Mycotoxins, drugs and other extrolites produced by species in *Penicillium* subgenus *Penicillium*

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Abstract: The 58 species in *Penicillium* subgenus *Penicillium* produce a large number of bioactive extrolites (secondary metabolites), including several mycotoxins. An overview of these extrolites is presented with original references to the reports on their production and their chemical constitution. 132 extrolite families are reported from the subgenus with an average of 5 extrolite families per species. This is an underestimate as several pigments, volatiles and uncharacterized extrolites are not included in this average. Several reported producers are reidentified and new producers of known extrolites are reported for the first time. Several extrolites are unique for one species, but most of the metabolites are produced by more than one species. The most widespread extrolites were roquefortine C, which is produced by 25 species, the cyclopenins that are produced by 17 species, patulin which is produced by 13 species, penicillic acid which is produced by 10 species, and terrestric acid and 2-methyl isoborneol that are produced by 8 species. Most species produce both polyketides, terpenes and amino acid derived extrolites and a large number of the species produce bioactive metabolites. The nephrotoxic mycotoxin ochratoxin A is produced by *P. verrucosum* and *P. nordicum*, and another nephrotoxin, citrinin, is produced by *P. expansum, P. radicicola* and *P. verrucosum*. Patulin is produced by *P. carneum, P. clavigerum, P. concentricum, P. coprobium, P. dipodomyicola, P. expansum, P. glandicola, P. gladioli, P. griseofulvum, P. marinum, P. paneum, P. sclerotigenum* and *P. vulpinum*. Another polyketide mycotoxin, penicillic acid, is produced by *P. aurantiogriseum, P. carneum, P. cyclopium, P. freii, P. melanoconidium, P. neoechinulatum, P. polonicum, P. radicicola, P. tulipae* and *P. viridicatum*. The tremorgenic verrucosidin is produced by *P. aurantiogriseum, P. melanoconidium* and *P. polonicum*, while another tremorgen, penitrem A, is produced by *P. carneum, P. clavigerum, P. crustosum, P. flavigenum, P. glandicola, P. melanoconidium* and *P. tulipae*. Asteltoxin is produced by *P. cavernicola, P. concentricum, P. confertum, P. formosanum* and *P. tricolor*. The mutagenic mycotoxin botryodiploidin is produced by *P. brevicompactum* and *P. paneum*. The chaetoglobosins are produced by *P. discolor, P. expansum* and *P. marinum*. The cytotoxic communesins are produced by *P. expansum* and *P. marinum*. Cyclopiazonic acid is produced by *P. camemberti, P. commune, P. dipodomyicola, P. griseofulvum* and *P. palitans*. The fumitremorgins, verruculogen, isochromantoxins and viriditoxin are produced by *P. mononematosum*. The immunosuppressive extrolite mycophenolic acid is produced by *P. bialowiezense, P. brevicompactum, P. carneum* and *P. roqueforti*. PR-toxin is produced by *P. chrysogenum* and *P. roqueforti*. Secalonic acid is produced by *P. chrysogenum* and *P. confertum*. The territrems are produced by *P. cavernicola* and *P. echinulatum*. Viridic acid is produced by *P. nordicum* and *P. viridicatum*, while viridicatumtoxin is produced by *P. aethiopicum*. The hepatotoxins xanthomegnin, viomellein and vioxanthin are produced by *P. clavigerum, P. cyclopium, P. freii, P. melanoconidium, P. tricolor* and *P. viridicatum*. Apart from these mycotoxins several alkaloids, such as festuclavine, rugulovasine, and roquefortine C are also produced by several species in *Penicillium* subgenus *Penicillium*. In most cases these extrolites are produced consistently by all isolates examined in a species. The important antibiotic penicillin is produced by all members of series *Chrysogena* and *P. griseofulvum*. The cholesterol-lowering agent compactin is produced by *P. solitum* and *P. hirsutum*. A large number of interesting lead-compounds are produced by species in the subgenus.

Keywords: secondary metabolites, drugs, mycotoxins, *Penicillium* subgenus *Penicillium*

Introduction

Some of the most well known extrolites are produced by species in *Penicillium* subgenus *Penicillium*, the most famous and economically important being penicillins produced by *Penicillium chrysogenum* (Raper and Thom, 1949), mycophenolic acid produced by *Penicillium brevicompactum* (Bentley, 2000) and compactins produced by *Penicillium solitum* (Frisvad and Filtenborg, 1989). Since the start of the discovery of these very important pharmaceuticals, this scientific field has been plagued by the problem that the producers of these drugs have been misidentified initially. Gosio (1896) called the producer of mycophenolic acid *P. glaucum*, Fleming (1929) called the producer of penicillin *P. rubrum*, and Brown *et al*. (1976) and Endo *et al*. (1976) identified their fungi producing compactins as *P. brevicompactum* and *P. citrinum*, respectively. Being an unusual practice, penicillin was named after the genus, and the term rubrin was fortunately never coined. In most other cases, the name of a pharmaceutical or mycotoxin has been coined to the originally discovered isolate, and this is of course unfortunate, when this isolate is misidentified. *Penicillium* subgenus

Penicillium is also well known because a large number of its species produce mycotoxins, and also here misidentifications flourish. Viridicatumtoxin is not produced by *P. viridicatum*, cyclopiazonic acid, cyclopiamine and cyclopiamide are not produced by *P. cyclopium*, verrucosidin is not produced by *P. verrucosum*, and communesins are not produced by *P. commune* (Frisvad, 1989a). For descreening of known compounds and for prevention of mycotoxin production, it is very important to establich accurate connections between fungal species and extrolite production, provided the fungal isolates are correctly identified. The aim of the following paper is to present an overview of extrolites, including mycotoxins and drugs, from all 58 species accepted in *Penicillium* subgenus *Penicillium* (Frisvad & Samson, 2004) and survey all known extrolites from these taxa.

Materials and methods

A large number of isolates, usually more than 8, but often up to 100 isolates, from each species were checked for production of extrolites, except in species where only few isolate are available. The fungi were inoculated on the media Czapek yeast autolysate agar (CYA) and yeast extract sucrose agar (YES), incubated for 7 days at 25ºC and extracted using the methods of Frisvad and Thrane (1987, 1993), Smedsgaard (1997) and Nielsen and Smedsgaard (2003). A large number of authentic standards were available for confirming the identity of the extrolites produced (Nielsen and Smedsgaard, 2003). Furthermore, the original producers of extrolites were often available and such cultures were re-identified and analyzed for the expected occurrence of extrolites.

Results and discussion

Uniqueness and taxonomic distribution of extrolites in* Penicillium *subgenus* Penicillium *compared to other subgenera and all other fungal genera.

All species in *Penicillium* subgenus *Penicillium* produced a profile of a large number of extrolites. These extrolites could be ordered into 3-9 extrolite biosynthetic families. The method employed secured that many of these extrolites families were detected and that they were efficiently extracted from the fungal cultures, even when using just three agar plugs for extraction as suggested by Smedsgaard (1997). The full profile of extrolites may be difficult to obtain using only one chromatographic method and two media. Fungal volatiles require GC-MS analysis (see Larsen and Frisvad, 1995a) and the non-volatile extrolites HPLC-DAD-MS analysis. The extraction method employed here has the advantage of avoiding simple sugars, amino acids, organic acids, but very polar metabolites, including most small bioactive peptides and proteins and several polar pigments are not necessarily extracted. Despite this, a very large number of extrolites could be detected, including acids, like terrestric acid, alkaloids, such as roquefortine C, polyketides, such as patulin, and terpenes, such as expansolide.

Some extrolites are apparently unique to one species and have therefore only been found in subgenus *Penicillium*. This is the case for amudol, auranthine, bis(2-ethylhexyl)phthalate, brevigellin, brevioxims, cyclopiamide, fumaryl-d,l-alanine, gladiolic acid, 2-(4-hydroxyphenyl)-2-oxo acetaldehyde oxime, italinic acid, lumpidine, marcfortines, 4-methoxy-6-n-propenyl-2-pyrone, methyl-4-(2-(2R)-hydroxyl-3-butynyloxy) benzoate, mycelianamide, N-acetyl-tryptamine, nalgiovensin, patulolides, pebrolides, penochalasins, penostatins, phenylpyropens, puberulic acid, sorrentanone, TAN-1612, verrucins, and viridamine. These metabolites have been detected in our study in these particular species (Table 1), but may later be discovered in other species.

Most of the metabolites were not only shared with other members of subgenus *Penicillium*, but also with taxa of the subgenera *Aspergilloides* and *Furcatum* and the genus *Aspergillus*. Extrolites unique for subgenus *Penicillium*, apart from those listed above, were adenophostins, alantrypinone, anacin, anicequol, aurantiamine, brevianamide A, brevicompanins, breviones, cyclopiamines, daldinine D, 3,5-dimethyl-6-hydroxyphthalide, dipodazin, isofumigaclavine A and B, isorugulosuvine, PR-toxin, penigequinolone, puberulines, sclerotigenine, tryptoquialanins, verrucosidins, and viridic acid. These metabolites may also be found later in other fungi.

Some metabolites are only found within the genus *Eupenicillium* and all its associated anamorph subgenera *Aspergilloides*, *Furcatum* and *Penicillium*, but not outside this phylogenetic group (these of course include the two groups listed above). These additional metabolites produced by soil borne forms also are: aurantionone, compactins, fulvic acids, isochromantoxins, penitrem A (but *Aspergillus* species produce other penitrems, Table 1), quinolactacins, terrestric and carolic acids, and xanthocillins.

Other extrolites from s/g *Penicillium* are shared with species in the genus *Aspergillus* and its teleomorphs: arisugacins, asperenones, asperphenamate, asperfuran, aspterric acid, asteltoxin, asterric acid, atrovenetins, cyclopiazonic acids, deoxybrevianamides, expansolide, fumigaclavines, fumiquinazolins, fumitremorgins, glyantrypine, gregatins, griseofulvins, meleagrin (or isomeleagrin), neoxaline, ochratoxins, penicillic acid, penitrems, pyripyropens, roquefortine C, silvathins, viridicatumtoxin, and xanthocillins. Most of these metabolites are produced by *Aspergillus fumigatus, A. terreus, A. giganteus* and *Emericella* species.

Table 1. Production of extrolites from *Penicillium* subgenus *Penicillium.* Several extrolites are families of precursors and major and minor biosynthetic relatives. 34 of the biosynthetic families are listed as a footnote to the table, including all known extrolites in any family. They may not all occur in *Penicillium* subgenus *Penicillium* species.

	Producer	Incorrectly identified or unidentified producer
Adenophostins (Takahashi *et al*., 1993)	?	*P. brevicompactum* (Takahashi *et al*., 1993)
Aib-containing polypeptides (Brückner and Reinecke, 1988, 1989)	*P. roqueforti* (Brückner and Reinecke, 1988) (called roquecin), *P. nalgiovense* (Brückner and Reinecke, 1989)	
Alantrypinone (Larsen *et al*., 1998a)	*P. thymicola* (Larsen *et al*., 1998a)	
Alternariol (Raistrick *et al*., 1953)	*P. coprophilum* (this publication)	
Amudol (Kamal *et al*., 1970a)	*P. griseofulvum* (reidentified here)	*P. martensii* (Kamal *et al*., 1970a)
Anacine (Boyes-Korkis *et al*., 1993, the structure has be revised by Larsen *et al*., 1999)	*P. aurantiogriseum* (Larsen et al., 1999a), *P. nordicum* (Larsen *et al*., 2001a), *P. polonicum* (Boyes-Korkis *et al*., 1993; Larsen *et al*., 1999a), *P. thymicola* (Larsen et al., 2001a)	(originally isolated from *P. polonicum* although cited as *P. aurantiogriseum*).
Anicequol (Igarashi *et al*., 2002)	?	*P. aurantiogriseum* (Igarashi *et al*., 2002)
Aristolochene (Proctor and Hohn, 1993)	*P. roqueforti* (Proctor and Hohn, 1993)	
Arisugacins (Kuno *et al*., 1996)	*P. cavernicola, P. echinulatum* (this publication)	*Penicillium* sp. (Kuno *et al*., 1996)
Asperenone- and asperrubrol-like compounds (Pattenden, 1969; Rabache *et al*., 1970; 1974), called met I (Suhr *et al*., 2002; Larsen *et al*., 2002)	*P. camemberti, P. cavernicola, P. commune, P. nordicum, P. palitans* *P. verrucosum*	
Asperfuran (Pfefferle *et al*., 1990)	*P. clavigerum* (Svendsen and Frisvad, 1994)	
Asperphenamate[1] (Clark and Hufford, 1978)	*P. brevicompactum* (Bird and Campbell, 1982), *P. bialowiezense, P. olsonii* (this publication)	
Aspterric acid (Tsuda *et al*., 1978)	*P. polonicum* (Frisvad and Lund, 1993)	*P. fructigenum* (Arai *et al*., 1989a)
Asteltoxin (Kruger *et al*., 1979)	*P. cavernicola* (this publication), *P. concentricum, P. confertum* (Svendsen and Frisvad, 1994), *P. formosanum* (this publication), *P. tricolor* (Frisvad *et al*., 1994)	
Asterric acid (Curtis *et al*., 1959)	*P. vulpinum* (Svendsen and Frisvad, 1994)	
Atrovenetin (Thomas, 1961; Narisimhachari *et al*., 1963)	*P. albocoremium* (Overy and Frisvad, 2003), *P. allii* (this publication)	
Aurantiamine (Larsen *et al*., 1992)	*P. aurantiogriseum* (Larsen *et al*., 1992), *P. freii, P. neoechinulatum* (Lund and Frisvad, 1994)	*P. terrestre* I (Solov'eva *et al*., 1995), *P. viridicatum* (Solov'eva *et al*., 1995)
Auranthine (Yeulet *et al*., 1986)	*P. aurantiogriseum* (Yeulet *et al*., 1986)	
Aurantioclavine, N-ethyl-aurantioclavine, clavicipitic acid (King *et al*., 1977)	*P. expansum, P. marinum* (this publication)	*P. aurantiovirens* (Kozlovsky *et al*., 1981), *P. vulpinum* (Kozlovsky *et al*., 2000)
Aurantionone (Ishikawa *et al*., 1992)	?	*P. aurantio-virens* (Ishikawa *et al*., 1992)
Barceloneic acid (Jayasuriya *et al*., 1995)	*P. concentricum* (this publication)	
Bis(2-ethylhexyl)phthalate (Amade *et al*., 1994)	*P. olsonii* (Amade *et al*., 1994)	
Botryodiploidin (Arsenault *et al*., 1969)	*P. brevicompactum* (Frisvad, 1989)	*P. carneolutescens* (Fijimoto *et al*., 1980)
Botryodiploidin	*P. paneum* (Boysen *et al*., 1996)	*P. roqueforti* (Moreau *et al*., 1982; Renauld *et al*., 1985)
Brevianamide A[2] (Birch and Wright, 1969)	*P. brevicompactum* (Birch and Wright, 1969), *P. viridicatum* (Wilson *et al*., 1973)	*P. commune* (Vinokurova *et al*., 2003), *P. ochraceum* (Robbers *et al*., 1975), *P. verrucosum* (El-Banna *et al*., 1987)

Brevicompanins (Kusano *et al*., 2000)	?	*P. brevicompactum* (Kusano *et al*., 2000)
Brevigellin (McCorkindale and Baxter, 1981)	*P. brevicompactum* (McCorkindale and Baxter, 1981)	
Breviones (Macías *et al*., 2000a & b)	*P. bialowiezense* (this publication) *P. olsonii* (this publication)	*P. brevicompactum* (Macías *et al*., 2000a & b)
Brevioximes[3] (Moya *et al*., 1997)	?	*P. brevicompactum* (Moya *et al*., 1997)
Chaetoglobosin A[4] (Silverton *et al*., 1976; Sekita *et al*., 1982a,b)	*P. discolor* (Frisvad *et al*., 1997), *P. expansum* (Frisvad and Filtenborg, 1989, Larsen *et al*., 1998b), *P. marinum* (this publication)	*P. aurantiovirens* (Springer *et al*., 1976), *P. aurantiogriseum* (Veselý *et al*., 1995), *Penicillium* sp. (Numata *et al*., 1995)
Chanoclavine-I (Acklin *et al*., 1966)	*P. griseofulvum*, *P. palitans* (Vinokurova *et al*., 1991), *P. roqueforti* (Vinokurova *et al*., 2001)	
Cholesterol, ergosta-7,22-dien-3 β-OH, ergosta-7,22-24(28)-trien-3β-OH, episterol, eburicol (Ariza *et al*., 2002)	*P. digitatum* (Ariza *et al*., 2002)	
Chrysogine[5] (Hikino *et al*., 1973)	*P. albocoremium* (Overy and Frisvad, 2003), *P. allii* (this publication), *P. chrysogenum* (Hikino *et al*., 1973), *P. nalgiovense, P. persicinum* (this publication), *P. radicicola, P. tulipae* (Overy and Frisvad, 2003)	
1,8-cineol = eucalyptol	*P. glandicola, P. venetum, P. vulpinum* (Larsen and Frisvad, 1995)	
Citreoisocoumarin[6] (Lai *et al*., 1991)	*P. nalgiovense* (Larsen and Breinholt, 1999), *P. paneum* (this publication) *P. roqueforti* (this publication)	*Penicillium* sp. (Lai *et al*., 1991)
Citrinin[7] (Hetherington and Raistrick, 1931)	*P. expansum* (Harwig *et al*., 1973)	
Citrinin (continued)	*P. radicicola* (Overy and Frisvad, 2003)	*P. albocoremium* (Frisvad and Filtenborg, 1989)
Citrinin (continued)	*P. verrucosum* (Frisvad, 1985a,b)	*P. viridicatum* (Krogh *et al*., 1970)
Communesin A, B, C & D (nomofungin) (Numata *et al*., 1993; Jadulco *et al*., 2004; Wigley *et al*., 2004)	*P. expansum* (Larsen *et al*., 1998b, Andersen *et al*., 2004), *P. marinum* (this publication)	*Penicillium* sp. (Numata *et al*., 1993; Ratnayake *et al*., 2001; 2003; May *et al*., 2003)
Compactin[8] (Brown *et al*., 1976)	*P. hirsutum,* (Frisvad and Filtenborg, 1989)	
Compactin (continued)	*P. solitum* (Frisvad and Filtenborg, 1989)	*Paecilomyces viridis* (Murakawa *et al*., 1994), *Penicillium aurantiogriseum* (Wagschal *et al*., 1996), *P. brevicompactum* (Brown *et al*., 1976), *P. citrinum* (Endo *et al.,* 1976), *P. cyclopium* (Doss *et al*., 1986)
Cyclopaldic acid[9] (Birkinshaw *et al*., 1952)	*P. commune* (Frisvad and Filtenborg, 1989)	*P. cyclopium* (Birkinshaw *et al*., 1952) *P. viridicatum* (Sankhala, 1957)
Cyclopaldic acid (continued)	*P. carneum* (Svendsen and Frisvad, 1994; Boysen *et al*., 1996), *P. mononematosum* (Frisvad and Filtenborg, 1989)	
Cyclopeptin, dehydrocyclopeptin, cyclopenin, cyclopenol, viridicatin, 3-methoxyviridicatin, viridicatol[34]	*P. albocoremium* (Frisvad and Filtenborg, 1989, Overy and Frisvad, 2003), *P. allii* (Frisvad and Filtenborg, 1989) *P. caseifulvum* (Lund *et al*., 1998), *P. commune* (this publication), *P. crustosum* (Taniguchi and Satomura, 1970; Frisvad and Filtenborg, 1989), *P. discolor* (Frisvad *et al*., 1998), *P. echinulatum* (Frisvad and Filtenborg, 1989) *P. freii* (Lund and Frisvad, 1994), *P. hirsutum* (this publication), *P. neoechinulatum* (Frisvad *et al*, 1987), *P. palitans* (this publication), *P. poloni-*	*P. carneo-lutescens* (Solov'eva *et al*., 1995), *P. hordei* (Solov'eva *et al*., 1995), *P. puberulum* (Austin and Meyers, 1953), *P. viridicatum* (Cunningham and Freeman, 1953, Solov'eva *et al*., 1995)

	cum (Frisvad and Filtenborg, 1989), *P. radicicola* (Overy and Frisvad, 2003) *P. solitum* (Frisvad and Filtenborg, 1989), *P. tulipae* (Overy and Frisvad, 2003), *P. venetum, P. vulpinum* (Frisvad and Filtenborg, 1989)	
Cyclopiamide (Holzapfel *et al*., 1990)	*P. griseofulvum* (this publication)	*P. cyclopium* (Holzapfel *et al*., 1990)
Cyclopiamine A & B (Bond *et al*., 1979)	*P. clavigerum, P. concentricum, P. coprobium, P. coprophilum, P. griseofulvum, P. vulpinum* (this publication)	*P. cyclopium* (Bond *et al*., 1979)
α-cyclopiazonic acid[10]	*P. camemberti* (Still *et al*., 1978) *P. commune* (Frisvad, 1985a & b; Pitt *et al*., 1986; Polonelli *et al*., 1987) *P. dipodomyicola* (Frisvad *et al*., 1987) *P. griseofulvum* (Leistner and Eckardt, 1979 as *P. patulum*; de Jesus *et al*., 1981), *P. palitans* (Frisvad, 1985a & b; Polonelli *et al., 1987*; Reshetilova *et al*., 1994)	*P. chrysogenum* (El-Banna *et al.,* 1987) *P. crustosum* (Leistner and Pitt, 1977) *P. cyclopium* (Holzapfel, 1968; Holzapfel *et al*., 1973), *P. echinulatum* (Eckardt and Leistner, 1979), *P. hirsutum* (El-Banna *et al*., 1987), *P. nalgiovense* (El-Banna *et al*., 1987), *P. puberulum* (Leistner and Pitt, 1977), *P. verrucosum* var. *album* (Leistner and Eckardt, 1979), *P. viridicatum* (Leistner and Pitt, 1977), *P. vulpinum* (Kozlovsky *et al*., 1997, 2000)
Cyclopin (Nafacy and Carver, 1963)	?	*P. cyclopium* (Nafacy and Carver, 1963)
Daldinine D (Ariza *et al*., 2001)	*P. discolor* (this publication), *P. hirsutum* (this publication), *P. thymicola* (Ariza *et al*., 2001)	
10-deacetylbaccatin III (and taxol = paclitaxel)	?	*P. aurantiogriseum* IHEM 14753 (El Jaziri and Diallo, 2000)
Dehydrofulvic acid[12]	*P. allii, P. concentricum, P. coprobium* (this publication), *P. griseofulvum* (Oxford *et al*, 1935; Dean *et al*., 1957), *P. italicum* (Arai *et al*., 1989b)	
Deoxybrevianamide E[11] (Scott *et al*., 1974; Arai *et al*., 1989b)	*P. italicum* (Scott *et al*., 1974; Arai *et al*., 1989b), *P. ulaiense* (this publication)	
2,5-dihydro-4-methoxy-2H-pyran-2-one (Gorst-Allman *et al*., 1982; Gorst-Allman and Steyn, 1983)	*P. italicum* (Gorst-Allman *et al*., 1982; Gorst-Allman and Steyn, 1983)	
2,3-dihydroxy benzoic acid	*?*	*P. roqueforti* (Hayashi *et al*., 1995)
3,5-dimethyl-6-hydroxyphthalide	*P. gladioli* (Birch and Pride, 1962)	
3,5-dimethyl-6-hydroxyphthalide.	*P. marinum* (this publication),	
Dipodazine	*P. cavernicola* (this publication), *P. dipodomyis,P. nalgiovense* (Sørensen *et al*., 1999), *P. thymicola* (this publication)	
Emodic acid and ω-hydroxy emodin (Anslow *et al*., 1940)	*P. chrysogenum*	*P. cyclopium* (Anslow *et al*., 1940)
11-(5'-epoxy-4'-hydroxy-3'-hydroxymethylcyclo-2'-hexenone)-Δ-8(12)-drimene (Ayer *et al*., 1990)	*P. brevicompactum* (Ayer *et al*., 1990)	
Expansolide (Massias *et al*., 1990)	*P. expansum* (Massias *et al*., 1990) *P.marinum* (this publication)	
Festuclavine	*P. roqueforti* (Vinukurova *et al*., 2001)	
Formylxanthocillin X (Arai *et al*., 1989)	*P. italicum* (Arai *et al*., 1989)	
Fumaryl-d,l-alanine (Birkinshaw *et al*., 1942)	*P. expansum*	*P. resticulosum* (Birkinshaw *et al*., 1942)
Fumigaclavine A, B, C[13] (Cole *et al*, 1977)	*P. clavigerum* (Vinokurova *et al*., 2003, *P. palitans* (Reshetilova *et al*., 1994)	*P. chrysogenum* (Kozlovsky *et al*., 1997), *P. crustosum* (Kawai *et al*., 1992) *P. oxalicum* (Vinokurova *et al*., 1991)
Fumiquinazoline F (Takahashi *et al*., 1995)	*P. thymicola* (Larsen *et al*., 1998a)	
Fumitremorgins[14]	*P. mononematosum* (Svendsen and Frisvad, 1994)	

Fungisporin (Sumiki and Miyao, 1952; Miyao, 1960; Studer, 1969)	*P. chrysogenum* (Sumiki and Miyao, 1952; Miyao, 1960; Studer, 1969) *P. vulpinum* (Sumiki and Miyao, 1952; Miyao, 1960; Studer, 1969)	
Geosmin	*P. carneum, P. crustosum* (Larsen and Frisvad, 1995), *P. clavigerum* (Larsen and Frisvad, 1994), *P. discolor, P. echinulatum* (Larsen and Frisvad, 1995), *P. expansum* (Mattheis and Roberts, 1992), *P. formosanum* (this publication)	
Gladiolic acid and dihydrogladiolic acid (Raistrick and Ross, 1952)	*P. gladioli* (Raistrick and Ross, 1952)	
Glyantrypine (Penn *et al*., 1992a)	*P. cavernicola,P. gladioli* (this publication)	
Gregatins[15] (Kobayashi and Ui, 1975, 1977)	*P. sclerotigenum* (this publication)	
Griseofulvin[16] (Oxford *et al*., 1939)	*P. aethiopicum*, *P. coprophilum* (Frisvad and Filtenborg, 1989), *P. dipodomyicola* (Frisvad *et al*., 1987), P. *griseofulvum* (Oxford *et al*., 1939), *P. persicinum* (this publication), *P. sclerotigenum* (Clarke and McKenzie, 1967)	*P. hordei* (Soloveva *et al*., 1995) *P. vulpinum* (Kozlovsky *et al*, 2000)
Hadacidin (Kaczka *et al*., 1962)	*P. camemberti, P. crustosum* (Dulaney and Gray, 1962)	
5-hydroxymethyl-furic acid	*P. italicum* (Arai *et al*., 1989b)	
2-(4-hydroxyphenyl)-2-oxo acetaldehyde oxime	*P. olsonii* (Amade *et al*., 1994)	
Isochromantoxin (3,7-dimethyl-8-hydroxy-6-methoxy-isochroman) (Cox *et al*.,. 1979), 3,7-dimethyl-1,8-dihydroxy-6-methoxy-isochroman (Malmstrøm *et al*., 2000)	*P.mononematosum* (Frisvad *et al*., 1987)	
Isofumigaclavine[17] A, B (= Roquefortine A & B) (Ohmomo *et al*., 1975)	*P. carneum* (this publication) *P. roqueforti* (Ohmomo *et al*., 1975, Vinokurova *et al*., 2001)	*P. crustosum* (Cole *et al*., 1983)
Isorugulosuvine (Kozlovsky *et al*, 1998)	?	*P. chrysogenum* (Kozlovsky *et al*, 1998) *P. expansum* (Kozlovsky *et al*., 2002), to be checked
Italinic and italicic acid	*P. italicum* (Arai *et al*., 1989b)	
Limonene	*P. olsonii, P. roqueforti, P. vulpinum* (Larsen and Frisvad, 1995)	
Lumpidine (Larsen *et al*., 2001b)	*P. nordicum* (Larsen *et al*., 2001b)	
Marcfortine A, B, C (Polonsky *et al*., 1980; Prangé *et al*., 1981)	*P. paneum* (this publication)	*P. roqueforti* (Polonsky *et al*., 1980; Prangé *et al*., 1981)
Meleagrin (Nozawa and Nakajima, 1979; Kawai *et al*., 1984) Meleagrin belongs to the roquefortine biosynthetic family.	*P. albocoremium* (Frisvad and Filtenborg, 1989, Overy and Frisvad, 2003), *P. allii,P. atramentosum* (Frisvad and Filtenborg, 1989), *P. chrysogenum* (Frisvad *et al*., 1987, Frisvad and Filtenborg, 1989), *P. concentricum* (this publication), *P. confertum* (Frisvad *et al*., 1987, Frisvad and Filtenborg, 1989), *P. coprophilum* (Frisvad and Filtenborg, 1989), *P. flavigenum* (Banke *et al*, 1997), *P. glandicola* (Frisvad and Filtenborg (1989), *P. hirsutum* (this publication), *P. melanoconidium* (this publication), *P. radicicola* (Overy and Frisvad, 2003), *P. tulipae* (Overy and Frisvad, 2003), *P. vulpinum* (Frisvad and Filtenborg, 1989)	*P. brevicompactum* (Solov'eva *et al*., 1995), *P. commune* (Vinokurova *et al.*, 2003), *P. expansum* (Kozlovsky *et al*., 2002), *P. hordei* (Solov'eva *et al*., 1995), *P. lanoso-coeruleum* (Solov'eva *et al*., 1995), *P.meleagrinum* (Nozawa and Nakajima, 1979; Kawai *et al*., 1984)
1-methoxy-3-methylbenzene	*P. carneum, P. coprophilum*, *P. expan-*	

	sum (Larsen and Frisvad, 1995)	
4-methoxy-6-n-propenyl-2-pyrone (Arai *et al*., 1989b)	*P. italicum* (Arai *et al*., 1989b)	
Methyl-4-(2-(2R)-hydroxyl-3-butynyloxy)benzoate (Arai *et al*., 1989a)	*P. polonicum* (Frisvad and Lund, 1993)	*P. fructigenum* (Arai *et al*., 1989a)
2-Methyl-isoborneol	*P. camemberti, P. commune*, *P. crustosum*, *P. discolor, P. polonicum, P. solitum* (Larsen and Frisvad, 1995), *P. thymicola* (Larsen *et al*., 2001a), *P. vulpinum* (Larsen and Frisvad, 1995)	
Mycelianamide (Oxford and Raistrick, 1948)	*P. griseofulvum* (Oxford and Raistrick, 1948; Birch *et al*., 1962)	
Mycophenolic acid[18] (Clutterbuck and Raistrick, 1933, Birkinshaw *et al*., 1948, 1952)	*P. bialowieziense* (Clutterbuck and Raistrick, 1933), *P. brevicompactum* (Clutterbuck and Raistrick, 1933; Birkinshaw *et al*., 1948, 1952), *P. carneum* (Boysen *et al*., 1996), *P. roqueforti* (Lafont *et al*., 1979)	*P. carneolutescens* (Fujimoto *et al*., 1980), *P. glaucum* (Gosio, 1896), *P. meleagrinum* (Umeda *et al*., 1974), *P. viridicatum* (Burton, 1949, Solov'eva *et al*., 1995)
N-acetyltryptamine	*P. expansum* (Kozlovsky *et al*., 2002), not checked	*P. chrysogenum* (Kozlovsky *et al*., 2002)
Nalgiovensin, nalgiolaxin (Raistrick and Ziffer, 1951; Birch and Massy-Westropp, 1957; Birch and Stapleford, 1967)	*P. nalgiovense* (Raistrick and Ziffer, 1951; Birch and Massy-Westropp, 1957; Birch and Stapleford, 1967)	
Neoxaline (Hirano *et al*., 1979; Konda *et al*., 1980) Neoxaline belongs to the roquefortine biosynthetic family.	*P. atramentosum* (this publication), *P. coprobium* (this publication), *P. coprophilum* (this publication)	
Nephrotoxic glycopeptides (Yeulet *et al*., 1988; Mac George and Mantle, 1990; Mantle *et al*., 1991; Mantle, 1994)	*P. aurantiogriseum* (Yeulet et al., 1988), *P. polonicum* (Frisvad, 1995)	*P. commune* (MacGeorge and Mantle, 1990)
Norlichexanthone (Santesson and Sundholm, 1969)	*P. clavigerum* (this publication) and all griseofulvin producers	
Ochratoxins[19] (van der Merwe *et al*., 1965)	*P. verrucosum* (Frisvad and Filtenborg, 1983, Frisvad 1985a,b; Pitt, 1987), *P. nordicum* (Frisvad and Filtenborg, 1983; Land and Hult, 1987; Larsen *et al*., 2001a)	*P. atramentosum* (Bridge *et al.,* 1989), *P. aurantiogriseum* (Mills *et al*., 1989, Skrinjar *et al*., 1995), *P. brevicompactum* (Paterson and Kemmelmeier, 1989); *P. camemberti* (Bridge *et al*., 1989), *P. chrysogenum* (Leistner and Pitt, 1977, Mills and Abramson, 1982; Mills *et al*., 1989), *P. commune* (Mintzlaff *et al*., 1972), *P. corymbiferum* (Krivobok *et al*., 1987), *P. cyclopium* (Ciegler *et al*., 1972), *P. expansum* (Krivobok *et al*., 1987), *P. glandicola* (Abramson *et al*., 1992), *P. griseofulvum* (Mantle and McHugh, 1993), *P. palitans* (Scott *et al*., 1972), *P. solitum* (Bridge *et al*., 1989; Mantle and McHugh, 1993), *P. viridicatum* (Walbeek *et al*, 1969; Ciegler *et al*., 1973; Mantle and McHugh, 1993)**
Oxaline (Nagel *et al*., 1976) Oxaline beongs to the roquefortine biosyntheitc family.	*P. allii* (this publication), *P. atramentosum* (Frisvad and Filtenborg, 1989), *P. concentricum* (this publication), *P. coprophilum, P. melanoconidium*, *P. vulpinum* (Frisvad and Filtenborg, 1989)	*P. hordei* (Solov'eva *et al*., 1995)
Pachybasin (Shibata and Takido, 1955; Curtis *et al*., 1971))	*P. vulpinum* (this publication)	
Palitantin (Birkinshaw and Raistrick, 1936a)	*P. commune* (Frisvad and Filtenborg, 1989), *P. discolor* (Frisvad *et al*., 1997), *P. echinulatum* (this publication), *P. palitans* (Birkinshaw and	

	Raistrick, 1936a; Chaplen and Thomas, 1960)	
Patulidin, CT2108A & B (Sakuda *et al*., 1995; Laakso *et al*., 2003)	*P. concentricum, P. glandicola* (this publication), *P. griseofulvum* mutant (Sakuda *et al*., 1995)	*P. solitum* (Laakso *et al*., 2003)
Patulin[20]	*P. carneum* (Frisvad and Filtenborg, 1989), *P. clavigerum* (Svendsen and Frisvad, 1994)*, P. concentricum* (Leistner and Eckardt, 1979), *P. coprobium* (Frisvad and Filtenborg, 1989), *P. dipodomyicola* (Frisvad *et al*., 1987), *P. expansum* (Anslow *et al*., 1943)*, P. glandicola* (Frisvad and Filtenborg, 1989), *P. gladioli* (this publication), *P. griseofulvum* (Anslow et al., 1943; Kent and Heatley, 1945; Simonart and Lathouwer, 1956) *P. marinum* (this publication), *P. paneum* (Boysen *et al*., 1996) *P. sclerotigenum* (this publication), *P. vulpinum* (Chain *et al*., 1942; Bergel *et al*., 1943)	*P. aurantiogriseum* (Steiman *et al*., 1989), *P. brevicompactum* (Paterson *et al*., 2003), *P. chrysogenum* (Leistner and Pitt, 1977), *P. commune* (Oh *et al*., 1998), *P. crustosum* (Northolt *et al*., 1978), *P. divergens* (Barta and Mecir, 1948), *P. echinulatum* (Okeke *et al*., 1993), *P. hirsutum, P. italicum* (Okeke *et a*l., 1993), *P. roqueforti* (Leistner and Pitt, 1977; Olivigni and Bullerman, 1978), *P. terrestre* (Atkinson, 1942, 1943, Raper and Thom, 1949), *P. verrucosum* (Oh *et al*., 1998), *P. viridicatum* (Frank, 1972)
Patulolides A, B & C (Sekeguchi *et al*., 1985; Rodphaya *et al*., 1986)	*P. griseofulvum* mutants (Sekeguchi *et al*., 1985; Rodphaya *et al*., 1986)	
Pebrolide, desacetylpebrolide, 1-deoxypebrolide (McCorkindale *et al*., 1981)	*P. brevicompactum* (McCorkindale *et al*., 1981)	
Penicillic acid[21] (Birkinshaw *et al*., 1936)	*P. aurantiogriseum* (Frisvad and Filtenborg, 1983, 1989), *P. carneum* (Boysen *et al*., 1996), *P. cyclopium* (Birkinshaw *et al*., 1936), *P. freii* (Lund and Frisvad, 1994) *P. melanoconidium* (Frisvad and Filtenborg, 1989; Lund and Frisvad, 1994), *P. neoechinulatum* (Frisvad and Filtenborg, 1989; Lund and Frisvad, 1994), *P. polonicum* (Frisvad and Filtenborg, 1989; Lund and Frisvad, 1994), *P. radicicola* (Overy and Frisvad, 2003), *P. tulipae* (Overy and Frisvad, 2003), *P. viridicatum* (Frisvad and Filtenborg, 1989, Lund and Frisvad, 1994)	*P. chrysogenum* (Leistner and Pitt, 1977), *P. commune* (Ciegler *et al*., 1972), *P. expansum* (Mintzlaf *et al*., 1972), *P. griseofulvum* (Reio, 1958), *P. palitans* (Ciegler and Kurtzman, 1970), *P. roqueforti* (Olivigni and Bullerman, 1978), *P. suavolens* (Karow *et al*., 1944)
Penicillins[22]	*P. chrysogenum* (Clutterbuck *et al*., 1933), *P. dipodomyis* (Frisvad *et al*., 1987), *P. flavigenum* (Banke *et al*., 1997), *P. griseofulvum* (Johns *et al*., 1946; Laich *et al*., 2002), *P. nalgiovense* (Andersen & Frisvad, 1994; Färber and Geisen, 1994)	*P. rubrum* (Fleming, 1929)
Penigequinolones[23] (Kimura *et al*., 1996)	*P. thymicola* (this publication)	
Penitrems[24]	*P. carneum* (Boysen *et al*., 1996), *P. clavigerum* (Patterson *et al*., 1979; Frisvad and Filtenborg, 1989), *P. crustosum* (Ciegler and Pitt, 1970; Hou et *al*., 1971, de Jesus *et al*., 1981b; 1983b & c), *P. flavigenum* (Banke *et al*, 1997), *P. glandicola* (Ciegler and Pitt, 1970, as *P. granulatum*; Frisvad and Filtenborg, 1989), *P. melanoconidium* (Frisvad and Filtenborg, 1989), *P. tulipae* (Overy and Frisvad, 2003)	*P. commune* (Wagener *et al.,* 1980), *P. cyclopium* (Wilson *et al*., 1968; Ciegler and Pitt, 1970; Hou et al., 1971; Vesonder *et al*., 1980), *P. lanosocoeruleum* (Wells and Cole, 1977), *P. martensii* (Ciegler and Pitt, 1970), *P. olivino-viride* (Ciegler and Pitt, 1970), *P. palitans* (Ciegler and Pitt, 1970; Hou *et al*., 1971), *P. puberulum* (Ciegler and Pitt, 1970; Hou *et al*., 1971)
Penochalasins A-H . (Numata *et al*., 1995; Iwamoto *et al*, 2001)	*P. marinum* (this publication)	*Penicillium* sp. (Numata *et al*., 1995; Iwamoto *et al*, 2001)
Penostatins A-I (Takahashi *et al*., 1996,	*P. marinum* (this publication)	*Penicillium* sp. (Takahashi *et al*., 1996,

Iwamoto *et al*., 1998)		Iwamoto *et al*., 1998)
Phenylalanine-proline diketopiperazine	*P. digitatum* (Tantaqoui-Elaraki *et al*., 1994)	
Phenylpyropene A, B & C (Kwon *et al*, 2002, Rho *et al*., 2002)	*P. griseofulvum* (Kwon *et al*, 2002, Rho *et al*., 2002), not confirmed in this study	
PR-toxin[25] (Wei *et al*., 1975)	*P. chrysogenum* (Frisvad and Filtenborg, 1989; Dai *et al*., 1993; Möller *et al*., 1997), *P. roqueforti* (Wei *et al*., 1975)	
Pseurotin[26] (Bloch *et al*., 1976; Bloch and Tamm, 1981)	*P. aurantiogriseum, P. cyclopium* (Frisvad and Lund, 1993)	
Puberulic acid, puberulonic acid	*P. cyclopium* (Birkinshaw *et al*., 1932)	
Puberulines[27] (fructigenins, verrucofortines, verrucosins)	*P. cyclopium, P. polonicum*, *P. tricolor* (Lund and Frisvad, 1994)	*P. carneolutescens* (Solov'eva *et al*., 1992),*P. hordei* (Solov'eva *et al*., 1992), *P. puberulum* (Solov'eva *et al*., 1992), *P. verrucosum* var. *cyclopium* (Solov'eva *et al*., 1989, 1995)
Pyripyropens (Ōmura *et al*., 1993)	*P. concentricum, P. coprobium* (this publication)	
Quinolactacin (Kakinuma *et al*., 2000, Takahashi *et al*., 2000; Kim *et al*., 2001)	*P. bialowiezense* (this publication)	
Raistrick phenols	*P. bialowiezense* (this publication; Andersen, 1991), *P. brevicompactum* (Clutterbuck *et al*., 1932; Oxford and Raistrick, 1933; Godin, 1953; 1955)	
Roquefortine C & D[28]	*P. albocoremium* (Frisvad and Filtenborg, 1989, Overy and Frisvad, 2003), *P. allii,P. atramentosum* (Frisvad and Filtenborg, 1989), *P. carneum* (Boysen *et al*., 1996), *P. chrysogenum* (El-banna *et al*., 1987; Frisvad and Filtenborg, 1989), *P. concentricum, P. confertum*, *P. coprobium*, *P. coprophilum* (Frisvad and Filtenborg, 1989), *P. crustosum* (Kozlovsky *et al*., 1981b, as *P. farinosum*; Kyriakidis *et al*., 1981), *P. expansum* (Ohmomo *et al*., 1980; Frisvad and Filtenborg, 1983), *P. flavigenum* (Banke *et al*., 1997), *P. glandicola* (Frisvad and Filtenborg, 1983, as *P. granulatum*; Frisvad and Filtenborg, 1989), *P. griseofulvum* (Ohmomo *et al*, 1980 as *P. urticae*; Frisvad and Filtenborg, 1983), *P. hirsutum* (as *P. corymbiferum* (Ohmomo *et al*., 1980; Frisvad and Filtenborg, 1989), *P. hordei* (Frisvad and Filtenborg, 1989), *P. marinum* (this publication), *P. melanoconidium* (Frisvad and Filtenborg, 1989), *P. paneum* (Boysen *et al*., 1996), *P. persicinum* (this publication), *P. radicicola* (Overy and Frisvad, 2003), *P. roqueforti* (Scott *et al*., 1976; Yamaguchi *et al*., 1991), *P. sclerotigenum* (Frisvad and Filtenborg, 1990), *P. tulipae* (Overy and Frisvad, 2003), *P. venetum* (Frisvad and Filtenborg, 1989), *P. vulpinum* (Frisvad and Filtenborg, 1983, as *P. claviforme*)	*P. aurantiogriseum* (Kozlovsky *et al*., 2003), *P. brevicompactum* (Solov'eva *et al*., 1995), *P. commune* (Wagener *et al*., 1980, Vinokurova *et al*., 2003), *P. cyclopium* (Kozlovsky and Reshetilova, 1987), *P. puberulum* (Solov'eva *et al*., 1995), *P. verrucosum* (Kozlovsky and Reshetilova, 1987), *P. viridicatum* (Solov'eva *et al*., 1995)
Rugulosuvine B (Kozlovsky *et al*., 2002)	*P. polonicum*	*P. expansum* (Kozlovsky *et al*., 2002)
Rugulovasine A & B[29] (Abe *et al*., 1969; Yamatodani *et al*., 1970)	*P. atramentosum* (Frisvad and Filtenborg, 1989), *P. caseifulvum*	*P. biforme* (Dorner *et al*., 1980), *P. palitans* III (Solov'eva *et al*., 1995), *P.*

	(Lund *et al*., 1998), *P. commune* (Frisvad and Filtenborg, 1989)	*raciborskii* (Solov'eva *et al*., 1995), *P. solitum* (Solov'eva *et al*., 1995), *P. viridicatum* (Solov'eva *et al*., 1995)
Sch 642305 (Chu *et al*., 2003)	?	*P. verrucosum* (Chu *et al*., 2003)
Sclerotigenine (Joshi *et al*., 1999)	*P. clavigerum* IBT 4899, IBT 19355 (Larsen *et al*., 2000), *P. commune* IBT 3427 (Larsen *et al*., 2000), *P. melanoconidium* (Larsen *et al*., 2000), *P. nordicum* (Larsen *et al*., 2000, 2001a), *P. sclerotigenum* (Joshi *et al*., 1999)	*P. verrucosum* (Larsen *et al*., 2000)
Secalonic acid D & F (Steyn, 1970)	*P. chrysogenum*, *P. confertum* (this publication)	*P. brevicompactum* (Soloveva *et al*. 1995)
Serantrypinone (Ariza *et al*., 2001)	*P. thymicola* (Ariza *et al*., 2001)	
Silvathins [30] (Ayer *et al*., 1990)	*P. brevicompactum* (Ayer *et al*., 1990)	
Solistatin (Sørensen *et al*., 1999)	*P. solitum* (Sørensen *et al*., 1999)	
Sorbicillin and bisvertinolone[31] (Cram and Tishler, 1948, Cram, 1948; Miller and Huang, 1995)	*P. chrysogenum* (Cram and Tishler, 1948, Cram, 1948; Miller and Huang, 1995)	
Sorrentanone (Miller and Huang, 1995)	*P. chrysogenum* (Miller and Huang, 1995), not verified by us	
TAN-1612 (Ishimaru *et al*., 1994)	*P. clavigerum* (Ishimaru *et al*., 1994)	
Terrestric acid[32] ((Birkinshaw and Raistrick, 1936b)	*P. aurantiogriseum* (Frisvad and Filtenborg 1989), *P. crustosum* (as *P. terrestre*) (Birkinshaw and Raistrick, 1936b), *P. hirsutum*, *P. hordei* (Frisvad and Filtenborg, 1989), *P. radicicola* (Overy and Frisvad, 2003), *P. tricolor* (Frisvad *et al*., 1994), *P. tulipae* (Overy and Frisvad, 2003), *P. venetum* (Frisvad and Filtenborg, 1989)	*P. jensenii* (Mantle, 1987), *P. puberulum* (Soloveva *et al*., 1995), *P. viridicatum* (Birkinshaw and Samant, 1960, Solov'eva *et al*., 1995)
Territrems (Ling *et al*., 1979)	*P. cavernicola, P. echinulatum* (this publication)	*Penicillium* sp. (Kuno *et al*., 1996)
Tryptophyltryptophyl diketopiperazine (Kozlovsky *et al*., 1997)	?	*P. aurantiogriseum* (Kozlovsky *et al*., 1997)
Tryptoquialanins (Ariza *et al*., 2002)	*P. aethiopicum* (this publication), *P. digitatum* (Ariza *et al*., 2002)	
Verrucine A & B (Larsen *et al*., 1999)	*P. verrucosum* (Larsen *et al*., 1999)	
Verrucolone[33] = arabenoic acid (Isaac *et al*., 1991; Larsen *et al*., 1998c; Rahbaek *et al*., 2003)	*P. italicum* (this publication), *P. olsonii, P. nordicum* (Rahbaek *et al*., 2003), *P, thymicola* (Larsen *et al*, 2001), *P. verrucosum* (Larsen *et al*., 1998c; Rahbaek *et al*., 2003)	
Verrucosidin and normethylverrucosidin (Burka *et al*., 1983)	*P. aurantiogriseum* (El-Banna *et al*., 1987; El-Banna and Leistner, 1989; Frisvad and Filtenborg, 1989), *P. melanoconidium* (Lund and Frisvad, 1994), *P. polonicum* (Frisvad and Filtenborg, 1989; Lund and Frisvad, 1994)	*P. verrucosum* var. *cyclopium* (Burka *et al*., 1983)
Viridamine (Holzapfel and Marsh, 1977)	*P. viridicatum* (Holzapfel and Marsh, 1977)	
Viridic acid (Holzapfel *et al*., 1986)	*P. nordicum* (Larsen *et al*., 2002), *P. viridicatum* (Holzapfel *et al*., 1986)	
Viridicatumtoxin (Hutchison *et al*., 1973; Kabuto *et al*., 1976)	*P. aethiopicum* (Frisvad and Filtenborg, 1989)	*P. viridicatum* (Kabuto *et al*., 1976, Hutchison *et al*., 1973), *P. expansum* (De Jesus *et al*., 1982)
Viriditoxin (Weisleder and Lillehøj, 1971; Lillehoj and Milburn, 1973, Suzuki *et al*., 1990).	*P. mononematosum* (this publication)	
Xanthocillins (Hagedorn *et al*., 1960; Achenbach *et al*., 1972; Pfeiffer *et al*, 1972),	*P. chrysogenum* (Hagedorn *et al*., 1960; Achenbach *et al*., 1972; Pfeiffer *et al*, 1972), *P. flavigenum* (this publication), *P. italicum* (Arai *et al*, 1989b)	
Xanthomegnin, viomellein, vioxan-	(*P. clavigerum*) (this publication), *P.*	*P. aurantiogriseum* (El-Banna *et al.,*

thin[35] (Höfle and Röser, 1978)	*cyclopium* (Stack and Mislivec, 1978), (*P. flavigenum*) (this publication), *P. freii, P. melanoconidium* (Lund and Frisvad, 1994), *P. tricolor* (Frisvad et al, 1997), *P. viridicatum* (Ciegler *et al*., 1981; Frisvad and Filtenborg, 1989; Lund and Frisvad, 1994)	1987), *P. crustosum* (Hald *et al*., 1983), *P. chrysogenum* (Singh *et al*., 2003)

*The original strain producing cyclopenol was *P. cyclopium* IMI 089374, this strain was later listed as *P. aurantiogriseum* by CABI, but is actually a *P. solitum* (Frisvad and Filtenborg, 1989). The latter authors later showed that *P. cyclopium* (but not *P. aurantiogriseum*) produced cyclopenol anyway.
**Ochratoxin A production in all these species could not be confirmed when reexamining the cultures claimed to be producers.

[1]**Asperphenamates**: Asperphenamate (Clark and Hufford, 1978), N-benzoyl phenylalanine, N-benzoyl phenylalaninol (Doerfler *et al*., 1981)
[2]**Brevianamides**: Brevianamide A, B, Brevianamide C & D (photolytic compounds) (Birch and Russell, 1972), tryptophanyl-proline anhydride (= brevianamide F) (Birch and Russell, 1972), breviananamide E (Birch and Wright, 1969)
[3]**Brevioxims**: Brevioxime (Moya *et al*., 1997), N-(2-Methyl-3-oxodecanoyl)pyrrole, N-(2-Methyl-3-oxodec-8-enoyl)pyrrole (Cantín *et al*., 1998), N-(2-Methyl-3-oxodecanoyl)-2-pyrroline (Moya *et al*., 1998)
[4]**Chaetoglobosins**: Chaetoglobosin A (Silverton *et al*., 1976), Chaetoglobosin A-F (Sekita *et al*., 1973; Sekita *et al*., 1976, Sekita *et al*., 1982a,b); Chaetoglobosin G & J (Sekita *et al*., 1977), Chaetoglobosin K (Springer *et al*., 1980), Chaetoglobosin L (Probst and Tamm, 1982), Chaetoglobosin M (Spöndlin and Tamm, 1988), Chaetoglobosin N (Convert *et al*., 1994), Chaetoglobosin O (Ichihara *et al*., 1996, Iwamoto *et al*., 2001), Chaetoglobosin P (Donoso *et al*., 1997), prochaetoglobosin I-IV (Oikawa *et al*., 1991, 1992), 19-O-acetylchaetoglobosin A (Probst and Tamm, 1981b), 19-O-acetylchaetoglobosin B & D (Probst and Tamm, 1981a)
[5]**Chrysogines**: Chrysogine, 2-pyrovoylaminobenzamide (Suter and Turner, 1967, *P. chrysogenum*), questiomycin A (Bar *et al*., 1971), N-acetyl-2-amino-3H-phenoxazin-3-one (Pfeifer *et al*., 1972, *P. chrysogenum*), N-formyl-2-aminophenol (Bar *et al*., 1971b, *P. chrysogenum*), 2-[(2-hydroxypropionyl)amino]benzamide (Dai *et al*., 1993)
[6]**Citreoisocoumarins**: Citreoisocoumarin, 6-methyl-citreoisocoumarin, dichlorodiaporthin, diaporthinol, diaporthinic acid (all in *P. nalgiovense*, Larsen and Breinholt, 1999)
[7]**Citrinins**: Citrinin, phenol A, 2,6-dihydroxy-4-(3-hydroxy-2-butyl)-m-toluic acid, 5-(2-formyloxy-1-methyl-resorcinol, dihydrocitrinone, sclerotinin A, decarboxycitrinin, decarboxydihydrocitrinone (from *P. citrinum*, Curtis *et al*., 1968)
[8]**Compactins**: Compactin (Brown *et al*., 1976), ML-236A, ML-236-C (Endo *et al*., 1976), 3α-hydroxy-3,5-dihydro ML-236C (Murakawa *et al*., 1994), dihydrocompactin (Tony Lam *et al*., 1981), solistatin (Sørensen *et al*., 1999)
[9]**Cyclopaldic acids**: Cyclopaldic acid, cyclopolic acid (Birkinshaw *et al*., 1952; Brillinger *et al*., 1978), 3-O-methyl-cyclopolic acid (Achenbach *et al*., 1982), 3-O-ethyl cyclopolic acid (Achenbach and Mühlenfeld, 1984), chromanol 1, chromanol 2, chromanol 3, chromanol 4, 5-O-isopentenyl cyclopolic acid, 5-O-isopentenyl-3-O-ethyl cyclopolic acid, (Achenbach *et al*., 1982), duricaulic acid (Achenbach *et al*., 1985), asperdurin (Mühlenfeld and Achenbach, 1988), 5,7-dihydroxy-6-methyl-1(3H)-isobenzofuranone, 5-hydroxy-7-methoxy-6-methyl-1(3H)-isobenzofuranone, 5,7-dihydroxy-4,6-dimethyl-1(3H)-isobenzofuranone, 5,7-dihydroxy-4-(methoxymethyl)-6-methyl-1(3H)-isobenzofuranone, 5-hydroxy-7-methoxy-4,6-dimethyl-1(3H)-isobenzofuranone, 5-hydroxy-4-(hydroxymethyl)-7-methoxy-6-methyl-1(3H)-isobenzofuranone, 5-hydroxy-7-methoxy-4-(methoxymethyl)-6-methyl-1(3H)-isobenzofuranone, 4-hydroxy-6-methoxy-5-methyl-1(3H)-isobenzofuranone, 3-ethoxy-4-)hydroxymethyl)-7-methoxy-6-methyl-5-[(3-methyl-2-butenyl)oxy]-1-(3H)-isobenzofuranone, 1,3-dihydro-3,7-dihydroxy-5-methoxy-6-methyl-4–isobenzofuranecarbonic acid (Sodium salt), 1,3-dihydro-3-hydroxy-5-methoxy-6-methyl-7–[(3-methyl-2-butenyl)oxy]-4-isobenzofuranecarbonic acid (Sodium salt) (Achenbach *et al*., 1985)
[10]**Cyclopiazonic acids**: α-cyclopiazonic acid (Holzapfel, 1968), β-cyclopiazonic acid (Holzapfel *et al*., 1970, de Jesus *et al*., 1981a), bissecodehydrocyclopiazonic acid (Ohmomo *et al*., 1973), cyclopiazonic acid imine (Holzapfel *et al*., 1970)
[11]**Deoxybrevianamides**: Deoxybrevianamide E, 12,13-dehydrodeoxybrevianamide E (Scott *et al*., 1974), 10,20-dehydro[12,13-dehydroprolyl]-2-(1',1'-dimethylallyltryptophyl)diketopiperazine, austamide, 12,13-dehydroaustamide (Steyn, 1973)
[12]**Fulvic acids**: Fulvic acid (*Eupenicillium brefeldianum* & *P. griseofulvum* Dean *et al*., 1957), dehydrofulvic acid, PI-3, PI-4 (*P. italicum*, Arai *et al*., 1989b), polivione (Demetriadou *et al*., 1985)
[13]**Fumigaclavines**: Fumigaclavine A, B, and C, pyroclavine, festuclavine, chanoclavine-I, agroclavine, 4-(γ,γ-dimethylallyl)tryptophane (Cole *et al*., 1983; Vinokurova *et al*., 1991, Osanai *et al*., 1999)
[14]**Fumitremorgins**: Fumitremorgin A, B (Yamazaki et al., 1974; 1975a & b; 1980a & b, Schroeder *et al*., 1975), Fumitremorgin C (Cole *et al*. 1977), TR-2 (Cole and Kirksey, 1973), verruculogen (Cole *et al*., 1972), 15-acetoxyverruculogen, demethoxyfumitremorgin C, 12,13-dihydroxyfumitremorgin C, trypostatin A, B (Cui *et al*., 1996a & b), spirotrypostatin B (Cui *et al*., 1996c)
[15]**Gregatins**: Gregatin A, B, C, D, E (Kobayashi and Ui, 1975; Clemo and Pattenden, 1982), graminin A (Kobayashi and Ui, 1977), cyclogregatin (Anke *et al*., 1988), aspertetronin A and B (Clemo and Pattenden, 1982)
[16]**Griseofulvins**: Griseofulvin, dechlorogriseofulvin, bromogriseofulvin (MacMillan, 1953, 1954), dehydrogriseofulvin, 4,6-dimethoxy-2'-methylgrisan-3,4',6'-trione (McMaster *et al*., 1960), griseophenone A, B, C (Rhodes et al., 1961), dihydrogriseofulvin (Kamal et al., 1970b), griseoxanthone B, C, Norlichexanthone (McMaster *et al*., 1960; Broadbent *et al*., 1975)
[17]**Isofumigaclavines**: Isofumigaclavine A & B (Ohmome *et al*., 1975; Cole *et al*., 1983), agroclavine (Abe *et al*., 1967), 8,9-epoxyagroclavine (Kozlovzky *et al*., 1982)
[18]**Mycophenolic acids**: Mycophenolic acid, 6-farnesyl-5,7-dihydroxy-4-methylphthalide (Canonica *et al*., 1971; Colombo *et al*., 1987), ethyl mycophenolate, mycophenolic acid diol lactone, mycochromenic acid (Campbell *et al*., 1966)

[19]**Ochratoxin**s: Ochratoxin A (van der Merwe *et al*, 1965), ochratoxin B (van der Merwe *et al*., 1965; Steyn and Holzapfel, 1967a), ochratoxin C (van der Merwe *et al*., 1965; Steyn *et al*., 1970), ochratoxin α, ochratoxin β, 4R-hydroxyochratoxin A (Hutchison *et al*., 1971), 4S-hydroxyochratoxin A, 10-hydroxyochratoxin A, 7-carboxy-3,4-dihydro-8-hydroxy-3-methylisocoumarin (Hutchison *et al*., 1971), ochratoxin A methylester, ochratoxin B methylester, ochratoxin B ethyl ester (Steyn and Holzapfel, 1967b), serin-ochratoxin A, hydroxyprolin-ochratoxin A, lysine-ochratoxin A (Hadidane *et al*., 1992)
[20]**Patulins**: Patulin, isopatulin (Sekiguchi *et al*., 1979), ascladiol, (+)-epiepoxydon, (+)-desoxyepiepoxydon (Nagasawa *et al*., 1978), pintulin (Mikami *et al*., 1996), m-hydroxybenzyl alcohol (Rebstock, 1964), 6-methylsalicylic acid, 6-formylsalicylic acid, 3-hydxroxyphthalic acid, m-cresol, toluquinol, toluquinone, m-hydroxybenzyl alcohol, m-hydroxybenzaldehyde, m-hydroxybenzoic acid, gentisyl alcohol, gentisyl quinine, gentisaldehyde, gentisic acid, isoepoxydon, phyllostine, neopatulin, dihydroepiepoformin (McMaster *et al*., 1960; Sekiguchi and Gaucher, 1979a, b; Priest and Light, 1989; Kuo *et al*., 1995), parahydroxybenzoic acid, pyrogallol (Bassett and Tanenbaum, 1958)
[21]**Penicillic acids**: Orsellinic acid, penicillic acid, dihydropenicillic acid (Eijk, 1969, Obana *et al*., 1995)
[22]**Penicillins**: δ-(α-aminoadipyl)-cysteinyl valine (Arnstein and Morris, 1960), Penicillin G, F, K, V, N, dihydropenicillin F, isopenicillin N (Crowfoot *et al*, 1949; Cole and Bachelor, 1963), 6-aminopenicillanic acid (Batchelor *et al*., 1959), α-aminoadipyl-serinylisodehydrovaline, α-aminoadipyl-alanyl-valine, α-aminoadipyl-serinyl-valine (Neuss *et al*., 1980), 6-oxo-piperidine-2-carboxylic acid (Brundidge *et al*., 1980)
[23]**Penigequinolones**: Penigequinolones A, B (Kimura *et al*., 1996; Larsen *et al*., 1999, in *P. scabrosum*), 3-methoxy-4,5-dihydrocy-4-(4'-methoxyphenyl)-quinolone, 5-deoxy-3-methoxy-4,5-dihydroxy-4-(4'-methoxyphenyl)-quinolone (Hayashi *et al*., 1997), peniprequinolone, 3-methoxy4-hydroxy-4-(4'-methoxyphenyl)quinolinone, 3-methoxy-4,6-dihydroxy-4-(4'-methoxyphenyl)quinolinone (Kusano *et al*., 2000)
[24]**Penitrems**: Penitrem A-F (de Jesus *et al*., 1983a & b), penitrem G (González *et al*., 2003), PC-M5', PC-M6 (Hosoe *et al*., 1990), PC-M5, PC-M4 (Yamaguchi *et al*., 1993), thomitrems (cultural artefacts, Rundberget and Wilkins, 2002), penitremone A-C (Naik *et al*., 1995), pennigritrem (Penn *et al*., 1992b), secopenitrem B = 10-oxo-11,33-dihydropenitrem B (Laakso *et al*., 1993), sulpinine A-C (Laakso *et al*., 1982), 6-bromopenitrem E (Hayashi *et al*., 1993)
[25]**PR-toxins**: PR-toxin (Wei *et al*., 1975, Eremofortine A, B, C, D, E (Moreau *et al*., 1980; Chalmers *et al*., 1981), PR-imine (Siemens and Zawistowski, 1993), PR-amide (Chang *et al*., 1993), Aristolochene (Hohn and Plattner, 1989; Proctor and Hohn, 1993), PR acid (Chang *et al*., 1998)
[26]**Pseurotins**: Pseurotin A (Bloch *et al*., 1976; Bloch and Tamm, 1981), pseurotin B, C, D, E (Breitenstein *et al*., 1981; 8-O-demethylpseurotin (Wenke *et al*., 1993), synerazol (Ando *et al*., 1991), azaspirene (Asami *et al*., 2002)
[27]**Puberulines:** Puberuline A (Solov'eva *et al*., 1997), puberuline B (= fructigenine A), verrucofortine (= verrucosine = fructigenine B), verrucosinol, dehydroverrucosine, demethylverrucosine, rugulosuvine, leucyltryptophanyldiketopiperazine (Solovyeva *et al*., 1989, 1992, Arai *et al*., 1989a; Hodge *et al*., 1988)
[28]**Roquefortines**: (E)-2-(1H-imidazole-4-yl methylene)-6-(1H-indole-3-yl-methyl)-2,5-piperazine diol (Kozlovsky *et al*., 1998), Roquefortine C, roquefortine D (= 3,12-dihydroroquefortine C) (Ohmomo *et al*., 1978), 16-hydroxyroquefortine C (Steyn and Vleggaar, 1983), roquefortine E (Musuko *et al*., 1994), N-ethylroquefortine C (Kozlovsky *et al*., 1998), glandicolin A, glandicolin B (Kozlovskii *et al*., 1994; Reshetilova *et al*., 1995), meleagrin, oxaline (Nagel *et al*., 1976), neoxaline (Hirano *et al*., 1979; Konda *et al*., 1980), PF-1, PF-2, PF-3, PF-4 (Kozlovsky *et al*., 1988)
[29]**Rugulovasines**: Rugulovasine A, B, Chlororugulovasine A, B (Cole *et al*. 1976a & b)
[30]**Silvatins**: cis-Bis(methylthio) silvatin, cis-1,4-Dimethyl-3,6-bis(methylthio)-3-(4'-hydroxyphenyl-methyl)-2,5-piperazinedione, 3-thiomethyl-3-[4'-(3''-methyl-2''-butenoyl) phenylmethyl]-2,5-piperazinedione, 6-hydroxy-3-methylthio-3-[4'-(3''-methyl-2''-butenoxy) phenylmethyl]-2,5-piperazinedione, 1,4-Dimethyl-3-hydroxcy-3-)4'-methoxyphenylmethyl)-2,5-piperazinedione (Ayer *et al*., 1990)
[31]**Sorbicillins**: Sorbicillin, Dihydrosorbicillin, bisvertioquinol, bisvertinolone, vertinolide (Trifonov *et al*., 1982, 1983, 1986 from *Verticillium intertextum*)
[32]**Terrestric acids**: Terrestic acid, viridicatic acid, carlosic acid, carlic acid, carolic acid, dehydrocarolic acid, carolinic acid, γ-methyl tetronic acid (Birkinshaw and Raistrick, 1936b; Bracken and Raistrick, 1947; Birkinshaw and Samant, 1960; Bentley *et al*., 1962; Boll *et al*., 1968; Jacobsen *et al*, 1978; Simonsen *et al*., 1980)
[33]**Verrucolones**: Verrucolone (= arabenoic acid) (Isaac *et al*., 1991), PC-2, LL-P888γ, verrucosapyrone A, B (Larsen *et al*., 1998c; Rahbaek *et al*., 2003), 5-hydroxy-3-methoxy-6-oxo-2-decenoic acid δ-lactone, pestalotin = LL-P880α, LL-P880β, 6-(1-hydroxypentyl)-4-methoxypyran-2-one
[34]**Viridicatols**: Cyclopeptin, dehydrocyclopeptin (Framm *et al*., 1973, *P. solitum*), cyclopenin, cyclopenol, viridicatin, viridicatol, 3-methoxyviridicatin (Bracken *et al*., 1954; Birkinshaw *et al*., 1963; Luckner, 1967; Mohammed and Luckner, 1963), deepoxy-methoxycyclopenol (Kusano *et al*., 2000)
[35]**Xanthomegnins**: xanthomegnin, viomellein, vioxanthin, rubrosulphin, viopurpurin, xanthoviridicatin D, G, E, F, 3,4-dehydroxanthomegnin, luteosporin, semi-vioxanthin, 7-de-O-methylsemivioxanthin, 3,4-dehydroviomellein, 3',4'-dehydroviomellein, 3,4,3',4'-bisdehydroxanthomegnin (Stack *et al*., 1977; 1979; Sedmera *et al*., 1981; de Jesus *et al*., 1983a; Singh *et al*., 2003).

A few metabolite families are produced by both *Eupenicillium* and and associated soil forms, s/g *Penicillium* and *Aspergillus.* These genera are quite phylogenetically unrelated and very widespread in Nature. It seems therefore that these compounds may occur several times during evolution: citrinin, fungisporin, patulins, penicillins, pseurotins, secalonic acids, viriditoxins, and xanthomegnins.

Some extrolites are produced by Penicillia phylogenetically related to *Eupenicillium* and to phylogenetically very different filamentous fungi, but not by *Aspergillus*: alternariol, aristolochene, barceloneic acid, botryodiploidin, chaetoglobosins, chanoclavins, cholesterol, chrysogines, eucalyptol, citreoisocoumarin, geosmin, limonene, 1-methoxy-3-methylbenzene, 2-methyl-isoborneol, mycophenolic acid, pachybasin, phenylalanine-prolin diketopiperazine, sorbicillins, verrucolones and pestalotins.

Some of the volatiles mentioned are even produced by prokaryotes, plants and animals (Cole and Cox, 1981, Turner, 1971; Turner and Aldridge, 1983).

Some metabolites, common for soil-borne Penicillia in the subgenera *Aspergilloides* and *Furcatum*, have **not** (yet) been found in *Penicillium* subgenus *Penicillium*, including anthglutin, antibiotic A26771B, austins, barnol, bredenine, canescin, chlorogentisyl alcohol, citreodiol, citreopyrone, citreoviridin, citromycetin, cividiclavine, curvulic acids, curvularins, decumbic acid, deoxyverucarin E, 2,3-dihydro-3,6-dihydroxy-2-methyl-4-pyrone, dipicolinic acid, ethisolide, furan-2-carboxylic acids, gliotoxin, herqueinones, herquline, hydroxyasperentins, janthitrems, lapidosin, leucogenol, monorden, nerolidol, nigrifortine (= amauromine), β-nitropropionic acid, oxathine carboxylic acid, paraherquamides, paraherquonine, paxilline, phoenicin, pulvilloric acid, questins, rotiorins, sclerotiorins, spinulosin, tetrahydroauroglaucin, and thujopsene (Mantle, 1987). It would be interesting to investigate why all these extrolites have not been found in *Penicillium* subgenus *Penicillium*, but rather in soil-borne Penicillia from the subgenera *Aspergilloides* and *Furcatum*.

Talaromyces and its associated anamorphs in *Penicillium* subgenus *Biverticillium* produce extrolites completely different from any *Eupenicillium* and its associated anamorphs, including mitorubrins, rubratoxins, islandicins, cyclochlorotins, penicillides etc. (Mantle, 1987, Frisvad *et al*., 1990a). The only common extrolites are some sterols, fungisporin and rugulosuvines, and rugulovasine A and B. Actually *Aspergillus* species share more extrolites with *Eupenicillium* than *Talaromyces*.

In general diketopiperazines are particularly common in *Penicillium* subgenus *Penicillium*, whereas they have not been found at all in *Talaromyces* and its associated anamorphs in *Biverticillium*. They have been found in *Eupenicillium, Penicillium* subgenus *Aspergilloides* and *Furcatum*, and *Aspergillus* and its associated teleomorphs, but the diketopiperazines are much less common in those taxonomic groups. Polyketides are common in all these groups, while terpenes or terpene units are most common in *Eupenicillium* and associated anamorphs and *Aspergillus*, and again most common in *Penicillium* subgenus *Penicillium*.

Extrolites produced by subgenus *Penicillium*

Some extrolites were very common in subgenus *Penicillium*. Roquefortine C was the most common extrolite of all, being produced by 25 species of the 58 examined (Table 1). Ten species are apparently unable to produce the advanced biosynthetic relatives glandicolin A, B, meleagrin, oxaline or neoxaline. The species that only produce roquefortine C (and its precursor roquefortine D), include *P. carneum*, *P. crustosum, P. dipodomyicola, P. expansum, P. griseofulvum, P. marinum, P. paneum, P. persicinum, P. roqueforti* and *P. sclerotigenum*. The remaining 15 roquefortine C producing species produce either meleagrin or oxaline or both. Only 6 species produce oxaline and 3 species have been found to produce neoxaline. These compounds have only been found in *Aspergillus aculeatus* outside *Penicillium* subgenus *Penicillium* yet (Hirano *et al*., 1979; Konda *et al*., 1980).

The cyclopenins have been found in 17 species of the 58 examined. In one species only the cyclopenins have been found (*P. caseifulvum*) but the remaining species produce the viridicatins. Characteristically members of series *Viridicata* and *Corymbifera* produce 3-O-methylviridicatin, while taxa in the other series accumulate viridicatin.

Patulin was also rather common, being produced by 13 species. This metabolite was common in the section *Penicillium* and *Roqueforti*, but not found in section *Viridicata*. Thus patulin may be found in dung, fruits, and silage, but not in cereals and most other type of foods.

Penicillic acid was produced by 10 species, all in series *Viridicata* and *Corymbifera*, and in one isolate in *P. carneum*. Terrestric acid often accompanied this metabolite in the same two series, but there appear to be no direct link between the two groups of small acid molecules.

The characteristic mouldy smell of geosmin (8 producers) and 2-methylisoborneol (8 producers) was common in subgenus *Penicillium*. Even though some of the terpenes were tentatively identified, the characteristic odour of those species confirms that these metabolites are indeed produced. Fourteen species in all produced these terpenes and *P. crustosum* and *P. discolor* produced both geosmin and 2-methylisoborneol. These volatiles were spread over seven series, but were most common in series *Camemberti* and *Solita*. In some series the profiles of volatiles are quite alike in all species in a series, notably *Verrucosa* and *Viridicata* (Larsen *et al*., 2001a). In other cases species from different series clustered based on volatile profiles (Larsen and Frisvad, 1995a).

Penitrem A is another extrolite that is present in individual species in several series; in this case the seven producers are present in 6 different series. Penitrem A is also produced by species in *Penicillium* subgenus *Aspergilloides* and *Furcatum,* including the species *P. canescens* (Shreeve *et al*., 1978), *P. janczewskii* (Mantle *et al*., 1978), *P. janthinellum* (Patterson *et al*., 1979), *P. simplicissimum* (Hayashi *et al*., 1993), *P. spinulosum* (Leistner and Pitt, 1977) and *P. frequentans* (Mintzlaff *et al*., 1972). Even though isolates which are claimed to produce penitrem A are not all correctly identified, it is clear that penitrem A is widespread in *Eupenicillium* and its anamorphic states. We have confirmed the penitrem A production in *P. janczewskii* and *P. ochrochloron* (Frisvad and Filtenborg, 1990a; Nielsen and Smedsgaard, 2003). The complicated penitrem biosynthetic pathway may have evolved several times during evolution, as it is rarely present in phylogenetically closely related species. Given the highly possible involvement of paxilline in the biosynthesis of the penitrems (Mantle and Penn, 1989) and the 17 genes in a cluster on chromosome V of *Penicillium paxilli* (approximately 50 kb) (Young *et al*., 2001) required for paxilline biosynthesis, the penitrems (A-G and four precursors) must require even more genes. In *Saccharomyces cerevisiae* there are 5 putative genes for extrolism (secondary metabolism) among 6449 genes (0.07%) and in *Neurospora crassa* there are at present 23 genes identified for extrolism out of the 3218 (0.7%) of an estimated total of 11,000 genes (Mannhaupt *et al*., 2003). We expect that in species in *Penicillium* subgenus *Penicillium*, the number of extrolite genes is much larger, because one to 11 biosynthetic families (pathways) have been recorded as shown in Table 1. This excludes volatile extrolites and uncharacterised extrolites (see Table 2). The average number of known biosynthetic extrolite families is five, which is an underestimate, as many pigments, volatiles and further uncharacterised extrolites are not included. Maybe each species in the subgenus have eight extrolite families consisting of an estimated average of 15 genes each, which will give an estimate of 120 extrolite genes. It is less probable that all species have all the genes required for the 132 extrolite families listed in Table 1, and that a major part of them are constantly silent genes. Sequencing of extrolites genes and whole genome sequencing will eventually reveal this, but a functional analysis of the extrolism of the species using several growth conditions and media may reveal many further extrolites (Nielsen *et al*., 2003).

Partly characterised extrolites

A large part of the extrolites detected using HPLC with UV detection were identifiable, as were the volatiles produced detected by GC-MS (Larsen and Frisvad, 1995a, b), but there are still several extrolites with characteristic chromophores that have not been chemically structure elucidated (Table 2). Some of these may be members of the same biosynthetic family, as an addition of a doublebond, a rearrangement within the molecule or other modifications may result in different chromophores in many cases (Frisvad, 1989b). There are still a high number of extrolites to be structure elucidated, however. Judged from the UV spectra many of these are polyketides (including several anthraquinones), terpenes and alkaloids. All the species produced ergosterol, but more specific sterol-like extrolites, such as anicequol (Igarashi *et al*, 2002) will probably also be discovered in the future in species in *Penicillium* subgenus *Penicillium*.

Some extrolites are very polar, for example the red extracellular pigments of *P. persicinum*, and some isolates of *P. brevicompactum* and *P. paneum.* Such extrolites will only be isolated if alternative extraction techniques are used. The most polar compounds will remain in the water phase if our standard method of extraction is used (Nielsen and Smedsgaard, 2003). Other extrolites may be missed if they form strong chelates and remain in the mycelium. Yet other extrolites may be missed if they do not have characteristic chromophores. HPLC-MS techniques may then be used to screen for such metabolites (Nielsen and Smedsgaard, 2003).

Biosynthesis and taxonomy

Nearly all species produced polyketides, 52 of 58 species produced at least one family of polyketides. Those that did not (*P. atramentosum, P. camemberti, P. caseifulvum, P. crustosum, P. dipodomyis* and *P. digitatum*) produced pigments that are in most cases polyketides anyway, so it is likely that **all** 58 species have genes for producing polyketides. Several species have three or four families of polyketides, including *P. brevicompactum, P. coprophilum, P. cyclopium, P. discolor, P. italicum, P. melanoconidium, P. mononematosum, P. olsonii, P. paneum, P. polonicum*, and *P. solitum* that have three polyketide families, *P. carneum, P. gladioli, P. griseofulvum, P. verrucosum*, and *P. vulpinum* that have four polyketide families and *P. clavigerum* and *P. concentricum* that have five families of polyketides. These efficient producers of several polyketides are placed in several different series in subgenus *Penicillium*, but some of the most prolific producers are from section *Penicillium*, series *Claviformia*.

All species produced terpenes, if sterols are included in the list. If sterols are excluded only *P. dipodomyis*, *P. gladioli*, and *P. nalgiovense* are without known structure elucidated terpenes; the remaining 55 species produce terpene extrolites or add terpene units to alkaloids or polyketides. Thus it is also highly probable that **all** species in subgenus *Penicillium* also produce terpenes.

Table 2. The distribution of biosynthetic extrolite families, volalites and estimated further chromophore families throughout all 58 species in *Penicillium* subgenus *Penicillium* (the third column is based on HPLC with diode array detection, UV-VIS spectra from 200 to 600 nm) The volatiles were tentatively identified based on mass spectra and retention times of standards when available (Larsen and Frisvad, 1995a, b), but many more volatiles were produced than could be identified. (NT: not tested).

Species	**No. of non-volatile extrolite families**	**Single volatiles detected (Larsen and Frisvad, 1995a, b)**	**Characteristic chromophore families (not yet structure elucidated)**
P. aethiopicum	3	9 (1 alcohol, 1 ketone, 6 esters, 1 terpene)	13
P. albocoremium	3	NT	8
P. allii	4	12 (2 alcohols, 10 terpenes)	11
P. atramentosum	2	9 (9 esters)	19
P. aurantiogriseum	8	10 (3 alkenes, 2 alcohols, 2 ketones, 3 terpenes)	25
P. bialowiezense	5	NT	13
P. brevicompactum	8	2 (2 alcohols)	7
P. camemberti	3	15 (1 alkene, 3 alcohols, 1 ketone, 4 esters, 6 terpenes)	5
P. carneum	7	15 (1 alkene, 3 alcohols, 1 ester, 6 terpenes)	5
P. caseifulvum	2	NT	3
P. cavernicola	6	NT	4
P. chrysogenum	12	9 (5 alkenes, 2 alcohols, 2 ketones)	8
P. clavigerum	6	11 (1 alkene, 5 esters, 5 terpenes)	12
P. commune	6	21 (3 alkenes, 4 alcohols, 3 ketones, 1 ester, 10 terpenes)	5
P. concentricum	7	11 (2 alcohols, 9 terpenes)	4
P. confertum	3	NT	1
P. coprobium	4	15 (9 alkenes, 2 alcohols, 1 ketone, 3 esters)	12
P. coprophilum	5	22 (7 alkenes, 5 alcohols, 4 ketones, 2 esters, 2 methoxy-alkyl-benzenes, 2 alkylfurans)	21
P. crustosum	4	21 (2 alkenes, 1 disulphide, 2 alcohols, 1 ketone, 11 esters, 3 terpenes)	7
P. cyclopium	7	Weak	20
P. digitatum	2	19 (11 esters, 8 terpenes)	7
P. dipodomyicola	3	NT	9
P. dipodomyis	2	NT	15
P. discolor	4	15 (3 alcohols, 1 ketone, 1 ester, 10 terpenes)	10
P. echinulatum	4	13 (2 alcohols, 1 ketone, 1 ester, 9 terpenes)	7
P. expansum	7	9 (2 alcohols, 6 terpenes, 1 methoxy-alkyl-benzene)	15
P. flavigenum	4	NT	29
P. formosanum	2	8 (1 alkane, 1 ester, 6 terpenes)	4
P. freii	4	5 (2 alkenes, 2 alcohols, 1 ketone)	8
P. gladioli	5	NT	6
P. glandicola	4	20 (2 alkenes, 2 alcohols, 2 ketones, 3 esters, 11 terpenes)	11
P. griseofulvum	11	15 (15 esters)	4
P. hirsutum	4	4 (2 alcohols, 2 terpenes)	16
P. hordei	2	2 (2 alcohols)	12
P. italicum	8	15 (3 alkenes, 2 alcohols, 1 ketone, 3 esters, 7 terpenes)	11
P. marinum	8	NT	7
P. melanoconidium	6	3 (1 alkene, 2 alcohols)	13

P. mononematosum	4	NT	19
P. nalgiovense	5	5 (1 alkene, 1 alcohol, 1 ketone, 1 ester, 1 terpene)	8
P. neoechinulatum	3	NT	13
P. nordicum	7	NT	3
P. olsonii	5	7 (3 alcohols, 3 ketones, 1 terpene)	7
P. palitans	4	NT	2
P. paneum	5	NT	11
P. persicinum	3	NT	3
P. polonicum	9	9 (1 ketone, 1 ester, 7 terpenes)	8
P. radicicola	7	11 (2 alcohols, 9 terpenes)	5
P. roqueforti	6	20 (1 alkene, 3 alcohols, 1 ketone, 1 ester, 14 terpenes)	9
P. sclerotigenum	5	NT	8
P. solitum	3	10 (2 alcohols, 4 esters, 4 terpenes)	11
P. thymicola	4	NT	4
P. tricolor	5	17 (5 alkenes, 4 alcohols, 1 ketone, 1 ester, 5 terpenes, 1 lactone)	8
P. tulipae	5	NT	3
P. ulaiense	1	NT	4
P. venetum	4	13 (1 alkene, 2 alcohols, 2 ketones, 8 terpenes)	20
P. verrucosum	6	7 (2 alcohols, 4 ketones, 1 terpene)	7
P. viridicatum	5	7 (2 alcohols, 2 ketones, 3 terpenes)	15
P. vulpinum	7	34 (7 alkenes, 2 alcohols, 1 ketone, 2 esters, 20 terpenes, 2-methyl-phenol, 1 meth-oxyalkane-benzene)	19

Of the 40 species examined for volatile sequiterpenes and diterpenes, only 10 species did not produce detectable amounts of these terpenes (Larsen and Frisvad, 1995a, b).

All species produce amino acid derived extrolites, and all species produce extrolites derived from tryptophan or anthranilic acid. However *P. bialowiezense, P. formosanum, P. gladioli* and *P. olsonii* only produced partly characterized indol-alkaloids. Twenty-one species (of the 58 species examined) produced known alkaloids derived from phenylalanine. Alkaloid extrolites also contained other amino acids, especially histidin, alanine, glycine, glutamine, tyrosine, proline, serine, valine, and leucine. Cysteine is incorporated into penicillins and methionine is used as a methyl-donor for other extolites, but the remaining 'protein' amino acids have not yet been detected as part of any extrolites in subgenus *Penicillium*. Some unusual amino acids are incorporated into some extrolites however (Table 3).

Threonine, ornithine, arginine, isoleucine, lysine, hydroxylysine, aspartic acid, glutamic acid, and asparagin have not yet been found in any small extrolites from subgenus *Penicillium*.

Influence of the growth substrate on extrolite production

All isolates and species in *Penicillium* subgenus *Penicillium* produced a large number of different extrolites, thus following the so-called OSMAC (one strain/many compounds) approach (Schiewe and Zeeck, 1999; Bull *et al*., 2000; Bode *et al*., 2002). Whereas Bode *et al*. (2002) suggested to use a series of different abiotic and biotic conditions to allow the isolate to produce several extrolites, Frisvad and Filtenborg (1983, 1989) reported that all isolates of *Penicillium* examined by them produced a large number of extrolites consistently in species specific profiles on just two media, CYA and YES. Our experience has been that most known extrolites are produced on these two media (Frisvad and Filtenborg, 1989), but in some special cases other media or growth conditions may add to the full phenotypic potential of any one isolate. A good quantitative example is the penicillins, which are produced in much higher amounts on media with a low content of glucose (Raper and Thom, 1949). In other cases the metabolite profile may be influenced by the pH of the growth medium. For example *P. crustosum* produces relatively large amounts of thomitrems as compared to penitrem A on rice, because the high amount of starch result in a significant lowering of the pH (Rundberget *et al*., 2004).

Table 3. Production of non-volatile extrolites and their biological activity in species in *Penicillium* subgenus *Penicillium*. The data in the biosynthetic origin column are based on Turner (1971), Turner and Aldridge (1983) and Mantle (1987) and the data in the Activity column are based on Korzybski *et al*., 1967, Cole and Cox (1981), Pearce (1997), Cole and Schweickert (2003a & b) and Cole *et al*., 2003 and the original references listed in Table 1. Antibiotics are here regarded as extrolites active against prokaryotes.

Species	Series	Extrolite biosynthetic family	Biosynthetic origin	Activity, [P]: Potential or actual-pharmaceutical [M]: Mycotoxin
P. aethiopicum	*Aethiopica*	Griseofulvins	Heptaketide, Cl	Antifungal[P] Teratogenic[M]
P. aethiopicum	*Aethiopica*	Viridicatumtoxin	Nonaketide	Antitumor[P] Nephrotoxin[M]
P. aethiopicum	*Aethiopica*	Tryptoquialanins	TRP, ALA, terpene (DMA)	?Tremorgen[M]
P. albocoremium	*Corymbifera*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. albocoremium	*Corymbifera*	Meleagrin	TPP, HIS, terpene (DMA)	Antibiotic[P]
P. albocoremium	*Corymbifera*	Atrovenetins	Heptaketides	Antioxidant[P]
P. albocoremium	*Corymbifera*	Cyclopenins	ANT, PHE, O_2	Herbicidal (Springer et al., 1988) Anti-HIV[P] (3-O-methylviridicatin, Heguy *et al*., 1998)
P. allii	*Corymbifera*	Fulvic acids	Heptaketide	
P. allii	*Corymbifera*	Atrovenetins	Heptaketides	Antioxidant[P]
P. allii	*Corymbifera*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. allii	*Corymbifera*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. allii	*Corymbifera*	Oxaline	TRP, HIS, terpene (DMA)	
P. allii	*Corymbifera*	Chrysogines	ANT	Anti auxin
P. atramentosum	*Camemberti*	Rugulovasines	TRP, terpene (DMA), Cl	Anti-hypotensive[P]
P. atramentosum	*Camemberti*	Roquefortine C	TRP, HIS, terpene (DMA)	Neurotoxin[M]
P. atramentosum	*Camemberti*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. atramentosum	*Camemberti*	Oxaline, neoxaline	TRP, HIS, terpene (DMA)	
P. aurantiogriseum	*Viridicata*	Penicillic acids	Tetraketides	Antibiotic[P] Antiviral[P] Antitumor[P] Cytotoxic[M] ?Carcinogenic[M]
P. aurantiogriseum	*Viridicata*	Verrucosidins	Nonaketide	Tremorgenic[M]
P. aurantiogriseum	*Viridicata*	Terrestric acids	TCA cycle, acetate	Cardiotoxin[M]
P. aurantiogriseum	*Viridicata*	Pseurotins	Hexaketide, PHE, MET	Angiogenesis inhibitor[P] Antifungal[P]
P. aurantiogriseum	*Viridicata*	Anacin	ANT, GLN, LEU	
P. aurantiogriseum	*Viridicata*	Auranthine	ANT, GLN	
P. aurantiogriseum	*Viridicata*	Aurantiamine	VAL, HIS, terpene (DMA)	Cell cycle inhibitor[P]
P. aurantiogriseum	*Viridicata*	Nephrotoxic glycopep-tides	Glycopeptide with ASP, GLU, GLY, TYR, LYS, ILE, PHE (Yeulet *et al*., 1988)	Nephrotoxic[M]
P. bialowiezense	*Olsonii*	Raistrick phenols	Pentaketide	
P. bialowiezense	*Olsonii*	Mycophenolic acid	Tetraketide, terpene (farnesyl)	Immunosuppresive [M,P]
P. bialowiezense	*Olsonii*	Asperphenamate	PHE	
P. bialowiezense	*Olsonii*	Breviones	Diterpenoid	Allelochemical

P. bialowiezense	*Olsonii*	Quinolactacins	ANT	Anti-larvae Acetylcholinesterase inhibitor[P]
P. brevicompactum	*Olsonii*	Raistrick phenols	Pentaketide	
P. brevicompactum	*Olsonii*	Mycophenolic acid	Tetraketide, terpene (farnesyl)	Immunosuppresive [M,P]
P. brevicompactum	*Olsonii*	Botryodiploidin	Tetraketide	Cancerogenic[M]
P. brevicompactum	*Olsonii*	Drimens	Terpene	
P. brevicompactum	*Olsonii*	Silvatins	TYR, GLY, MET, terpene (DMA)	Antifungal[P]
P. brevicompactum	*Olsonii*	Brevianamides	TRP, PRO, terpene (DMA)	Anti-insecticidal
P. brevicompactum	*Olsonii*	Pebrolides	Sesquiterpene	
P. brevicompactum	*Olsonii*	Brevigellin	PRO, ALA, N-benzoythreonine, β-aminobutyric acid, 3-(3-carboxypropyl) Δ^2-pyrroline	
P. camemberti	*Camemberti*	See also *P. commune* for rare extrolites		
P. camemberti	*Camemberti*	Hadacidin	GLY, formate, O_2, SER (Stevens and Emery, 1966)	Herbicidal Anticancer[P]
P. camemberti	*Camemberti*	Cyclopiazonic acid	TRP, terpene (DMA), acetoacetyl unit	Organ-damage in mammals[M]
P. camemberti	*Camemberti*	Met I (aspereynone like)	Terpene	
P. carneum	*Roqueforti*	Cyclopaldic acids	Tetraketide	Antibiotic[P]
P. carneum	*Roqueforti*	Penicillic acid	Tetraketide	Antibiotic[P] Antiviral[P] Antitumor[P] Cytotoxic[M] ?Carcinogenic[M]
P. carneum	*Roqueforti*	Patulin	Tetraketide	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. carneum	*Roqueforti*	Mycophenolic acid	Tetraketide, terpene (farnesyl)	Immunosuppressive[M, P]
P. carneum	*Roqueforti*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. carneum	*Roqueforti*	Penitrems	TRP, terpene	Tremorgen[M] Acutely toxic[M]
P. carneum	*Roqueforti*	Isofumigaclavines	TRP, terpene (DMA)	Weak pharmacological effects[P]
P. caseifulvum	*Camemberti*	Rugulovasines	TRP, terpene (DMA)	Hypotensive[P]
P. caseifulvum	*Camemberti*	Cyclopenin	ANT, PHE, O_2	Herbicidal
P. cavernicola	*Solita*	Territrems	?Polyketide, shikimate	Acetylcholinesterase inhibitors[P] Tremorgens[M]
P. cavernicola	*Solita*	Arisugacins	?Polyketide, shikimate	Acetylcholinesterase inhibitors[P]
P. cavernicola	*Solita*	Asteltoxin	Nonaketide	Mycotoxin[M]
P. cavernicola	*Solita*	Glyanthrypine	ANT, GLY	
P. cavernicola	*Solita*	Dipodazin	TRP, GLY	
P. cavernicola	*Solita*	Met I (asperenone-like)	Asperenone is a terpene	
P. chrysogenum	*Chrysogena*	Secalonic acids	Octaketides	Antibiotic[P] Antifungal[P] Antitumor[P] Antiulcer[P] Mycotoxin[M]
P. chrysogenum	*Chrysogena*	Sorbicillins and sorrentanone	Hexaketides	Antibiotics[P]
P. chrysogenum	*Chrysogena*	(Emodic acids)	Octaketides	
P. chrysogenum	*Chrysogena*	PR-toxin	Sesquiterpene	Inhibits RNA polymerase[M]

P. chrysogenum	*Chrysogena*	Penicillins	VAL, CYS, α-aminoadipic acid	Antibiotics[P]
P. chrysogenum	*Chrysogena*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. chrysogenum	*Chrysogena*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. chrysogenum	*Chrysogena*	Xanthocillins	Shikimic acid pathway	Antibiotic[P]
P. chrysogenum	*Chrysogena*	Chrysogine	ANT	Anti-auxin
P. chrysogenum	*Chrysogena*	Questiomycin	ANT	Antibiotic[P]
P. chrysogenum	*Chrysogena*	Penitrinic acid (Stodola *et al*, 1945)	($C_{15}H_{17}O_5N$)	(Yellow pigment)
P. chrysogenum	*Chrysogena*	Chrysogenin (Wolf *et al*., 1960)	($C_{18}H_{22}O_6$)	(Yellow pigment)
P. chrysogenum	*Chrysogena*	Negapillin (Shimi *et al*., 1966)		Antibiotic[P]
P. chrysogenum	*Chrysogena*	Notatin (Coulthard *et al*., 1945)	A protein (a glucose oxidase)	Antibiotic[P] Antiviral[P]
P. chrysogenum	*Chrysogena*	PAF (Marx *et al*., 1995)	A protein	Antifungal[P]
P. chrysogenum	*Chrysogena*	Fungisporin	D-PHE, L-PHE, D-VAL, L-VAL	
P. clavigerum	*Claviformia*	Patulin	Tetraketide	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. clavigerum	*Claviformia*	Asperfuran	Polyketide	Antifungal[P]
P. clavigerum	*Claviformia*	Norlichexanthone	Heptaketide	
P. clavigerum	*Claviformia*	TAN-1612	Nonaketide	Substance P inhibitor [P]
P. clavigerum	*Claviformia*	Xanthomegnins	Heptaketide	Hepato- and nephrotoxin[M]
P. clavigerum	*Claviformia*	Penitrems	TRP, terpene, Cl	Tremorgenic[M]
P. clavigerum	*Claviformia*	Cyclopiazonic acid	TRP, terpene (DMA), acetoacetyl unit	Organ-damage in mammals[M]
P. commune	*Camemberti*	Cyclopaldic acids	Tetraketide	Antibiotics[P]
P. commune	*Camemberti*	Palitantin, frequentin	Heptaketide	Frequentin is antifungal[P]
P. commune	*Camemberti*	Met I (asperenone like)	Asperenone is a terpene	
P. commune	*Camemberti*	Cyclopiazonic acid	TRP, terpene (DMA), acetoacetyl unit	Organ-damage in mammals[M]
P. commune	*Camemberti*	Rugulovasines	TRP, terpene (DMA), Cl	Anti-hypotensive[P]
P. commune	*Camemberti*	Cyclopenins	ANT, PHE, O_2	Herbicidal
P. concentricum	*Claviformia*	Patulin	Tetraketide	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. concentricum	*Claviformia*	Patulidins	Hexaketide	Antifungal (fatty acid synthase inhibitor)[P]
P. concentricum	*Claviformia*	Asteltoxin	Nonaketide	Mycotoxin[M]
P. concentricum	*Claviformia*	Barceloneic acid A	Polyketide	Farnesyl protein transferase inhibitor[P]
P. concentricum	*Claviformia*	Pyripyropens	Polyketide (3 mevalonate + 5 acetate), nicotinic acid (Tomoda *et al*., 1996)	Acyl-CoA: cholesterol acyltransferase inhibitor[P]
P. concentricum	*Claviformia*	Cyclopiamines	TRP, PRO, terpenes (2 x DMA), nitro	
P. concentricum	*Claviformia*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. concentricum	*Claviformia*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. concentricum	*Claviformia*	Oxaline	TRP, HIS, terpene (DMA)	
P. confertum	*Mononematosa*	Asteltoxin	Nonaketide	Mycotoxin[M]
P. confertum	*Mononematosa*	Secalonic acids	Octaketides	Antibiotic[P]

				Antifungal[P] Antitumor[P] Antiulcer[P] Mycotoxin[M]
P. confertum	*Mononematosa*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. confertum	*Mononematosa*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. coprobium	*Claviformia*	Patulin	Tetraketide	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. coprobium	*Claviformia*	Pyripyropens	Polyketide (3 mevalonate + 5 acetate), nicotinic acid	Acyl-CoA: cholesterol acyltransferase inhibitor[P]
P. coprobium	*Claviformia*	Cyclopiamines	TRP, PRO, terpenes (2 x DMA)	
P. coprobium	*Claviformia*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. coprobium	*Claviformia*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. coprobium	*Claviformia*	Neoxaline	TRP, HIS, terpene (DMA)	
P. coprophilum	*Claviformia*	Alternariol	Heptaketide	Antibiotic[P] Inhibit HeLa cells[P]
P. coprophilum	*Claviformia*	Griseofulvins	Heptaketide, Cl	Antifungal[P] Teratogenic[M]
P. coprophilum	*Claviformia*	Pyripyropens	Polyketide (3 mevalonate + 5 acetate), nicotinic acid	Acyl-CoA: cholesterol acyltransferase inhibitor[P]
P. coprophilum	*Claviformia*	Cyclopiamines	TRP, PRO, terpenes (2 x DMA)	
P. coprophilum	*Claviformia*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. coprophilum	*Claviformia*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. coprophilum	*Claviformia*	Oxaline & neoxaline	TRP, HIS, terpene (DMA)	
P. crustosum	*Camemberti*	Terrestric acid	TCA cycle, acetate	cardiotoxin[M]
P. crustosum	*Camemberti*	Penitrems	TRP, terpene	Tremorgen[M] Acutely toxic[M]
P. crustosum	*Camemberti*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. crustosum	*Camemberti*	Hadacidin	GLY, formate, O_2, SER	Herbicidal Anticancer[P]
P. crustosum	*Camemberti*	Cyclopenins	ANT, PHE, O_2	Herbicidal
P. cyclopium	*Viridicata*	Penicillic acid	Tetraketide	Antibiotic[P] Antiviral[P] Antitumor[P] Cytotoxic[M] ?Carcinogenic[M]
P. cyclopium	*Viridicata*	Xanthomegnins	Heptaketide	Hepato- and nephrotoxin[M]
P. cyclopium	*Viridicata*	Puberulic acids	Tetraketide	Antibiotic[P]
P. cyclopium	*Viridicata*	Puberulines	TRP, PHE, acetate, terpene (DMA)	
P. cyclopium	*Viridicata*	Verrucofortins	TRP, LEU, acetate, terpene (DMA)	
P. cyclopium	*Viridicata*	Cyclopenins	ANT, PHE, O_2	Herbicidal Anti-HIV[P] (3-O-methylviridicatin)
P. cyclopium (?)	*Viridicata*	Cyclopin	Protein (trypsin sensitive)	Antiviral
P. digitatum	*Digitata*	Tryptoquialanins	TRP, ALA, terpene (DMA)	
P. digitatum	*Digitata*	Phenylalanine proline diketopiperazine	PHE, PRO	

P. dipodomyicola	*Urticicolae*	Patulins	Tetraketide	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. dipodomyicola	*Urticicolae*	Griseofulvins	Heptaketide, Cl	Antifungal[P] Teratogenic[M]
P. dipodomyicola	*Urticicolae*	Cyclopiazonic acid	TRP, terpene (DMA), acetoacetyl unit	Organ-damage in mammals[M]
P. dipodomyis	*Chrysogena*	Dipodazin	TRP, GLY	
P. dipodomyis	*Chrysogena*	Penicillins	VAL, CYS, α-aminoadipic acid	Antibiotic[P]
P. discolor	*Solita*	Palitantin, frequentin	Heptaketide	Frequentin is antifungal[P]
P. discolor	*Solita*	Daldinin D	?Pentaketide	
P. discolor	*Solita*	Chaetoglobosins	Polyketide, TRP	Cytotoxic[M,P]
P. discolor	*Solita*	Cyclopenins	ANT, PHE, O_2	Herbicidal
P. echinulatum	*Solita*	Arisugacins	?Polyketide, shikimate	Acetylcholinesterase inhibitors[P]
P. echinulatum	*Solita*	Territrems	?Polyketide, shikimate	Acetylcholinesterase inhibitors[P] Tremorgens[M]
P. echinulatum	*Solita*	Palitantin, frequentin	Heptaketide	Frequentin is antifungal[P]
P. echinulatum	*Solita*	Cyclopenins	ANT, PHE, O_2	Herbicidal
P. expansum	*Expansa*	Patulin	Tetraketide	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. expansum	*Expansa*	Citrinin	Pentaketide, 2 MET	Antibiotic[P] Nephrotoxin[M]
P. expansum	*Expansa*	Expansolide	Terpene	
P. expansum	*Expansa*	Chaetoglobosins	Polyketide, TRP	Cytotoxins[M,P]
P. expansum	*Expansa*	Aurantioclavine	TRP, terpene (DMA)	
P. expansum	*Expansa*	N-acetyltryptamine	TRP, terpene (DMA)	Serotinin inhibitor[P]
P. expansum	*Expansa*	Communesins	TRP, tryptamine, acetate or sorbic acid	Cytotoxins[M,P]
P. expansum	*Expansa*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. expansum	*Expansa*	Fumaryl-d,l-alanine	ALA, fumaric acid	Antibiotic[P]
P. flavigenum	*Chrysogena*	Penicillins	VAL, CYS, α-aminoadipic acid	Antibiotic[P]
P. flavigenum	*Chrysogena*	Xanthocillins	Shikimic acid pathway	Antibiotic[P]
P. flavigenum	*Chrysogena*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. flavigenum	*Chrysogena*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. flavigenum	*Chrysogena*	Penitrems	TRP, terpene	Acutely toxic[M] Tremorgen[M]
P. formosanum	*Claviformia*	Patulin	Tetraketide	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. formosanum	*Claviformia*	Asteltoxin	Nonaketide	Mycotoxin[M]
P. freii	*Viridicata*	Penicillic acid	Tetraketide	Antibiotic[P] Antiviral[P] Antitumor[P] Cytotoxic[M] ?Carcinogenic[M]
P. freii	*Viridicata*	Xanthomegnins	Heptaketides	Hepato- and nephrotoxins[M]
P. freii	*Viridicata*	Aurantiamine	VAL, HIS, terpene (DMA)	Cell cycle inhibitor[P]
P. freii	*Viridicata*	Cyclopenins	ANT, PHE, O_2	Herbicidal Anti-HIV[P] (3-O-methylviridicatin)
P. gladioli	*Gladioli*	Gladiolic acids	Tetraketide	Antifungal[P]

				Antibiotic[P]
P. gladioli	*Gladioli*	3,5-dimethyl-6-hydroxyphthalide	Tetraketide	
P. gladioli	*Gladioli*	Patulin	Tetraketide	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. gladioli	*Gladioli*	Atrovenetins	Heptaketides	Antioxidant[P]
P. gladioli	*Gladioli*	Glyanthrypine	ANT, GLY	
P. glandicola	*Claviformia*	Patulin	Tetraketide	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. glandicola	*Claviformia*	Patulidins	Hexaketides	Antifungal (fatty acid synthase inhibitor)[P]
P. glandicola	*Claviformia*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. glandicola	*Claviformia*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. glandicola	*Claviformia*	Penitrems	TRP, terpene	Neurotoxin[M]
P. griseofulvum	*Urticicolae*	Patulins	Tetraketides	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. griseofulvum	*Urticicolae*	Griseofulvins	Heptaketide, Cl	Antifungal[P] Teratogenic[M]
P. griseofulvum	*Urticicolae*	(Patulidin)	Hexaketides	Antifungal (fatty acid synthase inhibitor)[P]
P. griseofulvum	*Urticicolae*	Fulvic acids	Heptaketides	
P. griseofulvum	*Urticicolae*	Mycelianamide	TYR, ALA, terpene	Antibiotic[P]
P. griseofulvum	*Urticicolae*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. griseofulvum	*Urticicolae*	Penicillins	VAL, CYS, α-aminoadipic acid	Antibiotic[P]
P. griseofulvum	*Urticicolae*	Cyclopiazonic acid	TRP, terpene (DMA), acetoacetyl unit	Organ damage in mammals[M]
P. griseofulvum	*Urticicolae*	Cyclopiamine	TRP, PRO, terpenes (2 x DMA), nitro	
P. griseofulvum	*Urticicolae*	Cyclopiamide	TRP, terpene (DMA)	
P. griseofulvum	*Urticicolae*	Chanoclavine-I	TRP, terpene (DMA)	
P. hirsutum	*Corymbifera*	Terrestric acids	TCA cycle, acetate	Cardiotoxin[M]
P. hirsutum	*Corymbifera*	Compactins	Nonaketides	Cholesterol lowering[P]
P. hirsutum	*Corymbifera*	Daldinin D	Hexaketide	
P. hirsutum	*Corymbifera*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. hirsutum	*Corymbifera*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. hordei	*Corymbifera*	Terrestric acids	TCA cycle, acetate	Cardiotoxin[M]
P. hordei	*Corymbifera*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. italicum	*Italica*	Italinic acids	?TCA cycle, acetate	
P. italicum	*Italica*	2,5-dihydro-4-methoxy-2H-pyran-2-one	Pentaketide	Mycotoxin[M]
P. italicum	*Italica*	Verrucolone	Pentaketide	Herbicidal
P. italicum	*Italica*	Fulvic acids	Heptaketides	
P. italicum	*Italica*	Deoxybrevianamide E	TRP, PRO, terpene (DMA)	
P. italicum	*Italica*	Xanthocillins	Shikimic acid pathway	Antibiotic[P]
P. italicum	*Italica*	4-methoxy-6-n-propenyl-2-pyrone	?Polyketide	
P. italicum	*Italica*	5-hydroxymethyl-2-furic acid	?Polyketide	
P. marinum	*Expansa*	Patulins	Tetraketides	Antibiotic[P] ?Carcinogenic[M]

				Cytotoxic[M] Generally toxic[M]
P. marinum	*Expansa*	3,5-dimethyl-6-hydroxyphthalide	Tetraketide	
P. marinum	*Expansa*	Expansolide	Terpene	
P. marinum	*Expansa*	Penostatins	Terpenes	Cytotoxins[P,M]
P. marinum	*Expansa*	Chaetoglobosins	Polyketide, TRP	Cytotoxins[M,P]
P. marinum	*Expansa*	Penochalasins	Polyketide, TRP, other amino acid?	Cytotoxins[M,P]
P. marinum	*Expansa*	Aurantioclavine	TRP, terpene (DMA)	
P. marinum	*Expansa*	N-acetyltryptamine	TRP	Serotonin inhibitor[P]
P. marinum	*Expansa*	Communesins	TRP, tryptamine, acetat or sorbic acid	Cytotoxins[M,P]
P. marinum	*Expansa*	Roquefortine C	TRP, HIS, terpene (DMA)	Neurotoxin[M]
P. melanoconidium	*Viridicata*	Penicillic acid	Tetraketide	Antibiotic[P] Antiviral[P] Antitumor[P] Cytotoxic[M] ?Carcinogenic[M]
P. melanoconidium	*Viridicata*	Verrucosidins	Nonaketide	Tremorgenic[M]
P. melanoconidium	*Viridicata*	Xanthomegnins	Heptaketides	Hepato- and nephrotoxins[M]
P. melanoconidium	*Viridicata*	Roquefortine C	TRP, HIS, terpene (DMA)	Neurotoxin[M]
P. melanoconidium	*Viridicata*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. melanoconidium	*Viridicata*	Oxaline	TRP, HIS, terpene (DMA)	
P. melanoconidium	*Viridicata*	Sclerotigenine	ANT	Antiinsectan
P. melanoconidium	*Viridicata*	Penitrem A	TRP, terpene	Tremorgenic[M] Acutely toxic[M] Anti-mite
P. mononematosum	*Mononematosa*	Isochromantoxins	Pentaketide	Mycotoxins[M]
P. mononematosum	*Mononematosa*	Cyclopaldic acids	Tetraketide	Antibiotic[P]
P. mononematosum	*Mononematosa*	Viriditoxin	Octaketide	Mycotoxin[M]
P. mononematosum	*Mononematosa*	Verrucologen and fumitremorgins	TRP, PRO, terpene (DMA), O_2	Anticancer[P] (fumitremorgin C) Acutely toxic[M] Tremorgens[M]
P. nalgiovense	*Chrysogena*	Nalgiovensins	Nonaketide	
P. nalgiovense	*Chrysogena*	Diaporthins	Hexaketide	
P. nalgiovense	*Chrysogena*	Dipodazin	TRP, GLY	
P. nalgiovense	*Chrysogena*	Penicillins	VAL, CYS, α-aminoadipic acid	Antibiotic[P]
P. nalgiovense	*Chrysogena*	Peptaibol	AIB, ILE, LEU, PRO, GLU, GLY	Antibiotic[P]
P. nalgiovense	*Chrysogena*	PAF (Geisen, 2000)	A protein	Antifungal[P]
P. neoechinulatum	*Viridicata*	Penicillic acid	Tetraketide	Antibiotic[P] Antiviral[P] Antitumor[P] Cytotoxic[M] ?Carcinogenic[M]
P. neoechinulatum	*Viridicata*	Aurantiamine	VAL, HIS, terpene (DMA)	Cell cycle inhibitor[P]
P. neoechinulatum	*Viridicata*	Cyclopenins	ANT, PHE, O_2	Herbicidal Anti-HIV[P] (3-O-methylviridicatin)
P. nordicum	*Verrucosa*	Verrucolones, pestalotins	Pentaketides	Herbicidal
P. nordicum	*Verrucosa*	Ochratoxin A	Pentaketide, PHE, Cl	Nephrotoxin[M] Antiinsectan
P. nordicum	*Verrucosa*	Met I (asperenone-like)	Asperenone is a terpene	
P. nordicum	*Verrucosa*	Anacine	ANT, GLN, LEU	
P. nordicum	*Verrucosa*	Sclerotigenin	ANT	Antiinsectan

P. nordicum	*Verrucosa*	Viridic acid	Dimethylamin-orthosubstituted PHE, carboxylic orthosubstituted PHE, LEU	Mycotoxin[M]
P. nordicum	*Verrucosa*	Lumpidin	TRP, PHE, homo-PRO	
P. olsonii	*Olsonii*	Verrucolones, pesta-lotins	Pentaketides	Herbicidal
P. olsonii	*Olsonii*	2-(4-hydroxyphenyl)-2-oxo acetaldehyde oxime	?Polyketide	
P. olsonii	*Olsonii*	Bis(2-ethylhexyl)phthalate	?Polyketide	
P. olsonii	*Olsonii*	Breviones	Diterpenoid	Allelochemical
P. olsonii	*Olsonii*	Asperphenamate	PHE	
P. palitans	*Camemberti*	Palitantin	Heptaketide	Frequentin is antifungal[P]
P. palitans	*Camemberti*	Cyclopiazonic acid	TRP, terpene (DMA), acetoacetyl unit	Organ damage in mam-mals[M]
P. palitans	*Camemberti*	Fumigaclavines	TRP, terpene (DMA)	
P. palitans	*Camemberti*	Met I (asperenone-like)	Asperenone is a terpene	
P. paneum	*Roqueforti*	Patulins	Tetraketides	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. paneum	*Roqueforti*	Botryodiploidin	Tetraketide	Mutagenic[M] Teratogenic[M] Anticancer[P]
P. paneum	*Roqueforti*	Citreoisocoumarins	Hexaketide	
P. paneum	*Roqueforti*	Roquefortine C	TRP, HIS, terpene (DMA)	Neurotoxin[M]
P. paneum	*Roqueforti*	Marcfortins	TRP, PRO, terpenes (DMA)	
P. persicinum	*Persicina*	Griseofulvins	Heptaketides, Cl	Antifungal[P] Teratogenic[M]
P. persicinum	*Persicina*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. persicinum	*Persicina*	Chrysogine	ANT	Anti-auxin
P. polonicum	*Viridicata*	Penicillic acid	Tetraketide	Antibiotic[P] Antiviral[P] Antitumor[P] Cytotoxic[M] ?Carcinogenic[M]
P. polonicum	*Viridicata*	Verrucosidin	Nonaketide	Tremorgen[M]
P. polonicum	*Viridicata*	Methyl-4-(2-(2R)-hydroxyl-3-butynyloxy) benzoate	?Polyketide	
P. polonicum	*Viridicata*	Aspterric acid	Terpene	
P. polonicum	*Viridicata*	Anacin	ANT, GLN, LEU	
P. polonicum	*Viridicata*	Puberulines	TRP, PHE, acetate, terpene (DMA)	
P. polonicum	*Viridicata*	Verrucofortines	TRP, LEU, acetate, terpene (DMA)	
P. polonicum	*Viridicata*	Cyclopenins	ANT, PHE, O_2	Herbicidal Anti-HIV[P] (3-O-methylviridicatin)
P. polonicum	*Viridicata*	Nephrotoxic glycopep-tides	Glycopeptide with ASP, GLU, GLY, TYR, LYS, ILE, PHE (Yeulet *et al*., 1988)	Nephrotoxic[M]
P. radicicola	*Corymbifera*	Penicillic acid	Tetraketide	Antibiotic[P] Antiviral[P] Antitumor[P] Cytotoxic[M]

				?Carcinogenic[M]
P. radicicola	*Corymbifera*	Citrinin	Pentaketide, 2 MET	Antibiotic[P] Nephrotoxic[M]
P. radicicola	*Corymbifera*	Terrestric acid	TCA cycle derived	Cardiotoxin[M]
P. radicicola	*Corymbifera*	Chrysogine	ANT	Anti-auxin
P. radicicola	*Corymbifera*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. radicicola	*Corymbifera*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic[P]
P. radicicola	*Corymbifera*	Cyclopenins	ANT, PHE, O_2	Herbicidal Anti-HIV[P] (3-O-methylviridicatin)
P. roqueforti	*Roqueforti*	Citreoisocoumarin	Hexaketide	
P. roqueforti	*Roqueforti*	Mycophenolic acids	Tetraketide, terpene (farnesyl)	Immunosuppressive[M, P]
P. roqueforti	*Roqueforti*	PR-toxin	Sesquiterpene	Inhibits RNA polymerase[M]
P. roqueforti	*Roqueforti*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. roqueforti	*Roqueforti*	Isofumigaclavines	TRP, terpene (DMA)	Weak pharmacological effects[P]
P. roqueforti	*Roqueforti*	α-aminoisobutyric acid peptide (peptaibol): roquecin	AIB, ALA, GLY and several other amino acids	Antibiotic[P]
P. sclerotigenum	*Expansa*	Patulins	Tetraketides	Antibiotic[P] ?Carcinogenic[M] Cytotoxic[M] Generally toxic[M]
P. sclerotigenum	*Expansa*	Griseofulvins	Heptaketide, Cl	Antifungal[P] Teratogenic[M]
P. sclerotigenum	*Expansa*	Gregatins	?	Phytotoxin Antibiotic[P]
P. sclerotigenum	*Expansa*	Sclerotigenin	ANT	Anti-insectan
P. sclerotigenum	*Expansa*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]
P. solitum	*Solita*	Compactins	Nonaketides	Cholesterol-lowering[P]
P. solitum	*Solita*	Solistatin	Nonaketide	Cholesterol-lowering[P]
P. solitum	*Solita*	Palitantin	Heptaketide	Frequentin is antifungal[P]
P. solitum	*Solita*	Cyclopenins	ANT, PHE, O_2	Herbicidal
P. thymicola	*Verrucosa*	Verrucolones and pestalotins	Pentaketides	Herbicidal
P. thymicola	*Verrucosa*	Daldinine D	Hexaketide	
P. thymicola	*Verrucosa*	Penigequinolones	ANT, PHE + ?terpene	Pollen growth inhibitor Nedmaticidal Toxic to *Artemisia*
P. thymicola	*Verrucosa*	Fumiquinazoline F & alantrypinone, serantrypinone	ANT, TRP, L-ALA (serantrypinone has SER instead of ALA)	
P. thymicola	*Verrucosa*	Anacine	ANT, GLN, LEU	
P. tricolor	*Viridicata*	Terrestric acid	TCA-cycle, acetate	Cardiotoxin[M]
P. tricolor	*Viridicata*	Asteltoxin	Nonaketide	Mycotoxin[M]
P. tricolor	*Viridicata*	Xanthomegnins	Heptaketide	Hepato- and nephrotoxins[M]
P. tricolor	*Viridicata*	Puberulins	TRP, PHE, acetate, terpene (DMA)	
P. tricolor	*Viridicata*	Verrucofortines	TRP, LEU, acetate, terpene (DMA)	
P. tulipae	*Corymbifera*	Terrestric acid	TCA-cycle, acetate	Cardiotoxin[M]
P. tulipae	*Corymbifera*	Penicillic acid	tetraketide	Antibiotic[P] Antiviral[P] Antitumor[P] Cytotoxic[M] ?Carcinogenic[M]
P. tulipae	*Corymbifera*	Chrysogine	ANT	Anti-auxin
P. tulipae	*Corymbifera*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic[P] Neurotoxin[M]

P. tulipae	*Corymbifera*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic^P
P. tulipae	*Corymbifera*	Neoxaline	TRP, HIS, terpene (DMA)	
P. tulipae	*Corymbifera*	Penitrem A	TRP, terpene, Cl	Tremorgen^M Acutely toxic^M
P. ulaiense	*Italica*	Deoxybrevianamide E	TRP, PRO, terpene (DMA)	
P. venetum	*Corymbifera*	Terrestric acid	TCA-cycle, acetate	Cardiotoxin^M
P. venetum	*Corymbifera*	Atrovenetins	Heptaketides	Antioxidants^P
P. venetum	*Corymbifera*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic^P Neurotoxin^M
P. venetum	*Corymbifera*	Cyclopenins	ANT, PHE, O_2	Herbicidal Anti-HIV^P (3-O-methylviridicatin)
P. verrucosum	*Verrucosa*	Verrucolones and pestalotins	Pentaketides	Herbicidal
P. verrucosum	*Verrucosa*	Ochratoxins	Pentaketide, PHE, Cl	Nephrotoxin^M, anti-insectan
P. verrucosum	*Verrucosa*	Citrinin	Pentaketide, 2 MET	Nephrotoxin^M Antibiotic^P
P. verrucosum	*Verrucosa*	Red brown anthraquinone (as indicated by the UV spectrum)	?Polyketide	
P. verrucosum	*Verrucosa*	Met I (like asperenone)	Asperenone is a terpene	
P. verrucosum	*Verrucosa*	Verrucins	ANT, GLN, PHE	
P. viridicatum	*Viridicata*	Penicillic acid	Tetraketide	Antibiotic^P Antiviral^P Antitumor^P Cytotoxic^M ?Carcinogenic^M
P. viridicatum	*Viridicata*	Xanthomegnins	Heptaketide	Hepato- and nephrotoxins^M
P. viridicatum	*Viridicata*	Brevianamides	TRP, PRO	Insecticidal
P. viridicatum	*Viridicata*	Viridic acid	Dimethylamin-orthosubstituted PHE, carboxylic orthosubstituted PHE, LEU	Acutely toxic^M
P. viridicatum	*Viridicata*	Viridamine	VAL, HIS, terpene (DMA)	
P. vulpinum	*Claviformia*	Asterric acid	Octaketide	
P. vulpinum	*Claviformia*	Pachybasin	Octaketide	
P. vulpinum	*Claviformia*	Patulin	Tetraketide	Antibiotic^P ?Carcinogenic^M Cytotoxic^M Generally toxic^M
P. vulpinum	*Claviformia*	Lichexanthone	Heptaketide	
P. vulpinum	*Claviformia*	Cyclopenins	ANT, PHE, O_2	Herbicidal
P. vulpinum	*Claviformia*	Roquefortine C	TRP, HIS, terpene (DMA)	Antibiotic^P Neurotoxin^M
P. vulpinum	*Claviformia*	Meleagrin	TRP, HIS, terpene (DMA)	Antibiotic^P
P. vulpinum	*Claviformia*	Oxaline	TRP, HIS, terpene (DMA)	
P. vulpinum	*Claviformia*	Cyclopiamine	TRP, PRO, terpenes (2 x DMA), nitro	

AIB: α-aminobutyric acid, ALA: alanine, ANT: anthranilic acid, ASP: asparagine, DMA: dimethylallyl, CYS: cysteine, GLN: glutamine, GLY: glycine, HIS: histidine, ILE: Isoleucine, LEU: leucine, MET: methionine, PHE: phenylalanine, PRO: proline, SER: serine, TCA: tricarboxylic acid, TYR: tyrosine, VAL: valine.

The extrolite families produced by species in *Penicillium* subgenus *Penicillium* are listed in Table 3. A very large number of polyketides, amino acid derived metabolites, terpenes, and extrolites with mixed biosynthetic origins were detected in most species. The number of polyketide biosynthetic families in subgenus *Penicillium* detected thus far is 49, whereas 3 families of extrolites are probably derived directly from the citric acid cycle (gregatins, italinic acid, terrestric acid), nine extrolite families are terpene derived, excluding ergosterol which was produced by all species examined. 45 extrolite families were primarily amino acid derived. Of these most were diketopiperazines, but small peptides such as penicillin and viridic acid were also found. The number of terpenes may seem low, but it should be noted that most of the amino acid derived extrolite families include the addition of one or more terpene units, such as dimethyl allyl groups. Some polyketides also involve addition of a terpene unit: mycophenolic acid, for example, includes a farnesyl group in the molecule. Finally the biosynthesis of several polyketides involves the use of the amino acid methionine as a methyl donor (citrinin for example) and some amino acids are directly added to the molecule: for example phenylalanine is added to a polyketide in ochratoxin A (Steyn *et al*., 1983) and in pseurotin A (Mohr and Tamm, 1981).

Consistency in extrolite production

In most cases the production of extrolites is consistent from isolate to isolate in a species (see Frisvad and Filtenborg, 1989, 1990b) For example all isolates of *P. griseofulvum* examined produced patulin, griseofulvin, cyclopiazonic acid and roquefortine C, without exceptions. Likewise all isolates of *P. freii* produced xanthomegnin, viomellein, vioxanthin, aurantiamine and the cyclopenins. Some extrolites were consistently produced in most species, while the production was rare in isolates of other species. For example few isolates of *P. freii* and *P. carneum* produce penicillic acid, and future molecular data will show whether the genes for penicillic acid production are present in all isolates of those two species. In other species, such as *P. aurantiogriseum, P. polonicum, P. melanoconidium* and *P. cyclopium*, penicillic acid production is very consistent.

Mycotoxin production

The Penicillia found in foods can produce several mycotoxins in these foods under certain conditions (Miller and Trenholm, 1994; Weidenbörner, 2001). Some of the most important mycotoxins, such as the fumonisins, trichothecenes, zearalenone, tenuazonic acid, sterigmatocystin and the aflatoxins are **not** produced by species in the genus *Penicillium*. There has been a report on aflatoxin production by *Penicillium puberulum* ATCC 15683 = NRRL A-12539 (Hodges *et al*., 1964), later reidentified by us to *P. polonicum*. An extract from this fungus "produced the typical bile duct proliferation type of liver damage that is characteristic of the aflatoxin effect" in Peking white ducklings (Hodges *et al*., 1964). Neither the original isolate nor any other isolate in series *Viridicata* produced any aflatoxins or their precursors. If the culture, originally isolated from rejected mouldy peanuts, was not contaminated with *A. flavus* or *A. parasiticus*, other fluorescing extrolites from *P. polonicum* may have caused the liver damage. In that case known compounds from *P. polonicum* should be screened for liver damaging effects.

Maskey *et al*. (2003) reported that sterigmatocystin was produced by *Penicillium chrysogenum* together with the antifungal 8-O-methylaverufin, 1,8-O-dimethylaverantin and several other metabolites of the sterigmatocystin pathway. The original isolate was sent to us and examined and showed to be a mixed culture of *Aspergillus versicolor*, a known producer of sterigmatocystin, and *P. chrysogenum*. The latter culture did not produce sterigmatocystin. Therefore we conclude that species in *Penicillium* subgenus *Penicillium* are not able to produce aflatoxins or sterigmatocystins.

Most of the 58 species produced mycotoxins. Species that apparently did not produce mycotoxins included *P. caseifulvum, P. digitatum, P. nalgiovense, P. olsonii, P. solitum, P. thymicola* and *P. ulaiense*. Even though most of the species produce mycotoxins under laboratory conditions, they may not do so under industrial conditions. For example one can find isolates of *P. camemberti* and *P. roqueforti* that do not produce the usual mycotoxins, so they can be safely used in the cheese industry. In other cases the mycotoxins are unstable in a food product (Teuber and Engel, 1983).

The nephrotoxic and possibly carcinogenic ochratoxins are only produced by *P. verrucosum* and *P. nordicum* (Table 1; Larsen *et al*., 2001a), despite several reports on ochratoxin production by other terverticillate Penicillia (Table 1). The former species is very common in cereals (Lund and Frisvad, 2003), while *P. nordicum* is common on dried meat products such as salami and ham. Both species can occur on cheese. Ochratoxin A production seems to specific to series *Verrucosa* in *Penicillium*, while it has been found in two closely related sections of *Aspergillus*, section *Flavi* and section *Circumdati* (Frisvad and Samson, 2000).

The nephrotoxin citrinin is produced by *Penicillium expansum, P. radicicola* and *P. verrucosum*. These three species are most common on apples and other pomaceous fruits, tap-root plants and cereals respectively.

The very toxic extrolite patulin is produced by 13 species, *P. carneum, P. clavigerum, P. concentricum, P. coprobium, P. dipodomyicola, P. expansum, P. glandicola, P. gladioli, P. griseofulvum, P. marinum, P. paneum, P. sclerotigenum* and *P. vulpinum*. The most important species concerning foods are *P. carneum* (in beer, wine, on rye-bread and on dry meat products), *P. expansum* (on pomaceous fruits and nuts), *P. griseofulvum* (on cereals), *P. paneum* (on rye-bread) and *P. sclerotigenum* (on yams). The remaining species are primarily dung-associated and hopefully very uncommon in foods.

Penicillic acid, another general toxin, is produced by *P. aurantiogriseum, P. carneum, P. cyclopium, P. freii, P. melanoconidium, P. neoechinulatum, P. polonicum, P. radicicola, P. tulipae* and *P. viridicatum*. Most of these species are common on cereals, whereas *P. radicicola* is common on tap-root plants and *P. carneum* is common in wine, beer, rye-bread and on dry meat products). *P. polonicum* is found often both in cereals and on dry meat products.

The tremorgenic mycotoxin verrucosidin, in combination with both nephrotoxic glycopeptides and penicillic acid are produced by *P. aurantiogriseum*, *P. polonicum* and possibly *P. melanoconidium*. The nephrotoxic glycopeptides have not been found yet in *P. melanoconidium*, however.

The tremorgenic mycotoxin penitrem A is produced by several taxonomically quite unrelated fungi: *P. carneum, P. clavigerum, P. crustosum, P. flavigenum, P. glandicola, P. melanoconidium* and *P. tulipae*.

The very toxic tremorgens verrucologen, fumitremorgin A and B are only produced by *P. mononematosum*. This species has not yet been found in foods.

Cyclopiazonic acid is a chelating mycotoxin that has been found in *P. camemberti, P. commune, P. dipodomyicola, P. palitans*, and *P. griseofulvum*. This toxin may be produced in cheeses (*P. commune, P. camemberti* and *P. palitans*) or on cereals (*P. griseofulvum*).

Secalonic acid D and F produced by some strains of *P. chrysogenum* and by the uncommon *P. confertum* may be a neglected mycotoxin. *P. chrysogenum* is common in dry foods and indoor air (Samson *et al*., 2004).

Useful extrolites: Lead compounds and drugs

All 58 species produced bioactive compounds. Often even mycotoxins may have pharmacologically interesting characteristics, and could at least be used for structure-activity studies. *P. nordicum*, *P. olsonii*, *P. thymicola*, *P. tricolor* and *P. ulaiense* did not contain known antibiotics or lead compounds, but they produced several partly characterised extrolites that may have interesting activities (Table 2).

The important antibiotic penicillin has made *Penicillium* famous, but this occurs only in a few species of *Penicillium.* All species in series *Chrysogena* (*P. chrysogenum, P. flavigenum, P. dipodomyis, P. nalgiovense*) produce penicillin as do *P. griseofulvum* (Johns *et al*., 1946). Penicillin production by *P. griseofulvum* was later confirmed by Laich *et al*. (2002), who also showed that part of the genes for penicillin production are present in *P. nordicum* (identified by them as *P. verrucosum*). It is interesting that most penicillin producers are often isolated from meat products like salami and ham. Production of penicillin could be predicted in *P. dipodomyicola* based on taxonomic and phylogenetic similarity and also in *P. olsonii* which has a high occurrence on meat products. Together with *P. nalgiovense, P. chrysogenum* and *P. nordicum, P. olsonii* was found commonly on naturally fermented sausages (Andersen, 1995). The potential production of penicillin by these species has not been examined yet.

Compactin (= mevistatin), the important cholesterol lowering agent, has only been found in *Penicillium solitum* and *P. hirsutum* in subgenus *Penicillium*. Until now the compactins have only been found in species growing at low temperatures, including *P. lanosum* from *Penicillium* subgenus *Furcatum* (Frisvad and Filtenborg, 1990a). The latter species is common in soil in cold and Alpine areas (Domsch *et al*., 1980). It has not been clear whether compactins are important for the ergosterol metabolism in some fungi which can grow in cold areas, or whether it is the antifungal effect of compactin (Brown *et al*., 1976) that is its functional value. As with most other extrolites, ecological rather than phylogenetic considerations may be used for prediction of their presence.

Mycophenolic acid (mycophenolic acid mofetil) is a very important drug with several potential applications (Bentley, 2000). It is presently used in heart transplantation to avoid organ rejection. This extrolite is produced by *P. brevicompactum, P. bialowiezense, P. carneum* and *P. roqueforti* in subgenus *Penicillium* (Table 1).

Griseofulvin has been used for many years for curing fungal infections of man, but is used less frequently now because of several side effects. This antifungal compound is produced by some related and some unrelated fungi: *P. griseofulvum* and *P. dipodomyicola* from series *Urticicolae* and, *P. aethiopicum*, *P. persicinum*, *P. sclerotigenum* and *P. coprophilum*.

Screening of 15,000 fungal extracts yielded 3-O-methylviridicatin as active against HIV virus (Heguy *et al*., 2003). The fungus producing this extrolites was not identified, but 3-O-methylviridicatin is common in subgenus *Penicillium*. 17 species in subgenus *Penicillium* and *P. scabrosum* in subgenus *Furcatum* (Frisvad *et al*., 1990b) produce this biosynthetic family.

Being cytotoxic, several extrolites from subgenus *Penicillium* species are potential anticancer agents including alternariol, aurantiamine, chaetoglobosins communesin A & B, fumitremorgin C, hadacidin, paclitaxel, penicillic acid, PR-toxin, and viridicatumtoxin (Table 1). Fumitremorgin C and paclitaxel appear to show most promise in cancer treatment.

Some extrolites are effective antioxidants, such as atrovenetins, aurantionone and 2,3-dihydroxy benzoic acid (Table 1).

Several extrolites listed in Tabel 1 are anti-insecticidal, including brevianamide A, ochratoxin A, and sclerotigenin (Gloer, 1995). Some of these compounds are probably too toxic to be used commercially (ochratoxin A), others may be promising.

Finally some compounds may be potential herbicides, including verrucolone (= arabenoic acid), chrysogines, cyclopenol, hadacidin and few others. This effect may be ecologically important as the compounds are primarily produced by species occurring on plants. For example *P. verrucosum* occurs on cereals and produces the herbicidal compound verrucolone. This compound is also found in *P. olsoni,* which is common on tomatoes and other plants and *P. italicum* which is common on citrus.

Prediction of antibiotic production from habitat

Some species may produce a surprisingly high number of antibiotic and antifungal compounds. *P. chrysogenum* has been reported to produce the antibiotic biosynthetic families penicillins, sorbicillins, secalonic acids (including sorrentanone), roquefortine C (and also meleagrin), xanthocillins, questiomycins, negapillin and notatin and the antifungal protein PAF (Table 2). The reason in this case must be that *P. chrysogenum* has been scrutinized since 1940 for antibiotics other than penicillin. *P. chrysogenum* is often found on cheese and salami, where bacteria often occur and also in indoor environments where bacteria are also common. It can be predicted that coprophilic fungi produce many antibiotics also, as they occur in a competive environment with many other fungi and bacteria, and indeed species from series *Claviformia* produce several antibiotics and antifungals (Table 2), including patulin, roquefortine C, meleagrin, griseofulvin and asperfuran. Some of the same extrolites are also found in series *Urticicolae* and *Expansa*, whereas patulin and griseofulvin have never been found in section *Viridicata*. Species in the latter section are more common on semi-dried foods and produce other extrolites such as xanthomegnins, verrucolones, ochratoxins, puberulins, penicillic acids, verrucosidins, cyclopenins, and atrovenetin.

In conclusion, species in *Penicillium* subgenus *Penicillium* produce a very large number of biologically active extrolites, including some of the most important pharmaceuticals and mycotoxins. The biosynthetic potential in this subgenus and its 58 species is very large and still not fully explored. We predict that several new interesting bioactive extrolites will be found in *Penicillium*.

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