

Phylogeny and nomenclature of the genus *Talaromyces* and taxa accommodated in *Penicillium* subgenus *Biverticillium*

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Abstract: The taxonomic history of anamorphic species attributed to *Penicillium* subgenus *Biverticillium* is reviewed, along with evidence supporting their relationship with teleomorphic species classified in *Talaromyces*. To supplement previous conclusions based on ITS, SSU and/or LSU sequencing that *Talaromyces* and subgenus *Biverticillium* comprise a monophyletic group that is distinct from *Penicillium* at the generic level, the phylogenetic relationships of these two groups with other genera of *Trichocomaceae* was further studied by sequencing a part of the *RPB1* (RNA polymerase II largest subunit) gene. *Talaromyces* species and most species of *Penicillium* subgenus *Biverticillium sensu* Pitt reside in a monophyletic clade distant from species of other subgenera of *Penicillium*. For detailed phylogenetic analysis of species relationships, the ITS region (incl. 5.8S nrDNA) was sequenced for the available type strains and/or representative isolates of *Talaromyces* and related biverticillate anamorphic species. Extrolite profiles were compiled for all type strains and many supplementary cultures. All evidence supports our conclusions that *Penicillium* subgenus *Biverticillium* is distinct from other subgenera in *Penicillium* and should be taxonomically unified with the *Talaromyces* species that reside in the same clade. Following the concepts of nomenclatural priority and single name nomenclature, we transfer all accepted species of *Penicillium* subgenus *Biverticillium* to *Talaromyces*. A holomorphic generic diagnosis for the expanded concept of *Talaromyces*, including teleomorph and anamorph characters, is provided. A list of accepted *Talaromyces* names and newly combined *Penicillium* names is given. Species of biotechnological and medical importance, such as *P. funiculosum* and *P. marneffeii*, are now combined in *Talaromyces*. Excluded species and taxa that need further taxonomic study are discussed. An appendix lists other generic names, usually considered synonyms of *Penicillium sensu lato* that were considered prior to our adoption of the name *Talaromyces*.

Key words: anamorph, DNA phylogeny, single name nomenclature, teleomorph, *Trichocomaceae*.

Taxonomic novelties: **Taxonomic novelties: New species** – *Talaromyces apiculatus* Samson, Yilmaz & Frisvad, sp. nov. **New combinations and names** – *Talaromyces aculeatus* (Raper & Fennell) Samson, Yilmaz, Frisvad & Seifert, *T. albobiverticillius* (H.-M. Hsieh, Y.-M. Ju & S.-Y. Hsieh) Samson, Yilmaz, Frisvad & Seifert, *T. allahabadensis* (B.S. Mehrotra & D. Kumar) Samson, Yilmaz & Frisvad, *T. aurantiacus* (J.H. Mill., Giddens & A.A. Foster) Samson, Yilmaz, & Frisvad, *T. boninensis* (Yaguchi & Udagawa) Samson, Yilmaz, & Frisvad, *T. brunneus* (Udagawa) Samson, Yilmaz & Frisvad, *T. calidicarius* (J.L. Chen) Samson, Yilmaz & Frisvad, *T. cecidicola* (Seifert, Hoekstra & Frisvad) Samson, Yilmaz, Frisvad & Seifert, *T. coalescens* (Quintan.) Samson, Yilmaz & Frisvad, *T. dendriticus* (Pitt) Samson, Yilmaz, Frisvad & Seifert, *T. diversus* (Raper & Fennell) Samson, Yilmaz & Frisvad, *T. duclauxii* (Delacr.) Samson, Yilmaz, Frisvad & Seifert, *T. echinosporus* (Nehira) Samson, Yilmaz & Frisvad, comb. nov. *T. erythromellis* (A.D. Hocking) Samson, Yilmaz, Frisvad & Seifert, *T. funiculosus* (Thom) Samson, Yilmaz, Frisvad & Seifert, *T. islandicus* (Sopp) Samson, Yilmaz, Frisvad & Seifert, *T. loliensis* (Pitt) Samson, Yilmaz & Frisvad, *T. marneffeii* (Segretain, Capponi & Sureau) Samson, Yilmaz, Frisvad & Seifert, *T. minioluteus* (Dierckx) Samson, Yilmaz, Frisvad & Seifert, *T. palmae* (Samson, Stolk & Frisvad) Samson, Yilmaz, Frisvad & Seifert, *T. panamensis* (Samson, Stolk & Frisvad) Samson, Yilmaz, Frisvad & Seifert, *T. paucisporus* (Yaguchi, Someya & Udagawa) Samson & Houbraken *T. phialosporus* (Udagawa) Samson, Yilmaz & Frisvad, *T. piceus* (Raper & Fennell) Samson, Yilmaz, Frisvad & Seifert, *T. pinophilus* (Hedgcock) Samson, Yilmaz, Frisvad & Seifert, *T. pittii* (Quintan.) Samson, Yilmaz, Frisvad & Seifert, *T. primulinus* (Pitt) Samson, Yilmaz & Frisvad, *T. proteolyticus* (Kamyschko) Samson, Yilmaz & Frisvad, *T. pseudostrumaticus* (Hodges, G.M. Warner, Rogerson) Samson, Yilmaz, Frisvad & Seifert, *T. purpurogenus* (Stoll) Samson, Yilmaz, Frisvad & Seifert, *T. rademirici* (Quintan.) Samson, Yilmaz & Frisvad, *T. radicus* (A.D. Hocking & Whitelaw) Samson, Yilmaz, Frisvad & Seifert, *T. ramulosus* (Visagie & K. Jacobs) Samson, Yilmaz, Frisvad & Seifert, *T. rubicundus* (J.H. Mill., Giddens & A.A. Foster) Samson, Yilmaz, Frisvad & Seifert, *T. rugulosus* (Thom) Samson, Yilmaz, Frisvad & Seifert, *T. sabulosus* (Pitt & A.D. Hocking) Samson, Yilmaz & Frisvad, *T. siamensis* (Manoch & C. Ramirez) Samson, Yilmaz & Frisvad, *T. sublevisporus* (Yaguchi & Udagawa) Samson, Yilmaz & Frisvad, *T. variabilis* (Sopp) Samson, Yilmaz, Frisvad & Seifert, *T. varians* (G. Sm.) Samson, Yilmaz & Frisvad, *T. verruculosus* (Peyronel) Samson, Yilmaz, Frisvad & Seifert, *T. viridulus* Samson, Yilmaz & Frisvad.

INTRODUCTION

The modern concept of *Penicillium* (referred to in this paper as *Penicillium sensu lato*), was derived from the pioneering monographic revisions of Thom (1930), Raper & Thom (1949), and formalised by the recognition of four subgenera, *Aspergilloides*, *Furcatum*, *Penicillium* and *Biverticillium* by Pitt (1980). Over the past decade, the realisation has grown that *Penicillium* subgenus *Biverticillium* is phylogenetically distinct from other subgenera of *Penicillium* and that this distinctiveness should be reflected in its formal taxonomy. Because of their usually symmetrical, biverticillate conidiophores, the group has been recognised since Wehmer (1914) segregated them in an informal subdivision of

Penicillium that he called "Verticillatae". The delineation, species composition and taxonomic rank of this group were modified in subsequent monographs by Thom (1930), Raper & Thom (1949), Pitt (1980), and Ramirez (1982), culminating in the widespread recognition of subgenus *Biverticillium* and the use of this name in many taxonomic and phylogenetic studies. Malloch (1985), based on a consideration of morphological and ecological factors, and anamorph-teleomorph connections, may have been the first to speculate that subgenus *Biverticillium* should be removed from *Penicillium* as a separate genus.

The teleomorph genera historically associated with *Penicillium sensu lato* are *Talaromyces* and *Eupenicillium* (in single name nomenclature, the latter is now considered a synonym of

Penicillium sensu stricto, see Houbraken & Samson 2011). The teleomorphs of these two groups produce distinctive ascomata. In *Talaromyces*, the soft ascomatal walls are comprised of multiple layers of interwoven hyphae and the ascomata mature quickly, usually within a few weeks in agar culture. In *Penicillium sensu stricto*, the sclerotium-like ascomata have rigid walls of thick-walled, isodiametric cells and the ascomatal maturity can take months and often ascospores do not form at all. Furthermore, in *Talaromyces* the ascus initials sometimes have morphologically distinguishable gametangia and the mature asci are produced in chains (Stolk & Samson 1972), while the ascomatal initials in *Penicillium sensu stricto* are irregularly interwoven, loosely branched hyphae masses (Emmons 1935), and the mature asci are single. Raper & Thom (1949) already recognised that there was considerable evidence that *Penicillium* subgenus *Biverticillium* constituted a natural and homogenous group. A comparison of the anamorphs of these two teleomorph types reveals a correlation with phialide shape, with anamorphs of *Talaromyces* (until now classified in *Penicillium* subgenus *Biverticillium*) having narrower phialides that are aculeate or lanceolate, and anamorphs in *Penicillium sensu stricto* having broader, ampulliform or flask-shaped phialides. One consequence of the differences in phialide shape is that the symmetrical nature of the conidiophores of species allied with *Talaromyces* tends to be emphasised, because in general the phialides are more densely packed. The colonies of subgenus *Biverticillium* can often be distinguished from those of *Penicillium sensu stricto* by the naked eye. They often have darker green conidia, more or less yellow pigmented and encrusted aerial hyphae, and colony reverses in yellow, orange or red to purplish red shades.

Once DNA-based studies of fungal phylogeny began, it quickly became apparent that the differences between *Penicillium sensu stricto* and *Talaromyces* were more than a matter of degree, and that there might be a significant problem with the generic concept of *Penicillium sensu lato*. *Penicillium sensu stricto* and *Talaromyces* occur as distinct clades within *Trichocomaceae*, which could be considered subfamilies (LoBuglio *et al.*, 1993, LoBuglio & Taylor 1993). Using small subunit nuclear ribosomal DNA sequences (18S), Berbee *et al.* (1995) showed that *Penicillium* is polyphyletic if subgenus *Biverticillium* is included, a conclusion reconfirmed in one of the first reviews of the impact of molecular phylogenetics on Ascomycete taxonomy (Sugiyama 1998) using an analysis of 18S rDNA sequences. Removal of subgenus *Biverticillium* transforms *Penicillium sensu stricto* into a monophyletic group. This dichotomy between *Penicillium sensu stricto* and *Talaromyces* was shown repeatedly in studies employing nuclear ribosomal RNA genes, for example by Peterson (2000), who analysed a combination of the nuclear ribosomal internal transcribed spacer regions (ITS) and large subunit ribosomal DNA (28S) sequences (Ogawa *et al.* 1997, Ogawa & Sugiyama 2000), and by Wang & Zhuang (2007) in a phylogeny based on calmodulin sequences. The results of these analyses are all confirmed in the multigene phylogenetic analyses presented elsewhere in this volume by Houbraken & Samson (2011), using genes selected for their ability to accurately reflect molecular phylogeny. As indicated by Houbraken & Samson (2011), when other genera assigned to *Trichocomaceae* are included in phylogenetic analyses, the division between subgenus *Biverticillium* and *Penicillium sensu stricto* becomes even clearer. In that study, intervening genera include *Aspergillus*, *Paecilomyces sensu stricto* (with *Byssochlamys* as a synonym), and several small and less well-known genera such as *Thermoascus*, *Penicilliopsis*, *Thermomyces* and the recently described *Rasamsonia* (Houbraken *et al.* 2011).

In a molecularly defined, phylogenetically accurate taxonomic system, maintaining subgenus *Biverticillium* in *Penicillium sensu stricto* is untenable. However, almost every aspect of the biology, biochemistry, and physiology of these two groups emphasises their fundamental distinctiveness, although sometimes with limited taxon sampling. For example, Pitt (1980) emphasised the distinctiveness of subgenus *Biverticillium* by using a low water-activity medium, G25N (which includes 25 % glycerol) in his standard plating regime. Strains assigned to this subgenus grow slowly on this medium, less than 10 mm diam at 25 °C in 7 d, whereas species of the other subgenera are more xerophilic and grow faster. Cell-wall components seem to differ significantly. Leal & Bernabé (1998) reported on the complex glucomannogalactan components of the water soluble polysaccharide fraction of several species of *Trichocomaceae*, suggesting that a characteristic heteropolysaccharide composed of 4 galactose: 1 mannose: 1 glucose was unique to species of subgenus *Biverticillium*. Species of *Penicillium sensu stricto* species were characterised by the presence of a β -(1-5)(1-6)-galactofuran polysaccharide in the same fraction. Cell wall components as reflected by their exoantigens were screened in about 50 species of *Penicillium sensu lato* using an ELISA reaction to antibodies raised to *P. digitatum* (subgenus *Penicillium*). These antibodies reacted well with all the species of subgenera *Furcatum*, *Penicillium* and *Aspergilloides*, but did not react with the four species of subgenus *Biverticillium* tested (*P. funiculosum*, *P. islandicum*, *P. rubrum*, and *P. tardum*) (Notermans *et al.* 1998). Kuraishi *et al.* (1991) first noted that the pattern of ubiquinones in *Penicillium sensu lato* and showed a distinct pattern in subgenus *Biverticillium*. Paterson (1998) examined 335 strains and 118 species of *Penicillium sensu lato* and determined that the Q9 ubiquinone type was predominant in the species of *Penicillium sensu stricto*. In contrast, species of *Talaromyces*, *Trichocoma* and subgenus *Biverticillium* had different versions of the Q10 ubiquinone type. Exceptions to these patterns can be explained by the small number of species whose classification in, or elimination from, subgenus *Biverticillium* has been uncertain or controversial. Frisvad *et al.* (1990a) provided an overview of the extrolites of *Talaromyces* species, and demonstrated the occurrence of characteristic extrolites such as mitorubins, bisanthaquinones such as rugulosin and skyrin, vermicellin, vermistatin, vermiculine, duclauxin and glauconic acid. None of these compounds were found in cultures of *Penicillium sensu stricto* (Frisvad *et al.* 1990b).

The soon to be published *International Code of Nomenclature for Algae, Fungi and Plants* removes the primacy of teleomorph-over anamorph-typified names, leaving both kinds of names competing equally for priority (Norvell 2011). Because of these changes, we apply the principle of 'one fungus - one name' and in the nomenclatural revision, priority is given to the oldest genus and species name irrespective of whether they were originally described for teleomorphs or anamorphs (Hawksworth *et al.* 2011). In this respect, *Penicillium* returns to the single named, but pleomorphic, nomenclatural and taxonomic system used by many of the founders of its taxonomy, and actively promoted by the Peoria school (Thom 1930, Raper & Thom 1949). *Talaromyces*, now also defined as a pleomorphic genus, is adopted for the anamorphic species formerly included in *Penicillium* subgenus *Biverticillium*. In this study, the phylogenetic relationships of species of subgenus *Biverticillium* and other members of the *Trichocomaceae* were studied by sequencing a part of the *RPB1* (RNA polymerase II largest subunit) gene. Furthermore, we discuss the taxonomy and nomenclature of species of this expanded concept of *Talaromyces*, based on phylogenetic, phenotypic and extrolite data. For detailed

phylogenetic analysis below genus level, the ITS regions (including the 5.8S nrDNA) of ex-type strains and/or representatives were sequenced. As discussed below, this paper is not meant as a monographic treatment, because many complexes have not yet been studied comprehensively.

MATERIALS AND METHODS

Sources of cultures

The fungi examined include type strains or representatives of all available species of *Talaromyces* and *Biverticillium*. The strains are maintained in the CBS-KNAW Fungal Biodiversity Centre (CBS) culture collection and an overview of strains used for phylogenetic analysis is shown in Table 1. In a few cases, the ex-type strain was unavailable and sequence data present in GenBank were used.

Morphology and physiology

Cultures were grown for 7 d on Czapek agar, Czapek yeast autolysate agar (CYA), oatmeal agar (OA) and/or malt extract agar (MEA) plates at 25 °C or, if required, another temperature. Medium compositions follow Samson *et al.* (2010). Cultures were grown for up to 3 wk for ascospore production.

Extrolite analysis

Nearly all species described in the genera *Penicillium sensu lato* (including those formerly classified in *Eupenicillium*), *Penicillium* subgenus *Biverticillium*, *Talaromyces*, *Aspergillus* and its many associated teleomorphic genera, and *Paecilomyces* (including those formerly or still classified in the associated teleomorph genus *Byssosclamyces*) were analysed qualitatively for their profiles of secondary metabolites as determined by HPLC with diode array detection. Many strains of each species were examined, whenever available, but in some cases only the ex-type culture was available. Cultures were inoculated on the media CYA, MEA (Blakeslee formula, using Difco malt extract), YES agar (Samson *et al.* 2010, Difco yeast extract) and OA. All cultures were analysed chemically using three agar plugs from a 7 d old culture grown at 25 °C (Smedsgaard 1997). Different methods were used for HPLC analysis, but the methods were essentially based on Frisvad & Thrane (1987, 1993). Since 1997, the method for Nielsen & Smedsgaard (2003) was used and after 2010 the UPLC method of Nielsen *et al.* (2011) was applied. Metabolites were identified via their diode-array based UV-VIS spectra and in some cases by their mass spectra, and by comparison to authenticated standards (Nielsen *et al.* 2011).

For the extrolites analyses, the biosynthetic families of the sampled genera were compared using UPGMA cluster analysis (NTSYS version 2.11). All metabolites were classified according to biosynthetic families; for example the viridicatin biosynthetic family consists of cyclophenol, cyclophenin, cycloheptin, dehydrocycloheptin, viridicatin, viridicatol and 3-methoxyviridicatin (Turner & Aldridge 1983). This family was scored as one character in the cluster analysis. The exometabolites were also combined into biosynthetic families and tabulated as such. For example, many species of *Talaromyces* and *Penicillium* subgenus *Biverticillium* produce the azaphilones mitorubrin, mitorubrinol, mitorubrinolol, mitorubrinolol acetate, mitorubrinic acid, funicone, deoxyfunicone, actofunicone,

3-O-methylfunicone, kasanosin A and B, diazaphilonic acid, and wortmin; they are here collectively called the mitorubrins, while the related metabolites vermistatins and penicidones are called vermistatins (see Šturdíková *et al.* 2000, Nicoletti *et al.* 2009, Osmanova *et al.* 2010). Some chlorinated azaphilones such as helicisins (Yoshida *et al.* 1995) and luteusins (Fujimoto *et al.* 1990, Yoshida *et al.* 1996a, b) are epimers of the sclerotiorins from *P. sclerotiorum*, and are treated as two families, albeit closely related to the mitorubrins.

DNA extraction, amplification and sequencing

Isolates used for molecular studies were grown on MEA for 7–14 d at the required temperature prior to DNA extraction. DNA was extracted from the cells using the UltraClean™ Microbial DNA Kit (MoBio Laboratories), following the protocols of the manufacturer. A part of the *RPB1* gene was amplified to study the phylogenetic relationships among *Penicillium* and other related genera. This fragment was amplified using the primer pair RPB1-F1843 5'-ATTTYGAYGGTGAYGARATGAAC-3' and RPB1-R3096 5'-GRACRGTDCRCATAYTTRACC-3' (Houbraken & Samson 2011). Primer RPB1-F1843 corresponds with position 1490–1512 of GenBank no. XM_002146871 (*P. marneffei*, ATCC 18224) and RPB1-R3096 corresponds with position 2610–2633. An additional primer, RPB1-R2623 5'-GCRTTGTTSARATCCTTMARRCTC-3' was occasionally used as an internal primer for sequencing (Houbraken & Samson 2011). The ITS regions were sequenced to study the relationship among *Talaromyces* and the related biverticillate anamorphic species. Fragments containing the ITS region were amplified using primers V9G (de Hoog & Gerrits van den Ende 1998) and LS266 (Masclaux *et al.* 1995). Sequencing reactions were performed with the Big Dye Terminator Cycle Sequencing Ready Reaction Kit v. 3.1 (Applied Biosystems) and carried out for both strands to ensure consistency of the consensus sequence.

Data analyses

For the DNA sequence analyses, alignments were performed using the software Muscle as implemented in the MEGA5 programme (Tamura *et al.* 2011). The RAxML (randomised accelerated maximum likelihood) software (v. 7.2.8, Stamatakis *et al.* 2008) was used for the Maximum Likelihood (ML) analysis. The robustness of trees in the ML analyses was evaluated by 100 bootstrap replications. The phylogram based on *RPB1* sequences is rooted with *Coccidioides immitis* (strain RS; full genome strain), and *Trichocoma paradoxa* (CBS 788.83) is used as an outgroup in the ITS analysis.

RESULTS

Phylogenetic generic delimitation of *Talaromyces* and biverticillate anamorphic species

The phylogenetic relationships of *Talaromyces* and species of *Penicillium* subgenus *Biverticillium* among other related genera were studied using partial *RPB1* sequences. One-hundred fifty-six strains were included in this analysis. The length of the alignment was 496 characters (exon data only, no introns observed) and 323 of those characters were variable. The proportion of gaps and

Table 1. Strains used in phylogenetic analysis of *Talaromyces*.

| Name | Collection no. | Origin | GenBank Accession number | |
|-------------------------------------|--|--|-------------------------------|----------|
| | | | RPB1 | ITS |
| " <i>Aphanoascus cinnabarinus</i> " | CBS 267.72 = ATCC 26215 | Soil, Japan | JN121625 | JN899376 |
| <i>Aspergillus aculeatus</i> | CBS 172.66 ^T = ATCC 16872 = IMI 211388 | Tropical soil | JN121590 | |
| <i>Aspergillus clavatoflavus</i> | CBS 473.65 ^{NT} = ATCC 16866 = IMI 124937 | Rain forest soil, Tulley, Queensland, Australia | JN121686 | |
| <i>Aspergillus flavus</i> | NRRL 3357 = CBS 128202 = ATCC 200026 | Peanut cotyledons, USA | Unpublished | |
| <i>Aspergillus fumigatus</i> | Af293 | Patient with invasive aspergillosis | Nierman <i>et al.</i> (2005) | |
| <i>Aspergillus niger</i> | CBS 513.88 | Derived from NRRL 3122 and currently used as enzyme production strain | Pel <i>et al.</i> (2007) | |
| <i>Aspergillus ochraceoroseus</i> | CBS 101887 = ATCC 42001 = IBT 14580 | Soil, Tai National Forest, Ivory Coast | JN121557 | |
| <i>Aspergillus ochraceus</i> | CBS 108.08 ^{NT} = ATCC 1008 = CBS 547.65 = IMI 016247 = IMI 016247iii = IMI 016247iv = NRRL 1642 = NRRL 398 | Unknown source | JN121562 | |
| <i>Aspergillus penicillioides</i> | CBS 130294 | Indoor environment, Germany | JN121578 | |
| <i>Aspergillus robustus</i> | CBS 649.93 ^T = CBS 428.77 = IBT 14305 | Surface soil from thorn-forest, near Mombasa, Kenya | JN121711 | |
| <i>Aspergillus sparsus</i> | CBS 139.61 ^{NT} = ATCC 16851 = IMI 019394 = IMI 019394ii = MUCL 31314 = NRRL 1933 | Soil, Costa Rica | JN121586 | |
| <i>Aspergillus steynii</i> | CBS 112812 ^T = IBT 23096 | Dried arabica green coffee bean, on parchment, internal infection, Chamumdesheran Estata, Karnataka, district Giris, India | JN121569 | |
| <i>Aspergillus sydowii</i> | CBS 264.81 | Grains and milling fractions, <i>Triticum aestivum</i> , India | JN121624 | |
| <i>Aspergillus versicolor</i> | CBS 245.65 = ATCC 11730 = ATCC 16020 = IMI 045554 = IMI 045554ii = IMI 045554iii = IMI 045554iv = MUCL 19008 | Cellophane, Indiana, USA | JN121614 | |
| <i>Aspergillus zonatus</i> | CBS 506.65 ^{NT} = ATCC 16867 = IMI 124936 | Forest soil, Province of Linon, Fortuna, Costa Rica | JN121691 | |
| <i>Byssosclamyces nivea</i> | CBS 100.11 ^T = ATCC 22260 | Unknown source | JN121511 | |
| <i>Byssosclamyces spectabilis</i> | CBS 101075 ^T = ATCC 90900 = FRR 5219 | Heat processed fruit beverage, Tokyo, Japan | JN121554 | |
| <i>Byssosclamyces verrucosa</i> | CBS 605.74 ^T = ATCC 34163 | Nesting material of <i>Leipoa ocellata</i> (Malleefowl), Pulletop Nature Reserve, New South Wales, Australia | JN680311 | |
| <i>Chrysosporium inops</i> | CBS 132.31 ^T = IMI 096729 = UAMH 802 | Skin of man, Italy | JN121584 | |
| <i>Coccidioides immitis</i> | Strain "RS" | Vaccine strain - origin unknown | Sharpton <i>et al.</i> (2009) | |
| <i>Emericella nidulans</i> | FGSC A4 (= ATCC 38163 = CBS 112.46) | Unknown source | Galagan <i>et al.</i> (2005) | |
| <i>Eurotium herbariorum</i> | CBS 516.65 ^{NT} = ATCC 16469 = IMI 211383 = NRRL 116 | Unpainted board, Washington, USA | JN121693 | |
| <i>Geosmithia viridis</i> | CBS 252.87 ^T = FRR 1863 = IMI 288716 | Soil, bank of creek flowing into Little River, New South Wales | JN680284 | JN899314 |
| <i>Hamigera avellanea</i> | CBS 295.48 ^T = ATCC 10414 = IMI 040230 = NRRL 1938 | Soil, San Antonio, Texas, USA | JN121632 | |
| <i>Hamigera striata</i> | CBS 377.48 ^{NT} = ATCC 10501 = IMI 039741 = NRRL 717 | Canned blueberries, USA | JN121665 | |
| <i>Monascus purpureus</i> | CBS 109.07 ^T = ATCC 16365 = ATCC 16426 = IMI 210765 = NRRL 1596 | Fermented rice grain, 'ang-quac' (purple coloured rice), Kagok-Tegal, imported from China, Prov. Quouan-toung, Java, Indonesia | JN121563 | |
| <i>Paecilomyces aeruginus</i> | CBS 350.66 ^T = IMI 105412 | Debris of <i>Glyceria maxima</i> , Attenborough, Notts., UK | JN121657 | JN899388 |
| <i>Paecilomyces pascuus</i> | CBS 253.87 ^T = FRR 1925 | Pasture grass, Otara, New Zealand | JN899292 | JN899321 |

Table 1. (Continued).

| Name | Collection no. | Origin | GenBank Accession number | |
|---|---|---|--------------------------|----------|
| | | | RPB1 | ITS |
| <i>Penicillioopsis clavariiformis</i> | CBS 761.68 = CSIR 1135 | Unknown source, Pretoria, South Africa | JN121716 | |
| <i>Penicillium aculeatum</i> | CBS 100105 = CBS 289.48 = ATCC 10409 = IMI 040588 = NRRL 2129 = NRRL A-1474 | Textile, USA | | JN899389 |
| | CBS 289.48 ^{NT} = ATCC 10409 = IMI 040588 = NRRL 2129 = NRRL A-1474 | Textile, USA | | JN899378 |
| <i>Penicillium aculeatum</i> var. <i>apiculatum</i> | CBS 312.59 ^T = ATCC 18315 = FRR 635 = IMI 068239 | Soil, Japan | JN680293 | JN899375 |
| <i>Penicillium allahabadense</i> | CBS 453.93 ^T = ATCC 15067 = CBS 304.63 | Soil of cultivated field, pH 6.9, Allahabad, India | JN680309 | JN899345 |
| <i>Penicillium arenicola</i> | CBS 220.66 ^T = ATCC 18321 = ATCC 18330 = IMI 117658 = NRRL 3392 | Soil from pine forest, Kiev, Ukraine | JN121601 | |
| <i>Penicillium aurantiacum</i> | CBS 314.59 ^T = ATCC 13216 = IMI 099722 = NRRL 3398 | Soil, Georgia | | JN899380 |
| <i>Penicillium aureocephalum</i> | CBS 102801 ^T | <i>Quercus ruber</i> , Gerona, Selva de Mar, Catalonia, Spain | | JN899392 |
| <i>Penicillium brunneum</i> | CBS 227.60 ^T = ATCC 18229 = FRR 646 = IFO 6438 = IHEM 3907 = IMI 078259 = MUCL 31318 | Milled rice imported into Japan, Thailand | JN680281 | JN899365 |
| <i>Penicillium calidicanium</i> | CBS 112002 ^T | Soil, Nantou County, Taiwan | JN899305 | JN899319 |
| <i>Penicillium canescens</i> | CBS 300.48 ^{NT} = ATCC 10419 = IMI 028260 = MUCL 29169 = NRRL 910 | Soil, England | JN121636 | |
| <i>Penicillium catenatum</i> | CBS 352.67 ^T = ATCC 18543 = IMI 136241 | Desert soil, Upington, Cape Province, South Africa | JN121659 | |
| <i>Penicillium cinnamopurpureum</i> | CBS 490.66 = ATCC 18337 = IMI 114483 | Cultivated soil, South Africa | JN121690 | |
| <i>Penicillium citrinum</i> | CBS 139.45 ^T = ATCC 1109 = IMI 091961 = MUCL 29781 = NRRL 1841 | Unknown source | JN121585 | |
| <i>Penicillium coalescens</i> | CBS 103.83 ^T | Soil under <i>Pinus</i> sp., near Vulladolid, Spain | | JN899366 |
| <i>Penicillium concavorugulosum</i> | CBS 898.73 ^T = ATCC 20202 | Unknown substrate, Japan | JN899304 | JN899390 |
| <i>Penicillium crateriforme</i> | CBS 184.27 ^T = FRR 1057 = IMI 094165 = LSHB P164 = MUCL 29224 = NRRL 1057 | Soil, Louisiana | JN680270 | JN899373 |
| <i>Penicillium dendriticum</i> | CBS 660.80 ^T = IMI 216897 | Leaf litter of <i>Eucalyptus pauciflora</i> , Kosciusko National Park, New South Wales, Australia | JN121714 | JN899339 |
| <i>Penicillium diversum</i> | CBS 320.48 ^T = ATCC 10437 = DSM 2212 = IMI 040579 = IMI 040579ii = NRRL 2121 | Leather, USA | JN680297 | JN899341 |
| <i>Penicillium duclauxii</i> | CBS 322.48 ^T = ATCC 10439 = IMI 040044 = MUCL 28672 = MUCL 29094 = MUCL 29212 = NRRL 1030 | Canvas, France | JN121643 | JN899342 |
| <i>Penicillium echinosporum</i> | CBS 293.62 ^T = ATCC 18319 = DSM 2230 = FRR 3411 = IMI 080450 = IMI 101214 | Wood pulp, Surrey, Kenley, UK | | JN899363 |
| <i>Penicillium erythromellis</i> | CBS 644.80 ^T = FRR 1868 = IMI 216899 | Soil from creek bank, Little River, New South Wales, Australia | JN680315 | JN899383 |
| <i>Penicillium euglaucum</i> | CBS 323.71 ^{NT} | Soil, Argentina | JN121644 | |
| <i>Penicillium expansum</i> | CBS 325.48 = ATCC 7861 = IBT 5101 = IMI 039761 = MUCL 29192 = NRRL 976 | Fruit of <i>Malus sylvestris</i> , USA | JN121645 | |
| <i>Penicillium fellutanum</i> | CBS 229.81 ^{NT} = ATCC 10443 = CBS 326.48 = FRR 746 = IFO 5761 = IMI 039734 = IMI 039734iii = NRRL 746 | Unknown source, USA | JN121605 | |
| <i>Penicillium funiculosum</i> | CBS 272.86 ^{NT} = IMI 193019 | <i>Lagenaria vulgaris</i> , India | JN680288 | JN899377 |
| <i>Penicillium glabrum</i> | CBS 125543 ^{NT} = IBT 22658 = IMI 91944 | Unknown source | JN121717 | |

Table 1. (Continued).

| Name | Collection no. | Origin | GenBank Accession number | |
|--------------------------------------|---|--|--------------------------|----------|
| | | | RPB1 | ITS |
| <i>Penicillium herquei</i> | CBS 336.48 ^T = ATCC 10118 = FRR 1040 = IMI 028809 = MUCL 29213 = NRRL 1040 | Leaf, France | JN121647 | |
| <i>Penicillium ilderdanum</i> | CBS 168.81 ^T = IJFM 5596 = IMI 253793 | Air, Madrid, Spain | | JN899311 |
| <i>Penicillium isariiforme</i> | CBS 247.56 ^T = ATCC 18425 = IMI 060371 = MUCL 31191 = MUCL 31323 = NRRL 2638 | Woodland soil, Zaire | JN121616 | |
| <i>Penicillium islandicum</i> | CBS 338.48 ^{NT} = ATCC 10127 = IMI 040042 = MUCL 31324 = NRRL 1036 | Unknown source, Cape Town, South Africa | JN121648 | JN899318 |
| <i>Penicillium janthinellum</i> | CBS 340.48 ^{NT} = ATCC 10455 = IMI 040238 = NRRL 2016 | Soil, Nicaragua | JN131650 | |
| <i>Penicillium javanicum</i> | CBS 341.48 ^T = ATCC 9099 = IMI 039733 = MUCL 29099 = NRRL 707 | Root of <i>Camellia sinensis</i> , Indonesia, Java | JN121651 | |
| <i>Penicillium kewense</i> | CBS 344.61 ^T = ATCC 18240 = IMI 086561 = MUCL 2685 = NRRL 3332 | Culture contaminant of mineral oil CMI 1959; Kew, Surrey, UK | JN121654 | |
| <i>Penicillium korosum</i> | CBS 762.68 ^T | Rhizosphere, India | | JN899347 |
| <i>Penicillium lapidosum</i> | CBS 343.48 ^T = ATCC 10462 = IMI 039743 = NRRL 718 | Canned blueberry, Washington, USA | JN121653 | |
| <i>Penicillium liani</i> | CBS 225.66 ^T = ATCC 18325 = ATCC 18331 = IMI 098480 = NRRL 3380 = VKM F-301 | Soil, China | JN680280 | JN899395 |
| <i>Penicillium loliense</i> | CBS 643.80 ^T = ATCC 52252 = FRR 1798 = IMI 216901 = MUCL 31325 | <i>Lolium</i> , Palmerston North, New Zealand | JN680314 | JN899379 |
| <i>Penicillium marneffeii</i> | CBS 388.87 ^T = ATCC 18224 = CBS 334.59 = IMI 068794ii = IMI 068794iii | <i>Rhizomys sinensis</i> (bamboo rat), Vietnam | JN899298 | JN899344 |
| <i>Penicillium minioluteum</i> | CBS 642.68 ^T = IMI 089377 = MUCL 28666 | Unknown source | JN121709 | JN899346 |
| <i>Penicillium mirabile</i> | CBS 624.72 ^T = CCRC 31665 = FRR 1959 = IMI 167383 = MUCL 31206 | Forest soil, Crimea, Ukraine | JN680312 | JN899322 |
| <i>Penicillium namylovskii</i> | CBS 353.48 ^T = ATCC 11127 = IMI 040033 = MUCL 29226 = NRRL 1070 | Soil under <i>Pinus</i> sp., Puszcza Bialowieska, square "652", Poland | JN121660 | |
| <i>Penicillium oblatum</i> | CBS 258.87 ^T = FRR 2234 | Spoiled baby food, Sydney, New South Wales, Australia | JN680285 | JN899364 |
| <i>Penicillium ochrosalmoneum</i> | CBS 489.66 = ATCC 18338 = IMI 116248ii | Cornmeal, South Africa | JN121689 | |
| <i>Penicillium osmophilum</i> | CBS 462.72 ^T = IBT 14679 | Agricultural soil, Wageningen, Netherlands | JN121683 | |
| <i>Penicillium palmae</i> | CBS 442.88 ^T = IMI 343640 | Seed, Wageningen, Netherlands | JN680308 | JN899396 |
| <i>Penicillium panamense</i> | CBS 128.89 ^T = IMI 297546 | Soil, Barro Colorado Island, Panama | JN899291 | JN899362 |
| <i>Penicillium phialosporum</i> | CBS 233.60 ^T = ATCC 18481 = FRR 203 = IMI 078256 | Milled Californian rice, California, USA | JN680282 | JN899340 |
| <i>Penicillium piceum</i> | CBS 361.48 ^T = ATCC 10519 = IMI 040038 = NRRL 1051 | Unknown source | | JN899370 |
| <i>Penicillium pinophilum</i> | CBS 631.66 ^{NT} = ATCC 36839 = CECT 2809 = DSM 1944 = IAM 7013 = IMI 114933 | PVC, Centre d'Études du Bouchet, M. Magnoux, France | JN680313 | JN899382 |
| <i>Penicillium pittii</i> | CBS 139.84 ^T = IMI 327871 | Clay soil, under poplar trees, bank of Duero River, Valladolid, Spain | JN680274 | JN899325 |
| <i>Penicillium primulinum</i> | CBS 321.48 ^T = ATCC 10438 = CBS 439.88 = FRR 1074 = IMI 040031 = MUCL 31321 = MUCL 31330 = NRRL 1074 | USA | JN680298 | JN899317 |
| <i>Penicillium proteolyticum</i> | CBS 303.67 ^T = ATCC 18326 = NRRL 3378 | Granite soil, Ukraine | JN680292 | JN899387 |
| <i>Penicillium pseudostromaticum</i> | CBS 470.70 ^T = ATCC 18919 = FRR 2039 | Feather, near Itasca State Park, Hubbard Co., Minnesota, USA | JN899300 | JN899371 |

Table 1. (Continued).

| Name | Collection no. | Origin | GenBank Accession number | |
|--|---|--|--------------------------|----------|
| | | | RPB1 | ITS |
| <i>Penicillium purpurogenum</i> | CBS 286.36 ^T = IMI 091926 | Unknown source | JN680271 | JN899372 |
| <i>Penicillium purpurogenum</i> var. <i>rubisclerotium</i> | CBS 274.95 | Sculpture, castle Troja, Prague, Czech Republic | JN899295 | JN899316 |
| | CBS 270.35 ^T = ATCC 4713 = ATCC 52244 = FRR 1064 = IBT 4302 = MUCL 29225 = NRRL 1064 = NRRL 1142 | <i>Zea mays</i> , Castle Rock, Virginia, USA | JN680287 | JN899381 |
| <i>Penicillium rademirici</i> | CBS 140.84 ^T = CECT 2771 = IMI 282406 = IMI 327870 | Air under willow tree, bank of river Duero, Herrera, Valladolid, Spain | | JN899386 |
| <i>Penicillium radicum</i> | CBS 100489 ^T = FRR 4718 | Root of seedling of <i>Triticum aestivum</i> , Wagga Wagga, New South Wales, Australia | | JN899324 |
| <i>Penicillium rotundum</i> | CBS 369.48 ^T = ATCC 10493 = IMI 040589 = NRRL 2107 | Wood, Chiriqui Prov., Panama | | JN899353 |
| <i>Penicillium rubicundum</i> | CBS 342.59 ^T = ATCC 13217 = IMI 099723 = NRRL 3400 | Soil, Georgia, USA | JN680301 | JN899384 |
| " <i>Penicillium rubrum</i> " | CBS 196.88 = FRR1714 | Unknown source | JN680278 | JN899312 |
| | CBS 206.89 = IFO 6580 | Japan | JN680279 | JN899313 |
| | CBS 263.93 | Bronchoalveolair lavage of immunocompetent female patient with pneumonia by <i>Nocardia</i> | JN680286 | JN899315 |
| <i>Penicillium rugulosum</i> | CBS 371.48 ^T = ATCC 10128 = IMI 040041 = MUCL 31201 = NRRL 1045 | Tuber (<i>Solanum tuberosum</i>), Connecticut, USA | JN680302 | JN899374 |
| <i>Penicillium sabulosum</i> | CBS 261.87 ^T = FRR 2743 | Spoiled pasteurized fruit juice, New South Wales, Sydney, Australia | JN899294 | |
| <i>Penicillium samsonii</i> | CBS 137.84 ^T = CECT 2772 = IMI 282404 = IMI 327872 | Fruit, damaged by insect, Valladolid, Spain | JN680273 | JN899369 |
| <i>Penicillium shearii</i> | CBS 290.48 ^T = ATCC 10410 = IMI 039739 = IMI 039739iv = NRRL 715 | Soil, Tela, Honduras | JN121631 | |
| <i>Penicillium siamense</i> | CBS 475.88 ^T = IMI 323204 | Forest soil, Lampang, Thum District, Ban Daen Tham, Thailand | | JN899385 |
| <i>Penicillium simplicissimum</i> | CBS 372.48 ^{NT} = ATCC 10495 = IMI 039816 | Flannel bag, Cape, South Africa | JN121662 | |
| <i>Penicillium stipitatum</i> | CBS 375.48 ^T = ATCC 10500 = NRRL 1006 = IMI 39805 | Rotting wood, Louisiana, USA | JN680303 | JN899348 |
| <i>Penicillium stolckiae</i> | CBS 315.67 ^T = IMI 136210 = ATCC 18546 | Peaty forest soil, Eastern Transvaal, South-Africa | JN680295 | |
| <i>Penicillium tardum</i> | CBS 258.37 ^T = NRRL 2116 | Unknown source | JN899293 | |
| | CBS 378.48 ^T = ATCC 10503 = IMI 040034 = NRRL 1073 | Dead twig, France | JN899297 | |
| <i>Penicillium tularense</i> | CBS 430.69 ^T = ATCC 22056 = IMI 148394 | Soil, under <i>Pinus ponderosa</i> and <i>Quercus kelloggii</i> , Tulare Co., Pine Flat, California, USA | JN121681 | |
| <i>Penicillium variabile</i> | CBS 385.48 ^{NT} = ATCC 10508 = IMI 040040 = NRRL 1048 | Cocos fibre, Johannesburg, South Africa | JN680304 | JN899343 |
| <i>Penicillium varians</i> | CBS 386.48 ^T = ATCC 10509 = IMI 040586 = NRRL 2096 | Cotton yarn, UK | JN680305 | JN899368 |
| <i>Penicillium verruculosum</i> | CBS 388.48 ^{NT} = ATCC 10513 = DSM 2263 = IMI 040039 = NRRL 1050 | Soil, Texas, USA | | JN899367 |
| <i>Penicillium victoriae</i> | CBS 274.36 ^T = IMI 058412 = MUCL 9651 | Dried leaf, Tobaheide, Sumatra | JN680289 | JN899393 |
| <i>Penicillium viridicatum</i> | CBS 390.48 ^{NT} = ATCC 10515 = IBT 23041 = IMI 039758 = IMI 039758ii = NRRL 963 | Air, District of Columbia, Washington D.C., USA | JN121668 | |
| <i>Phialosimplex caninus</i> | CBS128032 ^T = UAMH 10337 | Bone marrow aspirate ex canine, San Antonio, Texas, USA | JN121587 | |
| <i>Phialosimplex chlamyosporus</i> | CBS 109945 ^T = FMR 7371 = IMI 387422 | Disseminated infection in a dog | JN121566 | |
| <i>Phialosimplex sclerotialis</i> | CBS 366.77 ^T = IAM 14794 | Fodder of ray-grass and lucerne, France | JN121661 | |
| <i>Rasamsonia eburnea</i> | CBS 100538 ^T = IBT 17519 | Soil, Taipei, Taiwan | JN680325 | |

Table 1. (Continued).

| Name | Collection no. | Origin | GenBank Accession number | |
|---|---|---|--------------------------|----------|
| | | | RPB1 | ITS |
| <i>Rasamsonia argillacea</i> | CBS 101.69 ^T = IMI 156096 = IBT 31199 | Mine tip with a very high surface temperature; Staffordshire, UK | JN121556 | |
| <i>Rasamsonia byssochlamydoides</i> | CBS 413.71 ^T = IBT 11604 | Dry soil under Douglas fir, Oregon, USA | JN121675 | |
| <i>Rasamsonia emersonii</i> | CBS 393.64 ^T = DTO 4811 = IBT 21695 = ATCC 16479 = IMI 116815 = IMI 116815ii | Compost, Italy | JN121670 | |
| <i>Sagenoma viride</i> | CBS 114.72 ^T ATCC 22467 = NRRL 5575 | Soil, Australia | JN121571 | |
| <i>Sagenomella bohémica</i> | CBS 545.86 ^T = CCF 2330 = IAM 14789 | Peloids for balneological purposes, Frantiskovy Lázně Spa, West Bohemia, Czech Republic | JN121699 | JN899400 |
| <i>Sagenomella diversispora</i> | CBS 398.69 | Forest soil under <i>Populus tremuloides</i> , Petawawa, Ontario, Canada | JN121673 | |
| | CBS 399.69 = MUCL 15012 | Forest soil under <i>Thuja occidentalis</i> , Aberfoyle, Ontario, Canada | JN121674 | |
| <i>Sagenomella griseoviridis</i> | CBS 426.67 ^T = ATCC 18505 = IMI 113160 | Unknown source | JN121677 | |
| <i>Sagenomella humicola</i> | CBS 427.67 ^T = ATCC 18506 = IMI 113166 | Forest soil under <i>Thuja occidentalis</i> , Ontario, Canada | JN121678 | |
| <i>Sagenomella striatispora</i> | CBS 429.67 ^T = ATCC 18510 = IMI 113163 | Soil, Guelph, Ontario, Canada | JN121679 | |
| <i>Sagenomella verticillata</i> | CBS 415.78A | Gymnosperm forest soil, Sweden | JN680307 | |
| <i>Sclerocleista ornata</i> | CBS 124.53 ^{NT} = ATCC 16921 = IMI 055295 = MUCL 15643 = NRRL 2256 | Soil in oak forest, Dane Co., Madison, Wisconsin, USA | JN121581 | |
| <i>Talaromyces assiutensis</i> | CBS 118440 | Soil, Fes, Morocco | | JN899320 |
| | CBS 147.78 ^T | Soil, amended with crushed buffalo hoofs and incubated for 5 months at 35 °C, Egypt | JN680275 | JN899323 |
| <i>Talaromyces austrocalifornicus</i> | CBS 644.95 ^T = IBT 17522 | Soil, campus Univ. South California, Los Angeles, USA | JN680316 | JN899357 |
| <i>Talaromyces bacillisporus</i> | CBS 296.48 ^T = ATCC 10126 = IMI 040045 = NRRL 1025 | Begonia leaf, New York City, New York, USA | JN121634 | JN899329 |
| <i>Talaromyces barcinensis</i> | CBS 649.95 ^T = IBT 17518 | Soil, Barcelona, Spain | JN680318 | JN899349 |
| <i>Talaromyces brevicompactus</i> | CBS 102661 ^T = AS 3.4676 | Moulded vegetables, Prov. Sechuan, Wolong, China | JN680326 | |
| <i>Talaromyces convolutus</i> | CBS 100537 ^T = IBT 14989 | Soil, Kathmandu, Nepal | JN121553 | JN899330 |
| <i>Talaromyces cyanescens</i> | CBS 114900 = FMR 8388 | Tortosa, Catalina, Spain | | JN899391 |
| <i>Talaromyces derxii</i> | CBS 412.89 ^T = NHL 2981 | Cultivated soil, Okayama Prefecture, Kurashiki City, Higashitomi, Japan | JN680306 | JN899327 |
| | CBS 413.89 ^T = NHL 2982 | Cultivated soil, Okayama Prefecture, Kurashiki City, Higashitomi, Japan | JN899299 | JN899326 |
| <i>Talaromyces emodensis</i> | CBS 100536 ^T = IBT 14990 | Soil, Kathmandu, Nepal | JN121552 | JN899337 |
| <i>Talaromyces flavus</i> | CBS 310.38 ^{NT} = IMI 197477 = NRRL 2098 | Unknown substrate, New Zealand | JN121639 | JN899360 |
| <i>Talaromyces galapagensis</i> | CBS 751.74 ^T = IFO 31796 | Shaded soil under <i>Maytenus obovata</i> , Isla Santa Cruz, Galapagos Islands, Ecuador | JN680321 | JN899358 |
| <i>Talaromyces gossypii</i> | CBS 645.80 ^T = FRR 1966 = IMI 198365 | <i>Gossypium</i> , India | JN680317 | JN899334 |
| <i>Talaromyces helicus</i> var. <i>boninensis</i> | CBS 650.95 ^T = IBT 17516 | Lawn soil, Kominato, Chichijima, Ogasawara-mura, Tokyo-to, Japan | JN680319 | JN899356 |
| <i>Talaromyces helicus</i> var. <i>helicus</i> | CBS 335.48 ^T = ATCC 10451 = DSM 3705 = IMI 040593 = NRRL 2106 | Soil, Sweden | JN680300 | JN899359 |
| <i>Talaromyces helicus</i> var. <i>major</i> | CBS 652.66 ^T = IMI 100914 | Swamp soil, near Attenborough, Nottingham, UK | JN680320 | JN899335 |
| <i>Talaromyces indigoticus</i> | CBS 100534 ^T = IBT 17590 | Soil, Nagasaki-ken, Minamikushiyama-mura, Japan | JN680323 | JN899331 |
| <i>Talaromyces intermedius</i> | CBS 152.65 ^T = BDUN 267 = IFO 31752 = IMI 100874 | Alluvial pasture and swamp soil, Attenborough, Nottingham, England | JN680276 | JN899332 |

Table 1. (Continued).

| Name | Collection no. | Origin | GenBank Accession number | |
|----------------------------------|---|--|--------------------------|----------|
| | | | RPB1 | ITS |
| <i>Talaromyces leycettanus</i> | CBS 398.68 ^T = ATCC 22469 = IMI 178525 | Coal spoil tip soil, Leycett, Staffordshire, England, UK | JN121672 | |
| <i>Talaromyces luteus</i> | CBS 348.51 ^{NT} = IMI 089305 | Soil, UK | JN121656 | |
| <i>Talaromyces macrosporus</i> | CBS 317.63 ^T = FRR 404 = IMI 197478 | Apple juice, Stellenbosch, South Africa | JN680296 | JN899333 |
| <i>Talaromyces mimosinus</i> | CBS 659.80 ^T = FRR 1875 = IMI 223991 | Soil from creek bank, Nattai River, New South Wales, Australia | JN899302 | JN899338 |
| <i>Talaromyces muroii</i> | CBS 756.96 ^T = PF 1153 | Soil, Hualien County, Chingpu, Taiwan | JN680322 | JN899351 |
| <i>Talaromyces ocotl</i> | CBS 102855 ^T | Heat-treated soil from forest of <i>Pinus hartwegii</i> , Veracruz, Mexico | JN680327 | |
| <i>Talaromyces ohioensis</i> | CBS 127.64 ^T | Soil treated with cyanamide, Germany | JN680272 | JN899355 |
| <i>Talaromyces purpureus</i> | CBS 475.71 ^T = ATCC 24069 = ATCC 52513 = FRR 1731 = IMI 181546 | Soil, near Esterel, France | JN121687 | JN899328 |
| <i>Talaromyces subinflatus</i> | CBS 652.95 ^T = IBT 17520 | Copse soil, Hahajima, Ogasawara-mura, Tokyo-to, Japan | JN899301 | JN899397 |
| <i>Talaromyces tardifaciens</i> | CBS 250.94 ^T | Unknown source | JN680283 | JN599361 |
| <i>Talaromyces thermophilus</i> | CBS 236.58 ^T = ATCC 10518 = IMI 048593 = NRRL 2155 | <i>Parthenium argentatum</i> , decaying plant; California, USA | JN121611 | |
| <i>Talaromyces trachyspermus</i> | CBS 373.48 ^T = ATCC 10497 = IMI 040043 = NRRL 1028 | Unknown source, USA | JN121664 | JN899354 |
| <i>Talaromyces ucrainicus</i> | CBS 162.67 ^T = ATCC 22344 = FRR 3462 | Unknown source | JN680277 | JN899394 |
| <i>Talaromyces udagawae</i> | CBS 579.72 ^T = FRR 1727 = IMI 197482 | Soil, Misugimura, Japan | JN680310 | JN899350 |
| <i>Talaromyces unicus</i> | CBS 100535 ^T = CCRC 32703 = IBT 18385 | Soil, Chiayi County, Funlu, Taiwan | JN680324 | JN899336 |
| <i>Talaromyces wortmanii</i> | CBS 391.48 ^T = ATCC 10517 = IMI 040047 = NRRL 1017 | Unknown source | JN121669 | JN899352 |
| <i>Thermoascus aurantiacus</i> | CBS 396.78 | Sawdust, in lumber yard, Toronto, Ontario, Canada | JN121671 | |
| | CBS 891.70 = IMI 173037 | Wood, Firenze, Italy | JN121719 | |
| <i>Thermoascus crustaceus</i> | CBS 181.67 ^T = ATCC 16462 = IMI 126333 | <i>Parthenium argentatum</i> , decaying plant; Salinas, California, USA | JN121591 | |
| <i>Thermoascus thermophilus</i> | CBS 528.71 ^{NT} = IMI 123298 = NRRL 5208 | Wood and bark of <i>Pinus</i> , Sweden | JN121697 | |
| <i>Thermomyces lanuginosus</i> | CBS 218.34 = MUCL 8338 | Fruit shell of <i>Theobroma cacao</i> | JN121599 | |
| | CBS 224.63 = MUCL 8337 | Mushroom compost; Gossau-Zürich Switzerland | JN121602 | |
| | CBS 288.54 = MUCL 8340 | Stomach of bovine foetus, Netherlands | JN680291 | |
| <i>Trichocoma paradoxa</i> | CBS 103.73 | Unknown source, Japan | JN121558 | |
| | CBS 247.57 = MUCL 39666 = IBT 31159 | Unknown source, Hachijō, Japan | JN121617 | |
| | CBS 788.83 | Rotting stump of cut down tree, Myoji Temple near Hakui Noto Park, Ishikawa Pref., Japan | JN121718 | JN899398 |
| <i>Warcupiella spinulosa</i> | CBS 512.65 ^{NT} = ATCC 16919 = IMI 075885 = NRRL 4376 | Jungle soil, Berakas-Muara, Brunei | JN121692 | |

completely undetermined characters in the alignment was 0.60 %. Figure 1 shows that members of the subgenus *Biverticillium* and *Talaromyces* are accommodated in a well-supported (97 % bs), monophyletic clade (= *Talaromyces* s. str.) and that species of the *Penicillium* subgenera *Aspergilloides*, *Furcatum* and *Penicillium* form an independent, well-supported clade (*Penicillium* s. str.). The majority of described *Talaromyces* species belong to *Talaromyces* s. str., but some species are dispersed in other clades, including *Talaromyces ocotl*, *T. luteus*, *T. thermophilus*, *T.*

eburneus, *T. emersonii*, *T. byssochlamydoides*, *T. spectabilis*, *T. brevicompactus*, *T. striatus* and *T. leycettanus*. *Talaromyces ocotl* is in a well-supported clade with the type species of *Sagenomella*, *S. diversispora*, and other *Sagenomella* species. The former *T. emersonii*, *T. eburneus* and *T. byssochlamydoides* form a clade recently recognised and described as the genus *Rasamsonia* (Houbraken *et al.* 2011). *Talaromyces thermophilus* is also excluded from *Talaromyces* s. str. and is closely related to the type species of *Thermomyces*, *Therm. lanuginosus*. Basal to *Therm. lanuginosus*

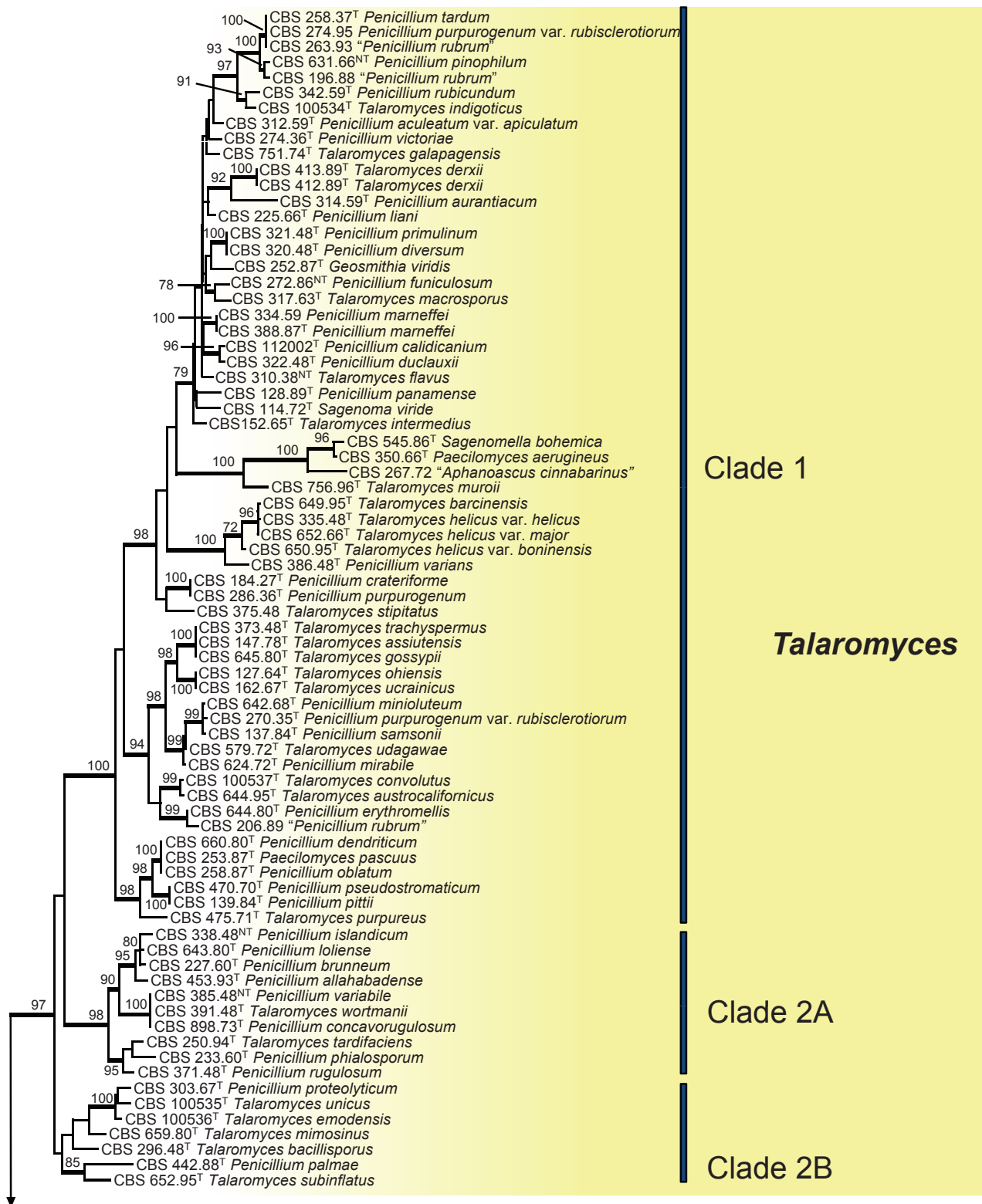


Fig. 1. Best-scoring Maximum Likelihood tree calculated using RAxML, based on partial *RPB1* sequences showing the relationships among members of *Talaromyces* and *Penicillium* subgenus *Biverticillium* and related genera. The bootstrap support percentages of the maximum likelihood (ML) analysis are presented at the nodes. Bootstrap support values less than 70% are not shown and branches with bootstrap support values > 70% are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Coccidioides immitis* (strain RS).

and *T. thermophilus* is *Talaromyces luteus*. This species is on a separate branch and no other closely related species were found in our analysis. The uniqueness of the species is supported by the production of large amounts of the prenylated diketopiperazines talathermophilins A and B, not found in any other species (Chu *et al.* 2010). The phylogenetic position of *T. leycettanus* is not convincingly defined. This species is positioned near *Warcupiella*

spinulosa and *Hamigera striata* (= *Talaromyces striatus*), but bootstrap support is lacking. *Talaromyces brevistipitatus* occurs on a well-supported branch with *H. avellanea*. Comparison of ITS and calmodulin sequences shows that this species is closely related to NRRL 2108, an undescribed, phylogenetically distinct *Hamigera* species (ITS 100% bs, calmodulin 99% bs) (Peterson *et al.* 2010). The majority of members of subgenus *Biverticillium sensu*

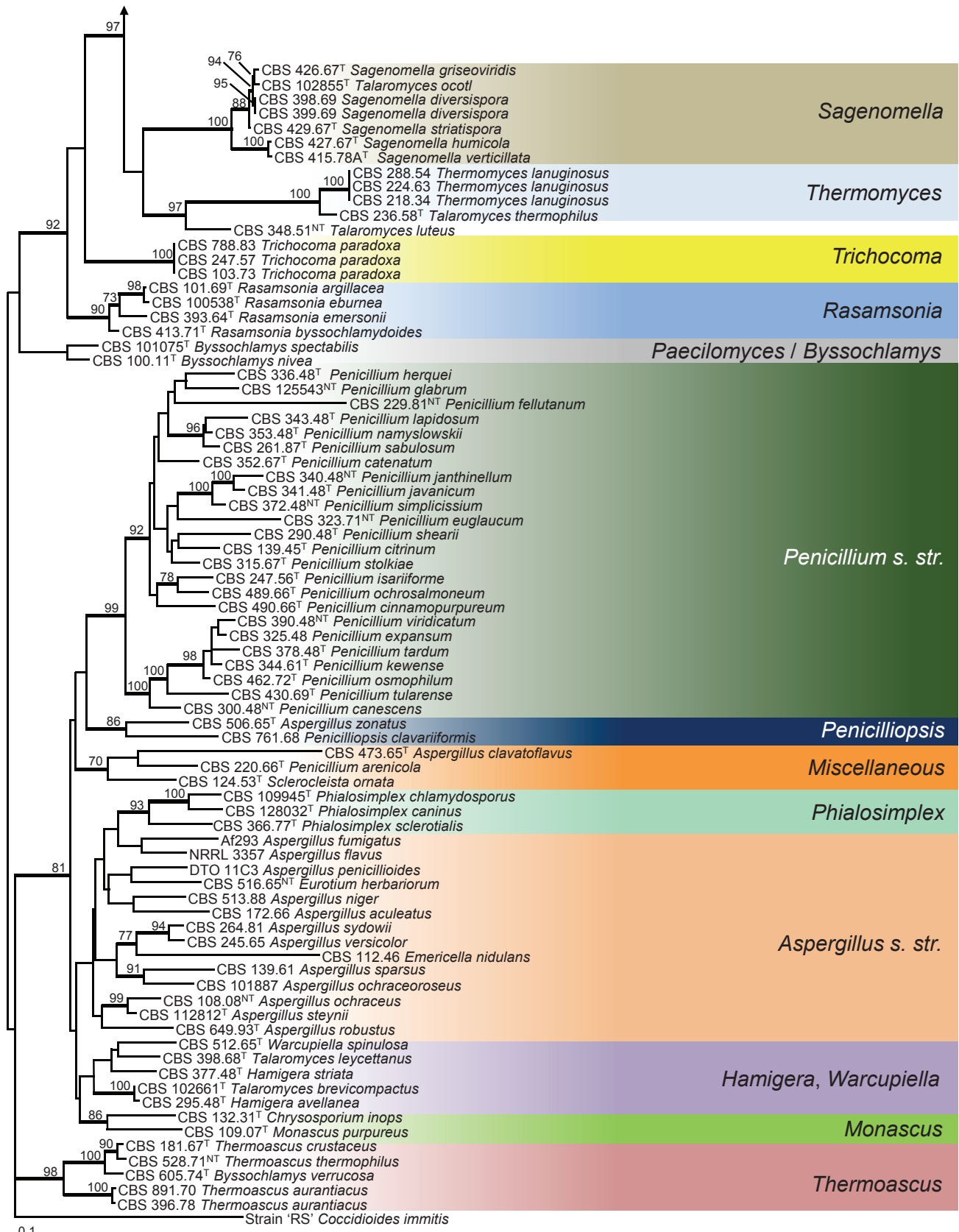


Fig. 1. (Continued).

Pitt (1980) are phylogenetically placed within *Talaromyces* s. str., with *P. isariiforme* as the only exception. This species belongs to *Penicillium* s. str. and is closely related to *P. ochrosalmoneum*. This relationship was also confirmed by extrolite data (see below).

Figure 1 indicates that the following species phylogenetically belong in *Talaromyces*: *Aphanoascus cinnabarinus* (CBS 267.72),

Sagenomella bohémica (CBS 545.86^T), *Paecilomyces aerugineus* (CBS 350.66^T), *Geosmithia viridis* (CBS 252.87^T) and *Sagenoma viride* (CBS 114.72^T). The former three strains are on a well-supported sister clade basal to *Talaromyces muroii* CBS 756.96.

Species delimitation and synonymies within *Talaromyces*

The ITS analysis (Fig. 2) was used in this study to provide a preliminary circumscription of the species belonging to the *Talaromyces* clade. Ninety-seven strains were included in the ITS analysis. The used primer pair V9G and LS266 also amplifies a part of the 18S and 28S rDNA; however, for analysis, only the span including the ITS regions and 5.8S rDNA was used. The length of the alignment was 483 characters and 221 characters were variable.

Most bootstrap support values in the ITS analysis are low, less than 70 %. Only a few branches are supported with values higher than 70 %. The majority of *Talaromyces* species are on a branch with 96 % bootstrap support (clade 1, Fig. 2). This clade is also present in the *RPB1* analysis (100 % bs). Another large clade was present in the ITS phylogram and this clade is supported with 96 % bootstrap (clade 2). This clade can be divided in two subclades (2A and 2B), both present in the *RPB1* analysis; however, the relationship among these subclades is not supported statistically. *Talaromyces dendriticus*, *T. oblatus*, and *Paecilomyces pascuus* are in the same lineage and the former two species share the same ITS sequence. *Talaromyces assiutensis* and *T. gossypii* also have similar ITS sequences and are phenotypically similar (Frisvad et al. 1990a).

Extrolite analysis

In general, *Talaromyces* species produce many biosynthetic families of polyketides and meroterpenoids, but rather few families of nonribosomal peptides and terpenes. By examining HPLC-DAD results from all described species of *Penicillium*, *Aspergillus* and their teleomorphs, and by searching the literature for families of exometabolites produced by these fungi, it is obvious that *Talaromyces* species have unique and specific extrolites (Table 2). Figure 3 shows the common exometabolite families in *Talaromyces/Biverticillium*, *Penicillium*, *Aspergillus* and other genera. *Aspergillus* and *Penicillium* share 91 biosynthetic families, but shares more of these with other fungal genera than with *Talaromyces*. A few exometabolites are shared among *Talaromyces*, *Penicillium* and *Aspergillus* including alternariols, asperphenamate, botryodiploidin, dehydrocarolic acid, emodins, geodins, gregatins, herqueinone, 3-hydroxyphthalic acid, italinic acid, lichexanthones, mellein, monordens, pinselin, rugulosuvines, rugulovasines, secalonic acids and zeorins. Most of these metabolites have relatively simple structures, and many occur in other genera less related phylogenetically to any of the penicilloid and aspergilloid genera. Considering the large number of shared exometabolite biosynthetic families in common between *Penicillium* and *Aspergillus*, *Talaromyces* is clearly different, which corresponds with all other data for these genera.

Among the few extrolites shared by *Penicillium*, *Aspergillus* and *Talaromyces* are the ergochromes, secalonic acid D & F. These anthraquinone derived metabolites are found in *P. isariiforme*, *P. chrysogenum*, *Aspergillus aculeatinus*, *P. dendriticum* and *P. pseudostromaticum* (Samson et al. 1989, Frisvad & Samson 2004, Houbraken et al. 2011). It is also possible that there are optical antipodes of these compounds produced in these genera, as was found in *Aspergillus versicolor* ((+) versicolamide) and *A. sclerotiorum* ((-)-versicolamide) (Williams 2011). If this is so, it may indicate that the extrolites of *Talaromyces* and *Penicillium* /

Aspergillus may also differ in stereochemical aspects. Another example of shared yet different extrolites is the azaphilones, which are common in species of *Talaromyces* and related biverticillate anamorphic species (Frisvad et al. 1990a, Nicoletti et al. 2009, Osmanova et al. 2010), but could not be found in *Aspergillus* and *Penicillium sensu stricto*. When similar compounds were found in *Talaromyces*, stereoisomers of the compounds were found in *Aspergillus* and *Penicillium*. For example, while sclerotiorins occur in *P. sclerotiorum*, the epimers are found in *Talaromyces helicus* and *T. luteus* (Yoshida et al. 1995, 1996a, b). Austdiol was isolated from *Aspergillus pseudoustus* (Vleggaar et al. 1974, Samson et al. 2011), but 7-epi-austdiol from a *Talaromyces* species (Liu et al. 2010).

Misidentifications of strains can make these comparisons difficult, but the overwhelming majority of extrolites found in *Talaromyces* are not found in *Aspergillus* or *Penicillium*. Although vermistatins, penisimplisins, penisimplicissins were reported from *Penicillium simplicissimum* (Komai et al. 2005), the producing strain was misidentified and actually represents a species of *Talaromyces*. The opposite has also happened, and metabolites attributed to a species of subgenus *Biverticillium* are later found to be produced by species of *Penicillium sensu stricto*. *Penicillium verruculosum* was reported to produce verruculogen, hence the name (Cole et al. 1972, Cole & Kirksey 1973), but the strain was later reidentified as *P. brasilianum* (Frisvad 1989).

Penicillium isariiforme (Samson et al. 1989) and *P. ochrosalmoneum* (Wicklow & Cole 1984) both produce large amounts of citreoviridin, supporting their close relationship indicated by the phylogenetic analyses, as noted above (Fig. 1).

DISCUSSION

The symmetrical, biverticillate penicillus was used as a defining character by Wehmer (1914), and Thom (1915a, b). Wehmer (1914) proposed to call this group the Verticillata, while Thom (1915a) referred to it as the *Penicillium luteum-purpurogenum* group. Biourge (1923) was the first who named this group as the subgenus *Biverticillium*, but included species such as *P. citrinum* (as *P. aurifluum*), *P. atramentosum* etc., which are no longer regarded as members of this subgenus (Houbraken et al. 2010). The characteristic lanceolate or acrose phialides was used as a more definitive morphological character of subgenus *Biverticillium* and related *Talaromyces* anamorphs (Raper & Thom 1949), because biverticillate branched conidiophores with flask-shaped phialides are mainly found in unrelated species such as *P. citrinum*. Although the lanceolate phialides occur in most species of subgenus *Biverticillium*, some species, e.g. *P. rugulosum*, have phialides that are not slender and have an apical portion tapering into a long acuminate point.

Thom (1930) treated some of the Penicillia in his *Biverticillate-Symmetrica* group and distinguished four sections: *Ascogena*, *Coremigena*, *Luteo-virida* (*Funiculosa* and *Luteo-purpurogena*) and *Miscellanea*. Later, Raper & Thom (1949) subdivided the group into the *P. luteum* series, *P. duclauxii* series, *P. funiculosum* series, *P. purpurogenum* series, *P. rugulosum* series and *P. herquei* series. This grouping is inconsistent with our phylogenetic analysis of the biverticillate group. The classification proposed by Pitt (1980) is more in concordance with the phylogenetic and taxonomic treatment proposed here, although he included a few species in *Penicillium* subgenus *Biverticillium*, namely *P. isariiforme*, *P. clavigerum* and

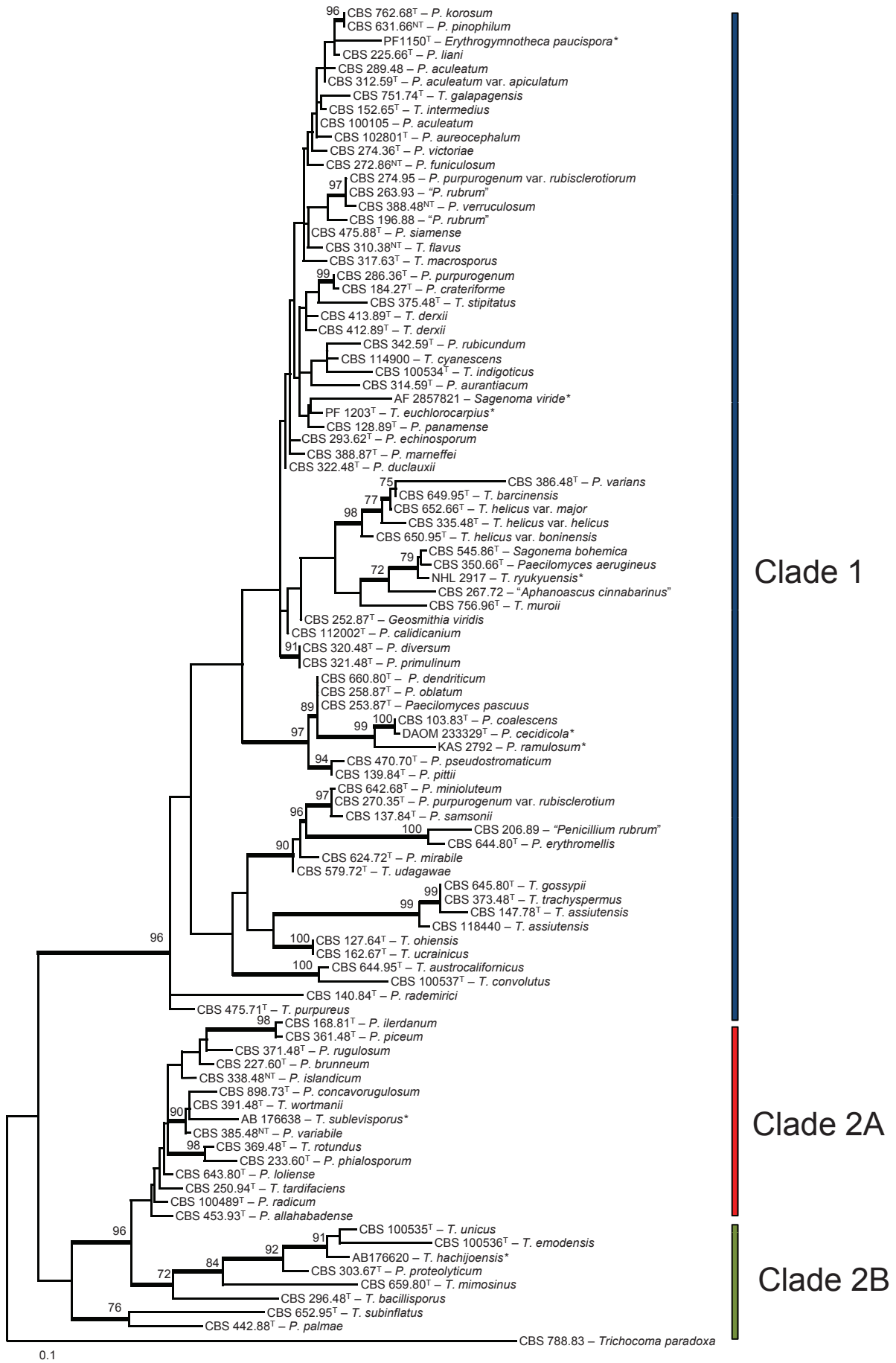


Fig. 2. Best-scoring Maximum Likelihood tree calculated using MEGA 5.0 based on ITS sequences showing the relationship among members of the *Talaromyces* and members of *Penicillium* subgenus *Biverticillium*. The bootstrap support percentages of the maximum likelihood (ML) analysis are presented at the nodes. Bootstrap support values less than 70 % are not shown and branches with bootstrap support values > 75 % are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Trichocoma paradoxa* (CBS 788.83). *T.* = *Talaromyces*; *P.* = *Penicillium*. Strains indicated with * are ITS sequencing obtained from GenBank.

Table 2. Secondary metabolite (exometabolite) biosynthetic families known from *Talaromyces* and *Penicillium* subgenus *Biverticillium*. (P) means also found in *Penicillium* and its teleomorphic state *Eupenicillium*, (A) means also found in species of *Aspergillus*. (Others) means also found in other fungi outside *Penicillium*, *Aspergillus*, *Talaromyces* and related genera.

| Secondary metabolite (exometabolite) biosynthetic families | | |
|--|---|---|
| AF-110 | 5-Hydroxymethylfurfural | Purpurogenones |
| Alternariols * (P and others) | Hydromethylmaltol | Rasfonin |
| Anthglutin | 4-Hydroxy-4,5-dicarboxy pentadecanoic acid (<i>T. spiculisporus</i>) | Rubratoxins |
| Apiculides (incl. NG-011's * (others)) | 7-Hydroxy-2,5-dimethylchromane | Rugulosins (& flavoskyrin) * (others) |
| AS-186-G | 3-Hydroxymethyl-6,8-dimethoxycoumarin | Rugulotrosins |
| Asperphenamates & asperglauclid * (A, P) | 3-Hydroxyphthalic acid * (P) | Rugulosuvine * (P) |
| Atrovetinin methyl acetal (<i>P. verruculosum</i>) | Islandic acids | Rugulovasines * (P) |
| Epi-Austdiols (7-epiaustdiol & 8-O-methylepiaustdiol) (the stereoisomer austdiol found in <i>Aspergillus</i>) | (+)-Isocitric acid + Decylcitric acid (<i>T. spiculisporus</i>) | Secalonic acids * (A, P, others) |
| Austins * (A, P) | Italinic acids * (P) | Speciferone* (others) |
| BE-24811 | Juglones | Spiculisporic acids (= minioluteic acids) |
| BE-31405's | Lichexanthone * (others) | SQ 30957 |
| Berkeleyamides | Luteusins | Stemphyperylene |
| Botryodipoidin * (P & others) | Maculosin * (others) | Stipitatic acids |
| Chrodinanine A | Mellein * (A) | Talaperoxides |
| Cordyanhydrides | Methyl-4-carboxy-5-hydroxyphthalaldehyde | Talaroconvolutins |
| Cyclochlorotines & islanditoxin | 3-Methyl-6-hydroxy-8-methoxy-3,4-dihydroisocoumarins | Talaroderxine |
| Dehydrocarolic acids * (A, P) | Miniolutelides, berkeleydione, berkeleytriones, berkeleyacetals, dhilirolides | Talaroflavones |
| Diethylphthalate (Artefact?) | Mitorubins & kasanosins & funicones | Talaromycins |
| 5,6-Dihydro-3,5-dihydroxy-6-hydroxymethyl-2H-pyran-2-one | Monascins & monascorubramin | Talarotoxins |
| 4,6-Dihydroxy-5-methylphthalide | Monordens * (A, others) | TAN-931 |
| (2E,2E',7S,7'E)-4,9-Dioxo-7-(4',9'-dioxo-2',7' decadienoxyloxy)-2-decanoic acid | NG-061 | Thailandolides |
| Diversonols | NK-374200 | Trachyspermic acids |
| Duclauxins | OF-4949's | Trachyspic acid |
| Emodins * (A, P, others) | Penicillipsin * (others) | Triacetic lactone |
| Erythroskyrins | Penisimplicins | (-)-2,3,4-Trihydroxy-butanamide |
| Flavomannin | Penisimplicissins | Vermicellins |
| Funiculosic acids | Penitric acid & penitricins | Vermiculins |
| Funiculosin | Pevalic acid | Vermilutins |
| Geodins * (A, P) | PF-1092A | Vermistatins & penicidones |
| Glauconic acids | Pinselic acid | Vertoskyrin |
| Gregatins and penicilliois * (A, P) | Pinselins * (A, others) | Wortmannilactones |
| Helicusins | Purpactins (= penicillides = vermioxocins) | Wortmannins * (others) |
| Herqueinones* (P) | Purpuride | Xanthoradones |
| | | Zeorins * (A, others) |

P. vulpinum (as *P. claviforme*) that are now classified in *Penicillium sensu stricto*. The same conclusion was shown by the early molecular results of LoBuglio & Taylor (1993), and subsequently supported by the physiological, morphological and extrolite characters reviewed in the Introduction, and generated during this study.

In general, *Penicillium sensu stricto* and *Aspergillus* share many more features with each other than they do with *Talaromyces*. This includes micro- and macro-morphology, good growth on low water activity media, and the many shared exometabolite families. *Talaromyces* produces a series of metabolites that are apparently unique to this genus (J.C. Frisvad unpubl. data). The characteristic yellow and red colony and mycelial colours in *Talaromyces* are often caused by accumulation of mitorubins and other azaphilones

and unique anthraquinones and mitorubins that are not found in *Aspergillus* and *Penicillium*. Some azaphilones are found in *Penicillium sclerotiorum* and *Penicillium hirayamae*, but only their optical antipodes are found in *Talaromyces*.

***Penicillium* and *Talaromyces* species excluded from the revised *Talaromyces* genus**

Figure 1 shows that a number of species described in the genus should be excluded from *Talaromyces s. str.* Phylogenetically, *T. ocofl* CBS 102855^T belongs to *Sagenomella*, as also suggested using phenotypic characters (Heredia *et al.* 2001). The anamorph of this species was not formally named, described only as

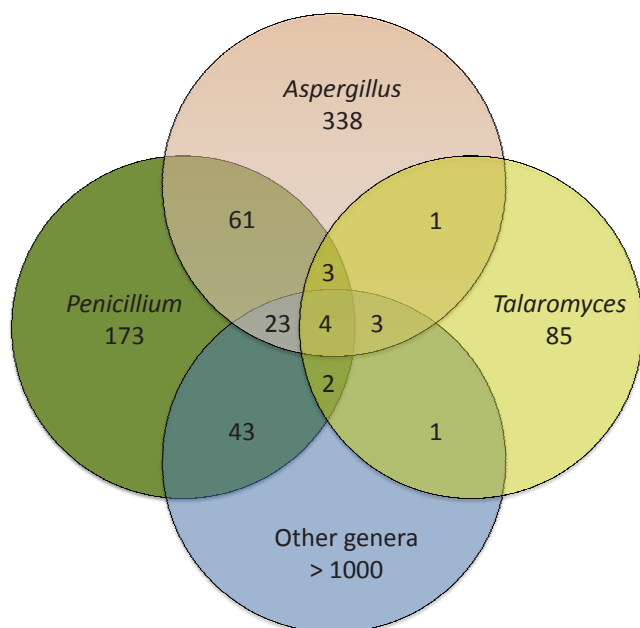


Fig. 3. Common exometabolite families in *Talaromyces/Biverticillium*, *Penicillium*, *Aspergillus* and other genera.

Sagenomella sp., and thus the new combination *Sagenomella ocofi* is proposed in the taxonomy section below.

Our analysis confirms the distinctiveness of the recently described genus *Rasamsonia* erected for thermotolerant or thermophilic species with distinctly rough-walled conidiphore stipes, olive-brown conidia, and ascomata, if present, with a scanty hyphal covering. *Talaromyces eburneus*, *T. emersonii*, *T. byssochlamydoides* were assigned to this genus, together with the anamorphic species originally described as *Geosmithia argillacea* and *G. cylindrospora* (Houbraken *et al.* 2011).

Talaromyces thermophilus is the only member of *Talaromyces* section *Thermophila* (Stolk & Samson 1972). LoBuglio *et al.* (1993) already noted that this species is the most divergent *Talaromyces* species, occupying a basal position to the major *Talaromyces* clade. Houbraken *et al.* (2011) showed that this species is closely related to *Thermomyces lanuginosus* and our partial *RPB1* sequence data confirm this relationship (Fig. 1). We did not examine type material of *Talaromyces thermocitrinus* (as '*thermocitrium*') and the conclusion of Mouchacca (2007), who tentatively placed this species in synonymy with *T. thermophilus*, is not followed here. *Talaromyces luteus* is further basal to *T. thermophilus* and *Therm. lanuginosus* and this species might represent a distinct genus. For the present, *T. thermophilus* and *T. luteus* will be retained in *Talaromyces*. More research is needed to confirm whether the assignment of these species to *Thermomyces* is warranted.

Udagawa & Suzuki (1994) described *Talaromyces spectabilis* with a *Paecilomyces* anamorph. Houbraken *et al.* (2008) transferred this species to *Byssochlamys* and showed that it is the teleomorph of *Paec. variotii*. In a single name system, *Paec. variotii* is the oldest genus and species name for this taxon, and thus the correct name for the holomorph.

Talaromyces brevicompactus, *T. striatus* (= *Hamigera striata*) and *T. leycettanus* are distant from *Talaromyces s. str.* and phylogenetically more closely related to *Penicillium s. str.* and *Aspergillus*. Figure 1 shows that *H. striata* and *T. leycettanus* are closely related. Further phylogenetic support for this relationship was presented in the studies of Ogawa & Sugiyama (2000) and Houbraken & Samson (2011). These two species are phylogenetically distant from

Talaromyces s. str. and more closely related to *Hamigera*. Peterson *et al.* (2010) delimited *Hamigera* phylogenetically but stated that *T. leycettanus* and *H. striata* do not belong to this genus, and followed Benjamin's (1955) placement of *H. striata* in *Talaromyces*. In this study, we retain *H. striata* and *T. leycettanus* in *Hamigera* and *Talaromyces*, respectively. A thorough study on *Hamigera* and related genera is needed to clarify the correct placement of these species. Kong (1999) described *Talaromyces brevicompactus*, stating that this species is closely related to *Hamigera avellanea* (as *Talaromyces avellaneus*). The anamorph of this species was described in *Merimbla*, thus confirming the relationship with *Hamigera*. Sequence comparisons of this species showed that it is similar to NRRL 2108, a phylogenetically undescribed *Hamigera* species (J. Houbraken, unpubl. data, Peterson *et al.* 2010). We wait with combining this species in *Hamigera* until a more data and strains become available.

Species described in other genera but phylogenetically within *Talaromyces*

Phylogenetic analysis shows that "*Aphanoascus cinnabarinus*", *Sagenomella bohemica*, *Paecilomyces aerugineus*, *Geosmithia viridis* and *Sagenoma viride* belong to *Talaromyces*. The genus *Sagenoma* is typified with *S. viride*, and therefore this genus can be considered as a synonym of *Talaromyces*. Our data support the conclusions of von Arx (1987), who correctly transferred this species in *Talaromyces*, and this is reflected in the taxonomy section below.

Houbraken & Samson (2011) discussed the confusion over *Aphanoascus cinnabarinus*, which has persisted since the description of the genus *Aphanoascus* by Zukai (1890). Most authors follow Apinis (1968) and consider the genus *Aphanoascus* to be typified by *A. fulvescens* Zukai. In addition, the neotypification of *A. cinnabarinus* by Udagawa & Takada (1973) was incorrect, because their neotype strain had a *Paecilomyces* anamorph, whereas Zukai's original description and illustrations clearly showed a *Chrysosporium*-like anamorph (Stolk & Samson 1983). Based on morphological features, Stolk & Samson (1983) indicated that *Chromocleista cinnabarina* (as *A. cinnabarinus sensu* Udagawa & Takada) belongs to the *Eurotiales* and suggested that this species is intermediate between *Thermoascus* and *Talaromyces*. Our phylogenetic study, and that of Houbraken & Samson (2011), clarified that *C. cinnabarina* belongs to *Talaromyces s. str.* The taxonomic position of *Chromocleista cinnabarina* (as *A. cinnabarinus sensu* Udagawa & Takada) will be discussed in a forthcoming paper. *Paecilomyces aerugineus* was proposed by Samson (1974) for *Spicaria silvatica* Oudemans *sensu* Apinis. This species resembles the anamorph of *A. cinnabarinus sensu* Udagawa & Takada and a more detailed study is necessary to clarify this relationship.

TAXONOMY

Penicillium itself has a long list of generic synonyms (see Seifert *et al.* 2011) that must be considered for the species formerly included in subgenus *Biverticillium*. These synonyms of *Penicillium* are discussed in the Appendix to this paper. As it turns out, none of these are appropriate for subgenus *Biverticillium*, leaving the comparatively young *Talaromyces* as the oldest well-known generic name as the new home for the anamorphic species of subgenus *Biverticillium*.

Yaguchi *et al.* (1994a) introduced *Erythrogymnotheca* for the single species *E. paucispora*. No specimens of *E. paucispora* were studied; however, examination of the available ITS data on GenBank and the original description shows that this species belongs in *Talaromyces*. As a consequence, *Erythrogymnotheca* is synonymised with *Talaromyces*. Comparison of an ITS sequence of *E. paucispora* (AB176603) shows that it is related to *P. korosum*, *P. pinophilum* and *P. liani* in *Talaromyces* (Fig. 2). The original description suggests that *Talaromyces* and *Erythrogymnotheca* differ in ascus characteristics and ascospore morphology. However, these genera also share characters. The ascomatal initials of *E. paucispora* approximate those of *Talaromyces flavus* and other species of *Talaromyces*. Furthermore, *E. paucispora* produces a loose hyphal yellow- or red-pigmented ascomata similar to those of other *Talaromyces* species and the main ubiquinone systems are Q-10 and Q-10 (H₂), also indicating a relationship with *Talaromyces* (Paterson 1998, Yaguchi *et al.* 1994a).

Matsushima (2001) described *Paratalaromyces* from soil collected in Taiwan, distinguishing it by a distinct *textura epidermoidea* layer in the ascomatal wall, and the presence of spinulose marginal hyphae. We have not seen the type but the description of *Paratalaromyces lenticularis* is similar to that of *Talaromyces unicus* (Tzean *et al.* 1992). We consider the genus a synonym here.

Visagie & Seifert (unpubl. data) report on the generic name *Lasioderma* Mont., typified by *L. flavo-virens* Durieu & Mont., which is conspecific with *Penicillium aureocephalum* Munt.-Cvetk., Hoyo & Gómez-Bolea. The name *Lasioderma* is widely used as an insect genus, and a formal proposal for the conservation of *Talaromyces* against this older name is being prepared.

***Talaromyces* C.R. Benj., Mycologia 47: 681. 1955.**

- = *Penicillium* Link subgenus *Biverticillium* Dierckx *apud* Biourge Cellule 33: 31. 1923.
- = *Penicillium* subg. *Biverticillata-Symmetrica* Thom, The Penicillia: 158. 1930.
- = *Sagenoma* Stolk & G.F. Orr, Mycologia 66: 676. 1974.
- = *Erythrogymnotheca* Yaguchi & Udagawa, Mycoscience 35: 219. 1994.
- = *Paratalaromyces* Matsush., Matsush. Mycol. Mem. 10: 111 (2003) [2001].

Ascomata cleistothecial, usually with a distinctly hyphal exterior wall, often yellow, occasionally white, creamish, pinkish or reddish. *Asci* 8-spored, globose to ellipsoidal, ascus initials sometimes with morphologically distinguishable gametangia, mature asci produced in chains. *Ascospores* one-celled, rarely smooth-walled, but often with surface ornamentation and wings, hyaline to yellow, in strains producing abundant red pigment occasionally red. *Conidiophores* comprising smooth or rough-walled elements, with long hyaline stipes, generally terminating in a single whorl of 3–10 metulae, appearing symmetrical in face view (in some species with a single subterminal lateral branch that afterwards repeats the branching pattern of the main axis, but then with the whole conidiophore appearing asymmetrical), each metula with a terminal whorl of phialides. *Conidiogenous cells* phialidic, aculeate or acerose, rarely ampulliform, periclinal thickening usually visible in the conidiogenous aperture, with or without a cylindrical collarette. *Conidia* aseptate, green in mass, in basipetal connected chains, usually ellipsoidal to fusiform.

Type species: Talaromyces vermiculatus (P.A. Dang.) C.R. Benj., Mycologia 47: 684. 1955.

The name *Talaromyces* was introduced by Benjamin (1955), and the type species is *T. vermiculatus* (P.A. Dang.) C.R. Benj. One of

the authors (RAS) personally visited several herbaria in Paris to locate holotype or other original material of *Penicillium vermiculatum* P.A. Dang. Dangeard (1907) described and illustrated both the anamorph and teleomorph under this name, but his material could not be located. To repair the shortcoming of the typification of *Talaromyces*, the lectotype for *P. vermiculatum* is here designated as Plate XVIII in Dangeard (1907, available at the Biodiversity Heritage Library, www.biodiversitylibrary.org). It was selected from among the plates XVI–XX because it includes the most detailed drawings of the anamorph, but also includes elements of the teleomorph. Herb. IMI 197477 is here designated as the epitype of *Penicillium vermiculatum* P.A. Dang. This specimen, which is also the holotype of *Penicillium dangeardii* J. Pitt, the seldom-used name for the anamorph of *T. flavus*, is derived from the equivalent cultures CBS 310.38, IMI 19447, and NRRL 2098. The latter strain was considered typical of *P. vermiculatum* by Raper & Thom (1949), the last major treatment to use this *Penicillium* name as a distinct species.

List of species

The following list includes previously accepted species of *Talaromyces* and proposals to transfer the species of *Penicillium* subgenus *Biverticillium* to *Talaromyces*.

Our phylogenetic studies demonstrate that several taxa represent complexes of morphologically cryptic phylogenetic species, requiring further study. For example, we analysed members of the *Penicillium purpurogenum* complex (including *P. purpurogenum*, *P. rubrum*, *P. crateriforme*, *P. sanguineum*) and found that several species group could be distinguished by sequencing certain genes (N. Yilmaz, unpubl. data) and had distinct macromorphological features and unique extrolite profiles. The full phylogenetic diversity of the *P. purpurogenum* species complex requires more investigation, and a more detailed account will be published elsewhere.

ACCEPTED SPECIES IN TALAROMYCES

Talaromyces aculeatus (Raper & Fennell) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560639.

Basionym: Penicillium aculeatum Raper & Fennell, Mycologia 40: 535. 1948.

Talaromyces albobiverticillius (H.-M. Hsieh, Y.-M. Ju & S.-Y. Hsieh) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560683.

Basionym: Penicillium albobiverticillium H.-M. Hsieh, Y.-M. Ju & S.-Y. Hsieh, Fung. Sci. 25: 26. 2010.

Talaromyces allahabadensis (B.S. Mehrotra & D. Kumar) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560640.

Basionym: Penicillium allahabadense B.S. Mehrotra & D. Kumar, Canad. J. Bot. 40: 1399. 1962.

Talaromyces apiculatus Samson, Yilmaz & Frisvad, **sp. nov.** MycoBank MB560641.

= *Penicillium aculeatum* var. *apiculatum* Abe, S., 1956, J. Gen. Appl. Microbiol., Tokyo 2: 124. 1956 (*nom. inval.*, Art. 36).

Penicillio aculeato simile, sed conidiis apiculatis distinguitur.

Typus: **Japan** from soil (CBS H-20755 – Holotype, culture ex-type CBS 312.59)

Note: Species similar to *Penicillium aculeatum* but differing by apiculate conidia.

Talaromyces assiutensis Samson & Abdel-Fattah, *Persoonia* 9: 501. 1978.

Anamorphic synonym: *Penicillium assiutense* Samson & Abdel Fattah (simultaneously published, identical holotype).

Talaromyces aurantiacus (J.H. Mill., Giddens & A.A. Foster) Samson, Yilmaz, & Frisvad, **comb. nov.** MycoBank MB560642.

Basionym: *Penicillium aurantiacum* J.H. Mill., Giddens & A.A. Foster, *Mycologia* 49: 797. 1957.

Talaromyces austrocalifornicus Yaguchi & Udagawa *Trans. Mycol. Soc. Japan* 34: 245. 1993.

Anamorphic synonym: *Penicillium austrocalifornicum* Yaguchi & Udagawa (simultaneously published, identical holotype).

Talaromyces bacillisporus (Swift) C. R. Benj., *Mycologia* 47: 682. 1955.

= *Penicillium bacillisporum* Swift, *Bull. Torrey Bot. Club* 59: 221, 1932.

Talaromyces boninensis (Yaguchi & Udagawa) Samson, Yilmaz, & Frisvad, **comb. nov.** MycoBank MB560643.

Basionym: *Talaromyces helicus* var. *boninensis* Yaguchi & Udagawa, *Transactions Mycological Society Japan* 33: 511. 1992.

Talaromyces brunneus (Udagawa) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560644.

Basionym: *Penicillium brunneum* Udagawa, *J. Agric. Sci. (Tokyo) Nogyo Daigaku* 5: 16. 1959.

Talaromyces calidicanus (J.L. Chen) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560645.

Basionym: *Penicillium calidicanium* J.L. Chen, *Mycologia* 94(5): 870. 2002.

Talaromyces cecidicola (Seifert, Hoekstra & Frisvad) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560646.

Basionym: *Penicillium cecidicola* Seifert, Hoekstra & Frisvad, *Stud. Mycol.* 50: 520. 2004.

Talaromyces coalescens (Quintan.) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560647.

Basionym: *Penicillium coalescens* Quintan., *Mycopathol.* 84: 115. 1984.

Talaromyces convolutus Udagawa, *Mycotaxon* 48: 141. 1993.

Anamorphic synonym: *Penicillium convolutum* Udagawa (simultaneously published, identical holotype).

Talaromyces dendriticus (Pitt) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560648.

Basionym: *Penicillium dendriticum* Pitt, *The Genus Penicillium*: 413. 1980.

Talaromyces dextrii Takada & Udagawa, *Mycotaxon* 31: 418. 1988.

Anamorphic synonym: *Penicillium dextrii* Takata & Udagawa (simultaneously published, identical holotype).

Talaromyces diversus (Raper & Fennell) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560649.

Basionym: *Penicillium diversum* Raper & Fennell, *Mycologia* 40: 539. 1948.

Talaromyces duclauxii (Delacr.) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560650.

Basionym: *Penicillium duclauxii* Delacr., *Bull. Soc. Mycol. France* 7: 107. 1891.

Talaromyces echinosporus (Nehira) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560651.

Basionym: *Penicillium echinosporum* Nehira, *J. Ferment. Technol., Osaka* 11: 861. 1933.

Note: *Penicillium asperosporum* G. Smith, *Trans. Brit. Mycol. Soc.* 48: 275. 1965. (= *Penicillium echinosporum* G. Sm., *Trans. Brit. Mycol. Soc.* 45: 387. 1962, non Nehira in *J. Ferment. Technol.* 11: 849. 1933) belongs in *Penicillium* section *Aspergilloides* (Houbraken & Samson 2011).

Talaromyces emodensis Udagawa, *Mycotaxon* 48: 146. 1993.

Anamorphic synonym: *Penicillium emodense* Udagawa (simultaneously published, identical holotype).

Talaromyces erythromellis (A.D. Hocking) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560652.

Basionym: *Penicillium erythromellis* A.D. Hocking *apud* Pitt, *The Genus Penicillium*: 459. 1980.

Talaromyces euchlorocarpus Yaguchi, Someya & Udagawa, *Mycoscience* 40: 133. 1999.

Anamorphic synonym: *Penicillium euchlorocarpium* Yaguchi, Someya & Udagawa (simultaneously published, identical holotype).

Note: We have not seen the type, but the description and the ITS sequences available in GenBank (AB176617) show that this is a distinct species of *Talaromyces*.

Talaromyces flavo-virens (Durieu & Mont.) Visagie, Llimona & Seifert, *ined.*

Note: A manuscript on this species and its relationship to *Penicillium aureocephalum* Munt.-Cvetk., Hoyo & Gómez-Bolea is being prepared for publication in *Mycotaxon*.

Talaromyces flavus (Klöcker) Stolk & Samson, *Stud. Mycol.* 2: 10. 1972.

Anamorphic synonym: *Penicillium dangeardii* Pitt, *The Genus Penicillium*: 472. 1980.

Talaromyces funiculosus (Thom) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560653.

Basionym: *Penicillium funiculosum* Thom, Bull. Bur. Anim. Ind. U.S. Dep. Agric. 118: 69. 1910.

Talaromyces galapagensis Samson & Mahoney, Trans. Brit. Mycol. Soc. 69: 158. 1977.

Anamorphic synonym: *Penicillium galapagense* Samson & Mahoney (simultaneously published, identical holotype).

Talaromyces hachijoensis Yaguchi, Someya & Udagawa, Mycoscience 37: 157. 1996.

Note: We have not seen the type but the description and the ITS sequences available in GenBank (AB176620) show that this is a distinct species of *Talaromyces*. It is unusual in the genus for its apparent lack of an anamorph.

Talaromyces helicus (Raper & Fennell) C.R. Benj., Mycologia 47: 684. 1955.

≡ *Penicillium helicum* Raper & Fennell, Mycologia 40: 515. 1948.

Talaromyces indigoticus Takada & Udagawa, Mycotaxon 46: 129. 1993.

Anamorphic synonym: *Penicillium indigoticum* Takada & Udagawa (simultaneously published, identical holotype).

Talaromyces intermedius (Apinis) Stolk & Samson, Stud. Mycol. 2: 21. 1972.

Anamorphic synonym: *Penicillium intermedium* Stolk & Samson, Stud. Mycol. 2: 21. 1972.

Talaromyces islandicus (Sopp) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560654.

Basionym: *Penicillium islandicum* Sopp, Skr. Vidensk.-Selsk. Christiania, Math.-Naturvidensk. Kl. 11: 161. 1912.

Talaromyces loliensis (Pitt) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560655.

Basionym: *Penicillium loliense* Pitt, The Genus *Penicillium*: 450. 1980

Talaromyces macrosporus (Stolk & Samson) Frisvad, Samson & Stolk, Ant. van Leeuwenhoek 57: 186. 1990.

Anamorphic synonym: *Penicillium macrosporum* Frisvad, Filt., Samson & Stolk. *nom. illegit.* Art. 53 (non *P. macrosporum* Berk. & Broome 1882).

Talaromyces marneffei (Segretain, Capponi & Sureau) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560656.

Basionym: *Penicillium marneffei* Segretain, Capponi & Sureau *apud* Segretain, Bull. Soc. Mycol. France 75: 416. 1959 [1960].

Talaromyces mimosinus A.D. Hocking *apud* Pitt, The Genus *Penicillium*: 507. 1980.

Anamorphic synonym: *Penicillium mimosinum* A. D. Hocking (simultaneously published, identical holotype).

Talaromyces minioluteus (Dierckx) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560657.

Basionym: *Penicillium minioluteum* Dierckx, Ann. Soc. Sci. Bruxelles 25: 87. 1901.

Talaromyces muroii Yaguchi, Someya & Udagawa, Mycoscience 35: 252. 1994.

Note: This species is unusual in *Talaromyces* because of its lack of a known anamorph.

Talaromyces palmae (Samson, Stolk & Frisvad) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560658.

Basionym: *Penicillium palmae* Samson, Stolk & Frisvad, Stud. Mycol. 31: 135. 1989.

Talaromyces panamensis (Samson, Stolk & Frisvad) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560659.

Basionym: *Penicillium panamense* Samson, Stolk & Frisvad, Stud. Mycol. 31: 136. 1989.

Talaromyces paucisporus (Yaguchi, Someya & Udagawa) Samson & Houbraken, **comb. nov.** MycoBank MB560684.

Basionym: *Erythrogymnotheca paucispora* Yaguchi, Someya & Udagawa, Mycoscience 35: 219. 1994.

Talaromyces phialosporus (Udagawa) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560660.

Basionym: *Penicillium phialosporum* Udagawa, J. Agric. Sci. (Tokyo) Nogyo Daigaku 5: 11. 1959.

Talaromyces piceus (Raper & Fennell) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560661.

Basionym: *Penicillium piceum* Raper & Fennell, Mycologia 40: 533. 1948.

Talaromyces pinophilus (Hedgcock) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560662.

Basionym: *Penicillium pinophilum* Hedgcock *apud* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 37. 1910.

Talaromyces pittii (Quintan.) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560663.

Basionym: *Penicillium pittii* Quintan., Mycopathol. 91: 69. 1985.

Talaromyces primulinus (Pitt) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560664.

Basionym: *Penicillium primulinum* Pitt, The Genus *Penicillium*: 455. 1980.

Talaromyces proteolyticus (Kamyschko) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560665.

Basionym: *Penicillium proteolyticum* Kamyschko, Not. Syst. Crypt. Inst. Bot. Acad. Sci. USSR 14: 228. 1961.

Talaromyces pseudostromaticus (Hodges, G.M. Warner, Rogerson) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560666.

Basionym: *Penicillium pseudostromaticum* Hodges, G.M. Warner & Rogerson, *Mycologia* 62: 1106. 1970.

Talaromyces purpureus (E. Müll. & Pacha-Aue) Stolk & Samson, *Stud. Mycol.* 2: 57. 1972.

Anamorphic synonym: *Penicillium purpureum* Stolk & Samson, *Stud. Mycol.* 2: 57. 1972.

Talaromyces purpurogenus (Stoll) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560667.

Basionym: *Penicillium purpurogenum* Stoll, *Beitr. Charakt. Penicillium-Arten*: 32. 1904.

Talaromyces rademirici (Quintan.) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560668.

Basionym: *Penicillium rademirici* Quintan., *Mycopathol.* 91: 69. 1985.

Talaromyces radicus (A.D. Hocking & Whitelaw) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560669.

Basionym: *Penicillium radicum* A.D. Hocking & Whitelaw, *Mycol. Res.* 102: 802. 1998.

Talaromyces ramulosus (Visagie & K. Jacobs) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560670.

Basionym: *Penicillium ramulosum* Visagie & K. Jacobs, *Mycologia* 101: 890. 2009.

Talaromyces rotundus (Raper & Fennell) C.R. Benj., *Mycologia* 47: 683. 1955.

≡ *Penicillium rotundum* Raper & Fennell, *Mycologia* 40: 518. 1948.

Talaromyces ryukuensis (S. Ueda & Udagawa) Arx, *Persoonia* 13: 282. 1987.

≡ *Sagenoma ryukuense* S. Ueda & Udagawa, *Mycotaxon* 20: 499. 1984.

Note: We have not seen the type but the description and the ITS sequences available in GenBank (AB176628) show that this is a distinct species of *Talaromyces*.

Talaromyces rubicundus (J.H. Mill., Giddens & A.A. Foster) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560671.

Basionym: *Penicillium rubicundum* J.H. Mill., Giddens & A.A. Foster, *Mycologia* 49: 797. 1957.

Talaromyces rugulosus (Thom) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560672.

Basionym: *Penicillium rugulosum* Thom, *Bull. Bur. Anim. Ind. US Dept. Agric.* 118: 60. 1910.

Talaromyces sabulosus (Pitt & A.D. Hocking) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560673.

Basionym: *Penicillium sabulosum* Pitt & A. D. Hocking, *Mycologia* 77: 818. 1985.

Talaromyces siamensis (Manoch & C. Ramírez) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560674.

Basionym: *Penicillium siamense* Manoch & C. Ramírez, *Mycopathol.* 101: 32. 1988.

Talaromyces stipitatus (Thom) C.R. Benj., *Mycologia* 47: 684. 1955.

≡ *Penicillium stipitatum* Thom, *Mycologia* 27: 138. 1935.

Talaromyces sublevisporus (Yaguchi & Udagawa) Samson, Yilmaz & Frisvad, **comb. et stat. nov.** MycoBank MB560675.

Basionym: *Talaromyces wortmannii* var. *sublevisporus* Yaguchi & Udagawa, *Mycoscience* 35: 63. 1994.

Note: We have not examined the ex-type of this species but from the ITS data (GenBank AB176638), this seems to be a separate species.

Talaromyces tardifaciens Udagawa, *Mycotaxon* 48: 150. 1993.

Anamorphic synonym: *Penicillium tardifaciens* Udagawa (simultaneously published, identical holotype).

Talaromyces trachyspermus (Shear) Stolk & Samson, *Stud. Mycol.* 2: 32. 1972.

Anamorphic synonym: *Penicillium spiculisporum* Leman, *Mycologia* 12: 268. 1920.

Talaromyces ucrainicus Udagawa, in Stolk & Samson, *Stud. Mycol.* 2: 34. 1972.

Anamorphic synonym: *Penicillium ucrainicum* Panasenko, *Mycologia* 56: 59. 1964.

Talaromyces udagawae Stolk & Samson, *Stud. Mycol.* 2: 36. 1972.

Anamorphic synonym: *Penicillium udagawae* Stolk & Samson (simultaneously published, identical holotype).

Talaromyces unicus Tzean, J.L. Chen & Shiu, *Mycologia* 84: 739. 1992.

Anamorphic synonym: *Penicillium unicum* Tzean, J.L. Chen & Shiu (simultaneously published, identical holotype).

Talaromyces variabilis (Sopp) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560676.

Basionym: *Penicillium variabile* Sopp, *Skr. Vidensk.-Selsk. Christiania, Math.-Naturvidensk. Kl.* 11: 169. 1912.

Talaromyces varians (G. Sm.) Samson, Yilmaz & Frisvad, **comb. nov.** MycoBank MB560677.

Basionym: *Penicillium varians* G. Sm., *Trans. Brit. Mycol. Soc.* 18: 89. 1933.

Talaromyces verruculosus (Peyronel) Samson, Yilmaz, Frisvad & Seifert, **comb. nov.** MycoBank MB560678.

Basionym: *Penicillium verruculosum* Peyronel, *Germi Atmosf. Fung. Micel.*: 22. 1913.

Talaromyces viridis (Stolk & G.F. Orr) von Arx, *Persoonia* 13: 2821. 1987.

≡ *Sagenoma viride* Stolk & G.F. Orr, *Mycologia* 66: 677. 1974.

Talaromyces viridulus Samson, Yilmaz & Frisvad, **nom. nov.** MycoBank MB560679.

Basionym: *Geosmithia viridis* Pitt & A.D. Hocking, *Mycologia* 77: 822. 1985 = *P. viride* (Pitt & A.D. Hocking) Frisvad, Samson &

Stolk, *Persoonia* 14: 229. 1990, *nom. illegit.* Art. 53 (non Fres. 1851 nec Rivera 1873 nec Sopp 1912 nec (Matr.) Biourge 1923). Non *Talaromyces viridis* (Stolk & G.F. Orr) Arx.

Talaromyces wortmannii (Klöcker) C.R. Benjamin, *Mycologia* 47: 683. 1955.

≡ *Penicillium wortmannii* Klöcker, *Compt-Rend. Trav. Carlsberg Lab.* 6: 100. 1903.

EXCLUDED SPECIES AND TAXA, WHICH NEED FURTHER TAXONOMIC STUDY

Penicillium concavorugulosum S. Abe, *J. Gen. Appl. Microbiol.* Tokyo 2: 127. 1956 (*nom. inval.* Art. 36).

Note: This species was invalidly described, but our ITS data (Fig. 2) show that it is related to *T. wortmannii*. Further study is required but extrolite data indicate that this species is unique (J.C. Frisvad, unpubl. data).

Penicillium crateriforme J.C. Gilman & E.V. Abbott, *Iowa State Coll. J. Sc.* 1: 293. 1927.

Note: Our ITS data (Fig. 2) show that this species is a synonym of *P. purpurogenum*.

Penicillium ilerdanum C. Ramírez, A.T. Martínez & Berer., *Mycopathol.* 72: 32. 1980.

Note: Frisvad *et al.* (1990b) considered this species synonymous with *Penicillium piceum* Raper & Fennell, which is confirmed by our ITS data (Fig. 2).

Penicillium isariiforme Stolk & J.A. Mey., *Trans. Brit. Mycol. Soc.* 40: 187. 1957.

Note: According to Houbraken & Samson (2011), this species, included in subgenus *Biverticillium* by Pitt (1980), is correctly classified in *Penicillium sensu lato*.

Penicillium korosum J.N. Rai, Wadhvani & J.P. Tewari, *Ant. van Leeuwenhoek* 35: 430. 1969.

Note: This species requires further investigation, but our ITS sequence (Fig. 2) indicates that it is similar to *P. pinophilum*.

Penicillium krugeri C. Ramírez, *Mycopathol.* 110: 23. 1990.

Note: We have been unable to examine authentic material, and the correct classification of this species is uncertain.

Penicillium lignorum Stolk, *Ant. van Leeuwenhoek* 35: 264. 1969.

Note: A preliminary phylogenetic analysis indicates that this species does not belong to *Talaromyces* and might represent a new genus (J. Houbraken, unpubl. data).

Penicillium mirabile Beliakova & Milko, *Mikol. Fitopatol.* 6: 145. 1972.

Note: The ex-type culture is in poor condition and although our ITS data (Fig. 2) indicate that it is a distinct species, it should be further investigated.

Penicillium oblatum Pitt & A.D. Hocking, *Mycologia* 77: 810. 1985.

Note: In our ITS phylogeny (Fig. 2), this species is close to *Paecilomyces pascuus* and *Penicillium dendriticum* and needs further study.

Penicillium pascuum (Pitt & A.D. Hocking) Frisvad, Samson & Stolk, *Persoonia* 14: 229. 1990.

≡ *Paecilomyces pascuus* Pitt & A. D. Hocking, *Mycologia* 77: 822. 1985.

Note: See on the position of this species under *P. oblatum* above.

Penicillium rubrum Stoll, *Beitr. Charakt. Penicillium-Arten:* 35. 1904.

Note: Although the name is well-known, the taxonomic position of the taxon remains doubtful because no type material has been located. A possible solution would be lectotypification from Stoll's illustrations, followed by epitypification to become a usable name.

Penicillium purpurogenum var. *rubrisclerotium* Thom, *Mycologia* 7: 137. 1915.

Note: Our ITS data (Fig. 2) indicate that this species is synonymous with *P. minioluteum*.

Penicillium samsonii Quintan., *Mycopathol.* 91: 69. 1985.

= *Talaromyces minioluteus* (Dierckx) Samson, Yilmaz, Frisvad & Seifert (see above).

Penicillium tardum Thom, *The Penicillia:* 485. 1930.

Note: Raper & Thom (1949) pointed out that there is confusion about the type culture and the status of this species will be subject of further studies.

Penicillium victoriae Szilv., *Archiv. Hydrobiol.* 14, Suppl. 6: 535. 1936.

= *Penicillium janthinellum* Biourge, *Cellule* 33: 258. 1923 (Pitt, 1980).

Note: Pitt (1980) synonymised this species under *Penicillium janthinellum*, but our studies showed that it clearly belongs in *Talaromyces*. Because there is only one strain, the exact identity of this fungus requires further study.

Talaromyces barcinensis Yaguchi & Udagawa, *Trans. Mycol. Soc. Japan* 34: 15. 1993.

Anamorphic synonym: *Penicillium barcinense* Yaguchi & Udagawa (simultaneously published, identical holotype).

Note: Our ITS sequence data show that this species is close to *Talaromyces helicus* and further study should determine its correct taxonomic position.

Talaromyces brevicompactus Kong, *Mycosystema* 18: 9. 1999.

Anamorphic synonym: *Merimbla brevicompacta* Kong, *Mycosystema* 18: 9. 1999 (simultaneously published, identical holotype).

Note: Fig. 1 shows that this species belongs in *Hamigera*. Comparison of partial β -tubulin and calmodulin sequences of the ex-type strain of *T. brevicompactus* with recent published data shows that this species represents a distinct species (J. Houbraken, unpubl. data). The new combination in *Hamigera* will be made elsewhere.

Talaromyces byssochlamydoides Stolk & Samson, *Stud. Mycol.* 2: 45. 1972.

Anamorphic synonym: *Paecilomyces byssochlamydoides* Stolk & Samson (simultaneously published, same holotype).

= *Rasamsonia byssochlamydoides* (Stolk & Samson) Houbraken & Frisvad, *Ant. van Leeuwenhoek*, *in press*.

Talaromyces eburneus Yaguchi, Someya & Udagawa, *Mycoscience* 35: 249. 1994.

Anamorphic synonym: *Geosmithia eburnea* Yaguchi, Someya & Udagawa (simultaneously described, holotype identical)

= *Rasamsonia eburnea* (Yaguchi, Someya & Udagawa) Houbraken & Frisvad, *Ant. van Leeuwenhoek*, *in press*.

Talaromyces emersonii Stolk, *Ant. van Leeuwenhoek* 31: 262. 1965.

Anamorphic synonym: *Penicillium emersonii* Stolk (simultaneously described, holotype identical), *Ant. van Leeuwenhoek* 31: 262. 1965.

= *Rasamsonia emersonii* (Stolk) Houbraken & Frisvad, *Ant. van Leeuwenhoek*, *in press*.

Talaromyces gossypii Pitt, *The Genus Penicillium*: 500. 1980

= *Talaromyces assiutensis*, Samson & Abdel-Fattah, *Persoonia* 9: 501. 1978 (*vide* Frisvad *et al.* 1990a).

Talaromyces lagunensis Udagawa, Uchiy. & Kamiya, *Mycoscience* 35: 403. 1994.

Anamorphic synonym: *Penicillium lagunense* Udagawa, Uchiy. & Kamiya (simultaneously published, identical holotype).

Note: We have been unable to examine authentic material, and the correct classification of this species is uncertain.

Talaromyces leycettanus H.C. Evans & Stolk, *Trans. Brit. Mycol. Soc.* 56: 45. 1971.

Anamorphic synonym: *Penicillium leycettanus* H.C. Evans & Stolk (simultaneously published, identical holotype).

= *Paecilomyces leycettanus* (H.C. Evans & Stolk) Stolk, Samson & H.C. Evans, *Persoonia* 6: 342. 1971.

Note: Houbraken & Samson (2011) showed that this species is phylogenetically unrelated to *Talaromyces* and close to *Hamigera*. Its taxonomic position requires further investigation.

Talaromyces luteus (Zukal) C.R. Benj., *Mycologia* 47: 681. 1955.

= *Penicillium luteum* Zukal, *Sitzungsber Kaiserl. Akad. Wiss. Math-Naturwiss. C1., Abt. 1*, 98: 561. 1890.

Note: Although the phenotype of this species resembles species of *Talaromyces*, our molecular analysis shows that it is phylogenetically unique and basal to *T. thermophilus*.

Talaromyces malagensis (Thüm.) Stalpers & Samson 1984, in Stalpers, *Stud. Mycol.* 24: 69. 1984.

Note: Stolk & Samson (1972) considered *Sporotrichum malagense* a dubious synonym of *T. udagawae*, based on their failure to find ascospores and conidia in the type material (herb. W). Later, Stalpers (1984) studied material preserved in herb. BR which is authentic and labelled as "type". It agrees with Thümen's original diagnosis and contains both fertile *Talaromyces* cleistothecia and a sporulating biverticillate anamorph. Therefore, the new combination to *Talaromyces* was proposed. The species resembles *T. udagawae* or *T. luteus*, but in the absence of a living culture we cannot determine its precise taxonomic identity.

Talaromyces ocotl Bills & Heredia, *Mycologia* 90: 533. 1998.

Note: Figure 1 shows that this species belongs to *Sagenomella* and the new combination is proposed here:

Sagenomella ocotl (Bills & Heredia) Samson, Houbraken & Frisvad, **comb. nov.** MycoBank MB560681.

Basionym: *Talaromyces ocotl* Bills & Heredia, *Mycologia* 93: 533. 1998.

Talaromyces ohioensis Pitt, *The Genus Penicillium*: 502. 1980.

Anamorphic synonym: *Penicillium ohioense* L. H. Huang & J. A. Schmitt, *Ohio J. Sci.* 75: 78. 1975.

Note: Pitt (1980) considered this species to be related to *T. luteus*, but our ITS data clearly show that is synonymous with *T. ucrainicus*.

Talaromyces panasenkoi Pitt, *The Genus Penicillium*: 482. 1980.

Anamorphic synonym: *Penicillium panasenkoi* Pitt (simultaneously published, identical holotype).

Note: Pitt (1980) proposed *T. panasenkoi* as a new species for the invalidly published *P. ucraininum* Panasenko; however, Stolk & Samson (1972) had already proposed *Talaromyces ucrainicus* Udagawa for this taxon. *Talaromyces panasenkoi* Pitt is therefore a synonym of *T. ucrainicus*.

Talaromyces retardatus Udagawa, Kamiya & Kaori Osada, *Trans. Mycol. Soc. Japan* 34: 9. 1993.

Anamorphic synonym: *Penicillium retardatum* Udagawa, Kamiya & Kaori Osada (simultaneously published, identical holotype).

Note: No strain was available for examination and the status of this species is thus unknown.

Talaromyces spectabilis Udagawa & Suzuki, *Mycotaxon* 50: 82. 1994.

= *Byssochlamys spectabilis* (Udagawa & Suzuki) Houbraken & Samson, *Appl. Environ. Microbiol.* 74: 1618. 2008.

= *Paecilomyces variotii* Bainier *Bull. Soc. mycol. Fr.* 23: 27. 1907.

Note: The oldest generic and species name for this species is *P. variotii*, which becomes the correct name for the holomorph.

Talaromyces striatus (Raper & Fennell) C.R. Benj., *Mycologia* 47: 682. 1955.

= *Hamigera striata* (Raper & Fennell) Stolk & Samson, *Persoonia* 6: 347. 1971.

Talaromyces thermocitrinus Subrahm. & Gopalkr., *Ind. Bot. Reporter* 35: 35. 1984 (as '*T. thermocitrinum*').

Note: We have not seen the type, but judging from the substrate (dust on books), and the mention of yellow cleistothecia, it is possible that this is an *Eurotium* species, a typical contaminant of books and other material in archives. However, its reported thermophily is different from known species of the mesophilic genus *Eurotium*.

Talaromyces thermophilus Stolk, *Ant. van Leeuwenhoek* 31: 268. 1965.

Basionym: *Penicillium dupontii* Griffon & Maubl., *Bull. Trimest. Soc. mycol. Fr.* 27: 73. 1911.

Note: Figure 1 shows that this species is related to *Thermomyces lanuginosus*, and should be transferred to *Thermomyces* (Houbraken *et al.* 2011, Houbraken & Samson 2011).

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APPENDIX: OTHER POSSIBLE GENERIC NAMES

As noted above in the Taxonomy section, in order to adopt *Talaromyces* as the generic name for the former *Penicillium* subgenus *Biverticillium*, older genera considered synonyms of *Penicillium sensu lato* had to be considered. These are treated below.

Aspergillopsis Sopp, *Vid.-Selsk. Skr. I. Math.-naturv. Kl.* 11: 201. 1912. (Taf. xx, Fig. 149, Taf. xxiii, Fig. 31).

Type species: *A. fumosus* Sopp 1912.

Note: This generic name is illegitimate (Art. 53), being a later homonym of *Aspergillopsis* Speg. 1910. Pitt (1980) considered Sopp's genus a tentative synonym of *Merimbla* Pitt.

Citromyces Wehmer, *Ber. dt. Bot. Ges.* 11: 338. 1893.

Type species: *C. pfefferianus* Wehmer 1893 = *Penicillium glabrum* (Wehmer) Westling 1911, *vide* Pitt 1980.

Note: Wehmer's genus was considered a synonym of *Penicillium* by many authors, including Raper & Thom (1949) and Pitt (1980), with *C. pfefferianus* considered a probable synonym of *P. glabrum* (subgenus *Aspergilloides*) by Pitt (1980). Therefore, the genus remains a synonym of *Penicillium sensu stricto*.

Coremium Link : *Fr., Mag. Ges. naturf. Freunde, Berlin* 3: 19. 1809 : Fries, *Syst. mycol.* 1: xlviii, 1821.

Type species: *C. glaucum* Link 1809.

Note: This genus was described in the same publication as *Penicillium*. Raper & Thom (1949) and Seifert & Samson (1985) both considered the type species to be a synonym of the type species of *Penicillium*, *P. expansum* Link 1809. Therefore, *Coremium* remains a synonym of *Penicillium sensu stricto*.

Eladia G. Sm., *Trans. Br. mycol. Soc.* 44: 47. 1961.

Type species: *Eladia saccula* (Dale) G. Sm. 1961 = *Penicillium sacculum* Dale 1926.

Note: This genus was considered a synonym of *Penicillium* by Stolk & Samson (1985), but was considered distinct by Pitt (1980), and von Arx (1981). In the multigene phylogenetic study by Houbraken & Samson (2011), *Eladia* is clearly included in *Penicillium sensu stricto* and that synonymy is accepted here.

Floccaria Grev., *Scott. Crypt. Fl., Vol. 6, Pl.* 301. 1828.

Type species: *F. glauca* Grev. 1828.

Note: There is no known extant type according to Seifert & Samson (1985), who searched for it in K and E. The illustration shows a synnematus fungus that could well be *P. expansum*, but there are no microscopic details. Therefore, this name can be discounted as a possible generic name for the species formerly ascribed to subgenus *Biverticillium*.

Geosmithia Pitt, *Can. J. Bot.* 57: 2021. 1980.

Type species: *Geosmithia lavendula* (Raper & Fennell) Pitt 1980 = *Penicillium lavendulum* Raper & Fennell 1948.

Note: Although von Arx (1981) considered *Geosmithia* a synonym of *Penicillium*, it is polyphyletic as presently circumscribed. Using SSU sequences, Ogawa *et al.* (1997) showed that *G. lavendula*, and a second common species *G. putterilli*, belong to the *Bionectriaceae*, *Hypocreales*. Similar results were obtained using ITS sequences by Kolařík *et al.* (2004), using LSU sequences by Schroers *et al.* (2005) and then multigene phylogenies by Kolařík & Kirkendall (2010). Despite this, some anamorphs attributed to *Geosmithia* have been described recently in *Talaromyces* (e.g. Yaguchi *et al.* 2005). Because the type species is not associated with the same order as *Penicillium*, *Geosmithia* need not be considered as a possible home for species of subgenus *Biverticillium*, but neither should it be considered a synonym of *Penicillium*.

Hormodendrum Bonord., *Handbuch allg. Mykol.*: 76. 1851.

Type species: *Amphitrichum olivaceum* Corda 1837 = *Hormodendrum olivaceum* (Corda) Bonord. 1851, lectotype selected by Clements & Shear 1931.

Note: *Hormodendron* has variously been treated as a synonym of *Penicillium* by von Arx (1974) and de Hoog & Hermanides-Nijhoff (1977) but more often as a synonym of *Cladosporium* Link, following

the study of the type specimen by Hughes (1958). There is no reason to consider this name further as a synonym of *Penicillium* or as a possible receptacle for the species of subgenus *Biverticillium*.

Merimbla Pitt, Can. J. Bot. 57: 2394. 1980.

Type species: *M. ingelheimensis* (F.H. Beyma) Pitt 1980 = *Penicillium ingelheimense* F.H. Beyma 1942.

Note: *Merimbla* was considered a possible synonym of *Penicillium* by von Arx (1981), but this has not generally been accepted. *Merimbla ingelheimensis* was considered the anamorph of *Hamigera avellanea* by Stolk & Samson (1971), but is now known to be a closely related but phylogenetically distinct species (Peterson *et al.* 2010). The *Hamigera* clade is phylogenetically distinct from subgenus *Biverticillium* in the multigene analyses of Peterson *et al.* (2010) and Houbraken & Samson (2011). In a single name system, we consider *Merimbla* a synonym of the older genus *Hamigera*.

Monilia Fr., Syst. mycol. 3: 409. 1832.

Type species: *M. caespitosa* (L. : Fr.) Fr. 1832 / *Mucor caespitosus* L. 1753.

Note: Donk (1963) suggested that *M. caespitosa* might be a species of *Penicillium* based on the protologue. However, this generic name was formally rejected to conserve usage of *Monilia* Bonorden for the well-known genus of fruit pathogens. Therefore, it is unavailable as a possible generic name for species included in subgenus *Biverticillium*.

Moniliger Letell., Fig. Champ., Pl. 668. 1839. Figs 3, 4.

Type species: not designated, two original species.

Note: According to Seifert *et al.* (2011), Letellier included two species, with illustrations clearly representing *Aspergillus*. The synonymy of *Moniliger* with *Penicillium* proposed by Kirk *et al.* (2008) thus seems unlikely, and the genus is better listed as a synonym of *Aspergillus*.

Penicillium Link : Fr., Mag. Ges. naturf. Freunde, Berlin 3: 16. 1809. : Fries, Syst. mycol. 3: 406. 1832.

Type species: *P. expansum* Link 1809, *vide* Thom 1910.

Note: With this revision, and that of Houbraken & Samson (2011), *Penicillium* is now used exclusively for the nominal Clade including *P. expansum*, and species in the now synonymous genus *Eupenicillium* F. Ludw. 1892 (Houbraken & Samson 2011).

Pritzeliella Henn., Hedwigia Beibl. 42: 88. 1903.

Type species: *P. caerulea* Henn. 1903.

Note: Clements & Shear (1931) suggested that *Pritzeliella* should be considered a synonym of *Penicillium* without further commenting on the identity of its type species. Seifert & Samson (1985) examined the holotype of *P. caerulea* and considered it a synonym of *Penicillium coprophilum* (subgenus *Penicillium*). Its status as a synonym of *Penicillium sensu stricto* thus remains unchanged.

Rhodocephalus Corda, Ic. Fung. 1: 21. 1837 (Tab. vi, Fig. 282).

Type species: *R. candidus* Corda 1837 = *Penicillium leucocephalum* Rabenh. 1844.

Note: Corda (1837) illustrated and described his species as having aseptate stipes, a branched, asymmetrical penicillate head, with long chains of asexual conidia. Rabenhorst (1844) renamed the species in *Penicillium*, changing the epithet, a conclusion followed by Lindau (1907). Thom (1930) and Raper & Thom (1949) disagreed, stating that the illustration in the protologue has branched conidial chains that would exclude the fungus from *Penicillium*. This a debatable conclusion, because the chains are simply overlapping in the illustration and there is no clear indication of branching. Pitt (1980) evidently did not examine the protologue when he suggested a synonymy with *Aspergillus candidus*. Hughes (1958) did not report on the type, and according to Holubová (in litt. to Seifert, 1991), there is no material of *Rhodocephalus* in the Corda herbarium (PRM). The asymmetrical conidiophores illustrated by Corda discount this as a possible genus for species of subgenus *Biverticillium*, but its exact identity is unknown.

Torulomyces Delitsch, Systematik der Schimmelpilze: 91. 1943 (Taf. 30, Figs 232–235).

Type species: *T. lagena* Delitsch 1943 = *Monocillium lagena* (Delitsch) Hashmi, W.B. Kendr. & Morgan-Jones 1972 = *Penicillium lagena* (Delitsch) Stolk & Samson 1983.

Note: *Torulomyces* was included as a synonym of *Penicillium sensu stricto* in the phylogenetic study of Houbraken & Samson (2011).

Yunnania H.-Z. Kong, Mycotaxon 69: 320. 1998.

Type species: *Y. penicillata* H.-Z. Kong 1998.

Note: Houbraken & Samson (2011) sequenced the ITS of authentic cultures of *Y. penicillata*, showing a relationship with the *Microascales*, suggesting a synonymy with *Scopulariopsis* or *Scedosporium* might be appropriate.

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