. *Conidia* aseptate, hyaline, smooth, ellipsoid, straight to slightly curved, distally broadly rounded, without recognisable hilum, (4.3–)5.5–7.7(–8.0) × (2.7–)3.0–3.8(–4.0) µm (av. = 6.8 × 3.5 µm, n = 150).

Culture characteristics: Colonies on OA reaching 30–35 mm diam after 7 d in darkness at 25 °C, flat, with entire margin, aerial mycelium scanty, finely floccose, whitish, reverse concolourous. Colonies on PDA reaching 27–28 mm diam, flat, with entire margin, aerial mycelium moderately dense, floccose, pale yellow, reverse concolourous. Colonies on SNA reaching 19–22 mm diam, flat, with entire margin, aerial mycelium moderate, floccose white, reverse whitish.

Notes: Phylogenetically, *M. synnematus* is closely related to *M. coccicola*, *M. coxeniae*, *M. odorus*, and *M. phyllostachydis* (Fig. 1). Morphologically, *M. synnematus* can be distinguished from *M. odorus* and *M. coccicola* by its larger conidia, (4.3–)5.5–7.7(–8.0) × (2.7–)3.0–3.8(–4.0) µm (av. = 6.8 × 3.4 µm) in *M. synnematus*, 3.2–5.5 × 2.1–3.3 (av. 4 × 2 µm) in *M. coccicola* and (3.4–)3.7–5.0(–6.6) × (1.8–)2.1–2.8(–3.0) µm (av. = 4.4 × 2.5 µm) in *M. odorus*. Furthermore, CBS 126677 (*M. synnematus*) and CBS 330.69 (*M. phyllostachydis*) have clearly different ITS (93.9 % identity, with 31 bp differences), LSU (97.6 %, 18 bp), *RPB2* (89.1 %, 81 bp), and *TEF1* (96.6 %, 27 bp) sequences, while *M. synnematus* (CBS 126677) has different ITS (95 % identity, with 24 bp differences) sequences when compared with *M. coxeniae* (BRIP 49559a).

Stephanonectria Schroers & Samuels, Sydowia 51: 116. 1999.

Type: *Stephanonectria keithii* (Berk. & Broome) Schroers & Samuels

Sexual morph on the natural substratum. *Stroma* superficial, reduced or erumpent through bark. *Perithecia* brown, KOH-, smooth to rough, minutely papillate. *Ostiolum* surrounded by a crown-like arrangement of cells. *Perithecial wall* consisting of two regions. Cells of the crown merging with the cells of the outer wall region, angular to oblong, outwards toothlike. *Ascospores* 1-septate, covered with short striae. *Asexual morph*. *Conidiophores* monomorphic, sporodochial, towards the margin of the colony solitary, irregularly penicillate, or sparsely aggregated, not showing regular patterns, with 1–5 phialides on each supporting cell; branches overall diverging, sometimes joined by anastomoses. *Phialides* cylindrical, sometimes widening in the middle or in the upper part, typically becoming narrower just underneath the apex, with apical periclinal thickening visible, without collarette. *Conidia* aseptate, hyaline, smooth, ellipsoidal, hilum median, slightly laterally displaced, or not visible (adapted from Schroers *et al*. 1999a).

Notes: *Stephanonectria* was introduced as a new genus because of characters of the ascomatal wall and aggregations of cells forming a crown-like structure around the ostiolum. The ascospores are covered with short striae that are more or less parallel with the long axis of the spore. The asexual morph was identified as being myrothecium-like (Schroers *et al.* 1999a) because of details seen in the shape of phialides. Despite the more irregular branching pattern of conidiophores, sporodochia seen in *S. keithii* are similar to those formed by many *Clonostachys* species. The use of "myrothecium-like" for the asexual morph in *Stephanonectria* (Schroers *et al.* 1999a) is therefore obsolete.

Stephanonectria chromolaenae R.H. Perera & K.D. Hyde, Fungal Diversity 118: 134. 2023. Fig. 7.

Typus: **Thailand**, Chiang Mai Province, Mae Rim District, on dead stem of *Chromolaena odorata* (*Asteraceae*), 18 Sep. 2017, R.H. Perera (**holotype** MFLU 19-0972, ex-type living culture MFLUCC 18-0589).

Description and illustration: Perera *et al*. (2023).

Additional materials examined: **Turkey**, isolated from soil, date unknown, G. Turhan, No. 10, culture CBS 475.91; soil, date unknown, G. Turhan, No. 13, culture CBS 476.91.

Notes: *Stephanonectria chromolaenae* was described from dead stems of *Chromolaena odorata*. Based on our phylogenetic analysis, *S. chromolaenae* and *S. keithii* formed a fully-supported clade within the genus *Stephanonectria* (Fig. 1).

Stephanonectria keithii (Berk. & Br.) Schroers & Samuels, Sydowia 51: 116. 1999.
Basionym: *Nectria keithii* Berk. & Br., Ann. Mag. Nat. Hist., Ser. 4, 27: 144. 1876.
Synonym: *Nectriella keithii* (Berk. & Br.) Sacc., Michelia 1: 279. 1879.

Typus: **UK,** Scotland, Forres, on decorticated stems of cabbage, collection date unknown, Rev. J. Keith, specimen IMI 77877.

Description and illustration: Schroers *et al*. (1999a).

Additional materials examined: **Netherlands**, Utrecht, Berenkuil, soil, Sep. 1972, collector unknown, culture CBS 943.72; Oostelijk Flevoland, agricultural soil, under permanent potato, J. W. Veenbaas-Rijks, Oct. 1969, culture CBS 434.70. **New Zealand**, Gisborne, Lake Waikaremoana, Ngamoko Trail, on Beilschrniedia tawa, 30 May 1983, G. J. Samuels *et al*., Samuels culture 83-165, CBS 100007 (PDD 46342; BPI 737629).

Notes: This species was originally described as *Nectria keithii* (Berkeley & Broome 1876). Schroers *et al*. (1999a) introduced a new genus *Stephanonectria* to accommodate *S. keithii*. The three strains included in the phylogenetic analysis cluster in a supported clade (Fig. 1; 87 % / 100 % / 1).

Sesquicillium W. Gams, Acta Bot. Neerl. 17. 455. 1968.

Type: *Sesquicillium buxi* (J.C. Schmidt ex Link) W. Gams

Sexual morph on the natural substratum. *Perithecial stroma* typically formed superficially on plant tissue, reduced, supporting solitary perithecia, typically consisting of prosenchymatous cells not integrating with cells of major perithecial wall regions,

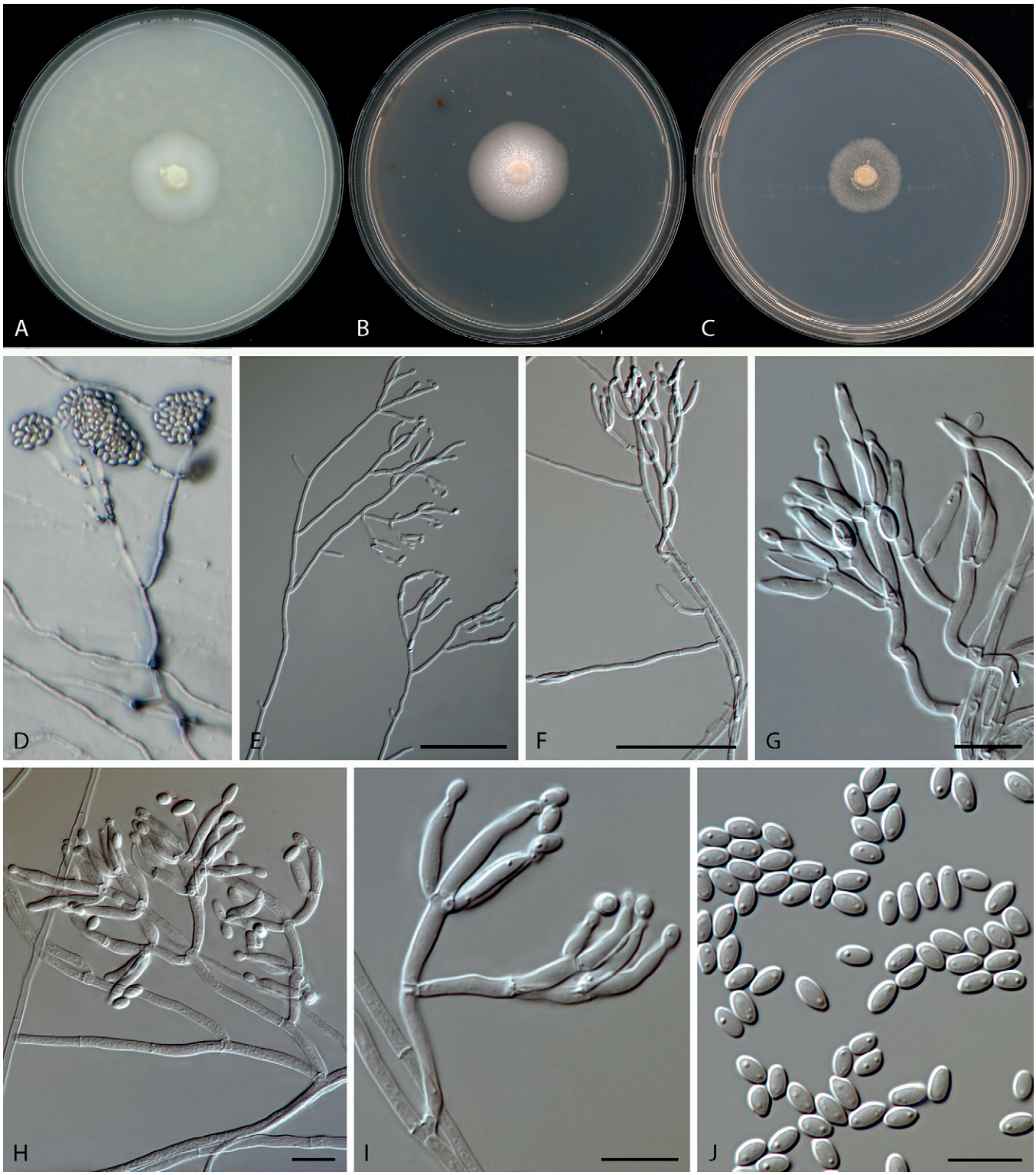

Fig. 7. *Stephanonectria chromolaenae* (CBS 475.91). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–I.** Conidiophores. **J.** Conidia. Scale bars: E, F = 50 µm; G–J = 10 µm.

sometimes erumpent through bark, supporting several perithecia and consisting of pseudoparenchymatous cells. *Perithecia* solitary, gregarious or loosely aggregated, crowded if formed on an erumpent stroma, globose to subglobose, 200–400 µm diam, sometimes smaller, up to 200 µm diam, pale yellow, pale to light orange, apically or laterally pinched when dry, not papillate, glabrous; ostiolar region somewhat sunken and slightly darker (brownish). *Perithecial wall* either consisting of two or one major wall region, sometimes with an additional outermost cell-layer that continues into the prosenchymatous stroma. *Asci* narrowly to broadly clavate, 8-spored, with flat or rounded apex, with or without visible ring. *Ascospores* typically 1-septate, equally 2-celled, sometimes aseptate, hyaline, spinulose, warted, with short striae or with warts arranged in striae, typically ellipsoidal to fusiform. *Asexual morph*. *Conidiophores* macronematous, mononematous, monomorphic penicillate or somewhat dimorphic, penicillate and verticillium-like, mostly arising from the agar surface or from sparsely formed aerial mycelium. Penicillate conidiophores bi- to quaterverticillate; branches of the penicilli divergent or adpressed; terminal whorls consisting of narrowly flask-shaped phialides and/or typically one or sometimes two successive intercalary phialides, of which the uppermost bears a solitary terminal phialide;

conidiogenous pegs of intercalary phialides typically short, formed laterally just below the upper septum. *Conidia* aseptate, smooth, hyaline, obovoid, ellipsoid, or fusoid, slightly curved or straight, generally with a slightly laterally displaced hilum and arranged in imbricate chains forming columns or, rarely, with a centrally located hilum and arranged in linear chains (adapted from Schroers 2001).

Notes: In this study, *Bionectria* subgenera *Epiphloea* and *Uniparietina* clustered in a statistically supported clade (Fig. 1; 97 % / 99 % / 1) that is sister to clades accommodating the other *Clonostachys* subgenera (Fig. 1). This separate clade includes *C. buxi* and *C. candelabrum* classified by Gams (1968) in *Sesquicillium*. The type species of the subgenus *Uniparietina* is *Bionectria coronata*, for which *S. buxi* is currently in use. Furthermore, the genus *Sesquicillium*, already used by Samuels (1989) for several below considerd species, is resurrected to accommodate the subgenera *Epiphloea* and *Uniparietina*.

Sesquicillium buxi (J.C. Schmidt ex Link) W. Gams, Acta Bot. Neerl. 17: 455. 1968.
Basionym: *Fusidium buxi* J.C. Schmidt ex Link, Willdenow, Sp. pl., Edn 4 6(2): 97. 1825.
Synonyms: *Fusisporium buxi* (J.C. Schmidt ex Link) Fr., Syst. Mycol. 3: 447. 1832.
Verticillium buxi (J.C. Schmidt ex Link) Auersw. & Fleischh., Hedwigia 6: 9. 1867.
Ramularia buxi (J.C. Schmidt ex Link) Fuckel, Symb. Mycol. p. 97. 1870.
Paecilomyces buxi (J.C. Schmidt ex Link) Bezerra, Acta Bot. Neerl. 12: 63. 1963.
Clonostachys buxi (J.C. Schmidt ex Link) Schroers, Stud. Mycol. 46: 193. 2001.
Nectriella coronata Juel, Arkiv før Botanik 19: 4. 1925.
Bionectria coronata (Juel) Schroers, Stud. Mycol. 46: 203. 2001.

Typus: **Germany**, Leipzig, Auerswald [**neotype** for *Fusidium buxi*: B, designated by Gams (1968)].

Descriptions and illustrations: Juel (1925), Gams (1968), Rossman *et al*. (1993), Schroers (2001).

Additional materials examined: **France**, Pyrénées Atlantiques, Île de Sauveterre de Béarn; 400 m alt., *Buxus sempervirens*, leaf litter, 17 Oct 1993, F. Candoussau, BPI 802851, culture CBS 696.93. **Netherlands**, *Buxus sempervirens*, collection date unknown, J.L. Bezerra, culture CBS 288.62; Culemborg, soil, collection date unknown, R. Fuld, culture JW182006; Netherlands, Utrecht, soil, collection date unknown, M. Wickham, culture JW199009; Ermelo, soil, collection date unknown, Marit en Mette Elmers, culture JW259005; Deurne, soil, collection date unknown, Martina Hoeben, culture JW58015; Eemnes, soil, collection date unknown, Herman Wim Vos, culture CBS 147861 = JW6017; Rijen, soil, collection date unknown, Gijs & Lotte Schijvenaars, culture JW94008. **Sweden**, Uppsala, Botanical Garden, on leaves of *Buxus sempervirens*, 10 Oct. 1924, O. Juel (type of *Nectriella coronata*: holotype S, isotype BPI). **UK**, England, Kew Gardens, *Buxus sempervirens*, leaf litter, Nov. 1967, W. Gams, CBS H-18217, culture CBS 202.69.

Notes: *Sesquicillium buxi* was originally described as *Fusidium buxi* (Link 1825). Later, it was transferred to the genus *Sesquicillium* (Gams 1968) as *S. buxi* (type species) with conidiophores having sparsely branched whorls, and intercalary phialides. By accepting a broader genus concept, Schroers (2001) combined *S. buxi* as *Clonostachys buxi*. In the present study, the phylogenetic analysis of the combined ITS, LSU, *TEF1*, *RPB2* and *TUB2* dataset reveals that taxa of *Sesquicillium* form the phylogenetic sister of *Clonostachys sensu stricto* (Fig. 1). Therefore, *S. buxi* is resurrected here.

Sesquicillium candelabrum (Bonord.) W. Gams, Acta Bot. Neerl. 17: 457. 1968. Fig. 8.
Basionym: *Verticillium candelabrum* Bonord., Handb. Allgem. Mykol. (Stuttgart): 97. 1851.
Synonyms: *Clonostachys candelabrum* (Bonord.) Schroers, Stud. Mycol. 46: 192. 2001.
Clonostachys chuyangsinensis Hong Yu bis & Yao Wang, Frontiers Microbiol. 14: 3. 2023.

Typus: **Switzerland**, Kt. Bern, Büetigen, Waldhaus Hörnli, Ischlag, strongly decayed *Fomitopsis pinicola*, 13 Oct. 2005, W. Gams (**epitype designed here** CBS H-25178, MBT 10012943, ex-epitype culture CBS 119045); Rabenhorst 'Fungi europaei' No. 2148, on leaves of *Laurus nobilis*, *leg*. P.A. Saccardo, Selva, 1875 (B), designated by Gams (1968) (**neotype** for *Verticillium candelabrum*).

Sexual morph unknown. *Asexual morph*. *Conidiophores* monomorphic, scattered on the agar surface or arising from strands of aerial hyphae, mono- to quaterverticillate, divergent or with branches at somewhat acute angles. *Conidiogenous cells* phialidic divergent or adpressed; *stipes* 20–90 µm long, 2.4–4.3 µm wide at base; *penicilli* 30–90 µm high, up to 100 µm wide; *terminal phialides* in adpressed whorls of 2–6, (6.6–)7.4–12.7(–14.4) long, (1.9–)2.0–2.7(–3.2) wide at base, (2.8–)2.9–3.6(–3.9) at widest point, 0.8–1.1(–1.2) wide near aperture (n = 80), flask-shaped or cylindrical, generally with widest point in the lower third, slightly tapering toward the apex; *intercalary phialides* below solitary terminal phialides, in whorls, sometimes below whorls of terminal phialides, (4.6–)5.4–11.0(–12.4) × (2.2–)2.5–3.5(–3.7) µm (av. 7.8 × 3.0 µm, n = 60); subterminally formed lateral pegs 1.5–3.5 µm long (n = 60). *Conidia* aseptate, hyaline, smooth, ellipsoidal to subglobose, slightly curved, sometimes with a laterally displaced hilum, broadly rounded at the end, (3.6–)3.9–4.9(–5.5) × (2.5–)2.6–3.2(–3.7) µm (av. = 4.3 × 2.9 µm, n = 150), arranged in imbricate chains.

Culture characteristics: Colony on OA attaining 31–32 mm after 7 d at 25 °C in darkness, flat, with entire margin, aerial mycelium moderate, finely to coarsely granular, floccose to felty, whitish, reverse concolourous. Colony on PDA attaining 24–26 mm diam, flat, with entire margin, aerial mycelium moderate, felty, whitish, reverse concolourous. Colony on SNA attaining 24–26 mm diam, flat, with entire margin, aerial mycelium sparsely developed, finely to coarsely granular, floccose to felty, whitish, reverse concolourous.

Additional materials examined: **China**, Yunnan Province, Kunming City, Wild Duck Forest Park (25°13'N, 102°87'E, 2 100 m alt.), from soil on the forest floor, 20 Aug. 2018, Y. Wang, culture YFCC 895; Yunnan Province, Kunming City, Songming County, Dashao Village (25°24'N, 102°55'E, 2 697 m alt.), from *Ophiocordyceps highlandensis*, 25 Aug. 2018, D.-X. Tang, culture YFCC 8591. **Netherlands**, Limburg Province, loampit near Tegelen, dead stem of *Equisetum hyemale*, Jun. 1968, W. Gams, culture CBS 205.69; North Holland Province, Bergen, needle of *Pinus pinaster*, 8 Oct. 1967, W. Gams, culture CBS 512.67; Amsterdam, soil, collection date unknown, J. Dijk, culture JW1015. Huis ter Heide, soil, collection date unknown, L. Grootscholten, culture JW31018; Kapel Avezaath, soil, collection date unknown, A. Panneman, culture JW79008. **UK**, England, Manchester, root of *Avena sativa*, Mar. 1966, G.S. Taylor, No. 2, culture CBS 513.67; soil, 1948, E.G. Jefferys, No. 650, culture CBS 194.53; Kew Gardens, leaf litter of *Buxus sempervirens*, Nov. 1967, W. Gams, culture CBS 204.69. **Vietnam**, Dak Lak Province, Chu Yang Sin National Park (12°29'N, 108°43'E, 1 659 m alt.), on a spider on the underside of a leaf, Oct. 22, 2017, collected by Y.-B. Wang, specimen YHH 896, culture YFCC 896).

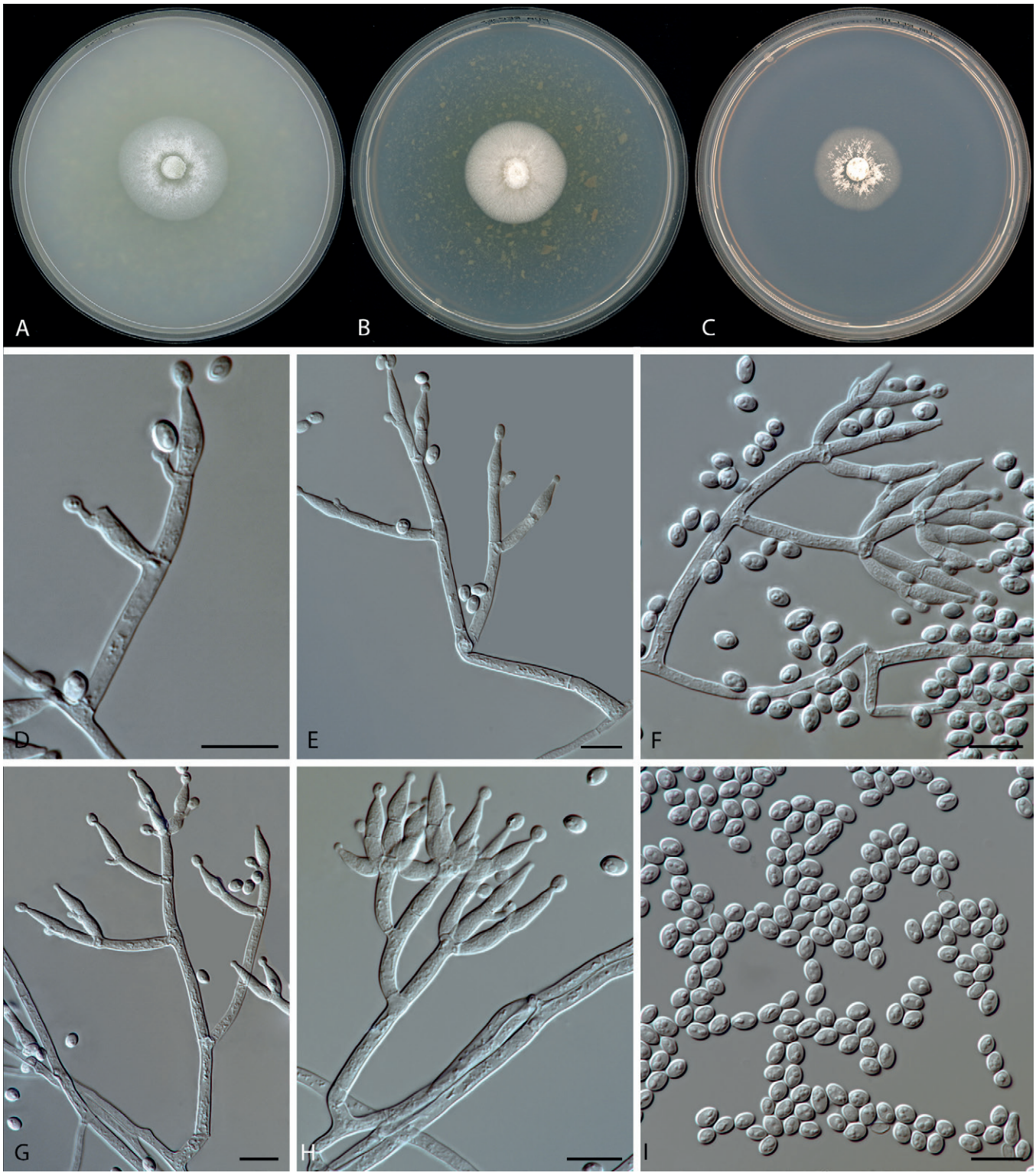

Fig. 8. *Sesquicillium candelabrum* (ex-type CBS 119045). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–H.** Conidiophores. **I.** Conidia. Scale bars = 10 µm.

Notes: *Sesquicillium candelabrum* was originally described as *Verticillium candelabrum*. Gams (1968) described the new genus *Sesquicillium* and introduced the combination *S. candelabrum*. Type material of the species described by Bonorden (1851) has not been preserved. Therefore, well-preserved fungarium material of Rabenhorst No. 2148 was designated as neotype for *Verticillium candelabrum* (Gams 1968). Schroers (2001) placed *S. candelabrum* into *Clonostachys* as both genera form (i) penicillate and sometimes dimorphic conidiophores, (ii) intercalary phialides (although less commonly in *Clonostachys*), and (iii) conidia with a laterally displaced hilum and arranged in imbricate chains. In our study, based on the phylogenetic analyses, both genera cluster in closely related, however, separate sister clades (Fig. 1). Therefore, *S. candelabrum* is resurrected here. Isolate CBS 119045, which was collected near the type locality, is herewith designed as ex-epitype, and the specimen CBS H-25178 as epitype of *Verticillium candelabrum*. In addition, according to the phylogenetic analyses, *C. chuyangsinensis* (Wang *et al*. 2023) is conspecific with *S. candelabrum* and included as synonym of *S. candelabrum*.

Sesquicillium essexcoheniae (Y.P. Tan *et al.*) L. Zhao & Crous, ***comb. nov.*** MycoBank MB 848448. Fig. 9.
Basionym: *Clonostachys essexcoheniae* Y.P. Tan *et al.*, Index of Australian Fungi 5: 3. 2023.

Typus: **Australia**, Queensland, Brisbane, from soil, 14 Jul. 2022, Y.P. Tan (**holotype** BRIP 75170a permanently preserved in a metabolically inactive state).

Description based on CBS 918.97: *Sexual morph* unknown. *Asexual morph*. *Conidiophores* monomorphic, penicillate, rising from the agar surface, up to quaterverticillate, branches typically divergent, phialides divergent or adpressed; *stipes* 20–70 µm long, 2–4 µm wide at base; *penicilli* 30–75 µm high, to 70 µm wide; *terminal phialides* (5.5–)7.2–9.8(–12.3) µm long, (1.6–)2.0–2.5(–2.9) µm wide at base, (2.5–)2.6–3.1(–3.5) µm at widest point, 0.8–1.2 µm wide near aperture (n = 80), in whorls of up to five, flask-shaped, slightly tapering toward the apex; *intercalary phialides* common, subapically formed lateral pegs to 3 µm long. *Conidia* aseptate, hyaline, smooth, ellipsoid to subglobose, slightly curved, with a slightly visible, typically laterally displaced hilum, broadly rounded at the end, (3.9–)4.3–5.6(–5.8) × (2.1–)

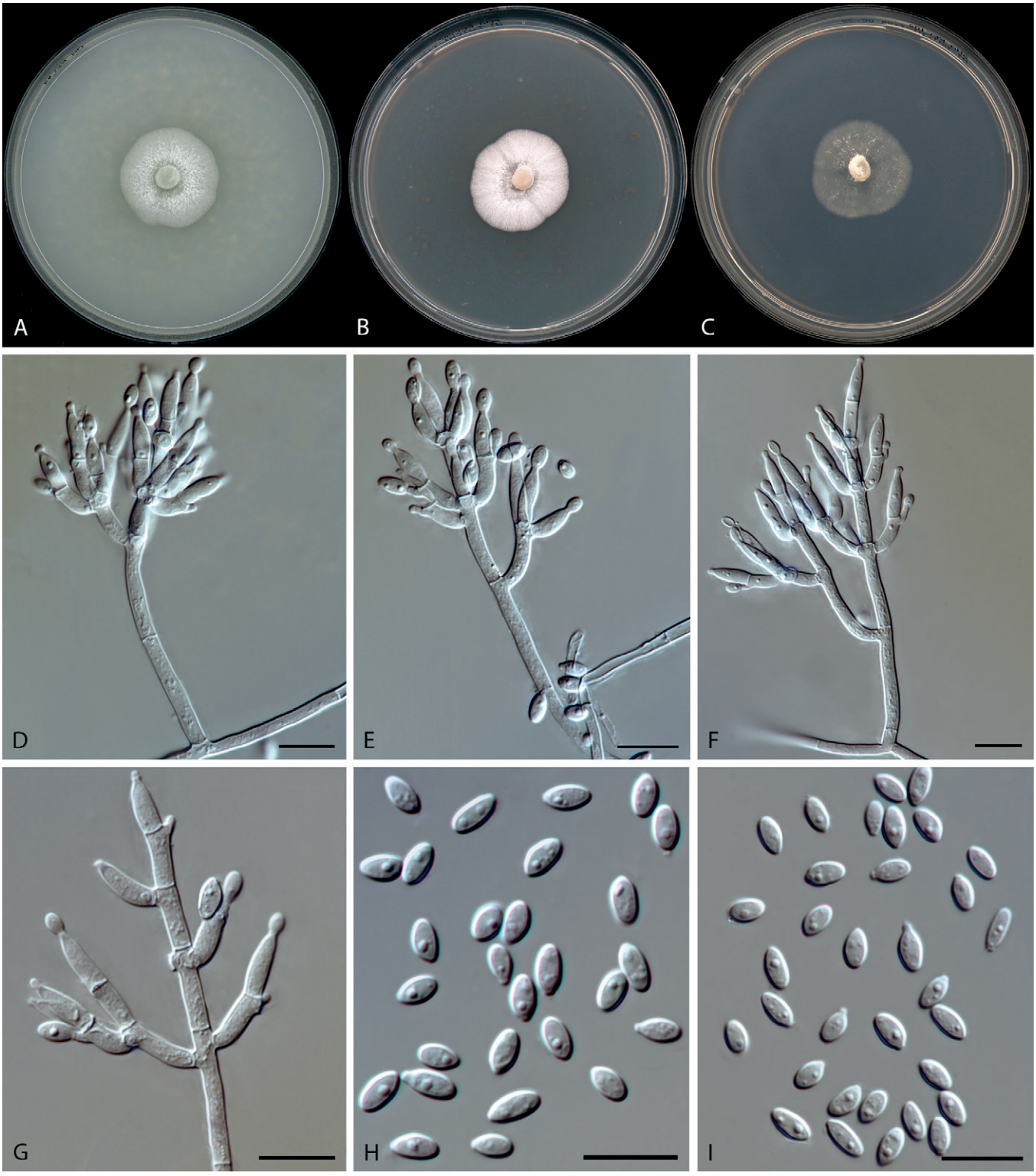

Fig. 9. *Sesquicillium essexcoheniae* (CBS 918.97). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–G.** Conidiophores. **H, I.** Conidia. Scale bars = 10 µm.

2.3–2.8(–3.0) µm (av. = 4.8 × 2.5 µm, n = 110), arranged in imbricate chains.

Culture characteristics: Colonies on OA reaching 27–28 mm diam after 7 d at 25 °C in darkness, flat, with entire margin, aerial mycelium moderate, finely to coarsely granular, floccose to felty, whitish, reverse concolourous. Colonies on PDA reaching 25–29 mm, flat, with crenate margin, aerial mycelium abundant, finely granular, felty to cottony, whitish, reverse concolourous. Colonies on SNA reaching 26–30 mm, flat, with entire margin, aerial mycelium scanty, finely granular, dirty white, reverse concolourous.

Additional material examined: **USA**, Puerto Rico, Caribbean National Forest, Luquillo Mts., Big Tree Trail, from *Sphaeriales*, 23 Feb. 1996, G.J. Samuels & H.J. Schroers, 101, culture CBS 918.97.

Notes: *Sesquicillium essexcoheniae* was described as *C. essexcoheniae* based on ITS sequence data (holotype BRIP 75170a), but without proper morphological illustrations and morphological characters (Tan & Shivas 2023). Accordingly, the identification of strain CBS 918.97 is based on a direct comparison of ITS sequences. Both sequences differ from each other by two single nucleotide indels. Phylogenetically, it is a member of the genus *Sesquicillium*. Multi-locus sequences deriving from CBS 918.97 places *S. essexcoheniae* in a statistically supported sister-group relationship with *S. rossmaniae* and *S. neerlandicum* (Fig. 1). Schroers (2001) included CBS 918.97 under *S. candelabrum* (as *C. candelabrum*) although the sequences of *S. essexcoheniae* (CBS 918.97) and *S. candelabrum* (CBS 119045) differ considerably (ITS: 91.6 % identity, with 37 bp differences; LSU: 98.6 %, 11 bp; *RPB2*: 84.9 %, 112 bp; and *TEF1*: 95.3 %, 40 bp).

Sesquicillium intermediophialidicum L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848449. Fig. 10.

Etymology: Name refers to the whorls of intercalary phialides regularly occurring below solitary terminal phialides.

Typus: **Cuba**, unknown substrate, 19 Mar. 1996, R.F. Castañeda (**holotype** designated here CBS H-25133, ex-type living culture CBS 685.96).

Sexual morph unknown. *Asexual morph*. *Conidiophores* monomorphic, penicillate, scattered on the agar surface or arising from strands of aerial hyphae, up to ter-verticillate, branches and phialides adpressed or somewhat divergent; *stipes* up to 300 µm long, 2.0–3.5 µm wide at base; *penicilli* up to 80 µm high, to 40 µm diam at widest point; *terminal phialides* adpressed, in whorls of up to five, straight to slightly curved, flask-shaped, slightly tapering in the upper part, with or without a visible collarette, (5.8–)6.5–9.8(–11.5) µm long, (1.8–)2.0–2.8(–3.2) µm wide at base, (2.4–)2.8–3.4(–3.9) µm at widest point, 1.0–1.3(–1.4) µm wide near aperture (n = 70); *intercalary phialides* regularly occurring below solitary terminal phialides, in whorls, sometimes in whorls together with terminal phialides, sometimes in chains of two, cylindrical, 5.6–11.5 × 2.2–3.8 µm wide; lateral pegs formed subapically, to 2 µm long. *Conidia* aseptate, ellipsoidal to oblong-ellipsoidal, hyaline, smooth-walled, almost straight or one side straight and the other slightly curved, with a rather rounded distal end, with a median or slightly laterally displaced hilum, (5.2–)6.0–8.7(–10.0) × (1.8–)2.0–2.4(–2.5) µm (av. = 7.3 × 2.2 µm, n = 170), arranged in imbricate chains.

Culture characteristics: Colonies on OA reaching 28–30 mm diam after 7 d in darkness at 25 °C, flat, with entire margin, membranous without aerial mycelium, whitish, reverse concolourous. Colonies on PDA reaching 26–29 mm diam, flat, with entire margin, aerial mycelium sparsely developed, finely felty, dirty white, reverse whitish. Colonies on SNA reaching 16–18 mm diam, flat, with dendritic margin, membranous without aerial mycelia, white, reverse concolourous.

Notes: Phylogenetically, *S. intermediophialidicum* is closely related to *S. saulense*, *S. spinulosisporum* and *S. phyllophilum* (Fig. 1). Conidial size ranges distinguish the three species from one another. Conidia are (5.2–)6.0–8.7(–10.0) × (1.8–)2.0–2.4(–2.5) µm in *S. intermediophialidicum*, 8.5–11.0(–12.0) × 3.5–4.0 µm in *S. saulense* (Lechat *et al*. 2019) and 4.5–6.5 × 3.5–4.0 µm in *S. spinulosisporum* (Lechat & Fournier 2018). In addition, *S. intermediophialidicum* (stipes up to 300 µm long) can be distinguished from *S. saulense* (15–30 µm) and *S. spinulosisporum* (11–35 µm) by its longer stipes. Schroers (2001) placed the strains of *S. intermediophialidicum* (CBS 685.96) under *S. phyllophilum* (as *C. phyllophila*).

Sesquicillium lasiacidis **(**Samuels**)** L. Zhao, Crous & Schroers, ***comb. nov.*** MycoBank MB 848454. Fig. 11.
Basionym: *Nectria lasiacidis* Samuels, Mem. New York Bot. Gard. 49: 273. 1989.
Synonyms: *Bionectria lasiacidis* (Samuels) Schroers, Stud. Mycol. 46: 187. 2001.
Clonostachys lasiacidis Schroers, Stud. Mycol. 46: 187. 2001.

Typus: **French Guiana**, *ca*. 3 h walk W of Marouini River, toward Roche Koutou, 02°55'N, 54°03'W, 150–350 m alt., on dead culms of *Lasiacis ligulata*, 18 Aug. 1987, G.J. Samuels, G.J.S. 5864; G.J.S. isolate 87-149 (**isotype** CBS H-7411; culture ex-type CBS 179.88).

Descriptions and illustrations: Samuels (1989), Schroers (2001).

Additional materials examined: **Germany**, root-associated soil using *Hordeum vulgare* as bait, 22 May 2018, J.G. Maciá-Vicente, culture CBS 147133. **Netherlands**, *Pinus nigra* var. *austriaca*, root collar, unknown date and collector, culture CBS 190.38; wheat field soil, collection date unknown, J.H. van Emden, specimen CBS H-18223, culture CBS 504.67; Eindhoven, soil, 2017, T. Tuinier, culture JW235005; Drenthe, soil, 2019, L. Jurjens, S. Bilstra & J. van Hoorn, culture NL19-085003; Drenthe, soil, 2019, L. Jurjens, S. Bilstra & J. van Hoorn, culture NL19-085006; Drenthe, soil, 15 Nov. 2019, N. Schoon & S. Krol, culture NL19-086015; Drenthe, soil, 2019, S. Schabel & M. Geerisma, culture NL19-089008.

Notes: Based on the phylogenetic analyses, *S. lasiacidis* has a close phylogenetic affinity to *S. candelabrum* (Fig. 1). Morphologically, *S. lasiacidis* differs from *S. candelabrum* in producing longer and narrower conidia, (5.6–)6.4–7.6(–8.2) × (1.8–)2.2–2.8(–3.2) µm *vs* (3.6–)3.9–4.9(–5.5) × (2.5–)2.6–3.2(–3.7) µm (Schroers 2001). Although phylogenetically closely related, isolate CBS 504.67, which produces shorter conidia, (3.2–)3.6–4.5 µm, may represent another phylogenetic species.

Sesquicillium neerlandicum L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848455. Fig. 12.

Etymology: Named after the Netherlands where the strains of this species were isolated in the context of a Dutch citizen science project of the Westerdijk Institute and Utrecht University, in collaboration with various schools, sampling garden soils in urban areas.

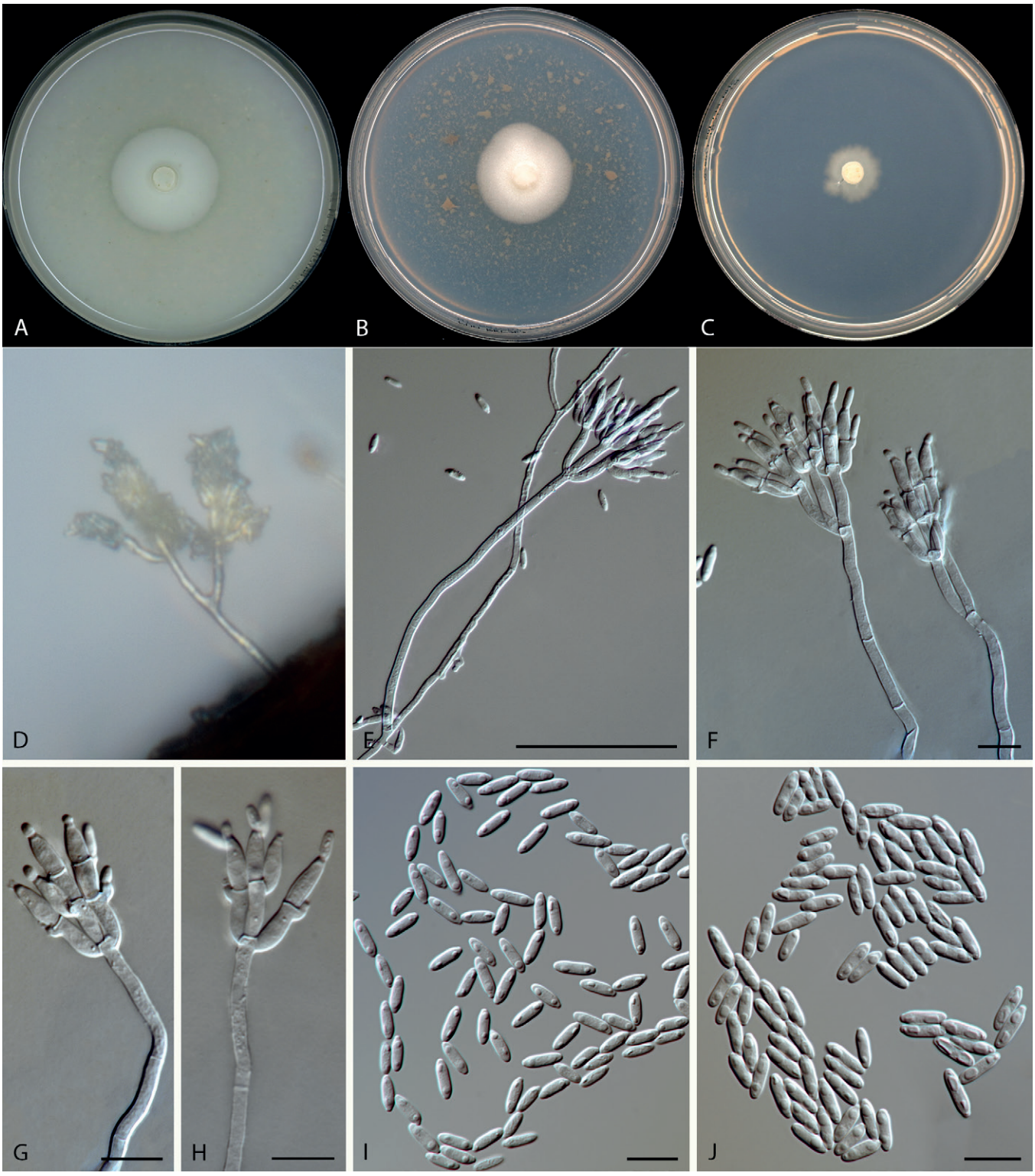

Fig. 10. *Sesquicillium intermediophialidicum* (ex-type CBS 685.96). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–H.** Conidiophores. **I, J.** Conidia. Scale bars: E = 50 µm; F–J = 10 µm.

Typus: **Netherlands**, Gelderland Province, Ravenswaaij, soil, Mar. 2017, L. & N. de Klijne (**holotype** designated here CBS H-25136, ex-type living culture CBS 148203 = JW 17023).

Sexual morph unknown. *Asexual morph*. *Conidiophores* monomorphic, scattered on the agar surface or arising from strands of aerial hyphae, penicillate, branches divergent or adpressed, bi- to quaterverticillate; *stipes* up to 80 µm long, to 2.4–4.4 µm wide at base, *penicilli* up to 100 µm high and 100 µm wide; *terminal phialides* in adpressed whorls of up to five, straight to slightly curved, narrowly flask-shaped, slightly tapering in the upper part, (5.4–)6.5–9.7(–12.7) µm long, 1.9–2.4 µm wide at base, 2.4–3.4 µm at widest point, 0.8–1.2 µm wide near apex (n = 38); *intercalary phialides* common, solitary or in pairs, subterminally formed lateral pegs up to 7 µm long. *Conidia* hyaline, aseptate, ellipsoidal to cylindrical, almost straight, without a laterally displaced hilum, with rounded distal end, (4.2–)4.5–5.6(–6.0) × (2.5–)2.7–3.2(–3.5) µm (av. = 5.1 × 3.0 µm, n = 150), arranged in imbricate chains.

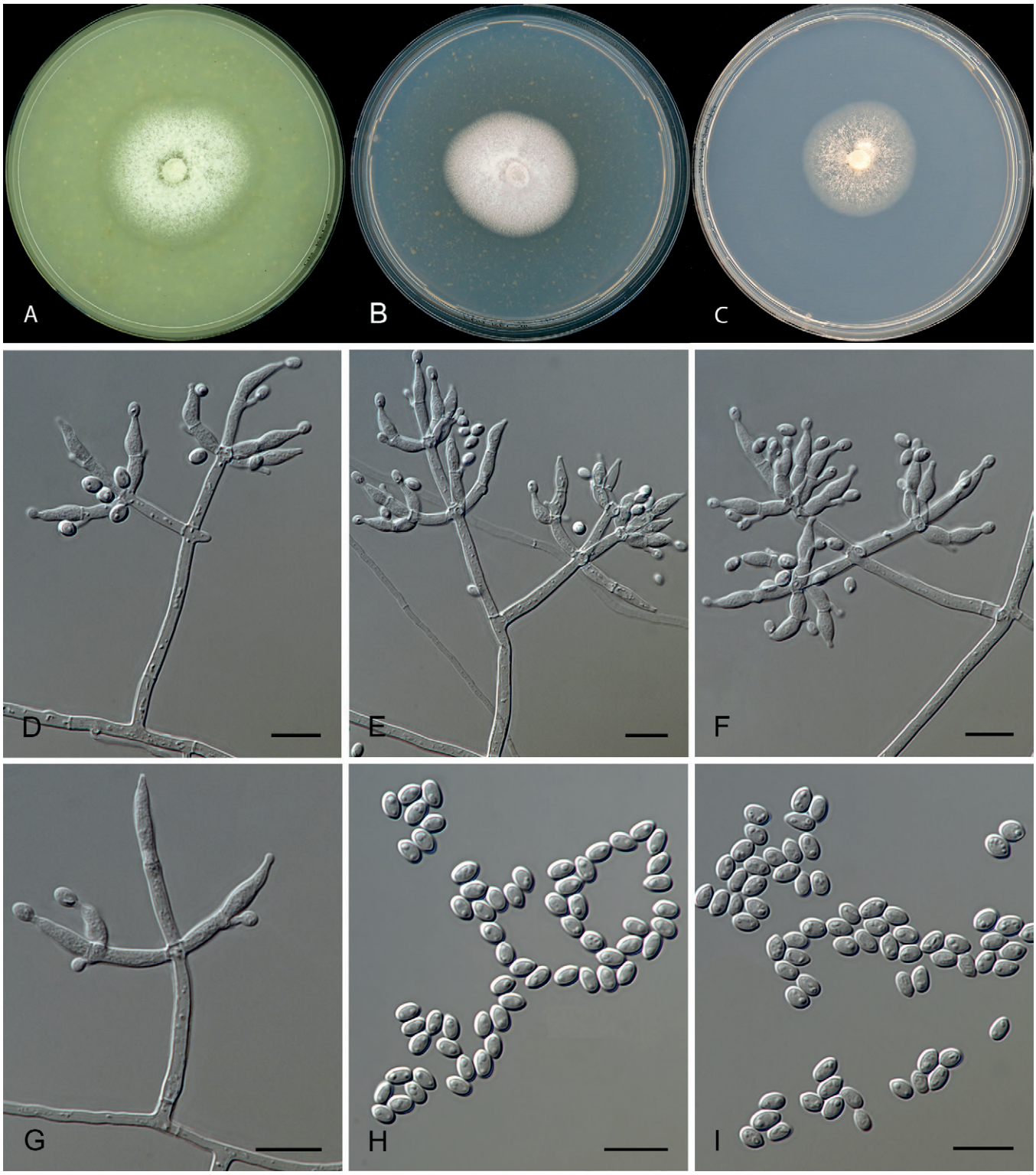

Fig. 11. *Sesquicillium lasiacidis* (CBS 504.67). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–G.** Conidiophores. **H, I.** Conidia. Scale bars = 10 µm.

Culture characteristics: Colonies on OA reaching 24–27 mm diam after 7 d at 25 °C in darkness, flat, with crenate margin, aerial mycelium moderate, felty, finely granular, dirty white, reverse concolourous. Colonies on PDA reaching 24–26 mm diam, flat, with crenate margin, aerial mycelium abundant, felty to cottony, finely to coarsely granular, whitish, reverse concolourous. Colonies on SNA reaching 23–25 mm diam, flat, with crenate margin, aerial mycelium sparse, finely to coarsely granular, whitish, reverse concolourous.

Additional materials examined: **Netherlands**, Gelderland Province, Kapel Avezaath, soil, Mar. 2017, A. Panneman, CBS 148215 = JW79004; Limburg Province, Ell, soil, Mar. 2017, K. Brennand, culture CBS 148213 = JW53028; North Holland Province, Hilversum, soil, Mar. 2017, H., J., A. & J. Bezemer, culture CBS 148201 = JW135005; South Holland Province, Hillegom, soil, Mar. 2017, M. & L. Fleur, culture CBS 148214 = JW71013; Utrecht Province, Nieuwegein, soil, Mar. 2017, J. Schmidt, culture CBS 148212 = JW45022; Utrecht Province, Utrecht, soil, Mar. 2017, G. Bleijlevens, culture CBS 148202 = JW143015; Utrecht, soil, Mar. 2017, R. van den Brink, culture CBS 148209 = JW263008; Utrecht, soil, Mar. 2017, R. van den Brink, culture CBS 148210 = JW263012.

Notes: *Sesquicillium neerlandicum* was isolated from Dutch garden soil. Its species clade and phylogenetic relatedness to *S.*

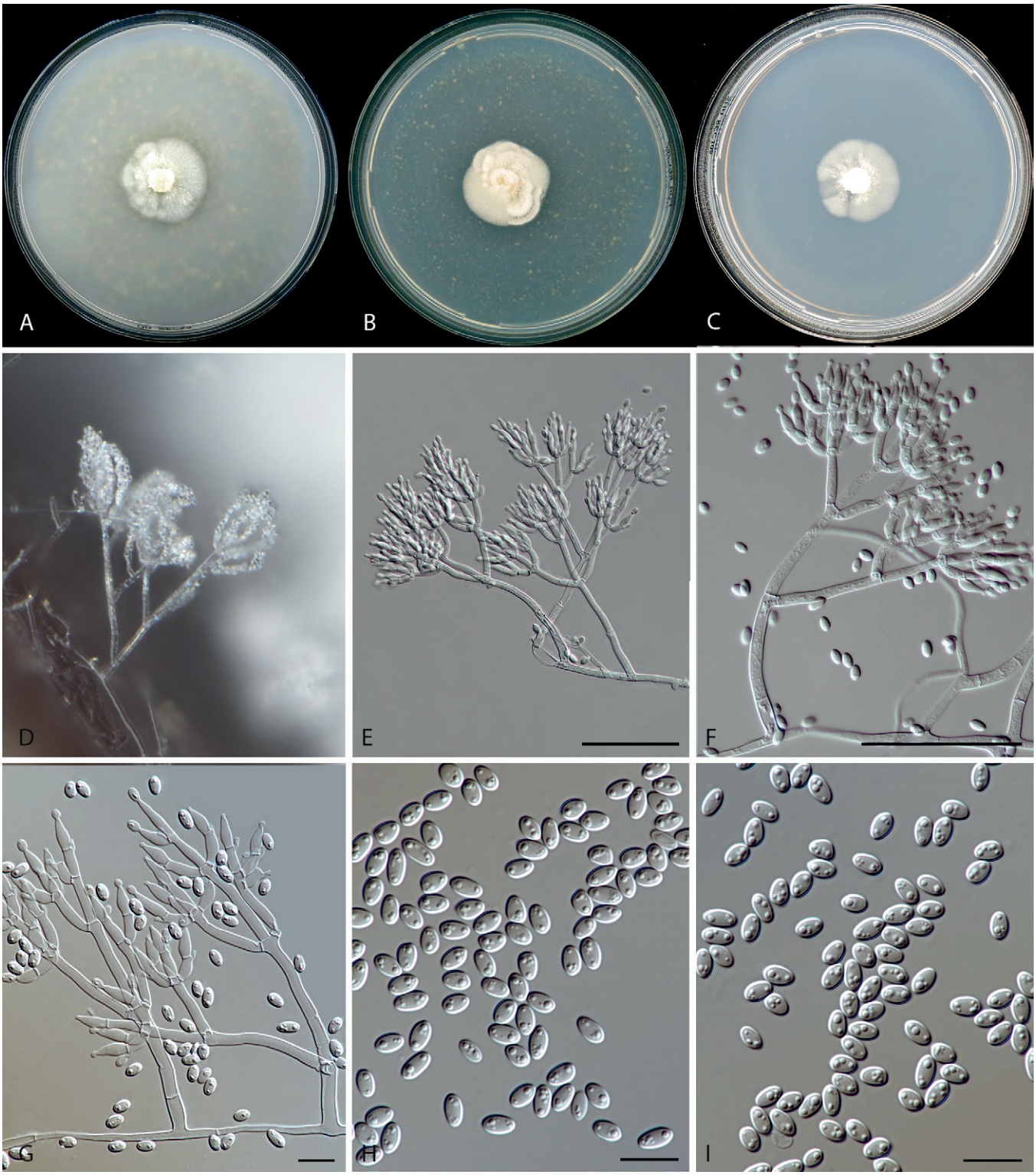

Fig. 12. *Sesquicillium neerlandicum* (ex-type CBS 148203). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–G.** Conidiophores. **H, I.** Conidia. Scale bars: E, F = 50 µm; G–I = 10 µm.

rossmaniae and *S. essexcoheniae* is statistically strongly supported (Fig. 1; 100 % / 100 % / 1). It differs from *S. rossmaniae* in the production of longer stipes (up to 80 µm long in *S. neerlandicum vs* 40 µm long in *S. rossmaniae*) and higher and wider penicilli (100 µm high and 100 µm wide in *S. neerlandicum vs* 50 µm high and 60 µm wide in *S. rossmaniae*). *Sesquicillium neerlandicum* differs from *S. essexcoheniae* in higher and wider penicilli (100 µm high and wide in *S. neerlandicum*, 30–75 µm high and 70 µm wide in *S. essexcoheniae*).

Sesquicillium phyllophilum (Schroers) L. Zhao, Crous & Schroers, ***comb. nov.*** MycoBank MB 848456.
Basionym: *Clonostachys phyllophila* Schroers, Stud. Mycol. 46: 193. 2001.

Typus: **France**, Forêt des buis, Coudrée (Haute Savoie), *Buxus* forest, on fallen leaves of *Viscum album*, Sep. 1996, H.-J. Schroers & T. Gräfenhan (**holotype** CBS H-7945, ex-type culture CBS 921.97).

Description and illustration: Schroers (2001).

Additional material examined: **Japan**, Tokyo, Shinjuku Gyoen Garden, Sep. 1983, W. Gams, culture CBS 662.83.

Notes: *Sesquicillium phyllophilum* was originally described as *Clonostachys phyllophila* by Schroers (2001) from fallen leaves of *Viscum album* collected in France. The present study places it phylogenetically in the genus *Sesquicillium* and therefore a new combination is proposed here (Fig. 1).

Sesquicillium rossmaniae (Schroers) L. Zhao, Crous & Schroers, ***comb. nov.*** MycoBank MB 848457.
Basionym: *Clonostachys rossmaniae* Schroers, Stud. Mycol. 46: 177. 2001.
Synonym: *Bionectria rossmaniae* Schroers, Stud. Mycol. 46: 177. 2001.

Typus: **French Guiana**, Piste de Saint-Elie, km 16 on road between Sinnamary and St. Elie, 'Ecerex', Orstom research area, 05°20'N, 00°53'W, on twigs of recently dead tree, Feb.–Mar. 1986, G.J. Samuels, G.J.S. 3970, G.J.S. isolate 86-246 (**isotype** CBS H-7944, ex-type culture CBS 211.93).

Description and illustration: Schroers (2001).

Additional materials examined: **French Guiana**, on bark of living liana, Jan.–Mar. 1986, G.J. Samuels, culture CBS 210.93; *ibid*. bark of recently dead tree, Jan.–Mar. 1986, G.J. Samuels, culture CBS 221.93.

Note: *Sesquicillium rossmaniae* was originally described as *Clonostachys* (*Bionectria*) *rossmaniae* by Schroers (2001) and is shown here to cluster with other species of *Sesquicillium* (Fig. 1). Phylogenetically, *S. rossmaniae* is closely related to *S. neerlandicum*, but with clearly different ITS (99.4 % identity, with 3 bp differences), *RPB2* (97.4 %, 19 bp), and *TEF1* (97.5 %, 20 bp) sequences. For morphological comparison, see notes under *S. neerlandicum*.

Sesquicillium saulense (Lechat & J. Fourn.) L. Zhao & Crous, ***comb. nov.*** MycoBank MB 848458.
Basionym: *Clonostachys saulensis* Lechat & J. Fourn., Ascomycete. org 11(3): 65. 2019.

Typus: **French Guana**, Saül, Gros Arbres trail, on dead bark of *Bauhinia* sp., 22 Aug. 2018, C. Lechat, CLLG18023-A5 (**holotype** LIP CLLG18023-A5, ex-type culture BRFM 2782).

Description and illustration: Lechat *et al*. (2019).

Notes: The culture was isolated from dead bark of *Bauhinia* sp. collected from Saül in French Guiana, and described as *Clonostachys saulensis* (Lechat *et al*. 2019). Phylogenetically, it falls in a well-supported lineage among other species of the genus *Sesquicillium* (Fig. 1).

Sesquicillium sesquicillii (Samuels) L. Zhao, Crous & Schroers, ***comb. nov.*** MycoBank MB 848459.
Basionym: *Nectria sesquicillii* Samuels, Mem. New York Bot. Gard. 49: 268. 1989.
Synonyms: *Bionectria sesquicillii* (Samuels) Schroers, Stud. Mycol. 46: 190. 2001.
Clonostachys sesquicillii Schroers, Stud. Mycol. 46: 190. 2001.

Typus: **Guyana**, Cuyuni-Mazaruni Region, No. VII, Mazaruni Subregion, No. VII-2, foothills immediately S of Mt. Ayanganna, *ca*. 1 km W of Pong River, 05°28'N, 60°04'W, 550–600 m alt., on twigs and lichen, 26 Feb. 1987, G.J. Samuels, J. Pipoly & G. Gharbarran, G.J.S. 4825, G.J.S. isolate 87-23 (**isotype** CBS H-7413, culture ex-type CBS 180.88).
Descriptions and illustrations: Samuels (1989), Schroers (2001).

Notes: *Sesquicillium sesquicillii* was originally described as *Nectria sesquicillii* by Samuels (1989) from twigs and a lichen. It was subsequently transferred to *Clonostachys* (Schroers 2001). According to our phylogenetic inference, the ex-type of *N. sesquicillii* falls in the highly supported *Sesquicillium* clade (Fig. 1; 97 % / 100 % / 1). Perithecia of *S. sesquicillii* are formed in dense groups on erumpent stromata (Schroers 2001: fig. 87a, b, d), while the perithecia of other *Sesquicillium* species are formed solitarily on superficial, thus, non-erumpent, typically reduced stromata.

Sesquicillium spinulosisporum (Lechat & J. Fourn.) L. Zhao & Crous, ***comb. nov.*** MycoBank MB 848460.
Basionym: *Clonostachys spinulosispora* Lechat & J. Fourn., Ascomycete.org 10(4): 128. 2018.

Typus: **French Guiana**, Régina, nouragues natural Reserve, Inselberg camp, primary rainforest, on aerial, dead palm leaf of *Astrocaryum vulgare* (*Arecaceae*), 16 Jun. 2012, *C. Lechat* [**holotype** CLLG12001 (LIP), ex-type culture CBS 133762].

Description and illustration: Lechat & Fournier (2018).

Notes: The type culture was isolated from a dead palm leaf of *Astrocaryum vulgare* (*Arecaceae*) collected from Régina in French Guiana and originally described as *C. spinulosispora*. The present study places it phylogenetically in the genus *Sesquicillium,* being closely related to *S. phyllophilum* (Fig. 1). *Sesquicillium spinulosisporum* can be distinguished from *S. phyllophilum* based on the absence of intercalary phialides and its shorter conidia (4.5–6.5 µm in *S. spinulosisporum vs* (5.4–)5.8–7(–8.8) µm in *S. phyllophilum*).

Sesquicillium symmetricum L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848461. Fig. 13.

Etymology: Name refers to the symmetrical conidia produced by this species.

Typus: **Colombia**, Dep. de Meta, Municipio de Villavicencio, 25 km from Villavicencio to Acacías, 550 m alt., agricultural soil, 18 Feb. 1978, O. Rangel (**holotype** designated here CBS H-25134, ex-type living culture CBS 124.79).

Sexual morph unknown. *Asexual morph*. *Conidiophores* monomorphic, penicillate, arising from the agar surface or aerial mycelium; *stipe* 20–130 µm long, 1.9–3.9 µm wide at base; *penicilli* up to 120 µm high, 90 µm wide; *terminal phialides* in whorls of up to six, adpressed or divergent at acute angles, narrowly flask-shaped, (8.7–)10.4–21.6(–22.6) µm long, (1.2–)1.6–2.5(–2.8) µm wide at base, (2.0–)2.5–3.6(–4.0) µm at widest point, (0.8–)0.9–1.2(–1.3) µm wide near aperture (n = 60); *intercalary phialides* present, subterminally formed lateral pegs 3–5 µm long. *Conidia* hyaline, ellipsoidal to obovoid to somewhat clavate, symmetrical, distally broadly rounded, without laterally displaced hilum, (5.5–)5.8–8.9(–9.8) × (2.2–)2.3–3.3(–3.9) µm (av. = 7.1 × 2.7 µm, n = 100), arranged in linear chains.

Culture characteristics: Colony on OA attaining 18–20 mm after 7 d at 25 °C in darkness, flat, with entire margin, aerial mycelium sparsely developed, finely felty, dirty white, reverse whitish. Colony on PDA attaining 20–21 mm, flat, with entire margin, aerial

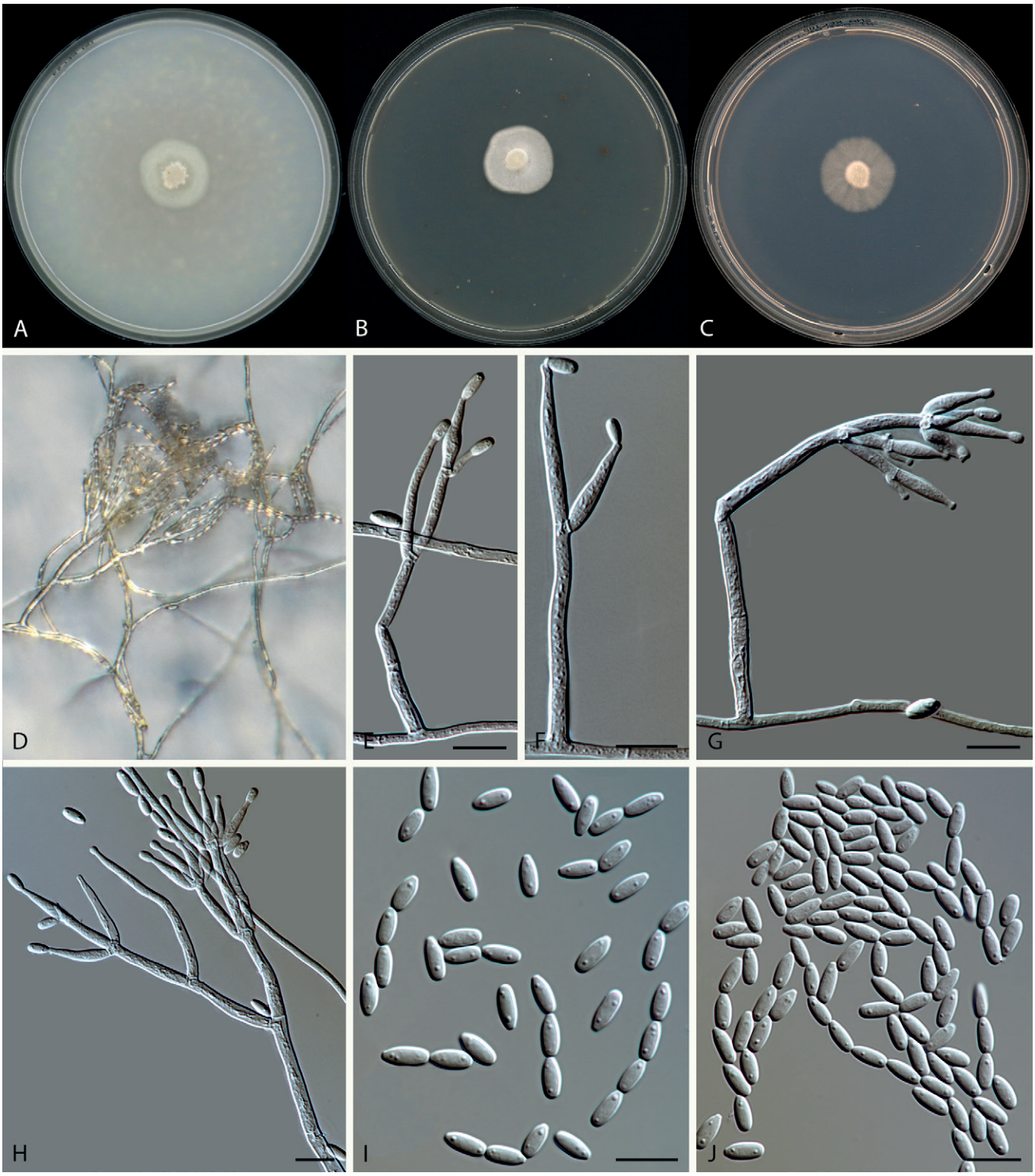

Fig. 13. *Sesquicillium symmetricum* (ex-type CBS 124.79). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–H.** Conidiophores. **I, J.** Conidia in linear chains. Scale bars = 10 µm.

mycelium moderate, felty, whitish, reverse concolourous. Colony on SNA attaining 20–21 mm, flat, with entire margin, aerial mycelium moderate, felty, dirty white, reverse concolourous.

Additional material examined: **Colombia**, Dep. de Meta, Municipio de Villavicencio, 25 km from Villavicencio to Acacías, 550 m alt., maize-field soil, collection and isolation date unknown, O. Rangel, culture CBS 485.78.

Notes: *Sesquicillium symmetricum* is closely related to *S. candelabrum*, *S. essexcoheniae*, *S. lasiacidis*, *S. neerlandicum*, and *S. rossmaniae* (Fig. 1). *Sesquicillium symmetricum* can be morphologically distinguished from *S. candelabrum*, *S. essexcoheniae, S. rossmaniae* and *S. neerlandicum* based on its longer conidia [(5.5–)5.8–8.9(–9.8) µm long, av. = 7.1 µm, in *S. symmetricum*; (3.6–)3.9–4.9(–5.5) µm av. = 4.3 µm in *S. candelabrum*; (3.9–)4.3–5.6(–5.8) µm, av. = 4.84 µm in *S. essexcoheniae*; (4.2–)4.6–5.4(–6.6) µm, av. = 5 µm in *S. rossmaniae*; [(4.6–)5.0–6.0 µm, av. = 5.05 µm in *S. neerlandicum*]. *Sesquicillium symmetricum* differs from *S. lasiacidis* in having longer phialides [(8.7–)10.4–21.6(–22.6) µm in *S. symmetricum*, 8.4–13.8 µm in *S.*

lasiacidis]. Due to the symmetrical shape of conidia and central placement of their hila, *S. symmetricum* produces not imbricate but linear conidial chains.

Sesquicillium tornatum (Höhn.) Schroers, ***comb. nov.*** MycoBank MB 848462.
Basionym: *Pseudonectria tornata* Höhn., Sitzungsber. Akad. Wiss. Wien, Math.-Naturwiss, Kl., Abt. 1. 118: 1470. 1909.
Synonyms: *Bionectria tornata* (Höhn.) Schroers, Stud. Mycol. 46: 184. 2001.
Clonostachys tornata (Höhn.) Rossman *et al.*, Stud. Mycol. 80: 242. 2015.
Sesquicillium asymmetricum Samuels, Mem. New York Bot. Gard. 49: 276. 1989.
Clonostachys asymmetrica (Samuels) Schroers, Stud. Mycol. 46: 184. 2001.
Nectria sesquiphialis Samuels, Mem. New York Bot. Gard. 49: 276. 1989.

Typus: Type for *Pseudonectria tornata*: **Indonesia**, Java, Tjibodas, on decaying leaves of *Pandanus* sp. (no **holotype** specimen recorded). Type for *Nectria sesquiphialis* and *Sesquicillium asymmetricum*: **Venezuela**, Edo, Bolivar, 110–111 km S of El Dorado on road between El Dorado and Sta Elena, on leaf of *Zingiberaceae*, 6 Aug 1972, R.F. Cain, G.J. Samuels & C. Blanco [**holotype** Dumont-VE 7184 (VEN), **isotype** NY, dried culture of C.T.R. isolate 72-193 (= ATCC 66892), derived from ascospores of Dumont-VE 7184, type of *N. sesquiphialis*, and filed with it (NY)].

Descriptions and illustrations: Von Höhnel (1909), Samuels (1989), Schroers (2001).

Notes: *Pseudonectria tornata* and *Nectria sesquiphialis*, including the asexual morph-typified *S. asymmetricum*, were synonymised based on sexual and asexual morph characters encountered in the type of *N. sesquiphialis* (Dumont-VE 7184) and *P. tornata* (FH no. 2899) (Schroers 2001: figs 81 *vs* 82) and sexual morph characters described by von Höhnel (1909). Asexual morph characters consisted of conidiophores showing intercalary phialides below solitary terminal phialides and size range and shape of conidia; sexual morph characters, the habit of superficially formed perithecia on decaying leaves of *Pandanus* sp., perithecial walls composed of two regions, and 1-septate ascospores (9–12.8 × 2–2 µm for *P. tornata*; 10.8–20.8 × 2–4 µm for *N. sesquiphialis*) (Schroers 2001). Accordingly, morphological character interpretations were used for linking *P. tornata* and *N. sesquiphialis* to *Bionectria* subgenus *Epiphloe* and combining *P. tornata* into *Bionectria* and the same arguments are here adopted for combining the species into *Sesquicillium*. Obtaining and analysing phylogenetic marker genes from strain ATCC 66892 (= C.T.R. isolate 72-193, ex-type strain of *N. sesquiphialis*) is therefore required to further support the here suggested taxonomy.

Clonostachys Corda, Pracht-Fl. Eur. Schimmelbild.: 31. 1839.

Type: *Clonostachys araucaria* Corda

Sexual morph. *Stromata* typically present, well developed if erumpent through bark, reduced if formed on associated fungus hosts, typically made of pseudoparenchymatous cells, rarely entirely superficial. *Perithecia* orange, yellowish orange, brownish orange, rarely brownish, KOH-, sometimes becoming paler in lactic acid, crowded in often large groups on stromata, rarely solitary, globose or somewhat higher than wide, sometimes obovoid, smooth or warted. *Perithecial wall* of two or three regions, rarely a single region, texture prosenchymatous or pseudoparenchymatous. Perithecial surface smooth, rough, or warted. *Perithecial warts*, if present, strongest developed in the upper part of the perithecia, irregularly scattered or radiating from the perithecial apex downwards. *Asci* 8-spored, apically rounded or flat, sometimes with prominent edges, with subapically thickened walls and apical ring. *Ascospores* typically 1-septate, coarsely or finely warted or striate, hyaline, ellipsoidal, tapering slightly towards their ends, sometimes with warts arranged in striae, rarely rough or smooth. *Asexual morph*. *Sporodochia* often on erumpent stroma when formed on the natural substratum or cushion-shaped in culture and without stroma; synnemata present in some species. *Conidiophores* frequently dimorphic (primary and secondary conidiophores), sometimes monomorphic. Primary conidiophores mononematous, early-formed, verticillum-like or narrowly penicillate. Secondary conidiophores mononematous, later-formed, penicillate, often aggregating into cushin-shaped, more or less distinct sporodochia, less commonly synnematous; *stipes* typically arising from submerged or aerial hypha or from aerial hyphal fascicles, ropes or strands; *penicilli* monoverticillate or bi- to more-level verticillate). *Conidiogenous cells* phialidic. *Phialides* on primary conidiophores almost cylindrical, slightly and gradually tapering; phialides on secondary conidiophores narrowly flask-shaped, widest in the lower third or middle, and slightly and continuously tapering toward tip or, in some species, intercalarly formed below terminal phialides and with subapically formed conidiogenous, lateral pegs. Conidiophores rarely with setae. *Conidia* aseptate, ellipsoid to subfusoid, typically with one more flattened side and a laterally displaced hilum resulting in a somewhat kidney-like appearance, hyaline or greenish hyaline, held in watery droplets or heads when formed on primary conidiophores or imbricate chains when formed on secondary conidiophores or sporodochia, conidial masses collapsing in either off-white, orange or greenish slimy masses.

Notes: *Clonostachys araucaria*, the type species of *Clonostachys*, was described as producing white colonies “on forest soil”, incubated at around 17 °C, and oblong-ellipsoidal, obviously hyaline, and imbricately arranged conidia that adhere in columns and are formed by a penicillate conidiophore (Corda 1839). Although type material is not available, it is clear that Corda’s drawing illustrates a secondary conidiophore formed by many *Clonostachys* species. Samuels (1988a) linked members of the *Nectria ochroleuca* group to *Clonostachys*, and Schroers *et al*. (1999b) classified *Clonostachys* as the asexual morph of *Bionectria*. Thereafter, *Clonostachys* binominals were also provided for sexual morph-typified *Bionectria* names to allow usage of *Clonostachys* binomials for all species considered at that time (Schroers 2001), and *Clonostachys* became the name selected in the single name system (Rossman *et al.* 2013).

Dimorphic conidiophores, described for *Clonostachys rosea* (as *Gliocladidum roseum*) for the first time by Bainier (1905, 1907), *i.e*., primary and secondary conidiophores, slightly curved conidia showing laterally displaced hila (*i.e*., a scar at the base of a conidium), perithecial walls consisting of three regions, warted ascospores and stromata erumpent through bark, characterise a core group of species of subgenus *Bionectria* (Fig. 1 and 2, terminal clade including *C. reniformis*). The group is further subdivided morphologically based on characteristics of both types of conidiophores, bearing either diverging or adpressed branches or phialides, while further differentiations of species based on morphological characters are difficult (Moreira *et al*. 2016). Species

of this core group show rather homogenous character patterns, however, two of its species do not produce dimorphic conidiophores but sporodochia only. This core group also includes *C. rosea* and *C. solani*, for which two forms were accepted based on either light or (partly dark) green conidial masses (Schroers 2001) and named by using the reduced species epithets from *Gliocladium catenulata* Gilman & Abbott or, respectively, *G. nigrovirens* van Beyma. We recommend using the form-based system in situations where users of names wish to emphasise the green phenotype trait of their strains. However, the use of the binominals *C. rosea* or *C. solani* is equally correct (Fig. 2, Supplementary Fig. S9).

Our phylogenetic concept of subgenus *Bionectria* presented here mirrors the earlier provided morphocentric concept (Schroers 2001) (Fig. 1), although Fig. 2 suggests that subgenus *Astromata* may have evolved from within subgenus *Bionectria*. However, the phylogenetic analysis also confirms relatedness of morphologically diverse taxa including, *e.g.*, *C. samuelsii* forming sporodochia only and symmetrical conidia, *C. ralfsii* with a differing perithecial wall anatomy, outstandingly large conidia and synnematous conidiomata, and several others including *C. compactiuscula*, *C. bambusae*, and *C. divergens*. Even after excluding the vast majority of sesquicillium-like species, the phylogenetic analyses furthermore support a morphologically broad concept for *Clonostachys* with diversifying character patterns. These include, *e.g.*, (i) reduced, non-erumpent stromata often on plant associated fungal hosts and sporodochia forming green conidial masses (subgen. *Astromata*), (ii) striate ascospores, perithecial walls consisting of two regions, with cells not integrating with cells of stromata (subgenus *Zebrinella*), (iii) penicilli with numerous intercalary phialides indistinguishable from those seen in *Sesquicillium* (*C. setosa*, *C. bambusae*), (iv) perithecia consisting of a single region only, superficially formed not on woody substrata but on a dicotyledonous leaf [*C. vesiculosa* (Luo & Zhuang 2010) that Schroers (2001) would most likely have classified in subgen. *Uniparietina*, now *Sesquicillium*], and (v) curved and smooth ascospores, cup-shaped conidiomata combined with symmetrical conidia, *etc.* (subgenus *Myronectria*).

Based on phylogenetic analysis and morphological characters employed in the present study, the genus *Clonostachys* has 49 known and 19 new species, distributed among four subgenera: *Astromata* (six species, four known and two new species), *Bionectria* (40 species, 32 known and eight new species), *Myronectria* (two species, one known and one new species) and *Zebrinella* (18 species, 10 known and eight new species). Additionally, there are two known species, namely *C. vesiculosa* (morphologically comparable with subgenus *Uniparietina*, now *Sesquicillium*) and *C. setosa* (sesquicillium-like), which do not belong to any of the subgenera.

Clonostachys aurantiaca L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848477. Fig. 14.

Etymology: From Latin *aurantiacus*, meaning orange. Referring to the production of orange ascomata.

Typus: **Cameroon**, Korup National Park, bark of recently fallen tree tropical wet forest, collection and isolation date unknown, G.J. Samuels (**holotype** designated here CBS H-25140, ex-type living culture CBS 124757).

Sexual morph produced in culture on OA. *Stroma* generally well-developed, erumpent, bearing perithecia, cells prosenchymatous, densely hyphal. *Perithecia* solitary or crowded in groups of to 10, sometimes overgrown by mycelium, globose to subglobose, 140–240 µm diam, yellowish to brownish orange, slightly papillate, scaly to warty. *Perithecial warts* whitish to pale orange, up to 70 µm high, cells subglobose to globose, of the same type as the cells of the outer perithecial wall region, (6.0–)7.0–13.0(–15.0) × (4.5–)6.5–11.5–12(–14.5) µm (n = 100), walls generally evenly thickened to 1 µm thick. *Perithecial wall* 25–50 µm thick composed of two regions; outer region 12–27 µm or 1–3 cells thick, cells merging with the cells of the warts, angular to subglobose, (5.5–)6.5–13.5(–15.0) × (4.0–)5.0–9.5(–12.0) µm (n = 100), with uniformly thickened walls around 1.5 µm thick; sometimes with vacuoles; middle region lacking; inner region 10–20 thick. *Asci* 8-spored, clavate, 39–60 × 7–16 µm (n = 35), apex flat, edges rounded, ring clearly visible. *Ascospores* 1-septate, striate, striae parallel, constriction at the median septum frequently observed in discharged ascospores, ellipsoid, (8.5–)9.0–12.0(–12.5) × 4.0–5.5(–6) µm (n = 80). *Asexual morph* not observed.

Culture characteristics: Colonies on OA reaching 29–33 mm diam after 7 d at 25 °C in darkness, with crenate margin, aerial mycelium moderate, felty to cottony, pale yellow, reverse concolourous. Colonies on PDA reaching 29–34 mm diam, with crenate margin, aerial mycelium moderate, felty, white yellowish, reverse pale yellow. Colonies on SNA reaching 26–31 mm diam, with crenate margin, aerial mycelium sparse, whitish, reverse concolourous.

Notes: Phylogenetically, *Clonostachys aurantiaca* is closely related to *C. fusca* (Figs 1, 2), but with clearly different ITS (98.0 % identity, with 11 bp differences), *RPB2* (98.9 %, 8 bp), and *TEF1* (98.2 %, 15 bp) sequences. For morphological comparison with *C. fusca*, see notes under *C. fusca*. Observed morphological characters, especially cell morphology of stroma not integrating with cells of the perithecial wall, perithecial walls consisting of two regions, perithecial warts consisting of cells with evenly thickened walls, and striate ascospores, support its classification in subgen. *Zebrinella.*

Clonostachys australiana L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848478. Fig. 15.

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

Typus: **Australia**, New South Wales, Blue Mountains Nat. Park, bark of recently dead tree, Aug. 1999, G.J. Samuels (**holotype** designated here CBS H-25138, ex-type living culture CBS 102421).

Sexual morph unknown. *Asexual morph*. *Conidiophores* dimorphic. *Primary conidiophores* sparsely branched, penicillate, or acremonium-like, arising from the agar surface or strands of aerial mycelium; *stipe* 30–110 µm long, 2.6–4.7 µm wide at base; *penicilli* 40–70 µm high; *terminal phialides* in apical whorls of up to five, straight, almost cylindrical, slightly tapering towards the tip, without or with a somewhat visible collarette, (12.4–) 16.6–30.8(–35.8) µm long, (1.4–)1.5–2.7(–3.1) µm wide at base, (1.0–)1.2–2.0(–2.2) µm wide near aperture (n = 60). *Secondary conidiophores,* penicillate, mono- to terverticillate, branches divergent or adpressed; *stipe* 20–60 µm long, 2.6–4.4 µm wide; *penicilli* 30–65 µm high, up to 65 µm wide; *terminal phialides* in loose whorls of up to nine, adpressed, straight or slightly curved, flask-shaped, widest in the lower third, slightly tapering in the upper part towards the tip, without a collarette, (6.5–)7.6–16.7(–23.3) µm long, (1.5–)1.6–2.7(–3.2) µm wide at

Fig. 14. *Clonostachys aurantiaca* (ex-type CBS 124757). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D, E.** Perithecia. **F.** Section through perithecium. **G.** Ostiole. **H.** Lateral perithecial wall showing two regions. **I.** Perithecial base and stroma or stroma below a perithecium. **J.** Immature asci with slightly visible ring. **K.** Mature asci. **L, M.** Discharged ascospores in optical section (L) and surface view (M). Scale bars: F = 50 µm; G–M = 10 µm.

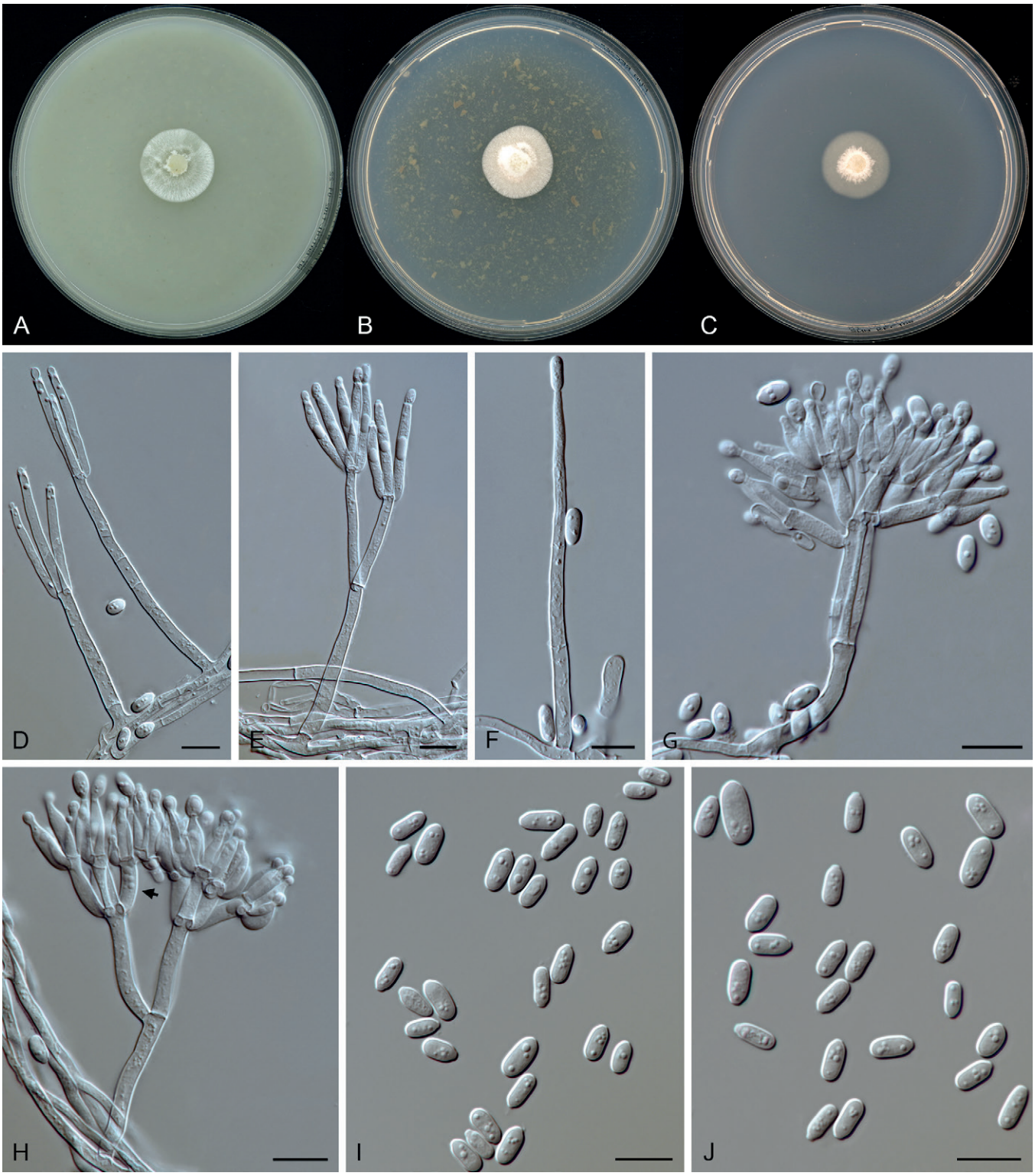

Fig. 15. *Clonostachys australiana* (ex-type CBS 102421). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–F.** Primary conidiophores. **G, H.** Secondary conidiophores. **I, J.** Conidia. Black arrows indicate intercalary phialides. Scale bars = 10 µm.

base, (2.2–)2.4–3.3(–3.9) µm at widest point, (0.9–)1.0–1.4(–1.5) µm wide near aperture (n = 90); *intercalary phialides* sometimes observed, bearing several or one terminal phialides, cylindrical, 8–14 × 2–4 µm wide, lateral conidiogenous pegs to 5.5 µm long. *Conidia* aseptate, hyaline, smooth, ellipsoid, broadly rounded, with a median or invisible hilum, (4.5–)5.4–7.7(–9.7) × (2.5–)2.7–3.6(–4.1) µm (av. 6.3 × 3.1 µm, n = 150), arranged in imbricate chains that may collapse into slimy masses.

Culture characteristics: Colonies on OA reaching 21–23 mm diam after 7 d at 25 °C in darkness, with entire margin, aerial mycelium moderate, felty to cottony, whitish, reverse concolourous. Colonies on PDA reaching 21–24 mm diam, with entire margin, aerial mycelium moderate, felty to cottony, whitish, reverse concolourous. Colonies on SNA reaching 19–20 mm diam, with entire margin, aerial mycelium moderate in the centre, sparse at periphery, felty, whitish, reverse concolourous.

Fig. 16. *Clonostachys bambusae* (ex-type CBS 139411). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–H.** Conidiophores. **I.** Conidia. Black arrows indicate intercalary phialides. Scale bars: D, E = 50 *µ*m; F–I = 10 µm.

Additional material examined: **Australia**, New South Wales, Blue Mountains Nat. Park, bark of recently dead tree, Aug. 1999, G.J. Samuels, culture CBS 102423.

Notes: Phylogenetically, *C. australiana* is closely related to *C. grammicosporopsis* (Figs 1, 2), but differs genetically in ITS (98.1 % identity, with 9 bp differences), LSU (98.9 %, 9 bp), and *TEF1* (96.7 %, 26 bp) sequences. Morphologically, *C. australiana* differs from *C. grammicosporopsis* in producing smaller conidia [(4.5–)5.4–7.7(–9.7) × (2.5–)2.7–3.6(–4.1) µm *vs* (4.8–)6.6–8.4(–11.6) × (2.2–)3.0–3.6(–4.6) µm] (Schroers 2001). Morphology of conidiophores and conidia are similar to other species in subgen. *Zebrinella.*

Clonostachys bambusae L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848479. Fig. 16.

Etymology: Referring to the host, bamboo, from which the type of this species was collected.

Typus: **Thailand**, Chiang Mai Province, Mae Teng Distr. Highway 1095 at 22 km marker, 750 m alt., dead leaf of bamboo, Aug. 2014, W. Gams (**holotype** designated here CBS H-25151, ex-type culture CBS 139411).

Sexual morph unknown. *Asexual morph. Conidiophores* monomorphic, penicillate, scattered on the agar surface or arising from strands of aerial hyphae, bi- to quaterverticillate, branches somewhat divergent to adpressed; *stipes* 35–140 µm long, to 4.6 µm wide at base; *penicilli* up to 100 µm high, 90 µm wide; *terminal phialides* almost adpressed in whorls of up to 5, narrowly flask-shaped, slightly tapering in the upper part, with a minute collarette, (7.3–)7.7–12.0(–12.6) µm long, (1.2–)1.7–2.6(–2.7) µm wide at base, 2.3–3.0(–3.4) µm at widest point, 0.9–1.3(–1.5) µm wide near aperture (n = 80); *intercalary phialides* rather frequent, formed solitarily below whorls of terminal phialides; almost cylindrical, 6.0–10.0 × 2.0–3.2 µm, lateral conidiogenous peg 2.0–5.0 µm long. *Conidia* aseptate, hyaline, smooth, oblong-ellipsoid, almost straight, but with a laterally displaced hilum, broadly rounded at the end, (5.6–)6.4–9.2(–10.3) × 1.6–2.0(–2.4) µm (av.= 7.7 ×1.9, n = 150), arranged in imbricate chains.

Culture characteristics: Colonies on OA reaching 32–36 mm diam after 7 d at 25 °C in darkness, flat, with crenate margin, aerial mycelium moderate, felty, dirty white to pale yellow, with concentric rings, reverse pale yellow. Colonies on PDA reaching 34–36 mm diam, flat, with crenate margin, aerial mycelium moderate, felty to cottony, dirty white, with concentric rings, reverse concolourous. Colonies on SNA reaching 28–31 mm diam, flat, with entire margin, aerial mycelium sparse, dirty white, reverse concolourous.

Notes: Phylogenetically, *C. bambusae* (CBS 139411) and *Clonostachys* sp. CBS 496.90 (Figs 1, 2) form a sister clade to the core group of subgenus *Bionectria* characterised by regularly formed dimorphic conidiophores and slightly curved conidia having a laterally displaced hilum. Monomorphic, penicillate conidiophores, with somewhat divergent to adpressed branches and frequent occurrence of intercalary phialides characterise *C. bambusae*. The two strains differ genetically in ITS (99.2 % identity, with 4 bp differences), LSU (99.6 %, 3 bp), *RPB2* (94 %, 43 bp), *TEF1* (98.5 %, 12 bp) and *TUB2* (98 %, 16 bp) sequences. Schroers (2001: fig. 93a) illustrated CBS 496.90 to directly compare conidiophores and intercalary phialides with those of *C. setosa*, which also is characterised by a sesquicillium-like asexual morph. Due to their phylogenetic affinity, *Clonostachys* sp., CBS 496.90 and *C. setosa* are to be classified in *Clonostachys* and not *Sesquicillium*.

Clonostachys buxicola L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848480. Fig. 17.

Etymology: Name refers to the host genus, from which this fungus was isolated, *Buxus*.

Typus: **France**, Pyrénées Atlantiques, Isle de Sauveterre de Bearn, on bark of dead *Buxus sempervirens*, 25 Oct. 1998, G.J. Samuels & F. Candoussau (**holotype** designed here CBS H-25137; ex-type culture CBS 102419).

Sexual morph unknown. *Asexual morph*. *Conidiophores* variable, somewhat penicillate or typically with short conidiophores gradually integrating into indistinct sporodochia. *Sporodochia* arising from the aerial mycelium or from agar surface, appearing at first as distinct white pustules, with time coalescing, arranged in tufts throughout the colony, covered with greenish grey to dark green conidial masses. *Penicillate mononematous conidiophores* arising from agar surface or aerial mycelium, with irregularly branched penicilli. *Sporodochial conidiophores* irregularly penicillate, ter- to quaterverticillate or more frequently branched; cells supporting phialides frequently widening distally; *terminal phialides* in whorls of 2–5, also singly, adpressed or divergent at acute angles, straight or curved, cylindrical or somewhat narrowly flask-shaped, generally slightly tapering in the upper part, without a visible collarette, (7.4–)8.7–16.9(–21.0) µm long, (1.4–)1.6–2.4 µm wide at base, 0.9–1.2 µm wide near aperture; *intercalary phialides* rare, solitary, mostly below a single terminal phialide, sometimes arising from ± square-shaped cells, the conidiogenous peg of intercalary phialides sometimes as long as terminal phialides. *Conidia* aseptate, greenish hyaline, smooth, ovoid to ellipsoid, straight or minutely curved, sometimes widest in the lower part, with a median or slightly laterally displaced, not protruding, distinctly flat or almost invisible hilum, (4.6–)5.2–8.0(–8.6) × (2.3–)2.7–3.5(–3.8) µm (av. = 6.4 × 3.1 µm, n = 200), arranged in linear chains.

Culture characteristics: Colonies on OA reaching 24–26 mm diam after 7 d at 25 °C in darkness, flat, with entire margin, and aerial mycelium sparsely developed, felty, dirty white, reverse concolourous. Colonies on PDA reaching 25–28 mm diam, flat, with entire margin, aerial mycelium moderate, felty, white, reverse concolourous. Colonies on SNA reaching 16–17 mm diam, flat, with irregular margin, finely granulose, felty, white, reverse concolourous.

Notes: Based on phylogenetic analysis, *C. buxicola* and *C. pityrodes*, both forming distinctly greenish pigmented conidial masses, were included in a fully-supported clade (Figs 1, 2). *Clonostachys buxicola* and *C. pityrodes* are morphologically similar, but have clearly differing ITS (96.3 % identity, with 18 bp differences), LSU (98.7 %, 10 bp), *RPB2* (84.2 %, 119 bp), *TEF1* (95.3 %, 38 bp), and *TUB2* (90.3 %, 104 bp) sequences. Both species form a unique lineage near the root of the *Clonostachys* clade (Figs 1, 2). *Clonostachys pityrodes* was placed in its own subgenus, subgenus *Myronectria*, because of morphological characters deviating from those of the other subgenera (Schroers 2001).

Clonostachys cylindrica L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848481. Fig. 18.

Etymology: Name refers to the cylindrical conidia produced by this species.

Typus: **Venezuela**, Estación Biológica de Rancho Grande, Parque Nacional Henry Pittie, Estado Aragua, 1 200 m alt., Nov. 1997, R.F. Castañeda (**holotype** designated here CBS H-25150, ex-type living culture CBS 101113).

Sexual morph unknown. *Asexual morph. Conidiophores* dimorphic. *Primary conidiophores* verticillium-like, or acremonium-like, arising from the agar surface or from aerial mycelium, with monoverticillate or more-level-verticillate divergent phialides, sometimes with side-branches; *stipe* up to 165 µm long, 2.3–4.5 µm wide at base; *penicilli* up to 134 µm high; *terminal phialides* in whorls of 4, in lower levels also solitary, straight, cylindrical, but slightly and continuously tapering towards the tip, with or without a minute collarette, (10.4–)18.4–39.0(–41.7) µm long, (1.7–)1.8–2.6(–3.1)

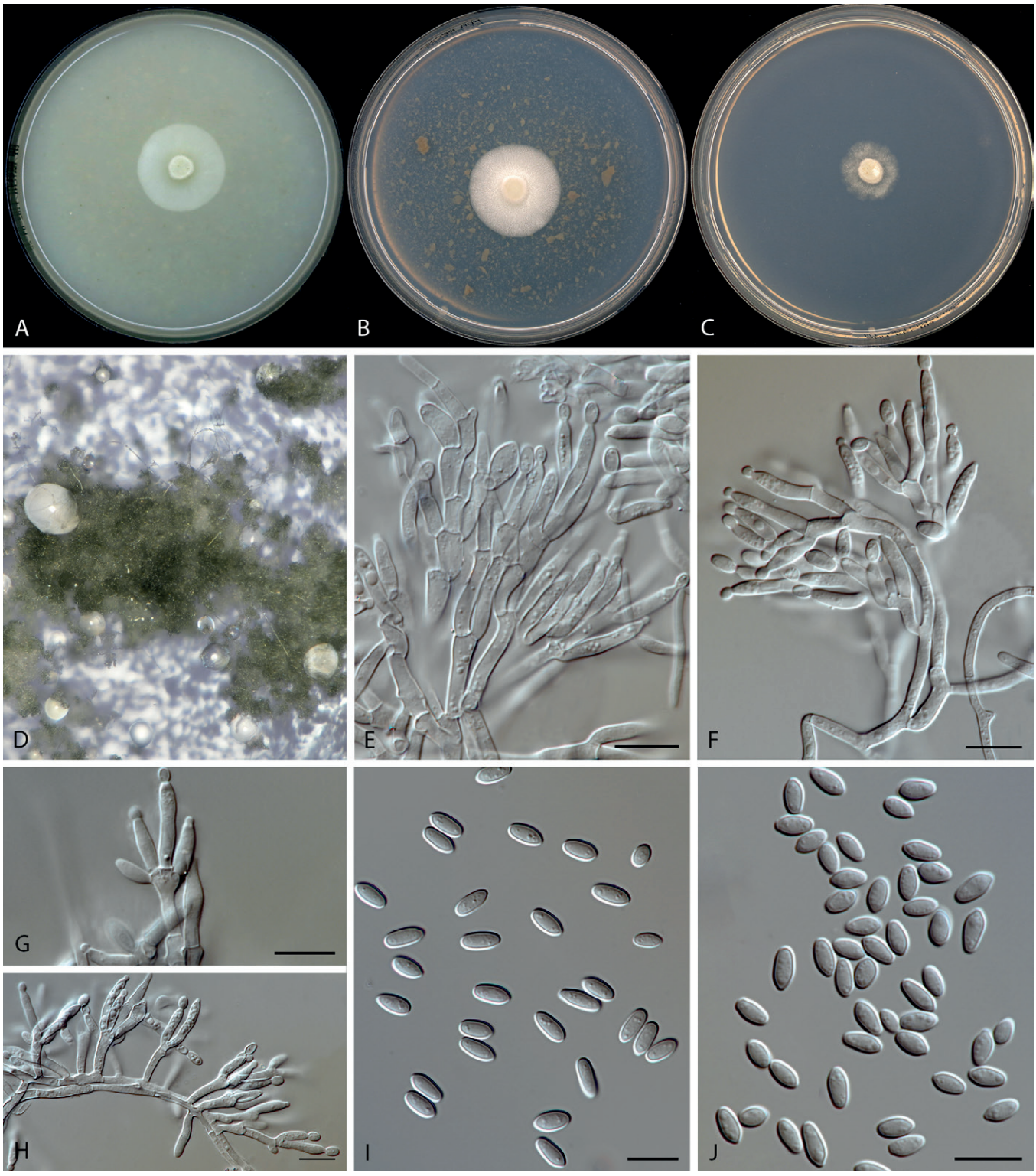

Fig. 17. *Clonostachys buxicola* (ex-type CBS 102419). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D.** Sporodochia producing green conidial masses on OA. **E, F.** Sporodochia. **G.** Phialides. **H.** Conidiophores. **I, J.** Conidia. Scale bars = 10 µm.

µm wide at base, (1.0–)1.2–1.6(–1.7) µm wide near aperture (n = 52), each producing a small, hyaline drop of conidia. *Secondary conidiophores* penicillate, scattered on the agar surface or arising from strands of aerial hyphae, up to terverticillate, branches adpressed or somewhat divergent; *stipes* 41–152 µm long, to 3.2–5.0 µm wide at base; *penicilli* up to 93 µm high, to 71 µm diam at widest point; *terminal phialides* adpressed, in whorls of up to seven, straight to slightly curved, narrowly flask-shaped, slightly tapering in the upper part, with or without a visible collarette, (7.7–)8.2–12.8(–15.7) µm long, (1.6–)1.8–2.9(–3.3) µm wide at base, (2.4–)3.0–4.0 µm at widest point, (0.9–)1.0–1.3(–1.4) µm wide near aperture (n = 100); *intercalary phialides* (5.4–)6.7–10.2(–12.3) × (2.8–)3.0–4.0(–4.3) with to 4.5 µm long lateral pegs, below a whorl of terminal phialides. *Conidia* aseptate, hyaline, smooth, cylindrical, straight or slightly curved, with a laterally displaced or sometime central hilum, (7.7–)8.6–11.9(–13.5) × (2.3–)2.5–3.3(–4.3) µm (av. = 10.1 × 2.9 µm, n = 150), arranged in imbricate chains.

Culture characteristics: Colonies on OA reaching 32–34 mm diam after 7 d at 25 °C in darkness, with entire margin, aerial mycelium

Fig. 18. *Clonostachys cylindrica* (ex-type CBS 101113). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–F.** Primary conidiophores. **G–I.** Secondary conidiophores. **J.** Conidia. Scale bars: E = 50 *µm*; D, F–J = 10 µm.

moderate, felty, whitish, reverse concolourous. Colonies on PDA reaching 35–38 mm diam, with entire margin, aerial mycelium moderate, felty to cottony, finely to coarsely granular, whitish, reverse concolourous. Colonies on SNA reaching 31–36 mm diam, with entire margin, aerial mycelium sparse, granular, whitish, reverse concolourous.

Notes: *Clonostachys cylindrica* resembles *C. compactiuscula* and *C. penicillata*, but these species can be distinguished based on conidial size [(7.7–)8.6–11.9(–13.5) × (2.3–)2.5–3.3(–4.3) µm in *C. cylindrica*) *vs* (3.9–)5.4–6.6–7.5(–12.4) × (1.5–)1.9–2.2–2.5(–3.2) µm in *C. compactiuscula* and (4.5–)5.0–6.8(–7.6) × (1.6–)1.7–2.2(–2.4) µm in *C. penicillata*. However, the morphologically differing *C. divergens* and *C. samuelsii* (sporodochial conidiophores) and *C. hongkongensis* and *C. rogersoniana* (broadly ellipsoidal to oval conidia) are also members of the two clades. *Clonostachys cylindrica* produces mononematous, dimorphic conidiophores, pale conidial masses, and clearly longer conidia (av. = 10.1 µm), while *C. divergens* (clostest phylogenetic sister lineage in Fig. 2) forms greenish pigmented conidial masses, and less than 5 µm long

conidia. Also the molecular sequences distinguish both species clearly (ITS: 96.3 % identity, with 18 bp differences; LSU: 99.4 %, 5 bp; and *TEF1*: 97.9 %, 17 bp).

Clonostachys ellipsoidea L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848482. Fig. 19.

Etymology: Name refers to the broadly ellipsoidal conidia produced by this fungus.

Typus: **Indonesia**, Java, Jogyakarta, date unknown, F.J.J. Jongeleen (**holotype** designated here CBS H-25144, ex-type living culture CBS 175.76).

Sexual morph unknown. *Asexual morph. Conidiophores* monomorphic, penicillate, arising from the sparse aerial mycelium, branches divergent or somewhat divergent, mono- to biverticillate; *stipes* 10–60 to µm long, to 4.3 µm wide at base; *terminal phialides* in loose apical whorls of 2–6, adpressed or divergent at acute angles, straight or curved, cylindrical and slightly tapering towards

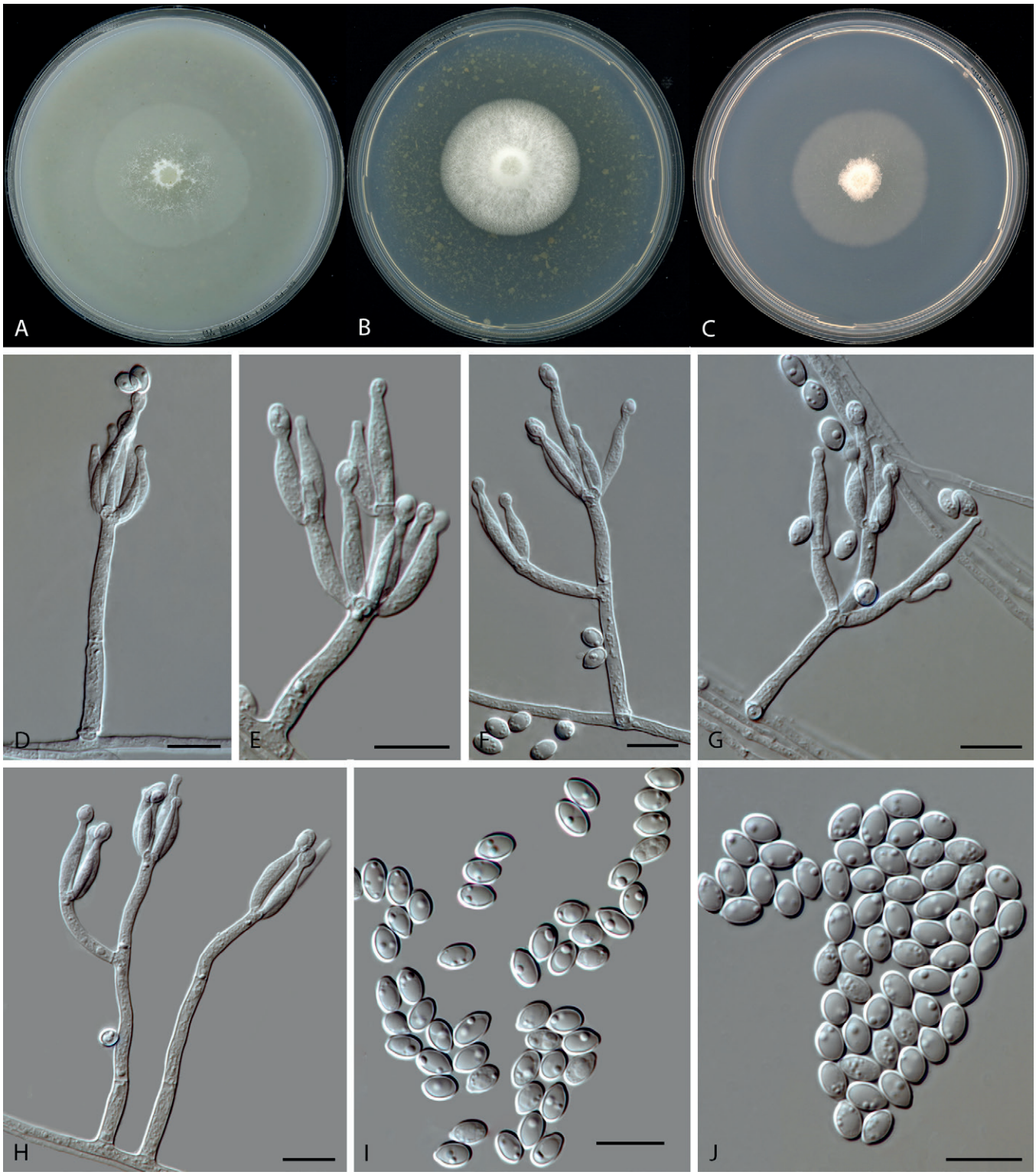

Fig. 19. *Clonostachys ellipsoidea* (ex-type CBS 175.76). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–H.** Conidiophores. **I, J.** Conidia. Scale bars = 10 µm.

the tip or narrowly flask-shaped and slightly widening in the middle, without visible collarette, (7.9–)8.5–18.9(–21.5) µm long, (1.4–)1.5–2.4(–2.7) µm wide at base, (2.2–)2.4–3.5(–3.9) µm at widest point, 1.0–1.4 µm wide near aperture (n = 100); *intercalary phialides* rare, conidiogenous pegs to 5 µm long, formed solitarily below whorls of terminal phialides. *Conidia* aseptate, hyaline, smooth, broadly ellipsoidal, rarely minutely curved, ends broadly rounded, hilum laterally displaced, almost median or invisible, (4.2–)4.8–5.9(–6.3) × (3.0–)3.2–3.7(–4.0) (av.= 5.3 × 3.5, n = 150), arranged in imbricate chains that may collapse into slimy masses.

Culture characteristics: Colonies on OA reaching 40–42 mm diam after 7 d at 25 °C in darkness, flat, with entire margin, aerial mycelium sparse, floccose, whitish, reverse concolourous. Colonies on PDA reaching 39–41 mm diam, with entire margin, aerial mycelium moderate, felty to cottony, whitish, reverse concolourous. Colonies on SNA reaching 38–40 mm diam, flat, with entire margin, aerial mycelium sparse, felty, finely granular, whitish, reverse concolourous.

Additional material examined: **India**, Amarkantak, Shahdol, soil, Jan. 1993, T. Okuda, No. TC 1304, culture CBS 102566.

Notes: Based on the phylogenetic analyses (Figs 1, 2), *C. ellipsoidea* is closely related to *C. leucaenae* (MFLUCC 20-0008), C. *pallens* (PAD S00004), *C. vacuolata* (CBS 191.93) and *C. venezuelae* (CBS 107.87). *Clonostachys ellipsoidea* differs from *C. leucaenae* in ITS (95.3 %, with 23 bp differences), LSU (98.3 %, 14 bp), from *C. pallens* in the ITS (92.5 % identity, with 14 bp differences) sequence, and from *C. venezuelae* (CBS 107.87) in ITS (95.5 % identity, with 23 bp differences), LSU (98.6 %, 11 bp), *RPB2* (96 %, 30 bp), *TEF1* (96.2 %, 30 bp), and *TUB2* (97.1 %, 30 bp) sequences. In addition, *C. ellipsoidea* differs from *C. vacuolata* in producing smaller and wider conidia (av. = 5.3 × 3.5 µm *vs* av. = 6.0 × 2.9 µm). Morphology of conidiophores and conidia supports classification of *C. ellipsoidea* in subgen. *Zebrinella.*

Clonostachys eriocamporesii R.H. Perera & K.D. Hyde, Fungal Diversity 100: 199. 2020. Fig. 20.

Typus: **Thailand**, Southern Thailand, on dead stems of *Pennisetum polystachion* (*Poaceae*), 11 Nov. 2017, A. Karunarathne, Bion 78 (**holotype** MFLU 18-2718, ex-type culture MFLUCC 19-0486).

Description based on CBS 647.91: *Sexual morph* unknown. *Asexual morph. Sporodochia* formed as distinct white pustules, with time coalescing to support dark greenish conidial masses. *Conidiophores* monomorphic, sporodochial, *phialides* straight or curved, cylindrical and slightly tapering towards the tip or narrowly flask-shaped and slightly widening in the middle, with or without a visible collarette, (7.6–)9.5–17.5(–19.6) µm long, (2.0–)2.2–3.2(–3.5) µm at base, (2.3–)2.5–3.5(–3.7) at widest point, (0.8–)0.9–1.2(–1.3) µm wide near aperture (n = 60). *Conidia* aseptate, greenish hyaline, ellipsoidal to narrowly clavate, straight or slightly curved, with or without a slightly protruding or slightly laterally displaced hilum and a rounded distal end, (4.4–)5.9–8.6(–12.6) × (2.4–)2.7–3.8(–4.2) µm (av. 7.4 × 3.2 µm, n = 150), arranged in linear chains.

Culture characteristics: Colonies on OA reaching 30–45 mm diam after 7 d at 25 °C in darkness, with entire margin, aerial mycelium moderate, felty to cottony, whitish, reverse concolourous. Colonies on PDA reaching 32–41 mm diam, with entire margin, aerial mycelium moderate, felty to cottony, whitish, reverse concolourous. Colonies on SNA reaching 27–32 mm diam, with entire margin, aerial mycelium moderate in the centre, sparsely at periphery, floccose, whitish, reverse concolourous.

Additional materials studied: **Germany**, Berlin, unknown date and collector, culture CBS 647.91. **Netherlands**, soil, Oct. 27, 2019, T. Vercruisse, culture CBS 148221= NL19-060010.

Notes: *Clonostachys eriocamporesii* was first described from dead stems of *Pennisetum polystachion* (Hyde *et al*. 2020a). According to our phylogenetic analyses (Figs 1, 2), *C. eriocamporesii* is closely related to *C. epichloe*, *C. fujianensis*, *C. miodochialis* and *C. obovatispora*. Morphologically, *C. eriocamporesii* differs from *C. epichloe*, *C. miodochialis* and *C. obovatispora*, in producing larger conidia [(4.4–)5.9–8.6(–12.6) × (2.4–)2.7–3.8(–4.2) av. 7.4 × 3.2 µm in *C. eriocamporesii*, (4.8–)6.0–7.0(–9.6) × (1.6–)2.2–2.8(–3.6) av. = 6.6 × 2.6 µm in *C. epichloe*, (5.2–)5.8–7.2(–8.0) × (1.8–)2.6–3.0(–3.4) av. = 6.6 × 2.8 µm in *C. miodochialis*, and (4.7–)5.8–7.6(–8.2) × (1.7–)2.0–2.5(–2.9) av. = 6.74 × 2.26 µm in *C. obovatispora*]. *Clonostachys eriocamporesii* (CBS 647.91) and *C. fujianensis* (CBS 127474) are clearly different by ITS (98.2 % identity, with 9 bp differences), LSU (99.6 %, 3 bp), *TEF1* (95.8 %, 34 bp), and *TUB2* (91.5 %, 90 bp) sequences.

Clonostachys farinosa (Henn.) Rossman, IMA Fungus 5: 86. 2014.
Basionym: *Nectriella farinosa* Henn., Hedwigia 36: 219. 1897.
Synonyms: *Nectria farinosa* (Henn.) Möller, in Schimper, Bot. Mitt. Tropen 9: 296. 1901.
Nectria byssicola Berk. & Broome, J. Linn. Soc. Bot. 14: 116. 1873.
Bionectria byssicola (Berk. & Broome) Schroers & Samuels, Z. Mykol. 63: 152. 1997.
Clonostachys byssicola Schroers, Stud. Mycol. 46: 80. 2001.
Clonostachys eriocamporesiana R.H. Perera & K.D. Hyde, Fungal Diversity 100: 197. 2020.
Clonostachys indica Prasher & R. Chauhan [as '*indicus*'], Kavaka 48: 22. 2017.
Clonostachys wenpingii (J. Luo & W.Y. Zhuang) Z.Q. Zeng & W.Y. Zhuang, Mycol. Progr. 13: 969. 2014.
Clonostachys granuligera (Starbäck) Forin & Vizzini, Persoonia 45: 240. 2020.
Clonostachys squamuligera (Sacc.) Forin & Vizzini, Persoonia 45: 245. 2020.
Clonostachys spinulosa R.H. Perera, E.B.G. Jones & K.D. Hyde, Fungal Diversity 118: 109. 2023.

Description and illustration: Schroers (2001).

Typus: **Venezuela**, Edo Sucre, between Los Pocitos and Santa Isabel, on unidentified wood, 11 Jul. 1972, G.J. Samuels & K.P. Dumont (**isotype** of *C. byssicola*, CBS H-7918, ex-type living culture CBS 364.78 = C.T.R. 72-123-ss7 = VE 4681).

Notes: *Nectria byssicola* was described by Berkeley & Broome (1873) from the portion '173d' (type specimen) as having pale orange, scurfy perithecia and ascospores. It was transferred to *Bionectria* as *B. byssicola* (Schroers & Samuels 1997). Subsequently, *Clonostachys byssicola* was newly described by Schroers (2001). However, with the introduction of the One Fungus–One Name concept, *B. byssicola* became a synonym for *C. byssicola*. Therefore, the oldest available name, *N. byssicola* (1873), cannot be recombined in *Clonostachys*. Accordingly, the

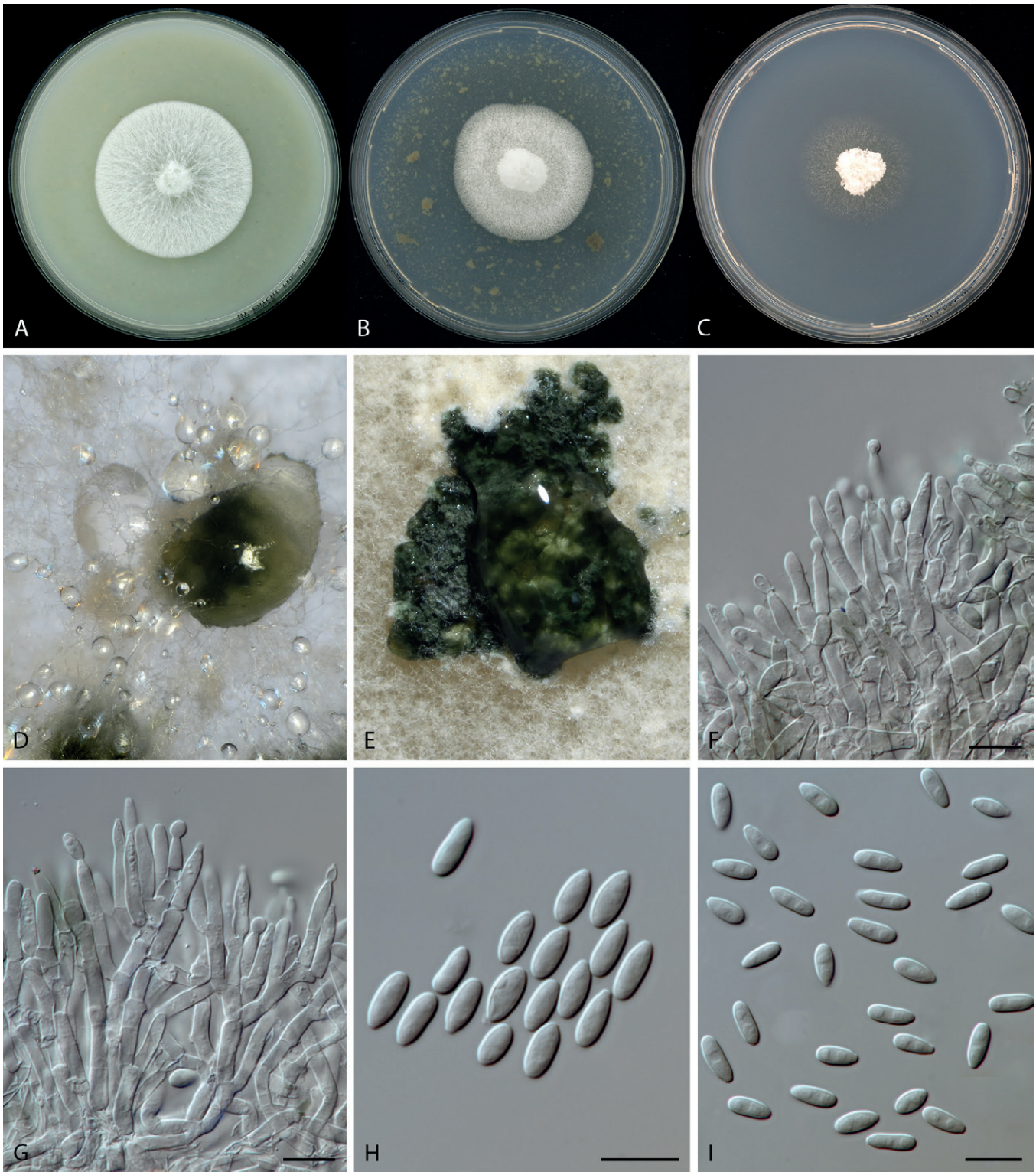

Fig. 20. *Clonostachys eriocamporesii* (CBS 647.91). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D.** Sporodochia after 1 wk. **E.** Sporodochia after 2 wk. **F, G.** Sporodochia. **H, I.** Conidia. Scale bars = 10 µm.

next available epithet, *Nectriella farinosa* (1897), was placed in *Clonostachys* and published as a new combination, *C. farinosa* (Rossman 2014). According to the multi-gene phylogenetic inferences, the ex-type strains of *C. eriocamporesiana* (MFLUCC 17-2620), *C. granuligera* (PAD S00011), *C. indica* (IBP2), *C. spinulosa* (MFLUCC 17-0131), *C. squamuligera* (PAD S00020) and *C. wenpingii* (CBS 124067) cluster near the ex-type culture of *C. byssicola* (CBS 364.78; Figs 1, 2) and together with several other strains identified by Schroers (2001) as *C. byssicola* (Fig. 2). Judged on the basis of gatherings of perithecia on recently dead trees, *C. farinosa* is one of the more frequently occurring species in tropical regions (Samuels 1976, Schroers 2001). A couple of asexual morph characters were discussed that could help identifying *C. farinosa* in cultures (Schroers 2001, as *C. byssicola*); however, distinguishing this species from others forming dimorphic conidiophores is difficult. It is therefore not surprising that rather numerous synonymous species were described since 2001 on the basis of asexual morph-typified material.

Fig. 21. *Clonostachys flava* (ex-type CBS 915.97). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–F.** Primary conidiophores. **G, H.** Secondary conidiophores. **I, J.** Conidia. Scale bars = 10 µm.

Clonostachys flava L. Zhao, Crous, & Schroers, ***sp. nov.*** MycoBank MB 848483. Fig. 21.

Etymology: Name refers to the yellow colonies of this species (OA, PDA, and SNA).

Typus: **French Guiana**, St. Laurent-Du-Marouni, Canton de Maripasoula, S. along Route De belizon, decaying bark, 200 m alt., 14 Sep. 1994, S.M. Huhndorf, BPI 737845, culture G.J.S. 94-75 (**holotype** designated here CBS H-25139, ex-type culture CBS 915.97).

Sexual morph known from natural specimen (not shown). *Asci* 49–70 × 8.5–10 µm. *Ascospores* 1-septate, hyaline, striate, ellipsoid, 9.7–10.8–12.8 × 3.3–4.0–4.9 µm. *Asexual morph. Conidiophores* dimorphic, mononematous, scattered on the agar surface or arising from strands of aerial hyphae. *Primary conidiophores* narrowly penicillate, adpressed, mono- to terverticillate; *stipe* 20–120 µm long, 2.2–4.0 µm wide at base; *penicilli* 40–100 µm high; *phialides* straight to slightly curved, almost cylindrical, slightly tapering towards the tip, sometimes with a short collarette, (22.4–)25.9–43.2(–46.9) µm long, (1.4–)1.6–2.4(–2.6) µm wide at base, (1.1–)1.2–1.6(–1.7) µm

wide near aperture (n = 50). *Secondary conidiophores* penicillate, ter- to quaterverticillate, branches adpressed or divergent, phialides adpressed or somewhat divergent; *phialides* in loose whorls of 2–5, straight or slightly curved, flask-shaped or somewhat cylindrical, widest in the lower third, slightly tapering in the upper part towards the tip, without a collarette, (11.4–)12.6–18.8(–20.7) µm long, (1.2–)1.5–2.3(–2.8) µm wide at base, (1.8–)2.0–2.7(–2.8) µm at widest point, (0.8–)0.9–1.3(–1.4) µm wide near aperture (n = 50). *Conidia* aseptate, hyaline, smooth, ellipsoid to obovoid, distally broadly rounded, apex minutely tapering, with a median, invisible, or rarely somewhat laterally displaced hilum, (4.7–)4.9–6.5(–7.8) × (2.4–)2.6–3.3(–3.4) µm (av. 5.7 × 3.0 µm, n = 150), arranged in imbricate chains that may collapse into slimy masses.

Culture characteristics: Colonies on OA reaching 22–30 mm diam after 7 d at 25 °C in the darkness, flat, with crenate margin, aerial mycelium abundant, felty to cottony, finely to coarsely granular, yellowish white to pale yellow, reverse yellowish to pale yellow. Colonies on PDA reaching 24–29 mm diam, flat, with entire margin, aerial mycelium abundant, felty to cottony, granular, yellowish white to pale yellow, reverse pale yellow to pale orange. Colonies on SNA reaching 22–24 mm diam, flat, with crenate margin, aerial mycelia sparsely developed, felty, finely granular, pale yellow, reverse concolourous.

Notes: Based on phylogenetic analyses, *C. flava* and *C. grammicospora* formed a well-supported clade (Figs 1, 2). Morphologically, the longer phialides (both in primary and secondary conidiophores) can be used to distinguish *C. flava* from *C. grammicospora* [primary conidiophore: (22.4–)25.9–43.2(–46.9) µm *vs* (11–)17.2–24.6(–43.4) µm; secondary conidiophore: (11.4–)12.6–18.8(–20.7) µm *vs* (4.4–)9.8–12.6(–18.6) µm]. Furthermore, CBS 915.97 (*C. flava*) and CBS 209.93 (*C. grammicospora*) have clearly different ITS (97.4 % identity, with 12 bp differences), LSU (99.5 %, 4 bp), *RPB2* (96.1 %, 29 bp), *TEF1* (96.9 %, 25 bp), and *TUB2* (96.8 %, 30 bp) sequences. Schroers (2001) listed CBS 915.97 under *C. grammicospora*, characterised by an ascospore size of (8.2–)10.6–12.6(–17.6) × (3.0–)3.8–4.6(–6.2) µm (av. 11.6 × 4.2 µm). Accordingly, *C. flava* forms similarly sized ascospores as specimen Raunkiaer 3103 (isotype of *Nectria grammicospora*, ascospores 10.7–13.1 × 3.8–4.9 µm) and specimen Samuels 3285 (type of *C. grammicospora*, ascospores 9–13.5 × 3.6–5.4 µm) (Samuels 1988b, Schroers 2001). Overall characters of the sexual morph of *C. flava* and *C. grammicospora* are similar. The morphology of conidiophores and conidia supports classification of *C. flava* in subgen. *Zebrinella*.

Clonostachys fujianensis L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848484.

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

Typus: **China**, Fujian, Bamboo stem, collection and isolation date unknown, W.Y. Zhuang & J. Luo (**holotype** designated here CBS H-25146, ex-type living culture CBS 127474).

Cultures sterile. *Clonostachys fujianensis* differs from its closest phylogenetic neighbours *C. eriocamporesii* (Fig. 2) by unique nucleotide substitutions and indels in the five investigated loci (see direct sequence comparisons deposited at doi: 10.6084/m9.figshare.22894592): *C. fujianensis* and *C. eriocamporesii* (CBS 647.91): ITS position 116 (C), 167 (gap), 171 (T), 182 (gap), 429 (gap), 477 (A), 478 (G), 481 (C), 533 (C), 534 (T), 548 (A), 564 (A); LSU position 1 007 (C), 1 008 (T), 1 045 (C); *TEF1* position 2 150 (C), 2 180 (T), 2 186 (T), 2 198 (C), 2 270 (T), 2 306 (T), 2 339 (A), 2 360 (T), 2 361 (G), 2 369 (C), 2 384 (A), 2 414 (T), 2 429 (C), 2 469 (G), 2 471 (T), 2 504 (G), 2 513 (T), 2 522 (C), 2 525 (C), 2 556 (G), 2 621 (T), 2 643 (A), 2 690 (C), 2 702 (C), 2 705 (T), 2 748 (C), 2 759 (C), 2 819 (C), 2 831 (C), 2 849 (C), 2 885 (C); *TUB2* position 2 945 (T), 2 946 (G), 2 996 (gap), 3 000–3 002 (gap), 3 006 (T), 3 007 (G), 3 009 (A), 3 011 (A), 3 012 (T), 3 013 (G), 3 014 (C), 3 015 (T, insertion), 3 018–3 021 (gap), 3 028 (G, insertion), 3 029 (A), 3 038 (T), 3 039 (G), 3 045 (G), 3 062 (A), 3 109 (C), 3 118 (T), 3 121 (T), 3 172 (T), 3 203 (G), 3 217 (T), 3 219 (C), 3 221 (T), 3 222 (C), 3 223 (T), 3 224 (C), 3 225–3 226 (gap), 3 227 (A), 3 229 (A), 3 236 (T), 3 239 (T), 3 242 (C), 3 244 (A), 3 245 (G), 3 246 (C), 3 248 (T), 3 252 (A), 3 255 (A), 3 257 (C), 3 258 (A), 3 261 (G), 3 269 (G), 3 271 (T), 3 272 (gap), 3 287 (A), 3 292 (C), 3 294 (G), 3 295 (G), 3 308 (T), 3 311 (C), 3 365 (C), 3 371 (A), 3 377 (T), 3 398 (T), 3 410 (T), 3 416 (T), 3 461 (G), 3 468 (G), 3 470 (G), 3 473 (T), 3 482 (C), 3 497 (C), 3 542 (C), 3 569 (A), 3 635 (T), 3 684 (T), 3 705 (T), 3 714 (G), 3 744 (C), 3 768 (T), 3 780 (G), 3 786 (T), 3 789 (C), 3 813 (T), 3 834 (T), 3 864 (G), 3 873 (C), 3 888 (C), 3 930 (T), 3 960 (C), 3 972 (T), 4 002 (A), 4 032 (C), 4 047 (T).

Notes: *Clonostachys fujianensis* was collected from stems of a bamboo. Unfortunately, it does not sporulate in culture. Phylogenetically, it is distinct from all other sequenced species (Figs 1, 2).

Clonostachys fusca L. Zhao, Crous & Schroers, ***sp. nov.*** MycoBank MB 848485. Fig. 22.

Etymology: Epithet derived from the brown ascomata produced by this species.

Typus: **French Guiana**, unknown, herbaceous stem, Jan.–Mar. 1986, G.J. Samuels (**holotype** designated here CBS H-25141, ex-type living culture CBS 207.93); also kept as G.J.S. 3731, culture G.J.S. 86-200.

Sexual morph produced in culture on OA. *Stroma* superficial or erumpent, bearing perithecia, cells prosenchymatous, densely hyphal. *Perithecia* crowded in groups of up to 20, globose to subglobose, 190–300 µm diam, pale to brownish orange or reddish brown. *Perithecial warts* whitish to pale orange, up to 70 µm high, cells subglobose to globose, of the same type as the cells of the outer perithecial wall region, (6.5–)7.5–17.0(–26.0) × (6.0–)7.0–16.0(–20.0) µm (av. = 11.6 × 10.7 µm, n = 100). *Perithecial wall* 20–45 µm thick composed of two regions; outer region 15–36 µm or 1–3 cells thick, cells merging with the cells of the warts, cells angular to subglobose, (5.5–)6.5–13.0(–15.0) × (3.5–)4.5–12.0(–15.5) µm (av. = 9.5 × 8.0 µm, n = 100), with evenly thickened walls around 1.5 µm thick, sometimes with vacuoles; middle region lacking; inner region 10–25 mm thick. *Asci* 8-spored, clavate, 35–70 × 7.5–12.0 µm (av. = 48.1 × 10.5 µm, n = 35), apex flat or sometimes rounded, edges rounded, ring clearly visible. *Ascospores* 0–1-septate, striate, striae parallel, constriction at the median septum frequently observed in discharged ascospores, ellipsoid, (11.5–)12.0–15.0(–16.0) × (4.0–)4.5–5.5 µm (av. = 13.2 × 4.8 µm, n = 80). *Asexual morph* not observed.

Culture characteristics: Colonies on OA reaching 33–36 mm diam after 7 d at 25 °C in darkness, with crenate margin, aerial mycelium moderate, felty to cottony, pale yellow, reverse concolourous. Colonies on PDA reaching 38–40 mm diam, with entire margin,

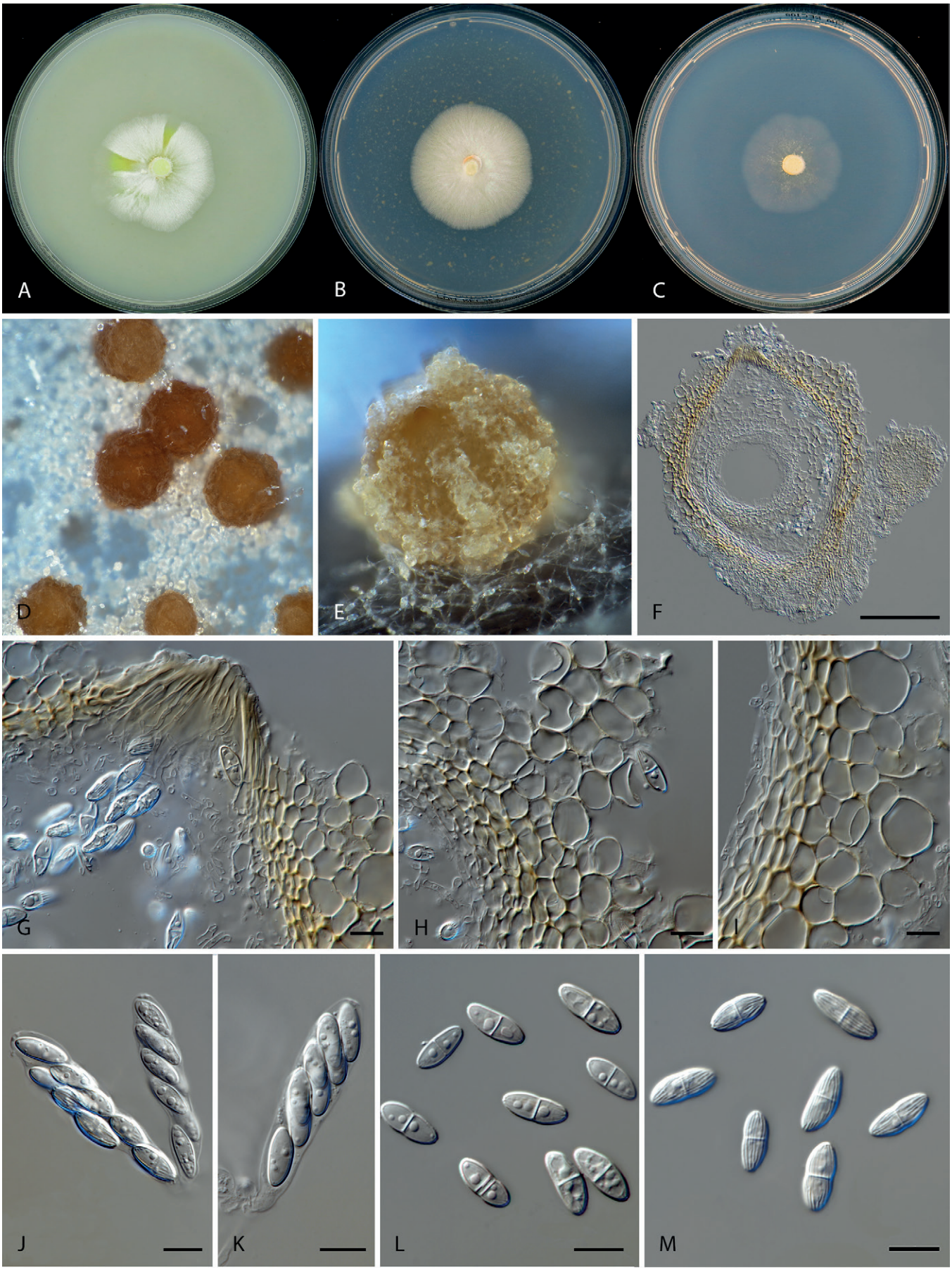

Fig. 22. *Clonostachys fusca* (ex-type CBS 207.93). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D, E.** Perithecia. **F.** Section through perithecium. **G.** Ostiole. **H.** Perithecial wart. **I.** Lateral perithecial wall showing two regions. **J, K.** Asci. **L, M.** Discharged ascospores in optical section (L) and surface view (M). Scale bars: F = 50 µm; G–M = 10 µm.

aerial mycelium moderate, felty, white yellow, reverse pale yellow. Colonies on SNA reaching 31–37 mm diam, with crenate margin, aerial mycelium sparse, felty, whitish, reverse concolourous.

Additional materials examined: **USA**, Puerto Rico, Caribbean National Forest, Luquillo Mts., Bisley Experimental Watershed, bark of recently dead tree, 21 Feb. 1996, G.J. Samuels, H.J. Schroers 74 & D.J. Lodge, BPI 749156, culture CBS 996.97; Puerto Rico, Caribbean National Forest, Liquillo Mts., trail to Cocle Falls from Rt 191, 475 m alt., bark, 23 Feb. 1996, G.J. Samuels & H.-J. Schroers, culture CBS 101925.

Notes: Based on phylogenetic analyses, *C. fusca* is closely related to *C. aurantiaca* (Figs 1, 2). Morphologically, *C. fusca* differs from *C. aurantiaca* in producing more crowded perithecia, and larger ascospores [(11.5–)12.0–15.0(–16.0) × (4.0–)4.5–5.5 µm *vs* (8.5–)9.0–12.0(–12.5) × 4.0–5.5(–6.0) µm]. Observed morphological characters, especially perithecial walls consisting of two regions, perithecial warts consisting of cells with evenly thickened walls and the striate ascospores support their classification in subgen. *Zebrinella.*

Clonostachys garysamuelsii L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848486. Fig. 23.

Etymology: Named in honour of Dr Gary J. Samuels, who collected many sexual morphs of *Clonostachys* and *Sesquicillium* species, isolated ascospores and deposited cultures in the CBS collection.

Typus: **Venezuela**, unknown, tree bark, date unknown, G.J. Samuels (**holotype** designated here CBS H-25154, ex-type culture CBS 123964).

Sexual morph unknown. *Asexual morph. Conidiophores* dimorphic. *Primary conidiophores* arising from the agar surface or strands of aerial mycelium, mononematous, acremonium- or verticillium-like, mono- to terverticillate; phialides adpressed or divergent; sometimes with main side branches arising from the lower part of the stipe; *stipe* varying in length, (8.0–)20.0–90.0 µm long, 2.0–3.5 µm wide at base; *penicilli* 40–70 µm high; *phialides* in whorls of 2–5, straight, generally slightly tapering towards the tip, with or without a visible collarette, (15.6–)16.8–41.4(–50.0) µm long, (1.6–)1.8–2.7 µm wide at base, (1.1–)1.2–1.8 µm wide near aperture (n = 60). *Secondary conidiophores* ter- to quinquiesverticillate, densely aggregated, formed in pustules or sporodochia on agar surface or from strands of aerial mycelium; branches divergent; *phialides* in loose whorls of 3–5, straight to slightly curved, narrowly flask-shaped, generally with widest point in the lower third, or almost cylindrical, tapering in the upper part, without a visible collarette, (7.8–)9.9–18.8(–20.2) µm long, (1.5–)1.7–2.5(–2.6) µm wide at base, (2.0–)2.2–2.8(–3.0) µm at widest point, 1.0–1.4(–1.5) µm wide near aperture (n = 50). *Conidia* aseptate, hyaline, smooth, ellipsoid, straight or minutely curved, some asymmetric with one more flattened side, ends broadly rounded, without a visible hilum, or with a hardly visible, laterally displaced hilum, (3.5–)4.5–7.1(–8.2) × (2.0–)2.3–3.3(–3.7) µm (av. = 5.7 × 2.7 µm, n = 150), arranged in imbricate chains that may collapse into slimy masses.

Culture characteristics: Colonies on OA reaching 30–35 mm diam after 7 d at 25 °C in darkness, flat, with entire margin, aerial mycelium moderate, felty, whitish, reverse concolourous. Colonies on PDA reaching 28–31 mm diam, flat, with entire margin, aerial mycelium moderate, felty to cottony, whitish, reverse concolourous. Colonies on SNA reaching 28–30 mm diam, flat, with entire margin, aerial mycelium sparse, felty, whitish, reverse concolourous.

Notes: According to the multi-gene phylogenetic inference, *C. garysamuelsii* groups together with *C. moreaui* and *C. oblongispora* (Fig. 2; support below threshold values) or *C. parasporodochialis* and *C. sporodochialis* (Fig. 1, poorly to well-supported). Morphologically, *C. garysamuelsii* differs from *C. moreaui* and *C. oblongispora* in producing smaller conidia [(3.5–)4.5–7.1(–8.2) × (2.0–)2.3–3.3(–3.7) µm *vs* 5.0–10.0(–12.0) × 3.5–5.0 µm and (9.0–)12.6–14.0(–19.8) × (2.6–)3.2–3.8(–4.2) µm]. However, *C. garysamuelsii* differs from *C. sporodochialis* in producing larger conidia [(3.5–)4.5–7.1(–8.2) × (2.0–)2.3–3.3(–3.7) µm *vs* (3.2–)4.4–5.4(–6.8) × (1.6–)2.0–2.2(–2.6) µm]. *Clonostachys garysamuelsii* can also be distinguished from *C. moreaui* and *C. parasporodochialis* by having dimorphic conidiophores, while conidiophores of *C. moreaui* and *C. parasporodochialis* are monomorphic (Lechat *et al.* 2020).

Clonostachys hongkongensis L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848487. Fig. 24.

Etymology: Named after the location where the fungus was collected, Hong Kong, China.

Typus: **China**, Hong Kong, Pokfulam Reservoir, wood, 14 Jun. 2001, unknown collector (**holotype** designated here CBS H-25149, ex-type living culture CBS 115291).

Sexual morph unknown. *Asexual morph. Conidiophores* dimorphic, mononematous. *Primary conidiophores* verticillium-like, arising from the agar surface or from aerial mycelium, with monoverticillate or more-level-verticillate divergent phialides, sometimes with side-branches; *stipe* up to 225 µm long, 2.3–4.6 µm wide at base; *penicilli* 40–130 µm high; *phialides* in whorls of 2–4, in lower levels also solitary, straight, cylindrical, slightly and continuously tapering towards the tip, with or without a minute collarette, (19.9–)20.4–39.1(–43.4) µm long, (1.6–)1.9–2.3(–2.6) µm wide at base, 1.1–1.5(–1.7) µm wide near aperture (n = 50), each producing a small, hyaline drop of conidia. *Secondary conidiophores* penicillate, scattered on the agar surface or arising from strands of aerial hyphae, bi- to quaterverticillate; branches adpressed or somewhat divergent; *stipes* 93–135 µm long, to 5 µm wide at base; *penicilli* 30–58 µm, to 55 µm diam at widest point; *terminal phialides* adpressed, in whorls of up to 4–5, straight to slightly curved, narrowly flask-shaped, slightly tapering in the upper part, with or without a visible collarette, (9.0–)10.3–14.5(–15.9) µm long, (1.5–)1.6–2.2(–3.0) µm wide at base, (2.2–)2.4–2.9(–3.4) µm at widest point, (0.8–)0.9–1.3 µm wide near aperture (n = 50); *intercalary phialides* rare, with to 3 µm long lateral pegs, below a whorl of terminal phialides (not shown). *Conidia* aseptate, hyaline, smooth, ellipsoid to obovoid, straight or slightly curved, with a laterally displaced or sometimes median hilum, (4.1–) 4.3–5.9(–6.3) × (2.8–)2.9–3.4 µm (av. = 4.8 × 3.1 µm, n = 70), arranged in imbricate chains.

Culture characteristics: Colonies on OA reaching 36–40 mm diam after 7 d at 25 °C in darkness, flat, with crenate margin, aerial mycelium moderate, finely to coarsely granular, felty to cottony, whitish to pale yellow, reverse yellowish. Colonies on PDA reaching 37–43 mm diam, flat, with crenate margin, aerial mycelium moderate, finely to coarsely granular, felty to cottony, whitish, reverse concolourous. Colonies on SNA reaching 39–40 mm diam, flat, with crenate margin, aerial mycelium sparse, finely to coarsely granular, whitish, reverse concolourous.

Additional material examined: **China**, Hong Kong, Pokfulam Reservoir, wood, 14 Jun. 2001, unknown collector, culture CBS 116542.

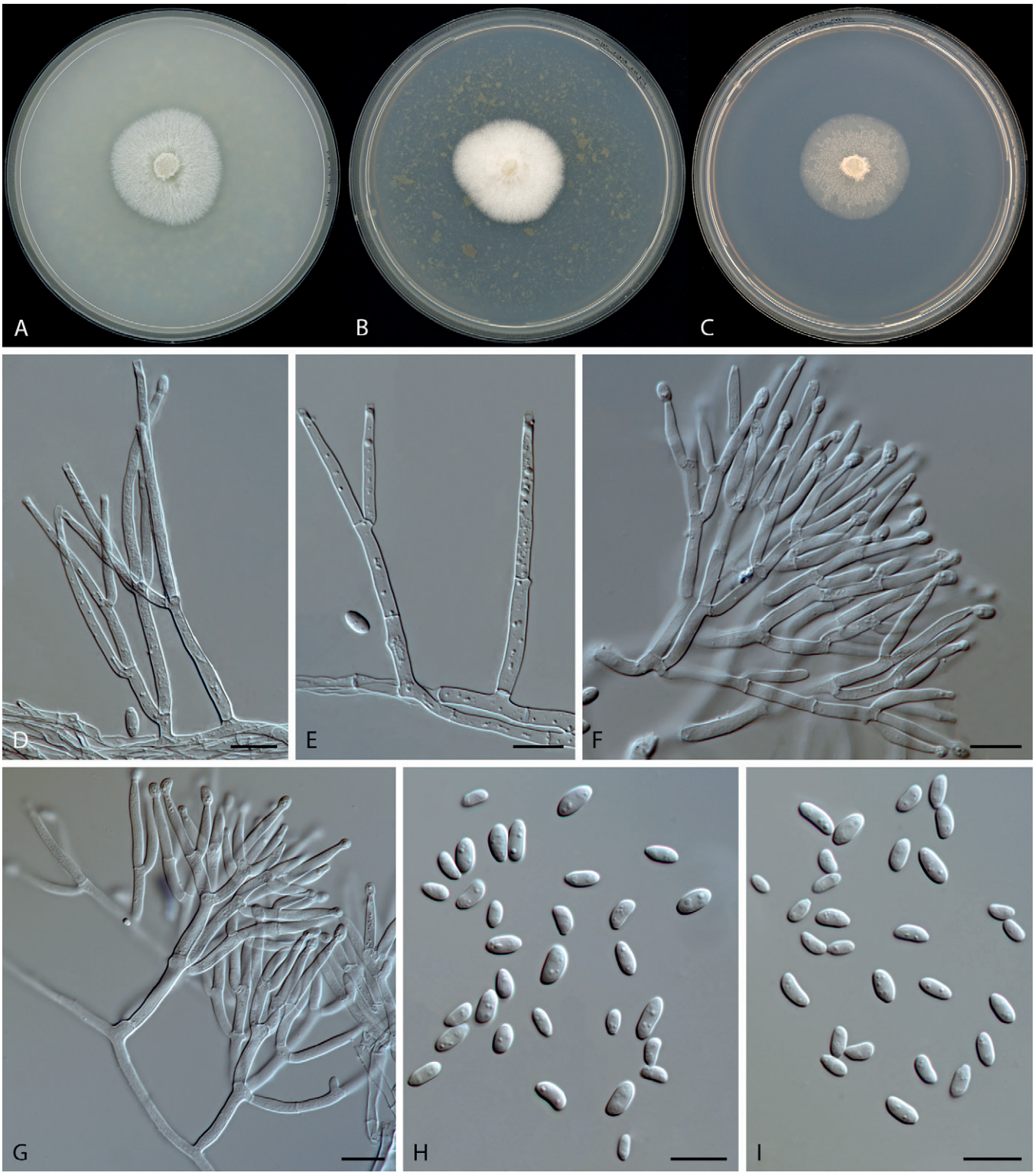

Fig. 23. *Clonostachys garysamuelsii* (ex-type CBS 123964). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D, E.** Primary conidiophores. **F, G.** Secondary conidiophores. **H, I.** Conidia. Scale bars = 10 µm.

Notes: Based on the multi-locus phylogenetic analyses (Figs 1, 2), *C. hongkongensis* has a close phylogenetic affinity to *C. cylindrica*, *C. divergens*, *C. rogersoniana* and *C. samuelsii*. Morphologically, *C. hongkongensis* differs from *C. cylindrica*, *C. divergens*, *C. rogersoniana* and *C. samuelsii* in producing shorter conidia [(4.1–)4.3–5.9(–6.3) µm *vs* (7.7–)8.6–11.9(–13.5) µm in *C. cylindrica*, (4.8–)5.8–6.4(–7.4) µm in *C. divergens*, (4.8–)5.8–7.2(–9.6) µm in *C. rogersoniana* and (4.4–)5.8–7.0(–11.6) µm in *C. samuelsii*]. Loosely branched sporodochia showing diverging branches and greenish conidial masses distinguish *C. divergens* from *C. hongkongensis*.

Clonostachys kunmingensis Hong Yu bis & Yao Wang, Frontiers Microbiol. 14: 8. 2023. Fig. 25.

Typus: **China**, Yunnan Province, Kunming City, Wild Duck Forest Park (25°13'N, 102°87'E, 2 100 m alt.), from soil on the forest floor, 10 Aug. 2019, Yao Wang (**holotype** YHH 898 dried specimen, ex-type culture YFCC 898).

Description based on CBS 101920: *Sexual morph* from natural specimen (not shown). *Asci* 49.1–59.1–66.9 × 6.7–8.4–10.0 µm (n

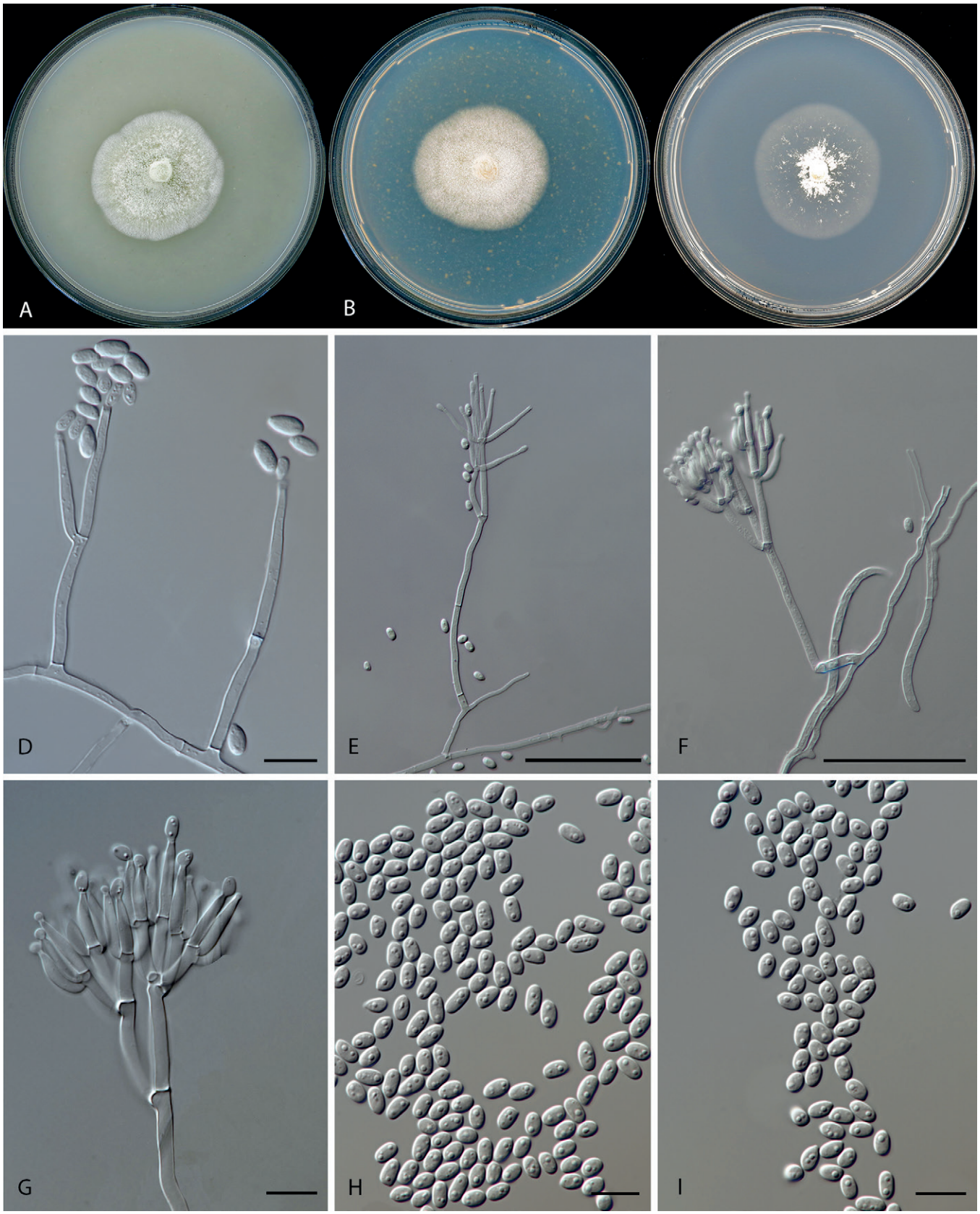

Fig. 24. *Clonostachys hongkongensis* (ex-type CBS 115291). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D, E.** Primary conidiophores. **F, G.** Secondary conidiophores. **H, I.** Conidia. Scale bars: E, F = 50 µm; D, G–I = 10 µm.

= 16). *Ascospores* 1-septate, hyaline, smooth or finely spinulose, ellipsoid, 10.1–12.7–16.6 × 3.6–4.2–4.9 µm (n = 24). *Asexual morph. Conidiophores* dimorphic, mononematous. *Primary conidiophores* arising from the agar surface or from strands of aerial mycelium, branches adpressed or somewhat divergent, phialides adpressed; *stipe* 30–140 µm long, 2.8–4.8 µm wide at base; *penicilli* 30–80 µm high; *phialides* in apical whorls of 2–5, also solitary arising from lower levels, straight, almost cylindrical, slightly tapering towards the tip, with a somewhat visible collarette, (15.4–)17.6–31.2(–32.5) µm long, (1.6–)1.9–2.5(–2.7) µm wide at base, 1.1–1.5(–1.6) µm wide near aperture (n = 80). *Secondary conidiophores* penicillate, bi- to quaterverticillate, primary branches

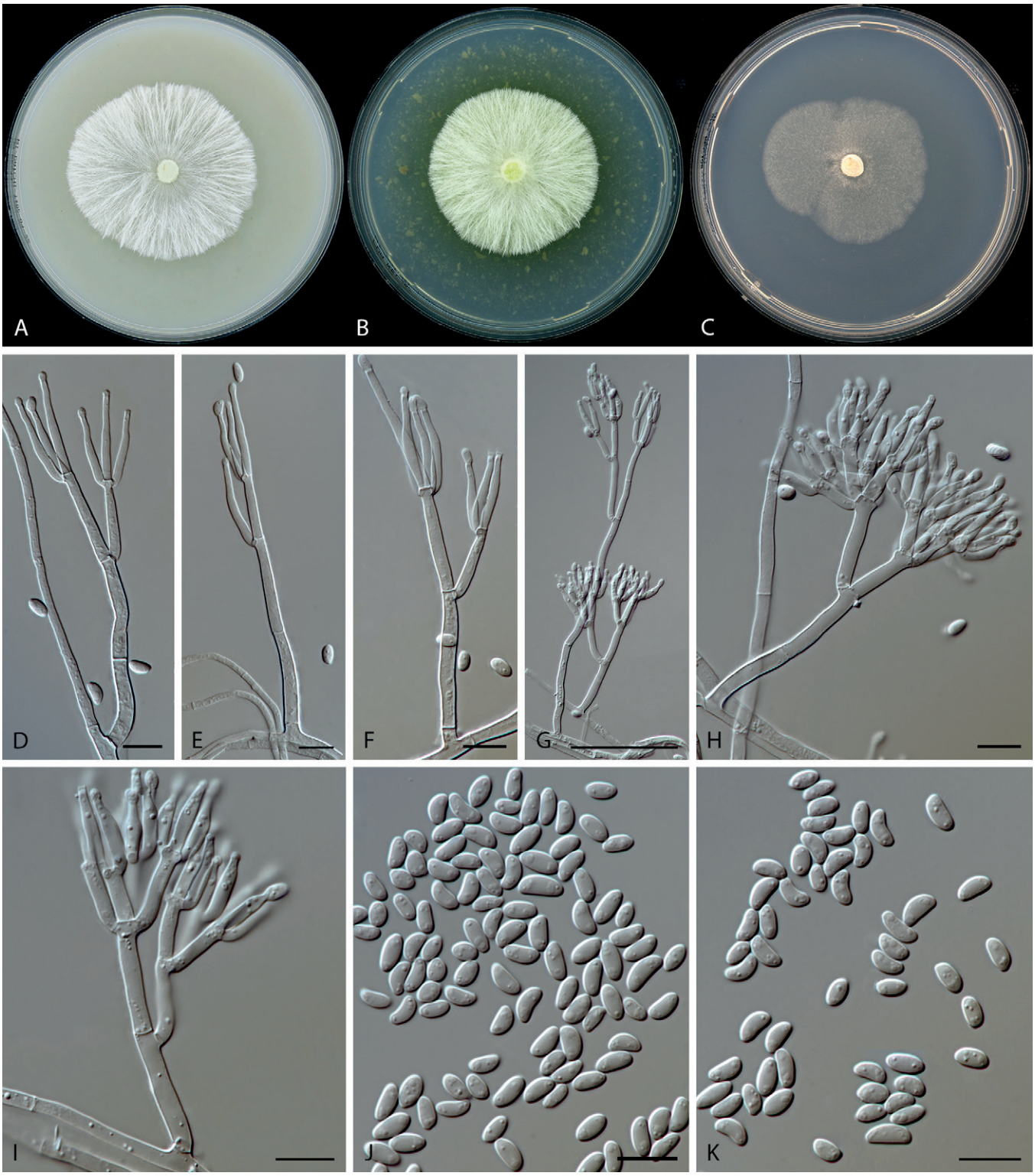

Fig. 25. *Clonostachys kunmingensis* (CBS 101920). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–F.** Primary conidiophores. **G–I.** Secondary conidiophores. **J, K.** Conidia. Scale bars: G = 50 µm; D–F, H–K = 10 µm.

typically divergent, higher level branches and phialides somewhat divergent to almost adpressed; *stipe* 20–120 µm long, 2.5–4.5 µm wide; *penicilli* 30–70 µm long; 25–65 µm wide; *terminal phialides* in loose whorls of up to 6, straight or slightly curved, flask-shaped, widest in the lower third, slightly tapering in the upper part towards the tip, without or with a collarette, (9.0–)10.0–16.7(–28.1) µm long, (1.2–)1.6–2.5(–2.8) µm wide at base, (1.9–)2.1–2.7(–2.8) µm at widest point, (0.9–)1.0–1.3 µm wide near aperture (n = 100); *intercalary phialides* sometimes observed, bearing one or several terminal phialides, conidiogenous pegs to 5 µm long. *Conidia* aseptate, hyaline, smooth, ellipsoid, commonly asymmetric with one more flattened sides, distally broadly rounded, with laterally displaced hilum, (3.7–)4.5–6.3(–7.1) × (2.1–)2.4–3.1(–3.3) µm (av. = 5.4 × 2.7 µm, n = 150), arranged in imbricate chains.

Culture characteristics: Colonies on OA reaching 51–53 mm diam after 7 d at 25 °C in darkness, flat, with fimbriate margin, aerial mycelium abundant, felty, whitish, reverse concolourous. Colonies on PDA reaching 46–50 mm diam, flat, with entire margin, aerial mycelium abundant, felty, pale yellow, with greenish tinge

diffusing into the medium outside the colony, reverse yellowish to light orange. Colonies on SNA reaching 38–45 mm diam, flat, with crenate margin, floccose, aerial mycelium scanty, whitish, reverse concolourous.

Material examined: **China**, Yunnan Province, Kunming City, Songming County, Dashao Village (25°24'N, 102°55'E, 2 750 m alt.), from soil on the forest floor, 24 Aug. 2019, Y. Wang, culture YFCC 892. **Jamaica**, Hanover Parish, Dolphin Head Mt., vic. Askenish, wood, collection and isolation date unknown, collected by D. Korf *et al*., isolated by C.T. Rogerson & G.J. Samuels MJ 946, C.T.R. 71-116, culture CBS 101920.

Notes: *Clonostachys kunmingensis* was described from soil in Kunming City, China, but its holomorph was encountered in the neotropics. Schroers (2001) filed CBS 101920 under *C. solani* due to overall branching patterns of the primary and secondary conidiophores. Based on our phylogenetic analysis, *C. kunmingensis* is closely related to *C. rhizophaga* (Figs 1, 2). Length of phialides in primary conidiophores distinguish both species [(15.4–)17.6–31.2(–32.5) µm in *C. kunmingensis*, (15.6–)22.0–34.2(–48.2) µm in *C. rhizophaga*]. *Clonostachys kunmingensis* (CBS 101920) has different ITS (99.2 % identity, with 4 bp differences), LSU (99.9 %, 1 bp), *RPB2* (97.5 %, 19 bp), *TEF1* (99.6 %, 3 bp), and *TUB2* (98.3 %, 18 bp) sequences when compared with *C. rhizophaga* (CBS 202.37).

Clonostachys longiphialidica L. Zhao, Crous, & Schroers, ***sp. nov.*** MycoBank MB 848488. Fig. 26.

Etymology: Names refers to the long conidiogenous peg of intercalary phialides produced by this species.

Typus: **Venezuela**, Dept. Rio Negro, Cerro de la Neblina, summit camp 5, valley at N base of Pico Phelps, 1 000–1 250 m alt., bark, cloud forest, 12 Apr 1984, G.J. Samuels, G.J.S. 1301 (**holotype** designated here CBS H-25142, ex-type living culture CBS 112.87, = G.J.S. 84-330).

Sexual morph from natural specimen (not shown). *Asci* 46.1–66.3 × 6.6–10.3 µm (n = 11). *Ascospores* 1-septate, hyaline, striate, ellipsoid, 10.4–12.7–15.8 × 3.4–4.2–5.3 µm (n = 27). *Asexual morph. Conidiophores* monomorphic, aggregated in pustules, arising from the agar surface or sparse aerial mycelium, adpressed or with more or less divergent branches, phialides adpressed or somewhat divergent, bi- to quaterverticillate; *stipe* 10–50 µm long, 1.9–3.4 µm wide at base; *penicilli* up to 75 µm long, 60 µm wide; *terminal phialides* in whorls of 2–6, cylindrical or slightly tapering toward the tip, or slightly widening in lower third, frequently with a small collarette, (7.6–)9.2–16.7(–24.2) µm long, (1.5–)1.7–2.8(–2.9) µm wide at base, (2.0–)2.3–3.3(–3.5) µm at widest point, (1.1–)1.2–1.5(–1.6) µm wide near aperture (n = 80); *intercalary phialides* rare, formed below whorls of terminal phialides, with to 8 µm long conidiogenous pegs. *Conidia* aseptate, hyaline, smooth, narrowly ellipsoid to cylindrical, straight or nearly straight, distally broadly rounded, (6.3–)6.7–8.5(–9.3) × (2.2–)2.4–3.0(–3.4), (av. = 7.5 × 2.7 µm, n = 150), arranged in imbricate chains that may collapse into slimy masses.

Culture characteristics: Colonies on OA reaching 40–42 mm diam after 7 d at 25 °C in darkness, with entire margin, aerial mycelium sparse, felty, whitish, reverse concolourous. Colonies on PDA reaching 37–43 mm diam, with entire margin, aerial mycelium moderate, felty to cottony, finely to coarsely granular, white yellowish, reverse pale yellow. Colonies on SNA reaching 39–44 mm diam, with entire margin, aerial mycelium moderate, felty to cottony, whitish, reverse concolourous.

Notes: *Clonostachys longiphialidica* is represented by a single strain isolated from bark in Venezuela. It is phylogenetically different from the closely related *C. vacuolata* (ITS: 96.0 % sequence similarity; LSU: 96.0 %, *RPB2*: 93.6 %, and *TEF1*: 97.6 %). Their morphological differences are discussed under *C. vacuolata*. Specimen G.J.S. 1301 was identified as *C. grammicospora* on the basis of ascospore morphology and characters of the perithecia (Schroers 2001: fig. 62a, c, e, f). However, its ascospores cover a slightly larger length range as Raunkiaer 3103 (isotype of *Nectria grammicospora*, ascospores 10.7–13.1 × 3.8–4.9 µm) and specimen Samuels 3285 (type of *C. grammicospora*, ascospores 9–13.5 × 3.6–5.4 µm) (Samuels 1988b, Schroers 2001). Sexual and asexual morphology suggest classification of *C. longiphialidica* in subgen. *Zebrinella*.

Clonostachys obovatispora L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848489. Fig. 27.

Etymology: Names refers to the obovate conidial shown by this species.

Typus: **Germany**, Frankfurt, Bergen-Enkheim, on living leaves with *Epichloe typhina*, 10 Jun. 2005, R. Kirschner (**holotype** designated here CBS H-25148, ex-type living culture CBS 118752).

Sexual morph unknown. *Asexual morph. Conidiophores* monomorphic, sporodochial. *Sporodochia* appearing at first as distinct white pustules, with time coalescing and with green coloured conidial masses; *phialides* in whorls of 2–4, flask-shaped to cylindrical, widest near the middle, narrowing in the uppermost part, without a visible collarette, (9.2–)9.8–16.4(–17.0) µm long, (1.6–)1.8–2.7(–2.9) µm at base, (2.3–)2.4–3.2(–3.5) at widest point, (0.7–)0.8–1.1(–1.2) µm wide near aperture (n = 60). *Conidia* aseptate, greenish hyaline to pale green, smooth, oblong-ellipsoid or clavate to obovoid, (4.7–)5.8–7.6(–8.2) × (1.7–)2.0–2.5(–2.9) (av. = 6.7 × 2.3 µm, n = 100), arranged in linear chains.

Culture characteristics: Colonies on OA reaching 27–30 mm diam after 7 d at 25 °C in darkness, with slightly lobate margin, aerial mycelium moderate, felty, finely to coarsely granular, whitish, reverse concolourous. Colonies on PDA reaching 26–27 mm diam, with slightly lobate margin, aerial mycelium moderate, felty to cottony, whitish, reverse concolourous. Colonies on SNA reaching 19–22 mm diam, flat, with entire margin, membranous without aerial mycelia, colourless, reverse colourless.

Notes: According to phylogenetic inferences in the present study (Figs 1, 2), *C. obovatispora* is closely related to *C. epichloe*, and *C. miodochialis*. However, *C. obovatispora* differs from *C. epichloe* (CBS 101037) in ITS (98.8 % identity, with 6 bp differences), LSU (99.3 %, 5 bp), *RPB2* (91.3 %, 66 bp), *TEF1* (95.8 %, 34 bp), and *TUB2* (95.1 %, 50 bp) sequences; *C. obovatispora* differs from *C. miodochialis* (CBS 997.69) in ITS (98.4 % identity, with 8 bp differences), LSU (99.5 %, 4 bp), *RPB2* (91.7 %, 62 bp), *TEF1* (96.1 %, 32 bp), and *TUB2* (95.3 %, 47 bp) sequences. Morphologically, *C. obovatispora* differs from *C. epichloe* and *C. miodochialis* in producing shorter phialides [(9.2–)9.8–16.4(–17.0) µm in *C. obovatispora vs* (7–)12–17(–29) µm in *C. epichloe*], and narrower conidia [(1.6–)2.2–2.6–2.8 (–3.6) µm in *C. obovatispora*

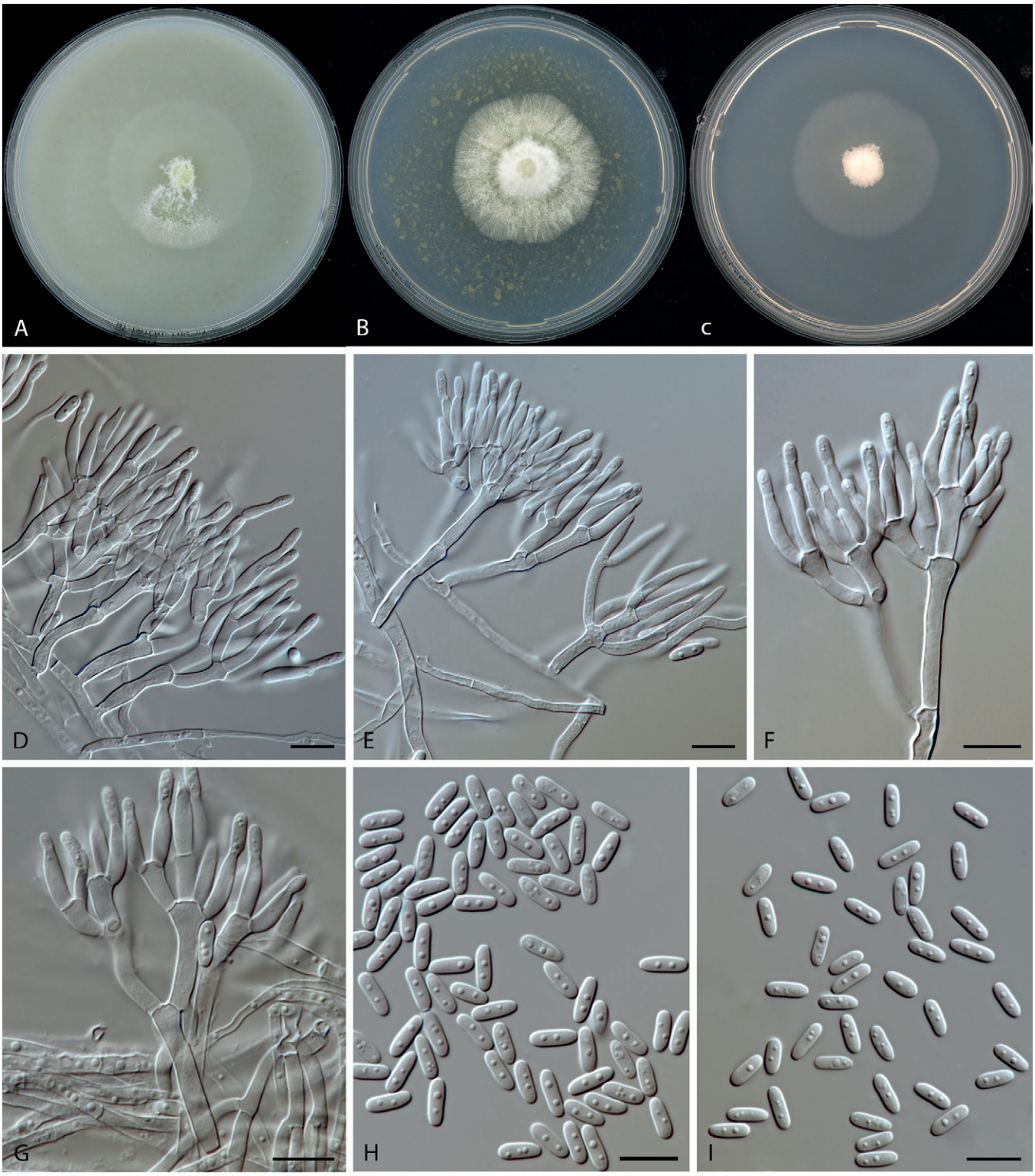

Fig. 26. *Clonostachys longiphialidica* (ex-type CBS 112.87). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–G.** Conidiophores. **H, I.** Conidia. Scale bars = 10 µm.

vs (1.8–)2.6–3(–3.4) µm in *C. miodochialis*)]. However, overall nature of morphological characters, *i.e.*, occurrence of sporodochia, greenish pigmentation of conidial masses and shape of conidia, is similar in these closely related species and aligns *C. obovatispora* well into the morphological concept of subgenus *Astramata*.

Clonostachys palmae L. Zhao, Crous & Schroers, ***sp. nov.*** MycoBank MB 848490. Fig. 28.

Etymology: Name refers to palm, the host from which the ex-type culture of this fungus was isolated.

Typus: **Indonesia**, Sulavesi, Eastern Dumoga-Bone Nat. Park, between Maddison's Camp, from palm leaves, 5 Oct. 1985, G.J. Samuels, 2156, culture G.J.S. 85-155 (**holotype** designated here CBS H-25153, ex-type culture CBS 119.87).

Sexual morph known from natural specimen (not shown). *Asci* 45–67.5 × 7.0–10.8 µm. *Ascospores* striate, ellipsoid with gently

Fig. 27. *Clonostachys obovatispora* (ex-type CBS 118752). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D, E.** Sporodochia. **F, G.** Phialides. **H, I.** Conidia. Scale bars = 10 µm.

tapering ends, 1-septate, 10.0–14.5 × 3.0–5.4 µm. *Asexual morph*. *Conidiophores* dimorphic. *Primary conidiophores* mononematous, arising from either the aerial mycelium or the agar surface, either unbranched, acremonium-like or verticillium-like, mono- to terverticillate, with divergent branches and phialides diverging at more or less acute angles; *stipe* 40–180 µm long, 2.4–4.6 µm wide at base; *penicilli* 50–100 µm high; *phialides* in apical whorls of 2–4, straight, cylindrical, slightly tapering towards the tip, with a minute visible collarette, (21.0–)22.4–42.2(–48.8) µm long, (1.6–)1.8–2.8(–3.0) µm wide at base, 1.2–1.8(–2.0) µm wide near aperture (n = 70). *Secondary conidiophores* broadly penicillate, arising from the agar surface or aerial mycelium ter- to quinquiesverticillate, aggregated in pustules or sporodochia; *phialides* slightly divergent or adpressed, in whorls of 2–4, flask-shaped, widest in the lower third or almost cylindrical, slightly tapering in the upper part towards the tip, without a visible collarette, (9.2–)11.0–19.0(–21.6) µm long, (1.5–)1.6–2.6(–2.9) µm wide at base, (2.1–)2.2–2.9(–3.1) at widest point, (1.0–)1.1–1.7(–1.8) µm wide near aperture (n = 80). *Conidia*

Fig. 28. *Clonostachys palmae* (ex-type CBS 119.87). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–F.** Primary conidiophores. **G, H.** Secondary conidiophores. **I, J.** Conidia. Scale bars = 10 µm.

aseptate, hyaline, smooth, ellipsoid, some slightly curved or asymmetric with one more flattened side, with a laterally displaced hilum, (4.5–)5.3–8.2(–10.2) × (2.4–)2.7–3.2(–3.6) (av. 6.5 × 2.9 µm, n = 150), arranged in imbricate chains.

Culture characteristics: Colonies on OA reaching 49–53 mm diam after 7 d at 25 °C in darkness, flat, with entire margin, aerial mycelium moderate, finely to coarsely granular, felty to cottony, whitish, reverse concolourous. Colonies on PDA reaching 54–61 mm diam, flat, with entire margin, aerial mycelium abundant, cottony, pale yellow, with greenish tinge diffusing into the medium outside the colony, reverse yellowish. Colonies on SNA reaching 41–45 mm diam, flat, with crenate margin, aerial mycelium moderate, felty, finely granular, whitish, reverse concolourous.

Notes: Measurements provided for asci and ascospores and description of the sexual morph are derived from observations and notes by G. Samuels. No specimen but a dried culture was

encountered when Schroers later re-examined specimen G.J. Samuels 2156. Schroers (2001) filed this specimen under *C. pseudostriata*. According to the multi-gene phylogenetic inference, phylogenetic relatedness of *C. palmae* to *C. pseudostriata* is highly supported (Figs 1, 2). However, *C. palmae* (CBS 119.87) has clearly different ITS (98.6 % identity, with 7 bp differences), LSU (99.7 %, 2 bp), *RPB2* (97.5 %, 19 bp), *TEF1* (98.1 %, 15 bp), and *TUB2* (97.0 %, 31 bp) sequences compared to *C. pseudostriata* (CBS 120.87). Striae formed on the surface of ascospores of *C. pseudostriata* consist of warts that are arranged in rows (Schroers 2001: fig. 44k), while ascosporal striae of species of subg. *Zebrinella* are continuous.

Clonostachys parasporodochialis L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848491. Fig. 29.

Etymology: Named after its close morphological and phylogenetic relationship to *C. sporodochialis*.

Typus: **Venezuela**, unknown, terminal branchlet of recently dead tree, Nov.–Dec. 1990, G.J. Samuels, 7760, culture G.J.S. 90-192 (**holotype** designated here CBS H-25156, ex-type culture CBS 192.93).

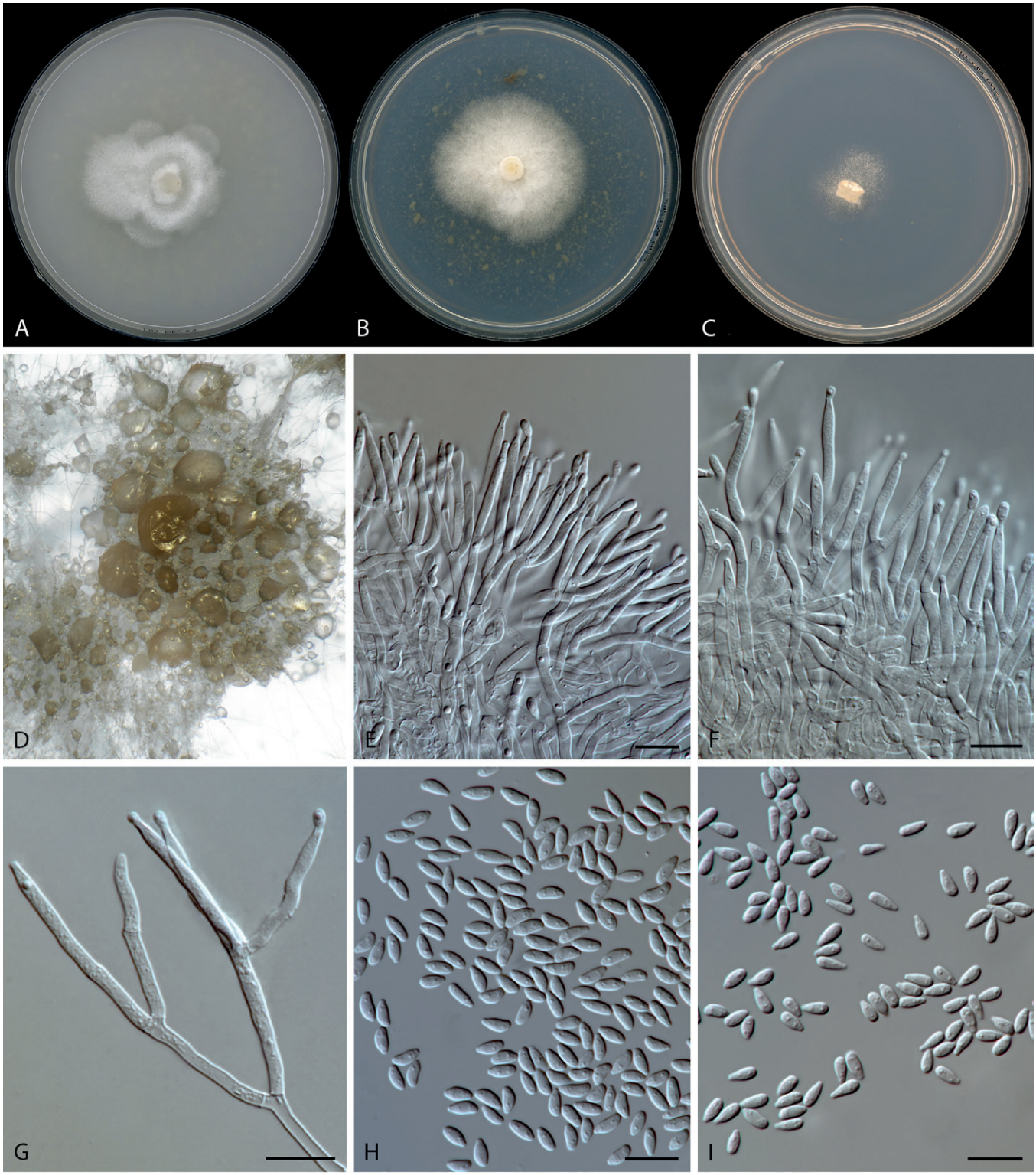

Fig. 29. *Clonostachys parasporodochialis* (ex-type CBS 192.93). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–F.** Sporodochia. **G.** Phialides. **H, I.** Conidia. Scale bars = 10 µm.

Sexual morph known from natural specimen (not shown). *Asci* 57.7–84.7 × 9.2–12.6 µm (n = 16). *Ascospores* 1-septate, hyaline, spinulose, ellipsoid, 8.6–13.0 × 2.6–4.4 µm. *Asexual morph. Conidiophores* monomorphic, sporodochial, penicillate, ter- to quaterverticillate, branches of conidiophores in young sporodochial pustules divergent, in developed sporodochia adpressed; *phialides* in apical whorls of 2–4, also arising from lower levels, slightly divergent or almost adpressed, straight, hardly narrowing towards the tip, almost cylindrical, without visible collarette, (7.5–)11.3–24.3(–28.4) µm long, (1.5–)1.7–2.3(–2.5) µm wide at base, (0.7–)0.8–1.1(–1.2) µm wide near aperture (n = 60). *Conidia* aseptate, hyaline, smooth, oblong-ellipsoid or obovoid, some minutely curved, asymmetric with one more flattened side, distally broadly rounded, with laterally displaced hilum, (3.5–)4.5–6.6(–8.2) × (1.8–)2.0–2.4(–2.7) µm (av. = 5.2 × 2.2 µm, n = 150), arranged in imbricate chains that may collapse into slimy masses.

Culture characteristics: Colonies on OA reaching 34–52 mm diam after 7 d at 25 °C in darkness, flat, irregular margin, aerial mycelium moderate, felty to cottony, whitish, reverse concolourous. Colonies on PDA reaching 36–48 mm diam, with entire margin, aerial mycelium moderate, felty, whitish, reverse concolourous. Colonies on SNA reaching 21–24 mm diam, flat, irregular margin, aerial mycelium sparse, felty, finely granular, whitish, reverse concolourous.

Notes: *Clonostachys parasporodochialis* forms a sister lineage to *C. sporodochialis* (Figs 1, 2). Substitutions in sequences distinguish both species. *Clonostachys parasporodochialis* (CBS 192.93) has clearly different ITS (99.0 % identity, with 5 bp differences), LSU (99.6 %, 3 bp), *RPB2* (95.8 %, 32 bp), and *TEF1* (99.3 %, 6 bp) sequences when compared with *C. sporodochialis* (CBS 101921). However, both species produce morphologically similar sporodochia in cultuers and no mononematous dimorphic conidiophores.

Clonostachys penicillata L. Zhao, Crous & Schroers, ***sp. nov.*** MycoBank MB 848492. Fig. 30.

Etymology: Name refers to its penicillate conidiophores.

Typus: **Germany**, Freiburg, forest soil, unknown date and collector (**holotype** designated here CBS H-25145, ex-type living culture CBS 729.87).

Sexual morph unknown. *Asexual morph. Conidiophores* mono-morphic, mononematous, penicillate, arising from the colony surface or sparse aerial mycelium, frequently branched, forming independent side-branches, branches bi- to quaterverticillate, divergent at acute angles, sometimes with setose extensions; *stipes* up to 130 µm high, 4.0 µm wide at base; branching part *ca.* 140 µm high, *penicilli* of independent units around 30–100 µm high, up to 90 µm wide; *terminal phialides* in adpressed whorls of up to six, narrowly flask-shaped, (7.0–)8.0–11.0(–12.0) µm long, (1.2–)1.6–2.3(–2.5) µm wide at base, (1.9–) 2.0–2.8 µm at widest point, 0.8–1.2(–1.3) µm wide near aperture (n = 50); *intercalary phialides* formed solitarily below whorls of terminal phialides, conidiogenous pegs to 4 µm long. *Conidia* aseptate, hyaline, smooth, ellipsoid to cylindrical, almost straight, with or without laterally displaced hilum, (4.5–)5.0–6.8(–7.6) × (1.6–)1.7–2.2(–2.4) µm (av. = 5.9 × 2.0 µm, n = 100), arranged in imbricate chains or columns.

Culture characteristics: Colonies on OA reaching 37–41 mm diam after 7 d at 25 °C in the darkness, with entire margin, aerial mycelium moderate, felty to cottony, whitish, reverse concolourous. Colonies on PDA reaching 35–38 mm diam, with crenate margin, aerial mycelium moderate, felty to cottony, yellowish white, reverse concolourous. Colonies on SNA reaching 29–30 mm diam, with entire margin, aerial mycelium sparse, felty, whitish, reverse concolourous.

Additional materials examined: **Netherlands**, Gelderland Province, Schovenhorst near Putten, decaying wood, unknown date and collector, culture CBS 653.70; Utrecht Province, Bilthoven, soil, 2017, B. de Bruin, culture CBS 148211 = JW34009.

Notes: According to the phylogenetic analyses in the current study, *C. penicillata* and *C. compactiuscula* form a statistically supported sister group relationship (Figs 1, 2). *Clonostachys penicillata* (CBS 729.87) and *C. compactiuscula* (CBS 913.97) share a low *RPB2* (96.8 %, 24 bp) and *TEF1* (98.0 %, 16 bp) sequence similarity and a higher ITS (99.6 % identity, with 2 bp differences) and LSU (99.5 %, 4 bp) similarity. Slightly smaller conidia in *C. penicillata* may distinguish these two closely related species; av. 5.9 × 2.0 µm in *C. penicillata*, *vs* av. 6.6 × 2.2 µm in *C. compactiuscula*. The two species occupy an isolated phylogenetic position (Fig. 2) as relatedness to the morphologically differing *C. ralfsii* is not supported (Figs 1, 2). *Clonostachys compactiuscula* occurs in temperate and tropical regions. However, its sexual morph is often seen in North America, while sexual morphs of the majority of *Clonostachys* species are typically seen in (sub)tropical regions.

Clonostachys reniformis L. Zhao & Crous, ***sp. nov.*** MycoBank MB 848493. Fig. 31.

Etymology: Name refers to the reniform shape of its conidia.

Typus: **Unknown**, substrate, date and collector unknown (**holotype** designated here CBS H-25152, ex-type culture CBS 695.86).

Sexual morph unknown. *Asexual morph. Conidiophores* dimorphic. *Primary conidiophores* mononematous, formed throughout the colony, dominating towards the margin, arising from the agar surface or from aerial hyphae, narrowly penicillate, divergent or adpressed, mono- to terverticillate; *stipe* 40–150 µm long, 2.5–4.0 µm wide at base; *penicilli* to 40–120 µm high; *phialides* in apical whorls of to four, also solitary, straight, cylindrical, slightly tapering towards the tip, with a visible collarette, (18.4–)19.5–35.6(–39.5) µm long, (1.4–)1.6–2.5(–2.9) µm wide at base, (1.0–)1.2–1.6(–1.7) µm wide near aperture (n = 60). *Secondary conidiophores* broadly penicillate, mostly formed from strands of aerial mycelium, mononematous to sporodochial, ter- to quaterverticillate or more frequently branched, branches almost divergent or sometimes adpressed, phialides almost adpressed; *stipe* 20–70 µm long, 2.0–4.5 µm wide at base; *penicilli* divergently branched, up to 80 µm high, 30–90 µm wide; *terminal phialides* in loose whorls of 2–5, straight to slightly curved, flask-shaped, widest in the lower third or almost cylindrical, slightly tapering in the upper part towards the tip, without a visible collarette (10.2–)10.8–18.0(–18.6) µm long, (1.3–)1.6–2.5(–2.7) µm wide at base, (2.1–)2.3–2.8(–3.0) µm at widest point, 1.0–1.3 µm wide near aperture (n = 50); *intercalary phialides* formed rarely, solitarily below whorls of terminal phialides. *Conidia* aseptate, hyaline, smooth, reniform, curved, some asymmetric with one more flattened side with a laterally displaced hilum, distally broadly rounded, (4.0–)4.4–6.3(–8.2) × (2.2–)2.4–3.2(–3.6) µm (av. = 5.1 × 2.7 µm, n = 150), arranged in imbricate chains.

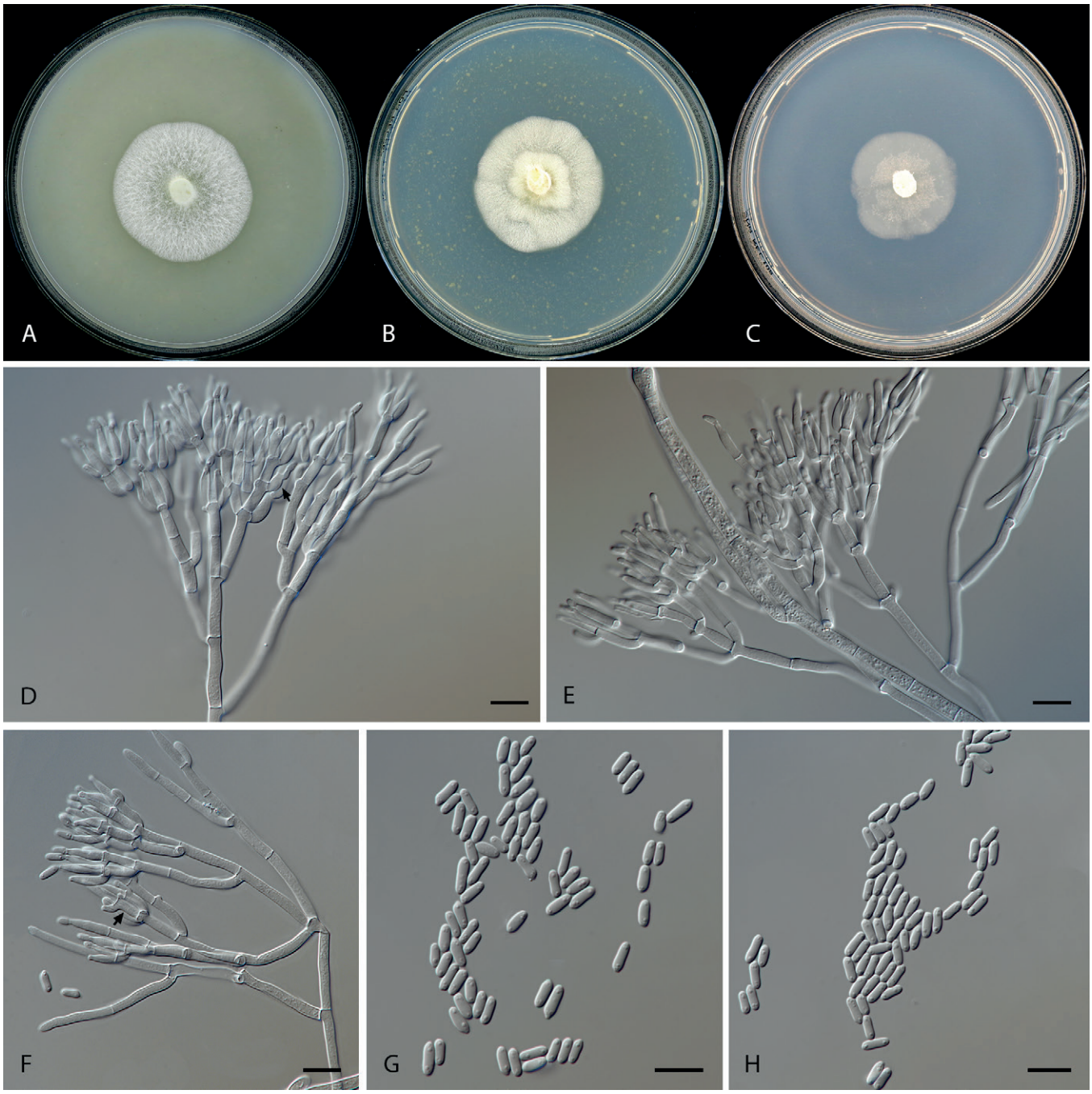

Fig. 30. *Clonostachys penicillata* (ex-type CBS 729.87). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–F.** Conidiophores. **G, H.** Conidia. Black arrows indicate intercalary phialides. Scale bars = 10 µm.

Culture characteristics: Colonies on OA reaching 46–48 mm diam after 7 d at 25 °C in darkness, flat, with crenate margin, aerial mycelium moderate, finely to coarsely granular, felty to cottony, yellowish white to pale yellow, reverse yellowish. Colonies on PDA reaching 46–51 mm diam, flat, with crenate margin, aerial mycelium abundant, felty, pale yellow, with greenish tinge diffusing into the medium outside the colony, reverse yellowish. Colonies on SNA reaching 35–37 mm diam, flat, with entire margin, aerial mycelium sparse, finely granular, felty, whitish, reverse concolourous.

Notes: According to the phylogenetic analysis in the current study, *C. reniformis* groups with *C. viticola* and *C. swieteniae* (Figs 1, 2). *Clonostachys reniformis* differs from *C. viticola* (CAA 944) in *TUB2* (98.9 % identity, with 5 bp differences), and from *C. swieteniae* in ITS (99.4 % identity, with 3 bp differences) and LSU (99.5 % identity, 4 bp). Morphologically, *C. reniformis* differs from *C. viticola* in producing longer primary conidiophores (stipe 40–150 µm, penicilli 40–120 µm in *C. reniformis vs* 70.5 ± 17.9 µm in *C. viticola*). *Clonostachys reniformis* can be distinguished from *C. swieteniae* by its shorter and narrower stipes of secondary conidiophores (20–70 × 2.0–4.5 *vs* 130–200 × 5.0–8.0 µm), and curved conidia with clearly laterally displaced hila, while hila are typically central in *C. swieteniae* (Perera *et al*. 2020).

Clonostachys rosea (Link) Schroers *et al*., Mycologia 91: 369. 1999.

Basionym: *Penicillium roseum* Link, Mag. Gesell. Naturf. Freunde, Berlin 7: 37. 1816.

Synonyms: *Gliocladium roseum* Bainier, Bull. Soc. Mycol. Fr. 23: 111. 1907.

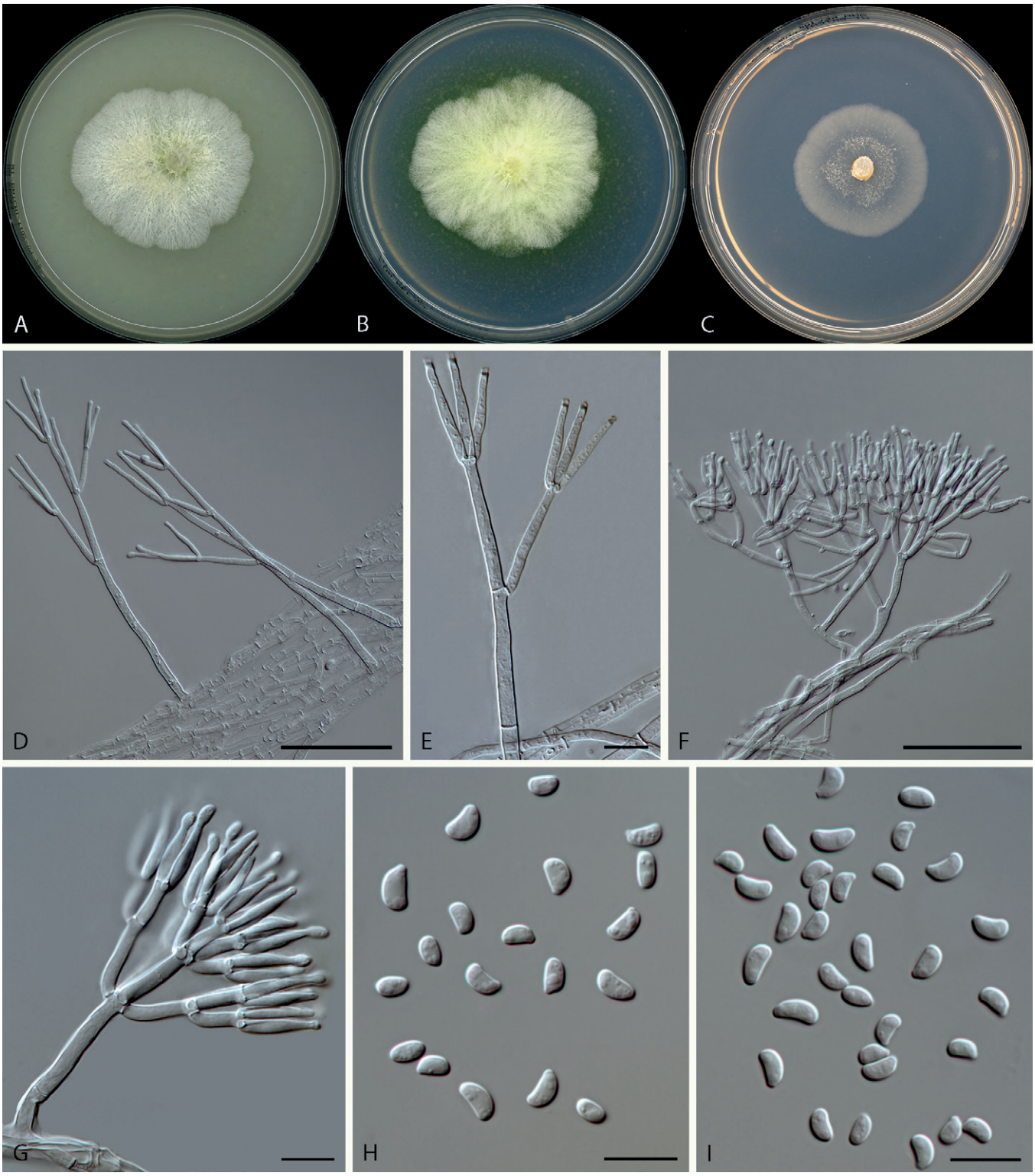

Fig. 31. *Clonostachys reniformis* (ex-type CBS 695.86). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D, E.** Primary conidiophores. **F, G.** Secondary conidiophores. **H, I.** Conidia. Scale bars: D, F = 50 *µm*; E, G–I = 10 µm.

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Description and illustration: Schroers (2001).

Typus: **Netherlands**, soil, on buried sclerotia of *Sclerotinia minor*, date unknown, A. van Zaayen & W. Gams (**neotype** CBS H-7917, ex-type culture CBS 710.86).

Additional materials studied: **China**, Guizhou, Qianlingshan Park, spider, Jun. 2016, W.H. Chen, culture QLS0625clo (type of *Clonostachys aranearum*). **France**, rotten cardboard, date unknown, G. Bainier, culture CBS 100502 (type of *Gliocladium roseum* Bainier). **USA**, on decaying bulb of *Lilium auratum*, Jan. 1955, E.B. Smalley, culture CBS 194.57 (ex-type strains of *Nectria gliocladioides* Smalley & Hansen); New York, causing lesions on stored carrot roots, date unknown, W.E. Rader, culture CBS 226.48 (ex-type strain of *Gliocladium aureum*).

Notes: *Clonostachys rosea* is the most commonly isolated species in the genus, with complex taxonomical and nomenclatural history (Schroers 2001). Based on our phylogenetic analyses, the recently described *C. aranearum* (Chen *et al*. 2016) is conspecific with *C. rosea* and included as synonym of *C. rosea*.

Clonostachys vacuolata L. Zhao, Crous & Schroers, ***sp. nov.*** MycoBank MB 848494. Fig. 32.

Etymology: Name refers to vacuoles formed by this species inside phialides.

Typus: **Venezuela**, Edo. Miranda: Parque Nacional Guatopo, trail between Agua Blanca and La Cruceta, 10°03'N, 66°26'W N, 500–600 m alt., bark, 27–30 Nov. 1990, G.J. Samuels VE-7664, B. Hein & S.M. Huhndorf (**holotype** designated here CBS H-25143, ex-type living culture CBS 191.93).

Sexual morph from natural specimen (not shown). *Asci* 48–74.4 × 9.5–16.6 µm. *Ascospores* 1-septate, hyaline, striate, ellipsoid, 13.2–14.7–17.6 × 4.4–5.4–6.3 µm (n=23). *Asexual morph*. *Conidiophores* monomorphic, densely aggregated, confluent, formed in pustules, not sporodochial, arising from the agar surface or sparse aerial mycelium, branches divergent, bi- to quaterverticillate, phialides somewhat divergent; *stipe* 10–55 µm long, 1.8–3.8 µm wide at base; *penicilli* 20–65 µm high, up to 70 µm wide, frequently higher than the length of the stipe; *terminal phialides* generally in whorls of 2–5, straight or slightly curved, cylindrical, or flask-shaped, with vacuoles, widest in the lower third or middle, slightly tapering in the upper part towards the tip, collarette absent, (7.0–)9.4–21.8(–25.7) µm long, (1.5–)1.7–2.4(–2.6) µm wide at base, (2.1–)2.2–2.9(–3.0) µm at widest point, (1.0–)1.1–1.5(–1.6) µm wide near aperture (n = 100); *intercalary phialides* rare, formed below whorls of terminal phialides. *Conidia* aseptate, hyaline, smooth, ellipsoid to obovoid, straight, or both ends broadly rounded, without visible hilum, (5.1–)5.4–6.8(–7.7) × (2.5–)2.7–3.1(–3.3) (av. = 6.0 × 2.9 µm, n = 100), arranged in imbricate chains that may collapse into slimy masses.

Culture characteristics: Colonies on OA reaching 37–40 mm diam after 7 d at 25 °C in darkness, with entire margin, aerial mycelium sparsely developed, felty, finely to coarsely granular, yellowish white, reverse concolourous. Colonies on PDA reaching 38–45 mm diam, with entire margin, and aerial mycelium moderate, felty, finely to coarsely granular, pale yellow, reverse concolourous. Colonies on SNA reaching 35–37 mm diam, with entire margin, aerial mycelium sparse, felty, whitish, reverse concolourous.

Notes: *Clonostachys vacuolata* clusters together with *C. longiphialidica*, *C. pallens*, *C. venezuelae* and *C. ellipsoidea* (Figs 1, 2). It can be morphologically distinguished from *C. longiphialidica* by producing shorter conidia [(5.1–)5.4–6.8(–7.7) µm *vs* (6.3–)6.7–8.5(–9.3) µm]. *Clonostachys vacuolata* differs from *C. ellipsoidea* in producing longer and narrower conidia (av. = 6.0 × 2.9 µm *vs* av. = 5.3 × 3.5 µm). A morphological comparison with *C. vacuolata* and *C. pallens* is difficult, because *C. palllens* was only described based on a sexual morph (Forin *et al.* 2020), while we observed only asexual morph characters in culture although working with the same strain. Schroers (2001) filed the specimen incorrectly under *C. grammicospora*, as the longer ascospores distinguish VE-7664 from this species. Sexual and asexual morphology suggest classification of *C. vacuolata* in subgen. *Zebrinella.*

Clonostachys venezuelae L. Zhao, Crous & Schroers, ***sp. nov.*** MycoBank MB 848495.

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

Typus: **Venezuela**, Edo Merida, 7 km NE of Merida, *ca*. 4 km inside San Javier del Valle resort, 24 Jul. 1971, K.P. Dumont & G.J. Samuels (**holotype** designated here CBS H-25240, ex-type living culture CBS 107.87); specimen VE 2865 (NY), culture C.T.R. 71-349.

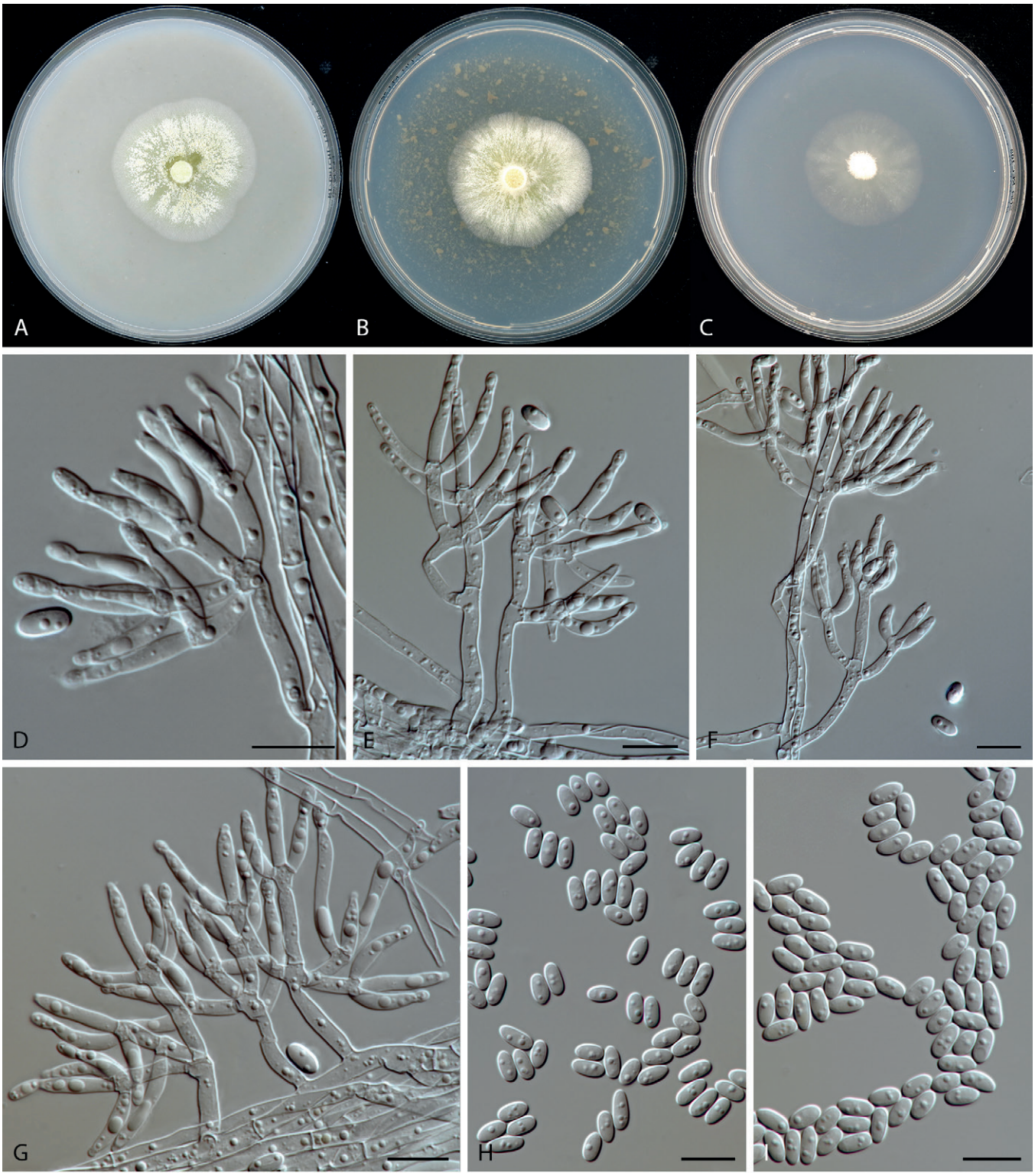

Fig. 32. *Clonostachys vacuolata* (ex-type CBS 191.93). **A–C.** Colonies on OA, PDA and SNA after 7 d at 25 °C. **D–G.** Conidiophores. **H, I.** Conidia. Scale bars = 10 µm.

Sexual morph known from natural specimen (not shown). *Asci* 63.0–90.0 × 10.0–16.0 µm (n = 14). *Ascospores* 1-septate, hyaline, striate, ellipsoid, (16.0–)17.9(–21.0) × 5.0–6.1–7.0 µm (n = 22). *Asexual morph* (not shown), from dried CMD culture, obtained from isolated ascospores. *Conidia* (8.3–)13.1(–18.8) × (3.8–)5.5(–6.8) µm (*fide* Schroers) or (5.0–)10.3(–18.0) × (3.0–)5.0(–7.0) µm (*fide* Samuels). Deposited CBS cultures not sporulating. *Clonostachys venezuelae* differs from its closest phylogenetic neighbours *C. pallens* and *C. ellipsoidea* by unique nucleotide substitutions and indels in the five investigated loci (see direct sequence comparisons deposited at doi: 10.6084/m9.figshare.22894592): *C. venezuelae* and *C. pallens*: ITS position 24 (C), 43 (C), 44 (T), 45 (A, insertion), 52 (C), 53 (gap), 67 (gap), 111 (C), 142 (G), 143 (A), 149(C), 153 (C), 157 (C), 158 (C), 162 (gap), 171 (C), 192 (C), 207 (A, insertion). *C. venezuelae* and *C. ellipsoidea*: ITS position 44 (T, insertion), 52 (C), 67 (gap), 69 (A), 111 (C), 143 (A), 150 (T), 153 (C), 158 (C), 162 (gap), 171 (C), 172 (T), 191 (C), 200 (A), 207 (A, insertion), 277 (T), 359 (C), 403 (T), 429 (A), 430 (G), 431 (C), 494

(C), 496 (A), 516 (G), 519 (C), 522 (C), 548 (G), 552 (C, insertion); LSU position 643 (A), 704 (C), 987 (A), 990 (A), 991 (G), 1 005 (T), 1 007 (T), 1 008 (C), 1 042 (T), 1 045 (T), 1 065 (C); *RPB2* position 1 398 (T), 1 407 (C), 1 422 (T), 1 493 (G), 1 599 (A), 1 614 (T), 1 620 (T), 1 650 (C), 1 701 (C), 1 710 (G), 1 719 (A), 1 743 (G), 1 779 (A), 1 782 (C), 1 788 (T), 1 803 (A), 1 804 (C), 1 809 (C), 1 812 (A), 1 833 (C), 1 862 (C), 1 870 (C), 1 900 (G), 1 916 (T), 2 002 (C), 2 011 (G), 2 047 (T), 2 105 (C), 2 126 (C); *TEF1* position 2 156 (G), 2 165 (T), 2 174(C), 2 180 (C), 2 186 (T), 2 198 (C), 2 255 (T), 2 375 (T), 2 391 (A), 2 392 (A), 2 *3*93 (G), 2 414 (C), 2 416 (G), 2 426 (T), 2 432 (C), 2 447 (T), 2 454 (T), 2 468 (T), 2 469 (C), 2 591 (C), 2 528 (C), 2 585 (T), 2 645 (C), 2 652 (C), 2 748 (T), 2 749 (T), 2 752 (C), 2 840 (C), 2 846 (T), 2 914(A); *TUB2* position 3 196 (A), 3 199 (C), 3 205–3 206 (gap), 3 207 (A), 3 209 (gap), 3 219 (G), 3 223 (C), 3 225 (C), 3 236 (A), 3 241 (G), 3 246 (G), 3 249 (T), 3 250 (T), 3 252 (A), 3 260 (T), 3 268 (A), 3 282 (T), 3 356 (C), 3 416 (C), 3 620 (C), 3 684 (A), 36 93 (T), 3 705 (C), 3 744 (C), 3 816 (C).

Notes: The CBS culture of *C. venezuelae* does not sporulate anymore, but the phylogenetic analyses show no similarity of this culture with other sequenced cultures (Figs 1, 2). However, the asexual morph is known from a dried culture filed together with specimen VE 2865 studied by G.J. Samuels (see Samuels 1988b) and Schroers (2001). Both filed the specimen under *C.* (*Nectria*) *subquaternata*. Sexual and asexual morphology suggest classification of *C. venezuelae* in subgen. *Zebrinella.*

DISCUSSION

In this study, we investigated 420 strains identified as *Clonostachys* and allied genera based on morphological characters and phylogenetic analyses. The current study presents the largest sampling of *Clonostachys* ever subjected to multi-locus sequencing analyses and provides a comprehensive phylogenetic backbone and framework for future studies of *Clonostachys*.

Most cultures examined previously by Schroers *et al*. (1999b) and Schroers (2000, 2001) were incorporated and newly compared with so far unstudied isolates. Based on phylogenetic analyses of five loci, ITS, LSU, *RPB2*, *TEF1*, *TUB2*, and morphological characters, a rich set of taxa were identified as new species of *Clonostachys*, *Mycocitrus*, *Nectriopsis*, and *Sesquicillium* (Fig. 1) and our data support that they all belong to the *Bionectriaceae*. *Sesquicillium microsporum* differs from other *Sesquicillium* species in size ranges of phialides and conidia (Samuels 1989) and a myxomyceticolous lifestyle (Rogerson & Stephenson 1993). Our phylogenetic analyses (Fig. 1) support an earlier hypothesis that *S. microsporum* is a species of *Nectriopsis* (Schroers 2001), which accommodates also other myxomyceticolous species (Samuels 1988a).

We clarified that *Clonostachys* accommodates the subgenera *Astromata*, *Bionectria*, *Myronectria* and *Zebrinella* with 19 new and 49 known species, while the genus *Sesquicillium*, with three new species and eight new combinations was resurrected for subgenera *Epiphloea* and *Uniparietina*. Although the purpose of describing subgenera in *Clonostachys*/*Bionectria* was to delineate groups of species with similar morphological characters, Schroers (2001) reported that some but not all subgenera are mono- or paraphyletic based on ITS and *TUB2* sequences.

In the present study, the subgenus *Astromata* (Clade V in Fig. 1) is comprised of six species, including known species *C. epichloe*, *C. eriocamporesii*, *C. miodochialis* and *C. oligospora*, which agrees with the suppositions in the previous study of Schroers (2001), and new species *C. fujianensis* and *C. obovatispora*. Most species of this group form perithecia either directly on their substrata such as fruiting bodies of other fungi or on clearly reduced stromata, sporodochial asexual morphs and greenish pigmented conidial masses, and conidia with a somewhat laterally protruding hilum, that results in a somewhat clavate spore shape (Schroers 2001).

Within subgenus *Bionectria* (Clade VI in Fig. 1), the known species *C. compactiuscula*, *C. divergens*, *C. ralfsii*, *C. rogersoniana* and *C. samuelsii* and the new species *C. bambusae*, *C. cylindrica*, *C. hongkongensis* and *C. penicillata* accumulate numerous nucleotide differences in sequences (Figs 1, 2) when compared to others. All these species cluster outside a well-supported clade comprising the above discussed core group with homogeneous species of the subgenus *Bionectria* characterised by dimorphic conidiophores (Fig. 1: 90 % / 99 % / 1; Fig. 2: 92 % / 98 % / 0.96). Also see the discussion under the taxonomic treatment of *Clonostachys* above.

The subgenus *Myronectria* (Clade III in Fig. 1), comprising two species, *C. pityrodes* and *C. buxicola*, is fully supported (Fig. 1: 100 % / 100 % / 1; Fig. 2: 100 % / 100 % / 1). It accommodates an individual branch within the supported *Clonostachys* clade and is unrelated to the other subgenera. Schroers (2001) erected subgenera *Myronectria* and *Astromata* due to the circumstance that they produce synnematous conidiophores and rather dark greenish pigmented conidial masses. *Clonostachys pityrodes* is also the only *Clonostachys* species forming somewhat curved, broadly rounded, and comparatively large ascospores.

The subgenus *Zebrinella* forms a monophyletic lineage in *Clonostachys* (Clade IV in Fig. 1: 93 % / 98 % / 1). Our phylogenetic analyses agree well with the previous study of Schroers (2001), who placed *C. chlorina*, *C. grammicospora*, *C. grammicosporopsis*, *C. intermedia*, *C. levigata*, *C. lucifer* and *C. subquaternata* into the subgenus *Zebrinella*. The subgenus, is, however, also well-supported on the basis of morphological characters. Clearly striate ascospores and perithecial walls showing two regions distinguish it from species of the subgenus *Bionectria* typically forming warted ascospores and perithecial walls consisting of three regions.

The subgenus *Epiphloea* is shown to be polyphyletic in the present study (Clades labelled I in Fig. 1), with the majority of species now accepted in *Sesquicillium*, while the sesquicillium-like *Clonostachys setosa* is accepted in *Clonostachys sensu stricto*. The subgenus *Uniparietina* (Clade II in Fig. 1) is represented by *Sesquicillium buxi* in the present study.

Species of *Sesquicillium* are characterised by macronematous conidiophores that form typically one, rarely two, intercalary phialides just below a single terminal phialide in their penicilli. They should be distinguished from intercalary phialides typically in micronematous conidiophores that look like hyphal cells possessing a lateral conidiogenous peg, for example, in some *Acremonium* (Gams 1971) and *Nectria sensu stricto* species (Seifert 1985). This revision, however, shows that high numbers of intercalary phialides are not only formed by species of *Sesquicillium* but also by *C. setosa* and *Clonostachys* sp. CBS 496.90, both classified therefore in subgenus *Epiphloea* by Schroers (2001). In addition, there are also quite many *Clonostachys* species producing intercalary phialides at least sporadically [see *C. australiana*, *C. longiphialidica*, *C. vacuolata*, *C. ellipsoidea*, *C. penicillata* (this study), *C. agarwalii*, *C. verrucispora*, *C. compactiuscula*, *C. rogersoniana*, *C. grammicospora*, *C. levigata*, and *C. chlorina* (Schroers 2001)]. It is thus the occurrence of intercalary phialides that link the genera *Clonostachys* and *Sesquicillium* morphologically (see also

Schroers 2000: fig. 5). Because *Clonostachys* and *Sesquicillium* are phylogenetically closely related sister genera (Fig. 1) it is not far-fetched assuming that their intercalary phialides are of homologous nature and perhaps plesiomorphic. The ancestor of these two genera may have possessed conidiophores forming solitary intercalary phialides below terminal phialides.

Recognition of *Sesquicillium* distinguishes species typically forming a reduced perithecial stroma superficially on plant tissue from species in *Clonostachys* often forming well-developed, through bark erumpent stromata. Also, the asexual morphs, when observed on the natural substratum, are typically mononematous and formed superficially in *Sesquicillium*, while they are often sporodochial and formed on stromata in *Clonostachys*. *Sesquicillium* accommodates a set of species that inhabit leaves, while this lifestyle is rarely seen in *Clonostachys*, where species may occur as endophytes in woody hosts and subcortical colonisers in recently dead trees, or on fungal hosts associating woody plants. It is possible that the ability to produce stromata erumpent through bark may have evolved in woody hosts (*Clonostachys*), while stromata were ecologically not required for the superficial lifestyle on plant tissues including leaves (*Sesquicillium*).

However, *Bionectria vesiculosa* (Luo & Zhuang 2010), here confirmed on the basis of available nrDNA sequences as a species of *Clonostachys*, clearly contradicts the concept mentioned above. The sexual morph of this species is astromatous, formed superficially on leaves, and, remarkably, its perithecial wall region consists of a single region only. A similar situation is encountered in *Sesquicillium buxi*, whose sexual morph consists of astromatous perithecia and a single perithecial wall region (Schroers 2001: fig. 96), nearly indistinguishable from *C. vesiculosa* (Luo & Zhuang 2010: fig. 1). While it was the asexual morph linking *Nectriella coronata* first to *Sesquicillium* (Gams 1968) and then to *Clonostachys* (Schroers 2000: fig. 5; Schroers 2001), ITS sequences supported classification of *C. vesiculosa* in *Clonostachys* (Luo & Zhuang 2010; Supplementary Fig. S1), while LSU places it in an unresolved polytomy among *Sesquicillium* and *Clonostachys* (Supplementary Fig. S2). Occurrence of superficially formed perithecia with a simple perithecial wall in both *Sesquicillium* and *Clonostachys* may allow hypothesising that these character patterns are (i) plesiomorphic and that (ii) also the common ancestor of *Sesquicillium* and *Clonostachys* formed perithecia superficially on plant tissue, perhaps on leaves. Most importantly, however, this concept allows hypothesising that (iii) a diversification of morphs, including perithecial wall anatomies and perithecial wall and stroma interfaces occurred then independently within *Sesquicillium* and *Clonostachys* and (iv) this morphological diversification allowed occupation of woody host-related ecological niches and perhaps even mycoparasitism, especially in *Clonostachys*.

Species of *Clonostachys* are widely distributed all over the world, with the highest known species diversity occurring in tropical regions. These species are commonly found in soils, litter, and dead plant substrata as saprotrophs. They have also been reported as endophytes and epiphytes of living plants (Torcato *et al.* 2020). Destructive mycoparasitism is especially well documented for *C. rosea* and a mycophilic habit was inferred for several *Clonostachys* species that formed their (a)sexual morph structures just on top of other wood associating fungi (Samuels 1976, Schroers *et al.* 1999b, Schroers 2001). However, while *C. rosea* has been exhaustively studied (see below), hardly any data are available for the many other species of *Clonostachys* and *Sesquicillium*. Sporadic reports have also emphasised parasitic interactions of *C. rosea* with myxomycetes, nematodes, ticks, molluscs, and leafhoppers (reviewed by Schroers 2001, Toledo *et al*. 2006, Zhang *et al*. 2008). However, these reports may rather illustrate the opportunistic nature of this species.

Clonostachys rosea was reported as an aggressive mycoparasite in the late 1950s (Barnett & Lilly 1962), and initial attempts to use it for biological control of plant diseases soon followed (Shigo 1958). Since then, there has been a wealth of new knowledge emerging concerning the ecology, physiology and genetics of *C. rosea*, and its applied use as a biological control agent (BCA) including its formulation, application strategy, efficiency and safety (Jensen *et al.* 2022). The biocontrol mechanisms of *C. rosea* against plant pathogenic fungi are primarily attributed to direct parasitism, secretion of fungal cell wall degrading enzymes, production of secondary metabolites such as antibiotics and toxins, and induction of plant resistance (Sun *et al.* 2020). Although most reports of biological control of plant diseases involves the species *C. rosea*, there is evidence to suggest that certain strains from other, closely related species, also possess biocontrol properties, such as *C. byssicola*, *C. chloroleuca*, *C. rhizophaga* and *C. solani* (García *et al.* 2003, Krauss *et al.* 2013, Sun *et al.* 2017, Broberg *et al.* 2021).

Biological control of plant pathogens via microbial antagonists is one promising component in future disease control strategies (Karlsson *et al*. 2015). As large-scale genomic sequencing becomes economically viable, the impact of single nucleotide polymorphisms (SNPs) on biocontrol-associated phenotypes can be easily studied across entire genomes of fungal populations. Recently, genome assemblies of four *C. rosea* strains have been published (Karlsson *et al*. 2015, Sun *et al*. 2015, Liu *et al.* 2016, Broberg *et al*. 2018, Wang 2021). The available genome resources are valuable for identifying biocontrol-related genes what will improve our understanding of the biological control ability of *C. rosea* and related species.

The present study should serve as phylogenetic backbone for future taxonomic studies of *Clonostachys*. Further studies are presently underway to generate full genome sequences of the species studied here in an attempt to identify additional taxa that have biocontrol properties of potential interest to industry.

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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Supplementary Material: https://studiesinmycology.org/

Fig. S1. Phylogenetic tree of representatives of the *Bionectriaceae* and outgroups resulting from a RAxML analysis of aligned ITS sequences. Bootstrap support values > 50 % are indicated at nodes. *Flammocladiella aceris* CBS 138906, *F. decora* CBS 142776, *F. anomiae* CLL 16017, *Tilachlidium brachiatum* CBS 363.97, and *T. brachiatum* CBS 505.67 are used as outgroup. Scale bar represents expected number of changes per site. "T" indicates ex-type strains.

Fig. S2. Phylogenetic tree of representatives of the *Bionectriaceae* and outgroups resulting from a RAxML analysis of aligned LSU sequences. Bootstrap support values > 50 % are indicated at nodes. *Flammocladiella aceris* CBS 138906, *F. decora* CBS 142776, *F. anomiae* CLL 16017, *Tilachlidium brachiatum* CBS 363.97, and *T. brachiatum* CBS 505.67 are used as outgroup. Scale bar represents expected number of changes per site. "T" indicates ex-type strains.

Fig. S3. Phylogenetic tree of representatives of the *Bionectriaceae* and outgroups resulting from a RAxML analysis of aligned *RPB2* sequences. Bootstrap support values > 50 % are indicated at nodes. *Flammocladiella aceris* CBS 138906 and *F. anomiae* CLL 16017, *Tilachlidium brachiatum* CBS 363.97 and *T. brachiatum* CBS 505.67 are used as outgroup. Scale bar represents expected number of changes per site. "T" indicates ex-type strains.

Fig. S4. Phylogenetic tree of representatives of the *Bionectriaceae* and outgroups resulting from a RAxML analysis of aligned *TEF1* sequences. Bootstrap support values > 50 % are indicated at nodes. *Flammocladiella aceris* CBS 138906 and *F. anomiae* CLL 16017 are used as outgroup. Scale bar represents expected number of changes per site. "T" indicates ex-type strains.

Fig. S5. Phylogenetic tree of *Clonostachys* species and outgroups resulting from a RAxML analysis of aligned ITS sequences. Bootstrap support values > 50 % are indicated at nodes. *Acremonium alternatum* CBS 407.66 and *A. stroudii* CBS 138820 are used as outgroup. Scale bar represents expected number of changes per site. "T" indicates ex-type strains.

Fig. S6. Phylogenetic tree of *Clonostachys* species and outgroups resulting from a RAxML analysis of the aligned LSU sequences. Bootstrap support values > 50 % are indicated at nodes. *Acremonium alternatum* CBS 407.66 and *A. stroudii* CBS 138820 are used as outgroup. Scale bar represents expected number of changes per site. "T" indicates ex-type strains.

Fig. S7. Phylogenetic tree of *Clonostachys* species and outgroups resulting from a RAxML analysis of aligned *RPB2* sequences. Bootstrap support values (1 000 replicates, GTR-GAMMA model) > 50 % are indicated at nodes. *Acremonium alternatum* CBS 407.66 and *A. stroudii* CBS 138820 are used as outgroup. Scale bar represents expected number of changes per site. "T" indicates ex-type strains.

Fig. S8. Phylogenetic tree of *Clonostachys* species and outgroups resulting from a RAxML analysis of aligned *TEF1* sequences. Bootstrap support values (1 000 replicates, GTR-GAMMA model) > 50 % are indicated at nodes. *Acremonium alternatum* CBS 407.66 and *A. stroudii* CBS 138820 are used as outgroup. Scale bar represents expected number of changes per site. "T" indicates ex-type strains.

Fig. S9. A detailed view of the collapsed clade (*Clonostachys rosea* and *Clonostachys rosea* f. *catenulata*) at the bottom of the phylogenetic tree presented in Fig. 2.

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