

Polyphasic taxonomy of *Penicillium* subgenus *Penicillium* A guide to identification of food and air-borne terverticillate *Penicillia* and their mycotoxins

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Abstract

Species in *Penicillium* subgenus *Penicillium* have terverticillate penicilli and are related to the ascomycete genus *Eupenicillium* series *Crustacea*. Many of its species are very common, being associated with stored foods of human beings and other animals, but also with animal dung and building materials, indoor air, and several other habitats. The taxonomy of this group has been regarded to be especially difficult, but here we propose a stable taxonomy of these species based on a polyphasic study of a large number of isolates. 58 species are accepted. Four new species, *P. cavernicola*, *P. freii*, *P. marinum* and *P. thymicola* are described and two new combinations are made: *P. melanoconidium* and *P. neoechinulatum*. The species are ordered in natural sections and series, i.e. series that are both ecologically and phylogenetically consistent. The sections are named *Coronata*, *Chrysogena*, *Roqueforti*, *Expansa*, *Digitata* and *Viridicata* and emended because they differ considerably from the circumscriptions made by Pitt (1979).

Some species with terverticillate penicilli, or rather twice biverticillate penicilli, including *P. arenicola*, *P. scabrosum*, *P. fennelliae* and *P. lanosum*, are regarded as phylogenetically and phenetically unrelated soil-borne forms and are not treated here. The phenotypic characters used include micro- and macro-morphology, physiology, including growth at 5, 15, 25, 30, 37°C, growth at 5 % NaCl and 15 % sucrose, and growth inhibition in presence of 1 % propionic acid, nutritional characters, including growth on urea, nitrite and creatine. All species have been analyzed for secondary metabolites (extrolites) and the profiles of these extrolites are highly species specific, and often of high consistency. In general features based on fungal differentiation (morphology and extrolites) are most diagnostic and consistent, but the classification proposed is also supported by the physiological and nutritional characters. The ecology and biogeography of the species is discussed and data on extrolites, both mycotoxins and pharmaceutically active compounds, is listed. Descriptions and colour illustrations of the colonies and micromorphology of the 58 accepted species are given. Keys to the taxa in the various series are given, but for a more detailed electronic database including partial beta tubulin sequences reference is made to <http://www.cbs.knaw.nl/penicillium.htm>.

Key words: *Penicillium* subgenus *Penicillium*, polyphasic taxonomy, terverticillate *Penicillia*, description, keys, foodborne species, indoor fungi

Taxonomic novelties: *P. cavernicola* Frisvad & Samson sp. nov., *P. freii* Frisvad & Samson, sp. nov., *P. marinum* Frisvad & Samson sp. nov., *P. thymicola* Frisvad & Samson sp. nov., *P. melanoconidium* (Frisvad) Frisvad & Samson comb. nov., *P. neoechinulatum* (Frisvad, Filt. & Wicklow) Frisvad & Samson, comb. nov.

Introduction

One of the first species to be described in *Penicillium* was *P. expansum*, a species producing terverticillate smooth-walled penicilli, synnemata and capable of producing rot in apples. *P. expansum* nomenclaturally typifies the genus *Penicillium* and has easily been recognized by later taxonomists based on the above characteristics. Even though it was later shown that some of these features are actually variable, such as conidiophore stipe surface occasionally being rough (Raper and Thom, 1949, Berny and Hennebert, 1985) and synnemata not always being produced, *P. expansum* is still regarded by most taxonomists as an unique species. However such phenotypic plasticity has

rendered the taxonomy of species with terverticillate penicilli very unstable and obviously features other than micromorphology and the few other characters usually employed are needed to stabilize the taxonomy and recognize and discover species. The introduction of DNA sequencing data has improved the situation, but it is clear that they are more suited for phylogenetic studies and is less satisfactory for classification and identification than phenotypic data.

In this paper we describe, illustrate and key out the 58 species in *Penicillium* subgenus *Penicillium*. As in the majority of fungal taxonomic monographs, a detailed phylogenetic and phenetic study of the spe-

cies is not presented, but will be published in additional papers in this volume and elsewhere as these two aspects, cladification and classification, are absolutely necessary in future monographs.

History

Several species of subgenus *Penicillium* were described by Dierckx (1901), Thom (1906, 1910), Westling (1911), Biourge (1923) and Zalesky (1927). Despite treatments of some of those species by Thom (1930) and Niethammer (1949), the first effective synthesis of the species was written by Raper and Thom (1949). They placed these species in their subsections *Asymmetrica-Lanosa*, *-Funiculosa*, *-Velutina* and *-Fasciculata*, with one species, *P. olsonii*, being placed in *Biverticillata-Symmetrica*. Abe (1956) mostly followed Raper and Thom (1949) and described some new varieties. Fassatova (1977) also treated many of the fasciculate species in her emended description of the series *Expansa*. Samson *et al.* treated most of the terverticillate species in three studies (1976, 1977a & b) and Ramirez (1982) followed their mainly micromorphologically based taxonomy. Pitt (1973; 1979) reintroduced some physiological characters, such as growth rates at different temperatures and water activities and gathered the terverticillate *Penicillia* with flask shaped phialides in subgenus *Penicillium*. He placed *P. gladioli* as a synonym of *Eupenicillium crustaceum* and *P. sclerotigenum* in subgenus *Furcatum*, and included *P. fennelliae* and *P. lanosum* in subgenus *Penicillium*. This overall concept of subgenus *Penicillium* is very similar to the present day placement of species in the subgenus (as presented by Frisvad *et al.*, 2000) or sequence based ribosomal DNA phylogeny (Peterson, 2000). The series classification of Pitt and Cruickshank (1990) based on colony diameters and micromorphology is, however, very different from that of Frisvad *et al.* (2000).

Secondary metabolites (extrolites), often recognisable as diffusible colours, colony reverse colours and exudate colours, have played a special role in fungal taxonomy. Usually colours, especially conidium colour, are regarded as part of morphology. These colours can be subdivided into melanin and protein melanin complexes that give fungal conidia their physical strength, hardness and radiation protection and other colours (and volatiles) that often acts as ecological signals (Wicklow, 1986). Raper and Thom (1949) mentioned citrinin as a common extrolite in several *P. citrinum* strains, but did not ascribe any taxonomic value to it. Ciegler *et al.* (1973) used extrolites in their subdivision of one species, *P. viridicatum*, but concluded that "production of similar metabolic products does not provide an adequate basis for recognition of a new taxon", based on the advice

of K.B. Raper. Frisvad (1981) was the first to suggest that extrolites could be used directly in *Penicillium* taxonomy and this was followed up by two studies on many of the species in subgenus *Penicillium* (Frisvad and Filtenborg, 1983; 1989, 1990a), where it was shown that extrolites are of particularly high value in a taxonomic sense (Frisvad *et al.*, 1998). Later a series of studies with increasingly advanced instrumentation has confirmed the value of both non-volatile and volatile extrolites in taxonomy (Lund and Frisvad, 1994; Svendsen and Frisvad, 1994; Larsen and Frisvad, 1995 a & b; Smedsgaard and Frisvad, 1996).

Extracellular enzyme production was suggested for use in *Penicillium* taxonomy by Frisvad (1981). Profiles of isozymes were introduced by Cruickshank and Pitt (1987a & b) for subgenus *Penicillium*, but were later shown to be difficult to reproduce (Paterson *et al.*, 1989). In some cases, isozyme profiles supported synonymies accepted by Samson *et al.* (1976) and Frisvad and Filtenborg (1983), e.g. the synonymy of *P. resticulosum* with *P. expansum* (Cruickshank and Pitt, 1987a), but rejected by Pitt (1979), in other cases for example the claimed synonymy of *P. aurantiovirens* with *P. expansum* (Pitt & Cruickshank, 1990) proved to be incorrect. In general the isozyme profiles appear to support the species series suggested in this paper. Isozyme profiles showed that *P. brevicompactum* and *P. olsonii* were closely related (Cruickshank & Pitt, 1987) in agreement with our emended series *Olsonii*, still Pitt and Cruickshank (1990) placed *P. brevicompactum* in series *Urticicola* and *P. olsonii* in series *Olsonii*. Using a more detailed protocol than that of Cruickshank (1983) and Cruickshank and Wade (1980), Banke *et al.* (1997) were able to classify isolates into species in the series *Chrysogena*. It seems that detailed analyses are needed to achieve resolution at the species level (Rosendahl and Banke, 1998). The latter authors also emphasize that variation within a species and statistics need to be considered. Filtenborg *et al.* (1996) suggested that extracellular enzymes may play an important role in the specific association of fungal species with their habitat, so these methods appear to be promising for future polyphasic taxonomic investigations.

Bridge *et al.* (1989 a & b) attempted to classify the terverticillate *Penicillia* by using a phenotypic approach. Their results were difficult to evaluate, because many isolates clustered tightly, even though they were actually very different. For example isolates of *P. expansum* and *P. aethiopicum* clustered even though they have no extrolites in common, while distinct taxa such as *P. coprophilum* had isolates placed in several different clusters (Frisvad and Filtenborg, 1989).

Table 1. Number of species accepted in different monographic treatments of *Penicillium* subgenus *Penicillium* (*P. arenicola*, *P. duclauxii*, *P. echinosporum*, *P. fagi*, *P. fennelliae*, *P. giganteum*, *P. isariiforme*, *P. kojigenum*, *P. lanosum*, *P. lavendulum*, *P. namyslowskii*, *P. oxalicum*, *P. pallidum*, *P. paxilli*, *P. putterillii*, and *P. skjabinii* not included).

Authors	Number of taxa accepted	New taxa described (accepted here)
Dierckx (1901)	14	10 (4)
Westling (1911)	31 (??)	11 (4)
Biourge (1923)	64	23 (0)
Zaleski (1927)	-	10 (2)
Thom (1930)	64	7 (1)
Niethammer (1949)	64	0 (0)
Raper and Thom (1949)	43	1 (1)
Abe (1952)	-	6 (0)
Samson et al. (1976, 1977 a&b)	22	6 (1)
Fassatova (1977)	-	4 (1)
Pitt (1979)	23	1 (0)
Ramirez (1982)	36	5 (0)
Bridge et al. (1989)	28	2 (0)
Frisvad & Filtenborg (1989)	38	12 (9)*
Pitt & Cruickshank (1990)	23	0 (0)
Frisvad et al. (2000)	50	2 (2)
Present work	58	6 (6)

* The three taxa not accepted here are two new combinations, one new variety was a synonym. Of the remaining nine taxa two were described as new species and seven have now been raised to species status.

Skouboe et al. (1996, 1999; 2000) and Boysen et al. (1996) sequenced the ITS1 and ITS2 region, including the 5.8 S region, of several terverticillate *Penicillia* and found rather few sequence differences among the species. *P. roqueforti*, *P. carneum* and *P. paneum* were quite different from the remaining species (Boysen et al., 1996), while morphologically different species such as *P. solitum* and *P. echinulatum* has no differences at all in this region (Skouboe et al., 2000).

Peterson (2000) also found few differences between terverticillate *Penicillium* species in the ribosomal DNA regions. Clearly the ribosomal DNA gene has too few informative differences to reveal the phylogeny of these *Penicillia*. Seifert & Louis-Seize (2000) used a part of the β -tubulin (exons 3-6 of *Ben A*) gene to indicate a more resolved phylogeny of series *Viridicata* and related species. More than one gene may be necessary to elucidate the phylogeny of the terverticillate *Penicillia*, but at this point in time the β -tubulin gene seems to be most promising for a one-gene phylogeny.

The number of taxa accepted in these different taxonomic treatments is listed in Table 1. The number of species has had two peaks, one around Biourge (1923) and Thom (1930) and the next in the present work. Biourge (1923) was particularly unsuccessful in describing new species that have been accepted in this study, not one of his 23 new species is accepted here. 23 of the species accepted here have been described recently.

Materials and Methods

Isolates examined:

As many isolates as possible of each species were investigated in order to determine the variability of each taxon. Cultures ex type were always examined, but occasionally these were not in good condition after many years of maintenance in culture collections. Therefore typical cultures have been included for comparison and verification of identity of newly identified isolates. They are indicated with an Y in the description of each taxon. Eight isolates of each taxon were examined in depth. These are listed after the description of each species. Some species are presently only represented by one isolate as yet, including *P. formosanum* and *P. confertum*.

Media and incubation

The media were all modified by adding coppersulphate and zink-sulphate to ensure proper development of the green pigmentation of the conidial colour in *Penicillium* isolates (Smith, 1949; Filtenborg et al., 1990). All fungi were grown on the following media (all percentages are weight/volume):

Czapek-Dox (Cz) agar (Raper and Thom, 1949):

NaNO ₃	0.3 %
Sucrose	3.0%
K ₂ HPO ₄ ·3H ₂ O	0.13%
MgSO ₄ ·7H ₂ O	0.05%
KCl	0.05%
FeSO ₄ ·7H ₂ O	0.001%
CuSO ₄ ·5H ₂ O.	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Agar	1.5%
Distilled water, pH 6.3 ± 0.2	

Czapek Yeast Autolysate (CYA) agar (Pitt, 1979):

NaNO ₃	0.3%
Yeast extract (Difco)	0.5%
Sucrose	3.0%
K ₂ HPO ₄ ·3H ₂ O	0.13%
MgSO ₄ ·7H ₂ O	0.05%
KCl	0.05%
FeSO ₄ ·7H ₂ O	0.001%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Agar	1.5%

Distilled water, pH 6.3 ± 0.2

Blakeslee Malt Extract Autolysate (MEA) agar:(Raper and Thom, 1949)

Malt extract (Difco)	3.0%
Bacteriological peptone	0.1%
Glucose	2.0%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Agar	2.0%

Distilled water, pH 5.3 ± 0.3

2% malt extract (ME2) agar (Samson et al., 2002):

Malt extract	2.0%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Agar	1.5%

Distilled water, pH 5.4 ± 0.3

Oat meal (OAT) agar (Samson et al., 2002):

Oat meal	3.0%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Agar	1.5%

Distilled water

Yeast extract sucrose (YES) agar (Frisvad, 1981; Filtenborg et al., 1990):

Yeast extract (Difco)	2.0%
Sucrose	15.0%
MgSO ₄ ·7H ₂ O	0.05%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Agar	2.0%

Distilled water

Creatine sucrose (CREA) agar (Frisvad, 1981, 1985, 1993):

Creatine·1H ₂ O	0.3 %
Sucrose	3.0%
K ₃ PO ₄ ·7H ₂ O	0.16%
MgSO ₄ ·7H ₂ O	0.05%
KCl	0.05%
FeSO ₄ ·7H ₂ O	0.001%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Bromecresol purple	0.005%
Agar	1.5%

Distilled water, Adjust pH to 8.0 ± 0.2

UNO agar (new medium suggested here):

Urea	0.1%
NaNO ₂	0.1%
Glucose	3.0%
K ₂ HPO ₄ ·3H ₂ O	0.13%
MgSO ₄ ·7H ₂ O	0.05%
FeSO ₄ ·7H ₂ O	0.001%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Bromecresol purple	0.005%
Dichloran	0.0002%
Agar	1.5%

Distilled water, pH 6.3± 0.2

Czapek yeast autolysate with 5 % NaCl (CYAS) agar (medium suggested here):

NaNO ₃	0.3%
NaCl	5.0%
Yeast extract (Difco)	0.5%
Sucrose	3.0%
K ₂ HPO ₄ ·3H ₂ O	0.13%
MgSO ₄ ·7H ₂ O	0.05%
KCl	0.05%
FeSO ₄ ·7H ₂ O	0.001%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Agar	1.5%

Distilled water, pH 6.3 ± 0.2

Czapek with 1000 ppm propionic acid (CzP) agar (modified after Frisvad, 1981):

Sodium propionate	0.1375%
NaNO ₃	0.3 %
Sucrose	3.0%
K ₂ HPO ₄ ·3H ₂ O	0.13%
MgSO ₄ ·7H ₂ O	0.05%
KCl	0.05%
FeSO ₄ ·7H ₂ O	0.001%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Agar	2.0%

Distilled water, after autoclaving adjust pH to 3.8 ± 0.1

Czapek with 50 ppm benzoic and sorbic acid (CzBS) agar (modified after Frisvad, 1981)

Sodium benzoate	0.009%
Potassium sorbate	0.0067%
NaNO ₃	0.3 %
Sucrose	3.0%
K ₂ HPO ₄ ·3H ₂ O	0.13%
MgSO ₄ ·7H ₂ O	0.05%
KCl	0.05%
FeSO ₄ ·7H ₂ O	0.001%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Agar	2.0%

Distilled water, after autoclaving adjust pH to 3.8 ± 0.1

Nitrite sucrose (NO2) agar (Abe, 1956; Frisvad, 1981):

NaNO ₂	0.3 %
Sucrose	3.0%
K ₂ HPO ₄ ·3H ₂ O	0.13%
MgSO ₄ ·7H ₂ O	0.05%
KCl	0.05%
FeSO ₄ ·7H ₂ O	0.001%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.001%
Agar	2.0%

Distilled water, pH 6.3 ± 0.2

Raulin-Thom (RT) agar (Raper and Thom, 1949)

Ammoniumtartrate	0.26%
(NH ₄)H ₂ PO ₄	0.04%
(NH ₄) ₂ SO ₄	0.016%
Sucrose	3.0%
Tartaric acid	0.26%
Magnesium(OH)carbonate	0.028%
K ₂ CO ₃	0.04%
FeSO ₄ ·7H ₂ O	0.006%
CuSO ₄ ·5H ₂ O	0.0005%
ZnSO ₄ ·7H ₂ O	0.007%
Agar	2.0%

Distilled water

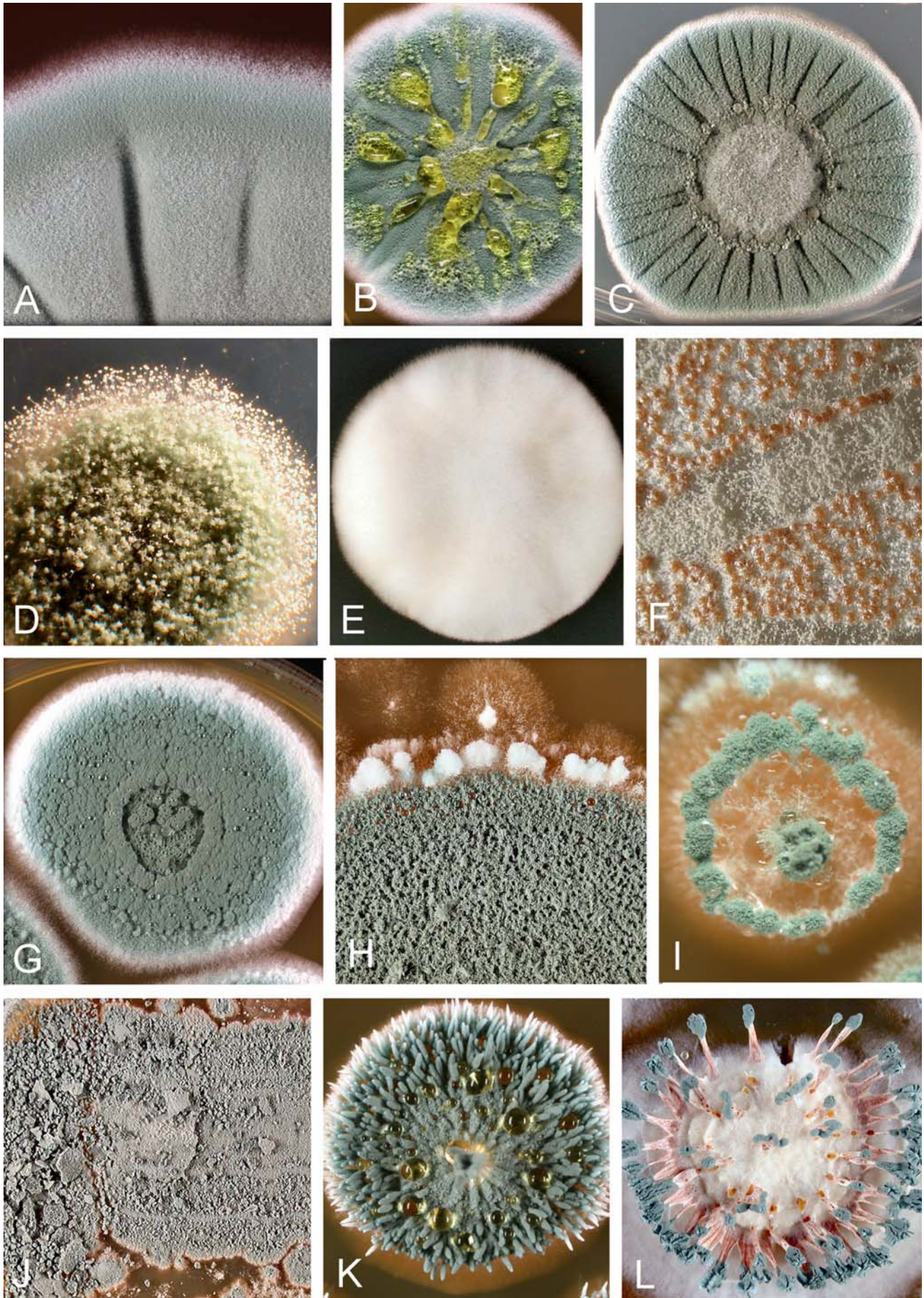


Fig. 1. A-B velvety colony of *P. persicinum* and *P. chrysogenum*, B. typical yellow exudate in *P. chrysogenum*, C. velvety colony of *P. commune* later becoming more fasciculate, D. large and compact conidial heads of *P. brevicompactum* E. floccose colony in *P. camemberti*, F. sclerotia in *P. olsonii*, G-I. fasciculate colonies of *P. expansum*, J. crusts of conidial masses of a 10 day old colony of *P. crustosum*, K-L. synnematosus growth in *P. clavigerum* and *P. vulpinum*

Cultures were three-point inoculated on media in 9 cm plastic Petri dishes using a dense conidium suspension and incubated in the dark at 25°C, except where otherwise noted. Depending on the ventilation in the incubators, Petri dishes were incubated uncovered or in perforated plastic bags to retard drying out of the media. The fungi were also grown at 15, 30 and 37°C on CYA. The cultures were examined after 7 days of growth and further examined after 14 days. Colony diameters were measured using a ruler and colours were measured using a Minolta colourimeter and also subjectively evaluated. Fasciculation of the colonies was evaluated using a scale from 1 to 4.

All species were examined using oil immersion with an Olympus BHH microscope with Normarski interphase contrast at up to 1000 x magnification. Digital micrographs were taken with a Nikon Coopix 990 and 995.

Microscopic slides were prepared from malt based media (MEA and ME2) and 60 % lactic acid without colour dye was used as a mounting medium.

Morphology and other phenotypic characters

Colony patterns and growth

Colonies in species of subgenus *Penicillium* have various patterns. When freshly isolated, these patterns are consistent but the typical features may be lost after regular transferring and maintaining of the cultures. The following colony pattern can be found:

Velvety (Fig. 1 A-B). Conidiophores are produced singly and form a compact felt. Typical velvety taxa are: *P. persicinum*, *P. chrysogenum*, *P. aethiopicum*. In *P. brevicompactum* and *P. olsonii*, the colonies are velvety but the conidial heads are large and compact and resemble *Aspergillus* heads, which make the colony appearance more or less granular (Fig. 1 D).

Floccose (Fig. 1 E): *P. camemberti* and some strains of *P. nalgiovense* have colonies with white aerial and fluffy mycelium

Fasciculate (Fig. 1 G-I): Fasciculation occurs when conidiophores are bundled together forming small tufts. These mostly are found at the edges of colonies. Typical fasciculate species are *P. expansum* and *P. concentricum*.

Synnematosus (Fig. 1 K-L): The conidiophores are defined as synnematosus when they consist of a distinct stalk and a head such as in *P. vulpinum*, *P. clavigerum*, *P. coprobium* and *P. formosanum*. Synnematosus growth largely depends on the medium and typical synnema can often be found on OA or on MEA. In cultures fasciculate conidiophores can also be found repeatedly.

Crustose (Fig. 1 J): Fresh isolates of *P. crustosum* form a crust of conidial masses when they are 7 days and older. This character is typical for the species and can be used as an aid for identification.

Exudate: Several species produce distinct exudates droplets e.g. yellow in *P. chrysogenum* (Fig 1 B) and dark brown in *P. venetum*.

Reverse: Various pigments are more or less typical for the species. On YES agar the reverse colours are particularly pronounced. Colours vary from uncoloured, cream to yellow, yellow to brown or red

Conidiophores: In culture mature conidiophores are produced in 5-7 days old colonies. The penicillus of species of subgenus *Penicillium* are typically two staged branched (terverticillate). However, in some taxa the penicillus is often biverticillate. In other species, more branches are present and quaterverticillate conidiophores can be formed. *P. digitatum* deviates from the typical conidiophore branching, because it is often irregular and only biverticillate. It is important that conidiophore branching and its elements can be best seen in microscopical slides made from MEA. On CYA, YES and other media the conidiophores are often swollen and have an atypical branching pattern.

Stipe (Fig. 2 N-R): The stipes of most taxa are straight. Curved stipes are typical for *P. vulpinum* and *P. clavigerum*. The stipe of the conidiophore can either be smooth, rough-walled or tuberculate (warty). Typical smooth stipes are found in for example *P. mononematosum*, *P. vulpinum* and *P. olsonii*. In *P. chrysogenum* and *P. expansum* mostly smooth walled stipe are present, but some strains have rough-walled stipes. Rough-walled to echinulate stipes are typical for *P. glandicola* and *P. hirsutum*. Typical tuberculate stipes are found in *P. roqueforti*, *P. paneum* and *P. carneum*.

Often stipe ornamentation depends on the media and age of the culture. On Czapek and YES agar the conidiophores often do not have ornamented stipes, but they are produced on MEA. We have also observed that stipe ornamentation depends on the availability of oxygen. In Petri dishes that are sealed with parafilm or in closed polyethylene bags the ornamentation is sometimes completely lacking. The lack of ornamentation in certain growth conditions is often evident in *P. roqueforti* cultures.

Phialides (Fig. 2 I-M): In subgenus *Penicillium*, the phialide shape can differ. Mostly the phialides are flask shaped consisting of a more or less cylindrical basal part with a short neck. The collarette of this neck can become thickened when conidia are produced. In *P. digitatum*, *P. ulaiense* and *P. italicum*, the cylindrical shape is more pronounced and the

phialides are longer. In *P. griseofulvum* and *P. dipodomyicola* the phialides are typical short.

Conidia (Fig. 2 A-H): Most taxa in subgenus *Penicillium* have globose smooth-walled conidia. Mainly ellipsoidal conidia are found in *P. formosanum* and *P. expansum*, while in *P. italicum*, *P. ulaiense*, and *P. persicinum*, they are typical cylindrical.

Sclerotia (Fig 1. F): In most species sclerotia are not produced. Only in *P. gladioli* and *P. sclerotigenum* are sclerotia present, while some isolates of *P. olsonii* from tropical soil also produce sclerotia. In 3 week old MEA colonies of *P. roqueforti*, soft sclerotium-like structures can be sometimes observed. In *P. italicum* large, white sclerotia at the margin of colonies growing on OA have been observed in cultures incubated in the dark at 0°C for three months. In old colonies of *P. persicinum*, sclerotia have been observed (Wang Long, personal communication). Sclerotial production is soon lost when cultures are transferred

Table 2. Degree of sporulation on YES after one week at 25°C: 0: None or very thin and poor sporulation, 1: Sporulation in the centre of the colony, 2: Strong sporulation on more than 90% of the colony

Species	Sporulation	Reverse colour
<i>P. aethiopicum</i>	2	Yellow to curry yellow
<i>P. albocoremium</i>	0	Brownish yellow / orange
<i>P. allii</i>	2	Yellow brown to warm brown
<i>P. atramentosum</i>	2	Yellow brown to dark brown
(<i>P. aurantiocandidum</i>)	0	Yellow
<i>P. aurantiogriseum</i>	0/1/2	Yellow
<i>P. bialowiezense</i>	2	Cream to cream beige
<i>P. brevicompactum</i>	2	Cream to cream beige*
<i>P. camemberti</i>	0	Cream yellow
<i>P. carneum</i>	2	Cream beige
<i>P. caseifulvum</i>	2/(1)	Orange or orange yellow
<i>P. cavernicola</i>	2/(1)	Yellow to yellow orange
<i>P. chrysogenum</i>	2	Citrine yellow
<i>P. clavigerum</i>	0	Light to dark yellow brown
<i>P. commune</i>	0/1/(2)	Cream to cream yellow **
<i>P. concentricum</i>	2	Orange
<i>P. confertum</i>	2	Yellow cream to curry
<i>P. coprobium</i>	2	Yellow cream to yellow brown
<i>P. coprophilum</i>	2	Yellow brown to dark brown
<i>P. crustosum</i>	2	Yellow
<i>P. cyclopium</i>	0/(1)	Yellow

<i>P. digitatum</i>	2 (0 in old strains)	Cream yellow
<i>P. dipodomyicola</i>	2	Yellow olive to dark olive
<i>P. dipodomyis</i>	2	Orange to orange yellow
<i>P. discolor</i>	2	Orange to vivid orange red
<i>P. echinulatum</i>	2	Yellow
<i>P. expansum</i>	2/1/0	Cream yellow to orange brown
<i>P. flavigenum</i>	2	Citrine yellow
<i>P. formosanum</i>	0	Yellow to yellow orange
<i>P. freii</i>	0/(1)	Yellow
<i>P. gladioli</i>	0	Cream yellow **
<i>P. glandicola</i>	2	Orange red to red
<i>P. griseofulvum</i>	2	Cream yellow to beige
<i>P. hirsutum</i>	2/(0)	Orange yellow
<i>P. hordei</i>	0	Yellow
<i>P. italicum</i>	2	Orange to red brown
(<i>P. lumpi</i>)	0/1	Cream
<i>P. marinum</i>	1/(2)	Cream yellow
<i>P. melanconidium</i>	2	Yellow
<i>P. mononematosum</i>	2	Cream to brown yellow
<i>P. nalgioense I</i>	0	Dark yellow brown
<i>P. nalgioense II</i>	2	Orange
<i>P. nordicum</i>	0/1/2	Cream to cream yellow
<i>P. neoehinulatum</i>	0	Yellow
<i>P. olsonii</i>	2	Yellow to yellow cream
<i>P. palitans</i>	2	Yellow
<i>P. paneum</i>	2	Cream yellow to beige*
<i>P. persicinum</i>	2	Red, with colour diffusing
<i>P. polonicum</i>	2	Yellow
<i>P. radicola</i>	0/(1)	Deep to butter yellow
<i>P. roqueforti</i>	2	Dark blackish green
<i>P. sclerotigenum</i>	2	Cream yellow
<i>P. solitum</i>	2/1/0	Yellow to orange yellow
<i>P. thymicola</i>	0/1/2	Yellow to orange, diffusing
<i>P. tulipae</i>	0/1/2	Deep yellow to yellowish orange
<i>P. tricolor</i>	0	Brown yellow to honey
<i>P. ulaiense</i>	2	Cream yellow to brown
<i>P. venetum</i>	2	Yellow brown
<i>P. verrucosum</i>	0/1	Red brown to terracotta
<i>P. viridicatum</i>	0/1/(2)	Yellow
<i>P. vulpinum</i>	0/(2)	Cream yellow to beige

* May become strawberry red with colour diffusing into the agar; ** Often turn to dark blackish brown with colour diffusing into the agar

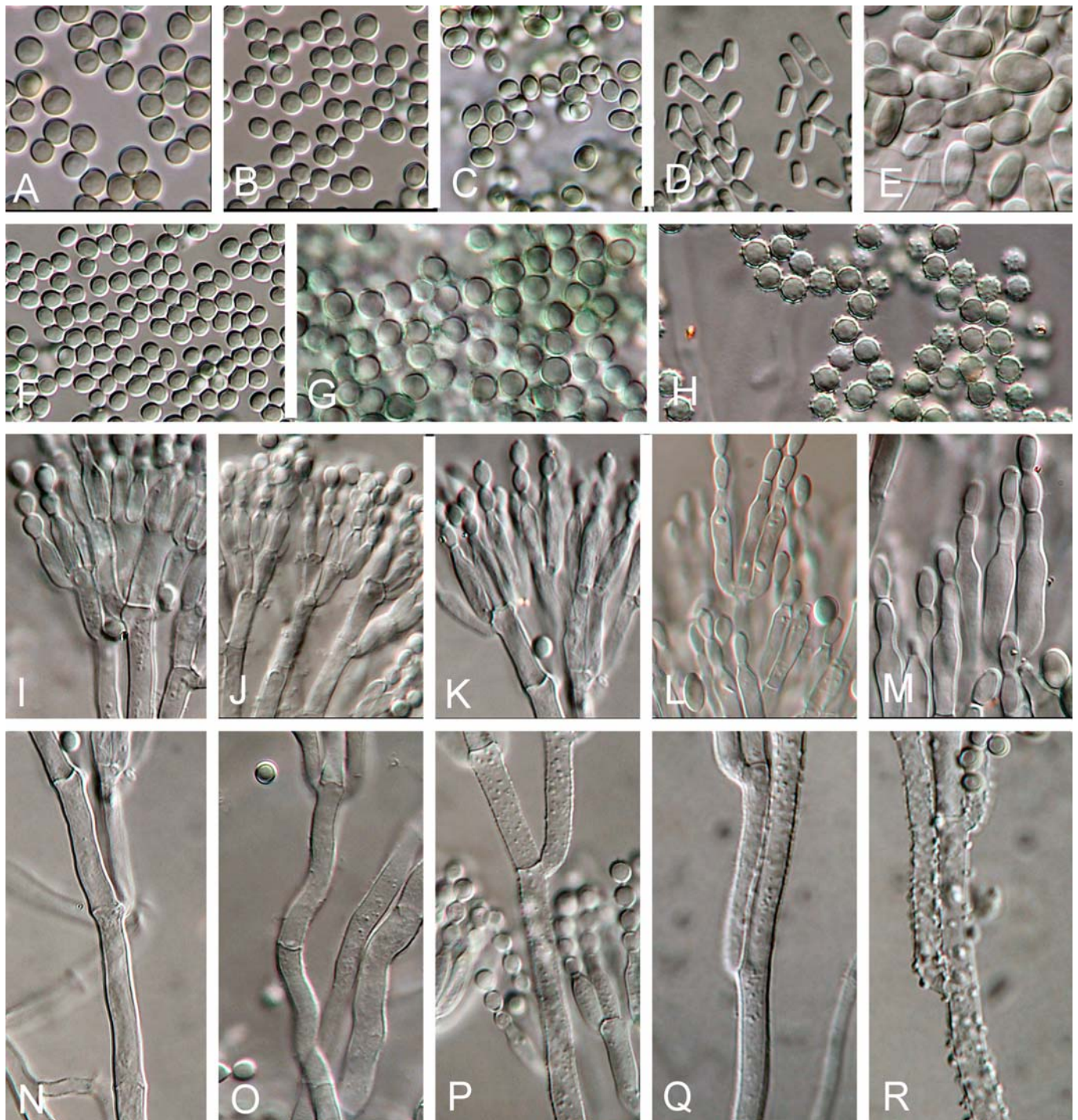


Fig 2. Morphological structures in *Penicillium* subgenus *Penicillium*. A-H. Conidia, A. Smooth, globose conidia in *P. roqueforti*, B. Globose to subglobose in *P. cyclopium*, C. ellipsoidal in *P. expansum*, D. cylindrical in *P. persicinum*, E. ellipsoidal to cylindrical in *P. digitatum*, F. subglobose to ellipsoidal in *P. confertum*, G. rough-walled conidia *P. discolor*, H. echinulate conidia in *P. echinulatum*. I-M. Phialide shape. I. flash-shaped in *P. chrysogenum*, J. flash-shaped but short in *P. griseofulvum*, K. flask-shaped but more elongated in *P. expansum*, L-M. phialides more or less cylindrical in *P. ulaiense* and *P. digitatum*, Conidiophore stipe, N. *P. expansum*, O. *P. clavigerum*, P. *P. tulipae*, Q. *P. roqueforti*, R. *P. glandicola*

Ehrlich test

All isolates were examined for production of cyclopiazonic acid and other alkaloids reacting with Ehrlich reagent (Lund, 1995a) using a filter paper method. Ehrlich reagent consists of 2 g of 4-dimethylamino-benzaldehyde in 96% ethanol (85 ml) added 15 ml 10 N HCl. A *ca.* four mm agar plug is cut out of the center of a colony grown on CYA (incubated 5-9 days at 25°C) and a round piece (1 cm diam.) of the wetted

filter paper (Whatman No. 1) is placed on the mycelial side of the plug. If a violet ring appears after 2- 6 min. the culture contains cyclopiazonic acid or related alkaloids (**Fig. 4**). If the reaction comes after 7-10 min. it is regarded as weak. After 10 min the violet ring will fade away. Some fungi produce alkaloids that will react with Ehrlich reagent to give pink to red or yellow rings.

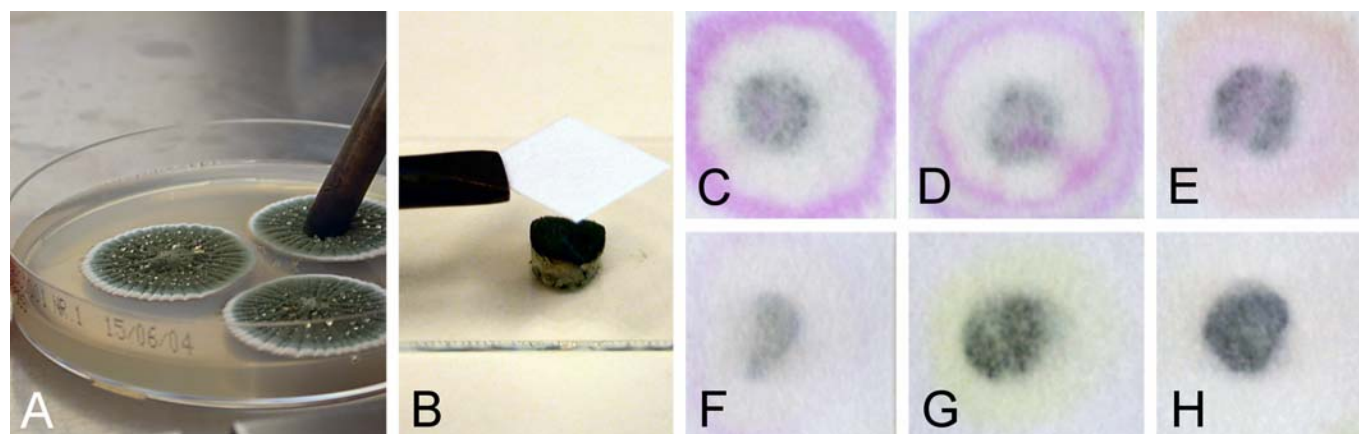


Fig 3. Ehrlich colour reactions. A. Taking a plug from a *Penicillium* colony. B. Adding a piece of filterpaper with Ehrlich solution. C. violet in *P. expansum*, D. violet in *P. palitans*, E. red brown in *P. allii*, F. weak violet in *P. discolor*, G. yellow in *P. olsonii*, H. no reaction in *P. italicum*

Table 3. Ehrlich results on CYA after one week at 25°C

Species	violet	notes	Always negative (occasionally yellow reaction)	
<i>P. albocoremium</i>	(+)		<i>P. aethiopicum</i>	
<i>P. bialowiezense</i>	(+)		<i>P. atramentosum</i>	
<i>P. camemberti</i>	(++)	(0 in old deteriorated cultures)	<i>P. brevicompactum</i>	(some cultures yellow, or faint yellow)
<i>P. carneum</i>	(+ / + +)		<i>P. cavernicola</i>	(yellow in some cultures)
<i>P. caseifulvum</i>	(+)		<i>P. chrysogenum</i>	(some cultures yellow or faint yellow)
<i>P. commune</i>	(+ / + / + / +)		<i>P. clavigerum</i>	(yellow, yellow to violet in some cultures)
<i>P. dipodomyicola</i>	(+ / + / +)		<i>P. concentricum</i>	(some cultures yellow, or faint yellow)
<i>P. discolor</i>	(+)		<i>P. confertum</i>	(faint yellow)
<i>P. expansum</i>	(+ / + / + / +)		<i>P. coprobium</i>	(some cultures faint yellow)
<i>P. griseofulvum</i>	(+ / + / +)	(0 in old deteriorated cultures)	<i>P. coprophilum</i>	
<i>P. hirsutum</i>	(+ / + / +)	(0 in some cultures)	<i>P. crustosum</i>	(occasionally faint yellow)
<i>P. hordei</i>	(+)		<i>P. digitatum</i>	
<i>P. marinum</i>	(+ / +)	(0 in some mutants)	<i>P. dipodomyis</i>	
<i>P. neoechinulatum</i>	(+ / + / +, +)	red violet)	<i>P. echinulatum</i>	
<i>P. palitans</i>	(+ / + / +)		<i>P. flavigenum</i>	
<i>P. polonicum</i>	(+ / + / +)		<i>P. formosanum</i>	
<i>P. radiculicola</i>	(w / +)		<i>P. gladioli</i>	
<i>P. roqueforti</i>	(+ / + / +)	(yellow in some cultures)	<i>P. glandicola</i>	(some cultures yellow++ or faintly yellow)
<i>P. tulipae</i>	(+ / + / +)		<i>P. italicum</i>	
Pink (to red) reaction			<i>P. mononematosum</i>	
<i>P. allii</i>			<i>P. nordicum</i>	(yellow green)
<i>P. aurantiogriseum</i>			<i>P. nalgioyense</i>	(occasionally faint yellow)
<i>P. cyclopium</i>		(red brown to pink to yellow brown)		
<i>P. freii</i>		(pink red)	<i>P. olsonii</i>	(yellow)
<i>P. lumpi</i>			<i>P. paneum</i>	(some cultures faintly violet)
<i>P. melanoconidium</i>			<i>P. persicinum</i>	
<i>P. viridicatum</i>		(also yellow to brown)	<i>P. sclerotigenum</i>	(occasionally faintly yellow)
Yellow reaction:			<i>P. solitum</i>	
<i>P. clavigerum</i>		(yellow to violet in some cultures)	<i>P. thymicola</i>	(yellow green)
<i>P. nordicum</i>		(yellow green)	<i>P. ulaiense</i>	
<i>P. olsonii</i>			<i>P. tricolor</i>	
<i>(P. scabrosum)</i>			<i>P. venetum</i>	
<i>P. thymicola</i>			<i>P. verrucosum</i>	(yellow in some cultures)
<i>P. viridicatum</i>		(yellow pink brown)	<i>P. vulpinum</i>	(some cultures yellow or faintly violet)

Extrolite analysis

CYA and YES were used for extrolite analysis. Agar plugs (6 mm diameter) were cut out of 7 days old cultures and kept in a -18°C freezer until extraction. The cultures were extracted according to the method of Smedsgaard (1987) using 500 μl ethylacetate / methanol / dichloromethane 3:2:1 (vol. / vol. / vol.) with 1 % formic acid and ultrasonicated for 10 minutes. The organic solvent was transferred to another vial and evaporated at 1 mbar in a Rotavapor centrifuge evaporator. The extract was redissolved in 400 μl methanol and analysed by HPLC with diode array detection (DAD) or electrospray mass spectrometric detection (ES-MS) (Frisvad and Thrane, 1987; 1993 and Smedsgaard, 1997; Nielsen and Smedsgaard, 2003). The extrolites were identified by their UV spectra and MS characteristics. Authentic analytical standards were employed for retention time and retention index comparison with the extrolites detected.

Taxonomy

Delimitation of *Penicillium* subgenus *Penicillium*

Penicillium subgenus *Penicillium* comprises species with terverticillate (two stage branched) conidiophores (Fig. 4). They all sporulate heavily and are often fasciculate. However the subgenus also appears to be a natural group, i.e. it is both phylogenetically and ecologically distinct. All species are related to animal nutrition and excretion and mans domesticated landscapes, e.g. they are found growing and sporulating on plant, algal, animal or fungal raw or processed materials and in dwellings of man and other animals. They all grow well at low temperatures and poorly, if at all, at 37°C . They also grow well at low water activities and at low pH values (Pitt and Hocking, 1998; Frisvad *et al.*, 2000).

Excluded taxa

Some species in other subgenera with similar penicilli or ecology are excluded from subgenus *Penicillium* for the reasons discussed below.

Species in the other subgenera are mainly soil or plant root associated (subgenus *Aspergilloides* and *Furcatum*) or are often associated with wood and textiles (subgenus *Biverticillium*). These ecologically based subdivisions are strongly supported by DNA sequence data (Peterson, 2000). DNA sequence data also indicate that most species in *Eupenicillium* series *Crustacea*, except *E. shearii*, are related to *P. chrysogenum* (Peterson, 2000). Some species e.g. *Eupenicillium crustaceum* *E. egyptiacum* and *E. molle* (Fig. 5) have many terverticillate structures, however, and yet should be included in subgenus *Penicillium*. In the present revision we have not included the *Eupenicillium* species because a major revision using a

polyphasic approach and mulilocus DNA sequences is needed to resolve the taxonomy of this teleomorph genus. Occasionally biverticillate species include *P. digitatum*, *P. sclerotigenum* and certain isolates of *P. chrysogenum*. The extrolites produced by these species, the plant pathogenicity (of *P. digitatum* and *P. sclerotigenum*) and DNA sequence data (Peterson, 2000) clearly shows that these taxa should be placed in subgenus *Penicillium*.

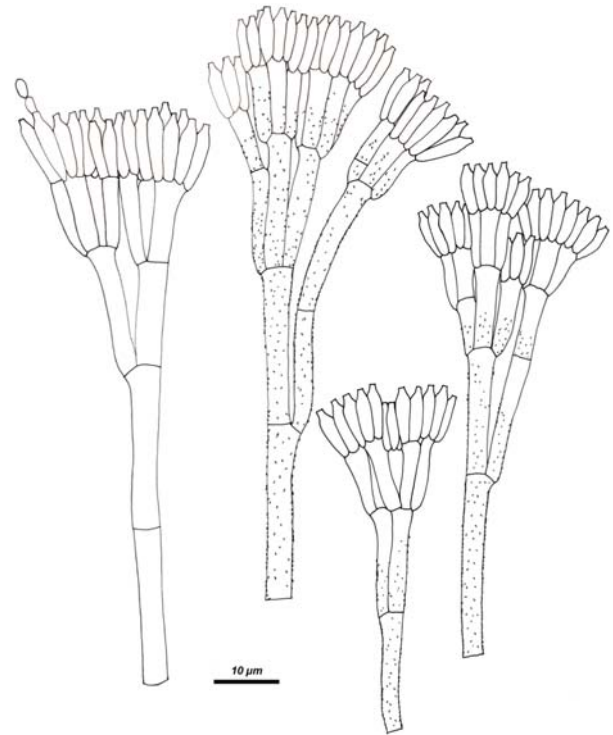


Fig 4. Conidiophore branching patterns in subgenus *Penicillium*

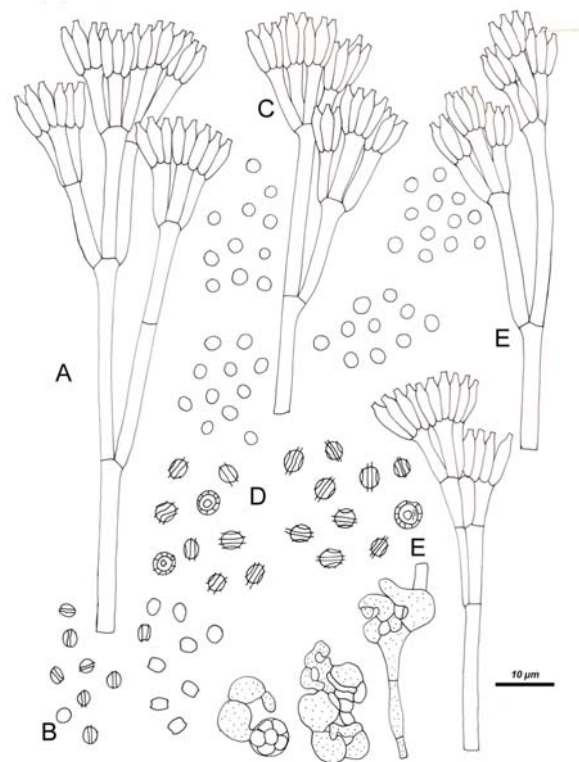


Fig 5. Conidiophores, conidia and ascogenous structures of a *Eupenicillium crustaceum* (A-B), *E. egyptiacum* (C-D) and *E. molle* (E).

P. oxalicum has biverticillate structures, but is pathogenic to cucumbers (Menzies *et al.*, 1995). It shows rich growth at 37 °C and is phylogenetically close to subgenus *Furcatum* (Peterson, 2000). On balance, this isolate have been excluded from subgenus *Penicillium* in this treatment. Other species in *Furcatum* are endophytes of plants; e.g. *P. nodositatum* forms myconodules with elder trees (Valla *et al.*, 1989). This species is biverticillate and asymmetric and thus belong to subgenus *Furcatum*.

Several soil-borne species can produce a few asymmetric terverticillate conidiophores, but in most cases, these can be recognized as twice biverticillate structures. The best examples of this are *P. lanosum* and *P. scabrosum*. *P. lanosum* (Fig. 6) was included among the asymmetric terverticillate *Penicillia* by Samson *et al.* (1976) and as a synonym of *P. puberulum* in subgenus *Penicillium* by Pitt (1979). *P. lanosum* and *P. scabrosum* produce extrolites that are both produced by subgenus *Furcatum* and subgenus *Penicillium* species (Frisvad *et al.*, 1990a & b). Based on phenetic and phylogenetic data we place the latter two species in subgenus *Furcatum*. This is in agreement with Domsch *et al.* (1980). These authors placed *P. scabrosum* (listed as *P. atrovenetum*, p. 545) and *P. lanosum* (p. 584) close to soil-borne *Penicillia* in subgenus *Furcatum*, *P. herquei* and *P. jensenii*, respectively.

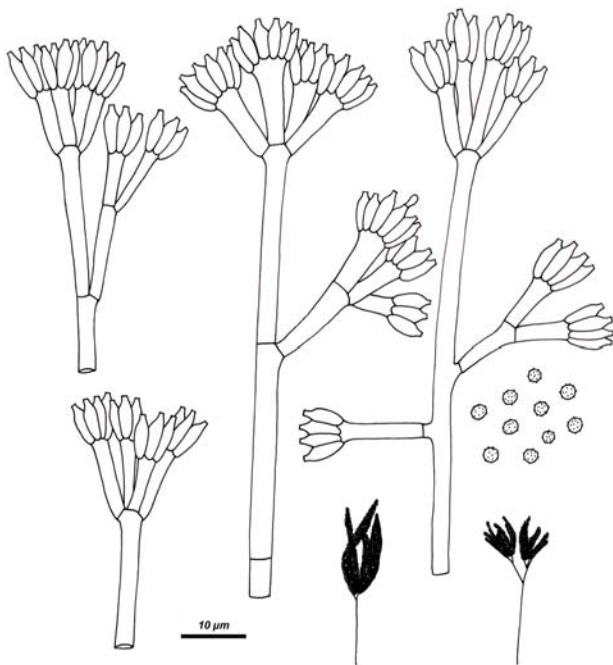


Fig. 6. Conidiophores and conidia of *Penicillium lanosum*.

P. arenicola was so different from all other *Penicillium* species that Pitt (1979) set it apart in section *Inordinate* Pitt, series *Arenicola* Pitt, with *P. canadense* as a synonym. The very irregular penicilli, the golden blonde to olive brown conidia, the dark brown reverse, the production of canadensolide and the specific occurrence in forest soil all suggest an en-

tirely unique placement in *Penicillium* and no links to any species in subgenus *Penicillium*. The only features in common with species in subgenus *Penicillium* are the often terverticillate *Penicilli* and the production of the extrolite asperphenamate. We have therefore omitted *P. arenicola* in this monograph.

Species concept

Many controversies exist regarding the infraspecific ranks of variety and subspecies. We have chosen to use only the species rank following the idea that varieties and subspecies are usually based on the neodarwinian idea that populations and races will gradually turn into new species, for example, after geographical separation and selection. As we do not subscribe to that mechanism as the only cause of speciation, in agreement with Schlichting and Pigliucci (1998), we here adopt the species level as the lowest formal taxonomic level.

We here adopt a phenotypic species concept in which each species is a homogeneous and distinct cluster in phenotypic space with a large distance to any other such cluster. Species discovered this way have proven to agree with other species concepts such as those based on ecology or phylogeny. The criteria applied are a **combination** of micromorphological, macromorphological, physiological and extrolite characters. Classifications and identifications based on any of those types of characters **alone** have been unsatisfactory among others because of the many taxa in *Penicillium*.

We will exemplify this with *Penicillium crustosum*. *P. crustosum* was described in 1930 by Thom and accepted in the *P. expansum* series by Raper and Thom (1949), even though a synonym of it, *P. terrestre* Jensen, was placed in the *P. terrestre* series based on slightly different colony texture. Samson *et al.* (1976) placed *P. crustosum* in synonymy with *P. verrucosum* var. *cyclopium* based on micromorphological similarities. Fassatiouva (1977) placed *P. crustosum* close to *P. expansum* and reduced it to variety status as *P. expansum* var. *crustosum*. Pitt (1979b) accepted *P. crustosum*, but included isolates of *P. aurantiogriseum* (*P. australicum*) and *P. solitum* (*P. verrucosum* var. *melanochlorum*), inconsistent with the high growth rate claimed to be characteristic for *P. crustosum*, while *P. solitum* and *P. aurantiogriseum* grow very slowly. Other strains of *P. solitum* and *P. aurantiogriseum* were placed under the latter species by Pitt (1979b). Bridge *et al.* (1989) reduced *P. crustosum* to a variety of *P. solitum* as *P. solitum* var. *crustosum*. Frisvad and Filtenborg (1989) accepted *P. crustosum* based on its consistent production of penitrem A, roquefortine C, terrestric acid and cyclopenol in combination with its high growth rate and extraordinarily high production of conidia. Some of the similar and dissimilar features of the species above (see also page 50) show why it is important to

combine a suite of characters in order to classify or identify these fungi correctly. Based on a smaller subset of these characters many species could be placed in synonymy, but taken as a whole the species are indeed very different. Interestingly *P. crustosum* is not phylogenetically close to any of the species mentioned above, but is rather phylogenetically related to *P. commune* and *P. camemberti* (Skouboe *et al.*, 1996; Peterson, 2000).

The sectional classification of *Penicillium* subgenus *Penicillium*

Overview:

Section *Coronata* –

- Ser. *Olsonii*

Section *Roqueforti*

- Ser. *Roqueforti*

Section *Chrysogena*

- Ser. *Chrysogena*
- Ser. *Mononematosa*
- Ser. *Aethiopica*
- Ser. *Persicina*

Section *Penicillium*

- Ser. *Expansa*
- Ser. *Urticicolae*
- Ser. *Claviformia*
- Ser. *Italica*
- Ser. *Gladioli*

Section *Digitata*

- Ser. *Digitata*

Section *Viridicata*

- Ser. *Viridicata*
- Ser. *Corymbifera*
- Ser. *Verrucosa*
- Ser. *Camemberti*
- Ser. *Solita*

These six sections are all phenotypically distinct.

Section *Coronata*

Section *Coronata* includes species that all produce compact, often multiramous penicilli with long stipes, and velutinous colonies. All species produces asperphenamate. Chemotaxonomically *Coronata* is most similar to sect. *Roqueforti*. *P. brevicompactum* share only few common extrolites with other species in subgenus *Penicillium*. Brevianamide A is also produced by *P. viridicatum* in section *Viridicata*. One or two of the three species produce a series of other unique extrolites including brevicompanins, breviones, pebrolides, silvatins, and Raistrick phenols. *P. brevicompactum* produces botryodiploidin in common with *P. paneum* in Sect. *Roqueforti*. Furthermore *P. brevicompactum* and *P. bialowiezense* produce

mycophenolic acid in common with *P. roqueforti* and *P. carneum* in Sect. *Roqueforti*.

Species in section *Coronata* are able to grow both at very low water activities and at low temperatures, but do not tolerate high growth temperatures. The species occur worldwide, from the tropical to arctic regions. *P. olsonii* is found mostly in the tropics and these tropical isolates occasionally produce sclerotia. The species have been found on plants growing in greenhouses, especially on tomatoes, but they are also common in soil worldwide. All species in section *Coronata* are common species encountered in indoor environments. All species grow poorly on creatine as sole N-source and they produce no or little acid on CREA. All species tolerate nitrite well and can use it as sole N-source.

Section *Roqueforti*

Section *Roqueforti* is unique in its high tolerance to propionic acid, acetic acid, lactic acid and other acids and to high concentrations of carbondioxide and probably developed this resistance in competition or corporation with lactic acid bacteria during evolution. The species included in *Roqueforti* have large smooth-walled globose conidia, rough-walled stipes and low velutinous colonies, growing fast on almost all substrates. Roquefortine C is common to all species in the section *Roqueforti* but is also produced by several species in all other sections, except *Coronata*. PR-toxins, marcfortins, isofumigaclavins are only produce by (some) section *Roqueforti* species, whereas mycophenolic acid and botryodiploidin are also found in section *Coronata*. Penitrem A produced by *P. carneum* is also produced by *P. glandicola* and *P. clavigerum* in section *Expansa*, and *P. tulipae* and *P. melanoconidium* in section *Viridicata*. Patulin produced by *P. carneum* and *P. paneum* in *Roqueforti* is also produced by many species in section *Expansa*. All species in section *Roqueforti* grow well on creatine and nitrite as sole N-sources, and are poor or non-producers of acid on CREA. Section *Roqueforti* members grow relatively poorly at low water activities compared to species in other sections of subgenus *Penicillium*, but grow well at low temperatures, whereas growth at 37°C is nil.

Section *Chrysogena*

Section *Chrysogena* include species that have rather short broad phialides with broad collula and divaricate penicillus structures and two additional monotypic series with unique morphologies (*Persicina* and *Aethiopica*). Most species share, as the only species in subgenus *Penicillium*, the ability to grow at 37°C. Penicilli can be biverticillate, terverticillate and/or quarterverticillate. All species have a velutinous to weakly floccose colony type and the all grow very or rather fast. They all grow very well at 30°C. Penicillin is common to all species in ser. *Chrysogena*, but is

also produced by *P. griseofulvum* in section *Expansa*. Anthraquinones and other yellow polyketides are produced by most species. Xanthocillins have been found in two species in *Chrysogena* (*P. chrysogenum* and *P. flavigenum*), in the related *Eupenicillium* *egyptiacum*, but only found in *P. italicum* in section *Expansa* outside *Chrysogena*. Chrysogine is also common in section *Chrysogena*, and only found in *P. tulipae* in section *Viridicata* outside *Chrysogena*. *P. mononematosum* is unique in this section, however, being characterized by the production of fumitremorgins, also found in *Eupenicillium crustaceum*, cyclopaldic acid (also found in *P. carneum* in section *Roqueforti* and *P. commune* in section *Viridicata*), and isochromantoxins (found in *P. steckii* in subgenus *Furcatum*). Roquefortine C and meleagrins are found in *P. chrysogenum*, but also by many other species in sections *Expansa* and *Viridicata*. Dipodazin has only been found in *P. dipodomyis* from this section and in *P. cavernicola* from section *Viridicata*. As mentioned earlier all species grow well at high temperatures, often producing colonies at 37°C. The species can all grow at very low water activities and high salt (NaCl) concentrations. Only species in section *Viridicata* seems to be more halotolerant. *P. aethiopicum*, as an exception, is not very halotolerant, however. No species use creatine well as sole N-source, but all species grow moderately well on nitrite as sole N-source and very well on UNO. The species are not resistant to acids, but grow well at relatively high pH values. Compared to other species in subgenus *Penicillium*, species in *Chrysogena* are those closest to *Eupenicillium* series *Crustacea* and other soil-borne *Penicillia*.

Section *Penicillium*

Series *Expansa* is characterized by smooth-walled ellipsoidal conidia, except *P. marinum* and *P. gladioli* which have globose to subglobose conidia. Most species have strongly fasciculate to coremiform colonies and conidiophores with smooth stipes and terverticillate to quarterverticillate structures. *P. gladioli* differs by having only slightly fasciculate colonies and rough-walled stipes.

In series *Urticicolae* the species are unique in having divaricate structures and very short phialides. Most species appear to be very competitive, producing patulin, griseofulvin, or fulvic acid or all of these (in *P. griseofulvum*). Furthermore all species in the section produce roquefortine C, except *P. gladioli*, *P. italicum* and *P. ulaiense*. Extrolites such as deoxybrevianamide E, italinic acid, cyclopamide, cyclopamine, communesins, expansolides, gladiolic acids, asperfuran, and pyripyropens are only known from section *Expansa* in subgenus *Penicillium*. *P. griseofulvum*, but also *P. commune* and *P. palitans* in section *Viridicata* produce cyclopiazonic acid. *P. expansum* produces chaetoglobosins, but these me-

tabolites are also produced by *P. discolor* in section *Viridicata*. All species tolerate both quite acidic and alkaline conditions and can grow at relatively low water activities, albeit not as low as the other sections. No species can grow at 37°C. All species are psychrotolerant. All species in series *Expansa* and *Claviformia* grow well on creatine as sole N-source, whereas species in the other series in the section grow poorly on creatine. Several plant pathogenic species are found in section *Expansa*. *P. expansum* produces rots in pomaceous fruits and *P. italicum* and *P. ulaiense* produce rot in citrus fruits. *P. sclerotigenum* produces rot in yams and *P. gladioli* produces a destructive rot in *Gladiolus* corms. Species in series *Claviformia* are all coprophilic, creatine positive and synnemata producing.

Section *Digitata*

Section *Digitata* (and series *Digitata*) is only 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*, biverticillate rather than terverticillate, divaricate and the conidia are olive-green. The conidia are large and ellipsoidal to cylindrical. The extrolites produced are tryptoquialanines, which it only shares with *P. aethiopicum* from series *Aethiopica* in section *Chrysogena*. The species grow poorly at low water activities and at higher temperatures, and it grows very poorly with no acid production on creatine as sole N-source. It is also the only species in subgenus *Penicillium* that grow poorly on Czapek agar. The species has only been found on rotting citrus fruits. It shares the citrus rotting ability and ellipsoidal to cylindroidal conidia with *P. italicum* and *P. ulaiense* from series *Italica* section *Expansa*, but shares no extrolites with those species. *P. digitatum* is the only species in subgenus *Penicillium* that cannot use nitrate as sole N-source.

Section *Viridicata*

Most species in section *Viridicata* have globose conidia and rough-walled conidiophore stipes, with *P. atramentosum* as an exception with smooth-walled stipes. However occasionally section *Viridicata* members do not produce rough-walled stipes. *Viridicata* also contain the only species with dark green rough walled conidia in subgenus *Penicillium*. Most species have a fasciculate colony texture and grow rather fast, except species in series *Verrucosa*, which grow slowly. Several extrolites are only found in section *Viridicata* in subgenus *Penicillium*: Xanthomegnins, penicillic acids, puberulic acids, ochratoxins, daldinin C, alantrypinone, anacins, verrucins, auranthine, aurantiamin, puberuline, verrucosidin, terrestrial acids, rugulovasines, asteltoxin, territrem, arisugacins, palitantin, compactins, barceloneic acid, and atrovenetins. Verrucolone (arabenoic acid) is

produced by all species in series *Verrucosa*, but also by *P. italicum* in series *Italica* section *Expansa* and *P. olsonii* in section *Coronata*. Viridicatins are produced by many species in section *Viridicata* and outside this section only by *P. vulpinum* in section *Expansa*. The combination of roquefortine C and penitrem A is produced by *P. crustosum*, *P. melanoconidium* and *P. tulipae* in section *Viridicata*, but also by *P. glandicola* in section *Expansa*. In section *Viridicata* roquefortine C production is restricted to *P. crustosum* in series *Camembertii*, *P. melanoconidium* in series *Viridicata* and all species in series *Corymbifera*. Citrinin is produced by *P. verrucosum* and *P. radicola* in section *Viridicata* but also by *P. expansum* in section *Expansa*. All species are psychrotolerant and grow well at low water activities. Section *Viridicata* species are common on stored or manufactured man-made foods. Series *Viridicata*, *P. verrucosum* and *P. hordei* are common on stored cereals, while series *Camemberti*, *Solita* and *P. nordicum* are common on cheese, nuts and other fat and protein rich substrates. Species in series *Corymbifera*, except *P. hordei*, are common on onions, root vegetables and flower bulbs.

TAXONOMIC AND NOMENCLATORAL NOTES ON SERIES, SPECIES AND SYNONYMY IN *PENICILLIUM* SUBGENUS *PENICILLIUM*

All holotypes, neotypes, epitypes listed below are those from the Names in Current Use (NCU) list (Pitt and Samson, 1993, Pitt et al., 2000) or otherwise indicated.

Section *Coronata* Pitt, Gen. Penicil.: 392, 1979

Series *Olsonii* Pitt, Gen. Penicil.: 392, 1979

= Series *P. brevicompactum* Raper & Thom, Man. Penicillia: 404, 1949 (nom. inval., arts 21,36)

Type species: *P. olsonii*

Accepted species:

P. bialowiezense K. Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B, 1927: 462, 1927.

Neotype : CBS 227.38

P. brevicompactum Dierckx, Ann. Soc. Scient. Brux. 25: 88, 1901.

= *P. griseobrunneum* Dierckx, Ann. Soc. Scient. Brux. 25: 88, 1901.

= *P. stoloniferum* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 68, 1910.

= *P. tabescens* Westling, Ark. Bot. 11: 100, 1911.

= *P. szaferei* K.M. Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B, 1927: 447, 1927.

= *P. hagemii* K.M. Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B, 1927: 448, 1927.

= *P. patris-mei* K.M. Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B, 1927: 496, 1927.

= *P. brunneostoloniferum* Abe, J. Gen. Appl. Microbiol. 2: 104, 1956 (nom. inval.)

= *P. brunneostoloniferum* Abe ex Ramírez, Man. Atlas Pen.: 412, 1982.

Neotype: IMI 040225

P. olsonii Bain. & Sartory, Ann. Mycol. 10: 398, 1912.

= *P. monstrosum* Sopp, Skr. Vidensk. Selsk. Christiana 11: 150, 1912.

= *P. volgaense*, Beljakova & Mil'ko, Mikol. Fitopatol. 6: 147, 1972.

= *P. brevicompactum* var. *magnum* Ramírez, Man. Atlas Penicil.: 398, 1982.

Neotype: IMI 192502

Section diagnosis: Conidiophores strictly mononematous, with a long stipe, bearing a short, compact and broad, basically two-stage-branched penicillus, sometimes because of the septation of the branches, the penicilli become more complex. Branches 1-6 per branching point, rarely more, closely appressed. The penicilli of the section *Coronata* are shorter, broader

and more compact than those of the other sections in subgenus *Penicillium*: Characteristically, the number of branches per verticil is larger and the metulae and branches are shorter and appear clavate or swollen. Phialides have a broadly cylindrical base and a short, narrow neck. Looking superficially like *Aspergillus* heads in the stereomicroscope, the conidia adhere in divergent to radiating tangled chains, whereas in the other sections of subgenus *Penicillium* they develop in parallel chains, which may become somewhat tangled in age. Conidia subglobose, pear-shaped to broadly ellipsoidal, with walls finely roughened, sometimes appearing smooth. All species produce asperphenamate and the unknown metabolite O (Svendsen and Frisvad, 1994; Frisvad et al., 1990a). The species are common in all parts of the world, with *P. olsonii* being more common in tropical regions. Thriving in mountainous areas of the tropics, especially coffee estates, they also thrive in greenhouses and are common on tomatoes. *P. brevicompactum* and *P. bialowiezense* are also common on mushrooms, where they can produce conspicuous green colonies directly on the basidiocarps. They have also been found in yoghurts, liver patees and many other processed foods at low water activities. See also the description of the section *Coronata* above. This section only contains one series: *Olsonii*.

The series lacks known teleomorphs state, but few tropical strains of *P. olsonii* can produce large white sclerotia (see Fig. 2 F).

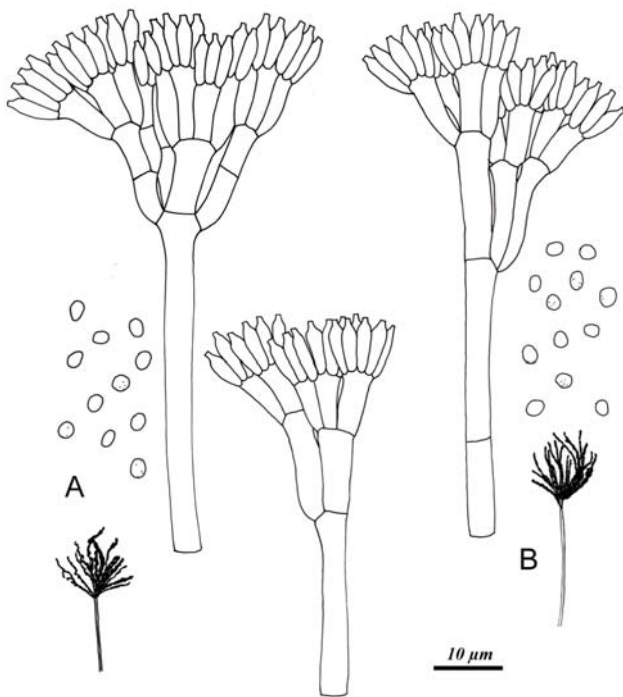


Fig. 7. Conidiophores and conidia of (A) *Penicillium olsonii* and (B) *P. brevicompactum*.

Series *Olsonii* contains only three closely related species: *P. olsonii*, *P. brevicompactum* and *P. bialowiezense*. They differ mainly in the complexity of

their penicilli. In *P. brevicompactum* and *P. bialowiezense* branches are often single, although occasionally two to three of them may occur per branching point, whereas typical penicilli of *P. olsonii* produce a compact verticil of up to six branches, developing on the apex and sometimes also on the subapical part of the stipe. However, deteriorated strains of *P. olsonii* produce smaller verticils of branches.

Penicilli of *P. olsonii* are sometimes suggestive of the conidial structures from the section *Inordinata* (which contains only *P. arenicola*). The shape of the phialides and the brown colour of the colonies distinguish *Inordinata* from the section *Coronata* and we have excluded the former section from subgenus *Penicillium*.

P. brevicompactum has many synonyms. Most of these were described by Zaleski and one more well-known species, *P. stoloniferum*, was accepted by Raper and Thom (1949). We have examined ex type strains of *P. griseobrunneum* (NRRL 867), *P. stoloniferum* (CBS 236.51), *P. hagemii* (CBS 316.59), *P. patris-mei* (CBS 210.28) and *P. brunneostoloniferum* (CBS 317.59). They all have the typical morphology of *P. brevicompactum* and furthermore all produce mycophenolic acid, brevianamide A and the Raistrick phenols and are clearly synonyms of this common species. Strains of *P. tabescens* and *P. szaferei* were not available for study, so we follow Raper and Thom (1949) and Pitt (1979) in suggesting these as synonyms of *P. brevicompactum*.

P. volgaense (CBS 626.72) and *P. brevicompactum* var. *magnum* (IJFM 5954) were entirely typical of *P. olsonii*. *P. monstrosum* was unavailable for study, but Sopp's protologue indicates that this was a *P. olsonii* rather than a *P. brevicompactum* as suggested by Raper and Thom (1949) and Pitt (1979).

Using multilocus DNA sequence analysis Peterson (2004) recognized *P. brevicompactum*, *P. olsonii* and a third clade which he assigned to *P. biourgeianum* Zaleski. Examination of the ex-type NRRL 865 of *P. biourgeianum* showed that it is identical with *P. bialowiezense*. Peterson (2004) found that the culture NRRL 863 of *P. bialowiezense* is identical with *P. polonicum*. However, in our study we examined the ex-type of *P. bialowiezense* CBS 227.38, which was originally deposited at CBS by K. Zaleski. Therefore NRRL 863, which was sent later to C. Thom, can be considered a contaminant. Our examination of NRRL 863 showed that it has the typical extrolite production of *P. cyclopium*. It is somewhat different from *P. cyclopium* by its good sporulation on YES and the dark reverse on CYA.

Section *Roqueforti* Frisvad & Samson sect. nov.

Sectio generis *Penicillium* subgeneris *Penicillium*, penicillis asymmetrice terverticillatis, stipitibus rugosis,

conidiis obscure viridibus, levibus, globosis; coloniae celeriter crescentes, velutinae, creatinum vel nitritum vel substratum nitrogeni assimilantes; 0.5% acido acetico vel 1% propionico addito et in atmosphaera CO₂ bene crescentes; sed 37°C non crescunt et 5% NaCl inhibuntur; roquefortinum formatur.

Typus *P. roqueforti* Raper & Thom

Series *Roqueforti* Raper & Thom ex Frisvad, Int.

Mod. Meth. Pen Asp. Clas., 277, 2000.

= Series *P. roqueforti* Raper & Thom, Man. Penicillia, 392, 1949 (nom. inval., arts 21,36)

Type species: *P. roqueforti*

Accepted species:

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

= *P. aromaticum casei* Sopp, Zentbl. Bakt. ParasitKde., Abt. II: 4: 164, 1898.

= *P. vesiculosum* Bain., Bull. Trimest. Soc. Mycol. Fr. 23: 10, 1907.

= *P. roqueforti* var. *weidemannii* Westling, Ark. Bot. 11: 71, 1911.

= *P. atroviride* Sopp, Skr. Vidensk. Selsk. Christiana 11: 149, 1912.

= *P. roqueforti* Sopp, Skr. Vidensk. Selsk. Christiana 11: 156, 1912.

= *P. virescens* Sopp, Skr. Vidensk. Selsk. Christiana 11: 157, 1912.

= *P. aromaticum* Sopp, Skr. Vidensk. Selsk. Christiana 11: 159, 1912.

= *P. aromaticum-casei* Sopp ex Sacc., Syll. Fung. 22: 1278, 1913.

= *P. suavolens* Biourge, Cellule 33: 200, 1923.

= *P. gorgonzolae* Weidemann apud Biourge, Cellule 33: 204, 1923.

= *P. weidemannii* (Westling) Biourge, Cellule 33: 204, 1923.

= *P. stilton* Biourge, Cellule 33: 206, 1923.

= *P. weidemannii* var. *fuscum* Arnaud, Boll. Ist. Sieroter. Milan. 6: 27 (1928).

= *P. biourgei* Arnaud, Boll. Ist. Sieroter. Milan. 6: 27 (1928).

= *P. roqueforti* var. *viride* Dattilo-Rubbo, Trans. Br. Mycol. Soc. 22: 178, 1938.

= *P. conservandi* Novobranova, Nov. Sist. Niz. Rast. 11: 233, 1974.

Neotype: IMI 024313

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

= *P. roqueforti* var. *carneum* Frisvad, Mycologia 81: 858, 1989.

Type: IMI 293204

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

Holotype: C 25000

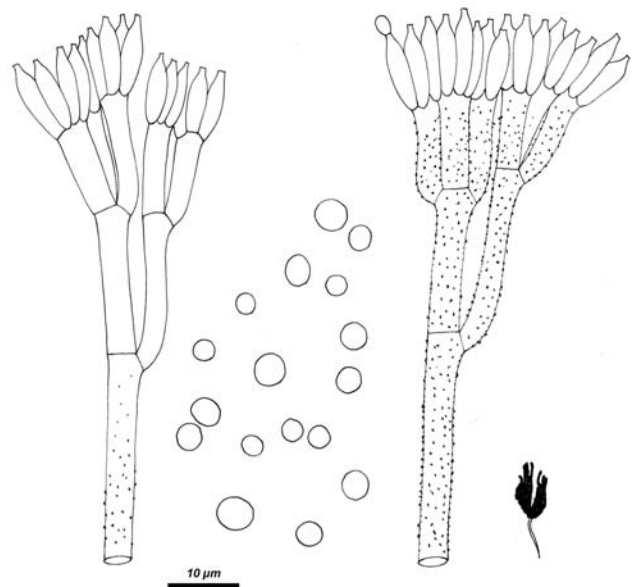


Fig. 8. Conidiophores and conidia of *P. roqueforti*

Section diagnosis: Conidiophores arising from submerged hyphae, up to 200 µm in length, relatively wide, and walls tuberculate (occasionally also smooth with stipe relatively short) bearing (one-) two-(three-)stage-branched penicilli with branches and usually also metulae tuberculate. All elements appressed. Phialides with a short, relatively wide neck. Conidia globose to subglobose, relatively large, smooth-walled, adhering in loose columns or in tangled chains. Conidial areas dark green or dark blue-green. Colony growth rate is fast for all species. All isolates in the series can grow at low pH values (for example on media containing 0.5 % acetic acid), at high alcohol concentrations and at elevated CO₂ levels. All species grow well on creatine and nitrite as the sole N-source. Roquefortine C is produced by all species. Isfumigaclavine and mycophenolic acid is produced by two of the three species. Members of the series appear to have a symbiotic relationship with lactic acid bacteria and certain acid-tolerant yeasts (Samson et al., 2002).

The section and series *Roqueforti* is separated from the section *Viridicata* by rapid growth, thin, strictly velutinous colonies, tuberculate stipes and branches, as well as by relatively large, globose, smooth-walled conidia. The series includes three species, *P. roqueforti*, *P. carneum* and *P. paneum*.

The three species in series *Roqueforti* are closely related (Boysen et al., 1996). *P. roqueforti* is the predominant mould occurring on cheeses of the Roquefort-type. Apart from blue-mould cheeses, *P. roqueforti* often occurs on other substrates, such as silage, rye bread and other acid preserved commodities. *P. roqueforti* produces small, soft white sclerotia-like structures after prolonged incubation (Samson et al., 1977a). Furthermore, its dark green reverse is distinctive.

P. carneum is mainly distinguished from *P. roqueforti* by its dark blue-green conidial areas, pale brown colony reverse, lower average growth rate and the profiles of extrolites. This species does not occur on blue cheeses. It has been isolated from meat products, silage and other substrates. *P. carneum* produces geosmin, distinguishing it from the other species. *P. paneum* also has a pale brown colony reverse. It can be distinguished from *P. carneum* by the profile of volatiles and by the profile of other extrolites.

A number of other epithets have been given to blue cheese moulds. In agreement with other authors, all of them are regarded as synonyms of *P. roqueforti*. The ex-type cultures of *P. gorgonzolae* (NRRL 857), *P. roqueforti* var. *viride* (CBS 234.38) and *P. conservandi* (CBS 498.73) were examined and found to be entirely typical of *P. roqueforti*.

Section *Chrysogena* Frisvad & Samson, sect. nov.

= Series *Chrysogena* Raper & Thom ex Stolk & Samson, Adv. Pen. Asp. Syst.: 180, 1985 = Series *P. chrysogenum* Raper & Thom, Man. Penicillia: 355, 1949 (nom. inval., arts 21, 36)

Sectio generis *Penicillium* subgeneris *Penicillium*, penicillis raro biverticillatis, vulgo terverticillatis, stipitibus levibus; coloniae celeriter crescentes in substratis 15% sucrosi continentibus, velutinae; in creatino velut substrato nitrogeni parce crescentes; 37°C plerumque sustinetur, sed 30°C omnes species bene crescentes; 5% NaCl addito stimulantur (*P. aethiopico* excepto).

Typus *P. chrysogenum* Thom

Accepted species:

P. chrysogenum Thom, Bull. Bur. Anim. Ind. USDA 118: 58, 1910.

- = *P. griseoroseum* Dierckx, Ann. Soc. Scient. Brux. 25: 86, 1901.
- = *P. brunneorubrum* Dierckx, Ann. Soc. Scient. Brux. 25: 88, 1901.
- = *P. citreoroseum* Dierckx, Ann. Soc. Scient. Brux. 25: 89, 1901.
- = *P. baculatum* Westling, Svensk Bot. Tidskr. 14: 139, 1910.
- = *P. notatum* Westling, Ark. Bot. 11: 95, 1911.
- = *P. meleagrimum* Biourge, Cellule 33: 147, 1923.
- = *P. flavidomarginatum* Biourge, Cellule 33: 150, 1923.
- = *P. cyaneofulvum* Biourge, Cellule 33: 174, 1923.
- = *P. roseocitreum* Biourge, Cellule 33: 184, 1923.
- = *P. rubens* Biourge, Cellule 33: 265, 1923.
- = *P. chlorophaeum* Biourge, Cellule 33: 271, 1923.
- = *P. camerunense* Heim apud Heim, Nouvel & Saccas, Bull. Acad. R. Belg. Cl. Sci. 35: 42, 1949.
- = *P. chrysogenum* var. *brevisterigma* Forster, Brit. Pat. 691: 242, 1953.

- = *P. aromaticum* f. *microsporium* Romankova, Uchen. Zap. Leningr. Gos. Univ. (Ser. Biol. Nauk. 40:) 191: 102, 1955.
- = *P. harmonense* Baghdadi, Nov. Sist. Niz. Rast. 5: 102, 1968.
- = *P. verrucosum* var. *cyclopium* strain ananas-olens Ramírez, Man. Atlas. Penicil.: 457, 1982.
- = *P. chrysogenum* mut. *fulvescens* Takashima, Arima & Abe ex Ramírez, Man. Atlas Penicil.: 365

Neotype: IMI 024314

P. flavigenum Frisvad & Samson, Mycological Research 101: 620, 1997.

Holotype: CBS 419.89

P. dipodomyis (Frisvad, Filt. & Wicklow) Banke, Frisvad and S. Rosendahl, Int. Mod. Meth. Pen. Asp. Clas., 270, 2000

= *P. chrysogenum* var. *dipodomyis* Frisvad, Filt. & Wicklow, Can. J. Bot. 65: 766, 1987.

= *P. dipodomyis* (Frisvad, Filt. & Wicklow) Banke, Frisvad & S. Rosendahl, Mycol. Res. 101: 622, 1997 (nom. inval.).

Holotype: IMI 296926

P. nalgiovense Laxa, Zentbl. Bakt. ParasitKde, Abt. II 86: 162, 1932.

Neotype: CBS 352.48

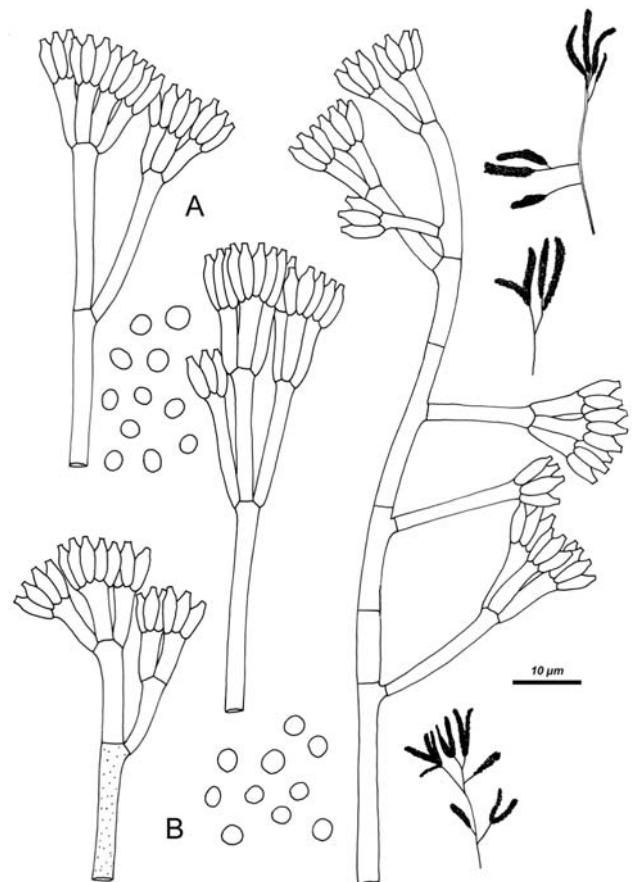


Fig 9. Conidiophores and conidia of (A) *P. chrysogenum* and (B) *P. dipodomyis*.

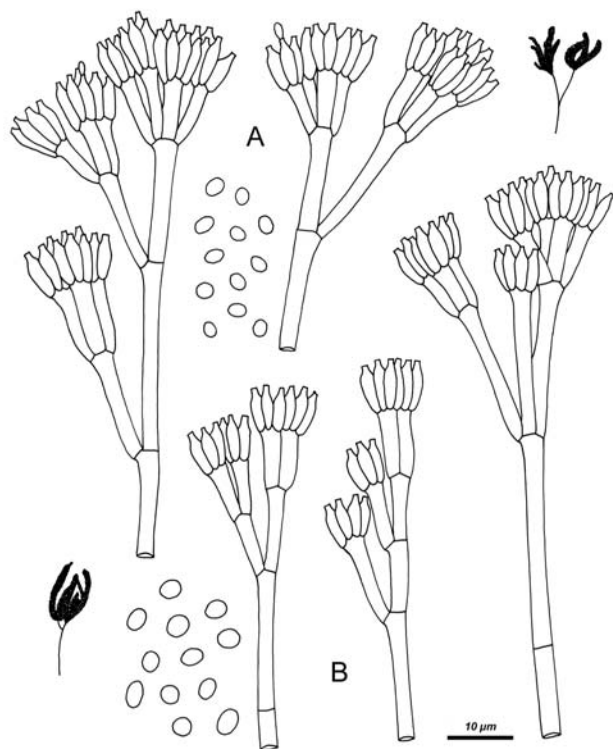


Fig. 10. Conidiophores and conidia of (A) *P. flavigenum* and (B) *P. atramentosum*

Section diagnosis: Conidiophores mononematous, (one-) two- or three-, occasionally more-stage-branched with the lower branches sometimes intergrading with a variable number of single, strongly divergent, subterminal and/or intergrading branches (metulae), arising lower along the stipe. Stipes usually long, with walls smooth or nearly so, rarely very finely roughened. Metulae are in somewhat appressed verticils of 3-5. Branches are usually single and divergent; only when arising at the first septum below the verticil of metulae, do they occasionally occur in a somewhat appressed verticil of three. Phialides when typical, are relatively small (rarely longer up to 10 µm in length), with a broadly cylindrical base and a short, sometimes inconspicuous, narrowed neck. Conidia (broadly) ellipsoidal to subglobose or globose with walls smooth or very finely roughened, adhering in columns. Teleomorph and sclerotia absent, even though there is a close affinity with *Eupenicillium egyptiacum*.

Raper and Thom (1949) and Pitt (1979: 330) suggested that *P. chrysogenum* had some affinities with species in subgenus *Furcatum* (e.g. *P. citrinum*). Pitt actually placed *P. griseoroseum* (a synonym) in his subgenus *Furcatum*, but because of the two-to three-stage-branched penicilli, he placed *P. chrysogenum* in subgenus *Penicillium*. Series *Chrysogena* is distinguished from series *Citrina* by the more complex conidiophores. The type strain of *P. griseoroseum* agrees in many respects with the type culture of *P. chrysogenum* but differs in producing one-stage-branched penicilli. According to Biourge's description (1923), *P. griseoroseum* was character-

ized by one- to two-stage-branched conidiophores, like those of *P. chrysogenum*. Consequently, the correct name of the present species should be *P. griseoroseum*. Since the name is in common use, *P. chrysogenum* was proposed for conservation (Frisvad *et al.*, 1990c; Kozakiewicz *et al.*, 1992) and the Committee for Fungi and Lichens accepted this.

P. chrysogenum has many synonyms. Three of those were described before *P. chrysogenum* and therefore would have nomenclatural priority, but the name *P. chrysogenum* has been conserved (see above). The following ex type strains of synonyms of *P. chrysogenum* have been examined: *P. griseoroseum* (NRRL 820), *P. notatum* (CBS 355.48), *P. meleagrimum* (authentic, CBS 349.48), *P. cyaneofulvum* (CBS 314.48), *P. harmonense* (CBS 412.69), *P. roseocitreum* (NRRL 889), *P. rubens* (NRRL 822), *P. chlorophaeum* (NRRL 817), *P. camerunense* (CBS 339.58), *P. fluorescens* (NRRL 819), *P. aromaticum* var. *microsporum* (CBS 302.67). All these isolates were indistinguishable from the ex type culture of *P. chrysogenum*, although there were some differences in the production of yellow pigment in the strains. *P. harmonense* differed in two kinds of extrolites and may be distinct, but more cultures of *P. harmonense* are needed to decide if this is the case. All the strains produce penicillin, roquefortine C and meleagrin.

The species in this section (Banke *et al.*, 1987) are united by their production of penicillin, their dry habitats, salt tolerance, strictly velutinous colony texture, divergent conidiophores and phialide shape, fast growth rates and production of yellow and orange pigments. Extrolite and isozyme data show that *P. chrysogenum* is most closely related to *P. flavigenum*, while *P. nalgiovense* (the starter culture strains) is more similar to *P. dipodomyis*.

Since strains of *P. chrysogenum* may develop up to five-, rarely more-stage-branched conidiophores, the species shows some morphological affinities with *P. griseofulvum* (series *Urticicolae*). However, the conidiophores of Section *Chrysogena* are generally less complicated and both the phialides and metulae are larger than those of *P. griseofulvum*.

Cultures of Section *Chrysogena* grow much more rapidly than those of the series *Tularenisia* in *Eupenicillium* and they do not produce ascomata or sclerotia. Moreover, the conidial chains of the *Chrysogena* usually form columns, whereas those of the *Tularenisia* adhere in parallel to tangled chains.

Three other species associated with dry habitats like deserts are included in the *Chrysogena*. *P. flavigenum* closely resembles *P. chrysogenum*. The conidia of *P. flavigenum* are a little more ellipsoidal and slightly smaller than those of *P. chrysogenum* and they adhere in at first loosely parallel, later tangled chains. The two species are mainly distinguished by their extrolites. *P. chrysogenum* and *P.*

dipodomys are mainly distinguished by their extrolites. Moreover, the stipes of *P. dipodomys* are slightly rough-walled and the conidia of *P. dipodomys* are darker green than those of *P. chrysogenum*. *P. nalgiovense* isolates from cheese are rather slow growing, produce large quantities of nalgiovensin and nalgiofaxin and only traces of penicillin, whereas the *P. nalgiovense* strains found on meat products are fast growing and produce large amounts of penicillin and smaller amounts of nalgiovensin and nalgiofaxin (Andersen and Frisvad, 1996). Starter cultures of *P. nalgiovense* have white conidia, because they have been selected for this character, but wild-type strains of *P. nalgiovense* from meat products have dark green conidia.

Scott et al. (*in press*) studied the phenotypic variation in *P. chrysogenum* from indoor environments and five unique multilocus haplotypes were revealed. Their phylogenetic analysis of allele sequences resolved in three strongly supported lineages. The majority of indoor isolates (90%) clustered together with the culture Alexander Flemming used for his penicillin experiments. A second clade contained the ex type cultures of *P. chrysogenum* and *P. notatum*. Scott et al. (*in press*) indicated that four taxa can be recognized with the *P. chrysogenum* complex and an expanded polyphasic study using strains from various substrates including multilocus sequence analysis is required to solve the delimitation of the taxa.

Series *Mononematosa* Frisvad, Int. Mod. Meth. Pen. Asp. Clas., 269, 2000.

Type species: *P. mononematosum*

Accepted species:

P. mononematosum (Frisvad, Filt. & Wicklow)

Frisvad, Mycologia 81: 857, 1989.

= *P. glandicola* var. *mononematosa* Frisvad, Filt. & Wicklow, Can. J. Bot. 65: 767, 1987.

= *P. granulatum* var. *mononematosa* (Frisvad, Filt. & Wicklow) Bridge, Kozak. & R.R.M. Paterson, Myc. Pap. 165: 38, 1992.

Holotype: IMI 296925

P. confertum (Frisvad, Filt. & Wicklow) Frisvad, Mycologia 81: 852, 1989

= *P. glandicola* var. *confertum*. Frisvad, Filt. & Wicklow, Can. J. Bot. 65: 769, 1987.

Holotype: IMI 296930

These non-fasciculate slow-growing species have complicated structures different from the usual appressed two-ramus structures seen in most other species in subgenus *Penicillium*. *P. mononematosum* has been found in deserts and warm salt marshes and usually in connection with burrows of rodents. The

only strain known of *P. confertum* has also been found in kangaroo rat burrows. These species were characteristic in the two numerical taxonomical studies where they have been included (Bridge *et al.*, 1989; Svendsen and Frisvad, 1994). The production of verrucologen and other fumitremorgins, cyclopaldic acid, isochromantoxin, asteltoxin, viriditoxin and metabolite A (Frisvad and Filtenborg, 1989; Svendsen and Frisvad, 1994) by *P. mononematosum* clearly sets this species apart from other terverticillate *Penicillia* and even indicates that *P. mononematosum* is more closely related to subgenus *Furcatum*. Both species bears some resemblance to *Chrysogena*, but in contrasts to that series they do not produce penicillin and they are slow growing.

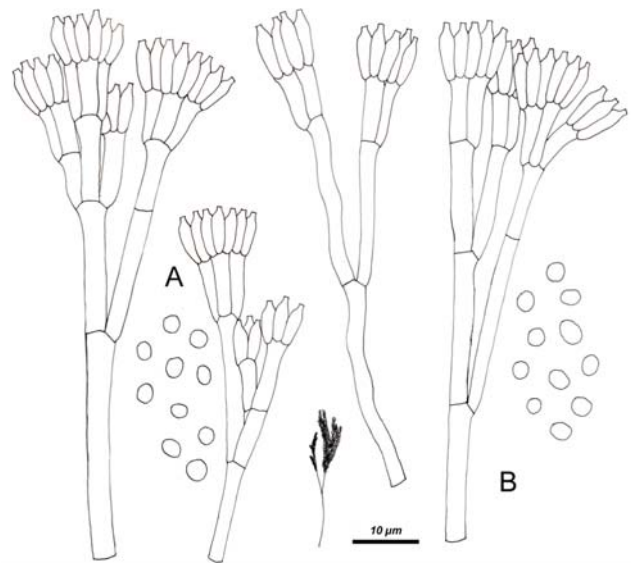


Fig. 11. Conidiophores and conidia of (A) *P. mononematosum* and (B) *P. confertum*.

Series *Aethiopica* Frisvad & Samson, **ser. nov.**

Series generis *Penicillium* subgeneris *Penicillium* sectionis *Chrysogena*, conidiophoris terverticillatis appressis, stipitibus levibus vel asperatis, conidiis levibus ellipsoideis; coloniae in reverso flavescetes, fasciculatae, 37°C bene crescentes sed 5% NaCl addito inhibitae; pigmenta haud in agarum diffundentia.

Typus *P. aethiopicum*

P. aethiopicum Frisvad, Mycologia 81: 848, 1989.

Holotype: IMI 285524

Series *Persicina* Frisvad and Samson, **ser. nov.**

Series generis *Penicillium* subgeneris *Penicillium* sectionis *Chrysogena*, conidiophoris terverticillatis appressis, stipitibus levibus, conidiis ellipsoideis vel cylindricis; coloniae pigmento rubido diffundente, 37°C bene crescunt.

Typus *P. persicinum* L. Wang, H. Zhou, Frisvad & Samson

P. persicinum L. Wang, H. Zhou, Frisvad & Samson, Ant. van Leeuwenhoek 86: 177

Holotype: HMAS 80638-1-4

These two species have only been found in warm climates. They both produce ellipsoidal conidia and griseofulvin. Growth at 37°C and production of chrysogine and roquefortine C by *P. persicinum* indicates an affinity with section *Chrysogenum*, while the ellipsoidal conidia and the production of griseofulvin by *P. persicinum* and *P. aethiopicum* indicate an affinity to section *Expansa*.

Section *Penicillium*

Series *Expansa* Raper & Thom ex Fassatióvá, Acta Univ. Carol. Biol 12: 324, 1977

= Series *P. expansum* Raper & Thom, Man. Penicillia: 508, 1949 (nom. inval., arts 21,36)

= Series *P. terrestre* Raper & Thom, Man. Penicillia: 446, 1949 (nom. inval., arts 21,36)

Type species: *P. expansum*

Accepted species:

P. expansum Link, Obs. Mycol. 1: 16, 1809.

= *Coremium leucopus* Pers., Mycol. Eur. 1: 42, 1822.

= *Coremium glaucum* Link ex Pers., Mycol. Eu. 1: 42, 1822.

= *Floccaria glauca* Grev., Scot. Crypt. Fl. 6: 301, 1828.

= *Coremium alphotobus* Secr., Mycol. Suisse 3: 539, 1833.

= *Coremium vulgare* Corda, Pracht-Fl.: 54, 1839.

= *P. glaucum* var. *coremium* Sacc., Syll. Fung. 4: 78, 1886.

= *P. elongatum* Dierckx, Corda, Pracht-Fl.: 54, 1839.

= *P. glaucum* var. *coremium* Sacc., Syll. Fung. 4: 78, 1886.

= *P. elongatum* Dierckx, Ann. Soc. Scient. Brux. 25: 87, 1901.

= *P. musae* Weidemann, Zentralbl. Bakt. ParasitKde., Abt. II, 19: 687, 1907.

= *P. juglandis* Weidemann, Zentralbl. Bakt. ParasitKde., Abt. II, 19: 683, 1907.

= *P. variabile* Wehmer, Mykol. Zentralbl. 2: 195, 1913.

P. leucopus (Pers.) Biourge, C.R. Séanc. Soc. Biol. 82: 877, 1919.

= *P. plumiferum* Demelius, Verh. Zool.-Bot. Ges. Wien 72: 76, 1922.

= *P. aeruginosum* Demelius, Verh. Zool.-Bot. Ges. Wien 72: 76, 1922.

= *P. malivorum* Ciferri, Riv. Pathol. Veg., Padova 14: 77, 1924.

= *P. kap-laboratorium* Sopp apud Biourge, Cellule 36: 454, 1925.

= *P. reticulosum* Birkinshaw, Raistrick & G. Smith, Biochem. J. 36: 830, 1942.

Neotype: CBS 325.48

P. marinum Frisvad & Samson, *sp. nov.*

A *Penicillio expanso* conidiophoris divaricatis et conidiis subglobosis (2.5-3.2 µm) distinguitur; coloniae in omnibus

substratis lentius crescentes, penostatinum formatur neque citrininum.

Typus: CBS 109550

P. sclerotigenum Yamamoto, Scient. Rep. Hyogo Univ. Agric., Agric. Biol. Ser. 2, 1: 69, 1955.

Lectotype: IMI 068616

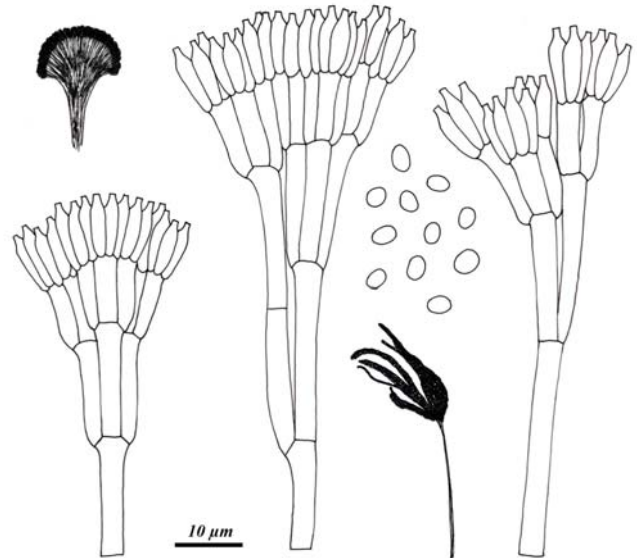


Fig. 12. Conidiophores and conidia of *P. expansum*

Conidiophores predominantly mononematous, occasionally also synnematus, especially in marginal areas of fresh isolates (of *P. expansum*). Synnemata, when present consisting of a white, sterile stalk and a green, fertile capitulum. Stipes long, usually smooth-walled, occasionally on MEA slightly roughened, bearing a terminal, regularly two- to three-stage-branched penicillus, with elements appressed. In *P. sclerotigenum* several one stage branched structures can be found. Phialides are robust, with a broadly cylindrical basal part and a relatively short, slightly narrowed, comparatively wide neck. Conidia are ellipsoidal to subglobose, smooth-walled, adhering in parallel, sometimes slightly tangled chains, occasionally forming loose columns. In *P. sclerotigenum* the conidia at first are ellipsoidal, hyaline, smooth-walled, often later becoming globose to subglobose with walls pigmented and more or less roughened, adhering in parallel to tangled chains.

Teleomorph absent but sclerotia present in *P. sclerotigenum*.

The series *Expansa* contains three species; two closely related *P. expansum* and *P. marinum* in addition to *P. sclerotigenum*. They are characterized by large regularly two- to three-stage-branched conidiophores with smooth walls and large ellipsoidal or subglobose conidia. The well-developed coremia, occasionally present in marginal areas of fresh isolates of *P. expansum*, are lacking in the two other species. *P. expansum*, *P. marinum* and *P. sclerotigenum* are distinguished from the smooth-walled

species of the *Claviformia* by the more rapid growth of their colonies and the more robust phialides.

P. expansum causes a destructive rot of pomaceous fruits, on which it produces conspicuous concentric zones of crust-like coremia. Well-developed coremia occur only occasionally on agar media. They may develop in small numbers in marginal areas of fresh isolates. After a few years of maintenance, the capacity to produce well-defined coremia is usually lost. The synnemata may be induced by long maintenance at low temperatures, in apples or on media with toxic constituents. The ex type culture of *P. resticulosum*, regarded as floccose by Raper and Thom (1949), produced synnemata on malt extract agar after 3 month of storage at 0°C. This species is considered as a synonym of *P. expansum*. The cultures become velutinous, producing mononematous to slightly synnematos conidiophores.

P. sclerotigenum produces a rot in yam tubers and has only been found in habitats with yams. It is characterized by rapid growth and sclerotium production and a quite large proportion of biverticillate asymmetric penicilli. The latter feature leads Pitt (1979) to place *P. sclerotigenum* in *Furcatum*. Fresh isolates, however, have many terverticillate structures.

The three species in the series share the ability to produce patulin, roquefortine C and geosmin and general colony appearance. Pitt (1979) placed *P. chrysogenum* and *P. atramentosum* in this series, but his series were based more on facilitating identification than phylogenetic or overall phenetic similarity.

P. resticulosum (CBS 150.45) is clearly a synonym of *P. expansum*, despite its occasionally cylindrical conidia. The other synonyms listed above are not available as living cultures anymore.

Series *Urticicolae* Fassatiová, Acta Univ. Carol. Biol. 12: 324, 1977

= Series *P. urticae*, Raper & Thom, Man. Penicillia: 531, 1949 (nom. inval., arts 21,36)

Type species: *P. griseofulvum*

Accepted species:

P. griseofulvum Dierckx, Ann. Soc. Scient. Brux. 25: 88, 1901.

= *P. patulum* Bain., Bull. Trimest. Soc. Mycol. Fr. 22: 208, 1906.

= *P. urticae* Bain., Bull. Trimest. Soc. Mycol. Fr. 23: 15, 1907.

= *P. flexuosum* Dale apud Biourge, Cellule 33: 264, 1923.

= *P. maltum* Hori & Yamamoto, Jap. J. Bacteriol. 9: 1105, 1954.

= *P. duninii* Sidibe, Mikol. Fitopatol. 8: 371, 1974.

Neotype: IMI 075832

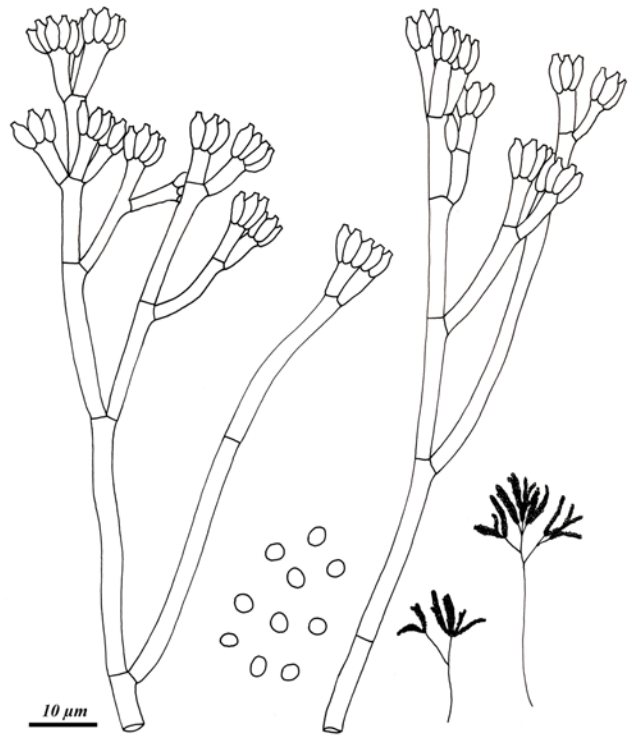


Fig. 13. Conidiophores and conidia of *P. griseofulvum*

P. dipodomycicola (Frisvad, Filt. & Wicklow) Frisvad, Int. Mod. Meth. Pen. Asp. Clas., 275.

P. griseofulvum var. *dipodomycicola* Frisvad, Filt. & Wicklow, Can. J. Bot. 65: 767, 1987.

Holotype: IMI 296935

Section diagnosis: Conidiophores mono- and synnematos. The stipes are long, often slightly sinuous, and smooth-walled. Penicilli are large, complicated, variable in pattern, loosely three- to five- or more-stage-branched, and all elements are smooth-walled. Branches single strongly divergent, bearing short, compact, one-(two-) stage-branched structures. Metulae 2-3 per verticil, comparatively short. Phialides very small, less than 6 μm in length, more or less swollen, with a very short or inconspicuous neck. Conidia ellipsoidal, smooth-walled, adhering in parallel chains, sometimes forming loose columns. Teleomorph and sclerotia absent.

Fassatiová (1977) proposed the series *Urticicola* to accommodate a single species: *P. urticae* (= *P. griseofulvum*). Pitt (1979) emended Fassatiová's concept by adding five species that like *P. griseofulvum* are characterized by relatively slow growth on CYA at 25°C. However, the added species produce regularly, two- to three-stage-branched penicilli and thus differ strongly from the complicated, loosely arranged, three- to five-stage-branched conidial structures, characteristic of *P. griseofulvum*. Moreover, the phialides are quite different. Because of its branched, synnematos conidiophores, most authors (Raper & Thom 1949, Fassatiová, 1977; Pitt, 1979;

Ramirez 1982) classified *P. griseofulvum* in Raper & Thom's subsection *Fasciculata*. However, in many respects, such as the complicated conidiophores, the divergent branches and the small metulae and phialides *P. griseofulvum* differs strongly from the section *Viridicata* and other series in *Expansa*. In fact *P. griseofulvum* and *P. dipodomyicola* represents unique species without very close relationships with other species. The three-to five- or more-stage-branched conidiophores are however, slightly reminiscent of *P. chrysogenum*. Penicillin production adds further to the similarity between these series. *P. griseofulvum* differs from the *Chrysogena* in producing synnematosus conidiophores, which are more complicated and irregular in structure. Moreover *P. griseofulvum* and *P. dipodomyicola* are also distinguished from the *Chrysogena* by the very small phialides and metulae.

The series *Urticicolae*, as delimited here is restricted to only two closely related species, *P. griseofulvum* and *P. dipodomyicola*. The series *Urticicolae* is placed in section *Expansa* because of the strongly ellipsoidal smooth-waled conidia, the synnemata and the production of patulin. The two species differ from series *Expansa* by their inability to use creatine as sole N-source and their very short phialides. Both species produce griseofulvin, cyclopiazonic acid and patulin

P. griseofulvum and *P. dipodomyicola* have most often been found on dry cereals and seeds. Both species are distinct, however, as *P. dipodomyicola* produce predominantly bi- to rarely ter-verticillate structures while *P. griseofulvum* has ter- to quarter-verticillate structures. Each species consistently produce other species specific extrolites (Frisvad and Filtenborg, 1989; Svendsen and Frisvad, 1994; Smedsgaard and Frisvad, 1997).

The ex type cultures of *P. patulum* (NRRL 994), *P. urticae* (CBS 384.48) and *P. flexuosum* (CBS 124.14) were inseparable from *P. griseofulvum*.

Series *Claviformia* Raper & Thom ex Stolk, Samson & Frisvad, Int. Mod. Con. Pen. Asp. Clas.: 132, 1990

Type species: *P. vulpinum*

Accepted species:

P. clavigerum Demelius, Verh. Zool.-Bot. Ges. Wien 72: 74, 1922.

Neotype: IMI 039807

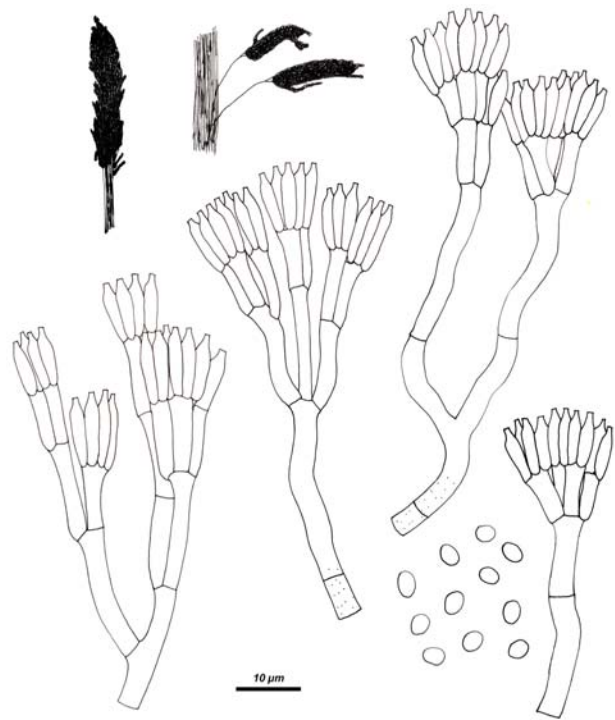


Fig 14. Conidiophores and conidia of *P. clavigerum*

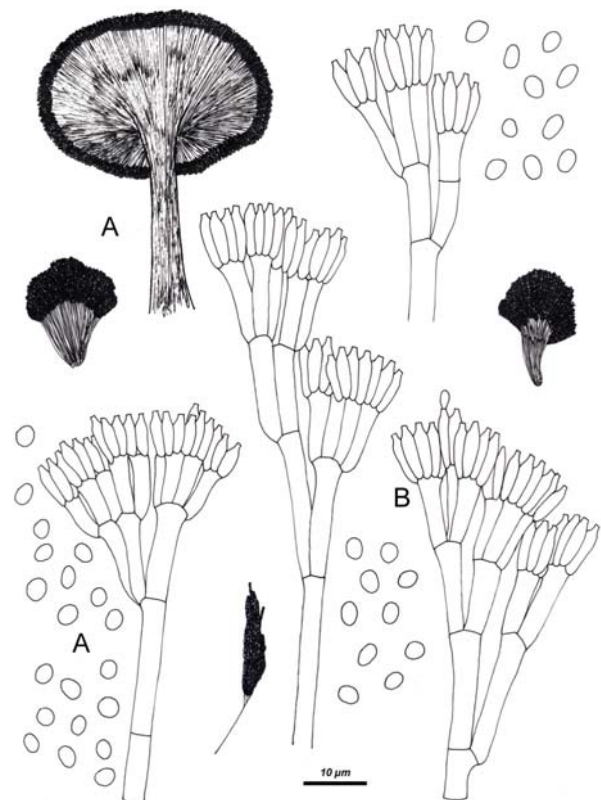


Fig. 15. Conidiophores and conidia of (A) *P. coprophilum* and (B). *P. coprobium*

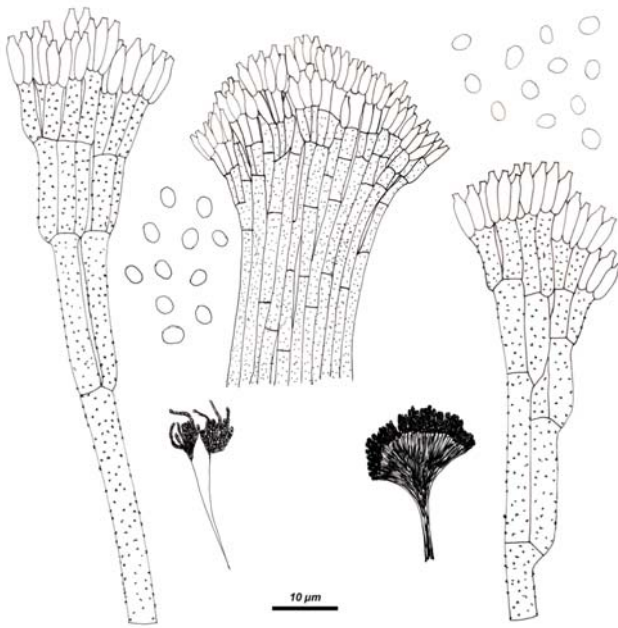


Fig. 16. Conidiophores and conidia of *P. glandicola*

P. concentricum, Samson, Stolck & Hadlok, Stud. Mycol. (Baarn) 11: 17, 1976.

P. glandicola var. *glaucovenetum* Frisvad, Mycologia 81: 855, 1989.

Holotype: CBS 477.75

P. coprobium Frisvad, Mycologia 81: 853, 1989.

Holotype: IMI 293209

P. coprophilum (Berk. & Curt.) Seifert & Samson, Adv. Pen. Asp. Syst.: 145, 1985.

Holotype: Cuba, Wright 666 (K). We designate CBS 110760 as epitype.

P. formosanum Hsieh, Su & Tzean, Trans. Mycol. Soc. R.O.C. 2: 159, 1987.

Holotype: PPEH 10001

P. glandicola (Oud.) Seifert & Samson, Adv. Pen. Asp. Syst.: 147, 1985.

= *P. granulatum* Bain., Bull. Trimest. Soc. Mycol. Fr. 21: 126, 1905.

= *P. divergens* Bain. & Sartory, Bull. Trimest. Soc. Mycol. Fr. 28: 270, 1912.

= *P. schneeggii* Boas, Mykol. Zentralbl. 5: 73, 1914.

= *P. granulatum* var. *globosum* Bridge, D. Hawksw., Kozak., Onions, R.R.M. Paterson, Sackin & Sneath, J. Gen. Microbiol. 135: 2957, 1989.

Holotype: Netherlands, Valkenburg, Jul 1901, Rick in herb. Oudemans (L), Epitype suggested here: CBS 498.75

P. vulpinum (Cooke & Masee) Seifert & Samson, Adv. Pen. Asp. Syst.: 144, 1985.

= *Coremium claviforme* (Bain.) Peck, Bull. N.Y. St. Mus. 131: 16, 1909.

= *Coremium silvaticum* Wehmer, Ber. Dt. Bot. Ges. 31: 373, 1914.

= *Penicillium silvaticum* (Wehmer) Biourge, Celule 33: 1056, 1923.

= *P. silvaticum* (Wehmer) Gäumann, Vergl. Morph. Pilze: 177, 1926.

= *P. claviforme* mut. *candicans* Abe & Uro ex Ramirez, Man, Atl. Penicil.: 488, 1982

= *P. claviforme* mut. *olivicolor* Abe & Uro ex Ramirez, Man, Atl. Penicil.: 490, 1982

Holotype: "on dung", *s.coll.*, in herb. Cooke (K),

Epitype suggested here CBS 126.23

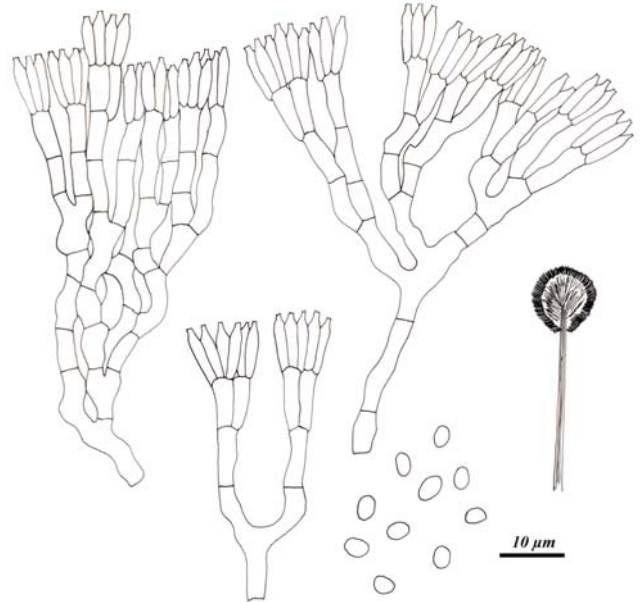


Fig. 17. Conidiophores and conidia of *P. vulpinum*

Series diagnosis: Cultures strongly fasciculate to coremiform, with a majority of the conidiophores aggregated onto loose or well-defined coremia. Mononematous structures in varying numbers also present. Coremia, developing commonly in concentric zones, usually consisting of a stalk, comprised of the stipes of conidiophores and an apical, feathery capitulum comprised of separate, diverging conidiophores, occasionally acicular with penicilli borne over nearly the entire length, though commonly more concentrated on the terminal part. Stipes of varying length, with walls smooth or roughened. Penicilli large, two- to three-stage-branched, with elements typically appressed, occasionally slightly divergent. Phialides with a cylindrical base and a short, but distinct, slightly narrowed neck. Conidia ellipsoidal to subglobose, smooth-walled, adhering in parallel chains, sometimes forming columns. Sclerotia rarely present.

Species of the *Claviformia* are characterized by more or less restricted colonies, producing loose to well-defined coremia in concentric zones. The coremia consist usually of a sterile stalk and a fertile, feathery capitulum, occasionally they are acicular with the penicilli covering nearly the entire stalk, though especially the terminal part (e.g. *P. clavigerum*).

In contrast to *P. vulpinum* the conidiophores of the remaining species of the series retain their individuality and they are somewhat divergently arranged, giving the coremia their feathery appearance. The coremia of *P. vulpinum* are compact. Generally the coremia of the *Claviformia* are larger and better developed on the natural substrate than on agar media.

In *P. clavigerum* colonies are strongly synnemataous. Synnemata are well-developed, acicular, with a pointed top, often not showing a clear differentiation into stalk and conidium-bearing area, usually simple, but sometimes branched near the top; conidiophores borne over nearly the entire length of the stalk, though usually more concentrated on the terminal area, one- to two-stage-branched with elements commonly appressed and smooth-walled. The stipes are variable in length, often long, sinuous, compressing the body of the synnemata. The phialides have a cylindrical basal part and a short, narrowed neck. Conidia are ellipsoidal and smooth-walled. *P. clavigerum* is mainly separated from the other species of the series *Claviformia* by the structure of the synnemata. The coremia of most synnemataous species of the subgenus *Penicillium* consist of a more or less, sterile stalk and a fertile capitulum, whereas the synnemata of *P. clavigerum* show no clear differentiation into stalk and capitulum. They are acicular and composed of a stalk, covered over nearly the entire length with conidiophores.

Pitt (1979) regarded *P. clavigerum* as a synonym of *P. duclauxii*, since the structure of their synnemata is alike. Yet, *P. clavigerum* does not produce the acerose phialides of the series *Duclauxii* (subgenus *Biverticillium*) but is characterized by the flask-shaped phialides typical of the subgenus *Penicillium* and consequently belongs in the latter subgenus. Moreover the penicilli and conidia, as well as the cultural appearance are quite different. *P. clavigerum* is placed here in the *Claviformia* (subgenus *Penicillium*) because of its morphological affinities with *P. coprophilum* and its biochemical affinities with *P. glandicola*. This classification based on morphology is supported by chemotaxonomic evidence (Samson *et al.*, 1989, p. 140). *P. duclauxii* produce duclauxin and other secondary metabolites typical of the genus *Talaromyces* and subgenus *Biverticillium* (Frisvad *et al.*, 1990d), and have no extrolites in common with *P. clavigerum* at all. In contrast to *P. vulpinum*, the conidiophores of *P. clavigerum*, like those of the remaining members of *Claviformia*, retain their individuality.

In *P. vulpinum*, the cultures are strongly coremiform. Coremia consisting of a sterile stalk and a subglobose to ellipsoidal, fertile capitulum, comprised of interwoven, anastomosing penicilli forming a hymenium-like layer. Conidiophore stipes of varying length, somewhat sinuous and interlaced, smooth-

walled. Penicilli dichotomously two- to four-stage-branched, with both branches per branching point nearly equal in length, all elements smooth-walled. Branches sinuous, gnarled, strongly interwoven, the ultimate branches bearing 2-3 metulae. Phialides slender, with a relatively long, cylindrical basal part and a short, slightly narrowed neck. Conidia ellipsoidal, smooth-walled, adhering in well-defined columns.

The characteristic, well-developed coremia and the dichotomously two- to four-stage-branched conidiophores distinguish *P. vulpinum* from all other species of *Penicillium*. Raper & Thom (1949) proposed the series *P. claviforme* to include the two species: *P. claviforme* (= *P. vulpinum*) and *P. clavigerum*. They included their *P. claviforme* series in the subsection *Fasciculata* since both species produce well-defined coremia. This assignment was accepted by Samson *et al.* (1976) and Ramirez (1982). According to Pitt (1979) *P. claviforme* and *P. clavigerum* should be classified in the series *Duclauxii* of the subgenus *Biverticillium*. However, the phialides of both species are characterized by a short, truncate neck. Acuminate necks, as occurring in the subgenus *Biverticillium* were not observed by us. Using DNA sequence data, LoBuglio *et al.*, 1994 also showed that these two strongly synnemataous species belong in subgenus *Penicillium*.

P. coprophilum, *P. coprobium* and *P. concentricum* resemble one another closely. Coremia, conidiophores, conidia as well as cultural characters (e.g. rate of growth and zonation of the cultures) are identical. Their profiles of metabolites are, however, quite different. Moreover they show differences in the colouration of their colony reverses. *P. coprobium* can produce white sclerotia, which are absent in the other two species. *P. concentricum* shows because of its conidia and smooth-walled stipes more affinities with *P. coprophilum* than with *P. glandicola*. It is regarded here as a separate species near *P. coprophilum*.

The *Claviformia* are separated from the *Corymbifera* by their ellipsoidal conidia and their better-developed coremia. They differ from the *Expansa* by their more restricted growth and the more prominent coremia. In addition the phialides of the *Claviformia* are slender as compared with the robust conidia-bearing structures of *P. expansum*.

This series is here amended to include all known synnemataous coprophilic species of *Penicillium*. They all have predominantly smooth walled ellipsoidal conidia and all species produce patulin. The members of this group have several features in common with species in series *Expansa* and *Urticicolae* including production of patulin and/or griseofulvin and roquefortine C, smooth walled stipes and smooth-walled ellipsoidal conidia and the production of synnemata.

Ex type cultures of *P. granulatum* (CBS 333.48), *P. schneegii* (NRRL 985) and *P. granulatum* var. *globosum* (IMI 299049) were all examined and found to agree with *P. glandicola*.

The ex type cultures of *P. claviforme* (CBS 126.23) and *P. silvaticum* (NRRL 1001) were both found to agree in all features with *P. vulpinum*.

Series *Italica* Raper & Thom ex Pitt, Gen. Penicil.: 381, 1979

= Series *P. italicum* Raper & Thom, Man. Penicillia: 523, 1949 (nom. inval., arts 21,36)

Type species: *P. italicum*

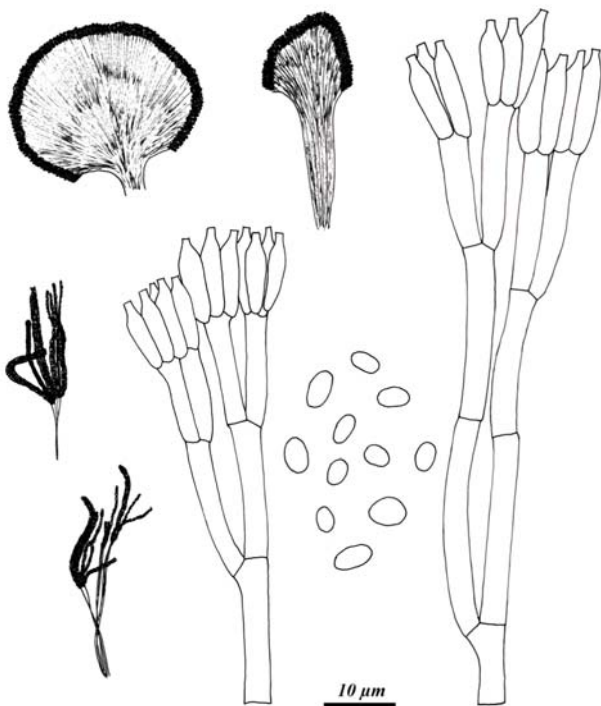


Fig. 18. Conidiophores and conidia of *P. italicum*

Accepted species:

P. italicum Wehmer, Hedwigia 33: 211, 1894.

= *Oospora fasciculata* (Grev.) Sacc. & Vogl. apud Sacc., Syll. Fung. 4: 11, 1886.

= *P. aeruginosum* Dierckx, Ann. Soc. Scient. Brux. 25: 87, 1901.

= *P. ventuosum* Westling, Ark. Bot. 11: 112, 1911.

= *P. digitatum* var. *latum* Abe, J. Gen. Appl. Microbiol. 2: 97, 1956.

= *P. japonicum* G. Smith, Trans. Br. Mycol. Soc. 46: 333, 1963.

= *P. italicum* var. *avellaneum* Samson & Gutter, Stud. Mycol. (Baarn) 11: 30, 1976.

Neotype: CBS 339.48

P. ulaiense Hsieh, Su & Tzean, Trans. Mycol. Soc. R.O.C. 2: 161, 1987.

Holotype: PPEH 29001.87

This is a natural series adapted to citrus fruits (Holmes *et al.*, 1994). The species share several extrolites, yet each species both produce species specific extrolites. The series has been emended to only include *P. italicum* and *P. ulaiense*, as the other species included in it were *P. fennelliae*, *P. digitatum* and *P. resticulosum* (Pitt, 1979) and these latter species are very different from the core species *P. italicum*.

Section diagnosis: Conidiophores mononematous to definitely synnematous, especially in marginal areas, one- to two-stage-branched, with all elements appressed and smooth-walled. Synnemata typically consisting of short to long stalks, up to 1 mm or more in length, erect or ascending, sometimes arising well below the agar surface, bearing terminal fertile parts. Stipes long sometimes slightly sinuous, forming the stalks of the synnemata. Metulae in verticils of 2-4. Phialides parallel, large, robust with a broad, cylindrical base and a wide neck, varying in length and merging almost imperceptibly into the conidial chain. Conidia cylindrical to ellipsoidal, smooth-walled, adhering in parallel chains occasionally forming loose columns. Colonies have greyish blue-green shades (rarely white or avellaneous). Teleomorph and sclerotia probably absent. Wehmer (1894) and Thom (1910) described sclerotia in *P. italicum*, but failed to find ascospores. Schwarz (1927) reported on a strain of *P. italicum*, which produced sclerotia upon oranges. After 12 weeks a few sclerotia developed asci. The smooth ascospores were provided with an equatorial ring, they measured 3.9 x 2.6 µm. Since then no ascomatal or sclerotial strain of *P. italicum* has been reported. Schwarz's description suggests that his strain represented a species of *Eupenicillium*, possibly *E. baarnense*.

The series is represented by two species, *P. italicum* and *P. ulaiense*. They cause a characteristic blue rot of citrus fruits. *P. italicum* grows much faster and has a more strongly coloured red-brown reverse on Cz based agars as compared to *P. ulaiense*. *P. italicum* and *P. ulaiense* are distinguished from *P. digitatum* by the synnematous conidiophores, the better developed one- to two-stage-branched penicilli as well as by the greyish, blue-green colonies. White or avellaneous mutants of *P. italicum* may occasionally be encountered.

P. italicum is somewhat reminiscent of *P. expansum* (series *Expansa*). However, *P. italicum* produces (one-) two-stage-branched conidiophores, whereas in *P. expansum* the penicilli range from two- to three-stage-branched. Moreover, the penicillic elements of *P. italicum* are larger, the conidia are also larger and more definitely ellipsoidal and the colonies differ strongly in appearance. In addition, *P. italicum* causes a blue rot of Citrus fruit, whereas *P. expansum* causes a rot of pomaceous fruits. *P. resticulosum*,

placed by Pitt (1979) in the *Italica*, seems in spite of its cylindrical to pyriform conidia, to be better classified in series *Expansa*. It is regarded to be an extreme variant of *P. expansum*. *P. japonicum* (CBS 327.59), placed by Pitt (1979) under *P. resticulosum*, is a typical *P. italicum*.

Series *Gladioli* Raper & Thom ex Stolk & Samson, Adv. Pen. Asp. Syst.: 183, 1985
= Series *P. gladioli*, Man. Penicillia: 471, 1949 (nom. inval., arts 21,36)

Type species: *P. gladioli*

Accepted species:

P. gladioli McCulloch & Thom, Science, N.Y. 67: 217, 1928.

= *P. gladioli* Machacek, Rep. Queb. Soc. Prot. Pl. 19: 77, 1928

Neotype: IMI 034911

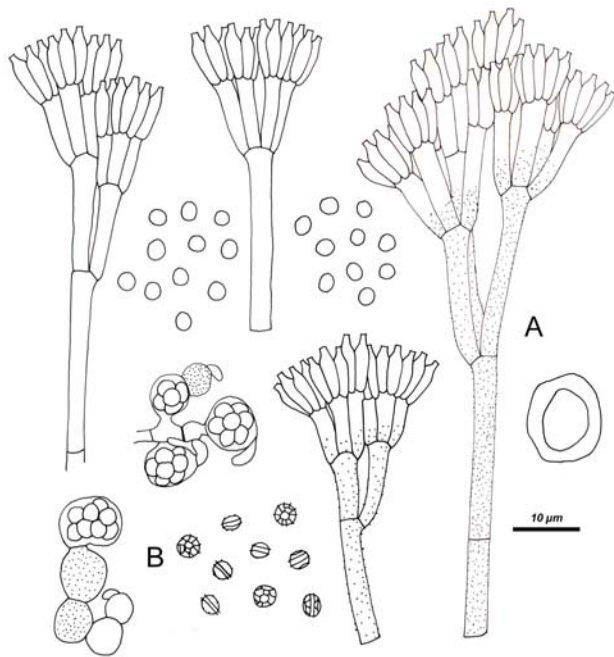


Fig. 19. Conidiophores and conidia of (A) *P. gladioli* and (B) *P. sinaicum*

Series diagnosis: Conidiophores are mononematous, occasionally slightly synnematus. Stipes are varying in length, but are typically long. They are bearing terminal, slender one-two-three-stage-branched penicilli, but with the lower branch often somewhat divergent, and stipes often rough walled. Metulae in verticils of 2-5; one to two, usually single, lower branches, each one with 2-4 apical metulae. Phialides consisting of a cylindrical base and a relatively short, narrowed neck. In *P. gladioli* conidia globose to subglobose (occasionally at first ellipsoidal), with walls smooth, adhering in parallel or tangled chains, sometimes forming ill-defined columns. Sclerotia

often present. There are no teleomorphs known, but *E. crustaceum* was regarded as the teleomorph of *P. gladioli* by Pitt (1979). Even though this pair of species is not representing the same species, they surely show a series of morphological similarities.

P. gladioli shows some affinities with the series *Corymbifera*. Both series are distinguished by the structure of their cultures. Species of the series *Corymbifera* are characterized by well-defined synnemata, whereas in *P. gladioli*, the conidiophores are usually mononematous, with only a few small fascicles occasionally present. Moreover the sclerotia which are typically present in *P. gladioli* are lacking in the *Corymbifera*. In both series the majority of species can cause a rot in below ground roots, bulbs, or onions.

Species of the series *Gladioli* show many affinities with those of the other series of the subgenus *Penicillium*, though especially with the series *Viridicata*. All of them agree in the structure of their conidiophores. The *Gladioli* are mainly distinguished from the other species of the present section by their hard, well-developed sclerotia and poor sporulation.

Section *Digitatum* Frisvad & Samson, sect. nov.

= Series *Digitata* Raper & Thom ex Stolk & Samson, Adv. Pen. Asp. Syst.: 183, 1985 = Series *P. digitatum* Raper & Thom, Man. Penicillia: 385, 1949 (nom. inval., arts 21,36)

Sectio generis *Penicillium* subgeneris *Penicillium*, penicillis biverticillatis vel raro terverticillatis, stipitibus levibus, metulis phialidibusque magnis, conidiis olivaceis, magnis, ellipsoideis vel cylindricis; coloniae in omnibus substratis velutinae; creatinum, nitritum et nitratum velut substratum nitrogeni parce assimilantur, in medio creatinum et sucrosium continente acidum haud formatur; 30°C et supra non crescentes neque 5% NaCl addito; fructus citricos putrescens.

Typus *P. digitatum*.

P. digitatum (Pers.:Fr.) Sacc., Fung. Ital.: 894, 1881.

= *Monilia digitata* Pers. ex Fr., Syst. Mycol. 3: 411, 1832.

= *Monilia digitata* Pers., Syn. Meth. Fung.: 693, 1801.

= *Aspergillus albus tenuissimus, graminis dactyloidis facie, seminibus rotundis* Mich., Nova Pl. Gen.: 213, 1729.

= *Mucor caespitosus* L., Sp. Pl. 2: 1186, 1753.

= *Penicillium olivaceum* Wehmer, Beitr. Kennt. Einh. Pilze 2: 73, 1895.

= *P. olivaceum* Sopp, Skr. Vidensk. Selsk. Christiana 11: 176, 1912.

= *P. olivaceum* var. *norvegicum* Sopp, Skr. Vidensk. Selsk. Christiana 11: 177, 1912.

= *P. olivaceum* var. *italicum* Sopp, Skr. Vidensk. Selsk. Christiana 11: 179, 1912.

= *P. digitatoides* Peyronel, Germi Atmosferici Fung. Micel.: 22, 1913.

= *P. lanosgrisellum* Biourge, Cellule 33: 196, 1923.

= *P. terraconense* Ramírez & Martínez, Mycopathologia 72: 187, 1980.

Lectotype: icon in Saccardo, Fung. Ital.: tab. 894 Jul. 1881, Epitype proposed here: CBS 112082.

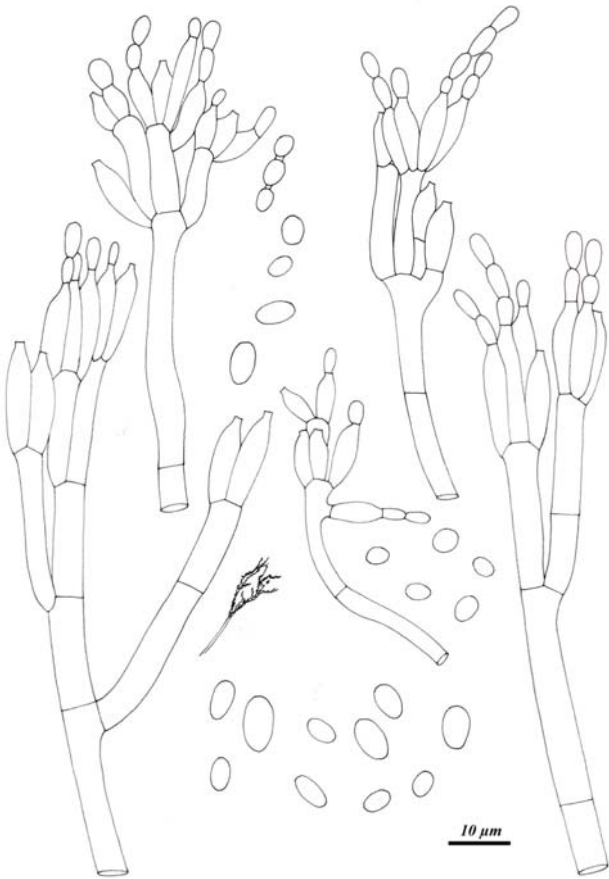


Fig. 20. Conidiophores and conidia of *P. digitatum*

This series comprises only the very distinct species *P. digitatum*. The olive coloured conidia and large irregular micromorphological structures and cylindrical phialides and conidia are unique in *Penicillium*. No relatives are known although it shows some resemblance to the anamorph structures of *Penicillioopsis* and its placement in subgenus *Penicillium* has been questioned (Stolk and Samson, 1985). There are no extrolites in common between *P. digitatum* and the two members of *Italica*.

Of the synonyms of *P. digitatum*, only *P. terraconense* was available as an ex type culture (CBS 177.81). This was a typical *P. digitatum*.

Section *Viridicata* Frisvad & Samson, sect. nov.

Sectio generis *Penicillium* subgeneris *Penicillium*, penicillis terverticillatis, stipitibus levibus vel plerumque asperulatis vel rugosis, conidiis globosis vel subglobosis; coloniae 5% NaCl addito plerumque stimulantur, 37°C haud crescentes, granulares vel modice fasciculatae; species praecipue in cerealibus, bulbis horticolis, *Allio cepa*, carne, nucibus mel productis e lacte derivatis inventae; patulinum, griseofulvinum vel deoxybrevianamidum E

haud producta, sed una vel complures substantiarum sequentium: verrucolonum, acidum penicillicum, xanthomegninum, rugulovasinum, acidum cyclopiazonicum, viridicatina, territrema.

Typus *P. viridicatum*.

Series *Viridicata* Raper & Thom ex Pitt, Gen. Penicil.: 334, 1979

= Series *P. viridicatum* Raper & Thom, Man. Penicillia: 481, 1949 (nom. inval., arts 21,36)

= Series *P. cyclopium* Raper & Thom, Man. Penicillia: 490, 1949 (nom. inval., arts 21,36)

= Series *P. ochraceum* Raper & Thom, Man. Penicillia: 475, 1949 (nom. inval., arts 21,36)

= *Ochracea* Fassatiová, Acta Univ. Carol. Biol. 12: 324, 1977

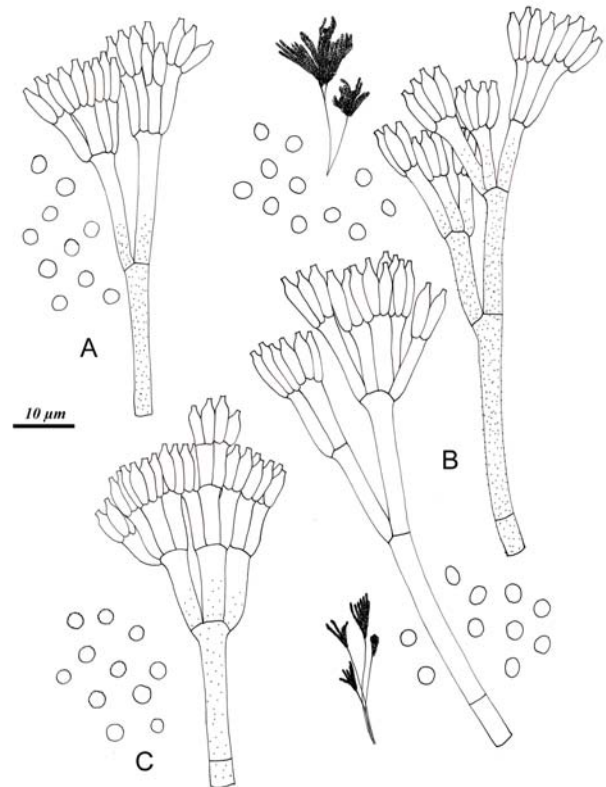


Fig. 21. Conidiophores and conidia of (A) *P. aurantiogriseum*, (B) *P. melanoconidium* and (C) *P. viridicatum*

Accepted species:

P. aurantiogriseum Dierckx, Ann. Soc. Scient. Brux. 25: 88, 1901

= *P. aurantiogriseum* var. *poznaniense* K.M. Zalesky, Bull. Int. Acad. Pol. Sci. Lett., Sér. B 1927: 444, 1927. Neotype: IMI 195050

P. cyclopium Westling, Ark. Bot. 11: 90, 1911.

= ?*P. aurantiocandidum* Dierckx, Ann. Soc. Scient. Brux. 25: 88, 1901.

= ?*P. puberulum* Bain., Bull. Trimest. Soc. Mycol. Fr. 23: 16, 1907.

= *P. porraceum* Biourge, Cellule 33: 188, 1923.

= *P. aurantiovirens* Biourge, Cellule 33: 119, 1923.

= ?*P. janthogenum* Biourge, Cellule 33: 143, 1923.

= *P. brunneoviolaceum* Biourge, Cellule 33: 145, 1923.

= *P. martensii* Biourge, Cellule 33: 152, 1923.

- = *P. aurantio-albidum* Biourge, Cellule 33: 197, 1923.
- = *P. johanniolii* K.M. Zalesky, Bull. Int. Acad. Pol. Sci. Lett., Sér. B 1927: 453, 1927.
- = *P. cyclopium* var. *aurantiovirens* (Biourge) Fassatióvá, Acta Univ. Carol. Biol. 12:326, 1977.
- = *P. cordubense* Ramírez & Martínez, Mycopathologia 74: 164, 1981
- = *P. viridicyclopium* Abe, J. gen. Appl. Microbiol. 2: 107, 1956.

Neotype: IMI 089372

***P. freii* Frisvad & Samson, sp. nov.**

A *Penicillio aurantiogriseo* coloniis crustosis et inertia 30°C crescendi distinguitur; xanthomegninum, viomelleinum, vioxanthinum, cyclopeptinum, dehydrocyclopeptinum, cyclopeninum, cyclophenolum, viridicatolum, 3-methoxyviridicatinum formantur, neque auranthinum, anacinum, acidum terrestricum.

Typus: IMI 285513

***P. melanoconidium* (Frisvad) Frisvad & Samson, comb. nov.**

Basionym: *P. aurantiogriseum* var. *melanoconidium* Frisvad, Mycologia 81:849, 1989.

Holotype: IMI 321503

***P. neoechinulatum* (Frisvad, Filt. & Wicklow) Frisvad & Samson, comb. nov.**

Basionym: *P. aurantiogriseum* var. *neoechinulatum* Frisvad, Filt. & Wicklow, Can. J. Bot. 65: 767, 1987.

Holotype: IMI 296937

***P. polonicum* K. Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B 1927: 445, 1927.**

= *P. aurantiogriseum* var. *polonicum* (K.M. Zalesky) Frisvad, Mycologia 81: 850.

= *P. carneolutescens* G. Smith, Trans. Br. Mycol. Soc. 22: 252, 1939.

Neotype: CBS 222.28

***P. tricolor* Frisvad, Seifert, Samson & Mills, Can. J. Bot. 72: 937, 1997 (check).**

Holotype: DAOM 216240

***P. viridicatum* Westling, Ark. Bot. 11: 88, 1911.**

= *P. olivoviride* Biourge, Cellule 33: 132, 1923.

= *P. blakesleei* K.M. Zalesky, Bull. Int. Acad. Pol. Sci. Lett., Sér. B, 1927: 441, 1927.

= *P. stephaniae* K.M. Zalesky, Bull. Int. Acad. Pol. Sci. Lett., Sér. B, 1927: 451, 1927.

= *P. ochraceum* Bain. apud Thom, Penicillia: 309, 1930.

= *P. verrucosum* var. *ochraceum* (Bain.) Samson, Stolk & Hadlok, Stud. Mycol. (Baarn) 11: 42, 1976.

= *P. olivicolor* Pitt, Gen. Penicil.: 368, 1979.

= *P. aurantiogriseum* var. *viridicatum* (Westling) Frisvad & Filt., Mycologia 81: 850, 1989.

Neotype: IMI 039758ii

All species included in the series *Viridicata* produce similar two-, occasionally three- stage-branched (terverticillate) conidiophores, as well as robust

phialides. The conidia of most species range from ellipsoidal or subglobose to globose, with walls smooth or nearly so (with the exception of the strongly roughened conidia of *P. neoechinulatum*).

Species of the *Viridicata* are very important spoilage and mycotoxin producing fungi in cereals, and consequently a correct identification is very important. Unfortunately, the identification of these species is often problematic, because of the great morphological variation within the species and the presence of morphologically intergrading strains.

Raper & Thom (1949) considerably reduced the number of species by regarding many of them as synonymns. However, they still maintained a great number of closely related species, which they distinguished by minor differences, such as colony texture and colour. In an attempt to simplify species determination in this series, Samson *et al.* (1976) proposed to emend the description of *P. verrucosum*, thus creating a large, variable species, which they divided into six varieties, mainly based on conidial colour. Pitt (1979) used colony diameter at different temperatures and water conditions together with conidial and colony pigmentation as means to separate the species of *Penicillium*. Frisvad (1981, 1983, 1985) introduced the application of physiological criteria, such as the production of extrolites (for details see above) in an attempt to come to a more accurate delimitation of species. In the present paper the species are based on both morphological and physiological characters (especially on profiles of extrolites). Since the morphological differences between most species of the *Viridicata* are very slight, the taxonomical importance of the extrolites is emphasized. Species of the series *Viridicata* show close affinities with the series *Corymbifera*, since the structure of the conidiophores is identical. Both series are distinguished by morphological criteria. In the *Viridicata* the conidiophores range from strictly mononematous to very slightly synnematos, whereas in the *Corymbifera* many conidiophores are aggregated into well-defined synnemata, usually appearing as conspicuous or loosely branched coremia. The *Viridicata* are mainly separated from the *Expansa* by their globose to subglobose conidia and by their weak growth on creatine as sole N-source.

This series has been discussed by Frisvad and Lund (1993) and Lund and Frisvad (1994). It is characterized by the seed and cereal habitats (good amylase production) and production of several extrolites. It is clearly a polythetic series concerning extrolites, as no metabolites are common to all nine species (Svendsen and Frisvad, 1994; Larsen and Frisvad, 1995; Smedsgaard and Frisvad, 1997).

The ex type culture of *P. aurantiogriseum* var. *poznaniense* (NRRL 972) is a typical *P. aurantiogriseum* and not a *P. crustosum* as claimed by Pitt (1979).

Two names, *P. aurantiocandidum* and *P. puberulum* predate *P. cyclopium*. The ex type culture of *P. aurantiocandidum* is very degenerated and deteriorating and its identity is questionable. It is proposed to treat *P. aurantiocandidum* as a *nomen dubium*. *P. puberulum* is based on neotype material consisting of a mixed culture. NRRL 1889 (also NRRL 2040) represents *P. cyclopium*, while NRRL 845 represents *P. commune*. This species is therefore also here regarded as a *nomen dubium*.

Ex type cultures of *P. aurantiovirens* (CBS 294.48), *P. brunneoviolaceum* (CBS 256.29), *P. aurantioalbum* (NRRL 887), *P. johanioli* (NRRL 956), *P. viridicyclopium* (CBS 349.59), *P. martensii* (authentic, CBS 111.43) and *P. cordubense* (CBS 162.81) were inseparable from *P. cyclopium*. The ex type culture of *P. carneolutescens* (CBS 278.39) proved to be a synonym of *P. polonicum*. Ex type cultures of *P. olivoviride* (CBS 264.29), *P. ochraceum* = *P. olivicolor* (CBS 246.32) were found to be synonyms of *P. viridicatum*.

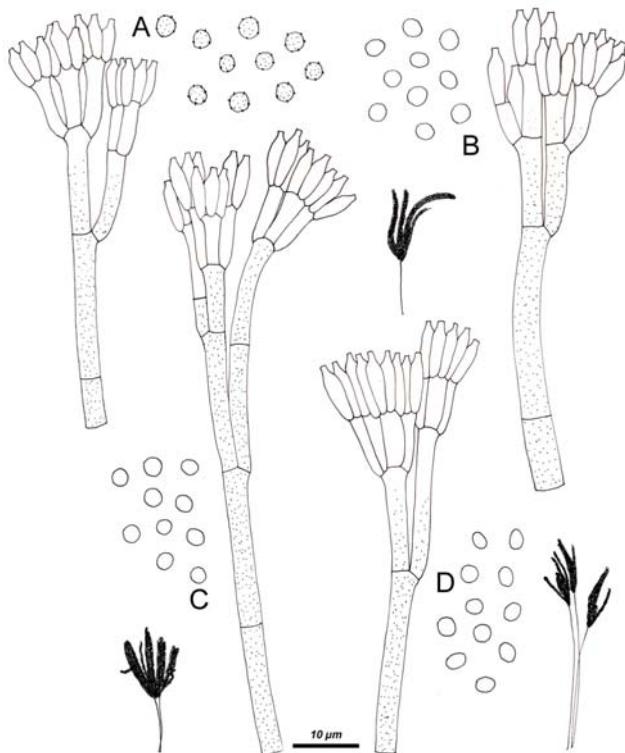


Fig. 22. Conidiophores and conidia of (A) *P. crustosum* (B) *P. neoechinulatum*, (C) *P. aethiopicum* and (D) *P. verrucosum*.

Series *Verrucosa* Frisvad, Int. Mod. Meth. Pen. Asp. Clas., 274, 2000.
Type species: *P. verrucosum*

Accepted species:

P. nordicum Dragoni & Cantoni ex Ramírez, Adv. Pen. Asp. Syst.: 139, 1985.

= *P. nordicum* Dragoni & Cantoni, Ind. Aliment 155: 283, 1979 (nom. inval., art 36).

= *P. mediolanense* Dragoni & Cantoni, Ind. Aliment 155: 281, 1979 (nom. inval., art 36)

Type: ATCC 44219

P. thymicola Frisvad & Samson, **sp. nov.**

A *Penicillio nordico* conidiis asperulatis et reverso luteo-aurantio coloniae in agaris CYA et YES distinguitur; fumiquinazolinum F, daldininum C, alantrypinonum formantur, neque anacina et ochratoxinum A.

Typus: CBS 111225

P. verrucosum Dierckx, Ann. Soc. Scient. Brux. 25: 88, 1901.

= *P. casei* Staub, Zentralbl. Bakt. ParasitKde. Abt. II, 31: 454, 1911.

Neotype: IMI 200310

Micromorphologically these species are similar to series *Viridicata*, *Corymbifera*, *Camembertii* and *Solita*. A number of differences set these species apart from any other member of the subgenus, however. They are all slow growing species that can grow on nitrite as sole N-source, but only weakly on creatine as sole N-source. The production of verrucolone is common to all species in *Verrucosa* (Larsen *et al.*, 2002). Some of the extrolites produced by *P. verrucosum* (the verrucins and a red brown pigment) are autapomorphic and only citrinin is shared with other *Penicillium* species. *P. verrucosum* has been found on cereals from temperate zones, whereas *P. nordicum* has been recovered from salted meat products and cheese from Northern and Southern Europe. *P. thymicola* is a less common species, but has been found on herbs from Southern Europe. These species have often been referred to species in *Viridicata*, but differs in a large number of features from those species, including growth on nitrite-sucrose agar and no acid production on creatine-sucrose agar.

P. casei (CBS 302.48) is a typical *P. verrucosum* in all aspects. *P. mediolanense* (ATCC 44220), an invalid name, is a synonym of *P. nordicum*.

Series *Corymbifera* Frisvad, Int. Mod. Meth. Pen.

Asp. Clas., 275, 2000

Type species: *P. hirsutum*

Accepted species:

P. albocoremium (Frisvad) Frisvad, Int. Mod. Tax. Meth. Pen. Asp. Clas.: 275, 2000.

Basionym: *P. hirsutum* var. *albocoremium* Frisvad, Mycologia 81: 856, 1989.

Holotype: IMI 285511

P. allii Vincent & Pitt, Mycologia 81: 300, 1989.

= *P. hirsutum* var. *allii* (Vincent & Pitt) Frisvad, Mycologia 81: 856, 1989.

Holotype: MU Vincent 114

P. hirsutum Dierckx, Ann. Soc. Scient. Brux. 25: 89, 1901.

= *P. corymbiferum* Westling, Ark. Bot. 11: 92, 1911.

= *P. verrucosum* var. *corymbiferum* (Westling) Samson, Stolk & Hadlok, Stud. Mycol.(Baarn) 11: 36, 1976.

= ? *P. hispalense* Ramírez & Martínez, Mycopathologia 74: 169, 1981.

Neotype: IMI 040213

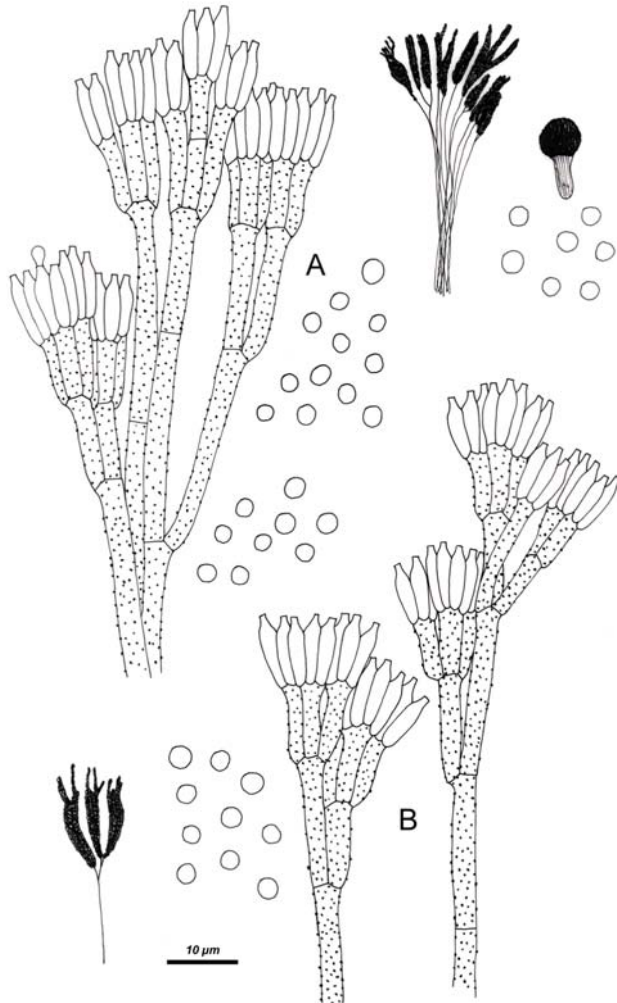


Fig. 23. Conidiophores and conidia of (A) *P. hirsutum* and (B) *P. allii*

P. hordei Stolk, Ant. van Leeuwenhoek 35: 270, 1969.

= *P. hirsutum* var. *hordei* (Stolk) Frisvad, Mycologia 81: 856, 1989.

Holotype: CBS 701.68

P. radicola Overy & Frisvad, Syst. Appl. Microbiol.: 633, 2003.

Holotype: C 60161

P. tulipae Overy & Frisvad, Syst. Appl. Microbiol. 634, 2003.

Holotype: C 60162

P. venetum (Frisvad) Frisvad, Int. Mod. Tax. Meth. Pen. Asp. Clas.: 275, 2000.

= *P. hirsutum* var. *venetum* Frisvad, Mycologia 81: 856, 1989.

Holotype: IMI 321520

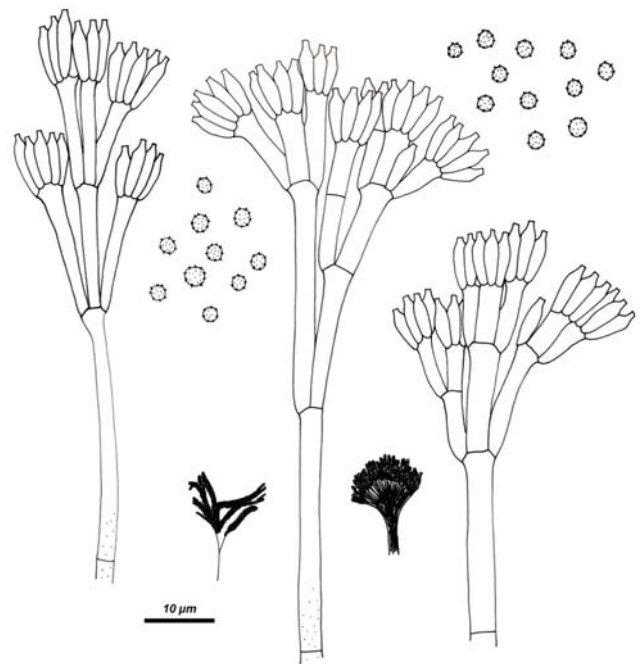


Fig. 24. Conidiophores and conidia of *P. hordei*

Section diagnosis: Conidiophores mononematous to strongly synnematus, usually with most conidiophores aggregated into small fascicles or well-developed coremia, but a variable number of them mononematous. Coremia commonly consisting of a stalk, comprised of the stipes of the conidiophores and an apical feather-like capitulum, comprised of separate, diverging conidiophores. Stipes variable in length, typically very long, with walls conspicuously or finely roughened, (occasionally smooth). Penicilli large, two- to three-stage-branched. Metulae in verticils of 2-6. Branches 1(2) per branching point. All elements of the penicillus appressed, the lower branch occasionally a little divergent. Phialides with a cylindrical base and a short, but distinct, slightly narrowed neck. Conidia globose to slightly subglobose, with walls smooth or roughened, adhering in parallel, occasionally tangled chains, sometimes forming diverging, loose columns. Teleomorph absent. Sclerotia not present.

Frisvad & Filtenborg (1989) recognized five varieties of *P. hirsutum*. It is preferred here to regard them as species because of their marked, morphological differences. Together seven species comprise the new series *Corymbifera*, which is characterized by deep fasciculate to coremiform colonies, conidiophores with walls strongly roughened (less pronounced in *P. hordei*, which produces finely roughened to smooth-walled stipes) globose, smooth-walled conidia (except the finely roughened conidia of *P. hordei*) and by the production of terrestrial acid

(except *P. allii* and *P. albocoremium*) and roquefortine C. The *Corymbifera* differ from the *Gladioli* in the absence of sclerotia, as well as in the pronounced fasciculation. Cultures of the *Viridicata* lack the production of well-developed coremia. The *Corymbifera* and *Claviformia* have the fasciculate to coremiform character of the colonies in common, though the coremia of the *Claviformia* are usually better developed. Both series differ mainly in the shape of the conidia.

These seven distinct fasciculate species are all associated with onions, tap root plants and flower bulbs, except *P. hordei* which is associated with barley and other cereals. *P. hordei* has, however, been found on lilaceous bulbs also. *P. albocoremium sensu lato* have recently been split into three species (Overy and Frisvad, 2003) in agreement with chemotaxonomic studies by Larsen and Frisvad (1995) and Smedsgaard and Frisvad (1997). In the extrolite study of Svendsen and Frisvad (1994) all these species clustered with *P. crustosum*, except *P. hordei*, which clustered with *P. aurantiogriseum*, another cereal-borne species. The seven species in this series seems to most closely related to *Viridicata* and *P. crustosum*.

Series *Solita* Frisvad, Int. Mod. Meth. Pen. Asp. Clas., 279, 2000
Type species: *P. solitum*

Accepted species:

P. discolor Frisvad & Samson, Ant. van Leeuwenhoek, 72: 120, 1997.
Holotype: IMI 285513

P. echinulatum Fassatiová, Acta Univ. Carol. Biol. 12: 326, 1977.
= *P. cyclopium* var. *echinulatum* Raper & Thom, Man. Penicil.: 497, 1949.
= *P. palitans* var. *echinoconidium* Abe, J. Gen. Appl. Microbiol. 2: 111, 1956.
Holotype: PRM 778523

P. solitum Westling, Ark. Bot. 11: 65: 1911.
= *P. majusculum* Westling, Ark. Bot. 11: 60, 1911.
= *P. conditaneum* Westling, Ark. Bot. 11: 63, 1911.
= *P. paecilomyceforme* Szilvinyi, Zentralbl. Bakt. ParasitKde., Abt. II, 103: 156, 1941.
= *P. casei* Staub var. *compactum* Abe, J. Gen. Appl. Microbiol. 2: 101, 1956.
= *P. mali* Novobr., Biol. Nauki 10: 105, 1972 (nom. inval., art. 36, 37, 38)
= *P. verrucosum* var. *melanochlorum* Samson, Stolk & Hadlok, Stud. Mycol. (Baarn) 11: 41, 1976.
= *P. mali* Gorlenko & Novobr., Mikol. Fitopatol. 17: 464, 1983 (nom. inval., art. 64)

= *P. melanochlorum* (Samson, Stolk & Hadlok) Frisvad, Adv. Pen. Asp. Syst.: 330, 1985.
Neotype: CBS 424.89

P. cavernicola Frisvad & Samson, **sp. nov.**
= *P. crustosum* var. *spinulosporum* Sasaki (nom. inval., Art. 36)
A *Penicillio echinulato* reverso violaceo-brunneo coloniae in agar CYA distinguitur; asteltoxinum, glyanthrypinum, aurantiaminum, dipodazinum formantur neque cyclopeptinum, dehydrocyclopeptinum, cyclopheninum, cyclophenolum, viridicatinum, viridicatolum.
Typus: CBS 100540

Micromorphologically these species resemble series *Viridicata*. This series contains three closely related species with rough or thick walled dark green conidia and rough walled conidiophore stipes. All species grow well on creatine as sole N-source. They all produce the viridicatin biosynthetic family except *P. cavernicola*. The three species were distinct yet included in the same main cluster in the HPLC analysis based on extrolites reported by Svendsen and Frisvad (1994). In an electrospray mass spectrometric (ES-MS) study of extrolites of the terverticillate *Penicillia*, *P. solitum* clustered with *P. echinulatum* when grown on CYA agar and *P. echinulatum* clustered with *P. discolor* as its nearest neighbour when cultures were grown on YES agar (Smedsgaard and Frisvad, 1997). The reason these species also clustered with several members of *Viridicata* and *P. crustosum* was that the viridicatin biosynthetic family was present in all these species and these dominated the ES-MS profiles. Concerning volatile secondary metabolites the three species were distinct and not very similar (Larsen and Frisvad, 1995).

P. solitum has several synonyms. The ex type cultures of *P. majusculum* (CBS 423.89), *P. paecilomyceforme* (CBS 160.42), *P. mali* (CBS 500.73), *P. casei* var. *compactum* (CBS 427.65) and *P. melanochlorum* (CBS 487.75) were examined and all were typical or deteriorated *P. solitum*.

P. palitans var. *echinoconidium* (CBS 337.59) was examined and is inseparable from *P. echinulatum*.

Series *Camemberti* Raper & Thom ex Pitt, Gen. Penicil.: 358, 1979

= Series *P. camemberti*, Raper & Thom, Man. Penicillia: 421, 1949 (nom. inval., arts 21,36)
= Series *P. commune*, Raper & Thom, Man. Penicillia: 429, 1949 (nom. inval., arts 21,36)
Type species: *P. camemberti*

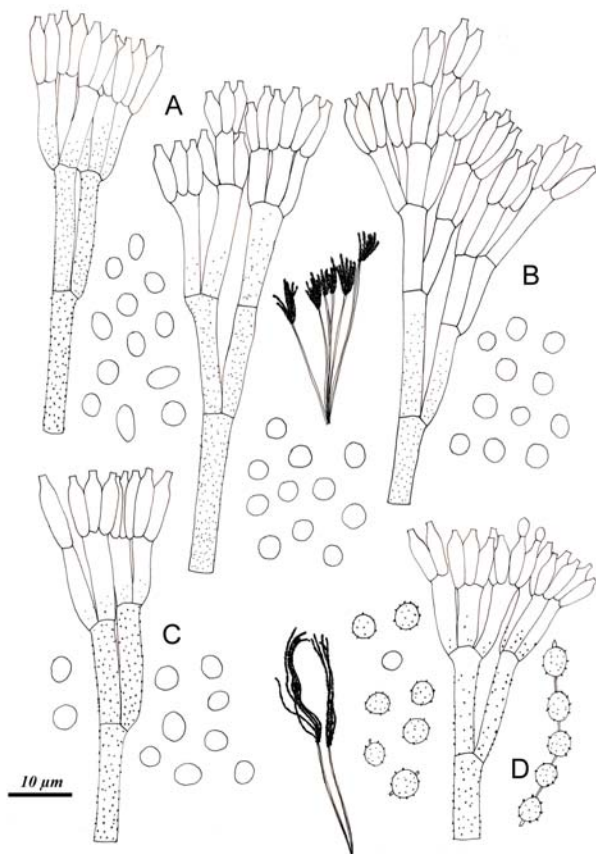


Fig. 25. Conidiophores and conidia of (A) *P. commune*, (B) *P. solitum*, (C) *P. camemberti* and (D) *P. echinulatum*.

Accepted species:

- P. commune*** Thom, Bull. Bur. Anim. Ind. USDA 118: 56, 1910.
 = *P. fuscoglaucum* Biourge, Cellule 33: 128, 1923.
 = *P. flavoglaucum* Biourge, Cellule 33: 130, 1923.
 = *P. lanosoviride* Thom, Penicillia: 314, 1930.
 = *P. ochraceum* Thom var. *macrosporum* Thom, Penicillia: 310, 1930.
 = *P. lanosoviride* Thom, Penicillia: 314, 1930.
 = *P. lanosogriseum* Thom, Penicillia: 327, 1930.
 = *P. psittacinum* Thom, Penicillia: 369, 1930.
 = *P. australicum* Sopp ex van Beyma, Ant. van Leeuwenhoek 10: 53, 1944.
 = *P. cyclopium* var. *album* G. Smith, Trans Brit. Mycol. Soc. 34: 18, 1951.
 = *P. roqueforti* var. *punctatum* Abe, J. Gen. Appl. Microbiol. 2: 99, 1956.
 = *P. caseiperdens* Frank, Beitr. Tax. Gat. Pen.: 91, 1966.
 = *P. verrucosum* var. *album* (G. Smith) Samson, Stolk & Hadlok, Stud. Mycol. (Baarn) 11:35, 1976.
 = *P. album* (G. Smith) Stolk & Samson, Adv. Pen. Asp. Syst.: 185, 1985.
 Neotype: IMI 039812

- P. camemberti*** Thom, Bull. Bur. Anim. Ind. USDA 82: 33, 1906.
 = *P. album* Epstein, Ark. Hyg. Bakt. 45: 360, 1902.

- = *P. epsteinii* Lindau, Rabenh. Krypt.-Fl. 1, Abt. 8: 166, 1904
 = *P. rogeri* Wehmer apud Lafar, Handb. Tech. Mykol. 4: 226, 1906.
 = *P. caseicola* Bain., Bull. Trimest. Soc. Mycol. Fr. 23: 94, 1907.
 = *P. camemberti* var. *rogeri* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 52, 1910.
 = *P. biforme* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 54, 1910.
 = *P. camemberti* Sopp, Skr. Vidensk. Selsk. Christiana 11: 179, 1912.
 = *P. candidum* Roger apud Biourge, Cellule 33: 193, 1923.

Lectotype: IMI 027831

- P. caseifulvum*** Lund, Filt. & Frisvad, J. Food Mycol 1: 97, 1998.
 Holotype: C 24999

- P. palitans*** Westling, Ark. Bot. 11: 83, 1911.
 Neotype: IMI 040215

- P. crustosum*** Thom, Penicillia: 399, 1930.
 = *P. pseudocasei* Abe, J. Gen. Appl. Microbiol. 2: 102, 1956.
 = *P. pseudocasei* Abe ex G. Smith, Trans. Brit. Mycol. Soc. 46: 335, 1963.
 = *P. terrestre* sensu Raper & Thom, Man. Penicil.: 450, 1949.
 = *P. farinosum* Novobranova, Nov. Sist. Niz. Rast. 11: 232, 1974.
 = *P. expansum* var. *crustosum* (Thom) Fassatiová, Acta Univ. Carol. Biol. 12: 329, 1977.
 = *P. solitum* var. *crustosum* (Thom) Bridge, D. Hawksw., Kozak., Onions, R.R.M. Paterson, Sackin & Sneath, J. Gen. Microbiol. 135: 2957, 1989.
 Neotype: IMI 091917

- P. atramentosum*** Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 65, 1910.
 Neotype: IMI 039752

These six species are united by their growth on creatine and nitrite as sole N-source and their association to proteinaceous and lipid-containing foods. Their micromorphology is similar to that of *Viridicata* (see above), except *P. atramentosum*, which has smooth stipes and a more divaricate penicillus structure similar to that of *P. chrysogenum*. Furthermore *P. atramentosum* is the most alkalitolerant of all terverticillate Penicillia. All species are particularly common on cheese, but may also be found on nuts. *P. camemberti* is the domesticated form of *P. commune* and is strictly associated to white mould cheese such as Camembert and Brie. *P. caseifulvum* is only found as a surface contaminant of blue cheeses, and may improve the flavour of these cheeses. *P. commune* and *P. atramentosum* were both described by Thom (1910) during his studies of cheese associated Penicillia and still these species are found as dominant

species on cheese (Lund *et al.*, 1996). Polonelli *et al.* (1997) found that *P. palitans* was close to *P. commune*, but disinct, and this was later confirmed by Lund (1995b). *P. crustosum* is also found on cheese, but is also common on nuts and in soil. Like *P. expansum* and *P. solitum*, *P. crustosum* can produce a rot in apples, albeit less severe than that of the two former species (Frisvad, 1981, Pitt *et al.*, 1991).

Isolates in four of the species produce rugulovarsine A and three of the species produce cyclopiazonic acid.

Ex type cultures of *P. fuscoglaucum* (CBS 261.29), *P. lanosoviride* (NRRL 930), *P. ochraceum* var. *macrosporum* (CBS 247.32), *P. lanosogriseum* (CBS 216.30), *P. psittacinum* (CBS 265.29), *P. australicum* (NRRL 935), *P. cyclopium* var. *album* = *P. verrucosum* var. *album* = *P. album* (CBS 343.51), and *P. roqueforti* var. *punctatum* (CBS 341.59) were all examined and found to be inseparable from *P. commune*.

Ex type cultures of *P. candidum* (NRRL 876), *P. rogeri* (CBS 123.08), *P. caseicola* (CBS 303.48) and *P. bifforme* (CBS 297.48) were found to be inseparable from *P. camemberti*.

Ex type or authentic cultures of *P. terrestre* (authentic, CBS 380.48), *P. pseudocasei* (CBS 340.59), and *P. farinosum* (CBS 499.73) were all typical *P. crustosum*.

ECOLOGY AND DISTRIBUTION OF SPECIES IN *PENICILLIUM* SUBGENUS *PENICILLIUM*

Most species in *Penicillium* subgenus *Penicillium* are associated to the foods and feeds of terrestrial animals or in some cases the dung of these animals (Frisvad *et al.*, 2000). However few *Penicillium* species, if any, are generalists, and they are associated to particular habitats (Frisvad, 1988; Filtenborg *et al.*, 1996). Some of these associations are so strong that they were recognized early on (Westerdijk, 1949), like the association of *P. italicum* and *P. digitatum* to citrus fruits, but most authors have regarded the *Penicillia* as ubiquitous "weed" organisms (Thom, 1930; Raper and Thom, 1949; Pitt, 1979). It is true that all *Penicillia* can grown on laboratory substrates, for example malt extract agar (made from barley) and oat meal agar, but this does not indicate that they are all associated to cereals, and even *P. digitatum* and *P. italicum* grow well on autoclaved cereal based laboratory media and do not require special media based on citrus peels. Actually malt extract and oat meal agar are excellent for inducing sclerotium and synnema production as

compared to chemically defined media or semi-synthetic media such as CYA and YES agar. On the other hand the latter media (containing the minerals, vitamins, amino acids etc. from yeast extract) are good for inducing the production of many extrolites (Frisvad and Filtenborg, 1989). The laboratory media have a strong influence on the phenotype of the *Penicillia*, but data from these substrates does not predict which habitats the fungi are associated to. The collection and examination of isolates used for this study has clearly shown that there are strong associations between the *Penicillium* species and their natural habitats. These associations are probably first of all based on chemical communications via extrolites and extracellular enzymes, but much more research is needed to explain these important association phenomena.

Abiotic factors also play a role, including the combination of temperature, redox potential, pH, pressure, water activity, and atmosphere (Andersen and Frisvad, 2001), but still none of these factors can explain the association of *P. italicum* to citrus fruits, *P. expansum* to pomaceous fruits, *P. commune* to cheeses and *P. aurantiogriseum* to cereals. Processing or treatment with chemicals may of course change the associated mycobiota of foods and feeds. There are examples of changed associations based on more extreme conditions. *P. italicum* and *P. digitatum* are strongly associated to citrus fruits, but if fungicide treatment is applied, a third species, *P. ulaiense*, associated to these non-climateric fruits will dominate (Holmes *et al.*, 1994). *P. expansum* is the dominating *Penicillium* pathogenic to apples, but if fungicides are used, *P. solitum* will dominate (Pitt *et al.*, 1991). The third known example of the influence of fungicides is natamycin treatment that will favour *P. discolor* at the expense of *P. commune*, the otherwise dominating species on cheese (Lund *et al.*, 1995; Frisvad *et al.*, 1997). Members of series *Roqueforti* are a special case, growing very well at low pH, often in conjunction with organic acids, and at high CO₂ content of the atmosphere. This has the consequence that *P. roqueforti*, *P. carneum* and *P. paneum* are the dominating species growing on rye bread, blue cheeses and silage, but the reason for these associations may very well be their co-evolution with lactic acid bacteria, which produce all the metabolic products, lactic acid, CO₂ etc., that members of series *Roqueforti* are easily tolerating. The reason *P. carneum* is more common on dried lactic acid fermented meat products (salami) than *P. roqueforti* may be that *P. carneum* produces patulin, which inhibits the growth of many bacteria.

Table 4. *Penicillium* species and their specific habitats

Typical habitat*	Species
Indoor air	<i>P. brevicompactum</i> , <i>P. chrysogenum</i> , <i>P. commune</i> , <i>P. polonicum</i> , <i>P. expansum</i> , <i>P. olsonii</i> ,
pomaceous fruit	<i>P. expansum</i> , <i>P. crustosum</i> , <i>P. solitum</i>
citrus	<i>P. italicum</i> , <i>P. digitatum</i> , <i>P. ulaiense</i>
nuts	<i>P. discolor</i>
onions	<i>P. radiculicola</i> , <i>P. albocoremium</i> , <i>P. allii</i>
bulbs and roots	<i>P. tulipae</i> , <i>P. hirsutum</i> , <i>P. venetum</i> , <i>P. gladioli</i>
silage	<i>P. paneum</i> , <i>P. carneum</i>
mushrooms	<i>P. brevicompactum</i>
cheese hard	<i>P. commune</i> , <i>P. discolor</i>
cheese soft	<i>P. camemberti</i> , <i>P. roqueforti</i> , <i>P. caseifulvum</i> ,
bread	<i>P. roqueforti</i> , <i>P. paneum</i> , <i>P. carneum</i>
salami & ham	<i>P. nalgiovense</i> , <i>P. nordicum</i>
cereal grains	<i>P. hordei</i> , <i>P. verrucosum</i> , <i>P. cyclopium</i> , <i>P. freii</i> , <i>P. tricolor</i> ,
oak	<i>P. glandicola</i>
dung	<i>P. coprophilum</i> , <i>P. coprobium</i> , <i>P. concentricum</i> , <i>P. vulpinum</i> , <i>P. formosanum</i> , <i>P. clavigerum</i>
soil	<i>P. persicinum</i> ,

* Listed are the typical habitats of the species. For a more detailed description of occurrence see the text.

Strong associations

P. italicum and *P. ulaiense* in series *Italica* and *P. digitatum* in series *Digitata* are strongly associated to citrus fruits. There is no strong evidence they are associated to any other plant products, although they are occasionally reported from soil and plant roots or stems. This may be caused by cross contamination from *P. digitatum* spoiling citrus fruits. When these fruits are spoiled a large number of air-borne conidia are produced. Fungi isolated directly from citrus fruits rots are most probably one of the three species listed above, and the same species are unlikely to thrive on any other substrate.

P. sclerotigenum has only been found in association with yam tubers and yam flour (*Discorea batatas* and *D. cayenensis*). It appears to be strictly associated to this particular habitat.

P. gladioli has only been found on *Gladiolus* bulbs, but has not been reported since 1970. We were unsuccessful to isolate this species in Europe in spite of our extensive efforts. Perhaps new ways of protecting flower bulbs from diseases have eradicated the species.

P. tulipae is primarily associated to *Tulipa*, but it has also been found on other flower bulbs such as *Chrysanthemum* and *Lilium*. It is also occasionally associated to other plant roots. *P. hirsutum* has been found on some of the same bulbs, but appears to be less strictly associated to plant roots, because it has also been found on butter and apples. However cross-contamination from plant roots cannot be excluded. *P. venetum* is most often found on roots of *Iris*, *Hyacinthus* and *Ornithogalum*, but has also been found on *Asparagus*.

P. allii is a very common garlic rotting organism while *P. albocoremium* and *P. radiculicola* are commonly found on other *Allium* spp., especially *Allium cepa*. However the latter two species are also common on other plant roots often used for human food.

P. verrucosum, *P. hordei*, and all members of series *Viridicata* are all typically associated to stored cereal grains. There may be a tendency of *P. viridicatum*, *P. melanoconidium*, *P. aurantiogriseum* and *P. polonicum* to grow on corn and wheat in warmer climates and for *P. cyclopium*, *P. freii*, *P. verrucosum*, *P. tricolor* and *P. hordei* to thrive in colder climates especially on barley and wheat. *P. neoehinulatum* from Series *Viridicata* however, has until now only been found on seeds gathered by kangaroo rats in the Sonoran desert. *P. polonicum*, *P. aurantiogriseum* and *P. viridicatum* may also cross-contaminate dried meat products, such as salami. The contamination source may be wheat flour.

P. glandicola have only been reliably been recorded from oak trees, acorns and cork and appears to be strictly associated to *Quercus* spp. The species name is thus well chosen. Its occasional occurrence in soil and in guts of deer may easily be explained by its association to oak trees.

P. roqueforti, *P. carneum* and *P. paneum* have only been found on substrates in which lactic acid bacteria have grown, or substrates that have the same characteristics. The substrates may have been preserved with organic acids that are quite similar to lactic acid, including sorbic acid, benzoic acid, propionic acid and acetic acid, or they may contain some alcohol and/or they may have high CO₂ or low O₂ content. Examples are rye bread, yoghurt, cheese or silage (Boysen *et al.*, 1996; Lund *et al.*, 1996)

P. camemberti, *P. caseifulvum*, *P. commune*, *P. palitans* and *P. atramentosum* appear to be mostly associated to cheese and other milk products (Lund *et al.*, 1995). *P. commune* and *P. palitans* have also been reported from dried meat products and nuts, but are much less common on such substrates. *P. atramentosum* has been found on Norwegian gamalost and on other cheeses, but is much more prevalent in alkaline soils (Kubatová, 1990). We have found it to be domi-

nating in limestone quarry soils in Denmark together with *P. scabrosum* (Banke and Frisvad, unpublished).

P. nordicum and *P. nalgiovense* are very salt tolerant and are mostly associated to dried or salted meat products, such as salami and dried hams. Both species also occur on cheese, but are less common there (Lund *et al.*, 1995)

P. marinum is probably associated to marine algae, but too few isolates have been found to substantiate this. The two extant isolates are from coastal sands.

P. coprophilum, *P. coprobium*, *P. concentricum*, *P. vulpinum*, *P. formosanum* and *P. clavigerum* all appear to be strongly associated to animal dung. This association is supported by several common features in these fungi, including production of ellipsoidal conidia, synnema, and patulin or griseofulvin in combination with roquefortine C. The same combination of features is also found in series *Urticicolae*, *P. expansum* and *P. sclerotigenum* and it is likely that the dung *Penicillia*, *Urticicolae* and *P. expansum* all share a common dung-borne ancestor.

Strong associations to several different habitats

P. echinulatum and *P. cavernicola* are often found on lipid rich substrates such as butter, margarine and cheese. *P. echinulatum* has also been found on wood shavings and in wet mechanical pulp. *P. cavernicola* has been found in caves with bats. There are too few isolates of these species reported to conclude what their primary habitats might be.

P. discolor has been found on natamycin treated cheeses, but was originally isolated from vegetable roots and weevil-damaged pecans (Frisvad *et al.*, 1997). It has often been isolated from walnuts, black walnuts, chestnuts and pecans, which may be its primary habitat.

Plurivorous species

The following species grow very well at low water activities and at a wide range of temperatures.

P. expansum, *P. solitum* and *P. crustosum* are all known for their rot of pomaceous fruits (Raper and Thom, 1949; Frisvad, 1981; Pitt *et al.*, 1991), but they also occur in other quite different habitats. *P. expansum* and *P. crustosum* have been found repeatedly on nuts and oilseeds, and all three apple rotting organisms have also been found on dried meat. *P. crustosum* has also been found occasionally in corn and rice and on cheese, so this species appear to be more of a generalist among these *Penicillia*. *P. expansum* has been found commonly on wood in Canadian buildings, while *P. crustosum* can be common on cardboard, leather, textiles and wood (K.A. Seifert, personal com.)

P. aethiopicum has been found on several tropical plant products and in tropical soil and no particular group of foods seems to be particularly prone to infection with this fungus.

P. chrysogenum, *P. dipodomyis*, *P. flavigenum*, *P. nalgiovense*, *P. mononematosum* and *P. confertum* are common in dry habitats and may originally have inhabited desert habitats and salty soils. They are able to grow on foods at low water activities. *P. chrysogenum* has been found on dried cereals, salted meat and many other low water activity foods, but is also common in indoor air environments together with *Aspergillus versicolor* (Samson *et al.*, 2004).

P. thymicola has been found on dried herbs and sorghum. *P. griseofulvum* and *P. dipodomyicola* are common on grasses and their seeds including dry barley and wheat. The former species may also be found on pasta and white bread.

P. brevicompactum, *P. bialowiezense* and *P. olsonii* are very common in soil from tropical rain forests and soil in green-houses in other areas of the world. These species have been found on mouldy mushroom, tomatoes, green coffee, in processed foods, and many other substrates. The two former species are also common in temperate forest soil (Zaleski, 1927), maybe because of their growth on basidiocarps.

P. percicinum has only been found in soil, so its primary habitat is unknown.

Abiotic and nutritional factors

All species in *Penicillium* subgenus *Penicillium* are able to grow at 25°C, so they are not psychrophiles according to the most common definitions. Most species are, however, capable of growing at 5°C and some are growing faster at 15 than 25°C. Species not able to grow at 30°C include *P. bialowiezense*, *P. marinum*, *P. formosanum*, *P. ulaiense*, *P. gladioli*, *P. digitatum*, *P. solitum*, *P. cavernicola*, *P. nordicum*, *P. thymicola*, *P. verrucosum*, *P. freii* and *P. tricolor*. Further species growing very poorly at 30°C include *P. brevicompactum*, *P. olsonii*, *P. expansum*, *P. coprobium*, *P. glandicola*, *P. vulpinum*, *P. italicum*, *P. camemberti*, *P. caseifulvum*, *P. commune*, *P. palitans*, *P. echinulatum*, and *P. hirsutum*. Species growing faster at 15°C than 25°C include *P. bialowiezense*, *P. marinum*, *P. thymicola*, *P. verrucosum* and *P. radicola*.

Most species in subgenus *Penicillium* tolerate 5% NaCl very well. Species that grow faster on media with 5% NaCl than without NaCl, include *P. bialowiezense*, *P. brevicompactum*, *P. olsonii*, *P. chrysogenum*, *P. dipodomyis*, *P. flavigenum*, *P. nalgiovense*, *P. confertum*, (*P. mononematosum*), (*P. marinum*), (*P. glandicola*), *P. gladioli*, (*P. commune*), *P. palitans*, *P. discolor*, *P. solitum*, *P. cavernicola*, *P. echinulatum*, *P. nordicum*, *P. thymicola*, *P. verrucosum*, *P. aurantiogriseum*, *P. cyclopium*, *P. freii*, *P. melanoconidium* (*P. neoehinulatum*), *P. polonicum*, *P. viridicatum*, *P. albocoremium*, *P. allii*, *P. hirsutum*, *P. hordei*, *P. radicola*, and *P. venetum*. Series

Roqueforti and *Italica*, *P. clavigerum*, *P. formosanum* and *P. digitatum* are strongly inhibited by 5% NaCl.

Most species can tolerate low pH, but members of series *Roqueforti* can grow in the presence of 1% propionic acid and 0.5% acetic acid. 50 ppm sorbic acid and benzoic acid inhibits most species, but series *Roqueforti* members actually grow faster on such media, maybe using the acids as further carbon sources. The species most strongly inhibited by these fungicidal preservatives are *P. atramentosum* and *P. digitatum*.

Creatine positive species are concentrated in series *Roqueforti*, *Expansa* (except *P. sclerotigenum*), *Claviformia* (except *P. clavigerum* and *P. formosanum*), *Camemberti*, and *Solita*.

Only one species in subgenus *Penicillium* cannot use nitrate as N-source, namely *P. digitatum*.

Mycotoxins produced by *Penicillium* subgenus *Penicillium* (for a more detailed list of all extrolites see Frisvad *et al.*, 2004)

The terverticillate *Penicillia* are well known for their mycotoxin production (Frisvad and Filtenborg, 1983; 1989). Some of the first terverticillate *Penicillia* shown to be toxigenic were *P. cyclopium* and *P. viridicatum* (Purchase, 1974). Unfortunately nearly all these reports were based on misidentified strains. For example *P. cyclopium* was reported to produce penitrem A, but the producing organism was *P. crustosum* (Pitt, 1979b, Frisvad, 1989). Penitrem A was reported to be produced by strains were identified as *P. commune*, *P. lanosocoeruleum*, *P. palitans*, *P. martensii*, *P. meleagrimum*, *P. piceum*, *P. verrucosum* var. *melanochlorum* and *P. verrucosum* var. *cyclopium*, but they all proved to be *P. crustosum* (Pitt, 1979b, Frisvad, 1989). Cyclopiazonic acid, cyclopiamine and cyclopiamide were named after a strain identified as *P. cyclopium*, but that strain proved to be *P. griseofulvum* (Frisvad, 1989). Other strains of *P. cyclopium* (Leistner and Pitt, 1977) were also claimed to be cyclopiazonic acid producers, but the strains proved to be *P. commune* (Frisvad, 1989). Other strains identified as *P. cyclopium* and *P. cyclopium* var. *album* were reported to produce cyclopaldic acid and cyclopolic acid (Birch and Kocor, 1960), but the producing strains were *P. commune* again (Frisvad, 1989). *P. viridicatum*, claimed responsible for producing viridicatumtoxin, was later reidentified to *P. expansum* (de Jesus *et al.*, 1982), but the producer was a *P. aethiopicum* (Frisvad, 1989). Strains identified as *P. viridicatum* (Walbeek *et al.*, 1969; Ciegler *et al.*, 1973) were reported to produce ochratoxin and often also citrinin, but all these strains proved to be *P. verrucosum* or *P. nordicum* (Frisvad and Filtenborg, 1983, Frisvad, 1985; Larsen *et al.*, 2002a). The strains producing citrinin and ochratoxin A were all *P. verrucosum* (Frisvad, 1985, 1989). *P. viridicatum* has also

been claimed to produce viridicatin (Cunningham and Freeman, 1953) and viridicatic acid (Birkinshaw and Samant, 1960); however, the first isolate was *P. solitum* and the second was *P. crustosum* (Frisvad, 1989).

Aflatoxins or sterigmatocystin have not been reliably reported from any *Penicillium* species. The report of aflatoxin production in *Penicillium puberulum* (Hodges *et al.*, 1964) could not be confirmed. The strain, *P. polonicum* ATCC 15683 = NRRL A-12539 = IBT 14609 did not produce any aflatoxin in our experiments.

Ochratoxin A has been reported from many *Penicillia*, but actually it is only produced by *P. verrucosum* and *P. nordicum* (Frisvad, 1985; Land and Hult, 1987; Pitt, 1987; Larsen *et al.*, 2002a). *P. verrucosum* is the species responsible for producing ochratoxin A in cereals, while *P. nordicum* can produce ochratoxin A in meat products and cheese.

The nephrotoxin citrinin has been found in *P. radiculicola*, *P. expansum*, and *P. verrucosum*. It may thus potentially occur in carrots and potatoes (*P. radiculicola*), cereals (*P. verrucosum*) and pomaceous fruits and nuts (*P. expansum*).

Some as yet only partially characterized nephrotoxic glycopeptides have been isolated from *P. polonicum* and *P. aurantiogriseum*, both species common in cereals and to a certain extent in meat products (Yeulet *et al.* 1988, Mantle, 1993; Frisvad, 1995)

The hepatotoxic and nephrotoxic extrolites xanthomegnin, viomellein, and vioxanthin have been recovered from *P. cyclopium*, *P. freii*, *P. melanoconidium*, *P. tricolor* and *P. viridicatum*, (Lund and Frisvad, 1994; Frisvad, 1995). All these species are very common in cereals

Penicillic acid has been found in *P. aurantiogriseum*, *P. aurantiocandidum*, *P. cyclopium*, *P. freii*, *P. melanoconidium*, *P. neoehinulatum*, *P. polonicum*, *P. tricolor* and *P. viridicatum*. It probably increase the nephrotoxicity of ochratoxin A as this has been shown experimentally in pigs (Stoev *et al.*, 2001). All the members of series *Viridicata* can produce penicillic acid and occur in cereals together with *P. verrucosum* and thus ochratoxin A and penicillic acid often co-occur. However, *P. verrucosum* has never been found in warm habitats.

The neurotoxin verrucosidin is produced by *P. aurantiogriseum* and *P. polonicum* and could therefore occur in cereals and possibly meat products.

The neurotoxin roquefortine C is produced by 26 species in subgenus *Penicillium*: *P. albocoremium*, *P. allii*, *P. atramentosum*, *P. carneum*, *P. chrysogenum*, *P. clavigerum*, *P. concentricum*, *P. coprobium*, *P. coprophilum*, *P. crustosum*, *P. expansum*, *P. flavigenum*, *P. glandicola*, *P. griseofulvum*, *P. hirsutum*, *P. hordei*, *P. marinum*, *P. melanoconidium*, *P. paneum*, *P. persicinum*, *P. radiculicola*, *P. roqueforti*, *P. sclerotigenum*, *P. tulipae*, *P. venetum*, and *P.*

vulpinum. It is probably most likely to be produced in cheeses, silage and meat products.

The highly toxic tremorgen penitrem A is produced by *P. carneum*, *P. crustosum*, *P. clavigerum*, *P. glandicola*, *P. melanoconidium*, and *P. radicola*. Of these species, *P. crustosum* is the most important, already implicated in many mycotoxicoses. This species is a very common spoilage organism of cheese, nuts, meat and many other products. *P. carneum* may also be involved in silage intoxications of cattle and it can grow at very acidic or microaerophilic conditions.

The generally toxic patulin has been found in 14 species in subgenus *Penicillium*: *P. carneum*, *P. clavigerum*, *P. concentricum*, *P. coprobium*, *P. dipodomyicola*, *P. expansum*, *P. formosanum*, *P. gladioli*, *P. glandicola*, *P. griseofulvum*, *P. marinum*, *P. paneum*, *P. sclerotigenum*, and *P. vulpinum*. The most probable problems with this mycotoxin may be in applejuice and other juices (producer *P. expansum*) and in very acidic products, such as silage (producers *P. carneum* and *P. paneum*). *P. griseofulvum* may potentially produce patulin in cereals and pasta and *P. sclerotigenum* may potentially produce patulin in yams. All these Patulin producers also produce other mycotoxins, at least in pure culture, and thus may be more toxic than expected based on patulin alone.

The ergot-like rugulovasins have been found in *P. atramentosum* and *P. commune*. These alkaloids may thus be present in cheese samples with growth of these two fungi.

The ergot-like alkaloids fumigaclavine A and B have been found in *P. palitans* and may thus be produced in cheese.

The similar isofumigaclavines are produced by *P. roqueforti* and *P. carneum* and may be a problem in silage and cheese.

The mycotoxin cyclopiazonic acid is produced by *P. camemberti*, *P. clavigerum*, *P. commune*, *P. griseofulvum*, and *P. palitans*. Production in cheese by *P. camemberti*, *P. commune* and *P. palitans* is not unlikely, whereas *P. griseofulvum* may produce it in cereals and pasta.

The mycotoxin botryodiplodin has been found in *P. brevicompactum* and in *P. paneum*. The frequency of producing isolates in each species and the significance of this mycotoxin is unknown.

The chaetoglobosins have been reported as mycotoxins (Cole and Cox, 1981) and are among the major extrolites of *P. expansum* and *P. discolor*.

The cytotoxic communesin B is produced by *P. marinum* and *P. expansum*. Its significance as a mycotoxin is also still unknown.

PR-toxin has been found in *P. roqueforti* and *P. chrysogenum*. Despite several reports of PR-toxin production by *P. chrysogenum* (Frisvad and Filtenborg, 1983; Hohn *et al.*, 1991; Dai *et al.*, 1993; Möller *et al.*, 1997), this has been difficult to reproduce as it

appears that the production of this toxin is strongly influenced by the type of yeast extract used in the media. PR-toxin has been found naturally occurring in maize causing mycotoxicosis (Vesely *et al.*, 1981).

The tripeptide mycotoxin viridic acid has been found in *P. viridicatum* (Holzapfel *et al.*, 1986) and *P. nordicum* (Larsen *et al.*, 2002b) and may be a problem in cereals and meat products. Viridicatumtoxin is produced by *P. aethiopicum*, *P. clavigerum* and by *P. brasilianum* in subgenus *Furcatum* (Frisvad and Filtenborg, 1990b).

The strongly acidic cardiotoxin terrestric acid is produced by *P. aurantiogriseum*, *P. crustosum*, *P. hirsutum*, *P. hordei*, *P. radicola*, *P. tricolor*, *P. tulipae*, and *P. venetum*. The significance of this metabolite is unknown.

The tryptoquialanins are chemically similar to the toxic tryptoquivalins (Cole and Cox, 1981). They are produced by *P. digitatum* and *P. aethiopicum* (Ariza *et al.*, 2002), but their potential natural occurrence in citrus fruits or tropical cereals, respectively, is unknown.

The tremorgenic territremes are produced by *P. echinulatum* and *P. cavernicola* (Smedsgaard *et al.*, in preparation). These species, especially the first, have been recovered from butter, margarine, liver pate, cheese and similar products.

Pharmaceuticals produced by *Penicillium* subgenus *Penicillium*

Interest in extrolites from species included in *Penicillium* subgenus *Penicillium* started early with the isolation of the antibiotic mycophenolic acid by Gosio (1889). This compound was later shown to be a potent pharmaceutical used as an immunosuppressing agent in organ transplantations (Bentley, 2000). Of species in subgenus *Penicillium*, mycophenolic acid is produced by *P. bialowiezense*, *P. brevicompactum*, *P. carneum* and *P. roqueforti*.

Of particular interest is penicillin, which was first discovered in a strain firstly identified as *P. rubrum* by Fleming (1928) and later reidentified as *P. notatum* (a synonym of *P. chrysogenum*) and later again isolated from a strain of *P. chrysogenum* from a canteloupe. Subsequently later research has shown that all strains examined of *P. chrysogenum* produce penicillin (Andersen and Frisvad, 1994) and furthermore that the other closely related species in series *Chrysogena* also produce penicillin, i.e. *P. dipodomyis*, *P. nalgiovense* and *P. flavigenum* (Frisvad *et al.*, 1987; Banke *et al.*, 1997). Another penicillin producer in subgenus *Penicillium* is *P. griseofulvum* (Laich *et al.*, 2002). The latter authors also found parts of the penicillin genes in *P. nordicum* (incorrectly identified as *P. verrucosum*).

The important anticholerolemic agent compactin was first reported from a strain of *P. brevicompactum* (Brown *et al.*, 1986), albeit via its antifungal activity.

Later other producers of compactin were reported as *P. citrinum* (Endo *et al.*, 1976; Lam *et al.*, 1981), *P. cyclopium* (Doss *et al.*, 1986; Basaraa *et al.*, 1998), *Paecilomyces viridis* (Murakawa *et al.*, 1994) and *P. aurantiogriseum* (Wagschal *et al.*, 1996). All these reports were based on misidentified strains, and the correct name of producer of compactin was shown to be *P. solitum* (Frisvad and Filtenborg, 1989). Further producers in subgenus *Penicillium* include *P. hirsutum* (Frisvad and Filtenborg, 1989).

The benzodiazepine-like alkaloids cyclopeptin, dehydrocyclopeptin, cyclophenin and cyclophenol were named after *P. cyclopium*, but the original was later re-identified as *P. solitum* (Frisvad and Filtenborg, 1989). *P. cyclopium* actually produces these alkaloids consistently (Lund and Frisvad, 1995). 3-methoxyviridicatin is of special interest, because it is active against HIV (Heguy *et al.*, 1998). 3-methoxyviridicatin is produced by *P. albocoremium*, *P. allii*, *P. aurantiocandidum*, *P. commune*, *P. crustosum*, *P. cyclopium*, *P. discolor*, *P. echinulatum*, *P. freii*, *P. hirsutum*, *P. neoehinulatum*, *P. palitans*, *P.*

polonicum, *P. radicicola*, *P. solitum*, *P. venetum* and *P. vulpinum*. Much more viridicatin than 3-methoxyviridicatin is produced by the creatine positive species *P. commune*, *P. crustosum*, *P. discolor*, *P. echinulatum*, *P. palitans*, *P. solitum* and *P. vulpinum*, however.

The antifungal pharmaceutical griseofulvin is produced by *P. aethiopicum*, *P. coprophilum*, *P. dipodomycicola*, *P. griseofulvum*, *P. persicinum*, and *P. sclerotigenum*.

The anticholerolemic agents, the pyripyropens, are produced by *P. coprobium* and *P. concentricum*.

The acetylcholinesterase inhibiting arisugacins are produced by the territreum producing species *P. echinulatum* and *P. cavernicola* (Smedsgaard, Svendsen and Frisvad, in preparation).

Many other extrolites have been found in the terverticillate *Penicillia* as lead compounds, and time will show if any of these have a future as important pharmaceuticals. Many of these are listed in the synoptic key below.

List of accepted species in subgenus *Penicillium*

1. *P. aethiopicum* Frisvad, Mycologia **81**: 848, 1989
2. *P. albocoremium* (Frisvad) Frisvad, Int. Mod. Tax. Meth. Pen. Asp. Clas.: 275, 2000
3. *P. allii* Vincent and Pitt, Mycologia **81**: 300, 1989
4. *P. atramentosum* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. **118**: 65, 1910
5. *P. aurantiogriseum* Dierckx, Ann. Soc. Scient. Brux. **25**: 88, 1901
6. *P. bialowiezense* K. Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B **1927**: 462, 1927
7. *P. brevicompactum* Dierckx, Ann. Soc. Scient. Brux. **25**: 88, 1901
8. *P. camemberti* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. **82**: 33, 1906
9. *P. carneum* (Frisvad) Frisvad, Microbiology, UK, **142**: 546, 1996
10. *P. caseifulvum* Lund, Filt. & Frisvad, J. Food Mycol. **1**: 97, 1998
11. *P. cavernicola* Frisvad & Samson sp. nov.
12. *P. chrysogenum* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. **118**: 58, 1910
13. *P. clavigerum* Demelius, Verh. Zool.-Bot. Ges. Wien **72**: 74, 1922
14. *P. commune* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. **118**: 56, 1910
15. *P. concentricum* Samson, Stolk and Hadlok, Stud. Mycol. (Baarn) **11**: 17, 1976.
16. *P. confertum* (Frisvad, Filt. & Wicklow) Frisvad, Mycologia **81**: 852, 1989.
17. *P. coprobium* Frisvad, Mycologia **81**: 853, 1989.
18. *P. coprophilum* (Berk. & Curt.) Seifert & Samson, Adv. Pen. Asp. Syst.: 145, 1985.
19. *P. crustosum* Thom, Penicillia: 399, 1930.
20. *P. cyclopium* Westling, Ark. Bot. **11**: 90, 1911.
21. *P. digitatum* (Pers.:Fr.) Sacc., Fung. Ital.: 894, 1881.
22. *P. dipodomyicola* (Frisvad, Filt. & Wicklow) Frisvad, Int. Mod. Tax. Meth. Pen. Asp. Clas.: 275, 2000.
23. *P. dipodomyis* (Frisvad, Filt. & Wicklow) Banke, Frisvad and S. Rosendahl, Int. Mod. Tax. Meth. Pen. Asp. Clas.: 271, 2000.
24. *P. discolor* Frisvad & Samson, Ant. van Leeuwenhoek **72**: 120, 1997.
25. *P. echinulatum* Fassatiová, Acta Univ. Carol. Biol. **12**: 326, 1977.
26. *P. expansum* Link, Obs. Mycol. **1**: 16, 1809
27. *P. flavigenum* Frisvad & Samson, Mycol. Res. **101**: 620, 1997
28. *P. formosanum* Hsieh, Su & Tzean, Trans. Mycol. Soc. R.O.C. **2**: 159, 1987
29. *P. freii* Frisvad & Samson, sp. nov.
30. *P. gladioli* McCulloch & Thom, Science, N.Y. **67**: 217, 1928
31. *P. glandicola* (Oud.) Seifert & Samson, Adv. Pen. Asp. Syst.: 147, 1985.
32. *P. griseofulvum* Dierckx, Ann. Soc. Scient. Brux. **25**: 88, 1901
33. *P. hirsutum* Dierckx, Ann. Soc. Scient. Brux. **25**: 89, 1901
34. *P. hordei* Stolk, Ant. van Leeuwenhoek **35**: 270, 1969
35. *P. italicum* Wehmer, Hedwigia **33**: 211, 1894
36. *P. marinum* Frisvad & Samson sp. nov.
37. *P. melanoconidium* (Frisvad) Frisvad & Samson, comb. nov.
38. *P. mononematosum* (Frisvad, Filt. & Wicklow) Frisvad, Mycologia **81**: 857, 1989
39. *P. nalgiovense* Laxa, Zentbl. Bakt. ParasitKde., Abt. II **86**: 162, 1932
40. *P. neoechinulatum* (Frisvad, Filt. & Wicklow) Frisvad & Samson, comb. nov.
41. *P. nordicum* Dragoni & Cantoni ex Ramírez, Adv. Pen. Asp. Syst.: 139, 1985
42. *P. olsonii* Bain. & Sartory, Ann. Mycol. **10**: 398, 1912
43. *P. palitans* Westling, Ark. Bot. **11**: 83, 1911
44. *P. paneum* Frisvad, Microbiology, UK **142**: 546, 1996
45. *P. persicinum* L. Wang, H. Zhou, Frisvad & Samson, Ant. van Leeuwenhoek **86**: 177, 2004
46. *P. polonicum* K. Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B **1927**: 445, 1927
47. *P. radicola* Overy and Frisvad, Syst. Appl. Microbiol. **26**: 633, 2003
48. *P. roqueforti* Thom, Bull. Bur. Anim. Ind. US Dept. Agric. **82**: 35, 1906
49. *P. sclerotigenum* Yamamoto, Scient. Rep. Hyogo Univ. Agric., Agric. Biol. Ser. 2, **1**: 69, 1955
50. *P. solitum* Westling, Ark. Bot. **11**: 65, 1911
51. *P. thymicola* Frisvad & Samson sp. nov.
52. *P. tricolor* Frisvad, Seifert, Samson & Mills, Can. J. Bot. **72**: 937, 1994
53. *P. tulipae* Overy & Frisvad, Syst. Appl. Microbiol. **26**: 634, 2003
54. *P. ulaiense* Hsieh, Su & Tzean, Trans. Mycol. Soc. R.O.C. **2**: 161, 1987
55. *P. venetum* (Frisvad) Frisvad, Int. Mod. Tax. Meth. Pen. Asp. Clas.: 275, 2000
56. *P. verrucosum* Dierckx, Ann. Soc. Scient. Brux. **25**: 88, 1901
57. *P. viridicatum* Westling, Ark. Bot. **11**: 88, 1911
58. *P. vulpinum* (Cooke & Massee) Seifert & Samson, Adv. Pen. Asp. Syst.: 144, 198

Keys to species (see also <http://www.cbs.knaw.nl/penicillium.htm>)

The identification of the 58 taxa of subgenus *Penicillium* is difficult, because the micromorphology of the strains is very similar. In addition of the structures and branching of the conidiophores, the shape and ornamentation of conidia it is often helpful to use colony characters including growth rate, colour of the conidia and reverse. In a few species a diffusing pigment is characteristic. For most species the isolates should be inoculated on four media: CYA, MEA, CREA and YES (for formulations see page 3-4) at 25°C (37°C on CYA).

Because of the difficulty to use morphological characters a dichotomous key is here only provided to the Sections and series, while the characters of the taxa in the individual series are described in the box keys.

A more electronic key is provided at <http://www.cbs.knaw.nl/penicillium.htm>. The following data sheet can be used to collect colony and morphological characters of the isolates.

Data sheet for identification of taxa of subgenus *Penicillium*.

CYA – Incubation 7 days at 25°C	Colony diameter in mm:
Colour obverse*	blue green / dark green / dull green / grey green / olive green / yellow; pure green / white
Colour reverse*	pale / yellow / orange / red / beige-light brown / brown / dark brown; blackish green
Ehrlich reaction	no reaction / violet / red-brown / yellow
CYA – Incubation 7 days at 30°C	Colony diameter in mm:
MEA – Incubation 7 days at 25°C	Colony diameter in mm:
Colony texture	velvety / granulate / weak fasciculate / fasciculate / weakly floccose / floccose
Colour colony obverse*	blue green / dark green / dull green / grey green / olive green / yellow; pure green / white
Prepare microscopic slide	One slide at the colony edge (for conidiophore) and one in the colony (for conidia)
CREA – Incubation 7–10 (14) days at 25°C	Colony diameter in mm:
Degree of growth	No or very weak / Weak to moderate / Moderate / Moderate to good / good
Acid production	None / Weak / Moderate / Good / High
Base production: after 7 days	Absent / Present
after 10-14 days	Absent / Present
YES – Incubation 7 days at 25°C	Colony diameter in mm:
Degree of sporulation	None / Weak / Moderate / Strong
Colour colony reverse*	pale / yellow / orange / red / beige-light brown / brown / dark brown; blackish green
Microscopic characters	
Conidia Length/width in µmµm
Ornamentation	Smooth / fine roughened / rough-walled / echinulate
Phialide length in µmµm
Metulae length in µmµm
Stipe width in µmµm
Ornamentation	Smooth / finely roughened / rough-walled / warted
Conidiophore adpressedness	Strongly adpressed / adpressed / neither adpressed nor divergent / divergent / strongly divergent
Conidiophore branching pattern*	Monoverticillate / biverticillate / terverticillate / quaterverticillate

* More than one character is possible to enter into the database

Synoptic key to series

1. *Aethiopica* Frisvad & Samson
2. *Camemberti* Raper & Thom ex Pitt
3. *Chrysogena* Raper & Thom ex Stolk & Samson
4. *Claviformia* Raper & Thom ex Stolk, Samson & Frisvad
5. *Corymbifera* Frisvad
6. *Digitata* Raper & Thom ex Stolk & Samson
7. *Expansa* Raper & Thom ex Fassatova
8. *Gladioli* Raper & Thom ex Stolk & Samson
9. *Italica* Raper & Thom ex Pitt
10. *Mononematosa* Frisvad
11. *Olsonii* Pitt
12. *Persicina* Frisvad & Samson
13. *Roqueforti* Raper & Thom ex Frisvad
14. *Solita* Frisvad
15. *Urticicolae* Fassatova
16. *Verrucosa* Frisvad
17. *Viridicata* Raper & Thom ex Pitt

Conidia cylindrical and ellipsoidal: 6, 9, 12

Conidia ellipsoidal: 1, ((2)), ((3)), 4, 6, 7 (except *P. marinum*), 9, 11, 12, 15

Conidia globose to subglobose: 2, 3, 5, (*P. marinum* in 7), 8, 10, 13, 14, 16, 17

Conidia rough-walled: *P. echinulatum*, *P. cavernicola* & *P. discolor* (in 14), *P. neoechinulatum* (in 17)

Conidia finely or clearly rough-walled: *P. hordei* (in 5), 11, 14, *P. thymicola* (in 16), *P. viricatum* & *P. neochinulatum* (in 17)

Conidia more than 6 µm: 6

Conidia olive coloured: 6

Conidia dark green: *P. palitans* & *P. atramentosum* (in 2), *P. dipodomyis* (in 3), 13, 14, *P. melanoconidium* (in 17)

Weak conidium production: *P. camemberti* and *P. caseifulvum* (in 2), 8

Stipes more than 500 µm long: 11

Stipes clearly rough walled: (1), (2), *P. glandicola* (in 4), 5, (8), 13, 14, 16, (17)

Stipes finely or strongly rough-walled: (1), (2), (*P. dipodomyis* (in 3)), (4), 5, ((*P. expansum* in 7)), 8, 13, 14, 16, (17)

Stipes smooth-walled: (1), *P. atramentosum* and *P. camemberti* (in 2), 3, 4 (except *P. glandicola*), 6, 7, (8), 9, 10, 11, 12, ((14, only stipes in agar)), 15, (17)

Phialides less than 6 µm: 15

Multiramulate: (11)

Biramulate: (3)

Divaricate rami: *P. atramentosum* (in 2), 3, 6, *P. marinum* (in 7), (4), (8), 10

Sinous stipes: (4), 10

Penicillus as long as it is broad: 11

Sclerotia: ((*P. coprobium* in 4)), *P. sclerotigenum* (in 7), 8, ((*P. olsonii* (in 11))), ((*P. roqueforti* (in 13)))

Acicular synnemata: *P. clavigerum* (in 4)

Capitulate synnemata: 4, (7), 9

Extracellular red colour on CYA: 12

Box keys to the individual series:**Section *Coronata* - Series *Olsonii***

Extrolites	<i>P. brevicompactum</i>	<i>P. olsonii</i>	<i>P. bialowiezense</i>
Mycophenolic acid	+	-	+
Brevianamide A	+	-	-
Raistrick phenols	+	-	+
Pebrolides	+	-	-
Silvatin derivatives	+	+?	-?
Asperphenamate	+	+	+
Botryodiploidin	+/-	-	-?
Breviones	-	+	+/-
Verrucolone	-	+	-
2-(4-hydroxyphenyl)-2-oxo acetalde- hyde oxime	-	+	-
Phenotypic characters			
Ehrlich reaction	-	-	w
Growth rate on CYA	8-30 mm	26-40 mm	11-25 mm
Growth rate on YES	14-36 mm	35-56 mm	18-30 mm
Reverse colour, YES	Cream to beige	Yellow, yellow/cream	Cream to beige
Conidium colour	Dull green	Greyish green	Dull green
Sclerotia	-	-/+	-
Multiramulate	-/(+)	+	-
Plants, vegetables etc.	+	+	+
Ornamentals, green houses	-/+	+	-
Mushrooms	+	-	-
Fruits	(+)	-	+

Section *Roqueforti* - Series *Roqueforti*

Extrolites	<i>P. roqueforti</i>	<i>P. carneum</i>	<i>P. paneum</i>
Roquefortine C	+	+	+
Isofumigaclavine A & B	+	+	-
Marcfortines	-	-	+
PR-toxin & eremofortines	+	-	-
Mycophenolic acid	+/-	+	-
Patulin	-	+	+
Penicillic acid	-	-/+	-
Cyclopaldic acid	-	+	-
Penitrem A	-	+	-
Botryodiploidin	-	-	+/-
Geosmin	-	+	-
Phenotypic characters			
Ehrlich reaction	+/++	+/++	-
Blackish green reverse, CYA	+	-	-
Reverse colour, YES	Blackish green	Cream beige	Cream yellow/beige#
Growth rate on CYA 30°C	(0-)6-11 mm	4-11(-26) mm	(10-)17-39 mm
Growth on CzP	12-25 mm	22-34 mm	5-34 mm
Small sclerotia	-/(+)	-	-
Habitat/substrate			
Blue cheese	+	-	-
Meat	-	+	-
Rye bread	+	(+)	+
Preserved foods	+	+	+
Beverages	+	+	-
Mouldy bakers yeast	+	+	-
Silage	+	(+)	+
Soil	+	-	-

Often turn to strawberry red in age, with colour diffusing into the medium

Section *Chrysogena* Series *Chrysogena* – including *P. atramentosum* in series *Camemberti*

Extrolites	<i>chrysogenum</i>	<i>flavigenum</i>	<i>dipodomyis</i>	<i>nalgiovense</i>	<i>nalgiovense</i> II	<i>atramentosum</i>
Penicillin	+	+	+	weak	+	-
Roquefortine C	+	+	-	-	-	+
Meleagrin	+	+	-	-	-	+
Oxaline	-	-	-	-	-	+
Chrysogine	+	+	-	-	+	-
Rugulovasine	-	-	-	-	-	+
Nalgiovensin	-	-	-	+	+	-
Nalzovins	-	-	-	-	+	-
Dipodazin	-	-	+	-	+/-	-
Xanthocillin X	+	+	-	-	-	-
Secalonic acids	+/-	+/-	-	-	-	-
Penitrem A	-	+	-	-	-	-
Phenotypic character						
Ehrlich reaction	-	-	-	-	-	-
Creatine, growth	weak	Weak	weak	weak	Weak	++
Creatine, acid	-/+?	?	-	-	-	-
Reverse, CYA	Cream, beige, yellow	Yellow	Creamish brown	Dark red brown	Yellowish	Dark brown
Reverse, YES	Yellow	Yellow	Orange to orange yellow	Orange brown	Orange	Dark brown
Dark green conidia	-(+)	-	+	-	+	+
Blue green conidia	+	+	-	-	-	-
Col. Diam. CYA						
Exudate	Yellow	Yellow	Clear	Brown	Clear	Brown
Stipe on MEA	Smooth	Smooth / rough	Finely rough	Smooth	Smooth	Smooth
Conidia on MEA	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth
Branching	Ter to quart	Ter	Ter to quar	Bi to ter	Ter to quarter	Ter
Conidial shape	El/sg	El/sg	Sg	Sg/g	El/sg	El
Odour	Fruity	Mouldy	None	None	None	Corn
Habitat/substrate						
On cheese	-(+)	-	-	+	-/+	-/+
On salami	+/-	-	-	-	+	-
In desert soil	+	+	+	-	-(+)	-
In basic soil	-	-	-	-	-	+
In other soil	-	-	-	-	-	+
In indoor air	+	-	-	-	-	-?

Bi = biverticillate; ter = terverticillate; quarter = quaterverticillate ; El = ellipsoid ; g = globose ; sg = subglobose

Series *Mononematosa* Box key to species in *Mononematosa*

Extrolites	<i>P. mononematosum</i>	<i>P. confertum</i>
Cyclopaldic acid	+	-
Fumitremorgins and verrucologen	+	-
Isochromantoxin	+	-
Viriditoxin	+	-
Asteltoxin	-	+
Meleagrin	-	+
Phenotypic character		
Ehrlich reaction	-	-
Diameter, 7 days, CYA 30°C	26-33 mm	17-21 mm
Reverse colour, YES	Yellow cream to curry	Cream to brown yellow

Series *Aethiopica* and series *Persicina*

Extrolites	<i>P. aethiopicum</i>	<i>P. persicinum</i>
Griseofulvin	+	+
Chrysogine	-	+
Roquefortine C	-	+
Tryptoquialanins	+	-
Viridicatumtoxin	+	-
Phenotypic character		
Ehrlich reaction	-	-
Ellipsoidal conidia	+	+
Cylindrical conidia	-	+
Rough stipes	+/-	-
Fasciculate	+	-
Red diffusible pigment	-	+
Diameter, 7 days, CYA, 30°C	29-35 mm	18-22 mm
Reverse colour, YES	Yellow to curry yellow	Strawberry red

Section *Expansa* - Series *Expansa* - including *P. crustosum* from series *Camemberti*

Extrolites	<i>P. expansum</i>	<i>P. marinum</i>	<i>P. crustosum</i>	<i>P. sclerotigenum</i>
Patulin	+	+	-	+
Roquefortine C	+	+	+	+
Communesins	+	+	-	-
Chaetoglobosins	+	+	-	-
Penostatins	-	+	-	-
Expansolide	+	+	-	-
Geosmin	+	-	+	-
Penitrem A	-	-	+	-
Cyclopenol etc.	-	-	+	-
Terrestric acid	-	-	+	-
Citrinin	+/-	-	-	-
Sclerotigenin	-	-	-	+
Griseofulvin	-	-	-	+
Gregatins	-	-	-	+
Phenotypic character				
Ehrlich reaction	++	++	-	-
Stipe	Smooth (to rough)	Smooth	Rough	Smooth
Conidium form	Ellipsoidal	Sg	Sg	Ellipsoidal
Synnemata	Fasciculate, synnemata occasionally	None	Not distinct	None
Sclerotia	-	-	-	+
Crustose	-	-	+	-
Colony diam., 7 d., CYA, 25°C	26-50 mm	17-27 mm	32-46 mm	40-62 mm
Colony diam., 7d., CYA, 30°C	0-3 mm	0 mm	15-26 mm	16-29 mm
Reverse colour, CYA	Brown to orange brown	Brown	Cream	Brown
Reverse colour, YES	Cream yellow to orange brown	Cream yellow	Yellow	Cream yellow
Apple rot	Pronounced	None	Restricted	None
Growth on CREA	++	++	++	w

Series *Urticicolae*

Extrolites	<i>P. griseofulvum</i>	<i>P. dipodomyicola</i>
Patulin	+	+
Griseofulvin	+	+
Roquefortine C	+	-
Cyclopiazonic acid	+	+
Cyclopiamine	+	-
Cyclopiamide	+	-
Mycelianamide	+/-	-
Fulvic acid	+	-
Penicillin	+	?
Phenotypic character		
Ehrlich reaction	+	++
Phialides ≤6.5 µm	+	+
Conidium colour	Grey green	Dull green
Reverse colour CYA	Creamish yellow	Dark brown
Branching	Ter to quarter	Biv to ter
Synnemata MEA	Distinct when fresh	Not distinct
Reverse colour, YES	Cream yellow to beige	Yellow olive to dark olive
CYAS, diam., 7 d., 25°C	17-23 mm	24-28 mm
CYA, diam., 30°C, 7 d.	17-22 mm	17-21 mm
Ehrlich reaction	++, violet	++, violet
Habitat/substrate		
Soil	+	+
Cereals	+	-
Desert seeds	+	(+)

Series *Claviformia*

Extrolites	<i>coprophilum</i>	<i>concentricum</i>	<i>glandicola</i>	<i>coprobium</i>	<i>clavigerum</i>	<i>formosanum</i>	<i>vulpinum</i>
Patulin	-	+	+	+	+	+	+
Griseofulvin	+	-	-	-	-	-	-
Roquefortine C	-	+	+	+	+?	-	+
Meleagrin	-	+	+	+	-	-	+
Pyripyropens	-	-	-	+	-	-	-
Xanthomegnin	-	-	-	-	+/-	-	-
Cyclopiazonic acid	-	-	-	-	+/-	-	-
Geosmin	-	-	-	-	+	+	-
Patulonide	-	+	+	-	-	-	-
Penitrem A	-	-	+	-	+	-	-
Ehrlich reaction	-	-	-	-	Yellow	-	-
Phenotypic characters							
CYA >> CYAS	-	-	-	-	+	+	-
CYA, diam., 7 d., 30°C	7-20 mm	0 mm	0-6 mm	0-4 mm	7-13 mm	0 mm	0-4 mm
Growth on UNO	++	++	++	++	w	w	+/++
Growth on CREA	++	++	++	++	w	w	++
Synnemata	Capitulate	Capitulate	Feathery	Capitulate	Acicular	Thin, feathery	Capitulate
Concentric rings	-	+	+	+	-	-	+
Conidium colour	Greenish grey	Blue green	Dull green	Dark dull green	Dull to grey green	Greenish white	Greenish grey
Conidiophore stipe	Sm/ro	Sm	Ro	Sm	Sm/ro	Sm	Sm
Colony reverse MEA	Brown	Orange	Orange	Cream	Cream/brown	Cream	Brown
Habitat/substrate							
Animal fur	-	-	-	-	+	-	-
Insects	-	-	-	-	-	-	+
Dung & dungy soil	+	+	+/-	+	+/-	+	+
Oak, acorn, cork	-	-	+	-	-	-	-

Series *Italica* - including *P. digitatum* from *Digitata*.

Extrolites	<i>P. italicum</i>	<i>P. ulaiense</i>	<i>P. digitatum</i>
Deoxybrevianamide E	+	+	-
Italinic acid	+	-	-
Formylxanthocillin X	+	-	-
PI-3	+	-	-
Tryptoquialanins	-	-	+
Ehrlich reaction	-	-	-
Biphenyl Resistant	-	+	-

Phenotypic characters

Synnemata	Occasional	Distinct	None
Conidia	Cylindrical to ellipsoidal	Long cylindrical	Large cylindrical
Conidium colour	Greenish grey	Greenish grey	Olive
Reverse colour CYA	Red brown	Cream	Beige
CYA, diam., 7 d., 25°C	26-50 mm	13-26 mm	15-55 mm
CYAS, diam., 7 d., 25°C	3-17 mm	0(-13) mm	0 mm

Series *Gladioli* including *P. sclerotigenum* from *Expansa*:

Extrolites	<i>P. gladioli</i>	<i>P. sclerotigenum</i>
Patulin	+/-	+
Atrovenetins	+	-
Gladiolic acid	+	-
Glyanthrypine	+	-
Gregatins	-	+
Sclerotigenin	-	+
Griseofulvin	-	+
Roquefortine C	-	+

Phenotypic characters

Ehrlich reaction	-	-
Sclerotia	Avellaneous, pale brown	Buff, avellaneous, orange brown
Conidia	Subglobose	Ellipsoidal
CYAS > CYA	+	-
CYA, 7 d., diam., 30°C	0 mm	16-29 mm

Section *Viridicata* Series *Viridicata*, including *P. verrucosum* in *Verrucosa*

Extrolites	AG	AC	CY	FR	ME	NE	PO	TR	VI	VE
Penicillic acid	+	+	+	-/+	+	+	+	-	-/+	-
Xanthomegnin	-	-	+	+	+/-	-	-	+	+	-
Asteltoxin	-	-	-	-	-	-	-	+	-	-
Cyclopenol etc.	-	+	+	+	-	+	+	-	-	-
Verrucofortine	-	+	+	-	-	-	+	+	-	-
Penitrem A	-	-	-	-	+	-	-	-	-	-
Terrestric acid	+	-	-	-	-	-	-	+	-	-
Brevianamide A	-	-	-	-	-	-	-	-	+/-	-
Viridamine	-	-	-	-	-	-	-	-	+	-
Aurantiamine	+	-	-	+	-	+	-	-	-	-
Auranthine	+	-	-	-	-	-	-	-	-	-
Anacine	+	-	-	-	-	-	+	-	-	-
Puberulonic acid	-	+	-	-	-	-	-	-	-	-
Verrucosidin	+	-	-	-	+	-	+	-	-	-
Ochratoxin A	-	-	-	-	-	-	-	-	-	+
Citrinin	-	-	-	-	-	-	-	-	-	+/-
Verruculone	-	-	-	-	-	-	-	-	-	+
Verrucinin	-	-	-	-	-	-	-	-	-	+
Pseurotin	+	+	+	-	-	-	+	-	-	-

Oxaline	-	-	-	-	+	-	-	-	-	-
Sclerotigenin	-	-	-	-	+	-	-	-	-	-
Viridic acid	-	-	-	-	-	-	-	-	+	-
Phenotypic characters										
Ehrlich reaction	p	+	P+	p	p	+	+	-	P+	-
Reverse on YES	y	y	Y	y	y	y	y	br	y	Red brown
CREA: acid	+	+	+	+	+	+	+	+	+	-
Growth on nitrite	-	-	-	-	-	-	-	-	-	+
RT reaction	+	+	+	+	-	+	+	-	+	-
Exudate	+	++	+	++	(+)	++	+	++	+	++
Conidium ornam.	sm	sm	Sm	sm	Sm	ro	sm	sm	fr	sm
Stipe ornam.	Ro/sm	Ro/sm	Ro/sm	Ro/sm	Ro/sm	ro	Ro/sm	Ro!!	ro	Ro!
Yellow green conidia	-	-	+	-	+	-	-	-	+	+
Blue green conidia	+	+	(+)	+	-	+	+	-	-	-
Grey green conidia	-	-	-	-	-	-	-	+	-	-
Dark green conidia	-	-	-	-	+	-	-	-	-	-
Good sporulation YES	+/-	-	-	-	+	-	+	+	+/-	-
Habitat/substrate										
Cereals	+	+	+	+	+	-	+	+	+	+
Desert seeds	-	-	-	-	-	+	-	-	+	-
Salami	(+)	-	-	-	(+)	-	+	-	-	+
Indoor air	-	-	-	-	-	-	+	-	-	-

AG: *P. auranthiogriseum*, AC: *P. cyclopium* II (formerly called *P. aurantiocandidum* or *P. aurantiovirens*), CY: *P. cyclopium*, FR: *P. freii*, ME: *P. melanoconidium*, NE: *P. neoechinulatum*, PO: *P. polonicum*, TR: *P. tricolor*, VI: *P. viridicatum*, VE: *P. verrucosum*, y: yellow, br: brown, sm: smooth, ro: rough, fr: finely roughened, p: pink reaction in Ehrlich test, P+: pink reaction and yellow and brown colours developing.

Series *Corymbifera*

Extrolites	<i>hirsutum</i>	<i>albocoremium</i>	<i>allii</i>	<i>hordei</i>	<i>venetum</i>	<i>radicicola</i>	<i>tulipae</i>
Roquefortine C	+	+	+	+	+	+	+
Penitrem A	-	-	-	-	-	-	+
Meleagrin	-	+	+	-	+	+	+
Cyclophenol, cyclophenin etc.	+/-	+	+	-	+	+	-
Fulvic acid	-	-	+	-	-	-	-
Compactin	+	-	-	-	-	-	-
Hordein	-	-	-	+	-	-	-
Terrestric acid	+	-	-	+	+	+	+
Atrovenetins	+	+	+	+	+	-	-
Citrinin	-	-	-	-	-	+	-
Phenotypic character							
Ehrlich reaction	+	+	p	+	-	+	+
Conidium ornam.	Smooth	Smooth	Smooth	Rough	Smooth	Smooth	Smooth
Conidium colour	Green	Greyish green	Green	Green	Blue green	Greyish green	Greysih green
Mycelium colour	Yellow	White	White	Yellow	White	White	White
Reverse colour, CYA	Yellow brown	Brownish yellow to brownish orange	Dark brown	Yellow	Dark yellow brown	Deep orange	Orange to light orange
Synnemata	Yellow	White feathery	None	Yellow, loose	None	White feathery	White feathery
Exudate	Dark brown	Clear	Dark brown	Yellow?	Dark brown	-	-
Habitat/substrate							
Flower bulbs	-/+?	+	-	-	+	-	-
Onions, garlic	+	+	+	-	-	-	-
Vegetables	-??	+	?	-	-	-	-
Cereals	-	-	-	+	-	-	-
Agricultural soil	+/-?	+	+	+	+	-	-

P: pink reaction in Ehrlich test

Series *Verrucosa* including *P. viridicatum* from *Viridicata*

Extrolites	<i>P. verrucosum</i>	<i>P. nordicum</i>	<i>P. nordicum</i> II	<i>P. thymicola</i>	<i>P. viridicatum</i>
Ochratoxin A	+	+	+	-	-
Citrinin	+/-	-	-	-	-
Daldinin D	-	-	-	+	-
Verrucolone, PC-2	+	+	+	+	-
Anacin	-	+	+	+	-
Verrucin	+	-	-	-	-
Lumpidin	-	-	+	-	-
Fumiquinazoline F	-	-	-	+	-
Alantrypinone	-	-	-	+	-
Penigequinolone	-	-	-	+/-	-
Dipodazin	-	-	-	+/-	-
Sclerotigenin	-	+	-	-	-
2-methylisoborneol	+	+	+	+	-
Xanthomegnin	-	-	-	-	+
Brevianamide A	-	-	-	-	+
Viridic acid	-	+	-	-	+
Viridamine	-	-	-	-	+
Phenotypic character					
Ehrlich reaction	-	yellow	pink	yellow	Yellow, pink, brown
Growth on nitrite	+	+	+	+	-
Reverse YES	Red brown	Cream	Cream	Yellow	Yellow
Habitat/substrate					
Cereals	+	-	-	-	+
Meat	-	+	+	-	-
Fish, salted	-	-	+	-	-
Herbs, sorghum	-	-	-	+	-

Series *Camemberti*

Extrolites	<i>P. commune</i>	<i>P. camemberti</i>	<i>P. palitans</i>	<i>P. caseifulvum</i>	<i>P. crustosum</i>	<i>P. atramentosum</i>
Cyclopiazonic acid	+	+	+	-	-	-
Rugulovasine	+	-	-	+	-	+
Cyclophenin	-/+	-	+	+	+	-
Roquefortine C	-	-	-	-	+	+
Oxaline	-	-	-	-	-	+
Cyclopaldic acid	+/-	-	-	-	-	-
Fumigaclavine	-	-	+	-	-	-
Palitantin	+	-	+	-	-	-
Terrestric acid	-	-	-	-	+	-
Penitrem A	-	-	-	-	+	-
Phenotypic character						
Ehrlich reaction	++	+/-	++	+	-	-
CYA, diam. 7 d., 30°C	0-4 mm	0-3 mm	0-7 mm	0 mm	15-26 mm	0 mm
Dark green conidia	-	-	+	-	-	+
Grey green conidia	+	+	-	+	(+)	-
Acid on CREA	+	+	+	+	++	-
Floccose colonies	-	+	-	+	-	-
Crustose colonies	-	-	-	-	+	-
Habitat/substrate						
Cheese	+	+	+	+	+	+
Meat	+	-	+	-	+	-
Nuts	+	-	-	-	+	-
Alkaline habitats	-	-	-	-	-	+

Similarities between *P. crustosum* and other species claimed to be identical or closely related to it

Extrolites	<i>P. crustosum</i>	<i>P. expansum</i>	<i>P. solitum</i>	<i>P. aurantiogriseum</i>
Terrestrial acid	+	-	-	+
Penitrem A	+	-	-	-
Roquefortine C	+	+	-	-
Cyclopenol	+	-	+	-
Compactin	-	-	+	-
Chaetoglobosins	-	+	-	-
Communesins	-	+	-	-
Patulin	-	+	-	-
Expansolide	-	+	-	-
Penicillic acid	-	-	-	+
Verrucosidin	-	-	-	+
Auranthine	-	-	-	+
Aurantiamine	-	-	-	+
Phenotypic character				
Ehrlich reaction	+	+	-	-
Ellipsoidal conidia	-	+	-	-
Rough stipes	+	- (+)	+	+
Conidial crusts	+	-	-	-
High growth rate	+	+	-	-
Growth on creatine	+	+	+	-
Habitat/substrate				
Apple rot	+	+	+	-
Cereal associated	-	-	-	+

Series *Solita*, including *P. neoechinulatum* from Series *Viridicata*.

Extrolites	<i>P. solitum</i>	<i>P. echinulatum</i>	<i>P. discolor</i>	<i>P. cavernicola</i>	<i>P. neoechinulatum</i>
Cyclopenol etc.	+	+	+	-	+
Territrems	-	+	-	+	-
Chaetoglobosins	-	-	+	-	-
Aurantiamin	-	-	-	+	+
Compactin	+	-	-	-	-
Palitantin	+	+	+	-	-
Penicillic acid	-	-	-	-	+
Phenotypic character					
Ehrlich reaction	-	-	+	-	+
Creatine, growth	+	+	+	+	-
Conidium colour	Dark green	Dark green	Dark green	Dark green	Blue green
Conidium ornam.	Smooth/rough	Rough	Rough/(sm)	Rough	Rough
Reverse on YES	Orange yellow	Yellow	Orange red*	Yellow	Yellow, diffusing
Habitat/substrate					
Cured meat products	+	+	-	-	-
Cheese	+	+	+	-	-
Butter, margarine	-	+	-	+	-
Vegetables	+	-	+	-	-
Seeds	-	-	-	-	+
Natamycin resistant	-	-	+/-	-	-
Indoor air	(+)	(+)	-	-	-

DISCUSSION

Species in subgenus *Penicillium* are among the most frequently encountered filamentous fungi. They occur on mouldy foods, feeds and other substrata and in building environments, yet these species have been called some of the most difficult to identify of all fungi (Thom, 1930). In this paper we present a new taxonomy of those important and ubiquitous species, which we believe will be stable for many years. Both cladification and classification of the species point to the same species and species series (Samson *et al.*, 2004; Frisvad *et al.*, 2004). Most other studies of filamentous fungi are based on a morphological treatment occasionally backed up with sequence data from one gene, usually rDNA ITS data. We believe that a polyphasic approach is necessary in any taxonomic study and have included other ecologically important facets of fungal biology in addition to morphology and nucleotide sequences.

The most useful phenotypic characters were extrolites, which are such an important part of the biology of these fungi that it is impressive that previous taxonomic schemes have been at all successful without them. Extrolites are an integral part of classification and identification and are often called "morphological" characters. For example flavour compounds, odours, basidiocarp colours and toxins are regularly used in Basidiomycete taxonomy, and these composite features are all mixtures of extrolites, although they are never mentioned as such. Modern separation and spectrometric methods have enabled identification of all these components and structural elucidation has made it possible to elucidate their biosynthesis.

It is possible to identify the species based on micro- and macro-morphology, colours and physiological features, but identification of extrolites using either TLC, HPLC-DAD, GC-MS, HPLC-MS or MS make identification much easier. Simple tests that detect specific extrolites are the Ehrlich test, colony reverse colours and the strong halo formation by some species in series *Viridicata*. More of these simple tests should be developed to aid identification, as chromatographic and spectrometric equipment is not available in most mycological laboratories.

Despite successful application in bacterial and yeast taxonomy, nutritional features have rarely been used in the systematics of filamentous fungi. Few characters have been used with good results; however, especially isolate reaction on creatine sucrose agar.

Earlier attempts to classify *Penicillium* subgenus *Penicillium* have been successful for some very distinct species, but isolates of the most widespread species have often been placed incorrectly when too few taxonomic features have been used (Raper and Thom, 1949; Samson *et al.* 1976; Pitt, 1979). Attempts to use a large number of features (Bridge *et al.*, 1989 a,b; Paterson *et al.*, 1989; Ahmad and Malloch, 1999,

2000) on the other hand has also resulted in many equivocal results. For example experience using the key based on the system of Bridge *et al.* (1992) resulted in a high number of isolates being identified as *P. solitum*, even though those isolates often represented other species. 35 species accepted in the present study were not accepted by Bridge *et al.* (1989a; 1992), even though typical isolates of some of them were included in their study such as *P. aethiopicum*, *P. carneum*, *P. concentricum*, *P. confertum*, *P. coprobium*, *P. coprophilum*, *P. dipodomyicola*, *P. dipodomyis*, *P. discolor*, *P. flavigenum*, *P. italicum*, *P. digitatum*, *P. nalgiovense*, *P. palitans*, *P. polonicum* and *P. venetum*. The extended medium regime of Ahmad and Malloch (1999, 2000) looked promising as aid for classification and identification of *Penicillium* subgenus *Penicillium*, but our experience has shown that the reactions on the new chemically well defined media are difficult to read accurately. The diagnostic tests were only effective for very distinct species such as *P. atramentosum* in our attempts to use the system of Ahmad and Malloch (1999, 2000). The limited numbers of nutritional and physiological tests we have used in our study were easier to read and gave clear results. In addition our use of YES agar (degree of conidium production, reverse colours) was of great help in recognizing the 58 species accepted by us.

Two features of our system will be a further help in identification of new isolates of *Penicillium* subgenus *Penicillium*. The isolates marked Y (current typical culture selected by us) in the following descriptions can be used as a current reference standard equivalent to the use of standards of chemical compounds for compound identification. Extrolites are a very efficient help in identifying species in *Penicillium*, but even without those we believe that accurate identification is possible. In order to allow the use of extrolites without having access to expensive analytical chemical equipment, we have advocated the use of the Ehrlich test to indicate production of indol alkaloids. We think that more of this kind of tests are needed in order to facilitate identification.

Reactions to abiotic factors (ecophysiology), especially temperature, water activity, pH and atmosphere are very significant, but have been underemphasized in most taxonomies of filamentous fungi. In agreement with Pitt (1979), we believe that these features will play a greater role in future taxonomy. Apart from being functionally and ecologically relevant, these features are often easy to record. We have selected a few of these characters (growth at 15, 25, 30 and 37 °C, 5 % NaCl) in order to keep the number of diagnostic media to a minimum, but other conditions such as high pH, low pH, low redox potential, and high carbon dioxide could have been employed. All species in series *Roqueforti* grow well at low oxygen tensions and high carbon dioxide tensions and *P. atramentosum* prefers an alkaline habitat. Media and conditions

reflecting such unique features have not been included in general in this study. Pitt (1979) used growth at 5, 25 and 37°C and growth on G25N (reduced water activity), but we believe that our combination of media reflects the most important abiotic factors and works better for the terverticillate *Penicillia*.

It is interesting that the classification proposed by Raper and Thom (1949) is closer to a phylogenetically sound taxonomy than that of Pitt (1979), perhaps because the latter work had an emphasis on the identification process. Our *Penicillium* series are much closer to those of Raper and Thom (1949) than those of Pitt (1979). It is paradoxical that Raper and Thom (1949) had a physiologically more correct classification without using physiological characters, whereas Pitt (1979) in introducing the use of temperature and water relations ended up with a classification that was less physiologically sound.

The number of species we accept (58) is quite high compared to those accepted by Samson *et al.* (1976, 1977a & b) or Pitt (1979) or Pitt and Cruickshank (1990). Many new species have been discovered, however, and they are all unique in the suite of diagnostic features that characterize them.

The section and series classification suggested here appears to be natural both in an ecological and phylogenetic sense. Most series suggested are not very different from those suggested by Raper and Thom (1949), including *Olsonii* (*P. brevicompactum* series), *Roqueforti*, *Chrysogena*, *Camemberti*, *Gladioli*, *Viridicata* (*P. ochraceum*, *P. viridicatum* and *P. cyclopium* series), *Corymbifera*, *Expansa*, *Claviformia*, *Digitata*, *Italica* and *Urticicola*. However, within some of these series, several changes were made: Concerning the series *Olsonii*, *P. olsonii* was placed by Raper and Thom (1949) in their *Biverticillata-Symmetrica*. This was later corrected by Pitt (1979). We now include *P. brevicompactum* and *P. bialowiezense* in this series, already suggested by Stolk and Samson (1985) and Frisvad *et al.*, 1990b, and supported by isozyme data (Cruickshank and Pitt, 1987). In *Roqueforti*, not recognized by Pitt (1979), Raper and Thom included *P. casei*, now placed in *Verrucosa* as a synonym of *P. verrucosum*. The current *Roqueforti* series is strongly supported by ITS sequence data (Boysen *et al.*, 1996; Skouboe *et al.*,

1999) and by the unique physiological and morphological characters by the three species included in it. Series *Chrysogena* was not recognized by Pitt (1979), but its members have a series of features supporting it, including production of penicillin by all species and growth at low water activities. The four species accepted by Raper and Thom (1949) have all been synonymized (Samson *et al.*, 1977a), but two new species have since been discovered and *P. nalgiovense* transferred to the series (Banke *et al.*, 1997). Several species in the Raper and Thom (1949) series *P. camemberti* and *P. commune* are now placed in series *Camemberti*, while some other floccose form are placed in *Viridicata* now. Series *Viridicata* now contains nine closely related species. The Raper and Thom (1949) concept of their three series *P. cyclopium*, *P. viridicatum* and *P. ochraceum* in addition to the *P. camemberti*, *P. commune* and *P. terrestre* series have been merged and has then been subdivided into four series here: *Viridicata*, *Verrucosa* (both containing species growing poorly on creatine as sole nitrogen source), and *Camemberti* and *Solita* (both containing species growing well on creatine as sole nitrogen source). Series *Corymbifera* no longer contains *P. glandicola*. It has been transferred to the series containing synnematus dung fungi *Claviformia*. Several new species have been added to *Corymbifera*, most of which are pathogenic to bulbs and onions. Series *Expansa* now contains three species, but not *P. crustosum*, which has been transferred to series *Camemberti*.

Raper and Thom (1949) placed many of the species according to colony texture, a feature that often is a result of fungal deterioration rather than taxonomic placement (Pitt, 1979). Pitt (1979) on the other hand emphasised colony diameters and had unrelated species in the same series because of their growth rate. His approach was based on a pragmatic approach to identify *Penicillia*. Although we strongly agree that identification should be a practical issue, simple keys for *Penicillium* identification are unrealistic. The keys provided in this paper will be helpful but only with a combination of DNA sequences, extrolite production and other phenotypical characters it will be possible to identify the taxa using electronic databases.

P. aethiopicum Frisvad, *Mycologia* 81: 848, 1989.

In *Penicillium* subgenus *Penicillium* section *Chrysogena* series *Aethiopica*

Type: Herb. IMI 285524

Culture ex type: CBS 484.84 = IBT 21501 = IBT 5903 = IMI 285524 = FRR 2942 (T, Y), ex *Hordeum vulgare*, Addis-Abeba, Ethiopia

Diagnostic features: Griseofulvin, viridicatumtoxin, tryptoquialanins, geosmin, ellipsoidal smooth-walled conidia, markedly sulcate colonies with a golden yellow reverse, growth at 37°C.

Similar species: Isolates of this species have earlier been identified as *P. expansum* (CSIR 1039, CSIR 1375, IMI 246656, IMI 279025), *P. crustosum*, *P. verrucosum* var. *cyclopium* or *P. aurantiogriseum* (CCM F-389), *P. verrucosum* var. *corymbiferum* (Leistner Sp. 1448 = CBS 109575), *P. viridicatum* (CSIR 1039), but differs from all those taxa by its growth at 37°C. It differs by all species in section *Chrysogena* by being fasciculate.

Description:

Conidia: Smooth-walled, ellipsoidal, 2.8-3.2 x 3.3-3.8 µm, in long columns

Phialides: 7-9 µm, short collula

Metulae: 12-17 µm

Rami: 15-25 µm

Stipes: 200-350 µm, smooth to rough-walled

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Sulcate on CYA

Conidium colour CYA: Dull green.

Exudate droplets on CYA: Copious, clear

Reverse colour on CYA: Golden yellow

Reverse colour on YES: Yellow to curry yellow

Diffusible colour: Occasional; pale orange

Ehrlich reaction: No reaction

Odour and volatile metabolites: Geosmin, ethylacetate, 2-methyl-3-butene-2-ol, 2-pentanone, ethyl isobutanoate, isobutyl acetate, ethyl 2-methyl-butanoate, ethyl isopentanoate, and isopentyl acetate (Larsen and Frisvad, 1995)

Extrolites: 1) Griseofulvin, dechlorogriseofulvin, lichexanthone, 2) Viridicatumtoxin, 3) Tryptoquialanine A & B

Growth on creatine: weak to moderate growth

Acid and base production on creatine: Weak to moderate

Growth on UNO: Very good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 26-38 mm; MEA: 25-40 mm; YES: 34-57 mm; CREA: 15-34 mm; Cz: 17-28 mm, OAT: 20-37 mm; CYAS: 23-32 mm; CzBS: 17-23 mm; CzP: 0 mm; UNO: 11-16 mm; DG18: 31-38 mm

Diam., 1 week: 15°C: 20-25 mm; 30°C: 29-34 mm; 37°C: 3-9 mm

CYA/CYAS: 1.4 [1.1-1.7]

CYA15°C/CYA 25°C: 0.6 [0.6-0.7]

CYA30°C/CYA 25°C: 0.9 [0.8-0.9]

CZBS/CZ: 0.6 [0.5-0.7]

CZP/CZ: 0

Distribution: Pantropical (South America, Africa, India, Southeast Asia), but also in greenhouses in subtropical and temperate climates.

Ecology and habitats: Maize, sorghum, wheat, barley, kemiri nuts, cow peas, soybeans, mung beans, peanuts, cashews (Frisvad and Filtenborg, 1989, Pitt and Hocking 1998)

Biotechnological applications: Viridicatumtoxin is a weak antitumor agent (Raju *et al.*, 82) and griseofulvin is an important antifungal agent (Cole and Cox, 1981). The species is not used commercially.

Biodeterioration & phytopathology: No data

Mycotoxins and mycotoxins: Viridicatumtoxin is a nephrotoxin (Hutchison *et al.*, 1973); the toxicity of the tryptoquialanins is unknown, but the closely related tryptoquivalins are regarded as tremorgens (Cole and Cox, 1981). No reported mycotoxicosis.

Typical cultures: IBT 11191 = CBS 270.97, locust bean gum flour, imported to Denmark; IBT 16873 = CBS 287.97, tropical room Victoria, Vancouver Island, BC, Canada; IBT 5753 = IBT 3352 = IBT 3916 = IBT 3906 = IBT 4706 = CBS 109575, salami, Germany; IBT 5906 = CBS 109577 = IMI 279025, *Vitis* sp. fruit, India; IBT 5750 = CBS 109574 = IMI 246656, maize, Bhagalpur, India; IBT 5905 = CBS 109576, pearl millet, Zimbabwe; IBT 21721 = CBS 109602, cassava chips, Africa; CSIR 1029; CSIR 1375 = NRRL 5880, maize, South Africa; IBT 4701 = IMI 293194 = ATCC 58633, cucumber in greenhouse, Denmark; CCM F-389, tropical soil; IBT 5752, soil, Amazonas, Brazil.

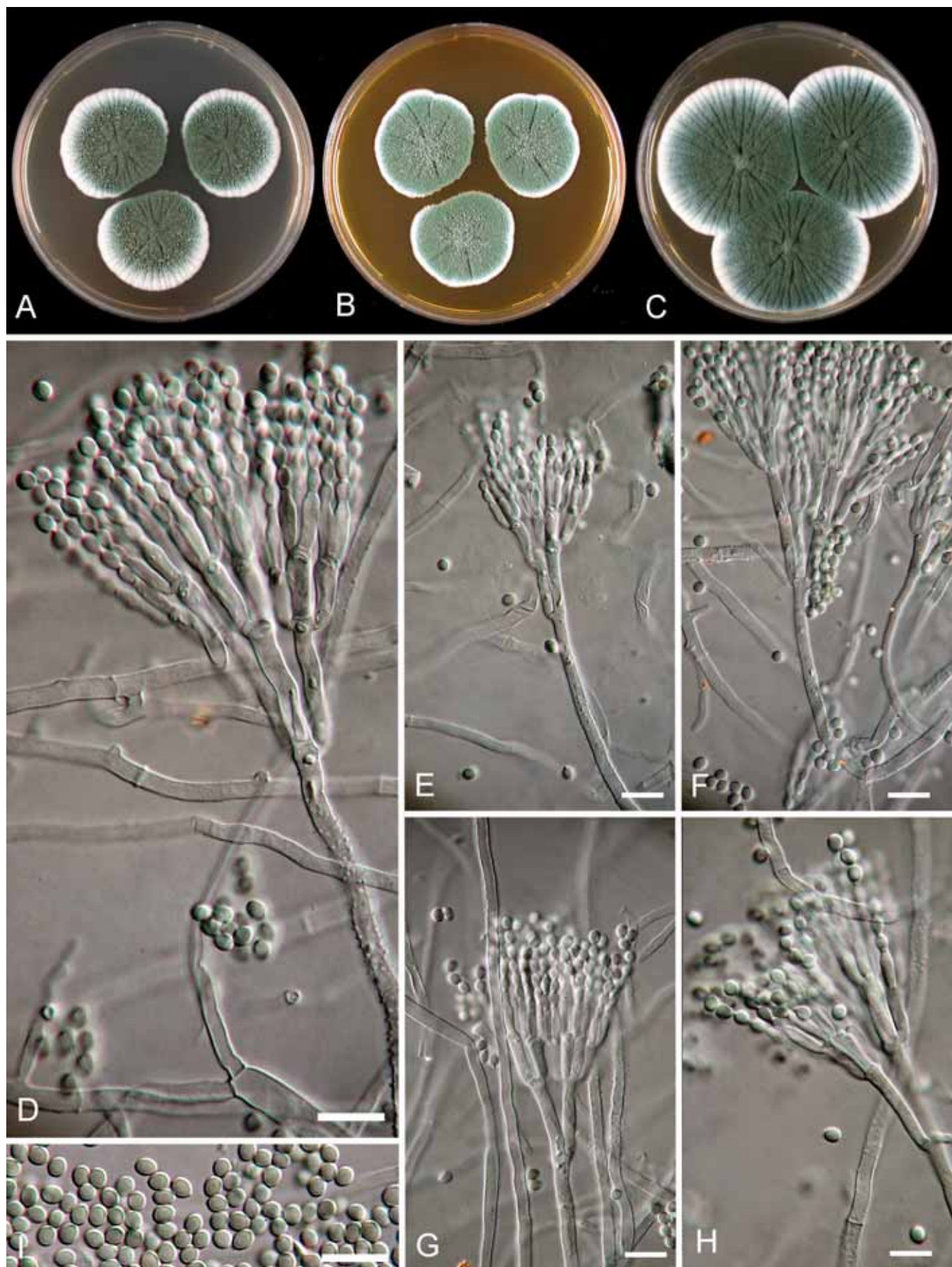


Fig. 26. *Penicillium aethiopicum*. 7-day old colonies at (A) CYA, (B), MEA, (C) YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. albocoremium (Frisvad) Frisvad, Int. Mod. Tax. Meth. Pen. Asp. Clas.: 275, 2000

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Corymbifera*

Type: Herb. IMI 285511, isotype Herb. C 60163

Culture ex type: IMI 285511 = CBS 472.84 = IBT 21502 = IBT 10682 = FRR 2931 = T12 (T,Y), ex salami, Hillerød, Denmark

Diagnostic features: Roquefortine C, meleagrin, orange brown reverse on CYA, smooth-walled conidia, warty conidiophore stipes, halotolerant, psychrotolerant.

Similar species: *P. albocoremium* differs from *P. tulipae* and *P. radicicola* by its dark orange brown reverse on CYA and good sporulation on YES agar. *P. hirsutum* and *P. venetum* differ from *P. albocoremium* by their production of deep violet brown exudate.

Description:

Structure: Asymmetric terverticillate to quarterverticillate

Conidia: Smooth-walled, globose to subglobose, 3.1-4.5 µm

Phialides: 7.9-11.7 µm x 2.2-3.5 µm, with short collula

Metulae: Rough walled, cylindrical, 8.5-18.8 µm x 2.4-4.5 µm

Rami: 9.8-24.9 µm x 2.9-4.8 µm

Stipes: 150-2000 µm, very rough and warted

Synnemata or fasciculation: Fasciculate to coremiform, white stipes

Sclerotia: None

Colony texture: Floccose to fasciculate

Conidium colour on CYA: Greyish green to dull green

Exudate droplets on CYA: Copious, clear to pale yellow

Reverse colour on CYA: Brownish orange

Reverse colour on YES: Brownish yellow to orange

Diffusible colour on CYA: None

Ehrlich reaction: +, red violet

Odour and volatile metabolites: No data

Extrolites: 1) Roquefortine C & D, meleagrin; 2) Atrovenetin; 3) Cyclopeptin, dehydrocyclopeptin, cyclopenin, cyclophenol, viridicatin

Growth on creatine: Weak to moderate

Acid and base production on creatine: W/+ (no base)

Growth on UNO: Very good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 28-38 mm; MEA: 25-31 mm; YES: 48-60 mm; CREA: 18-28 mm; Cz: 14-20 mm, OAT: 23-27 mm; CYAS: 35-41 mm; CzBS: 12-17 mm; CzP: 0 mm; UNO: 8-14 mm; DG18: 33-43 mm

Diam., 1 week: 15°C: 32-35 mm; 30°C: 8-14 mm; 37°C: 0 mm

CYA/CYAS: 0.9 [0.8-1.0]: halotolerant

CYA15°C/CYA 25°C: 1.0 [0.9-1.1]

CYA30°C/CYA 25°C: 0.3 [0.3-0.4]

CZBS/CZ: 0.7 [0.5-0.9]

CZP/CZ: 0

Distribution: Denmark, Slovenia, Israel

Ecology and habitats: Roots of *Apium graveolens*, *Petroselinum crispum*, *Allium cepa*, and *Zingiber officinale*, on *Fragaria vespa*, cakes, salami and in a saltern.

Biotechnological applications: none

Biodeterioration & phytopathology: Possibly causing a rot of onions (*Allium cepa*)

Mycotoxins and mycotoxins: Roquefortine C has been listed as a neurotoxin (Cole and Cox, 1981)

Typical cultures: IBT 22806 = CBS 109583, ex saltern, Slovenia; IBT 22521 = CBS 109585, ex *Allium cepa*, Denmark; IBT 21071 = CBS 109584, ex *Zingiber officinale* imported to Denmark; IBT 12813 = CBS 109587 = NRRL 941 = Thom 4733.48 (identified by Biourge as *P. corymbiferum*, identified as *P. cyclopium* by Raper and Thom, 1949); IBT 16884 = CBS 320.97 = CBS 109586, ex *Allium cepa*, Denmark; IBT 20068 = CBS 109582, ex cake, Denmark; IBT 19154 = CBS 109614, cake, Denmark; IBT 3457 & IBT 10673, ex *Fragaria vesca*, Denmark; IBT 3891 & IBT 10672 ex *Apium graveolens*, Denmark; IBT 10679, ex food, Denmark; IBT 10683, IBT 10685 & IBT 10689, ex indoor air, Denmark; IBT 10689, ex salami, Denmark; IBT 13001 ex *Petroselinum crispum*, Denmark; IBT 19397 ex date imported to Denmark; IBT 21596, ex *Allium cepa*, Denmark.

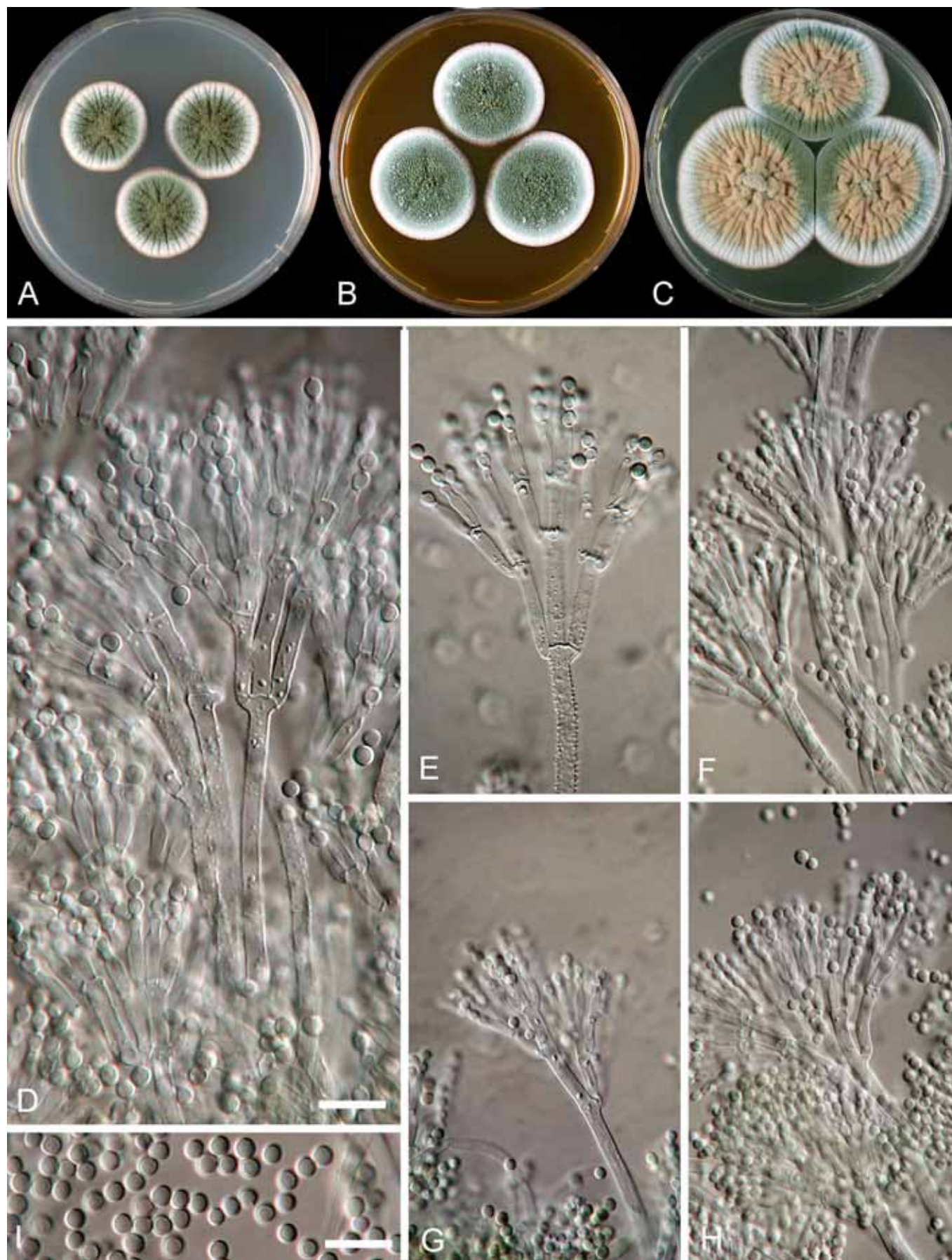


Fig. 27. *Penicillium albocoremium*. 7-day old colonies at (A) CYA, (B), MEA, (C) YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. allii Vincent and Pitt, Mycologia 81: 300, 1989

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Corymbifera*

Type: Herb. MU Vincent 114

Culture ex type: CBS 131.89 = IBT 21503 = IBT 6610 = ATCC 64868 = FRR 3184 (T,Y), ex garlic, Egypt

Diagnostic features: Smooth-walled conidia, fulvic acid or analogues, a dark brown reverse, garlic rot

Similar species: *P. allii* differs from *P. hirsutum* by not being coremiform and by fewer and more lightly coloured exudates droplets. It differs from *P. albocoremium*, *P. radicola* and *P. tulipae* by its much darker brown reverse.

Description:

Structure: Terverticillate, some irregular structures

Conidia: Smooth-walled, globose 3.0-4.5 µm

Phialides: 6.5-11 µm x 2.8-3.2 µm

Metulae: 7.5-13 µm x 2.2-3.8 µm

Rami: 10-25 µm x 3.2-4.5 µm

Stipes: Short, rough-walled, 75-400 µm x 3.5-5 µm

Synnemata or fasciculation: Weakly fasciculate (especially on OAT)

Sclerotia: None

Colony texture on CYA: Granular to weakly fasciculate, only sulcate in center of colony

Conidium colour on CYA: Dull green

Exudate droplets: Small clear, yellow or brown on CYA

Reverse colour on CYA: Dark brown

Diffusible colour on CYA: Amber to brown, often produced

Reverse colour on YES: Yellow brown to dark yellow brown

Ehrlich reaction: Pink to red

Odour and volatile metabolites: Isobutanol, isopentanol, several terpenes (Larsen and Frisvad, 1995)

Extrolites: 1) Roquefortine C, meleagrin, oxaline; 2) Cyclopeptin, dehydrocyclopeptin, cyclopenin, cyclopenol, viridicatin, viridicatinol; 3) Atrovenetins; 4) Dehydrofulvic acid, PI-3 and fulvic acid; 5) Chrysogine.

Growth on creatine: Weak

Acid and base production on creatine: No or weak acid, no base

Growth on UNO: Good

Growth on nitrite: Weak to moderate

Abiotic factors:

Diam., 1 week, 25°C: CYA: 26-40 mm (35-45 mm*); MEA: 20-37 mm (35-45 mm*); YES: 31-54 mm; CREA: 10-24 mm; Cz: 14-24 mm, OAT: 17-36 mm; CYAS: 27-39 mm; CzBS: 0-7 mm; CzP: 0 mm; UNO: 13-20 mm; DG18: 19-30 mm

Diam., 1 week: 5°C: 0 mm; 15°C: 24-30 mm; 30°C: 1-5 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.8-0.9], halotolerant

CYA15°C/CYA 25°C: 1.0 [0.9-1.1], psychrotolerant

CYA30°C/CYA 25°C: 0.1 [0.04-0.2]

CZBS/CZ: 0 (one isolate 0.5)

CZP/CZ: 0

* According to Vincent and Pitt (1989)

Distribution: Egypt, Argentina, Korea, Spain, Czech Republic, Germany, United Kingdom, Denmark, Georgia, USA, Ontario, Canada.

Ecology and habitats: Garlic, occasionally in onions and rice.

Biotechnological applications: None

Biodeterioration & phytopathology: *P. allii* produces a severe rot in garlic (Vincent and Pitt, 1989; Frisvad and Filtenborg, 1989).

Mycotoxins and mycotoxins: Only roquefortine C is a known mycotoxin.

Typical cultures: IBT 20212 = CBS 875.95, ex garlic, Spain; IBT 4112 = CBS 109581 = CCF 1875 = IMI 297905, ex *Oryza sativa*, Czech Republic; IBT 14490 = CBS 109578, Georgia, USA; IBT 13030 = CBS 411.92, ex garlic, Korea; IBT 11735 = CBS 109579, ex walnut surface; IBT 3772 = IBT 3056 = CBS 188.88, ex food, United Kingdom; IBT 5553 = CBS 109580 = ATCC 64636 = IMI 321505 = NRRL 13630, ex garlic, Denmark; CBS 161.42 = ATCC 8507 = FRR 942 = IMI 039803 = MUCL 29086 = MUCL 29176 = NRRL 942 = IBT 4515 = IBT 5460 (as *P. cyclopium*); FRR 1668 = IMI 192216, ex soil, Egypt; IMI 321506, ex garlic, Denmark, IBT 24593, ex garlic Argentina, CBS 409.92 & 410.92, ex onion, Korea.

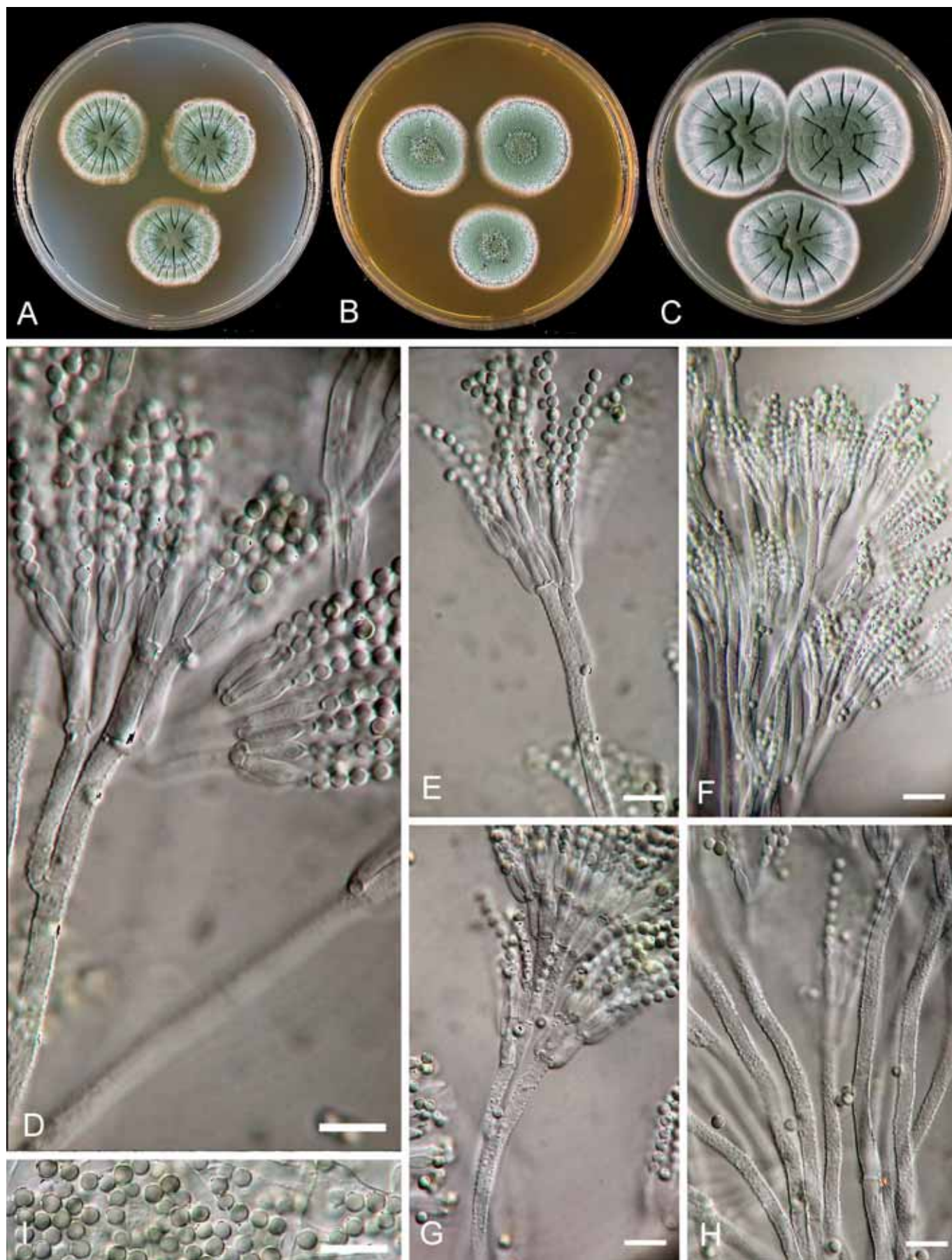


Fig. 28. *Penicillium allii*. 7-day old colonies at (A) CYA, (B) MEA, (C) YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

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

In *Penicillium* subgenus *Penicillium* section *Viridicata*
series *Camemberti*

Type: Herb. IMI 039752

Culture ex type: CBS 291.48 = IBT 6616 = ATCC 10104
= FRR 795 = IFO 8137 = IMI 039752ii = MUCL 29071 =
MUCL 29126 = NRRL 795 = QM 7483 (T), ex French
camembert cheese, USA.

Diagnostic features: globose smooth-walled conidia, good
growth on CREA with no acid production, no growth at
30°C, production of oxaline, rugulovasins and ethyl-2-
methyl-butanoate

Similar species: *P. atramentosum* differs from *P. chrysogenum* by its dark brown reverse and ability to grow on CREA. It differs from members of series *Roqueforti* by its smooth conidiophore stipes and from other species by its alkali tolerance and inability to produce acid on CREA.

Description:

Conidia: smooth-walled, globose to subglobose, 2.3-3.0 µm
Phialides: cylindrical with short collula, 7.5-10 µm x 2.3-
2.5 µm

Metulae: Cylindrical, 10-15 µm x 2.5-3.0 µm

Rami: One or two, often somewhat divergent, 15-20 µm x
3.0-4.0 µm

Stipes: Long 300-500 µm, smooth-walled (finely roughened
in CBS 109601), from subsurface hyphae

Synnemata or fasciculation: None

Sclerotia: None

Colony texture on CYA: Velutinous

Conidium colour on CYA: Dark green

Exudate droplets on CYA: Small droplets often produced,
pale to dark red brown

Reverse colour on CYA: Dark brown to rosy brown

Diffusible colour: Brownish orange

Ehrlich reaction: None, a violet reaction may be observed in
particular good rugulovasine producers

Odour and volatile metabolites: Ethyl-2-methyl-butanoate,
ethyl isopentanoate, ethyl acetate, methyl isobutanoate,
ethyl isobutanoate, isobutyl acetate (Larsen and Frisvad,
1995)

Extrolites: 1) Roquefortine C & D, meleagrin, oxaline,
neoxaline, 2) Rugulovasine A and B

Growth on creatine: Very good

Acid and base production on creatine: No acid produced

Growth on UNO: Very good

Growth on nitrite: Good growth

Abiotic factors:

Diam., 1 week, 25°C: CYA: 23-39 mm (30-45 mm*);
MEA: 13-34 mm (20-30 mm*); YES: 29-49 mm; CREA: 9-
28 mm; Cz: 14-25 mm, OAT: 10-32 mm; CYAS: 29-32
mm; CzBS: 0-15 mm; CzP: 0 mm; UNO: 9-16 mm; DG18:
24-33 mm

Diam., 1 week: 15°C: 20-25 mm; 30°C: 0 mm; 37°C: 0 mm
CYA/CYAS: 1.0 [0.8-1.2]

CYA15°C/CYA 25°C: 0.7 [0.6-1.0]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0 or 0.6 [0 or 0.4-0.8]

CZP/CZ: 0

Distribution: Denmark, Norway, Iceland, UK, the Nether-
lands, Switzerland, Slovenia, Spain, Costa Rica, Ontario,
Canada, Tanzania, Australia, New Zealand, Japan; when
found in the tropics usually found at higher elevations.

Ecology and habitats: Camembert, Danbo, Emmentaler
and Gammelost cheeses, blood sausage, walnuts, soil,
especially chalky soil, limestone quarries.

Biotechnological applications: None

Biodeterioration & phytopathology: Found on mouldy
cheeses and sausages.

Mycotoxins and mycotoxins: Roquefortine C and
rugulovasine A and B have been listed as mycotoxins (Cole
and Cox, 1981).

Typical cultures: IBT 21504 = CBS 194.88 (Y), pig feed,
Norway; IBT 21193 = CBS 109588, Mbizi rainforest soil,
Ufipa Plateau, 2000 m elev., Tanzania; IBT 11800 = CBS
490.84 = IMI 285530 = FRR 2947, *Capsicum anuum*,
Denmark; IBT 13139 = CBS 109601 = WT 37, ex soil,
conifer forest, Switzerland; IBT 10565 = CBS 109611, soil,
Urmston, UK; IBT 11801 = CBS 109613, hay, Iceland; IBT
14762 = CBS 109612, cheese, Hjørring, Denmark; IBT
23031 = CBS 243.73, ex man, Netherlands; IBT 22273, ex
soil, Wilson Botanical Garden, Costa Rica, 1100 m elev.;
IBT 15294, ex *Thymus vulgaris* imported to Denmark; IBT
4719 = FRR 1446 = IMI 192501, ex soil, Turramurra,
N.S.W., Australia; IBT 3417, rye bread, Denmark; IBT
3421, ex soil, the Netherlands; IBT 18891, ex air, Cake
factory, Denmark, IBT 3420, ex agricultural soil, IBT
23511, New Zealand; IBT 24774, saltern, Slovenia

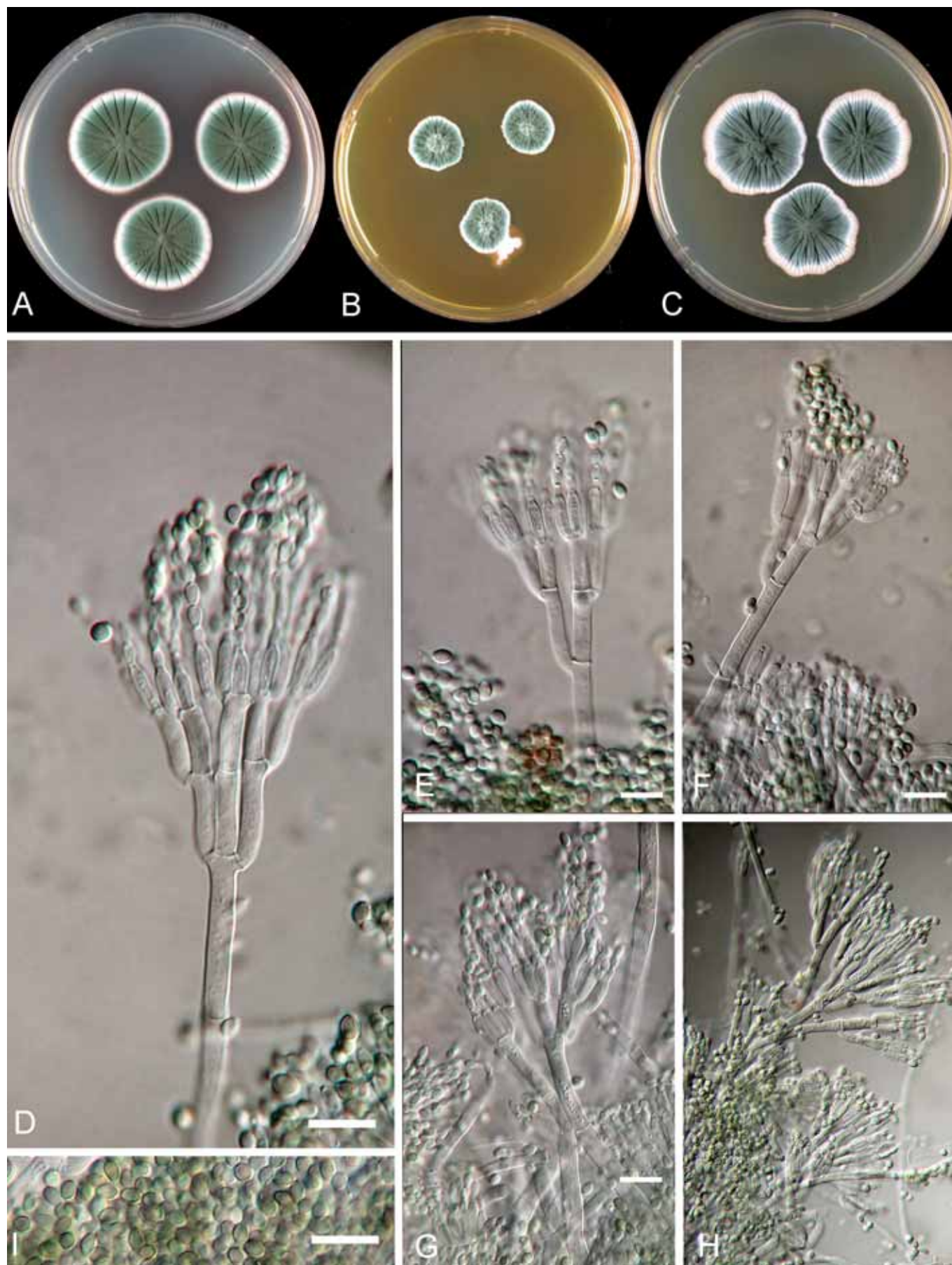


Fig. 29. *Penicillium atramentosum*. 7-day old colonies at (A) CYA, (B), MEA, (C) YES, D-H. Conidiophores. I. Conidia. White bar = 10 μ m.

P. aurantiogriseum Dierckx, Ann. Soc. Scient. Brux. 25: 88, 1901

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Viridicata*

Type: Herb. IMI 195050

Culture ex type: CBS 324.89 = IBT 14016 = IMI 195050 = ATCC 48920 = NRRL 971 = IBT 13458 = IBT 3502 = FRR 971 (T)

Diagnostic features: Anacine, aurantiamin, auranthine, penicillic acid, verrucosidin, pseurotin, smooth-walled conidia, dark brown halo on Raulin-Thom agar.

Similar species: *P. aurantiogriseum* can be distinguished from *P. viridicatum*, *P. melanoconidium* and *P. tricolor* by its blue green conidia. It differs from *P. freii* by its warm orange reverse and poor production of exudates droplets and from *P. polonicum* by its much slower growth rate on CYA. It differs from *P. cyclopium* by its more blue conidia on CYA and its better sporulation and more white obverse mycelium on YES. It differs from *P. neoehinulatum* by its smooth walled conidia.

Description:

Conidiophores terverticillate, few biverticillate and quarterverticillate

Conidia: 3-4 x 2.5-3.5 µm, globose to subglobose (rarely ellipsoidal), smooth-walled,

Phialides: 7.5-10 µm x 2.5-2.8 µm, cylindrical with collula

Metulae: 10-13 µm x 2.8-3.5 µm

Rami: 15-25 µm x 3-3.5 µm

Stipes: 180-400 µm x 3-4 µm, from subsurface hyphae, walls smooth to finely roughened

Synnemata or fasciculation: Weak fasciculation

Sclerotia: None

Colony texture: Velutinous to weakly fasciculate

Conidium colour on CYA: Blue green to grey green to dark dull green

Exudate droplets on CYA: Occasionally present, pale or light brown

Reverse colour on CYA: Curry-yellow to warm orange to reddish brown

Reverse colour on YES: Yellow

Diffusible colour: Often present, orange to red brown

Ehrlich reaction: Pink

Odour and volatile metabolites: Isobutanol, isopentanol, 3-heptanone, 3-octanone (Larsen and Frisvad, 1995)

Extrolites: 1) Anacine, 2) Aurantiamin, 3) Auranthine, 4) Penicillic acid, 5) Verrucosidin and normethylverrucosidin, 6) Pseurotin, 7) Terrestrial acid and viridicatic acid, 8) Nephrotoxic glycopeptides

Growth on creatine: Weak to moderate

Acid and base production on creatine: Strong acid production, no base production

Growth on UNO: Weak

Growth on nitrite: Very weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 11-32 mm; MEA: 16-40 mm; YES: 24-46 mm; CREA: 12-29 mm; Cz: 19-27 mm, OAT: 15-35 mm; CYAS: 23-38 mm; CzBS: 19-28 mm; CzP: 0 mm; UNO: 6-11 mm; DG18: 19-28 mm

Diam., 1 week: 15°C: 16-23 mm; 30°C: 12-17 mm; 37°C: 0 mm

CYA/CYAS: 0.7 [0.6-1.0], halotolerant

CYA15°C/CYA 25°C: 0.9 [0.7-1.3]

CYA30°C/CYA 25°C: 0.7 [0.6-0.7]

CZBS/CZ: 0.9 [0.7-1.0]

CZP/CZ: 0

RT: Strong reaction, dark brown halo and reverse

Distribution: Denmark, Sweden, United Kingdom, Germany, Norway, Czech Republic, former Yugoslavia, Bulgaria, Russia, Iran, New South Wales, Australia, Argentina, USA, Canada

Ecology and habitats: Cereals and foods and feeds based on cereals, less common in onions, garlic, also found in soil.

Biotechnological applications: None

Biodeterioration & phytopathology: This species is a major agent deteriorating cereals at cool temperatures.

Mycotoxins and mycotoxins: This species produces a mixture of mycotoxins: penicillic acid, verrucosidin and nephrotoxic glycopeptides. The toxicity of the many alkaloids produced is unknown. This species and *P. polonicum* may be involved in Balkan Endemic Nephropathy (Barnes *et al.*, 1977, Macgeorge and Mantle, 1990, 1991; Mantle *et al.*, 1991; Mantle and McHugh, 1993, Mantle, 1993; Lund and Frisvad, 1994, Frisvad, 1995). The original isolate (IMI 180922A) investigated by Barnes *et al.* (1977) as *P. aurantiogriseum* was correctly identified, while most of the other strains subsequently identified as such or as *P. commune* (Macgeorge and Mantle, 1990) were in fact *P. polonicum* (Frisvad, 1995).

Typical cultures: IBT 11325 = IBT 21505 = CBS 792.95 (Y), ex apple juice production plant, Denmark; IBT 11252 = CBS 642.95, ex chicken feed, Denmark; IBT 5134 = CBS 112021 = NRRL 3672; IBT 14264 = CBS 110327 = NRRL 953; IBT 15986 = CBS 112023, ex mixed pig feed, Stara Zagova, Bulgaria; IBT 13169 = CBS 110329 = RMF 7862, ex soil, Wyoming, USA; IBT 12482 = CBS 110330, ex wheat, Canada; IBT 24592, garlic, Argentina; IBT 22509, waste, Germany; IBT 11624, IBT 11635; IBT 12954, IBT 12480, IBT 11660 & IBT 11672, ex wheat, Canada; IBT 21558, Czech Republic; IBT 5268 = CCF 1275; IBT 11293, ex barley, Denmark; IBT 11321 = NRRL 3564; IBT 11309 = NRRL 3612; IBT 12834 = NRRL 3747; IBT 12836 = NRRL 6317; IBT 12726 = NRRL 6318; IBT 11301 = IMI 092235; IBT 3992 = IMI 180922A; IBT 14454, ex Lechuquilla Cave, Carlsbad, New Mexico, USA; IBT 12716, ex kangaroo rat, New Mexico, USA; VKM F-232, Russia.

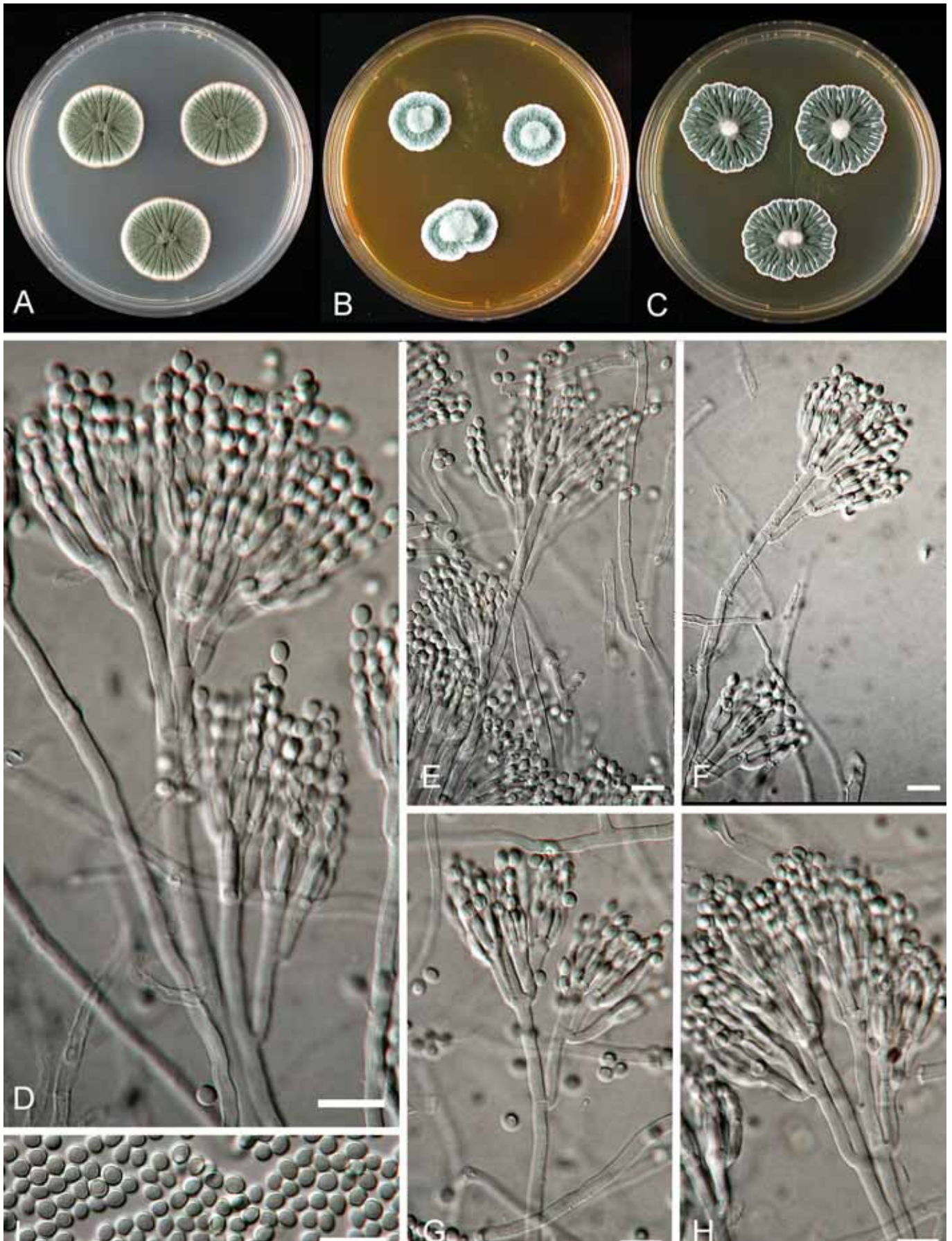


Fig. 30. *Penicillium aurantiigriseum*. 7-day old colonies at (A) CYA, (B), MEA, (C) YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. bialowiezense K. Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B 1927: 462, 1927

In *Penicillium* subgenus *Penicillium* section *Coronata* series *Olsonii*

Type: Herb. IMI 092237

Culture ex type: CBS 227.28 = IBT 23044 = IMI 092237 (T, Y), ex forest soil, Poland

Diagnostic features: ellipsoidal finely roughened conidia, long broad stipes with all elements short and appressed, quinolactacin, Raistrick phenols, mycophenolic acid, asperphenamate, poor growth on creatine, but good growth on nitrite-sucrose agar

Similar species: *P. bialowiezense* is closely related to *P. brevicompactum*. *P. bialowiezense* has shorter and less wide stipes than *P. brevicompactum*. *P. brevicompactum* consistently produces brevianamide A, while *P. bialowiezense* produces quinolactacin A consistently. Both species has shorter stipes and smaller colonies on CYA and YES than *P.olsonii*.

Description:

Conidiophores: Long, appressed, terverticillate

Conidia: Finely roughened subglobose to ellipsoidal, 2.5-3.5 µm x 2.0-3 µm

Phialides: Cylindrical with gradually tapering collula, 6.5-9 µm x 2.5-3 µm

Metulae: Cylindrical but apically inflated, 10-15 µm x 3-4.5 µm

Rami: 15-25 µm x 4-5 µm

Stipes: 250-400 µm x 4-6 µm, smooth-walled

Synnemata or fasciculation: None

Sclerotia: None

Colony texture on CYA: Velutinous

Conidium colour on CYA: Dull green to grey green

Exudate droplets on CYA: Often present, pale to reddish brown

Reverse colour on CYA: Beige to yellowish cream

Reverse colour on YES: Cream to cream beige

Diffusible colour on CYA: Pale or light brown

Ehrlich reaction: Red-violet

Odour and volatile metabolites: Not examined

Extrolites: 1) Raistrick phenols, 2) Mycophenolic acid, 3) Asperphenamate, 4) Breviones, 5) Quinolactacin A

Growth on creatine: Weak

Acid and base production on creatine: Weak acid production

Growth on UNO: Good

Growth on nitrite: Good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 11-25 mm; MEA: 9-16 mm; YES: 18-30 mm; CREA: 8-12 mm; Cz: 9-18 mm, OAT: 11-25 mm; CYAS: 21-31 mm; CzBS: 6-16 mm; CzP: 0 mm; UNO: 6-13 mm; DG18: 16-22 mm

Diam., CYA, 1 week: 15°C: 17-22 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.5-1.3], halotolerant

CYA15°C/CYA 25°C: 1.1 [0.8-1.9], psychrotolerant

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.8 [0.6-1.1]

CZP/CZ: 0

Distribution: Denmark, Faroe Islands, Poland, Italy, Slovenia, Chile, Wyoming, USA, Canada, Saudi-Arabia

Ecology and habitats: Forest soil, coffee cherries, mouldy mushrooms, seaweed, yoghurt, dried lamb meat, Brussels sprouts, sage, margarine, wheat bread, thyme, mouldy harness, air in factories.

Biotechnological applications: None

Biodeterioration & phytopathology: May degrade leather

Mycotoxins and mycotoxins: May grow in fruit yoghurts and cause intoxication, but the metabolites responsible are unknown (Frisvad, unpublished).

Typical cultures: IBT 13469, ex wheat, Denmark; IBT 20786 = CBS 110104, ex seaweed, Bellevue, Denmark; IBT 21225, ex soil under *Salix* sp. in dried root segment of Elisabeth Adams irrigation ditch, Centennial, Wyoming, USA; IBT 22460, ex soil under *Nothofagus* sp., Chile; IBT 22443 = CBS 110102, ex bread, Italy; IBT 13145, ex soil, conifer forest, Switzerland; IBT 21578 = CBS 112477, ex barley, Denmark; IBT 6510, ex *Thymus vulgaris*, Denmark; IBT 6500 = CBS 112478, ex margarine, Denmark.

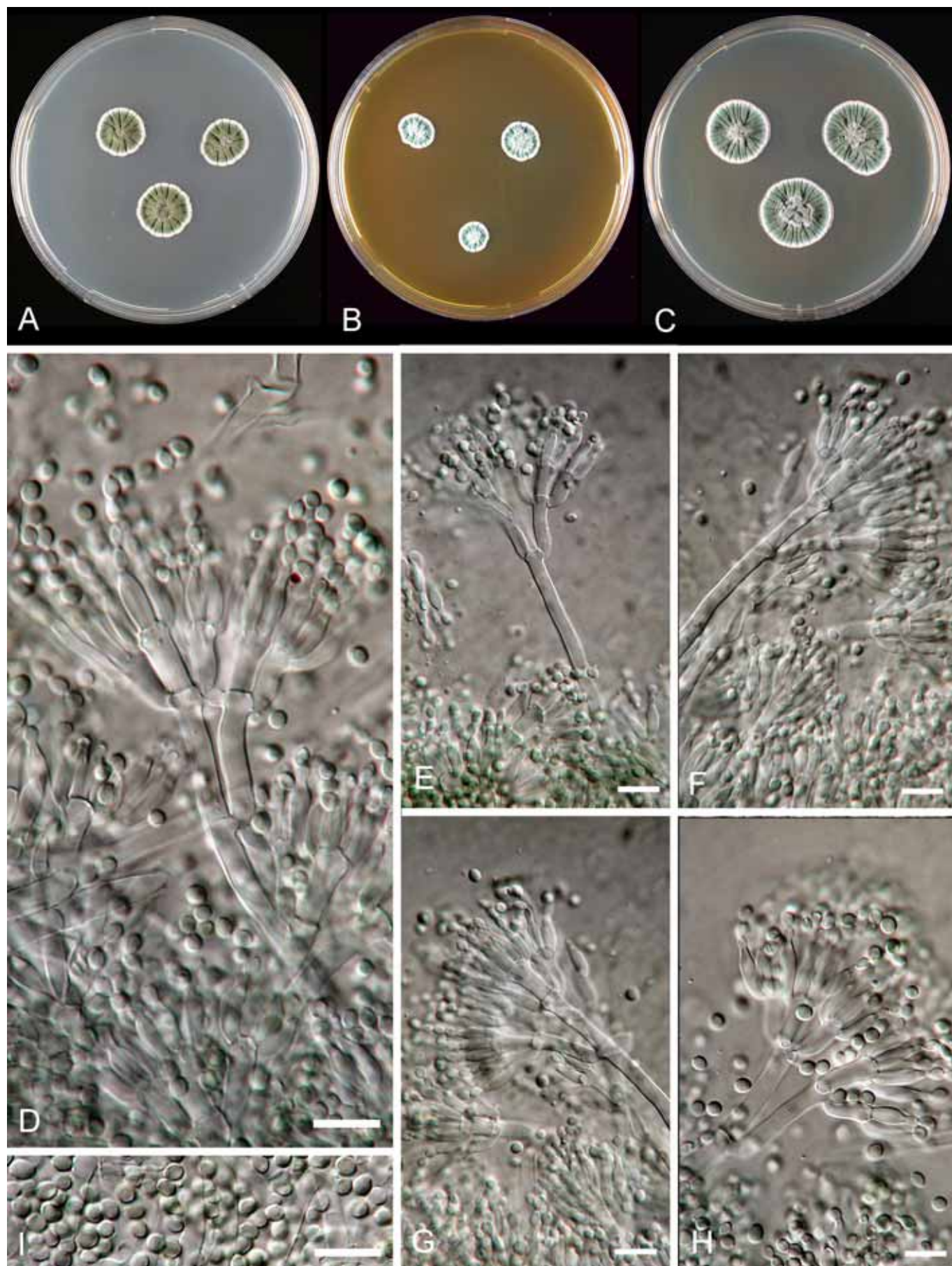


Fig. 31. *Penicillium bialowiezense*. 7-day old colonies at (A) CYA, (B), MEA, (C) YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. brevicompactum Dierckx, Ann. Soc. Scient. Brux. 25: 88, 1901

In *Penicillium* subgenus *Penicillium* section *Coronata* series *Olsonii*

Type: Herb. IMI 040225

Culture ex type: CBS 257.29 = CBS 110071 = IBT 23045 = IMI 040225 = ATCC 9056 = ATCC 10814 = FRR 862 = NRRL 862 = NRRL 863 = NRRL 2011 (T), ex unrecorded source.

Diagnostic features: Brevianamide A, mycophenolic acid, pebrolides, Raistrick phenols, finely roughened ellipsoidal conidia, short broad penicilli, apically inflated metulae.

Similar species: See *P. bialowiezense*.

Description:

Conidiophores: Long, appressed, terverticillate

Conidia: Finely roughened ellipsoidal, 2.5-3.5 µm x 2.0-2.5 µm

Phialides: Cylindrical with gradually tapering collula, 6.5-9 µm x 2.5-3 µm

Metulae: Cylindrical apically inflated, 10-15 µm x 3.5-4.5 µm

Rami: 15-25 µm x 4-5 µm

Stipes: 400-800 µm x 4-6 µm, smooth-walled

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Dull green to grey green

Exudate droplets on CYA: Pale to yellow or reddish brown

Reverse colour on CYA: beige to yellowish cream

Reverse colour on YES: Cream-coloured to beige, in few strains a conspicuous red reverse and diffusible pigment is produced

Diffusible colour on CYA: Pale or light brown

Ehrlich reaction: No reaction or yellow

Odour and volatile metabolites: Isobutanol, isopentanol (Larsen and Frisvad, 1995)

Extrolites: 1) Raistrick phenols; 2) Mycophenolic acids and mycochromenic acid, 3) Brevianamide A & B, 4) Asperphenamate, 5) Pebrolides, 6) Botryodiploidin, 7) 11-(5'-Epoxy-4'-hydroxy-3'-hydroxymethylcyclo-2'-hexenone)-Δ-8(12)-drimene, 8) Silvatins, 9) Brevigillide

Further extrolites reported: 10) Brevicompanins, 11) Brevioxims, 12) Adenophostins. The identity of the producing organisms has not been verified for the last three groups

Growth on creatine: Poor

Acid and base production on creatine: Most commonly no acid production, occasionally weak or good acid production

Growth on UNO: Good

Growth on nitrite: Moderate to good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 14-30 mm [atyp.: 8-11 mm]; MEA: 10-26 mm; YES: 20-36 mm; CREA: 4-18 mm; Cz: 9-18 mm, OAT: 16-26 mm; CYAS: (15-)21-26 mm; CzBS: 7-17 mm; CzP: 0 mm; UNO: 10-14 mm; DG18: 12-19 mm

Diam., CYA, 1 week: 15°C: 17-21 mm; 30°C: 0-3 mm; 37°C: 0 mm

CYA/CYAS: 0.9 [0.8-0.9], halotolerant

CYA15°C/CYA 25°C: 0.9 [0.7-1.0], psychrotolerant

CYA30°C/CYA 25°C: 0.1 [0-0.1]

CZBS/CZ: 0.9 [0.6-1.0]

CZP/CZ: 0

Distribution: Cosmopolitan. Denmark, Faroe Islands, Greenland, The Netherlands, Sweden, Svalbard, Norway, United Kingdom, Germany, Poland, France, Slovenia, Italy, Greece, Costa Rica, Venezuela, Columbia, Brazil, Chile, Connecticut, New Mexico, Wisconsin, South Carolina, USA, Canada, Ethiopia, India, Japan, Australia, Eastern Island (Chile). See also Domsch *et al.* (1980)

Ecology and habitats: Soil under conifers, agricultural soil, mouldy mushrooms, spruce cones, acorns, seaweed, sage, coffee cherries, apples, potatoes, barley, wheat, oats, sorghum, mouldy coffee beans, seaweed, air in factories, cod roe, mouldy bakers yeast, apricot puree, maple syrup, margarine, liver paté, salami and other processed foods, waste, dead insects, human bone, salt pans.

Biotechnological applications: Production of mycophenolic acid (mofetil) (brand name CellCept) (Bentley, 2000). This is used for treatment of many diseases, but is especially effective for prevention of rejection in heart and kidney transplantations (Bentley, 2000)

Biodeterioration & phytopathology: *P. brevicompactum* has been found growing actively on *Amanita citrina*, *Paxillus involutus*, *Flammulina velutipes*, *Boletus* spp., *Pleurotus ostreatus*, *Nectria rishbethii* and other macrofungi; it has also been found growing in cosmetics and on wood for building construction

Mycotoxins and mycotoxins: Mycophenolic acid is an antibiotic, with anti-tumor, anti-psoriasis and immunosuppressive features (Bentley, 2000) and may be of relevance for secondary mycotoxicosis (bacterial infections caused by intake of immunosuppressive mycotoxins). The other extrolites produced have not been reported to be mycotoxins in the strict sense of the word, except botryodiploidin. This mycotoxin is produced by some strains of *P. brevicompactum* (Fujimoto *et al.*, 1980 misidentified as *P. carneolutescens*; Frisvad, 1989)

Typical cultures: IBT 18329 = CBS 110067, ex soil under Juniper, Madrid, New Mexico, USA; IBT 21507 = IBT 6607 = CBS 480.84 = FRR 2938 (Y), ex *Raphanus* sp., Denmark; IBT 13151 = CBS 110068 = WSF 3531, ex soil, Wisconsin, USA; IBT 4342 = CBS 110072 = NRRL 867 = IMI 092219 = FRR 3719, ex unrecorded source (*P. griseobrunneum*); CBS 256.31 = IBT 23046 = IMI 089824 = NRRL 859 = FRR 859 = ATCC 10111 = IFO 5858, ex decomposing mushroom, Storrs, Connecticut, USA (*P. stoloniferum*); CBS 210.28 = IBT 23043 = IMI 092266, ex forest soil under conifers, Puszcza, Bialowieska, Poland (*P. patris-meae*); CBS 316.59 = IBT 23047 = IMI 092262 = NRRL 866 = FRR 866, ex soil under conifers, Tatra Mountains (*P. hagemii*); CBS 317.59 = IBT 23069 = IFO 5727 = FRR 1363 = IMI 068217 = ATCC 18311, ex soil, Japan (*P. brunneostoloniferum*); IBT 18098 = CBS 110069 = FRR 2455, ex artificial maple syrup, preserved with 650 ppm benzoic acid, Sydney, NSW, Australia.

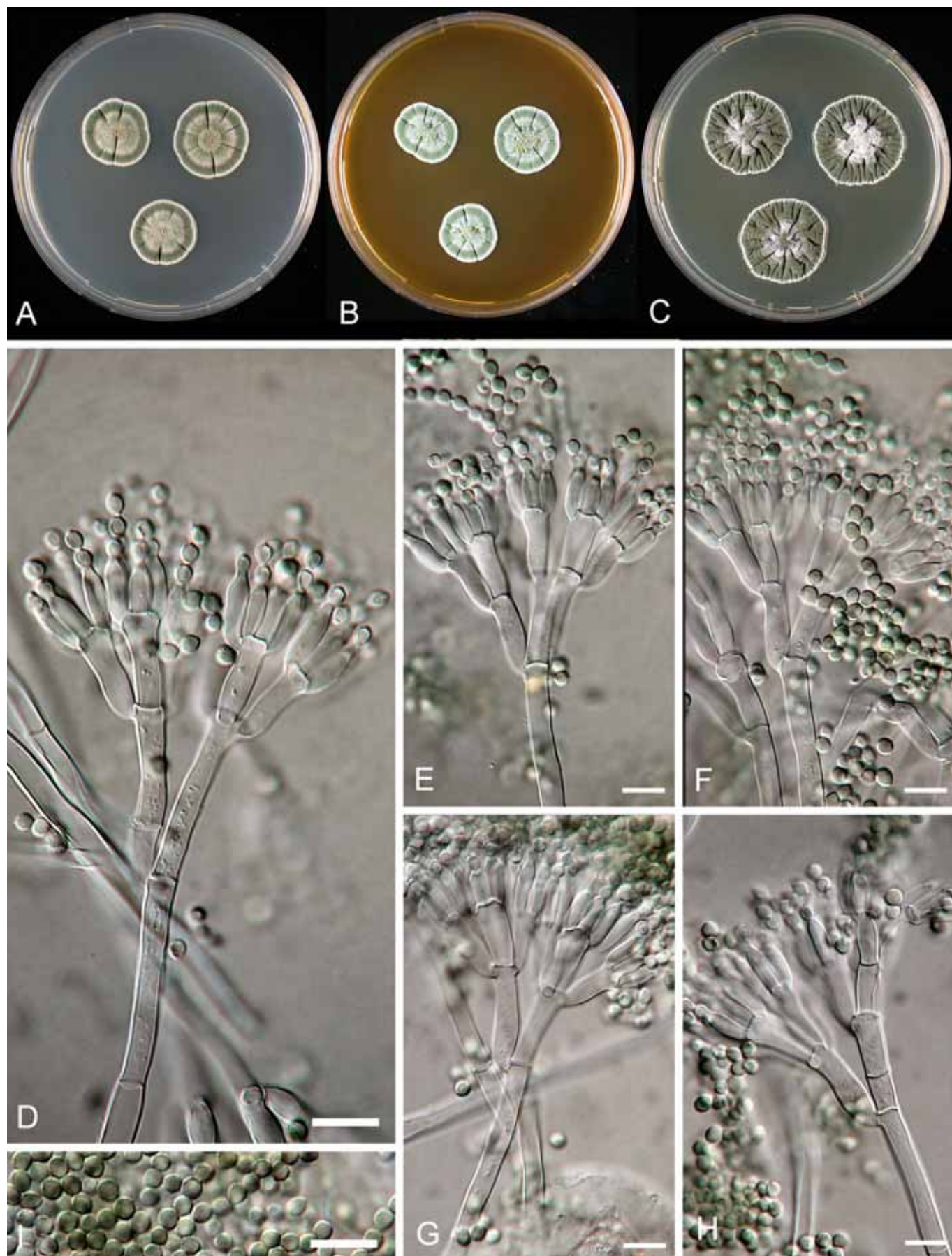


Fig. 32. *Penicillium brevicompactum*. 7-day old colonies at (A) CYA, (B), MEA, (C) YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. camemberti Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 82: 33, 1906

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Camemberti*

Type: Herb. IMI 027831

Culture ex type: CBS 299.48 = IBT 21508 = IBT 21604 = IMI 027831 = IMI 092200 = ATCC 1105 = ATCC 4845 = FRR 878 = LCP P11 = MUCL 29790 = NRRL 877 = NRRL 878 (T,Y)

Diagnostic features: Cyclopiazonic acid, white floccose colonies, poor sporulation

Similar species: Deteriorated strains of *P. commune* may look like *P. camemberti*. *P. camemberti* differs from *P. caseifulvum* by its poor sporulation and its inability to produce orange reverse colours on YES.

Description:

Conidiophores: Terverticillate to quaterverticillate, sometimes irregular structures

Conidia: Smooth-walled, globose to suglobose, 3.5-5 µm x 3.3-4.5 µm

Phialides: Cylindrical with long wide colulla, 10-13 µm x 2.5-3 µm

Metulae: Cylindrical 7.5-12 µm x 2.5-3.5 µm

Rami: Cylindrical, 15-25 µm x 3-4 µm

Stipes: 200-500 µm x 3-4 µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Floccose

Conidium colour on CYA: White or rarely grey green

Exudate droplets: None or few droplets (often large violet droplets on CREA)

Reverse colour on CYA: Pale, cream-coloured or yellowish

Reverse colour on YES: Cream yellow

Diffusible colour: none

Ehrlich reaction: Violet (no reaction in few old isolates)

Odour and volatile metabolites: 3-octanone, ethylacetat, isobutanol, ethyl isobutanoate, isobutyl acetate, styrene, 1-octen-3-ol, 3-octanol, ethyl hexanoate, 2-methyl-isoborneol (Larsen and Frisvad, 1995)

Extrolites: 1) Cyclopiazonic acids, 2) Cyclopaldic acid (rare), 3) Rugulovasine A & B (rare), 4) Aspereynone-like compounds, 5) Palitantin (rare)

Growth on creatine: Very good

Acid and base production on creatine: Moderate to good acid production followed by base production

Growth on UNO: Very good

Growth on nitrite: Weak or moderate

Abiotic factors:

Diam., 1 week, 25°C: CYA: 19-27 mm; MEA: 12-27 mm; YES: 23-38 mm; CREA: 9-17 mm; Cz: 13-20 mm, OAT: 10-21 mm; CYAS: 14-33 mm; CzBS: 6-17 mm; CzP: 0-1 mm; UNO: 13-18 mm; DG18: 14-27 mm

Diam., CYA, 1 week: 15°C: 14-26 mm; 30°C: 0-3 mm; 37°C: 0 mm

CYA/CYAS: 1 [0.8-1.2], halotolerant

CYA15°C/CYA 25°C: 1.0 [0.8-1.3], psychrotolerant

CYA30°C/CYA 25°C: 0 [0-0.2]

CZBS/CZ: 0.8 [0.5-1.3]

CZP/CZ: 0 [0-0.1]

Distribution: This domesticated species has been found in countries where white mould cheeses are produced and sold.

Ecology and habitats: On white mould cheeses (brie, camembert etc.). This species is a domesticated from of *P. commune* Thom. The species has never been found outside the white mould cheese environment. Occasionally cross-contaminating other cheeses in refrigerators.

Biotechnological applications: Production of white mould cheeses

Biodeterioration & phytopathology: -

Mycotoxicoeses and mycotoxins: Cyclopiazonic acid is produced by some strains

Typical cultures: IBT 21601 = CBS 123.08 = NRRL 874 = ATCC 10387 = IMI 091932 (*P. camemberti* var. *rogeri*), ex French camembert cheese; IBT 11754 = CBS 303.48 = ATCC 10423 = FRR 875 = IMI 028810 = MUCL 29156 = NRRL 875 = UPSC 3178 (*P. caseicola*), ex French camembert cheese; IBT 21602 = CBS 112325 = NRRL 876 (*P. candidum* Roger), IBT 3505 = CBS 112479 (NB *P. commune* like back-mutation), ex French camembert cheese, "Prairie", IBT 15441 = CBS 112562, ex brie, Denmark; IBT 11568 = CBS 249.77A, ex German camembert cheese, T65 = IBT 11755 = CBS 190.67, ex Dutch camembert cheese; IBT 14856 = CBS 112078, ex Appenzeller cheese, Switzerland; CBS 160.42; IBT 11570 = CBS 131.67 = MUCL 8446, ex French brie cheese; CBS 133.67, ex French camembert cheese; CBS 248.77, Germany; IBT 13592 = CBS 273.97, ex dust, Denmark; IBT 23943 = Kulmbach Sp. 2491, Germany; IBT 23941 = ATCC 42009 = Kulmbach Sp. 912, ex camembert cheese.

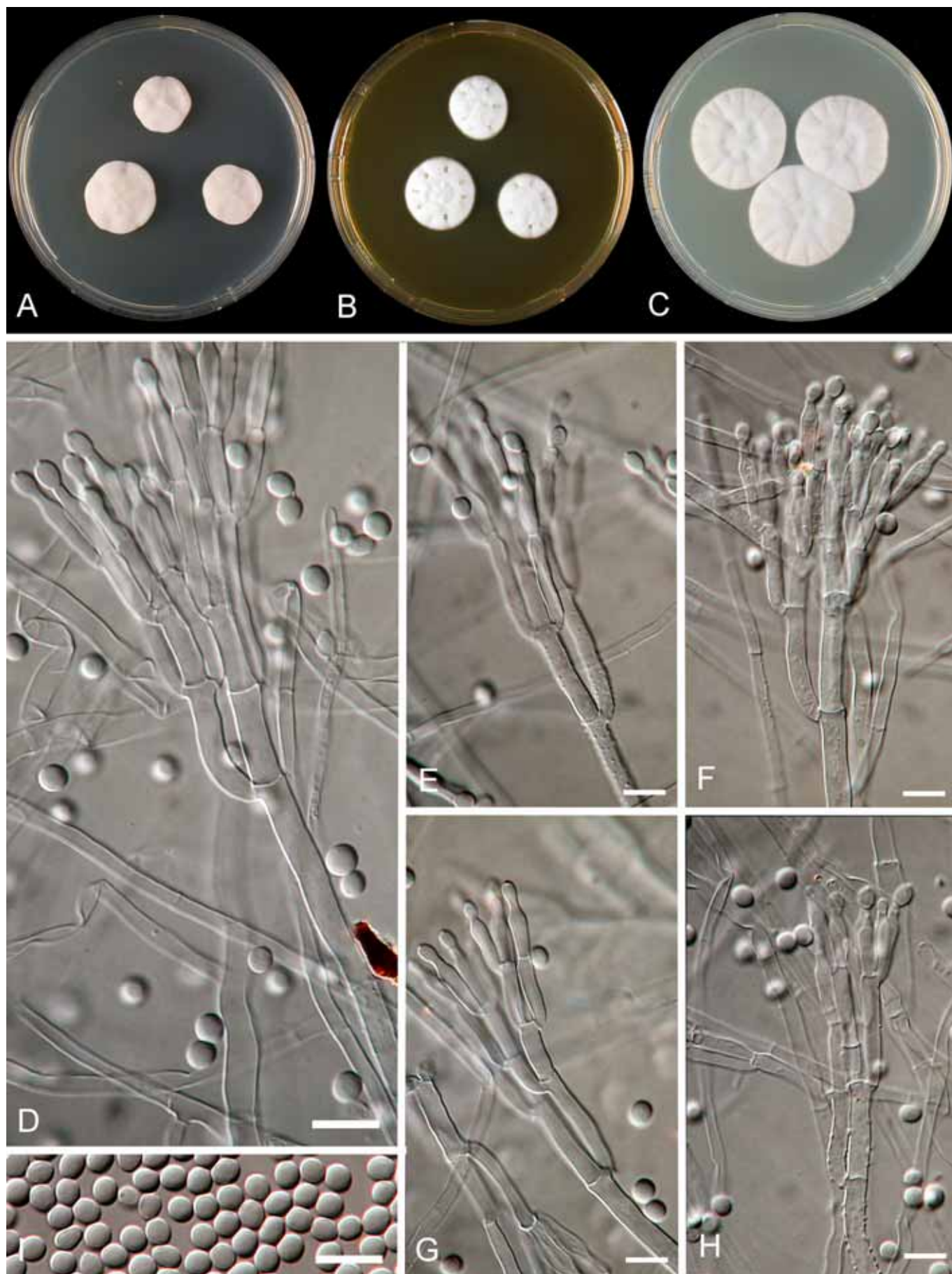


Fig. 32. *Penicillium camemberti*. 7-day old colonies at (A) CYA, (B) MEA, (C) YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

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

In *Penicillium* subgenus *Penicillium* section *Roqueforti* series *Roqueforti*

Type: Herb. IMI 293204

Culture ex type: CBS 112297 = IBT 6884 = IBT 18419 = IMI 293204 = ATCC 58624, ex rye bread, Denmark (T)

Diagnostic features: Mycophenolic acid, patulin, roquefortine C, isofumigaclavine A & B, penitrem A, globose large smooth-walled conidia, rough-walled stipes, high growth rate on all media, growth on propionic acid and acetic acid, growth at low oxygen and large carbon dioxide levels.

Similar species: *P. carneum* differs from *P. roqueforti* by its inability to produce the dark green reverse colour on CYA and from *P. paneum* by its strong smell of isobutanol and geosmin.

Description:

Conidiophores: Terverticillate, occasionally quarterverticillate, appressed elements, borne from subsurface hyphae

Conidia: smooth-walled, globose, 3.5-5 µm

Phialides: Cylindrical with short collula, 8-10 µm x 2.5-3.0 µm

Metulae: Cylindrical, 10-17 µm x 3-4 µm

Rami: Cylindrical, 17-35 µm x 3-4 µm

Stipes: Rough-walled often warted, 100-200 µm x 4-5 µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Pistacio green to dark American green

Exudate droplets on CYA: None or clear droplets

Reverse colour on CYA: Beige to brown

Reverse colour on YES: Cream beige to curry

Diffusible colour on CYA: None

Ehrlich reaction: Violet

Odour and volatile metabolites: Isopentanol, geosmin, 2-methyl-3-butene-2-ol, isobutanol, 1-octene, isopentyl acetate, 1-methoxy-3-methyl-benzene (Larsen & Frisvad, 1995)

Extrolites: 1) Cyclopaldic acid and chromanols, 2) Mycophenolic acids, 3) Patulin, 4) Penicillic acid (only produced by CBS 449.78); 5) Roquefortine C, 6) Penitrem A; 7) Isofumigaclavine A

Growth on creatine: Very good

Acid and base production on creatine: Acid production in margin of colony

Growth on nitrite: Good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 36-53 mm; MEA: 35-56 mm; YES: 51-74 mm; CREA: 27-35 mm; Cz: 23-34 mm, OAT: 34-72 mm; CYAS: 33-35 mm; CzBS: 17-38 mm; CzP: 23-34 mm; UNO: 28-36 mm; DG18: 39-44 mm

Diam., CYA, 1 week: 15°C: 32-36 mm; 30°C: 11-26 mm; 37°C: 0 mm

CYA/CYAS: 1.2 [1.1-1.2]

CYA15°C/CYA 25°C: 0.9 [0.8-0.9]

CYA30°C/CYA 25°C: 0.3 [0.3-0.6]

CZBS/CZ: 1.0 [0.7-1.1]

CZP/CZ: 0.9 [0.7-1.1]

High resistance to acid and good growth at high CO₂ levels.

Distribution: Denmark, Norway, Sweden, Germany, Great Britain, USA, Canada

Ecology and habitats: Dried meat, silage, rye bread, water, beer, (barley), cheddar cheese, mouldy bakers yeast, cork

Biotechnological applications: None

Biodeterioration & phytopathology: This fungus may deteriorate silage, other lactic acid fermentation products, and beer.

Mycotoxins and mycotoxins: Patulin, penitrem A, mycophenolic acid, (penicillic acid), isofumigaclavine A are all mycotoxins that can be produced potentially in silage and other acid containing products. *P. carneum* was involved in mycotoxicosis of a man drinking beer contaminated with *P. carneum* (IBT 11188) (reidentified by us, originally identified as *P. crustosum*). The beer contained both penitrem A and isofumigaclavine A (Cole *et al.*, 1983)

Typical cultures: IBT 21509 = IBT 3473 = IBT 6753 = CBS 449.78, ex cheddar cheese, USA (Y); IBT 6892 = CBS 468.95, ex salami, Germany; IBT 6885 = IBT 3472 = CBS 466.95, ex salami, Germany; IBT 3466 = CBS 467.95, ex water tank, Denmark; IBT 19478 = CBS 390.78, ex raw sausage, Germany; IBT 15600 = CBS 112489, ex chilled food, France; IBT 6888 = CBS 112487, ex *Hordeum vulgare*, Denmark; NRRL 1168 = IBT 16402, Ottawa, Canada; NRRL 855 = IBT 16434; IBT 11188, ex beer intoxicating man, Georgia, USA.

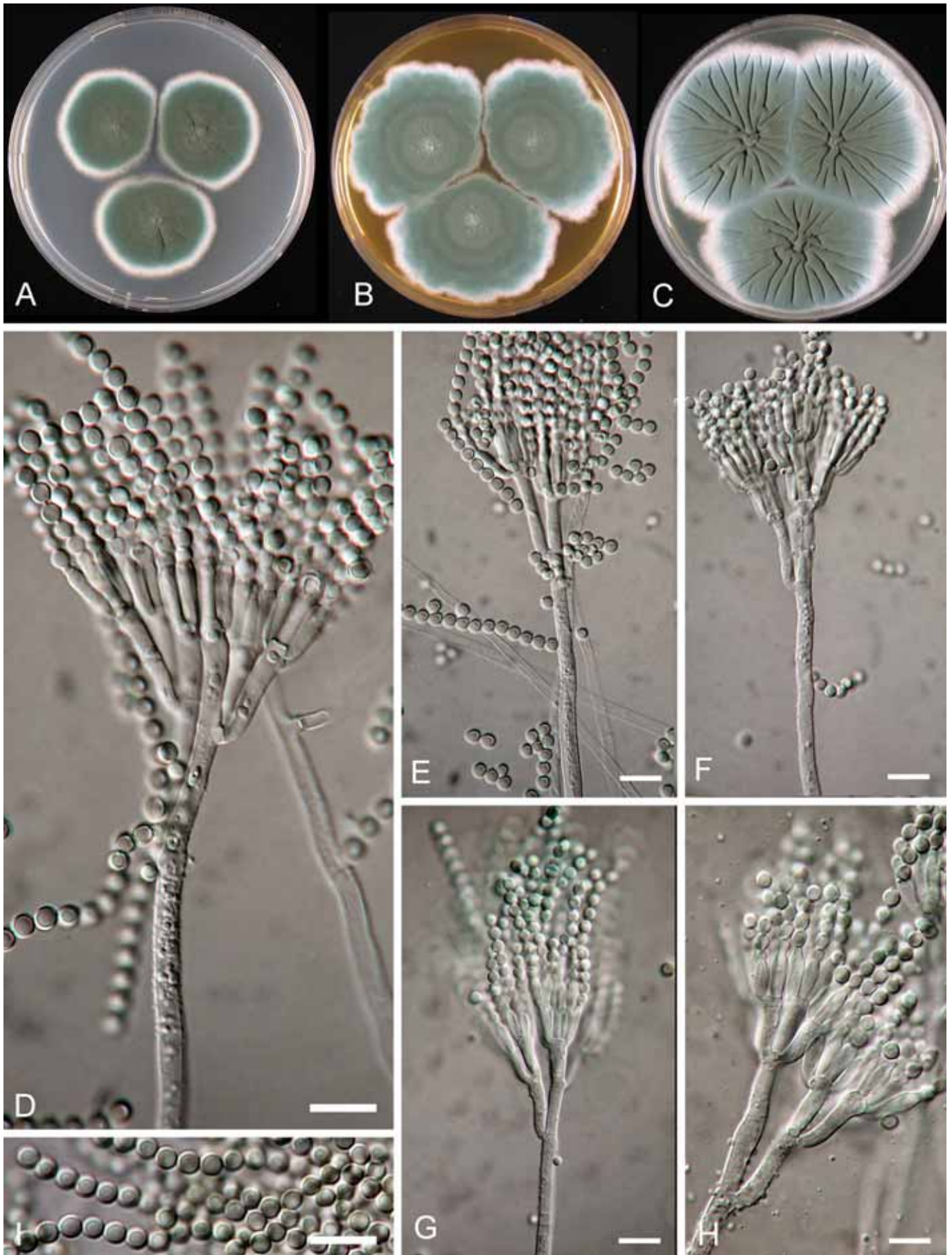


Fig. 33. *Penicillium carneum*. 7-day old colonies at (A) CYA, (B), MEA, (C) YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. caseifulvum Lund, Filt. & Frisvad, J. Food Mycol. 1: 97, 1998

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Camemberti*

Type: Herb. C 24999

Culture ex type: CBS 101134 = IBT 21510 = IBT 18282 (T,Y), ex Danish blue cheese

Diagnostic features: Cyclopeptin, rugulovasine A, smooth-walled conidia, floccose colonies, good growth on CREA, weak but consistent growth on CzP (1000 ppm propionic acid, pH 3.5)

Similar species: *P. caseifulvum* differs from *P. camemberti* by an orange reverse on YES agar.

Description:

Conidiophores: Born from aerial hyphae, terverticillate

Conidia: Smooth-walled, subglobose to broadly ellipsoidal, 3-5 µm x 2.5-3.5 µm

Phialides: Cylindrical with short narrow collula, 7-13 µm x 2.8-3.5 µm

Metulae: Cylindrical, 10-13 µm x 3.5-4.5 µm

Rami: Cylindrical, 12-25 µm x 4-5 µm

Stipes: 300-800 µm x

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Floccose

Conidium colour on CYA: Greyish green to greyish blue green (turquoise)

Exudate droplets on CYA: Small clear droplets at colony margin

Reverse colour on CYA: Creamish yellow to brown yellow

Reverse colour on YES: Vividly orange, rarely only cream yellow

Diffusible colour on CYA: None

Ehrlich reaction: Violet (weak reaction)

Odour and volatile metabolites: Not examined

Extrolites: 1) Cyclopeptin, 2) Rugulovasine A and B

Growth on creatine: Very good growth

Acid and base production on creatine: Good acid production followed by base production

Growth on UNO: Very good

Growth on nitrite: Very good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 15-24 mm; MEA: 16-28 mm; YES: 32-42 mm; CREA: 13-24 mm; Cz: 21-24 mm, OAT: 22-25 mm; CYAS: 23-33 mm; CzBS: 15-22 mm; CzP: 3-5 mm; UNO: 17-23 mm; DG18: 21-24 mm

Diam., CYA, 1 week: 5°C: 3-8 mm; 15°C: 18-23 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.7-1.0]

CYA15°C/CYA 25°C: 0.9 [0.8-1.1]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.9 [0.7-1.0]

CZP/CZ: 0.2 [0.1-0.2]

Distribution: Denmark, France, Germany

Ecology and habitats: Blue mould cheeses and some other German and French cheeses

Biotechnological applications: *P. caseifulvum* has been found to colonize some of the most highly regarded blue mould cheeses (unpublished results). White mould type cheeses have been made on an experimental basis with *P. caseifulvum*. These cheeses were turquoise on the surface and appeared to be of a very fine quality (unpublished results). Not producing cyclopiazonic acid, *P. caseifulvum* could be a potential new candidate for fermenting cheeses or salami.

Biodeterioration & phytopathology: The growth of *P. caseifulvum* on the surface of blue mould cheeses can be seen as biodeterioration, but also regarded as an indicator of very good quality.

Mycotoxicoses and mycotoxins: Rugulovasine A is a potential mycotoxin, but no relevant toxicity data (oral, skin or pulmonary toxicity) are available.

Typical cultures: IBT 19782 = CBS 108956, ex Danish blue cheese; IBT 18725 = CBS 108957, ex Danish blue cheesew, Bornhom; IBT 19801 = CBS 111838, ex French cheese (Saint Lactaire); IBT 19802 = CBS 111837, ex French goat cheese; IBT 23156 = CBS 112324, ex German Montagnolo cheese; IBT 23155 = CBS 112323, ex Danish blue cheese; IBT 20915 = CBS 111836, ex Danish blue cheese.

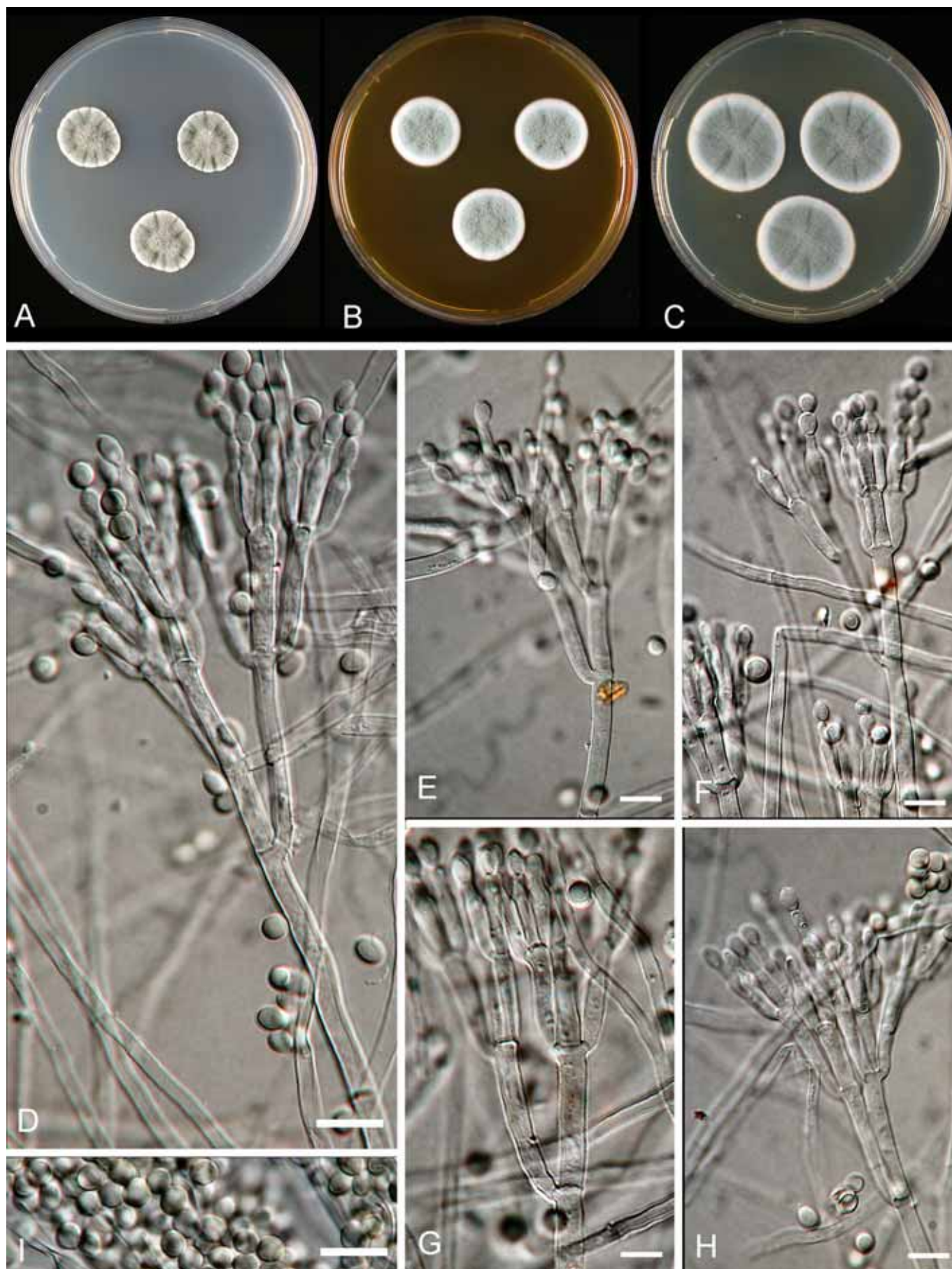


Fig. 35. *Penicillium caseifulvum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

***P. cavernicola* Frisvad & Samson, sp. nov.**

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Solita*

Type: Herb. CBS 100540

Culture ex type: IBT 14499 = CBS 100540, ex wall of the Lechuiguilla Cave, Carlsbad, New Mexico, USA (T)

Diagnostic features: Territrems, aurantiamine, asteltoxin, dark green rough-walled conidia, yellow brown reverse on CYA, good growth on CREA, no growth at 30°C

Similar species: Differs from *P. solitum*, *P. echinulatum* and *P. discolor* by its yellow brown reverse on CYA.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Rough-walled, globose to subglobose, 3.5-4.5 µm.

Phialides: Cylindrical tapering to a distinct collulum, 8-11 µm x 2.2-3.0 µm

Metulae: Cylindrical, 10-15 µm x 2.5-3.5 µm

Rami: Cylindrical, 12-20 µm x 3.2-4.2 µm

Stipes: Rough-walled, 300-550 µm x 3.5-4.2 µm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Dark green,

Exudate droplets on CYA: Present, clear

Reverse colour on CYA: Yellow brown

Reverse colour on YES: Strongly yellow

Diffusible colour on CYA: None

Ehrlich reaction: None (yellow in two isolates)

Odour and volatile metabolites: No data

Extrolites: 1) Territrems and arisugacins, 2) Asteltoxin, 3)

Aurantiamine, 4) Glyanthrypine, 5) Dipodazin, 6) Asperey-none-like compounds

Growth on creatine: Very good

Acid and base production on creatine: Weak to moderate acid, delayed base production

Growth on UNO: Moderate to good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 23-33 mm; MEA: 20-32 mm; YES: 28-44 mm; CREA: 18-23 mm; Cz: 20-23 mm, OAT: 17-28 mm; CYAS: 30-38 mm; CzBS: 12-18 mm; CzP: 0-1 mm; UNO: 13-19 mm; DG18: 22-27 mm

Diam., CYA, 1 week: 15°C: 16-27 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.8-0.9]

CYA15°C/CYA 25°C: 0.8 [0.6-0.9]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.7 [0.6-0.8]

CZP/CZ: 0.02 [0-0.04]

Distribution: Germany, New Mexico (USA), Venezuela, Japan

Ecology and habitats: Found twice on walls in caves, but also on butter and salami

Biotechnological applications: Can be potentially used to produce arisugacins.

Biodeterioration & phytopathology: May degrade lipid containing foods

Mycotoxicoeses and mycotoxins: Produces territrems, tremorgenic mycotoxins, but appear to be too rare to cause significant mycotoxicoeses

Typical cultures: IBT 5265 = CBS 109557 = FRR 1621 = IFO 5341, ex butter, Japan; IBT 3235 = CBS 109556 = Kulmbach Sp. 1894, ex salami, Germany; CBS 109558 = IBT 21194, ex bat cave, Venezuela (Y).

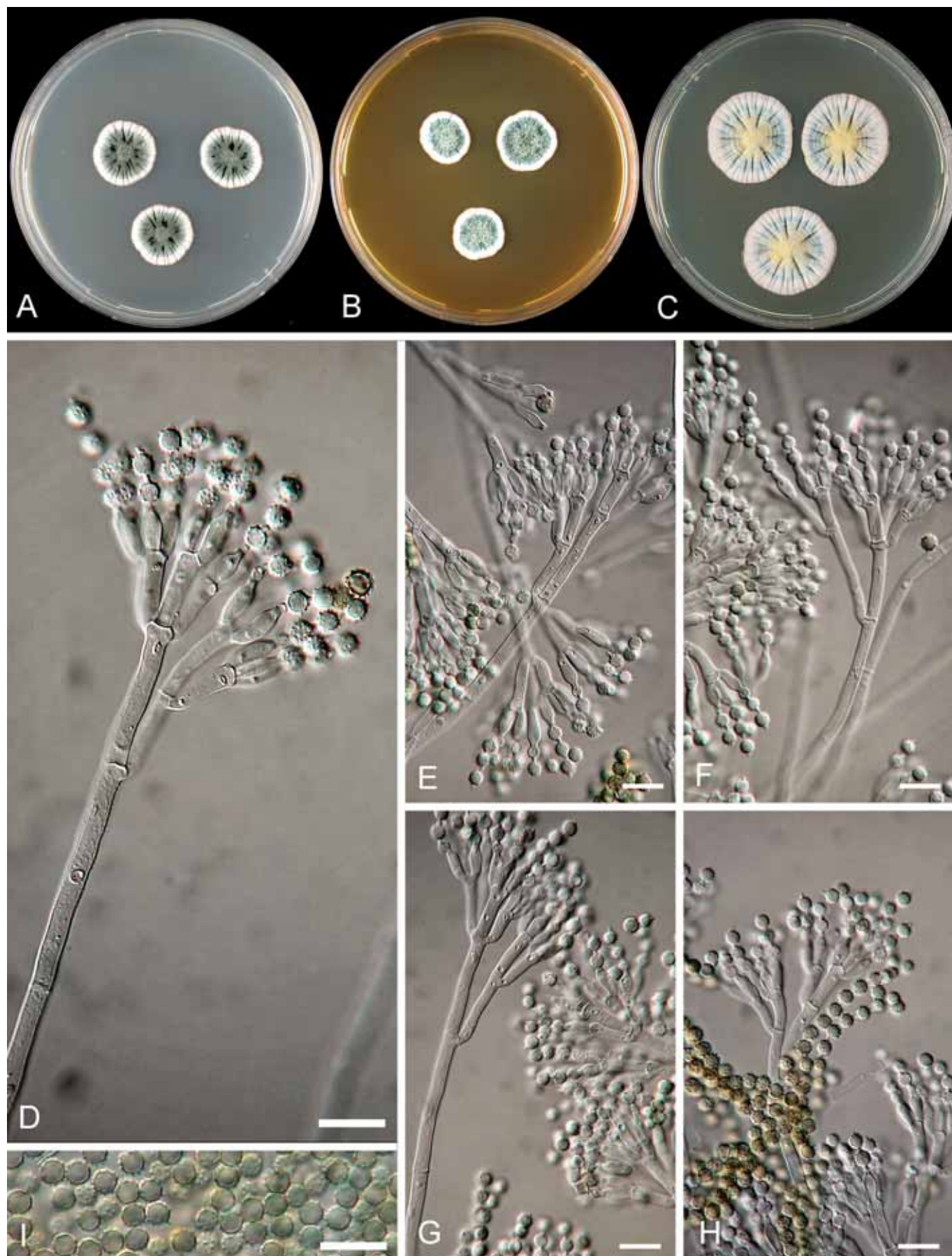


Fig. 36. *Penicillium cavernicola*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. chrysogenum Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 58, 1910

In *Penicillium* subgenus *Penicillium* section *Chrysogena* series *Chrysogena*

Type: Herb. IMI 024314

Culture ex type: CBS 306.48 = IBT 5233* = IMI 024314 = IMI 092208 = ATCC 10106 = CCRC 30564 = FRR 807 = MUCL 29079 = MUCL 29145 = NRRL 807 = NRRL 810 = QM 7500, ex cheese, Connecticut, USA (T)

Diagnostic features: Roquefortine C & D, chrysogine, penicillin F & G, globose to subglobose to broadly ellipsoidal smooth-walled conidia, relatively short phialides with short broad collula, high growth rate on YES with a yellow reverse and strong sporulation.

Similar species: *P. flavigenum* is most closely related to *P. chrysogenum*, but differs by the slower growth rate on CYAS and the deep yellow reverse on YES agar.

Description:

Conidiophores: Bi-, ter- and quarterverticillate, both appressed and divergent rami born from aerial and subsurface hyphae

Conidia: Smooth-walled, globose to subglobose to broadly ellipsoidal, 2.5-4 µm x 2.3-3.5 µm

Phialides: Cylindrical, with short broad collula, 7-9 µm x 2.3-2.5 µm

Metulae: Cylindrical, 8-12 µm x 2.5-4 µm

Rami: Cylindrical, 15-20 µm x 3-4 µm

Stipes: 200-300 µm x 3-4 µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Floccose to velutinous

Conidium colour on CYA: Blue green to green

Exudate droplets on CYA: Often present, copious, yellow

Reverse colour on CYA: Cream, yellow, rarely brown

Reverse colour on YES: Citrine Yellow

Diffusible colour: Yellow pigment often produced

Ehrlich reaction: No reaction or yellow reaction

Odour and volatile metabolites: 3-octanone, 1-heptene, 1,3-octadiene, 3-heptanone, 1-nonene, 1-octen-3-ol, 3-octanol, (pineapple odour at low water activities) (Larsen and Frisvad, 1995)

Extrolites: 1) Penicillins, 2) Roquefortine C and meleagrins, 3) Chrysogine, 4) Xanthocillins, 5) Secalonic acids, 6) Sorrentanone and sorbicillin 7) PR-toxin

Growth on creatine: Weak

Acid and base production on creatine: none or poor, no base production

Growth on UNO: Very good

Growth on nitrite: Occasionally good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 23-46 mm; MEA: 19-52 mm; YES: 40-64 mm; CREA: 16-26 mm; Cz: 18-33 mm, OAT: 18-42 mm; CYAS: 27-43 mm; CzBS: 7-24 mm; CzP: 0 mm; UNO: 15-29 mm; DG18: 29-41 mm

Diam., CYA, 1 week: 5°C: 1-4 mm; 15°C: 15-26 mm; 30°C: 14-27 mm; 37°C: 0-7 mm

CYA/CYAS: 0.9 [0.8-1.1]

CYA15°C/CYA 25°C: 0.6 [0.4-0.7]

CYA30°C/CYA 25°C: 0.6 [0.4-0.8]

CZBS/CZ: 0.6 [0.3-0.9]

CZP/CZ: 0

Distribution: Panglobal, very common

Ecology and habitats: Indoor environments, deserts, dried foods, salterns, cheese

Biotechnological applications: Production of penicillin and xanthocillin X, treatment of pulp mill waste, production of polyamine oxidase, polyamide oxidase, phospho-gluconate dehydrogenase, glucose oxidase, and also used for biotransformations.

Biodeterioration & phytopathology: Building materials are deteriorated

Mycotoxins and mycotoxins: PR-toxin, roquefortine C, secalonic acids have been regarded as mycotoxins

Typical cultures: IBT 14462 = CBS 776.95, ex Lechuquilla Cave, Carlsbad, New Mexico, USA; IBT 5304* = CBS 775.95, ex air in kitchen, Denmark; T84 = IBT 21511 = CBS 478.84 (Y), ex air, Denmark; IBT 22809 = CBS 111216, ex saltern, Slovenia; IBT 21928* = CBS 111215, ex sage; IBT 23019 = CBS 205.57 = ATCC 8537 = ATCC 9478 = CECT 2306 = IMI 015378 = NRRL 1209 = NRRL 824 = QM 6749, ex culture contaminant, UK; IBT 22777 = CBS 111214, ex wheat bread, Italy; IBT 5848* = CBS 112208, ex soil, China; IBT 23022* = CBS 412.69, ex soil, Syria (*P. harmonense*); IBT 6048 = IBT 4344* = CBS 355.48 = NRRL 821 = IMI 039759ii = ATCC 10108 = IHM 3181 = MUCL 31327 = QM 7601, ex decaying branch of *Hyssopus* sp., Norway (*P. notatum*); IBT 3363* = FRR 1142 = ATCC 48908, ex snack food, Sydney, NSW, Australia; IBT 19373* = CBS 289.53 = IMI 089373, ex gelatine, UK (the only strain found that does not produce meleagrins, but does produce emodic acid and ω-hydroxyemodin); CBS 307.48 = FRR 1951 = NRRL 1951 = IMI 040233 = CECT 2802 = QM 941 = VTT D-88381, ex *Citrullus lenotus*, Illinois, USA; IBT 4395 = IBT 6067 = NRRL 820 = IMI 092220 (*P. griseoroseum*); IBT 4350 = IBT 6062 = CBS 349.48 = NRRL 836 = ATCC 10468 = IFO 8143 = IMI 039762 = QM 7598 (AUT, *P. meleagrinum*); IBT 3361 = IMI 041606 (*P. camerunense*); IBT 3363 = IMI 092241 (*P. flavidomarginatum*); IMI 129964 (*P. aromaticum* var. *microsporum*)

*These isolates produce the unknown indole metabolite Ø

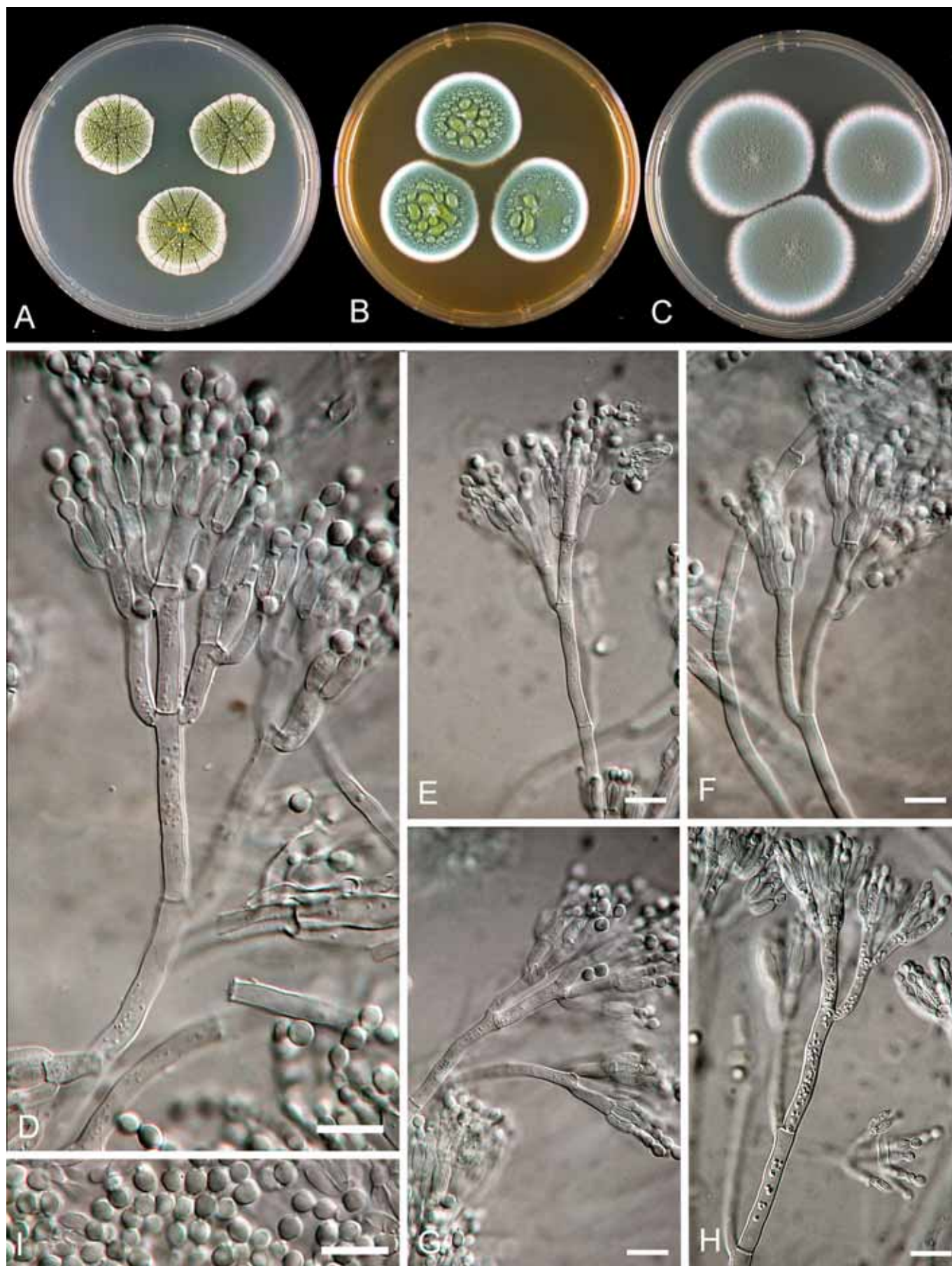


Fig. 37. *Penicillium chrysogenum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. clavigerum Demelius, Verh. Zool.-Bot. Ges. Wien 72: 74, 1922

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Claviformia*

Type: Herb. IMI 039807

Culture ex type: CBS 255.94 = CBS 310.48 = IBT 21512 = IBT 14993 = IMI 039807 = NRRL 1003 = ATCC 10427, ex man, Winnipeg, Manitoba, Canada (T, Y)

Diagnostic features: Long acicular synnemata especially on OAT and MEA, ellipsoidal smooth-walled conidia, patulin, penitrem A, asperfuran, very poor growth on CYAS, poor growth on CREA with no acid production.

Similar species: *P. clavigerum* differs from *P. vulpinum* by its thin acicular synnemata.

Description:

Conidiophores: Born on the synnemata rarely from aerial mycelium, sometimes sinuous, very long growing along the synnema, 3.5-4.5 µm wide

Conidia: Smooth-walled, ellipsoidal, 3-4 µm x 2.2-3 µm

Phialides: Cylindrical, slowly tapering to a short but distinct collum, 7-9 µm x 2-3 µm

Metulae: Cylindrical, 10-12 µm x 3.5-4 µm

Rami: 12-15 µm x 3.5-4.5 µm

Stipes: Smooth walled, rough at the base,

Synnemata or fasciculation: Long acicular synnemata with conidiophores born along the entire length

Sclerotia: None

Colony texture: Coremiform, synnemata 10-40 mm

Conidium colour on CYA: Grey green near tea green and slate olive

Exudate droplets on CYA: Absent

Reverse colour on CYA: Dark brown

Reverse colour on YES: Yellow to yellow or orange brown

Diffusible colour on CYA: Often present, yellow to orange brown,

Ehrlich reaction: No or yellow reaction in one isolate a violet reaction

Odour and volatile metabolites: Geosmin, thujopsene, ethyl acetate, ethyl isobutanoate, isobutyl acetate, ethyl 2-methylbutanoate, ethyl isopentanoate, styrene (Larsen & Frisvad, 1995)

Extrolites: 1) Patulin, 2) Asperfuran, 3) Norlichexanthone, 4) TAN-1612, 5) Penitrem A, 6) Cyclopiazonic acid, 7) Viomellein

Growth on creatine: Poor

Acid and base production on creatine: No acid (nor base) production

Growth on UNO: Weak

Growth on nitrite: Good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 13-31 mm; MEA: 17-37 mm; YES: 17-32 mm; CREA: 13-28 mm; Cz: 20-27 mm, OAT: 25-37 mm; CYAS: 0-8 mm; CzBS: 0-11 mm; CzP: 0 mm; UNO: 3-7 mm; DG18: 10-18 mm

Diam., CYA, 1 week: 15°C: 10-13 mm; 30°C: 7-13 mm; 37°C: 0 mm

CYA/CYAS: 6.3 [3-11.5]

CYA15°C/CYA 25°C: 0.6 [0.3-0.8]

CYA30°C/CYA 25°C: 0.5 [0.4-0.6]

CZBS/CZ: 0.6 [0-0.6] (5 isolates no growth on CzBS, 2 isolates 0.5 & 0.6)

CZP/CZ: 0

Distribution: UK, DC & Wyoming, USA, Alberta & Manitoba, Canada

Ecology and habitats: Found in soil, associated to rodents has been found twice in hospitals.

Biotechnological applications: None

Biodeterioration & phytopathology: None

Mycotoxins and mycotoxins: Penitrem A, patulin, cyclopiazonic acid, viomellein are produced, but *P. clavigerum* has not yet been found in foods.

Typical cultures: IBT 14991 = NRRL 1004, Inst. Of Health, Washington DC, USA; IBT 5523 = IBT 3507 = IBT 3830 = IMI 297557; USA; IBT 18977 = CBS 112482 = UAMH 2766, ex gopher hair, Cardston, Alta., Canada; IBT 18974 = CBS 112564 = UAMH 452, rodent survey, Alberta, Canada; IBT 18973 = CBS 112563 = UAMH 450, rodent survey, Alberta, Canada; IBT 19361 = CBS 112484 = IMI 299048, USA; IBT 20478 = CBS 112483, ex soil, rodent hole, Laramie Basin, Wyoming, USA; IBT 18976 = CBS 112436 = UAMH 2767, ex gopher hair, Cardston, Alta., Canada; IBT 19355 = IFO 5755 = FAT 1161, ex soil, Japan; IMI 224631 = CBS 189.89, ex soil, UK; IBT 3461 = IBT 3767 = IBT 3784 = IBT 5482 = IBT 5524, ex soil, UK.

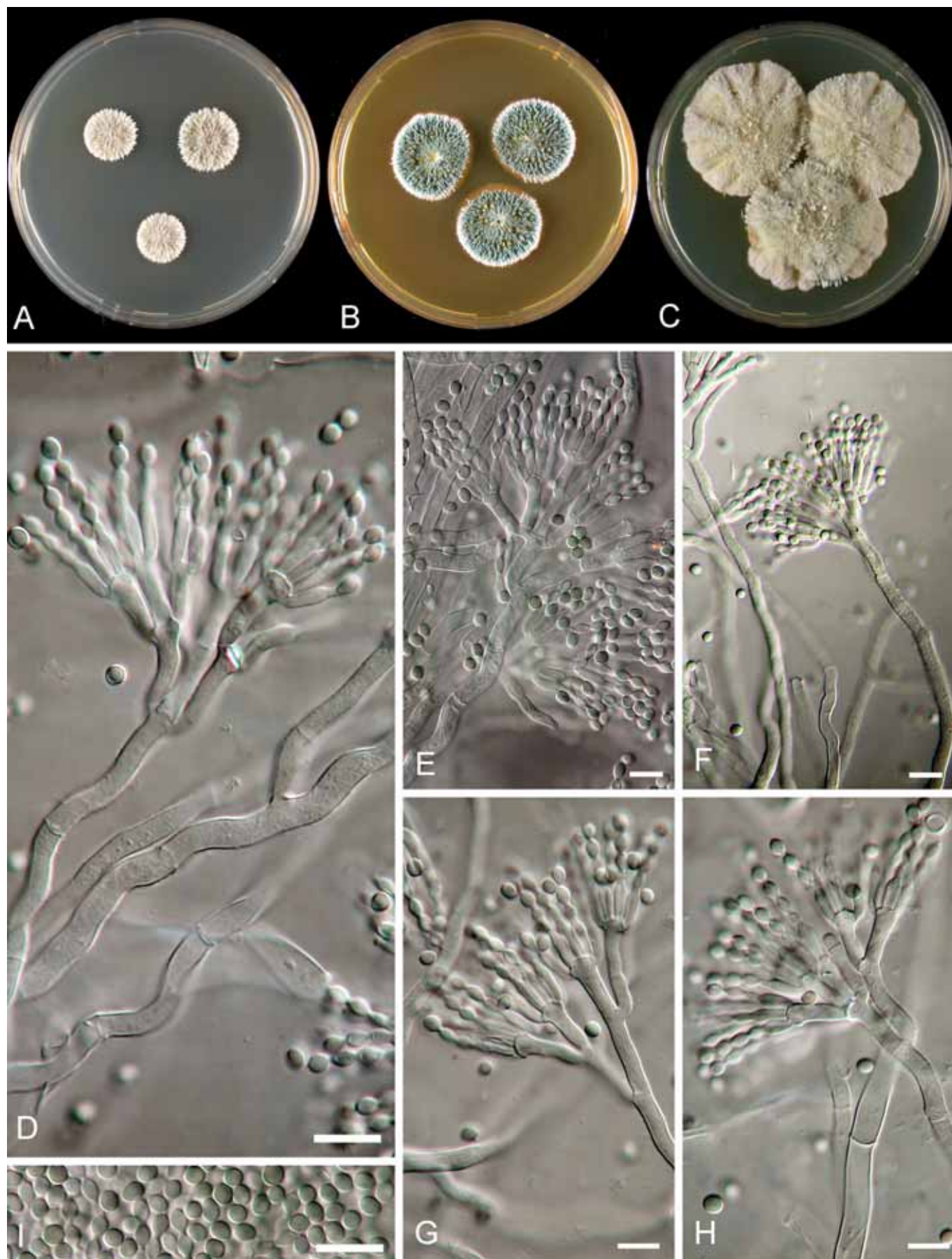


Fig. 38. *Penicillium clavigerum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. commune Thom, Bull. Bur. Anim. Ind. US Dept. Agric. 118: 56, 1910

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Camemberti*

Type: Herb. IMI 039812

Culture ex type: CBS 311.48 = IBT 6200 = IMI 039812 = FRR 890 = NRRL 890 = ATCC 10428 = IFO 5753 (T)

Diagnostic features: Cyclopiazonic acid, rugulovasine A & B, palitantin, subglobose to ellipsoidal smooth-walled conidia, good growth on CREA

Similar species: *P. palitans* can be distinguished from *P. commune* by its green conidia and good sporulation on YES agar. *P. camemberti* is much more floccose than *P. commune*.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose to (rarely) ellipsoidal, 3.5-4.5 µm.

Phialides: Cylindrical tapering to a distinct collulum, 9-12 µm x 2.5-3 µm

Metulae: Cylindrical, 10-15 µm x 3-4 µm

Rami: Cylindrical, 15-25 µm x 3-4 µm

Stipes: Rough-walled, 200-400 µm x 3-4 µm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Velutinous to floccose or weakly fasciculate

Conidium colour on CYA: Blue green to green

Exudate droplets on CYA: Often present, clear

Reverse colour on CYA: Cream coloured to beige or cream-yellow

Reverse colour on YES: Cream coloured to yellow

Diffusible colour on CYA: None

Ehrlich reaction: Strong violet reaction

Odour and volatile metabolites: Isobutanol, isopentanol, styrene, 3-octanone, β-caryophyllene (?), ethyl acetate, 3-heptanone, 1-octen-3-ol, 3-octanol, 2-methyl-isoborneol (Larsen and Frisvad, 1995)

Extrolites: 1) Cyclopaldic acid and chromanols, 2) Palitantin, 3) Rugulovasine A & B, 4) Cyclopiazonic acids, 5) Viridicatin, 6) Aspergynone-like metabolites (Frisvad and Filtenborg, 1989)

Growth on creatine: Very good

Acid and base production on creatine: Mostly strong acid and base production, few isolates only show acid production under the colony

Growth on UNO: Very good

Growth on nitrite: Good

Abiotic factors:

Diam., 1 week, 25°C: CYA: (15-)21-35 mm; MEA: (16-)20-37 mm; YES: 29-50 mm; CREA: 14-28 mm; Cz: 19-29 mm, OAT: 20-34 mm; CYAS: 19-34 mm; CzBS: 7-27 mm; CzP: 0-9 mm; UNO: 15-25 mm; DG18: 25-30 mm

Diam., CYA, 1 week: 15°C: 23-29 mm; 30°C: 0-4 mm; 37°C: 0 mm

CYA/CYAS: 1.0 [0.6-1.4]

CYA15°C/CYA 25°C: 1.0 [0.8-1.3]

CYA30°C/CYA 25°C: 0.0 [0-0.2]

CZBS/CZ: 0.8 [0.4-1.1]

CZP/CZ: 0.3 and three at 0 [0-0.3]

Distribution: Temperate regions, on cheese in refrigerators in warmer areas, Denmark, Greenland, Norway, UK, the Netherlands, Italy, Spain, Turkey, USA, Canada, Bahamas, Japan, Australia, New Zealand

Ecology and habitats: Cheese, nuts, wheat bread, dried fish, cherries, litchis, bromeliads, wood, *Sorbus* endophyte, bee larvae, and soil.

Biotechnological applications: None, however the domesticated form is *P. camemberti* (Pitt *et al.*, 1986; Polonelli *et al.*, 1987)

Biodeterioration & phytopathology: The major fungus deteriorating cheese (Lund *et al.*, 1995; Hocking and Faedo, 1992; Tzanetakis *et al.*, 1987; Kure and Skaar, 2000; Kure *et al.*, 2001). *P. palitans* is also quite common in Norwegian cheeses and may be separated from *P. commune* by differences in several features (Polonelli *et al.*, 1987; Lund, 1995b; Kure *et al.*, 2002). Fingerprinting has been used to separate isolates within these species (Lund and Skouboe, 1998; Hansen *et al.*, 2003; Lund *et al.*, 2003; Kure *et al.*, 2003).

Mycotoxins and mycotoxins: The production of cyclopiazonic acid was first reported from *P. griseofulvum*, at that time misidentified as *P. cyclopium* (Holzapfel, 1968; Hermansen *et al.*, 1984; Frisvad, 1989). Despite this it has later incorrectly been claimed that *P. cyclopium* produced it (Bennett and Klich, 2003). The production of cyclopiazonic acid was later reported from *P. camemberti* (Still *et al.*, 1978) and *P. commune* (Frisvad, 1985; Pitt *et al.*, 1986; Polonelli *et al.* 1987; El-Banna *et al.* (1987); Frisvad and Filtenborg, 1989). This mycotoxin may be produced directly on the cheese or may enter melt cheeses.

Typical cultures: IBT 21513 = CBS 468.84 = FRR 2926 = IMI 285507, ex liquorice root (Y); IBT 14135 = CBS 279.67, ex Roquefort cheese; IBT 3430 = CBS 112080 = IMI 291543, ex animal feed nuts, UK; IBT 10762 = CBS 112470, ex French cheese, Paris; IBT 10924 = CBS 269.97 = CBS 112079, ex feta cheese; IBT 14083 = CBS 111835, mummified bee larva, USA; IBT 21896 = CBS 112471, ex patient, the Netherlands; IBT 23305 = CBS 112472, ex ice, Svalbard, Norway; NRRL 845, contaminant in *P. puberulum* NRRL 1889; CBS 282.36 = NRRL 879 = IBT 16113, ex sweet water in glycerol still, UK (*P. lanosoviride*); CBS 247.32 = NRRL 873 = IBT 12807 (*P. ochraceum* var. *macrosporum*), ex mouldy tobacco, UK; NRRL 935 = IBT 21597 (*P. australicum*); CBS 327.48 = NRRL 948 = IBT 21599 (*P. flavoglaucum*); NRRL 930 = IBT 21605 (*P. lanosogriseum*); CBS 216.30 = NRRL 894 = IBT 21606 (*P. lanosogriseum*), ex leaf mould, Spouderwout, Bussum, the Netherlands; NRRL 932 = IBT 21598 = CBS 265.29 = CBS 254.31 = ATCC 10116 = FRR 932 = IMI 192904 (*P. psittacinum*), ex air; CBS 341.59 = ATCC 18381 = IMI 068234 = IFO 6237 = QM 7292 (*P. roqueforti* var. *punctatum*), ex cheese, Japan; IBT 3470 = IBT 3467 = IMI 295179 = ATCC 56608, ex turnips, Denmark; IBT 18102 = FRR 4192, ex cheddar cheese, Sydney, Australia; CBS 343.51 (*P. cyclopium* var. *album*); IBT 3469 = FRR 2160, ex cheddar cheese, Sydney, NSW, Australia.

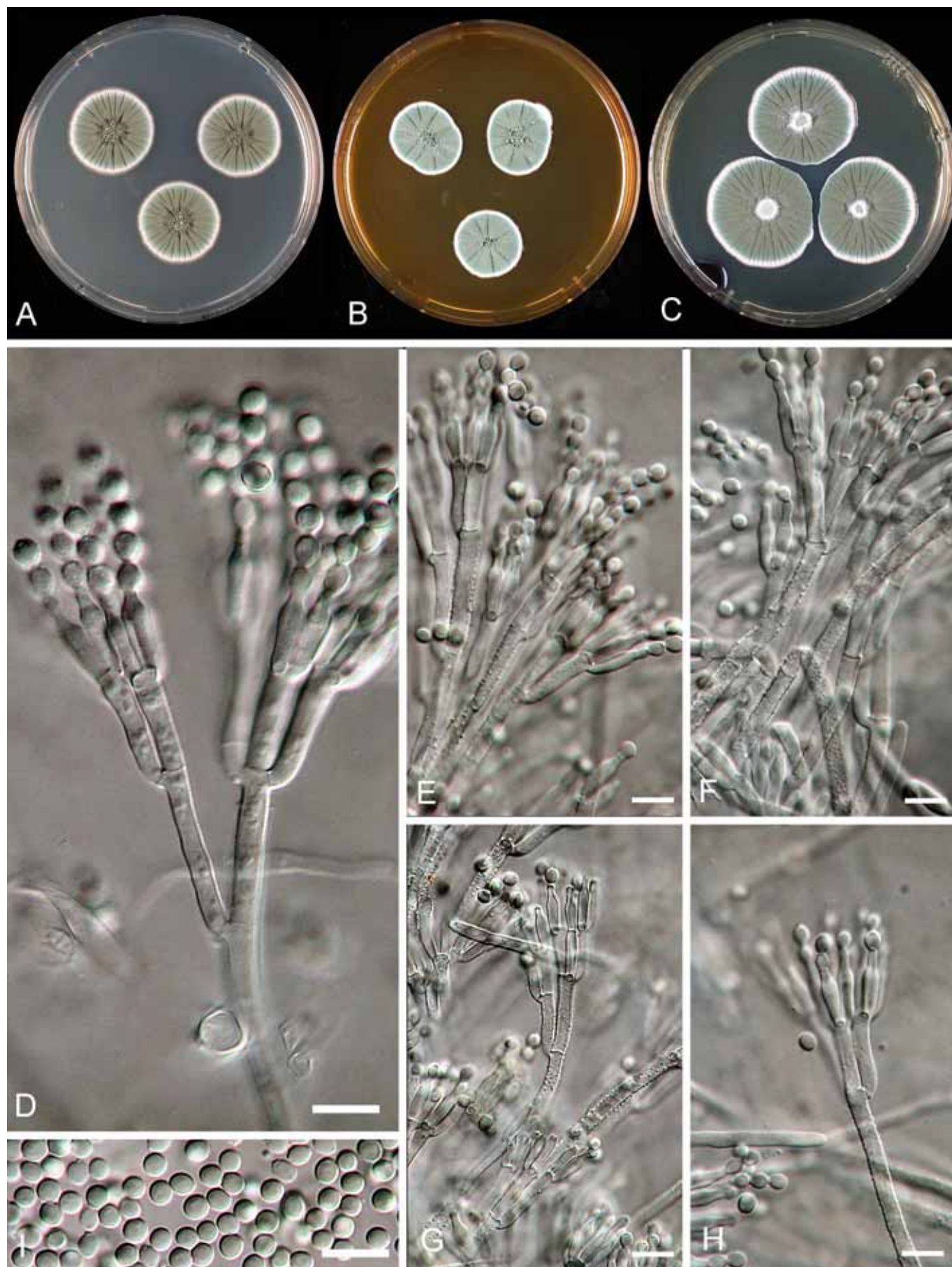


Fig. 39. *Penicillium commune*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. concentricum Samson, Stolk and Hadlok, Stud. Mycol. (Baarn) 11: 17, 1976

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Claviformia*

Type: Herb. CBS 477.75

Culture ex type: CBS 477.75 = IBT 14571 = IBT 6577 = FRR 1715, ex colon of a deer, Germany (T)

Diagnostic features: Patulin, patulidin, roquefortine C, meleagrins, oxaline, broadly ellipsoidal smooth-walled conidia, fasciculate, orange reverse on all substrates,

Similar species: *P. concentricum* is most similar to *P. glandicola*. The latter species produce very rough stipes in contrast to *P. concentricum*.

Description:

Conidiophores: Terverticillate, appressed and somewhat divergent elements, born from subsurface hyphae

Conidia: Smooth-walled, Broadly ellipsoidal, 3.2-3.7 µm x 2-2.5 µm

Phialides: Cylindrical tapering to a distinct collum, 5-10 µm x 2.2-2.5 µm

Metulae: Cylindrical, 9-13 µm x 3-3.5 µm

Rami: Cylindrical, 12-20 µm x 3-3.5 µm

Stipes: Smooth-walled (rarely finely rough-walled), 200-400 µm x 3-4 µm

Synnemata or fasciculation: Fasciculate

Sclerotia: None

Colony texture: Fasciculate

Conidium colour on CYA: Artemisia to lily green

Exudate droplets on CYA: Copious, clear to pale yellow

Reverse colour on CYA: Orange to orange red

Reverse colour on YES: Yellow to strongly orange

Diffusible colour on CYA: Orange

Ehrlich reaction: No reaction or yellow

Odour and volatile metabolites: Not examined

Extrolites: 1) Patulin, 2) Patulodin & CT 2108A & B, 3) Asteltoxin, 4) Barceloneic acid 5) Pyripyropens 6) Roquefortine C, meleagrins and oxaline, 7) Cyclopamine

Growth on creatine: Very good

Acid and base production on creatine: Good acid production or just visible under colony followed by weak base production

Growth on UNO: Very good

Growth on nitrite: Good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 12-25 mm; MEA: 7-16 mm; YES: 18-40 mm; CREA: 4-20 mm; Cz: 4-16 mm, OAT: 21-30 mm; CYAS: 15-21 mm; CzBS: 3-15 mm; CzP: 0 mm; UNO: 6-15 mm; DG18: 17-22 mm

Diam., CYA, 1 week: 15°C: 15-20 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 1.1 [0.8-1.3]

CYA15°C/CYA 25°C: 1.0 [0.8-1.3]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.7 [0.5-1.0]

CZP/CZ: 0

Distribution: Denmark, Sweden, Norway, Germany, United Kingdom, France, South Carolina, Wisconsin, Kansas, USA

Ecology and habitats: Deer dung, soil (with deer dung), salami, cheese, wheat flour; water tanks (*P. concentricum* can be regarded as a faecal indicator)

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: As in other coprophilic species, many antibiotically active extrolites are found, including patulin, patulidin, barceloneic acid and meleagrins, but *P. concentricum* has rarely been found in foods.

Typical cultures: IBT 21514 = IBT 20230 = CBS 101024, ex soil, University of South Carolina, USA (Y); IBT 5625, ex pig feed, Norway; IBT 5623 = IBT 4372 = IBT 3848 = CBS 185.89 = CBS 110762 = IMI 293197 = ATCC 58613 = FRR 3066, ex wheat flour, Denmark; IBT 5621 = IBT 3080 = CBS 285.36 = CBS 110765 = NRRL 2034 = ATCC 46510 = IMI 326061; IBT 22163 = CBS 110763, ex dung from white-tailed deer, Turkey Swamp, New Jersey, USA; IBT 13685 = CBS 110764, ex soil at Chateau Menthon, St. Bernard, France; IBT 6778 = IBT 3078 = CBS 191.88 = NRRL 13633 = IMI 321510 = ATCC 64635, ex soil, Denmark; IBT 13168 = RMF 8051; ex soil, Konza Grassland, LTER, Kansas; IBT 5629 = IBT 3079 = IMI 285527 = Kulmbach Sp. 831, ex salami, Germany; IBT 12736 = WSF 2352, soil in floodplain forest (Maple-Ash-Elm), Wisconsin, USA; IBT 3847 = CBS 631.70; IBT 5618, ex cheese, Denmark; UAMH 3893, ex oil-spilled soil, Norman Wells NWT, Canada.

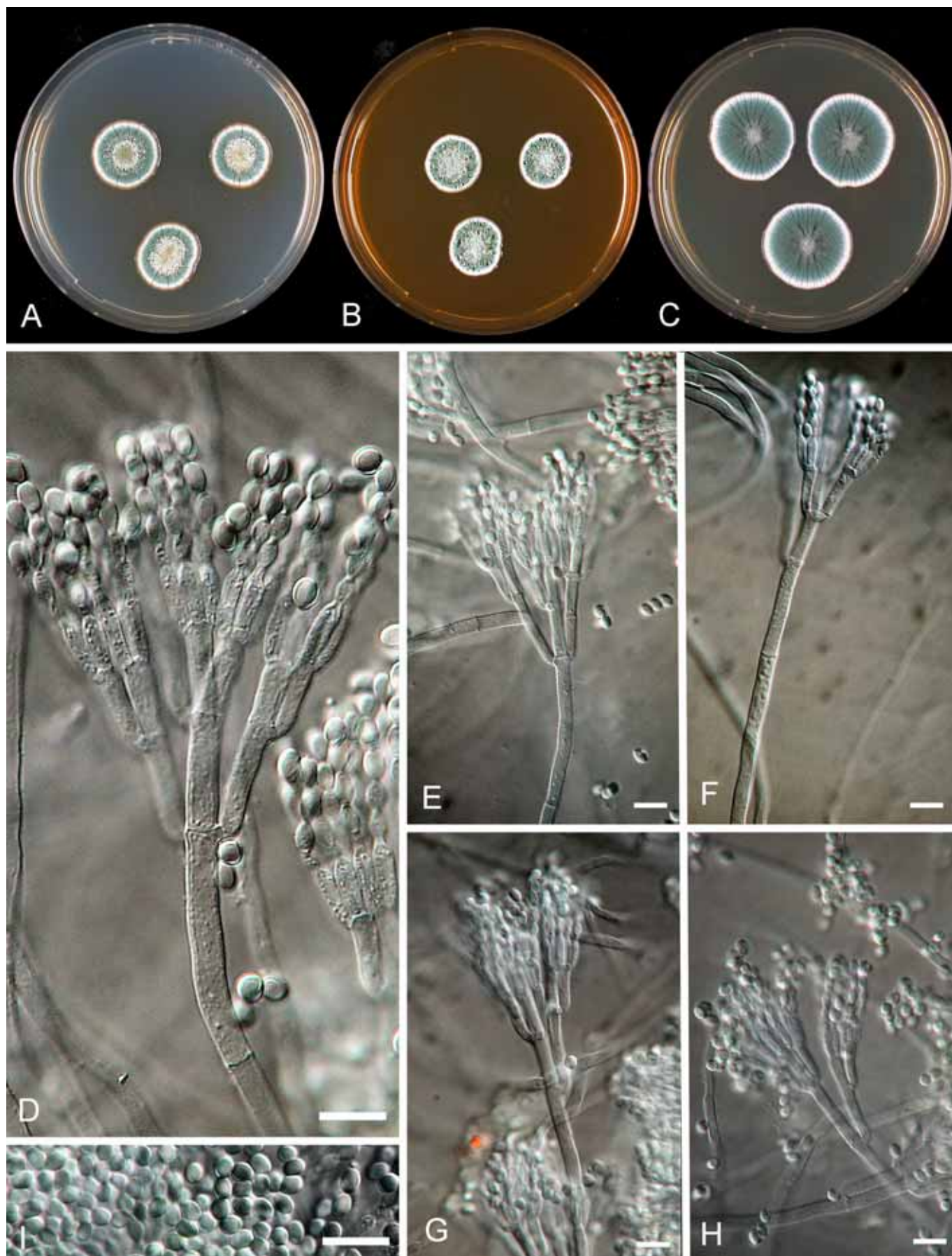


Fig. 40. *Penicillium concentricum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. confertum (Frisvad, Filt. & Wicklow) Frisvad,
Mycologia 81: 852, 1989

In *Penicillium* subgenus *Penicillium* section *Chrysogena*
series *Mononematosa*

Type: Herb. IMI 296930

Culture ex type: IBT 21515 = IBT 3098 = IBT 3093 = IBT
5672 = CBS 171.87 = IMI 296930 = NRRL 13488 = NRRL
A-26904, ex external fur-lined cheek pouch of *Dipodomys*
spectabilis, 6 km east of Portal, Arizona, USA (T,Y)

Diagnostic features: Asteltoxin, meleagrins, sinoid conidio-
phore stipes, good growth at 37°C.

Similar species: *P. confertum* is most closely related to
Penicillium mononematosum, but differs by its less compli-
cated penicilli and thin often sinoid stipes.

Description:

Conidiophores: Terverticillate, sinoid, appressed and
somewhat divergent elements, born from subsurface hyphae
Conidia: Smooth-walled, subglobose to broadly ellipsoidal,
3.2-3.7 µm x 2.2-3.0 µm

Phialides: Flask shaped with a distinct collulum, 7-9 µm x
2.5-3.0 µm

Metulae: Cylindrical, 10-15 µm x 3-4 µm

Rami: Cylindrical, 15-25 µm x 3-4 µm

Stipes: Thin, smooth-walled, sinoid, 150-300 µm x 2.5-3.5
µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Greyish green to greyish tur-
quoise

Exudate droplets on CYA: Copious, clear to pale

Reverse colour on CYA: Cream to beige

Reverse colour on YES: Yellowish cream to curry

Diffusible colour: None

Ehrlich reaction: None to faint yellow

Odour and volatile metabolites: Not examined

Extrolites: 1) Asteltoxin, 2) Secalonic acid D, 3) Roque-
fortine C & meleagrins

Growth on creatine: Weak

Acid and base production on creatine: Acid under colony,
no base production

Growth on UNO: Weak

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 20-24 mm; MEA: 17-29 mm;
YES: 26-36 mm; CREA: 18-24 mm; Cz: 14-24 mm, OAT:
23-29 mm; CYAS: 24-26 mm; CzBS: 1-2 mm; CzP: 0 mm;
UNO: 11-13 mm; DG18: 22-25 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 13-15 mm;
30°C: 18-20 mm; 37°C: 7-10 mm

CYA/CYAS: 0.9

CYA15°C/CYA 25°C: 0.6

CYA30°C/CYA 25°C: 0.8

CZBS/CZ: 0.04

CZP/CZ: 0

Distribution: Arizona & New Mexico, USA

Ecology and habitats: Kangaroo rat mounds, deserts

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: Asteltoxin, but the fungus
is apparently not food or feed-borne.

Typical cultures: IBT 16864, ex soil under *Atriplex gard-
neri*, Chetro Ketl, Chaco Canyon, New Mexico, USA.

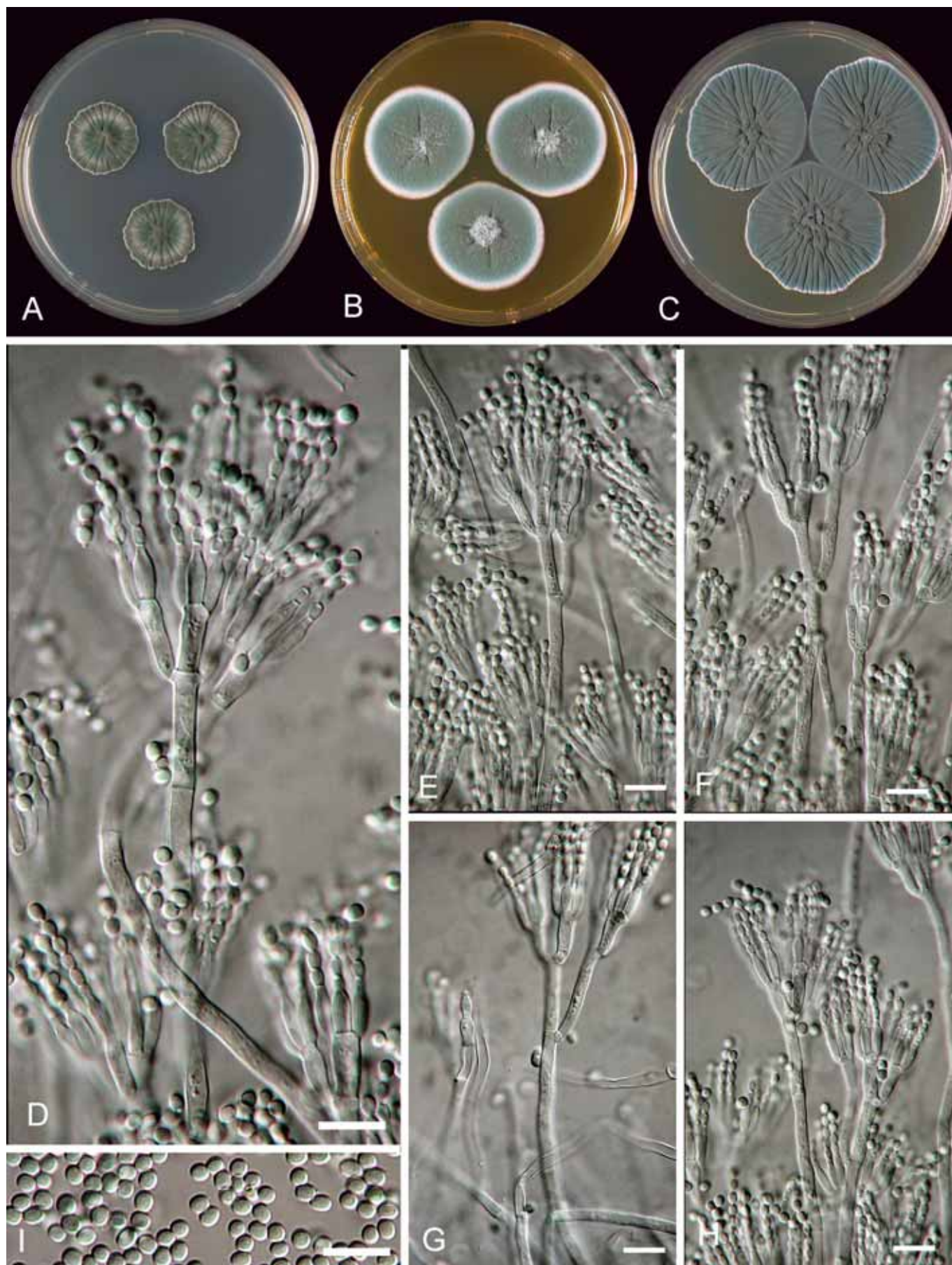


Fig. 41. *Penicillium confertum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. coprobium Frisvad, Mycologia 81: 853, 1989

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Claviformia*

Type: Herb. IMI 293209

Culture ex type: CBS 561.90 = IBT 3069 = IBT 4583 = IBT 6932 = IBT 21516 = IMI 293209 = ATCC 58615, ex pig feed, Norway (**T, Y**)

Diagnostic features: Patulin, roquefortine C, meleagrins, ellipsoidal smooth-walled conidia, fasciculate, small synnemata, pale reverse MEA, strong fruit-like smell.

Similar species: *P. coprophilum* differs from *P. coprobium* by uneven colony margins, and a dark brown reverse on CYA. *P. concentricum* has small colonies with a strong orange reverse on MEA, while the reverse of *P. coprobium* is cream coloured to light yellow.

Description (see also Kubatova (1993/1994) for colour photographs, as *P. coprophilum*):

Conidiophores: Terverticillate, appressed elements but divergent rami, born from subsurface hyphae

Conidia: Smooth-walled, broadly ellipsoidal, 3.2-4 µm x 2.5-3.0 µm

Phialides: Cylindrical tapering to a distinct collum, 6.5-10 µm x 2.0-2.5 µm

Metulae: Cylindrical, 9-13 µm x 2.5-3 µm

Rami: Cylindrical, 12-20 µm x 3-3.5 µm

Stipes: Smooth-walled, 200-400 µm x 3-4 µm

Synnemata or fasciculation: Fasciculate, synnemata up to 1 mm with white stalks and green heads best developed on OAT

Sclerotia: White to pink and rare only seen on MEA after 3 weeks in a glass Petri dish (rare)

Colony texture: Fasciculate, not sulcate or only weakly sulcate

Conidium colour on CYA: Grey green to dark green

Exudate droplets on CYA: Copious, clear to pale brown

Reverse colour on CYA: Greyish brown to yellow brown

Reverse colour on YES: Cream coloured to curry to olive

Diffusible colour: Pale orange brown

Ehrlich reaction: None (one isolate faint yellow)

Odour and volatile metabolites: Isobutanol, isopentanol, 1,3,5-heptatriene and two isomers, 2-pentanone, isobutyl acetate, 1-nonene, styrene, 1-undecene, (blackberry smell) (Larsen & Frisvad, 1995)

Extrolites: 1) Patulin, 2) Pyripyropens, 3) Cyclopiamin, 4) Roquefortine C, meleagrins and neoxaline (Frisvad and Filtenborg, 1989)

Growth on creatine: Very good

Acid and base production on creatine: No acid production or acid just under colony

Growth on UNO: Very good

Growth on nitrite: Good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 21-29 mm; MEA: 9-26 mm; YES: 25-34 mm; CREA: 3-15 mm; Cz: 12-17 mm, OAT: 18-31 mm; CYAS: 16-28 mm; CzBS: (0-) 4-17 mm; CzP: 0 mm; UNO: 5-16 mm; DG18: 23-29 mm

Diam., CYA, 1 week: 15°C: 14-19 mm; 30°C: 0-4 mm; 37°C: 0 mm

CYA/CYAS: 1.2 [0.9-1.3]

CYA15°C/CYA 25°C: 0.7 [0.5-0.9]

CYA30°C/CYA 25°C: 0.1 [0-0.2]

CZBS/CZ: 0.7 [one 0, 0.3-1.1]

CZP/CZ: 0

Distribution: Denmark, Norway, the Netherlands, Germany, United Kingdom, Czech Republic, Slovakia, Siberia, Russia, China, Kansas, USA

Ecology and habitats: Dung, soil and roots, cereal based animal feed, tea

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: Patulin and roquefortine C are produced, but *P. coprobium* has only been found sporadically on foods and feeds. The species may indicate faecal contamination of feeds.

Typical cultures: IBT 6895 = IBT 3068 = IBT 4516 = CBS 184.88 = ATCC 64630 = IMI 321497 = NRRL 13626, ex soil, Houtribdijk, the Netherlands; IBT 3070 = IBT 3707 = IBT 3777 = IBT 6899 = CBS 185.88, ex pig feed, Norway; IBT 6897 = IBT 3071 = CBS 267.97, ex rabbit dung; IBT 15439 = CBS 280.97, ex *Hordeum vulgare*, Denmark; IBT 6900 = CBS 562.90 = CCF 2005, ex Českomoravská Vrchovina hills, Czech Republic; IBT 18861 = CBS 110762 = CCF 2800, ex soil Vrchy hills, Eastern Bohemia, Czech Republic; IBT 19342 = CBS 110761 = FRR 3645 = PREM 47700, ex grass roots, mangrove, Natal, South Africa; IBT 13168 = RMF 8051; ex soil, Konza Grassland, LTER, Kansas; IBT 22719, ex soil under snow 3 km west of Uthoss, Siberia, Russia; IBT 24820, tea, China; IBT 14656, ex potato, Denmark; IBT 3066, ex walnut; IBT 4369 = IBT 3067 = IBT 10555 = IMI 321499, ex soil, Loosdrecht, the Netherlands; IBT 18862 = CCF 2802, ex soil at Hlinsko, Czech Republic; IBT 18859 = FFC 2803, ex soil, Strážovské vrchy hills, Slovakia.

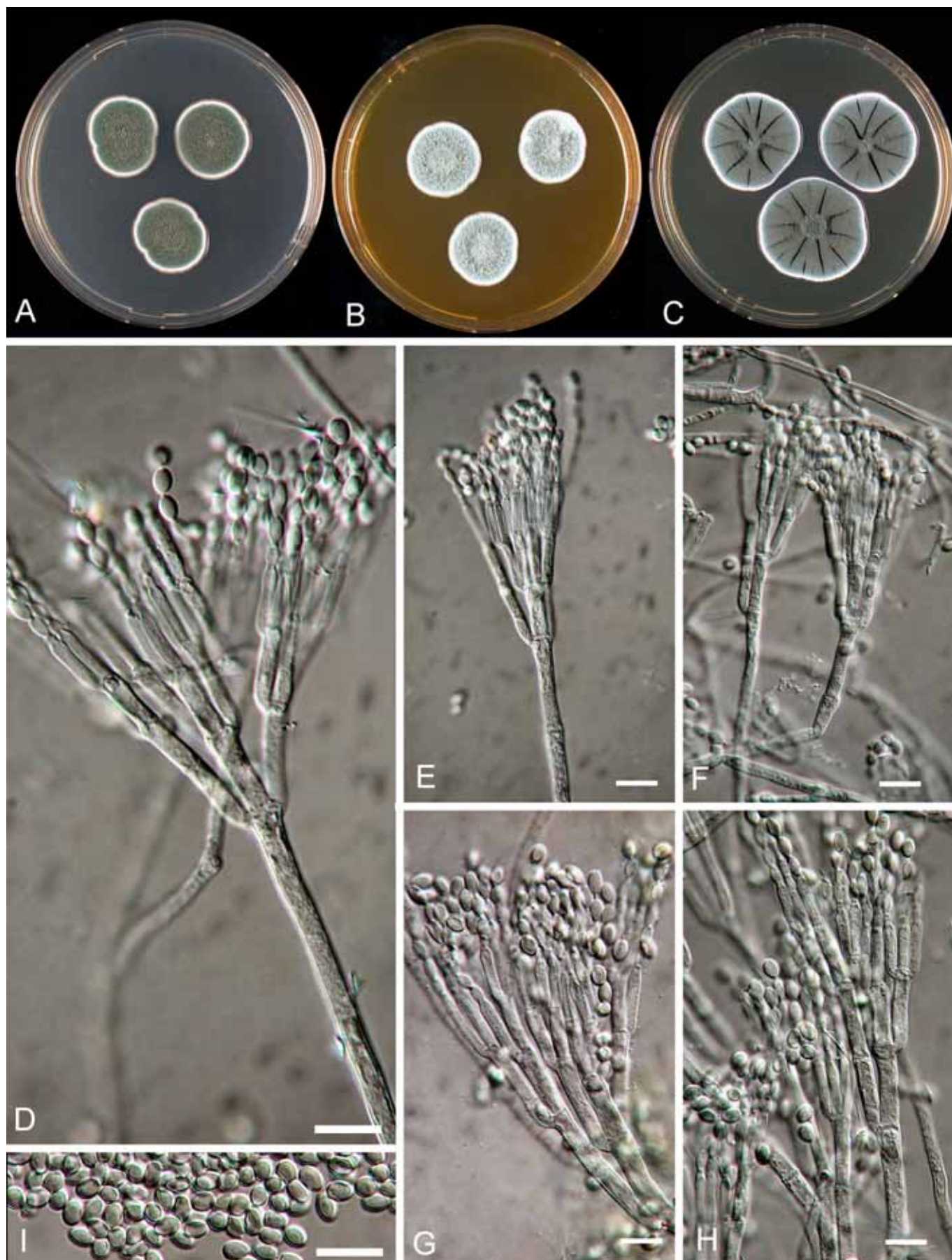


Fig. 42. *Penicillium coprobium*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. coprophilum (Berk. & Curt.) Seifert & Samson, Adv. Pen. Asp. Syst.: 145, 1985

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Claviformia*

Type: herb. K, Cuba, Wright, 666

Ex epi type cultures: CBS 110760 = IBT 5551 = IBT 3064, ex rabbit dung, Groeneveld, Baarn, the Netherlands (**epiT**)

Diagnostic features: Griseofulvin, roquefortine C, meleagrins, oxalin, broadly ellipsoidal smooth-walled conidia, synnemata produced, uneven margin of colonies on MEA, dark brown reverse on CYA

Similar species: See *P. coprobium*.

Description:

Conidiophores: Terverticillate, appressed elements but divergent rami, born from subsurface hyphae

Conidia: Smooth-walled, broadly ellipsoidal, 3.2-3.7 µm x 2.0-2.5 µm

Phialides: Cylindrical tapering to a short distinct collum, 6.5-10 µm x 2.2-2.5 µm

Metulae: Cylindrical, 9-13 µm x 3-3.5 µm

Rami: Cylindrical, 12-20 µm x 3-3.5 µm

Stipes: Smooth- and rough-walled, 200-400 µm x 3-4 µm

Synnemata or fasciculation: Fasciculate, synnemata up to 1.3 mm with white stalks and green heads

Sclerotia: None

Colony texture: Fasciculate to coremiform

Conidium colour on CYA: Green to dark green

Exudate droplet on CYA: Copious, clear to pale brown

Reverse colour on CYA: Dark brown

Reverse colour on YES: Curry to brown yellow

Diffusible colour on CYA: Brown

Ehrlich reaction: None

Odour and volatile metabolites: Isobutanol, isopentanol, 1-octene, styrene, 2-pentanone, 3-methyl-2-pentanone, methyl isopentanoate, 1-nonene, 2-heptanol, 2-octanone, 3,4-dimethyl-hexanone, 1-methoxy-3-methyl-benzene, 1-undecene (Larsen and Frisvad, 1995)

Extrolites: 1) Griseofulvin, 2) Alternariol, 3) Pyripyropens, 4) Roquefortine C, meleagrins, oxalin, neoxalin 5) Cyclopiazamin

Growth on creatine: Very good

Acid and base production on creatine: Good acid production followed by base production, occasionally only acid under the colony

Growth on UNO: Very good

Growth on nitrite: Good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 18-29 mm; MEA: 9-26 mm; YES: 25-34 mm; CREA: 3-15 mm; Cz: 12-17 mm, OAT: 18-31 mm; CYAS: 16-28 mm; CzBS: (0-) 4-17 mm; CzP: 0 mm; UNO: 5-16 mm; DG18: 23-29 mm

Diam., CYA, 1 week: 15°C: 14-19 mm; 30°C: 0-4 mm; 37°C: 0 mm

CYA/CYAS: 1.0 [0.9-1.2]

CYA15°C/CYA 25°C: 0.6 [0.6-0.8]

CYA30°C/CYA 25°C: 0.6 [0.3-0.7]

CZBS/CZ: 1.0 [0.9-1.3]

CZP/CZ: 7 isolates 0, two isolates 0.2 [0.2-0.3]

Distribution: Denmark, Norway, United Kingdom, Germany, South Carolina, New Jersey & Wisconsin (USA), Cameroon, Zambia, Ethiopia, South Africa, Australia, New Zealand

Ecology and habitats: Rabbit and deer dung, soil with herbivore dung, corn, rye bread, barley, compound feed, salami, hazelnuts

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: Roquefortine C and alternariol are produced, but the species did not produce conspicuous growth on the food substrate from which they were isolated.

Typical cultures: CBS 186.89 = IBT 21517 = IBT 3768 = IBT 5539 = NRRL 13627, ex *Andropogon sorghum* imported to Denmark (Y); IBT 23268 = CBS 102444, ex woodchip paper behind skirting board, Germany; IBT 5546 = CBS 473.75, ex *Zea mays*, Pretoria, South Africa; IBT 3063 = IBT 3845 = IBT 4753 = IBT 5552 = CBS 110759 Kulmbach Sp. 1370, ex salami, Germany; IBT 18704 = CBS 110758, ex rye bread, Denmark; IBT 22162 = CBS 110757, ex *Styria cifolia* (liquid amber), Turkey Swamp, New Jersey, USA; IBT 12724 = CBS 110767, ex *Hordeum vulgare*, the Netherlands; IBT 12992 = CBS 272.97 = CBS 110768, ex wheat, Denmark; FRR 1403, ex chicken feed, Brisbane, Qld., Australia; IBT 12750 = WSF 5238.

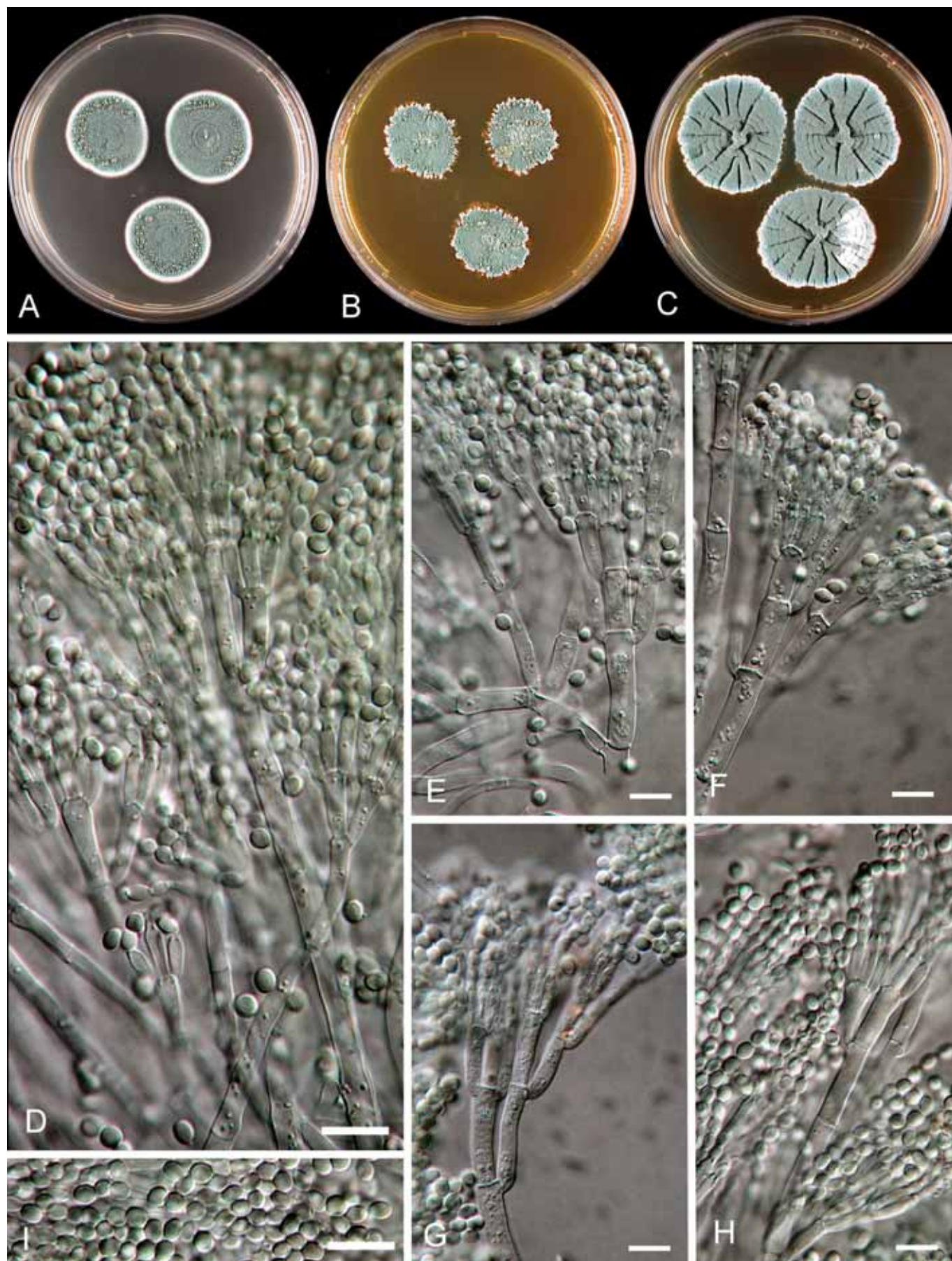


Fig. 43. *Penicillium coprophilum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. crustosum Thom, *Penicillia*: 399, 1930

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Camemberti*

Type: Herb. IMI 091917

Culture ex type: IBT 5528 = IBT 6175 = IMI 091917 = FRR 1669 = ATCC 52044 = NCTC 4002, ex lemon, Aberdeen, Scotland (T)

Diagnostic features: Penitrem A, roquefortine C, terrestrial acid, viridicatin, smooth-walled conidia, crustose on CYA and MEA after 7-10 days, high growth rate, good growth on CREA. Strong sporulation and high growth rate on YES agar.

Similar species: *P. expansum* has ellipsoidal conidia and usually smooth stipes and is not crustose. *P. commune* has smaller colony diameters, not a deep yellow reverse on YES and is not crustose. *P. palitans* has smaller colonies, darker and greener conidia and is not crustose.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 3-4 µm.

Phialides: Cylindrical tapering to a distinct collum, 9-12 µm x 2.5-3 µm

Metulae: Cylindrical, 10-15 µm x 3-3.5 µm

Rami: Cylindrical, 15-25 µm x 3.5-4 µm

Stipes: Rough-walled, 200-400 µm x 3.5-4.5 µm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Velutinous to weakly fasciculate, becoming crustose

Conidium colour on CYA: Dull green to grey green or blue green at the colony margin

Exudate droplets on CYA: Copious, clear or brown

Reverse colour on CYA: Cream-coloured to yellow brown

Reverse colour on YES: Strongly yellow

Diffusible colour: Pale brown or none

Ehrlich reaction: None

Odour and volatile metabolites: Ethyl acetate, isobutanol, ethyl propanoate, isopentanol, dimethyldisulphide, ethyl isobutanoate, isobutyl acetate, ethyl butanoate, ethyl-2-methyl butanoate, ethyl isopentanoate, isopentyl acetate, styrene, ethyl pentanoate, 3-octanone, ethyl hexanoate, ethyl octanoate, 2-methyl-isoborneol, geosmin.

Extrolites: 1) Penitrem A-G, 2) Roquefortine C-E, 3) Terrestrial acid and viridicatic acid, 4) Viridicatin (cyclopeptin, dehydrocyclopeptin, cyclopenin, cyclophenol, viridicatin, viridicatol), 5) Hadacidin, 6) Andrastin A

Growth on creatine: Very good

Acid and base production on creatine: Good acid production followed by base production

Growth on UNO: Very good

Growth on nitrite: Poor

Abiotic factors:

Diam., 1 week, 25°C: CYA: 32-46 mm; MEA: 25-46 mm; YES: 40-56 mm; CREA: 22-35 mm; Cz: 29-32 mm, OAT: 28-38 mm; CYAS: 29-39 mm; CzBS: 25-28 mm; CzP: 0-3 mm; UNO: 19-23 mm; DG18: 29-32 mm

Diam., CYA, 1 week: 15°C: 28-31 mm; 30°C: 15-26 mm; 37°C: 0 mm

CYA/CYAS: 1.3 [1.1-1.5]

CYA15°C/CYA 25°C: 0.7 [0.7-0.7]

CYA30°C/CYA 25°C: 0.5 [0.4-0.6]

CZBS/CZ: 0.9 [0.8-0.9]

CZP/CZ: 0.1 and four at 0 [0-0.1]

Distribution: Panglobal: Denmark, Norway, Germany, Slovenia, Greece, Bulgaria, Azores Islands, Portugal, Georgia & New Mexico (USA), Kazakhstan, Victoria B.C., Indonesia; Canada, Australia, New Zealand.

Ecology and habitats: Pecans, walnuts, chestnuts, apples, cream cheese, blue cheese, salami, indoor air, coffee beans, maize, cotton seed, compound feeds, cardboard.

Biotechnological applications: None

Biodeterioration & phytopathology: *P. crustosum* can produce a weak rot in apples (Frisvad, 1981). It is a major degrader of compound feeds for animals and cheeses.

Mycotoxicoses and mycotoxins: Penitrem A and roquefortine C from *P. crustosum* growing on cheese or nuts have been implicated in toxicoses of dogs (Richard *et al.*, 1981; Richard and Arp, 1979; Puls and Ladyman, 1988; Hocking *et al.*, 1988; Naudé *et al.*, 2002). The case of mycotoxicosis of a man after drinking beer (Cole *et al.*, 1983; Cysewski *et al.*, 1975) was caused by *P. carneum*, not *P. crustosum*). Cattle has also been intoxicated with penitrem A from *P. crustosum* (Wilson *et al.*, 1968; Dorner *et al.*, 1984). Strains identified as *P. palitans* (Ciegler, 1969), *P. commune* (Mintzlauff *et al.*, 1972; Wagener *et al.*, 1980), *P. lanosocoe-ruleum* (Wells and Cole, 1977), *P. cyclopium* (Wilson, 1968; Ciegler and Pitt, 1970; Vesonder *et al.*, 1980), *P. martensii*, *P. olivinoviride*, *P. puberulum* (Ciegler and Pitt, 1970) producing penitrem A and roquefortine C were all *P. crustosum* (Pitt, 1979b, Frisvad, 1989). The production of both toxins is very consistent in *P. crustosum* (El-Banna and Leistner, 1988; Frisvad and Filtenborg, 1989).

Typical cultures: IBT 21518 = IBT 14747 = CBS 101025, ex cheese, Azores Islands (Y); IBT 23265 = CBS 181.89, ex soil with *Agaricus bisporus*; IBT 6579 = IBT 3425 = CBS 471.84 = IMI 285510 = FRR 2929, ex *Thymus vulgaris*, Greece; IBT 6580 = IBT 5529 = CBS 110076 = FRR 1387, ex Portuguese wine corks, Sydney, NSW, Australia; IBT 18099 = CBS 110077 = FRR 1513, ex deteriorating preserved wood-stakes; North Qld., Australia; IBT 15977 = CBS 110075, ex mixed pig feed, Bulgaria; IBT 14519 = CBS 110074, ex Lechuiguilla Cave, Carlsbad, New Mexico; IBT 16510 = CBS 110073, ex soil, ex soil under *Betula* sp., Victoria B.C., Canada; IBT 11095 = CBS 499.73 = IMI 174717 = FRR 1478 = VKM F-1746 = ATCC 24721, ex grapes in storage, Alma-Ata, Kazakhstan (*P. farinosum*); IBT 11150 = CBS 340.59 = QM 7293 = ATCC 18379 = FRR 3457 = IFO 6235 = IMI 068235, ex soil, Japan (*P. pseudocasei*); IBT 3426 = ATCC 32014, ex weevil-damaged pecans, Georgia, USA; IBT 6578 = FRR 2223, ex weevil-damaged pecans, Georgia, USA; IBT 16885, ex mouldy onion, Denmark; IBT 18359 = CCRC 32633, Taiwan; IBT 23710 = IMI 206159, ex soil, New Zealand.

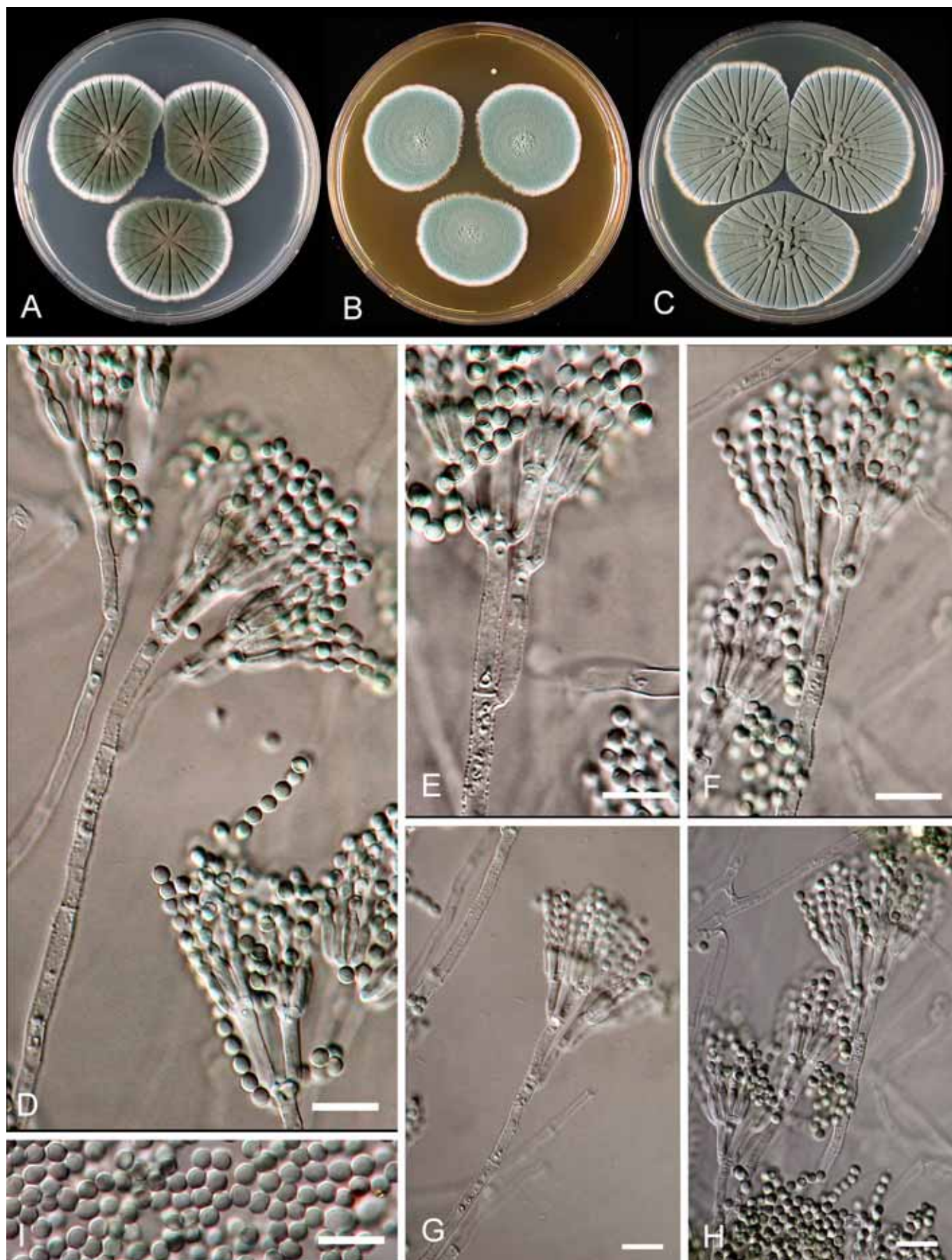


Fig. 44. *Penicillium crustosum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. cyclopium Westling, Ark. Bot. **11**: 90, 1911

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Viridicata*

Type: Herb. IMI 089372

Culture ex type: CBS 144.45 = CBS 114.74 = IBT 5130 = IMI 089372 = ATCC 8731 = ATHUM 2888 = CECT 2264 = DSM 1250 = LSHB 1923 = MUCL 15613 = QM 6839 = VKM F-265, ex fruit, Norway (**T**)

(*P. puberulum* Bain. 1907 is a *nomen dubium* as the culture ex neotype contains both material of *P. commune* (NRRL 845 = ATCC 8508) and *P. cyclopium* (NRRL 1889 = NRRL 2040))

Diagnostic features: Xanthomegnin, viomellein, vioxanthin, penicillic acid, blue green smooth-walled conidia, green on CYA and blue green on MEA

Similar species: See *P. aurantiogriseum*

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 2.6-3.2 µm.

Phialides: Cylindrical tapering to a distinct collulum, 8-9 µm x 2.6-2.8 µm

Metulae: Cylindrical, 9.5-14 µm x 3.2-4.4 µm

Rami: Cylindrical, 15-25 µm x 3.2-4.4 µm

Stipes: Rough-walled, 200-750 µm x 3.5-5 µm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Velutinous to weakly fasciculate

Conidium colour on CYA: Blue green to green, blue green on MEA

Exudate droplets on CYA: Copious, clear or light yellow

Reverse colour on CYA: Yellow to orange to red brown occasionally only cream yellow

Reverse colour on YES: Strongly yellow, also yellow obverse (poor sporulation on YES)

RT agar: Dark brown halo in most isolates

Diffusible colour: None or pink or red brown

Ehrlich reaction: pink to red or yellow brown

Odour and volatile metabolites: Close to the volatile profile of *P. aurantiogriseum*, but weaker

Extrolites: 1) Penicillic acid, 2) Xanthomegnin, viomellein and vioxanthin, 3) Puberulic acid and puberulonic acid 4) Puberuline and verrucofortine (rugulosuvine and leucyltryptophanyldiketopiperazine), 5) 3-Methoxyviridicatin (and cyclopeptin, dehydrocyclopeptin, cyclophenin, cyclophenol, viridicatol)

Growth on creatine: Poor growth

Acid and base production on creatine: Good acid production, no base production

Growth on UNO: Weak

Growth on nitrite: Poor.

Abiotic factors:

Diam., 1 week, 25°C: CYA: 18-34 mm; MEA: 21-35 mm; YES: 28-40 mm; CREA: 11-21 mm; Cz: 19-28 mm, OAT:

17-29 mm; CYAS: 25-34 mm; CzBS: 12-21 mm; CzP: 0 mm; UNO: 7-17 mm; DG18: 23-27 mm

Diam., CYA, 1 week: 15°C: 19-24 mm; 30°C: 2-6 mm; 37°C: 0 mm

CYA/CYAS: 0.9 [0.8-1.1]

CYA15°C/CYA 25°C: 0.8 [0.7-1.0]

CYA30°C/CYA 25°C: 0.2 [0.1-0.2]

CZBS/CZ: 0.8 [0.5-0.9]

CZP/CZ: 0

Distribution: Temperate regions with farming: Denmark, Sweden, United Kingdom, Norway, Canada, more rare in Saudi Arabia and California (USA)

Ecology and habitats: Cereals: wheat, barley, oats, maize, compound feeds, more rare on salami, seaweed and harness.

Biotechnological applications: None

Biodeterioration & phytopathology: Degrades cereals and animal feeds.

Mycotoxins and mycotoxins: This species is a very efficient producer of xanthomegnin, viomellein and vioxanthin, as are *P. freii*, *P. viridicatum* and *P. tricolor* (the latter is less common, however). These species are very commonly growing in low quality cereals and may cause liver and kidney diseases in domestic animals (Carlton *et al.*, 1968; Carlton and Tuite, 1970a & b; Budiarso *et al.*, 1968; 1971; Carlton *et al.*, 1972; Zwicker *et al.*, 1973). The latter reference reported on probable carcinogenicity of *P. viridicatum*, which always produces xanthomegnin, viomellein and vioxanthin, but also brevianamide A, viridic acid and viridamine distinguishing it from *P. cyclopium* (see also *P. viridicatum*). The mixture of penicillic acid and xanthomegnin, viomellein and vioxanthin is also present in most isolates of *Aspergillus ochraceus* (Frisvad and Samson, 2000). *A. ochraceus* give the same severe symptoms in mice and swine (Zimmerman *et al.*, 1976, 1977; 1979; Robbers *et al.*, 1978) as *P. viridicatum* indicating that xanthomegnin and viomellein are more important than previously thought. It appears that ochratoxin A from *P. verrucosum* (or some of the strains of *Aspergillus ochraceus*) mostly adds to the nephrotoxicity of mouldy cereals rather than to the hepatotoxicity. Xanthomegnin, viomellin and vioxanthin have been found to be naturally occurring in cereals (Hald *et al.*, 1983; Scudamore *et al.*, 1986) and the fungi responsible for this were *P. cyclopium* and *P. freii*.

Typical cultures: IBT 21519 = IBT 11415 = CBS 101136 (Y), ex harness, Saudi Arabia; IBT 5171 = CBS 477.84 = IMI 285516 = FRR 2935, ex *Hordeum vulgare*, Denmark; IBT 5167 = CBS 349.59 = QM 7314 = ATCC 18382 = FRR 1364 = IFO 6240 = IMI 068218 (*P. viridicyclopium*), ex soil, Japan; IBT 22027 = CBS 110335, ex wheat, UK; IBT 14369 = CBS 110336, ex wheat, UK; IBT 16769 = CBS 110337, ex malting barley, Denmark; IBT 3454 = CBS 110338; IBT 5141 = CBS 123.14 = NRRL 1889 = NRRL 2040 = ATCC 10483 = ATCC 8505 = ATCC 8732 = CCRC 31519 = FRR 2040 = IFO 7733 = IMI 034913 = LSHB Ad113 = QM 1556 = MUCL 29231 = MUCL 31198 = QM 1556 = VMK F-328 (*P. puberulum*), ex maize, Lincoln, Nebraska, USA; IBT 12480 = NRRL 970 = FRR 970 (*P. porraceum*); IBT 5362 = FRR 1347, from chicken feed implicated in fatty liver and kidney syndrome, Victoria, Australia.



Fig. 45. *Penicillium cyclopium*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. digitatum (Pers.:Fr.) Sacc., Fung. Ital.: 894, 1881

In *Penicillium* subgenus *Penicillium* section *Digitata* series *Digitata*

Type: Icon in Saccardo, Fung. Ital.: tab. 894 Jul. 1881

Epitype suggested: CBS 112082 = IBT 13068, ex *Citrus limon*, Italy (**epiT**)

Diagnostic features: Tryptoquialanines, large cylindrical to ellipsoidal smooth-walled olive green conidia, no growth on Czapek agar and CYAS

Similar species: None

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface or aerial hyphae

Conidia: Smooth-walled, ellipsoidal to cylindrical, 6-9 (-14) μm x 2.8-6 μm .

Phialides: Cylindrical tapering to a distinct collulum, 10-17 μm x 4-5 μm

Metulae: Cylindrical, 15-25 μm x 5-6 μm

Rami: Cylindrical, 20-30 μm x 5-6 μm

Stipes: Rough-walled, 60-160 μm x 5-7 μm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Olive green

Exudate droplets on CYA: Only in few isolates

Reverse colour on CYA: greyish olive to beige

Reverse colour on YES: cream yellow with light brown center

Diffusible colour: None

Ehrlich reaction: None

Odour and volatile metabolites: Ethylene, ethyl alcohol, ethyl acetate, methyl acetate, isopropyl acetate, octyl acetate, limonene, valencene (Birkinshaw et al., 1931; Larsen and Frisvad, 1995)

Extrolites: 1) Tryptoquialanins, 2) Cholesterol, ergosta-7,22-dien-3 β -OH, ergosta-7,22-24(28)-trien-3 β -OH, episterol, eburicol, 3) Phenylalanine-proline dike-topiperazine (2 isomers), 4) 3,5-Dimethoxyphenol, methoxyphenol (5 isomers), 1,1'-biphenyl-3-ol, 2-methoxy-4-propyl phenol (ethyl vanillin)

Growth on creatine: Very poor

Acid and base production on creatine: No acid

Growth on UNO: Good

Growth on nitrite: Neither growth on Czapek nor nitrite agar

Abiotic factors:

Diam., 1 week, 25°C: CYA: (15-)24-37(-55) mm; MEA: 26-54 mm; YES: 44-76 mm; CREA: 0-6 mm; Cz: 13-27 mm, OAT: 19-38 mm: CYAS: 0 mm; CzBS: 2-4 mm; CzP: 0 mm; UNO: 3-8 mm; DG18: 44-56 mm

Diam., 1 week: 15°C: 8-22 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: No growth on CYAS

CYA15°C/CYA 25°C: 0.7 [0.3-1.1]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.2 [0.1-0.3]

CZP/CZ: 0

Distribution: Italy, Spain, Cyprus, Turkey, Israel, Egypt, Saudi Arabia, Libya, Morocco, Nigeria, South Africa, Zimbabwe, Tanzania, Florida, California, USA, Cuba, Domenica, Argentina, Brazil, Australia, Indonesia, India, Bangla Desh, Pakistan, Japan, Korea, Taiwan, Viet Nam. On imported citrus fruits to Denmark, Sweden, United Kingdom, Netherlands, Belgium, France, Germany, the Netherlands, etc. (imported citrus fruits), Canada, Connecticut, North Carolina, Oklahoma, Wisconsin, USA.

Ecology and habitats: Citrus fruits are often degraded by *P. digitatum*. The species has been found on herbs, but citrus fruits may be the only real habitat. See also Domsch et al. (1980)

Biotechnological applications: None

Biodeterioration & phytopathology: *P. digitatum* is a major pathogen of citrus fruits (where it may co-occur with *P. italicum* and *P. ulaiense*) (Holmes et al., 1994)

Mycotoxicoeses and mycotoxins: Some metabolites were shown to be toxic in the chick embryo test (Faid and Tantaoui-Elaraki, 1989).

Typical cultures: IBT 21520 = IBT 15179 = CBS 101026 (Y), ex chili mix, Indonesia; IBT 12919 = CBS 351.97 = CBS 529.97, ex chervil, Denmark; IBT 15037 = CBS 112083, ex *Citrus sinensis*; IBT 5533 = CBS 112322 = FRR 288 = ATCC 52304, ex soil, foreshore of Whiteswan Lake, Saskatchewan, Canada; IBT 3816 = CBS 112081, ex mandarin; IBT 23020 = CBS 136.65 = DSM 2731, ex fruit of *Citrus medica limonum*, Netherlands; IBT 23021 = CBS 319.48 = NRRL 786 = ATCC 10030 = IFO 7006 = IMI 039748 = QM 7552 = DSM 2748, ex fruit of *Citrus* sp., Connecticut, USA; CBS 492.84 = IMI 293202 = ATCC 58617, ex *Lipidium sativum*.

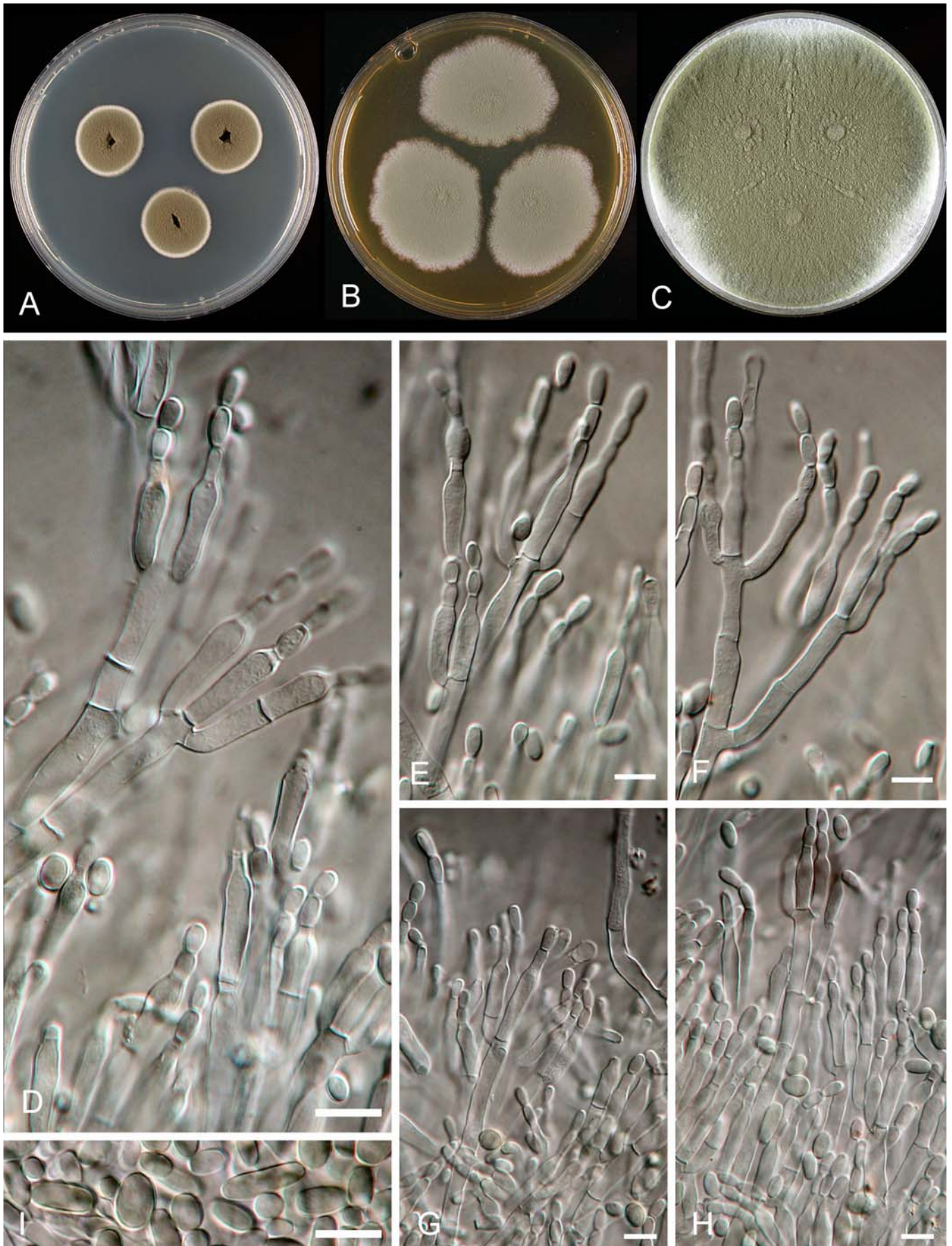


Fig. 46. *Penicillium digitatum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. dipodomyicola (Frisvad, Filt. & Wicklow)
Frisvad, Int. Mod. Tax. Meth. Pen. Asp. Clas.:
275, 2000

In *Penicillium* subgenus *Penicillium* section *Penicillium*
series *Urticicolae*

Type: Herb. IMI 296935

Culture ex type: CBS 173.87 = IBT 21521 = IMI 296935,
ex external fur-lined cheek pouch of kangaroo rat (*Dipodo-*
mys spectabilis), 6 km east of Portal, Arizona (**T, Y**)

Diagnostic features: Griseofulvin, cyclopiazonic acid,
patulin, broadly ellipsoidal smooth-walled conidia, short
phialides, dark brown reverse on CYA, dull green to dark
green conidia

Similar species: *P. dipodomyicola* has darker green conidia
and a darker brown reverse on CYA than *P. griseofulvum*

Description:

Conidiophores: Divergent biverticillate to terverticillate

Conidia: smooth-walled, broadly ellipsoidal, 2.5-3.5 x 2.2-
2.5 µm

Phialides: Cylindrical tapering to a distinct collulum, 4.5-
6.5 µm x 2.2-2.5 µm

Metulae: Cylindrical, 7.5-10 µm x 3.5-4 µm

Rami: Cylindrical, 15-25 µm x 3.5-4 µm

Stipes: Smooth-walled, 400-500 µm x 3-4 µm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Velvety to weakly granular

Conidium colour on CYA: Dark (grey) green to dark green

Exudate droplets on CYA: Often exudates droplets, clear to
yellow to red

Reverse colour: Dark brown

Diffusible colour: None

Ehrlich reaction: Strong, violet

Odour and volatile metabolites: No data

Extrolites: 1) Patulin, 2) Griseofulvin, 3) Cyclopiazonic
acid

Growth on creatine: Poor

Acid and base production on creatine: No acid

Growth on UNO: Very good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 20-30 mm; MEA: 22-30 mm;
YES: 32-45 mm; CREA: 14-18 mm; Cz: 14-18 mm, OAT:
21-27 mm: CYAS: 24-28 mm; CzBS: 13-19 mm; CzP: 0
mm; UNO: 12-16 mm; DG18: 24-26 mm

Diam., 1 week: 15°C: 17-22 mm; 30°C: 17-21 mm; 37°C: 0
mm

CYA/CYAS: 1.1 [1.0-1.3]

CYA15°C/CYA 25°C: 0.7 [0.6-0.8]

CYA30°C/CYA 25°C: 0.7 [0.6-0.7]

CZBS/CZ: 1.1 [1-1.1]

CZP/CZ: 0

Distribution: Deserts of Western USA, New South Wales,
Australia, Slovakia

Ecology and habitats: Mounds and cheek pouches of
kangaroo rats, on rice, in mixed chicken feed, and in soil
under sagebrush

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: Found on rice once and in
seeds from the desert

Typical cultures: IBT 16571 = CBS 110421, ex soil under
sagebrush, 16 km North of Rawlins, Wyoming, USA; IBT
19341 = CBS 110422 = FRR 3866, ex rice from Murrum-
didgee Irrigation Area fumigated with phosphine, Sydney,
N.S.W., Australia (identified as *P. waksmanii*); IBT 18044
= CBS 110423, ex soil under sagebrush, Rock Springs,
Wyoming; IBT 12706 = CBS 110424, ex kangaroo rat,
Sevilletta National Wildlife Refuge, Socorro County, New
Mexico, USA; IBT 10723 = CBS 110425 = NRRL A-
27015, ex kangaroo rat, Arizona, USA; IBT 16314 = CBS
110426, ex soil under sagebrush, 16 km North of Rawlins,
Wyoming, USA; IBT 4182 = CBS 110427 = NRRL A-
26936, ex kangaroo rat, Arizona, USA, IBT 4092 = IBT
10613 = NRRL A-27016; IBT 26223, ex chicken feed
mixture, Slovakia.



Fig. 47. *Penicillium dipodomyicola*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. dipodomyis (Frisvad, Filt. & Wicklow) Banke,
Frisvad & S. Rosendahl, Int. Mod. Tax. Meth.
Pen. Asp. Clas.: 271, 2000

In *Penicillium* subgenus *Penicillium* section *Chrysogena*
series *Chrysogena*

Type: Herb. IMI 296926

Culture ex type: IBT 5333 = CBS 110412 = NRRL 13485
= NRRL A-26836 = IMI 296926, ex cheek pouch of
kangaroo rat, 6 km east of Portal, Arizona (T)

Diagnostic features: Penicillin F & G, dipodazin, dark
green smooth-walled conidia

Similar species: *P. dipodomyis* is more consistently terverticillate than *P. nalgiovense*.

Description:

Conidiophores: Bi-, terverticillate, both appressed and
divergent rami born from aerial and subsurface hyphae,
some stipes sinoid

Conidia: Smooth-walled, globose to subglobose, 2.5-4 µm x
2.3-3.5 µm

Phialides: Cylindrical, with short broad collula, 7-9 µm x
2.3-2.5 µm

Metulae: Cylindrical, 8-12 µm x 2.5-4 µm

Rami: Cylindrical, 15-22 µm x 3-4 µm

Stipes: Smooth to finely rough-walled, 200-300 µm x 3-4
µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Dark green

Exudate droplets on CYA: Present, clear

Reverse colour on CYA: Cream coloured

Reverse colour on YES: Yellow to orange

Diffusible colour: None

Ehrlich reaction: None

Odour and volatile metabolites: Not tested

Extrolites: 1) Penicillin F and G, 2) Dipodazin

Growth on creatine: Poor

Acid and base production on creatine: No acid or acid under
colony, no base

Growth on UNO: Very good

Growth on nitrite: Good (one isolate weak)

Abiotic factors:

Diam., 1 week, 25°C: CYA: 25-34 mm; MEA: 18-30 mm;
YES: 28-45 mm; CREA: 13-18 mm; Cz: 13-20 mm, OAT:
20-26 mm; CYAS: 31-40 mm; CzBS: 13-18 mm; CzP: 0
mm; UNO: 11-19 mm; DG18: 26-34 mm

Diam., 1 week: 15°C: 17-21 mm; 30°C: 15-18 mm; 37°C:
0-4 mm

CYA/CYAS: 0.9 [0.8-1.0]

CYA15°C/CYA 25°C: 0.6 [0.6-0.7]

CYA30°C/CYA 25°C: 0.5 [0.4-0.6]

CZBS/CZ: 0.9 [0.8-1.0]

CZP/CZ: 0

Distribution: Western states of USA, Saudi Arabia

Ecology and habitats: Deserts, kangaroo rat mounds and
cheek pouches, soil near salt lakes, leather harness

Biotechnological applications: None

Biodeterioration & phytopathology: May deteriorate
leather

Mycotoxins and mycotoxins: None known

Typical cultures: IBT 21522 = CBS 170.87, ex kangaroo
rat, Arizona, USA (Y); IBT 11425 = CBS 110415, ex
harness, Saudi Arabia; IBT 12700 = CBS 110414, ex
kangaroo rat, Seville, New Mexico, USA; IBT 17759 =
CBS 110413; ex barley, Star Valley, Wyoming, USA; IBT
20227 = CBS 112578, ex soil with 14% salt, Antelope
Island, Salt Lake, Utah, USA; IBT 3353 = CBS 112570, ex
soil, Walnut Crater, Arizona, USA; IBT 3356 = CBS
112316; seeds of an *Amaranthus* sp., Arizona, USA.

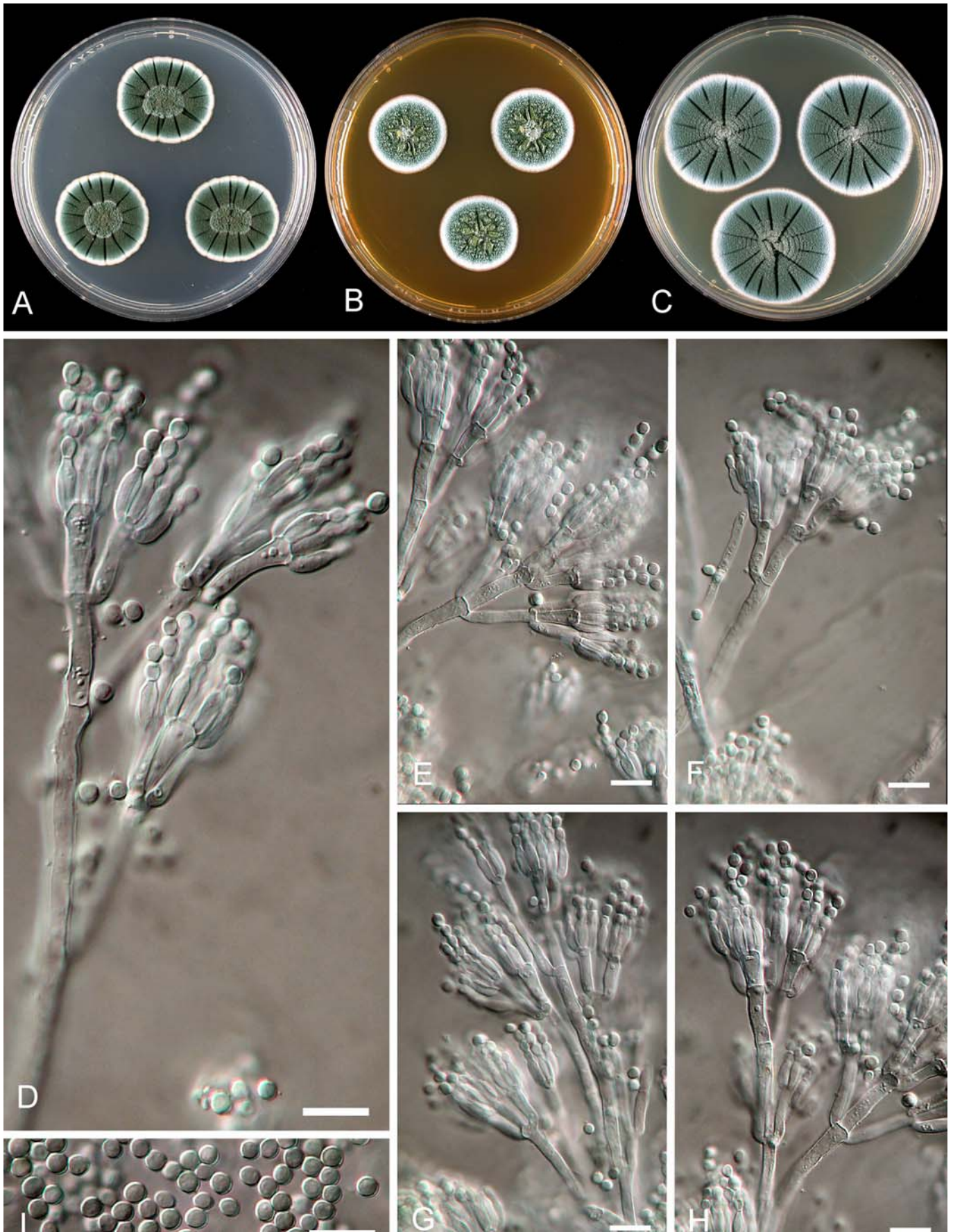


Fig. 48. *Penicillium dipodomyis*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. discolor Frisvad & Samson, Ant. Leeuwenhoek
72: 120, 1997

In *Penicillium* subgenus *Penicillium* section *Viridicata*
series *Solita*

Type: Herb. IMI 285513

Culture ex type: CBS 474.84 = IBT 21523 = IBT 5738 =
IBT 14440 = IMI 285513 = FRR 2933, ex *Raphanus sati-*
vus, Israel (Y, T)

Diagnostic features: Chaetoglobosin A, B, C, cyclopenol,
cyclopenin, dark green rough-walled conidia, brilliant red
diffusible colour on YES agar

Similar species: *P. echinulatum* and *P. cavernicola* differs
from *P. discolor* by the brilliant red diffusible pigment
produced by the latter species.

Description:

Conidiophores: Terverticillate, appressed elements, born
from subsurface hyphae

Conidia: Rough-walled, globose to subglobose, 3.5-4.0 µm.

Phialides: Cylindrical tapering to a distinct collum, 8-10
µm x 2-2.5 µm

Metulae: Cylindrical, 12-15 µm x 3-3.5 µm

Rami: Cylindrical, 12-20 µm x 3.2-4.2 µm

Stipes: Rough-walled, 200-250 µm x 3.5-4 µm

Synnemata or fasciculation: Fasciculate on MEA and OAT
Sclerotia: None

Colony texture on CYA: Velutinous to fasciculate

Conidium colour on CYA: Dark green

Exudate droplets on CYA: Clear

Reverse colour on CYA: Cream yellow

Reverse colour on YES: Orange turning into deep red with
age

Diffusible colour: Brilliant red diffusible colour on YES

Ehrlich reaction: Weak, violet

Odour and volatile metabolites: 2-methyl-3-butene-2-ol,
isobutanol, isopentanol, 3-octanone, 2-methyl-isoborneol,
geosmin, isobutyl acetate (Larsen & Frisvad, 1995)

Extrolites: 1) Palitantin, 2) Cyclopeptin, dehydro-
cyclopeptin, cyclopenol, cyclopenin, viridicatol, viridicatin,
3) Chaetoglobosin A, B, C etc., 4) Daldinin D

Growth on creatine: Very good

Acid and base production on creatine: Good acid and base
production

Growth on UNO: Very good

Growth on nitrite: Poor

Abiotic factors:

Diam., 1 week, 25°C: CYA: 21-36 mm; MEA: 20-33 mm;
YES: 28-51 mm; CREA: 17-28 mm; Cz: 23-30 mm, OAT:
21-30 mm; CYAS: 27-38 mm; CzBS: 19-24 mm; CzP: 0
mm; UNO: 14-23 mm; DG18: 25-29 mm

Diam., CYA, 1 week: 5°C: 3-6 mm; 15°C: 24-30 mm;
30°C: 0-12 mm (thin colonies); 37°C: 0 mm

CYA/CYAS: 0.94 [0.7-1.1]

CYA15°C/CYA 25°C: 0.9 [0.8-1.2]

CYA30°C/CYA 25°C: 0.2 [0-0.3]

CZBS/CZ: 0.8 [0.7-1.0]

CZP/CZ: 0

Distribution: Denmark, the Netherlands, Belgium, Czech
Republic, France, Germany, Italy, Georgia, North Carolina,
Colorado, New Mexico, USA, Canada, Israel, Kenya, India,
South Korea

Ecology and habitats: Hard cheese, blue cheese, acorns,
walnuts, chestnuts, black walnuts, pecans, hazel nuts,
radishes, onion, sunseed tubers, flower bulbs, apples

Biotechnological applications: None

Biodeterioration & phytopathology: Moulding natamycin
treated cheeses

Mycotoxins and mycotoxins: Chaetoglobosin A, B and
C could potentially be produced in vegetables, nuts and
cheese, and have been found naturally occurring in chest-
nuts (Overy *et al.*, 2003).

Typical cultures: IBT 15145 = CBS 278.97, ex dairy
cooling device, Denmark; IBT 11512 = CBS 271.97, ex
acorn, Kgs. Lyngby, Denmark; IBT 14472 = CBS 112557,
ex wall of Lechuguilla Cave, Carlsbad, New Mexico, USA;
IBT 16218 = IBT 16476 = CBS 112569; ex black walnut,
North Carolina; IBT 3088 = CBS 112558 = ATCC 32002 =
IBT 4229 = IBT 5730, ex weevil damaged pecan, Georgia,
USA; IBT 13522 = CBS 112568, ex cereal, Kenya; T182 =
IBT 19542 = CBS 112559, Czech Republic; IBT 16126 =
CBS 284.97, ex black walnut, Colorado, USA; CBS 969.97,
ex cheese, Germany; CBS 183.88 = IBT 3904 = IBT 4231 =
IBT 5734 = IBT 5920, ex *Corylus avellana*; CBS 221.92 =
IBT 14439, ex cheese, Netherlands; CBS 222.92, ex cheese,
Netherlands; CBS 547.95, ex cheese surface, Italy; CBS
548.95, ex cheese surface, Netherlands; CBS 549.95, ex air
in cheese plant, Belgium; CBS 550.95, ex cheese surface,
Austria; CBS 551.95, ex cheese surface, France, IBT 4232
= IBT 5733 = ATCC 32000, ex weevil damaged pecans,
IBT 5740, ex walnut, India; IBT 3086 = IBT 4224 = IBT
5744, ex *Helianthus tuberosus*, Denmark; IBT 3089 = IBT
4223 = IBT 5731, ex onion, Denmark; IBT 3179 = IBT
3769 = IBT 5736 = IBT 4237, ex onion, Denmark; IBT
3090, ex cheese, the Netherlands; IBT 3185 = IBT 4228 =
IBT 5740, ex pecan nut; IBT 3187 = IBT 4220 = IBT 5735,
ex walnut, Denmark; IBT 3557 = IBT 4227 = IBT 5737, ex
apple, Kgs. Lyngby, Denmark; IBT 11699, ex walnut,
France; IBT 11513, IBT 11626 & IBT 11511, all ex acorns,
Denmark; IBT 11724 & IBT 11725, ex cheese, Denmark;
IBT 13022, ex citrus fruits, Korea; IBT 15185, ex flower
bulb, Denmark; IBT 15186, ex blue cheese, France; IBT
16126 = RMF 9950, ex black walnut, North Carolina, USA.

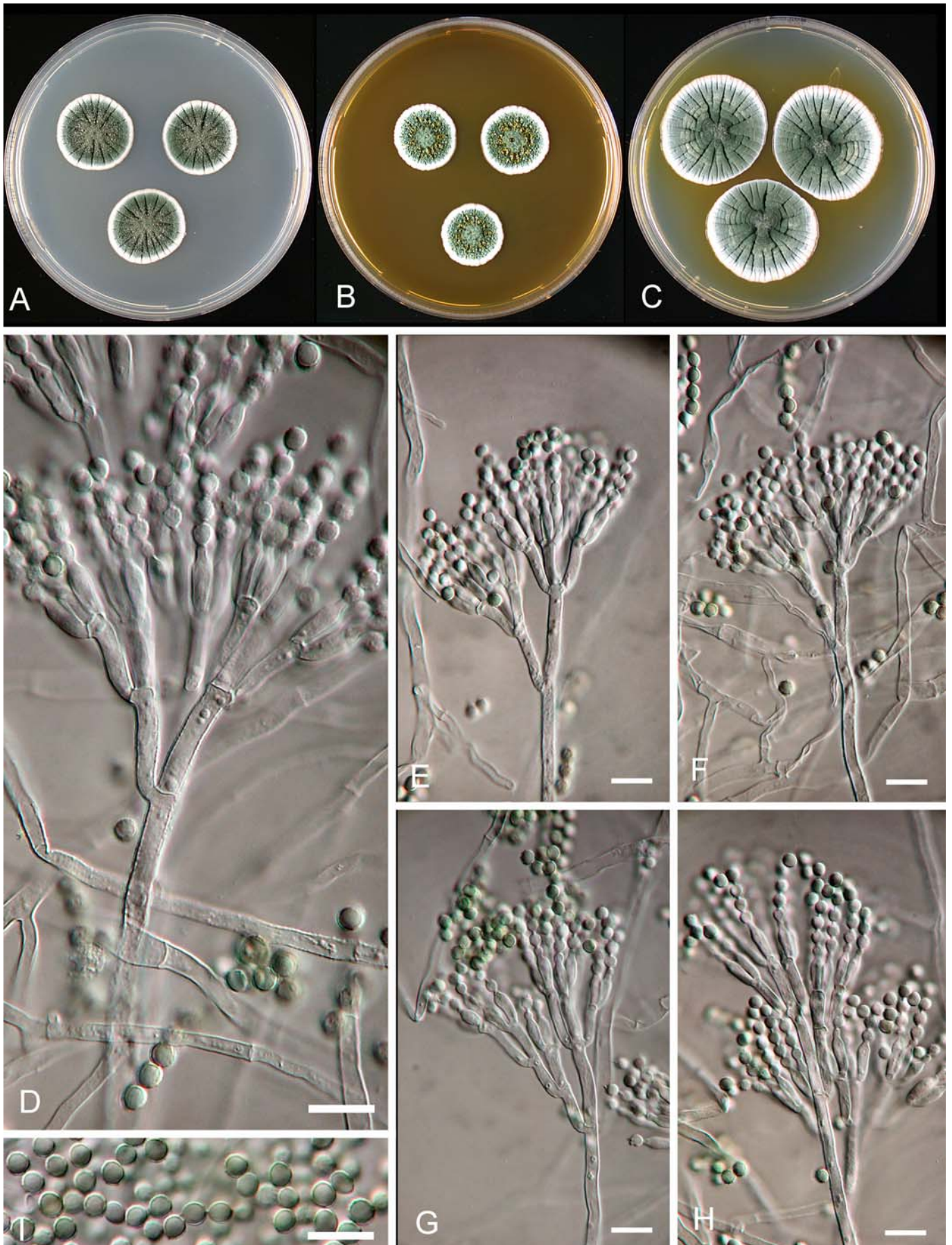


Fig. 49. *Penicillium discolor*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. echinulatum Fassatiová, Acta Univ. Carol. Biol. **12**: 326, 1977

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Solita*

Type: Herb. PRM 778523

Culture ex type: CBS 317.48 = IBT 6294 = IMI 040028 = ATCC 10434 = NRRL 1151 = FRR 1151 = IFO 7760 = MUCL 15615 = QM 7519, contaminant in a Petri dish, Ottawa, Canada (T)

Diagnostic features: Territrems, cyclopenins, dark green rough-walled conidia

Similar species: *P. echinulatum* differs from *P. solitum* by producing rough-walled conidia and from *P. discolor* by inability to produce a diffusible red pigment. *P. discolor* differs from *P. cavernicola* by the cream-coloured reverse on CYA, in contrast to the brown reverse of the latter species.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Rough-walled, globose to subglobose, 3.5-4.5 µm.

Phialides: Cylindrical tapering to a distinct collulum, 9-11 µm x 2.5-3.0 µm

Metulae: Cylindrical, 11-15 µm x 3-3.5 µm

Rami: Cylindrical, 12-20 µm x 3.5-4.2 µm

Stipes: Rough-walled, 250-500 µm x 3.5-4.2 µm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Velutinous to weakly fasciculate

Conidium colour on CYA: Dark green

Exudate droplets on CYA: Present, clear

Reverse colour on CYA: Cream coloured

Reverse colour on YES: Yellow

Diffusible colour: None

Ehrlich reaction: None

Odour and volatile metabolites: Ethyl acetate, isobutanol, isopentanol, 3-octanone, geosmin (Larsen and Frisvad, 1995)

Extrolites: 1) Palitantin, 2) Territrems and arisugacins, 3) Cyclopeptin, dehydrocyclopeptin, cyclopenin, cyclopenol, viridicatin, viridicatul

Growth on creatine: Very good

Acid and base production on creatine: Good acid production followed by base production

Growth on UNO: Very good

Growth on nitrite: Poor

Abiotic factors:

Diam., 1 week, 25°C: CYA: 20-40 mm; MEA: 18-35 mm; YES: 33-53 mm; CREA: 21-27 mm; Cz: 14-25 mm, OAT: 20-34 mm; CYAS: 32-39 mm; CzBS: 17-24 mm; CzP: 0 mm; UNO: 12-22 mm; DG18: 16-29 mm

Diam., CYA, 1 week: 5°C: 3-5 mm; 15°C: 25-31 mm; 30°C: 0-1 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.6-1.0]

CYA15°C/CYA 25°C: 0.9 [0.8-1.3]

CYA30°C/CYA 25°C: 0.03 [0.03-0.05]

CZBS/CZ: 0.9 [0.8-1.0]

CZP/CZ: 0

Distribution: Denmark, Sweden, the Netherlands, Germany, France, Wyoming, Arizonut, USA, Canada, Thailand, Japan, South Africa

Ecology and habitats: Lipids, margarine, cheese, wood and wood products, lemon grass

Biotechnological applications: None

Biodeterioration & phytopathology: Has been found in wet mechanical pulp, and may be able to degrade paper.

Mycotoxinoses and mycotoxins: Territrems are tremorgenic mycotoxins, but these have not been found to occur naturally.

Typical cultures: IBT 21524 = IBT 12879 = CBS 101027, ex wash basin, Denmark (Y); IBT 7000 = CBS 268.97, ex goat cheese, Paris, France; IBT 3232 = CBS 337.59 = ATCC 18487 = FAT 1019 = FRR 637 = IFO 6233 = IMI 068236 = QM 7304, unrecorded source, Japan (*P. palitans* var. *echinoconidium*); IBT 3234 = CBS 112287 = FRR 1963, ex cheddar cheese, Orange Free State, South Africa; IBT 21568 = CBS 112288; ex wood shaving, Denmark; IBT 16296 = CBS 290.97, ex root, Wyoming, USA; IBT 22503 = CBS 112289, ex waste, Germany; IBT 21839 = CBS 112286, ex lemon grass, Thailand; CBS 255.55, ex wet mechanical pulp, Sweden; IBT 4105 = CBS 347.97, ex adult bee gut, Arizona, USA.

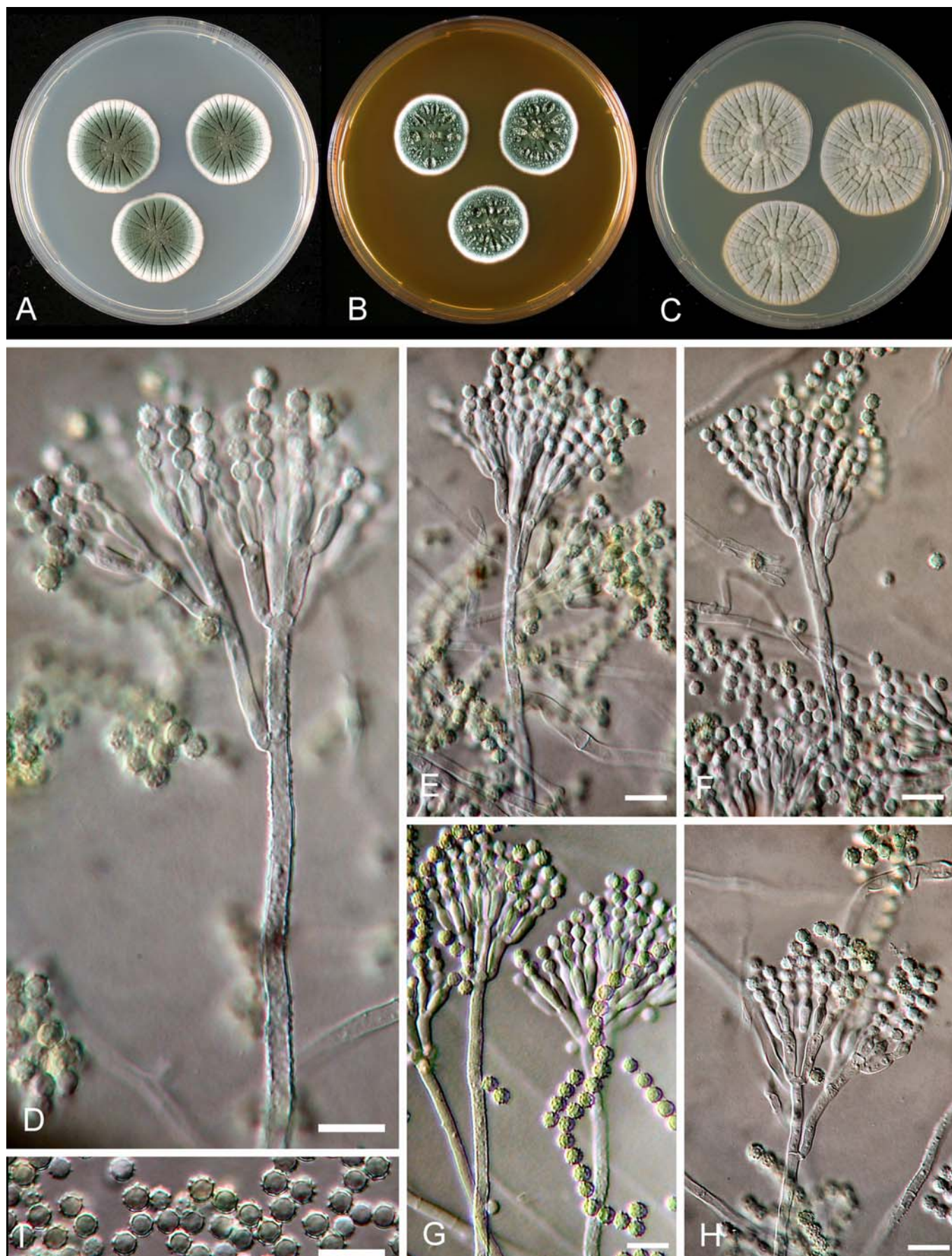


Fig. 50. *Penicillium echinulatum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. expansum Link, Obs. Mycol. 1: 16, 1809

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Expansa*

Type (neo): Herb. CBS 325.48

Culture ex neotype: CBS 325.48 = IBT 3486 = IBT 5101 = IBT 5854 = IMI 039761ii = ATCC 7861 = ATUM 2891 = FRR 976 = MUCL 29192 = NRRL 976 = VKM F-275, ex *Malus sylvestris*, USA (**T**)

Diagnostic features: Expansolide, patulin, chaetoglobosins, roquefortine C, communesin A & B, ellipsoidal smooth-walled conidia, apple rot

Similar species: See *P. marinum*. *P. expansum* differs from *P. crustosum* by inability to produce conidial crusts.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface and aerial hyphae

Conidia: Smooth-walled, ellipsoidal, 3-3.5 µm x 2.5-3 µm.

Phialides: Cylindrical tapering to a distinct collulum, 8-12 µm x 2.5-3.2 µm

Metulae: Cylindrical, 11-15 µm x 3-4 µm

Rami: Cylindrical, 15-25 µm x 3-4 µm

Stipes: Smooth walled, occasionally rough-walled at lower part of stipe, 200-500 µm x 3-4 µm

Synnemata or fasciculation: Capitulate synnemata produced in fresh strains or after cold storage on MEA or OAT

Sclerotia: None

Colony texture: Floccose to weakly fasciculate

Conidium colour on CYA: Blue green to green

Exudate droplets on CYA: Copious, clear

Reverse colour on CYA: Cream to yellow with brown center, orange brown or dark brown

Reverse colour on YES: Cream yellow or orange

Diffusible colour on CYA: Common, rosy brown

Ehrlich reaction: Strong, violet

Odour and volatile metabolites: Isobutanol, isopentanol, 1-methoxy-3-methyl-benzene, geosmin (Larsen and Frisvad, 1995; Mattheis and Roberts, 1992)

Extrolites: 1) Patulin, 2) Citrinin, 3) Chaetoglobosin A, B, C etc., 4) Communesin A and B, 5) Roquefortine C, 6) Expansolide A & B, 7) Fumaryl-d,l-alanine

Growth on creatine: Very good (poor in very few strains)

Acid and base production on creatine: Good acid production followed by base production

Growth on UNO: Good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 26-50 mm; MEA: 16-34 mm;

YES: 38-65 mm; CREA: 23-28 mm; Cz: 25-30 mm, OAT:

25-42 mm; CYAS: 23-41 mm; CzBS: 10-25 mm; CzP: 0 mm; UNO: 11-27 mm; DG18: 21-42 mm

Diam., CYA, 1 week: 5°C: 3-5 mm; 15°C: 26-34 mm; 30°C: 0-3 mm; 37°C: 0 mm

CYA/CYAS: 1.1 [0.7-1.6]

CYA15°C/CYA 25°C: 0.9 [0.8-1.3]

CYA30°C/CYA 25°C: 0.03 [0-0.09]

CZBS/CZ: 0.7 [0.4-0.8]

CZP/CZ: 0

Distribution: Denmark, United Kingdom, Sweden, Norway, the Netherlands, Belgium, Germany, France, Italy, Spain, Turkey, Czech Republic, Slovenia, Hungary, Moldavia, Russia, Israel, USA, Canada, Trinidad, Argentina, Ghana, Mozambique, Japan, Queensland and New South Wales, Australia, New Zealand. See also Domsch *et al.*, (1980)

Ecology and habitats: Apples, pears and other pomaceous fruits, cherries, peaches, plums and other stone fruits, tomatoes, papaya, *Albizia gummifera*, *Cydonia vulgaris*, *Dioscorea* spp., walnuts, acorns, pine cones, *Sorbus* endophyte, peanuts, dried meat, household waste, lumber, wall paper, indoor air, soil (see also Domsch *et al.*, 1980)

Biotechnological applications: None

Biodeterioration & phytopathology: Pathogen of pomaceous and other fruits

Mycotoxins and mycotoxins: Patulin, chaetoglobosin C, roquefortine C, citrinin and communesin A & B may be involved in mycotoxins, but it is only patulin that is regulated (especially in apple juice). Sugar beet waste, potato peel waste, fruit juices etc may have heavy growth of *P. expansum* and have resulted in toxicoses of domestic animals (Andersen *et al.*, 2004).

Typical cultures: IBT 21525 = CBS 481.84, ex *Brassica oleracea*, Denmark (**Y**); IBT 15598 = CBS 281.97, ex chilled food, Denmark; IBT 22804 = CBS 486.75, ex meat product, Germany; IBT 19300 = CBS 110402, ex lime quarry, Fakse, Denmark; IBT 13494 = VKM F-1971, Moldavia; IBT 15658 = CBS 110403 = FRR 4314, ex spoiled margarine, Sydney, Australia; Australia; IBT 16943 = CBS 110404, ex wheat, Hohenheim, Germany; T205 = IBT 15717 = CBS 110405, ex fungal mat on industrial cherry juice, Denmark; IBT 16705 = CBS 285.97, ex maize, Slovenia; CBS 150.45 = IMI 040227 = ATCC 10487 = NRRL 2021 = IFO 7734, culture contaminant (*P. resticolum*).

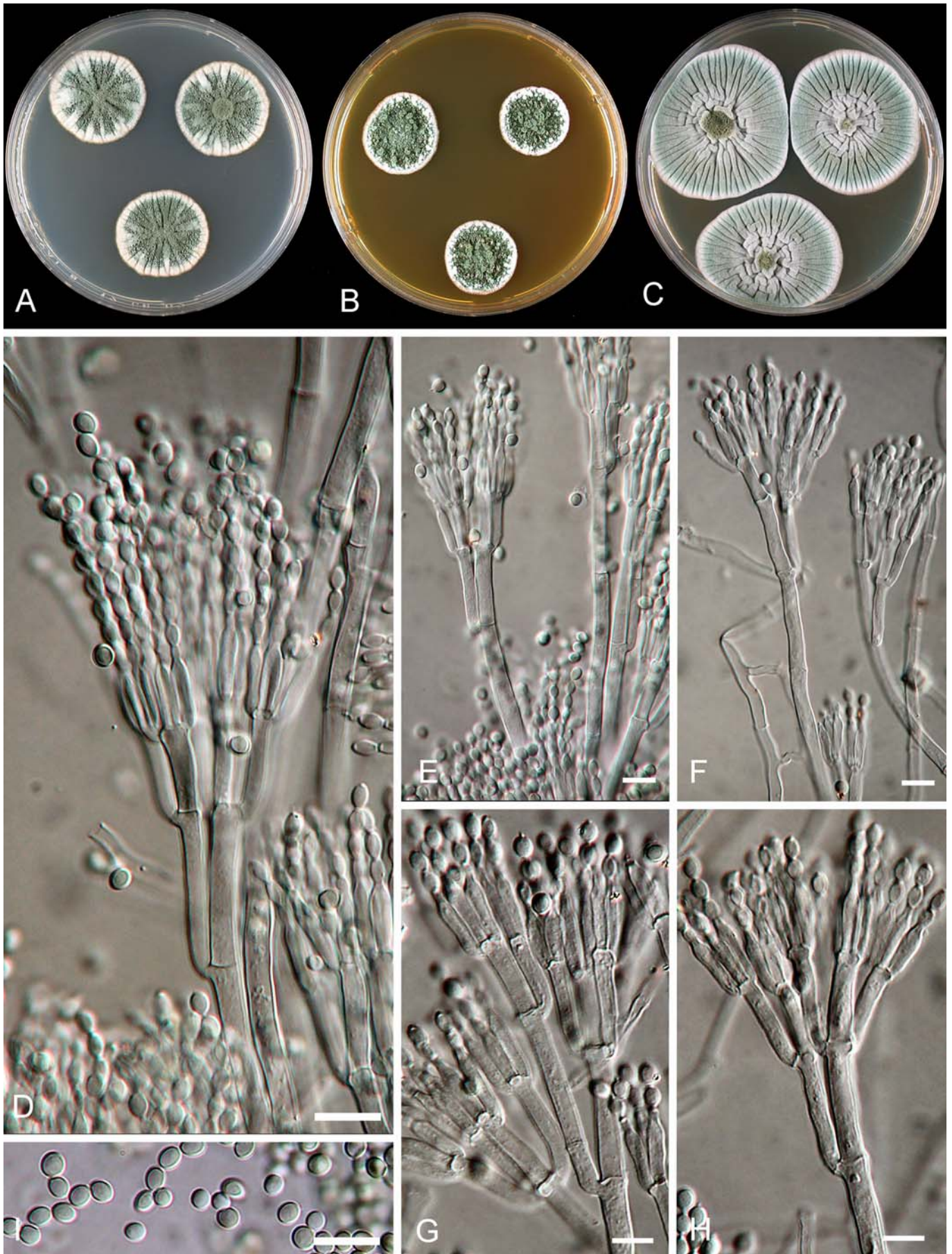


Fig. 51. *Penicillium expansum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

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

In *Penicillium* subgenus *Penicillium* section *Chrysogena* series *Chrysogena*

Type: Herb. CBS 419.89

Culture ex type: CBS 419.89 = CBS 190.88 = IBT 3091 = IBT 21526 = IBT 3780 = IBT 4727, ex wheat flour, Denmark (T)

Diagnostic features: Smooth-walled conidia, bright yellow droplets and reverse, diffusible pigment

Similar species: See *P. chrysogenum*.

Description:

Conidiophores: Terverticillate, both appressed and divergent rami born from aerial and subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 2.5-4 µm x 2.3-3.5 µm

Phialides: Cylindrical, with short broad collula, 7-9 µm x 2.3-2.5 µm

Metulae: Cylindrical, 8-12 µm x 2.5-4 µm

Rami: Cylindrical, 15-22 µm x 3-4 µm

Stipes: Smooth, 200-300 µm x 3-4 µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous to slightly floccose

Conidium colour on CYA: Blue green

Exudate droplets on CYA: Present, yellow

Reverse colour on CYA: Yellow

Reverse colour on YES: Yellow

Diffusible colour on CYA: Yellow

Ehrlich reaction: None

Odour and volatile metabolites: No data

Extrolites: 1) Penicillin F & G, 2) Xanthocillins, 3) Roquefortine C and meleagrins, 4) Penitrem A

Growth on creatine: Weak

Acid and base production on creatine: Acid under colony, no base

Growth on UNO: Very good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 22-31 mm; MEA: 24-36 mm; YES: 37-52 mm; CREA: 17-22 mm; Cz: 21-25 mm, OAT: 23-32 mm; CYAS: 23-39 mm; CzBS: 6-15 mm; CzP: 0 mm; UNO: 20-27 mm; DG18: 28-37 mm

Diam., 1 week: 15°C: 16-19 mm; 30°C: 15-21 mm; 37°C: 0-4 mm

CYA/CYAS: 0.9 [0.7-1.1]

CYA15°C/CYA 25°C: 0.7 [0.6-0.7]

CYA30°C/CYA 25°C: 0.7 [0.6-0.8]

CZBS/CZ: 0.4 [0.3-0.6]

CZP/CZ: 0

Distribution: Denmark, New Mexico, Arizona and Wyoming (USA), Canada, Tunisia

Ecology and habitats: Desert and cool desert soil, wheat, (nuts)

Biotechnological applications: none, but *P. flavigenum* is a potential producer of penicillin and xanthocillin X, both antibiotics

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: Penitrem A and roquefortine C may be potentially produced in cereals and nuts, but it is not known whether *P. flavigenum* can be a dominant species in cereals or nuts.

Typical cultures: IBT 16616 = CBS 110406, ex soil under *Chrysothamnus nauseosus*, Table Rock Road, Wyoming (Y); IBT 14060 = CBS 110407, ex hazel nut, Denmark; T209 = IBT 21794 = CBS 110408, ex saltern Slovenia; T210 = IBT 16864 = CBS 286.97, ex soil under *Atriplex gardneri*, New Mexico, USA; T211 = IBT 3230 = CBS 110409, ex mud from excavation, Tunisia; T212 = IBT 5908 = CBS 110410, ex soil under cactus, Marica Point, Grand canyon, Arizona, USA; IBT 11693 = CBS 110411, ex wheat, Canada; IBT 13687 = CBS 274.97, ex liquorice root, France; IBT 14531 = CBS 276.97, ex walls of Lecuguilla Cave, Carlsbad, New Mexico.

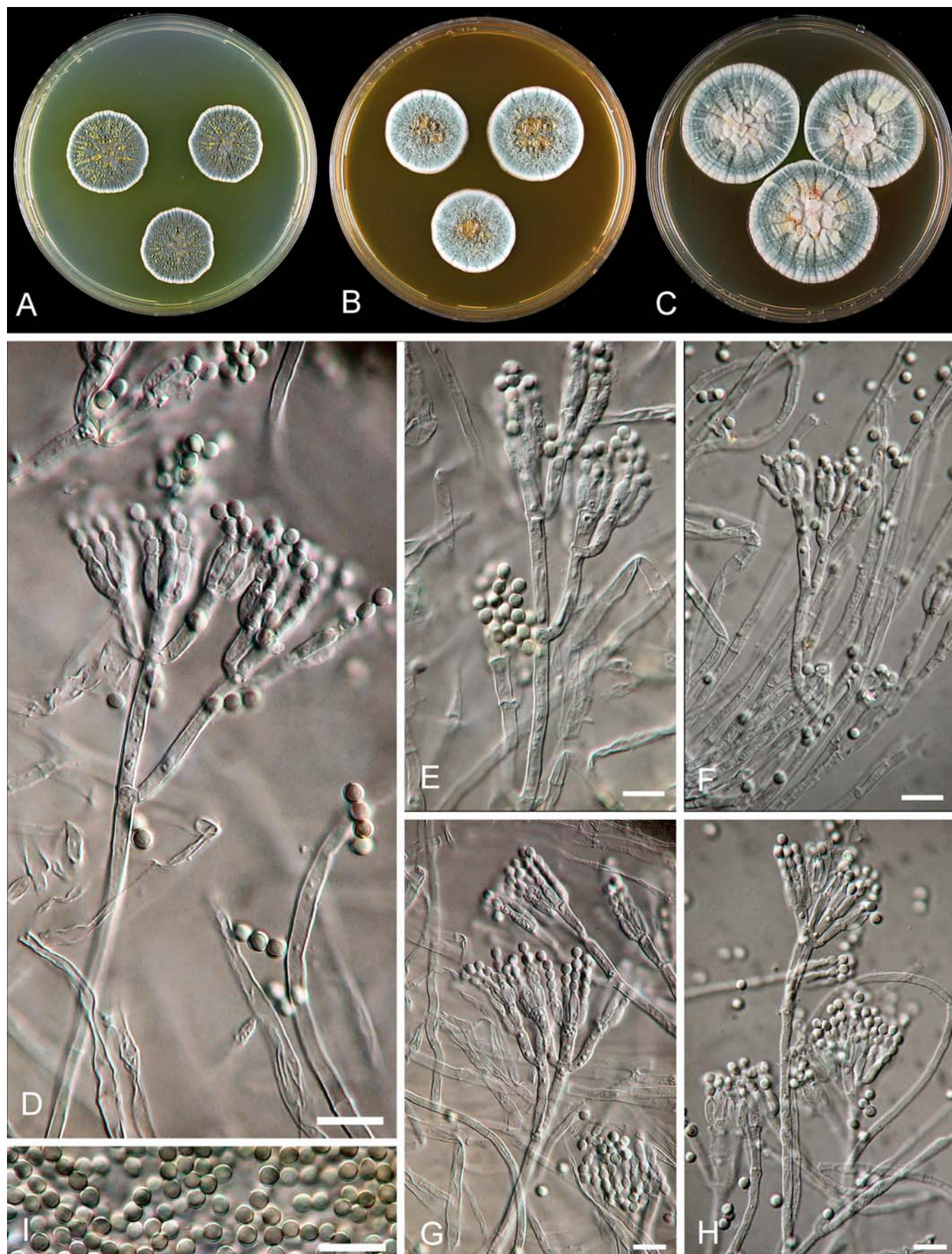


Fig. 52. *Penicillium flavigenum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

***P. formosanum* Hsieh, Su & Tzean**, Trans. Mycol. Soc. R.O.C. **2**: 159, 1987

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Claviformia*

Type: Herb. PPEH 10001

Culture ex type: IBT 21527 = IBT 19748 = CBS 211.92 = CBS 101028 = CCRC 32654, ex dungy soil, Hsihtou, Nantou County, Taiwan (T, Y)

Diagnostic features: Patulin, broadly ellipsoidal smooth-walled conidia, poor conidium production but yellow mycelium on CYA, poor growth on CREA and UNO, synnemata with yellow stipes, no growth at 30°C, very poor growth on CYAS

Similar species: *P. formosanum* is most closely related to *P. vulpinum* and *P. clavigerum*, but *P. formosanum* does not produce synnemata on CYA, while it produces yellow synnemata on MEA and OAT.

Description:

Conidiophores: Biverticillate or mostly terverticillate, appressed rami born from aerial and synnematal hyphae

Conidia: Smooth-walled, subglobose to broadly ellipsoidal, 2.8-4 µm x 2.4-3.5 µm

Phialides: Cylindrical, with short collula, 9-12 µm x 2.6-3.2 µm

Metulae: Cylindrical, 9-14 µm x 2.4-4.5 µm

Rami: Cylindrical, 10-25 µm x 3.2-4.5 µm

Stipes: Smooth, 100-300 µm x 3.5-4.5 µm

Synnemata or fasciculation: Yellow synnemata produced on OAT and MEA

Sclerotia: None

Colony texture: Weakly sulcate, fasciculate

Conidium colour on CYA: Few conidia, pale green (and light yellow mycelium)

Exudate droplets on CYA: Small exudates droplets, light yellow

Reverse colour on CYA: Light orange to yellow brown

Reverse colour on YES: Beige yellow

Diffusible colour on CYA: Light orange

Ehrlich reaction: None

Odour and volatile metabolites: Geosmin, ethyl acetate, citroenelle (Larsen and Frisvad, 1995)

Extrolites: 1) Patulin, 2) Asteltoxin

Growth on creatine: Weak

Acid and base production on creatine: No acid

Growth on UNO: Moderate

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 18-42 mm; MEA: 9-15 mm (19-26 mm, Tzean et al., 1994); YES: 28-55 mm; CREA: 3-18 mm; Cz: 3-5 mm, OAT: 16-30 mm; CYAS: 3-5 mm; CzBS: 0 mm; CzP: 0 mm; UNO: 4-6 mm; DG18: 17-19 mm
Diam., 1 week: 5°C: 0 mm; 15°C: 19-21 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 15.5

CYA15°C/CYA 25°C: 0.8

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0

CZP/CZ: 0

Distribution: Nantou County, Taiwan

Ecology and habitats: Probably a dung fungus

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxinoses and mycotoxins: Patulin production, but the species is not associated to foods

Typical cultures: No further strains known

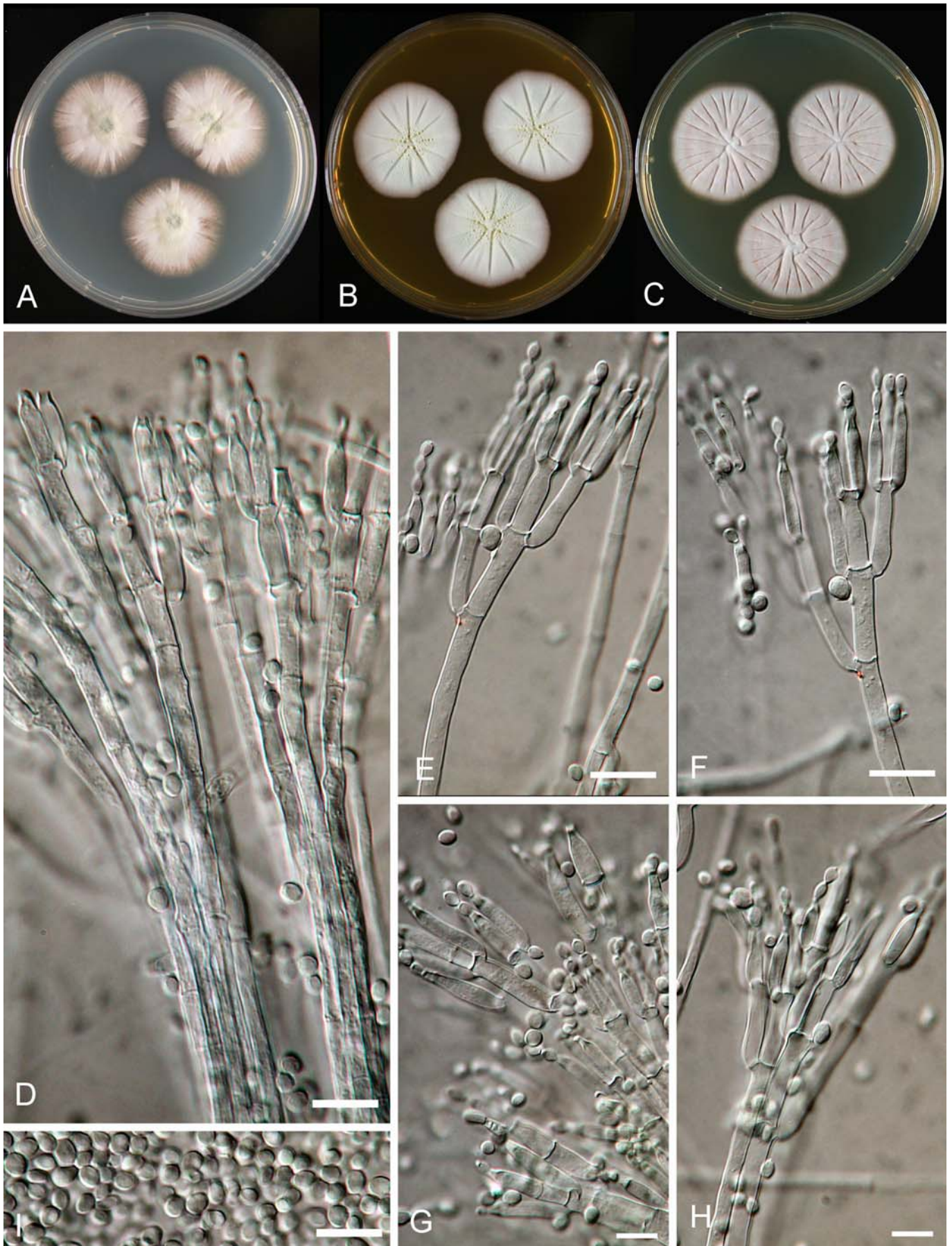


Fig. 53. *Penicillium formosanum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

***P. freii* Frisvad & Samson, sp. nov.**

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Viridicata*

Type: Herb. IMI 285513

Culture ex type: CBS 476.84 = IBT 5137 = IMI 285513, ex barley, Denmark (T)

Diagnostic features: Xanthomegnin, viomellein, vioxanthin, aurantiamine, blue green smooth-walled conidia, crustose, large clear exudates droplets

Similar species: See *P. aurantiogriseum*.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 2.6-3.4 μm .

Phialides: Cylindrical tapering to a distinct collulum, 7-9 μm x 2.2-2.8 μm

Metulae: Cylindrical, 9.5-14 μm x 3.2-4.2 μm

Rami: Cylindrical, 15-25 μm x 3.2-4.2 μm

Stipes: Smooth or finely rough walled, 100-650 μm x 3-4 μm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Velutinous to granular, crustose

Conidium colour on CYA: Blue green

Exudate droplets on CYA: Copious, clear

Reverse colour on CYA: Cream to yellow rarely brownish rose

Reverse colour on YES: Strongly yellow

Diffusible colour on CYA: If present, red brown

Ehrlich reaction: Pink reaction

Odour and volatile metabolites: Isobutanol, isopentanol, 3-octanone (Larsen and Friavad, 1995)

Extrolites: 1) Penicillic acid, 2) Xanthomegnin, viomellein and vioxanthin, 3) Aurantiamine, 4) Cyclopeptin, dehydrocyclopeptin, cyclopenin, cyclophenol, 3-methoxyviridicatin, viridicatinol

Growth on creatine: Weak

Acid and base production on creatine: Strong acid production, no base

Growth on UNO: Weak

Growth on nitrite: Very weak

RT agar: Strong reaction and dark brown halo

Abiotic factors:

Diam., 1 week, 25°C: CYA: 15-27 mm; MEA: 15-33 mm; YES: 25-40 mm; CREA: 11-23 mm; Cz: 13-24 mm, OAT: 16-32 mm; CYAS: 33-38 mm; CzBS: 15-23 mm; CzP: 0 mm; UNO: 6-11 mm; DG18: 12-23 mm

Diam., CYA, 1 week: 15°C: 17-23 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 0.6 [0.5-0.9]

CYA15°C/CYA 25°C: 0.8 [0.7-1.1]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 1.1 [0.7-1.3]

CZP/CZ: 0

Distribution: Denmark, Sweden, Norway, United Kingdom, Bulgaria, Ontario, Winnipeg, Canada, South Africa

Ecology and habitats: Cereals, mostly barley, wheat, rye and oats.

Biotechnological applications: None

Biodeterioration & phytopathology: Deteriorates cereals and barley especially at low temperature

Mycotoxins and mycotoxins: Involved in viomellein production (natural occurrence) in cereals (Hald *et al.*, 1983, misidentified as *P. crustosum*)

Typical cultures: IBT 11273 = CBS 794.95, ex chicken feed, Denmark; IBT 11310 = CBS 796.95, ex feed, Norway (Y); IBT 15065 = CBS 112022, ex barley, Pudria, Bulgaria; T218 = IBT 4363 = CBS 112290, ex wheat, United Kingdom; IBT 11996 = CBS 101486 = CSIR 1876, ex barley, South Africa; IBT 16693 = CBS 112293, ex pigfeed, Bulgaria; T221 = IBT 10107 = CBS 112292, ex barley, Denmark; T222 = IBT 11662 = CBS 112291, ex wheat, Canada; CBS 183.89, ex barley, Denmark; CBS 225.90 = IBT 5132, ex barley, Denmark.

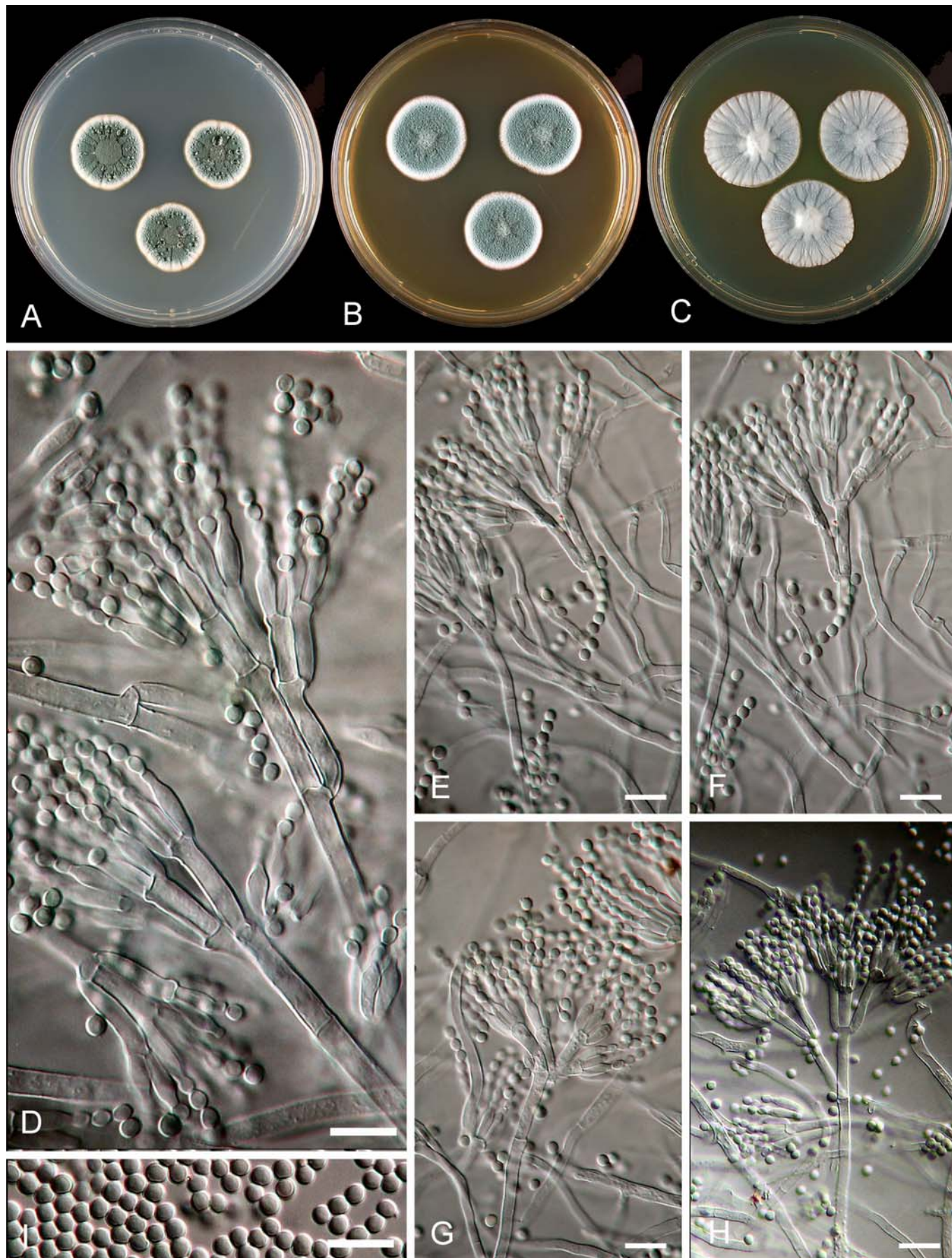


Fig. 54. *Penicillium freii*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. gladioli McCulloch & Thom, Science, N.Y. 67: 217, 1928

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Gladioli*

Type: Herb. IMI 034911

Culture ex type: CBS 332.48 = IBT 14772 = IMI 034911 = NRRL 939 = ATCC 10448 = FRR 339 = LCP 89.202 = MUCL 29174 = QM 1955, ex corm of *Gladiolus* sp. from Netherlands imported to Columbia, USA (T)

Diagnostic features: Gladiolic acid, patulin, glyanthrypine, smooth-walled conidia, sclerotia produced, gladiolus rot

Similar species: This species superficially resembles *Eupenicillium crustaceum*, but differs from that species by having rough walled stipes (Stolk and Samson, 1983)

Description:

Conidiophores: Terverticillate, appressed elements, occasionally with one or two lower branches

Conidia: Smooth-walled, subglobose, 2.6-3.4 µm.

Phialides: Cylindrical with short collula, 7.5-10 µm x 2.0-2.5 µm

Metulae: Cylindrical, 10-15 µm x 2.5-3.5 µm

Rami: Cylindrical, 15-25 µm x 2.5-3.5 µm

Stipes: Rough walled, 200-900 µm x 2.5-4 µm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: Abundant in fresh isolates, especially on OAT and MEA, hard, 150-300 (-600) µm, composed of thick walled cells (8-12 µm). Sclerotium colour cream to light pinkish tan

Colony texture: Floccose to slightly fasciculate

Conidium colour on CYA: Bluish grey green

Exudate droplets on CYA: Copious, clear

Reverse colour on CYA: Cream to light yellow or orange

Reverse colour on YES: Cream yellow

Diffusible colour on CYA: None

Ehrlich reaction: None

Odour and volatile metabolites: Not examined

Extrolites: 1) Gladiolic acid and dihydro-gladiolic acid, 2) Atrovenetins, 3) Glyanthrypine (Patulin in CBS 815.70)

Growth on creatine: moderate (very good in CBS 815.70)

Acid and base production on creatine: Moderate acid production

Growth on UNO: Weak

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 27-41 mm; MEA: 21-38 mm; YES: 30-52 mm; CREA: 12-27 mm; Cz: 18-26 mm, OAT: 25-41 mm; CYAS: 41-43 mm; CzBS: 22-24 mm; CzP: 0 mm; UNO: 4-23 mm; DG18: 27-30 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 17-23 mm;

30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.7-0.9]

CYA15°C/CYA 25°C: 0.8 [0.7-0.9]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 1.0 [0.9-1.2]

CZP/CZ: 0

Distribution: UK, Netherlands, USA, India

Ecology and habitats: *Gladiolus* corms is the only habitat known

Biotechnological applications: None

Biodeterioration & phytopathology: Pathogenic to *Gladiolus* corms, but the last isolation of *P. gladioli* is from India in 1970. The species may be extinct, maybe because of changed fungicide treatment plans.

Mycotoxins and mycotoxins: Patulin is produced, but *P. gladioli* is only known from *Gladiolus* bulbs.

Typical cultures: IBT 14699 = CBS 214.28, ex *Gladiolus* sp., USA; IBT 14773 = CBS 278.47 = ATCC 9437 = DSM 2436 = IFO 5766 = IMI 038567ii = NCTC 3994 = NRRL 938 = QM 6756, ex corm of *Gladiolus* sp., UK; IBT 21528 = IBT 14769 = CBS 815.70 = CBS 101029 = IMI 140809 = FRR 1548, ex corm of *Gladiolus*, India (Y).

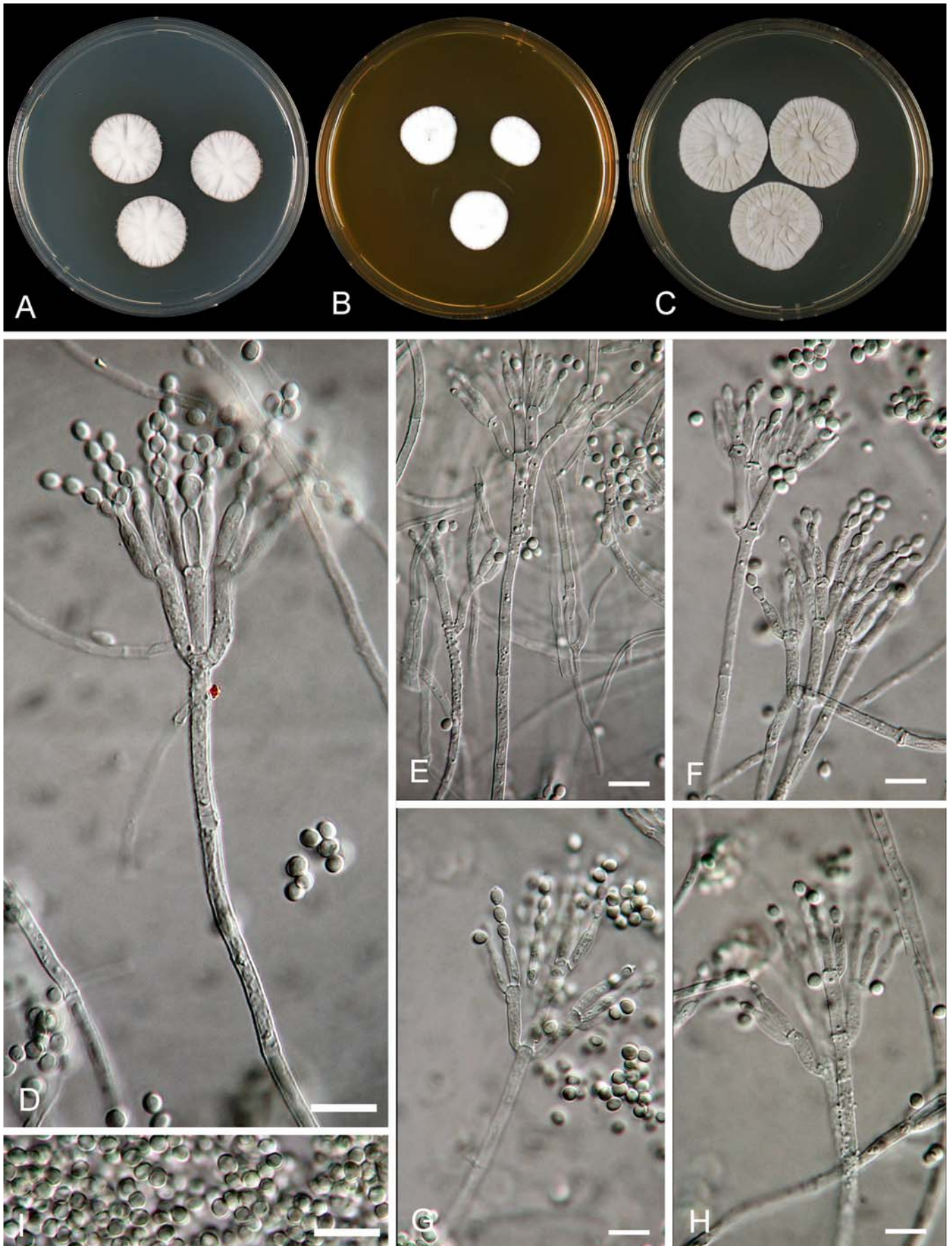


Fig. 55. *Penicillium gladioli*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. glandicola (Oud.) Seifert & Samson, Adv. Pen. Asp. Syst.: 147, 1985

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Claviformia*

Type: Netherlands, Valkenburg, Jul. 1901, *Rick* in herb. Oudemans (L)

Culture ex epitype: CBS 498.75 = IBT 21529 = IMI 154241, ex mouldy wine cork, Portugal (**epiT**, **Y**)

Diagnostic features: Patulin, patulidin, roquefortine C, meleagrins, penitrem A, ellipsoidal smooth-walled conidia, extremely tuberculate stipes

Similar species: *P. glandicola* resembles *P. concentricum*, but does not produce capitulate synnemata and very rough-walled stipes.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth-walled, ellipsoidal, 3-3.5 µm x 2.2-2.8 µm.

Phialides: Cylindrical tapering to a distinct collum, 8-11 µm x 2.2-3 µm

Metulae: Cylindrical, 8-14 µm x 3.5-4.5 µm (occasionally apically inflated)

Rami: Cylindrical, 12-20 µm x 3.5-4.2 µm

Stipes: Tuberculate walls, 100-200 µm x 3.5-4.5 µm

Synnemata or fasciculation: Strongly fasciculate, small feathery synnemata (1-3 mm)

Sclerotia: None

Colony texture: Strongly fasciculate

Conidium colour on CYA: Glaucous green to dull green

Exudate droplets on CYA: Present, clear to pale yellow

Reverse colour on CYA: yellow to orange or red brown

Reverse colour on MEA: Orange to orange red

Reverse colour on YES: Bright orange red

Diffusible colour: Yellow to red brown

Ehrlich reaction: None (few strains yellow reaction, however)

Odour and volatile metabolites: Isobutanol, 2-pentanone, isopentanol, β and γ-elemene, ethyl acetate, ethylisopentanoate, 4-heptanone, styrene, 1,8-cineol (Larsen and Frisvad, 1995)

Extrolites: 1) Patulin, 2) Patulidin, 3) Roquefortine C & D, glandicolin A / B, meleagrins, 4) Penitrem A

Growth on creatine: Very good

Acid and base production on creatine: Weak acid (mostly under colony)

Growth on UNO: Very good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 15-32 mm; MEA: 7-17 mm; YES: 22-40(-52) mm; CREA: 12-10 mm; Cz: 13-25 mm, OAT: 21-40 mm; CYAS: 19-25 mm; CzBS: 9-13 mm; CzP: 0 mm; UNO: 5-9 mm; DG18: 14-21 mm

Diam., CYA, 1 week: 5°C: 2-5 mm, 15°C: 17-23 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 0.9 [0.8-1.0]

CYA15°C/CYA 25°C: 0.8 [0.6-1.0]

CYA30°C/CYA 25°C: 0.05 [0-0.3]

CZBS/CZ: 0.5 [0.2-0.8]

CZP/CZ: 0

Distribution: Germany, Switzerland, Portugal, Illinois & South Carolina (USA), Malaysia. Domsch *et al.* (1980) list Peru, Japan, Egypt, Israel, Syria and Australia

Ecology and habitats: Oak trees and acorns, wine corks, dungy soil, forest soil and low pH soils (see also Domsch *et al.*, 1980)

Biotechnological applications: None

Biodeterioration & phytopathology: The volatiles and mycotoxins of *P. glandicola* may be present in wine corks and give bad taste (and traces of mycotoxins) to wine.

Mycotoxicoses and mycotoxins: Patulin, penitrem A, roquefortine C may be produced in silage, as *P. glandicola* (often called *P. granulatum*) has been reported from that source.

Typical cultures: IBT 6592 = CBS 333.48 = ATCC 10450 = FRR 2036 = IMI 040220 = MUCL 15621 = NRRL 2036 = QM 6868, ex soil, Illinois, USA (*P. granulatum*); IBT 14689 = CBS 111222, Switzerland; IBT 20584 = CBS 111221, growing on wood, Switzerland; IBT 4168 = CBS 111219 = IMI 296059, ex air in caves, workshop, Notts, UK; IBT 3291 = CBS 111218 = IMI 297593, ex soil in *Fagus-Prunus* forest, Switzerland; IBT 16918 = CBS 294.97 = CBS 111220, ex boiled cork, Portugal; IBT 13697 = CBS 112317 = VKM F-1277 (as *P. divergens*), Russia; IBT 3287 = CBS 494.75, ex colon of a deer, Germany; CBS 308.63, ex salami sausage, Netherlands; IBT 6778 = IBT 3290 = CBS 192.88 = IMI 321513, ex soil under *Quercus* sp., Columbia, South Carolina, USA; NRRL 985 = FRR 985 = IMI 092224 (*P. schneegii*); IBT 3288 = NRRL 3480, ex soil, USA; IBT 12298 = WSF 5122, ex soil, Wisconsin, USA; FRR 1386, ex wine corks, Portugal, imported to Sydney, Australia

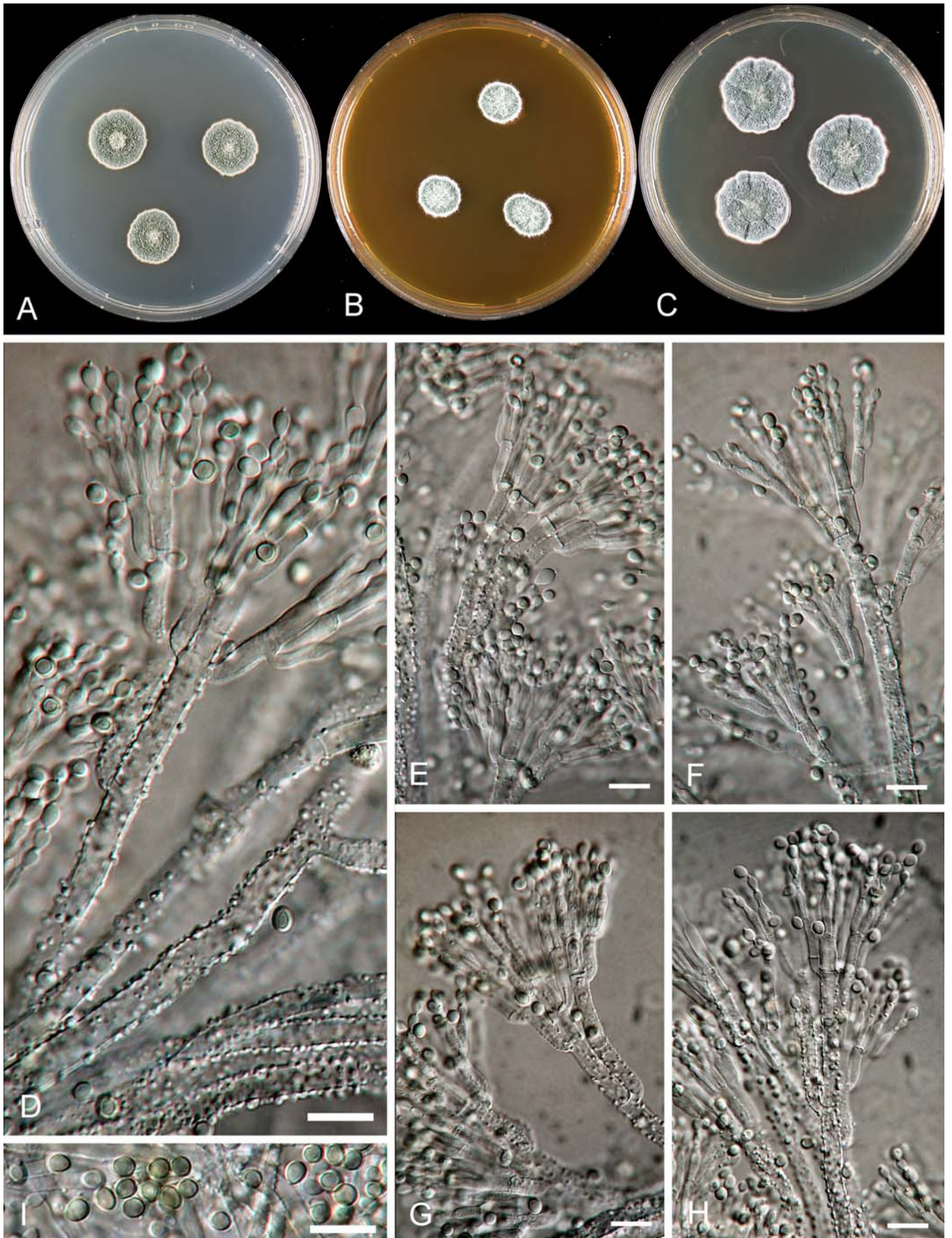


Fig. 56. *Penicillium glandicola*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. griseofulvum Dierckx, Ann. Soc. Scient. Brux.
25: 88, 1901

In *Penicillium* subgenus *Penicillium* section *Penicillium*
series *Urticicolae*

Type: Herb. IMI 075832

Culture ex type: Type: CBS 185.27 = IBT 6740 = ATCC 11885 = IMI 075832 = ATHUM 2893 = CECT 2605 = DSM 896 = IFO 7640 = IFO 7641 = LCP 79.3245 = MUCL 28643 = NRRL 2152 = NRRL 2300 = QM 6902 = VKM F-286, Belgium (T)

Diagnostic features: Griseofulvin, cyclopiazonic acid, patulin, roquefortine C, cyclopiamide, cyclopiamine, ellipsoidal smooth-walled conidia, very short phialides, grey conidia with only small element of green, very branched conidiophores

Similar species: *P. dipodomyicola* has a dark brown reverse and green conidia on CYA in contrast to *P. griseofulvum*.

Description:

Conidiophores: Divergent, undulate or sinuate, terverticillate to quinterverticillate

Conidia: Smooth-walled, broadly ellipsoidal, 2.5-3.5 x 2.2-2.5 µm

Phialides: Flask-shaped tapering to a distinct collulum, 4.5-6.5 µm x 2.2-2.5 µm

Metulae: Cylindrical, 7.5-10 µm x 3.5-4 µm

Rami: Cylindrical, 15-25 µm x 3.5-4 µm

Stipes: Smooth-walled, 400-500 µm x 3-4 µm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Velutinous to fasciculate

Conidium colour on CYA: Grey to grey green

Exudate droplets on CYA: Present, clear to yellow

Reverse colour: Cream, beige or brown

Diffusible colour: Weak pinkish brown

Ehrlich reaction: Violet

Odour and volatile metabolites: Ethylene, ethyl acetate, ethyl isobutanoate, isobutyl acetate, ethyl butanoate, ethyl 2-methyl-butanoate, ethyl isopentanoate, ethyl propanoate, propyl acetate, butyl acetate, isopropyl butanoate, 2-methyl-butyl acetate, isopentyl acetate, pentyl acetate, ethyl hexanoate, ethyl heptanoate (Larsen and Frisvad, 1995)

Extrolites: 1) Patulin, isopatulin, desoxypatulinic acid, 2) Griseofulvin, 3) Fulvic acid, 4) Triacetic acid lactone, 5) Cyclopiazonic acid, 6) Mycelianamide, 7) Roquefortine C and D, 8) Cyclopiamine, 9) Cyclopiamide, 10) Chanoclavine I, elymoclavine,

Growth on creatine: Weak

Acid and base production on creatine: No acid

Growth on UNO: Weak

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 19-32 mm; MEA: 14-32 mm; YES: 28-46 mm; CREA: 11-22 mm; Cz: 15-22 mm, OAT: 15-27 mm; CYAS: 17-23 mm; CzBS: 7-19 mm; CzP: 0 mm; UNO: 9-22 mm; DG18: 22-27 mm

Diam., 1 week: 5°C: 2-4 mm; 15°C: 18-21 mm; 30°C: 17-22 mm; 37°C: 0 mm

CYA/CYAS: 1.5 [1.3-1.7]

CYA15°C/CYA 25°C: 0.7 [0.6-0.8]

CYA30°C/CYA 25°C: 0.7 [0.7-0.8]

CZBS/CZ: 0.8 [0.4-1.2]

CZP/CZ: 0

Distribution: Denmark, Greenland, Norway, Netherlands, Belgium, Germany, British Isles, United Kingdom, France, Spain, Czech Republic, Russia, Iran, Israel, Alaska, New Mexico, Wyoming, Colorado, California (USA), Peru, Brazil, Mozambique, Somalia, South Africa, Pakistan, India, Australia

Ecology and habitats: Rice and other cereals, cherries, animal feed, dungy soil, deteriorating plants, grassland and cool desert soil. See also Domsch *et al.* (1980).

Biotechnological applications: Production of griseofulvin

Biodeterioration & phytopathology: Degradation of malt

Mycotoxicoeses and mycotoxins: There are indications of mycotoxicoesis when *P. griseofulvum* has grown in cereal based animal feeds (Domsch *et al.*, 1980). Patulin, cyclopiazonic acid, roquefortine C and probably other metabolites of *P. griseofulvum* are all toxic.

Typical cultures: IBT 21530 = CBS 485.84, ex *Hordeum vulgare*, Denmark (Y); IBT 14319 = CBS 110420 = IMI 351308, ex maize seed, Vratsa, Bulgaria; IBT 11633 = CBS 110419, ex wheat, Canada; IBT 13695 = CBS 110418 = VKM F-758, Russia; IBT 16399 = CBS 110417, ex cereal grain in field, Denmark; IBT 15163 = CBS 110416, ex malting barley, South Africa; IBT 21778 = IBT 18077 = CBS 112297 = RMF 3098A, ex soil in Pawnee National Grassland, Colorado, USA; IBT 17756 = CBS 295.97, ex soil with rabbit dung, New Mexico, USA; CBS 124.14 = FRR 992 = IMI 092273 = MUCL 29201 = NRRL 992 = VKM F-320, ex soil, Scotland (*P. flexuosum*); CBS 384.48 = ATCC 10120 = FRR 989 = IMI 039809 = VKM F-374, ex dead stem of *Urticaceae* (*P. urticae*), CBS 315.63 = LCP 79.3237, ex grain elevator, South Africa; CBS 746.70, ex soil, Italy; CBS 472.75, ex stored cereals, Yugoslavia; CBS 493.75, ex contents of a deer colon, Germany; CBS 100233, ex soil, Nepal; NRRL 994 = FRR 994 = ATCC 9260 = IMI 028808 (*P. patulum*).

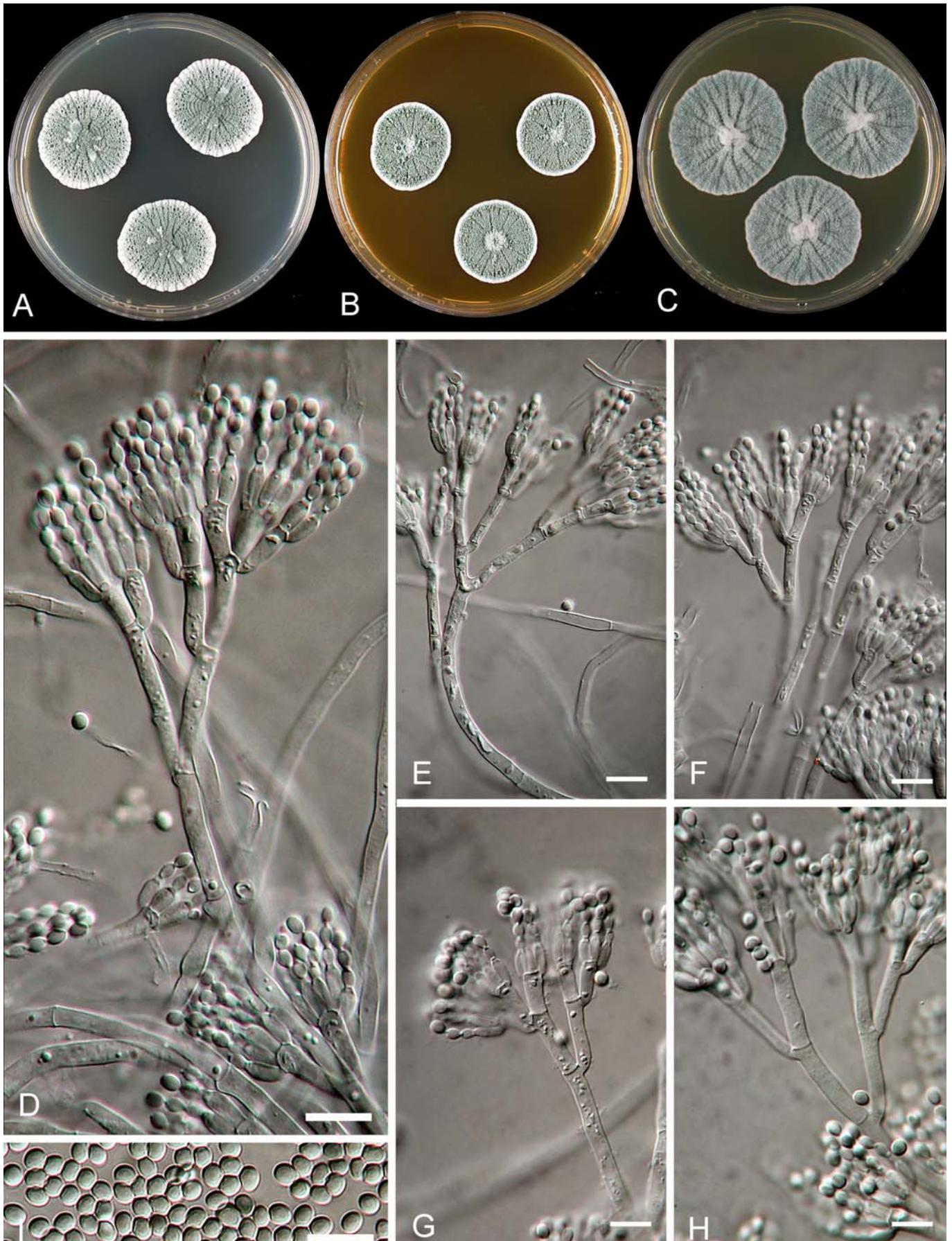


Fig. 57. *Penicillium griseofulvum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. hirsutum Dierckx, Ann. Soc. Scient. Brux. 25: 89, 1901

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Corymbifera*

Type: Herb. IMI 040213

Culture ex type: CBS 135.41 = IBT 21531 = IBT 10628 = IMI 040213 = ATCC 10429 = FRR 2032 = IFO 6092 = MUCL 15622 = NRRL 2032, ex aphid, Netherlands (T,Y)

Diagnostic features: Compactin, daldinin D, smooth-walled conidia, yellow synnemata

Similar species: *P. hirsutum* produce yellow synnemata in contrast to *P. radicicola*, *P. albocoremium* and *P. tulipae*.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 2.2-3.8 µm

Phialides: Cylindrical tapering to a distinct collulum, 8-12 µm x 2.4-3.2 µm

Metulae: Cylindrical, 7.5-13 µm x 3.2-4 µm

Rami: Cylindrical, 16-27 µm x 3.2-4 µm

Stipes: Rough-walled, 100-500 µm x 3.2-4 µm

Synnemata or fasciculation: Yellow synnemata produced, especially on OAT and MEA

Sclerotia: None

Colony texture: Velutinous to fasciculate

Conidium colour on CYA: Green

Exudate droplets on CYA: Yellow to dark orange or red brown

Reverse colour on CYA: Yellow to orange brown

Reverse colour on YES: Cream yellow to curry yellow

Diffusible colour on CYA: Yellow brown to brown

Ehrlich reaction: Red to violet

Odour and volatile metabolites: Isobutanol, isopentanol (Larsen & Frisvad, 1995)

Extrolites: 1) Terrestrial acid, 2) Daldinin D, 2) Compactins, 3) Roquefortine C & D, meleagrin

Growth on creatine: Moderate to good

Acid and base production on creatine: Acid production, no base production

Growth on UNO: Moderate to good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 19-43 mm; MEA: 22-45 mm; YES: 41-54 mm; CREA: 23-36 mm; Cz: 25-41 mm, OAT: 26-43 mm; CYAS: 28-42 mm; CzBS: 29-38 mm; CzP: 0 mm; UNO: 13-20 mm; DG18: 28-38 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 32-36 mm; 30°C: 2-9 mm; 37°C: 0 mm

CYA/CYAS: 0.9 [0.5-1.1]

CYA15°C/CYA 25°C: 1.0 [0.8-1.0(-1.9)]

CYA30°C/CYA 25°C: 0.09 [0.05-0.3]

CZBS/CZ: 1.0 [0.9-1.1]

CZP/CZ: 0

Distribution: Netherlands, Czech Republic, Illinois (USA), Korea, Taiwan. See also Domsch *et al.* (1980) under *P. verrucosum* var. *corymbiferum*, but this taxon may also include *P. allii*, *P. venetum*, *P. radicicola*, *P. albocoremium* and *P. tulipae*.

Ecology and habitats: Greenhouses, horse radish, tulip bulbs, aphids, butter.

Biotechnological applications: None

Biodeterioration & phytopathology: May degrade flower bulbs and vegetable roots

Mycotoxins and mycotoxins: It is not known whether roquefortine C will be produced in vegetable roots.

Typical cultures: IBT 12398 = CBS 349.75, ex bulb of *Tulipa* sp., Netherlands; IBT 10623 = CBS 110101 = CCF 1445, ex rotten apple, Prague, Czech Republic; IBT 10624 = CBS 110100 = NRRL 999, ex horse radish roots, Illinois, USA; IBT 19340 = CBS 110099 = FRR 3642 = PPEH 25001, Taiwan; IBT 13033 = CBS 437.92, ex *Tulipa* sp., Korea; IBT 18379 = CBS 110098 = CCRC 32022, ex butter, Taipei City, Taiwan; IBT 22221 = CBS 112318, ex chestnut, Denmark.

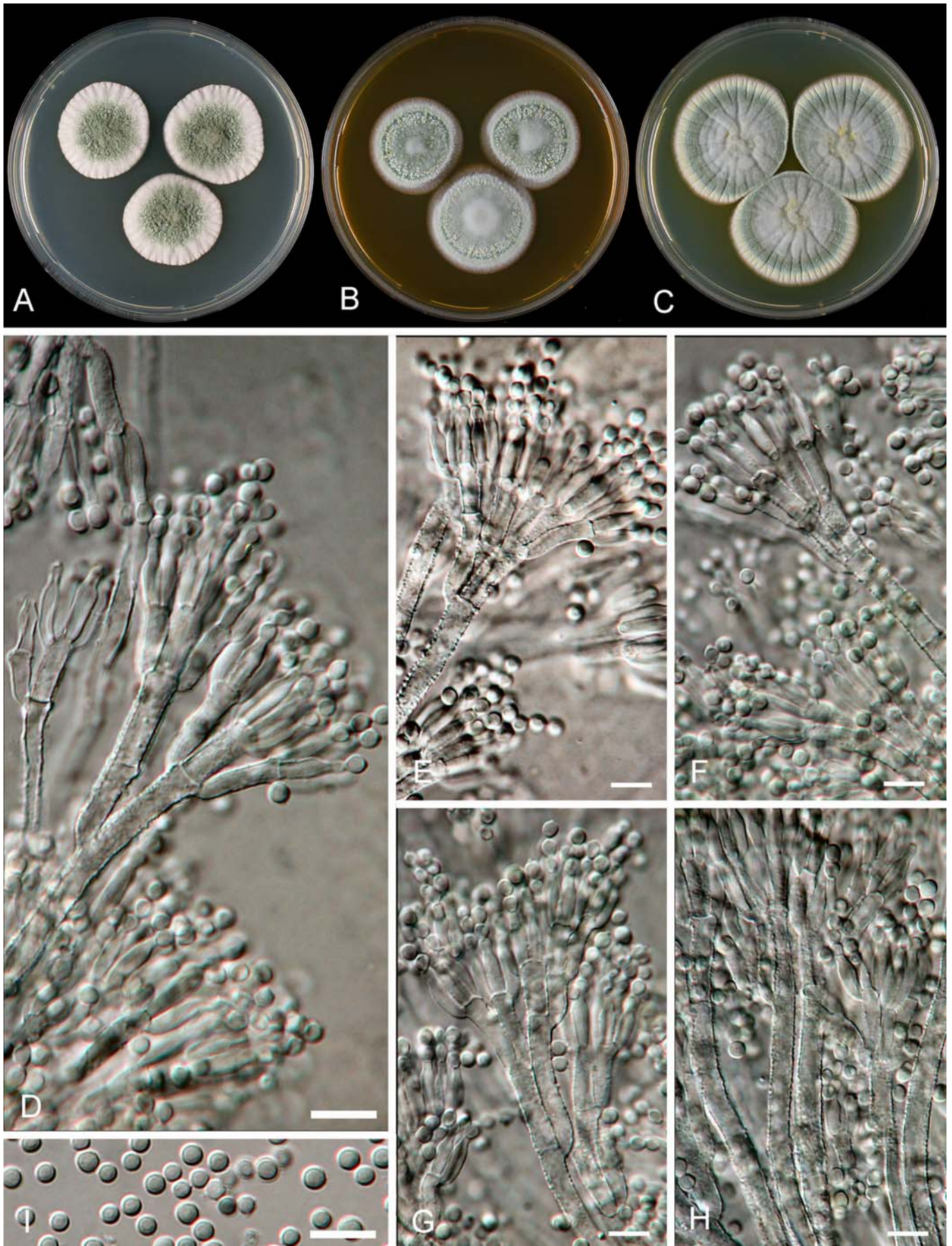


Fig. 58. *Penicillium hirsutum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. hordei Stolk, Ant. van Leeuwenhoek **35**: 270, 1969

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Corymbifera*

Type: Herb. CBS 701.68

Culture ex type: CBS 701.68 = IBT 17804 = IBT 6980 = IMI 151748 = ATCC 22053 = CECT 2290 = FRR 815 = MUCL 39559, ex *Hordeum vulgare*, Denmark (T)

Diagnostic features: Rough-walled conidia, yellow mycelium and synnemata, roquefortine C, terrestrial acid

Similar species: *P. hordei* differs from *P. hirsutum* and other members of series *Corymbifera* by its finely roughened conidia.

Description:

Conidiophores: Terverticillate, appressed or slightly divergent elements, born from subsurface and aerial hyphae

Conidia: Finely rough-walled, globose to subglobose, 2-3 µm

Phialides: Cylindrical tapering to a distinct collulum, 7-10 µm x 2-2.5 µm

Metulae: Cylindrical, 7.5-10 µm x 2.2-3.5 µm

Rami: Cylindrical, 16-27 µm x 3.2-4 µm

Stipes: Finely rough and smooth-walled, 75-1000 µm x 2.2-3 µm

Synnemata or fasciculation: Yellow synnemata, especially on MEA and OAT

Sclerotia: None

Colony texture: Floccose to fasciculate

Conidium colour on CYA: Green (artemisia to lily green)

Mycelium colour: yellow

Exudate droplets on CYA: Present, yellow to red brown droplets

Reverse colour on CYA: Yellow brown to reddish brown

Reverse colour on YES: Yellow

Diffusible colour on CYA: Yellow brown

Ehrlich reaction: Light violet

Odour and volatile metabolites: Isobutanol, isopentanol (Larsen & Frisvad, 1995)

Extrolites: 1) Terrestrial acid, carolic acid, carlosic acid, 2) Roquefortine C

Growth on creatine: Moderate to good

Acid and base production on creatine: Moderate to good acid production

Growth on UNO: Moderate to good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 27-41 mm; MEA: 23-35 mm; YES: 27-45 mm; CREA: 19-25 mm; Cz: 21-29 mm, OAT: 27-33 mm; CYAS: 37-40 mm; CzBS: 17-24 mm; CzP: 0-2 mm; UNO: 8-18 mm; DG18: 29-34 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 19-31 mm; 30°C: 10-17 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.7-1.0]

CYA15°C/CYA 25°C: 0.9 [0.7-1.0]

CYA30°C/CYA 25°C: 0.4 [0.3-0.5]

CZBS/CZ: 0.7 [0.5-0.9]

CZP/CZ: 0.02 [0-0.05]

Distribution: Denmark, Sweden, Netherlands, Germany, United Kingdom

Ecology and habitats: Barley, wheat, wheat field soils

Biotechnological applications: None

Biodeterioration & phytopathology: Cereal decomposition

Mycotoxins and mycotoxins: Roquefortine C is a potential mycotoxin in cereals

Typical cultures: IBT 21532 = IBT 4505 = CBS 560.90, ex *Hordeum vulgare*, Denmark (Y); IBT 3084 = CBS 473.84, ex *Lycopersicon esculentum*, Denmark; IBT 15999 = CBS 110097, ex cereal, Denmark; IBT 16374 = CBS 110122, ex wasted barley kernel, Denmark; IBT 4900 = CBS 559.90, ex fern in greenhouse, Netherlands; IBT 23023 = CBS 704.68, ex *Hordeum vulgare*, Netherlands; IBT 23024 = CBS 788.70 = IMI 197487, ex cereal, United Kingdom; IBT 11204 = CBS 112440, ex *Hordeum vulgare*, Denmark; IBT 6470 = CBS 558.90, ex wheat field soil, Denmark; IBT 6766 = 557.90, ex *Hordeum vulgare*, Denmark; IBT 3513 = CBS 220.90, ex *Hordeum vulgare*, Denmark; CBS 813.70, ex straw in soil, Denmark; CBS 703.68, ex *Hordeum vulgare*, Denmark; CBS 702.68 = IMI 197486 = FRR 1743, ex grain of *Hordeum vulgare*, Denmark.

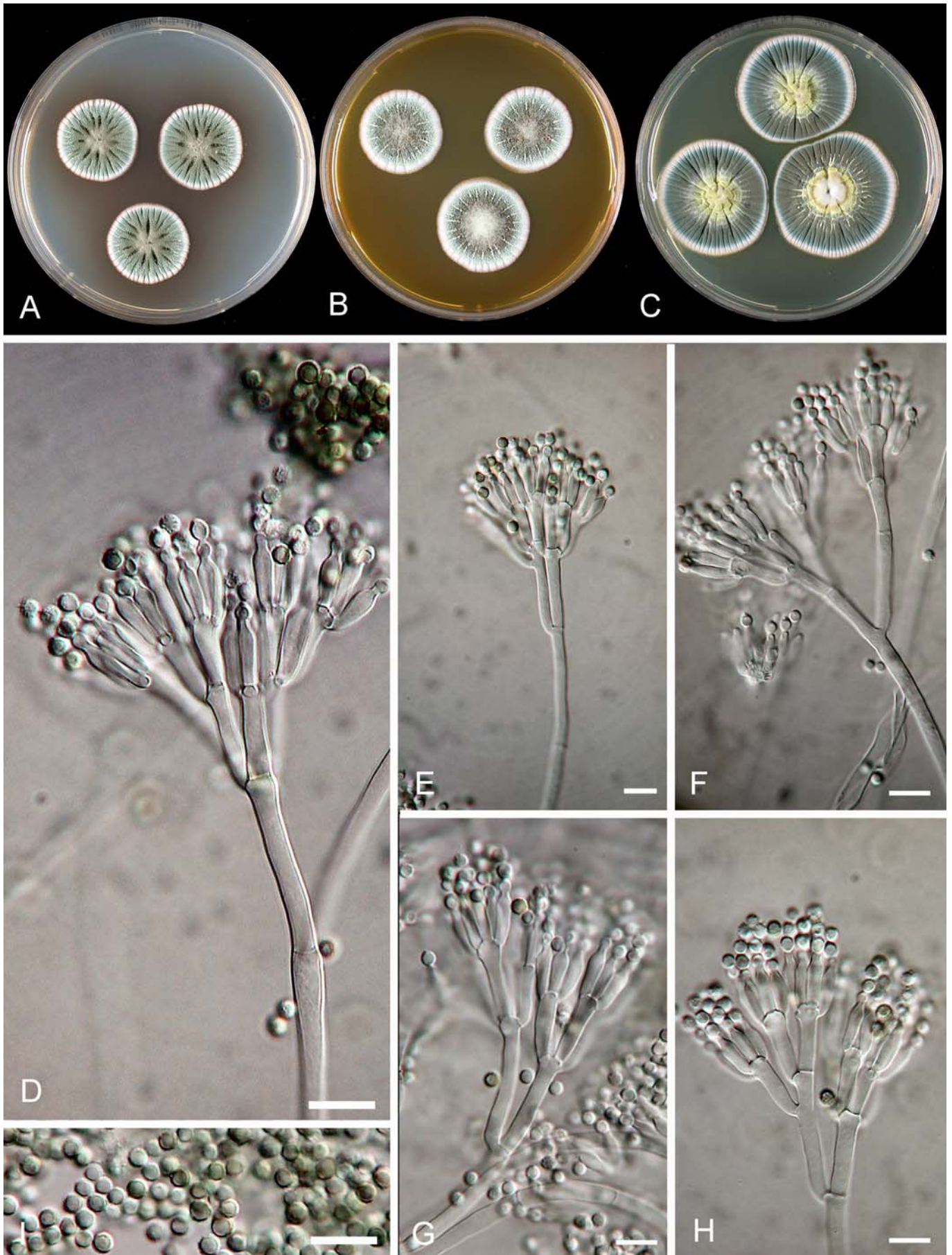


Fig. 59. *Penicillium hordei*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. italicum Wehmer, Hedwigia **33**: 211, 1894

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Italica*

Type (neo): CBS 339.48

Culture ex type: CBS 339.48 = IBT 23029 = IMI 039760 = ATCC 10454 = FRR 983 = NRRL 983, ex citrus fruit, Riverside, California, USA (T)

Diagnostic features: cylindrical to ellipsoidal smooth-walled conidia, poor growth and no acid production on CREA, crustose on YES, deoxybrevianamide E

Similar species: *P. italicum* grows much faster than *P. ulaiense* and is more colourful.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth-walled, ellipsoidal to cylindrical, 3.5-5 µm x 2.2-3.5 µm

Phialides: Cylindrical tapering to a distinct collulum, 8-15 µm x 2.5-4.5 µm

Metulae: Cylindrical, 14-20 µm x 3.5-4 µm

Rami: Cylindrical, 12-20 µm x 3.2-4.5 µm

Stipes: Smooth-walled, 100-300 µm x 3-5 µm

Synnemata or fasciculation: Fasciculate in the colony margins

Sclerotia: Reported in fresh isolates, colourless to light brown, 200-500 µm (Raper and Thom, 1949)

Colony texture: Velutinous to fasciculate, crustose

Conidium colour on CYA: Grey green

Exudate droplets on CYA: None or small clear droplets

Reverse colour on CYA: Pale, brownish orange or red brown

Reverse colour on YES: Red brown

Diffusible colour on CYA: None

Ehrlich reaction: None

Odour and volatile metabolites: Ethyl acetate, isopentanol, linalool, isobutanol, 1-octene, ethyl butanoate, ethyl 2-methyl-butanoate, 1-nonene, styrene, citronellene? (Larsen & Frisvad, 1995)

Extrolites: 1) Italinic and italicic acid, 2) 2,5-dihydro-4-methoxy-2H-pyran-2-one & verrucolone, 3) deoxybrevianamide E, 4) formylxanthocillin X, 5) dehydrofulvic acid,

PI-3 & PI-4, 6) 4-methoxy-6-n-propenyl-2-pyrone, 7) 5-hydroxymethyl-2-furic acid, 7) Absciscic acid

Growth on creatine: Weak

Acid and base production on creatine: No acid

Growth on UNO: Very good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 26-50 mm; MEA: 22-47 mm; YES: 31-71 mm; CREA: 6-12 mm; Cz: 19-34 mm, OAT: 24-38 mm; CYAS: 3-17 mm; CzBS: 14-32 mm; CzP: 0 mm; UNO: 5-19 mm; DG18: 23-48 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 17-34 mm; 30°C: 0-12 mm; 37°C: 0 mm

CYA/CYAS: 5.4 [2.2-11]

CYA15°C/CYA 25°C: 0.7 [0.6-0.8]

CYA30°C/CYA 25°C: 0.1 [0-0.2]

CZBS/CZ: 0.8 [0.4-0.9]

CZP/CZ: 0

Distribution: Italy, Spain, Portugal, (imported to Denmark, Germany, Netherlands, Australia etc.), Turkey, Israel, Egypt, Libya, Cyprus, Ghana, Zambia, Zimbabwe, South Africa, India, Australia, New Zealand

Ecology and habitats: Citrus fruits and debris in soil. See also Domsch *et al.* (1980)

Biotechnological applications: None

Biodeterioration & phytopathology: *P. italicum* is pathogenic to citrus fruits.

Mycotoxins and mycotoxins: The toxicity of the many extrolites produced by *P. italicum* is unknown.

Typical cultures: IBT 21533 = CBS 489.84, ex *Raphanus sativus*, Denmark (Y); IBT 23026 = CBS 495.75, ex soil, Uttar Pradesh, India; IBT 23028 = CBS 490.75, ex fruit of *Citrus* sp., Israel; IBT 23030 = CBS 278.58 = DSM 2428, ex fruit of *Citrus sinensis*, Netherlands; IBT 18097 = CBS 112437 = FRR 1312, ex fruit of *Citrus limon*, Sydney, N.S.W., Australia; IBT 15661 = CBS 112480, ex food product, Turkey; IBT 12955, ex mouldy fruit of *Citrus sinensis*, Denmark; CBS 719.73 = DSM 2417, ex *Citrus* sp., Israel (*P. italicum* var. *avellaneum*).

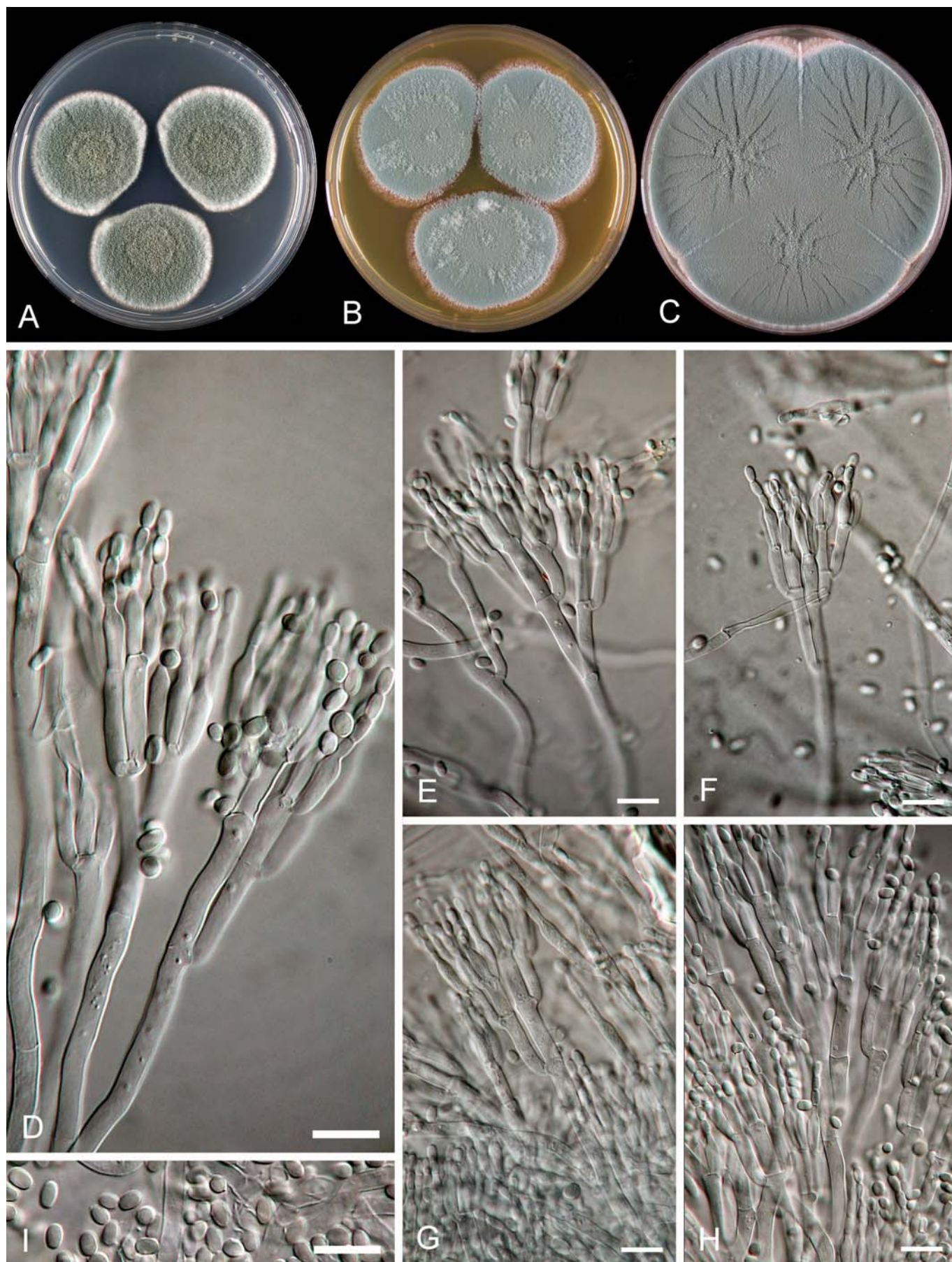


Fig. 60. *Penicillium italicum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

***P. marinum* Frisvad & Samson, sp. nov.**

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Expansa*

Type: Herb. CBS 109550

Culture ex type: CBS 109550 = IBT 14360, ex sandy soil, Japan (T, Y)

Diagnostic features: Expansolide, patulin, penostatins, subglobose smooth-walled conidia

Similar species: *P. expansum* is growing much faster than *P. marinum*. *P. marinum* cannot produce an apple rot like *P. expansum*.

Description:

Conidiophores: Terverticillate, with divergent rami born from aerial and subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 2.5-3.2 µm

Phialides: Cylindrical, with short broad collula, 8-12 µm x 2.2-3.5 µm

Metulae: Cylindrical, 10-16 µm x 2.5-4 µm

Rami: Cylindrical, 15-22 µm x 3-4 µm

Stipes: Smooth, 200-400 µm x 3-4 µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous to lanose

Conidium colour on CYA: Blue green to green on CYA,

Exudate droplets on CYA: Present, clear to yellow or orange

Reverse colour on CYA: Brown to dark brown

Reverse colour on YES: Cream yellow

Diffusible colour on CYA: None

Ehrlich reaction: Strong reaction

Odour and volatile metabolites: Unknown

Extrolites: 1) Patulin, 2) 3,5-dimethyl-6-hydroxyphthalide, 3) Expansolide, 4) Penostatins, 5) Aurantioclavine and

communesins, 6) Roquefortine C, 7) Chaetoglobosins and penochalasin

Growth on creatine: Good growth

Acid and base production on creatine: Acid under colony and often around colony

Growth on UNO: Good

Growth on nitrite: Good (except two of the mutants)

Abiotic factors:

Diam., 1 week, 25°C: CYA: 17-27 mm; MEA: 8-16 mm; YES: 23-40 mm; CREA: 14-18 mm; Cz: 11-17 mm, OAT: 17-25 mm; CYAS: 17-24 mm; CzBS: 4-13 mm; CzP: 0 mm; UNO: 6-12 mm; DG18: 15-23 mm

Diam., 1 week: 15°C: 17-24 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 1.0 [0.8-1.2]

CYA15°C/CYA 25°C: 1.1 [1.0-1.3], psychrotolerant

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.5 [0.3-0.8]

CZP/CZ: 0

Distribution: Tunisia, Japan

Ecology and habitats: Marine species found on an *Enteromorpha* sp. and in coastal sand.

Biotechnological applications: Potential production of penostatins and communesins

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: Patulin and communesins, but the species has not been found on foods or feeds

Typical cultures: IBT 16712 = CBS 109549, ex sandy soil, Tunisia

Mutant strains of CBS 109549: IBT 16715 = CBS 109548;

IBT 16713 = CBS 109547; IBT 16714 = CBS 109546;

IBT16716 = CBS 109545.



Fig. 61. *Penicillium marinum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

***P. melanoconidium* (Frisvad) Frisvad & Samson, comb. nov.**

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Viridicata*

Type: Herb. IMI 321503

Culture ex type: IBT 3444 = IMI 321503, ex wheat, Denmark (T)

Diagnostic features: Penicillic acid, sclerotigenin, verrucosidin, oxaline, dark green smooth-walled conidia, curry yellow reverse on CYA,

Similar species: *P. melanoconidium* has much darker green conidia than *P. viridicatum*. It differs from *P. polonicum* by its dark green rather than blue green conidia. The distinctive black brown halo produced by most members of series *Viridicata* is not produced by *P. melanoconidium*.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 2.5-3.5 µm.

Phialides: Cylindrical tapering to a distinct collum, 7.5-9 µm x 2.2-2.8 µm

Metulae: Cylindrical, 9.5-14 µm x 3.2-4.2 µm

Rami: Cylindrical, 15-23 µm x 3.2-4.2 µm

Stipes: Rough walled, 100-500 µm x 3-4 µm

Synnemata or fasciculation: Not observed

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Dark green

Exudate droplets on CYA: Present, clear

Reverse colour on CYA: Curry yellow

Reverse colour on YES: Yellow (strong sporulation on YES)

Diffusible colour: None

Ehrlich reaction: Pink

Odour and volatile metabolites: Isobutanol, isopentanol (Larsen & Frisvad, 1995)

Extrolites: 1) Penicillic acid, 2) Verrucosidin, 3) Xanthomegnin, viomellein and vioxanthin, 4) Penitrem A, 5)

Roquefortine C, meleagrin, oxaline, 6) Sclerotigenin

Growth on creatine: Weak

Acid and base production on creatine: Good acid production, no base

Growth on UNO: Weak

Growth on nitrite: Weak

RT: No black brown halo

Abiotic factors:

Diam., 1 week, 25°C: CYA: 17-27 mm; MEA: 18-36 mm; YES: 31-46 mm; CREA: 16-24 mm; Cz: 22-25 mm, OAT: 22-32 mm; CYAS: 34-40 mm; CzBS: 16-22 mm; CzP: 0 mm; UNO: 10-11 mm; DG18: 26-30 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 18-23 mm; 30°C: 13-18 mm; 37°C: 0 mm

CYA/CYAS: 0.7 [0.6-0.7]

CYA15°C/CYA 25°C: 0.9 [0.8-1.0]

CYA30°C/CYA 25°C: 0.6 [0.6-0.8]

CZBS/CZ: 0.8 [0.7-0.9]

CZP/CZ: 0

Distribution: Denmark, United Kingdom, Canada, Washington (USA)

Ecology and habitats: Barley, wheat, rye, oats, rice

Biotechnological applications: None

Biodeterioration & phytopathology: May deteriorate cereals

Mycotoxicoeses and mycotoxins: Penicillic acid, verrucosidin, xanthomegnin, viomellein vioxanthin may be produced in cereals

Typical cultures: IBT 3435x = CBS 109542, ex cereal, Denmark; IBT 21534 = IBT 11406 = CBS 641.95, ex mixed cereal feeds for birds, Denmark (Y); IBT 10031 = CBS 640.95, ex *Panicum miliaceum* imported to Denmark; IBT 3443 = CBS 218.90, ex *Hordeum vulgare*, Denmark; IBT 3445 = CBS 653.95, ex cereal, Denmark; IBT 22052 = CBS 109604 = PIL 333a, ex cereal, United Kingdom; IBT 15983 = CBS 109606, ex mixed pig feed, Bulgaria; IBT 6672 = CBS 109603 = NRRL 958, Pullman, Washington; IBT 15448 = CBS 109605; CBS 219.90 = IBT 3702, ex *Triticum aestivum*, United Kingdom; CBS 186.88, ex *Hordeum vulgare*, Denmark; ATCC 64627, ex wheat, Denmark; NRRL 13628, ex wheat, Denmark; IMI 351502, ex barley, Denmark.

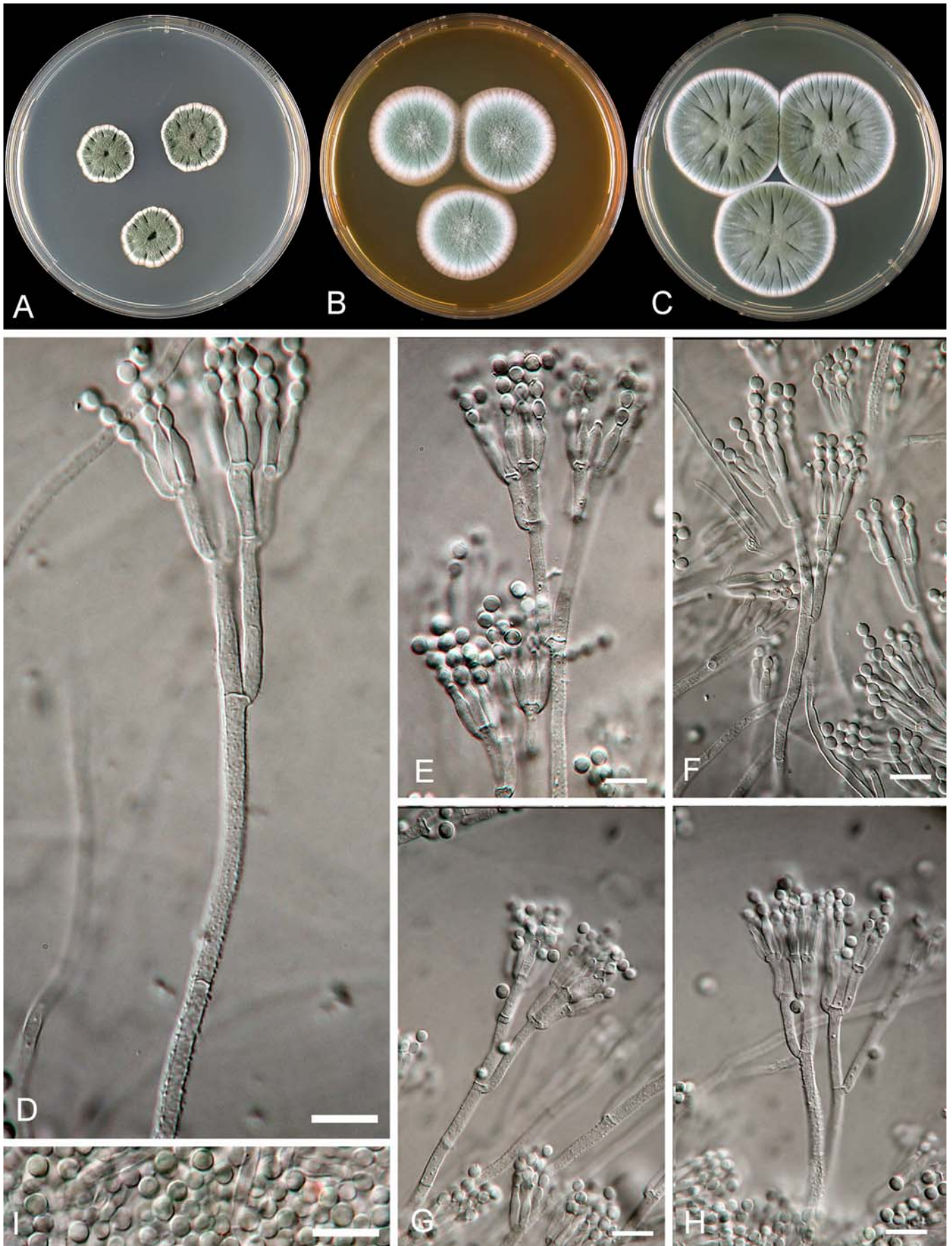


Fig. 62. *Penicillium melanoconidium*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. mononematosum (Frisvad, Filt. & Wicklow)
Frisvad, Mycologia **81**: 857, 1989

In *Penicillium* subgenus *Penicillium* section *Chrysogena* series *Mononematosia*

Type: Herb. IMI 296925

Culture ex type: CBS 172.87 = IBT 3072 = IBT 5518 = IBT 21535 = IMI 296925 = NRRL 13482 = NRRL A-26709, ex burrow system of *Dipodomys spectabilis*, 6 km east of Portal, Arizona (**T, Y**)

Diagnostic features: Fumitremorgins, verrucologen, cyclopaldic acid, divergent structures and often 2 rami, smooth-walled conidia, very good growth at 30°C

Similar species: See *P. confertum*

Description:

Conidiophores: Terverticillate to quaterverticillate, appressed and divergent elements, born from subsurface hyphae

Conidia: Smooth-walled, subglobose to broadly ellipsoidal, 3.2-3.7 µm x 2.5-3.2 µm

Phialides: Flask shaped with a distinct broad collulum, 7.5-10 µm x 2.5-3.2 µm

Metulae: Cylindrical, 10-15 µm x 3-4 µm

Rami: Cylindrical, 15-25 µm x 3-4 µm

Stipes: Broad smooth-walled 200-500 µm x 3-4.5 µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Blue green to green

Exudate droplets on CYA: Copious, clear

Reverse colour: Beige to greyish cream

Diffusible colour: None

Ehrlich reaction: None

Odour and volatile metabolites: Not examined

Extrolites: 1) Cyclopaldic acid, 2) Isochromantoxins, 3) fumitremorgins and verrucologen, 4) Viriditoxin

Growth on creatine: Weak to moderate

Acid and base production on creatine: Moderate acid production

Growth on UNO: Weak

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 19-34 mm; MEA: 13-35 mm; YES: 25-58 mm; CREA: 17-25 mm; Cz: 12-26 mm, OAT: 27-33 mm; CYAS: 20-38 mm; CzBS: 14-24 mm; CzP: 0 mm; UNO: 2-27 mm; DG18: 18-39 mm

Diam., CYA, 1 week: 5°C: 2-3 mm; 15°C: 18-24 mm; 30°C: 26-33 mm; 37°C: 0 mm

CYA/CYAS: 1.0 [0.7-1.4]

CYA15°C/CYA 25°C: 0.7 [0.6-0.8]

CYA30°C/CYA 25°C: 0.9 [0.8-1.2]

CZBS/CZ: 1.0 [0.6-1.3]

CZP/CZ: 0

Distribution: France, Arizona and New Mexico (USA), Egypt (type II)

Ecology and habitats: Cheek pouches and mounds of kangaroo rats, seeds of *Amaranthus* sp., Rocky Mountain desert soil, salt marsh soil (type II)

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxinoses and mycotoxins: Fumitremorgin A, B, verrucologen, isochromantoxin are toxic, but *P. mononematosum* has not been found to produce the mycotoxins in any food or feed samples.

Typical cultures: T118 = IBT 20392 = RMF 9577; IBT 6071 = CBS 112104 = NRRL A-26710 = NRRL 13483 = IMI 296932, ex cheek pouch of banner-tailed kangaroo rat, 6 km east of Portal, Arizona, USA; NRRL 13484, ex cheek pouch of banner-tailed kangaroo rat, 6 km east of Portal, Arizona, USA; IBT 12628 = CBS 112102, ex wine cork, Portugal; IBT 12410 = CBS 112103, ex kangaroo rat mound, Seville, New Mexico, USA; IBT 11891 = CBS 112105, squash, France; IBT 11682 = CBS 112106, Jerusalem artichoke, Denmark; IBT 5510 = CBS 112107, ex soil, Walnut Crater, Arizona, USA; IBT 5507 = IBT 4391 = CBS 112434 = IBT 4308 = CBS 112575 = CBS 112435 {type II}, ex salt marsh soil, Egypt; T291 = IBT 5509 = CBS 109616 (type II), ex salt marsh soil, Egypt.

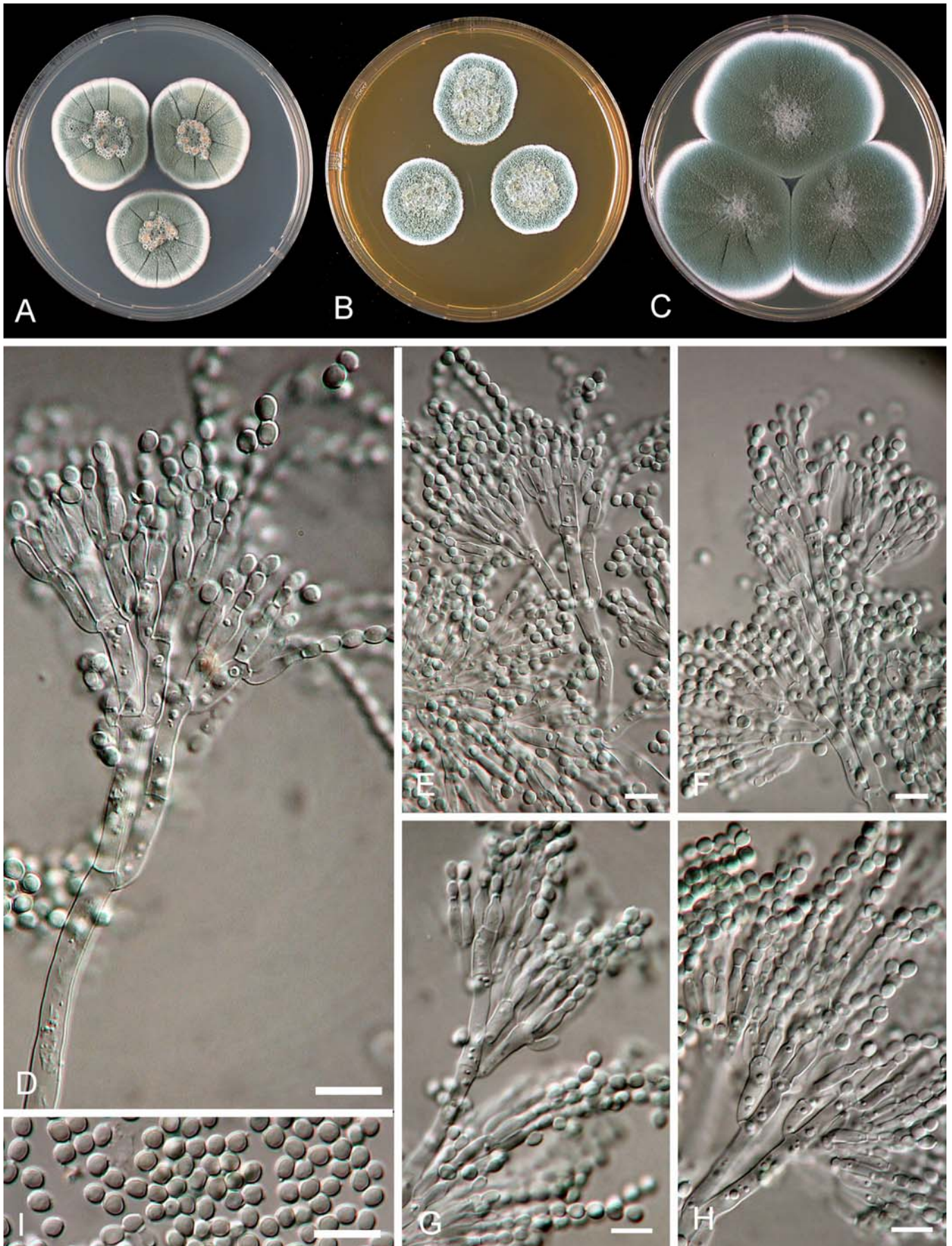


Fig. 63. *Penicillium mononematosum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. nalgiovense Laxa, Zentbl. Bakt. ParasitKde.,
Abt. II **86**: 162, 1932

In *Penicillium* subgenus *Penicillium* section *Chrysogena*
series *Chrysogena*

Type: Herb. CBS 352.48

Culture ex type: CBS 352.48 = CBS 101030 = IBT 21536
= IBT 3800 = IMI 039804 = ATCC 10472 = CCF 1728 =
CCRC 31671 = DSM 897 = FRR 911 = IFO 8112 = MUCL
31194 = NRRL 911 = QM 7600, ex Ellischauer cheese,
Czech Republic (T,Y)

Diagnostic features: Penicillin F & G, nalgiovensin,
smooth-walled conidia, orange reverse on YES, divergent
structures, dark green conidia in fresh isolates

Similar species: See *P. dipodomyis*.

Description:

Conidiophores: Bi-, ter- and quarterverticillate both diver-
gent metulae and rami born from aerial and subsurface
hyphae

Conidia: Smooth-walled, globose to subglobose to broadly
ellipsoidal, 3-4 µm x 2.3-3.5 µm

Phialides: Flask-shaped, with short wide collula, 8-10 µm x
2-2.5 µm

Metulae: Cylindrical, 7-15 µm x 2.5-3 µm

Rami: Cylindrical, 15-20 µm x 3-4 µm

Stipes: 200-300 µm x 3-4 µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Dark green (occasionally white)

Exudate droplets on CYA: clear

Reverse colour on CYA: cream to yellow to orange to dark
orange brown

Reverse colour on YES: Bright yellow to orange

Diffusible colour: yellow brown in CBS 352.48 and IBT
13039

Ehrlich reaction: None

Odour and volatile metabolites: Ethyl acetate, isobutanol,
styrene, 3-octanone

Extrolites: 1) Nalgiovensin, nalgolaxin, 2) Diaporthins, 3)
Penicillin F & G, 4) Dipodazin

Growth on creatine: Weak

Acid and base production on creatine: No acid

Growth on UNO: Very good

Growth on nitrite: Very good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 18-34 mm; MEA: 9-27 mm;
YES: 28-45 mm; CREA: 14-20 mm; Cz: 13-27 mm, OAT:
14-25 mm; CYAS: 31-42 mm; CzBS: 6-25 mm (0 mm in
one isolate); CzP: 0 mm; UNO: 13-17 mm; DG18: 25-35
mm

Diam., CYA, 1 week: 5°C: 1-4 mm; 15°C: 14-25 mm;
30°C: 5-16 mm (1 mm in one isolate); 37°C: 0 mm

CYA/CYAS: 0.8 [0.6-0.9]

CYA15°C/CYA 25°C: 0.7 [0.6-0.8]

CYA30°C/CYA 25°C: 0.4 [0.05-0.6]

CZBS/CZ: 0.6 [0-0.9]

CZP/CZ: 0

Distribution: Svalbard (Norway), Denmark, Germany,
Italy, Canada

Ecology and habitats: Cheese, salami, desert sand

Biotechnological applications: Fermentation of salami
(Hungary, Germany, Italy, Spain)

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: The toxicity of nalgioven-
sin, nalgolaxin, dipodazin and diaporthins are unknown.

Typical cultures: IBT 13039 = CBS 109607, ex cheese,
Crete, Greece; IBT 15040 = CBS 297.97 = CBS 258.94, ex
sandy soil, California, USA; IBT 13042 = CBS 109608, ex
salami; IBT 12108, ex cheese, Denmark; IBT 11965 = CBS
109610 = FRR 3284, ex salami, Germany; IBT 12383 =
CBS 318.92, ex salami; IBT 23346 = CBS 112438, ex ice,
Svalbard, Norway; IBT 22527 = CBS 112439, ex salami;
IBT 11970 = Sp 1785, ex salami, Germany; IBT 12640 =
CBS 315.92, ex salami, Denmark; IBT 12372 = CBS
316.92, ex salami, Denmark; IBT 12648 = CBS 317.92, ex
salami, Denmark; IBT 12383 = CBS 318.92, ex salami,
Denmark; IBT 12561 = CBS 319.92, ex salami, Denmark,
CBS 390.92, ex salami; IBT 12420 = CBS 321.92, ex
salami, Denmark; CBS 257.94, ex sandy soil, California.



Fig. 64. *Penicillium nalgioense*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. neoechinulatum (Frisvad, Filt. & Wicklow)
Frisvad & Samson, **comb. nov.**

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Viridicata*

Type: Herb. IMI 296937

Culture ex type: CBS 169.87 = CBS 101135 = IBT 3493 = IBT 21537 = IMI 296937 = NRRL 13486 = NRRL A-27178, ex cheek pouch of *Dipodomys spectabilis*, 8 km east of Portal, Arizona, USA (**T, Y**)

Diagnostic features: rough-walled conidia, weak growth on CREA, penicillic acid, cyclopenin, cyclopenol

Similar species: Other members of series *Viridicata* have smooth to very finely roughened conidia.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface and aerial hyphae

Conidia: Rough-walled, globose to subglobose, 2.6-3.4 µm.

Phialides: Cylindrical tapering to a distinct collulum, 7-9 µm x 2.2-2.8 µm

Metulae: Cylindrical apically swollen, 9.5-13 µm x 3.2-4.2 µm

Rami: Cylindrical, 15-25 µm x 3.2-4.2 µm

Stipes: Finely roughened and smooth walls, 100-550 µm x 3-4 µm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Floccose to weakly fasciculate

Conidium colour on CYA: Blue green

Exudate droplets on CYA: Copious, clear

Reverse colour on CYA: Yellow, orange to red brown

Reverse colour on YES: Yellow

Diffusible colour: Pink, orange or red brown

Ehrlich reaction: Strong, red violet

Odour and volatile metabolites: Not examined

Extrolites: 1) Penicillic acid, 2) Aurantiamine, 3)

Cyclopeptin, dehydrocyclopeptin, cyclopenin, cyclopenol, viridicatol, 3-methoxyviridicatin

Growth on creatine: Weak

Acid and base production on creatine: Strong acid production

Growth on UNO: Weak

Growth on nitrite: Weak

RT: Blackish brown halo

Abiotic factors:

Diam., 1 week, 25°C: CYA: 24-35 mm; MEA: 24-34 mm; YES: 26-43 mm; CREA: 14-23 mm; Cz: 22-27 mm, OAT: 22-32 mm; CYAS: 32-38 mm; CzBS: 15-26 mm; CzP: 0 mm; UNO: 8-12 mm; DG18: 20-27 mm

Diam., CYA, 1 week: 5°C: 2-4 mm, 15°C: 24-28 mm; 30°C: 13-17 mm; 37°C: 0 mm

CYA/CYAS: 1.0 [0.8-1.1]

CYA15°C/CYA 25°C: 0.8 [0.8-0.9]

CYA30°C/CYA 25°C: 0.4 [0.4-0.5]

CZBS/CZ: 0.9 [0.7-1.1]

CZP/CZ: 0

Distribution: Arizona (USA)

Ecology and habitats: Mounds and cheek pouches of kangaroo rats

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: Penicillic acid produced, but *P. neoechinulatum* has not been found in foods.

Typical cultures: IBT 23266 = IBT 5583 = CBS 101472 = NRRL A-26679 = IMI 321490; IBT 5603 = CBS 101468 = NRRL A-26677; IBT 5600 = CBS 110342 = NRRL A-26680; IBT 5414 = CBS 110341 = NRRL A-27001; IBT 5595 = CBS 110343 = NRRL A-26842; IBT 5424 = CBS 110339 = NRRL A-27003; IBT 5582 = CBS 110340 = NRRL A-26859; CBS 101469 = IBT 5591 = NRRL A-27147; CBS 101470 = IBT 5590 = NRRL A-27151; CBS 101471 = IBT 5587 = NRRL A-26838; all strains are from mounds or cheek pouches of kangaroo rats, live trapped 6 km east of Portal, Arizona, USA.

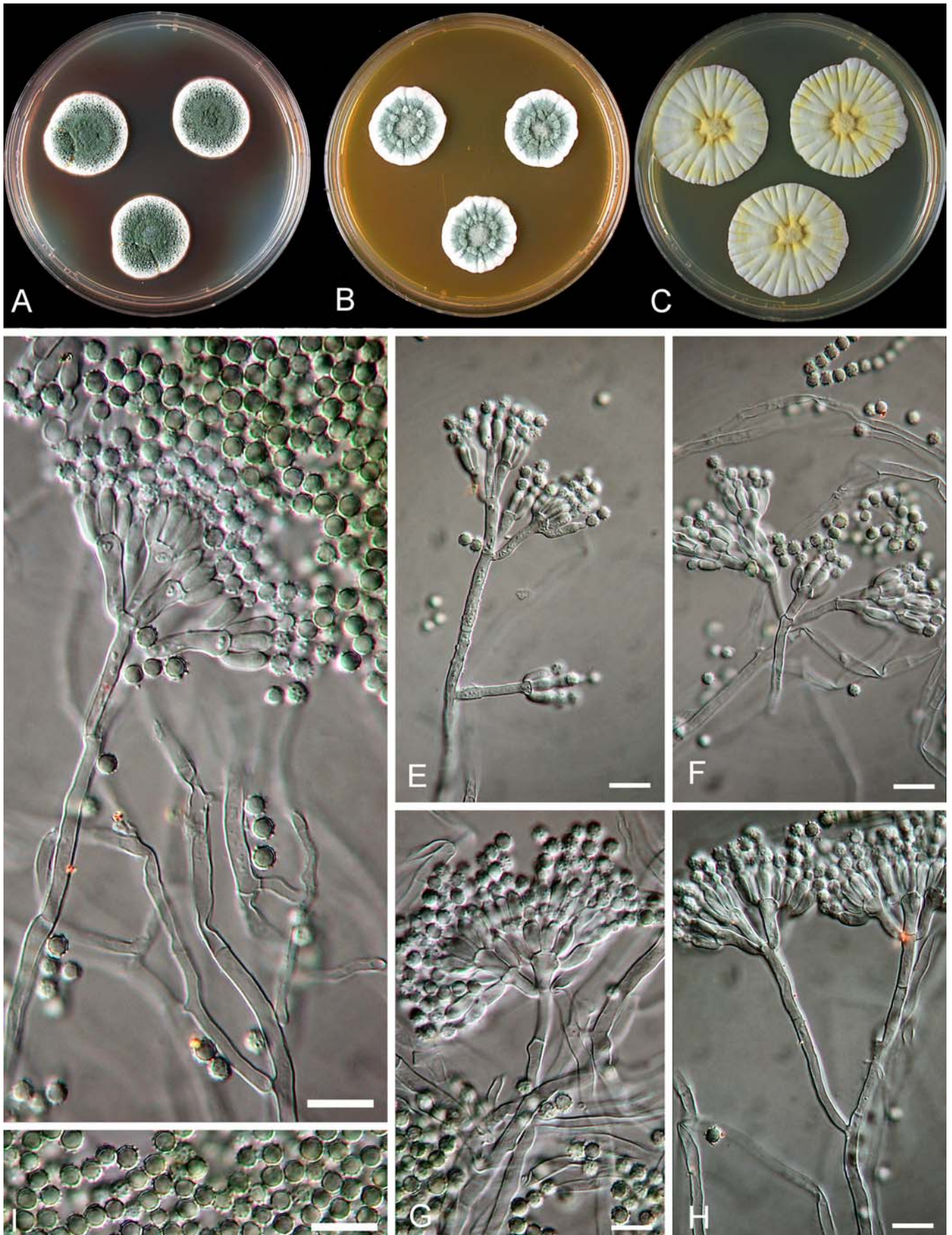


Fig. 65. *Penicillium neoechinulatum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. nordicum Dragoni & Cantoni ex Ramírez,
Adv. Pen. Asp. Syst.: 139, 1985

In *Penicillium* subgenus *Penicillium* section *Viridicata*
series *Verrucosa*

Type: ATCC 44219

Culture ex type: IBT 13307 = ATCC 44219, ex salami,
Italy (T)

Diagnostic features: smooth-walled conidia, ochratoxin A,
verrucolone, anacine, good growth on UNO and nitrite,
poor growth and no acid production of CREA, rough
conidiophore stipes

Similar species: *P. verrucosum* is the most similar and
closely related species, but *P. nordicum* has a cream yellow
reverse on YES in contrast to the red brown to terracotta
reverse of *P. verrucosum*.

Description:

Conidiophores: Terverticillate, appressed elements, born
from surface or subsurface hyphae

Conidia: Rough-walled, globose to subglobose, 2.6-3.4 µm.

Phialides: Cylindrical tapering to a distinct collulum, 7-9
µm x 2.2-2.8 µm

Metulae: Cylindrical, 8-13 µm x 3-4 µm

Rami: Cylindrical, 12-22 µm x 3-4 µm

Stipes: Rough walled, 200-450 µm x 3-4 µm

Synnemata or fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Velutinous to floccose, often weakly
fasciculate

Conidium colour on CYA: Green

Exudate droplets on CYA: Copious, clear to light yellow

Reverse colour on CYA: Cream often with brown center

Reverse colour on YES: Cream yellow

Diffusible colour on CYA: None

Ehrlich reaction: Yellow green reaction

Odour and volatile metabolites: As in *P. verrucosum*

Extrolites: 1) Verrucolone, 2) Ochratoxin A & B, 3) ana-
cine, 4) sclerotigenin, 5) lumpidin (only fish roe type), 6)
Viridic acid

Growth on creatine: Weak

Acid and base production on creatine: None

Growth on UNO: Very good

Growth on nitrite: Very good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 8-21 mm; MEA: 6-16 mm;
YES: 14-36 mm; CREA: 6-12 mm; Cz: 10-17 mm, OAT: 9-
19 mm; CYAS: 14-30 mm; CzBS: 4-10 mm; CzP: 0 mm;
UNO: 9-14 mm; DG18: 21-26 mm

Diam., CYA, 1 week: 5°C: 2-4 mm, 15°C: 8-21 mm; 30°C:
0 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.4-1.0]

CYA15°C/CYA 25°C: 1.0 [0.6-1.2]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.5 [0.3-0.7]

CZP/CZ: 0

Distribution: Greenland, Svalbard (Norway), Denmark,
Italy, Spain, Japan, Australia, Indonesia

Ecology and habitats: Refrigerated dry meat (salami, ham,
chicken), salted fish, fish roe, cheese and jam

Biotechnological applications: None

Biodeterioration & phytopathology: Degrading meat
products

Mycotoxinoses and mycotoxins: Ochratoxin A is produced
by all strains and can also be produced in meat products
(Spotti *et al.*, 2001). It may play a more prominent role in
Balkan Endemic Nephropathy than hitherto believed.

Typical cultures: IBT 5105 = CBS 112573 = NRRL 5547
= FRR 1642, ex salami, Italy; IBT 6728 = CBS 110770, ex
salami, Germany (Y); IBT 6734 = CBS 483.84, ex cheese,
Denmark; IBT 14172 = CBS 606.68, ex chicken meat,
Germany; IBT 12797 = CBS 112565 = NRRL A-19175, ex
sausage, Italy; IBT 14745 = CBS 110769, ex cheese, Spain;
IBT 12802 = CBS 110771 = NRRL 6061 = NRRL A-
19166, ex sausage, Italy; IBT 22949 = CBS 112321 = FRR
5205, ex wheat, southern part of Western Australia; ATCC
44220, ex salami, Italy (*P. mediolanense*); NRRL 5573 =
FRR 1641, ex salami, Italy; Fish roe type: IBT 6573 = CBS
109541, ex roe of *Lumpus*; IBT 12806 = CBS 109536 =
NRRL 1161, ex air in meat packing plant, Canada; IBT
13943 = CBS 109535, ex Serano ham, Spain; IBT 13958 =
CBS 109539, ex Spanish ham; IBT 22528 = CBS 109538,
ex fish roe, Denmark; IBT 22532 = CBS 109537, ex jam,
Japan.

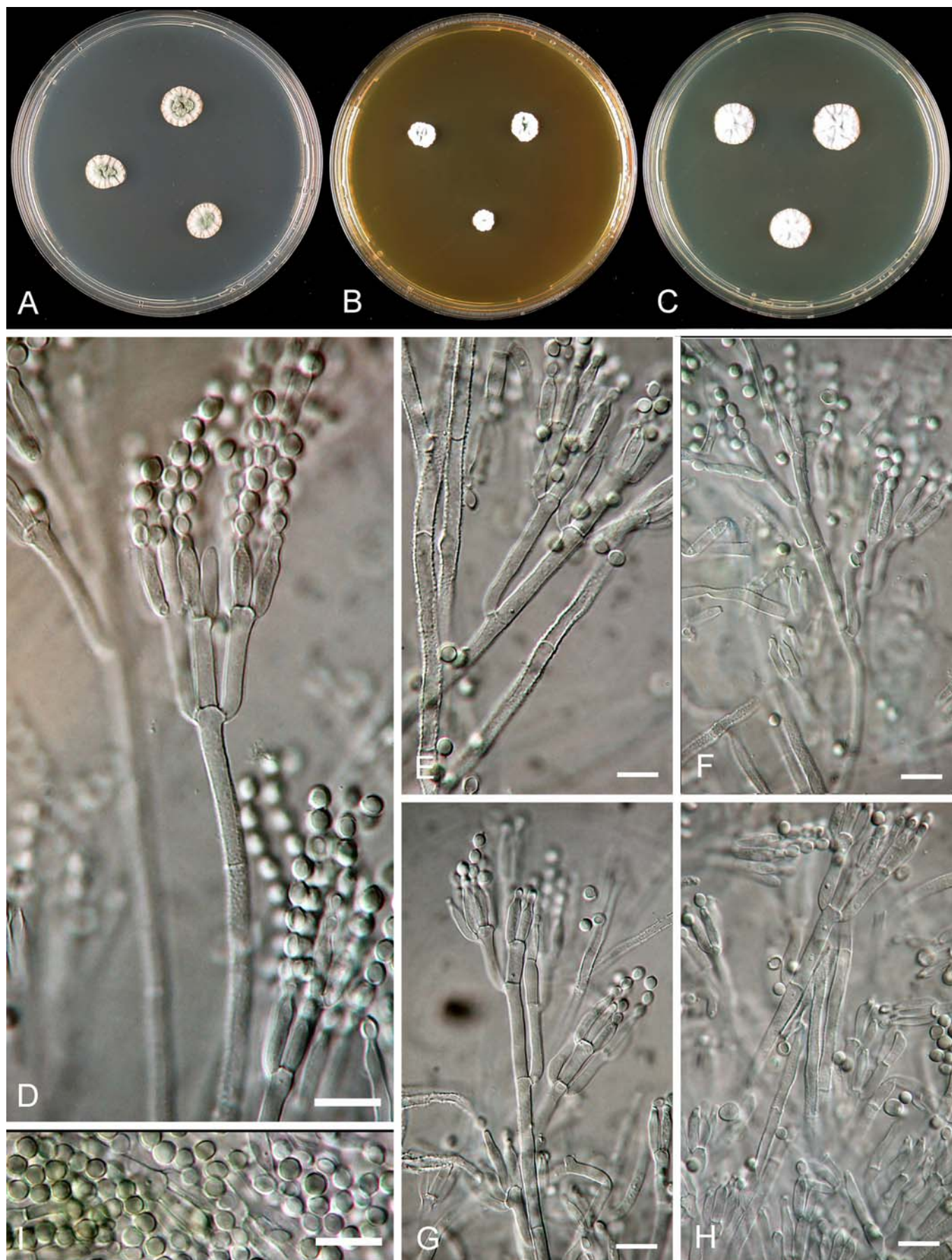


Fig. 66. *Penicillium nordicum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. olsonii Bain. & Sartory, Ann. Mycol. 10: 398, 1912

In *Penicillium* subgenus *Penicillium* section *Coronata* series *Olsonii*

Type (neo): Herb. IMI 192502

Culture ex type: CBS 232.60 = IBT 23473 = IMI 192502 = FRR 432, ex root of *Picea* sp., Austria (T)

Diagnostic features: Ellipsoidal finely roughened conidia, multiramulate penicilli, verruculone, ellipsoidal finely rough conidia

Similar species: *P. olsonii* grows much faster than *P. brevicompactum* and *P. bialowiezense* on CYA and YES.

Description:

Conidiophores: Long, multiramulate, appressed, terverticillate

Conidia: Finely roughened ellipsoidal, 3-4 µm x 2.5-3 µm

Phialides: Cylindrical with short collula, 9-12 µm x 2-3.2 µm

Metulae: Cylindrical but apically inflated, 10-12 µm x 2.5-4 µm

Rami: 8-18 µm x 4-5 µm

Stipes: 500-2000 µm x 4-6 µm, smooth-walled

Synnemata or fasciculation: None

Sclerotia: Occasionally large pale to light yellow sclerotia produced (IBT 20248)

Colony texture: Velutinous

Conidium colour on CYA: Greyish green to dull green

Exudate droplets on CYA: Clear to light yellow

Reverse colour: Cream to light yellow

Diffusible colour: None

Ehrlich reaction: Yellow reaction

Odour and volatile metabolites: 2-Butanone, isobutanol, isopentanol, 2-methyl-butanol, 2-heptanone, limonene, 2-nonanone (Larsen and Frisvad, 1995)

Extrolites: 1) Verruculone, 2) Asperphenamate, 3) 2-(4-Hydroxyphenyl)-2-oxo acetaldehyde oxime, 4) Bis (2-ethylhexyl)phthalate, 5) Breviones

Growth on creatine: Weak

Acid and base production on creatine: No acid or just under colony

Growth on UNO: Very good

Growth on nitrite: Very good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 26-40 mm; MEA: 19-36 mm; YES: 35-56; CREA: 13-17 mm; Cz: 20-24 mm, OAT: 17-33 mm; CYAS: 42-49; CzBS: 6-22; CzP: 0 mm; UNO: 7-20 mm; DG18: 32-49 mm

Diam., CYA, 1 week: 5°C: 2-5 mm, 15°C: 23-27 mm; 30°C: 0-2 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.6-0.9], halotolerant

CYA15°C/CYA 25°C: 0.7 [0.7-0.8]

CYA30°C/CYA 25°C: 0.03 [0-0.05]

CZBS/CZ: 0.8 [0.3-1.0]

CZP/CZ: 0

Distribution: Denmark, Norway, Netherlands, Russia, Costa Rica, Puerto Rico, Ontario, Canada

Ecology and habitats: Very common in greenhouses, peat soil, tomatoes, rarely on barley and cod roe, tropical soil

Biotechnological applications: None

Biodeterioration & phytopathology: Can deteriorate tomatoes and other vegetables in greenhouses.

Mycotoxins and mycotoxins: Unknown

Typical cultures: IBT 21538 = CBS 833.88, ex cactus pot soil, Denmark (Y); IBT 20248 = CBS 112481 = CBS 312.97, ex forest soil, 2000 feet, Costa Rica; IBT 21925 = CBS 112567, ex sage; IBT 23269 = CBS 381.75, ex *Fragaria* sp., Netherlands; IBT 18096 = CBS 112883 = FRR 2377, wooden artefact from New Guinea, Australian Museum, Sydney; IBT 23032 = CBS 349.61 = FRR 433, ex rubber life-raft, Netherlands; IBT 23033 = CBS 626.72 = IHEM 4512 = IMI 167384 = LCP 72.2195 = VKM F-1127, ex soil close to Volga, Russia (*P. volgaense*); IBT 13065 = CBS 112884, ex chilli pepper imported to Denmark; CBS 193.88, ex peat moss soil, Denmark; CBS 266.97 = IBT 14335, ex barley, Denmark; CBS 298.97 = IBT 14812, ex cod roe, Denmark; CBS 299.97 = IBT 15736, ex cherry tomato, Denmark.

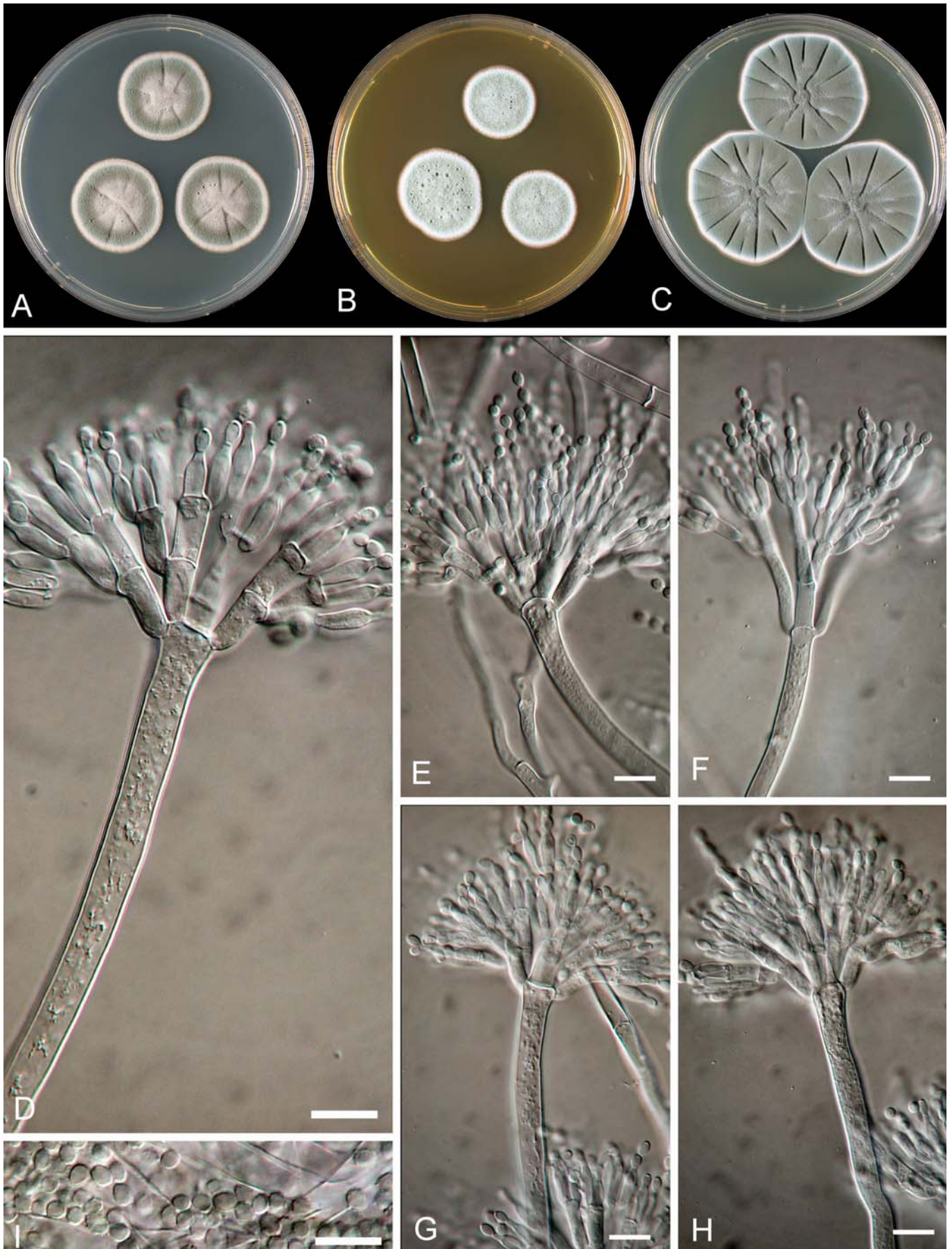


Fig. 67. *Penicillium olsonii*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. palitans Westling, Ark. Bot **11**: 83, 1911

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Camemberti*

Type: Herb. IMI 040215

Culture ex type: CBS 107.11 = IBT 23034 = IMI 040215 = ATCC 10477 = NRRL 2033 (T)

Diagnostic features: smooth-walled conidia, cyclopiazonic acid, fumigaclavine A & B; palitantin, dark green conidia, good growth on CREA

Similar species: *P. palitans* sporulates more heavily on YES and has greener conidia than *P. commune*. It is not crustose and grows more slowly than *P. crustosum*.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 3.5-4.5 μm .

Phialides: Cylindrical tapering to a distinct collulum, 9-12 μm x 2.5-3 μm

Metulae: Cylindrical, 10-15 μm x 3-4 μm

Rami: Cylindrical, 15-25 μm x 3-4 μm

Stipes: Rough-walled, 200-400 μm x 3-4 μm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Dark green to green

Exudate droplets on CYA: Present, clear to yellow

Reverse colour on CYA: Cream with a brown center

Reverse colour on YES: Yellow

Diffusible colour on CYA: None

Ehrlich reaction: Strong violet

Odour and volatile metabolites: No data

Extrolites: 1) Palitantin and frequentin, 2) Cyclopiazonic acid, 3) Fumigaclavine A & B

Growth on creatine: Very good

Acid and base production on creatine: Good acid production and subsequent base production

Growth on UNO: Very good

Growth on nitrite: Weak, occasionally good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 15-31 mm; MEA: 17-27 mm; YES: 28-46 mm; CREA: 16-28 mm; Cz: 19-28 mm, OAT: 22-30 mm; CYAS: 27-38 mm; CzBS: 15-27 mm; CzP: 0-1 mm; UNO: 16-27 mm; DG18: 25-33 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 21-30 mm; 30°C: 0-7 mm; 37°C: 0 mm

CYA/CYAS: 0.9 [0.7-1.1]

CYA15°C/CYA 25°C: 1.0 [0.9-1.1]

CYA30°C/CYA 25°C: 0.09 [0-0.2]

CZBS/CZ: 0.9 [0.6-1.2]

CZP/CZ: 0.01 [0-0.05]

Distribution: Denmark, Norway, Sweden, Russia, Japan, New Mexico (USA)

Ecology and habitats: Cheese, nuts, bread, liver pate

Biotechnological applications: None

Biodeterioration & phytopathology: May degrade cheese, but less common than *P. commune* on this substrate

Mycotoxins and mycotoxins: Cyclopiazonic acid and fumigaclavine may be formed in foods, but have not been found naturally occurring made by this species yet.

Typical cultures: IBT 6355 = CBS 491.84 = FRR 2948 = IMI 285507, ex mouldy liver pate; IBT 12714 = CBS 111834, ex kangaroo rat mound, Sevilletta, New Mexico; IBT 21540 = IBT 14740 = CBS 101031, Japan (Y); T327 = IBT 22531 = CBS 112207 = SUM 3170, Japan; IBT 14741, Japan; IBT 13514 = CBS 112203, ex wet barley, Denmark; T330 = IBT 13420 = CBS 112206 = VKM F-3088, Russia; T331 = IBT 13421 = CBS 112204 = VKM F-478, Russia; T332 = IBT 15975 = CBS 112205, ex mied pig feed, Stara Zagora, Bulgaria; IBT 18789 = CBS 112473, ex air in cake factory, Denmark; IBT 14757 = CBS 112474, ex wheat roll, Denmark.

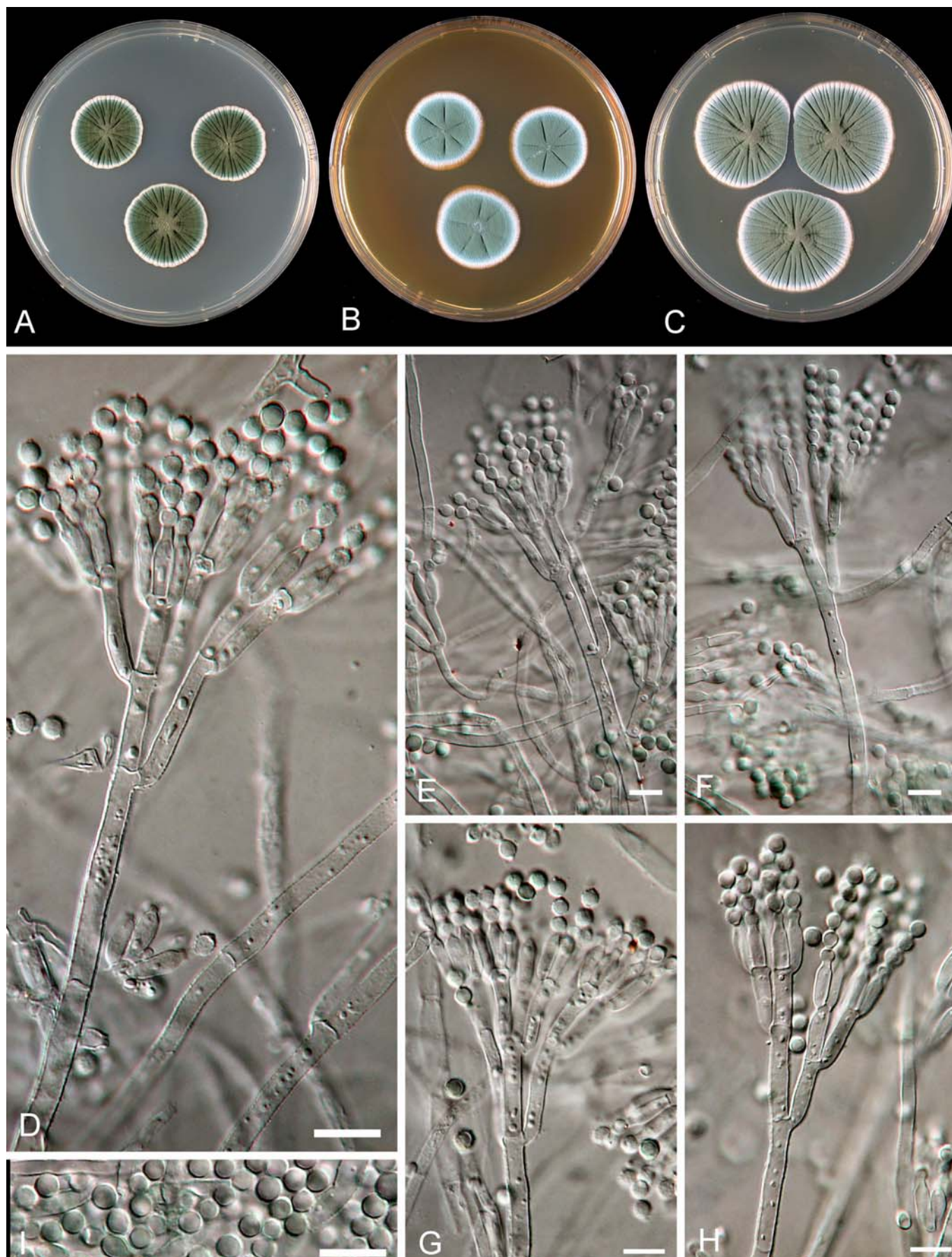


Fig. 68. *Penicillium palitans*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. paneum Frisvad, Microbiology, UK **142**: 546, 1996

In *Penicillium* subgenus *Penicillium* section *Roqueforti* series *Roqueforti*

Type: Herb. C 25000

Culture ex type: CBS 101032 = CBS 463.95 = IBT 21541 = IBT 12407 (**T, Y**) ex mouldy rye bread, Denmark

Diagnostic features: Marcfortines, patulin, globose smooth-walled conidia, growth on 0.5% acetic acid and 1% propionic acid (CzP)

Similar species: See *P. carneum*.

Description:

Conidiophores: Terverticillate, occasionally quarterverticillate, appressed elements, borne from subsurface hyphae

Conidia: smooth-walled, globose, 3.5-5 µm

Phialides: Cylindrical with short collula, 8-10 µm x 2.5-3.0 µm

Metulae: Cylindrical, 10-17 µm x 3-4 µm

Rami: Cylindrical, 17-33 µm x 3-4 µm

Stipes: Rough-walled, 100-250 µm x 4-5 µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture on CYA: Velutinous

Conidium colour on CYA: Blue green to green

Exudate droplets on CYA: Copious, clear

Reverse colour on CYA: Beige to brown

Reverse colour on YES: Cream beige often a pink to red water soluble pigment produced

Diffusible colour on CYA: None

Ehrlich reaction: None (weak violet reaction in one isolate)

Odour and volatile metabolites: Not examined

Extrolites: 1) Patulin, 2) Botryodiplodin, 3) Citreoisocoumarin, 4) Roquefortine C & D, 5) Marcfortine A, B & C

Growth on creatine: Very good

Acid and base production on creatine: None or weak acid at margin of colony

Growth on UNO: Very good

Growth on nitrite: Good growth

Abiotic factors:

Diam., 1 week, 25°C: CYA: 38-41 mm; MEA: 43-67 mm; YES: 52-71 mm; CREA: 14-30 mm; Cz: (9-)20-31 mm, OAT: 53-72 mm; CYAS: 20-28 mm; CzBS: 8-50 mm; CzP: 7-34 mm; UNO: 20-47 mm; DG18: 33-47 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 27-36 mm; 30°C: 10-39 mm; 37°C: 0 mm

CYA/CYAS: 2.0 [1.4-2.6]

CYA15°C/CYA 25°C: 0.7 [0.6-0.9]

CYA30°C/CYA 25°C: 0.6 [0.2-0.8]

CZBS/CZ: 1.3 [0.9-1.4]

CZP/CZ: 0.7 [0.2-0.9]

High resistance to acid and good growth at high CO₂ levels.

Distribution: Denmark, Norway, Sweden, Canada

Ecology and habitats: Mouldy rye bread and bakers yeast, silage, cassava chips

Biotechnological applications: none

Biodeterioration & phytopathology: Deteriorates silage

Mycotoxicoeses and mycotoxins: Botryodiplodin, patulin and roquefortine C may all be produced in silage.

Typical cultures: IBT 13321 = CBS 303.97, ex sweet carbonated water, Denmark; IBT 21729 = CBS 112296, ex cassava chips, Africa; IBT 21613 = CBS 112295, ex grass silage, Sweden; IBT 11839 = CBS 464.95, ex rye bread, Denmark; IBT 16402 = CBS 112294 = NRRL 1168, Ot-tawa, Canada; IBT 14356 = CBS 462.65, ex wine cork, Spain; IBT 19477 = IBT 3912 = CBS 167.91, ex grain, Sweden; IBT 21543 = CBS 479.84, ex mouldy bakers yeast, Denmark; IBT 21814 = CBS 112319, ex air, factory, Denmark; IBT 12392 = CBS 463.95, ex chocolate sauce, Norway; IBT 21736 = CBS 112320, ex cassava chips, Africa; IBT 13929 = CBS 465.95, ex mouldy bakers yeast, Denmark.

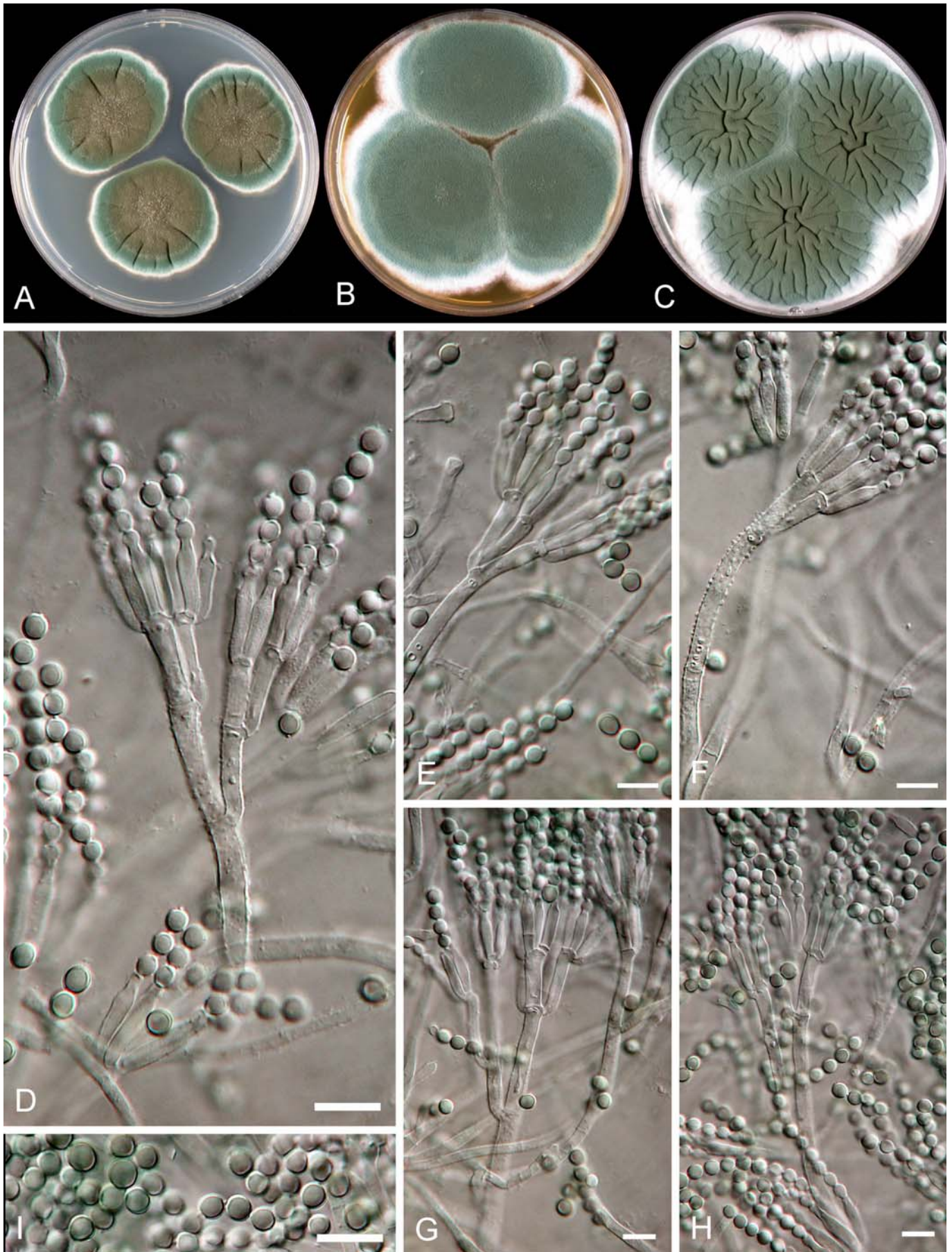


Fig. 69. *Penicillium paneum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. persicinum L. Wang, H. Zhou, Frisvad & Samson, Ant. van Leeuwenhoek 86: 177. 2004

Provisionally in *Penicillium* subgenus *Penicillium* section *Chrysogena* series *Persicina*

Type: Herb. HMAS 80638-1-4

Culture ex type: CBS 111235 = IBT 24565 = AS 3.5891 = T505, ex soil, Qinghai, China

Diagnostic features: Griseofulvin, chrysogine, roquefortine C, cylindrical to ellipsoidal smooth-walled conidia, pink diffusible pigment on CYA and YES

Similar species: *P. persicinum* differs from *P. italicum* by production of a pink diffusing pigment on CYA and YES and growth at 37°C.

Description:

Conidiophores: Terverticillate, occasionally quarterverticillate, appressed elements, borne from aerial hyphae

Conidia: smooth-walled, cylindrical and ellipsoidal, 3.5-4.5 µm x (1.5-) 2-3 (-3.5) µm

Phialides: Cylindrical with short collula, 7-11 µm x (2-) 2.5-3.5 (-4) µm

Metulae: Cylindrical, apically swollen up to 10 µm, 10-20 µm x 3.5-4.5(-5.4) µm

Rami: Cylindrical, 18-36 µm x 3.5-4.5 µm

Stipes: Rough-walled, 200-600 µm x 3.5-4.5 µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Gnaphalium green

Exudate droplets on CYA: None

Reverse colour on CYA: Peach to coral red

Reverse on YES: Pinkish red

Diffusible colour on CYA: Peach to coral red

Ehrlich reaction: None

Odour and volatile metabolites: Not examined

Extrolites: 1) Griseofulvins, 2) Roquefortine C & D, 3) Chrysogine, 2-pyrovoylaminobezamide, 2-acetyl-qionazolin-4(3H)-one

Growth on creatine: Weak

Acid and base production on creatine: No acid

Growth on UNO: Good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 22-30 mm; MEA: 22-26 mm; YES: 24-33 mm; CREA: 13-18 mm; Cz: 27-29 mm, OAT: 23-30 mm; CYAS: 19-21mm; CzBS: 10-12 mm; CzP: 0 mm; UNO: 26-30 mm; DG18: 20-22 mm

Diam., CYA, 1 week: 5°C: 0 mm; 15°C: 13-18 mm; 30°C: 19-21 mm; 37°C: 8-9 mm

CYA/CYAS: 1.4 [1.3-1.5]

CYA15°C/CYA 25°C: 0.6 [0.5-0.6]

CYA30°C/CYA 25°C: 0.8 [0.7-0.9]

CZBS/CZ: 0.4

CZP/CZ: 0

Distribution: China

Ecology and habitats: Soil

Biotechnological applications: None

Biodeterioration & phytopathology: -

Mycotoxins and mycotoxins: Roquefortine C is produced.

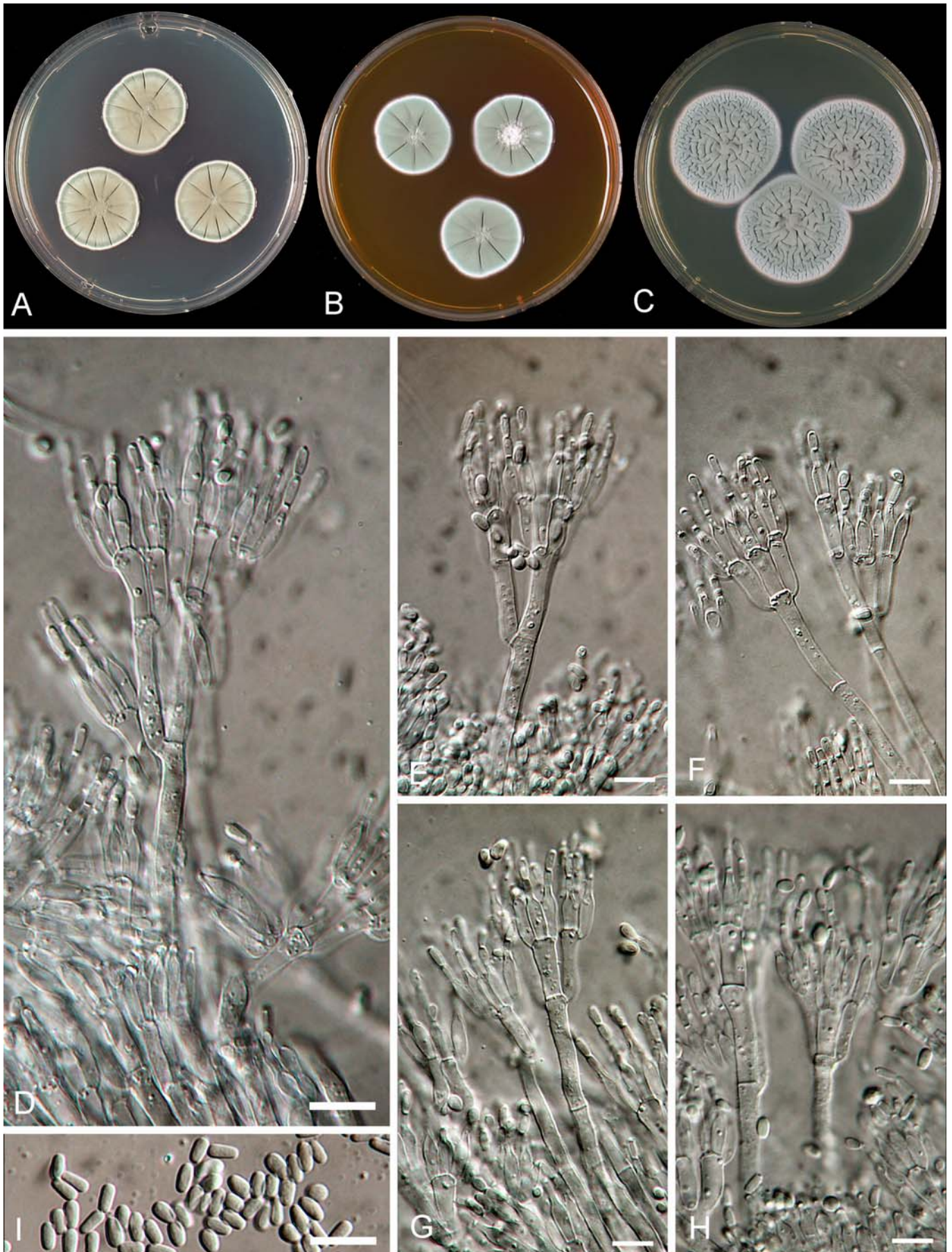


Fig. 70. *Penicillium persicinum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. polonicum K. Zaleski, Bull. Int. Acad. Pol. Sci. Lett., Sér. B **1927**: 445, 1927

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Viridicata*

Type: Herb. CBS 222.28

Culture ex type: CBS 222.28 = IBT 12821 = IMI 291194 = MUCL 29204 = NRRL 995, ex soil, Poland (T)

Diagnostic features: Penicillic acid, puberuline / verrucofortune, verrucosidin, cyclopenin, cyclophenol, smooth-walled conidia,

Similar species: *P. polonicum* grows faster than *P. aurantiogriseum* and other species in series *Viridicata* with blue green conidia on CYA and YES, sporulates better on YES and grow better on CREA. *P. polonicum* has blue green conidia in contrast to the pure green conidia of *P. melanoconidium* and *P. viridicatum*.

Description:

Conidiophores terverticillate, few biverticillate and quarterverticillate from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 3-4 x 2.5-3.5 µm

Phialides: Flask-shaped tapering to a distinct collulum, 7.5 - 10 µm x 2.5-2.8 µm

Metulae: Cylindrical, 10-13 µm x 2.8-3.5 µm

Rami: Cylindrical, 15-25 µm x 3-3.5 µm

Stipes: 180-400 µm x 3-4 µm, walls smooth to finely roughened

Synnemata or fasciculation: None

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Blue green

Exudate droplets on CYA: Present, clear

Reverse colour on CYA: Pale to cream or yellow brown to red brown

Reverse colour on YES: Yellow (strong sporulation)

Diffusible colour: None or beige brown to red brown

Ehrlich reaction: Weak, violet

Odour and volatile metabolites: gamma-elemene, ethyl acetate, 3-octanone, 2-methyl-isoborneol (Larsen & Frisvad, 1995)

Extrolites: 1) Penicillic acid, 2) Verrucosidin, 3) Puberuline and verrucofortune, 4) Cyclopeptin, dehydrocyclopeptin, Cyclophenol, cyclopenin, viridicatol, 3-methoxyviridicatin, 5) Anacine, 6) Aspterric acid, 7) Methyl-4-(2-(2R)-hydroxyl-3-butyloxy) benzoate, 8) Nephrotoxic glycopeptides

Growth on creatine: Moderate to good, colony often with a yellow center

Acid and base production on creatine: Very good, no base

Growth on UNO: Weak

Growth on nitrite: Weak

RT: Strong reaction, dark brown halo and reverse

Abiotic factors:

Diam., 1 week, 25°C: CYA: 24-43 mm; MEA: 28-40 mm; YES: 36-54 mm; CREA: 10-27 mm; Cz: 22-38 mm, OAT: 24-36 mm; CYAS: 36-49 mm; CzBS: 22-30 mm; CzP: 0 mm; UNO: 8-15 mm; DG18: 30-36 mm

Diam., 1 week: 5°C: 2-5 mm, 15°C: 27-30 mm; 30°C: 10-15 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.7-1.0], halotolerant

CYA15°C/CYA 25°C: 0.9 [0.7-1.0]

CYA30°C/CYA 25°C: 0.4 [0.2-0.4]

CZBS/CZ: 0.9 [0.8-1.0]

CZP/CZ: 0

Distribution: Denmark, Sweden, United Kingdom, Germany, Netherlands, Spain, Italy, BC, Canada, Kenya, Taiwan

Ecology and habitats: Wheat, barley, rye, oats, rice, corn, peanuts, dried meat, onions, vegetable field soil

Biotechnological applications: None

Biodeterioration & phytopathology: Deteriorate cereals

Mycotoxinoses and mycotoxins: This species produce penicillic acid, verrucosidin and nephrotoxic glycopeptides (see also *P. aurantiogriseum*). It may play a role in Balkan Endemic Nephropathy.

Typical cultures: IBT 14318 = CBS 110332 = NRRL 952; T334 = IBT 21542 = IBT 11245 = CBS 793.95 (Y), ex *Hordeum vulgare*, Denmark; IBT 14320 = CBS 101479 = IMI 321304, Vratsa, Bulgaria; IBT 22439 = CBS 112490, ex cassava chips, Africa; IBT 15982 = CBS 112561, ex mixed pig feed, Bulgaria; IBT 11383 = CBS 639.95, ex mixed cereal feed, Denmark; IBT 18382 = CBS 112560 = CCRC 32637, ex rhizosphere of garlic, Taichung, Taiwan; IBT 6285 = CBS 690.77 = IJFM 3752 = IMI 291200, ex air, Spain (*P. glaucocoeruleum*, *nomen nudum*); IBT 14609 = CBS 112020 = ATCC 15683, ex peanuts, USA (reported as aflatoxin producer); CBS 278.30 = ATCC 10421 = IFO 7723 = IMI 040218 = NRRL 2035 = QM 6867 = IBT 11782, ex dried flowers of *Humulus lupulus*, United Kingdom (*P. carneolutescens*); CBS 111.43 = ATCC 10467 = FRR 2027 = IFO 8142 = IMI 040211 = MUCL 15618 = NRRL 2027 = VKM F-310 = IBT 6156 = IBT 4349; CBS 316.48 = ATCC 10433 = FRR 1899 = IFO 5847 = IMI 040236ii = NRRL 1899 = QM 684 = IBT 12820; CBS 692.77 = IJFM 3751 = IMI 291195, ex air, Spain (*P. ochraceoviride*, *nomen nudum*); CBS 475.84 = FRR 2934 = IMI 285514; CBS 222.90 = IBT 3448, ex *Allium* sp., Denmark; CBS 224.90 = IBT 3522, ex *Triticum aestivum*, Denmark; CBS 228.90 = IBT 3447 = PREM 47750 = ATCC 64541, South Africa; CBS 654.95 = IBT 5131; CBS 793.95 = IBT 11245, ex *Hordeum vulgare*, Denmark; CBS 101478 = IBT 12826 = NRRL 6316, USA; CBS 101487 = IBT 14321, ex wheat, United Kingdom, IBT 11410 = NRRL 3608, IBT 5157 = NRRL 5570, IBT 12822 = NRRL 6314, IBT 12827 = NRRL 2029, IBT 12828 = NRRL 6315.



Fig. 71. *Penicillium polonicum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. radicicola Overy and Frisvad, Syst. Appl. Microbiol., **26**: 633, 2003

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Corymbifera*

Type: Herb. C 60161

Culture ex type: CBS 112430 = IBT 10696 (T, Y), ex *Armoracia rusticana* root, Denmark

Diagnostic features: Smooth-walled conidia, poor sporulation but fasciculate colonies on MEA, no sporulation on YES agar, orange reverse on CYA, production of citrinin, meleagrin, penicillic acid, and terrestric acid

Similar species: See *P. albocoremium*.

Description:

Conidiophores terverticillate, few quarterverticillate from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 2.8–4 µm

Phialides: Flask-shaped tapering to a distinct collulum, 7.8–11.2 µm x 2.6–3.5 µm

Metulae: Cylindrical, 10–17 µm x 2.5–4.8 µm

Rami: Cylindrical, 12–27 µm x 2.6–4.8 µm

Stipes: 150–2000 µm x 3–4 µm, walls smooth to finely roughened

Fasciculation: Weakly fasciculate

Sclerotia: None

Colony texture: Floccose to weakly fasciculate

Conidium colour on CYA: Greyish green to dull green

Exudate droplets on CYA: Present, clear

Reverse colour on CYA: Deep orange to Persian orange

Reverse colour on YES: Deep to butter yellow

Diffusible colour on CYA: None

Ehrlich reaction: Weak violet reaction

Odour and volatile metabolites: isobutanol, isopentanol, γ-murolene? (Larsen & Frisvad, 1995)

Extrolites: 1) Citrinin, 2) penicillic acid, 3) Terrestric acid
4) Roquefortine C & D, meleagrin, 5) Cyclopeptin, dehydrocyclopeptin, cyclopenin, cyclophenol, viridicatol, 3-methoxyviridicatin, 6) Chrysogine

Growth on creatine: Weak to moderate

Acid and base production on creatine: Good acid production

Growth on UNO: Weak

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 29–41 mm; MEA: 17–37 mm; YES: 37–50 mm; CREA: 15–27 mm; Cz: 17–30 mm, OAT: 28–40 mm; CYAS: 29–37 mm; CzBS: 11–24 mm; CzP: 0 mm; UNO: 10–15 mm; DG18: 22–36 mm

Diam., 1 week: 5°C: 2–5 mm, 15°C: 27–34 mm; 30°C: 1–10 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.7–1.0], halotolerant

CYA15°C/CYA 25°C: 1.2 [0.7–1.0], psychrotolerant

CYA30°C/CYA 25°C: 0.1 [0.1]

CZBS/CZ: 0.9 [0.8–1.0]

CZP/CZ: 0

Distribution: Denmark, United Kingdom, Iceland

Ecology and habitats: Carrots, potatoes, onions and tap-root plants, (snake dung)

Biotechnological applications: none

Biodeterioration & phytopathology: May cause a rot in vegetable roots and flower bulbs

Mycotoxins and mycotoxins: It is not known whether this species can produce citrinin, penicillic acid, terrestric acid or roquefortine C in carrots, onions or potatoes

Typical cultures: IBT 10693 = CBS 112429, ex *Apium graveolens*, Denmark; IBT 18894 = CBS 112576, ex butter cake, Denmark; IBT 3491 = CBS 112428, ex *Solanum tuberosum*, Denmark; IBT 22526 = CBS 109554, ex *Allium cepae*, Denmark; IBT 22520 = CBS 112427, ex *Allium cepae*, Denmark; IBT 22522 = CBS 112426, ex *Allium cepae*, Denmark; IBT 3489 = CBS 112425, ex carrot, Denmark; IBT 10695, ex *Colchicum* sp.; IBT 10698 = IMI 293206, ex carrot; IBT 10699, ex *Apium graveolens*; IBT 11646 & IBT 11647, ex carrot, Denmark; IBT 11649, ex *Allium fistulosum*, Denmark; IBT 15242, ex *Pastinaca sativa*, Denmark; IBT 18856, ex snake dung, United Kingdom; IBT 22536, ex soil, Iceland.

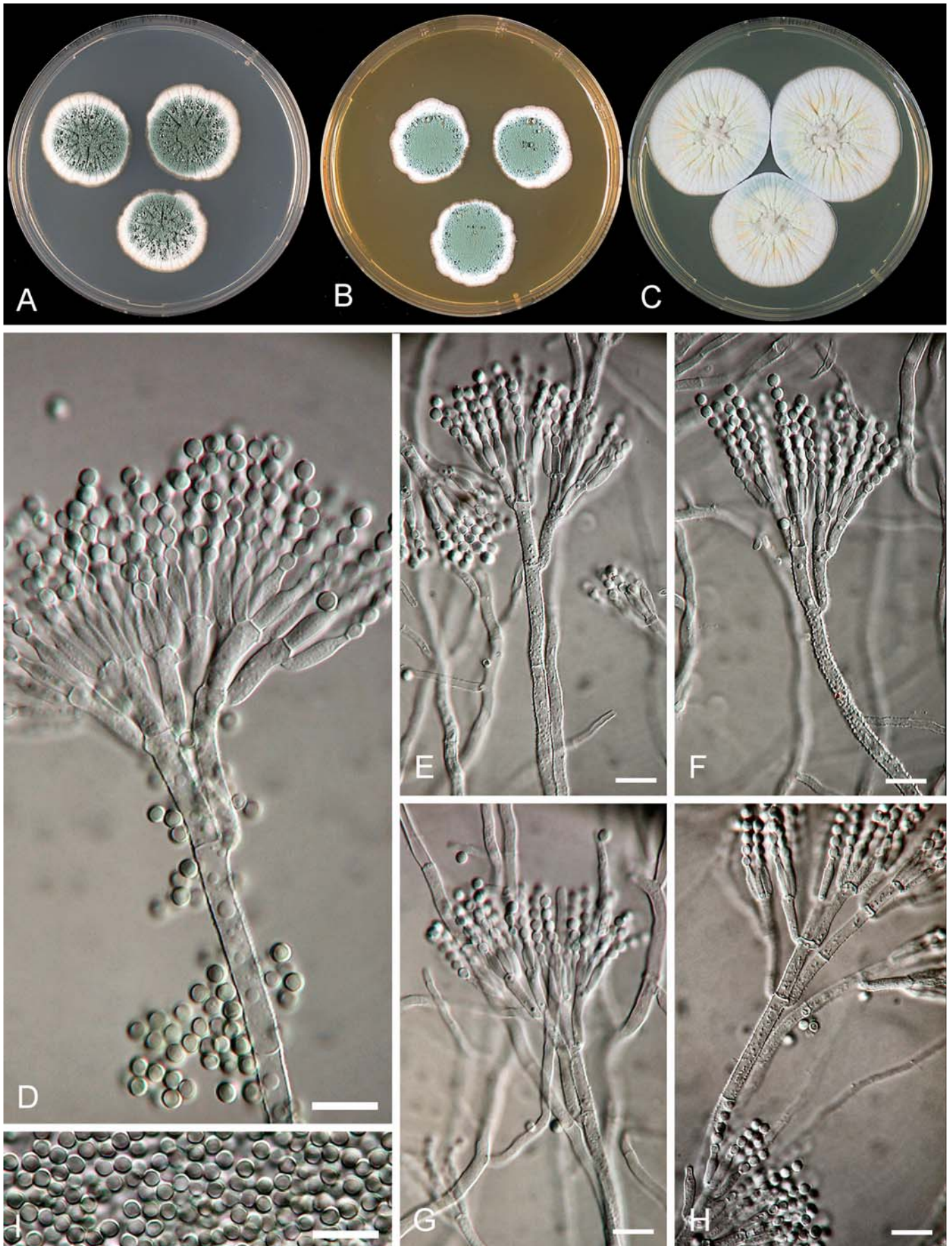


Fig. 72. *Penicillium radiculicola*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

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

In *Penicillium* subgenus *Penicillium* section *Roqueforti*
series *Roqueforti*

Type: Herb. IMI 024313

Culture ex type: CBS 221.30 = IBT 6754 = IMI 024313 =
ATCC 10110 = ATCC 1129 = CECT 2905 = IFO 5459 =
NCTC 588 = NRRL 849 = QM 1937 (T), ex French Roque-
fort cheese, USA

Diagnostic features: PR-toxin, roquefortine C, globose
smooth-walled conidia, good growth on media with 0.5%
acetic acid or 1% propionic acid, black green reverse on
CYA and YES

Similar species: *P. roqueforti* differs from *P. paneum* and
P. carneum by producing a dark greenish black reverse on
CYA and YES.

Description:

Conidiophores: Terverticillate, occasionally quarterverticil-
late, appressed elements, borne from subsurface hyphae

Conidia: smooth-walled, globose, 3.5-5 µm

Phialides: Cylindrical with short collula, 8-10 µm x 2.5-3.0
µm

Metulae: Cylindrical, 10-17 µm x 3-4 µm

Rami: Cylindrical, 17-33 µm x 3-4 µm

Stipes: Rough-walled, 100-250 µm x 4-5 µm

Synnemata or fasciculation: None

Sclerotia: Occasionally rudimentary sclerotia

Colony texture on CYA: Velutinous

Conidium colour on CYA: Green

Exudate droplets: None

Reverse colour on CYA: Blackish green

Reverse colour on YES: Blackish green

Diffusible colour on CYA: None

Ehrlich reaction: Violet (yellow in few old strains)

Odour and volatile metabolites: Isobutanol, isopentanol, 2-
methyl-butanol, isobutyl acetate, 1-octene, 3-octanone, β-
myrcene, p-cymene, limonene, linalool, eremophilene,
aristolochene, patchoulene isomer, β-elemene? (Larsen &
Frisvad, 1995)

Extrolites: 1) Citreoisocoumarin, 2) Mycophenolic acids, 3)
PR-toxins, 4) roquefortine C & D, 5) Isofumigaclavine A &
B, α-amino isobutyric acid peptides

Growth on creatine: Very good

Acid and base production on creatine: None

Growth on UNO: Very good

Growth on nitrite: Very good

Abiotic factors:

Diam., 1 week, 25°C: CYA: (17-) 40-77 mm; MEA: 26-43
mm; YES: 38-71 mm; CREA: 12-44 mm; Cz: 15-46 mm,
OAT: 34-61 mm; CYAS: 26-43 mm; CzBS: 28-41 mm;
CzP: 13-25 mm; UNO: 16-48 mm; DG18: 37-48 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 28-38 mm;
30°C: (0-) 6-11 mm; 37°C: 0 mm

CYA/CYAS: 1.3 [0.6-1.6]

CYA15°C/CYA 25°C: 0.8 [0.4-1.7]

CYA30°C/CYA 25°C: 0.2 [0-0.2]

CZBS/CZ: 1.2 [0.9-1.9]

CZP/CZ: 0.7 [0.4-1.3]

High resistance to acid and good growth at high CO₂ levels.

Distribution: Denmark, France, Netherlands, Belgium,
Germany, Sweden, Norway, United Kingdom, Ireland,
Czech Republic, Italy, Spain, Portugal, Turkey, USA,
Canada

Ecology and habitats: Blue mould cheeses, silage, rye
bread, mould bakers yeast, forest soil, wood

Biotechnological applications: Production of blue cheese

Biodeterioration & phytopathology: Deterioration of
silage

Mycotoxins and mycotoxins: PR-toxin, roquefortine C
and isofumigaclavine A & B. Mycophenolic acid is immu-
nosuppressive and may thus cause secondary (indirect)
mycotoxicosis.

Typical cultures: IBT 21543 = CBS 479.84, ex mouldy
bakers yeast, Denmark (Y); IBT 19479 = CBS 253.56, ex
Roquefort cheese, France; IBT 19475 = CBS 135.67 =
MUCL 8491, ex blue cheese, Germany; IBT 19480 = CBS
265.55 = IBT 16401 = NRRL 858 (light reverse), ex
Gorgonzola cheese, Italy; IBT 19476 = CBS 498.73 =
ATCC 24720 = FRR 1480 = IMI 174718 = IMI 291199 =
VKM F-1748 (light reverse), ex fruit of *Malus sylvestris*,
Russia (*P. conservandi*); IBT 19481 = CBS 234.38 = IMI
291202, ex blue Cheshire cheese, United Kingdom; IBT
16407 = CBS 112579 = NRRL 1165 (light reverse), ex
waste sulphite liquor, Ottawa, Canada; IBT 5308 = IBT
3915 = CBS 112571 = IMI 300728 (slow growing)(received
as *P. mali*); IBT 5309 = IBT 3905 = IMI 298084, ex soil in
Salix-Populus forest, South Wisconsin; IBT 16404 = NRRL
852, Grove City, Pennsylvania; IBT 16408 = NRRL 853,
State College of Washington, USA; IBT 16405 = NRRL
857 (*P. gorgonzolae* Weideman), IBT 16403 = NRRL 851,
Waycross, Georgia; IBT 19482 = CBS 257.55, ex blue
cheese, Denmark.

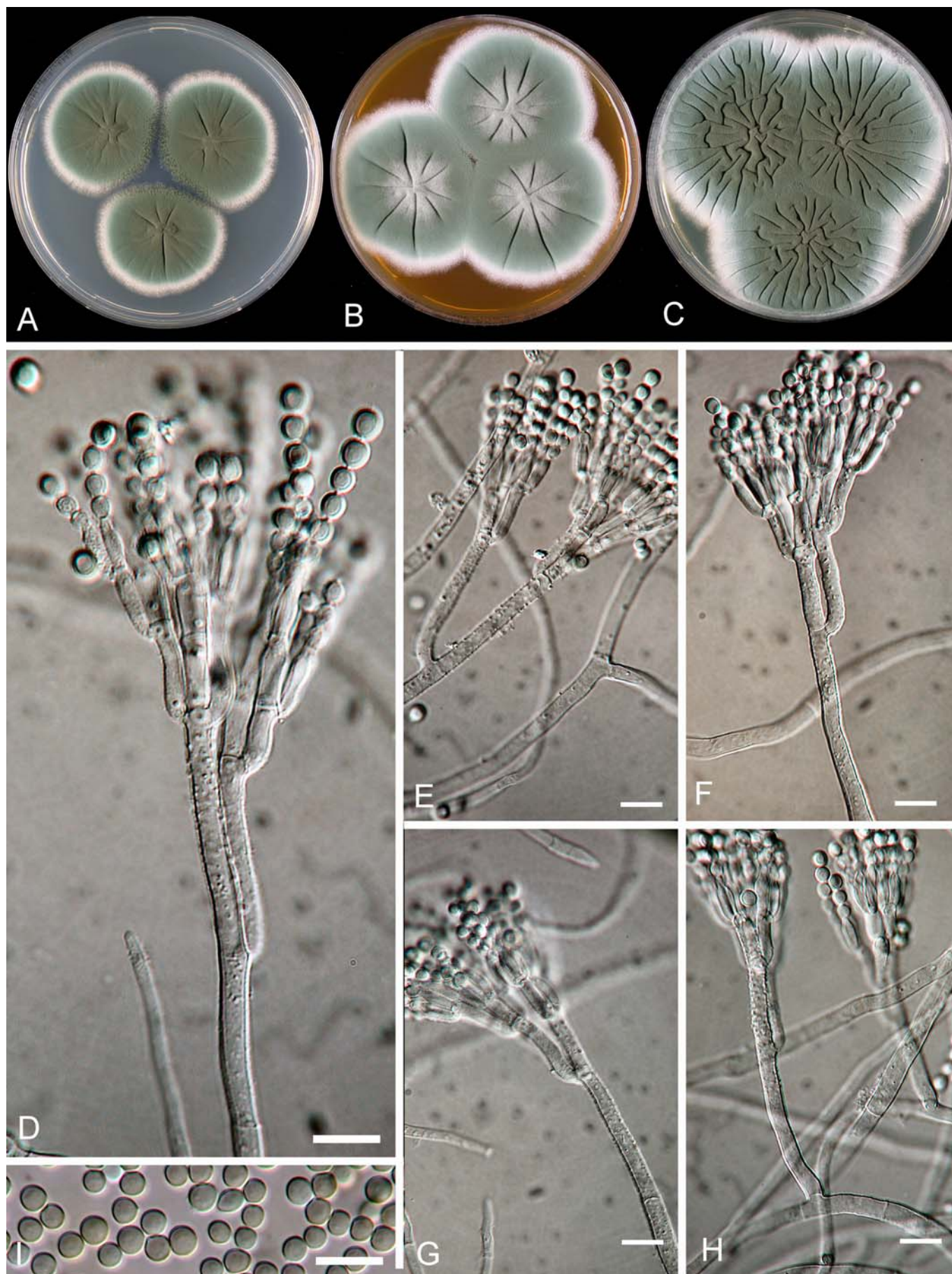


Fig. 73. *Penicillium roqueforti*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. sclerotigenum Yamamoto, Scient. Rep. Hyogo Univ. Agric., Agric. Biol. Ser. 2, 1: 69, 1955

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Expansa*

Type: Herb. IMI 068616

Culture ex type: CBS 349.59 = CBS 101033 = IBT 14346 = IBT 21544 = IMI 068616 = ATCC 18488 = IFO 6167 = NRRL 3461 = QM 7779 (T, Y), ex rotting tuber of *Dioscorea batatas*, Japan

Diagnostic features: Griseofulvin, sclerotigenin, patulin, gregatins, ellipsoidal smooth-walled conidia, high growth rates on all media

Similar species: *P. sclerotigenum* differs from *P. expansum* by poor growth on CREA, many biverticillate penicilli and production of sclerotia.

Description:

Conidiophores: Biverticillate and terverticillate, appressed elements, borne from surface hyphae

Conidia: smooth-walled, ellipsoidal, 4-5 µm x 2.5-3.5 µm

Phialides: Cylindrical with short collula, 8-12 µm x 2.5-3.0 µm

Metulae: Cylindrical, 13-22 µm x 3-4 µm, can be apically swollen

Rami: Cylindrical, 17-25 µm x 3-4 µm

Stipes: Rough-walled, 200-600 µm x 3-4 µm

Synnemata or fasciculation: None

Sclerotia: 150-300 µm, pseudoparenchymatous

Colony texture: Velutinous

Conidium colour on CYA: Dull green

Exudate droplets on CYA: None

Reverse colour on CYA: Light brown with a darker brown center

Diffusible colour on CYA: None

Ehrlich reaction: None

Odour and volatile metabolites: Not examined

Extrolites: 1) Patulin, 2) Griseofulvin, 3) Gregatins, 4) Sclerotigenin, 5) Roquefortine C & D

Growth on creatine: Weak

Acid and base production on creatine: No acid or some acid, no base

Growth on UNO: Very good

Growth on nitrite: Very good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 40-62 mm; MEA: 16-70 mm; YES: 53-80 mm; CREA: 33-45 mm; Cz: 33-48 mm, OAT: 46-67 mm; CYAS: 22-34 mm; CzBS: 0-17 mm; CzP: 0 mm; UNO: 19-34 mm; DG18: 30-51 mm

Diam., CYA, 1 week: 5°C: 0-1 mm; 15°C: 23-35 mm; 30°C: 16-29 mm; 37°C: 0 mm

CYA/CYAS: 2.0 [1.5-2.6]

CYA15°C/CYA 25°C: 0.6 [0.5-0.7]

CYA30°C/CYA 25°C: 0.4 [0.3-0.5]

CZBS/CZ: 0.3 [0-0.5]

CZP/CZ: 0

Distribution: Philippines, Japan, Taiwan, Russia, Jamaica.

Ecology and habitats: Yam tubers and yams products

Biotechnological applications: None

Biodeterioration & phytopathology: Pathogenic on yams

Mycotoxins and mycotoxins: Patulin, roquefortine C may be produced in yams, but this has not been examined.

Typical cultures: IBT 15061 = CBS 307.97 = IMI 361520, ex blue yams flour, Philippines; IBT 13938 = CBS 306.97 = IMI 267703, ex *Dioscorea cayennensis*, Jamaica; IBT 13826 = CBS 112566 = VKM F-2398, Russia.

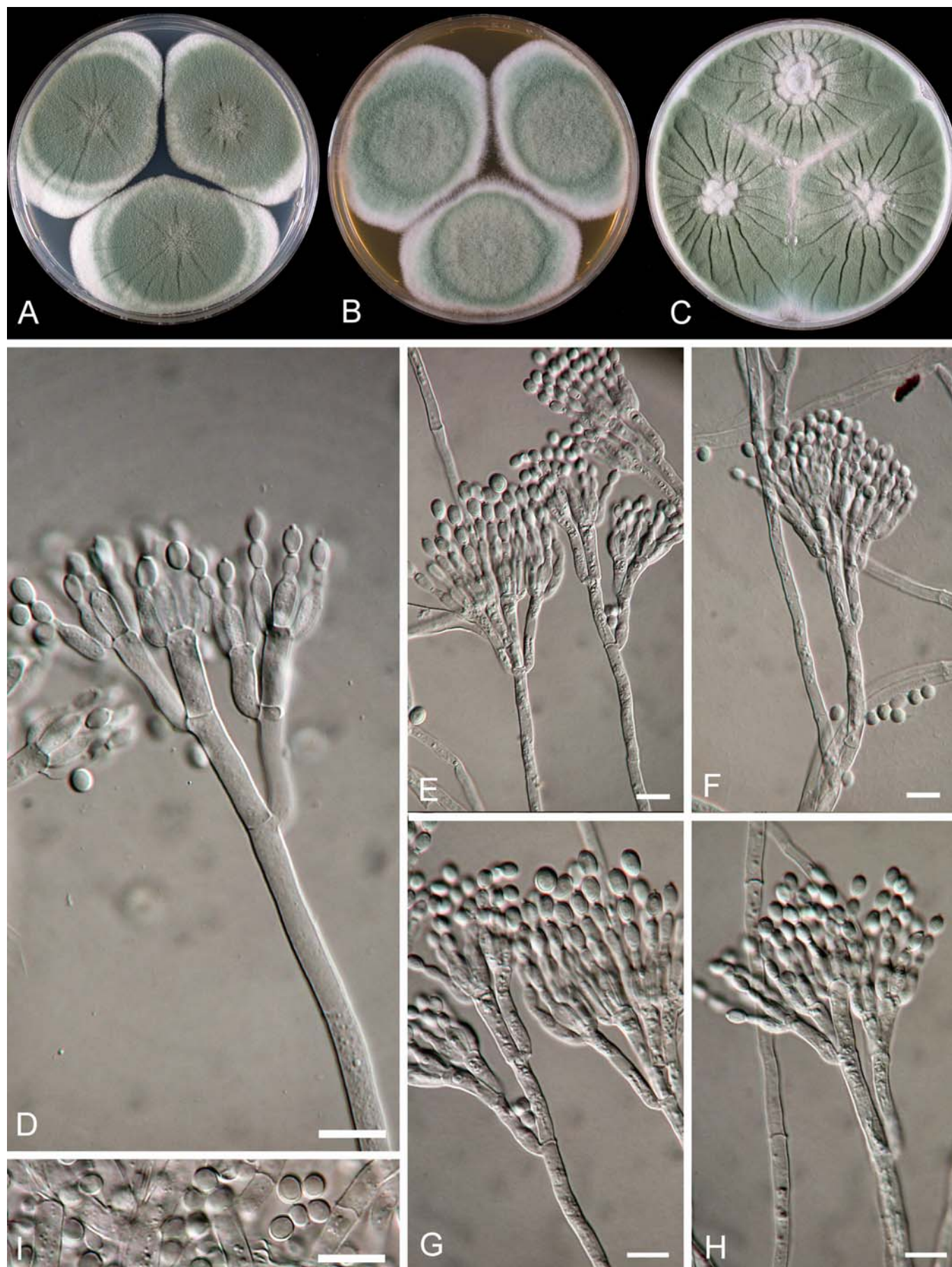


Fig. 74. *Penicillium sclerotigenum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. solitum Westling, Ark. Bot. **11**: 65, 1911

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Solita*

Type: Herb. CBS 424.89

Culture ex type: CBS 424.89 = CBS 288.36 = IBT 3948 = FRR 937 = IFO 7765 = IMI 039810 = IMI 092225 = ATCC 9923 = MUCL 28668 = MUCL 29173 = NRRL 937, Norway (**T**)

Diagnostic features: Compactin, cyclopenin, cyclopenol, dark green smooth to slightly rough-walled conidia, rough stipes, yellow orange reverse on YES agar

Similar species: *P. solitum* differs from *P. cavernicola*, *P. echinulatum* and *P. discolor* by having smooth to slightly rough-walled conidia, in contrast to the conspicuously rough-walled conidia of the other species with dark green conidia in series *Solita*. *P. solitum* differs from *P. palitans* by darker green conidia and a more orange reverse on YES.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth to slightly rough-walled, globose to subglobose, 3.5-4.5 µm.

Phialides: Cylindrical tapering to a distinct collulum, 9-11 µm x 2.5-3.0 µm

Metulae: Cylindrical, 11-15 µm x 3-3.5 µm

Rami: Cylindrical, 12-18 µm x 3.5-4.2 µm

Stipes: Rough-walled, 200-400 µm x 3.5-4.2 µm

Synnemata or fasciculation: None

Sclerotia: None

Colony texture on CYA: Velutinous

Conidium colour on CYA: Dark blue green to green

Exudate droplets on CYA: Often present, clear to light yellow (rarely brown)

Reverse colour on CYA: Cream to light beige

Reverse colour on YES: Yellow to orange

Diffusible colour: None

Ehrlich reaction: None

Odour and volatile metabolites: Isobutanol, isopentanol, 2-methyl-isoborneol (Larsen & Frisvad, 1995)

Extrolites: 1) Palitantin, 2) Compactins and solistatin, 3) Cyclopeptin, dehydrocyclopeptin, cyclopenin, cyclopenol., viridicatol, viridicatin

Growth on creatine: Good to very good

Acid and base production on creatine: Under colony or good, base production poor or delayed

Growth on UNO: Very good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 16-34 mm; MEA: 14-26 mm;

YES: 25-39 mm; CREA: 6-22 mm; Cz: 12-27 mm, OAT:

17-29 mm; CYAS: 30-38 mm; CzBS: 5-23 mm; CzP: 0 mm; UNO: 7-24 mm; DG18: 27-32 mm

Diam., CYA, 1 week: 5°C: 3-5 mm; 15°C: 18-30 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.7-0.9], halotolerant

CYA15°C/CYA 25°C: 0.9 [0.7-1.1]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.9 [0.3-1.4]

CZP/CZ: 0

Distribution: Denmark, Greenland, Svalbard, Norway, Sweden, United Kingdom, Netherlands, Germany, France, Russia, USA, BC, Canada

Ecology and habitats: Refrigerated dry meat, cheese, apples, pears, nuts

Biotechnological applications: Used for production of compactin, a cholesterol lowering agent. Compactin also has an antifungal effect. Present on naturally fermented lamb meat on Faroe Islands, but not used deliberately.

Biodeterioration & phytopathology: An important apple rotting organism (Frisvad, 1981; Pitt *et al*, 1991; Sanderson and Spotts, 1995). It may cause spoilage of cheese (Hocking and Faedo, 1992; Lund *et al.*, 1995)

Mycotoxins and mycotoxins: Unknown

Typical cultures: IBT 21545 = CBS 147.86, ex fruit of *Malus sylvestris*, Denmark (**Y**); IBT 21838 = CBS 109828, ex mouldy cheese, Denmark; IBT 22505 = CBS 109827, ex waste, Germany; IBT 23267 = CBS 500.73 = VKM F-1751 = ATCC 24727 = IMI 287746, ex *Malus sylvestris*, Russia (*P. mali*); IBT 3950 = IBT 23182 = CBS 487.75 = IMI 291192, ex meat product, Germany (*P. verrucosum* var. *melanochlorum* & *P. melanochlorum*); IBT 23035 = CBS 146.86, ex fruit of *Malus sylvestris*, Denmark; IBT 22583 = CBS 112019, ex wheat bread, Italy; IBT 14859 = CBS 112053, ex Manchego cheese, Spain; CBS 488.75 = IMI 291196, ex meat product, Germany; CBS 489.75 = IMI 291198, ex meat product, Germany; CBS 470.84 = IMI 285509 = FRR 2928, ex tuber of *Helianthus tuberosus*, Denmark; CBS 140.86, ex surface of *Malus sylvestris*, Denmark; CBS 141.86, ex air, Denmark; CBS 142.86, ex mouse nest, Denmark; CBS 143.86, ex mouldy salami, Denmark; CBS 143.86, ex mouldy salami, Denmark; CBS 144.86, ex soil, Sweden; CBS 145.86, ex mouldy peas, Denmark; CBS 422.89 = CBS 423.89 = FRR 955 = IMI 134650 = MUCL 29088 = MUCL 29183 = NRRL 954 = NRRL 955, ex fruit, Norway (*P. majusculum*); CBS 109275 = IBT 19846, ex French cheese, CBS 109276 = IBT 19803, ex French cheese.



Fig. 75. *Penicillium solitum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

***P. thymicola* Frisvad & Samson, sp. nov.**

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Verrucosa*

Type: Herb. CBS 111225

Culture ex type: CBS 111225 = IBT 5891, ex thyme, Greece (T)

Diagnostic features: Green rough-walled conidia, verrucolone, alantrypinone, fumiquinazoline F, halotolerant and psychrotolerant

Similar species: *P. thymicola* differs from *P. verrucosum* and *P. nordicum* by rough-walled conidia and a yellow reverse on CYA.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Rough-walled, globose to subglobose, 2.6-3.2 µm.

Phialides: Cylindrical tapering to a distinct collulum, 7-9 µm x 2.5-3.0 µm

Metulae: Cylindrical, 8-14 µm x 3.2-4.4 µm

Rami: Cylindrical, 10-20 µm x 3.5-4.5 µm

Stipes: Rough-walled, 200-500 µm x 3.5-4.2 µm

Synnemata or fasciculation: none

Sclerotia: None

Colony texture: Velutinous

Conidium colour on CYA: Green

Exudate droplets on CYA: None or yellow droplets

Reverse colour on CYA: Yellow

Reverse colour in YES: Yellow to orange

Diffusible colour: None

Ehrlich reaction: Yellow green

Odour and volatile metabolites: 2-methyl-isoborneol (Larsen *et al.*, 2001)

Extrolites: 1) Verrucolone & PC-2, 2) Daldinine D, 3) Fumiquinazoline F, 4) Alantrypinone and serantrypinone, 5) Anacine

Growth on creatine: Weak

Acid and base production on creatine: acid under colony, no base

Growth on UNO: Good

Growth on nitrite: Good

Abiotic factors:

Diam., 1 week, 25°C: CYA: 9-20 mm; MEA: 8-17 mm; YES: 15-26 mm; CREA: 5-13 mm; Cz: 7-12 mm, OAT: 8-13 mm; CYAS: 24-30 mm; CzBS: 2-10 mm; CzP: 0 mm; UNO: 6-11 mm; DG18: 18-21 mm

Diam., CYA, 1 week: 15°C: 19-24 mm; 30°C: 2-6 mm; 37°C: 0 mm

CYA/CYAS: 0.6 [0.4-0.7], halotolerant

CYA15°C/CYA 25°C: 1.4 [1.0-2.3], psychrotolerant

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.6 [0.3-1.0]

CZP/CZ: 0

Distribution: Czech Republic, Greece, Sudan, Wyoming (USA)

Ecology and habitats: Thyme and other herbs, sorghum, soil under cottonwood

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: The toxicity of the extrolites of *P. thymicola* is unknown.

Typical cultures: IBT 21560 = CBS 111226, ex air of archive, Moravia, Czech Republic, Czech Republic (Y); IBT 5254 = CBS 111227, ex sorghum, Sudan; IBT 5812 = CBS 111224; herb, Greece; IBT 16332 = CBS 111223, ex soil under *Populus angustifolia* in creek, Arlington, Wyoming, USA.

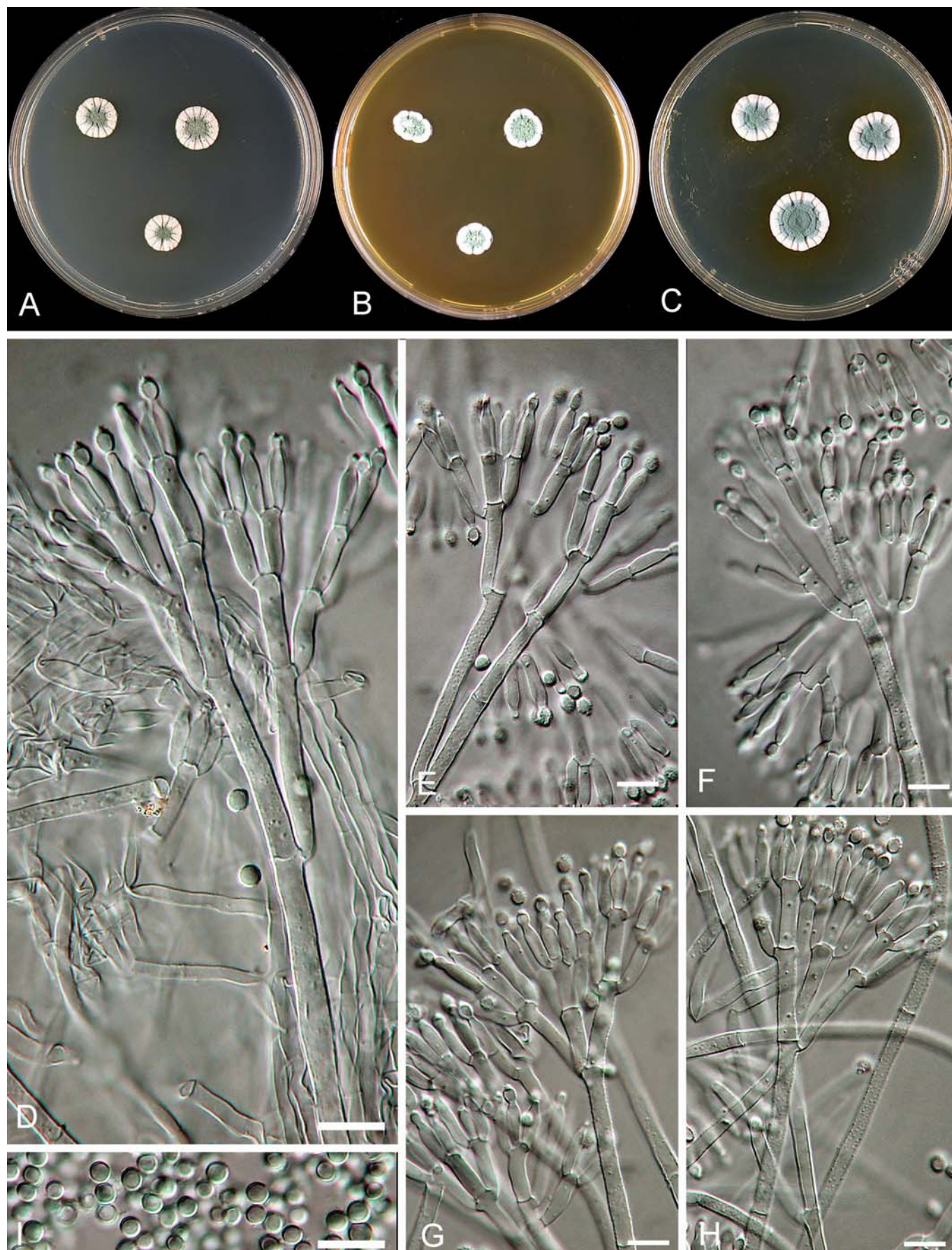


Fig. 76. *Penicillium thymicola*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. tricolor Frisvad, Seifert, Samson & Mills, Can. J. Bot. **72**: 937, 1994

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Viridicata*

Type: Herb. DAOM 216240

Culture ex type: CBS 635.93 = IBT 12493 = DAOM 216240, ex *Triticum aestivum*, Saskatchewan, Canada (T)

Diagnostic features: Terrestrial acid, xanthomegnin, viomellein, vioxanthin, smooth-walled conidia, rough walled stipes, grey (green) conidia, yellow brown reverse on CYA and YES

Similar species: *P. tricolor* differs from other members of series *Viridicata* by producing grey green conidia and a brown reverse on YES.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface and aerial hyphae

Conidia: Smooth-walled, globose to subglobose, 2.6-3.4 µm.

Phialides: Flask-shapes tapering to a distinct collulum, 7-9 µm x 2.2-2.8 µm

Metulae: Cylindrical apically swollen, 9.5-13 µm x 3.2-4.2 µm

Rami: Cylindrical, 15-25 µm x 3.2-4.2 µm

Stipes: Rough walled, 100-450 µm x 3-4 µm

Synnemata or fasciculation: None or very weak fasciculation

Sclerotia: None

Colony texture on CYA: Velutinous

Conidium colour on CYA: Grey green

Exudate droplets on CYA: Copious, brown

Reverse colour on CYA: Dark yellow brown

Reverse colour on YES: Yellow brown

Diffusible colour on CYA: light yellow brown

Ehrlich reaction: None

Odour and volatile metabolites: Isobutanol, isopentanol, 1-octene-3-ol, 3-octanone, 3-octanol, isobutyl acetate, 1-octene, styrene, γ-hexalactone (Larsen and Frisvad, 1995)

Extrolites: 1) Terrestrial acid, 2) Xanthomegnin, viomellein and vioxanthin, 3) Asteltxin, 4) Puberuline and verrucofortune

Growth on creatine: Weak

Acid and base production on creatine: Good acid production, no base

Growth on UNO: Weak

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 20-32 mm; MEA: 24-33 mm; YES: 30-40 mm; CREA: 20-28 mm; Cz: 22-30 mm, OAT: 23-30 mm; CYAS: 24-27 mm; CzBS: 21-25 mm; CzP: 0 mm; UNO: 13-16 mm; DG18: 19-23 mm

Diam., CYA, 1 week: 5°C: 2-4 mm, 15°C: 4-15 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 1.2 [1.0-1.3]

CYA15°C/CYA 25°C: 0.4 [0.1-0.5]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.8 [0.7-1.0]

CZP/CZ: 0

Distribution: Saskatchewan and Manitoba (Canada)

Ecology and habitats: Wheat and barley

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: Xanthomegnin, viomellein, vioxanthin and asteltxin, but the species seems to be rare in cereals

Typical cultures: IBT 21547 = IBT 11663 = CBS 637.93 = IMI 357306, ex *Triticum aestivum*, Saskatchewan, Canada (Y); IBT 12471 = CBS 636.93 = DAOM 216241, ex *Triticum aestivum*, Saskatchewan, Canada; IBT 12494 = CBS 101488 = IMI 357307 = DAOM 216242, ex *Triticum aestivum*, Manitoba, Canada.



Fig. 77. *Penicillium tricolor*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. tulipae Overy & Frisvad, Syst. Appl. Microbiol. **26**: 634, 2003

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Corymbifera*

Type: Herb. C 60162

Culture ex type: CBS 109555 = CBS 187.88 = IBT 3458, ex *Tulipa* sp., Denmark (T, Y)

Diagnostic features: Terrestrial acid, penitrem A, meleagrins, neoxaline, smooth-walled conidia, fast growing on all substrates, melon yellow to orange reverse on CYA

Similar species: *P. tulipae* differs from *P. albocoremium* and *P. radicola* by base production following acid production on CREA and better sporulation on YES agar.

Description:

Conidiophores terverticillate, few quarterverticillate from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 2.8-4.5 µm

Phialides: Flask-shaped tapering to a distinct collulum, 7.4 - 12.9 µm x 2.2-3.8 µm

Metulae: Cylindrical, 8.8-15.3 µm x 2.5-4.8 µm

Rami: Cylindrical, 10.6-24.9 µm x 2.6-5.1 µm

Stipes: 150-2000 µm x 3.5-4.5 µm, walls smooth to finely roughened

Synnemata or fasciculation: Loose fasciculation

Sclerotia: None

Colony texture on CYA: Velutinous to slightly floccose

Conidium colour on CYA: Greyish green to dull green

Exudate droplets on CYA: Present, clear to yellow or yellow brown

Reverse colour on CYA: Melon yellow to orange

Reverse colour on YES: Deep yellow to yellowish orange

Diffusible colour on CYA: None

Ehrlich reaction: Weak to moderate, violet

Odour and volatile metabolites: No data

Extrolites: 1) Terrestrial acid, 2) Penicillic acid (rare), 3) Chrysogine, 4) Roquefortine C, meleagrins, neoxaline, 5) Penitrem A

Growth on creatine: weak to moderate

Acid and base production on creatine: Good acid production

Growth on UNO: weak

Growth on nitrite: weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 39-48 mm; MEA: 26-40 mm; YES: 48-54 mm; CREA: 24-30 mm; Cz: 30-40 mm; OAT: 33-59 mm; CYAS: 30-40 mm; CzBS: 18-27 mm; CzP: 0 mm; UNO: 11-15 mm; DG18: 32-38 mm

Diam., 1 week: 5°C: 2-5 mm, 15°C: 28-37 mm; 30°C: 2-9 mm; 37°C: 0 mm

CYA/CYAS: 1.1 [1.0-1.3]

CYA15°C/CYA 25°C: 0.80 [0.7-0.9]

CYA30°C/CYA 25°C: 0.2 [0.1-0.2]

CZBS/CZ: 0.7 [0.6-0.9]

CZP/CZ: 0

Distribution: Denmark, the Netherlands, Korea, Germany

Ecology and habitats: *Tulipa*, *Lilium*, and *Chrysanthemum* bulbs, *Apium graveolens*, *Glycyrrhiza* sp., *Brassica oleracea*, *Helianthus tuberosus*

Biotechnological applications: None

Biodeterioration & phytopathology: Pathogenic to tulips and *Lilium*

Mycotoxins and mycotoxins: The natural occurrence of penitrem A, roquefortine C and penicillic acid may be produced in *Beta vulgaris*, *Helianthus tuberosus* etc. has yet to be determined.

Typical cultures: IBT 23036 = CBS 734.74, ex bulb of *Lilium* sp., Netherlands; IBT 10676 = CBS 111217, ex leave of *Tulipa* sp., Denmark; IBT 10687 = CBS 109552, ex agricultural soil, Germany; IBT 10631 = CBS 112431, ex *Glycyrrhiza* sp., Thailand; IBT 10691 = CBS 112432, ex *Apium graveolens*, Denmark; IBT 6173 = CBS 112433, ex *Helianthus tuberosus*, Denmark; IBT 6174, ex *Beta vulgaris*, Denmark; IBT 10632, ex *Beta vulgaris*, Denmark; IBT 10671, IBT 10675, IBT 10678, IBT 10680, IBT 15852, IBT 17812, ex *Tulipa* sp., Denmark; IBT 10674 & IBT 10686, ex *Brassica oleracea* ssp. *gemmifera*, Denmark; IBT 13024 = CBS 406.92, IBT 13025 = CBS 408.92, IBT 13029 = CBS 407.92, ex *Tulipa* sp., Korea; IBT 11648, ex *Apium graveolens*, Denmark; IBT 10681, ex *Chrysanthemum* sp., Denmark.



Fig. 78. *Penicillium tulipae*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

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

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Italica*

Type: Herb. PPEH 29001.87

Culture ex type: CBS 210.92 = IBT 18387 = IBT 23037 = CBS 261.94 = CCRC 32655, ex skin of decaying orange, Ulai, Taipei County, Taiwan (T)

Diagnostic features: Ellipsoidal to long cylindrical smooth-walled conidia, slow growth rate, neither growth nor acid on CREA, synnemata on MEA, very poor growth on CYAS

Similar species: *P. ulaiense* differs from *P. italicum* by much slower growth rates on all media and pale reverse colours on all media.

Description:

Conidiophores: Terverticillate, appressed elements, sinoid, born from surface hyphae

Conidia: Smooth-walled, cylindrical and ellipsoidal, 4.5-9.5 µm x 2.2-3.5 µm

Phialides: Cylindrical tapering to a short collulum, 9-15 µm x 3-4 µm

Metulae: Cylindrical, 10-15 µm x 3.5-4.5 µm

Rami: Cylindrical, 17-22 µm x 3.2-4 µm

Stipes: Smooth and rough walled, 50-250 µm x 4-5 µm

Synnemata or fasciculation: Synnematos, fasciculate

Sclerotia: None

Colony texture: Velutinous to strongly fasciculate, crustose

Conidium colour on CYA: Dull green to greyish green

Exudate droplets on CYA: Present, clear or none

Reverse colour on CYA: Pale to cream

Reverse colour on YES: Cream yellow to brown

Diffusible colour on CYA: None

Ehrlich reaction: None

Odour and volatile metabolites: None

Extrolites: 1) Deoxybrevianamide E and 12,13-dehydrodeoxybrevianamide E

Growth on creatine: Weak

Acid and base production on creatine: None

Growth on UNO: Weak

Growth on nitrite: Weak (one strain good growth)

Abiotic factors:

Diam., 1 week, 25°C: CYA: 13-26 mm; MEA: 13-23 mm; YES: 24-33 mm; CREA: 4-6 mm; Cz: 8-16 mm, OAT: 16-20 mm; CYAS: 0-13 mm; CzBS: 0-7 mm; CzP: 0 mm; UNO: 1-7 mm; DG18: 19-25 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 4-17 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: ≥6.6 [2-11]

CYA15°C/CYA 25°C: 0.7 [0.5-1.1]

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.2 [0-0.6]

CZP/CZ: 0

Distribution: Denmark, USA, South Africa, Taiwan

Ecology and habitats: Citrus fruits

Biotechnological applications: None

Biodeterioration & phytopathology: *P. ulaiense* produces rot in fungicide treated citrus fruits, the so-called whisker mould (Holmes *et al.*, 1994)

Mycotoxins and mycotoxins: None known

Typical cultures: IBT 23027 = CBS 136.41 = DSM 2734, ex *Citrus medica limonum*, South Africa; IBT 21548 = IBT 23038 = CBS 262.94, ex grapefruit cv. Marsh, California, USA (Y); IBT 13258 = CBS 314.97, ex apricot, Denmark; IBT 13078 = CBS 322.92, ex lemon, Denmark.

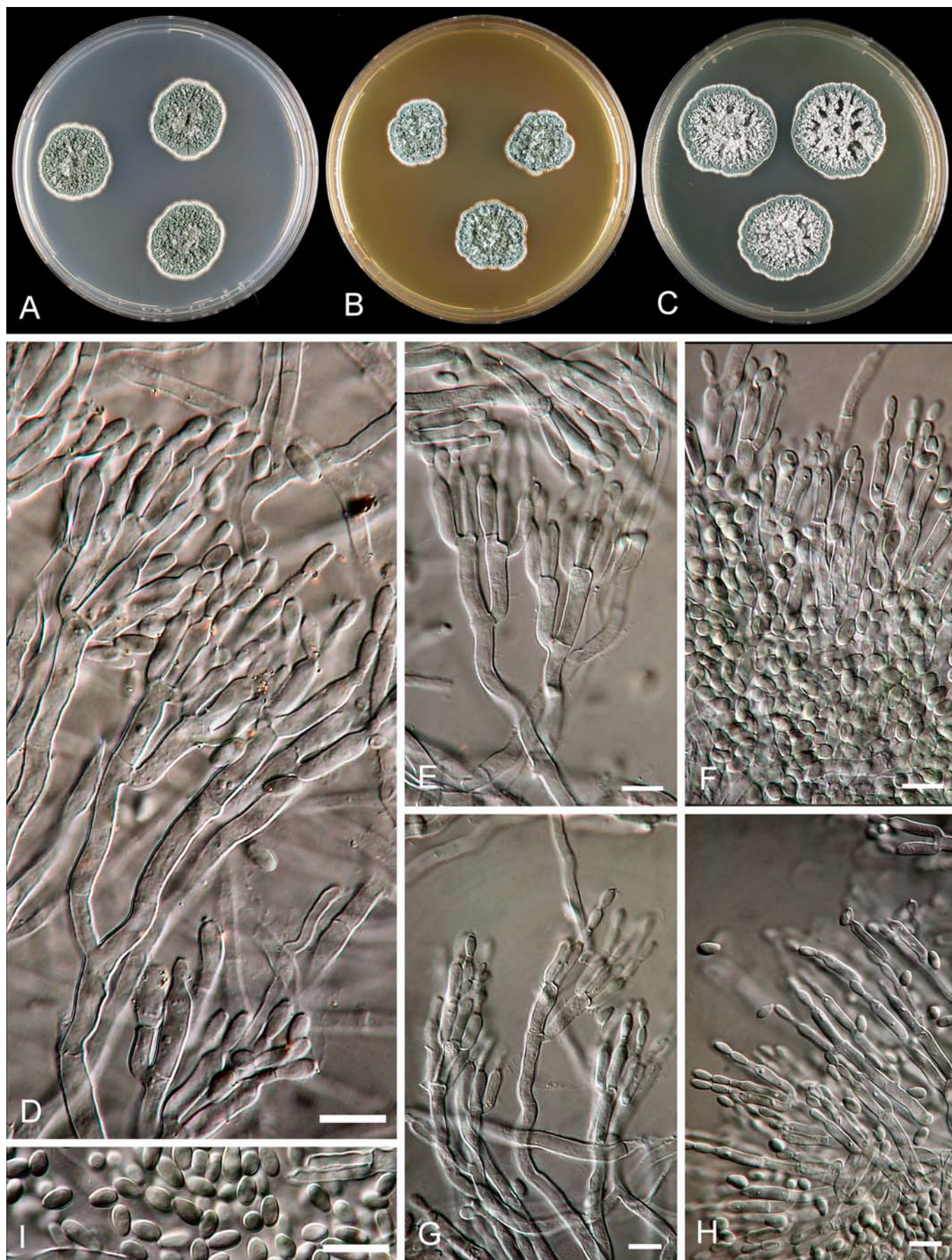


Fig. 79. *Penicillium ulaiense*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

P. venetum (Frisvad) Frisvad, Int. Mod. Tax. Meth. Pen. Asp. Clas.: 275, 2000

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Corymbifera*

Type: Herb. IMI 321520

Culture ex type: IBT 10661 = IMI 321520, ex *Armoracia rusticana*, Kgs. Lyngby, Denmark

Diagnostic features: Smooth-walled conidia, yellow brown exudates droplets and diffusible pigment,

Similar species: *P. venetum* produce conidia that are blue rather than blue green and yellow brown exudate droplets and diffusible pigment distinguishing it from *P. albocoremium*, *P. hirsutum*, *P. hordei*, *P. radicola*, and *P. tulipae*.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface hyphae

Conidia: Smooth-walled, globose to subglobose, 2.2-3.8 µm

Phialides: Cylindrical tapering to a distinct collulum, 8-12 µm x 2.4-3.2 µm

Metulae: Cylindrical, 7.5-13 µm x 3.2-4 µm

Rami: Cylindrical, 16-27 µm x 3.2-4 µm

Stipes: Rough-walled, 100-500 µm x 3.2-4 µm

Synnemata or fasciculation: weakly fasciculate

Sclerotia: None

Colony texture: Velutinous to weakly fasciculate

Conidium colour on CYA: Blue green

Exudate droplets on CYA: Copious, yellow to red brown

Reverse colour: Yellow and dark yellow brown center

Diffusible colour: Yellow brown to dark ochre

Ehrlich reaction: None

Odour and volatile metabolites: Isobutanol, 3-octanone, 1,8-cineol, isopentanol, 3-heptanone, limonene (Larsen and Frisvad, 1995)

Extrolites: 1) Terrestric acid, 2) Atrovenetins, 3) Roquefortine C, 4) Cyclopeptin, dehydrocyclopeptin, cyclopenin, cyclophenol, viridicatol, 3-methoxyviridicatin

Growth on creatine: Weak to moderate

Acid and base production on creatine: Acid under colony, no base

Growth on UNO: Weak

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 18-34 mm; MEA: 17-34 mm; YES: 34-47 mm; CREA: 15-24 mm; Cz: 15-26 mm, OAT: 23-34 mm; CYAS: 30-37 mm; CzBS: 14-23 mm; CzP: 0 mm; UNO: 14-21 mm; DG18: 19-31 mm

Diam., CYA, 1 week: 5°C: 2-4 mm; 15°C: 26-33 mm; 30°C: 2-7 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.7-1.0]

CYA15°C/CYA 25°C: 1.1 [0.8-1.3]

CYA30°C/CYA 25°C: 0.2 [0.1-0.3]

CZBS/CZ: 0.9 [0.9-1.0]

CZP/CZ: 0

Distribution: Denmark, the Netherlands, United Kingdom, Canada, Korea, Montana (USA), Transvaal (South Africa), Thailand

Ecology and habitats: *Iris* spp., *Asparagus*, *Ornithogalum* spp., *Hyacinthus* spp., *Armoracea* spp.

Biotechnological applications: None

Biodeterioration & phytopathology: Can cause a destructive rot in flower bulbs, pathogenic to *Iris* and *Ornithogalum*.

Mycotoxins and mycotoxins: Roquefortine C is produced, but *P. venetum* is rare on foods.

Typical cultures: IBT 21549 = CBS 405.92, ex *Iris* sp., Korea (Y); IBT 23039 = CBS 201.57 = ATCC 16025 = CECT 2812 = IMI 019759 = MUCL 19012 = QM 840, ex bulb of *Hyacinthus* sp., United Kingdom; IBT 23040 = CBS 253.96, ex *Asparagus*; IBT 16215 = IBT 16127 = CBS 110096, Canada; IBT 22111, ex *Hyacinthus* sp., Denmark; IBT 15191 = CBS 110095, ex flower bulb, Denmark; IBT 16308 = CBS 110094, ex metal polluted soil, pH 2.5-3.5, under moss, Glengarry Creek, Montana, USA; IBT 23814 = CBS 112441, ex *Asparagus*; CBS 502.75 = IMI 068414, ex *Ornithogalum* sp., Transvaal, South Africa; CBS 402.92, ex *Iris* sp., Korea; CBS 403.92, ex *Iris* sp., Korea; CBS 404.92, ex *Iris* sp., Korea; IBT 4662 = IMI 321519, ex Liquirice root, Thailand, IBT 24614, ex Hyacinth flower, Denmark.

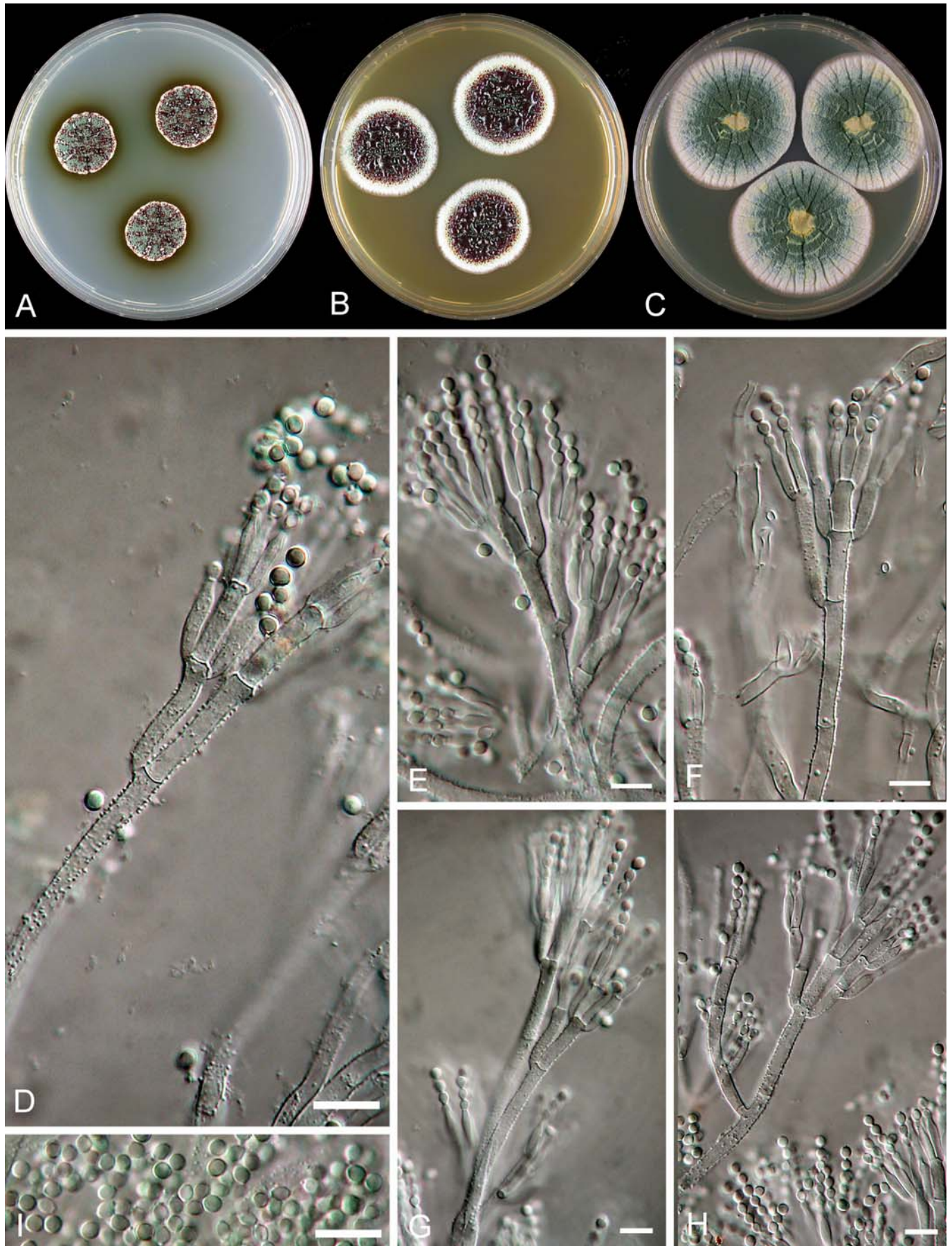


Fig. 80. *Penicillium venetum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. verrucosum Dierckx, Ann. Soc. Scient. Brux.
25: 88, 1901

In *Penicillium* subgenus *Penicillium* section *Viridicata*
series *Verrucosa*

Type: Herb. IMI 200310

Culture ex type: CBS 603.74 = ATCC 48957 =ATHUM
2897 = CECT 2906 = FRR 965 = IBT 4733 = IBT 12809 =
IMI 200310 = MUCL 28674 = MUCL 29089 = MUCL
29186 = NRRL 965 (T)

Diagnostic features: Ochratoxin A, citrinin, verrucolone,
verrucins, smooth-walled conidia, red brown reverse on
YES, slow growing on all media, no growth at 30°C

Similar species: *P. verrucosum* has a red-brown to terra-
cotta reverse on YES agar distinguishing it from *P. nordi-*
cum and *P. thymicola*.

Description:

Conidiophores: Terverticillate, appressed elements, born
from surface or subsurface hyphae

Conidia: Rough-walled, globose to subglobose, 2.6-3.2 µm.

Phialides: Cylindrical tapering to a distinct collulum, 7-9
µm x 2.2-2.8 µm

Metulae: Cylindrical, 8-13 µm x 3-4 µm

Rami: Cylindrical, 12-22 µm x 3-4 µm

Stipes: Rough walled, 200-450 µm x 3-4 µm

Synnemata or fasciculation: weakly fasciculate

Sclerotia: None

Colony texture on CYA: Velutinous to floccose to weakly
fasciculate

Conidium colour on CYA: Green

Exudate droplets on CYA: Copious, clear

Reverse colour on CYA: Cream yellow, often with brown
center

Reverse colour on YES: Red brown (terracotta)

Diffusible colour on CYA: None

Ehrlich reaction: None

Odour and volatile metabolites: 2-pentanone, 2-butanone,
isobutanol, isopentanol, 3-octanone (Larsen & Frisvad,
1995)

Extrolites: 1) Verrucolone = arabenoic acid, 2) Ochratoxin
A, 3) Citrinin, 4) Verrucin A & B

Growth on creatine: Weak

Acid and base production on creatine: None

Growth on UNO: Very good

Growth on nitrite: Very good

Abiotic factors:

Diam., 1 week, 25°C: CYA: (9-) 11-24 mm; MEA: (7-) 10-
22 mm; YES: (14-) 24-32 mm; CREa: 12-15 mm; Cz: 11-

16 mm, OAT: 10-14 mm; CYAS: 21-27 mm; CzBS: 3-8
mm; CzP: 0 mm; UNO: 9-13 mm; DG18: 25-31 mm

Diam., CYA, 1 week: 5°C: 2-5 mm, 15°C: 17-23 mm;
30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 0.7 [0.6-0.9], halotolerant

CYA15°C/CYA 25°C: 1.1 [1.0-1.2], psychrotolerant

CYA30°C/CYA 25°C: 0

CZBS/CZ: 0.5 [0.3-0.9]

CZP/CZ: 0

Distribution: Norway, Denmark, Sweden, United King-
dom, Germany, Poland, Netherlands, Belgium, Switzerland,
France, Portugal, Italy, Canada, USA, Russia; most com-
mon in cold temperate regions

Ecology and habitats: barley, oats, rye, wheat, cheese
(Lund and Frisvad, 2003; Staub, 1930)

Biotechnological applications: None

Biodeterioration & phytopathology: Deteriorate cereals
and produce brown spots on cheese (Staub, 1930)

Mycotoxicoeses and mycotoxins: Porcine mould nephrosis
is cause primarily by *P. verrucosum* in Northern temperate
regions (Lund and Frisvad, 2003). *P. verrucosum* was a
possible candidate to be involved in Balkan endemic neph-
ropathy. However, because *P. nordicum* is much more
prevalent in the Balkan countries and grows on dried meat
products, this species may play a contributing role to Balkan
Endemic Nephropathy in combination with other species in
series *Viridicata*.

Typical cultures: IBT 21550 = CBS 223.71, ex white bean,
Ontario, Canada (Y); IBT 5088 = CBS 321.90, ex *Triticum*
aestivum, United Kingdom; IBT 5061 = CBS 226.90, ex
Hordeum vulgare, Denmark; IBT 21573 = CBS 112485, ex
Hordeum vulgare, Denmark; IBT 22025 = CBS 112577 =
VTT D98495, ex *Hordeum vulgare*, Finland; IBT 22112 =
CBS 112486, ex wheat, United Kingdom; IBT 22682 =
CBS 112488, ex soil in spruce forest, 4 km east of Ze-
lenogorsk, Russia; IBT 22699 = CBS 111026, ex wheat,
Sweden; CBS 302.48 = IBT 3434 = IBT 4738 = IBT 6731 =
ATCC 10422 = IFO 8109 = IMI 039766 = NRRL 844 =
QM 7499, ex Swiss cheese (*P. casei*); CBS 222.71, Canada;
CBS 224.71 & CBS 225.71 & CBS 226.71G, ex unshelled
nut of *Arachis hypogea*, Canada; IBT 14257 = CBS
226.71A, and CBS 227.71B-E, ex toxic white beans, On-
tario, Canada; CBS 226.71F, ex poultry feed, Saskatche-
wan, Canada; CBS 221.90 = IBT 5007, ex *Hordeum vul-*
gare, Denmark; CBS 321.90, ex *Triticum aestivum*, United
Kingdom; CBS 815.96, ex rye, Gotland, Sweden.

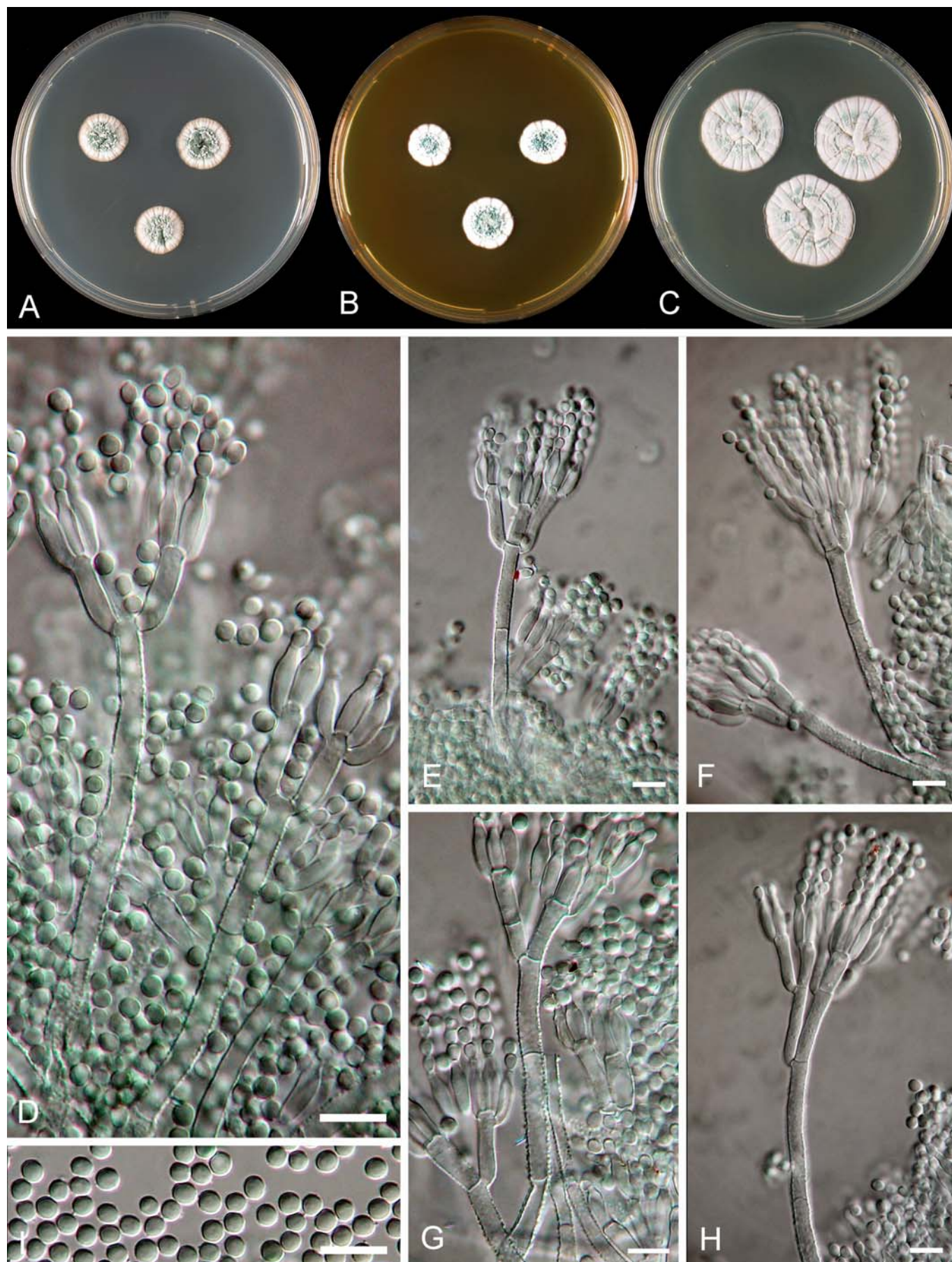


Fig. 81. *Penicillium verrucosum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μm.

P. viridicatum Westling, Ark. Bot. **11**: 88, 1911

In *Penicillium* subgenus *Penicillium* section *Viridicata* series *Viridicata*

Type (neo): Herb. IMI 039758

Culture ex type: CBS 390.48 = IBT 23041 = IMI 039758ii = ATCC 10515 = IFO 7736 = FRR 963 = NRRL 963 = IBT 4674 = IBT 3455 = IBT 5151 = QM 7683, ex air, Washington DC, USA (T)

Diagnostic features: Xanthomegnin, viomellein, vioxanthin, brevianamide A, viridic acid, penicillic acid, finely rough-walled conidia, yellow green to pure green conidia

Similar species: *P. viridicatum* has pure green conidia distinguishing it from all other species in series *Viridicata*, except *P. melanoconidium*, which, however, has dark green conidia. *P. viridicatum* produce acid on CREA and a bright yellow reverse on YES in contrast to *P. verrucosum* and *P. nordicum*.

Description:

Conidiophores: Terverticillate, appressed elements, born from subsurface and aerial hyphae

Conidia: Finely rough-walled, globose to subglobose, 2.6–3.4 µm.

Phialides: Flask-shapes tapering to a distinct collulum, 7–9 µm x 2.2–2.8 µm

Metulae: Cylindrical apically swollen, 9.5–13 µm x 3.2–4.2 µm

Rami: Cylindrical, 15–25 µm x 3.2–4.2 µm

Stipes: Rough walled, 200–450 µm x 3–4 µm

Synnemata or fasciculation: weakly fasciculate

Sclerotia: None

Colony texture on CYA: Velutinous to weakly fasciculate

Conidium colour on CYA: Green

Exudate droplets on CYA: clear to yellow droplets

Reverse colour: Yellow to orange brown

Diffusible colour: None or orange brown

Ehrlich reaction: Weak, yellow, pink or brown

Odour and volatile metabolites: 3-octanone, 3-heptanone, 1-octen-3-ol, 3-octanol (Larsen & Frisvad, 1995)

Extrolites: 1) Penicillic acid, 2) Xanthomegnin, viomellein and vioxanthin, 3) Brevianamide A, 4) Viridic acid, 5) Viridamine

Growth on creatine: Weak

Acid and base production on creatine: Good acid production, no base

Growth on UNO: Weak to moderate

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 19–35 mm; MEA: 25–34 mm; YES: (16–) 25–40 mm; CREA: 17–24 mm; Cz: 19–27 mm,

OAT: 21–32 mm; CYAS: 33–40 mm; CzBS: 16–25 mm; CzP: 0 mm; UNO: 9–18 mm; DG18: 22–33 mm

Diam., CYA, 1 week: 5°C: 2–4 mm, 15°C: 21–24 mm; 30°C: 6–18 mm; 37°C: 0 mm

CYA/CYAS: 0.8 [0.7–0.9], halotolerant

CYA15°C/CYA 25°C: 0.8 [0.7–0.9]

CYA30°C/CYA 25°C: 0.5 [0.2–0.6]

CZBS/CZ: 0.9 [0.8–1.1]

CZP/CZ: 0

Distribution: Denmark, Sweden, Great Britain, France, Bulgaria, Ohio, Michigan, Texas, Kansas, Indiana, Washington DC, Pennsylvania, Wisconsin, Montana, Arizona (USA), Canada, Ethiopia, Taiwan

Ecology and habitats: Corn, wheat, barley, beans, peas

Biotechnological applications: None

Biodeterioration & phytopathology: Deteriorates cereals

Mycotoxicoeses and mycotoxins: Xanthomegnin, viomellein, vioxanthin, and viridic acid are mycotoxins that can be potentially produced by *P. viridicatum* in cereals.

Typical cultures: IBT 21551 = IBT 15053 = CBS 101034 (Y), ex beans, Bulgaria; IBT 14246 = CBS 109826 = IMI 351305, ex cereal, Bulgaria; IBT 16939 = CBS 109823, ex *Triticum aestivum*, Germany; IBT 5145 = CBS 109825 = NRRL A-26909, ex mound of kangaroo rat, 8 km east of Portal, Arizona, USA; IBT 12824 = CBS 109824 = NRRL 3600, ex wheat, Pennsylvania, USA; IBT 12817 = NRRL 3586, ex wheat flour, Michigan, USA; IBT 18375 = CBS 112052 = CCRC 32632, ex corn seed, Alien, Kaosiung County, Taiwan; CBS 101473 = IBT 11636, ex *Hordeum vulgare*, Denmark; CBS 101474 = NRRL 5569 = FRR 1636 = IBT 5193, ex corn, Kansas, USA; CBS 101475 = IBT 5192, ex piece of a branch, Ethiopia; CBS 101476 = IBT 11664, ex field pea, Denmark; CBS 101477 = IBT 14245 = IMI 351306, ex cereal, Bulgaria; IBT 12823 = NRRL 2028 = NRRL 959, ex cultivated soil, Woburn, Bedford, UK (*P. olivinoviride*), IBT 5292 = NRRL 961, Buenos Aires, Argentina (as *P. olivinoviride*), IBT 12814 = CBS 356.48 = IMI 039823 = FRR 871 = NRRL 871 = ATCC 10474 = IBT 12814 = CBS 246.32 = IMI 092264 = IFO 5760 = MUCL 29155, ex corn, France (*P. ochraceum* and *P. olivicolor*), IBT 5289 = NRRL 870 = FRR 870 = ATCC 10112, ex diseased corn kernels, Cleveland, Ohio, USA (as *P. ochraceum*); IBT 5145 = NRRL A-26909, ex mound of *Dipodomys spectabilis*, 6 east of Portal, Arizona, USA; IBT 12818 = NRRL A-15402, ex wheat flour, Texas, USA; IBT 12825 = NRRL A-18563, ex wheat, Michigan; IBT 12829 = NRRL 869, ex diseased corn kernels, Cleveland, Ohio, USA (as *P. ochraceum*).

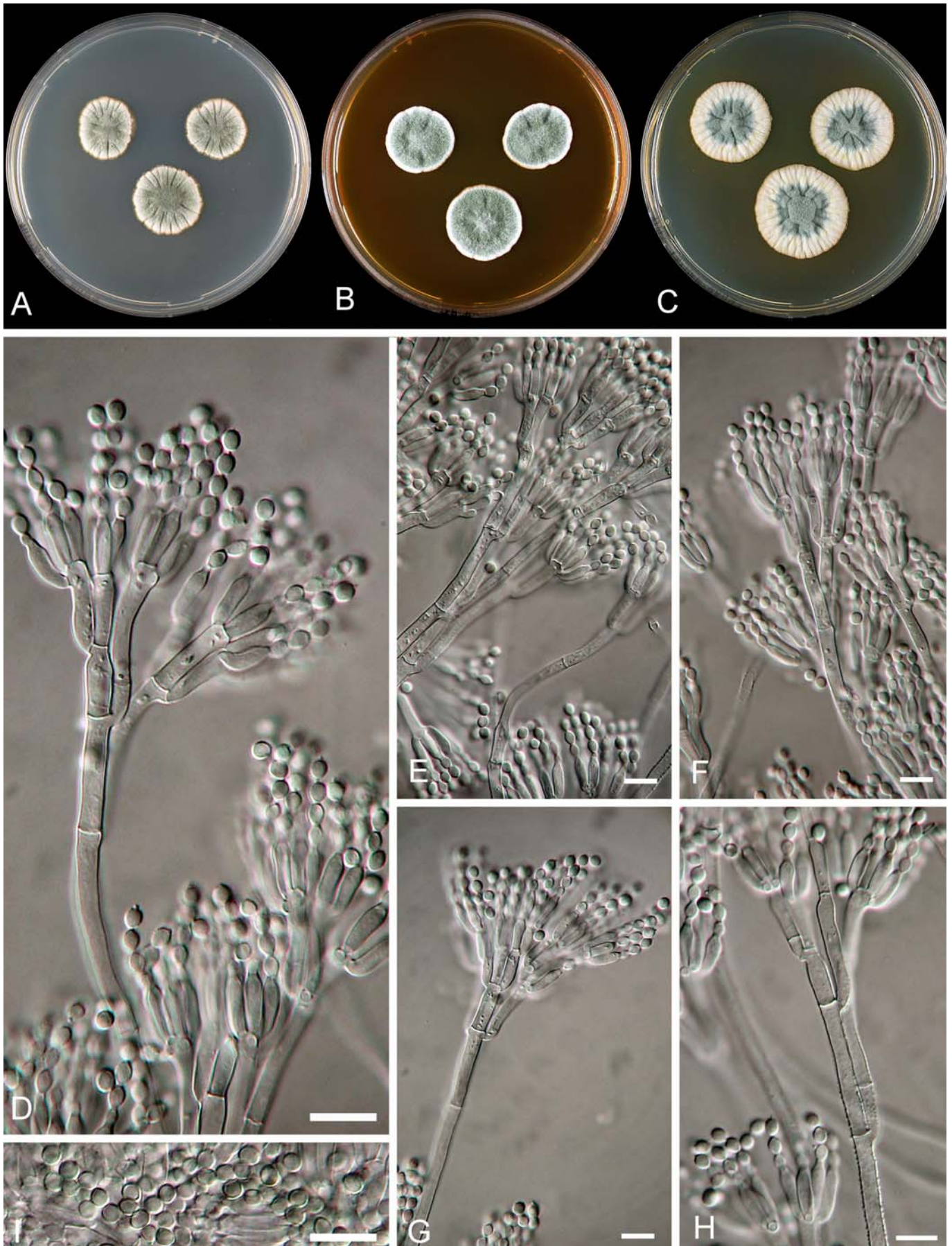


Fig. 82. *Penicillium viridiactum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 μ m.

P. vulpinum (Cooke & Masee) Seifert & Samson, Adv. Pen. Asp. Syst.: 144, 1985

In *Penicillium* subgenus *Penicillium* section *Penicillium* series *Claviformia*

Type: "on dung", *s. coll.*, in herb Cooke (K)

Epitype: Herb. CBS 126.23 (proposed here)

Culture ex epitype: CBS 126.23 = ATCC 10426 = IMI 040237 = NRRL 2031 = VKM F-257 (*P. claviforme*) (**epiT**)

Diagnostic features: Patulin, roquefortine C, meleagrins, oxaline, broadly ellipsoidal smooth-walled conidia, long synnemata with pink stipes

Similar species: *P. vulpinum* has capitulate synnemata with pink stipes in contrast to *P. clavigerum*, which has acicular synnemata without a differentiated capitulum.

Description:

Conidiophores: Terverticillate, sinoid, appressed elements, but divergent rami born on synnemata

Conidia: Smooth-walled, ellipsoidal, 4-4.5 µm x 3-3.5 µm.

Phialides: Cylindrical tapering to a sort collulum, 8-11 µm x 2.2-3 µm

Metulae: Cylindrical, 9-12 µm x 2-3 µm (occasionally apically inflated)

Rami: Cylindrical, 10-27 µm x 3-4 µm

Stipes: Smooth walls, 100-200 µm x 2.5-3.5 µm

Synnemata or fasciculation: Long conspicuous capitulate synnemata (2-5 mm)

Sclerotia: None

Colony texture on CYA: Coremiform

Conidium colour on CYA: Greenish grey

Exudate droplets on CYA: Clear

Reverse colour on CYA: Cream to reddish brown

Reverse on YES: Cream yellow to beige

Diffusible colour on CYA: None

Ehrlich reaction: None, yellow or weak violet reaction in few strains

Odour and volatile metabolites: 1-methoxy-3-methylbenzene, 1,8-cineol, 1,3-octadiene (2 isomers), beta-bisabolene?, 1,3,6-octatriene and two isomers, 6-methyl-5-heptene-2-one, 2-methyl-phenol, 1-hexene, 1-heptene, 1-octene, sabinene, beta-myrcene, limonene, alpha-terpinene, 2-methyl-phenol, 2-methyl-isoborneol, ethyl acetate, isobutanol, isopentanol, isobutyl acetate (Larsen & Frisvad, 1995)

Extrolites: 1) Asteric acid, 2) Patulin, 3) Pachybasin, 4) lichexanthone, 5) Cyclopeptin, dehydrocyclopeptin,

cyclopenin, cyclopenol, viridicatin, viridicatol, 6) Roquefortine C / D, meleagrins, oxaline 7) Cyclopamin

Growth on creatine: Very good

Acid and base production on creatine: moderate acid

Growth on UNO: Weak to good

Growth on nitrite: Weak

Abiotic factors:

Diam., 1 week, 25°C: CYA: 17-43 mm; MEA: 12-33 mm; YES: 26-48 mm; CREA: 11-23 mm; Cz: 11-22 mm, OAT: 19-38 mm; CYAS: 18-33 mm; CzBS: 0-5 mm; CzP: 0 mm; UNO: 10-18 mm; DG18: 10-19 mm

Diam., CYA, 1 week: 5°C: 2-3 mm, 15°C: 17-23 mm; 30°C: 0 mm; 37°C: 0 mm

CYA/CYAS: 0.9 [0.8-1.0]

CYA15°C/CYA 25°C: 0.8 [0.6-1.0]

CYA30°C/CYA 25°C: 0.05 [0-0.3]

CZBS/CZ: 0.5 [0.2-0.8]

CZP/CZ: 0

Distribution: Denmark, Netherlands, British Isles, United Kingdom, Poland, Germany, Austria, Czech Republic, Russia, Turkey, Cyprus, Israel, Syria, India, Taiwan, USA, Canada, Guinea, Colombia, Chile, Australia

Ecology and habitats: Dung, insects, soil (see Domsch *et al.*, 1980, as *P. claviforme*)

Biotechnological applications: None

Biodeterioration & phytopathology: Unknown

Mycotoxins and mycotoxins: Patulin, roquefortine C

Typical cultures: IBT 21552 = IBT 11932 = CBS 309.97 = CBS 101133 (Y), melon, Denmark; CBS 305.63 = IBT 10605 = IBT 3228 = IBT 10605 = MUCL 3132, ex greenhouse soil, Belgium; IBT 3099 = CBS 488.84 = IMI 285528, *Hordeum vulgare*, Denmark; IBT 10606 = IBT 3227 = CBS 308.97 = CBS 218.89 = ATCC 58612 = IMI 293198, insect, Denmark; IBT 19370 = CBS 110772 = IMI 300363, ex soil, Meghalaya, India; IBT 6311 = CBS 110773, United Kingdom; IBT 23042 = CBS 344.54, owl pellet?, Netherlands; IBT 23392 = CBS 112442, ex ant farm; CBS 305.65, ex insect, Amsterdam, Netherlands; CBS 295.65, ex soil, Savelsbos, Netherlands; NRRL 1001 (*Coremium silvaticum*); NRRL 2149, Germany; NRRL 1002.

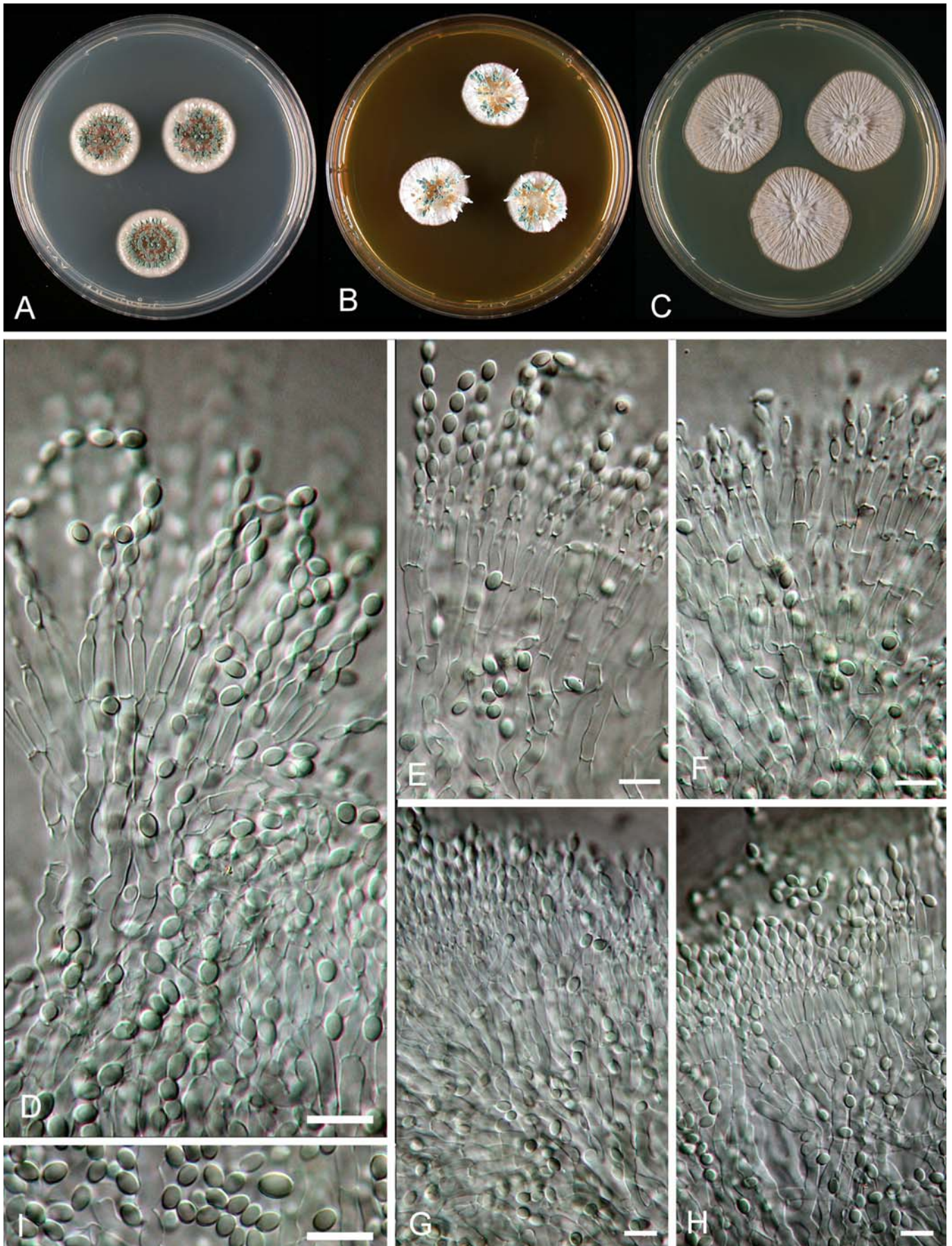


Fig. 83. *Penicillium vulpinum*. 7-day old colonies on A. CYA, B. MEA, C. YES, D-H. Conidiophores. I. Conidia. White bar = 10 µm.

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