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Identification and nomenclature of the genus *Penicillium*

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**Abstract:** *Penicillium* is a diverse genus occurring worldwide and its species play important roles as decomposers of organic materials and cause destructive rots in the food industry where they produce a wide range of mycotoxins. Other species are considered enzyme factories or are common indoor air allergens. Although DNA sequences are essential for robust identification of *Penicillium* species, there is currently no comprehensive, verified reference database for the genus. To coincide with the move to one fungus one name in the International Code of Nomenclature for algae, fungi and plants, the generic concept of *Penicillium* was re-defined to accommodate species from other genera, such as *Chromocleista*, *Eladia*, *Eupenicillium*, *Tolomycetes* and *Thysanophora*, which together comprise a large monophyletic clade. As a result of this, and the many new species described in recent years, it was necessary to update the list of accepted species in *Penicillium*. The genus currently contains 354 accepted species, including new combinations for *Aspergillus crystallinus*, *A. malodoratus* and *A. paradoxa*, which belong to *Penicillium* section *Paradoxa*. To add to the taxonomic value of the list, we also provide information on each accepted species MycoBank number, living ex-type strains and provide GenBank accession numbers to ITS, β-tubulin, calmodulin and RPB2 sequences, thereby supplying a verified set of sequences for each species of the genus. In addition to the nomenclatural list, we recommend a standard working method for species descriptions and identifications to be adopted by laboratories working on this genus.

**Key words:** Aspergillaceae, Fungal identification, phylogeny, media, nomenclature.

**Taxonomic novelties: New combinations:** *Penicillium crystallinus* (Kwon-Chung & Fennell) Samson, Houbraken, Visagie & Frisvad, *Penicillium malodoratum* (Kwon-Chung & Fennell) Samson, Houbraken, Visagie & Frisvad, *Penicillium paradoxa* (Fennell & Raper) Samson, Houbraken, Visagie & Frisvad.

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**INTRODUCTION**

*Penicillium* is well known and one of the most common fungi occurring in a diverse range of habitats, from soil to vegetation to indoor environments and various food products. It has a worldwide distribution and a large economic impact on human life. Its main function in nature is the decomposition of organic materials, where species cause devastating rots as pre- and postharvest pathogens on food crops (Frisvad & Samson 2004, Pitt & Hocking 2009, Samson et al. 2010), as well as producing a diverse range of mycotoxins (Frisvad et al. 2004). Some species also have positive impacts, with the food industry exploiting some species for the production of speciality cheeses, such as Camembert or Roquefort (Thom 1906, Nelson 1970, Karahadian et al. 1985, Giraud et al. 2010) and fermented sausages (Ludemann et al. 2010). Their degradative ability has resulted in species being screened for the production of novel enzymes (Raper & Thom 1949, Li et al. 2007, Adsul et al. 2007, Terrasan et al. 2010). Its biggest impact and claim to fame is the production of penicillin, which revolutionised medical approaches to treating bacterial diseases (Fleming 1929, Chain et al. 1940, Abraham et al. 1941, Thom 1945). Many other extrolites have since been discovered that are used for a wide range of applications (Frisvad et al. 2004), Pitt (1979) considered it axiomatic that *Penicillium* or one of its products has affected every modern human.

It is now more than 200 years since Link (1809) introduced the generic name *Penicillium*, meaning ‘brush’, and described the three species *P. candidum*, *P. glaucum* and the generic type *P. expansum*. Since then, more than 1000 names were introduced in the genus. Many of these names are not recognisable today because descriptions were incomplete by modern criteria. Some names were published invalidly, or are now considered synonyms of other species. Thom (1930) revised all species described until 1930 and accepted 300 species. In later studies, Raper & Thom (1949) accepted 137 species, Pitt (1979) accepted 150 species, and Ramirez (1982) accepted 252 species (numbers include species described in *Eupenicillium*). At that time, a morphological species concept was used for *Penicillium* classification and identification, with DNA sequencing starting to be used during the 1990’s. DNA sequencing created the threat that old names previously considered of uncertain application, because their ex-type cultures were no longer morphologically representative, could replace more commonly used but younger names. As such, the List of “Names in Current Use” (NCU) for the family *Trichocomaceae* (Pitt & Samson 1993) accepted 223 species and disregarded all other names as if not published. This list was updated by Pitt et al. (2000) who...
accepted 225 species. Species names not accepted on these lists were not to be disregarded permanently, as stated by Pitt et al. (2000), because they were not formally rejected under the nomenclatural code and could still be reintroduced in a revised taxonomy. In fact, this became common practice as many old species were shown to be distinct and were reintroduced (Peterson et al. 2005, Serra et al. 2008, Houbraken et al. 2011a,b, Houbraken et al. 2012a, Vsagie et al. 2013).

The abandonment of article 59 in the new International Code of Nomenclature for algae, fungi and plants (ICN) (McNeill et al. 2012) resulted in single name nomenclature for fungi. In anticipation of this change, Houbraken & Samson (2011) redefined the genera in the family Trichocomaceae based on a four gene phylogeny. They segregated the Trichocomaceae into three families, namely the Aspergillaceae (Aspergillus, Hamigera, Leiothecium, Monascus, Penicilliosis, Penicillium, Phialomyces, Sclerocleista, Warcupiella, Xeromyces), Thermoascaceae (Byssoclamys/Paeclomyces, Thermoascus) and the Trichocomaaceae (Rasamsonia, Sagenomella, Talaromyces, Themomyces, Trihocoma). Penicillium subgenus Biverticillium and Talaromyces were shown to form a monophyletic clade distinct from the other subgenera of Penicillium, with these names recombined as necessary into Talaromyces (Samson et al. 2011). The remaining Penicillium species formed a monophyletic clade together with species classified in Eupenicillium, Eladia, Hemicarpentes, Torulomyces, Thysanophora and Chromocleista. These generic names were synonymised with Penicillium, while their species were given Penicillium names (Houbraken & Samson 2011). The remaining three Aspergillus species, A. paradoxa (≡ Hemicarpentes paradoxa), A. malodoratus and A. crystallinus, phylogenetically belonging in Penicillium, are transferred to Penicillium below in the Taxonomy section. To accommodate the morphological variation, the generic diagnosis of Penicillium was amended in Houbraken & Samson (2011). Most importantly, in comparison with the prevailing generic concept (Raper & Thom 1949, Pitt 1979), it now excludes the acerose phialides and usually symmetrically branched conidioaphores of species now included in Talaromyces, and was expanded to include the conidioaphores with solitary phialides of species in section Torulomyces, and the darkly pigmented stipes that formerly characterised the genus Thysanophora, which show secondary growth by means of the proliferation of an apical penicillus. For infrageneric classification, the genus was divided into two subgenera, Aspergilloides and Penicillium, and 25 sections.

Thom (1954) attempted to explicitly define species concepts used for Penicillium. He was the pioneer of standardised working techniques and emphasised that Penicillium taxonomy demands a consistent, logical approach. He demonstrated these tendencies himself by taking into account infraspecies variation when delineating species. To minimise infraspecies variation, the importance of standardised working techniques were again emphasised by Pitt (1979), Samson & Pitt (1985), Okuda (1994) and Okuda et al. (2000). Although this was relatively effective when dealing with freshly isolated or wild-type strains, comparing strains using only morphology requires experience and nuance, because of the degeneration of characters in old reference material and the large number of species in the genus. New techniques incorporated into taxonomic studies resulted in the physiological species concept (Ciegle & Pitt 1970, Pitt 1973, Frisvad 1981, Frisvad & Filtenborg 1983, Cruickshank & Pitt 1987a,b, El-Banna et al. 1987, Frisvad & Filtenborg 1989, Paterson et al. 1989), phylogenetic species concept, including Genealogical Concordance Phylogenetic Species Recognition (GCPSR) (LoBuglio et al. 1993, Berbee et al. 1995, Boysen et al. 1996, Geiser et al. 1998, Skouboe et al. 1999, O'Donnell et al. 1998, Peterson 2000a, Taylor et al. 2000) and eventually led to the combined approach using morphological, extrolite and genetic data in a polyphasic species concept (Christensen et al. 2000, Frisvad & Samson 2004). In the modern taxonomy, however, sequence data and GCPSR carries more weight than morphology or extrolite data.

Even though Penicillium species are very common and the taxonomic structure of the genus is well defined, species identification is still problematic. Problems include an out-dated accepted species list and a lack of a verified, complete sequence database. The aim of this paper is to address these issues. In honour of Charles Thom and Kenneth B. Raper, the fathers of Penicillium taxonomy, and all the other mycologists who have contributed in the last 200 years towards our current understanding of the genus, we offer this contribution towards a practical, stable, consistent, logical approach to Penicillium taxonomy, identification and nomenclature.

RECOMMENDED METHODS FOR IDENTIFICATION AND CHARACTERISATION OF PENICILLIUM

Morphological species recognition

Morphology in the past has been central to the taxonomy of Penicillium and along with multigene phylogenetics and extrolite profiling comprises the polyphasic species concept adopted for Penicillium. Morphology is the physical architecture through which an organism functions in and adapts to its environment, but some aspects may vary or be induced by specific cues in the immediate environment. As a result, strains characterised in one laboratory might look different when grown in another because of subtle differences in nutrients, temperature, lighting or humidity. This sometimes makes comparisons between different studies very difficult. These effects can be minimised using strictly standardised working techniques for medium preparation, inoculation technique and incubation conditions (Samson & Pitt 1985, Okuda 1994, Okuda et al. 2000). We recommend the following standardised methods for laboratories identifying and describing Penicillium species (summarised in Fig. 1).

Macromorphology

Colony characters and diameters on specific media are important features for species identification. Czapek Yeast Autolysate agar (CYA) and Malt Extract agar (MEA, Oxoid) is recommended as standard media for Penicillium. Even though malt extract from Oxoid is recommended, many laboratories prefer Difco. It should be noted that two different MEA formulations are widely used in modern taxonomic studies. Blakeslee’s MEA was historically widely used, but lately CBS switched to a different formulation (given in Table 1). Both are suitable for characterisation, but studies should state which MEA (Oxoid or Difco) and formulation was used. The following alternative media can be used for observing additional taxonomic characters: Czapek’s agar (CZ), Yeast Extract Sucrose agar (YES), Oatmeal agar (OA), Creatine Sucrose agar (CREA), Dichloran 18 % Glycerol agar (DG18), Blakeslee’s MEA and CYA with 5 % NaCl (CYAS). CZ was used
Table 1. Media and stock solutions used for morphological characterisation.

| Solution Description | Formula | Amount | Method |
|----------------------|---------|--------|--------|
| Czapek stock solution (100 ml) (Pitt 1979) | NaNO₃, KCl, MgSO₄·7H₂O, FeSO₄·7H₂O, dH₂O | 30 g, 5 g, 5 g, 0.1 g, 100 ml | Store at 4–10 °C |
| Trace elements stock solution (100 ml) | CuSO₄·5H₂O, ZnSO₄·7H₂O, dH₂O | 0.5 g, 0.1 g, 100 ml | Store at 4–10 °C |
| Blakeslee’s Malt extract agar (MEAbl, Blakeslee 1915) | Malt extract (Oxoid), Peptone (Oxoid), Glucose, Trace elements, Agar, dH₂O | 20 g, 1 g, 20 g, 1 ml, 20 g, 1000 ml | Mix well and autoclave at 121 °C for 15 min. pH 5.3 ± 0.2. |
| Creatine sucrose agar (CREA, Frisvad 1981) | Sucrose, Creatine·H₂O, K₂PO₄·7H₂O, MgSO₄·7H₂O, KCl, FeSO₄·7H₂O, Trace elements stock solution, Bromocresol purple, Agar, dH₂O | 30 g, 3 g, 1.6 g, 0.5 g, 0.5 g, 0.01 g, 1 ml, 0.05 g, 20 g, 1000 ml | Mix well and autoclave at 121 °C for 15 min. pH 8.0 ± 0.2. |
| Czapek’s agar (CZ, Raper & Thom 1949) | Czapek concentrate, Sucrose, Trace elements stock solution, Agar, dH₂O | 10 ml, 30 g, 1 ml, 20 g, 1000 ml | Mix well and autoclave at 121 °C for 15 min. |
| Czapek Yeast Autolysate agar (CYA, Pitt 1979) | Czapek concentrate, Sucrose, Yeast extract (Difco), MgSO₄·7H₂O, Trace elements stock solution, Agar, dH₂O | 10 ml, 30 g, 5 g, 0.5 g, 1 ml, 20 g, 1000 ml | Mix well and autoclave at 121 °C for 15 min. pH 6.2 ± 0.2. |

(Continued.)

Table 1. (Continued).

| Solution Description | Formula | Amount | Method |
|----------------------|---------|--------|--------|
| Czapek Yeast Autolysate agar with 5 % NaCl (CYAS) | Czapek concentrate, Sucrose, Yeast extract (Difco), K₂HPO₄, Trace elements stock solution, Agar, NaCl, dH₂O | 10 ml, 30 g, 5 g, 1 g, 1 ml, 50 g, 1000 ml | Mix well and autoclave at 121 °C for 15 min. pH 6.2 ± 0.2. |
| Dichloran 18 % Glycerol agar (DG18, Hocking & Pitt 1980) | Dichloran-Glycerol-agar-base (Oxoid), Trace elements stock solution, Chloramphenicol, Agar, dH₂O | 31.5 g, 1 ml, 0.05 g, 20 g, 1000 ml | Mix well and autoclave at 121 °C for 15 min. After autoclaving, add 0.05 chlortetracycline. pH 5.6 ± 0.2. |
| Malt Extract agar (MEA, Samson et al. 2010) | Malt extract (Oxoid CM0059), Trace elements stock solution, dH₂O | 50 g, 1 ml, 1000 ml | Mix well and autoclave at 115 °C for 10 min. pH 5.4 ± 0.2. |
| Oatmeal agar (OA, Samson et al. 2010) | Oatmeal / flakes, Trace elements stock solution, Agar, dH₂O | 30 g, 1 ml, 20 g, 1000 ml | First autoclave flakes (121 °C for 15 min) in 1000 ml dH₂O. Squeeze mixture through cheese cloth and use flow through, topping up to 1000 ml with dH₂O with 20 g agar. Autoclave at 121 °C for 15 min. pH 6.5 ± 0.2. |
| Yeast extract sucrose agar (YES, Frisvad 1981) | Yeast extract (Difco), Sucrose, MgSO₄·7H₂O, Trace elements stock solution, Agar, dH₂O | 20 g, 150 g, 0.5 g, 1 ml, 20 g, 885 ml | Mix well and autoclave at 121 °C for 15 min. pH 6.5 ± 0.2. |
in the taxonomic treatments of Raper & Thom (1949) and Ramirez (1982) and is chemically well defined. However, it is not widely used for Penicillium studies. YES is the recommended medium for extrolite profiling of species. Sexual reproduction most commonly occurs when strains are grown on OA and thus often provide valuable taxonomic information. OA should be prepared using organic uncooked flakes and not the unsuitable quick cook oats (“3 minute oats”) or prefabricated OA formulations available. Acid production is observed by the colour reaction in CREA (from purple to yellow) and is often useful for distinguishing between closely related species. In some species acid production is followed by base production and is most often observed from the colony reverse. DG18 and CYAS often provide useful information with regards to growth rates on low water activity media. For consistent conidial colours, the addition of zinc-sulphate and copper-sulphate as trace elements (1 g ZnSO₄.7H₂O and 0.5 g CuSO₄.5H₂O in 100 ml distilled water) is of utmost importance because these metals vary widely in water sources in different locations and are critical for pigment production. For inorganic chemicals, analytical grade should be used. Experience has shown that the brand of agar used influences colony appearance. As such, it is important to test the agar for consistent character development and note the brand in species descriptions. Even though we do not recommend a brand here as standard, after extensive comparisons CBS opted to use So-Bi-Gel agar (Bie & Berntsøn, BBB 100030) for medium preparations. Medium formulations are given in Table 1.

Media are prepared in 90 mm Petri-dishes with a volume of 20 ml (Okuda et al. 2000). Glass Petri dishes was traditionally considered best for character observation. However, today it is not feasible using them, with polystyrene Petri dishes recommended. The Petri dishes should preferably be vented which allows for a bit of air exchange. Inoculations are made from spore suspensions in a semi-solid agar solution containing 0.2 % agar and 0.05 % Tween80 (Pitt 1979). In some laboratories, spore suspensions are made in a 30 % glycerol, 0.05 % agar and 0.05 % Tween80 solution. Variation between the two inoculation suspension solutions has not been shown. We recommend using a micropipette for inoculating the spore suspension in three-point fashion (0.5–1 μl per spot). They should not be wrapped with Parafilm, which by restricting air exchange often inhibits growth and sporulation (Okuda et al. 2000). When using walk-in incubators, laboratory rules often require plates to be placed in plastic containers or plastic bags. In this case, the boxes or bags should allow for enough aeration and care should be taken not to have too many plates in one box or in one incubator. For standard bench-top incubators, plates do not need to be incubated in boxes or bags, unless there is a strong air-current in the incubator. All media are incubated at the standard temperature of 25 °C for 7 d, with additional CYA plates at 30 and 37 °C that are useful to distinguish between species. It is crucial that temperatures are carefully checked as small differences have a large impact on colony growth. No effect on colonies has been shown for inoculating Petri dishes upside down or vice versa.

After 7 d, colony diameters are measured at the widest part of the colony. Important characters used for describing Penicillium include colony texture, degree of sporulation, the colour of conidia, the abundance, texture and colour of mycelia, the presence and colours of soluble pigments and exudates, colony reverse colours, and degree of growth and acid production (in some species acid production followed by base production) on CREA. The use of a standard colour chart is recommended for descriptions. Although many are available, the most commonly used colour chart in Penicillium is the Methuen Handbook of Color (Kornerup & Wanscher 1967), which although long out of print is available in many libraries. It is worth noting that colour names used by Raper & Thom (1949) were based on Ridgway (1912) and are also still in use. When colour charts are not available, it is recommended to publish full color phototemplates to accompany descriptions of new species. Some species produce specialised structures such as cleistothecia or sclerotia, mostly after longer incubation times, especially on OA. We thus recommend OA plates be incubated for prolonged periods to have a chance of observing these structures. For definitions and explanations of terms used in descriptions of Penicillium colonies, readers are referred to Frisvad & Samson (2004).

**Micromorphology**

Conidiophore and cleistothecium (when produced) characters of Penicillium are of great taxonomic importance. Conidiophore branching patterns (Fig. 2) were traditionally used in the classification of Penicillium (Thom 1930, Raper & Thom 1949, Pitt 1979). Although these branching patterns do not correspond perfectly with the sections currently accepted for Penicillium, characterising them accurately is still considered important. The conidiophores range from being simple (solitary phialides, Fig. 2A) to very complex patterns with multiple levels of branching resulting in overall symmetrical or asymmetrical patterns. Monoverticillate conidiophores (Fig. 2B) have a terminal whorl of phialides and in some species, the terminal cell of the conidiophore is slightly swollen or vesiculate; such species could be confused with diminutive Aspergillus conidiophores, but they have septa in the stipes unlike species of the latter genus. Divaricate conidiophores, previously also referred to as irregular (Pitt 1979, Fig. 2C), are best described as having a simple to complex branching pattern with numerous subterminal branches formed, but where conidiophore parts are divergent. Biverticillate conidiophores (Fig. 2D, E) have a whorl of three or more metulae between the end of the stipe and the phialides; the metulae may be of unequal or equal length, vary in their degree of divergence, are usually more or less cylindrical but can also be clavate or slightly vesiculate. Tertverticillate conidiophores (Fig. 2F) have another level of branching between the stipe and the metulae, often just a continuation of the stipe axis and one side branch, sometimes a true whorl of three or more branches. Quaterverticillate conidiophores (Fig. 2G) are produced by only a few species, and have one extra level of branching beyond the tertverticillate pattern. Tertverticillate and quaterverticillate conidiophores tend to be conspicuously asymmetrical. In colonies of many species, especially as cultures begin to degenerate, there may be more than one branching pattern or intermediate forms, and it can be challenging to decide which pattern is typical or most developed.

Other important microscopic characters include the wall texture/ornamentation of stipes and conidia, as well as dimensions, ornamentation and sometimes colours of all elements of the conidiophore (Fig. 1). In our experience, wall textures are very sensitive to minute differences in media composition and aeration. For best observation of conidial ornamentation, differential interference contrast (= Nomarski) is recommended if possible; ornamentation is sometimes most conspicuously visible in air pockets in the preparation.

For microscopic observations, slides are prepared from 7–10 d old MEA colonies. Remove material from the zones where adjacent colonies are closest or growing together, from
the part of the colony where the conidial colour is just starting to develop. For observing conidia, material removed from colony centers generally gives more uniform results. Lactic acid (60%) is the most commonly used mounting fluid, although other solutions such as Shear’s solution or lactic acid with cotton blue (Frisvad & Samson 2004, Samson et al. 2010) can also be used. We do not recommend lactophenol because of the corrosiveness and toxicity of phenol. Because of the abundant hydrophobic conidia produced by most species, drops of 70% ethanol are commonly used to wash away excess conidia and to prevent air being “trapped” when mounted in lactic acid. For photographing conidiophores, we often wash away the spores two or three times. Some species have dense colonies and then it is necessary to tease apart the conidiophores with very fine needles under the dissecting microscope.

**DNA barcoding for identification and multilocus sequence typing for phylogenetic species recognition**

**Sequence markers**
During the 1990’s, DNA sequencing became one of the most powerful tools for taxonomists, because it created the opportunity for inferring relationships between species without the need for
standardising culturing regimes and eliminated problems related to deteriorated cultures. It also created the opportunity for sequence based identifications. DNA barcoding was launched to make species identification of any eukaryotic organism possible for anybody, by using a standardised short DNA sequence and a curated reference database linked to authoritatively identified vouchers (Blaxter 2003, Tautz et al. 2003, Hebert et al. 2003, Blaxter et al. 2005, DeSalle et al. 2005, Ratnasingham & Hebert 2007, Seifert et al. 2007, Min & Hickey 2007a,b, Schoch et al. 2012). Only recently however, was the internal transcribed spacer rDNA area (ITS) accepted as the official barcode for fungi (Schoch et al. 2012). ITS is the most widely sequenced marker for fungi, and universal primers are available (Schoch et al. 2012). In Penicillium, it works well for placing strains into a species complex or one of the 25 sections, and sometimes provides a species identification (Visagie et al. 2014a). Unfortunately, for Penicillium and many other genera of ascomycetes, the ITS is not variable enough for distinguishing all closely related species (Skouboe et al. 1999, Seifert et al. 2007, Schoch et al. 2012). The open source sequence repository GenBank contains a large proportion of incorrectly identified sequences, making identifications of Penicillium using BLAST very tricky for inexperienced workers. This particular problem is addressed in a number of publications (Köljalg et al. 2005, Santamaria et al. 2012, Köljalg et al. 2013, Schoch et al. 2014). For Penicillium, the International Commission of Penicillium and Aspergillus (ICPA), in conjunction with the publication of an updated accepted species list presented below, decided to include GenBank accession numbers to reference barcode sequences for each species when available.

Because of the limitations associated with ITS as a species marker in Penicillium, a secondary barcode or identification marker is often needed for identifying isolates to species level. The requirements for a secondary identification marker are clear. It should be easy to amplify, distinguish among closely related species and most importantly, the reference data set should be complete, meaning that there should be representative sequences for all species. It would be an added bonus if this marker is useful for phylogenetic studies, as it will by default become the gene most widely sequenced in future. Based on these criteria, we propose the use of β-tubulin (BenA) as the best option for a secondary identification marker for Penicillium. BenA does, however, have problems associated with it. Although not influencing BLAST identifications, alignments across a diverse genus like Penicillium is difficult and often contains a large proportion ambiguously aligned sites, which can make phylogenies difficult. Also, there is evidence for the amplification of BenA paralogous genes in Aspergillus (Peterson 2008, Hubka & Kolářek 2012) and Talaromyces (Peterson & Jurjević 2013) and it can thus be assumed that the same might be happening in some Penicillium species, although this has not been shown. Other possible secondary marker options include calmodulin (CaM) or the RNA polymerase II second largest subunit (RPB2) genes. Both these genes have similar discriminatory power as BenA. RPB2 has the added advantage of lacking introns in the amplicon, allowing robust and easy alignments when used for phylogenies, but it is sometimes difficult to amplify and the database is incomplete. Similarly, we lack a complete CaM database. Thus, for routine identifications BenA is currently recommended, while for the description of new species, we suggest the use of ITS, BenA, CaM and RPB2 among the markers for multilocus sequence typing and GCPSR. We consider it good practise to include at least ITS and BenA sequences when describing new species, to allow others to more easily recognise the new species.

BenA can successfully be used for accurately identifying Penicillium species. However, as is the case for genes other than BenA, care should be taken in specific groups or situations. Intraspecies variation in BenA occurs in some Penicillium species as is observed in phylogenies published for Penicillium (Frisvad & Samson 2004, Barreto et al. 2011, Peterson et al. 2011, Houbraken et al. 2011b,c, Rivera & Seifert 2011, Rivera et al. 2012, Houbraken et al. 2012a, Visagie et al. 2013, 2014a, 2014b). This variation must be considered for identification purposes and especially when considering whether a strain might represent a new species. This means that in addition to the reference sequences of ex-type cultures sanctioned by ICPA, additional reference sequences are necessary to document sequence variation that differ from the ex-type. ICPA is currently working on populating such a validated database to capture infraspecies variation, but for the time being critical phylogenetic revisions of different sections should be referred to for reliable data. Alternatively, combining ITS, BenA, CaM and RPB2 from a suspected new species with sequences of the same markers from related species will aid in deciding whether a species is new or not, using GCPSR as explained in detail by Taylor et al. (2000). This is in fact common practise in most studies describing and characterising Penicillium species.

β-tubulin as a secondary marker in practise

As discussed above, BenA works well for species identifications in Penicillium. Penicillium chrysogenum and P. alli-sativi is one example where identification based on BenA should be made with care (Houbraken et al. 2012a). This is a consequence of the variation observed among strains of P. chrysogenum, which results in P. alli-sativi forming a clade within the P. chrysogenum clade in BenA species trees. Even though CaM distinguishes P. chrysogenum from P. alli-sativi, it does not distinguish P. chrysogenum and P. rubens. As a result, molecular identifications should be made with great care in section Chrysogena, with the revision by Houbraken et al. (2012a) used as guide. Penicillium kongii was recently introduced as a close relative of P. brevicaespactum (Wang & Wang 2013). Even though this species formed a coherent clade distinct from the P. brevicaespactum ex-type strain, on examining additional strains previously identified as P. brevicaespactum, the P. kongii clade is resolved within the P. brevicaespactum clade. This clade thus requires more work to resolve the species from the complex. A similar situation is observed for P. desertorum and the newly described P. glycyrhizaolaca (Chen et al. 2013), where more strains and additional genes included in the phylogeny will help to resolve species. Another species that cannot be identified using molecular data is P. camemberti, P. caseiflum and P. commune, which shares identical BenA and other gene sequences (Giraud et al. 2010). Although these could be considered taxonomic synonyms, their different applications and importance in the cheese industry suggest that it is of more value to keep them as separate species. Morphological identification is necessary in this case, with P. camemberti having white conidia, P. caseiflum having an orange reverse on YES and P. commune producing green conidia (Frisvad & Samson 2004).
**Table 2. Primers used for amplification and sequencing.**

| Locus                             | Primer name | Direction | Primer sequence (5′-3′) | Reference          |
|-----------------------------------|-------------|-----------|-------------------------|--------------------|
| Internal Transcribed Spacer (ITS) | ITS1        | Forward   | TCC GTA GGT GAA CCT GCG G | White et al. 1990  |
|                                   | ITS4        | Reverse   | TCC TCC GCT TAT TGA TAT GC | White et al. 1990  |
|                                   | V9G         | Forward   | TTA CGT CCC TGC CCT TTG TA | de Hoog & Gerrits van den Ende 1998 |
|                                   | LS266       | Reverse   | GCA TCC CCA AAC AAC TCG ACT C | Masciaux et al. 1995 |
| β-tubulin (BenA)                   | Bl2a        | Forward   | GGT AAC CAA ATC GCT GCT TTC | Glass & Donaldson 1995 |
|                                   | Bl2b        | Reverse   | ACC CTC AGT GTA GTG ACC CTT GGC | Glass & Donaldson 1995 |
| Calmodulin (CaM)                   | CMD5        | Forward   | CGG AGT ACA AGG ARG CCT TC | Hong et al. 2006   |
|                                   | CMD6        | Reverse   | CGG ATR GAG GTC ATR AGC TGG | Hong et al. 2006   |
|                                   | CF1         | Forward   | GCC GAC TCT TTG ACY GAR GAR | Peterson et al. 2005 |
|                                   | CF4         | Reverse   | TTT YTG CAT CAT RAG YTG GAC | Peterson et al. 2005 |
| RNA polymerase II second largest subunit (RPB2) | 5F          | Forward   | GAY GAY MGW GAT CAY TTY GG | Liu et al. 1999   |
|                                   | 7CR         | Reverse   | CCC ATR GCT TGY TTR CCC AT | Liu et al. 1999   |
|                                   | 5Feur       | Forward   | GAY GAY CGK GAY CAY TTC GG | Houbraken et al. 2012b |
|                                   | 7CReur      | Reverse   | CCC ATR GCY TGY TTR CCC AT | Houbraken et al. 2012b |

**Amplification and identification**

Primers used for amplification of the ITS, BenA, CaM and RPB2 genes are included in Table 2 and amplification profiles are given in Table 3. A standard thermal cycle with an annealing temperature of 55 °C is generally used. Sometimes amplification success is low for CaM, especially in sections Cansescentia and Ramosa. In this case, dropping the annealing temperature to 52 °C gives good results. The RPB2 amplification is more complicated. We recommend using a touch-up PCR (50–52–55 °C) with primer pair 5Feur and 7CReur for best amplification. When amplification is problematic, the alternative touch-up PCR (48–50–52 °C) profile can be used and/or the alternative primer pair 5F and 7CR.

After sequences are obtained, there is a number of ways to use them to identify the strain. The most widely used method is the BLAST search on NCBI. Using this method, one is able to search all sequences in the database, but as noted above, there are many unidentified and misidentified sequences in the database. For ITS the RefSeq data set, accessible from the NCBI homepage (http://www.ncbi.nlm.nih.gov/refseq/), is now available and can be used to query ITS sequences against a verified ITS database (Schoch et al. 2014). Unfortunately, the RefSeq database does not cover alternative genes. For this, we suggest setting up Local BLAST files and using the verified BenA database provided here.

**Extrolite data**

Extrolites are produced by the mycelium and sporulating structures of *Penicillium* species, and exudates, diffusible pigments, and reverse colours are also mixtures of secondary metabolites. Studies of extrolite profiles were very useful for unravelling some morphological species concepts into biologically meaningful segregate species before DNA sequencing provided similar possibilities. As an example, the *P. aurantiogriseum* complex, critical contaminants of grain, was divided first into species using extrolite profiles by Frisvad & Filtenborg (1983, 1989), delimitations that were subsequently supported by BenA sequencing (Seifert & Louis-Seize 2000).

Identification of unknown strains using extrolites is possible for well-equipped chemical laboratories. The best way of using extrolites as identification aids is to extract and then separate them by HPLC and then partially or fully identify as many of the secondary metabolites as possible, generally using mass spectroscopy based technology (Frisvad et al. 2008). The media used for identification, especially CYA and YES agars, are optimal for production of most major diagnostic extrolites in *Penicillium* after incubation for 7 d at 25 °C in darkness. Agar plugs are extracted with a mixture of dichloromethane, ethylacetate and methanol. The metabolites extracted can then be analysed using advanced separation and detection techniques.

**Table 3. Thermal cycle programs used for amplification.**

| Gene                  | Profile type | Initial denaturing | Cycles | Denaturing | Annealing | Elongation | Final elongation | Rest period |
|-----------------------|--------------|--------------------|--------|------------|-----------|------------|------------------|-------------|
| General ITS, BenA, CaM| standard     | 94 °C, 5 min       | 35     | 94 °C, 45 s| 55 °C, 45 s| 72 °C, 80 s | 72 °C, 7 min | 10 °C, ∞    |
| General alternative   | standard     | 94 °C, 5 min       | 35     | 94 °C, 45 s| 52 °C, 45 s| 72 °C, 60 s | 72 °C, 7 min | 10 °C, ∞    |
| RPB2                  | touch-up     | 94 °C, 5 min       | 5      | 94 °C, 45 s| 50 °C, 45 s| 72 °C, 60 s | 72 °C, 60 s | 72 °C, 7 min | 10 °C, ∞    |
|                       |              |                    |        | 5          | 52 °C, 45 s| 72 °C, 60 s |                  |             |
|                       |              |                    |        | 30         | 55 °C, 45 s| 72 °C, 60 s | 72 °C, 60 s | 10 °C, ∞    |
| RPB2 alt.             | touch-up     | 94 °C, 5 min       | 5      | 94 °C, 45 s| 48 °C, 45 s| 72 °C, 60 s | 72 °C, 60 s | 72 °C, 7 min | 10 °C, ∞    |
|                       |              |                    |        | 5          | 50 °C, 45 s| 72 °C, 60 s |                  |             |
|                       |              |                    |        | 30         | 52 °C, 45 s| 72 °C, 60 s | 72 °C, 60 s | 10 °C, ∞    |
for example ultra high performance liquid chromatography with
diode array detection and high resolution mass spectrometric
detection (UHPLC-DAD-HRMS) (Kildgaard et al. 2014, Kildgaard et al. 2014). However, simpler HPLC-diode array detection
methods can also be used (Frisvad & Thrane 1987, 1993).

Laboratories with less sophisticated equipment can perform
valuable confirmatory tests. Although Thin Layer Chromatography
(TLC) is no longer considered state of the art for chemical
research, it is still a useful technique for detecting coloured or
uncoloured extraites that can be used to confirm the identification
of a Penicillium strain. For example, P. brevicipitum consis-
tently produces large amounts of the colourless mycophenolic
acid, and this metabolite will make a green colour reaction with
ferric chloride (Clutterbuck & Raistrick 1933).

Sometimes only a few extraites are needed to confirm the
identity of a Penicillium isolate. If an isolate produces griseo-
fulvin and roquefortine C, it can only be P. coprophilum, P. griseofulvum or P. sclerotigenum and if the isolate also pro-
duces cyclopiazonic acid, it can only be P. griseofulvum (Frisvad
& Samson 2004).

Identification based purely on secondary metabolites is not
yet possible for all species of Penicillium, but future databases
will be better developed and an optimal battery of media for
secondary metabolite production may allow this method to be
used for identification of all species in the future.

**Misidentifications in Penicillium**

A few examples demonstrate why Penicillium identification is
difficult or how misleading results might be obtained in practise
using morphology or sequencing. For example, a fungus pro-
ducing penicillones A and B and chlortanspinones A, B and
terrestrols was identified as P. terrestr (patent strain CCTCC M
204077, strain unavailable) (Liu et al. 2005). The name P. terrestr was used by Raper & Thom (1949), but has since
been considered a synonym of P. crustosum. However, addi-
tional secondary metabolites produced by the isolate, such as
sorbicillin and trichodimerol, are never seen in P. crustosum
(Frisvad et al. 2004), suggesting the strain was P. chrysogenum or P. rubens. Liu et al. (2005) did not describe how their isolate
was identified. Another strain of P. chrysogenum or P. rubens,
SD-118 (HQ652873), was misidentified as a P. commune (Shang
et al. 2012, Zhao et al. 2012), based on “100 % sequence identity”
with P. commune (FJ499541). The production of chrysogine, sorbicillin and meleagrin indicated that the strain,
SD-118, was in fact P. chrysogenum. We propose that the use of
the reference sequence databases provided here, will minimise
these type of misidentifications.

**Matrix-assisted laser desorption/ionization time-of-flight mass spectrometry fingerprinting**

(MALDI-TOF MS)

Another detection technique receiving a lot of attention, especially
from the medical field, is matrix-assisted laser desorption/ioniza-
tion time-of-flight mass spectrometry fingerprinting (MALDI-TOF
MS). It was successfully applied to the identification of bacteria
(Hettick et al. 2006, Siegrist et al. 2007) and yeast species (Amiri-
Eliasi & Fenselau 2001, Kolecka et al. 2013). Only a limited
number of studies included or focused on Penicillium (Welham
et al. 2000, Hettick et al. 2008, Del Chierico et al. 2012,
Chalupová et al. 2014) and the closely related Aspergillus (Bille
et al. 2011, De Carolis et al. 2011, Iriart et al. 2012, Verwer et al.
2013). Although these studies promisingly report that MALDI-
TOF MS distinguish between species, a large degree of varia-
tion is observed within a species, even between duplicates of the
same strain (Hettick et al. 2008). This means that data from a high
number of strains will have to be included in the database to make
robust identifications feasible. Difficulties with identifications are
also reported in Aspergillus, where not all strains could be iden-
tified with 100 % accuracy (Iriart et al. 2012, Verwer et al. 2013).
Thus we can conclude that although this technique shows prom-
ise, a lot of work remains to make routine identifications feasible.

**TAXONOMY**

Phylogenetic analyses revealed that Hemicarpenteles paradoxus
should not be classified in Aspergillus, and together with its closest
relatives A. crystallinus and A. malodoratus, should be transferred
to Penicillium (Peterson 2000a, 2008, Houbraken & Samson 2011).
Houbraken & Samson (2011) included them in Penicillium sect.
Paradoxa together with P. atramentosum. The other Hemi-
carpenteles species were shown to belong in Aspergillus sect.
Clavati (H. acanthosporus ≡ A. acanthosporus ≡ Neocarpenteles
acanthosporus (Udagawa & Takada Udagawa & Uchiy.) (Peterson
2000b, Tamura et al. 2000, Varga et al. 2007, Peterson 2008),
while H. omatus and H. thaxteri are classified in Sclerocleista (Pitt
et al. 2000, Houbraken & Samson 2011).

Aspergillus paradoxus was described by Fennell & Raper
(1955) for strains producing small clavate vesicles suggestive of
those observed in aberrant strains of A. clavatus. Later, Raper
& Fennell (1965) placed A. paradoxus in the A. omatus species
group, based on the resemblance of its sclerotia to young
ascostelia of A. omatus and A. citrinosus. Rai et al. (1964,
1967) also isolated A. paradoxus from soil in India, and found
that conditions favouring sclerotia production also inhibited the
formation of conidial heads and the yellow pigment in the me-
dium. Sarbhy & Elphick (1968) observed that a strain of A.
paradoxus (CBS 793.68 = IMI 117502), isolated from dog
dung in the United Kingdom, produced mature unilocular clei-
stothecia with tough peridial walls, embedding smooth-walled
lenticular ascospores. They introduced the name Hemi-
carpenteles for the sexual morph, with H. paradoxus as type.
Houbraken & Samson (2011) noted that the sexual morph most
closely resembles Eupenicillium, both producing sclerotoid
ascostelia that ripen from the centre outwards (Sarbhy & Elphick
1968, Pitt 1979, Stolk & Samson 1983). In our fresh
isolates, some strains produce sclerotia abundantly while others
have only a few sclerotia. Only two fresh isolates produced
ascospores after incubation at 25 °C for three weeks on OA.
Aspergillus paradoxus, A. crystallinus and A. malodoratus (Figs
3–6) have a striking similarity with members of section Olsonii
and Coronata (Frisvad & Samson 2004, Samson et al. 2004),
in particular the long, wide, smooth-walled conidiophores termi-
nating in densely branched penicilli with metulae and phialides.
Particularly P. olsonii bears a morphological resemblance with
A. paradoxus and A. crystallinus.

Extritole data also suggest that A. paradoxus, A. crystallinus
and A. malodoratus belong in Penicillium (summarised in
Table 4). Pseurotins are found in both Penicillium and Aspergillus
species (Frisvad et al. 2004). Sorbicillins were previously only
confirmed in P. rubens and P. chrysogenum, and not so far in
Fig. 3. *Penicillium paradoxum*. A. Colonies: top row left to right, obverse CYA, YES, DG18 and MEA; bottom row left to right, reverse CYA, reverse YES, reverse DG18 and CREA. B. Young sclerotia. C. Phototropic conidiophores after two weeks growth. D–H. Conidiophores. I. Conidia. Scale bars: D–I = 10 μm.
Aspergillus, although Basaran & Demirbas (2010) reported sorbicillin production in A. parasiticus; we have never observed sorbicillins in any A. parasiticus strain. Penicillium atramentosum, also classified in section Paradoxa, produces andrastin A, atpensins, meleagrin and oxaline, roquefortine C & D and rugulovasine A & B (Frisvad et al. 2004, and reported here). Among Penicillium and Aspergillus species, the atpensins have only been found in P. atramentosum (Omura et al. 1988, Kawada et al. 2009), but the other listed extrolites are common in species of Penicillium sections Paradoxa and Chrysogena. Rugulovasins are an exception and have only been found in P. commune (Frisvad et al. 2004).

Aspergillus paradoxus produces brefeldin, an extrolite also reported in P. brefeldianum (Hutchinson et al. 1983), but never in Aspergillus apart from a report for A. clavatus (Wang et al. 2002) that could not be confirmed (Varga et al. 2007). The latter strain was probably actually A. ingratus, first regarded as belonging to Aspergillus section Clavati (Yaguchi et al. 1993) but now considered a synonym of A. paradoxus. Xanthocillins are produced by A. paradoxus strains, and also by P. chrysogenum and P. egyptiacum. Meleagrin is commonly produced in Penicillium sections Paradoxa and Chrysogena, and species of several other sections (Frisvad et al. 2004). The closely related extrolite, neoxaline, has been reported in A. japonicus (Hirano et al. 1979). Aspergillus crystallinus produces chrysogine, typical of P. rubens and P. chrysogenum (Frisvad et al. 2004, Houbraken et al. 2012a), and a compound also reported in A. nomius (Varga et al. 2011). Chrysophanic acid, produced in A. crystallinus, was found in Talaromyces islandicus (Howard & Raistrick 1950), and pachybasin was found in P. vulpinum (Frisvad et al. 2004). Aspergillus malodoratus produces andrastin A, meleagrin and oxaline.

Andrastin A is produced by several Penicillium species including P. rubens and P. chrysogenum (Houbraken et al. 2011a, 2012a), but has not been found in Aspergillus. On balance, chemotaxonomic evidence points to the placement of A. paradoxus, A. crystallinus and A. malodoratus in Penicillium.

From the phenotypic, molecular and extrolite data we can conclude that the three species formerly placed in Aspergillus belong to Penicillium. Consequently we propose the following new combinations:

**Penicillium paradoxum** (Fennell & Raper) Samson, Houbraken, Visagie & Frisvad, **comb. nov.** MycoBank MB547045. Figs 3, 4.

**Basionym:** Aspergillus paradoxus Fennell & Raper, Mycologia 47: 69. 1955. MycoBank MB292853

≡ Hemicarpenteles paradoxus Sarthoy & Elphick, Trans. Brit. Mycol. Soc. 51: 156. 1968. MycoBank MB265229

= Aspergillus ingratus Yaguchi, Someya & Udagawa, Trans. Mycol. Soc. Japan 34: 305. 1993. MycoBank MB361187

[Non Trichocoma paradoxa Jungh., Praemissa in floram cryptogramamicam Javae insulae: 9. 1838. MycoBank MB161024]

**Typus:** New Zealand. Wellington, dung of opossum, 1948, isolated by J.H. Warcup. Neotype IMI 061446, culture ex-type CBS 527.65 = NRRL 2162 = ATCC 16918 = IMI 061446

**Penicillium paradoxum** (and P. malodoratum) deviate from other Penicillium species by being phototropic (Raper & Fennell 1965) and occasionally having a well-developed vesicle that makes the conidiphore appears like an aspergillum (illustrated by Yaguchi et al. 1993 in the protologue of Aspergillus ingratus).
Fig. 5. *Penicillium crystallinum*. A. Colonies: top row left to right, obverse CYA, YES, DG18 and MEA; bottom row left to right, reverse CYA, reverse YES, reverse DG18 and CREA. B. Colony texture on MEA. C–G. Conidiophores. H. Conidia. Scale bars: C–H = 10 μm.
Fig. 6. *Penicillium malodoratum*. A. Colonies: top row left to right, obverse CYA, YES, DG18 and MEA; bottom row left to right, reverse CYA, reverse YES, reverse DG18 and CREA. B. Colony texture on MEA. C–G. Conidiophores. H. Conidia. Scale bars: C–H = 10 μm.
Table 4. Origin and extrolites of the strains examined in this study.

| Species         | Strain            | Origin                          | Extrolites                                      |
|-----------------|-------------------|---------------------------------|-------------------------------------------------|
| A. crystallinus | CBS 479.65T = IBT 21947 | Forest soil, Tilaran, Costa Rica | chrysophanic acid, chrysogine, meleagrin, pachybasin |
| A. malodoratum  | CBS 490.65T = IBT 21948 | Forest soil, Barranca, Costa Rica | andrastin A, oxaline, meleagrin                  |
| A. paradoxus    | CBS 123898 = IBT 29765 = DTO 76F5 | Dung of dog, the Netherlands | “astyl”, brefeldin A, “SLOF”                     |
|                 | CBS 123898 = IBT 29768 = DTO 76F6 | Dung of dog, the Netherlands | “astyl”, brefeldin A, pseudotin, “SLOF”, sorbicillins |
|                 | CBS 527.65T = IBT 19547 | Dung of opossum, New Zealand | “astyl”, brefeldin A, pseudotin, “SLOF”, sorbicillins |
|                 | CBS 643.95T = IBT 17513 = PF 1116 | Soil, USA, California (ex-type of A. ingratus) | “astyl”, brefeldin A, “PAS”, pseudotin, “SLOF”, sorbicillins |
|                 | CBS 793.68 = IBT 19572 | Dung of dog, UK | brefeldin A, “PAS”, pseudotin, “SLOF”, sorbicillins |
|                 | CBS 793.91 = IBT 12297 | Dung of dog, Denmark | brefeldin A, pseudotin, “SLOF”, sorbicillins |
|                 | IBT 29766 = DTO 76F7 | Dung of dog, the Netherlands | brefeldin A, pseudotin, “SLOF”, sorbicillins |
| IMI 173765      | IMI 17365          | Jet fuel, New Zealand           | “astyl”, brefeldin A, pseudotin, sorbicillins    |
| IMI 320026      | IMI 19365          | Air, UK                         | brefeldin A, pseudotin, sorbicillins            |

However, stipes were described as small, thin-walled and even sepalate, and the illustration by Raper & Fennell (1965) indicates a conidial head not unlike P. crystallinum and P. malodoratum. The latter authors also noted that A. crystallinus and A. malodoratum occasionally produced triseriate “sterigmata” and “conidial structures, particularly when small, tend to resemble those of the genus Penicillium”. Most isolates of P. paradoxum are apparently from dung. Penicillium paradoxum, P. malodoratus and P. crystallinum produce strong penetrating odours, similar to those known from coprophilous species in Penicillium series Claviformia, apparently an adaptation to the dung habitat.

**Penicillium crystallinum** (Kwon-Chung & Fennell) Samson, Houbraken, Visagie & Frisvad, comb. nov. MycoBank MB809315. Fig. 5.

Basionym: Aspergillus crystallinus Kwon-Chung & Fennell, The Genus Aspergillus: 471. 1965. MycoBank MB326624

Typus: Costa Rica, Province of Guanacaste, Tilaran, forest soil, 1962, isolated by K.J. Kwon & D.I. Fennell. Neotype IMI 139270, culture ex-type CBS 479.65 = NRRL 5082 = ATCC 16833 = IMI 139270.

*Penicillium crystallinum* is only known from its ex-type strain (CBS 479.65 = NRRL 5082 = ATCC 16833 = IMI 139270), isolated from forest soil in Costa Rica. Colonies contain numerous long, phototropic conidiophores. Raper & Fennell (1965) observed abundant soft sclerotium-like bodies with thick-walled cells, but we could not detect them. As the name suggests, this fungus produces an unpleasant odour on all media tested. Although A. malodoratus and A. crystallinus were isolated from forest soil in Costa Rica and have similar morphological characters, the taxa can be distinguished by the colony diameter, the length of the conidiophores and the size and shape of the conidia. Conidia of A. crystallinus are globose, 4–7 μm, echinulate, while those of A. malodoratus are subglobose to ellipsoidal, 3–5 × 3–4 μm and mainly smooth.

**PROPOSED LIST OF ACCEPTED SPECIES IN THE GENUS PENICILLIUM**

The following list includes species names that are accepted in the genus *Penicillium* on 8 August 2014. This list is updated from previous lists published by Pitt & Samson (1993) and Pitt et al. (2000). This revision was considered necessary following changes made to the ICN and the move to single name nomenclature (McNeill et al. 2012), the large number of species described since the 2000 list and new taxonomic information provided by molecular data.

The most dramatic changes in *Penicillium* are the incorporation of *Eupenicillium* and several other genera as synonyms (Houbraken & Samson 2011), and the transfer of species of the former *Penicillium* subgenus *Biverticillium* species to *Talaromyces* (Samson et al. 2011). *Aspergillus paradoxus*, A. crystallinus and A. malodoratus were shown to belong to *Penicillium* and were transferred above. Several species described as *Penicillium* belongs to other genera and not to *Penicillium* (Houbraken & Samson 2011). They are listed below the accepted species list.

Even though the updating of the accepted species list began for nomenclatural purposes, we aim to make this list more...
functional by including additional information linked to the species names. The list thus includes MycoBank numbers where complete nomenclatural data can be obtained, collection numbers of ex-type strains for future taxonomists requiring authenticated reference material, the species current sectional classification, and GenBank accession numbers for ITS barcodes and, where available, alternative molecular identification markers for BenA, CaM and RPB2.

Despite the considerable effort of time and effort spent on completing this list, there is the possibility of errors or oversights. As such we solicit and gratefully accept any comments on missing names, errors or new data that has become available, especially when publishing a new species. We would also appreciate suggestions for making the list more useful. The active version of the list is currently hosted on the ICPA website (http://www.aspergilluspenicillium.org) where it will be updated as new information comes to light. The website contains a portal for contributions, for the convenience of our users. The list published here contains only accepted species; the online version will in future also include data for synonyms. Similar lists are available for Aspergillus (Samson et al. 2014) and Talaromyces (Yilmaz et al. 2014).

**Penicillium** Link, Mag. Ges. Naturf. Freunde Berlin 3: 16. 1809. MycoBank MB9257.

− Coremium Link, Mag. Ges. Naturf. Freunde Berlin 3: 19. 1809, fide Raper & Thom 1949, Seifert & Samson 1985. [MB7782].
− Flococcia Gray, Scott, crypt. fll.: pl. 301. 1827, fide Seifert & Samson 1985. [MB8260].
− ?= Hormodendrum Bonord., Handbuch allg. Mykol.: 76. 1851, fide de Hoog & Henries-Nijhof 1977, but see Hughes 1958. [MB5588].
− = Walsia Sorokin, Trudy Inst. Mig. 18: 43. 1912. [MB104429].
− = Pithizelia Henn., Hedwigia 42: 88. 1903, fide Clements & Shear 1931. [MB9529].
− = Eupenicillium F. Ludwig, Lehrbuch der Niederer Kryptogamen: 263. 1892, fide Houbraken & Samson 2011. [MB1933].
− = Chloromyces Wehmer, Ber. Deut. Bot. Ges.: 11. 333. 1883, fide Thom 1930. [MB7972].
− = Aspergillopsis Skr, Videskr.-Selisk. Christiana Math.-Nat. Kl. 11: 204. 1912, non Aspergillopsis Spec. 1910, fide Pitt 1979. [MB22043].
− = Carpenetes Langeron, Crypt. Fr.: 344. 1922, fide Stolk & Scott 1967. [MB826].
− = Eupenicillium Link, Mag. Ges. Naturf. Freunde Berlin 3: 16. 1809. MycoBank MB9257. [MB10252].
− = Eikelia Smith, Trans. Brit. Mycol. Soc.: 44. 47. 1961, fide Samson 1967. [MB10314].
− = Thysanoptera Hendrick, Can. J. Bot.: 39. 820. 1961, fide Houbraken & Samson 2011. [MB10230].
− = Hemicarpenteles Sarbhyo & Elphick, Trans. Brit. Mycol. Soc.: 51. 156. 1968, fide Houbraken & Samson 2011. [MB2279].
− = Penicillium Link ex Gray sensu Pitt, The genus Penicillium: 154. 1979 (nom. inval., art 13e).
− = Chromocleista Yaguchi & Udagawa, Trans. Mycol. Soc. Japan 34: 101. 1993, fide Houbraken & Samson 2011. [MB25855].

**Penicillium abidanum** Stolk, Antonie van Leeuwenhoek 34: 49. 1968. = Eupenicillium abidanum Stolk, Antonie van Leeuwenhoek 34: 49. 1968. [MB335705].
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S.W. Peterson, J. Clin. Microbiol. (in press). [MB807056]. — Herb.: Ex-type: CBS 15867. Section Canescentia. ITS barcode: CaM = JN606622; RPB2 = JN606626; CaM = JN606423.

Penicillium cinerereum Biourge, Cellule 33: 308. 1923. [MB260765]. — Herb.: Ex-type: CBS 199224. Section: NERL. ITS barcode: CaM = JX141041; RPB2 = n.a.; CaM = n.a.

Penicillium cincinereum Chabrol, Bot. Mater. Old. Sporov. Rast. 6: 167. 1950. [MB302385]. — Herb.: Ex-type: CBS H-7469. Ex-type: CBS 222.66 + ATCC 22350 + FRR 3390 = ULMF 5024 + IMI 113676 + VKMF-656. Section Exilicaulis. ITS barcode: CaM = JX141100. (Alternative markers: BenA = JN606678; RPB2 = JN606626; CaM = JN606423.

Penicillium cinereum Biourge, Cellule 33: 284. 1923. [MB260472]. — Herb.: Ex-type: CBS 199224. Section: NERL. ITS barcode: CaM = JX141041; RPB2 = n.a.; CaM = n.a.

Penicillium conspicuum Bot. Int. Acad. Polon. Sci., Sér. B, Sci. Nat. 1927: 464. 1927. [MB206069]. — Herb.: unknown. Ex-type: CBS 217.28 + FRR 903 = MUCL 29167 + NERL 1741 + NERL 903. Section Citrina. ITS barcode: CaM = GU944603. (Alternative markers: BenA = JN606678; RPB2 = JN606626; CaM = JN606423.

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Penicillium clavipes Thom, U.S.D.A. Bur. Animal Industr. Bull. 118: 61. 1910. [MB165293]. — Herb.: IMI 921961. Ex-type: CBS 28673 = ATCC 2049 = ATCC 1910. Section Canescentia. ITS barcode: CaM = JX141100. (Alternative markers: BenA = EF629648; RPB2 = JN606533; CaM = EF629649.

Penicillium clavipes Thom, U.S.D.A. Bur. Animal Industr. Bull. 118: 61. 1910. [MB165293]. — Herb.: IMI 921961. Ex-type: CBS 28673 = ATCC 2049 = ATCC 1910. Section Canescentia. ITS barcode: CaM = JX141100. (Alternative markers: BenA = EF629648; RPB2 = JN606533; CaM = EF629649.

Penicillium clavipes Thom, U.S.D.A. Bur. Animal Industr. Bull. 118: 61. 1910. [MB165293]. — Herb.: IMI 921961. Ex-type: CBS 28673 = ATCC 2049 = ATCC 1910. Section Canescentia. ITS barcode: CaM = JX141100. (Alternative markers: BenA = EF629648; RPB2 = JN606533; CaM = EF629649.
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Penicillium coralligerum
Nicot & Pignat, Bull. Soc. Mycol. France 78: 245. 1963 [1962]. [MB335721]. = Herb.: IMI 99195. Ex-type: CBS 123.65 = ATCC 16968 = F556 = IFO 9578 = IHEM 4511 = IMI 199915 = LCP 58.1674 = NRRL 3466. Section Caneascensia. Its barcode: JN176167. (Alternative markers: BenA = KX834444; RPB2 = JN406632; CaM = KJ868994).
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18239 = FRR 2671 = IFO 8175 = IMI 071626 = LSH BB323 = NRRL

28643 = NRRL 2152 = NRRL 2300 = QM 6902 = VKMF-286. Section

7641 = IMI 075832 = IMI 075832ii = LCP 79.3245 = LSHBP 68 = MUCL

[MB120566].

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22353 = FRR 3429 = IFO 9147 = IMI 096157. Section

3745 = IMI 253783. Section

—

[MB809964].

CaM

BenA

907 = FRR 907 = Thom 4894.16. Section

2012. [MB801875].

6452. Section

Gracilenta.

hirayamae

Citrina.

29057. Section

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BenA

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Penicillium maclennaniae H.Y. Yip, Trans. Brit. Mycol. Soc. 77: 202. 1981. [MB112253]. — Herb.: DAR 35238. Ex-type: CBS 198.81 = DAR35238. Section Exilicaulis. ITS barcode: KC411689. (Alternative markers: BenA = KJ334468; RPB2 = n.a.; CaM = n.a.).

Penicillium macrocerotermorum L. Wang, X.M. Zhang & W.Y. Zhuang, Mycol. Res. 111: 1244. 2007. [MB492622]. — Herb.: HMAS 133177-1-4. Ex-type: CBS 116871 = A 3.6581. Section Gracilenta. ITS barcode: KJ934311. (Alternative markers: BenA = KJ334469; RPB2 = JN121432; CaM = DQ911123).

Penicillium madriti R. Serra & S.W. Peterson, Mycologia 99: 81. 2007. [MB130027]. — Herb.: HMAS 21872. Ex-type: CBS 213.60 = A 4083. Section Aspergilloides. ITS barcode: AF033485. (Alternative markers: BenA = KJ334470; RPB2 = JN060022; CaM = JF624796).

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Penicillium malodoratum G. Sm., Trans. Brit. Mycol. Soc. 44: 44. 1961. [MB335747]. — Herb.: IMI 86563. Ex-type: CBS 213.60 = A 3.6581. Section Cinnamopurpureum. ITS barcode: EU427300. (Alternative markers: BenA = EU427286; RPB2 = JN060062; CaM = KJ699697).

Penicillium malatcenense C. Ramirez & A.T. Martinez, Mycopathologia 72: 186. 1980. [MB111023]. — Herb.: IJF 7093. Ex-type: CBS 160.81 = A 3.6581. Section Melanoconidium. ITS barcode: AY674981. (Alternative markers: BenA = JX997082). 

Penicillium melanophilum R. Günther & Udagawa, Beih. Bot. Centralbl. 40: 434. 1927. [MB492618]. — Herb.: CBS H-21289. Ex-type: CBS 206.65 = A 3.6581. Section Lanata-Divaricata. ITS barcode: JN406613. (Alternative markers: BenA = AV499997; RPB2 = JX997067; CaM = JN799645).

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Penicillium malhamense (Yaguchi & Udagawa) Houbraken & Samson, Stud. Mycol. 70: 47. 2011. — Herb.: Chromocleista maclennaniae Yaguchi & Udagawa, Trans. Mycol. Soc. Japan 34: 102.1993. [MB561971]. — Herb.: CBS 647.95. Ex-type: CBS 647.95 = IOT 17515. Section Sclerotiora. ITS barcode: KCT773838. (Alternative markers: BenA = KCT77394; RPB2 = n.a.; CaM = KCT773820).

Penicillium malmoense (Kwon-Chung & Fennell, Gen. Mycol. 1: 215. 1980) Frisvad, Filt. & Wicklow, Stud. Mycol. 49: 20. 2004. — Herb.: CBS 172.87 = IOT 3072 = IOT 5158 = IBT 21535 = IMI 115235 = NRRL 13442 = NRRL A-26709. Section Chrysogena. ITS barcode: JX997082. (Alternative markers: BenA = AV499997; RPB2 = JX997067; CaM = JN799645).
Penicillium ochrochloron  
H.Z. Kong & Z.T. Qi, Mycosystema 1: 108. 1988.  
[MB135445]. — Herb.: CBS 227.89. Ex-type: CBS 227.89. Section Cinnamo- 
mpurea. Itsbarcode: KC411703. (Alternative markers: 
BenA = KJ834475; RPB2 = JN406603; CaM = KJ887003).

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KJ384513. (Alternative markers: BenA = KJ384476; RPB2 = n.a.; CaM = n.a.).

Penicillium nothofagi  
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2011. [MB53191]. — Herb.: CBS H-20655. Ex-type: CBS 130383 ≡ 
NRRL 2912 = QM 7604. Section Caneascencia. Its barcode: 
JN617888. (Alternative markers: BenA = KJ384477; RPB2 = JN406628; CaM = KJ866999).

Penicillium ochrochloron  
Bourge, Cellule 33: 269. 1923. [MB272701]. — Herb.: 
IMI 35808. Ex-type: CBS 358.62 = ATCC 358.62 = IMI 358.62. Section Cinnamopurpurea. Its barcode: 
GU981570. (Alternative markers: BenA = GU981672; RPB2 = KF296445; CaM = KF296373).

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Udagawa, J. Agric. Sci. Tokyo Nogyo Daigaku 5: 10. 
1959 ≡ Penicillium ochrosalmoneum D.B. Scott & Stolk, Antonie van 
Leuwenhoek 33: 302. 1967. [MB302409]. — Herb.: 
NHL 6048. Ex-type: CBS 489.66 ≡ ATCC 18338 ≡ CSIR 145 = IMI 1162481 = 
NRRL 35499. Section Ochrosalmonea. Its barcode: EF826961. (Alternative markers: 
BenA = EF506212; RPB2 = J121524; CaM = EF506237).

Penicillium ochrochrous  
M. Chr. & Backus, Mycologia 53: 459. 1961. [MB335755]. — Herb.: 
WSF 2000. Ex-type: CBS 294.62 ≡ ATCC 14769 = DSM2419 = IFO 7741 ≡ IMI 0942081 = 
NRRL 3007 = WSF2000. Section Aspergiloides. Its barcode: 
KCI41730. (Alternative markers: BenA = KJ384478; RPB2 = JN406583; CaM = KIM089363).

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NRRL 3058 = NRRL 13716. Section Breviscripta. Its barcode: 
EU987341. (Alternative markers: BenA = YH674445; RPB2 = J121164; 
CaM = DQ058165).

Penicillium onobense  
C. Ramírez & A.T. Martínez, Mycopathologia 74: 44. 
1981. [MB112525]. — Herb.: CBS 174.81. Ex-type: CBS 174.81 ≡ 
ATCC 24222 ≡ IFM 2062 = VKM-F-2183. Section Lanata-Divaricata. Its barcode: 
GU981575. (Alternative markers: BenA = GU981627; RPB2 = KF296447; 
CaM = KF296371).

Penicillium ornatum  
Udagawa, Trans. Mycol. Soc. Japan 6: 79. 1965 (nom. inval., Art. 36). 
[MB302412]. — Herb.: EUP 23262. Ex-type: CBS 262.60 ≡ 
ATCC 10480 = FRR 2662 = IFO 7732 = IMI 040587 = 
NRRL 2095 = QM 1878. Section Exilicaulis. Its barcode: 
AF178511. (Alternative markers: BenA = KF296446; RPB2 = KF296449; 
CaM = KF296372).

Penicillium paraherquei  
S. Abe ex G. Sm., Trans. Brit. Mycol. Soc. 46: 335. 
1963 ≡ Penicillium paraherquei S. Abe, J. Gen. Appl. Microbiol., Tokyo 2: 
131. 1956 (nom. inval., Art. 36). [MB302412]. — Herb.: 
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NRRL 2162 = ATCC 16918 = IMI 061446. Section Paraherquei. Its barcode: 
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CBS H-7099. Ex-type: CBS 623.72 = FRR 23262. Section Lanata-Divaricata. Its barcode: 
GU981627. (Alternative markers: BenA = KF296447; RPB2 = J121164; 
CaM = DQ058165).

Penicillium persicinum  
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2004. [MB500259]. — Herb.: CBS H-20663. Ex-type: CBS 126330 ≡ 
IBT 126330. Section Citrina. Its barcode: JN617876. (Alternative markers: 
BenA = JN060667; RPB2 = JN060617; CaM = JN060394).

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FRR 2661. Ex-type: CBS 260.87 = FRR 2662. Section Aspergil- 
oides. Its barcode: KC411718. (Alternative markers: BenA = KJ384381; 
RPB2 = JN406593; CaM = n.a.).

Penicillium pavilli  
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IMI 40226. Ex-type: CBS 360.48 = ATCC 10480 = FRR 2008 = IMI 
040226 = NRRL 2098 = QM 725. Section Citrina. Its barcode: 
GU944577. (Alternative markers: BenA = JN060844; RPB2 = JN060611; 
CaM = JN060566).

Penicillium penarajense  
Houbrekan et al., Int. J. Syst. Evol. Microbiol. 61: 1471. 
2011. [MB150824]. — Herb.: HUA 170335. Ex-type: CBS 113178 = 
IBT 23262. Section Lanata-Divaricata. Its barcode: GU981570. (Alternative markers: 
BenA = GU981646; RPB2 = KF296450; CaM = KF296381).

Penicillium persicinum  
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2004. [MB500259]. — Herb.: HMAS 80308-1-4. Ex-type: 
CBS 111235 ≡ AS 3.5891 = IBT 24569. Section Cystogonia. Its barcode: 
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CaM = J096654).}
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**IDENTIFICATION AND NOMENCLATURE OF Penicillium**

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Penicillium benomaliense RPB2 Herb.: CBS H-20666. Ex-type: CBS 101623 = IBT 2905. Section Citrina. ITS barcode: JN167661. (Alternative markers: BenA = JN606700; RPB2 = JN606622; CaM = JN605690). \[MB563202. \]

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Penicillium chrysogenum Chrysogena. \[MB213547. \]

Penicillium chrysogenum RPB2 Herb.: CBS H-5727. Ex-type: CBS 417.69 = IFO 2001 = IFO 3697 = IFO 8179 = IFO 2994 = CBS 221.30 = ATCC 10936 = CBS 104234 = CBS 31202 = VKMF-1074. Section Aspergilloides. ITS barcode: KM198565. (Alternative markers: BenA = KM088801; RPB2 = KM089573; CaM = KM089198). \[MB335762. \]

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Penicillium claviforme RPB2 Herb.: CBS H-21862. Ex-type: CBS 137953 = DTO 056-AS. Section Aspergilloides. ITS barcode: KM198541. (Alternative markers: BenA = KM088777; RPB2 = KM089551; CaM = KM089164). \[MB488823. \]

Penicillium claviforme †. Herb.: C 60161. Ex-type: CBS 112430 = IBT 10696. Section Sclerotiora. ITS barcode: KJ834557. (Alternative markers: BenA = AV164147; RPB2 = n.a.; CaM = n.a.). \[Houbraken & Samson, IMA Fungus 1: 174. 2010. \]

Penicillium claviforme RPB2 Herb.: CBS H-20666. Ex-type: CBS 101623 = IBT 2905. Section Citrina. ITS barcode: JN167661. (Alternative markers: BenA = JN606700; RPB2 = JN606622; CaM = JN605690). \[MB563202. \]

Penicillium claviforme RPB2 Herb.: CBS H-5727. Ex-type: CBS 417.69 = IFO 2001 = IFO 3697 = IFO 8179 = IFO 2994 = CBS 221.30 = ATCC 10936 = CBS 104234 = CBS 31202 = VKMF-1074. Section Aspergilloides. ITS barcode: KM198565. (Alternative markers: BenA = KM088801; RPB2 = KM089573; CaM = KM089198). \[MB335762. \]

Penicillium claviforme RPB2 Herb.: CBS H-5727. Ex-type: CBS 417.69 = IFO 2001 = IFO 3697 = IFO 8179 = IFO 2994 = CBS 221.30 = ATCC 10936 = CBS 104234 = CBS 31202 = VKMF-1074. Section Aspergilloides. ITS barcode: KM198565. (Alternative markers: BenA = KM088801; RPB2 = KM089573; CaM = KM089198). \[MB335762. \]

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Penicillium verhagenii Houbraken, Stud. Mycol. 78: 443. 2014. [MB809979]. — Herb.: CBS H-21865. Ex-type: CBS 137969 = DTO 193-A1. Section Aspergillioides. ITS barcode: KM189708. (Alternative markers: BenA = KM089855; RPB2 = KM089729; CaM = KM089342).

Penicillium verrucosum Dierckx, Ann. Sci. Soc. Bruxelles 25: 88. 1901. [MB212252]. — Herb.: IMI 200310. Ex-type: CBS 603.74 = ATCC 48957 = ATCUM2897 = CECT 2909 = FRR 965 = IBT 12809 = IBT 4733 = IMI 203013 = IMI 203016 = MUCU 28674 = MUCU 29089 = MUCU 29186 = NRRL 965. Section Fasciculata. ITS barcode: AY373939. (Alternative markers: BenA = AY674323; RPB2 = JN121539; CaM = DQ911138).

Penicillium vinaceum J.C. Gilman & E.V. Abbott, Iowa St. Coll. J. 1: 299. 1927. [MB281754]. — Herb.: IMI 29189. Ex-type: CBS 10514 = FRR 739 = IMI 029189 = NRRL 739 = QM 6746. Section Exilicaulis. ITS barcode: AF334361. (Alternative markers: BenA = HM646657; RPB2 = JN406641; CaM = HM646586).

Penicillium viridicatum [Cooke & Massee] Seifert & Samson, Adv. Mycol. 5: 368. 2005. — Herb.: CBS 126.23 = ATCC 10426 = IMI 040237 = NRRL 40: 353. 1990. [MB561965]. — Herb.: unknown. Ex-type: No culture available. Note: No material is available for this species. As such, we cannot confirm the taxonomic position of the species and consider it as doubtful.

Penicillium yezoense Hanzawa ex Houbraken, Stud. Mycol. 5: 99. 1968. [MB335738]. — Herb.: CBS H-20657. Ex-type: CBS 130375 = IBT 23253. Section Torulomyces. ITS barcode: AY674295. (Alternative markers: BenA = AJ478092; RPB2 = JN121511; CaM = n.a.).

Penicillium zanjiangii L. Wang, PloS ONE 9: e101454-P4. 2014. [MB809545]. — Herb.: HMAS 244922. Ex-type: CBS 137464 + NRRL 62806 = AS 3.15341. Section Aspergillioides. ITS barcode: KF769435. (Alternative markers: BenA = KF769411; RPB2 = n.a.; CaM = KF769422).

**Doubtful species**

Penicillium asymmetricum (Subram. & Sudha) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 \equiv Thysanophora asymmetrica Subram. & Sudha, Kavaka 12. 88. 1985. [MB561963]. — Herb.: unknown. Ex-type: No culture available. Note: No material is available for this species. As such, we cannot confirm the taxonomic position of the species and consider it as doubtful.

Penicillium coniferophilum Houbraken & Samson, Stud. Mycol. 70: 47. 2011 \equiv Thysanophora striata/pora Bannor & Cooke, Mycopathol. Mycol. Appl. 40: 353. 1970. [MB561968]. — Herb.: unknown. Ex-type: No culture available. Note: No material is available for this species. As such, we cannot confirm the taxonomic position of the species and consider it as doubtful.

Penicillium glaucoalbidum (Desm.) Houbraken & Samson, Stud. Mycol. 70: 47. 2011 \equiv Sclerotium glaucoalbidum Desm., Ann. Sci. Nat., Bot. 16: 329. 1851 \equiv Thysanophora glucosida (Desm.) M. Morelet, Ann. Soc. Sci. Nat. Archéol. Toulon Var 20: 104. 1968. [MB561965]. — Herb.: unknown. Ex-type: No culture available. Note: No material is available for this species. As such, we cannot confirm the taxonomic position of the species and consider it as doubtful.

Penicillium melanostipe Houbraken & Samson, Stud. Mycol. 70: 47. 2011 \equiv Thysanophora verrucosa Mercedo, Gené & Guarto, Myxotaxon 67: 419. 1998. [MB561970]. — Herb.: HAC (M) 9165. Ex-type: No culture available. Note: No material is available for this species. As such, we cannot confirm the taxonomic position of the species and consider it as doubtful.

Penicillium parviverrucosum (K. Ando & Pitt) Houbraken & Samson, Stud. Mycol. 70: 48. 2011 \equiv Torulomyces parviverrucosus (K. Ando & Pitt) Pitt, Mycological Research 93: 317. 1998. — Herb.: TNS-F-238516. Ex-type: KY 12720. Note: Material for this species is not available for study. As such, we cannot confirm the taxonomic position of the species and consider it as doubtful.

Penicillium taiwanense (Matsush.) Houbraken & Samson, Stud. Mycol. 70: 48. 2011 \equiv Phialomyces taiwanensis Matsush., Mitsuhashi Mycol. Mem. 4: 12. 1985 \equiv Thysanophora taiwanensis (Matsush.) Mercédo, Gené & Guarto, Myxotaxon 67: 421. 1998. [MB561969]. — Herb.: unknown. Ex-type: No culture available. Section Thysanophora. Note: No material is available for this species. As such, we cannot confirm the taxonomic position of the species and consider it as doubtful.

**Excluded species**

Penicillium arenicola Chalabuda, Bot. Mater. Otd. Sporov. Rast. 6: 162. 1950. [MB302375]. — Herb.: IMI 117658. Ex-type: CBS 18321 = ATCC 18330 = DSM 2435 = FRR 3932 = IMI 117658 = NRRL 3932 = VKM F-1035. ITS barcode: GU092964. (Alternative markers: BenA = n.a.; CaM = n.a.; RPB2 = JN121457). Note: Molecular data suggest that this species is related to Phialomyces (Houbraken & Samson 2011).

Penicillium canadense G. Sm., Trans. Br. Mycol. Soc. 39: 113. 1950 = Penicillium arenicola Chalab., Bot. Mater. Otd. Sporov. Rast. 6: 162. 1950. [MB302384]. — Herb.: unknown. Ex-type: CBS 245.56 + ATCC 18424 = FRR 2553 = IMI 061834 = LS8H BB300 = NRRL 2553 = QM 6970 = WB 4155. ITS barcode: GU092963. (Alternative markers: BenA = GU092758; CaM = n.a.; RPB2 = n.a.). Note: Molecular data suggest that this species is a synonym of P. arenicola and is related to Phialomyces (Houbraken & Samson 2011).

Penicillium kabanicum Baghdadi, Novosti Sist. Nizs. Rast.: 92. 1968. [MB335738]. — Herb.: CBS 575.90. Ex-type: CBS 575.90 = CBS 409.69 = FRR 513 = IMI 065000. (Alternative markers: BenA = n.a.; CaM = n.a.; RPB2 = n.a.). Note: Material for this species is not available. As such, we cannot confirm the taxonomic position of the species and consider it as doubtful.

Penicillium moldavicum Milko & Beliakova, Novosti Sist. Nizs. Rast. 1967: 255. 1967. [MB335751]. — Herb.: unknown. Ex-type: CBS 574.90 = ATCC 18355 = CBS 627.67 = FRR 665 = IMI 129966 = VKM F-922. ITS barcode:
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n.a. (Alternative markers: BenA = n.a.; CaM = n.a.; RPB2 = n.a.). Note: Molecular data suggest that this species does not belong to Penicillium (Houbraken, unpubl. data).

Penicillium nodositatum Vaila, Pl. Soil 114: 146. 1989. [MB126535]. — Herb.: CBS 330.90. Ex-type: CBS 333.90. ITS barcode: KC790403. (Alternative markers: BenA = RPB36599; CaM = n.a.; RPB2 = n.a.). Note: Molecular data suggest that this species is closely related to P. kabunicum and does not belong in Penicillium (Visage et al. 2013).

Penicillium resedanum McLennan & Ducker, Aust. J. Bot. 2: 360. 1954. [MB302422]. — Herb.: IMI 062877. Ex-type: CBS 181.71 = ATCC 22356 = FRR 578 = IMI 062877 = NRRL 578. ITS barcode: AF303398. (Alternative markers: BenA = n.a.; CaM = n.a.; RPB2 = n.a.). Note: Pitt (1979) noted that this species form acerose phialides with weak growth on G25N, suggesting a relationship with Talaromyces, which is confirmed by ITS data (Houbraken & Samson 2011).

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