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

R.A. Samson1, N. Yilmaz1,6, J. Houbraken1,6, H. Spierenburg1, K.A. Seifert6, S.W. Peterson3, J. Varga1 and J.C. Frisvad5

1CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands; 2Biodiversity (Mycology), Eastern Cereal and Oilseed Research Centre, Agriculture & Agri-Food Canada, 960 Carling Ave., Ottawa, Ontario, K1A 0C6, Canada; 3Bacterial Foodborne Pathogens and Mycology Research Unit, National Center for Agricultural Utilization Research, 1815 N. University Street, Peoria, IL 61604, U.S.A.; 4Department of Microbiology, Faculty of Science and Informatics, University of Szeged, H-6726 Szeged, Kízélp fasor 52, Hungary; 5Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands.

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 rDNA) was sequenced for the available type strains and/or representative isolates of Talaromyces species. Following the concepts of nomenclatural priority and single name nomenclature, we transfer all accepted species of Talaromyces subgenus Biverticillium to Talaromyces. A holomorph 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. marnierae, 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.

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, Fuscum, Penicillium and Biverticillium by Pitt (1980). Over the past decade, the realisation has grown that teleomorph-teleomorph connections, may have been the first to be described. Following the concepts of nomenclatural priority and single name nomenclature, the latter is now considered a synonym 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), and Ramírez (1982), culminating in the widespread recognition of subgenus Biverticillium and the use of this name in many taxonomic and phylogenetic studies. Malloch (1985), based on a consideration of morphological and ecological factors, and anamorph-teleomorph connections, may have been the first to speculate that subgenus Biverticillium should be removed from Penicillium as a separate genus.

The teleomorph genera historically associated with Penicillium sensu lato are Talaromyces and Eupenicillium (in single name nomenclature, the latter is now considered a synonym of...
Penicillium sensu stricto, see Houbraken & Samson 2011). The teleomorphs of these two groups produce distinctive ascocarps. In Talaromyces, the soft ascocarp walls are comprised of multiple layers of interwoven hyphae and the ascocarp mature quickly, usually within a few weeks in agar culture. In Penicillium sensu stricto, the sclerotium-like ascocarps have rigid walls of thick-walled, isodiametric cells and the ascocarp 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 ascocarp 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 acuate 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 Thermosascus, Penicillioopsis, 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, G2SN (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 glucosaminogalactan 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-typed names, leaving both kinds of names competing equally for priority (Norvell 2011). Because of these changes, we apply the principle of ‘one fungus - one name’ and in the nomenclatural revision, priority is given to the oldest genus and species name irrespective of whether they were originally described for teleomorphs or anamorphs (Hawksworth et al. 2011). In this respect, Penicillium returns to the single named, but pleomorphic, nomenclatural and taxonomic system used by many of the founders of its taxonomy, and actively promoted by the Peoria school (Thom 1930, Raper & Thom 1949). Talaromyces, now also defined as a pleomorphic genus, is adopted for the anamorphic species formerly included in Penicillium subgenus Biverticillium. In this study, the phylogenetic relationships of species of subgenus Biverticillium and other members of the Trichocomaceae were studied by sequencing a part of the RPB1 (RNA polymerase II largest subunit) gene. Furthermore, we discuss the taxonomy and nomenclature of species of this expanded concept of Talaromyces, based on phylogenetic, phenotypic and extrolite data. For detailed
phylogenetic analysis below genus level, the ITS regions (including the 5.8S nrDNA) of ex-type strains and/or representatives were sequenced. As discussed below, this paper is not meant as a monographic treatment, because many complexes have not yet been studied comprehensively.

MATERIALS AND METHODS

Sources of cultures

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

Morphology and physiology

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

Extrolite analysis

Nearly all species described in the genera Penicillium sensu lato (including those formerly classified in Eupenicillium), Penicillium subgenus Biverticillium, Talaromyces, Aspergillus and its many associated teleomorphic genera, and Paecilomyces (including those formerly or still classified in the associated teleomorph genus Byssoschlamys) 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 up to 3 wk for ascomata production.

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'-GRACRGTDCCRTCAYTTRACC-3' (Houbraken & Samson 2011). Primer RPB1-F1843 corresponds with position 1490–1512 of GenBank no. XM_002146871 (P. marneffei, ATCC 18224) and RPB1-R3096 corresponds with position 2610–2633. An addition primer, RPB1-R2623 5'-GCRGTTGATTCATTCCTMMRCCTC-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 MEGAS programme (Tamura et al. 2011). The RAxML (randomised accelerated maximum likelihood) software (v. 7.2.8, Stamatakis 2006) 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 Coccioides immitis (strain RS; full genome strain), and Trichoclora 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*.

<table>
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<th>Name</th>
<th>Collection no.</th>
<th>Origin</th>
<th>GenBank Accession number</th>
</tr>
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<tbody>
<tr>
<td>&quot;Aphanoascus cinnabarinus&quot;</td>
<td>CBS 267.72 = ATCC 26215</td>
<td>Soil, Japan</td>
<td>JN121625 JN899376</td>
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<td>Aspergillus aculeatus</td>
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<td>Tropical soil</td>
<td>JN121590</td>
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<td>Aspergillus clavatoflavus</td>
<td>CBS 473.65T = ATCC 16866 = IMI 124937</td>
<td>Rain forest soil, Tulley, Queensland, Australia</td>
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<tr>
<td>Aspergillus flavus</td>
<td>NRRL 3357 = CBS 128202 = ATCC 200026</td>
<td>Peanut cotyledons, USA</td>
<td>Unpublished</td>
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<td>Aspergillus fumigatus</td>
<td>A293</td>
<td>Patient with invasive aspergillosis</td>
<td>Nierman et al. (2005)</td>
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<tr>
<td>Aspergillus niger</td>
<td>CBS 513.88</td>
<td>Derived from NRRL 3122 and currently used as enzyme production strain</td>
<td>Pel et al. (2007)</td>
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<td>Aspergillus ochraceoroseus</td>
<td>CBS 101887 = ATCC 42001 = IBT 14580</td>
<td>Soil, Tai National Forest, Ivory Coast</td>
<td>JN121557</td>
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<td>Aspergillus ochraceus</td>
<td>CBS 108.08T = ATCC 1008 = CBS 547.65 = IMI 016247 = IMI 016247ii = IMI 016247iv = NRRL 1642 = NRRL 398</td>
<td>Unknown source</td>
<td>JN121562</td>
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<td>Aspergillus penicilloides</td>
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<td>Indoor environment, Germany</td>
<td>JN121578</td>
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<td>Surface soil from thorn-forest, near Mombasa, Kenya</td>
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<td>Aspergillus steynii</td>
<td>CBS 112812T = IBT 23096</td>
<td>Dried arabica green coffee bean, on parchment, internal infection, Chamumeshurun Estate, Karnataka, district Gris, India</td>
<td>JN121569</td>
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<td>Aspergillus sydowii</td>
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<td>Grains and milling fractions, <em>Triticum aestivum</em>, India</td>
<td>JN121624</td>
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<td>Aspergillus versicolor</td>
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<td>Cellophane, Indiana, USA</td>
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<td>Byssochlamys nivea</td>
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<td>Byssochlamys spectabilis</td>
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<td>Heat processed fruit beverage, Tokyo, Japan</td>
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<td>Byssochlamys verrucosa</td>
<td>CBS 605.74T = ATCC 34163</td>
<td>Nesting material of <em>Leipoa ocellata</em> (Malleefowl), Pullop Nature Reserve, New South Wales, Australia</td>
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<td>Chrysosporium inops</td>
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<td>Coccidioides immittis</td>
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<td>Vaccine strain - origin unknown</td>
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<td>Soil, bank of creek flowing into Little River, New South Wales</td>
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<td>Hamigera avellana</td>
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<td>Monascus purpureus</td>
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<td>Fermented rice grain, ‘ang-ucac’ (purple coloured rice), Kayok-Tegal, imported from China, Prov. Guoou-Tong, Java, Indonesia</td>
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<td>Paecilomyces aeruginus</td>
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<td>Debris of Glyceria maxima, Attenborough, Notts., UK</td>
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| Paecilomyces pascuus               | CBS 253.87T = FRR 1925 | Pasture grass, Otara, New Zealand           | JN899292 JN899321
### Table 1. (Continued).

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<td>Penicillium euglaucum</td>
<td>CBS 323.71T</td>
<td>Soil, Argentina</td>
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<td>Penicillium expansum</td>
<td>CBS 325.48T = ATCC 7861 = IBT 5101 = IMI 039761 = MUCL 29192 = NRRL 976</td>
<td>Fruit of Malus sylvestris, USA</td>
<td>JN121645</td>
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<td>Penicillium felutanum</td>
<td>CBS 228.81T = ATCC 10443 = CBS 326.48 = FRR 746 = FIO 5761 = IMI 039734 = IMI 039734ii = NRRL 746</td>
<td>Unknown source, USA</td>
<td>JN121605</td>
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<td>Penicillium fusiculosum</td>
<td>CBS 272.86T = IMI 193019</td>
<td>Lagenaria vulgaris, India</td>
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<td>Penicillium glabrum</td>
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<td><em>Penicillium herquei</em></td>
<td>CBS 338.48• ATCC 10118 = FRR 1040 = IMI 028809 = MUCL 29213 = NRRL 1040</td>
<td>Leaf, France</td>
<td>JN121647</td>
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<td><em>Penicillium ierlandanum</em></td>
<td>CBS 168.81• IJFM 5596 = IMI 253793</td>
<td>Air, Madrid, Spain</td>
<td>JN899311</td>
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<td><em>Penicillium isariiforme</em></td>
<td>CBS 247.56• ATCC 18425 = IMI 060371 = MUCL 31191 = MUCL 31323 = NRR 2638</td>
<td>Woodland soil, Zaire</td>
<td>JN121616</td>
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<tr>
<td><em>Penicillium islandicum</em></td>
<td>CBS 338.48• ATCC 10127 = IMI 040042 = MUCL 31324 = NRR 1036</td>
<td>Unknown source, Cape Town, South Africa</td>
<td>JN121648 JN899318</td>
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<td><em>Penicillium janthinellum</em></td>
<td>CBS 340.48• ATCC 10555 = IMI 040238 = NRR 2016</td>
<td>Soil, Nicaragua</td>
<td>JN131650</td>
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<td><em>Penicillium javanicum</em></td>
<td>CBS 341.48• ATCC 9099 = IMI 039733 = MUCL 29099 = NRR 707</td>
<td>Root of Camellia sinensis, Indonesia, Java</td>
<td>JN121651</td>
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<tr>
<td><em>Penicillium isariiforme</em></td>
<td>CBS 344.61• ATCC 18240 = IMI 086561= MUCL 2985 = NRR 3332</td>
<td>Culture contaminant of mineral oil CMI 1959; Kew, Surrey, UK</td>
<td>JN121654</td>
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<tr>
<td><em>Penicillium korosum</em></td>
<td>CBS 762.68• Rhizosphere, India</td>
<td>Rhizosphere, India</td>
<td>JN899347</td>
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<td><em>Penicillium loliense</em></td>
<td>CBS 343.48• ATCC 10462 = IMI 039743 = NRR 718</td>
<td>Canned blueberry, Washington, USA</td>
<td>JN121653</td>
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<td><em>Penicillium liani</em></td>
<td>CBS 225.66• ATCC 18325 = ATCC 18331 = IMI 098480 = NRR 3380 = VKM F-301</td>
<td>Soil, China</td>
<td>JN680280 JN899395</td>
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<td><em>Penicillium foliense</em></td>
<td>CBS 643.80• ATCC 52252 = FRR 1798 = IMI 216901 = MUCL 31325</td>
<td>Lolium, Palmerston North, New Zealand</td>
<td>JN680314 JN899379</td>
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<td><em>Penicillium mameffei</em></td>
<td>CBS 388.87• ATCC 18224= CBS 334.59• IMI 068794ii= IMI 068794ii</td>
<td>Rhizomys sinensis (bamboo rat), Vietnam</td>
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<td><em>Penicillium minnioluteum</em></td>
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<td>JN121709 JN899346</td>
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<td><em>Penicillium mirabile</em></td>
<td>CBS 624.72• CCR 31665 = FRR 1959 = IMI 167383 = MUCL 31206</td>
<td>Forest soil, Crimea, Ukraine</td>
<td>JN680312 JN899322</td>
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<tr>
<td><em>Penicillium namylowskii</em></td>
<td>CBS 353.48• ATCC 11127 = IMI 040033 = MUCL 29226 = NRR 1070</td>
<td>Soil under Pinus sp., Puszcza Białowieska, square &quot;652&quot;, Poland</td>
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<td><em>Penicillium obtatum</em></td>
<td>CBS 258.87• FRR 2234</td>
<td>Spoiled baby food, Sydney, New South Wales, Australia</td>
<td>JN680285 JN899364</td>
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<td><em>Penicillium ochrosalmoneum</em></td>
<td>CBS 489.66• ATCC 18338 = IMI 116248i</td>
<td>Cornmeal, South Africa</td>
<td>JN121689</td>
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<td><em>Penicillium osmophilum</em></td>
<td>CBS 462.72• ITB 14679</td>
<td>Agricultural soil, Wageningen, Netherlands</td>
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<td><em>Penicillium panamense</em></td>
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<td>Seed, Wageningen, Netherlands</td>
<td>JN680308 JN899396</td>
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<td><em>Penicillium phialosporum</em></td>
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<td>Soil, Barro Colorado Island, Panama</td>
<td>JN899291 JN899362</td>
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<td><em>Penicillium piceum</em></td>
<td>CBS 233.60• ATCC 18481 = FRR 203 = IMI 078256</td>
<td>Milled Californian rice, California, USA</td>
<td>JN680282 JN899340</td>
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<td><em>Penicillium pittii</em></td>
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<td><em>Penicillium pinophilum</em></td>
<td>CBS 631.68• ATCC 36839 = CECT 2809 = DSM 1944 = IAM 7013 = IMI 114933</td>
<td>PVC, Centre d’Études du Bouchet, M. Magnoux, France</td>
<td>JN680313 JN899332</td>
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<tr>
<td><em>Penicillium pittii</em></td>
<td>CBS 139.84• IMI 327871</td>
<td>Clay soil, under poplar trees, bank of Duero River, Valladolid, Spain</td>
<td>JN680274 JN899325</td>
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<tr>
<td><em>Penicillium primulinum</em></td>
<td>CBS 321.48• ATCC 10438 = CBS 439.88• FRR 1074 = IMI 040031 = MUCL 31321 = MUCL 31530 = NRR 1074</td>
<td>USA</td>
<td>JN680298 JN899317</td>
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<tr>
<td><em>Penicillium proteolyticum</em></td>
<td>CBS 303.67• ATCC 18326 = NRR 3376</td>
<td>Granite soil, Ukraine</td>
<td>JN680292 JN899387</td>
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<tr>
<td><em>Penicillium pseudostromaticum</em></td>
<td>CBS 470.70• ATCC 18919 = FRR 2039</td>
<td>Feather, near Itasca State Park, Hubbard Co., Minnesota, USA</td>
<td>JN899300 JN899371</td>
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<td>Penicillium purpurogenum</td>
<td>CBS 286.36° = IMI 091926</td>
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<td>Penicillium purpurogenum var. rubisclerotium</td>
<td>CBS 274.95</td>
<td>Sculpture, castle Troja, Prague, Czech Republic</td>
<td>JN899295 JN899316</td>
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<td>Penicillium rademirici</td>
<td>CBS 270.35° = ATCC 4713 = ATCC 52244 = FRR 1064 = IBT 4302 = MUCL 29225 = NRRL 1064 = NRRL 1142</td>
<td>Zea mays, Castle Rock, Virginia, USA</td>
<td>JN680287 JN899381</td>
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<td>Penicillium radiculum</td>
<td>CBS 140.64° = CECT 2771 = IMI 202406 = IMI 237870</td>
<td>Air under willow tree, bank of river Duero, Herrera, Valladolid, Spain</td>
<td>JN899386</td>
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<tr>
<td>Penicillium rotundum</td>
<td>CBS 100469° = FRR 4718</td>
<td>Root of seedling of Trichium aestivum, Wagga Wagga, New South Wales, Australia</td>
<td>JN899324</td>
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<tr>
<td>Penicillium rubicundum</td>
<td>CBS 369.48° = ATCC 10493 = IMI 040589 = NRRL 2107</td>
<td>Wood, Chiriqui Prov., Panama</td>
<td>JN899353</td>
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<td>Penicillium rubinum</td>
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<td>JN860301 JN899384</td>
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<td>Penicillium rugulosum</td>
<td>CBS 371.48° = ATCC 10128 = IMI 040041 = MUCL 31201 = NRRL 1045</td>
<td>Tuber (Solanum tuberosum), Connecticut, USA</td>
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<td>Penicillium rubulosum</td>
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<td>Spoiled pasteurized fruit juice, New South Wales, Sydney, Australia</td>
<td>JN899294</td>
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<td>Penicillium samsonii</td>
<td>CBS 137.84° = CECT 2772 = IMI 282404 = IMI 327872</td>
<td>Fruit, damaged by insect, Valladolid, Spain</td>
<td>JN680273 JN899369</td>
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<td>Penicillium sheari</td>
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<td>Soil, Tela, Honduras</td>
<td>JN121631</td>
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<tr>
<td>Penicillium siamense</td>
<td>CBS 475.68° = IMI 323204</td>
<td>Forest soil, Lampang, Thum District, Ban Daen, Than, Thailand</td>
<td>JN899385</td>
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<td>Penicillium simplicissimum</td>
<td>CBS 372.48° = ATCC 10495 = IMI 039816</td>
<td>Flannel bag, Cape, South Africa</td>
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<td>Penicillium stipitatum</td>
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<td>Penicillium stictatum</td>
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<td>Peaty forest soil, Eastern Transvaal, South-Africa</td>
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<td>Penicillium tardum</td>
<td>CBS 258.37° = NRRL 2116</td>
<td>Unknown source</td>
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<td>Penicillium tularensae</td>
<td>CBS 378.48° = ATCC 10503 = IMI 040034 = NRRL 1073</td>
<td>Dead twig, France</td>
<td>JN899297</td>
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<td>Penicillium variabile</td>
<td>CBS 430.69° = ATCC 22056 = IMI 148394</td>
<td>Soil, under Pinus ponderosa and Quercus kelloggii, Tulare Co., Pine Flat, California, USA</td>
<td>JN121681</td>
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<td>Penicillium varians</td>
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<td>Cocos fibre, Johannesburg, South Africa</td>
<td>JN880304 JN899343</td>
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<td>Penicillium verruculosum</td>
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<td>Penicillium victoriae</td>
<td>CBS 388.48° = ATCC 10513= DSM 2263= IMI 040039 = NRRL 1050</td>
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<td>Phialosimplex caninus</td>
<td>CBS 128032° = UAMH 10337</td>
<td>Bone marrow aspirate ex canine, San Antonio, Texas, USA</td>
<td>JN121587</td>
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<td>Phialosimplex chlamydosporus</td>
<td>CBS 109945° = FMR 7371 = IMI 387422</td>
<td>Disseminated infection in a dog</td>
<td>JN121566</td>
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<td>Phialosimplex sclerotialis</td>
<td>CBS 366.77° = IAM 14794</td>
<td>Fodder of ray-grass and lucerne, France</td>
<td>JN121661</td>
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<td>Rasamsonia eburnea</td>
<td>CBS 100538° = IBT 17519</td>
<td>Soil, Taipei, Taiwan</td>
<td>JN680325</td>
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<td>Rasamsonia argillacea</td>
<td>CBS 101.69 = IMI 156096 = IBT 31199</td>
<td>Mine tip with a very high surface temperature; Staffordshire, UK</td>
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<td>Rasamsonia byssochlamydoides</td>
<td>CBS 413.71 = IMI 11604</td>
<td>Dry soil under Douglas fir, Oregon, USA</td>
<td>JN121675</td>
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<td>Rasamsonia emersonii</td>
<td>CBS 393.64 = DTM 4811 = IBT 21695 = ATCC 16479 = IMI 116815 = IMI 116815</td>
<td>Compost, Italy</td>
<td>JN121670</td>
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<td>Sagenoma viride</td>
<td>CBS 114.72 = ATCC 22467 = NRRL 5579</td>
<td>Soil, Australia</td>
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<td>Sagenomella bohemica</td>
<td>CBS 545.86 = CCF 2330 = IAM 14789</td>
<td>Peloids for balneological purposes, Frantiskovy Lazne Spa, West Bohemia, Czech Republic</td>
<td>JN121699</td>
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<td>Sagenomella diversispora</td>
<td>CBS 398.69</td>
<td>Forest soil under Populus tremuloides, Petawawa, Ontario, Canada</td>
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<td>Sagenomella griseoviridis</td>
<td>CBS 426.67 = ATCC 18505 = IMI 113160</td>
<td>Unknown source</td>
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<td>Sagenomella humidola</td>
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<td>Forest soil under Thuja occidentalis, Ontario, Canada</td>
<td>JN121678</td>
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<td>Sagenomella striatisspores</td>
<td>CBS 429.67 = ATCC 18510 = IMI 113163</td>
<td>Soil, Guelph, Ontario, Canada</td>
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<td>Sagenomella verticillata</td>
<td>CBS 415.76A</td>
<td>Gymnosperm forest soil, Sweden</td>
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<td>Sclerocleista ornata</td>
<td>CBS 124.53 = ATCC 16921 = IMI 052985 = MUCL 15012</td>
<td>Soil in oak forest, Dane Co., Madison, Wisconsin, USA</td>
<td>JN121581</td>
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<td>Talaromyces assiutensis</td>
<td>CBS 118440</td>
<td>Soil, Fez, Morocco</td>
<td>JN899320</td>
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<td>Talaromyces austrocalifornicus</td>
<td>CBS 644.95 = IBT 17522</td>
<td>Soil, campus Univ. South California, Los Angeles, USA</td>
<td>JN680275</td>
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<td>Talaromyces bacillisporus</td>
<td>CBS 296.48 = ATCC 10126 = IMI 040045 = NRRL 1025</td>
<td>Begonia leaf, New York City, New York, USA</td>
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<td>Talaromyces barchinensis</td>
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<td>Soil, Barcelona, Spain</td>
<td>JN680318</td>
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<td>Talaromyces brevicompactus</td>
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<td>Moulded vegetables, Prov. Sechuan, Wolong, China</td>
<td>JN680326</td>
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<td>Talaromyces convolutus</td>
<td>CBS 100537 = IBT 14989</td>
<td>Soil, Kathmandu, Nepal</td>
<td>JN121553</td>
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<td>Talaromyces cyanescens</td>
<td>CBS 114900 = FMR 8388</td>
<td>Tortosa, Catalina, Spain</td>
<td>JN899391</td>
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<td>Talaromyces denuxi</td>
<td>CBS 412.89 = NHL 2381</td>
<td>Cultivated soil, Okayama Prefecture, Kurashiki City, Higashitomi, Japan</td>
<td>JN899327</td>
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<tr>
<td>Talaromyces emodensis</td>
<td>CBS 100536 = IBT 14990</td>
<td>Soil, Kathmandu, Nepal</td>
<td>JN121552</td>
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<td>Talaromyces flavus</td>
<td>CBS 310.38 = IMI 197477 = NRRL 2098</td>
<td>Unknown substrate, New Zealand</td>
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<td>Talaromyces galapagensis</td>
<td>CBS 751.74 = IFO 31796</td>
<td>Shaded soil under Maytenus obovata, Isla Santa Cruz, Galapagos Islands, Ecuador</td>
<td>JN680321</td>
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<td>Talaromyces gossypii</td>
<td>CBS 645.80 = FRR 1966 = IMI 198365</td>
<td>Gossypium, India</td>
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<td>Talaromyces helicus var. boninensis</td>
<td>CBS 650.95 = IBT 17516</td>
<td>Lawn soil, Kominato, Chichijima, Ogasawara-mura, Tokyo-to, Japan</td>
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<td>Talaromyces helicus var. helicus</td>
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<td>Soil, Sweden</td>
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<td>Talaromyces helicus var. major</td>
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<td>Swamp soil, near Attenborough, Nottingham, UK</td>
<td>JN899335</td>
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<td>Talaromyces indigoticus</td>
<td>CBS 100534 = IBT 17590</td>
<td>Soil, Nagasaki-ken, Minamikushiyama-mura, Japan</td>
<td>JN899331</td>
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<td>Talaromyces intermedius</td>
<td>CBS 152.65 = BDUN 267 = IFO 31792 = IMI 100874</td>
<td>Alluvial pasture and swamp soil, Attenborough, Nottingham, England</td>
<td>JN899332</td>
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<td><strong>Talaromyces leycettanus</strong></td>
<td>CBS 398.68 = ATCC 22469 = IMI 178525</td>
<td>Coal spoil tip soil, Leycett, Staffordshire, England, UK</td>
<td>JN121672</td>
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<td><strong>Talaromyces luteus</strong></td>
<td>CBS 348.51 = IMI 089305</td>
<td>Soil, UK</td>
<td>JN121656</td>
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<td><strong>Talaromyces macrosporus</strong></td>
<td>CBS 317.63 = FRR 404 = IMI 19746</td>
<td>Apple juice, Stellenbosch, South Africa</td>
<td>JN680296 JN899333</td>
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<td><strong>Talaromyces mimosinus</strong></td>
<td>CBS 659.80 = FRR 1875 = IMI 223991</td>
<td>Soil from creek bank, Nattai River, New South Wales, Australia</td>
<td>JN899302 JN899338</td>
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<td><strong>Talaromyces muroii</strong></td>
<td>CBS 756.96 = PF 1153</td>
<td>Soil, Huaiilen County, Chingpu, Taiwan</td>
<td>JN680322 JN899351</td>
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<tr>
<td><strong>Talaromyces ochraceus</strong></td>
<td>CBS 102855</td>
<td>Heat-treated soil from forest of Pinus hartwegii, Veracruz, Mexico</td>
<td>JN680327</td>
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<tr>
<td><strong>Talaromyces ochiensis</strong></td>
<td>CBS 127.64</td>
<td>Soil treated with cyanamide, Germany</td>
<td>JN680272 JN899355</td>
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<td><strong>Talaromyces purpureus</strong></td>
<td>CBS 475.71 = ATCC 24069 = ATCC 52513 = FRR 17831 = IMI 181546</td>
<td>Soil, near Estere, France</td>
<td>JN121687 JN899328</td>
</tr>
<tr>
<td><strong>Talaromyces subinflatus</strong></td>
<td>CBS 652.95 = IBT 17520</td>
<td>Copse soil, Hahajima, Ogasawara-mura, Tokyo-to, Japan</td>
<td>JN899301 JN899397</td>
</tr>
<tr>
<td><strong>Talaromyces tardifaciens</strong></td>
<td>CBS 250.94</td>
<td>Unknown source</td>
<td>JN680283 JN599361</td>
</tr>
<tr>
<td><strong>Talaromyces thermophilus</strong></td>
<td>CBS 236.58 = ATCC 10518 = IMI 046590 = NRRL 2155</td>
<td>Parthenium argentatum, decaying plant; California, USA</td>
<td>JN121611</td>
</tr>
<tr>
<td><strong>Talaromyces trachyspermus</strong></td>
<td>CBS 373.48 = ATCC 10497 = IMI 040043 = NRRL 1028</td>
<td>Unknown source, USA</td>
<td>JN121664 JN899354</td>
</tr>
<tr>
<td><strong>Talaromyces ucrainicus</strong></td>
<td>CBS 162.67 = ATCC 22344 = FRR 3462</td>
<td>Unknown source</td>
<td>JN680277 JN899394</td>
</tr>
<tr>
<td><strong>Talaromyces udagawae</strong></td>
<td>CBS 579.72 = FRR 1727 = IMI 197482</td>
<td>Soil, Misugimura, Japan</td>
<td>JN680310 JN899350</td>
</tr>
<tr>
<td><strong>Talaromyces unicus</strong></td>
<td>CBS 100535 = CCRC 32703 = IBT 18385</td>
<td>Soil, Chiayi County, Funlu, Taiwan</td>
<td>JN680324 JN899336</td>
</tr>
<tr>
<td><strong>Talaromyces worlmanii</strong></td>
<td>CBS 391.48 = ATCC 10517 = IMI 040047 = NRRL 1017</td>
<td>Unknown source</td>
<td>JN121669 JN899352</td>
</tr>
<tr>
<td><strong>Thermoascus aurantiacus</strong></td>
<td>CBS 396.78</td>
<td>Sawdust, in lumber yard, Toronto, Ontario, Canada</td>
<td>JN121671</td>
</tr>
<tr>
<td><strong>Thermoascus crustaceus</strong></td>
<td>CBS 891.70 = IMI 173037</td>
<td>Wood, Firenze, Italy</td>
<td>JN121719</td>
</tr>
<tr>
<td><strong>Thermoascus thermophilus</strong></td>
<td>CBS 181.67 = ATCC 16462 = IMI 126333</td>
<td>Parthenium argentatum, decaying plant; Salinas, California, USA</td>
<td>JN121591</td>
</tr>
<tr>
<td><strong>Thermomyces lanuginosus</strong></td>
<td>CBS 528.71 = IMI 123298 = NRRL 5208</td>
<td>Wood and bark of Pinus, Sweden</td>
<td>JN121697</td>
</tr>
<tr>
<td><strong>Thermomyces lanuginosus</strong></td>
<td>CBS 218.34 = MUCL 8338</td>
<td>Fruit shell of Theobroma cacao</td>
<td>JN121599</td>
</tr>
<tr>
<td><strong>Thermomyces lanuginosus</strong></td>
<td>CBS 224.63 = MUCL 8337</td>
<td>Mushroom compost; Gossau-Zürich Switzerland</td>
<td>JN121602</td>
</tr>
<tr>
<td><strong>Thermomonospora paradoxa</strong></td>
<td>CBS 268.54 = MUCL 8340</td>
<td>Stomach of bovine foetus, Netherlands</td>
<td>JN680291</td>
</tr>
<tr>
<td><strong>Trichocoma paradoxa</strong></td>
<td>CBS 103.73</td>
<td>Unknown source, Japan</td>
<td>JN121558</td>
</tr>
<tr>
<td><strong>Trichocoma paradoxa</strong></td>
<td>CBS 247.57 = MUCL 39666 = IBT 31159</td>
<td>Unknown source, Hachijō, Japan</td>
<td>JN121617 JN899398</td>
</tr>
<tr>
<td><strong>Warcupiella spinulosa</strong></td>
<td>CBS 788.83</td>
<td>Rotting stump of cut down tree, Myojo Temple near Hakui Noto Park, Ishikawa Pref., Japan</td>
<td>JN121718</td>
</tr>
</tbody>
</table>

**Note:** 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 ochraceus*, *T. luteus*, *T. thermophilus*, *T. eburneus*, *T. emersonii*, *T. byssoschlamydoides*, *T. spectabilis*, *T. brevicompactus*, *T. striatus* and *T. leycettanus*. *Talaromyces ochraceus* 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. byssoschlamydoides* 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 Penicillium varians.

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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 preylytic diketopiperazines talahtermophilins A and B, not found in any other species (Chu et al. 2010). The phylogenetic position of T. leyceettanus is not convincingly defined. This species is positioned near Warcupiella spinulosa and Hamigera striata (= Talaromyces striatus), but bootstrap support is lacking. Talaromyces brevispitiatus occurs on a well-supported branch with H. avellanea. Comparison of ITS and calmodulin sequences shows that this species is closely related to NRR 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...
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. ochrosalmonae. This relationship was also confirmed by extrolite data (see below).

Figure 1 indicates that the following species phylogenetically belong in Talaromyces: Aphanoascus cinnabarinus (CBS 267.72), Sagenomella bohemica (CBS 545.86), Paecilomyces aeruginus (CBS 350.66), Geosmithia viridis (CBS 252.87) and Sagenoma viride (CBS 114.72). The former three strains are on a well-supported sister clade basal to Talaromyces muroil 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 LS268 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. obliatus, 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 nonribosomal peptides and terpenes, it is obvious that Talaromyces species have unique and specific extrolites (Table 2). 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 this 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 aculeatusus, P. dendriticus 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). Austidiol was isolated from Aspergillus pseudousustus (Vleggaar et al. 1974, Samson et al. 2011), but 7-epi-austidiol 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, penisimplins, 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 Biverticillum 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. ochrosalmonene (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. Bourge (1923) was the first who named this group as the subgenus Biverticillum, but included species such as P. citrinum (as P. auriflum), P. atramentosum etc., which are no longer regarded as members of this subgenus (Houbraken et al. 2010). The characteristic lanceolate or acerose phialides was used as a more definitive morphological character of subgenus Biverticillum 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 Biverticillum, 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-Symmetra group and distinguished four sections: Ascogena, Coremigena, Luteo-virida (Funiculosa and Luteo-purpurgena) 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 Biverticillum, 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 paradoxus (CBS 788.83). T. = Talaromyces; P. = Penicillium. Strains indicated with * are ITS sequencing obtained from GenBank.
*P. vulpinum* (as *P. claviforme*) that are now classified in *Penicillium* sensu stricto. The same conclusion was shown by the early molecular results of LoBuglio & Taylor (1993), and subsequently supported by the physiological, morphological and extrolite characters reviewed in the Introduction, and generated during this study.

In general, *Penicillium sensu stricto* and *Aspergillus* share many more features with each other than they do with *Talaromyces*. This includes micro- and macro-morphology, good growth on low water activity media, and the many shared exometabolite families. *Talaromyces* produces a series of metabolites that are apparently unique to this genus (J.C. Frisvad unpubl. data). The characteristic yellow and red colony and mycelial colours in *Talaromyces* are often caused by accumulation of mitorubrins and other azaphilones and unique anthraquinones and mitorubrins that are not found in *Aspergillus* and *Penicillium*. Some azaphilones are found in *Penicillium sclerotiorum* and *Penicillium hirayamae*, but only their optical antipodes are found in *Talaromyces*. *Penicillium* and *Talaromyces* species excluded from the revised *Talaromyces* genus

Figure 1 shows that a number of species described in the genus should be excluded from *Talaromyces s. str.* Phylogenetically, *T. ochr CBS 102855* 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

### 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.

<table>
<thead>
<tr>
<th>Secondary metabolite (exometabolite) biosynthetic families</th>
<th>5-Hydroxymethylfurfural</th>
<th>Purpurogenones</th>
</tr>
</thead>
<tbody>
<tr>
<td>172</td>
<td>Alternariols * (P and others)</td>
<td>Hydromethylmaltol</td>
</tr>
<tr>
<td>Anthglutin</td>
<td>4-Hydroxy-4,5-dicarboxy pentadecanoic acid (<em>T. spiculísporus</em>)</td>
<td>Rubratoxins</td>
</tr>
<tr>
<td>Apiculides (incl. NG-011’s * (others))</td>
<td>7-Hydroxy-2,5-dimethylchromane</td>
<td>Rugulosins &amp; flavoskyrin * (others)</td>
</tr>
<tr>
<td>AS-186-G</td>
<td>3-Hydroxymethyl-6,8-dimethoxycoumarin</td>
<td>Rugulotosins</td>
</tr>
<tr>
<td>Asperphenamates &amp; asperglaucid * (A, P)</td>
<td>3-Hydroxyphthalic acid * (P)</td>
<td>Rugulosuvine * (P)</td>
</tr>
<tr>
<td>Atevenotrient methyl acetil (<em>P. verruculosum</em>)</td>
<td>Islandic acids</td>
<td>Rugulovasines * (P)</td>
</tr>
<tr>
<td>Epi-Ausdios (7-epiausdios &amp; 8-O-methylepiausdios) (the stereoisomer ausdios found in <em>Aspergillus</em>)</td>
<td>(+)-Isocitric acid + Decylic acid (<em>T. spiculísporus</em>)</td>
<td>Secalonics * (A, P, others)</td>
</tr>
<tr>
<td>Austins * (A, P)</td>
<td>Italicic acids * (P)</td>
<td>Speciferones* (others)</td>
</tr>
<tr>
<td>BE-24811</td>
<td>Juglones</td>
<td>Spiculisporic acids (&amp; miniluteic acids)</td>
</tr>
<tr>
<td>BE-31405’s</td>
<td>Lichexanthone * (others)</td>
<td>SQ 30957</td>
</tr>
<tr>
<td>Berkeleyamides</td>
<td>Luteins</td>
<td>Strepthymylpenole</td>
</tr>
<tr>
<td>Botyopodin * (P &amp; others)</td>
<td>Maculosin * (others)</td>
<td>Stilpatic acid</td>
</tr>
<tr>
<td>Chordiniline A</td>
<td>Mellein * (A)</td>
<td>Talapoxtides</td>
</tr>
<tr>
<td>Cordyhanhydrides</td>
<td>Methyl-4-carboxy-5-hydroxyphthalaldehydehydrate</td>
<td>Talaroconvolutins</td>
</tr>
<tr>
<td>Cyclochlorotines &amp; islanditoxin</td>
<td>3-Methyl-6-hydroxy-8-methoxy-3,4-dihydroisocoumarins</td>
<td>Talarodixine</td>
</tr>
<tr>
<td>Dehydrocarolic acids * (A, P)</td>
<td>Minioluteidos, berkeleydione, berkeleytriones, berkeleyacetales, dhiolides</td>
<td>Talaroflavones</td>
</tr>
<tr>
<td>Diethylphthalate (Artefact?)</td>
<td>Mitorurins &amp; kasanosins &amp; funicones</td>
<td>Talaromycins</td>
</tr>
<tr>
<td>5,6-Dihydro-3,5-dihydroxy-6-hydroxymethyl-2H-pyran-2-one</td>
<td>Monasncins &amp; monascorubramin</td>
<td>Talarotoxins</td>
</tr>
<tr>
<td>4,6-Dihydro-5-methylphthalaldehyde</td>
<td>Monordens * (A, others)</td>
<td>TAN-931</td>
</tr>
<tr>
<td>(2E,2E’,7S,7‘E)-4,9-Dioxo-7-(4’,9’-dioxo-2’,7’decadienoyloxy)-2-decanoic acid</td>
<td>NG-061</td>
<td>Thailandolides</td>
</tr>
<tr>
<td>Diverconols</td>
<td>NK-374200</td>
<td>Trachyspermic acids</td>
</tr>
<tr>
<td>Duclauixins</td>
<td>OF-4949’s</td>
<td>Trachyspermic acid</td>
</tr>
<tr>
<td>Emodins * (A, P, others)</td>
<td>Penicillospain * (others)</td>
<td>Triacetel lactone</td>
</tr>
<tr>
<td>Erythroskyrins</td>
<td>Penisimplicins</td>
<td>(-&gt;)-2,3,4-Trihydroxy-butanamide</td>
</tr>
<tr>
<td>Flavonominin</td>
<td>Penisimplicinsins</td>
<td>Vermicells</td>
</tr>
<tr>
<td>Funiculosic acids</td>
<td>Penitric acid &amp; penitricins</td>
<td>Vermiculins</td>
</tr>
<tr>
<td>Funiculosin</td>
<td>Pevalic acid</td>
<td>Vermillitins</td>
</tr>
<tr>
<td>Goodins * (A, P)</td>
<td>PF-1092A</td>
<td>Vermitastins &amp; penicidones</td>
</tr>
<tr>
<td>Glauconic acids</td>
<td>Pinseilic acid</td>
<td>Vertoskyrin</td>
</tr>
<tr>
<td>Gregatins and penizzlies * (A, P)</td>
<td>Pinseilin * (A, others)</td>
<td>Wortmannilactones</td>
</tr>
<tr>
<td>Helicins</td>
<td>Purpactins ( = penicilides = vermixocins)</td>
<td>Wortmannins * (others)</td>
</tr>
<tr>
<td>Herqueinones * (P)</td>
<td>Purpuride</td>
<td>Xanthoradones</td>
</tr>
<tr>
<td>Zeorins * (A, others)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

In general, *Penicillium sensu stricto* and *Aspergillus* share many more features with each other than they do with *Talaromyces*. This includes micro- and macro-morphology, good growth on low water activity media, and the many shared exometabolite families. *Talaromyces* produces a series of metabolites that are apparently unique to this genus (J.C. Frisvad unpubl. data). The characteristic yellow and red colony and mycelial colours in *Talaromyces* are often caused by accumulation of mitorubrins and other azaphilones and unique anthraquinones and mitorubrins that are not found in *Aspergillus* and *Penicillium*. Some azaphilones are found in *Penicillium sclerotiorum* and *Penicillium hirayamae*, but only their optical antipodes are found in *Talaromyces*.

### Penicillium and Talaromyces species 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. ochr CBS 102855* 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
Sagenomella sp., and thus the new combination Sagenomella ocoti is proposed in the taxonomy section below.

Our analysis confirms the distinctiveness of the recently described genus Rasasomonia erected for thermostolerant or thermophilic species with distinctly rough-walled conidiphore stipes, olive-brown conidia, and ascomata, if present, with a scanty hypal 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 thermocritinus (as 'thermocritinus') 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 Thermomyces 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, unpublished 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 Sagenomella is typified with S. viride, and therefore this genus can be considered as a synonym of Talaromyces. Our data support the conclusions of von Arx (1987), who correctly transferred this species in Talaromyces, and this is reflected in the taxonomy section below.

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

TAXONY

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 *Erythrogynnotheca* 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, *Erythrogynnotheca* 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 *Erythrogynnotheca* 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 *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* Donieu & 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.**


Ascomata cleistothecial, usually with a distinctly hyphal exterior wall, often yellow, occasionally white, creamish, pinkish or reddish. Asci 8-spored, globose to ellipsoidal, ascospor 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 acerosus, rarely ampulliform, periclinal thickening usually visible in the conidigenous apertures, 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 Benjamín (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 *Talaromyces dangeardi* 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 extrofile 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.


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


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

Penicillium aculeatum similis, sed conidios apiculatis distinguatur.

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.

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


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

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


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

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


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


**Talaromyces emodensis** Udagawa, Mycotaxon 48: 146. 1993.
Anamorphic synonym: *Penicillium emodense* Udagawa (simultaneously published, identical holotype).


**Talaromyces euchlorocarpus** Yaguchi, Someya & Udagawa, Mycoscience 40: 133. 1999.
Anamorphic synonym: *Penicillium euchlorocarpum* 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 & Gómez-Bolea is being prepared for publication in Mycotaxon.


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.


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


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

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


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


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


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.

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

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


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

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

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

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


Talaromyces viridulus Samson, Yilmaz & Frisvad, nom. nov. MycoBank MB560679.
Excluded species and taxa, which need further taxonomic study


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, unpublished data).


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


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


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


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


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


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


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.


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


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


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.


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


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.


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.


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.


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

≡ Rasamsomia byssochlamydoides (Stolk & Samson) Houbraken & Frisvad, Ant. van Leeuwenhoek, in press.


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

≡ Rasamsomia eburnea (Yaguchi, Someya & Udagawa) Houbraken & Frisvad, Ant. van Leeuwenhoek, in press.


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

≡ Rasamsomia emersonii (Stolk) Houbraken & Frisvad, Ant. van Leeuwenhoek, in press.


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.


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


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


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.


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.


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

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


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

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


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. T. panasenkoi Pitt is therefore a synonym of T. ucrainicus.


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.


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


**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 species is a *Eurotium* species, a typical contaminant of books and other material in archives. However, its reported thermophily is different from known species of the mesophilic *Eurotium* species.

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


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

**Aspergillossis** 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 *Aspergillossis* Speg. 1910. Pitt (1980) considered Sopp's genus a tentative synonym of *Merimbla* Pitt.


Type species: *C. pfefferianus* Wehmer 1893

* = *Penicillium glabrum* (Wehmer) Westling 1911, fide Pitt 1980.

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


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*.


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 Houbreken & Samson (2011), *Eladia* is clearly included in *Penicillium sensu stricto* and that synonymy is accepted here.


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

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


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 *Bioneuctriaceae*, *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 *Biverticillum*.


**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 *Penicillium* 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 *Biverticillum*.

**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*.


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

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

**Pritzelia** Henn., Hedwigia Beibl. 42: 88. 1903.

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

*Note:* Clements & Shear (1931) suggested that *Pritzelia* 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 Type species: *Penicillium leucocephalum* Rabenh. 1844.

*Note:* Corda (1837) illustrated and described his species as having asceptate stipes, a branched, asymmetrical penicillate head, with long chains of amorocconidia. 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 *Biverticillum*, but its exact identity is unknown.


**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).


**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.

**REFERENCES**


