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Catalog of *Penicillium* spp. causing blue mold of bulbs, roots, and tubers

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Abstract—Accuracy in assigning specific epithets to *Penicillium* isolates documented as agents of blue mold of edible and ornamental bulb, root, and tuber crops is highly variable—with methods ranging from appropriate (recent morpho-cultural criteria, metabolite production, DNA sequences), to plausible (older morpho-cultural criteria from monographs), to suspect (unspecified methods, identification via inappropriate literature). We provide a catalogue appropriate for plausibly assigned names accompanied by authorities, references, host distribution, and identification methodology. Names are categorized according to (i) segregates of *P. corymbiferum* (i.e., names in *P.* subg. *Penicillium*) and taxa in *P.* ser. *Corymbifera* associated with *Liliaceae* s.l.; (ii) taxa in *P.* subg. *Penicillium* other than *P.* ser. *Corymbifera* associated with *Liliaceae* s.l.; (iii) taxa other than *P.* subg. *Penicillium* associated with *Liliaceae* s.l.; (iv) associates of *Beta vulgaris* (beets and sugar beets); and (v) associates of mostly tropical or subtropical roots and tubers. Ambiguities or deficiencies in assignment of certain specific epithets are noted.

Key words—*Allium*, *Dioscorea, Iris, Manihot, Zingiber*

Introduction

Previously attributed to a small number of *Penicillium* species, blue mold pathogens on bulb and root crops have been assigned by modern molecular-genetic methods to an increasing number of species, many of which represent "cryptic" species segregated from other species described decades ago (Dugan & Everhart 2016). In comparing sets of investigations, results from artificial inoculations reveal substantial areas where host ranges agree as well as instances with contradictory results (Dugan & al. 2014, 2017; Overy & al. 2005). As new species are still being described and new host records published (e.g., Strausbaugh & Dugan 2017, Oh & al. 2015, Sang & al. 2014), there is a need for a catalog of names for *Penicillium* species causing blue mold diseases of bulb and root crops that also cites the literature on hosts and indicates how isolates were identified. Because numerous publications record *Penicillium* species on various bulb, root, or tuber hosts without clearly indicating how isolates were identified to species level, we emphasize literature with well-defined identification methods. Species names in *Penicillium* are provided with authors, dates, and publication references (Index Fungorum 2018) for species of greatest importance to this review (Tables 1–5). We divide our topic into three main sections: blue mold on bulbs of *Liliaceae* sensu lato (Tables 1–3), blue mold on beets and sugar beets (Table 4), and blue mold on roots and tubers, many of which are tropical or subtropical (Table 5). We also note pertinent subgeneric classifications for Tables 1–3.

Tables 1–5 concisely summarize methods used to assign specific epithets for each publication cited. In some instances pertinent isolates that may have been obtained at different times or simultaneously are those characterized molecularly and publicly available from culture collections. For instance, Frisvad & Samson (2004), who characterized isolates using morpho-cultural methods (including extrolites), published in the same issue as Samson & al. (2004), who characterized the same isolates emphasizing β-tubulin DNA sequences; we also include isolates used by Overy & al. (2005), also previously characterized and readily available. In other instances, plausibly correct names were assigned earlier based on older monographs (e.g., Pitt 1980; Ramirez 1982; Raper & Thom 1968, 1949) whose methods were current at the time but not yet molecular-genetic. We also note instances where species names have become established in pertinent literature but for which identification methods were not specified or are problematic. We accept subgeneric classifications by Frisvad & Samson (2004), Houbraken & Samson (2011), Pitt (1980), or Visagie & al. (2014). Authorities and publication references are provided at first mention in Tables 1–5. We do not provide full synonymies for *Penicillium* names (particularly where varieties have been elevated to species or where a fungus has been transferred to *Penicillium* from another genus), but we do reference specific instances of disagreement over synonymy.

For more complete lists of accepted species and synonyms, readers are encouraged to refer to Farr & Rossman (2018), Frisvad & Samson (2004), Pitt (1980, 2000), MycoBank (2018), Species Fungorum (2018), Visagie & al.

(2014), and other literature mentioned in tables and text. The primary purpose of this catalogue is to assess the degree of confidence one should place in assigning a specific epithet by documenting the method(s) by which the name was assigned.

Blue mold on bulbs of *Liliaceae* sensu lato

For decades, blue mold on edible or ornamental bulbs was attributed to *Penicillium corymbiferum* Westling, Ark. Bot. 11(1): 92 (1911), presently regarded as a synonym of *Penicillium hirsutum* (e.g., Frisvad & Samson 2004, Pitt 1980, Species Fungorum 2018). Frisvad & Samson (2004) treated these and the following species within *P.* subg. *Penicillium*, *P.* sect. *Viridicata* (= *P.* sect. *Fasciculata*; Houbraken & Samson 2011), *P.* ser. *Corymbifera*. *Penicillium* sect. *Corymbifera* is not strictly phylogenetic, but a traditional group of convenience based partially on host (edible or ornamental bulbs) (Frisvad & al. 2000, Frisvad & Samson 2004). Dugan & al. (2014) provided details on the typification of *Penicillium allii*, *P. corymbiferum*, and *P. hirsutum*, focusing on repercussions for identifying and naming the agents that rot garlic (*Allium sativum*) in the field and in storage.

Literature is here summarized for results of artificial inoculation of various edible bulbs (various cultivars or varieties of onion, *Allium cepa* L., and garlic, *A. sativum* L.) and ornamental bulbs (ornamental onions, *Allium aflatunense* B. Fedtsch. and *A. stipitatum* Regel; crocus, *Crocus sativus* L.; grass lily, *Ornithogalum umbellatum* L.; daffodil, *Narcissus* 'Ice Follies;' *Gladiolus* 'Black Walnut' and two unnamed cultivars; *Iris ×hollandica*; *Tulipa gesneriana* L. and *Tulipa* 'Purple Prince') (Dugan & al. 2011, 2014, 2017; Overy & al. 2005). Not all plant taxa were challenged by each set of investigators. Species and cultivars sometimes differed, as did inoculation and incubation details.

Blue mold on beets and sugar beets

The most frequently reported *Penicillium* species on *Beta vulgaris* L. subsp. *vulgaris* (table beets, cv. group 'Conditiva' and sugar beets, cv. group 'Altissima') is *P. vulpinum* (most often reported under its synonym, *P. claviforme* Bainier), which is readily identifiable by its conspicuous coremia (Bugbee 1975, Fugate & Campbell 2009). However, several other species have been conclusively identified, and others are indicated in literature using ambiguous or potentially obsolete identification methods. Blue mold of beet is not treated in Koike & al. (2007), Sherf & MacNab (1986), or Snowdon (1992), but *P. vulpinum* has commonly been listed among the most important storage rot pathogens along with an *Athelia*-like sp., *Botrytis cinerea* Pers., and *Phoma betae* A.B. Frank (Bugbee 1993, Strausbaugh & al. 2015). *Penicillium vulpinum* is an antagonist of *B. cinerea* (Bugbee 1976). *Penicillium* spp. have also been acknowledged to complicate the re-isolation of the slow growing *Athelia*-like sp. from sugar beet roots (Strausbaugh & al. 2015).

Rot lesions on sugar beet roots infested by *Penicillium* spp. in storage are normally associated with wounds created by harvest operations or other fungi (Fugate & Campbell 2009, Strausbaugh & al. 2015). Other *Penicillium* spp. documented as pathogenic on sugar beet roots in storage include: *P. cellarum, P. cyclopium*, *P. expansum*, *P. funiculosum*, and *P. polonicum* (Bugbee 1975, Bugbee & Nielsen 1978, Fugate & Campbell 2009, Strausbaugh 2018). A direct comparison of *P. cellarum*, *P. expansum*, and *P. polonicum* established that *P. expansum* and *P. polonicum* are the most virulent on sugar beet roots in long-term storage in Idaho (Strausbaugh 2018). In historical literature on sugar beet storage rots from the United States, *P. vulpinum* has been described as being the most prevalent *Penicillium* sp. in most environments (Bugbee 1993, Fugate & Campbell 2009). Sheikholeslami & al. (1998) also reported *P. vulpinum* on stored sugar beet roots in Iran. However, recent reports describe *P. expansum* as being the most prevalent species in sugar beet storages in the Czech Republic (Huijbregts 2013, Zahradníček 1996) and Japan (Uchino 2001), although the identification methods have not been detailed. In Idaho, both *P. expansum* and *P. cellarum* have recently been established as the most prevalent *Penicillium* spp. in long-term sugar beet piles (Strausbaugh 2018). Bugbee (1975) described *P. variabile* on stored roots in the Red River Valley (North Dakota), a fungus now regarded as a synonym of *P. expansum* in Farr & Rossman (2018), Frisvad & Samson (2004), and MycoBank (2018). *Penicillium variabile* is not included in the list of species accepted by Visagie & al. (2014) but is listed as an independent species by Species Fungorum (2018). Bugbee (1975) determined that *P. variabile* was not as virulent or as prevalent as *P. vulpinum* on sugar beet roots. *Penicillium* has also been cited from storages in Belgium, the Netherlands, and Sweden, but the species was not determined (Huijbregts & al. 2013). Some species described as pathogenic on sugar beet in storage—such as *P. cyclopium*, *P. funiculosum*, and *P. polonicum*—appear to be of minor importance.

Blue mold on edible roots and tubers

These crops, with the exception of horseradish, are primarily tropical to subtropical. Given that current criteria for assignment of species names have incorporated molecular-genetic methods, and given the technological challenges faced by scientists in developing countries, it is unsurprising that the quality of characterizing of *Penicillium* isolates from these crops varies considerably. Accordingly, several names are not cited in the tables, but covered in notes below the tables, with caveats indicated. Table 5 occasionally directs readers to a specific note. Details are provided where a trail of citations ultimately support plausible criteria and literature for assigning specific epithets. Other details note where we were unable to locate literature with definitive criteria. There are instances where specific epithets have been putatively (and invalidly) assigned by citing literature that does not actually provide species descriptions.

Table 1: *Penicillium* subg. *Penicillium* sensu Frisvad & Samson (2004), *P.* ser. *Corymbifera*; with comments on hosts in *Liliaceae* sensu lato

Penicillium albocoremium (Frisvad) Frisvad, Integr. Mod. Taxon. Meth. Penicill. Asperg. Classif: 275 (2000).

Pathogenic on garlic*, onion, iris, and tulip; less virulent on ornamental onion (*Allium stipitatum*) (Dugan & al. 2017; morpho-cultural, DNA sequence β-tubulin).

Pathogenic on onion, tulip; non-pathogenic on garlic*, gladiolus (Overy & al. 2005**; morpho-cultural, DNA sequence β-tubulin).

Additional substrates in Frisvad & Samson (2004).

Penicillium allii Vincent & Pitt, Mycologia 81: 300 (1989).

Pathogenic on garlic, onion; moderately pathogenic on grass lily and tulip*; non-pathogenic on crocus, daffodil, ornamental onion (*Allium stipitatum*), gladiolus, and iris (Dugan & al. 2014; morpho-cultural, DNA sequence β-tubulin).

Pathogenic on garlic; non-pathogenic on ornamental onions (*A. aflatunense*, *A. stipitatum*) (Dugan & al. 2011; morpho-cultural, DNA sequence β-tubulin).

Pathogenic on onion, garlic; non-pathogenic on tulip*, gladiolus (Overy & al. 2005; morpho-cultural, DNA sequence β-tubulin).

Additional substrates in Frisvad & Samson (2004).

Penicillium hirsutum Dierckx, Ann. Soc. Sci. Bruxelles 25: 89 (1901).

Pathogenic on crocus, garlic, onion, tulip, moderately pathogenic on gladiolus and iris; non-pathogenic on daffodil, ornamental onion, and grass lily (Dugan & al. 2014; morpho-cultural, DNA sequence β-tubulin).

Pathogenic on onion, garlic, tulip, gladiolus (Overy & al. 2005; morpho-cultural, DNA sequence β-tubulin).

Additional substrates in Frisvad & Samson (2004).

Penicillium hordei Stolk, Antonie van Leeuwenhoek 35: 270 (1969).

Pathogenic on tulip; non-pathogenic on onion, garlic, gladiolus (Overy & al. 2005; morpho-cultural, DNA sequence β-tubulin). However, typically on barley (*Hordeum vulgare* L.) or other cereals, or soil wherein such are cultivated (Frisvad & Samson 2004), but also once isolated from seed of *Lupinus albus* L. in Washington state (Alomran & al. 2013).

Penicillium radicicola Overy & Frisvad, Syst. Appl. Microbiol. 26: 633 (2003).

Pathogenic on garlic*, onion, and iris; non-pathogenic on *A. stipitatum* and tulip* (Dugan & al. 2017; morpho-cultural, DNA sequence β-tubulin).

Pathogenic on onion, tulip*; non-pathogenic on garlic*, gladiolus (Overy & al. 2005; morpho-cultural, DNA sequence β-tubulin).

Additional substrates in Frisvad & Samson (2004), e.g., carrot, sometimes without comment on pathogenicity.

Table 1, concluded

Penicillium tulipae Overy & Frisvad, Syst. Appl. Microbiol. 26: 634 (2003).

Pathogenic on garlic*, onion, iris, and tulip, moderately pathogenic on crocus, daffodil, and grass lily; non- pathogenic on ornamental onion and gladiolus* (Dugan & al. 2014; morpho-cultural, DNA sequence β-tubulin).

Pathogenic on onion (cultivar-dependent), tulip, gladiolus*; non-pathogenic on garlic* (Overy & al. 2005; morpho-cultural, DNA sequence β-tubulin).

Additional substrates in Frisvad & Samson (2004): bulbs of lily (*Lilium* sp.) and (without plant part specified) beet (*Beta vulgaris*) and Jerusalem artichoke (*Helianthus tuberosus* L.).

Penicillium venetum (Frisvad) Frisvad, Integ. Mod. Taxon. Meth. Penicill. Asper. Classif.: 275 (2000).

Pathogenic on garlic, onion (cultivar-dependent), gladiolus, grass lily, iris and tulip; non-pathogenic on crocus and daffodil (Dugan & al. 2014; morpho-cultural, DNA sequence β-tubulin).

Pathogenic on onion, garlic tulip, gladiolus (Overy & al. 2005; morpho-cultural, DNA sequence β-tubulin).

Additional substrates in Frisvad & Samson (2004): bulbs of *Hyacinthus* spp. (pathogenic), horseradish (*Armoracia rusticana* G. Gaertn. & al., pathogenic, see *P. hirsutum*, Table 5), and "licorice root" (*Glycyrrhiza glabra* L.; pathogenicity not specified).

* Indicates differences in results between investigators, possibly reflecting variation in isolates, inoculation, or incubation.

** Overy & al. (2005) challenged bulbs in more than one anatomical location. Results tabulated above regard lesion formation at any location as a positive result.

Table 2. *Penicillium* subg. *Penicillium* sensu Frisvad & Samson (2004) (other than *P.* ser. *Corymbifera*) with comments on hosts in *Liliaceae* sensu lato.

Penicillium aurantiogriseum Dierckx, Ann. Soc. Sci. Bruxelles 25: 88 (1901) [*P.* ser. *Viridicata* in Frisvad & Samson 2004 = *P.* sec. *Fasciculata* in Visagie & al. 2014]

Substrates in Frisvad & Samson (2004) include onion, garlic* (*Allium* spp., with pathogenicity implied rather than stated). Non-pathogenic on garlic* in Valdez & al. (2009; morpho-cultural via Ramirez 1982 and others).

Penicillium crustosum Thom, The *Penicillia:* 399 (1930) [*P.* ser. *Camemberti*].

Pathogenic on onion; moderately pathogenic on iris; non-pathogenic on *Allium stipitatum* and tulip (Dugan & al. 2017; morpho-cultural, DNA sequence β-tubulin).

Additional substrates in Frisvad & Samson (2004).

Penicillium expansum Link, Mag. Gesell. Naturf. Freunde, Berlin 3: 17 (1809) [*P.* ser. *Expansa*].

Pathogenic on iris, tulip, onion (cultivar-dependent); moderately pathogenic on garlic (Dugan & al. 2017; morpho-cultural, DNA sequence β-tubulin). Symptoms illustrated (Duduk & al. 2017; morpho-cultural, DNA sequence β-tubulin).

Additional substrates in Frisvad & Samson (2004). The species is most well known as inducing rot of apple (*Malus domestica* Borkh.) fruits.

Penicillium polonicum K.W. Zaleski, Bull. Int. Acad. Polon. C1 Sci. Math., Sér. B: 445 (1927) [*P.* ser. *Viridicata*]

Pathogenic on garlic, onion; non-pathogenic on *Allium stipitatum*, iris*, tulip (Dugan & al. 2017; morpho-cultural, DNA sequence β-tubulin).

Pathogenic on garlic, onion, moderately pathogenic on iris*; non-pathogenic on crocus, daffodil, ornamental onion, grass lily, and tulip (Dugan & al. 2014; morpho-cultural, DNA sequence β-tubulin). Multiple cultivars of onion; symptoms illustrated (Duduk & al. 2017; morpho-cultural, DNA sequence β-tubulin).

Additional substrates in Frisvad & Samson (2004) include *Allium* sp.

* Indicates differences in results between investigations, possibly reflecting variation in isolates, inoculation, or incubation.

TABLE 3. *Penicillium*, other than *P.* subg. *Penicillium* sensu Frisvad & Samson (2004); with comments on hosts in *Liliaceae* sensu lato.

Penicillium brasilianum Bat., Anais Soc. Biol. Pernambuco 15: 160 (1957)
[*P.* sec. *Lanata-Divaricata*, Visagie & al. 2014; but see also Pitt 1980]
Pathogenic on onion (but significantly less aggressive than the pathogenic *Aspergillus awamori* Nakaz. or *Fusarium oxysporum* Schltdl.—presumably *F. oxysporum* f. sp. *cepae*) (Sang & al. 2014; morpho-cultural, β-tubulin DNA sequences).

Penicillium citrinum Thom, Bull. U.S. Depart. Agric., Bureau Anim. Indust. 118: 61 (1910)
[*P.* sec. *Citrina*, Pitt 1980, Visagie & al. 2014]
Pathogenic on *Allium sativum* (Hernández-Anguiano 2006, using Pitt 1988).

Penicillium georgiense S.W. Peterson & B.W. Horn, Mycologia 101: 79 (2009)
[*P.* sec. *Charlesii*, Visagie & al. 2014]
Pathogenic on onion, moderately aggressive (lesions ~4-5mm at 10 days) (Oh & al. 2015: morpho-cultural, β-tubulin DNA sequences).

Penicillium glabrum (Wehmer) Westling, Ark. Bot. 11(1): 131 (1911).
[*P.* sec. *Aspergilloides*, Pitt 1980, Visagie & al. 2014]
Pathogenic on garlic, onion; moderately pathogenic on iris; non-pathogenic on *Allium stipitatum,* tulip (Dugan & al. 2017; morpho-cultural, DNA sequence β-tubulin). Symptoms illustrated (Duduk & al. 2017; morpho-cultural, DNA sequence β-tubulin). Typically confined to outer layers (Varga & al. 2008).

Penicillium paraherquei S. Abe ex G. Sm., Trans. Brit. Mycol. Soc. 46: 335 (1963)
[*P.* sec. *Furcatum*, Pitt, 2000; *P.* sec. *Lanata-Divaricata*, Visagie & al. 2014]
Pathogenic on garlic, onion (cultivar-dependent); non-pathogenic on *A. stipitatum*, iris, tulip (Dugan & al. 2017; morpho-cultural, β-tubulin DNA sequences).

Penicillium purpureogenum Stoll [as "*purpurogenum*"], Beitr. Morph. Biol. Char. *Penicillium:* 32 (1904) [*P.* ser. *Miniolutea*, Pitt 1980; but see Visagie & al. 2014].
≡ *Talaromyces purpureogenus* (Sopp) Samson & al., Stud. Mycol. 70: 177 (2011).
Treated either as an accepted species (Pitt 1980, 2000; Visagie & al. 2014; Farr & Rossman (2018); Species Fungorum 2018) or as a species complex requiring further study (Samson & al. 2011).
Pathogenic on onion, (Vélez-Rodríguez & Rivera-Vargas 2007; identification corroborated by CABI Bioscience Identification Services).

Comments on TABLES 1–3

Penicillium allii-sativi Frisvad & al. (Houbraken & al. 2012; Persoonia 29: 89): although the epithet refers to the substrate, *Allium sativum,* from which the type was isolated, it is not included in the tables because it is NOT a pathogen on garlic (Houbraken & al 2012).

Penicillium frequentans Westling, identified from morpho-cultural criteria, was isolated from tulip bulbs in Poland, and the closely related *P. spinulosum* Thom has been isolated from onion bulbs in Lithuania (Dugan & al. 2014, and sources cited there). *Penicillium frequentans* is regarded as either an independent species (MycoBank 2018, Visagie & al. 2014) or a synonym of *P. glabrum* (Pitt 1980, Farr & Rossman 2018, Species Fungorum 2018).

Penicillium gladioli L. McCulloch & Thom (not included in tables) "may be extinct" ...; pathogenic to *Gladiolus* corms" (Frisvad & Samson 2004). In spite of "may be extinct," one still sees this name assigned to penicillia reported on *Gladiolus* (e.g., Farr & Rossman 2018). See Pitt (1980) and Index Fungorum (2018) for its sometimes ambiguous nomenclatural history.

Penicillium paraherquei and *P. brasilianum* were previously considered synonyms of *P. simplicissimum* (Oudem.) Thom (Pitt 1980), and *P. paraherquei* (not cited in Farr & Rossman 2018) is still so regarded at Species Fungorum (2018). Isolates identified as *P. simplicissimum* based on Pitt (1980) are recorded from onion (cf. the sources and phylogenetic summary in Dugan & al. 2017). *Penicillium paraherquei* and *P. brasilianum* are accepted as independent species by Visagie & al. (2014) but are treated as synonyms in MycoBank (2018).

Penicillium purpureogenum is sometimes assigned the protologue citation La Cellule 33: 235 (1923). The correct protologue is provided in Table 3.

Some names in Sumner & al. (2008) are problematic because that publication does not explain clearly how a specific epithet was applied to agents of blue mold of onion. There are the cases of *P. citrinum* on onion (a species primarily on *Citrus* but see Hernández-Anguiano 2006); *P. cyclopium* on onion (from a 1978 publication in Sumner & al. 2008) is a synonym of *P. aurantiogriseum* in Farr & Rossman (2018) and Pitt (1980, 2000) but independent in MycoBank (2018) and Visagie & al. (2014); *P. aurantiogriseum* is documented on onion and garlic (see Table 2). *Penicillium digitatum* (Pers.) Sacc. is also mostly on citrus, but host-fungus indices in Farr & Rossman (2018) cite *P. digitatum* on *Iris*, in the same broad family as onion. The sole record in Farr & Rossman (2018) of *P. funiculosum* on onion is from a checklist of fungi in Pakistan, and Farr & Rossman (2018) have no records for *P. oxalicum* on onion. In addition, *P. discolor* Frisvad & Samson, a species noted for its presence on cheeses, is recorded from onion in two cases by Frisvad & Samson (2004), but with no indication of pathogenicity.

Table 4. *Penicillium* spp. on *Beta vulgaris.*

Penicillium cellarum C.A. Strausb. & Dugan, Pl. Dis. 101: 1783 (2017).

[*P.* sect. *Fasciculata*] Phylogenetically allied to: *P. aurantiogriseum* with ITS-5.8S, β-tubulin] (Visagie & al. 2014); *P. camemberti* with RPB2.

Pathogenic on sugar beet roots held in long-term storage piles (Strausbaugh & Dugan 2017; morpho-cultural, DNA sequences: β-tubulin, ITS-5.8S, RPB2). *P. cellarum* is recently described, yet to be evaluated on other crops.

Table 4 concluded

Penicillium cyclopium Westling, Ark. Bot. 11(1): 90 (1911).
Pathogenic on sugar beet roots (*Beta vulgaris*) (Bugbee & Nielsen 1978; morpho-cultural in Raper & Thom 1968).

Penicillium expansum
Pathogenic on stored sugar beet roots (*Beta vulgaris*) (Bugbee 1975; Strausbaugh 2018, morpho-cultural and DNA sequences: β-tubulin, ITS-5.8S, RPB2). Bugbee (1975; by implication, using Raper & Thom 1968) applied the name *P. variabile*, sometimes considered a synonym of *P. expansum* as noted above. Farr & Rossman (2018) do not presently list records of *P. expansum* on sugar beet.

Penicillium funiculosum Thom,
Bull. U.S. Dep. Agric., Bur. Anim. Indust. 118: 69 (1910) [*P.* subg. *Biverticillium*].
≡ *Talaromyces funiculosus* (Thom) Samson & al., Stud. Mycol. 70: 176 (2011).
Pathogenic on sugar beet roots (*Beta vulgaris*) (Bugbee & Nielsen 1978: morpho-cultural via Raper & Thom 1968).

Penicillium polonicum
Pathogenic on stored sugar beet roots (*Beta vulgaris*) in Idaho (Strausbaugh 2018; morph-cultural, DNA sequences: β-tubulin, ITS-5.8S, RPB2).

Penicillium tulipae
On *Beta vulgaris* (Overy & Frisvad 2003; morpho-cultural, extrolites, DNA sequence β-tubulin). *Penicillium tulipae* was twice isolated from *B. vulgaris* and given IBT accession numbers; no indication of pathogenicity provided.

Penicillium variabile Sopp, Skr. Vidensk.-Selsk.
Christiania, Math.-Naturvidensk. Kl. 11: 169 (1912) [*P.* subg. *Biverticillium*].
≡ *Talaromyces variabilis* (Sopp) Samson & al., Stud. Mycol. 70: 177 (2011).
Pathogenic on sugar beet (*Beta vulgaris*) (Bugbee 1975, deposited accession ATCC 28703 but without stating identification method; possibly via Raper & Thom 1968, as this was how Bugbee identified *P. cyclopium* and *P. funiculosum* above). *Penicillium variabile* was rare in sugar beet, relative to *P. vulpinum* (Bugbee 1975).

Penicillium vulpinum (Cooke & Massee) Seifert & Samson,
Adv. Penicill. Asper. System.: 144 (1986) ["1985"]
The synonym *Penicillium claviforme* is common in phytopathological literature. In older U.S. literature *P. claviforme* is the most prevalent *Penicillium* rotting sugar beet (Bugbee 1993). "Clavate coremia, usually produced at 25°C on both CYA and MEA, distinguish *Penicillium claviforme* from all other *Penicillium* species" (Pitt 1980). Bugbee (1975) presented a photo of coremia and deposited representative accession (ATCC 28702).
Additional substrates in Frisvad & Samson (2004).

Comments on Table 4:

Bugbee (1975) also cited Morochkovsky (1936, in Russian) describing additional *Penicillium* spp. inducing sugar beet rot: *P. stoloniferum* Thom (regarded as a synonym of *P. brevicompactum* by Farr & Rossman 2018, Pitt 1980, and Species Fungorum 2018), *P. bordzilowskii* Morochk. (later regarded as a synonym of *P. cyclopium* based on Samson & al. 1976), *P. expansum*, *P. duclauxii* Delacr., and *P. rubrum* Stoll. We have not read Morochkovsky's publication and do not know how the isolates were identified.

Liebe & al. (2016) listed *Penicillium paneum* Frisvad based on fungal ITS sequences present in stored beets. The ITS region alone is considered insufficient for species assignment in *Penicillium,* and definitive phylogenetic analyses use alternative or supplemental gene regions (e.g., Samson & al. 2004; Visagie & al. 2014). Although beets were sorted based on their degree of deterioration, Liebe & al. (2016) did not describe inoculations (i.e., Koch's postulates) and thus did not provide a direct measure of pathogenicity.

Table 5: *Penicillium* spp. on edible roots and tubers.

Penicillium albocoremium

On *Zingiber officinale* Roscoe, ginger (Frisvad & Samson 2004; morpho-cultural, DNA sequence β-tubulin). Pathogenicity is implied rather than stated.

Penicillium brevicompactum Dierckx, Ann. Soc. Sci. Bruxelles 25: 88 (1901), [*P.* ser. *Olsonii*].

Pathogenic on *Zingiber officinale*, ginger (Overy & Frisvad 2005; Varga & al. 2008, literature review, citing sources; morpho-cultural, metabolite profiles).

Penicillium crustosum

On *Dioscorea alata* L., purple yam (Pitt 1980, citing an IMI accession), with comment on pathogenicity. See comment on Snowdon (1992) below.

Penicillium expansum

On *Dioscorea* spp., yam (Frisvad & Samson 2004). On *Ipomoea* spp., see comment on Holmes & Clark (2013) below.

Penicillium hirsutum

On horseradish roots (*Armoracia rusticana;* Frisvad & Samson 2004) but without indicating pathogenicity; morpho-cultural, DNA sequence β-tubulin). "*P. hirsutum* is a major cause of loss of stored horseradish" (Beuchat 1987). However, Beuchat (1987) may have been referring to what was subsequently described as *P. hirsutum* var. *venetum* Frisvad (Frisvad & Filtenborg 1990), the basionym of *P. venetum*, Table 1.

Penicillium oxalicum Currie & Thom, J. Biolog. Chem. 22: 289 (1915)
[*P.* sec. *Lanata-Diviricata*, Visagei & al. 2014].

On sweet potato (*Ipomoea batatas* (L.) Lam.; Paul & al. 2018, with illustrations of symptoms; methods: morpho-cultural, DNA sequences: β-tubulin, ITS). See comment on Snowdon (1992) in notes.

On *Dioscorea* spp., see comment on Snowdon (1992) below. Pathogenic on cush-cush yam (*Dioscorea trifida* L.f.; Ricci & al. 1979; morpho-cultural, implying use of Raper & Thom 1949 for identification).

Pathogenic on *Dioscorea alata, D. cayenensis* Lam.*, D. dumetorum* (Kunth) Pax, and *D. rotundata* Poir. (Adeniji 1970: "Identifications were confirmed by the Commonwealth Mycological Inst., Kew, England.")

Penicillium polonicum

On Chinese yam [*Dioscorea batatas* Decne. (= *D. polystachya* Turcz.)], Kim & al. (2008; morpho-cultural, DNA sequence β-tubulin). No pathogenicity tests were performed.

Table 5 concluded

Penicillium purpureogenum

FRR 1977 "from cassava [*Manihot esculenta* Crantz] … Representative of species" (Pitt 1980); no indication of pathogenicity.

Penicillium sclerotigenum T. Yamam., Sci. Rep. Hyogo Univ. Agric., Ser. 2, Agr. Biol. 2: 69 (1955) [*P.* ser. *Expansa*].

On yam (*Dioscorea* spp.), tubers and products (Frisvad & Samson 2004).

On *Dioscorea batatas* (Kim & al. 2008), but without pathogenicity tests; methods: morpho-cultural, DNA sequence β-tubulin). Pitt's (1980) different classification placed *P. sclerotigenum* in *P.* subg. *Furcatum* but did describe the species as rotting *Dioscorea* spp. See comment on Snowdon (1992) in notes.

Comments on Table 5:

Holmes & Clark (2013) provided species names for penicillia causing blue mold on sweet potatoes but did not specify the identification methods. "*Penicillium* spp. identified from …isolates collected in North Carolina packing houses: *P. expansum* [the most common], *P. bilaiae* Chalab., *P. variabile, P. rugulosum* Thom, *P. solitum* Westling [variously treated as a synonym of *P. aurantiogriseum* (Pitt 1980), an independent species (Pitt 2000, Visagie & al. 2014), or as a separate species with *P. crustosum* a junior synonym (Species Fungorum 2018)], and *P. viridicatum* Westling [treated as a distinct species by Pitt (1980, 2000) and Visagie & al. (2014), but as a junior synonym of *P. aurantiogriseum* by Species Fungorum (2018)] (Holmes & Clark 2013, authors of species names added). The reference on *Penicillium* in Holmes & Clark (2013) is Harter & al. (1918), which states, "The species of *Penicillium* which we most frequently isolated … was given to Dr. Charles Thom … it belongs to the *expansum* group"). Holmes & Clark (2013) contained a good photo of *P. expansum* by Holmes, clearly showing synnemata typical of the species in vivo. Holmes, on the faculty at North Carolina State University (Department of Plant Pathology), was co-author on Edmunds & al. (2008) produced by the North Carolina State University Extension and co-author with John Pitt (Holmes & al. 1994); Holmes identified the isolates based on Pitt (1980, 2000) (Gerald Holmes, pers. comm.). Holmes & Clark (2013) did not provide explicit statements regarding pathogenicity of individual species.

Snowdon (1992) listed the following species on yams: *P. crustosum* ("very common on yams imported into the UK from Nigeria," but without supplying a citation); *P. cyclopium* (referring only to a previous section on that fungus, not on yam); *P. gladioli* ("has been found on importations to the USA from Cuba and Puerto Rico," but without a citation); *P. oxalicum* (citing Adeniji 1970—see Table 5—and Ricci & al. (1978), who provided no identification methods did reference Ricci & al. 1979, see Table 5);

P. sclerotigenum (citing Yamamoto & al. 1955 as well as Moura 1980, who in turn cited Moura & al. 1976). Snowdon (1992) also cited Plumbley & al. (1985), which does not contain information on identification methods, but refers to Plumbley & al. (1984, similarly devoid of such methods), who did cite earlier reports, including Ogundana & al. (1970), which stated "… microorganisms were isolated and identified" but which otherwise provided no methods or references by which *Penicillium* isolates could conceivably be identified to species. Nonetheless, growth rate, conidial size, and teleomorph absence detailed in Moura & al. (1976) convincingly led to *P. sclerotigenum* in the synoptic key to sclerotigenic species in Pitt (1980).

Snowdon (1992) also mentions *Penicillium* sp. on "cocoyams (taro [*Colocasia esculenta* (L.) Schott] and tannias [*Xanthosoma sagittifolium* (L.) Schott]);" and *Penicillium* spp. on sweet potatoes without providing specific epithets for penicillia on any of these crops. Farr & Rossman (2018) record the following on *Ipomoea*: *Penicillium chrysogenum* Thom, *P. citrinum, P. crustosum, P. decumbens* Thom, *P. expansum, P. funiculosum, P. glabrum, P. islandicum* Sopp, *P. italicum* Wehmer, *P. oxalicum, P. pinophilum* Hedgc., *P. purpureogenum,* and *P. simplicissimum,* but in each instance cite only a regional checklist. It is difficult to confirm reports of *Penicillium expansum* on yam (*Dioscorea*), and they are not cited in Farr & Rossman (2018).

For cassava (*Manihot* spp.), Farr & Rossman (2018) cite a checklist of fungi in Papua New Guinea and one research article from India listing three *Penicillium* species on *Manihot* spp. However, the *Penicillium* species listed in India were assessed as non-pathogenic in artificial inoculations, and no identification methods were provided nor can be inferred from the references listed.

Discussion

DNA sequence analyses, especially of β-tubulin but also of RPB2 and even ITS (for subgeneric groups), along with advances in understanding phylogenetic significance of metabolite production, has substantially reinforced morpho-cultural methods for identifying *Penicillium* isolates to species. Subgeneric assignment changes include transferal of *P. vulpinum* (Table 4) from *P.* subg. *Biverticillium* to *P.* subg. *Penicillium* (Pitt 2000), but the distinctive coremia in *P. vulpinum* consistently enabled assignment of that specific epithet to isolates regardless of higher level classification. Note that although Houbraken & Samson (2011) assigned *Penicillium* species to only two subgenera—*P.* subg. *Aspergilloides* and *P.* subg. *Penicillium*—

for heuristic reasons we use prior subgeneric assignments in Tables 1–3, given that most identification literature uses these prior classifications. Pitt (2000) also noted that he (Pitt 1980) "suggested that only 70–80% of isolates even from common sources are readily identifiable. The remainder can be identified, but their identification must increasingly rely on the skill and experience of the taxonomist and/or newer techniques such as metabolite profiles or molecular data." This comment explains the difference between the large strides in identifying agents of blue mold of edible and ornamental bulbs (primarily grown in economically and scientifically advanced temperate regions) and the somewhat lagging identification of agents of blue mold on tropical and subtropical roots and tubers (primarily grown in tropical regions with developing economies).

There are repeated instances in older phytopathological literature (from both advanced and developing economies) of cavalier treatment of identification. Much older and even some newer literature substituted repetitious "citation" recycling instead of explicitly specifying the monograph or species description on which the name ultimately rested. Through diligence, some confusions can be resolved by tracing a citation trail back to an early monograph (e.g., Raper & Thom 1949), but ultimately modern morpho-cultural observations and DNA sequence analyses must be provided.

Several online publications from developing regions cite various editions of H.L. Barnett & B.B. Hunter (Illustrated genera of imperfect fungi), T. Watanabe (Pictorial atlas of seed and soil fungi), and/or F.M. Dugan (The identification of fungi) for determining species names for *Penicillium* isolates derived from roots, tubers, or bulbs. Such manuals are useful for recognizing fungal families and genera, but as they are entirely inappropriate for applying specific epithets to *Penicillium* isolates, we omit literature citing those manuals for assigning species names. We expect inappropriate citations will diminish as comprehensive monographs on *Penicillium*—as well as equipment and skills needed for DNA sequence analyses—become more widely available. We accordingly anticipate increased knowledge of agents of *Penicillium* blue mold of crops such as cassava, sweetpotato, ginger, taro, and tannia.

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