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A critical review of producers of small lactone mycotoxins: patulin, penicillic acid and moniliformin

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Abstract

A very large number of filamentous fungi has been reported to produce the small lactone mycotoxins patulin, penicillic acid and moniliformin. Among the 167 reported fungal producers of patulin, only production by 29 species could be confirmed. Patulin is produced by 3 *Aspergillus* species, 3 *Paecilomyces* species, 22 *Penicillium* species from 7 sections of *Penicillium*, and one *Xylaria* species. Among 101 reported producers of penicillic acid, 48 species could produce this mycotoxin. Penicillic acid is produced by 23 species in section *Aspergillus* subgenus *Circumdati* section *Circumdati*, by *Malbranchea aurantiaca* and by 24 *Penicillium* species from 9 sections in *Penicillium* and one species that does not actually belong to *Penicillium* (*P. megasporum*). Among 40 reported producers of moniliformin, five species have been regarded as doubtful producers of this mycotoxin or are now regarded as taxonomic synonyms. Moniliformin is produced by 34 *Fusarium* species and one *Penicillium* species. All the accepted producers of patulin, penicillic acid and moniliformin were revised according to the new one fungus – one name nomenclatural system, and the most recently accepted taxonomy of the species.

Keywords: patulin, penicillic acid, moniliformin, terrestric acid, *Penicillium*, *Aspergillus*, *Fusarium*

1. Introduction

Small toxic lactones, especially patulin, penicillic acid and moniliformin are recognised mycotoxins (Bemi, 2004; Ciegler *et al.*, 1971; Gaucher, 1979; McKinley and Carlton, 1991; Moake *et al.*, 2005; Puel *et al.*, 2010; Schütt *et al.*, 1998; Scott, 1974; Wilson, 1976), even though only patulin is under regulation (EC, 2003). They share some properties apart from being toxic and having some structural similarities. They are all polar, acidic, secondary metabolites often produced in large amounts in foods and feeds (Ciegler *et al.*, 1971), even though they differ in the niches their producers occupy: patulin is often associated with fruits and penicillic acid and moniliformin with cereals. Patulin and penicillic acid were early on recognised as effective antibiotics (Chain *et al.*, 1942; Florey *et al.*, 1949; Korzybski *et al.*, 1967; Oxford *et al.*, 1942; Singh, 1967), and have later been show also to inhibit quorum sensing in bacteria (Rasmussen *et al.*, 2005). Patulin and penicillic acid also share a specific reaction with the sulfhydryl-

containing amino acids cysteine and glutathione (Larsen and Olson, 1992; Morgavi *et al.*, 2003). While this may help inactivating these mycotoxins in foods containing cysteine and glutathione, those data indicate that part of the toxic effect of the small lactones is the binding of S-containing amino acids in proteins.

Apart from being an effective antibiotic, patulin can also produce petit mutants in *Saccharomyces cerevisiae* (Mayer and Legator, 1969). Patulin can act as a phytotoxin (Ellis *et al.*, 1977; Florey *et al.*, 1949; Ismail and Papenbrock, 2015; Korzybski *et al.*, 1967; Scott, 1974) and is active against pathogenic fungi (Gilliver, 1946; Herrick, 1945; Sanders, 1946). Patulin was initially suggested for treatment of common cold (Birkinshaw *et al.*, 1943; Gye, 1943), as it is anti-viral (Detroy and Still, 1975) in addition to being antibacterial, but the trials on humans were quickly dropped because of the toxicity of patulin.

Patulin has been reported to be acutely toxic (Ciegler, 1977; Devaraj *et al.*, 1986; Drusch and Ragab, 2003; Engel and Teuber, 1984; Escoula *et al.*, 1977; Fung and Clark, 2004; Hayes *et al.*, 1979; Hopkins, 1993; McKinley and Carlton, 1980a,b; McKinley *et al.*, 1982; Wouters and Speijers, 1996), teratogenic (Ciegler *et al.*, 1976; Vesely and Vesela, 1991), cardiotoxic (Vesely and Vesela, 1991), it influences the colonic epithelial permeability (Maidana *et al.*, 2016; Mohan *et al.*, 2012), and it is immunotoxic (Bourdiol *et al.*, 1990; Escoula *et al.*, 1988; Paucod *et al.*, 1990; Sharma, 1993). Patulin is first of all found in pomaceous foods like apples and pears, but also in other fruits (Beretta *et al.*, 2000; Jackson and Dombrinck-Kurtzman, 2006; Yang *et al.*, 2014).

Penicillic acid was first reported by Alsberg and Black (1913) in an examination of fungal growth in maize and potential fungal involvement in pellagra. Its structure was elucidated by Birkinshaw *et al.* (1936) and its antibacterial effect against Gram positive and Gram negative bacteria was first reported by Oxford in 1942, Oxford *et al.* in 1942 and Geiger and Conn in 1945, as reviewed by Korzybski *et al.* (1967). Later the antibiotic effect of penicillic acid has also been reported by Ezzat *et al.* (2007). Penicillic acid is also very inhibitory towards *Phytophthora* species (Kang and Kim, 2004). Furthermore, penicillic acid is phytotoxic (Ismail and Papenbrock, 2015).

Penicillic acid has been shown to be acutely toxic to poultry, mice, rats and rabbits (Cole and Cox, 1981). Furthermore, it dilates blood vessels and possesses antidiuretic properties (Murnaghan, 1946). Penicillic acid has been involved in broiler chicken mycotoxicosis (Ghadevaru, 2013; Samadha and Balachandran, 2008; Sarmadha *et al.*, 2008) but gingerol has been shown to alleviate the toxic effects of penicillic acid (Pazhavinel *et al.*, 2015). Penicillic acid is cytotoxic (Grabsch *et al.*, 2006), hepatotoxic (Chan and Hayes, 1981), and has been claimed to be carcinogenic and cardiotoxic (Dickens and Jones, 1961, 1963, 1965; Vesely and Vesela, 1991), and a sodium, potassium and calcium channel blocker in frog hearts (Pandiyani *et al.*, 1990). It is also toxic to rat alveolar macrophages (Sorenson and Simpson, 1986).

Ochratoxin A and penicillic acid show synergistic toxicity on bovine macrophage cell lines (Oh *et al.*, 2015), in chickens (Kubena *et al.*, 1984; Micco *et al.*, 1989), in the corn ear worm and the fall armyworm (Dowd, 1989). The two toxins together also increase degeneration in kidney proximal tubules (Klarić *et al.*, 2013; Stoev, 2013; Stoev and Denev, 2013). The synergistic worm toxicity of penicillic acid and ochratoxin A is interesting as the fungi producing these combinations of toxins are often growing in corn and other cereals (Lund and Frisvad, 1994; Visagie *et al.*, 2014a). Other studies have only shown an additive toxic effect on porcine lymphocytes of ochratoxin A and penicillic acid (Bernhoft *et al.*, 2004; Stoev *et al.*, 1999). These two mycotoxins are often co-occurring as *Aspergillus* from section *Circumdati*

produce penicillic acid and ochratoxin simultaneously in most species from that section (Visagie *et al.*, 2014a). Furthermore, species from *Penicillium* section *Fasciculata* series *Viridicata* and *Verrucosa* co-occur in cereals (Lund and Frisvad, 1995), and thus penicillic acid and ochratoxin A are also both found often in contaminated cereals.

It has been suggested that ochratoxin A and penicillic acid may both be involved in Balkan Endemic Nephropathy (Stoev, 2017; Stoev *et al.*, 2001). *Penicillium polonicum* and *Penicillium aurantiogriseum*, both producing penicillic acid, verrucosidin and nephrotoxic glycopeptides, are often found in the Balkan countries, but *Penicillium verrucosum*, the main ochratoxin A producing *Penicillium* species in cereals, is found less often (MacGeorge and Mantle, 1990; Mantle, 1994; Mantle *et al.*, 2010; Miljkovic *et al.*, 2003; Stoev *et al.*, 2010; Yeulet *et al.*, 1988). Penicillic acid is mostly found in cereals (Bokhari and Flannigan, 1996; Chełkowski and Golinski, 1983; Chełkowski *et al.*, 1983, 1987; Kurtzman and Ciegler, 1970; Szebiotko *et al.*, 1981; Tangni and Pussemier, 2007) and some other products like cassava (Wareing *et al.*, 2001).

Terrestrial acid is rather closely related to penicillic acid, and is produced by *P. aurantiogriseum*, *Penicillium crustosum* (= *Penicillium terrestre*), *Penicillium hirsutum*, *Penicillium hordei*, *Penicillium radicolica*, *Penicillium tricolor*, *Penicillium tulipae*, *Penicillium venetum* and *Magnaporthe grisea* = *Pyricularia oryzae* (Birkinshaw and Raistrick, 1936; Frisvad and Samson, 2004; Frisvad *et al.*, 1994, 2004; Lund and Frisvad, 1994; Overy and Frisvad, 2003; Overy *et al.*, 2005; Sonjak *et al.*, 2005; Yu *et al.*, 2010). Production of terrestrial acid by *Penicillium griseoroseum* (Da Silva *et al.*, 2013), and *Penicillium viridicatum* (Birkinshaw and Samant, 1960) could not be confirmed (Frisvad and Samson, 2004), other metabolites produced by these organisms indicate they were in fact *P. crustosum* (Frisvad *et al.*, 2014). Terrestrial acid has also been reported from *P. hirsutum* var. *albocoremium* (Frisvad and Filtenborg, 1989), but this taxon was later subdivided in *Penicillium albocoremium*, *P. radicolica* and *P. tulipae*. Only the last two species produce terrestrial acid (Overy and Frisvad, 2003; Overy *et al.*, 2005). This small acidic lactone is also phytotoxic (Nukina, 1988) and cardiotoxic (Giarman, 1948, 1949), thus resembling penicillic acid in some of its bioactivities. *P. aurantiogriseum*, *P. radicolica* and *P. tulipae* can produce both penicillic acid and terrestrial acid (Frisvad *et al.*, 2004; Overy and Frisvad, 2003; Overy *et al.*, 2005).

Like penicillic acid, moniliformin has also been found in cereals and other plant products (Herrare *et al.*, 2017; Kovalsky *et al.*, 2016; Neme and Mohammed, 2017; Uhlig *et al.*, 2004). An important fact is that while moniliformin is mostly produced by important field-fungi, such as *Fusarium* spp., penicillic acid is produced by storage fungi only. Moniliformin has not been reported as an antibiotic or

quorum sensing inhibitor in bacteria (Bacon *et al.*, 2017), but moniliformin is acutely toxic to poultry (Burmeister *et al.*, 1979; Cole *et al.*, 1973; Sharma *et al.*, 2008) and rats (Chen *et al.*, 1990; Jonsson *et al.*, 2013, 2015; Thiel, 1978), in the latter study indicating a severe impact on the immune system. It inhibits several enzymes important in metabolism (Burka *et al.*, 1982). It is cardiotoxic and effects mammalian smooth muscle (Kamyar *et al.*, 2006; Peltonen *et al.*, 2010). Moniliformin is also phytotoxic and has plant growth-regulating properties (Cole *et al.*, 1973).

There is one example of co-production of penicillic acid and patulin by *Penicillium roqueforti* (Olivigni and Bullerman, 1977, 1978), but the producing organism was reidentified to *Penicillium carneum* later (Boysen *et al.*, 1996; Frisvad and Samson, 2004; Frisvad *et al.*, 2004). *Penicillium melanoconidium* has been reported to produce moniliformin and penicillic acid (Hallas-Møller *et al.*, 2016), but no species has been reported to produce patulin and moniliformin concomitantly.

It was the aim of this review to revise the lists of producers of patulin, penicillic acid and moniliformin according to the most recent taxonomic treatments of the genera *Aspergillus* (Chen *et al.*, 2016a,b, 2017; Frisvad, 2015; Frisvad and Larsen, 2015; Hubka *et al.*, 2015, 2016; Jurjevič *et al.*, 2015; Kocsubé *et al.*, 2016; Samson *et al.*, 2011a,b, 2014, 2017; Sklenář *et al.*, 2017; Varga *et al.*, 2007a,b, 2011a,b; Visagie *et al.*, 2014a, 2017), *Penicillium* (Frisvad and Samson, 2004; Houbraken *et al.*, 2016; Visagie *et al.*, 2014b) and *Fusarium* (Aoki *et al.*, 2014; Burgess, 2014; Gerlach and Nirenberg, 1982; Lesley and Summerell, 2016; Nelson *et al.*, 1983), as correct species-mycotoxin relations are important for prevention of mycotoxin formation in foods, feeds and biotechnological products.

2. Criteria for accepting a species as a producer of one or more small toxic lactones

Confirmation of mycotoxin production by a species of a filamentous fungus requires that both the fungus and the mycotoxin are correctly identified. Furthermore, it should be verified that the fungus examined is a pure culture. Also the fungal strain producing the mycotoxins should be available to the scientific community. In several cases the producing fungi were never accessioned in a culture collection, so the experiments could not be repeated and the identity of the fungal strain could not be verified or validated. If the mycotoxinogenic isolate was identified using a polyphasic approach, using a combination of morphological, physiological, chemical, and molecular features, the identifications are often correct. Molecular identification should be based on sequences of several genes, because ITS sequences are not always sufficient for correct identification at the species level (Raja *et al.*, 2017; Seifert *et al.*, 2007). Several independent reports of production of a

particular mycotoxin by a particular fungal species adds to the credulity of a species-mycotoxin connection (Frisvad, 1989; Frisvad and Samson, 2004). Often production of a particular secondary metabolite is taxonomically restricted to rather few, often phylogenetically related species, so unexpected mycotoxin formation from phylogenetically unrelated species to known producers should be confirmed with special care. It should be noted that some groups of species have been revised several times, so a name that was valid earlier now may just be a synonym or a rejected name. Furthermore, the one fungus – one name system introduced in 2011 has caused a lot of changes. For example species earlier called *Eurotium*, *Neosartorya*, *Emericella* are now all called *Aspergillus* (Samson *et al.*, 2014) and *Fusarium* is the preferred name for species formerly allocated to *Gibberella* (Geiser *et al.*, 2013). It also adds to the credulity of the reported specific mycotoxin production, if the toxin has been detected in a large number of isolates in the species examined.

It should also be documented that the growth medium used for mycotoxin production does not contain the mycotoxin already. Often secondary metabolites are accumulated, so repeated reporting of trace amounts of mycotoxins on media otherwise suited for production may indicate that the mycotoxin was already present in the growth medium. This is most important for media based on cereals, as these can contain trace amounts of mycotoxins if field or storage fungi have grown in such substrates. It is in general recommended to analyse control samples for mycotoxins and use chemically defined media in a confirmation of mycotoxin production, if unexpected results have been obtained using plant based media.

Chemical analysis, for example using HPLC methods for separation and combined with sensitive detection methods will also inherently carry the risk of carry over of mycotoxins, so here proper controls are also needed. Chromatographic and spectrometric verification of the identity of the mycotoxin is needed to guard against false positives. If the retention times in several chromatographic systems is equal to the retention time of an authentic chemical standard, this is valuable confirmation of identity, but on top of that high resolution mass spectra (MS) and/or UV spectra, as compared to an authentic standard are necessary to confirm identity. It is recommended to have at least 3 different independent confirmations of identity, and one of them should preferably be high resolution mass spectrometry (identical mass ions and relevant adducts as compared to a standard) and even the same mass fragmentation pattern as an authentic standard. Occasionally chemical identity is confirmed by nuclear magnetic resonance (NMR) characterisation, circular dichroism (CD) spectra, fourier transform infrared (FTIR) spectra, etc., especially the first time a secondary metabolite is structure elucidated and isolated from a

particular species. NMR, CD and FTIR can also be used for a very solid confirmation of identity. Other types of data, for example detection of biosynthetic precursors, and discovery of the gene cluster or part of it for the particular mycotoxin under scrutiny adds further data to support a mycotoxin-fungal species connection. The criteria for accepting a fungus as a producer of patulin, penicillic acid or moniliformin include the following: production has been reported several times and in several different strains (more than one time and from different research groups), fungal identification has been documented, the fungal producing strains are available for the scientific community, and at least three chromatographic and spectrometric kinds of confirmatory data have been provided. If, in addition, parts of the gene cluster for the mycotoxins have been found, NMR data for the mycotoxin have been made available, or the biosynthesis has been confirmed, for example by detecting biosynthetic precursors, the documentation for such relationships is of course even stronger.

3. Patulin and producing organisms

The biosynthesis of patulin, starting from 6-methyl salicylic acid is well known (Barad *et al.*, 2016c; Birch *et al.*, 1955; Bu'Lock and Ryan 1958; Dimroth *et al.*, 1976; Forrester and Gaucher, 1972a,b; Priest, 1989; Puel *et al.*, 2010; Scott *et al.*, 1971, 1972; Sekiguchi, 1983; Sekiguchi and Gaucher, 1978; Tanenbaum and Bassett, 1959), and the gene cluster for patulin has been found in different producing filamentous fungi (Ballester *et al.*, 2015; Barad *et al.*, 2016c; Dombrink-Kurtzman, 2007; Li *et al.*, 2015; Nielsen *et al.*, 2017; Puel *et al.*, 2010; Snini *et al.*, 2014; Tannous *et al.*, 2014). The role of patulin itself in the fruit infection process has not been fully elucidated (Barad *et al.*, 2016a,b), but it has been suggested that accumulation of both gluconic acid and patulin (Barad *et al.*, 2012, 2014, 2016a; Snini *et al.*, 2015) will make *Penicillium expansum* a more aggressive post-harvest pathogen. However, patulin may also be important for *P.expansum* itself in the competition with other microorganisms thriving in the fruit. It should be noted that the two other apple pathogenic Penicillia, *Penicillium solitum* and *P. crustosum*, do not produce patulin (Frisvad and Samson, 2004; Sanderson and Spotts, 1995), questioning the importance of patulin in the infection process.

The main end-product is patulin itself, but other related toxins are known, such as neopatulin, isopatulin, desoxyapatulinic acid, ascladiol, longianone and pintulin (Appell *et al.*, 2009; Bennett *et al.*, 1990, 1991; Ghisalberti *et al.*, 2000; Lykakis *et al.*, 2009; Mikami *et al.*, 1996; Scott *et al.*, 1972; Sekiguchi *et al.*, 1979).

Many strains producing patulin have been genome sequenced, including *P. expansum* (Ballester *et al.*, 2015; Barad *et al.*, 2016c; Julca *et al.*, 2015; Yin *et al.*, 2017; Yu *et*

al., 2014), *P. griseofulvum* (Banani *et al.*, 2016), *Penicillium antarcticum*, *P. carneum*, *Penicillium paneum*, and *Penicillium vulpinum* (Nielsen *et al.*, 2017). A comparison of the gene clusters for patulin production in the different species shows they are quite similar, and that *P. roqueforti* has part of the gene cluster needed to produce patulin, but lacks essential genes, making it unable to produce patulin (Nielsen *et al.*, 2017).

Patulin has been reported from 166 different species, varieties and chemotypes (Table 1), but the documentation for some of all these producers is occasionally doubtful. In many of the publications, the original producers reported are not available to the scientific community. For example, in the papers by Steiman *et al.* (1989), Okeke *et al.* (1993), and Oh *et al.* (1998), accession numbers of the fungi examined are not available, and thus it is not possible to verify the identity of the producers. In the paper by Okeke *et al.* (1993) some very efficient producers of patulin are reported, often known producers of patulin, such as *P. expansum*, while most of the trace producers of patulin are fungi not expected to produce patulin, such as *Trichothecium roseum*. It has been a general experience that when a fungus can produce patulin, it will always accumulate large amounts of the toxin, never a small trace of a toxin (Frisvad, personal observations). It is tempting to speculate that the detection of patulin in unexpected species was caused by carry over in the HPLC chromatographic system or because of contamination with efficient patulin producers. Patulin has been found in sections *Canescentia*, *Formosana*, *Gladioli*, *Osmophila*, *Penicillium*, *Ramosa* and *Robsamsonia* in *Penicillium*, but only in section *Clavati* in *Aspergillus*.

Patulin has the formula $C_7H_6O_4$, and a molecular mass of 154, and a monoisotopic mass of 154.026. Searching in the Microbial secondary metabolite database AntiBase with approximately 40,000 natural products, 95 secondary metabolites have the molecular mass of 154, while 13 fungal secondary metabolites had a monoisotopic mass of 154.026, including members of the patulin biosynthetic pathway patulin, isopatulin, neopatulin, gentisic acid, longianone and (-)-phyllostine. However, other secondary metabolites, such as terreic acid and terremutin also have the monoisotopic mass of 154.026. This may be the reason *Aspergillus terreus* was reported to produce patulin (Draughon and Ayers, 1980; El-Shanawany *et al.*, 2005; Escoula, 1974; Girisham and Reddy, 1986a,b; Giridhar and Reddy, 1998; Kent and Heatley, 1945; Reddy and Reddy, 1984, 1988), while it was probably terreic acid that was detected. Given several references on patulin production by *A. terreus*, it cannot be excluded that this species, or one of the closely related species, can produce it. Obviously for such small molecules, mass spectrometric (MS) verification is of value, but has to be combined with other data, such as an UV spectrum identical to that of patulin and retention time verification,

Table 1. Filamentous fungi claimed to produce patulin (also called clavacin, clavatin, claviformin, expansin and penicidin).

Fungal species	References	Synonymised species
<i>Acremonium implicatum</i>	Ismail <i>et al.</i> , 2016	
<i>Acremonium persicinum</i>	Okeke <i>et al.</i> , 1993	
<i>Acremonium sclerotigenum</i>	Okeke <i>et al.</i> , 1993	
<i>Acremonium zeae</i>	Steiman <i>et al.</i> , 1989	
<i>Alternaria alternata</i>	Drusch and Ragab, 2003; Leidou <i>et al.</i> , 2001; Steiman <i>et al.</i> , 1989	
<i>Alternaria papaveris</i>	Steiman <i>et al.</i> , 1989	
<i>Alternaria tenuissima</i>	Okeke <i>et al.</i> , 1993	
<i>Ascochyta imperfecta</i>	Steiman <i>et al.</i> , 1989	
<i>Aspergillus amstelodami</i>	Steiman <i>et al.</i> , 1989	
<i>Aspergillus candidus</i>	Frank, 1977	
<i>Aspergillus clavatus</i>	Bergel <i>et al.</i> , 1943, 1944; Diaz and Flannigan, 1997; Escoula, 1974; Lopez-Varga <i>et al.</i> , 2007; Paterson, 2004 (IDH gene); Umezawa <i>et al.</i> , 1947; Wiesner, 1942	
<i>Aspergillus echinulatus</i>	Steiman <i>et al.</i> , 1989	
<i>Aspergillus flavus</i>	Luque <i>et al.</i> , 2011	
<i>Aspergillus fumigatus</i>	Steiman <i>et al.</i> , 1989	
<i>Aspergillus giganteus</i>	Florey <i>et al.</i> , 1944; Okeke <i>et al.</i> , 1993; Paterson, 2004 (IDH gene); Varga <i>et al.</i> , 2007a	
<i>Aspergillus longivesica</i>	Varga <i>et al.</i> , 2007a	
<i>Aspergillus manginii</i>	Steiman <i>et al.</i> , 1989	
<i>Aspergillus ochraceus</i>	Abu-Seidah, 2003	
<i>Aspergillus oryzae</i>	Chunmei <i>et al.</i> , 2013; Luque <i>et al.</i> , 2011	
<i>Aspergillus parasiticus</i>	Steiman <i>et al.</i> , 1989	
<i>Aspergillus petrakii</i>	Okeke <i>et al.</i> , 1993	
<i>Aspergillus repens</i>	Steiman <i>et al.</i> , 1989	
<i>Aspergillus sydowii</i>	Chunmei <i>et al.</i> , 2013	
<i>Aspergillus tamarii</i>	Luque <i>et al.</i> , 2011	
<i>Aspergillus terreus</i>	Couch and Gaucher, 2004 (MSA gene); El-Shanawany <i>et al.</i> , 2005; Escoula, 1974; Draughon and Ayers; 1980; Giridhar and Reddy, 1998; Girisham and Reddy, 1986a;b; Kent and Heatley, 1945; Paterson, 2004 (IDH gene); Reddy and Reddy, 1984, 1988	
<i>Aspergillus varicolor</i>	Steiman <i>et al.</i> , 1989	
<i>Aspergillus versicolor</i>	Steiman <i>et al.</i> , 1989	
<i>Aureobasidium pullulans</i> var. <i>pullulans</i>	Steiman <i>et al.</i> , 1989	
'Basidio 2'	Steiman <i>et al.</i> , 1989	
<i>Botrytis allii</i>	Steiman <i>et al.</i> , 1989	
<i>Byssochlamys fulva</i>	Escoula, 1974; Paterson, 2004 (IDH gene); Sant'Ana <i>et al.</i> , 2010; rejected by Puel <i>et al.</i> , 2007	see <i>Paecilomyces fulvus</i>
<i>Byssochlamys nivea</i>	Escoula, 1974; Kis <i>et al.</i> , 1969; Paterson, 2004 (IDH gene); Sant'Ana <i>et al.</i> , 2010; Scurti <i>et al.</i> , 1973	see <i>Paecilomyces niveus</i>
<i>Calcarisporium arbuscula</i>	Okeke <i>et al.</i> , 1993; Steiman <i>et al.</i> , 1989	
<i>Chaetomium atrobrunneum</i>	Okeke <i>et al.</i> , 1993	
<i>Chondrostereum purpureum</i>	Okeke <i>et al.</i> , 1993	
<i>Chrysosporium pannorum</i>	Steiman <i>et al.</i> , 1989	now <i>Geomyces pannorum</i>
<i>Cladobotryum varium</i>	Steiman <i>et al.</i> , 1989	
<i>Cladobotryum verticillatum</i>	Steiman <i>et al.</i> , 1989	
<i>Cladorrhinium</i> sp.	Okeke <i>et al.</i> , 1993; Steiman <i>et al.</i> , 1989	
<i>Colletotrichum musae</i>	Steiman <i>et al.</i> , 1989	
<i>Coniothyrium</i> sp.	Okeke <i>et al.</i> , 1993	
<i>Cunninghamella bainieri</i>	Steiman <i>et al.</i> , 1989	
<i>Curvularia lunata</i>	Steiman <i>et al.</i> , 1989	
<i>Cylindrocarpon cylindroides</i>	Okeke <i>et al.</i> , 1993	
<i>Cylindrocarpon ianthotele</i>	Okeke <i>et al.</i> , 1993	
<i>Cylindrocarpon olidum</i>	Okeke <i>et al.</i> , 1993	

Table 1. Continued.

Fungal species	References	Synonymised species
<i>Dichotomomyces cejpai</i>	Okeke <i>et al.</i> , 1993	
<i>Emericella quadrilineata</i>	Luque <i>et al.</i> , 2011	
<i>Emericella rugulosa</i>	Luque <i>et al.</i> , 2011	
<i>Emericella varicolor</i>	Luque <i>et al.</i> , 2011	
<i>Eupenicillium brefeldianum</i>	Okeke <i>et al.</i> , 1993; Steiman <i>et al.</i> , 1989	
<i>Eupenicillium javanicum</i>	Okeke <i>et al.</i> , 1993	
<i>Eupenicillium</i> sp. 1	Okeke <i>et al.</i> , 1993	
<i>Eupenicillium</i> sp. 2	Okeke <i>et al.</i> , 1993	
<i>Fusarium culmorum</i>	Steiman <i>et al.</i> , 1989	
<i>Fusarium proliferatum</i> var. <i>proliferatum</i>	Steiman <i>et al.</i> , 1989	
<i>Fusarium</i> sp.	Xie <i>et al.</i> , 2011	
<i>Gymnoascus</i> sp.	Karow and Forster, 1944; Kuehn, 1958	
<i>Gymnoascus reesii</i>	Okeke <i>et al.</i> , 1993; Steiman <i>et al.</i> , 1989	
<i>Mortierella bainieri</i>	Steiman <i>et al.</i> , 1989	
<i>Mucor hiemalis</i>	Steiman <i>et al.</i> , 1989	
<i>Mucor racemosus</i> var. <i>globosus</i>	Steiman <i>et al.</i> , 1989	
<i>Oidiodendron echinulatum</i>	Steiman <i>et al.</i> , 1989	
<i>Oidiodendron tenuissimum</i>	Steiman <i>et al.</i> , 1989	
<i>Paecilomyces lilacinus</i>	Okeke <i>et al.</i> , 1993; Steiman <i>et al.</i> , 1989	
<i>Paecilomyces variotii</i>	Escoula, 1975; Paterson, 2004 (IDH gene)	
<i>Paecilomyces fulvus</i>	renamed here from <i>Byssochlamys fulva</i>	
<i>Paecilomyces niveus</i>	renamed here from <i>Byssochlamys nivea</i>	
<i>Paecilomyces saturatus</i>	Samson <i>et al.</i> , 2009	
<i>Penicillium antarcticum</i>	Vansteelandt <i>et al.</i> , 2012	
<i>Penicillium asperosporum</i>	Moslem <i>et al.</i> , 2011	
<i>Penicillium aurantiogriseum</i>	Luque <i>et al.</i> , 2011; Moslem <i>et al.</i> , 2010; Oh <i>et al.</i> , 1998; Okeke <i>et al.</i> , 1993; Paterson, 2004 (IDH gene); Paterson <i>et al.</i> , 2003; Steiman <i>et al.</i> , 1989	
<i>Penicillium brevicompactum</i>	Paterson, 2004 (IDH gene); Paterson <i>et al.</i> , 2003	
<i>Penicillium camemberti</i>	Luque <i>et al.</i> , 2011	
<i>Penicillium canescens</i>	Steiman <i>et al.</i> , 1989	
<i>Penicillium carneum</i>	Boysen <i>et al.</i> , 1996; Dombrinck-Kurtzman, 2007; Nielsen <i>et al.</i> , 2006	
<i>Penicillium chrysogenum</i>	Chunmei <i>et al.</i> , 2013; Leistner and Pitt, 1977; Oh <i>et al.</i> , 1998; Steiman <i>et al.</i> , 1989	
<i>Penicillium citreonigrum</i>	Steiman <i>et al.</i> , 1989	
<i>Penicillium citrinum</i>	El-Samawaty <i>et al.</i> , 2013; Frank, 1977; Oh <i>et al.</i> , 1998	
<i>Penicillium claviforme</i>	Afiyatullof <i>et al.</i> , 2015; Bergel <i>et al.</i> , 1943; Borkowska Opacka and Escoula, 1977; Chain <i>et al.</i> , 1942; Frisvad and Filtenborg, 1983	see <i>P. vulpinum</i>
<i>Penicillium clavigerum</i>	Dombrinck-Kurtzman, 2007; Dombrinck-Kurtzman and Blackburn, 2005; Svendsen and Frisvad, 1994	
<i>Penicillium commune</i>	Luque <i>et al.</i> , 2011; Oh <i>et al.</i> , 1998	
<i>Penicillium compactum</i>	Houbraken <i>et al.</i> , 2016	
<i>Penicillium concentricum</i>	Dombrinck-Kurtzman, 2007; Frisvad and Samson, 2004; Frisvad <i>et al.</i> , 2004; Leistner and Eckardt, 1979	
<i>Penicillium concentricum</i> II	Frisvad and Filtenborg, 1983; Houbraken <i>et al.</i> , 2016	see <i>P. coprobium</i>
<i>Penicillium coprobium</i>	Frisvad and Filtenborg, 1989; Frisvad and Samson, 2004; Frisvad <i>et al.</i> , 2004; Dombrinck-Kurtzman and Blackburn, 2005; Houbraken <i>et al.</i> , 2016	
<i>Penicillium corylophilum</i>	Paterson, 2004 (IDH gene); Vismer <i>et al.</i> , 1996	
<i>Penicillium crustosum</i>	Northolt <i>et al.</i> , 1978; Yun <i>et al.</i> , 2006	
<i>Penicillium cyaneofulvum</i>	Berestetskii <i>et al.</i> , 1974	
<i>Penicillium cyaneum</i>	Okeke <i>et al.</i> , 1993	

Table 1. Continued.

Fungal species	References	Synonymised species
<i>Penicillium cyclopium</i>	Efimenko and Yakimov, 1960; Frank, 1972; 1977; Leistner and Pitt, 1977	
<i>Penicillium dipodomyicola</i>	Dombrinck-Kurtzman, 2007; Frisvad and Samson, 2004; Frisvad <i>et al.</i> , 1987, 2004; Houbraken <i>et al.</i> , 2016; Luque <i>et al.</i> , 2011	
<i>Penicillium dipodomys</i>	Koteswara Rao <i>et al.</i> , 2011	
<i>Penicillium divergens</i>	Barta and Mecir, 1948,	see <i>P. glandicola</i>
<i>Penicillium diversum</i>	Okeke <i>et al.</i> , 1993	
<i>Penicillium duclauxii</i>	Okeke <i>et al.</i> , 1993	
<i>Penicillium echinulatum</i>	Okeke <i>et al.</i> , 1993	
<i>Penicillium equinum</i>	Burton, 1949; Burton and Pausacker, 1947	see <i>P. expansum</i>
<i>Penicillium expansum</i>	Luijk, 1938; Andersen <i>et al.</i> , 2004; Anslow <i>et al.</i> , 1943; Borkowska Opacka and Escoula, 1977; Casquete <i>et al.</i> , 2017; Chunmei <i>et al.</i> , 2013; Dombrinck-Kurtzman, 2007; Dombrinck-Kurtzman and Blackburn, 2005; El-Samawaty <i>et al.</i> , 2013; Frisvad and Filtenborg, 1983; Harwig <i>et al.</i> , 1973; Larsen <i>et al.</i> , 1998; Okeke <i>et al.</i> , 1993; Paster <i>et al.</i> , 1995; Paterson, 2004 (IDH gene); Paterson <i>et al.</i> , 2003; Sommer <i>et al.</i> , 1974; Steiman <i>et al.</i> , 1989; Welke <i>et al.</i> , 2011	
<i>Penicillium fellutanum</i>	Vismer <i>et al.</i> , 1996	
<i>Penicillium funiculosum</i>	Steiman <i>et al.</i> , 1989; Vismer <i>et al.</i> , 1996; Yassin <i>et al.</i> , 2010	
<i>Penicillium glabrum</i>	Okeke <i>et al.</i> , 1993	
<i>Penicillium gladioli</i>	Dombrinck-Kurtzman, 2007; Frisvad and Samson, 2004; Frisvad <i>et al.</i> , 2004	
<i>Penicillium glandicola</i>	Frisvad and Filtenborg, 1989; Houbraken <i>et al.</i> , 2016; Paterson, 2004 (IDH gene)	
<i>Penicillium glandicola</i> var. <i>glaucovenetum</i>	Dombrinck-Kurtzman, 2007; Frisvad and Filtenborg, 1989; Paterson, 2004 (IDH gene)	see <i>P. concentricum</i>
<i>Penicillium granulatum</i>	Borkowska Opacka and Escoula, 1977; Frisvad <i>et al.</i> , 1983	see <i>P. glandicola</i>
<i>Penicillium griseofulvum</i>	Chunmei <i>et al.</i> , 2013; Dombrinck-Kurtzman, 2007; Dombrinck-Kurtzman and Blackburn, 2005; Frisvad and Filtenborg, 1983, 1989; Frisvad <i>et al.</i> , 1987; Houbraken <i>et al.</i> , 2016; Kent and Heatley, 1945; Moslem <i>et al.</i> , 2010; Okeke <i>et al.</i> , 1993; Oh <i>et al.</i> , 1998; Paterson, 2004 (IDH gene); Simonart and Lathouwer, 1956; Steiman <i>et al.</i> , 1989; Welke <i>et al.</i> , 2011	
<i>Penicillium griseofulvum</i> var. <i>dipodomyicola</i>	Frisvad and Filtenborg, 1989; Frisvad <i>et al.</i> , 1987; Paterson, 2004 (IDH gene)	see <i>P. dipodomyicola</i>
<i>Penicillium hirsutum</i>	Okeke <i>et al.</i> , 1993; Paterson <i>et al.</i> , 2004	
<i>Penicillium italicum</i>	Okeke <i>et al.</i> , 1993	
<i>Penicillium janczewskii</i>	only IDH gene found, Paterson, 2004	
<i>Penicillium lanosum</i>	Kharchenko, 1970	
<i>Penicillium lapidosum</i>	Myrchink, 1967	
<i>Penicillium leucopus</i>	Anslow <i>et al.</i> , 1943; Brian <i>et al.</i> , 1956; Umezawa <i>et al.</i> , 1947	see <i>P. expansum</i>
<i>Penicillium lignorum</i>	Okeke <i>et al.</i> , 1993	
<i>Penicillium maltum</i>	Ukai <i>et al.</i> , 1954	see <i>P. griseofulvum</i>
<i>Penicillium marinum</i>	Frisvad and Samson, 2004; Frisvad <i>et al.</i> , 2004	
<i>Penicillium melanoconidium</i>	Luque <i>et al.</i> , 2011	
<i>Penicillium melinii</i>	Frisvad and Filtenborg, 1990; Karow and Forster, 1944; Okeke <i>et al.</i> , 1993; Paterson, 2004 (IDH gene)	
<i>Penicillium miczynskii</i>	Chunmei <i>et al.</i> , 2013	
<i>Penicillium novae-zeelandiae</i>	Burton, 1949; Burton and Pausacker, 1947; Frisvad and Filtenborg, 1990	
<i>Penicillium paneum</i>	Boysen <i>et al.</i> , 1996; Dombrinck-Kurtzman, 2007; Frisvad and Samson, 2004; Nielsen <i>et al.</i> , 2006	
<i>Penicillium patulum</i>	Anslow <i>et al.</i> , 1943; Birkinshaw <i>et al.</i> , 1943; Chain <i>et al.</i> , 1942; Frisvad, 1981	see <i>P. griseofulvum</i>
<i>Penicillium polonicum</i>	Luque <i>et al.</i> , 2011	
<i>Penicillium psychrosexualis</i>	Houbraken <i>et al.</i> , 2010	
<i>Penicillium puberulum</i>	El-Samawaty <i>et al.</i> , 2013; Moslem <i>et al.</i> , 2011	
<i>Penicillium purpurogenum</i>	Xie <i>et al.</i> , 2011	

Table 1. Continued.

Fungal species	References	Synonymised species
<i>Penicillium raistrickii</i>	Veselá and Veselý, 1995	
<i>Penicillium rivolii</i>	Berestetskii <i>et al.</i> , 1975	
<i>Penicillium roqueforti</i>	Bullerman, 1978; Cakmakci <i>et al.</i> , 2015; Chunmei <i>et al.</i> , 2013; Erdogan <i>et al.</i> , 2003; Leistner and Pitt, 1977; Malekinejad <i>et al.</i> , 2015; Olivigni and Steiman <i>et al.</i> , 1989; Müller and Amend, 1997; Paterson <i>et al.</i> , 2003; Vismer <i>et al.</i> , 1996	
<i>Penicillium roqueforti</i> chemotype II	Frisvad and Filtenborg, 1983	see <i>P. paneum</i>
<i>Penicillium roqueforti</i> var. <i>carneum</i>	Frisvad and Filtenborg, 1989; Vismer <i>et al.</i> , 1996	see <i>P. carneum</i>
<i>Penicillium rugulosum</i>	Leistner and Pitt, 1977; Vismer <i>et al.</i> , 1996	
<i>Penicillium samsonianum</i>	Houbraken <i>et al.</i> , 2016	
<i>Penicillium sclerotigenum</i>	Dombrinck-Kurtzman, 2007; Frisvad <i>et al.</i> , 2004	
<i>Penicillium selandiae</i>	<i>nomen nudum</i> , in IMI Culture Collection Catalogue, 2010; Frisvad, unpublished	see <i>P. antarcticum</i>
<i>Penicillium simplicissimum</i>	Okeke <i>et al.</i> , 1993; Paterson, 2004 (IDH gene)	
<i>Penicillium</i> sp.	Atkinson, 1942	
<i>Penicillium spinulosum</i>	only IDH gene, Paterson, 2004	
<i>Penicillium terrestre</i>	Atkinson <i>et al.</i> , 1944	
<i>Penicillium thomii</i>	Borkowska Opacka and Escoula, 1977	
<i>Penicillium urticae</i>	Kent and Heatley, 1945; Yamamoto, 1954	see <i>P. griseofulvum</i>
<i>Penicillium variabile</i>	Leistner and Pitt, 1977; Steiman <i>et al.</i> , 1989	
<i>Penicillium verrucosum</i>	Luque <i>et al.</i> , 2011; Moslem <i>et al.</i> , 2013; Oh <i>et al.</i> , 1998	
<i>Penicillium viridicatum</i>	Frank, 1972	
<i>Penicillium vulpinum</i>	Dombrinck-Kurtzman, 2007; Frisvad <i>et al.</i> , 2004; Houbraken <i>et al.</i> , 2016; Ismaiel and Papenbrock, 2015; Ismaiel <i>et al.</i> , 2016	
<i>Pestalotiopsis</i> sp.	Okeke <i>et al.</i> , 1993	
<i>Phialophora hoffmannii</i>	Okeke <i>et al.</i> , 1993	
<i>Pseudodiplodia</i> sp.	Steiman <i>et al.</i> , 1989	
<i>Rhinochadiella atrovirens</i>	Steiman <i>et al.</i> , 1989	
<i>Scopulariopsis</i> sp.	Steiman <i>et al.</i> , 1989	
<i>Scopulariopsis flava</i>	Okeke <i>et al.</i> , 1993	
<i>Scytalidium lignicola</i>	Okeke <i>et al.</i> , 1993	
<i>Spicelleum roseum</i>	Okeke <i>et al.</i> , 1993	
<i>Sporormiella minimoides</i>	Steiman <i>et al.</i> , 1989	
<i>Sporothrix schenckii</i>	Steiman <i>et al.</i> , 1989	
<i>Stemphylium</i> sp.	Okeke <i>et al.</i> , 1993	
<i>Stemphylium vesicarium</i>	Laidou <i>et al.</i> , 2001	
<i>Talaromyces purpureogenus</i>	Ismaiel <i>et al.</i> , 2016	
<i>Talaromyces trachyspermus</i>	Okeke <i>et al.</i> , 1993	
<i>Trametes squalens</i>	Steiman <i>et al.</i> , 1989	
<i>Trichoderma pseudokoningii</i>	Steiman <i>et al.</i> , 1989	
<i>Trichoderma polysporum</i>	Steiman <i>et al.</i> , 1989	
<i>Trichophyton mentagrophytes</i>	Steiman <i>et al.</i> , 1989	
<i>Trichophyton persicolor</i>	Okeke <i>et al.</i> , 1993	
<i>Trichothecium roseum</i>	Okeke <i>et al.</i> , 1993	
<i>Xylaria longiana</i>	Edwards <i>et al.</i> , 1999; Goss <i>et al.</i> , 1999; Lykakis <i>et al.</i> , 2009	

¹ Confirmed producers are in bold.

and comparison to an authentic standard (Kildgaard *et al.*, 2014). A MS/MS analysis will only yield few fragments for patulin, and thus several other verification tests have to be done to ensure that the metabolite detected is indeed patulin. In the paper by Luque *et al.* (2011) patulin was reported for several known producers and in addition species, such as *Aspergillus flavus*, *Penicillium camemberti*, and *P. verrucosum*. In tests of those fungi for patulin this has never been verified in those species (Frisvad *et al.*, 2004; Varga *et al.*, 2011b). Luque *et al.* (2011) used micellar capillary electrophoresis (retention time) and/or HPLC-MS (retention time and MS) in addition to reporting on a PCR amplicon (496 basepairs) for the FC2/IDH gene involved in the patulin biosynthesis, and despite this, they detected patulin in species that do obviously not produce patulin. Other records of patulin producers are correct, but sometimes the fungi are just synonyms of another species. An example of this is *Penicillium griseofulvum*, a very efficient and consistent producer of patulin, and three of its synonyms *P. maltum*, *P. patulum* and *P. urticae* (Pitt, 1979) have been repeatedly reported to produce patulin (Table 1).

Given the dubious accounts of patulin production by many species, a revision of confirmed and efficient producers of patulin is given in Table 1 (species in bold). Only 29 species can be reliably said to produce patulin. Among these *P. expansum* is the most important, producing patulin in apples, pears, plums and other fruits (Dombrink-Kurtzman and McGovern, 2007; Filtenborg *et al.*, 1996; Frisvad and Samson, 2004). *Penicillium sclerotigenum*, specifically associated to sweet potatoes, is also an important patulin-producing species (Yamamoto *et al.*, 1955), as is *P. griseofulvum* that may produce patulin in wheat and malted barley (Jiménez *et al.*, 1991; Ukai *et al.*, 1954; Yamamoto *et al.*, 1954). Similarly *Aspergillus clavatus* can produce patulin in malted barley (Lopez-Diaz and Flannigan, 1997). *Penicillium dipodomyicola*, another efficient patulin producer is occasionally found in foods (Dombrink-Kurtzman and McGovern, 2007; Frisvad and Samson, 2004). Members of *Penicillium* section *Roquefortorum* all produce patulin, except *P. roqueforti*. Since *P. roqueforti* is used for blue mould cheese production, it is particularly important to know whether this fungus produces this mycotoxins. The data of Nielsen *et al.* (2017) show that *P. roqueforti* has most of the gene cluster needed for production of patulin, but some genes are missing, explaining the inability of *P. roqueforti* to produce patulin. The reports of patulin production by *P. roqueforti* (Cakmakci *et al.*, 2015; Chunmei *et al.*, 2013; Erdogan *et al.*, 2003; Leistner and Pitt, 1977; Malekinejad *et al.*, 2015; Müller and Amend, 1997; Olivigni and Bullerman, 1978; Paterson *et al.*, 2003; Steiman *et al.*, 1989; Vismer *et al.*, 1996) appear to be caused by misidentifications, because the closely related species *P. carneum* and *P. paneum* both produce patulin (Boysen *et al.*, 1996). *Paecilomyces fulvus* (formerly *Byssosclamyces fulva*),

Paecilomyces niveus (formerly *Byssosclamyces nivea*) and *Paecilomyces saturatus* have all been reported to produce patulin. There has been some doubt whether *Pae. fulvus* can produce patulin (reported by Escoula, 1974; Paterson, 2004 and Sant'Ana *et al.*, 2010, but rejected by Puel *et al.*, 2007), but these species all have heat resistant ascospores (Samson *et al.*, 2009), and thus may survive in pasteurised fruit juices and produce patulin (Rice *et al.*, 1977; Sant'Ana *et al.*, 2010). *Paecilomyces niveus* and *Penicillium paneum* can grow in substrates with a high concentration of acetic acid and thus can also be found in silage, and may produce patulin there (Gallo *et al.*, 2015; O'Brien *et al.*, 2006; Scurti *et al.*, 1973). *P. antarcticum* is a marine-derived *Penicillium* species and may produce patulin on seaweed or even in shellfish (Geiger *et al.*, 2013; Vansteelandt *et al.*, 2012). *Penicillium marinum* is also marine-derived and may produce patulin in the same seaborne organisms (Frisvad and Samson, 2004).

The remaining species producing patulin are of less consequence for mycotoxin production in foods. *Penicillium gladioli* may potentially produce patulin in gladiolus bulbs, and *Penicillium glandicola* can potentially produce patulin on acorns, but flower bulbs and acorns are not used for food or feed. *Penicillium compactum*, *Penicillium novae-zeelandiae* and *Penicillium samsonianum* are soil or grass-borne fungi (Houbraken *et al.*, 2016) and *Aspergillus longivesica*, *Aspergillus giganteus*, *Penicillium clavigerum*, *Penicillium concentricum*, *Penicillium coprobium*, *Penicillium formosanum*, and *P. vulpinum* are all dung fungi and of no consequence for food safety (Frisvad and Samson, 2004).

For all of the species listed above, patulin has been detected in a large number of isolates of the producing species, for example patulin was detected in 83 out of 85 isolates of *P. expansum* by Andersen *et al.* (2004), and produced by 350/357 isolates out of *P. expansum*, by 40 out of 40 isolates in *P. griseofulvum*, by 13/13 isolates in *P. coprobium*, by 14/14 isolates in *P. glandicola*, by 14/15 strains of *P. concentricum* (= *P. glandicola* var. *glaucovenetum*), by 10/12 isolates of *P. carneum* (= *P. roqueforti* var. *carneum*), by 4/4 isolates of *P. dipodomyicola* (= *P. griseofulvum* var. *dipodomyicola*) and by 6/6 isolates of *P. vulpinum* (Frisvad and Filtenborg, 1989), showing a high consistency in patulin production by these species.

4. Penicillic acid and producing organisms

Penicillic acid is the main product of the biosynthetic pathway that starts with orsellinic acid and has penicillic acid as end product (Axberg and Gatenbeck, 1975a,b; Eldridge *et al.*, 1977). However there are other members of the penicillic acid pathway, including 5,6-dihydropenicillic acid, 5,6-dihydro-6-hydroxyenicillic acid, 6-methoxy-5,6-dihydropenicillic acid, coculnol, and (4R,5R)-4,5-

dihydroxy-3-methoxy-5-methylcyclohex-2-en-1-one (He *et al.*, 2004; Kimura *et al.*, 1996; Nonaka *et al.*, 2015; Obana *et al.*, 1995a,b; Phainuphong *et al.*, 2017; Qi *et al.*, 2015; Raphael, 1947a,b; Shiono *et al.*, 2005).

Penicillic acid has been reported in 101 species, varieties and chemotypes of fungi (Table 2), of which 48 are regarded as well documented. Some of the data may be incorrect connections between fungal species and penicillic acid because of carry over in the chromatographic system, or contamination by penicillic acid producing species. In the paper by Gutarowska *et al.* (2010), *Aspergillus niger* and *Aspergillus flavus* are reported to produce penicillic acid, and this has never been reported from these *Aspergilli* in any other papers. Again the isolates have not been accessioned in any fungal collection, but furthermore, the concomitant detection of penicillic acid and viridicatin indicates that the cultures of *A. flavus* and *A. niger* were contaminated with *Penicillium cyclopium*, which is a known producer of these two secondary metabolites. In the control sample on malt extract agar (MEA) with no fungi inoculated, Gutarowska *et al.* (2010) found kojic acid, indicating that a kojic acid producer had been growing in the barley malt before it was made into malt extract.

Producers of penicillic acid are especially common in *Penicillium* section *Viridicata* and in *Aspergillus* section *Circumdati* (Frisvad and Samson, 2000; Frisvad *et al.*, 2004a; Visagie *et al.*, 2014a). One can therefore expect a mycotoxin cocktail in mouldy cereals consisting of citrinin, ochratoxin A, penicillic acid, verrucosidin, nephrotoxic glycopeptides, xanthomegnin, viomellein, vioxanthin, moniliformin, and penitrem A when associated storage fungal species, such as *P. verrucosum*, *P. aurantiogriseum*, *P. polonicum*, *P. viridicatum*, *P. cyclopium* and *Penicillium freii* have grown on those cereals in a worst case scenario (Frisvad and Samson, 2004; Frisvad *et al.*, 2004; Hallas-Møller *et al.*, 2016; Lund and Frisvad, 1994). Most species in *Aspergillus* section *Circumdati*, such as *Aspergillus westerdijkiae*, *Aspergillus steynii* and *Aspergillus ochraceus* also produce one or more of the mycotoxins ochratoxin A, penicillic acid, xanthomegnin, viomellein and vioxanthin (Visagie *et al.*, 2014a). Penicillic acid has been found in many sections of *Penicillium*, including *Brevicompecta*, *Canescentia*, *Chrysogena*, *Exilicaulis*, *Fasciculata*, *Lanata-Divaricata*, *Ramosa*, *Roquefortorum* and *Turbatum*, so this is found in many phylogenetic groups of *Penicillium*. Penicillic acid has only been found in one section of *Aspergillus*: *Circumdati*.

Other species listed in Table 2 producing penicillic acid include soil borne species, such as *Penicillium baarnense*, *Penicillium egyptiacum*, and *Penicillium jamesonlandense*, grass-associated fungi, such as *Penicillium brasilianum* and dung fungi, such as *Penicillium bovisimosum* also produce

penicillic acid, but such fungi will probably not grow in foods or feeds, and are less relevant for food safety.

Among the common species producing penicillic acid, there is a high consistency in producing this mycotoxin. In *P. aurantiogriseum*, more than 278 isolates out of 385 examined produced penicillic acid, and it was produced by 17/17 isolates of *P. melanoconidium*, by 35/53 isolates of *Penicillium neoechinulatum*, by 234/276 isolates of *P. polonicum*, and by 324/350 isolates of *P. viridicatum* (Frisvad and Filtenborg, 1989).

Terrestrial acid, often co-occurring with penicillic acid, is produced by cereal borne fungi such as *P. aurantiogriseum*, *P. tricolor* and *P. hordei*, by onion and bulb associated fungi, such as *P. radicumicola*, *P. tulipae*, and *P. venetum* in addition to being produced by the apple, cheese and nut associated *P. crustosum* and the rice associated fungus *M. grisea* (Frisvad and Samson, 2004; Yu *et al.*, 2010) (Table 3). This toxin may thus co-occur in cereals with penicillic acid, moniliformin, ochratoxin A, verrucosidins, and xanthomegnins (Frisvad and Samson, 2004).

5. Moniliformin and producing microorganisms

Moniliformin is a mycotoxin that was first reported from *Fusarium moniliforme* (Cole *et al.*, 1973), but has since been reported to be produced by many species in that genus (Table 4). It is biosynthesised from two acetyl units (Franck and Breipohl, 1984; Gathercole *et al.*, 1986). Most of the producers of moniliformin have been confirmed by data from later papers (Table 4), and rejected producers mostly are only synonyms of names later accepted. Most of these 40 species reported to produce moniliformin do indeed produce it, except for 6 species, where Schütt *et al.* (1998) could not confirm production by these species. It should be noted that moniliformin production is difficult to verify because of the low molecular weight and simple MS fragmentation pattern, so often TLC and the characteristic UV spectrum has been used to confirm identity. In the database on natural products called AntiBase, among more than 40,000 compounds, only one has a formula of $C_4H_2O_3$, so simple HR-MS data are also confirmative of production. In addition to its production by *Fusarium* species, *Penicillium melanoconidium* has been reported to produce moniliformin (Hallas-Møller *et al.*, 2016). A large number of these species are cereal-borne, including *P. melanoconidium* which has, however, only been found on stored cereals. However, other species of *Fusarium* are pathogens on potatoes, tomatoes, onions, etc. (Lesley and Summerell, 2016), and thus moniliformin can occur in many cereals, fruits and vegetables. Furthermore, moniliformin is produced by isolates of *Fusarium fusaroides* from millet, sorghum, dried fish and peanuts (Rabie *et al.*, 1978). In addition *Fusarium* species produce several other mycotoxins concomitantly, such as trichothecenes, zearalenone,

Table 2. Filamentous fungi claimed as producers of penicillic acid.¹

Fungal species	References	Synonymised species
<i>Aspergillus affinis</i>	Visagie <i>et al.</i> , 2014a	
<i>Aspergillus auricomus</i>	Ciegler 1972; Frisvad <i>et al.</i> , 2004a; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus bridgeri</i>	Frisvad <i>et al.</i> , 2004a; Kumar <i>et al.</i> , 2011; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus cervinus</i>	He <i>et al.</i> , 2004	
<i>Aspergillus cretensis</i>	Frisvad <i>et al.</i> , 2004a; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus elegans</i>	Obana <i>et al.</i> , 1995b	
<i>Aspergillus flavus</i>	Gutarowska <i>et al.</i> , 2010	
<i>Aspergillus flocculosus</i>	Frisvad <i>et al.</i> , 2004a; Montenegro <i>et al.</i> , 2012; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus fumigatus</i>	Şenyuva <i>et al.</i> , 2008	
<i>Aspergillus insulicola</i>	Frisvad <i>et al.</i> , 2004a; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus melleus</i>	Ciegler, 1972; Frisvad <i>et al.</i> , 2004a; Gill-Carey 1949; Obana <i>et al.</i> , 1995b; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus muricatus</i>	Frisvad and Samson, 2000; Frisvad <i>et al.</i> , 2004a; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus neobridgeri</i>	Frisvad <i>et al.</i> , 2004a; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus nidulans</i>	Abu-Seidah, 2003	
<i>Aspergillus niger</i>	Gutarowska <i>et al.</i> , 2010	
<i>Aspergillus occultus</i>	Visagie <i>et al.</i> , 2014a	
<i>Aspergillus ochraceopetaliformis</i>	Visagie <i>et al.</i> , 2014a	
<i>Aspergillus ochraceus</i>	Ciegler, 1972; El-Shanawany <i>et al.</i> , 2005; Frisvad <i>et al.</i> , 2004a; Garza <i>et al.</i> , 1993; Karow <i>et al.</i> , 1944; Northolt <i>et al.</i> , 1979; Obana <i>et al.</i> , 1995b; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus ostianus</i>	Ciegler, 1972; Frisvad <i>et al.</i> , 2004a; Namikoshi <i>et al.</i> , 2003; Obana <i>et al.</i> , 1995b; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus pallidofulvus</i>	Visagie <i>et al.</i> , 2014a	
<i>Aspergillus persii</i>	Frisvad <i>et al.</i> , 2004a; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus petrakii</i>	Frisvad <i>et al.</i> , 2004a	see <i>A. ochraceus</i>
<i>Aspergillus pseudoelegans</i>	Frisvad <i>et al.</i> , 2004a	
<i>Aspergillus pulvericola</i>	Visagie <i>et al.</i> , 2014a	
<i>Aspergillus quercinus</i>	Gill-Carey, 1949	
<i>Aspergillus salwaensis</i>	Visagie <i>et al.</i> , 2014a	
<i>Aspergillus roseoglobulosus</i>	Frisvad <i>et al.</i> , 2004a; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus sclerotiorum</i>	Ciegler, 1972; Frisvad <i>et al.</i> , 2004a; Kang and Kim, 2004; Kang <i>et al.</i> , 2007; Obana <i>et al.</i> , 1995b; Visagie <i>et al.</i> , 2014a; Zheng <i>et al.</i> , 2010	
<i>Aspergillus</i> sp.	Li <i>et al.</i> , 2010	
<i>Aspergillus subramaniani</i>	Visagie <i>et al.</i> , 2014a	
<i>Aspergillus sulphureus</i>	Ciegler, 1972; Frisvad <i>et al.</i> , 2004a; Gill-Carey, 1949	
<i>Aspergillus violaceus</i>	Abu-Seidah, 2003	
<i>Aspergillus wentii</i>	He <i>et al.</i> , 2004	
<i>Aspergillus westerdijkiae</i>	Frisvad <i>et al.</i> , 2004a; Visagie <i>et al.</i> , 2014a	
<i>Aspergillus westlandensis</i>	Visagie <i>et al.</i> , 2014a	
<i>Eupenicillium bovisimosum</i>	Tuthill and Frisvad, 2002	see <i>P. bovisimosum</i>
<i>Exophiala</i> sp.	Zhang <i>et al.</i> , 2008	
<i>Malbranchea aurantiaca</i>	Martinez-Luis <i>et al.</i> , 2005	
<i>Paecilomyces ehrlichii</i>	Gorbach and Friederick, 1949	
<i>Penicillium atramentosum</i>	Bridge <i>et al.</i> , 1989	
<i>Penicillium aurantiogriseum</i>	Bridge <i>et al.</i> , 1989; Bokhari and Flannigan, 1996; El-Banna <i>et al.</i> , 1987; Frisvad and Filtenborg 1983; Frisvad <i>et al.</i> , 2004b; Garza <i>et al.</i> , 1993; Khaddor <i>et al.</i> , 2007; Lund and Frisvad 1994; Mills <i>et al.</i> , 1995a,b; Oh <i>et al.</i> , 1998	
<i>Penicillium aurantiogriseum</i> var. <i>polonicum</i>	Frisvad and Filtenborg, 1989	see <i>P. polonicum</i>
<i>Penicillium aurantiogriseum</i> var. <i>neoechinulatum</i>	Frisvad <i>et al.</i> , 1987	see <i>P. neoechinulatum</i>

Table 2. Continued.

Fungal species	References	Synonymised species
<i>Penicillium aurantiogriseum</i> var. <i>melanoconidium</i>	Frisvad and Filtenborg, 1989	see <i>P. melanoconidium</i>
<i>Penicillium aurantiovirens</i>	Lund and Frisvad, 1994; Wirth and Klosek, 1972	presently regarded as a synonym of <i>P. cyclopium</i>
<i>Penicillium baarnense</i>	Burton, 1949; Mosbach, 1960	
<i>Penicillium bovisomum</i>	Tuthill and Frisvad, 2002; Visagie <i>et al.</i> , 2014b	
<i>Penicillium brasilianum</i>	Frisvad, 1989; Frisvad and Filtenborg, 1990 Schurman <i>et al.</i> , 2010	
<i>Penicillium brevicompactum</i>	Paterson <i>et al.</i> , 1987	
<i>Penicillium canescens</i>	Keromnes and Thouvenot, 1985; Kharchenko, 1970	
<i>Penicillium carneum</i>	Boysen <i>et al.</i> , 1996; Frisvad <i>et al.</i> , 2004	
<i>Penicillium castellae</i>	Quintanilla, 1982	see <i>P. raistrickii</i>
<i>Penicillium chrysogenum</i>	Jiménez <i>et al.</i> , 1991; Leistner and Pitt, 1977; Oyero and Oyefulo, 2009	
<i>Penicillium citrinum</i>	Delgado <i>et al.</i> , 2011; El-Samawaty <i>et al.</i> , 2013	
<i>Penicillium claviforme</i>	Ueno, 1994	
<i>Penicillium commune</i>	Ciegler <i>et al.</i> , 1972; Mintzlaff <i>et al.</i> , 1972	
<i>Penicillium cordubense</i>	Skóra <i>et al.</i> , 2017	see <i>P. polonicum</i>
<i>Penicillium cremeogriseum</i>	Frisvad and Filtenborg, 1990	
<i>Penicillium cyclopium</i>	Bentley and Keil, 1962; Birkinshaw <i>et al.</i> , 1936; Ciegler <i>et al.</i> , 1972; Frisvad and Samson, 2004; Jiménez <i>et al.</i> , 1991; Keromnes and Thouvenot, 1985; Lei <i>et al.</i> , 2010; Lindenfelser and Ciegler, 1977; Lund and Frisvad, 1994; Mintzlaff <i>et al.</i> , 1972; Northolt <i>et al.</i> , 1979	
<i>Penicillium expansum</i>	Ciegler <i>et al.</i> , 1972; Mintzlaff <i>et al.</i> , 1972; Patterson and Damoglou, 1985	
<i>Penicillium fennelliae</i>	Van Eijk, 1969	
<i>Penicillium freii</i>	Frisvad <i>et al.</i> , 2004; Lund and Frisvad, 1994	
<i>Penicillium frequentans</i>	Yamaji <i>et al.</i> , 2005	
<i>Penicillium funiculosum</i>	Nasser, 2008	
<i>Penicillium granulatum</i>	Bridge <i>et al.</i> , 1989	
<i>Penicillium griseofulvum</i>	Moslem <i>et al.</i> , 2010; Reio, 1958	
<i>Penicillium griseum</i>	Gorbach and Friederick, 1949	
<i>Penicillium hirsutum</i>	Bridge <i>et al.</i> , 1989; Ezzat <i>et al.</i> , 2007	
<i>Penicillium hirsutum</i> var. <i>albocoremium</i>	Frisvad and Filtenborg, 1989	
<i>Penicillium islandicum</i>	Nasser, 2008	
<i>Penicillium jamesonlandense</i>	Frisvad <i>et al.</i> , 2006	
<i>Penicillium janczewskii</i>	Frisvad and Filtenborg, 1990	
<i>Penicillium janthinellum</i>	Ciegler <i>et al.</i> , 1972; Mintzlaff <i>et al.</i> , 1972	
<i>Penicillium lilacinum</i>	Kharchenko, 1970	
<i>Penicillium lividum</i>	Gorbach and Friederick, 1949	
<i>Penicillium madriti</i>	Birkinshaw and Gowlland, 1962	also named <i>P. madriti</i>
<i>Penicillium martensii</i>	Kurtzman and Ciegler, 1970; Lillehoj <i>et al.</i> , 1972; Mintzlaff <i>et al.</i> , 1972; Northolt <i>et al.</i> , 1979; Wirth <i>et al.</i> , 1956	
<i>Penicillium megalosporum</i>	Nozawa <i>et al.</i> , 1989; not a <i>Penicillium</i> (Frisvad and Filtenborg, 1990; Visagie <i>et al.</i> , 2014b)	
<i>Penicillium melanoconidium</i>	Lund and Frisvad 1994; Frisvad and Samson, 2004	
<i>Penicillium neoechinulatum</i>	Lund and Frisvad 1994; Frisvad and Samson, 2004	
<i>Penicillium ochraceum</i>	Tsunoda <i>et al.</i> , 1978	see <i>P. viridicatum</i>
<i>Penicillium olivinoviride</i>	Kobayashi <i>et al.</i> , 1971	see <i>P. viridicatum</i>
<i>Penicillium oxalicum</i>	Oh <i>et al.</i> , 1998	

Table 2. Continued.

Fungal species	References	Synonymised species
<i>Penicillium palitans</i>	Ciegler and Kurtzman, 1970	
<i>Penicillium paraherquei</i>	Leistner and Eckardt, 1979	
<i>Penicillium piscarium</i>	Leistner and Pitt, 1977	
<i>Penicillium polonicum</i>	Frisvad and Samson, 2004; Lund and Frisvad, 1994; Skóra <i>et al.</i> , 2017	
<i>Penicillium puberulum</i>	Alsberg and Black 1913; El-Samawaty <i>et al.</i> , 2013; Moslem <i>et al.</i> , 2011	see <i>P. cyclopium</i>
<i>Penicillium pulvillum</i>	Frisvad and Filtenborg, 1990	
<i>Penicillium radicolica</i>	Frisvad and Samson, 2004; Overy and Frisvad, 2003, 2005	
<i>Penicillium raistrickii</i>	Bridge <i>et al.</i> , 1989; Frisvad, 1988; Frisvad and Filtenborg, 1990	
<i>Penicillium rolfsii</i>	Frisvad, 1989	
<i>Penicillium roqueforti</i>	Bridge <i>et al.</i> , 1989; Cakmakci <i>et al.</i> , 2012, 2015; Erdogan <i>et al.</i> , 2003; Moubasher <i>et al.</i> , 1978; Malekinejad <i>et al.</i> , 2015; Mioso <i>et al.</i> , 2015; Müller and Amend, 1997; Olivigni and Bullerman, 1978	
<i>Penicillium simplicissimum</i>	Betina <i>et al.</i> , 1969; Ciegler <i>et al.</i> , 1972; El-Banna <i>et al.</i> , 1987; Mintzclaff <i>et al.</i> , 1972; Takahashi <i>et al.</i> , 2008	
<i>Penicillium solitum</i>	Bridge <i>et al.</i> , 1989	
<i>Penicillium</i> sp.	Komagata <i>et al.</i> , 1996; Tachibana <i>et al.</i> , 2008	
<i>Penicillium stoloniferum</i>	Alsberg and Black, 1913; Clutterbuck <i>et al.</i> , 1932 Ciegler <i>et al.</i> , 1972; Lindenfelser and Ciegler, 1977	
<i>Penicillium suaveolens</i>	Karow <i>et al.</i> , 1944	see <i>P. carneum</i>
<i>Penicillium subrubescens</i>	Mansouri <i>et al.</i> , 2013	
<i>Penicillium thomii</i> / <i>P. thomii</i>	Karow <i>et al.</i> 1944; Casquete <i>et al.</i> , 2017	
<i>Penicillium tulipae</i>	Frisvad and Samson, 2004; Overy and Frisvad, 2003; Overy <i>et al.</i> , 2005;	
<i>Penicillium vanderhammenii</i>	Houbraken <i>et al.</i> , 2011	
<i>Penicillium verrucosum</i>	Gedek <i>et al.</i> , 1981; Moslem, 2013; Oh <i>et al.</i> , 1998	
<i>Penicillium viridicatum</i>	Bresler <i>et al.</i> , 1995; Ciegler <i>et al.</i> , 1972, 1973; Frisvad and Samson, 2004; Jiménez <i>et al.</i> , 1991; Lund and Frisvad, 1994; Mintzclaff <i>et al.</i> , 1972; Northolt <i>et al.</i> , 1979; Oh <i>et al.</i> , 1998	
<i>Trichoderma</i> spp. ²	Lebed <i>et al.</i> , 1978	

¹ Confirmed producers are in bold.
² In this case penicillic acid is referring to a member of the penicilin biosynthetic pathway.

enniatins and several other mycotoxins or emerging mycotoxins (Brase *et al.*, 2009; Gruber-Dorninger *et al.*, 2017; Neme and Mohammed, 2017). Since moniliformin is produced by so many species one can maybe expect that apart from its mammal and plant toxicity, it could have antibiotic or quorum sensing inhibition abilities.

6. Conclusions

The small acidic lactone mycotoxins, such as patulin, penicillic acid and moniliformin can occur in many foods and feeds, and are toxic by themselves, but often there may be a potential synergistic or additive effect with other co-occurring mycotoxins. Based on the species producing patulin, fruit products are most prone to contamination with this mycotoxin. Penicillic acid is more common on stored cereals, as the best producers are mostly cereal-borne.

Moniliformin is produced by a large number of *Fusarium* species, and many of those are common on cereals, but also on fruits and vegetables. Among a large number of species reported to produce patulin and penicillic acid, only 29 and 48 species, respectively, have been reliably reported to produce them. The species producing them are mostly belonging to *Penicillium* and *Aspergillus*. Moniliformin is produced by 34 *Fusarium* species and by one species of *Penicillium*. The revised lists of producers of these mycotoxins will aid in preventive mycotoxin work, but also help in de-selecting known producers of these antibiotic toxins, when screening for new antibiotics.

Table 3. Filamentous fungi reported as producers of terrestrial acid.¹

Fungal species	References	Synonymised species
Magnaporthe oryzae	Couch and Kohn, 2002 (taxonomy); Yu <i>et al.</i> , 2010	
<i>Pyricularia oryzae</i>	Yu <i>et al.</i> , 2010	see <i>M. oryzae</i>
Penicillium aurantiogriseum	Frisvad and Samson, 2004; Lund and Frisvad, 1994	
<i>Penicillium aurantiogriseum</i> var. <i>aurantiogriseum</i>	Frisvad and Filtenborg, 1989	see <i>P. aurantiogriseum</i>
Penicillium crustosum	Frisvad and Filtenborg, 1989; Frisvad and Samson, 2004; Sonjak <i>et al.</i> , 2005	
<i>Penicillium griseoroseum</i>	Da Silva <i>et al.</i> , 2013	
Penicillium hirsutum	Frisvad and Samson, 2004; Overy and Frisvad, 2003; Overy <i>et al.</i> , 2005	
<i>Penicillium hirsutum</i> var. <i>albocoremium</i>	Frisvad and Filtenborg, 1989	
<i>Penicillium hirsutum</i> var. <i>hirsutum</i>	Frisvad and Filtenborg, 1989	see <i>P. hirsutum</i>
<i>Penicillium hirsutum</i> var. <i>hordei</i>	Frisvad and Filtenborg, 1989	see <i>P. hordei</i>
<i>Penicillium hirsutum</i> var. <i>venetum</i>	Frisvad and Filtenborg, 1989	see <i>P. venetum</i>
Penicillium hordei	Frisvad and Samson, 2004; Overy <i>et al.</i> , 2005	
<i>Penicillium terrestre</i>	Birkinshaw and Samant, 1960	see <i>P. crustosum</i>
Penicillium tricolor	Frisvad and Samson, 2004; Frisvad <i>et al.</i> , 1994	
Penicillium radiculicola	Overy and Frisvad, 2003; Overy <i>et al.</i> , 2005	
Penicillium tulipae	Overy and Frisvad, 2003; Overy <i>et al.</i> , 2005	
Penicillium venetum	Frisvad and Samson, 2004; Overy and Frisvad, 2003; Overy <i>et al.</i> , 2005	
<i>Penicillium viridicatum</i>	Birkinshaw and Samant, 1960	

¹ Confirmed producers are in bold.

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Table 4. Filamentous fungi reported as producers of moniliformin.¹

Fungal species	References
<i>Fusarium acuminatum</i>	Bosch and Mirocha, 1992; Hussein <i>et al.</i> , 1991; Logrieco <i>et al.</i> , 1992; Rabie <i>et al.</i> , 1982; Schütt <i>et al.</i> , 1998
<i>Fusarium acutatum</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium anthophilum</i>	Marasas <i>et al.</i> , 1986; Schütt <i>et al.</i> , 1998
<i>Fusarium arthrosporioides</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium avenaceum</i>	Bosch and Mirocha, 1992; Rabie <i>et al.</i> , 1982; Schütt <i>et al.</i> , 1998
<i>Fusarium begoniae</i>	Fotso <i>et al.</i> , 2002; Schütt <i>et al.</i> , 1998
<i>Fusarium beomiforme</i>	Marasas <i>et al.</i> , 1991; Schütt <i>et al.</i> , 1998
<i>Fusarium bulbicola</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium chlamydosporum</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium concentricum</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium concolor</i> ²	Rabie <i>et al.</i> , 1982
<i>Fusarium culmorum</i> ²	Scott <i>et al.</i> , 1987
<i>Fusarium denticulatum</i>	Fotso <i>et al.</i> , 2002; Schütt <i>et al.</i> , 1998
<i>Fusarium denticulatum</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium dlamini</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium equiseti</i> ²	Bosch and Mirocha, 1992; Hussein <i>et al.</i> , 1991; Rabie <i>et al.</i> , 1982
<i>Fusarium fujikuroi</i> (Bakane strains)	Marasas <i>et al.</i> , 1986, 1991; Schütt <i>et al.</i> , 1998
<i>Fusarium fusaroides</i>	Rabie <i>et al.</i> , 1978, 1982
<i>Fusarium lactis</i>	Fotso <i>et al.</i> , 2002; Schütt <i>et al.</i> , 1998
(<i>Fusarium moniliforme</i>) ²	Cole <i>et al.</i> , 1973; Burmeister <i>et al.</i> , 1979; Hussein <i>et al.</i> , 1991; Marasas <i>et al.</i> , 1986; Rabie <i>et al.</i> , 1982; Tseng, 1993
<i>Fusarium moniliforme</i> var. <i>subglutinans</i> (<i>Fusarium sacchari</i> var. <i>subglutinans</i>) ² = <i>Fusarium subglutinans</i> (see this)	Bosch and Mirocha, 1992; Bosch <i>et al.</i> , 1992; Hussein <i>et al.</i> , 1991; Kriek <i>et al.</i> , 1977; Lew <i>et al.</i> , 1996; Logrieco <i>et al.</i> , 1993; Marasas <i>et al.</i> , 1986; Rabie <i>et al.</i> , 1982
<i>Fusarium napiforme</i>	Marasas <i>et al.</i> , 1991; Schütt <i>et al.</i> , 1998
<i>Fusarium nisikadoi</i>	Fotso <i>et al.</i> , 2002; Schütt <i>et al.</i> , 1998
<i>Fusarium nygamai</i>	Marasas <i>et al.</i> , 1988; 1991; Schütt <i>et al.</i> , 1998
<i>Fusarium oxysporum</i>	Abbas <i>et al.</i> , 1995; Hussein <i>et al.</i> , 1991; Rabie <i>et al.</i> , 1982; Schütt <i>et al.</i> , 1998
<i>Fusarium phyllophilum</i>	Fotso <i>et al.</i> , 2002; Schütt <i>et al.</i> , 1998
<i>Fusarium proliferatum</i>	Logrieco and Botalico, 1988; Logrieco <i>et al.</i> , 1995; Marasas <i>et al.</i> , 1986; Miller <i>et al.</i> , 1995; Scarpino <i>et al.</i> , 2015; Schütt <i>et al.</i> , 1998
<i>Fusarium pseudoanthophilum</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium pseudocircinatum</i>	Fotso <i>et al.</i> , 2002; Schütt <i>et al.</i> , 1998
<i>Fusarium pseudonygamai</i>	Fotso <i>et al.</i> , 2002; Schütt <i>et al.</i> , 1998
<i>Fusarium ramigenum</i>	Fotso <i>et al.</i> , 2002; Schütt <i>et al.</i> , 1998
<i>Fusarium redolens</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium sacchari</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium semitectum</i>	Rabie <i>et al.</i> , 1982;
<i>Fusarium sporotrichioides</i> ²	Scott <i>et al.</i> ; 1987
<i>Fusarium subglutinans</i>	Bosch and Mirocha, 1992; Bosch <i>et al.</i> , 1992; Hussein <i>et al.</i> , 1991; Kriek <i>et al.</i> , 1977; Marasas <i>et al.</i> , 1986; Lew <i>et al.</i> , 1996; Logrieco <i>et al.</i> , 1993; Rabie <i>et al.</i> , 1982; Schütt <i>et al.</i> , 1998
<i>Fusarium temperatum</i>	Scaufflaire <i>et al.</i> , 2011; Sewram <i>et al.</i> , 1999
<i>Fusarium thapsinum</i>	Schütt <i>et al.</i> , 1998
<i>Fusarium tricinctum</i>	Schütt <i>et al.</i> , 1998
<i>Penicillium melanoconidium</i>	Hallas-Møller <i>et al.</i> , 2016

¹ Confirmed producers are in bold.² Not confirmed by Schütt *et al.* (1998), regarded here as the authoritative statement regarding taxonomy of the *Fusaria*.

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