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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
*Cct*8	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
*RPB*2	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
*Tsr*1	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*

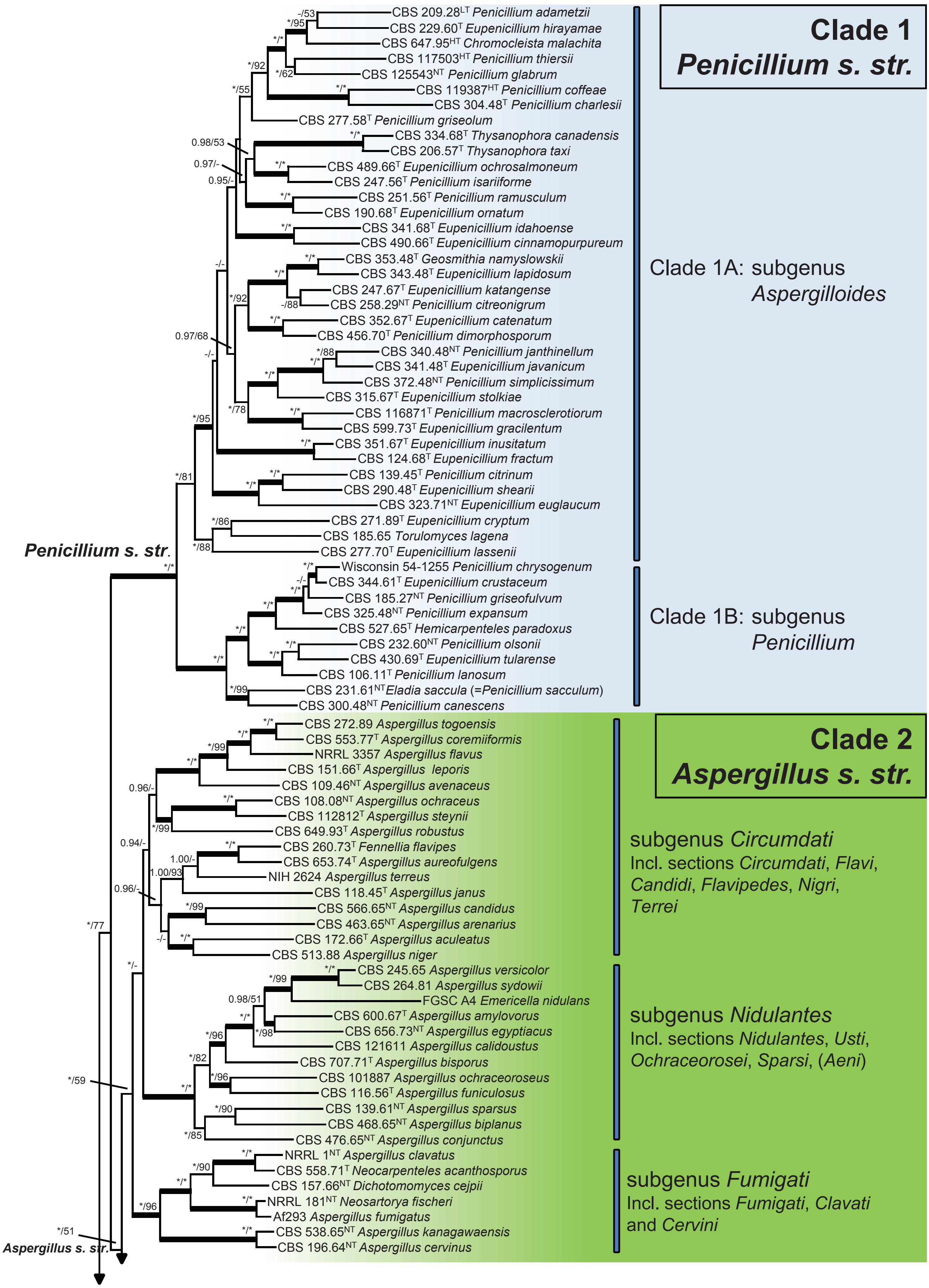

Fig. 1. Best-scoring Maximum Likelihood tree using RAxML based on combined data set of partial *Cct8*, *Tsr1*, *RPB1 and RPB2* sequences showing the relationship among members of *Trichocomaceae*. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) 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).

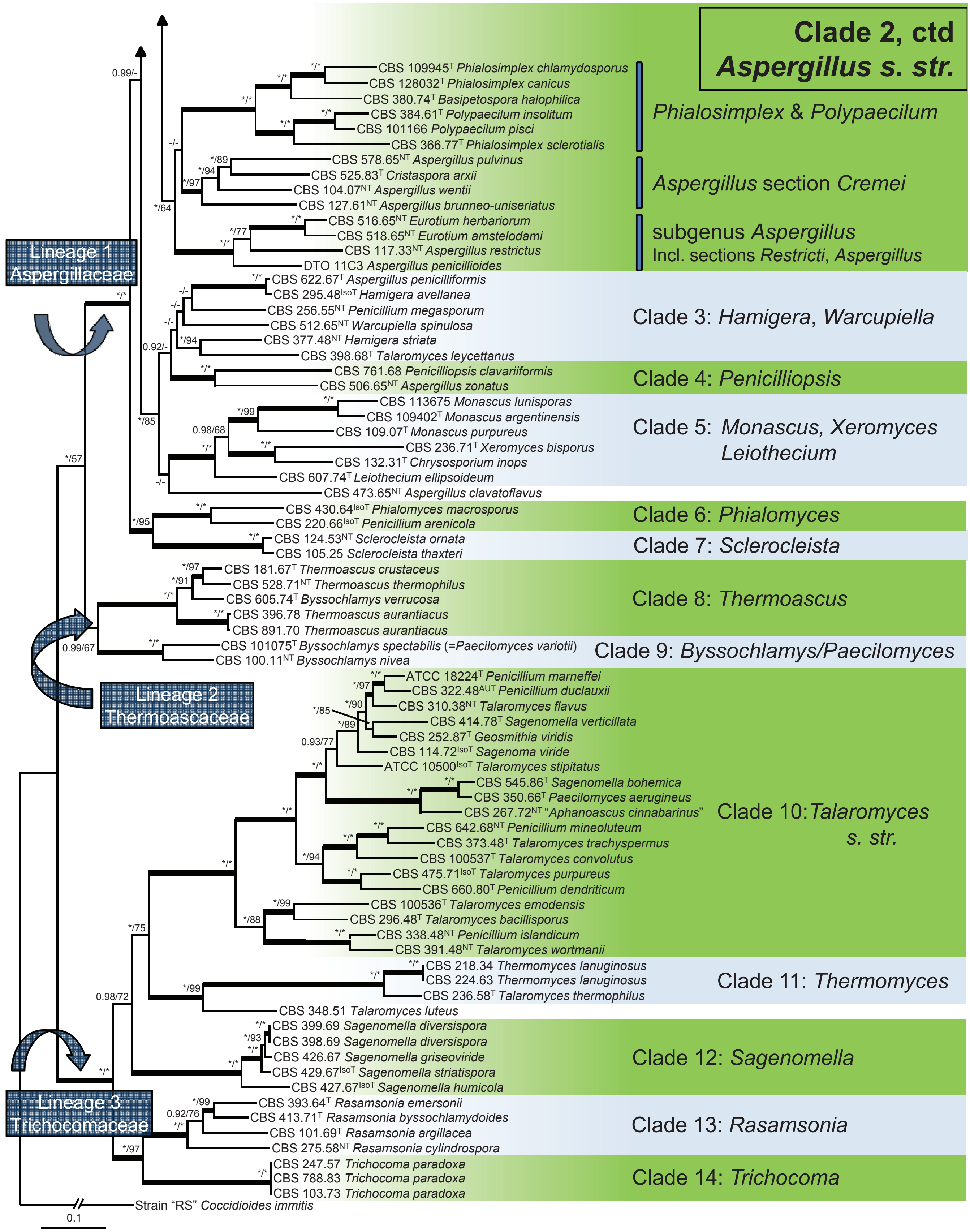

Fig. 1. (Continued).

(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$^{\text{isoT}}$ (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$^{\text{T}}$) 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*.

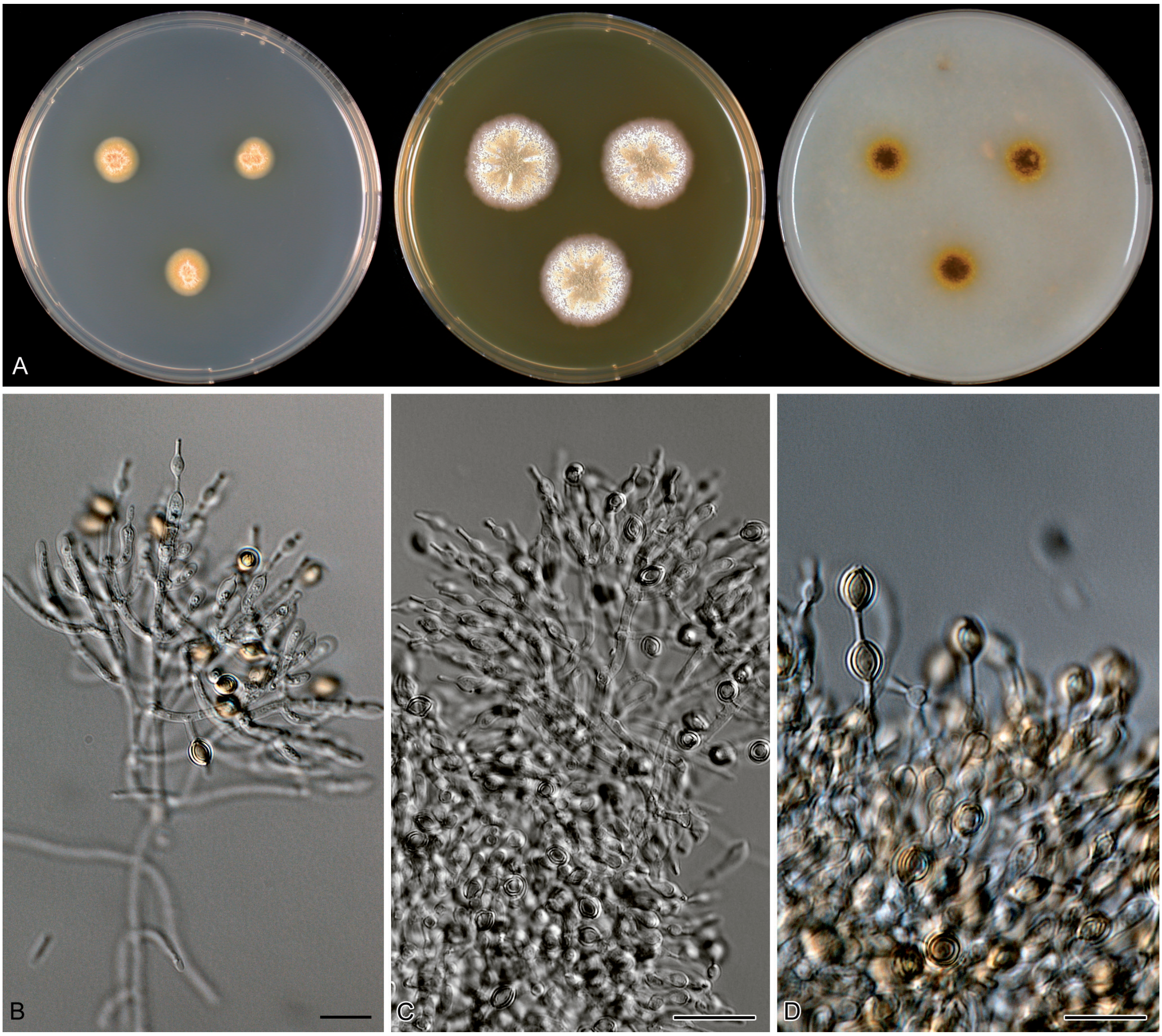

Fig. 2. *Phialotubus microsporus* CBS 861.70$^{\text{isoT}}$. A. Colonies grown for 7 d at 25 °C, from left to right: CYA, MEA, OA. B–D. Conidiophores and conidia. Scale bar = 10 µm.

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

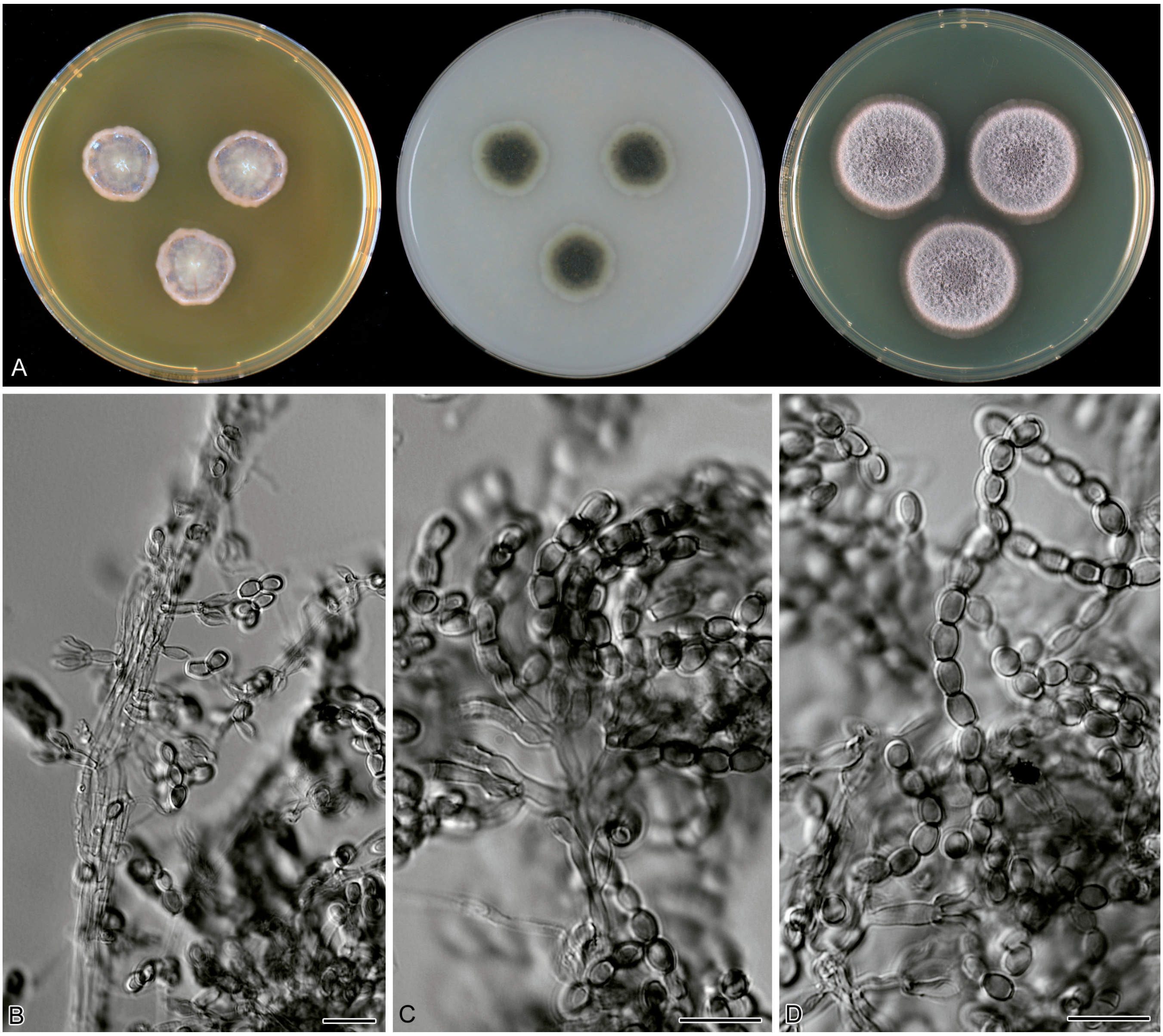

Fig. 3. *Yunnania penicillata* CBS 130296^T. A. Colonies grown for 7 d at 25 °C, from left to right: MEA, OA, CYA. B–D. Conidiophores and conidia.

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

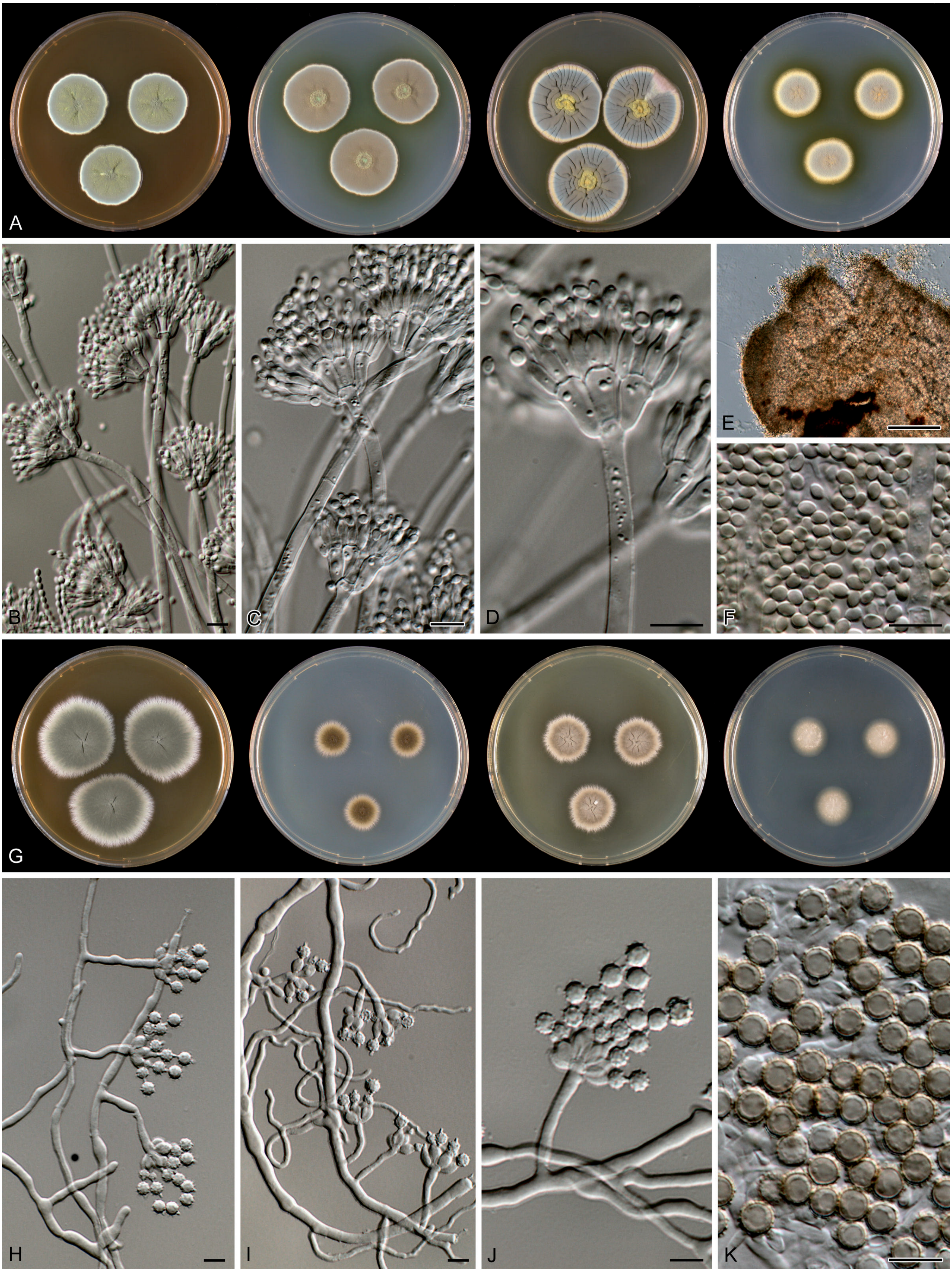

Fig. 4. A–F. *Penicillium malachiteum* CBS 647.95^{HT}. A. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. B–D. Conidiophores. E. Immature cleistothecia. F. Conidia. G–K. *Penicillium sacculum* CBS 123567. G. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES,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

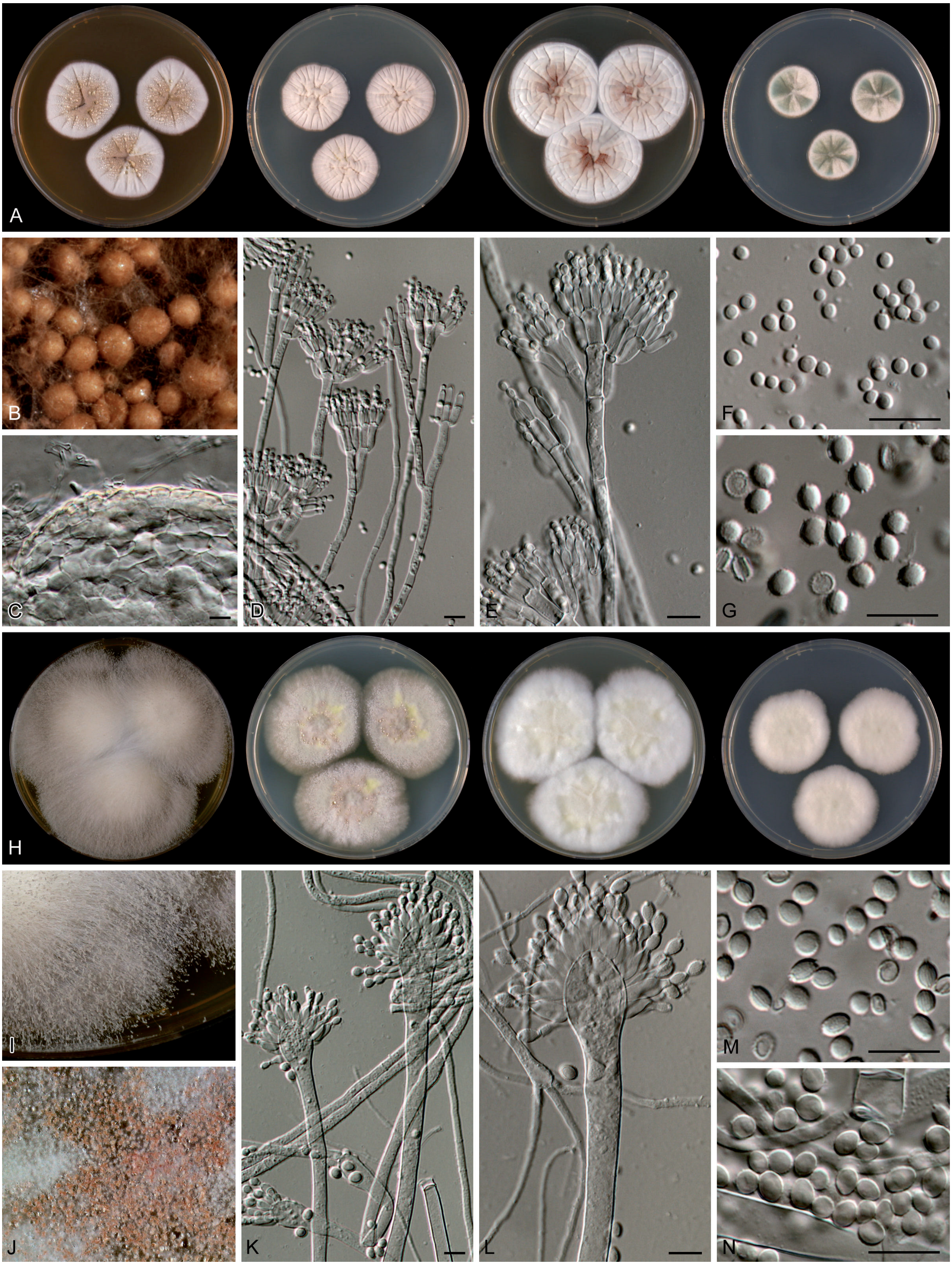

Fig. 5. A–G. *Penicillium kewense* CBS 344.61^{T}. A. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. B–C. Cleistothecia. D-E. Conidiophores. F. Conidia. G. Ascospores. H–N. *Aspergillus paradoxus* (= *P. paradoxum*, R.A. Samson unpubl. results) CBS 130295. H. Colonies grown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

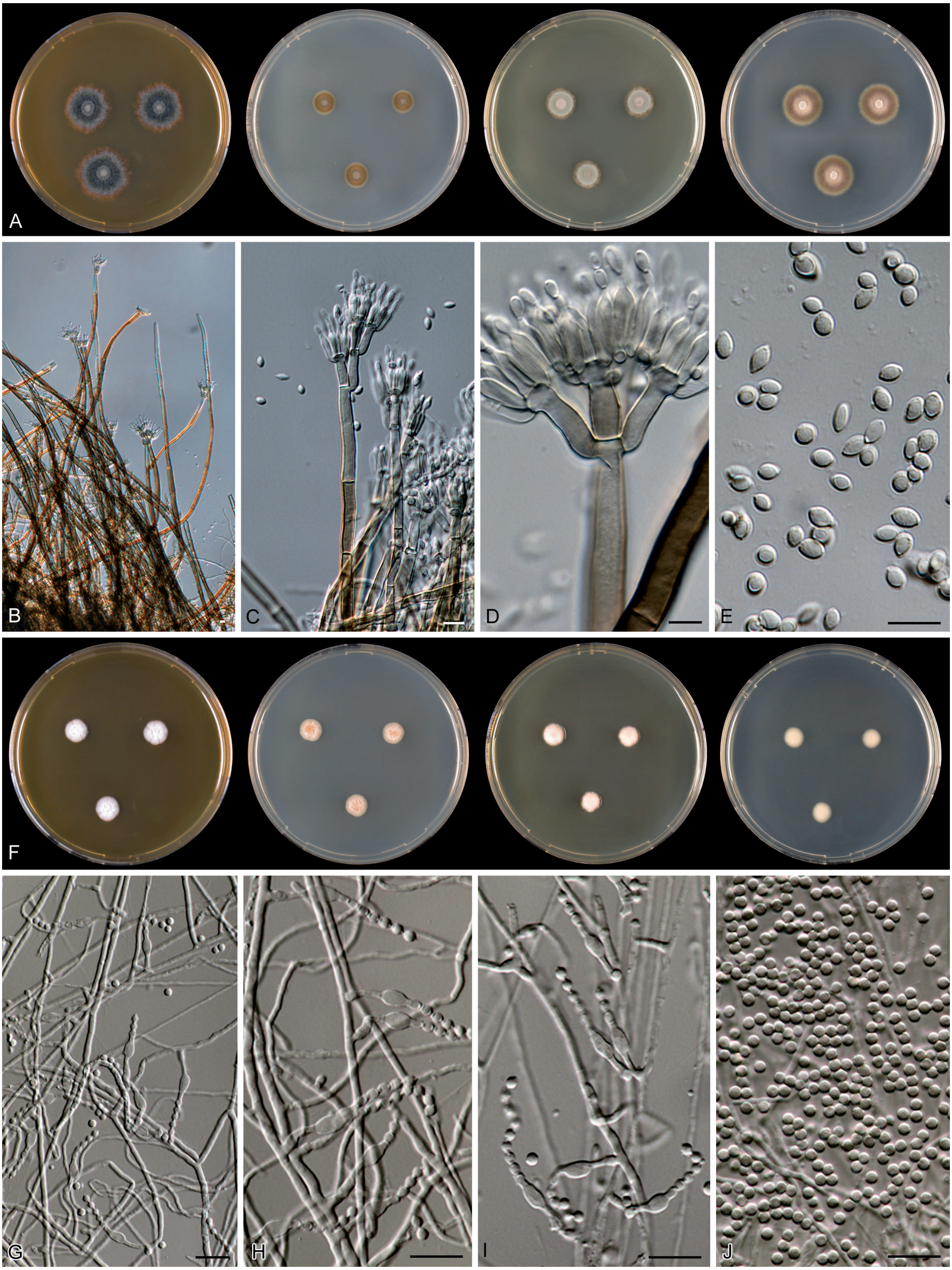

Fig. 6. A–H. *Penicillium glaucoalbidum* CBS 292.60. A. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. B–D. Conidiophores. E. Conidia. F–J. *Penicillium lagena* CBS 337.97. F. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. G–I. Conidiophores. J. Conidia.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

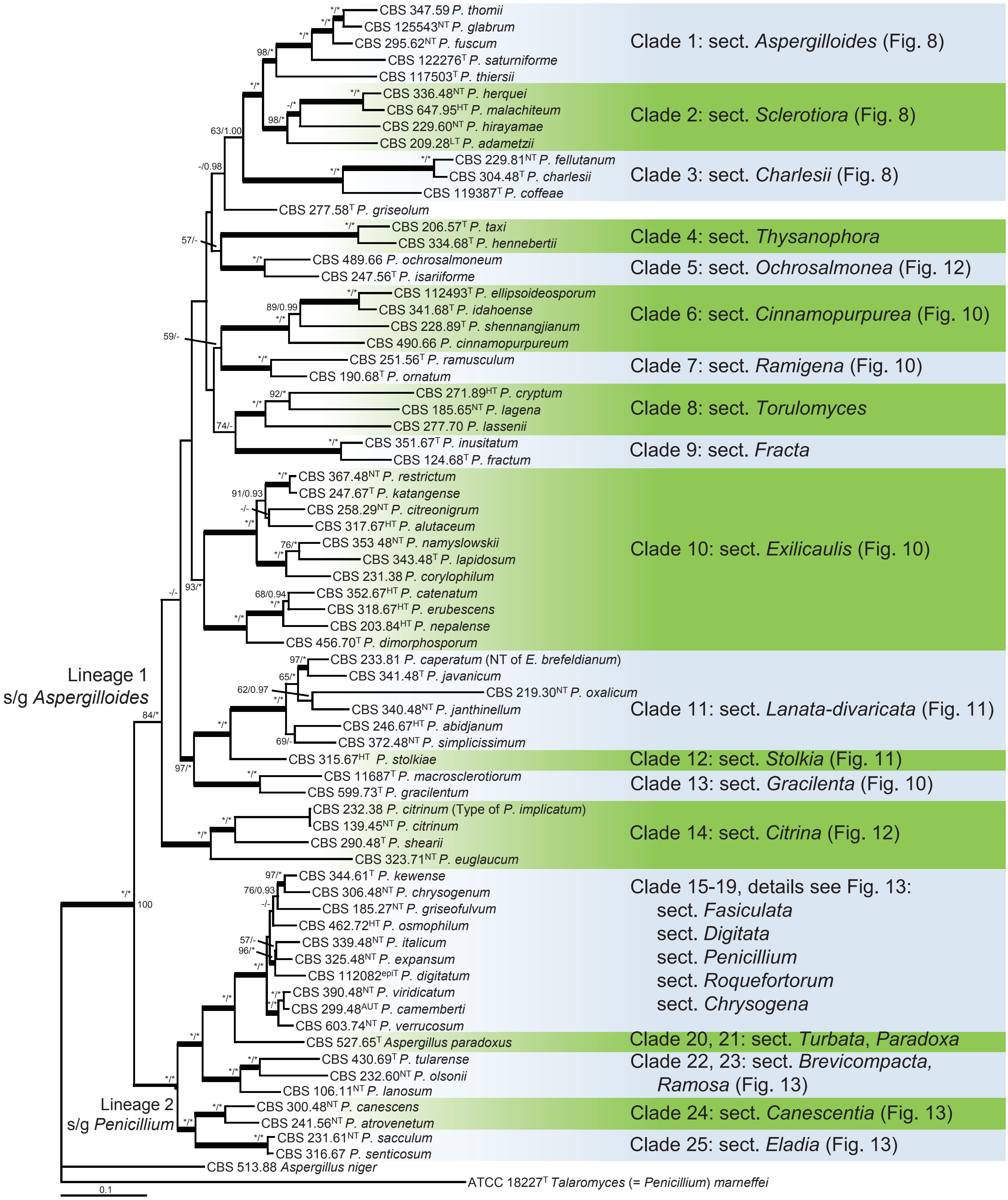

Fig. 7. Best-scoring Maximum Likelihood tree using RAxML based on combined data set of partial *Cct8*, *Tsr1*, *RPB1 and RPB2* sequences showing the relationship among members of *Penicillium s. str. Penicillium s. str.* is divided in two lineages (s/g *Aspergilloides* and *Penicillium*) and 25 sections. 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 18227^{T}.

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.

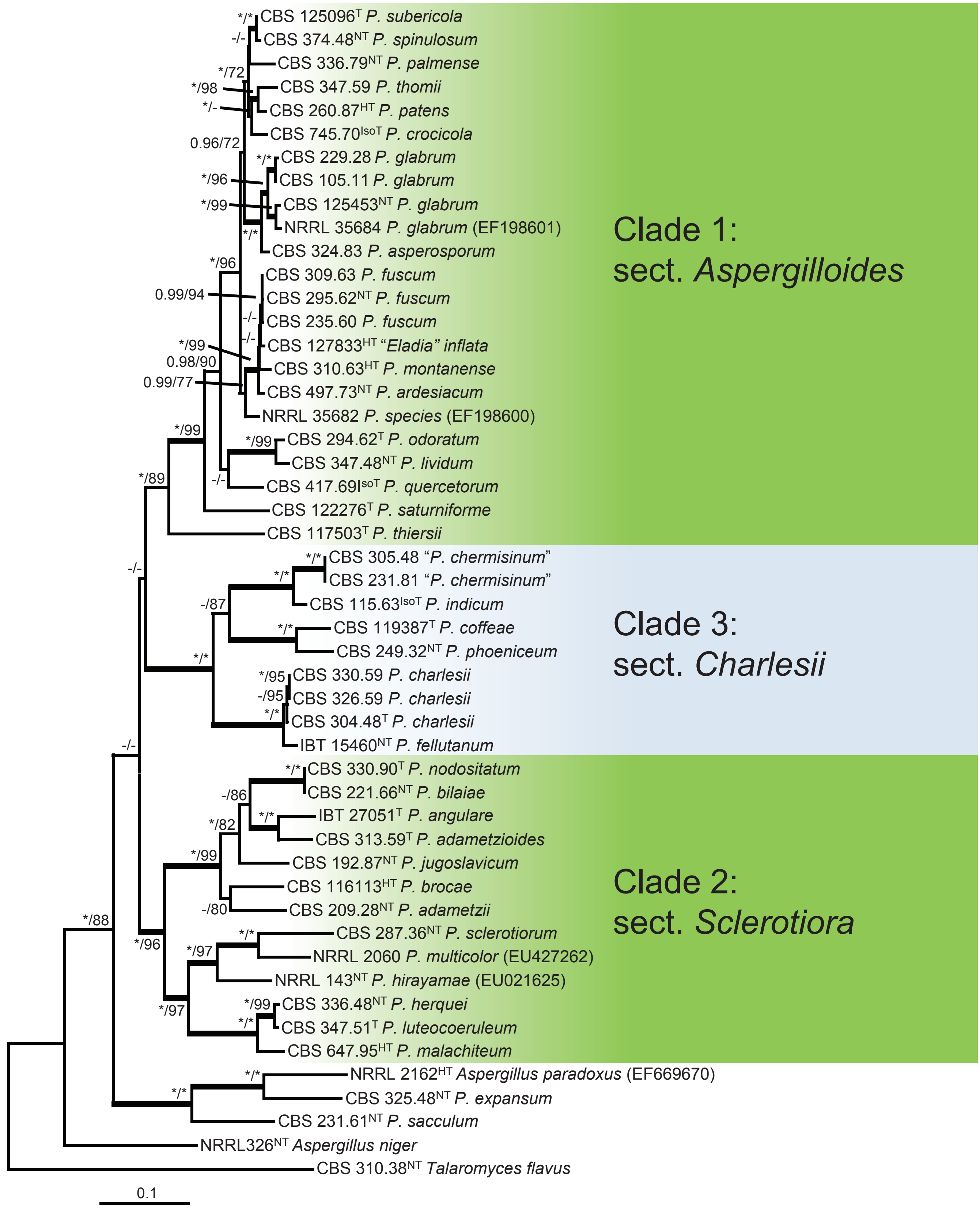

Fig. 8. Best-scoring Maximum Likelihood tree using RAxML based on partial *RPB2* sequences and giving an overview of the members accommodated in sections *Aspergilloides*, *Sclerotiora* and *Charlesii*. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (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 310.38^{NT}.

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.

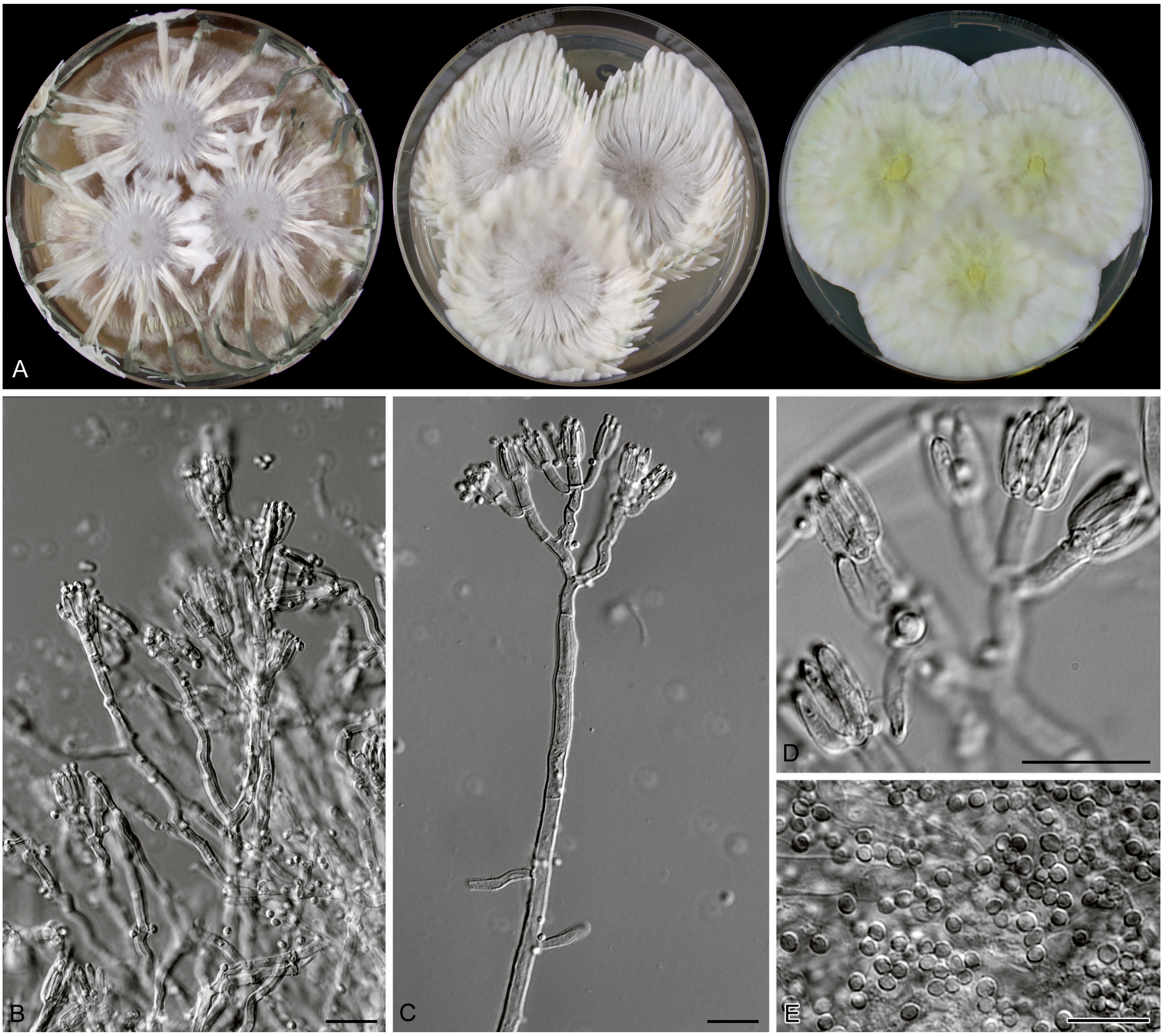

Fig. 9. *Penicillium isariiforme* CBS 247.56. A. Colonies grown for 14 d at 25 °C, from left to right: MEA, YES, CYA. B–D. Conidiophores. E. Conidia. Scale bar = 10 µm.

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.

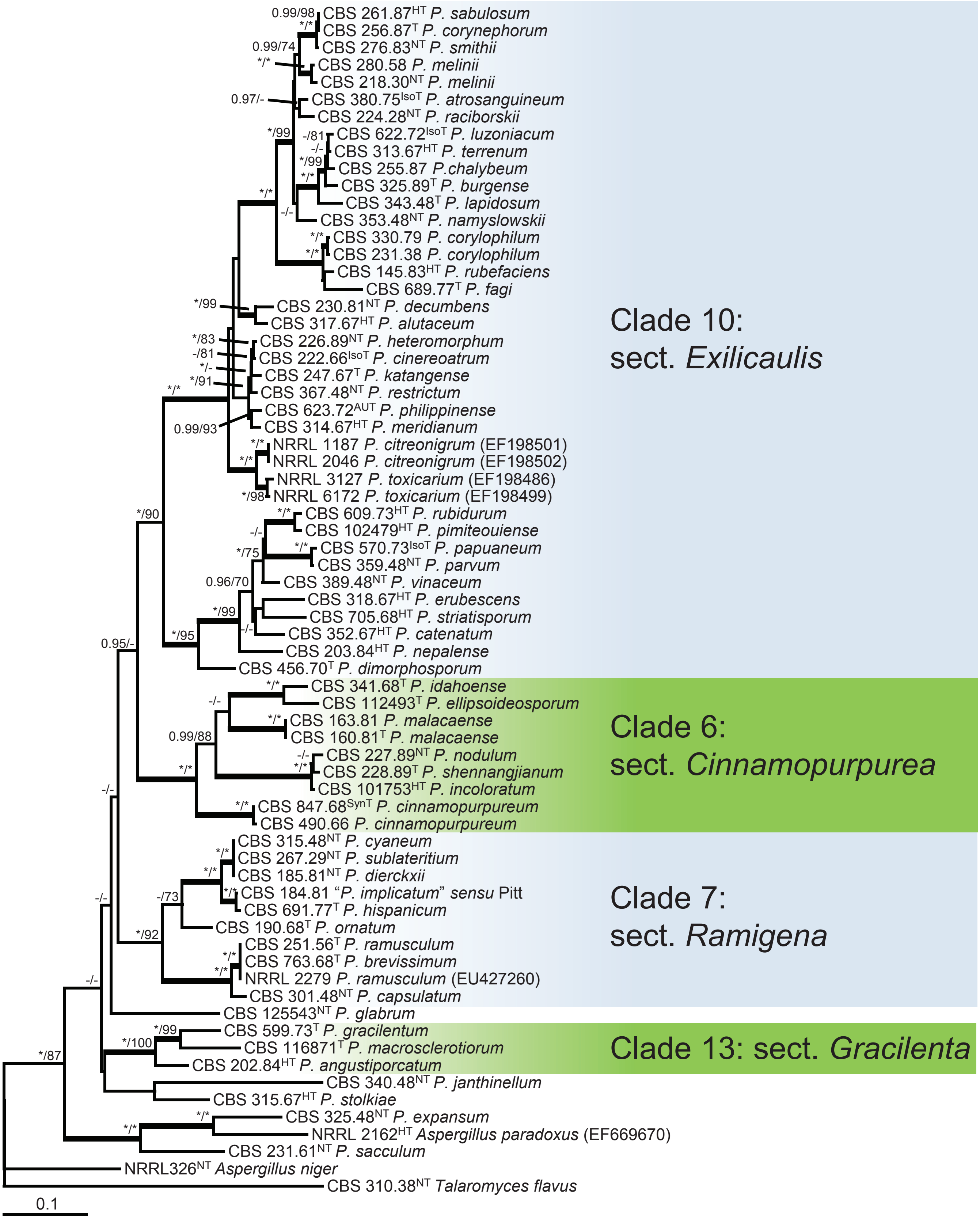

Fig. 10. Best-scoring Maximum Likelihood tree using RAxML based on partial *RPB2* sequences and giving an overview of the members accommodated in sections *Exilicaulis*, *Cinnamopurpurea*, *Ramigena* and *Gracilenta*. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum 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 310.38^{NT}.

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

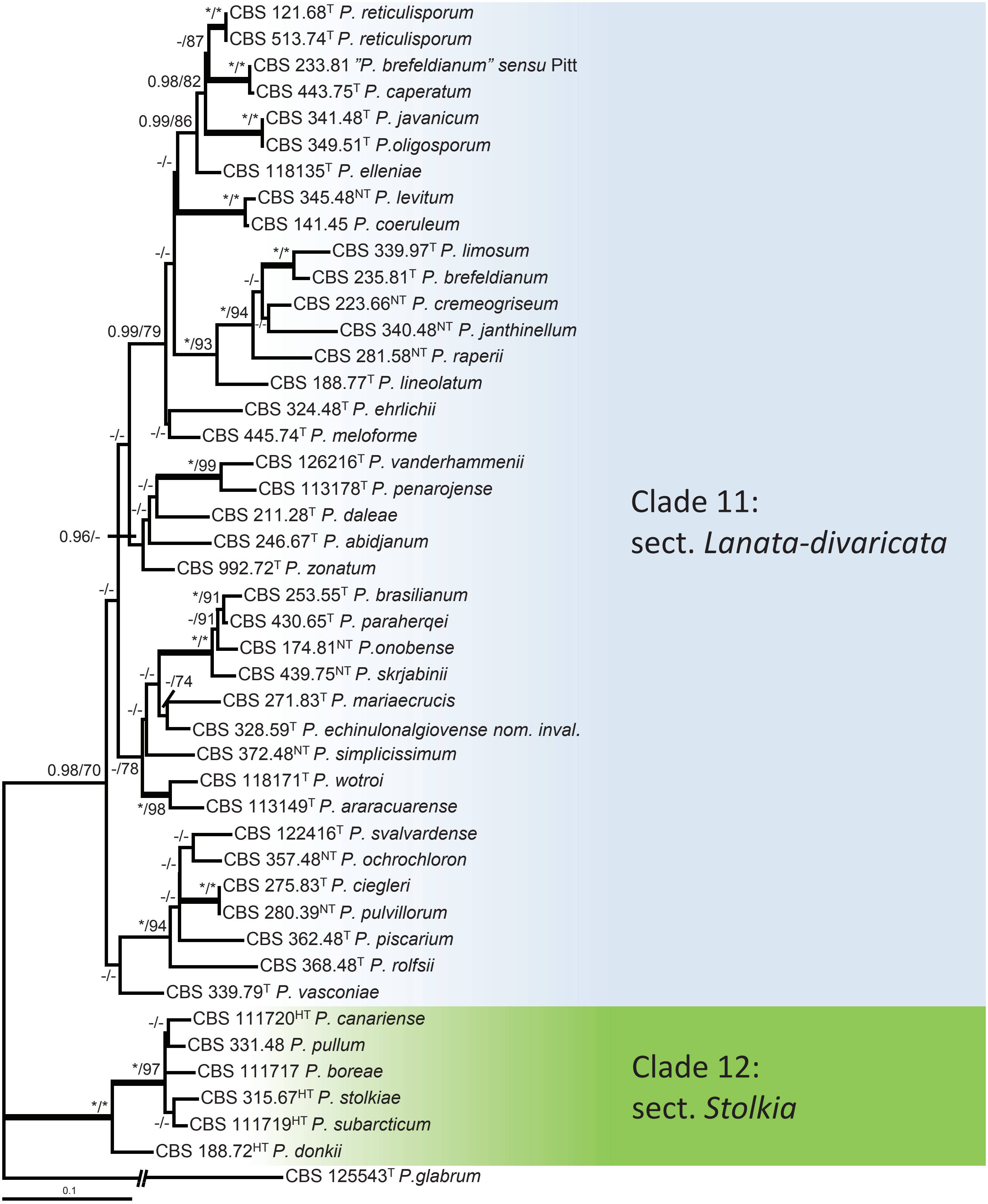

Fig. 11. Best-scoring Maximum Likelihood tree using RAxML based on partial β-tubulin sequences and giving an overview of the members accommodated in sections *Lanata-divaricata* and *Stolkia*. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis 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.

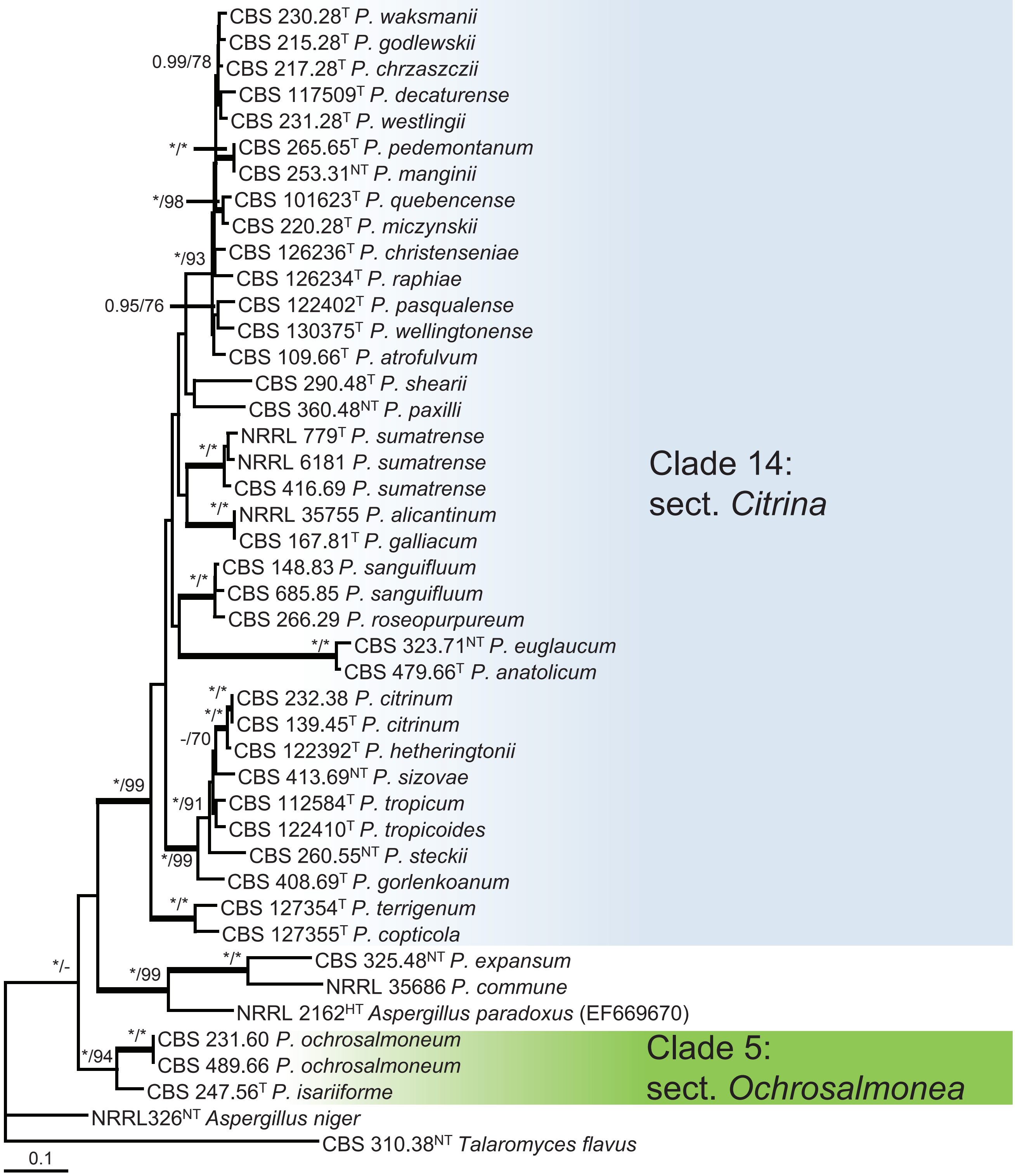

Fig. 12. Best-scoring Maximum Likelihood tree using RAxML based on partial *RPB2* sequences and giving an overview of the members accommodated in sections *Citrina* and *Ochrosalmonea*. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are 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

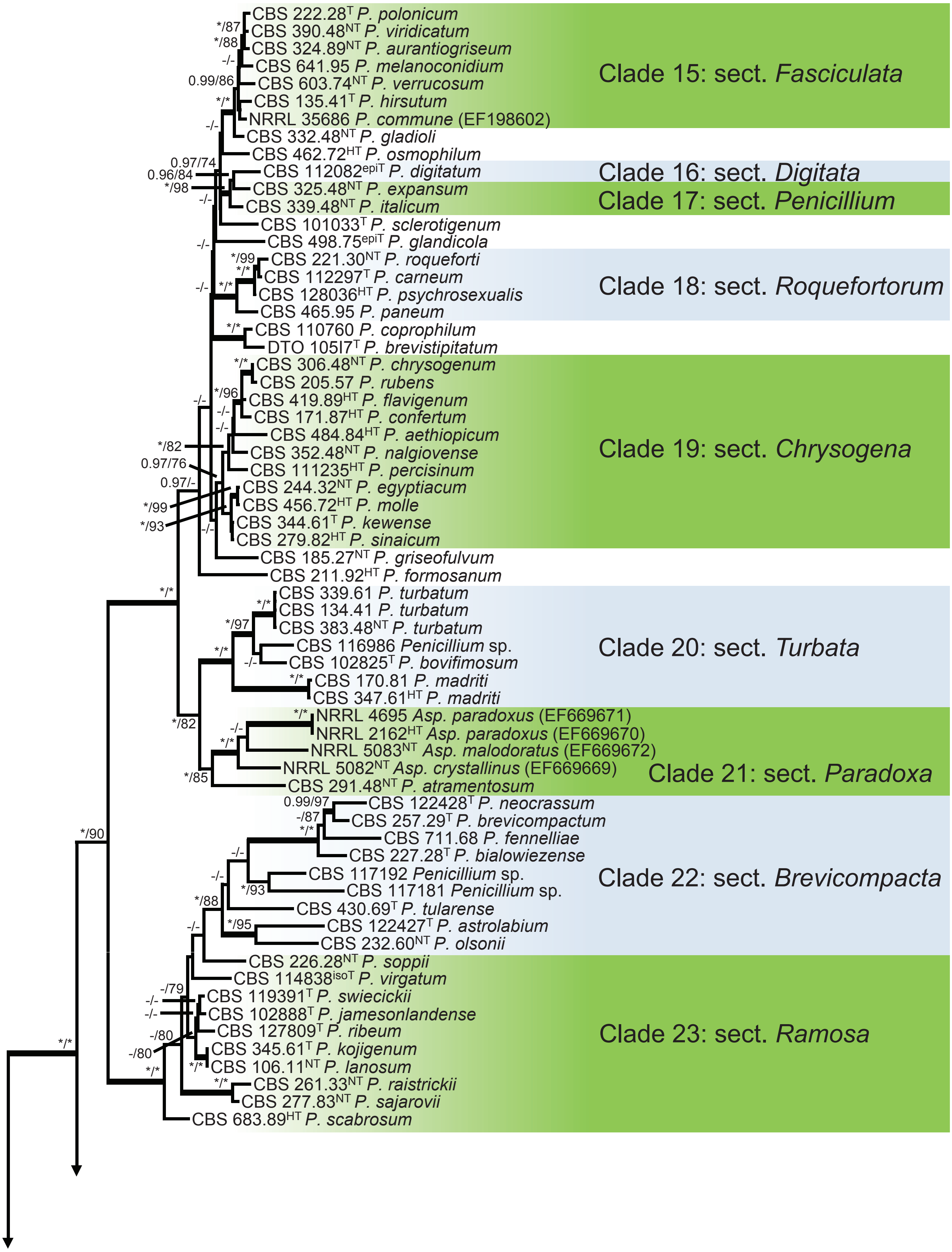

Fig. 13. Best-scoring Maximum Likelihood tree using RAxML based on partial *RPB2* sequences and giving an overview of the members accommodated in subgenus Penicillium (clades 15–25). The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are 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 310.38^{NT}.

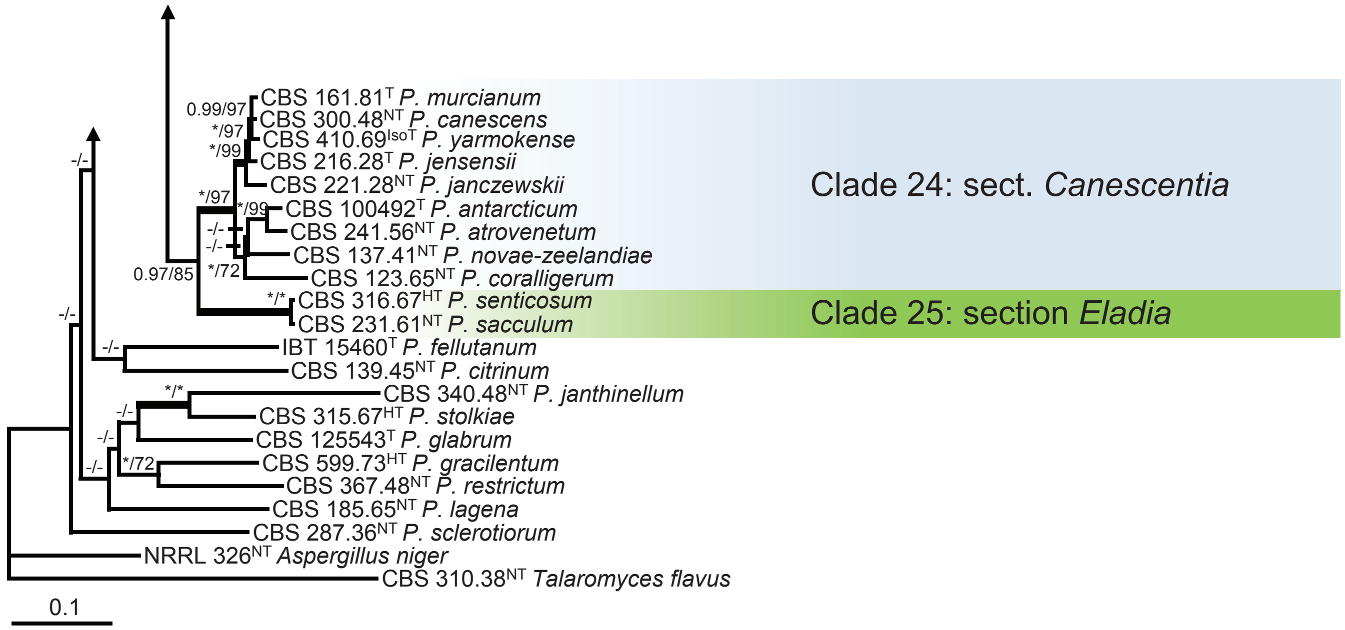

Fig. 13. (Continued).

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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