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

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**Abstract**: Species of *Trichocomaceae* occur commonly and are important to both industry and medicine. They are associated with food spoilage and mycotoxin production and can occur in the indoor environment, causing health hazards by the formation of β-glucans, mycotoxins and surface proteins. Some species are opportunistic pathogens, while others are exploited in biotechnology for the production of enzymes, antibiotics and other products. *Penicillium* belongs phylogenetically to *Trichocomaceae* and more than 250 species are currently accepted in this genus. In this study, we investigated the relationship of *Penicillium* to other genera of *Trichocomaceae* and studied in detail the phylogeny of the genus itself. In order to study these relationships, partial RPB1, RPB2 (RNA polymerase II genes), Tar1 (putative ribosome biogenesis protein) and Cct8 (putative chaperonin complex component TCP-1) gene sequences were obtained. The *Trichocomaceae* are divided in three separate families: *Aspergillaceae*, *Thermoascaceae* and *Trichocomaceae*. The *Aspergillaceae* are characterised by the formation flask-shaped or cylindrical phialides, asci produced inside cleistothecia or surrounded by Hülle cells and mainly ascosporas with a furrow or slit, while the *Trichocomaceae* are defined by the formation of lanceolate phialides, asci borne within a tuft or layer of loose hyphae and ascosporas lacking a slit. *Thermoascus* and *Paeilomyces*, both members of *Thermoascaceae*, also form ascospores lacking a furrow or slit, but are differentiated from *Trichocomaceae* by the production of ascii from croziers and their thermotolerant or thermophilic nature. Phylogenetic analysis shows that *Penicillium* is polyphyletic. The genus is re-defined and a monophyletic genus for both anamorphs and teleomorphs is created (*Penicillium* sensu stricto). The genera *Thyssanophora*, *Eupenicillium*, *Chromocleista*, *Hemicarpenteles* and *Torulomyces* belong in *Penicillium* s. str. and new combinations for the species belonging to these genera are proposed. Analysis of *Penicillium* below genus rank revealed the presence of 25 clades. A new classification system including both anamorph and teleomorph species is proposed and these 25 clades are treated here as sections. An overview of species belonging to each section is presented.

**Key words**: *Aspergillus*, *Eupenicillium*, nomenclature, *Penicillium*, *Talaromyces*, taxonomy.

**Taxonomic novelties**: New sections, all in *Penicillium*: sect. *Sceliotrema* Houbraken & Samson, sect. *Charlesia* Houbraken & Samson, sect. *Thyssanophora* Houbraken & Samson, sect. *Cinamnoporpurne* Houbraken & Samson, sect. *Trichocomaceae* Houbraken & Samson, sect. *Citrina* Houbraken & Samson, sect. *Trichocomaceae* Houbraken & Samson, sect. *Paradoxa* Houbraken & Samson, sect. *C漼esenta* Houbraken & Samson.

**New combinations**: *Penicillium asymmetricum* (Subramanian & Sudha) Houbraken & Samson, *P. boviiformum* (Tuhlil & Frisvad) Houbraken & Samson, *P. glaucoalbidum* (Desmazières) Houbraken & Samson, *P. lavee* (K. Ando & Manochn) Houbraken & Samson, *P. longisporum* (Kendrick) Houbraken & Samson, *P. malalchemiun* (Yaguchi & Udawg) Houbraken & Samson, *P. saturniforme* (Wang & Zhuang) Houbraken & Samson, *P. taiwenense* (Matsushima) Houbraken & Samson.

**New names**: *Penicillium confenophilum* Houbraken & Samson, *P. henneni* Houbraken & Samson, *P. melanosiotpe* Houbraken & Samson, *P. porphyreum* Houbraken & Samson.

**INTRODUCTION**

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

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

*Penicillium* is an anamorph genus and belongs phylogenetically to *Trichocomaceae* (Berbee 1995, Peterson 2000a). The name *Penicillium* is derived from *penicillus*, which means "little brush" and was introduced by Link in 1809. Many new species were described in the 19th century, and Dierckx (1901) was the first researcher who introduced a subgeneric classification system for the genus.
He proposed the subgenera Aspergilloides, Biverticillium and Eupenicillium and Biourge (1923) followed Dierckx’s classification system and expanded it with two sections, four series and six subsections. Thom (1930: 155–159) did not accept Dierckx’s and Biourge’s subgeneric classification system and introduced a new system with four divisions (subgenera), 12 sections and 18 subsections (series). His system was mainly based on colony characteristics and conidiophore branching and the monographs of Raper & Thom (1949) and Ramirez (1982) are in line with that of Thom (1930). Pitt (1980) did not follow Thom’s concept and, based on conidiophore characters, phialide shapes and growth characteristics, divided Penicillium into four subgenera, 10 sections and 21 series. In addition, he treated Eupenicillium separately from Penicillium and subdivided the former genus into eight series. In 1985, Stolk & Samson proposed another taxonomic scheme for Penicillium anamorphs and this classification was primary based on phialide shape and conidiophore branching. They divided Penicillium in 10 sections and 18 series and this taxonomic scheme treated strict anamorphs, as well as anamorphs of sexual Penicillium species. More recently, Frisvad & Samson (2004) studied subgenus Penicillium and five sections and 17 series were recognised.

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

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

Pleomorphism in fungi was first demonstrated by Tulasne (1851). Together with his discovery, he was already aware of the problem raised by the nomenclature of composite species and he stated that the imperfect forms must someday be submerged in the Ascomycota. He thus established a first principle of pleomorphic nomenclature and suggested the precedence of the perfect state name over imperfect names (Hennebert 1971).

In 1910, “dual nomenclature” was introduced and this was established in the International Code of Botanical Nomenclature (ICBN). The problem of naming fungi that exhibit pleomorphic life cycles was addressed in previous versions of article 59 of the ICBN and implied that more than one name for a single taxon can be used (Cline 2005). Recently, the proposal to revise article 59 was accepted at the 2011 IBC Nomenclature Section at Melbourne and the principle of “one fungus : one name” was established (Norvell et al. 2011).

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

MATERIAL AND METHODS

Strains

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

DNA extraction, amplification and sequencing

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

| CBS no. | Name                                      | Other collections | Origin                  | GenBank accession or reference |
|---------|-------------------------------------------|-------------------|-------------------------|-------------------------------|
| CBS 267.72NT | Aphanoascus cinnabarinus*                  | ATCC 26215        | Soil, Japan             | JN121625                      |
| CBS 172.66NT | Aspergillus aculeatus*                    | ATCC 16872 = IMI 211388 | Tropical soil           | JN121590                      |
| CBS 600.67NT | Aspergillus amylovorus*                   | ATCC 18351 = IMI 129961 = MUCL 15648 | Wheat starch, Kharkiv, Ukraine | JN121705                      |
| CBS 463.65NT | Aspergillus arenarius*                    | ATCC 16830 = IMI 055632 = IMI 055632ii | Soil, Mysore, Karnataka, India | JN121684                      |
| CBS 653.74NT | Aspergillus aureofulgens*                 | ATCC 1002 = IMI 091889 = NRRL 303 | Unknown source           | JN121702                      |
| CBS 109.46NT | Aspergillus avenaceus*                    | ATCC 16681 = IMI 016140 = NRRL 517 | Seed of Pisum sativum (pea), England, UK | JN121565                      |
| CBS 468.65NT | Aspergillus biplanus*                     | ATCC 16858 = IMI 235602 | Soil, Tilaran, Costa Rica | JN121685                      |
| CBS 566.65NT | Aspergillus candidus*                     | ATCC 16816 = IMI 107684 | Soil, West Malaysia, Malaysia | JN121595                      |
| CBS 473.65NT | Aspergillus clavatoflavus*                | ATCC 16686 = IMI 124037 | Rain forest soil, Tully, Queensland, Australia | JN121686                      |
| CBS 707.71NT | Aspergillus clavatus**                    | NRRL 1 (= ATCC 1007 = CBS 513.65 = IMI 19549) | Unknown source           | Fedorova et al. (2008)        |
| CBS 127.61NT | Aspergillus brunneouniseriatus*           | ATCC 16916 = IMI 227677 | Soil under Dalbergia sissio, India | JN121579                      |
| CBS 121611 | Aspergillus calidoustus*                  | ATCC 16796 = IMI 135421 | Forest soil, Palm, Province of Puntarenas, Costa Rica | JN121688                      |
| CBS 553.77NT | Aspergillus coremiformis*                 | ATCC 38576 = 223069 | Soil, Ivy Coast         | JN121700                      |
| CBS 656.73NT | Aspergillus egyptiacus*                   | IMI 141415        | Sandy soil, under Olea europaea (olive tree), Mediterranean Coast, Ras-el-Hikma, Egypt | JN121713                      |
| CBS 128202 | Aspergillus flavus/                        | NRRL 3357 (= ATCC 200026) | Peanut cotyledons, USA | Unpublished                    |
| CBS 118.45NT | Aspergillus fumigatus/                    | A293              | Patient with invasive aspergilosis | Nierman et al. (2005)         |
| CBS 116.56NT | Aspergillus funiculosus*                  | ATCC 16846 = IMI 054397 = IMI 054397ii | Soil, Ibadan, Nigeria | JN121572                      |
| CBS 118.45NT | Aspergillus janus*                       | ATCC 16835 = IMI 016065 = IMI 016065ii = MUCL 31307 = NRRL 1787 | Soil, Panama             | JN121576                      |
| CBS 538.65NT | Aspergillus kanagawaensis*                | ATCC 16143 = IMI 126690 | Forest soil under Pinus banksiana, Wisconsin, USA | JN121698                      |
| CBS 151.66NT | Aspergillus leporis*                      | ATCC 16490        | Dung of Lepus townsendi (white-tailed Jackrabbit), near Saratoga, Wyoming, USA | JN121589                      |
| CBS 513.88 | Aspergillus niger*                        | ATCC 16143 = IMI 126690 | Forest soil under Pinus banksiana, Wisconsin, USA | JN121598                      |

*Other collections refer to cultures deposited in the Centraalbureau voor Schimmelcultures (CBS), Nederland; the American Type Culture Collection (ATCC), Rockville, Maryland, USA; the Deutsche Sammlung von Mikroorganismen und Zellkulturen (DSM), Braunschweig, Germany; the Japan Culture Collection Center (JCM), Tokyo, Japan; the Institute of Microbial Chemistry (IMC), Tokyo, Japan; and the National Collection of Industrial Bacteria (NCIB) and the National Collection of Industrial Fungi (NCIIF), York, UK.**
| CBS no. | Name                          | Other collections    | Origin                                           | GenBank accession or reference† |
|--------|-------------------------------|----------------------|-------------------------------------------------|---------------------------------|
| CBS 101887 | *Aspergillus ochraceoroseus* | ATCC 42001 = IBT 14580 | Soil, Tai National Forest, Ivory Coast          | JN121557 JN121416 JN121723 JN121871 |
| CBS 108.08^t | *Aspergillus ochraceus* | ATCC 1008 = CBS 547.65 = IMI 016247 = IMI 016247iv = IMI 016247ivv = NRRRL 1642 = NRRRL 398 | Unknown source                 | JN121562 JN121421 JN121728 JN121875 |
| CBS 622.67^t | *Aspergillus penicilloformis* | ATCC 18328 = IMI 129968 = IMI 132431 | Soil under Nicotiana tabacum, Moldavia, Romania | JN121708 JN121542 JN121848 JN121934 |
| CBS 130294 | *Aspergillus penicilloides* | DTO 11C3            | Indoor environment, Germany                     | JN121578 JN121437 JN121744 JN121886 |
| CBS 578.65^t | *Aspergillus pulvinus* | ATCC 16842 = IMI 139628 | Forest soil, Liberia, Province of Guanacaste, Costa Rica | JN121703 JN121536 JN121842 JN121930 |
| CBS 117.33^t | *Aspergillus restrictus* | ATCC 16912 = CBS 541.65 = IMI 016267 = MUCL 31313 = NRRRL 154 = NRRRL 4155 | Cloth, UK                        | JN121574 JN121432 JN121740 JN121884 |
| CBS 649.93^t | *Aspergillus robustus* | CBS 428.77 = IBT 14305 | Surface soil from thorn-forest, near Mombasa, Kenya | JN121711 JN121544 JN121850 JN121935 |
| CBS 139.61^t | *Aspergillus sparsus* | ATCC 16851 = IMI 016394 = IMI 016394i = MUCL 31314 = NRRRL 1933 | Soil, Costa Rica                 | JN121586 JN121444 JN121751 JN121891 |
| CBS 112812^t | *Aspergillus steynii* | IBT 23096            | Dried arabica green coffee bean, on parchment, internal infection, Chamumadeshuran Estata, Kamataka, district Girs, India | JN121569 JN121428 JN121735 JN121880 |
| CBS 264.81 | *Aspergillus sydowi* | NIH 2624            | Grains and milling fractions, Triticum aestivum, India | JN121624 JN121476 JN121782 JN121902 |
| CBS 272.89 | *Aspergillus togoensis* | NRRL 13550          | Clinical isolate, unpublished                    | JN121627 JN121480 JN121785 JN121904 |
| CBS 245.65 | *Aspergillus versicolor* | ATCC 11730 = ATCC 16020 = IMI 045554 = IMI 045554ii = IMI 045554iii = IMI 045554iv = MUCL 19008 | Cellophane, Indiana, USA          | JN121614 JN121468 JN121775 JN121899 |
| CBS 104.07^nt | *Aspergillus wentii* | ATCC 1023 = IMI 017295 = IMI 017295ii = NRRRL 1269 = NRRRL 375 | Soybeans, Java, Indonesia          | JN121559 JN121418 JN121725 JN121873 |
| CBS 506.65^nt | *Aspergillus zonatus* | ATCC 16867 = IMI 124936 | Forest soil, Province of Linon, Fortuna, Costa Rica | JN121691 JN121526 JN121832 JN121921 |
| CBS 380.74^t | *Basipetospora halophilica* | IFO 9650            | Undaria pinnatifida (Wakame), Osaka, Japan       | JN121666 JN121509 JN121815 JN121910 |
| CBS 100.11^nt | *Byssoclamys nivea* | ATCC 22260          | Unknown source                                  | JN121511 JF417414 JF417381 JF417514 |
| CBS 101075^t | *Byssoclamys spectabilis* | ATCC 90900 = FRR 5219 | Heat processed fruit beverage; Tokyo Japan        | JN121554 JF417446 JF417412 JF417546 |
| CBS 605.74^t | *Byssoclamys verrucosa* | ATCC 34163          | Nesting material of Leipoa occellata (Malleefowl), Pulletop Nature Reserve, New South Wales, Australia | JN680311 JN121540 JN121746 JN121932 |
| CBS no. | Name                        | Other collections | Origin                                      | GenBank accession or reference | RPB1   | RPB2   | Ts1    | Cct8    |
|---------|-----------------------------|-------------------|---------------------------------------------|--------------------------------|--------|--------|--------|--------|
| CBS 132.31* | Chrysosporium inops* | IMI 096729 = UAMH 802 | Skin man, Italy                           | JN121584                      | JN121443 | JN121750 | JN121890 |
|          | Coccidioides immitis**     | Strain "RS"       | Vaccine strain - origin unknown          | Sharpton et al. (2009)       |        |        |        |        |
| CBS 525.83* | Cristaspora arxii*        | ATCC 52744 = FMR 416 | Soil, Taragona, Spain                     | JN121695                      | JN121529 | JN121835 | JN121924 |
| CBS 157.66* | Dichotomomycyes caespit*  | FGSC A4 (= ATCC 38163 = CBS 112.46) | Orchard soil, near Tiraspol, Moldova | JN121589                      | JN121447 | JN121754 | JN121984 |
| CBS 229.60* | Eupenicillium hirayamae*   | ATCC 18312 = IMI 078255 = IMI 078255i = NRRL 143 | Milled rice, Thailand              | JN121604                      | JN121459 | JN121766 | JN121946 |
| CBS 518.65* | Eurotium amstelodami*     | ATCC 16464 = IMI 229971 = NRRL 90 | Unknown substrate                        | JN121694                      | JN121528 | JN121834 | JN121923 |
| CBS 516.65* | Eurotium herbariorum*     | ATCC 16469 = IMI 211363 = NRRL 116 | Unpainted board, Washington, USA          | JN121693                      | JN121527 | JN121833 | JN121922 |
| CBS 260.73* | Fennelia flavipes*        | ATCC 24484 = IMI 171883 = NRRL 5504 | Cellulose material buried in forest soil, Pak Thong Chai, Thailand | JN121623                      | JN121475 | JN121781 | JN121901 |
| CBS 252.87* | Geosmithia viridis*       | IMI 288716        | Soil; bank of creek flowing into Little River; New South Wales; Australia | JN121620                      | JF417422 | JF417389 | JF417522 |
| CBS 296.48* | Hamigera avellanea*       | ATCC 10414 = IMI 040230 = NRRL 1938 | Soil; San Antonio, Texas, USA             | JN121632                      | JF417424 | JF417391 | JF417524 |
| CBS 377.48* | Hamigera striata*         | ATCC 10501 IMI 039741 = NRRL 717 | Canned blueberries, USA                  | JN121665                      | JN121508 | JN121814 | JN121909 |
| CBS 527.65* | Hemicarpenteles paradoxus* | ATCC 16919 = IMI 061446 = NRRL 2162 | Dung of Opossum, Wellington, New Zealand | JN121696                      | JN121530 | JN121836 | JN121989 |
| CBS 607.74* | Leiothecium ellipsosideum* | ATCC 32453        | Soil, between rocks, Mystras, Peloponnesos, Greece | JN121707                      | JN121541 | JN121847 | JN121933 |
| CBS 109402* | Monascus argentinensis*   | FMR 7393          | Soil sample, El Infemil, Taf del Valle, Tucumán province, Argentina | JN121564                      | JN121423 | JN121730 | JN121877 |
| CBS 113675 | Monascus lunisporas*      | FMR 6679          | Soil sample, Corcovado Mountain, Tijuca National Park, Rio de Janeiro, Brazil | JN121570                      | JN121429 | JN121736 | JN121881 |
| CBS 109.07* | Monascus purpureus*       | ATCC 16365 = ATCC 16426 = IMI 210765 = NRRL 1596 | Fermented rice grain, 'ang-quaç' (purple coloured rice), Kagok-Tegal, imported from China, Prov. Quoan-toung, Java, Indonesia | JN121563                      | JN121422 | JN121729 | JN121876 |
| CBS 558.71* | Neocarpenteles acanthosporum* | ATCC 22931 = IMI 164621 | Soil, Bougainville Island, Solomon Islands | JN121701                      | JN121534 | JN121840 | JN121928 |
|          | Neosartorya fischeri*     | NRRL 181          | Canned fruit                               | JN121657                      | JN121502 | JN121808 | JN121907 |
| CBS 350.66* | Paecilomyces aerugineus*  | IMI 105412        | Debris of Glyceria maxima, Attenborough, Notts., UK | JN121657                      | JN121502 | JN121808 | JN121907 |
| CBS 761.68 | Penicilliaopsis clavaniformis* | CSIR 1135   | Unknown source, Pretoria, South Africa     | JN121716                      | JN121549 | JN121855 | JN121940 |
| CBS 246.67* | Penicillium abidjanum**   | ATCC 18385 = FRR 1156 = IMI 136244 | Savannah soil, near Abidjan, Ivory Coast | JN121615                      | JN121469 | JN121777 | JN121954 |
| CBS 209.28* | Penicillium adametzii**   | ATCC 10407 = IMI 039751 = MUCL 29106 = NRRL 737 | Soil under conifers, Poznan, Poland | JN121598                      | JN121455 | JN121762 | JN121944 |
Table 1. (Continued).

| CBS no. | Name | Other collections | Origin | GenBank accession or reference |
|---------|------|-------------------|--------|-------------------------------|
| CBS 317.67HT | *Penicillium alutaceum* | ATCC 18542 = FR 1158 = IFO 31729 = IMI 136243 | Soil, near Pretoria, South Africa | JN121641 JN121489 JN121795 JN121968 |
| CBS 220.66HT | *Penicillium arenicola* | ATCC 18321 = ATCC 18330 = IMI 117056 = NRRL 3392 | Soil from pine forest, Kiev, Ukraine | JN121601 JN121457 JN121764 JN121897 |
| CBS 241.56HT | *Penicillium atrovenetum* | ATCC 13352 = FRR 2571 = IFO 8138 = IMI 061837 | Soil, Sussex Downs, England | JN121614 JN121467 JN121774 JN121953 |
| CBS 299.48HT | *Penicillium camemberti* | ATCC 1105 = IMI 028260 = MUCL 29169 = NRRL 910 | French Camembert cheese, Connecticut, USA | JN121635 JN121484 JN121790 JN121963 |
| CBS 300.48HT | *Penicillium canescens* | ATCC 10419 = IMI 026260 = MUCL 29196 = NRRL 910 | Soil, England | JN121636 JN121485 JN121791 JN121964 |
| CBS 233.81 | *Penicillium caperatum* | FRR 71 = IMI 216895 | Neotype of E. brefeldianum | JN121610 JN121465 JN121772 JN121952 |
| CBS 352.67HT | *Penicillium catenatum* | ATCC 18543 = IMI 136241 | Desert soil, Upington, Cape Province, South Africa | JN121659 JN121504 JN121810 JN121980 |
| CBS 304.48T | *Penicillium charlesi* | ATCC 8730 = CBS 342.51 = IMI 040232 = NRRL 1887 = NRRL 778 | Unknown source, UK | JN121637 JN121486 JN121792 JN121965 |
| CBS 306.48T | *Penicillium chrysogenum* | ATCC 10106 = FR 807 = IBT 5233 = IMI 024314 = IMI 092208 = MUCL 29079 = MUCL 29145 = NRRL 807 = NRRL 810 | Cheese, Storrs, Connecticut | JN121638 JN121487 JN121793 JN121966 |
| CBS 490.66 | *Penicillium cinnamopurpureum* | ATCC 18337 = IMI 114483 | Moldy cantaloupe | Wisconsin 54-1255 van den Berg et al (2008) |
| CBS 258.29T | *Penicillium citreonigrum* | ATCC 48736 = 002209 = MUCL 28648 = MUCL 29062 = MUCL 29116 = NRRL 761 | Rotten stem, Belgium | JN121622 JN121474 JN121780 JN121957 |
| CBS 139.45T | *Penicillium citrinum* | ATCC 1109 = IMI 091961 = MUCL 29781 = NRRL 1841 | Unknown | JN121585 JF417416 JF417383 JF417516 |
| CBS 232.38 | *Penicillium citrinum* | Thom 4733.73 | Type of P. implicatum; unknown source, Belgium | JN121608 JN121463 JN121770 JN121950 |
| CBS 119387T | *Penicillium coffaea* | IBT 27866 = NRRL 35363 | Peduncle, Coffea arabica, Oahu, Hawaii, USA | JN121577 JN121436 JN121743 JN121862 |
| CBS 231.38 | *Penicillium corylophilum* | ATCC 10452 = IFO 7726 = IMI 039817 = NRRL 872 | Type of P. humuli; Humulus lupulus (hops), Weihenstephan, Germany | JN121606 JN121461 JN121768 JN121948 |
| CBS 271.89T | *Penicillium cryptum* | ATCC 60138 = IMI 296794 = NRRL 13460 | Soil from Quercus-Betula forest, Hemplestead Lake State Park, Long Island, New York | JN121626 JN121478 JN121784 JN121958 |
| CBS no. | Name                      | Other collections | Origin                                                                                                                                                                                                 | GenBank accession or reference |
|--------|---------------------------|-------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------|
| CBS 660.80² | *Penicillium dendriticum* | IMI 216897        | Leaf litter of Eucalyptus pauciflora, Kosciusko National Park, New South Wales, Australia                                                                                                                 | JN121714 JN121547 JN121853 JN121938 |
| CBS 112082³ | *Penicillium digitatum*   | IBT 13068         | Citrus limon, Italy                                                                                                                                                                                     | JN121567 JN121426 JN121733 JN121858 |
| CBS 456.70² | *Penicillium dimorphosporum* | ATCC 22783 = ATCC 52501 = FRR 1120 = IMI 140680 | Mangrove swamp soil, below high tide level, Torraadded, Westerport Bay, Sawtell’s Inlet, Victoria, Australia                                                                                       | JN121683 JN121517 JN121823 JN121985 |
| CBS 322.48² | *Penicillium duclauxii*   | ATCC 10439 = IMI 040044 = MUCL 28672 = MUCL 29094 = MUCL 29212 = NRRRL 1030 | Canvas, France                                                                                                                                                                                        | JN121643 JN121491 JN121797 JN121905 |
| CBS 112493³ | *Penicillium ellipsoideosporum* | AS 3.5688         | Banyan seeds, Pingxiang, Guanbxi Province, China (data after Wang et al. 2007)                                                                                                                     | JN121568 JN121427 JN121734 JN121859 |
| CBS 318.67² | *Penicillium erubescens*  | ATCC 18544 = FRR 814 = IFO 31734 = IMI 136204 | Nursery soil, Pretoria, South Africa                                                                                                         | JN121642 JN121490 JN121796 JN121969 |
| CBS 323.71² | *Penicillium euglaucum*   | Soil, Argentina                                                                                      |                                                                                                                                               | JN121644 JN121492 JN121798 JN121970 |
| CBS 325.48² | *Penicillium expansum*    | ATCC 7861 = IBT 5101 = IMI 039761 = MUCL 29192 = NRRRL 976 | Fruit of Malus sylvestris, USA                                                                                                                 | JN121645 JF417427 JF417394 JF417527 |
| CBS 229.81³ | *Penicillium fellutanum*  | ATCC 10443 = CBS 326.48 = FRR 746 = IFO 5761 = IMI 039734 = IMI 039734 = NRRRL 746                                                                 | Unknown source, USA                                                                                                                        | JN121605 JN121460 JN121767 JN121947 |
| CBS 124.68³ | *Penicillium fractum*     | ATCC 18567 = FRR 3448 = IMI 136701 = NRRRL 3448 | Soil, Univ. Shinshu, Ueda-shi, Nagano Pref, Japan                                                                                             | JN121582 JN121441 JN121748 JN121864 |
| CBS 295.62³ | *Penicillium fuscur*      | ATCC 14770 = IFO 7743 = IMI 0694209 = MUCL 31196 = NRRRL 3018 = WSF 15c | Type of *E. pinetorum* and neotype of Citromyces fuscus; pine-birch forest soil, Vilas County, Wisconsin, USA | JN121633 JN121483 JN121789 JN121962 |
| CBS 12554³ | *Penicillium glabrum*     | IBT 22658 = IMI 91944 | Unknown                                                                                                                                   | JN121717 JF417447 JF417413 JF417547 |
| CBS 599.73³ | *Penicillium gracilentum* | ATCC 28047 = ATCC 48258 = IMI 216900 | Soil, Brown River, Port Moresby, Central Dist., Papua New Guinea                                                                           | JN121704 JN121537 JN121843 JN121990 |
| CBS 185.27³ | *Penicillium griseofulvum*| ATCC 11885 = IBT 6740 = IMI 075832 = MUCL 28643 = NRRRL 2152 = NRRRL 2300 | Unknown source, Belgium                                                                                                                   | JN121592 JN121449 JN121756 JN121865 |
| CBS 277.58³ | *Penicillium griseolum*   | ATCC 18239 = IMI 071626 = NRRRL 2671 | Acidic dune sand, Dorset, Stufland, England                                                                                               | JN121629 JN121490 JN121786 JN121959 |
| CBS 336.48³ | *Penicillium herquei*     | ATCC 10118 = FRR 1040 = IFO 31747 = IMI 028609 = MUCL 29213 = NRRRL 1040 | Leaf, France                                                                                                                               | JN121647 JN121494 JN121800 JN121972 |
| CBS 341.68³ | *Penicillium idahoense*   | ATCC 22055 = IMI 148393 | Soil, Latah Co., Univ. of Idaho Plant Science Farm, Idaho, USA                                                                            | JN121652 JN121499 JN121805 JN121976 |
| CBS 351.67³ | *Penicillium inulpatum*   | ATCC 18622 = IMI 136214 | Forest soil, Knysna Valley, Cape Province, South Africa                                                                              | JN121658 JN121503 JN121809 JN121979 |
| CBS no.  | Name                                      | Other collections | Origin                                      | GenBank accession or reference1 |
|---------|-------------------------------------------|-------------------|---------------------------------------------|---------------------------------|
| CBS 247.56T | *Penicillium isariiforme*                | ATCC 18425 = IMI 060071 = MUCL 31191 = MUCL 31323 = NRRL 2638 | Woodland soil, Zaire          | JN121616 JN121470 JN121720 JN121993 |
| CBS 338.48T | *Penicillium islanticum*                 | ATCC 10127 = IMI 040042 = MUCL 31324 = NRRL 1036 | Unknown source, Cape Town, South Africa | JN121648 JN121495 JN121801 JN121906 |
| CBS 339.48T | *Penicillium italicum**                 | ATCC 10454 = IMI 983 = IBT 23029 = IMI 039760 = MUCL 15608 = NRRL 983 | Fruit, Citrus Experiment Station, Riverside, California, USA | JN121649 JN121496 JN121802 JN121973 |
| CBS 340.48T | *Penicillium janthinellum*               | ATCC 10455 = IMI 040238 = NRRL 2016 | Soil, Nicaragua                       | JN131650 JN121497 JN121803 JN121974 |
| CBS 341.48T | *Penicillium javanicum*                  | ATCC 9099 = FRR 707 = IMI 039733 = MUCL 29099 = NRRL 707 | Type of *P. javanicum*, *E. javanicum* and *P. indonesiae*; root of Camellia sinensis (green tea), Buitenzorg, Java, Indonesia | JN121651 JN121498 JN121804 JN121975 |
| CBS 247.67T | *Penicillium katangense*                 | ATCC 18388 = IMI 136206 = NRRL 5182 | Soil, Katanga, Zaire                  | JN121618 JN121471 JN121777 JN121955 |
| CBS 344.61T | *Penicillium kawaiense*                  | ATCC 18240 = IMI 086661 = MUCL 2685 = NRRL 3332 | Culture contaminant of mineral oil, Kew, Surrey, England, UK | JN121654 JF417428 JF417395 JF417528 |
| CBS 106.11T | *Penicillium lanosum*                    | ATCC 10454 = IMI 040224 = MUCL 29232 = NRRL 2009 | Unknown source, Germany             | JN121561 JN121420 JN121727 JN121857 |
| CBS 343.48T | *Penicillium lapidosum*                  | ATCC 10462 = IMI 039743 | Canned blueberry, Washington, USA        | JN121653 JN121500 JN121806 JN121977 |
| CBS 277.70T | *Penicillium lasseni*                    | ATCC 22054 = IMI 148395 | Soil under conifers, Tehama Co., Lassen National Forest, 1300 m alt., California, USA | JN121630 JN121481 JN121787 JN121960 |
| CBS 116871T | *Penicillium macroclerotiorum*           | AS 3.6581 | Soil, Chongqing, Wushan County, Sichuan Province, China | JN121573 JN121432 121739 JN121860 |
| CBS 647.95T | *Penicillium malachitum*                 | IBT 17515 | Soil, Nihondaira Pref. Park, Shimizu-shi, Shimizu-ken, Japan | JN121710 JN121543 JN121849 JN121991 |
| CBS 256.55T | *Penicillium marneffei**                 | ATCC 18224 (CBS 334.59 = IMI 88794) | Bamboo rat (Rhizomys sinensis); Vietnam | Unpublished |
| CBS 642.68T | *Penicillium minioluteum*                | IMI 089377 = MUCL 28666 | Unknown                                     | JN121709 JF417443 JF417409 JF417543 |
| CBS 353.48T | *Penicillium namyslowskii*               | ATCC 11127 = IMI 216904 = NRRL 2232 | Soil under *Pinus* sp.; Puszcza Bialowieska, Poland | JN121660 JF417430 JF417397 JF417530 |
| CBS 203.84T | *Penicillium nepalense**                 | NHL 6482 | Rice soil, Boudha, Kathmandu, Nepal         | JN121596 JN121453 JN121760 JN121868 |
| CBS 489.66T | *Penicillium ochroalbicans*              | ATCC 18338 = IMI 116248ii | Type of *E. ochroalbicans*; cornmeal, South Africa | JN121689 JN121524 JN121830 JN121987 |
| CBS 232.60T | *Penicillium olsonii**                   | IBT 23473 = IMI 192502 | Root, Picea abies, alt. 1980 m., Pitztal, Austria | JN121609 JN121464 JN121771 JN121952 |
| CBS 190.68T | *Penicillium ornatum*                    | ATCC 18608 = IMI 137977 = NRRL 3471 | Soil, Moto-machi, Oshima Islands, Japan | JN121594 JN121451 JN121758 JN121867 |
| CBS 462.72T | *Penicillium osmophilum**                | IBT 14679 | Agricultural soil, Wageningen, the Netherlands | JN121683 JN121518 JN121824 JN121986 |

Table 1. (Continued).

| CBS no.  | Name                                      | Other collections | Origin                                      | GenBank accession or reference1 |
|---------|-------------------------------------------|-------------------|---------------------------------------------|---------------------------------|
| CBS 203.84T | *Penicillium nepalense**                 | NHL 6482 | Rice soil, Boudha, Kathmandu, Nepal         | JN121596 JN121453 JN121760 JN121868 |
| CBS 489.66T | *Penicillium ochroalbicans*              | ATCC 18338 = IMI 116248ii | Type of *E. ochroalbicans*; cornmeal, South Africa | JN121689 JN121524 JN121830 JN121987 |
| CBS 232.60T | *Penicillium olsonii**                   | IBT 23473 = IMI 192502 | Root, Picea abies, alt. 1980 m., Pitztal, Austria | JN121609 JN121464 JN121771 JN121952 |
| CBS 190.68T | *Penicillium ornatum*                    | ATCC 18608 = IMI 137977 = NRRL 3471 | Soil, Moto-machi, Oshima Islands, Japan | JN121594 JN121451 JN121758 JN121867 |
| CBS 462.72T | *Penicillium osmophilum**                | IBT 14679 | Agricultural soil, Wageningen, the Netherlands | JN121683 JN121518 JN121824 JN121986 |
| CBS no. | Name                                      | Other collections | Origin                                      | GenBank accession or reference	 | RPB1  | RPB2  | Tsr1  | Cct8  |
|--------|-------------------------------------------|-------------------|---------------------------------------------|---------------------------------|--------|--------|--------|--------|
| CBS 219.30<sup>cd</sup> | *Penicillium oxalicum**                          | ATCC 1126 = FRR 787 = IMI 192332 = MUCL 20047 = NRRL 767 | Soil, Connecticut               | JN121600 | JN121456 | JN131763 | JN121944 |
| CBS 251.56<sup>e</sup> | *Penicillium ramusculum*                         | ATCC 12392 = IMI 063546 = NRRL 3459 | Culture contaminant, Brazil       | JN121620 | JN121472 | JN121778 | JN121956 |
| CBS 367.48<sup>cd</sup> | *Penicillium restrictum**                         | ATCC 11257 = FRR 1748 = IMI 040228 = NRRL 1748 | Soil, Honduras                   | JN121662 | JN121506 | JN121812 | JN121981 |
| CBS 231.61<sup>cd</sup> | *Penicillium saucculum (syn. Eladia saccula)* | ATCC 18350 = IMI 051498 | Soil, Madrid, Spain                | JN121607 | JN121462 | JN121769 | JN121949 |
| CBS 122276<sup>cd</sup> | *Penicillium saturniforme**                        | AS 3.6886 | Soil, Jiling Province, China             | JN121580 | JN121439 | JN121746 | JN121863 |
| CBS 290.48<sup>e</sup> | *Penicillium shearii*                              | ATCC 10410 = IMI 039739 = NRRL 715 | Soil, Tela, Honduras               | JN121631 | JN121482 | JN121788 | JN121961 |
| CBS 228.89<sup>cd</sup> | *Penicillium shennangianum**                      | AS 3.4526 | Mouldy pea, Hubei Province, Shennongjia, China | JN121603 | JN121458 | JN121766 | JN121945 |
| CBS 372.48<sup>cd</sup> | *Penicillium simplicissimum*                        | ATCC 10495 = IFO 5762 = IMI 039816 | Flannel bag, Cape, South Africa    | JN121662 | JN121507 | JN121813 | JN121981 |
| CBS 315.67<sup>cd</sup> | *Penicillium stolkiae*                             | ATCC 18546 = IMI 136210 | Peaty forest soil, Eastern Transvaal, South Africa | JN121640 | JN121488 | JN121794 | JN121967 |
| CBS 117503<sup>e</sup> | *Penicillium thiersii*                             | IFT 27050 = NRRL 28162 | Old, black stroma, encrusting the surface of dead Acer saccharum log, alt. 300 m., New Glarus Woods State Park, Wisconsin, USA | JN121575 | JN121434 | JN121741 | JN121861 |
| CBS 347.59 | *Penicillium thomii**                             | IFO 6031 = IMI 068221 | Type of P. thomii var. flavescens; soil, Japan | JN121655 | JN121501 | JN121807 | JN121978 |
| CBS 430.69<sup>e</sup> | *Penicillium tularense*                            | ATCC 22056 = IMI 148394 | Soil, under Pinus ponderosa and Quercus kelloggi, Tulare Co., Pine Flat, California | JN121681 | JN121516 | JN121822 | JN121984 |
| CBS 603.74<sup>cd</sup> | *Penicillium verrucosum**                          | ATCC 48987 = FRR 965 = IBT 12809 = IBT 4733 = IMI 200310 = IMI 200310ii = MUCL 28674 = MUCL 29089 = MUCL 29186 = NRRL 965 | Unknown source, Belgium          | JN121706 | JN121539 | JN121845 | JN121991 |
| CBS 390.48<sup>cd</sup> | *Penicillium viridicatum**                         | ATCC 10515 = IBT 23041 = IMI 039758 = IMI 039758ii = NRRL 963 | Air, District of Columbia, Washington D.C., USA | JN121668 | JN121511 | JN121817 | JN121983 |
| CBS 430.64<sup>cd</sup> | *Phialomyces macrosorpus*                          | ATCC 16661 = IMI 110130 = MUCL 9776 | Soil, near Rotorua, New Zealand      | JN121680 | JN121515 | JN121821 | JN121915 |
| CBS 128032<sup>a</sup> | *Phialosimplex caninus*                            | UAMH 10337 | Bone marrow aspirate ex dog, San Antonio, Texas, USA | JN121587 | JN121445 | JN121752 | JN121892 |
| CBS 109945<sup>e</sup> | *Phialosimplex chlamydosporus*                     | FMR 7371 = IMI 367422 | Disseminated infection in a dog        | JN121566 | JN121425 | JN121732 | JN121879 |
| CBS 366.77<sup>cd</sup> | *Phialosimplex sclerotialiis*                      | IAM 14794 | Fodder of ray-grass and lucerne, France    | JN121661 | JN121505 | JN121811 | JN121908 |
| CBS 384.61<sup>e</sup> | *Polypaecilum insolitum*                           | ATCC 18164 = IMI 075202 = MUCL 3078 | Ear of human, Leeds, Yorkshire, England, UK | JN121667 | JN121510 | JN121816 | JN121911 |
| CBS 101166 | *Polypaecilum pisci*                               | IBT 23041 = IMI 039758 = IMI 039758ii = NRRL 963 | Yeast extract, Netherlands          | JN121555 | JN121415 | JN121722 | JN121870 |
| CBS 101.69<sup>e</sup> | *Rasamsonia argillacea*                            | DTO 97E4 = IMI 156096 = IBT 31199 | Mine tip with a very high surface temperature; Staffordshire, UK | JN121556 | JF417415 | JF417382 | JF417515 |
| CBS no. | Name | Other collections | Origin | GenBank accession or reference |
|---------|------|-------------------|--------|-------------------------------|
| CBS 413.71 | *Rasamsonia byssoclamydoides* | DTO 149D6 = IBT 11604 | Dry soil under Douglas fir; Oregon, USA | JN121675 JF417437 JF417403 JF417537 |
| CBS 275.58^*t | *Rasamsonia cylindrospora* | DTO 138F8 = IBT 31202 = ATCC 18223 = IMI 071823 | Culture contaminant; Berkshire, England, UK | JN121628 JF417423 JF417390 JF417523 |
| CBS 393.64^*t | *Rasamsonia emersonii* | DTO 481 = IBT 21696 = ATCC 16479 = IMI 116815i | Compost; Italy | JN121670 JF417434 JF417401 JF417534 |
| CBS 114.72^*t | *Sagenomia viride* | ATCC 22467 = NRRL 5575 | Soil, Australia | JN121571 JN121430 JN12137 JN121882 |
| CBS 545.86^*t | *Sagenomella bohemica* | CCF 2330 = IAM 14789 | Peloids for balneological purposes, Frantiskovy Lázné Spa, West Bohemia, Czech Republic | JN121699 JN121532 JN121838 JN121927 |
| CBS 398.69 | *Sagenomella diversispora* | MUCL 15012 | Forest soil under *Populus tremuloides*; Petawawa, Ontario, Canada | JN121673 JF417435 JF417402 JF417536 |
| CBS 399.69 | *Sagenomella diversispora* | | | JN121674 JN121513 JN121819 JN121913 |
| CBS 426.67 | *Sagenomella griseoviridis* | ATCC 18505 = IMI 113160 | Unknown source | JN121677 JF417438 JF417404 JF417538 |
| CBS 398.68 | *Sagenomella leycettan* | ATCC 16921 = IMI 055295 = NRRL 2292 | Soil; Guelph, Ontario, Canada | JN121581 JN121440 JN121747 JN121888 |
| CBS 105.25 | *Sclerocleista thaxteri* | IMI 089305 | Dung of caterpillar, USA | JN121560 JN121419 JN121726 JN121874 |
| CBS 100537 | *Talaromyces convolutus* | ATCC 10126 = IMI 040045 = NRRL 1025 | Begonia leaf; New York City, New York, USA | JN121634 JF417425 JF417392 JF417525 |
| CBS 100538 | *Talaromyces emodensis* | IBT 14989 | Soil, Kathmandu, Nepal | JN121553 JN121414 JN121721 JN121869 |
| CBS 310.39^*t | *Talaromyces flavus* | IMI 197477 = NRRL 2098 | Unknown substrate; New Zealand | JN121639 JF417426 JF417393 JF417526 |
| CBS 398.60 | *Talaromyces luteus* | ATCC 24469 = IMI 176525 | Coal spoil tip soil; Leycester, Staffordshire, England, UK | JN121672 JF417435 JF417402 JF417535 |
| CBS 100537 | *Talaromyces luteus* | IMI 089305 | Soil, UK | JN121656 JF417429 JF417396 JF417529 |
| CBS 475.71^*t | *Talaromyces porpureus* | ATCC 24069 = ATCC 52513 = FRR 1731 = IMI 181546 | Soil, near Esterel, France | JN121687 JN121522 JN121628 JN121919 |
| CBS 398.60 | *Talaromyces stipitatus* | ATCC 10500 (= NRRL 1006 = CBS 375.48 = IMI 39805) | Rotting wood; Louisiana, USA | JN121611 JF417420 JF417387 JF417520 |
| CBS 236.58^*t | *Talaromyces thermophilus* | ATCC 10518 = IMI 046593 = NRRL 2155 | Parthenium argentatum, decaying plant; California, USA | JN121611 JF417420 JF417387 JF417520 |
| CBS 373.48^*t | *Talaromyces trachyspermus* | ATCC 10497 = IMI 040043 = NRRL 1028 | Unknown source, USA | JN121664 JF417432 JF417399 JF4174532 |
| CBS 391.48^*t | *Talaromyces wortmanii* | ATCC 10517 = IMI 040047 = NRRL 1017 | Unknown source | JN121669 JF417433 JF417400 JF417533 |
| CBS 891.70 | *Thermoascus aurantiacus* | IMI 173037 | Wood; Firenze, Italy | JN121719 JF417444 JF417410 JF417544 |
Table 1. (Continued).

| CBS no.  | Name                      | Other collections | Origin                                      | GenBank accession or reference1 |
|----------|---------------------------|-------------------|---------------------------------------------|---------------------------------|
| CBS 396.78 | Thermoascus aurantiacus* | JCM 12816         | Sawdust, in lumber yard, Toronto, Ontario, Canada | JN121671 JN121512 JN121818 JN121912 |
| CBS 181.67 | Thermoascus crustaceus*   | ATCC 16462 = IMI 126333 | Panthirnium argentatum, decaying plant; Salinas, California, USA | JN121591 JF417417 JF417384 JF417517 |
| CBS 528.71 | Thermoascus thermophilus* | IMI 123298 = NRRL 5208 | Wood and bark of Pinus; Sweden               | JN121697 JF417442 JF417408 JF417542 |
| CBS 218.34 | Thermodermomyces lanuginosus* | MUCL 8338      | Fruit shell of Theobroma cacao             | JN121599 JF417418 JF417385 JF417518 |
| CBS 224.63 | Thermodermomyces lanuginosus* | MUCL 8337      | Mushroom compost; Gossau-Zürich Switzerland | JN121602 JF417419 JF417386 JF417519 |
| CBS 334.68 | Thysanophora canadensis*  | ATCC 18741 = IMI 137644 = MUCL 21216 | Needle of Tsuga canadensis, Bell's Corners, Ontario, Canada | JN121647 JN121493 JN121799 JN121971 |
| CBS 206.57 | Thysanophora taxii*       | ATCC 18484 = MUCL 11402 | Litter, Berlin, Germany                    | JN121597 JN121454 JN121761 JN121942 |
| CBS 185.65 | Torulomyces lagena*       | MUCL 8221       | Bog soil under Thuja plicata, Guelph, Ontario, Canada | JN121593 JN121450 JN121757 JN121866 |
| CBS 247.57 | Trichocoma paradoxa*      | MUCL 39666 = IBT 31159 | Unknown source; Hachijō, Japan              | JN121617 JF417421 JF417388 JF417521 |
| CBS 103.73 | Trichocoma paradoxa*      |                     | Unknown source, Japan                       | JN121558 JN121417 JN121724 JN121872 |
| CBS 788.83 | Trichocoma paradoxa*      |                     | Rotting stump of cut down tree, Myojij Temple near Hakui Noto Park, Ishikawa Pref., Japan | JN121718 JN121550 JN121856 JN121941 |
| CBS 512.65 | Warcziella spinulosa*     | ATCC 16919 = IMI 075885 = NRRL 4376 | Jungle soil; Berakas-Muara, Brunei          | JN121692 JF417441 JF417407 JF417541 |
| CBS 236.71 | Xeromyces bisporus*       | IMI 063718      | Mouldy stick of liquorice, Homebush, New South Wales, Australia | JN121612 JN121466 JN121773 JN121898 |

1 Sequences derived from published full genome data. * Strains used in the study of Trichocomaceae (Fig. 1); ** Strains used in for the preparation of Figs 1 and 7. CBS, culture collection of the CBS-KNAW Fungal Biodiversity Centre, Utrecht, Netherlands (WDCM 133) http://www.cbs.knaw.nl/databases/index.htm; DTO, internal culture collection of CBS-KNAW Fungal Biodiversity Centre; IMI, CABI Genetic Resources Collection, Surrey, UK (WDCM 214) http://www.cabi.org/; IBT, culture collection of Center for Microbial Biotechnology (CMB) at Department of Systems Biology, Technical University of Denmark (WDCM 758) http://www.biocentrum.dtu.dk/; NRRL, ARS Culture Collection of the CBS-KNAW Fungal Biodiversity Centre, Utrecht, Netherlands (WDCM 133) http://www.cbs.knaw.nl/databases/index.htm; MUCL, Mycothèque de l’Université catholique de Louvain, Leuven, Belgium (WDCM 308).

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

The RBPI fragment was amplified using the primer pair RBPI-F1843 and R3096, and RBPI-R2623 was occasionally used as an internal primer for sequencing. A part of the RBPI locus was amplified using the primer pair RBPI-2F and RBPI-2CR (Liu et al. 1999) or the primer pair RBPI-2F Eur and RBPI-2CR Eur. The internal sequencing primers RBPI-F311 and RBPI-R310 were occasionally used when poor results were obtained with the regular forward and reverse primers. A part of the Cct8 gene was performed using the primer pair Cct8-F660 and Cct8-R1595. No amplicons could be obtained in the case of 5–10 % of the analysed strains. In those cases, amplicons were generated using the primer pair Cct8-R1595 and Cct8-F94. A part of the Tar1 gene was amplified using the forward primers Tar1-F1526Pc or Tar1-F1526 in combination with Tar1-R2434. Annealing temperatures and primers used for amplification and sequencing are shown in Table 2.

The PCR reactions were performed in 25 μL reaction mixtures containing 1 μL genomic DNA 2.5 μL PCR buffer, 0.75 μL MgCl2 (50 mM), 16.55 μL demineralised sterile water, 1.85 μL dNTP (1 mM), 0.50 μL of each primer (100 mM) and 0.1 μL Taq polymerase (5 U/μL, BioTaq, Bioline). The PCR program typically was: 5 cycles of 30 s denaturation at 94 °C, followed by primer annealing for 30 s at 51 °C, and extension for 1 min at 72 °C; followed by 5 cycles with an annealing temperature at 49 °C and 30 cycles at 47 °C, finalised with an extension for final 10 min at 72 °C. Excess primers and dNTP's were removed from the PCR product using the QIAQuick PCR purification kit (Qiagen). Purified PCR fragments were resuspended in 30–50 μL of water. PCR products were sequenced directly in both directions with the same primers and DYEnamic...
Phylogenetic analysis

The protein coding nucleotide sequences were translated into amino acid data prior to alignment and subsequently aligned using the Muscle software in the MEGA5 package. Combined sequence data sets were used in the study on the phylogeny of Trichocomaceae. Phylogenetic analysis was performed with two sets of four chains (one cold and three heated) and the stoprule option, stopping the analysis at an average standard deviation of split frequencies of 0.01. The sample frequency was set to 100; the first 25 percent of trees were removed as burnin. The phylograms obtained with the RAxML analysis were used for presenting the data. Bootstrap values lower than 70 % were considered unreliable because their wide range of error and Bayesian posterior probabilities are considered unreliable below 0.95 (Murphy et al. 2001, Wilcox et al. 2002, Alfaro & Holder 2006). Therefore, only posterior probability (pp) values higher than 0.95 and bootstrap (bs) values higher than 70 % were plotted on the phylograms. Coccidioides immitis (strain RS), a member of Onygenales, was chosen to root the phylogram used in the study on the relationships of Penicillium species among Trichocomaceae. Penicillium (= Talaromyces) marneffei ATCC 18227T was selected as an outgroup for the analysis of the phylogeny of Penicillium. Various phylograms were prepared for assignment of species to sections. All data sets were based on partial RPB2 sequences and rooted with Talaromyces flavus CBS 310.38T, with exception of the phylogram of sections Lanata-divaricata and Stolkia, which is based on partial β-tubulin data. Penicillium glabrum CBS 125543T was used as an outgroup.

RESULTS

Phylogeny of Trichocomaceae

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

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

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

| Locus | Primer | Sequence (5′–3′) | Annealing (°C) | Fragment size (bp) | References |
|-------|--------|------------------|----------------|-------------------|------------|
| Cct8  | F94    | (Fwd) CGCAAC AAGATGYGTBATYAAACCA | 50–52 | 94-R1595: 1400–1450 | Houbraken et al. 2011d |
|       | F660   | (Fwd) GIGTKGTBAAGATCATGGGWWG | 50–52 | 660-R1595: 850–900 | Houbraken et al. 2011d |
|       | R1595  | (Rev) RTCMACRCNGTGGTTCCCATGA | 50–52 | This study |
| RPB1  | F1843  | ATTTYGAGYGGTGYARATGAAC | 48–53 | This study |
|       | R3096  | GRACRGTDCTCTATYTTTRACC | 48–53 | This study |
|       | R2623  | GCRTTGTSARATCTTAMRRCTC | 48–53 | This study |
| RPB2  | 5F     | GAYGAYMGWATCATYTTYGG | 48–51 | 5F: 1220 Liu et al. 1999 |
|       | 7CR    | CCCATRGCCTTGYTRCCCAT | 48–51 | This study |
|       | 5F_Eur | (Fwd) GAYGAYCGKGAYCAYTTCGG | 48–51 | Houbraken et al. 2011d |
|       | 7CR_Eur| (Rev) CCCATRGCYGTTYTRCCCAT | 48–51 | Houbraken et al. 2011d |
|       | F311   | CATGAYCARCGIAAYATGGA | 48–51 | This study |
|       | R310   | CACATRTICGGYTRCATGAAA | 48–51 | This study |
| Tsrl  | F1526Pc| GARTAYCCBCARTCNGAGATGT | 48–50 | 1526Pc: 820 Houbraken et al. 2011d |
|       | F1626  | GARTAYCCBCARTCNGAIAATGT | 48–50 | This study |
|       | R2434  | (Rev) ASAGAYTGVARDCGCTTTRAACCA | 48–50 | Houbraken et al. 2011d |

ET Terminator Cycle Sequencing Kit (Amersham Bioscience, Roosendaal, The Netherlands). The cycle sequencing reaction mixture had a total reaction volume of 10 μL, and contained 1 μL of template DNA, 0.85 μL BigDye reagent, 3 μL buffer, 4.75 μL demineralised water and 0.4 μL primer (10 mM). Sequencing products were purified according to the manufacturers’ recommendations with Sephadex G-50 superfine columns (Amersham Bioscience, Roosendaal, The Netherlands) in a multiscreen HV plate (Millipore, Amsterdam, The Netherlands) and with MicroAmp Optical 96-well reaction plate (AB Applied Biosystems, Nieuwerkerk a/d Yssel, The Netherlands). Contigs were assembled using the forward and reverse sequences with the programme SeqMan from the LaserGene package (DNAStar Inc., Madison, WI).

Phylogenetic analysis

The protein coding nucleotide sequences were translated into amino acid data prior to alignment and subsequently aligned using the Muscle software in the MEGA5 package. After aligning, the amino acid data were translated into nucleotide data and used in the phylogenetic analysis. Combined sequence data sets were used in the study on the phylogeny of Trichocomaceae and Penicillium. Before combining the data sets, each data set was analysed using RAxML (Stamatakis 2008). The number of bootstrap runs was set to 100. The program compat.py (from http://www.lutzonilab.net) was conducted to determine the relationship among members of Trichocomaceae. A total of 157 species were included in the analysis and the total length of the alignment was 3 111 base pairs long, respectively. The GTR+I+G model was optimal for all four partitions.

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

### DISCUSSION

**Part One: Phylogenetic analysis of Trichocomaceae**

#### Choice of genes

Parts of the *RPB1*, *RPB2*, *Cct8* and *Tsr1* genes were only used for the construction of the phylogenetic relationships among members of *Trichocomaceae* and *Penicillium* species, and the ability of these genes for species recognition remains largely unexplored. The regions E and F (according Matheny et al. 2002) of the *RPB1* gene were analysed. No additional sequence data of *Trichocomaceae* were published on this part of the *RPB1* gene and comparison with other studies is therefore difficult. The regions 5–7 of the *RPB2* gene are commonly used in taxonomic studies of *Penicillium* and *Aspergillus* and proved to be a good marker for species recognition (e.g. Peterson 2008, Serra et al. 2008, Peterson & Horn 2009, Peterson et al. 2010, Barreto et al. 2011). However, *RPB1* and *RPB2*, as well as *TEF1a*, β-tubulin, and γ-actin, were not found among the best performing genes for fungal systematics (Aguileta et al. 2008). Aguileta et al. (2008) studied, using a bioinformatics approach, the performance of single-copy protein-coding genes for fungal phylogenetics. Their analyses of 30 published fungal genomes revealed that MCM7 (MS456), *Tsr1* (MS277) and *Cct8* (FG610) were among the best single-copy genes in phylogenetic utility. *MCM7*, the best gene for recovering a larger-scale phylogeny across fungal groups, was excluded in the current study since it was not variable enough within the genus *Penicillium* (Marthey et al. 2008). *Tsr1* and *Cct8* were also used in other (phylogenetic) studies of groups belonging to *Trichocomaceae*.

### Phylogeny of Penicillium sensu stricto

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

| Table 3. Details of each analysis of the data sets used for generating Figs 8, 10–13. |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Figure | Clades, acc. Fig. | Locus | No. isolates | Length alignment | Best-fit model |
| 8     | 1, 2, 3           | RPB2  | 50           | 916             | SYM+H+G        |
| 10    | 6, 7, 10 and 13   | RPB2  | 69           | 916             | GTR+H+G        |
| 11    | 11, 12            | β-tubulin | 45           | 528             | HKY+H+G        |
| 12    | 5, 14             | RPB2  | 44           | 849             | SYM+H+G        |
| 13    | 15–25             | RPB2  | 86           | 916             | GTR+H+G        |
Fig. 1. Best-scoring Maximum Likelihood tree using RAxML based on combined data set of partial Cct8, Tar1, RPB1 and RPB2 sequences showing the relationship among members of Trichocomaceae. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (pp/bs). Values less than 50 % supported in the ML or less than 0.90 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate full support (100 % bs or 1.00 pp). The branches with more than 95 % bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with Coccidioides immitis (strain RS).
(López-Villavicencio et al. 2010, Peterson et al. 2010). Analysis of the Tsr1 gene generated the best resolved trees, when compared with Cct8, MCM7 and ITS (López-Villavicencio et al. 2010). The sequenced parts of the RPB1, RPB2, Tsr1 and Cct8 genes mainly contain exons, and the alignment of these loci is therefore unambiguous. This is the main advantage over ITS regions where alignment above genus can be difficult. Furthermore, the ITS region is generally considered unreliable as a phylogenetic marker, especially above genus rank. β-tubulin and calmodulin sequences are often used in taxonomical studies of Penicillium, Paecilomyces

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**Fig. 1.** (Continued).
and Aspergillus (e.g. Samson et al. 2004, Houbraken et al. 2007, Samson et al. 2009, Varga et al. 2011). However, a large part of these genes consists of intron data and these regions cannot be aligned above genus level, resulting in loss of information in these data sets. In addition, there is evidence that β-tubulins are present in the genome in multiple copies and thus have the potential of being phylogenetically misleading (Landvik et al. 2001, Peterson 2008).

**Phylogenetic analysis of Trichocomaceae**

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

**Phenotypic classification and delimitation of Aspergillaceae, Trichocomaceae and Thermoascaceae**

Several studies on the classification of Trichocomaceae and Eurotiales based on phenotypic characters were published (Malloch & Cain 1972, Fennell 1973, Benny & Kimbrough 1980, Malloch 1985a, b, von Arx 1987) and an overview of selected studies is shown in Table 4. Some of these classifications differ significantly from each other. We compared the results of these studies with the current proposed phylogenetic classification and this showed that our phylogenetic classification largely corresponds with the phenotypic classification described by Malloch (1985a, b). Malloch (1985a, b) divided Trichocomaceae into two subfamilies, Trichomoideae and Dichlaenoideae, based on phenotypic characters including cleistothecial initials, peridium, ascus structure and ascospore morphology. Malloch’s list of genera belonging to Dichlaenoideae largely corresponds with the genera we place in Aspergillaceae and his definition of Trichomoideae is comparable with our phylogenetically defined Trichocomaceae. There are two main differences: a) Monascus is treated here in Aspergillaceae and b) the genera Byssochlamys and Thermoascus are accommodated in Thermoascaceae; these were treated by Malloch (1985a, b) in Trichomoideae and Dichlaenoideae, respectively. Using the characters proposed by Malloch in his classification, Aspergillaceae are characterised by the production of ascii inside cleistothecia, stromata, or are surrounded by Hülle cells and mainly have oblate to ellipsoidal ascospores with a furrow or slit. The conidia are mostly formed on flask shaped or cylindrical phialides. The Trichocomaceae are defined by having ascii borne within a tuft or layer of loose hyphae, and ascospores are lacking slits or furrows. The phialides of species belonging to this family are mostly lanceolate or cylindrical. Apinis (1967) introduced Thermoascaceae and noted that the common essential character of genera of this family is the production of firm, somewhat sclerotoid, pseudoparenchymatous cleistothecia. The inclusion of Byssochlamys in this family does not fit in that description because it produces almost naked ascospores. Based on the relative branch length in Fig. 1, another possibility would be to delimit the Thermoascus clade (clade 8) and the Byssochlamys/ Paecilomyces clade (clade 9) as separate families. However, there are characters shared by Thermoascus and Byssochlamys including the production of ascii in croziers and the formation of smooth or finely roughened ascospores lacking a furrow or slit. The relationship between these two genera is also illustrated by Byssochlamys verrucosa and Thermoascus crustaceus. Byssochlamys verrucosa phenotypically belongs to Byssochlamys, but is positioned phylogenetically in Thermoascus (Fig. 1) and Therm. crustaceus shares a Paecilomyces anamorph with members of the Byssochlamys/Paecilomyces clade. In addition, most members of both genera are thermotolerant or thermophilic. The genera Chaetosartorya, Crisstaspora, Dichlaena, Dichotomomyces, Eupenicillium, Edyuillia, Emericella, Eurotium, Hamigera, Hemicarpenteles, Hemisartorya, Neoasartorya, Penicillipios, Petromyces, Scleroticlestra, Thermoascus and Warcupiella were placed by Malloch (1985a, b) in Aspergillaceae (as subfamily Dichlaenoideae). The majority of these genera are also included in our classification, and exceptions are Edyuillia, which is synonymised with Eurotium (von Arx 1974) and Thermoascus, which is classified in Thermoascaceae. The main difference is the placement of Monascaceae as Aspergillaceae. Benny & Kimbrough (1980) placed the genera Ascorhiza, Leiothecium, Monascus and Xeromyces in Monascaceae and suggested a relationship with Ascosphaerales. Later, several authors included this family in Pezizales (Malloch 1981, Hawksworth & Pitt 1983). Von Arx (1987), in his revision of Eurotiales, included Monascus in Orygenaceae, and reduced Monascaceae to synonymy. More recently, Monascaceae was placed in Eurotiales (LoBuglio et al. 1993, Hawksworth et al. 1995). Fennell (1973) noted that species of both Monascaceae and Eurotiaeaceae, which approximates our definition Aspergillaceae, form a distinct cleistothecial wall. Nevertheless, Fennell (1973) separated these families based on the formation of aleurioconidia by members of Monascaceae, but our results show that this feature is insufficient for family delimitation. Anamorph genera were not treated by Malloch (1985a, b) and Fig. 1 shows that the genera Aspergillus, Basiptetospora, Eladia, Fraseriella, Penicillium, Phialomyces, Phialosimplex, Polypaecilum, Thysanophora and Torulomyces are classified in Aspergillaceae. The teleomorph genera Chromocleista, Fennellia, Neocarpenteles and Neopetromyces,
which were not treated in Malloch’s study (1985a, b), also belong to this family.

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

### Phylogeny of Aspergillaceae

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

#### Clade 1: Penicillium sensu stricto

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

Clade 2: Aspergillus

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

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

The type species of the genera Polypaeciligum and Phialosimplex and the ex-type strain of Basidiospora halophilica form a strongly supported clade (100 % bs, 1.00 pp) within Aspergillus s. str. This clade is related to Aspergillus sections Cremei, Aspergillus
and Restricti (64 % bs, 1.00 pp). Recently, Phialosimplex was introduced for species with simple phialides borne laterally on vegetative hyphae. These phialides form chains of conidia and are mostly monophyletic, but a second opening can also be formed (polyphialides). Sagemella chlamydosporus and S. sclerotialis were transferred to this genus and Phialosimplex canicus was described as a new species (Sigler et al. 2010). The transfer of S. sclerotialis to Phialosimplex created a paraphyletic genus with Polypaecilum embedded in it. The type species of Polypaecilum, P. insolitum, produces its conidia on polyphialides and this feature is shared with members of Phialosimplex (Smith 1961a). The formation of chlamydomycoses and the occurrence in patient material are also shared features of both genera. This indicates that these genera could be congeneric and more research is needed to clarify their taxonomic status. Basipetospora halophilica also belongs to this diverse clade. The production of short solitary conidiophores is also shared features of both genera. This indicates that these genera have similar phenotypic characters including the formation of stalked ascomata and the production of aleurioconidia from dehiscing asci. These features clearly set this clade and this genus is polyphyletic.

Clade 3: Hamigera

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

Clade 4: Penicilliosis

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

Clade 5: Monascus, Xeromyces and Leiothecium

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

Clade 6: Phialomyces

The type species of Phialomyces, Phial. macrosporus (Misra & Talbot 1968), is positioned in clade 6 and is closely related to Penicillium arenicola (100 % bs, 1.00 pp). Merimbla humicoloides (=Penicillium humicoloides sensu Peterson et al. 2010) also belongs to this clade (R.A. Samson, unpubl. data). All three species are phylogenetically distinct form Penicillium s. str. Pitt (1980)
placed *P. arenicola* in a separate section and series and noted that this species may not be a true *Penicillium*. Phenotypically, *Phial. macrosporos*, *M. humicoloidei* and *P. arenicola* form conidia in shades of gold-brown, a feature uncommon for *Penicillium* species. These species can produce terverticillate conidiophores, a character also present in subgenus *Penicillium* (clade 1B). Our results indicate that *P. arenicola* and *M. humicoloidei* should be transferred to another genus.

**Clade 7: Sclerocleista**

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

**Phylogeny of Thermoascaceae**

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

**Clade 8: Thermoascus**

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

**Clade 9: Paecilomyces**

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

**Phylogeny of Trichocomaceae**

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

**Clade 10: Talaromyces**

The majority of *Penicillium* species assigned to the subgenus *Biverticillum* belong in clade 10 (incl. type of subgenus *Biverticillum*, *P. minoluteum*) together with the type species of the genera *Talaromyces* and *Sagenoma*. These species are phylogenetically distant from *Penicillium* s. *str.* and therefore these species are transferred to the genus *Talaromyces* (Samson et al. 2011, this study). Phenotypically, *Talaromyces* differs from *Penicillium* s. *str.* by the formation of symmetrically branched conidiophores with lanceolate phialides, and the production of soft ascomata without a well-defined, persistant wall. Members of the *Talaromyces* clade grow slower on the agar medium G25N than *Penicillium* s. *str.* members (Pitt 1980). Also differences in ubiquinones and extrolites patterns are observed between *Penicillium sensu stricto* and *Talaromyces*. The Q9 ubiquinone system was present in most *Penicillium sensu stricto* species, while nearly all *Talaromyces* have Q10(H2) (Paterson 1998). In addition, extrolites such as mitorubrins, certain bisanthraquinones (*rugulosin, skyrin*), duclauxin and glauconic acid were detected in *Talaromyces*, but never found in *Penicillium sensu stricto* (Frisvad et al. 1998). The taxonomic and phylogenetic structure of *Talaromyces* is considered further by Samson et al. (2011).

The neotype strain of *Aphanoascus cinnabarinus sensu Ugadaga and Takada also belongs to this clade. Much taxonomic confusion followed after the proposal of *Aphanoascus* by Zukal (1890). Most authors follow Apinis (1968) and maintain *Aphanoascus* that is typified by *A. fulvescens*. In addition, the neotypification of *A. cinnabarinus* by Ugadaga & Takada (1973) was incorrect, because their neotype strain had a *Paecilomyces* anamorph, while Zukal's original description and illustrations showed structures of a *Chrysosporium* anamorph (Stolk & Samson 1983). Based on morphological characters, Stolk & Samson (1983) suggested that *Chromocleista cinnabaria* (as *A. cinnabarinus sensu Ugadaga & Takada*) belongs to *Eurotiidae*, and that this species occupies an intermediate position between the genera *Thermoascus* and *Talaromyces*. The result of our multigene phylogeny shows that *C. cinnabaria* belongs to *Talaromyces* s. *str.*
This data is in concordance with the 18S rDNA sequence data of Ogawa & Sugiyama (2000), which shows that C. cinnabarina forms a monophyletic group with T. macrosporus and T. bacillisporus. No specimens of Erythrogymnotheca were studied, but an ITS sequence of the type species of this genus (E. paucispora) is deposited GenBank (AB176603) and a BLAST search on GenBank and internal CBS databases shows that this sequence belongs to Talaromyces s. str.

Clade 11: Thermomyces

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

Clade 12: Sagenomella

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

Clade 13: Rasamsonia

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

Clade 14: Trichocoma

The monotypic genus Trichocoma is typified by Trichocoma paradoxa and is characterised by asci born in hyphal masses or tufts that can be up to 10–20 mm long (Kominami et al. 1952, Malloch 1965b). The anamorph of this species resembles an anamorph of Talaromyces. However, Trichocoma produces conidia in shades of brown. Rasamsonia is phylogenetically related to Trichocoma, and can be differentiated by the presence of scanty ascocatal coverings and its ability to grow at temperatures above 40 °C.

Excluded genera: Geosmithia, Phialotubus and Yunnania

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

Geosmithia

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

Phialotubus

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

Yunnania

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

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

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

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

Type: *Aspergillus* Fr: Fr.

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

Type: *Thermoascus* Miehe

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

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

Type: *Trichocoma* Junghuhn

Part Two: Delimitation of *Penicillium*

**Authority**

The generic name *Penicillium* is attributed to Link (1809). Link included three species within *Penicillium*, *P. glaucum*, *P. candidum* and *P. expansum*. He illustrated *P. candidum*, which clearly shows structures of a *Penicillium* species. Later, *Penicillium expansum* was selected by Thom (1910) and later (co-)authors as the lectotype of *Penicillium*. The generic name *Penicillium* was attributed by Fries (1832: 406) to Link (1809). Hawksworth et al. (1976) proposed to conserve the generic name *Penicillium* as *Penicillium* Link ex Grey over *Penicillium* Fries 1832 (proposal no. 420), and lectotypified...
the genus with *Penicillium expansum* Link ex Grey. This proposal was countered by Jørgensen & Gunnerbeck (1977) because Fries listed "Mucor crustaceus" L. as a typical species of *Penicillium* and not as the type species of this genus. The proposal of Hawksworth et al. (1976) was therefore rejected (Petersen 1980). The general starting point for fungal names is Linnaeus 1753, but there are a few exceptions and these are mentioned in the ICBN under art. 13e. One exception is that names used by E.M. Fries’ “Systema mycologicum” 1821–1832 have a protected status. These names are sanctioned and have priority over older synonyms and homonyms. The authority used here is therefore *Penicillium* Link: Fries.

**Generic diagnosis**

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

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

"Vegetative mycelium abundant, entirely submerged or more or less effused, irregularly branching, septate, hyaline or brightly coloured and forming a dense and compact mycelia colony with well-defined margins. Conidiophores borne from undifferentiated subsurface, superficial or aerial hyphae, rarely subapically proliferation under terminal penicillus. Stipes relatively narrow and thin walled, 2–5 µm,"
and in some species apically swollen, hyaline, in some species brown. Conidial apparatus usually a well defined structure (brush or broom), named the Penicillus; penicilli comprised of phialides born directly basipetally, single celled, commonly between 2–5 µm in diameter, rarely exceeding 6 µm, en masse coloured in shades of green, rarely white, olive or brown. Chlamydospores absent. Sclerotia occasionally produced, composed of thick-walled cells, usually hard.

**Synonyms of Penicillium**

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

**Penicillium**

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

- *Penicillium* Link, Obs. Mycol 1: 16. 1809 (nom. inval., art. 13e).
- *Cornellium* Link ex Gray, Nat. Arr. Br. Pl. 1: 563. 1821.
- *Eupenicillium* Link, Libr. Nied. Krypt. 4: 90. 1821.
- *Citromyces* Wehmer, Bieitr. Kennt. Pilze 1: 1. 1893.
- *Carpenteles* Langeron, C. Séanc. Soc. Biol. Paris 87: 344. 1922.
- *Torulomyces* De Bie, Systematik der Schimmelpilze: 91. 1943.
- *Thysanophora* Kendrick, Can. J. Bot. 39: 820. 1961.
- *Eladia* Smith, Trans. Brit. Mycol. Soc. 44: 47. 1961.
- *Hemicarpenteles* Sarby & Elphick, Trans. Brit. Mycol. Soc. 51: 156. 1968.
- *Penicillium* Link ex Gray sensu Pitt, The Genus *Penicillium*: 154. 1980 (nom. inval., art. 13e).
- *Chromocleista* Yaguchi & Udagawa, Trans. Mycol. Soc. Japan 34: 101. 1993.

Subgenus *Aspergilloides* Dierckx, Annl. Soc. Scient. Brux. 25: 85. 1901.

- Subgenus *Monoverticillium* Bourg, Cellule 33: 265. 1923.
- Subgenus *Fuscum* Pitt, The Genus *Penicillium*: 233. 1980.

Subgenus *Penicillium* Dierckx, Annl. Soc. Scient. Brux. 25: 85. 1901.

Chromocleista

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

**Citromyces**

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

**Eladia**

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

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

**Eupenicillium and Carpenteles**

The genus *Eupenicillium* was introduced by Ludwig (1892) for an ascomycete species that Brefeld (1874) described and
Fig. 4. A–F. *Penicillium malachiteum* CBS 647.95T. A. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. B–D. Conidiophores. E. Immature cleistothecia. F. Conidia. G–K. *Penicillium sacculum* CBS 123567. G. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. H–J. Conidiophores. K. Conidia. Scale bar = 10 µm.
illustrated as *P. crustaceum*. Unaware of Ludwig's publication, Langeron (1922) introduced the genus *Carpenteles* for ascospore-producing *Penicillium* species. Because we include sexual and asexual species in our definition of *Penicillium*, *Eupenicillium* and *Carpenteles* are considered synonyms of *Penicillium*. In most cases a *Penicillium* anamorph name is already available for these *Eupenicillium* species; however, in the case of *E. bivolimosum* and *E. saturniforme*, only the teleomorph was described and no *Penicillium* names linked to these species exist (Tuthill & Frisvad 2002, Wang & Zhuang 2009). The new combinations *Penicillium* bivolimosum and *Penicillium* saturniforme are proposed below for these two species.

**Hemicarpenteles**

The genus *Hemicarpenteles* was created by Sarbhoy & Elphick (1968) and *H. paradoxus* was designated as type (IMI 117502 = CBS 793.68T). This species is characterised by the presence of an *Aspergillus* anamorph and sclerotoid ascomata (Fig. 5). This unique combination led to the proposition of a new genus. If only ascomata development and characteristics were considered, then *H. paradoxus* is most similar to *Eupenicillium*, because both genera form sclerotoid cleistothecia that ripen from the centre outwards (Sarbhoy & Elphick 1968, Pitt 1980, Stolk & Samson 1983). Figure 1 shows the phylogenetic positioning of *H. paradoxus* in the genus *Penicillium*. The placement of this species in *Penicillium* is remarkable, since this species has an *Aspergillus* anamorph. The positioning of *H. paradoxus* in *Penicillium* is also supported by analysis of the ITS and D1/D2 regions of the 28S rDNA and partial calmodulin and β-tubulin data (Peterson 2000a, 2008). *Aspergillus* and *Penicillium* species are currently classified in *Aspergillus* and phylogenetic studies showed that this species is related to *Neocarpenteles* *acanthosporus* (Peterson & Sigler 2002). Another characteristic of *Penicillium* species is brown, this feature sufficient to keep *Thysanophora* as a separate genus. However, that would create a paraphyletic clade in *Penicillium* or the need for at least eight genera to restore monophyly. To avoid both scenarios it is chosen here to transfer this genus to *Penicillium*. *Thysanophora* comprises eight accepted species, namely *T. longispora*, *T. canadensis*, *T. taxi*, *T. striatisspora*, *T. asymmetrica*, *T. verrucosa*, *T. glaucoalbida* and *T. taiwanensis* (Minter 2007). *Thysanophora* penicillioides is regarded as a synonym of *T. glauco-albida*, because following the ICN, the latter epithet has priority (Morelet 1968, Minter 2007). No type material was present in the CBS culture collection of *T. striatisspora*, *T. asymmetrica*, *T. verrucosa*, *T. glaucoalbida* and *T. taiwanensis*. Only the species descriptions were studied and the species delimitation of Mercado-Sierra (1998) is largely followed. With exception of *T. taxi*, which was originally described as *Penicillium* *taxi* (Schneider 1956), all accepted species of *Thysanophora* are transferred here to *Penicillium* and new combinations are proposed below.

**Torulomyces**

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

Currently, eight species are described in *Torulomyces*: *T. bruneus*, *T. indicus*, *T. laevis*, *T. lagena*, *T. macrosporus*, *T. ovatus*, *T. parviverrucosus* and *T. viscosus*. Isolate CBS 185.85 was designated as the neotype of *P. lagena*, and *Eupenicillium limoneum* was considered to be the teleomorph of this species (Stolk & Samson 1983). Unfortunately, the ex-type culture of *E. limoneum* (CBS 650.82T) maintained in the CBS collection is dead. Stolk & Samson (1983) are followed here and *E. limoneum* is kept in synonymy with *P. lagena*. Delitsch’s species *Torulomyces viscosus* remains doubtful since no type material is available and the diagnosis lacks critical details (Stolk & Samson 1983, Ando et al. 1998). No ex-type material of *Torulomyces macrosporus* could be obtained; based on its protologue (Matsumiha 1987), *T. macrosporus* may belong to *Monocillium* (Ando et al. 1998). *Torulomyces laevis*, *T. ovatus* and *T. parviverrucosus* were described by Ando et al. (1998) and in the same publication *Monocillium humicola var. bruneus* was combined with *T. bruneus*. The type strain of *T. bruneus* CBS 382.64 is closely related to *Torulomyces lagena* CBS 185.65; these isolates have identical ITS sequences, but differ in their partial β-tubulin, calmodulin and RPB2 sequences (ITS 100 %; calmodulin 98.3 % and β-tubulin 98.4 % and RPB2 sequence positions).
Fig. 5. A–G. Penicillium kewense CBS 344.61T. A. Colonies grown for 7 d at 25 °C, from left to right: MEA, CYA, YES, DG18. B–C. Cleistothecia. D–E. Conidiophores. F. Conidia. G. Ascospores. H–N. Aspergillus paradoxus (= P. paradoxum, R.A. Samson unpubl. results) CBS 130295. H. Colonies grown for 7 d at 25 °C, from left to right: MEA (14 d), CYA, YES, DG18. I. Detail of conidiophores. J. Cleistothecia. K–L. Conidiophores. M. Ascospores. N. Conidia. Scale bar = 10 µm.

98.3 %; unpubl. data). Ando et al. (1998) is followed here and this species is kept as separate. No type material of T. laevis, T. ovatus and T. parviverrucosus was available for analysis, but a detailed study of the species descriptions suggests they warrant separate species status. New combinations in Penicillium are proposed below. Various isolates with similar morphology to P. lagena are
maintained in the CBS collections (CBS 185.65, CBS 382.64, CBS 287.66, CBS 337.97, CBS 120415, CBS 110532, DTO 82A8, DTO 92D1), and preliminary sequencing results show a sequence variation among these strains, suggesting the presence of multiple species (unpubl. data). A thorough taxonomic study should be performed to elucidate the species diversity in this clade.
The genus *Monocillium* needs further attention. This genus was established for a single species, *M. indicum* (Saksena 1955). Based on conidium morphogenesis, Hashmi et al. (1972) placed *Monocillium* in synonymy with *Toralomyces*, and later Kendrick & Carmichael (1973) made the combination *Toralomyces indicus*. However, a BLAST search with the ITS sequence of the type strain of *M. indicum* (UAMH 1499, GenBank GQ169328) showed that the closest relatives are among *Hypocreaceae* (Sigler et al. 2010). This is in agreement with Gams (1971), who showed that *Monocillium* species are anamorphs related to *Niesslia* species.

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

**Classification**

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

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

**Accepted species and their position in the sections of *Penicillium***

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

**Clade 1: section Aspergilloides**

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

**In: Penicillium subgenus Aspergilloides.**

**Type:** *Penicillium aurantiobrunneum* Dierckx

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

- *Penicillium ardesiacum* Novobranova, Novosti Sist. Nizs. Rast. 11: 228. 1974.
- *Penicillium asperosporum* Smith, Trans. Br. Mycol. Soc. 48: 275. 1965.
- *Penicillium crocicola* Yamamoto, Scient. Rep. Hyogo Univ. Agric., Agric. Biol. Ser. 2, 2: 28. 1966.
- *Penicillium fuscum* (Sopp) Biourge, Cellule 33: 103. 1923 (Stolk & Samson 1983).
- *Penicillium georgiense* Peterson & Horn, Mycologia 101: 79. 2009.
- *Penicillium glabrum* (Wehner) Westling, Ark. Bot. 11: 131. 1911 (syn. *P. terlikowskii*; Barreto et al. 2011).
- *Penicillium kananaskense* Ramirez, Mycopathol. 91: 96. 1985 (Frisvad et al. 1990c).
- *Penicillium lividum* Westling, Ark. Bot. 11: 134. 1911.
- *Penicillium montanense* Christensen & Backus, Mycologia 54: 574. 1963.
- *Penicillium odoratum* Christensen & Backus, Mycologia 53: 459. 1962 (this study, Fig. 8).
- *Penicillium palmense* Ramirez & Martinez, Mycopathol. 66: 80. 1978.
- *Penicillium patens* Pitt & Hocking, Mycotaxon 22: 197. 1985.
- *Penicillium quercetorum* Baghdadi, Nov. Sist. Niz. Rast. 5: 110. 1968.
| Section      | Type species          | Section      | Type species          | Section      | Type species          | Section      | Type species          | Section      | Type species          |
|--------------|-----------------------|--------------|-----------------------|--------------|-----------------------|--------------|-----------------------|--------------|-----------------------|
| Ascogena     | P. luteum             | Aspergilloides | P. aurantiobrunneum   | Aspergilloides | P. glabrum           | Aspergilloides | P. aurantiobrunneum   |                |                       |
| Brevi-compacta | P. brevicompactum     | Coremigenum  | P. duclauxii          | Brevicillium  | P. miniluteum        | Brevipecta*   | P. olsonii            |                |                       |
| Coremigena   | P. duclauxii          | Coronatum    | P. olsonii           | Coremigenum  | P. duclauxii         | Caneoscentia  | P. canescens          |                |                       |
| Fasciculata  | Fasiculate Penicilli e.g. P. hirsutum | Cylindrorphorum | P. italicum          | Divaricatum  | P. janthinellum      | Charlesii    | P. charlesii          |                |                       |
| Furiculosa   | Undefined; similar to Lanata-divaricata | Divaricatum  | P. janthinellum      | Eladia       | P. sacculum          | Chrysogena*   | P. chrysogenum        |                |                       |
| Lanata-divaricata | P. janthinellum-type  | Exilicaulis  | P. restrictum        | Geosmithia   | P. lavendulum        | Cinnamopurpurea | P. cinnamopurpureum   |                |                       |
| Lanata-typica | P. camemberti         | Furacatum    | P. oxalicum          | Inordinate   | P. arenicola         | Citrina       | P. citrinum           |                |                       |
| Luteo-virida | P. miniluteum         | Inordinate   | P. arenicola         | Penicillium  | P. expansum          | Digiata*      | P. digitatum          |                |                       |
| Miscellanea  | Miscellaneous species and genera | Penicillium  | P. expansum          | Ramsomum     | P. lanosum           | Eladia       | P. sacculum           |                |                       |
| (Monoverticillata)-stricta | Undefined section | Simplicium  | P. miniluteum       | Torulomyces  | P. lagenata          | Exilicaulis  | P. restrictum         |                |                       |
| (Monoverticillata)-Ramigena | Citromycetes species |            |                       |              |                       |              |                       |                |                       |
| Velutina     | Undefined section     |              |                       |              |                       |              |                       |                |                       |

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

Clade 1: sect. Aspergilloides (Fig. 8)
Clade 2: sect. Sclerotiora (Fig. 8)
Clade 3: sect. Charlesi (Fig. 8)
Clade 4: sect. Thysanophora
Clade 5: sect. Ochrosalmonela (Fig. 12)
Clade 6: sect. Cinnamopurpurea (Fig. 10)
Clade 7: sect. Ramigena (Fig. 10)
Clade 8: sect. Torulomyces
Clade 9: sect. Fracta
Clade 10: sect. Exilicaulis (Fig. 10)
Clade 11: sect. Lanata-divaricata (Fig. 11)
Clade 12: sect. Stolkia (Fig. 11)
Clade 13: sect. Gracilenta (Fig. 10)
Clade 14: sect. Citrina (Fig. 12)
Clade 15-19, details see Fig. 13: sect. Fusiculata, sect. Digitata, sect. Penicillum, sect. Roquefortorum, sect. Chrysogena
Clade 20, 21: sect. Turbata, Paradoxa
Clade 22, 23: sect. Brevicompacta, Ramosa (Fig. 13)
Clade 24: sect. Canescentia (Fig. 13)
Clade 25: sect. Eladia (Fig. 13)

Fig. 7. Best-scoring Maximum Likelihood tree using RAxML based on combined data set of partial Cdc6, Tsr1, RPB1 and RPB2 sequences showing the relationship among members of Penicillium s. str. Penicillium s. str. is divided in two lineages (s/g Aspergilloides and Penicillium) and 25 sections. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (bs/pp). Values less than 70 % supported in the ML or less than 0.95 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate good support (100 % bs or 1.00 pp). The branches with more than 95 % bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with Penicillium (= Talaromyces) marneffei ATCC 18227T.

Penicillium saturniforme (Wang & Zhuang) Houbraken & Samson, Stud. Mycol. 70: 48. 2011 (this study).
Penicillium spinulosum Thom, Bull. Bur. Anim. Ind. U.S. Dep. Agric. 118: 76. 1910.
Penicillium suberica Barreto, Frisvad & Samson, Fungal Diversity 49: 32. 2011.

Penicillium thiersii Peterson, Bayer & Wicklow, Mycologia 96: 1283. 2004.
Penicillium thomii Maire, Bull. Soc. Hist. Nat. Afrique N. 8: 189. 1917.
Fig. 8. Best-scoring Maximum Likelihood tree using RAxML based on partial RPB2 sequences and giving an overview of the members accommodated in sections Aspergilloides, Sclerotiora and Charlesii. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (pp/bs). Values less than 70% supported in the ML or less than 0.95 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate good support (100% bs or 1.00 pp). The branches with more than 95% bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with Talaromyces flavus CBS 310.38T.

Clade 1: section Aspergilloides

Clade 2: section Sclerotiora

Clade 3: section Charlesii

In: Penicillium subgenus Aspergilloides

Type: Penicillium sclerotiorum van Beyma

Houbraken & Samson

Mycobank MB563124.

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

*Penicillium adametzii* Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 507. 1927.

*Penicillium adametzioidei* Abe ex Smith, Trans. Br. Mycol. Soc. 46: 335. 1963.

*Penicillium angulare* Peterson, Bayer & Wicklow, Mycologia 96: 1289. 2004.

*Penicillium biliae* Chalabuda, Bot. Mater. Otd. Sporov. Rast. 6: 165. 1950.

*Penicillium brocae* Peterson, Pérez, Vega & Infantef, Mycologia 95: 143. 2003.

*Penicillium caurni* Rivera & Seifert, Stud. Mycol. 70: 147. 2011.

*Penicillium guanacastense* Rivera, Urb & Seifert, Mycotaxon, in press. 2011.

*Penicillium herquei* Bainier & Sartory, Bull. Soc. Mycol. France 28: 121. 1912.

*Penicillium hirayamae* Udagawa, J. Agric. Sci. Tokyo Nogyo Daigaku 5: 6. 1959.

*Penicillium jacksonii* Rivera & Seifert, Stud. Mycol. 70: 151. 2011.

*Penicillium johnkrugei* Rivera & Seifert, Stud. Mycol. 70: 151. 2011.

*Penicillium jugoslavicum* Ramirez & Muntañola-Cvetkovic, Mycopathol. 88: 65. 1984.

*Penicillium malachitenum* (Yaguchi & Udagawa) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).

*Penicillium mallochii* Rivera, Urb & Seifert Mycotalon, in press. 2011.

*Penicillium nodositatum* Valla, Plant and Soil 114: 146. 1989.

*Penicillium sclerotiorum* van Beyma, Zentralbl. Bakteriol., 2. Abt., 96: 418. 1937.

*Penicillium viticola* Nonaka & Masuma, Mycoscience 52: 339. 2011.

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

*Penicillium* in *Penicillium* subgen. *Aspergilloides*. *Solum* in *CYA* and have conidiophores with an apical swelling. Species of this section can be strictly monoverticillate, but *P. charlesii* and *P. fellutanum* can also be irregularly biverticillate. Included species are based on the data presented in Fig. 8 and Peterson (2000a) and Peterson et al. (2005).

*Penicillium charlesii* Smith, Trans. Br. Mycol. Soc. 18: 90. 1933.

*Penicillium coffeae* Peterson, Vega, Posada & Nagai, Mycologia 97: 662. 2005.

*Penicillium fellutanum* Bourge, Cellule 33: 262. 1923.

*Penicillium georgiense* Peterson & Horn, Mycologia 101: 79. 2009.

*Penicillium indicum* Sandhu & Sandhu, Can. J. Bot. 41: 1273. 1963 (syn. *P. gerundense*, Peterson & Horn 2009).

*Penicillium phoeniceum* van Beyma, Zentralbl. Bakteriol., 2. Abt., 88: 136. 1933.

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

Secio in *Penicillium* subgen. *Aspergilloides*. Colonii pulli, conidiophorae pigmentatae, compactae et incremento secundario stipitis per proliferationem penicillii apicali.

*Penicillium* in *Penicillium* subgen. *Aspergilloides* Type: *Penicillium charlesii* Smith

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

*Penicillium charlesii* Smith, Trans. Br. Mycol. Soc. 18: 90. 1933.

*Penicillium coffeae* Peterson, Vega, Posada & Nagai, Mycologia 97: 662. 2005.

*Penicillium fellutanum* Bourge, Cellule 33: 262. 1923.

*Penicillium georgiense* Peterson & Horn, Mycologia 101: 79. 2009.

*Penicillium indicum* Sandhu & Sandhu, Can. J. Bot. 41: 1273. 1963 (syn. *P. gerundense*, Peterson & Horn 2009).

*Penicillium phoeniceum* van Beyma, Zentralbl. Bakteriol., 2. Abt., 88: 136. 1933.

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

Secio in *Penicillium* subgen. *Aspergilloides*. Colonii pulli, conidiophorae pigmentatae, compactae et incremento secundario stipitis per proliferationem penicillii apicali.

*Penicillium* in *Penicillium* subgen. *Aspergilloides* Type: *Penicillium glauco-albidum* Desmazières

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

*Penicillium asymmetircicum* (Subramanian & Sudha) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).

*Penicillium coniferophilum* Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).

*Penicillium glauco-albidum* (Desmazières) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).

*Penicillium hennebertii* Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).

*Penicillium longisporum* (Kendrick) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).

*Penicillium taiwanense* (Matsushima) Houbraken & Samson, Stud. Mycol. 70: 48. 2011 (this study).

*Penicillium taxi* Schneider, Zentralblatt für Bakteriologie und Parasitenkunde, Abteilung 2, 110: 43. 1956.

Clade 5: section *Ochrosalmonea* Houbraken & Samson, sect. nov. MycoBank MB563127.
In: *Penicillium* subgenus *Aspergilloides*

**Type:** *Penicillium ochrosalmoneum* Udagawa

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

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

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

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

Clade 6: section *Cinnamopurpurea* Houbraken & Samson, sect. nov. MycoBank MB8563128.

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

In: *Penicillium* subgenus *Aspergilloides*

**Type:** *Penicillium cinnamopurpureum* Udagawa

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Fig. 9. *Penicillium isariiforme* CBS 247.56. A. Colonies grown for 14 d at 25 °C, from left to right: MEA, YES, CYA. B–D. Conidiophores. E. Conidia. Scale bar = 10 µm.
Members of section *Cinnamopurpurea* grow slowly on MEA and CYA and can be strictly monovervitectillate, but species with biverticillate conidiophores are also present in this section. The majority of the species have distinct vesicular conidiophores. This section is phenotypically related to section *Omnata*; however, statistical support for this relationship is lacking in our phylogenetic analysis (Fig. 7).

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

*Penicillium chermesinum* is also placed in this section. This species was neotypified with NRRL 2048 (= CBS 231.81), because the type culture, NRRL 735, no longer adequately represented the type strains of *P. indicum* (sect. *Ramigena*, Fig. 10) and *P. cinnamopurpureum* (Peterson 2000a) while the neotype of this species, NRRL 2048 (AY742693) is related to *P. indicum* in section *Charlesii*. Based on the data presented in Fig. 10 and Peterson & Horn (2009), the following species are accommodated in *Cinnamopurpurea*.

*Penicillium chermesinum* Biourge, Cellule 33: 284. 1923.

*Penicillium cinnamopurpureum* Udagawa, J. Agric. Food Sci., Tokyo 5: 1. 1959.

*Penicillium ellipsoideosporum* Wang & Kong, Mycosistema 19: 463. 2000.

*Penicillium idahoense* Paden, Mycopath. Mycol. Appl. 43: 261. 1971 (Peterson & Horn 2009, this study).

*Penicillium incoloratum* Huang & Qi, Acta Mycol. Sin. 13: 264. 1994.

*Penicillium malacaense* Ramirez & Martinez, Mycopathologia 72: 186. 1980 (syn. *P. ovetense*, this study) (Peterson & Horn 2009).

*Penicillium nodulum* Kong & Qi, Mycosistema 1: 108. 1988.

*Penicillium parvulum* Peterson & Horn, Mycologia 101: 75. 2009.

*Penicillium shennangiangii* Kong & Qi, Mycosistema 1: 110. 1988.

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

In: *Penicillium* subgenus *Aspergilloides*

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

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

*Penicillium capsulatum* Raper & Fennell, Mycologia 40: 528. 1948.

*Penicillium cyaneum* (Bainier & Sartory) Biourge, Cellule 33: 102. 1923.

*Penicillium dierckxii* Biourge, Cellule 33: 313. 1923.

*Penicillium hispanicum* Ramírez, Martínez & Ferrer, Mycopath. 66: 77. 1978 (syn. *Penicillium implicatum sensu* Pitt).

*Penicillium ornatum* Udagawa, Trans. Mycol. Soc. Japan 9: 49. 1968.

*Penicillium ramulosum* Batista & Maia, Anais Soc. Biol. Pernamb. 13: 27. 1955 (syn. *P. brevissimum* Rai & Wadhwani) this study, Peterson & Horn 2009).

*Penicillium sublatentum* Biourge, Cellule 33: 315. 1923.

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

In: *Penicillium* subgenus *Aspergilloides*

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

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

*Penicillium cryptum* Gochenaur, Mycotaxon 26: 349. 1986.

*Penicillium lagena* (Delitsch) Stolk & Samson, Stud. Mycol. 23: 100. 1983.

*Penicillium laeve* (K. Ando & Manoch) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).

*Penicillium lassenii* Paden, Mycopath. Mycol. Appl. 43: 266. 1971.

*Penicillium ovatum* (K. Ando & Nawawi) Houbraken & Samson, Stud. Mycol. 70: 48. 2011 (this study).

*Penicillium parviverrucosum* (K. Ando & Pitt) Houbraken & Samson, Stud. Mycol. 70: 48. 2011 (this study).

*Penicillium porphyreum* Houbraken & Samson, Stud. Mycol. 70: 48. 2011 (this study).

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

Sectio in Penicillio subgen. Aspergilloide. Colonis in agar tarde crescentibus; ascosporis spinulosis; phialidibus ampulliformibus vel lanceolatis; conidios ellipsoides.
In: *Penicillium* subgenus Aspergilloides

Type: *Penicillium ornatum* Udagawa

*Penicillium inusitatum* and *P. fractum* belong to section *Fracta* and both are able to form a teleomorph. Pitt (1980) noted that these two species are closely related, differing principally in conidiophore structure. Both species share unusual ascospore morphology for...
Penicillium species: the ascospores are spheroidal without flanges or furrows and ornamented by spines. Furthermore, both species grow slowly on agar media, form ampulliform to lanceolate phialides and elliptical conidia. Phylogenetically, section *Fracta* might be related to section *Torulomyces* (72 % bs, < 0.95 pp). However, ascospores produced by the members of the latter section have two ridges (*P. lagena, P.lassenii, P. cryptum*).

**Penicillium fractum** Udagawa, Trans. Mycol. Soc. Japan 9: 51. 1968.

**Penicillium insitusatum** Scott, Mycopathol. Mycol. Appl. 36: 20. 1968.

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

In: *Penicillium* subgenus *Aspergilloides*

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

Pitt (1980) defined section *Exilicaulis* for monoverticillate species with stipes lacking a terminal vesicular swelling. The phylogenetic delimitation is broader and also several species with an additional segment, two ridges (*P. lassenii*, *P. lagena*). Furthermore, both species belong to section *Fracta*, but our data shows that this species is closely related to *P. nanyslowskii*.

**Penicillium corynephorum** Zaleski, Bull. Int. Acad. Polonc. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 194. 1927.

**Penicillium neapalense** Takada & Udagawa, Trans. Mycol. Soc. Japan 24: 146. 1983.

**Penicillium parvum** Raper & Fennell, Mycologia 40: 508. 1948 (this study).

**Penicillium philippinense** Udagawa & Y. Horie, J. Jap. Bot. 47: 341. 1972.

**Penicillium pimiteouiense** Zaleski, Bull. Int. Acad. Polonc. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 454. 1927.

**Penicillium restrictum** Gilman & Abbott, Iowa State Coll. J. Sci. 1: 287. 1927.

**Penicillium rubefaciens** Quintanilla, Mycopathol. 80: 73. 1982.

**Penicillium rubidurum** Udagawa & Horie, Trans. Mycol. Soc. Japan 14: 381. 1973.

**Penicillium smithii** Quintanilla, Avances Nutr. Mejora Anim. Aliment. 23: 340. 1982 (syn. *P. corynephorum, P. sabulosum*).

**Penicillium striatissporum** Stolk, Ant. van Leeuwenhoek 35: 36. 1969.

**Penicillium terrenum** Scott, Mycopathol. Mycol. Appl. 36: 1. 1968.

**Penicillium toxicarum** Miyake, Rep. Res. Inst. Rice Improvement 1: 1940 (nom. inval., Art. 36) (Serra et al. 2008).

**Penicillium velutinum** van Beyma, Zentralbl. Bakteriol., 2. Abt., 91: 297. 1927.

**Penicillium vinaceum** Gilman & Abbott, Iowa State Coll. J. Sci. 1: 299. 1927.

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

= section *Funiculosa* Thom, The Penicillia: 358. 1930.
= section *Divaricatum* Pitt, The Genus *Penicillium*: 238. 1980.
= section *Furcatum* Pitt, The Genus *Penicillium*: 272. 1980.

= Eupenicillium section *Javanica* (Pitt) Stolk & Samson, Stud. Mycol. 23: 55. 1983.

In: *Penicillium* subgenus *Aspergilloides*

Type: *Penicillium janthinellum* Biourge

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

Section *Funiculosa* is placed in synonymy with this section. Thom (1930) already noted that species belonging section...
Funiculosa have affinity with members of section Lanata-typica and that separation is hard to define. This observation is supported by our data: many species mentioned in Thom’s section Funiculosa belong to section Lanata-divaricata. Raper & Thom’s (1949) subsection Divaricata largely corresponds with our section Lanata-divaricata. They noted that members of their subsection have a definite relationship to Penicillium javanicum. Stolk & Samson (1983) also discussed this relationship and they placed 26 species in synonymy with Eupenicillium javanicum and P. simplicissimum. Recently, a phylogenetic study showed that many of these synonyms should be treated as separate species (Peterson 2000a, Houbraken et al. 2011c). This section largely corresponds with Peterson’s (2000a) group 5 and the list provided here for this section is mainly based on this data supplemented with data of Houbraken et al. (2011c). Penicillium cluniae, P. griseopurpureum and P. glaucoroseum were not included in these studies, though unpublished data shows that these three species also belong to this section.

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

Penicillium abdijanum Stolk, Ant. van Leeuwenhoek 34: 49. 1968. Penicillium araracuarens Houbraken, C. López-Q, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 61: 1469. 2011. Penicillium brasiliense Batista, Anais Soc. Biol. Pernambuco 15: 162. 1957. Penicillium brebeldianum Dodge, Mycologia 29: 92. 1933 (syn. P. dodgel).

Penicillium caperatum Udagawa & Horie, Trans. Mycol. Soc. Japan 14: 371. 1973 (syn. E. brebeldianum sensu Pitt). Penicillium cluniae Quintanilla, Avances Nutr. Mejora Anim. Alimient. 30: 174. 1990. (unpubl. data)

Penicillium coeruleum Sopp apud Biourge, Cellule 33: 102. 1923. Penicillium cremeosorum Chalabuda, Bot. Mater. Otd. Sporov. Rast. 6: 168. 1950.

Penicillium daleae Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér B, Sci. Nat., 1927. 495. 1927. Penicillium ehrlichii Klebahn, Ber. Deutsch. Bot. Ges. 48: 374. 1930.

Penicillium eilenia Houbraken, C. López-Q, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 61: 1470. 2011.

Penicillium gracilisemum Demelus, Verh. Zool.-Bot. Ges. Wien 72: 72. 1923. (unpubl. data)

Penicillium griseopurpureum Smith, Trans. Br. Mycol. Soc. 48: 275. 1965 (unpubl. data).

Penicillium janthinellum Biourge, Cellule 33: 258. 1923. Penicillium javanicum van Beyma, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect., 26: 17. 1929 (syn. P. oligosporum, P. indonesiae). Penicillium levitum Raper & Fennell, Mycologia 40: 511. 1948 (syn. P. rasile).

Penicillium limosum Ueda, Mycoscience 36: 451. 1995. Penicillium lineolatum Udagawa & Horie, Mycotaxon 5: 493. 1977. Penicillium ludwigii Udagawa, Trans. Mycol. Soc. Japan 10: 2. 1969. Penicillium mariaeae Crus Quintanilla, Avances Nutr. Mejora Anim. Alimient. 23: 334. 1982.

Penicillium meloforme Udagawa & Horie, Trans. Mycol. Soc. Japan 14: 376. 1973.

Penicillium ochrochororum Biourge, Cellule 33: 269. 1923. Penicillium onobense Ramírez & Martínez, Mycopathol. 74: 44. 1981.

Penicillium oxalicum Currie & Thom, J. Biol. Chem. 22: 289. 1915. Penicillium paraherquei Abe ex Smith, Trans. Br. Mycol. Soc. 46: 335. 1963.

Penicillium penarojense Houbraken, C. López-Q, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 61: 1471. 2011.

Penicillium piscarium Westling, Ark. Bot. 11: 86. 1911. Penicillium pulvillorum Turff, Trans. Br. Mycol. Soc. 23: 186. 1939 (Syn. P. ciegi). Penicillium raperi Smith, Trans. Br. Mycol. Soc. 40: 486. 1957. Penicillium reticulisorum Udagawa, Trans. Mycol. Soc. Japan 9: 52. 1968. (syn. P. arvensce).

Penicillium rolfsii Thom, Penicillia: 489. 1930. Penicillium simplicissimum (Oudemans) Thom, Penicillia: 335. 1930.

Penicillium skrjabinii Schmotina & Goloviche, Mikoł. Fitopatol. 8: 530. 1974.

Penicillium svalbardense Frisvad, Sonjak & Gunde-Cimeran, Ant. van Leeuwenhoek 92: 48. 2007.

Penicillium vanderhammenii Houbraken, C. López-Q, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 61: 1473. 2011.

Penicillium vasconiae Ramírez & Martínez, Mycopathol. 72: 189. 1980. Penicillium wotroi Houbraken, C. López-Q, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 61: 1474. 2011.

Penicillium zonatum Hodges & Perry, Mycologia 65: 697. 1973.

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

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

In: Penicillium subgenus Aspergilloides

Type: Penicillium stolkiae Scott

Brown conidiophores occur in two phylogenetic unrelated sections of Penicillium s. str. One includes species belonging to section Thysanophora (previously assigned to the genus Thysanophora) (Iwamoto et al. 2002, Peterson & Sigler 2002) and the second lineage is centered around P. stolkiae, another species with conidiophores that also may be hyaline to definitely brown (Stolk & Samson 1983). Peterson & Sigler (2002) described four species with darkly melanised conidiophores, which are all closely related to P. stolkiae, namely P. subarticm, P. canariense, P. pullum and
None of these species demonstrate the sympodial proliferation of subapical metulae and phialides present in section Thysanophora. The following species are placed in section Stolkia based on the data presented in Fig. 11 and of Peterson & Sigler (2002).

**Fig. 11.** Best-scoring Maximum Likelihood tree using RAxML based on partial β-tubulin sequences and giving an overview of the members accommodated in sections Lanata-divaricata and Stolkia. The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (pp/bs). Values less than 70 % supported in the ML or less than 0.95 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate good support (100 % bs or 1.00 pp). The branches with more than 95 % bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with *Penicillium glabrum* CBS 125543T.
Penicillium stalkiae Scott, Mycopathol. Mycol. Appl. 36: 8. 1968.
Penicillium subarcticum Peterson & Sigler, Mycol. Res. 106: 1116. 2002.

Clade 13: section Gracilenta Houbraken & Samson, sect. nov. MycoBank MB563131.
Sectio in Penicillo subgen. Aspergilloide. Colononia 37 °C haud crescentibus, reverso olivaceo-brunneo vel brunneo, conidiis saepe late ellipsoidis vel ellipsoidis.

In: Penicillium subgenus Aspergilloides

Type: Penicillium gracilentum Udagawa & Horie

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

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

Clade 14: section Citrina Houbraken & Samson, sect. nov. MycoBank MB563132.
Sectio in Penicillo subgen. Aspergilloide. Formatione conidiophorum symmetricorum biverticillatorum.

In: Penicillium subgenus Aspergilloides

Type: Penicillium citrinum Thom

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

Penicillium anatolicum Stolk, Ant. van Leeuwenhoek 34: 46. 1968.
Penicillium argentinense Houbraken, Frisvad & Samson, Stud. Mycol. 70: 78. 2011.
Penicillium atrofulvum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 80. 2011.
Penicillium aurantiacobrunneum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 80. 2011.
Penicillium cairnsense Houbraken, Frisvad & Samson, Stud. Mycol. 70: 83. 2011.
Penicillium christenseniae Houbraken, Frisvad & Samson, Stud. Mycol. 70: 85. 2011.
Penicillium chrzaszczii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 464. 1927.
Penicillium citrinum Thom, Bull. Bur. Anim. Ind. U.S. Dep. Agric. 118: 61. 1910.
Penicillium copticola Houbraken, Frisvad & Samson, Stud. Mycol. 70: 88. 2011.
Penicillium cosmopolitanum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 91. 2011.
Penicillium decaturense Peterson, Bayer & Wicklow, Mycologia 96: 1290. 2004.
Penicillium euglaucum van Beyma, Ant. van Leeuwenhoek 6: 269. 1940.
Penicillium gallicum Ramirez, Martinez & Berenguier, Mycopathol. 72: 30. 1980.
Penicillium godlewskii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 466. 1927.
Penicillium gorlenkoanum Baghdadi, Nov. Sist. Niz. Rast. 5: 97. 1968.
Penicillium hetheringtonii Houbraken, Frisvad & Samson, Fung. Div. 44: 125. 2010.
Penicillium manginin Düché & Heim, Trav. Cryptoq. Louis L. Mangin: 450. 1931 (syn. P. pedemontanum, Houbraken et al. 2011b).
Penicillium miczynskii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 492. 1927.
Penicillium neomiczynskii Cole, Houbraken, Frisvad & Samson, Stud. Mycol. 70: 105. 2011.
Penicillium nothofagi Houbraken, Frisvad & Samson, Stud. Mycol. 70: 105. 2011.
Penicillium panchosmum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 108. 2011.
Penicillium pasqualense Houbraken, Frisvad & Samson, Stud. Mycol. 70: 108. 2011.
Penicillium paxilli Bainier, Bull. Soc. Mycol. France 23: 95. 1907.
Penicillium quebecense Houbraken, Frisvad & Samson, Stud. Mycol. 70: 111. 2011.
Penicillium raphiae Houbraken, Frisvad & Samson, Stud. Mycol. 70: 114. 2011.
Penicillium roseopurpureum Dierckx, Ann. Soc. Sci. Bruxelles 25: 86. 1901.
Penicillium sanguifluum (Sopp) Biourge, La Cellule 33: 105. 1923.
Penicillium shearii Stolk & Scott, Persoonia 4: 396. 1967.
Penicillium sizovae Baghdadi, Novosti Sist. Nizs. Rast. 1968: 103. 1968.
Penicillium steckii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 469. 1927.
Penicillium sumatrense Szilvinyi, Archiv. Hydrobiol. 14, Suppl. 6: 535. 1936.
Penicillium terrigenum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 125. 2011.
Penicillium tropicoides Houbraken, Frisvad & Samson, Fung. Div. 44: 127. 2010.
Penicillium tropicum Houbraken, Frisvad & Samson, Fung. Div. 44: 129. 2010.
Penicillium ubiquetum Houbraken, Frisvad & Samson, Stud. Mycol. 70: 127. 2011.
Penicillium vancouverense Houbraken, Frisvad & Samson, Stud. Mycol. 70: 131. 2011.
Penicillium waksmanii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 468. 1927.
Penicillium wellingtonense Cole, Houbraken, Frisvad & Samson, Stud. Mycol. 70: 133. 2011.
Penicillium westlingii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 473. 1927.
Clade 14: sect. *Citrina*

- CBS 230.28T *P. waksmanii*
- CBS 215.28T *P. godlewskii*
- CBS 217.28T *P. chrysaszczi*
- CBS 117509T *P. decaturense*
- CBS 231.28T *P. westlingii*
- */* CBS 265.65T *P. pedemonatum*
- CBS 253.31NT *P. manginii*
- CBS 101623T *P. quebencense*
- CBS 220.28T *P. miczynskii*
- CBS 126236T *P. christenseni*
- CBS 126234T *P. raphae*
- CBS 122402T *P. pasqualense*
- CBS 130375T *P. wellingtonense*
- CBS 109.66T *P. atrofulvum*
- CBS 290.48T *P. shearii*
- CBS 360.48NT *P. paxilli*
- NRRL 779T *P. sumatrense*
- NRRL 6181 *P. sumatrense*
- CBS 416.69 *P. sumatrense*
- NRRL 35755 *P. alicantinum*
- CBS 167.81T *P. galliacum*
- CBS 148.83 *P. sanguifluum*
- CBS 685.85 *P. sanguifluum*
- CBS 266.29P. *roseopurpureum*
- */* CBS 323.71NT *P. euglaucum*
- CBS 479.66T *P. anatolicum*
- CBS 232.38 *P. citrinum*
- CBS 139.45T *P. citrinum*
- CBS 122392T *P. hetheringtonii*
- CBS 413.69NT *P. sizovae*
- CBS 112584T *P. tropicum*
- CBS 122410T *P. tropicoides*
- CBS 260.55NT *P. steckii*
- CBS 408.69T *P. gorenkoanum*
- CBS 127354T *P. ferrigenum*
- CBS 127355T *P. coptica*
- */* CBS 325.48NT *P. expansum*
- NRRL 35686 *P. commune*
- */* CBS 21622NT *Aspergillus paradoxus* (EF669670)
- CBS 231.60T *P. ochrosalmoneum*
- CBS 489.66P. *ochrosalmoneum*
- CBS 247.56T *P. isariforme*
- NRRL326NT *Aspergillus niger*
- CBS 310.38NT *Talaromyces flavus*

Clade 5: sect. *Ochrosalmonea*

- */* NRRL 326NT *Aspergillus niger*
- NRRL 326NT *Aspergillus flavus*
- CBS 310.38NT *Talaromyces flavus*

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

Clade 15: Section *Fasciculata* Thom, The Penicillia: 374. 1930.
- Section *Lanata-typica* Thom, The Penicillia: 305. 1930.
- Section *Viridicata* Frisvad & Samson. Stud. Mycol. 49: 27. 2004.

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium hirsutum* Dierckx

Sections *Lanata-typica* and *Viridicata* are placed in synonymy with section *Fasciculata*. *Lanata-typica* was erected for species with vegetative aerial mycelium consisting of lanose, cottony or floccose colonies and only a small portion of the species currently present this section produce such structures (*P. camemberti*, *P. commune*, *P. caseifulvum*). Most species of section *Fasciculata* have a granulose or fasciculate colony texture and therefore the name *Fasciculata* is given priority to *Lanata-typica*. The current definition of *Fasciculata*...
is similar to that of *Viridicata* (Frisvad & Samson 2004). All species grow rather quickly, except species in series *Verrucosa*, which grow slowly. Most species in this section have globose conidia and rough-walled conidiophore stipes. All species are psychrotolerant and grow well at low water activities (Frisvad & Samson 2004). Frisvad & Samson (2004) accommodated 28 species in section *Viridicata (= Fasciculata*). We excluded *P. atramentosum* from this section and placed this species in section *Paradoxa*. This species was placed in section *Fasciculata* based on its ability to grow on creatine as sole nitrogen source and its occurrence on cheese. However, Frisvad & Samson (2004) also noted that its ability to grow at very high pH values and the formation of smooth-walled stipes sets it apart from section *Fasciculata*. *Penicillium osmophilum* is tentatively accommodated in section *Viridicata*. Figure 13 shows that this species is most closely related to this section, but bootstrap support is lacking.

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

*Penicillium viridicatum* Westling, Ark. Bot. 11: 88. 1911.  
Clade 16: *Section Digitata* (as "Digitatum") Frisvad & Samson, Stud. Mycol. 49: 26. 2004.  
In: *Penicillium* subgenus *Penicillium*  
Type: *Penicillium digitatum* (Pers.:Fr.) Sacc.  
Section *Digitata* is represented by one species, *P. digitatum*. This species is unique in its combination of features. Conidiophore and conidial structures are irregular and exceptionally large for *Penicillium*, usually biverticillate rather than terverticillate and the conidia are olive-green. The conidia are large and ellipsoidal to cylindrical (Frisvad & Samson 2004). Partial β-tubulin (Samson et al. 2004) and RPB2 data (Fig. 13) show that this section is situated in subgenus *Penicillium*. Frisvad & Samson (2004) is followed here and this section is retained for *P. digitatum*.

*Penicillium digitatum* (Pers.:Fr.) Sacc., Fung. Ital.: 894. 1881.  
Clade 17: *Section Penicillium*  
− *Bulliardium* Bourge, La Cellule 33: 107. 1923 (= *Asymetrica*).  
In: *Penicillium* subgenus *Penicillium*  
Type: *Penicillium expansum* Link

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

*Penicillium brevistipitatum* Wang & Zhuang, Mycotaxon 93: 234. 2005.  
*Penicillium clavigerum* Demelius, Verh. Zool.-Bot. Ges. Wien 72: 74. 1922.  
*Penicillium concentricum* Samson, Stolk & Hadlok, Stud. Mycol. 11: 17. 1976.  
*Penicillium coprophilum* Frisvad, Mycologia 81: 853. 1989.  
*Penicillium coprophilum* (Berk. & Curt.) Seifert & Samson, Adv. Pen. Asp. Syst.: 145. 1985.  
*Penicillium dipodomyicola* (Frisvad, Filt. & Wicklow) Frisvad, Int. Mod. Meth. Pen. Asp. Clas.: 275. 2000.  
*Penicillium expansum* Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamten Naturk. 3: 16. 1809.  
*Penicillium forsanum* Hsieh, Su & Tzean, Trans. Mycol. Soc. R.O.C. 2: 159. 1987.  
*Penicillium gladioli* McCulloch & Thom, Science, N.Y. 67: 217. 1928.  
*Penicillium glandicola* (Oud.) Seifert & Samson, Adv. Pen. Asp. Syst.: 147. 1985.  
*Penicillium griseofulvum* Dierckx, Ann. Soc. Scient. Brux. 25: 88. 1901.  
*Penicillium italicum* Wehmer, Hedwigia 33: 211. 1894.  
*Penicillium marinum* Frisvad & Samson, Stud. Mycol. 49: 20. 2004.
Penicillium* sclerotigenum* Yamamoto, Scient. Rep. Hyogo Univ. Agric., Agric. Biol. Ser. 2, 1: 69. 1955.

Penicillium alba* Hsieh, Su & Tzean, Trans. Mycol. Soc. R.O.C. 2: 161. 1987.

Penicillium vulpinum* (Cooke & Massee) Seifert & Samson, Adv. Pen. Asp. Syst.: 144. 1985.

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

In: Penicillium subgenus Penicillum

Type: Penicillium roqueforti Thom

Frisvad & Samson (2004) erected section Roqueforti for rapidly growing species forming strictly velutinous colonies. All species form terverticillate rough walled conidiophores and are able to grow at low pH values (e.g. on media containing 0.5 % acetic acid), at high alcohol concentrations and at elevated CO₂ levels. Members of this section appear to have a symbiotic relationship with lactic acid bacteria and certain acid-tolerant yeasts. Currently, four species are described in this section (Frisvad & Samson 2004, Houbraken et al. 2010a):

Penicillium carneum* (Frisvad) Frisvad, Microbiology, UK, 142: 546. 1996.

Penicillium paneum* Frisvad, Microbiology (UK) 142: 546. 1996.

Penicillium psychrophorossexualis* Houbraken & Samson, IMA Fungus 1:174. 2010.

Penicillium roqueforti* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 82: 35. 1906.

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

In: Penicillium subgenus Penicillum

Type: Penicillium chrysogenum Thom

Members of the section Chrysogena are characterised by the formation of ter- and/or quarterverticillate, smooth walled conidiophores with relatively small phialides. Colonies have a velvety texture and species are tolerant to salt and the majority is capable to produce penicillin relatively small phialides. Colonies have a velvety texture and species are characterised by the formation of a teleomorph in Clade 19: section Chrysogena. Frisvad & Samson (2004) erected section Chrysogena (Frisvad & Samson 2004). Four teleomorph species belong to section Turbata and are characterised by the formation of a teleomorph in Clade 19: section Chrysogena. Frisvad & Samson (2004, Houbraken c et al. 2011). Pitt (1980) transferred the teleomorphic Chrysogena (Frisvad & Samson 2004). Four teleomorph species belong to section

Penicillium confertum* (Frisvad et al.) Frisvad, Mycologia 81: 852. 1990.

Penicillium dipodomyis* (Frisvad, Filtenborg & Wicklow) Banke, Frisvad & Rosendahl, Int. Mod. Meth. Pen. Asp. Clas., 270. 2000.

Penicillium egyptiacum* van Beyma, Zentralbl. Bakteriol., 2. Abt., 88: 137. 1933. (syn. P. nilense).

Penicillium flavigenum* Frisvad & Samson, Mycol. Res. 101: 620. 1997.

Penicillium kewense* Smith, Trans. Br. Mycol. Soc. 44: 42. 1961 (syn. E. crustaceum).

Penicillium molle* Pitt, The Genus Penicillium: 148, 1980 ["1979].

Penicillium mononematosum* (Frisvad et al.) Frisvad, Mycologia 81: 857. 1990.

Penicillium nalgiovense* Laxa, Zentralbl. Bakteriol., 2. Abt., 86: 160. 1932.

Penicillium persicinum* Wang, Zhou, Frisvad & Samson, Ant. van Leeuwenhoek 86: 177. 2004.

Penicillium rubens* Bourge, Cellule 33: 265. 1923.

Penicillium sicaicum* Udagawa & Ueda, Mycotaxon 14: 266. 1982.

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

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

In: Penicillium subgenus Penicillum

Type: Penicillium turbatum Westling

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

Penicillium bovificosum* (Tuthill & Frisvad) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 (this study).

Penicillium matri* Smith, Trans. Br. Mycol. Soc. 44: 44. 1961.

Penicillium turbatum* Westling, Ark. Bot. 11: 128. 1911 (syn. E. baumense, P. baumense, this study).

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

Secio in Penicillo subgen. Penicillo. Speciebus saepe cum conidiophoris typi Aspergillus et odore molesti effereinti.

In: Penicillium subgenus Penicillum

Type: Aspergillus paradoxous Fennell & Raper

Aspergillus paradoxous, A. malodoratus, A. crystallinus and P. ateramentosum form a well-supported clade (85 % bs, 1.00 pp). Phylogenetic and extrolite analysis shows that the first three species belong in Penicillum and will be transferred to this genus (R.A. Samson, unpubl. data). Besides a similar type of Aspergillus anamorph, these three species also produce a strong, unpleasant smell. Penicillium ateramentosum is phylogenetically basal to these three species. This species is alkaliphilic and unpublished results show that this character is shared with A. paradoxous. More research
Fig. 13. Best-scoring Maximum Likelihood tree using RAxML based on partial RPB2 sequences and giving an overview of the members accommodated in subgenus Penicillium (clades 15–25). The BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes (pp/bs). Values less than 70% supported in the ML or less than 0.95 in the Bayesian analysis are indicated with a hyphen, whereas asterisks indicate good support (100% bs or 1.00 pp). The branches with more than 95% bootstrap support and 1.00 posterior probability values are thickened. The bar indicates the number of substitutions per site. The tree is rooted with Talaromyces flavus CBS 310.38NT.
is needed to determine whether *A. malodoratus* and *A. crystallinus* also share this feature.

*Penicillium atramentosum* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 65. 1910.

*Aspergillus crystallinus* Kwon-Chung & Fennell, The Genus *Aspergillus*: 471. 1965.

*Aspergillus malodoratus* (Kwon-Chung & Fennell), The Genus *Aspergillus*: 468. 1965.

*Aspergillus paradoxus* Fennell & Raper, Mycologia 47: 69.

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

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

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium brevicompactum* Dierckx

Members of the section *Brevicompacta* are characterised by conidiophores with long and broad stipes. The conidial heads look superficially like *Aspergillus* heads in the stereomicroscope. Section *Coronata*, typified with *P. olsonii*, is placed here in synonymy. Recently, *P. neocrassum* and *P. astrolobatum* were described in this section (Serra & Peterson 2007) and partial RPB2 data (Fig. 13) show that also *P. tularensis* and *P. fennelliae* belong here. The production of the extrolites asperphenamate and the unknown metabolite O (Frisvad & Samson 2004) is shared by these metabolites are also produced by the other members of this section are on a well-supported branch with clade in two sections based on phenotypic characters and extrolite patterns. Members of the section *Lanosa* form biverticillate or terverticillate conidiophores with divergent rami (twice biverticiliate), while members of sect. *Brevicompacta* have appressed branches. *Penicillium jamesonlandense*, *P. lanosum*, *P. raistrickii*, *P. soppii* and *P. wiecickii* produce different combinations of cycloaspeptide, kojic acid and griseofulvin (Frisvad & Fitlenborg 1990, Frisvad et al. 2006) and these extrolites are not detected in this section (Frisvad & Samson 2004). More research is needed to determine if the other members of this section also produce cycloaspeptide, kojic acid and/or griseofulvin.

*Penicillium scabrosum* Stolk, Ant. van Leeuwenhoek 35: 261. 1969.

*Penicillium neocrassum* Serra & Peterson, Mycologia 99: 81. 2007.

*Penicillium olsonii* Bainier & Sartory, Ann. Mycol. 10: 398. 1912.

*Penicillium tularensis* Paden, Mycopathol. Mycol. Appl. 43: 264. 1971.

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

In: *Penicillium* subgenus *Penicillium*

Type: *Penicillium lanosum* Westling

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

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

![Phylogeny of Penicillium and Trichocomaceae](image_url)
Penicillium jamesonlondense Frisvad & Overy, Int. J. Syst. Evol. Microbiol. 56: 1435. 2006.

Penicillium kajigenum Smith, Trans. Br. Mycol. Soc. 44: 43. 1961.

Penicillium lansum Westling, Ark. Bot. 11: 97. 1911.

Penicillium raistricki Smith, Trans. Br. Mycol. Soc.18: 90. 1933.

Penicillium ribeum Frisvad & Overy, Int. J. Syst. Evol. Microbiol. 56: 1436. 2006.

Penicillium saporii Quintanilla, Avances Nutr. Mejora Anim. Aliment. 22: 539. 1981.

Penicillium scabrosum Frisvad, Samson & Stolk, Persoonia 14: 177. 1990.

Penicillium simile Davolos, Pietrangeli, Persiani & Maggi, J. Syst. Evol. Microbiol., in press.

Penicillium soppii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 476. 1927.

Penicillium sweicickii Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B 1927: 474. 1927.

Penicillium virgatum Nirenberg & Kwasna, Mycol. Res. 109: 977. 2005.

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

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

In: Penicillium subgenus Penicillium

Type: Penicillium canescens Sopp

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

Penicillium canescens Sopp, Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 11: 181. 1912.

Penicillium jensenii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 494. 1927.

Penicillium yarmokense Baghdadi, Nov. Sist. Niz. Rast. 5: 99. 1968.

Penicillium janczewskii Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., 1927: 488. 1927.

Penicillium antarcticum Hocking & McRae, Polar Biology 21: 103. 1999.

Penicillium atrovenetum Smith, Trans. Br. Mycol. Soc. 39: 112. 1956.

Penicillium novae-zeelandiae van Beyma, Ant. van Leeuwenhoek 6: 275. 1940.

Penicillium coralligerum Nicot & Pionnat, Bull. Soc. Mycol. France 78: 245. 1963 (“1962”).

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

In: Penicillium subgenus Penicillium

Type: Penicillium sacculum Dale

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

Penicillium sacculum Dale apud Biourge, Cellule 33: 323. 1923.

Penicillium senticosum Scott, Mycopathol. Mycol. Appl. 36: 5. 1968.

Excluded and unclassified Penicillia

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

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

Penicillium griseolum is listed as a synonym of P. restrictum (Pitt et al. 2000). However, Fig. 7 shows that these species are phylogenetically unrelated. In our study, we did not find any species closely related to P. griseolum and this species might represent a separate section. We have chosen not to proceed with the description of this new section for this species until additional related species are described.
Penicillium arenicola Chalabuda, Bot. Mater. Otd. Sporov. Rast. 6: 162. 1950 (= clade 6, related to Phialomyces).

Penicillium inflatum Stolk & Malla, Persoonia 6: 197. 1971. (= Aspergillus inflatus, R.A. Samson, unpubl. data).

Penicillium kabunicum Baghdadi, Novosti Sist. Nizs. Rast.: 98. 1968 (unrelated to Penicillium, J. Houbraken, unpubl. data).

Penicillium lineatum Pitt, The Genus Penicillium: 485. 1980 ["1979"] (= Hamigera striata).

Penicillium megasporum Orpurt & Fennell, Mycologia 47: 233. 1955 (= clade 3, related to Hamigera and Warcupiella).

Penicillium moldavicum Milko & Beliakova, Novosti Sist. Nizs. Rast.: 1967: 255. 1967 (unrelated to Penicillium, J. Houbraken, unpubl. data).

Penicillium syriacum Baghdadi, Novosti Sist. Nizs. Rast.: 111. 1968 (nomen ambiguum, Christensen et al. 1999).

Character analysis

The classification proposed in the monographs of Raper & Thom (1949), Pitt (1980) and Ramírez (1982) is not concordant with the new classification system proposed here. One of the most important characters in these monographs is the branching pattern of the Penicillium conidiophore. Our study shows that monoverticillate (Aspergillloid) conidiophores occur in various sections (e.g. clades 1, 2, 6, 8, 10, 12, 25). Sections Aspergilloides (clade 1) and Eladia (clade 25) comprise only strictly monoverticillate species, while mono- and biverticillate species are intermingled in the other clades.

The occurrence of both structures in multiple phylogenetic clades (sections) indicates that reduction of the Penicillium conidiophore might have occurred various times. Most of the species belonging to section Citrina (clade 14) are symmetrically biverticillate and occasionally additional branches with the same branching pattern as the main axis (“double symmetrically biverticillate”) occurs. Species belonging to section Lanata-divaricata are mainly divaricate and the metulae are borne terminally, subterminally and in intercalary positions. Terverticillate conidiophores mainly occur in clades 15–18 and section Chrysogena (clade 19) comprises species with quarterverticillate conidiophores. The monoverticillate species Penicillium sacculum and P. senticosum belong to clade 25.

The clade is positioned in subgenus Penicillium and has therefore a unique branching pattern for this subgenus. Growth rates on agar media are also frequently used for classification. Some sections mainly comprise fast growing species (e.g. clades 1, 2, 11, 16, 18, 19, 25) while in other clades slow growing species predominate (e.g. clades 3, 6, 8, 9). The new proposed sectional classification will serve as a starting point to investigate phenotypic characters used for classification.

TAXONOMIC IMPLICATIONS

Penicillium asymmetricum (Subramanian & Sudha) Houbraken & Samson, comb. nov. MycoBank MB561963.

Basionym: Thysanophora asymmetrica Subramanian & Sudha, Kavaka 12: 88. 1985.

Penicillium bovifimosum (Tuthill & Frisvad) Houbraken & Samson, comb. nov. MycoBank MB561957.

Basionym: Eupenicillium bovifimosum Tuthill & Frisvad, Mycologia 94: 241. 2002.

Penicillium coniferophilum Houbraken & Samson, nom. nov. MycoBank MB561968.

Basionym: Thysanophora striatspora Barron & Cooke, Mycopathologia et Mycologia Applicata 40: 353. 1970, non Penicillium striatsporum Stolk, Ant. van Leeuwenhoek 35: 268. 1969.

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

Penicillium glaucoalbidum (Desmazières) Houbraken & Samson, comb. nov. MycoBank MB561965.

Basionym: Sclerotium glaucoalbidum Desmazières, Annales des Sciences Naturelles, Botanique 16: 329. 1851.

= Thysanophora glaucoalbida (Desm.) Morelet, Annales de la Société des Sciences Naturelles et Archéologie de Toulon et Var 20: 104. 1968.

= Thysanophora penicillioides (Roumeguère) Kendrick, Can. J. Bot. 39: 820. 1961.

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

Penicillium hennebertii Houbraken & Samson, nom. nov. MycoBank MB561964.

Basionym: Thysanophora canadensis Stolk & Hennebert, Persoonia 5: 189. 1968, non Penicillium canadense Smith, Trans. Br. mycol. Soc. 39: 113. 1956.

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

Penicillium laeve (K. Ando & Manoch) Houbonen & Samson, comb. nov. MycoBank MB561960.

Basionym: Torulomyces laevis K. Ando & Manoch, Mycoscience 39: 317. 1998.

Penicillium longisporum (Kendrick) Houbraken & Samson, comb. nov. MycoBank MB561966.

Basionym: Thysanophora longispora Kendrick, Can. J. Bot. 39: 826. 1961.

Penicillium malachiteum (Yaguchi & Udagawa) Houbraken & Samson, comb. nov. MycoBank MB561971.

Basionym: Chromoleista malachitae Yaguchi & Udagawa, Trans. Mycol. Soc. Japan 34: 102. 1993.

= Geosmithia malachitae Yaguchi & Udagawa, Trans. Mycol. Soc. Japan 34: 102. 1993.

Penicillium melanostipe Houbraken & Samson, nom. nov. MycoBank MB561970.

Basionym: Thysanophora verrucosa Mercado, Gené & Guaro, Mycotaxon 67: 481. 1998, non Penicillium verrucosum Dierckx, Annales de la Société Scientifique de Bruxelles 25: 88. 1901.

Note: The name Penicillium verrucosus is already occupied and therefore the name melanostipe, which is referring to the pigmented stipe of this species, is proposed.
Penicillium ovatum (K. Ando & Nawawi) Houbraken & Samson, comb. nov. MycoBank MB561961. Basionym: Torulozymes ovatus K. Ando & Nawawi, Mycoscience 39: 317. 1998.

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

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

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

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

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

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

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Yaguchi T, Someya A, Udagawa S (1994). Two new species of the British Mycological Society 44: 437–440.

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### Table S1. *Penicillium* strains used in the study of the infrageneric classification (addition to those mentioned in Table 1).

| Name | Collection no. | Origin | GenBank accession no. |
|------|----------------|--------|-----------------------|
| Aspergillus crystallinus | NRRL 5082** | Forest soil, Costa Rica | EF69669** |
| Aspergillus malodoratus | CBS 5083** | Forest soil, Costa Rica | EF69672** |
| Aspergillus paradoxus | NRRL 2162** | Holotype of *Hemicarpenteles paradoxus*; dung of opossum, Wellington, New-Zealand | EF69670** |
| Eladias infata | CBS 127833** | Unknown source, India | EF69671** |
| P. abidjanum | CBS 246.67** | Savannah soil, Ivory Coast | GU981650** |
| P. adametzioides | CBS 247.65** | Soil, Japan | JN406578** |
| P. aethiopicum | CBS 248.84** | Grain of *Hordeum vulgare*, Addis Abeba, Ethiopia | JN406549** |
| P. albicans | CBS 249.66** | Soil, Turkey | JN406576** |
| P. angulare | CBS 250.84** | Old polypore, New Mexico, USA | JN406570** |
| P. angustipurcatum | CBS 251.84** | Forest soil, Nandanda, Nepal | JN406577** |
| P. antarcticum | CBS 255.67** | Soil scraping, near nest site of Southern Fulmar Adery, Windmill Islands, Wilkes Land, Antarctica | JN406549** |
| P. araracuarense | CBS 256.67** | Leaf litter exposed for 6 months, 36-year old forest, Araracuara, Colombia | GU981629** |
| P. ardesiacum | CBS 257.67** | Soil near *Vitis vinifera*, Alma-Ata Region, Kazakhstan | JN406547** |
| P. asperosporum | CBS 258.83** | Holotype of *P. echinosporum*; resin of *Eucalyptus tereticornis*, Prov. Guizhon, Guiyang, China | JN406574** |
| P. astrolabium | CBS 259.27** | Wine grapes, Portugal | JN406634** |
| P. atramentosum | CBS 259.48** | French Camembert cheese, Storrs, Connecticut, USA | JN406584** |
| P. atrofulvum | CBS 260.66** | Soil, Katanga, Zaire | JN606620** |
| P. atrosanguineum | CBS 261.66** | Grain in silo *Triticum aestivum*, Praha, Czech Republic | JN406573** |
| P. aurantiogriseum | CBS 262.89** | Soil under conifers, Białowieża Forest, Poland | JN406600** |
| P. boreae | CBS 263.47** | Soil, Kiev, Ukraine | JN406610** |
| P. brevicompactum | CBS 264.29** | Petroleum contaminated soil, near Norman Wells, Northwest-Territories, Canada | JN606775** |
| P. brevispathum | CBS 265.29** | Dry cow manure, Wyoming, USA | JN406649** |
| P. brocace | CBS 266.64** | Herbarium specimen, Recife, Brazil | GU981629** |
| P. caperatum | CBS 267.61** | Neotype of *E. brevispathum* fide Pitt (1979, p. 119); soil, Murrumbidgee Irrigation Area, NSW, Australia | GU981659** |
| Name                    | Collection no. | Origin                                      | GenBank accession no. |
|-------------------------|----------------|---------------------------------------------|-----------------------|
| *P. caperatum*          | CBS 443.75 = ATCC 28046 | Soil, Papua New Guinea                      | GU981660**          |
| *P. capsulatum*         | CBS 301.49 = ATCC 10420 = IJFM 5120 = IMI 040576 = NRRL 2056 | Optical instrument, Canal Zone, Panama       | JN406582**          |
| *P. carneum*            | CBS 112297 = IBT 6884 | Mouldy rye bread, Denmark                   | JN406642**          |
| *P. chalybeum*          | CBS 255.87 = FRR 2658 = IMI 288722 | Dried fish, Decapterus sp., Indonesia       | JN406594**          |
| *P. charlesi*           | CBS 326.59 = ATCC 18225 = IMI 068223 | Type of Penicillium dembuncs var. atrovirens and *P. atrovirens*; soil, Japan | JN406571**          |
| *P. charlesi*           | CBS 330.59 = IMI 068224 = MUCL 15638 | Type of *P. fellutanum var. nigrocastaneum*; soil, Japan | JN406570**          |
| *P. ‘chermesinum’*      | CBS 305.48 = ATCC 10424 = IMI 040577 = NRRL 2049 | Air, Panama                                 | JN406581**          |
| *P. christensenae*      | CBS 126236 = IBT 23355 | Soil in native forest, “Lowland forest” east / north east side of Costa Rica about 30 km inland from Limon and the Caribbean. | JN606624**          |
| *P. ciegleri*           | CBS 275.83 = IMI 257691 | Forest soil, Kiev, Ukraine                  | GU981671**          |
| *P. cinereum*           | CBS 222.66 = ATCC 22350 = IJFM 5024 = IMI 113676 | Rye grain, Spain                            | GU981660**          |
| *P. cinamopurpureum*    | CBS 847.68 = ATCC 18489 = CBS 429.65 | Milled rice, Japan                          | JN406533**          |
| *P. citreonigrum*       | NRRL 1187 = IMI 092212 = MUCL 29230 = MUCL 29783 = NRRL 1187 | Type of *P. citreoiviride*; unknown source  | EF198501**          |
| *P. coeruleum*          | CBS 141.45 = NCTC 6595 | As *Citreomyces coeruleus*; unknown source   | GU981655**          |
| *P. commune*            | NRRL 35686      | Unknown source                              | EF198602**          |
| *P. confertum*          | CBS 171.87 = IBT 21515 = IBT 3098 = IBT 5672 = IMI 296930 = NRRL 13488 = NRRL A-26904 | Cheek pouch of Dipodomy spectabilis, Arizona, USA | JN406622**          |
| *P. coralligerum*       | CBS 123.65 = ATCC 16966 = FRR 3465 = IMI 099159 = NRRL 3465 | Seed of *Hordeum vulgare* (barley), France | JN406632**          |
| *P. corylophilum*       | CBS 330.79 = IJFM 5147 | Authentic strain of *P. citreoviride* Abe ex Ramírez; air, Barcelona, Spain | JN406569**          |
| *P. corynephorum*       | CBS 256.87 = FRR 2683 = IMI 288724 | Dried fish, Decapterus sp., Indonesia       | JN406599**          |
| *P. creneogerisum*      | CBS 233.66 = ATCC 18323 = IJFM 5011 = IMI 197492 = NRRL 3369 | Forest soil, Kiev, Ukraine                  | GU981624**          |
| *P. crocicola*          | CBS 745.70 = ATCC 18313 | Crocus sativus (Saffron), Japan              | JN406535**          |
| *P. cyanum*             | CBS 315.48 = ATCC 10432 = IMI 039744 = NRRL 775 | Unrecorded source, France                   | JN406575**          |
| *P. daeleae*            | CBS 211.28 = ATCC 10436 = IFO 6087 = IFO 9072 = IMI 034910 = MUCL 29234 = NRRL 2025 | Soil under conifer, Poland                  | GU981649**          |
| *P. decaturense*        | CBS 117509 = IBT 27117 = NRRL 28152 | Old resupinate fungus, Ramsey Lake State Park, Decatur, Illinois, USA | JN606621**          |
| *P. decumbens*          | CBS 230.81 = IMI 190875 = MUCL 29107 = NRRL 741 | Unrecorded source, Miami, Florida, USA       | JN406601**          |
| *P. dierckxii*          | CBS 185.81 = IMI 092216 = MUCL 28865 = NRRL 755 | Unknown source, Belgium                     | JN406619**          |
| *P. donkii*             | CBS 188.72 = ATCC 48439; = IFO 31746 = IMI 197489 = MUCL 31188 | Arable soil, Alaska, USA                    | JN617718**          |
| *P. echinulonalgiovense*| CBS 328.59 = ATCC 18314 = IFO 6229 = IMI 068213 | Soil, Japan                                 | GU981631**          |
| *P. egyptiacum*         | CBS 244.32 = ATCC 10441 = IBT 14684 = IMI 040580 = NRRL 2090 | Soil, Cairo, Egypt                          | JN406598**          |
## SUPPLEMENTARY INFORMATION

### Table S1. (Continued).

| Name                | Collection no. | Origin                                      | GenBank accession no. |
|---------------------|----------------|----------------------------------------------|-----------------------|
| *P. ehrlichii*      | CBS 324.48T = ATCC 10442 = IMI 039737 = NRRL 708 | Poland                        | GU981652T             |
| *P. elleniae*       | CBS 118135’ = IBT 23229                          | Leaf litter exposed for 6 months, mature forest, Araracuara, Colombia | GU981663T             |
| *P. fagi*           | CBS 689.77* = CCM F-696 = JLMF 3049 = IMI 253806 | Fallen leaf, on Andosol, alt. 800 m. Fagus sylvatica, Navarra, Spain | JN406540T<sup>###</sup> |
| *P. fellutanum*     | IBT 15460<sup>**</sup> = NRRL 746 = IMI 39734 = ATCC 10443 | Unrecorded source, USA | JN406646T<sup>###</sup> |
| *P. fennelliae*     | CBS 711.68<sup>**</sup> = ATCC 22050 = ATCC 52492 = IMI 151747 = MUCL 31322 | Floor, Zaire | JN406536T<sup>###</sup> |
| *P. flavigenum*     | CBS 419.69<sup>**</sup> = IBT 21526 = IBT 3091 = IMI 293207 | Rhizosphere soil of *Brassica campestris* var. *toria*, Lyngby, Denmark | JN406551T<sup>###</sup> |
| *P. fagi*           | CBS 235.60<sup>**</sup> = ATCC 52498 = IMI 330521 | Type of *P. macedonense*; forest soil, former Yugoslavia, Macedonia | JN406580T<sup>###</sup> |
| *P. gallaicum*      | CBS 167.81<sup>**</sup> = ATCC 24232 = IMI 253794 = IBT 22016 | Air, Madrid, Spain | JN606609T<sup>###</sup> |
| *P. glabrum*        | CBS 105.11<sup>**</sup> | Type of *P. frequentans*, unknown substrate, former West-Germany, Germany | JN406647T<sup>###</sup> |
| *P. gladioli*       | CBS 229.28 = IMI 092231 = MUCL 29111 = NRRL 751 = NRRRL 35564 | Type of *P. paccoski;* soil, under conifer Poland | JN406902T<sup>###</sup> |
| *P. gladioli*       | CBS 332.48<sup>**</sup> = ATCC 10448 = IBT 14772 = IMI 034911 = IMI 034911<sup>ii</sup> = MUCL 29174 = NRRL 939 | Boiled cork, Portugal | EF198601T<sup>###</sup> |
| *P. glandicola*     | CBS 498.75<sup>**</sup> = IBT 21529 = IMI 154241 | Gladiolus corm, imported from the Netherlands, Washington DC, District of Columbia, USA | JN406567T<sup>###</sup> |
| *P. godlewskii*     | CBS 215.28<sup>**</sup> = ATCC 10449 = ATCC 48714 = IFO 7724 = IMI 040591 = MUCL 29243 = NRRL 2111 | Soil under pine, Bialowieza, Poland | JN606626T<sup>###</sup> |
| *P. gorlenkoanum*   | CBS 408.69<sup>**</sup> = IMI 140339 | Soil, Syria | JN606601T<sup>###</sup> |
| *P. heteromorphum*  | CBS 226.89<sup>**</sup> | Soil, Hubei Province, Shennongjia, China | JN406605T<sup>###</sup> |
| *P. heteromorphum*  | CBS 122392<sup>**</sup> | Soil, Treasure Island, Florida, USA | JN606606T<sup>###</sup> |
| *P. hinayamae*      | NRRRL 143<sup>**</sup> = CBS 527.65 = 229.60 = ATCC 18312 = IMI 076255 = IMI 078255<sup>ii</sup> = NRRL 143 | Milled rice, Thailand | EU021625T<sup>###</sup> |
| *P. hirsutum*       | CBS 135.41<sup>**</sup> = ATCC 10429 = IBT 21531 = IMI 040213 = MUCL 15622 = NRRRL 2032 | Aphid, green fly, Baarn, Netherlands | JN406629T<sup>###</sup> |
| *P. hispanicum*     | CBS 184.81 = FRR 2061 = IMI 190235 = NRRL 2061 | Neotype of *P. implicatum sensu Pitt*; soil, New Delhi, India | JN406620T<sup>###</sup> |
| *P. hispanicum*     | CBS 691.77<sup>**</sup> = ATCC 38667 = FRR 3223 = IMI 253785 | *Citrus limonium*, Madrid, Spain | JN406539T<sup>###</sup> |
| *P. incoloratum*    | CBS 101753<sup>**</sup> = AS 3.4672 | Seed of *Phaseolus angularis*, Beijing, China | JN406651T<sup>###</sup> |
| *P. indicum*        | CBS 115.63<sup>**</sup> = ATCC 18324 = FRR 3387 = IMI 166620 | Sputum, man, Delhi, India | JN406640T<sup>###</sup> |
| *P. jamesonlandense*| CBS 102888<sup>**</sup> = DAOM 234087 = IBT 21984 = IBT 24411 | Soil near Cassiope tetragona and *Phyllodoce oreorea*, East Greenland, Jameson Land near Hugin Lake, Greenland | JN406648T<sup>###</sup> |
| *P. janczewskii*    | CBS 221.28<sup>**</sup> = IMI 191499 = NRRL 919 | Soil under *Pinus sp.*, Poland | JN406612T<sup>###</sup> |
| *P. janthinellum*   | CBS 340.48<sup>**</sup> = ATCC 10455 = IMI 040238 = NRRL 2016 | Soil, Nicaragua | GU981625T<sup>###</sup> |
| *P. javanicum*      | CBS 341.48<sup>**</sup> = ATCC 9099 = IFO 31735 = IMI 039733 = MUCL 29090 = NRRL 707 | Root of *Camellia sinensis*, Indonesia, Java | GU981657T<sup>###</sup> |
| *P. jenseni*        | CBS 216.28<sup>**</sup> = ATCC 10456 = IMI 068323 = NRRL 3431 | Forest soil, Poland | JN406614T<sup>###</sup> |
| *P. jugoslavicum*   | CBS 192.87<sup>**</sup> = IFO 7785 = IMI 314508 | Seed of *Helianthus annuus* (sunflower), former Yugoslavia | JN406618T<sup>###</sup> |
| *P. kojigenum*      | CBS 345.61<sup>**</sup> = ATCC 18227 = IMI 086562 = MUCL 2457 = NRRL 3442 | Roadside soil, Kirkcudbrightshire, Gelston, Scotland | JN406564T<sup>###</sup> |
### Table S1. (Continued).

| Name                   | Collection no.                                                                 | Origin                                      | GenBank accession no. |
|------------------------|-------------------------------------------------------------------------------|----------------------------------------------|-----------------------|
| *P. levitum*           | CBS 345.48<sup>NT</sup> = ATCC 10464 = IFO 6101 = IMI 039735 = NRRL 705       | Modeling clay, USA                           | GU981654<sup>BT</sup> |
| *P. limosum*           | CBS 339.97                                                                     | Marine sediment, Nagasaki prefecture, Japan  | GU981621<sup>FR</sup> |
| *P. lineaturn*         | CBS 188.77<sup>NT</sup> = NHL 2776                                           | Soil from copse, Japan                      | GU981620<sup>FR</sup> |
| *P. lividum*           | CBS 347.48<sup>NT</sup> = ATCC 10102 = IMI 039736 = NRRL 754                  | Soil, Scotland                              | JN406563<sup>FR</sup> |
| *P. lutococerulum*     | CBS 347.51<sup>T</sup> = ATCC 18237 = IMI 107651 = NRRL 3450                  | Wakamato corn and rice cake, Nehira, Osaka   | JN406562<sup>FR</sup> |
| *P. luzoniacum*        | CBS 622.72<sup>NT</sup> = DSM 2418 = NHL 6128                               | Soil from pine forest, Luzon Island, Sinipsip near Baguio, Philippines | JN406543<sup>FR</sup> |
| *P. madriti*           | CBS 347.61<sup>NT</sup> = ATCC 18233 = IMI 086563 = MUCL 2456 = MUCL 31193 = NRRL 3452 | Garden soil, Madrid, Spain                  | JN406561<sup>FR</sup> |
| *P. malacaense*        | CBS 160.81<sup>NT</sup> = ATCC 42241 = IJFM 5144 = IMI 253791                | Type of *P. castellonense*; air, Madrid, Spain | JN406623<sup>FR</sup> |
| *P. maniaeaeccus*      | CBS 271.83<sup>N</sup> = IMI 256075                                         | Secale cereale, Spain                       | GU981630<sup>BT</sup> |
| *P. melanconidium*     | CBS 641.95 = IBT 11406 = IBT 21534                                           | Soil, Denmark                               | JN406529<sup>FR</sup> |
| *P. melinii*           | CBS 218.30<sup>NT</sup> = ATCC 10469 = IFO 040216 = MUCL 29235 = NRRL 2041 | Forest soil, USA                           | JN406613<sup>FR</sup> |
| *P. multicolor*        | CBS 253.31<sup>NT</sup> = NRRL 2134 = IMI 191732 = IIB 18224                 | Type of *P. radulatum*; Calluna heathland soil, England | JN406586<sup>FR</sup> |
| *P. meloforme*         | CBS 445.74<sup>NT</sup> = ATCC 28049 = IMI 216903 = NHL 6648                 | Soil, Papua New Guinea                      | GU981655<sup>BT</sup> |
| *P. meridianum*        | CBS 314.67<sup>NT</sup> = ATCC 18545 = IIMI 136209                         | Grassland soil, Pretoria, South Africa      | JN406576<sup>FR</sup> |
| *P. miczynskii*        | CBS 220.28<sup>NT</sup> = ATCC 10470 = DSM 2437 = IFO 7730 = IIMI 040030 = MUCL 29228 = NRRL 1077 = IIB 25491 | Soil under conifer, Tatry mountains, Poland | JN406623<sup>FR</sup> |
| *P. molle*             | CBS 456.72<sup>NT</sup> = ATCC 24075 = IIMI 084589                        | Soile, Pakistan                             | JN406550<sup>FR</sup> |
| *P. montanense*        | CBS 310.63<sup>NT</sup> = ATCC 14941 = IIMI 099468 = MUCL 31326 = NRRL 3407 | Coniferous forest soil, Ravalli Co., Montana, USA | JN406579<sup>FR</sup> |
| *P. multicolor*        | NRRL 2060 = IIMI 092040 = NRRL 2060                                         | Weathering treated cellophane, Florida, USA  | EU42726<sup>FR</sup> |
| *P. murcianum*         | CBS 161.81<sup>NT</sup> = ATCC 42239 = IJFM 7031 = IMI 253800               | Sandy soil, Madrid, Spain                   | JN406625<sup>FR</sup> |
| *P. nalgiovense*       | CBS 352.48<sup>NT</sup> = ATCC 10472 = IIB 21536 = IMI 039804 = MUCL 31194 = NRRL 911 | Ellischauser cheese, fomer Czechoslovakia   | JN406560<sup>FR</sup> |
| *P. neocrassum*        | CBS 122426 = NRRL 35639                                                       | Wine grapes, Madeira Island, Portugal        | JN406633<sup>FR</sup> |
| *P. nodosatatum*       | CBS 330.90<sup>T</sup>                                                         | Soil, Alberta, Canada                       | JN406568<sup>FR</sup> |
| *P. nodum*             | CBS 227.89<sup>NT</sup>                                                         | Mouldy pork, Hubei Province, Shennongjia, China | JN406603<sup>FR</sup> |
| *P. novae-zeelandiae*  | CBS 137.41<sup>NT</sup> = ATCC 10473 = IIMI 040564 = NRRL 2128              | Apothecium of *Sclerotinia*, Palmerston North, New Zealand | JN406628<sup>FR</sup> |
| *P. ochrochloron*      | CBS 357.48<sup>NT</sup> = ATCC 10540 = IIMI 039806 = NRRL 926               | Copper sulphate solution, Washington, USA    | GU981672<sup>FR</sup> |
| *P. ochrosalmonum*     | CBS 489.60<sup>NT</sup> = ATCC 18338 = IIMI 116248                           | Cammeal, South Africa                       | JN406631<sup>FR</sup> |
| *P. odoratum*          | CBS 294.62<sup>T</sup> = ATCC 14769 = CBS 296.62 = IIMI 094206 = NRRL 3007 | Peaty soil in Picea-Larix bog, Taylor Co., Wisconsin, USA | JN406583<sup>FR</sup> |
| *P. oligosporum*       | CBS 349.51<sup>T</sup>                                                         | Japan                                        | GU981658<sup>FR</sup> |
| *P. onobense*          | CBS 174.81<sup>NT</sup> = ATCC 42225 = IJFM 7029                            | Soil, Navarra, Spain                        | GU981627<sup>FR</sup> |
| *P. palense*           | CBS 336.79<sup>NT</sup> = ATCC 38660 = IJFM 3840                          | Gran Canaria, Las Palmas, Spain             | JN406569<sup>FR</sup> |
| *P. paneum*            | CBS 465.95 = IIB 13929                                                        | Mouldy baker’s yeast, Vangede, Denmark      | JN406549<sup>FR</sup> |
**SUPPLEMENTARY INFORMATION**

| Name             | Collection no.          | Origin                                                                 | GenBank accession no. |
|------------------|-------------------------|------------------------------------------------------------------------|-----------------------|
| P. papuaneum     | CBS 570.73 = ATCC 28050 = ATCC 48363 | Forest soil under *Pinus* sp. Central Dist., Port Moresby, Papua New Guinea | JN406545***/22 |
| P. paraherquei   | CBS 430.65 = FAT 824    | Soil, Japan                                                            | GU81628***/27 |
| P. parvum        | CBS 359.48 = ATCC 10479 = IFO 7732 = IMI 040087 = NRRL 2095 = QM 1589 | Soil, Nicaragua                                                   | JN406559***/22 |
| P. pasqualense   | CBS 122402 = IBT 28047  | Air in bakery, Averthorn, the Netherlands                              | JN606617***/21 |
| P. patens        | CBS 260.87 = FRR 2662   | Dried fish, Rastrelliger kanagurta, Indonesia                         | JN406593***/22 |
| P. paxilli       | CBS 360.48 = ATCC 10480 = IMI 040226 = NRRL 2008 = IBT 16202           | Ex-type; optical instrument, Barro Colorado Island, Panama           | JN606611***/22 |
| P. penarjense    | CBS 113178 = IBT 23262  | Leaf litter exposed 6 months, mature forest, Peña Roja, Colombia      | GU81646***/27 |
| P. percinsense   | CBS 111235 = AS 3.5891 = IBT 24565                                   | Soil, Qinghai prov., China                                            | JN406644***/22 |
| P. philippinense | CBS 623.72 = DSM 2420 = NHL 6130                                     | Twig peduncle and fruit, Luzon Island, Sinipsip near Baguio, Philippines | JN406542***/22 |
| P. phoeniceum    | CBS 349.32 = ATCC 10481 = IJFM 5122 = IMI 040585 = NRRL 2070          | Sooty mould on *Phoenix* sp. (palm)                                   | JN406597***/22 |
| P. pimiteoiense  | CBS 102479 = NRRL 25542  | Kidney epithelial cell culture flask, Peoria, Illinois, USA            | JN406650***/22 |
| P. piscarium     | CBS 362.48 = ATCC 10482 = IMI 040032 = NRRL 1075                      | Cod-liver oil emulsion, Norway                                       | GU81668***/27 |
| P. polonicum     | CBS 222.28 = IBT 12821 = IMI 291194 = MUCL 29204 = NRRL 995          | Soil, Puszczja Białowieska Forest, Poland                            | JN406609***/22 |
| P. psychrosexuals| CBS 128036 = DSM 2420 = NHL 6130                                     | Wooden crate in cold-store of apples, Netherlands                    | JN406537***/22 |
| P. pullum        | CBS 331.48 = ATCC 10447 = IFO 6097 = IMI 039747 = NRRL 721            | Soil, Tennessee, USA                                                 | JN611719***/27 |
| P. pulvillorum   | CBS 280.39 = IFO 7763 = NRRL 2026                                     | Acidic soil, UK                                                      | GU81670***/27 |
| P. quebecense    | CBS 101623 = IBT 29050                                              | Air in sawmill, Quebec, Canada                                       | JN606622***/22 |
| P. quercetorum   | CBS 417.69 = ATCC 48727 = IMI 140342 = MUCL 31203                     | Soil, Sweden                                                        | JN406552***/22 |
| P. raciborskii   | CBS 224.28 = ATCC 10488 = IMI 040568 = MUCL 29246 = NRRL 2150         | Soil, under conifer Poznan area, "Dluga Goslina", Poland             | JN406607***/22 |
| P. raistrickii   | CBS 261.33 = ATCC 10490 = IMI 040221 = NRRL 1044 = NRRL 2039          | Cotton yarn, UK                                                    | JN406592***/22 |
| P. ramusculum    | NRRL 2279                                                           | Unknown source                                                    | EU427260***/27 |
| P. raperi        | CBS 281.58 = ATCC 22355 = IFO 8179 = IMI 071625 = NRRL 2674          | Soil, Bedford, UK                                                  | GU81662***/27 |
| P. raphiae       | CBS 126234 = IBT 22407                                              | Soil under *Raphia* (?) palm in primary forest, Las Alturas, elev. 1530 m, Costa Rica | JN606619***/22 |
| P. reticulisporm | CBS 513.74 = DSM 2207 = IFO 9712                                     | Type of *P. arvense* and *E. arvense*; soil, Japan                  | GU81666***/27 |
| P. ribeum        | CBS 121.68 = ATCC 18565 = IMI 136699 = NHL 6102 = NRRL 3446          | Soil, Japan                                                        | GU81665***/27 |
| P. raffii        | CBS 127809 = IBT 16537 = IBT 24431 = DAOM 234091                    | Red currant, Wyoming, USA                                           | JN40663***/22 |
| P. roqueforti    | CBS 368.48 = ATCC 10491 = IFO 7735 = IMI 040029 = MUCL 29229 = NRRL 1078 | Pineapple, Florida, USA                                           | GU81667***/27 |
| P. roseopurpureum| CBS 221.30 = ATCC 10110 = ATCC 1129 = IBT 6754 = IMI 024313 = NRRL 849 | French Roquefort cheese, USA                                       | JN406611***/22 |
| P. rubidunum     | CBS 266.29 = ATCC 10492 = IMI 040573 = MUCL 29654 = MUCL 29237 = NRRL 2064 = NRRL 2064A | Unrecorded source                                                | JN606613***/22 |
| P. rubefaciens   | CBS 145.83 = ATCC 10491 = IFO 7735 = IMI 040029 = MUCL 29229 = NRRL 1078 | Sandy soil under pine tree, Valladolid, Spain                     | JN406627***/22 |
| P. rubens        | CBS 202.57 = ATCC 8537 = ATCC 9478 = IBT 23019 = IMI 015378 = NRRL 1209 = NRRL 824 | Contaminant of bacterial culture (Fleming's strain), UK             | JN406616***/22 |
| P. sabulosum     | CBS 609.73 = ATCC 28051 = ATCC 48238 = IMI 228551                    | Soil, East Sepik Dist., Wewak, Papua New Guinea                     | JN406544***/22 |
| P. sabulosum     | CBS 261.87 = FRR 2743                                               | Spoiled pasteurized fruit juice, Sydney, New South Wales, Australia | JN406591***/22 |
### Table S1. (Continued)

| Name                  | Collection no. | Origin                                                                 | GenBank accession no. |
|-----------------------|----------------|------------------------------------------------------------------------|-----------------------|
| *P. sajarovii*        | CBS 277.83\*NT = CECT 2751 = IMI 259992 | Secale cereale (rye) Zamora, Castrocontrigo, Spain | JN406588\*NT          |
| *P. sanguifluum*      | CBS 148.83 = CECT 2753 | Sandy soil under pine tree, Valladolid, Spain | JN606614\*NT          |
|                       | CBS 685.85 = LFM 19078 = IBT 4904 = IBT 10578 = IBT 10579 | Ex-type of *P. flaccidum*, sandy soil, National Park of Torres del Paine, near Lake Sarmiento, Tierra del Fuego, Chile | JN606615\*NT          |
| *P. scabrum*          | CBS 683.89\*NT = FRR 2960 = IBT 3736 = IMI 285533 | Zea mays, Denmark | JN406541\*NT          |
| *P. sclerotigenum*    | CBS 101033\* = ATCC 343.59 = IBT 14346 = IBT 10578 = IBT 10579 | Sandy soil, National Park of Torres del Paine, near Lake Sarmiento, Tierra del Fuego, Chile | JN406552\*NT          |
| *P. scabrosum*        | CBS 267.83\*NT = ATCC 10496 = IMI 040217 = MUCL 29233 = NRRL 2023 | Soil, Pushczza Bialowieska Forest, square “652”, Poland | JN406606\*NT          |
| *P. sclerotiorum*     | CBS 287.36\*NT = ATCC 10496 = IMI 040569 = NRRL 2074 | Air, Buitenzorg, Java, Indonesia | JN406589\*NT          |
| *P. simplicissimum*   | CBS 372.48\*NT = ATCC 10496 = IMI 039816 | Flannel bag, South Africa | GU981632\*NT          |
| *P. sinaicum*         | CBS 279.82\*NT = ATCC 10496 = IMI 040569 = NRRL 2074 | Soil, Pushczza Bialowieska Forest, square “652”, Poland | JN406588\*NT          |
| *P. sordosativum*     | CBS 439.75\*NT = IMI 140344 | Soils, Buitenzorg, Java, Indonesia | JN606609\*NT          |
| *P. skrjabinii*       | CBS 439.75\*NT = IMI 140344 | Soils, Buitenzorg, Java, Indonesia | JN606609\*NT          |
| *P. smithii*          | CBS 276.83\*NT = CECT 2744 | Secale cereale (rye), Zamora, Torneros, Spain | JN406589\*NT          |
| *P. soppii*           | CBS 226.28\*NT = ATCC 10496 = IMI 040217 = MUCL 29233 = NRRL 2023 | Soil, Pushczza Bialowieska Forest, square “652”, Poland | JN406606\*NT          |
| *P. spiculicola*      | CBS 374.48\*NT = ATCC 10496 = IMI 040569 | Culture contaminant, Hannover, Germany | JN406558\*NT          |
| *P. steckii*          | CBS 260.50\*NT = ATCC 10496 = DSM 1252 = IMI 040563 = NRRL 2140 | Cotton fabric treated with copper naphthenate; Panama | JN606602\*NT          |
| *P. stolkae*          | CBS 315.67\*NT = ATCC 18546 | Peaty forest soil, Eastern Transvaal, South Africa | JN617717\*NT          |
| *P. striatiporum*      | CBS 705.68\*NT = ATCC 22052 = IMI 151749 = MUCL 31202 | Leaf litter, Acacia karroo (Sweet Thorn), Potchefstroom, South Africa | JN406538\*NT          |
| *P. subarcticum*      | CBS 111719\*NT = NRRL 31108 | Petroleum contaminated soil, near Norman Wells, Northwest-Territories, Canada | JN617716\*NT          |
| *P. subericola*       | CBS 125096\* | Non-boiled cork, Coruche, Portugal | JN406621\*NT          |
| *P. subliterrarium*   | CBS 267.29\*NT = ATCC 10502 = IMI 040594 = MUCL 28655 = NRRL 2071 | Unrecorded source, Belgium | JN406590\*NT          |
| *P. sumatrense*       | NRRL 6181 | Unknown source | JN606612\*NT          |
|                       | NRRL 779\* = CBS 281.36 = NRRL 779 = ATCC 48669 = IBT 29658 = IBT 4978 | Soil, Toba Heath, Sumatra, Indonesia | JN617717\*NT          |
|                       | CBS 416.69 = IMI 140336 = IBT 2964 | Isotype of *P. baradicum*; soil under cornel, Damascus, Syria | JN606612\*NT          |
| *P. svalbardense*     | CBS 122416\* = IBT 23856 = EX-F 1307 | Glacial ice, Svalbard, Greenland | GU981635\*NT          |
| *P. swiecickii*       | CBS 119391\*NT = FRR 918 = IBT 27865 = IMI 191500 = NRRL 918 | Pine forest soil, Poland | JN406635\*NT          |
| *P. terrenum*         | CBS 313.67\*NT = ATCC 18547 = IMI 136208 | Soil in subtropical forest, Eastern Transvaal, South Africa | JN406577\*NT          |
| *P. terrigenum*       | CBS 127354\* = IBT 30769 | Soil, Hawaii, USA | JN606609\*NT          |
| *P. toxicarium*       | NRRL 31271 | Unknown source | EF198540\*NT          |
|                       | NRRL 6172 | Unknown source | EF198541\*NT          |
| *P. tropicoides*      | CBS 122410\* | Soil rainforest, near Hua-Hin, Thailand | JN606609\*NT          |
| *P. tropicum*         | CBS 112584\* = ATCC 24580 | Soil between Coffea arabica, Karnataka, India | JN606609\*NT          |
| *P. turbatum*         | CBS 134.41 = ATCC 10415 = IMI 040590 = NRRL 2086 | Neotype of *P. baarnense*; soil, Baarn, Netherlands | JN406630\*NT          |
|                       | CBS 339.61 = NRRL 2087 | Contaminant of *P. euglaucum* culture, see also Stolk Scott (1967); leaf litter of Acacia mollissima, Natal, South Africa | JN406565\*NT          |
| *P. vanderhammenii*   | CBS 126216\* = DTO 97A3 = IBT 23203 | Leaf litter exposed for 6 months, mature forest, Araracuara, Colombia | GU981647\*NT          |
**SUPPLEMENTARY INFORMATION**

| Name              | Collection no. | Origin                                           | GenBank accession no. |
|-------------------|----------------|--------------------------------------------------|-----------------------|
| *P. vasconiae*    | CBS 339.79 = CBS 175.81, UFM 3008                | Acid washed brown soil, Spain                     | GU981653**          |
| *P. vinaceum*     | CBS 389.48** = ATCC 10514 = IMI 029189 = NRRL 739 | Soil, Utah, USA                                    | JN406555**         |
| *P. virgatum*     | CBS 114838** = BBA 65745                          | Soil near soy bean plant North of Noumea, Port Laguerre, New Caledonia | JN406641**         |
| *P. wakmanii*     | CBS 230.28** = ATCC 10516 = IFO 7737 = IMI 039746 = IMI 039746i = MUCL 29120 = NRRL 777 = IBT 5003 = IBT 6994 | Woodland soil, Puszczka Białowieska Forest, Poland | JN606627** |
| *P. waksmanii*    | CBS 118171** = IBT 23253                          | Soil under conifer, Denga Goolina, Poznan, Poland | JN606658**         |
| *P. wellingtonense* | CBS 130375 = IBT 23557         | Soil, New Zealand                                    | JN606616**         |
| *P. westlingii*   | CBS 231.28** = IMI 092272 = IBT 15088             | Soil under conifer, Denga Goolina, Poznan, Poland | JN606629**         |
| *P. wotroi*       | CBS 118171** = IBT 23253                          | Leaf litter exposed for 6 months, mature forest, Araracuara, Colombia | GU981637**         |
| *P. yarmokense*   | CBS 410.69** = FRR 520 = IMI 140346               | Soil, Syria                                        | JN406553**         |
| *P. zonatum*      | CBS 999.72** = ATCC 24353                         | Coastal marsh soil, USA, North Carolina            | GU981651**         |
| *Penicillium* sp. | CBS 116986 = IBT 3265 | Soil, Wales                                        | JN406638**         |
|                   | CBS 117161 = IBT 6005 = IMI 304286                | Barley, Denmark                                     | JN406637**         |
|                   | CBS 117192 = IBT 22220 = IBT 24432                | Chestnut, France                                    | JN406636**         |