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Phylogenetic and taxonomic studies on the genera *Penicillium* and *Talaromyces*

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Cover: Top from left to right: Young cleistothecium of *Talaromyces trachyspermus*, ascospores of *T. macrosporus*, conidiophore of *Penicillium sumatrense*. Bottom from left to right: Conidiophores of *P. calidicanium*, MEA Petri dish with 7 d old culture of *P. isariiforme*, scanning electron micrograph of ascospores of *P. shearii*.

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Phylogeny of *Penicillium* and the segregation of *Trichocomaceae* into three families

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Abstract: Species of *Trichocomaceae* occur commonly and are important to both industry and medicine. They are associated with food spoilage and mycotoxin production and can occur in the indoor environment, causing health hazards by the formation of β-glucans, mycotoxins and surface proteins. Some species are opportunistic pathogens, while others are exploited in biotechnology for the production of enzymes, antibiotics and other products. *Penicillium* belongs phylogenetically to *Trichocomaceae* and more than 250 species are currently accepted in this genus. In this study, we investigated the relationship of *Penicillium* to other genera of *Trichocomaceae* and studied in detail the phylogeny of the genus itself. In order to study these relationships, partial *RPB1*, *RPB2* (RNA polymerase II genes), *Tsr1* (putative ribosome biogenesis protein) and *Cct8* (putative chaperonin complex component TCP-1) gene sequences were obtained. The *Trichocomaceae* are divided in three separate families: *Aspergillaceae*, *Thermoascaceae* and *Trichocomaceae*. The *Aspergillaceae* are characterised by the formation flask-shaped or cylindrical phialides, asci produced inside cleistothecia or surrounded by Hülle cells and mainly ascospores with a furrow or slit, while the *Trichocomaceae* are defined by the formation of lanceolate phialides, asci borne within a tuft or layer of loose hyphae and ascospores lacking a slit. *Thermoascus* and *Paecilomyces*, both members of *Thermoascaceae*, also form ascospores lacking a furrow or slit, but are differentiated from *Trichocomaceae* by the production of asci from croziers and their thermotolerant or thermophilic nature. Phylogenetic analysis shows that *Penicillium* is polyphyletic. The genus is re-defined and a monophyletic genus for both anamorphs and teleomorphs is created (*Penicillium sensu stricto*). The genera *Thysanophora*, *Eupenicillium*, *Chromocleista*, *Hemicarpenteles* and *Torulomyces* belong in *Penicillium s. str.* and new combinations for the species belonging to these genera are proposed. Analysis of *Penicillium* below genus rank revealed the presence of 25 clades. A new classification system including both anamorph and teleomorph species is proposed and these 25 clades are treated here as sections. An overview of species belonging to each section is presented.

Key words: *Aspergillus*, *Eupenicillium*, nomenclature, *Penicillium*, *Talaromyces*, taxonomy.
Taxonomic novelties: New sections, all in *Penicillium*: sect. *Sclerotiora* Houbraken & Samson, sect. *Charlesia* Houbraken & Samson, sect. *Thysanophora* Houbraken & Samson, sect. *Ochrosalmonea* Houbraken & Samson, sect. *Cinnamopurpurea* Houbraken & Samson, *Fracta* Houbraken & Samson, sect. *Stolkia* Houbraken & Samson, sect. *Gracilenta* Houbraken & Samson, sect. *Citrina* Houbraken & Samson, sect. *Turbata* Houbraken & Samson, sect. *Paradoxa* Houbraken & Samson, sect. *Canescentia* Houbraken & Samson.
New combinations: *Penicillium asymmetricum* (Subramanian & Sudha) Houbraken & Samson, *P. bovifimosum* (Tuthill & Frisvad) Houbraken & Samson, *P. glaucoalbidum* (Desmazières) Houbraken & Samson, *P. laeve* (K. Ando & Manoch) Houbraken & Samson, *P. longisporum* (Kendrick) Houbraken & Samson, *P. malachiteum* (Yaguchi & Udagawa) Houbraken & Samson, *P. ovatum* (K. Ando & Nawawi) Houbraken & Samson, *P. parviverrucosum* (K. Ando & Pitt) Houbraken & Samson, *P. saturniforme* (Wang & Zhuang) Houbraken & Samson, *P. taiwanense* (Matsushima) Houbraken & Samson.
New names: *Penicillium coniferophilum* Houbraken & Samson, *P. hennebertii* Houbraken & Samson, *P. melanostipe* Houbraken & Samson, *P. porphyreum* Houbraken & Samson.

INTRODUCTION

The *Trichocomaceae* comprise a relatively large family of fungi well-known for their impact, both positive and negative, on human activities. The most well-known species of this family belong to the genera *Aspergillus*, *Penicillium* and *Paecilomyces*. Species belonging to *Trichocomaceae* are predominantly saprobic and represent some of the most catabolically and anabolically diverse microorganisms known. Some species are capable of growing at extremely low water activities (*i.e.* xerotolerant and/or osmotolerant), low temperatures (psychrotolerant) and high temperatures (thermotolerant). Members of *Trichocomaceae* secrete secondary metabolites (extrolites) that are known as mycotoxins (*e.g.* aflatoxins, ochratoxins, patulin), while other extrolites are used as pharmaceuticals, including antibiotics such as penicillin and the cholesterol-lowering agent lovastatin. Furthermore, members of *Trichocomaceae* are also known for their production of organic acids and diverse enzymes that degrade a wide variety of complex biomolecules (Geiser *et al*. 2006, Pitt & Hocking 2009, Samson *et al*. 2010).

The taxon *Trichocomaceae* was introduced by Fischer (1897) and the classification of this family was studied extensively using phenotypic characters (Malloch & Cain 1972, Subramanian 1972, Malloch 1985a, b, von Arx 1986). These studies include only teleomorph genera because *Trichocomaceae* is based on *Trichocoma*, a teleomorph genus, and thus not applicable for anamorph genera (Malloch 1985b). However, it is noted that anamorph genera with phialidic structures are linked to *Trichocomaceae* (Malloch & Cain 1972). Currently, only the phylogenetic relationships within certain genera of *Trichocomaceae*, *e.g. Aspergillus*, *Penicillium* and *Paecilomyces*, are elucidated (Peterson 2000a, b, Samson *et al*. 2004, Peterson 2008, Samson *et al*. 2009), but the relationships among the genera are still poorly studied.

Penicillium is an anamorph genus and belongs phylogenetically to *Trichocomaceae* (Berbee 1995, Peterson 2000a). The name *Penicillium* is derived from *penicillus*, which means "little brush" and was introduced by Link in 1809. Many new species were described in the 19th century, and Dierckx (1901) was the first researcher who introduced a subgeneric classification system for the genus.

He proposed the subgenera *Aspergilloides*, *Biverticillium* and *Eupenicillium* and Biourge (1923) followed Dierckx's classification system and expanded it with two sections, four series and six subsections. Thom (1930: 155–159) did not accept Dierckx's and Biourge's subgeneric classification system and introduced a new system with four divisions (subgenera), 12 sections and 18 subsections (series). His system was mainly based on colony characteristics and conidiophore branching and the monographs of Raper & Thom (1949) and Ramírez (1982) are in line with that of Thom (1930). Pitt (1980) did not follow Thom's concept and, based on conidiophore characters, phialide shapes and growth characteristics, divided *Penicillium* into four subgenera, 10 sections and 21 series. In addition, he treated *Eupenicillium* separately from *Penicillium* and subdivided the former genus into eight series. In 1985, Stolk & Samson proposed another taxonomic scheme for *Penicillium* anamorphs and this classification was primary based on phialide shape and conidiophore branching. They divided *Penicillium* in 10 sections and 18 series and this taxonomic scheme treated strict anamorphs, as well as anamorphs of sexual *Penicillium* species. More recently, Frisvad & Samson (2004) studied subgenus *Penicillium* and five sections and 17 series were recognised.

The first attempt to make a subgeneric classification of *Eupenicillium* was undertaken by Pitt (1980) and eight series were introduced. This classification was based on a combination of various characters, such as growth rates in standard conditions, colony morphology and microscopical characters of both teleomorphic and anamorphic states. In the monograph of Stolk & Samson (1983), four sections were introduced for the classification of *Eupenicillium*, and Pitt's concept of using series of species was abandoned.

To date, only a limited number of studies have investigated the phylogenetic relationship of *Penicillium* at genus level. Berbee (1995), based of 18S rDNA sequences, demonstrated that *Penicillium* is polyphyletic. The genus splits up in two clades: one clade includes *Talaromyces* species and members of the subgenus *Biverticillium* and the other clade includes *Eupenicillium* species and *Penicillium* species accommodated in the subgenera *Penicillium*, *Furcatum* and *Aspergilloides* (LoBuglio & Taylor 1993, LoBuglio *et al*. 1993, Berbee *et al*. 1995, Ogawa *et al*. 1997, Wang & Zhuang 2007). Peterson (2000a) studied the phylogeny of *Eupenicillium* and members of the subgenera *Penicillium*, *Furcatum* and *Aspergilloides* in more detail. He subsequently divided the studied species in six groups and showed that many subgeneric taxa in *Penicillium* are polyphyletic. Furthermore, his data indicated that the current classification systems based on conidiophore branching is not congruent with the phylogeny and a new subgeneric classification system is needed.

Pleomorphism in fungi was first demonstrated by Tulasne (1851). Together with his discovery, he was already aware of the problem raised by the nomenclature of composite species and he stated that the imperfect forms must someday be submerged in the Ascomycota. He thus established a first principle of pleomorphic nomenclature and suggested the precedence of the perfect state name over imperfect names (Hennebert 1971). In 1910, "dual nomenclature" was introduced and this was established in the International Code of Botanical Nomenclature (ICBN). The problem of naming fungi that exhibit pleomorphic life cycles was addressed in previous versions of article 59 of the ICBN and implied that more than one name for a single taxon can be used (Cline 2005). Recently, the proposal to revise article 59 was accepted at the 2011 IBC Nomenclature Section at Melbourne and the principle of "one fungus : one name" was established (Norvell *et al*. 2011).

In the present study, the phylogenetic relationships between *Penicillium* and other members of the family *Trichocomaceae* are studied using a combined analysis of four loci (*RPB1*, *RPB2*, *Tsr1* and *Cct8*). In this study, the principle "one fungus - one name" is applied and priority is given to the oldest family, genus and section names using the single-name nomenclature (Hawksworth *et al*. 2011, Norvell 2011). *Penicillium* is delimited, various genera are placed in synonymy, and new combinations in *Penicillium* are made for the species belonging to the genera *Thysanophora*, *Eupenicillium*, *Chromocleista*, *Hemicarpenteles* and *Torulomyces*. Subsequently, the phylogeny of *Penicillium* is studied and a new sectional classification system is proposed. In addition, an overview of species in each section is presented.

MATERIAL AND METHODS

Strains

The first part of this study treats the phylogenetic relationships of the *Penicillium* species among *Trichocomaceae*. A selection of strains is made in order to study these relationships and in most cases the types of the genera were selected. The second part deals with the phylogeny of *Penicillium.* For this study, the type species of the various subgenera and sections in *Penicillium* and *Eupenicillium* were selected, and this selection is supplemented with other related species. An overview of strains used in the study of the phylogeny of *Trichocomaceae* and *Penicillium* presented in Table 1. In the third part of this study, a new sectional classification system for *Penicillium* is proposed and lists of species in each section are compiled. For the preparation of these lists, mostly type strains were selected of accepted *Penicillium* and *Eupenicillium* species. This selection is based on the overview of "accepted species and their synonyms in the *Trichocomaceae*" by Pitt *et al*. (2000) and supplemented with species described after 2000. An overview of these strains is shown in Table S1 (Supplementary Information - online only) and partly in Table 1 (species names indicated with two asterisks). All strains are maintained in the CBS-KNAW culture collection and additional strains were obtained from IBT (culture collection of Center for Microbial Biotechnology (CMB) at Department of Systems Biology, Technical University of Denmark), NRRL (ARS Culture Collection, U.S. Department of Agriculture, Peoria, Illinois, USA), ATCC (American Type Culture Collection, Manassas, VA, USA) and IMI (CABI Genetic Resources Collection, Surrey, UK).

DNA extraction, amplification and sequencing

Genomic DNA was extracted using the Ultraclean Microbial DNA isolation kit (MoBio Laboratories, Carlsbad, CA, USA), according to the manufacturer's instructions. Parts of the following loci were amplified and sequenced for the species listed in Table 1: 1. *RPB1*, RNA polymerase II largest subunit (regions E and F; according Matheny *et al.* 2002), 2. *RPB2*, RNA polymerase II second largest subunit (regions 5–7), 3. *Cct8*, subunit of the cytosolic chaperonin Cct ring complex, related to Tcp1p and required for the assembly of actin and tubulins *in vivo* (Stoldt *et al.* 1996, Kim *et al.* 1994), 4. *Tsr1*, protein required for processing of 20S pre-rRNA in the cytoplasm

Table 1. Strains used in phylogenetic analysis of *Trichocomaceae* and other families.

CBS no.	Name	Other collections	Origin	GenBank accession or reference[1]			
				RPB1	***RPB2***	***Tsr1***	***Cct8***
CBS 267.72[NT]	*Aphanoascus cinnabarinus**	ATCC 26215	Soil, Japan	JN121625	JN121477	JN121783	JN121903
CBS 172.66[T]	*Aspergillus aculeatus**	ATCC 16872 = IMI 211388	Tropical soil	JN121590	JN121448	JN121755	JN121895
CBS 600.67[T]	*Aspergillus amylovorus**	ATCC 18351 = IMI 129961 = MUCL 15648	Wheat starch, Kharkiv, Ukraine	JN121705	JN121538	JN121844	JN121931
CBS 463.65[NT]	*Aspergillus arenarius**	ATCC 16830 = IMI 055632 = IMI 055632ii	Soil, Mysore, Karnataka, India	JN121684	JN121520	JN121825	JN121917
CBS 653.74[T]	*Aspergillus aureofulgens**		Natural truffle soil, Provence, France	JN121712	JN121545	JN121851	JN121936
CBS 109.46[NT]	*Aspergillus avenaceus**	ATCC 16861 = IMI 016140 = NRRL 517	Seed of *Pisum sativum* (pea), England, UK	JN121565	JN121424	JN121731	JN121878
CBS 468.65[NT]	*Aspergillus biplanus**	ATCC 16858 = IMI 235602	Soil, Tilaran, Costa Rica	JN121685	JN121520	JN121826	JN121917
CBS 707.71[T]	*Aspergillus bisporus**	ATCC 22527 = NRRL 3693	Soil injected into mouse, Clarksburg, Maryland, USA	JN121715	JN121548	JN121854	JN121939
CBS 127.61[NT]	*Aspergillus brunneouniseriatus**	ATCC 16916 = IMI 227677	Soil under Dalbergia sissoo, India	JN121583	JN121442	JN121749	JN121889
CBS 121611	*Aspergillus calidoustus**		Patient (case 4), man with allogeneic HSCT, probably lung infection, man, Washington, USA	JN121579	JN121438	JN121745	JN121887
CBS 566.65[NT]	*Aspergillus candidus**	ATCC 1002 = IMI 091889 = NRRL 303	Unknown source	JN121702	JN121535	JN121841	JN121929
CBS 196.64[NT]	*Aspergillus cervinus**	ATCC 15508 = IMI 107684	Soil, West Malaysia, Malaysia	JN121595	JN121452	JN121759	JN121896
CBS 473.65[NT]	*Aspergillus clavatoflavus**	ATCC 16866 = IMI 124937	Rain forest soil,Tulley, Queensland, Australia	JN121686	JN121521	JN121827	JN121918
	Aspergillus clavatus[1]*	NRRL 1 (= ATCC 1007 = CBS 513.65 = IMI 15949)	Unknown source	Fedorova *et al.* (2008)			
CBS 476.65[NT]	*Aspergillus conjunctus**	ATCC 16796 = IMI 135421	Forest soil, Palmar, Province of Puntarenas, Costa Rica	JN121688	JN121523	JN121829	JN121920
CBS 553.77[T]	*Aspergillus coremiiformis**	ATCC 38576 = 223069	Soil, Ivory Coast	JN121700	JN12153	JN121839	JN121926
CBS 656.73[NT]	*Aspergillus egyptiacus**	IMI 141415	Sandy soil, under *Olea europaea* (olive tree), Mediterranean Coast, Ras-el-Hikma, Egypt	JN121713	JN121546	JN121852	JN121937
CBS 128202	*Aspergillus flavus*[1]*	NRRL 3357 (= ATCC 200026)	Peanut cotyledons, USA	Unpublished			
	Aspergillus fumigatus[1]*	Af293	Patient with invasive aspergillosis	Nierman *et al.* (2005)			
CBS 116.56N[T]	*Aspergillus funiculosus**	ATCC 16846 = IMI 054397 = IMI 054397ii	Soil, Ibadan, Nigeria	JN121572	JN121431	JN121738	JN121883
CBS 118.45[T]	*Aspergillus janus**	ATCC 16835 = IMI 016065 = IMI 016065ii = MUCL 31307 = NRRL 1787	Soil, Panama	JN121576	JN121435	JN121742	JN121885
CBS 538.65[NT]	*Aspergillus kanagawaensis**	ATCC 16143 = IMI 126690	Forest soil under *Pinus banksiana*, Wisconsin, USA	JN121698	JN121531	JN121837	JN121925
CBS 151.66[T]	*Aspergillus leporis**	ATCC 16490	Dung of *Lepus townsendii* (white-tailed Jackrabbit), near Saratoga, Wyoming, USA	JN121589	JN121446	JN121753	JN121893
CBS 513.88	*Aspergillus niger*[1]*		Derived from NRRL 3122 and currently used as enzyme production strain.	Pel *et al.* (2007)			

Table 1. (Continued).

CBS no.	Name	Other collections	Origin	GenBank accession or reference[1]			
				RPB1	*RPB2*	*Tsr1*	*Cct8*
CBS 101887	*Aspergillus ochraceoroseus**	ATCC 42001 = IBT 14580	Soil, Tai National Forest, Ivory Coast	JN121557	JN121416	JN121723	JN121871
CBS 108.08^{NT}	*Aspergillus ochraceus**	ATCC 1008 = CBS 547.65 = IMI 016247 = IMI 016247iii = IMI 016247iv = NRRL 1642 = NRRL 398	Unknown source	JN121562	JN121421	JN121728	JN121875
CBS 622.67^{T}	*Aspergillus penicilliformis**	ATCC 18328 = IMI 129968 = IMI 132431	Soil under *Nicotiana tabacum*, Moldavia, Romania	JN121708	JN121542	JN121848	JN121934
CBS 130294	*Aspergillus penicillioides**	DTO 11C3	Indoor environment, Germany	JN121578	JN121437	JN121744	JN121886
CBS 578.65^{NT}	*Aspergillus pulvinus**	ATCC 16842 = IMI 139628	Forest soil, Liberia, Province of Guanacaste, Costa Rica	JN121703	JN121536	JN121842	JN121930
CBS 117.33^{NT}	*Aspergillus restrictus**	ATCC 16912 = CBS 541.65 = IMI 016267 = MUCL 31313 = NRRL 154 = NRRL 4155	Cloth, UK	JN121574	JN121432	JN121740	JN121884
CBS 649.93^{T}	*Aspergillus robustus**	CBS 428.77 = IBT 14305	Surface soil from thorn-forest, near Mombasa, Kenya	JN121711	JN121544	JN121850	JN121935
CBS 139.61^{NT}	*Aspergillus sparsus**	ATCC 16851 = IMI 019394 = IMI 019394ii = MUCL 31314 = NRRL 1933	Soil, Costa Rica	JN121586	JN121444	JN121751	JN121891
CBS 112812^{T}	*Aspergillus steynii**	IBT 23096	Dried arabica green coffee bean, on parchment, internal infection, Chamumdeshuran Estata, Karnataka, district Giris, India	JN121569	JN121428	JN121735	JN121880
CBS 264.81	*Aspergillus sydowii**		Grains and milling fractions, *Triticum aestivum*, India	JN121624	JN121476	JN121782	JN121902
	Aspergillus terreus[1]*	NIH 2624	Clinical isolate	Unpublished			
CBS 272.89	*Aspergillus togoensis**	NRRL 13550	Seed, near La Maboké, Central African Republic	JN121627	JN121480	JN121785	JN121904
CBS 245.65	*Aspergillus versicolor**	ATCC 11730 = ATCC 16020 = IMI 045554 = IMI 045554ii = IMI 045554iii = IMI 045554iv = MUCL 19008	Cellophane, Indiana, USA	JN121614	JN121468	JN121775	JN121899
CBS 104.07^{NT}	*Aspergillus wentii**	ATCC 1023 = IMI 017295 = IMI 017295ii = NRRL 1269 = NRRL 375	Soybeans, Java, Indonesia	JN121559	JN121418	JN121725	JN121873
CBS 506.65^{NT}	*Aspergillus zonatus**	ATCC 16867 = IMI 124936	Forest soil, Province of Linon, Fortuna, Costa Rica	JN121691	JN121526	JN121832	JN121921
CBS 380.74^{T}	*Basipetospora halophilica**	IFO 9650	Undaria pinnatifida (Wakame), Osaka, Japan	JN121666	JN121509	JN121815	JN121910
CBS 100.11^{NT}	*Byssochlamys nivea**	ATCC 22260	Unknown source	JN121511	JF417414	JF417381	JF417514
CBS 101075^{T}	*Byssochlamys spectabilis**	ATCC 90900 = FRR 5219	Heat processed fruit beverage; Tokyo Japan	JN121554	JF417446	JF417412	JF417546
CBS 605.74^{T}	*Byssochlamys verrucosa**	ATCC 34163	Nesting material of *Leipoa ocellata* (Malleefowl), Pulletop Nature Reserve, New South Wales, Australia	JN680311	JN121540	JN121746	JN121932

Table 1. (Continued).

CBS no.	Name	Other collections	Origin	GenBank accession or reference[1]			
				RPB1	***RPB2***	***Tsr1***	***Cct8***
CBS 132.31[T]	*Chrysosporium inops**	IMI 096729 = UAMH 802	Skin man, Italy	JN121584	JN121443	JN121750	JN121890
	Coccidioides immitis[1]**	Strain "RS"	Vaccine strain - origin unknown	Sharpton *et al.* (2009)			
CBS 525.83[T]	*Cristaspora arxii**	ATCC 52744 = FMR 416	Soil, Tarragona, Spain	JN121695	JN121529	JN121835	JN121924
CBS 157.66[NT]	*Dichotomomyces cejpii**		Orchard soil, near Tiraspol, Moldova	JN121589	JN121447	JN121754	JN121894
	Emericella nidulans[1]**	FGSC A4 (= ATCC 38163 = CBS 112.46)	Unknown source	Galagan *et al.* (2005)			
CBS 229.60[T]	*Eupenicillium hirayamae**	ATCC 18312 = IMI 078255 = IMI 078255ii = NRRL 143	Milled rice, Thailand	JN121604	JN121459	JN121766	JN121946
CBS 518.65[NT]	*Eurotium amstelodami**	ATCC 16464 = IMI 229971 = NRRL 90	Unknown substrate	JN121694	JN121528	JN121834	JN121923
CBS 516.65[NT]	*Eurotium herbariorum**	ATCC 16469 = IMI 211383 = NRRL 116	Unpainted board, Washington, USA	JN121693	JN121527	JN121833	JN121922
CBS 260.73[T]	*Fennellia flavipes**	ATCC 24484 = IMI 171883 = NRRL 5504	Cellulose material buried in forest soil, Pak Thong Chai, Thailand	JN121623	JN121475	JN121781	JN121901
CBS 252.87[T]	*Geosmithia viridis**	IMI 288716	Soil; bank of creek flowing into Little River; New South Wales; Australia	JN121620	JF417422	JF417389	JF417522
CBS 295.48[IsoT]	*Hamigera avellanea**	ATCC 10414 = IMI 040230 = NRRL 1938	Soil; San Antonio, Texas, USA	JN121632	JF417424	JF417391	JF417524
CBS 377.48[NT]	*Hamigera striata**	ATCC 10501 IMI 039741 = NRRL 717	Canned blueberries, USA	JN121665	JN121508	JN121814	JN121909
CBS 527.65[T]	*Hemicarpenteles paradoxus**	ATCC 16918 = IMI 061446 = NRRL 2162	Dung of *Opossum*, Wellington, New Zealand	JN121696	JN121530	JN121836	JN121989
CBS 607.74[T]	*Leiothecium ellipsoideum**	ATCC 32453	Soil, between rocks, Mystras, Peloponnesos, Greece	JN121707	JN121541	JN121847	JN121933
CBS 109402[T]	*Monascus argentinensis**	FMR 7393	Soil sample, El Infiernillo, Tafi del Valle, Tucumán province, Argentina	JN121564	JN121423	JN121730	JN121877
CBS 113675	*Monascus lunisporas**	FMR 6679	Soil sample, Corcovado Mountain, Tijuca National Park, Rio de Janeiro, Brazil	JN121570	JN121429	JN121736	JN121881
CBS 109.07[T]	*Monascus purpureus**	ATCC 16365 = ATCC 16426 = IMI 210765 = NRRL 1596	Fermented rice grain, 'ang-quac' (purple coloured rice), Kagok-Tegal, imported from China, Prov. Quouan-toung, Java, Indonesia	JN121563	JN121422	JN121729	JN121876
CBS 558.71[T]	*Neocarpenteles acanthosporum**	ATCC 22931 = IMI 164621	Soil, Bougainville Island, Solomon Islands	JN121701	JN121534	JN121840	JN121928
	*Neosartorya fischeri**	NRRL 181	Canned fruit				
CBS 350.66[T]	*Paecilomyces aerugineus**	IMI 105412	Debris of *Glyceria maxima*, Attenborough, Notts., UK	JN121657	JN121502	JN121808	JN121907
CBS 761.68	*Penicilliopsis clavariiformis**	CSIR 1135	Unknown source, Pretoria, South Africa	JN121716	JN121549	JN121855	JN121940
CBS 246.67[HT]	*Penicillium abidjanum***	ATCC 18385 = FRR 1156 = IMI 136244	Savannah soil, near Abidjan, Ivory Coast	JN121615	JN121469	JN121777	JN121954
CBS 209.28[LT]	*Penicillium adametzii**	ATCC 10407 = IMI 039751 = MUCL 29106 = NRRL 737	Soil under conifers, Poznan, Poland	JN121598	JN121455	JN121762	JN121944

Table 1. (Continued).

CBS no.	Name	Other collections	Origin	GenBank accession or reference[1]			
				RPB1	*RPB2*	*Tsr1*	*Cct8*
CBS 317.67[HT]	*Penicillium alutaceum***	ATCC 18542 = FRR 1158 = IFO 31728 = IMI 136243	Soil, near Pretoria, South Africa	JN121641	JN121489	JN121795	JN121968
CBS 220.66[IsoT]	*Penicillium arenicola**	ATCC 18321 = ATCC 18330 = IMI 117658 = NRRL 3392	Soil from pine forest, Kiev, Ukraine	JN121601	JN121457	JN121764	JN121897
CBS 241.56[NT]	*Penicillium atrovenetum***	ATCC 13352 = FRR 2571 = IFO 8138 = IMI 061837	Soil, Sussex Downs, England	JN121614	JN121467	JN121774	JN121953
CBS 299.48[AUT]	*Penicillium camemberti***	ATCC 1105 = ATCC 4845 = FRR 878 = IBT 21508 = IMI 027831 = IMI 092200 = MUCL 29790 = NRRL 877 = NRRL 878	French Camembert cheese, Connecticut, USA	JN121635	JN121484	JN121790	JN121963
CBS 300.48[NT]	*Penicillium canescens**	ATCC 10419 = IMI 028260 = MUCL 29169 = NRRL 910	Soil, England	JN121636	JN121485	JN121791	JN121964
CBS 233.81	*Penicillium caperatum*	FRR 71 = IMI 216895	Neotype of *E. brefeldianum*; soil, Murrumbidgee Irrigation Area, N.S.W., Australia	JN121610	JN121465	JN121772	JN121952
CBS 352.67[HT]	*Penicillium catenatum**	ATCC 18543 = IMI 136241	Desert soil, Upington, Cape Province, South Africa	JN121659	JN121504	JN121810	JN121980
CBS 304.48[T]	*Penicillium charlesii**	ATCC 8730 = CBS 342.51 = IMI 040232 = NRRL 1887 = NRRL 778	Unknown source, UK	JN121637	JN121486	JN121792	JN121965
CBS 306.48[NT]	*Penicillium chrysogenum***	ATCC 10106 = FRR 807 = IBT 5233 = IMI 024314 = IMI 092208 = MUCL 29079 = MUCL 29145 = NRRL 807 = NRRL 810	Cheese, Storrs, Connecticut	JN121638	JN121487	JN121793	JN121966
	*Penicillium chrysogenum[1]**	Wisconsin 54-1255	Moldy cantaloupe Peoria, Illinois, USA	van den Berg *et al.*(2008)			
CBS 490.66	*Penicillium cinnamopurpureum**	ATCC 18337 = IMI 114483	Type of *E. cinnamopurpureum*; cultivated soil, South Africa	JN121690	JN121525	JN121831	JN121988
CBS 258.29[NT]	*Penicillium citreonigrum**	ATCC 48736 = 092209 = MUCL 28648 = MUCL 29062 = MUCL 29116 = NRRL 761	Rotting stem, Belgium	JN121622	JN121474	JN121780	JN121957
CBS 139.45[NT]	*Penicillium citrinum**	ATCC 1109 = IMI 091961 = MUCL 29781 = NRRL 1841	Unknown	JN121585	JF417416	JF417383	JF417516
CBS 232.38	*Penicillium citrinum***	Thom 4733.73	Type of *P. implicatum*; unknown source, Belgium	JN121608	JN121463	JN121770	JN121950
CBS 119387[T]	*Penicillium coffeae**	IBT 27866 = NRRL 35363	Peduncle, *Coffea arabica*, Oahu, Aiea, Hawaii, USA	JN121577	JN121436	JN121743	JN121862
CBS 231.38	*Penicillium corylophilum***	ATCC 10452 = IFO 7726 = IMI 039817 = NRRL 872	Type of *P. humuli*; *Humus lupulus* (hops), Weihenstephan, Germany	JN121606	JN121461	JN121768	JN121948
CBS 271.89[HT]	*Penicillium cryptum**	ATCC 60138 = IMI 296794 = NRRL 13460	Soil from *Quercus-Betula* forest, Hempstead Lake State Park, Long Island, New York	JN121626	JN121478	JN121784	JN121958

Table 1. (Continued).

CBS no.	Name	Other collections	Origin	GenBank accession or reference[1]			
				RPB1	***RPB2***	***Tsr1***	***Cct8***
CBS 660.80[T]	*Penicillium dendriticum**	IMI 216897	Leaf litter of *Eucalyptus pauciflora*, Kosciusko National Park, New South Wales, Australia	JN121714	JN121547	JN121853	JN121938
CBS 112082[epiT]	*Penicillium digitatum***	IBT 13068	*Citrus limon*, Italy	JN121567	JN121426	JN121733	JN121858
CBS 456.70[T]	*Penicillium dimorphosporum**	ATCC 22783 = ATCC 52501 = FRR 1120 = IMI 149680	Mangrove swamp soil, below high tide level, Tooraddin, Westernport Bay, Sawtell's Inlet, Victoria, Australia	JN121683	JN121517	JN121823	JN121985
CBS 322.48[AUT]	*Penicillium duclauxii**	ATCC 10439 = IMI 040044 = MUCL 28672 = MUCL 29094 = MUCL 29212 = NRRL 1030	Canvas, France	JN121643	JN121491	JN121797	JN121905
CBS 112493[T]	*Penicillium ellipsoideosporum***	AS 3.5688	Banyan seeds, Pingxiang, Guanbxi Province, China (data after Wang *et al*. 2007)	JN121568	JN121427	JN121734	JN121859
CBS 318.67[HT]	*Penicillium erubescens***	ATCC 18544 = FRR 814 = IFO 31734 = IMI 136204	Nursery soil, Pretoria, South Africa	JN121642	JN121490	JN121796	JN121969
CBS 323.71[NT]	*Penicillium euglaucum**		Soil, Argentina	JN121644	JN121492	JN121798	JN121970
CBS 325.48	*Penicillium expansum**	ATCC 7861 = IBT 5101 = IMI 039761= MUCL 29192 = NRRL 976	Fruit of *Malus sylvestris*; USA	JN121645	JF417427	JF417394	JF417527
CBS 229.81[NT]	*Penicillium fellutanum***	ATCC 10443 = CBS 326.48 = FRR 746 = IFO 5761 = IMI 039734 = IMI 039734iii = NRRL 746	Unknown source, USA	JN121605	JN121460	JN121767	JN121947
CBS 124.68[T]	*Penicillium fractum**	ATCC 18567 = FRR 3448 = IMI 136701 = NRRL 3448	Soil, Univ. Shinshu, Ueda-shi, Nagano Pref, Japan	JN121582	JN121441	JN121748	JN121864
CBS 295.62[NT]	*Penicillium fuscum***	ATCC 14770 = IFO 7743 = IMI 094209 = MUCL 31196 = NRRL 3008 = WSF 15c	Type of *E. pinetorum* and neotype of *Citromyces fuscus*; pine-birch forest soil, Vilas County, Wisconsin, USA	JN121633	JN121483	JN121789	JN121962
CBS 125543[NT]	*Penicillium glabrum**	IBT 22658 = IMI 91944	Unknown	JN121717	JF417447	JF417413	JF417547
CBS 599.73[T]	*Penicillium gracilentum**	ATCC 28047 = ATCC 48258 = IMI 216900	Soil, Brown River, Port Moresby, Central Dist., Papua New Guinea	JN121704	JN121537	JN121843	JN121990
CBS 185.27[NT]	*Penicillium griseofulvum**	ATCC 11885 = IBT 6740 = IMI 075832 = IMI 075832ii = MUCL 28643 = NRRL 2152 = NRRL 2300	Unknown source, Belgium	JN121592	JN121449	JN121756	JN121865
CBS 277.58[T]	*Penicillium griseolum**	ATCC 18239 = IMI 071626 = NRRL 2671	Acidic dune sand, Dorset, Stufland, England	JN121629	JN121480	JN121786	JN121959
CBS 336.48[NT]	*Penicillium herquei***	ATCC 10118 = FRR 1040 = IFO 31747 = IMI 028809 = MUCL 29213 = NRRL 1040	Leaf, France	JN121647	JN121494	JN121800	JN121972
CBS 341.68[T]	*Penicillium idahoense**	ATCC 22055 = IMI 148393	Soil, Latàh Co., Univ. of Idaho Plant Science Farm, Idaho, USA	JN121652	JN121499	JN121805	JN121976
CBS 351.67[T]	*Penicillium inusitatum**	ATCC 18622 = IMI 136214	Forest soil, Knysna Valley, Cape Province, South Africa	JN121658	JN121503	JN121809	JN121979

Table 1. (Continued).

CBS no.	Name	Other collections	Origin	GenBank accession or reference[1]			
				RPB1	*RPB2*	*Tsr1*	*Cct8*
CBS 247.56[NT]	*Penicillium isariiforme**	ATCC 18425 = IMI 060371 = MUCL 31191 = MUCL 31323 = NRRL 2638	Woodland soil, Zaire	JN121616	JN121470	JN121720	JN121993
CBS 338.48[NT]	*Penicillium islandicum**	ATCC 10127 = IMI 040042 = MUCL 31324 = NRRL 1036	Unknown source, Cape Town, South Africa	JN121648	JN121495	JN121801	JN121906
CBS 339.48[NT]	*Penicillium italicum***	ATCC 10454 = FRR 983 = IBT 23029 = IMI 039760 = MUCL 15608 = NRRL 983	Fruit, Citrus Experiment Station, Riverside, California, USA	JN121649	JN121496	JN121802	JN121973
CBS 340.48[NT]	*Penicillium janthinellum**	ATCC 10455 = IMI 040238 = NRRL 2016	Soil, Nicaragua	JN131650	JN121497	JN121803	JN121974
CBS 341.48[T]	*Penicillium javanicum**	ATCC 9099 = FRR 707 = IMI 039733 = MUCL 29099 = NRRL 707	Type of *P. javanicum*, *E. javanicum* and *P. indonesiae*; root of *Camellia sinensis* (green tea), Buitenzorg, Java, Indonesia	JN121651	JN121498	JN121804	JN121975
CBS 247.67[T]	*Penicillium katangense**	ATCC 18388 = IMI 136206 = NRRL 5182	Soil, Katanga, Zaire	JN121618	JN121471	JN121777	JN121955
CBS 344.61[T]	*Penicillium kewense**	ATCC 18240 = IMI 086561= MUCL 2685 = NRRL 3332	Culture contaminant of mineral oil, Kew, Surrey, England, UK	JN121654	JF417428	JF417395	JF417528
CBS 106.11[NT]	*Penicillium lanosum**	ATCC 10458 = IMI 040224 = MUCL 29232 = NRRL 2009	Unknown source, Germany	JN121561	JN121420	JN121727	JN121857
CBS 343.48[T]	*Penicillium lapidosum**	ATCC 10462 = IMI 039743 = NRRL 718	Canned blueberry, Washington, USA	JN121653	JN121500	JN121806	JN121977
CBS 277.70[T]	*Penicillium lassenii**	ATCC 22054 = IMI 148395	Soil under conifers, Tehama Co., Lassen National Forest, 1300 m alt., California, USA	JN121630	JN121481	JN121787	JN121960
CBS 116871[T]	*Penicillium macrosclerotiorum**	AS 3.6581	Soil, Chongqing, Wushan County, Sichuang Province, China	JN121573	JN121432	121739	JN121860
CBS 647.95[HT]	*Penicillium malachiteum**	IBT 17515	Soil, Nihondaira Pref. Park, Shimizu-shi, Shimizu-ken, Japan	JN121710	JN121543	JN121849	JN121991
	Penicillium marneffei[1]*	ATCC 18224 (CBS 334.59 = IMI 68794)	Bamboo rat (*Rhizomys sinensis*); Vietnam	Unpublished			
CBS 256.55[NT]	*Penicillium megasporum**	ATCC 12322 = IMI 216904 = NRRL 2232	Heath soil,Suffolk, England	JN121621	JN121473	JN121779	JN121900
CBS 642.68[NT]	*Penicillium minioluteum**	IMI 089377 = MUCL 28666	Unknown	JN121709	JF417443	JF417409	JF417543
CBS 353.48[NT]	*Penicillium namyslowskii**	ATCC 11127 = IMI 040033 = MUCL 29226 = NRRL 1070	Soil under *Pinus* sp.; Puszcza Bialowieska, Poland	JN121660	JF417430	JF417397	JF417530
CBS 203.84[HT]	*Penicillium nepalense***	NHL 6482	Rice soil, Boudha, Kathmandu, Nepal	JN121596	JN121453	JN121760	JN121868
CBS 489.66[T]	*Penicillium ochrosalmoneum**	ATCC 18338 = IMI 116248ii	Type of *E. ochrosalmoneum*; cornmeal, South Africa	JN121689	JN121524	JN121830	JN121987
CBS 232.60[NT]	*Penicillium olsonii**	IBT 23473 = IMI 192502	Root, *Picea abies*, alt. 1980 m., Pitztal, Austria	JN121609	JN121464	JN121771	JN121952
CBS 190.68[T]	*Penicillium ornatum**	ATCC 18608 = IMI 137977 = NRRL 3471	Soil, Moto-machi, Oshima Islands, Japan	JN121594	JN121451	JN121758	JN121867
CBS 462.72[HT]	*Penicillium osmophilum***	IBT 14679	Agricultural soil, Wageningen, the Netherlands	JN121683	JN121518	JN121824	JN121986

Table 1. (Continued).

CBS no.	Name	Other collections	Origin	GenBank accession or reference[1]			
				RPB1	***RPB2***	***Tsr1***	***Cct8***
CBS 219.30[NT]	*Penicillium oxalicum***	ATCC 1126 = FRR 787 = IMI 192332 = MUCL 29047 = NRRL 787	Soil, Connecticut	JN121600	JN121456	JN131763	JN121944
CBS 251.56[T]	*Penicillium ramusculum**	ATCC 12292 = IMI 063546 = NRRL 3459	Culture contaminant, Brazil	JN121620	JN121472	JN121778	JN121956
CBS 367.48[NT]	*Penicillium restrictum***	ATCC 11257 = FRR 1748 = IMI 040228 = NRRL 1748	Soil, Honduras	JN121662	JN121506	JN121812	JN121981
CBS 231.61[NT]	*Penicillium sacculum* (syn. *Eladia saccula*)*	ATCC 18350 = IMI 051498	Soil, Madrid, Spain	JN121607	JN121462	JN121769	JN121949
CBS 122276[T]	*Penicillium saturniforme***	AS 3.6886	Soil, Jiling Province, China	JN121580	JN121439	JN121746	JN121863
CBS 290.48[T]	*Penicillium shearii**	ATCC 10410 = IMI 039739 = IMI 039739iv = NRRL 715	Soil, Tela, Honduras	JN121631	JN121482	JN121788	JN121961
CBS 228.89[T]	*Penicillium shennangjianum***	AS 3.4526	Mouldy pea, Hubei Province, Shennongjia, China	JN121603	JN121458	JN121766	JN121945
CBS 372.48[NT]	*Penicillium simplicissimum**	ATCC 10495 = IFO 5762 = IMI 039816	Flannel bag, Cape, South Africa	JN121662	JN121507	JN121813	JN121981
CBS 315.67[T]	*Penicillium stolkiae**	ATCC 18546 = IMI 136210	Peaty forest soil, Eastern Transvaal, South Africa	JN121640	JN121488	JN121794	JN121967
CBS 117503[T]	*Penicillium thiersii**	IBT 27050 = NRRL 28162	Old, black stroma, encrusting the surface of dead *Acer saccharum* log, alt. 300 m., New Glarus Woods State Park, Wisconsin, USA	JN121575	JN121434	JN121741	JN121861
CBS 347.59	*Penicillium thomii***	IFO 6031 = IMI 068221	Type of *P. thomii* var. *flavescens*; soil, Japan	JN121655	JN121501	JN121807	JN121978
CBS 430.69[T]	*Penicillium tularense**	ATCC 22056 = IMI 148394	Soil, under *Pinus ponderosa* and *Quercus kelloggii*, Tulare Co., Pine Flat, California	JN121681	JN121516	JN121822	JN121984
CBS 603.74[NT]	*Penicillium verrucosum***	ATCC 48957 = FRR 965 = IBT 12809 = IBT 4733 = IMI 200310 = IMI 200310ii = MUCL 28674 = MUCL 29089 = MUCL 29186 = NRRL 965	Unknown source, Belgium	JN121706	JN121539	JN121845	JN121991
CBS 390.48[NT]	*Penicillium viridicatum***	ATCC 10515= IBT 23041 = IMI 039758 = IMI 039758ii = NRRL 963	Air, District of Columbia, Washington D.C., USA	JN121668	JN121511	JN121817	JN121983
CBS 430.64[IsoT]	*Phialomyces macrosporus**	ATCC 16661 = IMI 110130 = MUCL 9776	Soil, near Rotorua, New Zealand	JN121680	JN121515	JN121821	JN121915
CBS 128032[T]	*Phialosimplex caninus**	UAMH 10337	Bone marrow aspirate ex dog, San Antonio, Texas, USA	JN121587	JN121445	JN121752	JN121892
CBS 109945[T]	*Phialosimplex chlamydosporus**	FMR 7371 = IMI 387422	Disseminated infection in a dog	JN121566	JN121425	JN121732	JN121879
CBS 366.77[T]	*Phialosimplex sclerotialis**	IAM 14794	Fodder of ray-grass and lucerne, France	JN121661	JN121505	JN121811	JN121908
CBS 384.61[T]	*Polypaecilum insolitum**	ATCC 18164 = IMI 075202 = MUCL 3078	Ear of human, Leeds, Yorkshire, England, UK	JN121667	JN121510	JN121816	JN121911
CBS 101166	*Polypaecilum pisci**		Yeast extract, Netherlands	JN121555	JN121415	JN121722	JN121870
CBS 101.69[T]	*Rasamsonia argillacea**	DTO 97E4 = IMI 156096 = IBT 31199	Mine tip with a very high surface temperature; Staffordshire, UK	JN121556	JF417415	JF417382	JF417515

Table 1. (Continued).

CBS no.	Name	Other collections	Origin	GenBank accession or reference[1]			
				RPB1	*RPB2*	*Tsr1*	*Cct8*
CBS 413.71^{T}	*Rasamsonia byssochlamydoides**	DTO 149D6 = IBT 11604	Dry soil under Douglas fir; Oregon, USA	JN121675	JF417437	JF417403	JF417537
CBS 275.58^{NT}	*Rasamsonia cylindrospora**	DTO 138F8 = IBT 31202 = ATCC 18223 = IMI 071623	Culture contaminant; Berkshire, England, UK	JN121628	JF417423	JF417390	JF417523
CBS 393.64^{T}	*Rasamsonia emersonii**	DTO 48I1 = IBT 21695 = ATCC 16479 = IMI 116815 = IMI 116815ii	Compost; Italy	JN121670	JF417434	JF417401	JF417534
CBS 114.72^{IsoT}	*Sagenoma viride**	ATCC 22467 = NRRL 5575	Soil, Australia	JN121571	JN121430	JN121737	JN121882
CBS 545.86^{T}	*Sagenomella bohemica**	CCF 2330 = IAM 14789	Peloids for balneological purposes, Frantiskovy Lázne Spa, West Bohemia, Czech Republic	JN121699	JN121532	JN121838	JN121927
CBS 398.69	*Sagenomella diversispora**		Forest soil under *Populus tremuloides*; Petawawa, Ontario, Canada	JN121673	JF417435	JF417402	JF417536
CBS 399.69	*Sagenomella diversispora**	MUCL 15012	Forest soil under *Thuja occidentalis*, Aberfoyle, Ontario, Canada	JN121674	JN121513	JN121819	JN121913
CBS 426.67	*Sagenomella griseoviridis**	ATCC 18505 = IMI 113160	Unknown source	JN121677	JF417438	JF417404	JF417538
CBS 427.67^{IsoT}	*Sagenomella humicola**	ATCC 18506 = IMI 113166	Forest soil under *Thuja occidentalis*; Ontario, Canada	JN121678	JF417439	JF417405	JF417539
CBS 429.67^{IsoT}	*Sagenomella striatispora**	ATCC 18510 = IMI 113163	Soil; Guelph, Ontario, Canada	JN121679	JF417440	JF417406	JF417540
CBS 414.78^{T}	*Sagenomella verticillata**	IAM 14697	Conifer forest soil, Sweden	JN121676	JN121514	JN121820	JN121914
CBS 124.53^{NT}	*Sclerocleista ornata**	ATCC 16921 = IMI 055295 = MUCL 15643 = NRRL 2256	Soil in oak forest, Dane Co., Madison, Wisconsin, USA	JN121581	JN121440	JN121747	JN121888
CBS 105.25	*Sclerocleista thaxteri**	IMI 055296 = NRRL 2292	Dung of caterpillar, USA	JN121560	JN121419	JN121726	JN121874
CBS 296.48^{T}	*Talaromyces bacillisporus**	ATCC 10126 = IMI 040045 = NRRL 1025	Begonia leaf; New York City, New York, USA	JN121634	JF417425	JF417392	JF417525
CBS 100537^{T}	*Talaromyces convolutus**	IBT 14989	Soil, Kathmandu, Nepal	JN121553	JN121414	JN121721	JN121869
CBS 100536^{T}	*Talaromyces emodensis**	IBT 14990	Soil; Kathmandu, Nepal	JN121552	JF417445	JF417411	JF417545
CBS 310.38^{NT}	*Talaromyces flavus**	IMI 197477 = NRRL 2098	Unknown substrate; New Zealand	JN121639	JF417426	JF417393	JF417526
CBS 398.68^{T}	*Talaromyces leycettanus**	ATCC 22469 = IMI 178525	Coal spoil tip soil; Leycett, Staffordshire, England, UK	JN121672	JF417435	JF417402	JF417535
CBS 348.51^{NT}	*Talaromyces luteus**	IMI 089305	Soil, UK	JN121656	JF417429	JF417396	JF417529
CBS 475.71^{IsoT}	*Talaromyces purpureus**	ATCC 24069 = ATCC 52513 = FRR 1731 = IMI 181546	Soil, near Esterel, France	JN121687	JN121522	JN121828	JN121919
	Talaromyces stipitatus[1]*	ATCC 10500 (= NRRL 1006 = CBS 375.48 = IMI 39805)	Rotting wood; Louisiana, USA	Unpublished			
CBS 236.58^{T}	*Talaromyces thermophilus**	ATCC 10518 = IMI 048593 = NRRL 2155	*Parthenium argentatum*, decaying plant; California, USA	JN121611	JF417420	JF417387	JF417520
CBS 373.48^{T}	*Talaromyces trachyspermus**	ATCC 10497 = IMI 040043 = NRRL 1028	Unknown source, USA	JN121664	JF417432	JF417399	JF4174532
CBS 391.48^{NT}	*Talaromyces wortmanii**	ATCC 10517 = IMI 040047 = NRRL 1017	Unknown source	JN121669	JF417433	JF417400	JF417533
CBS 891.70	*Thermoascus aurantiacus**	IMI 173037	Wood; Firenze, Italy	JN121719	JF417444	JF417410	JF417544

Table 1. (Continued).

CBS no.	Name	Other collections	Origin	GenBank accession or reference[1]			
				RPB1	***RPB2***	***Tsr1***	***Cct8***
CBS 396.78	*Thermoascus aurantiacus**	JCM 12816	Sawdust, in lumber yard, Toronto, Ontario, Canada	JN121671	JN121512	JN121818	JN121912
CBS 181.67^{T}	*Thermoascus crustaceus**	ATCC 16462 = IMI 126333	*Parthenium argentatum*, decaying plant; Salinas, California, USA	JN121591	JF417417	JF417384	JF417517
CBS 528.71^{NT}	*Thermoascus thermophilus**	IMI 123298 = NRRL 5208	Wood and bark of *Pinus*; Sweden	JN121697	JF417442	JF417408	JF417542
CBS 218.34	*Thermomyces lanuginosus**	MUCL 8338	Fruit shell of *Theobroma* cacao	JN121599	JF417418	JF417385	JF417518
CBS 224.63	*Thermomyces lanuginosus**	MUCL 8337	Mushroom compost; Gossau-Zürich Switzerland	JN121602	JF417419	JF417386	JF417519
CBS 334.68^{T}	*Thysanophora canadensis**	ATCC 18741 = IMI 137644 = MUCL 21216	Needle of *Tsuga canadensis*, Bell's Corners, Ontario, Canada	JN121647	JN121493	JN121799	JN121971
CBS 206.57^{T}	*Thysanophora taxi**	ATCC 18484 = MUCL 11402	Litter, Berlin, Germany	JN121597	JN121454	JN121761	JN121942
CBS 185.65	*Torulomyces lagena**	MUCL 8221	Bog soil under *Thuja plicata*, Guelph, Ontario, Canada	JN121593	JN121450	JN121757	JN121866
CBS 247.57	*Trichocoma paradoxa**	MUCL 39666 = IBT 31159	Unknown source; Hachijô, Japan	JN121617	JF417421	JF417388	JF417521
CBS 103.73	*Trichocoma paradoxa**		Unknown source, Japan	JN121558	JN121417	JN121724	JN121872
CBS 788.83	*Trichocoma paradoxa**		Rotting stump of cut down tree, Myojoji Temple near Hakui Noto Park, Ishikawa Pref., Japan	JN121718	JN121550	JN121856	JN121941
CBS 512.65^{NT}	*Warcupiella spinulosa**	ATCC 16919 = IMI 075885 = NRRL 4376	Jungle soil; Berakas-Muara, Brunei	JN121692	JF417441	JF417407	JF417541
CBS 236.71^{T}	*Xeromyces bisporus**	IMI 063718	Mouldy stick of liquorice, Homebush, New South Wales, Australia	JN121612	JN121466	JN121773	JN121898

[1] Sequences derived from published full genome data. * Strains used in the study of *Trichocomaceae* (Fig. 1); ** Strains used in for the preparation of Figs 1 and 7. CBS, culture collection of the CBS-KNAW Fungal Biodiversity Centre, Utrecht, Netherlands (WDCM 133) http://www.cbs.knaw.nl/databases/index.htm; DTO, internal culture collection of CBS-KNAW Fungal Biodiversity Centre; IMI, CABI Genetic Resources Collection, Surrey, UK (WDCM 214) http://www.cabi.org/; IBT, culture collection of Center for Microbial Biotechnology (CMB) at Department of Systems Biology, Technical University of Denmark (WDCM 758) http://www.biocentrum.dtu.dk/; NRRL, ARS Culture Collection, U.S. Department of Agriculture, Peoria, Illinois, USA (WDCM 97) http://nrrl.ncaur.usda.gov/; ATCC, American Type Culture Collection, Manassas, VA, USA (WDCM 1) http://www.atcc.org/; MUCL, Mycotheque de l'Universite catholique de Louvain, Leuven, Belgium (WDCM 308).

(Gelperin *et al*. 2001, Léger-Silvestre *et al*. 2004). Partial *RPB2* data was obtained for the majority of species listed in Table S1. Exceptions are strains used in the study of Houbraken *et al*. (2011c); in that case, published partial β-tubulin sequences were used.

The *RPB1* fragment was amplified using the primer pair *RPB1*-F1843 and R3096, and *RPB1*-R2623 was occasionally used as an internal primer for sequencing. A part of the *RPB2* locus was amplified using the primer pair *RPB2*-5F and *RPB2*-7CR (Liu *et al.* 1999) or the primer pair *RPB2*-5F_Eur and *RPB2*-7CR_Eur. The internal sequencing primers *RPB2*-F311 and *RPB2*-R310 were occasionally used when poor results were obtained with the regular forward and reverse primers. Amplification of a part of the *Cct8* gene was performed using the primer pair *Cct8*-F660 and *Cct8*-R1595. No amplicons could be obtained in the case of 5–10 % of the analysed strains. In those cases, amplicons were generated using the primer pair *Cct8*-R1595 and *Cct8*-F94. A part of the *Tsr1* gene was amplified using the forward primers *Tsr1*-F1526Pc or *Tsr1*-F1526 in combination with *Tsr1*-R2434. Annealing temperatures and primers used for amplification and sequencing are shown in Table 2.

The PCR reactions were performed in 25 µL reaction mixtures containing 1 µL genomic DNA 2.5 µL PCR buffer, 0.75 µL $MgCl_2$ (50 mM), 16.55 µL demineralised sterile water, 1.85 µL dNTP (1 mM), 0.50 µL of each primer (100 mM) and 0.1 µL Taq polymerase (5 U/µL, BioTaq, Bioline). The PCR program typically was: 5 cycles of 30 s denaturation at 94 °C, followed by primer annealing for 30 s at 51 °C, and extension for 1 min at 72 °C; followed by 5 cycles with an annealing temperature at 49 °C and 30 cycles at 47 °C, finalised with an extension for final 10 min at 72 °C. Excess primers and dNTP's were removed from the PCR product using the QIAQuick PCR purification kit (Qiagen). Purified PCR fragments were resuspended in 30–50 µL of water. PCR products were sequenced directly in both directions with the same primers and DYEnamic

Table 2. Primers used in this study for amplification and sequencing.

Locus	Primer	Sequence (5'–3')	Annealing (°C)	Fragment size (bp)	References
Cct8	F94	(Fwd) CGCAAC AAGATYGTBATYAACCA	50–52	F94-R1595: 1400–1450	Houbraken *et al*. 2011d
	F660	(Fwd) GIGTKGTBAAGATCATGGGWGG		F660-R1595: 850–890	Houbraken *et al*. 2011d
	R1595	(Rev) RTCMACRCCNGTIGTCCAGTA			Houbraken *et al*. 2011d
RPB1	F1843	(Fwd) ATTTYGAYGGTGAYGARATGAAC	48–53	*ca*. 1000	This study
	R3096	(Rev) GRACRGTDCCRTCATAYTTRACC			This study
	R2623	GCRTTGTTSARATCCTTMARRCTC			This study
RPB2	5F	GAYGAYMGWGATCAYTTYGG	48–51	*ca*. 1220	Liu *et al*. 1999
	7CR	CCCATRGCTTGYTTRCCCAT			Liu *et al*. 1999
	5F_Eur	(Fwd) GAYGAYCGKGAYCAYTTCGG			Houbraken *et al*. 2011d
	7CR_Eur	(Rev) CCCATRGCYTGYTTRCCCAT			Houbraken *et al*. 2011d
	F311	CATGATYCARCGIAAYATGGA			This study
	R310	CCATRTTICGYTGRATCATGAA			This study
Tsr1	F1526Pc	(Fwd) GARTAYCCBCARTCNGAGATGT	48–50	*ca*. 820	Houbraken *et al*. 2011d
	F1626	(Fwd) GARTAYCCBCARTCNGAIATGT			This study
	R2434	(Rev) ASAGYTGVARDGCCTTRAACCA			Houbraken *et al*. 2011d

ET Terminator Cycle Sequencing Kit (Amersham Bioscience, Roosendaal, The Netherlands). The cycle sequencing reaction mixture had a total reaction volume of 10 µL, and contained 1 µL of template DNA, 0.85 µL BigDye reagent, 3 µL buffer, 4.75 µL demineralised water and 0.4 µL primer (10 mM).

Sequencing products were purified according to the manufacturers' recommendations with Sephadex G-50 superfine columns (Amersham Bioscience, Roosendaal, The Netherlands) in a multiscreen HV plate (Millipore, Amsterdam, The Netherlands) and with MicroAmp Optical 96-well reaction plate (AB Applied Biosystems, Nieuwerkerk a/d Yssel, The Netherlands). Contigs were assembled using the forward and reverse sequences with the programme SeqMan from the LaserGene package (DNAStar Inc., Madison, WI).

Phylogenetic analysis

The protein coding nucleotide sequences were translated into amino acid data prior to alignment and subsequently aligned using the Muscle software in the MEGA5 package. After aligning, the amino acid data were translated into nucleotide data and used in the phylogenetic analysis. Combined sequence data sets were used in the study on the phylogeny of *Trichocomaceae* and *Penicillium*. Before combining the data sets, each data set was analysed using RAxML (Stamatakis *et al.* 2008). The number of bootstrap runs was set to 100. The program compat.py (from http://www.lutzonilab.net) was used to detect major topological incongruences among single gene data sets (Kauff & Lutzoni 2002). Conflicts were considered significant when a sequence was differentially resolved between two gene trees with greater than 70 % bootstrap support. If no conflicts were detected, then the data sets were combined.

Statistical support was measured by Maximum Likelihood (ML) analysis using the RAxML (randomised axelerated maximum likelihood) software (Stamakis *et al*. 2008). The robustness of trees in the ML analyses was evaluated by 1000 bootstrap replications. A second measure for statistical support was performed by Bayesian tree inference (BI) analysis using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003). Prior to analysis, the most suitable substitution model was determined using MrModeltest v. 2.3 (Nylander 2004), utilising the Akaike Information Criterion (AIC). The Bayesian analysis was performed with two sets of four chains (one cold and three heated) and the stoprule option, stopping the analysis at an average standard deviation of split frequencies of 0.01. The sample frequency was set to 100; the first 25 percent of trees were removed as burnin. The phylograms obtained with the RAxML analysis were used for presenting the data. Bootstrap values lower than 70 % were considered unreliable because their wide range of error and Bayesian posterior probabilities are considered unreliable below 0.95 (Murphy *et al*. 2001, Wilcox *et al*. 2002, Alfaro & Holder 2006). Therefore, only posterior probability (pp) values higher than 0.95 and bootstrap (bs) values higher than 70 % were plotted on those phylograms. *Coccidioides immitis* (strain RS), a member of *Onygenales*, was chosen to root the phylogram used in the study on the relationships of *Penicillium* species among *Trichocomaceae*. *Penicillium* (= *Talaromyces*) *marneffei* ATCC 18227^{T} was selected as an outgroup for the analysis of the phylogeny of *Penicillium*. Various phylograms were prepared for assignment of species to sections. All data sets were based on partial *RPB2* sequences and rooted with *Talaromyces flavus* CBS 310.38^{NT}, with exception of the phylogram of sections *Lanata-divaricata* and *Stolkia*, which is based on partial β-tubulin data. *Penicillium glabrum* CBS 125543^{T} was used as an outgroup.

RESULTS

Phylogeny of *Trichocomaceae*

A phylogenetic study using four combined loci (*RPB1*, *RPB2*, *Cct8* and *Tsr1*) was conducted to determine the relationship among members of *Trichocomaceae*. A total of 157 species were included in the analysis and the total length of the alignment was 3 111 characters, 1 939 of those characters were variable. The length of the *Cct8*, *Tsr1*, *RPB1* and *RPB2* partitions were 714, 669, 768, 960 base pairs long, respectively. The GTR+I+G model was optimal for all four partitions.

The result of the analysis is shown in Fig. 1 and indicates that *Trichocomaceae* can be divided into three lineages. Lineage 1 is divided into seven clades (clades 1–7) and these clades are on a well-supported branch (100 % bs, 1.00 pp). The type species

Table 3. Details of each analysis of the data sets used for generating Figs 8, 10–13.

Figure	Clades, acc. Fig. 7	Locus	No. isolates	Length alignment	Best-fit model
8	1, 2, 3	*RPB2*	50	916	SYM+I+G
10	6, 7, 10 and 13	*RPB2*	69	916	GTR+I+G
11	11, 12	β-tubulin	45	528	HKY+I+G
12	5, 14	*RPB2*	44	849	SYM+I+G
13	15–25	*RPB2*	86	916	GTR+I+G

of the genera *Chromocleista* (*C. malachitea*), *Eladia* (*E. saccula*), *Eupenicillium* (*E. crustaceum*), *Hemicarpenteles* (*H. paradoxus*), *Penicillium* (*P. expansum*), *Thysanophora* (*T. penicillioides*) and *Torulomyces* (*T. lagena*) belong to clade 1. This clade is named *Penicillium sensu stricto* and is divided into two subclades: clade 1A and 1B. The types of subgenera *Aspergilloides* and *Furcatum* are accommodated in clade 1A and the type of subgenus *Penicillium* belongs to clade 1B. Clade 2 is moderately supported (< 70 % bs, 1.00 pp) and contains the type species of the genera *Aspergillus* (*A. glaucus*), *Cristaspora* (*C. arxii*), *Phialosimplex* (*P. caninus*), *Polypaecilum* (*P. insolitum*) and the teleomorphs of *Aspergillus* (*Fennellia*, *Eurotium*, *Emericella*, *Neocarpenteles*, *Dichotomyces*, *Neosartorya*, *Sclerocleista*). Not all teleomorph genera of *Aspergillus* are represented in our analysis; however, previous data has shown the genera *Chaetosartorya*, *Neopetromyces* and *Petromyces* also belong to this lineage (Peterson 2008). This clade is subdivided into six groups. Four of the six groups represent the *Aspergillus* subgenera as defined by Peterson (2008). In addition, also *Aspergillus* section *Cremei* and a clade with *Phialosimplex* and *Polypaecilum* are present. Clade 3 comprises the type species of *Hamigera* (*H. avellanea*), *Warcupiella* (*W. spinosa*) and *Raperia* (*R. spinulosa*) but this clade is poorly supported (< 70 % bs, < 0.95 pp). Clade 4 contains *P. clavariiformis*, the type species *Penicilliopsis*. The type species of the genera *Basipetospora* (*B. rubra*), *Fraseriella* (*F. bisporus*), *Leiothecium* (*L. ellipsoideum*), *Monascus* (*M. ruber*), *Xeromyces* (*X. bisporus*) cluster together in clade 5. *Phialomyces* (*P. macrosporus*) and *Sclerocleista* (*S. ornata*) belong to clade 6 and 7, respectively. Lineage 2 is subdivided into two clades: the type species of *Thermoascus, Coonemeria* and *Dactylomyces* belong to clade 8, and the types of the genera *Byssochlamys* (*B. nivea*) and *Paecilomyces* (*P. variotii*) belong to clade 9. The posterior probability value indicates a strong relationship between these two clades (0.99); however, the maximum likelihood analysis resulted in a bootstrap value lower than 70 % (67 %). The posterior probability and bootstrap values are also contradictory regarding the relationship between lineages 1 and 2 (< 70 % bs, 1.00 pp). Lineage 3 is subdivided into five clades (clades 10–14) and these clades are on a strongly supported branch (100 % bs, 1.00 pp). Clade 10 is centered on the type species of *Talaromyces*, *T. flavus*, and the type species of *Sagenoma* (*S. viride*) also belongs in this clade. The type species of *Thermomyces* (*T. lanuginosus*), *Sagenomella* (*S. diversispora*), *Rasamsonia* (*R. emersonii*) and *Trichocoma* (*T. paradoxa*) belong in clades 11–14, respectively.

Phylogeny of *Penicillium sensu stricto*

The phylogenetic relationship among members of *Penicillium s. str.* was studied using the same four combined loci (*RPB1*, *RPB2*, *Cct8* and *Tsr1*). In total, 72 strains were included in the analysis and the total length of the alignment was 3 393 characters, and 1 805 of them were variable. *Penicillium* (= *Talaromyces*) *marneffei* was used as an outgroup. The length of the *Cct8*, *Tsr1*, *RPB1* and *RPB2* partitions were 723, 759, 955, 957 base pairs, respectively. The best-fit model GTR+I+G was optimal for all four partitions. The result of the analysis is shown in Fig. 7 and confirms the result above that *Penicillium s. str.* can be divided into two distinct lineages. Similarly, the type species of subgenus *Aspergilloides*, *P. aurantiobrunneum* (= *P. glabrum*) and *Furcatum* (*P. citrinum*), belong to lineage 1 and the type of subgenus *Penicillium* belongs to lineage 2. Lineage 1 is subdivided in 14 clades (Fig. 7). These clades (1–14) were in most cases supported with a bootstrap value higher than 95 % and a posterior probability of 1.00. Lineage 2 is subdivided into 11 clades (15–25). Clades 20–25 are on well-supported branches; however, the overall bootstrap and posterior probability values of clades 15–19 are low. The numbering of the clades is therefore based on the analysis of the partial β-tubulin data in Samson *et al*. (2004), because well-supported clades (sections) were present in that phylogenetic treatment. Five separate phylograms (Figs 8, 10–13) were prepared in order to determine which species belong to which clade (section). Details of these analyses are summarised in Table 3.

DISCUSSION

Part One: Phylogenetic analysis of *Trichocomaceae*

Choice of genes

Parts of the *RPB1*, *RPB2*, *Tsr1* and *Cct8* genes were only used for the construction of the phylogenetic relationships among members of *Trichocomaceae* and *Penicillium* species, and the ability of these genes for species recognition remains largely unexplored. The regions E and F (according Matheny *et al*. 2002) of the *RPB1* gene were analysed. No additional sequence data of *Trichocomaceae* were published on this part of the *RPB1* gene and comparison with other studies is therefore difficult. The regions 5–7 of the *RPB2* gene are commonly used in taxonomic studies of *Penicillium* and *Aspergillus* and proved to be a good marker for species recognition (*e.g.* Peterson 2008, Serra *et al*. 2008, Peterson & Horn 2009, Peterson *et al*. 2010, Barreto *et al*. 2011). However, *RPB1* and *RPB2*, as well as TEF1α, β-tubulin, and γ-actin, were not found among the best performing genes for fungal systematics (Aguileta *et al*. 2008). Aguileta *et al*. (2008) studied, using a bioinformatics approach, the performance of single-copy protein-coding genes for fungal phylogenetics. Their analyses of 30 published fungal genomes revealed that *MCM7* (= MS456), *Tsr1* (= MS277) and *Cct8* (= FG610) were among the best single-copy genes in phylogenetic utility. *MCM7*, the best gene for recovering a larger-scale phylogeny across fungal groups, was excluded in the current study since it was not variable enough within the genus *Penicillium* (Marthey *et al*. 2008). *Tsr1* and *Cct8* were also used in other (phylogenetic) studies of groups belonging to *Trichocomaceae*

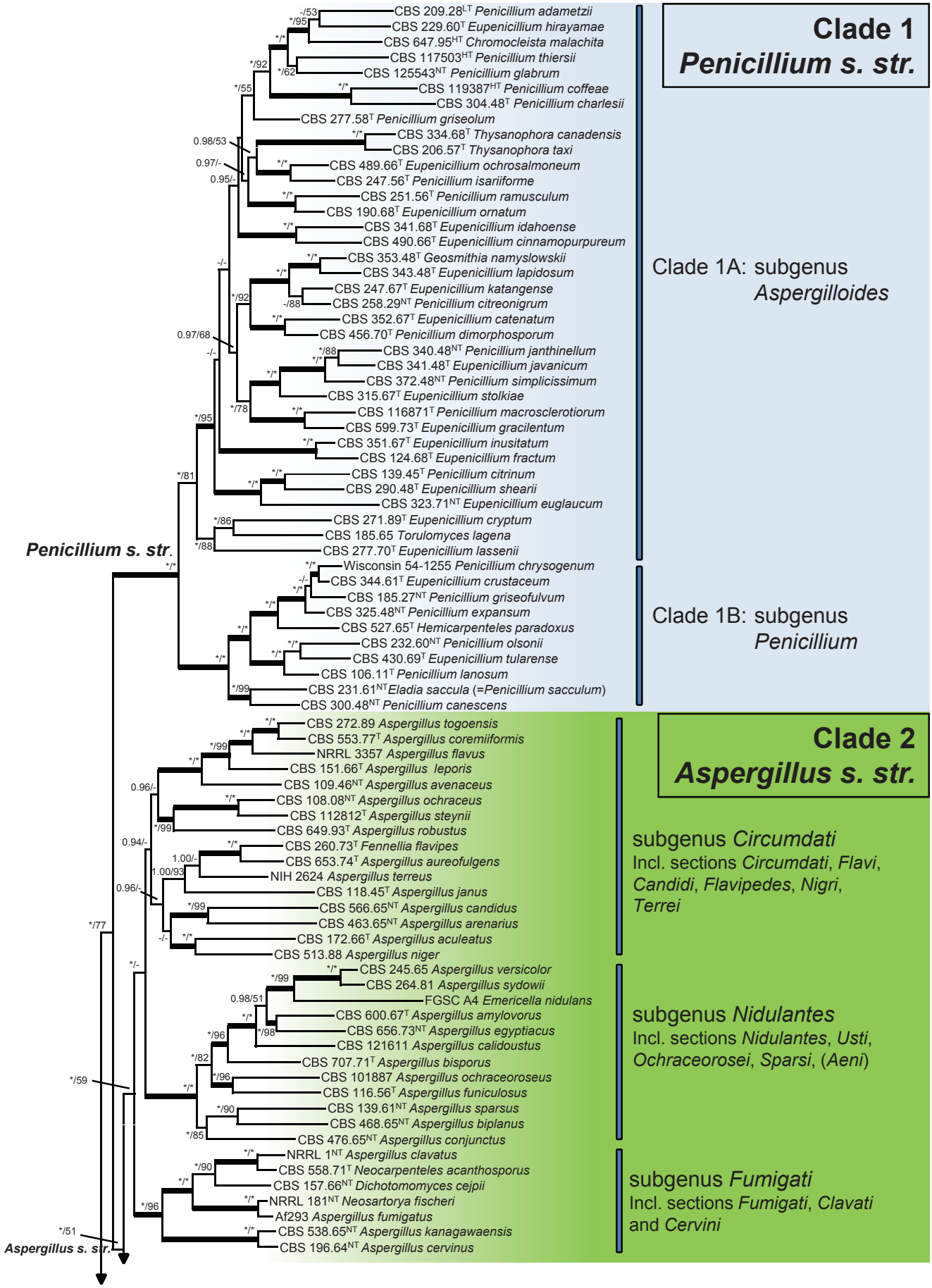

Fig. 1. Best-scoring Maximum Likelihood tree using RAxML based on combined data set of partial *Cct8*, *Tsr1, RPB1 and RPB2* sequences showing the relationship among members of *Trichocomaceae*. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (pp/bs). Values less than 50 % supported in the ML or less than 0.90 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate full support (100 % bs or 1.00 pp). The branches with more than 95 % bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Coccidioides immitis* (strain RS).

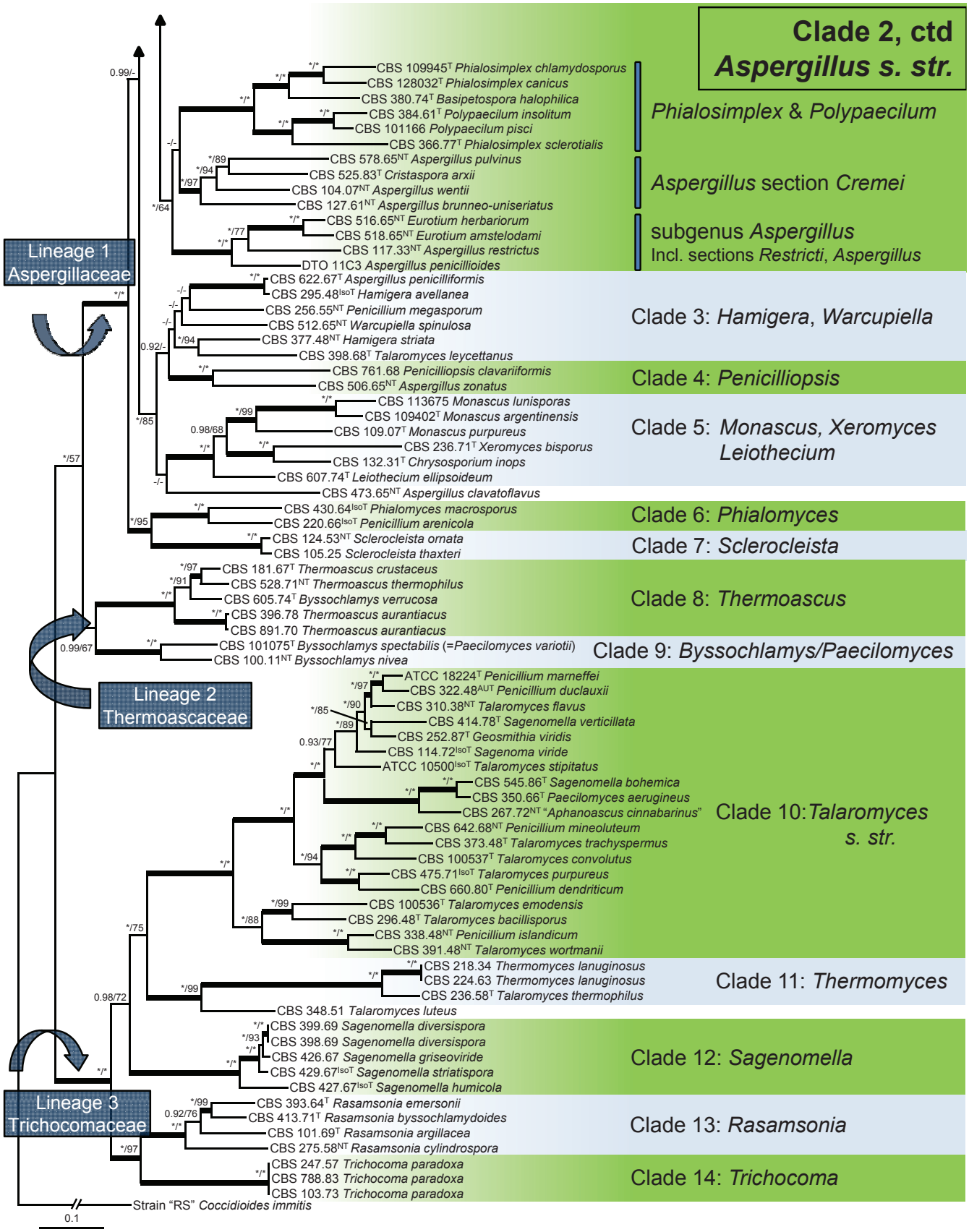

Fig. 1. (Continued).

(López-Villavicencio *et al*. 2010, Peterson *et al*. 2010). Analysis of the *Tsr1* gene generated the best resolved trees, when compared with *Cct8*, *MCM7* and ITS (López-Villavicencio *et al*. 2010). The sequenced parts of the *RPB1*, *RPB2*, *Tsr1* and *Cct8* genes mainly contain exons, and the alignment of these loci is therefore unambiguous. This is the main advantage over ITS regions where alignment above genus can be difficult. Furthermore, the ITS region is generally considered unreliable as a phylogenetic marker, especially above genus rank. β-tubulin and calmodulin sequences are often used in taxonomical studies of *Penicillium*, *Paecilomyces*

and *Aspergillus* (*e.g.* Samson *et al*. 2004, Houbraken *et al*. 2007, Samson *et al*. 2009, Varga *et al*. 2011). However, a large part of these genes consists of intron data and these regions cannot be aligned above genus level, resulting in loss of information in these data sets. In addition, there is evidence that β-tubulins are present in the genome in multiple copies and thus have the potential of being phylogenetically misleading (Landvik *et al*. 2001, Peterson 2008).

Phylogenetic analysis of Trichocomaceae

Three lineages are recognised in *Trichocomaceae* (Fig. 1) and we propose to treat these three lineages as distinct families: *Trichocomaceae*, *Aspergillaceae* and *Thermoascaceae*. Lineage 1 corresponds with *Aspergillaceae* and this name is the oldest available family name within the analysed group of related genera. Malloch & Cain (1972) did not accept this family name since it was based on the asexual (anamorph) form-genus *Aspergillus* and therefore not applicable for ascomycete perfect (sexual) states. Because we are applying a single-name system and give priority to the oldest name, the family name *Aspergillaceae* is re-instated. Phylogenetically, *Monascaceae* belong to *Aspergillaceae* and this is in agreement with other studies that show that *Monascus* (type genus of *Monascaceae*) is related to *Penicillium* and/or *Aspergillus* (Berbee *et al*. 1995, Ogawa *et al*. 1997, Ogawa & Sugiyama 2000, Peterson 2008, Pettersson *et al*. 2011). In contrast, Stchigel *et al*. (2004), who used ITS sequence data to determine the molecular relationships of *Monascaceae* taxa, concluded that *Monascus* and *Xeromyces* form a well-supported, monophyletic clade (81 % bs), separate from *Eurotiales* (Stchigel & Guarro 2007). These contradictory results can be explained by a deeper taxon sampling in this study combined with a phylogeny based on sequences of four protein-coding genes instead of ITS sequences alone. The *Thermoascaceae* (= lineage 2) were introduced by Apinis (1967) and typified by *Thermoascus*. Lineage 3 corresponds to *Trichocomaceae* and this family was introduced by Fischer (1897) (as *Trichocomataceae*) and is typified by *Trichocoma*. The *Eurotiaceae* were placed in synonymy with this family because the name *Trichocomaceae* predates *Eurotiaceae* (Malloch & Cain 1972). The current analysis shows that *Eurotiaceae* (type genus *Eurotium*) should be placed in synonymy with *Aspergillaceae*. The family names *Hemicarpenteleaceae*, *Penicilliopsidaceae*, *Phialomycetaeae*, *Warcupiellaceae*, *Xeromycetaceae* and *Talaromycetaceae* were introduced by Locquin (1972, 1984) but all lack a Latin description and are invalidly published.

Phenotypic classification and delimitation of Aspergillaceae, Trichocomaceae and Thermoascaceae

Several studies on the classification of *Trichocomaceae* and *Eurotiales* based on phenotypic characters were published (Malloch & Cain 1972, Fennell 1973, Benny & Kimbrough 1980, Malloch 1985a, b, von Arx 1987) and an overview of selected studies is shown in Table 4. Some of these classifications differ significantly from each other. We compared the results of these studies with the current proposed phylogenetic classification and this showed that our phylogenetic classification largely corresponds with the phenotypic classification described by Malloch (1985a, b). Malloch (1985a, b) divided *Trichocomaceae* into two subfamilies, *Trichomoideae* and *Dichlaenoideae*, based on phenotypic characters including cleistothecial initials, peridium, ascus structure and ascospore morphology. Malloch's list of genera belonging to *Dichlaenoideae* largely corresponds with the genera we place in *Aspergillaceae* and his definition of *Trichomoideae* is comparable with our phylogenetically defined *Trichocomaceae*. There are two main differences: a) *Monascus* is treated here in *Aspergillaceae* and b) the genera *Byssochlamys* and *Thermoascus* are accommodated in *Thermoascaceae*; these were treated by Malloch (1985a, b) in *Trichomoideae* and *Dichlaenoideae*, respectively. Using the characters proposed by Malloch in his classification, *Aspergillaceae* are characterised by the production of asci inside cleistothecia, stromata, or are surrounded by Hülle cells and mainly have oblate to ellipsoidal ascospores with a furrow or slit. The conidia are mostly formed on flask shaped or cylindrical phialides. The *Trichocomaceae* are defined by having asci borne within a tuft or layer of loose hyphae, and ascospores are lacking slits or furrows. The phialides of species belonging to this family are mostly lanceolate or cylindrical. Apinis (1967) introduced *Thermoascaceae* and noted that the common essential character of genera of this family is the production of firm, somewhat sclerotioid, pseudoparenchymatous cleistothecia. The inclusion of *Byssochlamys* in this family does not fit in that description because it produces almost naked ascomata. Based on the relative branch length in Fig. 1, another possibility would be to delimit the *Thermoascus* clade (clade 8) and the *Byssochlamys*/*Paecilomyces* clade (clade 9) as separate families. However, there are characters shared by *Thermoascus* and *Byssochlamys* including the production of asci in croziers and the formation of smooth or finely roughened ascospores lacking a furrow or slit. The relationship between these two genera is also illustrated by *Byssochlamys verrucosa* and *Thermoascus crustaceus*. *Byssochlamys verrucosa* phenotypically belongs to *Byssochlamys*, but is positioned phylogenetically in *Thermoascus* (Fig. 1) and *Therm. crustaceus* shares a *Paecilomyces* anamorph with members of the *Byssochlamys*/*Paecilomyces* clade. In addition, most members of both genera are thermotolerant or thermophilic.

The genera *Chaetosartorya*, *Cristaspora*, *Dichlaena*, *Dichotomomyces*, *Eupenicillium*, *Edyuillia*, *Emericella*, *Eurotium*, *Hamigera*, *Hemicarpenteles*, *Hemisartorya*, *Neosartorya*, *Penicilliopsis*, *Petromyces*, *Sclerocleista*, *Thermoascus* and *Warcupiella* were placed by Malloch (1985a, b) in *Aspergillaceae* (as subfamily *Dichlaenoideae*). The majority of these genera are also included in our classification, and exceptions are *Edyuilla*, which is synonymised with *Eurotium* (von Arx 1974) and *Thermoascus*, which is classified in *Thermoascaceae*. The main difference is the placement of *Monascaceae* is *Aspergillaceae*. Benny & Kimbrough (1980) placed the genera *Ascorhiza*, *Leiothecium*, *Monascus* and *Xeromyces* in *Monascaceae* and suggested a relationship with *Ascosphaerales*. Later, several authors included this family in *Pezizales* (Malloch 1981, Hawksworth & Pitt 1983). Von Arx (1987), in his revision of *Eurotiales*, included *Monascus* in *Onygenaceae*, and reduced *Monascaceae* to synonymy. More recently, *Monascaceae* was placed in *Eurotiales* (LoBuglio *et al*. 1993, Hawksworth *et al.* 1995). Fennell (1973) noted that species of both *Monascaceae* and *Eurotiaceae*, which approximates our definition *Aspergillaceae*, form a distinct cleistothecial wall. Nevertheless, Fennell (1973) separated these families based on the formation of aleurioconidia by members of *Monascaceae*, but our results show that this feature is insufficient for family delimitation. Anamorph genera were not treated by Malloch (1985a, b) and Fig. 1 shows that the genera *Aspergillus*, *Basipetospora*, *Eladia*, *Fraseriella*, *Penicillium*, *Phialomyces*, *Phialosimplex*, *Polypaecilum*, *Thysanophora* and *Torulomyces* are classified in *Aspergillaceae*. The teleomorph genera *Chromocleista*, *Fennellia*, *Neocarpenteles* and *Neopetromyces,*

Table 4. Overview of the classifications of the *Trichocomaceae* and *Eurotiaceae* by Benny & Kimbrough (1980), Malloch (1985b), von Arx (1987) and the current study.

Benny & Kimbrough (1980)	von Arx (1987)	Malloch (1985b)	Current study
***Trichocomaceae*:**	***Eurotiaceae*:**	***Trichomoideae*:**	***Aspergillaceae*:**
Aphanoascus	*Chaetosartorya*	*Byssochlamys*	*Aspergillus* (incl. teleomorphs, syn. *Stilbothamnium*)
Byssochlamys	*Cristaspora*	*Dendrosphaera*	*Hamigera* (incl. *Merimbla*)
Chaetosartorya	*Dichlaena*	*Sagenoma*	*Leiothecium*
	Dichotomomyces	*Talaromyces*	*Monascus* (incl. *Basipetospora*)
Dichleana	*Emericella*	*Trichocoma*	*Penicilliopsis*
Edyuillia	*Eupenicillium*	***Dichlaenoideae*:**	*Penicillium* (syn. *Chromocleista, Eladia, Eupenicillium, Hemicarpenteles, Thysanophora*, *Torulomyces*)
Emericella	*Eurotium*	*Chaetosartorya*	*Phialomyces*
Eupenicillium	*Fennellia*	*Cristaspora*	*Phialosimplex*
Eurotium	*Hemicarpenteles*	*Dichlaena*	*Polypaecilum*
Fennellia	*Mallochia*[2]	*Dichotomomyces*	*Sclerocleista*
Hamigera	*Neosartorya*	*Eupenicillium*	*Warcupiella* (incl. *Raperia*)
Hemicarpenteles	*Saitoa*	*Edyuillia* (=*Eurotium*)	*Xeromyces*
Hemisartorya		*Emericella*	***Thermoascaceae*:**
Neosartorya		*Eurotium*	*Paecilomyces* (incl. *Byssochlamys*)
Penicilliopsis		*Fennellia*	*Thermoascus* (syn. *Coonemeria*, *Dactylomyces*)
Petromyces		*Hamigera*	***Trichocomaceae*:**
Roumegueriella[1]		*Hemicarpenteles*	*Dendrosphaera* (tentatively, *fide* Malloch 1985b)
Sagenoma		*Hemisartorya*[3]	*Rasamsonia*
Sclerocleista		*Neosartorya*	*Sagenomella*
Talaromyces		*Penicilliopsis*	*Talaromyces* (syn. *Sagenoma, Erythrogymnotheca*)
Trichocoma		*Petromyces*	*Thermomyces*
Warcupiella		*Sclerocleista*	*Trichocoma*
***Monascaceae*:**		*Thermoascus*	**Unknown status:**
Ascorhiza		*Warcupiella*	*Ascorhiza* (no strains available/studied)
Leiothecium			*Pseudocordyceps*
Monascus			*Sarophorum*
Xeromyces			*Dichleana*

[1]Benny & Kimbrough (1980) accommodated *Roumegueriella* in the *Trichocomaceae*; however, Sung *et al*. (2007) showed that this genus belongs to the *Bionectriaceae* (*Hypocreales*) and is excluded in our study of the *Trichocomaceae*. [2]The type species *Mallochia*, *M. echinulata*, has a close relationship with *Amaurascopsis reticulata* and both species belong to the *Onygenales* (Solé *et al*. 2002). [3]Comparison of the ITS sequence of the type strain of the type of *Hemisartorya*, *H. maritima* (CBS 186.77), showed to have a 100 % homology with the type of *A. versicolor* CBS 583.65 (J. Houbraken, unpubl. data).

which were not treated in Malloch's study (1985a, b), also belong to this family.

The genera *Byssochlamys*, *Dendrosphaera*, *Sagenoma*, *Talaromyces* and *Trichocoma* were placed by Malloch (1985a, b) in *Trichocomaceae* (as subfamily *Trichomoideae*), and anamorphs in *Paecilomyces* or *Penicillium* were linked to it. The results of our phylogenetic analysis (Fig. 1) confirm the positioning of the genera *Sagenoma*, *Talaromyces* and *Trichocoma* in this family. In addition, the recently described genus *Rasamsonia* (Houbraken *et al*. 2011d), and the asexual genera *Thermomyces* and *Sagenomella* are classified in this family. Phylogenetic analysis shows that *Byssochlamys* is more closely related to *Thermoascus*. Fennell (1973) also observed the relationship between these two genera and stated that *Byssochlamys* is transitional between *Thermoascaceae* and *Aspergillaceae* (as *Eurotiaceae*). No strains of the genus *Dendrosphaera* were available and its position remains questionable. Kobayasi (1971) described an aleurioconidial state in *Dendrosphaera eberhardtii* and Benny & Kimbrough (1980) therefore suggested placing this species in *Onygenales* (which makes *Dendrosphaeraceae* a family of *Onygenales*). On the other hand, Malloch (1985b) noted that *D. eberhardtii* and *T. paradoxa* produce similar brushes of soft hyphae bearing asci and ascospores suggesting the placement in *Trichocomaceae*. Following Malloch (1985b), we tentatively place this genus in *Trichocomaceae*, and consequently, *Dendrosphaeraceae* are synonymised with *Trichocomaceae*.

Phylogeny of Aspergillaceae

Seven clades (Fig. 1, clades 1–7) can be distinguished in *Aspergillaceae*. Each clade is discussed and phenotypic characters of the members belonging to those clades are compared with those of *Penicillium*.

Clade 1: *Penicillium sensu stricto*

Penicillium sensu lato is polyphyletic and species of this genus occur in the phylogenetically redefined families *Aspergillaceae* and *Trichocomaceae* (Fig. 1). The type species of *Penicillium*, *Penicillium expansum*, and the type species of *Eupenicillium*, *E. crustaceum*, form a clade within *Aspergillaceae*, defined here as *Penicillium sensu stricto*. The Penicillia not belonging to *Penicillium*

s. str. are mainly classified in *Trichocomaceae*, in a clade together with the type species of *Talaromyces*, *T. flavus* (clade 10). The presence of two major clades in *Penicillium* is concordant with earlier studies using rDNA sequences (Berbee & Taylor 1995, Ogawa *et al*. 1997, Sugiyama 1998, Ogawa & Sugiyama 2000, Tamura *et al.* 2000). More recently, Wang & Zhuang (2007) used partial calmodulin sequences for the phylogenetic analysis of *Penicillium* and their data also supported the presence of two lineages in *Trichocomaceae*. However, their placement of *Talaromyces trachyspermus* on a single lineage is contradictory with our data. The *Penicillium s. str.* clade is most closely related to the *Aspergillus* clade (clade 2) and is phylogenetically more distant from genera with similar anamorphs such as *Paecilomyces*, *Merimbla* and the *Penicillium* species assigned to *Trichocomaceae* in this study. The phylogenetic study shows that various other genera belong to *Penicillium s. str.* The type species of the genera *Chromocleista*, *Torulomyces*, *Thysanophora*, *Hemicarpenteles* and *Eladia* are positioned in *Penicillium s. str.* These genera are considered here as synonyms of *Penicillium,* and the species are transferred as appropriate. Two well-supported subclades (Fig. 1A, B) can be distinguished within *Penicillium s. str.* Pitt (1980) classified *Penicillium* in four subgenera: *Aspergilloides*, *Furcatum*, *Penicillium* and *Biverticillium*. This system was mainly based on conidiophore branching and shape of the phialides. The type species of subgenus *Penicillium* (*P. expansum*) belongs to clade 1B and mainly comprises the species which are ter- and/or quarterverticillate. The type species of the subgenera *Aspergilloides* and *Furcatum* (*P. aurantiobrunneum* (= *P. glabrum*) and *P. citrinum*, respectively) are positioned in clade 1A, and monoverticillate and biverticillate species with flask shaped phialides more frequently occur in this clade. The type species of subgenus *Biverticillium*, *Penicillium minioluteum*, does not belong to *Penicillium s. str.* and is recombined as *Talaromyces minioluteus* elsewhere (Samson *et al.* 2011). Species with symmetrical biverticillate conidiophores and lanceolate phialdes belong to this clade. These observations confirm other studies that also showed that the current phenotype-based subgeneric classification, which is mainly based on the branching system of the *Penicillium* conidiophores, is incongruent with the molecular phylogeny (Peterson 2000a, Wang & Zhuang 2007). It is proposed here to abandon the current subgeneric classification and to synonymise subgenus *Furcatum* with *Aspergilloides*, because the latter is an older name. The subgenera *Aspergilloides* and *Penicillium* correspond to clades 1A and 1B, respectively. The phylogenetic structure within these clades is examined with more depth in Part 3 of the discussion.

Clade 2: *Aspergillus*

A limited number of *Aspergillus* species and related teleomorphs are included in this study. The majority of the studied *Aspergillus* strains form a clade with 51 % bootstrap and 1.00 posterior probability support and this clade is defined here as *Aspergillus sensu stricto*. *Aspergillus s. str.* is phylogenetically closely related to *Penicillium s. str.* (77 % bs, 1.00 pp). These genera are morphologically distinct. *Aspergillus* forms nonseptate stipes, which often terminate in a distinct inflated part (vesicle) and have a foot-cell (Raper & Fennell 1965). Furthermore, the phialides are produced synchronously from the vesicle in *Aspergillus*. The distinction between these two genera is largely supported by the phylogeny. However, there are a few exceptions. *Aspergillus paradoxus*, *A. crystallinus* and *A. malodoratus* phylogenetically belong to *Penicillium* (R.A. Samson, unpubl. data). However, Raper & Fennell (1965) also noted that *A. crystallinus* and *A. malodoratus* produce triseriate structures that resemble *Penicillium*. In addition, there are also Aspergilli, which look similar to *Penicillium*. An example is *Penicillium inflatum*, which phylogenetically belongs to *Aspergillus* section *Cremei* and will be transferred from *Penicillium* to *Aspergillus* (R.A. Samson, unpubl. data). In addition, *Aspergillus sydowii* regularly produces small penicilli, and *A. restrictus* can produce diminutive vesiculate monoverticillate stipes, similar in appearance to those of some *Penicillium* species.

The classification of the genus *Aspergillus* is traditionally based on morphological characters. Raper & Fennell (1965) divided the genus into 18 groups. More recently, Peterson (2008) studied the relationship among Aspergilli using a multigene phylogeny and accepted 5 subgenera (*Aspergillus*, *Circumdati*, *Fumigati*, *Nidulantes* and *Ornati*) and 16 sections. Our data largely corresponds with Peterson's phylogeny, and four of the six subclades in Fig. 1 represent the *Aspergillus* subgenera as defined by Peterson (2008). However, there are some discrepancies. Sections *Restricti* and *Aspergillus* of the subgenus *Aspergillus* are on a well supported branch (100 % bs, 1.00 pp), confirming Peterson's data. Peterson (2008) placed sections *Clavati* and *Fumigati* in a single subgenus and, because of lack of statistical support, tentatively placed section *Cervini* in this subgenus. The representatives of section *Cervini* (*Aspergillus cervinus*, *A. kanagawaensis*) used in our study show that this section is basal to sections *Fumigati* and *Clavati* and belongs in the subgenus *Fumigati*. This confirms the phenotypic data of Gams *et al*. (1985), who placed sections *Fumigati* and *Cervini* in subgenus *Fumigati*. Phylogenetically, the monophyletic subgenus *Circumdati* as proposed by Peterson (2008) contains sections *Circumdati*, *Candidi*, *Flavi*, *Flavipedes*, *Nigri*, *Terrei* and *Cremei*. The relationship between the former six sections is poorly supported in our analysis (30 % bs, 0.94 pp) and more studies on the phylogenetic structure of *Aspergillus* are needed. In contrast to previous published results (Peterson 1995, 2008), section *Cremei* appeared to be unrelated to the other sections of subgenus *Circumdati*. The studied members of section *Cremei* (*A. pulvinus*, *A. wentii*, *A. brunneouniseriatus*) formed a well supported clade with the type species of *Cristaspora* (*C. arxii*) and this clade is more closely related to members of the subgenus *Aspergillus* (64 % bs, 1.00 pp) than to subgenus *Circumdati*. The subgenus *Nidulantes* contains sections *Nidulantes*, *Ochraceorosei*, *Usti*, *Sparsi* and *Aeni* (Frisvad *et al.* 2005, Peterson 2008, Varga *et al.* 2010). These results were confirmed in our study, with exception of section *Aeni*, because no representatives were included in our study. Section *Ornati* in subgenus *Ornati* is not positioned in *Aspergillus s. str.* and species belonging to this section are placed in the clade 7. Peterson (2008) suggested that it would be possible to change the classification of *Aspergillus* by splitting the genus based on teleomorphic states associated with particular monophyletic groups. However, he advocated keeping *Aspergillus* as a monophyletic genus, since this would reflect the actual relationships of species displaying an aspergillum whereas dividing the form genus into several genera based on teleomorphs would de-emphasise the relationships for most biologists not intimately familiar with the genus. Teleomorph genera associated with *Aspergillus* anamorphs include *Chaetosartorya, Dichotomomyces, Emericella, Eurotium*, *Fennellia*, *Neocarpenteles, Neopetromyces*, *Neosartorya* and *Petromyces*.

The type species of the genera *Polypaecilum* and *Phialosimplex* and the ex-type strain of *Basipetospora halophilica* form a strongly supported clade (100 % bs, 1.00 pp) within *Aspergillus s. str.* This clade is related to *Aspergillus* sections *Cremei*, *Aspergillus*

and *Restricti* (64 % bs, 1.00 pp). Recently, *Phialosimplex* was introduced for species with simple phialides borne laterally on vegetative hyphae. These phialides form chains of conidia and are mostly monophialidic, but a second opening can also be formed (polyphialides). *Sagenomella chlamydosporus* and *S. sclerotialis* were transferred to this genus and *Phialosimplex canicus* was described as a new species (Sigler *et al*. 2010). The transfer of *S. sclerotialis* to *Phialosimplex* created a paraphyletic genus with *Polypaecilum* embedded in it. The type species of *Polypaecilum*, *P. insolitum*, produces its conidia on polyphialides and this feature is shared with members of *Phialosimplex* (Smith 1961a). The formation of chlamydospores and the occurrence in patient material are also shared features of both genera. This indicates that these genera could be congeneric and more research is needed to clarify their taxonomic status. *Basipetospora halophilica* also belongs to this diverse clade. The production of short solitary conidiophores or conidiogeneous cells by this species is a shared character with members of *Phialosimplex*, *Polypaecilum* and many other genera; however, formation of polyphialides by this species was not described (Pitt & Hocking 1985). Furthermore, *Polypaecilum* morphs related to *Thermoascus* and *Dichotomyces* are not part of this clade and this genus is polyphyletic.

Clade 3: *Hamigera*

Hamigera, *Warcupiella* and the related anamorphs *Merimbla* and *Raperia* are positioned in clade 3. The statistical support of this clade is low (< 70 % bs, < 0.90 pp) and the studied species might not be related. We decided to place the species *Hamigera avellanea*, *Hamigera striata*, *Penicillium megasporum*, *Talaromyces leycettanus* and *Warcupiella spinosa* in our taxon sampling based on data presented in previous studies, in which it was demonstrated that these species are related (Ogawa & Sugiyama 2000, Tamura *et al*. 2000, Peterson 2008, Peterson *et al.* 2010). *Penicillium giganteum*, *Merimbla ingelheimensis*, *Hamigera paravellanea, H. insecticola*, *H. inflata*, *H. terricola*, *H. pallida*, *H. fusca* were not included in our study, but are also members of this clade (Ogawa & Sugiyama 2000, Peterson *et al.* 2010). *Hamigera striata* and *Talaromyces leycettanus* are on a strongly supported branch (94 % bs, 1.00 pp). Ogawa & Sugiyama (2000) showed in their 18S rDNA analysis that both species are related (83 % bs), confirming our data. Peterson *et al.* (2010) did not accept *H. striata* in *Hamigera* because of lack of statistical support and followed Benjamin's (1955) placement of this species in *Talaromyces*. Our results indicate that *Talaromyces* is phylogenetically distant and we therefore maintain *H. striata* in *Hamigera*. *Talaromyces leycettanus* also warrants further attention. Stolk & Samson (1972) noted that the anamorph of *T. leycettanus*, *Paecilomyces leycettanus*, seems to occupy an intermediate form between *Penicillium* and *Paecilomyces*. The complex conidiophore of *T. leycettanus* resembles *Merimbla* (= anamorph of *Hamigera*) (Peterson *et al.* 2010), supporting its placement in this diverse clade. *Warcupiella* is monotypic, represented by *Warcupiella spinulosa* (Subramanian 1972) and this species was originally described as *Aspergillus spinulosus* (Raper & Fennell 1965). Later, *Raperia* was introduced by Subramanian & Rajendran (1979) to accommodate the anamorph of *W. spinulosa* (von Arx 1986). Our results and others (Tamura *et al*. 2000, Peterson 2008) show that *W. spinulosa* does not belong to *Penicillium* or *Aspergillus*, and is more closely related to *Hamigera avellanea*. The relationship between *Warcupiella*/*Raperia* and *Hamigera* was also noted by von Arx (1986), and he transferred *W. spinulosa* to *Hamigera*. *Penicillium megasporum*, another member of this clade, has little affinity with *Penicillium s. str.* as noted by Pitt (1980), who created *Penicillium* series *Megaspora* for this species and *P. asperosporum*. Peterson *et al*. (2010) described the penicillus structure of *P. megasporum* as similar as that of *Merimbla*, but that phylogenetic analysis did not support inclusion of *P. megasporum* in the *Hamigera* clade. Our analysis lacks high bootstrap support to confidentially place *P. megasporum*, *W. spinulosa* and *T. leycettanus* in *Hamigera*. More research is needed to elucidate the classification of this diverse clade.

Clade 4: *Penicilliopsis*

Clade 4 comprises *Aspergillus zonatus* and *Penicilliopsis clavariiformis* and these two species form a strongly supported clade. *Penicilliopsis* is typified by *P. clavariiformis* and characterised by seed-borne, stipitate stromata. The anamorph genera *Pseudocordyceps*, *Sarophorum* and *Stilbodendron* are phenotypically related (Samson & Seifert 1985, Hsieh & Ju 2002). The former two genera have conidiogenous structures similar to those of *Penicillium* and the latter has *Aspergillus*-like conidiogenous structures. The sclerotia of *Stilbothamnium* morphologically resemble ascomata of *Penicilliopsis*. However, phylogenetically, the type species of *Stilbothamnium*, *Aspergillus togoensis*, belongs to *Aspergillus* subgenus *Circumdati* section *Flavi* and is unrelated to *Penicilliopsis* (Fig. 1). More research is needed to clarify the relationship between *Penicillium*, *Penicilliopsis* and the associated anamorph genera *Pseudocordyceps* and *Sarophorum*.

Clade 5: *Monascus*, *Xeromyces* and *Leiothecium*

The teleomorph genera *Monascus*, *Xeromyces* and *Leiothecium* belong in clade 5, as do the anamorph genera *Fraseriella* and *Basipetospora* (Pettersson *et al*. 2011, our data). Benny & Kimbrough (1980) placed *Monascus*, *Xeromyces* and *Leiothecium* in *Monascaceae* and this family is transferred here to *Aspergillaceae* (see part 1, phylogeny of *Aspergillaceae*). These genera have similar phenotypic characters including the formation of stalked ascomata and the production of aleurioconidia from undifferentiated conidiogenous cells. These features clearly set these genera apart from *Penicillium s. str*. and *Aspergillus*. Our results confirm those of Pettersson *et al*. (2011) and we follow their opinion in retaining *Xeromyces* for xerophilic *Monascus*-like species and *Monascus* for the species that grow at higher water activities. In addition, Pettersson *et al*. (2011) suggested that *Chrysosporium inops* should be transferred to a new genus. However, Fig. 1 shows that this species is closely related to *X. bisporus* and the xerophilic nature of boths species indicates a close relationship (Pitt & Hocking 2009, Pettersson *et al*. 2011). *Leiothecium* is basal to *Monascus* and the connection between these two genera was also noted by Samson & Mouchacca (1975). *Aspergillus clavatoflavus* is basal to this clade, but the relationship lacks statistical support. The micromorphology is *A. clavatoflavus* differs from the members of clade 5 and therefore this species is placed outside this clade, awaiting more conclusive data.

Clade 6: *Phialomyces*

The type species of *Phialomyces*, *Phial. macrosporus* (Misra & Talbot 1968), is positioned in clade 6 and is closely related to *Penicillium arenicola* (100 % bs, 1.00 pp). *Merimbla humicoloides* (= *Penicillium humicoloides sensu* Peterson *et al*. 2010) also belongs to this clade (R.A. Samson, unpubl. data). All three species are phylogenetically distinct form *Penicillium s. str.* Pitt (1980)

placed *P. arenicola* in a separate section and series and noted that this species may not be a true *Penicillium*. Phenotypically, *Phial. macrosporus*, *M. humicoloides* and *P. arenicola* form conidia in shades of gold-brown, a feature uncommon for *Penicillium* species. These species can produce terverticillate conidiophores, a character also present in subgenus *Penicillium* (clade 1B). Our results indicate that *P. arenicola* and *M. humicoloides* should be transferred to another genus.

Clade 7: *Sclerocleista*

Sclerocleista ornata and *S. thaxteri* are basal to *Phial. macrosporus* and *P. arenicola* (Fig. 1). *Sclerocleista ornata* was originally described as *Aspergillus ornatus* (Raper *et al.* 1953), and later transferred to *Sclerocleista* (Subramanian 1972). *Sclerocleista thaxteri* was originally described in *Sclerocleista* and later von Arx (1974) transferred this species to *Hemicarpenteles*. The two species are closely related, and phylogenetically distant from *H. paradoxus,* the type species of *Hemicarpenteles* (Fig. 1, *Penicillium s. str*.). Peterson (2008) placed *Sclerocleista* basal to the Aspergilli, suggesting a monophyletic *Aspergillus* clade; however, our data do not support this conclusion. *Sclerocleista* differs from *Penicillium s. str.* in having an *Aspergillus*-type anamorph and purple coloured cleistothecia filled with lenticular ascospores (Raper & Fennell 1965).

Phylogeny of Thermoascaceae

Figure 1 shows that two clades (clade 8 and 9) are present in *Thermoascaceae* (= lineage 2). The phylogeny of these two clades and the comparison of the species belonging to these two clades with *Penicillium s. str*. is discussed below.

Clade 8: *Thermoascus*

Thermoascus aurantiacus, *T. crustaceus* and *T. thermophilus* are together with *Byssochlamys verrucosa* in a separate clade. The taxonomy of *Thermoascus* is treated in various studies. Apinis (1967) split *Thermoascus* in two: *Thermoascus* was retained for its type species *T. aurantiacus*, and *T. thermophilus* and *T. crustaceus* were transferred to *Dactylomyces*. Later, Mouchacca (1997) divided *Dactylomyces* further in two, creating *Coonemeria* for *T. crustaceus*. Although these species have different anamorphs (*Paecilomyces*/*Polypaecilum*), our phylogenetic study (Fig. 1) shows that these three species are closely related and should be retained in *Thermoascus*. Samson *et al*. (2009) noted that *Byssochlamys verrucosa* is misidentified in *Byssochlamys* but related to *Thermoascus*, and this observation is confirmed here. *Thermoascus* has a similar type of sclerotioid cleistothecium as members of *Penicillium s. str.* (Stolk & Samson 1983). These two genera differ mainly in ascomatal development. Ascomata of *Thermoascus* are initiated by an ascogonial coil (Stolk 1965, Subramanian & Rajendran 1980), whereas in *Penicillium s. str*. the formation begins with sclerotium-like bodies inside which the ascogonia develop. Furthermore, the anamorphs of *Thermoascus* are not of the *Penicillium* type, but can be similar to *Paecilomyces*.

Clade 9: *Paecilomyces*

The types of *Paecilomyces* (*P. variotii*) and *Byssochlamys* (*B. nivea*) occur together on a branch with 100 % bootstrap support. Using a polyphasic approach, Samson *et al.* (2009) showed that the genera *Byssochlamys* and *Paecilomyces s. str.* are closely related and form a monophyletic group. *Paecilomyces* was introduced by Bainier (1907) and has priority over *Byssochlamys* (Westling 1909). Phylogenetic analysis of the 18S rDNA demonstrated that *Paecilomyces sensu* Samson (1974) is polyphyletic across two subclasses, *Sordariomycetidae* and *Eurotiomycetidae*. The type species of this genus, *Paecilomyces variotii*, and its thermophilic relatives belong in the *Eurotiales* (Luangsa-ard *et al.* 2004). Figure 1 shows that *Paecilomyces s. str.* is also phylogenetically distinct from *Penicillium*. Morphological characters also support this conclusion. The conidia of *Paecilomyces s. str.* are olive-brown and formed in phialides that have a broad base and end in a long and slender neck, while the conidia of *Penicillium* species are green and formed in flask or cylindrical shaped phialides. In addition, the conidiophores of *Paecilomyces s. str.* are more irregularly branched than those of *Penicillium*. The teleomorphs are also different: those of *Paecilomyces* (formerly known as *Byssochlamys*) are almost naked while *Penicillium s. str*. produces cleistothecia with a distinct wall.

Phylogeny of Trichocomaceae

Five clades (clades 10–15) can be recognised in the more narrowly delimited *Trichocomaceae*. The species treated in these clades are phylogenetically distinct from *Penicillium s. str*., but some are phenotypically similar.

Clade 10: *Talaromyces*

The majority of *Penicillium* species assigned to the subgenus *Biverticillium* belong in clade 10 (incl. type of subgenus *Biverticillium*, *P. minioluteum*) together with the type species of the genera *Talaromyces* and *Sagenoma*. These species are phylogenetically distant from *Penicillium s. str.* and therefore these species are transferred to the genus *Talaromyces* (Samson *et al*. 2011, this study). Phenotypically, *Talaromyces* differs from *Penicillium s. str.* by the formation of symmetrically branched conidiophores with lanceolate phialides, and the production of soft ascomata without a well-defined, persistant wall. Members of the *Talaromyces* clade grow slower on the agar medium G25N than *Penicillium s. str*. members (Pitt 1980). Also differences in ubiquinones and extrolites patterns are observed between *Penicillium sensu stricto* and *Talaromyces*. The Q9 ubiquinone system was present in most *Penicillium sensu stricto* species, while nearly all *Talaromyces* have Q10(H_2) (Paterson 1998). In addition, extrolites such as mitorubrins, certain bisanthraquinones (rugulosin, skyrin), duclauxin and glauconic acide were detected in *Talaromyces*, but never found in *Penicillium sensu stricto* (Frisvad *et al*. 1998). The taxonomic and phylogenetic structure of *Talaromyces* is considered further by Samson *et al*. (2011).

The neotype strain of *Aphanoascus cinnabarinus sensu* Udagawa and Takada also belongs to this clade. Much taxonomic confusion followed after the proposal of *Aphanoascus* by Zukal (1890). Most authors follow Apinis (1968) and maintain *Aphanoascus* that is typified by *A. fulvescens*. In addition, the neotypification of *A. cinnabarinus* by Udagawa & Takada (1973) was incorrect, because their neotype strain had a *Paecilomyces* anamorph, while Zukal's original description and illustrations showed structures of a *Chrysosporium* anamorph (Stolk & Samson 1983). Based on morphological characters, Stolk & Samson (1983) suggested that *Chromocleista cinnabarina* (as *A. cinnabarinus sensu* Udagawa & Takada) belongs to *Eurotiales,* and that this species occupies an intermediate position between the genera *Thermoascus* and *Talaromyces*. The result of our multigene phylogeny shows that *C. cinnabarina* belongs to *Talaromyces s. str.*

This data is in concordance with the 18S rDNA sequence data of Ogawa & Sugiyama (2000), which shows that *C. cinnabarina* forms a monophyletic group with *T. macrosporus* and *T. bacillisporus*. No specimens of *Erythrogymnotheca* were studied, but an ITS sequence of the type species of this genus (*E. paucispora*) is deposited GenBank (AB176603) and a BLAST search on GenBank and internal CBS databases shows that this sequence belongs to *Talaromyces s. str*.

Clade 11: *Thermomyces*

Talaromyces thermophilus belongs to the same clade as the type of *Thermomyces*, *T. lanuginosus*. *Talaromyces thermophilus* and *Therm. lanuginosus* share similar characters, including their ability to grow at high temperatures and the formation of thick-walled chlamydospores or chlamydospore-like conidia. These characters are not shared by members of *Penicillium s. str. Talaromyces luteus* is basal to this clade. This species is not thermophilic and phenotypically different from *Thermomyces* and *Tal. thermophilus*, and it is therefore excluded from clade 11.

Clade 12: *Sagenomella*

Clade 12 is centered around the type species of *Sagenomella*, *S. diversispora*, and this genus is phylogenetically unrelated to *Penicillium s. str. Sagenomella* was described by Gams (1978) for *Acremonium*-like fungi and is characterised by connected conidial chains and sympodially proliferating, often centrally swollen phialides. These characters are not present in *Penicillium s. str.* Molecular data showed that *Sagenomella sensu* Gams is polyphyletic (Endo *et al*. 1998, Thanh *et al.* 1998, our results). Sigler *et al.* (2010) transferred *S. chlamydospora* and *S. sclerotialis* to the new genus *Phialosimplex* and *Sagenomella bohemica* belongs in *Talaromyces* (Samson *et al*. 2011). The close relationship of this genus with *Talaromyces* indicates that *Sagenomella* is a reduced form of *Talaromyces*.

Clade 13: *Rasamsonia*

The thermophiles *Talaromyces emersonii* and *T. byssochlamydoides* were transferred to *Rasamsonia* (Houbraken *et al.* 2011d), leaving *T. thermophilus* as sole thermophile in *Talaromyces*. However, our phylogenetic analysis shows that this species belongs to *Thermomyces* and not to *Talaromyces*. The genus *Rasamsonia* was erected for thermotolerant or thermophilic species, which have cylindrical phialides usually gradually tapering towards the apices, conidiophores with distinctly rough walled stipes, olive-brown conidia and ascomata, if present, with a scanty covering. This clade contains the species *R. argillacea*, *R. brevistipitata*, *R. byssochlamydoides*, *R. cylindrospora*, *R. eburnea* and *R. emersonii* (Houbraken *et al*. 2011d).

Clade 14: *Trichocoma*

The monotypic genus *Trichocoma* is typified by *Trichocoma paradoxa* and is characterised by asci born in hyphal masses or tufts that can be up to 10–20 mm long (Kominami *et al*. 1952, Malloch 1985b). The anamorph of this species resembles an anamorph of *Talaromyces*. However, *Trichocoma* produces conidia in shades of brown. *Rasamsonia* is phylogenetically related to *Trichocoma*, and can be differentiated by the presence of scanty ascomatal coverings and its ability to grow at temperatures above 40 °C.

Excluded genera: Geosmithia, Phialotubus and Yunnania

The genera *Geosmithia, Phialotubus* and *Yunnania* have sometimes been hypothesised to be related to *Penicillium* (Gams 1978, Pitt 1980, Kong 1998). Our data shows that these genera do not belong to the *Eurotiales* and details are provided below.

Geosmithia

The genus *Geosmithia* is typified by *G. lavendula* (Pitt 1978) and is a polyphyletic morphogenus introduced to classify *Penicillium* species, which are characterised by: a) cylindroidal phialides and conidia, b) rugulose to rugose conidiophores walls, metulae and phialides and c) conidial colour other than green (with the exception of *G. namyslowskii*). Anamorphs of *Geosmithia* have affinities with hypocrealean (*Hypocreales*: *Bionectriaceae*) and eurotialean (*Eurotiales*: *Trichocomaceae*) fungi, and the type species of *Geosmithia*, *G. lavendula*, is related to *Acremonium alternatum*, the type species of *Acremonium* (Ogawa *et al.* 1997, Rossman *et al*. 2001, Summerbell *et al*. 2011). Currently, there are 16 described species (Pitt 1980, Yaguchi *et al.* 1993, 1994, Pitt *et al.* 2000, Kolařík *et al.* 2004, 2005, 2010), and eight of these species (*G. fassatiae*, *G. flava*, *G. langdonii*, *G. lavendula*, *G. morbida*, *G. obscura*, *G. pallida*, and *G. putterillii*) belong to the *Hypocreales*. *Geosmithia argillacea* (teleomorph *Talaromyces eburneus sensu* Yaguchi *et al*. 2005), *G. eburnea* (teleomorph *Talaromyces eburneus sensu* Yaguchi *et al*. 1994), *G. emersonii* (teleomorph *Talaromyces emersonii*) and *G. cylindrospora* are closely related to each other and were recently transferred to *Rasamsonia* (Houbraken *et al*. 2011d, see clade 13 above). *Geosmithia swiftii* (teleomorph *Talaromyces bacillisporus*) and *G. viridis* belong to *Talaromyces s. str.* and *G. namyslowskii* and *G. malachiteum* (described as the anamorph of *Chromocleista malachitea*) belong to *Penicillium s. str.* (Fig. 1). Zaleski (1927) originally described *Geosmithia namyslowskii* as *Penicillium namyslowskii* and the new combination of *Penicillium malachiteum* is made elsewhere in this article.

Phialotubus

Phialotubus (Roy & Leelavathy 1966) is monotypic with *Phialotubus microsporus* as the type. This species is characterised by the formation of cylindrical phialides with long hyaline thread-like projections, which get prolonged into the hyaline tube-like projection when conidia are formed (Fig. 2). The conidia are fusiform in shape and produced in chains (Roy & Leelavathy 1966, Gams 1978, Arx 1981). These characters suggest a close connection with the *Eurotiales*, for example with *Paecilomyces*, *Phialomyces*, *Sagenomella* and *Torulomyces*. However, a BLAST search on GenBank with an ITS sequence of strain CBS 861.70^{isoT} (GenBank no. JN831360) did not retrieve any high similarity matches with members of the *Eurotiales*. The overall similarity matches were low and this species probably belongs to the class *Sordariomycetes*.

Yunnania

Kong (1998) proposed the genus *Yunnania* and typified it with *Y. penicillata*. The truncated conidia and the black or brownish black colonies resemble those of *Scopulariopsis*. In addition, the conidia are produced by annelides (Fig. 3). Examination of the type strain of *Y. penicillata* (CBS 130296^{T}) showed that this species is morphologically related to *Scedosporium*. A BLAST search on GenBank with an ITS sequence of this species (GenBank no. JN831361) did not retrieve a high similarity match, but showed that this species belongs to the order *Microascales*.

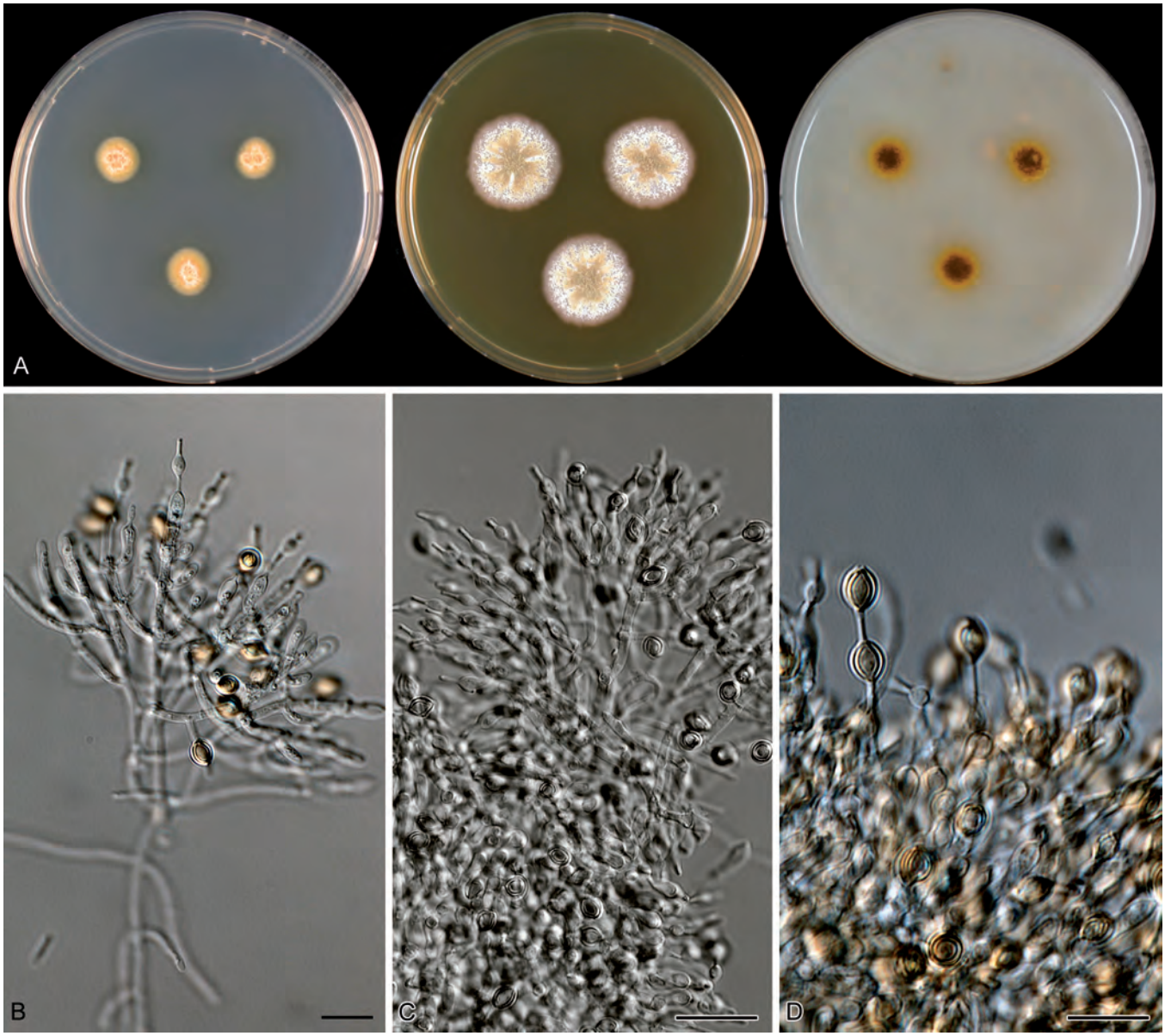

Fig. 2. *Phialotubus microsporus* CBS 861.70^{isoT}. A. Colonies grown for 7 d at 25 °C, from left to right: CYA, MEA, OA. B–D. Conidiophores and conidia. Scale bar = 10 µm.

Taxonomic implications

Aspergillaceae Link, Abh. dt. Akad. Wiss. Berlin 1824: 165. 1826.

= *Eurotiaceae* Clements and Shear, Gen. Fung. 50. 1931.
= *Monascaceae* J. Schröter, Nat. Pflanzenfamilien 1: 148. 1894.
= *Hemicarpenteleaceae* Locquin, Tribune Méd. (Paris) 1. 1972. *nom. inval.* (Art. 36).
= *Penicilliaceae* Vuillemin, Pl. Jungh. 10: 172. 1910. (as Penicilliacées *nom. inval.* Art. 32.1b).
= *Penicilliopsidaceae* Locquin, Tribune Méd. (Paris) 1. 1972. *nom. inval.* (Art. 36).
= *Phialomycetaeae* Locquin, Mycologie générale et structurale: 212. 1984. *nom. inval.* (Art. 36).
= *Warcupiellaceae* Locquin, Mycologie générale et structurale: 167. 1984. *nom. inval.* (Art. 36).
= *Xeromycetaceae* Locquin, Tribune Méd. (Paris) 1. 1972. *nom. inval.* (Art. 36).

Type: *Aspergillus* Fr: Fr.

Thermoascaceae Apinis, Trans. Br. Mycol. Soc 50: 581. 1967.

Type: *Thermoascus* Miehe

Trichocomaceae E. Fischer, Nat. Pflanzenfam. 1: 310. 1897. (as *Trichocomataceae*)

= *Talaromycetaceae* Locquin, Mycologie générale et structurale: 176. 1984. *nom. inval.* (Art. 36).
= *Dendrosphaeraceae* Ciferri ex Benny & Kimbrough, Mycotaxon 12: 22. 1980.

Type: *Trichocoma* Junghuhn

Part Two: Delimitation of *Penicillium*

Authority

The generic name *Penicillium* is attributed to Link (1809). Link included three species within *Penicillium*, *P. glaucum*, *P. candidum* and *P. expansum*. He illustrated *P. candidum*, which clearly shows structures of a *Penicillium* species. Later, *Penicillium expansum* was selected by Thom (1910) and later (co-)authors as the lectotype of *Penicillium*. The generic name *Penicillium* was attributed by Fries (1832: 406) to Link (1809). Hawksworth *et al.* (1976) proposed to conserve the generic name *Penicillium* as *Penicillium* Link ex Grey over *Penicillium* Fries 1832 (proposal no. 420), and lectotypified

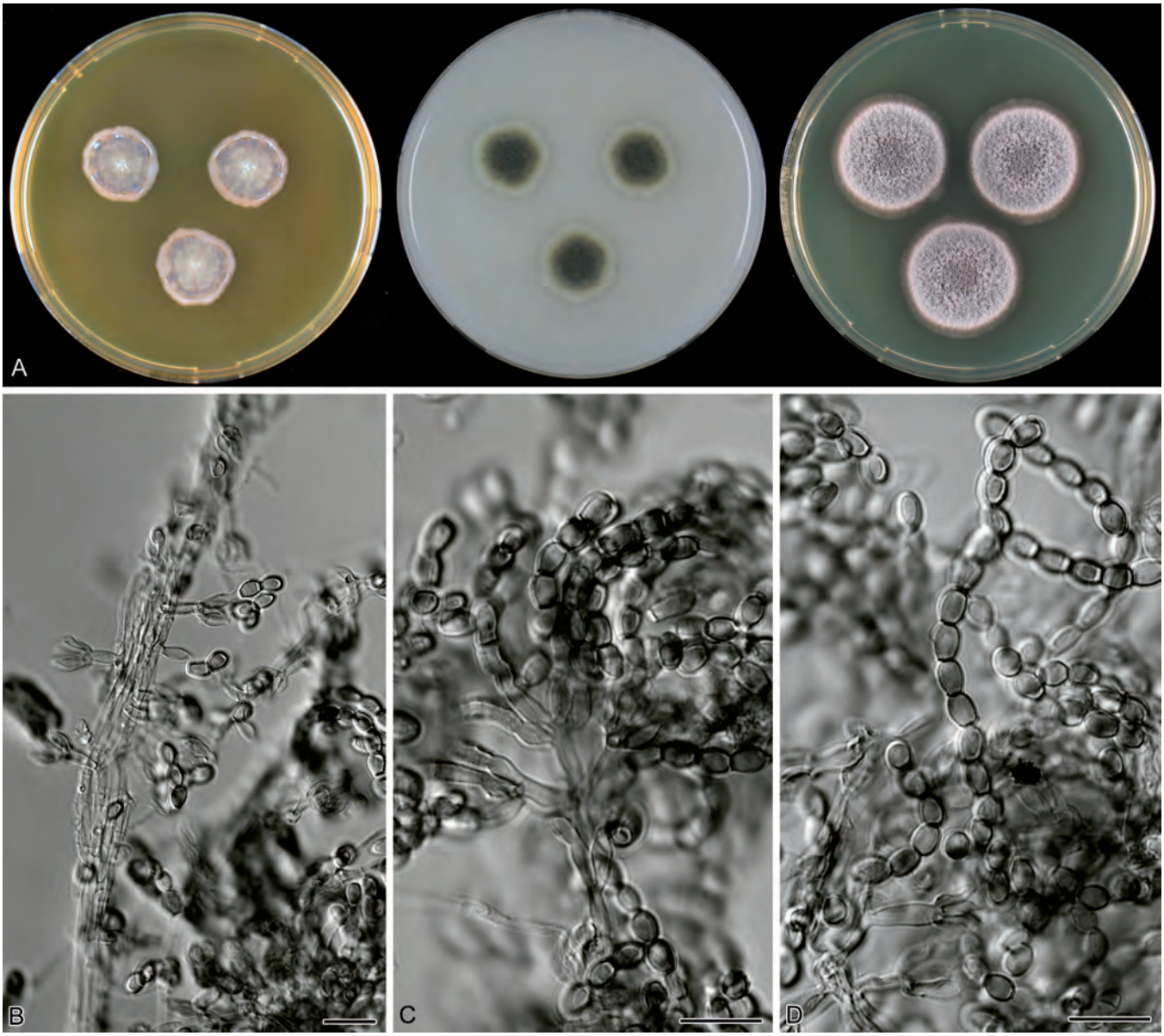

Fig. 3. *Yunnania penicillata* CBS 130296[T]. A. Colonies grown for 7 d at 25 °C, from left to right: MEA, OA, CYA. B–D. Conidiophores and conidia.

the genus with *Penicillium expansum* Link ex Grey. This proposal was countered by Jørgensen & Gunnerbeck (1977) because Fries listed "*Mucor crustaceus* L." as a typical species of *Penicillium* and not as the type species of this genus. The proposal of Hawksworth *et al*. (1976) was therefore rejected (Petersen 1980). The general starting point for fungal names is Linnaeus 1753, but there are a few exceptions and these are mentioned in the ICBN under art. 13e. One exception is that names used by E.M. Fries' "Systema mycologicum" 1821–1832 have a protected status. These names are sanctioned and have priority over older synonyms and homonyms. The authority used here is therefore *Penicillium* Link : Fries.

Generic diagnosis

The concept of *Penicillium* has been refined and restated often in mycological history. The concept of Raper & Thom (1949) is followed here; however, there are some emendations. In our concept, *Penicillium* includes species with pigmented stipes (*Thysanophora* species, *P. stolkiae* and related species), as well as species formerly ascribed to the genera *Eladia*, *Torulomyces*, *Chromocleista* and *Hemicarpenteles*. Details regarding the position of these genera in *Penicillium* are presented below. Another important difference between our and Raper & Thom's (1949) concept is the exclusion of *Talaromyces* and related *Penicillium* species. In our concept, only teleomorphs producing pseudoparenchymatous and sclerotioid ascomata are included ("Eupenicillium-type"), and *Talaromyces* species, with soft ascomata without a well-defined, persistent wall, are excluded (Samson *et al*. 2011). Also the *Penicillium* species, which have lanceolate phialides and metulae with equal lengths as the phialides, are excluded. These species are also phylogenetically distinct (Fig. 1). Our emended generic diagnosis is derived from Raper & Thom (1949) and is presented here:

Penicillium Link : Fries, Systema Mycologicum 3: 406. 1832.

Vegetative mycelium abundant, entirely submerged or more or less effused, irregularly branching, septate, hyaline or brightly coloured and forming a dense and compact mycelia colony with well-defined margins. *Conidiophores* borne from undifferentiated subsurface, superficial or aerial hyphae, rarely subapically proliferation under terminal penicillus. *Stipes* relatively narrow and thin walled, 2–5 µm,

and in some species apically swollen, hyaline, in some species brown. *Conidial apparatus* usually a well defined structure (brush or broom), named the Penicillus; penicilli comprised of phialides born directly on the stipe, or with one, two or rarely more verticils of metulae and rami as supporting cells. *Conidiogenous cells* phialides, borne in succession, *i.e.* not synchronouse, rarely exceeding 15 µm in length, ampulliform, rarely cylindrical. *Conidia* in unbranched chains, borne basipetally, single celled, commonly between 2–5 µm in diameter, rarely exceeding 6 µm, *en masse* coloured in shades of green, rarely white, olive or brown. *Chlamydospores* absent. *Sclerotia* occasionally produced, composed of thick-walled cells, usually hard. *Cleistothecia*, if produced, usually hard, globose to subglobse, pseudoparenchymatous or sclerochymatous, ripening from the center outward and often tardily; white, pale, yellow, orange or brown coloured, occasionally black or red. *Asci* ellipsoidal to globose, usually 8-spored, 5–15 µm. *Ascospores* lenticular, usually with equatorial ridges, 2–5 µm.

Synonyms of Penicillium

The re-definition of the genus *Penicillium* has several taxonomic implications. Based on the phylogenetic data presented in Fig. 1 in combination with a review of literature, we place the genera *Chromocleista*, *Carpenteles*, *Citromyces*, *Eladia*, *Eupenicillium*, *Hemicarpenteles, Thysanophora* and *Torulomyces* in synonymy with *Penicillium*. More genera are congeneric with *Penicillium* and a more extended list can be found in Seifert *et al*. (2011: 333). Each genus is discussed here and new combinations are proposed below for the species accommodated in these genera.

Penicillium Link : Fries, Systema Mycologicum 3: 406. 1832.
- = *Penicillium* Link, Obs. Mycol 1: 16. 1809 (*nom. inval.*, Art. 13e).
- = *Coremium* Link ex Gray, Nat. Arr. Br. Pl. 1: 563. 1821.
- = *Eupenicillium* Ludwig, Lehrb. Nied. Kryptog.: 263. 1892.
- = *Citromyces* Wehmer, Bleitr. Kennt. Pilze 1: 1. 1893.
- = *Carpenteles* Langeron, C.r. Séanc. Soc. Boil. Paris 87: 344. 1922.
- = *Torulomyces* Delitsch, Systematik der Schimmelpilze: 91. 1943.
- = *Thysanophora* Kendrick, Can. J. Bot. 39: 820. 1961.
- = *Eladia* Smith, Trans. Brit. Mycol. Soc. 44: 47. 1961.
- = *Hemicarpenteles* Sarbhoy & Elphick, Trans. Brit. Mycol. Soc. 51: 156. 1968.
- = *Penicillium* Link ex Gray *sensu* Pitt, The Genus *Penicillium*: 154. 1980 (*nom. inval*., art 13e).
- = *Chromocleista* Yaguchi & Udagawa, Trans. Mycol. Soc. Japan 34: 101. 1993.

Subgenus ***Aspergilloides*** Dierckx, Annls. Soc. Scient. Brux. 25: 85. 1901.
- = Subgenus *Monoverticillium* Biourge, Cellule 33: 265. 1923.
- = Subgenus *Furcatum* Pitt, The Genus *Penicillium*: 233. 1980.

Subgenus ***Penicillium***
- = Subgenus *Eupenicillium* Dierckx, Annls Soc. Scient. Brux. 25: 85. 1901.

Chromocleista

The genus *Chromocleista*, defined by the type species *C. malachitea*, belongs to *Penicillium* and is related to *P. herquei* (see Figs 1, 7). This genus was created by Yaguchi *et al.* (1993) for species that form bright coloured sclerotioid cleistothecia with a *Geosmithia* anamorph (Fig. 4). The close relationship with *Eupenicillium* was noted in the original description, but the presence of the *Geosmithia* anamorph was, according to the authors, sufficient to create a new genus. Using 18S rDNA sequence data, Ogawa & Sugiyama (2000) showed that *C. malachitea* groups with *Eupenicillium javanicum*, *E. crustaceum*, *P. chrysogenum* and *Geo. namyslowskii*. Furthermore, they indicated that the *Geosmithia*-anamorph of *Chromocleista malachitea* resembles *P. herquei* and the former species could be placed in synonymy. Comparison of the β-tubulin sequences and *RPB2* sequences of the (neo)type cultures of *P. herquei* CBS 336.48^{NT} and *C. malachitea* CBS 647.95^{T} showed homologies of 92.8 % and 94.7 % respectively. Furthermore, a BLAST search with the ITS, *RPB2* and β-tubulin sequence data of *C. malachitea* CBS 647.95^{T} on GenBank and local databases did not retrieve any high similarity matches with other described species and therefore this species is combined with *Penicillium* below.

Citromyces

Citromyces was introduced by Wehmer (1893) for monoverticillate *Penicillium* species. Many authors have agreed that this genus is a synonym of *Penicillium* (Westling 1911, Biourge 1923, Thom 1930, Raper & Thom 1949, Pitt 1980). *Citromyces* largely encompasses subgenus *Aspergilloides* as defined by Pitt (1980). In our classification system, *Citromyces* corresponds with section *Aspergilloides*.

Eladia

Thom (1930) and Raper & Thom (1949) regarded *Penicillium sacculum* Dale as a *Scopulariopsis*, and Smith (1961b) introduced the genus *Eladia* to accommodate this species and typified it with *E. saccula*. Smith (1961b) did not indicate why this species should not be considered a *Penicillium*. Pitt (1980) accepted the positioning of *E. saccula* in a separate genus and he noted that this genus is closely related to *Penicillium*, but differing in three features (Fig. 4): a) the phialides are born irregularly on stipes, b) phialides have a short collula and distinct thickening of the wall; c) the conidial chains are very short. Stolk & Samson (1985) did not accept this genus and transferred *E. saccula* to *Penicillium* and this position was retained in the list of accepted species in *Trichocomaceae* (Pitt *et al.* 2000). Our molecular data support the positioning of Smith's neotype of *Eladia succula* (CBS 231.61^{NT}) in *Penicillium* (Figs 1 and 7). This species is most closely related to *P. canescens* and *P. atrovenetum* (Fig. 7, clades 24, 25). The relationship of *P. sacculum* with these species (and also with *e.g. P. janczewskii*) was also suggested by Stolk & Samson (1985), who emphasised that all these species have swollen phialides with an abruptly narrowed neck and often short conidial chains.

Six species were described in *Eladia*: *E. saccula*, *E. inflata*, *E. minima*, *E. striatispora*, *E. pachyphialis* and *E. tibetensis*. The current name for *Eladia saccula* is *Penicillium sacculum* Dale (1926). Ex-type strains of *E. inflata* (CBS 127833) and *E. minima* (CBS 127834) were examined and comparison of the *RPB2* region (Fig. 8) showed that *E. inflata* and *P. fuscum* (= *E. pinetorum*, CBS 295.62^{T}) are closely related. *Eladia minima* is closely related to *P. heteromorphum* (CBS 226.89^{T}) and *P. philippinense* (CBS 623.72^{T}). *Eladia minima* is closely related to *P. heteromorphum, P. restrictum, Eup. katangense* and *Eup. philippinense* (data not shown). More research is needed to determine species boundaries in this group of phylogenetical related species. No living ex-type material could be obtained for *Eladia striatispora*. Drawings of *E. striatispora* show a clear resemblance with *P. striatisporum*, and therefore *E. striatispora* is regarded as a synonym of *P. striatisporum* (Stolk 1969, Matsushima 1971, Kobayasi 1971). No type material could be obtained from *E. pachyphialis* and *E. tibetensis* and their taxonomic position remains uncertain.

Eupenicillium and *Carpenteles*

The genus *Eupenicillium* was introduced by Ludwig (1892) for an ascomycete species that Brefeld (1874) described and

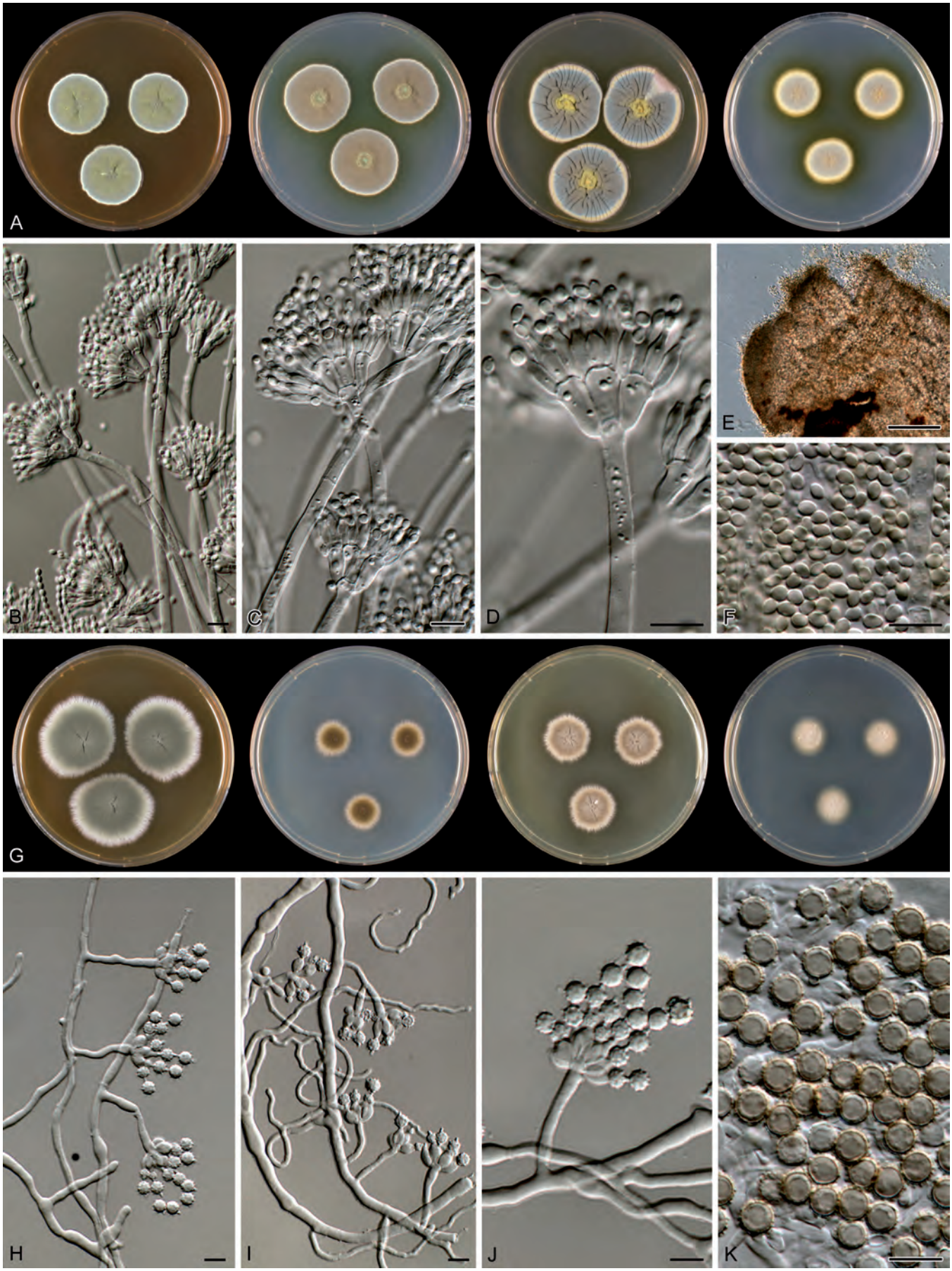

Fig. 4. A–F. *Penicillium malachiteum* CBS 647.95^{HT}. A. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. B–D. Conidiophores. E. Immature cleistothecia. F. Conidia. G–K. *Penicillium sacculum* CBS 123567. G. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. H–J. Conidiophores. K. Conidia. Scale bar = 10 µm.

illustrated as *P. crustaceum*. Unaware of Ludwig's publication, Langeron (1922) introduced the genus *Carpenteles* for ascus-producing *Penicillium* species. Because we include sexual and asexual species in our definition of *Penicillium*, *Eupenicillium* and *Carpenteles* are considered synonyms of *Penicillium*. In most cases a *Penicillium* anamorph name is already available for these *Eupenicillium* species; however, in the case of *E. bovifimosum* and *E. saturniforme*, only the teleomorph was described and no *Penicillium* names linked to these species exist (Tuthill & Frisvad 2002, Wang & Zhuang 2009). The new combinations *Penicillium bovifimosum* and *Penicillium saturniforme* are proposed below for these two species.

Hemicarpenteles

The genus *Hemicarpenteles* was created by Sarbhoy & Elphick (1968) and *H. paradoxus* was designated as type (IMI 117502^T = CBS 793.68^T). This species is characterised by the presence of an *Aspergillus* anamorph and sclerotioid ascomata (Fig. 5). This unique combination led to the proposition of a new genus. If only ascoma development and characteristics were considered, then *H. paradoxus* is most similar to *Eupenicillium*, because both genera form sclerotioid cleistothecia that ripen from the centre outwards (Sarbhoy & Elphick 1968, Pitt 1980, Stolk & Samson 1983). Figure 1 shows the phylogenetic positioning of *H. paradoxus* in the genus *Penicillium*. The placement of this species in *Penicillium* is remarkable, since this species has an *Aspergillus* anamorph. The positioning of *H. paradoxus* in *Penicillium* is also supported by analysis of the ITS and D1/D2 regions of the 28S rDNA and partial calmodulin and β-tubulin data (Peterson 2000a, 2008) and the name *Penicillium paradoxum* will therefore be proposed (R.A. Samson, unpubl. data). The placement of an *Aspergillus*-type anamorph in the genus *Penicillium* might be confusing, when using solely phenotypic characters for identification. Three other species are described in *Hemicarpenteles*: *H. acanthosporus*, *H. ornatus* and *H. thaxteri*. The former species was transferred to *Neocarpenteles acanthosporus* (Udagawa & Uchiyama 2002) and phylogenetic studies showed that this species is related to *Aspergillus* section *Clavati* (Tamura *et al.* 2000, Varga *et al.* 2007, Peterson 2000b, 2008). *Hemicarpenteles ornatus* and *H. thaxteri* are currently classified in *Sclerocleista* (Fig. 1, clade 7) (Pitt *et al.* 2000).

Thysanophora

Thysanophora was proposed by Kendrick (1961), based on *Haplographium penicillioides*. *Haplographium penicillioides* was transferred to *Thysanophora* because this species produces conidia from phialides in a basipetal succession and in dry chains, while *Haplographium* species produce ameroconidia in slime. Roumeguère (1890) noted in his description of *H. penicillioides* that this species also forms *Penicillium*-like conidiophores ("l'appareil fructifère ressemble à celui d'un *Penicillium*"). Preuss' description of three new *Penicillium* species (*P. finitimum*, *P. flexuosum* and *P. fuscipes*) in 1851 from pine needles might be the first report of members *Thysanophora*. The habitat and descriptions certainly indicate this placement, but unfortunately, no type specimens were maintained (Kendrick 1961).

Thysanophora species produce dark coloured colonies, have dark and stout conidiophores and the majority of species have secondary growth of the stipe by means of the proliferation of an apical penicillius (Fig. 6). Based on the combined *RPB1*, *RPB2*, *Tsr1* and *Cct8* data, it is clear that members of the genus *Thysanophora* belong to *Penicillium*. Members of this genus form a separate clade within this genus (Figs 1, 7), confirming earlier results using rDNA sequences (Iwamoto *et al*. 2002, Peterson & Sigler 2002). Although stipe pigmentation of *Thysanophora* species is brown, this feature is thus not a useful phylogenetic character for separating this genus from *Penicillium* (Iwamoto *et al*. 2002). Melanised conidiophores appear in two separated lineages in *Penicillium*, namely in *Thysanophora,* and in a second lineage centered on *P. stolkiae* (Peterson & Sigler 2002). Another characteristic of *Thysanophora* is the secondary growth of the stipes. This character is not present in any other *Penicillium* species and could be argued as a feature sufficient to keep *Thysanophora* as a separate genus. However, that would create a paraphyletic clade in *Penicillium* or the need for at least eight genera to restore monophyly. To avoid both scenarios it is chosen here to transfer this genus to *Penicillium*. *Thysanophora* comprises eight accepted species, namely *T. longispora*, *T. canadensis*, *T. taxi*, *T. striatispora*, *T. asymmetrica*, *T. verrucosa*, *T. glaucoalbida* and *T. taiwanensis* (Minter 2007). *Thysanophora penicillioides* is regarded as a synonym of *T. glauco-albida*, because following the ICBN, the latter epithet has priority (Morelet 1968, Minter 2007). No type material was present in the CBS culture collection of *T. striatispora*, *T. asymmetrica*, *T. verrucosa*, *T. glaucoalbida* and *T. taiwanensis*. Only the species descriptions were studied and the species delimitation of Mercado-Sierra (1998) is largely followed. With exception of *T. taxi*, which was originally described as *Penicillium taxi* (Schneider 1956), all accepted species of *Thysanophora* are transferred here to *Penicillium* and new combinations are proposed below.

Torulomyces

The genus *Torulomyces* was erected for two species (*T. lagena* and *T. viscosus*) which form dry connected chains in a basipetal manner (Delitsch 1943). Stolk & Samson (1983) transferred *Torulomyces lagena*, the type species, to *Penicillium*. This transfer was based on morphological similarities, such as the phialide shape and cultural appearances (Fig. 6). Later, Pitt & Samson (1993) did not accept this transfer to *Penicillium*, and *Torulomyces* was re-instated. Our phylogenetic data support Stolk & Samson's (1983) proposal to transfer *Torulomyces* to *Penicillium* and other species described in *Torulomyces* need to be combined with *Penicillium*.

Currently, eight species are described in *Torulomyces*: *T. brunneus*, *T. indicus*, *T. laevis*, *T. lagena*, *T. macrosporus*, *T. ovatus*, *T. parviverrucosus* and *T. viscosus*. Isolate CBS 185.65 was designated as the neotype of *P. lagena*, and *Eupenicillium limoneum* was considered to be the teleomorph of this species (Stolk & Samson 1983). Unfortunately, the ex-type culture of *E. limoneum* (CBS 650.82^T) maintained in the CBS collection is dead. Stolk & Samson (1983) are followed here and *E. limoneum* is kept in synonymy with *P. lagena*. Delitsch's species *Torulomyces viscosus* remains doubtful since no type material is available and the diagnosis lacks critical details (Stolk & Samson 1983, Ando *et al.* 1998). No ex-type material of *Torulomyces macrosporus* could be obtained; based on its protologue (Matsushima 1987), *T. macrosporum* may belong to *Monocillium* (Ando *et al.* 1998). *Torulomyces laevis*, *T. ovatus* and *T. parviverrucosus* were described by Ando *et al.* (1998) and in the same publication *Monocillium humicola* var. *brunneum* was combined with *T. brunneus*. The type strain of *T. brunneus* CBS 382.64^T is closely related to *Torulomyces lagena* CBS 185.65^{NT}; these isolates have identical ITS sequences, but differ in their partial β-tubulin, calmodulin and *RPB2* sequences (ITS 100 %; calmodulin 98.3 % and β-tubulin 98.4 % and *RPB2*

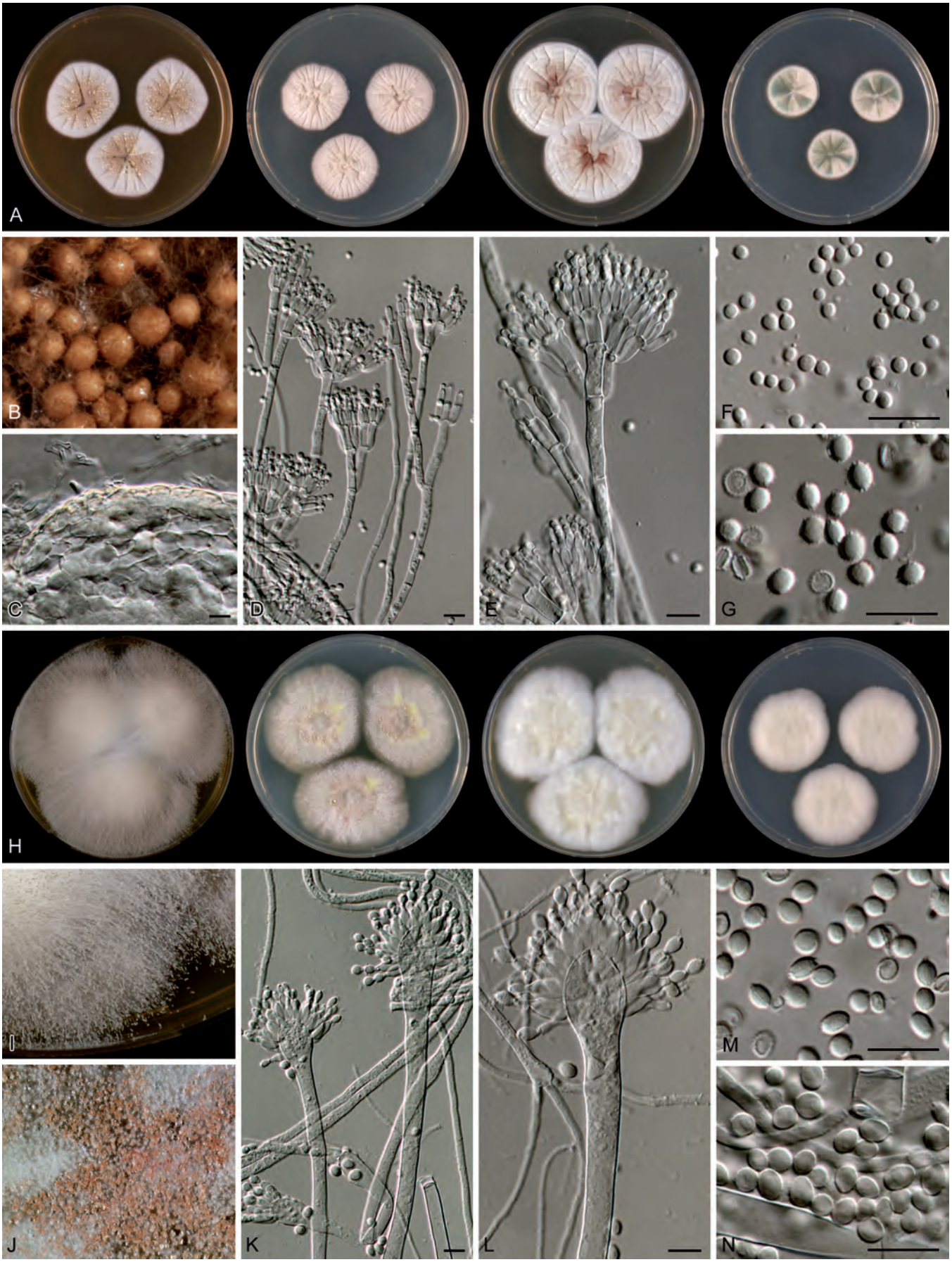

Fig. 5. A–G. *Penicillium kewense* CBS 344.61^{T}. A. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. B–C. Cleistothecia. D-E. Conidiophores. F. Conidia. G. Ascospores. H–N. *Aspergillus paradoxus* (= *P. paradoxum*, R.A. Samson unpubl. results) CBS 130295. H. Colonies grown for 7 d at 25 °C, from left to right: MEA (14 d), CYA, YES, DG18. I. Detail of conidiophores. J. Cleistothecia. K–L. Conidiophores. M. Ascospores. N. Conidia. Scale bar = 10 µm.

98.3 %; unpubl. data). Ando *et al.* (1998) is followed here and this species is kept as separate. No type material of *T. laevis*, *T. ovatus* and *T. parviverrucosus* was available for analysis, but a detailed study of the species descriptions suggests they warrant separate species status. New combinations in *Penicillium* are proposed below. Various isolates with similar morphology to *P. lagena* are

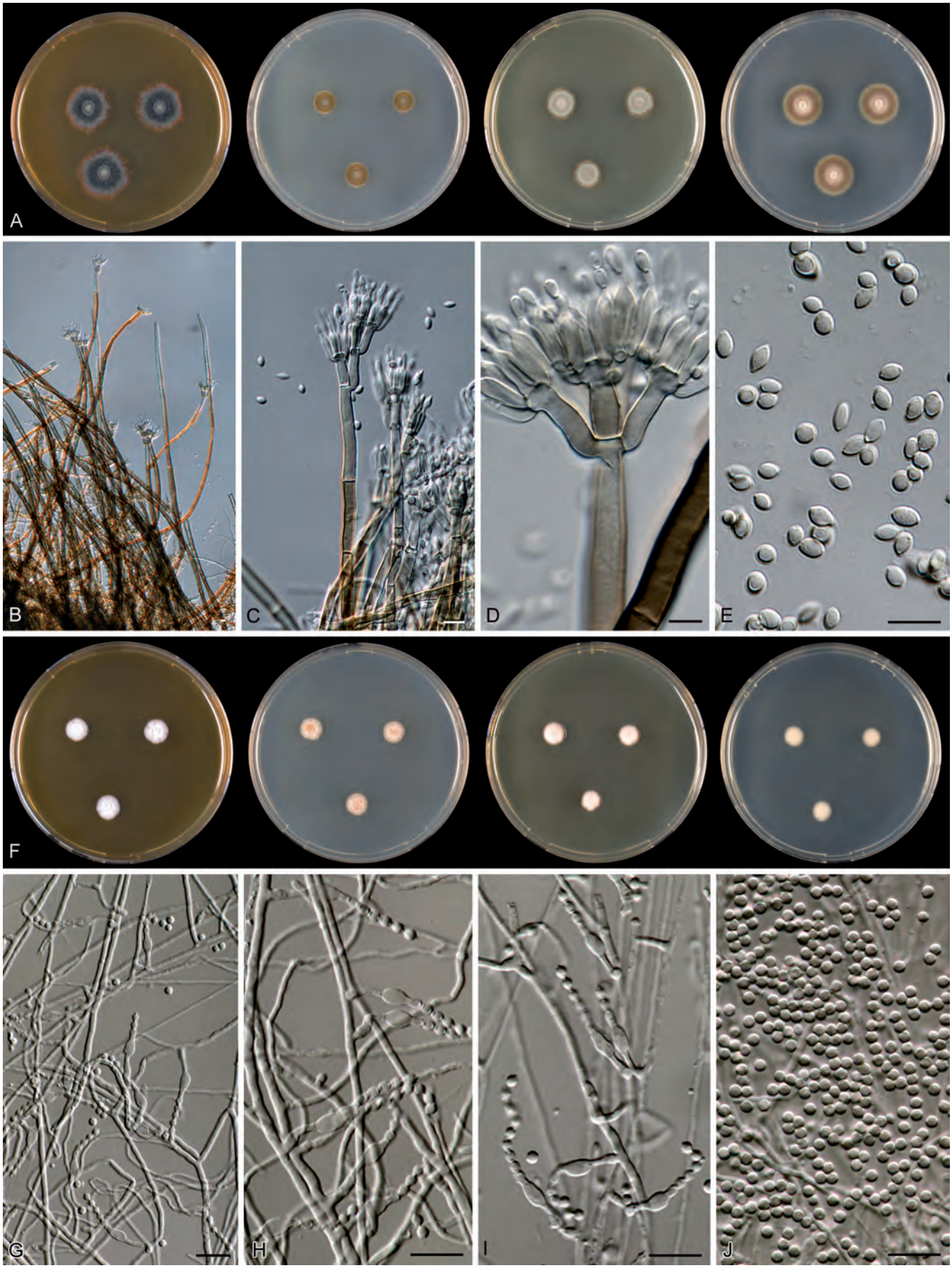

Fig. 6. A–H. *Penicillium glaucoalbidum* CBS 292.60. A. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. B–D. Conidiophores. E. Conidia. F–J. *Penicillium lagena* CBS 337.97. F. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. G–I. Conidiophores. J. Conidia. Scale bar = 10 µm.

maintained in the CBS collections (CBS 185.65, CBS 382.64, CBS 287.66, CBS 337.97, CBS 120415, CBS 110532, DTO 82A8, DTO 92D1), and preliminary sequencing results show a sequence variation among these strains, suggesting the presence of multiple species (unpubl. data). A thorough taxonomic study should be preformed to elucidate the species diversity in this clade.

The genus *Monocillium* needs further attention. This genus was established for a single species, *M. indicum* (Saksena 1955). Based on conidium morphogenesis, Hashmi *et al.* (1972) placed *Monocillium* in synonymy with *Torulomyces*, and later Kendrick & Carmichael (1973) made the combination *Torulomyces indicus*. However, a BLAST search with the ITS sequence of the type strain of *M. indicum* (UAMH 1499, GenBank GQ169328) showed that the closest relatives are among *Hypocreaceae* (Sigler *et al.* 2010). This is in agreement with Gams (1971), who showed that *Monocillium* species are anamorphs related to *Niesslia* species.

Part Three: Sectional delimitation within *Penicillium s. str.*

Classification

Dierckx (1901) proposed the first infrageneric classification of *Penicillium* and introduced the subgenera *Aspergilloides*, *Biverticillium* and *Eupenicillium* (Biourge 1923). Biourge (1923) expanded this subdivision and accepted two subgenera, two sections, four series and six subsections. The sections *Bulliardium* (*Asymetrica*) was introduced by Biourge (1923) and in this section *Penicillium* species with branched conidiophores were included. No type species was designated and species with terverticillate conidiophores belong to Biourge´s definition of his section *Bulliardium* (*Asymetrica*). We decided to synonymise this section with section *Penicillium*. The section *Biverticillium* belongs to *Talaromyces s. str.* and is not treated here (Fig. 1). In the classical work of Thom (1930: 155–159), *Penicillium* is divided in four subgenera (although not named as such), and 12 sections and 17 subsections. Raper & Thom (1949) introduced various new sections, subsections and series and Ramírez (1982) largely followed Raper and Thom's classification. Neither provided Latin descriptions for their newly introduced sections (and series), and these names are therefore regarded as *nomen invalidum* are not considered further here. Pitt (1980) divided *Penicillium* into four subgenera, 10 sections and 21 series. Five years later, Stolk & Samson (1985) proposed another taxonomic scheme for *Penicillium* anamorphs. In the latter taxonomic scheme, both sexual and asexual species were treated. More recently, Samson & Frisvad (2004) revised subgenus *Penicillium* and five sections and 17 series were recognised. An overview of sections and their type species of the studies of Thom (1930), Pitt (1980), Stolk & Samson (1985) and Frisvad & Samson (2004) is shown in Table 5.

The classification of *Eupenicillium* does not have such a long history: Pitt (1980) was the first, and introduced eight series. In the monograph of Stolk & Samson (1983), four sections were introduced for the grouping of the *Eupenicillium* species and Pitt's infrageneric concept of classifying species in series was abandoned.

Accepted species and their position in the sections of Penicillium

The phylogenetic relationship among *Penicillium s. str.* was studied using combined sequence data of four loci. Based on these results (Fig. 7), *Penicillium* is subdivided into two subgenera and 25 sections. An overview of these sections is presented in Table 5, together with the type species of each section. In our study, a new sectional subdivision is proposed and older names at different ranks (*e.g.* subgeneric, subsection and series names) and invalid names (Raper & Thom 1949, Ramírez 1982) are not considered. Assignment of the species to the various sections was mainly based on the overviews presented in Figs 8 and 10–13 and other published molecular-based data. The accepted *Penicillium* and *Eupenicillium* species mentioned in the list of "accepted species and their synonyms in *Trichocomaceae*" (Pitt *et al*. 2000) were used as a starting point for dividing the species among the various sections, updated species described after 2000. In various cases, the same *Penicillium* and *Eupenicillium* species share the same ex-type specimen. However, if the type material of the *Penicillium* morph differs from the *Eupenicillium* morph, then both ex-type strains were included in the study and additional comments are given in the text.

Clade 1: section *Aspergilloides*

= *Eupenicillium* sect. *Pinetorum* (Pitt) Stolk & Samson, Stud. Mycol. 23: 88. 1983.

In: *Penicillium* subgenus *Aspergilloides*.

Type: *Penicillium aurantiobrunneum* Dierckx

Most members of this section grow quickly on agar media, form velvety colonies and are predominantly monoverticillate. This section corresponds to group 2 of Peterson (2000a). Two teleomorph species are positioned in this section: *P. fuscum* and *P. saturniforme*. Stolk (1968) found ascospores in an old culture of the type strain of *P. pinetorum* and described the ascosporic state as *Eupenicillium pinetorum*. Later, the anamorph of *E. pinetorum* was linked to *P. fuscum* (Stolk & Samson 1983); the latter name is older than *P. pinetorum* and therefore used here. The taxonomic position of *P. lapidosum* warrants further attention. Peterson (2000a) suggested that this species is conspecific with *P. thomii*. However, our results show that the type strain of this species (CBS 343.48^{T}) is phylogenetically related to *P. namyslowskii* (Fig. 7, clade 10) and therefore unrelated to section *Aspergilloides*. Based on the data presented in Fig. 8 and literature (Peterson 2000a, Peterson & Horn 2009, Wang & Zhuang 2009, Barreto *et al.* 2011), we place the following species in section *Aspergilloides*:

Penicillium ardesiacum Novobranova, Novosti Sist. Nizs. Rast. 11: 228. 1974.
Penicillium asperosporum Smith, Trans. Br. Mycol. Soc. 48: 275. 1965.
Penicillium crocicola Yamamoto, Scient. Rep. Hyogo Univ. Agric., Agric. Biol. Ser. 2, 2: 28. 1956.
Penicillium fuscum (Sopp) Biourge, Cellule 33: 103. 1923 (Stolk & Samson 1983).
Penicillium georgiense Peterson & Horn, Mycologia 101: 79. 2009.
Penicillium glabrum (Wehmer) Westling, Ark. Bot. 11: 131. 1911 (syn. *P. terlikowskii*; Barreto *et al*. 2011).
Penicillium kananaskense Seifert, Frisvad & McLean, Can. J. Bot. 72: 20. 1994 (unpubl. data, K.A. Seifert).
Penicillium lapatayae Ramírez, Mycopathol. 91: 96. 1985 (Frisvad *et al*. 1990c).
Penicillium lividum Westling, Ark. Bot. 11: 134. 1911.
Penicillium montanense Christensen & Backus, Mycologia 54: 574. 1963.
Penicillium odoratum Christensen & Backus, Mycologia 53: 459. 1962 (this study, Fig. 8).
Penicillium palmense Ramírez & Martínez, Mycopathol. 66: 80. 1978.
Penicillium patens Pitt & Hocking, Mycotaxon 22: 197. 1985.
Penicillium quercetorum Baghdadi, Nov. Sist. Niz. Rast. 5: 110. 1968.

Table 5. Overview of sectional classification in different studies of *Penicillium*

Thom (1930)		Pitt (1980)		Stolk & Samson (1985)		Current study	
Section	**Type species**	**Section**	**Type species**	**Section**	**Type species**	**Section**	**Type species**
Ascogena	*P. luteum*	*Aspergilloides*	*P. aurantiobrunneum*	*Aspergilloides*	*P. glabrum*	*Aspergilloides*	*P. aurantiobrunneum*
Brevi-compacta	*P. brevicompactum*	*Coremigenum*	*P. duclauxii*	*Biverticillium*	*P. minioluteum*	*Brevicompacta**	*P. olsonii*
Coremigena	*P. duclauxii*	*Coronatum*	*P. olsonii*	*Coremigenum*	*P. duclauxii*	*Canescentia*	*P. canescens*
Fasciculata	Fasiculate Penicillia e.g. *P. hirsutum*	*Cylindrosporum*	*P. italicum*	*Divaricatum*	*P. janthinellum*	*Charlesii*	*P. charlesii*
Funiculosa	Undefined; similar to *Lanata-divaricata*	*Divaricatum*	*P. janthinellum*	*Eladia*	*P. sacculum*	*Chrysogena**	*P. chrysogenum*
Lanata-divaricata	*P. janthinellum*-type	*Exilicaulis*	*P. restrictum*	*Geosmithia*	*P. lavendulum*	*Cinnamopurpurea*	*P. cinnamopurpureum*
Lanata-typica	*P. camemberti*	*Furcatum*	*P. oxalicum*	*Inordinate*	*P. arenicola*	*Citrina*	*P. citrinum*
Luteo-virida	*P. minioluteum*	*Inordinate*	*P. arenicola*	*Penicillium*	*P. expansum*	*Digitata**	*P. digitatum*
Miscellanea	Miscellaneous species and genera	*Penicillium*	*P. expansum*	*Ramosum*	*P. lanosum*	*Eladia*	*P. sacculum*
(Monoverticillata)-*stricta*	Undefined section	*Simplicium*	*P. minioluteum*	*Torulomyces*	*P. lagena*	*Exilicaulis*	*P. restrictum*
(Monoverticillata)-*Ramigena*	*Citromyces* species					*Fasciculata**	*P. viridicatum*
Velutina	Undefined section					*Fracta*	*P. fractum*
						Gracilenta	*P. gracilentum*
						Lanata-divaricata	*P. janthinellum*
						Ochrosalmonea	*P. ochrosalmoneum*
						Paradoxa	*A. paradoxus*
						*Penicillium**	*P. expansum*
						Ramigena	*P. cyaneum*
						Ramosa	*P. lanosum*
						*Roquefortorum**	*P. roqueforti*
						Sclerotiora	*P. sclerotiorum*
						Stolkia	*P. stolkiae*
						Thysanophora	*S. glauco-albidum*
						Torulomyces	*P. lagena*
						Turbata	*P. turbatum*

* Frisvad & Samson (2004) divided subgenus *Penicillium* in six sections. This sectional classification is supported by extrolite, phenotypic and physiological data and their subdivision is followed here. The results of our analysis based on partial *RPB2* data (Fig. 13) do not confirm these sections; however, partial β-tubulin data largely confirmed their polyphasic classification (Samson *et al*. 2004).

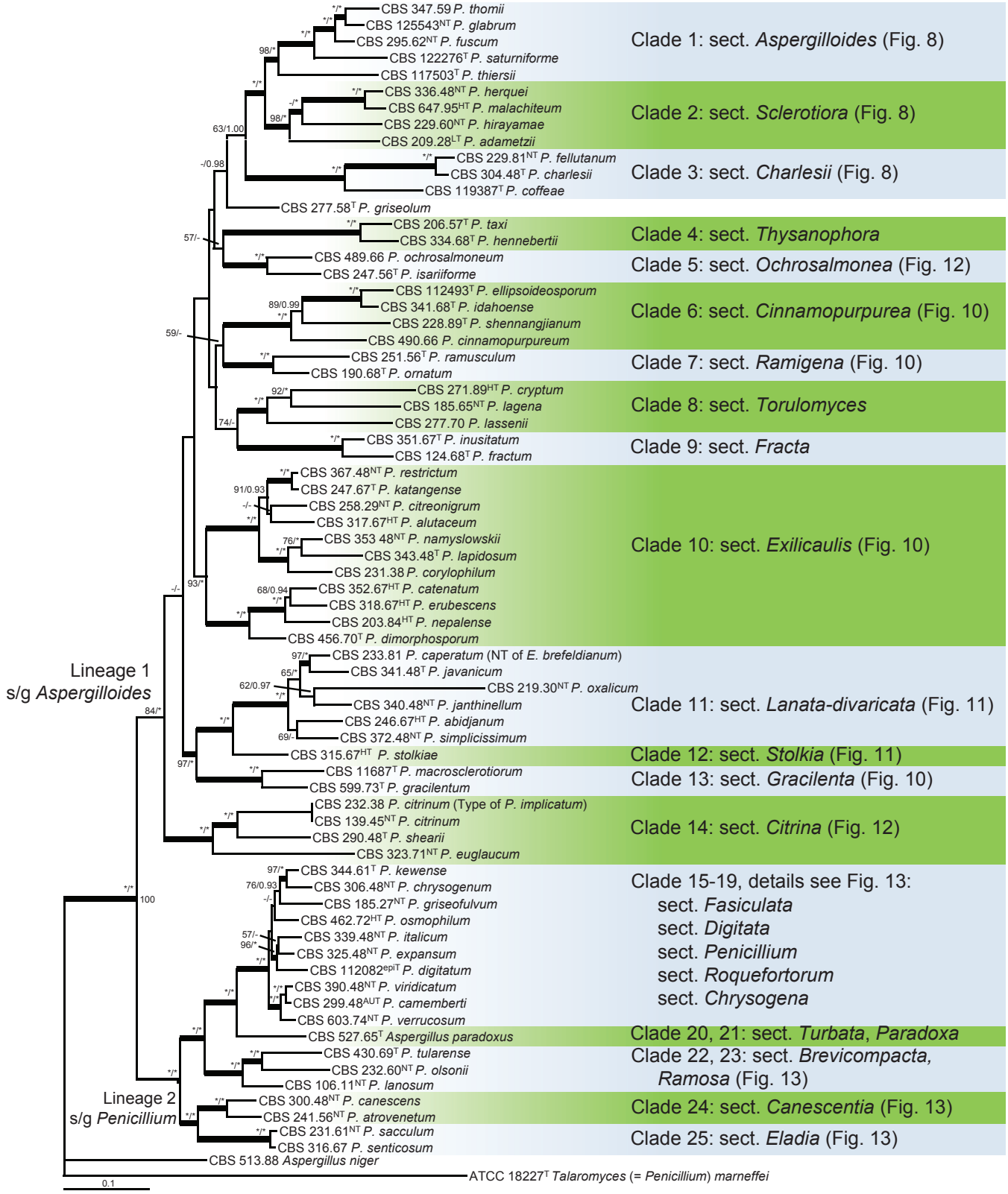

Fig. 7. Best-scoring Maximum Likelihood tree using RAxML based on combined data set of partial *Cct8*, *Tsr1, RPB1 and RPB2* sequences showing the relationship among members of *Penicillium s. str. Penicillium s. str.* is divided in two lineages (s/g *Aspergilloides* and *Penicillium*) and 25 sections. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (bs/pp). Values less than 70 % supported in the ML or less than 0.95 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate good support (100 % bs or 1.00 pp). The branches with more than 95 % bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Penicillium* (= *Talaromyces*) *marneffei* ATCC 18227T.

Penicillium saturniforme (Wang & Zhuang) Houbraken & Samson, Stud. Mycol. 70: 48. 2011 (this study).

Penicillium spinulosum Thom, Bull. Bur. Anim. Ind. U.S. Dep. Agric. 118: 76. 1910.

Penicillium subericola Barreto, Frisvad & Samson, Fungal Diversity 49: 32. 2011.

Penicillium thiersii Peterson, Bayer & Wicklow, Mycologia 96: 1283. 2004.

Penicillium thomii Maire, Bull. Soc. Hist. Nat. Afrique N. 8: 189. 1917.

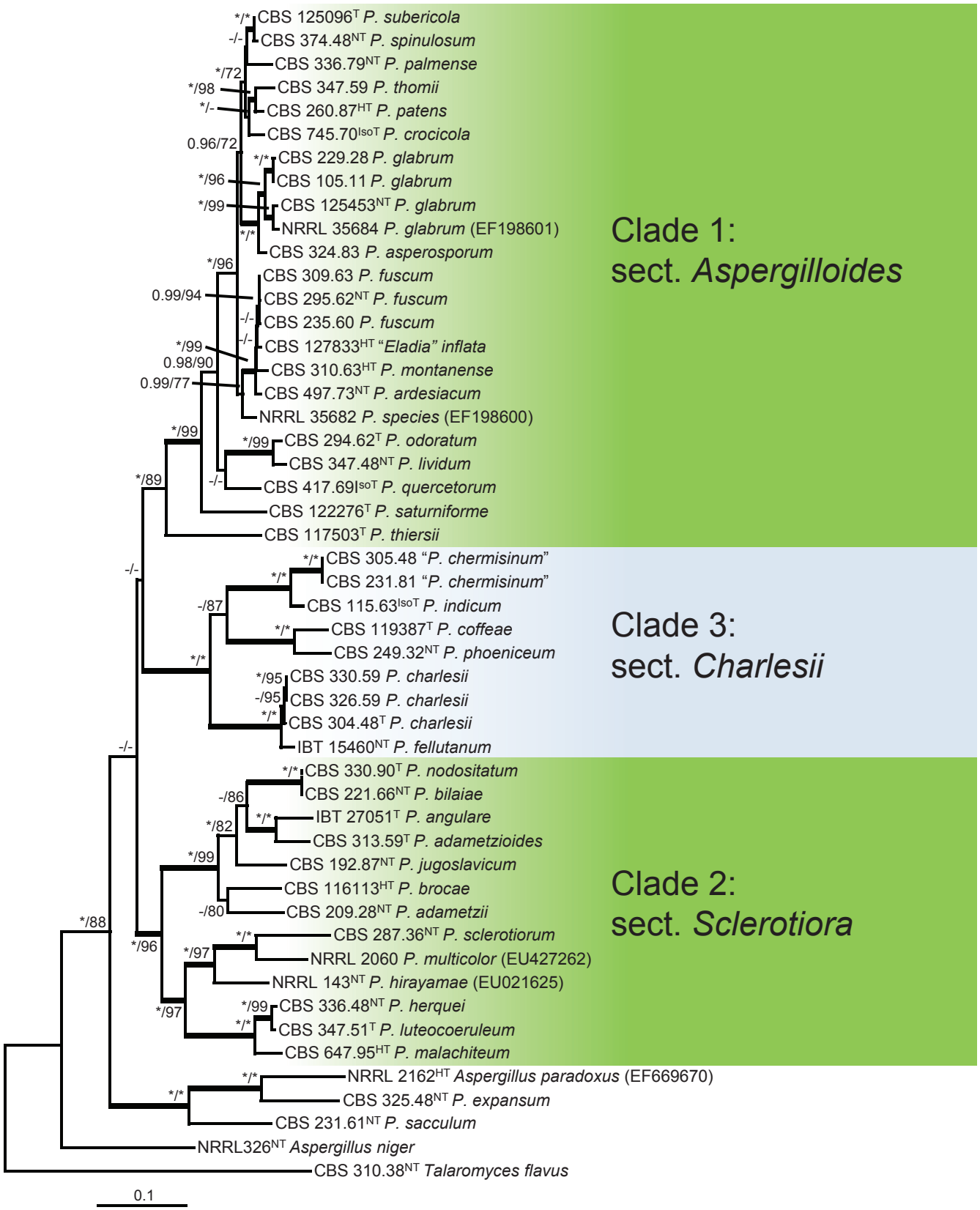

Fig. 8. Best-scoring Maximum Likelihood tree using RAxML based on partial *RPB2* sequences and giving an overview of the members accommodated in sections *Aspergilloides*, *Sclerotiora* and *Charlesii*. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (pp/bs). Values less than 70 % supported in the ML or less than 0.95 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate good support (100 % bs or 1.00 pp). The branches with more than 95 % bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Talaromyces flavus* CBS 310.38NT.

Clade 2: section *Sclerotiora* Houbraken & Samson, sect. nov. MycoBank MB563124.

Sectio in Penicillio subgen. Aspergilloide. Mycelio saepe colorato, plus minusve flavido et/vel aurantiaco. Sclerotis/cleistotheciis claris. colore.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium sclerotiorum* van Beyma

Members of section *Sclerotiora* generally have monoverticillate conidiophores; however, exceptions are *P. malachiteum*, *P. nodositatum* and *P. herquei*, which form symmetrically biverticillate conidiophores. The mycelium of members of sect. *Sclerotiora* is pigmented in shades of yellow and/or orange, reverse colony colours in shades of yellow, orange or red, and sclerotia and cleistothecia are, if present, bright coloured. Species belonging to this section occur regularly in and are abundant upon substrata exposed to soil. This section corresponds with group 3 of Peterson (2000a). Our list of species belonging to this section was composed based on the data presented in Fig. 8 and studies by Peterson (2000a), Peterson *et al.* (2003, 2004), Peterson & Horn (2009), Nonaka *et al*. (2011) and Rivera & Seifert (2011). Isolate NRRL 2060 is included in Fig. 8 and Peterson & Horn (2009) treated this strain as the type of *P. multicolor*. However, Raper & Thom's (1949) isolates of *P. multicolor* differ in significant features from the original description of Grigorieva-Manoilova & Poradielova (1915) (Pitt 1980), and Rivera & Seifert (2011) treated this species as a synonym of *P. fellutanum*. *Penicillium nodositatum* shares identical partial *RPB2* sequences with *P. bilaiae* and might be conspecific with the latter species. More research is needed because the former species produces biverticillate conidiophores and the latter strictly monoverticillate structures (Pitt 1980, Valla *et al.* 1989).

Penicillium adametzii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 507. 1927.
Penicillium adametzioides Abe ex Smith, Trans. Br. Mycol. Soc. 46: 335. 1963.
Penicillium angulare Peterson, Bayer & Wicklow, Mycologia 96: 1289. 2004.
Penicillium bilaiae Chalabuda, Bot. Mater. Otd. Sporov. Rast. 6: 165. 1950.
Penicillium brocae Peterson, Pérez, Vega & Infante, Mycologia 95: 143. 2003.
Penicillium cainii Rivera & Seifert, Stud. Mycol. 70: 147. 2011.
Penicillium guanacastense Rivera, Urb & Seifert, Mycotaxon, *in press*. 2011.
Penicillium herquei Bainier & Sartory, Bull. Soc. Mycol. France 28: 121. 1912.
Penicillium hirayamae Udagawa, J. Agric. Sci. Tokyo Nogyo Daigaku 5: 6. 1959.
Penicillium jacksonii Rivera & Seifert, Stud. Mycol. 70: 151. 2011.
Penicillium johnkrugii Rivera & Seifert, Stud. Mycol. 70: 151. 2011.
Penicillium jugoslavicum Ramírez & Muntañola-Cvetkovic, Mycopathol. 88: 65. 1984.
Penicillium malachiteum (Yaguchi & Udagawa) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).
Penicillium mallochii Rivera, Urb & Seifert Mycotaxon, *in press*. 2011.
Penicillium nodositatum Valla, Plant and Soil 114: 146. 1989.
Penicillium sclerotiorum van Beyma, Zentralbl. Bakteriol., 2. Abt., 96: 418. 1937.
Penicillium viticola Nonaka & Masuma, Mycoscience 52: 339. 2011.

Clade 3: section *Charlesia* Houbraken & Samson, sect. nov. MycoBank MB563125.

Sectio in Penicillio subgen. Aspergilloide. Solum in CYA, conidiophoris ad apicem inflatis.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium charlesii* Smith

The phylogeny of this section was studied by Peterson *et al*. (2005). In the same study, an overview was presented of phenotypic characters to differentiate species within section *Charlesii*. It was stated that the overall phenotypic similarity of these species is striking; however, no shared characters were given. With exception of *P. indicum*, all members of section *Charlesii* grow restricted on CYA and have conidiophores with an apical swelling. Species of this section can be strictly monoverticillate, but *P. charlesii* and *P. fellutanum* can also be irregularly biverticillate. Included species are based on the data presented in Fig. 8 and Peterson (2000a) and Peterson *et al*. (2005).

Penicillium charlesii Smith, Trans. Br. Mycol. Soc. 18: 90. 1933.
Penicillium coffeae Peterson, Vega, Posada & Nagai, Mycologia 97: 662. 2005.
Penicillium fellutanum Biourge, Cellule 33: 262. 1923.
Penicillium georgiense Peterson & Horn, Mycologia 101: 79. 2009.
Penicillium indicum Sandhu & Sandhu, Can. J. Bot. 41: 1273. 1963 (syn. *P. gerundense*, Peterson & Horn 2009).
Penicillium phoeniceum van Beyma, Zentralbl. Bakteriol., 2. Abt., 88: 136. 1933.

Clade 4: section *Thysanophora* Houbraken & Samson, sect. nov. MycoBank MB563126.

Sectio in Penicillio subgen. Aspergilloide. Coloniis pullis, conidiophoris pigmentatis, compactis et incremento secundario stipitis per proliferationem penicillii apicali.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Sclerotium glauco-albidum* Desmazières

The genus *Thysanophora* is placed in synonymy with *Penicillium* (see above). The section is characterised by the formation dark coloured colonies, pigmented and stout conidiophores and the majority of species have secondary growth of the stipe by means of the proliferation of an apical penicillius. Nine specific epithets have been combined with *Thysanophora*, and eight are accepted species. Mercado-Sierra *et al.* (1998) is largely followed here and the following species belong in section *Thysanophora*:

Penicillium asymmetricum (Subramanian & Sudha) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).
Penicillium coniferophilum Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).
Penicillium glaucoalbidum (Desmazières) Houbraken & Samson, Stud. Mycol.70: 47. 2011 (this study).
Penicillium hennebertii Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).
Penicillium longisporum (Kendrick) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).
Penicillium melanostipe Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).
Penicillium taiwanense (Matsushima) Houbraken & Samson, Stud. Mycol. 70: 48. 2011 (this study).
Penicillium taxi Schneider, Zentralblatt für Bakteriologie und Parasitenkunde, Abteilung 2, 110: 43. 1956.

Clade 5: section *Ochrosalmonea* Houbraken & Samson, sect. nov. MycoBank MB563127.

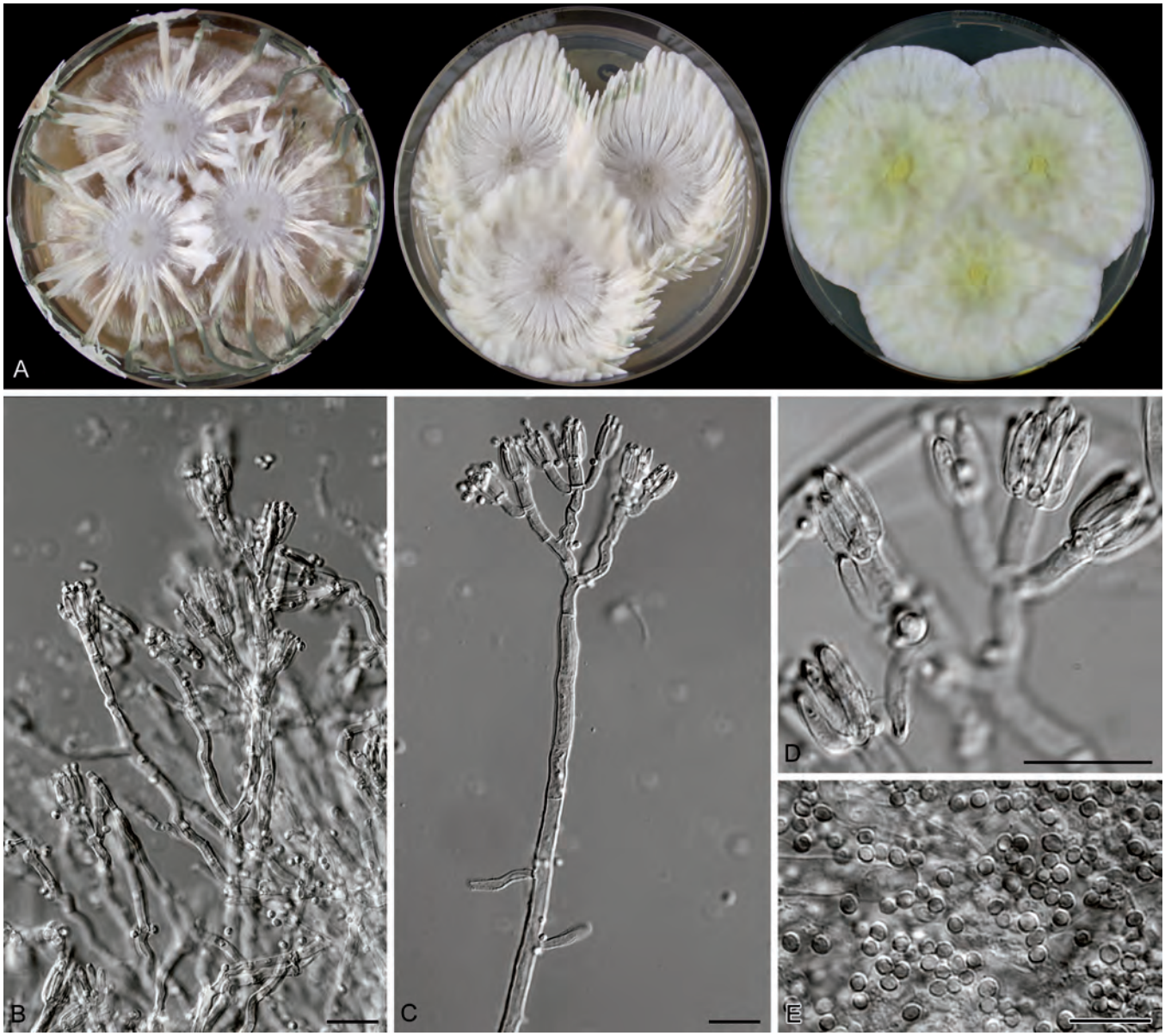

Fig. 9. *Penicillium isariiforme* CBS 247.56. A. Colonies grown for 14 d at 25 °C, from left to right: MEA, YES, CYA. B–D. Conidiophores. E. Conidia. Scale bar = 10 µm.

Sectio in Penicillio subgen. Aspergilloide. Mycelio conspicue pigmentoso, flavido; phialidibus ampulliformibus vel acerosis; conidiis apiculatis.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium ochrosalmoneum* Udagawa

Penicillium ochrosalmoneum and *P. isariiforme* are accommodated in section *Ochrosalmonea* (Fig. 5, clade 5). Both species seem macroscopically dissimilar. *Penicillium isariiforme* grows quickly on agar media MEA and CYA (Pitt 1980) and forms characteristic feather-like synnemata (Samson *et al*. 1976, Fig. 9). In contrast, *P. ochrosalmoneum* isolates grow slowly on agar media and forms a velutinous colony surface (Pitt 1980). However, both species form conspicuous yellow coloured mycelium, ampulliform to acerose shaped phialides and apiculate conidia. The classification of *P. isariiforme* in *Penicillium* was subject of various studies. This species was classified in subgenus *Biverticillium* (= *Talaromyces s. str*.) (Pitt 1980, Frisvad & Filtenborg 1983), but also in subgenus *Penicillium* (= *Penicillium s. str*.) (Ramírez 1982, Samson *et al*. 1976). Figure 7 shows that *P. isariiforme* phylogenetically belongs to subgenus *Aspergilloides* in *Penicillium s. str*.

The holotype of *Eup. ochrosalmoneum* is CBS 489.66 and CBS 231.60 is the ex-type of *P. ochrosalmoneum*. The strains share identical partial *RPB2* sequences and therefore *E. ochrosalmoneum* is regarded as conspecific with *P. ochrosalmoneum* (Fig. 12). Based on the data presented in Fig. 12, the following species belong in section *Ochrosalmonea*.

Penicillium isariiforme Stolk & Meyer, Trans. Br. Mycol. Soc. 40: 187. 1957.

Penicillium ochrosalmoneum Udagawa, J. Agric. Sci. Tokyo Nogyo Daigaku 5: 10. 1959.

Clade 6: section *Cinnamopurpurea* Houbraken & Samson, sect. nov. MycoBank MB563128.

Sectio in Penicillio subgen. Aspergilloide. Sect. Ornatis similis, sed conidiophoris semper simplicibus vel biverticillate divaricates; stipitibus cum conidiophoris distincte vesiculosis.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium cinnamopurpureum* Udagawa

Members of section *Cinnamopurpurea* grow slowly on MEA and CYA and can be strictly monoverticillate, but species with biverticillate conidiophores are also present in this section. The majority of the species have distinct vesicular conidiophores. This section is phenotypically related to section *Ornata*; however, statistical support for this relationship is lacking in our phylogenetic analysis (Fig. 7).

Penicillium cinnamopurpureum was originally described by Abe (1956) without a Latin diagnosis, and validated by Udagawa (1959). Stolk & Samson (1983) considered *P. dierckxii* the anamorph of *Eupenicillium cinnamopurpureum* and Pitt (1980) linked *P. phoeniceum* to *E. cinnamopurpureum*. Our data show that *P. phoeniceum* (sect. *Charlesii*, Fig. 8) and *P. dierckxii* (sect. *Ramigena*, Fig. 10) are phylogenetically distinct from *P. cinnamopurpureum*. Furthermore, partial *RPB2* data show that the type strains of *P. cinnamopurpureum* (CBS 847.68) and *E. cinnamopurpureum* (CBS 490.66) are similar (Fig. 10).

Penicillium chermesinum is also placed in this section. This species was neotypified with NRRL 2048 (= CBS 231.81), because the type culture, NRRL 735, no longer adequately represented Biourge's protologue (Pitt 1980). Molecular analysis shows that these two species are phylogenetically unrelated. The ITS-partial 28S rDNA sequences of NRRL 735^{T} (= GenBank no. AF033413) is related to *P. cinnamopurpureum* (Peterson 2000a) while the neotype of this species, NRRL 2048^{NT}, (AY742693) is related to *P. indicum* in section *Charlesii*. Based on the data presented in Fig. 10 and Peterson & Horn (2009), the following species are accommodated in *Cinnamopurpurea.*

Penicillium chermesinum Biourge, Cellule 33: 284. 1923.
Penicillium cinnamopurpureum Udagawa, J. Agric. Food Sci., Tokyo 5: 1. 1959.
Penicillium ellipsoideosporum Wang & Kong, Mycosystema 19: 463. 2000.
Penicillium idahoense Paden, Mycopath. Mycol. Appl. 43: 261. 1971 (Peterson & Horn 2009, this study).
Penicillium incoloratum Huang & Qi, Acta Mycol. Sin. 13: 264. 1994.
Penicillium malacaense Ramírez & Martínez, Mycopathologia 72: 186. 1980 (syn. *P. ovetense*, this study) (Peterson & Horn 2009).
Penicillium nodulum Kong & Qi, Mycosystema 1: 108. 1988.
Penicillium parvulum Peterson & Horn, Mycologia 101: 75. 2009.
Penicillium shennangjianum Kong & Qi, Mycosystema 1: 110. 1988.

Clade 7: section *Ramigena* Thom, The Penicillia: 225. 1930.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium cyaneum* (Bainier & Sartory) Biourge

This section is based on Thom's section *Ramigena*. Thom (1930) introduced this section for species where monoverticillate conidiophores are evident, but divaricate branching at various levels without a definiteness of organisation or arrangement is consistently observed. Most species illustrated by Banier & Sartory (1913) as species of *Citromyces* are accommodated in this section (*fide* Thom 1930). Members of the section *Ramigena* share the following characters: a slow growth rate on agar media, a monoverticillate branching system with non-vesiculate stipes. Conidia are relatively large (3–4 µm), smooth and ellipsoidal or pyriform (Pitt 1980). *Penicillium ornatum* is the sole member known in this section with a teleomorph (Udagawa 1968, Pitt 1980). The ascospores of this species are ornamented with two and sometimes four longitudinal flanges. The ex-type culture of *P. implicatum* in the CBS collection (CBS 232.38) is a *Penicillium citrinum*, and therefore this species is not accepted as distinct (Frisvad *et al*. 1990b, Houbraken *et al*. 2010b). Pitt (1980) neotypified *P. implicatum* with CBS 184.81 and Fig. 10 shows that this strain is closely related to the type of *Penicillium hispanicum* CBS 691.77. This neotypification is not accepted here and *P. implicatum sensu* Pitt is considered as a synonym of *P. hispanicum*. Pitt *et al*. (2000) accepted *P. dierckxii*, *P. cyaneum* and *P. sublateritium* as single species in their overview of accepted species in *Penicillium*. This concept is followed here; however, partial *RPB2* data (Fig. 10) shows that these three species are very closely related and might represent one species.

Penicillium capsulatum Raper & Fennell, Mycologia 40: 528. 1948.
Penicillium cyaneum (Bainier & Sartory) Biourge, Cellule 33: 102. 1923.
Penicillium dierckxii Biourge, Cellule 33: 313. 1923.
Penicillium hispanicum Ramírez, Martínez & Ferrer, Mycopathol. 66: 77. 1978 (syn. *Penicillium implicatum sensu* Pitt).
Penicillium ornatum Udagawa, Trans. Mycol. Soc. Japan 9: 49. 1968.
Penicillium ramusculum Batista & Maia, Anais Soc. Biol. Pernamb. 13: 27. 1955 (syn. *P. brevissimum* Rai & Wadhwani) (this study, Peterson & Horn 2009).
Penicillium sublateritium Biourge, Cellule 33: 315. 1923.

Clade 8: section *Torulomyces* (Delitsch) Stolk & Samson, Adv. Pen. Asp. Syst.: 169. 1985.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium lagena* (Delitsch) Stolk & Samson

The genus *Torulomyces* is synonymised with *Penicillium* and consequently the majority of the species described in *Torulomyces* are transferred to *Penicillium* (this study). Figure 7 shows that *P. lagena* is related to *P. cryptum* and *P. lassenii*. These species have a slow growth rate on the agar media CYA and MEA and form short-stiped monoverticillate or terminal biverticillate conidiophores. Phialides are predominantly singly formed in *P. lagena*, short, 4–7 µm long, with a narrowed base and a swollen middle that tapers abruptly into a narrow neck (Fig. 6).

Penicillium cryptum Gochenaur, Mycotaxon 26: 349. 1986.
Penicillium lagena (Delitsch) Stolk & Samson, Stud. Mycol. 23: 100. 1983.
Penicillium laeve (K. Ando & Manoch) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).
Penicillium lassenii Paden, Mycopathol. Mycol. Appl. 43: 266. 1971.
Penicillium ovatum (K. Ando & Nawawi) Houbraken & Samson, Stud. Mycol. 70: 48. 2011 (this study).
Penicillium parviverrucosum (K. Ando & Pitt) Houbraken & Samson, Stud. Mycol. 70: 48. 2011 (this study).
Penicillium porphyreum Houbraken & Samson, Stud. Mycol. 70: 48. 2011 (this study).

Clade 9: section *Fracta* Houbraken & Samson, sect. nov. MycoBank MB563129.

Sectio in Penicillio subgen. Aspergilloide. Coloniis in agaro tarde crescentibus; ascosporis spinulosis; phialidibus ampullifomibus vel lanceolatis; conidiis ellipsoideis.

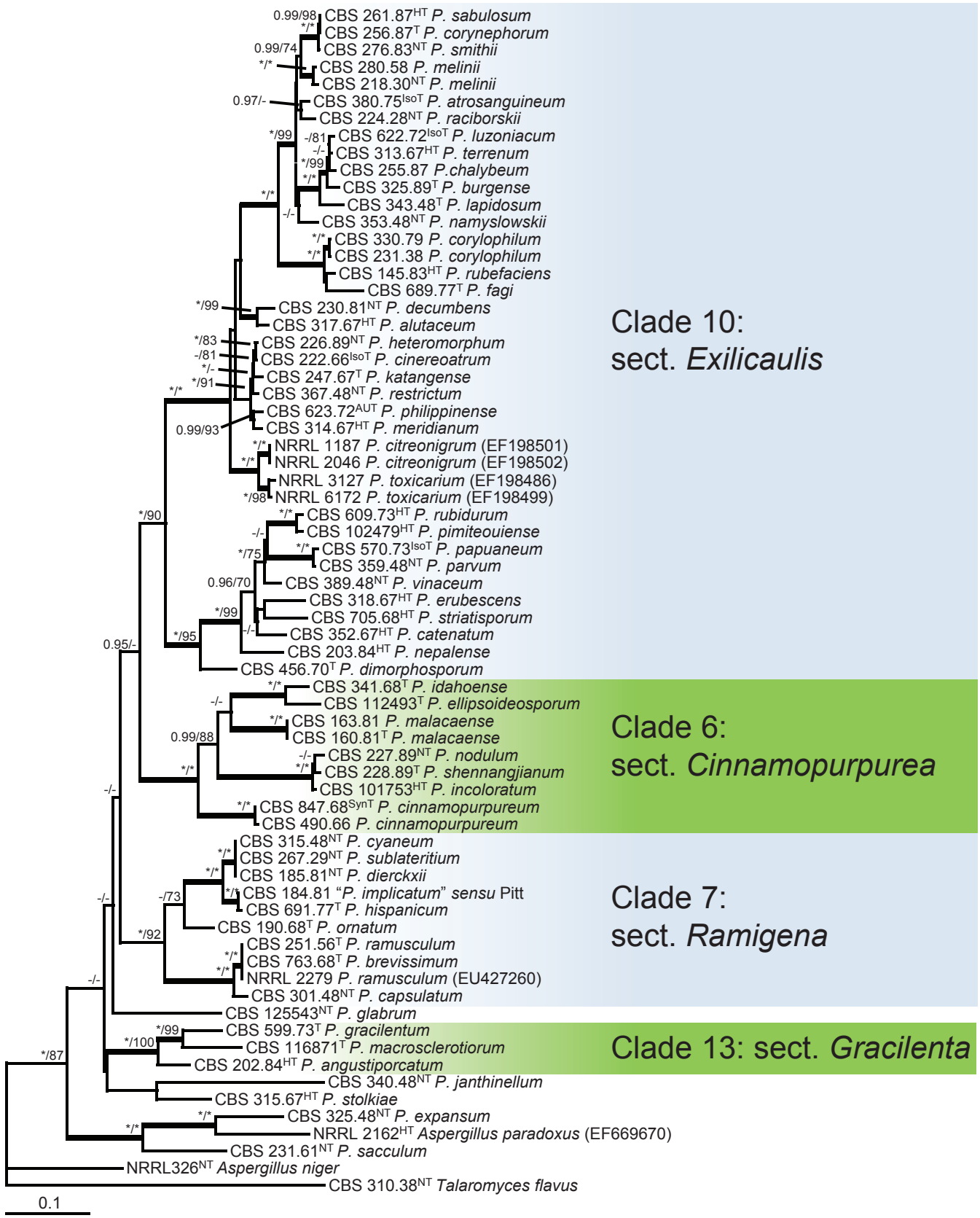

Fig. 10. Best-scoring Maximum Likelihood tree using RAxML based on partial *RPB2* sequences and giving an overview of the members accommodated in sections *Exilicaulis*, *Cinnamopurpurea*, *Ramigena* and *Gracilenta*. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (pp/bs). Values less than 70 % supported in the ML or less than 0.95 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate good support (100 % bs or 1.00 pp). The branches with more than 95 % bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Talaromyces flavus* CBS 310.38NT.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium ornatum* Udagawa

Penicillium inusitatum and *P. fractum* belong to section *Fracta* and both are able to form a teleomorph. Pitt (1980) noted that these two species are closely related, differing principally in conidiophore structure. Both species share unusual ascospore morphology for

Penicillium species: the ascospores are spheroidal without flanges or furrows and ornamented by spines. Furthermore, both species grow slowly on agar media, form ampulliform to lanceolate phialides and ellipsoidal conidia. Phylogenetically, section *Fracta* might be related to section *Torulomyces* (72 % bs, < 0.95 pp). However, ascospores produced by the members of the latter section have two ridges (*P. lagena*, *P. lassenii*, *P. cryptum*).

Penicillium fractum Udagawa, Trans. Mycol. Soc. Japan 9: 51. 1968.
Penicillium inusitatum Scott, Mycopathol. Mycol. Appl. 36: 20. 1968.

Clade 10: section *Exilicaulis* Pitt, The Genus *Penicillium*: 205. 1980.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium restrictum* Gilman & Abbott
= *Eupenicillium* section *Lapidosa* (Pitt) Stolk & Samson, Stud. Mycol. 23: 55. 1983.

Pitt (1980) defined section *Exilicaulis* for monoverticillate species with stipes lacking a terminal vesicular swelling. The phylogenetic delimitation is broader and also several species with an additional branch are included (*e.g. P. raciborski*, *P. melinii*, *P. velutinum*, *P. corylophilum*). This section largely corresponds with group 4 of Peterson (2000a); the only difference is that Peterson placed *P. turbatum* in this clade, while our data shows that this species belongs to section *Turbata* (group 6 *fide* Peterson (2000a)). Based on Fig. 10 and data of Peterson *et al*. and Peterson 2000a, the following species are included in section *Exilicaulis*:

Penicillium alutaceum Scott, Mycopathol. Mycol. Appl. 36: 17. 1968.
Penicillium atrosanguineum Dong, Ceská Mycol. 27: 174. 1973.
Penicillium burgense Quintanilla, Avances Nutr. Mejora Anim. Aliment. 30: 176. 1990.
Penicillium catenatum Scott, Mycopathol. Mycol. Appl. 36: 24. 1968.
Penicillium chalybeum Pitt & Hocking, Mycotaxon 22: 204. 1985.
Penicillium cinerascens Biourge, Cellule 33: 308. 1923.
Penicillium cinereoatrum Chalabuda, Bot. Mater. Otd. Sporov. Rast. 6: 167, 1950 (Frisvad *et al*. 1990c).
Penicillium citreonigrum Dierckx, Ann. Soc. Sci. Bruxelles 25: 86. 1901.
Penicillium corylophilum Dierckx, Ann. Soc. Sci. Bruxelles 25: 86. 1901.
Penicillium decumbens Thom, Bull. Bur. Anim. Ind. U.S. Dep. Agric. 118: 71. 1910.
Penicillium dimorphosporum Swart, Trans. Br. Mycol. Soc. 55: 310. 1970.
Penicillium dravuni Janso, Mycologia 97: 445. 2005.
Penicillium erubescens Scott, Mycopathol. Mycol. Appl. 36: 14. 1968.
Penicillium fagi Ramírez & Martínez, Mycopathol. 63: 57. 1978.
Penicillium flavidostipitatum Ramírez & González, Mycopathol. 88: 3. 1984 (preliminary sequencing results show that this species is closely related to *P. namyslowskii*).
Penicillium guttulosum Gilman & Abbott, Iowa State Coll. J. Sci. 1: 298. 1927 (Peterson *et al*. 2011).
Penicillium heteromorphum Kong & Qi, Mycosystema 1: 107. 1988.
Penicillium katangense Stolk, Ant. van Leeuwenhoek 34: 42. 1968.
Penicillium lapidosum Raper & Fennell, Mycologia 40: 524. 1948.
Penicillium maclennaniae Yip, Trans. Br. Mycol. Soc. 77: 202. 1981.
Penicillium melinii Thom, Penicillia: 273. 1930.
Penicillium menonorum Peterson, IMA Fungus 2: 122. 2011.
Penicillium meridianum Scott, Mycopathol. Mycol. Appl. 36: 12. 1968.
Penicillium namyslowskii Zaleski, Bull. Int. Aead. Polonc. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 479. 1927.
Penicillium nepalense Takada & Udagawa, Trans. Mycol. Soc. Japan 24: 146. 1983.
Penicillium parvum Raper & Fennell, Mycologia 40: 508. 1948 (this study).
Penicillium philippinense Udagawa & Y. Horie, J. Jap. Bot. 47: 341. 1972.
Penicillium pimiteouiense Peterson, Mycologia 91: 271. 1999.
Penicillium raciborskii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 454. 1927.
Penicillium restrictum Gilman & Abbott, Iowa State Coll. J. Sci. 1: 297. 1927.
Penicillium rubefaciens Quintanilla, Mycopathol. 80: 73. 1982.
Penicillium rubidurum Udagawa & Horie, Trans. Mycol. Soc. Japan 14: 381. 1973.
Penicillium smithii Quintanilla, Avances Nutr. Mejora Anim. Aliment. 23: 340. 1982 (syn. *P. corynephorum*, *P. sabulosum*).
Penicillium striatisporum Stolk, Ant. van Leeuwenhoek 35: 268. 1969.
Penicillium terrenum Scott, Mycopathol. Mycol. Appl. 36: 1. 1968.
Penicillium toxicarium Miyake, Rep. Res. Inst. Rice Improvement 1: 1. 1940 (*nom. inval*., Art. 36) (Serra *et al*. 2008).
Penicillium velutinum van Beyma, Zentralbl. Bakteriol., 2. Abt., 91: 353. 1935.
Penicillium vinaceum Gilman & Abbott, Iowa State Coll. J. Sci. 1: 299. 1927.

Clade 11: Section *Lanata-divaricata* Thom, The Penicillia: 328. 1930.

= section *Funiculosa* Thom, The Penicillia: 358. 1930.
= section *Divaricatum* Pitt, The Genus *Penicillium*: 238. 1980.
= section *Furcatum* Pitt, The Genus *Penicillium*: 272. 1980.
= *Eupenicillium* section *Javanica* (Pitt) Stolk & Samson, Stud. Mycol. 23: 55. 1983.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium janthinellum* Biourge

Most of the species, but not all, of section *Lanata-divaricata* grow rapidly and form broadly spreading colonies. The majority of the species belonging to this section are strongly divaricate and the metulae are born terminally, subterminally and in intercalary positions, and in the latter case intergrading with monoverticillate conidiophores. Furthermore, the terminal cluster often consists of a prolongation of the main axis. Species belonging to section *Lanata-divaricata* are mainly soil inhabitants, but may also occur on leaf litter and vegetable remains in the later stage of decomposition (Raper & Thom 1949, Houbraken *et al*. 2011c). Many species of this section are unusually tolerant for heavy metals and some species have been proposed as efficient biosorbent agents in the bioleaching of zinc oxide, copper, lead and nickel (Burgstaller *et al*. 1992, Valix *et al*. 2001, Li *et al*. 2008).

Section *Funiculosa* is placed in synonymy with this section. Thom (1930) already noted that species belonging section

Funiculosa have affinity with members of section *Lanata-typica* and that separation is hard to define. This observation is supported by our data: many species mentioned in Thom's section *Funiculosa* belong to section *Lanata-divaricata*. Raper & Thom's (1949) subsection *Divaricata* largely corresponds with our section *Lanata-divaricata*. They noted that members of their subsection have a definite relationship to *Penicillium javanicum.* Stolk & Samson (1983) also discussed this relationship and they placed 26 species in synonymy with *Eupenicillium javanicum* and *P. simplicissimum*. Recently, a phylogenetic study showed that many of these synonyms should be treated as separate species (Peterson 2000a, Houbraken *et al*. 2011c). This section largely corresponds with Peterson's (2000a) group 5 and the list provided here for this section is mainly based on this data supplemented with data of Houbraken *et al*. (2011c). *Penicillium cluniae*, *P. griseopurpureum* and *P. glaucoroseum* were not included in these studies, though unpublished data shows that these three species also belong to this section.

The typification of *P. brefeldianum*, *P. javanicum*, *P. levitum* and *P. ehrlichii* warrants further attention. Dodge (1933) described *P. brefeldianum* as a holomorphic species. Pitt (1980) did not accept teleomorph species in *Penicillium* and a neotype (CBS 233.81 = FRR 71 = IMI 216895) was selected because the original type culture of *P. brefeldianum* distributed by Dodge no longer produced cleistothecia. Subsequently, Dodge's strain (CBS 235.81 = FRR 710 = IMI 216896 = NRRL 710) was used for the description of the anamorph of *Eupenicillium brefeldianum* (as *Penicillium dodgei*). Teleomorphs are allowed in *Penicillium* and therefore Dodge's *P. brefeldianum* is re-instated. Furthermore, Fig. 11 shows that Dodge's type strain (CBS 235.81) differs from Pitt's neotype (CBS 233.81) and this neotype is similar to the type of *P. caperatum* (CBS 443.75^{T}). *Penicillium levitum*, *P. javanicum* and *P. ehrlichii* were described including a teleomorph. Pitt (1980) introduced the new species names *P. rasile*, *P. indonesiae* and *P. klebahnii* respectively, for the anamorphs of *P. levitum, P. javanicum* and *P. ehrlichii*. These names are not used here for the same the reason as mentioned under *P. brefeldianum*.

Penicillium abidjanum Stolk, Ant. van Leeuwenhoek 34: 49. 1968.
Penicillium araracuarense Houbraken, C. López-Q, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 61: 1469. 2011.
Penicillium brasilianum Batista, Anais Soc. Biol. Pernambuco 15: 162. 1957.
Penicillium brefeldianum Dodge, Mycologia 25: 92. 1933 (syn. *P. dodgei*).
Penicillium caperatum Udagawa & Horie, Trans. Mycol. Soc. Japan 14: 371. 1973 (syn. *E. brefeldianum sensu* Pitt).
Penicillium cluniae Quintanilla, Avances Nutr. Mejora Anim. Aliment. 30: 174. 1990. (unpubl. data)
Penicillium coeruleum Sopp *apud* Biourge, Cellule 33: 102. 1923.
Penicillium cremeogriseum Chalabuda, Bot. Mater. Otd. Sporov. Rast. 6: 168. 1950.
Penicillium daleae Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 495. 1927.
Penicillium ehrlichii Klebahn, Ber. Deutsch. Bot. Ges. 48: 374. 1930.
Penicillium elleniae Houbraken, C. López-Q, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 61: 1470. 2011.
Penicillium glaucoroseum Demelius, Verh. Zool.-Bot. Ges. Wien 72: 72. 1923. (unpubl. data)
Penicillium griseopurpureum Smith, Trans. Br. Mycol. Soc. 48: 275. 1965 (unpubl. data).
Penicillium janthinellum Biourge, Cellule 33: 258. 1923.
Penicillium javanicum van Beyma, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect., 26: 17. 1929 (syn. *P. oligosporum*, *P. indonesiae*).
Penicillium levitum Raper & Fennell, Mycologia 40: 511. 1948 (syn. *P. rasile*).
Penicillium limosum Ueda, Mycoscience 36: 451. 1995.
Penicillium lineolatum Udagawa & Horie, Mycotaxon 5: 493. 1977.
Penicillium ludwigii Udagawa, Trans. Mycol. Soc. Japan 10: 2. 1969.
Penicillium mariaecrucis Quintanilla, Avances Nutr. Mejora Anim. Aliment. 23: 334. 1982.
Penicillium meloforme Udagawa & Horie, Trans. Mycol. Soc. Japan 14: 376. 1973.
Penicillium ochrochloron Biourge, Cellule 33: 269. 1923.
Penicillium onobense Ramírez & Martínez, Mycopathol. 74: 44. 1981.
Penicillium oxalicum Currie & Thom, J. Biol. Chem. 22: 289. 1915.
Penicillium paraherquei Abe ex Smith, Trans. Br. Mycol. Soc. 46: 335. 1963.
Penicillium penarojense Houbraken, C. López-Q, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 61: 1471. 2011.
Penicillium piscarium Westling, Ark. Bot. 11: 86. 1911.
Penicillium pulvillorum Turfitt, Trans. Br. Mycol. Soc. 23: 186. 1939 (Syn. *P. ciegleri*).
Penicillium raperi Smith, Trans. Br. Mycol. Soc. 40: 486. 1957.
Penicillium reticulisporum Udagawa, Trans. Mycol. Soc. Japan 9: 52. 1968. (syn. *P. arvense*).
Penicillium rolfsii Thom, Penicillia: 489. 1930.
Penicillium simplicissimum (Oudemans) Thom, Penicillia: 335. 1930.
Penicillium skrjabinii Schmotina & Golovleva, Mikol. Fitopatol. 8: 530. 1974.
Penicillium svalbardense Frisvad, Sonjak & Gunde-Cimerman, Ant. van Leeuwenhoek 92: 48. 2007.
Penicillium vanderhammenii Houbraken, C. López-Q, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 61: 1473. 2011.
Penicillium vasconiae Ramírez & Martínez, Mycopathol. 72: 189. 1980.
Penicillium wotroi Houbraken, C. López-Q, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 61: 1474. 2011.
Penicillium zonatum Hodges & Perry, Mycologia 65: 697. 1973.

Clade 12: section *Stolkia* Houbraken & Samson, sect. nov. MycoBank MB563130.

Sectio in Penicillio subgen. Aspergilloide. Conidiophoris pigmentatis, metulis subapicalibus sympodialiter proliferantibus; phialidibus nullis.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium stolkiae* Scott

Brown conidiophores occur in two phylogenetic unrelated sections of *Penicillium s. str*. One includes species belonging to section *Thysanophora* (previously assigned to the genus *Thysanophora*) (Iwamoto *et al*. 2002, Peterson & Sigler 2002) and the second lineage is centered around *P. stolkiae*, another species with conidiophores that also may be hyaline to definitely brown (Stolk & Samson 1983). Peterson & Sigler (2002) described four species with darkly melanised conidiophores, which are all closely related to *P. stolkiae*, namely *P. subarticum*, *P. canariense*, *P. pullum* and

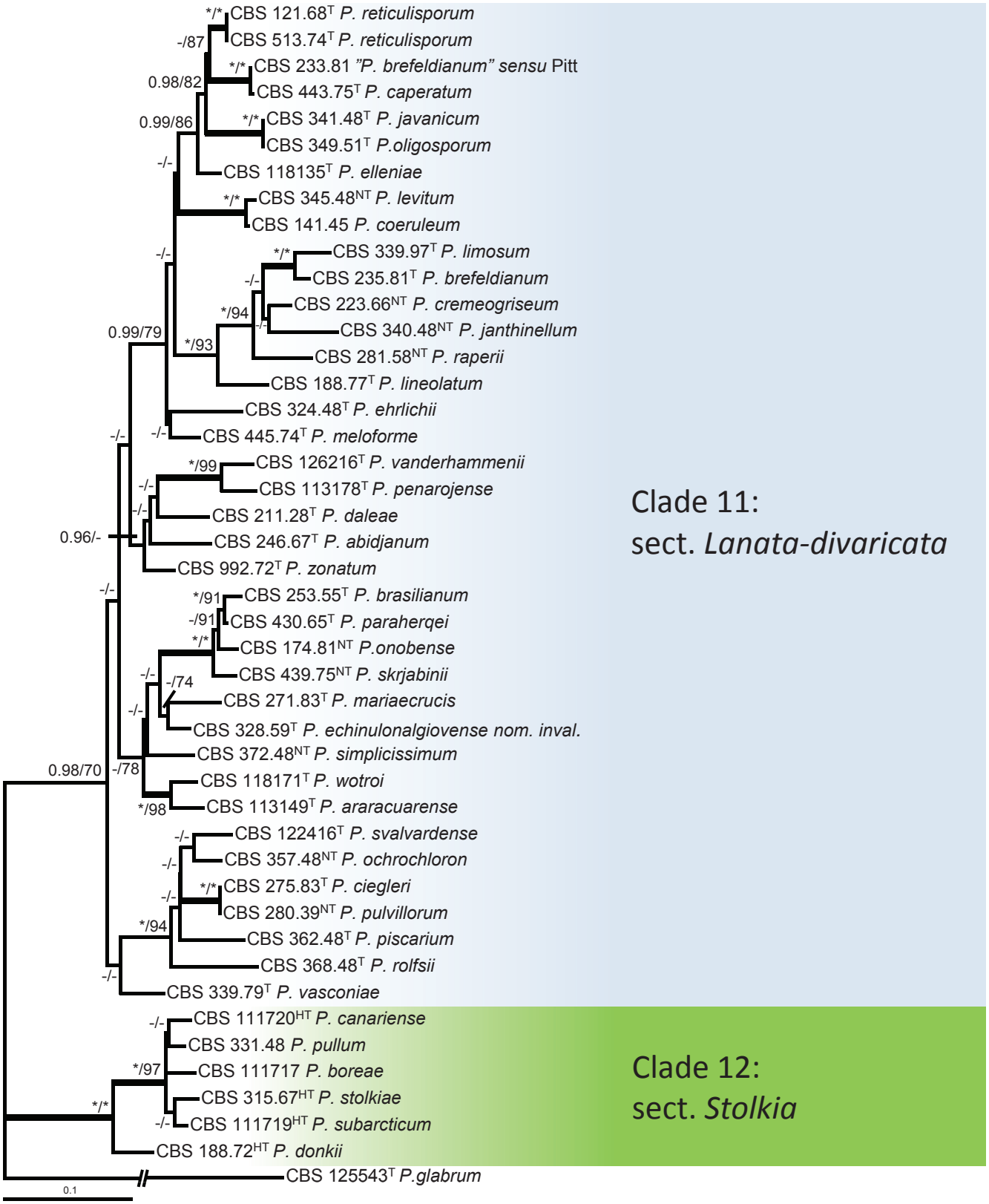

Fig. 11. Best-scoring Maximum Likelihood tree using RAxML based on partial β-tubulin sequences and giving an overview of the members accommodated in sections *Lanata-divaricata* and *Stolkia*. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (pp/bs). Values less than 70 % supported in the ML or less than 0.95 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate good support (100 % bs or 1.00 pp). The branches with more than 95 % bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Penicillium glabrum* CBS 125543T.

P. boreae. None of these species demonstrate the sympodial proliferation of subapical metulae and phialides present in section *Thysanophora*. The following species are placed in section *Stolkia* based on the data presented in Fig. 11 and of Peterson & Sigler (2002).

Penicillium boreae Peterson & Sigler, Mycol. Res. 106: 1112. 2002.
Penicillium canariense Peterson & Sigler, Mycol. Res. 106: 1113. 2002.
Penicillium donkii Stolk, Persoonia 7: 333. 1973.
Penicillium pullum Peterson & Sigler, Mycol. Res. 106: 1115. 2002.

Penicillium stolkiae Scott, Mycopathol. Mycol. Appl. 36: 8. 1968.
Penicillium subarcticum Peterson & Sigler, Mycol. Res. 106: 1116. 2002.

Clade 13: section *Gracilenta* Houbraken & Samson, sect. nov. MycoBank MB563131.

Sectio in Penicillio subgen. Aspergilloide. Coloniis 37 °C haud crescentibus, reverso olivaceo-brunneo vel brunneo, conidiis saepe late ellipsoideis vel ellipsoideis.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium gracilentum* Udagawa & Horie

Four species are placed in section *Gracilenta*. Comparison of the phenotypic characters did not reveal many significant similarities among these species. All species did not grow at 37 °C and have an olive-brown to brown reverse on agar media. With exception of *P. macrosclerotiorum*, all species produced broadly ellipsoidal to ellipsoidal conidia (Abe 1956, Udagawa & Horie 1973, Pitt 1980, Takada & Udagawa 1983, Wang *et al*. 2007). The taxonomy and phylogeny of these species is not well studied and future research might reveal more shared characters.

Penicillium angustiporcatum Takada & Udagawa, Trans. Mycol. Soc. Japan 24: 143. 1983.
Penicillium estinogenum Komatsu & Abe ex Smith, Trans. Br. Mycol. Soc. 46: 335. 1963.
Penicillium macrosclerotiorum Wang, Zhang & Zhuang, Mycol. Res. 111: 1244. 2007.
Penicillium gracilentum Udagawa & Horie, Trans. Mycol. Soc. Japan 14: 373. 1973.

Clade 14: section *Citrina* Houbraken & Samson, sect. nov. MycoBank MB563132.

Sectio in Penicillio subgen. Aspergilloide. Formatione conidiophorum symmetricorum biverticillatorum.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium citrinum* Thom

Species of section *Citrina* are commonly occurring in soil and the majority of the species form symmetrical biverticillate conidiophores. This section corresponds with group 1 of Peterson (2000a). The taxonomy of section *Citrina* is recently revised by Houbraken *et al*. (2010b, 2011b) and based on this data and Fig. 12, the following species are placed in section *Citrina*:

Penicillium anatolicum Stolk, Ant. van Leeuwenhoek 34: 46. 1968.
Penicillium argentinense Houbraken, Frisvad & Samson, Stud. Mycol. 70: 78. 2011.
Penicillium atrofulvum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 80. 2011.
Penicillium aurantiacobrunneum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 80. 2011.
Penicillium cairnsense Houbraken, Frisvad & Samson, Stud. Mycol. 70: 83. 2011.
Penicillium christenseniae Houbraken, Frisvad & Samson, Stud. Mycol. 70: 85. 2011.
Penicillium chrzaszczii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 464. 1927.
Penicillium citrinum Thom, Bull. Bur. Anim. Ind. U.S. Dep. Agric. 118: 61. 1910.
Penicillium copticola Houbraken, Frisvad & Samson, Stud. Mycol. 70: 88. 2011.
Penicillium cosmopolitanum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 91. 2011.
Penicillium decaturense Peterson, Bayer & Wicklow, Mycologia 96: 1290. 2004.
Penicillium euglaucum van Beyma, Ant. van Leeuwenhoek 6: 269. 1940.
Penicillium galliacum Ramírez, Martínez & Berenguer, Mycopathol. 72: 30. 1980.
Penicillium godlewskii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 466. 1927.
Penicillium gorlenkoanum Baghdadi, Nov. Sist. Niz. Rast. 5: 97. 1968.
Penicillium hetheringtonii Houbraken, Frisvad & Samson, Fung. Div. 44: 125. 2010.
Penicillium manginii Duché & Heim, Trav. Cryptog. Louis L. Mangin: 450. 1931 (syn. *P. pedemontanum*, Houbraken *et al*. 2011b).
Penicillium miczynskii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 482. 1927.
Penicillium neomiczynskii Cole, Houbraken, Frisvad & Samson, Stud. Mycol. 70: 105. 2011.
Penicillium nothofagi Houbraken, Frisvad & Samson, Stud. Mycol. 70: 105. 2011.
Penicillium pancosmium Houbraken, Frisvad & Samson, Stud. Mycol. 70: 108. 2011.
Penicillium pasqualense Houbraken, Frisvad & Samson, Stud. Mycol. 70: 108. 2011.
Penicillium paxilli Bainier, Bull. Soc. Mycol. France 23: 95. 1907.
Penicillium quebecense Houbraken, Frisvad & Samson, Stud. Mycol. 70: 111. 2011.
Penicillium raphiae Houbraken, Frisvad & Samson, Stud. Mycol. 70: 114. 2011.
Penicillium roseopurpureum Dierckx, Ann. Soc. Sci. Bruxelles 25: 86. 1901.
Penicillium sanguifluum (Sopp) Biourge, La Cellule 33: 105. 1923.
Penicillium shearii Stolk & Scott, Persoonia 4: 396. 1967.
Penicillium sizovae Baghdadi, Novosti Sist. Nizs. Rast. 1968: 103. 1968.
Penicillium steckii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 469. 1927.
Penicillium sumatrense Szilvinyi, Archiv. Hydrobiol. 14, Suppl. 6: 535. 1936.
Penicillium terrigenum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 125. 2011.
Penicillium tropicoides Houbraken, Frisvad & Samson, Fung. Div. 44: 127. 2010.
Penicillium tropicum Houbraken, Frisvad & Samson, Fung. Div. 44: 129. 2010.
Penicillium ubiquetum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 127. 2011.
Penicillium vancouverense Houbraken, Frisvad & Samson, Stud. Mycol. 70: 131. 2011.
Penicillium waksmanii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 468. 1927.
Penicillium wellingtonense Cole, Houbraken, Frisvad & Samson, Stud. Mycol. 70: 133. 2011.
Penicillium westlingii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 473. 1927.

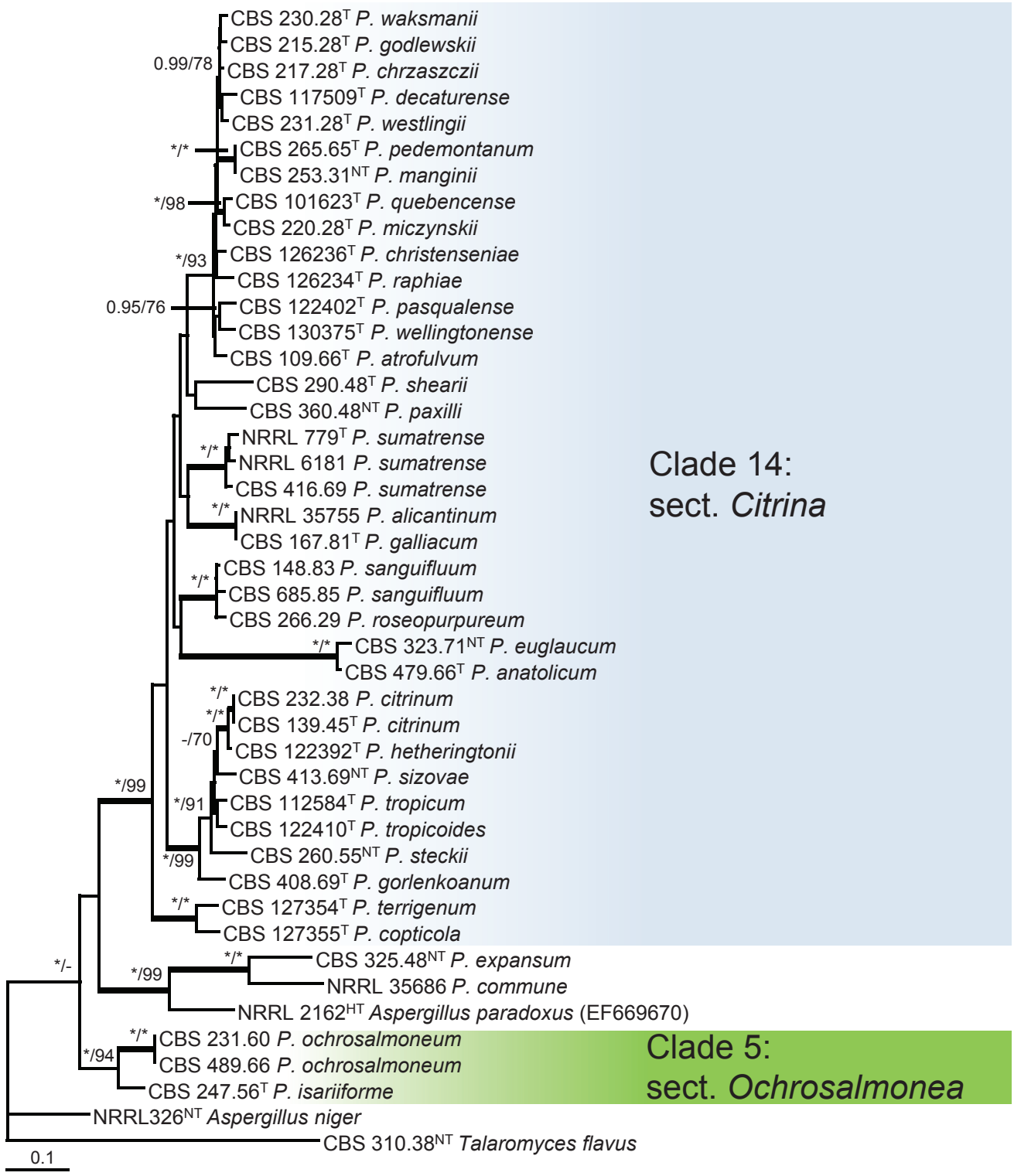

Fig. 12. Best-scoring Maximum Likelihood tree using RAxML based on partial *RPB2* sequences and giving an overview of the members accommodated in sections *Citrina* and *Ochrosalmonea*. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (pp/bs). Values less than 70 % supported in the ML or less than 0.95 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate good support (100 % bs or 1.00 pp). The branches with more than 95 % bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Talaromyces flavus* CBS 310.38^{NT}.

Clade 15: Section *Fasciculata* Thom, The Penicillia: 374. 1930.

= Section *Lanata-typica* Thom, The Penicillia: 305. 1930.
= Section *Viridicata* Frisvad & Samson, Stud. Mycol. 49: 27. 2004.

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium hirsutum* Dierckx

Sections *Lanata-typica* and *Viridicata* are placed in synonymy with section *Fasciculata*. *Lanata-typica* was erected for species with vegetative aerial mycelium consisting of lanose, cottony or floccose colonies and only a small portion of the species currently present this section produce such structures (*P. camemberti, P. commune*, *P. caseifulvum*). Most species of section *Fasciculata* have a granulose or fasciculate colony texture and therefore the name *Fasciculata* is given priority to *Lanata-typica*. The current definition of *Fasciculata*

is similar to that of *Viridicata* (Frisvad & Samson 2004). All species grow rather quickly, except species in series *Verrucosa*, which grow slowly. Most species this section have globose conidia and rough-walled conidiophore stipes. All species are psychrotolerant and grow well at low water activities (Frisvad & Samson 2004). Frisvad & Samson (2004) accommodated 28 species in section *Viridicata* (= *Fasciculata*). We excluded *P. atramentosum* from this section and placed this species in section *Paradoxa*. This species was placed in section *Fasciculata* based on its ability to grow on creatine as sole nitrogen source and its occurrence on cheese. However, Frisvad & Samson (2004) also noted that its ability to grow at very high pH values and the formation of smooth-walled stipes sets it apart from section *Fasciculata*. *Penicillium osmophilum* is tentatively accommodated in section *Viridicata*. Figure 13 shows that this species is most closely related to this section, but bootstrap support is lacking.

Penicillium albocoremium (Frisvad) Frisvad, Int. Mod. Tax. Meth. Pen. Asp. Clas.: 275. 2000.
Penicillium allii Vincent & Pitt, Mycologia 81: 300. 1989.
Penicillium aurantiogriseum Dierckx, Ann. Soc. Scient. Brux. 25: 88. 1901.
Penicillium camemberti Thom, Bull. Bur. Anim. Ind. USDA 82: 33. 1906.
Penicillium caseifulvum Lund, Filt. & Frisvad, J. Food Mycol. 1: 97. 1998.
Penicillium cavernicola Frisvad & Samson, Stud. Mycol. 49: 31. 2004.
Penicillium commune Thom, Bull. Bur. Anim. Ind. USDA 118: 56. 1910.
Penicillium crustosum Thom, Penicillia: 399. 1930.
Penicillium cyclopium Westling, Ark. Bot. 11: 90. 1911.
Penicillium discolor Frisvad & Samson, Ant. Van Leeuwenhoek, 72: 120. 1997.
Penicillium echinulatum Fassatiová, Acta Univ. Carol. Biol. 12: 326. 1977.
Penicillium freii Frisvad & Samson, Stud. Mycol. 49: 28. 2004.
Penicillium hirsutum Dierckx, Ann. Soc. Scient. Brux. 25: 89. 1901.
Penicillium hordei Stolk, Ant. van Leeuwenhoek 35: 270. 1969.
Penicillium melanoconidium (Frisvad) Frisvad & Samson, Stud. Mycol. 49: 28. 2004.
Penicillium neoechinulatum (Frisvad, Filt. & Wicklow) Frisvad & Samson, Stud. Mycol. 49: 28. 2004.
Penicillium nordicum Dragoni & Cantoni ex Ramírez, Adv. Pen. Asp. Syst.: 139. 1985.
Penicillium osmophilum Stolk & Veenbaas-Rijks, Ant. van Leeuwenhoek 40: 1. 1974.
Penicillium palitans Westling, Ark. Bot. 11: 83. 1911.
Penicillium polonicum Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B 1927: 445. 1927.
Penicillium radicicola Overy & Frisvad, Syst. Appl. Microbiol.: 633. 2003.
Penicillium solitum Westling, Ark. Bot. 11: 65. 1911.
Penicillium thymicola Frisvad & Samson, Stud. Mycol. 49: 29. 2004.
Penicillium tricolor Frisvad, Seifert, Samson & Mills, Can. J. Bot. 72: 937. 1994.
Penicillium tulipae Overy & Frisvad, Syst. Appl. Microbiol. 634. 2003.
Penicillium venetum (Frisvad) Frisvad, Int. Mod. Tax. Meth. Pen. Asp. Clas.: 275. 2000.
Penicillium verrucosum Dierckx, Ann. Soc. Scient. Brux. 25: 88. 1901.
Penicillium viridicatum Westling, Ark. Bot. 11: 88. 1911.

Clade 16: Section *Digitata* (as "*Digitatum*") Frisvad & Samson, Stud. Mycol. 49: 26. 2004.

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium digitatum* (Pers.:Fr.) Sacc.

Section *Digitata* is represented by one species, *P. digitatum*. This species is unique in its combination of features. Conidiophore and conidial structures are irregular and exceptionally large for *Penicillium*, usually biverticillate rather than terverticillate and the conidia are olive-green. The conidia are large and ellipsoidal to cylindrical (Frisvad & Samson 2004). Partial β-tubulin (Samson *et al*. 2004) and *RPB2* data (Fig. 13) shows that this section is situated in subgenus *Penicillium*. Frisvad & Samson (2004) is followed here and this section is retained for *P. digitatum*.

Penicillium digitatum (Pers.:Fr.) Sacc., Fung. Ital.: 894. 1881.

Clade 17: Section *Penicillium*

= *Bulliardium* Biourge, La Cellule 33: 107. 1923 (= *Asymetrica*).

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium expansum* Link

Frisvad & Samson (2004) are followed here in their delimitation of section *Penicillium*. The recently described species *P. brevistipitatum* is added to this list, because it is closely related to *P. coprophilum* (Fig. 13). The analysis of our partial *RPB2* data (Fig. 13) indicate sthat this section is polyphyletic. In contrast, partial β-tubulin data (Samson *et al*. 2004) showed that members of this section are on a single branch with 100 % bootstrap support. Frisvad & Samson (2004) are followed and the following species are accommodated in section *Penicillium*:

Penicillium brevistipitatum Wang & Zhuang, Mycotaxon 93: 234. 2005.
Penicillium clavigerum Demelius, Verh. Zool.-Bot. Ges. Wien 72: 74. 1922.
Penicillium concentricum Samson, Stolk & Hadlok, Stud. Mycol. 11: 17. 1976.
Penicillium coprobium Frisvad, Mycologia 81: 853. 1989.
Penicillium coprophilum (Berk. & Curt.) Seifert & Samson, Adv. Pen. Asp. Syst.: 145. 1985.
Penicillium dipodomyicola (Frisvad, Filt. & Wicklow) Frisvad, Int. Mod. Meth. Pen. Asp. Clas.: 275. 2000.
Penicillium expansum Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 3: 16. 1809.
Penicillium formosanum Hsieh, Su & Tzean, Trans. Mycol. Soc. R.O.C. 2: 159. 1987.
Penicillium gladioli McCulloch & Thom, Science, N.Y. 67: 217. 1928.
Penicillium glandicola (Oud.) Seifert & Samson, Adv. Pen. Asp. Syst.: 147. 1985.
Penicillium griseofulvum Dierckx, Ann. Soc. Scient. Brux. 25: 88. 1901.
Penicillium italicum Wehmer, Hedwigia 33: 211. 1894.
Penicillium marinum Frisvad & Samson, Stud. Mycol. 49: 20. 2004.

Penicillium sclerotigenum Yamamoto, Scient. Rep. Hyogo Univ. Agric., Agric. Biol. Ser. 2, 1: 69. 1955.
Penicillium ulaiense Hsieh, Su & Tzean, Trans. Mycol. Soc. R.O.C. 2: 161. 1987.
Penicillium vulpinum (Cooke & Massee) Seifert & Samson, Adv. Pen. Asp. Syst.: 144. 1985.

Clade 18: section *Roquefortorum* (as "*Roqueforti*") Frisvad & Samson, Stud. Mycol. 49: 16. 2004.

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium roqueforti* Thom

Frisvad & Samson (2004) erected section *Roqueforti* for rapidly growing species forming strictly velutinous colonies. All species form terverticillate rough walled conidiophores and are able to grow at low pH values (*e.g.* on media containing 0.5 % acetic acid), at high alcohol concentrations and at elevated CO_2 levels. Members of this section appear to have a symbiotic relationship with lactic acid bacteria and certain acid-tolerant yeasts. Currently, four species are described in this section (Frisvad & Samson 2004, Houbraken *et al*. 2010a):

Penicillium carneum (Frisvad) Frisvad, Microbiology, UK, 142: 546. 1996.
Penicillium paneum Frisvad, Microbiology (UK) 142: 546. 1996.
Penicillium psychrosexualis Houbraken & Samson, IMA Fungus 1:174. 2010.
Penicillium roqueforti Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 82: 35, 1906.

Clade 19: section *Chrysogena* Frisvad & Samson, Stud. Mycol. 49: 17. 2004.

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium chrysogenum* Thom

Members of the section *Chrysogena* are characterised by the formation of ter- and/or quarterverticillate, smooth walled conidiophores with relatively small phialides. Colonies have a velvety texture and species are tolerant to salt and the majority is capable to produce penicillin (Frisvad & Samson 2004). Four teleomorph species belong to section *Chrysogena*: *P. sinaicum, P. egyptiacum, P. molle* and *P. kewense* (Fig. 13). *Penicillium egyptiacum* was described as a holomorphic species (van Beyma 1933). Pitt (1980) transferred the teleomorphic state to *Eupenicillium* (*E. egyptiacum*) and introduced a new name for the *Penicillium* morph (*P. nilense*). This name is not used here and *P. egyptiacum* is re-instated. There are several taxonomic problems concerning *P. kewense*. Brefeld (1874) was the first who described the formation of a teleomorph in *Penicillium*. He identified the studied species as "*Penicillium crustaceum* Fries, *Penicillium glaucum* Link". It is, however, very questionable whether the strains studied by Brefeld truly represented the species described by Link and Fries (Stolk & Scott 1967). Stolk & Scott (1967) are followed here; they agreed that the fungus described by Smith (1961b) as *Penicillium kewense* resembles Brefeld's fungus. Based on the data of Samson *et al*. (2004), Houbraken *et al.* (2011a) and Fig. 13, the following species are accommodated in section *Chrysogena*.

Penicillium aethiopicum Frisvad, Mycologia 81: 848. 1990.
Penicillium chrysogenum Thom, Bull. Bur. Anim. Ind. U.S. Dep. Agric. 118: 58. 1910.
Penicillium confertum (Frisvad *et al*.) Frisvad, Mycologia 81: 852. 1990.
Penicillium dipodomyis (Frisvad, Filtenborg & Wicklow) Banke, Frisvad & Rosendahl, Int. Mod. Meth. Pen. Asp. Clas., 270. 2000.
Penicillium egyptiacum van Beyma, Zentralbl. Bakteriol., 2. Abt., 88: 137. 1933. (syn. *P. nilense*).
Penicillium flavigenum Frisvad & Samson, Mycol. Res. 101: 620. 1997.
Penicillium kewense Smith, Trans. Br. Mycol. Soc. 44: 42. 1961 (syn. *E. crustaceum*).
Penicillium molle Pitt, The Genus *Penicillium*: 148, 1980 ["1979"].
Penicillium mononematosum (Frisvad *et al*.) Frisvad, Mycologia 81: 857. 1990.
Penicillium nalgiovense Laxa, Zentralbl. Bakteriol., 2. Abt., 86: 160. 1932.
Penicillium persicinum Wang, Zhou, Frisvad & Samson, Ant. van Leeuwenhoek 86: 177. 2004.
Penicillium rubens Biourge, Cellule 33: 265. 1923.
Penicillium sinaicum Udagawa & Ueda, Mycotaxon 14: 266. 1982.

Clade 20: section *Turbata* Houbraken & Samson, sect. nov. MycoBank MB563133.

Sectio in Penicillio subgen. Penicillo. Conidiophoris delicatis et symmetricis, biverticillatis; formatione acoris extroliti penicillici.

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium turbatum* Westling

Section *Turbata* is phylogenetically closely related to section *Paradoxa*, and *P. matriti*, *P. bovifimosum* and *P. turbatum* are accommodated in this section. These species form rather delicate and symmetric biverticillate Penicillium conidiophores. Furthermore, penicillic acid is produced by all these species, and *P. bovifimosum*, *P. turbatum* and selected strains of *P. matriti* produce a fumagillin-like compound (Tuthill & Frisvad 2002).

Penicillium bovifimosum (Tuthill & Frisvad) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).
Penicillium matriti Smith, Trans. Br. Mycol. Soc. 44: 44. 1961.
Penicillium turbatum Westling, Ark. Bot. 11: 128. 1911 (syn. *E. baarnense, P. baarnense*, this study).

Clade 21: section *Paradoxa* Houbraken & Samson, sect. nov. MycoBank MB563134.

Sectio in Penicillio subgen. Penicillo. Speciebus saepe cum conidiophoris typi Aspergillus et odore molesti efferenti.

In: *Penicillium* subgenus *Penicillium*

Type: *Aspergillus paradoxus* Fennell & Raper

Aspergillus paradoxus, *A. malodoratus*, *A. crystallinus* and *P. atramentosum* form a well-supported clade (85 % bs, 1.00 pp). Phylogenetic and extrolite analysis shows that the first three species belong in *Penicillium* and will be transferred to this genus (R.A. Samson, unpubl. data). Besides a similar type of *Aspergillus* anamorph, these three species also produce a strong, unpleasant smell. *Penicillium atramentosum* is phylogenetically basal to these three species. This species is alkaliphilic and unpublished results show that this character is shared with *A. paradoxus*. More research

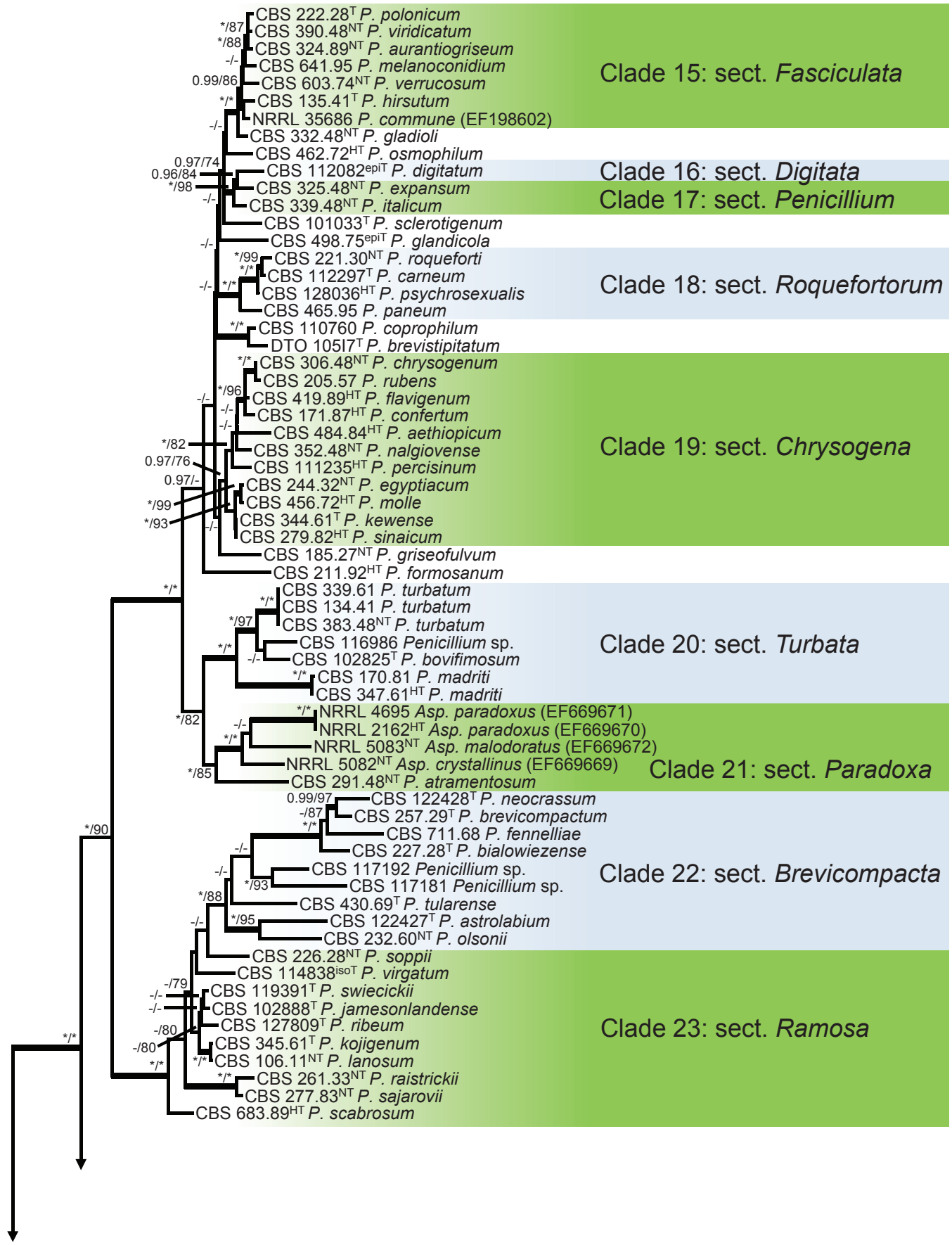

Fig. 13. Best-scoring Maximum Likelihood tree using RAxML based on partial *RPB2* sequences and giving an overview of the members accommodated in subgenus Penicillium (clades 15–25). The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (pp/bs). Values less than 70 % supported in the ML or less than 0.95 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate good support (100 % bs or 1.00 pp). The branches with more than 95 % bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Talaromyces flavus* CBS 310.38NT.

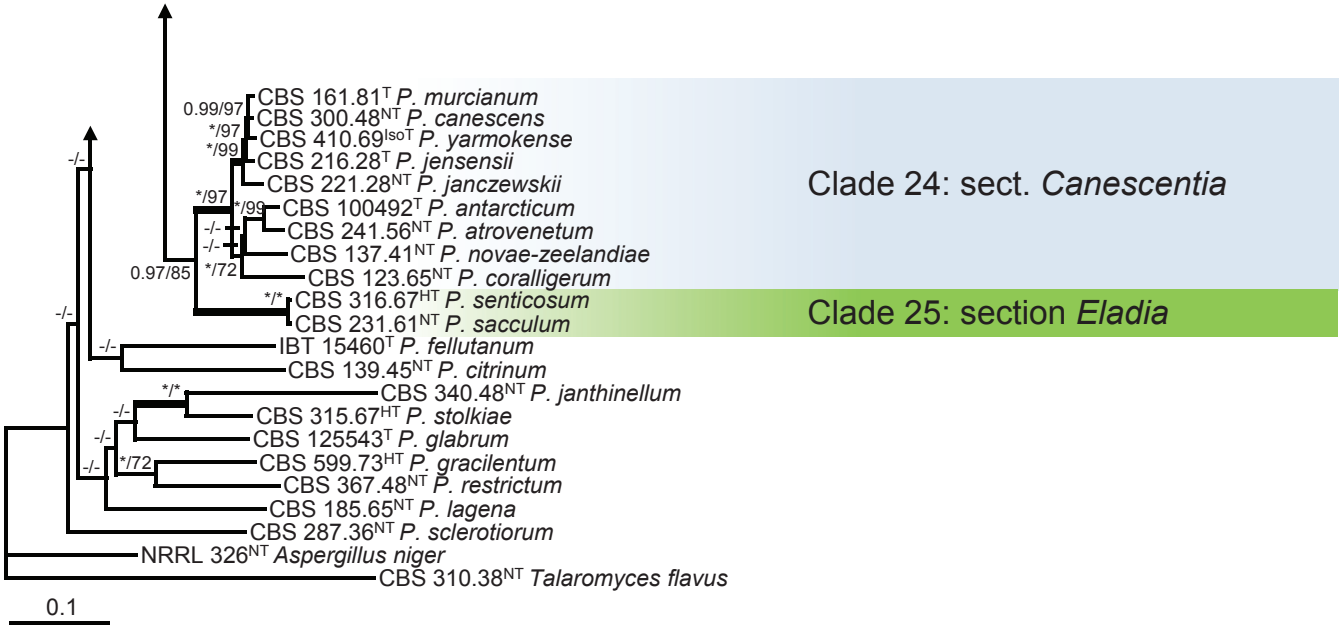

Fig. 13. (Continued).

is needed to determine whether *A. malodoratus* and *A. crystallinus* also share this feature.

Penicillium atramentosum Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 65. 1910.
Aspergillus crystallinus Kwon-Chung & Fennell, The Genus *Aspergillus*: 471. 1965.
Aspergillus malodoratus (Kwon-Chung & Fennell), The Genus *Aspergillus*: 468. 1965.
Aspergillus paradoxus Fennell & Raper, Mycologia 47: 69.

Clade 22: section *Brevicompacta* Thom, The Penicillia: 289. 1930.

= section *Coronata* Pitt, The Genus *Penicillium*: 392, 1980.

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium brevicompactum* Dierckx

Members of the section *Brevicompacta* are characterised by conidiophores with long and broad stipes. The conidial heads look superficially like *Aspergillus* heads in the stereomicroscope. Section *Coronata*, typified with *P. olsonii*, is placed here in synonymy. Recently, *P. neocrassum* and *P. astrolobatum* were described in this section (Serra & Peterson 2007) and partial *RPB2* data (Fig. 13) show that also *P. tularense* and *P. fennelliae* belong here. The production of the extrolites asperphenamate and the unknown metabolite O (Frisvad & Samson 2004) is shared by *P. olsonii*, *P. brevicompactum* and *P. bialowiezense*. More research in needed to determine whether these metabolites are also produced by the other members of section *Brevicompacta*. Based on literature (Frisvad & Samson 2004, Peterson 2004, Serra & Peterson 2007) and partial *RPB2* data (Fig. 13) the following species are accommodated in section *Brevicompacta*:

Penicillium astrolobatum Serra & Peterson, Mycologia 99: 80. 2007.
Penicillium bialowiezense Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B, 1927: 462. 1927 (syn. *P. biourgeianum*).
Penicillium brevicompactum Dierckx, Ann. Soc. Scient. Brux. 25: 88. 1901.
Penicillium fennelliae Stolk, Ant. van Leeuwenhoek 35: 261. 1969.
Penicillium neocrassum Serra & Peterson, Mycologia 99: 81. 2007.
Penicillium olsonii Bainier & Sartory, Ann. Mycol. 10: 398. 1912.
Penicillium tularense Paden, Mycopathol. Mycol. Appl. 43: 264. 1971.

Clade 23: section *Ramosa* (as "*Ramosum*") Stolk & Samson, Adv. Pen. Asp. Syst.: 179. 1985.

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium lanosum* Westling

Figure 13 shows that section *Ramosa* is not well resolved and members of this section are on a well-supported branch with section *Brevicompacta* members (100 % bs, 1.00 pp). We split this clade in two sections based on phenotypic characters and extrolite patterns. Members of the section *Lanosa* form biverticillate or terverticillate conidiophores with divergent rami (twice biverticillate), while members of sect. *Brevicompacta* have appressed branches. *Penicillium jamesonlandense, P. lanosum*, *P. ribeum*, *P. raistrickii*, *P. soppii* and *P. swiecickii* produce different combinations of cycloaspeptide, kojic acid and griseofulvin (Frisvad & Filtenborg 1990, Frisvad *et al*. 2006) and these extrolites are not been found in section *Brevicompacta* (Frisvad & Samson 2004). More research is needed to determine if the other members of this section also produce cycloaspeptide, kojic acid and/or griseofulvin.

Penicillium scabrosum is basal to the members of sections *Brevicompacta* and *Ramosa*. This species is tentatively accommodated in sect. *Ramosa* based on the formation of divaricate branches (Frisvad *et al*. 1990a). In contrast, cyclopenin, cyclopenol, viridicatin, penigequinolone A and B and fumagillin are produced by *P. scabrosum* and these extrolites are not detected in species belonging to sect. *Ramosa* (Frisvad *et al*. 1990a, Larsen *et al*. 1999). In the original description of *P. virgatum*, a relationship with *P. daleae* was suggested (Kwasna & Nirenberg 2005). However, these two species are unrelated and our partial *RPB2* data suggest *P. virgatum* is related to members of section *Ramosa* (Fig. 13). Based on data presented in Fig. 13 and in Frisvad *et al*. (2006), the following species are placed in section *Ramosa*:

Penicillium jamesonlandense Frisvad & Overy, Int. J. Syst. Evol. Microbiol. 56: 1435. 2006.
Penicillium kojigenum Smith, Trans. Br. Mycol. Soc. 44: 43. 1961.
Penicillium lanosum Westling, Ark. Bot. 11: 97. 1911.
Penicillium raistrickii Smith, Trans. Br. Mycol. Soc.18: 90. 1933.
Penicillium ribeum Frisvad & Overy, Int. J. Syst. Evol. Microbiol. 56: 1436. 2006.
Penicillium sajarovii Quintanilla, Avances Nutr. Mejora Anim. Aliment. 22: 539. 1981.
Penicillium scabrosum Frisvad, Samson & Stolk, Persoonia 14: 177. 1990.
Penicillium simile Davolos, Pietrangeli, Persiani & Maggi, J. Syst. Evol. Microbiol., *in press*.
Penicillium soppii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 476. 1927.
Penicillium swiecickii Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B 1927: 474. 1927.
Penicillium virgatum Nirenberg & Kwasna, Mycol. Res. 109: 977. 2005.

Clade 24: section *Canescentia* Houbraken & Samson, sect. nov. MycoBank MB563135.

Sectio in Penicillio subgen. Penicillo. Structuris symmetricis biverticillatis, raro cum ramulis pluribus. Phialidibus simplicibus, brevibus (7–9 µm), cum collo brevi, interdum distincte attenuato.

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium canescens* Sopp

Members of section *Canescentia* are soil-borne and are characterised by the formation of symmetrical biverticillate structures with infrequently an additional branch. Phialides are simple and short (7–9 µm) with a broadly cylindrical to slightly or more definitely swollen base and a short, occasionally more pronounced narrowed neck. This section has not been a subjected to a thorough phylogenetic study and unpublished sequence results show that several synonyms should be raised to species level. Partial *RPB2* data (Fig. 13) shows that following species are placed in section *Canescentia*.

Penicillium canescens Sopp, Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 11: 181. 1912.
Penicillium jensenii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 494. 1927.
Penicillium yarmokense Baghdadi, Nov. Sist. Niz. Rast. 5: 99. 1968.
Penicillium janczewskii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 488. 1927.
Penicillium antarcticum Hocking & McRae, Polar Biology 21: 103. 1999.
Penicillium atrovenetum Smith, Trans. Br. Mycol. Soc. 39: 112. 1956.
Penicillium novae-zeelandiae van Beyma, Ant. van Leeuwenhoek 6: 275. 1940.
Penicillium coralligerum Nicot & Pionnat, Bull. Soc. Mycol. France 78: 245. 1963 ["1962"].

Clade 25: section *Eladia* (Smith) Stolk & Samson, Adv. Pen. Asp. Syst.: 169. 1985.

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium sacculum* Dale

The genus *Eladia* is synonymised with *Penicillium* and two species are placed here in section *Eladia*: *P. sacculum* and *P. senticosum* (Fig. 7, clade 25 and Fig. 13). *Penicillium sacculum* and *P. senticosum* grow rather well on MEA (and poorly on Czapek agar) and their colonies on MEA are velvety and dull-green, brownish-green or olive-brown coloured. Phialides are born irregularly on the stipes, subterminally as well as terminally, short, 4–7 µm, with a swollen base, and at the apex tapering abruptly into a short narrow neck. Conidia are distinctly ornamented (Smith 1961b, Pitt 1980, Stolk & Samson 1983, Stolk & Samson 1985). No type material could be obtained from *Eladia pachyphialis* and *Eladia tibetensis* and their taxonomic position remains uncertain. Based on their protologues, it is likely that these species belong to *Penicillium*.

Penicillium sacculum Dale *apud* Biourge, Cellule 33: 323. 1923.
Penicillium senticosum Scott, Mycopathol. Mycol. Appl. 36: 5. 1968.

Excluded and unclassified Penicillia

Over 250 *Penicillium* and *Eupenicillium* species are mentioned in the list of accepted *Penicillium* species (Pitt *et al*. 2000) and a fair amount of these do not belong to *Penicillium s. str*. The majority of these excluded species are currently classified in *Talaromyces* and an overview of species is given by Samson *et al*. (2011). Only a small number of species do not belong to either genus. These include *P. arenicola*, *P. inflatum*, *P. kabunicum*, *P. lineatum*, *P. megasporum* and *P. moldavicum*. Figure 1 shows that *P. arenicola* is closely related to *Phialomyces* (clade 6) and *P. megasporum* belongs to the clade 3 (*Hamigera*/*Warcupiella*). Both species should be transferred to other genera. Unpublished data (R.A. Samson) shows that *P. inflatum* belongs to *Aspergillus* and this species will be combined in that genus. *Penicillium kabunicum* and *P. moldavicum* are phylogenetically related and were included in the initial analyses of *Trichocomaceae*. Both species were together on a single branch and did not fit with any members of this family (J. Houbraken, unpubl. data). These two species belong to another (related) family and might represent a new genus. *Penicillium lineatum* was described as the anamorph of *Hamigera striata* (Pitt 1980). *Hamigera striata* is accommodated in clade 3 (Fig. 1) and does therefore not belong to *Penicillium s. str*. *Penicillium syriacum* was included in the list of accepted names (Pitt *et al*. 2000), but the illustration and description of *P. syriacum* by Baghdadi (1968) and examination of ex-type material from ATCC, CBS and IMI indicated a mixed culture. This species is considered a *nomen ambiguum* (Christensen *et al*. 1999).

The phylogenetic position of *P. resedanum* needs further attention. Pitt (1980) and Ramírez (1982) placed *P. resedanum* in section *Aspergilloides* based on the formation of monoverticillate conidiophores. Pitt (1980) already noted that this species form acerose phialides with weak growth on G25N, suggesting a relationship with *Talaromyces* (and subgenus *Biverticillium*). A BLAST search on GenBank with ITS sequences of NRRL 578^T (AF033398) indicates a relationship with *Talaromyces*.

Penicillium griseolum is listed as a synonym of *P. restrictum* (Pitt *et al.* 2000). However, Fig. 7 shows that these species are phylogenetically unrelated. In our study, we did not find any species closely related to *P. griseolum* and this species might represent a separate section. We have chosen not to proceed with the description of this new section for this species until additional related species are described.

Penicillium arenicola Chalabuda, Bot. Mater. Otd. Sporov. Rast. 6: 162. 1950 (= clade 6, related to *Phialomyces*).
Penicillium inflatum Stolk & Malla, Persoonia 6: 197. 1971. (= *Aspergillus inflatus*, R.A. Samson, unpubl. data).
Penicillium kabunicum Baghdadi, Novosti Sist. Nizs. Rast.: 98. 1968 (unrelated to *Penicillium*, J. Houbraken, unpubl. data).
Penicillium lineatum Pitt, The Genus *Penicillium*: 485. 1980 ["1979"] (= *Hamigera striata*).
Penicillium megasporum Orpurt & Fennell, Mycologia 47: 233. 1955 (= clade 3, related to *Hamigera* and *Warcupiella*).
Penicillium moldavicum Milko & Beliakova, Novosti Sist. Nizs. Rast. 1967: 255. 1967 (unrelated to *Penicillium*, J. Houbraken, unpubl. data).
Penicillium syriacum Baghdadi, Novosti Sist. Nizs. Rast. 1968: 111. 1968 (*nomen ambiguum,* Christensen *et al.* 1999).

Character analysis

The classification proposed in the monographs of Raper & Thom (1949), Pitt (1980) and Ramírez (1982) is not concordant with the new classification system proposed here. One of the most important characters in these monographs is the branching pattern of the *Penicillium* conidiophore. Our study shows that monoverticillate (Aspergilloid) conidiophores occur in various sections (*e.g.* clades 1, 2, 6, 8, 10, 12, 25). Sections *Aspergilloides* (clade 1) and *Eladia* (clade 25) comprise only strictly monoverticillate species, while mono- and biverticillate species are intermingled in the other clades. The occurrence of both structures in multiple phylogenetic clades (sections) indicates that reduction of the *Penicillium* conidiophore might have occurred various times. Most of the species belonging to section *Citrina* (clade 14) are symmetrically biverticillate and occasionally additional branches with the same branching pattern as the main axis ("double symmetrically biverticillate") occurs. Species belonging to section *Lanata-divaricata* are mainly divaricate and the metulae are borne terminally, subterminally and in intercalary positions. Terverticillate conidiophores mainly occur in clades 15–18 and section *Chrysogena* (clade 19) comprises species with quarterverticillate condiophores. The monoverticillate species *Penicillium sacculum* and *P. senticosum* belong to clade 25. This clade is positioned in subgenus *Penicillium* and has therefore a unique branching pattern for this subgenus. Growth rates on agar media are also frequently used for classification. Some sections mainly comprise fast growing species (*e.g.* clades 1, 2, 11, 16, 18, 19, 25) while in other clades slow growing species predominate (*e.g.* clades 3, 6, 8, 9). The new proposed sectional classification will serve as a starting point to investigate phenotypic characters used for classification.

TAXONOMIC IMPLICATIONS

Penicillium asymmetricum (Subramanian & Sudha) Houbraken & Samson, **comb. nov.** MycoBank MB561963.
Basionym: *Thysanophora asymmetrica* Subramanian & Sudha, Kavaka 12: 88. 1985.

Penicillium bovifimosum (Tuthill & Frisvad) Houbraken & Samson, **comb. nov.** MycoBank MB561957.
Basionym: *Eupenicillium bovifimosum* Tuthill & Frisvad, Mycologia 94: 241. 2002.

Penicillium coniferophilum Houbraken & Samson, **nom. nov.** MycoBank MB561968.
Basionym: *Thysanophora striatispora* Barron & Cooke, Mycopathologia et Mycologia Applicata 40: 353. 1970, non *Penicillium striatisporum* Stolk, Ant. van Leeuwenhoek 35: 268. 1969.

Note: The name *P. striatisporum* is already occupied and therefore a new name is proposed.

Penicillium glaucoalbidum (Desmazières) Houbraken & Samson, **comb. nov.** MycoBank MB561965.
Basionym: *Sclerotium glaucoalbidum* Desmazières, Annales des Sciences Naturelles, Botanique 16: 329. 1851.
= *Thysanophora glaucoalbida* (Desm.) Morelet, Annales de la Société des Sciences Naturelles et Archéologie de Toulon et Var 20: 104. 1968.
= *Thysanophora penicillioides* (Roumeguère) Kendrick, Can. J. Bot. 39: 820. 1961.

Note: Virtually all of the published information relating to *P. glaucoalbidum* has used the binomial *Thys. penicillioides*. Iwamoto *et al*. (2005) aggregated sequence data of seven European and North American *P. glaucoalbidum* (as *Thys. penicillioides*) strains with Japanese strains. The strains formed nine lineages and according to phylogenetic species recognition by the concordance of genealogies, respective lineages correspond to phylogenetic species.

Penicillium hennebertii Houbraken & Samson, **nom. nov.** MycoBank MB561964.
Basionym: *Thysanophora canadensis* Stolk & Hennebert, Persoonia 5: 189. 1968, non *Penicillium canadense* Smith, Trans. Br. mycol. Soc. 39: 113. 1956.

Note: A new name was sought for this species, as the species name "canadensis" is already occupied.

Penicillium laeve (K. Ando & Manoch) Houbraken & Samson, **comb. nov.** MycoBank MB561960.
Basionym: *Torulomyces laevis* K. Ando & Manoch, Mycoscience 39: 317. 1998.

Penicillium longisporum (Kendrick) Houbraken & Samson, **comb. nov.** MycoBank MB561966.
Basionym: *Thysanophora longispora* Kendrick, Can. J. Bot. 39: 826. 1961.

Penicillium malachiteum (Yaguchi & Udagawa) Houbraken & Samson, **comb. nov.** MycoBank MB561971.
Basionym: *Chromocleista malachitea* Yaguchi & Udagawa, Trans. Mycol. Soc. Japan 34: 102. 1993.
= *Geosmithia malachitea* Yaguchi & Udagawa, Trans. Mycol. Soc. Japan 34: 102. 1993.

Penicillium melanostipe Houbraken & Samson, **nom. nov.** MycoBank MB561970.
Basionym: *Thysanophora verrucosa* Mercado, Gené & Guarro, Mycotaxon 67: 419. 1998, non *Penicillium verrucosum* Dierckx, Annales de la Société Scientifique de Bruxelles 25: 88. 1901.

Note: The name *Penicillium verrucosus* is already occupied and therefore the name melanostipe, which is referring to the pigmented stipe of this species, is proposed.

Penicillium ovatum (K. Ando & Nawawi) Houbraken & Samson, **comb. nov.** MycoBank MB561961.
Basionym: *Torulomyces ovatus* K. Ando & Nawawi, Mycoscience 39: 317. 1998.

Penicillium parviverrucosum (K. Ando & Pitt) Houbraken & Samson, **comb. nov.** MycoBank MB561962.
Basionym: *Torulomyces parviverrucosus* K. Ando & Pitt, Mycoscience 39: 317. 1998.

Penicillium porphyreum Houbraken & Samson, **nom. nov.** MycoBank MB561959.
Basionym: *Monocillium humicola* Barron var. *brunneum* M. Christensen & Backus, Mycologia 56: 498. 1964, non *Penicillium brunneum* Udagawa, J. agric. Sci. Tokyo Nogyo Daigaku 5: 16. 1959.
= *Torulomyces brunneus* (M. Christensen & Backus) K. Ando, Mycoscience 39: 314. 1998.

Note: The name *Penicillium brunneum* is already occupied (Udagawa *et al.* 1959) and therefore the name *P. porphyreum* is proposed. The epithet porphyreum refers to the red-brown reverse of this species.

Penicillium saturniforme (Wang & Zhuang) Houbraken & Samson, **comb. nov.** MycoBank MB561958.
Basionym: *Eupenicillium saturniforme* Wang & Zhuang, Mycopathologia 167: 300. 2009.

Penicillium taiwanense (Matsushima) Houbraken & Samson, **comb. nov.** MycoBank MB561969.
Basionym: *Phialomyces taiwanensis* Matsushima, Matsushima Mycological Memoirs 4: 12. 1985.
= *Thysanophora taiwanensis* (Matsush.) Mercado, Gené & Guarro, Mycotaxon 67: 421. 1998.

Note: This species was originally described as *Phialomyces taiwanensis*. Based on micro-morphological features, Mercado-Sierra *et al*. (1998) transferred this species to *Thysanophora taiwanensis*.

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Taxonomy of *Penicillium* section *Citrina*

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Abstract: Species of *Penicillium* section *Citrina* have a worldwide distribution and occur commonly in soils. The section is here delimited using a combination of phenotypic characters and sequences of the nuclear ribosomal RNA gene operon, including the internal transcribed spacer regions ITS1 and ITS2, the 5.8S nrDNA (ITS) and partial *RPB2* sequences. Species assigned to section *Citrina* share the production of symmetrically biverticillate conidiophores, flask shaped phialides (7.0–9.0 µm long) and relatively small conidia (2.0–3.0 µm diam). Some species can produce greyish-brown coloured cleistothecia containing flanged ascospores. In the present study, more than 250 isolates presumably belonging to section *Citrina* were examined using a combined analysis of phenotypic and physiological characters, extrolite profiles and ITS, β-tubulin and/or calmodulin sequences. Section *Citrina* includes 39 species, and 17 of those are described here as new. The most important phenotypic characters for distinguishing species are growth rates and colony reverse colours on the agar media CYA, MEA and YES; shape, size and ornamentation of conidia and the production of sclerotia or cleistothecia. Temperature-growth profiles were made for all examined species and are a valuable character characters for species identification. Species centered around *P. citrinum* generally have a higher maximum growth temperature (33–36 °C) than species related to *P. westlingii* (27–33 °C). Extrolite patterns and partial calmodulin and β-tubulin sequences can be used for sequence based identification and resolved all species. In contrast, ITS sequences were less variable and only 55 % of the species could be unambiguously identified with this locus.

Key words: citreoviridin, citrinin, soil fungi, taxonomy, phylogeny.
Taxonomic novelties: *Penicillium argentinense* Houbraken, Frisvad & Samson, *P. atrofulvum* Houbraken, Frisvad & Samson, *P. aurantiacobrunneum* Houbraken, Frisvad & Samson, *P. cairnsense* Houbraken, Frisvad & Samson, *P. christenseniae* Houbraken, Frisvad & Samson, *P. copticola* Houbraken, Frisvad & Samson, *P. cosmopolitanum* Houbraken, Frisvad & Samson, *P. neomiczynskii* Cole, Houbraken, Frisvad & Samson, *P. nothofagi* Houbraken, Frisvad & Samson, *P. pancosmium* Houbraken, Frisvad & Samson, *P. pasqualense* Houbraken, Frisvad & Samson, *P. quebecense* Seifert, Houbraken, Frisvad & Samson, *P. raphiae* Houbraken, Frisvad & Samson, *P. terrigenum* Seifert, Houbraken, Frisvad & Samson, *P. ubiquetum* Houbraken, Frisvad & Samson, *P. vancouverense* Houbraken, Frisvad & Samson, *P. wellingtonense* Cole, Houbraken, Frisvad & Samson.

INTRODUCTION

Raper & Thom (1949) introduced the "*Penicillium citrinum* series" for *Penicillium* species with restricted growth on Czapek's agar and producing terminal verticils of metulae in combination with relatively small conidia (2.5–3.2 µm). *Penicillium citrinum*, *P. corylophilum* and *P. steckii* were classified in this series. Ramírez (1982) followed Raper & Thom's concept, and added *P. matritii*. Pitt (1980) formalised series *Citrina*, and using similar criteria as Raper & Thom, he accepted seven species: *P. citrinum*, *P. corylophilum*, *P. miczynskii*, *P. humuli*, *P. herquei*, *P. paxilli* and *P. inflatum*. In his description of series *Citrina*, Pitt (1980) noted that it encompasses a rather diverse collection of species, which in some cases show relatively little affinity with each other. This observation was supported by the taxonomic and phylogenetic study of Houbraken *et al*. (2010). Seven species were recognised in series *Citrina*, and of all the species mentioned above, only *P. citrinum* and *P. steckii* were maintained. Peterson (2000) was among the first to study the phylogeny of *Penicillium* with sequence data. Using ITS sequences, he constructed a phylogeny of *Penicillium* and showed that *P. citrinum* is related to *P. westlingii*, *P. sumatrense*, *P. paxilli*, *P. waksmanii*, *P. miczynskii*, *Eupenicillium anatolicum* and *E. shearii*. Recently, a new sectional classification for *Penicillium* was proposed and section *Citrina* was introduced (Houbraken & Samson 2011). This classification was based on a combined analysis of sequence data of four loci and the species belonging to section *Citrina* are the same as those belonging to Peterson's group 1. Peterson *et al*. (2004) and Houbraken *et al*. (2010) studied certain species of this section in more detail, however, a modern overview of species and their synonyms is lacking.

Members of section *Citrina* are very abundant and have a worldwide distribution. It is even claimed that *P. citrinum* may well be one of the most commonly occurring eukaryotic life forms on earth (Pitt 1980). Species of this section are very common in soil, but are also isolated from indoor environments and foodstuffs (Pitt & Hocking 2009, Samson *et al*. 2010). The distribution of species appears to be climate-related. *Penicillium citrinum* is more common in (sub)tropical soils, and present only in low numbers in soils from temperate regions (the Netherlands, Poland, Canada), where *P. westlingii* and related species predominate.

Members of section *Citrina* are also known for their ability to produce the mycotoxins citrinin and citreoviridin. The nephrotoxic compound citrinin is consistently produced by *P. citrinum*, but also by other related species including *P. gorlenkoanum*, *P. hetheringtonii*, *P. miczynskii*, *P. chrzaszczii*, *P. manginii* and *P. westlingii*, and citreoviridin is produced by *P. miczynskii* and *P. manginii* (Pollock 1947, Frisvad 1989, Frisvad & Filtenborg 1990, Frisvad *et al*. 2006, Houbraken *et al*. 2010). Many other extrolites are reported to be produced by members of section *Citrina*; however, some of these extrolites are erroneously linked to certain species (Frisvad 1989, Frisvad & Filtenborg 1990, Houbraken *et al*. 2010).

Table 1. Isolates in *Penicillium* section *Citrina* examined in this study.

Species	CBS no.	Other numbers	Substrate and locality
P. anatolicum		DTO 23A1 = IBT 30775	Contaminant of CBS 316.67
	CBS 308.89	CBS H-20648 = DTO 23E6 = IBT 30768	Soil, Keewadin Island, Florida, USA
	CBS 467.67	CBS H-20647 = DTO 23A2 = CSIR 1095 = IBT 30763	Sandy soil, Kosi Bay, Natal, South Africa
	CBS 478.66^{T}	DTO 22I5 = DTO 22I6 = ATCC 18621 = CSIR 940 = IFO 31729 = IMI 136242 = IBT 30765	Soil, Turkey
	CBS 479.66	DTO 22I6 = IBT 16177 = IBT 30764	Soil, Turkey
P. argentinense	CBS 130371^{T}	CBS H-20641 = DTO 16B7 = IBT 30761	Soil, Valdes Peninsula peninsula, prov. Chubet, Argentinia
	CBS 130373	DTO 18B1 = IBT 30760	Soil, Spaanderswoud, Bussum, the Netherlands
	CBS 130374	DTO 18B6 = IBT 30761	Soil, Spaanderswoud, Bussum, the Netherlands
	CBS 130381	DTO 132D5	*Phaenocoma* leaf bracts, South Africa
P. atrofulvum	CBS 109.66^{T}	CBS H-20650 = DTO 31B2 = FRR 799 = IBT 30032 = IBT 29667	Soil, Katanga, Zaire
	CBS 126331	DTO 120G7	Soil of oak forest; Ras Rajel, Tunesia
	CBS 126332	DTO 118D4	Soil of oak forest; Fey el Rih, Tunesia
	CBS 261.64	DTO 22H4 = IBT 16171	Unrecorded source, the Netherlands
P. aurantiacobrunneum	CBS 126228^{T}	CBS H-20662 = DTO 78G2 = IBT 18753	Air sample, Cake factory, Give, Denmark
	CBS 126229	DTO 82C3 = IBT 23001	Soil, *Nothofagus* sp., Chile
	CBS 126230	DTO 82C9 = IBT 29145	Wood litter, Eves Bush, Marlborough, New Zealand
	CBS 126277	DTO 76D1 = IBT 29115	Soil, New Zealand
P. cairnsense	CBS 117962	DTO 55A5 = KAS 2100 = IBT 29675	Decaying basidioma of *Lactarius* sp.; Algonquin Park, Ontario, Canada, 45.593086° -78.519914°
	CBS 117982	DTO 5A7 = KAS 2122 = IBT 29857	Nut of *Carya cordiformis* (bitternut); Fireman's Park, Niagara Falls, Ontario, Canada, 43.142051° -79.115903°
	CBS 118028	CBS H-20653 = DTO 55B2 = KAS 2178	Ants (*Camponotus* spp.), New Brunswick, Canada
	CBS 124324	DTO 30B9 = IBT 29068	Soil, near lake Barrine, Australia
	CBS 124325^{T}	DTO 30E6 = IBT 29042	Soil, Atherton Tableland, Australia
	CBS 124326	DTO 30E8 = IBT 29069	Soil, Atherton Tableland, Australia
	CBS 126225	DTO 82B6 = IBT 18352 = CCRC 33163	Soil, Sun-Moon Lake, Nantou County, Taiwan
	CBS 126226	DTO 85A4 = IBT 30006	Soil, 2 mtr. from road, Ranomafana, Madagascar
P. christenseniae	CBS 126236^{T}	CBS H-20656 = DTO 76C3 = IBT 23355	Soil in native forest near base of aerial tram. "Lowland forest" east / north east side of Costa Rica about 30 km inland from Limon and the Caribbean
	CBS 126237	DTO 78A5 = RMF 9554 = IBT 18183	Litter of *Manilkara bidenta* or *Guarea guidonia*, rainforest, El verde in the Luquillo Experimental Forest, Caribbean National Forest, Puerto Rico
P. chrzaszczii	CBS 124320	DTO 42A8 = IBT 30635	Soil, Poland
	CBS 126430	DTO 42G9 = IBT 30634	Soil, Poland
	CBS 176.81	DTO 23D7 = ATCC 42242 = IJFM 7097 = VKM F-2198 = IBT 16265	Type of *P. turolense*; leaves litter of *Fagus silvatica*, near Nancy, France
	CBS 217.28^{T}	22E4 = FRR 903 = MUCL 29167 = NRRL 903 = NRRL 1741 = IBT 18226 = IBT 11222 = IBT 16409	Woodland soil, Puszcza Bialowieska Forest, Poland
P. citrinum	CBS 101275	DTO 23G2 = IBT 29060	Leaf, Panama
	CBS 115992	DTO 23G6	Compost, the Netherlands
	CBS 117.64	DTO 22H3 = IBT 30003	Epoxy softener, the Netherlands
	CBS 122394	DTO 7B8	Soil, Malaysia
	CBS 122395	DTO 20A3	Coconut milk; produced in Indonesia, imported into the Netherlands
	CBS 122397	DTO 6D6	Soil, Treasure Island, Florida, USA
	CBS 122398	DTO 31F9	Peanut, Indonesia
	CBS 122451	DTO 48C2 = NRRL 2145 = IBT 16140	Color mutant; unrecorded source
	CBS 122452	DTO 32B6 = IBT 30061	Color mutant, coffee beans, Thailand
	CBS 122726	DTO 58A4 = NRRL 783 = IBT 16149	Representative of *P. sartoryi*, unrecorded source

Table 1. (Continued).

Species	CBS no.	Other numbers	Substrate and locality
P. citrinum	CBS 139.45^{T}	DTO 22F3 = ATCC 1109 = ATCC 36382 = CECT 2269 = FRR 1841 = IMI 091961 = IMI 092196 = MUCL 29781 = NRRL 1841 = IBT 16200 = NRRL 1842 = IBT 16207	Type of *P. citrinum* and *P. aurifluum*, unrecorded source
	CBS 232.38	DTO 37B7 = Thom 4733.73 = IBT 21675	Type of *P. implicatum;* unrecorded source
	CBS 241.85	IMI 092267 = MUCL 29788 = IBT 21934	Type of *P. phaeojanthinellum*; unrecorded source
	CBS 252.55	DTO 22G4 = ATCC 12068 = FRR 3463 = NRRL 3463 = QM 6946 = IBT 19474	Isotype of *P. botryosum*; herbarium specimen, Recife, Brazil
	CBS 865.97	DTO 23F8	Patient with acute myeloid leukemia, autopsy of lung and pericardium
P. copticola	CBS 127355^{T}	CBS H-20643 = DTO 19H7 = IBT 30771	Tortilla, USA
	CBS 127356	DTO 104E8 = IBT 30772	Dried flower of *Cannabis*, the Netherlands
	CBS 130382	DTO 162G5	Air of a toilet in a kindergarten, Trier, Germany
P. cosmopolitanum		DTO 82C8 = IBT 29104	Forest soil, Hokitika, New Zealand
		DTO 42G4 = IBT 29692	Soil, Poland
	CBS 122406	DTO 17E3	Soil under oak, Spaanderswoud, Bussum, the Netherlands
	CBS 122435	DTO 38D6 = IBT 29040	Organic soil of mixed forest, Rijnsweerd, Utrecht
	CBS 124315	DTO 42F6 = IBT 30684	Soil, Poland
	CBS 124316	DTO 42D3 = IBT 29677	Soil, Poland
	CBS 126990	DTO 42F4 = IBT 30691	Soil, Poland
	CBS 126991	DTO 42G6 = IBT 30693	Soil, Poland
	CBS 126992	DTO 41B1 = IBT 30719	Soil, Poland
	CBS 126993	DTO 40E9 = IBT 30690	Soil, Poland
	CBS 126994	DTO 40I4 = IBT 30697	Soil, Poland
	CBS 126995^{T}	CBS H-20665 = DTO 92E8 = IBT 30681	Soil heathland, Cartier heide, Eersel, the Netherlands
	CBS 126996	DTO 42G1 = IBT 30683	Soil, Poland
	CBS 126997	DTO 42A1 = IBT 29690	Soil, Poland
	CBS 126998	DTO 41A4 = IBT 30757	Soil, Poland
	CBS 126999	DTO 39D5 = IBT 30687	Soil, Poland
	CBS 127000	DTO 92G6 = IBT 30678	Soil heathland, Cartier heide, Eersel, the Netherlands
	CBS 127001	DTO 92E9 = IBT 30682	Soil heathland, Cartier heide, Eersel, the Netherlands
	CBS 127002	DTO 42E1 = IBT 30680	Soil, Poland
	CBS 127038	DTO 76B6 = IBT 21692	Soil, near Lyngby Lake, Denmark
	CBS 200.86	DTO 23E4 = IBT 16144 = IBT 29697	Root of *Pseudotsuga menziesii*, the Netherlands
	CBS 251.70	DTO 23B1 = IBT 29071	Root of gymnosperm, Denmark
	CBS 552.86	DTO 23E5 = IBT 29681 = IBT 30689	Root of *Pseudotsuga menziesii*, the Netherlands
	CBS 586.70	DTO 23B5 = IBT 30686	Root of gymnosperm, Denmark
	CBS 637.70	DTO 23B6	Root of gymnosperm, Denmark
P. decaturense	CBS 117504	DTO 3A9 = IBT 27057 = NRRL 29675	*Trichaptum biformis*, on dead hardwood branch, Chehaw Park, Albany, Georgia, USA
	CBS 117505	DTO 3B1 = IBT 27058 = NRRL 29708	Basidiomycete on dead hardwood, Reed Bingham State park (hardwood swamp area), Adel, Georgia, USA
	CBS 117506	DTO 3B2 = IBT 27059 = NRRL 29828	*Trichaptum biformis*, on dead hardwood branch, Wakulla Springs State Park, Crawfordsville, Florida, USA
	CBS 117507	DTO 3F5 = IBT 27111 = NRRL 28160	*Ischnoderma*, old basidiomata, found on dead hardwood log, North Picture Ridge Road, Peoria, Illinois, USA
	CBS 117508	DTO 3F6 = IBT 27114 = NRRL 29840	Polypore found on a dead pine branch, Blountstown, Torreya State Park, Illinois, USA
	CBS 117509^{T}	DTO 3F7 = IBT 27117 = NRRL 28152	Old resupinate fungus, Ramsey Lake State Park, Decatur, Illinois, USA
	CBS 117510	DTO 3F8 = IBT 27120 = NRRL 28119	Wood decaying fungus
	CBS 119390	DTO 9F2 = IBT 27868 = NRRL 29807	Pyrenomycete stroma on dead hardwood; sabal palm swamp, Hickory Mounds, Florida, USA
P. euglaucum	CBS 130372	DTO 16G1 = IBT 30776	Soil, Azul, prov. Buenos Aires, Argentina
	CBS 323.71^{NT}	DTO 23B9 = IBT 30767	Soil, Argentina

Table 1. (Continued).

Species	CBS no.	Other numbers	Substrate and locality
P. gallaicum	CBS 164.81	DTO 34G2 = IJFM 7026 = IMI 253797 = VKM F-2193 = IBT 22014	Type of *P. alicantinum*; air, Madrid, Spain
	CBS 167.81^{T}	DT 34G3 = IJFM 5597 = DTO 34G3 = ATCC 42232 = IMI 253794 = VKM F-2190 = IBT 22016	Air, Madrid, Spain
	CBS 418.69	DTO 23A9 = NRRL 3759 = IBT 30046 = IMI 140303 = FRR 519	Type of *P. syriacum nomen dubium*; soil, Berza, Damascus, Syria
P. godlewskii	CBS 117273	DTO 2H8 = IBT 29661	Butter, the Netherlands
	CBS 124319	DTO 39C7 = IBT 29678	Soil, Bialowieska, Poland
	CBS 126419	DTO 40E3 = IBT 30692	Soil, Bialowieska, Poland
	CBS 126420	DTO 39C4 = IBT 30637	Soil, Bialowieska, Poland
	CBS 126421	DTO 42G2 = IBT 30636	Soil, Bialowieska, Poland
	CBS 126422	DTO 76B5 = IBT 21219	Sand under pine, summit of Eagle Rock, Medicine Bow National Forest near Laramie, Wyoming, USA
	CBS 126423	DTO 42E7 = IBT 30638	Soil, Bialowieska, Poland
	CBS 126424	DTO 58C6 = IBT 30640	Unknown substrate, Germany
	CBS 215.28^{T}	DTO 22E2 = ATCC 10449 = ATCC 48714 = FRR 2111 = I FO 7724 = IMI 040591 = MUCL 29243 = NRRL 2111 = QM 7566 = VKM F-1826	Soil under pine, Bialowieska, Poland
	CBS 218.28	ATCC 10457 = FRR 2147 = IFO 30869 = IFO 7674 = IMI 040567 = MUCL 29245 = NRRL 2147 = QM 7588 = IBT 4998 = IBT 5045	Type strain of *P. kapuscinskii*, ex sandy soil, Baltic, Poland
P. gorlenkoanum	CBS 408.69^{IsoT}	DTO 34E3 = FRR 511 = IMI 140339 = VKM F-1079 = IBT 19235	Soil, Syria
	CBS 411.69	DTO 23A6 = IMI 140337 = VKM F-1070 = IBT 16117	Type strain of *P. damascenum*; soil, Ima, Damascus region, Syria
P. hetheringtonii		DTO 30H7	Soil, Lookout Kuranda, Australia
	CBS 122392^{T}	DTO 5H9 = IBT 29057	Soil, Treasure Island, Florida, USA
	CBS 124286	DTO 30H5 = IBT 29061	Soil, Lookout Kuranda, Australia
	CBS 124287	DTO 32E3	Soil, Lake Easchem, Australia
P. manginii	CBS 108.66	DTO 22I3 = IBT 16132 = IBT 30406	Soil, Latosol, near Kipushi, Katanga, Congo
	CBS 122403	DTO 21B2	Indoor air of house, Eindhoven
	CBS 126232	DTO 87E5	Soil of rainforest, Ranoma fana, Madagascar
	CBS 126233	CBS H-20654 = DTO 76B7 = IBT 22405	Soil under *Cyathea* tree ferns, on Rio Jaba Trail near Quebrada Culebra, Wilson Botanical Garden/ La Cruces Biological Station, Costa Rica
	CBS 253.31^{NT}	DTO 22E9 = NRRL 2134 = IMI 191732 = FRR 2134 = IBT 18224	Soil, unknown locality
	CBS 265.65	DTO 22H6 = ATCC 18334 = IMI 143926 = NRRL 3379 = IBT 18186	Type of *P. pedemontanum*, mycorrhizae of *Fagus silvatica*, Italy
	CBS 327.79	DTO 23D5 = IJFM 3782 = IBT 29651	Air, Madrid, Spain
	CBS 343.52	DTO 22G2 = BRL 111A = IBT 16157	Soil, Norway
	CBS 378.65	DTO 22H8 = NRRL 3555 = IBT 18223 = IBT 30412 = IBT 29064	Soil, near Baya, Katanga, Congo
	CBS 407.65	DTO 22H9 = IMI 096225	Hay, Haslemere, Surrey, UK
	CBS 408.65	DTO 22I1 = FRR 1836 = IMI 099085 = IBT 3998	Soil, Cambridge, England, UK
	CBS 409.65	DTO 22I2 = IMI 096290	Rhizosphere of *Triticum aestivum*, Rothamsted, UK
P. miczynskii	CBS 124323	DTO 42F2 = IBT 30584	Soil, Bialowieza National Park, Poland
	CBS 126222	DTO 16A2 = IBT 29054	Soil, Los Alerces National Park, Chubut, Argentina
	CBS 126223	DTO 76B2 = IBT 18227 = RMF 7771	A1 horizon soil in conifer forest (lodgepole pine), Cinnabar Park, Wyoming, USA
	CBS 126224	DTO 82C7 = IBT 26903	Soil, Spread Creek, Wyoming, USA
	CBS 220.28^{T}	DTO 22E5 = ATCC 10470 = DSM 2437 = FRR 1077 = IFO 7730 = IMI 040030 = MUCL 29228 = NRRL 1077 = IBT 5491	Soil under conifer, Tatry mountains, Poland
P. neomiczynskii	CBS 126231^{T}	CBS H-20661 = DTO 78C2 = IBT 23560	Soil, New Zealand
P. nothofagi	CBS 127004	DTO 80D2 = IBT 17235	Soil, Brazil
	CBS 130383	CBS H-20655 = DTO 76C2 = IBT 23018	Soil under *Nothofagus,* Chile

Table 1. (Continued).

Species	CBS no.	Other numbers	Substrate and locality
P. pancosmium		DTO 82D1 = IBT 29160	Unknown source, New Zealand
	CBS 118007	DTO 55A9 = KAS 2150 = IBT 29670	Porcupine dung, Dufferin, Dufferin County Forest, 1 km N. of Mansfield, Ontario, Canada
	CBS 118018	DTO 55B1 = KAS 2163 = IBT 29871	Nut of *Juglans cinerea* (butternut); Fireman's Park, Niagara Falls, Ontario, Canada, 43.142051° -79.115903°
	CBS 124293	DTO 84H4 = IBT 22166	Growth on *Piptosphaeria* (on *Betula* sp), Lambs Lane, New Jersey, USA
	CBS 126431	DTO 118I8 = IBT 30707	Soil of oak forest; Fey el Rih, Tunesia
	CBS 126432	DTO 100A1	Soil, Portugal
	CBS 126433	DTO 82C2 = IBT 22969	Soil under *Nothofagus*, Chile
	CBS 126434	DTO 120A1 = IBT 30648	Soil; Ras Rajel, Tunesia
	CBS 126435	DTO 119A4 = IBT 30643	Soil of oak forest, Fey el Rih, Tunesia
	CBS 276.75^{T}	CBS H-20651 = DTO 31B4 = DAOM 147467 = IBT 29991	Old *Armillaria mellea*, on hardwood log; Meach Lake, Gatineau Park, Gatineau County, Quebec, Canada
P. pasqualense	CBS 122402	DTO 28C2 = IBT 29047	Air in bakery, Averhorn, the Netherlands
	CBS 124327	DTO 57D3	Soil, Katandra Nature Reserve, NSW, Australia
	CBS 126329	DTO 78B3 = IBT 17865	Soil and debris under *Juniperus* sp., Wind River canyon, 10 km south of Thermopolis, Wyoming, USA
	CBS 126330^{T}	CBS H-20663 = DTO 80D5 = IBT 14235	Soil, Easter Island, Chile
P. paxilli	CBS 101273	DTO 23F9 = IBT 30832	Leaf, Panama
	CBS 117190	DTO 31A8 = IBT 16459	Soil, Galapagos Islands, Ecuador
	CBS 117191	DTO 31A9 = IBT 20977 = IBT 21034 = IBT 21005	Mangrove, Venezuela
	CBS 118002	KAS 2144	*Coustania superba*, Panama
	CBS 118052	KAS 2206 = IBT 29839	Nut of *Carya cordiformis* (bitternut); Fireman's Park, Niagara Falls, Ontario, Canada, 43.142051° -79.115903°
	CBS 127360	DTO 52F9 = IBT 30839	Melon imported in the Netherlands, Brazil
	CBS 127361	DTO 30A6 = IBT 29070	Soil, near lake Cratez, Barrine, Queensland, Australia
	CBS 162.96	DTO 23F3 = IBT 30847	Wood in tropical rainforest, Madang Province, Finisterre Range, Papua-New Guinea
	CBS 360.48^{T}	DTO 31A6 = ATCC 10480 = FRR 2008 = IMI 040226 = NRRL 2008 = QM 725 = IBT 16202	Optical instrument, Barro Colorado Island, Panama
	CBS 547.77	DTO 31A7 = ATCC 26601 = FRR 1900 = IBT 3128 = IBT 3329 = IBT 5531	*Carya illinoensis, Juglandaceae*, Georgia, USA
P. quebecense	CBS 101623^{T}	CBS H-20666 = DTO 9B8 = IBT 29050	Air in sawmill, Quebec, Canada
P. raphiae	CBS 126234^{T}	CBS H-20660 = DTO 78B8 = IBT 22407	Soil under *Raphia* (?) palm in primary forest, Las Alturas, elev. 1530 m, Costa Rica
	CBS 126235	CBS H-20664 = DTO 84I9 = IBT 30001	Soil under baobab tree; Montagne d'Ambre National Park, Madagascar
P. roseopurpureum	CBS 127025	DTO 28F5 = IBT 30782	Indoor air of house, Eindhoven, the Netherlands
	CBS 127026	DTO 28F6 = IBT 30781	Indoor air of house, Eindhoven, the Netherlands
	CBS 127027	DTO 76C9 = IBT 27944	Soil under *Pinus flexilis*, Bear Mountain, Wyoming, USA
	CBS 127028	DTO 76D3 = IBT 27930	Soil under *Artemisia cana*, Bear Mountain, Wyoming, USA
	CBS 266.29^{NT}	DTO 9E3 = ATCC 10492 = ATHUM 2895 = FRR 2064 = IMI 040573 = MUCL 28654 = MUCL 29237 = NRRL 2064 = NRRL 2064A	Unrecorded source
	CBS 281.39	DTO 9E7 = FRR 2066 = MUCL 28670 = MUCL 29240 = NRRL 2066 = IBT 30783	Type of *P. carminoviolaceum*; plant material in ethanol, unknown location
P. sanguifluum	CBS 110.64	DTO 9E6 = IBT 29045	Soil, Erzurum, Turkey
	CBS 118020	DTO 128C8 = KAS 2165	Ants (*Camponotus* spp.), New Brunswick, Canada
	CBS 118024	DTO 128C9 = KAS 2171	Ants (*Camponotus* spp.), New Brunswick, Canada
	CBS 127029	DTO 15H6 = IBT 30793	Soil, Parque Nacional Los Alerces, Argentina
	CBS 127030	DTO 6D7 = IBT 30759	Chestnut, Corsica, France
	CBS 127031	CBS H-20642 = DTO 17G5 = IBT 29051	Soil, Calahonda, Costa del Sol, Spain
	CBS 127032^{NT}	CBS H-20645 = DTO 20B7 = IBT 29041	Soil, Calahonda, Costa del Sol, Spain
	CBS 127033	DTO 99I9 = IBT 30786	Unknown, Catia Rodriguez
	CBS 127034	DTO 119I1 = IBT 30785	Soil, Ras Rajel, Tunesia

Table 1. (Continued).

Species	CBS no.	Other numbers	Substrate and locality
P. sanguifluum	CBS 127035	DTO 120G9 = IBT 30784	Soil, Ras Rajel, Tunesia
	CBS 127036	DTO 121D8	Soil, Ras Rajel, Tunesia
	CBS 148.83	DTO 9E2 = CECT 2753	Type of *P. vaccaeorum*; sandy soil under pine tree, Valladolid, Spain
	CBS 300.67	DTO 9E5 = IBT 30787	Sandy greenhouse soil, the Netherlands
	CBS 643.73	DTO 9E4 = IBT 30789	Soil, sandy beach ridge, Manitoba, Canada
	CBS 685.85	DTO 36B9 = IJFM 19078 = IBT 4904 = IBT 10578 = IBT 10579	Type of *P. lacussarmientei*, sandy soil, National Park of Torres del Paine, near Lake Sarmiento, Tierra del Fuego, Chile
P. shearii		DTO 78C5 = IBT 28734	Unknown source, Brazil
	CBS 118059	DTO 23H7 = KAS 2214 = IBT 30164	Soil eaten by chimpanzees, Mahale Mountains National Park, Tanzania
	CBS 127358	DTO 54B8 = IBT 30837	Soil, Langkawi, Malaysia
	CBS 127359	DTO 99H1 = IBT 30821	Soil, Portugal
	CBS 290.48^{T}	DTO 22F6 = IMI 39739 = ATCC 10410 = NRRL 715 = IFO 6088 = IBT 24588	Soil, Tela, Honduras
	CBS 342.68	DTO 23A3 = IBT 14785 = IBT 14786	Soil, Congo
	CBS 343.54	DTO 22G3 = NRRL 3325 = IBT 14695	Soil, Congo
	CBS 502.78	DTO 23D4 = IBT 24589	Cassava field soil, Colombia
	CBS 513.73	NHL 6444 = IBT 14698	Soil, Cape Hoskins, Waississi, New Britain Island, Papua-New Guinea
	CBS 578.70	DTO 23B4 = IBT 30815	Soil, San Blas, Nayarit State, Mexico
P. sizovae	CBS 115968	DTO 23G5	Cropped soil, Italy
	CBS 117183	DTO 23H2	*Papaver somniferum*, the Netherlands
	CBS 117184	DTO 23H3 = IBT 22812	Salty water in saltern, Slovenia
	CBS 122386	DTO 5C5	Glue, the Netherlands
	CBS 122387	DTO 19H1	Margarine, the Netherlands
	CBS 139.65	DTO 22H5	Sea salt, Portugal
	CBS 413.69^{NT}	DTO 23A7 = FRR 518 = IMI 140344 = VKM F-1073	Soil, Syria
P. steckii		DTO 49G1 = IBT 14692 = NRRL 2142	Exposed fabric, Panama
	CBS 122388	DTO 49F9 = IBT 14691 = NRRL 6336	Baled coastal grass hay, Bermuda
	CBS 122389	DTO 49F8 = IBT 19353 = IFO 6024	Unrecorded source
	CBS 122390	DTO 48D3 = IBT 21096	*Caranx crysos* (blue runner, fish), sand bottoms with corals, surface water 23°C, dept 2–3 m at Cabruta, Mochima Bay, Venezuela
	CBS 122391	DTO 7D2	Potting soil, the Netherlands
	CBS 122417	DTO 48D2 = IBT 20952	Ascidie (tunicate, urochordata), sand bottoms with corals, surface water 23 °C, dept 2–3 m at Cabruta, Mochima Bay, Venezuela
	CBS 122418	DTO 48D1 = IBT 6452	*Cynara scolymus* (Artichoke), Egypt
	CBS 260.55^{NT}	DTO 22G5 = ATCC 10499 = CECT 2268 = DSM 1252 = IMI 040583 = NRRL 2140 = QM 6413	Cotton fabric treated with copper naphthenate; Panama
	CBS 325.59	DTO 22G7 = ATCC 20203 = ATCC 18307 = CECT 2273 = FRR 636 = IFO 6227 = IMI 068229 = QM 7291	Type of *P. corylophiloides*; soil, Japan
	CBS 789.70	DTO 23B7 = IBT 3145	Unrecorded source
P. sumatrense	CBS 115708	DTO 23G4 = IBT 29691	Soil, Presicce, Apulia, Italy
	CBS 117185	DTO 23H4 = IBT 24845 = IBT 29668	Bromeliad leaf tissue, *Orthophyton burle-marxii*, Selby Botanical Garden, Sarasota, Florida, USA
	CBS 127362	DTO 5I2 = IBT 29048	Soil, Land's end Garden, Treasure Island, Florida, USA
	CBS 127363	DTO 15E6 = IBT 30841	Packaging material, imported into the Netherlands
	CBS 127364	DTO 30H8 = IBT 29059	Soil, Lookout Kuranda, Queensland, Australia
	CBS 127365	DTO 99B6 = IBT 30840	Soil, Portugal
	CBS 127366	DTO 120H3 = IBT 30831	Soil, Ras Rajel, Tunisia
	CBS 130377	DTO 78A8 = IBT 27264	Bromeliad leaf, *Aechmia magdalenae*, Panama
	CBS 130378	DTO 78B2 = IBT 28809	Forest fruit, Uganda
	CBS 130380	DTO 80D6 = IBT 13201	Utility Pole, USA (no. JP 923, as *P. steckii*)

Table 1. (Continued).

Species	CBS no.	Other numbers	Substrate and locality
P. sumatrense	CBS 281.36^{T}	DTO 22F1 = NRRL 779 = FRR 779 = ATCC 48669 = IBT 29658 = IBT 4978	Soil, Toba Heath, Sumatra, Indonesia
	CBS 335.59	DTO 31B8 = ATCC 18378 = FAT 803 = FRR 639 = IFO 6232 = IMI 068232 = QM 7313 = IBT 14696	Type of *P. meleagrinum* var. *viridiflavum*; soil, Japan
	CBS 416.69	DTO 23A8 = FRR 508 = IMI 140336 = VKM F-1069 = IBT 29648	Isotype of *P. baradicum*; soil under cornel, Damascus, Syria
P. terrigenum	CBS 117967	KAS 2104 = IBT 29807	Mushroom fairy ring, Oshawa, Ontario, Canada
	CBS 117993	KAS 2133 = IBT 29908	Leaf surface, Puerto Rico
	CBS 127354^{T}	CBS H-20667 = DTO 9D4 = IBT 30769	Soil, Hawaii, USA
P. cf. *terrigenum*	CBS 127357	CBS H-20644 = DTO 19H8 = IBT 30770	Tortilla, USA
P. tropicoides	CBS 122410^{T}	DTO 10C4 = IBT 29043	Type; soil rainforest, near Hua-Hin, Thailand
	CBS 122436	DTO 10C8	Soil rainforest, near Hua-Hin, Thailand
P. tropicum		DTO 78C4 = IBT 27056	Leaf, Florida, USA
	CBS 112584^{T}	DTO 31B1 = IBT 24580	Soil under *Coffea arabica*, Mertha Subbagudigy, Karnataka, India
	CBS 130379	DTO 80D3 = IBT 16462 = DMG 1004	Soil, Galapagos Islands, Ecuador
P. ubiquetum	CBS 124317	DTO 30A8 = IBT 30705	Soil near lake Cratez, Barrine, Queensland, Australia
	CBS 124318	DTO 32D7 = IBT 30704	Soil, Lake Easchem, Queensland, Australia
	CBS 124450	DTO 84G8 = IBT 13179 = WSF 2210	A1 horizon soil, maple-elm-ash forest, Wisconsin, USA
	CBS 126436	DTO 30E2 = IBT 30397	Soil, wet forest, Atherton Tableland, Queensland, Australia
	CBS 126437^{T}	CBS H-20659 = DTO 78B5 = IBT 22226	Soil, Wilson Botanical Garden, Costa Rica
	CBS 126438	DTO 87B4 = IBT 30011	Soil under tree; Montagne d'Ambre, Madagascar
	CBS 126439	DTO 85B6 = IBT 30644	Soil, Ranoma fana, Madagascar
P. vancouverense	CBS 117962	DTO 55A4 = KAS 2098 = IBT 29801	Nut of *Juglans cinerea* (butternut); Fireman's Park, Niagara Falls, Ontario, Canada, 43.142051° -79.115903°
	CBS 122400	DTO 38F5	Organic soil, mixed forest Rijnsweerd, Utrecht, the Netherlands
	CBS 122401	DTO 21B1 = IBT 29063	Indoor air of house, Eindhoven
	CBS 124328	DTO 30D3 = IBT 29736	Soil, wet forest, Atherton Tableland, QLD, Australia
	CBS 124329	DTO 38D2 = IBT 30044	Organic soil, mixed forest Rijnsweerd, Utrecht, the Netherlands; dilution plate
	CBS 126321	DTO 78B6 = IBT 22265	Soil, Pacific slope of Volcan Barva at ca. 2000 m, just above Porrosati, in Heredia Province, under *Ticodendron* in wet montane forest, Costa Rica, November 2000
	CBS 126322	DTO 76B4 = IBT 20820	Soil under Maple tree, Vancouver, BC, Canada
	CBS 126323^{T}	CBS H-20646 = DTO 82B8 = IBT 20700	Soil under Maple tree, Vancouver, BC, Canada
	CBS 126324	DTO 76B9 = IBT 22472	Type; soil under *Nothofagus glauca*, Costa Azul School Forest of Universidad Catolica del Maule (35 37c / 72 c45w), Chile
	CBS 126325	DTO 30D1 = IBT 29058	Soil, wet forest, Atherton Tableland, QLD, Australia
	CBS 126326	DTO 76D2 = IBT 29309	Soil under Cypress, Pebble beach, Asilomar, California, USA
	CBS 126327	DTO 82C4 = IBT 20692	Soil under Maple tree, Vancouver, BC, Canada
	CBS 126328	DTO 85B2 = IBT 30004	Soil rainforest, Ranoma Fana, Madagascar
	CBS 130376	DTO 78A4 = IBT 16486	Soil under fern on slope on the way to the beach, "path 3", University of Vancouver, Vancouver, BC, Canada
P. waksmanii		DTO 78C1 = IBT 23508	Soil, New Zealand
	CBS 117502	DTO 3A8 = IBT 27053 = ATCC 48699 = FRR 906 = NRRL 906	Type of *P. rivolii*; forest soil, Poland
	CBS 117525	DTO 3A7 = IBT 27052 = NRRL 28095	Dead polypore, New Mexico, USA
	CBS 124295	DTO 84H6 = IBT 24654	Soil under conifer, Selatræd, Osterøy, Faroe Islands
	CBS 124321	DTO 42F8 = IBT 29680	Soil, Poland
	CBS 124322	CBS H-20652 = DTO 42G7 = IBT 29993	Soil, Poland
	CBS 126425	DTO 76A7 = IBT 13531	*Tilia* swamp, Denmark
	CBS 126426	CBS H-20658 = DTO 78A3 = IBT 15841 = DAOM 174586	Washed organic soil particle, Alberta, Canada
	CBS 126427	DTO 42A6 = IBT 29674	Soil, Poland

Table 1. (Continued).

Species	CBS no.	Other numbers	Substrate and locality
P. waksmanii	CBS 126428	DTO 82C6 = IBT 24649	Soil under tax tree, Selatræd, Osterøy, Faroe Islands
	CBS 126429	DTO 76C7 = IBT 23558x	Culture contaminant of IBT 23558
	CBS 230.28^{T}	DTO 22E6 = ATCC 10516 = FRR 777 = IFO 7737 = IMI 039746 = IMI 039746i = MUCL 29120 = NRRL 777 = QM 7681 = IBT 5003 = IBT 6994	Woodland soil, Purczcza Bialowieska Forest, Poland
P. wellingtonense	CBS 130375	CBS H-20657 = DTO 76C6 = IBT 23557	Soil, New Zealand
P. westlingii	CBS 118037	KAS 2189 = IBT 29822	Moose dung, Haliburton, Algonquin Park, Wildlife Research Station, Ontario, Canada
	CBS 118051	KAS 2205 = IBT 29838	Nut of *Juglans nigra* (black walnut); Fireman's Park, Niagara Falls, Ontario, Canada, 43.142051° -79.115903°
	CBS 118166	KAS 2117 = IBT 29853	Acorns of *Quercus*, Simcoe, Cawaja Beach, Ontario, Canada
	CBS 122407	DTO 28F9 = IBT 30688	Indoor air of house, Eindhoven, the Netherlands
	CBS 122408	DTO 18D7 = IBT 30677	Soil under oak, Spaanderswoud, Bussum, the Netherlands
	CBS 122409	DTO 17H7 = IBT 29062	Soil under oak, Spaanderswoud, Bussum, the Netherlands
	CBS 124311	DTO 39D4 = IBT 30774	Soil, Poland
	CBS 124312	DTO 30D6 = IBT 29067	Soil of rainforest, Atherton Tableland, Queensland, Australia
	CBS 124313	CBS H-20649 = DTO 30E3 = IBT 29992	Soil, Atherton Tableland, Queensland, Australia
	CBS 127003	DTO 32E1 = IBT 29659	Soil, Lake Easchem, Queensland, Australia
	CBS 127005	DTO 39D8 = IBT 30758	Soil, Poland
	CBS 127006	DTO 92G3	Soil heathland, Cartier heide, Eersel, the Netherlands
	CBS 127007	DTO 42H1 = IBT 30756	Soil, Poland
	CBS 127008	DTO 80I4 = IBT 30685	Indoor environment, Germany
	CBS 127037	DTO 78B7 = IBT 22399	Soil under *Cyathea* fern tree, on Rio Jaba trail, near Quebrada, Culebra, Wilson Botanical garden, Las Cruces Biological state park, Costa Rica
	CBS 127039	DTO 78B4 = IBT 22164	On *Ganoderma lucidum*, Turkey Swamp, New Jersey, USA
	CBS 127040	DTO 78G4 = DTO 78G3 = IBT 22985	Soil, St. Teresa Forest reserve, Brazil
	CBS 231.28^{T}	DTO 22E7 = IMI 092272 = IBT 15088	Soil under conifer, Denga Goolina, Poznan, Poland
	CBS 688.77	DTO 23D2 = IJFM 3046 = IBT 19471	Type of *P. citrinum* var. *pseudopaxilli*; andosol soil, Navarra, Spain

In this study, we delimited *Penicillium* section *Citrina* using a combination of ITS (internal spacer region and 5.8S rDNA gene) and partial *RPB2* gene sequences. After delimitation, the taxonomy of this section was studied in-depth using a polyphasic approach. Over 250 strains belonging to section *Citrina*, including type and freshly isolated strains, were included. Sequences of a part of the β-tubulin and calmodulin gene in combination with extrolite profiles, physiological and macro- and micromorphological characters were used for species delimitation.

MATERIAL AND METHODS

Strains

Data on the strains used in this study are listed in Table 1. More detailed information can be found in the on-line database of the CBS. These fungi are permanently preserved in the culture collection of the CBS-KNAW Fungal Biodiversity Centre, Utrecht, the Netherlands and placed in the working collection of the department of Applied and Industrial Mycology (DTO), housed at CBS.

DNA extraction, PCR amplification and sequencing

Strains were grown for 7 to 14 d on MEA prior to DNA extraction. DNA extraction was performed using the Ultraclean™ Microbial DNA isolation Kit (MoBio, Solana Beach, U.S.A.) according to the manufacturer's instructions. The extracted DNA was stored at -20 °C until used. The ITS regions and parts of the β-tubulin, calmodulin and *RPB2* genes were amplified and sequenced according the method described previously (Houbraken *et al*. 2007, 2011a, 2011b, Houbraken & Samson 2011).

Data analysis

The sequence data was optimised using the software package Seqman from DNAStar Inc. Sequences were aligned using the software Muscle in the MEGA5 programme (Tamura *et al*. 2011). The RAxML (randomised axelerated maximum likelihood) software (Stamatakis *et al*. 2008) was used in order to perform the Maximum Likelihood (ML) analysis on the combined data sets. Combined data sets were analysed as two distinct data partitions and individual branch length optimisation was applied per partition. Maximum Likelihood analysis on the individual data sets was performed with the MEGA5 software. Trees were redrawn from tree files using TREEVIEW (Page 1996). Section *Citrina* was delimitated

using a combination of ITS and *RPB2* sequences. *Coccidioides immitis* (strain RS) was used as an outgroup for this analysis. The phylogeny of different lineages within section *Citrina* was studied using a combination of partial β-tubulin and calmodulin sequences. These phylograms were rooted with *P. corylophilum* CBS 330.79, a member of section *Exilicaulis* (Houbraken & Samson 2011). Also the ITS region was sequenced for the majority of strains, and this locus was used to determine the effectiveness for species recognition. Unique, newly generated sequences were deposited in GenBank with accession numbers JN606358–JN606858.

Morphological analysis

Macroscopical characters were studied on the agar media Czapek yeast extract agar (CYA), CYA supplemented with 5 % NaCl (CYAS), yeast extract sucrose agar (YES), creatine sucrose agar (CREA), dichloran 18 % glycerol agar (DG18), oatmeal agar (OA) and malt extract agar (Oxoid) (MEA). The strains were inoculated at three points on 90-mm Petri dishes and incubated for 7 d at 25 °C in darkness. In addition, CYA plates were inoculated and incubated for 7 d at 15, 30 and 37 °C (CYA15°C, CYA30°C and CYA37°C, respectively). All media were prepared as described by Samson *et al*. (2010). The temperature-growth response of the strains was studied on CYA. Strains were inoculated at 3 points and incubated at 18, 21, 24, 27, 30, 33, 36 and 40 °C for 7 d in darkness. After incubation, the colony diameter on the various agar media was measured. Also the degree of sporulation, obverse and reverse colony colours and the production of soluble pigments was determined. Colony colours were not described using colour standards as good colour charts are rarely available and frequently used colour plates differ between the various copies of the same book. Instead, we choose to take pictures of the colonies with a Nikon Coolpix 990. The isolates were also examined for production of alkaloids reacting with Ehrlich reagent using a filter paper method (Lund 1995). The appearance of a violet ring within 10 min was regarded as a positive reaction, all other colours were considered negative.

Fungal material was examined using light microscopy (Olympus BH2 or Zeiss Axioskop 2 Plus). Microscopic mounts were prepared in 85 % lactic acid from MEA or OA and a drop of alcohol was added to remove air bubbles and excess conidia. Detailed examination of the ornamentation of the ascospores was performed by scanning electron microscopy (SEM). A quick sample preparation method was developed (J. Dijksterhuis unpubl. data), and this method is explained here in brief. Fungal cultures with ripe ascomata were flooded with 10 mM ACES buffer (pH 6.8, N-[2-acetamido]-2-aminoethane-sulfonic acid) supplemented with 0.05 % Tween 80. The ascomata were disconnected by vortexing with glass beads (1 mm) and filtered through sterile glass wool. Ascospores were spun down at 1,100×g (10 min) and washed twice in ACES buffer. In the last washing step, sterile demineralised water was used and the suspension was sonicated for 30 s prior to centrifugation. Filter disks with 1 µm pore size were placed on a Whatman filter paper (grade no. 1). Small aliquots of the ascospore-suspension were transferred on the filter disk, resulting in a quick removal of the water. The filter disks with the ascospores were fixed on aluminium stubs with carbon conductive double-sided tape and air-dried. Samples were examined in a JEOL 5600LV scanning electron microscope (JEOL, Tokyo, Japan).

Extrolite analysis

Strains listed in Table 1 were grown for 7 d at 25 °C on YES and CYA prior to extrolite extraction. Five agar plugs were taken along a diameter of the fungal colony and pooled together into the same vial. The extraction solvent ethyl acetate / dichloromethane / methanol (3:2:1, v/v/v) with 1 % (v/v) formic acid was added to the vial and subsequently ultrasonicated for 50 min. The extracts were transferred to 1.5 ml autosampler screw-cap vials, evaporated to dryness and re-dissolved in 400 µl methanol by ultrasonication for 10 min. Subsequently, the extracts were filtered through 0.45 µm filter (Minisart RC4, Sartorius, Germany) and kept at -18° C prior to analysis. The extracts were analysed by ultra high performance liquid chromatography (U-HPLC) using alkylphenone retention indices and diode array UV-VIS detection as described by Frisvad & Thrane (1987) and Nielsen *et al*. (2011). Identification of extrolites was performed by comparison of the UV-Visible spectra and retention times of the extrolites with those present in the collection at Department of Systems Biology, Kgs. Lyngby, Denmark. During our investigations many compounds were found, which could not be chemically identified. However, these extrolites proved to be important components for the species extrolite profile and they are listed between quotation marks.

RESULTS

Delimitation of section *Citrina*

In order to determine the species belonging to section *Citrina*, a phylogenetic study using combined sequence data of two loci (ITS and *RPB2*) was performed. 52 taxa were included in the analysis and the total length of the alignment was 1491 characters. The ITS partition was 575 characters long and had 174 variable sites, while the *RPB2* partition included 915 base pairs and 424 of them were variable. Figure 1 shows the results of this analysis. Members of section *Citrina* form a well-supported lineage on the phylogram (100 %). The majority of the branches in the backbone of this section are poorly supported. Two species-rich lineages are present in this section: one lineage is centered on *P. citrinum* and the other on *P. westlingii*. Three other well-supported lineages are present and these are centered on *P. sanguifluum*/*P. roseopurpureum*, *P. copticola*/*P. terrigenum* and *P. anatolicum*/*P. euglaucum*. These lineages appear to be less species-rich than those centered on *P. citrinum* and *P. westlingii*. *Penicillium shearii* and *P. paxilli* occurred on single branches and the relationship with other members of section *Citrina* remains unsolved. An overview of species classified by other authors in the *P. citrinum* series (Raper & Thom 1949, Ramírez 1982) or series *Citrina* (Pitt 1980) is presented in Table 2. Several of these species do not phylogenetically belong to section *Citrina* (Fig. 1), including *P. corylophilum* (synonyms: *P. obscurum*, *P. chloroleucon*, *P. citreovirens*, *P. humuli*), *P. soppii* (synonym: *P. matris-meae*), *P. herquei* (synonym: *P. luteocoeruleum nom. inval.*), *P. coralligerum*, *P. atrosanguineum, P. matriti* and *Aspergillus inflatus* (basionym: *P. inflatum*, R.A. Samson, unpublished data).

Species belonging to section *Citrina* share several characters. The majority of species produce symmetrically biverticillate conidiophores, flask shaped phialides (7.0–9.0 µm long) and relatively small-sized conidia (2.0–3.0 µm diam). The conidiophores of some species have an additional branch, which itself can also be biverticillate branched. Six of the 39 species produced greyish

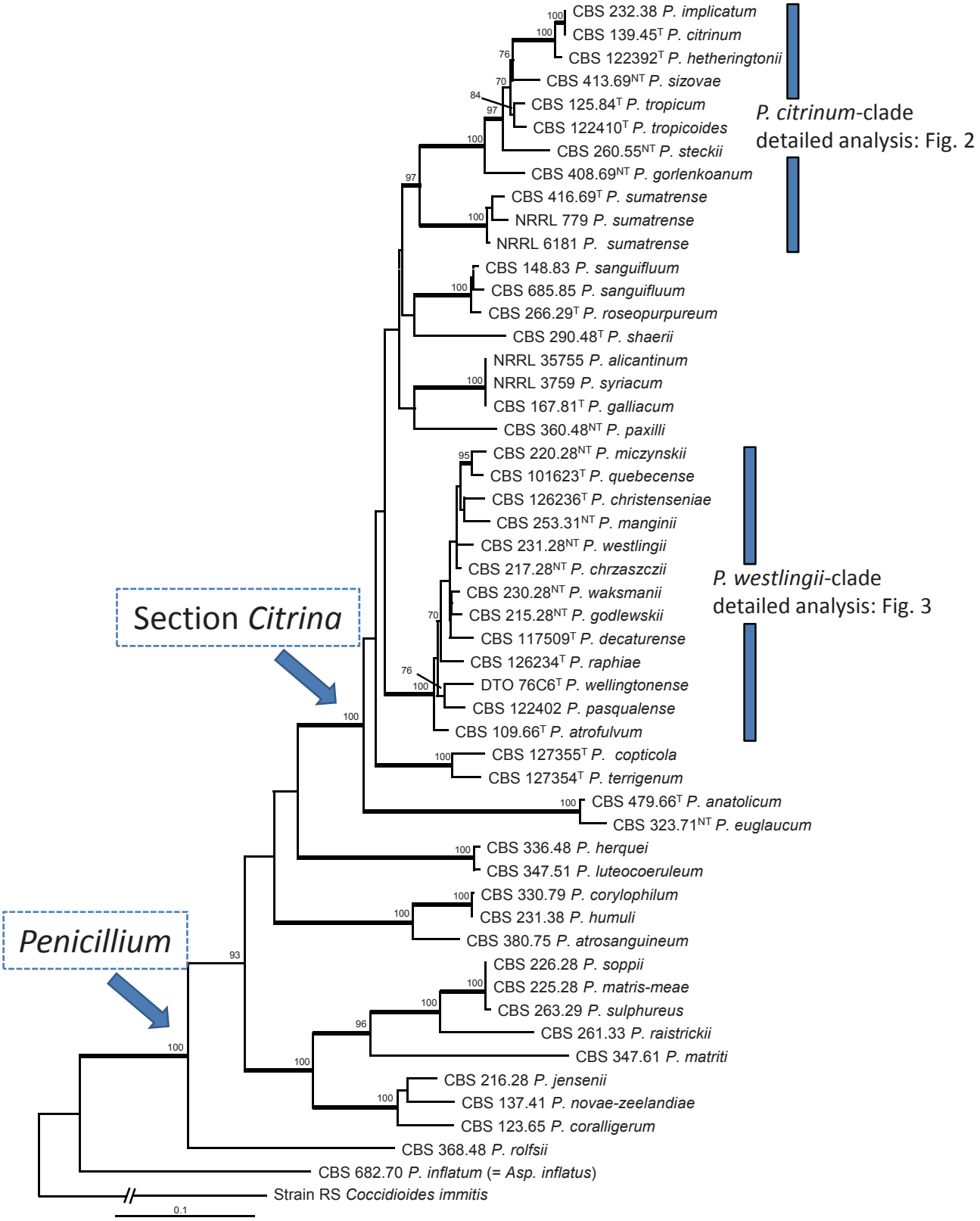

Fig. 1. Best-scoring Maximum Likelihood tree using RAxML based on a combination of partial *RPB2* and ITS sequences. Members of section *Citrina* are in a well-supported lineage (100 % bs) and some species previously belonging to series *Citrina* are placed in other lineages. Bootstrap percentages of the Maximum Likelihood (ML) analysis are presented at the nodes. Values less than 70 % supported in the ML are not shown and branches with more than 95 % bootstrap support are thickened. The bar indicates the number of substitutions per site. The phylogram is rooted with *Coccidioides immitis* (Strain RS).

brown cleistothecia and these cleistothecia contain flanged ascospores. The extrolite citrinin was produced by 16 of the 39 species and was most commonly produced by species belonging to section *Citrina*. The majority of the species grows poorly on CREA and do not have a violet reaction with Ehrlich reagent.

Phylogeny of section *Citrina*

Section *Citrina* was studied in detail with partial β-tubulin and calmodulin sequences. Three separated analyses were performed: one with species related to *P. citrinum* (= *P. citrinum*-clade) (Fig. 2), one with species related to *P. westlingii* (*P. westlingii*-clade) (Fig.

Table 2. Overview of species classified by Raper & Thom (1949), Pitt (1980) and Ramírez (1982) in the series *P. citrinum* or related *P. miczynskii* (Christensen *et al*. 1999). The names in bold are excluded from section *Citrina* in the current study.

Raper & Thom (1949)	Pitt (1980)	Ramírez (1982)	Christensen *et al*. (1999)
P. citrinum	*P. citrinum*	*P. citrinum*	*P. miczynskii*
P. corylophilum	***P. corylophilum***	***P. corylophilum***	*P. manginii*
P. steckii	*P. miczynskii*	*P. steckii*	***P. atrosanguineum***
	P. inflatum	***P. matriti***	***P. soppii***
	P. paxilli		*P. syriacum nomen ambiguum*
	P. herquei		*P. chrzaszcii nomen ambiguum*
	P. humuli		***P. sulphureum*** *nomen dubium*
			(*P. rolfsii*)*
			(*P. raistrickii*)*

* *P. raistrickii* and *P. rolfsii* were included in this study for comparison purposes and were not claimed to be related to *P. miczynskii*.

3) and one with all the other members of section *Citrina* (Fig. 4). Details on the partitions and variable sites are given in Table 3. Individual gene trees can be found in supplementary Figs 1–6.

Fifty-three strains were included in the analysis of the members belonging to the *P. citrinum*-clade and the total length of the alignment was 938 characters. This clade includes eight accepted species: *P. citrinum*, *P. hetheringtonii*, *P. sizovae*, *P. tropicoides*, *P. tropicum*, *P. steckii*, *P. gorlenkoanum* and *P. sumatrense*. The former seven species are accommodated in a well-supported lineage (100 %), and statistical support for the relationship of the latter species is lacking. However, this species was included in this analysis based on the results presented in Fig. 1, which confidently included this species in this clade (97 %).

One hundred and sixty-six isolates were included in the analysis of the *P. westlingii*-clade, and the total length of the alignment was 921 characters. Twenty-one species are present in this clade, and 14 of those are newly described here. The *P. westlingii*-clade can be subdivided into different subclades. *Penicillium cosmopolitanum*, *P. westlingii*, *P. nothofagi*, *P. pancosmium*, *P. decaturense*, *P. ubiquetum*, *P. waksmanii*, *P. godlewskii* and *P. chrzaszczii* are on a well-supported lineage (99 %). Another subclade only includes the newly described species *P. vancouverense*, *P. wellingtonense*, *P. pasqualense*, *P. atrofulvum* (96 %); *P. raphiae* and *P. christenseniae* are basal to this clade (82 %). *Penicillium cairnsense, P. quebecense*, *P. miczynskii*, *P. aurantiacobrunneum* and *P. neomiczynskii* are on another well-supported branch (98 %) and *P. manginii* is on a separate well-supported branch (100 %).

The phylogenetic relationships of the species not belonging to the *P. citrinum* or *P. westlingii*-clades are shown in Fig. 4. Sixty strains were included and the total length of the alignment was 1208 characters long. Six different lineages are present and comprise 10 species. *Penicillium paxilli* formed one clade, and this clade is related to a lineage containing the new species *P. copticola* and *P. terrigenum* (97 %). *Penicillium shearii* and *P. gallaicum* formed single lineages, while *P. sanguifluum* and *P. roseopurpureum* were together on a well-supported branch (100 %). *Penicillium euglaucum*, *P. anatolicum* and *P. argentinense* were also together on a well-supported branch (100 %).

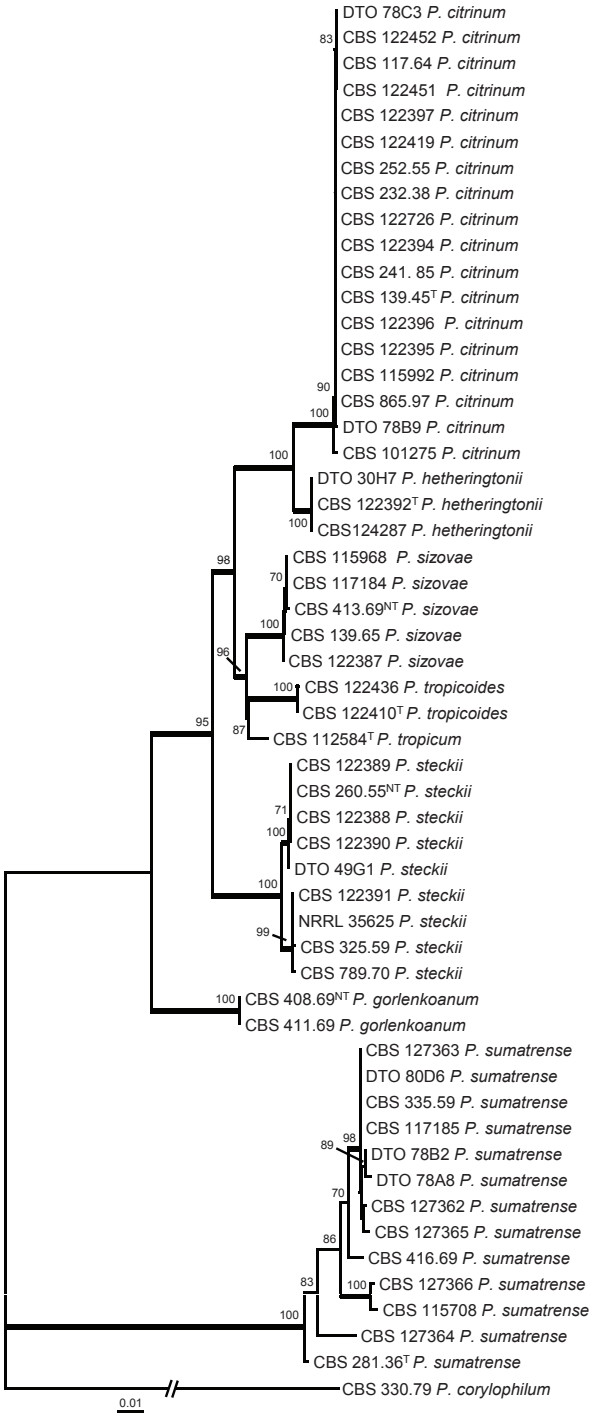

Fig. 2. Best-scoring Maximum Likelihood tree using RAxML based on a combination of partial β-tubulin and calmodulin sequences, showing the relationship among members of the *P. citrinum*-clade. Bootstrap percentages of the maximum likelihood (ML) analysis are presented at the nodes. Values less than 70 % supported in the ML are not shown and branches with more than 95 % bootstrap support are thickened. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. corylophilum* (CBS 330.79).

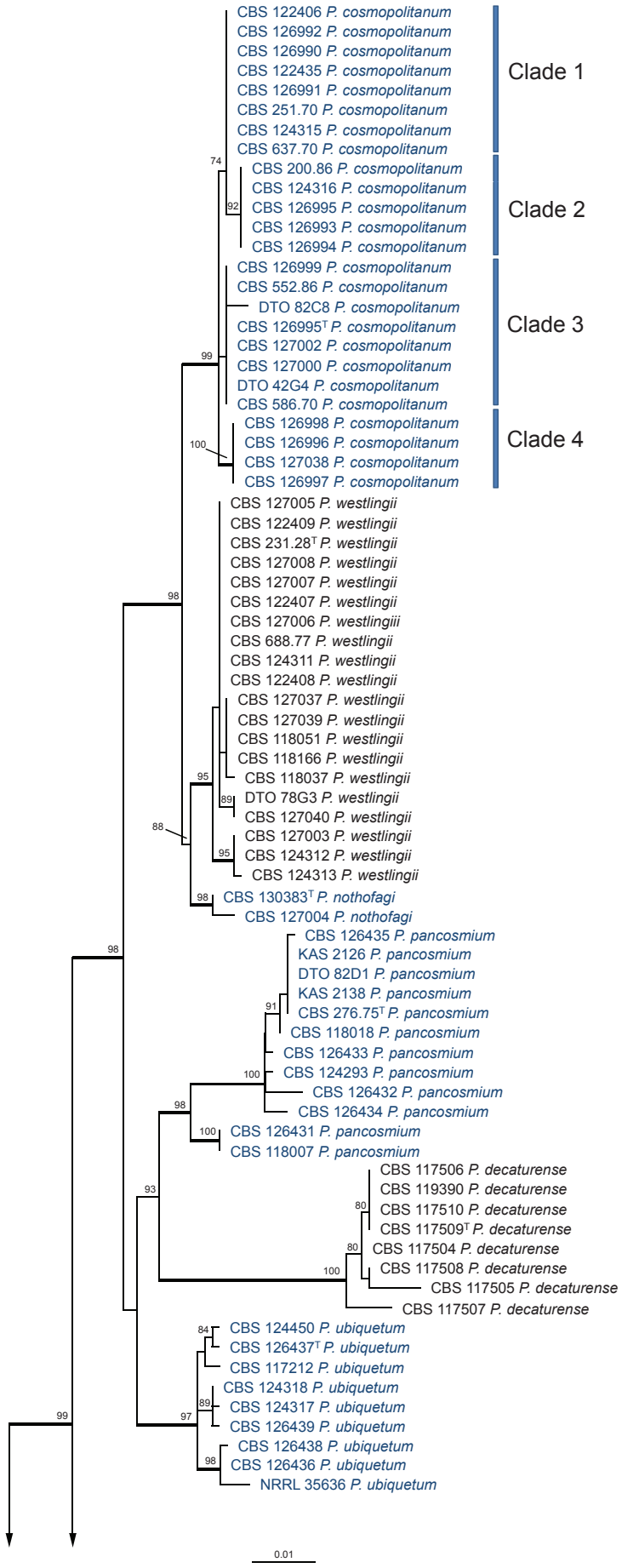

Fig. 3. Best-scoring Maximum Likelihood tree using RAxML based on a combination of partial β-tubulin and calmodulin sequences, showing the phylogenetic relationship among members of the *P. westlingii*-clade. Newly described species belonging to this section are presented in dark blue. Bootstrap percentages of the maximum likelihood (ML) analysis are presented at the nodes. Values less than 70 % supported in the ML are not shown and branches with more than 95 % bootstrap support are thickened. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. corylophilum* (CBS 330.79).

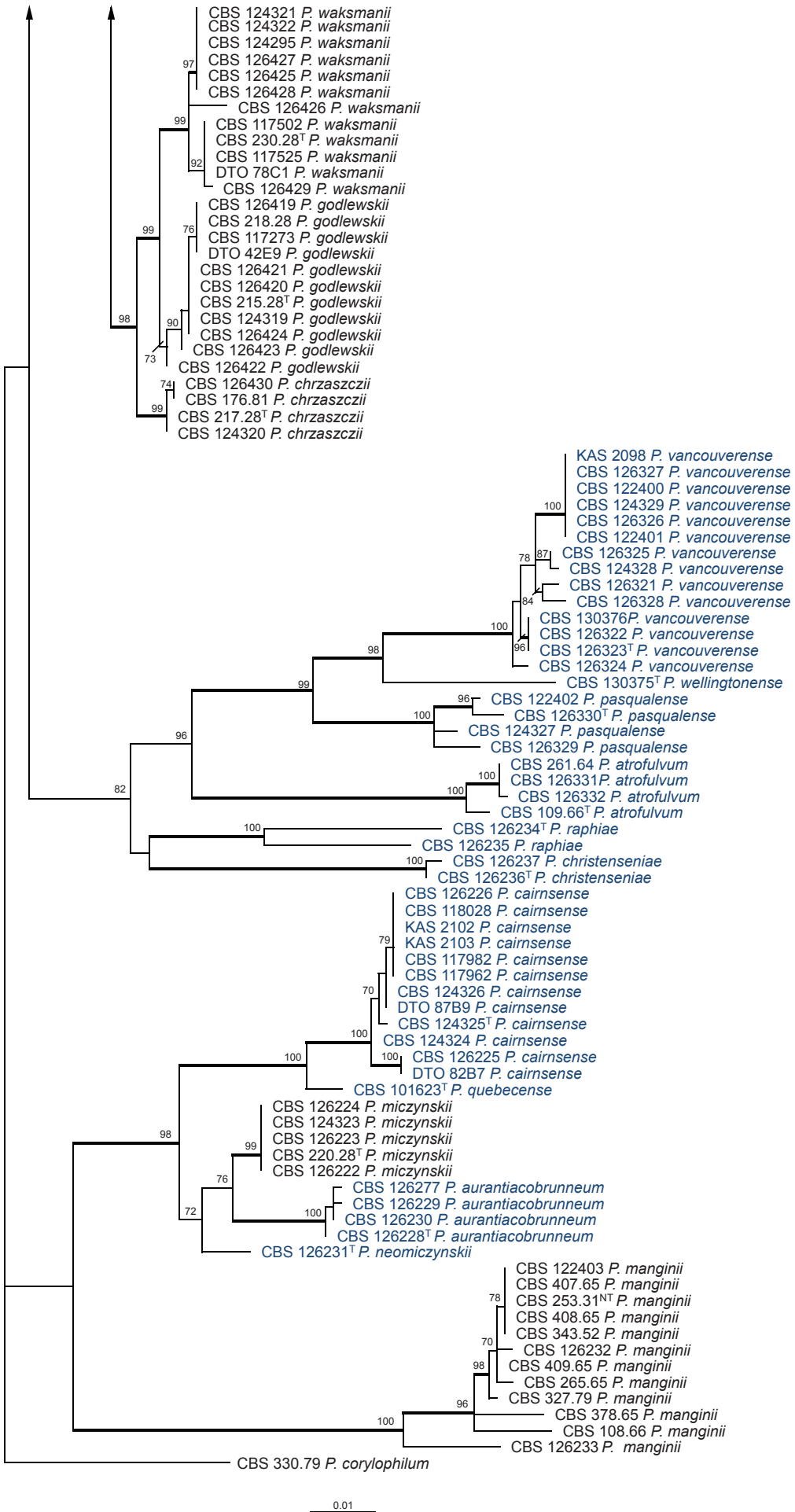

Fig. 3. (Continued).

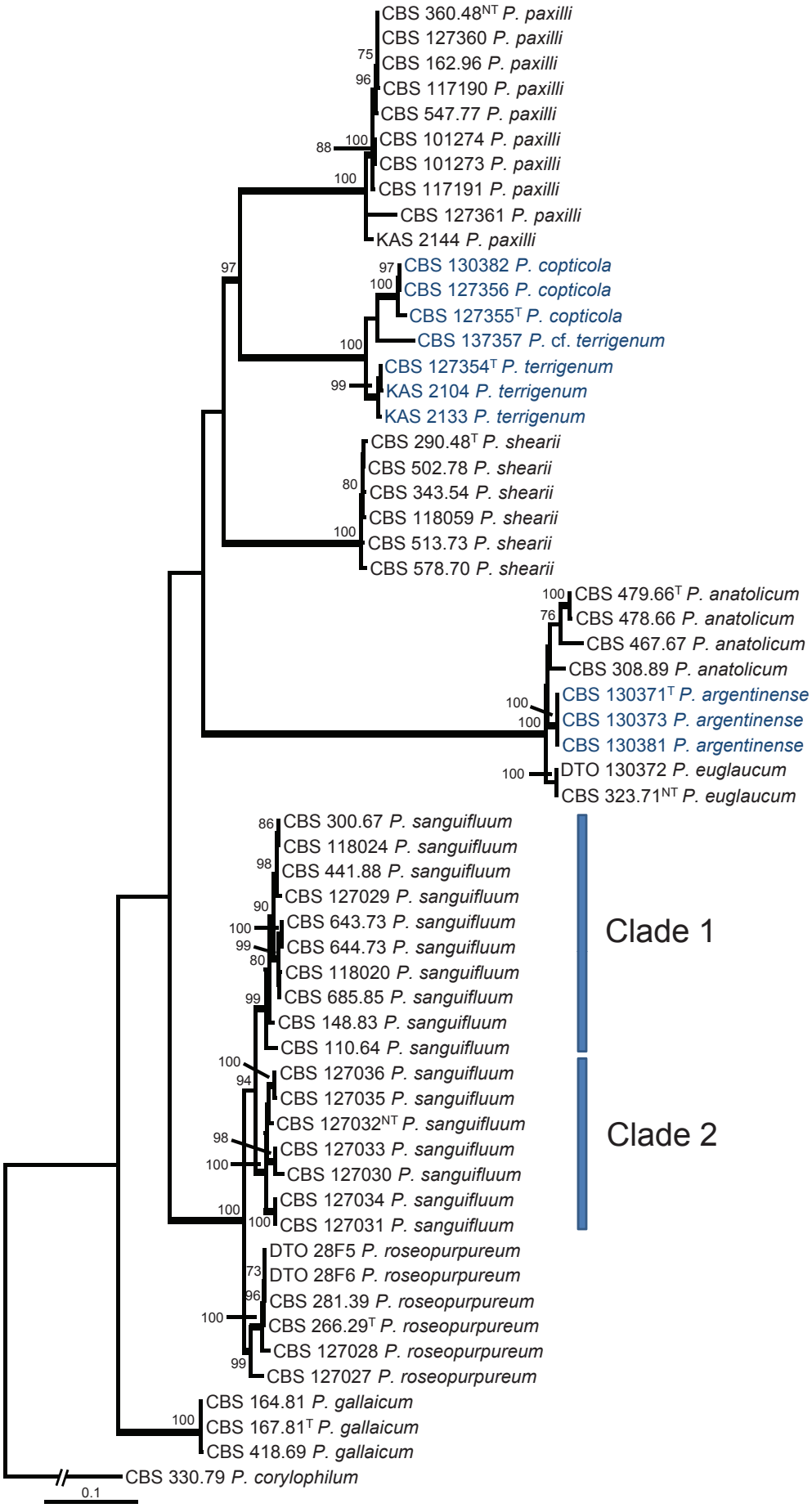

Fig. 4. Best-scoring Maximum Likelihood tree using RAxML based on a combination of partial β-tubulin and calmodulin sequences, showing the phylogenetic relationship among selected members of section *Citrina*. Newly described species belonging to this section are presented in dark blue. Bootstrap percentages of the maximum likelihood (ML) analysis are presented at the nodes. Values less than 70 % supported in the ML are not shown and branches with more than 95 % bootstrap support are thickened. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. corylophilum* (CBS 330.79).

Table 3. Parameters of matrices used to generate phylogenies.

Figure	No. species	β-tubulin		Calmodulin	
		Length	Variable sites	Length	Variable sites
Fig. 2, *P. citrinum*-clade	8	474	149	464	178
Fig. 3, *P. westlingii*-clade	21	452	148	469	225
Fig. 4, other sect. *Citrina* species	10	475	212	733	349

Morphology and physiology

Macro-morphology

Various phenotypic differences were observed among the investigated species. Growth rates on CYA, MEA, YES and DG18 are useful diagnostic features for species recognition. Some species, *e.g. P. wellingtonense*, *P. nothofagi* grow very restricted on CYA (5–15 mm), while others grow rapidly (*P. sumatrense*, *P. decaturense*, *P. quebecense*, 30–45 mm). Reverse colours on CYA and YES and the production of soluble pigments were also useful characters for differentiating species belonging to section *Citrina*. The colour of the mycelium was white and inconspicuous in most species, but certain species had (light) yellow coloured mycelium (*e.g. P. vancouverense*, *P. miczynskii*, *P. cairnsense*). Creatine agar, which is used for identification of species belonging to subgenus *Penicillium* (Frisvad 1985, Frisvad & Samson 2004) was also tested, but had little discriminatory power. Most species showed weak growth with no or weak acid production. Exceptions are *P. christenseniae*, *P. steckii* and *P. copticola* and certain strains of *P. pasqualense*, *P. tropicoides, P. tropicum* and *P. atrofulvum*. Another important feature was the production of sclerotia or cleistothecia. Six species formed cleistothecia on OA: *P. shearii*, *P. euglaucum*, *P. anatolicum*, *P. argentinense*, *P. tropicum* and *P. tropicoides*. These cleistothecia were coloured in greyish-brown shades and often took more than 6 wk to ripen. The ascospores of these species were ellipsoidal, with two narrow, closely appressed equatorial ridges. The ornamentation of the valves varied among the species, from finely roughened (*P. anatolicum*, *P. tropicum*) to warted (*P. tropicoides*) or reticulate (*P. argentinense*, *P. euglaucum*). Eight species produced sclerotia and these structures remained sterile after prolonged incubation up to 6 mo on OA, MEA and CYA. The production of sclerotia was species specific and most prominently present in freshly isolated strains. With exception of *P. gallaicum*, all sclerotium producing species belong to the *P. westlingii*-clade (*P. atrofulvum*, *P. aurantiacobrunneum*, *P. cairnsense*, *P. manginii, P. miczynskii*, *P. pasqualense*, *P. quebecense*). Some of the sclerotia of the latter six species were flecked, caused by short segments of pigmented external hyphae (Christensen *et al*. 1999). *Penicillium atrofulvum* produces black sclerotia, and all others were in shades of orange-brown. The Ehrlich reaction was of poor added value for differentiating among species of section *Citrina*. With exception of *P. aurantiacobrunneum*, all strains were negative in their Ehrlich reaction.

Micro-morphology

The micro-morphology was similar for most species and the majority has symmetrically branched biverticillate condiophores. Some species have additional branches and in some species these branches have the same branching pattern as the main axis ("double symmetrically biverticillate", *e.g.* in *P. pasqualense*). *Penicillium roseopurpureum*, *P. sanguifluum* and *P. galliacum* are exceptions in section *Citrina* and these species do not produce symmetrically branched conidiophores. They are predominantly monoverticillate, however, examination of older parts of the culture showed presence of divergent lower branch-like metulae or symmetrically biverticillate structures. The majority of the members of section *Citrina* have smooth walled stipes; however, there are exceptions, *e.g. P. paxilli* and certain isolates of *P. manginii* and *P. atrofulvum*. Conidia generally measure 2.0–3.0 µm and vary from smooth to rough-walled and from globose to ellipsoidal.

Temperature-growth curves

One of the main characters for identification of species in section *Citrina* is the optimum and maximum growth temperature on CYA. Temperature-growth curves were made, if possible, for at least four strains of each species. An overview of typical growth profiles is shown in Figs 5–9 and Table 4. The result of this analysis shows that optimum and maximum growth temperature is a species-specific character and an important feature for identification of members of section *Citrina*. Often phylogenetically related species also have similar optimum and maximum growth temperatures. Members of the *P. westlingii*-clade generally have maximum growth temperatures at or below 30 °C and an optimum between 21 and 24 °C. The exceptions in this clade are *P. pasqualense, P. quebecense* and *P. decaturense*. These species grow well at 30 °C (5–15 mm), and some strains can even grow at 33 °C. Members of the *P. citrinum*-clade, in contrast, have higher optimum and maximum growth temperatures. With exception of *P. tropicoides*, all species were able to grow at 33 °C. Furthermore, all examined *P. citrinum* strains consistently grew at 37 °C. Some strains of *P. sizovae* (five of seven) and *P. hetheringtonii* (one of four) were able to grow at this temperature, though more restrictedly than *P. citrinum*. Not only members of the *P. citrinum*-clade were able to grow at 37 °C. This feature is shared by *P. shearii*, *P. gallaicum* and *P. euglaucum* and related species.

Extrolites

Extrolite analysis showed that all species have a unique profile of metabolites. An overview of extrolites produced by all section *Citrina* species is given in Table 5. The extrolite profiles of each species are included in the species descriptions (see Taxonomy). Citrinin was most frequently detected and 41 % of the *Citrina* species were able to produce this extrolite. These citrinin producing strains were not present in a certain clade within section *Citrina*. In contrast, the tentatively named extrolite "MIF" (26 %) was only produced by species belonging to the *P. westlingii*-clade, and citreoviridin (23 %) and terrein (26 %) were almost exclusively produced by this clade. These extrolites could have been present in a common ancestor for all the species in the *P. westlingii*-clade. In general, the extrolite profiles were congruent with phenotype and phylogeny. Exceptions are in *e.g. P. manginii*, *P. vancouverense*, *P. waksmanii*, where strains could be divided in different subgroups based on extrolite profiles. More detailed chemical investigations are needed and these species might actually represent species complexes.

Table 4. Overview of main characters for identification of species belonging to section *Citrina*.

Penicillium sp.	Colony diameter (mm)		Cleistothecia / sclerotia	Maximum growth temperature (colony diameter, mm)*	Shape, ornamentation and size conidia	Typical feature(s)	Similar species
	CYA	MEA					
P. anatolicum	21–30	15–21	Cleistothecia	33 °C (15–25; 1/4) 36 °C (0–15; 3/4)	Globose to subglobose, finely roughened, 2.0–2.5 µm	Yellow soluble pigments	*P. argentinense*, *P. euglaucum*, *P. gallaicum*
P. argentinense	21–27	20–25	Cleistothecia	36 °C (mc–10)	Globose, smooth, 2.0-2.5 µm	Soluble pigment absent	*P. anatolicum*, *P. euglaucum*, *P. gallaicum*
P. atrofulvum	30–40	28–38	Sclerotia	27 °C (13–21)	Ellipsoidal, smooth, 2.0–3.0 × 2.0–2.5 µm	Dark sclerotia	None
P. aurantiacobrunneum	24–30	22–28	Sclerotia	27 °C (15–20; 2/4) 30 °C (0–mc; 2/4)	(Sub)globose, smooth, 2.0–3.0 µm	Ehrlich reaction positive	*P. miczynskii*, *P. neomiczynskii*
P. cairnsense	29–39	28–38	Sclerotia	30 °C (5–10; 1/4) 33 °C (0–5; 3/4)	(Sub)globose to broadly ellipsoidal, smooth, 2.0–3.0 × 1.8–2.5 µm	Red or blackish reverse on YES and/or DG18	*P. quebecense*
P. christenseniae	31–37	21–28	Absent	27 °C (15–22)	Globose to subglobose, finely roughened, 2.0–3.0 µm	Short stipes, moderate growth on CREA	*P. cosmopolitanum*, *P. pancosmium*, *P. ubiquetum*, *P. westlingii*
P. chrzaszczii	25–33	21–28	Absent	27 °C (15–25)	(Sub)globose, finely roughened, 2.0–3.0 µm	No sporulation of CYA, yellow soluble pigments on CYA, reverse on DG18 in shades of yellow	*P. cosmopolitanum*, *P. waksmanii*, *P. westlingii*
P. citrinum	27–33	18–25	Absent	36 °C (8–17)	(Sub)globose, smooth, 1.8–2.5 µm	Growth at 37 °C, yellow reverse on CYA, soluble pigment on CYA and YES	*P. gorlenkoanum*, *P. hetheringtonii*
P. copticola	31–37	25–34	Absent	33 °C (5–10)	Broadly ellipsoidal, smooth, 2.5–3.0 × 2.0–2.5 µm	Good growth on CREA	*P. christenseniae*, *P. steckii*, *P. terrigenum*,
P. cosmopolitanum	25–32	20–29	Absent	27 °C ((8–) 18–28)	Globose, roughened, 2.5–3.0 µm	No or weak sporulation on CYA and YES; reverse CYA beige-brown with orange coloured sulcations	*P. chrzaszczii*, *P. pancosmium*, *P. ubiquetum*, *P. westlingii*
P. decaturense	32–40	27–34	Absent	30 °C (5–15; 3/5) 33 °C (0–10; 2/5)	(Sub)globose, finely roughened, 2.0–2.5 µm	Colony diameters on CYA30°C 5–15 mm	*P. cosmopolitanum*, *P. pancosmium*, *P. ubiquetum*, *P. westlingii*
P. euglaucum	23–29	22–26	Cleistothecia	36 °C (5–15)	Globose, finely roughened, 2.0–2.5 µm	Ascospores 3.0–4.0 × 2.5–3.0 µm	*P. anatolicum*, *P. argentinense*, *P. gallaicum*
P. gallaicum	19–25	24–30	Sclerotia	36 °C (3–10)	(Sub)globose, smooth, 2.0–2.5 µm	Monoverticillate conidiophores	*P. anatolicum*, *P. argentinense*, *P. euglaucum*
P. godlewskii	15–25	12–20	Absent	27 °C (mc–10)	(Sub)globose, finely roughened, 2.0–2.5 µm	No growth at 30 °C and small colonies at 27 °C	None
P. gorlenkoanum	26–31	20–27	Absent	33 °C (6–12; 1/3) 36 °C (0–mc; 2/3)	(Sub)globose, finely roughened, 2.0–2.5 (–3.0) µm	Crème-brown reverse on CYA	*P. citrinum*, *P. hetheringtonii*
P. hetheringtonii	26–32	17–23	Absent	36 °C (7–14)	(Sub)globose, smooth to finely roughened, 2.0–2.5 µm	Growth at 36 °C	*P. citrinum*, *P. gorlenkoanum*
P. manginii	28–40	25–37	Sclerotia	27 °C (20–35; 5/8) 30 °C (0–10; 3/8)	(Broadly) ellipsoidal, smooth, 2.5–3.0 × 2.0–2.5 µm	Yellow mycelium on CYA15°C, fast growth rate on YES with red soluble pigments	*P. miczynskii*

Table 4. (Continued)..

Penicillium sp.	Colony diameter (mm)		Cleistothecia / sclerotia	Maximum growth temperature (colony diameter, mm)*	Shape, ornamentation and size conidia	Typical feature(s)	Similar species
	CYA	MEA					
P. miczynskii	21–27	17–25	Sclerotia	27 °C (12–25)	Subglobose to broadly ellipsoidal, smooth, 2.0–3.0 × 2.0–2.5 µm	Soluble pigments, if produced, yellow	*P. aurantiacobrunneum*, *P. manginii*, *P. neomiczynskii*
P. neomiczynskii	21–27	12–18	Absent	27 °C (8–15)	Subglobose-broadly ellipsoidal, smooth, 2.0–3.0 × 2.0–2.5 µm	Reverse on CYA yellowish brown, soluble pigments yellow-brown	*P. aurantiacobrunneum, P. miczynskii*
P. nothofagi	5–10	4–8	Absent	24 °C (10-15)	Globose to subglobose, finely roughened, 2.5–3.5 µm	Restricted growth on CYA, MEA and YES	*P. wellingtonense*
P. pancosmium	(23–) 28–35	(20–) 25–31	Absent	27 °C (15–25; 3/5) 30 °C (0–mc; 2/5)	Globose to subglobose, finely roughened, 2.0–3.0 µm	Reverse on YES yellow-orange or orange, dull-green or grey-green conidia on CYA	*P. ubiquetum*
P. pasqualense	25–35	(15–)25–30	Sclerotia	30 °C (6–15; 2/4) 33 °C (0–mc, 2/4)	(Sub)globose, spinose, 2.5–3.5 µm	Dark brown reverse on CYA, conidia (dark) blue green, spinose	None
P. paxilli	30–37	28–35	Absent	33 °C (mc–15)	Subglobose-broadly ellipsoidal, smooth or nearly so, 2.0–3.0 µm	Rough walled stipes, predominantly biverticillate with appressed terminal whorl of 4-8 metulae	*P. raphiae*
P. quebecense	38–42	30–35	Sclerotia	33 °C (3–10)	Subglobose, smooth, 2.0–3.0 µm	Dark red reverse on YES	*P. cairnsense*
P. raphiae	32–36	21–25	Absent	27 °C (15–22)	Broadly ellipsoidal,smooth or finely roughened, 2.0–2.5 × 1.8–2.5 µm	Symmetrically biverticillate conidiophores, broadly ellipsoidal conidia	*P. paxilli*
P. roseopurpureum	7–16	9–19	Absent	30 °C (mc–15)	(Sub)globose, smooth to finely roughened, 1.8–2.5 µm	Monoverticillate conidiophores, reverse on CYA in shades of red with red-brown diffusible pigments	*P. sanguifluum*
P. sanguifluum	(15–) 18–26	17–26	Absent	33 °C (mc–10)	Globose to subglobose, smooth to finely roughened, 2.0–2.5 µm	Monoverticillate conidiophores, reverse on CYA in shades of red with red-brown diffusible pigments	*P. roseopurpureum*
P. shearii	28–40	26–37	Cleistothecia	36 °C (8–20)	Subglobose-broadly ellipsoidal, smooth, 2.5–3.0 × 1.8–2.5 µm	Abundant production of dark grey coloured cleistothecia, growth at 37 °C	*P. tropicum*, *P. tropicoides*
P. sizovae	28–39	27–35	Absent	36 °C (4–8)	(Sub)globose, finely roughened, 2.0–2.5 µm	Fast growth rate on MEA and YES, pale reverse on CYA, growth at 36 °C	*P. steckii*
P. steckii	24–32	21–30	Absent	33 °C (mc–12 (–24); 5/6) 36°C (0–12; 1/6)	Broadly ellipsoidal towards fusiform, smooth, 2.3–3.0 × 2.0–2.5 µm.	Weak to moderate growth on CREA	*P. christenseniae*, *P. copticola*, *P. sizovae*, *P. sumatrense*, *P. terrigenum*
P. sumatrense	33–42	27–36	Absent	30 °C (10–30; 2/9) 33°C ((0–) 5–20; 7/9)	Subglobose-broadly ellipsoidal, finely roughened, 2.0–2.5 µm	Good growth on YES with yellow reverse	*P. steckii*
P. terrigenum	28–36	25–32	Absent	33 °C (10–15)	Broadly ellipsoidal, smooth, 2.0–3.0 × 2.0–2.5 µm	Poor growth on CREA	*P. copticola*, *P. steckii*
P. tropicoides	24–30	18–23	Cleistothecia	30 °C (10–16)	Broadly ellipsoidal, smooth, 2.0–3.0 × 1.8–2.5 µm	Abundant production of drab-grey cleitothecia, no growth at 33 °C	*P. shearii*, *P. tropicum*
P. tropicum	24–31	23–27	Cleistothecia	33 °C (8–18)	Broadly ellipsoidal, smooth, 2.0–3.0 × 2.0–2.5 µm	Abundant production of brownish-grey cleitothecia, growth at 33 °C	*P. shearii*, *P. tropicoides*

Table 4. (Continued)..

Penicillium sp.	Colony diameter (mm)		Cleistothecia / sclerotia	Maximum growth temperature (colony diameter, mm)*	Shape, ornamentation and size conidia	Typical feature(s)	Similar species
	CYA	MEA					
P. ubiquetum	24–34	18–26	Absent	27 °C (15–25)	(Sub)globose, finely roughened, 1.8–2.5 µm	Reverse on YES orange to pinkish-red, conidia dull green or dark green on CYA	*P. pancosmium*
P. vancouverense	20–30	16–23	Absent	27 °C (mc–15)	Subglobose, finely roughened, 2.0–3.0 µm	Light yellow mycelium (most pronouncedly on YES), colonies restricted	*P. manginii P. miczynskii*
P. waksmanii	(20–) 25–32	18–24 (–30)	Absent	27 °C (10–25)	(Sub)globose, finely roughened, 2.0–3.0 µm	Beige-brown reverse on CYA	*P. chrzaszczii, P. godlewskii*
P. wellingtonense	10–15	8–13	Absent	24 °C (15–20)	Subglobose to broadly ellipsoidal, smooth to finely roughened 2.5–3.5 µm	Slow growth on MEA and CYA, reverse on CYA in shade of orange	*P. nothofagi*
P. westlingii	(25–) 30–36	25–34	Absent	27 °C ((8–) 15–27; 11/14) 30 °C (0–mc; 3/14)	Globose, roughened, 1.8–2.5 µm	No or weak sporulation on CYA and YES; reverse CYA pale, pale-beige or pinkish-beige	*P. chrzaszczii, P. cosmopolitanum, P. pancosmium, P. ubiquetum*

mc = micro colonies, 1–2 mm in diam.

*The maximum growth temperature is determined at intervals of 3 °C (see material & methods). The highest temperature with visible growth is listed and the colony diameter is mentioned between brackets. If the maximum growth varied within a species, then both temperatures are listed together with the number of isolates showing growth at that temperature.

DISCUSSION

The species in section *Citrina* are very common in soil, but are also found in foods, indoor air and many other substrates. The description of 17 new species may help determining more accurately the mycobiota of soils, which may be important for biodiversity, ecological and climate change studies. Even though the species treated here are both phylogenetically and ecologically related, section *Citrina* was treated very differently in previous taxonomic studies (Raper & Thom 1949, Pitt 1980, Ramírez 1982). The inclusion of physiological, chemical and nucleotide sequence based data has changed the perception of series and sections in filamentous fungi and these taxonomic groupings are now both phylogenetically and ecologically consistent. Disregarding the many different species concepts proposed, a polyphasic approach to taxonomy has proven to give clear results that are predictive (*e.g.* Frisvad & Samson 2004). The species in section *Citrina* grow optimally at 23–26 °C, can grow at low water activities, in substrates containing NaCl, and often produce citrinin, citreoviridin, anthraquinones, indol-alkaloids, paxillin, and/or isochromantoxins. On the other hand, no species in section *Citrina* produce asperentins, atpenins, austins, brevianamides, chaetoglobosins, chrysogines, communesins, compactins, curvulic acids, cycloaspeptides, expansolides, fumitremorgins, fumagillins, gliotoxins, griseofulvins, kojic acids, mycophenolic acids, ochratoxins, paraherquamides, patulins, penicillic acids, penicillins, penigequinolones, penitrems, psychrophilins, pyripyropens, terrestric acids, tryptoquialanins, tryptoquivalins, viridicatumtoxins, verruculones, viridicatins, xanthocillins, xanthoepocins, xanthomegnins, and several other extrolites, often found in *Penicillium* subgenus *Penicillium* or section *Lanata-divaricata* (as series *Simplicissima*) (Frisvad & Filtenborg 1990, Frisvad & Samson 2004). Despite this, a large number of extrolites could not be identified (Table 5) and may prove to be new interesting drug leads.

TAXONOMY

Species delimitation

In this study, we applied a polyphasic approach for species recognition. Phenotypic and physiological characters combined with extrolite profiles and DNA sequences were used for species delimitation. New species were introduced when the results of these approaches were congruent. In some cases, these approaches were incongruent. In general, the phylogenetic analysis based on partial β-tubulin and calmodulin sequences generated more taxonomic units (clades) than the analyses based on phenotypic and physiological characters. If no distinct differences in phenotype and/or extrolite patterns were detected between those closely related clades, then we decided to keep them as one species, until more evidence becomes available to warrant describing them as species. More details on these decisions are given in the "taxonomy and phylogeny" part in the species descriptions.

Identification

As mentioned above, current species delimitation is based on a combination of characters. An overview of useful phenotypic and physiological characters for identification is given in Table 4. Although there are differences in phenotype and physiology among these species, identification based on these features

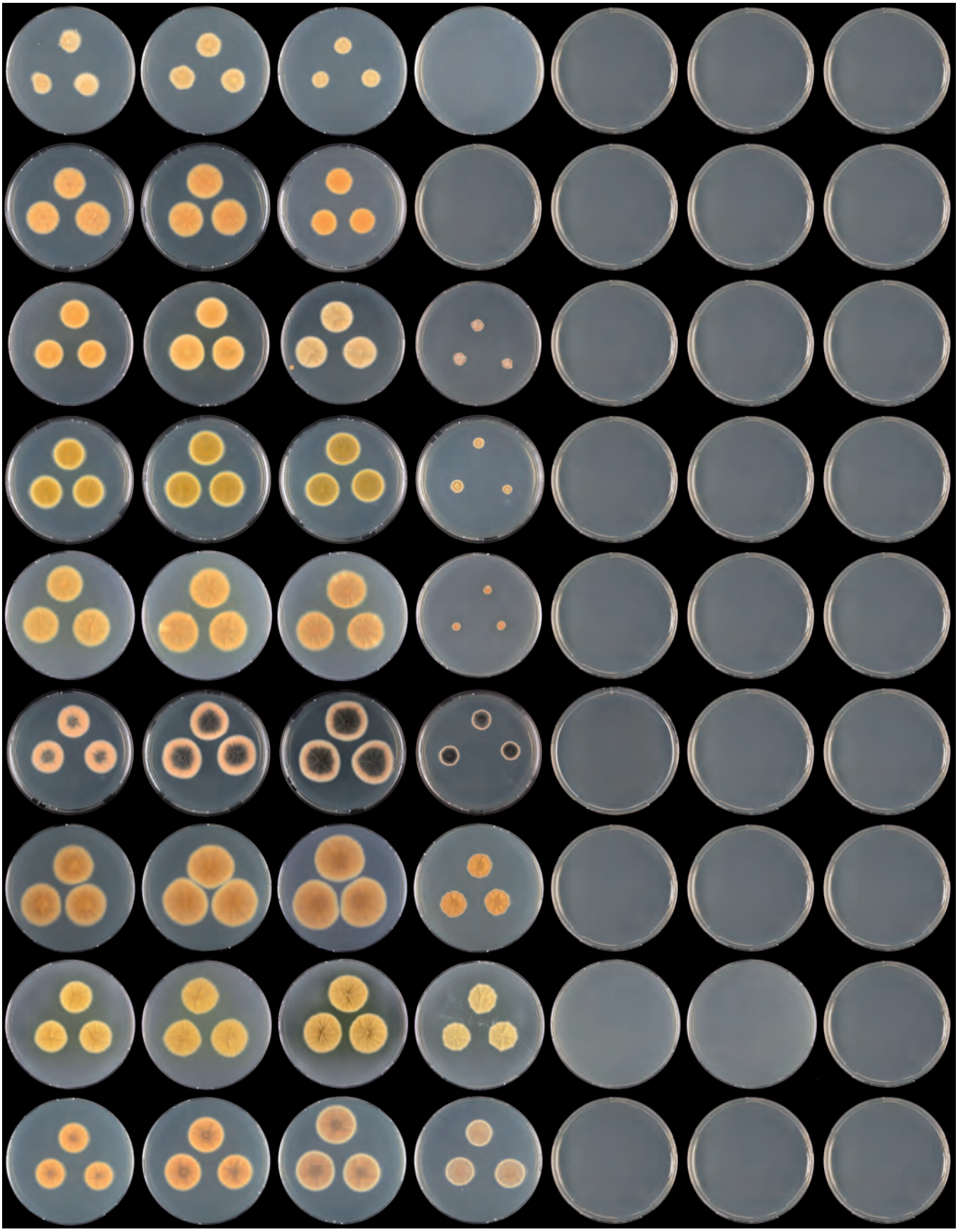

Fig. 5. Overview of growth rates on CYA (reverse) after 7 d at various temperatures. Row, left to right: 21, 24, 27, 30, 33, 36 °C; columns, top to bottom: *P. nothofagi*, *P. wellingtonense*, *P. godlewskii*, *P. vancouverense*, *P. neomiczynskii*, *P. atrofulvum*, *P. christenseniae*, *P. miczynskii*, *P. waksmanii*.

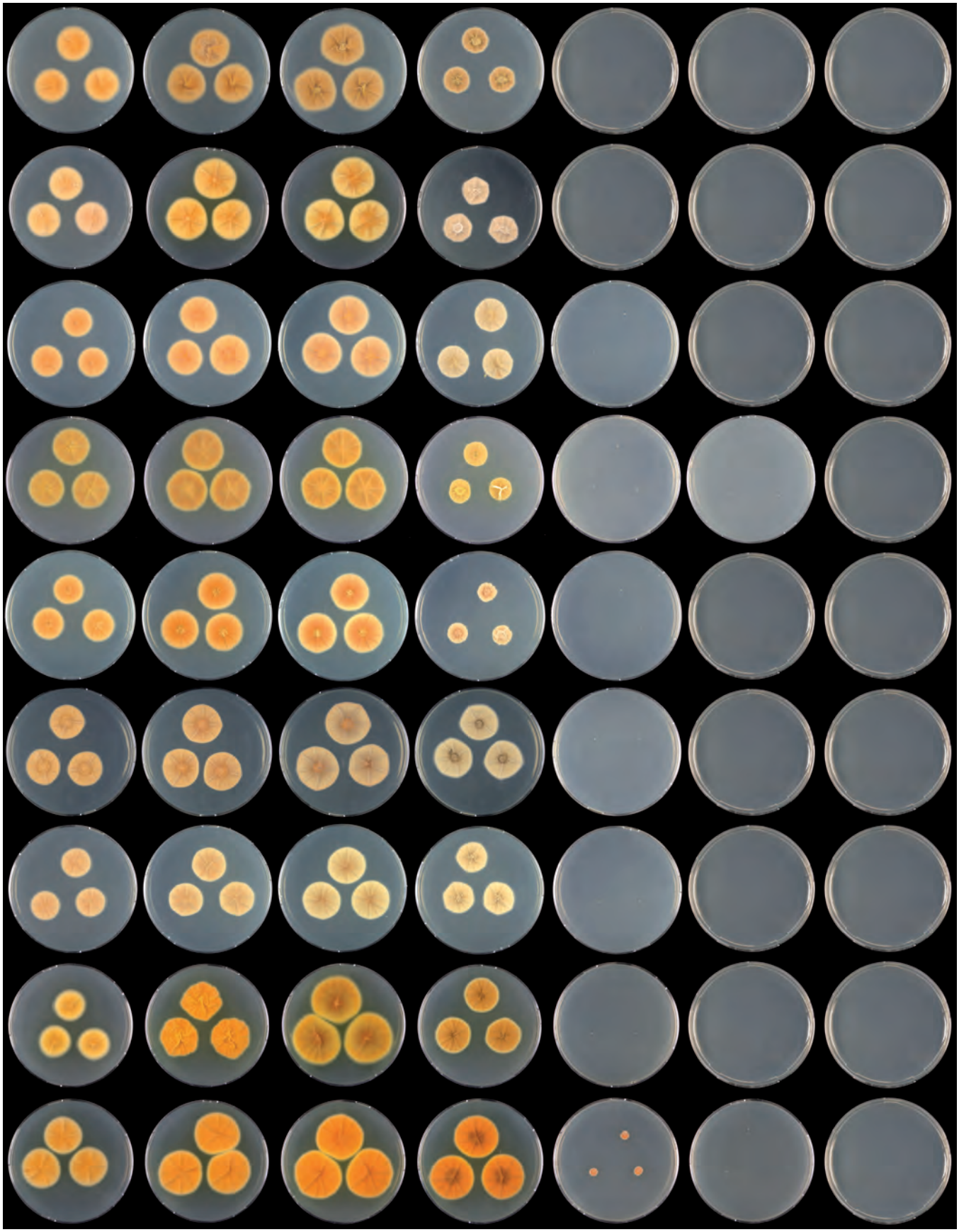

Fig. 6. Overview of growth rates on CYA (reverse) after 7 d at various temperatures. Row, left to right: 21, 24, 27, 30, 33, 36 °C; columns, top to bottom: *P. raphiae*, *P. chrzaszczii*, *P. ubiquetum*, *P. aurantiacobrunneum*, *P. pancosmium*, *P. cosmopolitanum*, *P. westlingii*, *P. manginii*, *P. manginii*.

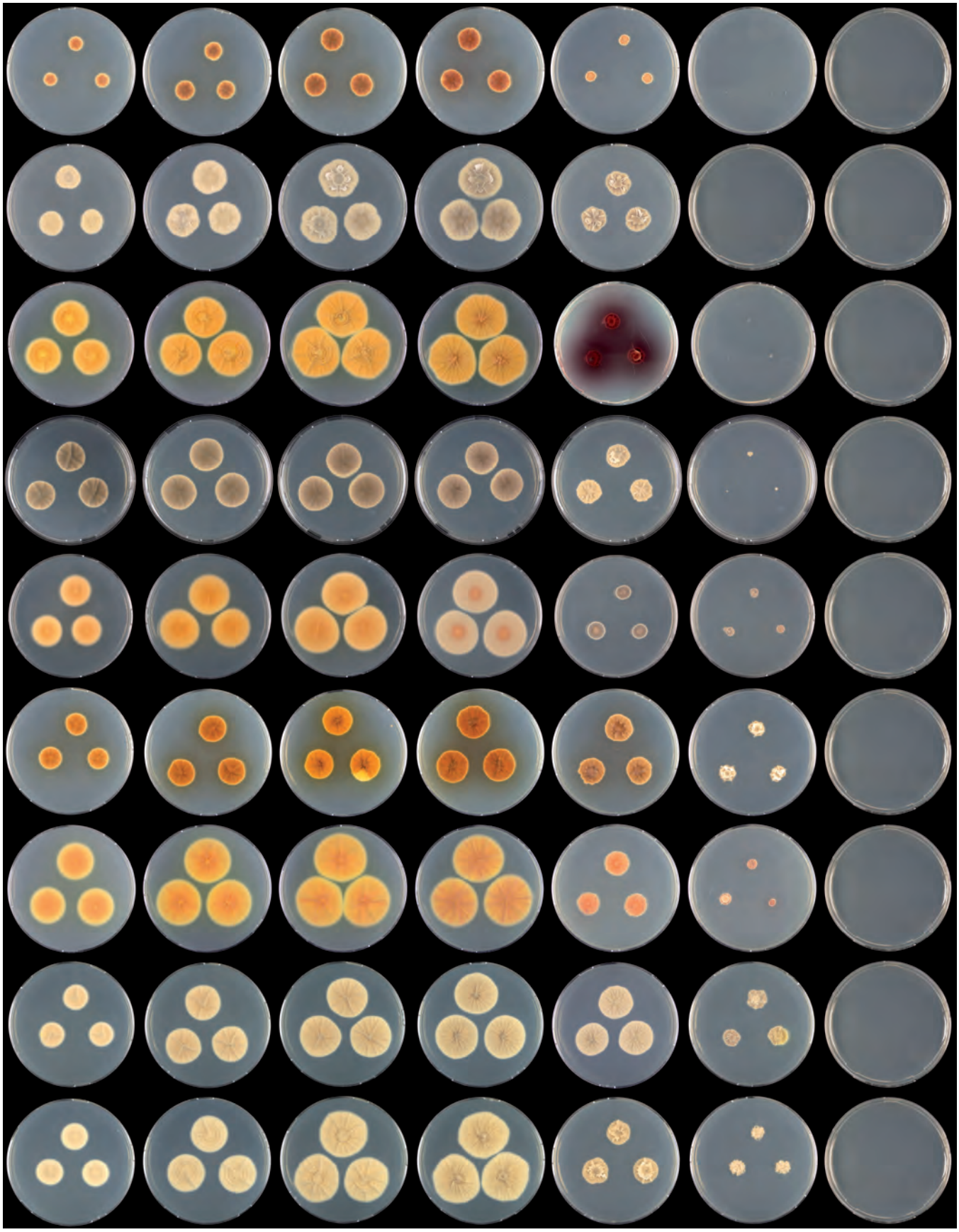

Fig. 7. Overview of growth rates on CYA (reverse) after 7 d at various temperatures. Row, left to right: 21, 24, 27, 30, 33, 36 °C; columns, top to bottom: *P. roseopurpureum*, *P. tropicoides*, *P. cairnsense*, *P. pasqualense*, *P. decaturense*, *P. sanguifluum*, *P. quebecense*, *P. terrigenum*, *P. copticola*.

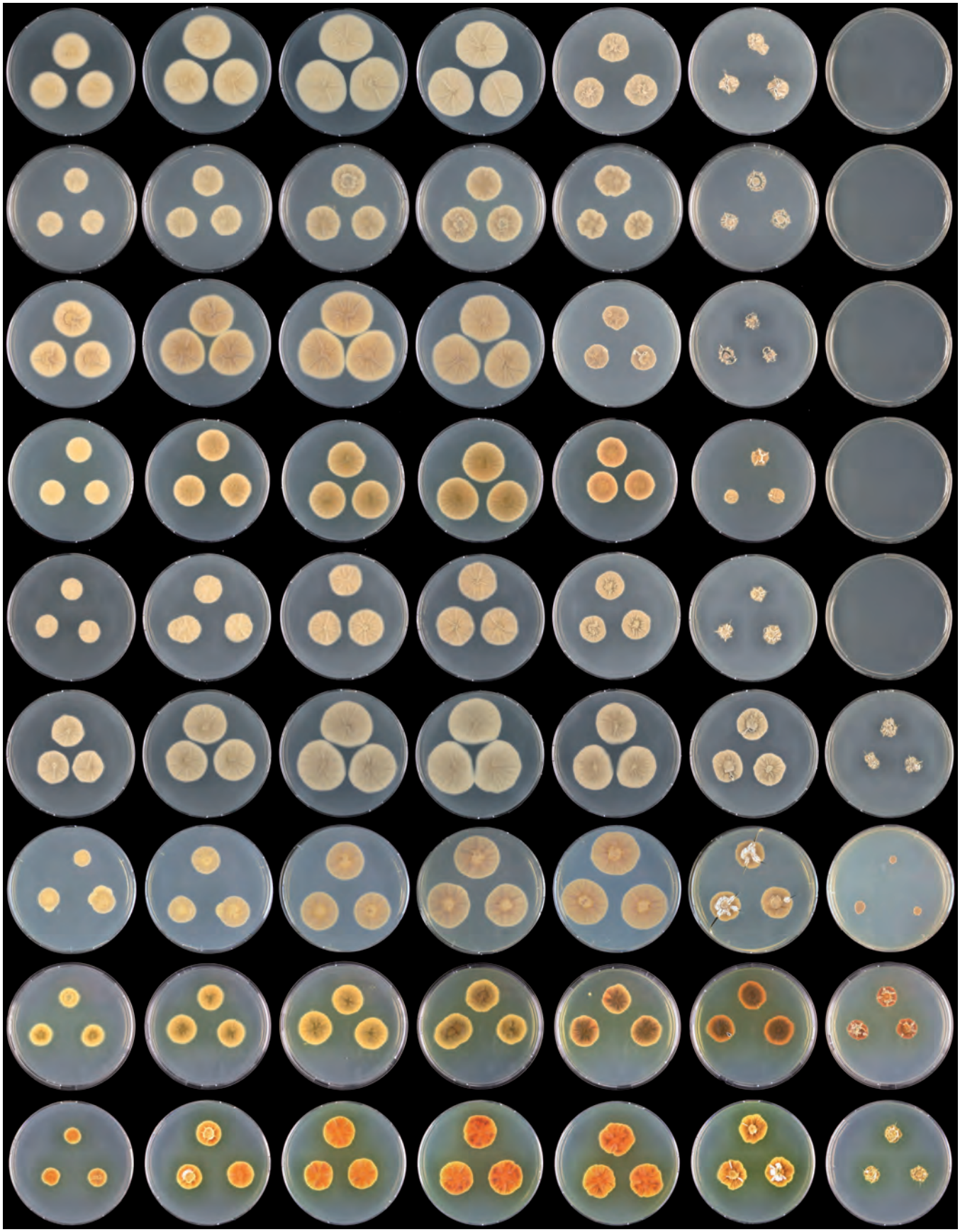

Fig. 8. Overview of growth rates on CYA (reverse) after 7 d at various temperatures. Row, left to right: 21, 24, 27, 30, 33, 36 °C; columns, top to bottom: *P. paxilli*, *P. tropicum*, *P. sumatrense*, *P. gorlenkoanum*, *P. steckii*, *P. sizovae*, *P. argentinense*, *P. euglaucum*, *P. anatolicum*.

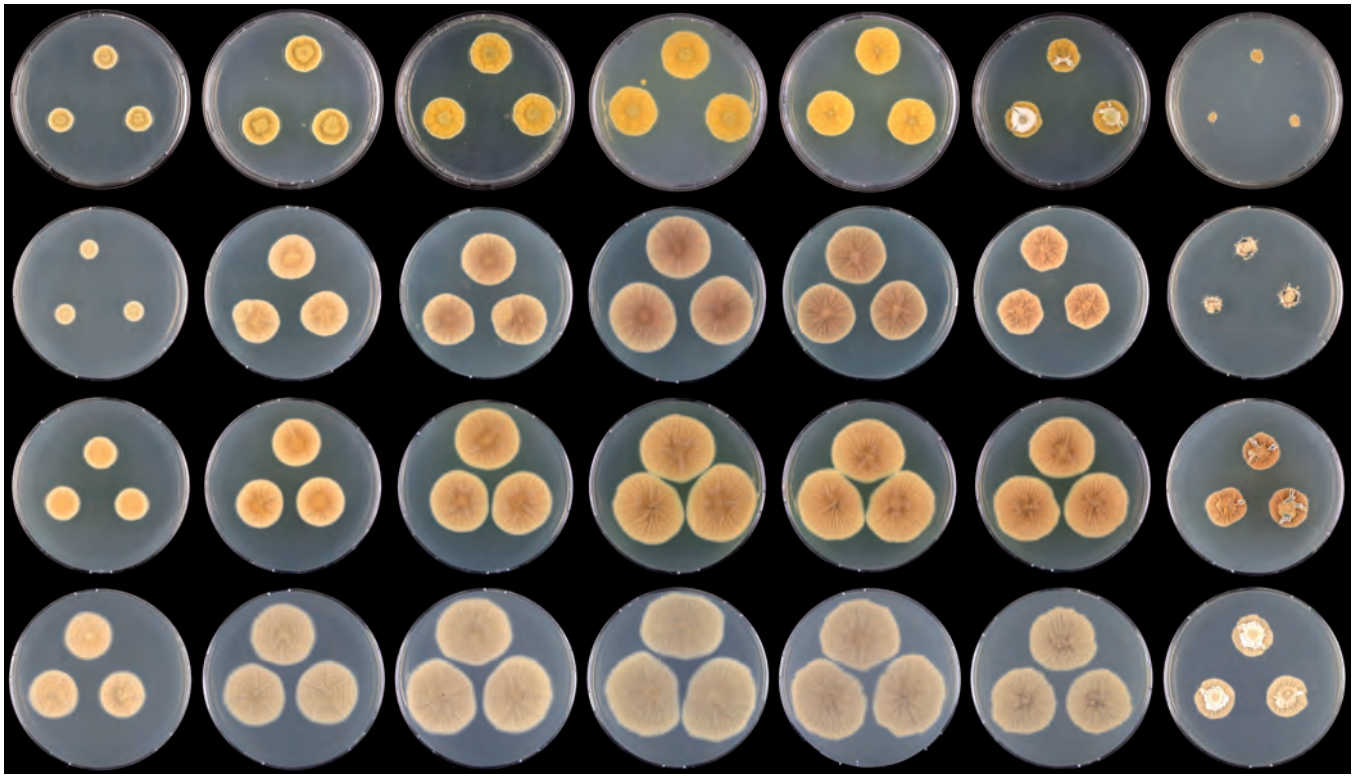

Fig. 9. Overview of growth rates on CYA (reverse) after 7 d at various temperatures. Row, left to right: 21, 24, 27, 30, 33, 36 °C; columns, top to bottom: *P. gallaicum*, *P. hetheringtonii*, *P. citrinum*, *P. shearii*.

remains difficult for non-specialists. Molecular based identification (sequencing) is nowadays common practice. Currently, ITS is the accepted barcode (C. Schoch *et al*., unpubl. data); however, this locus is inadequate for species recognition in section *Citrina*. 55 % of the species could be unambiguously identified using ITS sequences. Especially in the *P. westlingii*-clade, many species share the same ITS sequence. Partial calmodulin and β-tubulin sequences had sufficient discriminatory power to differentiate all species of section *Citrina*. It is therefore recommended to sequence either gene for correct species identification.

List of accepted species and their synonyms

Our polyphasic taxonomic approach revealed that *Penicillium* section *Citrina* includes 39 species including 17 new species. An overview of species belonging to section *Citrina* is presented in Table 4. Species belonging section *Citrina* and their synonyms are listed in Table 6 and the current classification is compared with those of Pitt (1980), Ramírez (1982) and Pitt *et al*. (2000).

Species descriptions

Penicillium anatolicum Stolk, Ant. van Leeuwenhoek 34: 46. 1968. Fig. 10.

= *Eupenicillium anatolicum* Stolk, Ant. van Leeuwenhoek 34: 46. 1968.

Typus: ex soil, Turkey (CBS 479.66, holotype; cultures ex-type CBS H-20647 = DTO 16B7 = IBT 16177 = IBT 30764).

Description: Colony diam, 7 d, in mm: CYA 18–30; CYA15°C 4–8; CYA30°C 23–32; CYA37°C 0–5; MEA 15–21; YES 23–30; DG18 20–28; ratio CYAS:CYA 0.85–1.0; creatine agar 11–18, weak growth, weak or no acid, and no base production.

Sporulation on CYA moderate, conidia grey green, cleistothecia abundantly produced in freshly isolated strains and covered under a felt of conidiophores, mycelium inconspicuous, clear exudate produced in small droplets, soluble pigment strong yellow, margin entire, reverse yellow-brown. Sporulation on YES moderate, conidia blue-green, mycelium pale-yellow, soluble pigments yellow, reverse (vivid) yellow. Sporulation on DG18 weak to moderate, conidia blue-green, mycelium white, reverse vivid yellow. Moderate sporulation on MEA, conidia dull-green with a blue element, colony texture slightly floccose, mycelium white. Ehrlich reaction negative.

Cleistothecia produced on most agar media, yellow-brown when young, becoming brown at age; globose or subglobose, up to 200 µm diam, occasionally larger, consisting of sclerotioid masses of polygonal cells, ripening after 4–5 wk or more. Ascospores ellipsoidal, with 2 distinct, appressed equatorial ridges, smooth to slightly roughened valves under light microscope, but showing warts and small ridges when viewed with SEM, 2.5–3.5 × 2.0–3.0 µm. Conidiophores predominantly biverticillate, stipes variable in length 20–200 µm, smooth walled, 2.0–3.0 µm wide. Metulae in verticils of 2–3 (–4), unequal in length, divaricate, slightly inflated at the apex, 10–20 × 2.0–4.0 µm. Phialides ampulliform, 6.0–8.0 × 2–3 µm. Conidia globose, finely roughened, 2.3–2.8 µm diam.

Extrolites: Anthraquinones, bisanthrons, curvularin, dehydrocurvularin, sorbicillins, "POTO", "3-T".

Diagnostic characters: Yellow soluble pigments (sorbicillins), metulae of unequal length, with inflated apex.

Similar species: *Penicillium anatolicum* is phylogenetically related to *P. euglaucum* and *P. argentinense*. The ascospores of *P. euglaucum* are larger than those of *P. anatolicum* and *P. argentinense*. In addition, *P. argentinense* does not produce

Table 5. Extrolites produced by species assigned to *Penicillium* section *Citrina*.

Species	Extrolites produced
P. anatolicum	Anthraquinones, bisanthrons, curvularin, dehydrocurvularin, sorbicillins, "POTO", "3-T"
P. argentinense	Curvularin, dehydrocurvularin, "AURANMUF", "OXIM"
P. atrofulvum	"ALK", "GULLA", "SOLIS", "3T"
P. aurantiacobrunneum	Benzomalvins, citreoviridin, terrein, "OTOT"
P. cairnsense	CBS 126226, CBS 117982, CBS 118028 and CBS 117962: benzomalvins, citreoviridin, phoenicin, decaturin; CBS 124325, CBS 126225 and DTO 87B9: citreoviridin, terrein and/or quinolactacin; other extrolites: "KUM", "MIF", "MIM", "RAI", "SENGA"
P. christenseniae	Citrinin, quinolactacin, "FON", "KUM", "MIF", "RYLA"
P. chrzaszczii	Citrinin, terrein, "MIF", "MIM", "RAI", "3T", "VERN"
P. citrinum	Citrinin, quinolactacins, citrinadins, perinadine, several anthraquinones, "CITY", "met k", "shamix"
P. copticola	"GULLA", "HAEN", "PRS", "VERSI"
P. cosmopolitanum	Citrinin, okaramin, perinadine, territrems, "CURVO", "HAEN", "PHOE", "ROTO", "SENGA", "TRIP", "VERSI", "XANTHOC"
P. decaturense	Daldinin D, decaturin A, deoxyoxalicine B, terrein, "SENGA", "SNIL", "SVOL", "VERSI", "XANTHOC"
P. euglaucum	Terrein, "ALK", "FRIL", "GLAD", "RAI", "SPOKO", "3-T"
P. gallaicum	Citreoviridin, "KOKSO", "3-S", "TIDL", "VYL"
P. godlewskii	Citrinin, citreoviridin, decaturin, okaramin, perinadine, "TRIP"
P. gorlenkoanum	Citrinin, costaclavin, chanoclavine-I, "KUSK", "PHOE", "WK", "WS", "WT" and "WØ"
P. hetheringtonii	Citrinadine, citrinin, quinolactacin, anthraquinones, "SHAMIX", "FON", "CITY", "PR1-x"
P. manginii	Citrinin, citreomontanin, citreoviridin A, citreoviridinol A_1 and A_2, epicitreoviridinol, phoenicin, "MIF", "MIM"
P. miczynskii	Citreoviridin, cyclopiazonic acid, quinolactacin, terrein, "met OE", "MIF", "TERRIT", "XANTHOC"
P. neomiczynskii	Citreoviridin, terrein, "MIF", "OFSO"
P. nothofagi	Citrinin, "CURVU", "SENTRIP", "SKAEM"
P. pancosmium	Citrinin, daldinin D, decaturin, terrein, "MELI", "ORAN", "SENGA", "XANTHOC"
P. pasqualense	Pyrenocines, indol alkaloids, "PAS"
P. paxilli	Paxillin, dehydroxypaxillin, 1'-O-acetylpaxillin, meleagrin, "PU", "PUX", "TOTO"
P. quebecense	Citreoviridin, phoenicin, terrein, "SENOE" (verrucofortine-type molecule), "MIF", "MIM", "SENGA", "alk-770"
P. raphiae	CBS 126234^T: citrinin, "FON", "MIF","KUM", "LOST","PHOE", and "TRIP"; CBS 126235: citrinin, quinolactacin,"FON", "MIF", "KUM", "MIM", "REJS", "SENGA", and "XANTHOC"
P. roseopurpureum	Bisanthrons, roseopurpurin, sorbicillins, "AQ", "SEL"
P. sanguifluum	Bisanthrons, roseopurpurin, β-hydroxycurvularin, dehydrocurvularin, curvularin, "FOSI", "FYKS", "SNIT", "TIDL", "VERN"
P. shearii	Paxillin, paspalinine, shearinin A & B, "XX" and several indole alkaloids
P. sizovae	Quinolactacin, tanzawaic acid E, verrucolone, "AFSI", "CHAE and "PNUF"
P. steckii	Isochromantoxins, quinolactacin, tanzawaic acid E, "ALTI", "EXPO", "FON", "FOS", "GLOO", "GYF", "PHOE", "RAI", "STOK", "SVUL", "VERN"
P. sumatrense	Curvularin, dehydrocurvularin, "POTO", "SAAT", "TERRIT", "TIDL", "VOX"
P. terrigenum	"HAEN", "ISOC", "PRS", "VERSI"
P. tropicoides	Isochromantoxins, several apolar indol-alkaloids, "CITY", "HOLOX", "PR1-x", "RAIMO"
P. tropicum	Several apolar indol-alkaloids, "CITY","EMON", "HOLOX" and "RAIMO
P. ubiquetum	Citrinin, terrein, "ALK", "GLYF", "RAI", "TRIP", "XANTHOC"; CBS 126438, CBS 126436: anthraquinone bisanthorns, citrinin, okaramins, and "SENGA"
P. vancouverense	Citrinin, citreoviridin, "MIF", "PAS", "met OE"
P. waksmanii	Citrinin, cyclopiamin, meleagrin (only produced by one isolate), "GLYF", "PAS", "SENGA".
P. wellingtonense	Citrinin, decaturin, "MIF", "met Q", "POF", "RAI", "TRIP", "XANTHOC"
P. westlingii	Citrinin, curvularin, dehydrocurvularin,"PHOE", "TRIP", "XANTHOC"

yellow soluble pigments. *Penicillium gallaicum* also yellow soluble pigments (citreoviridins), but forms predominantly monoverticillate conidiophores and produces sclerotia instead of ascomata.

Distribution and ecology: Soil seems to be the primary habitat; isolated in Turkey, Florida, USA and South-Africa.

Barcode & molecular based ID: GenBank no. GU944598. This species can be identified with ITS, β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: Stolk & Samson (1983) reduced *E. anatolicum* to synonymy with *E. euglaucum*, and *P. citreonigrum* was considered to be the anamorph. Peterson (2000) found that *E. anatolicum* is phylogenetically distinct from *E. euglaucum* and not closely related to *P. citreonigrum*. In contrast, our data show that *P. anatolicum* and *P. euglaucum* are closely related and both species are phylogenetically distinct from *P. citreonigrum* (Houbraken & Samson 2011). CBS 308.89 warrants further attention. This strain is phylogenetically related to *P. anatolicum* (Fig. 4), though without statistical support. This strain resembles *P. anatolicum* in many aspects, but differs in having a more restricted growth rate on DG18.

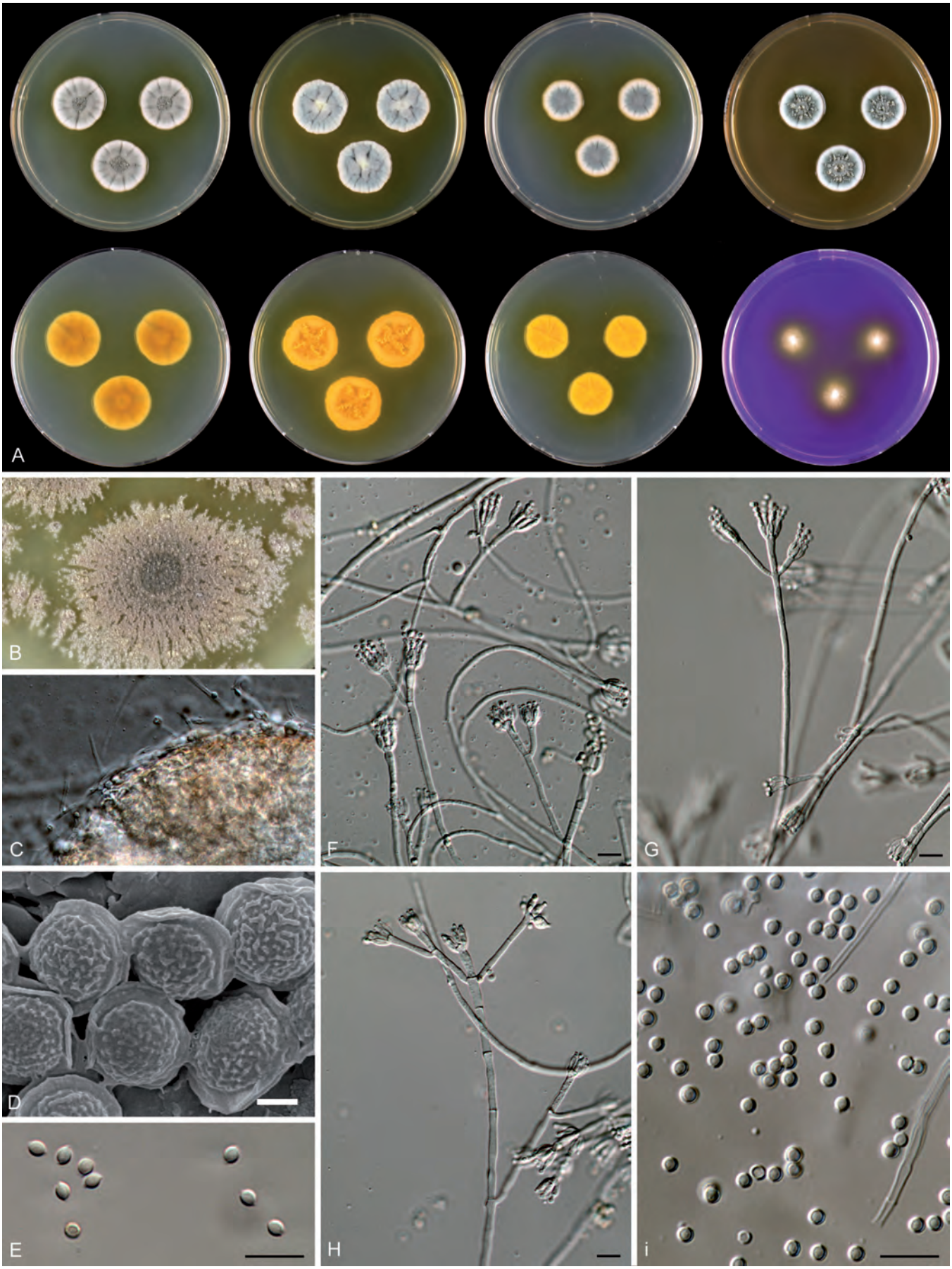

Fig. 10. *Penicillium anatolicum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–C. Ascomata. D–E. Ascospores. F–H. Conidiophores. I. Conidia. Scale bars = 10 µm.

Table 6. Taxonomic disposition of members of section *Citrina* in different studies of *Penicillium*.

Original species name	Pitt (1980)	Ramírez (1982)	Pitt *et al*. (2000)	Current study
Citromyces cesiae	*P. roseopurpureum*	*P. cyaneum*, p.655	*P. roseopurpureum*	*P. roseopurpureum*
Citromyces sanguifluus	*P. roseopurpureum*	*P. roseopurpureum*	*P. roseopurpureum*	*P. sanguifluum*
Citromyces subtilis	*P. citrinum*	*P. sartoryi*	*P. citrinum*	*P. citrinum*
E. anatolicum	*E. anatolicum*	Not treated	*E. anatolicum*	*P. anatolicum*
E. euglaucum	Not treated	Not treated	Not treated	*P. euglaucum*
E. shearii	*E. shearii*	Not treated	*E. shearii*	*P. shearii*
E. tropicum	Not treated	Not treated	Not treated	*P. tropicum*
P. alicantinum	Not treated	*P. alicantinum*	*P. citreonigrum*	*P. gallaicum*
P. aurifluum	*P. citrinum*	*P. citrinum*	*P. citrinum*	*P. citrinum*
P. baradicum	*P. citrinum*	*P. baradicum*	*P. citrinum*	*P. sumatrense*
P. botryosum	*P. citrinum*	*P. botryosum*	*P. citrinum*	*P. citrinum*
P. carminoviolaceum	*P. roseopurpureum*	*P. roseopurpureum*	*P. roseopurpureum*	*P. roseopurpureum*
P. chrzaszczii	*P. miczynskii*	*P. jensenii*	*P. miczynskii*	*P. chrzaszczii*
P. citrinum	*P. citrinum*	*P. citrinum*	*P. citrinum*	*P. citrinum*
P. corylophiloides nom. inval.	*P. jensenii*	*P. corylophilum*	*P. jensenii*	*P. steckii*
P. damascenum	*P. melinii*	*P. damascenum*	*P. melinii*	*P. gorlenkoanum*
P. decaturense	Not treated	Not treated	Not treated	*P. decaturense*
P. gallaicum	Not treated	*P. gallaicum*	*P. citreonigrum*	*P. gallaicum*
P. godlewskii	*P. jensenii*	*P. godlewskii*	*P. jensenii*	*P. godlewskii*
P. gorlenkoanum	*P. citrinum*	*P. gorlenkoanum*	*P. citrinum*	*P. gorlenkoanum*
P. hetheringtonii	Not treated	Not treated	Not treated	*P. hetheringtonii*
P. implicatum	*P. implicatum*	*P. implicatum*	*P. implicatum*	*P. citrinum*
P. kapuscinskii	*P. canescens*	*P. kapuscinskii*	*P. canescens*	*P. godlewskii*
P. lacussarmientei	Not treated	Not treated	*P. roseopurpureum*	*P. sanguifluum*
P. manginii	*P. miczynskii*	*P. miczynskii*	*P. manginii*	*P. manginii*
P. meleagrinum var. *viridiflavum*	*P. janthinellum*	*P. janthinellum*	*P. janthinellum*	*P. sumatrense*
P. miczynskii	*P. miczynskii*	*P. miczynskii*	*P. miczynskii*	*P. miczynskii*
P. paxilli	*P. paxilli*	*P. paxilli*	*P. paxilli*	*P. paxilli*
P. pedemontanum	*P. miczynskii*	*P. pedemontanum*	*P. pedemontanum*	*P. manginii*
P. phaeojanthinellum	*P. fellutanum*	*P. fellutanum*	*P. fellutanum*	*P. citrinum*
P. rivolii	*P. jensenii*	*P. janthinellum*	*P. jensenii*	*P. waksmanii*
P. roseopurpureum	*P. roseopurpureum*	*P. roseopurpureum*	*P. roseopurpureum*	*P. roseopurpureum*
P. sartoryi	*P. citrinum*	*P. sartoryi*	*P. citrinum*	*P. citrinum*
P. sizovae	*P. fellutanum*	*P. sizovae*	*P. sizovae*	*P. sizovae*
P. steckii	*P. citrinum*	*P. steckii*	*P. steckii*	*P. steckii*
P. sumatrense	*P. corylophilum*	*P. corylophilum*	*P. corylophilum*	*P. sumatrense*
P. tropicoides	Not treated	Not treated	Not treated	*P. tropicoides*
P. turolense	Not treated	*P. turolense*	*P. westlingii*	*P. chrzaszczii*
P. vaccaeorum	Not treated	Not treated	*P. roseopurpureum*	*P. sanguifluum*
P. waksmanii	*P. waksmanii*	*P. waksmanii*	*P. waksmanii*	*P. waksmanii*
P. westlingii	*P. waksmanii*	*P. waksmanii*	*P. westlingii*	*P. westlingii*

Penicillium argentinense Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563185. Fig. 11.

Etymology: Named after Argentina, the location of the type culture.

Differt ab omnibus speciebus affinibus coloniis ad 37 °C haud crescentibus, reverso pallido vel psammocolorato coloniae in agaro CYA et YES, sine pigmentis solubilibus.

Typus: ex soil, Valdes Peninsula, Chubet, Argentinia, M.B. Pildain. (CBS H-20641 – holotypus, cultures ex-type CBS 130371 = DTO 16B7 = IBT 30761).

Description: Colony diam, 7 d, in mm: CYA 21–27; CYA15°C 3–7; CYA30°C 22–30; no growth on CYA37°C; MEA 20–25; YES 22–29; DG18 14–20; ratio CYAS:CYA 1.0–1.1; creatine agar 8–14, weak growth, weak acid and no base production.

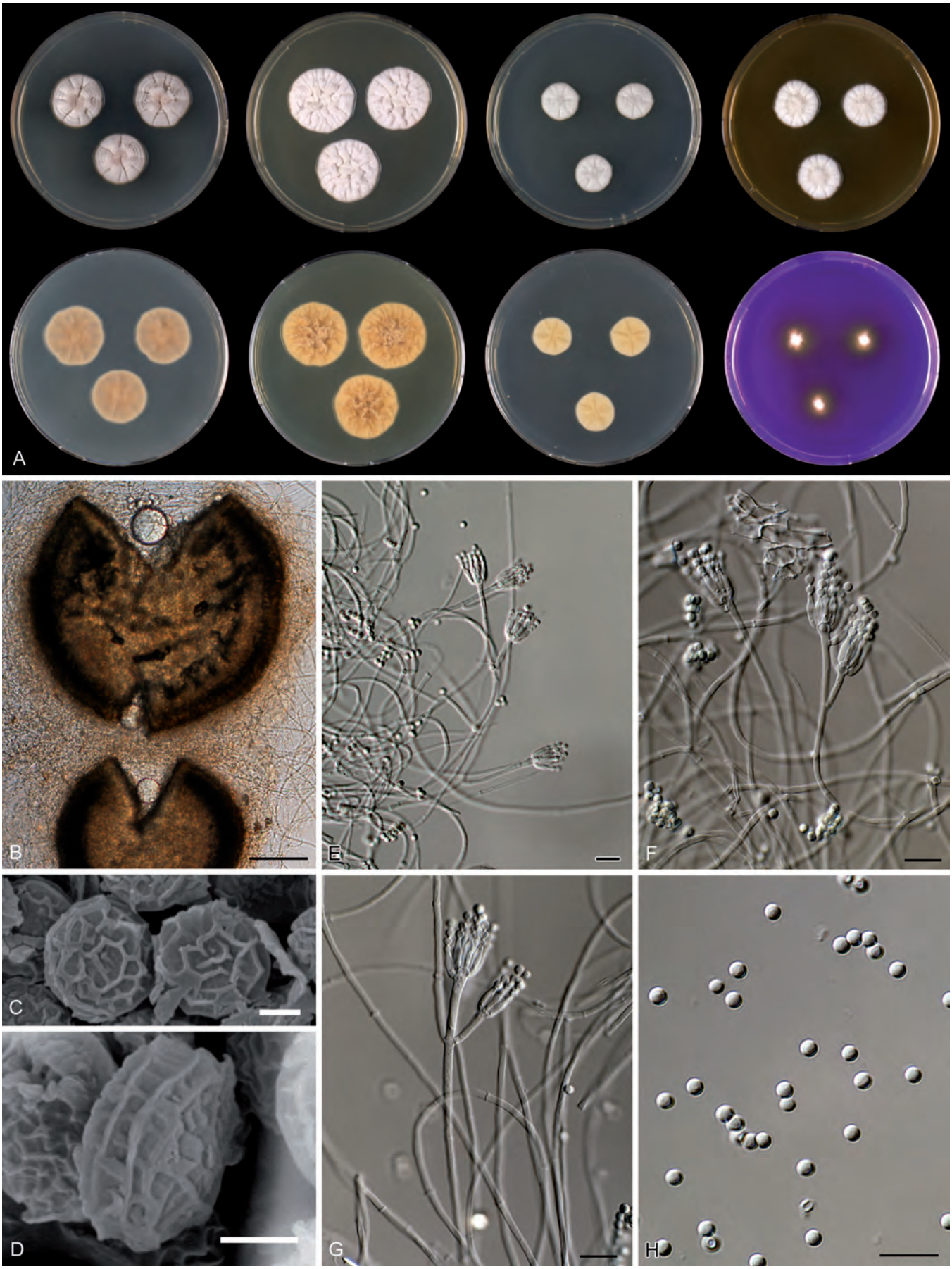

Fig. 11. *Penicillium argentinense*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Ascomata. C–D. Ascospores. E–G. Conidiophores. H. Conidia. Scale bars = 10 µm.

Sporulation on CYA absent after 7 d and sporulation sparsely after prolonged incubation, cleistothecia sparsely produced and inconspicuous when young and becoming brownish grey in age, mycelium white, exudate clear, produced in small droplets, soluble pigments absent, margin entire, reverse pale or beige. Sporulation on YES absent, mycelium white, soluble pigments absent, reverse in shades of pale-beige, becoming brown in the centre after prolonged incubation. Sporulation on DG18 absent, mycelium white, reverse pale to pale-cream. Sporulation on MEA absent, remaining sterile after prolong incubation, mycelium white. Ehrlich reaction negative.

Cleistothecia only produced on CYA and oatmeal agar, globose or subglobose, up to 100–200 µm diam, consisting of sclerotioid masses of polygonal cells, slowly ripening in more than 6 wk. Ascospores ellipsoidal, with 2 inconspicuous equatorial ridges, roughened valves under light microscope, reticulate when viewed with SEM, 2.5–3.0 × 2.0–2.5 µm. Conidiophores monoverticillate or biverticillate, stipes variable in length 30–200 µm, smooth walled, thin, measuring 1.5–2.5 µm, ending with a slightly inflated apex, 2.0–4.0 µm. Metulae, when present, as additional branch, 10–20 × 1.5–3.0 µm wide. Phialides ampulliform, occasionally positioned subapically, 7.0–9.0 × 2–3 µm. Conidia globose, smooth, 2.0–2.5 µm diam.

Extrolites: Curvularin, dehydrocurvularin, "AURANMUF", "OXIM".

Diagnostic characters: No growth at 37 °C, pale or beige reverse on CYA and YES, soluble pigments absent.

Similar species: See *P. anatolicum.*

Distribution and ecology: This species has a worldwide distribution. It has been isolated from soil in Argentina and the Netherlands and *Phaenocoma* leaf bracts from South Africa.

Barcode & molecular based ID: JN831359. This species can be identified with ITS, β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: None.

Penicillium atrofulvum Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563183. Fig. 12.

Etymology: Named after the black coloured sclerotia produced by this species.

Differt ab omnibus speciebus affinibus formatione sclerotiorum atratorum, reverso atrocolorato coloniae in agaro diverso et conidiophoris symmetricis biverticillatis.

Typus: ex soil, Katanga near Kipushi, Zaire; No. 153, C. Lanneau (CBS H-20650 – holotypus, cultures ex-type CBS 109.66 = DTO 31B2 = FRR 799 = IBT 30032).

Description: Colony diam, 7 d, in mm: CYA 30–40; CYA15°C 15–25; CYA30°C and CYA37°C: no growth; MEA 28–38; YES 40–47; DG18 28–35; ratio CYAS:CYA 1.0–1.2; creatine agar 13–22, weak to moderate growth and no acid production.

Moderate to good sporulation on CYA, velvety, conidia dark-green or dull green, mycelium inconspicuous, exudate absent or sparsely produced as small clear droplets, soluble pigment absent, margin entire, reverse dark brown to dark green and almost black underneath the sclerotia. Good sporulation on YES, conidia dull green, mycelium inconspicuous, soluble pigments absent, reverse black with beige margins. Good sporulation on on DG18, conidia grey green, reverse pale with a black centre. Colonies on MEA grey or dull-grey green, colony texture floccose, mycelium white. Ehrlich reaction negative.

Sclerotia black, partly embedded in the agar, irregular in shape, up to 50–800 µm diam, often produced under a thick felt of conidiophores, rather soft, confluent and forming coriaceous masses, sometimes concentrated along radial lines, consisting of dark pigmented, polygonal, thick walled cells. Asci and ascospores are not observed. Conidiophores predominantly symmetrically biverticillate, stipes 300–500 µm long, smooth or finely rough walled, 2.5–3.5 µm wide; metulae in a compact terminal whorls of 3–5, equal in length, 10–14 × 2.5–3.5 µm; phialides ampulliform, 7–9 × 2.0–3.0 µm. Conidia ellipsoidal, smooth walled, variable in size, but not in shape, 2.0–3.0 × 2.0–2.5 µm.

Extrolites: "ALK", "GULLA", "SOLIS", "3T".

Diagnostic characters: The formation of dark sclerotia, black coloured reverse on various agar media, symmetrical biverticillate conidiophores.

Similar species: None; this species is unique because of the formation of dark coloured sclerotia.

Distribution and ecology: This species has a worldwide occurrence and is isolated from soil in the Netherlands, Zaire and Tunisia.

Barcode & molecular based ID: GenBank no. JN617663. This species has unique ITS, β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: *Penicillium atrofulvum* phenotypically resembles *P. novae-zeelandiae* by the production of black coloured sclerotia and symmetrical biverticillate conidiophores. The lectotype of *P. novae-zeelandiae* (CBS 137.41^{T} = NRRL 2128^{T}) is related to *P. canescens*, *P. jensenii* and *P. coralligerum* in section *Canescentia* (Peterson & Horn 2009, Houbraken & Samson 2011). According to the original description of van Beyma (1940), this ex-type strain of *P. novae-zeelandiae* (CBS 137.41) produces black coloured sclerotia. However, this strain no longer shows this diagnostic feature. Phenotypically, *P. novae-zeelandiae* can be differentiated from *P. atrofulvum* by the formation of warted stipes and globose conidia. Furthermore, *P. novae-zeelandiae* produces patulin, an extrolite not formed by *P. atrofulvum* (Frisvad & Filtenborg 1990).

Penicillium aurantiacobrunneum Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563206. Fig. 13.

Etymology: Named after the orange-brown coloured sclerotia, produced by this species.

Differt ab omnibus speciebus affinibus divisione elementorum "Ehrlich" roseoviolacea, ratione CYAS:CYA 1.0–1.2, sclerotiis pallide aurantiacis.

Typus: ex air sample of cake factory, Give, Denmark, A. Svendsen (CBS H-20662 – holotype, cultures ex-type CBS 126228 = DTO 78G2 = IBT 18753).

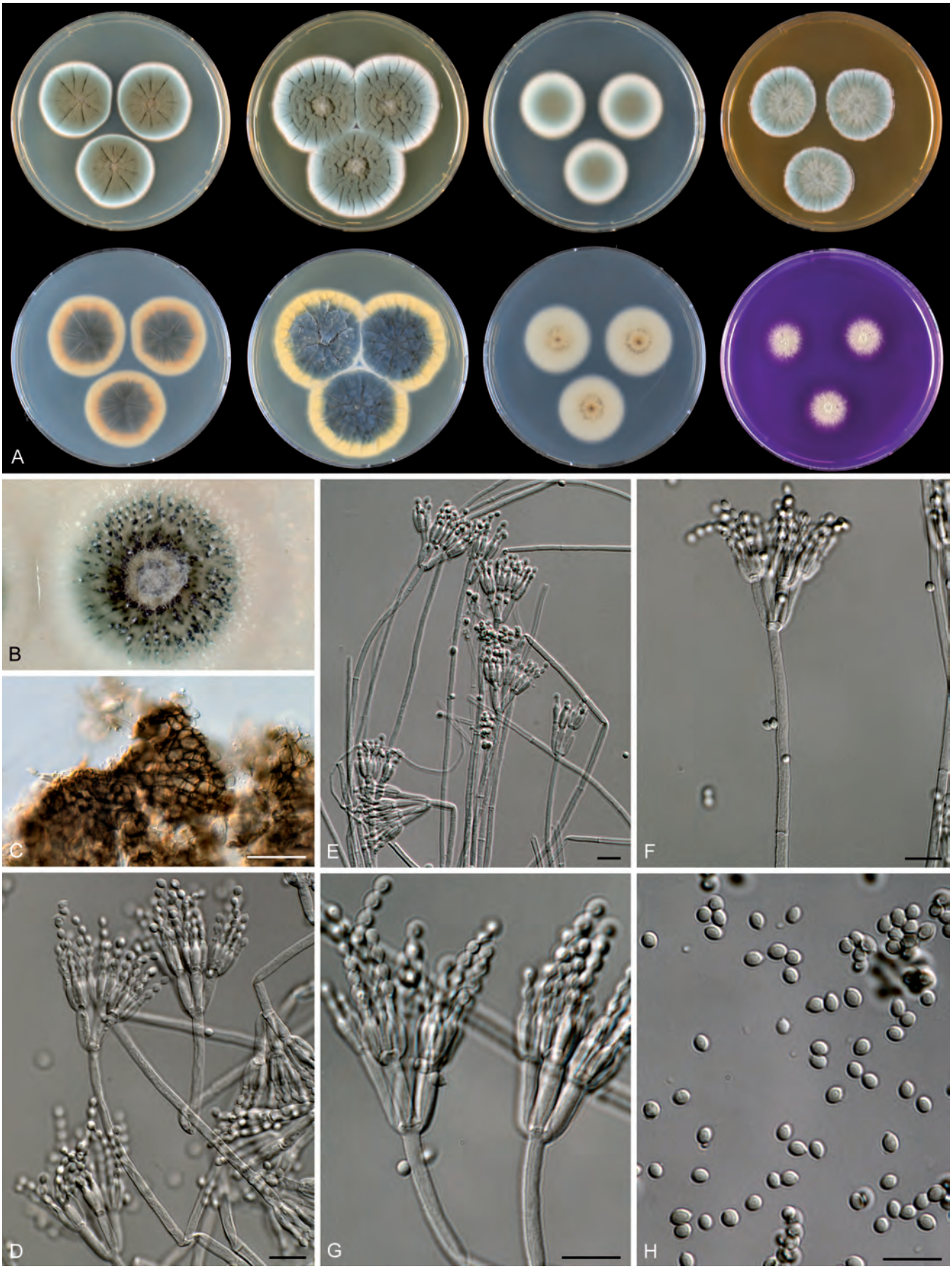

Fig. 12. *Penicillium atrofulvum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–C. Sclerotia. D–G. Conidiophores. H. Conidia. Scale bars = 10 µm.

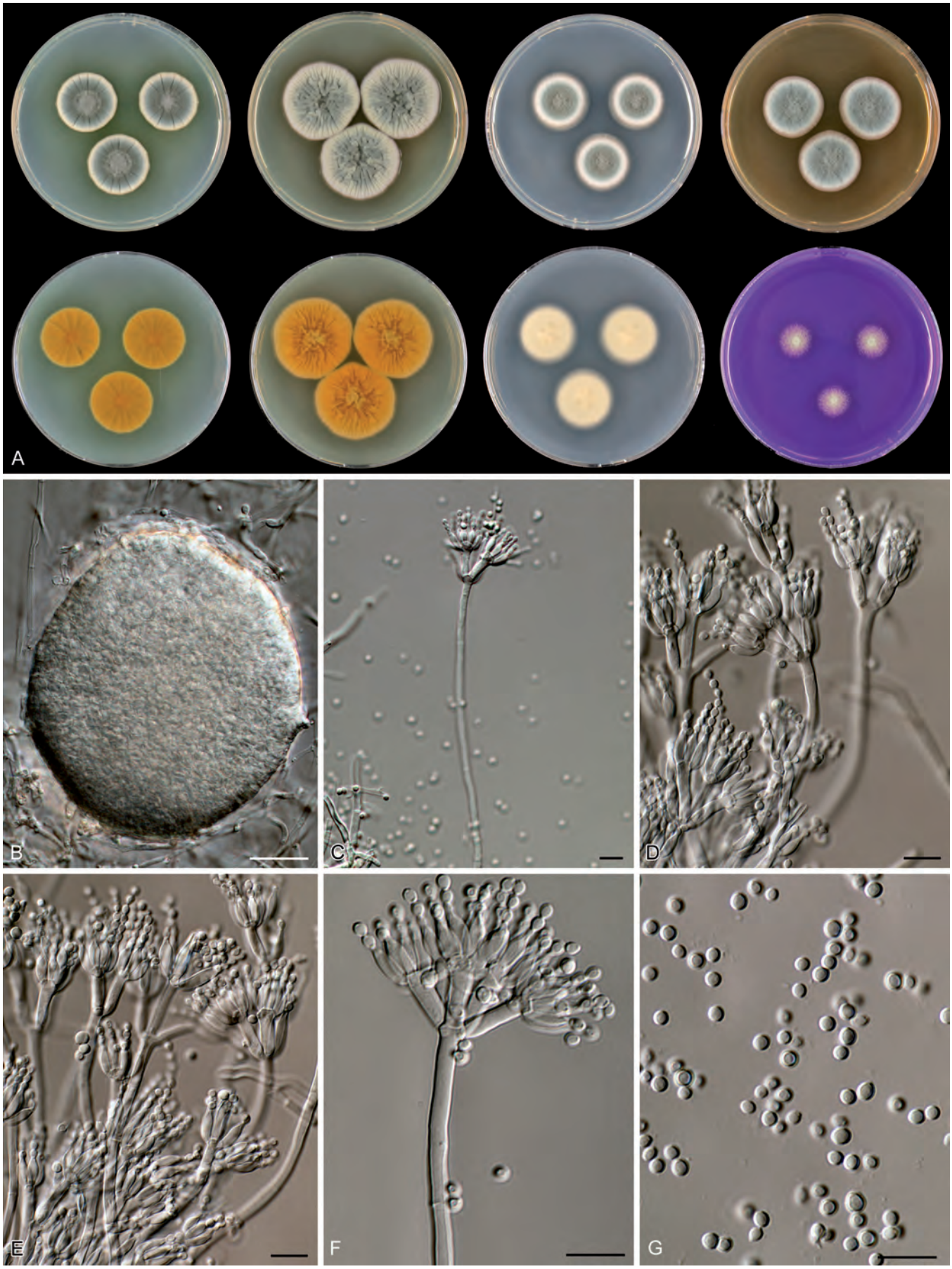

Fig. 13. *Penicillium aurantiacobrunneum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Sclerotia. C–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Description: Colony diam, 7 d, in mm: CYA 24–30; CYA30°C germination–3; CYA37°C: no growth; MEA 22–28 mm; YES 31–35 mm; DG18 21–29; ratio CYAS:CYA 1.0–1.2; creatine agar 12–18 mm, weak growth and no acid production.

Good sporulation on CYA with velvety to floccose surface, conidia dull blue green, mycelium inconspicuous or pale-yellow, exudate absent or sparsely produced as small clear droplets, soluble pigments yellow, margin entire or slightly polygonal, reverse yellow-orange. Moderate to good sporulation on YES, conidia light green, soluble pigments yellow, reverse yellow-orange or yellow brown. Good sporulation on DG18, conidia dull-grey green, reverse pale or pale yellow. Good sporulation on MEA, conidia grey green or bluish grey green, colony texture velvety to floccose. Ehrlich reaction positive (pinkish-violet).

Sclerotia white when young, becoming pale orange to orange-brown, 150–250 µm, sparsely produced on oatmeal agar under a layer of conidiophores and large exudates droplets; hard, consisting of polygonal cells; no asci or ascospores observed. Conidiophores 200–400 µm long, predominant biverticillate, occasionally terverticillate, stipes smooth, 2.5–3.5 µm wide. Metulae in terminal whorls of 3–6 and mostly equal in length, 10–14 × 2.5–3.5 µm. Phialides ampulliform with short neck, 7–9 × 2.5–3.5 µm. Conidia subglobose, smooth, rather large variation in size within an isolate, 2.0–3.0 µm diam.

Extrolites: Benzomalvins, citreoviridin, terrein, "OTOT".

Diagnostic characters: Ehrlich reaction pinkish-violet, ratio CYAS:CYA 1.0–1.2, pale orange sclerotia.

Similar species: See *P. miczynskii*. *Penicillium aurantiacobrunneum* morphologically resembles *P. miczynskii* and *P. neomiczynskii*, but can be differentiated by the pinkish-violet Ehrlich reaction of the former species.

Distribution and ecology: Worldwide distribution; from soil (New Zealand, Chile) and air (Denmark).

Barcode & molecular based ID: GenBank no. JN617670. *Penicillium aurantiacobrunneum* and *P. miczynskii* share the same ITS sequence. Partial β-tubulin and/or calmodulin sequences can be used to identify these species.

Taxonomy and phylogeny: None.

Penicillium cairnsense Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563184. Fig. 14.

Etymology: Named after Cairns (Australia), the city near the location where the type culture was collected.

Differt ab omnibus speciebus affinibus reverso rubro vel subnigro coloniae in agaro YES et/vel DG18, coloniis in agaro CYA 29–39 mm, constrictis, sed in agaro CYA30 continenter crescentibus, ratione CYAS:CYA 1.0–1.2, sclerotiis pallide aurantiacis vel aurantiaco-brunneis.

Typus: ex soil, Atherton Tableland, Australia, J. Houbraken (CBS H-20686 – holotype, cultures ex-type CBS 124325 = DTO 30E6 = IBT 29042).

Description: Colony diam, 7 d, in mm: CYA 29–39; CYA30°C 5–12; CYA37°C: no growth; MEA 28–38 mm; YES 40–50 mm; DG18 25–34; ratio CYAS:CYA 1.0–1.2; creatine agar 17–26 mm, weak growth and no acid production.

Good sporulation on CYA, velvety to slightly floccose, conidia dull green, mycelium light yellow, exudate produced in many minute droplets and clear to light yellow coloured, soluble pigments yellow, margin polygonal, reverse yellow-orange or orange, but also in shades of yellow brown, light brown or brown. Good sporulation on YES, conidia dull green, soluble pigments produced in most isolates and red, reverse brownish red or blackish red. Good sporulation on DG18, conidia dull-grey green, mycelium white, reverse (dark) red with red soluble pigments diffusing into the agar or pale yellow. Good sporulation on MEA, conidia dull-grey green, colony texture velvety. Ehrlich reaction negative.

Sclerotia white when young, becoming pale orange to orange-brown in age, 125–250 (–300) µm, produced on oatmeal agar in a velvety layer with small exudate droplets; consisting of polygonal cells and red-brown pigmented spots are present on the surface of the sclerotia; asci and ascospores not observed. Conidiophores predominantly biverticillate, but also a large portion terverticillate, additional branch both direct under terminal whorl and further down the stipe, 200–400 µm long, stipes smooth or occasionally finely roughened, 2.0–3.5 µm wide. Metulae in terminal whorls of 3–6 (–8) and often unequal in length, 9–13 (–15) × 2.5–3.5 µm. Phialides ampulliform, with short neck, 7–9 × 2–3 µm. Conidia smooth walled, subglobose to broadly ellipsoidal, 2.0–3.0 × 2.0–2.5 µm; a small portion of the conidia larger, globose, 3.0–3.5 µm diam.

Extrolites: The extrolite pattern of *P. cairnsense* is rather diverse. CBS 126226, CBS 117982, CBS 118028 and CBS 117962 produce the extrolites benzomalvins, citreoviridin, phoenicin and decaturin; CBS 124325, CBS 126225 and DTO 87B9 produce citreoviridin, terrein and/or quinolactacin. Other extrolites: "KUM", "MIF", "MIM", "RAI", "SENGA".

Diagnostic characters: Red or blackish reverse on YES and/or DG18, colonies on CYA 29–39 mm, restricted, but consistent growth on CYA30, ratio CYAS:CYA 1.0–1.2, pale orange to orange-brown sclerotia.

Similar species: See *P. miczynskii*. *Penicillium quebecense* is morphologically similar, but has a CYAS:CYA ratio lower than 1.

Barcode & molecular based ID: GenBank no. JN617669 (CBS 124325^T), JN617664 (CBS 117982). The strains CBS 124324, CBS 124326, CBS 124325^T, CBS 126225 have identical and unique ITS sequences. The *P. cairnsense* strains isolated nuts of *Carya cordiformis* (bitternut), Niagara Falls, Ontario, Canada (CBS 117982 and CBS 117962) differ one base pair from CBS 124325^T and share ITS sequences with the type cultures of *P. quebecense* and *P. neomiczynskii*.

Distribution and ecology: Worldwide; isolated from soil, ants (*Camponotus* sp.), decaying basidioma of *Lactarius* sp. and nut of *Carya cordiformis* (bitternut).

Taxonomy and phylogeny: Pitt (1980) mentioned in the description of *P. miczynskii* that some isolates of this species can produce red soluble pigment on MEA. These isolates were probably *P. cairnsense*, *P. quebecense* or *P. manginii*.

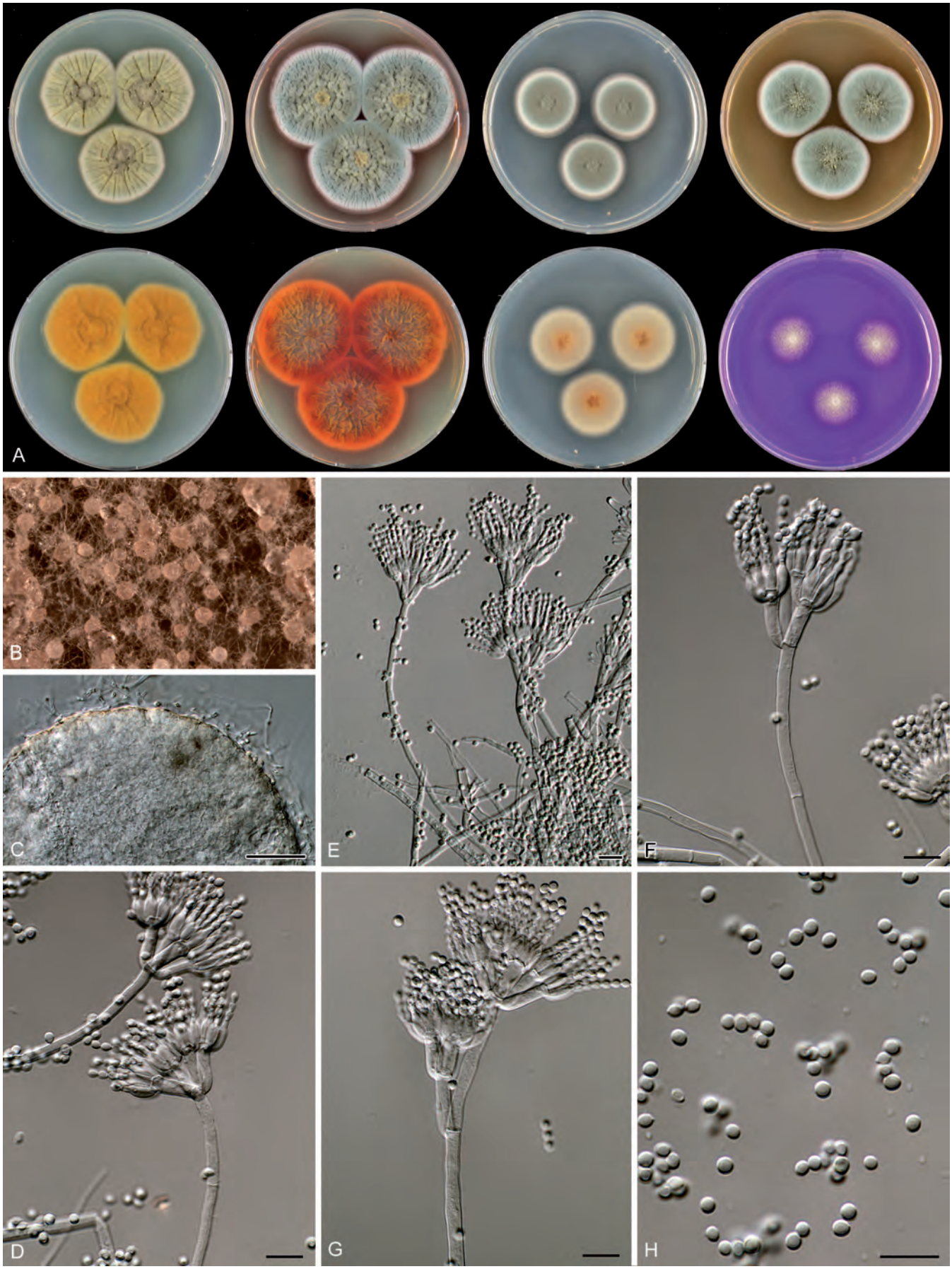

Fig. 14. *Penicillium cairnsense*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–C. Sclerotia. D–G. Conidiophores. H. Conidia. Scale bars = 10 µm.

Penicillium christenseniae Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563187. Fig. 15.

Etymology: Named after Martha Christensen who collected and isolated the type culture of this species.

Differt ab omnibus speciebus affinibus stipitibus brevibus et conidiophoris compactis, coloniis in agaro MEA velutinis, in agaro CREA modice crescentibus et haud crescentibus in agaro CYA ad 30 °C.

Typus: ex soil in native forest, east/north east side of Costa Rica, about 30 km inland from Limon and the Caribbean, M. Christensen (CBS H-20656 – holotypus, cultures ex-type CBS 126236 = DTO 76C3 = IBT 23355).

Description: Colony diam, 7 d, in mm: CYA 31–37; CYA15°C 20–26; CYA30°C and CYA37°C no growth; MEA 21–28; YES 33–38; DG18 21–26; ratio CYAS:CYA 1.0–1.2 creatine agar 16–22, moderate growth and no acid production.

Good sporulation on CYA, velvety, conidia dull green, mycelium white, exudate produced in clear droplets, soluble pigments absent, margin entire, reverse light brown with orange sulcations in centre. Good sporulation on YES, conidia dull green, mycelium inconspicuous, soluble pigments absent. Good sporulation on DG18, conidia dull or dull-grey green, reverse bright yellow or yellow-orange. Good sporulation on MEA, conidia dull-grey green, colony texture velvety, mycelium inconspicious. Ehrlich reaction negative.

Sclerotia absent. Conidiophores predominantly symmetrically biverticillate and occasionally with an additional branch; stipes relatively short, up to 250 µm, smooth walled, width, 2.0–3.0 µm; metulae in a compact terminal whorls of 4–8 (–10), rather equal in length, vesiculate, 10–15 × 2.0–3.0 µm; phialides ampulliform, 7–9 × 2.0–3.0 µm. Conidia globose to subglobose, finely roughened, 2.0–3.0 µm diam.

Extrolites: Citrinin, quinolactacin, “FON”, “KUM”, “MIF”, “RYLA”.

Diagnostic characters: This species is characterised by its short stipes (compared with other related species) and compact conidiophores, velvety colonies on MEA, moderate growth on CREA and no growth on CYA incubated at 30 °C.

Similar species: This species produces finely rough walled globose conidia and does not grow at 30 °C, which is also observed in species such as *P. westlingii*, *P. waksmanii* and *P. godlewskii*. However, the moderate growth on CREA, the velvety colonies on MEA and short stipes are characteristic for this species.

Distribution and ecology: Soil of a native forest and litter of *Manilkara bidenta* or *Guarea guidonia*; Costa Rica and Puerto Rico, USA.

Barcode & molecular based ID: GenBank no. JN617674. *Penicillium christenseniae* has unique β-tubulin, calmodulin and ITS sequences.

Taxonomy and phylogeny: This species is phylogenetically unique and belongs to the *P. westlingii*-clade. However, it does shares the production of quinolactacin and “FON” with *P. steckii*.

Penicillium chrzaszczii Zaleski, Bull. Int. Acad. pol. Sci. Lett., Sér. B.: 464. 1927. Fig. 16.

= *P. turolense* Ramírez & Martínez, Mycopathol. 74: 36. 1981.

Typus: ex woodland soil, Puszcza Bialowieska Forest, Poland (CBS 217.28 **–** lectotype, designated here; cultures ex-type IBT 18226 = IBT 11222 = IBT 16409 = DTO 22E4 = FRR 903 = MUCL 29167 = NRRL 903 = NRRL 1741).

Description: Colony diam, 7 d, in mm: CYA 25–33; CYA15°C 16–22; CYA30°C and CYA37°C no growth; MEA 21–28; YES 28–36; DG18 20–27; ratio CYAS:CYA 0.95–1.1; creatine agar 15–20, weak growth and no acid production.

No or weak sporulation on CYA, velvety, conidia grey-green, mycelium inconspicuous, exudate absent or sparsely present as minute clear droplets, soluble pigments present in fresh isolates and weak yellow coloured, margin slightly polygonal, reverse (pale) yellow-orange. Sporulation on YES absent, mycelium white, soluble pigments absent, reverse vivid yellow or yellow-orange. No or poor sporulation on DG18, white mycelium, yellow soluble pigments produced in time, reverse pale or vivid yellow. Weak to moderate sporulation on MEA, conidia grey green when young and becoming dull green in age, colony texture floccose. Ehrlich reaction negative.

Sclerotia absent. Conidiophores symmetrically biverticillate and often with an divergent branch, often starting 40–60 µm below the terminal verticil; stipes rather long, up to 500 µm, smooth, 2.5–3.5 µm wide; metulae in a compact terminal verticil, 4–7 (–9), unequal in length, vesiculate, 10–14 × 2.5–3.5 µm; phialides ampulliform, 7–9 × 2–3 µm. Conidia globose to subglobose, finely roughened, 2.0–3.0 µm diam.

Extrolites: Citrinin, terrein, “MIF”, “MIM”, “RAI”, “3T”, “VERN” (also see Christensen *et al*. 1999).

Diagnostic characters: No or poor sporulation on CYA, finely roughened conidia, no growth at 30 °C, often with terverticillate structures, yellow soluble pigment production on CYA, reverse on DG18 in shades of yellow (pale or vivid).

Similar species: Phylogenetically, *P. chrzaszczii* is related to *P. godlewskii* and *P. waksmanii*. The reverse on CYA of *P. waksmanii* is in shades of beige-brown, while *P. godlewskii* and *P. chrzaszczii* have reverses in shades of yellow and/or orange. *Penicillium godlewskii* is more restricted in its growth on CYA (15–25 mm) than *P. chrzaszczii* (25–33 mm). *Penicillium chrzaszczii* can be distinguished from *P. miczynskii* and related species by the formation of globose, roughened conidia.

Distribution and ecology: This species is not commonly occurring and was previously isolated from soil in Poland and France.

Barcode & molecular based ID: GenBank no. GU944603.This species shares identical ITS sequences with *P. decaturense*, but can be identified based on partial β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: *Penicillium chrzaszczii* was described by Zaleski (1927) in the subsection “*concentrice-undulata*”, which is characterised by concentric sulcated colonies. This feature was

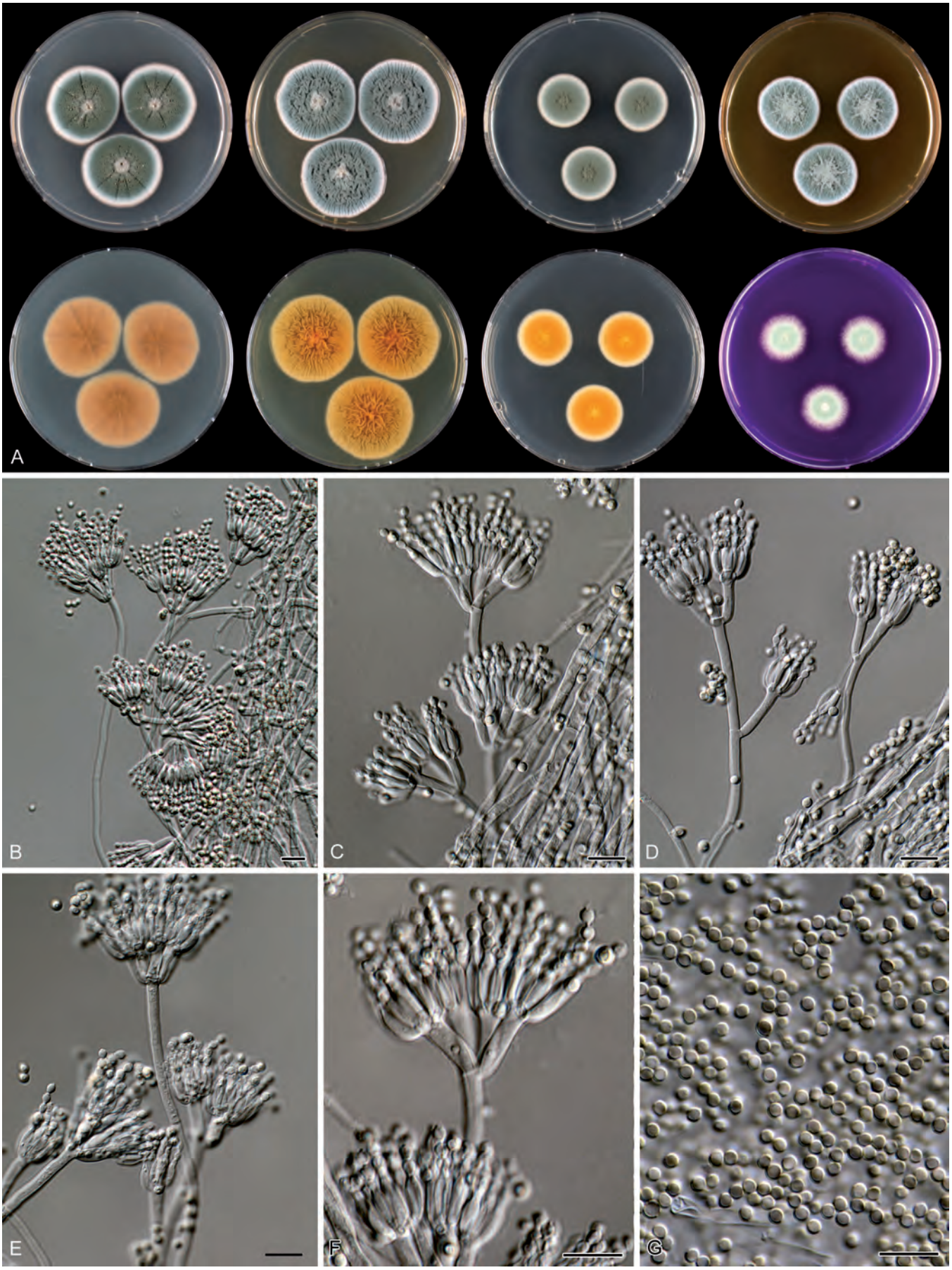

Fig. 15. *Penicillium christenseniae*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

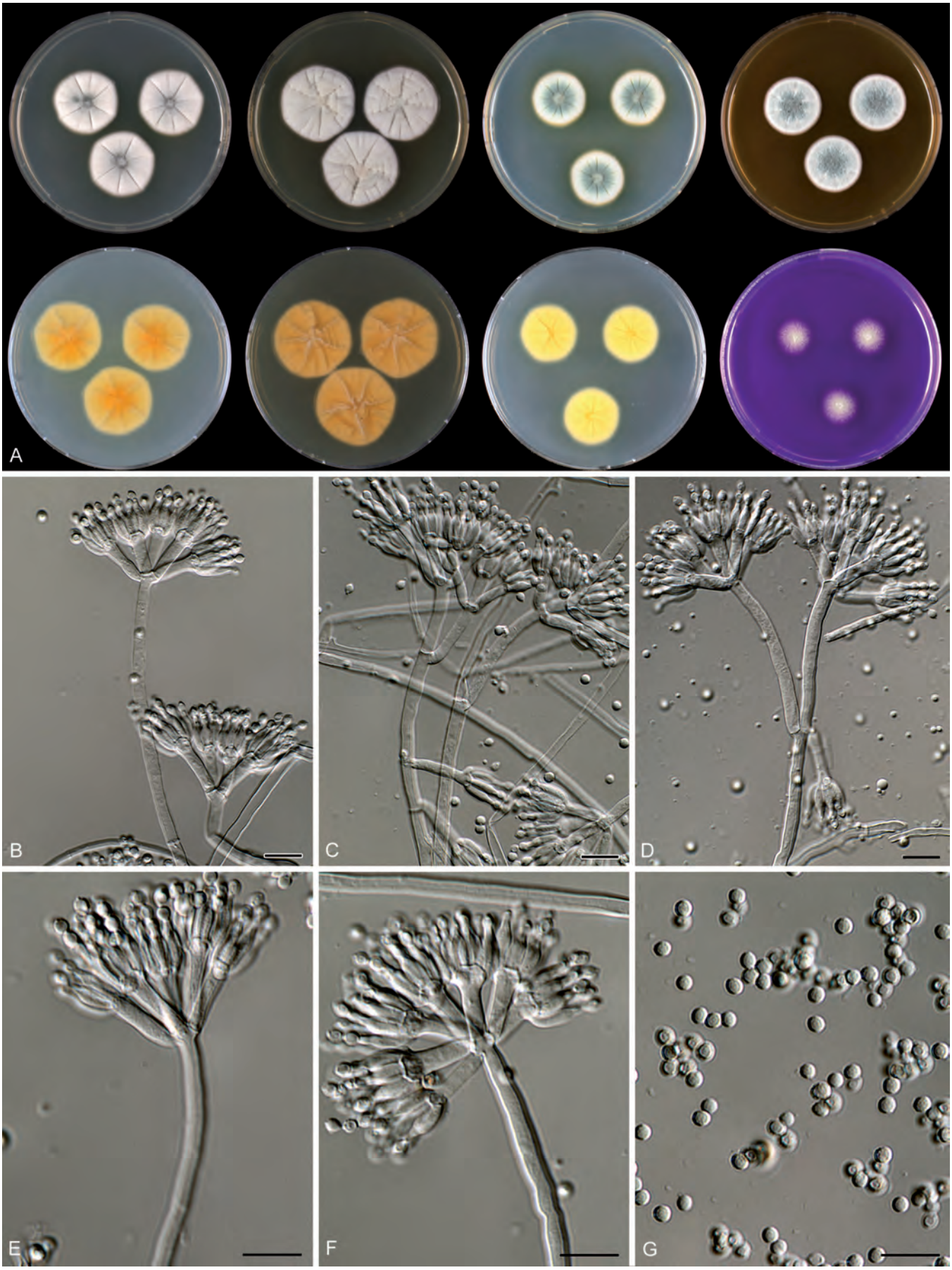

Fig. 16. *Penicillium chrzaszczii*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

not observed on the agar media used in this study. Raper & Thom (1949) placed *P. chrzaszczii* in synonymy with *P. jensenii* and Pitt (1980) synonymised this species with *P. miczynskii*. Molecular data indicate that *P. turolense* (CBS 176.81) is a synonym of *P. chrzaszczii*. Our strain of *P. turolense* is degenerated and sporulates weakly on most agar media. The original description shows typical ornamented conidia and biverticillate conidiophores (Ramírez & Martinez 1981) and therefore this species can be confidentially placed in synonymy.

Penicillium citrinum Thom, Bull. U.S. Dep. Agric., Bur. Animal Indus. 118: 61. 1910. Fig. 17.

= *Citromyces subtilis* Bainier & Sartory, Saccardo's Syll. fung. XXV: 684. 1912.
= *Penicillium subtile* (Bainier & Sartory) Biourge, Cellule 33: 106. 1923. (*nom. illegit*.,Art. 64; non Berk. 1841.
= *Penicillium aurifluum* Biourge, Cellule 33: 250. 1923.
= *Penicillium phaeojanthinellum* Biourge, Cellule 33: 289. 1923.
= *Penicillium implicatum* Biourge, Cellule 33: 278. 1923.
= *Penicillium sartoryi* Thom [as *'sartorii'*], The Penicillia: 233. 1930.
= *Penicillium botryosum* Bat. & H. Maia, Anais Soc. Biol. Pernambuco 15: 157. 1957.

Typus: unrecorded source (IMI 92196ii, type of both *P. citrinum* and *P. aurifluum*; cultures ex-type DTO 22F3 = CBS 139.45 = Biourge 53 = Thom 4733.14 = ATCC 1109 = ATCC 36382 = CECT 2269 = FRR 1841 = IMI 091961 = IMI 092196 = LSHB P25 = LSHB P6 = LSHB Ad95 = MUCL 29781 = NRRL 1841 = NRRL 1842).

Description: Colony diam, 7 d, in mm: CYA 27–33; CYA15°C 5–10; CYA30°C 27–40; CYA37°C 2–12; MEA 18–25; YES 29–37; DG18 15–23; ratio CYAS:CYA 0.9–1.2; creatine agar 10–19, poor growth, no or weak acid.

Moderate sporulation on CYA, conidia grey green or blueish grey green, mycelium inconspicuous, small exudate droplets produced by some strains and clear or pale yellow coloured, soluble pigments yellow, margin entire, reverse brownish-yellow. Moderate to good sporulation on YES, conidial colour variable: grey green to dark green, soluble pigment present in majority of strains and strong yellow or yellow-orange coloured, reverse yellow to yellow-orange. Moderate to good sporulation on DG18, conidia grey green, reverse pale and occasionally pale with yellow centre. Moderate to good sporulation on MEA, conidia grey green with a strong blue element, colony texture velvety. Ehrlich reaction negative.

Sclerotia absent. Conidiophores arising from mycelial mat, predominant symmetrically biverticillate, terverticillate structures abundantly produced in fresh isolates; stipes smooth, 100–300 × 2.0–3.0 µm. Metulae in whorls of 3–4 (–6), 12–16 × 2.0–3.0 µm. Phialides ampulliform, 7.5–10 × 2.0–2.5 µm. Conidia globose to subglobose, smooth, 2.0–2.5 × 2.0–2.5 µm.

Extrolites: Citrinin, quinolactacins, citrinadins, perinadine, several anthraquinones, "CITY", "met k" and "shamix" (Houbraken *et al*. 2010).

Diagnostic characters: Growth on CYA when incubated at 37 °C, 2–12 mm in diam, reverse on CYA in shades of yellow, soluble pigment production on CYA and YES, globose, smooth walled conidia.

Similar species: *Penicillium citrinum* belongs to the *P. citrinum*-clade and can be differentiated by other members of this series by its ability to grow at 37 °C and the formation of yellow or yellow-orange soluble pigments on YES.

Distribution and ecology: This species has a worldwide distribution and occurs more frequently in the (sub)tropics than in temperate regions. *Penicillium citrinum* is isolated from soils, but also from indoor air, food and as an endophyte of root, stem, leaves of coffee plants (Posada *et al*. 2007) and roots of *Ixeris repens* (Khan *et al*. 2008; identity based on ITS sequences deposited in GenBank).

Barcode & molecular based ID: GenBank no. GU944562. A gap of 36–38 bp was observed in the alignment of the ITS1 region of all *P. citrinum* isolates, when compared to most other species of this series. This species has unique ITS, partial β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: *Penicillium implicatum* is synonymised with *P. citrinum* (Houbraken *et al*. 2010). Pitt (1980) considered the type strain of *P. implicatum* lost and designated IMI 190235 (= CBS 184.81) as the neotype. However, the type culture of *P. implicatum*, deposited by Thom, is maintained at the CBS under CBS 232.38 and resembles *P. citrinum* in many aspects (Frisvad *et al*. 1990a, Houbraken *et al*. 2010). Houbraken *et al*. (2010) placed *P. phaeojanthinellum* and *P. botryosum* in synonymy with *P. citrinum* and more details about the taxonomy of *P. citrinum* can be found there.

Penicillium copticola Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563205. Fig. 18.

Etymology: Referring to pastery, the substrate where the type strain was growing on.

Differt ab omnibus speciebus affinibus coloniis in agaro CREA bene crescentibus, in agaro CYA ad 33 °C quoque crescentibus, coloniis in agaro MEA floccosis, conidiophoris biverticillatis.

Typus: ex tortilla, USA, J. Murray (CBS H-20643 – holotypus, cultures ex-type CBS 127355 = DTO 19H7 = IBT 30771).

Description: Colony diam, 7 d, in mm: CYA 31–37; CYA15°C 7–11; CYA30°C 13–17; CYA37°C no growth; MEA 25–34; YES 35–41; DG18 27–35; ratio CYAS:CYA 1.0–1.2; creatine agar 18–25, good growth, weak acid production followed by (delayed) base reaction.

Moderate or good sporulation on CYA, velvety, conidia dull green or dull-pure green, mycelium inconspicuous, exudate produced as minute clear droplets, soluble pigments absent, reverse pale beige or crème. Good sporulation on YES, conidia dull green, soluble pigment absent, reverse yellow to dark beige, with a darker greenish centre. Dull green conidia on DG18, reverse transparent or pale with a pale-cream centre. Colonies on MEA pure green or dull-pure green, colony texture floccose. Ehrlich reaction negative.

Sclerotia absent. Conidiophores predominantly symmetrically biverticillate, young conidophores monoverticillate, stipes up to 500 µm long, smooth, 2.0–3.0 µm wide; metulae in a compact terminal whorls of 2–4, equal or unequal in length, 12–16 × 2.0–3.5 µm, occasionally vesiculate. Phialides ampulliform to cylindrical, 7.5–9 × 2.0–3.0 µm. Conidia broadly ellipsoidal, smooth, 2.5–3.0 × 2.0–2.5 µm.

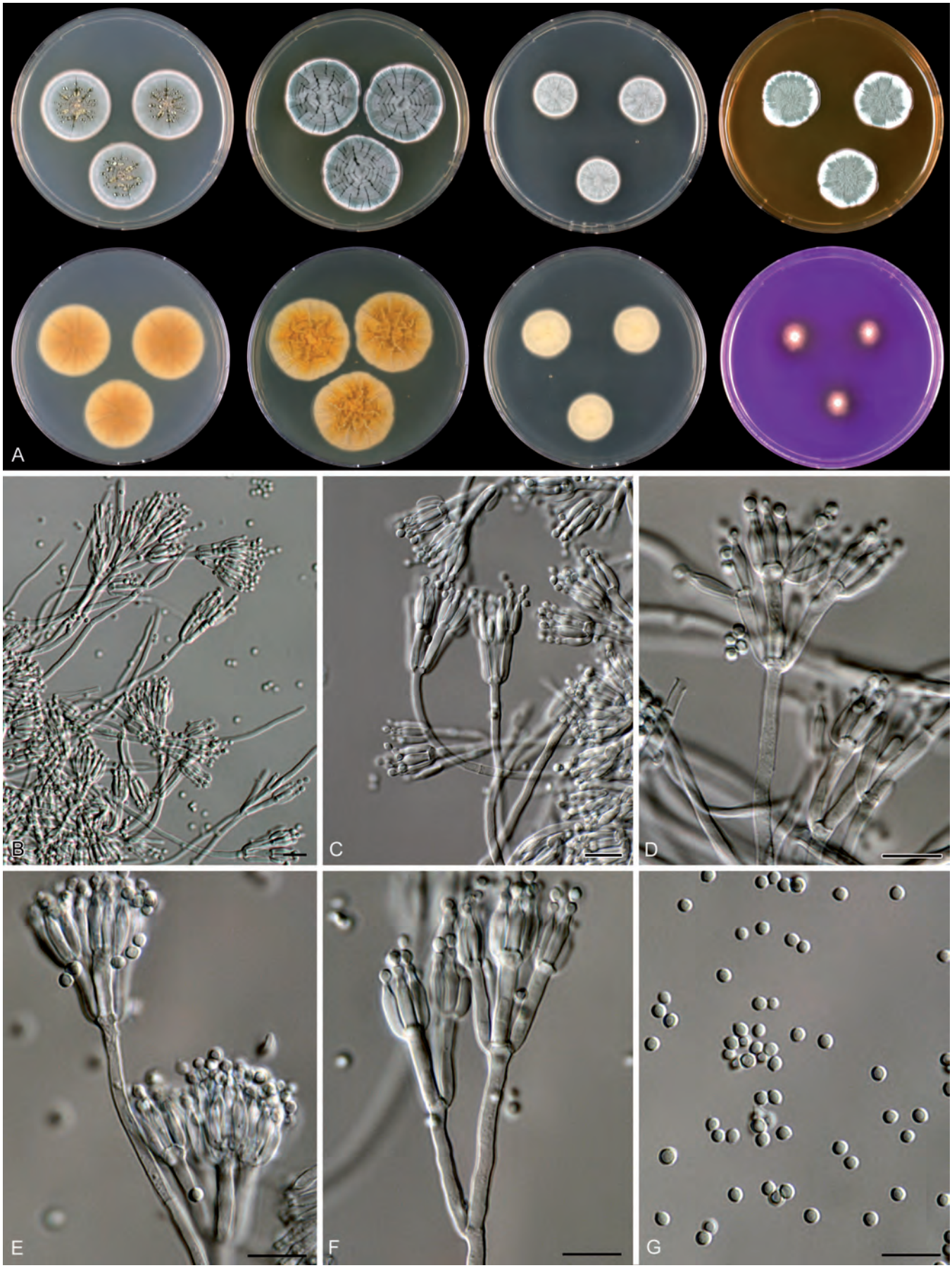

Fig. 17. *Penicillium citrinum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

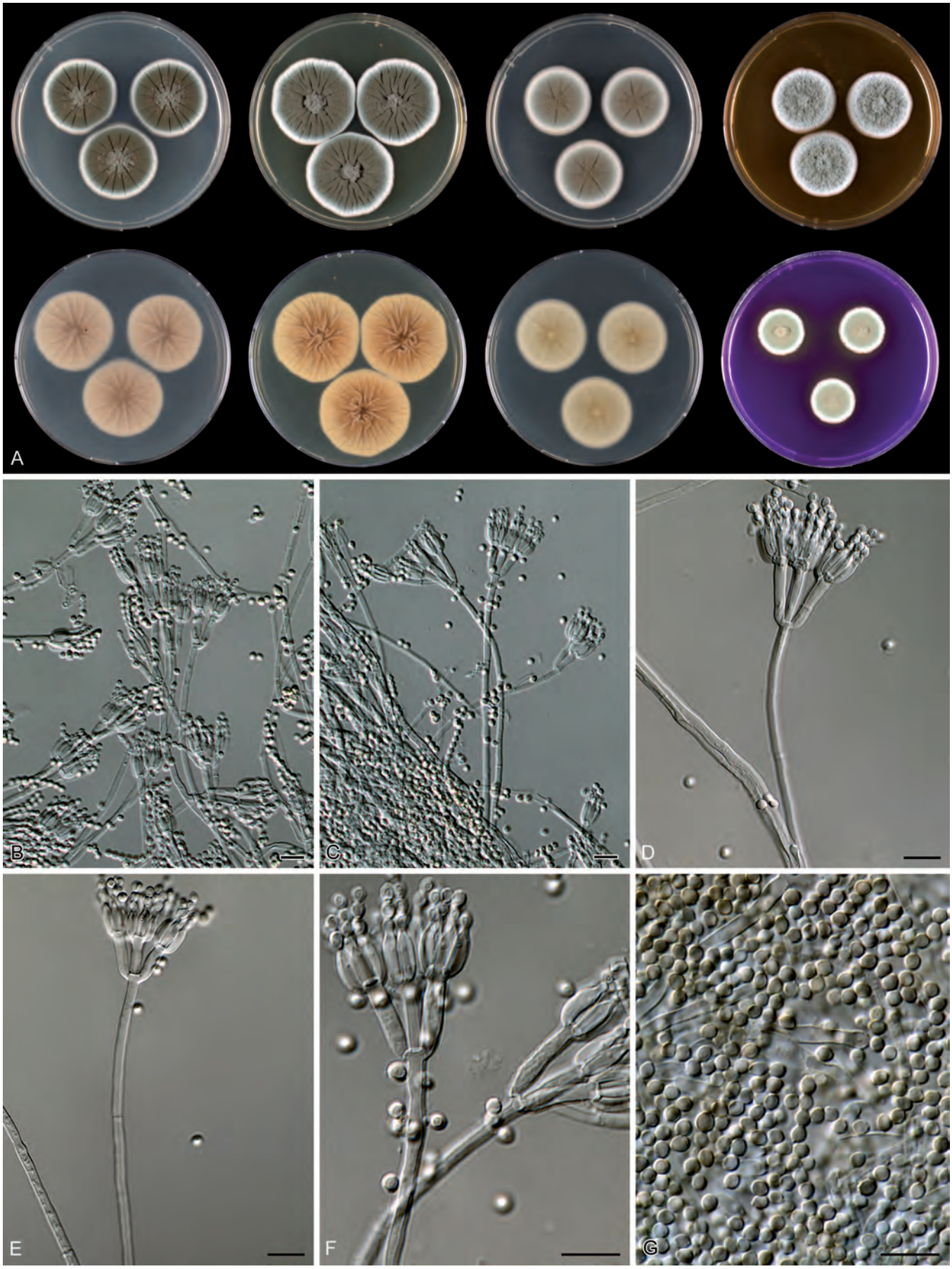

Fig. 18. *Penicillium copticola*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Extrolites: "GULLA", "HAEN", "PRS", "VERSI".

Diagnostic characters: Good growth on CREA with base production, growth on CYA incubated at 33 °C, floccose colonies on MEA, biverticillate conidiophores.

Similar species: See *P. terrigenum*.

Distribution and ecology: This species has a worldwide distribution. It is isolated from tortillas (USA), seed from ripe coffee berry (Hawaii, USA; NRRL 32575, GenBank DQ123664^{ITS}), dried flowers of *Cannabis sativa*, the Netherlands and air of a toilet in Germany.

Barcode & molecular based ID: GenBank JN617685. This species can be identified with ITS, partial β-tubulin and/or calmodulin sequences.

Taxonomy and phylogeny: Isolate NRRL 32575 was listed as *Penicillium* sp. by Vega *et al*. (2006) and comparison of the ITS sequence of this strain deposited in GenBank (DQ123664) shows that it is *P. copticola*.

Penicillium cosmopolitanum Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563188. Fig. 19.

Etymology: Named after the worldwide distribution of this species.

Differt ab omnibus speciebus affinibus conidiis exasperatis, coloniis haud crescentibus ad 30 °C, reverso psammocolorato-brunneo in agaro CYA, reverso pallide flavido vel eburneo in agaro YES, conidiis in agaro CYA et YES haud vel vix formantibus.

Typus: ex heathland soil, Cartier heide, Eersel, the Netherlands, J. Houbraken (CBS H-20665 – holotypus, cultures ex-type CBS 126995 = DTO 92E8 = IBT 30681).

Description: Colony diam, 7 d, in mm: CYA 25–32; CYA15°C 15–20; CYA30°C and CYA37°C no growth; MEA 20–29; YES 27–36; DG18 16–25; ratio CYAS:CYA 0.8–1.0 (–1.1); creatine agar 10–18, weak growth and no acid production.

Sporulation on CYA in most isolates absent or weak, occasionally moderate to good, velvety, conidia dull green, mycelium white, exudate occasionally present as small clear droplets, soluble pigments absent, margin polygonal or entire, reverse beige-brown with orange coloured sulcations giving the colony a pinkish tinge, some isolates pale beige or beige (CBS 200.86 and CBS 124316). Sporulation on YES mostly absent, mycelium white, soluble pigments absent, reverse cream, cream-buff or light beige. Sporulation on DG18 moderate to good, conidia dull or grey green, reverse transparent, pale beige or cream. Colonies on MEA poorly sporulating, conidia blueish green or dull green, colony texture floccose. Ehrlich reaction negative.

Sclerotia absent. Conidiophores symmetrically biverticillate, often with an divergent branch that is shorter than the main axis, occasionally quaterverticillate; stipes long, up to 500 µm, smooth, 2.5–4.0 µm wide; metulae in a compact terminal verticil, 3–6 (–8), more or less even in length, vesiculate and non-vesiculate, 9–13 (–15) × 2.0–3.5 µm; phialides ampulliform, 6.5–8.5 × 2–3 µm. Conidia globose, rough, 2.5–3.0 µm diam.

Extrolites: Citrinin, okaramin, perinadine, territrems, "CURVO", "HAEN", "PHOE", "ROTO", "SENGA", "TRIP", "VERSI", "XANTHOC".

Diagnostic characters: Rough walled conidia, no growth at 30 °C, reverse on CYA beige-brown, reverse on YES pale yellow to cream, no or weak sporulation on CYA and YES.

Similar species: See *P. westlingii*.

Distribution and ecology: This species is frequently isolated from soils in the Netherlands, Poland, Denmark and New Zealand.

Barcode & molecular based ID: GenBank no. JN617691 (Fig. 3, clade 1, 2 and 3), JN617682 (Fig. 3; clade 4). Clades 1, 2 and 3 in *P. cosmopolitanum* have identical ITS sequences, and these sequences are also shared by certain isolates of *P. westlingii* (CBS 124312, CBS 124313, CBS 127003, CBS 127040, see also description of *P. westlingii*). Members of clade 4 share ITS sequences with certain strains of *P. godlewskii* and *P. nothofagi*.

Taxonomy and phylogeny: Molecular analysis of partial β-tubulin and calmodulin data shows that this species can be subdivided into four subclades (Fig. 3). No clear morphological differences were observed among these clades, although strains of clade 2 have slightly paler reverse colours on CYA (*e.g.* CBS 126995^{T}, CBS 200.86).

Penicillium decaturense S.W Peterson, Bayer & Wicklow, Mycologia 96: 1290. 2004. Fig. 20.

Typus: ex old resupinate fungus, Ramsey Lake State Park, Decatur, Illinois, USA (BPI 842267 – holotypus, cultures ex-type CBS 117509 = IBT 27117 = DTO 3F7 = NRRL 28152).

Description: Colony diam, 7 d, in mm: CYA 32–40; CYA15°C 12–18; CYA30°C 5–15; CYA37°C no growth; MEA 27–34; YES 39–47; DG18 23–30; ratio CYAS:CYA 0.9–1.1; creatine agar 11–18, weak growth and no acid production.

Good sporulation on CYA, velvety, condia dark-green or blue-grey-green, mycelium inconspicuous, exudate production variable, absent, sparsely or predominant, clear or light yellow, soluble pigments absent, margin entire, reverse orange-beige to skin coloured, occasionally with beige-brown centre. Good sporulation on YES, conidia dark green, mycelium white, soluble pigments absent, reverse yellow-orange, in some isolates yellow. Good sporulation on DG18, conidia dull-grey green, reverse pale, cream or pale yellow. Good sporulation on MEA, conidia blue-green or blueish-dark green, colony texture floccose to velvely. Ehrlich reaction negative.

Sclerotia absent. Conidiophores symmetrically biverticillate, occasionally with an divergent branch that is shorter than the main axis; stipes up to 300 µm, smooth to very finely rough, 2.0–3.5 µm; metulae in a compact terminal verticil, 3–5 (–7), unequal in length, vesiculate, 10–16 x 2.0–3.5 µm; phialides ampulliform, broad, 7.0–9.0 × 2.0–3.5 µm. Conidia globose to subglobose, finely roughened, 2.0–2.5 µm diam.

Extrolites: Daldinin D, decaturin A and deoxyoxalicine B (Zhang *et al.* 2003), terrein, "SENGA", "SNIL", "SVOL", "VERSI", "XANTHOC".

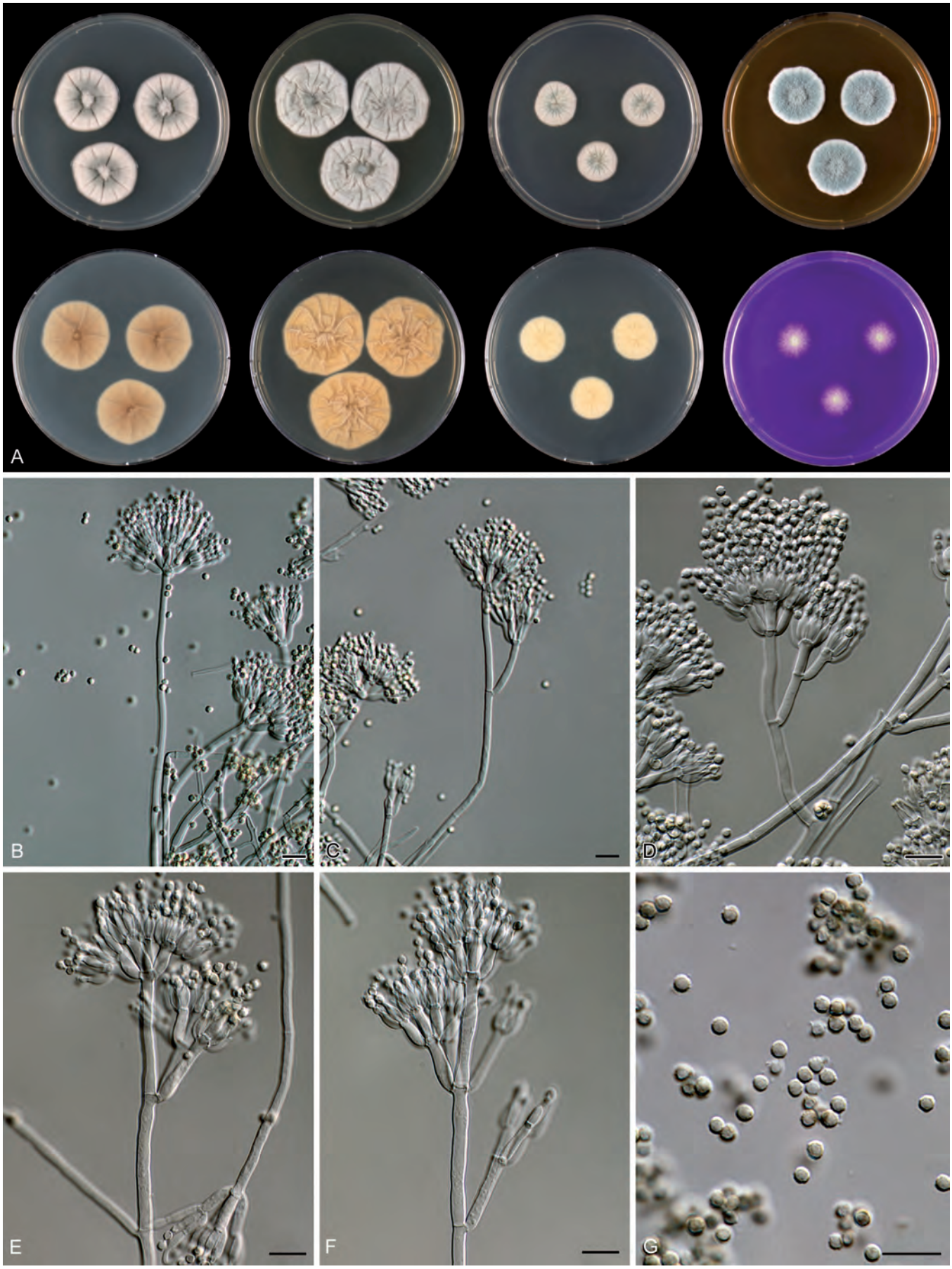

Fig. 19. *Penicillium cosmopolitanum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

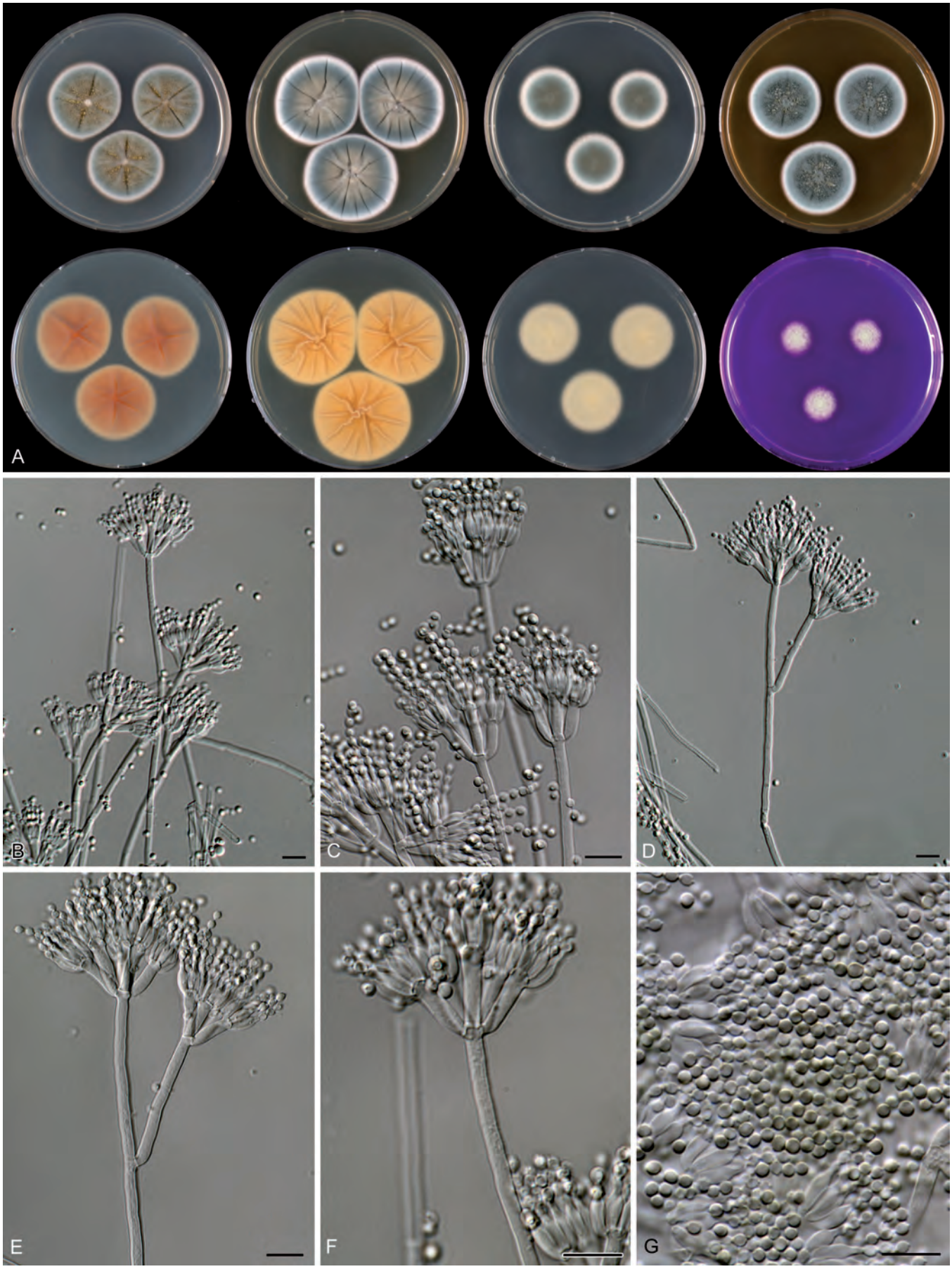

Fig. 20. *Penicillium decaturense*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Diagnostic characters: Finely roughened conidia, all examined isolates grow at 30 °C and some up to 33 °C, fast growing: 32–40 mm on CYA in 7 d at 25 °C.

Similar species: *Penicillium decaturense* forms finely roughened (sub)globose conidia. This feature is shared by several other species, such as *P. godlewskii*, *P. pancosmium*, *P. ubiquetum, P. cosmopolitanum*, *P. westlingii* and *P. chrzaszczii*. This species can be differentiated from the above mentioned species by its ability to grow consistently at 30 °C (5–15 mm).

Distribution and ecology: This species has been isolated as a colonist of fungal sporocarps (*Trichaptum biformis* and *Ischnoderma* sp.), collected in Illinois, Georgia and Florida, USA (Peterson *et al*. 2004).

Barcode & molecular based ID: GenBank no. GU944604. This species shares ITS sequences with *P. chrzaszczii*. Partial β-tubulin and calmodulin sequences can be used for identification.

Taxonomy and phylogeny: This species is a unique member of the *P. westlingii*-clade, because it is able to grow up to 33 °C. *Penicillium decaturense* is phylogenetically related to *P. pancosmium*.

Penicillium euglaucum van Beyma, Ant. van Leeuwenhoek 6: 269. 1940. Fig. 21.

= *Eupenicillium euglaucum* (van Beyma) Stolk & Samson, Stud. Mycol. 23: 90. 1983.

Typus: ex soil, Argentina (CBS 323.71 – neotype, Stolk & Samson 1983; cultures ex-type DTO 23B9 = IBT 30767).

Description: Colony diam, 7 d, in mm: CYA 23–29; CYA15°C 3–8; CYA30°C 21–30; CYA37°C (0–)5–15; MEA 22–26; YES 23–30; DG18 23–29; ratio CYAS:CYA 0.9–1.1; creatine agar 8–16, weak growth, weak acid and no base production.

Sporulation on CYA absent or inconspicuous in fresh isolates, moderate to good sporulation in cultures maintained for longer periods in culture, conidia blue-grey green, cleistothecia abundantly produced, pale yellow when young, becoming warm grey in age, mycelium inconspicuous or light yellow, exudate produced in large clear or light yellow coloured droplets, soluble pigment production strong, yellow coloured, margin entire, reverse yellow or yellow-brown and becoming dark brown in age. Sporulation on YES inconspicuous in fresh cultures, cleistothecia abundantly produced in age, warm-grey coloured, mycelium light yellow, strong yellow soluble pigments production, reverse in shades of yellow-brown. Sporulation on DG18 weak in fresh cultures and strong in degenerated cultures, conidia grey-green, mycelium white, reverse yellow. Sporulation on MEA inconspicuous and not influencing the colony colour, cleistothecia abundantly produced light yellow to grey coloured when young and becoming warm grey in age. Ehrlich reaction negative.

Cleistothecia abundantly produced on CYA, MEA and YES, globose or subglobose, up to 400 µm diam, consisting of sclerotioid masses of polygonal cells, ripening after 4–5 wk or more; warm-grey on MEA and CYA, grayish-brown on oatmeal agar. Ascospores ellipsoidal, with 2 appressed equatorial ridges, finely roughened valves in light microscope, reticulate with SEM, 3.0–4.0 x 2.5–3.0 µm. Conidiophores simple when young becoming biverticillate in age, stipes 5–60 (–100) µm long, occasionally longer, smooth walled or nearly so, 1.5–3.0 µm wide. Metulae, when present, in verticils of 2–3 (–4), unequal in length, 10–20 × 1.5–3.0 µm, often inflated at the apex, 2.5–5.0 µm wide. Phialides ampulliform, 7.0–9.0 × 2–3 µm. Conidia globose, finely roughened, 2.0–2.5 µm diam.

Extrolites: Terrein, “ALK”, “FRIL”, “GLAD”, “RAI”, “SPOKO”, “3-T”.

Diagnostic characters: *Penicillium euglaucum* is characterised by the production of warm-grey coloured cleistothecia, strong yellow soluble pigment production, good growth at 30 °C and ascospores 3.0–4.0 x 2.5–3.0 µm.

Similar species: See *P. anatolicum*.

Distribution and ecology: *Penicillium euglaucum* is isolated from Argentinean soil.

Barcode & molecular based ID: GenBank no. JN617699. This species has unique ITS, β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: *Penicillium euglaucum* was neotypified by Stolk & Samson (1983) with CBS 323.71, which resembles van Beyma’s original notes of *P. euglaucum*. They noted that *Penicillium citreonigrum* is the anamorph of *E. euglaucum* and thirty-seven species were placed in synonymy with these two species (Stolk & Samson 1983). Houbraken & Samson (2011) show that the type culture of *P. citreonigrum*, CBS 258.29, is phylogenetically unrelated to *P. euglaucum*. Analysis of the other synonyms mentioned shows that *P. euglaucum* is unrelated to any of those species (J. Houbraken, unpublished results) and therefore *P. euglaucum* is not as commonly occurring as suggested by Stolk & Samson (1983).

Penicillium gallaicum Ramírez, Martínez & Berenguer, Mycopathol. 72: 29. 1980. Fig. 22.

= *Penicillium alicantinum* Ramírez & Martínez, Mycopathol. 72: 185. 1980.
= *Penicillium syriacum* Baghdadi, Novosti Sist. Nizs. Rast. 1968: 111. 1968 (*pro parte*).

Typus: ex air, Madrid, Spain (IJFM 5597 – holotype, cultures ex type DTO 34G3 = CBS 167.81 = ATCC 42232 = IMI 253794 = VKM F-2190 = IBT 22016).

Description: Colony diam, 7 d, in mm: CYA 19–25; CYA15°C 3–6; CYA30°C 18–25; CYA37°C 0–5; MEA 24–30; YES 26–32; DG18 24–30; ratio CYAS:CYA 0.9–1.1; creatine agar 7–17, weak growth and acid production absent or only beneath the colony.

Sporulation on CYA absent, weak or moderate, conidia dull or pale grey green, mycelium pale yellow or pale crème, exudates present as droplets pale yellow, strong yellow-orange soluble pigments production, margin entire, reverse yellow-orange and becoming yellow brown in age or yellow-brown. Sporulation on YES absent or weak, conidia grey-green, mycelium white or pale beige, soluble pigments yellow-orange, reverse orange or orange-brown. Sporulation on DG18 absent or weak, obverse dull-grey green because of conidia or as white mycelium, reverse vivid yellow or yellow with conidial colour visible through the colony. Colonies on MEA weakly sporulating, mycelium white, crème or light grey coloured. Ehrlich reaction negative.

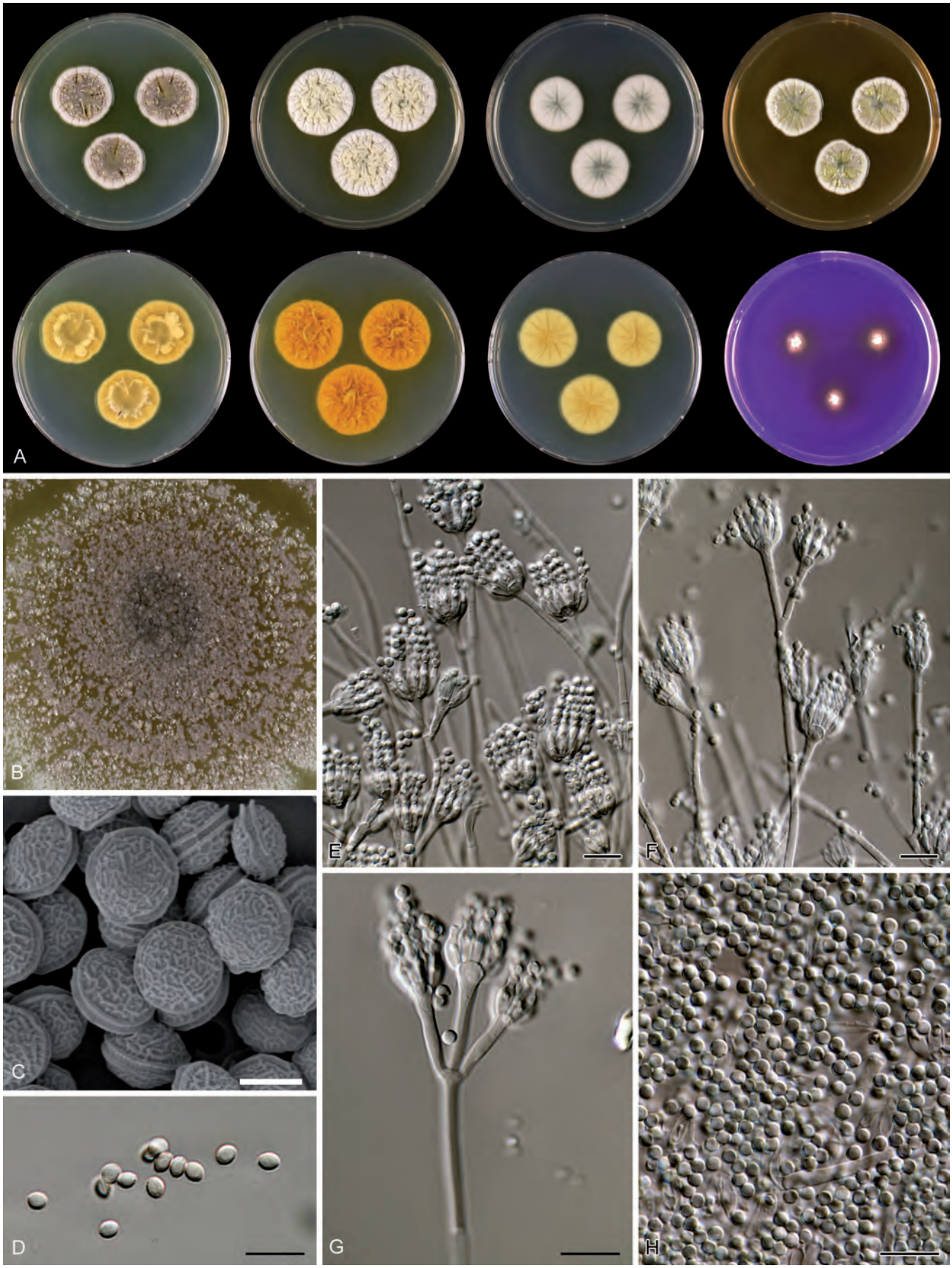

Fig. 21. *Penicillium euglaucum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Ascomata. C–D. Ascospores. E–G. Conidiophores. H. Conidia. Scale bars = 10 µm.

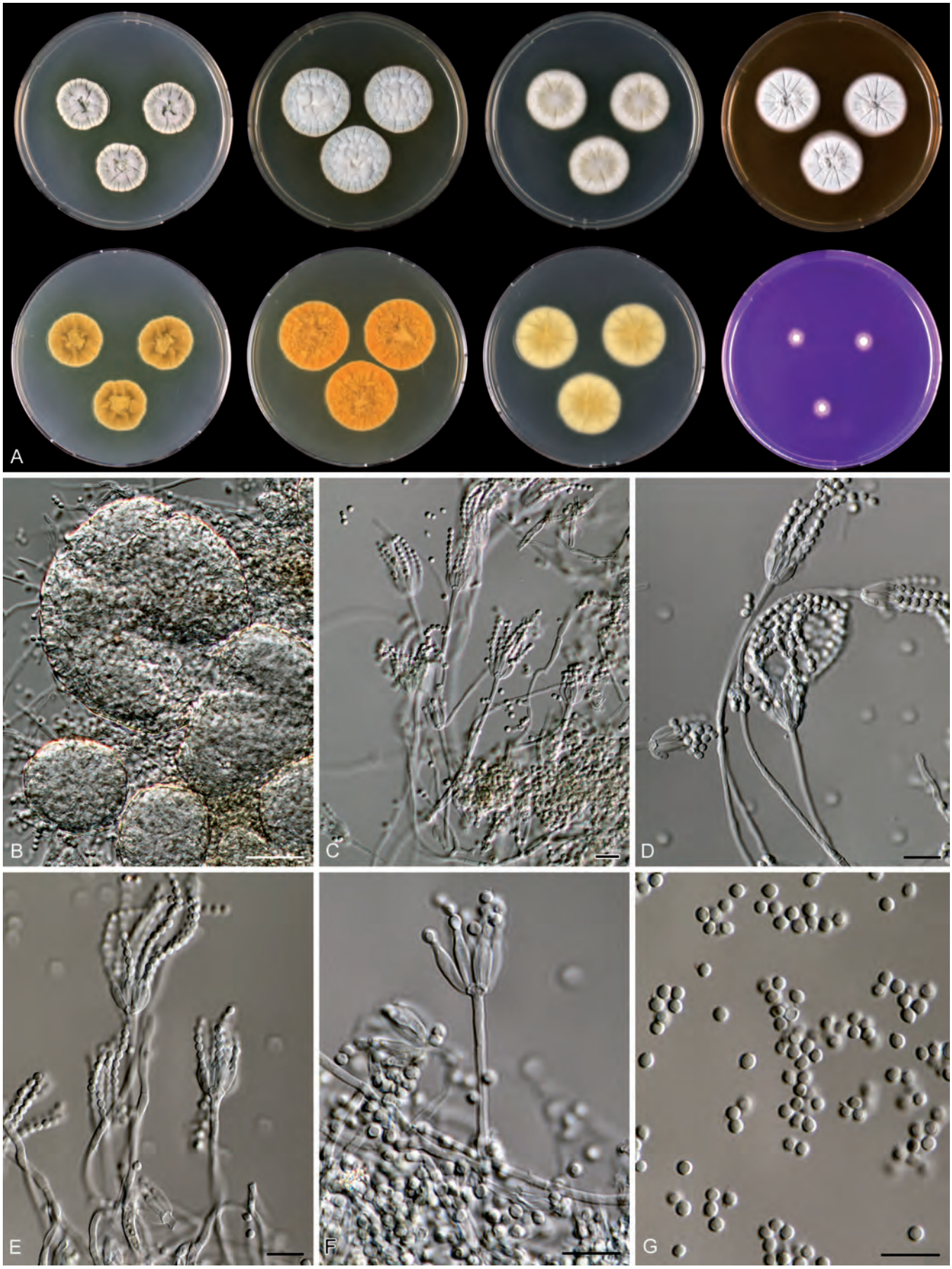

Fig. 22. *Penicillium gallaicum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Sclerotia. C–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Sclerotia inconspicuously formed under a layer of mycelium or conidiophores; white and soft when young, becoming hard and orange-brown in age, 60–100 (–150) µm; asci and ascospores not observed after prolonged incubation. Conidiophores monoverticillate occasionally with additional branch, stipes up to 50 µm, smooth walled, 2.0–3.0 µm. Phialides ampulliform, 8.0–10 × 2–3.5 µm. Conidia globose or subglobose, smooth, 2.0–2.5 µm diam.

Extrolites: Citreoviridin (Frisvad *et al*. 1990b), "KOKSO", "3-S", "TIDL", "VYL".

Diagnostic characters: Short monoverticillate conidiophores, yellow-orange soluble pigments on CYA and YES, and yellow-orange reverse becoming brown yellow brown on CYA, sclerotia production.

Similar species: *Penicillium gallaicum* is unique in section *Citrina* and shares monoverticillate conidiophores with *P. roseopurpureum* and *P. sanguifluum*. However, these species produce reddish soluble pigments. Macromorphologically, *P. gallaicum* resembles *P. citreonigrum* and both species produce citreoviridin (Frisvad *et al*. 1990b).

Distribution and ecology: Three strains were studied, two from air in Madrid, Spain and one from soil in Syria.

Barcode & molecular based ID: GenBank no. JN617690. This species has unique ITS, β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: Christensen *et al*. (1999) examined ex-type material of *P. syriacum* and indicated that this strain is a mixed culture. One of the isolates originating from the type of *P. syriacum* (CBS 418.69) is a *P. galliacum*. This strain has monoverticillate conidiophores and does not resemble Baghdadi's original description (Baghdadi 1968).

Penicillium godlewskii Zaleski, Bull. Int. Acad. pol. Sci. Lett., Sér. B.: 466. 1927. Fig. 23.

= *Penicillium kapuscinskii* Zaleski, Bull. Int. Acad. pol. Sci. Lett., Sér. B: 484. 1927.

Typus: ex soil under pine, Bialowieska, Poland (CBS 215.28 – lectotype, designated here; cultures ex type DTO 22E2 = ATCC 10449 = ATCC 48714 = FRR 2111 = IFO 7724 = IMI 040591 = MUCL 29243 = NRRL 2111 = QM 7566 = VKM F-1826).

Description: Colony diam, 7 d, in mm: CYA 15–25; CYA15°C 13–20; CYA30°C and CYA37°C no growth; MEA 12–20; YES 20–30; DG18 15–23; ratio CYAS:CYA 1.0–1.4; creatine agar 10–17, weak growth and no acid production.

Moderate to good sporulation on CYA, velvety, conidia grey-green, mycelium inconspicuous, exudate absent, soluble pigment absent, margin entire to slightly polygonal, reverse in shades of orange, often beige-orange. Sporulation on YES variable, absent to good, mycelium white, soluble pigments absent, reverse beige, beige-orange or yellow-orange. Moderate to good sporulation on DG18, conidia dull-green or grey-green, reverse pale. Moderate to good sporulation on MEA, conidia grey green, becoming blue-grey green in age, colony texture velvety with floccose centre. No reaction with Ehrlich test.

Sclerotia absent. Conidiophores symmetrically biverticillate and often with an divergent branch, starting often 30–50 µm under terminal verticil; stipes long, up to 700 µm, smooth and rather broad, 2.5–4.0 µm; metulae in a compact terminal verticil, 5–8 (–10), unequal in length, vesiculate, 9–13 (–15) × 2.5–3.5 µm; phialides ampulliform, 6.5–8.5 × 2–3 µm. Conidia globose to subglobose, finely roughened, 2.0–2.5 µm diam.

Extrolites: Citrinin, citreoviridin, decaturin, an okaramin, perinadine, "TRIP".

Diagnostic characters: Finely roughened conidia, weak growth on CYA incubated at 27 °C (0–5 mm), reverse on CYA in shades of yellow-orange.

Similar species: See *P. chrzaszczii.*

Distribution and ecology: Soil appears to be the primary habitat, but also isolated from butter; known from Poland, Germany and the Netherlands.

Barcode & molecular based ID: GenBank no. JN617692. *Penicillium godlewskii* shares ITS sequences with *P. nothofagi* and certain strains of *P. cosmopolitanum* (Fig. 3, clade 4) (CBS 126997, CBS 127038). *Penicillium godlewskii* can be identified using partial β-tubulin and/or calmodulin sequences.

Taxonomy and phylogeny: *Penicillium godlewskii* was described by Zaleski (1927). Raper & Thom (1949) gave it as a separate species status in their monograph, while Pitt (1980) placed this species in synonymy with *P. jensenii*. Type material of this species (CBS 215.28^{T}) is degenerated. Sequences generated from this strain indicate that *P. godlewskii* is distinct and belongs to the *P. westlingii*-clade. Raper & Thom (1949) placed *P. kapuscinskii* in the *Penicillium nigricans* series and Pitt (1980) accommodated this species in the *Canescentia* series. The main reason for this was the formation of ornamented conidia. However, molecular data indicate that this species is a synonym of *P. godlewskii*, a species that also forms (finely) roughened conidia. Furthermore, the original drawing of Zaleski (1927:55) shows that *P. kapuscinskii* produces symmetrically biverticillate structures, indicating a relation with section *Citrina*. The isolate maintained in the CBS collection is degenerated and produces conidiophores sparsely.

Penicillium gorlenkoanum Baghdadi, Nov. sist. Niz. Rast., 1968: 97. 1968. Fig. 24.

= *Penicillium damascenum* Baghdadi, Nov. sist. Niz. Rast., 1968: 101. 1968.

Typus: ex soil, Syria (CBS 408.69 – type; cultures ex-type DTO 34E3 = FRR 511 = IMI 140339 = VKM F-1079).

Description: Colony diam, 7 d, in mm: CYA 26–31; CYA15°C 8–12; CYA30°C 20–30; CYA37°C no growth; MEA 20–27; YES 26–30; DG18 18–26; ratio CYAS:CYA 1.0–1.1; creatine agar 13–19, weak growth and no or weak acid production.

Moderate or good sporulation on CYA, velvety with floccose centre, conidia grey, dull green or dark green, mycelium inconspicuous, exudate droplets minute and clear or weak yellow coloured, soluble pigments absent, margin entire, reverse pale yellow or crème-brown. Degree of sporulation on YES variable: weak (CBS 409.69) to strong (CBS 408.69), conidia grey green,

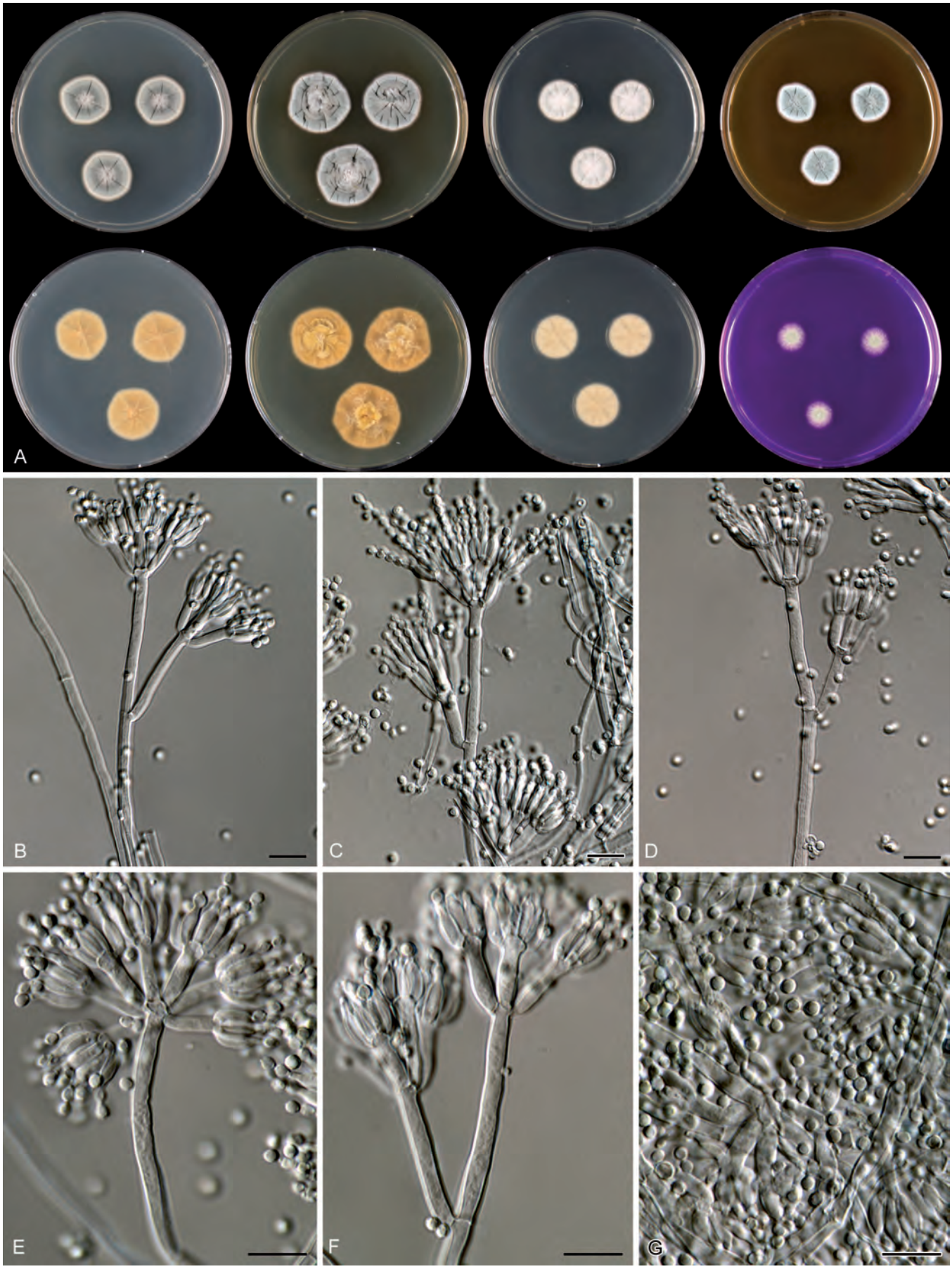

Fig. 23. *Penicillium godlewskii*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Fig. 24. *Penicillium gorlenkoanum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

soluble pigment absent, reverse pale yellow. Sporulation on DG18 variable, absent to strong, condia grey green or dark dull green, reverse pale or pale-light yellow. Variable sporulation on MEA, conidia grey green, colony texture velvety to floccose. Ehrlich reaction negative.

Sclerotia absent. Conidiophores from aerial hyphae, predominantly irregularly biverticillate, stipes smooth, width 2.0–2.7. Metulae terminal in whorls of 2–3, 12–17 × 2.2–3.0 µm. Phialides ampulliform, 7.5–9.0 × 2.0–3.0 µm. Conidia globose to subglobose, smooth to finely roughened, variable in size, predominantly 2.0–2.5 µm, smaller portion of conidia larger, 2.5–3.0 µm diam.

Extrolites: Citrinin, costaclavin, chanoclavine-I (Kozlovskiĭ *et al*. 1981a, 1981b), "KUSK", "PHOE", "WK", "WS", "WT" and "WØ" (Houbraken *et al*. 2010).

Diagnostic characters: No growth at 37 °C, production of chanoclavine-I.

Similar species: *Penicillium gorlenkoanum* is related to *P. citrinum* and related species. It can be distinguished from these species by the production of chanoclavine-I, a crème-brown reverse on CYA, absence of cleistothecia, and no growth at 37 °C.

Distribution and ecology: This species is only known from Syrian soil.

Barcode & molecular based ID: GenBank no. GU944581. This species has unique ITS, β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: Only two strains of this species were available for examination (CBS 408.69 and CBS 409.69) and both lacked typical terminal metulae in whorls of 5–8, as reported and shown in the original descriptions (Baghdadi 1969). This might be a result of degeneration of these cultures during preservation. The conidial size and the original drawings of the conidiophores indicate that this species belongs to section *Citrina*. Combined morphological, molecular and extrolite data show that *Penicillium gorlenkoanum* is conspecific with and *P. damascenum*.

Penicillium hetheringtonii Houbraken, Frisvad & Samson, Fung. Divers. 44: 125. 2010. Fig. 25.

Typus: ex soil, Treasure Island, Florida, USA, R.A. Samson (CBS 122392 – holotype, cultures ex-type DTO 5H9 = IBT 29057).

Description: Colony diam, 7 d, in mm: CYA 26–32; CYA15°C 7–11; CYA30°C 26–34; CYA37°C 0–2; MEA 17–23; YES 27–35; DG18 16–25; ratio CYAS:CYA 0.8–1.0; creatine agar 13–17, poor growth on creatine agar, no acid production.

Moderate to good sporulation on CYA, velvety, conidia dull green or dark green, mycelium inconspicuous, small hyaline exudate droplets, diffusible pigments absent, margin entire, reverse colour crème-brown. Moderate to good sporulation on YES, conidia dark green, mycelium inconspicuous, soluble pigments absent, reverse orange. Good sporulation on DG18, conidia grey green, reverse in shades of yellow (varying from pale to bright). Good sporulation on MEA, conidia dark grey green, colony texture velvety and floccose in centre. Ehrlich reaction negative.

Sclerotia absent. Conidiophores borne from surface hyphae, predominant symmetrically biverticillate, terverticillate conidiophores occasionally present; stipes smooth, 2.5–3.5 µm wide. Metulae in compact whorls of 4–8 (–12), 11–15 × 2.5–3.5 µm, vesticulated, even in length. Phialides ampulliform, 7.0–9.2 × 2.0–3.0 µm. Conidia globose to subglobose, smooth to finely roughened, 2.0–2.5 µm diam.

Extrolites: Citrinadine, citrinin, quinolactacin, two anthraquinones,"SHAMIX", "FON", "CITY", "PR1-x" (Houbraken *et al*. 2010).

Diagnostic characters: Metulae in verticils of 4–8 (–12), crème-brown reverse on YES, lacking diffusible soluble pigments on YES and CYA, CYAS:CYA 0.8–1.0, production of uncharacterised metabolite PR1-x.

Similar species: *Penicillium hetheringtonii* resembles *P. citrinum* in having similar growth rates on agar media and an orange reverse on YES, but differs from *P. citrinum* in having broader stipes, 4–8 closely appressed metulae and lacking the production of soluble pigments on YES and CYA.

Distribution and ecology: This species probably has a worldwide distribution and has a preference for warmer climates. It has been isolated from soil in Florida, USA and Queensland, Australia.

Barcode & molecular based ID: GenBank no. GU944558. This species can be identified with ITS sequences. It has a 36–38 bp deletion in the ITS1 when compared with other members of section *Citrina*. This deletion was also observed in all isolates of *P. citrinum* and CBS 327.79 (*P. manginii*).

Taxonomy and phylogeny: None.

Penicillium manginii Duché & Heim, Recl. Trav. Cryptog. Louis Mangin: 20. 1931. Fig. 26.

= *Penicillium pedemontanum* Mosca & Fontana, Allionia 9: 40. 1963.

Typus: unrecorded source (CBS 253.31 – neotype, designated by Pitt *et al*. 2000; cultures ex-type DTO 22E9 = NRRL 2134 = IMI 191732 = FRR 2134 = IBT 18224).

Description: Colony diam, 7 d, in mm: CYA 28–40; CYA15°C 19–27; CYA30°C 0–8; CYA37°C no growth; MEA 25–37; YES 35–47; DG18 18–27; ratio CYAS:CYA (0.85–) 1.0–1.3; creatine agar 16–22, weak growth and no acid production.

Moderate to good sporulation on CYA, velvety, conidia grey-green, mycelium light-yellow, exudate in some strains produced as minute clear or yellow droplets, soluble pigment yellow, margin in most isolates entire, in some strains polygonal, reverse orange or orange with red centre. Moderate to good sporulation on YES, conidia grey green, mycelium light-yellow, strong red soluble pigment production, reverse blackish-red or dark red-brown. Moderate to good sporulation on DG18, conidia grey green, reverse in most isolates deep-red with red soluble pigments, occasionally yellow or pale, conidia. Sporulation variable on MEA, varying from absent to good, conidia grey green, colony texture velvety, becoming floccose in age. Ehrlich reaction negative.

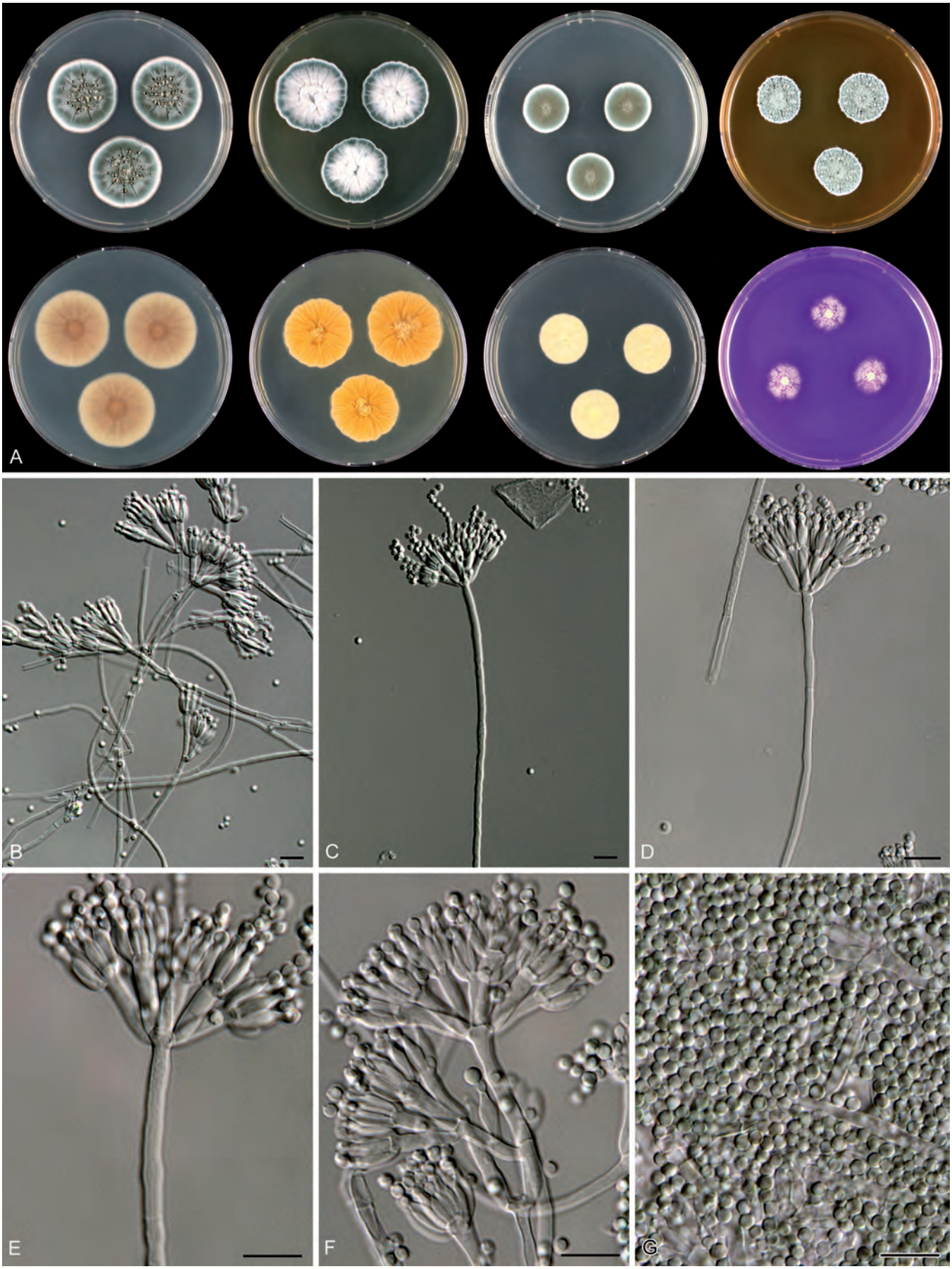

Fig. 25. *Penicillium hetheringtonii*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

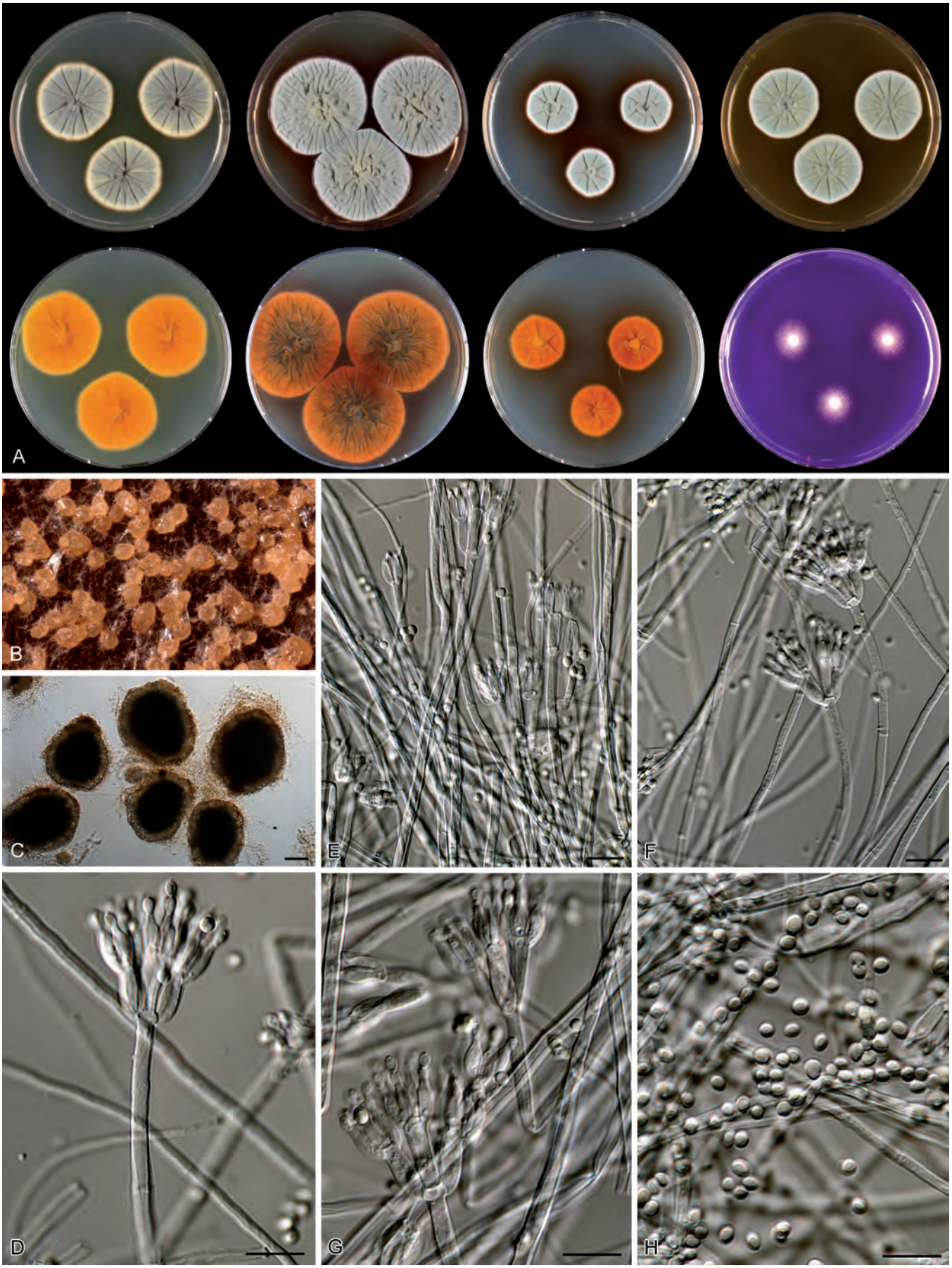

Fig. 26. *Penicillium manginii*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–C. Sclerotia. D–G. Conidiophores. H. Conidia. Scale bars = 10 µm.

Sclerotia light yellow-brown and soft when young, becoming orange brown and hard in age, consisting of large polygonal cells, with red brown pigmented hyphe present on the sclerotial body, 100–250 µm, irregular in shape. No ascospores observed after incubation on OA for 3 mo. Conidiophores predominantly symmetrically biverticillate and, depending on the isolate, additional branches can occur; stipes 200–500 µm long, finely rough walled occasionally smooth walled, width variable, 2.0–4.0 µm; metulae in a compact terminal whorls of 2–4 (–6), even in length, non-vesiculate, 10–14 × 2.0–3.5 µm; phialides ampulliform, 7–9 × 2.0–3.0 µm. Conidia (broadly) ellipsoidal, smooth, 2.5–3.0 × 2.0–2.5 µm.

Extrolites: Citrinin, citreomontanin (Rebuffat *et al*. 1980), citreoviridin A (Nagel *et al*. 1972, Rebuffat *et al*. 1984, Frisvad & Filtenborg 1990), citreoviridinol A_1 and A_2 (Rebuffat *et al*. 1984), epicitreoviridinol (Lai *et al*. 1990), phoenicin, "MIF", "MIM". Phoenicin was not detected in CBS 235.31, CBS 263.29, CBS 378.65 and CBS 126233, but all other 20 strains of *P. manginii* examined produced this compound. This compound contributes to the red colour of the diffusible pigment of *P. manginii*, but the species also produces some red anthraquinone secondary metabolites. Citrinin was produced by CBS 235.31, CBS 265.65, CBS 263.29, CBS 408.65, CBS 409.65, CBS 122403, CBS 126232 and seven additional strains. Citreoviridin was produced by all strains examined. CBS 126233 shares extrolites with other strains of *P. manginii*, but is unique in producing decaturins and aflavinin-type apolar sclerotial indolterpenes.

Diagnostic characters: Yellow mycelium (citreoviridins) (CYA15°C), fast growth rate on YES with red soluble pigments, light brown or orange brown sclerotia.

Similar species: The production of yellow mycelium is shared with *P. vancouverense*, but *P. manginii* grows faster, produces red soluble pigment and can have finely rough walled stipes.

Distribution and ecology: Worldwide. Isolated from soil in Norway, Congo, Madagascar and UK; air in the Netherlands and Spain, mycorrhizae of *Fagus sylvatica*, Italy and rhizosphere of *Triticum aestivum*, UK.

Barcode & molecular based ID: GenBank no. GU944599. The ITS region of the majority of the analysed *P. manginii* isolates were invariable. Isolate CBS 327.79 was an exception and had 37 bp deletion in the ITS1 region. This deletion in also observed in *P. citrinum* and *P. hetheringtonii*, but not in other strains of the *P. westlingii*-clade. Phylogenetic analysis of partial β-tubulin and calmodulin data shows that isolates CBS 378.65, CBS 108.66 and CBS 126233 are deviating from the majority of the analysed *P. manginii* isolates and each strain has a unique sequence. However, these three strains have similar ITS sequences (0, 1 and 4 bp difference, respectively) as the type of *P. manginii*, CBS 253.31^T.

Taxonomy and phylogeny: *Penicillium manginii* was placed in synonymy with *P. miczynskii* by Raper & Thom (1949), Pitt (1980) and Ramírez (1982), but this was not followed by Stolk & Samson (1983), who maintained it as a separate species on the basis of conidiophore ornamentation and conidial shape. Molecular data supports the conclusions of Stolk & Samson (1983). *Penicillium pedemontanum* is synonymised with *P. manginii*. The type of *P. pedemontanum* (CBS 265.65^T) once produced large light brown sclerotia, but the culture maintained at CBS has lost this ability.

Molecular data shows variation among the analysed *P. manginii* isolates and this species is probably a complex. Of all *P. manginii* strains analysed, CBS 378.65 was the only strain with a CYAS:CYA ratio lower than 1 (0.85). CBS 126233 produced decaturins and aflavinin-type apolar sclerotial indolterpenes and did not produce red soluble pigments. However, this latter feature was also observed in some other *P. manginii* strains. These strains might represent new species, but we wait with the description until more strains are collected and investigated. Several strains originally identified as *P. pulvillorum* (Nagel *et al*. 1972) proved to be *P. manginii* (CSIR 1405, CSIR 1406, IMI 059911, IMI 089983, IMI 096225, IMI 096290 and IMI 099085). Comparison of deposited calmodulin sequences of NRRL 29865 (AY443481) and NRRL 29736 (AY443483) suggests that these strains are closely related to *P. manginii* and might represent a new species.

Penicillium miczynskii Zaleski, Bull. Int. Acad. pol. Sci. Lett., Sér. B.: 482. 1927. Fig. 27.

Typus: ex soil under conifer, Tatry mountains, Poland (IMI 40030 – lectotype, Pitt 1980; cultures ex-type CBS 220.28 = ATCC 10470 = DSM 2437 = FRR 1077 = IFO 7730 = IMI 040030 = MUCL 29228 = NRRL 1077 = QM 1957 = IBT 5491)

Description: Colony diam, 7 d, in mm: CYA 21–27; CYA15°C 15–23; CYA30°C and CYA37°C: no growth; MEA 17–25 mm; YES 26–33 mm; DG18 18–25; ratio CYAS:CYA 0.85–1.0; creatine agar 9–13 mm, weak growth and no acid production.

Degree of sporulation on CYA generally poor, occasionally good sporulation (CBS 126223), velvety, conidia grey green, mycelium white or light yellow, exudate absent or sparsely produced as small clear droplets, soluble pigments absent and in some strains yellow, margin of most isolates polygonal, occasionally entire, reverse beige to beige brown in the majority of strains, occasionally yellow-orange (CBS 126222). No or weak sporulation on YES, soluble pigments absent (except CBS 126223, which has strong sporulation and yellow soluble pigments), reverse yellow-orange or yellow-brown. Moderate to good sporulation on DG18, conidia grey green, reverse (bright) yellow. Sporulation on MEA variable, conidia grey green, colony texture velvety to slightly floccose. No reaction with Ehrlich test; with exception of CBS 126222.

Sclerotia produced on oatmeal agar under large, clear exudate droplets and a thin layer of conidiophores. Sclerotia pale orange becoming orange-brown in age, 125–250 (–300 µm), soft when young becoming hard with age, consisting of polygonal cells, red-brown pigmented spots often present on the surface. Asci and ascospores not observed. Conidiophores predominantly symmetrical biverticillate with occasionally an additional branch, stipes 200–400 µm long, smooth walled, 2.5–4.0 µm wide; metulae in terminal whorls of 3–6 (–8) and often uneven in length, 10–12 × 2.5–4.0 µm; phialides ampulliform, 7–9 × 2.0–3.0 µm. Conidia subglobose to broadly ellipsoidal, smooth, 2.0–3.0 × 2.0–2.5 µm.

Extrolites: Citreoviridin, cyclopiazonic acid, quinolactacin, terrein, "met OE", "MIF", "TERRIT", "XANTHOC".

Diagnostic characters: Colonies on CYA 21–27 mm; no growth on CYA30, ratio CYAS:CYA 0.85–1.0, orange-brown sclerotia.

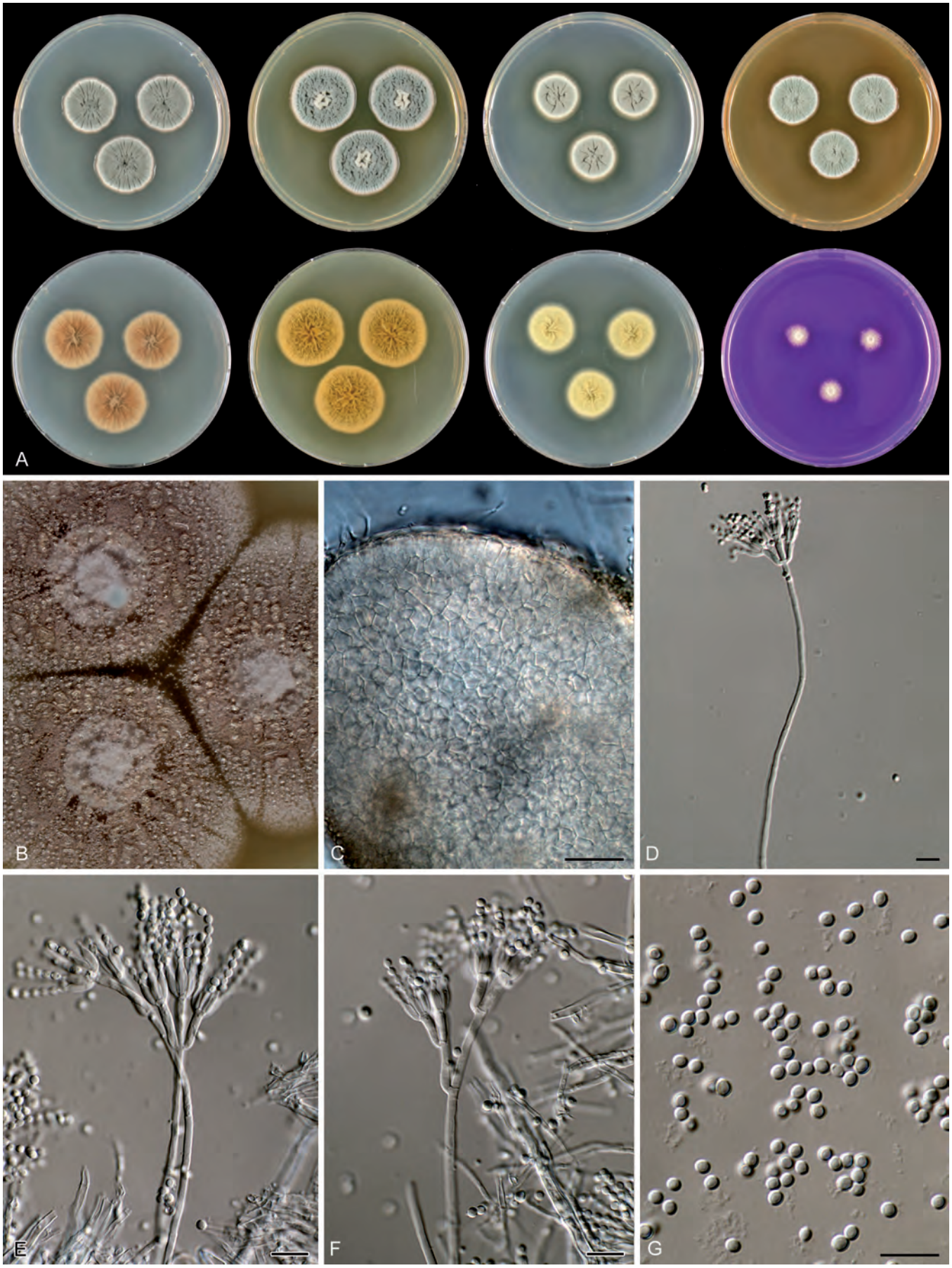

Fig. 27. *Penicillium miczynskii*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–C. Sclerotia. D–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Similar species: This species is phylogenetically related to *P. cairnsense*, *P. aurantiacobrunneum*, *P. neomiczynskii* and *P. quebecense*. *Penicillium miczynskii* deviates from *P. cairnsense* and *P. quebecense* in having smaller colony diameters on YES, MEA and CYA and does not grow at 30 °C. In addition, *P. cairnsense* and *P. quebecense* often produce red soluble pigments and have many exudate droplets on CYA. The ratio CYAS:CYA of *P. miczynskii* is lower than 1 and this character can be used to distinguish *P. miczynskii* from the morphologically similar species *P. aurantiacobrunneum* and *P. neomiczynskii.*

Distribution and ecology: Worldwide, commonly occurring in soil.

Barcode & molecular based ID: GenBank no. GU944600. *Penicillium miczynksii* and *P. aurantiacobrunneum* share the same ITS sequence. These species can be distinguished by partial β-tubulin and/or calmodulin sequences.

Taxonomy and phylogeny: *Penicillium miczynskii* was described by Zaleski (1927) and the taxonomy of this species was considered in various taxonomic studies (Raper & Thom 1949, Pitt 1980, Ramírez 1982, Christensen *et al*. 1999). Thom (1930: 488) placed this species in a miscellaneous group after his section *Biverticillata-Symmetica*, while Raper & Thom (1949) included it in the *P. janthinellum* series. Subsequently, Pitt (1980) placed this species in the series *Citrina* and broadened the species concept to include sclerotigenic strains. The ex-type culture CBS 220.28 does not produce sclerotia, but most recently isolated strains do. This feature appears to be quite common for *P. miczynskii* isolates and other phylogenetically related species. Although Pitt (1980) synonymised *P. chrzaszczii*, *P. soppii*, *P. matris-meae*, *P. manginii*, *P. pedemontanum*, *P. atrosanguineum* and *P. syriacum* with *P. miczynskii*, our study shows that none of these species are conspecific with *P. miczynskii*.

Penicillium neomiczynskii AJL Cole, Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563192. Fig. 28.

Etymology: This species is closely related to *P. miczynskii*.

Differt ab omnibus speciebus affinibus ratione CYAS:CYA 1.1–1.2, coloniis in agaro CYA ad 30 °C haud crescentibus, coloniis in agaro MEA 12–18 mm.

Typus: ex soil, New Zealand, T. Cole (CBS H-20661 – holotypus, cultures ex-type CBS 126231 = DTO 78C2 = IBT 23560).

Description: Colony diam, 7 d, in mm: CYA 21–27; CYA30°C no growth; CYA37°C: no growth; MEA 12–18 mm; YES 25–31 mm; DG18 16–22; ratio CYAS:CYA 1.1–1.2; creatine agar 9–13 mm, weak growth and no acid production.

Good sporulation on CYA, velvety to floccose, conidia grey-blue green, mycelium inconspicuous, exudate in minute clear droplets, soluble pigments yellow-brown, margin irregular, reverse yellowish brown. Good sporulation on YES, conidia grey green, soluble pigments absent, reverse yellow-beige. Good sporulation on DG18, conidia dull green, mycelium inconspicuous, reverse pale. Good sporulation on MEA, conidia dull green, colony texture velvety. Ehrlich reaction negative.

Sclerotia absent. Conidiophores 200–400 µm long, both symmetrically biverticillate and terverticillate, stipes smooth, 2.5–3.5 µm wide. Metulae in a terminal whorl of 3–6 metulae, often unequal in length, 10–13 × 2.5–3.5 µm. Phialides ampulliform, 7–9 × 2.5–3.0 µm. Conidia subglobose to broadly ellipsoidal, smooth, 2.0–3.0 × 2.0–2.5 µm, larger conidia also present, globose, 3.0–3.5 µm diam.

Extrolites: Citreoviridin, terrein, "MIF", "OFSO".

Diagnostic characters: CYAS:CYA ratio 1.1–1.2, no growth on CYA30°C, colonies on MEA 12–18 mm.

Similar species: *Penicillium neomiczynskii* resembles *P. miczynskii* and *P. aurantiacobrunneum*. It differs from *P. aurantiacobrunneum* in its negative Ehrlich reaction and can be differentiated from *P. miczynskii* by its CYAS:CYA ratio of 1.1–1.2.

Distribution and ecology: *Penicillium neomiczynskii* is only known from its type culture, which was isolated from soil from New Zealand.

Barcode & molecular based ID: GenBank no. JN617671. The sequences of the ITS regions of *P. neomiczynskii* are identical to those of the type of *P. cairnsense* (CBS 124325^T) and *P. quebecense* (CBS 101623^T). Partial β-tubulin and calmodulin sequences can be used for identification of this species.

Taxonomy and phylogeny: This species is phylogenetically and morphologically related to *P. miczynskii* and *P. aurantiacobrunneum*.

Penicillium nothofagi Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563189. Fig. 29.

Etymology: Isolated from soil under *Nothofagus* sp.

Differt ab omnibus speciebus affinibus coloniis in agaro CYA, MEA et YES restricte crescentibus, conidiis leniter vel distincte exasperates.

Typus: ex soil under *Nothofagus* sp., Chile (CBS H-20655 – holotypus, cultures ex-type CBS 130383 = DTO 76C2 = IBT 23018).

Description: Colony diam, 7 d, in mm: CYA 5–10; CYA15°C 8–14; CYA30°C and CYA37°C 0; MEA 4–8; YES 10–15; DG18 10–15; ratio CYAS:CYA 2.0–3.0; creatine agar 3–6, weak growth and no acid production.

Moderate sporulation on CYA, velvety, conidia dark green conidia, mycelium inconspicuous, exudates absent, soluble pigment absent, margin entire, reverse pale beige. Sporulation on YES absent, mycelium white, soluble pigments absent, reverse beige. Moderate sporulation on DG18, conidia dull green to grey green, reverse pale to pale-cream. No sporulation on MEA after 7 d of incubation, after 14 d moderate sporulation, conidia blue green, colony texture velvety to granulose. Ehrlich reaction negative.

Sclerotia absent. Conidiophores mostly symmetrically biverticillate and occasionally with an additional divergent branch; stipes variable in length, 50–400 µm long, smooth, 2.0–3.0 µm wide; metulae in a divergent terminal verticil, 2–4 (–7), unequal in length, with a distinct vesicle, long compared to related species, 11–17 × 2.5–3.5 µm, additional branches up to 25 µm; phialides ampulliform, 7.5–10 × 2.5–3.5 µm. Conidia globose to subglobose, finely to distinct roughened, 2.5–3.5 µm diam.

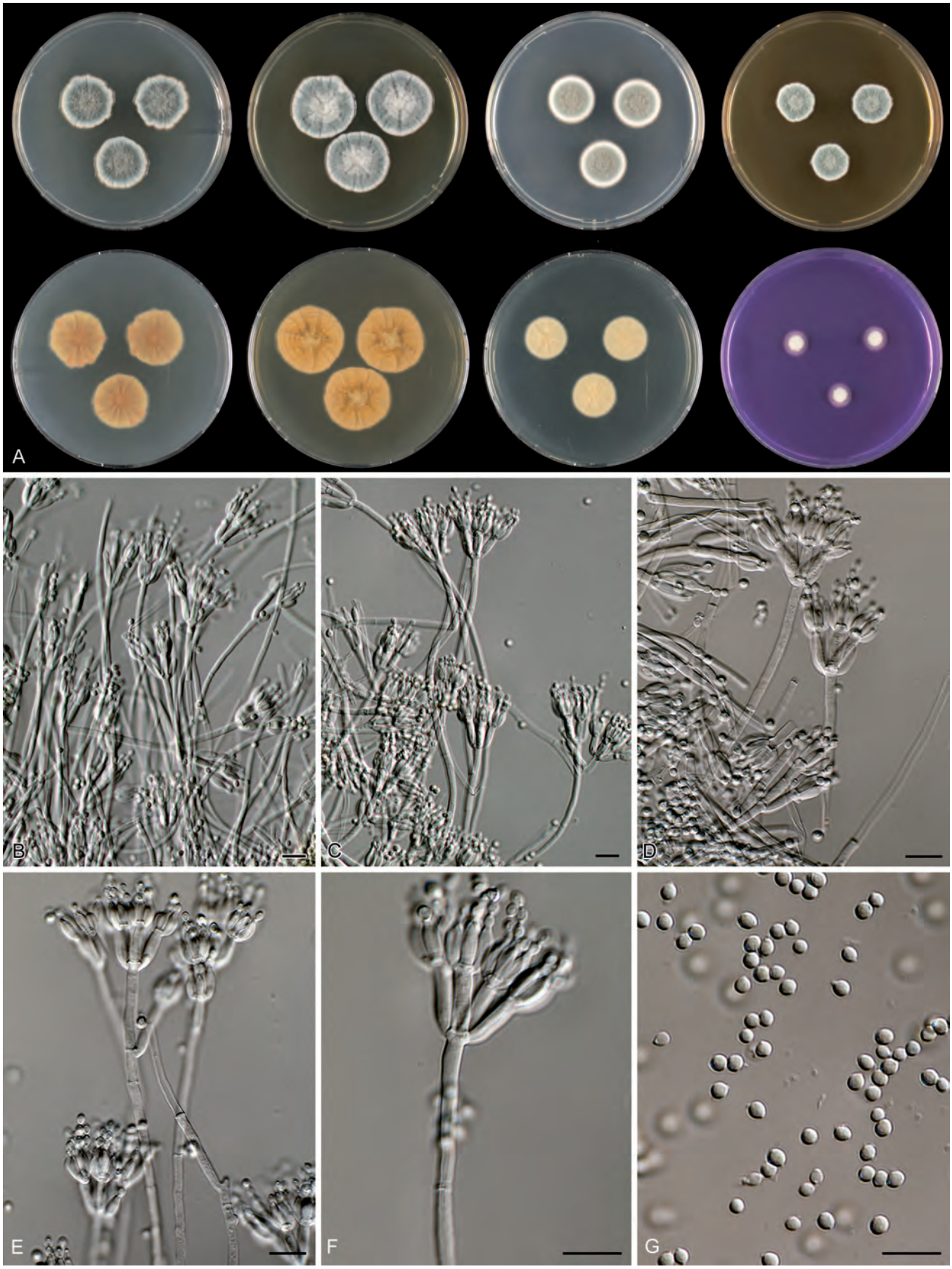

Fig. 28. *Penicillium neomiczynskii*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

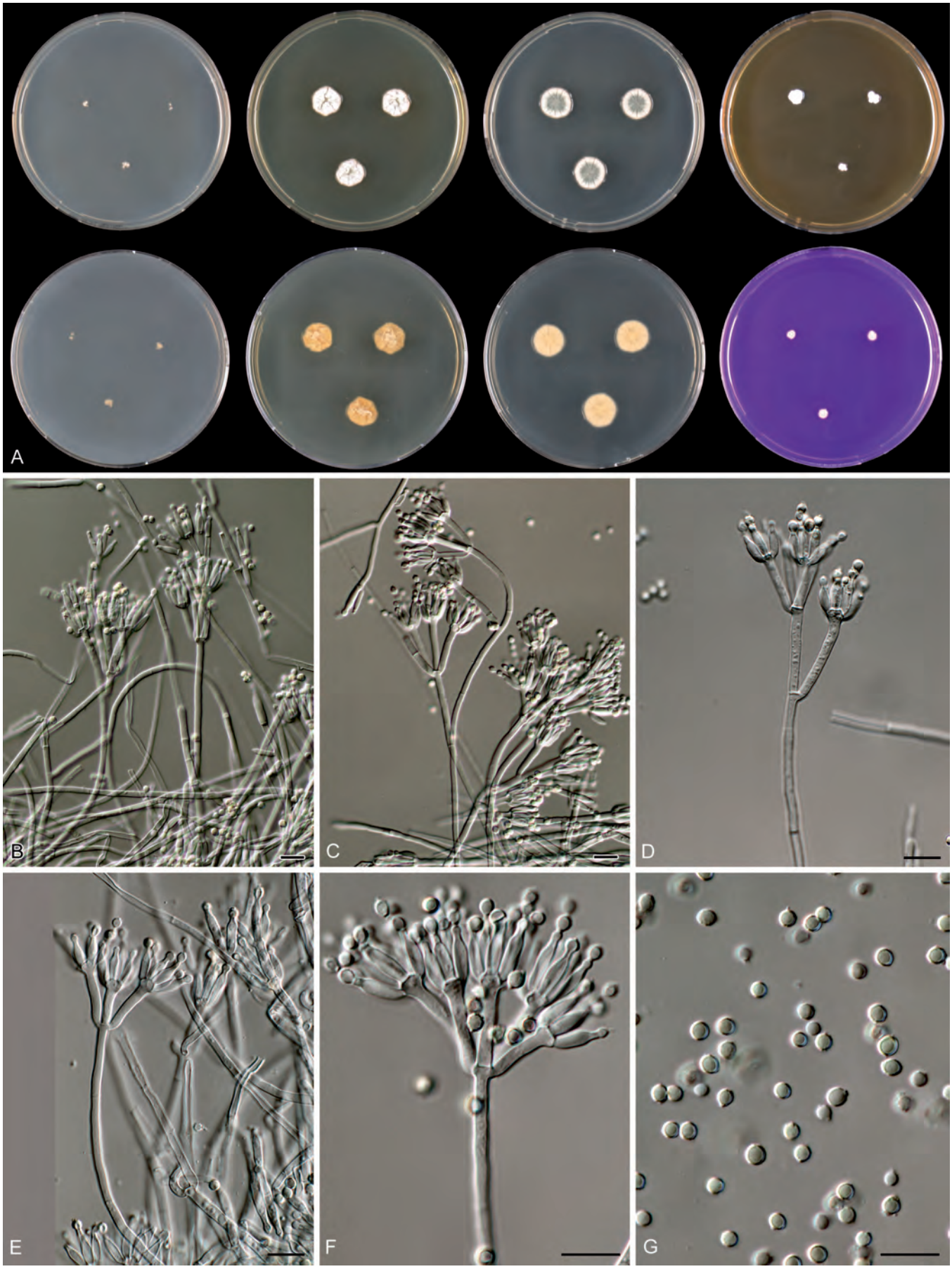

Fig. 29. *Penicillium nothofagi*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Extrolites: Citrinin, “CURVU”, “SENTRIP”, “SKAEM”.

Diagnostic characters: Restricted growth on CYA, MEA and YES, finely to distinct rough walled conidia.

Similar species: This species is phylogenetically related to *P. westlingii* and *P. cosmopolitanum*. It differs from those species by a slower growth rate on the CYA, YES and MEA. *Penicillium wellingtonense* is phenotypically similar, but produces has an orange coloured reverse on CYA and subglobose to broadly ellipsoidal conidia.

Distribution and ecology: Soil under *Nothofagus* sp. in Chile and soil, Brazil.

Barcode & molecular based ID: GenBank no. JN617712. CBS 130383^{T} shares ITS sequences with *P. godlewskii* and with *P. cosmopolitanum* strains belonging to subclade 4 (Fig. 3).

Taxonomy and phylogeny: Phylogenetically related to *P. westlingii* and *P. cosmopolitanum*.

Penicillium pancosmium Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563191. Fig. 30.

Etymology: Referring to the worldwide distribution of this species.

Differt ab omnibus speciebus affinibus conidiis subtiliter exasperatis, coloniis ad 30 °C haud crescentibus, ad 28–35 mm diam post hebdomatem, reverso flavo-aurantiaco vel aurantiaco in agaro YES.

Typus: ex old *Armillaria mellea*, on hardwood log; Meach Lake, Gatineau Park, Gatineau County, Quebec, Canada (CBS H-20651 – holotypus, cultures ex-type CBS 276.75 = DTO 31B4 = DAOM 147467 = IBT 29991).

Description: Colony diam, 7 d, in mm: CYA (23–) 28–35; CYA15°C 15–21; CYA30°C 0 or germination; CYA37°C no growth; MEA (20–)25–31; YES (26–) 30–40; DG18 (16–) 22–30; ratio CYAS:CYA 0.9–1.1; creatine agar 15–20, weak growth and no acid production.

Good sporulation on CYA, velvety or floccose, conidia dull-green or grey-green, mycelium inconspicuous, exudate absent or sparsely present as minute clear droplets, soluble pigments absent in most isolates, except CBS 118007, which produces light red pigments, margin entire or polygonal, reverse pale, light beige or pinkish beige (towards skin colour), often with orange pigments in sulcations. Sporulation on YES variable, absent to strong, mycelium white, soluble pigments absent or yellow, reverse yellow-orange or orange. Variable sporulation on DG18, condia dull green, reverse pale or cream. Good sporulation on MEA, conidia blue-green or blueish-grey green, colony texture floccose. Ehrlich reaction negative.

Sclerotia absent. Conidiophores symmetrically biverticillate, often with an divergent branch that is shorter than the main axis; stipes long, up to 500 µm, smooth, 2.5–4.0 µm; metulae in a compact terminal verticil, 4–6 (–8), unequal in length, vesiculate, 9–13 (–15) × 2.0–3.5 µm; phialides ampulliform, broad, 6.5–9 × 2–3 µm. Conidia globose to subglobose, finely roughened, 2.0–3.0 µm diam, except CBS 126432, which has finely roughened ellipsoidal conidia, 2.5–3.0 × 1.8–2.5 µm.

Extrolites: Citrinin, daldinin D, decaturin, terrein, “MELI”, “ORAN”, “SENGA”, “XANTHOC”.

Diagnostic characters: Finely roughened conidia, no growth at 30 °C, colonies attaining a diameter of 28–35 mm in 7 d at 25 °C, reverse on YES yellow-orange or orange.

Similar species: *Penicillium pancosmium* is phylogenetically related to *P. ubiquetum*. The species are phenotypically similar, but the latter has an orange-red reverse on YES and dark-dull green conidia on CYA, while *P. pancosmium* forms a yellow-orange or orange reverse on YES and has dull green or grey green conidia on CYA. Futhermore, *P. pancosmium* tends to grow faster on MEA than *P. ubiquetum*. *Penicillium chrzaszczii* produces yellow reverse on DG18 and sporulation on CYA is absent or poor, while *P. pancosmium* and *P. ubiquetum* isolates sporulate well on CYA and have a pale (or very pale yellow) reverse on DG18.

Distribution and ecology: Isolated from soil, old *Armillaria mellea* on a hardwood log, *Piptoporus* (on *Betula* sp), nut of *Juglans cinerea* (butternut) and porcupine dung. This species has a worldwide distribution and was isolated in Tunisia, Canada (Ontario and Quebec) and USA (New Jersey).

Barcode & molecular based ID: GenBank no. JN617660. This species has unique ITS, β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: Based on partial β-tubulin and calmodulin data, CBS 118007 and CBS 126431 are phylogenetically closely related, but distinct from CBS 276.75^{T}. These isolates differ from the other *P. pancosmium* strains in having smaller colonies and a pinkish-brown reverse on CYA. CBS 126432 differs in having ellipsoidal conidia and a different β-tubulin, calmodulin and ITS sequence than CBS 276.75^{T}. It needs to be noted that the variation within *P. pancosmium* is large, and it could be that this species represents a complex.

Penicillium pasqualense Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563190. Fig. 31.

Etymology: Referring to Easter Island, the locality of the type strain.

Differt ab omnibus speciebus affinibus (sect. *Citrina*) coloniis in agaro CYA30 crescentibus, reverse atro-brunneo in agaro CYA, conidiis leviter majoribus.

Typus: ex soil, Easter Island, Chile (CBS H-20663 – holotypus, cultures ex-type CBS 126330 = DTO 80D5 = IBT 14235).

Description: Colony diam, 7 d, in mm: CYA 25–35; CYA15°C 15–20; CYA30°C 5–15; CYA37°C 0; MEA (15–) 25–30; YES 25–35; DG18 17–25; ratio CYAS:CYA 0.75–0.95; creatine agar 13–18, varying from weak (CBS 122402 & CBS 126330) to moderate (CBS 124327) growth, no or weak acid production.

Good sporulation on CYA (except CBS 126329), velvety, conidia dull dark green, mycelium inconspicuous, exudate produced in both small and large droplets, which are clear or pale yellow coloured, soluble pigment absent, margin entire, reverse dark brown or blackish brown. Weak to moderate sporulation on YES, conidia dull green, soluble pigments absent, reverse beige-brown or brown. Good sporulation on DG18, conidia dull-green, reverse pale with a cream centre. Good sporulation on MEA, conidia

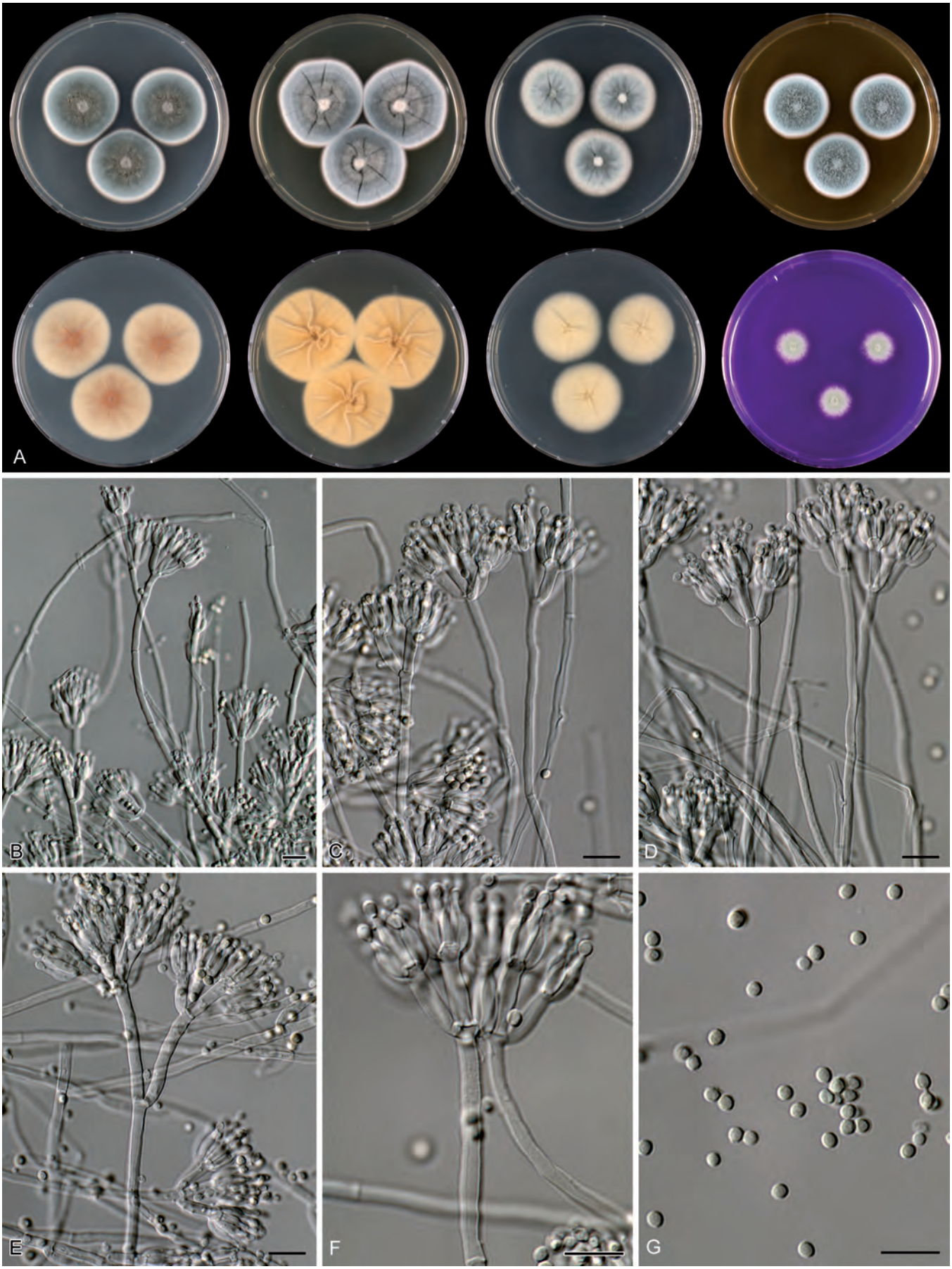

Fig. 30. *Penicillium pancosmium*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

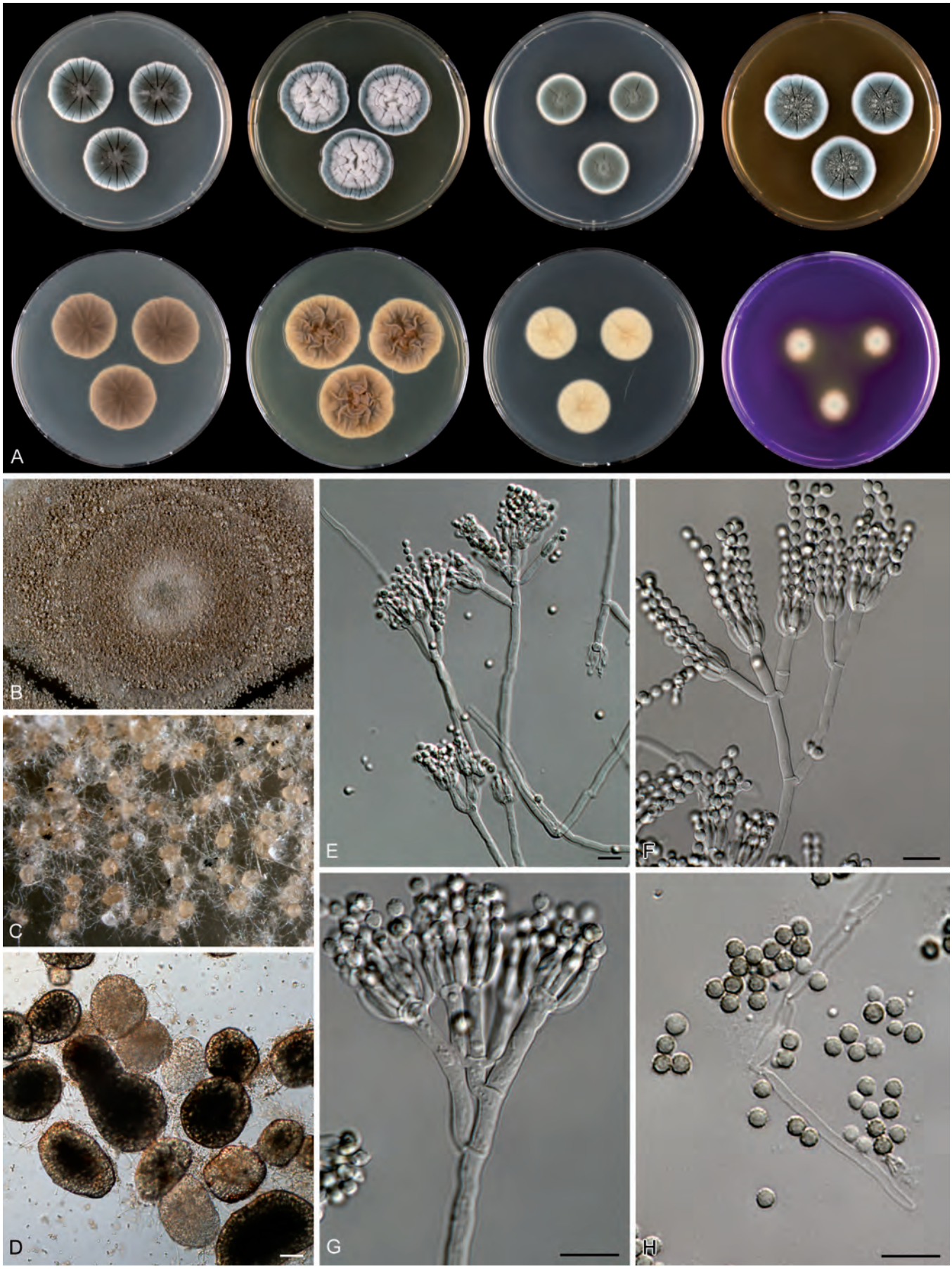

Fig. 31. *Penicillium pasqualense*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–D. Sclerotia. E–G. Conidiophores. H. Conidia. Scale bars = 10 µm.

dark green or dark-blue green, colony texture velvety to floccose, reverse medium-brown. Ehrlich reaction negative.

Sclerotia orange brown or brown, hard, consisting of hyaline polygonal cells with very thick walls, red-brown mycelium strands present present on the sclerotium. Asci and ascospores not observed. Conidiophores predominantly symmetrically biverticillate and often additional branches occur which are equal in length as the main axis and also consist of symmetrically biverticillate structures ("double symmetrically biverticillate"); stipes rather long, 200–400 µm, smooth, 2.5–3.0 µm wide; metulae in a divergent terminal vertical, 2–4, unequal in length, longer than in related species, 11–17 × 2.5–3.5 µm, branches longer up to 25 µm; phialides ampulliform, 7.5–10 × 2.5–3.5 µm. Conidia globose to subglobose, spinose, 2.5–3.5 µm diam.

Extrolites: Pyrenocines, indol alkaloids, "PAS".

Diagnostic characters: Growth on CYA30, dark brown reverse on CYA, orange brown or brown sclerotia, dark blue green spinose conidia on MEA, slightly larger conidia than most other members of section *Citrina*.

Similar species: The formation of orange-brown sclerotia indicates a relationship with *P. miczynskii* and related species, but *P. pasqualense* is less colourful, has a dark brown reverse on CYA and forms typical dark blue green, spinose conidia on MEA.

Distribution and ecology: This species was isolated from various soils and indoor air of a bakery. World-wide distribution: Easter Island, Chile, NSW, Australia, the Netherlands and Wyoming, USA.

Barcode & molecular based ID: GenBank no. JN617676. *Penicillium pasqualense* can be identified using ITS, partial β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: Phylogenetic analysis of partial β-tubulin and calmodulin data shows that this species is related to *P. vancouverense* and *P. wellingtonense* (99 % bs), but can differentiated by various phenotypic characters, such as growth at 30 °C, spinose conidia and sclerotium formation. The divergent long metulae and branching pattern of this species superficially resemble some species related to *P. simplicissimum* and *P. janthinellum*. It shares the production of of pyrenocines with *P. paxilli*.

Penicillium paxilli Banier, Bull. trimest. Soc. mycol. Fr. 23: 95. 1907. Fig. 32.

Typus: ex optical instrument, Barro Colorado Island, Panama (IMI 40226 – neotype, Pitt 1980; cultures ex-type CBS 360.48 = DTO 31A6 = ATCC 10480 = FRR 2008 = NRRL 2008 = QM 725 = IBT 16202).

Description: Colony diam, 7 d, in mm: CYA 30–37; CYA15°C 10–20; CYA30°C (9–) 18–25; CYA37°C no growth; MEA 28–35; YES 38–46; DG18 (25–) 30–37; ratio CYAS:CYA 1.0–1.3; creatine agar 11–20, weak growth and no acid production.

Good sporulation on CYA, velvety, conidia dull green or dull-blue green, mycelium white, exudate droplets clear, occasionally absent, soluble pigments absent, margin slightly polygonal, reverse pale or pale with pale beige centre. Strong sporulation on YES, conidia dull green or dull-blue green, mycelium white, soluble pigments absent, reverse (pale) crème or pale yellow. Strong sporulation on DG18, conidia dull green, reverse commonly pale, occasionally pale with pale yellow centre. Strong sporulation on MEA, conidia dull green, also dull green and blue green, colony texture floccose. Ehrlich reaction negative.

Extrolites: Paxillin, dehydroxypaxillin, 1'-O-acetylpaxillin (Frisvad & Filtenborg 1990), meleagrin, pyrenocines, "PU", "PUX", "TOTO". The paxillin biosynthetic pathway of *P. paxilli* (ATCC 26601 = CBS 547.77) was intensively studied (*e.g.* Young *et al*. 2001, McMillan *et al*. 2003).

Diagnostic characters: Rough walled stipes, predominantly biverticillate with appressed terminal whorl of 4–8 metulae, good growth on CYA incubated at 30 °C and good growth on DG18.

Similar species: *Penicillium paxilli* can be distinguished from *P. citrinum* by its inability to grow at 37 °C; from *P. sumatrense* and *P. hetheringtonii* by its pale reverse on CYA, and from *P. steckii* by its rough walled stipes.

Distribution and ecology: This species has a worldwide distribution and has a preference for (sub)tropic regions. *Penicillium paxilli* was isolated from various substrates, such as soil, wood in a tropical rainforest, the surface of a melon, mangrove, leaves, nut of *Carya cordiformis* (bitternut), termite mounds, *Garcinia* sp. (Rungjindamai *et al*. 2006) and as an endophyte of wild rubber trees (*Hevea brasiliensis*) (Gazis & Chaverri 2010).

Barcode & molecular based ID: GenBank no. GU944577. This species can be identified with ITS and partial β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: Analysis of partial β-tubulin and calmodulin sequences shows variation among various isolates of *P. paxilli* and this species might be a complex. A thorough population study is needed to clarify the taxonomy of this species.

Penicillium quebecense Seifert, Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563202. Fig. 33.

Etymology: Named after the location where the type strain was isolated, Quebec (Canada).

Differt ab omnibus speciebus affinibus reverso atro-rubro coloniae in agaro YES, coloniis in agaro CYA usque ad 38–42 mm et in agaro CYA30 16–20 mm, ratione CYAS:CYA 0.85–1.0, sclerotiis pallide aurantiacis efferentibus.

Typus: ex air in sawmill, Quebec, Canada (CBS H-20666 – holotypus, cultures ex-type CBS 101623 = DTO 9B8 = IBT 29050).

Description: Colony diam, 7 d, in mm: CYA 38–42; CYA30°C 16–20; CYA37°C: no growth; MEA 30–35 mm; YES 42–48 mm; DG18 24–29; ratio CYAS:CYA 0.85–1.0; creatine agar 17–24 mm, weak growth and no acid production.

Good sporulation on CYA, velvety, conidia dull grey green, many minute clear exudate droplets, soluble pigments yellow, margin entire, reverse yellow, yellow-orange in the centre. Good sporulation on YES, conidia dull green, soluble pigments red, reverse deep dark red in center with brown edge. Good sporulation on DG18, conidia grey green, reverse

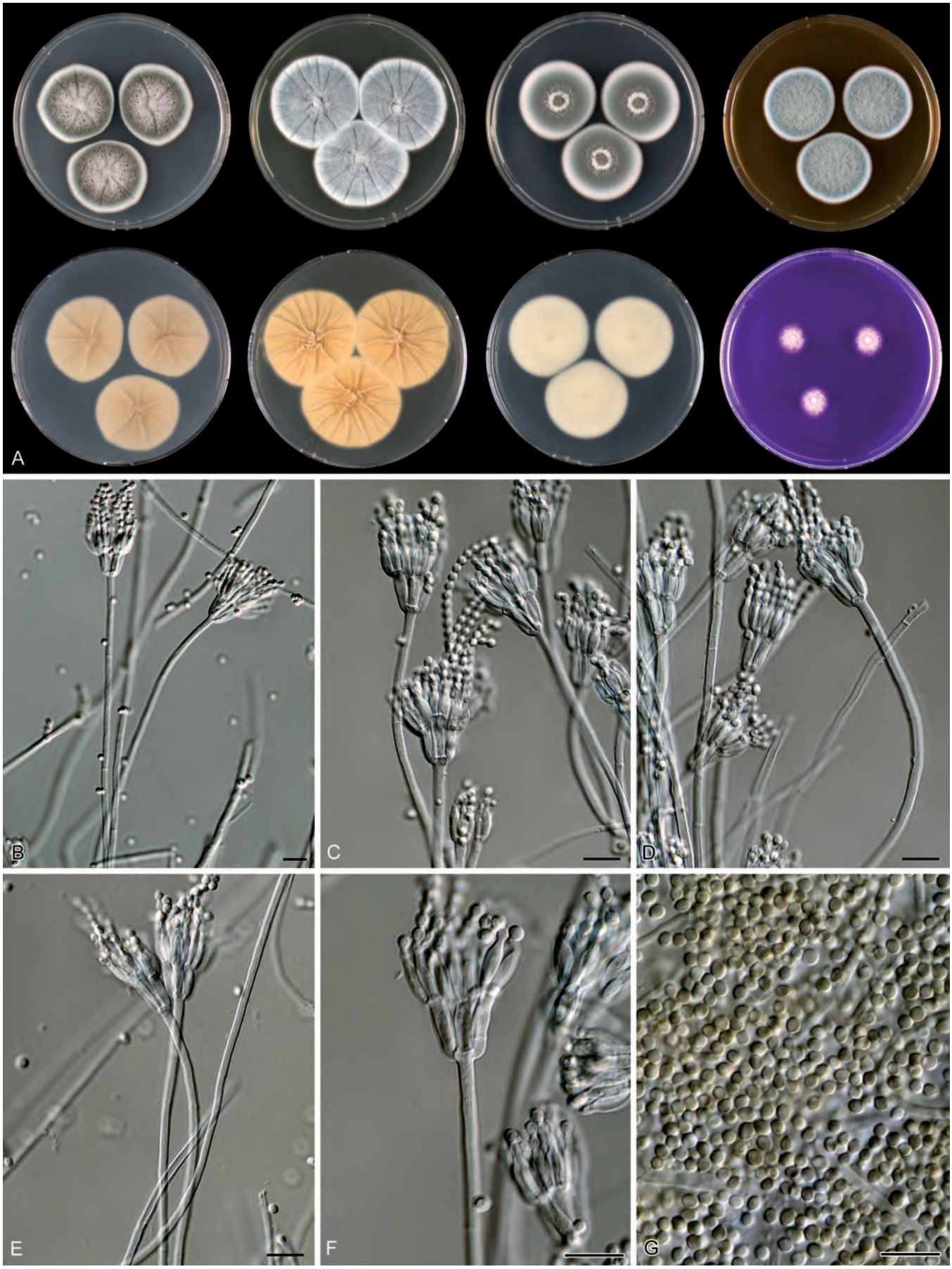

Fig. 32. *Penicillium paxilli*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

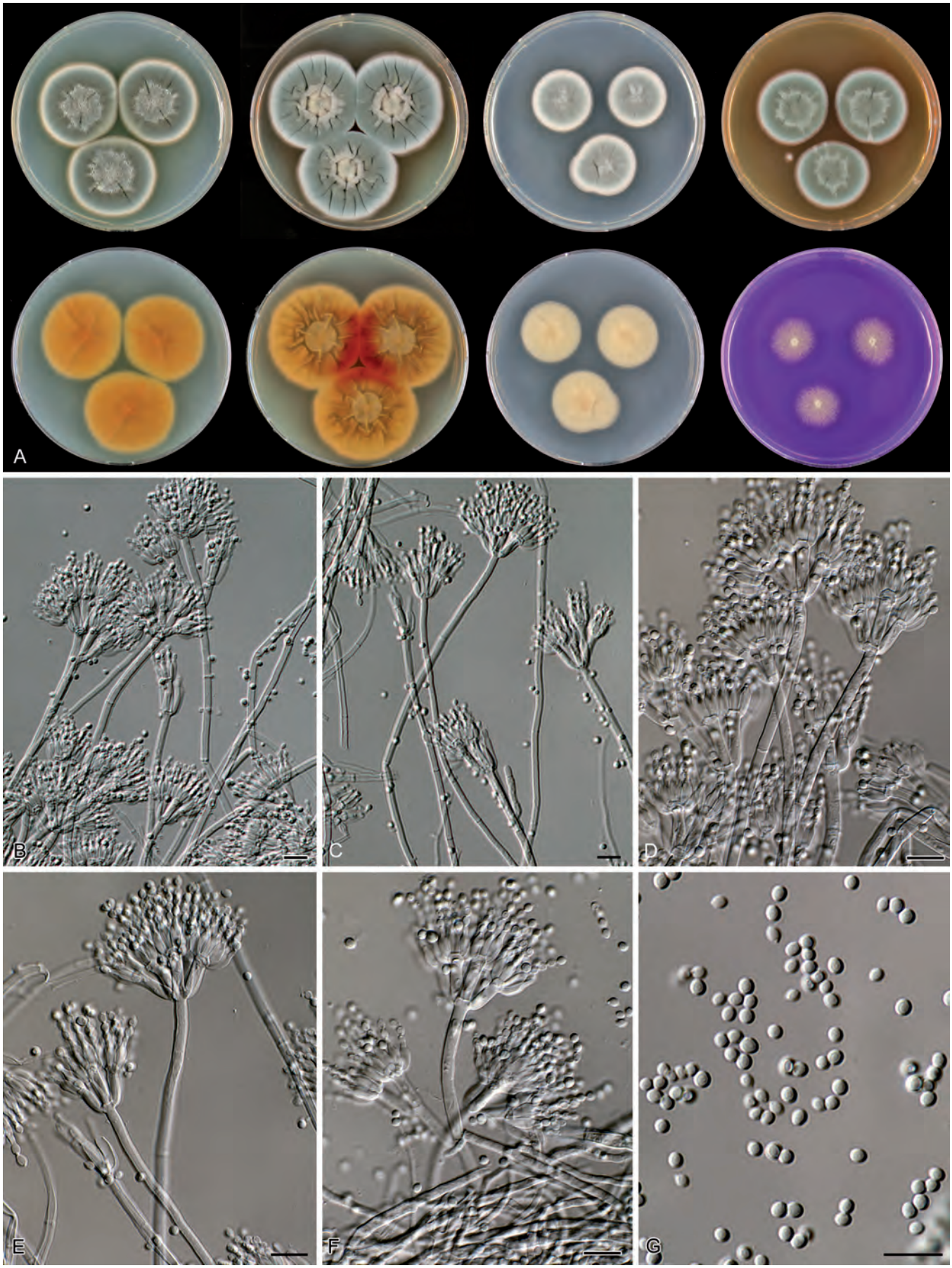

Fig. 33. *Penicillium quebecense*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

pale. Moderate to good sporulation on MEA, conidia grey green, colony texture velvety. Ehrlich reaction negative.

Sclerotia white when young, becoming pale orange in age, 150–250 µm, inconspicuously, produced on oatmeal agar under a dense layer of conidiophores, hard, consisting of polygonal cells; no asci or ascospores observed. Conidiophores 200–400 µm long, predominantly biverticillate, rarely terverticillate, stipes smooth, 2.5–3.5 µm wide. Metulae, in terminal whorl of 3–7, mostly equal in length, 10–14 x 2.5–3.5 µm. Phialides ampulliform, 7–9 × 2–3 µm. Conidia subglobose, smooth, 2.0–2.5 × 2.0–3.0 µm diam.

Extrolites: Citreoviridin, phoenicin, terrein, "SENOE" (verrucofortine-type molecule), "MIF", "MIM", "SENGA", "alk-770".

Diagnostic characters: Dark red reverse on YES, colonies on CYA 38–42 mm, colonies on CYA30 16–20 mm, ratio CYAS:CYA 0.85–1.0, pale orange sclerotia.

Similar species: *Penicillium quebecense* morphologically resembles *P. cairnsense*, but differs in a higher growth rate at CYA30°C. Additional strains should be compared to determine if this character is consistent among multiple strains.

Distribution and ecology: This species is only known from its type culture, isolated from the air in a sawmill in Quebec, Canada.

Barcode & molecular based ID: GenBank no. JN617661. The ITS regions of *P. quebecense* are identical to those of the type of *P. cairnsense* (CBS 124325^T) and *P. neomiczynskii* (CBS 126231^T). Partial β-tubulin and calmodulin sequences can be used for the identification of this species.

Taxonomy and phylogeny: None.

Penicillium raphiae Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563203. Fig. 34.

Etymology: This species was isolated from soil under *Raphia* palm.

Differt ab omnibus speciebus affinibus coloniis in agaro CYA30 haud crescentibus, conidiis late ellipsoideis, conidiophoris saepe symmetrice biverticillatis.

Typus: ex soil under *Raphia* palm in primary forest, Las Alturas, Costa Rica (CBS H-20660 – holotypus, cultures ex-type CBS 126234 = DTO 78B8 = IBT 22407).

Description: Colony diam, 7 d, in mm: CYA 32–36; CYA15°C 18–22; CYA30°C and CYA37°C no growth; MEA 21–25; YES 31–35; DG18 23–27; ratio CYAS:CYA 1.0–1.2; creatine agar 10–15, weak growth and no acid production.

Good sporulation on CYA, velvety, conidia blue-green, mycelium inconspicuous, exudate absent, soluble pigments absent, margin slightly irregular or polygonal, reverse creme to light-brown. Good sporulation on YES, conidia grey green, soluble pigments absent, reverse (light-) brown. Good sporulation on DG18, conidia light blue green or dull green, reverse cream or light yellow. Moderate to good sporulation on MEA, conidia light-blue green, colony texture velvety. Ehrlich test negative.

Sclerotia absent. Conidiophores predominantly symmetrically biverticillate and occasionally with additional branch; stipes up to 300–500 µm long, smooth or finely rough walled, 2.0–3.0 µm wide; metulae in compact terminal whorls of 4–8 (–10), equal in length, non-vesiculate, 10–14 × 2.0–3.5 µm. Phialides ampulliform, 7–9 × 2.0–3.0 µm. Conidia smooth or finely rough walled, broadly ellipsoidal, 1.8–2.5 × 2.0–2.5 µm.

Extrolites: CBS 126234^T produces citrinin, "FON", "MIF","KUM", "LOST","PHOE", and "TRIP"; CBS 126235, possibly a *P. raphiae*, produces citrinin, quinolactacin,"FON", "MIF", "KUM", "MIM", "REJS", "SENGA", and "XANTHOC".

Diagnostic characters: No growth on CYA30, broadly ellipsoidal conidia, predominantly symmetrically biverticillate conidiophores.

Similar species: The species is phenotypically related to *P. steckii*, *P. copticola* and *P. terrigenum*. *Penicillium raphiae* does not grow at 30 °C, while the other related species do grow at this temperature.

Distribution and ecology: This species is only known from its type strain, which was isolated from soil in a primary forest under *Raphia* palm in Costa Rica.

Barcode & molecular based ID: GenBank no. JN617673. This species has unique ITS, partial β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: This species is phylogenetically unique in the *P. westlingii*-clade. Sequence and extrolite data indicate that CBS 126235 is a new species. However, CBS 126234^T and CBS 126235 are phenotypically similar and we wait with the description of this species until more strains are collected and studied.

Penicillium roseopurpureum Dierckx, Annls Soc. Scient. Brux. 25: 86. 1901. Fig. 35.

= *Penicillium carminoviolaceum* Dierckx Annls Soc. Scient. Brux. 25: 86. 1901.
= *Citromyces cesiae* Bainier & Sartory, Bull. Trimest. Soc. Mycol. Fr. 29:148. 1913.
= *Penicillium cesiae* (Bainier & Sartory) Biourge, La Cellule 33: 101. 1923.

Typus: unrecorded source (IMI 40573 – neotype, cultures ex-type CBS 266.29 = DTO 9E3 = ATCC 10492 = ATHUM 2895 = FRR 2064 = IMI 040573 = MUCL 28654 = MUCL 29237 = NRRL 2064 = NRRL 2064A).

Description: Colony diam, 7 d, in mm: CYA 7–16; CYA15°C 7–13; CYA30°C and CYA37°C no growth; MEA 9–19; YES 12–18; DG18 14–22; ratio CYAS:CYA 1.2–1.9; creatine agar 3–6, weak growth and no acid production.

Sporulation absent or sparse on CYA and becoming velvety in time, with pale grey green conidia, mycelium white or pale yellow, exudate absent or sparsely present as dark red brown droplets, soluble pigments orange, reverse red brown or orange brown, margin varying form entire to irregular, reverse in shades of brown (red-brown, caramel or yellow-brown). Sporulation on YES variable or poor, mycelium white or pale yellow, soluble pigments absent or yellow-brown, reverse yellow with red-brown centre, orange-red or yellow. No sporulation on DG18, white mycelium, reverse yellow-orange, vivid yellow or pale yellow. Sporulation on MEA sparsely, becoming grey-green in time, colony texture velvety or floccose. Ehrlich reaction negative.

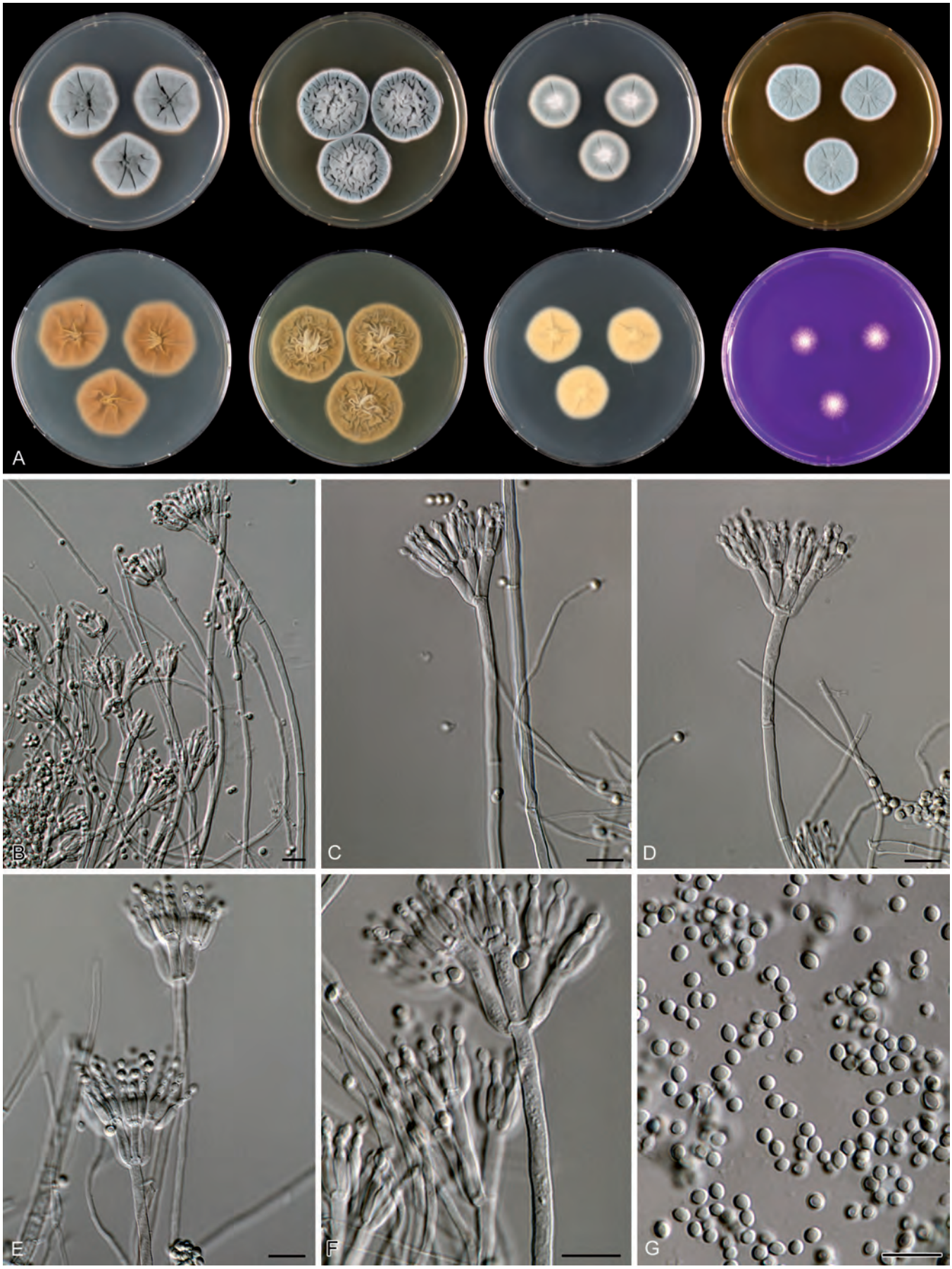

Fig. 34. *Penicillium raphiae*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

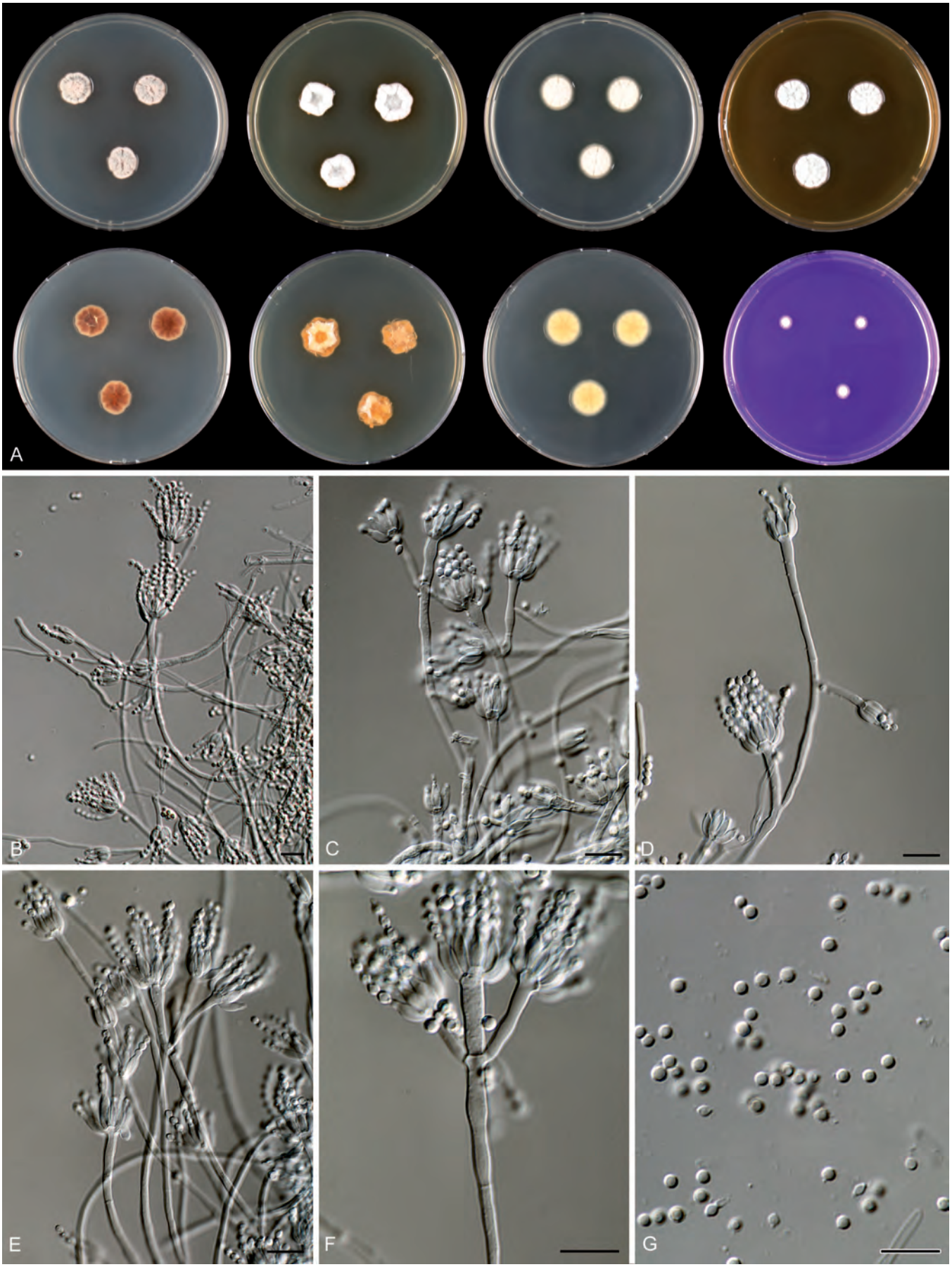

Fig. 35. *Penicillium roseopurpureum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Sclerotia absent. Conidiophores monoverticillate when young, becoming irregularly branched with divergent lower branch-like metulae or symmetrically biverticillate in age; length of stipe of main conidiophore 50–150 µm, lower branch-like metulae shorter, smooth, 2.0–3.0 µm wide; metulae branch-like, irregularly formed and in some cases difficult to distinguish from stipes, when produces terminally, then unequal in length, often gradually enlarging at the apex, giving a clavate appearance or distinct vesiculate, 15–25 × 2.0–3.5 µm at base, terminal up to 5.0 µm diam; phialides ampulliform, formed terminally and subterminally, 6.0–8.0 × 2–3 µm. Conidia globose to subglobose, smooth or very finely roughened, 1.8–2.5 µm diam.

Extrolites: Bisanthrons, roseopurpurin, sorbicillins (produced by some isolates), "AQ" (other anthraquinones apart from roseopurpurin), "SEL".

Diagnostic characters: Monoverticillate or furcate conidiophores with lower branch-like metulae, reverse on CYA in shades of red, often with red-brown diffusible pigments, restricted growth on agar media and no growth on CYA30°C.

Similar species: *Penicillium sanguifluum* is related to *P. roseopurpureum*, but the latter grows slower on CYA and does not grow on CYA incubated at 30 °C. Furthermore, *P. roseopurpureum* has a higher CYAS:CYA ratio than *P. sanguifluum*.

Distribution and ecology: This species was isolated from soil (Wyoming, USA) and indoor air (the Netherlands).

Barcode & molecular based ID: GenBank no. GU944605. This species shares ITS sequences with most members of clade 1 of *P. sanguifluum* (Fig. 4).

Taxonomy and phylogeny: Phylogenetic analysis shows that *P. roseopurpureum* belongs to section *Citrina*. This species is characterised by the formation of monoverticillate conidiophores, becoming irregularly branched with divergent lower branch-like metulae or symmetrically biverticillate condiophores in older parts of the colony. This branching pattern is unusual for members of section *Citrina*, which are in general symmetrically biverticillate. Figure 4 shows that the type strain of *P. carminoviolaceum* (CBS 281.39) belongs to *P. roseopurpureum*. No cultures of *P. cesiae* were available for analysis. Raper & Thom (1949) and Pitt (1980) are followed here and this species is considered as a synonym of *P. roseopurpureum*.

Penicillium sanguifluum (Sopp) Biourge, La Cellule 33: 105. 1923. Fig. 36.

Basionym: *Citromyces sanguifluus* Sopp, Skr. udgivne Videnskabs-Selsk. Christiania 11: 115. 1912.

= *Penicillium lacussarmientei* Ramírez, Mycopathol. 96: 29. 1986.

= *Penicillium vaccaeorum* Quintanilla, Mycopathol. 80: 77. 1982.

Typus: ex soil, Calahonda, Costa del Sol, Spain, L. Janson (CBS H-20645 – neotype, designated here; cultures ex-type CBS 127032 = DTO 20B7 = IBT 29041).

Description: Colony diam, 7 d, in mm: CYA (15–) 18–26; CYA15°C 7–14; CYA30°C microcolony–13; CYA37°C no growth; MEA 17–26; YES 18–28; DG18 16–22; ratio CYAS:CYA 0.9–1.2; creatine agar 5–14, weak growth and no or poor acid production. Sporulation on CYA variable, absent to moderate, velvety, conidia grey-green, mycelium white or pale beige, exudate absent or dark red brown, strong red soluble pigment production, margin entire or irregular, reverse dark red brown or red. Sporulation on YES absent or sparse, mycelium white, pale beige or pale yellow, soluble pigments absent or orange, reverse orange, orange-brown with or without orange-red centre. Sporulation absent or sparse on DG18, conidia dull-green, reverse in shades or yellow (yellow-orange, yellow or pale yellow). Colonies on MEA sporulating sparsely, colony texture floccose. Ehrlich reaction negative.

Sclerotia not produced. Conidiophores produced on trailing hyphe, monoverticillate, short, 15–50 µm, smooth, or with branch-like metulae scarcely formed, 1–3, unequal in length, strongly vesiculate, (10–) 13–18 × 2.0–3.0 µm at base, vesicle up to 5 µm; phialides ampulliform, terminally and subterminally formed, 6.5–8 × 2–3 µm. Conidia globose to subglobose, smooth or finely roughened, 2.0–2.5 µm diam.

Extrolites: Bisanthrons, roseopurpurin, β-hydroxycurvularin, dehydrocurvularin, curvularin, "FOSI", "FYKS", "SNIT", "TIDL", "VERN".

Diagnostic characters: Monoverticillate conidiophores, dark red brown reverse on CYA with red brown soluble pigment production, growth on CYA30°C.

Similar species: See *P. roseopurpureum*.

Distribution and ecology: This species appears to have preference for sandy soils and has a worldwide distribution. *Penicillium sanguifluum* is isolated from soils in Spain, Manitoba, Canada, the Netherlands, Turkey, Chile and Argentina.

Barcode & molecular based ID: GenBank no. JN617711 (clade 1) and JN617681 (clade 2). Two subclades are present in *P. sanguifluum* (Fig. 4). CBS 127032^T is positioned in clade 2 and shares identical ITS sequences with other members of this clade. Members of clade 1 share ITS sequences with *P. roseopurpureum*. This clade also includes the type cultures of *P. lacussarmientei* and *P. vaccaeorum*.

Taxonomy and phylogeny: *Penicillium sanguifluum* was considered a synonym of *P. roseopurpureum* (Raper & Thom 1949, Pitt 1980). Examination of the protologue of *Citreomyces sanguifluus* showed that this species is not *P. roseopurpureum* (Sopp 1912: 115). It has an optimal growth between 25 and 30 °C and the published Figure (Sopp 1912: XXII, Fig. 3) shows rather well developed colonies. These characters fit better with *P. sanguifluum* than with *P. roseopurpureum*. CBS 127032^T approximates the orginal description of *P. sanguifluum* and it is designated here as the neotype of this species. This study shows that the faster growth rate is a good feature for distinguishing *P. roseopurpureum* and *P. sanguifluum*. *Penicillium vaccaeorum* and *P. lacussarmientei* were considered synonyms of *P. roseopurpureum* by Frisvad *et al*. (1990b). They noted that both species are fast growing variants of *P. roseopurpureum*, and these species are treated here as synonyms of *P. sanguifluum*. *Penicillium sanguifluum* and *P. roseopurpureum* deviate from other members of section *Citrina* by its monoverticillate or furcate conidiophores. Partial β-tubulin and calmodulin sequences show that two subclades are present in *P. sanguifluum* (Fig. 4). No phenotypic differences were observed

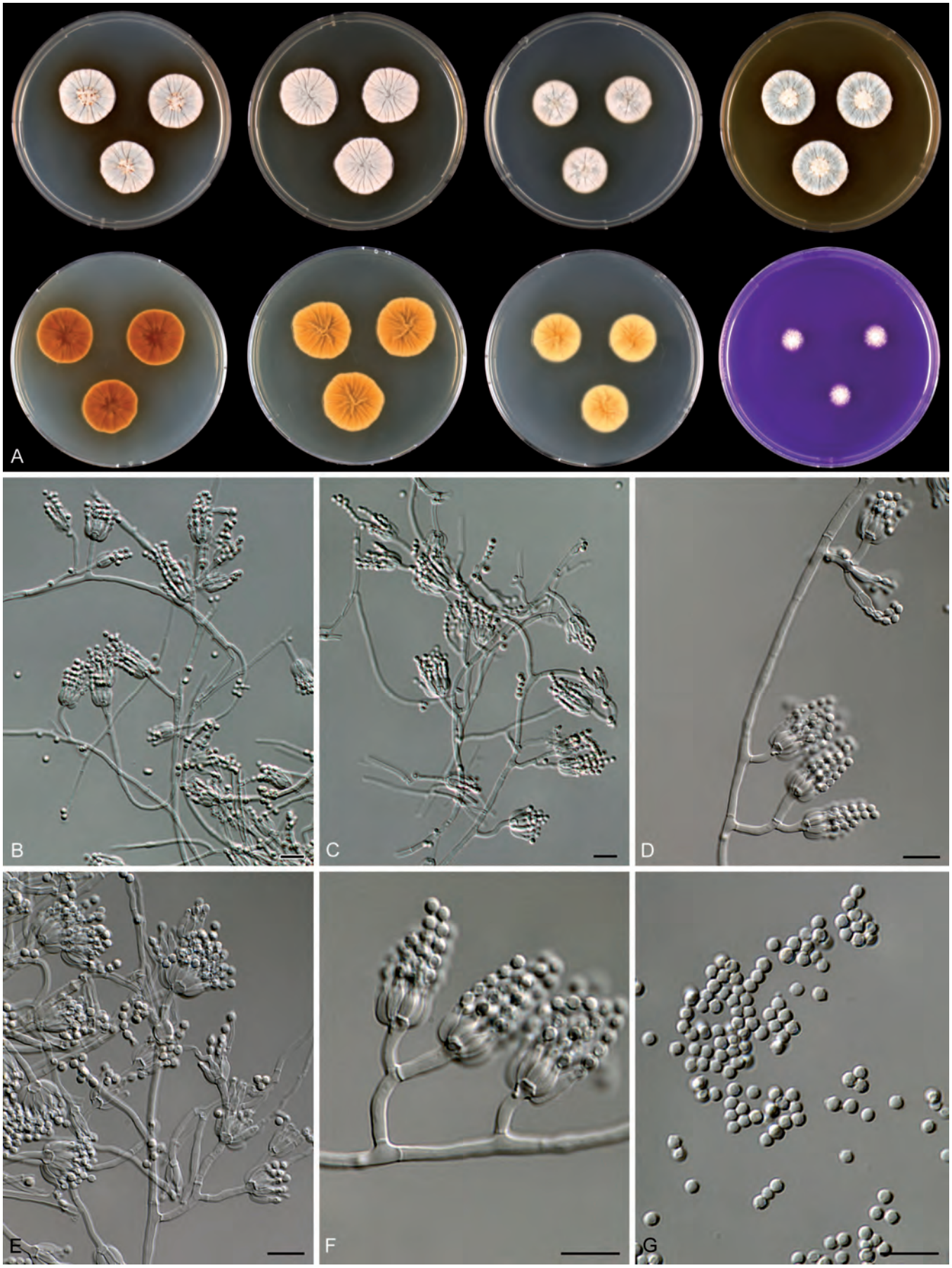

Fig. 36. *Penicillium sanguifluum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

between these two clades, and therefore we did not describe them as two distinct species.

Penicillium shearii Stolk & Scott, Persoonia 4: 396. 1967. Fig. 37.

= *Carpenteles asperum* Shear, Mycologia 26: 107. 1934 (misapplied).
= *Penicillium asperum* (Shear) Raper & Thom Man. Penicillia: 263. 1949 (misapplied).
= *Eupenicillium shearii* Stolk & Scott, Persoonia 4: 396. 1967.

Typus: ex soil, Tela, Honduras (CBS 290.48 – holotypus, cultures ex-type DTO 22F6 = IMI 39739 = ATCC 10410 = NRRL 715 = IFO 6088 = IBT 24588).

Description: Colony diam, 7 d, in mm: CYA 28–40; CYA15°C 6–10; CYA30°C 22–36; CYA37°C (0–) 5–19; MEA 26–37; YES 25–37; DG18 28–37; ratio CYAS:CYA (0.7–) 0.9–1.1; creatine agar 10–20, weak growth, acid and base production absent.

Sporulation on CYA absent or sparse; cleistothecia abundantly produced, dark grey coloured, mycelium inconspicuous, large clear exudate droplets, soluble pigments absent, margin entire, reverse (light) brown. Sporulation on YES absent or weak, cleistothecia abundantly produced and dark-grey, mycelium white, soluble pigments absent, reverse (pale) yellow-brown. Sporulation on DG18 absent in fresh isolates or weakly produced in older cultures, conidia grey green, mycelium white, reverse pale or pale yellow. Sporulation on MEA absent or weak, not influencing the colony colour, cleistothecia abundantly produced and grey. Ehrlich reaction negative.

Cleistothecia abundantly produced on CYA, MEA and YES, globose or subglobose, up to 500 µm diam, consisting of sclerotioid masses of polygonal cells, ripening after 4–5 wk or more. Ascospores ellipsoidal, 2.5–3.5 × 2.0–2.5 µm, with 2 appressed equatorial ridges up to 0.5 µm wide, valves roughened (towards warted). Conidiophores biverticillate, occasionally with additional branch, stipes 100–500 µm long, smooth walled or nearly so, 2.0–3.0 µm wide. Metulae in verticils of 2–5 (–8), unequal in length, 10–14 × 2.0–3.0 µm. Phialides ampulliform, 7.0–9.0 × 2–3 µm. Conidia subglobose or broadly ellipsoidal, smooth or nearly so, 2.5–3.0 × 1.8–2.5 µm.

Extrolites: Paxillin, paspalinine, shearinin A & B, "XX" and several indole alkaloids (Belofsky *et al*. 1995, Tuthill & Frisvad 2004).

Diagnostic characters: Abundant production of dark grey coloured cleistothecia, growth at 37 °C, ascospores produced after prolonged incubation.

Similar species: *Penicillium tropicum* and *P. tropicoides* are phenotypically similar species; however, these two species do not grow on CYA at 37 °C. *Penicillium shearii* can be differentiated from *P. euglaucum* and *P. anatolicum* by the absence of yellow soluble pigments and from *P. argentinense* by its ability to grow at 37 °C.

Distribution and ecology: *Penicillium shearii* has a worldwide distribution and has a preference for tropical and subtropical soils (Honduras, Colombia, Mexico, Congo, Papua-New Guinea, Tanzania, Malaysia; Tuthill & Frisvad (2004) also isolated this species in Venezuela, Ivory Coast, Australia, Costa Rica and India).

Barcode & molecular based ID: GenBank no. GU944606. This species can be identified with ITS, partial β-tubulin and/or calmodulin sequences.

Taxonomy and phylogeny: According to Shear (1934), the type strain of *P. shearii* (CBS 290.48) represented Brefeld's ascosporic species "*Penicillium glaucum* Link". He proposed *Carpenteles asperum* as a new name for Brefeld's fungus. However, CBS 290.48 does not produce asci in chains, as described and figured by Brefeld (1874), and consequently *C. asperum* Shear as well as the combination *P. asperum* (Shear) Raper & Thom are interpreted as misapplied names. That Shear's fungus differs from Brefeld's is nomenclaturally irrelevant because Shear clearly regarded Brefeld's organism to be the type for his new name. Stolk & Scott (1967) proposed the name *Eupenicillium shearii* for Shear's fungus and named the anamorph *P. shearii*.

Stolk & Samson (1983) described *P. soppii* as the anamorph of *E. shearii* (= *P. shearii*) and as a consequence *P. shearii* was synonymised with *P. soppii*. However, molecular data shows that *P. soppii* is distinct (Fig. 1) and phylogenetically unrelated to *P. shearii*. Furthermore, *P. soppii* does not grow at 37 °C and no ascospores or asci are produced in the sclerotia of this species.

Penicillium sizovae Baghdadi, Nov. sist. Niz. Rast., 1968: 103. 1968. Fig. 38.

Typus: ex soil, Syria (CBS 413.69 – neotype, designated by Pitt *et al*. 2000; cultures ex-type DTO 23A7 = FRR 518 = IMI 140344 = VKM F-1073).

Description: Colony diam, 7 d, in mm: CYA 28–39; CYA15°C 8–15; CYA30°C 28–34; CYA37°C 0–4; MEA 27–35; YES 40–50; DG18 23–32; ratio CYAS:CYA 0.95–1.2; creatine agar 15–23, poor growth, weak acid production.

Good sporulation on CYA, velvety, conidia grey green, mycelium inconspicuous, small clear exudate droplets, soluble pigments absent, margin entire, reverse pale and occasionally pale crème-brown. Moderate to good sporulation on YES, conidia dark green, soluble pigments absent, reverse pale or pale yellow-crème. Most isolates moderate to good sporulation on DG18, occasionally absent or poor, conidia dull green or grey green, reverse pale and conidial colour shining through the agar. Good sporulation on MEA, conidia grey green, colony texture floccose. No reaction with Ehrlich reagent.

Sclerotia absent. Conidiophores from aerial hyphae and the mycelial mat, predominantly symmetrically biverticillate, occasionally with an additional branch; stipes smooth, 100–300 × 2.5–3.2 µm. Metulae in whorls of 2–5, 11–16 × 2.5–3.2 µm, uniform in length. Phialides ampulliform, 7.0–9.5 × 2.0–3.0 µm. Conidia globose to subglobose, finely roughened, 2.0–2.5 µm diam.

Extrolites: Quinolactacin, tanzawaic acid E, verrucolone, "AFSI", "CHAE and "PNUF" (Houbraken *et al*. 2010).

Diagnostic characters: Fast growing on MEA and YES, pale reverse on CYA, finely roughened conidia.

Similar species: *Penicillium sizovae* is phylogenetically related to *P. citrinum*, *P. hetheringtonii*, *P. steckii* and *P. gorlenkoanum*. It

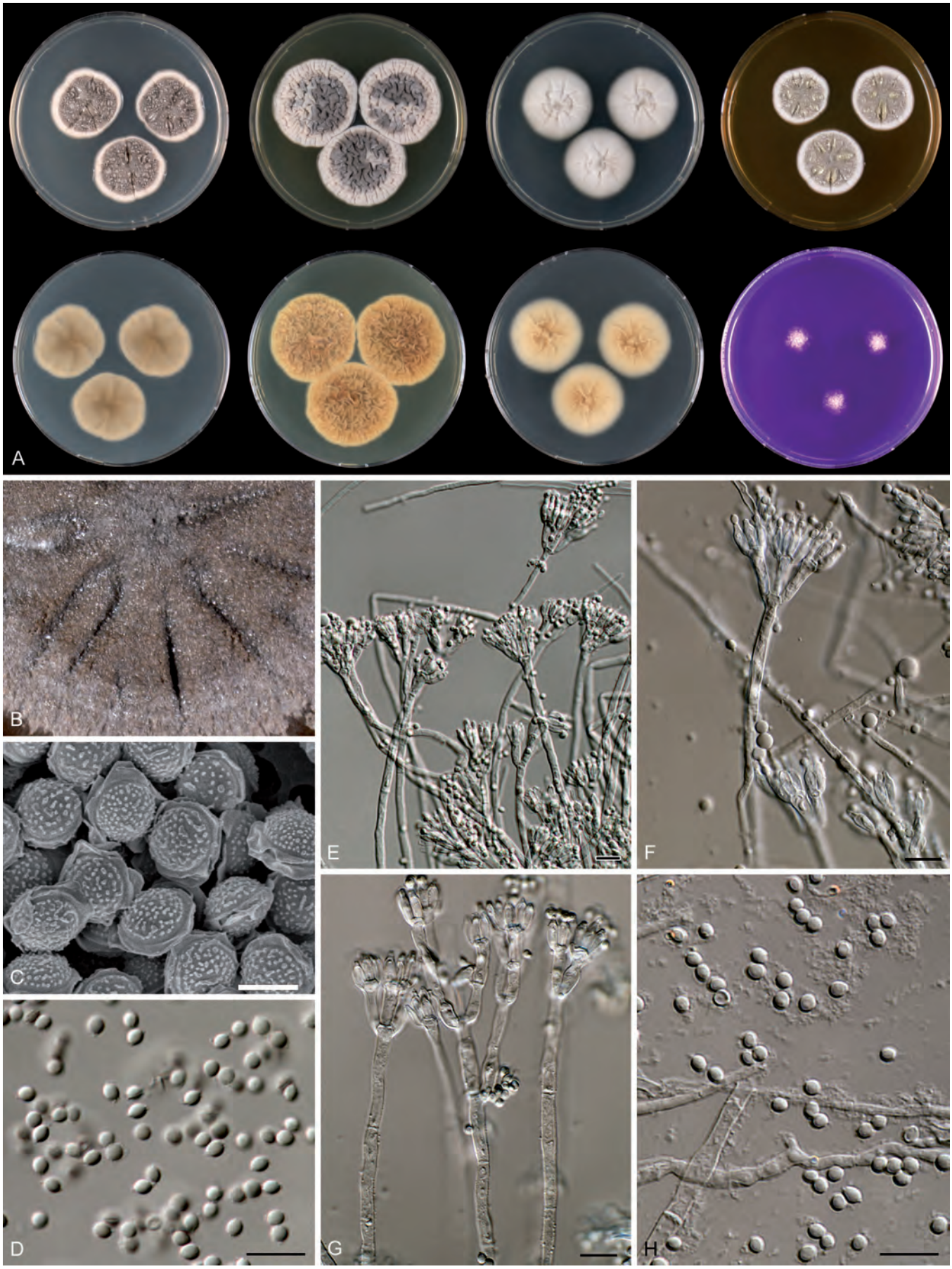

Fig. 37. *Penicillium shearii*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Sclerotia. C–D. Ascospores. E–G. Conidiophores. H. Conidia. Scale bars = 10 µm.

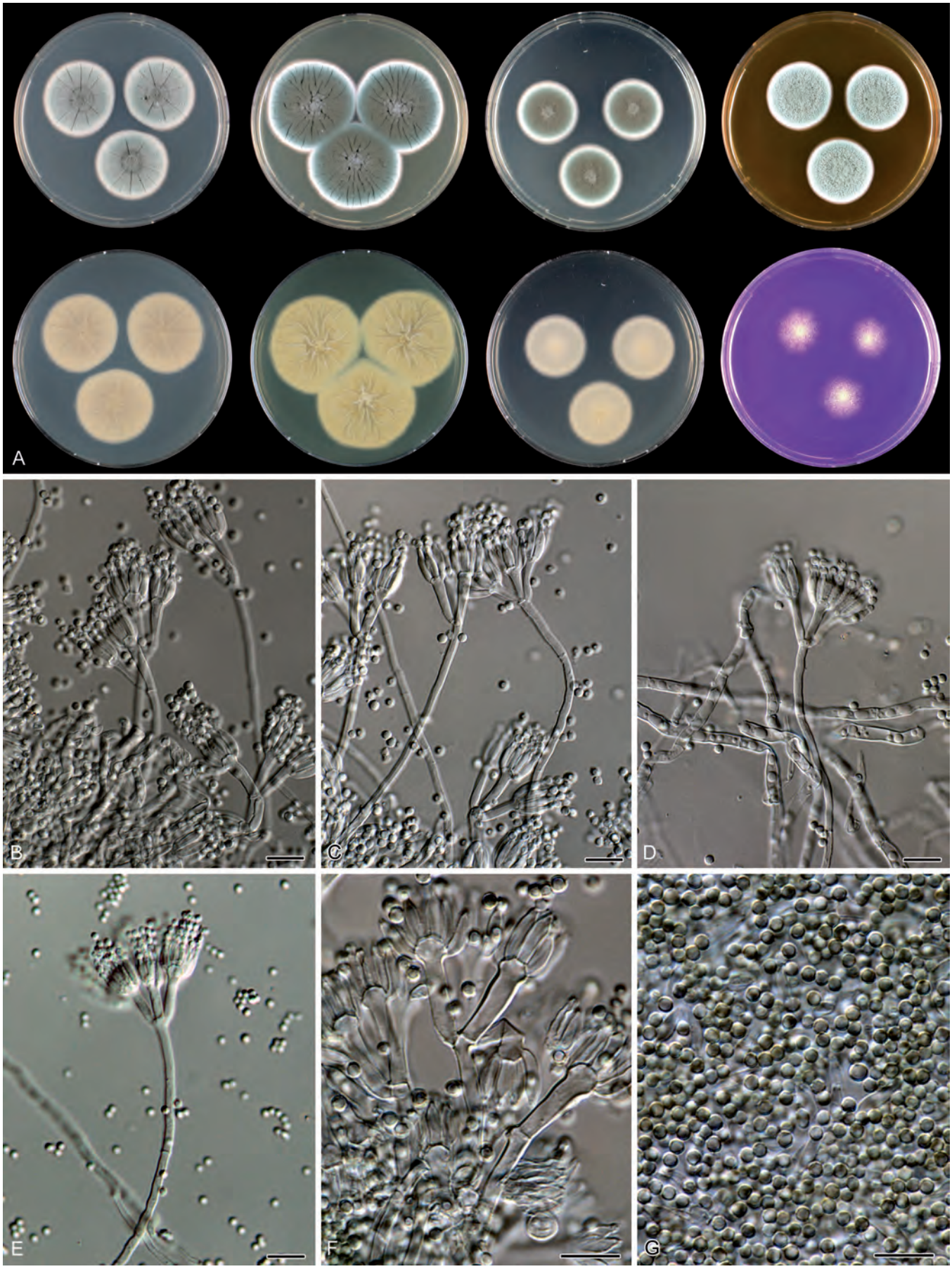

Fig. 38. *Penicillium sizovae*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

can be differentiated from these species by the formation of finely roughened conidia and its high growth rate on MEA and YES.

Distribution and ecology: This species has been isolated from soil, margarine, sea salt, salty water in saltern, glue and *Papaver somniferum* in the Netherlands, Portugal, Syria, Italy, Slovenia.

Barcode & molecular based ID: GenBank no. GU944588. This species has unique ITS, β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: Pitt (1980) placed *P. sizovae* in synonymy with *P. fellutanum*, but this species was later accepted and reinstated by Pitt & Samson (1993). CBS 413.69^{NT} is degenerated and shows both conidiophores with terminal metulae, as well as subterminal and intercalary metulae. These features could explain the earlier proposed synonymy in *P. fellutanum* (Houbraken *et al*. 2010).

Penicillium steckii Zaleski, Bull. Int. Acad. pol. Sci. Lett., Sér. B.: 469. 1927. Fig. 39.

= *Penicillium corylophiloides* S. Abe, J. gen. appl. Microbiol, Tokyo 2: 89. 1956 (*nom. inval*., Art. 36).

Typus: ex cotton fabric treated with copper naphthenate, Panama (IMI 40583 – neotype, designated by Pitt *et al*. 2000; cultures ex-type CBS 260.55 = DTO 22G5 = ATCC 10499 = CECT 2268 = DSM 1252 = NRRL 2140 = QM 6413 = NDRC 52B4C).

Description: Colony diam, 7 d, in mm: CYA 24–32; CYA15°C 7–13; CYA30°C 15–23; CYA37°C no growth; MEA 21–30; YES 29–40; DG18 24–36; ratio CYAS:CYA 1.0–1.2; creatine agar 11–19, weak to moderate growth, no or weak acid production.

Moderate or good sporulation on CYA, velvety, conidia grey green, mycelium inconspicuous, small clear or weak yellow exudate droplets, soluble pigments absent, reverse in shades of crème (crème, pale crème, yellow-crème or brown crème). Moderate to good sporulation on YES, conidia grey green, occasionally dull green, soluble pigments absent, reverse in most isolates (pale) yellow, sometimes orange. Good sporulation on DG18, conidia grey green conidia, reverse variable, pale, cream, (bright) yellow or yellow-orange. Good sporulation on MEA, conidia grey green or dull green, colony texture velvety. Ehrlich reaction negative, with the exception of CBS 122391.

Sclerotia absent. Conidiophores borne from surface hyphae, predominantly symmetrically biverticillate, occasionally with an additional branch; stipes smooth, 100–300 × 2.2–3.0 µm. Metulae in whorls of 3–6, 13–18 × 2.5–3.3 µm, equal in length. Phialides ampulliform, 7.0–10 × 2.2–3.0 µm. Conidia broadly ellipsoidal, in some strains slightly fusiform, smooth, 2.3–3.0× 2.0–2.5 µm.

Extrolites: Isochromantoxins (Cox *et al*. 1979, Malmstrøm *et al*. 2000), quinolactacin, tanzawaic acid E, "ALTI", "EXPO", "FON", "FOS", "GLOO", "GYF", "PHOE", "RAI", "STOK", "SVUL", and "VERN" (Houbraken *et al*. 2010).

Diagnostic characters: No growth at 37 °C, moderate growth at 33 °C; reverse colours on CYA in shades of crème, broadly ellipsoidal conidia.

Similar species: *Penicillium steckii* is phylogenetically related to *P. sizovae*, *P. citrinum*, *P. hetheringtonii* and *P. gorlenkoanum*. This species is characterised by the formation of broadly ellipsoidal conidia, which are not formed by any of the other species mentioned. *Penicillium tropicoides* and *P. tropicum* also form broadly ellipsoidal conidia, but also produce cleistothecia and ascospores.

Distribution and ecology: This species has a worldwide distribution and has been isolated in Japan, the Netherlands, Panama, Venezuela, Bermuda, Egypt, Venezuela, Indonesia and Slovenia. *Penicillium steckii* is isolated from cotton fabric treated with copper naphthenate, (potting) soil, hypersaline water, blue runner fish, baled coastal grass hay, artichokes, *Ascidie* (tunicate, urochordata), and as an endophyte of root of coffee plant (Posada *et al*. 2007).

Barcode & molecular based ID: GenBank no. GU944597. This species has a unique ITS sequence. A subgroup in the *P. steckii* clade was observed. This subgroup, characterised by a single basepair difference on position 164 of the ITS2 region, included the type strain of *P. corylophiloides nom. inval*. (CBS 325.59).

Taxonomy and phylogeny: Abe (1956) described *P. corylophiloides* without a Latin diagnosis and designation of a holotype. According to Abe (1956), *P. corylophiloides* could be differentiated from *P. citrinum* and *P. steckii* by the formation of ellipsoidal conidia. Houbraken *et al*. (2010) showed that *P. steckii* also formed broadly ellipsoidal conidia and both species were placed in synonymy. Following the phylogenetic species concept, *P. steckii* and *P. corylophiloides* are separate species; however, no differences in morphology, physiology or extrolites patterns could be observed and are therefore they are placed in synonymy (Houbraken *et al*. 2010).

Penicillium sumatrense von Szilvinyi, Archiv. Hydrobiol. 14, Suppl 6: 533. 1936. Fig. 40.

= *Penicillium baradicum* Baghdadi, Novosti Sistematiki Nizshikh Rastenii 5: 107. 1968.

= *Penicillium meleagrinum* var. *viridiflavum* Abe, J. Gen. Appl. Microbiol., Tokyo 2: 92. 1956 (*nom. inval*.).

Typus: ex soil, Toba Heath, Sumatra, Indonesia (CBS 281.36 – lectotype, designated here; cultures ex-type DTO 22F1 = NRRL 779 = FRR 779 = ATCC 48669 = IBT 29658 = IBT 4978).

Description: Colony diam, 7 d, in mm: CYA 33–42; CYA15°C 10–16; CYA30°C (10–) 15–25; CYA37°C no growth; MEA 27–36; YES (26–) 32–42 (–47); DG18 (20–) 25–34; ratio CYAS:CYA 0.9–1.1; creatine agar 15–23, weak growth and acid production absent.

Moderate or good sporulation on CYA, occasionally absent, velvety, conidia dull-green or dark-green, mycelium inconspicuous, exudate absent or present as small or large (pale)-yellow droplets, occasionally clear or light brown, soluble pigments in most strains absent, in some isolates weakly produced and light brown coloured, margin entire, reverse in shades of beige, beige-brown or brown. Good sporulation on YES, conidia dull-green, mycelium inconspicuous, soluble pigments absent, reverse yellow. Good sporulation on DG18; conidia grey-green or dull-green, reverse pale or pale yellow. Sporulation on MEA variable, conidia blue-green, light green or grayish-green, mycelium inconspicuous, floccose colony texture in fresh isolates, velvety in strains maintained for longer periods in the collection. Ehrlich reaction negative.

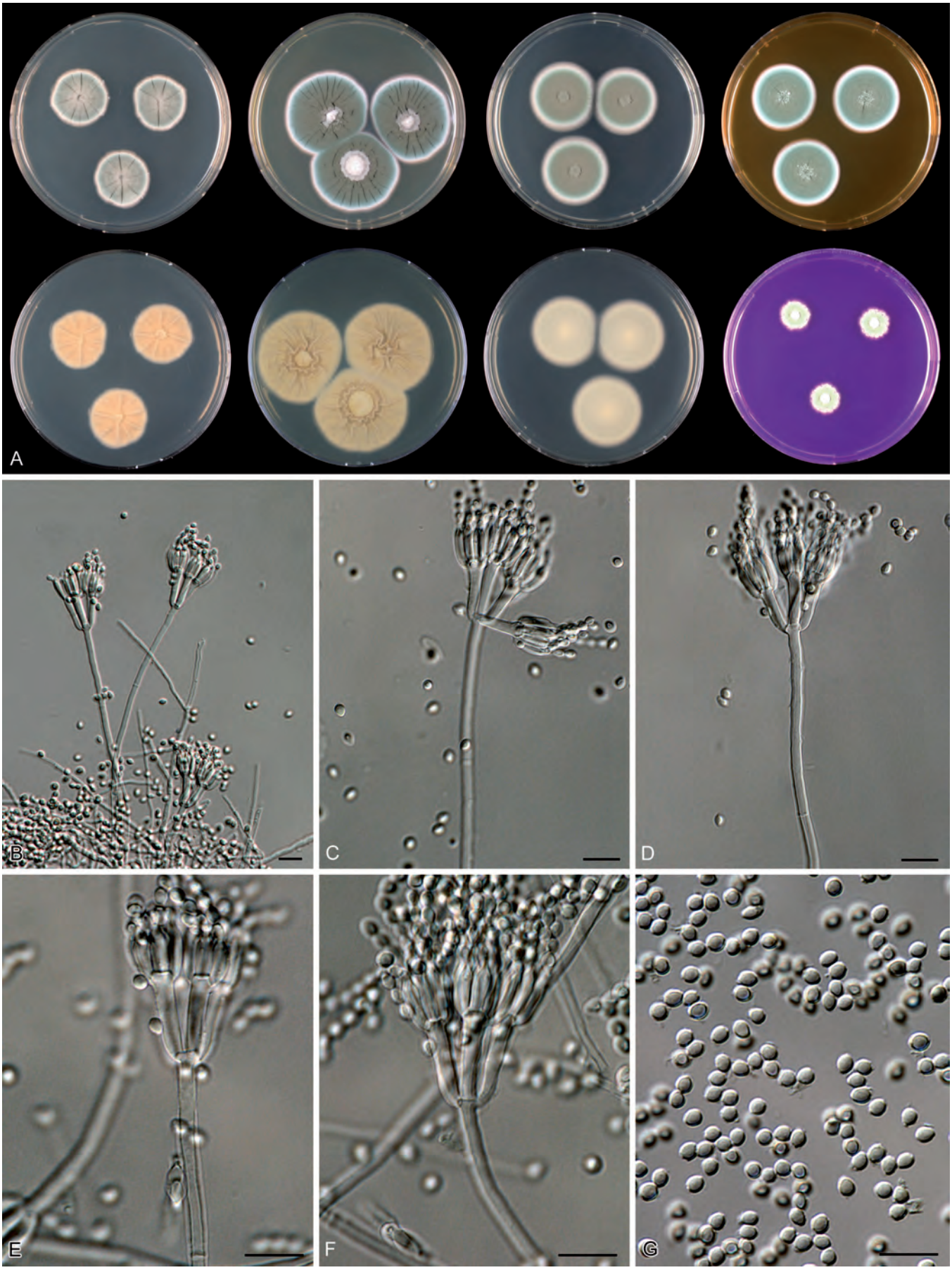

Fig. 39. *Penicillium steckii*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

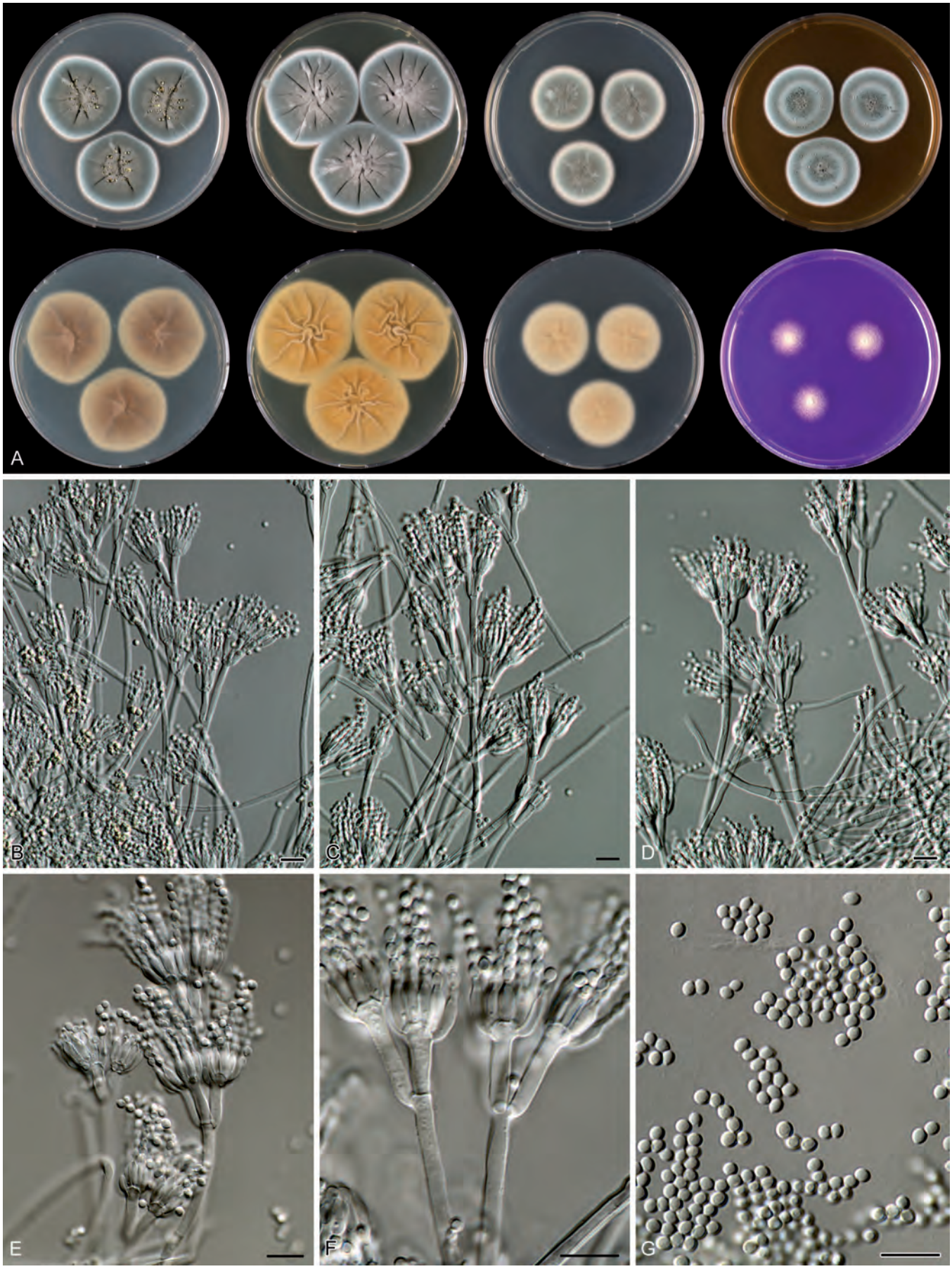

Fig. 40. *Penicillium sumatrense*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Sclerotia absent. Conidiophores predominantly biverticillate, occasionally with an additional branch, stipes up to 200 µm long with smooth or finely rough walls, 2.0–3.0 µm wide. vMetulae in terminal verticils and fairly compact, 3–6, uneven in length, vesiculate and rather long (10–) 12–16 × 2.0–3.0 µm. Phialides ampulliform, 8.0–10 × 2–3.5 µm. Conidia subglobose or broadly ellipsoidal, finely roughened, occasionally smooth, 2.0–2.5 µm diam.

Extrolites: Curvularin (Vesonder *et al*. 1976, Malmstrøm *et al*. 2000), dehydrocurvularin, "POTO", "SAAT", "TERRIT", "TIDL", "VOX".

Diagnostic characters: Growth on CYA incubated at 33 °C (cultures, which are maintained for long periods in culture collections, have a lower maximum growth temperature), beige-brown reverse on CYA, high growth rate on YES with yellow reverse.

Similar species: *Penicillium sumatrense* is phylogenetically distinct and differs from *P. citrinum* and *P. hetheringtonii* by its inability to grow at 37 °C. *Penicillium paxilli* has a pale reverse on CYA, appressed whorls of metulae and roughened stipes; *P. steckii* and *P. sizovae* lack a distinct yellow reverse on YES.

Distribution and ecology: This species has a worldwide distribution, but has a preference for (sub)tropical regions. Its main habitat is soil, but it has also been isolated from marine environments (Malmstrøm *et al*. 2000), as an endophyte of *Vitis vinifera* (Z. Wang & X. Qian, unpublished, GenBank no. EU030367), cork (Serra *et al*. 2008), packaging material imported into the Netherlands, pomegranates and bromeliad leaf tissue.

Barcode & molecular based ID: GenBank no. GU944578. This species has unique ITS, tubulin and calmodulin sequences.

Taxonomy and phylogeny: *Penicillium sumatrense* was formally considered a synonym of *P. corylophilum* (Pitt 1980), but Peterson (2000) and Houbraken & Samson (2011) showed that these two species are phylogenetically unrelated. The former species belongs to section *Citrina* (Peterson's group 1), and the latter to section *Exilicaulis* (Peterson's group 4). *Penicillium meleagrinum* var. *viridiflavum* was described without a Latin diagnosis, making the description invalid (Art. 36). Pitt *et al*. (2000) synonymised this species with *P. janthinellum*; however, Serra *et al*. (2008) showed that *P. meleagrinum* var. *viridiflavum* is genetically close to the type strain of *P. sumatrense*. The congruence of the phylograms from four different loci indicated that this could be a separate species (Serra *et al*. 2008). Our data (Fig. 4) also shows sequence variation among the analysed *P. sumatrense* strains. However, no differences in phenotype and extrolite patterns were detected among these strains and therefore they are maintained as one species. More research is needed to clarify the population structure of this species.

Penicillium terrigenum Seifert, Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563204. Fig. 41.

Etymology: Referring to soil, the substrate from where the type strain was isolated.

Differt ab omnibus speciebus affinibus coloniis in agaro CYA bene crescentibus ad 33 °C, conidiis ellipsoideis, laevibus, conidiophoris biverticillatis.

Typus: ex soil, Hawaii, USA, R. A. Samson (CBS H-20667 – holotypus, cultures ex-type CBS 127354 = DTO 9D4 = IBT 30769).

Description: Colony diam, 7 d, in mm: CYA 28–36; CYA15°C 7–15; CYA30°C 18–23; CYA37°C no growth; MEA 25–32; YES 34–41; DG18 28–34; ratio CYAS:CYA 1.0–1.3; creatine agar 15–22, weak growth and no acid production.

Sporulation on CYA variable, velvety and floccose at the centre, conidia dull-grey green, mycelium white, exudate produced as minute clear droplets, soluble pigments absent, margin entire to slightly irregular, reverse pale or crème. Weak to moderate sporulation on YES, mycelium white, soluble pigment absent, reverse creme-yellow, occasionally with a green shade. Good sporulation on DG18, conidia dull green, reverse pale. Moderate to good sporulation on MEA, conidia dull or dull-grey green, colony texture floccose. Ehrlich reaction negative.

Sclerotia absent. Conidiophores predominantly symmetrically biverticillate, occasionally with an additional branch, stipes long, up to 500 µm, smooth to finely rough walled or distinctly rough walled (CBS 117967), 2.5–3.5 µm wide; metulae in a compact terminal whorls of 3–7, slightly vesiculate, equal in length, (10–) 12–16 × 2.0–3.5 µm; phialides ampulliform to cylindrical, 7.5–9 × 2.5–3.5 µm. Conidia broadly ellipsoidal, smooth, 2.0–3.0 × 2.0–2.5 µm.

Extrolites: "HAEN", "ISOC", "PRS", "VERSI".

Diagnostic characters: Good on CYA incubated at 33 °C, broadly ellipsoidal smooth walled conidia, biverticillate conidiophores.

Similar species: This species is phylogenetically related to *P. copticola*, but can be distinguished by its poor growth on CREA. Morphologically, this species is similar to *P. steckii*, which also forms broadly ellipsoidal conidia and is also able to grow at 33 °C. *Penicillium steckii* sporulates better on CYA and YES and has velvety colonies.

Distribution and ecology: This species is isolated from Hawaiian soil, a leaf surface, USA, a mushroom fairy ring in Oshawa, Ontario, Canada and soil in Portugal. A BLAST analysis showed that this species was also isolated from a French pastry product (brioche) (GenBank FJ471589, ITS).

Barcode & molecular based ID: GenBank no. JN617684. This species can be identified with ITS, β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: CBS 127357 has an intermediate position between *P. copticola* and *P. terrigenum* (Fig. 4) and represents a new species. This strain resembles *P. terrigenum* in many aspects such as poor grow on CREA and the formation of broadly ellipsoidal conidia. However, it differs from *P. copticola* and *P. terrigenum* in its inability to grow at 33 °C. A more in-depth study with more *P. copticola* and *P. terrigenum* strains is needed to elucidate the taxonomy of this clade.

Penicillium tropicoides Houbraken, Frisvad & Samson, Fung. Divers. 44: 127. 2010. Fig. 42.

Typus: ex rainforest soil, near Hua-Hin, Thailand (CBS 122410 – holotypus, cultures ex-type DTO 10C4 = IBT 29043).

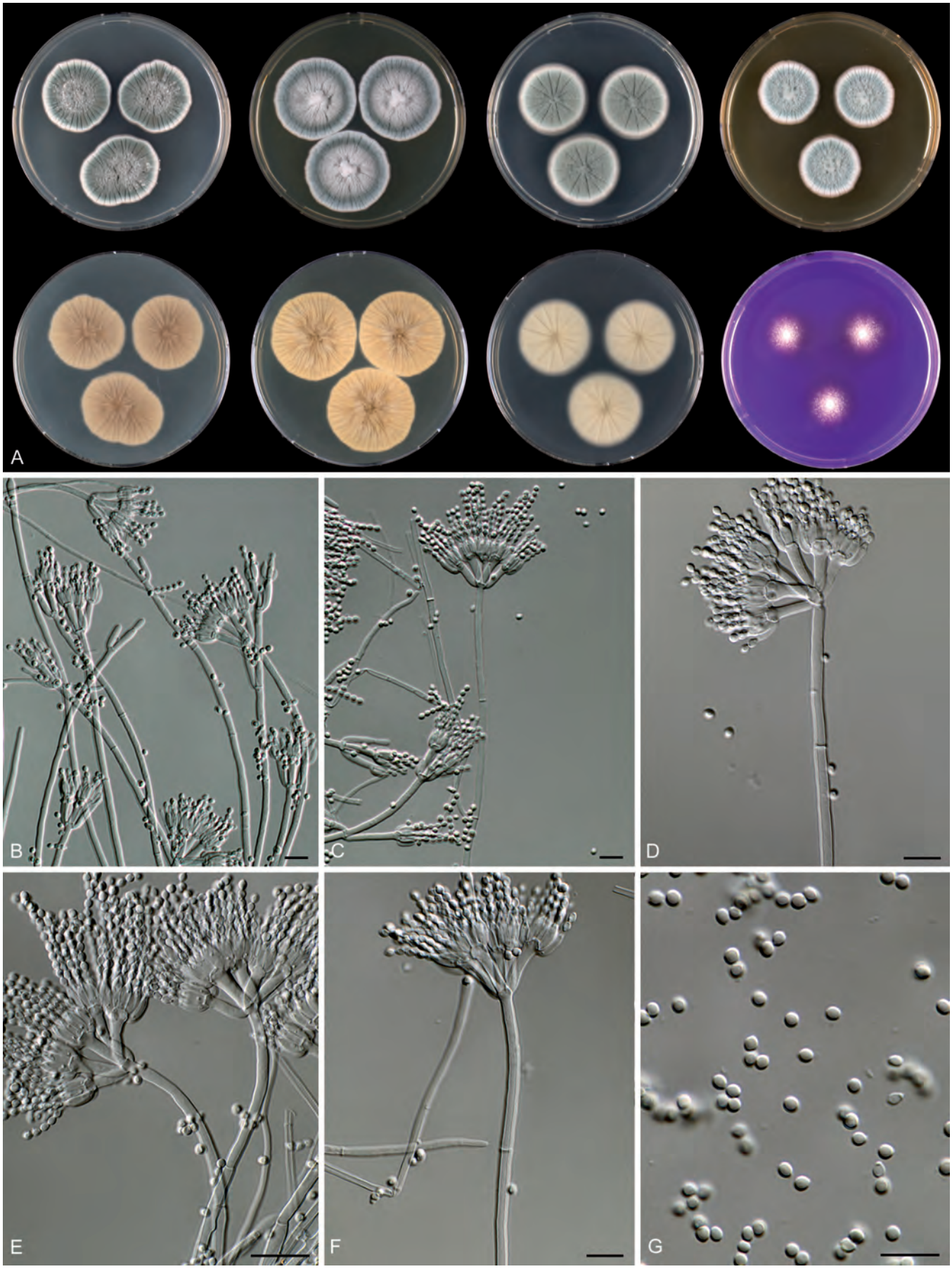

Fig. 41. *Penicillium terrigenum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Description: Colony diam, 7 d, in mm: CYA 24–30; CYA15°C 5–11; CYA30°C 15–25; CYA37°C no growth; MEA 18–23; YES 36–43; DG18 16–23; ratio CYAS:CYA 1.1–1.4; creatine agar 13–16, poor to moderate growth and weak acid production (under colony).

Sporulation on CYA inconspicuous or sparsely produced in fresh isolated strains, becoming more conidial after several transfers, conidia blue grey green, cleistothecia abundantly produced and determining colony colour, drab grey, mycelium inconspicuously, colonies typical with large hyaline exudate droplets, soluble pigments absent, margin slightly irregular, reverse crème-brown. Weak sporulation on YES, cleistothecia abundant present, drab-grey, soluble pigment absent, mycelium inconspicuously, reverse yellow. Weak to good sporulation on DG18, reverse yellow. Colonies on MEA ascomatal and sporulation absent or sparse, cleistothecia darb grey. Ehrlich reaction negative.

Cleistothecia sclerotioid, 200–300 µm diam, ripening slowly and mature after 3 mo on MEA and OA. Ascospores ellipsoidal, 2.5–3.5 × 1.5–2.5 µm, with two narrow, closely appressed equatorial ridges, valves smooth by light microscopy, warted with anastomosing ribs by SEM. Conidiophores arising from the mycelial mat, symmetrically biverticillate, stipes smooth, 100–250 µm long, 2.5–3.5 µm wide. Metulae in whorls of 2–5, 13–17 × 3.0–4.0 µm, uniform in length. Phialides ampulliform, 8.5–10.5 x 2.0–3.0 µm. Conidia broadly ellipsoidal, smooth, 2.0–3.0 × 2.0–2.5 µm.

Extrolites: Isochromantoxins, several apolar indol-alkaloids, "CITY", "HOLOX", "PR1-x", "RAIMO" (Houbraken *et al*. 2010).

Diagnostic characters: Slow growth at 30 °C, no growth at 37 °C, abundant production of drab-grey cleistothecia, maturing after prolonged incubation, over 3 months.

Similar species: *Penicillium tropicoides* morphologically resembles *P. tropicum.* The difference between *P. tropicoides* and *P. tropicum* is the slower maturation of the cleistothecia, slower growth rate at 30 °C and the production of isochromantoxins by *P. tropicoides*. *Penicillium shearii* is related, but can be differentiated by a higher maximum growth temperature than *P. tropicoides* and *P. tropicum*.

Distribution and ecology: *Penicillium tropicoides* is isolated form rainforest soil in Thailand.

Barcode & molecular based ID: GenBank no. GU944584. *Penicillium tropicoides* and *P. tropicum* have no differences in their ITS regions, but these species can be differentiated with β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: None.

Penicillium tropicum Houbraken, Frisvad & Samson, Fung. Divers. 44: 129. 2010. Fig. 43.

= *Eupenicillium tropicum* Tuthill & Frisvad Mycological Progress 3: 14. 2004.

Typus: ex soil beneath *Coffea arabica*, Karnataka, India (SC42-1 – holotype, cultures ex-type DTO 31B1 = CBS 112584 = IBT 24580).

Description: Colony diam, 7 d, in mm: CYA 24–31; CYA15°C 9–13; CYA30°C 25–30; CYA37°C no growth; MEA 23–27; YES 33–37; DG18 20–25; ratio CYAS:CYA 1.0–1.1; creatine agar 16–20, poor growth and weak acid production.

Sporulation on CYA sparse, conidia blue grey green, cleistothecia abundantly produced, orange-tan, becoming warm shades of grey (brownish-grey) in age, mycelium inconspicuous; exudate copious produced in large, hyaline droplets, soluble pigments absent, reverse crème coloured. Weak sporulation on YES, cleistothecia abundantly produced, deep dull grey, mycelium inconspicuous, soluble pigment absent, reverse crème-yellow. Good sporulation on DG18, conidia blue-grey green, reverse pale or very pale yellow. Colonies on MEA ascomatal, in shades of grey, sporulation absent or inconspicuous. Ehrlich reaction negative.

Cleistothecia sclerotioid, 200–300 µm diam, ripening within 3–6 wk on MEA and OA. Ascospores ellipsoidal, 2.5–3 × 2–2.5 µm, with two narrow, closely appressed equatorial flanges and finely roughened valves. Conidiophores arising from the mycelial mat, symmetrically biverticillate, stipes smooth, 2.5–3.5 µm wide; metulae in whorls of 2–5 (–8), 12–16 × 2.5–3.5 µm. Phialides ampulliform, 8.0–10.5 × 2.0–3.0 µm. Conidia broadly ellipsoidal, smooth, 2.3–3.0 × 2.0–2.5 µm.

Extrolites: Several apolar indol-alkaloids, "CITY","EMON", "HOLOX" and "RAIMO" (Tuthill & Frisvad 2004, Houbraken *et al*. 2010).

Diagnostic characters: No growth at 37 °C, abundant production of cleistothecia in warm shades of grey (brownish grey), maturing within 2–5 wk, colonies on CYA incubated at 30 °C reaching a diameter of 25–30 mm.

Similar species: See *P. tropicoides*.

Distribution and ecology: *Penicillium tropicum* has been isolated from (sub)tropical soils (*e.g.* India, Costa Rica, Ecuador and Galapagos Islands).

Barcode & molecular based ID: GenBank no. GU944582. *Penicillium tropicum* and *P. tropicoides* have no differences in their ITS regions, but these species can be differentiated with β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: None**.**

Penicillium ubiquetum Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563201. Fig. 44.

Etymology: Named after the worldwide distribution of this species.

Differt ab omnibus speciebus affinibus conidiis subtiliter exasperatis, coloniis ad 30 °C haud crescentibus, coloniis in agaro MEA ad 25 °C post hebdomatem usque ad 18–26 mm, reverso plus minusve aurantiaco vel roseo-rubro in agaro YES.

Typus: ex soil, Wilson Botanical Garden, Costa Rica, M. Christensen (CBS H-20659 – holotypus, cultures ex-type CBS 126437 = DTO 78B5 = IBT 22226).

Description: Colony diam, 7 d, in mm: CYA 24–34; CYA15°C 14–18; CYA30°C and CYA37°C no growth; MEA 18–26; YES 30–36; DG18 18–27; ratio CYAS:CYA 1–1.3; creatine agar 13–18, weak to moderate growth and no acid production.

Good sporulation on CYA, velvety, conidia dull-green to dark green, mycelium inconspicuous, exudates clear, soluble pigments absent, margin entire, reverse flesh coloured,

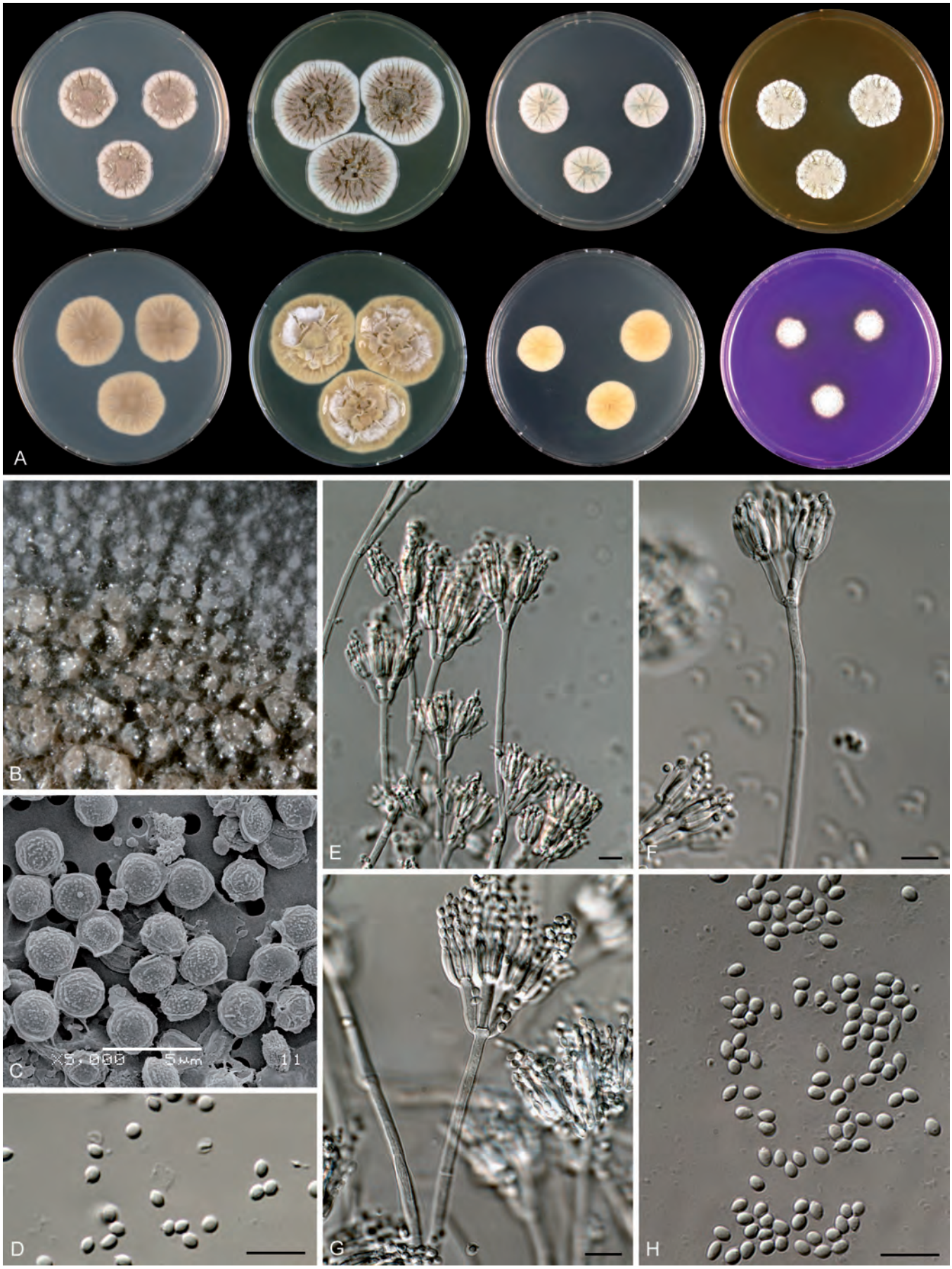

Fig. 42. *Penicillium tropicoides*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Ascomata. C–D. Ascospores. E–G. Conidiophores. H. Conidia. Scale bars = 10 µm.

Fig. 43. *Penicillium tropicum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Sclerotia. C. Ascospores. D–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

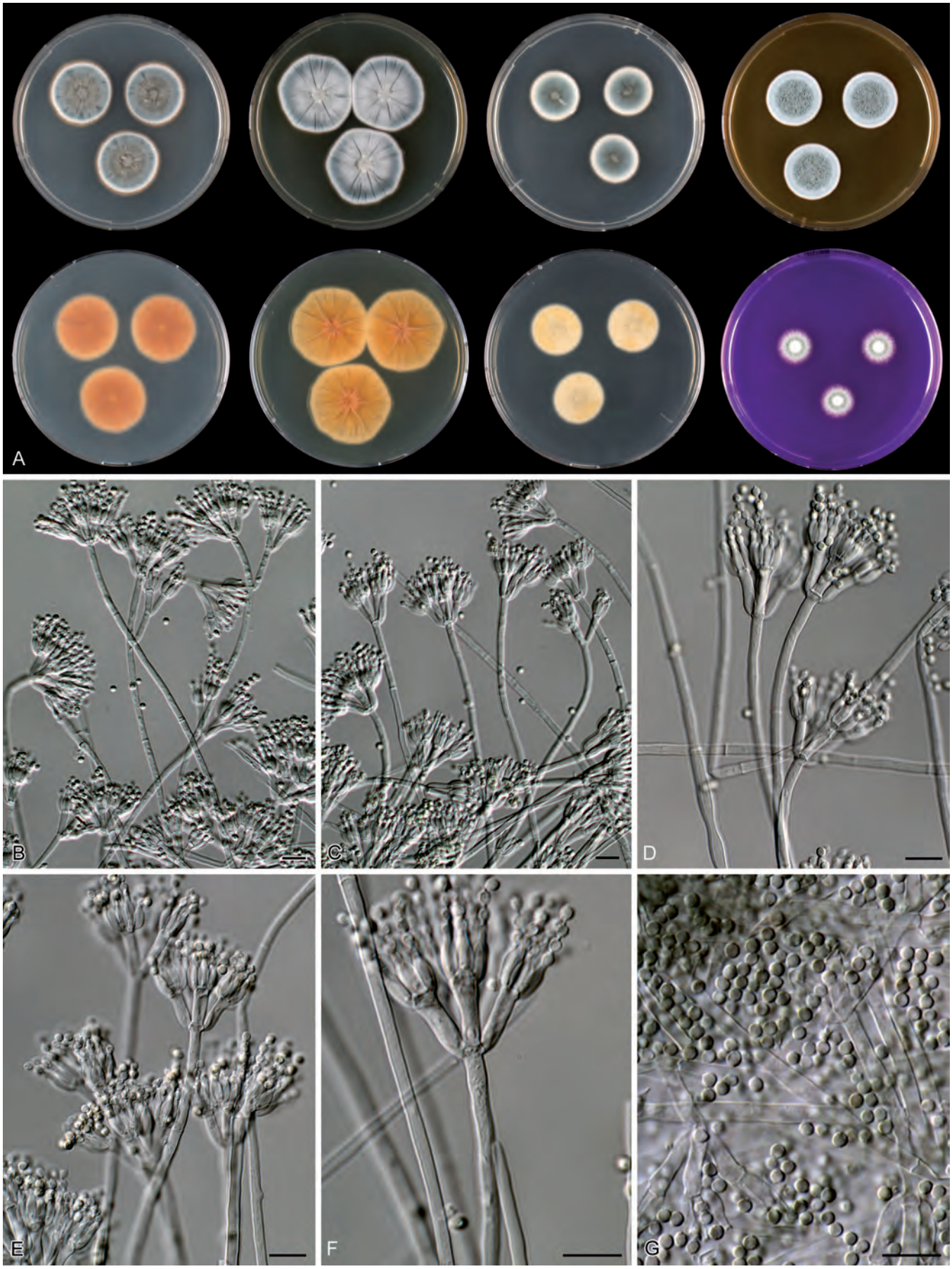

Fig. 44. *Penicillium ubiquetum*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

pinkish-brown with orange centre, often with orange pigmented sulcations. Good sporulation on YES, mycelium white, soluble pigments absent, reverse in shades of orange to pinkish-red. Good sporulation on DG18, conidia in shades of dull green, reverse pale, pale with yellow centre or bright yellow. Moderate to good sporulation MEA, conidial colour variable: blue-green or bluish-grey green or dark-blue green, colony texture floccose. Ehrlich reaction negative.

Sclerotia absent. Conidiophores symmetrically biverticillate, occasionally with an divergent branch that is shorter than the main axis; stipes shorter than most related species, up to 300 µm, smooth, 2.5–4.0 µm wide; metulae in a compact terminal verticil, 3–7 (–9), unequal in length, vesiculate, (8–) 10–15 × 2.0–3.5 µm. Phialides ampulliform, stout, 6.0–8.0 × 1.5–3.0 µm. Conidia globose to subglobose, finely roughened, strongly pigmented cell wall, 1.8–2.5 µm diam.

Extrolites: Citrinin, terrein, "ALK", "GLYF", "RAI", "TRIP", "XANTHOC", isolates in one subclade, CBS 126438 & CBS 126436 produce anthraquinone bisanthrons, citrinin, okaramins, and "SENGA".

Diagnostic characters: Finely roughened conidia, no growth at 30 °C, colonies on MEA attaining a diameter of 18–26 mm in 7 d at 25 °C, reverse on YES in shades of orange to pinkish-red.

Similar species: See *P. pancosmium.*

Distribution and ecology: Soil appears to be the primary habitat, but this species is also isolated from cork bark (GenBank no.v EF198586, as *P. decaturense*). Worldwide distribution: Queensland, Australia, Wisconsin, USA, Madagascar, Costa Rica, Italy, Portugal.

Barcode & molecular based ID: GenBank no. JN617680 (1) and JN617677 (2). *Penicillium ubiquetum* can be divided in two groups based on ITS sequences. ITS sequences of group 1 are unique (incl. CBS 126437^{T}); group 2 ITS sequences of *P. ubiquetum* are identical with *P. waksmanii* (CBS 126438, CBS 126436 and NRRL 35636). Figure 3 shows that the latter isolates also form a subgroup based on partial β-tubulin and calmodulin sequences.

Taxonomy and phylogeny: CBS 126438 and CBS 126436 have a distinct extrolite pattern and differ in their ITS sequence with other *P. ubiquetum* strains. However, no phenotypic or physiological differences were observed among these and other *P. ubiquetum* strains, and therefore these strains are all regarded as one species.

Penicillium vancouverense Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563207. Fig. 45.

Etymology: Named after the location of the type strain, Vancouver (Canada).

Differt ab omnibus speciebus affinibus mycelio flavido (vulgo in CYA15°C et/vel YES), conidiis glaucoviridibus in agaro MEA et conidiis subtiliter exasperatis, crassitunicatis.

Typus: ex soil under Maple tree, Vancouver, BC, Canada, J.C. Frisvad (CBS H-20646 – holotypus, cultures ex-type. CBS 126323 = DTO 82B8 = IBT 20700).

Description: Colony diam, 7 d, in mm: CYA 20–30; CYA15°C 17–25; CYA30°C and CYA37°C: no growth; MEA 16–23; YES 23–33; DG18 17–25; ratio CYAS:CYA 1.0–1.3; creatine agar 8–17, weak growth and no acid production.

Weak to moderate sporulation on CYA, velvety to floccose, conidia grey-green, mycelium light-yellow, often with minute clear or yellow exudates droplets, soluble pigment production variable, if produced yellow coloured, margin entire, reverse in shades of orange-brown or brown. Moderate to good sporulation on YES, conidia dull green, occasionally dull-blue green, mycelium in shades of yellow, soluble pigments absent, reverse beige or beige-brown. Good sporulation on DG18, conidia dull-green, reverse pale or yellow. Moderate to good sporulation on MEA, conidia blue green, colony texture velvety to floccose. Ehrlich reaction negative, with exception of CBS 126324.

Sclerotia absent. Conidiophores predominantly symmetrically biverticillate and, depending on the isolate, additional branches occur; stipes 200–400 µm long, smooth or finely rough walled, width variable, 2.0–4.0 µm; metulae in a compact terminal whorls of 3–6 (–7), unequal in length, often vesiculate, 10–14 × 2.5–3.5 µm. Phialides ampulliform, 7–9 × 2.0–3.5 µm. Conidia subglobose, finely roughened and with a distinct thick and pigmented cell wall, 2.0–3.0 µm diam.

Extrolites: The extrolite patterns of *P. vancouverense* isolates are somewhat diverse. All strains produce citrinin, citreoviridin, "MIF", "PAS" and "met OE". Some strains also produce "CANOT", "MIM", "PHOE" and "XANTHOC".

Diagnostic characters: Light yellow mycelium (especially on CYA15°C and/or YES), blue green conidia on MEA and finely roughened, thick walled conidia.

Similar species: *Penicillium vancouverense* is phylogentically related to *P. pasqualense*, but the latter species does not have yellow mycelium and has a dark-brown reverse on CYA. *Penicillium manginii* and some strains of *P. miczynskii* and related species also form yellow mycelium; *P. manginii* can be differentiated by the faster growth rate on CYA and the red soluble on YES; *P. miczynskii* and related species have smooth walled, subglobose to broadly ellipsoidal conidia.

Distribution and ecology: *Penicillium vancouverense* has a worldwide distribution (the Netherlands, Costa Rica, Chile, California, USA, Queensland, Australia, Madagascar, BC and Ontario, Canada). Soil appears to be the primary habitat, but this species is also isolated from indoor air of a house and a nut of *Juglans cinerea* (butternut).

Barcode & molecular based ID: GenBank no. JN617675. With the exception of isolate CBS 126321, all investigated strains have the same unique ITS sequence. Isolate CBS 126321 has one base pair difference in the ITS region compared with the type isolate CBS 126324^{T}.

Taxonomy and phylogeny: *Penicillium miczynskii* is characterised by the production of yellow pigmented mycelium, exudates and reverses (Pitt 1980, Christensen *et al*. 1999). These features are also characteristic for *P. vancouverense* and it is therefore likely that *P. vancouversense* isolates were previously identified as

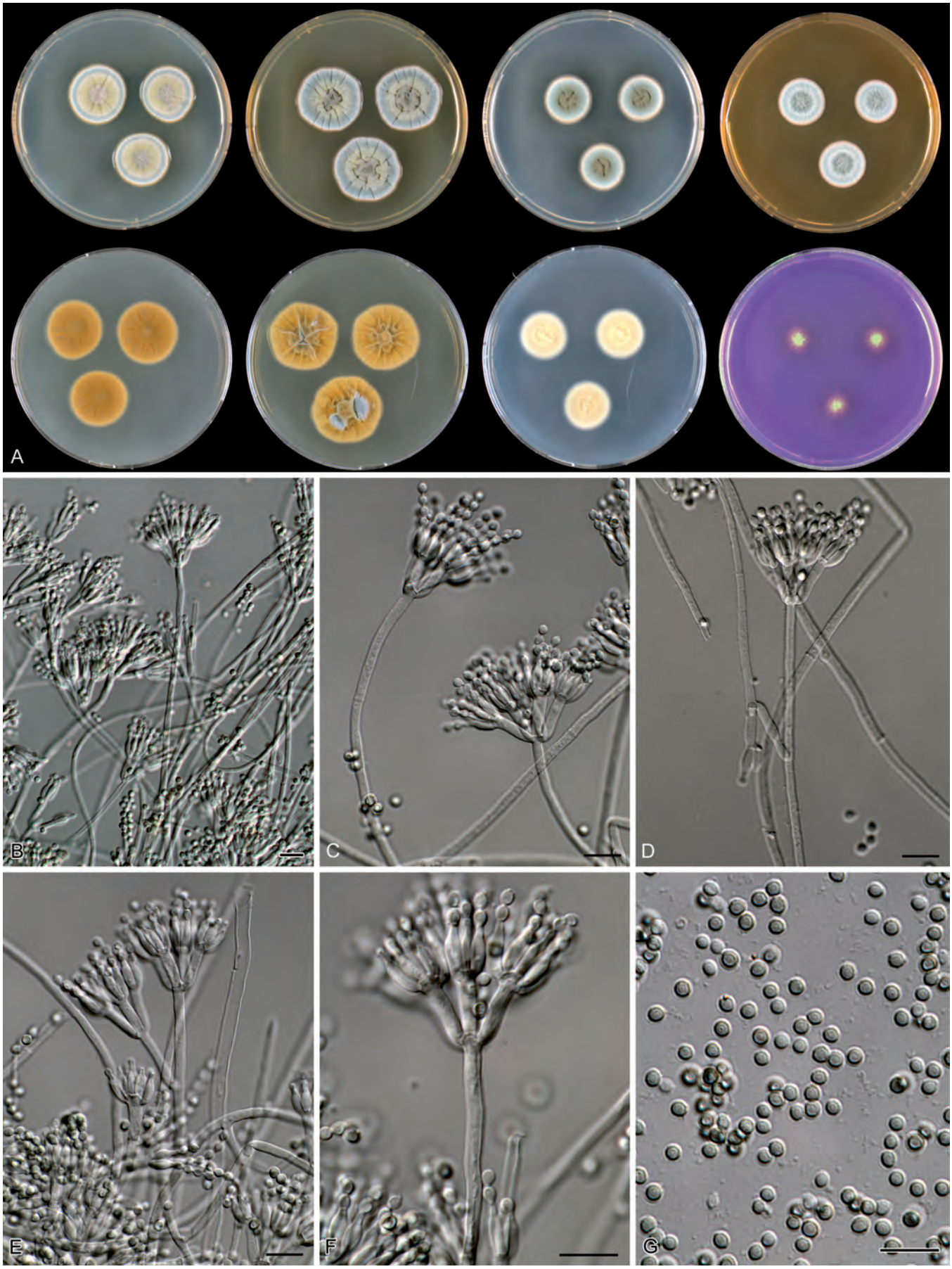

Fig. 45. *Penicillium vancouverense*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

P. miczynskii. This study shows that *P. miczynskii* forms smooth walled conidia and stipes. There is some variation in extrolite profiles and sequences detected among the *P. vancouverense* isolates. The different extrolite profiles do not correlate with the clustering observed in the phylogenetic study.

Penicillium waksmanii Zaleski, Bull. Int. Acad. pol. Sci. Lett., Sér. B.: 468. 1927. Fig. 46.

= *Penicillium rivolii* Zaleski, Bull. Int. Acad. pol. Sci. Lett., Sér. B: 471. 1927.

Typus: ex woodland soil, Purczcza Bialowieska Forest, Poland (Herb. IMI 39746i – lectotype, Pitt 1980; cultures ex-type CBS 230.28 = DTO 22E6 = ATCC 10516 = FRR 777 = IFO 7737 = IMI 039746 = MUCL 29120 = NRRL 777 = QM 7681 = IBT 5003 = IBT 6994).

Description: Colony diam, 7 d, in mm: CYA (20–) 25–32; CYA15°C 10–19; CYA30°C and CYA37°C no growth; MEA 18–24(–30); YES 25–33; DG18 16–27; ratio CYAS:CYA 1.0–1.2; creatine agar 10–18, weak growth and no acid production.

Moderate sporulation on CYA, velvety, conidia dull green, mycelium inconspicuous, exudate absent or as very small clear droplets, soluble pigment absent, entire margins, reverse beige or beige-brown. Sporulation on YES moderate, mycelium white, conidia dull green, soluble pigments absent, reverse beige or beige-brown. Grey green conidia on DG18, reverse pale. Colonies on MEA dull-grey green, colony texture velvety with floccose centre. Ehrlich reaction negative.

Sclerotia absent. Conidiophores symmetrically biverticillate and often with a divergent branch, stipes up to 200–500 µm long, smooth, 2.5–3.5 µm wide; metulae in a compact terminal verticil, 5–6 (–8), unequal in length, vesiculate, 10–14 × 2.5–3.5 µm; phialides ampulliform, 7.0–9.0 × 2–3 µm. Conidia globose to subglobose, finely roughened, 2.0–2.5 µm diam.

Extrolites: Citrinin, cyclopiamin, meleagrin (only produced by one isolate), “GLYF”, “PAS”, “SENGA”.

Diagnostic characters: Finely roughened conidia, no growth at 30 °C, reverse on CYA in shades of brown and a pale reverse on DG18.

Similar species: See *P. chrzaszczii*.

Distribution and ecology: Soil appears to be primary habitat, but this species was also isolated from a dead polypore; strains have been isolated from Poland, New Mexico, USA and New Zeeland.

Barcode & molecular based ID: GenBank no. GU944602. Some strains of *P. ubiquetum* (NRRL 35636 and CBS 126436) share ITS sequences with *P. waksmanii*. Partial β-tubulin and calmodulin sequences can be used for identification.

Taxonomy and phylogeny: Pitt (1980) accommodated *P. waksmanii* in the series *Fellutana* of the subgenus *Furcatum* based on the production of irregular conidiophores, while members of the series *Citrina* produce regular, terminal penicilli. Microscopical analysis of freshly isolated *P. waksmanii* strains from Polish soil show that this species also forms regularly biverticillate structures, often with an additional branch. Furthermore, phylogenetical analysis clearly indicates a close relationship with *P. godlewskii*. Peterson (2000) suggested that *P. rivolii* was a distinct species, because 2 nucleotide differences were observed between the ITS2 region of *P. waksmanii* and *P. rivolii*. However, this observation could not be confirmed and our data suggests that the names are conspecific. Zaleski (1927) described the production of orange pigment in this species. This is not observed in our ex-type strain and recent isolated strains of *P. waksmanii*. CBS 126426 produces, as the only isolate in this species, an anthraquinone, which may be the orange pigment.

Penicillium wellingtonense AJL Cole, Houbraken, Frisvad & Samson, **sp. nov.** MycoBank MB563208. Fig. 47.

Etymology: Named after location of the type strain, Wellington (New Zealand).

Differt ab omnibus speciebus affinibus, coloniis in agaro CYA, MEA et YES constricte crescentibus, ratione incrementi meliore ad 15 °C quam 25 °C.

Typus: ex soil, Wellington, New Zealand, A.J.L. Cole (CBS H-20657 – holotypus, cultures ex-type CBS 130375 = DTO 76C6 = IBT 23557).

Description: Colony diam, 7 d, in mm: CYA 10–15; CYA15°C 18–23; CYA30°C and CYA37°C no growth; MEA 8–13; YES 20–25; DG18 13–17; ratio CYAS:CYA 1.2–1.4; creatine agar 8–12, weak growth and no acid production.

Moderate sporulation on CYA, velvety, conidia grey-green, mycelium inconspicuous, exudate absent, soluble pigment absent, reverse orange. Good sporulation on YES, conidia grey-green, soluble pigments absent, reverse beige-brown. Dull-green colonies on DG18, soluble pigments yellow, reverse reverse bright yellow. Colonies on MEA blue-green, colony texture velvety and wrinkled surface. Ehrlich reaction negative.

Sclerotia absent. Conidiophores predominantly symmetrically biverticillate and occasionally with a branch; stipes rather long, 200–400 µm, smooth, 2.5–3.5 µm wide; metulae in a compact terminal vertical, 3–7, unequal in length, short and stout, 9–12 × 3.0–4.0 µm; phialides ampulliform, 7.5–9.5 × 2.5–3.5 µm. Conidia subglobose to broadly ellipsoidal, smooth to finely roughened, variable in size, 2.5–3.0 × 2.5–3.0 µm.

Extrolites: Citrinin, decaturin, “MIF”, “met Q”, “POF”, “RAI”, “TRIP”, “XANTHOC”.

Diagnostic characters: Restricted growth on CYA, MEA and YES and a higher growth rate at 15 °C than at 25 °C.

Similar species: This species is unique in its slow growth rate. *Penicillium nothofagi* is phenotypically similar. This species has a pale-beige reverse on CYA and *P. wellingtonense* has an orange reverse on CYA.

Distribution and ecology: This species is only known from its type culture, isolated from soil, New Zealand.

Barcode & molecular based ID: GenBank no. JN617713. This species has a unique β-tubulin, calmodulin and ITS sequence.

Taxonomy and phylogeny: *Penicillium wellingtonense* is

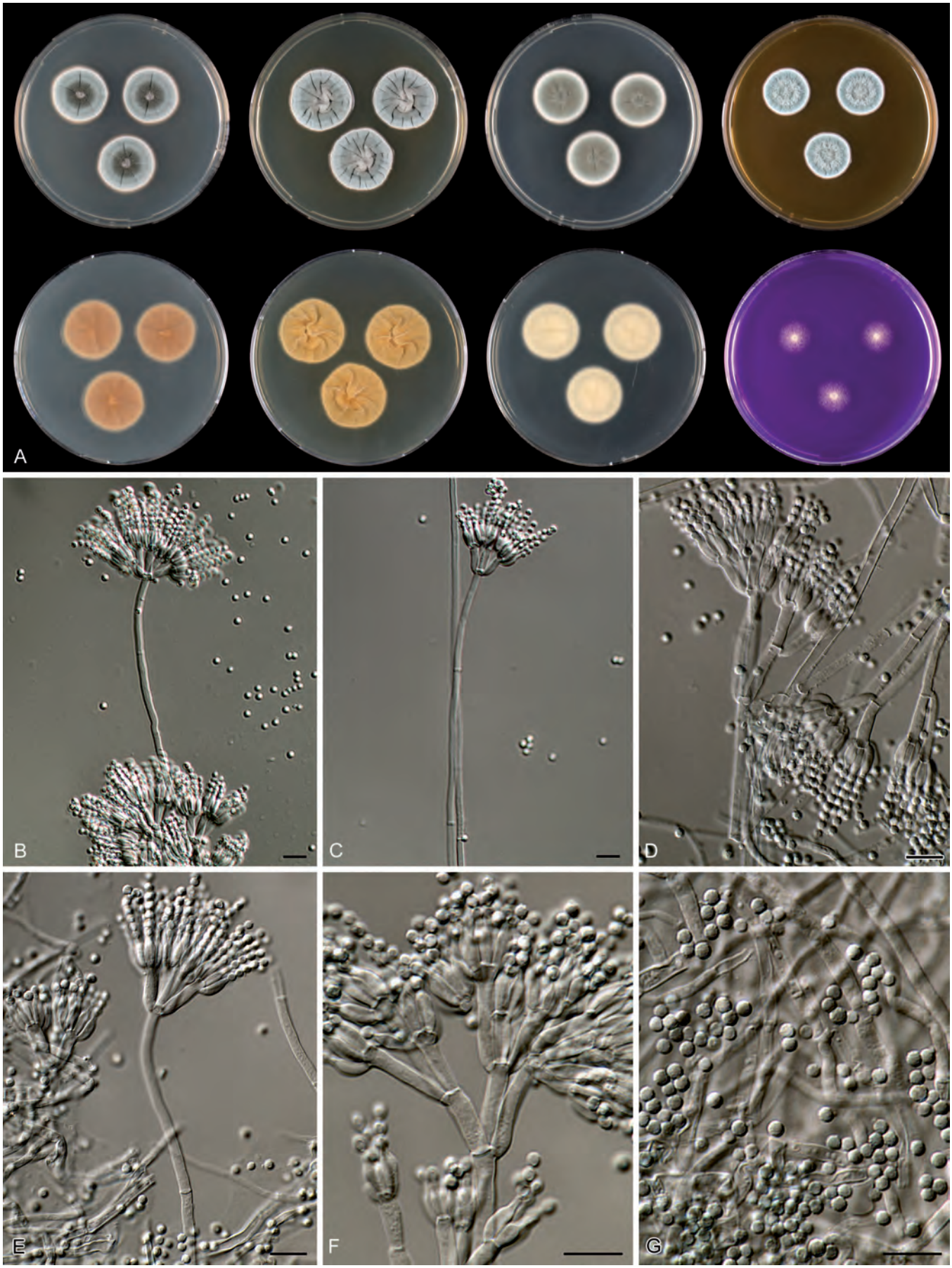

Fig. 46. *Penicillium waksmanii*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

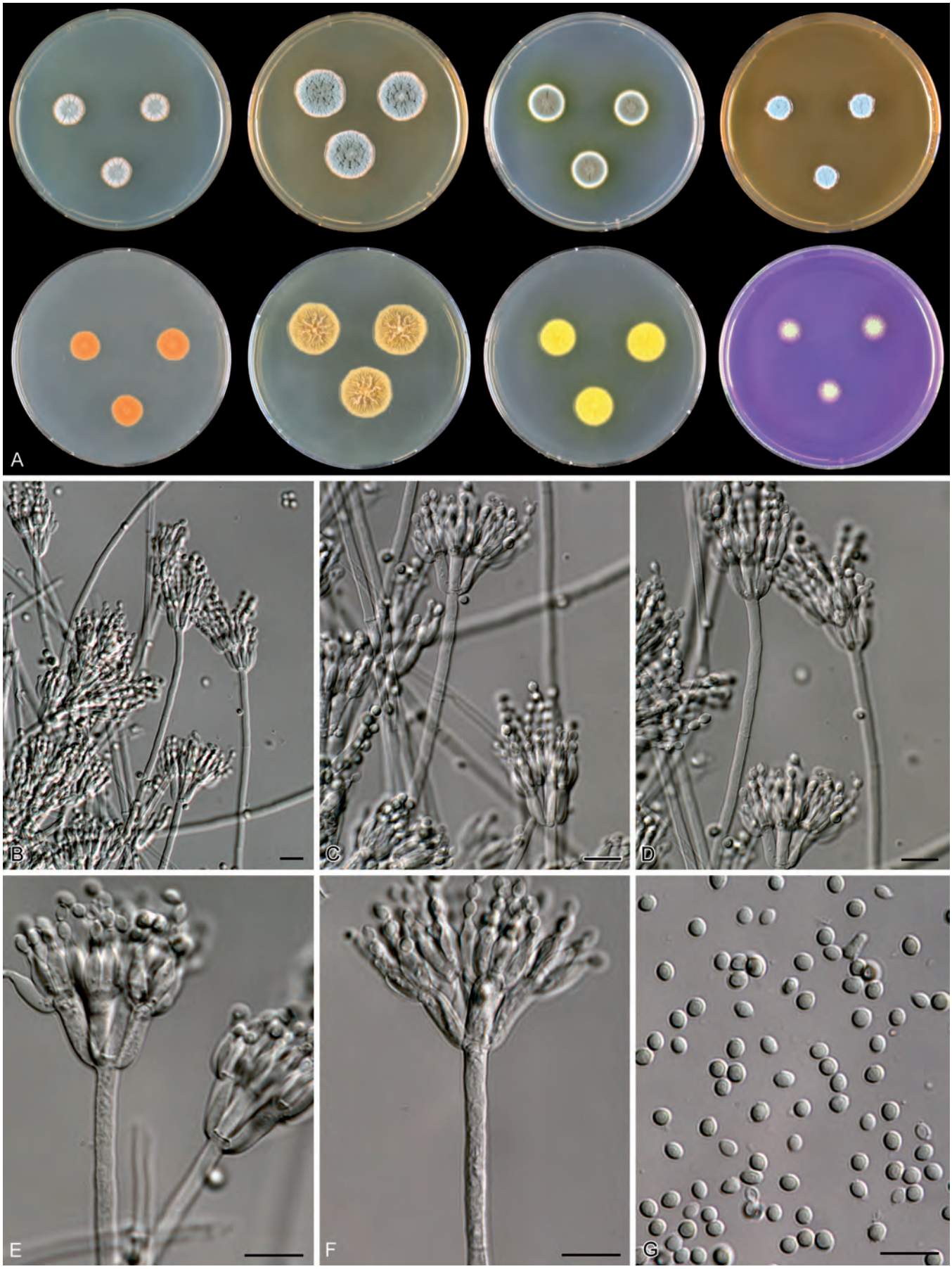

Fig. 47. *Penicillium wellingtonense*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

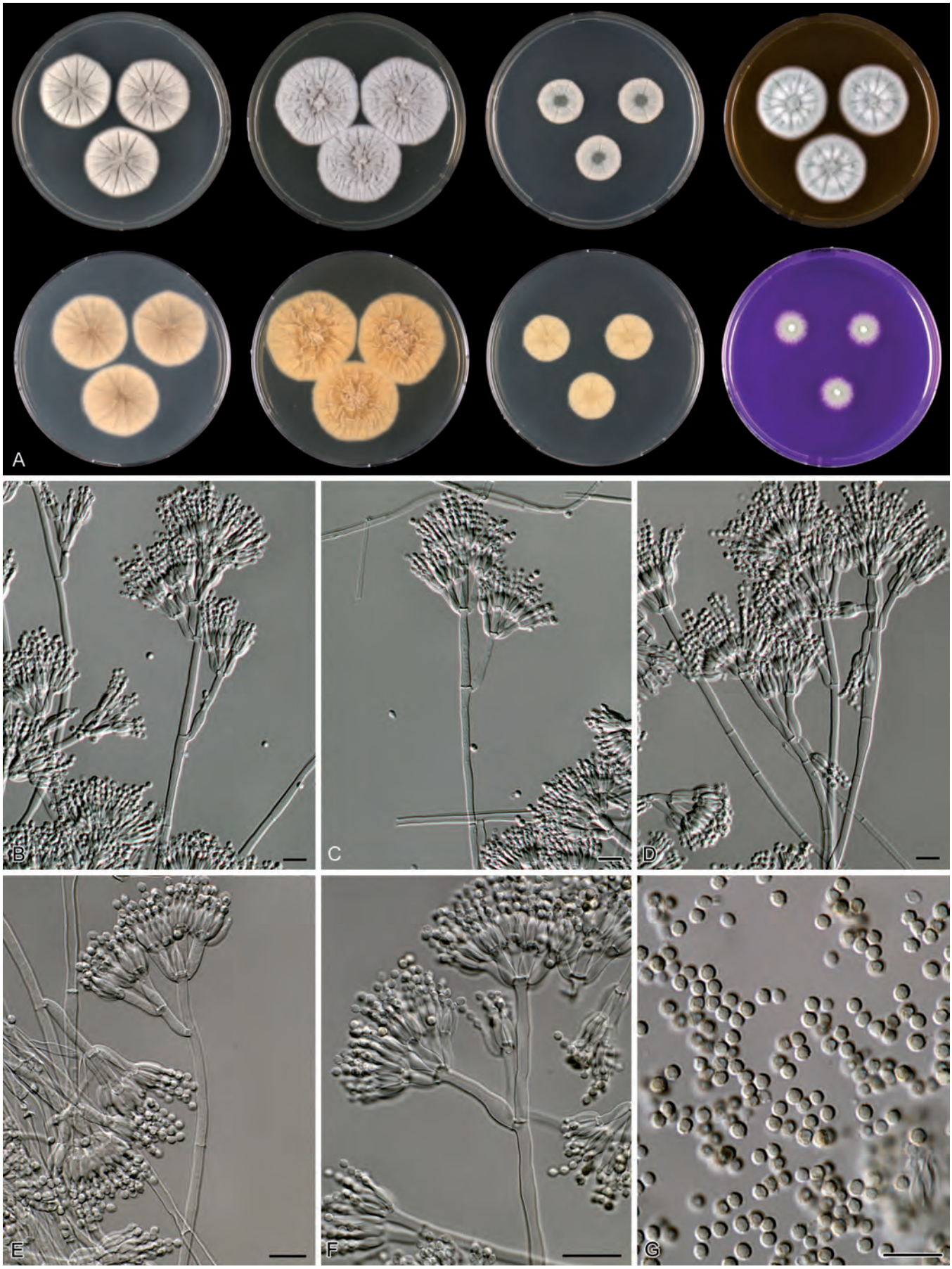

Fig. 48. *Penicillium westlingii*. A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

phylogenetically basal to *P. vancouverense*.

Penicillium westlingii Zaleski, Bull. Int. Acad. pol. Sci. Lett., Sér. B.: 473. 1927. Fig. 48.

= *P. citrinum var. pseudopaxilli* Martínez & Ramírez*, nomen nudum.*

Typus: ex soil under conifer, Denga Goolina, Poznan, Poland (IMI 92272 – neotype, designated by Pitt *et al*. 2000; cultures ex-type CBS 231.28 = DTO 22E7 = IBT 15088).

Description: Colony diam, 7 d, in mm: CYA (25–) 30–36; CYA15°C 15–22; CYA30°C no growth or germination (0–3); CYA37°C no growth; MEA 25–34; YES 33–40; DG18 16–28; ratio CYAS:CYA 0.9–1.1; creatine agar 10–17, weak or moderate growth and no acid production.

No or sparse sporulation on CYA, white mycelium, exudate absent, soluble pigments absent, margin polygonal, reverse pale, pale-beige or pinkish beige. Sporulation on YES absent, mycelium white, soluble pigments absent, reverse pale yellow (cream) to cream-buff. Variable sporulation on DG18, conidia dull green or grey green, reverse pale or pale-cream. Colonies on MEA poorly sporulating, conidia blueish-dark green, colony texture floccose. Ehrlich reaction negative.

Sclerotia absent. Conidiophores symmetrically biverticillate, often with a divergent branch that is shorter than the main axis, occasionally quaterverticillate, stipes up to 500 µm long, smooth, 2.5–4.0 µm wide; metulae in a compact terminal verticil, 3–6 (–8), mostly uniform in length, both vesiculate and non-vesiculate, 8–14 (–16) × 2.0–3.5 µm. Phialides ampulliform, 6.5–8.5 × 2–3 µm. Conidia globose, finely or distinct roughened, 1.8–2.5 µm diam.

Extrolites: Citrinin, curvularin, dehydrocurvularin,"PHOE", "TRIP", "XANTHOC".

Diagnostic characters: Finely roughened conidia, no (or at most very restricted) growth at 30 °C, reverse on CYA pale or pale-beige or pinkish beige, YES pale yellow to cream, no sporulation on CYA and YES.

Similar species: *Penicillium westlingii* is phylogenetically related to *P. nothofagi* and *P. cosmopolitanum*. It differs from *P. nothofagi* by its faster growth rate on CYA, YES and MEA. *Penicillium cosmopolitanum* generally has warmer reverse colours on CYA (with orange coloured sulcations) and larger conidia (2.5–3.0 µm diam). *Penicillium westlingii* is morphologically similar to *P. pancosmium* and *P. ubiquetum*, but the latter two species sporulate well on CYA. *Penicillium waksmanii* is also similar, but *P. westlingii* has a lighter reverse on CYA and a faster growth rate on CYA and YES.

Distribution and ecology: This species commonly occurs in soils in temperature regions, but is also isolated from a nut of *Juglans nigra* (black walnut), acorns of *Quercus*, moose dung and indoor environments.

Barcode & molecular based ID: GenBank no. GU944601. The majority of the investigated *P. westlingii* isolates have the same and unique ITS sequence, though several *P. westlingii* isolates (CBS 124312, CBS 124313, CBS 127003, CBS 127040) share sequences with certain isolates of *P. cosmopolitanum*. These strains also appear in separate subclades in Fig. 4.

Taxonomy and phylogeny: Raper & Thom (1949) and Pitt (1980) placed *P. westlingii* in synonymy of *P. waksmanii*. Pitt (1980) noted that *P. westlingii* grows faster than *P. waksmanii*, but decided that this was insufficient to describe *P. westlingii* as a separate species. Peterson (2000) showed that *P. westlingii* and *P. waksmanii* are genetically distinct and numerous (99 total) nucleotide differences were detected. Re-examination of these sequences shows that the deposited sequence of *P. westlingii* NRRL 800^{T} (GenBank no. AF033423) is not the same as CBS 231.28^{T}. Comparison of the sequence of NRRL 800 shows that *P. westlingii* is the same or very closely related to *P. citrinum*, while the sequence obtained in this study indicates a relation with *P. waksmanii*.

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A taxonomic and phylogenetic revision of the *Penicillium sclerotiorum* complex

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Abstract: The morphological concept of *Penicillium sclerotiorum* (subgenus *Aspergilloides*) includes strains with monoverticillate, vesiculate conidiophores, and vivid orange to red colony colours, with colourful sclerotia sometimes produced. Multigene phylogenetic analyses with the nuclear ribosomal internal transcribed spacer (ITS) region, cytochrome c oxidase subunit 1 (*cox1*), β-tubulin (*benA*), translation elongation factor 1-α (*tef1-α*), and calmodulin (*cmd*), reveal that the *P. sclerotiorum* morphospecies is a complex of seven phylogenetically distinct species, three of which were recently described, namely *P. guanacastense, P. mallochii,* and *P. viticola*. Three previously unidentified species are described here as *P. cainii, P. jacksonii,* and *P. johnkrugii*. The phylogenetic species are morphologically similar, but differ in combinations of colony characters, sclerotium production, conidiophore stipe roughening and branching, and conidial shape. Ecological characters and differences in geographical distribution further characterise some of the species, but increased sampling is necessary to confirm these differences. The fungal DNA barcode, the ITS, and the animal DNA barcode, *cox1*, have lower species resolving ability in our phylogenetic analyses, but still allow identification of all the species. *Tef1-α* and *cmd* were superior in providing fully resolved, statistically well-supported phylogenetic trees for this species complex, whereas *benA* resolved all species but had some issues with paraphyly. *Penicillium adametzioides* and *P. multicolor,* considered synonyms of *P. sclerotiorum* by some previous authors, do not belong to the *P. sclerotiorum* complex.

Key words: DNA barcoding, multigene phylogeny, sclerotia, soil-borne hyphomycetes.
Taxonomic novelties: New species: *Penicillium cainii* K.G. Rivera, Malloch & Seifert, *P. jacksonii* K.G. Rivera, Houbraken & Seifert, *P. johnkrugii* K.G. Rivera, Houbraken & Seifert.

INTRODUCTION

Penicillium sclerotiorum was first isolated from air in Java, Indonesia, by K.B. Boedijn, and then described by van Beyma (1937). The species has monoverticillate, vesiculate conidiophores and vivid orange to red colony colours, and some strains produce orange sclerotia that give the species its name. Cultures identified as *P. sclerotiorum* have been isolated from many countries in Africa, Asia, and North America, suggesting a cosmopolitan distribution, but it has been reported infrequently (Pitt 1980, Ramírez 1982). Strains commonly originate from soil, and occasionally textiles, but are also isolated from house dust (Vesper *et al.* 2005), diseased grape fruit and stems (De Lucca *et al.* 2008), and as a potential endophyte of *Coffea arabica* berries (Vega *et al.* 2006). Air sampling revealed higher concentrations of *P. sclerotiorum* outdoors than in indoor environments in India (Sawane & Saoji 2004).

Penicillium sclerotiorum is now classified in *Penicillium* subgenus *Aspergilloides*, section *Sclerotiora* by Houbraken & Samson (2011). As noted by Peterson (2000) and discussed at length by Houbraken & Samson (2011), the monoverticillate conidiophore, although a useful phenotypic character for identification, is phylogenetically uninformative and the concept of subgenus *Aspergilloides* promoted by Pitt (1980) has been substantially revised. Species with such conidiophores are phylogenetically intermingled with species with divaricate or symmetrically biverticillate conidiophores. Pitt (1980) classified *P. sclerotiorum* in his broadly circumscribed subgenus *Aspergilloides* series *Glabra,* which Peterson's phylogenetic studies distributed among his Clades 2, 3, and 5 (Peterson 2000). Peterson's 'Clade 3' of *Penicillium* included the predominantly monoverticillate species *P. adametzii*, *P. adametzioides, P. bilaiae,* and the biverticillate *P. herquei*, all now classified in section *Sclerotiora* by Houbraken & Samson (2011). Three biverticillate species were included by Houbraken & Samson (2011) in section *Sclerotiora*, namely *P. herquei,* classified by Pitt (1980) in *Penicillium* subgenus *Furcatum* section *Furcatum,* and the subsequently described *P. malachiteum* and *P. nodositatum.* Sclerotia are sporadically produced by species across many sections of *Penicillium,* with the orange sclerotia of *P. thomii* (section *Aspergilloides*) perhaps the most conspicuous and commonly encountered example.

Our recent studies of *Penicillium* strains isolated from the guts of tropical leaf-eating caterpillars in Costa Rica (Rivera *et al.* 2011) led to the description of two phylogenetically distinct species, *P. mallochii* and *P. guanacastense*, which although they do not produce sclerotia, otherwise conform to the morphological concepts of *P. sclerotiorum* of Pitt (1980) and Stolk & Samson (1983). This led to the realisation that the morphological concept of *P. sclerotiorum* includes a complex of phylogenetically distinct species, and to the taxonomic revision presented in this paper. Among the modern revisions of this taxon by Raper & Thom (1949), Pitt (1980), Ramírez (1982), and Stolk & Samson (1983), only the latter proposed synonyms for *P. sclerotiorum*; we reconsidered the status of *P. adametzioides* and *P. multicolor* as possible names for some of the phylogenetic lineages we observed. This paper provides a polyphasic taxonomic revision of 29 strains from this complex, based on morphological and microscopic characters, and phylogenetic analyses of five genes: β-tubulin (*benA*), cytochrome c oxidase subunit 1 (*cox1*), the internal transcriber spacer (ITS) region, translation elongation factor 1-α (*tef1-α*), and calmodulin (*cmd*). The ITS and *cox1* genes are of particular relevance as DNA barcodes, with ITS now functioning as the sanctioned DNA barcode for fungi (Schoch *et al.*, in prep.), and *cox1* as the DNA barcode for animals (Hebert *et al.* 2003).

Table 1. Accession numbers of cultures, isolation details and GenBank accession numbers for the five genes used for phylogenetic analysis of the *Penicillium sclerotiorum* complex.

Species	Accession number	Location	Host or substrate	GenBank Accession numbers				
				ITS	*benA*	*tef1-α*	*cmd*	*cox1*
P. adametzii	CBS 209.28 (T)	Poland, Poznan	Soil under conifers	JN714929	JN625957	JN626136	–	JN626049
	KAS 3463	Malaysia, Kedah	Forest soil	JN714930	JN625958	JN626137	–	JN626050
	KAS 3464	Malaysia, Kedah	Forest soil	JN714931	JN625959	JN626138	–	JN626051
	KAS 3465	Malaysia, Kedah	Forest soil	JN714932	JN625960	JN626139	–	JN626052
	KAS 3466	Malaysia, Kedah	Forest soil	JN714933	JN625961	JN626140	–	JN626053
P. adametziodes	DAOM 239916	Canada, Ontario, Vineland	Riesling grapes	JN686434	JN799643	–	JN686387	JN686410
	CBS 313.59 (T)	Japan	Soil	JN686433	JN799642	–	JN686388	JN686411
P. bilaiae	NRRL 3391 (T)	Ukraine, Kiev	Soil	JN714937	JN625966	JN626145	JN626009	JN626058
	ATCC 20851	Canada, Alberta, Lethbridge	Soil	JN714934	JN625964	JN626141	JN626005	JN626054
	ATCC 22348	Ukraine, Kiev	Soil	JN714935	JN625962	JN626143	JN626007	JN626056
	DAOM 197974	Canada, Alberta	Soil	JN714936	JN625965	JN626144	JN626008	JN626057
P. cainii	DAOM 239914 (T)	Canada, Ontario, Niagara, Niagara Falls, Fireman's Park	Nuts of *Juglans nigra*	JN686435	JN686366	JN686456	JN686989	JN686412
	DAOM 239915	Canada, Ontario, Niagara, Niagara Falls, Fireman's Park	Nuts of *Carya ovata*	JN686436	JN686367	JN686457	JN686390	JN686413
P. guanacastense	DAOM 239912(T)	Costa Rica, Santa Rosa, Área de Conservación Guanacaste	Gut of the caterpillar *Eutelia* sp. reared on leaves of *Spondias mombin*	JN626098	JN625967	JN626146	JN626010	JN626059
	DAOM 239913	Costa Rica, Santa Rosa, Área de Conservación Guanacaste	Gut of the caterpillar *Eutelia* sp. reared on leaves of *Spondias mombin*	JN626099	JN625968	JN626147	JN626011	JN626060
P. herquei	CBS 336.48 (T)	France	Leaf of *Agauria pirifolia*	JN626101	JN625970	JN626149	JN626013	JN626062
	CBS 136.22	France		JN626100	JN625969	JN626148	JN626012	JN626061
	CBS 347. 51	Japan, Nehira	Wakamoto corn and rice cake	JN626102	JN625971	JN626150	JN626014	JN626063
	CBS 110644	USA, Wisconsin	Forest soil	JN626103	JN625972	JN626151	JN626015	JN626064
P. hirayamae	CBS 229.60 (T)	Thailand	Milled rice	JN626095	JN625955	JN626135	JN626003	JN626046
	CBS 238.65	South Africa	Corn meal	JN626096	JN625956	JN626134	JN626004	JN626047
P. jacksonii	DAOM 239937 (T)	Australia, Queensland, Barrine Lake	Forest soil	JN686437	JN686368	JN686458	JN686391	JN686414
	DAOM 239938	Australia, Queensland, Barrine Lake	Forest soil	JN686438	JN686369	JN686459	JN686392	JN686415
P. johnkrugii	DAOM 239939	Malaysia, Kedah, Langkawi, Gunung Raya Rainforest	Rainforest soil	JN686443	JN686374	JN792190	JN686397	JN686420
	DAOM 239940	Malaysia, Kedah, Langkawi, Gunung Raya Rainforest	Forest soil	JN686444	JN686375	JN792191	JN686398	JN686421
	DAOM 239941	Malaysia, Kedah, Langkawi, Gunung Raya Rainforest	Forest soil	JN686445	JN686376	JN792192	JN686399	JN686422
	DAOM 239942	Malaysia, Kedah, Langkawi, Gunung Raya Rainforest	Forest soil	JN686446	JN686377	JN792193	JN686400	JN686423
	DAOM 239943 (T)	Malaysia, Kedah, Langkawi, Gunung Raya Rainforest	Forest soil	JN686447	JN686378	JN792194	JN686401	JN686424

Table 1. (Continued)..

Species	Accession number	Location	Host or substrate	GenBank Accession numbers				
				ITS	*benA*	*tef1-α*	*cmd*	*cox1*
	DAOM 239944	Malaysia, Kedah, Langkawi, Gunung Raya Rainforest	Forest soil	JN686448	JN686779	JN792195	JN686402	JN686425
	DAOM 239945	Malaysia, Kedah, Langkawi, Gunung Raya Rainforest	Forest soil	JN686449	JN686780	JN792196	JN686403	JN686426
	DAOM 239946	Malaysia, Kedah, Langkawi, Gunung Raya Rainforest	Forest soil	JN686450	JN686781	JN792197	JN686404	JN686427
	KAS 3479	Malaysia, Kedah, Langkawi, Gunung Raya Rainforest	Forest soil	JN686451	JN686782	JN792198	JN686405	JN686428
P. levitum	NRRL 705 (T)	USA, New York	Modeling clay	JN626097	JN714938	JN714928	JN714939	JN626048
P. mallochii	DAOM 239917 (T)	Costa Rica, Santa Rosa, Área de Conservación Guanacaste	Caterpillar on *Spondias mombin*	JN626104	JN625973	JN626152	JN626016	JN626065
	DAOM 239919	Costa Rica, Santa Rosa, Área de Conservación Guanacaste	Midgut of the caterpillar *Citheronia lobesis* feeding on *Spondias mombin*	JN626106	JN625975	JN626154	JN626018	JN626067
	DAOM 239922	Costa Rica, Santa Rosa, Área de Conservación Guanacaste	Hindgut of the caterpillar *Rothschildia lebeau* reared on leaves of *Spondias mombin*	JN626109	JN625978	JN626157	JN626020	JN626070
	DAOM 239925	Costa Rica, Santa Rosa, Área de Conservación Guanacaste	Guts of the caterpillar *Citheronia lobesis* reared on leaves of *Cochlospermum vitifolium*	JN626112	JN625980	JN626159	JN626023	JN626072
	DAOM 239926	Costa Rica, Santa Rosa, Área de Conservación Guanacaste	Frass of the caterpillar *Rothschildia lebeau* reared on leaves of *Spondias mombin*	JN626111	JN625981	JN626160	JN626024	JN626073
	DAOM 239927	Costa Rica, Santa Rosa, Área de Conservación Guanacaste	Gut of the caterpillar *Rothschildia lebeau* reared on leaves of *Spondias mombin*	JN626113	JN625982	JN626161	JN626025	JN626074
P. multicolor	CBS 501.73 (T)	USSR	Soil	JN799647	JN799645	JN799648	JN799646	JN799644
P. sclerotiorum	NRRL 2074 (T)	Indonesia, Java, Buitenzorg	Air	JN626132	JN626001	JN626180	JN626044	JN626093
	NRRL 32583	USA, Hawai'i, Kuauai	Coffee seeding crown	JN626133	JN626002	JN626181	JN626045	JN626094
	DAOM 239930	Thailand, Hua Hin	Forest soil	JN626129	JN625998	JN626177	JN626041	JN626090
	DAOM 239931	Australia, Queensland, Barron Falls	Forest soil	JN626130	JN625999	JN626178	JN626042	JN626091
	DAOM 239932	Australia, Queensland, Barron Falls	Forest soil	JN626131	JN626000	JN626179	JN626043	JN626092
	CBS 128.65	Zaire, Leopoldville, Nsang–Ngidinga River	Forest litter	JN686452	JN686783	JN686464	JN686406	JN686429
	CBS 258.55	Turkey, Istanbul	Culture contaminant	JN686453	JN686784	JN686465	JN686407	JN686430
	CBS 118889	Korea	Soil	JN686454	JN686785	JN686466	JN686408	JN686431
P. viticola	DAOM 239933	Australia, Queensland, Barron Falls	Forest soil	JN686439	JN686370	JN686460	JN686393	JN686416
	DAOM 239934	Australia, Queensland, Atherton	Forest soil	JN686440	JN686371	JN686461	JN686394	JN686417
	DAOM 239935	Australia, Queensland, Atherton	Rainforest soil	JN686441	JN686372	JN686462	JN686395	JN686418
	DAOM 239936	Australia, Queensland, Atherton	Rainforest soil	JN686442	JN686373	JN686463	JN686396	JN686419
Penicillium sp.	CBS 248.65	South Africa	Corn meal	JN686455	JN686786	JN686467	JN686409	JN686432

Abbreviations: CBS - CBS-KNAW Biodiversity Centre culture collection, Utrecht, the Netherlands. DAOM - culture collection and herbarium of the National Mycological Collections, Agriculture & Agri-Food Canada, Ottawa. NRRL - culture collection of USDA-ARS, National Center for Agricultural Utilization Research, Peoria, IL, USA. ATCC - American Type Culture Collection, Manassas, VA, USA. KAS - personal culture collection of Keith A. Seifert.

MATERIALS AND METHODS

Fungal isolates and herbarium specimens

We focused on cultures identified as *P. sclerotiorum,* and the related species in Clade 3 from the phylogenetic study of Peterson (2000). They were obtained from the CBS Fungal Biodiversity Centre (CBS) and USDA-ARS, National Center for Agricultural Utilization Research (NRRL) culture collections, and the personal research collections of K.A. Seifert and C. André Lévesque (Ottawa, ON, Canada), D. Malloch (formerly University of Toronto, ON, Canada), and J. Houbraken and R.A. Samson (CBS). Representative strains are deposited in the Canadian Collection of Fungal Cultures (DAOM) and CBS. Table 1 includes the metadata for the 29 strains used in this study. We note that cultures of this complex do not preserve well in sterile water at 4 ºC, often dying within one year. Some *P. sclerotiorum* strains (DAOM 239931, 239932) and all *P. johnkrugii* strains were isolated from ethanol treated soils from Australia and Malaysia (Houbraken, pers. comm.).

Morphological analysis

All strains were inoculated at three points onto Blakeslee's Malt Extract Agar (MEA, for microscopic analysis and colony characters), Czapek Yeast Agar (CYA, for colony characters; Pitt 1973), Czapek Agar (CZ, for ability to grow and sporulate in the absence of ammonia; Raper & Thom 1949), Yeast Extract Sucrose Agar (YES to stimulate colony pigmentation by enhancing secondary metabolite production; Filtenborg *et al.* 1990), Oatmeal Agar (OA, to stimulate sclerotial or ascomatal development) and Creatine Sucrose Agar (CREA, to test for acid production; Frisvad 1993). All measurements and observations were performed in duplicate from cultures inoculated at different times. Plates were incubated in the dark at 25 ºC for 7 days.

Microscopic observations employed a BX 50 light microscope (Olympus Canada, Richmond Hill, ON), using tissue removed from 7 d old colonies grown on MEA, and mounted in 85 % lactic acid. Microphotographs were taken and characters measured with an Evolution MP Camera using Image-Pro Plus v. 6 (both from Media Cybernetics, MD, USA). For each strain, automated measurements of 25 conidia were made from phase contrast images using the count/size algorithm of Image-Pro, and manual measurements were made for ten phialides, stipes, branches, vesicles, sclerotia and sclerotial cells. Variations in microscopic dimensions are presented as mean ± standard error. Alphanumeric colony colour codes are based on Kornerup & Wanscher (1978). Colony photographs were taken using a copy stand and a Coolpix P5000 camera (Nikon Canada, Mississauga, ON) under incandescent light.

DNA extractions, PCR and DNA sequencing

Genomic DNA was extracted from strains grown on MEA or CYA using the UltraClean™ Microbial DNA Isolation Kit (MoBio Laboratories, Montreal, Canada) following the manufacturer's protocol. *BenA* was amplified and sequenced with primers Bt2a and Bt2b (Glass & Donaldson 1995); ITS with primers ITS1 and ITS4 (White *et al.* 1990); *cox1* with primers PF and AR (Seifert *et al.* 2007); *tef1-α* with primers EF1c and EF6 (Peterson *et al.* 2004); and *cmd* with primers CMD5 and CMD6 (Hong *et al.* 2006).

PCR reactions were performed in 10 µl reaction mixtures containing 1 µl genomic DNA, 1X PCR Buffer, 0.1 mm of dNTPs, 0.08 µM of each primer, and 0.5X Taq polymerase. Amplifications were performed in a TGradient (Biometra, Montreal, Canada) or a Genius (Techne, Duxford, Cambridge, UK) thermocycler. The PCR parameters for ITS, *cox1*, *benA* were denaturation at 95 ºC for 1 min, followed by primer annealing at 56 ºC for 45 s, and primer extension at 72 ºC for 90 s for 35 cycles, plus a final 10 min elongation step at 72 ºC. The profile for *tef1-α* and *cmd* was denaturation at 94 ºC for 1 min, annealing at 62 ºC for 30 s, primer extension at 72 ºC for 90 s for 42 cycles, then a final elongation step at 72 ºC for 10 min. PCR products were visualised by gel electrophoresis in a 1 % agarose gel containing ethidium bromide (0.05 µg/mL).

Sequencing reactions were performed directly on PCR amplicons using forward and reverse primers. Reactions with a total volume of 10 µl contained 1 µl amplicon, 0.5 µl of ready-made BigDye and terminator mix v. 7 and 0.125X BigDye buffer (Applied Biosystems, Foster City, CA, USA), and 0.161 µM of primer. Reactions were performed in the thermocyclers noted above, programmed for denaturation at 95 ºC for 1 min, followed by primer annealing at 56 ºC for 30 s and primer extension at 72 ºC for 1 min for 30 cycles, plus a final 10 min elongation step at 72 ºC. Sequence reaction mixtures were precipitated using ethanol/EDTA/sodium acetate precipitation. Samples were analysed on an ABI 3130XL Genetic Analyzer (Applied Biosystems, Foster City, CA, USA).

Two strains of *P. herquei* (CBS 336.48^{T}, 110644) produced two amplicons (*ca*. 360 bp and 470 bp long) for *benA*. PCR products with multiple bands were cloned using Promega's pGEM®-T Vector Kit and JM109 High Efficiency Competent Cells (Madison, WI, USA) following the manufacturer's protocol. Fifteen transformed colonies were selected for PCR and sequencing.

Consensus sequences were assembled using Sequencher v. 4.8 (Genes Codes Corporation, Ann Arbor, MI, USA) and SeqMan in the LASERGENE package v. 8 (DNASTAR Inc., Madison, WI, USA). Alignments were constructed using the online version of MAFFT v. 6 (Katoh *et al.* 2009), and adjusted to optimise homology using BioEdit 7.0.9 (Hall 1999).

Maximum parsimony (MP) analyses were performed using heuristic searches in PAUP v. 4 (Swofford 2002) with the tree bisection-reconnection (TBR) branch swapping algorithm. Uninformative characters were removed for all analyses, gaps were treated as missing data, and maxtrees were set to 5000. Consensus trees were calculated, and the robustness of the gene trees was tested using a full heuristic search, saving 10 trees per replicate (1000 replicates).

Maximum likelihood (ML) analyses were performed using Phylogenies for Maximum Likelihood (PhyML) v. 2.4.4 (Guindon *et al.* 2005). Tree searches for each alignment were run under the nucleotide substitution models obtained from ModelTest 3.7, namely GTR+G (*benA*, *cox1,* ITS, *tef1-a*), and GTR+I+G (*cmd*), using the Alkaike Information Criteria (AIC) (Posada & Crandall 1998). The starting tree for branch swapping was obtained using the modified neighbour joining algorithm BIONJ (Gascuel 1997), as implemented in PhyML. The robustness for each tree was tested by performing 1000 bootstrap replicates.

Bayesian inference (BI) analyses were performed using MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001), using the same models noted for ML above. All Bayesian analyses were performed using random starting trees, and were run for four chains with one million generations for all genes, sampling every 100 generations, generating 10,001 trees, with the first 2,500 discarded as 'burn-in' for each chain.

Table 2. Comparative summary of colony and microscopic characters of species in the *P. sclerotiorum* complex.

Species	Colony characters on CYA			Morphological characters					Substrate/host	Geographical distribution
				Conidiophores			Conidia			
	Conidium colours	Diam (mm)	Sclerotia	Roughening	Length > 135 µm	Branching	Roughening	Shape		
P. sclerotiorum	Greenish grey/orange	18–40	Present	Smooth to finely rough	All	Unbranched	Finely rough	Subglobose to ellipsoidal	Soil, litter, coffee beans, air	Pantropical and subtropical
P. cainii	Deep blue to deep green	23–29	Absent	Rough	No	Unbranched or ~10 % branched	Finely rough	Globose	Nuts of *Juglandaceae*	Canada
P. guanacastense	Greenish grey	25–33	Absent	Finely rough	No	~10 % branched	Finely rough	Globose	Caterpillars feeding on leaves	Costa Rica
P. jacksonii	Deep green	30–33	Absent	Smooth to rough	No	Unbranched or < 65 % branched	Finely rough	Globose	Soil	Australia
P. johnkrugii	White	30–38	Present	Smooth to finely rough	Most	Unbranched	Finely rough	Globose to subglobose	Soil	Malaysia
P. mallochii	Turquoise grey/greenish grey	29–39	Absent	Smooth to finely rough	Most	~10 % branched	Finely rough	Globose to subglobose	Caterpillars feeding on leaves	Costa Rica
P. viticola	Greenish grey	26–36	Absent	Rough	No	Unbranched or ~10 % branched	Smooth	Globose	Grape vines, soil	Australia, Japan

Individual gene trees and a combined data set with all five genes were analysed by MP, ML and BI individually. A partition homogeneity test (PHT) was performed in PAUP v. 4 (Swofford 2002) using all genes to determine whether combining the genes was advisable. Missing *cmd* sequences for *P. adametzii* strains and missing *tef1-α* sequences for DAOM 239916 were replaced by N's to indicate missing data. Parsimony parameters were set to TBR, 1000 replicates, 10 trees saved per replicate, and maxtrees were set to 5000.

All new sequences used for our analyses are deposited in GenBank under accession numbers JN625955–JN799648 (Table 1). Alignments are in TreeBase under study S12031.

RESULTS

Analysis of morphological characters

Morphological species descriptions for *P. cainii*, *P. jacksonii*, *P. johnkrugii*, *P. viticola*, and the revised species description for *P. sclerotiorum* are provided in the Taxonomy section. Together with the descriptions of *P. guanacastense* and *P. mallochii* in Rivera *et al.* (2011), this constitutes a monographic revision of the *P. sclerotiorum* species complex. Most species can be identified by subtle phenotypic characters with the aid of Table 2 and the dichotomous key at the end of the paper. Several species seem to be ecologically distinct, but the apparent geographical disjunctions are preliminary and more sampling is needed to confirm these patterns.

In general, the species of this complex grow 20–40 mm diam in 7 d on CYA, and slightly slower, about 15–35 mm, on MEA. The conidial colours are green, often with grey or turquoise tinges; some species can be distinguished by subtle colour differences. Reverse colours are typically orange or red on CYA, and variations from this can be useful for species identification. Conidiophores are usually monoverticillate, but in several species up to about 10 % of conidiophores may have a single branch, and in some strains of *P. jacksonii* more than half of the conidiophores may be branched. Stipe roughening is usually slight, except for the conspicuous roughening in *P. cainii* and *P. viticola*. Stipe length varies considerably among the species; although ranges overlap, there seems to be a division between species with most conidiophores shorter or longer than 135 µm. We evaluated the width of the vesicles of monoverticillate conidiophores; they vary between 3–6 µm wide, and although there are minor statistical differences, we do not think this is a useful character for species recognition. Similarly, the number of phialides per vesicle, a highly variable character that is difficult to count confidently, is not useful as a species character. The conidia of most species in the complex are globose or subglobose and about 2–3 µm diam (L/W ratio 1:1 to about 1.2:1). Conidia of *P. sclerotiorum sensu stricto* are the most ellipsoidal in the complex. The conidia of most species are slightly roughened, although this is rather inconspicuous, and does not seem to be a useful character for species recognition, at least as observed with the light microscope.

Sclerotium production is inconsistent within some species, particularly *P. sclerotiorum,* where only four of eight strains produced them. The ex-type strain is very unpredictable, sometimes producing colonies completely covered with sclerotia, and in other transfers producing none at all. Sclerotia are normally visible after 7 d in fresh strains, but production is sometimes delayed to 10–14 d in some transfers of older strains. All strains of *P. johnkrugii*

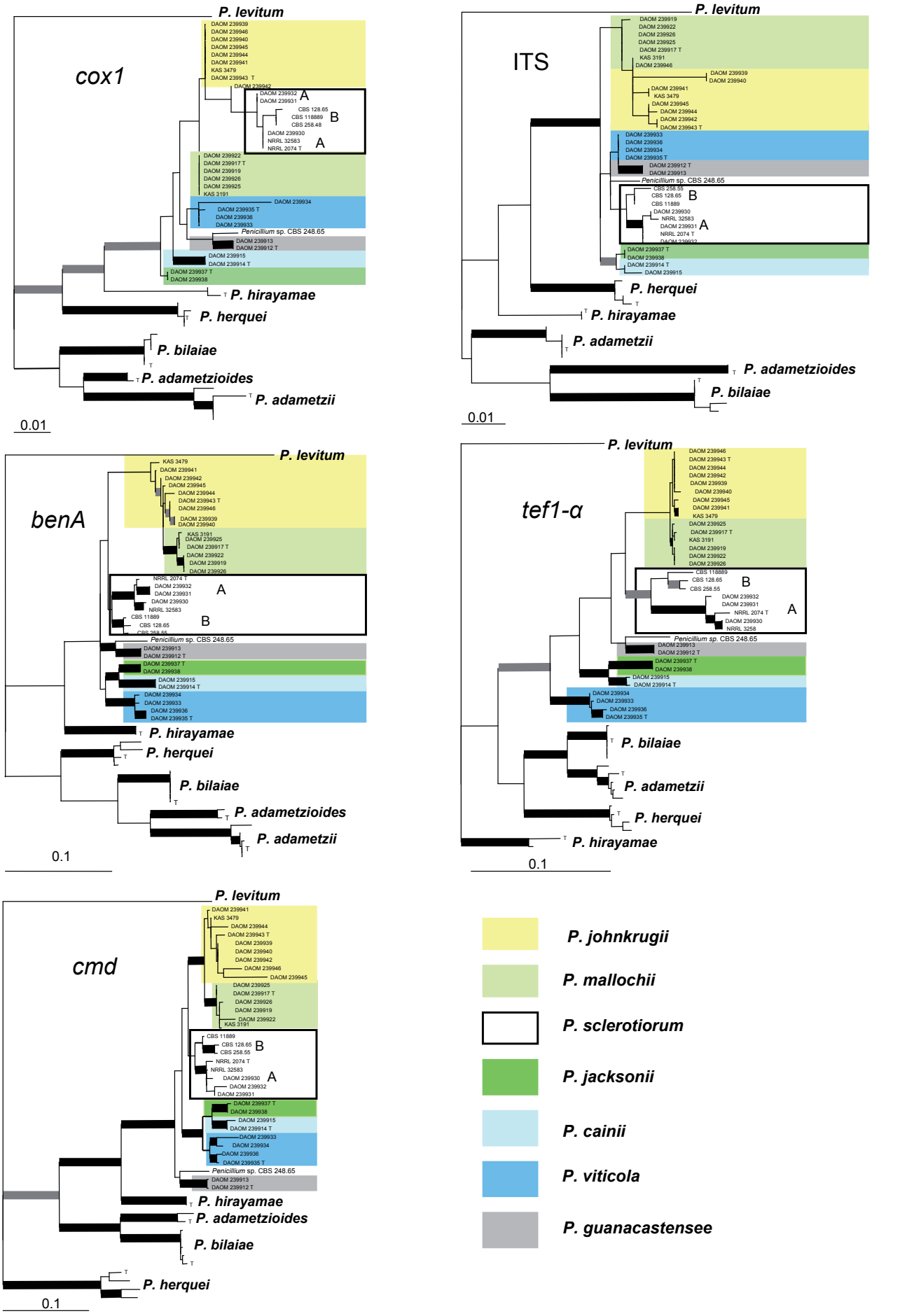

Fig. 1. Maximum likelihood (ML) trees generated for *cox1*, ITS, *benA*, *tef1-α* and *cmd* with PhyML using the GRT+G model (except *cmd*, GTR+I+G model), showing the clades representing the seven species of the *P. sclerotiorum* complex. Bold black branches have ML support > 0.90, MP bootstrap support > 90 %, and BI > 0.95; bold grey branches have ML support > 0.700, MP bootstrap support > 70 %, and BI > 0.95 (see Table 3 for details).

Table 3. Statistical support for species clades for individual gene trees using Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI).

		P. cainii	*P. guanacastense*	*P. jacksonii*	*P. johnkrugii*	*P. mallochii*	*P. sclerotiorum*		*P. viticola*
							A	B	
ITS	MP bootstrap (%)	< 70	92.00	< 70	< 70 *	< 70 *	85.00	< 70	< 70
	ML probability	0.82	0.99	0.93	0.718*	0.772*	0.19	0.76	0.49
	BI posterior probability	0.63	1.00	0.99	0.00	0.00	1.00	0.89	0.00
cox1	MP bootstrap (%)	98.00	96.00	92.00	0.00	< 70	< 70	< 70	72.00
	ML probability	1.00	1.00	1.00	0.237*	0.502*	0.00	0.00	0.79
	BI posterior probability	1.00	1.00	0.94	0.68*	0.99*	1.00	0.99	0.94
tef1-α	MP bootstrap (%)	100.00	100.00	100.00	<70	99.00	100.00	84.00	100.00
	ML probability	1.00	1.00	1.00	0.66	0.83	0.99	0.85	0.98
	BI posterior probability	1.00	1.00	1.00	0.55	0.95	1.00	0.86	1.00
benA	MP bootstrap (%)	100.00	100.00	100.00	< 70 *	< 70 *	99.00	100.00	100.00
	ML probability	1.00	1.00	1.00	1.00*	0.975*	1.00	1.00	1.00
	BI posterior probability	1.00	1.00	1.00	1.00*	1.00*	1.00	1.00	1.00
cmd	MP bootstrap (%)	100.00	100.00	100.00	<70	100.00	77.00	87.00	82.00
	ML probability	1.00	1.00	1.00	0.68	1.00	0.94	1.00	0.85
	BI posterior probability	1.00	1.00	1.00	0.92	1.00	1.00	1.00	0.99

* indicates analyses where *P. johnkrugii* and *P. mallochi*i were paraphyletic.

produced abundant sclerotia on all media, visible within 7 d. The colourful sclerotia often dramatically affect colony appearance, particularly, as occurs in *P. sclerotiorum*, when sclerotial colonies have much reduced, or absent, conidiation. *Penicillium cainii*, *P. guanacastense, P. jacksonii*, *P. mallochii,* and *P. viticola* strains produced no sclerotia on the media tested. All strains of all species were left for eight months in the dark at 25 °C on OA; ascospores were not produced in any of the sclerotial strains.

On MEA, several species, notably *P. guanacastense* and *P. mallochii*, have a tendency towards crustose colonies, with planar sheets of conidia dislodging *en masse* onto the Petri dish lid or slipping sideways across the agar. The phenomenon is less dramatic than in the terverticillate species *P. crustosum* and similar to that seen in monoverticillate species related to *P. glabrum.*

We included CREA to determine whether it had any diagnostic value for this group, but most strains of all species produced abundant acid, turning the entire plate yellow within 1 wk, and they did not produce any base to restore the original purple medium. All strains sporulated poorly and grew weakly or moderately. Only the slightly different but overlapping growth rates, and the presence of sclerotia, are recorded in the species descriptions. We do not consider this medium helpful for diagnosis in this group.

Phylogeny

Multigene phylogenetic analyses (ITS, *cox1, benA, cmd,* and *tef1-α*) revealed that strains previously identified as *P. sclerotiorum* comprise a complex of phylogenetically distinct species. The complex includes *P. sclerotiorum*, the newly described species in this paper, *P. cainii, P. jacksonii,* and *P. johnkrugii*, and the recently described *P. guanacastense, P. mallochii* (Rivera *et al.* 2011), and *P. viticola* (Nomura *et al.* 2011). Representative ML trees for each gene are presented in Fig. 1; the log likelihood values for these trees are *benA* -3725.72122, *cmd* -4537.96193, *cox1* -1919.56534, ITS -1846.917238, and *tef1-α* -4663.651570. The MP and BI trees are not shown, but differences in topology are discussed and support values for each analysis are mapped onto the ML trees and included in Table 3. Sequences were obtained for all genes and strains, except no *cmd* or *tef1-α* PCR products were obtained for the outgroup species *P. adametzii* and *P. adametzioides.* We experimented with denaturation temperatures as low as 40°C for 1 min, and for *cmd* with the primer combinations CF4 and CF5, CF4 and CMD6, and CMD5 and CF5 (Peterson *et al.* 2004, Hong *et al.* 2006), without success. Two strains of the outgroup species *P. herquei*, CBS 336.48^T and CBS 110644, yielded multiple bands after *benA* amplification; the most similar copy to that of the other species was selected for alignment.

In general, the trees of the two DNA barcode markers, ITS and *cox1,* were less resolved and although most species formed monophyletic groups in the strict consensus trees, bootstrap support was low for several (Table 3). Paraphyly was a problem with *P. johnkrugii* and *P. mallochii* in all analyses of these genes. Although both species formed coherent groups that could successfully be identified using these DNA barcodes, *P. mallochii* generally arose from within *P. johnkrugii*. However, these two species are easily distinguished morphologically by the presence or absence of sclerotia, and are ecologically distinct and geographically disjunct. All of the recognised species received strong support as distinct monophyletic clades in all *cmd* and *tef1-α* analyses. *BenA* was intermediate in providing better support for the species than ITS or *cox1*, but the issue of paraphyly of *P. johnkrugii* and *P. mallochii* remained. As noted below, *P. sclerotiorum* resolves into two clades in most analyses (except *cox1*), but we elected not to describe clade B as a distinct species because we did not have sporulating strains. Strain CBS 248.65, identified as *P. sclerotiorum*, did not group with the *P. sclerotiorum* ex-type group or any of the newly described species, and appears to represent a distinct species in the *P. sclerotiorum* complex. The strain did not produce the typical vivid orange to red reverse colony colours and sporulated poorly, and we elected to leave it undescribed pending the isolation of more vigorously sporulating strains. The PHT value for the combined data set for five genes was 0.0001, suggesting

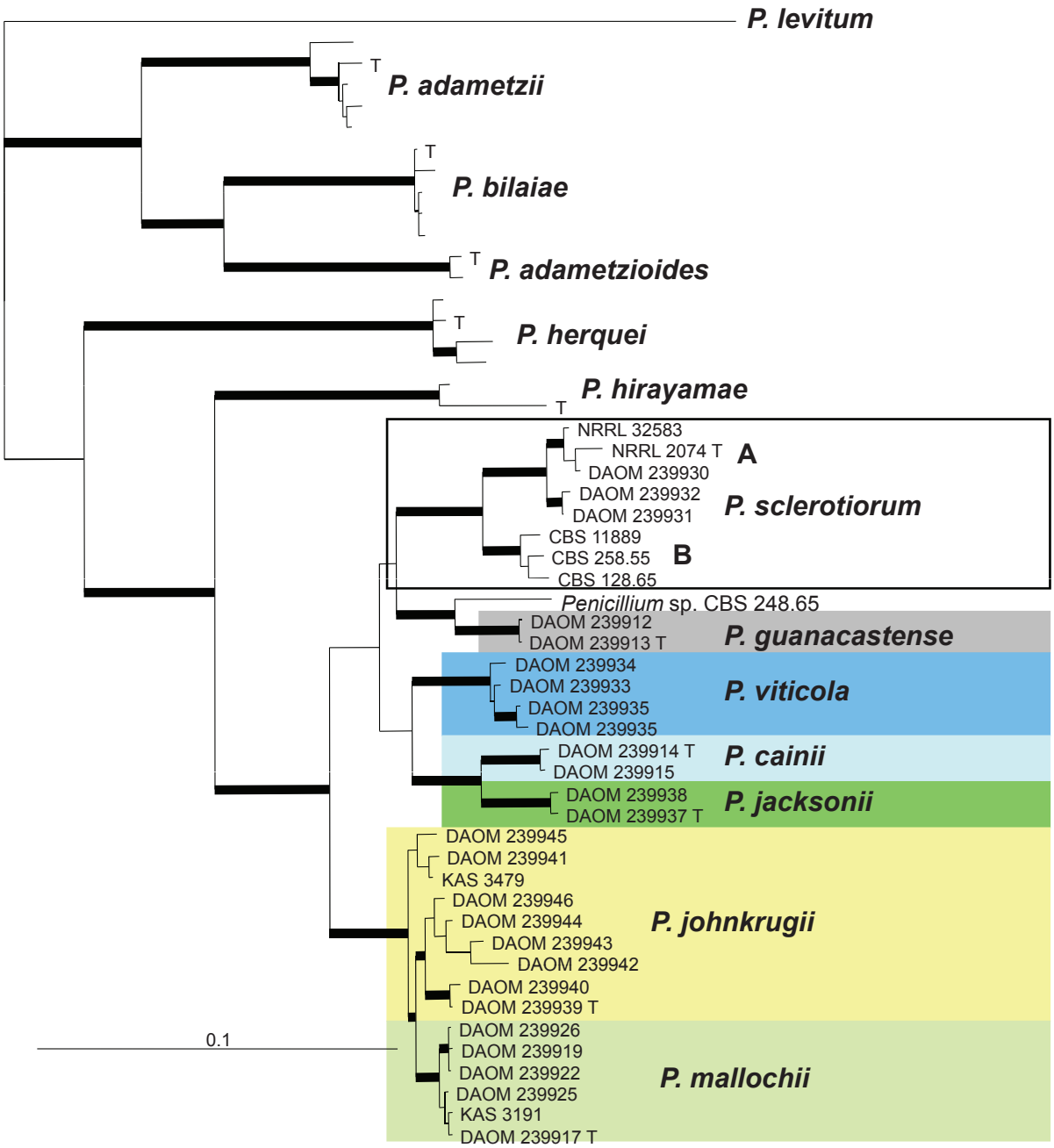

Fig. 2. Bayesian inference (BI) tree for the combined *cox1*, ITS, *BenA*, and *tef1-α* data set generated using MrBayes using the GTR model (except *cmd*, GTR+I+G model), showing the relationships among the seven species of the *P. sclerotiorum* complex. Bold black branches have ML support > 0.90, MP bootstrap support > 90 %, and BI > 0.95 (see Table 3 for details).

that the total combined data set was incongruent. Subsequent PHT analysis of gene pairs revealed that the *cmd* partition was incongruent with the other genes, and thus it was excluded from the construction of the Bayesian multigene phylogeny shown in Fig. 2. In all trees, *P. johnkrugii* and *P. mallochii* were siblings with strong statistical support. In the MP and BI trees, *P. sclerotiorum* and *P. guanacastense* were siblings, lacking strong statistical support (not shown), but in the ML tree (log likelihood -18058.213184), *P. sclerotiorum* was sibling to a clade including *P. cainii*, *P. jacksonii*, and *P. viticola*, again lacking strong statistical support. *Penicillium cainii* and *P. jacksonii* were consistently grouped together, with *P. viticola* as a sister group, all with strong statistical support.

We examined two of the species proposed as synonyms of *P. sclerotiorum* by Stolk & Samson (1983) and found that they did not belong to the revised complex. The ex-type strain of *P. adametzioides*, CBS 313.59, is sterile, and individual gene trees (Fig. 1) and the combined gene trees (Fig. 2) reveals that this is a distinct species, not part of the *P. sclerotiorum* complex, but still part of section *Sclerotiora* as defined by Houbraken & Samson (2011). Preliminary phylogenetic analyses with all five genes excluded the ex-type strain of *P. multicolor,* CBS 501.73, from the *P. sclerotiorum* complex, and BLAST results with *benA*, ITS, *tef1-α,* and *cmd* sequences had 100 % sequence similarity to *P. fellutanum*, classified by Houbraken & Samson (2011) in subgenus *Aspergilloides* section *Charlesii*. Morphologically, this strain grew slower, 13–15 mm after 7 d on all media, and lacked the vivid red to orange colony colours and vesiculate conidiophores usually observed in the *P. sclerotiorum* complex. We observed only monoverticillate conidiophores in the culture, not the metulate conidiophores emphasised in the description of *P. fellutanum* by Pitt (1980), but our strain of the ex-type was degenerated and sporulated poorly. *Penicillium multicolor* is not accepted as a synonym for *P. sclerotiorum* here, and it is probably a synonym of *P. fellutanum*.

TAXONOMY

Penicillium sclerotiorum J.F.H. Beyma, Zentralbl. Bakteriol., 2 Abt. 96: 416. 1937. MycoBank MB277708. Figs 3A, 4.

Colonies on CYA after 7 d at 25 ºC: 18–40 mm diam, low and velutinous, *ca.* 1 mm deep, with 8–11 sulcae and 2–3 wrinkles in some strains, sporulation dense in absence of sclerotia, very sparse or absent when orange sclerotia produced, conidia Greenish Grey (25–27E2), aerial mycelium sparse or absent, exudate moderately produced and light yellow in some strains, margin entire, reverse Orange to Reddish Yellow (3A7–4A6), Brown (7E4–8) or pale, some strains with darker colours turning orange towards the centre, vivid orange soluble pigments present in some strains. Colonies on CZ resembling those on CYA, 15–30 mm diam, with fewer sulcae, the sclerotia tending to be darker or reddish orange when present, exudate droplets light yellow to red when present, reverse less pigmented in some strains and then Yellowish White (1–4A2–3).

Colonies on MEA after 7 d at 25 ºC: 15–32 mm diam, planar, strictly velutinous when sporulating, orange sclerotia produced by some strains, in some strains with yellow sclerotia towards the centre, conidia of medium abundance, Grey (25–28D–F1) or Greyish Green (25–28C2), aerial mycelium sparse or absent, exudates not produced, margin entire, reverse Orange (6B7–8), Reddish Orange (7A–B7–8), Reddish Yellow (4A6) or Pale (1A2), soluble pigments not produced.

Colonies on YES after 7 d at 25 ºC: (20–) 33–38 (–44) mm diam, dense and with 16–20 sulcae and 6–8 wrinkles present in some strains, light orange and orange sclerotia present in some strains, conidia Turquoise Grey (24B–F2), Grey (27B1), Greenish Grey (25–27C–D2), with raised concentric rings of aerial mycelium, exudates not produced, margin entire, reverse Reddish Yellow (4A6–7), Orange (7C8) turning Pastel Yellow (3A4) near the margins or Pale Yellow (4A3), soluble pigments not produced.

Colonies on CREA after 7 d at 25 ºC: (13–) 20–28 mm diam, sclerotia present in some strains.

Conidiophores monoverticillate on MEA, borne directly from agar surface, stipes smooth to finely roughened, septate, (88–) 190–400 µm × 2–3 µm, unbranched, vesicles 4–7 µm wide (mean for different strains 4.6–5.9 ± 0.6). Phialides ampulliform to cylindrical, 8–11 × 2.5–3 µm, with short to long necks, periclinal thickenings not obvious. Conidia produced in columns, ellipsoidal, finely roughened, 2–3 µm diam (means for different strains = 2.5–3.0 ± 0.1 × 2–2.5 ± 0.1 µm, n = 25), mean L/W ratio 1.3:1. Sclerotia yellow, orange or reddish orange, subglobose to ellipsoidal, 180–320 µm diam; sclerotial cells 7–11 × 5–8 µm.

Habitat: Air, forest soil, berries of *Coffea arabica*.

Distribution: Asia (Indonesia), Australia, Pacifica (Hawai'i), but see notes below.

Typification: **Indonesia**, Java, Buitenzorg, isol. ex air, K.B. Boedijn, **holotype** IMI 40569 (not seen) **ex-type** NRRL 2074*, with equivalent culture collection numbers CBS 287.36, ATCC 10494. DNA barcodes: ITS JN626132, *cox1* JN626093.

Other cultures examined (Clade A): NRRL 32583, DAOM 239930, 239931*, 239932*. (Clade B): CBS 258.55, 126.65, 118889 (see Table 1).
* indicates sclerotium producing strains.

Notes: *Penicillium sclerotiorum* is the only species in the complex with clearly ellipsoidal conidia. About half the strains we examined produced orange sclerotia, and as noted above in the analysis of morphological characters, the ex-type strain produces abundant sclerotia in some transfers, and few or none in others. When sclerotia are observed, strains need only be compared with *P. johnkrugii,* which differs in colony colours on CYA and CZ, and by its subglobose conidia. Because of the revision of the complex here, it is difficult to evaluate the geographical distribution of *P. sclerotiorum* as reported in the literature. However, even from our limited sampling it is clear that this species is relatively widely distributed in tropical and subtropical areas, and that it is usually associated with soil. Similarly, as reviewed in more detail in the Discussion, the metabolites attributed to this morphological species need to be reevaluated in light of the revised species concept.

A phylogenetic division within *P. sclerotiorum* was suggested by all gene trees, the first comprising the ex-type group (marked A in Figs 1, 2), and group B comprising strains that did not produce conidia or sclerotia. We excluded the latter from our morphological description of *P. sclerotiorum* above, which thus describes Clade A. Description of Clade B as a new species may be warranted if sporulating strains can be isolated.

Penicillium cainii K.G. Rivera, Malloch & Seifert, **sp. nov.** MycoBank MB563159. Figs 3D, 5.

Etymology: Named for Roy F. Cain, a faculty member of the University of Toronto, a world authority on coprophilous Ascomycota, who was the Ph.D. supervisor of David Malloch and John Krug.

Coloniae in agaro CYA post 7 dies ad 25 °C 23–29 mm diam, conidia veneta vel viridia, exudatum flavum, in reverso flaviscentes vel flavi-brunneum. Coloniae in agaro MEA post 7 dies ad 25 °C 28–35 mm diam. Conidiophora monoverticillata vel raro metula singula, stipites 69–79 µm × 2.5–3 µm, parietibus asperulatis, ad apicem in vesiculam 4–6 µm latam inflati; metulae adsunt 31–34 µm longae. Cellulae conidiogenae phialidicae, ampulliformes, 7.5–10 × 2–3 µm. Conidia globosa vel subglobosa, levia vel plusminusve asperulata, 2.0–2.5 µm diam.

Colonies on CYA after 7 d at 25 ºC: 23–29 mm diam, dense and velutinous, *ca.* 1 mm deep, with 14–18 sulcae and 1–2 radial wrinkles in some strains, sclerotia absent, conidia medium in abundance, Deep Blue to Deep Green (23–27E2), 1–2 mm of white mycelia at the margin, clear yellow exudates produced moderately by some strains, margin entire, reverse Golden Yellow (5B7) and Brownish Yellow (5C8–9), Yellowish White (2–3A2) towards the edges, soluble pigments not produced, margin entire. Colonies on CZ after 7 d at 25 ºC: 18–21 mm diam, similar to colonies on CYA but lacking sulcae and radial wrinkles, conidia Turquoise Grey (24B–F2), with a concentric ring of paler shades of this colour towards the centre, margin entire, reverse Brownish Yellow (5–6C8), turning Yellowish Grey (3–4B2) towards the edges.

Colonies on MEA after 7 d at 25 ºC: 28–35 mm diam, planar, dense and velutinous, sclerotia not produced, conidia Greenish Grey (28E2) and Dull Green (27C–D2–4), aerial mycelium not present, exudate not produced, margin entire, reverse Orange to Dark Orange (5A–B8), Yellowish White (2–3A2) towards the edges, and soluble pigments not produced.

Colonies on YES after 7 d at 25 ºC: 31–34 mm diam, dense and velutinous, with 21–23 sulcae and 8–10 radial wrinkles, sclerotia not produced, conidia Greenish Grey (27D–F2), 2 mm of white mycelia at the margin, clear dark orange exudates droplets produced in negligible amounts in some strains, margin entire, reverse Brownish Orange to Reddish Orange (7B–D8), Greyish Brown (2B3) towards the edges, wrinkled towards the centre, soluble pigments not produced.

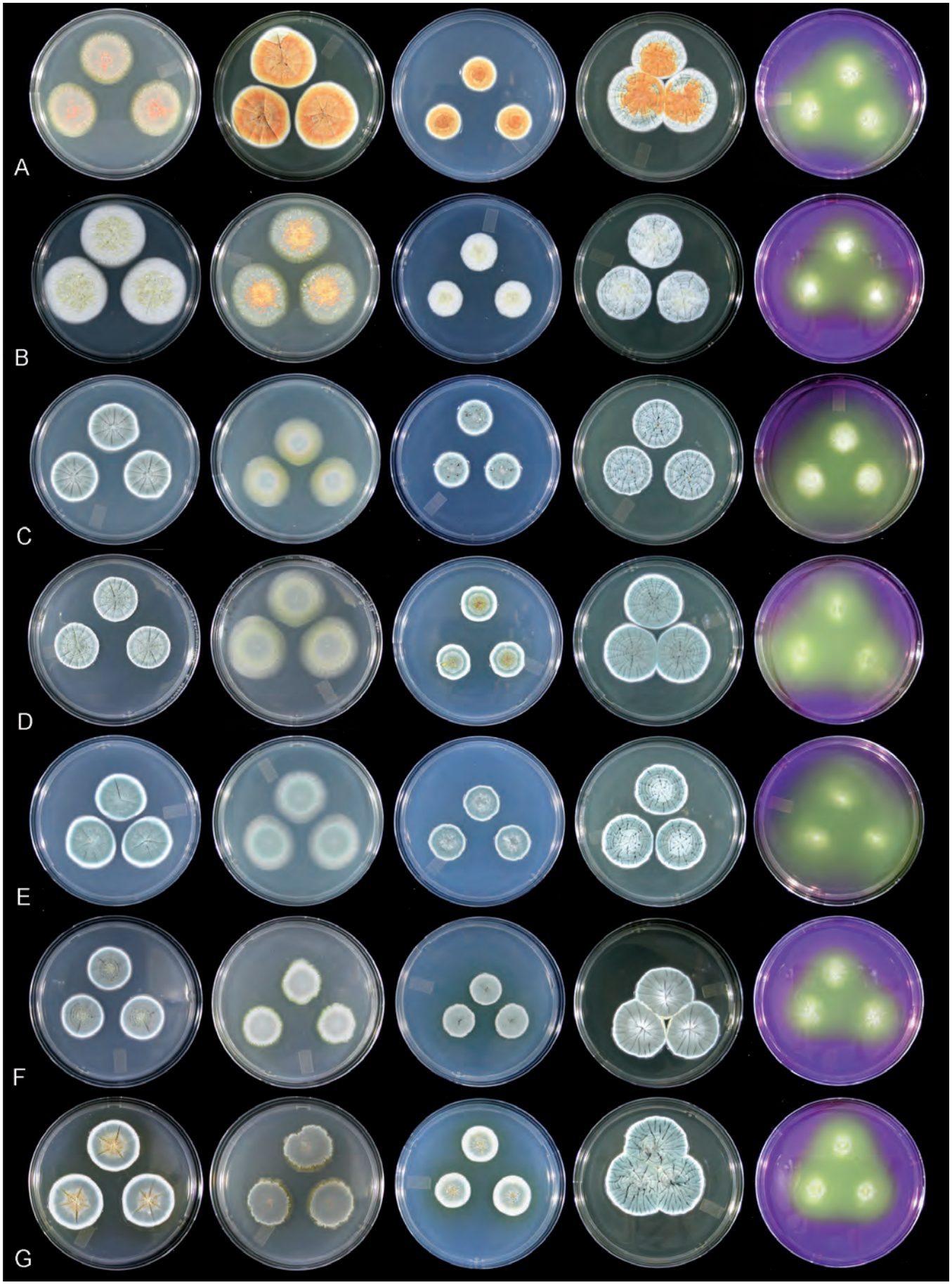

Fig. 3. Colonies of the seven species of the *P. sclerotiorum* complex grown for 7 d at 25 ºC on five media, right to left CYA, MEA, CZ, YES and CREA. A. *P. sclerotiorum*. B. *P. johnkrugii*. C. *P. viticola*. D. *P. cainii*. E. *P. jacksonii*. F. *P. mallochii*. G. *P. guanacastense*. All ex-type strains except A DAOM 239931, C DAOM 239935.

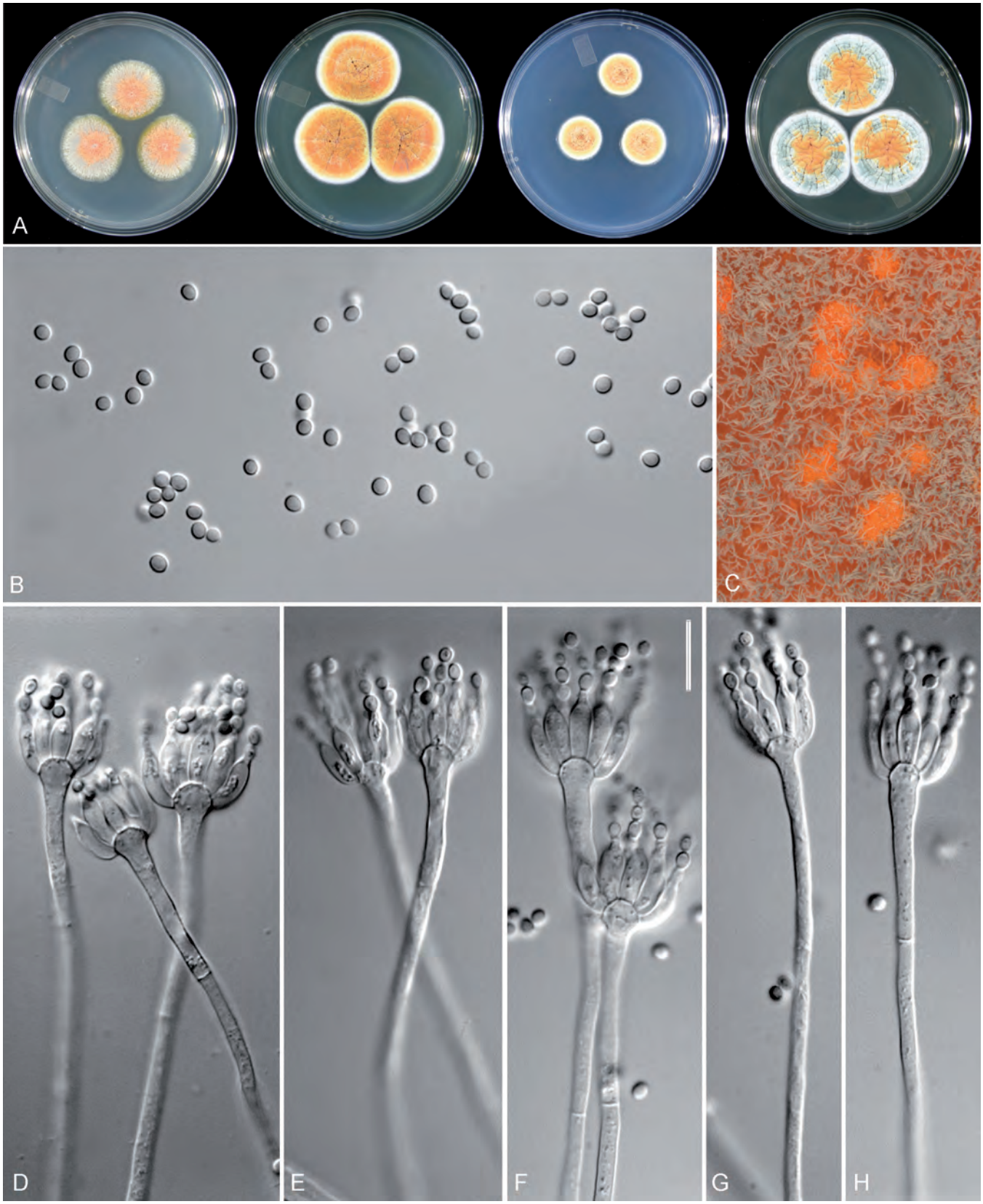

Fig. 4. *Penicillium sclerotiorum*, DAOM 239931. A. Colonies grown for 7 d on at 25 ºC CYA, MEA, CZ, YES. B. Conidia. C. Close-up of colony on MEA, showing conidial columns and orange hyphae around sclerotia. D–H. Conidiophores. Scale bar in F = 10 µm for all micrographs.

Colonies on CREA after 7 d at 25 ºC: (13–) 25–31 mm diam.

Conidiophores mostly monoverticillate on MEA, borne from agar surface, stipes rough-walled, septate, 70–80 µm × 2.5–3 µm, vesicle 3.5–5.0 µm wide, unbranched or in some strains with *ca*. 10 % of conidiophores with a single branch 31–34 µm long. Phialides ampulliform, 7.5–10 × 2–3 µm, with a distinguishable neck and inconspicuous periclinal thickening. Conidia globose, finely roughened, 2.0–2.5 µm diam (mean for different strains = 2.3–2.4 x 2.1–2.2 ± 0.035 µm), mean L/W ratio 1.07:1.

Habitat: Nuts of *Juglans nigra* and *Carya ovata*.

Distribution: North America (Canada: Ontario).

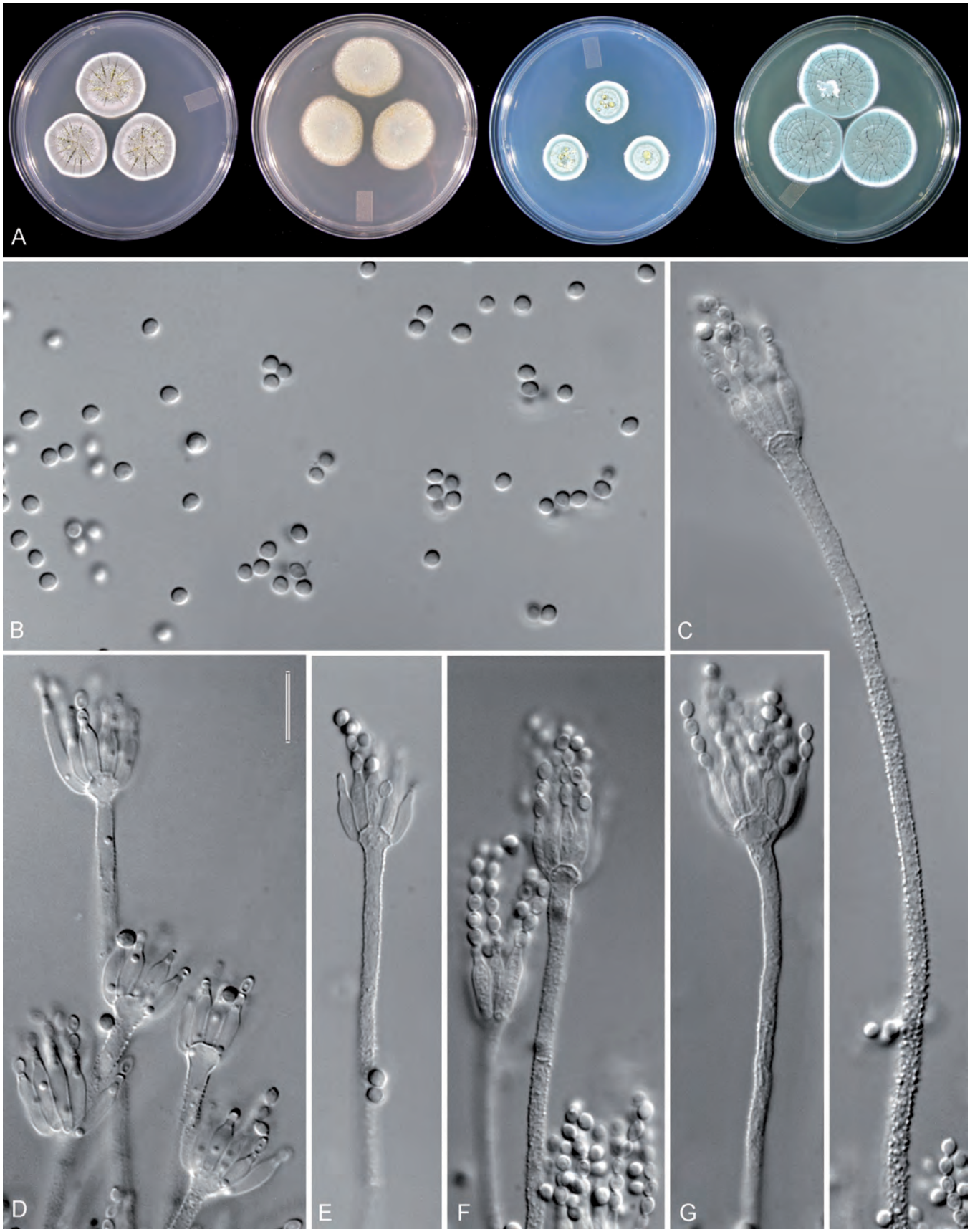

Fig. 5. *Penicillium cainii*. A. Colonies of DAOM 239915 grown for 7 d on at 25 ºC CYA, MEA, CZ, YES. B–G. Microphotographs of ex-type strain. B. Conidia. C–G. Conidiophores. Scale bar in D = 10 µm for all micrographs.

Typification: **Canada**, Ontario, Niagara, Niagara Falls, Fireman's Park, N43º 08' 49" W79º 07' 04, isol. ex nuts of black walnut, *Juglans nigra,* D. Malloch W-10, May 1996, **holotype** DAOM 239914 (dried culture). The **ex-type** strain has the same accession number and is maintained in the Canadian Collection of Fungal Cultures. DNA barcodes: ITS JN686435, *cox1* JN686412.

Other culture examined: Same location and date as type, isol. ex nuts of shagbark hickory, *Carya ovata,* D. Malloch W-15, DAOM 239915.

Notes: *Penicillium cainii* produces short conidiophores with conspicuously roughened stipes, and these microscopic characters combined with the substrate of nuts of various species of the family

Juglandaceae make the species easily recognisable. Neither strain produced sclerotia. Colonies resemble those of *P. sclerotiorum*, *P. mallochii*, *P. guanacastense*, and *P. viticola* on CYA, MEA, and YES, but colonies on CZ differ by the production of a concentric ring of a light shade of turquoise grey and clear yellow exudate droplets in the centre of the colony. The vesicles terminating the monoverticillate conidiophores tend to be more clavate than swollen, but this is a difficult character to interpet.

Penicillium jacksonii K.G. Rivera, Houbraken & Seifert, **sp. nov.** MycoBank MB563160. Figs 3E, 6.

Etymology: Named for H.S. Jackson, faculty member at the University of Toronto, an authority on rusts, but an avid collector of all fungi, and the Ph.D. advisor of R.F. Cain.

Coloniae in agaro CYA post 7 dies ad 25 °C 30–33 mm diam, conidia viridia, exudatum flavum, in reverso flaviscentes. Coloniae in agaro MEA post 7 dies ad 25 °C 31–37 mm diam. Conidiophora monoverticillata vel modice metula singula, stipites 83–134 × 2–3 µm, parietibus plusminusve asperulatis, apicem in vesiculam 3–6 µm latam inflati; metulae adsunt 28–48 µm longae. Cellulae conidiogenae phialidicae, ampulliformes, 6–5 (–13) × 2–3 µm. Conidia globosa vel subglobosa, levia vel plusminusve asperulata, 2.5–3 µm diam.

Colonies on CYA after 7 d at 25 ºC: 30–33 mm diam, dense and velutinous, *ca.* 1 mm deep, with 10–11 sulcae but no radial wrinkles, conidia produced abundantly, Deep Green (25–26E2), with concentric rings of paler shades of these colours, aerial mycelium present towards the centre, clear yellow exudate produced sparsely by some strains, with a margin 1–3 mm of white mycelia, margin entire, reverse Yellow (3A6–7), Vivid Yellow (2–3A8), or near the edges Yellowish White (2A2), soluble pigments not produced. Colonies on CZ after 7 d at 25 ºC: 19–23 (–30) mm diam, similar to colonies on CYA but lacking sulcae, conidia Greenish Grey (26–27E2), aerial mycelium present throughout the colony, one strain floccose near the centre, with 1–2 mm of white mycelia near the margin, reverse Brownish Yellow (5C8–9), Deep Yellow (4A8), Yellowish White towards the edges (1A2), soluble pigments not produced

Colonies on MEA after 7 d at 25 ºC: 31–37 mm diam, planar and velutinous, moderately dense, sporulation dense, conidia Dull Green (26–27E3), with concentric ring near the edges of paler shades of these colours, margin entire, reverse pale.

Colonies on YES after 7 d at 25 ºC: 30–32 mm diam, dense, velutinous, with 8–10 sulcae in the centre and 19–23 sulcae at the margin, and 6–9 radial wrinkles, sporulation good, conidia Greenish Grey (25E2), with concentric rings of paler shades of this colour present in some strains, aerial mycelia absent or white patches present occasionally, margin entire, reverse Yellowish White (3A2) or Reddish Yellow (4A6), soluble pigments not produced.

Colonies on CREA after 7 d at 25 ºC: 26–33 mm diam.

Conidiophores monoverticillate and/or once-branched on MEA, borne from agar surface, stipes smooth to rough, septate, 80–135 × 2–3 µm, vesicle 3–6 µm wide (mean for different strains 4.4–4.7 ± 0.4 µm), in some strains all unbranched, in others with *ca*. 65 % of conidiophores with a single branch 28–48 µm long. Phialides ampulliform, 6–5(–13) × 2–3 µm wide, with distinguishable collarette and inconspicuous periclinal thickening. Conidia globose, walls finely roughened, 2.5–3 µm diam (mean for different strains 2.8 × 2.5–2.6 ± 0.035 µm), mean L/W ratio 1.1:1.

Habitat: Forest soil.

Distribution: Queensland, Australia.

Typification: **Australia**, Queensland, Barrine Lake, S17° 15' 1" E145° 38' 7" E, isol. from soil pretreated with ethanol, Sept. 2006, leg. J. Houbraken, L. Janson, **holotype** DAOM 239937 (dried culture). The **ex-type** strain has the same accession number and is maintained in the Canadian Collection of Fungal Cultures. DNA barcodes: ITS JN686437, *cox1* JN686414.

Other culture examined: Same data as type, DAOM 239938.

Notes: *Penicillium jacksonii* produces short conidiophores, but otherwise has few microscopic characters that clearly distinguish it from related species. It is unusual in the *P. sclerotiorum* complex for the production of a high proportion of conidiophores with a single branch, but this is an inconsistent character and some transfers are strictly monoverticillate. Colonies of *P. jacksonii* colonies are similar to those of *P. mallochii*, *P. guanacastense*, *P. viticola,* and *P. cainii* on CYA, MEA, and on YES, but the conidia are perhaps the darkest green of the species. The most closely related species, *P. cainii* (Fig. 2), has conspicuously roughened conidiophores.

Penicillium johnkrugii K.G. Rivera, Houbraken & Seifert, **sp. nov.** MycoBank MB563161. Figs 3B, 7, 8.

Etymology: Named for John Krug, faculty member at the University of Toronto and a research associate at the Royal Ontario Museum (ROM). Like his PhD supervisor, RF Cain, he was a specialist on coprophilous fungi, but also an avid lichen collector. He introduced KGR to the world of fungal taxonomy.

Coloniae in agaro CYA post 7 dies ad 25 °C 30–38 mm diam, alba, conidia sparsa, sclerotia abundans, grisea vel aurantia, *ca*. 135–550 × 130–430 µm, exudatum plusminusve flavum, in reverso aurantiae vel flaviscentes. Coloniae in agaro MEA post 7 dies ad 25 °C 26–36 mm diam. Conidiophora monoverticillata, stipites 88–229 µm × 2–2.5 µm, parietibus plusminusve asperulatis, apicem in vesiculam 4–6 µm latam inflati. Cellulae conidiogenae phialidicae, ampulliformes, 7–11 × 2–3(–5) µm. Conidia globosa vel subglobosa, levia vel plusminusve asperulata, 2–3 µm diam.

Colonies on CYA after 7 d at 25 ºC: 30–38 mm diam, planar, surface mycelia White (1–3A1), *ca*. 1 mm deep, with 5–9 sulcae and 2–3(–9) radial wrinkles, sclerotia white, conidia not produced, light yellow exudate droplets produced in low to moderate amounts, margin entire, reverse Reddish Yellow to Orange (4–6AB7–8) and Yellowish Grey (3–4B2) towards the edges, stellate with radial wrinkles, soluble pigments absent. Colonies on CZ after 7 d at 25 ºC: 15–23 mm diam, occasionally 10–19 mm diam, velutinous and dense, 4–6 sulcae and 1–2 radial wrinkles present in some strains, sclerotia white, with sparse to negligible sporulation, conidia Greenish Grey (25–27D2), light yellow exudates droplets sparsely produced, reverse Yellow to Deep Yellow (3A6–8) and Orange (5–6B8), some strains Yellowish White (3A3) or Pastel Yellow (3A4) towards the centre, soluble pigments absent.

Colonies on MEA after 7 d at 25 ºC: 26–36 mm diam, planar, low and velutinous, sclerotia orange, yellow towards the centre, and white towards the margin, conidia Greenish Grey (24–27DE 3–5), conidia and sclerotia sectoring in some strains, aerial mycelium not present, exudates not produced, margin entire, reverse Orange (5–6B8), Vivid Yellow (3A8), Yellowish Grey (3–4B2) towards the centre, soluble pigment not produced.

Colonies on YES after 7 d at 25 ºC: 28–38 mm diam, velutinous, with 11–17 sulcae and 6–10 radial wrinkles, sclerotia white, sporulation poor, conidia Greenish Grey (25D2), yellow exudate droplets produced sparsely by some strains, white mycelia

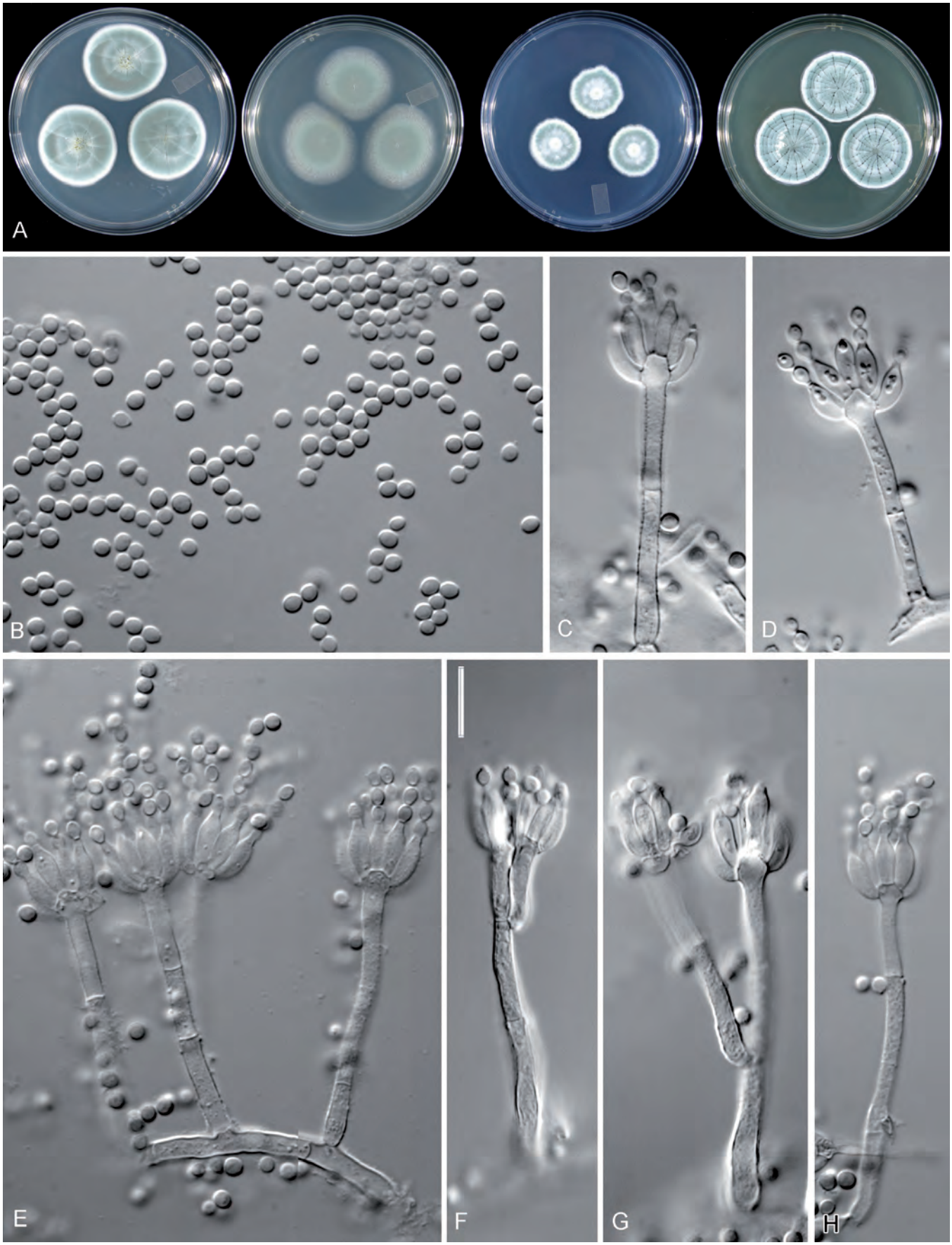

Fig. 6. *Penicillium jacksonii*. A. Colonies of DAOM 239938 grown for 7 d on at 25 ºC CYA, MEA, CZ, YES. B–H. Microphotographs of ex-type strain. B. Conidia. C–H. Conidiophores. Scale bar in F = 10 µm for all micrographs.

at the marginal 1 mm, margin entire, reverse Yellow (3A3–4) and Orange (5–6B8), some strains Pastel Yellow (3A3–4) towards the edges, stellate with radial wrinkles or wrinkled, soluble pigments not produced.

Colonies on CREA after 7 d at 25 ºC: 14–22 mm diam, sclerotia present.

Conidiophores strictly monoverticillate on MEA, borne from agar surface, stipes smooth to finely roughened, septate, 85–230

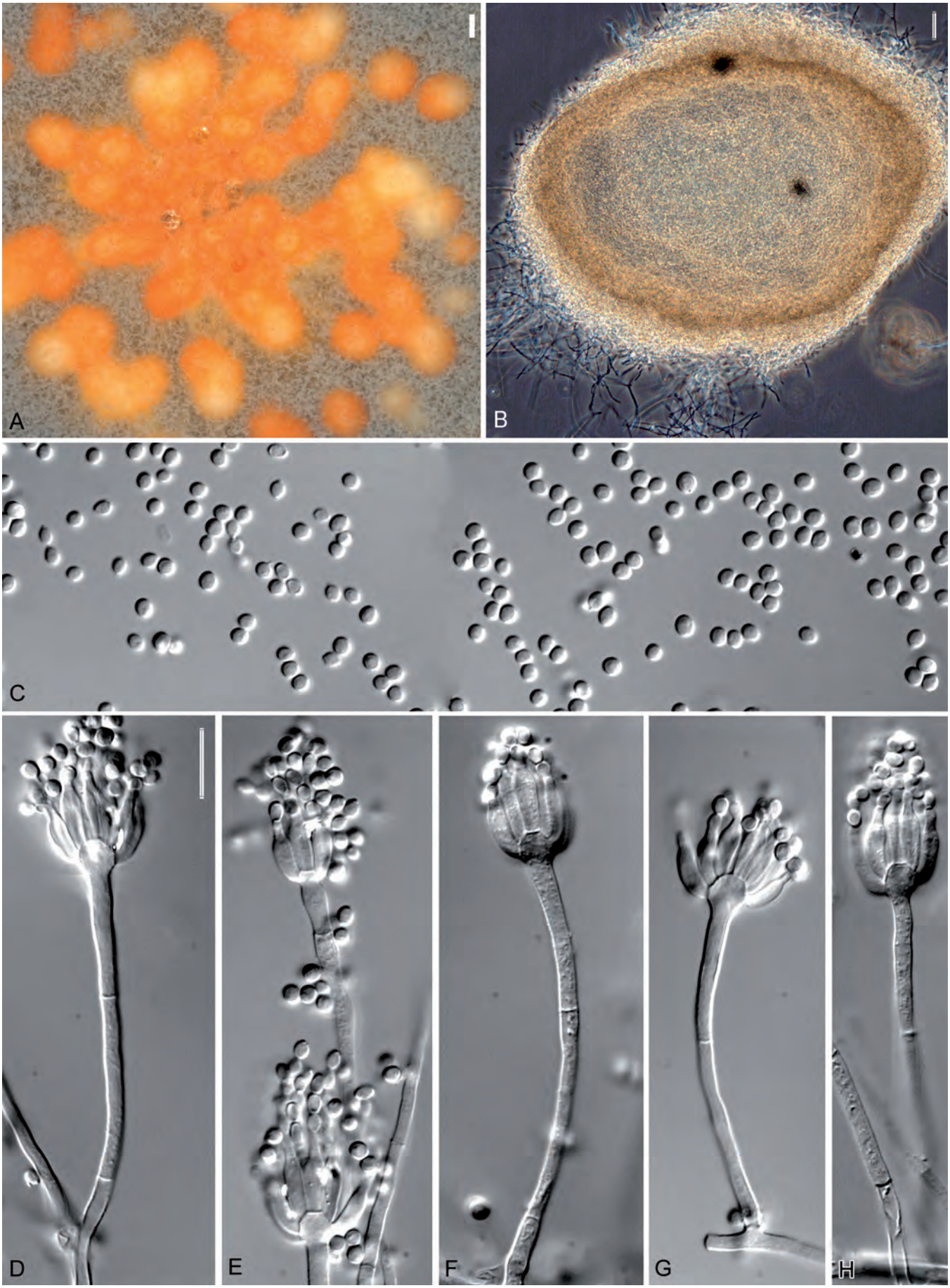

Fig. 7. *Penicillium johnkrugii*, ex-type strain A. Sclerotia on MEA. B. Micrograph of sclerotium. C. Conidia. D–H. Conidiophores. Scale bars A = 200 µm, B = 20 µm, in D = 10 µm for micrographs (C–H).

× 2–2.5 µm, vesiculate, 4–6 µm wide (means for different strains 4.6–5.4 ± 0.3). Phialides ampulliform to cylindrical, 7–11 × 2–3(–5) µm, with short to distinguishable necks, periclinal thickenings not obvious. Conidia globose to subglobose, finely roughened, 2–3 µm

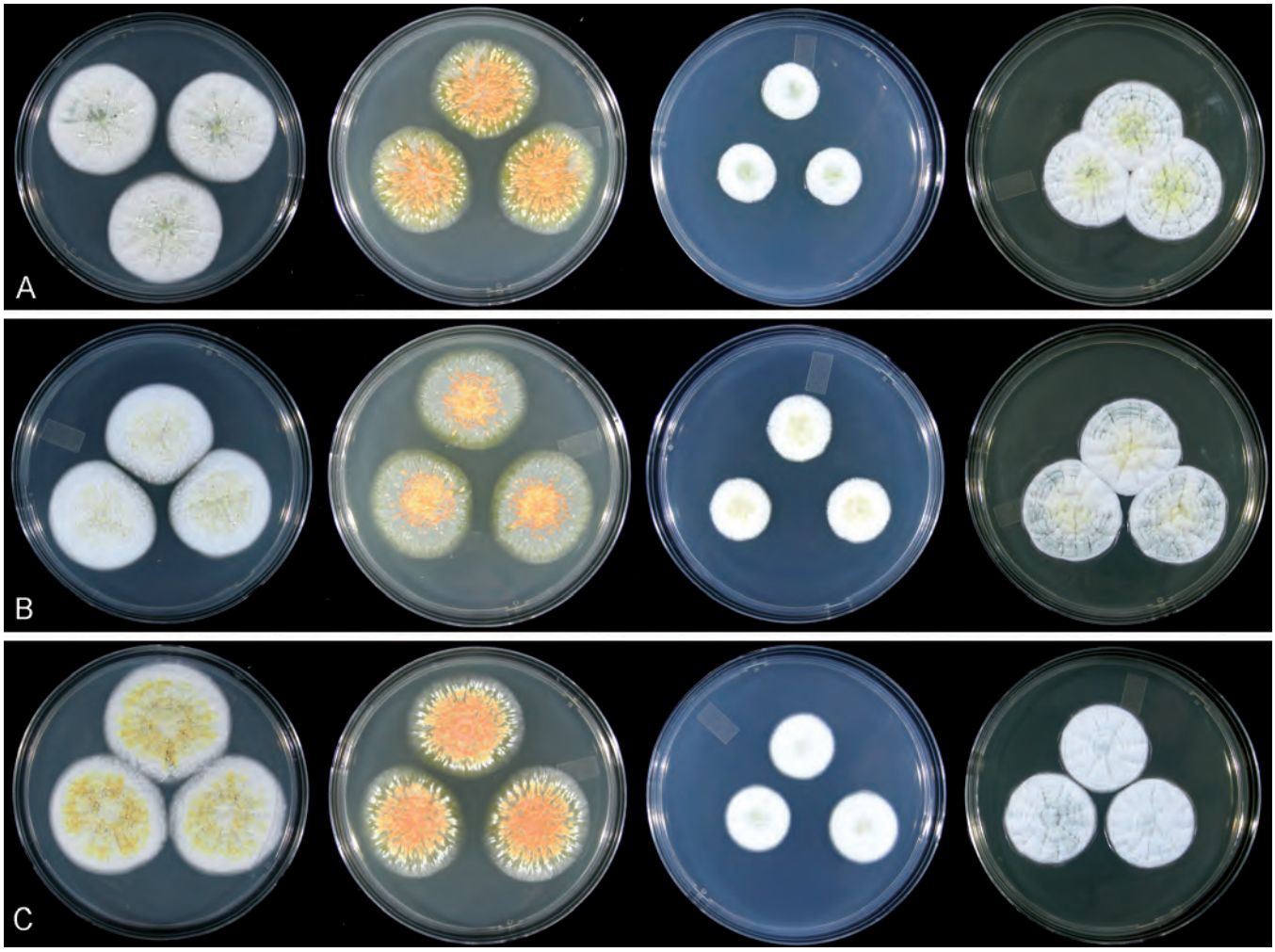

Fig. 8. *Penicillium johnkrugii*, three strains grown for 7 d on at 25 ºC CYA, MEA, CZ, YES. A. DAOM 239942. B. DAOM 239943 (T). C. DAOM 239944.

diam (means for different strains 2.7–2.9 ± 0.01 × 2.3–2.5 ± 0.01 µm, n = 25), mean L/W ratio 1.1:1. Sclerotia produced on all media, subglobose to ellipsoidal, at first white, becoming orange or yellow, 136–552 × 131–433 µm, sclerotial cells 5–8 × 3–6 µm.

Habitat: Forest soil.

Distribution: Langkawi, Malaysia.

Typification: **Malaysia**, Kedah, Langkawi, N 6° 19' 24" E 99° 51' 45", isol. ex soil after ethanol treatment, Nov. 2007, leg. R.A. Samson, isol. J. Houbraken, **holotype** DAOM 239943 (dried culture). The **ex-type** strain has the same accession number and is maintained in the Canadian Collection of Fungal Cultures. DNA barcodes: ITS JN686447, *cox1* JN686424.

Other cultures examined: Same data as type and presumably from the same soil sample, DAOM 239939, DAOM 239940, DAOM 239941, DAOM 239942, DAOM 239944, DAOM 239945, DAOM 239946.

Notes: *Penicillium johnkrugii* is distinct within the *P. sclerotiorum* complex for its production of white colonies and abundant grayish sclerotia on CYA and CZ; on other media, the sclerotia tend to be yellow or orange. The species is morphologically similar to *P. sclerotiorum*. Both have vivid yellow to orange reverse colony colours although *P. johnkrugii* differs by subglobose conidia and more conspicuously vesiculate conidiophores.

Penicillium johnkrugii and *P. mallochii* were paraphyletic in some analyses of *benA, cox1,* and ITS. Monophyletic recognition of the species occurred in all *tef1-α* analyses, and in the MP and ML trees for ITS, and ML and BI trees for *cmd*. Despite these phylogenetic issues, all genes provided diagnostic sequences for *P. johnkrugii,* and the species is morphologically distinct.

The strain DAOM 239944 did not cause any colour changes when grown on CREA.

Penicillium viticola Nonaka & Masuma, Mycoscience 52: 339. 2011. MycoBank MB516048. Figs 3C, 9.

Colonies on CYA after 7 d at 25 ºC: 26–30 (–36) mm diam, dense and velutinous, *ca*. 1 mm deep, with 6–13(–17) sulcae and 2–3 radial wrinkles, sclerotia absent, conidia Greenish Grey (25–27E2), with Bluish Grey (22D–F2) concentric rings, pale yellow exudate droplets produced sparsely by some strains, with white aerial mycelium in the central 2–3 mm and marginal 2–3 mm, margin entire, reverse Light Yellow (5C8), Yellowish Grey (3–4B2), Orange Grey (6B7–8), sometime Yellowish Grey (3–4B2) or Yellowish White (1A2–3) near the margin, stellate with some radial wrinkles, soluble pigments not produced. Colonies on CZ after 7 d at 25 ºC: 17–25 mm diam, similar to those on CYA, but some strains floccose at the centre, with 5–6 sulcae and 2–3 wrinkles in some strains, mycelia at margin 1–2 mm, reverse Reddish Yellow (4A7) and Brownish Yellow (5C8) in some strains.

Colonies on MEA after 7 d at 25 ºC: 23–35 (–40) mm diam, planar and moderately dense, velutinous, sclerotia not observed, conidia Greenish Grey (25–27E2), aerial mycelium not observed, exudates not produced, margin entire, reverse Orange Yellow to Orange (4–6B7–8), Brownish Orange (7C7–8), Pastel Yellow

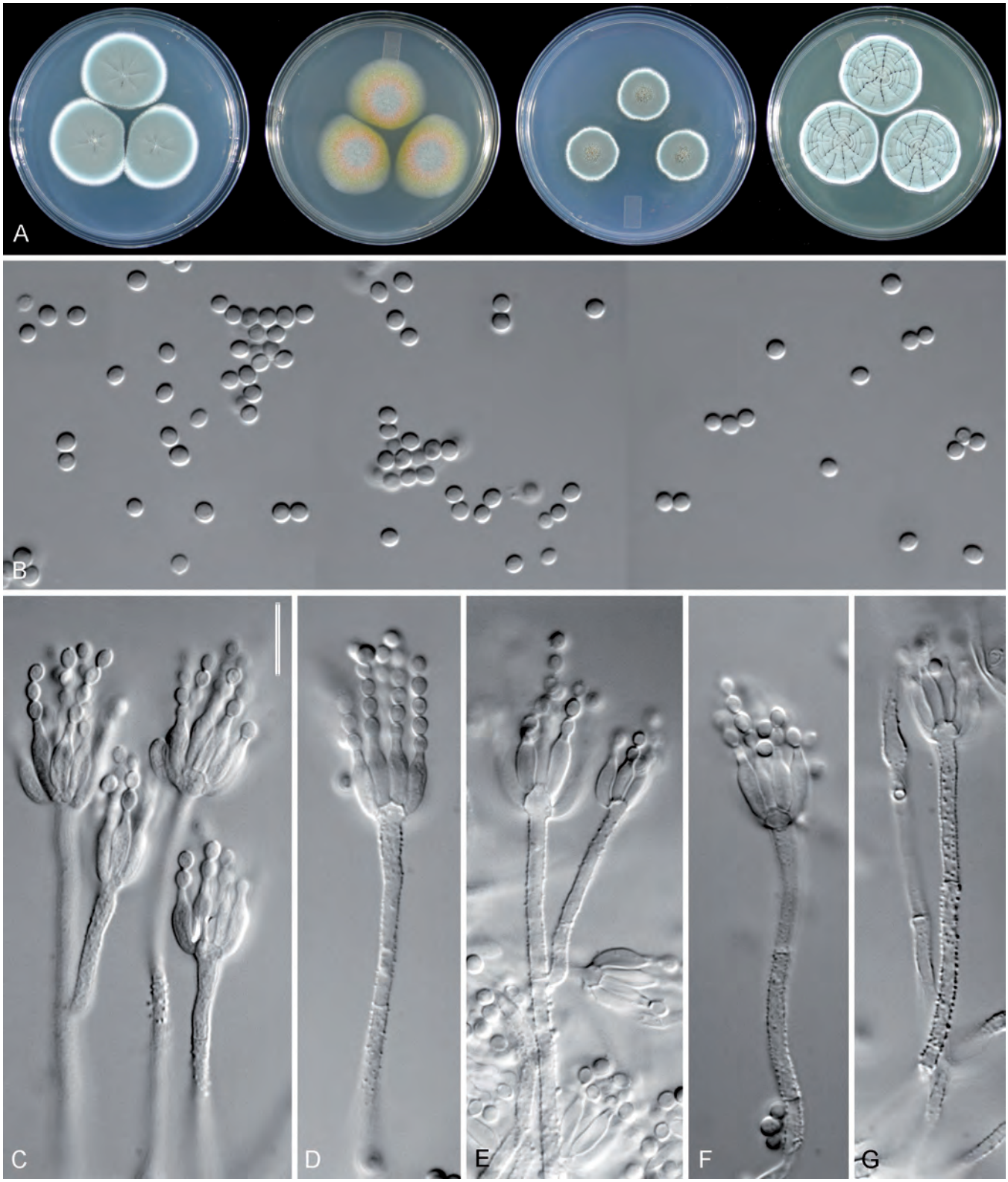

Fig. 9. *Penicillium viticola*. A. Colonies of DAOM 239933 grown for 7 d on at 25 ºC CYA, MEA, CZ, YES. B–G. Microphotographs of DAOM 239935. B. Conidia. C–G. Conidiophores. Scale bar in C 10 µm for all micrographs.

or Reddish Yellow (4A6–7) near the edges, soluble pigment not produced.

Colonies on YES after 7 d at 25 ºC: 29–33 mm diam, less commonly 34–36 mm diam, dense and velutinous, densely sulcate, especially near the edges (with 15–21 sulcae), with 7–9 radial wrinkles, sclerotia not produced, conidia Greenish Grey (25–26D–E2) and Turquoise Grey (24D2), concentric rings of different shades of turquoise grey present in some strains, white mycelia 2–3 mm at margins, clear vivid yellow exudate droplets produced sparsely by some strains, margin entire, reverse Reddish Yellow (7B8), Orange (6B8), Greyish Yellow (2–4B3), some strains Yellowish Grey (2B–C3) or Dull Yellow (3B3–4) towards the edges, wrinkled towards the centre with visible sulcae and radial wrinkles towards the margin, soluble pigment not observed.

Colonies on CREA after 7 d at 25 ºC: 23–29 mm diam.

Conidiophores predominantly monoverticillate on MEA, borne from agar surface, stipes rough, septate, 30–135 × 2–3 µm wide, moderately vesiculate, vesicles 4–6 µm wide (means for different strains 4.6–5.0 ± 0.3 µm), mostly unbranched, sometimes with about 10 % of conidiophores with a single branch 22–55 × 2–3 µm

wide. Phialides ampulliform, 7–10 × 2–3 µm, with a distinguishable collarette. Conidia borne in columns, globose, smooth, 2–3 µm diam (means for different strains 2.6–2.7 × 2.3–2.6 ± 0.01 µm), mean L/W ratio 1.1:1.

Typification: **Japan**, Yamanashi, isol. ex grape (*Vitus* sp.), 11 Jul 2006, K. Nonaka, **holotype** TNS-F-38702, **ex-type** culture JCM 17636 = FKI-4410 (not seen). DNA barcode: ITS AB606414 (Nonaka *et al*. 2011).

Other cultures examined: DAOM 239933, DAOM 239934, DAOM 239935, DAOM 239936, see Table 1 for details.

Habitat: Rainforest soil, and vines of *Vitus* sp.

Distribution: Asia (Japan), Australia (Queensland).

Notes: *Penicillium viticola* produces short, rough-walled conidiophores, slightly less roughened than those of the closely related species *P. cainii*, but rougher than all other species of the complex. The colony characters of *P. viticola* colony morphology resemble those of *P. mallochii*, *P. guanacastense*, *P. cainii*, and *P. sclerotiorum* on CYA and MEA. On CZ, it resembles *P. mallochii* and *P. guanacastense*. Microscopically it lacks the more vesiculate conidiophore apices observed in *P. mallochii*, *P. guanacastense,* and *P. sclerotiorum*.

Penicillium viticola was described by Nonaka *et* al. (2011) when our own revision was completed, and we were unable to examine the type strain. Their description matches ours in most respects, with only minor differences in growth rates, colony colours and exudate production that may be attributed to subtle variations in media. The published calmodulin tree in Nonaka *et al*. (2011) inadvertently included a mislabeled sequence for *P. viticola* that indicated a relationship with *P. angulare*; the sequence deposited by the authors (AB540173) is correct (R. Masuma, pers. comm.). With the *benA* sequence for the type strain (AB540174), this species is firmly established as a member of the *P. sclerotiorum* complex, and conspecific with our Australian strains, as it is treated here.

Iwatsuki *et al.* (2010) reported the production of tropolone compounds by the ex-type strain of *P. viticola* (in the publication named only as *Penicillium* sp.), including the anti-malarial compound puberulic acid, stipitatic acid and their novel analogues, viticolins A–C.

DISCUSSION

The *Penicillium sclerotiorum* complex now includes seven phylogenetically distinct but morphologically similar species. In this paper, three species in the *P. sclerotiorum* complex were described, added to the two species recently described from Costa Rica (*P. guanacastense, P. mallochii*; Rivera *et al.* 2011) and one recently described from Japan (*P. viticola*, Nonaka *et al.* 2011). Members of the complex can be recognised by the general suite of characters used by previous authors to delineate the species, namely moderately fast growing colonies on CYA and MEA, with a tendency to produce orange or reddish colony reverses, monoverticillate conidiophores with some conidiophores having a single branch, vesiculate conidiophore apices, and globose to ellipsoidal conidia in greyish green, dull green, or turquoise green colours. Careful examination of colony and microscopic characters revealed subtle morphological differences among species. The species differ by some conidial colours, variation in the roughening of the stipe, stipe lengths, and inconspicuously in the extent of vesiculation of the conidiophore apex and in conidial shape. Sclerotia are produced abundantly and consistently by *P. johnkrugii*, in most but not all fresh strains of *P. sclerotiorum,* and have not been seen in the other species. Sclerotium production is a difficult taxonomic character, because they may be constant or inconstant within a species or even a strain. Physiological experiments with *Aspergillus caelatus* show that a pH of 6–10 and temperatures of 28–30 ºC are optimal for sclerotia formation, production peaks at a C:N ratio of 8.6, and the sugar used in CYA (sucrose) suppresses production by 12 % (McAlpin 2004). Similar results have been seen in other *Aspergillus* species (Rudolph 1962), *Sclerotinia rolfsii* (Wheeler & Sharan 1965), and *Verticillium* species (Wyllie & DeVay 1970).

Five of the species so far have restricted geographical distributions, but sampling is still very meagre. *Penicillium johnkrugii* was isolated from soil from Langkawi, Malaysia, *P. jacksonii* from soil from Queensland, Australia, *P. cainii* from nuts collected in Niagara Falls, Ontario, while *P. mallochii* and *P. guanacastense* were isolated from the guts of two different caterpillar families reared in the Área de Conservación Guanacaste, Costa Rica. *Penicillium sclerotiorum* has the broadest known distribution (Table 1), while *P. viticola* has a disjunct distribution (soil from Australia, grapes from Japan) that hints at a broader distribution and a so-far undefined ecology.

Extrolite profiling is a common practice for characterising *Penicillium* species and contributed significantly to developing polyphasic species concepts in *Penicillium* subgenus *Penicillium* (Frisvad & Samson 2004). We were unable to study extrolites in this study, but there are indications that the *P. sclerotiorum* complex may be metabolically diverse, providing further characters for delimiting these morphologically similar species. Secondary metabolites with antibacterial and antifungal activities were reported for some strains identified as *P. sclerotiorum sensu lato,* including the antimicrobial compounds sclerotin (Curtin & Reilly 1940), isochromphilone VI and pencolide (De Lucca *et al.* 2008). Pairet *et al.* (1995) reported two azapholines from *P. sclerotiorum* as antagonists of endothelin-A and endothelin-B receptors, vasoconstriction peptides implicated in hypertension, heart and renal failure, ischemia, and cerebral vasospasms. We could not trace strains from these studies and therefore it is unclear what phylogenetic species produce these compounds. As noted above, only the production of puberulic acid, stipitatic acid and viticolins A–C can be attributed with any certainly to the phylogenetically defined *P. viticola,* but only the ex-type has been examined for these metabolites (Iwatsuki *et al.* 2010).

Phylogenetic analyses using maximum parsimony, maximum likelihood, and Bayesian inference algorithms, and DNA sequence data *benA*, ITS, *cox1*, *tef1-α,* and *cmd*, gave consistent results. The less variable genes did not provide robust statistical support for all species of the complex, but the results did not conflict with the other gene trees. The recognised species generally conform to the Genealogical Concordance Phylogenetic Species Recognition (Taylor *et al*. 2000) concept, although some of the species are only represented by two strains. There were problems with paraphyly of *P. johnkrugii* and *P. mallochii* in some *benA, cox1,* and ITS analyses, but all five genes yielded species specific sequences for all species, and each species formed a cohesive (if not strictly monophyletic) group that reaffirmed the species concepts proposed here. We have listed accession numbers of ITS and *cox1* barcodes in the paragraphs on Typification above, although all tested genes would work as barcodes in this complex.

The partition homogeneity test (PHT) indicated that the *cmd* was incongruent with the other genes, and this gene was not included

in combined phylogenetic analyses. Incongruency in phylogenetic signal between genes suggests different evolutionary histories for these genes (Scott *et al.* 2006). Visual comparisons of the *cmd* results suggest that the variable position of *P. guanacastense* within the ingroup, and a generally discordant arrangement of outgroups, probably led to the failure of the PHT. From the perspective of recognising phylogenetic species, the species groupings remained constant for all genes. From the perspective of accurately determining sister group relationships among species, the rejection of *cmd* is unfortunate.

The designation of *P. adametzioides* and *P. multicolor* as synonyms of *P. sclerotiorum,* as proposed by Stolk & Samson (1983), was not accepted here. *Penicillium adametzioides* is a distinct phylogenetic species, also noted by Peterson (2000) and accepted by Houbraken & Samson (2011). According to our molecular data, *P. multicolor* is a synonym of *P. fellutanum*, but the degenerated morphology of the ex-type strain we examined leaves this conclusion tentative.

KEY TO SPECIES

1. Conidiophore stipes distinctly roughened 2
1. Conidiophore stipes at most finely roughened 3

2. On CYA conidial colours with a blue tinge, colonies usually less than 30 mm diam; on nuts ..... *P. cainii*
2. On CYA, conidia colours lacking blue tinge, colonies 26–36 mm diam; on grape vines or in soil ..... *P. viticola*

3. Sclerotia produced 4
3. Sclerotia not produced 5

4. Colonies on CYA white, sclerotia white or grey, turning orange on MEA; conidia globose or subglobose ..... *P. johnkrugii*
4. Colonies on CYA with obvious green areas, sclerotia orange; conidia subglobose to ellipsoidal ..... *P. sclerotiorum*

5. Associated with caterpillars feeding on leaves in the neotropics; colonies on MEA crustose 6
5. Soilborne; colonies on MEA not crustose 7

6. Associated with Saturnid caterpillars; conidiophores 50–380 µm long ..... *P. mallochii*
6. Associated with Noctuid caterpillars; conidiophores 85–100 µm long ..... *P. guanacastense*

Note: Colony photographs of *P. guanacastense* and *P. mallochii* on CYA, MEA, CZ, YES and CREA are included in Fig. 3; the species are described in Rivera *et al.* (2011).

7. Colony reverse colours on CYA and MEA pale; some strains with > 50 % of conidiophores with a single branch, other strains all monoverticillate; conidia globose ..... *P. jacksonii*
7. Colony reverse colours on CYA and MEA yellow, orange or in vivid red colours; conidiophores strictly monoverticillate; conidia subglobose to ellipsoidal ..... *P. sclerotiorum* (non-sclerotial strains)

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Phylogeny and nomenclature of the genus *Talaromyces* and taxa accommodated in *Penicillium* subgenus *Biverticillium*

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Abstract: The taxonomic history of anamorphic species attributed to *Penicillium* subgenus *Biverticillium* is reviewed, along with evidence supporting their relationship with teleomorphic species classified in *Talaromyces.* To supplement previous conclusions based on ITS, SSU and/or LSU sequencing that *Talaromyces* and subgenus *Biverticillium* comprise a monophyletic group that is distinct from *Penicillium* at the generic level, the phylogenetic relationships of these two groups with other genera of *Trichocomaceae* was further studied by sequencing a part of the *RPB1* (RNA polymerase II largest subunit) gene. *Talaromyces* species and most species of *Penicillium* subgenus *Biverticillium sensu* Pitt reside in a monophyletic clade distant from species of other subgenera of *Penicillium*. For detailed phylogenetic analysis of species relationships, the ITS region (incl. 5.8S nrDNA) was sequenced for the available type strains and/or representative isolates of *Talaromyces* and related biverticillate anamorphic species. Extrolite profiles were compiled for all type strains and many supplementary cultures. All evidence supports our conclusions that *Penicillium* subgenus *Biverticillium* is distinct from other subgenera in *Penicillium* and should be taxonomically unified with the *Talaromyces* species that reside in the same clade. Following the concepts of nomenclatural priority and single name nomenclature, we transfer all accepted species of *Penicillium* subgenus *Biverticillium* to *Talaromyces*. A holomorphic generic diagnosis for the expanded concept of *Talaromyces*, including teleomorph and anamorph characters, is provided. A list of accepted *Talaromyces* names and newly combined *Penicillium* names is given. Species of biotechnological and medical importance, such as *P. funiculosum* and *P. marneffei,* are now combined in *Talaromyces*. Excluded species and taxa that need further taxonomic study are discussed. An appendix lists other generic names, usually considered synonyms of *Penicillium sensu lato* that were considered prior to our adoption of the name *Talaromyces*.

Key words: anamorph, DNA phylogeny, single name nomenclature, teleomorph, *Trichocomaceae*.
Taxonomic novelties: Taxonomic novelties: New species – *Talaromyces apiculatus* Samson, Yilmaz & Frisvad, sp. nov. **New combinations and names** – *Talaromyces aculeatus* (Raper & Fennell) Samson, Yilmaz, Frisvad & Seifert, *T. albobiverticillius* (H.-M. Hsieh, Y.-M. Ju & S.-Y. Hsieh) Samson, Yilmaz, Frisvad & Seifert, *T. allahabadensis* (B.S. Mehrotra & D. Kumar) Samson, Yilmaz & Frisvad, *T. aurantiacus* (J.H. Mill., Giddens & A.A. Foster) Samson, Yilmaz, & Frisvad, *T. boninensis* (Yaguchi & Udagawa) Samson, Yilmaz, & Frisvad, *T. brunneus* (Udagawa) Samson, Yilmaz & Frisvad, *T. calidicanius* (J.L. Chen) Samson, Yilmaz & Frisvad, *T. cecidicola* (Seifert, Hoekstra & Frisvad) Samson, Yilmaz, Frisvad & Seifert, *T. coalescens* (Quintan.) Samson, Yilmaz & Frisvad, *T. dendriticus* (Pitt) Samson, Yilmaz, Frisvad & Seifert, *T. diversus* (Raper & Fennell) Samson, Yilmaz & Frisvad, *T. duclauxii* (Delacr.) Samson, Yilmaz, Frisvad & Seifert, *T. echinosporus* (Nehira) Samson, Yilmaz & Frisvad, comb. nov. *T. erythromellis* (A.D. Hocking) Samson, Yilmaz, Frisvad & Seifert, *T. funiculosus* (Thom) Samson, Yilmaz, Frisvad & Seifert, *T. islandicus* (Sopp) Samson, Yilmaz, Frisvad & Seifert, *T. loliensis* (Pitt) Samson, Yilmaz & Frisvad, *T. marneffei* (Segretain, Capponi & Sureau) Samson, Yilmaz, Frisvad & Seifert, *T. minioluteus* (Dierckx) Samson, Yilmaz, Frisvad & Seifert, *T. palmae* (Samson, Stolk & Frisvad) Samson, Yilmaz, Frisvad & Seifert, *T. panamensis* (Samson, Stolk & Frisvad) Samson, Yilmaz, Frisvad & Seifert, *T. paucisporus* (Yaguchi, Someya & Udagawa) Samson & Houbraken *T. phialosporus* (Udagawa) Samson, Yilmaz & Frisvad, *T. piceus* (Raper & Fennell) Samson, Yilmaz, Frisvad & Seifert, *T. pinophilus* (Hedgcock) Samson, Yilmaz, Frisvad & Seifert, *T. pittii* (Quintan.) Samson, Yilmaz, Frisvad & Seifert, *T. primulinus* (Pitt) Samson, Yilmaz & Frisvad, *T. proteolyticus* (Kamyschko) Samson, Yilmaz & Frisvad, *T. pseudostromaticus* (Hodges, G.M. Warner, Rogerson) Samson, Yilmaz, Frisvad & Seifert, *T. purpurogenus* (Stoll) Samson, Yilmaz, Frisvad & Seifert, *T. rademirici* (Quintan.) Samson, Yilmaz & Frisvad, *T. radicus* (A.D. Hocking & Whitelaw) Samson, Yilmaz, Frisvad & Seifert, *T. ramulosus* (Visagie & K. Jacobs) Samson, Yilmaz, Frisvad & Seifert, *T. rubicundus* (J.H. Mill., Giddens & A.A. Foster) Samson, Yilmaz, Frisvad & Seifert, *T. rugulosus* (Thom) Samson, Yilmaz, Frisvad & Seifert, *T. sabulosus* (Pitt & A.D. Hocking) Samson, Yilmaz & Frisvad, *T. siamensis* (Manoch & C. Ramírez) Samson, Yilmaz & Frisvad, *T. sublevisporus* (Yaguchi & Udagawa) Samson, Yilmaz & Frisvad, *T. variabilis* (Sopp) Samson, Yilmaz, Frisvad & Seifert, *T. varians* (G. Sm.) Samson, Yilmaz & Frisvad, *T. verruculosus* (Peyronel) Samson, Yilmaz, Frisvad & Seifert, *T. viridulus* Samson, Yilmaz & Frisvad.

INTRODUCTION

The modern concept of *Penicillium* (referred to in this paper as *Penicillium sensu lato*), was derived from the pioneering monographic revisions of Thom (1930), Raper & Thom (1949), and formalised by the recognition of four subgenera, *Aspergilloides*, *Furcatum*, *Penicillium* and *Biverticillium* by Pitt (1980). Over the past decade, the realisation has grown that *Penicillium* subgenus *Biverticillium* is phylogenetically distinct from other subgenera of *Penicillium* and that this distinctiveness should be reflected in its formal taxonomy. Because of their usually symmetrical, biverticillate conidiophores, the group has been recognised since Wehmer (1914) segregated them in an informal subdivision of *Penicillium* that he called "Verticillatae". The delineation, species composition and taxonomic rank of this group were modified in subsequent monographs by Thom (1930), Raper & Thom (1949), Pitt (1980), and Ramírez (1982), culminating in the widespread recognition of subgenus *Biverticillium* and the use of this name in many taxonomic and phylogenetic studies. Malloch (1985), based on a consideration of morphological and ecological factors, and anamorph-teleomorph connections, may have been the first to speculate that subgenus *Biverticillium* should be removed from *Penicillium* as a separate genus.

The teleomorph genera historically associated with *Penicillium sensu lato* are *Talaromyces* and *Eupenicillium* (in single name nomenclature, the latter is now considered a synonym of

Penicillium sensu stricto, see Houbraken & Samson 2011). The teleomorphs of these two groups produce distinctive ascomata. In *Talaromyces,* the soft ascomatal walls are comprised of multiple layers of interwoven hyphae and the ascomata mature quickly, usually within a few weeks in agar culture. In *Penicillium sensu stricto,* the sclerotium-like ascomata have rigid walls of thick-walled, isodiametric cells and the ascomatal maturity can take months and often ascospores do not form at all. Furthermore, in *Talaromyces* the ascus initials sometimes have morphologically distinguishable gametangia and the mature asci are produced in chains (Stolk & Samson 1972), while the ascomatal initials in *Penicillium sensu stricto* are irregularly interwoven, loosely branched hyphae masses (Emmons 1935), and the mature asci are single. Raper & Thom (1949) already recognised that there was considerable evidence that *Penicillium* subgenus *Biverticillium* constituted a natural and homogenous group. A comparison of the anamorphs of these two teleomorph types reveals a correlation with phialide shape, with anamorphs of *Talaromyces* (until now classified in *Penicillium* subgenus *Biverticillium*) having narrower phialides that are aculeate or lanceolate, and anamorphs in *Penicillium sensu stricto* having broader, ampulliform or flask-shaped phialides. One consequence of the differences in phialide shape is that the symmetrical nature of the conidiophores of species allied with *Talaromyces* tends to be emphasised, because in general the phialides are more densely packed. The colonies of subgenus *Biverticillium* can often be distinguished from those of *Penicillium sensu stricto* by the naked eye. They often have darker green conidia, more or less yellow pigmented and encrusted aerial hyphae, and colony reverses in yellow, orange or red to purplish red shades.

Once DNA-based studies of fungal phylogeny began, it quickly became apparent that the differences between *Penicillium sensu stricto* and *Talaromyces* were more than a matter of degree, and that there might be a significant problem with the generic concept of *Penicillium sensu lato*. *Penicillium sensu stricto* and *Talaromyces* occur as distinct clades within *Trichocomaceae,* which could be considered subfamilies (LoBuglio *et al.*, 1993, LoBuglio & Taylor 1993). Using small subunit nuclear ribosomal DNA sequences (18S), Berbee *et al.* (1995) showed that *Penicillium* is polyphyletic if subgenus *Biverticillium* is included, a conclusion reconfirmed in one of the first reviews of the impact of molecular phylogenetics on Ascomycete taxonomy (Sugiyama 1998) using an analysis of 18S rDNA sequences. Removal of subgenus *Biverticillium* transforms *Penicillium sensu stricto* into a monophyletic group. This dichotomy between *Penicillium sensu stricto* and *Talaromyces* was shown repeatedly in studies employing nuclear ribosomal RNA genes, for example by Peterson (2000), who analysed a combination of the nuclear ribosomal internal transcribed spacer regions (ITS) and large subunit ribosomal DNA (28S) sequences (Ogawa *et al*. 1997, Ogawa & Sugiyama 2000), and by Wang & Zhuang (2007) in a phylogeny based on calmodulin sequences. The results of these analyses are all confirmed in the multigene phylogenetic analyses presented elsewhere in this volume by Houbraken & Samson (2011), using genes selected for their ability to accurately reflect molecular phylogeny. As indicated by Houbraken & Samson (2011), when other genera assigned to *Trichocomaceae* are included in phylogenetic analyses, the division between subgenus *Biverticillium* and *Penicillium sensu stricto* becomes even clearer. In that study, intervening genera include *Aspergillus*, *Paecilomyces sensu stricto* (with *Byssochlamys* as a synonym), and several small and less well-known genera such as *Thermoascus*, *Penicilliopsis, Thermomyces* and the recently described *Rasamsonia* (Houbraken *et al.* 2011).

In a molecularly defined, phylogenetically accurate taxonomic system, maintaining subgenus *Biverticillium* in *Penicillium sensu stricto* is untenable. However, almost every aspect of the biology, biochemistry, and physiology of these two groups emphasises their fundamental distinctiveness, although sometimes with limited taxon sampling. For example, Pitt (1980) emphasised the distinctiveness of subgenus *Biverticillium* by using a low water-activity medium, G25N (which includes 25 % glycerol) in his standard plating regime. Strains assigned to this subgenus grow slowly on this medium, less than 10 mm diam at 25 °C in 7 d, whereas species of the other subgenera are more xerophilic and grow faster. Cell-wall components seem to differ significantly. Leal & Bernabé (1998) reported on the complex glucomannogalactan components of the water soluble polysaccharide fraction of several species of *Trichocomaceae*, suggesting that a characteristic heteropolysaccharide composed of 4 galactose: 1 mannose: 1 glucose was unique to species of subgenus *Biverticillium*. Species of *Penicillium sensu stricto* species were characterised by the presence of a β-(1-5)(1-6)-galactofuran polysaccharide in the same fraction. Cell wall components as reflected by their exoantigens were screened in about 50 species of *Penicillium sensu lato* using an ELISA reaction to antibodies raised to *P. digitatum* (subgenus *Penicillium*). These antibodies reacted well with all the species of subgenera *Furcatum, Penicillium* and *Aspergilloides*, but did not react with the four species of subgenus *Biverticillium* tested (*P. funiculosum, P. islandicum, P. rubrum, and P. tardum*) (Notermans *et al.* 1998). Kuraishi *et al*. (1991) first noted that the pattern of ubiquinones in *Penicillium sensu lato* and showed a distinct pattern in subgenus *Biverticillium*. Paterson (1998) examined 335 strains and 118 species of *Penicillium sensu lato* and determined that the Q9 ubiqinone type was predominant in the species of *Penicillium sensu stricto*. In contrast, species of *Talaromyces, Trichocoma* and subgenus *Biverticillium* had different versions of the Q10 ubiquinone type. Exceptions to these patterns can be explained by the small number of species whose classification in, or elimination from, subgenus *Biverticillium* has been uncertain or controversial. Frisvad *et al*. (1990a) provided an overview of the extrolites of *Talaromyces* species, and demonstrated the occurrence of characteristic extrolites such as mitorubins, bisanthaquinones such as rugulosin and skyrin, vermicellin, vermistatin, vermiculine, duclauxin and glauconic acid. None of these compounds were found in cultures of *Penicillium sensu stricto* (Frisvad *et al*. 1990b).

The soon to be published *International Code of Nomenclature for Algae, Fungi and Plants* removes the primacy of teleomorph- over anamorph-typified names, leaving both kinds of names competing equally for priority (Norvell 2011). Because of these changes, we apply the principle of 'one fungus - one name' and in the nomenclatural revision, priority is given to the oldest genus and species name irrespective of whether they were originally described for teleomorphs or anamorphs (Hawksworth *et al*. 2011). In this respect, *Penicillium* returns to the single named, but pleomorphic, nomenclatural and taxonomic system used by many of the founders of its taxonomy, and actively promoted by the Peoria school (Thom 1930, Raper & Thom 1949). *Talaromyces,* now also defined as a pleomorphic genus, is adopted for the anamorphic species formerly included in *Penicillium* subgenus *Biverticillium.* In this study, the phylogenetic relationships of species of subgenus *Biverticillium* and other members of the *Trichocomaceae* were studied by sequencing a part of the *RPB1* (RNA polymerase II largest subunit) gene. Furthermore, we discuss the taxonomy and nomenclature of species of this expanded concept of *Talaromyces,* based on phylogenetic, phenotypic and extrolite data. For detailed

phylogenetic analysis below genus level, the ITS regions (including the 5.8S nrDNA) of ex-type strains and/or representatives were sequenced. As discussed below, this paper is not meant as a monographic treatment, because many complexes have not yet been studied comprehensively.

MATERIALS AND METHODS

Sources of cultures

The fungi examined include type strains or representatives of all available species of *Talaromyces* and *Biverticillium*. The strains are maintained in the CBS-KNAW Fungal Biodiversity Centre (CBS) culture collection and an overview of strains used for phylogenetic analysis is shown in Table 1. In a few cases, the ex-type strain was unavailable and sequence data present in GenBank were used.

Morphology and physiology

Cultures were grown for 7 d on Czapek agar, Czapek yeast autolysate agar (CYA), oatmeal agar (OA) and/or malt extract agar (MEA) plates at 25 °C or, if required, another temperature. Medium compositions follow Samson *et al.* (2010). Cultures were grown for up to 3 wk for ascomata production.

Extrolite analysis

Nearly all species described in the genera *Penicillium sensu lato* (including those formerly classified in *Eupenicillium*), *Penicillium* subgenus *Biverticillium, Talaromyces*, *Aspergillus* and its many associated teleomorphic genera, and *Paecilomyces* (including those formerly or still classified in the associated teleomorph genus *Byssochlamys*) were analysed qualitatively for their profiles of secondary metabolites as determined by HPLC with diode array detection. Many strains of each species were examined, whenever available, but in some cases only the ex-type culture was available. Cultures were inoculated on the media CYA, MEA (Blakeslee formula, using Difco malt extract), YES agar (Samson *et al*. 2010, Difco yeast extract) and OA. All cultures were analysed chemically using three agar plugs from a 7 d old culture grown at 25 °C (Smedsgaard 1997). Different methods were used for HPLC analysis, but the methods were essentially based on Frisvad & Thrane (1987, 1993). Since 1997, the method for Nielsen & Smedsgaard (2003) was used and after 2010 the UPLC method of Nielsen *et al*. (2011) was applied. Metabolites were identified via their diode-array based UV-VIS spectra and in some cases by their mass spectra, and by comparison to authenticated standards (Nielsen *et al.* 2011).

For the extrolites analyses, the biosynthetic families of the sampled genera were compared using UPGMA cluster analysis (NTSYS version 2.11). All metabolites were classified according to biosynthetic families; for example the viridicatin biosynthetic family consists of cyclopenol, cyclopenin, cyclopeptin, dehydrocyclopeptin, viridicatin, viridicatol and 3-methoxyviridicatin (Turner & Aldridge 1983). This family was scored as one character in the cluster analysis. The exometabolites were also combined into biosynthetic families and tabulated as such. For example, many species of *Talaromyces* and *Penicillium* subgenus *Biverticillium* produce the azaphilones mitorubrin, mitorubrinal, mitorubrinol, mitorubrinol acetate, mitorubrinic acid, funicone, deoxyfunicone, actofunicone, 3-O-methylfunicone, kasanosin A and B, diazaphilonic acid, and wortmin; they are here collectively called the mitorubrins, while the related metabolites vermistatins and penicidones are called vermistatins (see Šturdíková *et al*. 2000, Nicoletti *et al*. 2009, Osmanova *et al*. 2010). Some chlorinated azaphilones such as helicusins (Yoshida *et al*. 1995) and luteusins (Fujimoto *et al*. 1990, Yoshida *et al*. 1996a, b) are epimers of the sclerotiorins from *P. sclerotiorum*, and are treated as two families, albeit closely related to the mitorubrins.

DNA extraction, amplification and sequencing

Isolates used for molecular studies were grown on MEA for 7–14 d at the required temperature prior to DNA extraction. DNA was extracted from the cells using the UltraClean™ Microbial DNA Kit (MoBio Laboratories), following the protocols of the manufacturer. A part of the *RPB1* gene was amplified to study the phylogenetic relationships among *Penicillium* and other related genera. This fragment was amplified using the primer pair RPB1-F1843 5'-ATTTYGAYGGTGAYGARATGAAC-3' and RPB1-R3096 5'-GRACRGTDCCRTCATAYTTRACC-3' (Houbraken & Samson 2011). Primer RPB1-F1843 corresponds with position 1490–1512 of GenBank no. XM_002146871 (*P. marneffei*, ATCC 18224) and RPB1-R3096 corresponds with position 2610–2633. An addition primer, RPB1-R2623 5'-GCRTTGTTSARATCCTTMARRCTC-3' was occasionally used as an internal primer for sequencing (Houbraken & Samson 2011). The ITS regions were sequenced to study the relationship among *Talaromyces* and the related biverticillate anamorphic species. Fragments containing the ITS region were amplified using primers V9G (de Hoog & Gerrits van den Ende 1998) and LS266 (Masclaux *et al*. 1995). Sequencing reactions were performed with the Big Dye Terminator Cycle Sequencing Ready Reaction Kit v. 3.1 (Applied Biosystems) and carried out for both strands to ensure consistency of the consensus sequence.

Data analyses

For the DNA sequence analyses, alignments were performed using the software Muscle as implemented in the MEGA5 programme (Tamura *et al*. 2011). The RAxML (randomised accelerated maximum likelihood) software (v. 7.2.8, Stamatakis *et al*. 2008) was used for the Maximum Likelihood (ML) analysis. The robustness of trees in the ML analyses was evaluated by 100 bootstrap replications. The phylogram based on *RPB1* sequences is rooted with *Coccidioides immitis* (strain RS; full genome strain), and *Trichocoma paradoxa* (CBS 788.83) is used as an outgroup in the ITS analysis.

RESULTS

Phylogenetic generic delimitation of *Talaromyces* and biverticillate anamorphic species

The phylogenetic relationships of *Talaromyces* and species of *Penicillium* subgenus *Biverticillium* among other related genera were studied using partial *RPB1* sequences. One-hundred fifty-six strains were included in this analysis. The length of the alignment was 496 characters (exon data only, no introns observed) and 323 of those characters were variable. The proportion of gaps and

Table 1. Strains used in phylogenetic analysis of *Talaromyces.*

Name	Collection no.	Origin	GenBank Accession number	
			RPB1	**ITS**
"*Aphanoascus cinnabarinus*"	CBS 267.72 = ATCC 26215	Soil, Japan	JN121625	JN899376
Aspergillus aculeatus	CBS 172.66^{T} = ATCC 16872 = IMI 211388	Tropical soil	JN121590	
Aspergillus clavatoflavus	CBS 473.65^{NT} = ATCC 16866 = IMI 124937	Rain forest soil,Tulley, Queensland, Australia	JN121686	
Aspergillus flavus	NRRL 3357 = CBS 128202 = ATCC 200026	Peanut cotyledons, USA	Unpublished	
Aspergillus fumigatus	Af293	Patient with invasive aspergillosis	Nierman *et al.* (2005)	
Aspergillus niger	CBS 513.88	Derived from NRRL 3122 and currently used as enzyme production strain	Pel *et al.* (2007)	
Aspergillus ochraceoroseus	CBS 101887 = ATCC 42001 = IBT 14580	Soil, Tai National Forest, Ivory Coast	JN121557	
Aspergillus ochraceus	CBS 108.08^{NT} = ATCC 1008 = CBS 547.65 = IMI 016247 = IMI 016247iii = IMI 016247iv = NRRL 1642 = NRRL 398	Unknown source	JN121562	
Aspergillus penicillioides	CBS 130294	Indoor environment, Germany	JN121578	
Aspergillus robustus	CBS 649.93^{T} = CBS 428.77 = IBT 14305	Surface soil from thorn-forest, near Mombasa, Kenya	JN121711	
Aspergillus sparsus	CBS 139.61^{NT} = ATCC 16851 = IMI 019394 = IMI 019394ii = MUCL 31314 = NRRL 1933	Soil, Costa Rica	JN121586	
Aspergillus steynii	CBS 112812^{T} = IBT 23096	Dried arabica green coffee bean, on parchment, internal infection, Chamumdeshuran Estata, Karnataka, district Giris, India	JN121569	
Aspergillus sydowii	CBS 264.81	Grains and milling fractions, *Triticum aestivum*, India	JN121624	
Aspergillus versicolor	CBS 245.65 = ATCC 11730 = ATCC 16020 = IMI 045554 = IMI 045554ii = IMI 045554iii = IMI 045554iv = MUCL 19008	Cellophane, Indiana, USA	JN121614	
Aspergillus zonatus	CBS 506.65^{NT} = ATCC 16867 = IMI 124936	Forest soil, Province of Linon, Fortuna, Costa Rica	JN121691	
Byssochlamys nivea	CBS 100.11^{T} = ATCC 22260	Unknown source	JN121511	
Byssochlamys spectabilis	CBS 101075^{T} = ATCC 90900 = FRR 5219	Heat processed fruit beverage, Tokyo, Japan	JN121554	
Byssochlamys verrucosa	CBS 605.74^{T} = ATCC 34163	Nesting material of *Leipoa ocellata* (Malleefowl), Pulletop Nature Reserve, New South Wales, Australia	JN680311	
Chrysosporium inops	CBS 132.31^{T} = IMI 096729 = UAMH 802	Skin of man, Italy	JN121584	
Coccidioides immitis	Strain "RS"	Vaccine strain - origin unknown	Sharpton *et al.* (2009)	
Emericella nidulans	FGSC A4 (= ATCC 38163 = CBS 112.46)	Unknown source	Galagan *et al.* (2005)	
Eurotium herbariorum	CBS 516.65^{NT} = ATCC 16469 = IMI 211383 = NRRL 116	Unpainted board, Washington, USA	JN121693	
Geosmithia viridis	CBS 252.87^{T} = FRR 1863 = IMI 288716	Soil, bank of creek flowing into Little River, New South Wales	JN680284	JN899314
Hamigera avellanea	CBS 295.48^{T} = ATCC 10414 = IMI 040230 = NRRL 1938	Soil, San Antonio, Texas, USA	JN121632	
Hamigera striata	CBS 377.48^{NT} = ATCC 10501 = IMI 039741 = NRRL 717	Canned blueberries, USA	JN121665	
Monascus purpureus	CBS 109.07^{T} = ATCC 16365 = ATCC 16426 = IMI 210765 = NRRL 1596	Fermented rice grain, 'ang-quac' (purple coloured rice), Kagok-Tegal, imported from China, Prov. Quouan-toung, Java, Indonesia	JN121563	
Paecilomyces aerugineus	CBS 350.66^{T} = IMI 105412	Debris of *Glyceria maxima*, Attenborough, Notts., UK	JN121657	JN899388
Paecilomyces pascuus	CBS 253.87^{T} = FRR 1925	Pasture grass, Otara, New Zealand	JN899292	JN899321

Table 1. (Continued).

Name	Collection no.	Origin	GenBank Accession number	
			RPB1	**ITS**
Penicilliopsis clavariiformis	CBS 761.68 = CSIR 1135	Unknown source, Pretoria, South Africa	JN121716	
Penicillium aculeatum	CBS 100105 = CBS 289.48 = ATCC 10409 = IMI 040588 = NRRL 2129 = NRRL A-1474	Textile, USA		JN899389
	CBS 289.48^{NT} = ATCC 10409 = IMI 040588 = NRRL 2129 = NRRL A-1474	Textile, USA		JN899378
Penicillium aculeatum var. *apiculatum*	CBS 312.59^{T} = ATCC 18315 = FRR 635 = IMI 068239	Soil, Japan	JN680293	JN899375
Penicillium allahabadense	CBS 453.93^{T} = ATCC 15067 = CBS 304.63	Soil of cultivated field, pH 6.9, Allahabad, India	JN680309	JN899345
Penicillium arenicola	CBS 220.66^{T} = ATCC 18321 = ATCC 18330 = IMI 117658 = NRRL 3392	Soil from pine forest, Kiev, Ukraine	JN121601	
Penicillium aurantiacum	CBS 314.59^{T} = ATCC 13216 = IMI 099722 = NRRL 3398	Soil, Georgia		JN899380
Penicillium aureocephalum	CBS 102801^{T}	*Quercus ruber*, Gerona, Selva de Mar, Catalanıa, Spain		JN899392
Penicillium brunneum	CBS 227.60^{T} = ATCC 18229 = FRR 646 = IFO 6438 = IHEM 3907 = IMI 078259 = MUCL 31318	Milled rice imported into Japan, Thailand	JN680281	JN899365
Penicillium calidicanium	CBS 112002^{T}	Soil, Nantou County, Taiwan	JN899305	JN899319
Penicillium canescens	CBS 300.48^{NT} = ATCC 10419 = IMI 028260 = MUCL 29169 = NRRL 910	Soil, England	JN121636	
Penicillium catenatum	CBS 352.67^{T} = ATCC 18543 = IMI 136241	Desert soil, Upington, Cape Province, South Africa	JN121659	
Penicillium cinnamopurpureum	CBS 490.66 = ATCC 18337 = IMI 114483	Cultivated soil, South Africa	JN121690	
Penicillium citrinum	CBS 139.45^{T} = ATCC 1109 = IMI 091961 = MUCL 29781 = NRRL 1841	Unknown source	JN121585	
Penicillium coalescens	CBS 103.83^{T}	Soil under *Pinus* sp., near Vulladolid, Spain		JN899366
Penicillium concavorugulosum	CBS 898.73^{T} = ATCC 20202	Unknown substrate, Japan	JN899304	JN899390
Penicillium crateriforme	CBS 184.27^{T} = FRR 1057 = IMI 094165 = LSHB P164 = MUCL 29224 = NRRL 1057	Soil, Luisiana	JN680270	JN899373
Penicillium dendriticum	CBS 660.80^{T} = IMI 216897	Leaf litter of *Eucalyptus pauciflora*, Kosciusko National Park, New South Wales, Australia	JN121714	JN899339
Penicillium diversum	CBS 320.48^{T} = ATCC 10437 = DSM 2212 = IMI 040579 = IMI 040579ii = NRRL 2121	Leather, USA	JN680297	JN899341
Penicillium duclauxii	CBS 322.48^{T} = ATCC 10439 = IMI 040044 = MUCL 28672 = MUCL 29094 = MUCL 29212 = NRRL 1030	Canvas, France	JN121643	JN899342
Penicillium echinosporum	CBS 293.62^{T} = ATCC 18319 = DSM 2230 = FRR 3411 = IMI 080450 = IMI 101214	Wood pulp, Surrey, Kenley, UK		JN899363
Penicillium erythromellis	CBS 644.80^{T} = FRR 1868 = IMI 216899	Soil from creek bank, Little River, New South Wales, Australia	JN680315	JN899383
Penicillium euglaucum	CBS 323.71^{NT}	Soil, Argentina	JN121644	
Penicillium expansum	CBS 325.48 = ATCC 7861 = IBT 5101 = IMI 039761= MUCL 29192 = NRRL 976	Fruit of *Malus sylvestris*, USA	JN121645	
Penicillium fellutanum	CBS 229.81^{NT} = ATCC 10443 = CBS 326.48 = FRR 746 = IFO 5761 = IMI 039734 = IMI 039734iii = NRRL 746	Unknown source, USA	JN121605	
Penicillium funiculosum	CBS 272.86^{NT} = IMI 193019	*Lagenaria vulgaris*, India	JN680288	JN899377
Penicillium glabrum	CBS 125543^{NT} = IBT 22658 = IMI 91944	Unknown source	JN121717	

Table 1. (Continued).

Name	Collection no.	Origin	GenBank Accession number	
			RPB1	**ITS**
Penicillium herquei	CBS 336.48^{T} = ATCC 10118 = FRR 1040 = IMI 028809 = MUCL 29213 = NRRL 1040	Leaf, France	JN121647	
Penicillium ilerdanum	CBS 168.81^{T} = IJFM 5596 = IMI 253793	Air, Madrid, Spain		JN899311
Penicillium isariiforme	CBS 247.56^{T} = ATCC 18425 = IMI 060371 = MUCL 31191 = MUCL 31323 = NRRL 2638	Woodland soil, Zaire	JN121616	
Penicillium islandicum	CBS 338.48^{NT} = ATCC 10127 = IMI 040042 = MUCL 31324 = NRRL 1036	Unknown source, Cape Town, South Africa	JN121648	JN899318
Penicillium janthinellum	CBS 340.48^{NT} = ATCC 10455 = IMI 040238 = NRRL 2016	Soil, Nicaragua	JN131650	
Penicillium javanicum	CBS 341.48^{T} = ATCC 9099 = IMI 039733 = MUCL 29099 = NRRL 707	Root of *Camellia sinensis*, Indonesia, Java	JN121651	
Penicillium kewense	CBS 344.61^{T} = ATCC 18240 = IMI 086561= MUCL 2685 = NRRL 3332	Culture contaminant of mineral oil CMI 1959; Kew, Surrey, UK	JN121654	
Penicillium korosum	CBS 762.68^{T}	Rhizosphere, India		JN899347
Penicillium lapidosum	CBS 343.48^{T} = ATCC 10462 = IMI 039743 = NRRL 718	Canned blueberry, Washington, USA	JN121653	
Penicillium liani	CBS 225.66^{T} = ATCC 18325 = ATCC 18331 = IMI 098480 = NRRL 3380 = VKM F-301	Soil, China	JN680280	JN899395
Penicillium loliense	CBS 643.80^{T} = ATCC 52252 = FRR 1798 = IMI 216901 = MUCL 31325	*Lolium*, Palmerston North, New Zealand	JN680314	JN899379
Penicillium marneffei	CBS 388.87^{T} = ATCC 18224= CBS 334.59 = IMI 068794ii = IMI 068794iii	*Rhizomys sinensis* (bamboo rat), Vietnam	JN899298	JN899344
Penicillium minioluteum	CBS 642.68^{T} = IMI 089377 = MUCL 28666	Unknown source	JN121709	JN899346
Penicillium mirabile	CBS 624.72^{T} = CCRC 31665 = FRR 1959 = IMI 167383 = MUCL 31206	Forest soil, Crimea, Ukraine	JN680312	JN899322
Penicillium namylowskii	CBS 353.48^{T} = ATCC 11127 = IMI 040033 = MUCL 29226 = NRRL 1070	Soil under *Pinus* sp., Puszczeza Bialowieska, square “652”, Poland	JN121660	
Penicillium oblatum	CBS 258.87^{T} = FRR 2234	Spoiled baby food, Sydney, New South Wales, Australia	JN680285	JN899364
Penicillium ochrosalmoneum	CBS 489.66 = ATCC 18338 = IMI 116248ii	Cornmeal, South Africa	JN121689	
Penicillium osmophilum	CBS 462.72^{T} = IBT 14679	Agricultural soil, Wageningen, Netherlands	JN121683	
Penicillium palmae	CBS 442.88^{T} = IMI 343640	Seed, Wageningen, Netherlands	JN680308	JN899396
Penicillium panamense	CBS 128.89^{T} = IMI 297546	Soil, Barro Colorado Island, Panama	JN899291	JN899362
Penicillium phialosporum	CBS 233.60^{T} = ATCC 18481 = FRR 203 = IMI 078256	Milled Californian rice, California, USA	JN680282	JN899340
Penicillium piceum	CBS 361.48^{T} = ATCC 10519 = IMI 040038 = NRRL 1051	Unknown source		JN899370
Penicillium pinophilum	CBS 631.66^{NT} = ATCC 36839 = CECT 2809 = DSM 1944 = IAM 7013 =IMI 114933	PVC, Centre d'Études du Bouchet, M. Magnoux, France	JN680313	JN899382
Penicillium pittii	CBS 139.84^{T} = IMI 327871	Clay soil, under poplar trees, bank of Duero River, Valladolid, Spain	JN680274	JN899325
Penicillium primulinum	CBS 321.48^{T} = ATCC 10438 = CBS 439.88 = FRR 1074 = IMI 040031 = MUCL 31321 = MUCL 31330 = NRRL 1074	USA	JN680298	JN899317
Penicillium proteolyticum	CBS 303.67^{T} = ATCC 18326 = NRRL 3378	Granite soil, Ukraine	JN680292	JN899387
Penicillium pseudostromaticum	CBS 470.70^{T} = ATCC 18919 = FRR 2039	Feather, near Itasca State Park, Hubbard Co., Minnesota, USA	JN899300	JN899371

Table 1. (Continued).

Name	Collection no.	Origin	GenBank Accession number	
			RPB1	**ITS**
Penicillium purpurogenum	CBS 286.36^{T} = IMI 091926	Unknown source	JN680271	JN899372
Penicillium purpurogenum var. *rubisclerotium*	CBS 274.95	Sculpture, castle Troja, Prague, Czech Republic	JN899295	JN899316
	CBS 270.35^{T} = ATCC 4713 = ATCC 52244 = FRR 1064 = IBT 4302 = MUCL 29225 = NRRL 1064 = NRRL 1142	*Zea mays*, Castle Rock, Virginia, USA	JN680287	JN899381
Penicillium rademirici	CBS 140.84^{T} = CECT 2771 = IMI 282406 = IMI 327870	Air under willow tree, bank of river Duero, Herrera, Valladolid, Spain		JN899386
Penicillium radicum	CBS 100489^{T} = FRR 4718	Root of seedling of *Triticum aestivum*, Wagga Wagga, New South Wales, Australia		JN899324
Penicillium rotundum	CBS 369.48^{T} = ATCC 10493 = IMI 040589 = NRRL 2107	Wood, Chiriqui Prov., Panama		JN899353
Penicillium rubicundum	CBS 342.59^{T} = ATCC 13217 = IMI 099723 = NRRL 3400	Soil, Georgia, USA	JN680301	JN899384
"*Penicillium rubrum*"	CBS 196.88 = FRR1714	Unknown source	JN680278	JN899312
	CBS 206.89 = IFO 6580	Japan	JN680279	JN899313
	CBS 263.93	Bronchoalveolair lavage of immunecompetent female patient with pneumonia by Nocardia	JN680286	JN899315
Penicillium rugulosum	CBS 371.48^{T} = ATCC 10128 = IMI 040041 = MUCL 31201 = NRRL 1045	Tuber (*Solanum tuberosum*), Connecticut, USA	JN680302	JN899374
Penicillium sabulosum	CBS 261.87^{T} = FRR 2743	Spoiled pasteurized fruit juice, New South Wales, Sydney, Australia	JN899294	
Penicillium samsonii	CBS 137.84^{T} = CECT 2772 = IMI 282404 = IMI 327872	Fruit, damaged by insect, Valladolid, Spain	JN680273	JN899369
Penicillium shearii	CBS 290.48^{T} = ATCC 10410 = IMI 039739 = IMI 039739iv = NRRL 715	Soil, Tela, Honduras	JN121631	
Penicillium siamense	CBS 475.88^{T} = IMI 323204	Forest soil, Lampang, Thurn District, Ban Daen Tham, Thailand		JN899385
Penicillium simplicissimum	CBS 372.48^{NT} = ATCC 10495 = IMI 039816	Flannel bag, Cape, South Africa	JN121662	
Penicillium stipitatum	CBS 375.48^{T} = ATCC 10500 = NRRL 1006 = IMI 39805	Rotting wood, Louisiana, USA	JN680303	JN899348
Penicillium stolkiae	CBS 315.67^{T} = IMI 136210 = ATCC 18546	Peaty forest soil, Eastern Transvaal, South-Africa	JN680295	
Penicillium tardum	CBS 258.37^{T} = NRRL 2116	Unknown source	JN899293	
	CBS 378.48^{T} = ATCC 10503 = IMI 040034 = NRRL 1073	Dead twig, France	JN899297	
Penicillium tularense	CBS 430.69^{T} = ATCC 22056 = IMI 148394	Soil, under *Pinus ponderosa* and *Quercus kelloggii*, Tulare Co., Pine Flat, California, USA	JN121681	
Penicillium variabile	CBS 385.48^{NT} = ATCC 10508= IMI 040040 = NRRL 1048	Cocos fibre, Johannesburg, South Africa	JN680304	JN899343
Penicillium varians	CBS 386.48^{T} = ATCC 10509 = IMI 040586 = NRRL 2096	Cotton yarn, UK	JN680305	JN899368
Penicillium verruculosum	CBS 388.48^{NT} = ATCC 10513= DSM 2263= IMI 040039 = NRRL 1050	Soil, Texas, USA		JN899367
Penicillium victoriae	CBS 274.36^{T} = IMI 058412 = MUCL 9651	Dried leaf, Tobaheide, Sumatra	JN680289	JN899393
Penicillium viridicatum	CBS 390.48^{NT} = ATCC 10515= IBT 23041 = IMI 039758 = IMI 039758ii = NRRL 963	Air, District of Columbia, Washington D.C., USA	JN121668	
Phialosimplex caninus	CBS128032^{T} = UAMH 10337	Bone marrow aspirate ex canine, San Antonio, Texas, USA	JN121587	
Phialosimplex chlamydosporus	CBS 109945^{T} = FMR 7371 = IMI 387422	Disseminated infection in a dog	JN121566	
Phialosimplex sclerotialis	CBS 366.77^{T} = IAM 14794	Fodder of ray-grass and lucerne, France	JN121661	
Rasamsonia eburnea	CBS 100538^{T} = IBT 17519	Soil, Taipei, Taiwan	JN680325	

Table 1. (Continued).

Name	Collection no.	Origin	GenBank Accession number	
			RPB1	**ITS**
Rasamsonia argillacea	CBS 101.69^{T} = IMI 156096 = IBT 31199	Mine tip with a very high surface temperature; Staffordshire, UK	JN121556	
Rasamsonia byssochlamydoides	CBS 413.71^{T} = IBT 11604	Dry soil under Douglas fir, Oregon, USA	JN121675	
Rasamsonia emersonii	CBS 393.64^{T} = DTO 48I1 = IBT 21695 = ATCC 16479 = IMI 116815 = IMI 116815ii	Compost, Italy	JN121670	
Sagenoma viride	CBS 114.72^{T} ATCC 22467 = NRRL 5575	Soil, Australia	JN121571	
Sagenomella bohemica	CBS 545.86^{T} = CCF 2330 = IAM 14789	Peloids for balneological purposes, Frantiskovy Lázne Spa, West Bohemia, Czech Republic	JN121699	JN899400
Sagenomella diversispora	CBS 398.69	Forest soil under *Populus tremuloides*, Petawawa, Ontario, Canada	JN121673	
	CBS 399.69 = MUCL 15012	Forest soil under *Thuja occidentalis*, Aberfoyle, Ontario, Canada	JN121674	
Sagenomella griseoviridis	CBS 426.67^{T} = ATCC 18505 = IMI 113160	Unknown source	JN121677	
Sagenomella humicola	CBS 427.67^{T} = ATCC 18506 = IMI 113166	Forest soil under *Thuja occidentalis,* Ontario, Canada	JN121678	
Sagenomella striatispora	CBS 429.67^{T} = ATCC 18510 = IMI 113163	Soil, Guelph, Ontario, Canada	JN121679	
Sagenomella verticillata	CBS 415.78A	Gymnosperm forest soil, Sweden	JN680307	
Sclerocleista ornata	CBS 124.53^{NT} = ATCC 16921 = IMI 055295 = MUCL 15643 = NRRL 2256	Soil in oak forest, Dane Co., Madison, Wisconsin, USA	JN121581	
Talaromyces assiutensis	CBS 118440	Soil, Fes, Morocco		JN899320
	CBS 147.78^{T}	Soil, amended with crushed buffalo hoofs and incubated for 5 months at 35 °C, Egypt	JN680275	JN899323
Talaromyces austrocalifornicus	CBS 644.95^{T} = IBT 17522	Soil, campus Univ. South California, Los Angelos, USA	JN680316	JN899357
Talaromyces bacillisporus	CBS 296.48^{T} = ATCC 10126 = IMI 040045 = NRRL 1025	Begonia leaf, New York City, New York, USA	JN121634	JN899329
Talaromyces barcinensis	CBS 649.95^{T} = IBT 17518	Soil, Barcelona, Spain	JN680318	JN899349
Talaromyces brevicompactus	CBS 102661^{T} = AS 3.4676	Moulded vegetables, Prov. Sechuan, Wolong, China	JN680326	
Talaromyces convolutus	CBS 100537^{T} = IBT 14989	Soil, Kathmandu, Nepal	JN121553	JN899330
Talaromyces cyanescens	CBS 114900 = FMR 8388	Tortosa, Catalina, Spain		JN899391
Talaromyces derxii	CBS 412.89^{T} = NHL 2981	Cultivated soil, Okayama Prefecture, Kurashiki City, Higashitomii, Japan	JN680306	JN899327
	CBS 413.89^{T} = NHL 2982	Cultivated soil, Okayama Prefecture, Kurashiki City, Higashitomii, Japan	JN899299	JN899326
Talaromyces emodensis	CBS 100536^{T} = IBT 14990	Soil, Kathmandu, Nepal	JN121552	JN899337
Talaromyces flavus	CBS 310.38^{NT} = IMI 197477 = NRRL 2098	Unknown substrate, New Zealand	JN121639	JN899360
Talaromyces galapagensis	CBS 751.74^{T} = IFO 31796	Shaded soil under *Maytenus obovata*, Isla Santa Cruz, Galapagos Islands, Ecuador	JN680321	JN899358
Talaromyces gossypii	CBS 645.80^{T} = FRR 1966 = IMI 198365	*Gossypium*, India	JN680317	JN899334
Talaromyces helicus var. *boninensis*	CBS 650.95^{T} = IBT 17516	Lawn soil, Kominato, Chichijima, Ogasawara-mura, Tokyo-to, Japan	JN680319	JN899356
Talaromyces helicus var. *helicus*	CBS 335.48^{T} = ATCC 10451 = DSM 3705 = IMI 040593 = NRRL 2106	Soil, Sweden	JN680300	JN899359
Talaromyces helicus var. *major*	CBS 652.66^{T} = IMI 100914	Swamp soil, near Attenborough, Nottingham, UK	JN680320	JN899335
Talaromyces indigoticus	CBS 100534^{T} = IBT 17590	Soil, Nagasaki-ken, Minamikushiyama-mura, Japan	JN680323	JN899331
Talaromyces intermedius	CBS 152.65^{T} = BDUN 267 = IFO 31752 = IMI 100874	Alluvial pasture and swamp soil, Attenborough, Nottingham, England	JN680276	JN899332

Table 1. (Continued).

Name	Collection no.	Origin	GenBank Accession number	
			RPB1	**ITS**
Talaromyces leycettanus	CBS 398.68^{T} = ATCC 22469 = IMI 178525	Coal spoil tip soil, Leycett, Staffordshire, England, UK	JN121672	
Talaromyces luteus	CBS 348.51^{NT} = IMI 089305	Soil, UK	JN121656	
Talaromyces macrosporus	CBS 317.63^{T} = FRR 404 = IMI 197478	Apple juice, Stellenbosch, South Africa	JN680296	JN899333
Talaromyces mimosinus	CBS 659.80^{T} = FRR 1875 = IMI 223991	Soil from creek bank, Nattai River, New South Wales, Australia	JN899302	JN899338
Talaromyces muroii	CBS 756.96^{T} = PF 1153	Soil, Hualien County, Chingpu, Taiwan	JN680322	JN899351
Talaromyces ocotl	CBS 102855^{T}	Heat-treated soil from forest of *Pinus hartwegii*, Veracruz, Mexico	JN680327	
Talaromyces ohiensis	CBS 127.64^{T}	Soil treated with cyanamide, Germany	JN680272	JN899355
Talaromyces purpureus	CBS 475.71^{T} = ATCC 24069 = ATCC 52513 = FRR 1731 = IMI 181546	Soil, near Esterel, France	JN121687	JN899328
Talaromyces subinflatus	CBS 652.95^{T} = IBT 17520	Copse soil, Hahajima, Ogasawara-mura, Tokyo-to, Japan	JN899301	JN899397
Talaromyces tardifaciens	CBS 250.94^{T}	Unknown source	JN680283	JN599361
Talaromyces thermophilus	CBS 236.58^{T} = ATCC 10518 = IMI 048593 = NRRL 2155	*Parthenium argentatum*, decaying plant; California, USA	JN121611	
Talaromyces trachyspermus	CBS 373.48^{T} = ATCC 10497 = IMI 040043 = NRRL 1028	Unknown source, USA	JN121664	JN899354
Talaromyces ucrainicus	CBS 162.67^{T} = ATCC 22344 = FRR 3462	Unknown source	JN680277	JN899394
Talaromyces udagawae	CBS 579.72^{T} = FRR 1727 = IMI 197482	Soil, Misugimura, Japan	JN680310	JN899350
Talaromyces unicus	CBS 100535^{T} = CCRC 32703 = IBT 18385	Soil, Chiayi County, Funlu, Taiwan	JN680324	JN899336
Talaromyces wortmanii	CBS 391.48^{T} = ATCC 10517 = IMI 040047 = NRRL 1017	Unknown source	JN121669	JN899352
Thermoascus aurantiacus	CBS 396.78	Sawdust, in lumber yard, Toronto, Ontario, Canada	JN121671	
	CBS 891.70 = IMI 173037	Wood, Firenze, Italy	JN121719	
Thermoascus crustaceus	CBS 181.67^{T} = ATCC 16462 = IMI 126333	*Parthenium argentatum*, decaying plant; Salinas, California, USA	JN121591	
Thermoascus thermophilus	CBS 528.71^{NT} = IMI 123298 = NRRL 5208	Wood and bark of *Pinus*, Sweden	JN121697	
Thermomyces lanuginosus	CBS 218.34 = MUCL 8338	Fruit shell of *Theobroma* cacao	JN121599	
	CBS 224.63 = MUCL 8337	Mushroom compost; Gossau-Zürich Switzerland	JN121602	
	CBS 288.54 = MUCL 8340	Stomach of bovine foetus, Netherlands	JN680291	
Trichocoma paradoxa	CBS 103.73	Unknown source, Japan	JN121558	
	CBS 247.57 = MUCL 39666 = IBT 31159	Unknown source, Hachijô, Japan	JN121617	
	CBS 788.83	Rotting stump of cut down tree, Myojoji Temple near Hakui Noto Park, Ishikawa Pref., Japan	JN121718	JN899398
Warcupiella spinulosa	CBS 512.65^{NT} = ATCC 16919 = IMI 075885 = NRRL 4376	Jungle soil, Berakas-Muara, Brunei	JN121692	

completely undetermined characters in the alignment was 0.60 %. Figure 1 shows that members of the subgenus *Biverticillium* and *Talaromyces* are accommodated in a well-supported (97 % bs), monophyletic clade (= *Talaromyces s. str*.) and that species of the *Penicillium* subgenera *Aspergilloides*, *Furcatum* and *Penicillium* form an independent, well-supported clade (*Penicillium s. str*.). The majority of described *Talaromyces* species belong to *Talaromyces s. str*., but some species are dispersed in other clades, including *Talaromyces ocotl*, *T. luteus*, *T. thermophilus*, *T. eburneus*, *T. emersonii*, *T. byssochlamydoides, T. spectabilis*, *T. brevicompactus*, *T. striatus* and *T. leycettanus*. *Talaromyces ocotl* is in a well-supported clade with the type species of *Sagenomella*, *S. diversispora*, and other *Sagenomella* species. The former *T. emersonii*, *T. eburneus* and *T. byssochlamydoides* form a clade recently recognised and described as the genus *Rasamsonia* (Houbraken *et al*. 2011). *Talaromyces thermophilus* is also excluded from *Talaromyces s. str*. and is closely related to the type species of *Thermomyces, Therm. lanuginosus*. Basal to *Therm. lanuginosus*

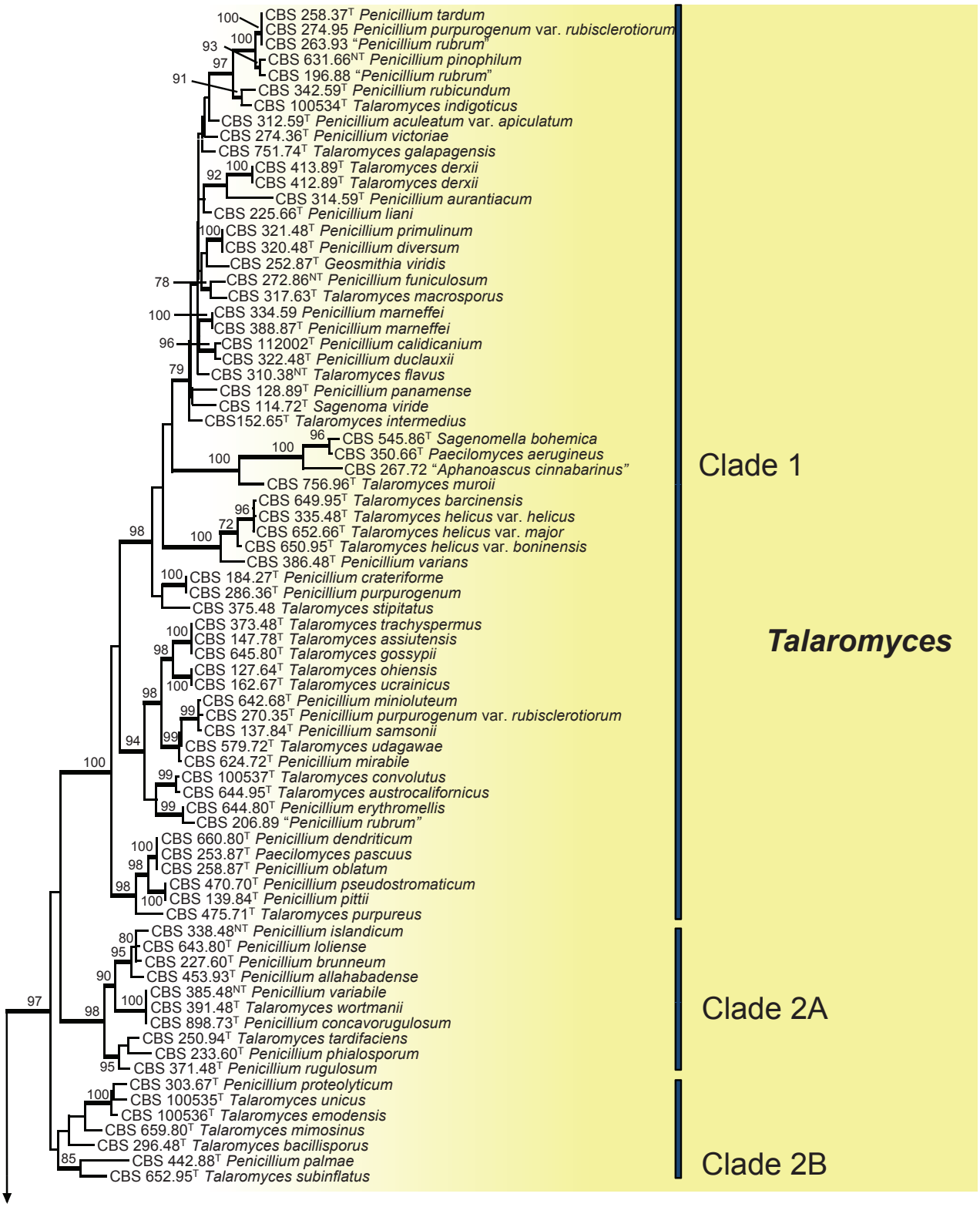

Fig. 1. Best-scoring Maximum Likelihood tree calculated using RAxML, based on partial *RPB1* sequences showing the relationships among members of *Talaromyces* and *Penicillium* subgenus *Biverticillium* and related genera. The bootstrap support percentages of the maximum likelihood (ML) analysis are presented at the nodes. Bootstrap support values less than 70 % are not shown and branches with bootstrap support values > 70 % are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Coccidioides immitis* (strain RS).

and *T. thermophilus* is *Talaromyces luteus*. This species is on a separate branch and no other closely related species were found in our analysis. The uniqueness of the species is supported by the production of large amounts of the prenylated diketopiperaziners talathermophilins A and B, not found in any other species (Chu *et al*. 2010). The phylogenetic position of *T. leycettanus* is not convincingly defined. This species is positioned near *Warcupiella spinulosa* and *Hamigera striata* (= *Talaromyces striatus*), but bootstrap support is lacking. *Talaromyces brevistipitatus* occurs on a well-supported branch with *H. avellanea*. Comparison of ITS and calmodulin sequences shows that this species is closely related to NRRL 2108, an undescribed, phylogenetically distinct *Hamigera* species (ITS 100 % bs, calmodulin 99 % bs) (Peterson *et al*. 2010). The majority of members of subgenus *Biverticillium sensu*

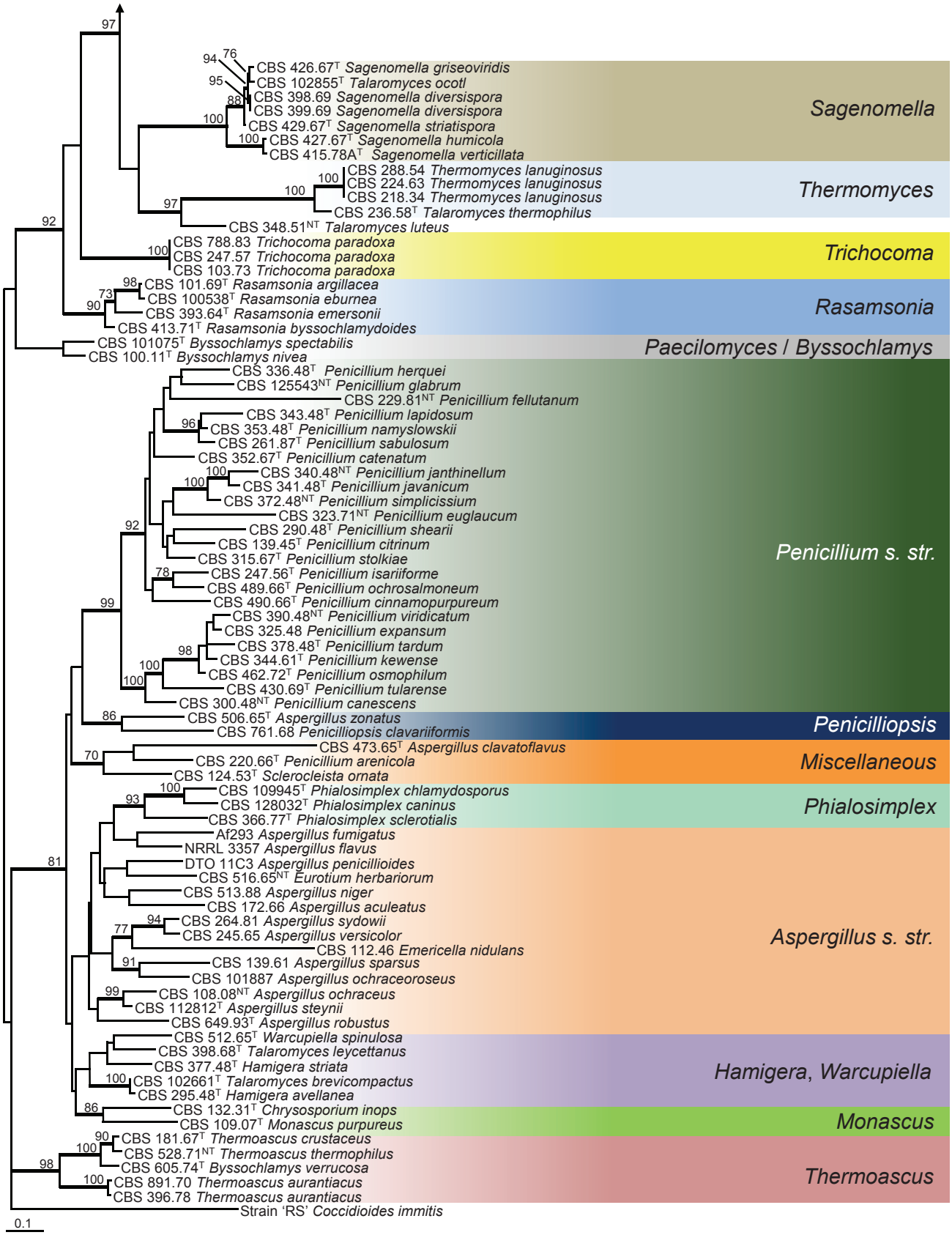

Fig. 1. (Continued).

Pitt (1980) are phylogenetically placed within *Talaromyces s. str.*, with *P. isariiforme* as the only exception. This species belongs to *Penicillium s. str.* and is closely related to *P. ochrosalmoneum*. This relationship was also confirmed by extrolite data (see below).

Figure 1 indicates that the following species phylogenetically belong in *Talaromyces*: *Aphanoascus cinnabarinus* (CBS 267.72), *Sagenomella bohemica* (CBS 545.86^{T}), *Paecilomyces aerugineus* (CBS 350.66^{T}), *Geosmithia viridis* (CBS 252.87^{T}) and *Sagenoma viride* (CBS 114.72^{T}). The former three strains are on a well-supported sister clade basal to *Talaromyces muroii* CBS 756.96.

Species delimitation and synonymies within *Talaromyces*

The ITS analysis (Fig. 2) was used in this study to provide a preliminary circumscription of the species belonging to the *Talaromyces* clade. Ninety-seven strains were included in the ITS analysis. The used primer pair V9G and LS266 also amplifies a part of the 18S and 28S rDNA; however, for analysis, only the span including the ITS regions and 5.8S rDNA was used. The length of the alignment was 483 characters and 221 characters were variable.

Most bootstrap support values in the ITS analysis are low, less than 70 %. Only a few branches are supported with values higher than 70 %. The majority of *Talaromyces* species are on a branch with 96 % bootstrap support (clade 1, Fig. 2). This clade is also present in the *RPB1* analysis (100 % bs). Another large clade was present in the ITS phylogram and this clade is supported with 96 % boostrap (clade 2). This clade can be divided in two subclades (2A and 2B), both present in the *RPB1* analysis; however, the relationship among these subclades is not supported statistically. *Talaromyces dendriticus*, *T. oblatus*, and *Paecilomyces pascuus* are in the same lineage and the former two species share the same ITS sequence. *Talaromyces assiutensis* and *T. gossypii* also have similar ITS sequences and are phenotypically similar (Frisvad *et al*. 1990a).

Extrolite analysis

In general, *Talaromyces* species produce many biosynthetic families of polyketides and meroterpenoids, but rather few families of nonribosomal peptides and terpenes. By examining HPLC-DAD results from all described species of *Penicillium, Aspergillus* and their teleomorphs, and by searching the literature for families of exometabolites produced by these fungi, it is obvious that *Talaromyces* species have unique and specific extrolites (Table 2). Figure 3 shows the common exometabolite families in *Talaromyces*/*Biverticillium*, *Penicillium*, *Aspergillus* and other genera. *Aspergillus* and *Penicillium* share 91 biosynthetic families, but shares more of these with other fungal genera than with *Talaromyces*. A few exometabolites are shared among *Talaromyces, Penicillium* and *Aspergillus* including alternariols, asperphenamate, botryodiploidin, dehydrocarolic acid, emodins, geodins, gregatins, herqueinone, 3-hydroxyphtalic acid, italinic acid, lichexanthones, mellein, monordens, pinselin, rugulosuvines, rugulovasines, secalonic acids and zeorins. Most of these metabolites have relatively simple structures, and many occur in other genera less related phylogenetically to any of the penicilloid and aspergilloid genera. Considering the large number of shared exometabolite biosynthetic families in common between *Penicillium* and *Aspergillus*, *Talaromyces* is clearly different, which corresponds with all other data for these genera.

Among the few extrolites shared by *Penicillum, Aspergillus* and *Talaromyces* are the ergochromes, secalonic acid D & F. These anthraquinone derived metabolites are found in *P. isariiforme*, *P. chrysogenum*, *Aspergillus aculeatinus*, *P. dendriticum* and *P. pseudostromaticum* (Samson *et al*. 1989, Frisvad & Samson 2004, Houbraken *et al*. 2011). It is also possible that there are optical antipodes of these compounds produced in these genera, as was found in *Aspergillus versicolor* ((+) versicolamide)) and *A. sclerotiorum* ((-)-versicolamide) (Williams 2011). If this is so, it may indicate that the extrolites of *Talaromyces* and *Penicillium* / *Aspergillus* may also differ in stereochemical aspects. Another example of shared yet different extrolites is the azaphilones, which are common in species of *Talaromyces* and related biverticillate anamorphic species (Frisvad *et al*. 1990a, Nicoletti *et al*. 2009, Osmanova *et al*. 2010), but could not be found in *Aspergillus* and *Penicillium sensu stricto*. When similar compounds were found in *Talaromyces,* stereoisomers of the compounds were found in *Aspergillus* and *Penicillium*. For example, while sclerotiorins occur in *P. sclerotiorum*, the epimers are found in *Talaromyces helicus* and *T. luteus* (Yoshida *et al*. 1995, 1996a, b). Austdiol was isolated from *Aspergillus pseudoustus* (Vleggaar *et al*. 1974, Samson *et al*. 2011), but 7-epi-austdiol from a *Talaromyces* species (Liu *et al*. 2010).

Misidentifications of strains can make these comparisons difficult, but the overwhelming majority of extrolites found in *Talaromyces* are not found in *Aspergillus* or *Penicillium*. Although vermistatins, penisimplisins, penisimplicissins were reported from *Penicillium simplicissimum* (Komai *et al*. 2005), the producing strain was misidentified and actually represents a species of *Talaromyces*. The opposite has also happened, and metabolites attributed to a species of subgenus *Biverticillium* are later found to be produced by species of *Penicillium sensu stricto*. *Penicillium verruculosum* was reported to produce verruculogen, hence the name (Cole *et al*. 1972, Cole & Kirksey 1973), but the strain was later reidentified as *P. brasilianum* (Frisvad 1989).

Penicillium isariiforme (Samson *et al*. 1989) and *P. ochrosalmoneum* (Wicklow & Cole 1984) both produce large amounts of citreoviridin, supporting their close relationship indicated by the phylogenetic analyses, as noted above (Fig. 1).

DISCUSSION

The symmetrical, biverticillate penicillus was used as a defining character by Wehmer (1914), and Thom (1915a, b). Wehmer (1914) proposed to call this group the Verticillata, while Thom (1915a) referred to it as the *Penicillium luteum-purpurogenum* group. Biourge (1923) was the first who named this group as the subgenus *Biverticillium*, but included species such as *P. citrinum* (as *P. aurifluum*), *P. atramentosum* etc., which are no longer regarded as members of this subgenus (Houbraken *et al*. 2010). The characteristic lanceolate or acerose phialides was used as a more definitive morphological character of subgenus *Biverticillium* and related *Talaromyces* anamorphs (Raper & Thom 1949), because biverticillate branched conidiophores with flask-shaped phialides are mainly found in unrelated species such as *P. citrinum*. Although the lanceolate phialides occur in most species of subgenus *Biverticillium,* some species, *e.g. P. rugulosum,* have phialides that are not slender and have an apical portion tapering into a long acuminate point.

Thom (1930) treated some of the Penicillia in his *Biverticillate-Symmetrica* group and distinguished four sections: *Ascogena*, *Coremigena*, *Luteo-virida* (*Funiculosa* and *Luteo-purpurogena*) and *Miscellanea*. Later, Raper & Thom (1949) subdivided the group into the *P. luteum* series, *P. duclauxii* series, *P. funiculosum* series, *P. purpurogenum* series, *P. rugulosum* series and *P. herquei* series. This grouping is inconsistent with our phylogenetic analysis of the biverticillate group. The classification proposed by Pitt (1980) is more in concordance with the phylogenetic and taxonomic treatment proposed here, although he included a few species in *Penicillium* subgenus *Biverticillium*, namely *P. isariiforme, P. clavigerum* and

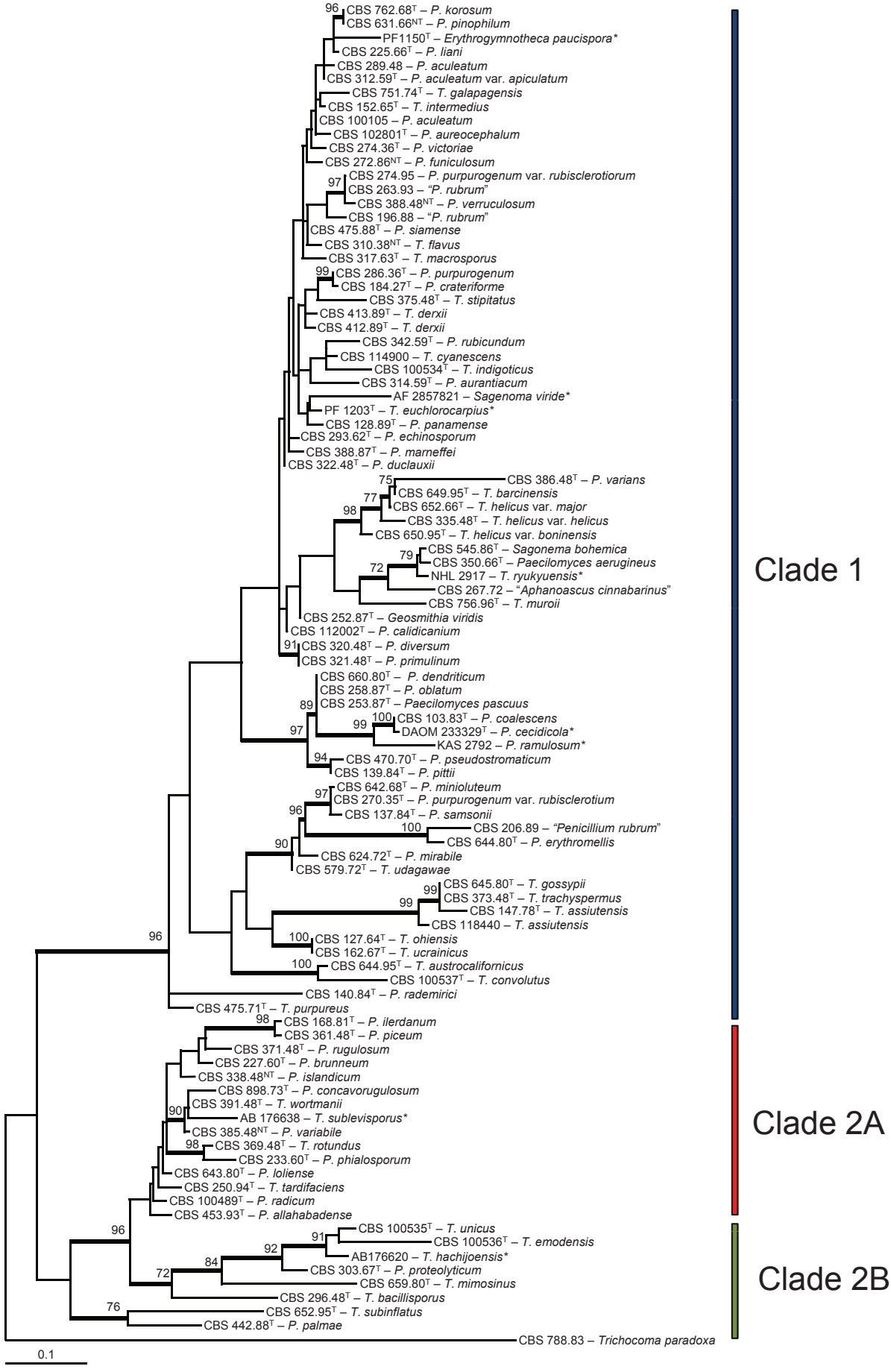

Fig. 2. Best-scoring Maximum Likelihood tree calculated using MEGA 5.0 based on ITS sequences showing the relationship among members of the *Talaromyces* and members of *Penicillium* subgenus *Biverticillium*. The bootstrap support percentages of the maximum likelihood (ML) analysis are presented at the nodes. Bootstrap support values less than 70 % are not shown and branches with bootstrap support values > 75 % are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Trichocoma paradoxa* (CBS 788.83). *T.* = *Talaromyces*; *P.* = *Penicillium*. Strains indicated with * are ITS sequencing obtained from GenBank.

Table 2. Secondary metabolite (exometabolite) biosynthetic families known from *Talaromyces* and *Penicillium* subgenus *Biverticillium*. (P) means also found in *Penicillium* and its teleomorphic state *Eupenicillium*, (A) means also found in species of *Aspergillus*. (Others) means also found in other fungi outside *Penicillium*, *Aspergillus*, *Talaromyces* and related genera.

Secondary metabolite (exometabolite) biosynthetic families		
AF-110	5-Hydroxymethylfurfural	Purpurogenones
Alternariols * (P and others)	Hydromethylmaltol	Rasfonin
Anthglutin	4-Hydroxy-4,5-dicarboxy pentadecanoic acid (*T. spiculisporus*)	Rubratoxins
Apiculides (incl. NG-011's * (others))	7-Hydroxy-2,5-dimethylchromane	Rugulosins (& flavoskyrin) * (others)
AS-186-G	3-Hydroxymethyl-6,8-dimethoxycoumarin	Rugulotrosins
Asperphenamates & asperglaucid * (A, P)	3-Hydroxyphthalic acid * (P)	Rugulosuvine * (P)
Atrovenetinon methyl acetal (*P. verruculosum*)	Islandic acids	Rugulovasines * (P)
Epi-Austdiols (7-epiaustdiol & 8-O-methylepiaustdiol) (the stereoisomer austdiol found in *Aspergillus*)	(+)-Isocitric acid + Decylcitric acid (*T. spiculisporus*)	Secalonic acids * (A, P, others)
Austins * (A, P)	Italinic acids * (P)	Speciferone* (others)
BE-24811	Juglones	Spiculisporic acids (= minioluteic acids)
BE-31405's	Lichexanthone * (others)	SQ 30957
Berkeleyamides	Luteusins	Stemphyperylenole
Botryodipoidin * (P & others)	Maculosin * (others)	Stipitatic acids
Chrodinanine A	Mellein * (A)	Talaperoxides
Cordyanhydrides	Methyl-4-carboxy-5-hydroxyphthalaldehydrate	Talaroconvolutins
Cyclochlorotines & islanditoxin	3-Methyl-6-hydroxy-8-methoxy-3,4-dihydroisocoumarins	Talaroderxine
Dehydrocarolic acids * (A, P)	Miniolutelides, berkeleydione, berkeleytriones, berkeleyacetals, dhilirolides	Talaroflavones
Diethylphthalate (Artefact?)	Mitorubrins & kasanosins & funicones	Talaromycins
5,6-Dihydro-3,5-dihydroxy-6-hydroxymethyl-2H-pyran-2-one	Monascins & monascorubramin	Talarotoxins
4,6-Dihydroxy-5-methylphthalide	Monordens * (A, others)	TAN-931
(2E,2E',7S,7'E)-4,9-Dioxo-7-(4',9'-dioxo-2',7'decadienoyloxy)-2-decanoic acid	NG-061	Thailandolides
Diversonols	NK-374200	Trachyspermic acids
Duclauxins	OF-4949's	Trachyspic acid
Emodins * (A, P, others)	Penicilliopsin * (others)	Triacetic lactone
Erythroskyrins	Penisimplicins	(-)-2,3,4-Trihydroxy-butanamide
Flavomannin	Penisimplicissins	Vermicellins
Funiculosic acids	Penitrinic acid & penitricins	Vermiculins
Funiculosin	Pevalic acid	Vermilutins
Geodins * (A, P)	PF-1092A	Vermistatins & penicidones
Glauconic acids	Pinselic acid	Vertoskyrin
Gregatins and penicilliols * (A, P)	Pinselin * (A, others)	Wortmannilactones
Helicusins	Purpactins (= penicillides = vermixocins)	Wortmannins * (others)
Herqueinones* (P)	Purpuride	Xanthoradones
		Zeorins * (A, others)

P. vulpinum (as *P. claviforme*) that are now classified in *Penicillium sensu stricto*. The same conclusion was shown by the early molecular results of LoBuglio & Taylor (1993), and subsequently supported by the physiological, morphological and extrolite characters reviewed in the Introduction, and generated during this study.

In general, *Penicillium sensu stricto* and *Aspergillus* share many more features with each other than they do with *Talaromyces*. This includes micro- and macro-morphology, good growth on low water activity media, and the many shared exometabolite families. *Talaromyces* produces a series of metabolites that are apparently unique to this genus (J.C. Frisvad unpubl. data). The characteristic yellow and red colony and mycelial colours in *Talaromyces* are often caused by accumulation of mitorubrins and other azaphilones and unique anthraquinones and mitorubrins that are not found in *Aspergillus* and *Penicillium*. Some azaphilones are found in *Penicillium sclerotiorum* and *Penicillium hirayamae*, but only their optical antipodes are found in *Talaromyces*.

Penicillium and *Talaromyces* species excluded from the revised *Talaromyces* genus

Figure 1 shows that a number of species described in the genus should be excluded from *Talaromyces s. str.* Phylogenetically, *T. ocotl* CBS 102855^T belongs to *Sagenomella,* as also suggested using phenotypic characters (Heredia *et al*. 2001). The anamorph of this species was not formally named, described only as

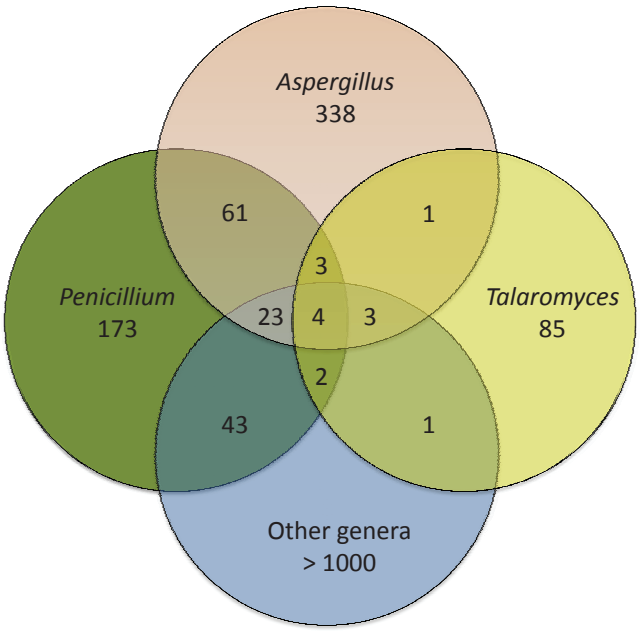

Fig. 3. Common exometabolite families in *Talaromyces*/*Biverticillium*, *Penicillium*, *Aspergillus* and other genera.

Sagenomella sp., and thus the new combination *Sagenomella ocotl* is proposed in the taxonomy section below.

Our analysis confirms the distinctiveness of the recently described genus *Rasamsonia* erected for thermotolerant or thermophilic species with distinctly rough-walled conidiphore stipes, olive-brown conidia, and ascomata, if present, with a scanty hyphal covering. *Talaromyces eburneus*, *T. emersonii*, *T. byssochlamydoides* were assigned to this genus, together with the anamorphic species originally described as *Geosmithia argillacea* and *G. cylindrospora* (Houbraken *et al*. 2011).

Talaromyces thermophilus is the only member of *Talaromyces* section *Thermophila* (Stolk & Samson 1972). LoBuglio *et al*. (1993) already noted that this species is the most divergent *Talaromyces* species, occupying a basal position to the major *Talaromyces* clade. Houbraken *et al*. (2011) showed that this species is closely related to *Thermomyces lanuginosus* and our partial *RPB1* sequence data confirm this relationship (Fig. 1). We did not examine type material of *Talaromyces thermocitrinus* (as '*thermocitrinum*') and the conclusion of Mouchacca (2007), who tentatively placed this species in synonymy with *T. thermophilus,* is not followed here. *Talaromyces luteus* is further basal to *T. thermophilus* and *Therm. lanuginosus* and this species might represent a distinct genus. For the present, *T. thermophilus* and *T. luteus* will be retained in *Talaromyces.* More research is needed to confirm whether the assignment of these species to *Thermomyces* is warranted.

Udagawa & Suzuki (1994) described *Talaromyces spectabilis* with a *Paecilomyces* anamorph. Houbraken *et al*. (2008) transferred this species to *Byssochlamys* and showed that it is the teleomorph of *Paec. variotii*. In a single name system, *Paec. variotii* is the oldest genus and species name for this taxon, and thus the correct name for the holomorph.

Talaromyces brevicompactus, *T. striatus* (= *Hamigera striata*) and *T. leycettanus* are distant from *Talaromyces s. str.* and phylogenetically more closely related to *Penicillium s. str.* and *Aspergillus*. Figure 1 shows that *H. striata* and *T. leycettanus* are closely related. Further phylogenetic support for this relationship was presented in the studies of Ogawa & Sugiyama (2000) and Houbraken & Samson (2011). These two species are phylogenetically distant from *Talaromyces s. str.* and more closely related to *Hamigera*. Peterson *et al*. (2010) delimited *Hamigera* phylogenetically but stated that *T. leycettanus* and *H. striata* do not belong to this genus, and followed Benjamin's (1955) placement of *H. striata* in *Talaromyces*. In this study, we retain *H. striata* and *T. leycettanus* in *Hamigera* and *Talaromyces*, respectively. A thorough study on *Hamigera* and related genera is needed to clarify the correct placement of these species. Kong (1999) described *Talaromyces brevicompactus,* stating that this species is closely related to *Hamigera avellanea* (as *Talaromyces avellaneus*). The anamorph of this species was described in *Merimbla*, thus confirming the relationship with *Hamigera*. Sequence comparisons of this species showed that it is similar to NRRL 2108, a phylogenetically undescribed *Hamigera* species (J. Houbraken, unpubl. data, Peterson *et al*. 2010). We wait with combining this species in *Hamigera* until a more data and strains become available.

Species described in other genera but phylogenetically within *Talaromyces*

Phylogenetic analysis shows that *"Aphanoascus cinnabarinus"*, *Sagenomella bohemica*, *Paecilomyces aerugineus*, *Geosmithia viridis* and *Sagenoma viride* belong to *Talaromyces*. The genus *Sagenoma* is typified with *S. viride,* and therefore this genus can be considered as a synonym of *Talaromyces*. Our data support the conclusions of von Arx (1987), who correctly transferred this species in *Talaromyces*, and this is reflected in the taxonomy section below.

Houbraken & Samson (2011) discussed the confusion over *Aphanoascus cinnabarinus,* which has persisted since the description of the genus *Aphanoascus* by Zukal (1890). Most authors follow Apinis (1968) and consider the genus *Aphanoascus* to be typified by *A. fulvescens* Zukal. In addition, the neotypification of *A. cinnabarinus* by Udagawa & Takada (1973) was incorrect, because their neotype strain had a *Paecilomyces* anamorph, whereas Zukal's original description and illustrations clearly showed a *Chrysosporium*-like anamorph (Stolk & Samson 1983). Based on morphological features, Stolk & Samson (1983) indicated that *Chromocleista cinnabarina* (as *A. cinnabarinus sensu* Udagawa & Takada) belongs to the *Eurotiales* and suggested that this species is intermediate between *Thermoascus* and *Talaromyces*. Our phylogenetic study, and that of Houbraken & Samson (2011), clarified that *C. cinnabarina* belongs to *Talaromyces s. str.* The taxonomic position of *Chromocleista cinnabarina* (as *A. cinnabarinus sensu* Udagawa & Takada) will be discussed in a forthcoming paper. *Paecilomyces aerugineus* was proposed by Samson (1974) for *Spicaria silvatica* Oudemans *sensu* Apinis. This species resembles the anamorph of *A. cinnabarinus sensu* Udagawa & Takada and a more detailed study is necessary to clarify this relationship.

TAXONOMY

Penicillium itself has a long list of generic synonyms (see Seifert *et al.* 2011) that must be considered for the species formerly included in subgenus *Biverticillium*. These synonyms of *Penicillium* are discussed in the Appendix to this paper. As it turns out, none of these are appropriate for subgenus *Biverticillium,* leaving the comparatively young *Talaromyces* as the oldest well-known generic name as the new home for the anamorphic species of subgenus *Biverticillium*.

Yaguchi *et al*. (1994a) introduced *Erythrogymnotheca* for the single species *E. paucispora*. No specimens of *E. paucispora* were studied; however, examination of the available ITS data on GenBank and the original description shows that this species belongs in *Talaromyces*. As a consequence, *Erythrogymnotheca* is synonymised with *Talaromyces*. Comparison of an ITS sequence of *E. paucispora* (AB176603) shows that it is related to *P. korosum*, *P. pinophilum* and *P. liani* in *Talaromyces* (Fig. 2). The original description suggests that *Talaromyces* and *Erythrogymnotheca* differ in ascus characteristics and ascospore morphology. However, these genera also share characters. The ascomatal initials of *E. paucispora* approximate those of *Talaromyces flavus* and other species of *Talaromyces*. Furthermore, *E. paucispora* produces a loose hyphal yellow- or red-pigmented ascomata similar to those of other *Talaromyces* species and the main ubiquinone systems are Q-10 and Q-10 (H_2), also indicating a relationship with *Talaromyces* (Paterson 1998, Yaguchi *et al*. 1994a).

Matsushima (2001) described *Paratalaromyces* from soil collected in Taiwan, distinguishing it by a distinct *textura epidermoidea* layer in the ascomatal wall, and the presence of spinulose marginal hyphae. We have not seen the type but the description of *Paratalaromyces lenticularis* is similar to that of *Talaromyces unicus* (Tzean *et al.* 1992). We consider the genus a synonym here.

Visagie & Seifert (unpubl. data) report on the generic name *Lasioderma* Mont., typified by *L. flavo-virens* Durieu & Mont., which is conspecific with *Penicillium aureocephalum* Munt.-Cvetk., Hoyo & Gómez-Bolea. The name *Lasioderma* is widely used as an insect genus, and a formal proposal for the conservation of *Talaromyces* against this older name is being prepared.

Talaromyces C.R. Benj., Mycologia 47: 681. 1955.

= *Penicillium* Link subgenus *Biverticillium* Dierckx *apud* Biourge Cellule 33: 31. 1923.

= *Penicillium* subg. *Biverticillata-Symmetrica* Thom, The Penicillia: 158. 1930.

= *Sagenoma* Stolk & G.F. Orr, Mycologia 66: 676. 1974.

= *Erythrogymnotheca* Yaguchi & Udagawa, Mycoscience 35: 219. 1994.

= *Paratalaromyces* Matsush., Matsush. Mycol. Mem. 10: 111 (2003) [2001].

Ascomata cleistothecial, usually with a distinctly hyphal exterior wall, often yellow, occasionally white, creamish, pinkish or reddish. *Asci* 8-spored, globose to ellipsoidal, ascus initials sometimes with morphologically distinguishable gametangia, mature asci produced in chains. *Ascospores* one-celled, rarely smooth-walled, but often with surface ornamentation and wings, hyaline to yellow, in strains producing abundant red pigment occasionally red. *Conidiophores* comprising smooth or rough-walled elements, with long hyaline stipes, generally terminating in a single whorl of 3–10 metulae, appearing symmetrical in face view (in some species with a single subterminal lateral branch that afterwards repeats the branching pattern of the main axis, but then with the whole conidiophore appearing asymmetrical), each metula with a terminal whorl of phialides. *Conidiogenous cells* phialidic, aculeate or acerose, rarely ampulliform, periclinal thickening usually visible in the conidiogenous aperture, with or without a cylindrical collarette. *Conidia* aseptate, green in mass, in basipetal connected chains, usually ellipsoidal to fusiform.

Type species: *Talaromyces vermiculatus* (P.A. Dang.) C.R. Benj., Mycologia 47: 684. 1955.

The name *Talaromyces* was introduced by Benjamin (1955), and the type species is *T. vermiculatus* (P.A. Dang.) C.R. Benj. One of the authors (RAS) personally visited several herbaria in Paris to locate holotype or other original material of *Penicillium vermiculatum* P.A. Dang. Dangeard (1907) described and illustrated both the anamorph and teleomorph under this name, but his material could not be located. To repair the shortcoming of the typification of *Talaromyces*, the lectotype for *P. vermiculatum* is here designated as Plate XVIII in Dangeard (1907, available at the Biodiversity Heritage Library, www.biodiversitylibrary.org). It was selected from among the plates XVI−XX because it includes the most detailed drawings of the anamorph, but also includes elements of the teleomorph. Herb. IMI 197477 is here designated as the epitype of *Penicillium vermiculatum* P.A. Dang. This specimen, which is also the holotype of *Penicillium dangeardii* J. Pitt, the seldom-used name for the anamorph of *T. flavus,* is derived from the equivalent cultures CBS 310.38, IMI 19447, and NRRL 2098. The latter strain was considered typical of *P. vermiculatum* by Raper & Thom (1949), the last major treatment to use this *Penicillium* name as a distinct species.

List of species

The following list includes previously accepted species of *Talaromyces* and proposals to transfer the species of *Penicillium* subgenus *Biverticillium* to *Talaromyces*.

Our phylogenetic studies demonstrate that several taxa represent complexes of morphologically cryptic phylogenetic species, requiring further study. For example, we analysed members of the *Penicillium purpurogenum* complex (including *P. purpurogenum, P. rubrum, P. crateriforme, P. sanguineum*) and found that several species group could be distinguished by sequencing certain genes (N. Yilmaz, unpubl. data) and had distinct macromorphological features and unique extrolite profiles. The full phylogenetic diversity of the *P. purpurogenum* species complex requires more investigation, and a more detailed account will be published elsewhere.

ACCEPTED SPECIES IN *TALAROMYCES*

Talaromyces aculeatus (Raper & Fennell) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560639.
Basionym: *Penicillium aculeatum* Raper & Fennell, Mycologia 40: 535. 1948.

Talaromyces albobiverticillius (H.-M. Hsieh, Y.-M. Ju & S.-Y. Hsieh) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560683.
Basionym: *Penicillium albobiverticillium* H.-M. Hsieh, Y.-M. Ju & S.-Y. Hsieh, Fung. Sci. 25: 26. 2010.

Talaromyces allahabadensis (B.S. Mehrotra & D. Kumar) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560640.
Basionym: *Penicillium allahabadense* B.S. Mehrotra & D. Kumar, Canad. J. Bot. 40: 1399. 1962.

Talaromyces apiculatus Samson, Yilmaz & Frisvad, **sp. nov.** MycoBank MB560641.

= *Penicillium aculeatum* var. *apiculatum* Abe, S., 1956, J. Gen. Appl. Microbiol., Tokyo 2: 124. 1956 (*nom. inval.,* Art. 36).

Penicillio aculeato simile, sed conidiis apiculatis distinguitur.

Typus: **Japan** from soil (CBS H-20755 – Holotype, culture ex-type CBS 312.59)

Note: Species similar to *Penicillium aculeatum* but differing by apiculate conidia.

Talaromyces assiutensis Samson & Abdel-Fattah, Persoonia 9: 501. 1978.
Anamorphic synonym: *Penicillium assiutense* Samson & Abdel Fattah (simultaneously published, identical holotype).

Talaromyces aurantiacus (J.H. Mill., Giddens & A.A. Foster) Samson, Yilmaz, & Frisvad, **comb. nov.** MycoBank MB560642.
Basionym: *Penicillium aurantiacum* J.H. Mill., Giddens & A.A. Foster, Mycologia 49: 797. 1957.

Talaromyces austrocalifornicus Yaguchi & Udagawa Trans. Mycol. Soc. Japan 34: 245. 1993.
Anamorphic synonym: *Penicillium austrocalifornicum* Yaguchi & Udagawa (simultaneously published, identical holotype).

Talaromyces bacillisporus (Swift) C. R. Benj., Mycologia 47: 682. 1955.
≡ *Penicillium bacillisporum* Swift, Bull. Torrey Bot. Club 59: 221, 1932.

Talaromyces boninensis (Yaguchi & Udagawa) Samson, Yilmaz, & Frisvad, **comb. nov.** MycoBank MB560643.
Basionym: *Talaromyces helicus var. boninensis* Yaguchi & Udagawa, Transactions Mycological Society Japan 33: 511. 1992.

Talaromyces brunneus (Udagawa) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560644.
Basionym: *Penicillium brunneum* Udagawa, J. Agric. Sci. (Tokyo) Nogyo Daigaku 5: 16. 1959.

Talaromyces calidicanius (J.L. Chen) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560645.
Basionym: *Penicillium calidicanium* J.L. Chen, Mycologia 94(5): 870. 2002.

Talaromyces cecidicola (Seifert, Hoekstra & Frisvad) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560646.
Basionym: *Penicillium cecidicola* Seifert, Hoekstra & Frisvad, Stud. Mycol. 50: 520. 2004.

Talaromyces coalescens (Quintan.) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560647.
Basionym: *Penicillium coalescens* Quintan., Mycopathol. 84: 115. 1984.

Talaromyces convolutus Udawaga, Mycotaxon 48: 141. 1993.
Anamorphic synonym: *Penicillium convolutum* Udagawa (simultaneously published, identical holotype).

Talaromyces dendriticus (Pitt) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560648.
Basionym: *Penicillium dendriticum* Pitt, The Genus *Penicillium*: 413. 1980.

Talaromyces derxii Takada & Udagawa, Mycotaxon 31: 418. 1988.
Anamorphic synonym: *Penicillium derxii* Takata & Udagawa (simultaneously published, identical holotype).

Talaromyces diversus (Raper & Fennell) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560649.
Basionym: *Penicillium diversum* Raper & Fennell, Mycologia 40: 539. 1948.

Talaromyces duclauxii (Delacr.) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560650.
Basionym: *Penicillium duclauxii* Delacr., Bull. Soc. Mycol. France 7: 107. 1891.

Talaromyces echinosporus (Nehira) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560651.
Basionym: *Penicillium echinosporum* Nehira, J. Ferment. Technol., Osaka 11: 861. 1933.

Note: *Penicillium asperosporum* G. Smith, Trans. Brit. Mycol. Soc. 48: 275. 1965. (= *Penicillium echinosporum* G. Sm., Trans. Brit. Mycol. Soc. 45: 387. 1962, non Nehira in J. Ferment. Technol. 11: 849. 1933) belongs in *Penicillium* section *Aspergilloides* (Houbraken & Samson 2011).

Talaromyces emodensis Udagawa, Mycotaxon 48: 146. 1993.
Anamorphic synonym: *Penicillium emodense* Udagawa (simultaneously published, identical holotype).

Talaromyces erythromellis (A.D. Hocking) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560652.
Basionym: *Penicillium erythromellis* A.D. Hocking *apud* Pitt, The Genus *Penicillium*: 459. 1980.

Talaromyces euchlorocarpius Yaguchi, Someya & Udagawa, Mycoscience 40: 133. 1999.
Anamorphic synonym: *Penicillium euchlorocarpium* Yaguchi, Someya & Udagawa (simultaneously published, identical holotype).

Note: We have not seen the type, but the description and the ITS sequences available in GenBank (AB176617) show that this is a distinct species of *Talaromyces.*

Talaromyces flavo-virens (Durieu & Mont.) Visagie, Llimona & Seifert*, ined*.

Note: A manuscript on this species and its relationship to *Penicillium aureocephalum* Munt.-Cvetk., Hoyo & Gómez-Bolea is being prepared for publication in Mycotaxon.

Talaromyces flavus (Klöcker) Stolk & Samson, Stud. Mycol. 2: 10. 1972.
Anamorphic synonym: *Penicillium dangeardii* Pitt, The Genus *Penicillium*: 472. 1980.

Talaromyces funiculosus (Thom) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560653.
Basionym: *Penicillium funiculosum* Thom, Bull. Bur. Anim. Ind. U.S. Dep. Agric. 118: 69. 1910.

Talaromyces galapagensis Samson & Mahoney, Trans. Brit. Mycol. Soc. 69: 158. 1977.
Anamorphic synonym: *Penicillium galapagense* Samson & Mahoney (simultaneously published, identical holotype).

Talaromyces hachijoensis Yaguchi, Someya & Udagawa, Mycoscience 37: 157. 1996.

Note: We have not seen the type but the description and the ITS sequences available in GenBank (AB176620) show that this is a distinct species of *Talaromyces.* It is unusual in the genus for its apparent lack of an anamorph.

Talaromyces helicus (Raper & Fennell) C.R. Benj., Mycologia 47: 684. 1955.
≡ *Penicillium helicum* Raper & Fennell, Mycologia 40: 515. 1948.

Talaromyces indigoticus Takada & Udagawa, Mycotaxon 46: 129. 1993.
Anamorphic synonym: *Penicillium indigoticum* Takada & Udagawa (simultaneously published, identical holotype).

Talaromyces intermedius (Apinis) Stolk & Samson, Stud. Mycol. 2: 21. 1972.
Anamorphic synonym: *Penicillium intermedium* Stolk & Samson, Stud. Mycol. 2: 21. 1972.

Talaromyces islandicus (Sopp) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560654.
Basionym: *Penicillium islandicum* Sopp, Skr. Vidensk.-Selsk. Christiania, Math.-Naturvidensk. Kl. 11: 161. 1912.

Talaromyces loliensis (Pitt) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560655.
Basionym: *Penicillium loliense* Pitt, The Genus *Penicillium*: 450. 1980

Talaromyces macrosporus (Stolk & Samson) Frisvad, Samson & Stolk, Ant. van Leeuwenhoek 57: 186. 1990.
Anamorphic synonym: *Penicillium macrosporum* Frisvad, Filt., Samson & Stolk. *nom. illegit.* Art. 53 (non *P. macrosporum* Berk. & Broome 1882).

Talaromyces marneffei (Segretain, Capponi & Sureau) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560656.
Basionym: *Penicillium marneffei* Segretain, Capponi & Sureau *apud* Segretain, Bull. Soc. Mycol. France 75: 416. 1959 [1960].

Talaromyces mimosinus A.D. Hocking *apud* Pitt, The Genus *Penicillium*: 507. 1980.
Anamorphic synonym: *Penicillium mimosinum* A. D. Hocking (simultaneously published, identical holotype).

Talaromyces minioluteus (Dierckx) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560657.
Basionym: *Penicillium minioluteum* Dierckx, Ann. Soc. Sci. Bruxelles 25: 87. 1901.

Talaromyces muroii Yaguchi, Someya & Udagawa, Mycoscience 35: 252. 1994.

Note: This species is unusual in *Talaromyces* because of its lack of a known anamorph.

Talaromyces palmae (Samson, Stolk & Frisvad) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560658.
Basionym: *Penicillium palmae* Samson, Stolk & Frisvad, Stud. Mycol. 31: 135. 1989.

Talaromyces panamensis (Samson, Stolk & Frisvad) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560659.
Basionym: *Penicillium panamense* Samson, Stolk & Frisvad, Stud. Mycol. 31: 136. 1989.

Talaromyces paucisporus (Yaguchi, Someya & Udagawa) Samson & Houbraken, **comb.nov.** MycoBank MB560684.
Basionym: *Erythrogymnotheca paucispora* Yaguchi, Someya & Udagawa, Mycoscience 35: 219. 1994.

Talaromyces phialosporus (Udagawa) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560660.
Basionym: *Penicillium phialosporum* Udagawa, J. Agric. Sci. (Tokyo) Nogyo Daigaku 5: 11. 1959.

Talaromyces piceus (Raper & Fennell) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560661.
Basionym: *Penicillium piceum* Raper & Fennell, Mycologia 40: 533. 1948.

Talaromyces pinophilus (Hedgcock) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560662.
Basionym: *Penicillium pinophilum* Hedgcock *apud* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 37. 1910.

Talaromyces pittii (Quintan.) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560663.
Basionym: *Penicillium pittii* Quintan., Mycopathol. 91: 69. 1985.

Talaromyces primulinus (Pitt) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560664.
Basionym: *Penicillium primulinum* Pitt, The Genus *Penicillium*: 455. 1980.

Talaromyces proteolyticus (Kamyschko) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560665.
Basionym: *Penicillium proteolyticum* Kamyschko, Not. Syst. Crypt. Inst. Bot. Acad. Sci. USSR 14: 228. 1961.

Talaromyces pseudostromaticus (Hodges, G.M. Warner, Rogerson) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560666.

Basionym: *Penicillium pseudostromaticum* Hodges, G.M. Warner & Rogerson, Mycologia 62: 1106. 1970.

Talaromyces purpureus (E. Müll. & Pacha-Aue) Stolk & Samson, Stud. Mycol. 2: 57. 1972.
Anamorphic synonym: *Penicillium purpureum* Stolk & Samson, Stud. Mycol. 2: 57. 1972.

Talaromyces purpurogenus (Stoll) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560667.
Basionym: *Penicillium purpurogenum* Stoll, Beitr. Charakt. *Penicillium*-Arten: 32. 1904.

Talaromyces rademirici (Quintan.) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560668.
Basionym: *Penicillium rademirici* Quintan., Mycopathol. 91: 69. 1985.

Talaromyces radicus (A.D. Hocking & Whitelaw) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560669.
Basionym: *Penicillium radicum* A.D. Hocking & Whitelaw, Mycol. Res. 102: 802. 1998.

Talaromyces ramulosus (Visagie & K. Jacobs) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560670.
Basionym: *Penicillium ramulosum* Visagie & K. Jacobs, Mycologia 101: 890. 2009.

Talaromyces rotundus (Raper & Fennell) C.R. Benj., Mycologia 47: 683. 1955.
≡ *Penicillium rotundum* Raper & Fennell, Mycologia 40: 518. 1948.

Talaromyces ryukyuensis (S. Ueda & Udagawa) Arx, Persoonia 13: 282. 1987.
≡ *Sagenoma ryukyuense* S. Ueda & Udagawa, Mycotaxon 20: 499. 1984.

Note: We have not seen the type but the description and the ITS sequences available in GenBank (AB176628) show that this is a distinct species of *Talaromyces*.

Talaromyces rubicundus (J.H. Mill., Giddens & A.A. Foster) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560671.
Basionym: *Penicillium rubicundum* J.H. Mill., Giddens & A.A. Foster, Mycologia 49: 797. 1957.

Talaromyces rugulosus (Thom) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560672.
Basionym: *Penicillium rugulosum* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 60. 1910.

Talaromyces sabulosus (Pitt & A.D. Hocking) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560673.
Basionym: *Penicillium sabulosum* Pitt & A. D. Hocking, Mycologia 77: 818. 1985.

Talaromyces siamensis (Manoch & C. Ramírez) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560674.
Basionym: *Penicillium siamense* Manoch & C. Ramírez, Mycopathol. 101: 32. 1988.

Talaromyces stipitatus (Thom) C.R. Benj., Mycologia 47: 684. 1955.
≡ *Penicillium stipitatum* Thom, Mycologia 27: 138. 1935.

Talaromyces sublevisporus (Yaguchi & Udagawa) Samson, Yilmaz & Frisvad, **comb. et stat. nov.** MycoBank MB560675.
Basionym: *Talaromyces wortmannii var. sublevisporus* Yaguchi & Udagawa, Mycoscience 35: 63. 1994.

Note: We have not examined the ex-type of this species but from the ITS data (GenBank AB176638), this seems to be a separate species.

Talaromyces tardifaciens Udagawa, Mycotaxon 48: 150. 1993.
Anamorphic synonym: *Penicillium tardifaciens* Udagawa (simultaneously published, identical holotype).

Talaromyces trachyspermus (Shear) Stolk & Samson, Stud. Mycol. 2: 32. 1972.
Anamorphic synonym: *Penicillium spiculisporum* Leman, Mycologia 12: 268. 1920.

Talaromyces ucrainicus Udagawa, in Stolk & Samson, Stud. Mycol. 2: 34. 1972.
Anamorphic synonym: *Penicillium ucrainicum* Panasenko, Mycologia 56: 59. 1964.

Talaromyces udagawae Stolk & Samson, Stud. Mycol. 2: 36. 1972.
Anamorphic synonym: *Penicillium udagawae* Stolk & Samson (simultaneously published, identical holotype).

Talaromyces unicus Tzean, J.L. Chen & Shiu, Mycologia 84: 739. 1992.
Anamorphic synonym: *Penicillium unicum* Tzean, J.L. Chen & Shiu (simultaneously published, identical holotype).

Talaromyces variabilis (Sopp) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560676.
Basionym: *Penicillium variabile* Sopp, Skr. Vidensk.-Selsk. Christiania, Math.-Naturvidensk. Kl. 11: 169. 1912.

Talaromyces varians (G. Sm.) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560677.
Basionym: *Penicillium varians* G. Sm., Trans. Brit. Mycol. Soc. 18: 89. 1933.

Talaromyces verruculosus (Peyronel) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560678.
Basionym: *Penicillium verruculosum* Peyronel, Germi Atmosf. Fung. Micel.: 22. 1913.

Talaromyces viridis (Stolk & G.F. Orr) von Arx, Persoonia 13: 2821. 1987.
≡ *Sagenoma viride* Stolk & G.F. Orr, Mycologia 66: 677. 1974.

Talaromyces viridulus Samson, Yilmaz & Frisvad, **nom. nov**. MycoBank MB560679.
Basionym: *Geosmithia viridis* Pitt & A.D. Hocking, Mycologia 77: 822. 1985 = *P. viride* (Pitt & A.D. Hocking) Frisvad, Samson &

Stolk, Persoonia 14: 229. 1990, *nom. illegit.* Art. 53 (non Fres. 1851 nec Rivera 1873 nec Sopp 1912 nec (Matr.) Biourge 1923). Non *Talaromyces viridis* (Stolk & G.F. Orr) Arx.

Talaromyces wortmannii (Klöcker) C.R. Benjamin, Mycologia 47: 683. 1955.
≡ *Penicillium wortmannii* Klöcker, Compt-Rend. Trav. Carlsberg Lab. 6: 100. 1903.

EXCLUDED SPECIES AND TAXA, WHICH NEED FURTHER TAXONOMIC STUDY

Penicillium concavorugulosum S. Abe, J. Gen. Appl. Microbiol, Tokyo 2: 127. 1956 (*nom. inval.* Art. 36).

Note: This species was invalidly described, but our ITS data (Fig. 2) show that it is related to *T. wortmanii*. Further study is required but extrolite data indicate that this species is unique (J.C. Frisvad, unpubl. data).

Penicillium crateriforme J.C. Gilman & E.V. Abbott, Iowa State Coll. J. Sc. 1: 293. 1927.

Note: Our ITS data (Fig. 2) show that this species is a synonym of *P. purpurogenum*.

Penicillium ilerdanum C. Ramírez, A.T. Martínez & Berer., Mycopathol. 72: 32. 1980.

Note: Frisvad *et al*. (1990b) considered this species synononymous with *Penicillium piceum* Raper & Fennell, which is confirmed by our ITS data (Fig. 2).

Penicillium isariiforme Stolk & J.A. Mey., Trans. Brit. Mycol. Soc. 40: 187. 1957.

Note: According to Houbraken & Samson (2011), this species, included in subgenus *Biverticillium* by Pitt (1980), is correctly classified in *Penicillium sensu lato.*

Penicillium korosum J.N. Rai, Wadhwani & J.P. Tewari, Ant. van Leeuwenhoek 35: 430. 1969.

Note: This species requires further investigation, but our ITS sequence (Fig. 2) indicates that it is similar to *P. pinophilum*.

Penicillium krugeri C. Ramírez, Mycopathol. 110: 23. 1990.

Note: We have been unable to examine authentic material, and the correct classification of this species is uncertain.

Penicillium lignorum Stolk, Ant. van Leeuwenhoek 35: 264. 1969.

Note: A preliminary phylogenetic analysis indicates that this species does not belong to *Talaromyces* and might represent a new genus (J. Houbraken, unpubl. data).

Penicillium mirabile Beliakova & Milko, Mikol. Fitopatol. 6: 145. 1972.

Note: The ex-type culture is in poor condition and although our ITS data (Fig. 2) indicate that is a distinct species, it should be further investigated.

Penicillium oblatum Pitt & A.D. Hocking, Mycologia 77: 810. 1985.

Note: In our ITS phylogeny (Fig. 2), this species is close to *Paecilomyces pascuus* and *Penicillium dendriticum* and needs further study.

Penicillium pascuum (Pitt & A.D. Hocking) Frisvad, Samson & Stolk, Persoonia 14: 229. 1990.
≡ *Paecilomyces pascuus* Pitt & A. D. Hocking, Mycologia 77: 822. 1985.

Note: See on the position of this species under *P. oblatum* above.

Penicillium rubrum Stoll, Beitr. Charakt. *Penicillium*-Arten: 35. 1904.

Note: Although the name is well-known, the taxonomic position of the taxon remains doubtful because no type material has been located. A possible solution would be lectotypification from Stoll's illustrations, followed by epitypification to become a usable name.

Penicillium purpurogenum var. *rubrisclerotium* Thom, Mycologia 7: 137. 1915.

Note: Our ITS data (Fig. 2) indicate that this species is synonymous with *P. minioluteum.*

Penicillium samsonii Quintan., Mycopathol. 91: 69. 1985.
= *Talaromyces minioluteus* (Dierckx) Samson, Yilmaz, Frisvad & Seifert (see above).

Penicillium tardum Thom, The Penicillia: 485. 1930.

Note: Raper & Thom (1949) pointed out that there is confusion about the type culture and the status of this species will be subject of further studies.

Penicillium victoriae Szilv., Archiv. Hydrobiol. 14, Suppl. 6: 535. 1936.
= *Penicillium janthinellum* Biourge, Cellule 33: 258. 1923 (Pitt, 1980).

Note: Pitt (1980) synonymised this species under *Penicillium janthinellum*, but our studies showed that it clearly belongs in *Talaromyces*. Because there is only one strain, the exact identity of this fungus requires further study.

Talaromyces barcinensis Yaguchi & Udagawa, Trans. Mycol. Soc. Japan 34: 15. 1993.
Anamorphic synonym: *Penicillium barcinense* Yaguchi & Udagawa (simultaneously published, identical holotype).

Note: Our ITS sequence data show that this species is close to *Talaromyces helicus* and further study should determine its correct taxonomic position.

Talaromyces brevicompactus Kong, Mycosystema 18: 9. 1999.
Anamorphic synonym: *Merimbla brevicompacta* Kong, Mycosystema 18: 9. 1999 (simultaneously published, identical holotype).

Note: Fig. 1 shows that this species belongs in *Hamigera*. Comparison of partial β-tubulin and calmodulin sequences of the ex-type strain of *T. brevicompactus* with recent published data shows that this species represents a distinct species (J. Houbraken, unpubl. data). The new combination in *Hamigera* will be made elsewhere.

Talaromyces byssochlamydoides Stolk & Samson, Stud. Mycol. 2: 45. 1972.
Anamorphic synonym: *Paecilomyces byssochlamydoides* Stolk & Samson (simultaneously published, same holotype).
= *Rasamsonia byssochlamydoides* (Stolk & Samson) Houbraken & Frisvad, Ant. van Leeuwenhoek, *in press*.

Talaromyces eburneus Yaguchi, Someya & Udagawa, Mycoscience 35: 249. 1994.
Anamorphic synonym: *Geosmithia eburnea* Yaguchi, Someya & Udagawa (simultaneously described, holotype identical)
≡ *Rasamsonia eburnea* (Yaguchi, Someya & Udagawa) Houbraken & Frisvad, Ant. van Leeuwenhoek, *in press*.

Talaromyces emersonii Stolk, Ant. van Leeuwenhoek 31: 262. 1965.
Anamorphic synonym: *Penicillium emersonii* Stolk (simultaneously described, holotype identical), Ant. van Leeuwenhoek 31: 262. 1965.
= *Rasamsonia emersonii* (Stolk) Houbraken & Frisvad, Ant. van Leeuwenhoek, *in press*.

Talaromyces gossypii Pitt, The Genus *Penicillium*: 500. 1980
= *Talaromyces assiutensis*, Samson & Abdel-Fattah, Persoonia 9: 501. 1978 (*fide* Frisvad *et al*. 1990a).

Talaromyces lagunensis Udagawa, Uchiy. & Kamiya, Mycoscience 35: 403. 1994.
Anamorphic synonym: *Penicillium lagunense* Udagawa, Uchiy. & Kamiya (simultaneously published, identical holotype).

Note: We have been unable to examine authentic material, and the correct classification of this species is uncertain.

Talaromyces leycettanus H.C. Evans & Stolk, Trans. Brit. Mycol. Soc. 56: 45. 1971.
Anamorphic synonym: *Penicillium leycettanus* H.C. Evans & Stolk (simultaneously published, identical holotype).
≡ *Paecilomyces leycettanus* (H.C. Evans & Stolk) Stolk, Samson & H.C. Evans, Persoonia 6: 342. 1971.

Note: Houbraken & Samson (2011) showed that this species is phylogenetically unrelated to *Talaromyces* and close to *Hamigera*. Its taxonomic position requires further investigation.

Talaromyces luteus (Zukal) C.R. Benj., Mycologia 47: 681. 1955.
≡ *Penicillium luteum* Zukal, Sitzungsber Kaiserl. Akad. Wiss. Math-Naturwiss. C1., Abt. 1, 98: 561. 1890.

Note: Although the phenotype of this species resembles species of *Talaromyces,* our molecular analysis shows that it is phylogenetically unique and basal to *T. thermophilus*.

Talaromyces malagensis (Thüm.) Stalpers & Samson 1984, in Stalpers, Stud. Mycol. 24: 69. 1984.

Note: Stolk & Samson (1972) considered *Sporotrichum malagense* a dubious synonym of *T. udagawae,* based on their failure to find ascospores and conidia in the type material (herb. W). Later, Stalpers (1984) studied material preserved in herb. BR which is authentic and labelled as "type". It agrees with Thümen's original diagnosis and contains both fertile *Talaromyces* cleistothecia and a sporulating biverticillate anamorph. Therefore, the new combination to *Talaromyces* was proposed. The species resembles *T. udagawae* or *T. luteus*, but in the absence of a living culture we cannot determine its precise taxonomic identity.

Talaromyces ocotl Bills & Heredia, Mycologia 90: 533. 1998.

Note: Figure 1 shows that this species belongs to *Sagenomella* and the new combination is proposed here:

Sagenomella ocotl (Bills & Heredia) Samson, Houbraken & Frisvad, **comb. nov.** MycoBank MB560681.
Basionym: *Talaromyces ocotl* Bills & Heredia, Mycologia 93: 533. 1998.

Talaromyces ohiensis Pitt, The Genus *Penicillium*: 502. 1980.
Anamorphic synonym: *Penicillium ohiense* L. H. Huang & J. A. Schmitt, Ohio J. Sci. 75: 78. 1975.

Note: Pitt (1980) considered this species to be related to *T. luteus*, but our ITS data clearly show that is synonymous with *T. ucrainicus.*

Talaromyces panasenkoi Pitt, The Genus *Penicillium*: 482. 1980.
Anamorphic synonym: *Penicillium panasenkoi* Pitt (simultaneously published, identical holotype).

Note: Pitt (1980) proposed *T. panasenkoi* as a new species for the invalidly published *P. ucraininum* Panasenko; however, Stolk & Samson (1972) had already proposed *Talaromyces ucrainicus* Udagawa for this taxon. *Talaromyces panasenkoi* Pitt is therefore a synonym of *T. ucrainicus.*

Talaromyces retardatus Udagawa, Kamiya & Kaori Osada, Trans. Mycol. Soc. Japan 34: 9. 1993.
Anamorphic synonym: *Penicillium retardatum* Udagawa, Kamiya & Kaori Osada (simultaneously published, identical holotype).

Note: No strain was available for examination and the status of this species is thus unknown.

Talaromyces spectabilis Udagawa & Suzuki, Mycotaxon 50: 82. 1994.
= *Byssochlamys spectabilis* (Udagawa & Suzuki) Houbraken & Samson, Appl. Environ. Microbiol. 74: 1618. 2008.
= *Paecilomyces variotii* Bainier Bull. Soc. mycol. Fr. 23: 27. 1907.

Note: The oldest generic and species name for this species is *P. variotii*, which becomes the correct name for the holomorph.

Talaromyces striatus (Raper & Fennell) C.R. Benj., Mycologia 47: 682. 1955.
= *Hamigera striata* (Raper & Fennell) Stolk & Samson, Persoonia 6: 347. 1971.

Talaromyces thermocitrinus Subrahm. & Gopalkr., Ind. Bot. Reporter 35: 35. 1984 (as '*T. thermocitrinum*').

Note: We have not seen the type, but judging from the substrate (dust on books), and the mention of yellow cleistothecia, it is possible that this is an *Eurotium* species, a typical contaminant of books and other material in archives. However, its reported thermophily is different from known species of the mesophilic genus *Eurotium*.

Talaromyces thermophilus Stolk, Ant. van Leeuwenhoek 31: 268. 1965.
Basionym: *Penicillium dupontii* Griffon & Maubl., Bull. Trimmest. Soc. mycol. Fr. 27: 73. 1911.

Note: Figure 1 shows that this species is related to *Thermomyces lanuginosus*, and should be transferred to *Thermomyces* (Houbraken *et al*. 2011, Houbraken & Samson 2011).

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APPENDIX: OTHER POSSIBLE GENERIC NAMES

As noted above in the Taxonomy section, in order to adopt *Talaromyces* as the generic name for the former *Penicillium* subgenus *Biverticillium,* older genera considered synonyms of *Penicillium sensu lato* had to be considered. These are treated below.

Aspergillopsis Sopp, Vid.-Selsk. Skr. I. Math.-naturv. Kl. 11: 201. 1912. (Taf. xx, Fig. 149, Taf. xxiii, Fig. 31).

Type species: *A. fumosus* Sopp 1912.

Note: This generic name is illegitimate (Art. 53), being a later homonym of *Aspergillopsis* Speg. 1910. Pitt (1980) considered Sopp's genus a tentative synonym of *Merimbla* Pitt.

Citromyces Wehmer, Ber. dt. Bot. Ges. 11: 338. 1893.

Type species: *C. pfefferianus* Wehmer 1893 = *Penicillium glabrum* (Wehmer) Westling 1911, *fide* Pitt 1980.

Note: Wehmer's genus was considered a synonym of *Penicillium* by many authors, including Raper & Thom (1949) and Pitt (1980), with *C. pfefferianus* considered a probable synonym of *P. glabrum* (subgenus *Aspergillioides*) by Pitt (1980). Therefore, the genus remains a synonym of *Penicillium sensu stricto.*

Coremium Link : Fr., Mag. Ges. naturf. Freunde, Berlin 3: 19. 1809 : Fries, Syst. mycol. 1: xlviii, 1821.

Type species: *C. glaucum* Link 1809.

Note: This genus was described in the same publication as *Penicillium*. Raper & Thom (1949) and Seifert & Samson (1985) both considered the type species to be a synonym of the type species of *Penicillium, P. expansum* Link 1809. Therefore, *Coremium* remains a synonym of *Penicillium sensu stricto.*

Eladia G. Sm., Trans. Br. mycol. Soc. 44: 47. 1961.

Type species: *Eladia saccula* (Dale) G. Sm. 1961 = *Penicillium sacculum* Dale 1926.

Note: This genus was considered a synonym of *Penicillium* by Stolk & Samson (1985), but was considered distinct by Pitt (1980), and von Arx (1981). In the multigene phylogenetic study by Houbraken & Samson (2011), *Eladia* is clearly included in *Penicillium sensu stricto* and that synonymy is accepted here.

Floccaria Grev., Scott. Crypt. Fl., Vol. 6, Pl. 301. 1828.

Type species: *F. glauca* Grev. 1828.

Note: There is no known extant type according to Seifert & Samson (1985), who searched for it in K and E. The illustration shows a synnematous fungus that could well be *P. expansum*, but there are no microscopic details. Therefore, this name can be discounted as a possible generic name for the species formerly ascribed to subgenus *Biverticillium*.

Geosmithia Pitt, Can. J. Bot. 57: 2021. 1980.

Type species: *Geosmithia lavendula* (Raper & Fennell) Pitt 1980 = *Penicillium lavendulum* Raper & Fennell 1948.

Note: Although von Arx (1981) considered *Geosmithia* a synonym of *Penicillium*, it is polyphyletic as presently circumscribed. Using SSU sequences, Ogawa *et al.* (1997) showed that *G. lavendula,* and a second common species *G. putterilli,* belong to the *Bionectriaceae, Hypocreales*. Similar results were obtained using ITS sequences by Kolařík *et al.* (2004), using LSU sequences by Schroers *et al.* (2005) and then multigene phylogenies by Kolařík & Kirkendall (2010). Despite this, some anamorphs attributed to *Geosmithia* have been described recently in *Talaromyces* (*e.g.* Yaguchi *et al.* 2005). Because the type species is not associated with the same order as *Penicillium*, *Geosmithia* need not be considered as a possible home for species of subgenus *Biverticillium*, but neither should it be considered a synonym of *Penicillium*.

Hormodendrum Bonord., Handbuch allg. Mykol.: 76. 1851.

Type species: *Amphitrichum olivaceum* Corda 1837 = *Hormodendrum olivaceum* (Corda) Bonord. 1851, lectotype selected by Clements & Shear 1931.

Note: *Hormodendron* has variously been treated as a synonym of *Penicillium* by von Arx (1974) and de Hoog & Hermanides-Nijhoff (1977) but more often as a synonym of *Cladosporium* Link, following

the study of the type specimen by Hughes (1958). There is no reason to consider this name further as a synonym of *Penicillium* or as a possible receptacle for the species of subgenus *Biverticillium*.

Merimbla Pitt, Can. J. Bot. 57: 2394. 1980.

Type species: *M. ingelheimensis* (F.H. Beyma) Pitt 1980 = *Penicillium ingelheimense* F.H. Beyma 1942.

Note: *Merimbla* was considered a possible synonym of *Penicillium* by von Arx (1981), but this has not generally been accepted. *Merimbla ingelheimensis* was considered the anamorph of *Hamigera avellanea* by Stolk & Samson (1971), but is now known to be a closely related but phylogenetically distinct species (Peterson *et al.* 2010). The *Hamigera* clade is phylogenetically distinct from subgenus *Biverticillium* in the multigene analyses of Peterson *et al*. (2010) and Houbraken & Samson (2011). In a single name system, we consider *Merimbla* a synonym of the older genus *Hamigera.*

Monilia Fr., Syst. mycol. 3: 409. 1832.

Type species: *M. caespitosa* (L. : Fr.) Fr. 1832 / *Mucor caespitosus* L. 1753.

Note: Donk (1963) suggested that *M. caespitosa* might be a species of *Penicillium* based on the protologue. However, this generic name was formally rejected to conserve usage of *Monilia* Bonorden for the well-known genus of fruit pathogens. Therefore, it is unavailable as a possible generic name for species included in subgenus *Biverticillium*.

Moniliger Letell., Fig. Champ., Pl. 668. 1839. Figs 3, 4.

Type species: not designated, two original species.

Note: According to Seifert *et al*. (2011), Letellier included two species, with illustrations clearly representing *Aspergillus.* The synonymy of *Moniliger* with *Penicillium* proposed by Kirk *et al*. (2008) thus seems unlikely, and the genus is better listed as a synonym of *Aspergillus*.

Penicillium Link : Fr., Mag. Ges. naturf. Freunde, Berlin 3: 16. 1809. : Fries, Syst. mycol. 3: 406. 1832.

Type species: *P. expansum* Link 1809, *fide* Thom 1910.

Note: With this revision, and that of Houbraken & Samson (2011), *Penicillium* is now used exclusively for the nominal Clade including *P. expansum,* and species in the now synonymous genus *Eupenicillium* F. Ludw. 1892 (Houbraken & Samson 2011).

Pritzeliella Henn., Hedwigia Beibl. 42: 88. 1903.

Type species: *P. caerulea* Henn. 1903.

Note: Clements & Shear (1931) suggested that *Pritzeliella* should be considered a synonym of *Penicillium* without further commenting on the identity of its type species. Seifert & Samson (1985) examined the holotype of *P. caerulea* and considered it a synonym of *Penicillium coprophilum* (subgenus *Penicillium*). Its status as a synonym of *Penicillium sensu stricto* thus remains unchanged.

Rhodocephalus Corda, Ic. Fung. 1: 21. 1837 (Tab. vi, Fig. 282).

Type species: *R. candidus* Corda 1837 = *Penicillium leucocephalum* Rabenh. 1844.

Note: Corda (1837) illustrated and described his species as having aseptate stipes, a branched, asymmetrical penicillate head, with long chains of ameroconidia. Rabenhorst (1844) renamed the species in *Penicillium,* changing the epithet, a conclusion followed by Lindau (1907). Thom (1930) and Raper & Thom (1949) disagreed, stating that the illustration in the protologue has branched conidial chains that would exclude the fungus from *Penicillium.* This a debatable conclusion, because the chains are simply overlapping in the illustration and there is no clear indication of branching. Pitt (1980) evidently did not examine the protologue when he suggested a synonymy with *Aspergillus candidus*. Hughes (1958) did not report on the type, and according to Holubová (in litt. to Seifert, 1991), there is no material of *Rhodocephalus* in the Corda herbarium (PRM). The asymmetrical conidiophores illustrated by Corda discount this as a possible genus for species of subgenus *Biverticillium*, but its exact identity is unknown.

Torulomyces Delitsch, Systematik der Schimmelpilze: 91. 1943 (Taf. 30, Figs 232–235).

Type species: *T. lagena* Delitsch 1943 = *Monocillium lagena* (Delitsch) Hashmi, W.B. Kendr. & Morgan-Jones 1972 = *Penicillium lagena* (Delitsch) Stolk & Samson 1983.

Note: *Torulomyces* was included as a synonym of *Penicillium sensu stricto* in the phylogenetic study of Houbraken & Samson (2011).

Yunnania H.-Z. Kong, Mycotaxon 69: 320. 1998.

Type species: *Y. penicillata* H.-Z. Kong 1998.

Note: Houbraken & Samson (2011) sequenced the ITS of authentic cultures of *Y. penicillata*, showing a relationship with the *Microascales*, suggesting a synonymy with *Scopulariopsis* or *Scedosporium* might be appropriate.

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SUPPLEMENTARY INFORMATION

Table S1. *Penicillium* strains used in the study of the infrageneric classification (addition to those mentioned in Table 1).

Name	Collection no.	Origin	GenBank accession no.
Aspergillus crystallinus	NRRL 5082^{NT} = CBS 479.65 = ATCC 16833 = IMI 139270	Forest soil, Costa Rica	EF669669^{RPB2}
Aspergillus malodoratus	NRRL 5083^{NT} = CBS 490.65 = IMI 172289 = ATCC 16834	Forest soil, Costa Rica	EF669672^{RPB2}
Aspergillus paradoxus	NRRL 2162^{HT} = ATCC 16918 = IMI 061446	Holotype of *Hemicarpenteles paradoxus*; dung of opossum, Wellington, New-Zealand	EF669670^{RPB2}
	NRRL 4695 = IMI 086829	Unknown source, India	EF669671^{RPB2}
Eladia infata	CBS 127833^{HT}	Soil, Sichuan Prov., Kangding County, China	JN406643^{RPB2}
P. abidjanum	CBS 246.67^{HT} = ATCC 18385 = IMI 136244	Savannah soil, Ivory Coast	GU981650^{BT}
P. adametzioides	CBS 313.59^{T} = ATCC 18306 = IMI 068227 = NRRL 3405	Soil, Japan	JN406578^{RPB2}
P. aethiopicum	CBS 484.84^{HT} = FRR 2942 = IBT 21501 = IBT 5903 = IMI 285524	Grain of *Hordeum vulgare*, Addis Abeba, Ethiopia	JN406548^{RPB2}
P. alicantinum	NRRL 35755	Unknown source	EU427254^{RPB2}
P. anatolicum	CBS 479.66^{HT} = IBT 30764	Soil, Turkey	JN606593^{RPB2}
P. angulare	CBS 130293^{T} = IBT 27051 = NRRL 28157	Old polypore, New Mexico, USA	JN406554^{RPB2}
P. angustipurcatum	CBS 202.84^{HT} = NHL 6481	Forest soil, Gandaki, near Nandanda, Nepal	JN406617^{RPB2}
P. antarcticum	CBS 100492^{T} = FRR 4989	Soil scraping, near nest site of Southern Fulmar Ardery Island, Windmill Islands, Wilkes Land, Antarctica	JN406653^{RPB2}
P. araracuarense	CBS 113149^{T} = IBT 23247	Leaf litter exposed for 6 months, 36-year old forest, Araracuara, Colombia	GU981642^{BT}
P. ardesiacum	CBS 497.73^{NT} = ATCC 24719 = IMI 174719	Soil near *Vitis vinifera*, Alma-Ata Region, Kazakhstan	JN406547^{RPB2}
P. asperosporum	CBS 324.83 = IMI 080450	Holotype of *P. echinosporum*; resin of *Eucalyptus tereticornis*, Prov. Guizhon, Guiyang, China	JN406574^{RPB2}
P. astrolabium	CBS 122427^{T} = NRRL 35611	Wine grapes, Portugal	JN406634^{RPB2}
P. atramentosum	CBS 291.48^{NT} = ATCC 10104 = IBT 6616 = IMI 039752 = IMI 039752ii = MUCL 29071 = MUCL 29126 = NRRL 795	French Camembert cheese, Storrs, Connecticut, USA	JN406584^{RPB2}
P. atrofulvum	CBS 109.66^{T} = IBT 30032	Soil, Katanga, Zaire	JN606620^{RPB2}
P. atrosanguineum	CBS 380.75^{IsoT} = FRR 1726 = IMI 197488	Grain in silo *Triticum aestivum*, Praha, Czech Republic	JN406557^{RPB2}
P. aurantiogriseum	CBS 324.89^{NT} = ATCC 48920 = IBT 14016 = IMI 195050 = MUCL 29090 = NRRL 971	Unrecorded source	JN406573^{RPB2}
P. bialowiezense	CBS 227.28^{T} = IBT 23044 = IMI 092237	Soil under conifers, Bialowiezska Puszcza, Poland	JN406604^{RPB2}
P. bilaiae	CBS 221.66^{NT} = ATCC 22348 = ATCC 48731 = IJFM 5025 = IMI 113677 = MUCL 31187	Soil, Kiev, Ukraine	JN406610^{RPB2}
P. boreae	CBS 111717 = NRRL 31002	Petroleum contaminated soil, near Norman Wells, Northwest-Territories, Canada	JN617715^{BT}
P. bovifimosum	CBS 102825^{T} = RMF 9598	Dry cow manure, Wyoming, USA	JN406649^{RPB2}
P. brasilianum	CBS 253.55^{HT} = ATCC 12072 = FRR 3466	Herbarium specimen, Recife, Brazil	GU981629^{BT}
P. brefeldianum	CBS 235.81^{T} = IFO 31731 = IMI 216896 = NRRL 710	Type of *P. brefeldianum* and *P. dodgei*; human alimentary tract	GU981623^{BT}
P. brevicompactum	CBS 257.29^{NT} = ATCC 10418 = ATCC 9056 = IBT 23045 = IMI 040225 = MUCL 28647 = MUCL 28813 = MUCL 28935 = MUCL 30240 = MUCL 30241 = MUCL 30256 = MUCL 30257 = NRRL 2011 = NRRL 862 = NRRL 864	Unrecorded source, Belgium	JN406594^{RPB2}
P. brevissimum	CBS 763.68^{T}	Mixed cereal feed for birds, Lucknow, India	JN406534^{RPB2}
P. brevistipitatum	CBS 122277^{T} = AS 3.6887	Soil, China	JN406528^{RPB2}
P. brocae	CBS 116113^{HT} = IBT 26293 = NRRL 31472	Faeces of coffee berry borer, Chiapas, Tapachula, Mexico	JN406639^{RPB2}
P. burgense	CBS 325.89^{T}	Uncultivated soil, Highlands north of Burgos, Spain	JN406572^{RPB2}
P. canariense	CBS 111720^{HT} = NRRL 31003	Soil, Canary Islands, Spain	JN617714^{BT}
P. caperatum	CBS 233.81 = IFO 31730 = IMI 216895	Neotype of *E. brefeldianum fide* Pitt (1979, p. 119); soil, Murrumbidgee Irrigation Area, NSW, Australia	GU981659^{BT}

SUPPLEMENTARY INFORMATION

Table S1. (Continued).

Name	Collection no.	Origin	GenBank accession no.
P. caperatum	CBS 443.75^{T} = ATCC 28046	Soil, Papua New Guinea	GU981660^{BT}
P. capsulatum	CBS 301.48^{NT} = ATCC 10420 = IJFM 5120 = IMI 040576 = NRRL 2056	Optical instrument, Canal Zone, Panama	JN406582^{RPB2}
P. carneum	CBS 112297^{T} = IBT 6884	Mouldy rye bread, Denmark	JN406642^{RPB2}
P. chalybeum	CBS 255.87 = FRR 2658 = IMI 288722	Dried fish, *Decapterus* sp., Indonesia	JN406596^{RPB2}
P. charlesii	CBS 326.59 = ATCC 18225 = IMI 068223	Type of *Penicillium decumbens* var. *atrovirens* and *P. atrovirens*; soil, Japan	JN406571^{RPB2}
P. charlesii	CBS 330.59 = IMI 068224 = MUCL 15638	Type of *P. fellutanum* var. *nigrocastaneum*; soil, Japan	JN406570^{RPB2}
P. 'chermesinum'	CBS 305.48 = ATCC 10424 = IMI 040577 = NRRL 2049	Air, Panama	JN406581^{RPB2}
	CBS 231.81 = IMI 191730 = NRRL 2048	Neotype of *P. chermesinum sensu* Pitt; deteriorating military equipment Florida, USA	JN406600^{RPB2}
P. christensenae	CBS 126236^{T} = IBT 23355	Soil in native forest, "Lowland forest" east / north east side of Costa Rica about 30 km inland from Limon and the Caribbean.	JN606624^{RPB2}
P. chrzaszczii	CBS 217.28^{T} = MUCL 29167 = NRRL 903 = NRRL 1741 = IBT 18226 = IBT 11222 = IBT 16409	Woodland soil, Puszcza Bialowieska Forest, Poland	JN606628^{RPB2}
P. ciegleri	CBS 275.83^{T} = IMI 257691	Rye grain, Spain	GU981671^{BT}
P. cinereoatrum	CBS 222.66^{IsoT} = ATCC 22350 = IJFM 5024 = IMI 113676	Forest soil, Kiev, Ukraine	JN406608^{RPB2}
P. cinnamopurpureum	CBS 847.68^{T} = ATCC 18489 = CBS 429.65	Milled rice, Japan	JN406533^{RPB2}
P. citreonigrum	NRRL 1187 = IMI 092212 = MUCL 29230 = MUCL 29783 = NRRL 1187	Type of *P. citreoviride*; unknown source	EF198501^{RPB2}
	NRRL 2046 = CBS 308.48 = ATCC 10425 = IMI 40575 = NRRL 2046	Deteriorating military equipment, Florida, USA	EF198502^{RPB2}
P. coeruleum	CBS 141.45 = NCTC 6595	As *Citreomyces coeruleus*; unknown source	GU981655^{BT}
P. commune	NRRL 35686	Unknown source	EF198602^{RPB2}
P. confertum	CBS 171.87^{HT} = IBT 21515 = IBT 3098 = IBT 5672 = IMI 296930 = NRRL 13488 = NRRL A-26904	Cheek pouch of *Dipodomys spectabilis*, Arizona, USA	JN406622^{RPB2}
P. coprophilum	CBS 110760 = IBT 5551	Rabbit dung, Baarn, Netherlands	JN406645^{RPB2}
P. copticola	CBS 127355^{T} = IIBT 30771	Tortilla, USA	JN606599^{RPB2}
P. coralligerum	CBS 123.65^{NT} = ATCC 16968 = FRR 3465 = IMI 099159 = NRRL 3465	Seed of *Hordeum vulgare* (barley), France	JN406632^{RPB2}
P. corylophilum	CBS 330.79 = IJFM 5147	Authentic strain of *P. citreovirens* Abe ex. Ramírez; air, Barcelona, Spain	JN406569^{RPB2}
P. corynephorum	CBS 256.87^{T} = FRR 2663 = IMI 288724	Dried fish, *Decapterus* sp., Indonesia	JN406595^{RPB2}
P. cremeogriseum	CBS 223.66^{NT} = ATCC 18323 = IJFM 5011 = IMI 197492 = NRRL 3389	Forest soil, Kiev, Ukraine	GU981624^{BT}
P. crocicola	CBS 745.70^{IsoT} = ATCC 18313	*Crocus sativus* (Saffron), Japan	JN406535^{RPB2}
P. cyaneum	CBS 315.48^{NT} = ATCC 10432 = IMI 039744 = NRRL 775	Unrecorded source, France	JN406575^{RPB2}
P. daleae	CBS 211.28^{T} = ATCC 10435 = IFO 6087 = IFO 9072 = IMI 034910 = MUCL 29234 = NRRL 2025	Soil under conifer, Poland	GU981649^{BT}
P. decaturense	CBS 117509^{T} = IBT 27117 = NRRL 28152	Old resupinate fungus, Ramsey Lake State Park, Decatur, Illinois, USA	JN606621^{RPB2}
P. decumbens	CBS 230.81^{NT} = IMI 190875 = MUCL 29107 = NRRL 741	Unrecorded source, Miami, Florida, USA	JN406601^{RPB2}
P. dierckxii	CBS 185.81^{NT} = IMI 092216 = MUCL 28665 = NRRL 755	Unknown source, Belgium	JN406619^{RPB2}
P. donkii	CBS 188.72^{HT} = ATCC 48439; = IFO 31746 = IMI 197489 = MUCL 31188	Arable soil, Alaska, USA	JN617718^{BT}
P. echinulonalgiovense	CBS 328.59^{T} = ATCC 18314 = IFO 6229 = IMI 068213	Soil, Japan	GU981631^{BT}
P. egyptiacum	CBS 244.32^{NT} = ATCC 10441 = IBT 14684 = IMI 040580 = NRRL 2090	Soil, Cairo, Egypt	JN406598^{RPB2}

SUPPLEMENTARY INFORMATION

Table S1. (Continued).

Name	Collection no.	Origin	GenBank accession no.
P. ehrlichii	CBS 324.48^{HT} = ATCC 10442 = IMI 039737 = NRRL 708	Poland	GU981652^{BT}
P. elleniae	CBS 118135^{T} = IBT 23229	Leaf litter exposed for 6 months, mature forest, Araracuara, Colombia	GU981663^{BT}
P. fagi	CBS 689.77^{T} = CCM F-696 = IJFM 3049 = IMI 253806	Fallen leaf, on Andosol, alt. 800 m. *Fagus sylvatica*, Navarra, Spain	JN406540^{RPB2}
P. fellutanum	IBT 15460^{NT} = NRRL 746 = IMI 39734 = ATCC 10443	Unrecorded source, USA	JN406646^{RPB2}
P. fennelliae	CBS 711.68^{HT} = ATCC 22050 = ATCC 52492 = IMI 151747 = MUCL 31322	Flour, Zaire	JN406536^{RPB2}
P. flavigenum	CBS 419.89^{HT} = IBT 21526 = IBT 3091 = IMI 293207	Rhizosphere soil of *Brassica campestris* var. *toria*, Lyngby, Denmark	JN406551^{RPB2}
P. formosanum	CBS 211.92^{HT} = IBT 19748 = IBT 21527	Soil, Hsitou, Taiwan	JN406615^{RPB2}
P. fuscum	CBS 235.60 = ATCC 18483	Type of *P. silvaticum*; forest soil, USSR	JN406599^{RPB2}
	CBS 309.63 = ATCC 18322	Type of *P. macedonense*; forest soil, former Yugoslavia, Macedonia	JN406580^{RPB2}
P. gallaicum	CBS 167.81^{T} = ATCC 42232 = IMI 253794 = IBT 22016	Air, Madrid, Spain	JN606609^{RPB2}
P. glabrum	CBS 105.11	Type of *P. frequentans*, unknown substrate, former West-Germany, Germany	JN406647^{RPB2}
	CBS 229.28 = IMI 092231 = MUCL 29111 = NRRL 751	Type of *P. paczoskii*; soil, under conifer Poland	JN406602^{RPB2}
	NRRL 35684	Boiled cork, Portugal	EF198601^{RPB2}
P. gladioli	CBS 332.48^{NT} = ATCC 10448 = IBT 14772 = IMI 034911 = IMI 034911ii = MUCL 29174 = NRRL 939	*Gladiolus* corm, imported from the Netherlands, Washington DC, District of Columbia, USA	JN406567^{RPB2}
P. glandicola	CBS 498.75^{EpiT} = IBT 21529 = IMI 154241	Corm, Portugal	JN406546^{RPB2}
P. godlewskii	CBS 215.28^{T} = ATCC 10449 = ATCC 48714 IFO 7724 = IMI 040591 = MUCL 29243 = NRRL 2111	Soil under pine, Bialowieska, Poland	JN606626^{RPB2}
P. gorlenkoanum	CBS 408.69^{IsoT} = IMI 140339	Soil, Syria	JN606601^{RPB2}
P. heteromorphum	CBS 226.89^{NT}	Soil, Hubei Province, Shennongjia, China	JN406605^{RPB2}
P. hetheringtonii	CBS 122392^{T}	Soil, Treasure Island, Florida, USA	JN606606^{RPB2}
P. hirayamae	NRRL 143^{NT} = CBS 527.65 = 229.60 = ATCC 18312 = IMI 078255 = IMI 078255ii = NRRL 143	Milled rice, Thailand	EU021625^{RPB2}
P. hirsutum	CBS 135.41^{T} = ATCC 10429 = IBT 21531 = IMI 040213 = MUCL 15622 = NRRL 2032	Aphid, green fly, Baarn, Netherlands	JN406629^{RPB2}
P. hispanicum	CBS 184.81 = FRR 2061 = IMI 190235 = NRRL 2061	Neotype of *P. implicatum sensu* Pitt; soil, New Delhi, India	JN406620^{RPB2}
	CBS 691.77^{T} = ATCC 38667 = IJFM 3223 = IMI 253785	*Citrus limonium*, Madrid, Spain	JN406539^{RPB2}
P. incoloratum	CBS 101753^{HT} = AS 3.4672	Seed of *Phaseolus angularis*, Beijing, China	JN406651^{RPB2}
P. indicum	CBS 115.63^{IsoT} = ATCC 18324 = FRR 3387 = IMI 166620	Sputum, man, Delhi, India	JN406640^{RPB2}
P. jamesonlandense	CBS 102888^{T} = DAOM 234087 = IBT 21984 = IBT 24411	Soil near *Cassiope tetragona* and *Phyllodoce coerulea*, East Greenland, Jameson Land near Hugin Lake, Greenland	JN406648^{RPB2}
P. janczewskii	CBS 221.28^{NT} = IMI 191499 = NRRL 919	Soil under *Pinus* sp., Poland	JN406612^{RPB2}
P. janthinellum	CBS 340.48^{NT} = ATCC 10455 = IMI 040238 = NRRL 2016	Soil, Nicaragua	GU981625^{BT}
P. javanicum	CBS 341.48^{HT} = ATCC 9099 = IFO 31735 = IMI 039733 = MUCL 29099 = NRRL 707	Root of *Camellia sinensis*, Indonesia, Java	GU981657^{BT}
P. jensenii	CBS 216.28^{T} = ATCC 10456 = IMI 068233 = NRRL 3431	Forest soil, Poland	JN406614^{RPB2}
P. jugoslavicum	CBS 192.87^{NT} = IJFM 7785 = IMI 314508	Seed of *Helianthus annuus* (sunflower), former Yugoslavia	JN406618^{RPB2}
P. kojigenum	CBS 345.61^{T} = ATCC 18227 = IMI 086562 = MUCL 2457 = NRRL 3442	Roadside soil, Kirkcudbrightshire, Gelston, Scotland	JN406564^{RPB2}

SUPPLEMENTARY INFORMATION

Table S1. (Continued).

Name	Collection no.	Origin	GenBank accession no.
P. levitum	CBS 345.48^{NT} = ATCC 10464 = IFO 6101 = IMI 039735 = NRRL 705	Modeling clay, USA	GU981654^{BT}
P. limosum	CBS 339.97	Marine sediment, Nagasaki prefecture, Japan	GU981621^{BT}
P. lineolatum	CBS 188.77^{HT} = NHL 2776	Soil from copse, Japan	GU981620^{BT}
P. lividum	CBS 347.48^{NT} = ATCC 10102 = IMI 039736 = NRRL 754	Soil, Scotland	JN406563^{RPB2}
P. luteocoeruleum	CBS 347.51^{T} = ATCC 18237 = IMI 107651 = NRRL 3450	Wakamoto corn and rice cake, Nehira, Osaka Univ. Fac. Techn., Japan	JN406562^{RPB2}
P. luzoniacum	CBS 622.72^{IsoT} = DSM 2418 = NHL 6128	Soil from pine forest, Luzon Island, Sinipsip near Baguio, Philippines	JN406543^{RPB2}
P. madriti	CBS 347.61^{HT} = ATCC 18233 = IMI 086563 = MUCL 2456 = MUCL 31193 = NRRL 3452	Garden soil, Madrid, Spain	JN406561^{RPB2}
	CBS 170.81 = ATCC 42229 = IJFM 5144 = IMI 253791	Type of *P. castellonense*; air, Madrid, Spain	JN406623^{RPB2}
P. malacaense	CBS 160.81^{T} = ATCC 42241 = IJFM 7093 = IMI 253801	Air, Madrid, Spain	JN406626^{RPB2}
	CBS 163.81 = ATCC 42237 = IJFM 7029	Type of *P. ovetense*; sandy soil, Madrid, Spain	JN406624^{RPB2}
P. manginii	CBS 253.31^{NT} = NRRL 2134 = IMI 191732 = IBT 18224	Soil, unknown source	JN606618^{RPB2}
P. mariaecrucis	CBS 271.83^{T} = IMI 256075	*Secale cereale*, Spain	GU981630^{BT}
P. melanoconidium	CBS 641.95 = IBT 11406 = IBT 21534	Soil, Denmark	JN406529^{RPB2}
P. melinii	CBS 218.30^{NT} = ATCC 10469 = IMI 040216 = MUCL 29235 = NRRL 2041	Forest soil, USA	JN406613^{RPB2}
	CBS 280.58 = ATCC 18383 = IMI 071624 = NRRL 2672	Type of *P. radulatum*; Calluna heathland soil, England	JN406586^{RPB2}
P. meloforme	CBS 445.74^{HT} = ATCC 28049 = IMI 216903 = NHL 6468	Soil, Papua New Guinea	GU981656^{BT}
P. meridianum	CBS 314.67^{HT} = ATCC 18545 = IMI 136209	Grassland soil, Pretoria, South Africa	JN406576^{RPB2}
P. miczynskii	CBS 220.28^{T} = ATCC 10470 = DSM 2437 = IFO 7730 = IMI 040030 = MUCL 29228 = NRRL 1077 = IBT 5491	Soil under conifer, Tatry mountains, Poland	JN606623^{RPB2}
P. molle	CBS 456.72^{HT} = ATCC 24075 = IMI 084589	Soil, Pakistan	JN406550^{RPB2}
P. montanense	CBS 310.63^{HT} = ATCC 14941 = IMI 099468 = MUCL 31326 = NRRL 3407	Coniferous forest soil, Ravalli Co., Montana, USA	JN406579^{RPB2}
P. multicolor	NRRL 2060 = IMI 092040 = NRRL 2060	Weathering treated cellophane, Florida, USA	EU427262^{RPB2}
P. murcianum	CBS 161.81^{T} = ATCC 42239 = IJFM 7031 = IMI 253800	Sandy soil, Madrid, Spain	JN406625^{RPB2}
P. nalgiovense	CBS 352.48^{NT} = ATCC 10472 = IBT 21536 = IMI 039804 = MUCL 31194 = NRRL 911	Ellischauer cheese, fomer Czechoslovakia	JN406560^{RPB2}
P. neocrassum	CBS 122428^{T} = NRRL 35639	Wine grapes, Madeira Island, Portugal	JN406633^{RPB2}
P. nodositatum	CBS 330.90^{T}	Soil, Alberta, Canada	JN406568^{RPB2}
P. nodulum	CBS 227.89^{NT}	Mouldy pork, Hubei Province, Shennongjia, China	JN406603^{RPB2}
P. novae-zeelandiae	CBS 137.41^{T} = ATCC 10473 = IMI 040584ii = NRRL 2128	Apothecium of *Sclerotinia*, Palmerston North, New Zealand	JN406628^{RPB2}
P. ochrochloron	CBS 357.48^{NT} = ATCC 10540 = IMI 039806 = NRRL 926	Copper sulphate solution, Washington, USA	GU981672^{BT}
P. ochrosalmoneum	CBS 489.66^{HT} = ATCC 18338 = IMI 116248ii	Cornmeal, South Africa	JN606631^{RPB2}
P. odoratum	CBS 294.62^{T} = ATCC 14769 = CBS 296.62 = IMI 094208ii = NRRL 3007	Peaty soil in Picea-Larix bog, Taylor Co., Wisconsin, USA	JN406583^{RPB2}
P. oligosporum	CBS 349.51^{T}	Japan	GU981658^{BT}
P. onobense	CBS 174.81^{T} = ATCC 42225 = IJFM 3026	Soil, Navarra, Spain	GU981627^{BT}
P. palmense	CBS 336.79^{T} = ATCC 38669 = IJFM 3840	Gran Canaria, Las Palmas, Spain	JN406566^{RPB2}
P. paneum	CBS 465.95 = IBT 13929	Mouldy baker's yeast, Vangede, Denmark	JN406549^{RPB2}

SUPPLEMENTARY INFORMATION

Table S1. (Continued).

Name	Collection no.	Origin	GenBank accession no.
P. papuaneum	CBS 570.73^{IsoT} = ATCC 28050 = ATCC 48363	Forest soil under *Pinus* sp. Central Dist., Port Moresby, Papua New Guinea	JN406545^{RPB2}
P. paraherquei	CBS 430.65^{AUT} = FAT 824	Soil, Japan	GU981628^{BT}
P. parvum	CBS 359.48^{NT} = ATCC 10479 = IFO 7732 = IMI 040587 = NRRL 2095 = QM 1878	Soil, Nicaragua	JN406559^{RPB2}
P. pasqualense	CBS 122402 = IBT 29047	Air in bakery, Averhorn, the Netherlands	JN606617^{RPB2}
P. patens	CBS 260.87^{HT} = FRR 2662	Dried fish, *Rastrelliger kanagurta*, Indonesia	JN406593^{RPB2}
P. paxilli	CBS 360.48^{T} = ATCC 10480 = IMI 040226 = NRRL 2008 = IBT 16202	Ex-type; optical instrument, Barro Colorado Island, Panama	JN606610^{RPB2}
P. penarojense	CBS 113178^{T} = IBT 23262	Leaf litter exposed 6 months, mature forest, Peña Roja, Colombia	GU981646^{BT}
P. percisinum	CBS 111235^{T} = AS 3.5891 = IBT 24565	Soil, Qinghai prov., China	JN406644^{RPB2}
P. philippinense	CBS 623.72^{AUT} = DSM 2420 = NHL 6130	Twig peduncle and fruit, Luzon Island, Sinipsip near Baguio, Philippines	JN406542^{RPB2}
P. phoeniceum	CBS 249.32^{NT} = ATCC 10481 = IJFM 5122 = IMI 040585 = NRRL 2070	Sooty mould on *Phoenix* sp. (palm)	JN406597^{RPB2}
P. pimiteoiense	CBS 102479^{T} = NRRL 25542	Kidney epithelial cell culture flask, Peoria, Illinois, USA	JN406650^{RPB2}
P. piscarium	CBS 362.48^{T} = ATCC 10482 = IMI 040032 = NRRL 1075	Cod-liver oil emulsion, Norway	GU981668^{BT}
P. polonicum	CBS 222.28^{T} = IBT 12821 = IMI 291194 = MUCL 29204 = NRRL 995	Soil, Puszcza Bialowieska Forest, Poland	JN406609^{RPB2}
P. psychrosexualis	CBS 128036^{HT}	Wooden crate in cold-store of apples, Netherlands	JN406537^{RPB2}
P. pullum	CBS 331.48 = ATCC 10447 = IFO 6097 = IMI 039747 = NRRL 721	Soil, Tennessee, USA	JN617719^{BT}
P. pulvillorum	CBS 280.39^{NT} = IFO 7763 = NRRL 2026	Acidic soil, UK	GU981670^{BT}
P. quebecense	CBS 101623^{T} = IBT 29050	Air in sawmill, Quebec, Canada	JN606622^{RPB2}
P. quercetorum	CBS 417.69^{IsoT} = ATCC 48727 = IMI 140342 = MUCL 31203	Soil, Syria	JN406552^{RPB2}
P. raciborskii	CBS 224.28^{T} = ATCC 10488 = IMI 040568 = MUCL 29246 = NRRL 2150	Soil, under conifer Poznan area, "Dluga Goslina", Poland	JN406607^{RPB2}
P. raistrickii	CBS 261.33^{T} = ATCC 10490 = IMI 040221 = NRRL 1044 = NRRL 2039	Cotton yarn, UK	JN406592^{RPB2}
P. ramusculum	NRRL 2279	Unknown source	EU427260^{RPB2}
P. raperi	CBS 281.58^{NT} = ATCC 22355 = IFO 8179 = IMI 071625 = NRRL 2674	Soil, Bedford, UK	GU981622^{BT}
P. raphiae	CBS 126234T = IBT 22407	Soil under *Raphia* (?) palm in primary forest, Las Alturas, elev. 1530 m, Costa Rica	JN606619^{RPB2}
P. reticulisporum	CBS 513.74 = DSM 2207 = IFO 9712	Type of *P. arvense* and *E. arvense*; soil, Japan	GU981666^{BT}
	CBS 121.68^{AUT} = ATCC 18565 = IMI 136699 = NHL 6102 = NRRL 3446	Soil, Japan	GU981665^{BT}
P. ribeum	CBS 127809^{T} = IBT 16537 = IBT 24431 = DAOM 234091	Red currant, Wyoming, USA	JN406631^{RPB2}
P. rolfsii	CBS 368.48^{T} = ATCC 10491 = IFO 7735 = IMI 040029 = MUCL 29229 = NRRL 1078	Pineapple, Florida, USA	GU981667^{BT}
P. roqueforti	CBS 221.30^{NT} = ATCC 10110 = ATCC 1129 = IBT 6754 = IMI 024313 = NRRL 849	French Roquefort cheese, USA	JN406611^{RPB2}
P. roseopurpureum	CBS 266.29^{NT} = ATCC 10492 = IMI 040573 = MUCL 28654 = MUCL 29237 = NRRL 2064 = NRRL 2064A	Unrecorded source	JN606613^{RPB2}
P. rubefaciens	CBS 145.83^{HT}	Sandy soil under pine tree, Valladolid, Spain	JN406627^{RPB2}
P. rubens	CBS 205.57 = ATCC 8537 = ATCC 9478 = IBT 23019 = IMI 015378 = NRRL 1209 = NRRL 824	Contaminant of bacterial culture (Fleming's strain), UK	JN406616^{RPB2}
P. rubidurum	CBS 609.73^{HT} = ATCC 28051 = ATCC 48238 = IMI 228551	Soil, East Sepik Dist., Wewak, Papua New Guinea	JN406544^{RPB2}
P. sabulosum	CBS 261.87^{HT} = FRR 2743	Spoiled pasteurized fruit juice, Sydney, New South Wales, Australia	JN406591^{RPB2}

SUPPLEMENTARY INFORMATION

Table S1. (Continued).

Name	Collection no.	Origin	GenBank accession no.
P. sajarovii	CBS 277.83^{NT} = CECT 2751 = IMI 259992	*Secale cereale* (rye) Zamora, Castrocontrigo, Spain	JN406588^{RPB2}
P. sanguifluum	CBS 148.83 = CECT 2753	Sandy soil under pine tree, Valladolid, Spain	JN606614^{RPB2}
	CBS 685.85 = IJFM 19078 = IBT 4904 = IBT 10578 = IBT 10579	Ex-type of *P. lacussarmientei*, sandy soil, National Park of Torres del Paine, near Lake Sarmiento, Tierra del Fuego, Chile	JN606615^{RPB2}
P. scabrosum	CBS 683.89^{HT} = FRR 2950 = IBT 3736 = IMI 285533	*Zea mays*, Denmark	JN406541^{RPB2}
P. sclerotigenum	CBS 101033^{T} = ATCC 18488 = CBS 343.59 = IBT 14346 = IBT 21544 = IMI 68616 = NRRL 3461	Rotting tuber, *Dioscorea batatas,* Myogo Pref., Tamba Prov., Sasayama, Japan	JN406652^{RPB2}
P. sclerotiorum	CBS 287.36^{NT} = ATCC 10494 = IMI 040569 = NRRL 2074	Air, Buitenzorg, Java, Indonesia	JN406585^{RPB2}
P. simplicissimum	CBS 372.48^{NT} = ATCC 10495 = IFO 5762 = IMI 039816	Flannel bag, South Africa	GU981632^{BT}
P. sinaicum	CBS 279.82^{HT} = NHL 2894	*Secale cereale* (rye) Suez Canal, 30 km N of Port Said, Sinai Peninsula, Egypt	JN406587^{RPB2}
P. sizovae	CBS 413.69^{NT} = IMI 140344	Soil, Syria	JN606603^{RPB2}
P. skrjabinii	CBS 439.75^{NT} = IMI 196528	Soil, Russia (far East)	GU981626^{BT}
P. smithii	CBS 276.83^{NT} = CECT 2744 = IMI 259693	*Secale cereale* (rye), Zamora, Torneros, Spain	JN406589^{RPB2}
P. soppii	CBS 226.28^{NT} = ATCC 10496 = IMI 040217 = MUCL 29233 = NRRL 2023	Soil, Puszcza Bialowieska Forest, square “652”, Poland	JN406606^{RPB2}
P. spinulosum	CBS 374.48^{NT} = ATCC 10498 = IMI 024316 = MUCL 13910 = MUCL 13911 = NRRL 1750	Culture contaminant, Hannover, Germany	JN406558^{RPB2}
P. steckii	CBS 260.55^{NT} = ATCC 10499 = DSM 1252 = IMI 040583 = NRRL 2140	Cotton fabric treated with copper naphthenate; Panama	JN606602^{RPB2}
P. stolkiae	CBS 315.67^{HT} = IMI 136210 = ATCC 18546	Peaty forest soil, Eastern Transvaal, South-Africa	JN617717^{BT}
P. striatisporum	CBS 705.68^{HT} = ATCC 22052 = IMI 151749 = MUCL 31202	Leaf litter, *Acacia karroo* (Sweet Thorn), Potchefstroom, South Africa	JN406538^{RPB2}
P. subarcticum	CBS 111719^{HT} = NRRL 31108	Petroleum contaminated soil, near Norman Wells, Northwest-Territories, Canada	JN617716^{BT}
P. subericola	CBS 125096^{T}	Non-boiled cork, Coruche, Portugal	JN406621^{RPB2}
P. sublateritium	CBS 267.29^{NT} = ATCC 10502 = IMI 040594 = MUCL 28655 = NRRL 2071	Unrecorded source, Belgium	JN406590^{RPB2}
P. sumatrense	NRRL 6181	Unknown source	EF198540^{RPB2}
	NRRL 779^{T} = CBS 281.36 = NRRL 779 = ATCC 48669 = IBT 29658 = IBT 4978	Soil, Toba Heath, Sumatra, Indonesia	EF198541^{RPB2}
	CBS 416.69 = IMI 140336 = IBT 29648	Isotype of *P. baradicum*; soil under cornel, Damascus, Syria	JN606612^{RPB2}
P. svalbardense	CBS 122416^{T} = IBT 23856 = EX-F 1307	Glacial ice, Svalbard, Greenland	GU981669^{BT}
P. swiecickii	CBS 119391^{T} = FRR 918 = IBT 27865 = IMI 191500 = NRRL 918	Pine forest soil, Poland	JN406635^{RPB2}
P. terrenum	CBS 313.67^{HT} = ATCC 18547 = IMI 136208	Soil in subtropical forest, Eastern Transvaal, South Africa	JN406577^{RPB2}
P. terrigenum	CBS 127354^{T} = IBT 30769	Soil, Hawaii, USA	JN606600^{RPB2}
P. toxicarium	NRRL 31271	Unknown source	EF198486^{RPB2}
	NRRL 6172	Unknown source	EF198499^{RPB2}
P. tropicoides	CBS 122410^{T}	Soil rainforest, near Hua-Hin, Thailand	JN606608^{RPB2}
P. tropicum	CBS 112584^{T} = IBT 24580	Soil between *Coffea arabica*, Karnataka, India	JN606607^{RPB2}
P. turbatum	CBS 134.41 = ATCC 10415 = IMI 040590 = NRRL 2086	Neotype of *P. baarnense*; soil , Baarn, Netherlands	JN406630^{RPB2}
	CBS 339.61 = NRRL 2087	Contaminant of *P. euglaucum* culture, see also Stolk Scott (1967); leaf litter of *Acacia mollissima*, Natal, South Africa	JN406565^{RPB2}
	CBS 383.48^{NT} = ATCC 9782 = CBS 237.60 = IMI 039738 = MUCL 29115 = NRRL 757 = NRRL 758	Rotten twig *Taxus baccata*	JN406556^{RPB2}
P. vanderhammenii	CBS 126216^{T} = DTO 97A3 = IBT 23203	Leaf litter exposed for 6 months, mature forest, Araracuara, Colombia	GU981647^{BT}

SUPPLEMENTARY INFORMATION

Table S1. (Continued).

Name	Collection no.	Origin	GenBank accession no.
P. vasconiae	CBS 339.79^{T} = CBS 175.81, IJFM 3008	Acid washed brown soil, Spain	GU981653^{BT}
P. vinaceum	CBS 389.48^{NT} = ATCC 10514 = IMI 029189 = NRRL 739	Soil, Utah, USA	JN406555^{RPB2}
P. virgatum	CBS 114838^{IsoT} = BBA 65745	Soil near soy bean plant North of Noumea, Port Laguerre, New Caledonia	JN406641^{RPB2}
P. waksmanii	CBS 230.28^{NT} = ATCC 10516 = IFO 7737 = IMI 039746 = IMI 039746i = MUCL 29120 = NRRL 777 = IBT 5003 = IBT 6994	Woodland soil, Puszcza Bialowieska Forest, Poland	JN606627^{RPB2}
P. wellingtonense	CBS 130375 = IBT 23557	Soil, New Zealand	JN606616^{RPB2}
P. westlingii	CBS 231.28^{T} = IMI 092272 = IBT 15088	Soil under conifer, Denga Goolina, Poznan, Poland	JN606625^{RPB2}
P. wotroi	CBS 118171^{T} = IBT 23253	Leaf litter exposed for 6 months, mature forest, Araracuara, Colombia	GU981637^{BT}
P. yarmokense	CBS 410.69^{IsoT} = FRR 520 = IMI 140346	Soil, Syria	JN406553^{RPB2}
P. zonatum	CBS 992.72^{HT} = ATCC 24353	Coastal marsh soil, USA, North Carolina	GU981651^{BT}
Penicillium sp.	CBS 116986 = IBT 3265	Soil, Wales	JN406638^{RPB2}
	CBS 117181 = IBT 6005 = IMI 304286	Barley, Denmark	JN406637^{RPB2}
	CBS 117192 = IBT 22220 = IBT 24432	Chestnut, France	JN406636^{RPB2}

SUPPLEMENTARY INFORMATION

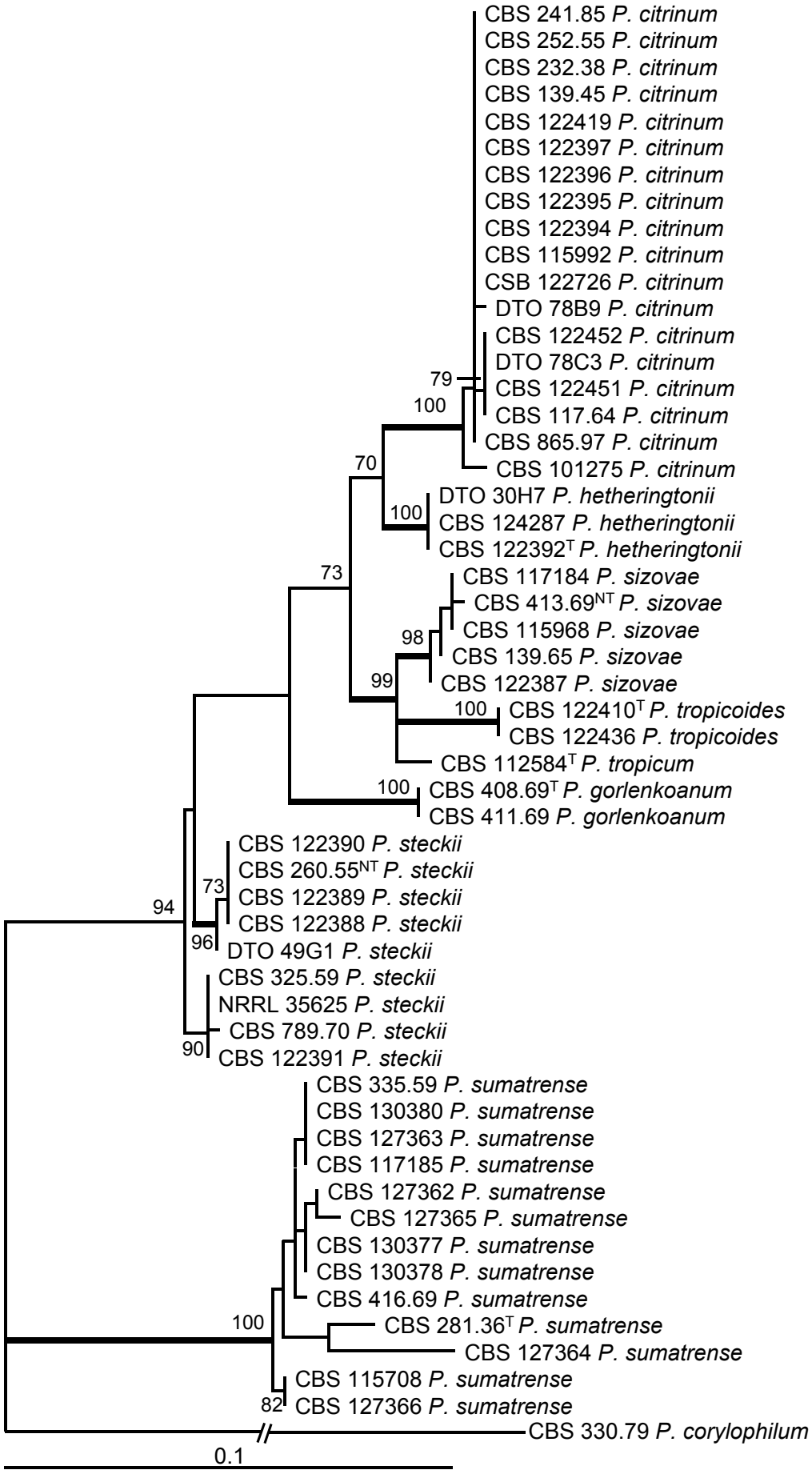

Fig. S1. Maximum Likelihood tree based on a partial β-tubulin sequence data of the *P. citrinum*-clade. Numbers above branches are bootstrap values. Only values above 70 % are shown and branches with more than 95 % bootstrap support are thickened. The phylogram is rooted with *P. corylophilum* (CBS 330.79).

SUPPLEMENTARY INFORMATION

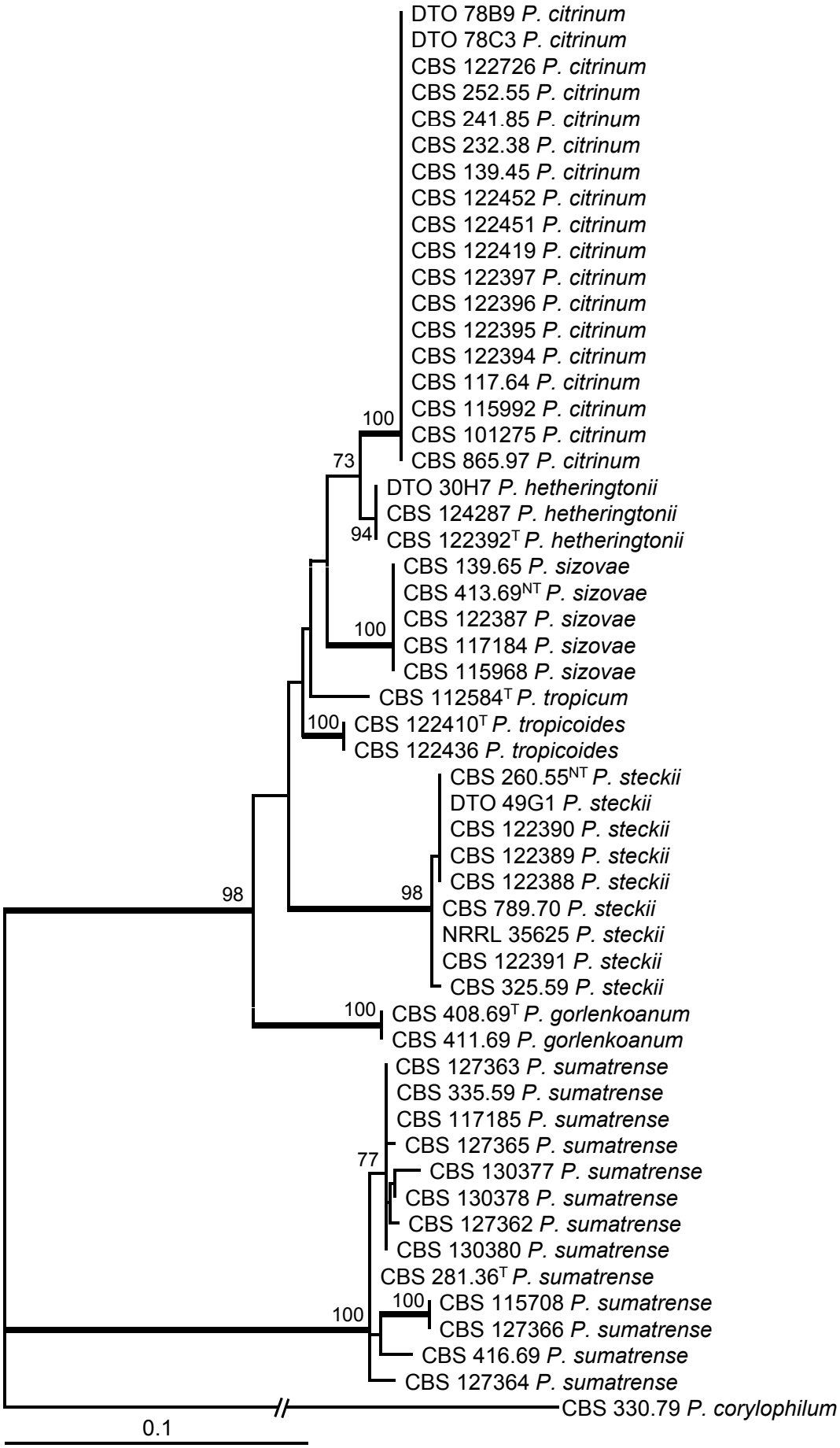

Fig. S2. Maximum Likelihood tree based on a partial calmodulin sequence data of the *P. citrinum*-clade. Numbers above branches are bootstrap values. Only values above 70 % are shown and branches with more than 95 % bootstrap support are thickened. The phylogram is rooted with *P. corylophilum* (CBS 330.79).

SUPPLEMENTARY INFORMATION

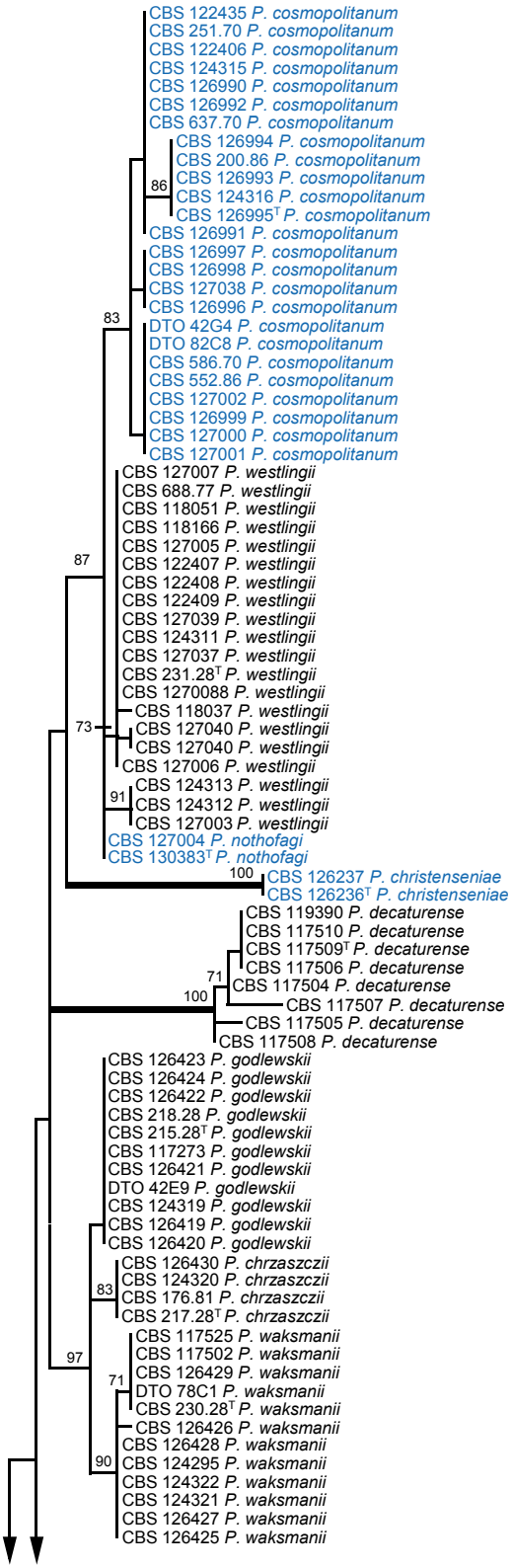

Fig. S3. Maximum Likelihood tree based on a partial β-tubulin sequence data of the *P. westlingii*-clade. Numbers above branches are bootstrap values. Only values above 70 % are shown and branches with more than 95 % bootstrap support are thickened. The phylogram is rooted with *P. corylophilum* (CBS 330.79).

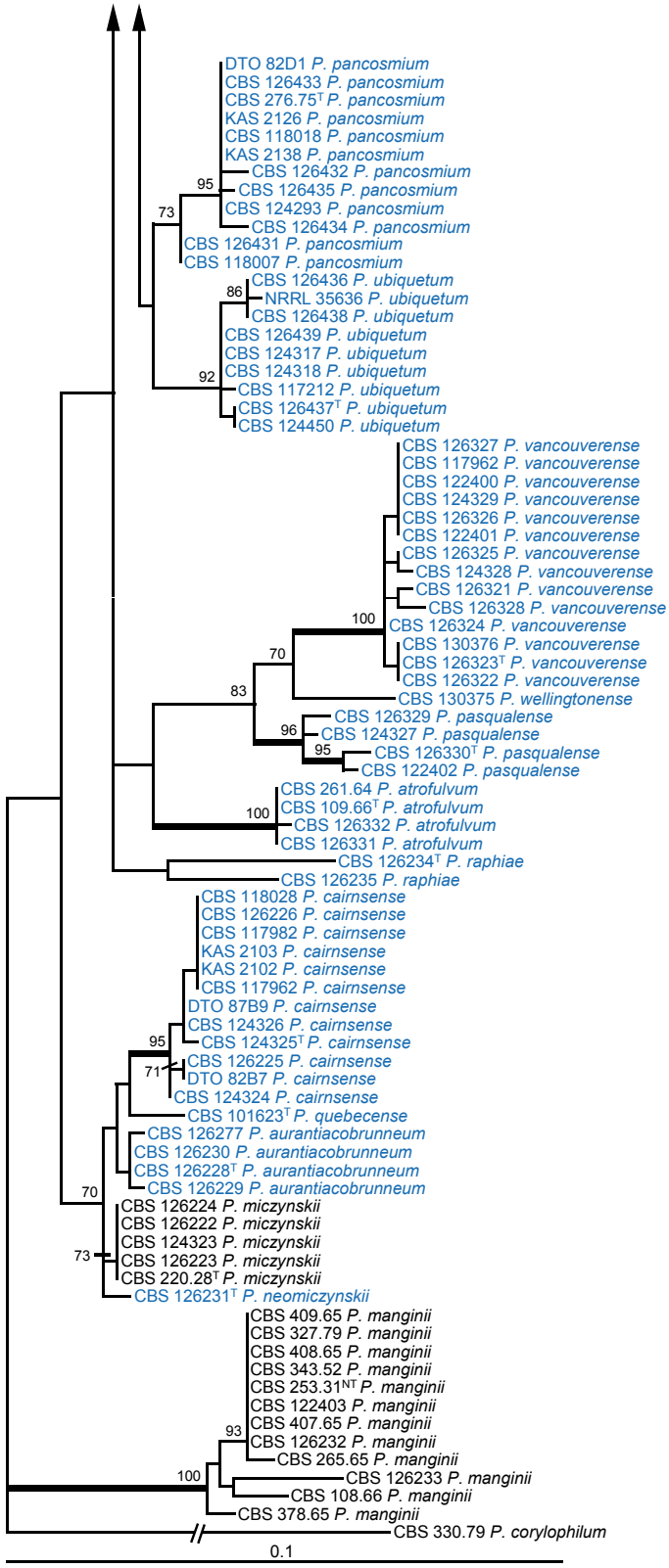

Fig. S3. (Continued).

SUPPLEMENTARY INFORMATION

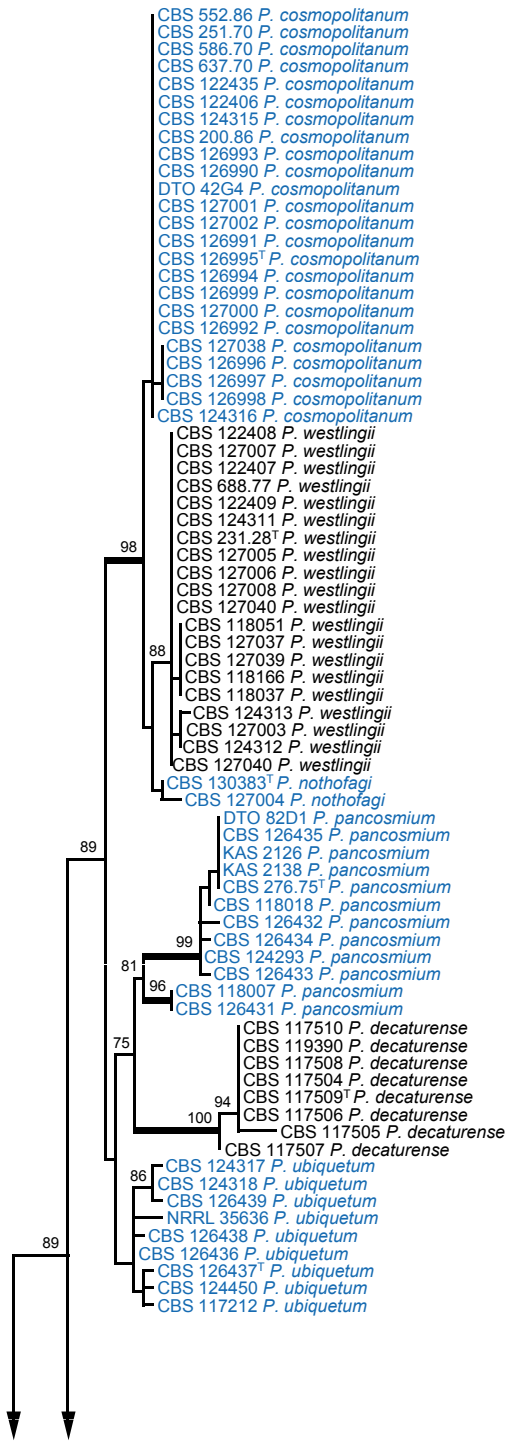

Fig. S4. Maximum Likelihood tree based on a partial calmodulin sequence data of the *P. westlingii* -clade. Numbers above branches are bootstrap values. Only values above 70 % are shown and branches with more than 95 % bootstrap support are thickened. The phylogram is rooted with *P. corylophilum* (CBS 330.79).

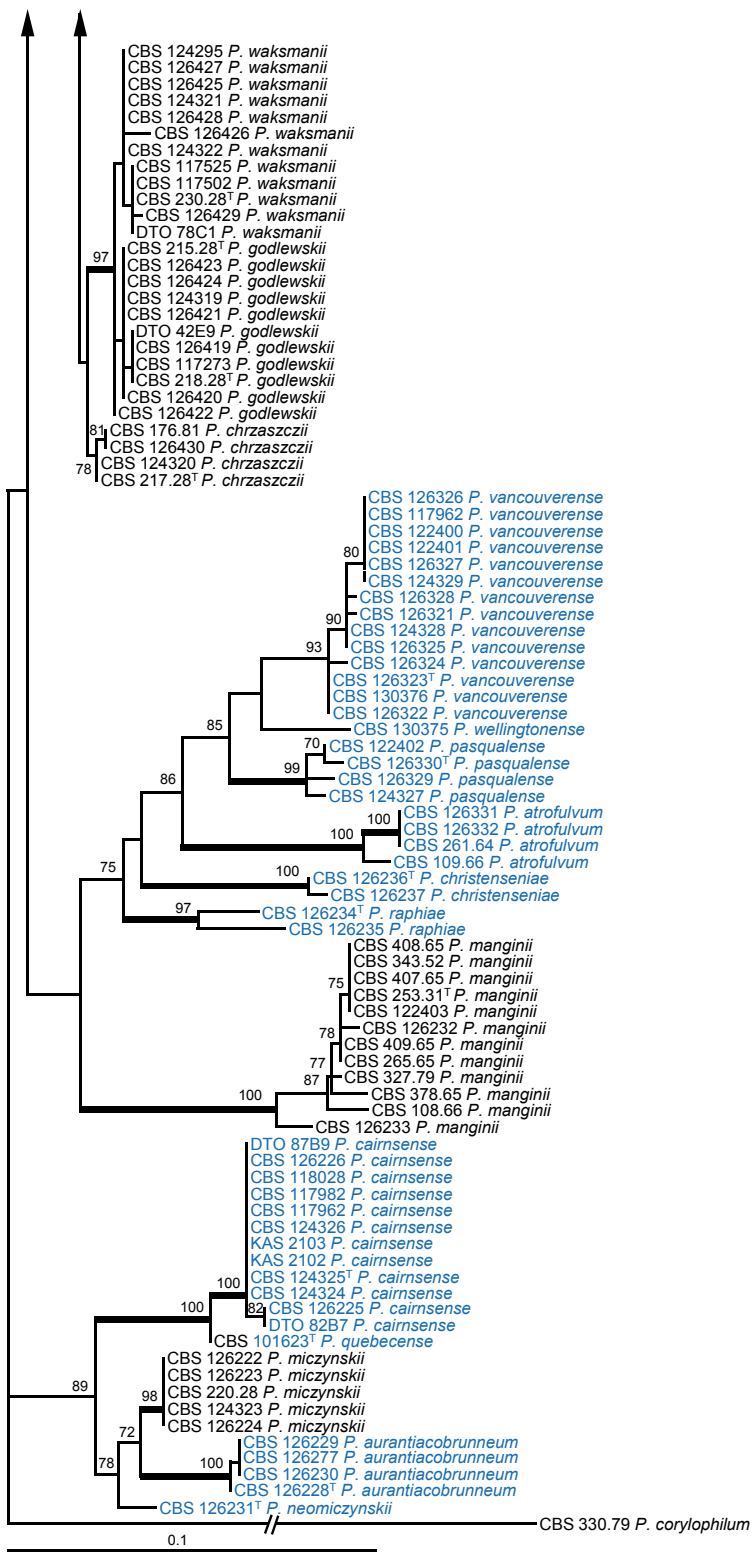

Fig. S4. (Continued).

SUPPLEMENTARY INFORMATION

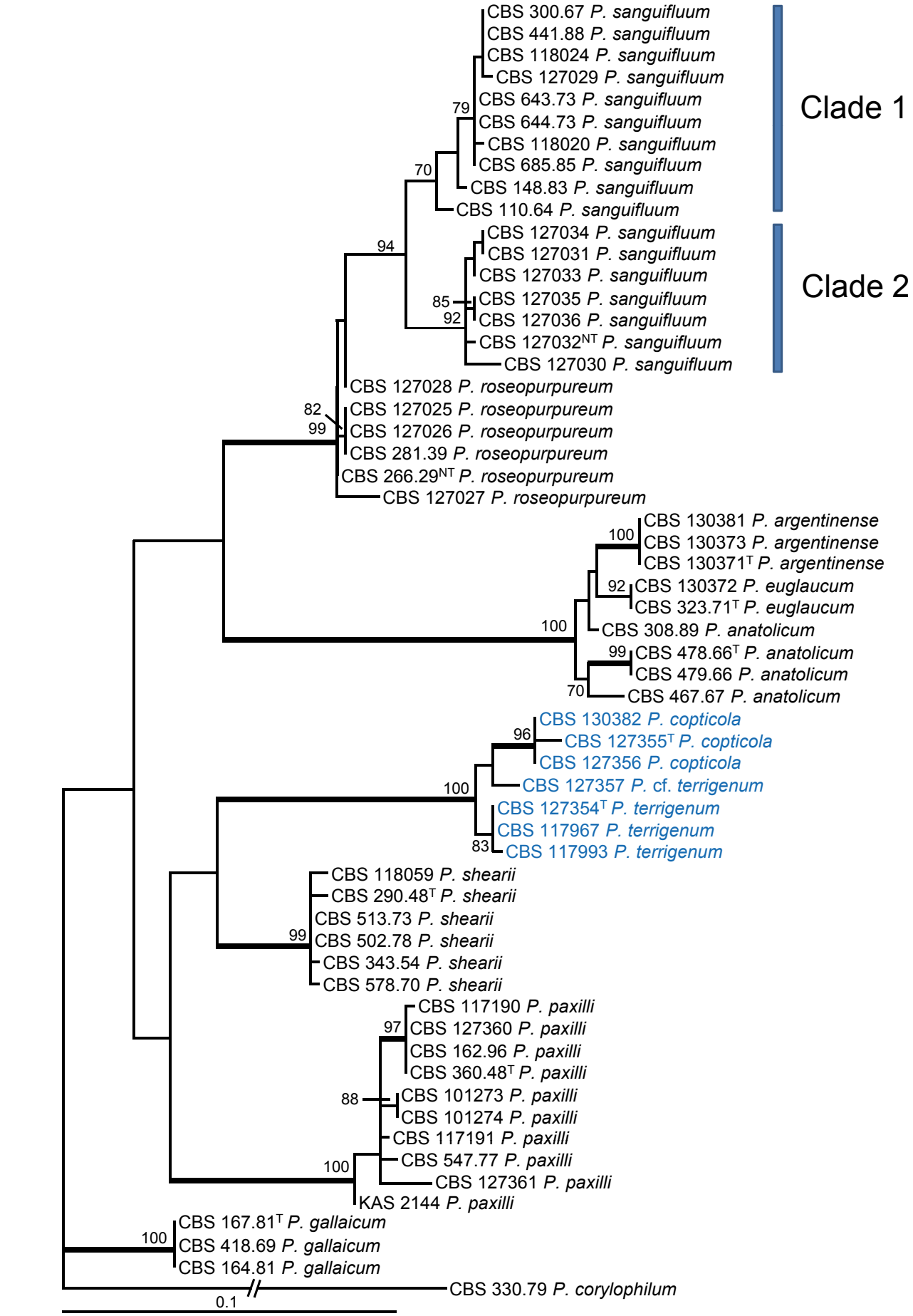

Fig. S5. Maximum Likelihood tree based on a partial β-tubulin sequence data of selected members of section *Citrina*. Numbers above branches are bootstrap values. Only values above 70 % are shown and branches with more than 95 % bootstrap support are thickened. The phylogram is rooted with *P. corylophilum* (CBS 330.79).

SUPPLEMENTARY INFORMATION

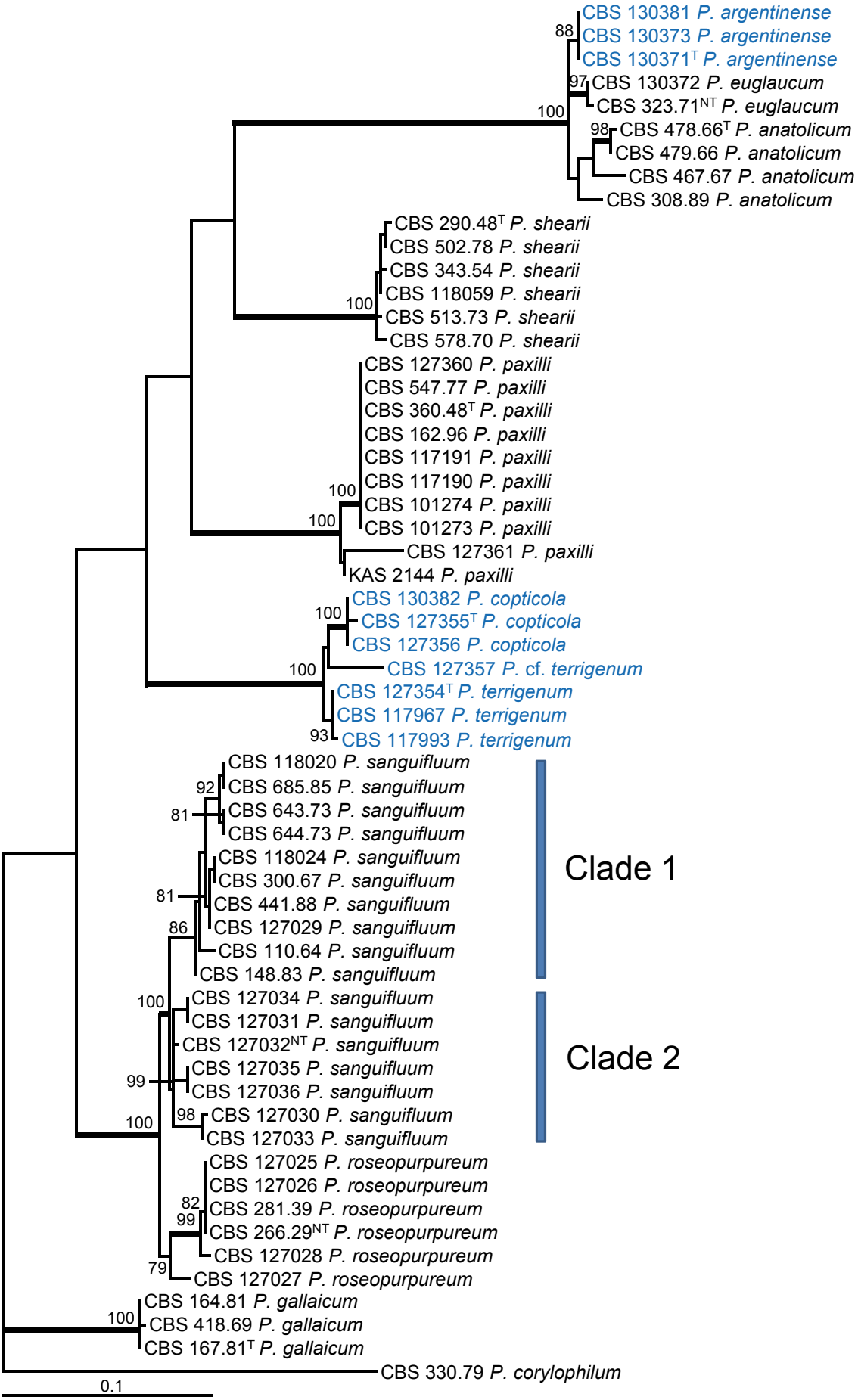

Fig. S6. Maximum Likelihood tree based on a partial calmodulin sequence data of selected members of section *Citrina*. Numbers above branches are bootstrap values. Only values above 70 % are shown and branches with more than 95 % bootstrap support are thickened. The phylogram is rooted with *P. corylophilum* (CBS 330.79).