

Taxonomy of *Aspergillus* section *Flavi* and their production of aflatoxins, ochratoxins and other mycotoxins

J.C. Frisvad^{1*}, V. Hubka^{2,3}, C.N. Ezekiel⁴, S.-B. Hong⁵, A. Nováková³, A.J. Chen^{6,9}, M. Arzanlou⁷, T.O. Larsen¹, F. Sklenář^{2,3}, W. Mahakarnchanakul⁸, R.A. Samson⁹, and J. Houbraken^{9*}

¹Department of Biotechnology and Biomedicine, DTU-Bioengineering, Technical University of Denmark, 2800 Kongens Lyngby, Denmark; ²Department of Botany, Faculty of Science, Charles University in Prague, Benátská 2, 128 01 Prague 2, Czech Republic; ³Institute of Microbiology of the CAS, v.v.i., Vídeňská 1083, 142 20 Prague 4, Czech Republic; ⁴Department of Microbiology, Babcock University, Ilishan Rémo, Nigeria; ⁵Korean Agricultural Culture Collection, National Academy of Agricultural Science, RDA, Suwon, South Korea; ⁶Institute of Medical Plant Development, Chinese Academy of Medical Sciences and Peking Union Medical College, Beijing 100193, PR China; ⁷Department of Plant Protection, University of Tabriz, Tabriz, Iran; ⁸Department of Food Science and Technology, Faculty of Agro-Industry, Kasetsart University, Bangkok 10900, Thailand; ⁹Westerdijk Fungal Biodiversity Institute, Uppsalalaan 8, 3584 CT Utrecht, the Netherlands

*Correspondence: J.C. Frisvad, jcf@bio.dtu.dk; J. Houbraken, j.houbraken@westerdijkinstitute.nl

Abstract: Aflatoxins and ochratoxins are among the most important mycotoxins of all and producers of both types of mycotoxins are present in *Aspergillus* section *Flavi*, albeit never in the same species. Some of the most efficient producers of aflatoxins and ochratoxins have not been described yet. Using a polyphasic approach combining phenotype, physiology, sequence and extrolite data, we describe here eight new species in section *Flavi*. Phylogenetically, section *Flavi* is split in eight clades and the section currently contains 33 species. Two species only produce aflatoxin B₁ and B₂ (*A. pseudotamarii* and *A. togoensis*), and 14 species are able to produce aflatoxin B₁, B₂, G₁ and G₂: three newly described species *A. aflatoxiformans*, *A. austwickii* and *A. cerealis* in addition to *A. arachidicola*, *A. minisclerotigenes*, *A. mottae*, *A. luteovirescens* (formerly *A. bombycis*), *A. nomius*, *A. novoparasiticus*, *A. parasiticus*, *A. pseudocaelatus*, *A. pseudonomius*, *A. sergii* and *A. transmontanensis*. It is generally accepted that *A. flavus* is unable to produce type G aflatoxins, but here we report on Korean strains that also produce aflatoxin G₁ and G₂. One strain of *A. bertholletius* can produce the immediate aflatoxin precursor 3-O-methylsterigmatocystin, and one strain of *Aspergillus sojae* and two strains of *Aspergillus alliaceus* produced versicolorins. Strains of the domesticated forms of *A. flavus* and *A. parasiticus*, *A. oryzae* and *A. sojae*, respectively, lost their ability to produce aflatoxins, and from the remaining phylogenetically closely related species (belonging to the *A. flavus*-, *A. tamarii*-, *A. bertholletius*- and *A. nomius*-clades), only *A. caelatus*, *A. subflavus* and *A. tamarii* are unable to produce aflatoxins. With exception of *A. togoensis* in the *A. coremiiformis*-clade, all species in the phylogenetically more distant clades (*A. alliaceus*-, *A. coremiiformis*-, *A. leporis*- and *A. avenaceus*-clade) are unable to produce aflatoxins. Three out of the four species in the *A. alliaceus*-clade can produce the mycotoxin ochratoxin A: *A. alliaceus* s. str. and two new species described here as *A. neoalliaceus* and *A. vandermerwei*. Eight species produced the mycotoxin tenuazonic acid: *A. bertholletius*, *A. caelatus*, *A. luteovirescens*, *A. nomius*, *A. pseudocaelatus*, *A. pseudonomius*, *A. pseudotamarii* and *A. tamarii* while the related mycotoxin cyclopiazonic acid was produced by 13 species: *A. aflatoxiformans*, *A. austwickii*, *A. bertholletius*, *A. cerealis*, *A. flavus*, *A. minisclerotigenes*, *A. mottae*, *A. oryzae*, *A. pipericola*, *A. pseudocaelatus*, *A. pseudotamarii*, *A. sergii* and *A. tamarii*. Furthermore, *A. hancockii* produced speradine A, a compound related to cyclopiazonic acid. Selected *A. aflatoxiformans*, *A. austwickii*, *A. cerealis*, *A. flavus*, *A. minisclerotigenes*, *A. pipericola* and *A. sergii* strains produced small sclerotia containing the mycotoxin aflatrem. Kojic acid has been found in all species in section *Flavi*, except *A. avenaceus* and *A. coremiiformis*. Only six species in the section did not produce any known mycotoxins: *A. aspearensis*, *A. coremiiformis*, *A. lanosus*, *A. leporis*, *A. sojae* and *A. subflavus*. An overview of other small molecule extrolites produced in *Aspergillus* section *Flavi* is given.

Key words: *Aspergillus*, Section *Flavi*, Aflatoxins, Cyclopiazonic acid, Tenuazonic acid.

Taxonomic novelties: *Aspergillus aflatoxiformans* Frisvad, Ezekiel, Samson & Houbraken, *Aspergillus aspearensis* Houbraken, Frisvad, Arzanlou & Samson, *Aspergillus austwickii* Frisvad, Ezekiel, Samson & Houbraken, *Aspergillus cerealis* Houbraken, Frisvad, Ezekiel & Samson, *Aspergillus neoalliaceus* A. Nováková, Hubka, Samson, Frisvad & Houbraken, *Aspergillus pipericola* Frisvad, Samson & Houbraken, *Aspergillus subflavus* Hubka, A. Nováková, Samson, Frisvad & Houbraken, *A. vandermerwei* Frisvad, Hubka, Samson & Houbraken.

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INTRODUCTION

Aspergillus subgenus *Circumdati* section *Flavi* contains some of the most important species in the genus, which are of significance in biotechnology, foods and health (Varga *et al.* 2011). *Aspergillus flavus* is reported, after *A. fumigatus* (section *Fumigati*), as the second leading cause of invasive aspergillosis and it is the most common cause of superficial infection (Hedayati *et al.* 2007). *Aspergillus oryzae* and *A. sojae* appear to be the domesticated forms of the aflatoxigenic species *A. flavus* and *A. parasiticus*, respectively, and are used extensively in the food and biotechnology industries (Houbraken *et al.* 2014). A large number of species in *Aspergillus* section *Flavi* are common in crops, and some of them produce several mycotoxins, such as aflatoxins, 3-nitropropionic acid, tenuazonic acid and cyclopiazonic acid

(Varga *et al.* 2011). Despite many publications in various research fields, the taxonomy of the aflatoxigenic species in *Aspergillus* section *Flavi* is still not fully elucidated, and several new species (some with aflatoxigenic potential) have been described since 2011, such as *A. novoparasiticus* (Gonçalves *et al.* 2012a,b), *A. mottae*, *A. transmontanensis*, *A. sergii* (Soares *et al.* 2012), *A. bertholletius* (Taniwaki *et al.* 2012), *A. hancockii* (Pitt *et al.* 2017) and *A. korhogoensis* (Carvajal-Campos *et al.* 2017). Additionally, there have also been some disagreements on the proper species names of strains formerly identified as *A. flavus* with large or small sclerotia (Probst *et al.* 2012, 2014).

Initially, *A. flavus* was reported to produce aflatoxin of the B and G type (Nesbitt *et al.* 1962, Codner *et al.* 1963). Later it was recognised that strains of *A. flavus* can only produce aflatoxin B₁ and B₂ (Varga *et al.* 2009, Amaike & Keller 2011) and that the

strains producing aflatoxin B and G were *A. parasiticus*, exemplified by strain NRRL 2999, which was initially identified as *A. flavus* (Christensen *et al.* 1973) and three years later re-identified as *A. parasiticus* (Buchanan & Ayres 1976). Although it was considered that *A. flavus* only produces B type aflatoxins, some reports indicate that *A. flavus* strains can also produce the G type aflatoxins (Camiletti *et al.* 2017, Barayani *et al.* 2015, Wicklow & Shotwell 1983, Okoth *et al.* 2018, Saldan *et al.* 2018). This contradictory data needs further investigation and it is important to determine whether *A. flavus sensu stricto* can produce aflatoxins of the G type or not. Most species in *Aspergillus* section *Flavi* produce both types of aflatoxins, while species outside section *Flavi* can only accumulate sterigmatocystin and aflatoxins of the B type (Geiser *et al.* 2007, Varga *et al.* 2009, Rank *et al.* 2011).

Raper & Fennell (1965) stated that *A. flavus* strains produced globose to subglobose sclerotia that are normally 400–700 µm in size, rarely exceeding 1 mm, but that some strains produced sclerotia that were uniformly and consistently smaller. They also mentioned strains that produced vertically elongate sclerotia, and such strains were later shown to be *A. nomius* or *A. pseudonomius* (Kurtzman *et al.* 1997, Varga *et al.* 2011, Massi *et al.* 2014). Also Hesseltine *et al.* (1970) reported *A. flavus* isolates with small sclerotia while most isolates had large sclerotia. They listed NRRL 3251 as one of the rare examples of a strain with small sclerotia that produced aflatoxin B₁ and B₂ only, and stated that this could represent a new species. Another strain similar to NRRL 3251 that also produce small-sized sclerotia is the genome sequenced strain ATCC MYA384 (= AF70) (Moore *et al.* 2015). These *A. flavus* strains with small sclerotia that produce B type aflatoxins (*A. flavus* S_B) are more common in USA than in Africa (Probst *et al.* 2014). Later Saito & Tsuruta (1993) found many strains with small sclerotia from agricultural soil in Thailand. They described their strains and NRRL 3251 as *A. flavus* var. *parvisclerotigenus*. In 2005, Frisvad *et al.* (2005) raised *A. flavus* var. *parvisclerotigenus* to species level and neotypified the species with a strain isolated from a peanut in Nigeria producing aflatoxin B₁, B₂, G₁ and G₂ (CBS 121.62 = IMI 093070 = NRRL A-11612). This neotypification is questionable as the original type only produced B type aflatoxins. Other strains producing small sclerotia, often referred to as *A. flavus* group S_{BG} (= “*A. flavus* strains producing small sized sclerotia and aflatoxin B and G”) represent multiple species. One of the “*A. flavus* group S_{BG}” taxa was described as *A. minisclerotigenes* (from Argentina originally) (Pildain *et al.* 2008) and is also found in Central, East and Southern Africa and Australia (Probst *et al.* 2014), while *A. parvisclerotigenus sensu Frisvad et al.* (2005) has been found in West Africa: Benin, Burkina Faso, Nigeria, Senegal and Sierra Leone (Probst *et al.* 2014). Another important group of strains is identified as *A. flavus* S_B and these strains are regarded as the agent causing lethal levels of aflatoxins in Kenyan maize. It remains questionable whether these are truly *A. flavus* or that these strains represent a species that has not yet been named (Cotty and Cardwell, 1999, Cardwell and Cotty, 2002, Donner *et al.* 2009, Okoth *et al.* 2012, 2018, Probst *et al.* 2007, 2010, 2012, 2014). However, a later study shows *A. flavus sensu stricto* and *A. minisclerotigenes* are the predominant species in Kenyan maize (Okoth *et al.* 2018).

The genomes of *A. oryzae* RIB 40 (Machida *et al.* 2005, Galagan *et al.* 2005, Inglis *et al.* 2013, Umemura *et al.* 2013a,b), and other strains of *A. oryzae* (Zhao *et al.* 2012, 2013, 2014), *A. flavus* NRRL 3357 (= ATCC 200026) (Payne *et al.* 2006, Fedorova *et al.* 2008, Nierman *et al.* 2015), ATCC

MYA384 (= AF70) (Moore *et al.* 2015) and other strains (Faustinelli *et al.* 2016), *A. parasiticus* ATCC 56775 (= NRRL 5862 = SU-1) (Linz *et al.* 2014), *A. sojae* NBRC 4239 (Sato *et al.* 2011), *A. bombycis* NRRL 26010 (Moore *et al.* 2016), *A. nomius* NRRL 13137 (= NBRC 33223) (Horn *et al.* 2009c, Moore *et al.* 2015), *A. hancockii* FRR 3425 (Pitt *et al.* 2017) and *A. arachidicola* (Moore *et al.* 2018) have been published. Gene clusters for several secondary metabolites, and the regulation of these gene clusters in *A. flavus* are known, including those for aflatoxins, aflatrem, aflavarins, aflavinines, asparosones, cyclopiazonic acid, kojic acid, leporins and penicillin (Chang *et al.* 2009, Georgianna *et al.* 2010, Marui *et al.* 2010, Terebayashi *et al.* 2010, Chang & Ehrlich 2011, Marui *et al.* 2011, Amare & Keller 2014, Ehrlich & Mack, 2014, Tang *et al.* 2015, Cary *et al.* 2015a,b, 2017, Gilbert *et al.* 2016, Ammar *et al.* 2017, Chang *et al.* 2017, Ibara *et al.* 2018). Genome sequencing of more strains in section *Flavi* will help elucidating how the gene clusters for aflatoxins and ochratoxins evolved. Sexual reproduction appears to be important for the variation between isolates of *A. flavus*, so acquisition of new alleles and mitochondrial inheritance are factors that should be taken into consideration (Horn *et al.* 2016).

For food safety purposes, correct species identification is of high importance (Kim *et al.* 2014, Samson *et al.* 2006, Probst *et al.* 2007, 2010, 2012, 2014, Varga *et al.* 2011), as different species may have different mycotoxin profiles and physiology. For example, *A. flavus* strains used to prevent aflatoxin production in crops, themselves unable to produce aflatoxins, may produce other potentially toxic secondary metabolites (Ehrlich, 2014). Detection of these species in foods using sophisticated analytical techniques requires an accurate and reliable taxonomic system (Frisvad *et al.* 2007, Godet & Munaut, 2010, Luo *et al.* 2014a,b, Faustinelli *et al.* 2017, Kaya-Celiker *et al.* 2015). Occasionally, strains producing important mycotoxins are apparently misidentified. An example of a dubious link between fungal species and mycotoxins is the production of the *A. fumigatus* metabolites fumigaclavine A (Jahardhanan *et al.* 1984) and fumitremorgins (Ma *et al.* 2016) by an *A. tamarii* strain. There is evidence that aflatoxigenic species can hybridize (Olate *et al.* 2012, 2015), so it should be examined whether some of the species producing aflatoxins may be hybrids. Furthermore, cells of *A. flavus* are multinucleate (Runa *et al.* 2015), and it is unknown whether such nuclei contain the same genetic material.

In this manuscript we present an update on the taxonomy of section *Flavi* and describe eight new species using a polyphasic approach combining physiology, morphology, sequence and extrolite data. A list of accepted species (and their synonyms) belonging to section *Flavi* is presented. The ability of the new species to produce aflatoxin and ochratoxin A is studied and an overview on the mycotoxin producing potential of all section *Flavi* species is presented.

MATERIALS AND METHODS

Isolation of microfungi

A part of the strains used in the study was recently isolated during various surveys in different countries (Czech Republic, Nigeria, Iran). Soil and drilosphere (soil in immediate proximity of

earthworm burrows) samples and samples from *Allolobophora hrabei* casts and intestines were collected in 2011–2013, always in spring and autumn, in the period of earthworm activity. Soil and drilosphere samples were collected by soil corer from the top 5 cm soil layer and *A. hrabei* casts were collected from the soil surface. Microscopic fungi were isolated by a dilution plate method (dilution 10⁴) and a soil washing technique (Garrett 1981, Kreisel & Schauer 1987) using three isolation media: dichloran rose bengal chloramphenicol agar (DRBC), Sabouraud's glucose agar (SGA) and beer wort agar (BWA). Rose bengal and chloramphenicol were added to the two latter media to suppress bacterial growth (Atlas 2010). Isolation from the *A. hrabei* intestine was done according to Nováková & Pižl (2003). Agar media were incubated for 7 days at 25 °C in darkness. For cultures from Nigeria, food (local rice, maize, mushroom, peanut cake and sesame) samples from various markets and agricultural soil samples from the top 2 cm of the soil were collected between October 2010 and February 2012. Cultures from food samples, except those from local rice and maize, were reported in other studies (Ezekiel *et al.* 2013a, 2013b, 2014). The isolates were previously reported as unnamed taxon S_{BG} based on phenotype (macro- and microscopic characters on 5/2 agar (5 % V-8 juice and 2 % agar, pH 5.2)) and aflatoxin production (on neutral red desiccated coconut agar) or *A. parvisclerotigenus* based on ITS, β -tubulin and calmodulin gene sequences. Local rice and maize grains were milled while soil was sieved prior to isolation of moulds on modified Rose Bengal Agar (mRBA; Cotty 1994) by dilution plating (Samson *et al.* 1995). Cultures on mRBA and 5/2 agar were incubated for 3 and 5 days, respectively, at 31 °C in darkness. Isolated colonies were purified on 5/2 agar. For cultures from Iran, soil samples were collected at 10–15 cm depth from Aspear Island in Urmia Lake, during 2011 and 2012. Isolations were carried out using the soil dilution plate on three culture media: malt extract agar (MEA), glucose peptone yeast extract agar (GPY) and potato dextrose agar (PDA) supplemented with various NaCl concentrations (0 to 3 %) (Arzanlou *et al.* 2016).

Strains

The recently isolated strains (see previous paragraph) were supplemented with strains from the 1) CBS culture collection, housed at the Westerdijk Fungal Biodiversity Institute, 2) CCF, Culture Collection of Fungi, Prague, Czech Republic, 3) DTO, the working collection of the Applied and Industrial Mycology department housed at the Westerdijk Institute, 4) IBT, the culture collection of at the Department of Biotechnology and Biomedicine, Technical University of Denmark, 5) KACC, Korean Agricultural Culture Collection, Wanju, South Korea. Interesting strains and strains representing new species were deposited into the public CBS culture collection.

Morphological characterisation

Cultures for macromorphological observations were inoculated in a three point position onto the agar media creatine sucrose agar (CREA), Czapek yeast extract agar (CYA), CYA supplemented with 5 % NaCl (CYAS), dichloran 18 % glycerol agar (DG18), malt extract agar (Oxoid) (MEA), oatmeal agar (OA) and yeast extract sucrose agar (YES). All media were prepared as described by Samson *et al.* (2014). Additional CYA plates were

inoculated and incubated at 37 °C (CYA37°C) and 42 °C (CYA42°C). Colony texture, degree of sporulation, obverse and reverse colony colours, production of soluble pigments, exudates and sclerotia/ascomata were determined and recorded after 7 d of incubation. Colours names and codes used in descriptions refer to Rayner (1970). The production of sclerotia was observed with the naked eye. Digital images of these structures were made from CYA plates (incubate at 25 or 37 °C) and captured using a Nikon SMZ25 dissecting microscope. For micromorphological observations, mounts were made in lactic acid (60 %) from colonies on MEA and a drop of ethanol was used to wash excess conidia. The possible production of a sexual state was observed on OA, MEA and CYA plates incubated up to six weeks. Structures were studied and captured by using a Zeiss AX10 Imager A2 light microscope equipped with a Nikon DS-Ri2 camera and the software package NIS-Elements D v4.50. Photoplates were prepared in Adobe® Photoshop® CS6.

DNA extraction, amplification and sequencing

DNA was extracted from 3–7 days-old colonies with the DNA extraction kit ArchivePure DNA yeast and Gram2+ kit (5PRIME Inc., Gaithersburg, Maryland) with modifications described by Hubka *et al.* (2015) or the Utraclean™ Microbial DNA isolation kit (MoBio, Solana Beach U.S.A.). The ITS rDNA region was amplified using forward primers ITS1 and ITS5 (White *et al.* 1990) and reverse primers ITS4S (Kretzer *et al.* 1996 or NL4 (O'Donnell 1993), or the primer pair V9G (de Hoog & Gerrits van den Ende, 1998) and LS266 (Masclaux *et al.* 1995); a part of the *BenA* gene encoding β -tubulin using the forward primers Bt2a (Glass & Donaldson 1995) or Ben2f (Hubka & Kolařík 2012) and the reverse primer Bt2b (Glass & Donaldson 1995); partial *CaM* gene encoding calmodulin using forward primers CF1M or CF1L and reverse primer CF4 (Peterson 2008), or the primer pair cmd5 and cmd6 (Hong *et al.* 2005); partial *RPB2* gene using forward primers fRPB2-5F (Liu *et al.* 1999), RPB2-F50-CanAre (Jurjević *et al.* 2015), RPB2-5F_Eur (Houbraken *et al.* 2012) and reverse primers RPB2-7CR_Eur (Houbraken *et al.* 2012) and fRPB2-7cR (Liu *et al.* 1999). PCR protocols were described by Hubka *et al.* (2014, 2016) and Samson *et al.* (2014). Automated sequencing was performed with the same primers as used in PCR reactions.

Phylogenetic analysis

The sequence data were inspected, assembled and optimised using the software package Seqman (v. 10.0.1) from DNASTar Inc. Sequences were aligned with MAFFT v.7 (Katoh & Standley 2013) using the L-INS-i method. Maximum likelihood (ML) analysis on the combined data sets was performed using the RAxML v. 7.2.6 (randomized axelerated maximum likelihood) software (Stamatakis & Alachiotis 2010). The combined data sets were analysed as three distinct partitions (*BenA*, *CaM* and *RPB2*). For each individual data set, the most optimal substitution model was calculated in the MEGA7 v. 7.0.25 software (Kumar *et al.* 2016) utilising the Akaike Information Criterion (AIC). Maximum Likelihood analysis of the individual data sets was analysed performed using MEGA7 and the robustness of the trees was evaluated by 1 000 bootstrap replicates. A second measure for statistical support was performed using MrBayes v. 3.2.2 (Ronquist *et al.* 2012) and the previously obtained most

Table 1. Isolates examined belonging to *Aspergillus* section *Flavi*.

Species	Isolate number	Provenance	GenBank accession no.				
			ITS	BenA	CaM	RPB2	
<i>Aspergillus aflatoxiformans</i>	CBS 143679 = DTO 228-G2 ^T = IBT 32085	Agricultural soil, Minna, Niger State, Nigeria, ex type of <i>Aspergillus aflatoxiformans</i>	MG662388	MG517706	MG518076	MG517897	
	CBS 121.62 = IMI 093070 = NRRL A-11612 = IBT 3651 = IBT 3850 = DTO 010-H7 = DTO 223-C2 = DTO 228-H6	<i>Arachis hypogea</i> , Nigeria, PKC Austwick, 1962 (former suggested neotype of <i>Aspergillus parvisclerotigenus</i>)	EF409240	MG517719	MG518089	MG517910	
	CBS 133264 = DTO 215-F3	Edible mushroom, Lagos State, Nigeria	–	JX627690	JX627694	MG517871	
	CBS 133265 = DTO 215-F4	Edible mushroom, Lagos State, Nigeria	–	JX627691	JX627695	MG517872	
	CBS 133923 = DTO 215-F1	Peanut cake, Niger State, Minna, Nigeria	–	MG517680	MG518051	MG517869	
	CBS 133924 = DTO 215-F2	Peanut cake, Niger State, Minna, Nigeria	–	MG517681	MG518052	MG517870	
	CBS 133925 = DTO 215-F5 DTO 087-A2	Peanut cake, Kaduna, Nigeria Soil near road, Ifaty, Madagascar	– MG662405	MG517682 MG517652	MG518053 MG517990	MG517873 MG517840	
	DTO 228-G1 = IBT 32079	Stored rice grains from market, Abeokuta, Ogun State, Nigeria	MG662389	MG517705	MG518075	MG517896	
	DTO 228-G3 = IBT 32086 = CBS 135587	Sesame kernels from market, Plateau State, Vwring, Nigeria	MG662387	MG517707	MG518077	MG517898	
	DTO 228-G4 = IBT 32087 = CBS 135588	Sesame kernels from market, Plateau State, Vwring, Nigeria	–	MG517708	MG518078	MG517899	
	DTO 228-G5 = IBT 32088 = CBS 135589	Sesame kernels from market, Plateau State, B/Ladi, Nigeria	–	MG517709	MG518079	MG517900	
	DTO 228-G6 = IBT 32089 = CBS 135404	Sesame kernels from market, Plateau State, B/Ladi, Nigeria	–	MG517710	MG518080	MG517901	
	DTO 228-G7 = IBT 32090 = CBS 135405	Sesame kernels from market, Plateau State, B/Ladi, Nigeria	–	MG517711	MG518081	MG517902	
	DTO 228-H2 = IBT 16807	Mexican sesame seed imported to Denmark and sold in Lyngby, JC Frisvad, 1995	–	MG517715	MG518085	MG517906	
	DTO 228-H3 = IBT 16808	Mexican sesame seed imported to Denmark and sold in Lyngby, JC Frisvad, 1995	–	MG517716	MG518086	MG517907	
	DTO 228-H7 = IBT 32083	Agricultural soil, Minna State, Nigeria	–	MG517720	MG518090	MG517911	
	<i>Aspergillus alliaceus</i>	CBS 536.65 ^{NT} = DTO 046-B1 = NRRL 315 = IMI 051982 = QM 1885 = ATCC 10760 = WB 315 = Thom 4656 = IBT 13377 = CCF 5607	Dead blister beetle (<i>Microbasis albida</i>), Washington D.C., USA, M.M. High, neotype of <i>Aspergillus alliaceus</i>	EF661551	EF661465	EF661534	MG517825
		CBS 110.26 = DTO 034-B2 = DTO 046-A7 = IBT 14351 = NRRL 316 = WB 316 = IMI 016125 = Thom 4660 = CCF 5603	<i>Allium cepa</i>	MH279383	MG517632	MG518004	MG517815
		CBS 143682 = DTO 326-D5 = S757 = CCF 5416 = IBT 33356	Intestine of <i>Allolobophora hrabei</i> , National Reservation Pouzdřanská step - Kolby, Czech Republic, A. Nováková, 2013	MH279421	MG517764	MG518134	MG517955
		CBS 511.69 = DTO 368-C3 = IBT 13379 = CCF 5682	Soil, Turkey	MH279439	MG517786	MG518156	MG517976
CBS 542.65 = DTO 034-A9 = DTO 203-B1 = NRRL 4181 = ATCC 16891 = IBT 13378 = IMI 116711 = QM 1892 = WB 4181 = JH Warcup SA 117		Soil, Australia, ex type of <i>Petromyces alliaceus</i>	EF661556	EF661466	EF661536	EU021644	
DTO 363-E8 = NRRL 318 = IBT 21073 = CCF 5601		Unknown source	MH279430	MG517776	MG518146	MG517967	
DTO 363-E9 = IBT 23440 = EXF-670 = CCF 5605		Saltern, Secovlje, Slovenia, P. Zalar	MH279431	MG517777	MG518147	MG517968	
		Mixed feed, Spain	MH279432	MG517778	MG518148	MG517969	

Table 1. (Continued).

Species	Isolate number	Provenance	GenBank accession no.			
			ITS	<i>BenA</i>	<i>CaM</i>	<i>RPB2</i>
	DTO 363-F1 = IBT 21992 = A196 = CCF 5604					
	DTO 363-F2 = IBT 21754 = IMI 017295 = CCF 5606	Contaminant in ex type culture of <i>Aspergillus wentii</i>	MH279433	MG517779	MG518149	–
	DTO 368-C4 = IMI 226007 = IBT 14130 = CCF 5680	Soil, Calicut University, India	MH279440	MG517787	MG518157	MG517977
	IBT 21770	Prairie soil, Nebraska, USA	MH279446	MG517790	MG518161	MG517980
	Mo2	Soil above the Movile cave, Romania, 2011, A. Nováková	MH279443	MG517791	LT558734	MG517981
	NRRL 1206 = Thom 5741	Unknown source	EF661543	EF661463	EF661535	EU021622
	NRRL 20602 = ATCC	Clinical isolate from human ear,	EF661548	EF661464	EF661537	EU021628
	58745 = IBT 14317 = UAMH 2476	Alberta, Canada, ex type of <i>Aspergillus albertensis</i>				
	S862 = CCF 4954	Soil above the Movile cave, Romania, A. Nováková, 2013	MH279444	MG517615	MG518160	MG517795
	S916 = CCF 5434	<i>Allolobophora hrabei</i> casts, National Monument Ječmeniště, Czech Republic, A. Nováková, 2013	MH279442	MG517616	MG518159	MG517796
	S98 = CCF 4953	Soil above Movile cave, Romania, A. Nováková, 2012	MH279445	MG517614	LT558735	MG517794
<i>Aspergillus arachidicola</i>	CBS 117610 ^T = DTO 009- G3 = IBT 25020	<i>Arachis glabrata</i> leaf, Mercedes, Corrientes province, Argentina, ex type of <i>Aspergillus arachidicola</i>	MF668184	EF203158	EF202049	MG517802
	CBS 117611 = DTO 009- G4 = IBT 27185	<i>Arachis glabrata</i> leaf, Mercedes, Corrientes province, Argentina	–	MG517620	MG518006	MG517803
	CBS 117615 = DTO 010- H5 = IBT 28178	<i>Arachis glabrata</i> leaf, Ituzaingó, Corrientes province, Argentina	–	MG517627	MG517999	MG517810
	DTO 228-H9	Leaf of <i>Protea roupelliae</i> var. <i>roupelliae</i> , Buffelskloof, South Africa	MG662384	MG517721	MG518091	MG517912
<i>Aspergillus aspearensis</i>	CBS 143672 ^T = DTO 203- D9 = CCTU758 = IBT 32590 = IBT 34544	Soil, Aspear Island, Urmia Lake, Iran, soil, ex type of <i>Aspergillus aspearensis</i>	MG662398	MG517669	MG518040	MG517857
	DTO 203-D4 = CBS 143671 = CCTU753 = IBT 34543	Soil, Aspear Island, Urmia Lake, Iran	MG662399	MG517667	MG518038	MG517855
	DTO 203-E1 = CBS 143673 = CCTU759 = IBT 32591	Soil, Aspear Island, Urmia Lake Iran	MH279394	MG517670	MG518041	MG517858
<i>Aspergillus austwickii</i>	CBS 143677 ^T = DTO 228- F7 = IBT 32590 = IBT 32076	Stored rice grains from market, Abeokuta, Ogun State, Nigeria, ex type of <i>Aspergillus austwickii</i>	MG662391	MG517702	MG518072	MG517893
	CBS 135406 = DTO 228- G8 = IBT 32091	Sesame kernels from market, Plateau State, B/Ladi, Nigeria	MG662386	MG517712	MG518082	MG517903
	CBS 143678 = DTO 228- F8 = IBT 32077	Stored rice grains from market, Abeokuta, Ogun State, Nigeria	–	MG517703	MG518073	MG517894
	DTO 228-F9 = IBT 32078	Stored rice grains from market, Abeokuta, Ogun State, Nigeria	MG662390	MG517704	MG518074	MG517895
<i>Aspergillus avenaceus</i>	CBS 109.46 ^T = DTO 009- H6 = DTO 006-A2 = NRRL 517 = ATCC 16861 = IMI 016140 = LCP 89.2592 = LSHB BB 155 = QM 6741 = WB 317 = IBT 4376 = IBT 4555 CBS 102.45 = NCTC 6548	Green pea (<i>Pisum sativum</i>), United Kingdom, G.E. Turfitt, 1938, ex type of <i>Aspergillus avenaceus</i>	AF104446	FJ491481	FJ491496	JN121424
		Unknown source, United Kingdom	–	FJ491480	FJ491495	–
<i>Aspergillus bertholletius</i>	CBS 143687 = DTO 223- D3 = IBT 29228 = CCT 7615 ^T = ITAL 270/06	Soil close to <i>Bertholletia excelsa</i> trees, Amazonian rainforest, Brazil, ex type of <i>Aspergillus bertholletius</i>	JX198673	MG517689	JX198674	MG517880
	IBT 29227 = ITAL 275/06 = CCT 7618	Soil close to <i>Bertholletia excelsa</i> trees, Amazonian rainforest	–	–	–	–
	IBT 30617 = ITAL 272/06 = CCT 7617	Soil close to <i>Bertholletia excelsa</i> trees, Amazonian rainforest	–	–	–	–

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Table 1. (Continued).

Species	Isolate number	Provenance	GenBank accession no.				
			ITS	BenA	CaM	RPB2	
<i>Aspergillus caelatus</i>	DTO 223-D4 = IBT 30618 = ITAL 271/06 = CCT 7616	Soil close to <i>Bertholletia excelsa</i> trees, Amazonian rainforest	–	–	–	–	
	IBT 31739 = ITAL 262 = CCT 7614	<i>Bertholletia excelsa</i> nut shell, Market, Amazon	–	–	–	–	
	CBS 763.97 ^T = DTO 046-A8 = NRRL 25528 = IBT 21091	Soil, USA, ex type of <i>Aspergillus caelatus</i>	AF004930	MG517640	MG518018	MG517823	
	CBS 764.97 = NRRL 25404	Soil, USA	–	EF203129	EF202036	–	
	DTO 276-I2	Corn silage, Cordoba, Argentina	–	MG517738	MG518108	MG517929	
	DTO 285-H9	Soil from corn field, Thailand	–	MG517751	MG518121	MG517942	
	DTO 285-I1	Soil from corn field, Thailand	–	MG517752	MG518122	MG517943	
	NRRL 25566 = IBT 29770 = DTO 073-B7	Soil, Japan	–	MG517651	MG518025	MG517839	
	NRRL 25567 = IBT 29773 = DTO 073-B8	Soil, Japan	–	–	–	–	
	NRRL 25568 = IBT 29772 = DTO 073-B9	Soil, Japan	–	–	–	–	
	NRRL 25569 = IBT 29771 = DTO 073-C1	Soil, Japan	–	–	–	–	
	NRRL 26100	Soil of peanut field, 2.5 km east of Herod, Georgia, USA	EF661550	EF661471	EF661523	EF661437	
	<i>Aspergillus cerealis</i>	CBS 143674 ^T = DTO 228-E7 = IBT 32067	Stored rice grains from market, Shagamu, Ogun State, Nigeria, ex type of <i>Aspergillus cerealis</i>	MG662394	MG517693	MG518063	MG517884
		CBS 143675 = DTO 228-E8 = IBT 32068	Stored rice grains from market, Shagamu, Ogun State, Nigeria	–	MG517694	MG518064	MG517885
CBS 143676 = DTO 228-E9 = IBT 32069		Stored maize grains from market, Shagamu, Ogun State, Nigeria	MG662393	MG517695	MG518065	MG517886	
DTO 228-E6 = IBT 32076		Stored rice grains from market, Shagamu, Ogun State, Nigeria	MG662395	MG517692	MG518062	MG517883	
DTO 228-F1 = IBT 32070		Stored maize grains from market, Shagamu, Ogun State, Nigeria	MG662392	MG517696	MG518066	MG517887	
DTO 228-F2 = IBT 32071		Stored maize grains from market, Shagamu, Ogun State, Nigeria	–	MG517697	MG518067	MG517888	
DTO 228-F3 = IBT 32072		Stored maize grains from market, Shagamu, Ogun State, Nigeria	–	MG517698	MG518068	MG517889	
DTO 228-F4 = IBT 32073		Stored maize grains from market, Shagamu, Ogun State, Nigeria	–	MG517699	MG518069	MG517890	
DTO 228-F5 = IBT 32074		Stored maize grains from market, Shagamu, Ogun State, Nigeria	–	MG517700	MG518070	MG517891	
DTO 228-F6 = IBT 32075		Stored maize grains from market, Shagamu, Ogun State, Nigeria	–	MG517701	MG518071	MG517892	
MACI219 = NRRL 66709		Peanut pods, Pokaha, Karhogo region, North part of Côte d'Ivoire (Ivory Coast)	KY689208	KY628791	KY661266	–	
MACI254 = NRRL 66710		Peanut pods, Gbandokaha, Karhogo region, North part of Côte d'Ivoire, 2014, probably ex type of <i>Aspergillus korhogoensis</i>	KY689209	KY628792	KY661267	–	
MACI264 = NRRL 66711		Peanut pods, Gbandokaha, Karhogo region, North part of Côte d'Ivoire, 2014	KY689210	KY628793	KY661268	–	
MACI46 = NRRL 66708		Peanut pods, Karhogo region, North part of Côte d'Ivoire, 2014	KY689207	KY628790	KY661265	–	
<i>Aspergillus coremiiformis</i>	CBS 553.77 ^T = DTO 046-A3 = ATCC 38576 = IHEM 4503 = IMI 223069 = NRRL 13603 = NRRL 13756 = IBT 3822 = IBT 13506 = IBT 21944	Soil, Tai National Forest, Ivory Coast, ex type of <i>Aspergillus coremiiformis</i>	AJ874114	FJ491482	FJ491488	JN121533	

Table 1. (Continued).

Species	Isolate number	Provenance	GenBank accession no.			
			ITS	<i>BenA</i>	<i>CaM</i>	<i>RPB2</i>
<i>Aspergillus flavus</i>	CBS 100927 ^T = NRRL 1957 = ATCC 16883 = CBS 569.65 = IMI 124930 = IBT 3605 = IBT 3610 AF70	Cellophane diaphragm of an optical mask, South Pacific Islands, ex type of <i>Aspergillus flavus</i>	AF027863	EF661485	EF661508	EF661440
		Seed of upland cotton (<i>Gossypium hirsutum</i>), Arizona, USA, genome sequenced	–	genome*	genome*	genome*
	CBS 110.55 = DTO 046- A1 = ATCC 12073 = NRRL 4743 = IMUR 236 = QM 6951 = WB 4743 = IBT 3819	Air contaminant, Brazil, ex type of <i>Aspergillus fasciculatus</i>	FJ491463	EF203135	MG518005	MG517821
	CBS 117637 = DTO 009- F9 = IBT 27177	<i>Arachis hypogea</i> seed, Provincia de Formosa, Las Lomitas, Argentina	–	MG517618	MG518010	MG517800
	CBS 117638 = DTO 009-G1	<i>Arachis hypogea</i> seed, Provincia de Corrientes, Empedrado, Argentina	–	MG517619	MG518011	MG517801
	CBS 117732 = NRRL 3251 = IBT 3597 = IBT 3618	Walnut, USA (small sclerotia)	–	–	–	–
	CBS 118.62 = DTO 010- H6 = IFO 7600 = IMI 091548 = NRRL A-11608 = RIB 1406	<i>Arachis hypogea</i> , Brazil	–	MG517628	MG517996	MG517811
	CBS 119368 = DTO 011- I2 = KACC 41730	Wheat, Boun-up, Boukun, Chungbuk Prov., South Korea	–	MG517630	MG518002	MG517813
	CBS 120.51 = DTO 046- A4 = ATCC 16859 = IFO 8135 = IMI 045644 = LCP 56.1517 = LSHB BB213 = NRRL 2097 = NRRL A-2022 = QM 6871 = WB 2097 = IBT 3636	Culture contaminant, London, England, ex type of <i>Aspergillus thomii</i>	EF661549	MG517639	MG518012	MG517822
	CBS 128202 = NRRL 3357 = ATCC 200026 = IBT 3696 = IBT 28518 = IBT 29624	Peanut cotyledons, USA, genome sequenced	JX535495	genome*	genome*	genome*
	CBS 133263 = DTO 215-E9	Edible mushroom from market, Lagos State, Nigeria	–	JX627689	JX627693	MG517868
	CBS 143688 = DTO 359- D8 = KACC 46894 = IBT 34547	Air, South Korea	–	MG517774	MG518144	MG517965
	CBS 143689 = DTO 359- D9 = KACC 46895 = IBT 34548	Air, South Korea	–	MG517775	MG518145	MG517966
	CBS 485.65 = DTO 046- B7 = ATCC 16870 = IFO 5324 = IMI 124932 = LCP 89.3556 = NRRL 4818 = WB 4818 = IBT 3641 = IBT 3657	Butter, Japan, ex type of <i>Aspergillus flavus</i> var. <i>columnaris</i> and <i>A. flavus</i> var. <i>asper</i>	EF661563	MG517643	MG518014	MG517828
	CBS 501.65 = DTO 046- B5 = ATCC 16862 = IMI 044882 = NRRL 4998 = WB 4998 = IBT 4378 = IBT 4402	Cotton lintafelt, England, ex neotype of <i>Aspergillus subolivaceus</i>	EF661563	MG517642	MG518015	MG517827
	CBS 542.69 = DTO 046- B4 = IMI 141553 = NRRL 3751 = GKC 1421(1) = IBT 3649	Stratigraphic core sample, soil, Niigata Pref., Kambara, Japan, ex type of <i>Aspergillus kambarensis</i>	EF661554	MG517641	MG518016	MG517826
	CBS 574.65 = DTO 303- C3 = ATCC 1010 = IMI 016142 = IMI 124935 = NRRL 506 = NRRL 1653	Corn (<i>Zea mays</i>), Vermont, USA, representative of <i>A. effusus</i> fide Thom & Church (1926) and Thom & Raper (1945) (Raper & Fennell 1965:377)	JN185448	JN185446	JN185447	JN185449
	DTO 016-I5 = dH 16719	Infection of leg (after liver transplantation), male 43 year old, China	–	MG517631	MG518003	MG517814
	DTO 062-C7	Peanut, Indonesia	–	MG517645	MG517985	MG517832
	DTO 062-C8	Peanut, Indonesia	–	MG517646	MG517986	MG517833
	DTO 062-H7	Peanut, Indonesia	–	MG517647	MG517987	MG517834
	DTO 066-C3	Corn kernels, Indonesia	–	MG517650	MG517989	MG517837

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Table 1. (Continued).

Species	Isolate number	Provenance	GenBank accession no.			
			ITS	BenA	CaM	RPB2
	DTO 087-A3	Forest soil, Ifaty, Madagascar	–	MG517653	MG517991	MG517841
	DTO 087-A4	Forest soil, Ifaty, Madagascar	–	MG517654	MG517992	MG517842
	DTO 215-E5	Laboratory contaminant, Nigeria	–	MG517679	MG518050	MG517867
	DTO 258-C9	Corn kernels, from East.Europe, imported to the Netherlands	–	MG517725	MG518095	MG517916
	DTO 258-D6	Corn kernels, from East.Europe, imported to the Netherlands	–	MG517728	MG518098	MG517919
	DTO 276-H7	Poultry feedstuff, Cordoba, Argentina	–	MG517734	MG518104	MG517925
	DTO 276-H8	Poultry feedstuff, Cordoba, Argentina	–	MG517735	MG518105	MG517926
	DTO 276-H9	Poultry feedstuff, Cordoba, Argentina	–	MG517736	MG518106	MG517927
	DTO 276-I1	Poultry feedstuff, Cordoba, Argentina	–	MG517737	MG518107	MG517928
	DTO 276-I3	Corn silage, Cordoba, Argentina	–	MG517739	MG518109	MG517930
	DTO 276-I4	Chinchilla feedstuffs, Cordoba, Argentina	–	MG517740	MG518110	MG517931
	DTO 276-I5	Chinchilla feedstuffs, Cordoba, Argentina	–	MG517741	MG518111	MG517932
	DTO 276-I6	Chinchilla feedstuffs, Cordoba, Argentina	–	MG517742	MG518112	MG517933
	DTO 276-I7	Chinchilla feedstuffs, Cordoba, Argentina	–	MG517743	MG518113	MG517934
	DTO 276-I8	Chinchilla feedstuffs, Cordoba, Argentina	–	MG517744	MG518114	MG517935
	DTO 281-E2	Rice, Thailand	–	MG517745	MG518115	MG517936
	DTO 281-H8	Rice, Thailand	–	MG517746	MG518116	MG517937
	DTO 285-F6	Soil from corn-field, Thailand	–	MG517748	MG518118	MG517939
	DTO 285-G3	Soil from corn-field, Thailand	–	MG517749	MG518119	MG517940
	DTO 285-I4	Soil from corn-field, Thailand	–	MG517753	MG518123	MG517944
	DTO 300-C7	Corn kernels, imported into the Netherlands	–	MG517754	MG518124	MG517945
	DTO 300-D7	Corn kernels, imported into the Netherlands	–	MG517755	MG518125	MG517946
	DTO 359-D7 = IBT 34546 = KACC 46893	Air, South Korea	–	–	–	–
	DTO 359-E1 = IBT 34551 = KACC 46897	Corn, South Korea	–	–	–	–
	DTO 359-E2 = IBT 34550 = KACC 46913	Soil, South Korea	–	–	–	–
	DTO 359-E3 = KACC 46917	Soil, Gyeonggi, Suwon, Korea	–	–	–	–
	NRRL 20521	Corn, Mississippi, USA	EF661547	EF661492	EF661514	EF661447
	NRRL 3518 = NRRL A-14304	Wheat flour, Peoria, Illinois, USA	EF661552	EF661487	EF661510	EF661442
	NRRL 4822	Unknown source	EF661564	EF661490	EF661513	EF661445
<i>Aspergillus hancockii</i>	FRR 3425 ^T = CBS 142004 = DTO 360-G7	Cultivated soil, Queensland, Australia, ex type of <i>Aspergillus hancockii</i>	KX858342	MBFL 01001228. 1:26000- 28000	MBFL 01000377. 1:5000- 7000	MBFL 01000137: 9000- 11000
	CBS 142001 = FRR 5050 = DTO 360-G4 = IBT 35030	Soil, Lockhart, New South Wales, Australia, J.I. Pitt, 2003	–	–	–	–
	CBS 142002 = FRR 6103 = DTO 360-G5 = IBT 35031	Dried peas, Victoria, Australia, M. Bull, 1997	–	–	–	–
<i>Aspergillus lanosus</i>	CBS 650.74 ^T = IMI 130727 = QM 9183 = IBT 33634	Soil under <i>Tectona grandis</i> , Uttar Pradesh, India	FJ491471	MG517633	MG518017	EU021642
<i>Aspergillus leporis</i>	CBS 151.66 ^T = IBT 3609 = DTO 199-B2 = CBS 129302 = RMF 99 = WB 5188 = ATCC	Dung of <i>Lepus townsendii</i> , near Saratoga, Wyoming, USA, ex type of <i>Aspergillus leporis</i>	MH279391	MG517662	MG518033	MG517850

Table 1. (Continued).

Species	Isolate number	Provenance	GenBank accession no.			
			ITS	<i>BenA</i>	<i>CaM</i>	<i>RPB2</i>
	16490 = LCP 89.2583 = NRRL 3216					
	CBS 125914 = DTO 195-C3 = R1251	A1 horizon soil, open area in sagebrush grassland, Rock Springs, Wyoming, USA (DOE site, 11 km west of Rock Springs)	MH279389	MG517660	MG518031	MG517848
	CBS 129235 = DTO 303-C5	Plant root tissue at non-seleniferous soil, Nunn, Colorado, USA	–	MG517760	MG518130	MG517951
	CBS 129310 = RMF 9587 = DTO 201-H1	A1 horizon soil, Canyonlands National Park, Utah, USA	MH279392	MG517663	MG518034	MG517851
	CBS 129330 = RMF 7757 = DTO 202-A2	Soil beneath <i>Atriplex confertifolia</i> , near Jim Bridger Power Plant, Sweetwater County, Wyoming, USA	MH279393	MG517664	MG518035	MG517852
	CBS 129596 = DTO 206-A8 = RMF G74	A1 horizon soil from bunchgrass rhizosphere, sagebrush grassland, Rock Springs, Wyoming, USA	MH279395	MG517673	MG518044	MG517861
	CBS 132153 = DTO 210-E1	Surface soil, near Dubois, Wyoming, USA	MH279396	MG517674	MG518045	MG517862
	CBS 132177 = RMF 2050 = DTO 210-G5	A1 Horizon soil, Grand Teton National Park, Wyoming, USA	MH279397	MG517676	MG518047	MG517864
	CBS 349.81 = IBT 3600 = NRRL 6599 = DTO 303-C4 = ATCC 44565 = Strain O168	Soil, Wyoming, USA	EF661569	EF661500	EF661542	EF661460
	IBT 12296 = IBT 13578 = ATCC 76617	Soil under grass, Canyon de Chelly, Arizona, USA	–	–	–	–
	IBT 16309 = RMF A39	Soil under <i>Atriplex gardneri</i> , cool desert, 10 km north of Rock Springs, Great Divide Basin, Wyoming, USA	–	–	–	–
	IBT 16585	Soil under <i>Atriplex confertifolia</i> , cool desert, 10 km north of Rock Springs, Great Divide Basin, Wyoming, USA	–	–	–	–
	CBS 132178 = RMF 2110 = DTO 210-G6	A1 Horizon soil, Grand Teton National Park, Wyoming, USA	MH279398	MG517677	MG518048	MG517865
<i>Aspergillus luteovirescens</i>	CBS 620.95 ^T = DTO 010-H1	Unknown source, ex type of <i>Aspergillus luteovirescens</i>	MG662406	MG517625	MG517998	MG517808
	CBS 117187 = NRRL 25010 = IBT 23536	Frass in a silkworm rearing house, Japan, 1987, ex type of <i>Aspergillus bombycis</i>	AF104444	EF661498	EF661533	EF661458
	DTO 073-C3 = NRRL 29236 = IBT 29777	Frass in a silkworm rearing house, 1983, Ibaraki Prefecture, Japan	–	–	–	–
	DTO 073-C4 = NRRL 29237 = IBT 29780	Frass in a silkworm rearing house, 1983, Ibaraki Prefecture, Japan	–	–	–	–
	DTO 073-C5 = NRRL 29241 = IBT 29779	Frass in a silkworm rearing house, 1983, Oita Prefecture, Japan	–	–	–	–
	ITAL 246 = IBT 31534	Brazil nut, Amazon, Brazil	–	–	–	–
	NRRL 25593 = IBT 23535	Frass in a silkworm rearing house, Japan, 1987	AF104445	EF661497	EF661532	EF661457
	NRRL 29235 = DTO 073-C2 = IBT 23537 = IBT 29778	Frass in a silkworm rearing house, Indonesia, 1999	AF338641	AY017575	AY017622	–
<i>Aspergillus minisclerotigenes</i>	CBS 117635 ^T = DTO 009-F7 = IBT 25032	<i>Arachis hypogea</i> , Manfredi, Córdoba province, Argentina, ex type of <i>Aspergillus minisclerotigenes</i>	EF409239	EF203148	MG518009	MG517799
	CBS 117633 = DTO 009-F5	<i>Arachis hypogea</i> seed, Provincia de Formosa, Las Lomitas, Argentina	MG662408	EF203153	MG518007	MG517797
	CBS 117634 = DTO 009-F6 = IBT 27197		MG662402	MG517617	MG518008	MG517798

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Table 1. (Continued).						
Species	Isolate number	Provenance	GenBank accession no.			
			ITS	BenA	CaM	RPB2
	DTO 045-F4 = FRR 4086	<i>Arachis hypogea</i> seed, Provincia de Cordoba, Alejandro, Argentina Freshly pulled peanuts, Interlaw Road, Kingaropy, Queensland, Australia	–	MG517635	MG518021	MG517817
	DTO 045-F5 = FRR 4937	Soil, Australia	–	MG517636	MG518022	MG517818
	DTO 045-F6 = FRR 5309	Soil, Coalston Lakes, Queensland, Australia	–	MG517637	MG518023	MG517819
	DTO 045-I9 = NRRL A- 11611 = NRRL 6444 = IBT 3840	Soil of peanut field, Nigeria	MH279386	MG517638	MG518024	MG517820
	DTO 228-G9 = IBT 32094	Agricultural soil, Jos, Plateau State, Nigeria	–	MG517713	MG518083	MG517904
	DTO 228-H1 = IBT 32111	Agricultural soil, Minna, Niger State, Nigeria	–	MG517714	MG518084	MG517905
	DTO 228-H5 = IBT 24629	Curry powder from Kenya imported to Denmark	–	MG517718	MG518088	MG517909
<i>Aspergillus mottae</i>	CBS 130016 ^T = DTO 223- C8 = IBT 32309 = MUM 10.231 MUM 10.233	Maize kernel, Braga, Portugal, ex type of <i>Aspergillus mottae</i> Maize, Portugal	JF412767	MG517687	MG518058	MG517878
			–	HM803090	HM803013	HM802982
<i>Aspergillus neoalliaceus</i>	CBS 143681 ^T = DTO 326- D3 = S765 = CCF 5433 = IBT 33110 = IBT 33353	Soil, Czech Republic, National Reservation Pouzdřanská step - Kolby, A. Nováková, 2013, ex type of <i>Aspergillus neoalliaceus</i>	MH279420	MG517763	MG518133	MG517954
	CBS 134375 = S77 = CCF 4424	Soil, National Monument Ječmeniště, Czech Republic, A. Nováková, 2012	MH279441	MG517613	MG518158	MG517793
	DTO 326-D6 = S768 = CCF 5414 = IBT 33111 = IBT 33357	Drilosphere soil, National Reservation Pouzdřanská step – Kolby, Czech Republic, A. Nováková, 2013	MH279422	MG517765	MG518135	MG517956
	DTO 326-D7 = B6 = CCF 5408 = IBT 32726	Soil, National Reservation Pouzdřanská step – Kolby, Czech Republic, A. Nováková, 2010	MH279423	MG517766	MG518136	MG517957
	DTO 326-E1 = S756 = CCF 5410 = IBT 33359	Soil, National monument Ječmeniště, Czech Republic, A. Nováková, 2013	MH279424	MG517768	MG518138	MG517959
	DTO 326-E2 = S766 = CCF 5412 = IBT 33355	<i>Allolobophora hrabei</i> cast, National Reservation Pouzdřanská step – Kolby, Czech Republic, A. Nováková, 2013	MH279425	MG517769	MG518139	MG517960
	DTO 326-E4 = S764 = CCF 5411 = IBT 33358	Soil, National monument Ječmeniště, Czech Republic, A. Nováková, 2013	MH279426	MG517770	MG518140	MG517961
	DTO 326-E5 = S913 = CCF 5415 = IBT 33351	Soil, National monument Ječmeniště, Czech Republic, A. Nováková, 2013	MH279427	MG517771	MG518141	MG517962
	DTO 326-E7 = S767 = CCF 5413 = IBT 33109 = IBT 33352	Soil, National Reservation Pouzdřanská step – Kolby, Czech Republic, A. Nováková, 2013	MH279428	MG517772	MG518142	MG517963
	CCF 5815 = S1429	Soil, above the Liliəcilor de la Gura Dobrogei cave, Dobrogea, Romania, A. Nováková, 2016	–	–	–	–
	CCF 5840 = S988	Soil, above the Limanu cave, Dobrogea, Romania, A. Nováková, 2014	–	–	–	–
<i>Aspergillus nomius</i>	CBS 260.88 ^T = NRRL 13137 = IBT 3656 = IBT4966 = FDA M93 CBS 117629 = NRRL 25585 = IBT 23530 CBS 399.93 = DTO 301-I8 = AS 3.4626 = IBT 14647	Wheat, USA, A.F. Schindler, 1965, ex type of <i>Aspergillus nomius</i> Silk worm frass, Japan, 1987 Soil, Guandong, Zhaoqing, China, ex type of <i>Aspergillus zhaoqingensis</i>	AF027860	EF661494	EF661531	EF661456
			–	–	–	–
			FJ491472	MG517757	MG518127	MG517948

Table 1. (Continued).

Species	Isolate number	Provenance	GenBank accession no.			
			ITS	<i>BenA</i>	<i>CaM</i>	<i>RPB2</i>
	DTO 161-F1	Bamboo sample, Walailak, Thailand	MH279387	MG517656	MG518026	MG517844
	DTO 161-F2	Bamboo sample, Addis Abeba, Ethiopia	MH279388	MG517657	MG518027	MG517845
	DTO 226-I5	Storage room of cassava, Yogyakarta, Indonesia	–	MG517690	MG518060	MG517881
	DTO 227-B8	Storage room of cassava, Yogyakarta, Indonesia	–	MG517691	MG518061	MG517882
	DTO 243-E8	HIV-Care room, Indonesia	–	MG517722	MG518092	MG517913
	DTO 247-F9	House dust, Mexico	–	MG517723	MG518093	MG517914
	DTO 247-G8	House dust, Mexico	–	MG517724	MG518094	MG517915
	DTO 318-F4	Heat treated pectin, Germany	–	MG517761	MG518131	MG517952
	DTO 321-F2	Cystic fibrosis patient material, the Netherlands	MH279419	MG517762	MG518132	MG517953
	IMI 190557 = NRRL 20745 = IBT 19368	Dried <i>Curcuma longa</i> , Central Crops Research Institute, India	AF338612	AY017543	AY017590	–
	NRRL 13138 = IBT 4493 = IBT 4495 = IBT 5054	Sub-isolate from a mixed culture, U.L. Diener, 1967	–	–	–	–
	NRRL 3161 = IBT 3661 = IBT 4975	<i>Cycas circinalis</i> , Guam, USA, A.C. Keyl, 1965	AF338642	EF661493	EF661530	EF661453
<i>Aspergillus novoparasiticus</i>	CBS 126849 ^T = DTO 223-C3 = DTO 223-C4 = FMR 10121 = LEMI 250 = IBT 32311	Sputum of leukemic patient, Sao Paulo, Brazil, ex type of <i>Aspergillus novoparasiticus</i>	MG662397	MG517684	MG518055	MG517875
	CBS 126850 = DTO 223-C5 = FMR 10158 = LEMI 149 IOP = IBT 32312	Air sample, Sao Paulo, Brazil	MH279415	MG517686	MG518057	MG517877
<i>Aspergillus oryzae</i>	CBS 102.07 ^T = CBS 110.47 = CBS 100925 = ATCC 1011 = ATCC 12891 = ATCC 4814 = ATCC 7651 = ATCC 9102 = CECT 2094 = IFO 4075 = IFO 5375 = IMI 016266ii = IMI 016266 = IMI 044242 = LSHBA c.19 = NCTC 598 = NRRL 447 = NRRL 692 = QM 6735 = Thom 113 = WB 447 = IBT 21451	Unknown source, ex type of <i>Aspergillus oryzae</i>	EF661560	EF661483	EF661506	EF661438
	NRRL 458 = ATCC 10063 = ATCC 9376 = IMI 051983	Unknown source	EF661562	EF661484	EF661507	EF661439
	RIB40 = ATCC 42149 = JCM 13832 = NRRL 5590 = IBT 28103	Horsebean, Muruka soy saúce factory, Mimaki-mura, Kuse-gun, Kyoto, Japan, genome sequenced	–	genome*	genome*	genome*
	Strain 100-8	Mutant of <i>A. oryzae</i> 3.042, which is used in soy sauce fermentation, China, genome sequenced	–	genome*	genome*	genome*
<i>Aspergillus parasiticus</i>	CBS 100926 ^T = NRRL 502 = ATCC 1018 = ATCC 6474 = ATCC 7865 = IMI 015957 = IMI 015957ii = IMI 015957iv = IMI 015957vi = IMI 015957vii = IMI 015957ix = NRRL 1731 = IBT 3607	Sugar cane mealy bug (<i>Pseudococcus calceolariae</i>), Hawaii, USA, ex neotype of <i>Aspergillus parasiticus</i>	AF027862	EF661481	EF661516	EF661449
	CBS 104.22 = DTO 009-H2 = IFO 5867	Unknown source	–	MG517621	MG517994	MG517804
	CBS 119.51 = DTO 009-H3 = IFO 5337	Unknown substrate, Japan	–	MG517622	MG518000	MG517805
	CBS 138.52 = DTO 009-H4	Unknown substrate, Japan	–	MG517623	MG517997	MG517806
	CBS 260.67 = DTO 046-C2 = ATCC 15517 = CCM F-550 = CECT 2680 = DSM 2038 = IFO 30179 = IHEM	Unknown source, Japan, ex type of <i>Aspergillus parasiticus</i> var. <i>globosus</i>	MG662400	EF203156	MG518013	MG517830

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Table 1. (Continued).

Species	Isolate number	Provenance	GenBank accession no.			
			ITS	BenA	CaM	RPB2
	4387 = IMI 120920 = IMI 229041 = MUCL 31311 CBS 580.65 = DTO 046- B9 = ATCC 1014 = ATCC 16863 = IMI 016127ii = LSHB Ac22 = NCTC 974 = NRRL 424 = QM 7475 = VKM F- 2041 = WB 424 = IBT 3664 = IBT 3670 = IBT 10828	Soil, Georgia, USA, ex type of <i>Aspergillus terricola</i> var. <i>americana</i>	MG662404	MG517644	MG518030	MG517829
	CBS 822.72 = DTO 046- A9 = ATCC 22789 = IFO 30109 = IMI 089717 = RIB 4002 = TRI M 39 = IBT 4377 = IBT 4408 CBS 921.70 = ATCC 26691 = CECT 2681 = IHEM 4383 = NRRL 2999 = IBT 3634 = IBT 15675	<i>Arachis hypogea</i> , Uganda, ex type of <i>Aspergillus toxicarius</i>	MG662401	EF203163	MG518019	MG517824
	Unknown source, Uganda	AB008418	–	–	–	
	DTO 203-C4	Soil, Aspear Island, Iran	–	MG517666	MG518037	MG517854
	DTO 203-H7	Soil, Kabodan Island, Iran	–	MG517672	MG518043	MG517860
	DTO 258-D1	Corn kernels from East-Europe imported to the Netherlands	–	MG517726	MG518096	MG517917
	DTO 258-D4	Corn kernels from East-Europe imported to the Netherlands	–	MG517727	MG518097	MG517918
	DTO 283-C6	Soil from corn field, Thailand	–	MG517747	MG518117	MG517938
	DTO 285-G9	Soil from corn field, Thailand	–	MG517750	MG518120	MG517941
	DTO 301-E6	Corn kernels, imported to the Netherlands	–	MG517756	MG518126	MG517947
	DTO 303-C2	Unknown source	–	MG517759	MG518129	MG517950
	NRRL 13005 = IBT 4564	Microarthropod in beech forest litter, Michigan, USA (produces sclerotia)	–	–	–	–
	NRRL 4123	Toxic grain	EF661555	EF661479	EF661518	EF661451
	NRRL 6433 = IBT 4375	Corn, North Carolina, USA	EF661568	EF661480	EF661519	EF661452
<i>Aspergillus pipericola</i>	CBS 143680 ^T = DTO 228- H4 = IBT 24628	Black pepper, unknown origin, imported to Denmark, ex type of <i>Aspergillus pipericola</i>	MG662385	MG517717	MG518087	MG517908
<i>Aspergillus pseudocaelatus</i>	CBS 117616 ^T = DTO 010- H4 = IBT 27191	<i>Arachis burkartii</i> leaf, Mercedes, Corrientes province, Ituzaingó, Argentina	EF409242	MG517626	MG517995	MG517809
	ITAL 103CC = IBT 29230	Peanuts, Brazil	–	–	–	–
	ITAL 1300F/09 = IBT 30532	Brazil nuts, Amazon, Brazil	–	–	–	–
<i>Aspergillus pseudonomius</i>	CBS 119388 ^T = DTO 009- F1 = NRRL 3353 = IBT 27864 = IBT 14897 DTO 177-G7	Diseased alkali bee (<i>Nomius</i> sp.), Wyoming, USA	AF338643	EF661495	EF661529	EF661454
	DTO 262-F3	Soil of corn-field, Phayao, Thailand	–	MG517659	MG518029	MG517847
	DTO 267-D6	Indoor environment of child hospital, Izmir, Turkey	–	MG517729	MG518099	MG517920
	DTO 267-H7	House dust, Micronesia	MH279416	MG517731	MG518101	MG517922
	DTO 267-I4	House dust, Thailand	MH279417	MG517732	MG518102	MG517923
	IBT 12657 = DTO 303-A4	House dust, Thailand	–	MG517733	MG518103	MG517924
	ITAL 823/07	Seed, unknown location	MH279418	MG517758	MG518128	MG517949
	ITAL 849F = IBT 32759	Brazil nut, Amazon, Brazil	–	–	–	–
	NRRL 6552	Brazil nut, Amazonas, Brazil	–	–	–	–
	NRRL 6552	Diseased pine sawfly, Wisconsin, USA, C.R. Benjamin, 1967	–	EF661496	EF661528	EF661455
<i>Aspergillus pseudotamarii</i>	CBS 766.97 ^T = NRRL 25517 = DTO 046-C1 = IBT 21092	Soil, teafield, Japan	AF272574	EF661477	EF661521	EU021631
	CBS 117625 = NRRL 25518 = IBT 21090	Soil, teafield, Japan	–	–	–	–
	CBS 117628 = NRRL 25519 = IBT 21093	Soil, teafield, Japan	–	–	–	–
	CBS 765.97 = NRRL 443 ITAL 791F/09 = IBT 30530	Unknown source Brazil nut, Amazonas, Brazil	AF004931	EF661476	EF661520	EU021650
			–	–	–	–

Table 1. (Continued).

Species	Isolate number	Provenance	GenBank accession no.				
			ITS	<i>BenA</i>	<i>CaM</i>	<i>RPB2</i>	
<i>Aspergillus sergii</i>	ITAL 792F/09 = IBT 30531	Brazil nut, Amazonas, Brazil	–	–	–	–	
	CBS 130017 ^T = DTO 223-C9 = IBT 32292 = IBT 32293	Fruits of <i>Prunus dulcis</i> , Trans-Os-Montes processing plant, Faro, Portugal, ex type of <i>Aspergillus sergii</i>	EF412769	MG517688	MG518059	MG517879	
<i>Aspergillus sojae</i>	CBS 100928 ^T = DTO 046-C3 = ATCC 42251 = IAM 2669 = IFO 4244 = IFO 30112 = IMI 191300 = RIB 1045 = SRRRC 1126 = K. Sakaguchi SH-10-6 = IBT 21642 = IBT 32109	Koji of soy sauce, shoyu brewing, 1942, ex neotype of <i>Aspergillus sojae</i>	KJ175434	EF203168	EF202041	MG517831	
	CBS 100929 = NISL 1909 = IBT 21643	Soy sauce, Japan	–	–	–	–	
	CBS 100930 = NISL 1939 = IBT 21644	Soy sauce, Japan	–	–	–	–	
	CBS 100931 = NISL 1905 = IBT 21645	Soy sauce, Japan	–	–	–	–	
	CBS 100932 = IAM 2665 = IFO 4239 = NISL 1777 = IBT 21646	Soy sauce, Japan	–	–	–	–	
	CBS 100933 = NISL 1939 = IBT 21647	Soy sauce, Japan	–	–	–	–	
	CBS 100934 = IAM 2718 = IFO 4274 = RIB 1050 = NISL 1849 = IBT 21648	Soy sauce, Japan	–	–	–	–	
	CBS 100935 = NISL 1920 = IBT 21649	Soy sauce, Japan	–	–	–	–	
	CBS 100936 = IAM 2678 = RIB 1024 = IBT 21650	Soy sauce, Japan (produces versicolorins)	–	–	–	–	
	CBS 126.59 = IFO 5241 = IMI 191304 = Ohashi 1124 = IBT 3669 = IBT 3682	Miso brewing, Okayama Agricultural Experiment Station, Japan	–	–	–	–	
	CBS 133.52 = ATCC 9362 = CECT 2095 = IMI 087159 = NRRL 1947 = NRRL 1988 = NRRL 4841 = WB 4841 = IBT 3595	Soy sauce, unknown origin	EF661546	EF661482	EF661517	EF661450	
	DTO 173-C3 = IFM 46699	Unknown source	–	MG517658	MG518028	MG517846	
	NRRL 5594 = IBT 4600	Unknown source	–	–	–	–	
	<i>Aspergillus subflavus</i>	CBS 143683 ^T = DTO 326-E8 = S778 = CCF 4957 = NRRL 66254 = IBT 34939	Soil, near Mobile Cave, Romania, A. Nováková, 2013, ex type of <i>Aspergillus subflavus</i>	MH279429	MG517773	MG518143	MG517964
		S843b	Moonmilk, Na Špičáku cave, Czech Republic, A. Nováková, 2013	MH279449	MG517792	MG518164	MG517983
	<i>Aspergillus tamarii</i>	CBS 104.13 ^T = NRRL 20818 = QM 9374 = IBT 3648	Activated carbon, unknown origin, ex neotype of <i>Aspergillus tamarii</i>	AF004929	EF661474	EF661526	EU021629
		CBS 133097 = DTO 213-H5 = NRRL 4959	Unknown source, representative of <i>Aspergillus tamarii</i> var. <i>crassus</i>	MG662403	MG517678	MG518049	MG517866
		CBS 133393 = NRRL 4966 = IMI 016124 = IBT 3628	Seed, cacao, unknown origin	EU021614	EU021673	EU021686	EU021652
		DTO 010-G9 = CBS 167.63 = NRRL 4680 = ATCC 15054 = IMI 172295 = QM 8903 = WB 4680 = IBT 22566	Mouldy bread, India (ex type of <i>Aspergillus indicus</i> and <i>A. terricola</i> var. <i>indicus</i>). Isolation of dihydrocanadensolide, fumaric acid, fumaryl-D,L-alanine, indazonic acid = cyclopiazonic acid, kojic acid, succinic acid and 3-nitropropionic acid show that these metabolites can be produced by <i>A. tamarii</i> (Birch et al., 1968)	MG662407	MG517624	MG518001	MG517807
		DTO 065-A4	Indoor environment, Germany	MH279381	MG517648	MG517984	MG517835

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Table 1. (Continued).

Species	Isolate number	Provenance	GenBank accession no.			
			ITS	BenA	CaM	RPB2
	DTO 066-A1	Corn kernels, Indonesia	-	MG517649	MG517988	MG517836
	DTO 145-C3	Indoor environment, Germany	MH279382	MG517655	MG517993	MG517843
	DTO 266-D7	House dust, Mexico	-	MG517730	MG518100	MG517921
	DTO 364-E3	Air in chocolate factory, the Netherlands	MH279435	MG517781	MG518151	MG517971
	NRRL 425	Unknown source, representative of <i>Aspergillus lutescens nomen nudum</i>	EF661558	EF661475	EF661524	EU021648
	NRRL 426 = DTO 010-H3 = CBS 579.65 = IBT 3681 = IBT 3826 = IBT 10827	Unknown substrate, USA, ex neotype of <i>Aspergillus terricola</i>	EF661559	EF661472	EF661525	EU021649
	NRRL 4911 = CBS 484.65 = IBT 3659	Air contaminant, Brazil, ex neotype of <i>Aspergillus flavofurcatus</i>	EF661565	EF661473	EF661527	EU021651
<i>Aspergillus togoensis</i>	CBS 205.75 ^T = LCP 67.3456 = NRRL 13551 = IBT 14899 = IBT 21943	Decaying fruit of <i>Landolphia</i> sp., Central African Republic, ex type of <i>Aspergillus togoensis</i>	-	-	-	-
	CBS 272.89 = DTO 034-C1 = NRRL 13550 = IBT 14989 = IBT 21943	Seed, La Maboké, Central African Republic	AJ874113	FJ491477	FJ491489	JN121479
<i>Aspergillus trans-montanensis</i>	CBS 130015 ^T = MUM 10.214 = IBT 32313	Almond, Portugal, ex type of <i>Aspergillus trans-montanensis</i>	JF412774	HM803101	HM803020	HM802980
	MUM 10.205	Almond, Portugal	JF412771	HM803087	HM803021	HM802979
	MUM 10.211	Almond, Portugal	JF412772	HM803102	HM803023	HM802968
	MUM 10.221	Almond, Portugal	JF446612	HM803093	HM803028	HM802972
<i>Aspergillus vandermerwei</i>	CBS 612.78 ^T = DTO 069-D2 = DTO 034-B5 = NRRL 5108 = IBT 13876 = CCF 5683	Unknown source, Buenos Aires, Argentina, ex type of <i>Aspergillus vandermerwei</i>	EF661567	EF661469	EF661540	MG517838
	DTO 199-A9 = CBS 129201 = DMSA 706 = IBT 16758 = CCF 5679	Unknown source, USA, California	MH279390	MG517661	MG518032	MG517849
	DTO 210-F8 = CBS 132171 = IBT 16423 = RMF 7709	Native shortgrass prairie, soil (1 m deep), Pawnee National Grassland, Colorado, USA	-	MG517675	MG518046	MG517863
	DTO 363-F3 = NRRL 1237 = IBT 21072 = CCF 5602	Unknown source	MH279434	MG517780	MG518150	MG517970
	DTO 368-B9 = IBT 16661 = CCF 5684	Soil under crested wheat grass, 2 km south of Pryor, Colorado, USA	MH279436	MG517783	MG518153	MG517973
	DTO 368-C1 = NRRL 1236 = IBT 13865 = CCF 5685	Unknown source	MH279437	MG517784	MG518154	MG517974
	DTO 368-C2 = CBS 126709 = RMF 9585 = IBT 20468 = CCF 5681	Grassland, A1 soil horizon soil, Canyonlands National park, Utah, USA	MH279438	MG517785	MG518155	MG517975
	IBT 16662	Soil under <i>Senecio</i> sp. (<i>Asteraceae</i>), Pablo Alto, Chaco Canyon, New Mexico, USA	MH279447	MG517788	MG518162	MG517978
	IBT 20491	A1 soil horizon, Canyonlands National park, Utah, USA	MH279448	MG517789	MG518163	MG517979

Culture collections: ATCC: American Type Culture Collection, Maryland, USA, CBS, Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands, CCF: Culture Collection of Fungi, Prague, Czech republic, CCM: Czech Collection of Microorganisms, Brno, Czech Republic, CCTU: Culture Collection of Tabriz University, Iran, DSM: Deutsche Sammlung von Mikroorganismen und Cell-kulturen, Braunschweig, Germany, DTO: The fungal working collection at Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands, IAM: Center for Cellular and Molecular Research, University of Tokyo, Tokyo, Japan (collection transferred to JCM), IFO (= NRBC) Institute of Fermentation, Osaka, Japan, IMI, CABI Fungal collection, Egham, UK, ITAL: Instituto de Tecnologia Alimentos, Campinas, Brazil, LCP: Laboratoire de Cryptogamie, Paris, France, KACC: Korean Agricultural Culture Collection, Seoul, South Korea, MUM: Micoteca da Universidade do Minho, Portugal, NRRL, Northern Regional Research Lab, NCAUR, Peoria, Illinois, USA, QM: Quartermaster Collection, now at NRRL, Peoria, Illinois, USA, RIB: National Research Institute of Brewing, Higashihiroshima, Hiroshima, Japan, RMF: Rocky Mountain Fungi, collected by Martha Christensen, and situated in Laramie, Wyoming, USA, Thom: The original collection of Charles Thom, now at NRRL, WB: Wisconsin Bacteriology collection, Madison, Wisconsin, cultures now deposited at CBS, ATCC, IMI and IBT.

optimal substitution model was used in the analyses. The Markov Chain Monte Carlo (MCMC) analysis used four chains and started from a random tree topology. Burn-in was set to 25 % and Tracer v. 1.5.0 (Rambaut & Drummond 2009) was used to confirm the convergence of chains. The phylograms obtained during the ML analysis were used for presenting the data. Phylograms were redrawn from the tree files using TREEVIEW (Page 1996) and optimized using Adobe® Illustrator® CS5.1. Bootstrap (BS) values lower than 70 % and posterior probability (pp) values lower than 0.95 were removed from the phylograms. The phylogenetic relationship of species belonging to section *Flavi* is studied using a combined data set of partial *BenA*, *CaM* and *RPB2* gene sequences. The relationship of strains (and species) belonging to five clades (*A. alliaceus*-, *A. flavus*-, *A. leporis*-, *A. nomius*- and *A. tamarii*-clade) is studied in more detail. The reason of these detail analyses is that either these clades contain new species and/or we found that the taxonomy of those clades was not well re-solved. *Aspergillus muricatus* NRRL 35674^T was used as out-group in the overview of section *Flavi*, *Aspergillus tamarii* NRRL 20818 in the *A. flavus*- and *A. leporis*-clade phylogenies and *A. bertholletius* CBS 143687^T in the *A. alliaceus*-, *A. nomius*- and *A. tamarii*-clade phylogenies.

Extrolite analysis

Strains were grown for 7 d at 25 °C on YES and CYA prior to extrolite extraction. The strains of the recently described species were inoculated on Czapek yeast autolysate (CYA) agar, malt extract agar (MEA) (Blakeslee formula), MEA-Ox (Oxoid formula), yeast extract sucrose (YES) agar, oat meal (OAT) agar, potato dextrose agar (PDA) (Difco), Wickerhams antibiotic test medium (WATM) and Raulin Thom oat meal (RTO) agar (Nielsen *et al.* 2011a,b, Frisvad 2012), and *Aspergillus flavus* parasiticus agar (AFPA) (Pitt *et al.* 1983).

Strains listed in Table 1 were tested for production of small molecule extrolites according to the agar plug extraction method of Filtenborg *et al.* (1983) as modified by Smedsgaard (1997). The HPLC-DAD method was following Frisvad & Thrane (1987), as modified by Nielsen & Smedsgaard (2003) and Nielsen *et al.* (2011a,b). After extracting the agar plugs with ethylacetate /dichloromethane / methanol (3:2:1, vol/vol/vol) containing 1 % formic acid, the solvent was evaporated and the mixture of extrolites were re-dissolved in methanol, filtered and 1 µl was injected into a Agilent high performance liquid chromatograph with a diode array detector. Samples made after 2015 were extracted with ethylacetate / isopropanol (3:1, vol/vol), with 1 % formic acid. Selected strains were

analyzed by Ultra high performance liquid chromatography-diode array detection-high resolution quadrupole time of flight mass spectrometry (UHPLC-DAD-HRQTOFMS) according to the method of Kildgaard *et al.* (2014) and Klitgaard *et al.* (2014) using an Agilent Infinity 1290 HPLC system (Agilent Technologies, Santa Clara, CA, USA) as described in detail by Kildgaard *et al.* (2014).

RESULTS

Phylogenetic analysis

Various analyses were performed to study the phylogenetic relationship between species in section *Flavi*. Details on the number of included isolates, the length of the data sets and information on the used substitution model for each dataset are listed in Table 2.

A phylogenetic study based on a combined data sets of loci (*BenA*, *CaM*, *RPB2*) was conducted to determine the relationship among *Aspergillus* section *Flavi* members. *Aspergillus* section *Flavi* could be subdivided into distinct eight clades: the *A. alliaceus*-, *A. avenaceus*-, *A. bertholletius*-, *A. coremiiformis*-, *A. flavus*-, *A. leporis*-, *A. nomius*- and *A. tamarii*-clade (Fig. 1). The *A. flavus*-clade is phylogenetically most closely related *A. tamarii*-clade and these clades form, together with the *A. nomius*- and the *A. bertholletius*-clades, a fully supported lineage. The phylogenetic relationship of the *A. bertholletius*-clade with the other clades remains partly unresolved in our analysis. In the ML analysis, the three *A. bertholletius* strains are placed with moderate statistical support (BS 83 %) in a basal position to the *A. tamarii*- and *A. flavus*-clades; however, no support was found in the Bayesian analysis (< 0.95 pp). The *A. alliaceus*- and *A. coremiiformis*-clades are also phylogenetically related (92 % BS, 1.00 pp) and these clades form a sister lineage to the *A. flavus*-, *A. tamarii*-, *A. bertholletius*- and *A. nomius*-clades. *Aspergillus leporis* and related species (*A. leporis*-clade) take a basal position to aforementioned clades and the *A. avenaceus*-clade, only represented by *A. avenaceus*, is basal in section *Flavi*.

The *A. flavus*-clade is the most species-rich clade of section *Flavi* and contains 15 species (Figs 2, 3), including the five new species described in this manuscript (see Taxonomy; *A. aflatoxiformans*, *A. austwickii*, *A. cerealis*, *A. pipericola*, *A. subflavus*). Analysis of the combined data set reveals four well-supported lineages in the *A. flavus*-clade. One main lineage is centered on *A. flavus* and contains *A. aflatoxiformans*,

Table 2. Details of the length and substitution model of each data set.

Description data set	No. isolates	<i>BenA</i> , length alignment	<i>BenA</i> , substitution model	<i>CaM</i> , length alignment	<i>CaM</i> , substitution model	<i>RPB2</i> , length alignment	<i>RPB2</i> , substitution model	Combined
Overview	38	574	K2 + G	617	TN93 + G	880	TN93 + G + I	2071
<i>A. alliaceus</i> -clade	41	431	K2	485	TN93 + G	760	K2 + G	1676
<i>A. flavus</i> -clade	133–138	481	K2	529	TN93 + G	843	TN93 + G	1853
<i>A. leporis</i> -clade	16	510	K2 + G	555	TN93 + G	968	TN93 + G	2033
<i>A. nomius</i> -clade	25	504	K2 + G	528	TN93 + G	923	TN93	1955
<i>A. tamarii</i> -clade	23	502	K2 + G	539	HKY	920	K2 + G	1961

BenA|CaM|RPB2

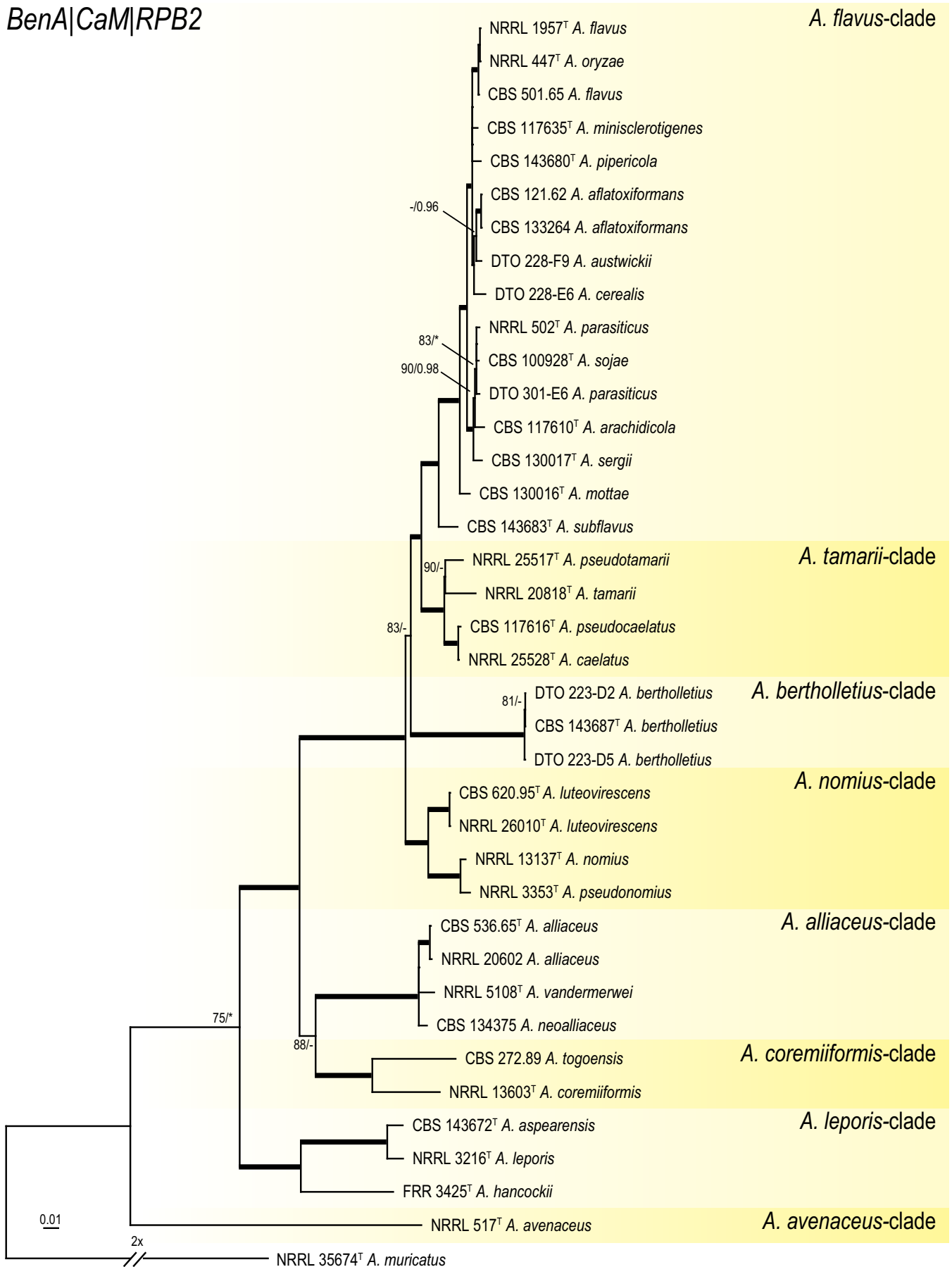


Fig. 1. Phylogeny inferred from a concatenated nucleotide data set (partial *BenA*, *CaM* and *RPB2* sequences) using ML analysis showing the relationship of species accommodated in *Aspergillus* section *Flavi*. The bar indicates the number of substitutions per site. The BI posterior probabilities values and bootstrap percentages of the ML analysis are presented at the node (BS/pp). Values less than 70 % bootstrap support in the ML analysis and less than 0.95 posterior probability in the Bayesian analysis are indicated with a hyphen. Branches with high support (> 95 % bs; 1.00 pp) are thickened and the BS and pp values indicated with an asterisks.

A. austwickii, *A. cerealis*, *A. flavus*, *A. minisclerotigenes*, *A. oryzae* and *A. pipericola* and the other main lineage (centered on *A. parasiticus*) includes *A. arachidicola*, *A. novoparasiticus*, *A. parasiticus*, *A. sergii*, *A. sojae* and *A. transmontanensis*. *Aspergillus mottae* has a basal position to the *A. flavus* and *A. parasiticus* lineages and *A. subflavus* is basal to all *A. flavus*-clade species. Almost all species could be resolved in the phylogenetic analysis of the combined data set. There are two exceptions: *A. oryzae* resides in a clade with *A. flavus* and *A. sojae* forms a clade with *A. parasiticus*. With the exception of *A. flavus/A. oryzae* and *A. parasiticus/A. sojae*, almost all species could be recognised using *BenA*, *CaM* or *RPB2* sequences only. The exception is *A. novoparasiticus* and this species shares *BenA* sequences with *A. parasiticus* isolates. Strains CBS 485.65 (ex-type of *A. flavus* var. *columnaris* and *A. flavus* var. *asper*), CBS 501.65 (*A. subolivaceus*), CBS 542.69 (*A. kambarensis*), CBS 120.51 (*A. thomii*) and CBS 110.55 (*A. fasciculatus*) belong to the *A. flavus/A. oryzae* clade and CBS 260.67 (*A. parasiticus* var. *globosus*), CBS 580.645 (*A. terricola* var. *americana*) and CBS 822.72 (*A. toxicarius*) reside in the *A. parasiticus/A. sojae* clade. Two interesting *A. flavus* strains (from air, Korea) that produce aflatoxins of the B and G type (CBS 143688, CBS 143689) cluster in all analyses with other *A. flavus/A. oryzae* strains. Also two strains with small sized sclerotia (DTO 281-H8; NRRL 3251) belong to the *A. flavus/A. oryzae* lineage.

Phylogenetic analysis reveals the presence of four species (*A. caelatus*, *A. pseudocaelatus*, *A. pseudotamarii* and *A. tamarii*) in the *A. tamarii*-clade (Fig. 4). The genetic distance between *A. caelatus* (CBS 763.97, DTO 073-B7, DTO 276-I2, NRRL 25528, NRRL 26100) and *A. pseudocaelatus* (DTO 285-H9, DTO 285-I1, CBS 117616) strains is low. In the phylogeny based on the combined data set, these strains resolve in two distinct clades. This clade is fully supported in the Bayesian analysis (1.00 pp); however, it lacks confident bootstrap support in the ML analysis (< 70 %). Representative strains of *A. flavofurcatus* (NRRL 4911), *A. indicus* and *A. terricola* var. *indicus* (CBS 167.63) cluster together with the type of *A. tamarii* (NRRL 20818) in all analyses.

Three species are accommodated in the *A. nomius*-clade: *A. luteovirescens*, *A. nomius* and *A. pseudonomius* (Fig. 5). Three well-supported, distinct clades could be recognised in the *BenA* analysis, representing the species accommodated in this clade. Not all species were resolved in the *CaM* and *RPB2* analysis. The statistical support in the *CaM* phylogram was low. *Aspergillus nomius* strain DTO 321-F2 clustered with the included *A. pseudonomius* strains; however, statistical support was lacking. Phylogenetic analysis of the *RPB2* data set could not resolve *A. nomius* and *A. pseudonomius* and strains of those species appear intermixed on one well-supported branch. The ex-type of *A. zhaoqingensis* (CBS 399.93) clusters together with the *A. nomius* strains in three out of the four analyses (*BenA*, *CaM* and combined analysis), and the ex-type of *A. bombycis* NRRL 26010^T clusters with *A. luteovirescens* strains (incl. CBS 620.95^{NT}).

Four distinct groups in the *A. alliaceus*-clade can be recognised after assessment of the phylograms using the Genealogical Concordance Phylogenetic Species Recognition (GCPSR; Taylor *et al.* 2000) concept (Figs 6, 7). These groups represent two known (*A. alliaceus*, *A. lanosus*) and two new species (described here as *A. neoalliaceus* and *A. vandermerwei*). The deeper nodes in the phylograms often have a low statistical

support and the relationship among species in the *A. alliaceus*-clade therefore remains unknown. A high *BenA*, *CaM* and *RPB2* sequence diversity is present in the *A. vandermerwei*. Following the GCPSR concept, two groups can be recognised in *A. vandermerwei*: one includes CBS 129201, CBS 132171 and DTO 368-B9, and the other contains CBS 126709, DTO 368-C1, DTO 363-F3, IBT 20491, IBT 16662 and NRRL 5108^T. The ex-type strain of *A. albertensis*, NRRL 20602, resides in the clade containing *A. alliaceus* isolates.

A set of strains isolated from soil of Aspear Island in Urmia Lake (Iran) formed a distinct lineage related to *A. leporis* and the name *A. aspearensis* is proposed for this group of isolates (Fig. 8). The third species in this clade is the recently described species *A. hancockii* (Pitt *et al.* 2017). All species can be recognised using the GCPSR concept.

Extrolite analysis

An overview of mycotoxins and other extrolites produced by *Aspergillus* section *Flavi* is given in Tables 3 and 4. The *A. avenaceus*- and *A. leporis*-clades are basal to the other clades in section *Flavi* (Fig. 1), but do not have the ability to produce aflatoxins or ochratoxins. Furthermore, *A. avenaceus* does not produce kojic acid, an extrolite produced by the majority of species in section *Flavi* (Table 3). Aflatoxins or precursors of aflatoxins are produced in all the other clades (the *A. flavus*-, *A. tamarii*-, *A. bertholletius*-, *A. nomius*-, *A. alliaceus*- and *A. coremiiformis* clades). Ochratoxin A and B are only found in the *A. alliaceus*-clade. Among the species in *Aspergillus* section *Flavi*, two species produced aflatoxin B₁ and B₂ only: *A. pseudotamarii* and *A. togoensis*. Sixteen species produced aflatoxin B₁, B₂, G₁ and G₂: *A. aflatoxiformans*, *A. arachidicola*, *A. austwickii*, *A. cerealis*, *A. luteovirescens*, *A. minisclerotigenes*, *A. mottae*, *A. nomius*, *A. novoparasiticus*, *A. parasiticus*, *A. pipericola*, *A. pseudocaelatus*, *A. pseudonomius*, *A. sergii*, *A. transmontanensis* and some strains of *A. flavus* (Table 3, Supplementary Fig. S1). One strain of *A. bertholletius* produced the aflatoxin B₁ precursor O-methylsterigmatocystin (Taniwaki *et al.* 2012, and this result was confirmed here). Seven strains of *A. flavus sensu stricto* from Korea were found to produce aflatoxins of the B and G type (Table 3). Most isolates of *A. alliaceus*, *A. neoalliaceus* and *A. vandermerwei* produced large amounts of ochratoxin A (Table 3; Supplementary Table S1, Supplementary Fig. S2). One strain of *A. sojae* and two strains of *A. alliaceus* produced versicolorins (Table 3), precursors of the aflatoxins. Another important mycotoxin, tenuazonic acid, is produced by eight species (*A. bertholletius*, *A. caelatus*, *A. luteovirescens*, *A. nomius*, *A. pseudocaelatus*, *A. pseudonomius*, *A. pseudotamarii* and *A. tamarii*) (Supplementary Fig. S3). The related mycotoxin cyclopiazonic acid was produced by 14 species: *A. aflatoxiformans*, *A. austwickii*, *A. bertholletius*, *A. cerealis*, *A. flavus*, *A. hancockii* (only speradine F found in this species), *A. minisclerotigenes*, *A. mottae*, *A. oryzae*, *A. pipericola*, *A. pseudocaelatus*, *A. pseudotamarii*, *A. sergii* and *A. tamarii* (Table 4, Supplementary Fig. S4).

Morphology and physiology

Species in section *Flavi* produce spreading, transparent colonies on CREA that measure (25–)35–50(–55) mm after 7 d and acid production is generally absent. Weak acid production is present in

some strains of certain species (*A. caelatus*, *A. pseudocaelatus*, *A. pseudotamarii*, *A. tamarii*); however, this is not a consistent character at species level. A colony diameter larger than 5 mm after 7 d incubation on CYA at 42 °C (CYA42°C) was observed in *A. aflatoxiformans*, *A. arachidicola*, *A. austwickii*, *A. cerealis*, *A. flavus*, *A. minisclerotigenes*, *A. novoparasiticus*, *A. oryzae*, *A. parasiticus*, *A. sergii* and *A. sojae* (Figs 9–12, Table 5). Some strains inconsistently grew on CYA42°C: certain strains of *A. alliaceus*, *A. lanosus*, *A. neoalliaceus*, *A. nomius*, *A. pipericola* produced restricted colonies on CYA42°C (1–5 (–8) mm), while no growth was observed in other isolates. *Aspergillus cor-miiformis* and *A. togoensis* did not grow on CYA incubated at 37 °C and *A. avenaceus* produced restricted colonies at that temperature (7 mm after 7 d); all other species grow well on CYA37 °C. Species belonging to section *Flavi* grow rapidly and generally attain a diameter of more than 50 mm on CYA, MEA and YES after 7 d; the exception is *A. coremiiformis* (CYA 30 mm, MEA 46 mm, YES 48 mm). The conidial colour can be in shades of brown, green and yellow. The majority of species have conidia in shades of (dark) yellow-green (e.g. *A. flavus*, *A. austwickii*, *A. arachidicola*, *A. nomius*, *A. parasiticus*, *A. transmontanensis*); conidia in shades of brown are produced by e.g. *A. bertholletius*, *A. caelatus*, *A. pseudocaelatus*, *A. tamarii* and yellow shades are present in isolates of *A. alliaceus*, *A. lanosus*, *A. neoalliaceus* and *A. vandermerwei*. A majority of species, 28 out of 33 species in *Aspergillus* section *Flavi*, can produce sclerotia (Table 5); however, not always on the media used in this study. Sclerotium production was often best on CYA incubated at 25 °C or 37 °C, followed by MEA and YES. The sclerotia produced by section *Flavi* species become dark brown or black coloured at age and have different shapes and sizes. Examples are shown in Figs 13 and 14. Species belonging to the *A. flavus*-clade generally produce globose to ellipsoidal sclerotia that can be large (e.g. *A. flavus*, *A. parasiticus*, *A. transmontanensis*, 400–700 (–1000) µm; *A. subflavus* 375–650 µm), intermediate (*A. sergii* 300–550 µm) or small (*A. aflatoxiformans*, *A. austwickii*, *A. cerealis*, *A. minisclerotigenes*, *A. pipericola* 100–375 µm; *A. mottae* 150–375 µm). Although the majority of *A. flavus* strains produce large-sized sclerotia, some isolates have sclerotia less than 350 µm in diam (Fig. 13, Table 5). Species in the *A. alliaceus*-clade produce large sclerotia (1000–2500 × 500–1200 µm) that are oblong to oval shaped, brownish black coloured, which occasionally have a white tip on the top (Fig. 14A). The sclerotia produced by species in the *A. leporis*-clade are ellipsoidal or irregular shaped and vary in size. Sclerotia of *A. leporis* measure 1000–3000 × 800–1800 µm (Fig. 14D), those of *A. aspearensis* are 800–1500 × 400–700 µm in size (Fig. 14E) and *A. hancockii* sclerotia are 500–1200 × 500–800 µm (Fig. 14C).

DISCUSSION

Mycotoxins and other extrolites

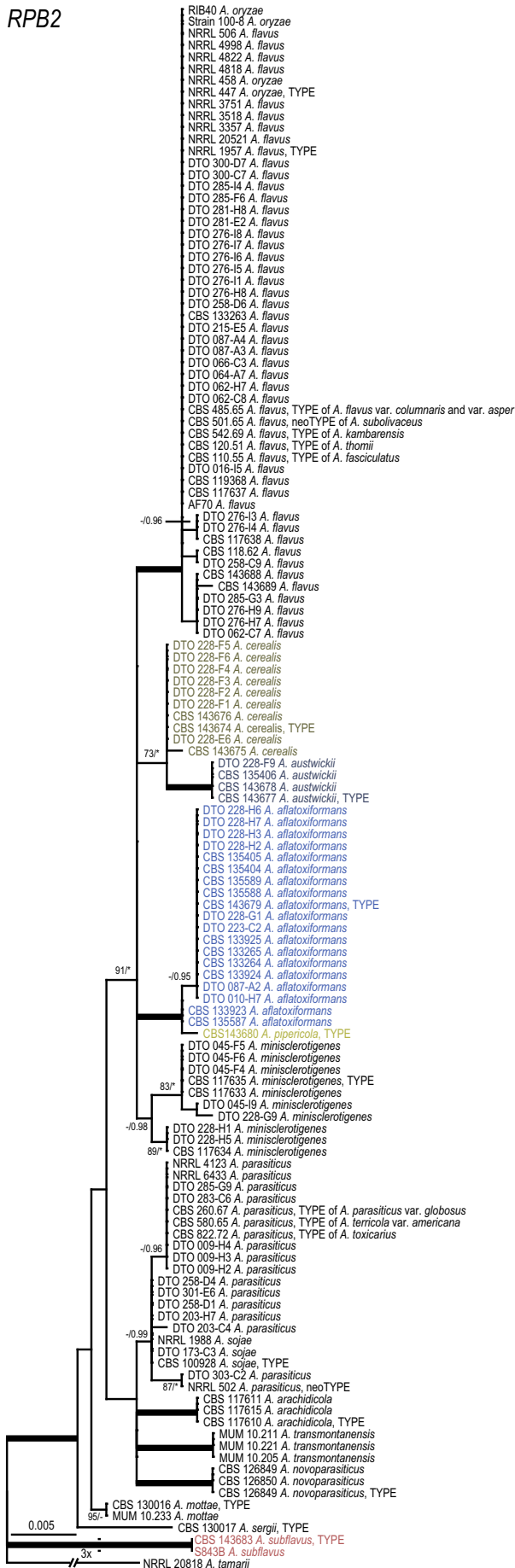
Among the 33 species (including the two domesticated species) in section *Flavi*, 18 species can produce aflatoxins and one strain

of one species, *A. bertholletius*, can produce the immediate aflatoxin precursor 3-O-methylsterigmatocystin. No fungal species have yet been found that could produce both aflatoxins and ochratoxins. In the *A. alliaceus*-clade (*A. alliaceus*, *A. neoalliaceus*, *A. vandermerwei*) the conidia are of a yellow shade and these species are able to produce ochratoxin A, but never aflatoxins. Ochratoxin A and B production seem to be an autapomorphy in that clade. On the other hand, two *A. alliaceus* isolates produced versicolorins (Table 3), which is an intermediate compound in the aflatoxin biosynthetic pathway. This shows that a part of the gene cluster for aflatoxin production may also be present in some species of the *A. alliaceus*-clade. In the species with yellow-green or brownish green conidia (*A. flavus*, *A. tamarii*, *A. nomius* and *A. togoensis* clades) several species produce aflatoxins, but never ochratoxins. It is interesting to note that if the ancestor to these five clades produced aflatoxins, then the species in the *A. alliaceus* clade must have lost the ability to produce aflatoxins, but gained the ability to produce ochratoxins. It has been shown that both ochratoxins and aflatoxins are insecticidal and that kojic acid and aflatoxin are synergistic in insect toxicity (Dowd 1988, Wicklow *et al.* 1996). Ochratoxin A and aflatoxin B₁ may have similar functions in nature; hence they are never co-produced by any species. It has not been examined whether kojic acid and ochratoxin have a synergistic toxic effect on insects, but kojic acid is produced in large amounts by most species in *Aspergillus* section *Flavi* (Varga *et al.* 2011, Table 3). It should also be noted that aflavinines, aflatrems and aflavazole, found in the sclerotia of many species in section *Flavi*, are also insecticidal (Gloer *et al.* 1988, TePaske *et al.* 1990, 1992), and thus a number of secondary metabolites from these species may act in concert in repelling insects.

Aspergillus section *Flavi* contains several species that produce some of the most important mycotoxins known, especially aflatoxins, ochratoxins and cyclopiazonic acid. Eight species are able to produce the B and G type aflatoxins in addition to cyclopiazonic acid: *A. aflatoxiformans*, *A. austwickii*, *A. cerealis*, *A. minisclerotigenes*, *A. mottae*, *A. pipericola*, *A. sergii*, and *A. pseudocaelatus*, while *A. flavus* and *A. pseudotamarii* produce the B type aflatoxins in addition to cyclopiazonic acid. However, Okoth *et al.* (2018) found that some of their strains of *A. minisclerotigenes* produced aflatoxin B only. *A. togoensis* also produces aflatoxin B₁, but not cyclopiazonic acid. *A. togoensis* is more similar to the aflatoxin B₁ producers in *Aspergillus* subgenus *Nidulantes* section *Ochraceorosei*, *A. ochraceorosei* and *A. rambellii*, in that all three species accumulate both sterigmatocystin and aflatoxin B₁ (Frisvad *et al.* 2005). These three species have all been isolated from tropical rainforest in the Tai National Forest of Ivory Coast (Bartoli & Maggi 1978), indicating that aflatoxin accumulation pattern is also influenced by the general ecological niches these species occupy. Species producing aflatoxin of the B and G type also include *A. nomius*, *A. luteovirescens* and *A. novoparasiticus*, and of those, *A. nomius* produces tenuazonic acid in addition to aflatoxins. *A. bertholletius* is the only species producing both tenuazonic acid and cyclopiazonic acid in addition to an aflatoxin precursor. Species that produce cyclopiazonic acid or tenuazonic acid without producing aflatoxins include *A. caelatus*, *A. tamarii* and *A. oryzae*. The

Fig. 2. ML Phylogeny showing the relationship of species accommodated in the *A. flavus*-clade (left, *BenA*; right, *CaM*). The bar indicates the number of substitutions per site. The BI posterior probabilities values and bootstrap percentages of the ML analysis are presented at the node (BS/pp). Values less than 70 % bootstrap support in the ML analysis and less than 0.95 posterior probability in the Bayesian analysis are indicated with a hyphen. Branches with high support (> 95 % bs; 1.00 pp) are thickened and the BS and pp values indicated with an asterisks.

RPB2



BenA|CaM|RPB2

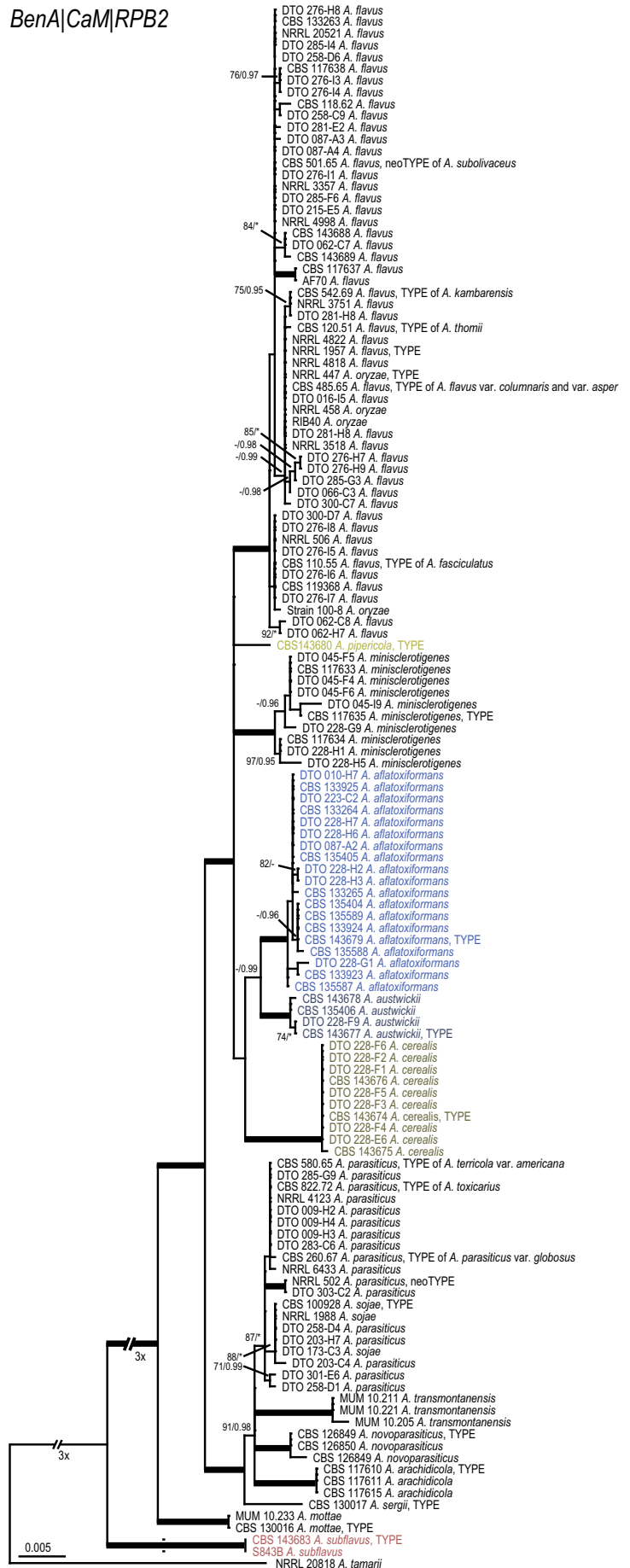


Fig. 3. Phylogeny showing the relationship of species accommodated in the *A. flavus*-clade (left, RPB2; right, combined data set of BenA, CaM and RPB2). The bar indicates the number of substitutions per site. The BI posterior probabilities values and bootstrap percentages of the ML analysis are presented at the node (BS/pp). Values less than 70 % bootstrap support in the ML analysis and less than 0.95 posterior probability in the Bayesian analysis are indicated with a hyphen. Branches with high support (> 95 % bs; 1.00 pp) are thickened and the BS and pp values indicated with an asterisks.

biosynthetic family of cyclopiazonic acids (CPAs) now includes 43 members, including speradines, aspergillines, cyclopiamides and asperorydines (Uka *et al.*, 2017, Liu *et al.*, 2018). Of these 30 members, 22 CPAs have been recovered in *A. flavus* (Uka *et al.*, 2017). Okoth *et al.* (2018) reported on cyclopiazonic acid production by an *A. parasiticus* strain No. 90, and stated that genetic recombination may be the reason for this rare mycotoxin-species connection. Besegmez & Heperkan (2015) also reported on trace CPA production by *A. parasiticus* strains. We have never observed CPA production in any strain of *A. parasiticus* or its domesticated form *A. sojae*. Genome sequencing and annotation of the CPA producing strain No. 90 may help explaining this unexpected result. Since the aflatoxin and CPA gene clusters are neighbours, and CPA is a pathogenicity factor in *A. flavus* (Chalivandra *et al.*, 2017), *A. parasiticus* may have the CPA cluster as mostly silent.

It has long been perceived that *A. flavus*, the most common species in section *Flavi*, can produce aflatoxin B₁ and B₂, but not aflatoxin G₁ and G₂. Here we report on strains of *A. flavus sensu stricto* from Korea that produce both types of aflatoxin. The only earlier reliable report that *A. flavus* can produce aflatoxins of the G type was published in 1983 (Wicklow & Shotwell 1983), and it was stated that the G type aflatoxins were only detected in the sclerotia of the genome sequence strain NRRL 3357 (Wicklow & Shotwell 1983, Nierman *et al.* 2015). The strains from South Korea are placed in *A. flavus* both based on phylogeny (Figs 2, 3) and extrolite data. Besides the production of aflatoxin G, the extrolite profile of those Korean strains fit well with other *A. flavus* strains, and including the partially characterized diketopiperazine flavimin that has until now only been found in this species.

Various isolates in section *Flavi* are able to produce small sclerotia, while those of *A. flavus* are usually large (Wicklow & Shotwell 1983). Sclerotia in *A. flavus* and *A. parasiticus* contain aflatoxins. Furthermore, sclerotium production is associated with specific secondary metabolites, including indoloterpenes such as aflatrems, aflavazole, aflavinines, anominine, aspernomine, paspalines and polyketides such as aflavarins (Table 3; Gallagher & Wilson 1978, Cole *et al.* 1981, TePaske *et al.* 1990, 1992). Aflatrems were detected in *A. aflatoxiformans*, *A. austwickii*, *A. cerealis*, *A. flavus* and *A. sergii*, and aflavazole was detected in *A. sergii* and *A. cerealis* (Table 2). The sclerotium associated polyketides aflavarins are also antiinsectan, but has until now only been found in *A. flavus* (TePaske *et al.* 1992). The ochratoxin A producing *A. alliaceus* produce similar isokotanin polyketides in the sclerotia in addition to anominine and paspaline (Gloer *et al.* 1989, Staub *et al.* 1993, Laakso *et al.* 1994), showing the chemical relatedness between *A. alliaceus* and *A. flavus*. *Aspergillus nomius* is also capable of producing anominine in addition to aspernomine (Staub *et al.* 1992, Bradshaw *et al.* 2010). The sclerotia of *A. leporis* and *A. aspearensis* also contain some aflavinin related metabolites, in addition to unique extrolites (Table 3). While *A. hancockii* is unique in producing the mycotoxins 7-hydroxytrichothecolone and fumitremorgin A found in other Aspergilli outside section *Flavi* (Pitt *et al.* 2017), in general this latter species is chemically unique.

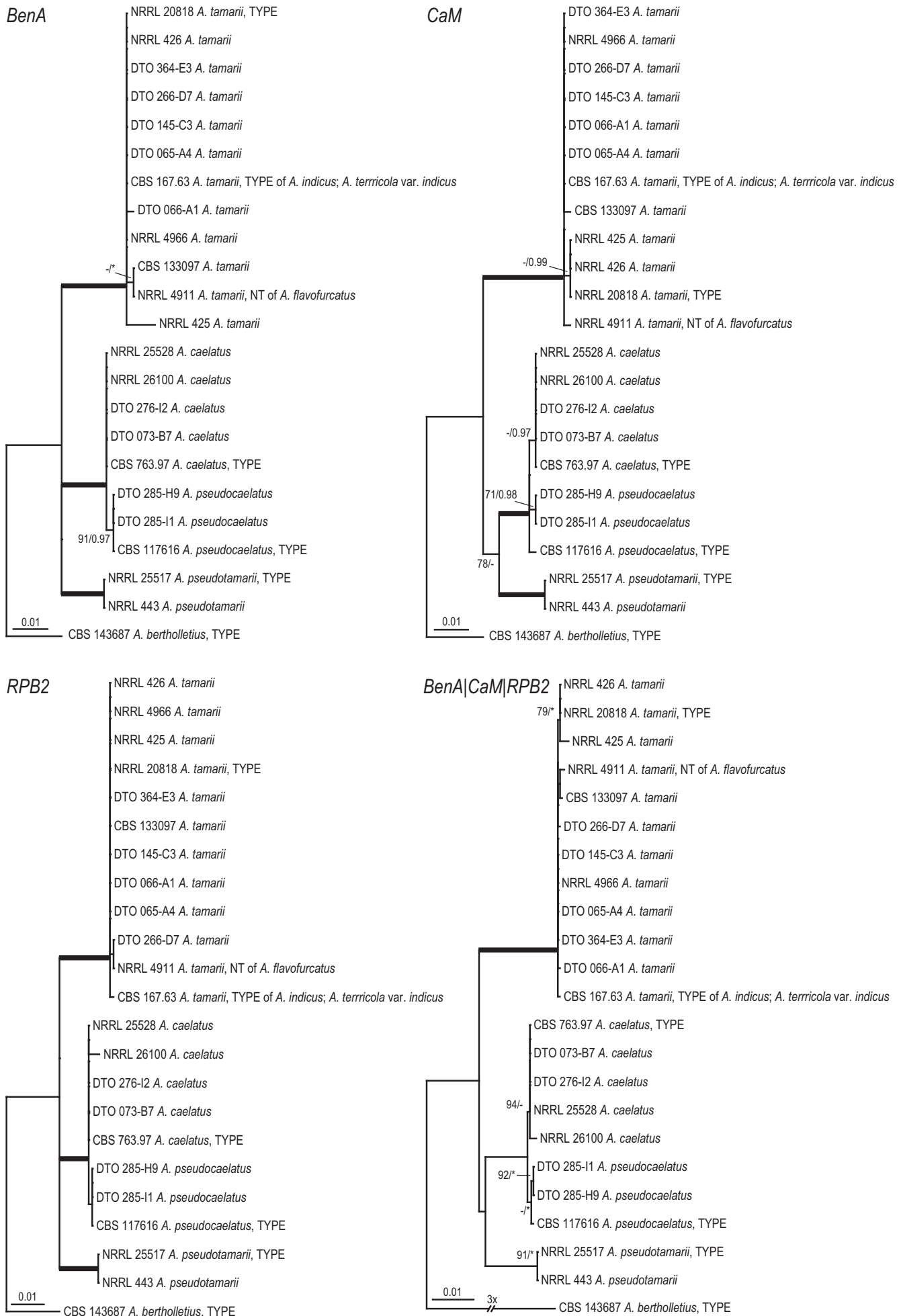
Aspergillus leporis, *A. aspearensis* and *A. hancockii* are related species in the *Aspergillus leporis* clade (Fig. 8). They share few secondary metabolites among them, but do share kojic acid with *A. flavus* and all other species in *Flavi* except *A. avenaceus* and *A. coremiiformis*. Furthermore, leporine A and other leporines, first found in *A. leporis*, were later also found in *A. flavus* (Sun *et al.* 2014, Arroya-Manzanares *et al.* 2015, Cary *et al.* 2015a,b). Aspergillic acid, found in *A. flavus* (Table 3) and leporins found in *A. flavus* and *A. leporis* are strong iron-chelating metabolites. In

A. flavus, an aspergillic acid ferri ion complex is readily expressed on the *Aspergillus flavus parasiticus* agar (AFPA) as an orange reverse, while the leporines are mostly non-expressed (Arroya-Manzanares *et al.* 2015, Cary *et al.* 2015a,b) in that species. *A. leporis*, not being able to produce aspergillic acid, produces leporins more readily. Apart from kojic acid and leporins, *A. leporis* produces leporazines A, B and C (Reategui *et al.* 2013). These latter epithiodiketopiperazines are not produced by *A. flavus* that produces chlorine containing epithiodiketopiperazine heteroisoextrolites instead that are called aspirochlorins (Klausmeyer *et al.* 2005). Aspirochlorine has been mentioned as a mycotoxin, and has been detected in some strains of *A. oryzae*, the domesticated form of *A. flavus* (Monti *et al.* 1999, Champhamjon *et al.* 2014).

Occasionally cultures reported to produce new secondary metabolites contain a large number of *A. flavus* metabolites, and are likely to have been contaminated with *A. flavus*. For example, *Pseudoallescheria boydii* F19-1 was reported to produce aflavinine, β -aflatrems, asperfuran, aspergillic acids, cyclopiamide E, 24,25-dehydro-10,11-dihydro-20-hydroxyaflavinine, O-methylsterigmatocystin, pseuboydone E, speradine B and C, in addition to several *A. fumigatus* metabolites (Lan *et al.* 2016), so it would be interesting to examine whether the reported pseudoboydones are secondary metabolites from *A. flavus* or *A. fumigatus*, and maybe not from *P. boydii*. In other cases, metabolites from other Aspergilli less closely related species to *A. flavus* were reported from this species, including terrein, hydroxysydonic acid, gregatin B and aspyrone (Saldan *et al.* 2018), such data have to be scrutinized and confirmed. We have not been able to detect the latter four secondary metabolites in any strain from *Aspergillus* section *Flavi*.

Morphology and ecology

Aspergillus flavus is the most common species in section *Flavi* causing contamination of food and feed (Klich 2007). The species can be delineated into two major morphotypes: the “L-type”, producing large sclerotia (average diameter >400 μ m) and the “S-type”, producing small sclerotia (average diameter <400 μ m) (Cotty 1989). In our study we show that *A. aflatoxiformans*, *A. arachidicola*, *A. austwickii*, *A. cerealis*, *A. minisclerotigenes*, *A. mottae*, *A. pipericola* can produce S-type sclerotia. These species also produce aflatoxins B and G, and strains reported as “strain S_{BG}” can potentially be any of those species (Doster *et al.* 1996, Freitas-Silva & Venâncio, 2011, Probst *et al.* 2007, 2010, 2012, 2014, Wagacha *et al.* 2013, Arone *et al.* 2016). The majority of investigated *A. flavus* strains produce L-type sclerotia, but S-type *A. flavus* strains occur as well (e.g. NRRL 3251, DTO 281-H8). Contamination events resulting in severe aflatoxicoses in Kenya have been attributed to section *Flavi* strains that produce S-type sclerotia and B-type aflatoxins (S_B). Based on the phylogenetic analysis of nitrate reductase (*niaD*) and aflatoxin pathway transcription factor (*afIR*) gene sequences, Probst *et al.* (2014) hypothesise that the Kenyan S_B-type isolates comprise a new aflatoxin-producing species. No cultures linked to this outbreak were available in this study for detailed taxonomic analysis. Recent analysis of Eastern Kenyan S-type *Flavi* strains, isolated from the area experiencing acute aflatoxicosis, showed that these strain are *A. flavus* or *A. minisclerotigenes* (Okoth *et al.* 2018). Based on these data, the unnamed Kenyan S_B strain is an *A. flavus* producing small sized sclerotia. Interestingly, Okoth *et al.* (2018) also reported *A. flavus* strains that produced B



and G aflatoxins in Eastern Kenya; hence *A. flavus* S_{BG} also exists. Taken together, *A. flavus* produces variable sized sclerotia (S or L) and if aflatoxin is produced, then it can be aflatoxin B only or more rarely B and G (S_B , S_{BG} or L morphotype).

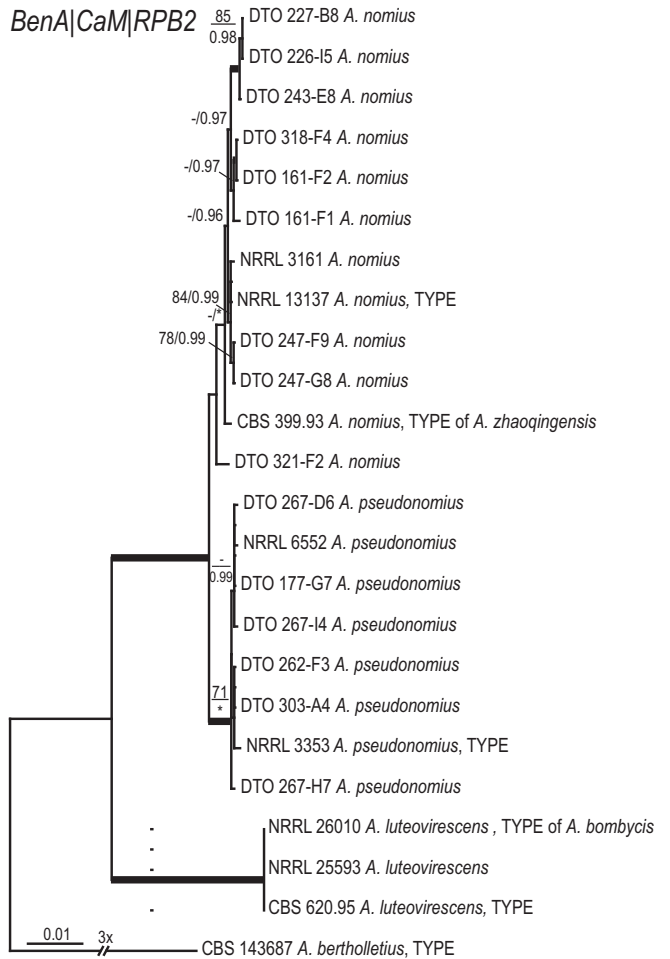
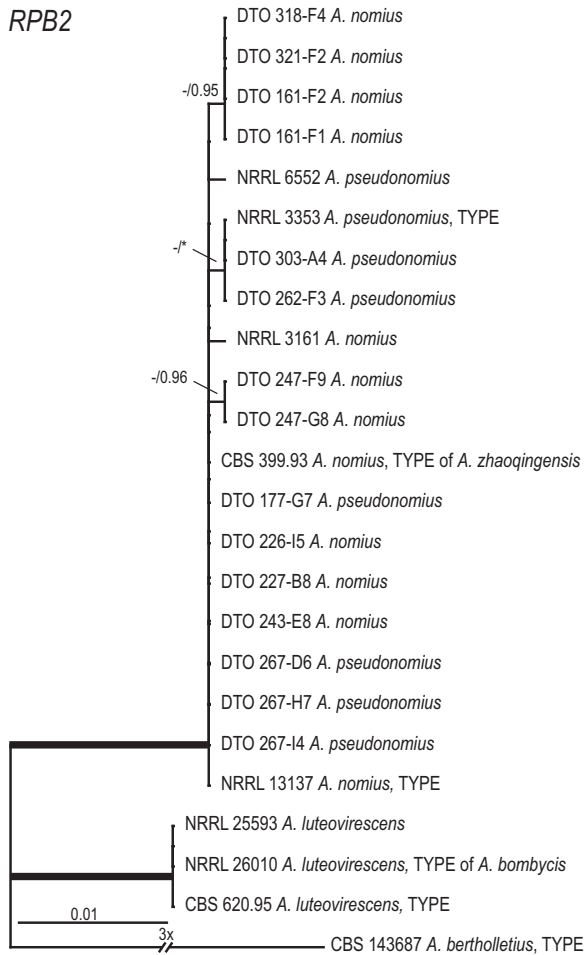
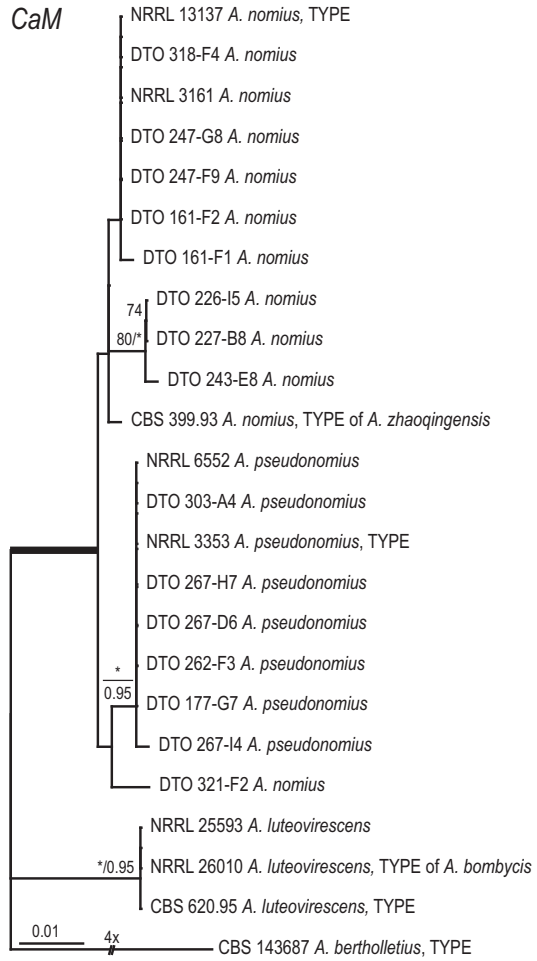
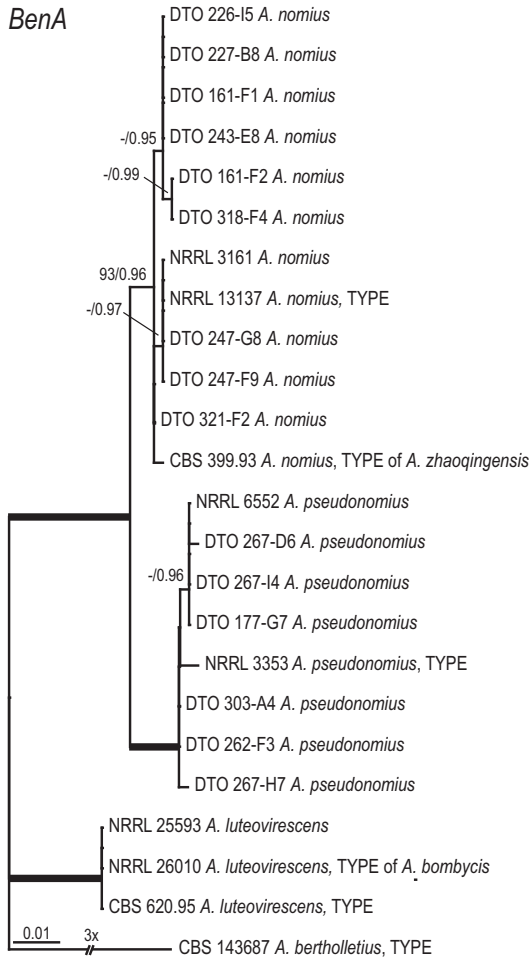
Some species in section *Flavi* are widespread and occur foremost in subtropical and tropical climates. *A. flavus*, *A. parasiticus* and *A. tamarii* have been reported from a large number of oil-seeds and nuts (Hedayati *et al.* 2007, Amaike & Keller 2011, Varga *et al.* 2009, 2011, 2015). However, many authors report on the occurrence of other section *Flavi* species and the presence of other species is therefore more common than first thought. For example, *A. minisclerotigenes* has been found mostly in South America (Pildain *et al.* 2008), while *A. aflatoxiformans*, *A. cerealis* and *A. austwickii*, reported as *A. flavus* S_{BG} , are most common in Africa and Thailand (Probst *et al.* 2007, 2010, 2012, 2014, Mutegi *et al.* 2012, Guezlane-Tebibel *et al.* 2013). Interestingly, many of the (recently) described species producing mycotoxins have been found in foods and are quite common: *A. aflatoxiformans* (also reported under its synonym *A. parvisclerotigenus*) (in African corn, Perrone *et al.* 2014a,b; Mexican and Nigerian sesame, Ezekiel *et al.* 2014, this study; edible mushrooms, Ezekiel *et al.* 2013b; peanut, Frisvad *et al.* 2005), *A. arachidicola* (in wild peanuts, Pildain *et al.* 2008; in Brazil nuts, Gonçalves *et al.* 2012a,b, Calderari *et al.* 2013, Taniwaki *et al.* 2017; in corn, Viaro *et al.* 2017), *A. austwickii* (stored rice grains and sesame kernels, this study), *A. caelatus* (in Brazil nuts, Gonçalves *et al.* 2012a,b, Taniwaki *et al.* 2017; in peanuts, Guezlane-Tebibel *et al.* 2013, Martins *et al.* 2017), *A. cerealis* (rice and maize grains, this study; peanut, Carvajal-Campos *et al.* 2017), *A. luteovirescens* (in Brazil nuts, Gonçalves *et al.* 2012a,b, Calderari *et al.* 2013, Taniwaki *et al.* 2017), *A. nomius* (in Brazil nuts, Olsen *et al.* 2008, Gonçalves *et al.* 2012a,b, Calderari *et al.* 2013, Massi *et al.* 2014, Taniwaki *et al.* 2017; in cocoa Copetti *et al.* 2011), *A. pseudonomius* (in Brazil nuts, Massi *et al.* 2014, Taniwaki *et al.* 2017) and to a lesser extent *A. novoparasiticus* (in corn, Viaro *et al.* 2017), *A. pseudocaelatus* (in corn, Viaro *et al.* 2017; in Brazil nuts, Taniwaki *et al.* 2017), and *A. pseudotamarii* (in Brazil nuts, Calderari *et al.* 2013, Taniwaki *et al.* 2017). Originally, *A. pseudotamarii* was found in tea field soil (Ito *et al.* 2001), *A. luteovirescens* in silkworm environments (Peterson *et al.* 2001), *A. nomius* in bees and in soil and silkworm excrements (Kurtzman *et al.* 1987, Ito *et al.* 1998), and *A. novoparasiticus* as a clinical isolate (Gonçalves *et al.* 2012a,b). Other species such as *A. mottae*, *A. sergii*, *A. transmontanensis* have been found in corn and almonds in Portugal, but not since their original discovery (Soares *et al.* 2012). *A. togoensis* producing sterigmatocystin, aflatoxin B and other secondary metabolites (Wicklow *et al.* 1989, McAlpin *et al.* 2000, Rank *et al.* 2011) has until now only been found on seeds of *Landolphia* and *Strychnos* (Samson & Seifert 1986, Wicklow *et al.* 1989, Wicklow & McAlpin 1990). Among the ochratoxin producing species *A. alliaceus*, *A. neoalliaceus* and *A. vandermerwei*, the first species has been detected in onions (Walker & Murphy 1934), peanuts (Wagacha *et al.* 2013), wheat (Hajjaji *et al.* 2006, Riba *et al.* 2008) and tree nuts and figs (Varga *et al.* 1997, Bayman *et al.* 2002), while *A. neoalliaceus* and

A. vandermerwei have only been found in soil (Table 1). *A. leporis* and the species related to it, *A. aspearensis* and *A. hancockii* have also only been isolated from soil (States & Christensen 1966, Christensen, 1981, Varga *et al.* 2011, Pitt *et al.* 2017), so even though mycotoxins have been detected such as antibiotic Y in *A. leporis* (Varga *et al.* 2011) and a potentially toxic trichothecolone from *A. hancockii* (Pitt *et al.* 2017), these species have never been found in foods or feeds. Concerning aflatoxin producers, it is not only *A. flavus* and *A. parasiticus* that should be regarded as important producers in foods and feeds, *A. aflatoxiformans* (= *A. parvisclerotigenus*), *A. arachidicola*, *A. austwickii*, *A. luteovirescens*, *A. cerealis*, *A. minisclerotigenes*, *A. nomius*, *A. novoparasiticus*, *A. pseudonomius*, *A. pseudocaelatus* and *A. pseudotamarii* are also aflatoxin producers to be considered.

With exception of *A. coremiiformis*, all species were able to grow on CYA incubated for 7 d at 37 °C. The majority of species belonging to the *A. flavus*-clade were able to grow moderate or well at 42 °C (> 5 mm). The only exceptions are *A. mottae*, *A. subflavus* (no growth observed) and *A. pipericola* (CYA42°C (1–5 (–8) mm). Some members of the *A. alliaceus*-clade were also able to grow at 42 °C, though not consistently (0–8 mm). Growth on creatine agar proved not to be useful to distinguishing species in section *Flavi* as most species grow poorly on this medium and acid production was not consistent at species level. Some isolates are capable of producing synnemata or synnemata-like structures on Czapek-Dox based media (Bartoli & Maggi 1978, McAlpin 2001, Danmek *et al.* 2014) including *A. togoensis*, *A. caelatus*, *A. coremiiformis* and *A. flavus*, but not *A. oryzae*, *A. nomius*, *A. parasiticus*, and *A. pseudotamarii* (Danmek *et al.* 2014). Synnema production has also been reported from tropical rainforest species such as the species *Aspergillus dybowskii*, *A. vitellinus* and *A. amazonensis* (Samson & Seifert 1986), so synnema production may be an ancestral character state in section *Flavi*. In some of the species, sclerotia are readily formed on most laboratory media, while others are only produced at specific conditions, or only by some isolates. Factors inducing sclerotium formation include corn or corn steep liquor (Wicklow & Shotwell 1983, Wicklow 1985, Wicklow & McAlpin 1990, TePaske *et al.* 1990, 1991, 1992, Rank *et al.* 2012). In our study we used agar media commonly applied in taxonomic studies investigating *Aspergilli* (Samson *et al.* 2014) and we found that sclerotium production most commonly present on CYA incubated at 25 or 37 °C.

Aspergillus section *Flavi* is the only section in *Aspergillus* where domesticated species have been accepted as valid species. *A. oryzae* is the domesticated form of *A. flavus*, and can be distinguished from the wild type by larger and more smooth conidia having more brown conidium colour *en masse*, a more floccose colony texture and weaker sporulation, absence of sclerotia, no production of aspergillic acid, and no production of aflatoxins (Wicklow 1984, Klich & Pitt 1988, Geiser *et al.* 2000, Machida *et al.* 2005, Payne *et al.* 2006, Hunter *et al.* 2011, Gibbons *et al.* 2012). These phenotypical differences may be caused by the interaction of domesticated yeasts (Gibbons & Rinker 2015). *Aspergillus sojae* is the domesticated form of

Fig. 4. Phylogeny showing the relationship of species accommodated in the *A. tamarii*-clade. The bar indicates the number of substitutions per site. The BI posterior probabilities values and bootstrap percentages of the ML analysis are presented at the node (BS/pp). Values less than 70 % bootstrap support in the ML analysis and less than 0.95 posterior probability in the Bayesian analysis are indicated with a hyphen. Branches with high support (> 95 % bs; 1.00 pp) are thickened and the BS and pp values indicated with an asterisks.



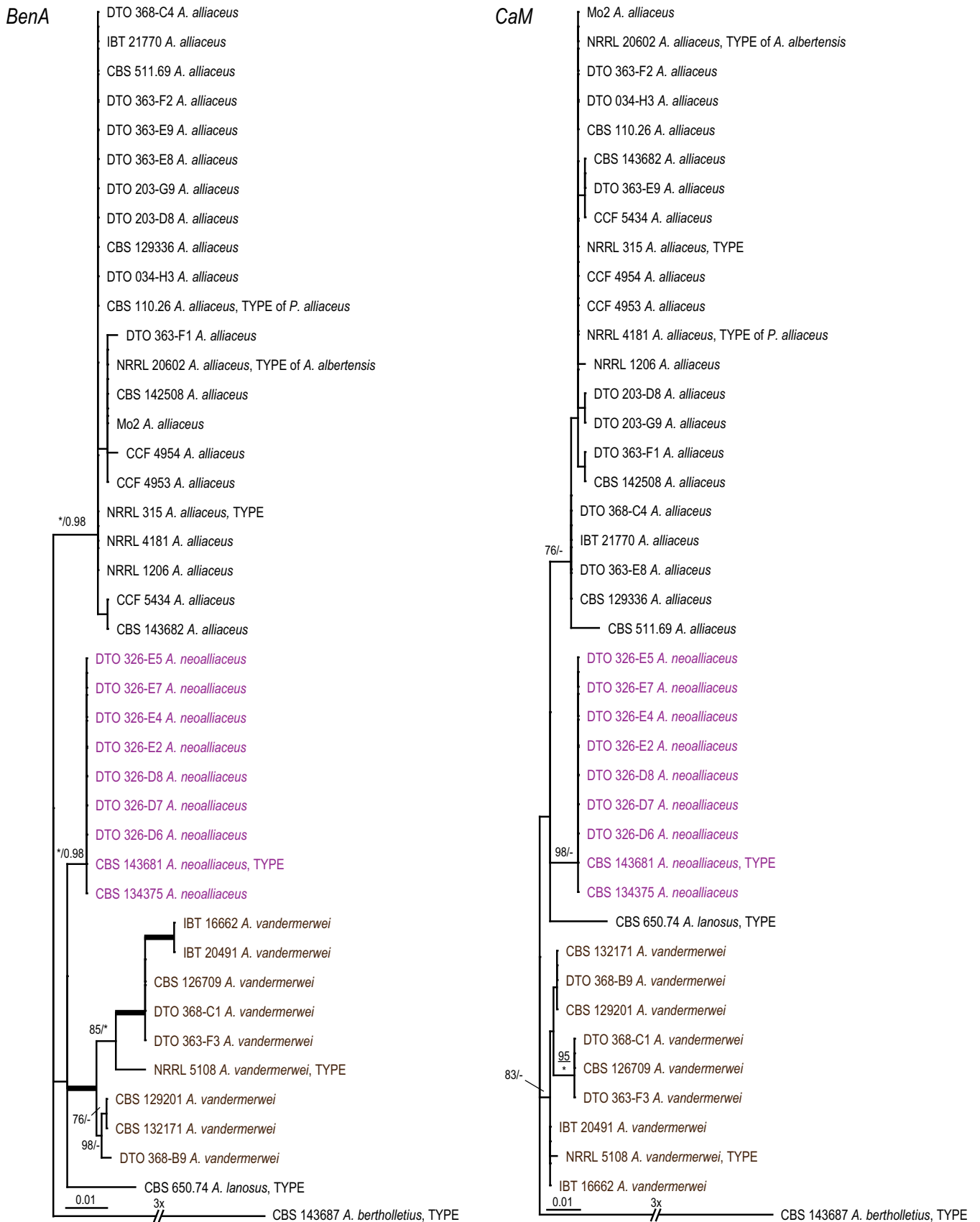


Fig. 6. ML Phylogeny showing the relationship of species accommodated in the *A. alliaceus*-clade (left, *BenA*; right, *CaM*). The bar indicates the number of substitutions per site. The BI posterior probabilities values and bootstrap percentages of the ML analysis are presented at the node (BS/pp). Values less than 70 % bootstrap support in the ML analysis and less than 0.95 posterior probability in the Bayesian analysis are indicated with a hyphen. Branches with high support (> 95 % bs; 1.00 pp) are thickened and the BS and pp values indicated with an asterisks.

Fig. 5. Phylogeny showing the relationship of species accommodated in the *A. nomius*-clade. The bar indicates the number of substitutions per site. The BI posterior probabilities values and bootstrap percentages of the ML analysis are presented at the node (BS/pp). Values less than 70 % bootstrap support in the ML analysis and less than 0.95 posterior probability in the Bayesian analysis are indicated with a hyphen. Branches with high support (> 95 % bs; 1.00 pp) are thickened and the BS and pp values indicated with an asterisks.

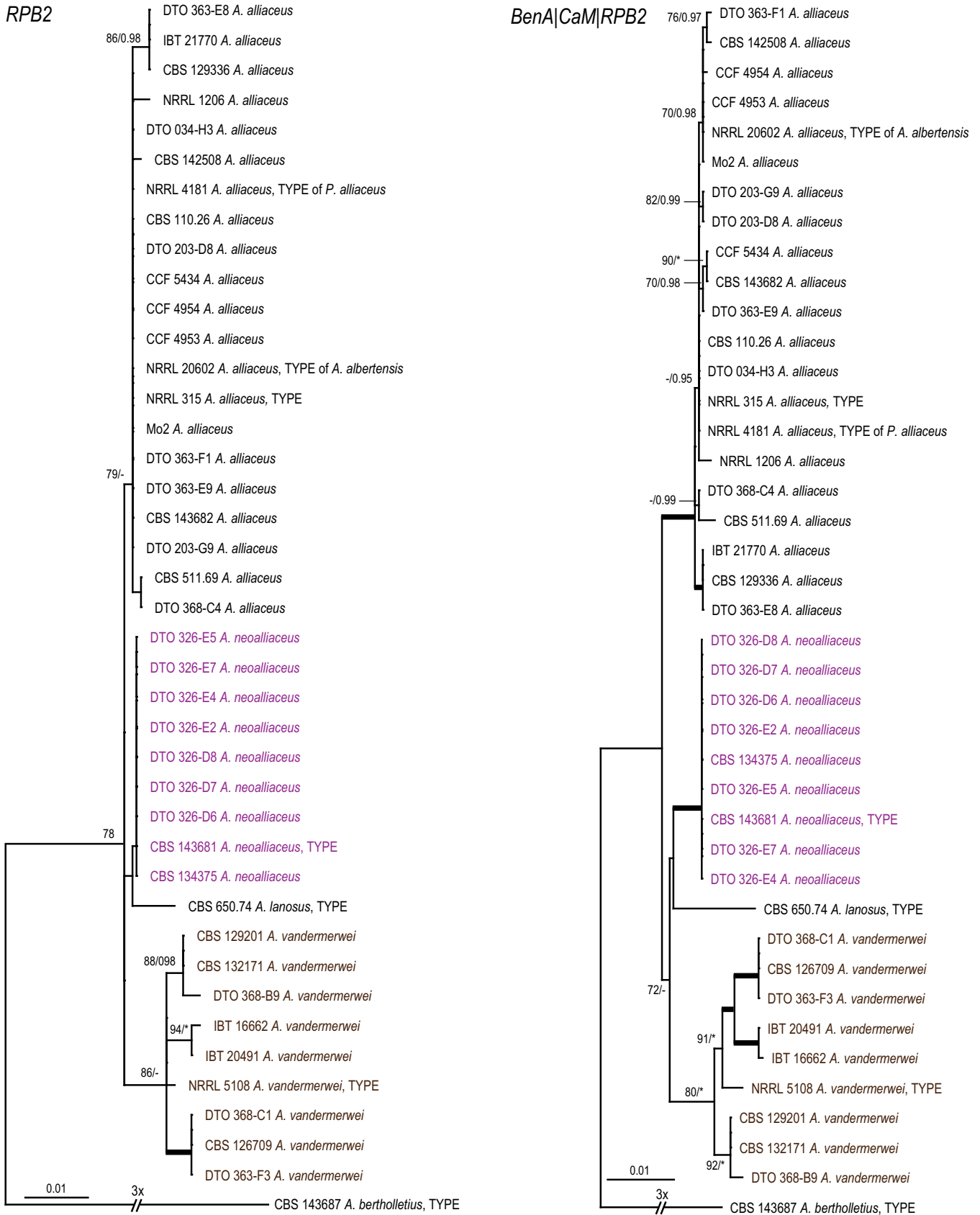


Fig. 7. Phylogeny showing the relationship of species accommodated in the *A. alliaceus*-clade (left, *RPB2*; right, combined data set of *BenA*, *CaM* and *RPB2*). The bar indicates the number of substitutions per site. The BI posterior probabilities values and bootstrap percentages of the ML analysis are presented at the node (BS/pp). Values less than 70 % bootstrap support in the ML analysis and less than 0.95 posterior probability in the Bayesian analysis are indicated with a hyphen. Branches with high support (> 95 % bs; 1.00 pp) are thickened and the BS and pp values indicated with an asterisks.

A. parasiticus, but these two species are morphologically and chemically very similar. Even though *A. sojae* does not produce aflatoxins, one strain was found to produce versicolorin, which is an aflatoxin precursor.

TAXONOMIC IMPLICATIONS

While most *A. flavus* strains produce large sclerotia (> 400 μm), some strains uniformly produce small sclerotia (Raper & Fennell,

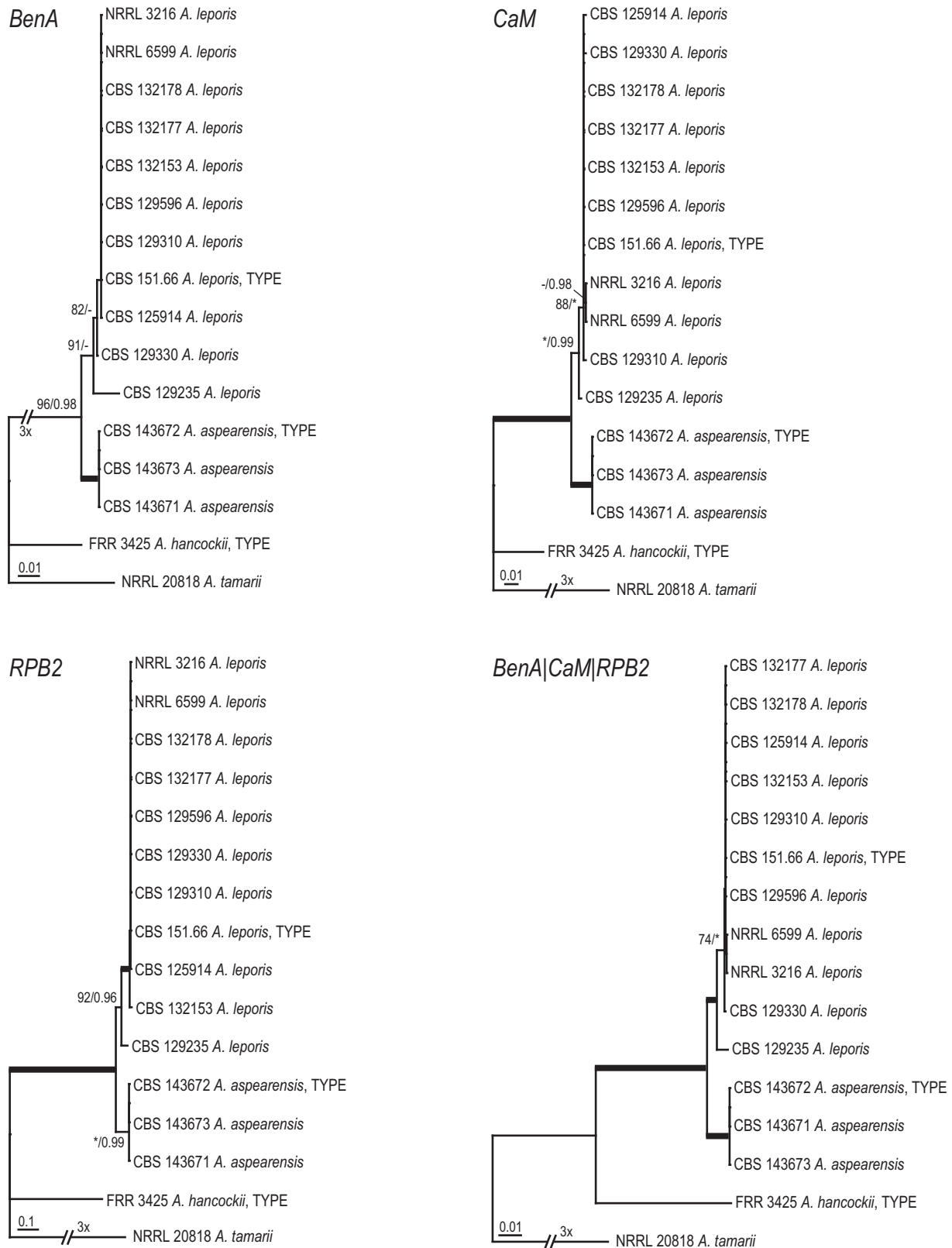


Fig. 8. Phylogeny showing the relationship of species accommodated in the *A. leporis*-clade. The bar indicates the number of substitutions per site. The BI posterior probabilities values and bootstrap percentages of the ML analysis are presented at the node (BS/pp). Values less than 70 % bootstrap support in the ML analysis and less than 0.95 posterior probability in the Bayesian analysis are indicated with a hyphen. Branches with high support (> 95 % bs; 1.00 pp) are thickened and the BS and pp values indicated with an asterisks.

1965, Hesseltnine *et al.* 1970). Hesseltnine *et al.* (1970) listed NRRL 3251 as an example of a strain with small sclerotia that produced aflatoxin B₁ and B₂ only. Saito & Tsuruta (1993) studied strains with small sclerotia isolated from agricultural soil in Thailand, including NRRL 3251. They subdivided their strains into two

groups: group I produced aflatoxins B₁ and B₂ (*A. flavus* S_B) and group II produced aflatoxins B₁, B₂, G₁ and G₂ (*A. flavus* S_{BG}). They described their species with small sclerotia as *A. flavus* var. *parvisclerotigenus*. This species was typified with NFRI 1538 (S_B-type; ex maize field, Chiang Mai, Thailand), but this material is not

Table 3. Mycotoxin and other extrolite production by *Aspergillus* section *Flavi* species.

Species	Extrolites reported in literature	Extrolites detected in this study	Examined strains
<i>Aspergillus aflatoxiformans</i>	–	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aflatrems, aflavarins, aflavinines, aspergillilic acid, aspirochlorin, cyclopiazonic acid, kojic acid, paspaline, paspalinine, versicolorins, metabolite gfn (UV absorptions 240 nm & 397 nm, RI 1148)	DTO 228-G1, DTO 228-G2 ^T , DTO 228-G3, DTO 228-G4, DTO 228-G5, DTO 228-G6, DTO 228-G7, DTO 228-H2, DTO 228-H3, DTO 228-H6, DTO 228-H7, CBS 133923, CBS 133924, CBS 133264, CBS 133265, CBS 133925, DTO 087-A2, CBS 121.62, DTO 010-H7
<i>A. alliaceus</i>	Anominine (Laakso <i>et al.</i> 1994, Nozawa <i>et al.</i> 1994), asperlicin A-E (Liesch <i>et al.</i> 1985, 1988), 7-O-demethyl-3,8'-bisiderin, 7-O-demethyl-6,6'-bisiderin (Nozawa <i>et al.</i> 1994), 14-(N,N-dimethyl-L-leucinoxy) paspalinine, 14-hydroxypaspalinine (Junker <i>et al.</i> 2006), isokotanins A-C (Laakso <i>et al.</i> 1994), kojic acid (Manabe <i>et al.</i> 1984), kotanin (Nozawa <i>et al.</i> 1994), ochratoxin A and B (Ciegler 1972, Bayman <i>et al.</i> 2002), paspaline (Laakso <i>et al.</i> 1994)	Anominine (8/13 strains), antarone A (4/13 strains), asperlicins (5/13 strains), isokotanins (7/13 strains), kojic acid (13/13 strains), met I ¹ (10/13 strains), ochratoxin A & B (13/13 strains), paspaline (10/13 strains), versicolorin (2/13 strains: DTO 363-F1, DTO 363-E8). For more details, see Supplementary Table S1 .	CBS 542.65 ^T , CBS 511.69, DTO 326-D5, DTO 363-E8, DTO 363-E9, DTO 363-F1, DTO 363-F2, DTO 368-C4, IBT 21770, NRRL 315, NRRL 316, NRRL 317, NRRL 20602
<i>A. arachidicola</i>	Aflatoxin B ₁ , B ₂ , G ₁ & G ₂ (Pildain <i>et al.</i> 2008, aspergillilic acid (Pildain <i>et al.</i> 2008), chrysogine (Pildain <i>et al.</i> 2008), ditryptophenaline (Varga <i>et al.</i> 2011), kojic acid (Pildain <i>et al.</i> 2008), parasiticolides (Pildain <i>et al.</i> 2008)	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aspergillilic acid (only in CBS 117613 & CBS 117614), chrysogine (chrysogine precursor in CBS 117614), ditryptophenaline, kojic acid, miyakamides, parasiticolides	CBS 117610, CBS 117611, CBS 117612, CBS 117613, CBS 117614, CBS 117615
<i>A. aspearensis</i>	–	An aflavinine, kojic acid, mevinolins, paspalinines	DTO 203-D9, DTO 203-E1, DTO 203-D4
<i>A. austwickii</i>	–	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aflatrems, aflavarins, cyclopiazonic acid, kojic acid, paspaline, paspalinine, versicolorins, metabolite gfn	DTO 228-F7 ^T , DTO 228-F8, DTO 228-F9, DTO 228-G8
<i>A. avenaceus</i>	Avenaciolide (Brookes <i>et al.</i> 1963), aspirochlorine (Varga <i>et al.</i> 2011), 4-isoavenaciolide (Turner, 1971, Turner & Aldridge, 1983), 3-nitropropionic acid (Brookes <i>et al.</i> 1963)	An altersolanol (only in IMI 238253 = IBT 19369 & IMI 232294 = IBT 19371), aspirochlorin, avenaciolides, pseurotin A (only in IMI 093340 = IBT 19372), 2-(4-hydroxyphenyl)-2-oxo acetaldehyde oxime (only in NRRL 4517 = IBT 18842)	CBS 109.46 ^T , IMI 093340, IMI 232294, IMI 238253, NRRL 4517
<i>A. bertholletius</i>	Cyclopiazonic acid, kojic acid, O-methylsterigmatocystin, parasiticolide, tenuazonic acid, ustilaginoidin C (Taniwaki <i>et al.</i> 2009)	Cyclopiazonic acid, kojic acid, O-methylsterigmatocystin (only the ex-type strain), parasiticolides (only two strains: IBT 31546, IBT 31739), tenuazonic acid, ustilaginoidin C	IBT 29228, IBT 30618, IBT 30617, IBT 30619, IBT 29227
<i>A. caelatus</i>	Aspirochlorin (Pildain <i>et al.</i> 2008), kojic acid (Frivsvad & Samson 2000), tenuazonic acid (Varga <i>et al.</i> 2011)	An altersolanol, aspirochlorin, kojic acid, tenuazonic acid, in addition to an indole alkaloid ("alkca") (RI 928) that has only been found in <i>A. caelatus</i> , <i>A. pseudocaelatus</i> and <i>A. pseudotamarii</i>	CBS 763.97 ^T , CBS 764.97, NRRL 25566, NRRL 25567, NRRL 25568, NRRL 25569
<i>A. cerealis</i>	–	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aflatrems, aflavarins, aflavazole, cyclopiazonic acid, kojic acid, paspaline, paspalinine, versicolorins	CBS 143674 ^T , DTO 228-E6, DTO 228-E8, DTO 228-E9, DTO 228-F1, DTO 228-F2, DTO 228-F3, DTO 228-F4, DTO 228-F5, DTO 228-F6
<i>A. coremiiformis</i>	Indole alkaloids (Varga <i>et al.</i> 2011)	No known extrolites found	CBS 553.77 ^T
<i>A. flavus</i>	Aflatoxin B ₁ and B ₂ (Nesbitt <i>et al.</i> 1962, Codner <i>et al.</i> 1963, Varga <i>et al.</i> 2009, Rank <i>et al.</i> 2012 and many others), aflatrem & β-aflatrem (Gallagher & Wilson 1978, TePaske <i>et al.</i> 1992, Rank <i>et al.</i> 2012, Sun <i>et al.</i> 2014), aflavarin A-C (TePaske <i>et al.</i> 1992), aflavazole (TePaske <i>et al.</i> 1990), asparosones (Cary <i>et al.</i> 2014, Malysheva <i>et al.</i> 2014, Chang <i>et al.</i> 2017), aspergillilic acid (White & Hill 1943, Assante <i>et al.</i> 1981), aspergillomarasmine A & B (Robert <i>et al.</i> 1962, Haenni <i>et al.</i> 1965), aspirochlorins (Sakata <i>et al.</i> 1982, 1987, Klausmeyer	Aflatoxin B ₁ and B ₂ , aflatrems (only in sclerotium producers), aflavarins (only in sclerotium producers), aflavinines (only in sclerotium producers), aspergillilic acid, aspirochlorin, citreoisocoumarin, cyclopiazonic acids, ditryptophenaline, flavimin, kojic acid, miyakamides, paspaline & paspalinine (only in sclerotium producers), ustilaginoidin C (ATCC 26850, CBS 116.48, CBS 113.49, CBS 120.51, CBS 110.55, CBS 131.62, CBS 117.62, CBS 118.62, CBS 119.62, CBS 118.62, CBS 119.62, CBS 242.65, CBS 501.65, CBS 569.65 ^T = CBS 100927 = NRRL 1957, CBS 625.66, CBS 542.69, CBS 289.95, CBS 816.96, CBS 970.97, CBS 117625, CBS 117632, CBS 127422, NRRL 453, NRRL 3251, NRRL 3357, NRRL 5565, NRRL 6551, NRRL 6556, NRRL 29254	

Table 3. (Continued).

Species	Extrolites reported in literature	Extrolites detected in this study	Examined strains
	<p><i>et al.</i> 2005, Rank <i>et al.</i> 2012), bright-greenish-yellow-fluorescence (6,6'-bis[5-hydroxy-2-(hydroxymethyl)-4H-pyran-4-one], "dikojic acid") (Zeringue <i>et al.</i> 1999), cAATrp (Uka <i>et al.</i> 2017), cyclopiamide A-G & J (Ma <i>et al.</i> 2015, Uka <i>et al.</i> 2017), α-cyclopiazonic acid, β-cyclopiazonic acid, iso-α-cyclopiazonic acid, α-cyclopiazonic acid imine (Luk <i>et al.</i> 1977, Rank <i>et al.</i> 2012, Sun <i>et al.</i> 2014, Uka <i>et al.</i> 2017), (S)-(-)-6,8-di-O-methylcitreisocoumarin (Sun <i>et al.</i> 2014), ditryptophenaline (Springer <i>et al.</i> 1977, Rank <i>et al.</i> 2012, Sun <i>et al.</i> 2014), gliotoxin (Lewis <i>et al.</i> 2005, Kupfahl <i>et al.</i> 2008), 3-hydroxy-speradine A (Uka <i>et al.</i> 2017), kojic acid (Birkinshaw <i>et al.</i> 1931, Manabe <i>et al.</i> 1984, Rank <i>et al.</i> 2012, Sun <i>et al.</i> 2014), leporins (Sun <i>et al.</i> 2014, Arroya-Manzanares <i>et al.</i> 2015), miyakamides (Shiomi <i>et al.</i> 2002), 3-nitropropionic acid (Bush <i>et al.</i> 1951, Becker and Schmidt 1964, Doxtater and Alexander 1966, Konoshita <i>et al.</i> 1968, Hatcher & Schmidt 1971, Iwasaki & Kozikowskii 1973), 2-oxo-cyclopiazonic acid (Uka <i>et al.</i> 2017), parasiticolide A (Shiomi <i>et al.</i> 2002), paspaline, β-PC-M6, 13-desoxypaxilline, 4b-deoxy-β-aflatrem, 9-isopentenylpaxilline D, paspalicine & paspalinine (Cole <i>et al.</i> 1981, Rank <i>et al.</i> 2012, Sun <i>et al.</i> 2014), penicillin G (Bush & Goth 1943, Bush <i>et al.</i> 1945, Adler & Wintersteiner 1948, Guida 1948, Blinc & Johanides 1956), speradine A-D, F & H (Ma <i>et al.</i> 2015, Uka <i>et al.</i> 2017), ustiloxin (Umemura <i>et al.</i> 2013a,b, 2014, Ye <i>et al.</i> 2016). Reported to be produced by <i>Aspergillus flavus</i> CBS 131.61: Aflatoxin B₁, G₁, aspergillic acid, aspyrone, betaine, chrysogine, diacetyl parasiticolide A, flufuran, gregatin B, hydroxysydonic acid, nicotinic acid, phomaligin A, spinulosin and terrein (Saldan <i>et al.</i> 2018)</p>	<p>CBS 816.96, CBS 970.97, CBS 117625, CBS 117632, CBS 127422, NRRL 453, NRRL 3251, NRRL 3357, NRRL 5565, NRRL 6551, NRRL 6556, NRRL 29254). Some columnar isolates of <i>A. flavus</i> produce aflatoxin B₂ (IBT 12654, NRRL 5821). Special Korean strains: DTO 359-E4: Aflatoxin B₁, B₂, G₁, G₂, kojic acid, ustilaginoidin C; DTO 359-D7, DTO 359-D8, DTO 359-D9, DTO 359-E1, DTO 359-E2, DTO 359-E8: aflatoxin B₁, B₂, G₁, G₂, cyclopiazonic acid, flavimin², kojic acid, ustilaginoidin C</p>	
<i>A. hancockii</i>	Dehydroterrestric acid, eupenifeldin, fumitremorgin A, hancockiamide A-F, 7-hydroxytrichothecolone, kojic acid, onychocin A & B, speradine F (Pitt <i>et al.</i> 2017)	An aflavarin, dehydroterrestric acid, fumitremorgin A, hancockiamide A, 7-hydroxytrichothecolone, onychocin A & B, a speradine	CBS 142002, CBS 142001
<i>A. lanosus</i>	Griseofulvin (Frisvad & Samson, 2000), kojic acid (Frisvad & Samson, 2000), ochratoxin A & B (Baker <i>et al.</i> 2003, Palumbo <i>et al.</i> 2007)	An altersolanol, an aspericin, griseofulvin, kojic acid, met I1. For more details, see Supplementary Table S1.	CBS 650.74 ^T
<i>A. leporis</i>	Antibiotic Y (Frisvad & Samson, 2000), kojic acid (Frisvad & Samson, 2000), leporins (TePaske <i>et al.</i> 1991), leporazines (Reategui <i>et al.</i> 2013), pseurotin A (Frisvad & Samson, 2000)	Antibiotic Y, clavatols, 7-hydroxytrichothecolone?, kojic acid, leporine A, leporazines, paspalines, pseurotin A	CBS 151.66, CBS 349.81, ATCC 76617, IBT 16309, IBT 16585
<i>A. luteovirescens</i>	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ (Pildain <i>et al.</i> 2008), aspergillic acid (Varga <i>et al.</i> 2011), kojic acid (Morton <i>et al.</i> 1945, Varga <i>et al.</i> 2011)	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , an altersolanol (only in NRRL 29235 & NRRL 29253), aspergillic acid, chrysogine (only in NRRL 29253), kojic acid, sporogen AO1, tenuazonic acid (in IBT 31534, NRRL 29235, NRRL 29237). CBS 620.95 ^T only produced kojic acid.	CBS 620.92 ^T , CBS 117187, DTO 073-C2, DTO 073-C3, DTO 073-C5, IBT 31534, NRRL 25593, NRRL 29237, NRRL 29253
<i>A. minisclerotigenes</i>	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aflavarins, aflatrems, aflavinines, aspergillic acid, cyclopiazonic acid, kojic acid, paspalinine (Pildain <i>et al.</i> 2008)	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aflatrems, aflavarins, aflavazole (in DTO 228-H1 & IBT 27213), aflavinines, aspergillic acid, cyclopiazonic acid, kojic acid, parasiticolides, paspalinine	CBS 117635 ^T , CBS 117620, CBS 117634, CBS 117637, CBS 117639, DTO 228-G9, DTO 228-H1, DTO 228-H5, IBT 27213, NRRL 6444

(continued on next page)

Table 3. (Continued).

Species	Extrolites reported in literature	Extrolites detected in this study	Examined strains
<i>A. mottae</i>	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ (Soares <i>et al.</i> 2012)	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , an aflavinin, aspergillilic acid, cyclopiazonic acid, kojic acid, 3-O-methylsterigmatocystin, parasiticol, paspalinine, versicolorins	CBS 130016 ^T = DTO 223-C8 = IBT 32309 = MUM 10.231
<i>A. neoalliaceus</i>	–	Anominine (6/9 strains), brefeldin A (5/9 strains), kojic acid (9/9 strains), ochratoxin A and B (9/9 strains), paspaline (7/9 strains). For more details, see Supplementary Table S1 .	CBS 143681 ^T , CBS 134375, DTO 326-D7, DTO 326-D8, DTO 326-D1, DTO 326-E4, DTO 326-E2, DTO 326-E7, DTO 326-D6, DTO 326-E5
<i>A. nomius</i>	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ (Kurtzman <i>et al.</i> 1987), anominine (Gloer <i>et al.</i> 1989, Bradshaw <i>et al.</i> 2010), aspergillilic acid (Frisvad & Samson 2000), aspernomine (Staub <i>et al.</i> 1992), kojic acid (Frisvad & Samson 2000), paspaline (Staub <i>et al.</i> 1992), pseurotin (Frisvad & Samson 2000), tenuazonic acid (Frisvad & Samson 2000)	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , anominine, aspergillilic acid, aspernomine, kojic acid, a miyakamide, 3-O-methylsterigmatocystin, parasiticol, paspaline, paspalinine, pseurotin A, tenuazonic acid, versicolorins and other aflatoxin precursors	CBS 260.88 ^T , CBS 399.93, CBS 117629, IMI 190557, NRRL 13138, NRRL 3161
<i>A. novoparasiticus</i>	Aflatoxins B ₁ , B ₂ , G ₁ , G ₂ (Gonçalves <i>et al.</i> 2012a,b)	Aflatoxins B ₁ , B ₂ , G ₁ , G ₂ , (aspirochlorin, ditryptophenaline, kojic acid, miyakamides, parasiticolide, and a tetracyclic compound	CBS 126849, CBS 126830
<i>A. oryzae</i>	Aflavinines (Rank <i>et al.</i> 2012), asperfuran (Pfefferle <i>et al.</i> 1990), aspergillomarasmins (Robert <i>et al.</i> 1962, Barbier <i>et al.</i> 1963), asperopterin A & B (Matsuura <i>et al.</i> 1972), aspirochlorins (Sakata <i>et al.</i> 1983, Champhamjon <i>et al.</i> 2014), cyclopiazonic acid and speradines (Orth 1977, Tokuoka <i>et al.</i> 2015), 14-deacetyl parasiticolide A & B and dideacetyl parasiticolide A, confertifolin, dideacetyl astellolide A & B (Rank <i>et al.</i> 2012, Shinohara <i>et al.</i> 2016a,b), 13-desoxyxaxilline (Rank <i>et al.</i> 2012), ditryptoleucine (Rank <i>et al.</i> 2012), kojic acid (Birkinshaw <i>et al.</i> 1931), kojistatin (Sato <i>et al.</i> 1996, Yamada <i>et al.</i> 1998), maltoryzin (Iizuka and Iida, 1962), 3-nitropropionic acid (Nakamura & Shimoda 1954, Yokotsuka <i>et al.</i> 1969, Orth 1977), oryzamides (Rank <i>et al.</i> 2012), paspaline and β-PC-M6 (Rank <i>et al.</i> 2012), penicillin (Saito 1946–47), speradine B-F (Hu <i>et al.</i> 2014a,b), sporogen AO1 (Tamogami <i>et al.</i> 1996), TMC-2A, B & C (Nonoka <i>et al.</i> 1997, Asai <i>et al.</i> 1998)	Asperfuran (CBS 102.22, CBS 134.52, IBT 3629), aspirochlorin (CBS 102.07 ^T , CBS 134.52, CBS 570.65, CBS 819.72, RIB 40), citreoisocoumarin (CBS 102.22, CBS 570.65, CBS 205.89, NRRL 6270), a cyclopiamide (IBT 3593, IBT 3629, NRRL 695), cyclopiazonic acid (CBS 102.07 ^T = CBS 110.47 ^T , CBS 570.65, CBS 205.89, IBT 3593, IBT 3629, NRRL 484), ditryptoleucine (RIB 40), kojic acid (CBS 102.07, CBS 134.52, CBS 570.65, CBS 205.89, IBT 3595, IBT 3629, NRRL 695), miyakamides / oryzamides (CBS 102.07 ^T = CBS 110.47 ^T , CBS 570.65, RIB 40), parasiticolides / astellolides (CBS 570.65, CBS 819.72, CBS 205.89, NRRL 695, RIB 40), paspalines (RIB 40), sporogen AO1 (NRRL 6270). According to verified strains of <i>A. oryzae</i> , isolates of the species can also produce penicillins and 3-nitropropionic acid	CBS 102.07 ^T (= CBS 110.47 ^T = CBS 100925 ^T), CBS 102.22, CBS 134.52, CBS 570.65, CBS 205.89, IBT 3593, IBT 3629, NRRL 484, NRRL 695, NRRL 6270, RIB 40
<i>A. parasiticus</i>	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ (Codner <i>et al.</i> 1963, Schroeder 1966, Basaran & Demirbas 2010), asparasone A (Sobolev <i>et al.</i> 1997), aspergillilic acid (Assante <i>et al.</i> 1981), aspersitin (Hamasaki <i>et al.</i> 1975), dibutylphthalate (an artefact?) (Basaran & Demirbas 2010), fumagillol (Basaran & Demirbas 2010), italicic acid (Basaran & Demirbas 2010), kojic acid (Birkinshaw <i>et al.</i> 1931, Basaran & Demirbas 2010), parasperone and ustilaginoindin C (Brown <i>et al.</i> 2003), parasitenone (Son <i>et al.</i> 2002), parasiticol (Stubblefield <i>et al.</i> 1970), parasiticolide A (= astellolide A) (Büchi <i>et al.</i> 1983, Rank <i>et al.</i> 2012), penicillin G (Arnstein & Cook 1947), pyrogallol (Basaran & Demirbas 2010), sequioatones (Stierle <i>et al.</i> 1999, 2001), sequioiamonascins (Stierle <i>et al.</i> 2003), sorbicillin (Basaran & Demirbas 2010)	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aspergillilic acid, kojic acid, parasperone, parasiticol, parasiticolide A and B	CBS 100926 ^T , CBS 822.72, CBS 580.65, CBS 260.67, CBS 921.70, NRRL 6433, NRRL 13005
<i>A. pipericola</i>	–	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aflatrem, aflavinins, aflavarins, cyclopiazonic acid, paspaline, paspalinine	CBS 143680 ^T

Table 3. (Continued).

Species	Extrolites reported in literature	Extrolites detected in this study	Examined strains
<i>A. pseudocaelatus</i>	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , cyclopiazonic acid, kojic acid (Varga <i>et al.</i> 2011)	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aspirochlorin, cyclopiazonic acid, ditryptophenaline, kojic acid, tenuazonic acid, "alkca"	CBS 117616, IBT 29230, DTO 350-B8
<i>A. pseudonomius</i>	Aflatoxin B ₁ , chrysogine, kojic acid (Varga <i>et al.</i> 2011)	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ (ex type isolate only produce type B aflatoxins), aspergilliacid, chrysogine, kojic acid, a miyakamide, tenuazonic acid	CBS 119388 ^T , DTO 079-I4, IBT 12657, IBT 32759, NRRL 5919 (= IBT 23354), NRRL 6343 = IBT 4496 = IBT 4985
<i>A. pseudotamarii</i>	Aflatoxin B ₁ , B ₂ , cyclopiazonic acid, kojic acid (Ito <i>et al.</i> 2001, Varga <i>et al.</i> 2011)	Aflatoxin B ₁ , B ₂ , aflavinines, an altersolanol (in CBS 766.97 CBS 117625 & CBS 117628), aspirochlorin (in CBS 766.97 & IBT 30530), cyclopiazonic acid, kojic acid, paspaline & paspalinine (in CBS 117628), tenuazonic acid, "alkca"	CBS 766.97, CBS 117625, CBS 117628; IBT 30530, IBT 30531
<i>A. sergii</i>	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ (Soares <i>et al.</i> 2012)	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aflatrem, aflavazole, an aflavarin, aflavinins, asperfuran, aspergilliacid, cyclopiazonic acid, kojic acid, paspalinine, versicolorins	CBS 130017 ^T , DTO 223-C9
<i>A. sojae</i>	Asperfuran (Varga <i>et al.</i> 2011), aspergilliacid (Pildain <i>et al.</i> 2008), aspirochlorin, chrysogine (Varga <i>et al.</i> 2011), kojic acid (Tanaka <i>et al.</i> 2002)	Asperfuran, aspergilliacid, aspirochlorin, chrysogine, kojic acid, miyakamides, versicolorins (only CBS 100936)	CBS 100928 ^T , CBS 133.52, CBS 126.59, CBS 100929, CBS 100930, CBS 100932, CBS 100933, CBS 100934, CBS 100935, CBS 100936, NRRL 5594
<i>A. subflavus</i>	–	Aflavinines, aspirochlorin, kojic acid, a parasiticolide	CBS 143683 ^T
<i>A. tamarii</i>	Aspirochlorin (Berg <i>et al.</i> 1976), (-)-canadensolide (Berg <i>et al.</i> 1976), cyclopiazonic acid (Dorner 1983), dihydrocanadensolide, fumaric acid, fumaryl-D,L-alanine (Birch <i>et al.</i> 1968), fumigaclavine A (Jahardhanan <i>et al.</i> 1984), kojic acid (Birkinshaw <i>et al.</i> 1931, Manabe <i>et al.</i> 1984), 3-nitropropionic acid (Birch <i>et al.</i> 1968), speradine A (Tsuda <i>et al.</i> 2003), succinic acid (Birch <i>et al.</i> 1968)	Aspirochlorin (8/15 strains), citreoisocoumarin (2/15 strains), cyclopiazonic acid (9/15 strains), kojic acid (13/15 strains), tenuazonic acid (4/15 strains)	CBS 103.14 ^T , CBS 104.14, CBS 129.49, CBS 109.63, CBS 167.63, CBS 484.65, CBS 575.65, CBS 579.65, CBS 591.68, CBS 117626, CBS 126844, IBT 29248, IBT 29229, NRRL 4860, NRRL 8101
<i>A. togoensis</i>	Aflatoxin B ₁ (Rank <i>et al.</i> 2011), sterigmatocystin (Wicklow <i>et al.</i> 1989)	Aflatoxin B ₁ , a bisiderin, paspaline, paspalinine, sterigmatocystin (CBS 205.75 ^T), paxilline (CBS 272.89)	CBS 205.75, CBS 272.89
<i>A. transmontanensis</i>	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ (Soares <i>et al.</i> 2012)	Aflatoxin B ₁ , B ₂ , G ₁ , G ₂ , aspirochlorin, kojic acid, a miyakamide	CBS 130015 ^T
<i>A. vandermerwei</i>	–	An altersolanol, anominine, an asperlicin, aspirochlorin, bostrycin?, brefeldin A, kojic acid, isokotanins, ochratoxin A, ochratoxin B. Griseofulvin produced by CBS 126708. For more details, see Supplementary Table S1.	DTO 069-D2 ^T , IBT 16662, IBT 20491, CBS 612.78, CBS 129201, DTO 363-F3, DTO 368-B9, CBS 126709, DTO 368-C1, CBS 132171

available for further study. Isolation of *Aspergillus* section *Flavi* strains from soil of maize fields in Chiang Mai (Thailand) revealed the presence of strains with small sclerotia (DTO 281-H8) and these strains are identified here as *A. flavus*. Furthermore, NRRL 3251 belongs, like NFRI 1538^T, to group I (Saito & Tsuruta 1993) and also NRRL 3251 is an *A. flavus*. We therefore treat *Aspergillus flavus* var. *parvisclerotigenus* as a synonym of *A. flavus* that produces S-type sclerotia and B-type aflatoxins (S_B). When Frisvad *et al.* (2005) raised *A. flavus* var. *parvisclerotigenus* to species status as *A. parvisclerotigenus*, they based it on a neotype from a peanut in Nigeria that produces aflatoxins B₁, B₂, G₁ and G₂ (CBS 121.62 = IMI 093070 = NRRL A-11612). The production of small sclerotia in combination with B and G type aflatoxins is linked Saito & Tsuruta's (1993) group II and is therefore in conflict with the protologue of *A. flavus* var. *parvisclerotigenus* (Saito & Tsuruta 1993), making the neotypification of *A. parvisclerotigenus* by Frisvad *et al.* (2005) incorrect [Art. 9.18 (McNeill *et al.* 2012)]. This conclusion is also backed up by ecological data because

A. parvisclerotigenus sensu Frisvad was not detected in Thai agricultural soils. Actually, *A. parvisclerotigenus sensu* Frisvad *et al.* (2005) is mainly found in West Africa: Benin, Burkina Faso, Nigeria, Senegal and Sierra Leone (Probst *et al.* 2014, Perrone *et al.* 2014a,b), but also in Madagascar and from Mexican sesame (this study). Ehrlich *et al.* (2007) also examined many soil samples in Thailand and found a high number of *Aspergillus nomius*, a species also producing B and G type aflatoxins, suggesting that group II of Saito & Tsuruta (1993) could be an *A. nomius*.

Because of the doubtful status of *A. parvisclerotigenus sensu* Frisvad *et al.* (2005), we introduce *A. aflatoxiformans* here for isolates that produce small sclerotia and B and G type aflatoxins, and treat *A. parvisclerotigenus* as a synonym of *A. flavus*. Furthermore, three other new species related to *A. flavus* are introduced (*A. austwickii*, *A. cerealis*, *A. subflavus*), two new species related to *A. alliaceus* (ochratoxin producers; *A. neoalliaceus*, *A. vandermerwei*) and one related to *A. leporis* (*A. aspearensis*).

Table 4. Mycotoxin producing species in *Aspergillus* section *Flavi*.

Species	Aflatoxin B ₁ ¹	Aflatoxin G ₁ ¹	Aflatre ¹	Cyclopiazonic acid	3-nitropropionic acid ²	Tenuazonic acid	Ochratoxin A
<i>Aspergillus aflatoxiformans</i>	+	+	+	+	-	-	-
<i>A. alliaceus</i>	-	-	-	-	-	-	+
<i>A. arachidicola</i>	+	+	-	-	-	-	-
<i>A. aspearensis</i>	-	-	-	-	-	-	-
<i>A. austwickii</i>	+	+	+	+	-	-	-
<i>A. avenaceus</i>	-	-	-	-	+	-	-
<i>A. bertholletius</i>	- ³	-	-	+	-	+	-
<i>A. caelatus</i>	-	-	-	-	-	+	-
<i>A. cerealis</i>	+	+	+	+	-	-	-
<i>A. coremiiformis</i>	-	-	-	-	-	-	-
<i>A. flavus</i>	+	(+) ⁴	+	+	+	-	-
<i>A. hancockii</i> ⁵	-	-	-	-	-	-	-
<i>A. lanosus</i>	-	-	-	-	-	-	-
<i>A. leporis</i>	-	-	-	-	-	-	-
<i>A. luteovirescens</i>	+	+	-	-	-	+	-
<i>A. minisclerotigenes</i>	+	+	+	+	-	-	-
<i>A. mottae</i>	+	+	-	+	-	-	-
<i>A. neoalliaceus</i>	-	-	-	-	-	-	+
<i>A. nomius</i>	+	+	-	-	-	+	-
<i>A. novoparasiticus</i>	+ ⁶	+ ⁶	-	-	-	-	-
<i>A. oryzae</i>	-	-	-	+	+	-	-
<i>A. parasiticus</i>	+	+	-	-	-	-	-
<i>A. pipericola</i>	+	+	+	+	-	-	-
<i>A. pseudocaelatus</i>	+	+	-	+	-	+	-
<i>A. pseudonomius</i>	+	+	-	-	-	+	-
<i>A. pseudotamarii</i>	+	-	-	+	-	+	-
<i>A. sergii</i>	+	+	+	+	-	-	-
<i>A. sojae</i>	-	-	-	-	-	-	-
<i>A. subflavus</i>	-	-	-	-	-	-	-
<i>A. tamarii</i>	-	-	-	+	+	+	-
<i>A. togoensis</i>	+	-	-	-	-	-	-
<i>A. transmontanensis</i>	+	+	-	-	-	-	-
<i>A. vandermerwei</i>	-	-	-	-	-	-	+

¹ 3-Nitropropionic acid, reported in Bush *et al.* 1951, Brookes *et al.* 1953, Becker & Schmidt 1964, Doxtater & Alexander 1966, Birch *et al.* 1968, Kinosita *et al.* 1968, Yokotsuka *et al.* 1969, Hatcher & Schmidt 1971, Turner 1971, Iwasaki & Kozikowski 1973, Orth 1977, Turner & Aldridge 1983.

² Only sclerotium producing strains can produce the mycotoxin aflatre.

³ The ex-type strain can produce the aflatoxin precursor 3-O-methylsterigmatocystin.

⁴ Only a few strains of *A. flavus* produce aflatoxins of the G type (this paper).

⁵ *A. hancockii* produces the mycotoxins fumitremorgin A, 7-hydroxytrichothecolone and speradine A, a compound related to cyclopiazonic acid and in the cyclopiazonic acid biosynthetic family.

⁶ Aflatoxin B₁, B₂, G₁, and G₂ were reported by Gonçalves *et al.* 2012, but could not be verified in the ex-type culture used in this study; however, fresh strains of *A. novoparasiticus* produce the four aflatoxins.

Aspergillus aflatoxiformans Frisvad, Ezekiel, Samson & Houbraken, **sp. nov.** MycoBank MB823770. Fig. 15.

Eymology: Referring to the copious production of aflatoxins.

Diagnosis: *Aspergillus aflatoxiformans* is closely related to *A. austwickii* and *A. cerealis*, but *A. austwickii* grows slowly on YES, and *Aspergillus cerealis* grows slowly on DG18.

Typus: Nigeria, Niger State, Minna, agricultural soil, 2011, collected by C.N. Ezekiel (holotype CBS H-23361, culture ex-type: CBS 143679 = DTO 228-G2 = IBT 32085).

ITS barcode: MG662388. (Alternative markers: *BenA* = MG517706; *CaM* = MG518076; *RPB2* = MG517897).

Colony diam, 7 d (mm): CYA 50–51; CYA 37 °C 39–40; CYA 42 °C 9–19; MEA 47–50; MEA 37 °C 30–32; MEA 40 °C 22–25; OA 60–70; YES >75; CREA 42–46; CYAS 44–50; DG18 35–38.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation moderately dense; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse pale luteous (11). DG18 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation moderately dense; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse pale luteous (11). OA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense; conidia *en masse* yellow-green (71), sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). CREA 25 °C, 7 d: Growth poor; acid production absent. AFPA: orange reverse.

Micromorphology: Sclerotia 100–250 µm, globose to ellipsoidal, dark brown to black. Conidial heads consistently yellow-green; radiate or loosely columnar, uniseriate. Conidiophores with rough stipes, hyaline, 250–500 × 8–13 µm. Vesicles subglobose to subclavate, 23–38 µm wide, fertile over three fourth of the surface; phialides hyaline, flask-shaped, 7.5–12.5 × 3–5.5 µm. Conidia smooth, subglobose, 3.5–5 × 3–4.5 µm.

Notes: *Aspergillus parvisclerotigenus* was neotypified with CBS 121.62 (ex *Arachis hypogea*, Nigeria; Frisvad *et al.* 2005). This neotypification was incorrect because *A. flavus* var. *parvisclerotigenus* originates from Thailand and produces aflatoxin B while *A. parvisclerotigenus sensu* Frisvad *et al.* (2005) was neotypified with a strain from Nigeria that produces aflatoxin B and G. *Aspergillus flavus* var. *parvisclerotigenus* and *A. parvisclerotigenus* are placed in synonymy with *A. flavus* (see also below; List of accepted species and their synonyms in *Aspergillus* section *Flavi*) and using the proposed taxonomy, CBS 121.62 is identified as *A. aflatoxiformans*.

Aspergillus aspearensis Houbraken, Frisvad, Arzanlou & Samson, **sp. nov.** MycoBank MB823771. Fig. 16.

Eymology: Named after Aspear Island (Urmia Lake, Iran), from where the type was isolated.

Diagnosis: Yellow-green, biseriate conidial heads, rough conidiophores, smooth, globose conidia measuring 2.5–3.5 µm.

Typus: Iran, Aspear Island, Urmia Lake, soil, 2012, collected by U. Ghosta & R. Samad (holotype CBS H-23358, culture ex-type: CBS 143672 = DTO 203-D9 = IBT 32590 = IBT 34544).

ITS barcode: MG662398. (Alternative markers: *BenA* = MG517669; *CaM* = MG518040; *RPB2* = MG517857). **Colony diam, 7 d (mm):** CYA 28–70; CYA 37 °C 15–25; CYA 42 °C no growth; MEA 50–65; MEA 37 °C 17–25; OA 50–65; YES >75; CREA 30–40; CYAS 28–65; DG18 45–75.

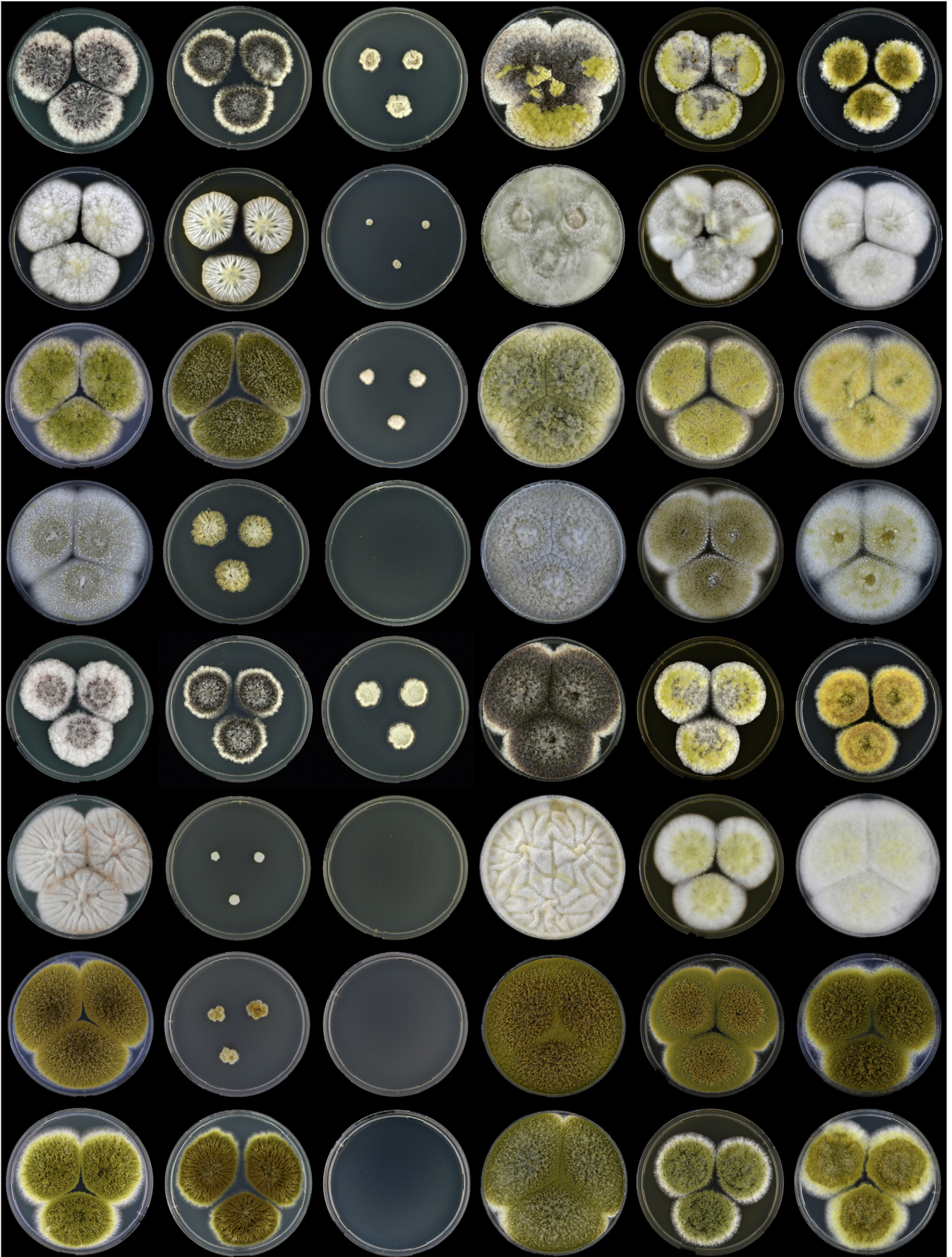


Fig. 9. Left to right: 7 d old colonies on CYA, CYA 37 °C, CYA 42 °C, YES, MEA, DG18; top to bottom: *A. aflatoxiformans* CBS 143679, *A. alliaceus* CBS 542.65, *A. arachidicola* CBS 117610, *A. aspearensis* CBS 143672, *A. austwickii* CBS 143677, *A. avenaceus* CBS 109.46, *A. bertholletius* CBS 143687, *A. caelatus* CBS 763.97.

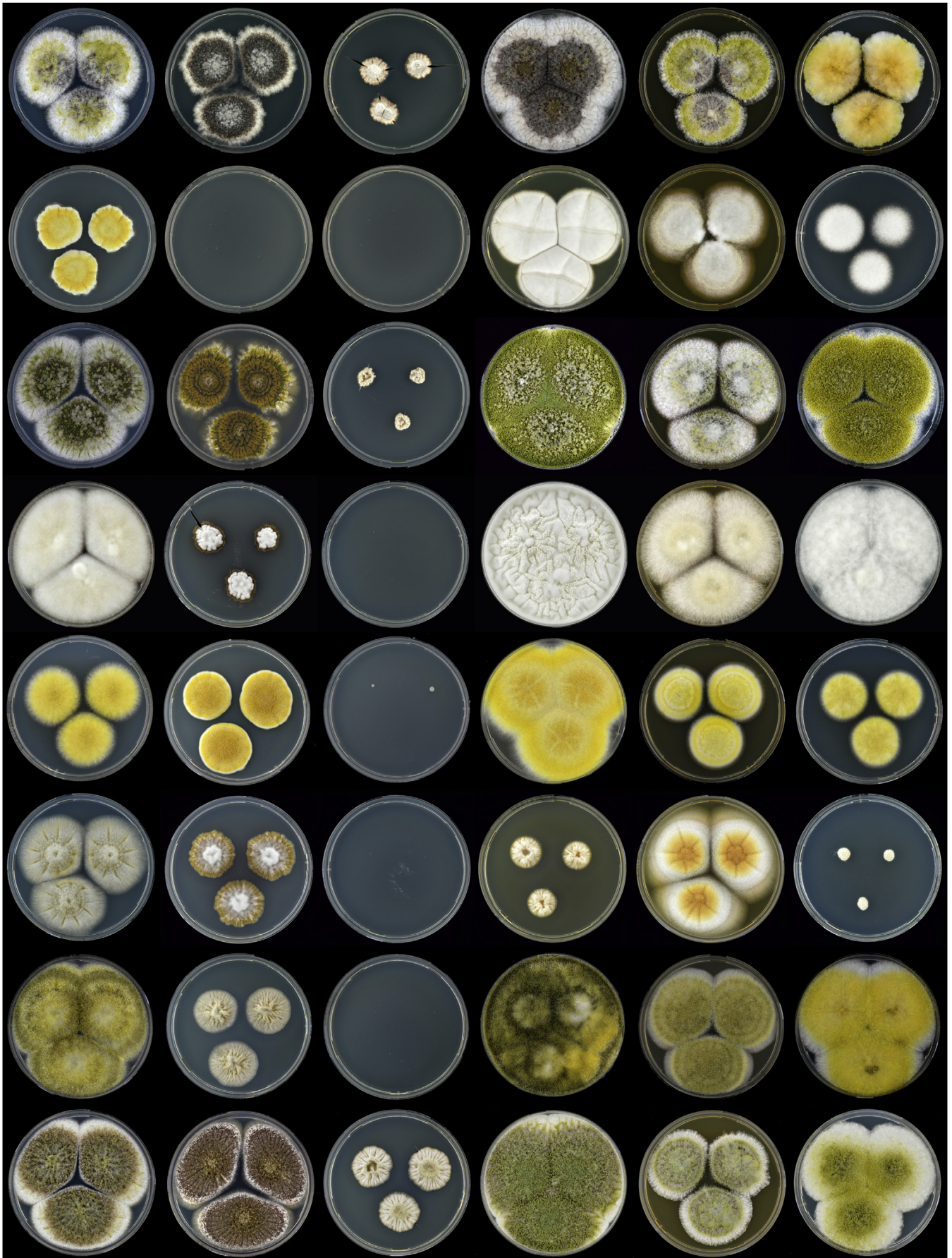


Fig. 10. Left to right: 7 d old colonies on CYA, CYA 37 °C, CYA 42 °C, YES, MEA, DG18; top to bottom: *A. cerealis* CBS 143674, *A. coremiiformis* CBS 553.77, *A. flavus* DTO 258-C9, *A. hancockii* CBS 142002, *A. lanosus* CBS 650.74, *A. leporis* CBS 129235, *A. luteovirescens* DTO 073-C2 (=NRRL 29235), *A. minisclerotigenes* DTO 045-F5 (=FRR 4937).

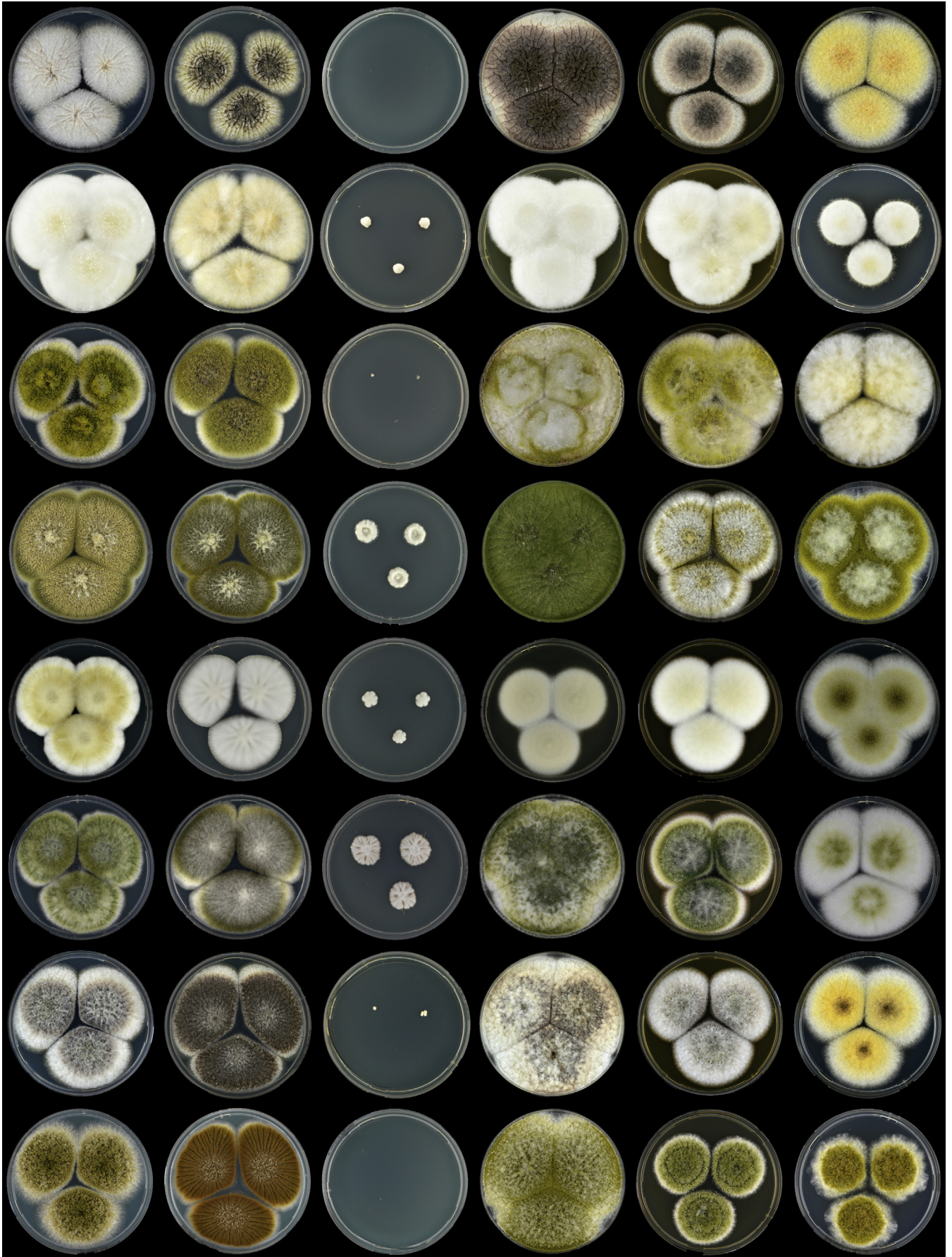


Fig. 11. Left to right: 7 d old colonies on CYA, CYA 37 °C, CYA 42 °C, YES, MEA, DG18; top to bottom: *A. mottae* CBS 130016, *A. neoalliaceus* DTO 326-E7 (=CCF 5413), *A. nomius* DTO 247-G8, *A. novoparasiticus* CBS 126849, *A. oryzae* CBS 100925, *A. parasiticus* CBS 100926, *A. pipericola* CBS 143680, *A. pseudocaelatus* CBS 117616.

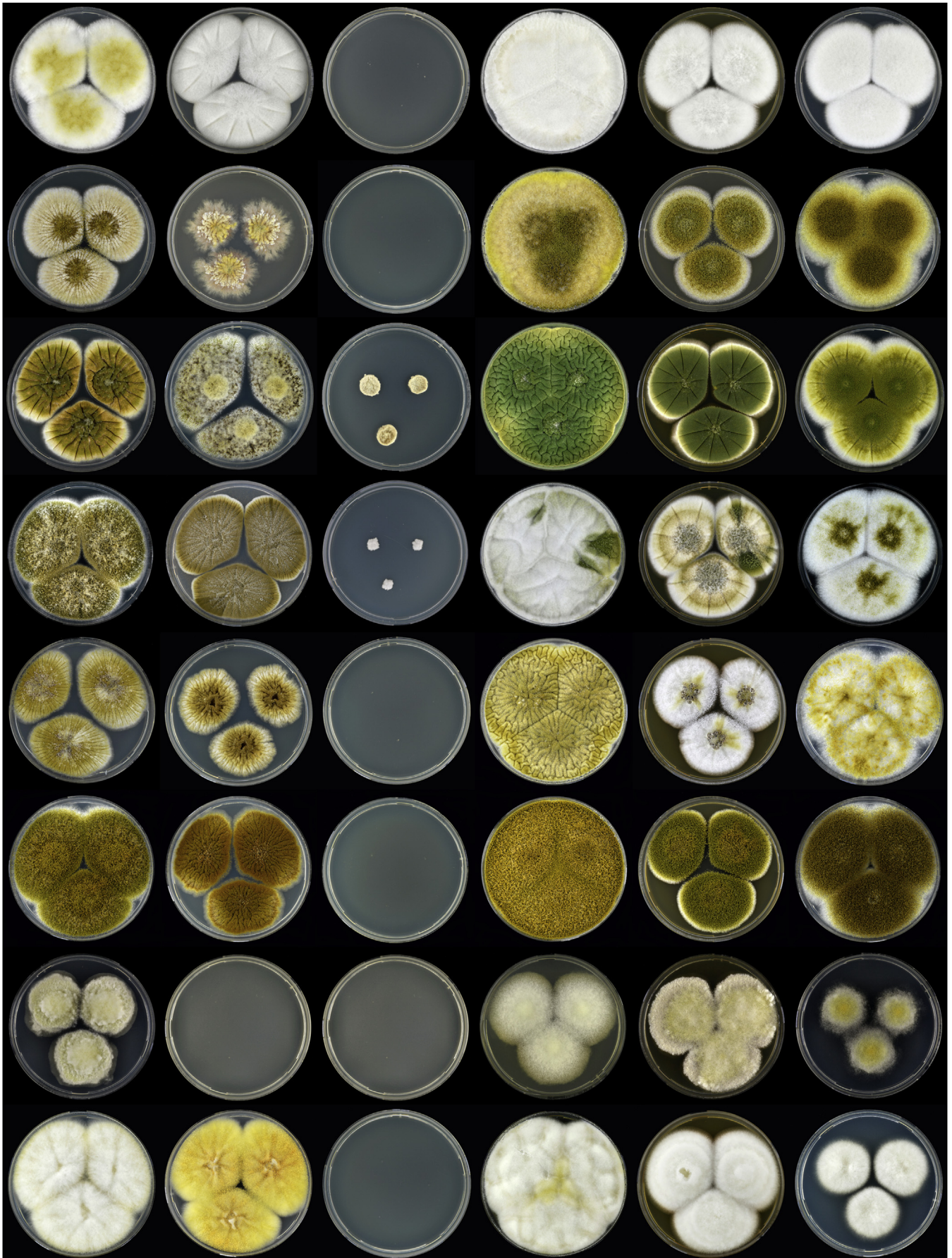


Fig. 12. Left to right: 7 d old colonies on CYA, CYA 37 °C, CYA 42 °C, YES, MEA, DG18; top to bottom: *A. pseudonomius* CBS 119388, *A. pseudotamarii* CBS 766.97, *A. sergii* CBS 130017, *A. sojae* CBS 100928, *A. subflavus* CBS 143683, *A. tamarii* DTO 266-D7, *A. togoensis* CBS 272.89, *A. vandermerwei* DTO 368-C2 (= IBT 20468).

Table 5. Sclerotium and synnema production in species in *Aspergillus* section *Flavi*.

Species				Colony diam CYA42°C (mm)	Conidial colour on MEA and/or CYA
	Large sclerotia	Small sclerotia	Synnemata		
<i>A. aflatoxiformans</i>	(+)	+	-	9–19	yellow-green
<i>A. alliaceus</i>	+ ¹	-	-	0–5	brownish yellow
<i>A. arachidicola</i>	+	(+)	-	10–24	(dark) yellow-green
<i>A. aspearensis</i>	+ ¹	-	-	0	yellow-green
<i>A. austwickii</i>	(+)	+	-	5–20	yellow-green
<i>A. avenaceus</i>	+	-	-	0	beige
<i>A. bertholletius</i>	-	-	-	0	brown
<i>A. caelatus</i>	+	-	+ ²	0	olive brown
<i>A. cerealis</i>	(+)	+	-	13–19	yellow-green
<i>A. coremiiformis</i>	-	-	+ ³	0	orange-brown
<i>A. flavus</i>	+	(+)	(+) ⁴	10–25	yellow-brown
<i>A. hancockii</i>	+ ¹	-	-	0	greyish green to olive
<i>A. lanosus</i>	-	-	-	0–3	dull yellow
<i>A. leporis</i>	+ ¹	-	-	0	beige to olive
<i>A. luteovirescens</i>	+	-	-	0	yellow-green
<i>A. minisclerotigenes</i>	(+)	+	-	18–30	yellow-green
<i>A. mottae</i>	(+)	+	-	0	yellow-green
<i>A. neoalliaceus</i>	+ ¹	-	-	0–10	greenish yellow
<i>A. nomius</i>	+	-	-	0–5	yellow-green
<i>A. novoparasiticus</i>	+	-	-	9–17	dark green to brown
<i>A. oryzae</i>	(+) ⁵	-	-	8–15	pale brown
<i>A. parasiticus</i>	+	-	-	10–20	dark yellow-green
<i>A. pipericola</i>	-	+	-	0–3	pale green
<i>A. pseudocaelatus</i>	+	-	-	0	olive brown
<i>A. pseudonomius</i>	+	-	-	0 (–11)	(dark) yellow-green
<i>A. pseudotamarii</i>	+	-	-	0	dark green-brown
<i>A. sergii</i>	+	-	-	8–12	yellow-green
<i>A. sojiae</i>	-	-	-	6–14	dark yellow green or brown
<i>A. subflavus</i>	+	-	-	0	yellow-green
<i>A. tamarii</i>	+	-	-	0	dark green-brown
<i>A. togoensis</i>	+ ⁶	-	+ ⁶	0	yellow-brown to orange-brown
<i>A. transmontanensis</i> ⁷	+	-	-	0	dark yellow-green
<i>A. vandermerwei</i>	+	-	-	0	pale greenish yellow

¹ Bullet-shaped sclerotia (this study, States & Christensen 1966, Wicklow 1985, Pitt *et al.* 2017).

² According McAlpin (2004).

³ Bartoli *et al.* (1978).

⁴ McAlpin (2001), Danmek *et al.* (2014).

⁵ *A. oryzae sensu stricto* isolates do not produce sclerotia, but non-domesticated strains from agricultural sources, including the genome sequenced sclerotium producing RIB 40, claimed to be *A. oryzae*, produce sclerotia.

⁶ *A. togoensis* produces sclerotia on rice after 6 weeks of incubation (Wicklow *et al.* 1989, Wicklow & McAlpin 1990), and is also able to form synnemata (Christensen 1981, Wicklow & McAlpin 1990, Varga *et al.* 2011, McAlpin *et al.* 2000).

⁷ data from Soares *et al.* (2012).

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation moderately dense; conidia *en masse* yellow-green (71); sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation moderately dense to dense; conidia

en masse yellow-green (71); sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse ochraceous (44). YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; conidia *en masse* yellow-green (71); sclerotia present; soluble pigments absent; exudates absent; reverse buff (45). DG18 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire;

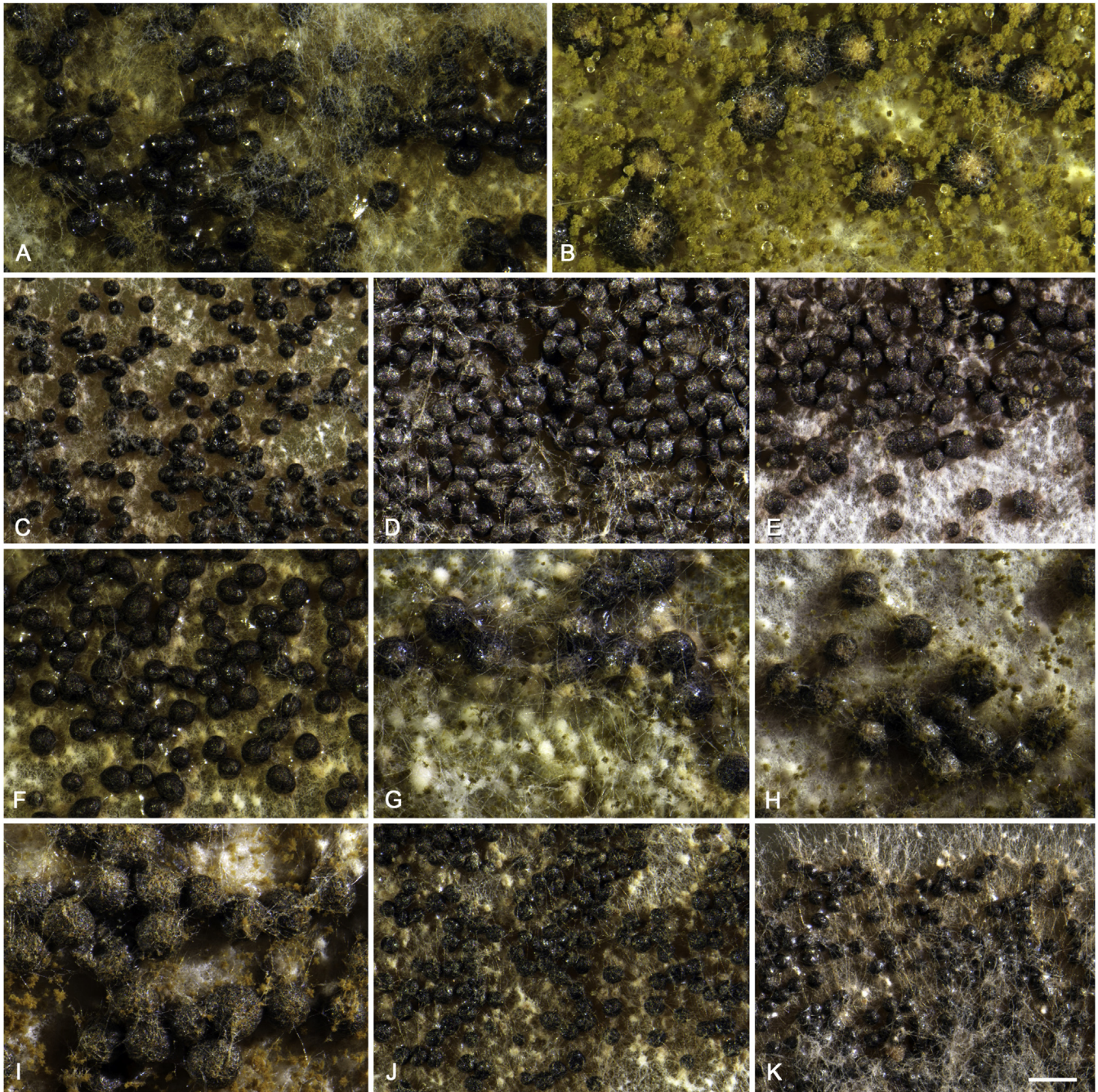


Fig. 13. Sclerotia production by various species belonging to *A. flavus*-clade. A. *A. flavus* DTO 281-H8; B. *A. flavus* DTO 282-A1; C. *A. aflatoxiformans* CBS 135404; D. *A. austwickii* CBS 143677; E. *A. minisclerotigenes* DTO 045-F5; F. *A. mottae* CBS 130016; G. *A. parasiticus* DTO 285-G9; H. *A. sergii* CBS 130017; I. *A. subflavus* CBS 143683; J. *A. cerealis* CBS 143675; K. *A. pipericola* CBS 143680. Scale bar = 500 μ m.

mycelium white; texture floccose; sporulation sparse to moderately dense; conidia *en masse* yellow-green (71); soluble pigments absent; exudates absent; reverse buff (45). OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture floccose; sporulation sparse to moderately dense; conidia *en masse* yellow-green (71); sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). CREA 25 °C, 7 d: Growth poor; acid production absent.

Micromorphology: Sclerotia grey-black, ellipsoidal to irregular, 800–1500 \times 400–700 μ m. Conidial heads yellow-green; radiate, biseriate. Conidiophores with rough stipes, hyaline, 400–800 \times 4.5–7 μ m. Vesicles globose, 16–30 μ m wide, fertile over the upper half to two thirds; metulae hyaline, 7–9.5 \times 3–5 μ m; phialides hyaline, flask-shaped, 5.5–8.5 \times 2–4 μ m. Conidia smooth, globose, 2.5–3.5 μ m.

Notes: *Aspergillus aspearensis* is related to *A. leporis* and *A. hancockii*, but produces different secondary metabolites. The only common extrolite between these three species is kojic acid (Table 3).

Aspergillus austwickii Frisvad, Ezekiel, Samson & Houbraken, **sp. nov.** MycoBank MB823772. Fig. 17.

Etymology: Named in honour of Peter K.C. Austwick, a pioneer in the discovery of aflatoxins.

Diagnosis: *Aspergillus austwickii* is closely related to *A. aflatoxiformans* and *A. cerealis*, but *A. aflatoxiformans* grows faster on YES, and *A. cerealis* grows slowly on DG18.

Typus: Nigeria, Ogun State, Abeokuta, stored rice grains from market, 2012, collected by C.N. Ezekiel (holotype CBS H-23360,

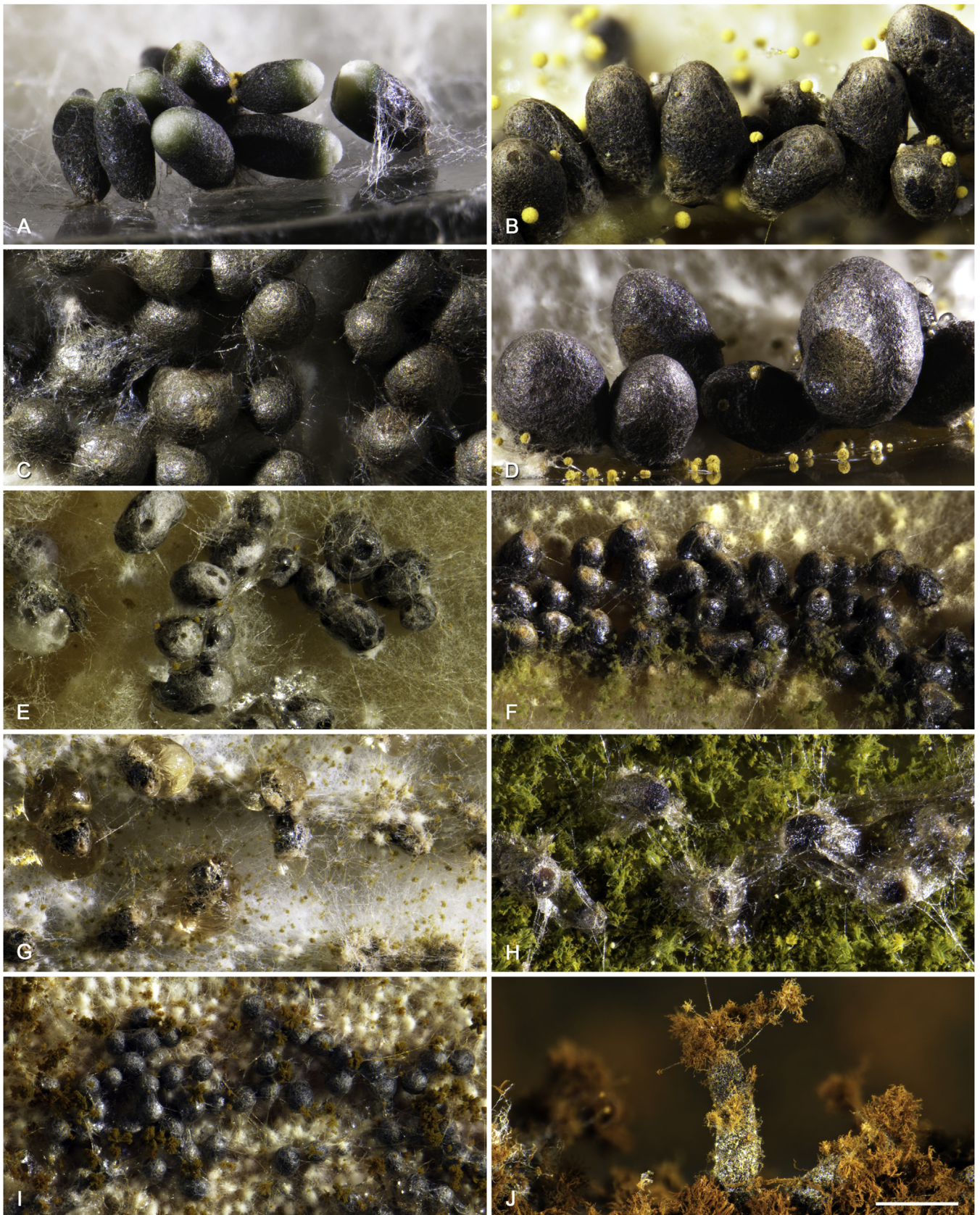


Fig. 14. Sclerotia production by species belonging to *Aspergillus* section *Flavi* (and outside the *A. flavus*-clade; see Fig. 13). A. *A. alliaceus* CBS 143682; B. *A. neoalliaceus* CBS 143681; C. *A. hancockii* CBS 142004; D. *A. leporis* CBS 129203; E. *A. aspearensis* CBS 143672; F. *A. nomius* CBS 260.88; G. *A. pseudonomius* DTO 267-H7; H. *A. caelatus* DTO 285-I1; I. *A. pseudotamarii* CBS 766.97; J. *A. bombycis* DTO 238-E5. Scale bar = 1000 μ m.

culture ex-type: CBS 143677 = DTO 228-F7 = IBT 32076 = IBT 32590).

ITS barcode: MG662391. (Alternative markers: *BenA* = MG517702; *CaM* = MG518072; *RPB2* = MG517893).

Colony diam, 7 d (mm): CYA 46–48; CYA 37 °C 37–38; CYA 42 °C 5–20; MEA 45–47; MEA 37 °C 35–37; MEA 40 °C 22–24; OA 60–62; YES 60–65; CREA 40–42; CYAS 46–50; DG18 35–38.

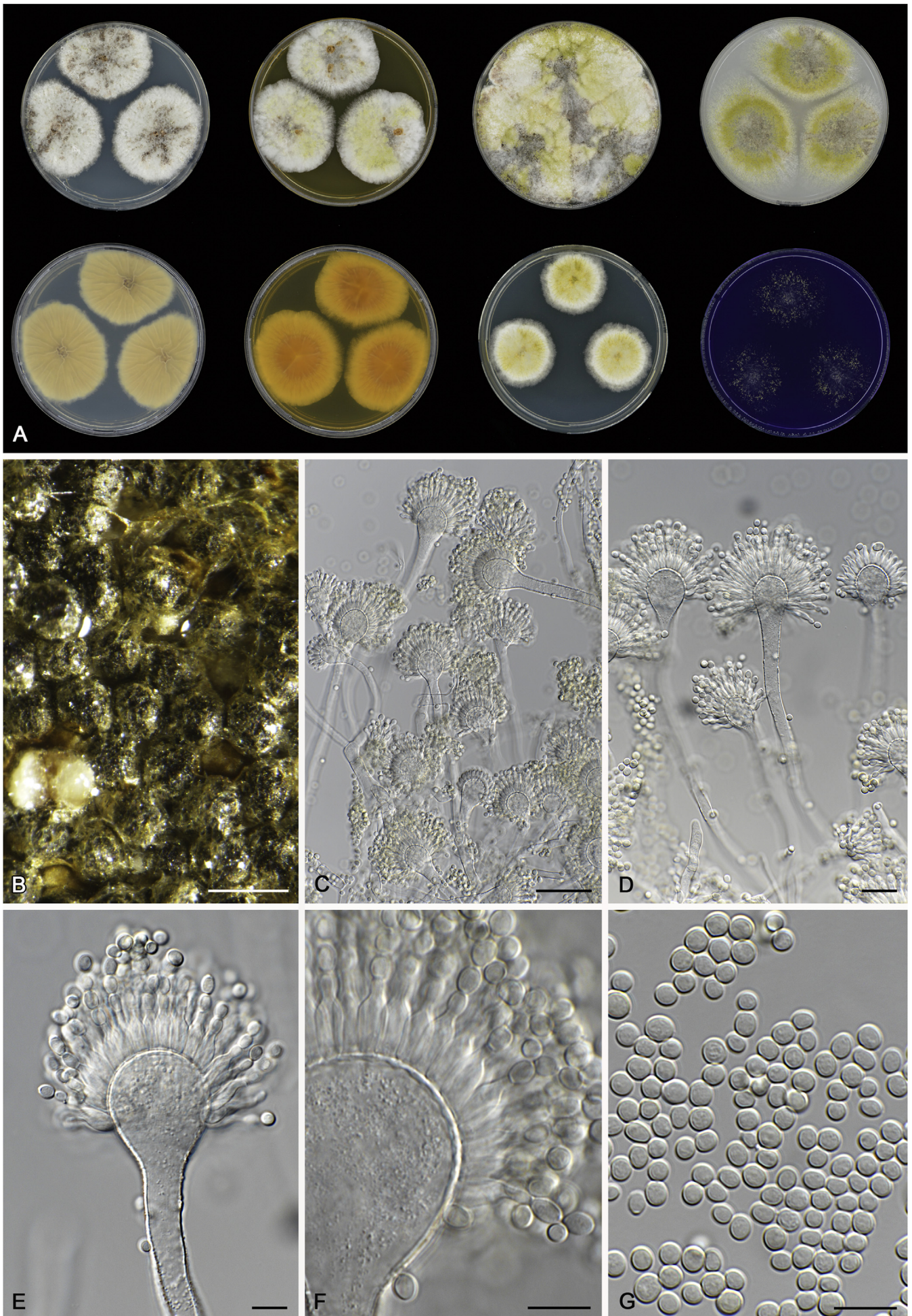


Fig. 15. *Aspergillus aflatoxiformans* CBS 143679^T. A. 7 d old colonies: top row left to right, obverse CYA, obverse MEA, YES and OA; bottom row left to right, reverse CYA, reverse MEA, DG18 and CREA. B. Sclerotia on MEA. C–F. Conidiophores and conidia. G. Conidia. Scale bars: B = 500 μ m; C = 100 μ m; D = 20 μ m; E–G = 10 μ m.

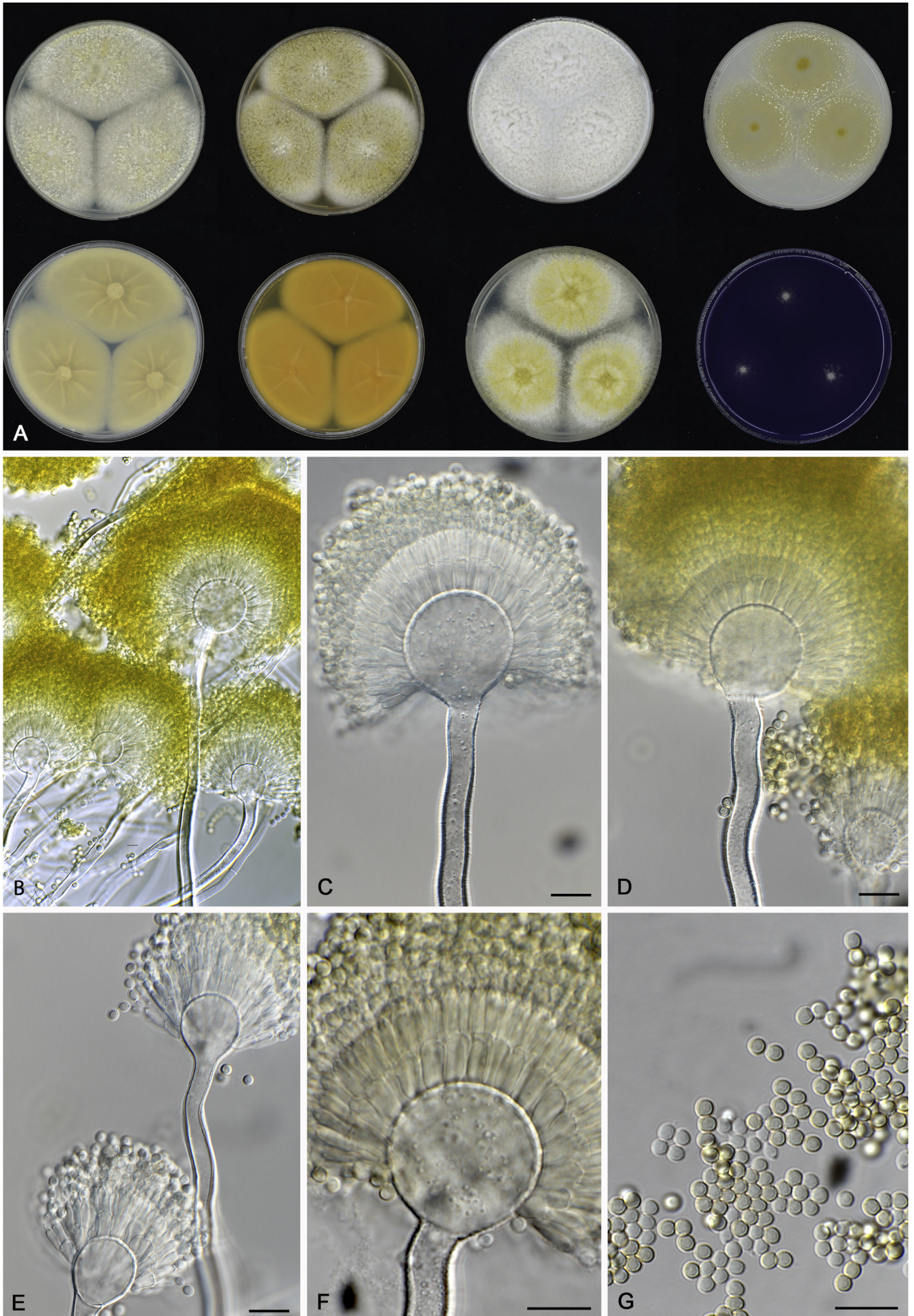


Fig. 16. *Aspergillus aspearensis* CBS 143672^T. A. 7 d old colonies: top row left to right, obverse CYA, obverse MEA, YES and OA; bottom row left to right, reverse CYA, reverse MEA, DG18 and CREA. B–F. Conidiophores and conidia. G. Conidia. Scale bars: B = 20 µm; C–G = 10 µm.

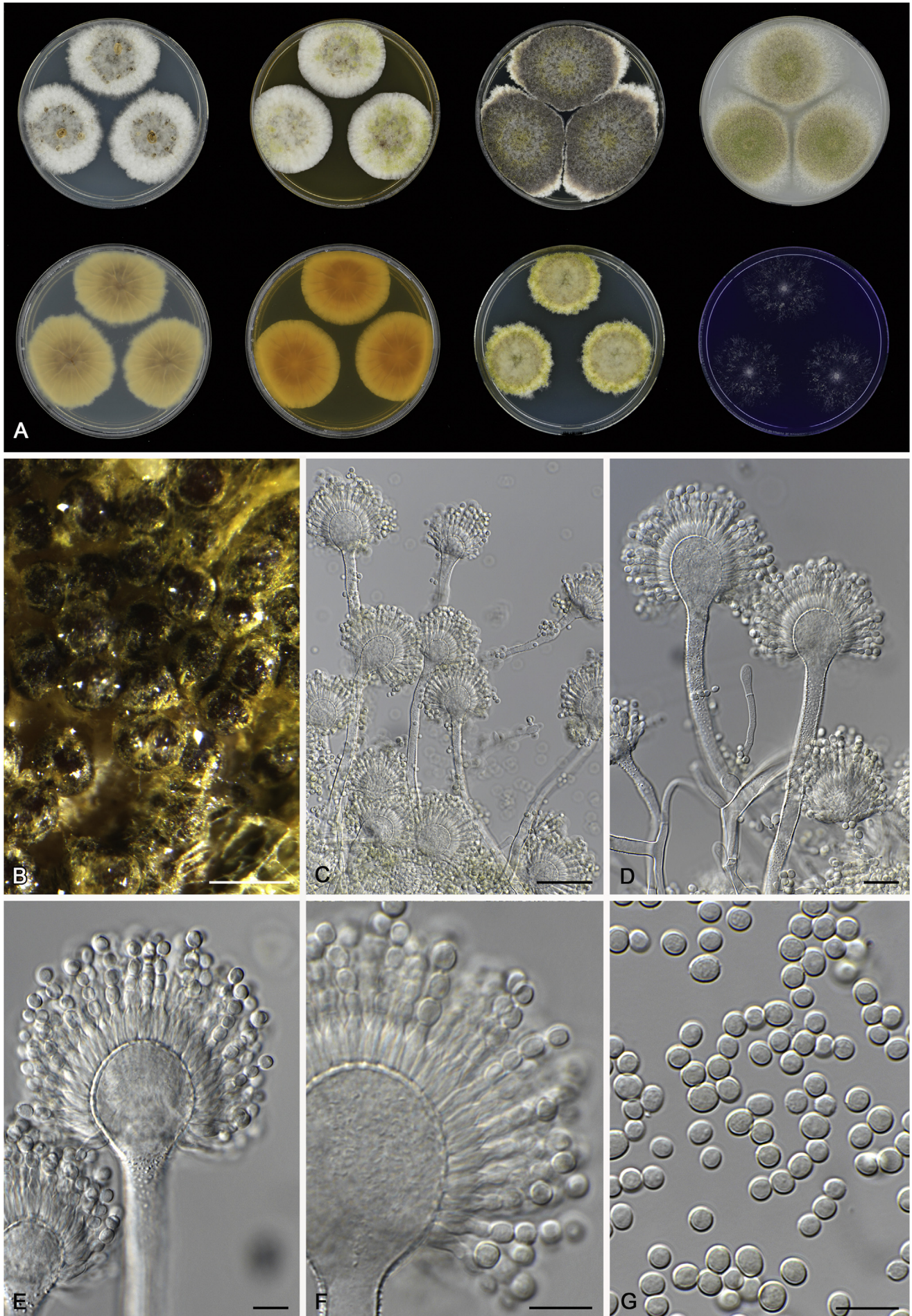


Fig. 17. *Aspergillus austwickii* CBS 143677^T. A. 7 d old colonies: top row left to right, obverse CYA, obverse MEA, YES and OA; bottom row left to right, reverse CYA, reverse MEA, DG18 and CREA. B. Sclerotia on MEA. C–F. Conidiophores and conidia. G. Conidia. Scale bars: B = 500 μ m; C = 100 μ m; D = 20 μ m; E–G = 10 μ m.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation moderately dense; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse ochraceous (44). YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse ochraceous (44). DG18 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates absent; reverse pale luteous (11). OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense; conidia *en masse* yellow-green (71), sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). CREA 25 °C, 7 d: Growth poor; acid production absent. AFPA: orange reverse.

Micromorphology: Sclerotia 100–300 µm, globose to ellipsoidal, dark brown to black. Conidial heads consistently yellow-green; radiate or loosely columnar, uniseriate. Conidiophores with rough stipes, hyaline, 200–500 × 7.5–12.5 µm. Vesicles subglobose to subclavate, 23–33 µm wide, fertile over three fourth of the vesicle surface; phialides hyaline, flask-shaped, 7–10 × 2.5–4.5 µm. Conidia smooth, subglobose, 4–6 × 3.5–5 µm.

Aspergillus cerealis Houbraken, Frisvad, Ezekiel & Samson, **sp. nov.** MycoBank MB823773. Fig. 18.

Etymology: Named based on its occurrence on cereals.

Diagnosis: *Aspergillus cerealis* is closely related to *A. aflatoxiformans* and *A. austwickii*, but *A. cerealis* grows more slowly on DG18 than the other two species. In addition, *A. cerealis* is biseriata, while *A. aflatoxiformans* and *A. austwickii* are uniseriate. *Aspergillus cerealis* produces aflavazole, as do some strains of *A. flavus*, *A. minisclerotigenes* and *A. sergii*.

Typus: Nigeria, Ogun State, Shagamu, stored rice grains from market, 2011, collected by C.N. Ezekiel (holotype CBS H-23359, culture ex-type: CBS 143674 = DTO 228-E7 = IBT 32067).

ITS barcode: MG662394. (Alternative markers: *BenA* = MG517693; *CaM* = MG518063; *RPB2* = MG517884).

Colony diam, 7 d (mm): CYA 60–65; CYA 37 °C 49–51; CYA 42 °C 13–19; MEA 52–55; MEA 37 °C 34–36; MEA 40 °C 18–21; OA 60–63; YES >75; CREA 45–46; CYAS 60–65; DG18 24–27.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation moderately dense; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse

ochraceous (44). YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse ochraceous (44) at centre, pale luteous (11) at edge. DG18 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse pale luteous (11). OA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense; conidia *en masse* yellow-green (71), sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). CREA 25 °C, 7 d: Growth poor; acid production absent.

Micromorphology: Sclerotia 100–250 µm, globose to ellipsoidal, dark brown to black. Conidial heads consistently yellow-green; radiate or loosely columnar, biseriata. Conidiophores with rough stipes, hyaline, 1000–2000 × 7–12 µm. Vesicles globose to subglobose, 37–57 µm wide, fertile over entire surface; metulae hyaline, 7–12.5 × 4–6.5 µm; phialides hyaline, flask-shaped, 5–11 × 2.5–4.5 µm. Conidia smooth, subglobose to ellipsoidal, 3–5 × 2.5–4 µm.

Aspergillus neoalliaceus A. Nováková, Hubka, Samson, Frisvad & Houbraken, **sp. nov.** MycoBank MB823775. Fig. 19.

Etymology: Referring to the closely related species *Aspergillus alliaceus*, but deviating in several features hence *A. neoalliaceus*.

Diagnosis: Colonies pale to intense yellow when young, turning to cinnamon in age. Conidia smooth, subglobose to ellipsoidal, 2.5–4 × 2–3.5 µm. Sclerotia present.

Typus: Czech Republic, National Reservation Pouzdřanská step, Kolby, soil, 2013, collected by A. Nováková (holotype CBS H-23363, culture ex-type: CBS 143681 = DTO 326-D3 = CCF 5433 = IBT 33110 = IBT 33353).

ITS barcode: MH279420. (Alternative markers: *BenA* = MG517763; *CaM* = MG518133; *RPB2* = MG517954).

Colony diam, 7 d (mm): CYA 65–75; CYA 37 °C 50–55; CYA 42 °C 0–8; MEA 65–70; MEA 37 °C 43–50; MEA 40 °C 15–18; OA 65–70; YES >75; CREA 55–60; CYAS 65–75; DG18 65–75.

Colony characters: CYA 25 °C, 7 d: Colonies deep, sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; conidia *en masse* pale luteous (11); soluble pigments absent; exudates present as clear droplets; reverse saffron (10). MEA 25 °C, 7 d: Colonies deep, sulcate; margins entire; mycelium white; texture floccose; sporulation sparse, conidia *en masse* pale luteous (11) white sclerotia present, turn to dark brown after 10 d; soluble pigments absent; exudates present as clear droplets; reverse sienna (8) at centre, fading into ochraceous (44). YES 25 °C, 7 d: Colonies deep, sulcate; margins entire; mycelium white; texture floccose; sporulation absent, large amount of sclerotia present at the edge of colony; soluble pigments absent; exudates present as clear droplets; reverse orange (7) at centre, luteous (12) at edge. DG18 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse luteous (12) at centre, fading into pale luteous (11) or white. OA 25 °C, 7 d: Colonies

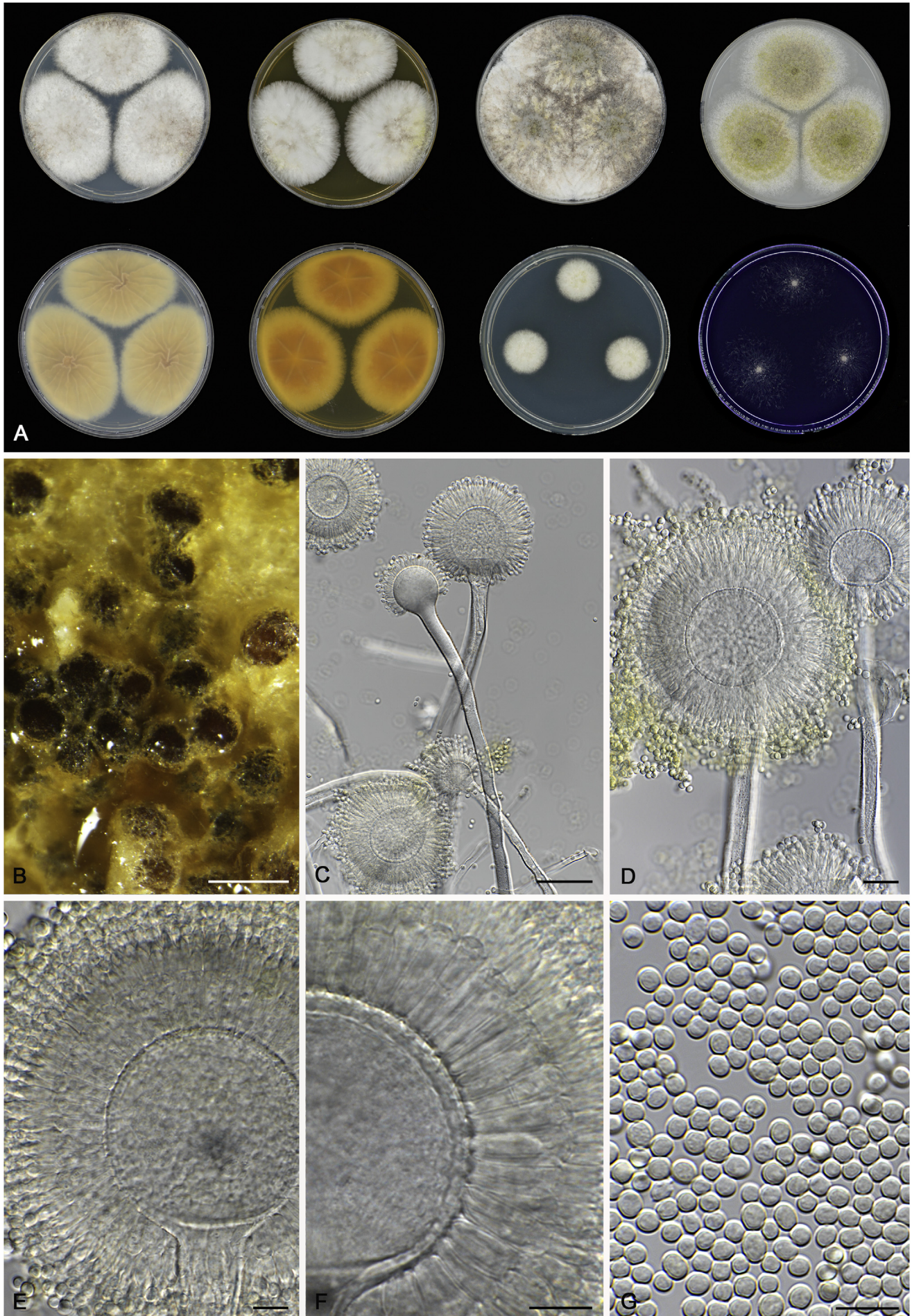


Fig. 18. *Aspergillus cerealis* CBS 143674^T. A. 7 d old colonies: top row left to right, obverse CYA, obverse MEA, YES and OA; bottom row left to right, reverse CYA, reverse MEA, DG18 and CREA. B. Sclerotia on MEA. C–F. Conidiophores and conidia. G. Conidia. Scale bars: B = 500 μ m; C = 100 μ m; D = 20 μ m; E–G = 10 μ m.

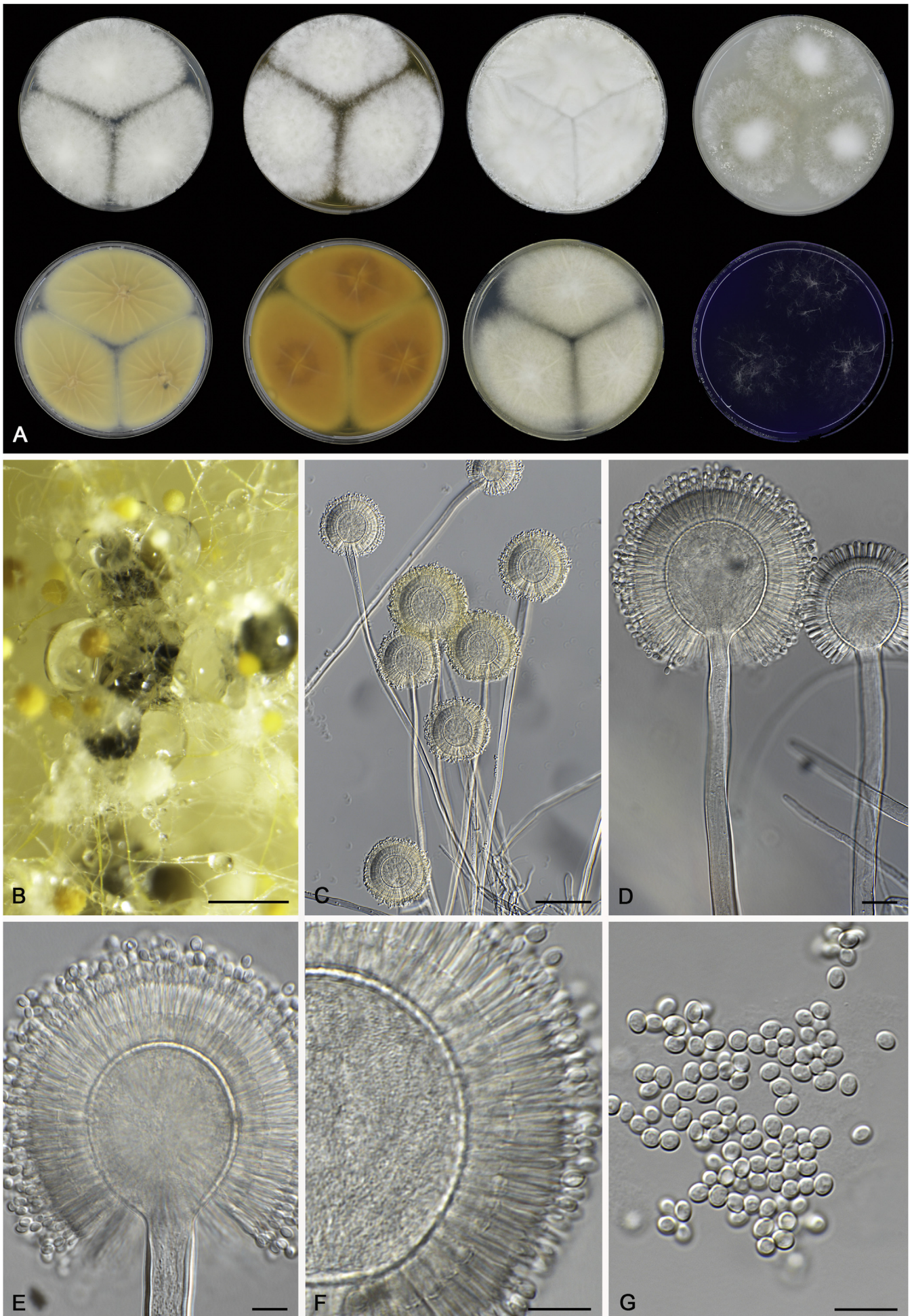


Fig. 19. *Aspergillus neoalliaceus* CBS 143681^T. A. 7 d old colonies: top row left to right, obverse CYA, obverse MEA, YES and OA; bottom row left to right, reverse CYA, reverse MEA, DG18 and CREA. B. Sclerotia on MEA. C–F. Conidiophores and conidia. G. Conidia. Scale bars: B = 500 μm; C = 100 μm; D = 20 μm; E–G = 10 μm.

moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation absent, sclerotia present at the edge of colony; soluble pigments absent; exudates present as clear droplets; reverse pale luteous (11). CREA 25 °C, 7 d: Growth poor; acid production absent.

Micromorphology: Sclerotia brownish black, ovate, oblong or oval, 1200–2500 × 800–1200 µm. Conidial heads pale to intense yellow when young, shifting to cinnamon in age; radiate, splitting into columns in age, biseriate. Conidiophores with smooth stipes, hyaline, 2000–3000 × 8.5–13.5 µm. Vesicles globose to subglobose, 40–77 µm wide, fertile over entire surface; metulae hyaline 6.5–11 × 3.5–6 µm; phialides hyaline, flask-shaped, 8–11 × 2–3.5 µm. Conidia smooth, subglobose to ellipsoidal, 2.5–4 × 2–3.5 µm.

Aspergillus pipericola Frisvad, Samson & Houbraken, **sp. nov.** MycoBank MB823774. Fig. 20.

Etymology: Referring to pepper, the substrate from which the type was isolated.

Diagnosis: Sporulation is absent on most of media, produces subglobose to ellipsoidal conidia measuring 3.5–5.5 × 3.5–5 µm. This species produces small sclerotia and grows restricted at CYA incubated at 42 °C.

Typus: Denmark, black pepper, 2011, collected by J.C. Frisvad (holotype CBS H-23362, culture ex-type: CBS 143680 = DTO 228-H4 = IBT 24628).

ITS barcode: MG662385. (Alternative markers: *BenA* = MG517717; *CaM* = MG518087; *RPB2* = MG517908). **Colony diam, 7 d (mm):** CYA 58–72; CYA 37 °C 70–75; CYA 42 °C 1–5 (–8); MEA 61–72; MEA 37 °C 54–55; OA 52–55; YES >75; CREA 58–65; CYAS 28–30; DG18 62–65.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation absent; dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse cinnamon (62). MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation absent; dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse ochraceous (44). YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation absent; dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse ochraceous (44) to orange (7). DG18 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium saffron (10); texture floccose; sporulation sparse; conidia *en masse* white to pale luteous (11); soluble pigments absent; exudates absent; reverse ochraceous (44) to orange (7). OA 25 °C, 7 d: Colonies moderately deep, plane; margins entire white; texture floccose; sporulation absent; dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). CREA 25 °C, 7 d: Growth poor; acid production absent. AFPA: orange reverse.

Micromorphology: Sclerotia 75–250 µm, globose to ellipsoidal, dark brown to black. Conidial heads white to pale luteous; radiate, biseriate. Conidiophores with smooth stipes, hyaline,

900–1200 × 10–16 µm. Vesicles globose, 30–48 µm wide, fertile over entire surface; metulae hyaline, 5.5–8 × 3.5–5 µm; phialides hyaline, flask-shaped, 6–10 × 3.5–5.5 µm. Conidia rough, subglobose to ellipsoidal, 3.5–5.5 × 3.5–5 µm.

Aspergillus subflavus Hubka, A. Nováková, Samson, Frisvad & Houbraken, **sp. nov.** MycoBank MB823776. Fig. 21.

Etymology: The species superficially resembles *Aspergillus flavus*, hence the name *Aspergillus subflavus*.

Diagnosis: Colonies yellow-green when young, turn to olive-green in age, uniseriate conidiophores and rough, globose conidia measuring 4.5–6.5 µm. *Aspergillus subflavus* produces sclerotia that measure 375–650 µm and this species is unable to grow on CYA incubated at 42 °C.

Typus: Romania, above Movile Cave, Dobrogea, Mangalia soil, Sept. 2013, collected by A. Nováková (holotype CBS H-23364, culture ex-type: CBS 143683 = DTO 326-E8 = CCF 4957 = NRRL 66254 = IBT 34939).

ITS barcode: MH279429. (Alternative markers: *BenA* = MG517773; *CaM* = MG518143; *RPB2* = MG517964). **Colony diam, 7 d (mm):** CYA 55–60; CYA 37 °C 15–18; CYA 42 °C No growth; MEA 52–53; MEA 37 °C 7–10; MEA 40 °C No growth; OA 55–60; YES >75; CREA 25–27; CYAS 65–70; DG18 65–75.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation dense; conidia *en masse* yellow-green (68), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation dense; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse ochraceous (44). YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation dense; conidia *en masse* yellow-green (71), dark brown sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse pale luteous (11). DG18 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation dense; conidia *en masse* yellow-green (71); soluble pigments absent; exudates absent; reverse buff (45). OA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation sparse; conidia *en masse* yellow-green (71), sclerotia present; soluble pigments absent; exudates present as clear droplets; reverse buff (45). CREA 25 °C, 7 d: Growth poor; acid production absent.

Micromorphology: Sclerotia 375–650 µm, globose to ellipsoidal, dark brown to black. Conidial heads yellow-green when young, shifting to olive-green in age; loosely radiate, uniseriate. Conidiophores with smooth stipes, hyaline, 300–450 × 7–12.5 µm. Vesicles globose to subglobose, 20–32 µm wide, fertile over three fourth of entire surface; phialides hyaline, flask-shaped, 7.5–13 × 4.5–7 µm. Conidia rough-walled, globose, 4.5–6.5 µm.

Aspergillus vandermerwei Frisvad, Hubka, Samson & Houbraken, **sp. nov.** MycoBank MB823777. Fig. 22.



Fig. 20. *Aspergillus pipericola* CBS 143680^T. A. 7 d old colonies: top row left to right, obverse CYA, obverse MEA, YES and OA; bottom row left to right, reverse CYA, reverse MEA, DG18 and CREA. B. Sclerotia on MEA. C–F. Conidiophores and conidia. G. Conidia. Scale bars: B = 500 µm; C = 20 µm; D, E = 10 µm; F–G = 10 µm.

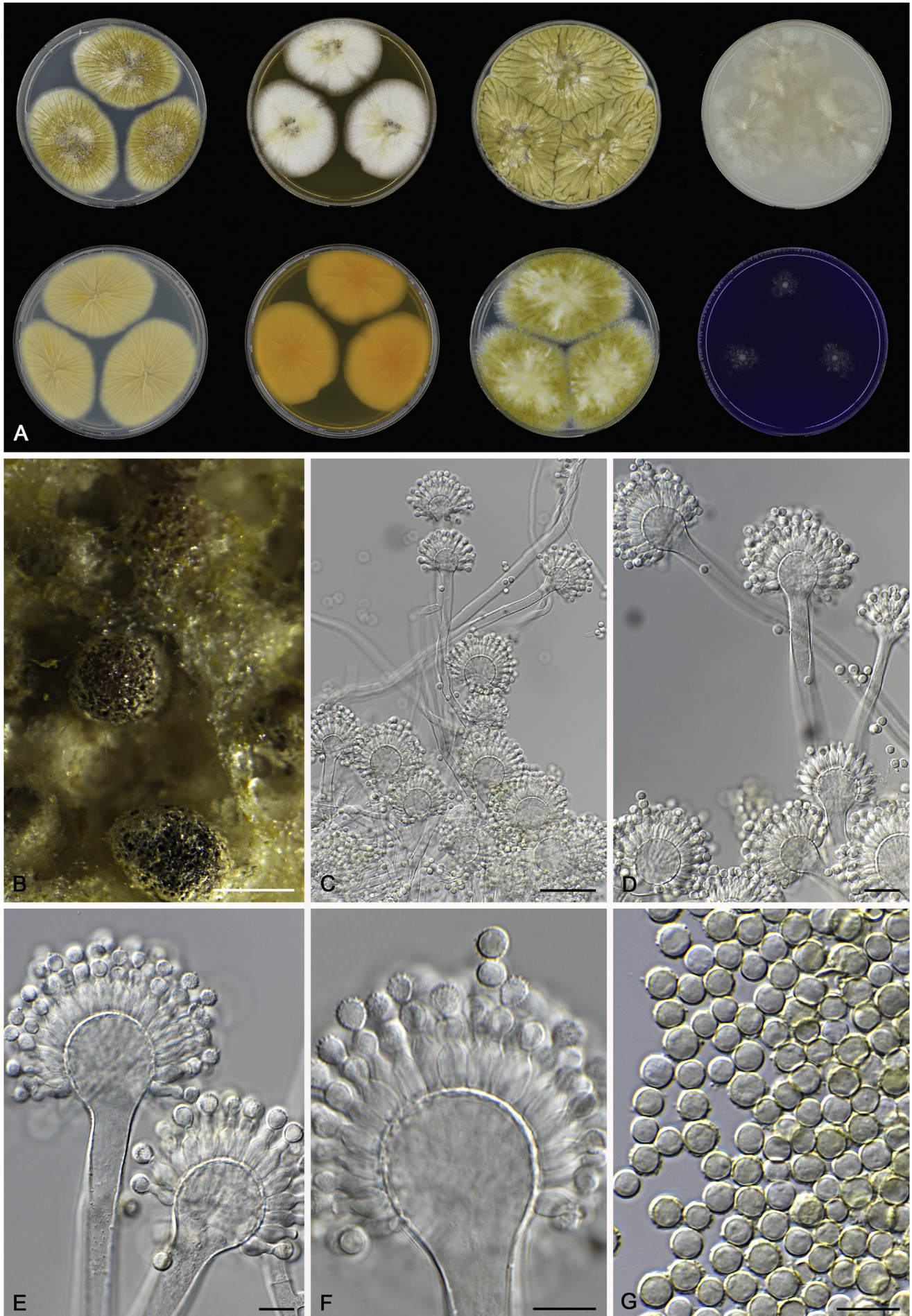


Fig. 21. *Aspergillus subflavus* CBS 143683^T. A. 7 d old colonies: top row left to right, obverse CYA, obverse MEA, YES and OA; bottom row left to right, reverse CYA, reverse MEA, DG18 and CREA. B. Sclerotia on MEA. C–F. Conidiophores and conidia. G. Conidia. Scale bars: B = 500 μ m; C = 100 μ m; D = 20 μ m; E–G = 10 μ m.

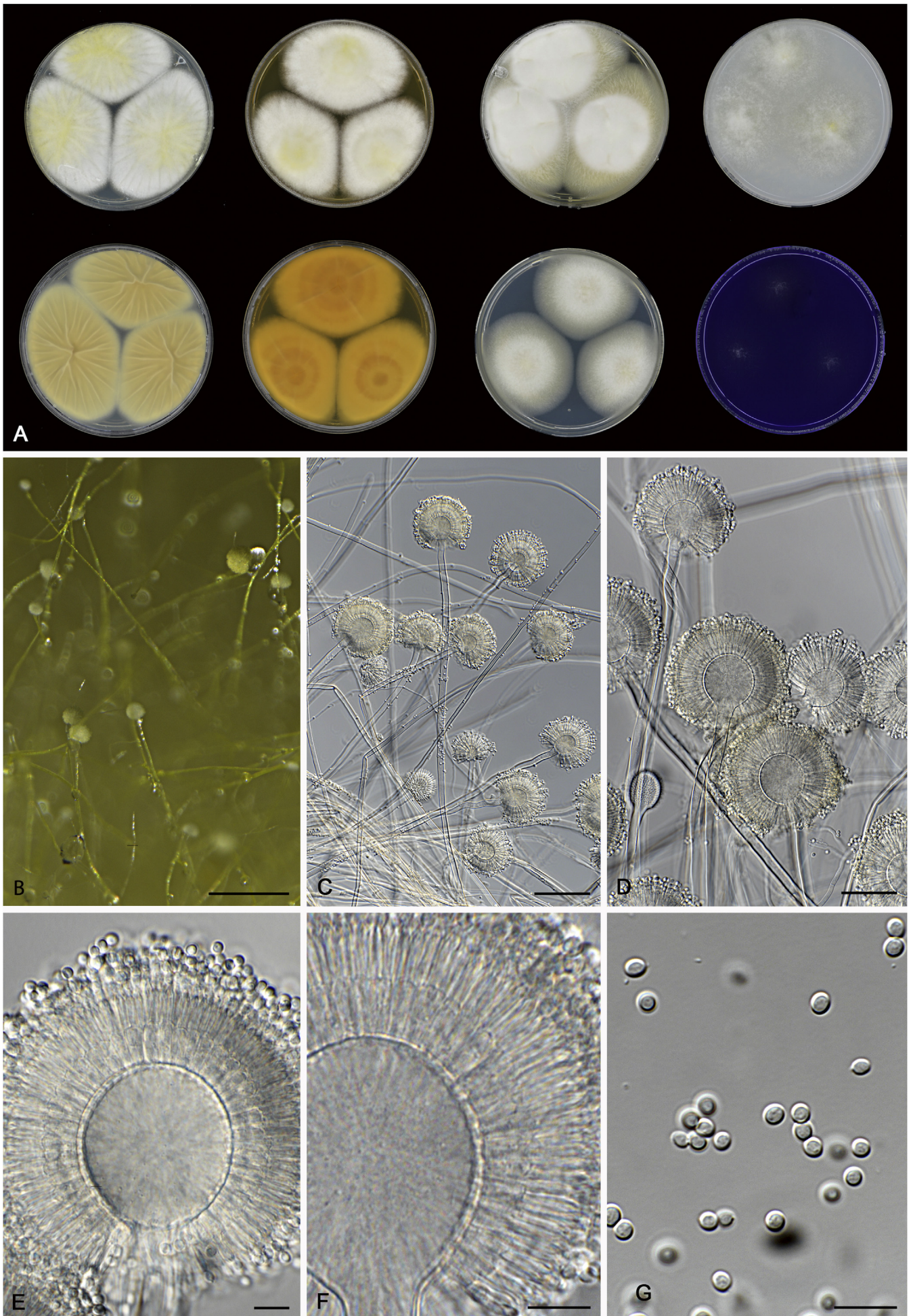


Fig. 22. *Aspergillus vandermerwei* CBS 612.78^T. A. 7 d old colonies: top row left to right, obverse CYA, obverse MEA, YES and OA; bottom row left to right, reverse CYA, reverse MEA, DG18 and CREA. B. Conidial head on MEA. C–F. Conidiophores and conidia. G. Conidia. Scale bars: B = 500 μm; C = 100 μm; D = 50 μm; E–G = 10 μm.

Etymology: Named after K.J. van der Merwe, who contributed to the research on ochratoxin A (Van der Merwe et al. 1965).

Diagnosis: *Aspergillus vandermerwei* is closely related to *A. neoalliaceus*, but *A. vandermerwei* grows slowly on CYA and MEA at 40 °C, and does not produce sclerotia.

Typus: **Argentina**, Buenos Aires, unknown source, 1950, isolated by J. Winitzky (holotype CBS H-23381, culture ex-type: CBS 612.78 = DTO 069-D2 = DTO 034-B5 = NRRL 5108 = CCF 5683 = IBT 13876).

ITS barcode: EF661567. (Alternative markers: *BenA* = EF661469; *CaM* = EF661540; *RPB2* = MG517838).

Colony diam, 7 d (mm): CYA 65–73; CYA 37 °C 32–34; CYA 42 °C no growth; MEA 61–68; MEA 37 °C 23–25; MEA 40 °C 1–4; OA 65–75; YES 72–75; CREA 45–50; CYAS 47–50; DG18 53–56.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation moderately dense; conidia *en masse* pale luteous (11); soluble pigments absent; exudates present as clear droplets; reverse buff (45). MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation moderately dense; conidia *en masse* pale luteous (11); soluble pigments absent; exudates present as clear droplets; reverse sienna (8) at centre, fading into ochraceous (44). YES 25 °C, 7 d: Colonies moderately dense, sulcate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates present as clear droplets; reverse pale luteous (11). DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse pale luteous (11). OA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation sparse; conidia *en masse* pale luteous (11); soluble pigments absent; exudates present as clear droplets; reverse pale luteous (11). CREA 25 °C, 7 d: Growth poor; acid production absent.

Micromorphology: Conidial heads pale to intense yellow when young, shifting to cinnamon in age; radiate, biseriolate. Conidiophores with smooth stipes, hyaline, 2000–3000 × 9.5–15.5 µm. Vesicles globose to subglobose, 35–57 µm wide, fertile over entire surface; metulae hyaline 7–8.5 × 3–4.5 µm; phialides hyaline, flask-shaped, 7.5–10 × 2–3.5 µm. Conidia smooth, subglobose to ellipsoidal, 3–4 × 2.5–3.5 µm.

List of accepted species and their synonyms in *Aspergillus* section *Flavi*

Below an overview of accepted species in *Aspergillus* section *Flavi* (in bold font) and their synonyms. *Aspergillus oryzae* and *A. sojae* are domesticated forms of *A. flavus* and *A. parasiticus*, respectively. Partial calmodulin gene sequencing, the recommended method for identification of Aspergilli, can't differentiate these domesticated forms from their wild types. Differentiation between *A. oryzae/A. sojae* and *A. flavus/A. parasiticus* is first of all based on the inability of the domesticated forms to produce aflatoxins. The second character for identification is the origin of the strain. *Aspergillus oryzae* and *A. sojae* strains are isolated from fermented (food) products or are used in biotechnology. Strains obtained from other environments, even if they are non-

aflatoxin producers, are identified as *A. flavus*. The representatives or ex-type strains of the synonyms listed under *A. oryzae* and *A. sojae* were isolated from fermented foods. However, their ability to produce aflatoxins was not studied and this should be done to confirm the proposed classification.

Aspergillus aflatoxiformans Frisvad, Ezekiel, Samson & Houbraken, published here [MB823770]. — Herb.: CBS H-23361. Ex-type: CBS 143679 = DTO 228-G2 = IBT 32085. ITS barcode: MG662388. (Alternative markers: *BenA* = MG517706; *CaM* = MG518076; *RPB2* = MG517897).

Aspergillus alliaceus Thom & Church, Aspergilli: 163. 1926. [MB256402]. — Herb.: CBS H-7812 (neotype, designated here; MBT 381967). Ex-type: CBS 536.65 = DTO 034-B3 = DTO 046-B1 = ATCC 10060 = DSM 813 = IFO 7538 = IMI 051982 = IMI 051982ii = NRRL 315 = QM 1885 = WB 315. ITS barcode: EF661551. (Alternative markers: *BenA* = EF661465; *CaM* = EF661534; *RPB2* = MG517825). **Notes:** *Petromyces alliaceus* was based on TRTC 46232 (= ATCC 16891 = CBS 542.65 = NRRL 1481; ex soil Australia) and Samson et al. (2014) listed this strain as type of *A. alliaceus* as well. However, *A. alliaceus* was based on two strains, one from rotted onions (CBS 110.26 = NRRL 316 = Thom 4660) and the other from a dead blister-beetle (CBS 536.65 = NRRL 315 = Thom 4656; USA) (Thom & Church 1926: 163). NRRL 315 produces a sexual state (Fennell & Warcup 1959) and this strain is therefore selected as neotype of *A. alliaceus*.

Synonyms: *Petromyces alliaceus* Malloch & Cain, Can. J. Bot. 50: 2623. 1972. [MB319449]. — Herb.: TRTC 46232. Ex-type: DTO 203-B1 = CBS 542.65 = NRRL 4181 = ATCC 16891 = IMI 126711 = WB 4181. ITS barcode: EF661556. (Alternative markers: *BenA* = EF661466; *CaM* = EF661536; *RPB2* = EU021644).

Synceleistostroma alliaceum (as '*alliacea*') Subram., Curr. Sci. 41: 6. 1972. [MB324391]. — Herb.: n/a. Ex-type: CBS 536.65 = DTO 034-B3 = DTO 046-B1 = ATCC 10060 = DSM 813 = IFO 7538 = IMI 051982 = IMI 051982ii = NRRL 315 = QM 1885 = WB 315. ITS barcode: EF661551. (Alternative markers: *BenA* = EF661465; *CaM* = EF661534; *RPB2* = MG517825).

Aspergillus alliaceus var. *macrosterigmatus* Glins., Thamavit & Sittir. [nom. inval., Art. 39.1, 40.1 (McNeill et al. 2012)], J. Sci. Soc. Thailand: 43. 1977. [MB347783]. — Herb.: n/a. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a). **Notes:** This species was described without a Latin diagnosis and without designation of type material and is therefore invalidly published. This species is tentatively synonymized with *A. alliaceus*, but could also belong to section *Circumdati*.

Aspergillus albertensis J.P. Tewari, Mycologia 77: 114. 1985. [MB105069]. — Herb.: UAMH 2976. Ex-type: NRRL 20602 = ATCC 58745 = UAMH 2976. ITS barcode: EF661548. (Alternative markers: *BenA* = EF661464; *CaM* = EF661537; *RPB2* = EU021628).

Petromyces albertensis J.P. Tewari, Mycologia 77: 114. 1985. [MB105626]. — Herb.: UAMH 2976. Ex-type: NRRL 20602 = ATCC 58745 = UAMH 2976. ITS barcode: EF661548. (Alternative markers: *BenA* = EF661464; *CaM* = EF661537; *RPB2* = EU021628).

Aspergillus arachidicola Pildain, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 58: 730. 2008. [MB505189]. — Herb.: unknown. Ex-type: DTO 009-G3 = CBS 117610 = IBT 117610 = IBT 25020. ITS barcode: EF409241. (Alternative

markers: *BenA* = EF203158; *CaM* = EF202049; *RPB2* = MG517802).

Aspergillus aspearensis Houbraken, Frisvad, Arzanlou & Samson, published here [MB823771]. — Herb.: CBS H-23358. Ex-type: CBS 143672 = DTO 203-D9 = CCTU 758 = IBT 32590 = IBT 34544. ITS barcode: MG662398. (Alternative markers: *BenA* = MG517669; *CaM* = MG518040; *RPB2* = MG517857).

Aspergillus austwickii Frisvad, Ezekiel, Samson & Houbraken, published here [MB823772]. — Herb.: CBS H-23360. Ex-type: CBS 143677 = DTO 228-F7 = IBT 32590 = IBT 32076. ITS barcode: MG662391. (Alternative markers: *BenA* = MG517702; *CaM* = MG518072; *RPB2* = MG517893).

Aspergillus avenaceus G. Sm., Trans. Brit. Mycol. Soc. 26: 24. 1943. [MB284296]. — Herb.: CBS H-6739. Ex-type: CBS 109.46 = NRRL 517 = ATCC 16861 = IMI 16140 = LCP 89.2592 = LSHBBB 155 = QM 6741 = WB 517. ITS barcode: AF104446. (Alternative markers: *BenA* = FJ491481; *CaM* = FJ491496; *RPB2* = JN121424).

Aspergillus bertholletius Taniwaki, Pitt & Frisvad, PLoS ONE 7: e42480-P6. 2012. [MB800125]. — Herb.: CCT 7615. Ex-type: DTO 223-D3 = ITAL 270/06 = IBT 29228. ITS barcode: JX198673. (Alternative markers: *BenA* = MG517689; *CaM* = JX198674; *RPB2* = MG517880).

Aspergillus caelatus B.W. Horn, Mycotaxon 61: 186. 1997. [MB436955]. — Herb.: BPI 737601. Ex-type: DTO 046-A8 = CBS 763.97 = NRRL 25528 = ATCC 201128. ITS barcode: AF004930. (Alternative markers: *BenA* = EF661470; *CaM* = EF661522; *RPB2* = EF661436).

Aspergillus cerealis Houbraken, Frisvad, Ezekiel & Samson, published here [MB823773]. — Herb.: CBS H-23359. Ex-type: CBS 143674 = DTO 228-E7 = IBT 32067. ITS barcode: MG662394. (Alternative markers: *BenA* = MG517693; *CaM* = MG518063; *RPB2* = MG517884).

Synonym: *Aspergillus korhogoensis* A. Carvajal-Campos, A.L. Manizan, S. Tadrast, D.K. Akaki, R. Koffi-Nevry, G.G. Moore, S.O. Fapohunda, S. Bailly, D. Montet, I.P. Oswald, S. Lorber, C. Brabet & O. Puel [*nom. inval.*, art. 42.1 (McNeill *et al.* 2012)], Toxins 9, 353: 11. 2017. [MB823357]. — Herb.: MAC1254. Ex-type: NRRL 66710. ITS barcode: KY689209. (Alternative markers: *BenA* = KY628792; *CaM* = KY661267; *RPB2* = n/a). *Notes:* An identifier issued by a recognized repository for that name was not cited in the protologue and this species is therefore not validly described [Art. 42.1 (McNeill *et al.* 2012)].

Aspergillus coremiiformis Bartoli & Maggi, Trans. Brit. Mycol. Soc. 71: 386. 1979. [MB309214]. — Herb.: RO 102 S. Ex-type: CBS 553.77 = NRRL 13603 = ATCC 38576 = IMI 223069 = NRRL 13756. ITS barcode: EF661544. (Alternative markers: *BenA* = EU014104; *CaM* = EU014112; *RPB2* = EU021623).

Aspergillus flavus Link, Mag. Ges. Naturf. Freunde Berlin 3: 16. Fr. 1809. [MB209842]. — Herb.: IMI 124930. Ex-type: CBS 569.65 = NRRL 1957 = ATCC 16883 = IMI 124930 = QM 9947 = WB 1957. ITS barcode: AF027863. (Alternative markers: *BenA* = EF661485; *CaM* = EF661508; *RPB2* = EF661440). *Synonyms:* *Monilia flava* (Link) Pers., Mycol. Eur. 1: 30. 1822. [MB496075]. — Herb.: n/a. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a).

Sterigmatocystis lutea Tiegh (*nom. nudum*), Bull. Soc. France 24: 103. 1877. [MB228931]. — Herb.: n/a. Ex-type: CBS 133153 = DTO 214-B2 = WB 508 = NRRL 508 (representative strain, Raper & Fennell 1965: 377). ITS barcode: MH279413. (Alternative markers: *BenA* = MH279880; *CaM* = MH279857; *RPB2* = n/a). *Notes:* This species probably served as the basis of Bainier's description of *Sterigmatocystis lutea*.

Sterigmatocystis lutea Bainier, Bull. Soc. France 27: 30. 1880. [MB219510]. — Herb.: n/a. Ex-type: CBS 133153 = DTO 214-B2 = WB 508 = NRRL 508 (representative strain, Raper & Fennell 1965: 377). ITS barcode: MH279413. (Alternative markers: *BenA* = MH279880; *CaM* = MH279857; *RPB2* = n/a).

Aspergillus variabilis Gasperini, Atti Soc. Toscana Nat. Sci. Pisa Mem. 8 (Fasc. 1): 326. 1887. [MB161681]. — Herb.: n/a. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a). *Notes:* see *Aspergillus oryzae* var. *variabilis*.

Sterigmatocystis variabilis (Gasperini) Sacc., Syll. Fung. 10: 525. 1892. [MB197900]. — Herb.: n/a. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a).

Aspergillus microviridicitrinus Costantin & Lucet, Ann. Sci. Nat. Botan. 2: 158. 1905. [MB535523]. — Herb.: n/a. Ex-type: CBS 124.62 = DTO 067-l8 = IMI 089340 = LSHB BB422 (received at CBS as *A. microviridicitrinus*). ITS barcode: MH279385. (Alternative markers: *BenA* = MH279865; *CaM* = MH279842; *RPB2* = n/a).

Aspergillus wehmeri Costantin & Lucet, Ann. Sci. Nat. Botan. (IX) 2: 162. 1905. [MB455472]. — Herb.: n/a. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a).

Aspergillus effusus Tirab., Ann. Bot. (Rome): 16. 1908. [MB212765]. — Herb.: n/a. Ex-type: CBS 574.65 = DTO 303-C3 = WB 506 = NRRL 506 = ATCC 1010 = IHEM 4388 = IMI 016142 = IMI 124935 = LCP 89.2587 = LSHB Ac21 = NCTC 973 = NRRL 1653 = QM 740 (representative strain, *vide* Thom & Church 1926, Thom & Raper 1945; Raper & Fennell 1965: 377). ITS barcode: JN185448. (Alternative markers: *BenA* = JN185446; *CaM* = JN185447; *RPB2* = JN185449).

Aspergillus oryzae var. *fulvus* Yamam. (?), Rept. Govt. Brewing Exptl. Sta. Japan 42. 1912. [MB486957]. — Herb.: n/a. Ex-type: CBS 133118 = DTO 213-l2 = NRRL 4894 = WB 4894 = IMI 359792 (representative, Raper & Fennell 1965: 374). ITS barcode: MH279408. (Alternative markers: *BenA* = MH279875; *CaM* = MH279852; *RPB2* = n/a). *Notes:* NRRL 4894 was deposited by the Faculty of Engineering, Osaka University in the NRRL collection as *A. oryzae* var. *fulvus* Yamamoto (Wicklow *et al.* 2002). Raper & Fennell (1965: 374) listed this strain as a representative of *A. oryzae* var. *fulvus* and *A. flavus* var. *oryzae* f. *fulvus*.

Aspergillus jeanselmei M. Ota, Anns Parasitol. Humaine Comp.: 146. 1923. [MB268405]. — Herb.: n/a. Ex-type: CBS 108.24 = DTO 389-C1 = NRRL 507 = WB 507 = Thom 5665 (probably ex-type; deposited by M. Ota in the CBS culture collection as *A. jeanselmei*). ITS barcode: MH279454. (Alternative markers: *BenA* = MH279882; *CaM* = MH279859; *RPB2* = n/a). No information was found on the source of this species and it is therefore tentatively placed in synonymy with *A. flavus*.

Sterigmatocystis jeanselmei (N. Ota) Nann., Repertorio sistematico dei miceti dell' uomo e degli animali 4: 229. 1934. [MB252829]. — Herb.: n/a. Ex-type: CBS 108.24 = DTO 389-C1 = NRRL 507 = WB 507 = Thom 5665 (probably ex-type; deposited by M. Ota in the CBS culture collection as

A. jeanselmei). ITS barcode: MH279454. (Alternative markers: *BenA* = MH279882; *CaM* = MH279859; *RPB2* = n/a). Notes: see *Aspergillus jeanselmei*.

Aspergillus luteus (Tiegh.) C.W. Dodge, Medical mycology. Fungous diseases of men and other mammals: 625. 1935. [MB253119]. — Herb.: n/a. Ex-type: CBS 133153 = DTO 214-B2 = WB 508 = NRRL 508 (representative strain, Raper & Fennell 1965: 365). ITS barcode: MH279413. (Alternative markers: *BenA* = MH279880; *CaM* = MH279857; *RPB2* = n/a).

Aspergillus flavus var. *asper* Y. Sasaki, J. Fac. Agric. Hokkaido Imp. Univ. 49: 143. 1950. [MB351898]. — Herb.: n/a. Ex-type: CBS 485.65 = DTO 046-B7 = ATCC 16870 = IFO 5324 = IMI 124932 = LCP 89.3556 = NRRL 4818 = WB 4818 = IBT 3641 = IBT 3657 = JCM 2225 = AHU B-18 (Y. Sasaki). ITS barcode: EF661563. (Alternative markers: *BenA* = MG517643; *CaM* = MG518014; *RPB2* = MG517828).

Aspergillus thomii G. Sm., Trans. Br. Mycol. Soc. 34: 17. 1951. [MB292861]. — Herb.: n/a. Ex-type: CBS 120.51 = ATCC 16859 = IFO 8135 = IMI 045644 = LCP 56.1517 = LSHB BB213 = NRRL 2097 = NRRL A-2022 = QM 6871 = WB 2097. ITS barcode: EF661549. (Alternative markers: *BenA* = MG517639; *CaM* = MG518012; *RPB2* = MG517822).

Aspergillus oryzae var. *wehmeri* (Costantin & Lucet) Y. Ohara, Res. Bull. Fac. Agric., Gifu Univ.: 80. 1953. [MB353278]. — Herb.: n/a. Ex-type: CBS 133063 = DTO 213-H4 = WB 4823 = NRRL 4823 = BCRC 33516 = CCRC 33516 = IAM 2960 = IFO 5770 = JCM 22428 = NBRC 5770 = RIB 1358 = RIFY 5024 = Y. Ohara KK-20 (Ohara's type, Raper & Fennell 1965: 368). ITS barcode: MH279407. (Alternative markers: *BenA* = MH279874; *CaM* = MH279851; *RPB2* = n/a).

Aspergillus flavus var. *microviridicitrinus* (Costantin & Lucet) Nehira, J. Ferment. Technol., Osaka 35: 56. 1957. [MB500159]. — Herb.: n/a. Ex-type: CBS 124.62 = DTO 067-I8 = IMI 089340 = LSHB BB422 (received at CBS as *A. microviridicitrinus*). ITS barcode: MH279385. (Alternative markers: *BenA* = MH279865; *CaM* = MH279842; *RPB2* = n/a).

Aspergillus flavus var. *oryzae* f. *fulvus* (Yamam.?) Nehira, J. Ferment. Technol., Osaka 35: 56. 1957. [MB347785]. — Herb.: n/a. Ex-type: CBS 133118 = DTO 213-I2 = NRRL 4894 = WB 4894 = IMI 359792 (representative, Raper & Fennell 1965: 374). ITS barcode: MH279408. (Alternative markers: *BenA* = MH279875; *CaM* = MH279852; *RPB2* = n/a). Notes: see *Aspergillus oryzae* var. *fulvus*.

Aspergillus flavus var. *proliferans* Anguli, Rajam, Thirum., Rangiah & Ramamurthi [*nom. inval.*, Art. 39.1 (McNeill et al. 2012)], Indian Journal of Microbiology 5: 94. 1965. [MB349038]. — Herb.: n/a. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a).

Aspergillus subolivaceus Raper & Fennell, Gen. *Aspergillus*: 385. 1965. [MB326661]. — Herb.: IMI 44882. Ex-type: CBS 501.65 = DTO 046-B5 = NRRL 4998 = ATCC 16862 = IMI 44882 = NRRL 20625 = QM 8902 = WB 4998. ITS barcode: AF257795. (Alternative markers: *BenA* = MG517642; *CaM* = MG518015; *RPB2* = MG517827).

Aspergillus flavus var. *columnaris* Raper & Fennell, Gen. *Aspergillus*: 366. 1965. [MB349037]. — Herb.: WB 4818. Ex-type: CBS 485.65 = DTO 046-B7 = ATCC 16870 = IFO 5324 = JCM 2225 = IMI 124932 = LCP 89.3556 = NRRL 4818 = WB 4818 = IBT 3641 = IBT 3657 = AHU B-18 (Y. Sasaki). ITS barcode: EF661563. (Alternative markers: *BenA* = MG517643; *CaM* = MG518014; *RPB2* = MG517828).

Aspergillus flavus var. *parvisclerotigenus* Mich. Saito & Tsuruta, Proc. Jpn. Assoc. Mycotoxicol. 37: 32. 1993. [MB361049]. — Herb.: NFRI 1538. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a). Notes: The original type culture and herbarium specimen of *A. flavus* var. *parvisclerotigenus* is unavailable. Strains with the same phenotype (small sclerotia and aflatoxin B production) are identified as *A. flavus* and this species is therefore considered as a synonym of *A. flavus*.

Aspergillus parvisclerotigenus (Mich. Saito & Tsuruta) Frisvad & Samson, Syst. Appl. Microbiol., 28: 450. 2005. [MB500166]. — Herb.: CBS 121.62 (neotype). Ex-type: DTO 223-C2 = CBS 121.62 = IMI 93070 = NRRL A-11612 = IBT 3651. ITS barcode: EF409240. (Alternative markers: *BenA* = MG517683; *CaM* = MG518054; *RPB2* = MG517874). Notes: The original type culture and herbarium specimen of *A. flavus* var. *parvisclerotigenus* is unavailable (Frisvad et al. 2005) and it was therefore neotypified with CBS 121.62 (ex *Arachis hypogea*, Nigeria). *Aspergillus flavus* var. *parvisclerotigenus* originates from Thailand and produces aflatoxin B while *A. parvisclerotigenus sensu* Frisvad et al. (2005) was neotypified with a strain from Nigeria that produces aflatoxin B and G. The neotypification of *A. parvisclerotigenus* is therefore incorrect (this study). *Aspergillus parvisclerotigenus sensu* Frisvad et al. is in this study described as a new species named *Aspergillus aflatoxiformans*.

Petromyces flavus B.W. Horn, I. Carbone & G.G. Moore, Mycologia 101: 424. 2009. [MB512910]. — Herb.: BPI 878851. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a). Notes: The holotype of *Petromyces flavus* is a dried slant culture of *A. flavus* NRRL 29473 (MAT1-1) crossed with *A. flavus* NRRL 29478 (MAT1-2) that produces cleistothecia and ascospores.

Aspergillus hancockii Pitt PLoS ONE e0170254: 16. 2017. [MB818219]. — Herb.: FRR 3425. Ex-type: CBS 142004 = DTO 360-G7. ITS barcode: KX858342. (Alternative markers: *BenA* = MBFL01001228.1:26000-28000; *CaM* = MBFL01000377.1:5000-7000; *RPB2* = MBFL01000137:9000-11000).

Aspergillus lanosus Kamal & Bhargava, Trans. Brit. Mycol. Soc. 52: 336. 1969. [MB326640]. — Herb.: IMI 130727. Ex-type: CBS 650.74 = DTO 034-B7 = NRRL 3648 = IMI 130727 = QM 9183 = WB 5347. ITS barcode: EF661553. (Alternative markers: *BenA* = MG517633; *CaM* = MG518017; *RPB2* = EU021642).

Aspergillus luteovirescens Blochwitz, Ann. Mycol. 31 (1-2): 80. 1933. [MB269992]. — Herb.: CBS H-23401 (neotype, designated here; MBT 381966). Ex-type: CBS 620.95 = DTO 010-H1 = CBS 116.32 (dead) = IMI 348034 = NRRL 4858 = WB 4858. ITS barcode: MG662406. (Alternative markers: *BenA* = MG517625; *CaM* = MG517998; *RPB2* = MG517808). *Synonym*: *Aspergillus bombycis* S.W. Peterson, Yoko Ito, B.W. Horn & T. Goto, Mycologia 93: 691. 2001. [MB474687]. — Herb.: BPI 745225. Ex-type: CBS 117187 = DTO 046-B8 = NRRL 26010 = IBT 23536 = IMI 386978 = NBRC 100700. ITS barcode: AF104444. (Alternative markers: *BenA* = AY017547; *CaM* = AY017594; *RPB2* = EF661458).

Aspergillus leporis States & M. Chr., Mycologia 58: 738. 1966. [MB326641]. — Herb.: NY RMF 99. Ex-type: CBS 151.66 = NRRL 3216 = ATCC 16490 = NRRL A-14256 = NRRL A-15810 = QM 8995 = RMF99 = WB 5188. ITS barcode:

AF104443. (Alternative markers: *BenA* = EF661499; *CaM* = EF661541; *RPB2* = EF661459).

Aspergillus minisclerotigenes Vaamonde, Frisvad & Samson, Int. J. Syst. Evol. Microbiol. 58: 733. 2008. [MB505188]. — Herb.: unknown. Ex-type: CBS 117635 = DTO 009-F7 = DTO 303-C6 = IBT 25032. ITS barcode: EF409239. (Alternative markers: *BenA* = EF203148; *CaM* = MG518009; *RPB2* = MG517799).

Aspergillus mottae C. Soares, S.W. Peterson & Venâncio, Mycologia 104: 692. 2012. [MB561841]. — Herb.: MUM-H 10.231. Ex-type: CBS 130016 = DTO 223-C8. ITS barcode: JF412767. (Alternative markers: *BenA* = HM803086; *CaM* = MG518058; *RPB2* = MG517878).

Aspergillus neoalliaceus A. Nováková, Hubka, Samson, Frisvad & Houbraken, published here [MB823775]. — Herb.: CBS H-23363. Ex-type: CBS 143681 = DTO 326-D3 = S765 = CCF 5433 = IBT 33110 = IBT 33353. ITS barcode: MH279420. (Alternative markers: *BenA* = MG517763; *CaM* = MG518133; *RPB2* = MG517954).

Aspergillus nomius Kurtzman *et al.*, Antonie van Leeuwenhoek 53: 151. 1987. [MB133392]. — Herb.: BPI NRRL 13137. Ex-type: CBS 260.88 = NRRL 13137 = ATCC 15546 = FRR 3339 = IMI 331920 = LCP 89.3558 = NRRL 6108 = NRRL A-13671 = NRRL A-13794. ITS barcode: AF027860. (Alternative markers: *BenA* = AF255067; *CaM* = AY017588; *RPB2* = EF661456).

Synonyms: *Aspergillus zhaoqingensis* Z.T. Qi & Z.M. Sun, Acta Mycol. Sin.: 22. 1991. [MB130300]. — Herb.: HMAS 58980. Ex-type: CBS 399.93 = DTO 301-I8 = AS 3.4626. ITS barcode: FJ491472. (Alternative markers: *BenA* = MG517757; *CaM* = MG518127; *RPB2* = MG517948).

Petromyces nomius B.W. Horn, I. Carbone & G.G. Moore, Mycologia 103: 176. 2011. [MB518289]. — Herb.: BPI 880386. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a). *Notes:* The holotype of *Petromyces nomius* is a dried slant culture of *A. nomius* NRRL 26886 (MAT1-1/MAT1-2) crossed with *A. nomius* NRRL 58994 (MAT1-2) that produces cleistothecia and ascospores.

Aspergillus novoparasiticus S.S. Gonçalves, Stchigel, Cano, Godoy-Martinez, Colombo & Guarro, Med. Mycol. 50: 158. 2011. [MB516612]. — Herb.: CBS H-20401. Ex-type: CBS 126849 = DTO 223-C3 = LEMI 250 = FMR 10121. ITS barcode: MG662397. (Alternative markers: *BenA* = MG517684; *CaM* = MG518055; *RPB2* = MG517875).

Aspergillus oryzae (Ahlb.) Cohn, Jahresber. Schles. Ges. Vaterl. Cult. 61: 226. 1884. [MB184394]. — Herb.: IMI 16266. Ex-type: CBS 100925 = CBS 102.07 = NRRL 447 = ATCC 1011 = ATCC 12891 = ATCC 4814 = ATCC 7561 = ATCC 9102 = IAM13118 = IFO 4075 = IFO 537 = IFO 5375 = IMI 16266 = IMI 44242 = LSHBA c .19 = NCTC 598 = NRRL 692 = QM 6735 = Thom 113 = WB 447. ITS barcode: EF661560. (Alternative markers: *BenA* = EF661483; *CaM* = EF661506; *RPB2* = EF661438).

Synonyms: *Eurotium oryzae* Ahlb., Dingler's Polytechn. J.: 330. 1878. [MB225012]. — Herb.: n/a. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a).

Aspergillus pseudoflavus Saito, Centbl. Bakt. Parasitkde, Abt. 2 18: 34. 1907. [MB188103]. — Herb.: n/a. Ex-type: CBS 133059 = DTO 213-F2 = WB 4787 = NRRL 4787 = IMI

360437 = IFO 4083 = JCM 2066 = IAM 2956 = ATU, A-68-6 (representative; Raper & Fennell 1965: 375, Wicklow *et al.* 2002). ITS barcode: MH279402. (Alternative markers: *BenA* = MH279869; *CaM* = MH279846; *RPB2* = n/a). *Notes:* NRRL 4787 is one of K. Saito's strains upon which Ohara (1953) based his recognition of *A. oryzae* var. *pseudoflavus* (Saito) Ohara (Raper & Fennell 1965: 375). This strain was isolated from fermented food and therefore identified here as *A. oryzae*. The blue-green pigmentation reported by Saito for old colonies has been observed in strain NRRL 483 (= CBS 132943 = DTO 213-C8 = WB 483 = IMI 360438 = Thom 3526) (Raper & Fennell 1965: 376). NRRL 483 was isolated by Wehmer (before 1914; data NRRL culture collection) and is according Raper & Fennell (1965: 376) a representative of *A. pseudoflavus*. However, the source of Wehmer's strain is probably not a fermented food product and this strain is therefore tentatively identified as *A. flavus*.

Aspergillus gymnosardae Yukawa, J. Coll. Agric. Imp. Univ. Tokyo: 362. 1911. [MB167015]. — Herb.: n/a. Ex-type: CBS 114.32 = DTO 067-H4 = QM 9703 (received as *A. gymnosardae* at CBS, originating from Japan). ITS barcode: MH279399. (Alternative markers: *BenA* = MH279866; *CaM* = MH279843; *RPB2* = n/a). *Notes:* WB 505 (= CBS 132941 = DTO 213-C6 = NRRL 505) is another representative of this species and was received from Japan. *Aspergillus gymnosardae* was reported as essential to the ripening of the tuna fish preparation, "katsuobushi" (Raper & Fennell 1965:373).

Sterigmatocystis pseudoflava (Saito) Sacc., Syll. Fung. 22: 1260. 1913. [MB194870]. — Herb.: n/a. Ex-type: CBS 133059 = DTO 213-F2 = WB 4787 = NRRL 4787 = IMI 360437 = IFO 4083 = JCM 2066 = IAM 2956 = ATU, A-68-6 (representative; Raper & Fennell 1965: 375, Wicklow *et al.* 2002). ITS barcode: MH279402. (Alternative markers: *BenA* = MH279869; *CaM* = MH279846; *RPB2* = n/a). *Notes:* see *Aspergillus pseudoflavus*.

Aspergillus oryzae var. *globosus* Sakag. & K. Yamada, J. Agric. Chem. Soc. Japan 20: 72. 1944. [MB351901]. — Herb.: n/a. Ex-type: CBS 133107 = DTO 214-A9 = WB 5004 = NRRL 5004 = IMI 359789 = IFO 4242 = IAM 2667 = NBRC 4242 = RIB 1301 = JCM 2242 = K. Sakaguchi SH 10-5. ITS barcode: MH279411. (Alternative markers: *BenA* = MH279878; *CaM* = MH279855; *RPB2* = n/a). *Notes:* NRRL 5004 was isolated from rom Shoyu-koji, Chiba Prefecture, Japan and represents *A. oryzae* var. *globosus* and *A. flavus* var. *oryzae* f. *globosus*.

Aspergillus oryzae var. *magnasporus* Sakag. & K. Yamada, J. Agric. Chem. Soc. Japan 20: 72. 1944. [MB346544]. — Herb.: n/a. Ex-type: CBS 133158 = DTO 214-B7 = WB 4804 = NRRL 4804 = JCM 22379 = IAM 2673 = Sakaguchi strain SH-8-4 (representative, Raper & Fennell 1965: 366). ITS barcode: MH279414. (Alternative markers: *BenA* = MH279881; *CaM* = MH279858; *RPB2* = n/a). *Notes:* CBS 133158 was isolated from Shoyu-koji in Japan and this strain is a representative of *A. oryzae* var. *magnasporus* (Raper & Fennell 1965: 366).

Aspergillus oryzae var. *microsporus* Sakag. & K. Yamada, J. Agric. Chem. Soc. Japan 20: 73. 1944. [MB346545]. — Herb.: n/a. Ex-type: CBS 133108 = DTO 214-B1 = NRRL 5003 = WB 5003 = IMI 359796 = IFO 4233 = K. Sakaguchi A5-1 (representative, Raper & Fennell 1965:374). ITS barcode: MH279412. (Alternative markers: *BenA* = MH279879; *CaM* = MH279856; *RPB2* = n/a).

Aspergillus candidus var. *amyolyticus* Takaoka [*nom. inval.* Art. 39.1 (McNeill *et al.* 2012)], J. Agr. Chem. Soc. Japan 23:57.

1949. [MB493812]. — Herb.: n/a. Ex-type: CBS 466.91 = DTO 389-C8 = NRRL 5032 = IFO 6215 = WB 5032 = IMI 360440. ITS barcode: MH279451. (Alternative markers: *BenA* = MH279886; *CaM* = MH279862; *RPB2* = n/a). Notes: This species produces white coloured conidia. No information was found on the source of this species but this species is generally accepted as *A. oryzae* (Raper & Fennell 1965).

Aspergillus oryzae var. *effusus* (Tirab.) Y. Ohara, Res. Bull. Fac. Agric. Gifu Univ.: 81. 1951. [MB123955]. — Herb.: n/a. Ex-type: CBS 133112 = DTO 213-I7 = WB 5030 = NRRL 5030 = IMI 360436 = IFO 5321 (representative of Ohara's *A. oryzae* var. *effusus*; Raper & Fennell 1965: 377, Wicklow et al. 2002). ITS barcode: MH279409. (Alternative markers: *BenA* = MH279876; *CaM* = MH279853; *RPB2* = n/a). Notes: NRRL 5030 is the basis for I. Ohara's recognition of *A. oryzae* var. *effusus* (Wicklow et al. 2002). According Raper & Fennell (1965: 377), Ohara's strain (NRRL 5030 = CBS 133112) differs from the original description of *A. effusus* (represented by NRRL 506 = CBS 574.65). CBS 574.65 was isolated from *Zea mays* from Vermont, USA and based on ecology and sequence data this strain is identified as *A. flavus*. CBS 133112 was isolated from fermented food and is therefore identified as *A. oryzae*.

Aspergillus oryzae var. *pseudoflavus* (Saito) Y. Ohara, Res. Bull. Fac. Agric. Gifu Univ.: 81. 1951. [MB349041]. — Herb.: n/a. Ex-type: CBS 133059 = DTO 213-F2 = WB 4787 = NRRL 4787 = IMI 360437 = IFO 4083 = JCM 2066 = IAM 2956 = ATU, A-68-6 (representative; Raper & Fennell 1965: 375, Wicklow et al. 2002). ITS barcode: MH279402. (Alternative markers: *BenA* = MH279869; *CaM* = MH279846; *RPB2* = n/a). Notes: see *Aspergillus pseudoflavus*.

Aspergillus oryzae var. *sporo-flavus* Y. Ohara, Res. Bull. Fac. Agric. Gifu Univ.: 81. 1951. [MB349042]. — Herb.: n/a. Ex-type: CBS 133064 = DTO 213-E8 = WB 4824 = NRRL 4824 = IAM 2957 = IFO 5785 = JCM 2067 = NBRC 5785 = RIB 1366 = Y. Ohara, MM-1-1 (Raper & Fennell 1965: 368). ITS barcode: MH279401. (Alternative markers: *BenA* = MH279868; *CaM* = MH279845; *RPB2* = n/a). Notes: NRRL 4824 was isolated from miso-koji in Japan and represents *A. oryzae* var. *sporo-flavus* (Raper & Fennell 1965: 368).

Aspergillus oryzae var. *microvesiculosus* Y. Ohara, J. Agric. Chem. Soc. Japan 26: 550. 1952. [MB346546]. — Herb.: n/a. Ex-type: CBS 133042 = DTO 213-F4 = WB 4803 = NRRL 4803 = IMI 359794 = IFO 4203 = IAM 2633 = JCM 2233 = JCM 2246 = NBRC 4203 = RIB 1160 = K. Sakaguchi M 1-2 (representative, Raper & Fennell 1965: 375). ITS barcode: MH279403. (Alternative markers: *BenA* = MH279870; *CaM* = MH279847; *RPB2* = n/a). Notes: NRRL 4803 was listed as a representative of *A. oryzae* var. *microvesiculosus* (Raper & Fennell 1965: 375). This strain was isolated from koji for miso, Kumamoto Prefecture by Prof. Ken-ichiro Sakaguchi, The University of Tokyo and is therefore identified as *A. oryzae*.

Aspergillus oryzae var. *tenuis* Y. Ohara, J. Agric. Chem. Soc. Japan 26: 550. 1952. [MB351902]. — Herb.: n/a. Ex-type: CBS 133044 = DTO 213-G1 = WB 4799 = NRRL 4799 = IMI 359791 = IFO 4134 = CCRC 31251 = IAM 2601 = IAM 2958 = IHEM 5780 = JCM 10114 = JCM 2068 = JCM 22426 = NBRC 4134 = RIB 1362 = RIB 3010. ITS barcode: MH279404. (Alternative markers: *BenA* = MH279871; *CaM* = MH279848; *RPB2* = n/a). Notes: NRRL 4799 belongs to T. Takahashi's "*A. oryzae* - D," and was isolated from koji for sake, and is the basis for *A. oryzae* var. *tenuis* (Wicklow et al. 2002).

Aspergillus sojae var. *gymnosardae* (Yukawa) Y. Ohara, Res. Bull. Fac. Agric. Gifu Univ.: 77. 1953. [MB349044]. — Herb.: n/a. Ex-type: CBS 133045 = DTO 213-G4 = WB 4806 = NRRL 4806 = IMI 360439 = IFO 4294 = NBRC 4294 = JCM 2226 (representative; Raper & Fennell 1965:376, Wicklow et al. 2002). ITS barcode: MH279405. (Alternative markers: *BenA* = MH279872; *CaM* = MH279849; *RPB2* = n/a). Notes: WB 4806 (= CBS 133045 = DTO 213-G4 = NRRL 4806 = IMI 360439 = IFO 4294 = NBRC 4294 = JCM 222) was isolated from katsuobushi (dried bonito) and is the basis for I. Ohara's recognition of *A. sojae* var. *gymnosardae* (Raper & Fennell 1965:376, Wicklow et al. 2002). See also notes of *A. gymnosardae*.

Aspergillus flavus var. *oryzae* f. *magnasporus* (Sakag. & K. Yamada) Nehira, J. Ferment. Technol., Osaka 35: 56. 1957. [MB347787]. — Herb.: n/a. Ex-type: CBS 133158 = DTO 214-B7 = WB 4804 = NRRL 4804 = JCM 22379 = IAM 2673 = Sakaguchi strain SH-8-4 (representative, Raper & Fennell 1965: 366). ITS barcode: MH279414. (Alternative markers: *BenA* = MH279881; *CaM* = MH279858; *RPB2* = n/a). Notes: See *Aspergillus oryzae* var. *magnasporus*.

Aspergillus oryzae var. *variabilis* (Gasperini) Y. Ohara, Res. Bull. Fac. Agric. Gifu Univ.: 84. 1953. [MB346548]. — Herb.: n/a. Ex-type: CBS 133062 = DTO 213-G6 = IAM 2959 = IFO 5768 = JCM 2247 = NBRC 5768 = NRRL 4822 = QM 8892 = RIB 1364 = WB 4822 = Y. Ohara, KK-9 (representative strain). ITS barcode: EF661564. (Alternative markers: *BenA* = EF661490; *CaM* = EF661513; *RPB2* = EF661445). Notes: NRRL 4822 fails to conform to Gasperini's (and Ohara's) description (*vide* Raper & Fennell 1965: 368) and it's questionable whether this strain is a good representative of *A. oryzae* var. *variabilis* and *A. variabilis*.

Aspergillus flavus var. *oryzae* f. *globosus* (Sakag. & K. Yamada) Nehira, J. Ferment. Technol., Osaka 35: 56. 1957. [MB347786]. — Herb.: n/a. Ex-type: CBS 133107 = DTO 214-A9 = WB 5004 = NRRL 5004 = IMI 359789 = IFO 4242 = IAM 2667 = NBRC 4242 = RIB 1301 = JCM 2242 = K. Sakaguchi SH 10-5. ITS barcode: MH279411. (Alternative markers: *BenA* = MH279878; *CaM* = MH279855; *RPB2* = n/a). Notes: See *Aspergillus oryzae* var. *globosus*.

Aspergillus flavus var. *oryzae* f. *microsporus* (Sakag. & K. Yamada) Nehira, J. Ferment. Technol., Osaka 35: 56. 1957. [MB347788]. — Herb.: n/a. Ex-type: CBS 133108 = DTO 214-B1 = NRRL 5003 = WB 5003 = IMI 359796 = IFO 4233 = K. Sakaguchi A5-1 (representative, Raper & Fennell 1965: 374). ITS barcode: MH279412. (Alternative markers: *BenA* = MH279879; *CaM* = MH279856; *RPB2* = n/a).

Aspergillus parasiticus f. *gymnosardae* (Yukawa) Nehira, J. Ferment. Technol., Osaka 35: 56. 1957. [MB347794]. — Herb.: n/a. Ex-type: CBS 114.32 = DTO 067-H4 = QM 9703 (received as *A. gymnosardae* at CBS, originating from Japan). ITS barcode: MH279399. (Alternative markers: *BenA* = MH279866; *CaM* = MH279843; *RPB2* = n/a). Notes: see *Aspergillus gymnosardae*.

Aspergillus oryzae var. *brunneus* Murak., J. Gen. Appl. Microbiol. (Tokyo) 17: 304. 1971. [MB352617]. — Herb.: RIB 1172. Ex-type: CBS 817.72 = DTO 389-C2 = IHEM 4381 = MUCL 31309 = IAM 2648 = IFO 30102 = JCM 2240 = K. Sakaguchi, S-3-8, ACTU 0-10-8. ITS barcode: MH279453. (Alternative markers: *BenA* = MH279883; *CaM* = MH279860; *RPB2* = n/a). Notes: Isolated from sake-koji, Japan.

Aspergillus oryzae var. *viridis* (as "*viride*") Murak., J. Gen. Appl. Microbiol. (Tokyo) 17: 303. 1971. [MB352619]. — Herb.: RIB 128. Ex-type: CBS 819.72 = DTO 389-D2 = ATCC 22788 = IFO 30113 = IHEM 4382 = JCM 2248 = MUCL 31310 = VTT D-88355. ITS barcode: MH279450. (Alternative markers: *BenA* = MH279887; *CaM* = MH279863; *RPB2* = n/a). Notes: this species was described from sake-koji, Japan.

Aspergillus flavus subsp. *flavus* var. *oryzae* (Ahlb.) Kurtzman, M.J. Smiley, Robnett & Wicklow, Mycologia 78: 957. 1986. [MB130238]. — Herb.: n/a. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a).

Aspergillus parasiticus Speare, Bull. Div. Pathol. Physiol., Hawaiian Sugar Planters Assoc. Exp. Sta. 12: 38. 1912. [MB191085]. — Herb.: IMI 15957ix. Ex-type: CBS 100926 = CBS 103.13 = NRRL 502 = ATCC 1018 = ATCC 6474 = ATCC 7865 = IMI 15957 = IMI 15957ii = IMI 15957iv = IMI 15957ix = IMI 15957vi = IMI 15957vii = LCP 89.2566 = LSHBA c 14 = NCTC 975 = NRRL 1731 = NRRL 3315 = NRRL A-13360 = NRRL A-14693 = Thom 3509 = WB 502. ITS barcode: AY373859. (Alternative markers: *BenA* = EF661481; *CaM* = AY017584; *RPB2* = EF661449).

Synonyms: *Aspergillus terricola* var. *americanus* Marchal, Am. J. Bot. 8: 125. 1921. [MB124083]. — Herb.: WB 424. Ex-type: CBS 580.65 = DTO 046-B9 = ATCC 1014 = ATCC 16863 = IMI 016127 = IMI 016127ii = LSHB Ac22 = NCTC 974 = NRRL 424 = QM 7475 = VKM F-2041 = WB 424. ITS barcode: MG662404. (Alternative markers: *BenA* = MG517644; *CaM* = MG518030; *RPB2* = MG517829).

Aspergillus chungii Y.K. Shih, Lingnan Sci. J.: 365. 1936. [MB251412]. — Herb.: n/a. Ex-type: CBS 115.37 = DTO 303-C2 = NRRL 4868 = IMI 093122 = WB 4868. ITS barcode: FJ491464. (Alternative markers: *BenA* = MG517759; *CaM* = MG518129; *RPB2* = MG517950).

Aspergillus parasiticus var. *globosus* Murak., J. Gen. Appl. Microbiol. (Tokyo) 12: 195. 1966. [MB353279]. — Herb.: ATCC 15517. Ex-type: CBS 260.67 = DTO 046-C2 = ATCC 15517 = CCM F-550 = CECT 2680 = DSM 2038 = IFO 30179 = IHEM 4387 = IMI 120920 = IMI 229041 = MUCL 31311. ITS barcode: MG662400. (Alternative markers: *BenA* = EF203156; *CaM* = MG518013; *RPB2* = MG517830).

Aspergillus toxicarius Murak., J. Gen. Appl. Microbiol. (Tokyo) 17: 307. 1971. [MB309247]. — Herb.: IMI 089717. Ex-type: CBS 822.72 = DTO 046-A9 = DTO 389-C9 = ATCC 22789 = IFO 30109 = IMI 089717 = RIB 4002 = TPI M 39. ITS barcode: MG662401. (Alternative markers: *BenA* = EF203163; *CaM* = MG518019; *RPB2* = MG517824).

Aspergillus flavus subsp. *parasiticus* var. *parasiticus* (Speare) Kurtzman, M.J. Smiley, Robnett & Wicklow, Mycologia 78: 958. 1986. [MB130237]. — Herb.: IMI 15957ix. Ex-type: CBS 100926 = CBS 103.13 = NRRL 502 = ATCC 1018 = ATCC 6474 = ATCC 7865 = IMI 15957 = IMI 15957ii = IMI 15957iv = IMI 15957ix = IMI 15957vi = IMI 15957vii = LCP 89.2566 = LSHBA c 14 = NCTC 975 = NRRL 1731 = NRRL 3315 = NRRL A-13360 = NRRL A-14693 = Thom 3509 = WB 502. ITS barcode: AY373859. (Alternative markers: *BenA* = EF661481; *CaM* = AY017584; *RPB2* = EF661449).

Aspergillus americanus (Marchal & É.J. Marchal) Kozak., Mycol. Pap. 161: 163. 1989. [MB127757]. — Herb.: . Ex-type: CBS 580.65 = DTO 046-B9 = ATCC 1014 = ATCC 16863 = IMI 016127 = IMI 016127ii = LSHB Ac22 = NCTC 974 = NRRL 424 = QM 7475 = VKM F-2041 = WB 424. ITS

barcode: MG662404. (Alternative markers: *BenA* = MG517644; *CaM* = MG518030; *RPB2* = MG517829).

Petromyces parasiticus B.W. Horn, I. Carbone & J.H. Ramirez-Prado, Mycologia 101: 276. 2009. [MB513282]. — Herb.: BPI 878821. Ex-type: n/a. ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a). Notes: The holotype of *Petromyces parasiticus* is a dried slant culture of *A. parasiticus* NRRL 29538 (MAT1-1) crossed with *A. parasiticus* NRRL 29570 (MAT1-2) that produces cleistothecia and ascospores.

Aspergillus pipericola Frisvad, Samson & Houbraken, published here [MB823774]. — Herb.: CBS H-23362. Ex-type: CBS 143680 = DTO 228-H4 = IBT 24628. ITS barcode: MG662385. (Alternative markers: *BenA* = MG517717; *CaM* = MG518087; *RPB2* = MG517908).

Aspergillus pseudocaelatus Varga, Samson & Frisvad, Stud. Mycol. 69: 63. 2011. [MB560397]. — Herb.: CBS H-20632. Ex-type: CBS 117616 = DTO 010-H4. ITS barcode: EF409242. (Alternative markers: *BenA* = MG517626; *CaM* = MG517995; *RPB2* = MG517809).

Aspergillus pseudonomius Varga, Samson & Frisvad, Stud. Mycol. 69: 67. 2011. [MB560398]. — Herb.: CBS H-20633. Ex-type: CBS 119388 = DTO 009-F1 = NRRL 3353 = IBT 27864. ITS barcode: AF338643. (Alternative markers: *BenA* = EF661495; *CaM* = EF661529; *RPB2* = EF661454).

Aspergillus pseudotamaris Yoko Ito, S.W. Peterson, Wicklow & T. Goto, Mycol. Res. 105: 237. 2001. [MB466527]. — Herb.: BPI 746098. Ex-type: CBS 766.97 = DTO 046-C1 = NRRL 25517. ITS barcode: AF272574. (Alternative markers: *BenA* = EF203125; *CaM* = EF202030; *RPB2* = EU021631).

Aspergillus sergii P. Rodrigues, S.W. Peterson, Venâncio & N. Lima, Mycologia 104: 693. 2012. [MB561842]. — Herb.: MUM-H 10.219. Ex-type: CBS 130017 = DTO 223-C9 = DTO 223-D1. ITS barcode: JF412769. (Alternative markers: *BenA* = MG517688; *CaM* = MG518059; *RPB2* = HM802985).

Aspergillus sojae Sakag. & K. Yamada, J. Agric. Chem. Soc. Japan 20: 72. 1944. [MB102834]. — Herb.: IMI 191300. Ex-type: CBS 100928 = DTO 046-C3 = IMI 191300. ITS barcode: KJ175434. (Alternative markers: *BenA* = KJ175494; *CaM* = KJ175550; *RPB2* = MG517831).

Synonym: *Aspergillus flavus* subsp. *parasiticus* var. *sojae* (Sakag. & K. Yamada ex Murak.) Kurtzman, M.J. Smiley, Robnett & Wicklow, Mycologia 78: 958. 1986. [MB130239]. — Herb.: IMI 191300. Ex-type: CBS 100928 = DTO 046-C3 = IMI 191300. ITS barcode: KJ175434. (Alternative markers: *BenA* = KJ175494; *CaM* = KJ175550; *RPB2* = MG517831).

Aspergillus subflavus Hubka, A. Nováková, Samson, Frisvad & Houbraken, published here [MB823776]. — Herb.: CBS H-23364. Ex-type: CBS 143683 = DTO 326-E8 = S778 = CCF 4957 = NRRL 66254 = IBT 34939. ITS barcode: MH279429. (Alternative markers: *BenA* = MG517773; *CaM* = MG518143; *RPB2* = MG517964).

Aspergillus tamaris Kita, Centralbl. Bakteriell. 2. Abth. 37: 433. 1913. [MB191425]. — Herb.: CBS 104.13. Ex-type: CBS 104.13 = NRRL 20818 = QM 9374. ITS barcode: AF004929. (Alternative markers: *BenA* = EF661474; *CaM* = EF661526; *RPB2* = EU021629).

Synonyms: *Aspergillus terricola* É.J. Marchal, Revue Mycol. (Toulouse): 101. 1893. [MB191770]. — Herb.: IMI 172294. Ex-type: CBS 579.65 = ATCC 16860 = IMI 172294 = NRRL 426 = WB 426. ITS barcode: EF661559. (Alternative markers: *BenA* = EF661472; *CaM* = EF661525; *RPB2* = EU021649). *Notes:* The name *Aspergillus terricola* competes with *Aspergillus tamarii*. The former species has priority based on publication date (1893 vs 1913). Marchal's (1893) description of *A. terricola* is incomplete and he describes the *A. terricola* as strictly uniseriate (Raper & Fennell 1965). Although this character can vary on different media and culture ages, it remains questionable whether Marchal was dealing with an *A. tamarii*. Because no type is known to be preserved of *A. terricola*, the species was neotypified with IMI 172294 (= CBS 579.65 = ATCC 16860 = NRRL 426 = WB 426) (Samson & Gams 1985). In contrast, the lectotype culture of *A. tamarii* CBS 104.13 (ex koji, Japan) was received at CBS from G. Kita. Based on these data, the identity of *A. terricola* is unclear while *A. tamarii* is unambiguously defined with an original culture.

Aspergillus flavus mut. *rufa* Blochwitz, Ann. Mycol. 27: 196. 1929 [MB123823]. — Herb.: n/a. Ex-type: n/a (Raper & Fennell 1965: 384). ITS barcode: n/a. (Alternative markers: *BenA* = n/a; *CaM* = n/a; *RPB2* = n/a).

Aspergillus lutescens Bainier ex Thom & Raper, A manual of the Aspergilli: 251. 1945. [MB284305]. — Herb.: NRRL 425. Ex-type: NRRL 425 = QM 7418 = Thom 4640.478. ITS barcode: EF661558. (Alternative markers: *BenA* = EF661475; *CaM* = EF661524; *RPB2* = EU021648).

Aspergillus terricola var. *bronzeus* Saincl., Centralbl. Gesamte Forstwesen: 118. 1949. [MB351905]. — Herb.: n/a. Ex-type: CBS 129.49 = DTO 389-C6. ITS barcode: KJ175440. (Alternative markers: *BenA* = MH279884; *CaM* = KJ175555; *RPB2* = n/a).

Aspergillus parasiticus var. *rugosus* Y. Ohara, Res. Bull. Fac. Agric. Gifu Univ.: 78. 1953. [MB353280]. — Herb.: n/a. Ex-type: CBS 133375 = DTO 389-C7 = WB 4960 = NRRL 4960. ITS barcode: MH279452. (Alternative markers: *BenA* = MH279885; *CaM* = MH279861; *RPB2* = n/a).

Aspergillus tamarii var. *crassus* Y. Ohara, Res. Bull. Fac. Agric. Gifu Univ.: 76. 1953. [MB353282]. — Herb.: n/a. Ex-type: CBS 133097 = DTO 213-H5 = NRRL 4959 = WB 4959. ITS barcode: MG662403. (Alternative markers: *BenA* = MG517678; *CaM* = MG518049; *RPB2* = MG517866).

Aspergillus effusus var. *furcatus* Bat. & H. Maia, Anais Soc. Biol. Pernambuco 13: 93. 1955. [MB351896]. — Herb.: DMUR 8. Ex-type: CBS 133104 = DTO 214-A6 = WB 4910 = NRRL 4910 = IMI 360444. ITS barcode: MH279410. (Alternative markers: *BenA* = MH279877; *CaM* = MH279854; *RPB2* = n/a).

Aspergillus flavofurcatus Bat. & H. Maia, Anais Soc. Biol. Pernambuco 13: 94. 1955. [MB292844]. — Herb.: DMUR 318. Ex-type: CBS 484.65 = NRRL 4911 = ATCC 16864 = IHEM 4385 = IMI 124938 = LCP 89.2591 = MUCL 31304 = WB 4911. ITS barcode: EF661565. (Alternative markers: *BenA* = EF661473; *CaM* = EF661527; *RPB2* = EU021651).

Aspergillus indicus B.S. Mehrotra & Agnihotri, Mycologia 54: 403. 1963. [MB326637]. — Herb.: Allahabad A-29. Ex-type: CBS 167.63 = DTO 010-G9 = NRRL 4680 = ATCC 15054 = IMI 172295 = QM 8903 = WB 4680. ITS barcode: MG662407. (Alternative markers: *BenA* = MG517624; *CaM* = MG518001; *RPB2* = MG517807).

Aspergillus terricola var. *indicus* (B.S. Mehrotra & Agnihotri) Raper & Fennell, Gen. *Aspergillus*: 412. 1965. [MB353283]. —

Herb.: Allahabad A-29. Ex-type: CBS 167.63 = DTO 010-G9 = NRRL 4680 = ATCC 15054 = IMI 172295 = QM 8903 = WB 4680. ITS barcode: MG662407. (Alternative markers: *BenA* = MG517624; *CaM* = MG518001; *RPB2* = MG517807).

Aspergillus togoensis (Henn.) Samson & Seifert, Adv. *Penicillium Aspergillus* Syst.: 419. 1985. [MB114720]. — Herb.: BR B 1009. Ex-type: CBS 205.75 = NRRL 13551 = LCP 67.3456 (CBS 272.89 = DTO 034-C1 (representative strain)). ITS barcode: AJ874113. (Alternative markers: *BenA* = FJ491477; *CaM* = FJ491489; *RPB2* = JN121479).

Aspergillus transmontanensis P. Rodrigues, S.W. Peterson, N. Lima & Venâncio, Mycologia 104: 694. 2012. [MB561843]. — Herb.: MUM-H 10.214. Ex-type: DTO 223-C7 = CBS 130015. ITS barcode: JF412774. (Alternative markers: *BenA* = HM803101; *CaM* = HM803020; *RPB2* = HM802980).

Aspergillus vandermerwei Frisvad, Hubka, Samson & Houbraken, published here [MB823777]. — Herb.: CBS H-23381. Ex-type: CBS 612.78 = DTO 069-D2 = DTO 034-B5 = NRRL 5108 = CCF 5683 = IBT 13876. ITS barcode: EF661567. (Alternative markers: *BenA* = EF661469; *CaM* = EF661540; *RPB2* = MG517838).

Chemical synoptic key for *Aspergillus* section *Flavi*

Species list

- 1 *A. aflatoxiformans*
- 2 *A. alliaceus*
- 3 *A. arachidicola*
- 4 *A. aspearensis*
- 5 *A. austwickii*
- 6 *A. avenaceus*
- 7 *A. bertholletius*
- 8 *A. caelatus*
- 9 *A. cerealis*
- 10 *A. coremiiformis*
- 11 *A. flavus*
- 12 *A. hancockii*
- 13 *A. lanosus*
- 14 *A. leporis*
- 15 *A. luteovirescens*
- 16 *A. minisclerotigenes*
- 17 *A. mottae*
- 18 *A. neoalliaceus*
- 19 *A. nomius*
- 20 *A. novoparasiticus*
- 21 *A. oryzae*
- 22 *A. parasiticus*
- 23 *A. pipericola*
- 24 *A. pseudocaelatus*
- 25 *A. pseudonomius*
- 26 *A. pseudotamarii*
- 27 *A. sergii*
- 28 *A. sojae*
- 29 *A. subflavus*
- 30 *A. tamarii*
- 31 *A. togoensis*
- 32 *A. transmontanensis*
- 33 *A. vandermerwei*

Aflatoxin B type: 1, 3, 5, 9, 11, 15, 16, 17, 19, 20, 22, 23, 24, 25, 26, 27, 31, 32

Aflatoxin G type: 1, 3, 5, 9, (11), 15, 16, 17, 19, 20, 22, 23, 24, 25, 27, 32
 Aflatrem: 1, 5, 9, 11, 16, 23, 27
 Aflavarins, isokotanins, kotanins, siderins: 1, 2, 5, 9, 11, 12, 16, 23, 27, 33
 Aflavazol: 9, 11, 16, 27
 Aflavinines: 1, 4, 11, 16, 17, (21), 23, 26, 27, 29
 "Alkca": 8, 24, 26
 Altersolanols: 2, 6, 8, 13, 15, 26, 33
 Anominine: 2, 18, 19, 33
 Antarone A: 2
 Antibiotic Y: 14
 Asperfuran: 11, 21, 27, 28
 Aspernommin: 19
 Asperopterin*: 21
 Aspergillic acid: 1, 3, 5, 9, 11, 15, 16, 17, 19, 20, 22, 23, 24, 26, 27, 28, 32
 Aspergillomarasmines*: 11, 21
 Aspirochlorin: 1, 6, 8, 11, 20, 21, 24, 26, 28, 29, 30, 32, 33
 Asperlicin: 2, 13, 33
 Brefeldin A: 18, 33
 Chrysogine: 3, 15, 26, 28
 Citreoisocoumarin: 11, 21, (30)
 Clavatols: 14
 Cyclopiazonic acid: 1, 5, 7, 9, 11, (12, speradine F), 16, 17, 21, 23, 24, 26, 27, 30
 Dehydroterrestric acid: 12
 Dityptoleucine: 21
 Dityptophenaline: 3, 11, 20, 24
 Eupenifeldin*: 12
 Flavimin (not structure elucidated): 11
 Fumaryl-D,L-alanine*: 30
 "Gfn": 1, 5
 Griseofulvin: 13, (33)
 Hancockiamides: 12
 7-Hydroxytrichothecolone: 12
 Kojic acid: 1, 2, 3, 4, 5, 7, 8, 9, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 32, 33
 Leporins: 11, 14
 Leporzines: 14
 "Met I": 2, 13
 Mevinolin: 4
 Miyakamides / oryzamides: 3, 11, 15, 19, 20, 21, 26, 28, 32
 3-Nitropropionic acid*: 6, 11, 21, 30
 Ochratoxins: 2, 18, 33
 Onycins: 12
 Parasiticolides/astelolides: 3, 7, 11, 16, 21, 22, 29
 Paspaline, paspalinine: 1, 2, 4, 5, 9, 11, 14, 16, 17, 18, 19, (21), 23, 26, 27, 31
 Paxillin: 31
 Penicillins*: 11, 21, 22
 Pseurotin A: (6), 14, 19
 Sporogen AO1: 15, 21
 Tenuazonic acid: 7, 8, 15, 19, 24, 25, 26, 30
 "Tetracyclic compound": 20
 Ustilaginoidin C: 7, 11, 22
 Versicolorins: 1, (2), 3, 5, (7), 9, 11, 15, 16, 17, 19, 20, 22, 23, 24, 25, 26, 27, (28), 31, 32
 *Note: The strains in this study were not screened for these extrolites. The data are based on literature and only isolates with verified identity are included.

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APPENDIX A. SUPPLEMENTARY DATA

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.simyco.2018.06.001>.

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