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ARTICLE

A phylogenetic revision of *Penicillium* sect. *Exilicaulis*, including nine new species from fynbos in South Africa

Cobus M. Visagie[1,2,3], Keith A. Seifert[1], Jos Houbraken[2], Robert A. Samson[2], and Karin Jacobs[3]

[1]Biodiversity (Mycology), Agriculture and Agri-Food Canada, Ottawa, ON K1A0C6, Canada; corresponding author e-mail: cobusvisagie9@gmail.com

[2]CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, NL-3584 CT Utrecht, The Netherlands

[3]Department of Microbiology, University of Stellenbosch, Private Bag X1, Stellenbosch 7600, South Africa

Abstract: A survey of the fynbos biome in South Africa resulted in the isolation of 61 *Penicillium* species from *Protea repens* infructescences, air, and soil samples. Fourteen of these belong to *Penicillium* sect. *Exilicaulis* and therefore we considered it an opportunity to re-evaluate the taxonomy of the section. Phylogenetic comparisons of the ITS, β-tubulin, calmodulin and *RPB2* gene regions of the 76 section *Exilicaulis* species, revealed 52 distinct species, including nine new species from fynbos. Morphological comparisons confirmed the novelty for most of these, however, new species closely related to *P. rubefaciens* did not show significant or consistent morphological differences and we thus placed a bias on phylogenetic data applying the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) concept. In this paper we describe the nine new species and update the accepted species list and resolve synonyms in the section. Importantly, we reveal that *P. citreosulfuratum* is the correct name for the clade previously considered to represent *P. toxicarium fide* Serra *et al.* (2008).

The nine new species are: *Penicillium atrolazulinum*, *P. consobrinum*, *P. cravenianum*, *P. hemitrachum*, *P. pagulum*, *P. repensicola*, *P. momoii*, *P. subturcoseum,* and *P. xanthomelinii* spp. nov.

Key words:
Citreovirdin
cryptic species
DNA barcode
mites
vector

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INTRODUCTION

Pitt (1980) introduced the name *Penicillium* sect. *Exilicaulis*, typified by *P. restrictum*, for species with monoverticillate conidiophores and non-vesiculated stipes. In the recent re-classification of *Penicillium* based on phylogenetic data (Houbraken & Samson 2011), section *Exilicaulis* was redefined to include biverticillate species such as *P. corylophilum*, *P. melinii,* and *P. raciborskii*. With a limited strain and species sampling, Houbraken & Samson (2011) separated species into two main clades. This was also supported by a more comprehensive *RPB2* (RNA polymerase II second largest subunit) phylogeny revealing a well-supported main *P. corylophilum* clade (containing biverticillate species), whereas monoverticillate species resolved in several basal clades.

Section *Exilicaulis* has received some taxonomic attention in recent years, including the introduction of new species (Langlois *et al.* 2014, Peterson *et al.* 1999, 2011), but more importantly species and their metabolites were shown to be toxic and to affect human health (Kremer *et al*. 1989, Lyratzopoulos *et al.* 2002, McMullin *et al*. 2014, Miyake 1940, Ohnishi *et al.* 2002, Peterson *et al*. 1999, Rosa *et al*. 2010, Unoura *et al.* 2011, Yoshida *et al*. 1992). Serra *et al*. (2008) studied the diversity of *Penicillium* species in cork bark with a focus on some species of sect. *Exilicaulis*, stressing the importance of applying the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) concept (Taylor *et al*. 2000) to *Penicillium*. This approach to species delineation has become standard in *Penicillium*, especially in studies focused on resolving the taxonomy of specific sections (Houbraken & Samson 2011, Houbraken *et al*. 2011, 2014, Peterson *et a*l. 2011, Rivera & Seifert 2011, Visagie *et al.* 2013). This concept was also applied in section *Exilicaulis*, but the focus was mostly on a subset of species from the *P. parvum*-clade (Langlois *et al*. 2014, Peterson *et al.* 1999, 2011) and the *P. citreonigrum* complex (Serra *et al.* 2008), but did not include all species belonging to these clades.

During a survey of species diversity in the fynbos biome, situated in the Western Cape of South Africa, *Penicillium* was one of the dominant genera isolated, with roughly 61 species found. Fourteen belong to section *Exilicaulis* and nine of those represent new species. Here we compare the morphology of these new species with all others previously classified in section *Exilicaulis* and apply GCPSR using phylogenies of the rDNA region (ITS), β-tubulin (*BenA*), calmodulin (*CaM*), and *RPB2* genes. This paper follows previous papers reporting new *Penicillium* species isolated during this survey belonging to sections *Aspergilloides* (Houbraken *et al.* 2014), *Citrina* (Visagie *et al.* 2014c), *Lanata-Divaricata* (Visagie *et al*. 2015), *Sclerotiora* (Visagie *et al*. 2013), and *Torulomyces* (Visagie *et al*. 2016a).

MATERIAL AND METHODS

Sampling and isolation

Soil, air and *Protea repens* infructescence samples were taken from three fynbos sampling sites at Stellenbosch (33°56'47"S 18°52'49"E), Riverlands (33°29'46"S 18°35'60"E), and Struisbaai (33°45'06"S 18°58'59"E). Potato dextrose agar (PDA) containing streptomycin (100 ppm), chloramphenicol (50 ppm) and dichloran (0.002 g/L) was used as isolation medium. Isolation plates were incubated at 25 °C for 7 d, after which colonies resembling *Penicillium* were transferred to oatmeal agar (OA).

Isolations from soil were made using a dilution series by adding 5 g soil to 100 mL dH_2O and diluting this tenfold three times resulting in suspensions 10^{-1}, 10^{-2} and 10^{-3} of the original. In triplicate, 1 mL from each dilution was spread onto PDA plates. Isolations from *Protea repens* infructescences included sampling from bracts and mite populations. Firstly, infructescences were cut open and the mites shaken onto 1 % water agar plates with chloroform used to temporarily sedate mites. Mites were transferred onto PDA plates using a fine needle and incubated on a lab bench (± 21 °C) on soapy water traps to prevent cross contamination by awaken mites roaming on plates. Roughly 15 bracts from infructescences were suspended in 100 mL dH_2O. This solution was diluted tenfold six times resulting in suspensions 10^{-4}, 10^{-5} and 10^{-6} of the original and spread plates prepared similarly to the soil spread plates. Air was sampled close to the same sampled *Protea repens* bushes using a MAS-Eco® air sampler set to a volume of 50 L.

Reference strains

Reference strains used for this study (Table 1), were obtained from the public collection of CBS (CBS-KNAW Fungal Biodiversity Centre, Utrecht) and cultures from the working collection of the Applied and Industrial Mycology group at the same institute (DTO). Strains isolated during this study are kept in a private collection at the department of Microbiology, Stellenbosch University, South Africa (CV). These strains were also deposited in DTO, with a subset of strains deposited into DAOMC (Canadian Collection of Fungal Cultures, Ottawa) and CBS.

DNA extraction, sequencing and phylogenetic analysis

DNA was extracted from strains grown on MEA for 7 d using the ZR Fungal/Bacterial DNA kit (ZymoResearch, CA), with extracts stored at 4 °C. Amplification of the ITS region, partial β-tubulin (*BenA*), calmodulin (*CaM*), and RNA polymerase II second largest subunit (*RPB2*) were made using primers and amplification profiles described in Visagie *et al*. (2014b). PCR and sequencing reactions followed similar methods to Visagie *et al.* (2013). For some strains, the partial *RPB2* gene was sequenced using internal sequencing primers *RPB2Int388F* and *RPB2Int-527R* as described in Houbraken & Samson (2011). Sequence contigs were assembled using CodonCode Aligner v. 4.0.1 (CodonCode Centerville, MA, USA). Newly generated sequences were deposited in GenBank with accession numbers provided in Table 1.

Fynbos strains isolated during this study were added to a sequence database that includes all ex-type strains of species belonging to section *Exilicaulis*. All data sets were aligned using MAFFT v. 7.164b (Katoh & Standley 2013) implementing the L-INS-i option. For multigene phylogenies, aligned data sets for each gene or region were concatenated in SeaView v. 4.4.1 (Gouy *et al.* 2010).

Phylogenies were constructed using both Maximum Likelihood (ML) and Bayesian tree inference (BI) analyses. ML analyses were done using MEGA v. 6.06 (Tamura *et al*. 2013). The most suitable model for each data set was selected based on the lowest Akaike information criterion (AIC) value in MEGA. ML analyses were run by calculating an initial Bio-Neighbour-Joining tree, followed by a Heuristic search with the Nearest-Neighbour-Interchange (NNI) option. Bootstrap analysis with 1000 replicates was used to represent support for nodes. For BI, the most suitable model for each data set was selected in MrModeltest v. 2.3 (Nylander *et al.* 2004) based on the lowest AIC value. Subsequent analyses were run in MrBayes v. 3.2.1 (Ronquist & Huelsenbeck 2003) using three sets of four chains (one cold and three heated) and stopped when the average standard of deviation for split frequencies reached 0.01. The sample frequency was then set at 100 and 25 % of trees were removed as burn-in. ML phylograms were used for representing phylogenies obtained from ML and BI analyses, with bootstrap values (≥ 80 %) and/or posterior probabilities (≥ 0.95 pp) both indicated above thickened branches.

Morphology

Fynbos strains were characterised on Czapek yeast autolysate agar (CYA), Blakeslee's malt extract agar (MEA; Bacto), yeast extract sucrose agar (YES), 25 % glycerol nitrate agar (G25N), and creatine sucrose agar (CREA), incubated at 25 °C for 7 d, with additional CYA plates incubated at 30 and 37 °C. CREA contains bromocresol purple and is used as a rapid method for detecting acid production by colonies, indicated by a colour change in the medium from purple to yellow (Frisvad 1981). Media preparation, inoculation technique, incubation conditions and microscope preparations were standardised according to the recommended methods published in Visagie *et al.* (2014b). Colour names and codes used in descriptions are based on Kornerup & Wanscher (1967). An Olympus SZX12 dissecting microscope and Olympus BX50 light microscope equipped with an Evolution MP digital microscope camera and ImagePro v. 6.0 software were used for microphotography. Photographic plates were prepared in Adobe Photoshop CS6.

RESULTS

Sampling and isolations

Penicillium sect. *Exilicaulis* was the dominant group isolated from the fynbos, with 740 isolates accounting for roughly 43 % of the total obtained. Strains belonging to the section were sorted into morpho-groups based on colony characters on CYA and MEA, with a subset of strains from each group subsequently sequenced and compared with reference sequences. The dominance of *P. citreosulfuratum* (197 isolates in total, with only three each from air and soil) and

Table 1. Strains used in this study.

Species name	Collection numbers	Substrate, Location	GenBank accession numbers			
			ITS	BenA	CaM	RPB2
P. alutaceum	CBS 317.67 = ATCC 18542 = FRR 1158 = IFO 31728 = IMI 136243	Soil, Pretoria region, South Africa; ex-type	AF033454	KJ834430	KP016768	JN121489
P. arabicum	CBS 414.69 = ATCC 22347 = DSM2205 = FRR 507 = IMI 140335 = VKMF-1077	Soil, Syria; ex-type	KC411758	KP016750	KP016770	KP064574
P. atrolazulinum	CBS 139136 = DAOM 241083 = DTO 180-H4 = CV 55	Air sample, Stellenbosch, South Africa; ex-type	JX140913	JX141077	JX157416	KP064575
P. atrolazulinum	CBS 139164 = DAOM 241085 = DTO 183-D7 = CV 1778	Bract from *Protea repens* infructescens, Struisbaai, South Africa	JX140907	JX141114	JX157501	KP064601
P. atrolazulinum	CBS 139172 = DTO 184-E8 = CV 125	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141079	JX157423	KP064576
P. atrolazulinum	CBS 139173 = DTO 184-F3 = CV 137	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141080	JX157424	KP064577
P. atrolazulinum	CBS 139174 = DTO 184-H9 = CV 365	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141099	JX157446	KP064593
P. atrolazulinum	CBS 139177 = DTO 186-D7 = CV 1791	Bract from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141115	JX157502	KP064602
P. atrolazulinum	CBS 139178 = DTO 186-E3 = CV 1854	Bract from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141117	JX157505	KP064603
P. atrolazulinum	CBS 139182 = DTO 186-G9 = CV 2025	Mite from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141118	JX157512	KP064604
P. atrolazulinum	DTO 184-F4 = CV 139	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141081	JX157425	KP064578
P. atrolazulinum	DTO 184-F6 = CV 152	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141082	JX157427	KP064579
P. atrolazulinum	DTO 184-F8 = CV 173	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141083	JX157429	KP064580
P. atrolazulinum	DTO 184-F9 = CV 176	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141084	JX157430	KP064581
P. atrolazulinum	DTO 184-G1 = CV 180	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141086	JX157432	KP064582
P. atrolazulinum	DTO 184-G2 = CV 197	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141087	JX157433	KP064583
P. atrolazulinum	DTO 184-G4 = CV 199	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141088	JX157434	KP064584
P. atrolazulinum	DTO 184-G7 = CV 235	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141089	JX157435	KP064585
P. atrolazulinum	DTO 184-G8 = CV 252	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141091	JX157437	KP064586
P. atrolazulinum	DTO 184-G9 = CV 264	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141092	JX157438	KP064587
P. atrolazulinum	DTO 184-H1 = CV 278	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141093	JX157439	KP064588
P. atrolazulinum	DTO 184-H2 = CV 282	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141094	JX157440	KP064589
P. atrolazulinum	DTO 184-H3 = CV 285	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141095	JX157442	KP064590
P. atrolazulinum	DTO 184-H5 = CV 307	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141096	JX157443	KP064591
P. atrolazulinum	DTO 184-H6 = CV 332	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141097	JX157444	KP064592
P. atrolazulinum	DTO 184-I2 = CV 438	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141100	JX157448	KP064594
P. atrolazulinum	DTO 184-I4 = CV 458	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141101	JX157449	KP064595
P. atrolazulinum	DTO 185-A2 = CV 500	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141102	JX157450	KP064596
P. atrolazulinum	DTO 185-B9 = CV 635	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141103	JX157456	KP064597
P. atrolazulinum	DTO 185-C1 = CV 644	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141105	JX157457	KP064598

Table 1. (Continued).

Species name	Collection numbers	Substrate, Location	GenBank accession numbers			
			ITS	BenA	CaM	RPB2
P. atrolazulinum	DTO 185-D1 = CV 777	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	n.a.	JX141106	JX157458	KP064599
P. atrolazulinum	DTO 186-D2 = CV 1736	Mite from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141112	JX157498	KP064600
P. atrolazulinum	DTO 186-H9 = CV 2222	Bract from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141119	JX157513	KP064605
P. atrosanguineum	CBS 380.75 = FRR 1726 = IMI 197488	*Triticum aestivum* in silo, Prague, Czech Republic; ex-type	JN617706	KJ834435	KP016771	JN406557
P. burgense	CBS 325.89	Soil, Burgos, Spain; ex-type	KC411736	KJ834437	KP016772	JN406572
P. canis	NRRL 62798	Ilial bone lesion in Rhodesian ridgeback dog, USA; ex-type	KJ511291	KF900167	KF900177	KF900196
P. catenatum	CBS 352.67 = ATCC 18543 = CSIR 1097 = IFO 31774 = IMI 136241	Desert soil, Upington, South Africa; ex-type	KC411754	KJ834438	KP016774	JN121504
P. cf restrictum	CBS 139137 = DAOM 241050 = DTO 180-I4 = CV 90	Soil, Stellenbosch, South Africa	JX140928	JX141054	JX157417	KP064643
P. cf restrictum	CBS 139139 = DAOM 241054 = DTO 180-I6 = CV 93	Soil, Stellenbosch, South Africa	JX140930	JX141055	JX157419	KP064607
P. cf restrictum	CBS 139148 = DAOM 241057 = DTO 182-B6 = CV 872	Soil, Malmesbury, South Africa	KP016817	JX141059	JX157464	KP064661
P. cf restrictum	CBS 139149 = DAOM 241052 = DTO 182-C3 = CV 896	Soil, Malmesbury, South Africa	KP016819	JX141060	JX157467	KP064609
P. cf restrictum	CBS 139150 = DAOM 241055 = DTO 182-C5 = CV 900	Soil, Malmesbury, South Africa	KP016816	JX141061	JX157468	KP064610
P. cf restrictum	CBS 139152 = DAOM 241058 = DTO 182-E1 = CV 943	Soil, Malmesbury, South Africa	n.a.	JX141063	JX157473	KP064611
P. cf restrictum	CBS 139153 = DAOM 241051 = DTO 182-E3 = CV 948	Soil, Malmesbury, South Africa	KP016818	JX141064	JX157474	KP064612
P. cf restrictum	CBS 139170 = DTO 184-E4 = CV 96	Soil, Stellenbosch, South Africa	n.a.	JX141056	JX157420	KP064644
P. cf restrictum	CBS 139171 = DTO 184-E6 = CV 101	Soil, Stellenbosch, South Africa	n.a.	JX141057	JX157421	KP064608
P. chalabudae	CBS 219.66 = ATCC 18322 = ATCC 18329 = FRR 3393 = VKMF-1037	Soil, Ukraine; ex-type	KP016811	KP016748	KP016767	KP064572
P. cinerascens	NRRL 748 = ATCC 48693 = BIOURGE 90 = FRR 748 = IMI 92234 = QM 7555 = Thom 4733.34	Unknown; ex-type	AF033455	JX141041	JX157405	KP064614
P. cinereoatrum	CBS 222.66 = ATCC 22350 = FRR 3390 = IJFM 5024 = IMI 113676 = VKMF-856	Forest soil, Kiev, Ukraine; ex-type	KC411700	KJ834442	KP125335	JN406608
P. citreonigrum	CBS 258.29 = ATCC 48736 = FRR 761 = IMI 092209 = LSHBP 20 = LSHBP 98 = MUCL 28648 = MUCL 29062 = MUCL 29116 = NRRL 761	Rotting stem, Belgium; ex-type of *P. citreonigrum* and *P. subcinearum*	AF033456	EF198621	EF198628	JN121474
P. citreonigrum	CBS 308.48 = ATCC 10425 = FRR 2046 = IMI 040575 = NRRL 2046	Military equipment, Florida, USA; ex-type of *P. citreoviride*	EF198647	EF198623	KP016778	KP064616
P. citreonigrum	CBS 321.59 = ATCC 18308 = FAT123 = IFO 6224 = IMI 068225 = NRRL 3404 = QM 7290	Soil, Japan; ex-type of *P. aeneum*	KP016812	KP016749	KP016769	KP064573
P. citreonigrum	NRRL 1187	Unknown	EF198646	EF198622	EF198626	EF198501

Table 1. (Continued).

Species name	Collection numbers	Substrate, Location	GenBank accession numbers			
			ITS	BenA	CaM	RPB2
P. citreosulfuratum	CBS 139135 = DTO 180-G1 = CV 11	Air sample, Stellenbosch, South Africa	JX140937	JX141162	JX157415	KP064675
P. citreosulfuratum	CBS 139140 = DTO 181-E1 = CV 283	Bract from *Protea repens* infructescens, Stellenbosch, South Africa	JX140943	JX141163	JX157441	KP064676
P. citreosulfuratum	CBS 139156 = DTO 182-G3 = CV 1000	Soil, Malmesbury, South Africa	JX140935	JX141164	JX157536	KP064677
P. citreosulfuratum	CBS 139158 = DTO 183-B2 = CV 1454	Bract from *Protea repens* infructescens, Malmesbury, South Africa	JX140939	JX141167	JX157485	KP064678
P. citreosulfuratum	CBS 139162 = DTO 183-C5 = CV 1532	Bract from *Protea repens* infructescens, Malmesbury, South Africa	JX140940	JX141168	JX157492	KP064679
P. citreosulfuratum	CBS 139165 = DTO 183-G2 = CV 2015	Bract from *Protea repens* infructescens, Struisbaai, South Africa	JX140942	JX141169	JX157537	KP064680
P. citreosulfuratum	IMI 92228 = DTO 290-I4	Unknown; ex-type	KP016814	KP016753	KP016777	KP064615
P. citreosulfuratum	NRRL 31271	Unknown, Strain of *P. toxicarium* Miyake *fide* Serra *et al*. (2008)	EF198660	EF198614	EF198641	EF198486
P. citreosulfuratum	NRRL 6172	Unknown, Strain of *P. toxicarium* Miyake *fide* Serra *et al*. (2008)	EF198650	EF198620	EF198631	EF198499
P. consobrinum	CBS 139141 = DAOM 241071 = DTO 181-F8 = CV 436	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	JX140887	JX141134	JX157447	KP064618
P. consobrinum	CBS 139144 = DAOM 241072 = DTO 181-H9 = CV 547	Soil, Stellenbosch, South Africa; ex-type	JX140888	JX141135	JX157453	KP064619
P. consobrinum	CBS 139147 = DAOM 241073 = DTO 182-B5 = CV 865	Air sample, Malmesbury, South Africa	JX140889	JX141138	JX157463	KP064622
P. consobrinum	CBS 139151 = DAOM 241074 = DTO 182-C9 = CV 911	Soil, Malmesbury, South Africa	JX140890	JX141141	JX157469	KP064625
P. consobrinum	CBS 139155 = DAOM 241075 = DTO 182-F5 = CV 977	Soil, Malmesbury, South Africa	JX140891	JX141144	JX157477	KP064628
P. consobrinum	DTO 185-D4 = CV 815	Air sample, Malmesbury, South Africa	n.a.	JX141136	JX157461	KP064620
P. consobrinum	DTO 185-D5 = CV 817	Air sample, Malmesbury, South Africa	n.a.	JX141137	JX157462	KP064621
P. consobrinum	DTO 185-E2 = CV 888	Soil, Malmesbury, South Africa	n.a.	JX141139	JX157465	KP064623
P. consobrinum	DTO 185-E5 = CV 894	Soil, Malmesbury, South Africa	n.a.	JX141140	JX157466	KP064624
P. consobrinum	DTO 185-F5 = CV 917	Soil, Malmesbury, South Africa	n.a.	JX141142	JX157470	KP064626
P. consobrinum	DTO 185-G3 = CV 941	Soil, Malmesbury, South Africa	n.a.	JX141143	JX157472	KP064627
P. consobrinum	DTO 185-I4 = CV 1095	Mite from *Protea repens* infructescens, Malmesbury, South Africa	n.a.	JX141145	JX157483	KP064629
P. consobrinum	DTO 186-A6 = CV 1457	Bract from *Protea repens* infructescens, Malmesbury, South Africa	n.a.	JX141146	JX157486	KP064630
P. corylophilum	CBS 127807 = IMI 92263 = NRRL 793 = FRR 793	Unknown; ex-type of *P. obscurum*	KP016815	KP016761	KP016797	KP064654
P. corylophilum	CBS 127808 = NRRL 799 = IMI 92202	Unknown; ex-type of *P. chloroleucon*	KP016813	KP016752	KP016776	KP064613
P. corylophilum	CBS 231.38 = ATCC 10452 = IFO 7726 = IMI 039817 = NRRL 872	*Humulus lupulus,* Weihenstephan, Germany; ex-type of *P. humuli*	JN617696	KP016756	KP016787	KP064645
P. corylophilum	CBS 254.37 = IMI 092201 = LSHBP 12 = MUCL 28669 = NRRL 769	Unknown; ex-type of *P. candidofulvum*	KC411712	KP016751	KP016773	KP064606

Table 1. (Continued).

Species name	Collection numbers	Substrate, Location	GenBank accession numbers			
			ITS	BenA	CaM	RPB2
P. corylophilum	CBS 259.67 = ATCC 22351 = FRR 3403 = IFO 9146 = IMI 103148	Litter of *Betula*, UK; ex-type of *P. coeruleoviride*	KC411717	KP016754	KP016779	KP064617
P. corylophilum	CBS 312.48 = TCC9784 = ATHUM2890 = CECT 2270 = FRR 802 = IMI 039754 = MUCL 28671 = MUCL 29073 = MUCL 29131 = NRRL 802 = QM 7510	Unknown; ex-type of *P. corylophilum* and *P. citreovirens*	AF033450	JX141042	KP016780	KP064631
P. corylophilum	CBS 330.79 = IJFM 5147	Air sample, Barcelona, Spain; authentic *P. citreovirens* strain	GU944557	GU944519	GU944607	JN406569
P. corylophilum	DTO 180-E4 = CV 2853	Soil, Malmesbury, South Africa	FJ230997	JX141044	JX157523	KP064633
P. corylophilum	DTO 180-E5 = CV 2854	Soil, Malmesbury, South Africa	FJ230996	JX141045	JX157522	KP064634
P. corylophilum	DTO 184-C9 = CV 2852	Soil, Malmesbury, South Africa	FJ230998	JX141043	JX157521	KP064632
P. cravenianum	CBS 139138 = DAOM 241082 = DTO 180-I5 = CV 92	Soil, Stellenbosch, South Africa; ex-type	JX140900	JX141076	JX157418	KP064636
P. decumbens	CBS 230.81 = FRR 741 = IMI 190875 = MUCL 29107 = NRRL 741	Unknown source, Florida, USA; ex-type	AY157490	KJ834446	KP016782	JN406601
P. dimorphosporum	CBS 456.70 = NRRL 5207 = ATCC 22783 = ATCC 52501 = FRR 1120 = IMI 149680	Mangrove swamp soil, Tooraddin, Australia; ex-type	AF081804	KJ834448	KP016783	JN121517
P. dravuni	BPI 844248	Great Astrolabe Reed from *Dictosphaeria versluyii*, Dravuni, Fiji; ex-type	AY494856	n.a.	n.a.	n.a.
P. erubescens	CBS 318.67 = ATCC 18544 = CSIR 1040 = FRR 814 = IFO 31734 = IMI 136204 = NRRL 6223	Nursery soil, Pretoria, South Africa; ex-type	AF033464	HQ646566	EU427281	JN121490
P. fagi	CBS 689.77 = CCMF-696 = IJFM 3049 = IMI 253806 = VKMF-2178	Fallen leaf (*Fagus sylvatica*) on Andosol soil, Spain; ex-type	AF481124	KJ834449	KP016784	JN406540
P. griseolum	CBS 277.58 = ATCC 18239 = FRR 2671 = IFO 8175 = IMI 071626 = LSHBB323 = NRRL 2671 = QM 7523	Acidic dune sand, Dorset, England; ex-type	EF422848	EF506213	EF506232	KP064638
P. guttulosum	CBS 141171 = NRRL 907 = ATCC 48734 = FRR 907 = Thom 4894.16	Soil, Utah, USA; ex-type	HQ646592	HQ646576	HQ646587	KP064639
P. hemitrachum	CBS 139133 = DAOM 241097 = DTO 180-D7 = CV 2844	Soil, Malmesbury, South Africa	FJ231002	JX141047	JX157525	KP064641
P. hemitrachum	CBS 139134 = DAOM 241098 = DTO 180-D8 = CV 2845	Soil, Malmesbury, South Africa; ex-type	FJ231003	JX141048	JX157526	KP064642
P. hemitrachum	CBS 139154 = DAOM 241099 = DTO 182-F1 = CV 964	Soil, Malmesbury, South Africa	JX140916	JX141046	JX157475	KP064640
P. heteromorphum	CBS 226.89	Soil, Shennongjia, China; ex-type	KC411702	KJ834455	KP016786	JN406605
P. katangense	CBS 247.67 = ATCC 18388 = IMI 136206 = NRRL 5182	Soil, Katanga, DR Congo; ex-type	AF033458	KP016757	KP016788	KP064646
P. kurssanovii	CBS 625.67 = ATCC 18387 = FRR 3381 = IJFM 5045 = IMI 129965 = NRRL 3381 = VKMF-1244	Maize-field soil, Záporožská district, Ukraine; ex-type	EF422849	KP016758	KP016789	KP064647
P. laeve	CBS 136665 = KY 12727 = NBRC 109724	Forest soil, Thailand; ex-type	KF667369	KF667365	KF667367	KF667371

Table 1. (Continued).

Species name	Collection numbers	Substrate, Location	GenBank accession numbers			
			ITS	BenA	CaM	RPB2
P. lapidosum	CBS 343.48 = ATCC 10462 = CCT4477 = IFO 6100 = IMI 039743 = NRRL 718 = QM 1928	Canned blueberry, Washington, USA; ex-type	AF033409	KJ834465	FJ530984	JN121500
P. maclennaniae	CBS 198.81 = DAR 35238	Rhizoplane of *Gahnia radula*, Victoria, Australia; ex-type	KC411689	KJ834468	KP016791	KP064648
P. melinii	CBS 139142 = DAOM 241100 = DTO 181-H6 = CV 535	Soil, Stellenbosch, South Africa	JX140919	JX141050	JX157451	KP064650
P. melinii	CBS 139143 = DAOM 241101 = DTO 181-H8 = CV 542	Soil, Stellenbosch, South Africa	JX140920	JX141051	JX157452	KP064651
P. melinii	CBS 139168 = DAOM 241102 = DTO 183-H8 = CV 2393	Bract from *Protea repens* infructescens, Struisbaai, South Africa	JX140917	JX141052	JX157527	KP064652
P. melinii	CBS 139169 = DAOM 241103 = DTO 183-I1 = CV 2404	Bract from *Protea repens* infructescens, Struisbaai, South Africa	JX140918	JX141053	JX157528	KP064653
P. melinii	CBS 218.30 = ATCC 10469 = FRR 2041 = IFO 7675 = IMI 040216 = MUCL 29235 = NRRL 2041 = QM 7599	Forest soil, USA; ex-type	AF033449	KJ834471	KP016792	JN406613
P. melinii	CBS 280.58 = ATCC 18383 = IMI 071624 = LSHBB333 = NRRL 2672 = QM 7526	Calluna heathland soil, England; ex-type of *P. radulatum*	KC411727	KP016763	KP016801	KP064658
P. melinii	CBS 285.65	*Pinus banksiana*, Petawawa, Canada	n.a.	KP016764	KP016802	KP064659
P. melinii	CBS 340.61	Soil, Padova, Italy	n.a.	KP016760	KP016793	KP064649
P. menonorum	NRRL 50410	Garden soil, California, USA; ex-type	HQ646591	HQ646573	HQ646584	KF900194
P. meridianum	CBS 314.67 = ATCC 18545 = CSIR 1052 = IMI 136209	Grassland soil, Pretoria, South Africa; ex-type	AF033451	KJ834472	KP016794	JN406576
P. momoii	CBS 139157 = DAOM 241077 = DTO 182-G4 = CV 1015	Mite from *Protea repens* infructescens, Malmesbury, South Africa; ex-type	JX140895	JX141073	JX157479	KP064673
P. namyslowskii	CBS 202.87 = IJFM 7824	Sand dune soil, Utah, USA; ex-type of *P. flavidostipitatum*	KC411691	KJ834451	KP016785	KP064637
P. namyslowskii	CBS 204.87	Sandy soil, Chile; ex-type of *P. turris-painense*	KC411693	KP016766	KP016809	KP064681
P. namyslowskii	CBS 353.48 = ATCC 11127 = IMI 040033 = MUCL 29226 = NRRL 1070	Soil under *Pinus,* Belarus, Poland; ex-type	AF033463	JX141067	KP016795	JF417430
P. nepalense	CBS 203.84 = NHL 6482	Rice soil, Kathmandu, Nepal; ex-type	KC411692	KJ834474	KP016796	JN121453
P. ovatum	CBS 136664 = KY 12726	Forest soil under litter of *Pinus caribaea,* Kuala Lumpur, Malayasia; ex-type	KF667370	KF667366	KF667368	KF667372
P. pagulum	CBS 139166 = DAOM 241069 = DTO 183-H2 = CV 2224	Bract from *Protea repens* infructescens, Struisbaai, South Africa; ex-type	JX140898	JX141070	JX157519	KP064655
P. pagulum	CBS 139167 = DAOM 241070 = DTO 183-H3 = CV 2236	Bract from *Protea repens* infructescens, Struisbaai, South Africa	JX140899	JX141071	JX157520	KP064656
P. parvum	CBS 359.48 = ATCC 10479 = IFO 7732 = IMI 040587 = NRRL 2095 = QM 1878	Soil, Nicaragua; ex-type	AF033460	HQ646568	KF900173	JN406559
P. parvum	CBS 570.73 = ATCC 28050 = ATCC 48363 = FRR 1559 = NHL 6463	Soil, Port Moresby, Papua New Guinea; ex-type *P. papuanum*	KC411767	KP016762	KP016798	KP064657

Table 1. (Continued).

Species name	Collection numbers	Substrate, Location	GenBank accession numbers			
			ITS	BenA	CaM	RPB2
P. philippinense	CBS 623.72 = FRR 1532 = NHL 6130	Soil from pine forest, Luzon Island, Philippines; ex-type	KC411770	KJ834482	KP016799	JN406543
P. pimiteouiense	CBS 102479 = NRRL 25542	Kidney epithelial cell culture flask, Preoria, USA; ex-type	AF037431	HQ646569	HQ646580	JN406650
P. raciborskii	CBS 224.28 = ATCC 10488 = DSM2422 = FRR 2150 = IFO 7676 = IMI 040568 = LSHBP 92 = MUCL 29246 = NRRL 2150	Soil under conifer, Długa Goślina, Poland; ex-type	AF033447	JX141069	KP016800	JN406607
P. repensicola	CBS 139159 = DAOM 241079 = DTO 183-B5 = CV 1486	Bract from *Protea repens* infructescens, Malmesbury, South Africa	JX140892	JX141149	JX157489	KP064666
P. repensicola	CBS 139160 = DAOM 241080 = DTO 183-B8 = CV 1495	Bract from *Protea repens* infructescens, Malmesbury, South Africa; ex-type	JX140893	JX141150	JX157490	KP064660
P. repensicola	CBS 139161 = DAOM 241081 = DTO 183-C2 = CV 1514	Bract from *Protea repens* infructescens, Malmesbury, South Africa	JX140894	JX141151	JX157491	KP064667
P. repensicola	CBS 139175 = DTO 186-A8 = CV 1479	Bract from *Protea repens* infructescens, Malmesbury, South Africa	KP016820	JX141147	JX157487	KP064664
P. repensicola	CBS 139176 = DTO 186-A9 = CV 1484	Bract from *Protea repens* infructescens, Malmesbury, South Africa	n.a	JX141148	JX157488	KP064665
P. repensicola	DTO 186-B5 = CV 1546	Bract from *Protea repens* infructescens, Malmesbury, South Africa	n.a.	JX141152	JX157493	KP064668
P. restrictum	CBS 367.48 = ATCC 11257 = FRR 1748 = IMI 040228 = NRRL 1748 = QM 1962	Soil, Honduras; ex-type	AF033457	KJ834486	KP016803	JN121506
P. rubefaciens	CBS 139145 = DAOM 241076 = DTO 181-I5 = CV 597	Mite from *Protea repens* infructescens, Stellenbosch, South Africa	JX140896	JX141072	JX157454	KP064662
P. rubefaciens	CBS 145.83 = CECT 2752	Sandy soil under *Pinus* sp., Valladolid, Spain; ex-type	KC411677	KJ834487	KP016804	JN406627
P. rubidurum	CBS 609.73 = NRRL 6033 = ATCC 28051 = ATCC 48238 = FRR 1558 = IMI 228551 = NHL 6460	Soil, Wewak, Papua New Guinea; ex-type	AF033462	HQ646574	HQ646585	JN406545
P. smithii	CBS 256.87 = FRR 2663 = IMI 288724	Dried fish *(Decapterus* sp.), Indonesia; ex-type of *P. corynephorum*	KC411716	KP016755	KP016781	KP064635
P. smithii	CBS 261.87 = FRR 2743	Pasteurised fruit juice, Sydney, Australia; ex-type of *P. sabulosum*	KC411719	KP016765	KP016805	KP064672
P. smithii	CBS 276.83 = CECT 2744 = IMI 259693	Secale cereale, Zamora, Spain; ex-type	KC411723	KJ834492	KP016806	JN406589
P. striatisporum	CBS 705.68 = ATCC 22052 = CCRC 31679 = FRR 827 = IMI 151749 = MUCL 31202	Leaf litter of *Acacia karroo,* Potchefstroom, South Africa; ex-type	AF038938	JX141156	KP016807	JN406538
P. subturcoseum	CBS 139129 = DAOM 241093 = DTO 180-C5 = CV 2817	Soil, Malmesbury, South Africa	FJ231004	JX141158	JX157533	KP064669
P. subturcoseum	CBS 139130 = DAOM 241094 = DTO 180-C6 = CV 2820	Soil, Malmesbury, South Africa	FJ231005	JX141159	JX157534	KP064670
P. subturcoseum	CBS 139131 = DAOM 241095 = DTO 180-C7 = CV 2826	Soil, Malmesbury, South Africa	FJ231007	JX141160	JX157535	KP064671
P. subturcoseum	CBS 139132 = DAOM 241096 = DTO 180-C9 = CV 2835	Soil, Malmesbury, South Africa; ex-type	FJ231006	JX141161	JX157532	KP064674
P. subturcoseum	CBS 139146 = DAOM 241078 = DTO 182-A7 = CV 795	Air sample, Malmesbury, South Africa	JX140934	JX141157	JX157459	KP064663
P. terrenum	CBS 254.87 = FRR 2660	Dried fish *(Decapterus* sp.), Indonesia; ex-type of *P. chalybeum*	KC411713	KJ834440	KP016775	JN406596

Table 1. (Continued).

Species name	Collection numbers	Substrate, Location	GenBank accession numbers			
			ITS	BenA	CaM	RPB2
P. terrenum	CBS 313.67 = ATCC 18547 = CSIR 1022 = IMI 136208	Soil, South Africa; ex-type	AM992111	KJ834496	KP016808	JN406577
P. terrenum	CBS 622.72 = DSM2418 = NHL 6128 = NRRL 5824	Forest soil under *Pinus* sp., Luzon Island, Philippines; ex-type of *P. luzoniacum*	AF033446	KP016759	KP016790	JN406544
P. velutinum	CBS 250.32 = ATCC 10510 = CECT 2318 = IJFM 5108 = IMI 040571 = NRRL 2069 = QM 7686 = VKMF-379	Sputum from man, Appeldoorn, Netherlands; ex-type	AF033448	JX141170	KP016810	KP064682
P. vinaceum	CBS 389.48 = ATCC 10514 = FRR 739 = IMI 029189 = NRRL 739 = QM 6746	Soil, Utah, USA; ex-type	AF033461	HQ646575	HQ646586	JN406555
P. xanthomelinii	CBS 139163 = DAOM 241104 = DTO 183-C7 = CV 1677	Soil, Struisbaai, South Africa; ex-type	JX140921	JX141120	JX157495	KP064683
P. xanthomelinii	CBS 139179 = DTO 186-F4 = CV 1923	Mite from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141126	JX157509	KP064689
P. xanthomelinii	CBS 139180 = DTO 186-F9 = CV 1942	Mite from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141128	JX157510	KP064690
P. xanthomelinii	CBS 139181 = DTO 186-G4 = CV 1969	Mite from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141129	JX157511	KP064691
P. xanthomelinii	DAOM 241105 = DTO 183-F6 = CV 1905	Bract from *Protea repens* infructescens, Struisbaai, South Africa	JX140924	JX141125	JX157508	KP064688
P. xanthomelinii	DTO 183-D3 = CV 1745	Mite from *Protea repens* infructescens, Struisbaai, South Africa	JX140922	JX141121	JX157499	KP064684
P. xanthomelinii	DTO 183-E7 = CV 1844	Mite from *Protea repens* infructescens, Struisbaai, South Africa	JX140923	JX141122	JX157504	KP064685
P. xanthomelinii	DTO 186-E5 = CV 1871	Bract from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141123	JX157506	KP064686
P. xanthomelinii	DTO 186-E8 = CV 1886	Bract from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141124	JX157507	KP064687
P. xanthomelinii	DTO 186-I7 = CV 2312	Bract from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141130	JX157514	KP064692
P. xanthomelinii	DTO 186-I9 = CV 2329	Bract from *Protea repens* infructescens, Struisbaai, South Africa	n.a.	JX141131	JX157515	KP064693

Table 2. Overiview and details used for phylogenetic analyses.

		Dataset			
		***P. citreonigrum* clade**	***P. corylophilum* clade**	***P. melinii* clade**	***P. parvum* clade**
BenA dataset	Length (bp)	449	420	454	427
	Substitution model (BI)	K80+G	SYM+G	HKY+G	SYM+G
	Substitution model (ML)	K2+I	K2+G	K2+G	K2+G
CaM dataset	Length (bp)	495	504	490	530
	Substitution model (BI)	K80+I	SYM+I	GTR+G	GTR+I+G
	Substitution model (ML)	K2+G	K2+G	K2+G	K2+G
RPB2 dataset	Length (bp)	877	695	838	888
	Substitution model (BI)	GTR+I+G	SYM+I+G	SYM+G	GTR+I+G
	Substitution model (ML)	K2+G	K2+G	TN93+G	K2+G
Concatenated dataset	Length (bp)	1821	1619	1782	1845
	Substitution model (BI)	GTR+G	SYM+I+G	GTR+I+G	GTR+I+G
	Substitution model (ML)	K2+I	TN93+G	K2+G	T92+I+G

P. atrolazulinum (321 total, six each from air and soil) in *Protea repens* infructescences and from their mite communities was especially apparent.

Phylogeny

An ITS phylogeny (Fig. 1) was used to compare all ex-type strains from section *Exilicaulis* species and sort them into smaller clades for the *BenA*, *CaM*, *RPB2* and combined phylogenies (Figs 2–6). The aligned ITS barcode data set was 526 bp long with K2+G+I and GTR+G+I the most suitable substitution models for ML and BI respectively. Table 2 summarises the most suitable substitution models used for the remaining phylogenies. The ITS phylogeny distributed strains into six main clades, similar to the results of Houbraken & Samson (2011). Species with biverticillate conidiophores were resolved in a well-supported clade distinct from monoverticillate species. We also divided the biverticillate clade into subclades, referred to here as the *P. melinii*- and *P. corylophilum*-clades, to present the data concisely. The monoverticillate species resolved in four clades, referred to here as the *P. restrictum-, P. citreonigrum-, P. decumbens-,* and *P. parvum*-clades. ITS performs poorly as a DNA barcode marker in the *P. melinii-, P. corylophilum*-, and *P. restrictum*-clades, although it still can be used to identify the important *P. corylophilum*. On the other hand, ITS can successfully identify all species from the *P. citreonigrum-, P. decumbens*-, and *P. parvum*-clades.

Penicillium melinii-clade (Fig. 2) — Phylogenetic data divided the fynbos strains into three clades, two representing new species described below as *P. hemitrachum* and *P. xanthomelinii*. The remaining strains were placed in a clade with *P. melinii* and *P. radulatum*. Although there is sequence variation within the clade, phylogenies were in conflict and following GCPSR we identified our strains as *P. melinii* and consider *P. radulatum* a synonym. Ex-type strains of *P. terrenum, P. chalybeum,* and *P. luzoniacum* were included in a coherent clade and we consider them to represent one species with *P. terrenum* the oldest name. Similarly, we consider *P. flavidostipitatum* and *P. turris-painense* synonyms of *P. namyslowskii*, while *P. corynephorum* and *P. sabulosum* are synonyms of *P. smithii*.

Penicillium corylophilum-clade (Figs 3–4) — The largest group of fynbos isolates belong to this clade, with nine species identified. GCPSR revealed seven coherent clades distinct from known species, which are introduced as new species below. *Penicillium repensicola* and *P. subturcoseum* strains were consistently resolved in coherent clades as close relatives. *Penicillium momoii* and *P. cravenianum* were represented by single isolates that shifted phylogenetic positions depending on the gene used. However, the combined phylogeny places *P. cravenianum* as a close relative to *P. pagulum*, while *P. momoii* seems most similar to *P. rubefaciens*. Sequence variation was observed in the clades described as *P. atrolazulinum*, *P. consobrinum* and *P. pagulum*. However, no coherent clades were observed within strains of *P. atrolazulinum* and *P. consobrinum*. For *P. pagulum*, only two strains were isolated and although they exhibited sequence variation, they were morphologically identical. Remaining fynbos isolates were identified as *P. corylophilum* and *P. rubefaciens*. Ex-type strains of *P. candidofulvum, P. coeruleoviride, P. corylophilum, P. chloroleucon, P. citreovirens, P. humuli,* and *P. obscurum* clustered together. Again, this clade displays sequence variation, but the only consistent branch is the one encompassing the entire clade. As a result, we accept *P. corylophilum* as the correct name for the clade and consider the remaining species synonyms.

Penicillium citreonigrum-clade (Fig. 5) — Based on the multigene analyses, we accept three species in this clade, namely *P. citreonigrum, P. cinerascens* and *P. citreosulfuratum*. *Penicillium toxicarium* (CBS 351.51) was recently shown to be synonymous with *P. trzebinskii* (Houbraken *et al*. 2014). On the other hand, Serra *et al*. (2008) pointed out that *P.*

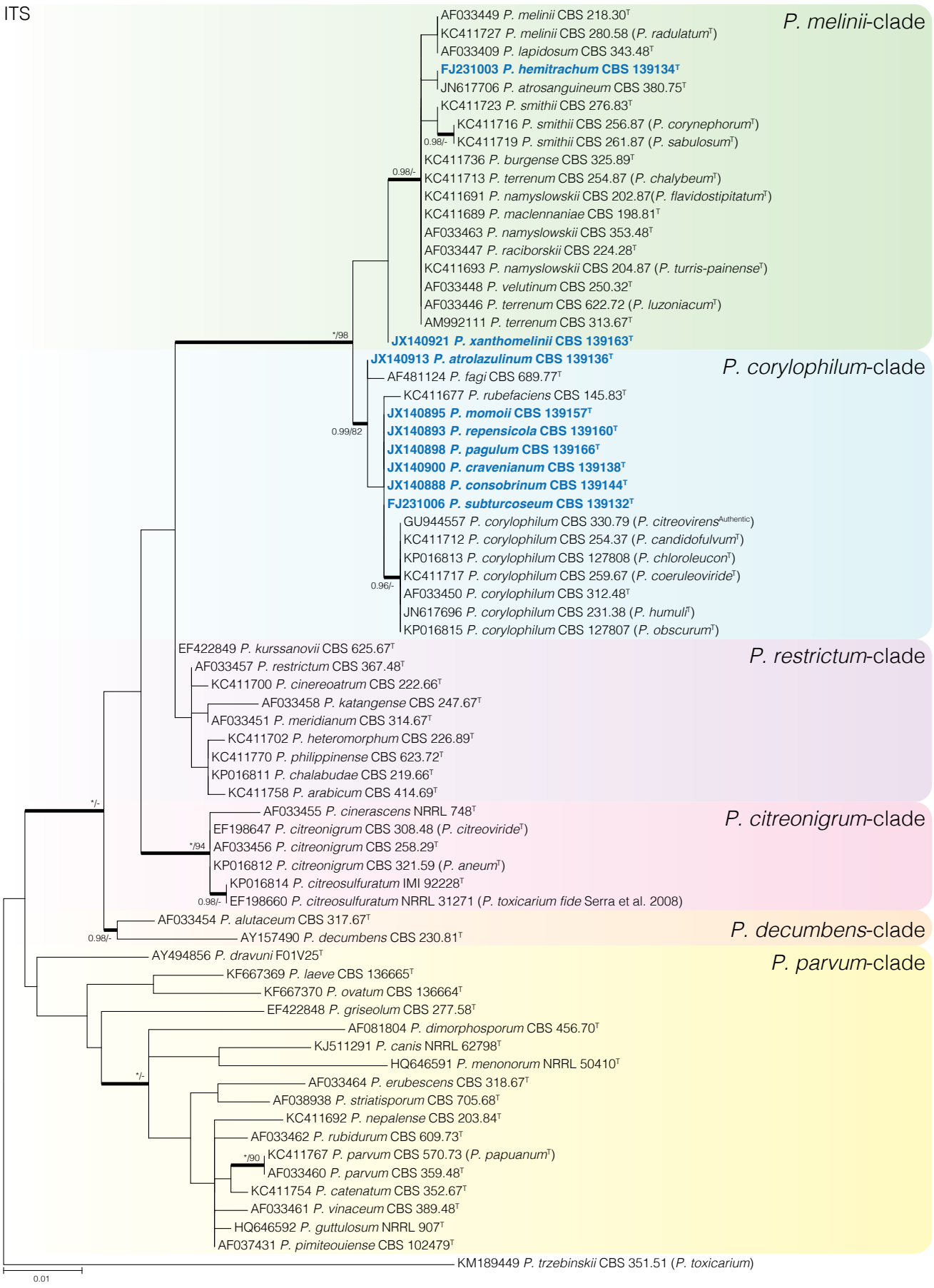

Fig. 1. Phylogenetic tree of *Penicillium* sect. *Exilicaulis* species ex-type strains using the ITS region. *Penicillium toxicarium* (CBS 351.51) was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80 respectively, are given above thickened branches. Names in bold indicate fynbos strains, names in blue indicate new species strains, T = ex-type strain.

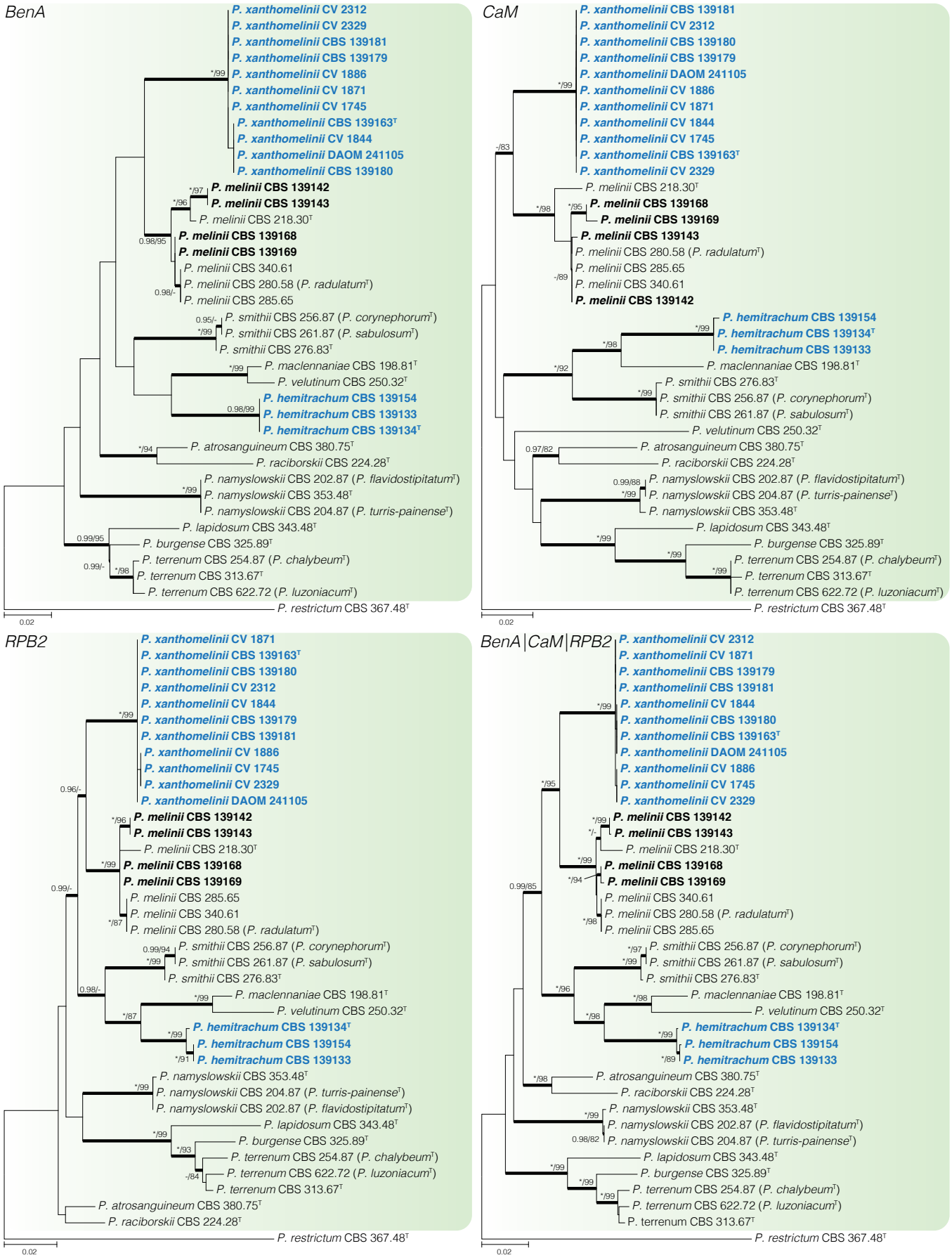

Fig. 2. Phylogenetic tree of *Penicillium* sect. *Exilicaulis* species belonging in the *P. melinii*-clade using *BenA, CaM, RPB2* and combined data sets. *Penicillium restrictum* was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80 respectively, are given above thickened branches. Names in bold indicate fynbos strains, names in blue indicate new species strains, T = ex-type strain.

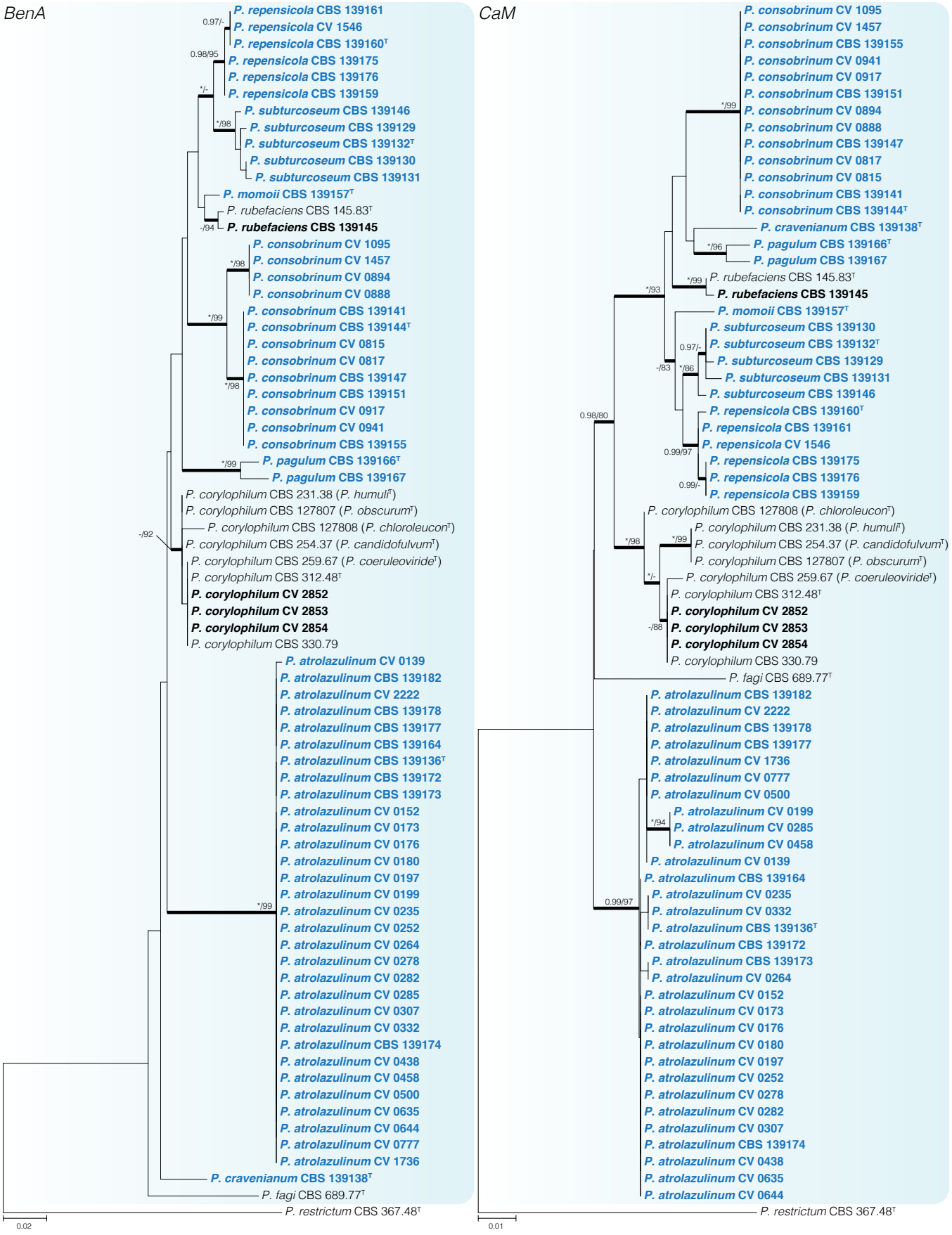

Fig. 3. Phylogenetic tree of *Penicillium* sect. *Exilicaulis* species belonging in the *P. corylophilum*-clade using *BenA* and *CaM*. *Penicillium restrictum* was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80 respectively, are given above thickened branches. Names in bold indicate fynbos strains, names in blue indicate new species strains, T = ex-type strain.

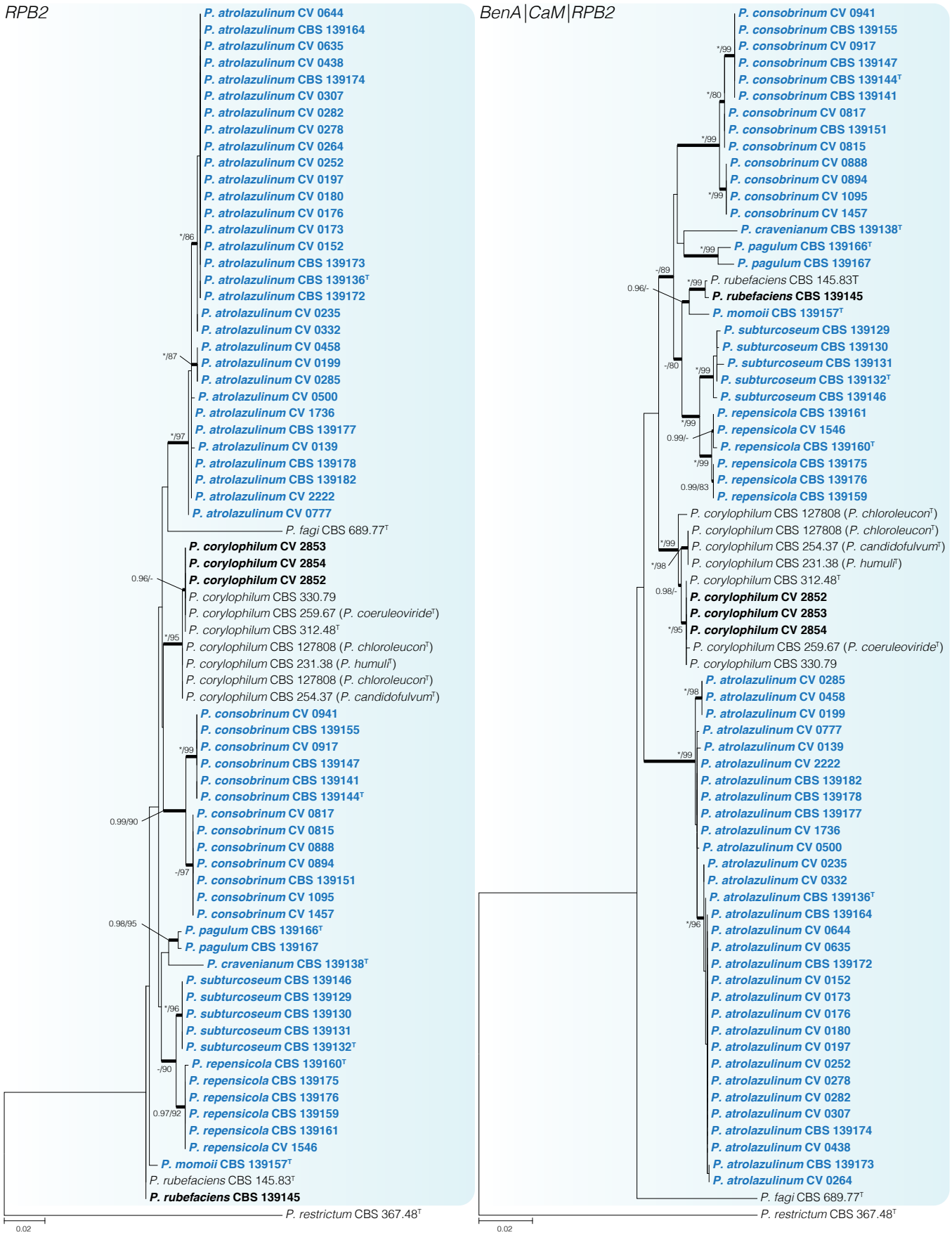

Fig. 4. Phylogenetic tree of *Penicillium* sect. *Exilicaulis* species belonging in the *P. corylophilum*-clade using *RPB2* and combined data sets. *Penicillium restrictum* was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80 respectively, are given above thickened branches. Names in bold indicate fynbos strains, names in blue indicate new species strains, T = ex-type strain.

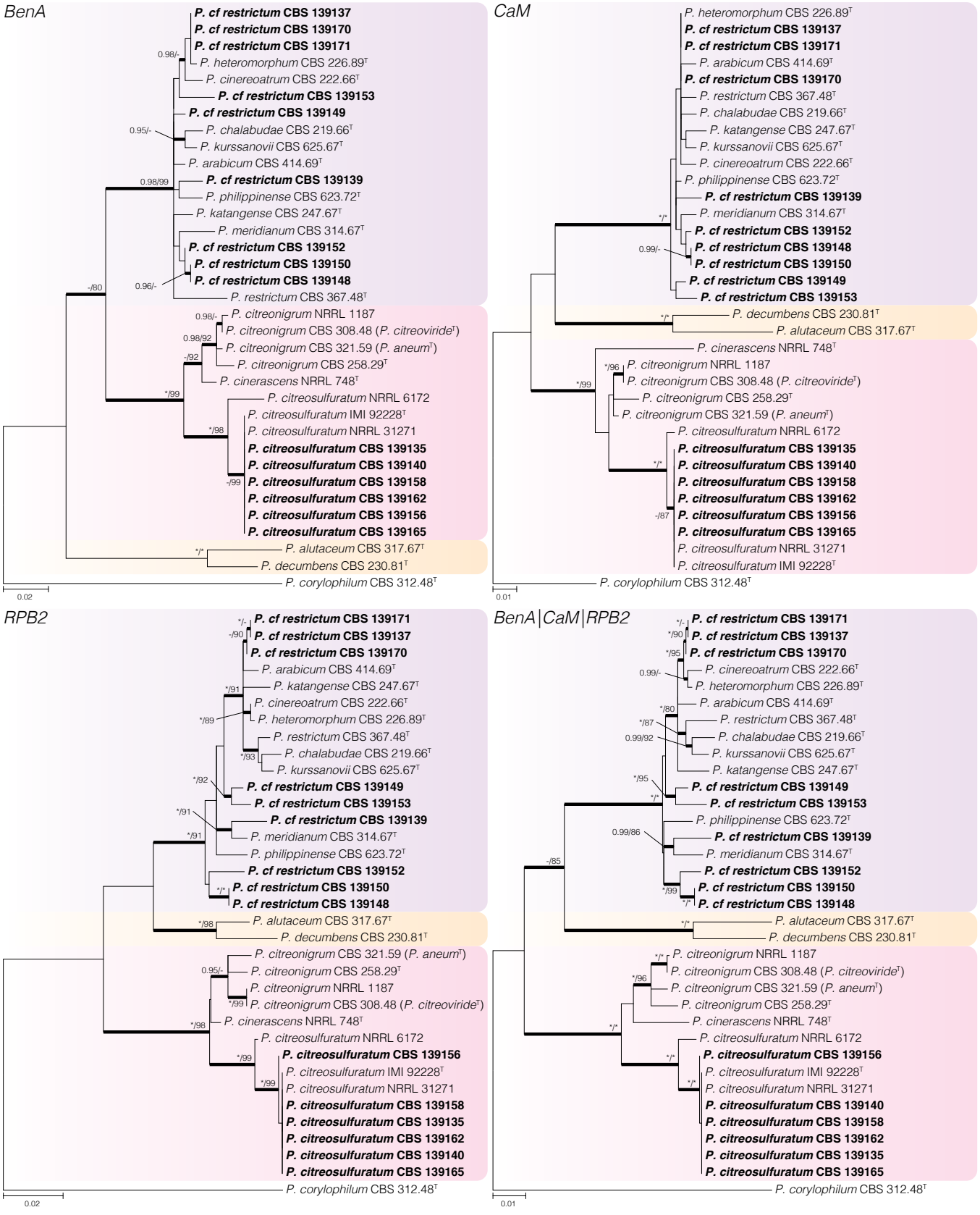

Fig. 5. Phylogenetic tree of *Penicillium* sect. *Exilicaulis* species belonging in the *P. citreonigrum-*, *P. decumbens*- and *P. restrictum*-clades using *BenA, CaM, RPB2* and combined data sets. *Penicillium corylophilum* was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80 respectively, are given above thickened branches. Names in bold indicate fynbos strains, T = ex-type strain.

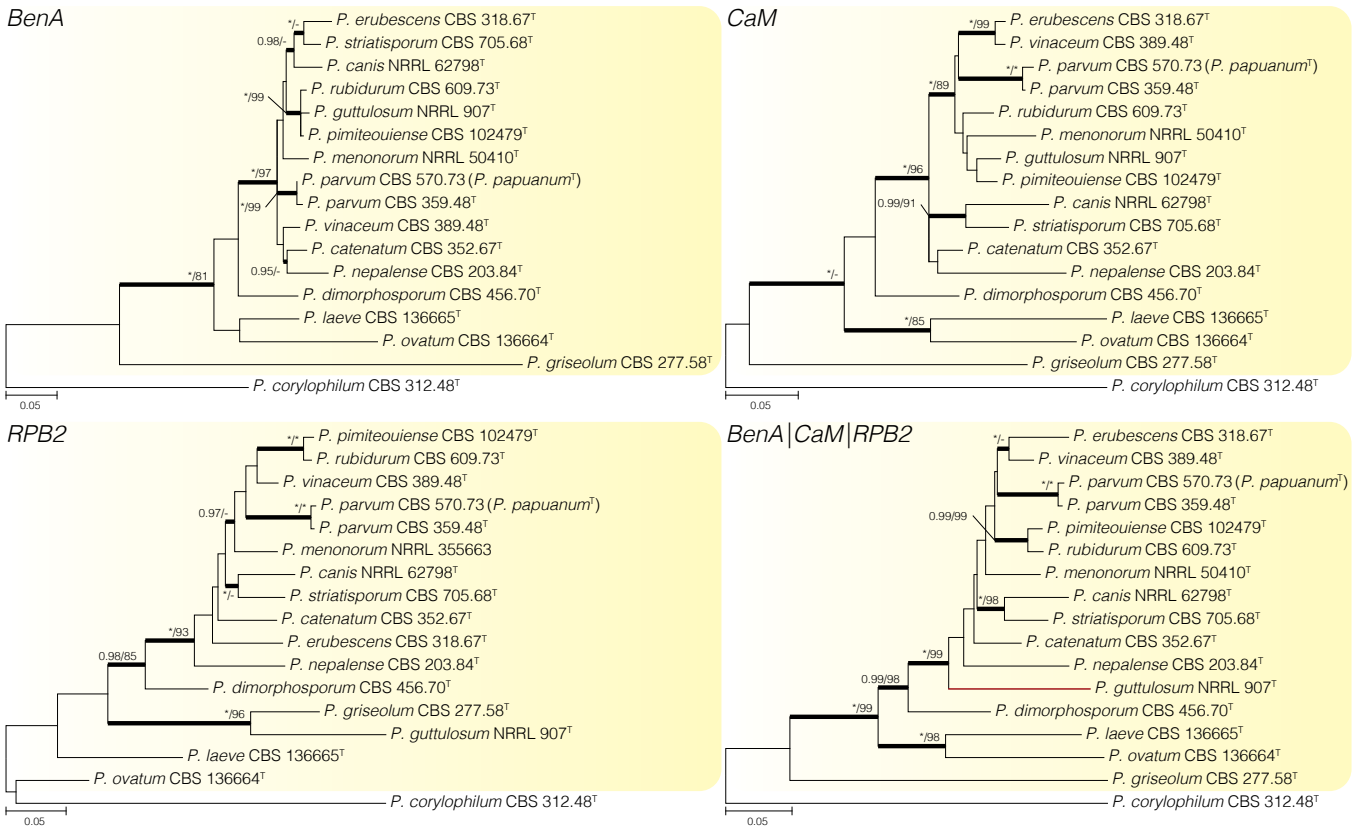

Fig. 6. Phylogenetic tree of *Penicillium* sect *Exilicaulis* species belonging in the *P. parvum*-clade using *BenA, CaM, RPB2* and combined data sets. *Penicillium corylophilum* was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80 respectively, are given above thickened branches. Names in bold indicate fynbos strains, names in blue indicate new species, T = ex-type strain. In the combined phylogeny, the *RPB2* sequence (KF900194) for *P. menonorum* (NRRL 50410) was too short for the phylogeny and was replaced with a representative sequence (KF900193) from different strain (NRRL 35663).

toxicarium should be considered a distinct species and closely related to *P. citreonigrum*; unfortunately, they did not identify which strain in their analysis represented the ex-type. Here we show that strains they named as *P. toxicarium* cluster in a clade with *P. citreosulfuratum*, the latter representing the oldest and thus correct name for the species. *Penicillium cinerascens* is also shown to be a distinct species and the closest relative of *P. citreonigrum*.

Penicillium decumbens-clade (Fig. 5) — *Penicillium decumbens* and *P. alutaceum* were resolved as close relatives in a distinct clade and all genes easily distinguish between the two.

Penicillium restrictum-clade (Fig. 5) — This clade includes nine previously described species in a complex and fynbos isolates may represent as many as six new species. However, strains isolated from house dust identified as "*P. restrictum*" (Visagie *et al.* 2014a) potentially also represent new species and from discussions with colleagues we are aware that there may be even more. Therefore we temporarily identify the fynbos strains as *P. cf. restrictum,* with the suggestion that this complex needs a comprehensive revision. *Penicillium arabicum* (syn. *P. decumbens fide* Pitt 1980)*, P. albocinerascens* (syn. *P. adametzii fide* Pitt 1980), and *P. kurssanovii* (syn. *P. restrictum fide* Pitt 1980) were not included in the list of accepted species by Visagie *et al*. (2014b). From our phylogenies, it is clear that they represent distinct species within the species concept currently adopted in this particular clade.

Penicillium parvum-clade (Fig. 6) — None of the fynbos strains resolved in this clade. Our phylogeny confirms the results of Houbraken & Samson (2011), who considered *P. papuanum* a synonym of *P. parvum.*

Morphology

Based on morphological characters, *Penicillium* sect. *Exilicaulis* can be split into two parts that correlate with the two main groups in the phylogenies. Species from the *P. corylophilum* and *P. melinii* clades typically produce biverticillate conidiophores with metulae on one conidiophore which are often of unequal length. The remaining clades contain species that typically produce non-vesiculate monoverticillate conidiophores with short stipes.

Fynbos isolates of the biverticillate clades typically produce conidiophores with rough stipes (but are smooth in *P. corylophilum*), and metulae and conidia which are roughened. Morphological differences observed were consistently supported by the phylogenies. Strains identified as *P. melinii* produce typical divergent, slender conidiophores with spinose, globose conidia. The rough walled phialides observed in fynbos isolates have not previously been observed in this species. All strains examined in this study produced a brownish colony reverse on CYA and sometimes produced brownish to red exudates on top

of the colonies. Strains identified as *P. corylophilum* had smooth walled stipes, the only biverticillate species in this section with this character state. The strain identified as *P. rubefaciens* (CBS 139145) was identical with the ex-type strain (CBS 145.83). *Penicillium rubefaciens* sporulates poorly and grows rather restrictedly on CYA at 25 °C attaining 15–23 mm diam, recalling the observations of Quintanilla (1982). The species is morphologically similar to *P. consobrinum, P. repensicola, P. momoii,* and *P. subturcoseum,* but can be distinguished by the colony growth rates as discussed below.

Monoverticillate fynbos isolates were identified as *P. citreosulfuratum* and *P. cf. restrictum*. *Penicillium citreosulfuratum* was one of the most commonly isolated species from inside *Protea repens* infructescences, but was also obtained from soil and air samples. Because of its prevalence, and the confusion surrounding the species concept and name, which was also commonly found in cork from Portugal but at the time identified as *P. toxicarium* (Serra *et al.* 2008), we provide a description for the species below. As mentioned, phylogenetically strains identified as *P. cf. restrictum* probably represent new species, but the morphological differences are minor and inconsistent between strains, e.g. CBS 139150, CBS 139170 and CBS 139171 which have both smooth and spiny conidia. Therefore, with currently available data there is not enough evidence to introduce new species names amongst this limited set of strains here.

TAXONOMY

Penicillium atrolazulinum Visagie & K. Jacobs, **sp. nov.**
MycoBank MB811001
(Figs 7–8)

Etymology: Latin, *atrolazulinum,* dark blue. Named in reference to the characteristic dark blue colony reverse on CYA, MEA and YES.

Diagnosis: Differs from close relatives in having dark colony reverses, while conidiophores have relatively long stipes and metulae that often have a green pigmentation.

Type: **South Africa:** Stellenbosch, isol. ex air sample, Mar. 2009, isol. *C. M. Visagie* (CBS H-22043 [dried culture] – holotype; CBS 139136 = DAOMC 241083 = DTO 180-H4 = CV 55 – ex-type cultures).

ITS barcode: JX140913. Alternative identification markers: *BenA* = JX141077, *CaM* = JX157416, *RPB2* = KP064575.

Colony diam, 7 d (in mm): CYA 20–50; CYA 30 °C 12–27; CYA 37 °C no growth, rarely up to 5; MEA 30–50; YES 28–47; G25N 6–15; CREA 18–25.

Colony characters: CYA, 25 °C, 7d: Colonies low to moderately deep, plane to very faintly sulcate; margins low, narrow to wide (1–5 mm), entire to somewhat irregular; mycelia white, sometimes green when embedded; texture mostly velutinous, floccose regions present; sporulation moderately dense, conidia *en masse* dull to greyish green (24D4–6; 25D4–6; 25E4–26E4); exudate clear to almost a hazy yellow, sometimes absent; soluble pigment mostly absent, sometimes yellowish orange; reverse dark blue to dark turquoise (23F8–24F8), pale yellow (1A3–2A3) at margin, some strains dark green (27F6–7) at centre, pastel yellow (3A4) at margin. MEA, 25 °C, 7d: Colonies low, plane; margins low to almost subsurface, wide (4–5 mm), entire; mycelia white, sometimes green when embedded; texture velutinous, floccose areas present; sporulation dense to moderately dense, conidia *en masse* dull green to greyish green (26E4–6) at centre, greyish green (25D6) near margin, some strains greyish turquoise (24C6–E4–5); exudate absent; soluble pigment absent; reverse dark blue to dark turquoise (24F8–25F8), greyish green (29C3) near margin, some strains dark green (28F6–7) at centre, (30C5) near margin. YES, 25 °C, 7d: Colonies low, to moderately deep, random furrows and ridges present; margins low, wide, regular, entire; mycelia white, sometimes green when embedded; texture velutinous, with loosely funiculose mycelia present; sporulation moderately dense, conidia *en masse* similar to CYA; exudate absent; soluble pigment absent, some strains yellowish orange; reverse dark blue to dark turquoise (24F8–25F8), pale yellow (1A3–2A3) at margin, some strains dark green (25F8) at centre, greyish yellow to yellow (3B5–3B8) near margin. CREA, 25 °C, 7d: Acid not produced.

Micromorphology: Conidiophores typically borne from green mycelia embedded in medium, stipes mostly hyaline but sometimes green, mostly biverticillate, infrequently terverticillate, monoverticillate side branches sometimes present; Stipes very short to very long, typically rough, a minor proportion smooth to finely rough, 40–400 × 2.5–4 µm; Branches two when present, 13–39.5 × 2.5–4 µm; Metulae mostly 3–5 per stipe, sometimes only two, divergent 38–69° (52.8±9.2), 11–23 × 2.5–4 µm (15.4±2.7 × 3.1±0.4), vesicle 3.5–6 µm (4.7±0.5); Phialides ampulliform, 6–9 per metula, sometimes up to sixteen, 7–9.5 × 2.5–4 µm (8.3±0.6 × 3±0.3); Conidia smooth, globose to subglobose, 2–3 × 2–2.5 µm (2.3±0.2 × 2.2±0.1), average width/length = 0.95, *n* = 32.

Notes: *Penicillium atrolazulinum* typically produces conidiophores with roughened stipes borne from greenish to blue submerged mycelia. This green pigmentation is present in some conidiophores, although most are hyaline, and gives this species its most striking feature, the dark turquoise to green colony reverse observed on most media. Although these characters are consistent, infraspecific variation is observed among strains, especially in colony diameter and appearance on CYA. Some strains, for instance, produce yellowish orange soluble pigments, which mask the characteristic reverse colour. Although a large degree of morphological variation is observed, the phylogenies confirm this as one species (Figs 3–4). Morphologically, *P. fagi* closely resembles the new species, producing dark colony reverses and similar conidiophores (Martinez & Ramírez 1978). In general, *P. atrolazulinum* produces longer stipes and metulae than *P. fagi.* Also, the green conidiophore stipes sometimes observed in the new species are unreported for *P. fagi.* Phylogenetically, *P. atrolazulinum* is distinct from all previously described species (Figs 3–4).

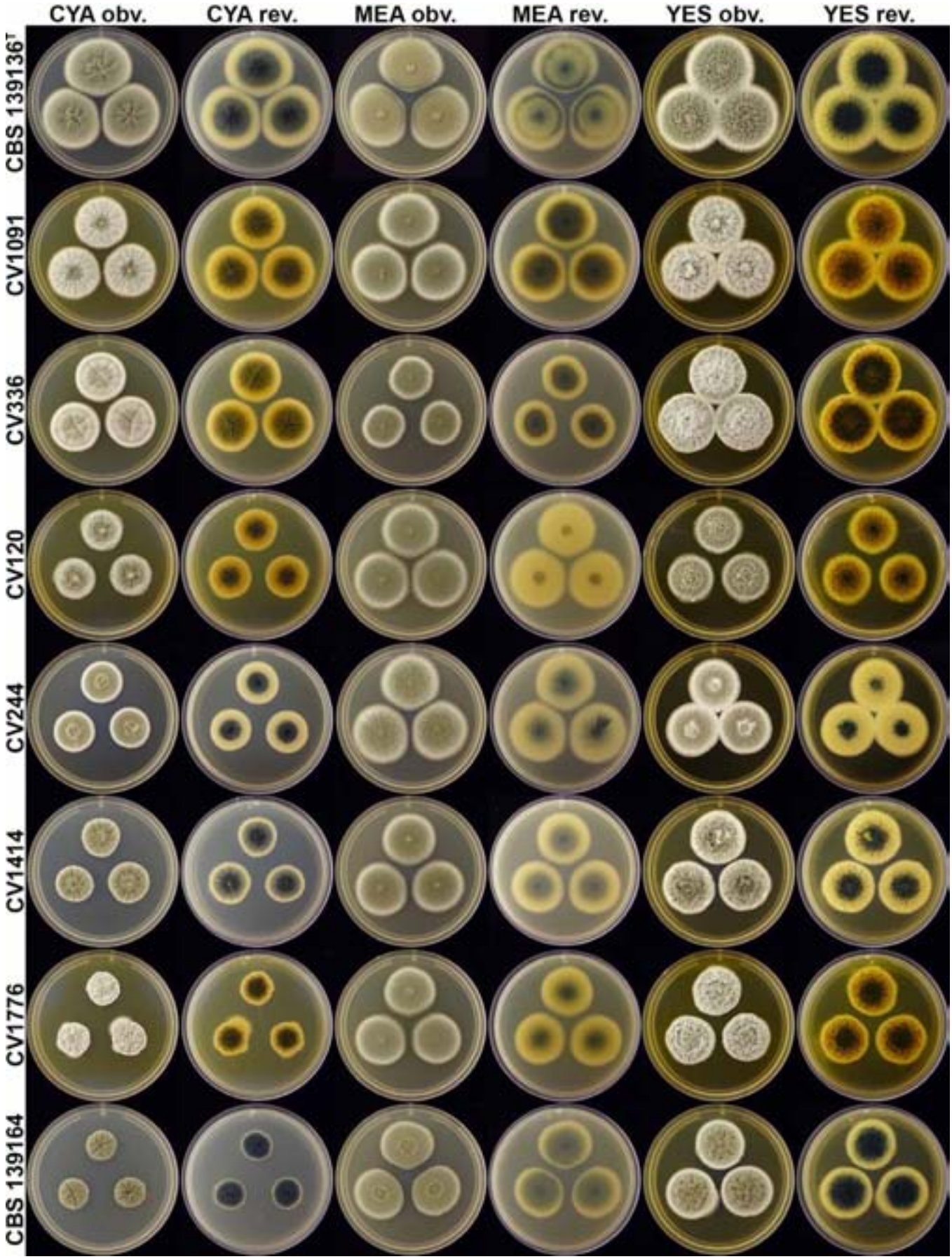

Fig. 7. *Penicillium atrolazulinum* colonies (top to bottom rows; CBS 139136, CV 1091, CV 336, CV 120, CV 244, CV 1414, CV 1776, CBS 139164), showing variation typical of the species.

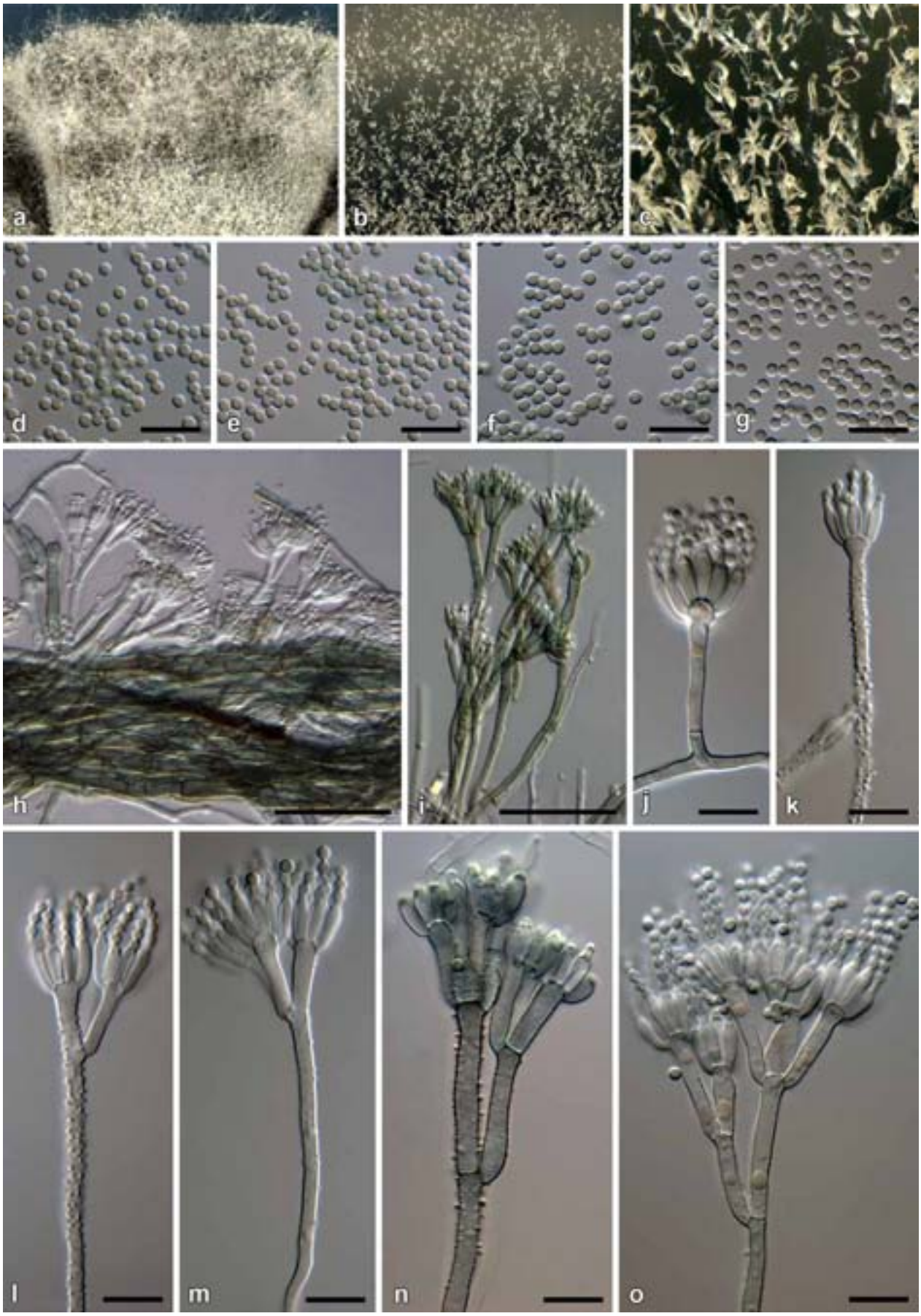

Fig. 8. *Penicillium atrolazulinum* conidiophores. a. Texture on CYA. b, c. Texture on MEA. d–g. Conidia (d. CBS 139136. e. CV 120. f. CBS 139164. g. CV 1776). h. Green mycelia embedded in medium, from where conidiophores are borne. i–o. Conidiophores. Bars h– i = 50 µm; d–g, l–o = 10 µm.

Penicillium burgense Quintan. ex Visagie, **sp. nov.**
MycoBank MB816641
Synonym: *Penicillium burgense* Quintan., *Av. Aliment Majora Anim*. **30**: 176 (1990); *nom. inval*. (Art. 40.7).

Diagnosis: Differs from its close relatives, *P. lapidosum* and *P. terrenum*, by lacking ascospore production and typically more complexly branched conidiophores. Also, faster growth reported at 37 °C (Quintanilla 1990).

Type: **Spain:** highlands north of Burgos, isol. ex soil, date unknown, isol. *J.A. Quintanilla* (CBS H-22567 [dried culture] – holotype; CBS 325.89 – ex-type cultures).

ITS barcode: KC411736. Alternative identification markers: *BenA* = KJ834437, *CaM* = KP016772, *RPB2* = JN406572.

Notes: *Penicillium burgense* was invalidly described by Quintanilla (1990) because no collection or herbarium was specified with his "1538" type designation (Art. 40.7). His original strain was sent to the CBS collection (CBS 325.89), the Netherlands. A dried specimen of his strain was used here to correct the typification and application of the name.

Penicillium chalabudae Visagie, **nom. nov.**
MycoBank MB816642
Replaced name: *Penicillium albocinerascens* Chalab., *Not. Syst. Crypt. Inst. bot. Acad. Sci. USSR* **6**: 166 (1950); *nom. illegit*. (Art. 53.1).
Non *Penicillium albocinerascens* (Maublanc) Biourge, *Cellule* 33: 100 (1923) *fide* (Pitt 1980).

Diagnosis: Morphologically this species has all the characters associated with the *P. restrictum* species complex. Multigene analysis confirms the species as unique.

Etymology: Latin, *chalabudae,* named after T.V. Chalabuda.

Type: **Ukraine:** Kiev, ex soil sample, isol. *T.V. Chalabuda* (CBS H-15439 [dried culture] – holotype; CBS 219.66 = ATCC 18322 = ATCC 18329 = FRR 3393 = VKM F-1037 – ex-type cultures).

ITS barcode: KP016811. Alternative identification markers: *BenA* = KP016748, *CaM* = KP016767, *RPB2* = KP064572.

Notes: Chalabuda (1950) used the epithet "*albocinerascens*" for his new species, not realising that Biourge (1923) already used the name. As such, Chalabuda's species is illegitimate (Art. 53.1) and we introduce the new name *P. chalabudae* for CBS H-15439. The species phylogenetically belongs in the *P. restrictum* species complex and has unique sequences.

Penicillium citreosulfuratum Biourge, *Cellule* **33**: 285 (1923).
MycoBank MB260947
(Fig. 9)
Synonym: *Penicillium toxicarium* I. Miyake, *Rep. Res. Inst. Rice Improvement*: 1 (1940); *nom. inval*. (Art. 39.1).
Non *Penicillium toxicarium* I. Miyake ex C. Ramírez, *Man. Atlas Penicillia*: 125 (1982) = *Penicillium trzebinskii* K.M. Zalessky 1927 *fide* (Houbraken *et al*. 2014).

Type: **France:** source unknown, Biourge, *Cellule* **33**: fig. 86 nº 21 (– ***lectotype designated here***, MBT203135; K(M) IMI 92228 [dried culture] – ***epitype designated here***, MBT203136; IMI 92228 = DTO 290-I4 = Biourge 21 = MUCL 29785 – ex-type cultures).

ITS barcode: KP016814. Alternative identification markers: *BenA* = KP016753, *CaM* = KP016777, *RPB2* = KP064615.

Colony diam, 7 d (in mm): CYA 20–25; CYA 30 °C 20–25; CYA 37 °C 3–7; MEA 15–18; YES 27–33; G25N 12–15; CREA 10–13.

Colony characters: CYA, 25 °C, 7d: Colonies radially and concentrically sulcate, moderately deep; margins low, narrow, entire; mycelia yellow; texture floccose; sporulation sparse to moderate, conidia *en masse* greyish to dark green (25D6–F6–26E6); exudate clear, absent in some strains; soluble pigment yellow; reverse yellow (3A6–3A8) to orange-yellow (4B8). MEA, 25 °C, 7d: Colonies low, plane; margins low, narrow, entire; mycelia white at margins, yellow elsewhere; texture floccose; sporulation moderately dense, conidia *en masse* dull to greyish green (25E4–26E5); exudate absent; soluble pigment yellow; reverse greenish yellow (1A6) at point of inoculation, fading into greyish yellow (1B6–2B6). YES, 25 °C, 7d: Colonies low to moderately deep, radially and concentrically sulcate; margins low, very narrow, entire; mycelia white at edges, yellow centrally; texture floccose; sporulation sparse, conidia *en masse* greenish white (27A2), dull green (27E4) in more dense areas; exudate absent; soluble pigment absent; reverse light yellow to yellow (3A4–6) to deep yellow (4A8) in some isolates. CREA, 25 °C, 7d: Acid not produced.

Micromorphology: Conidiophores mostly monoverticillate but sometimes with very short stipes that could be interpreted as subterminal branches, with biverticillate conidiophores sometimes present; Stipes/branches smooth, when terminal 70–290 × 2–2.5 µm, when borne sub-terminally 18–90 × 2–2.5 µm; Metulae typically 2, sometimes 3, divergent, 8–29 × 1.5–2.5 µm (18±4.5 × 2.1±0.2), vesicle 2.5–4 µm (3.4±0.3); Phialides ampulliform, 5–10 per metula, 5–9 × 2–3 µm (6.7±0.9 × 2.4±0.2); Conidia smooth, globose, 1.5–2 × 1.5–2 µm (1.8±0.1 × 1.8±0.1), average width/length = 0.98, *n* = 50.

Notes: *Penicillium citreosulfuratum* is distinguished by the compact yellow colonies and the soluble pigments produced on most media. The conidiophores are typically smooth walled, short, and slender and sometimes can be interpreted as either monoverticillate with very short stipes or as irregularly biverticillate (divaricate). In the strains examined, most conidiophores were strictly monoverticillate. *Penicillium citreosulfuratum* is closely related to *P. citreonigrum* and *P. cinerascens* (Figs 1, 5). These three species are morphologically difficult to distinguish. Ex-type strains of *P. citreonigrum* and *P. cinerascens* do not grow at 37 °C, whereas all *P. citreosulfuratum* strains studied had

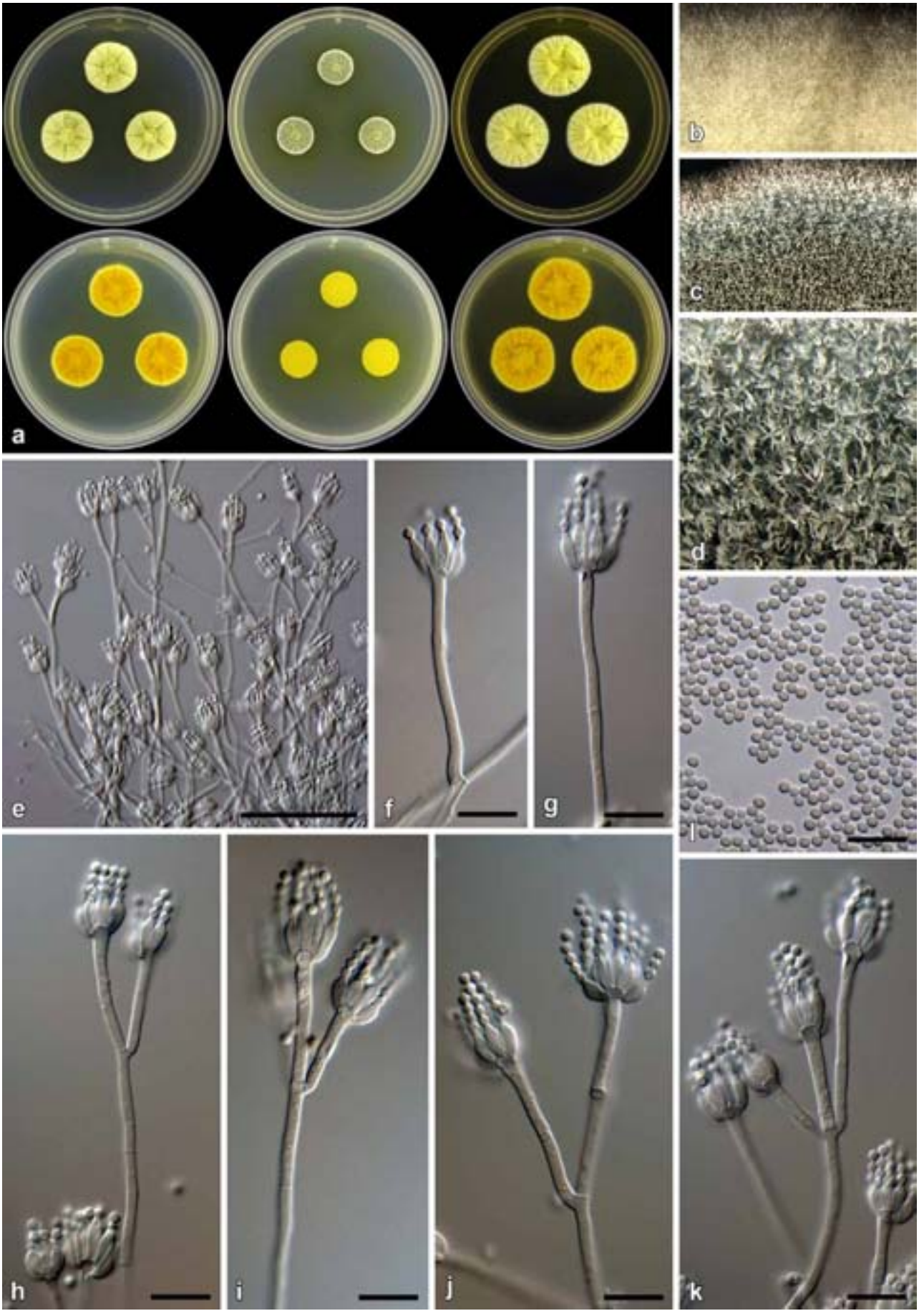

Fig. 9. *Penicillium citreosulfuratum* (CBS 139135). a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse). b. Texture on CYA. c–d. Texture on MEA. e–k. Conidiophores. l. Conidia. Bars e = 50 µm, f–l = 10 µm.

at least restricted growth at that temperature. For accurate identification of these species, we suggest the use of ITS or *BenA* sequences. *Penicillium toxicarium* became the informal name for this species following the publication of Serra *et al.* (2008), but they did not provide information on the type material of that species. *P. citreosulfuratum* is, however, clearly the correct name for this species because it is the oldest name and type material is available.

Penicillium consobrinum Visagie & K. Jacobs, **sp. nov.**
MycoBank MB811002
(Fig. 10)

Etymology: Latin, *consobrinum,* cousin, named in reference to its close relationship with other species in the *P. corylophilum* clade.

Diagnosis: Differs from close relatives by showing no growth on CYA at 37 °C, but colonies on MEA 48–52 mm.

Type: **South Africa:** Stellenbosch, isol. ex soil sample, Mar. 2009, isol. *C. M. Visagie* (CBS H-22045 [dried culture] – holotype; CBS 139144 = DAOMC 241072 = DTO 181-H9 = CV547 – ex-type cultures).

ITS barcode: JX140888. Alternative identification markers: *BenA* = JX141135, *CaM* = JX157453, *RPB2* = KP064619.

Colony diam, 7 d (in mm): CYA 29–34; CYA 30 °C 25–32; CYA 37 °C no growth; MEA 48–52; YES 40–45; G25N 11–15; CREA 17–20.

Colony characters: CYA, 25 °C, 7d: Colonies low to moderately deep, faintly radially sulcate, often having sterile areas at centre, giving colony a greyish green colour; margins low, very narrow (1 mm), entire; mycelia white; texture mostly velutinous, floccose at colony centre; sporulation moderately dense, conidia *en masse* greyish green (25E6–7) and greyish turquoise (24B3–4); exudate mostly absent, sometimes clear exudate present; soluble pigment absent; reverse brown (5F7–6F7) at centre, becoming pale yellow (4A3) near margin. MEA, 25 °C, 7d: Colonies low, plane; margins low to subsurface, wide (4 mm), entire; mycelia white; texture velutinous; sporulation dense, conidia *en masse* greyish green (25E6–7); exudate absent; soluble pigment absent; reverse greyish yellow (2B5) at centre, fading into greyish green to greyish yellow (30B3–C3–4). YES, 25 °C, 7d: Colonies low to moderately deep, radially and faintly concentrically sulcate, random furrows present; margins low, narrow, entire; mycelia white; texture mostly velutinous, floccose areas present; sporulation moderately dense to dense in regions, conidia *en masse* similar to CYA; exudate absent; soluble pigment absent; reverse dark green (25F8) at centre, fading into greyish green (28C4) to greyish yellow (1B4) near margin. CREA, 25 °C, 7d: Acid not produced.

Micromorphology: Conidiophores biverticillate with a minor proportion terverticillate and having subterminal branches; Stipes rough, 75–400 × 2.5–3.5 µm; Branches 2 when present, 16–70 × 2.5–3.5 µm; Metulae 2–5 per stipe, divergent, sometimes slightly appressed, 25–76° (46±10.4), 12–25 × 2.5–3.5 µm (17±2.3 × 2.9±0.3), vesicle 3.5–5.5 µm (4.5±0.5); Phialides ampulliform, 12–16 per metula, 6.5–10 × 2–3.5 µm (8.3±0.6 × 2.8±0.3); Conidia finely roughened, globose, 2–3 × 2–3 µm (2.3±0.2 × 2.3±0.2), average width/length = 0.97, *n* = 79.

Notes: *Penicillium consobrinum* typically produces colonies with a dark green reverse on YES and a brown reverse on CYA. Conidiophores are rough walled with finely roughened, globose conidia. Colony characters closely resemble those of *P. corylophilum*, but the latter produces smooth walled conidiophores. Phylogenetically, *P. consobrinum* belongs to a clade with *P. cravenianum, P. pagulum, P. repensicola, P. rubefaciens, P. momoii,* and *P. subturcoseum*. In that clade, *P. cravenianum* is distinguished from other species by the slow growth on MEA (16–20 mm). *Penicillium pagulum,* on the other hand, grows poorly on CYA at 25 °C (15–20 mm). *Penicillium rubefaciens* does not grow on CYA at 37 °C, whereas *P. pagulum* has restricted growth (1–5 mm) at that temperature. *Penicillium consobrinum* also does not grow at 37 °C, but on MEA grows faster than *P. rubefaciens* (48–52 *vs*. 25–30 mm). The remaining three species, *P. repensicola* (7–15 mm), *P. momoii* (5–8 mm), and *P. subturcoseum* (1–2 mm), can grow on CYA at 37 °C, with *P. repensicola* strains consistently growing fastest, while *P momoii* grew faster (only based on the one strain) than *P. subturcoseum*. The sporulation of *P. repensicola* strains is also consistently much denser on CYA at 25 °C than other species in this clade. *Penicillium momoii* grows only slightly more restrictedly on MEA and G25N compared to *P. subturcoseum*. Morphological differences are sometimes minor, which makes identification difficult, but these differences correlate with the phylogenies applying GCPSR (Figs 3–4).

Penicillium cravenianum Visagie & K. Jacobs, **sp. nov.**
MycoBank MB811003
(Fig. 11)

Etymology: Latin, *cravenianum*, named after Danie Craven, former president of the South African Rugby Board and ex-student of Stellenbosch University. The species was isolated from the foot of the mountain next to the Danie Craven Rugby Stadium.

Diagnosis: Differs from close relatives by showing restricted growth on MEA at 25 °C (16–20 mm).

Type: **South Africa:** Stellenbosch, isol. ex soil sample, Mar. 2009, isol. *C. M. Visagie* (CBS H-22044 [dried culture] – holotype; CBS 139138 = DAOMC 241082 = DTO 180-I5 = CV 92 – ex-type cultures).

ITS barcode: JX140900. Alternative identification markers: *BenA* = JX141076, *CaM* = JX157418, *RPB2* = KP064636.

Colony diam, 7 d (in mm): CYA 28–30; CYA 30 °C 25–28; CYA 37 °C no growth; MEA 16–20; YES 28–34; G25N 8–11; CREA 19–22.

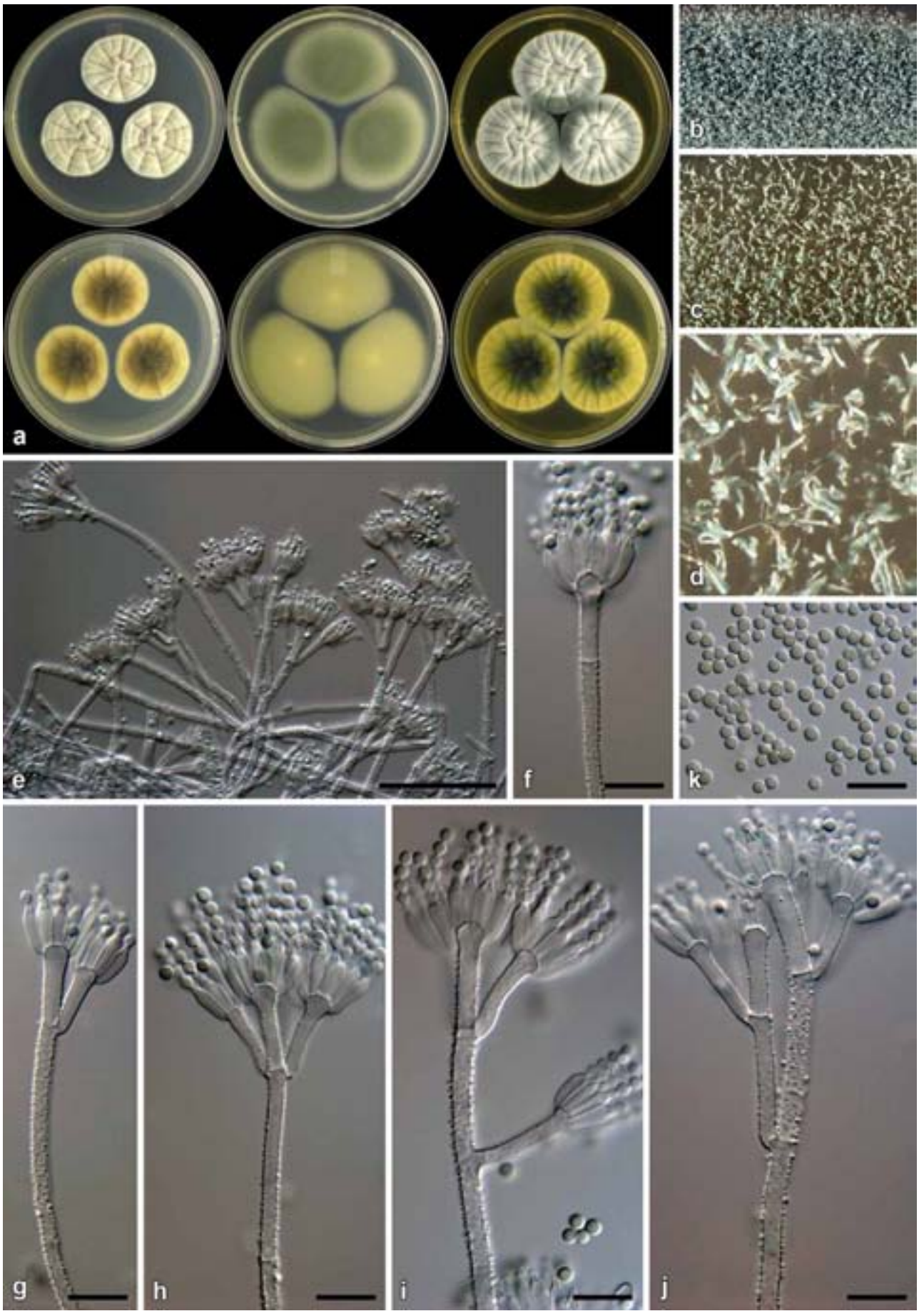

Fig. 10. *Penicillium consobrinum* (CBS 139144). a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse). b. Texture on CYA. c–d. Texture on MEA. e–j. Conidiophores. k. Conidia. Bars e = 50 µm, f–k = 10 µm.

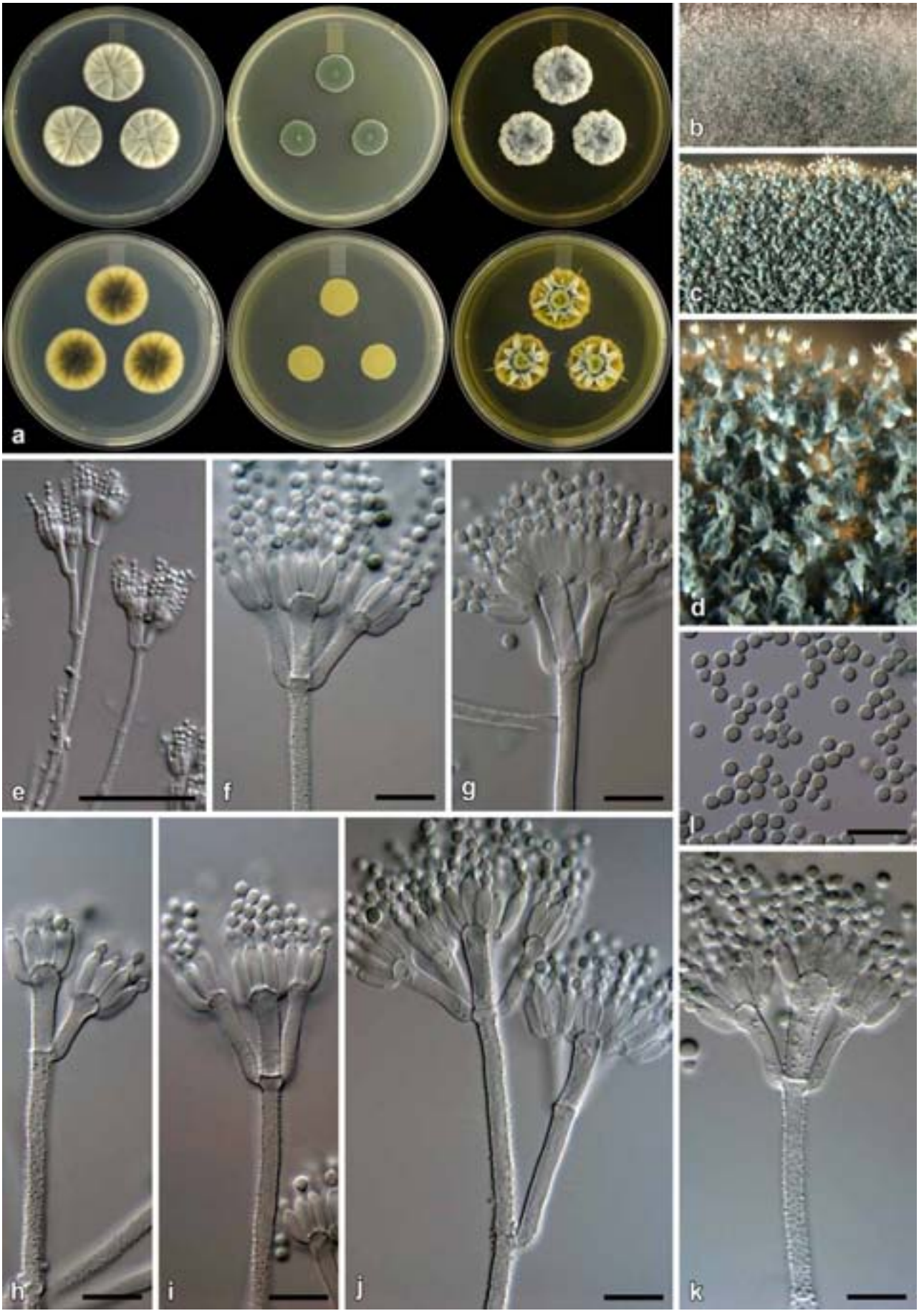

Fig. 11. *Penicillium cravenianum* (CBS 139138). a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse). b. Texture on CYA. c–d. Texture on MEA. e–k. Conidiophores. l. Conidia. Bars e = 50 µm, f–l = 10 µm.

Colony characters: CYA, 25 °C, 7d: Colonies low to moderately deep, radially and concentrically sulcate; margins low, narrow, entire; mycelia white; texture velutinous; sporulation sparse to sometimes moderate, conidia *en masse* dull green (30E3–4) at centre, dull green to greyish green (25D4–5) elsewhere; exudate absent; soluble pigment absent; reverse dark green to olive (30F5–8–1F5–8) at centre, pale yellow (2A3–3A3) near edge. MEA, 25 °C, 7d: Colonies low, plane; margins subsurface, narrow, entire; mycelia white; texture velutinous, floccose near centre; sporulation dense, conidia *en masse* dark green (25F8–26F8); exudate absent; soluble pigment absent; reverse yellow (3B8) at centre, fading into dull yellow (3B4) margin. YES, 25 °C, 7d: Colonies low, radially and concentrically sulcate, with randomly raised furrows; margins narrow, entire; mycelia white; texture floccose; sporulation sparse to sometimes moderately dense, conidia *en masse* similarly coloured as CYA; exudate absent; soluble pigment absent; reverse greyish green (28D6–E6) at centre, light to greyish yellow (3A5–B5) at margin. CREA, 25 °C, 7d: Acid not produced.

Micromorphology: Conidiophores mostly biverticillate, some terverticillate; stipes rough, 120–325 × 2.5–4 µm; Branches 2 when present, 16–48 × 2.5–4 µm; Metulae 2–6 per stipe, slightly divergent, 31–73° (51±10.3), 11–22 × 2.5–4.5 µm (15.4±2.1 × 3.1±0.4), vesicle 3.5–5.5 µm (4.7±0.5); Phialides ampulliform, 8–12 per metula, 7–9.5 × 2.5–3.5 µm (8.1±0.6 × 3±0.2); Conidia finely rough, globose to broadly ellipsoidal, 2.5–3 × 2–3 µm (2.6±0.2 × 2.4±0.1), average width/length = 0.93, *n* = 112.

Notes: *Penicillium cravenianum* characteristically produces colonies with restricted growth on MEA, somewhat resembling those of *P. brevicompactum*, and conidiophores with rough walls. These characters distinguish it from all close relatives in the *P. corylophilum* clade (Figs 3–4). *Penicillium brevicompactum* produces smooth walled conidiophores. See also under *P. consobrinum*.

Penicillium hemitrachum Visagie & K. Jacobs, **sp. nov.**
MycoBank MB811004
(Fig. 12)

Etymology: Latin, meaning half rough walled, named in reference to the rough and smooth walled metulae produced on the same conidiophore.

Diagnosis: Differs from close relatives by producing fast growing colonies especially on CYA at 30 °C; conidiophores have a brownish to green pigmentation, have rough walled stipes, while different metulae from the same conidiophore can be rough or smooth; conidia globose 2–2.5 µm.

Type: **South Africa:** Malmesbury, isol. ex air sample, Feb. 2007, isol. *C. M. Visagie* (CBS H-22042 [dried culture] – holotype; CBS 139134 = DAOMC 241098 = DTO 180-D8 = CV 2845 – ex-type cultures).

ITS barcode: FJ231003. Alternative identification markers: *BenA* = JX141048, *CaM* = JX157526, *RPB2* = KP064642.

Colony diam, 7 d (in mm): CYA 54–58; CYA 30 °C 60–62; CYA 37 °C 4–9; MEA 68–70; YES 68–70; G25N 10–18; CREA 20–25.

Colony characters: CYA, 25 °C, 7d: Colonies low, radially sulcate, concentrically sulcate in fresh cultures, grey sterile hyphae present covering some conidial areas; margins low, narrow, entire; mycelia white; texture velutinous, some floccose areas present; sporulation dense, conidia *en masse* dull to greyish green (26E3–6), lighter dull green (26D3) near margin; exudate absent; soluble pigment yellow sometimes inconspicuous; reverse olive (3F6–7) in central areas, dull green (28D4–E4) elsewhere. MEA, 25 °C, 7d: Colonies mm, low, plane; margins low to subsurface, wide; mycelia white; texture velutinous, some floccose mycelia present; sporulation dense, conidia *en masse* dull green to greyish green (28F4–F6); exudate absent; soluble pigment yellow; reverse greyish yellow (1B6) at point of inoculation, greyish green (1D6) elsewhere. YES, 25 °C, 7d: Colonies low, randomly sulcate; margins low, narrow; mycelia white; texture velutinous, floccose mycelia present near centre; sporulation dense, conidia *en masse* similar to CYA; exudate absent; soluble pigment absent; reverse similar to CYA. CREA, 25 °C, 7d: Acid not produced.

Micromorphology: Conidiophores mostly biverticillate, sometimes monoverticillate, having a brownish to green pigment, smooth and rough metulae commonly present on the same conidiophore; Stipes rough, conidiophores with short stipes often smooth, 20–180 × 2–3.5 µm; Metulae 2–4 per stipe, divergent, 38–67° (52±8.8), 9.5–18 × 2–3.5 µm (13.6±1.9 × 2.9±0.3), vesicle 3–6 µm (4.2±0.6); Phialides ampulliform, mostly 8–12 per metula, some only 4–6, 7–9 × 2–3.5 µm (7.7±0.5 × 2.8±0.2); Conidia finely rough, globose, 2–2.5 × 2–2.5 µm (2.4±0.1 × 2.4±0.1), average width/length = 0.98, *n* = 108.

Notes: *Penicillium hemitrachum* produces fast growing colonies, especially on CYA at 30 °C, but grows restrictedly at 37 °C. Colony appearance on MEA can easily be confused with *Aspergillus fumigatus*. Conidiophores often have a green pigmentation and are borne from green mycelia. Interestingly, some conidiophores have smooth and rough walled metulae on the same conidiophore. Phylogenetically the new species is related to *P. maclennaniae, P. smithii* and *P. velutinum* (Fig. 2). The fast growth rate of *P. hemitrachum, P. maclennaniae* and *P. velutinum* distinguish them from *P. smithii.* However, *P. maclennaniae* produces conidiophores lacking pigment and produces larger conidia (3.8–4.0 µm *fide* Yip 1981) than *P. hemitrachum,* while *P. velutinum* has smooth non-pigmented stipes and grows slightly slower on CYA at 25 °C.

Penicillium momoii Visagie & K. Jacobs, **sp. nov.**
MycoBank MB811007
(Fig. 13)

Etymology: Latin, *momoii*, named for Momo the dog, from the hide and seek book *Find Momo* by Andrew Knapp (Knapp 2014), reflecting the challenge of locating a single specimen

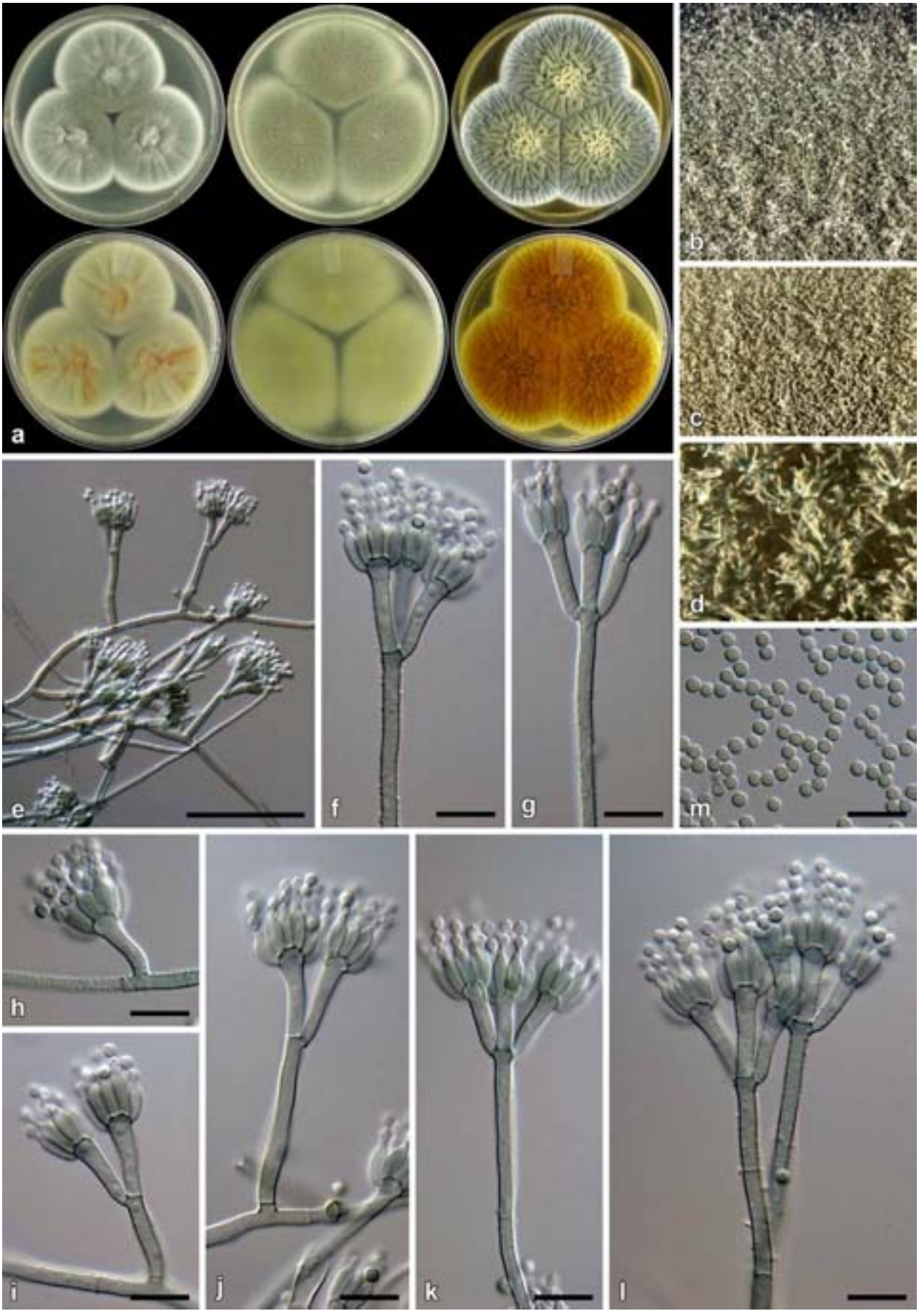

Fig. 12. *Penicillium hemitrachum* (CBS 139134). a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse). b. Texture on CYA. c–d. Texture on MEA. e–l. Conidiophores. m. Conidia. Bars e = 50 µm, f–m = 10 µm.

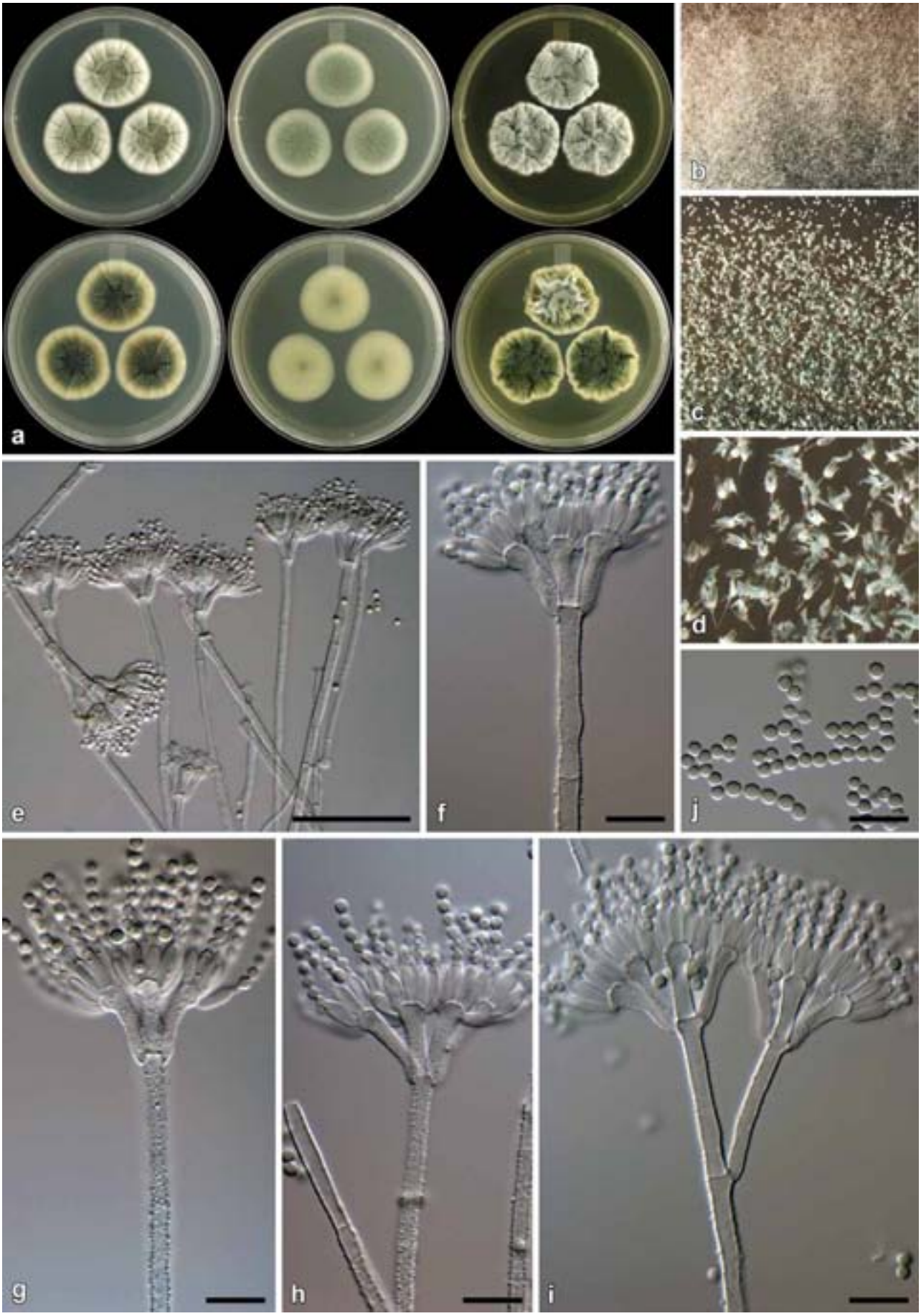

Fig. 13. *Penicillium momoii* (CBS 139157). a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse). b. Texture on CYA. c–d. Texture on MEA. e–i. Conidiophores. j. Conidia. Bars e = 50 µm, f–j = 10 µm.

of a unique species among thousands of morphologically similar cultures.

Diagnosis: Differs from close relatives by being able to grow on CYA at 37 °C (5–8 mm), grows more restricted on MEA and G25N than *P. subturcoseum* and *P. repensicolum* colonies sporulate much denser.

Type: **South Africa:** Malmesbury, isol. ex mite from *Protea repens* infructescence, Jun. 2009, isol. *C. M. Visagie* (CBS H-22046 dried culture] – holotype; CBS 139157 = DAOMC 241077 = DTO 182-G4 = CV 1015 – ex-type cultures).

ITS barcode: JX140895. Alternative identification markers: *BenA* = JX141073, *CaM* = JX157479, *RPB2* = KP064673.

Colony diam, 7 d (in mm): CYA 30–32; CYA 30 °C 27–28; CYA 37 °C 5–8; MEA 30–31; YES 28–31; G25N 15–16; CREA 15–17.

Colony characters: CYA, 25 °C, 7d: Colonies low to moderately deep, radially and concentrically sulcate; margins low, narrow to wide, somewhat irregular; mycelia white; texture floccose; sporulation moderately dense at centre, conidia *en masse* greyish green (27E5–7); exudate absent; soluble pigment absent; reverse greyish to dark green (25E7–F7) at centre, greenish white (26A2–27A2) at margin. MEA, 25 °C, 7d: Colonies low, plane; margins low, narrow, entire; mycelia white; texture velutinous, with floccose areas present; sporulation dense, conidia *en masse* greyish green (27E5–7); exudate absent; soluble pigment absent; reverse greyish to dull yellow (2B3–3B3) at centre, dull green (28D4–30D4) elsewhere. YES, 25 °C, 7d: Colonies low to moderately deep, radially and concentrically sulcate, random furrows also present; margins low, narrow, entire; mycelia white; texture velutinous, some floccose areas; sporulation ranging from moderately sparse to moderately dense at centre, conidia *en masse* greyish green (27E5–7); exudate absent; soluble pigment absent; reverse pigmentation greyish green to dark green (26E7–28F7–8) at centre, pale yellow (2A3) at margin. CREA, 25 °C, 7d: Acid not produced.

Micromorphology: Conidiophores biverticillate, a minor proportion monoverticillate, terverticillate not common; Stipes rough walled to warted, 100–400 × 2.5–3.5 µm; Branches 2 when present, 20–30 × 2.5–3.5 µm; Metulae 2–5 per stipe, divergent, sometimes slightly appressed, 41–102° (64±14), 12–19 × 2.5–3.5 µm (14.8±1.6 × 3.1±0.2), vesicle 4.5–6 µm (5.1±0.4); Phialides ampulliform, 10–12 per metula, 7.5–9.5 × 2.5–3 µm (8.3±0.5 × 2.8±0.2); Conidia rough, globose, 2–3 × 2–3 µm (2.5±0.1 × 2.5±0.1), average width/length = 0.98, *n* = 31.

Notes: See under *P. consobrinum*.

Penicillium pagulum Visagie & K. Jacobs, **sp. nov.**
MycoBank MB811005
(Fig. 14)

Etymology: Latin, *pagulum*, small village; in reference to the small colonies produced on CYA at 25 °C.

Diagnosis: Differs from close relatives by its restricted growth on CYA at 25 °C (15–20 mm).

Type: **South Africa:** Struisbaai, isol. ex bract from *Protea repens* infructescence, Aug. 2009, isol. *C. M. Visagie* (CBS H-22049 [dried culture] – holotype; CBS 139166 = DAOMC 241069 = DTO 183-H2 = CV 2224 – ex-type cultures).

ITS barcode: JX140898. Alternative identification markers: *BenA* = JX141070, *CaM* = JX157519, *RPB2* = KP064655.

Colony diam, 7 d (in mm): CYA 15–20; CYA 30 °C 12–15; CYA 37 °C 1–5; MEA 25–32; YES 26–34; G25N 5–10; CREA 19–24.

Colony characters: CYA, 25 °C, 7d: Colonies low, radially sulcate; margins low, narrow, entire; mycelia white; texture velutinous, some floccose areas; sporulation sparse, conidia *en masse* greyish turquoise (24B5–E5); exudate absent; soluble pigment absent; reverse olive (2F5–3F5). MEA, 25 °C, 7d: Colonies low, plane; margins subsurface, wide, entire; mycelia white; texture velutinous; sporulation dense, conidia *en masse* greyish to dark green (25E5–F5); exudate absent; soluble pigment absent; reverse greyish yellow (3B7) at centre, greyish green (30C5) at margin. YES, 25 °C, 7d: Colonies low, radially and concentrically sulcate; margins low, narrow, entire; mycelia white; texture velutinous, some floccose areas present; sporulation moderately dense, conidia *en masse* greyish turquoise (24B3) in some regions, greyish turquoise (24E5) in others; exudate absent; soluble pigment absent; reverse dark green (25F8), orange (6B7) at margin. CREA, 25 °C, 7d: Acid not produced.

Micromorphology: Conidiophores biverticillate, a minor proportion terverticillate; Stipes finely rough, 100–250 × 2.5–4 µm; Branches 2 when present, 21–32 × 2.5–4 µm; Metulae 2–5 per stipe, divergent, 28–62° (41±8.4), 13–24 × 2.5–4 µm (16.8±2.5 × 3.1±0.4), vesicle 3.5–5 µm (4.3±0.5); Phialides ampulliform, 9–14 per metula, 8–10.5 × 2.5–3.5 µm (9.3±0.6 × 3±0.2); Conidia finely rough, globose to subglobose, 2–3 × 2–3 µm (2.6±0.2 × 2.5±0.2), average width/length = 0.97, *n* = 35.

Notes: *Penicillium pagulum* displays restricted growth on CYA, which distinguishes it from all phylogenetically closely related species (Figs 3–4). See also under *P. consobrinum*.

Penicillium repensicola Visagie & K. Jacobs, **sp. nov.**
MycoBank MB811006
(Fig. 15)

Etymology: Latin, *repensicola*, dwelling in "*repens*"; in reference to the type strain, which was isolated from *Protea repens*.

Diagnosis: Differs from close relatives by being able to grow on CYA at 37 °C (7–15 mm), faster than its closest relatives *P. momoii* and *P. subturcoseum*. Colonies also sporulate much denser than the latter two.

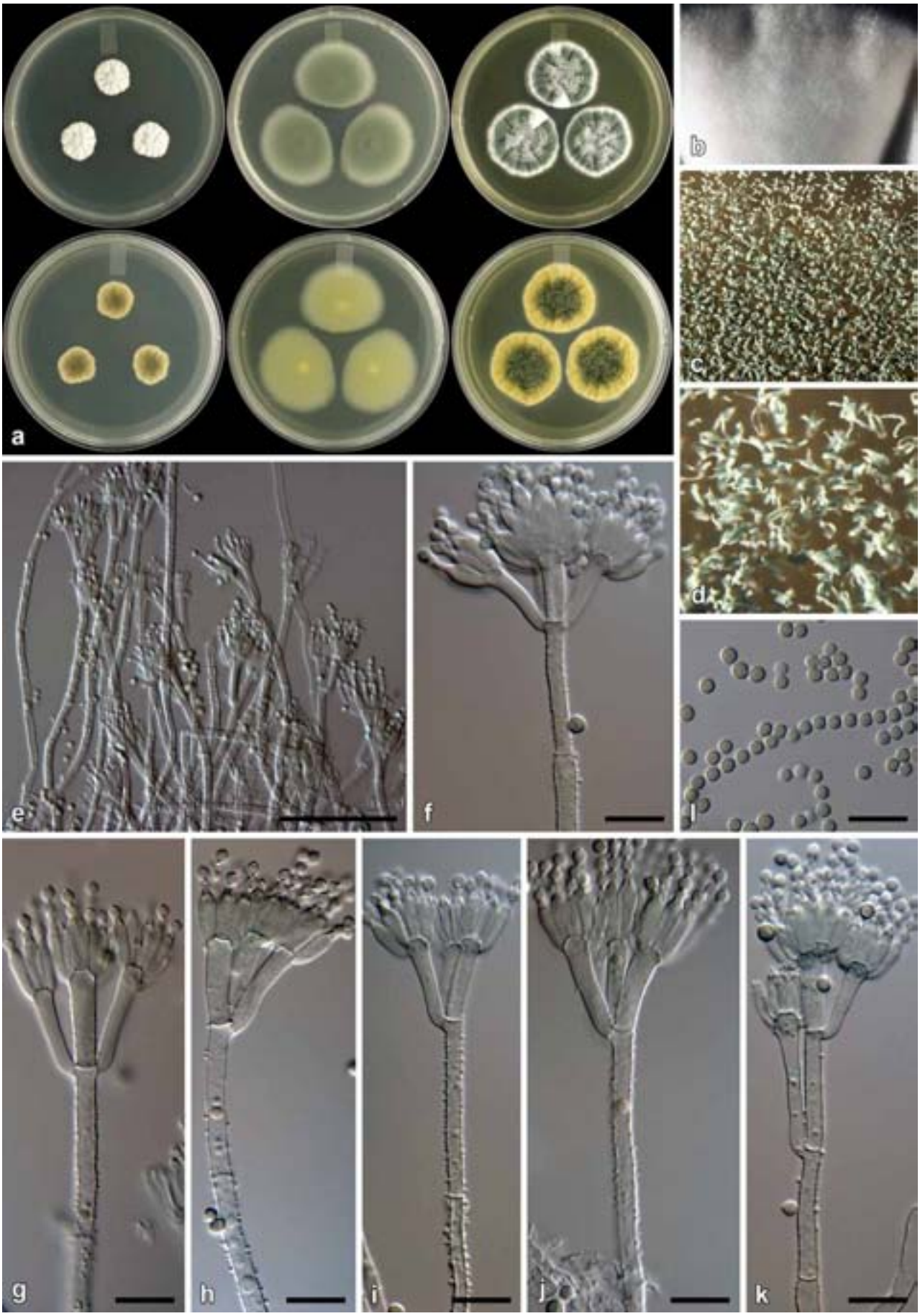

Fig. 14. *Penicillium pagulum* (CBS 139166). a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse). b. Texture on CYA. c–d. Texture on MEA. e–k. Conidiophores. l. Conidia. Bars e = 50 µm, f–l = 10 µm.

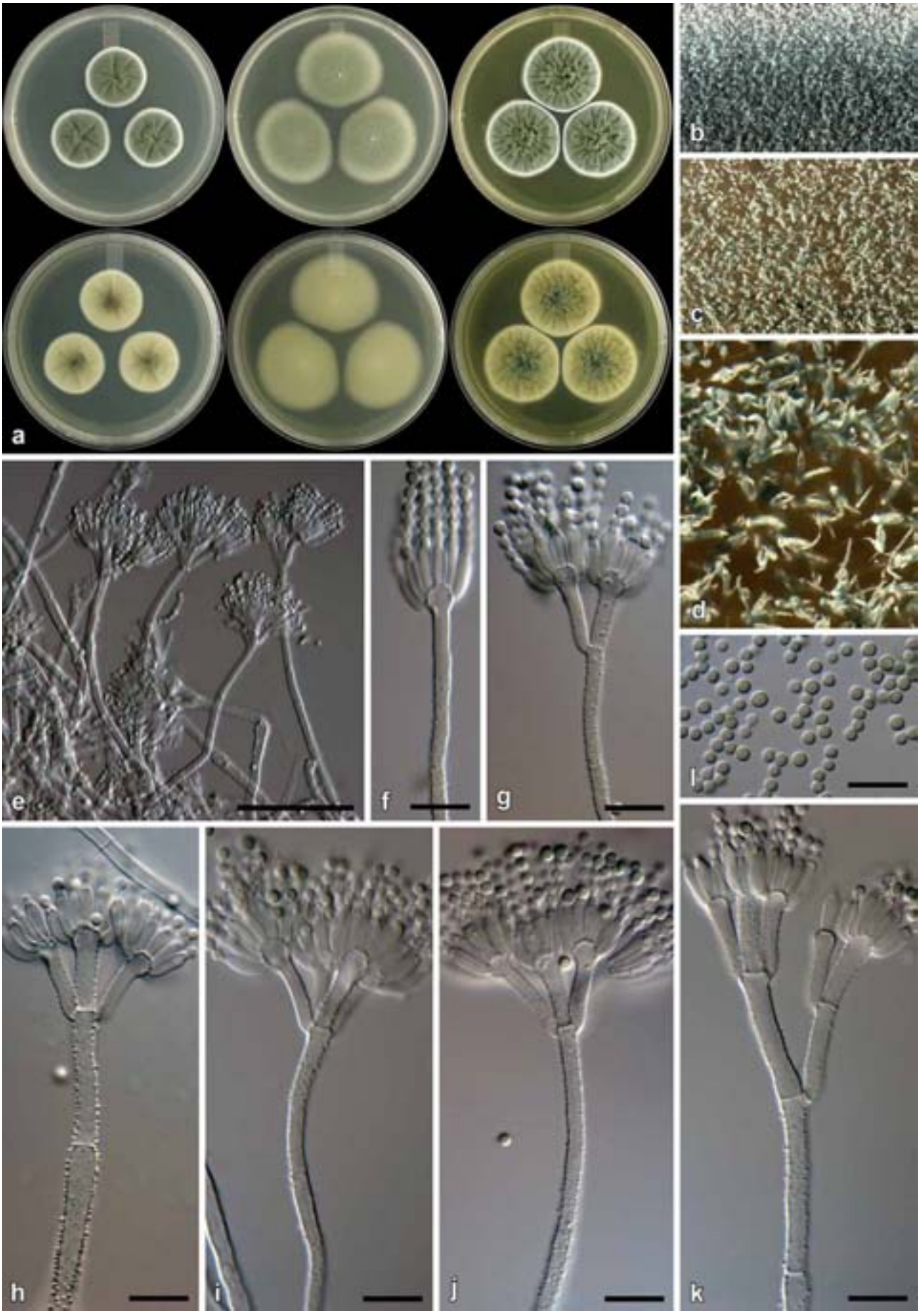

Fig. 15. *Penicillium repensicola* (CBS 139160). a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse). b. Texture on CYA. c–d. Texture on MEA. e–k. Conidiophores. l. Conidia. Bars e = 50 µm, f–l = 10 µm.

Type: **South Africa:** Malmesbury, isol. ex bract from *Protea repens* infructescence, Jun. 2009, isol. *C. M. Visagie* (CBS H-22047 [dried culture] – holotype; CBS 139160 = DAOMC 241080 = DTO 183-B8 = CV 1495 – ex-type cultures).

ITS barcode: JX140893. Alternative identification markers: *BenA* = JX141150, *CaM* = JX157490, *RPB2* = KP064660.

Colony diam, 7 d (in mm): CYA 23–32; CYA 30 °C 20–28; CYA 37 °C 7–15; MEA 30–43; YES 28–38; G25N 10–22; CREA 15–17.

Colony characters: CYA, 25 °C, 7d: Colonies low to moderately deep, radially and concentrically sulcate; margins low, narrow to wide, entire; mycelia white; texture velutinous; sporulation moderately dense, conidia *en masse* dark green (25F7–26F7); exudate absent; soluble pigment absent; reverse dark green to olive green (30F8–3F8) at centre, greenish white (26A2–27A2) at margin. MEA, 25 °C, 7d: Colonies low, plane; margins low, narrow, entire; mycelia white; texture velutinous, floccose areas present; sporulation dense, conidia *en masse* greyish green (27E5–7); exudate absent; soluble pigment absent; reverse sometimes olive brown (4F8) and sometimes greyish to dull yellow (2B3–3B3) at centre, dull green (28D4–30D4) elsewhere. YES, 25 °C, 7d: Colonies low to moderately deep, radially and concentrically sulcate, random furrows also present; margins low, narrow, entire; mycelia white; texture velutinous and floccose; sporulation moderately dense, conidia *en masse* dark green (25F7–26F7); exudate absent; soluble pigment absent; reverse pigmentation greyish to dark green (26E7–28F7–8) at centre, pale yellow (2A3) at margin. CREA, 25 °C, 7d: Acid not produced.

Micromorphology: Conidiophores biverticillate, a minor proportion monoverticillate, terverticillate not common; Stipes rough walled to warted, 80–260 × 2.5–3.5 µm; Branches 2 when present, 17–26 × 2.5–3.5 µm; Metulae 2–5 per stipe, divergent, sometimes slightly appressed, 50–92° (65±10), 13–22 × 2.5–3.5 µm (16±1.9 × 3±0.3), vesicle 4–6 µm (5±0.6); Phialides ampulliform, 10–12 per metula, 7–10 × 2.5–3.5 µm (8.5±0.6 × 2.8±0.3); Conidia rough, globose, 2–3 × 2–3 µm (2.4±0.2 × 2.4±0.2), average width/length = 0.97, *n* = 37.

Notes: See under *P. consobrinum*.

Penicillium subturcoseum Visagie & K. Jacobs, **sp. nov.**
MycoBank MB811008
(Fig. 16)

Etymology: Latin, *subturcoseum*, turquoise beneath; in reference to the colony reverse colour on CYA.

Diagnosis: Differs from close relatives by being able to grow on CYA at 37 °C (1–2 mm), even though growth is more restricted at this temperature than *P. momoii* and *P. repensicola*. Also, *P. repensicola* colonies sporulate much denser than the other two, while *P. subturcoseum* colonies show more restricted growth on MEA and G25N than *P. momoii.*

Type: **South Africa:** Malmesbury, isol. ex soil sample, Feb. 2007, isol. *C. M. Visagie* (CBS H-22041 [dried culture] – holotype; culture ex-type CBS 139132 = DAOMC 241096 = DTO 180-C9 = CV 2835 ex-type cultures).

ITS barcode: FJ231006. Alternative identification markers: *BenA* = JX141161, *CaM* = JX157532, *RPB2* = KP064674.

Colony diam, 7 d (in mm): CYA 29–39; CYA 30 °C 20–28; CYA 37 °C 1–2; MEA 34–43; YES 28–38; G25N 18–22; CREA 15–17.

Colony characters: CYA, 25 °C, 7d: Colonies low, radially and concentrically sulcate; margins low, narrow, somewhat irregular; mycelia white; texture velutinous, floccose areas present; sporulation moderately dense, conidia *en masse* greyish green (25E6); exudate absent; soluble pigment absent; reverse dark turquoise (24F7) to dark green (25F7). MEA, 25 °C, 7d: Colonies low, plane; margins low, narrow, entire; mycelia white; texture velutinous; sporulation moderately dense to dense, conidia *en masse* greyish to dark green (25E5–F8); exudate absent; soluble pigment absent; reverse greenish grey (29B2), sometimes dark green (25F8). YES, 25 °C, 7d: Colonies low to moderately deep, radially and concentrically sulcate, random furrows present; margins low, narrow, entire; mycelia white; texture velutinous and floccose; sporulation ranging from moderately sparse to moderately dense, conidia *en masse* similarly as CYA; exudate absent; soluble pigment absent; reverse greyish green to dark green (26E7–28F7–8) at centre, pale yellow (2A3) at margin. CREA, 25 °C, 7d: Acid not produced.

Micromorphology: Conidiophores biverticillate, a minor proportion monoverticillate, terverticillate not common; Stipes rough walled to warted, 45–350 × 2.5–3.5 µm; Branches 2 when present, 20–30 × 2.5–3.5 µm; Metulae 2–5 per stipe, divergent, sometimes slightly appressed, 27–100° (58.7±15), 12–21 × 2.5–4 µm (16±1.8 × 3±0.39), vesicle 4–6.5 µm (5.1±0.7); Phialides ampulliform, 10–12 per metula, 7–9.5 × 2.5–3.5 µm (8.3±0.7 × 2.9±0.3); Conidia rough, globose, 2–3 × 2–3 µm (2.4±0.2 × 2.4±0.2), average width/length = 0.97, *n* = 69.

Notes: See under *P. consobrinum*.

Penicillium xanthomelinii Visagie & K. Jacobs, **sp. nov.**
MycoBank MB811009
(Fig. 17)

Etymology: Latin, *xanthomelinii*, *xantho-* yellow; in reference to the yellow colony reverse and the phylogenetic placement as a close relative of *P. melinii.*

Diagnosis: Differs from close relative, *P. melinii,* by faster colony growth on most media, production of yellow soluble pigments on CYA and lacking brown colours in colonies common in *P. melinii*.

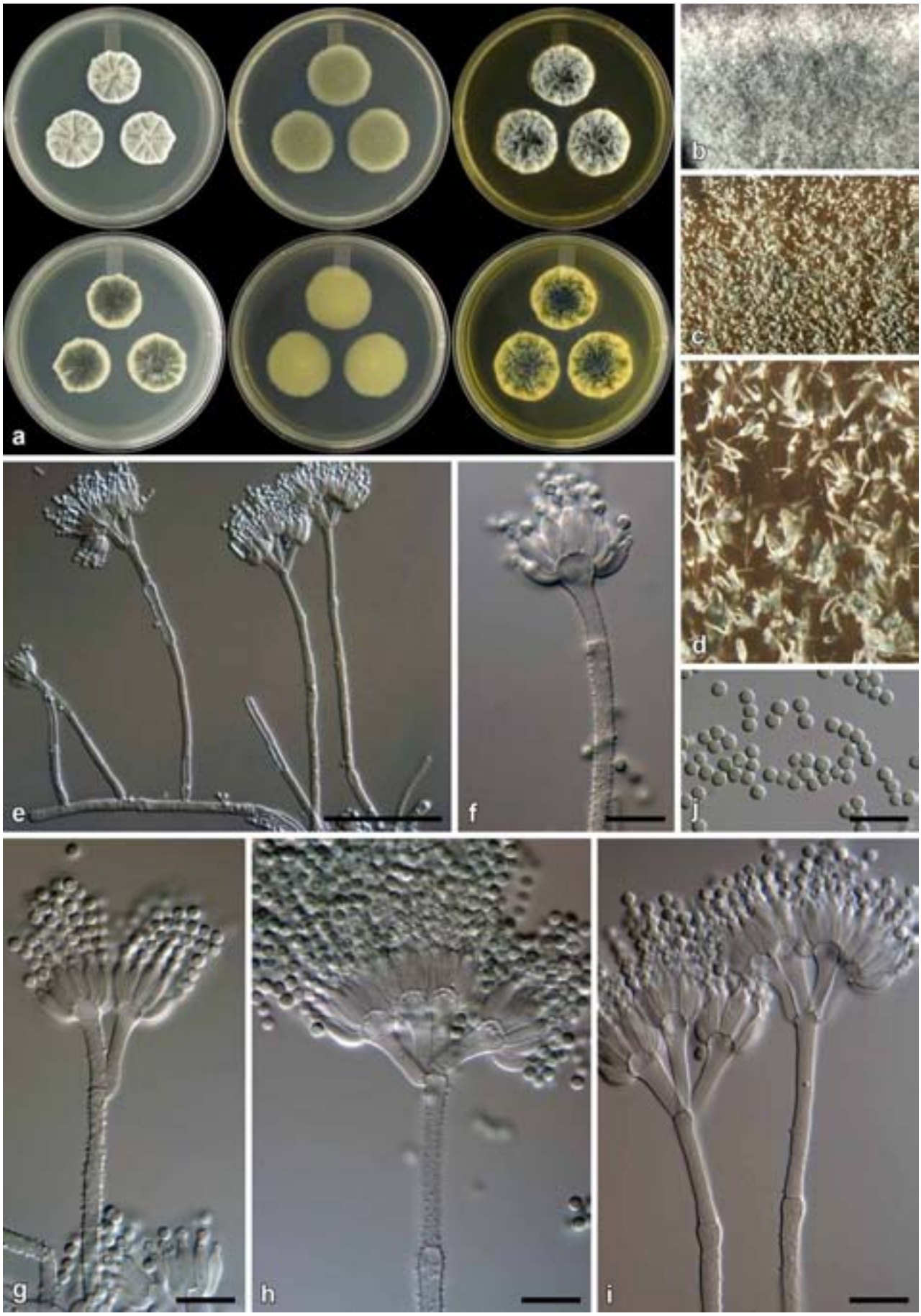

Fig. 16. *Penicillium subturcoseum* (CBS 139132). a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse). b. Texture on CYA. c–d. Texture on MEA. e–i. Conidiophores. j. Conidia. Bars e = 50 µm, f–j = 10 µm.

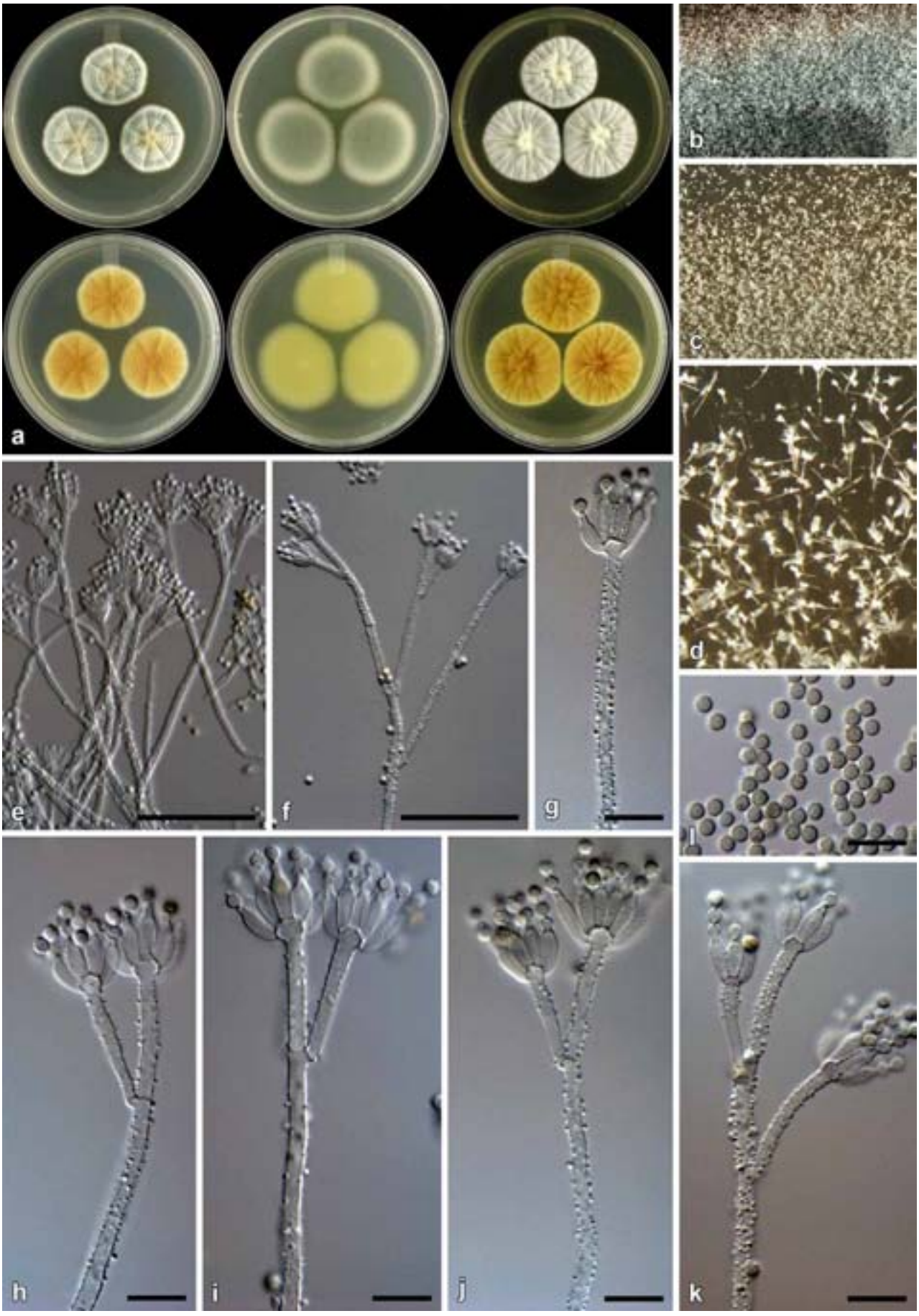

Fig. 17. *Penicillium xanthomelinii* (CBS 139163). a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse). b. Texture on CYA. c– d. Texture on MEA. e–k. Conidiophores. l. Conidia. Bars e–f = 50 µm, g–l = 10 µm.

Type: **South Africa:** Struisbaai, isol. ex soil sample, Aug. 2009, isol. *C. M. Visagie* (CBS H-22048 [dried culture] – holotype; CBS 139163 = DAOMC 241104 = DTO 183-C7 = CV 1677 – ex-type cultures).

ITS barcode: JX140921. Alternative identification markers: *BenA* = JX141120, *CaM* = JX157495, *RPB2* = KP064683.

Colony diam, 7 d (in mm): CYA 30–33; CYA 30 °C 17–21; CYA 37 °C no growth; MEA 39–45; YES 31–38; G25N 7–10; CREA 18–20.

Colony characters: CYA, 25 °C, 7d: Colonies low, radially and concentrically sulcate; margins low, narrow, entire; mycelia white; texture velutinous at margin, floccose areas at centre; sporulation moderately dense, conidia *en masse* greyish dark green (24E5–F5), and various shades of greyish green (24D5–25B3–C3); exudate deep yellow to orange-brown, less pronounced in some isolates; soluble pigment deep yellow to orange-brown, inconspicuous; reverse brown (7E7–8) at colony centre, greyish orange to orange (5C5–8) elsewhere, greyish yellow (2B3–C3) near the yellowish white (2A2) margin. MEA, 25 °C, 7d: Colonies low, plane; margins low, moderately wide, entire; mycelia white; texture velutinous, floccose areas present; sporulation moderately dense to dense, conidia *en masse* greyish green (25E5–F4–5); exudate absent; soluble pigment absent; reverse light yellow (3A5) at centre, greyish green (1C6–D6–7) elsewhere, margin greyish yellow (1B3). YES, 25 °C, 7d: Colonies low moderately deep near centre, radially and concentrically sulcate, random furrows also present; margins low, narrow, entire; mycelia white; texture velutinous, floccose areas present at centre; sporulation moderately dense, conidia *en masse* dull green (27E3–4), in less dense sporulating regions greyish green (27C2–3); exudate absent in most isolates, some with minute yellow to orange-brown droplets; soluble pigment absent; reverse golden yellow to orange (5B7–8) at centre, orange-yellow (4B8) elsewhere, becoming yellow (3B6) at margin. CREA, 25 °C, 7d: Acid not produced.

Micromorphology: Conidiophores biverticillate, subterminal monoverticillate branches common; Stipes rough walled to warted, 80–350 × 2–3 µm; Branches 2 when present, divergent, 25–85 × 2–3 µm; Metulae 2–4 per stipe, divergent, 20–67° (36.5±8.9), 14–31 × 2–3 µm (20.9±3.7 × 2.5±0.3, vesicle 3–5 µm (4±0.5); Phialides ampulliform, sometimes roughened, 8–14 per metula, often rough walled, 6.5–10 × 2.5–3.5 µm (8.3±0.7 × 3±0.3); Conidia spinose, globose, 2.5–3 × 2.5–3 µm (2.8±0.1 × 2.8±0.1, average width/length = 0.98, *n* = 61.

Notes: *Penicillium xanthomelinii* characteristically produces rough walled to warted, divergent and irregular conidiophores, and commonly also has rough walled phialides and spinose conidia. *Penicillium melinii*, also isolated in this study, is the closest relative. However, *P. melinii* grows more restrictedly on most media. In addition, *P. melinii* produces brown colours in colonies, which are absent in *P. xanthomelinii*, while the latter produces yellow soluble pigments on CYA. Phylogenetically, *P. xanthomelinii* strains form a coherent group separate from *P. melinii* and its previously assigned synonyms (Fig. 2).

Penicillium sect. *Exilicaulis*: accepted species and synonyms

The following list includes accepted *Penicillium* sect. *Exilicaulis* species and their synonyms based on our findings in this study. For each entry we include (in order): (1) reference to original description; (2) MycoBank number associated with the name; (3) type specimen information; (4) living ex-type cultures available in various collections; and (5) GenBank accession numbers to reference sequences obtained from ex-type cultures. Accepted species are indicated by bold text. Synonyms are included in regular text below appropriate accepted names. The list also includes *Eupenicillium* (teleomorphic/sexual state) names that in all cases were introduced based on the same type strain as that of the *Penicillium* (anamorphic/asexual state) name, often both introduced in the same paper. Because these names refer to different morphs of the same specimen, they refer in principle to different parts of that specimen. We indicate these cases with "*p.p.*" added after relevant herbarium accession numbers. Here we also correct typifications for *P. cinereoatrum* and *P. guttulosum.*

Citromyces griseus: See under *Penicillium restrictum*.
Eupenicillium alutaceum: See under *Penicillium alutaceum*.
Eupenicillium catenatum: See under *Penicillium catenatum*.
Eupenicillium erubescens: See under *Penicillium erubescens*.
Eupenicillium katangense: See under *Penicillium katangense*.
Eupenicillium lapidosum: See under *Penicillium lapidosum*.
Eupenicillium luzoniacum: See under *Penicillium terrenum*.
Eupenicillium meridianum: See under *Penicillium meridianum*.
Eupenicillium nepalense: See under *Penicillium nepalense*.
Eupenicillium parvum: See under *Penicillium parvum*.
Eupenicillium papuanum: See under *Penicillium parvum*.
Eupenicillium philippinense: See under *Penicillium philippinense*.
Eupenicillium rubidurum: See under *Penicillium rubidurum*.
Eupenicillium terrenum: See under *Penicillium terrenum*.
Geosmithia namyslowskii: See under *Penicillium namyslowskii*.
Penicillium aeneum: See under *Penicillium citreonigrum*.
Penicillium albocinerascens: See under *Penicillium chalabudae.*

Penicillium alutaceum D.B. Scott, *Mycopathol. Mycol. Appl*. **36**: 17 (1968). [MB335708]. — Herb.: CBS 317.67 *p.p.* (holotype). Ex-type cultures: CBS 317.67 = ATCC 18542 = FRR 1158 = IFO 31728 = IMI 136243. ITS barcode: AF033454. (Alternative markers: *BenA* = KJ834430; *RPB2* = JN121489; *CaM* = KP016768).

Synonym: *Eupenicillium alutaceum* D.B. Scott, *Mycopathol. Mycol. Appl*. **36**: 17 (1968). [MB330719]. — Herb.: CBS 317.67 *p.p.* (holotype). Ex-type cultures: CBS 317.67 = ATCC 18542 = FRR 1158 = IFO 31728 = IMI 136243. ITS barcode: AF033454. (Alternative markers: *BenA* = KJ834430; *RPB2* = JN121489; *CaM* = KP016768).

Penicillium arabicum Baghd., *Nov. Sist. Nizsh. Rast*. **5**: 105 (1968). [MB335711]. — Herb.: designated as T16 in Universitate Mosquensi (holotype); CBS H-7471 (isotype). Ex-type cultures: CBS 414.69 = ATCC 22347 = DSM 2205 = FRR 507 = IMI 140335 = VKM F-1077.

ITS barcode: KC411758. (Alternative markers*BenA* = KP016750; *RPB2* = KP064574; *CaM* = KP016770).

Penicillium atrolazulinum Visagie & K. Jacobs. *IMA Fungus* **7**: 91 (2016) [MB811001]. — Herb.: CBS H-22043 (holotype). Ex-type cultures: CBS 139136 = DAOMC 241083 = DTO 180-H4 = CV 55. ITS barcode: JX140913. (Alternative markers: *BenA* = JX141077; *RPB2* = KP064575; *CaM* = JX157416).

Penicillium atrosanguineum B.X. Dong, *Česká Mycol*. **27**: 174 (1973). [MB319260]. — Herb.: PRC 1397 (holotype), CBS H-15524 (isotype). Ex-type cultures: CBS 380.75 = FRR 1726 = IMI 197488. ITS barcode: JN617706. (Alternative markers: *BenA* = KJ834435; *RPB2* = JN406557; *CaM* = KP016771).

Penicillium bertai: See under *Penicillium citreonigrum*.

Penicillium burgense Quintan. ex Visagie. *IMA Fungus* **7**: 94 (2016). [MB816641]. — Herb.: CBS H-22567 (dried specimen, holotype). Ex-type culture: CBS 325.89. ITS barcode: KC411736. (Alternative markers: *BenA* = KJ834437; *RPB2* = JN406572; *CaM* = KP016772).

Synonym: *Penicillium burgense* Quintan. *Av. Aliment Majora Anim*., **30**: 176 (1990); *nom. inval*. (Art. 40.7) [MB130241]. — Herb.: Sáez 1538. Ex-type culture: CBS 325.89. ITS barcode: KC411736. (Alternative markers: *BenA* = KJ834437; *RPB2* = JN406572; *CaM* = KP016772).

Penicillium caerulescens: See under *Penicillium raciborskii*.

Penicillium candidofulvum: See under *Penicillium corylophilum*.

Penicillium canis S.W. Peterson, *J. Clin. Microbiol.* **52**: 2450 (2014). [MB807056]. — Herb.: BPI 892763 (holotype). Ex-type culture: NRRL 62798. ITS barcode: KJ511291. (Alternative markers: *BenA* = KF900167; *RPB2* = KF900196; *CaM* = KF900177).

Penicillium catenatum D.B. Scott, *Mycopathol. Mycol. Appl*. **36**: 24 (1968). [MB335719]. — Herb.: CBS 352.67 *p.p*. (holotype). Ex-type cultures: CBS 352.67 = ATCC 18543 = CSIR 1097 = IFO 31774 = IMI 136241. ITS barcode: KC411754. (Alternative markers: *BenA* = KJ834438; *RPB2* = JN121504; *CaM* = KP016774).

Synonym: Eupenicillium catenatum D.B. Scott, *Mycopathol. Mycol. Appl*. **36**: 24 (1968). [MB330723]. — Herb.: CBS 352.67 *p.p*. (holotype). Ex-type cultures: CBS 352.67 = ATCC 18543 = CSIR 1097 = IFO 31774 = IMI 136241. ITS barcode: KC411754. (Alternative markers: *BenA* = KJ834438; *RPB2* = JN121504; *CaM* = KP016774).

Penicillium chalybeum: See under *Penicillium terrenum*.

Penicillium chloroleucon: See under *Penicillium corylophilum*

Penicillium chalabudae Visagie. *IMA Fungus* **7**: 94 (2016). [MB816642]. — Herb.: CBS H-15439 (holotype). Ex-type cultures: CBS 219.66 = ATCC 18322 = ATCC 18329 = FRR 3393 = VKM F-1037. ITS barcode: KP016811. (Alternative markers: *BenA* = KP016748; *RPB2* = KP064572; *CaM* = KP016767).

Synonym: *Penicillium albocinerascens* Chalab., *Not. Syst. Crypt. Inst. bot. Acad. Sci. USSR* **6**: 166 (1950); non (Maublanc) Biourge 1923; *nom. illegit*. (Art. 53.1). [MB302374]. — Herb.: CBS H-15439 (isotype). Ex-type cultures: CBS 219.66 = ATCC 18322 = ATCC 18329 = FRR 3393 = VKM F-1037. ITS barcode: KP016811. (Alternative markers: *BenA* = KP016748; *RPB2* = KP064572; *CaM* = KP016767).

Penicillium cinerascens Biourge, *Cellule* **33**: 308 (1923). [MB260785]. — Herb.: K(M) IMI 92234 (neotype, Pitt *et al*. 2000). Ex-type cultures: NRRL 748 = ATCC 48693 = BIOURGE 90 = FRR 748 = IMI 92234 = QM 7555 = Thom 4733.34. ITS barcode: AF033455. (Alternative markers: *BenA* = JX141041; *RPB2* = KP064614; *CaM* = JX157405).

Penicillium cinereoatrum Chalab., *Not. Syst. Crypt. Inst. bot. Acad. Sci. USSR*. **6**: 167 (1950). [MB302385]. — Herb.: CBS H-7469 (***epitype designated here***, MBT204705); loc. cit.: Fig. 7 -- ***lectotype designated here***, MBT204706).. Ex-type cultures: CBS 222.66 = NRRL3390 = ATCC 22350 = FRR 3390 = IJFM 5024 = IMI 113676 = VKM F-856. ITS barcode: KC411700. (Alternative markers: *BenA* = KJ834442; *RPB2* = JN406608; *CaM* = KP125335).

Penicillium citreonigrum Dierckx, *Ann. Soc. Sci. Bruxelles* **25**: 86 (1901). [MB165197]. — Herb.: K(M) IMI 92209i (neotype, Pitt 1980). Ex-type cultures: CBS 258.29 = ATCC 48736 = FRR 761 = IMI 092209 = LSHBP 20 = LSHBP 98 = MUCL 28648 = MUCL 29062 = MUCL 29116 = NRRL 761. ITS barcode: AF033456. (Alternative markers: *BenA* = EF198621; *RPB2* = JN121474; *CaM* = EF198628).

Synonyms: *Penicillium subcinereum* Westling, *Ark. Bot*. **11** (1): 137 (1911). [MB215824]. — Herb.: unknown. Ex-type cultures: CBS 258.29 = ATCC 48736 = FRR 761 = IMI 092209 = LSHBP 20 = LSHBP 98 = MUCL 28648 = MUCL 29062 = MUCL 29116 = NRRL 761. ITS barcode: AF033456. (Alternative markers: *BenA* = EF198621; *RPB2* = JN121474; *CaM* = EF198628). Note: Same type as *Penicillium citreonigrum*.

Penicillium citreoviride Biourge, *Cellule* **33**: 297 (1923). [MB357253]. — Herb.: unknown. Ex-type cultures: CBS 308.48 = ATCC 10425 = FRR 2046 = IMI 040575 = NRRL 2046 (authentic according to Raper & Thom 1949). ITS barcode: EF198647. (Alternative markers: *BenA* = EF198623; *RPB2* = KP064616; *CaM* = KP016778).

Penicillium bertai Talice & Mackinnon, *Annls Parasit. Hum. Comp*. **7**: 97 (1929) (*fide* Pitt 1980). [MB258372]. — Herb.: unknown. Ex-type culture: No culture available.

Penicillium citreoviride var. *aeneum* S. Abe, *J. Gen. Appl. Microbiol*. **2**: 58 (1956); *nom. inval*. (Art. 39.1,). [MB123735]. — Herb.: unknown. Ex-type cultures: CBS 321.59 = ATCC 18308 = FAT123 = IFO 6224 = IMI 068225 = NRRL 3404 = QM 7290. ITS barcode: KP016812. (Alternative markers: *BenA* = KP016749; *RPB2* = KP064573; *CaM* = KP016769).

Penicillium aeneum G. Sm., *Trans. Brit. Mycol. Soc*. **46**: 334 (1963). [MB335706]. — Herb.: IMI 68225 (holotype). Ex-type cultures: CBS 321.59 = ATCC 18308 = FAT123 = IFO 6224 = IMI 068225 = NRRL 3404 = QM 7290. ITS barcode: KP016812. (Alternative markers: *BenA* = KP016749; *RPB2* = KP064573; *CaM* = KP016769).

Penicillium citreosulfuratum Biourge, *Cellule* **33**: 285 (1923). [MB260947]. — Herb.: icon in Biourge (1923) Cellule 33: fig. 86 no 21 (lectotype); K(M) IMI 92228 (epitype). Ex-type cultures: IMI 92228 = DTO 290-I4. ITS barcode: KP016814. (Alternative markers: *BenA* = KP016753; *RPB2* = KP064615; *CaM* = KP016777).

Synonym: *Penicillium toxicarium* I. Miyake, *Rep. Res. Inst. Rice Improvement* **1**: 1 (1940); *nom. inval*. (Art. 39.1). [MB335772]. — Herb.: unknown. Ex-type culture: No culture available. ITS barcode: n.a. (Alternative markers: *BenA* = n.a.; *RPB2* = n.a.; *CaM* = n.a.). Note: Non *Penicillium toxicarium* I. Miyake ex C. Ramírez, *Man. Atlas Penicillia*: 125 (1982) = ***Penicillium trzebinskii*** K.M. Zalessky, *Bull. Int. Acad. Polon. Sci., sér. B., Sci. Nat*. **1927**: 498 (1927) (*fide* Houbraken *et a*l. 2014). [MB280795]. — Herb.: unknown. Ex-type culture: CBS 351.51. Section *Aspergilloides*. ITS barcode: KM189449. (Alternative markers: *BenA* = KM088673; *RPB2* = KM089445; *CaM* = KM089058).

Penicillium citreovirens: See under *Penicillium corylophilum.*

Penicillium citreoviride: See under *Penicillium citreonigrum*.

Penicillium citreoviride var*. aeneum*: See under *Penicillium citreonigrum*.

Penicillium coeruleoviride: See under *Penicillium corylophilum*.

Penicillium consobrinum Visagie & K. Jacobs, *IMA Fungus* **7**: 96 (2016). [MB811002]. — Herb.: CBS H-22045 (holotype). Ex-type cultures: CBS 139144 = DAOMC 241072 = DTO 181-H9 = CV547. ITS barcode: JX140888. (Alternative markers: *BenA* = JX141135; *RPB2* = KP064619; *CaM* = JX157453).

Penicillium corylophilum Dierckx, *Ann. Soc. Sci. Bruxelles* **25**: 86 (1901). [MB178294]. — Herb.: K(M) IMI 39754 (neotype, Pitt 1980). Ex-type cultures: CBS 312.48 = TCC9784 = ATHUM2890 = CECT 2270 = FRR 802 = IMI 039754 = MUCL 28671 = MUCL 29073 = MUCL 29131 = NRRL 802 = QM 7510. ITS barcode: AF033450. (Alternative markers: *BenA* = JX141042; *RPB2* = KP064631; *CaM* = KP016780).

Synonyms: Penicillium candidofulvum Dierckx, Annls Soc. Scient. Brux. 25: 86, 1901. [MB175508]. — Herb.: unknown. Ex-type cultures: CBS 254.37 = IMI 092201 = LSHBP 12 = MUCL 28669 = NRRL 769. ITS barcode: KC411712. (Alternative markers: *BenA* = KP016751; *RPB2* = KP064606; *CaM* = KP016773).

Penicillium chloroleucon Biourge, Cellule **33**: 270 (1923). [MB260541]. — Herb.: unknown. Ex-type cultures: CBS 127808 = IMI 92202. ITS barcode: KP016813. (Alternative markers: *BenA* = KP016752; *RPB2* = KP064613; *CaM* = KP016776).

Penicillium coeruleoviride G. Sm., *Trans. Brit. Mycol. Soc*. **48**: 275 (1965). [MB335720]. — Herb.: K(M) IMI 103148 (holotype). Ex-type cultures: CBS 259.67 = ATCC 22351 = FRR 3403 = IFO 9146 = IMI 103148. ITS barcode: KC411717. (Alternative markers: *BenA* = KP016754; *RPB2* = KP064617; *CaM* = KP016779).

Penicillium humuli J.F.H. Beyma, *Zentralbl. Bakteriol. Parasitenk*., *Abt*.2 **99**: 393 (1939). [MB267441]. — Herb.: unknown. Ex-type cultures: CBS 231.38 = ATCC 10452 = IFO 7726 = IMI 039817 = NRRL 872. ITS barcode: JN617696. (Alternative markers: *BenA* = KP016756; *RPB2* = KP064645; *CaM* = KP016787).

Penicillium obscurum Biourge, *Cellule* **33**: 267 (1923). [MB272613]. — Herb.: unknown. Ex-type cultures: CBS 127807 = IMI 92263 = NRRL 793 = FRR 793. ITS barcode: KP016815. (Alternative markers: *BenA* = KP016761; *RPB2* = KP064654; *CaM* = KP016797).

Penicillium citreovirens S. Abe, *J. Gen. Appl. Microbiol*. **2**: 87 (1956); *nom. inval*. (Art. 39.1). [MB302387]. — Herb.: unknown. Ex-type cultures: CBS 312.48 = TCC9784 = ATHUM 2890 = CECT 2270 = FRR 802 = IMI 039754 = MUCL 28671 = MUCL 29073 = MUCL 29131 = NRRL 802 = QM 7510. ITS barcode: GU944557. (Alternative markers: *BenA* = GU944519; *RPB2* = JN406569; *CaM* = GU944607). Note: Same type as *Penicillium corylophilum*.

Penicillium corynephorum: See under *Penicillium smithii.*

Penicillium cravenianum Visagie & K. Jacobs, *IMA Fungus* **7**: 96 (2016). [MB811003]. — Herb.: CBS H-22044 (holotype). Ex-type cultures: CBS 139138 = DAOMC 241082 = DTO 180-I5 = CV 92. ITS barcode: JX140900. (Alternative markers: *BenA* = JX141076; *RPB2* = KP064636; *CaM* = JX157418).

Penicillium decumbens Thom, *USDA Bur. Animal Industr. Bull*. **118**: 71 (1910). [MB156582]. — Herb.: K(M) IMI 190875 (neotype, Pitt 1980). Ex-type cultures: CBS 230.81 = FRR 741 = IMI 190875 = MUCL 29107 = NRRL 741. ITS barcode: AY157490. (Alternative markers: *BenA* = KJ834446; *RPB2* = JN406601; *CaM* = KP016782).

Penicillium dimorphosporum H.J. Swart, *Trans. Brit. Mycol. Soc*. **55**: 310 (1970). [MB120334]. — Herb.: CBS 456.70 (holotype). Ex-type cultures: CBS 456.70 = NRRL 5207 = ATCC 22783 = ATCC 52501 = FRR 1120 = IMI 149680. ITS barcode: AF081804. (Alternative markers: *BenA* = KJ834448; *RPB2* = JN121517; *CaM* = KP016783).

Penicillium dravuni Janso, *Mycologia* **97**: 445 (2005). [MB501442]. — Herb.: BPI 844248 (holotype). Ex-type culture: F01V25. ITS barcode: AY494856. (Alternative markers: *BenA* = n.a.; *RPB2* = n.a.; *CaM* = n.a.).

Penicillium erubescens D.B. Scott, *Mycopathol. Mycol. Appl*. **36**: 14 (1968). [MB335726]. — Herb.: CBS 318.67 *p.p.* (holotype). Ex-type cultures: CBS 318.67 = ATCC 18544 = CSIR 1040 = FRR 814 = IFO 31734 = IMI 136204 = NRRL 6223. ITS barcode: AF033464. (Alternative markers: *BenA* = HQ646566; *RPB2* = JN121490; *CaM* = EU427281).

Synonym: Eupenicillium erubescens D.B. Scott, *Mycopathol. Mycol. Appl*. **36**: 14 (1968). [MB330727]. — Herb.: CBS 318.67 *p.p*. (holotype). Ex-type cultures: CBS 318.67 = ATCC 18544 = CSIR 1040 = FRR 814 = IFO 31734 = IMI 136204 = NRRL 6223. ITS barcode: AF033464. (Alternative markers: *BenA* = HQ646566; *RPB2* = JN121490; *CaM* = EU427281).

Penicillium fagi C. Ramírez & A.T. Martínez, *Mycopathologia* **63**: 57 (1978). [MB283595]. — Herb.: IJFM 3049 (holotype). Ex-type cultures: CBS 689.77 = CCMF-696 = IJFM 3049 = IMI 253806 = VKMF-2178. ITS barcode: AF481124. (Alternative markers: *BenA* = KJ834449; *RPB2* = JN406540; *CaM* = KP016784).

Penicillium flavidostipitatum: See under *Penicillium namyslowskii*.

Penicillium gilmanii: See under *Penicillium restrictum*.

Penicillium griseolum G. Sm., *Trans. Br. Mycol. Soc*. **40**: 485 (1957). [MB302401]. — Herb.: LSHTM BB 323 (holotype), K(M) IMI 071626 (isotype). Ex-type cultures: CBS 277.58 = ATCC 18239 = FRR 2671 = IFO 8175

= IMI 071626 = LSHBB323 = NRRL 2671 = QM 7523. ITS barcode: EF422848. (Alternative markers: *BenA* = EF506213; *RPB2* = KP064638; *CaM* = EF506232).

Penicillium griseum: See under *Penicillium restrictum*.

Penicillium guttulosum J.C. Gilman & E.V. Abbott, *Iowa St. Coll. J. Sci.* **1**: 298 (1927). [MB266689]. — Herb.: CBS H-22566 (***epitype designated here***), MBT204703; *loc. cit*.: Fig. 33 – ***lectotype designated here***, MBT204704). Ex-type cultures: CBS 141171 = NRRL 907 = ATCC 48734 = FRR 907 = Thom 4894.16. ITS barcode: HQ646592. (Alternative markers: *BenA* = HQ646576; *RPB2* = KP064639; *CaM* = HQ646587).

Penicillium hemitrachum Visagie & K. Jacobs, *IMA Fungus* **7**: 99 (2016). [MB811004]. — Herb.: CBS H-22042 (holotype). Ex-type cultures: CBS 139134 = DAOMC 241098 = DTO 180-D8 = CV 2845. ITS barcode: FJ231003. (Alternative markers: *BenA* = JX141048; *RPB2* = KP064642; *CaM* = JX157526).

Penicillium heteromorphum H.Z. Kong & Z.T. Qi, *Mycosystema* **1**: 107 (1988). [MB135444]. — Herb.: CBS 226.89 (neotype, Frisvad *et al*. 1990). Ex-type culture: CBS 226.89. ITS barcode: KC411702. (Alternative markers: *BenA* = KJ834455; *RPB2* = JN406605; *CaM* = KP016786).

Penicillium humuli: See under *Penicillium corylophilum*.

Penicillium katangense Stolk, *Antonie van Leeuwenhoek* **34**: 42 (1968). [MB120725]. — Herb.: CBS 247.67 *p.p*. (holotype). Ex-type cultures: CBS 247.67 = ATCC 18388 = IMI 136206 = NRRL 5182. ITS barcode: AF033458. (Alternative markers: *BenA* = KP016757; *RPB2* = KP064646; *CaM* = KP016788).

Synonym: Eupenicillium katangense Stolk, *Antonie van Leeuwenhoek* **34**: 42 (1968). [MB330732]. — Herb.: CBS 247.67 *p.p*. (holotype). Ex-type cultures: CBS 247.67 = ATCC 18388 = IMI 136206 = NRRL 5182. ITS barcode: AF033458. (Alternative markers: *BenA* = KP016757; *RPB2* = KP064646; *CaM* = KP016788).

Penicillium kurssanovii Chalab., *Bot. Mater. Otd. Sporov. Rast*. **6**: 168 (1950). [MB274327]. — Herb.: unknown. Ex-type cultures: CBS 625.67 = ATCC 18387 = FRR 3381 = IJFM 5045 = IMI 129965 = NRRL 3381 = VKMF-1244. ITS barcode: EF422849. (Alternative markers: *BenA* = KP016758; *RPB2* = KP064647; *CaM* = KP016789).

Penicillium laeve (K. Ando & Manoch) Houbraken & Samson, *Stud. Mycol*. **70**: 47 (2011). [MB561960]. — Herb.: TNS-F-238517 (holotype). Ex-type cultures: CBS 136665 = KY 12727 = NBRC 109724. ITS barcode: KF667369. (Alternative markers: *BenA* = KF667365; *RPB2* = KF667371; *CaM* = KF667367).

Synonym: *Torulomyces laevis* K. Ando & Manoch, *Mycoscience* **39**: 317 (1998). [MB447110].

Penicillium lapidosum Raper & Fennell, *Mycologia* **40**: 524 (1948). [MB289094]. — Herb.: K(M) IMI 39743 *p.p*. (holotype). Ex-type cultures: CBS 343.48 = ATCC 10462 = CCT4477 = IFO 6100 = IMI 039743 = NRRL 718 = QM 1928. ITS barcode: AF033409. (Alternative markers: *BenA* = KJ834465; *RPB2* = JN121500; *CaM* = FJ530984).

Synonym: Eupenicillium lapidosum D.B. Scott & Stolk, *Antonie van Leeuwenhoek* **33**: 298 (1967). [MB330733]. — Herb.: K(M) IMI 39743 *p.p*. (holotype). Ex-type cultures: CBS 343.48 = ATCC 10462 = CCT4477 = IFO 6100 = IMI 039743 = NRRL 718 = QM 1928. ITS barcode: AF033409. (Alternative markers: *BenA* = KJ834465; *RPB2* = JN121500; *CaM* = FJ530984).

Penicillium luzoniacum: See under *Penicillium terrenum*.

Penicillium maclennaniae H.Y. Yip, *Trans. Brit. Mycol. Soc*. **77**: 202 (1981). [MB112523]. — Herb.: DAR 35238 (holotype). Ex-type cultures: CBS 198.81 = DAR 35238. ITS barcode: KC411689. (Alternative markers: *BenA* = KJ834468; *RPB2* = KP064648; *CaM* = KP016791).

Penicillium melinii Thom, *Penicillia*: 273 (1930). [MB270876]. — Herb.: K(M) IMI 40216 (neotype, Pitt 1980). Ex-type cultures: CBS 218.30 = ATCC 10469 = FRR 2041 = IFO 7675 = IMI 040216 = MUCL 29235 = NRRL 2041 = QM 7599. ITS barcode: AF033449. (Alternative markers: *BenA* = KJ834471; *RPB2* = JN406613; *CaM* = KP016792).

Synonym: Penicillium radulatum G. Sm., *Trans. Brit. Mycol. Soc.* **40**: 484 (1957). [MB302420]. — Herb.: LSHTM BB 333 (holotype). Ex-type cultures: CBS 280.58 = ATCC 18383 = IMI 071624 = LSHBB333 = NRRL 2672 = QM 7526. ITS barcode: KC411727. (Alternative markers: *BenA* = KP016763; *RPB2* = KP064658; *CaM* = KP016801).

Penicillium menonorum S.W. Peterson, *IMA Fungus* **2**: 122 (2011). [MB519297]. — Herb.: BPI 881018 (holotype). Ex-type culture: NRRL 50410. ITS barcode: HQ646591. (Alternative markers: *BenA* = HQ646573; *RPB2* = KF900194; *CaM* = HQ646584).

Penicillium meridianum D.B. Scott, *Mycopathol. Mycol. Appl*. **36**: 12 (1968). [MB335750]. — Herb.: CBS 314.67 *p.p*. (holotype). Ex-type cultures: CBS 314.67 = ATCC 18545 = CSIR 1052 = IMI 136209. ITS barcode: AF033451. (Alternative markers: *BenA* = KJ834472; *RPB2* = JN406576; *CaM* = KP016794).

Synonym: Eupenicillium meridianum D.B. Scott, *Mycopathol. Mycol. Appl*. **36**: 12 (1968). [MB330736]. — Herb.: CBS 314.67 *p.p*. (holotype). Ex-type cultures: CBS 314.67 = ATCC 18545 = CSIR 1052 = IMI 136209. ITS barcode: AF033451. (Alternative markers: *BenA* = KJ834472; *RPB2* = JN406576; *CaM* = KP016794).

Penicillium momoii Visagie & K. Jacobs, *IMA Fungus* **7**: 99 (2016). [MB811007]. — Herb.: CBS H-22046 (holotype). Ex-type cultures: CBS 139157 = DAOMC 241077 = DTO 182-G4 = CV 1015. ITS barcode: JX140895. (Alternative markers: *BenA* = JX141073; *RPB2* = KP064673; *CaM* = JX157479).

Penicillium namyslowskii K.M. Zalessky, *Bull. Int. Acad. Polonc. Sci*., *Cl. Sci. Math*., *sér*. B, *Sci. Nat*. 1927: 479 (1927). [MB272006]. — Herb.: CBS 353.48 (neotype, Pitt 1979). Ex-type cultures: CBS 353.48 = ATCC 11127 = IMI 040033 = MUCL 29226 = NRRL 1070. ITS barcode: AF033463. (Alternative markers: *BenA* = JX141067; *RPB2* = JF417430; *CaM* = KP016795).

Synonyms: Geosmithia namyslowskii (K.M. Zalessky) Pitt, *Can. J. Bot.* **57**: 2024 (1979). [MB314414].

Penicillium flavidostipitatum C. Ramírez & C.C. González, *Mycopathologia* **88**: 3 (1984). [MB106338]. — Herb.: CBS 202.87 (neotype, Frisvad *et al*. 1990). Ex-type cultures: CBS 202.87 = IJFM 7824. ITS barcode: KC411691. (Alternative markers: *BenA* = KJ834451; *RPB2* = KP064637; *CaM* = KP016785).

Penicillium turris-painense C. Ramírez, *Mycopathologia* **91**: 93 (1985). [MB274385]. — Herb.: unknown. Ex-type culture: CBS 204.87. ITS barcode: KC411693. (Alternative markers: *BenA* = KP016766; *RPB2* = KP064681; *CaM* = KP016809).

Penicillium nepalense Takada & Udagawa, *Trans. Mycol. Soc. Japan* **24**: 146 (1983). [MB108327]. — Herb.: NHL 6482 *p.p*. (holotype). Ex-type cultures: CBS 203.84 = NHL 6482. ITS barcode: KC411692. (Alternative markers: *BenA* = KJ834474; *RPB2* = JN121453; *CaM* = KP016796).

Synonym: Eupenicillium nepalense Takada & Udagawa, *Trans. Mycol. Soc. Japan* **24**: 146 (1983). [MB107965]. — Herb.: NHL 6482 *p.p*. (holotype). Ex-type cultures: CBS 203.84 = NHL 6482. ITS barcode: KC411692. (Alternative markers: *BenA* = KJ834474; *RPB2* = JN121453; *CaM* = KP016796).

Penicillium obscurum: See under *Penicillium corylophilum*.

Penicillium ovatum (K. Ando & Nawawi) Houbraken & Samson, *Stud. Mycol*. **70**: 48 (2011). [MB561961]. — Herb.: TNS-F-238518 (holotype). Ex-type cultures: CBS 136664 = KY 12726. ITS barcode: KF667370. (Alternative markers: *BenA* = KF667366; *RPB2* = KF667372; *CaM* = KF667368).

Synonym: *Torulomyces ovatus* K. Ando & Nawawi, *Mycoscience* **39**: 317 (1998). [MB447111]. — Herb.: TNS-F-238518 (holotype). Ex-type cultures: CBS 136664 = KY 12726. ITS barcode: KF667370. (Alternative markers: *BenA* = KF667366; *RPB2* = KF667372; *CaM* = KF667368).

Penicillium pagulum Visagie & K. Jacobs, *IMA Fungus* **7**: 102 (2016). [MB811005]. — Herb.: CBS H-22049 (holotype). Ex-type cultures: CBS 139166 = DAOMC 241069 = DTO 183-H2 = CV 2224. ITS barcode: JX140898. (Alternative markers: *BenA* = JX141070; *RPB2* = KP064655; *CaM* = JX157519).

Penicillium papuanum: See under *Penicillium parvum*.

Penicillium parvum Raper & Fennell, *Mycologia* **40**: 508 (1948). [MB289101]. — Herb.: CBS 359.48 *p.p.* (holotype). Ex-type cultures: CBS 359.48 = ATCC 10479 = IFO 7732 = IMI 040587 = NRRL 2095 = QM 1878. ITS barcode: AF033460. (Alternative markers: *BenA* = HQ646568; *RPB2* = JN406559; *CaM* = KF900173).

Synonyms: Eupenicillium parvum (Raper & Fennell) Stolk & D.B. Scott, *Persoonia 4*: 402 (1967). [MB330739].

Eupenicillium papuanum Udagawa & Y. Horie, *Trans. Mycol. Soc. Japan* **14**: 378 (1973). [MB313983]. — Herb.: NHL 6463 *p.p*. (holotype). Ex-type cultures: CBS 570.73 = ATCC 28050 = ATCC 48363 = FRR 1559 = NHL 6463. ITS barcode: KC411767. (Alternative markers: *BenA* = KP016762; *RPB2* = KP064657; *CaM* = KP016798).

Penicillium papuanum Udagawa & Y. Horie, *Trans. Mycol. Soc. Japan* **14**: 378 (1973). [MB319290]. — Herb.: NHL 6463 *p.p*. (holotype). Ex-type cultures: CBS 570.73 = ATCC 28050 = ATCC 48363 = FRR 1559 = NHL 6463. ITS barcode: KC411767. (Alternative markers: *BenA* = KP016762; *RPB2* = KP064657; *CaM* = KP016798).

Penicillium philippinense Udagawa & Y. Horie, *J. Jap. Bot*. **47**: 341 (1972). [MB319291]. — Herb.: NHL 6130 *p.p*. (holotype). Ex-type cultures: CBS 623.72 = FRR 1532 = NHL 6130. ITS barcode: KC411770. (Alternative markers: *BenA* = KJ834482; *RPB2* = JN406543; *CaM* = KP016799).

Synonym: *Eupenicillium philippinense* Udagawa & Y. Horie, *J. Jap. Bot.* **47**: 341 (1972). [MB313984]. — Herb.: NHL 6130 p.p. (holotype). Ex-type cultures: CBS 623.72 = FRR 1532 = NHL 6130. ITS barcode: KC411770. (Alternative markers: *BenA* = KJ834482; *RPB2* = JN406543; *CaM* = KP016799).

Penicillium pimiteouiense S.W. Peterson, *Mycologia* **91**: 271 (1999). [MB460126]. — Herb.: BPI 806262 (holotype). Ex-type cultures: CBS 102479 = NRRL 25542. ITS barcode: AF037431. (Alternative markers: *BenA* = HQ646569; *RPB2* = JN406650; *CaM* = HQ646580).

Penicillium raciborskii K.M. Zalessky, *Bull. Int. Acad. Polon. Sci*., *sér*. B, *Sci. Nat*. **1927**: 454 (1927). [MB276002]. — Herb.: K(M) IMI 40568 (neotype, Pitt *et al*. 2000). Ex-type cultures: CBS 224.28 = ATCC 10488 = DSM2422 = FRR 2150 = IFO 7676 = IMI 040568 = LSHBP 92 = MUCL 29246 = NRRL 2150. ITS barcode: AF033447. (Alternative markers: *BenA* = JX141069; *RPB2* = JN406607; *CaM* = KP016800).

Synonym: Penicillium caerulescens Quintan., *Mycopathologia* **82**: 101 (1983) (*fide* Frisvad *et al*. 1990). [MB108323]. — Herb.: unknown. Ex-type culture: Q1147 (personal collection of Quintanilla). ITS barcode: n.a. (Alternative markers: *BenA* = n.a.; *RPB2* = n.a.; *CaM* = n.a.).

Penicillium radulatum: See under *Penicillium melinii*.

Penicillium repensicola Visagie & K. Jacobs, *IMA Fungus* **7**: 102 (2016). [MB811006]. — Herb.: CBS H-22047 (holotype). Ex-type cultures: CBS 139160 = DAOMC 241080 = DTO 183-B8 = CV 1495. ITS barcode: JX140893. (Alternative markers: *BenA* = JX141150; *RPB2* = KP064660; *CaM* = JX157490).

Penicillium restrictum J.C. Gilman & E.V. Abbott, *Iowa St. Coll. J. Sci*. **1**: 297 (1927). [MB276289]. — Herb.: K(M) IMI 40228 (neotype, Pitt 1980). Ex-type cultures: CBS 367.48 = ATCC 11257 = FRR 1748 = IMI 040228 = NRRL 1748 = QM 1962. ITS barcode: AF033457. (Alternative markers: *BenA* = KJ834486; *RPB2* = JN121506; *CaM* = KP016803).

Synonyms: Penicillium gilmanii Thom, *Penicillia*: 345 (1930) (*fide* Pitt 1980). [MB265991]. — Herb.: unknown. Ex-type culture: No culture available.

Penicillium griseum (Sopp) Biourge, *Cellule* **33**: 103 (1923) (*fide* Pitt 1980). [MB152791]. — Herb.: unknown. Ex-type culture: No culture available.

Citromyces griseus Sopp, *Skr. VidenskSelsk. Christiana* **11**: 119 (1912). [MB491119].

Penicillium rubefaciens Quintan., *Mycopathologia* **80**: 73 (1982). [MB109998]. — Herb.: CBS 145.83 (neotype, Frisvad *et al*. 1990). Ex-type cultures: CBS 145.83 = CECT 2752. ITS barcode: KC411677. (Alternative markers: *BenA* = KJ834487; *RPB2* = JN406627; *CaM* = KP016804).

Penicillium rubidurum Udagawa & Y. Horie, *Trans. Mycol. Soc. Japan* **14**: 381 (1973). [MB319295]. — Herb.: NHL 6460 *p.p*. (holotype). Ex-type cultures: CBS 609.73 = NRRL 6033 = ATCC 28051 = ATCC 48238 = FRR 1558 = IMI 228551 = NHL 6460. ITS barcode: AF033462.

(Alternative markers: *BenA* = HQ646574; *RPB2* = JN406545; *CaM* = HQ646585).

Synonym: Eupenicillium rubidurum Udagawa & Y. Horie, *Trans. Mycol. Soc. Japan* **14**: 381 (1973). [MB313985]. — Herb.: NHL 6460 *p.p*. (holotype). Ex-type cultures: CBS 609.73 = NRRL 6033 = ATCC 28051 = ATCC 48238 = FRR 1558 = IMI 228551 = NHL 6460. ITS barcode: AF033462. (Alternative markers: *BenA* = HQ646574; *RPB2* = JN406545; *CaM* = HQ646585).

Penicillium sabulosum: See under *Penicillium smithii*.

Penicillium smithii Quintan., *Av. Aliment. Majora Anim*. **23**: 340 (1982). [MB114173]. — Herb.: CBS 276.83 (neotype, Pitt *et al.* 2000). Ex-type cultures : CBS 276.83 = CECT 2744 = IMI 259693. ITS barcode: KC411723. (Alternative markers: *BenA* = KJ834492; *RPB2* = JN406589; *CaM* = KP016806).

Synonyms: Penicillium corynephorum Pitt & A. D. Hocking, *Mycotaxon* **22**: 202 (1985). [MB105609]. — Herb.: FRR 2663 (holotype). Ex-type cultures: CBS 256.87 = FRR 2663 = IMI 288724. ITS barcode: KC411716. (Alternative markers: *BenA* = KP016755; *RPB2* = KP064635; *CaM* = KP016781).

Penicillium sabulosum Pitt & A. D. Hocking, *Mycologia* **77**: 818 (1985). [MB104604]. — Herb.: FRR 2743 (holotype). Ex-type cultures: CBS 261.87 = FRR 2743. ITS barcode: KC411719. (Alternative markers: *BenA* = KP016765; *RPB2* = KP064672; *CaM* = KP016805).

Talaromyces sabulosus (Pitt & A.D. Hocking) Samson, Yilmaz & Frisvad, Stud. Mycol. 70: 177 (2011). [MB560673].

Penicillium striatisporum Stolk, *Antonie van Leeuwenhoek* **35**: 268 (1969). [MB335769]. — Herb.: CBS 705.68 (holotype). Ex-type cultures: CBS 705.68 = ATCC 22052 = CCRC 31679 = FRR 827 = IMI 151749 = MUCL 31202. ITS barcode: AF038938. (Alternative markers: *BenA* = JX141156; *RPB2* = JN406538; *CaM* = KP016807).

Penicillium subcinereum: See under *Penicillium citreonigrum*.

Penicillium subturcoseum Visagie & K. Jacobs, *IMA Fungus* **7**: 105 (2016). [MB811008]. — Herb.: CBS H-22041 (holotype). Ex-type cultures: CBS 139132 = DAOMC 241096 = DTO 180-C9 = CV 2835. ITS barcode: FJ231006. (Alternative markers: *BenA* = JX141161; *RPB2* = KP064674; *CaM* = JX157532).

Penicillium terrenum D.B. Scott, *Mycopathol. Mycol. Appl*. **36**: 1 (1968). [MB335771]. — Herb.: CBS 313.67 *p.p*. (holotype). Ex-type cultures: CBS 313.67 = ATCC 18547 = CSIR 1022 = IMI 136208. ITS barcode: AM992111. (Alternative markers: *BenA* = KJ834496; *RPB2* = JN406577; *CaM* = KP016808).

Synonyms: *Eupenicillium terrenum* D.B. Scott, *Mycopathol. Mycol. Appl.* **36**: 1 (1968). [MB330745]. — Herb.: CBS 313.67 *p.p*. (holotype). Ex-type cultures: CBS 313.67 = ATCC 18547 = CSIR 1022 = IMI 136208. ITS barcode: AM992111. (Alternative markers: *BenA* = KJ834496; *RPB2* = JN406577; *CaM* = KP016808).

Penicillium luzoniacum Udagawa & Y. Horie, *J. Jap. Bot.* **47**: 338 (1972). [MB319284]. — Herb.: CBS H-7120 *p.p*. (isotype). Ex-type cultures: CBS 622.72 = DSM2418 = NHL 6128 = NRRL 5824. ITS barcode: AF033446. (Alternative markers: *BenA* = KP016759; *RPB2* = JN406544; *CaM* = KP016790).

Eupenicillium luzoniacum Udagawa & Y. Horie, *J. Jap. Bot*. **47**: 338 (1972). [MB313979]. — Herb.: CBS H-7120 *p.p*. (isotype). Ex-type cultures: CBS 622.72 = DSM2418 = NHL 6128 = NRRL 5824. ITS barcode: AF033446. (Alternative markers: *BenA* = KP016759; *RPB2* = JN406544; *CaM* = KP016790).

Penicillium chalybeum Pitt & A.D. Hocking, *Mycotaxon* **22**: 204 (1985). [MB105608]. — Herb.: FRR 2660 (holotype). Ex-type cultures: CBS 254.87 = FRR 2660. ITS barcode: KC411713. (Alternative markers: *BenA* = KJ834440; *RPB2* = JN406596; *CaM* = KP016775).

Penicillium toxicarium: See under *Penicillium citreosulfuratum*.

Penicillium turris-painense: See under *Penicillium namyslowskii*.

Penicillium velutinum J.F.H. Beyma, *Zentralbl. Bakteriol. Parasitenk*., *Abt*. 2 **91**: 353 (1935). [MB283175]. — Herb.: K(M) IMI 40571 (neotype, Pitt 1980). Ex-type cultures: CBS 250.32 = ATCC 10510 = CECT 2318 = IJFM 5108 = IMI 040571 = NRRL 2069 = QM 7686 = VKMF-379. ITS barcode: AF033448. (Alternative markers: *BenA* = JX141170; *RPB2* = KP064682; *CaM* = KP016810).

Penicillium vinaceum J.C. Gilman & E.V. Abbott, *Iowa St. Coll. J. Sci*. **1**: 299 (1927). [MB281754]. — Herb.: K(M) IMI 29189 (neotype, Pitt 1980). Ex-type cultures: CBS 389.48 = ATCC 10514 = FRR 739 = IMI 029189 = NRRL 739 = QM 6746. ITS barcode: AF033461. (Alternative markers: *BenA* = HQ646575; *RPB2* = JN406555; *CaM* = HQ646586).

Penicillium xanthomelinii Visagie & K. Jacobs, *IMA Fungus* **7**: 105 (2016). [MB811009]. — Herb.: CBS H-22048 (holotype). Ex-type cultures: CBS 139163 = DAOMC 241104 = DTO 183-C7 = CV 1677. ITS barcode: JX140921. (Alternative markers: *BenA* = JX141120; *RPB2* = KP064683; *CaM* = JX157495).

Talaromyces sabulosus: See under *Penicillium smithii*.

Torulomyces laevis: See under *Penicillium leave*.

Torulomyces ovatus: See under *Penicillium ovatum*.

DISCUSSION

Penicillium sect. *Exilicaulis* is a taxonomically diverse group currently containing 83 *Penicillium* species names, including 11 *Eupenicillium* basionyms and one variety. Using four genes and applying GCPSR, we accept 43 of these species and introduce nine new species isolated from the fynbos biome in South Africa. The difficulty of distinguishing some species in section *Exilicaulis* using morphology alone is clear in the *P. corylophilum*-clade, where some complexes differ only inconspicuously whereas some neighbouring phylogenetically coherent species display considerable phenotypic variation. For example, we introduce six new species closely related to *P. rubefaciens,* but there are only minor morphological differences between some of these, although they are all phylogenetically distinct; i.e. they are “cryptic species”. The contrary example is *P. atrolazulinum,* which from a morphological perspective might represent multiple species (Fig. 7), but phylogenetically is only one (Figs 3–4). This again emphasizes the importance of sequence-based identifications and species circumscriptions in *Penicillium*, a

genus now containing 406 accepted species (Visagie *et al*. 2014b), making it one of the larger fungal genera. This number is ever increasing with 41 species introduced since the end of 2014 (Perrone *et al*. 2015, Peterson *et al*. 2015, Rong *et al*. 2015, Visagie *et al*. 2015, 2016a, b, You *et al*. 2014). At least five new fynbos species remain undescribed adding to the already 27 described during our fynbos diversity project. From experience we know that the fynbos biome still has a huge reservoir of undescribed species, especially when we start exploring other regions and more microhabitats similar to that of *Protea repens*. It would not be surprising if the number of new species described from this unique South African floral region reaches a century. The fynbos, however, represents a small proportion of the world inventory and it begs the question as to how many species remain undescribed from the world's other 24 biodiversity hotspots (Myers *et al*. 2000). Species estimates is a controversial subject but the general consensus for fungi is a conservative 1.5 million (Hawksworth 1991, 2001). To make such an estimate for *Penicillium* is of course very much speculative, as we simply do not have the type of dataset that Hawksworth (1991, 2001) had (i.e. plant:fungi ratio). With that being said, the total number of *Penicillium* may well reach close to 1000 when considering the possibility of cryptic species, the number of new species that we know will be described in the next few years and the many unexplored or under-sampled habitats in the world. We therefore again emphasize how important it is that new descriptions be accompanied by sequence data of preferably the ITS and *BenA* regions as a minimum requirement.

The ITS is the accepted DNA barcode for fungi (Schoch *et al*. 2014), but contains insufficient variation to distinguish several species of sect. *Exilicaulis*. This is also true for other groups of *Penicillium* and resulted in Visagie *et al*. (2014b) proposing *BenA* as a secondary identification marker for the genus. This gene was selected as it is easy to sequence, reference data is openly available and mostly complete, and most importantly works well for species identifications across the genus. In section *Exilicaulis*, ITS distinguishes species in the *P. citreonigrum*-, *P. decumbens-,* and *P. parvum*-clades, but performs poorly elsewhere. In comparison, *BenA* distinguishes all species in the section and is sufficient for identification purposes. *CaM* would work equally as well, but for *RPB2* we experienced difficulties amplifying and sequencing, and internal primers were often needed to obtain clean sequences. These genes are, however, useful for applying GCPSR to delineate species, and thus can be recommended for widespread use in taxonomic studies of *Penicillium*.

Correct identification of *Penicillium* sect. *Exilicaulis* species is important because they have important roles in a wide range of habitats. *Penicillium corylophilum* was recently reported as a common indoor contaminant (McMullin *et al*. 2014, Visagie *et al.* 2014a), where it can produce several extrolites that may cause allergies in humans (Kremer *et al.* 1989, McMullin *et a*l. 2014, Ohnishi *et al*. 2002, Unoura *et al.* 2011). *Penicillium pimiteouiense* and *P. canis* were respectively isolated from polycystic kidney cell structures (Peterson *et a*l. 1999) and a dog suffering with osteomyelitis (Langlois *et al.* 2014), and could be significant to animal health. Another medical example is *P. decumbens,* commonly reported from indoor air (Samson *et al*. 2010), which was isolated from a para-vertebral infection (Lyratzopoulos *et al*. 2002) and was reported as the causative agent of a fungus ball (Yoshida *et a*l. 1992).

Penicillium citreosulfuratum (as "*P. toxicarium*") was closely associated with cork bark (*Quercus suber)* in Portugal (Serra *et al.* 2008), and although not considered a health concern, may contribute to mouldy flavours in wine. *Penicillium citreosulfuratum* ("*P. toxicarium*" in Serra *et al*.) and *P. citreonigrum* (syn. *P. citreoviride*) are good producers of citreoviridin (Peterson *et al.* 2015), a mycotoxin linked to yellow rice disease or acute cardiac beri-beri in Japan (Miyake 1940, Sakabe *et al.* 1977, Udagawa & Tatsuno 2004, Uraguchi 1969) and more recently in Brazil (Almeida *et al*. 2012, Rosa *et al.* 2010). Citreoviridin production is associated with numerous species from various substrates (Cole *et al.* 1981, Wicklow & Cole 1984, Wicklow *et al.* 1988, Wigmann *et al*. 2015); Peterson *et al.* (2015) updated identifications from previous studies, confirming that many *Penicillium* species do produce citreoviridin.

We consider *P. citreosulfuratum* the correct name for *P. toxicarium*. It is unknown whether the ex-type culture of *P. citreosulfuratum* (IMI 92228) produces citreoviridin. *Penicillium cinerascens* has *P. citreonigrum* and *P. citreosulfuratum* as its closest relatives and does not produce citreoviridin. The description of *P. toxicarium* by Miyake (1940) was invalid because he did not include a Latin diagnosis. Ramírez (1982) later validated the name based on an ex-type strain CBS 351.51, noting that the culture had changed noticeably from the original description; that strain was evidently a contaminant and did not represent the species observed by Miyake. Houbraken *et al*. (2014) showed that sequences obtained from CBS 351.51 are identical to *P. trzebinskii* in section *Aspergilloides.* Serra *et al*. (2008) identified a number of isolates from cork bark (*Q. suber*) collected in Portugal as *P. toxicarium* and obtained sequences showing a close relationship to *P. citreonigrum*. Since then, numerous sequences have been deposited in GenBank as *P. toxicarium* based on that application of the name. Unfortunately, Serra *et al.* (2008) did not epitypify the name or indicate which strain they considered to be the ex-type. Although we agree that this clade possibly represents Miyake's (1940) original species, our data show that *P. citreosulfuratum* is the correct and older name for the clade, and we reduce *P. toxicarium* to a synonym. Adopting this name also resolves the confusion surrounding the application of *P. toxicarium*.

Several species accepted here were previously considered synonyms of other species, including *P. arabicum*, *P. albocinerascens* and *P. kurssanovii*, all part of the *P. restrictum*-clade. Although the section represents a species complex, these three species have unique sequences and are thus considered distinct. Unfortunately, no ex-type cultures are available for *P. bertai* (= *P. citreonigrum*), *P. gilmanii* (= *P. restrictum*) and *P. griseum* (= *P. restrictum*), and we thus accept the synonymies proposed by Pitt (1980). *Penicillium glaucolanosum* was considered synonymous with *P. decumbens* (Pitt 1980), but does not belong in section *Exilicaulis* and is probably a synonym of *P. janthinellum* (Houbraken & Samson 2011).

The ecology of *Penicillium* species inside *Protea repens* infructescences is intriguing. After a flowering season, usually between fall and winter, *Protea repens* inflorescences close and become woody (serotinous) and then only mites and insects can enter or exit. *Penicillium atrolazulinum* and *P. citreosulfuratum* had a close association with *Protea repens* infructescences and their mite communities. Reasons for this dominance are unclear but seem unlikely to be a coincidence because they dominated isolations from three very distinct collection sites, during three different flowering seasons. Perhaps there is an unknown selective pressure favouring their growth inside these infructescences, or mites could perhaps carry them into flowers where they start to outcompete other species for available nutrients when the flower closes. A mutualistic association between mites and a fungus in *Protea* infructescences was previously reported for *Ophiostoma*, but no association was found with any *Penicillium* species (Roets *et al.* 2007). During isolations from living mites, we observed that they commonly fed on colonies from these two *Penicillium* species. In Petri dishes, they would almost exclusively lay their eggs in *P. citreosulfuratum* colonies. The relationships among the flowers, mites, and the two *Penicillium* species should be investigated further to address this apparent feeding preference. Similar behaviour has been noted for other penicillia: Kobayashi *et al*. (2008) and Li *et al.* (2012) found *P. herquei* to almost exclusively colonize leaf rolls of *Euops chinensis*, with Li *et al*. (2012) suggesting a mutualistic relationship based on the fungus significantly improving development of larvae. Similarly, *P. coffeae* was described as an associate of the coffee-berry borer (*Hypothenemus hampei*) with speculation that the fungus might provide the beetle with the exogenous sterols necessary for development (Peterson *et al.* 2003). That mites preferred to feed and lay eggs in *P. citreosulfutatum* colonies suggests a similar mutualism. One hypothesis is that the fungus provides necessary nutrients to mites, while the mites act as vectors of dispersal to and from enclosed *Protea repens* infructescences. With regard to species distribution, it would be interesting to investigate whether *P. citreosulfuratum*: (1) is present in other *Protea* species; (2) is present in *Protea* farmed for export; and (3) includes strains capable of producing citreoviridin.

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