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

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**Abstract:** The taxonomic history of anamorphic species attributed to *Penicillium* subgenus *Biverticillium* is reviewed, along with evidence supporting their relationship with teleomorph species classified in *Talaromyces*. To complement previous conclusions based on ITS, SSU, and LSU sequencing, the realisation has grown that the distinctiveness of *Talaromyces* 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 and related biverticillate anamorphic species. Extröte 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 homomorphic generic diagnosis for the expanded concept of Talaromyces, including teleomorph and anamorph characters, is provided. A list of accepted Talaromyces names and newly combined Penicillium names is given. Species of biotechnological and medical importance, such as *P. funiculosum* and *P. marneffei*, are now combined in Talaromyces. Excluded species and taxa that need further taxonomic study are discussed. An appendix lists other generic names, usually considered synonyms of *Penicillium sensu lato* that were considered prior to our adoption of the name Talaromyces.


**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*).
in 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 matures quickly, usually within a few weeks in agar culture. In Penicillium sensu stricto, the sclerotium-like ascocarp has 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 ascus 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 ascus 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 Byssoschlamys as a synonym), and several small and less well-known genera such as Thermoascus, Penicilliosis, 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 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) (Nortman 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, Trichochoma 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, vermicillin, vermistatin, vermiculine, duclauxin and gluconic acid. None of these compounds were found in cultures of Penicillium sensu stricto (Frisvad et al. 1990b).

The soon to be published International Code of Nomenclature for Algae, Fungi and Plants removes the primacy of teleomorph-over anamorph-typified names, leaving both kinds of names competing equally for priority (Norvell 2011). Because of these changes, we apply the principle of ‘one fungus - one name’ and in the nomenclatural revision, priority is given to the oldest genus and species name irrespective of whether they were originally described for teleomorphs or anamorphs (Hawksworth et al. 2011). In this respect, Penicillium returns to the single named, but pleomorphic, nomenclatural and taxonomic system used by many of the founders of its taxonomy, and actively promoted by the Peoria school (Thom 1930, Raper & Thom 1949), Talaromyces, now also defined as a pleomorphic genus, is adopted for the anamorphic species formerly included in Penicillium subgenus Biverticillium. In this study, the phylogenetic relationships of species of subgenus Biverticillium and other members of the Trichocomaceae were studied by sequencing a part of the rPB1 (RNA polymerase II largest subunit) gene. Furthermore, we discuss the taxonomy and nomenclature of species of this expanded concept of Talaromyces, based on phylogenetic, phenotypic and extrolite data. For detailed
phylogenetic analysis below genus level, the ITS regions (including the 5.8S nrDNA) of ex-type strains and/or representatives were sequenced. As discussed below, this paper is not meant as a monographic treatment, because many complexes have not yet been studied comprehensively.

MATERIALS AND METHODS

Sources of cultures

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

Morphology and physiology

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

Extrolite analysis

Nearly all species described in the genera Penicillium sensu lato (including those formerly classified in Eupenicillium), Penicillium subgenus Biverticillium, Talaromyces, Aspergillus and its many associated teleomorphic genera, and Paecilomyces (including those formerly or still classified in the associated teleomorph genus 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 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 cyclopelenol, cyclopelenin, cyclopeptin, dehydrocyclopeptin, viridicatin, viridicalot 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, mitorubrinol acetate, mitorubrinic acid, funicorne, deoxyfunicorne, actofunicorne, 3-O-methylfunicone, kasanosin A and B, diazaphilonic acid, and wortmin; they are here collectively called the mitorubrins, while the related metabolites vermistatins and penicidones are called vermistatins (see Šturdíková et al. 2000, Nicoletti et al. 2009, Osmanova et al. 2010). Some chlorinated azaphilones such as helicusins (Yoshida et al. 1995) and luteusins (Fujimoto et al. 1990, Yoshida et al. 1996a, b) are epimers of the sclerotorins from P. sclerotiorum, and are treated as two families, albeit closely related to the mitorubrins.

DNA extraction, amplification and sequencing

Isolates used for molecular studies were grown on MEA for 7–14 d at the required temperature prior to DNA extraction. DNA was extracted from the cells using the UltraClean™ Microbial DNA Kit (MoBio Laboratories), following the protocols of the manufacturer. A part of the RPB1 gene was amplified to study the phylogenetic relationships among Penicillium and other related genera. This fragment was amplified using the primer pair RPB1-F1843 5’-ATTTYGAYGGTGAYGARATGAAC-3’ and RPB1-R3096 5’-GRACRGTDCCRTCATAYTTRACC-3’ (Houbraken & Samson 2011). Primer RPB1-F1843 corresponds with position 1490–1512 of GenBank no. XM_002146871 (P. marneffei, ATCC 18224) and RPB1-R3096 corresponds with position 2610–2633. An addition primer, RPB1-R2623 5’-GCRTTGTGATCCTTMMARCTC-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 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>
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<th>Collection no.</th>
<th>Origin</th>
<th>GenBank Accession number</th>
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<td><em>Aphanoascus cinnabarinus</em></td>
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<td><em>Aspergillus flavus</em></td>
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<td>Peanut cotyledons, USA</td>
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<td><em>Aspergillus fumigatus</em></td>
<td>A293</td>
<td>Patient with invasive aspergillosis</td>
<td>Nierman et al. (2005)</td>
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<td><em>Aspergillus niger</em></td>
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<td>Derived from NRRL 3122 and currently used as enzyme production strain</td>
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<td><em>Coccidioides immitis</em></td>
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<td>Vaccine strain - origin unknown</td>
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<td><em>Emericella nidulans</em></td>
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<td><em>Monascus purpureus</em></td>
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<td>Penicillium canescens</td>
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<td>Soil, England</td>
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<td>Penicillium catenatum</td>
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<td>Desert soil, Upington, Cape Province, South Africa</td>
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<td>Penicillium cinnamopurpureum</td>
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<td>Cultivated soil, South Africa</td>
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<td>Penicillium citrinum</td>
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<td>Penicillium coalescens</td>
<td>CBS 103.83</td>
<td>Soil under Pinus sp., near Vulladolid, Spain</td>
<td>JN899366</td>
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<td>Penicillium concavosporosum</td>
<td>CBS 898.73 = ATCC 20202</td>
<td>Unknown substrate, Japan</td>
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<td>Penicillium crateriforme</td>
<td>CBS 184.27 = FRR 1057 = IMI 094165 = LSHB P164 = MUCL 29022 = NRRL 10577</td>
<td>Soil, Louisiana</td>
<td>JN899373</td>
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<td>Penicillium dendriticum</td>
<td>CBS 660.80 = IMI 216897</td>
<td>Leaf litter of Eucalyptus pauciflora, Kosciusko National Park, New South Wales, Australia</td>
<td>JN121714</td>
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<td>Penicillium diversum</td>
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<td>Penicillium duclauxii</td>
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<td>Canvas, France</td>
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<td>Penicillium echinosporum</td>
<td>CBS 293.62 = ATCC 18319 = DSM 2230 = FRR 3411 = IMI 080450 = IMI 101214</td>
<td>Wood pulp, Surrey, Kenley, UK</td>
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<td>Penicillium erythromellis</td>
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<td>Soil from creek bank, Little River, New South Wales, Australia</td>
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<td>Penicillium euglacum</td>
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<td>Penicillium expansum</td>
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<td>Penicillium felleatum</td>
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<td>Penicillium funiculosum</td>
<td>CBS 272.86 = IMI 193019</td>
<td>Lagenaria vulgaris, India</td>
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<td>Penicillium glabrum</td>
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<td><strong>Penicillium herquei</strong></td>
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<td><strong>Penicillium ilerdanum</strong></td>
<td>CBS 168.81T = IJFM 5596 = IMI 253793</td>
<td>Air, Madrid, Spain</td>
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<td><strong>Penicillium isariiforme</strong></td>
<td>CBS 247.56T = ATCC 18425 = IMI 060371 = MUCL 31191 = MUCL 31323 = NRRL 2638</td>
<td>Woodland soil, Zaire</td>
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<td><strong>Penicillium islandicum</strong></td>
<td>CBS 338.48T = ATCC 10127 = IMI 040042 = MUCL 31324 = NRRL 1036</td>
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<td><strong>Penicillium janthinellum</strong></td>
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<td>Root of Camellia sinensis, Indonesia, Java</td>
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<td><strong>Penicillium kewense</strong></td>
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<td><strong>Penicillium korosum</strong></td>
<td>CBS 762.68T</td>
<td>Rhizosphere, India</td>
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<td><strong>Penicillium liani</strong></td>
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<td>Soil, China</td>
<td>JN680280 JN899395</td>
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<td><strong>Penicillium foliense</strong></td>
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<td>Lolium, Palmerston North, New Zealand</td>
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<td><strong>Penicillium mameffei</strong></td>
<td>CBS 388.87T = ATCC 18224 = CBS 334.59T = IMI 068794ii = IMI 068794ii</td>
<td>Rhizomys sinensis (bamboo rat), Vietnam</td>
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<td><strong>Penicillium namylowskii</strong></td>
<td>CBS 353.48T = ATCC 11127 = IMI 040033 = MUCL 29226 = NRRL 1070</td>
<td>Soil under Pinus sp., Puszceza Bialowieska, square &quot;652&quot;, Poland</td>
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<td><strong>Penicillium obtatum</strong></td>
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<td>Spoiled baby food, Sydney, New South Wales, Australia</td>
<td>JN680285 JN899364</td>
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<td><strong>Penicillium ochroalboneum</strong></td>
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<td>Commeal, South Africa</td>
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<td><strong>Penicillium osmophilum</strong></td>
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<td>Agricultural soil, Wageningen, Netherlands</td>
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<td><strong>Penicillium palmae</strong></td>
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<td>Seed, Wageningen, Netherlands</td>
<td>JN680308 JN899336</td>
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<td><strong>Penicillium panamense</strong></td>
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<td>Soil, Barro Colorado Island, Panama</td>
<td>JN899291 JN899362</td>
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<td><strong>Penicillium phialosporum</strong></td>
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<td>Milled Californian rice, California, USA</td>
<td>JN680282 JN899340</td>
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<td>PVC, Centre d'Études du Bouchet, M. Magnoux, France</td>
<td>JN680313 JN899382</td>
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<td><strong>Penicillium pittii</strong></td>
<td>CBS 139.84T = IMI 327871</td>
<td>Clay soil, under poplar trees, bank of Duero River, Valladolid, Spain</td>
<td>JN680274 JN899325</td>
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<td><strong>Penicillium primulinum</strong></td>
<td>CBS 321.48T = ATCC 10438 = CBS 439.88 = FRR 1074 = IMI 040031 = MUCL 31321 = MUCL 31530 = NRRL 1074</td>
<td>USA</td>
<td>JN680298 JN899317</td>
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<td><strong>Penicillium proteolyticum</strong></td>
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<td>Granite soil, Ukraine</td>
<td>JN680292 JN899387</td>
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<td><strong>Penicillium pseudostromaticum</strong></td>
<td>CBS 470.70T = ATCC 18919 = FRR 2039</td>
<td>Feather, near Itasca State Park, Hubbard Co., Minnesota, USA</td>
<td>JN899300 JN899371</td>
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Table 1. (Continued).

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<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 = MUC1 29225 = NRRL 1064 = NRRL 1142</td>
<td>Zea mays, Castle Rock, Virginia, USA</td>
<td>JN680287 JN899381</td>
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<td>Penicillium radicum</td>
<td>CBS 140.64 = CECT 2771 = IMI 202406 = IMI 327870</td>
<td>Air under willow tree, bank of river Duero, Herrera, Valladolid, Spain</td>
<td>JN899386</td>
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<td>Penicillium radicum var. rubisclerotum</td>
<td>CBS 100469 = FRR 4718</td>
<td>Root of seedling of Trillium aestivum, Wagga, New South Wales, Australia</td>
<td>JN899324</td>
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<td>Penicillium rotundum</td>
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<td>Wood, Chinqui Prov., Panama</td>
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<td>Penicillium rubicundum</td>
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<td>Japan</td>
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<td>Penicillium rubinum</td>
<td>CBS 263.93</td>
<td>Bronchoalveolar lavage of immunocompetent female patient with pneumonia by Nocardia</td>
<td>JN899315</td>
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<td>Penicillium rugulosum</td>
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<td>Tuber (Solanum tuberosum), Connecticut, USA</td>
<td>JN880302 JN899374</td>
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<td>Penicillium sabulosum</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 137.64 = CECT 2772 = IMI 282404 = IMI 327872</td>
<td>Fruit, damaged by insect, Valladolid, Spain</td>
<td>JN880273 JN899369</td>
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<td>Penicillium shearii</td>
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<td>Soil, Tela, Honduras</td>
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<td>Penicillium siamense</td>
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<td>Forest soil, Lampaing, Thum District, Ban Daen, Tharn, 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>Rotting wood, Louisiana, USA</td>
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<td>Peaty forest soil, Eastern Transvaal, South-Africa</td>
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<td>Penicillium tularense</td>
<td>CBS 378.48 = ATCC 10503 = IMI 040034 = NRRL 1073</td>
<td>Dead twig, France</td>
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<td>Penicillium tularense</td>
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<td>Soil, under Pinus ponderosa and Quercus kelloggi, Tulare Co., Pine Flat, California, USA</td>
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<td>Penicillium variabile</td>
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<td>Cocos fibre, Johannesburg, South Africa</td>
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<td>Penicillium varians</td>
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<td>Penicillium verruculosum</td>
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<td>Penicillium victoriae</td>
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<td>Penicillium viridicatum</td>
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<td>Phialosimplex caninus</td>
<td>CBS128032 = UAMH 1033</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>
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<td>Phialosimplex sclerotis</td>
<td>CBS 366.77 = IAM 1479</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>
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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>
<td>JN121556</td>
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<td>Rasamsonia byssochlamyoides</td>
<td>CBS 413.71T = I1 11604</td>
<td>Dry soil under Douglas fir, Oregon, USA</td>
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<td>Rasamsonia emersonii</td>
<td>CBS 393.64T = DTO 481T = IBT 21695 = ATCC 16479 = IMI 116815 = IMI 116815i</td>
<td>Compost, Italy</td>
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<td>Sagenoma viride</td>
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<td>Soil, Australia</td>
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<td>Sagenomella bohemica</td>
<td>CBS 545.86T = CCF 2330 = IAM 14789</td>
<td>Peloids for balneological purposes, Frantiskovy Lázne Spa, West Bohemia, Czech Republic</td>
<td>JN121699 JN899400</td>
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<td>Sagenomella diversispora</td>
<td>CBS 398.69</td>
<td>Forest soil under <em>Populus tremuloides</em>, Petawawa, Ontario, Canada</td>
<td>JN121673</td>
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<td>Sagenomella griseoviridis</td>
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<td>Sagenomella humicola</td>
<td>CBS 427.67T = ATCC 18506 = IMI 113166</td>
<td>Forest soil under <em>Thuja occidentalis</em>, Ontario, Canada</td>
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<td>Sagenomella striatiispora</td>
<td>CBS 429.67T = ATCC 18510 = IMI 113163</td>
<td>Soil, Guelph, Ontario, Canada</td>
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<td>Sagenomella verticillata</td>
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<td>Gymnosperm forest soil, Sweden</td>
<td>JN680307</td>
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<td>Sclerocleista ornata</td>
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<td>T alaromyces assiutensis</td>
<td>CBS 118440</td>
<td>Soil, Fes, Morocco</td>
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<td>T alaromyces austrocalifornicus</td>
<td>CBS 644.95T = I1 17522</td>
<td>Soil, campus Univ. South California, Los Angeles, USA</td>
<td>JN899323</td>
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<td>T alaromyces bacillisporus</td>
<td>CBS 296.48T = ATCC 10126 = IMI 040045 = NRRL 1025</td>
<td>Begonia leaf, New York City, New York, USA</td>
<td>JN121634 JN899329</td>
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<td>T alaromyces barcinensis</td>
<td>CBS 649.95T = I1 17518</td>
<td>Soil, Barcelona, Spain</td>
<td>JN680318 JN899349</td>
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<td>T alaromyces brevicompactus</td>
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<td>Moulded vegetables, Prov. Sechuan, Wolong, China</td>
<td>JN680326</td>
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<td>T alaromyces convolutus</td>
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<td>Soil, Kathmandu, Nepal</td>
<td>JN121553 JN899330</td>
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<td>T alaromyces cyanescens</td>
<td>CBS 114900 = FMR 8388</td>
<td>Tortosa, Catalina, Spain</td>
<td>JN899391</td>
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<td>T alaromyces denxii</td>
<td>CBS 412.89T = NHL 2961</td>
<td>Cultivated soil, Okayama Prefecture, Kurashiki City, Higashihommii, Japan</td>
<td>JN899327 JN899326</td>
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<td>T alaromyces emodensis</td>
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<td>Soil, Kathmandu, Nepal</td>
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<td>T alaromyces flavus</td>
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<td>Unknown substrate, New Zealand</td>
<td>JN121639 JN899360</td>
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<tr>
<td>T alaromyces galapagensis</td>
<td>CBS 751.74T = IFO 31796</td>
<td>Shaded soil under Maytenus obovata, Isla Santa Cruz, Galapagos Islands, Ecuador</td>
<td>JN680321 JN899358</td>
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<tr>
<td>T alaromyces gossypii</td>
<td>CBS 645.80T = FRR 1966 = IMI 198365</td>
<td>Gossypium, India</td>
<td>JN680317 JN899334</td>
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<tr>
<td>T alaromyces helicus var. boninensis</td>
<td>CBS 650.95T = I1 17516</td>
<td>Lawn soil, Kominato, Chichijima, Ogasawara-mura, Tokyo-to, Japan</td>
<td>JN680319 JN899356</td>
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<td>T alaromyces helicus var. helicus</td>
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<td>Soil, Sweden</td>
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<td>T alaromyces helicus var. major</td>
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<td>T alaromyces indigoticus</td>
<td>CBS 100534T = I1 17590</td>
<td>Soil, Nagasaki-ken, Minamikushiyma-mura, Japan</td>
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<tr>
<td>T alaromyces intermedius</td>
<td>CBS 152.66T = BDUN 267 = IFO 31792 = IMI 100874</td>
<td>Alluvial pasture and swamp soil, Attenborough, Nottingham, England</td>
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Table 1. (Continued).

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<td>Apple juice, Stellenbosch, South Africa</td>
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<td>Talaromyces mimosinus</td>
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<td>Soil from creek bank, Nattai River, New South Wales, Australia</td>
<td>JN899302</td>
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<tr>
<td>Talaromyces muroii</td>
<td>CBS 756.96 = PF 1153</td>
<td>Soil, Huaiilen County, Chingpu, Taiwan</td>
<td>JN680322</td>
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<td>Talaromyces occid</td>
<td>CBS 102855</td>
<td>Heat-treated soil from forest of Pinus hartwegii, Veracruz, Mexico</td>
<td>JN680327</td>
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<td>Talaromyces ohiensis</td>
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<td>Soil treated with cyanamide, Germany</td>
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<td>Copse soil, Hadajima, Ogasawara-mura, Tokyo-to, Japan</td>
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<td>Talaromyces thermophilus</td>
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<td>Parthenium argentatum, decaying plant; California, USA</td>
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<td>Thermoascus crustaceus</td>
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<td>Trichomycota paradoxoida</td>
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<tr>
<td>Thermomyces thermophilus</td>
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<td>Unknown source, Hachijō, Japan</td>
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<td>Trichomyces Hallii</td>
<td>CBS 788.83</td>
<td>Rotting stump of cut down tree, Myojji Temple near Hakui Noto Park, Ishikawa Pref., Japan</td>
<td>JN121718</td>
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<td>Warcupiella spinulosa</td>
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<td>Jungle soil, Berakas-Mura, Brunei</td>
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</table>

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 occid, T. luteus, T. thermophilus, T. eburneus, T. emersonii, T. byssochlamydoides, T. spectabilis, T. brevicompactus, T. striatus and T. leycettanus. Talaromyces occid 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.
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 talathermophils 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. 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).](image-url)
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. ochrocinereum*. 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’), *Paeilomyces aeruginus* (CBS 350.66’), *Geosmithia viridis* (CBS 252.87’) and *Sagenomella viride* (CBS 114.72’). The former three strains are on a well-supported sister clade basal to *Talaromyces murroi* CBS 756.96.
Species delimitation and synonymsies 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 nonribosomal peptides and terpenes, it is obvious that *Talaromyces* species produce many biosynthetic families, but share more in concordance with the phylogenetic and taxonomic treatment of subgenus *Biverticillum*. 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. brasiliennum* (Frisvad 1989).

**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 *Biverticillum*, but included species such as *P. citrinum* (as *P. aurifilum*), *P. atramentosum* etc., which are no longer regarded as members of this subgenus (Houbraken et al. 2010). The characteristic lanceolate or acerose phialides were used as a more definitive morphological character of subgenus *Biverticillum* and related *Talaromyces* amanorphs (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-Symmetica* 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. fuscumoseum* 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 *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 pseustudiosus* (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, penisimpilsins, penisimpilcissins 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. brasiliennum* (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).
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 Biverticillum. 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 786.83), 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. ochi 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

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**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.

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<table>
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<th>Secondary metabolite (exometabolite) biosynthetic families</th>
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<td>Rasfomin</td>
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<td>Anthglutin</td>
<td>4-Hydroxy-4,5-dicarboxy pentadecanoic acid (T. spiculiporus)</td>
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<td>Rugulosina &amp; flavoskyrin * (others)</td>
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<td>3-Hydroxyethyl-6,8-dimethylcoarin</td>
<td>Rugulotosins</td>
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<tr>
<td>Asperpenamates &amp; asperglaucid * (A, P)</td>
<td>3-Hydroxyphiatic acid * (P)</td>
<td>Rugulosuvine * (P)</td>
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<tr>
<td>Atroventerin methyl acetal (P. verruculosum)</td>
<td>Islandic acids</td>
<td>Rugulovasines * (P)</td>
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<td>Epi-Austidiol (7-epiaustidiol &amp; 8-O-methylepiastidiol)</td>
<td>(+)-Iositoic acid + Decylic acid (T. spiculiporus)</td>
<td>Secalonic acids * (A, P, others)</td>
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<td>Maculosin * (others)</td>
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<tr>
<td>Helicinins</td>
<td>Puractins (= penicillides = vermoxicins)</td>
<td>Wortmannins * (others)</td>
<td></td>
</tr>
<tr>
<td>Herqueinones * (P)</td>
<td>Purpuride</td>
<td>Xanthoradones</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Zeorins * (A, others)</td>
<td></td>
</tr>
</tbody>
</table>
Sagenomella sp., and thus the new combination Sagenomella ocuti is proposed in the taxonomy section below.

Our analysis confirms the distinctiveness of the recently described genus Rasasomia 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. byssoschlamydoides 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 thermotrichus (as ‘Thermotrichum’) 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 Byssoschlamys and showed that it is the teleomorph of Paec. varioti. In a single name system, Paec. varioti 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. leycettanuus 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. leycettanuus 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. leycettanuus 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. leycettanuus in Hamigera and Talaromyces, respectively. A thorough study on Hamigera and related genera is needed to clarify the correct placement of these species. Kong (1999) described Talaromyces brevicompactus, stating that this species is closely related to Hamigera avellanea (as Talaromyces avellaneus). The anamorph of this species was described in Merimbla, thus confirming the relationship with Hamigera. Sequence comparisons of this species showed that it is similar to NRRL 2108, a phylogenetically undescribed Hamigera species (J. Houbraken, unpubl. data, Peterson et al. 2010). We wait with combining this species in Hamigera until a more data and strains become available.

**Species described in other genera but phylogenetically within Talaromyces**

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

Houbraken & Samson (2011) discussed the confusion over Aphanoascus cinnabarinus, which has persisted since the description of the genus Aphanoascus by Zukal (1890). Most authors follow Apinis (1968) and consider the genus Aphanoascus to be typified by A. fulvescens Zukal. In addition, the neotypification of A. cinnabarinus by Udagawa & Takada (1973) was incorrect, because their neotype strain had a Paecilomyces anamorph, whereas Zukal’s original description and illustrations clearly showed a Chrysosporium-like anamorph (Stolk & Samson 1983). Based on morphological features, Stolk & Samson (1983) indicated that Chromocleista cinnabrina (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. cinnabrina belongs to Talaromyces s. str. The taxonomic position of Chromocleista cinnabrina (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 ascocoma similar to those of other *Talaromyces* species and the main ubiquinone systems are Q-10 and Q-10 (H2), also indicating a relationship with other *Talaromyces* species (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* Dunie & Mont., which is conspecific with *Penicillium aureocephalum* Munt.-Cvte., 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.

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

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

*Penicillium Link subgenus Biverticillium Dierckx apud Bourge Cellule 33: 31. 1923.*

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 ascus 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, and then with the whole conidiophore appearing asymmetrical), each metula with a terminal whorl of phialides. *Conidigenous cells* phialidic, aculeate or acerose, rarely ampulliform, periclinal thickening usually visible in the conidigenous aperture, with or without a cylindrical collarate. *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**


*Penicillium apiculatus* Samson, Yilmaz & Frisvad, **sp. nov.** MycoBank MB560641.
Penicillo aculeato simile, sed conidios apiculatis distinguetur.

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


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


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


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


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


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

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


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

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


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


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


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

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


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 & Frisvad, ined.

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


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

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

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.


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


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

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


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

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

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

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. 

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

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

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

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

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

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

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

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

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

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 tardificaciens 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.

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

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 synonynous 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 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. brevicompectus 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 bysschlamydoides Stolk & Samson (simultaneously published, same holotype).
≡ Rasamsonia bysschlamydoides (Stolk & Samson) Houbraken & Frisvad, Ant. van Leeuwenhoek, in press.


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


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* Subrah. & Gopalkr., Ind. Bot. Reporter 35: 35. 1984 (as ‘*T. thermocitrinus*’).

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.


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).

**ACKNOWLEDGEMENTS**

We are appreciative of discussions with Dave Malloch, and contributions by Ellen Hoekstra in the early years of this project. Cubus Visagie (South Africa) and Xavier Llimona (Spain) allowed us to access unpublished data on *P. aureoscelaphum* and the genus *Lasiodermia*. We are also grateful for nomenclatural advice received from Scott Redhead and Uwe Braun. We also thank Sung-Yuan Hsieh for providing the ITS sequence and the culture of *Penicillium albobicverticillium*.

**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


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 Houbraken & 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. puterillii*, belong to the Bionectriaceae, Hypocreales. Similar results were obtained using ITS sequences by Kolačić et al. (2004), using LSU sequences by Schroers et al. (2005) and then multigene phylogenies by Kolačić & 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., Handbucht allg. Mykol.: 76. 1851.

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

Note: *Hormodendrum* 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.


**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*.


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

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

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

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

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

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

**Type species:** *R. candidus* Cordy 1837 Type species: *Penicillium leucoceaphalum* Rabenh. 1844.

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


*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**


