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Review Article

Incidence and significance of black aspergilli in agricultural commodities: a review, with a key to all species accepted to-date

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ABSTRACT

Black aspergilli (*Aspergillus* species of Section *Nigri*) present dark colonies, often black, and uniseriate or biseriate conidial heads. Currently 26 species and one variety are accepted within this section. They have been isolated from a wide variety of food worldwide and are considered as common causes of food spoilage and biodeterioration of other materials. They are commonly present in cereals and vineyards and have the ability to cause *Aspergillus* rot of black berry. Some species of this section, like *A. niger* and *A. awamori*, are a common source of extracellular enzymes such as amylases and lipases, and organic acids, such as citric and gluconic acid, used as additives in food processing and are used for biotechnological purposes. These products hold the GRAS (Generally Recognised as Safe) status. Other species are able to produce ochratoxins (OTA) and fumonisins. This review briefly shedlighted on the taxonomy of this important group of *Aspergillus* along with the species incidence, mycotoxin production in agricultural commodities as well as their significance as plant pathogens. A provisional key for identification (based on phenotypic characteristics) is provided for all described species to-date.

Keywords: Ochratoxins; Fumonisins; Biotechnology; *Aspergillus carbonarius*; Cereals; Grapes.

1. TAXONOMICAL OVERVIEW

Thom and Raper [1] and Raper and Fennell [2] published major monographic treatments on the genus *Aspergillus* and respectively accepted 89 and 150 species. Now the genus comprises 339 species [3] or 344 [4]. Many of these species can be conveniently separated into several distinct morphospecies, and several of these are based on colors according to the earlier classification [2]. However, phylogenetic analyses of sequence data resulted in separating the *Aspergillus* genus into eight subgenera [5]. Following these analyses, the economically important species that produce the ochratoxins were divided to include those species of the subgenus *Circumdati*, the sections *Circumdati* (=*Aspergillus ochraceus* group) and *Nigri* (*A. niger* group). There are no known teleomorphic species of section *Nigri*. In recent years, members of the *Aspergillus* section *Nigri* have undergone an extensive taxonomic revision resulting in several new taxa. Mosseray [6] described 35 black aspergilli species, while Raper and Fennell [2] reduced this number to 12. Later, Al-Musallam [7] revised the taxonomy of the *A. niger* group and recognized seven species, based on morphological features, and described *A. niger* as an aggregate consisting of seven varieties and two *formae*. The black *Aspergillus* species were classified into the Section *Nigri* in the subgenus *Circumdati* by Gams et al. [8], formerly '*A. niger* species group' by Raper and Fennell [2]. They present dark colonies, often black, and uniseriate or biseriate conidiophores. In 1989, Kozakiewicz [9] suggested 17 taxa in the *A. niger* group and distinguished two groups: echinulate and verrucose, depending on their conidial ornamentations. In the past, it was very common that all *Aspergillus* isolates developing black colonies were identified as *A.niger* by non-taxonomists, because of the similarities in morphology. To solve this problem, Abarca et al. [10] published a review in the taxonomy of black aspergilla and proposed an identification key to distinguish the most common taxa based on uniseriate and biseriate character of the conidial heads. A provisional key of section *Nigri*, based on phenotypic characteristics, extrolites and β-tubulin sequencing, was also proposed [11] who accepted 15 species in this section: *A. aculeatus, A. brasilensis, A. carbonarius, A. costaricaensis, A. ellipticus, A. foetidus, A. heteromorphus, A. homomorphus, A. japonicus, A. lacticoffeatus, A. niger, A. piperis, A. sclerotioniger, A. tubingensis* and *A. vadensis*. Later on some more new species were described: *A. ibericus* [12], *A. aculeatinus, A. sclerotiocarbonarius* [13], *A. uvarum* [14], *A. saccharolyticus* [15]. Also in 2011, 4 additional species were described: *A. fijiensis, A. indologenus, A. eucalypticola, A. neoniger* and 2 others were validated; *A. violaceofuscus* and *A. acidus,* however *A. foetidus* was synonymized to *A. niger* based on molecular and physiological data and 2 other species described previously, *A. coreanus* and *A. lacticoffeatus,* were found to be colour mutants of *A. acidus* and *A. niger*, respectively [16]. Also in the study of Hubka and Kolarik [17] on β-tubulin paralogue *tubC,* stated that *A. japonicus* should be treated as a synonym with *A. violaceofuscus*, and *A. fijiensis* is reduced to synonymy with *A. brunneoviolaceus*. In 2012, two uniseriate species were described from indoor air (*A. floridensis* and *A. trinidadensis*) and *A. fijiensis* was confirmed as a synonym with *A. brunneoviolaceus* [18]. Currently and after these revisions, *Aspergillus* section *Nigri* is considered to comprise 26 defined species and one variety [5, 10, 11, 13, 14, 16-19] (refer to Table 1), although it remains under investigation, which may result in further changes.

2. DISTRIBUTION AND INCIDENCE OF THE BLACK ASPERILLI IN AGRICULTURAL COMMODITIES

It was indicated that most members of the genus *Aspergillus* occurred in the tropical latitudes below 25 degree north and south, with greater than expected frequencies in the subtropical to warm temperate zones at latitudes between 26 and 35 degrees [20]. Also, it was suggested that species abundance peaked in the subtropics is attributed to several biotic and abiotic interacting factors with the major factor temperature [20]. In general, the black species of aspergilli (particularly *A. niger* var. *niger*) were found to occur more frequently in forest and cultivated soils and less frequency in desert soils [20, 21]. *A.niger* is one of the most common species of the genus *Aspergillus*. It is one of the fungi that have been labelled with the GRAS (generally recognized as safe) status from the US Food and Drug Administration [22]. But instead of the safe categorization, *A. niger* has been found to be an opportunistic reason for infections of humans. If inhaled, in sufficient quantity it can cause severe lung problems i.e., aspergillosis in humans. It is also associated with various plant diseases resulting in huge economic loss. It is also reported to produce ochratoxin A and fumonisin B_2 in stored commodities [10, 23]. Black *Aspergillus* species were found as dominant in almost all agricultural commodities in all continents such as cereals (maize, wheat, barley, sorghum, millet, rye, oat, etc.), cereal products, beans, nuts (peanuts, almond and hazelnuts, coconut etc.), grape and grape products, fruits and fruit juices, and vegetables (refer to Table 2).

Table 1. List of species accepted to-date (ordered alphabetically).

1.	*A. aculeatinus* Noonim, Frisvad, Varga & Samson 2008
2.	*A. aculeatus* Lizuka 1953
3.	*A. brasiliensis* Varga, Frisvad & Samson 2007
4.	*A. brunneoviolaceus* Bat. & H. Maia 1955 (=*A. fijiensis* Varga, Frisvad & Samson 2011)
5.	*A. carbonarius* (Bainier) Thom 1916
6.	*A. ellipticus* Raper & Fennell 1965
7.	*A. eucalypticola* Varga, Frisvad & Samson 2011
8.	*A. floridensis* Ž. Jurjević, G. Perrone & S.W. Peterson 2012
9.	*A. helicothrix* Al-Musallam 1980
10.	*A. heteromorphus* Batista & Maia 1957
11.	*A. homomorphus Steiman,* Guiraud, Sage & Seigle-Mur. ex Samson & Frisvad 2004
12.	*A. ibericus* Serra, Cabanes & Perrone 2006
13.	*A. indologenus* Frisvad, Varga & Samson 2011
14.	*A. luchuensis* Inui 1901 (=*A. acidus* Kozak. 1989, =*Aspergillus awamori* Nakaz 1907)
15.	*A. neoniger* Varga, Frisvad & Samson 2011
16.	*A. niger* van Tieghem 1867 (=*A. foetidus* Thom & Raper 1945)
17.	*A. niger* var. *taxi* Zhou, Zhao & Ping 2009
18.	*A. piperis* Samson & Frisvad 2004
19.	*A. saccharolyticus* Sørensen, Lubeck & Frisvad 2011
20.	*A. sclerotiocarbonarius* Noonim, Frisvad, Varga & Samson 2008
21.	*A. sclerotioniger* Samson & Frisved 2004
22.	*A. trinidadensis* Ž. Jurjević, G. Perrone & S. W. Peterson 2012
23.	*A. tubingensis* (Schober) Mosseray 1934
24.	*A. uvarum* Perrone, Varga & Kozakiewicz 2007
25.	*A. vadensis* Samson, de Vries, Frisvad & Visser 2005
26.	*A. violaceofuscus* Gasperini 1887 (=*A. japonicus* Saito 1906)
27.	*A. welwitschiae* (Bres.) Henn. apud Wehmer 1907 (=*A. awamori* sensu Perrone et al. 2011)

3. OCHRATOXIN PRODUCTION IN AGRICULTURAL COMMODITIES AND BY THE ASSOCIATED BLACK ASPERGILLI

Ochratoxin A (OTA, Fig. 1) is a very strong nephrotoxin and potential carcinogen, teratogenic and immunosuppressive, classified as Group 2B by the International Agency for Research on Cancer [60]. The Joint FAO/WHO Expert Committee on Food Additives (JECFA) established 100 ng kg^{-1} bw as the tolerable weekly intake (PTWI) recommended for OTA [61], which is also regulated by the European Commission. The regulation levels in food and feed products are established at 10 μg kg^{-1} in dry grapes, 2 μg kg^{-1} in grape juice, must and wine, and 0.5 μg kg^{-1} in food for babies and infants.

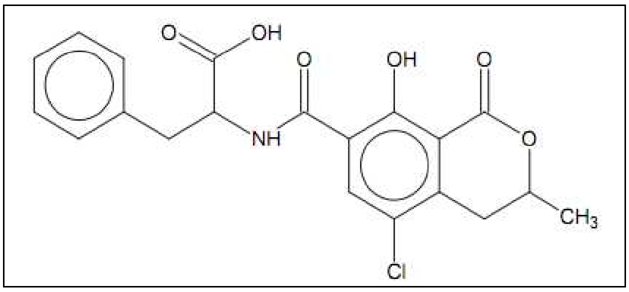

Figure 1. Chemical structure of OTA.

Dichotomous key for identification of species of section *Nigri* (based on phenotypic characteristics, designed by MA Ismail)

1.	Uniseriate (all species with no growth at 40 ºC) …………..	2
1.	Biseriate (growth at 40 ºC) ……..	9
2.	Versicle size up to 80 µm or more …………………….…………..............................	3
2.	Versicle size not exceed 45 µm …………………………………..................................	7
3.	Stipe width up to 30 µm, conidia 3.5-5 µm, sclerotia if present cream, up to 0.5 mm diam	*A. aculeatus*
3.	Stipe width not exceed 20 µm ………..………………………………….............................	4
4.	Conidia large 4-7(8) x 3.5-7, up to 13 x 10 µm if from monophialide	*A. trinidadensis*
4.	Conidia small, less than 6 µm in length ……………………..………..............................	5
5.	Conidia 2.5-4.5 µm, sclerotia if present white to cream, 0.4-0.6 mm diam ….....................	*A. aculeatinus*
5.	Conidia smaller, globose to ellipsoidal 3.5-5.0(6) x 3.5-5.0 (5.5) µm …............................	6
6.	Sclerotia if present buff to orange brown up to 0.8 mm diam ………............................	*A. brunneoviolaceus* (=*A. fijiensis*)
6.	Sclerotia if present buff yellowish, 0.2-1.1 mm diam ………………..	*A. floridensis*
7.	Stipe width (5-)10-18 (-24) µm, vesicle 20-30 µm, conidia globose-ellipsoidal (3-) 4-7 (-9) x 3.0-7.0 µm, sclerotia if present dark brown to black, 0.5-0.8 mm diam ………... ..	*A. uvarum*
7.	Not as above (stipe width and conidia smaller, vesicles larger)	8
8.	Stipe width 2-5 µm, vesicles 10-30 (-45) µm, conidia 3.5-4.0 x 4.0-5.5 µm, sclerotia if present white to cream, up to 0.5 mm diam. …..	*A. violaceofuscus* (=*A. japonicas*)
8.	Stipe width 5-7 µm, vesicles 25-40 µm, conidia 5.0-6.2 µm, sclerotia absent	*A. saccharolyticus*
8.	Stipe width 5-11 µm, vesicles 20-45 µm, conidia 3-4 µm, sclerotia absent…………….....	*A. indologenus*
9.	Conidial small, never exceed 5µm……………………………………..........................	10
9.	Conidia large, exceed 5 µm……………………………...	20
10.	Vesicle not exceed 45 µm……………………………………………....................	11
10.	Vesicles larger……………………………………………………............................	13
11.	No growth at 40 ºC, vesicles up to 30 µm, stipe width not exceed 7 µm; sclerotia 300-600 mm diam., white when young …………………………....................................	*A. heteromorphous*
11.	Growth at 40 ºC, vesicles up to 35 or 45 µm, stipe width up to 13 or 15 µm….................	12
12.	Vesicles not exceed 35 µm, stipe brown to black, short, not exceed 150 µm, sclerotia absent………………………………………..	*A. vadensis*
12.	Vesicles up to 45 µm, stipe pale brown, long, up to 1700 µm, sclerotia produced by some strains, white ……………………………..	*A. brasiliensis*
12.	Vesicles 30-55 µm, stipe hyaline, stipe width 8-14 µm, sclerotia absent, conidia globose 2.5-3.5 µm…………………………..	*A. eucalypticola*
12.	Vesicles 30-50 µm, stipe hyaline, stipe width 8-12µm, sclerotia absent, conidia 3.5-5.0 µm	*A. neoniger*
12.	Vesicle 20-40 µm, stipe hyaline, stipe width 10-13 (up to 30) µm, sclerotia absent, conidia 3.5-4.5 µm ………………………………..	*A. luchuensis* (=*A.acidus)*
13.	Sporulation abundant & heavy, vesicles up to 80 µm…………………............................	14
13.	Sporulation poor ………………………………………………………................................	18

Dichotomous key for identification of species of section *Nigri* (based on phenotypic characteristics, designed by MA Ismail)

14.	Sclerotia absent………………………………………………………...................................	15
14.	Sclerotia present………………………………………………………...............................	17
15.	Stipe length up to 1000 µm & width up to 12 µm…..……………….................................	*A. foetidus*
15.	Stipe width 8-12 µm, sclerotia absent, vesicle 30-50 µm ……………...............................	*A. niger*
15.	Stipe width up to 14 µm, conidia 2.5-3.5 µm ……….………………..................................	*A. eucalypticola*
15.	Stipe width 10-13 (-30) µm, conidia 3.5-4.5 µm, vesicle 20-40 µm …...............................	*A. luchuensis (=A.acidus)*
15.	Stipe longer, up to 3000 µm or more, stipe width up to 20 µm or more	16
16.	Stipe smooth, colorless or brownish only in the upper portion; stipe width 15-20 µm	*A. niger*
16.	Stipe very rough, brown on ageing; stipe width 20-33 µm…………….............................	*A. niger* var. *taxi*
16.	Stipes longer up to 6000 µm, smooth to coarse, brownish, stipe width 15-20 (-30) µm	*A. tubingensis*
17.	Sclerotia white, 1200-1800 µm; reverse yellow to orange to reddish brown in age, stipe width up to 12 µm ……………………………...	*A. foitidus*
17.	Sclerotia white to pink to black, 500-800 µm, reverse white; stipe width 15-20 (30) µm .	*A. tubingensis*
18.	Sclerotia present, yellowish or pinkisk; stipes hyaline………………................................	19
18.	Sclerotia absent, vesicle 40-65 µm, stipes orange brown…………….............................	*A. lacticoffeatus*
19.	Vesicle 40-55 µm, stipe width 7-10 µm, metulae 20-35 µm long …….............................	*A. piperis*
19.	Vesicles 40-80 (-90) µm; stipe width 12-22 µm, metulae 30-60 µm long …….................	*A. costaricaensis*
20.	Growth at 40 ºC, sclerotia absent……………………………….………..............................	*A. ibericus*
20.	No growth at 40 ºC……………………………………………………..................................	21
21.	Sclerotia absent………………………………….……………………...............................	22
21.	Sclerotia present………………………………………………………...............................	24
22.	Conidia strongly ellipsoidal, 7-10 X 2.5-3, spinulose; vesicles 75-100 µm; stipe long up to 5000-8000 (-1 cm) X 12-20 µm………………..	*A. ellipticus*
22.	Conidia not ellipsoidal……………………………………………………............................	23
23.	Stipe width 35-40 µm, conidia globose, 7-9 µm, metulae length less than 15 µm, vesicle 40-80 (-100) µm…………………………..	*A. carbonarius*
23.	Stipe width9-15 µm, conidia 5-7 (-9) µm, metulae length less than 15 µm, vesicles not exceed 50-65 µm…………………………………...	*A. homomorphus*
24.	Sclerotia cup-shaped with coiled setae; stipe width 8.5-13.5 µm, (with brownish stipe, vesicle, conidia, setae & sclerotia) ………………..	*A. helicothrix*
24.	Characters not as above……………………………………………....................................	25
25.	Conidia strongly ellipsoidal, 7-10 X 2.5-3 µm, spinulose, sclerotia dull yellow to brown in age, 500-1500 µm…………………………...	*A. ellipticus*
25.	Conidia globose………………………………………………….......................................	26
26.	Conidia 4.5-6.5µm, vesicle pyriform 30-50 µm, sclerotia yellow to orange to red brown; sporulation poor, stipe width less than 18 µm …..	*A. sclerotioniger*
26.	Conidia up to 9 µm; vesicle up to 100 µm, stipe width wider ………...............................	27
27.	Sclerotia yellow to orange to red brown, no growth at 9 ºC, stipe width 13-27 µm ……………………………………………………..	*A. sclerotiocarbonarius*
27.	Sclerotia pink to yellow, growth at 9 ºC, stipe width 35-40, sporulation abundant	*A. carbonarius*

Table 2. Black aspergilli in agricultural commodities.

Commodity	Species	Country	References
Grape & grape products	*A. brasiliensis, A. niger, A. awamori, A. aculeatus, A. tubingensis, A. ibericus, A, carbonarius, A. japonicus, A. uvarum, A. acidus,*	Worldwide	[12, 14, 24-29]
Grapes	*A. carbonarius, A. tubingensis, A. japonicus, A. ibericus, A. niger* aggregate	Greece	[30]
Grapes	*A. carbonarius, A. niger* aggregate	Italy	[31, 32]
Wine grapes	*A. niger* var. *niger, A. niger* var. *awamori, A. foetidus*	Argentina	[33]
Maize	*A. japonicus, A. niger* var. *niger*	Worldwide	[27, 34-36]
Maize	*A. niger* aggregate	Portugal	[37]
Maize kernels	*A. heteromorphus, A. carbonarius, A. aculeatus, A. niger, A. japonicus, A. brasiliesis*	Kenya	[38]
Wheat	*A. niger*	Egypt	[39]
Sorghum	*A. niger*	Egypt	[36]
Milled rice	*A. niger*	Uganda & Pakistan	[40-42]
Paddy & mild rice	*A. niger*	Uganda	[43]
Peanuts	*A. japonicus, A. niger* var. *niger, A. carbonarius, A. niger var. awamori*	Worldwide	[27, 35, 44]
Peanuts	*A. niger, A. carbonarius*	Uganda & Kenya	[45]
Peanuts	*A. niger*	Egypt	[39]
Lentil & sesame	*A. niger*	Egypt	[36]
Coffee bean	*A. aculeatus, A. aculeatinus, A. carbonarius, A. sclerotiocarbonarius, A. sclerotioniger, A. niger, A. lacticoffeatus, A. japonicus, A. tubingensis*	Worldwide	[11, 27, 35]
Coffee beans	*A. niger* group	Colombia	[46]
Coffee beans	*A. niger, A. carbonarius*	Saudi Arabia	[47]
Beans, wheat, millet	*A. niger*	Nigeria	[48]
Cereal products (baby foods)	*A. niger, A. carbonarius*	Canada, England & Kenya	[49, 50]
Cereal products (baby foods)	*A. carbonarius, A. niger, A. phoenicis*	Uganda	[51, 52]
Spices	*A. niger* var. *niger*	Worldwide	[27, 35, 53]
Black pepper	*A. piperis*	Worldwide	[27, 35]
Desiccated coconut	*A. niger, A. carbonarius, A. japonicus*	Uganda & Kenya	[45]
Fruit juice & beverages	*A. niger, A. japonicus*	Egypt	[54]
Apricot, fig, grapes & plum	*A. awamori, A. carbonarius, A. japonicus, A. niger, A. tubingensis, A. sclerotioniger, A. aculeatus, A. aculeatinus*	Iraq	[55]
Cocoa bean, coffee bean & dried cassava	*A. carbonarius, A. niger, A. tubingensis, A. aculeatus*	Indonesia	[56]
Cocoa beans	*A. carbonarius, A. tubingensis, A. niger*	Sierra Leona, Equatorial Guinea & Ecuador	[57]
Olive oil	*A. niger*	Morocco	[58]
Vegetables	*A. brasiliensis, A. niger, A. japonicus, A. vadensis*	Egypt	[59]

Table 3. Ochratoxins produced naturally in agricultural commodities due to infection by black aspergilla (*A. carbonarius* and *A. niger*).

Commodities	Country	Reference
Grape	Worldwide	[28, 31, 73-76]
Grape	Italy	[32]
Grape juice	Europe	[77]
Wine	Europe, worldwide	[28, 74, 77]
Raisins	California, USA	[29]
Dried vine fruits	Worldwide	[7, 28, 76]
Cereals	Europe	[77]
Coffee	Europe	[74, 77]
Dry fruits	Europe	[77]
Cocoa	Europe	[77]
Figs	Central Europe	[74]
Peanuts	Argentina	[44]
Rice and rice products*	Worldwide	[78-83]
Cereal grains (wheat, barley, corn, oats, sorghum)*	Worldwide (UK, Italy, Ivory Coast, Japan, Tunesia)	[81, 84-88]
Cereal flour (wheat, rye, maize, oats)*	Worldwide	[78, 82, 88- 90]
Infant cereal food*	Worldwide	[86, 91, 92]

*Means that aspergilli and penicillia may be involved in ohratoxin production.

OTA is produced by fungi of the genera *Aspergillus* and *Penicillium*. The major species implicated in OTA production includes *Aspergillus ochraceus, A. sulphureus, Petromyces alliaceus, Penicillium verrucosum, A. carbonarius,* and to a lesser extent *A. niger* [62, 63]. Ueno et al. [64] were the first to report on ochratoxin A (OA) production by a black *Aspergillus* species, *A. foetidus*. This was later confirmed [33, 65].

OTA is a frequent natural contaminant of many foodstuffs such as cocoa beans, coffee beans, cassava flour, cereals, peanuts, dried fruits and wine [66]. Studies revealed that whenever OTA was detected in high levels, AFB1 was absent or present at very low levels and vice versa which suggests some sort of competition between these toxins at the production level in foodstuffs. OTA has also been reported as a contaminant of tiger nuts and fermented maize dough in West Africa [67]. Ochratoxin A contamination of agricultural products including cereals and grains influences chronic effect on human exposure [68]. Natural occurrence of mould infection and OTA contamination in maize and maize-based products is a worldwide problem [69]. *A. niger* is commonly isolated from maize [70] and a high incidence of *A. carbonarius* has been also reported [71]. Both species are the main source of ochratoxins in corn and other food products in both subtropical and tropical zones of the world [35] and to a lesser extent in grapes, wine, dried vine fruits and grape juice [72] (refer to Table 3).

A. carbonarius was recognized as the major OTA-producer [65, 93-96], near 100% of isolaes produce OTA when grown in pure culture [97-101]. The closely related species *A. niger* has also been reported reliably as a producer [64, 97, 98, 102]. However all reports agree that OTA production by *A. niger* is very uncommon. Also, it was observed that *A. niger* “aggregate”, although the most common, showed a low percentage of OTA producing strains, from 4 to 10% [101, 103]; none of the strains belonging to *A. uvarum* was able to produce OTA [14]. *A. lacticoffeatus* and *A. sclerotioniger*, both isolated from coffee [11], and from raisin samples [104], are also reported as OTA producers (Table 4).

The most distinguishing characteristics to differentiate *A. niger* aggregate species (*A. niger, A. tubingensis* and *Aspergillus awamori*) from *A. carbonarius* are growth at 37°C and conidial diameter [19]. All 12 of the ochratoxigenic isolates of *A. carbonarius* showed restricted growth at 37°C, while all of the nonochratoxigenic isolates of *A. niger* aggregate grew well at 37°C. This effect was more pronounced at 40°C, at which the ochratoxigenic strains did not grow and the nonochratoxigenic strains grew well. In addition, all OTA-producing strains formed large (7-10 µm diameter), and all OTA-nonproducing strains formed smaller conidia (<4 µm diameter) [29] (refer to the Key).

Table 4. Ochratoxins produced by black aspergilli isolated from agricultural commodities.

Species	Ochratoxins	References
A. aculeatus	+	[10]
A. carbonarius	+	[11, 17, 19, 24, 25, 27-31, 35, 44, 47, 56, 57, 73, 74]
A. foetidus	+	[33]
A. japonicus	+	[27, 35, 44]
A. lacticoffeatus	+	[11]
A. niger var. *niger*	+	[11, 24, 27, 28, 33, 35, 44, 47, 56-58, 73, 74, 102]
A. niger aggregate/ Section *Nigri*	+	[31, 37, 106]
A. sclerotioniger	+	[11, 19]
A. tubingensis	+	[27, 30, 35, 57]
A. welwitschiae (=*A. awamori*)	+	[19, 28, 33, 44, 107]

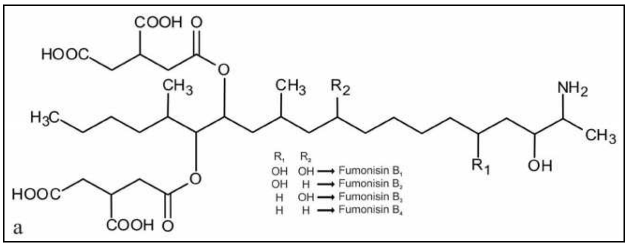

Figure 2. Chemical structures of fumonisins [113].

4. FUMONISINS PRODUCTION IN AGRICULTURAL COMMODITIES AND BY THE ASSOCIATED BLACK ASPERGILLI

Fumonisins (Fig. 2) were discovered in South Africa in 1988 [108, 109]. They are known to be produced by *Fusarium verticillioides* (formerly known as *F. moniliforme*), *F. proliferatum*, *F. oxysporum*, *F. globosum*, several other *Fusarium* spp., and *Alternaria alternata* f. sp. *lycopersici*. Fumonisins are frequently found in corn and corn-based foods [110, 111]. FB1 is the most commonly found, not only in corn (maize) and corn-based foods, but also in rice, sorghum, cowpea seeds, beans, soybeans and beer. FB1 can cause two diseases of farm animals: leucoencephalomalacia in horses and porcine pulmonary oedema. It is also carcinogenic, hepatotoxic, nephrotoxic and embryotoxic in laboratory animals. In humans fumonisins are associated with oesophageal cancer and neural tube defects based on studies in Transkei [109] and Texas [112]. The International Agency for Research on Cancer (IARC) designated FB1 in Group 2B as 'possibly carcinogenic to humans' [60].

Findings of fumonisins in agricultural commodities are shown in Table 5. In recent years fumonsins have been found in a wide variety of foods such as, cassava products in Tanzania [114], garlic and onion powders [115] and garlic bulbs [116], black radish [117], black tea [118, 119], figs in Turkey [120, 121], peanuts in Cote d'Ivoire, Cameroon and China [87, 122, 123], and soybeans in Japan [124]. Fumonisins have been found in dietary and medicinal wild plants in South Africa [125] and in other medicinal plants: leaves of orange tree, leaves/flowers of linden tree and chamomile in Portugal [118], mint and stinging nettle in Turkey [119]. Of particular note and interest is that for some foods, FB1 is not the major fumonisin as it is for maize and other grains. FB2 (without FB1) occurred in wine from several countries [126, 127], such as red wine must in Italy [126] and beer [128]. Table 5 shows some commodities contaminated with fumonisins.

Fumonisin production has also been proved by *A. niger* isolates originating from coffee beans and grapes [129, 130]. Further reports claimed that *A. niger* and *A. awamori* from grapes, raisins and coffee beans produced fumonisins particularly FB2 [129, 131], B2 and B4 [107, 126, 130, 132], although other isomers in smaller quantities [107] and a FB1 isoform, named FB6 were also detected [131]. No fumonisins were found in other black *Aspergillus* species from grapes, including *A. carbonarius* [126].

Whereas *F. verticillioides* produces fumonisins on agar media based on plant extracts such as barley malt, oat, rice, potatoes, and carrots, *A. niger* is able to produce fumonisins in high quantities on agar media with low water activity [63]. Recently, dried vine fruit samples (raisins, sultanas) were found contaminated with fumonisin-producing black aspergilli and several fumonisin isomers, including fumonisins B1-4, 3-epi-FB3, 3-epi-FB4, iso-FB1, and two iso-FB2,3 forms [107]. Several strains collected from figs, dates and onions were also able to produce fumonisins, thus black aspergilla are suspected to be responsible for fumonisin contamination of grape-derived products, figs and onions. Figs and onions were also contaminated with low but significant amount of fumonisins [107]. Frisvad et al. [133] studied 180 strains of *A. niger* from various sources and found about 80% producing FB2 (refer to Table 6). Although the percentage of fumonisin-producing strains was very high, the absence of at least part of the fumonisin biosynthetic gene cluster has been reported in *A. niger* [134].

5. *ASPERILLUS NIGER* AS A PLANT PATHOGEN

A. niger has been identified as the responsible species in diseases of food crops, such as maize seedling blight, maize ear rot and seedling blight of peanuts. It causes also a disease called black mold on certain fruits and vegetables such as grapes, onions and peanuts [74, 141] (refer to Table 7).

Table 5. Fumonisins B1 and B2 produced naturally from some agricultural commodities due to infection by black aspergilli (*A. niger/A. awamori*).

Commodities	Country	Reference
Grape, raisins, figs, onion	Central Europe	[74]
Coffee beans	Central Europe	[63]
Grapes, raisins & wine	Central Europe	[127, 130, 135, 136]
Maize kernels	South Africa	[137]

Table 6. Fumonisins produced by black aspergilli isolated from agricultural commodities.

Species	Fumonisins	Reference
A. carbonarius	B_1, B_4 and several fumonisin isomers	[74]
A. niger var. *niger*	B_1, B_4	[27, 35, 63, 126, 130, 131, 138]
A. niger aggregate/ Section *Nigri*	B_2	[28, 37]
A. welwitschiae (=*A. awamori)*	+	[19, 107, 139, 140]

Table 7. Plant diseases caused by *Aspergillus niger*.

Disease & host	Reference
Almond chlorosis	[74, 142]
Apricot, peach ripe fruit rot	[74, 142]
Bulb (black) rot of onions & garlic	[74, 142]
Black rot of cherry	[143]
Carrot sooty rot	[74, 142]
Citrus black mold	[74, 142]
Crown rot of peanuts	[74, 142, 144]
Fig smut	[74, 142]
Fruit rot of banana	[145]
Fruit rot of grapes	[146]
Grape bunch rot	[74, 142]
Kernel rot of maize	[35]
Mango black mold rot	[74, 142, 147]
Pistachio fruit rot	[74, 142]
Rot of tomatoes	[148]
Stem rot of *Dracaena*	[149]
Strawberry fruit rot	[74, 142]
Tuber rot of yam	[150]
Vine canker	[74, 142]

6. CONCLUSION

This review outlines a taxonomic overview on all described and accepted *Asperillus* species in section *Nigri* up-to-date with a key for identification based on their phenotypic features, however these features are not enough for species delimitation and other tools (e.g. molecular techniques and/or some physiological and biochemical characteristics) are needed to support their identity. The incidence and implication of species in agricultural commodities are also discussed. Capabilities of some species of the section to produce ochratoxins and/or fumonisins are of special significance in these commodities due to their health hazard to human.

TRANSPARENCY DECLARATION

The author declares that has no conflict of interest.

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