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Neopetromyces gen. nov. and an overview of teleomorphs of *Aspergillus* subgenus *Circumdati*

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Abstract: Species in the anamorph genus *Aspergillus* are associated with several teleomorphic genera in the *Eurotiales* and the most important mycotoxin producers are concentrated in *Aspergillus* subgenus *Circumdati*. A new genus, *Neopetromyces*, is proposed for the recently described *Petromyces muricatus*, because this species differs distinctly from the two other species, *P. alliaceus* and *P. albertensis. Neopetromyces muricatus* has flesh-coloured ascostromata and an anamorph in *Aspergillus* subgenus *Circumdati* section *Circumdati*, whereas other *Petromyces* species have black ascostromata and anamorphs in *Aspergillus* subgenus *Circumdati* section *Flavi.* The ascostromata of *P. alliaceus* and its synonym *P. albertensis* resemble those of *A. flavus* and *A. nomius.* Another species from section *Circumdati*, *A. lanosus*, is reassigned to section *Flavi.* All these taxa grow well at 37°C, and produce kojic acid and nominine/aflavinines. *Neopetromyces muricatus* is morphologically similar to *A. melleus* and related species in *Aspergillus* subgenus *Circumdati* section *Circumdati.* This similarity is further supported by physiological similarities, low growth rates at 37°C, and similarities in profiles of natural products. This new classification is in accord with DNA sequence data. Strains identified as *A. melleus* producing ochratoxin A proved to be the anamorph of *N. muricatus*, while no strains of *A. melleus sensu stricto* produced ochratoxin A. This is the first report on ochratoxin A production of *N. muricatus*. Ochratoxin A is thus produced by some species in both sections *Flavi* and *Circumdati*. Several options are discussed for integrating the taxonomy and nomenclature of anamorphs and teleomorphs that lack coincident generic concepts.

Key words: *Petromyces*, mycotoxins, *Aspergillus flavus, Aspergillus ochraceus*, aflatoxin, ochratoxin A, sclerotia

Introduction

Some of the most important mycotoxin-producing species of *Aspergillus* are classified in the sections *Flavi* and *Circumdati* of subgenus *Circumdati* and their placement in these sections has rarely been questioned. The three known producers of aflatoxin, *A. flavus*, *A. parasiticus* and *A. nomius*, which have green conidia, are placed in section *Flavi*, while the ochratoxin A-producing species with ochre-coloured conidia are placed in section *Circumdati* (Samson, 1992). No signs of ascospore production have been detected in any of the sclerotium-producing species in *Flavi* (Table 2). All produce black sclerotia resembling those of *Petromyces alliaceus* and *P. albertensis* in section *Circumdati.* All other species in section *Circumdati* have coloured sclerotia (white, cream, buff, clay, pale yellow to yellow, pale pink or pink to vinaceous-purple, orange to rufous or brown) (Raper and Fennell, 1965) except *P. alliaceus, P. albertensis* and *A. robustus* M. Christensen & Raper (Raper and Fennell, 1965; Christensen, 1982; Tewari, 1985). Kozakiewicz (1989) classified *P. alliaceus* with *A. wentii* and *A. alliaceus* in the *A. wentii*-group, and later reported on ochratoxin A production by both *A. wentii* and *P. albertensis* (Varga *et al.*, 1996). However, Peterson (1995) placed *A. wentii* with the xerophilic ascomycete genus *Chaetosartorya* and *Petromyces* within section *Flavi*.

Recent ribosomal DNA sequence data, including ITS data, indicate that *P. muricatus* is different from *P. albertensis* and *P. alliaceus* and that the latter two species are phylogenetically closely related to section *Flavi* rather than section *Circumdati* (Peterson, 1995; Nikkuni *et al.*, 1998). In a study of *Penicillium* species, *Petromyces muricatus* and *Pet. albertensis,* used as outgroups, were clearly different (Skouboe *et al.*, 1999). This led us to reexamine species of *Petromyces* and *Chaetosartorya* and associated anamorphs using morphological and chemotaxonomic data, with an emphasis on the taxonomic placement of producers of ochratoxin A and aflatoxins.

Materials and methods

Strains of *Aspergillus* and associated teleomorphs were obtained from the CBS (Centraalbureau voor Schimmelcultures, Baarn, NL) and IBT (Department of Biotechnology, Technical University of Denmark, Lyngby, Denmark). All strains were inoculated on Czapek agar, Czapek-yeast autolysate (CYA) agar, Yeast extract-sucrose (YES) agar, malt extract agar according to Blakeslee (MEA), and 2 % malt (mout) extract (ME) agar at 25°C and on CYA at 37°C [for recipes see Samson *et al.*, 1996, pp. 309–311; in Lyngby Difco malt extract, yeast extract, peptone and Czapek broth were used, in combination with So-Bi-Gel Agar (Bie & Bernsten, Denmark)].

The fungi were examined morphologically and chemically after incubation for one week. All isolates were examined for qualitative profiles of extrolites using thin-layer chromatography (TLC) (using two eluents) and high performance liquid chromatography (HPLC) with diode array detection, following the methods of Frisvad & Thrane (1987, 1993). Standards of ochratoxin A, aflatoxin B1, B2, G1, G2, kojic acid, penicillic acid, xanthomegnin, viomellein, circumdatin A, B, C, D, 4-hydroxymellein, griseofulvin, tenuazonic acid, antibiotic Y, aspergillic acid, parasiticol, nominine, aflavinin, cyclopiazonic acid, paspaline, and paspalinine were also used to confirm the results.

Results

Petromyces alliaceus and *P. albertensis* produced kojic acid, paspaline, nominine, ochratoxin A, and had unknown metabolite 1 in common (Table 1). They are thus regarded as synonyms, in agreement with Udagawa *et al.* (1994).

The production of these metabolites agrees with previous reports: Gill-Carey (1949) found kojic acid in *A. alliaceus*, and Nozawa *et al.* (1994) and Laakso *et al.* (1994) independently found nominine, paspaline and kotanins in two different strains of *P. alliaceus*. Ochratoxin A was reported from isolates of *A. alliaceus* independently by Ciegler (1972) and Hesseltine *et al.* (1972). Kojic acid, nominine and paspaline are all metabolites commonly found in typical members of section *Flavi* (Birkinshaw *et al.*, 1931; Gloer, 1995), but not in species of section *Circumdati*. The similarity of *P. alliaceus* to species of section *Flavi* is further supported by similarities in sclerotium colour (black sclerotia are formed in many strains of *A. flavus, A. parasiticus, A. tamarii, A. nomius, A. leporis* and *A. avenaceus*) (Raper and Fennell, 1965; Christensen, 1981; 1982); all these species have a very high growth rate at 37°C.

In contrast, *P. muricatus* produces light yellow sclerotioid ascomata, does not produce kojic acid and grows slowly at 37°C and so is much more similar to typical members of section *Circumdati*. This is substantiated by the production of penicillic acid, xanthomegnin, viomellein and vioxanthin by *P. muricatus* (Table 1) and all other members of the section (Table 2) (Durley *et al.*, 1975; Robbers *et al.*, 1978; Stack & Mislivec, 1978; Rahbæk *et al.*, 1997, 1999). Our results using HPLC and diode-array detection confirmed these earlier reports. HPLC analysis of *A. robustus* showed that it had no secondary metabolites in common with either section *Flavi* or *Circumdati* and may be unrelated to any of these sections.

The remaining species until now referred to section *Flavi* are the domesticated forms *A. oryzae* and *A. sojae* and the probable synonyms of *A. flavus* or *A. tamarii: A. kambarensis, A. subolivaceus, A. thomii, A. flavofurcatis, A. americanus* and *A. terricola* (Samson, 1979; Christensen, 1981; Kozakiewicz, 1989) and *A. caelatus* (Horn, 1997). All these species also grow rapidly at 37°C and produce kojic acid. *Aspergillus clavatoflavus* Raper & Fennell, *A. coremiiformis* Bartoli & Maggi and *A. zonatus* Kwon-Chung & Fennell are morphologically and biochemically different and do not belong in section *Flavi* (Kozakiewicz, 1989; Samson, 1992).

Taxonomic part

The sections *Flavi* and *Circumdati* of subgenus *Circumdati* contain the most important mycotoxin producers known in the genus *Aspergillus*. The taxonomic and phylogenetic placement of the toxigenic species in these sections is therefore of great interest. Species in these sections traditionally have been separated primarily on conidium colour *en masse*, i.e. pale pure

Table 1. Production of natural products of some important *Petromyces* and *Neopetromyces* species and some anamorphic *Aspergillus* species from these genera.

Anamorphic section	Natural products
Aspergillus section Circumdati – Neopetromyces	
N. muricatus IMI 368521a (T)	Ochratoxin A, penicillic acid, xanthomegnin, viomellein, aspergillic acid
A. muricatus NRRL 3520*	Ochratoxin A, penicillic acid, xanthomegnin, viomellein
A. muricatus NRRL 5226*	Ochratoxin A, penicillic acid, xanthomegnin, viomellein
A. muricatus NRRL 5227*	Ochratoxin A, penicillic acid, xanthomegnin, viomellein, vioxanthin
A. melleus CBS 546.65 (NT)	Penicillic acid, 4-hydroxymellein, circumdatin D, xanthomegnin, viomellein, vioxanthin
A. melleus NRRL 394	Penicillic acid, 4-hydroxymellein, xanthomegnin, viomellein
A. melleus NRRL 386	Penicillic acid, 4-hydroxymellein, xanthomegnin, viomellein
A. melleus IMI 49108	Penicillic acid, 4-hydroxymellein, circumdatin B and D, xanthomegnin, viomellein
Aspergillus section *Flavi – Petromyces*	
P. alliaceus UAMH 2476**	Kojic acid, ochratoxin A + B, paspaline, met. I
P. alliaceus CBS 542.65 (NT)	Kojic acid, ochratoxin A + B, paspaline, nominine, asperlicine, kotanins
P. alliaceus IMI 017295***	Kojic acid, ochratoxin A, asperlicine
P. alliaceus IBT 21770	Kojic acid, ochratoxin A + B, nominine, kotanins, asperlicin
P. alliaceus NRRL 1237	Kojic acid, asperlicin
P. alliaceus NRRL 318	Kojic acid, ochratoxin A, met I
P. alliaceus CBS 511.69	Kojic acid, ochratoxin A + B, paspaline, nominine, kotanins, met I
P. alliaceus CBS 110.26	Kojic acid, ochratoxin A + B, paspaline, met I
P. alliaceus NRRL 315	Kojic acid, ochratoxin A + B, paspaline, nominine, kotanins, asperlicin, met I
P. alliaceus NRRL 317	Kojic acid, ochratoxin A + B, paspaline, nominine, kotanins, asperlicin, met I
A. lanosus IMI 130727 (T)	Kojic acid, met I, griseofulvin
A. lanosus IBT 16758	Kojic acid
A. lanosus IMI 226007	Kojic acid, met I, griseofulvin
A. flavus NRRL 1957 (T)	Kojic acid, cyclopiazonic acid, aspergillic acid
A. flavus CBS 573.65	Kojic acid, aflatoxin B1, paspaline, paspalinine, nominine, aspergillic acid
A. parasiticus IMI 15957vi (T)	Kojic acid, aflatoxin B1, G1, parasiticol, parasiticolide A, aspergillic acid
A. nomius NRRL 13137 (T)	Kojic acid, aflatoxin B1, G1, pseurotin, tenuazonic acid, nominine, aspergillic acid
A. tamarii CBS 104.13 (T)	Kojic acid, cyclopiazonic acid, fumigaclavine A
A. caelatus NRRL 25528 (T)	Kojic acid
A. leporis CBS 157.66 (T)	Kojic acid, pseurotin, antibiotic Y, leporin
A. avenaceus CBS 109.46 (T)	Avenaciolide

*Formerly identified as *A. melleus*
** Ex type of *Petromyces albertensis*
***Received as ex-type of *Aspergillus wentii*, but does not represent that species. The ex-type cultures received from ATCC (1023) and CBS (104.07) were typical *A. wentii*.

yellow, orange-yellow, buff or ochraceus in section *Circumdati*, yellow, citrine, very light yellow- green, deep yellow-green, olive-brown, bronze or brown in section *Flavi* (Raper and Fennell, 1965; Christensen, 1981) and yellow-brown in *Chaetosartorya*. The differences in conidium colour between these sections is not sharp and clearly of minor importance compared to the many other differences. For example, the name *A. flavus* refer to a yellow conidium colour, which is present in young conidial heads of many species in *Flavi*, and all three sections contain species with conidia with some shade of brown.

Section *Flavi* includes the three aflatoxin-producing species *A. flavus*, *A. nomius* and *A. parasiticus*, and now *P. alliaceus*, an ochratoxin A producer, can be added to this group (see descriptions in Raper and Fennell, 1965; Fennell and Warcup, 1959; Horie *et al.*, 1993). Kojic acid is a common metabolite in all species except one (*A. avenaceus*) in section *Flavi*, whereas penicillic acid, xanthomegnin and viomellein are common for most species in section *Circumdati*. Several other natural products are common to several members of each section, such as cyclopiazonic acid in section *Flavi* and circumdatins and 4-hydroxymellein in section *Circumdati*. Two natural product families are in common for at least some species in both sections, aspergillic acids and ochratoxins, whereas another section in subgenus *Circumdati*, section *Nigri*, includes producers of nominine and ochratoxin A (Abarca *et al.*, 1994; Gloer, 1995; Ono *et al.*, 1995; Horie, 1995; Téren *et al.*, 1996; Wicklow *et al.*, 1996, Heenan *et al.*, 1998).

Molecular data agree with the classification proposed here (Table 2). Peterson (1995) found that *P. alliaceus* was in the same clade as members of section *Flavi*, based on 28S rDNA sequences. Using ITS and 18S sequence data, Nikkuni *et al.* (1998) found that taxa in section *Flavi*, such as *A. flavus*, *A. tamarii*, *A. parasiticus* and *A. nomius*, were in one clade and phylogenetically distantly related to *A. ochraceus*. A recent study of ITS sequences of the terverticillate penicillia used *Petromyces albertensis* and *P. muricatus* as outgroups (Skouboe *et al.*, 1999). This study clearly showed that *P. albertensis* differs significantly from *P. muricatus*. Data from Nikkuni *et al.* (1998) and Peterson (1995) show that *Petromyces alliaceus* (= *P. albertensis*) represents one clade together with section *Flavi*, while *P. muricatus* is the teleomorph in another clade, with species of section *Circumdati*.

Classification based on morphological, natural products and physiological data thus points to the same grouping as cladification based on molecular data, even though the principles involved are fundamentally different.

Because *Petromyces muricatus* is significantly different from the two other species of *Petromyces* described, we propose a new genus for the former:

NEOPETROMYCES Frisvad and Samson, *gen. nov.*

Diagnosis Latina in Mycotaxon 52: 208, 1994.

Species typica: *Petromyces muricatus* Udagawa, Uchiyama & Kamiya

Neopetromyces muricatus (Udagawa, Uchiyama & Kamiya) Frisvad & Samson, *comb. nov.*

≡ *Petromyces muricatus* Udagawa, Uchiyama & Kamiya — Mycotaxon 52: 208. 1994 (Basionym).

Holotypus: Herb. IMI 368521a (living culture ex type: IMI 368521a).

The genus and species is illustrated by Udagawa *et al.* (1994).

Discussion

The ascomycetous teleomorph genera connected with *Aspergillus* differ in morphology, natural products, physiology, and DNA sequences. *Eurotium* Link, and subgenus *Aspergillus* sections *Aspergillus* and *Restricti* are osmophilic and most species produce emodin, physcion, erythroglaucin, tetrahydroauroglaucin and echinulins (Turner and Aldridge, 1983). Another osmophilic genus is *Chaetosartorya*, which includes many species (*C. chrysella, A. flaschentraegeri, A. wentii, A. sepultus, A. dimorphicus*) that produce emodin, sulochrin, wentilacton and citraconic anhydride derivatives (Dorner *et al.*, 1980; Assante *et al.*, 1979, 1980; Wells *et al.*, 1975). Species in this group share physcion with *Eurotium*. Thus, these two groups can be considered related both ecologically and phylogenetically.

Hemicarpenteles A. K. Sarbhoy & Elphick and *Aspergillus* section *Clavati* contain alkaliphilic species that often produce patulin, kotanins, tryptoquivalins and cytochalasins and appear to be a sister group to the thermophilic *Neosartorya* and *Aspergillus* section *Fumigati* (Geiser *et al.*, 1998). Several species in the latter genus and section produce gliotoxin, tryptoquivalins, pseurotins, trypacidin, pyripyropens, fumigatins, asperfuran, fumitremorgins and fumagillin) (Frisvad & Samson, 1990; Samson *et al.*, 1990).

The hülle cell-producing species of *Emericella* Berk. and sections *Nidulantes*, *Usti* and *Versicolores* contain many producers of sterigmatocystin and shamixanthone (Turner & Aldridge, 1983), while the distantly related *Fennellia* B.J. Wiley & E.G. Simmons and sections *Flavipedes* and *Terrei* often produce citrinin and citreoviridin.

These ascomycete genera and *Sclerocleista* Subram. are all rather unique and this is confirmed by biochemical and molecular characters (Kuraishi *et al.*, 1990; Samson, 1992; Geiser *et al.*, 1998). The genus *Aspergillus* is therefore a diverse form genus maintained for practical information retrieval purposes, yet it may form a holophyletic group *in toto*. An interesting solution could be to use the name in a cladificatory way referring to a major clade containing all the species referred to the former anamorphic genus *Aspergillus*. On the other hand, all these nomenclatural names have until now been used in a Linnean classificatory sense. A fully correct genus name would be the

Table 2. Species in the three genera *Petromyces*, *Neopetromyces* and *Chaetosartorya*.

Petromyces Malloch & Cain, including *Aspergillus* subgenus *Circumdati* section *Flavi*

**P. alliaceus* Malloch & Cain (syn *P. albertensis* J. P. Tewari)
**A. avenaceus* G. Sm.
**A. caelatus* Horn
**A. flavus* Link [+ domesticated form, *A. oryzae* (Ahlb.) Cohn] (syn. *A. kambarensis* Sugiyama, *A. subolivaceus* Raper & Fennell, *A. thomii* G. Sm.)
A. lanosus Kamal & Bhargava
**A. leporis* States & M. Christensen
**A. nomius* Kurtzman *et al.* (syn. *A. zhaoquinensis*)
**A. parasiticus* Speare (domesticated form *A. sojae* Sakad. & K. Yamada ex Murak.) (syn. *A. toxicarius* Murakami)
**A. tamarii* Kita (syn. *A. flavofurcatus* Bat. & H. Maia, *A. terricola* E. J. Marchal)
Tentatively placed here: *A. americanus*

Neopetromyces including *Aspergillus* subgenus *Circumdati* section *Circumdati*

N. muricatus (Udagawa, Uchiyama & Kamiya) Frisvad & Samson
A. auricomus (Guég.) Saito
A. bridgeri M. Christensen
A. elegans Gasperini
A. insulicola Montem. & A.R. Santiago
A. melleus Yukawa
A. ochraceus K. Wilh.
A. ostianus Wehmer
A. petrakii Vörös
A. sclerotiorum G.A. Huber
A. sulphureus (Fresen.) Wehmer

*****Chaetosartorya*** Subram., including *Aspergillus* subgenus *Circumdati* section *Wentii* and section *Cremei*

C. chrysella (Kwon-Chung & Fennell) Subram.
C. cremea (Kwon-Chung & Fennell) Subram.
C. stromatioides B.J. Wiley & E.G. Simmons
A. dimorphicus B.S. Mehrotra & Prasad
A. flaschentraegeri Stolk
A. gorakhpurensis Kamal & Bhargava
A. itaconicus Kinosh.
A. pulvinus Kwon-Chung & Fennell
A. sepultus Tuthill & M. Christensen
A. wentii Wehmer

* At least some isolates produce black sclerotia.
**Based on Peterson (1995), *A. sepultus* has been added because it is obviously similar to *A. wentii*.

holomorphic (teleomorphic) name, so species in *Eurotium* and *Emericella* (always having the perfect state) can easily be named correctly. Giving 'correct' names for the other species in *Aspergillus* is more problematic.

There are at least five alternatives:

1) The genus for genus concept would require at least 9 different (mostly new) anamorph genera, with *Aspergillus* maintained only for *Eurotium* anamorphs and *Aspergillus* subgenus *Aspergillus* section *Restricti*. This approach would be disastrous for communication, information retrieval and practical applications of *Aspergillus* strains and more than 9 new sections, series etc. would have to be described, memorized and used.

2) Use the *Aspergillus* name only as was practiced by Raper and Fennell (1965). We also cannot recommend this approach because it would violate several rules of the ICBN and much information related to names such as *Eurotium* and *Emericella* would be lost (i.e. biological, chemical or ecological predictions from names would be impossible). For example, use of these two generic names indicates heat resistance for species so designated, related to ascospore formation.

3) Teleomorph names should always be used,

whether or not a teleomorph is known. For Aspergilli for which we do not know a teleomorph, we might have to invent names based on imaginary strains (this would in theory be possible using DNA sequence data). For example, *Aspergillus flavus* would thus be called the *Aspergillus* anamorph of '*Petromyces flavus*'. This we also cannot recommend, because a taxonomy based on long-extinct or perhaps never existing teleomorphs is an unscientific 'ghost' taxonomy.

4) The *Aspergillus* name is used followed by (in parenthesis) the phylogenetically and classificatorically correct name. Examples: *A. tetrazonus* Samson & W. Gams [aff. *Neosartorya quadricincta* (E. Yuill.) Malloch & Cain] or *A. sparsus* Raper & Thom (aff. unknown, or the nearest known and described named teleomorph). The only problem with this solution is the long citation.

5) When known and observed, the teleomorph name is used for the holomorph (e.g. *Eurotium herbariorum* Link). When the teleomorph name is known but ascomata are not actually observed, use the *Aspergillus* name followed by the genus (in parentheses) with which it is phylogenetically and classificatorically associated [e.g. *Aspergillus flavus* (aff. *Petromyces*)]. Finally, when the teleomorph is unknown, use the *Aspergillus* name followed by section name in parenthesis [e.g. *A. sparsus* (aff. sect. *Sparsi*)]. We recommend the last solution in which the use of the parenthetic addition is voluntary. The same solution can be used for other fungal genera.

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