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**Aspergillus section Nidulantes (formerly Emericella): Polyphasic taxonomy, chemistry and biology**

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**Abstract:** Aspergillus section Nidulantes includes species with striking morphological characters, such as biseriate conidiophores with brown-pigmented stipes, and if present, the production of ascocoma embedded in masses of Hülle cells with often reddish brown ascospores. The majority of species in this section have a sexual state, which were named Emericella in the dual name nomenclature system. In the present study, strains belonging to subgenus Nidulantes were subjected to multilocus molecular phylogenetic analyses using internal transcribed spacer region (ITS), partial β-tubulin (BenA), calmodulin (CaM) and RNA polymerase II second largest subunit (RPB2) sequences. Nine sections are accepted in subgenus Nidulantes including the new section Cavencolus. A polyphasic approach using morphological characters, extritoxins, physiological characters and phylogeny was applied to investigate the taxonomy of section Nidulantes. Based on this approach, section Nidulantes is subdivided in seven clades and 65 species, and 10 species are described here as new. Morphological characters including colour, shape, size, and ornamentation of ascospores, shape and size of conidia and vesicles, growth temperatures are important for identifying species. Many species of section Nidulantes produce the carcinogenic mycotoxin sterigmatocystin. The most important mycotoxins in Aspergillus section Nidulantes are aflatoxins, sterigmatocystin, emestrin, fumitremorgins, asteltoxins, and pxillxin while other extrolites are useful drugs or drug lead candidates such as echinocandins, mulundocandins, calbistrins, varitriols, variecolins and terrain. Aflatoxin B1 is produced by four species: A. astellatus, A. miraensis, A. olivicola, and A. venezuelensis.

**Key words:** Ascomycetes, Eurotiales, Multi-gene phylogeny, Sterigmatocystin.


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**INTRODUCTION**

The species of *Aspergillus* fall into distinct clusters, which have been called “groups” by Thom & Church (1926), Thom & Raper (1945) and Raper & Fennell (1965). These groups do not have nomenclatural standing and therefore Gams et al. (1985) introduced formal names for these groups as subgenera and sections. Subgenus Nidulantes contained five sections, namely sections Nidulantes, Versicoles, Usti, Terrei, and Flavipedes. Several investigations were conducted for nearly 20 years to test the taxonomic hypotheses based on phenotypic analysis. Peterson (2008) and Peterson et al. (2008) assessed phylogenetic relationships across Aspergillus using four loci and they accepted sections Nidulantes, Usti, Ochraceorosei, Sparsi and three hypothetical sections Raperi, Silvati, Bispori. Varga et al. (2010a, 2010b) introduced sections Aenei and Sparsi based on CaM, BenA and ITS sequence data, whereas Houbraken et al. (2014) accepted eight sections namely Aenei, Bispori, Cremei, Nidulantes, Ochraceorosei, Silvati, Sparsi and Usti in subgenus Nidulantes. Until now approximately 100 species have been described in this subgenus. The indoor relevant species in Aspergillus subgenus Nidulantes section Versicoles are closely related to species in section Nidulantes (Raper & Fennell 1965, Klich 1983, Jurjevic et al. 2012).

Aspergillus section Nidulantes accommodates *Aspergillus nidulans* and other species producing biseriate conidiophores with pale brown pigmented stipes, and if present, the ascocoma embedded in masses of Hülle cells (Frisvad & Samson 2004, Horie 1978, 1979, 1980, Kong & Qi 1986, Horie et al. 1989, 1990, 1996a,b, 1998, 2000, Raper & Fennell 1965, Samson & Mouchacca 1975, Stichigl & Guarro 1997, Thom & Raper 1939, Zalar et al. 2008 and others). The majority of section Nidulantes species are able to produce a sexual state and those species were, in the dual name nomenclature system, assigned to the genus Emericella. Because of the adoption of the “one fungus: one name” nomenclatural system, all Emericella species have been transferred to Aspergillus (Samson et al. 2014). Most former Emericella species belong to Aspergillus subgenus Nidulantes section Nidulantes. The only exceptions are: 1) *Aspergillus heterothallicus* (= Emericella heterothallica), the only known heterothalic species in subgenus Nidulantes, currently classified in Aspergillus subgenus Nidulantes section Usti (Houbraken et al. 2007, Samson et al. 2011), and 2) *A. bioclor* (= *A. biclor*), *A. discophorus* (= *A. discophora*), *A. foeniculica*
Aspergillus subgenus Nidulantes section Aenei (Varga et al. 2010a).

The morphology of the ascospores including colour, shape, size and ornamentation are of particular importance for species delineation and identification in Emericella (Thom & Raper 1939, Christensen & Raper 1978, Horie 1980, Christensen & States 1982, Ismail et al. 1995, Zalar et al. 2008, Matsuzawa et al. 2012, Guarro et al. 2013). Nowadays multiple methods are applied for species recognition and for example Frisvad & Samson (2004) applied a polyphasic analysis and described A. venezuelensis (= E. venezuelensis) based on morphological characters, extrolites and phylogenetic analyses. Using molecular phylogenetics, morphological data and growth temperatures Matsuzawa et al. (2012) discussed the species concept in Emericella and found that several species including A. nidulans (= A. nidulans), A. subtilis (= E. subtilata), A. montenegroi (= E. montenegroi), A. nidulans var. latus (= E. nidulans var. lata), A. quadrilineatus (= E. quadrilineata), A. mivijii (= E. mivijii), A. parvathecius (= E. parvathecius) and A. acristatus (= E. acristata) were undistinguishable by phylogenetic analysis alone. Therefore, they suggested to evaluate phylogenetic, morphological and physiological characters to identify species in this genus or section.

Aspergillus section Nidulantes species are widely distributed in nature and are believed to play significant roles in decomposition processes (Raper & Fennell 1965). The most well-known species A. nidulans, with the whole genome being sequenced in 2005 (Gaiaughan et al. 2005), occupies a place of prominence second only to Neurospora in the field of fungal genetics, being used to study a wide range of subjects including recombination, DNA repair, mutation, cell cycle control, nucleokinesis, pathogenesis, metabolism, and experimental evolution (Pontercorvo et al. 1954, Herbert & Arst 1976, Dean & Timberlake 1989, Schoustra et al. 2006, Todd et al. 2007). In addition to its role as genetic model, A. nidulans has been demonstrated as causative agent of diverse infections in humans. It was identified in cases of oto-mycosis, mycetoma, keratitis, siniusitis and pulmonary aspergillosis and was recognised as a major cause of invasive aspergillosis (IA) in patients with chronic granulomatous disease (CGD) (Bayle et al. 1968, Doby & Kombila-Favry 1978, Joshi et al. 1985, Segal et al. 1998, Henriot et al. 2012). Other species in section Nidulantes and Versicolores such as A. delacroixii (= A. spinulosporus), A. dentatus, A. protuberus, A. quadrilineatus, A. subtilis, A. unguis, A. sydowi, A. stellatus, A. versicolor and A. hongkongensis have also been reported in human infections (Polacheck et al. 1992, de Hoog et al. 2000, Verweij et al. 2008, Arabatzis et al. 2011, Yu et al. 2013, de Fontbrune et al. 2014, Sabino et al. 2014, Tsang et al. 2016).

Members of Aspergillus section Nidulantes produce a high number of secondary metabolites: such as aflatoxins and sterigmatocystins, echinocandins and mulundocandins, penicillins, terreins, and many others (Turner 1971, Cole & Cox 1981, Turner & Aldridge 1983, Frisvad 1985, Liu & Shen 2011, Saito et al. 2016). In general, similar metabolites can occur in phylogenetically closely related species, for example A. variecolor (= E. variecolor), A. filifera (= E. filifera), A. stella-maris (= E. stella-maris), A. olivicola (= E. olivicola), A. venezuelensis (= E. venezuelensis) and A. astellatus (= E. astellata) all produce the octaketides shaximithanones, emericellin and arugosins, while A. pluriseminatus (= E. pluriseminata), a phylogenetically species distant from these, showed an entirely distinctive extrolite profile (Zalar et al. 2008). Anidulafungin, a semisynthetic lipopeptide antifungal drug of the echinocandin type, is derived from a fermentation product of A. spinulosporus (syn. A. nidulans var. echinulatus) (Nyfeler & Keller-Schierlein 1974), A. parvathecius, A. navahoensis, A. quadrilineatus, A. rugulosus and A. pachycristatus (= Aspergillus nidulans var. roseus) nomen nudum) (Boczekker & Kastner 1981, Klich et al. 2001, de la Cruz et al. 2012, Matsuzawa et al. 2012, Bills et al. 2014, Yue et al. 2015). Aflatoxin production is observed in A. astellata (= E. astellata), A. venezuelensis (= E. venezuelensis) and A. olivicola (= E. olivicola) (Frisvad & Samson 2004, Frisvad et al. 2004, Zalar et al. 2008). Recently, a fungal natural product aspergillomarasmine A (AMA) was identified from extracts of A. versicolor (strain WAC-138). This compound combined with a carbapenem antibiotic has therapeutic potential to address the clinical challenge of MBL (metallo-β-lactamase)-positive carbapenem-resistant Gram-negative pathogens (King et al. 2014).

In this study, we delineate the sections of Aspergillus subgenus Nidulantes using a phylogenetic analysis of a combined data set of partial ITS, β-tubulin (BenA), calmodulin (CaM) and RNA polymerase II second largest subunit (RPB2) gene sequences. Subsequently, the taxonomy of section Nidulantes was investigated using a polyphasic approach including sequence analyses, morphological and physiological characterisation, and extrolite profiles.

**MATERIAL AND METHODS**

**Fungal strains**

Isolates used in this study were obtained from: 1) CBS, culture collection of CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; 2) IBT, culture collection of the DTU Systems Biology, Lyngby, Denmark; and 3) CGMCC, China General Microbiological Culture Collection Centre, Beijing, China. Isolates deposited in the working collection of the Applied and Industrial Mycology department (DTO) housed at CBS-KNAW were also included in this study. An overview of strains is listed in Table 1.

**DNA extraction, PCR amplification and sequencing**

Strains were grown for 1 wk on MEA prior to DNA extraction. DNA was extracted using the UltracleanTM Microbial DNA isolation Kit (MoBio, Solana Beach, U.S.A.) and stored at ~20 °C. ITS, BenA, CaM, and RPB2 were amplified and sequenced using methods and primers as previously described (Houben & Samson 2011, Samson et al. 2014).

**Phylogenetic analysis**

The phylogenetic relationship between species was studied using a combined data set containing ITS, BenA, CaM and RPB2 sequences, individual single gene phylogenies were also generated to resolve relationships among the species. Sequence alignments were generated with MAFFT v. 7 (Katoh & Standley 2013). The most suitable substitution model was determined using FindModel (Posada & Crandall 1998). Bayesian analyses
<table>
<thead>
<tr>
<th>Species name</th>
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<th>Substrate and origin</th>
<th>GenBank accession nr.</th>
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<td><em>amoenus</em></td>
<td>Nidulantes</td>
<td>NRRL 4838&lt;sup&gt;T&lt;/sup&gt;</td>
<td>Berberis sp. fruit, Germany</td>
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<td><em>A. angustatus</em></td>
<td>Nidulantes</td>
<td>CBS 273.65&lt;sup&gt;T&lt;/sup&gt; = DTO 319-H8</td>
<td>Mangiferina indica root, Mali</td>
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<td><em>A. askiburgiensis</em></td>
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<td>CBS 134374&lt;sup&gt;T&lt;/sup&gt; = CCF 4716 = CCF 4428 = NRRL 62818 = IBT 33114 = IBT 32911</td>
<td>Ex cave sediment, Czech Republic</td>
<td>LN873939 LN873952 LN873965 LN873984</td>
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<td>Soil from cave, Somerset, England, UK</td>
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<td>Canvas haversack for respirator, Australia</td>
<td>EU448273 AY339994 EU443975 KU866936</td>
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<td>Kangaroo rat cheek pouch, Sevilleta National Wildlife Refuge, New Mexico, USA</td>
<td>KU866588 KU866624 KU866711 KU866966</td>
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<td><em>A. aureolatus</em></td>
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<td>Air, Beograd, Serbia</td>
<td>EF652501 EF652325 EF652413 EF652237</td>
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<td>Cape town, South Africa</td>
<td>KU866663 KU866898 KU866726 KU866985</td>
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<td>CBS 314.89&lt;sup&gt;T&lt;/sup&gt; = DTO 047-I4</td>
<td>Forest soil, at base of Diospyros mespiliformis (ebony tree), Okavango Delta, Island Forest Area, Botswana</td>
<td>KU866572 KU866812 KU866695 KU866949</td>
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<td><em>A. caespitosus</em></td>
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<td>Desert soil, Western Desert, Egypt</td>
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<td>NRRL 58592&lt;sup&gt;T&lt;/sup&gt;</td>
<td>Soil under Saccharum oficinarum, Nakorn Pathom, Thailand</td>
<td>KU866767 KU866897 KU866789 KU867054</td>
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<td>Indoor air sample, California, USA</td>
<td>JQ301891 JN853980 JN854043 JN853832</td>
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<td>Grey soil, Egypt</td>
<td>EF652505 EF652329 EF652417 EF652241</td>
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<td>Grey soil, Egypt</td>
<td>KU866619 KU866861 KU866757 KU867020</td>
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<td>Dromia erythropus (crab, Crustacea), Morro of Garapita, Mochima Bay, Venezuela</td>
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<td>Dromia erythropus (crab, Crustacea), Morro of Garapita, Mochima Bay, Venezuela</td>
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<td>CBS 271.91(^1) = IFM 4997 = NHL 2999 = ATCC 76117 = IBT 14808 = DTO 046-A2</td>
<td>Soil with steppe-type vegetation of Sabaneta, Falcon State, Coro City, Venezuela</td>
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<td>CBS 989.72 = IBT 22830 = DTO 048-A3</td>
<td>Arid soil, of recent reclamation and cultivated with corn, New Valley Region, Western Desert, Dakhla Oasis, 12 km NW of Mut, Egypt</td>
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<td><em>A. falcifer</em></td>
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<td>CBS 126188 = IBT 23426 = RMF N172 = DTO 060-A1</td>
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<td>Hypersaline water, Secovlje salterns, Adriatic coast, Slovenia</td>
<td>EU448277 EF428372 EU443973 KU866932</td>
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<td>CBS 128791 = IFM 54282 = CBM FA-865 = DTO 098-H8 (ex-type of <em>A. chinensis</em>)</td>
<td>Kara Kuri Lake, near Mt.Kungur, Xinjiang Province, China</td>
<td>AB249003 AB248345 AB476806 KU866982</td>
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<td>Hypersaline water, Secovlje salterns, Slovenia</td>
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<td>Herbal drug of Tribulus terrestris, India</td>
<td>KX432635 KX432632 KX432635 KU867034</td>
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<td><em>A. hongkongensis</em></td>
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<td>HKU49(^7) = NBRC 110693 = NCPF 7870 = BCRC FU30360</td>
<td>From the big toenail of a man with onychomycosis in Hong Kong, China</td>
<td>AB987907 LC000552 LC000565 LC000578</td>
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<td><em>A. israelensis</em></td>
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<td>CBS 140627(^7) = IBT 24293 = DTO 325-E2</td>
<td>Evaporation pond, Ein Bokek, Dead Sea, Israel</td>
<td>KU866677 KU866915 KU867097 KU867062</td>
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| A. striatus | Nidulantes | CBS 592.65T = IBT 22824 = ATCC 16815 = NRRL 4699 = CBS 283.67 = IHEM 4515 = IMI 096679 = LCP 82.3319 = WB 4699 = DTO 320-D3 | Mangrove mud, Kagh Islands | EF652470 EF652294 EF652382 EF652206 |}
| A. subversicolor | Nidulantes | NRRL 58999T | Green coffee berries, India | JG019894 JN853970 JN853799 |}
| A. sulphureoviridis | Nidulantes | CBS 140626T = IBT 21868 = DTO 325-D1 | Indoor air, factory, Denmark | KU866673 KU866911 KU867058 |}
| A. sydowi | Nidulantes | CBS 593.65T = IBR 250 = IMI 211384 = NRRL 254 | Clinical Isolate, Waycross, Georgia, USA | EF652450 EF652274 EF652362 EF652186 |}
| A. tabacinus | Nidulantes | CBS 122718T = NRRL 4791 = IFO 4098 = QM 9766 = WB 4791 | Tobacco | EF652478 EF652302 EF652390 EF652214 |}
| A. tenesseensis | Nidulantes | NRRL 13150T | Toxic dairy cattle feed, Tennessee, USA | JQ019895 JN853976 JN853806 |}
| A. undulatus | Nidulantes | CBS 261.88T = AS 3.4510 = IBT 28027 = DTO 011-A1 | Soil, Hubei Province, Shennongjia, China | EU448275 EF423863 EU443898 KU866928 |}
| A. varians | Nidulantes | CBS 505.65T = NRRL 4793 = ATCC 16836 = IFO 4114 = IMI 172297 = WB 4793 = IBT 22568 = DTO 073-B5 | Unknown source | EF652479 EF652303 EF652391 EF652215 |}
| A. venenatus | Nidulantes | NRRL 13147T | Toxic dairy cattle feed, Tennessee, USA | JQ019896 JN854003 JN854014 JN853803 |}
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<td>Man skin scrapings, Illinois</td>
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<td>A. discophorus</td>
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were deposited in GenBank.

than 1 pp and 95 % bs are thickened. Newly obtained sequences less than 70 % bs are not shown. Branches with values more analysis are labelled at the nodes. Values less than 0.95 pp and probabilities (pp) values and bootstrap (bs) percentages of phylogeny. The resulting trees were visualized with FigTree

2003). The sample frequency was set to 100 and the

ments (0.1 g ZnSO4$\cdot$7H2O and 0.5 g CuSO4$\cdot$5H2O in 100 ml distilled water) were added to all media to obtain stable pigment

Macroscopic characters were studied on the agar media Czapek Yeast Autolysate agar (CYA), CYA supplemented with 5 % NaCl (CYAS), yeast extract sucrose agar (YES), creatine sucrose agar (CREA), dichloran 18 % glycerol agar (DG18), oatmeal agar (OA) and malt extract agar (MEA; Oxoid CM0059), trace elements (0.1 g ZnSO4$\cdot$7H2O and 0.5 g CuSO4$\cdot$5H2O in 100 ml distilled water) were added to all media to obtain stable pigment production and consistent conidial colours (Samson et al. 2010). The isolates were inoculated at three points on 90 mm plates and incubated for 7 d at 25 °C in darkness. In addition, CYA plates were incubated at 37 and 40 °C (CYA 37 °C and CYA 40 °C, respectively), while additional MEA plates were incubated at 37 °C (MEA 37 °C). After 7 d of incubation, colony diameters were recorded. Colony texture, degree of sporulation, obverse

were performed with MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003). The sample frequency was set to 100 and the first 25 % of the trees removed as burn-in. Maximum likelihood analyses including 500 bootstrap replicates were run using RAxML (Gamma model of rate heterogeneity) (Stamatakis et al. 2008). Aspergillus flavipes (NRRL 302$^T$) was used as outgroup in the Aspergillus subgenus Nidulantes phylogeny and Aspergillus ustus (CBS 261.67$^T$) as outgroup in the section Nidulantes phylogeny. The resulting trees were visualized with FigTree v1.4.2 and annotated using Adobe Illustrator CS5. BI posterior probabilities (pp) values and bootstrap (bs) percentages of analysis are labelled at the nodes. Values less than 0.95 pp and less than 70 % bs are not shown. Branches with values more than 1 pp and 95 % bs are thickened. Newly obtained sequences were deposited in GenBank.

Morphological analysis

Macroscopic characters were studied on the agar media Czapek Yeast Autolysate agar (CYA), CYA supplemented with 5 % NaCl (CYAS), yeast extract sucrose agar (YES), creatine sucrose agar (CREA), dichloran 18 % glycerol agar (DG18), oatmeal agar (OA) and malt extract agar (MEA; Oxoid CM0059), trace elements (0.1 g ZnSO4$\cdot$7H2O and 0.5 g CuSO4$\cdot$5H2O in 100 ml distilled water) were added to all media to obtain stable pigment production and consistent conidial colours (Samson et al. 2010). The isolates were inoculated at three points on 90 mm plates and incubated for 7 d at 25 °C in darkness. In addition, CYA plates were incubated at 37 and 40 °C (CYA 37 °C and CYA 40 °C, respectively), while additional MEA plates were incubated at 37 °C (MEA 37 °C). After 7 d of incubation, colony diameters were recorded. Colony texture, degree of sporulation, obverse and reverse colony colours, production of soluble pigments, exudates and ascomata were determined. Acid production on CREA is indicated by a change in the pH sensitive bromocresol purple dye from purple to yellow around growing colonies. For ascomata production, OA, MEA and CYA plates were incubated at 25 °C for up to four wks.

Light microscope preparations were made from 1 wk old colonies grown on MEA, for species which do not sporulate on MEA, other media (YES, OA or DG 18) were used for preparations and were indicated in species descriptions. Ascomata, ascii and ascospores were observed from OA. Lactic acid (60 %) was used as mounting fluid. Alcohol (96 %) was used to remove excess conidia and prevent air bubbles. A Zeiss Stereo Discovery V20 dissecting microscope and Zeiss AX10 Imager A2 light microscope both equipped with a Nikon DS-Ri2 camera and software NIS-Elements D v4.50 were used to capture digital images. The temperature growth profile of the strains was studied on CYA. Strains were inoculated at one point in the centre of the plates and incubated at 18, 21, 24, 30, 33, 37, 40, 45 and 50 °C for 5 d in darkness. Species in the clade Versicocoli were studied extensively by Jurjevic et al. (2012) and are not included here.

Cryo Scanning Electron Microscopy (cryoSEM)

Mature ascocarps were harvested from 30–50 day old cultures on OA. Ascocarps were crushed and ascospores were picked using a dissecting needle and carefully transferred into distilled deionized water. A drop (5 μl) of this suspension was transferred to a polycarbonate membrane (1.0 Micron, 47 mm, GE Water and Process Technologies, Trevose, PA, USA). Polycarbonate membranes were placed on filter paper circles (0.7 mm, Schleicher & Schuell)
to ensure that fluid was quickly absorbed through the pores of the membranes. The quick removal of fluid resulted in an equal distribution of ascospores and also more ascospores that could be viewed from the equatorial side as compared with passive evaporation of a droplet. The polycarbonate membranes with ascospore depositions were carefully cut out with a surgical knife and transferred to an aluminium stub. After drying at room temperature for one wk, the stubs were sputter-coated with gold three times for 30 s in a JEOL JFC-1300 Auto-fine coater and then viewed using a JEOL 5600LV scanning electron microscope (JEOL, Tokyo, Japan). Electron micrographs were acquired with the F4 scan at an acceleration voltage of 10 kV.

**Extrolite analysis**

Representatives of 48 section Nidulantes species were analysed for extrolite production using the method originally described by Frisvad & Thrane (1987, 1993) and modified by Smedsgaard (1997), and using the UHPLC-DAD method described in Kildgaard et al. (2014) and Kiltgaard et al. (2014). Strains were inoculated and incubated on CYA and YES agar for 7 d at 25 °C (Hubka et al. 2014, 2016). Strains were then transferred to an aluminium stub. After drying at room temperature spore depositions were carefully cut out with a surgical knife and viewed from the equatorial side as compared with passive evaporation of ascospores and also more ascospores that could be released through the pores of the membranes. The presence of extrolites was confirmed using a JEOL JSM 6360 scanning electron microscope. Electron micrographs were acquired with the F4 scan at an acceleration voltage of 10 kV.

**RESULTS**

**Phylogeny**

The phylogenetic relationships among Aspergillus subgenus Nidulantes species were studied using concatenated sequence data of four loci: ITS, BenA, CaM and RPB2. In total, 130 ex-type strains were included in the analysis and the total length of the aligned data set was 2483 characters, containing 498, 527, 537 and 921 bp for ITS, BenA, CaM and RPB2 respectively. For Bayesian analyses, GTR+G model was used for ITS, BenA, CaM and RPB2. Fig. 1 shows the results of the analysis and reveals the presence of nine lineages in subgenus Nidulantes. These lineages are treated here as sections, namely Aenei, Nidulantes, Usti, Raperi, Silvati, Bispori, Ochraceorosei, Sparsi and the newly introduced section Cavernicolus. The members of sections Nidulantes and Versicolores form a well-supported group (1 pp, 100 % ML), which is in agreement with previous studies (Peterson 2008, Peterson et al. 2008). On the basis of the phylogenetic analysis we follow Hubka et al. (2016) and include Versicolores within section Nidulantes. Based on our results, 65 species are well resolved in section Nidulantes. Section Cavernicolus (1 pp, 85 % ML) contains five species previously assigned to section Usti, namely A. californicus, A. cavernicolus, A. egyptiacus, A. kassunensis and A. subseptissili. Most of species in this section produce short conidiophores, except A. californicus, which produces long, light brown conidiophores, resembling typical section Usti species (Samson et al. 2011). Aspergillus fusicolus included in section Sparsi by Peterson (2008), clusters with A. ochraceoroseus and A. rambelli with poor bootstrap and Bayesian statistics.

To define relationships within section Nidulantes, an aligned concatenated data set with a total length of 2,400 characters (ITS 533; BenA 472; CaM 505; RPB2 890 bp) was analysed. For Bayesian analysis, GTR+G was used for BenA, CaM and ITS and K2P+G for RPB2. Members of section Nidulantes are resolved into seven well supported clades (Fig. 2). The A. nidulans clade contains 23 species including the type species of section Nidulantes-A. nidulans. Aspergillus denticus is phylogenetically identical with A. nidulans and therefore considered a synonym. Similarly, four species (A. parvathecius, A. nidulans var. acrinitus, A. floriformis and A. miyajii) are synonymised with A. quadrilineatus. Aspergillus sublatus and A. montenegroi are synonymised with A. latus; A. rugulosus var. lauzulina and A. cleistominutus are synonymised with A. rugulosus; A. similiis is synonymised with A. violaceus. The relation between the clades A. aurantiobrunneus, A. speluncicus and A. versicolor are uncertain, A. aurantiobrunneus clade clusters outside clades A. speluncicus and A. versicolor in the subgenus phylogeny (Fig. 1), while it clusters with A. speluncicus clade in the phylogeny (Fig. 2), both of the phylogenies do not have bootstrap and Bayesian statistics. The A. stellatus clade contains species with either stellate or appended ascospores. Aspergillus chinensis is considered a synonym of A. filifer based on phylogenetic and morphological characters as suggested by Matsuzawa et al. (2012) and Hubka et al. (2016).

**Morphology**

Morphological characters of Aspergillus section Nidulantes are summarised in Tables 2–4. Ascospores can be globose, sub-globose, stellate or appended (Figs 3–6). The ornamentation on the ascospore convex is informative for species identification. For example in the A. nidulans clade, the ascospore ornamentation can be irregularly wrinkled (A. corrugatus), finely pitted (A. foveolatus), rugolose (A. rugulosus) or echinulate (A. spinulosporus). Ascospore crests are two in number in most species, four crests are only observed in A. quadrilineatus. Ascospore colour is also taxonomically informative, for example the violet ascospores can easily differentiate A. violaceus from other section Nidulantes species (Fig. 5). In A. aurantiopurpureus, orange ascospores can turn to violet in older cultures (Fig. 4), which is firstly observed in section Nidulantes. However, ascospore colour can be variable in some species. Peintner & Rainer (1999) reported an isolate of A. nidulans (CBS 100522) with blue ascospores; another example is A. miraensis, which was originally described with violet ascospores (Zhang et al. 2013), but shows orange to reddish brown ascospores in our study. Ascomata, when present, are mostly 200–600 μm, but it may be highly variable depending on the media, and in some species like A. quadrilineatus and A. violaceus, variable size of ascomata were observed in different strains even under same cultivation condition. Thus the ascoma size is not recommended as a distinguishing feature.

In general, species in Aspergillus section Nidulantes produce more or less brown-pigmented conidiophores, typically smooth but occasionally showing surface protuberances. Vesicles are usually globose, sub-globose or subclavate, narrower than 30 μm. Conidia are typically globose and echinulate, green in mass, in some cases (A. asperescens and A. varians) conidia are ellipsoidal (Figs 7, 8). For non-ascosporic species, size and shape of conidiophores and conidia are taxonomically informative (Table 2).

Macromorphology including temperature growth profile, production of cleistothecia, mycelium colour, sporulation, soluble pigments, and exudate is also important distinguishing character. Species within the A. nidulans clade grow optimally at 37°C but
Fig. 1. Phylogenetic tree of subgenus Nidulantes inferred from concatenated 4 loci: ITS, BenA, CaM and RPB2. Branches with values more than 1 pp and 95% bs are thickened. The phylogram is rooted with Aspergillus flavipes (NRRL 302²).
do not grow at 50 °C (Table 5, Figs 9, 10), while species in the other six clades cannot grow at 40 °C, some species such as *A. asperescens*, *A. aureolatus*, *A. pluriseminatus*, *A. spelunceus* and *A. varians* cannot grow at 36 °C (Table 5, Figs 11, 12).

**Extrolites**

Forty eight species were analysed for extrolites and produced several shared or unique small molecule extrolites and often had species specific profiles (mentioned after each species description). An overview of reported extrolites from section *Nidulantes* species is shown in Table 6. Sterigmatocystins, shamixanthones, and violaceols are common to many species and are also found in some species of sections *Usti* and *Aenei* (Houbraken et al. 2007, Varga et al. 2010a, Samson et al. 2011). The shamixanthones are produced by 19 species in section *Nidulantes*. The ascospore / Hülle cell-associate metabolite asperthecin is produced by 20 species in the section. The desertorin polyketides are produced by 13 species, while violaceol polyketides are found in 19 species. The falconensins and falconensons are produced by the closely related species *A. aurantiopurpureus*, *A. falconensis*, *A. fruticulosus*, *A. navahoensis* and *A. revurvatus*. Emericellin is found in 18 species, asperugin polyketides is produced by 14 species and the shikimic derived emerins are formed by two species. The dithiodiketopiparazine mycotoxin emestrin is produced by six closely related species: *A. foveolatus*, *A. jaipurensis*, *A. quadrilineatus*, *A. rugulosus*, *A. striatus* and *A. violaceus*. The important antibiotic echinocandin and mulundocandin producers include *A. mulundensis*, *A. navahoensis*, *A. pachycristatus*, *A. quadrilineatus*, and *A. rugulosus* (Bills et al. 2016, de la Cruz et al. 2012). One of the originally reported producers was first identified as *A. spinulosporus* (as *Emericella echinulata*), but was later re-identified as *A. rugulosus* (*Emericella rugulosa*) (Dreyfuss 1986).

The mycotoxin sterigmatocystin has not only been found in most species of sections *Nidulantes*, *Aenei* and *Usti*, but also in some species of section *Ochraceorosei* (Table 7) (Frisvad 1985, Horie & Yamazaki 1985, Rank et al. 2011, Jurjevic et al. 2013). In *Aspergillus* section *Nidulantes* 35 species could produce sterigmatocystin, four additional species (*A. multicolor*, *A. purpureus*, *A. stellatus* and *A. violaceus*) have been reported to produce sterigmatocystin, but this could not be confirmed here, and two species remains to be examined for production of sterigmatocystin (*A. omanensis* and *A. sulphureoviridis*) (Table 7). Aflatoxin B1 is produced by four species: *A. astellatus*, *A. miraensis*, *A. olivcola*, and *A. venezuelensis*. This is the first report of aflatoxin production by *A. miraensis*. Other mycotoxins are also produced by a few species in section *Nidulantes*, such as verruculogen and fumitremorgins in *A. caespitosus* and asteltoxin produced by...
Fig. 2. Phylogenetic tree of section Nidulantes inferred from concatenated 4 loci: ITS, BenA, CaM and RPB2. Branches with values more than 1 pp and 95% bs are thickened. The phylogram is rooted with *Aspergillus ustus* (CBS 261.67T).
Fig. 2. (Continued).
A. olivicola, A. qinqixianii, A. stellatus and A. filifer. Thus the most important mycotoxins in Aspergillus section Nidulantes are aflatoxins, sterigmatocystin, emestrin, fumitremorgins, asteltoxins, and paxillin while other extrolites are useful drugs or drug lead candidates such as echinocandins, mulundocandins, calbistrins, varietriols, variecolins and terrein, and some can be regarded as both mycotoxins and drug lead candidates, for example viridicatumtoxin. It is interesting to note that many of these compounds are also produced by other Aspergillus species in phylogenetically different subgenera, showing that species in section Nidulantes are quite closely related to these other species in many features (Frisvad & Larsen 2015).

**DISCUSSION**

**Sectional classification in subgenus Nidulantes**

Based on a multigene phylogeny, nine sections are proposed within subgenus Nidulantes. Eight of them were introduced in previous studies (Peterson 2008, Peterson et al. 2008, Varga et al. 2010a, b). Five species previously assigned in section Usti, namely A. Californicus, A. cavenicola, A. egyptiacus, A. kassunensis and A. subsessilis form a monophyletic clade outside section Usti. The bootstrap support of this distinct clade is low (Hubka et al. 2016), but the species within this clade do share some phenotypic characters, most of them (except A. Californicus) produce short conidiophores, which is not common in section Usti. Based on these observations, we propose Aspergillus section Cavennicolus to accommodate these species within subgenus Nidulantes. Section Aenei was included in section Nidulantes as Aspergillus aeneus clade (Hubka et al. 2016). However in our study, section Aenei locates outside section Nidulantes with full support, which agrees with Varga et al. (2010a). Phenotypically the homothallic species in section Aenei (A. discophorus, A. bicolor, A. spectabilis and A. foeniculicola) produce similar ascospores with A. nidulans clade, but none of them is able to grow at 40 °C. Based on these observations, section Aenei is kept to accommodate these species. The placement of A. funiculosus in a certain group is doubtful, Raper & Fennell (1965) accepted A. funiculosus as the only uniseriate species in section Sparsi (Aspergillus sparsus group), our phylogenetic results show that A. funiculosus is more closely to A. ochraceoroseus, however is not supported by bootstrap and Bayesian statistics as shown by Hubka et al. (2016), the belonging of this species needs further study.

**Clade classification in section Nidulantes**

Matsuzawa et al. (2012) performed the first multilocus analysis based on BenA, CaM and actin in the genus Emericella, eight clades were introduced for 37 species, clades I, II, III, IV, V and VI
are equal with our A. nidulans clade, clades VII and VIII are equal with our A. stellatus clade, anamorphic species were not included in their analysis. Hubka et al. (2016) constructed a phylogenetic analysis for section Nidulantes, six statistically supported clades were designated, namely clades A. aeneus, A. speleuncus, A. versicolor, A. stellatus, A. nidulans and A. unguis, five of them are confirmed in our study, while Aspergillus aeneus clade is treated as section Aenei as discussed above. Besides these clades, additional two clades are introduced here, namely clades A. aurantiobrunneus and A. multicolor. The A. aurantiobrunneus clade contains A. aurantiobrunneus and A. purpureus. Hubka et al. (2016) included A. aurantiobrunneus in A. speleuncus clade although the grouping was not well supported (100/80/1 ML/MP/PP), A. purpureus was not included in their study. In our study, these two species form a full supported branch (1 pp, 100 % ML), morphologically they all produce globose and subglobose ascospores and grow restrictedly on all tested media. In contrast all species in A. speleuncus clade are anamorphic, and grow faster. Another newly introduced clade is A. multicolor clade, this clade contains A. multicolor, A. mulundensis and A. pluriseminatus, and
### Table 3: Most important micromorphological characters for section Nidulantes species with stellate ascospores (μm).

<table>
<thead>
<tr>
<th>Species name</th>
<th>Anamorphic characters</th>
<th>Teleomorphic characters</th>
<th>Convex surfaces of ascomata</th>
<th>Anamorphic characters of ascospores</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. angustatus</td>
<td>–</td>
<td>430 – 500</td>
<td>3 – 5</td>
<td>Orange to reddish brown 9 – 12</td>
</tr>
<tr>
<td>A. miraensis</td>
<td>–</td>
<td>320 – 600</td>
<td>2 – 6</td>
<td>Orange to reddish brown 8 – 10</td>
</tr>
<tr>
<td>A. olivicola</td>
<td>–</td>
<td>400 – 480</td>
<td>2 – 3</td>
<td>Orange to reddish brown 7.5 – 11</td>
</tr>
<tr>
<td>A. pluriseminatus</td>
<td>–</td>
<td>370 – 430</td>
<td>2 – 3</td>
<td>Orange to reddish brown 6.5 – 11.5</td>
</tr>
<tr>
<td>A. venezuelensis</td>
<td>–</td>
<td>1000 – 12</td>
<td>5 – 8</td>
<td>Orange to reddish brown 10 – 14</td>
</tr>
</tbody>
</table>

Data derived from Stchigel & Guarro 1997.

**Aspergillus section Nidulantes**

Anamorphic present or absent, if present conidiophores more or less brown-pigmented, typically smooth but occasionally showing surface protuberances, usually sinuous; vesicles usually globose, subglobose or subclavate, biseriate, metulae and phialides usually about equal in length. Conidia globose to subglobose, ovate to ellipsoidal, echinulate or finely rough, less commonly smooth. Ascomata produced in most species, but lacking in others: emericell-like, cleistothecial, superficial, solitary or clustered, globose to subglobose, non-ostiolate, reddish brown, violet, brown or blackish, typically surrounded by a heavy to discontinuous layer of Hülle cells; Hülle cells hyaline, pale brown, orange brown or pink, globose, subglobose, pyriform or ovoid. Asci 8 spored, globose to subglobose or stellate, evanescent. Ascospores one-celled, orange, purplish, violet, reddish brown or brown, globose to subglobose or stellate, usually with equatorial crests, smooth or with different patterns of ornamentation, entire, dentate, defecitive or with filiform appendages.

**Aspergillus nidulans clade**

Description: Conidiophores (if present) typically smooth but occasionally showing surface protuberances, hyaline to yellowish brown; vesicles globose to subclavate, fertile over the upper half to two thirds; Conidia echinulate, globose to subglobose. Ascomata (if present), cleistothecial, superfi cial, reddish brown, violet or dark brown, globose to subglobose, surrounded by numerous Hülle cells; Hülle cells hyaline to pale brown, globose, subglobose pyriform or ovoid. Asci 8 spored, globose to subglobose. Ascospores orange, reddish brown, brown or violet, in surface view globose to subglobose, spore bodies smooth or with verrucose, echinulate, reticulate or pitted ornamentation. Ascospore crests entire, dentate, defecive or with irregular protuberance, inconspicuous in some species, mostly two in number, four crests are present in *A. quadrilineatus*. Most species grow optimally around 37 °C, do not grow at or above 50 °C. *A. botswanensis, A. fruticulosus, A. latilabatus* and *A. recurvatus* do not grow at 45 °C (Table 5). Twenty-three species are accepted in this clade, 22 of them are homothallic, *A. recurvatus* is the only anamorphic species.

Accepted species:

**Aspergillus botswanensis** A.J. Chen, Frisvad & Samson, this study. [MB816095]

**Aspergillus corrugatus** Udagawa & Y. Horie, Mycotaxon 4: 535. 1976. [MB309216]

Table 4. Most important micromorphological characters for *Aspergillus* section *Nidulantes* species with globose or appendiged ascospores (μm).

<table>
<thead>
<tr>
<th>Species name</th>
<th>Ascomata Hülle cells</th>
<th>Ascospore color</th>
<th>Spore bodies</th>
<th>Ornamentation of convex surfaces</th>
<th>Conidiophores Vesicles Metulae Phialides Conidia</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. botswanensis</em></td>
<td>90–180</td>
<td>Brown</td>
<td>5–6 × 3.5–5</td>
<td>Tuberculate to reticulate</td>
<td>0.4–0.8</td>
</tr>
<tr>
<td><em>A. corrigatus</em></td>
<td>200–360</td>
<td>Orange to reddish brown</td>
<td>3.5–4.5 × 3.5–4</td>
<td>Irregularly wrinkled</td>
<td>0.5–1</td>
</tr>
<tr>
<td><em>A. desertorum</em></td>
<td>100–300</td>
<td>Reddish brown</td>
<td>6.5–7.5 × 6–7.5</td>
<td>Tuberculate</td>
<td>0.5</td>
</tr>
<tr>
<td><em>A. falconensis</em></td>
<td>300–700</td>
<td>Orange to reddish brown</td>
<td>4–6 × 3–3.5</td>
<td>Smooth</td>
<td>1–2</td>
</tr>
<tr>
<td><em>A. foveolatus</em></td>
<td>100–280</td>
<td>Orange to reddish brown</td>
<td>4–5 × 3.5–4.5</td>
<td>Finely pitted</td>
<td>0.5–1</td>
</tr>
<tr>
<td><em>A. fraticulosus</em></td>
<td>230–500</td>
<td>Orange to reddish brown</td>
<td>4.5–5.5 × 3–5</td>
<td>Smooth</td>
<td>0.8–1</td>
</tr>
<tr>
<td><em>A. jaipurensis</em></td>
<td>150–500</td>
<td>Purplish red</td>
<td>6–7.5 × 5–5.5</td>
<td>Smooth</td>
<td>0.8–1</td>
</tr>
<tr>
<td><em>A. latilatius</em></td>
<td>100–160</td>
<td>Orange or reddish brown</td>
<td>5.5–7.5 × 6–5</td>
<td>Smooth</td>
<td>0.5–1</td>
</tr>
<tr>
<td><em>A. latus</em></td>
<td>150–400</td>
<td>Light orange, orange or reddish brown</td>
<td>3.5–5 × 3–5</td>
<td>Smooth, incompletely reticulate or ribbed</td>
<td>1–1.5</td>
</tr>
<tr>
<td><em>A. navahoensis</em></td>
<td>140–400</td>
<td>Orange to reddish brown</td>
<td>3.5–4.5 × 3–3.5</td>
<td>Smooth</td>
<td>0.7–1</td>
</tr>
<tr>
<td><em>A. nidulans</em></td>
<td>150–420</td>
<td>Orange to reddish brown</td>
<td>3.5–5 × 3–4.5</td>
<td>Smooth</td>
<td>0.5–1 (entire or dentate)</td>
</tr>
<tr>
<td><em>A. omanensis</em></td>
<td>180–370</td>
<td>Brownish red</td>
<td>4.5–5.5 × 4–4.5</td>
<td>Tuberculate or verruculose</td>
<td>1</td>
</tr>
<tr>
<td><em>A. pachyclistatus</em></td>
<td>200–500</td>
<td>Orange to reddish brown</td>
<td>4–5 × 3.5–4</td>
<td>Smooth</td>
<td>0.7–1</td>
</tr>
<tr>
<td><em>A. purpureus</em></td>
<td>90–200</td>
<td>Brown</td>
<td>6–7 × 4.5–5</td>
<td>Smooth</td>
<td>0.3–0.6</td>
</tr>
<tr>
<td><em>A. quadrilineatus</em></td>
<td>100–700</td>
<td>Orange to reddish brown</td>
<td>4–4.5 × 3–4.5</td>
<td>Smooth</td>
<td>0.5–1 (entire, defective or with irregular protuberances)</td>
</tr>
<tr>
<td><em>A. rubulosus</em></td>
<td>220–350</td>
<td>Orange, greyish violet</td>
<td>4–4.5 × 3.5–4</td>
<td>Rugulose</td>
<td>0.5–0.6</td>
</tr>
<tr>
<td><em>A. savannensis</em></td>
<td>65–120</td>
<td>Orange to reddish brown</td>
<td>4–5 × 3.5–4</td>
<td>Smooth</td>
<td>0.5–1</td>
</tr>
<tr>
<td><em>A. spinulosporus</em></td>
<td>200–550</td>
<td>Orange to reddish brown</td>
<td>3.5–4.5 × 3–4.5</td>
<td>Echinulate</td>
<td>0.8–1</td>
</tr>
<tr>
<td><em>A. stercorarius</em></td>
<td>70–150</td>
<td>Orange or reddish brown</td>
<td>4.5–6 × 3.5–4.5</td>
<td>Smooth</td>
<td>0.3–0.4</td>
</tr>
<tr>
<td><em>A. striatus</em></td>
<td>180–500</td>
<td>Orange</td>
<td>6–7 × 5–5.5</td>
<td>With concentric thickenings</td>
<td>–</td>
</tr>
<tr>
<td><em>A. sulphureoviridis</em></td>
<td>350–600</td>
<td>Orange to reddish brown</td>
<td>4.5–5.5 × 3.5–4.5</td>
<td>Smooth</td>
<td>0.8–1.2</td>
</tr>
</tbody>
</table>


**Aspergillus jaipurensis** A.J. Chen, Frisvad & Samson, this study. [MB816093].

**Aspergillus latilabiatus** A.J. Chen, Frisvad & Samson, comb. nov., this study. [MB816100].

**Aspergillus navahoensis** M. Chr. & States, Mycologia 74: 226. 1982. [MB110496].


**Aspergillus quadrilineatus** Thom & Raper, Mycologia 31: 660. 1939. [MB277104].


**Aspergillus rugulosus** Thom & Raper, Mycologia 31: 660. 1939. [MB277104].

**Aspergillus savannensis** A.J. Chen, Frisvad & Samson, this study. [MB816096].

**Aspergillus aurantiopurpureus** A.J. Chen, Frisvad & Samson, this study. [MB816087].

**Aspergillus stercorarius** A.J. Chen, Frisvad & Samson, this study. [MB816094].


**Aspergillus sulphureoviridis** A.J. Chen, Frisvad & Samson, this study. [MB816097].

**Aspergillus violaceus** Fennell & Raper, Mycologia 47: 75. 1955. [MB292863].

### Aspergillus stellatus clade

**Description:** Conidiophores (if present) smooth, hyaline to yellowish brown; vesicles globose to subclavate, fertile over the upper half to two thirds; Conidia echinulate, globose to subglobose. Ascomata (if present), cleistothecial, superficial, reddish brown, violet or dark brown, globose to subglobose, surrounded by numerous Hülle cells; Hülle cells hyaline to pale brown, globose, subglobose or ovoid. Asci 8 spored, subglobose to polygonal or stellate. Ascospores orange, reddish brown, brown or violet brown, globose, stellate or appendaged. Most species do not grow at 40 °C, three species (A. astellatus, A. miraensis and A. stella-maris) do not grow at 37 °C (Table 5). Twelve species are accepted in this clade, 11 of them are homothallic, A. caespitosus is the only anamorphic species.

**Accepted species:**

**Aspergillus angustatus** A.J. Chen, Frisvad & Samson, this study. [MB816090].
Aspergillus caesipitosus Raper & Thom, Mycologia 36: 563. 1944. [MB284298].
Aspergillus dromiae A.J. Chen, Frisvad & Samson, this study. [MB816089].
Aspergillus versicolor clade

Description: Fide Jurjevic et al. (2012) conidiophores smooth to tuberose, hyaline to yellow or brownish; vesicles pyriform, spathulate or subglobose, fertile over half, two thirds or entire vesicle; Conidia smooth, spinulose or finely roughened, globose, subglobose or ellipsoidal. Hülle cells present in six species: A. cvjetkovicii, A. fructus, A. griseaourantiacus, A. protuberus, A. puulaauensis and A. venenatus, hyaline, globose, subglobose, ellipsoid or pyriform. All species do not grow at 37 °C. Sixteen species are accepted, all of them are anamorphic species. (Jurjevic et al. 2012, Visagie et al. 2014, Tsang et al. 2016).

Accepted species:

accepted, *A. pluriseminatus* is homothallic, *A. multicolor* and *A. mulundensis* are anamorphic species.

Accepted species

**Aspergillus multicolor** Sappa, Allonia 2: 87. 1954. [MB292849].

**Aspergillus mulundensis** Bills & Frisvad, J Antibiot. 69: 143. 2016. [MB813062].


*Aspergillus unguis* clade

Description: Conidiophores smooth, hyaline to yellowish brown; vesicles globose to subclavate, fertile over the upper half to one third; Conidia smooth to echinulate, globose to subglobose. Most species do not grow at 40 °C (Hubka et al. 2016 reported several *A. unguis* strains with restrict growth at 40 °C), two species: *A. croceus* and *A. israelensis* do not grow at 37 °C. Three species are accepted, *A. croceus* and *A. israelensis* are anamorphic, all *A. unguis* strains observed in this study

![Range of conidiophore and conidia phenotypes](image_url)

Table 5. Temperature profiles (5 days, in mm) on CYA for Aspergillus section Nidulantes species.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>18 °C</td>
</tr>
<tr>
<td>A. asperescens</td>
<td>12</td>
</tr>
<tr>
<td>A. astellatus</td>
<td>7</td>
</tr>
<tr>
<td>A. aurantiobruneus</td>
<td>0</td>
</tr>
<tr>
<td>A. aureolatus</td>
<td>7</td>
</tr>
<tr>
<td>A. israelensis</td>
<td>6</td>
</tr>
<tr>
<td>A. miraesimus</td>
<td>15</td>
</tr>
<tr>
<td>A. pluriseminatus</td>
<td>0</td>
</tr>
<tr>
<td>A. purpureus</td>
<td>0</td>
</tr>
<tr>
<td>A. speluncicus</td>
<td>4</td>
</tr>
<tr>
<td>A. stell-maris</td>
<td>17</td>
</tr>
<tr>
<td>A. varians</td>
<td>12</td>
</tr>
<tr>
<td>A. viridicatenatus</td>
<td>–</td>
</tr>
<tr>
<td>A. angustatus</td>
<td>–</td>
</tr>
<tr>
<td>A. coesiptosus</td>
<td>–</td>
</tr>
<tr>
<td>A. froromae</td>
<td>–</td>
</tr>
<tr>
<td>A. filifer</td>
<td>–</td>
</tr>
<tr>
<td>A. filifer (ex-type of A. chinensis)</td>
<td>–</td>
</tr>
<tr>
<td>A. multicolor</td>
<td>–</td>
</tr>
<tr>
<td>A. mulludensis</td>
<td>–</td>
</tr>
<tr>
<td>A. olivicola</td>
<td>–</td>
</tr>
<tr>
<td>A. angiospori</td>
<td>–</td>
</tr>
<tr>
<td>A. stelatus</td>
<td>–</td>
</tr>
<tr>
<td>A. undulatus</td>
<td>–</td>
</tr>
<tr>
<td>A. unguis</td>
<td>–</td>
</tr>
<tr>
<td>A. venezuelensis</td>
<td>–</td>
</tr>
<tr>
<td>A. aurantiopurpureus</td>
<td>–</td>
</tr>
<tr>
<td>A. botswanensis</td>
<td>–</td>
</tr>
<tr>
<td>A. corrugatus</td>
<td>–</td>
</tr>
<tr>
<td>A. desertorum</td>
<td>–</td>
</tr>
<tr>
<td>A. falconensis</td>
<td>–</td>
</tr>
<tr>
<td>A. foveolatus</td>
<td>–</td>
</tr>
<tr>
<td>A. fructiculosus</td>
<td>–</td>
</tr>
<tr>
<td>A. jaipurensis</td>
<td>–</td>
</tr>
<tr>
<td>A. laticlavius</td>
<td>–</td>
</tr>
<tr>
<td>A. latus</td>
<td>–</td>
</tr>
<tr>
<td>A. latus (ex-type of A. sublatus)</td>
<td>–</td>
</tr>
<tr>
<td>A. navahoensis</td>
<td>–</td>
</tr>
<tr>
<td>A. niulans</td>
<td>–</td>
</tr>
<tr>
<td>A. niulans (ex-type of A. dentatus)</td>
<td>–</td>
</tr>
<tr>
<td>A. pachyptistatus</td>
<td>–</td>
</tr>
<tr>
<td>A. quadrihirtus</td>
<td>–</td>
</tr>
<tr>
<td>A. quadriminatus (ex-type of A. floriformis)</td>
<td>–</td>
</tr>
<tr>
<td>A. quadriminatus (ex-type of A. niulans var. acrictus)</td>
<td>–</td>
</tr>
<tr>
<td>A. quadriminatus (ex-type of A. parvathecius)</td>
<td>–</td>
</tr>
<tr>
<td>A. recurvatus</td>
<td>–</td>
</tr>
<tr>
<td>A. rugulosus</td>
<td>–</td>
</tr>
<tr>
<td>A. rugulosus (ex-type of A. cleistominutus)</td>
<td>–</td>
</tr>
<tr>
<td>A. savannensis</td>
<td>–</td>
</tr>
<tr>
<td>A. spinulosporus</td>
<td>–</td>
</tr>
<tr>
<td>A. stercorarius</td>
<td>–</td>
</tr>
<tr>
<td>A. striatus</td>
<td>–</td>
</tr>
<tr>
<td>A. sulphureoviolaceus</td>
<td>–</td>
</tr>
<tr>
<td>A. violaceus</td>
<td>–</td>
</tr>
<tr>
<td>A. violaceus (ex-type of A. simili)</td>
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</tr>
</tbody>
</table>

*Species marked in green have optimal temperature around 27 °C, and do not grow at 37 °C; species marked in yellow have optimal temperature around 30 °C, and do not grow at 40 °C; species marked in orange have optimal temperature around 31 °C, and do not grow at 50 °C (four species do not grow at 45 °C).*

are anamorphic, but A. unguis NRRL 2393 was reported to tardily produce ascospores (Fennell & Raper 1955, Hubka et al. 2016).

Accepted species

**Aspergillus croceus** Hubka, A. Nováková, Frisvad, S.W. Peterson & M. Kolarík, Plant Syst. Evol. 302: 1291. [MB816281].

**Aspergillus israelensis** A.J. Chen, Frisvad & Samson, this study [MB816091].


**Aspergillus aurantiobruneus** clade

**Description**: Grow restrictedly on all tested media, anamorphic structures are hardly produced. Conidiophores smooth, hyaline to pale brown; vesicles globose to subclavate, fertile over two thirds to whole surface; Conidia echinulate, globose, subglobose, ellipsoidal to cylindrical. Ascomata cleistothecial, superficial, reddish brown, globose to subglobose, surrounded by numerous Hülle cells; Hülle cells hyaline to pale brown, globose, subglobose or ovoid. Ascii 8 spored, globose to subglobose. Ascospores light orange to brown, globose to subglobose. All species do not grow at 37 °C. Two homothallic species are accepted in this clade.

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Fig. 9. Temperature growth profile of *Aspergillus* sect. *Nidulantes* species on CYA, from left to right 30, 33, 37, 40, 45, 50 °C.
### Temperature Growth Profile of Aspergillus sect. Nidulantes on CYA

<table>
<thead>
<tr>
<th>Species</th>
<th>30 °C</th>
<th>33 °C</th>
<th>37 °C</th>
<th>40 °C</th>
<th>45 °C</th>
<th>50 °C</th>
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<td>A. nidulans</td>
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<td>A. nidulans (ex-type of A. dentatus)</td>
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<td>A. recurvatus</td>
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<td>A. savannensis</td>
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<tr>
<td>A. spinulosporus</td>
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<td>A. stercorarius</td>
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<td>A. striatus</td>
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<td>A. sulphureoviridis</td>
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<tr>
<td>A. violaceus</td>
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</tr>
<tr>
<td>A. violaceus (ex-type of A. similis)</td>
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Fig. 10. Temperature growth profile of Aspergillus sect. Nidulantes species on CYA, from left to right 30, 33, 37, 40, 45, 50 °C.
Table 6. Extrolites reported from species of *Aspergillus* section Nidulantes.

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<thead>
<tr>
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<th>Extrolites reported</th>
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<td><em>A. astellatus</em></td>
<td>Aflatoxin B₁</td>
<td>Frisvad et al. 2004</td>
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<tr>
<td></td>
<td>Asperthecin</td>
<td>Frisvad 1985</td>
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<tr>
<td></td>
<td>Austin, dehydroaustin</td>
<td>Simpson et al. 1982 (as “variant” of “Aspergillus variecolor”)</td>
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<td></td>
<td>2-(3,4-dihydroxyhepta-1,5-dienyl)-6-methoxybenzyl alcohol &amp; terrein</td>
<td>Dunn &amp; Johnstone 1979</td>
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<tr>
<td></td>
<td>Desferritriacylfusigen</td>
<td>de la Cruz et al. 2012</td>
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<td></td>
<td>Sterigmatocystin</td>
<td>Frisvad et al. 2004</td>
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<td></td>
<td>Tajixanthone, shamixanthone</td>
<td>Ahmed et al. 1992</td>
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<td><em>A. aurantiobrunneus</em></td>
<td>Emeremophiline</td>
<td>Fujimoto et al. 2000</td>
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<td></td>
<td>Emericol A-D, variecolin, variecolol</td>
<td>Yoganathan et al. 2004</td>
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<tr>
<td></td>
<td>Desferritriacylfusigen</td>
<td>de la Cruz et al. 2012</td>
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<td></td>
<td>Sterigmatocystin</td>
<td>Rabie et al. 1977</td>
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<td>Variecoacetal A &amp; B</td>
<td>Yoganathan et al. 2004</td>
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<td>Variecoladone, variecolin</td>
<td>Fujimoto et al. 2000, Yoganathan et al. 2004</td>
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<td><em>A. caespitosus</em></td>
<td>Asperline, (S,S,₆S)-5,6-dihydro-5-acetoxy-6-(1,2-trans-propenyl)-2H-pyran-2-one</td>
<td>Mizuba et al. 1975</td>
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<td></td>
<td>Penicillin G</td>
<td>Dulaney et al. 1947b, Gill-Carey 1949</td>
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<td></td>
<td>Cyclopamine B</td>
<td>Steyn et al. 1981</td>
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<td></td>
<td>6-methoxymellein</td>
<td>Dunn et al. 1979</td>
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<td></td>
<td>Trisdechlorornidulin</td>
<td>Steyn et al. 1981</td>
</tr>
<tr>
<td><em>A. corrugatus</em></td>
<td>Asperthecin</td>
<td>Frisvad 1985</td>
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<tr>
<td></td>
<td>Emericorrugatin A &amp; B</td>
<td>Fujimoto et al. 1998</td>
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<tr>
<td></td>
<td>norsolorinic acid</td>
<td>Fujimoto et al. 1998</td>
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<td><em>A. croceus</em></td>
<td>Kotonins, norsolorinic acid, orfandin, siderin,</td>
<td>Hubka et al. 2016</td>
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<td>sterigmatocystin, versicolorins</td>
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<td><em>A. desertorum</em></td>
<td>Desertorin A-C, 4,7-dihydroxy-5-methylcoumarin, 7-demethysiderin</td>
<td>Nozawa et al. 1987a, Rizzacasa &amp; Sargent 1988, Mazzaferrro et al. 2015</td>
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<td>Nozawa et al. 1987a</td>
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<td>Paullin</td>
<td>Nozawa et al. 1987b</td>
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<td>Silvaticol</td>
<td>Nozawa et al. 1987a</td>
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<td><em>A. falconensis</em></td>
<td>3,3’-Dihydroxy-5,5’-dimethyldiphenyl ether</td>
<td>Itabashi et al. 1993</td>
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<td></td>
<td>Falconenson A-B</td>
<td>Ogasawara et al. 1997</td>
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<td></td>
<td>Hopane-6α,7β,22-triol, hopane-7β,22-diol</td>
<td>Itabashi et al. 1996</td>
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<td>Mitorubrin, monomethylidydromitorubrin,</td>
<td>Ogasawara &amp; Kawai 1998</td>
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<td></td>
<td>monomethylmitorubrin</td>
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<tr>
<td></td>
<td>Zeorin</td>
<td>Itabashi et al. 1996</td>
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<tr>
<td><em>A. foveolatus</em></td>
<td>Asperthecin</td>
<td>Frisvad 1985</td>
</tr>
<tr>
<td></td>
<td>Dethiosecoemestrin, emestrin, emestrin B, secoemestrin C</td>
<td>Seya et al. 1986a,b, Ooike et al. 1997</td>
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<td>Secoemestrin D, emericellenes A-E</td>
<td>Xu et al. 2013, identity of producer was <em>Emericella</em> sp.</td>
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<td>de la Cruz et al. 2012</td>
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<td>Nozawa et al. 1989</td>
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<td>Violaceic acid</td>
<td>Ooike et al. 1997</td>
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<tr>
<td>A. fruticulosus</td>
<td>Sterigmatocystin</td>
<td>Frisvad 1985</td>
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<td>A. latus</td>
<td>Asperthecin</td>
<td>Frisvad 1985</td>
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<td>Nidulalin A &amp; B</td>
<td>Kawahara et al. 1994</td>
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<td>A. multicolor</td>
<td>Asticolourin A-C, averufin, 5,6-dimethoxyhydrosterigmatocystin, 5,6-dimethoxyserigmatocystin, sterigmatocystin, versicolourin C</td>
<td>Rabie et al. 1984, Hamasaki et al. 1977, 1980 (from IFO 8133, we could not confirm sterigmatocystin production by A. multicolor)</td>
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<td>A. mutundensis</td>
<td>Dexoymulundocandin, mulundocandin</td>
<td>Roy et al. 1987, Mukhopadhyay et al. 1987, 1992</td>
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<td>A. navahoensis</td>
<td>Averufin, norsolorinic acid, 6,7,8-trihydroxy-3-methylisocoumarin</td>
<td>Yamazaki et al. 1988</td>
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<td>Desferritriacetylfusigen</td>
<td>de la Cruz et al. 2012</td>
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<td>Echinocandin B</td>
<td>de la Cruz et al. 2012</td>
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<td>Sterigmatocystin</td>
<td>Frisvad 1985</td>
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<td>A. nidulans</td>
<td>Aloe-emodin, chrysophanol, cichorine, 2-ω-dihydroxymedin, 3-(2,6-dihydroxyphenyl)-4-hydroxy-6-methyl-1(3H)isobenzofuranone, emodic acid, emodin, emodin anthrone, endocrocin, endocrocin anthrone, ω-hydroxymedin</td>
<td>Ahmed et al. 1987, Sanchez et al. 2011, Schroekhh et al. 2009</td>
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<td>Arugosin A</td>
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<td>Arugosin H</td>
<td>Nielsen et al. 2011</td>
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<td>Asperfuraranone, preasperfuraranone</td>
<td>Chiang et al. 2009</td>
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<td>Aspermidine A &amp; B</td>
<td>Scherlach et al. 2010</td>
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<td>Asperugin A &amp; B</td>
<td>Ballantine et al. 1965, 1967</td>
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<td>Asperquinolone A-D, aniquazoline A-D, aflaquinolone A, aniduquinolone A-C, 6-deoxyaflaquinolone E, isoaflaquinolone E, 14-hydroxyaflaquinolone F</td>
<td>Scherlach &amp; Hertweck 2006, An et al. 2013a,b, Neff et al. 2012, These quinones and quinazolins were isolated from strains that may be misidentified, the strains are not available</td>
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<td>Aspyridone A &amp; B, preaspyridone</td>
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<td>Atrochrysone, atrochrysone carboxylic acid</td>
<td>Kleijirup et al. 2012</td>
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<td>Averufin</td>
<td>Ishida et al. 1972</td>
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<td>3-Benzyl-4-phenyl-2,5-furandione, 3-Carboxy-2,4-diphenylbut-2-enic anhydride</td>
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<td>Citreoisocoumarin</td>
<td>Watanabe et al. 1998, 1999</td>
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<td>Cordycepin</td>
<td>Kodama et al. 1979, Yoshino 1979</td>
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<td>Cordylol C, C-10-deoxyferulin</td>
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<td>2’,2’-Deoxycoforycin = co-viderabin = pentostatin, 3-deoxyadenosine</td>
<td>Kaczkia et al. 1964, Woo &amp; Dion 1974, Kodama et al. 1979</td>
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<td>Middleton et al. 1978, de la Cruz et al. 2012</td>
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<td>Diorcinol, orcinol, orsellinaldehyde, orsellinic acid, violecel I &amp; II</td>
<td>Sanchez et al. 2010, Nahlik et al. 2010</td>
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<td>Echinocandin B (only in CBS 240.90)</td>
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<td>Emericellamide A-F</td>
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<td>Emericellin = varicoxanthone B</td>
<td>Ishida et al. 1975a,b, Sanchez et al. 2011</td>
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<td>Emeridine A-B, emerphenolicin A-D, aspermidine A-B, austina, austinitol, dehydroaustin, acetoxydehydroaustin</td>
<td>Zhang et al. 2011, identity of producer is questionable</td>
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<td>Emerin</td>
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<td>Epishamixanthone</td>
<td>Sanchez et al. 2011</td>
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<td>F-9775A, F-9775B, paeciloxanthone</td>
<td>Sanchez et al. 2010</td>
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<td>Ferricrocin</td>
<td>Eisendle et al. 2003</td>
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<td>Ferrirhodin</td>
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<td>8-Hydroxy-1-(hydroxymethyl)-3-methyl-9H-xanthen-9-one</td>
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<td>Hydroxypreaspyridone</td>
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<td>Lecanoric acid</td>
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<td>Methyl-(2E,6E)-10,11-dihydroxy-3,7,11-trimethyl-2,6-dodecadienoate, methyl (2E,6E)-10,11-epoxid-3,7,11-trimethyl-2,6-dodecadienoate, methyl-(2E,6E)-10-hydroxy-11-formyl-3,7,11-trimethyl-2,6-dodecadienoate, methyl (2,6,10)-3,7,11-trimethyl-2,6-dodecadienoate</td>
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<td>Monodictyphenone</td>
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<td>Nidolol</td>
<td>Aucamp &amp; Holzapfel 1968</td>
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<td>Nidurufin, versicolourin A-C</td>
<td>Aucamp &amp; Holzapfel 1970</td>
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<td>Penicillin G</td>
<td>Dulaney 1947a,b, Holt &amp; MacDonald 1968</td>
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<td>Sanghaspironin A-B</td>
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<td>Sporogenic fatty acids</td>
<td>Mazur et al. 1990</td>
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<td>Terrequinone A</td>
<td>Bok et al. 2006</td>
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<td>6,7,9-Trihydroxy-3-methylcyclohepta(c)-pyran-8(1H)-one = antibiotic C</td>
<td>Turner &amp; Aldridge 1983</td>
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<td>Tricycethylfurarinine</td>
<td>Eisendle et al. 2003</td>
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<td>YWA1 &amp; 2</td>
<td>Watanabe et al. 1999, Fuji et al. 2001</td>
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<td>A. olivicola</td>
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<td>Emericellin (as arugosin E)</td>
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<td>Shamixanthone</td>
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<td>Siderin</td>
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<td>Terrein</td>
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<td><em>A. pluriseminatus</em></td>
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<td>Emindol SA, emindol SB, emindol SC</td>
<td>Kawai et al. 1994, Hosoe et al. 2006</td>
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<td>Epurpurin A-C</td>
<td>Takahashi et al. 1996</td>
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<td>Sterigmatocystin</td>
<td>Horie &amp; Yamazaki 1985</td>
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<td>Variecolactone</td>
<td>Takahashi et al. 1999</td>
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<td>Variecolin, variecolol</td>
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<td>Averufin, 7-methoxyaverufin, sterigmatocystin, versicolourin</td>
<td>Ahmad &amp; Sultana 1985</td>
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<td>Desferritriacetylfusigen</td>
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<td>Echinocandin B &amp; E</td>
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<td>Emericellin = variecoxanthone B</td>
<td>Kralj et al. 2006 (as <em>Emericella nidulans</em> var acristata)</td>
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<td>Emerstirin, aurantioemestrin, dethiosecoemestrin</td>
<td>Ooike et al. 1997</td>
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<td>3,5-Dibromo-2,4-dihydroxy-6-methyl benzoic acid methylester</td>
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<td>Yamazaki &amp; Maebayashi 1982a,b, Asami et al. 2012</td>
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1The strain of Emericella echinulata = A. spinulosporus = A. delacroixii of Benz et al. 1974 was claimed to be an A. rugulosus (Emericella rugulosa) by Dreyfuss 1986.

2Not structure elucidated.

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<td><em>A. ustus</em> (trace; not confirmed in later studies)</td>
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Accepted species


**Phylogenetic species recognition**

Based on a concatenated sequence analysis, 65 species are well resolved in section *Nidulantes*. ITS, the recommended official DNA barcode for fungi (Schoch et al. 2012), performs well in recognizing species in clades *A. unguis*, *A. spelunceus* and *A. multicolor*. However it is not variable sufficiently for recognizing species in other clades. *BenA*, *CaM* and *RPB2* can identify 63 species respectively, with *A. quadrilineatus* sharing identical *BenA* with *A. latus*, *A. qinqixianii* and *A. filifer* sharing identical *CaM* and *A. rugulosus* and *A. pachycristatus* sharing identical *RPB2* sequences. Matsuzawa et al. (2012) stated that *A. nidulans* (= *E. nidulans*), *A. dentatus* (= *E. dentata*), *A. latus* (= *E. nidulans* var. *lata*), *A. sublatus* (= *E. sublata*), *A. montenegro* (= *E. montenegro*), *A. acristerus* (= *E. acristera*), *A. miyajii* (= *E. miyajii*), *A. quadrilineatus* (= *E. quadrilineata*) and *A. parvathecius* (= *E. parvathecia*) were undistinguishable by phylogenetic analysis alone. These are confirmed in this study, to follow the genealogical concordance phylogenetic species recognition concept (GCPSR), several species are considered as synonyms here: *A. dentatus* is synonymised with *A. nidulans*; *A. sublatus* and *A. montenegro* are synonymised with *A. latus*; *A. acristerus*, *A. miyajii* and *A. parvathecius* are synonymised with *A. quadrilineatus* as did Hubka et al. 2016. Overall species in *A. nidulans* clade are phylogenetically similar, both phylogenetic and morphological data are important to define the species boundary. Speices in other six clades are more divergent phylogenetically, the only exceptions are *A. qinqixianii* and *A. filifer*, they share identical *CaM* sequences, only small differences are present in *BenA* (99.7 % similarity, 344/345 bp), *actin* (98.9 % similarity, 366/370 bp) (Matsuzawa et al. 2012, Hubka et al. 2016) and *RPB2* (99.7 % similarity, 912/914 bp).

**Morphological species recognition**

For homothallic species in section *Nidulantes*, the ascospore shape, ornamentation, color and size are of particular importance for differentiating species (Thom & Raper 1939, Christensen & Raper 1978, Horie 1980, Christensen & States 1982, Ismail et al. 1995, Zalar et al. 2008, Matsuzawa et al. 2012, Guarro et al. 2012). In *A. nidulans* clade, most species have unique ascospore morphology (Figs 3–5). However in some species, ascospore morphology shows a range of diversity. For example most of *A. nidulans* strains have entire
Fig. 11. Temperature growth profile of Aspergillus sect. Nidulantes species on CYA, from left to right 18, 21, 24, 27, 30, 33 °C.
Fig. 12. Temperature growth profile of Aspergillus sect. Nidulantes species on CYA, from left to right 21, 24, 27, 30, 33, 37 °C.
crests, but atypical dentate crests are presented in one strain (CBS 114.63), similarly in *A. quadrilineatus*, the crests in ascospores can be entire, defective or with irregular protuberance. In *A. stellatus* clade, species with stellate ascospores are morphologically very similar, molecular identification is recommended for distinguishing these species. Anamorphic structures are also important for species recognition, especially for anamorphic species. But the anamorphic structures can be affected by media and incubation conditions, here we follow the standardized method for laboratories working with *Aspergillus* (Samson et al. 2014), MEA is recommended for anamorphic description and OA is recommended for teleomorphic description in section *Nidulantes*.

**SPECIES DESCRIPTIONS**

*Aspergillus angustatus* A.J. Chen, Frisvad & Samson, sp. nov. MycoBank MB816090. Fig. 13.

Etymology: The name refers to the narrow vesicles of the aspergilla.

Diagnosis: Moderately dense or dense sporulation on CYA, MEA and YES, stellate ascospores and narrow vesicles measuring 8–12 μm.


**ITS barcode**: EU448283. (Alternative markers: *BenA* = AV339993; *CaM* = EU443984; *RPB2* = KU867013).

**Colony diam**, 7 d (mm): CYA 37–38; CYA 37 °C 16–17; CYA 40 °C No growth; MEA 48–50; MEA 37 °C 1–2; OA 42–44; YES 52–53; CREA 13–15; CYAS 33–34; DG18 27–28.

**Colony characters**: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white to light yellow; texture velvety to granular due to ascomata production; sporulation moderately dense, conidia *en masse* olive green; soluble pigments absent; exudates clear droplets; reverse dark brown at centre, light buff at edge; ascomata present after 1 wk. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture velvety; sporulation dense, conidia *en masse* dark green; soluble pigments absent; exudates clear to light yellow droplets; reverse dark brown at centre, cream yellow at edge; ascomata present after 1 wk. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white to light yellow; texture granular due to ascomata production; sporulation moderately dense, conidia *en masse* olive green; soluble pigments absent; exudates absent; reverse dark brown at centre, cream yellow at edge; ascomata present after 1 wk. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture velvety; sporulation dense, conidia *en masse* olive green; soluble pigments absent; exudates absent; reverse pale brown. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture velvety; sporulation moderately dense, conidia *en masse* yellow green; soluble pigments absent; exudates clear droplets; reverse pale brownish green; ascomata present after 1 wk. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology**: Ascomata cleistothecial, superficial, reddish brown, globose to subglobose, 430–780 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale brown, globose to ovoid, 17–35 μm. Asc 8 spored, stellate. Ascospores orange to reddish brown, in surface view stellate, 9–12 μm; spore bodies smooth, globose to subglobose, 3–4 × 3–3.5 μm; in side view broadly lenticular, with two stellate equatorial crests; undissected part of crests 0.5–1 μm broad, with 1.5–3 μm long extensions; crests ornamented with longitudinal, 0.3–0.4 μm wide pleats. Conidiophores with smooth stipes, pale brown, 200–400 × 4.5–6 μm; vesicles hyaline to pale brown, subglobose to subclavate, 8–12 μm wide, fertile over the upper half; metulae hyaline, 6–8 × 3–4.5 μm; phialides hyaline, flask-shaped, 7–8.5 × 2.5–3.5 μm. Conidia echinulate, globose to subglobose, 3–4.5 μm, green in mass.

**Extritoles**: asperthecin, a desertorin, emericellin, 2-ω-hydroxy-yemodin, shamixanthones.

**Distinguishing characters**: *Aspergillus angustatus* is morphologically and phylogenetically closely related to *A. dromiae*; however, *A. angustatus* sporulates well on CYA, MEA and YES, compared to the absent sporulation in *A. dromiae*. Furthermore, *A. dromiae* has wider vesicles (12–17 μm) than *A. angustatus*.


**Typus**: Holotype PRM 924055; isotype 924056. Culture ex-type: CBS 134374 = CCF 4716 = CCF 4428 = NRRL 62818 = DSM 871 = IBT 33114 = IBT 32911.

**ITS barcode**: LNN73939. (Alternative markers: *BenA* = LNN73952; *CaM* = LNN78365; *RPB2* = LNN73984).

**Colony characters**: Fide Hubka et al. (2016) colonies of both isolates assigned to *A. askiburgiensis* show numerous differences, and they are described separately. Colonies of CCF 4716 on CYA at 25 °C attained 24–35 mm diam in 14 days (19–20 mm in 7 days), velutinous, irregularly wrinkled with margin submerged 2–3 mm, pale orange yellow (ICC–NBS No. 73) with olive-gray (113) marginal parts, sporulation visible, olive-gray, no exudate, dark orange yellow (72) soluble pigment, reverse strong brown (55) to dark brown (59) with strong orange yellow margin (68). Colonies of CCF 4085 attained 18–19 mm diam in 14 days (12–13 mm in 7 days), floccose, plane to irregularly wrinkled, moderate yellow (87) with greyish olive (110) to dark olive (108) tint in central part (sporulation), 1 mm broad marginal zone yellowish white (92), no exudate or small brownish orange (54) droplets, reverse moderate yellowish brown (77) with light orange yellow 2–3 mm margin, no soluble pigment. No growth on CYA at 37 °C. Colonies of CCF 4716 on MEA at 25 °C attained 23–28 mm diam in 14 days (15–18 mm in 7 days), plane to very slightly furrowed, velutinous, yellowish white (92) to pale yellow (89), no exudate, no soluble pigment, reverse deep orange yellow (69) with vivid yellow margin (82). Colonies of CCF 4085 attained 14–15 mm diam in 14 days (10–11 mm in 7 days), plane, with 2 mm broad colorless leather-like marginal zone, colony centre velutinous (good sporulation), moderate olive brown (95) to moderate olive (107), no exudate, no soluble.
Fig. 13. Aspergillus angustatus CBS 273.65T. A. 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–D. Conidiophores and conidia. E. Ascomata. F. Hüle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
pigment, reverse light greyish olive (109) with moderate yellow colony centre and colorless margin. Colonies of CCF 4716 on CZA at 25 °C attained 15–16 mm diam in 14 days (9–10 mm in 7 days), effuse, plane, yellowish white (92) with dark greyish yellowish brown (81) colored ring (sporulation) in the colony centre (6–8 mm diam), no exudate, brilliant yellow orange (67) soluble pigment, reverse deep yellowish brown (75) with dark yellowish brown (78) colony centre. Colonies of CCF 4085 attained 19–20 mm diam in 14 days (10–11 mm in 7 days), submerged, plane, moderate olive (107) to dark olive (108) sporulation, no exudate, no soluble pigment, reverse colorless. Colonies of CCF 4716 on CREA at 25 °C attained 15–17 mm diam in 14 days (10–11 mm in 7 days), effuse, yellowish white (92) to greyish greenish yellow (105), no acid production. Colonies of CCF 4085 attained 17–18 mm diam in 14 days (11–12 mm in 7 days), submerged, plane, good sporulation in colony centre, no exudate, no soluble pigment, no acid production.

**Micromorphology:** Fide Hubka et al. (2016) stipes on MEA brown, smooth, non-septate or occasionally with septum, most commonly 40–180 × 3–8.5 μm diam, diminutive conidiophores occasionally present; vesicles pyriform, subglobose, less frequently globose, 5.5–18.5 μm diam; biseriate; metulae cylindrical, 4–6 μm long, covering 1/2–3/4 of the vesicles; phialides ampulliform, 5–8 μm long; conidia subglobose or globose, green in mass, 2.5–4 × (4–4.5) μm diam, first almost smooth or finely roughened but later definitely spinulose. Hülle cells arranged in clusters, ellipsoidal or pyriform, 16–24 × 10–16.5 μm, or subglobose to globose, 11–20 μm diam, produced after 14 or more days of cultivation at 25 °C. Sexual state not observed.

**Extróiltes:** Fide Hubka et al. (2016) sterigmatocystin, versicolorins, cf. monasolorubamin.

**Distinguishing characters:** This species is closely related to A. spelunceus, A. asperescens and A. aureolatus, but A. spelunceus produces longer conidiophores (130–300 μm), A. asperescens produces larger ellipsoidal conidia (4–7 × 3–5 μm) and A. aureolatus is characterized by orange marginal zone of colonies.

**Notes:** Aspergillus askiburgiensis was described from European caves. For an illustration of the species, readers are referred to Hubka et al. (2016).

**Aspergillus asperescens** Stolk, Antonie van Leeuwenhoek 20: 303. 1954. MycoBank MB809583. Fig. 14.

**Typus:** IMI 46813. Culture ex-type: CBS 110.51 = NRRL 2252 = ATCC 11079 = DSM 871 = IMI 046813 = GM 1946 = WB 2252 = WB 5038 = IBT 19363 = DTO 021-F4.

**ITS barcode:** EF652475. (Alternative markers: BenA = EF652299; CaM = EF652387; RPB2 = EF652211).

**Colony diam, 7 d (mm):** CYA 23–29; CYA 37 °C No growth; CYA 40 °C No growth; MEA 22–29; MEA 37 °C No growth; OA 23–27; YES 27–30; CREA 11–14; CYAS 17–20; DG18 10–15.

**Colony characters:** CYA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white and light yellow; texture velvety; sporulation moderately dense, conidia en masse olive; soluble pigments absent; exudates absent; reverse buff. MEA 25 °C, 7 d: Colonies moderately deep, plane to slightly sulcate; margins entire; mycelium white; texture velvety to floccose; sporulation moderately dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse pale brown to brown. YES 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white and light yellow; texture velvety; sporulation dense, conidia en masse olive; soluble pigments absent; exudates absent; reverse yellow green at central, cream white at edge. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture velvety; sporulation moderately dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse pale yellow green. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata not observed. Conidiophores with smooth stipes, yellowish brown, 200–400 × 6–8 μm; vesicles hyaline to pale yellowish brown, hemispherical to globose, 6–15 μm wide, fertile over the upper half; metulae hyaline to pale yellowish brown, 6–9 × 3–4 μm; phialides hyaline to pale yellowish brown, flask-shaped, 7.5–9 × 3–4 μm. Conidia in young cultures subglobose to ellipsoidal, smooth, 4–7 × 3–5 μm, in cultures older than two wks, rough conidia are formed.

**Extróiltes:** a calbistrin, dehydroaustin, sterigmatocystin, versicolorins, violaceolins.

**Distinguishing characters:** Aspergillus asperescens can be distinguished from other species by large, subglobose to ellipsoidal conidia that turn distinctly roughened with age.

**Notes:** Aspergillus asperescens was assigned in the A. nidulans series because of its yellow-green radiate conidial heads, brown conidiophores and Hülle cells (Stolk 1954). During our study, Hülle cells were not observed in the type culture; however, the characteristic asexual morphology and phylogeny prove its position in section Nidulantes.

**Aspergillus astellatus** (Fennell & Raper) Houbraken, Visagie & Samson, Stud. Mycol. 78: 154. 2014. MycoBank MB809577. Fig. 15.


**Typus:** IMI 061455. Culture ex-type: CBS 261.93 = CBS 134.55 = NRRL 2396 = ATCC 16817 = IMI 61455 = IMI 61455ii = NRRL A-1634 = QM 1910 = WB 2396 = IBT 21902 = IBT 22589 = DTO 010-17.

**ITS barcode:** EF652446. (Alternative markers: BenA = EF652270; CaM = EF652385; RPB2 = EF652182).

**Colony diam, 7 d (mm):** CYA 12–16; CYA 37 °C No growth; CYA 40 °C No growth; MEA 25–27; MEA 37 °C No growth; OA 20–23; YES 20–23; CREA 3–5; CYAS 12–13; DG18 13–18.
Fig. 14. Aspergillus asperescens CBS 110.51T. A. 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. G. Conidia. Scale bars: B = 30 μm; C–E,G = 10 μm; F = 8 μm.
Fig. 15. Aspergillus astellatus CBS 261.93\(^T\). A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 \(\mu\)m; C,D,F,G = 10 \(\mu\)m; E = 1000 \(\mu\)m; H = 2 \(\mu\)m.
Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, plane; margins entire to slightly irregular; mycelium brown; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse dark brown to black. MEA 25 °C, 7 d: Colonies moderately deep, plane to sulcate; margins entire; mycelium white to blue violet; texture granular due to ascomata production; sporulation absent to sparse; soluble pigments absent; exudates clear to light brown droplets; reverse dark brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium violet; texture floccose to granular due to ascomata production; sporulation absent to sparse; soluble pigments absent; exudates absent; reverse dark brown to dark gray. DG18 25 °C, 7 d: Colonies moderately deep, plane to slightly sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse white to yellowish brown. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white and light yellow; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse light brown to greyish olive. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, superficial, violet to brown, globose to subglobose, 330–500 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 15–27 μm. Asci 8 spored, globose to subglobose. Ascospores reddish brown, in surface view globose, spore bodies smooth, 5.5–6 × 3.5–5 μm; in side view lenticular, with two equatorial crests measuring 2–3.5 μm wide; crests ornamented with longitudinal, 0.3–0.4 μm wide pleats. Conidiophores with smooth stipes, light brown, 80–200 × 3–4 μm; vesicles hyaline to pale brown, subclavate to subglobose, 5–7 μm wide, fertile over the upper half; metulae hyaline, 4.5–5.5 × 2–3 μm; phialides hyaline, flask-shaped, 4.5–5 × 2–4 μm. Conidia echinulate, globose to subglobose, 2.5–6 μm.

Extrolites: aflatoxin B1 and B2, asperthecin, 2-µ-hydroxyemodin, shamoxanthone, sterigmatocystin and versicolorin.

Distinguishing characters: Aspergillus astellatus is characterized by ascospores with two wide undисsected crests up to 5.5 μm wide. Phylogenetically it is close to A. venezuelensis and A. stella-maris, but the latter two produce stellate ascospores. All three species can produce sterigmatocystin and shamoxanthones. Only A. venezuelensis and A. astellatus produce aflatoxin B1, and A. venezuelensis and A. stella-maris produce emericellin (Table 6).


ITS barcode: EF652465. (Alternative markers: BenA = EF652289; CaM = EF652377; RPB2 = EF652201).

Colony diam, 7 d (mm): CYA 9–12; CYA 37 °C No growth; CYA 40 °C No growth; MEA 10–11; MEA 37 °C No growth; OA 9–10; YES 11–12; CREA No growth; CYAS 11–13; DG18 15–16.

Colony characters: CYA 25 °C, 7 d: Colonies deep, plane; margins entire; mycelium white and orange; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse wood brown. MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse yellowish brown. YES 25 °C, 7 d: Colonies deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse cream yellow. DG18 25 °C, 7 d: Colonies deep, plane; margins entire; mycelium white and orange; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse light yellow. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse white. CREA 25 °C, 7 d: No growth.

Micromorphology: Ascomata cleistothecial, superficial, reddish brown, globose to subglobose, 60–300 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale brown, globose to ovoid, 14–25 μm. Ascii 8 spored, globose to subglobose. Ascospores light orange, in surface view globose to subglobose, spore bodies smooth, 4–5 × 3–4.5 μm; in side view lenticular, with two equatorial crests measuring 0.8–1 μm. Conidiophores with smooth stipes, light brown, 50–200 × 3.5–4.5 μm; vesicles hyaline to pale brown, globose to subclavate, 7–12 μm wide, fertile over the two thirds to whole surface; metulae hyaline to pale brown, 4–6 × 2.5–3.5 μm; phialides hyaline to pale brown, flask-shaped, 6.5–7.5 × 2.5–3 μm. Conidia echinulate, globose to subglobose, 2.5–3.5 μm (Anamorphic structures were observed from YES).


Distinguishing characters: Aspergillus aurantiobrunneus grows restrictedly on CYA, MEA, YES and OA, which differs from other morphologically similar species such as A. fruticulosisus and A. pachycristatus. Phylogenetically it is close to A. purpureus, but A. purpureus produces larger ascospores (6–7 × 4.5–5 μm) and narrower ascospore crests (0.3–0.6 μm).

Aspergillus aurantiopurpureus A.J. Chen, Frisvad & Samson, sp. nov. MycoBank MB816087. Fig. 17.

Etymology: Name refers to its ascospore colour, which is orange or reddish brown, later turns to violet.

Diagnosis: Yellow mycelium, smooth ascospores with crests measuring 0.8–1.2 μm wide, ascospores are first orange later turn to violet.


ITS barcode: KU866588. (Alternative markers: BenA = KU866824; CaM = KU866711; RP2 = KU866966).
Fig. 16. Aspergillus aurantiobrunneus CBS 465.65T. A. 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–D. Conidiophores and conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Fig. 17. Aspergillus aurantiopurpureus CBS 140608 T. A. 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, C. Conidiophores. D. Conidia. E. Ascomata. F. Hüllie cells. G, H. Ascospores. Scale bars: B = 30 μm; C, D, F, G = 10 μm; E = 1000 μm; H = 2 μm.
Colony diam, 7 d (mm): CYA 32–35; CYA 37 °C 23–30; CYA 40 °C 28–30; MEA 38–41; MEA 37 °C 33–35; OA 25 °C 40–45; YES 42–49; CREA 6–7; CYAS 20–22; DG18 14–17.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins slightly irregular; mycelium yellow; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse reddish brown. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium light yellow and white; texture floccose; sporulation sparse; soluble pigments absent; exudates clear droplets; reverse reddish brown. YES 25 °C, 7 d: Colonies deep, slightly sulcate; margins slightly irregular, surrounded by an orange halo; mycelium white; texture velvety; sporulation dense, conidia en masse greyish green to olive green; soluble pigments absent; exudates absent; reverse orange to reddish brown. CYA 25 °C, 7 d: Colonies deep, slightly sulcate; margins slightly irregular, surrounded by an orange halo; mycelium white; texture velvety; sporulation dense, conidia en masse yellow green to blue green; soluble pigments absent; exudates clear droplets; reverse orange to reddish brown. CYA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium yellow; texture velvety; sporulation dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse orange. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium yellow to light yellow; texture floccose; sporulation sparse; soluble pigments light brown; exudates clear droplets; reverse yellowish brown. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology**: Ascomata cleistothecial, enveloped by interwoven hyphae, blackish to dark brown, globose to subglobose, 200–320 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 11.5–20.5 μm. Asci 8 spored, globose to subglobose. Ascospores first orange to reddish brown, later turn to violet, in surface view globose, spore bodies smooth, 3.5–4.5 × 3–3.5 μm; in side view lenticular, with two equatorial crests measuring 0.8–1.2 μm wide; crests ornamented with longitudinal, 0.3–0.4 μm wide pleats. Conidiophores with smooth stipes, light brown, 130–260 × 3.5–5 μm; vesicles hyaline; subclavate to subglobose, 8–11.5 μm wide, fertile over the upper half; metulae hyaline, 5–6 × 2.5–4 μm; phialides hyaline, flask-shaped, 5–6.5 × 3–3.5 μm. Conidia echinulate, globose to subglobose, 3–3.5 μm, green in mass.

**Extrólites**: cyclopaldic acid, desertorins, falconensins, cf. falconensins, shamxanthones, sterigmatocystin.

**Distinguishing characters**: Phylogenetically it is close to *Aspergillus navahoensis*, but can be easily distinguished by wider pleated stipes and ascospore colour.


*ITS barcode*: EF652501. (Alternative markers: BenA = EF652325; CaM = EF652413; RP2B = EF652237).

*Colony diam, 7 d (mm)*: CYA 19–25; CYA 37 °C No growth; CYA 40 °C No growth; MEA 17–24; MEA 37 °C No growth; OA 16–18; YES 21–25; CREA 11–16; CYAS 18–21; DG18 11–17.

*Colony characters*: CYA 25 °C, 7 d: Colonies moderately deep, plane; margins slightly irregular, surrounded by an orange halo; mycelium white; texture velvety; sporulation dense, conidia en masse greyish green to olive green; soluble pigments absent; exudates absent; reverse orange to reddish brown. MEA 25 °C, 7 d: Colonies deep, slightly sulcate; margins slightly irregular, surrounded by an orange halo; mycelium white; texture velvety; sporulation dense, conidia en masse yellow green to blue green; soluble pigments absent; exudates clear droplets; reverse orange to reddish brown. YES 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins slightly irregular, surrounded by an golden to orange halo; mycelium white; texture velvety; sporulation dense, conidia en masse greyish green; soluble pigments absent; exudates absent; reverse orange. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium yellow; texture velvety; sporulation dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse orange. OA 25 °C, 7 d: Colonies low, plane; margins slightly irregular, surrounded by an orange halo; mycelium white; texture velvety; sporulation dense, conidia en masse dark green; soluble pigments light brown; exudates clear droplets; reverse yellowish brown. CREA 25 °C, 7 d: Acid production absent.

*Micromorphology*: Ascomata not observed. Conidiophores with smooth stipes, yellowish brown, 80–200 × 4–5.5 μm, reduced conidial heads are formed, sometimes clusters of sterigmata appear along the ascending conidiophores; typical vesicles hyaline to pale yellowish brown, globose, 9–12 μm wide, fertile over the upper half to two thirds; metulae hyaline to pale green, 5–8.5 × 2–4 μm; phialides hyaline to pale green, flask-shaped, 5×7 × 2.5–3 μm. Conidia globose to subglobose, echinulate, 3.5–5 μm, green in mass.

*Extrólites*: austalides (tentatively identified), a desertorin, an emerin, sterigmatocystin, versicolorins.

**Distinguishing characters**: The striking orange halo surrounding the colony and globose vesicles can distinguish *Aspergillus aureolatus* from related non-ascosporic species.

**Aspergillus botswanensis** A.J. Chen, Frisvad & Samson, sp. nov. MycoBank MB816095. Fig. 19.

**Etymology**: Name refers to its origin, isolated from forest soil from Botswana.

**Diagnosis**: Brown ascospores ornamented with tuberculate to irregular reticulate ornamentation.

**Typus**: Botswana, Okavango Delta, Island Forest Area, at base of Diospyros mespiliformis (ebony tree), forest soil, 1986, collected by D. Pearce (holotype CBS H-22494, culture ex-type CBS 314.89 = DTK-M1–C1).

*ITS barcode*: KJU866572. (Alternative markers: BenA = KJU866812; CaM = KJU866945; RP2B = KJU866949).
Fig. 18. Aspergillus aureolatus CBS 190.65T. A. 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–G. Conidiophores. H. Conidia. Scale bars: B–C = 30 μm; D–H = 10 μm.
Fig. 19. Aspergillus botswanensis CBS 314.89T. A. 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. Ascomata. C. Asci. D–H. Ascospores. E. Hülle cells. Scale bars: B = 1000 μm; C–E = 10 μm; F–H = 2 μm.
Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium light yellow to white; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse orange brown. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium light yellow and white; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse orange brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white; texture velvety; sporulation absent; soluble pigments absent; exudates absent; reverse buff yellow. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse yellow. OA 25 °C, 7 d: Colonies low, plane, margins entire; mycelium white; texture granular due to ascomata production; sporulation absent; soluble pigments absent; exudates absent; reverse pale olive. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, enveloped by interwoven mycelium, dark brown, globose, 90–180 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 12–16.5 μm. Ascii 8 spored, globose to ovoid. Ascospores brown, in surface view globose to subglobose; spore bodies resembling Hülle cells are observed on CYA plates, measuring 5–6 × 3.5–5 μm; in side view broadly lenticular, with two low equatorial crests, 0.4–0.8 wide. Anamorph absent.

Extrolites: asperthecin, desertorins, emericellin, an emindol, 2-ω-hydroxyemodin, paxillin, terrequinone A.

Distinguishing characters: The ascospores of Aspergillus botswanaensis resemble those of A. violaceus, but A. violaceus produces constantly violet ascospores with regular reticulate ornamentation. Phylogenetically, A. botswanaensis is close to A. desertorum, A. stercorarius and A. savannensis, but can be differed by its unique ascospore ornamentation.

**Aspergillus caesiptosus** Raper & Thom, Mycologia 36: 563, 1944. MycoBank MB284298. Fig. 20.


ITS barcode: EF652428. (Alternative markers: BenA = EF652252; CaM = EF652340; RPB2 = EF652164).

Colony diam, 7 d (mm): CYA 42–46; CYA 37 °C 7–30; CYA 40 °C No growth; MEA 46–54; MEA 37 °C 12–34; OA 45–55; YES 51–60; CREA 9–12; CYAS 25–35; DG18 32–35.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture velvety; sporulation sparse to moderately dense, conidia en masse grayish green; soluble pigments absent; exudates clear droplets; reverse vinaceous buff to grey olivaceous. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate to sulcate; margins entire; mycelium white; texture floccose; sporulation moderate density, conidia en masse yellow green to olive green; soluble pigments absent; exudates absent or clear droplets; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture velvety; sporulation moderately dense, conidia en masse yellow green to blue green; dark brown soluble pigments present after 2 wks; exudates absent; reverse olive to yellowish brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture velvety; sporulation dense, conidia en masse dark green; soluble pigments absent; exudates absent; reverse pale yellow green. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture velvety; sporulation dense, conidia en masse yellow green; soluble pigments absent to pale yellow; exudates absent; reverse greenish yellow to yellow. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata not observed. Conidiophores with smooth stipes, pale brown, 200–300 × 3–6 μm; vesicles hyaline to pale brown, hemisphere to subclavate, 10–15 μm wide, wide over the upper half; metulae hyaline to pale brown, 5–8 × 3.5–3.5 μm; phialides hyaline, flask-shaped, 6.5–8 X 3.4–5.5 μm. Conidia globose, echinulate, 3–4 μm, green in mass.

Extrolites: asperlicine, emodin, fumitremorgin B, 2-ω-hydroxyemodin, 6-methoxymellein, mellein (tentatively identified), secalonic acid D, TR-2, verruculogen.

Distinguishing characters: Aspergillus caespitosus is close to A. asperescens and A. unguis, but can be distinguished from A. asperescens by its globose conidia; from A. unguis by its longer conidiophores and wider vesicles. These three species share no extrolites, and can be easily distinguished chemically. A. caespitosus is the only species in section *Nidulantes* that produces fumitremorgins.

Notes: Abundant, thick walled, irregularly globose, ovoid or elliptical Hülle cells were mentioned in the original descriptions (Raper & Thom 1944); however, they are not confirmed in this study. Only some degenerated terminal or intercalary cells resembling Hülle cells are observed on CYA plates, measuring 7–16 × 5–10 μm.

**Aspergillus corrugatus** Udagawa & Y. Horie, Mycotaxon 4: 535. 1976. MycoBank MB309216. Fig. 21.


ITS barcode: KU866574. (Alternative markers: BenA = KU866814; CaM = KU866896; RPB2 = KU866951).

Colony diam, 7 d (mm): CYA 48–49; CYA 37 °C 53–54; CYA 40 °C 48–49; MEA 43–44; MEA 37 °C >60; OA 40–42; YES >60; CREA 10–13; CYAS 23–27; DG18 14–15.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white to light yellow; texture floccose; sporulation absent; soluble pigments light brown; exudates absent; reverse reddish brown to brown. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium salmon at centre, white at edge; texture floccose; sporulation sparse; soluble pigments absent; exudates clear droplets; reverse reddish brown to brown. YES 25 °C, 7 d:
Fig. 20. Aspergillus caespitosus CBS 10345T. A. 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,C,F. Conidophores. D,E. Terminal or intercalary cells resembling Hülle cells. G. Conidia. Scale bars: B–C,E,G = 10 μm; F = 8 μm; D = 1000 μm.
Fig. 21. *Aspergillus corrugatus* CBS 191.77T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Colony moderately deep, sulcate; margins entire; mycelium white to light yellow; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse brown. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white to buff; texture floccose; sporulation moderately dense, conidia en masse greyish green; soluble pigments absent; exudates absent; reverse cream white. OA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white and light yellow; texture floccose; sporulation sparse; soluble pigments light brown; exudates absent; reverse yellowish brown. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, reddish brown to brown, globose to subglobose, 200–360 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 16–23 μm. Ascii 8 spored, globose to ovate. Ascosporae orange to reddish brown, in surface view globose to subglobose, spore bodies with irregularly wrinkled ornamentation, globose to subglobose, 3.5–4.5 × 3.5–4 μm; in side view lenticular, with two pleated equatorial crests measuring 0.5–1 μm. Conidiothecia with smooth stipes, yellowish brown, 40–120 × 3.5–5.5 μm; vesicles pale brown, subclavate, 8–10 μm wide, fertile over the upper half to two thirds; metulae hyaline, pale green to brown, 5–8 × 2.5–4 μm; phialides hyaline to pale green, flask-shaped, 6–9 × 2.5–3.5 μm. Conidia echinulate, globose to subglobose, 2.5–3.5 μm.

**Extrolites:** asperthecin, asperugins, an austalide (tentatively identified), emecorrugatin, gregatins, shamixanthone, sterigmatocystin, versicolorins.

**Distinguishing characters:** Aspergillus corrugatus is close to *A. foveolatus*, *A. rugulosus* and *A. spinulosporus*, but differs in its ascospore ornamentation. The convex walls are irregularly wrinkled in *A. corrugatus*, in contrast to the finely pitted convex walls in *A. foveolatus*, rugulose walls in *A. rugulosus* and echinulate walls in *A. spinulosporus*.


_Typeus:_ Holotype PRM 924053; isotype 924054. Culture ex-type: CBS 134396 = CCF 4405 = NRRL 62495 = IBT 33602.

**ITS barcode:** LN873931. (Alternative markers: _BenA_ = LN873944; _CaM_ = LN873957; _RPB2_ = LN873976).

**Colony characters:** _Fide Hubka et al._ (2016) colonies on CYA at 25 °C attain 20–37 mm diam in 14 days (11–16 mm in 7 days), velutinous, plane, delicately furrowed to wrinkled with floccose vivid orange (No. 48) colony centre, colony margin plane, 2–3 mm wide, strong brown (No. 55), sporulation color greyish olive (110), greyish olive green (No. 127) to dark olive (No. 108). Hülle cells visible in some strains after 14 days, no exudate, no soluble pigment, reverse dark reddish brown (No. 44) with paler 1-mm-wide colony margin. No growth on CYA at 37 °C. Colonies on MEA at 25 °C attain 17–32 mm diam in 14 days (9–13 mm in 7 days), velutinous, plane to delicately furrowed with paler floccose central part, 3–5 mm in diam, deep orange (No. 69) with paler colony margin, brilliant yellow (83)-colored margins in some strains, sporadic sporulation in greyish olive (No. 110) to greyish olive green (No. 127), but in some strains more intense sporulation in greyish green (No. 150), no exudate, no soluble pigment, reverse brownish orange (No. 54) to strong brown (No. 55) with strong orange (No. 50) 1–2 mm margin. Colonies on CZA at 25 °C attain 19–28 mm diam in 14 days (7–12 mm in 7 days), velutinous to floccose, plane, mycelium light brownish gray (No. 63), brownish gray (No. 64) to strong reddish brown (No. 40) with medium brown (No. 58) to strong brown (No. 55) higher colony centre (12 mm) with sporulation (zone up to 12 mm in diam) in greyish olive green (No. 127), in some strains whitish mycelial overgrowth in the colony centre, no exudate or small droplets of dark brown (No. 59) exudate, soluble pigment medium pink (No. 5) to medium red (No. 15), reverse vivid deep red (No. 13) to dark reddish brown (No. 44) with deep red (No. 13) margin. Colonies on CREA at 25 °C attain 9–20 mm diam in 14 days (8–12 mm in 7 days), plane, submerged orange-colored mycelium, sparse sporulation, no acid production.

**Micromorphology:** _Fide Hubka et al._ (2016) stipes on MEA light brown to brown, rough-walled, warty to crustose, non-septate or occasionally with septum (sometimes separating vesicle and stipe), most commonly 90–200 × 3.5–5 μm diam, occasionally longer; vesicles pyriform, spathulate or clavate, 7–15 μm diam; metulae cylindrical, 7.5–10.5 μm long, covering 1/3–1/2 of vesicle; phialides ampulliform (6.5–) 7–9 (−9.5) μm long; conidia globose or subglobose, green in mass, 2–3 (−3.5) μm diam, smooth to finely roughened. Hülle cells arranged in clusters, globose, subglobose or pyriform, 8–18.5 × 8–11 (−17) μm, produced after 14 or more days cultivation at 25 °C. Sexual state not observed.

**Extrolites:** _Fide Hubka et al._ (2016) kotanins, norsolorinic acid, orflandin, siderin, sterigmatocystin, versicolorins.

**Distinguishing characters:** This species is closely related to _A. unguis_ and _A. israelensis_, but the latter two produce narrower vesicles, (8–10 μm) in _A. unguis_ and (7–10 μm) in _A. israelensis_.

**Notes:** For an illustration of the species, readers are referred to Hubka et al. (2016).


_Typeus:_ Holotype PRM 924053; isotype 924054. Culture ex-type: CBS 134396 = CCF 4405 = NRRL 62495 = IBT 33602.

**ITS barcode:** EF652505. (Alternative markers: _BenA_ = EF652329; _CaM_ = EF652417; _RPB2_ = EF652241).

**Colony diam:** CYA 20–35; CYA 37 °C 29–53; CYA 40 °C 29–47; MEA 32–40; MEA 37 °C 43–60; OA 30–36; YES 41–50; CREA 0–2; CYAS 0–23; DG18 0–17.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium saffron and white; texture floccose; sporulation absent; soluble pigments absent; exudates light brown droplets; reverse yellowish brown. MEA
Fig. 22. Aspergillus desertorum CBS 653.73T. A. 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. Ascomata. C, E–G. Ascospores. D. Hüllle cells. Scale bars: B = 30 μm; C–D = 10 μm; E–G = 2 μm.
25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse orange to reddish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture velvety; sporulation absent; soluble pigments absent; exudates absent; reverse light brown. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white and light yellow; texture floccose; sporulation absent; soluble pigments light yellow; exudates light brown droplets; reverse greyish yellow. Violet ascomata present after 1 wk. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology: Ascomata cleistothecial, superficial, violet to brown reddish, globose to subglobose, 100–300 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale brown, globose, ovoid or pyriform, 10–25 μm. Asci 8 spored, globose to subglobose. Ascospores reddish brown, in surface view globose to subglobose, spore bodies turbulcuate, 6.5–7.5 × 6–7.5 μm; in side view broadly lenticular, with two low equatorial crests measuring 0.5 μm wide: Anamorph absent.

**Extrólites:** asperthecin, calbistrins, desertorin A, B & C, emindols, nidulol, paaxillin, silvaticol, terrequinone A.

**Distinguishing characters:** Aspergillus dromiae is characterized by large ascospores, which are ornamented with two low crests. Its ascospores resemble those of A. purpureus and A. stercorarius, but A. purpureus produces smooth ascospores and grows slower on all tested media, A. stercorarius produces smooth and smaller ascospores (4.5–6 × 3.5–4.5 μm).

*Aspergillus dromiae* A.J. Chen, Frisvad & Samson, sp. nov. MycoBank MB816089. Fig. 23.

**Etymology:** Name refers to its origin, isolated from *Dromia erythropus* (crab, Crustacea).

**Diagnosis:** Stellate ascospores, echinulate conidia measuring 3.5–4.5 μm, vesicles measuring 12–17 μm.

**Typus:** *Venezuela,* Mochima Bay, Morro of Garapá, *Dromia erythropus* (crab, Crustacea), isolated by J.C. Frisvad (holotype CBS H-22489, culture ex-type CBS 140633 = IBT 25166 = DTO 059-H5).

**ITS barcode:** KU866580. (Alternative markers: BenA = KU866885; CaM = KU866703; RP2B = KU866958).

**Colony diam.** 7 d (mm): CYA 39–40; CYA 37 °C 10–11; CYA 40 °C No growth; MEA 45–47; MEA 37 °C 1–2; OA 40–45; YES 45–50; CREA 10–11; CYAS 33–34; DG18 18–27.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium greyish olive; texture floccose; sporulation absent; soluble pigments absent; exudates clear to light brown droplets; reverse dark olive; ascomata present after 1 wk. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium light yellow and white; texture granular at centre due to ascomata production; sporulation absent; soluble pigments absent; exudates clear droplets; reverse dark brown at centre, yellowish brown at edge; ascomata present after 1 wk. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white and light yellow; texture floccose to granular due to ascomata production; sporulation absent; soluble pigments absent; exudates absent; reverse yellowish brown; ascomata present after 1 wk. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse greenish yellow. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture granular due to ascomata production; sporulation absent; soluble pigments absent; exudates clear droplets; reverse pale yellow green; ascomata present after 1 wk. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, reddish brown to dark brown, globose to subglobose, 450–800 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellow brown, globose to ovoid, 16–31 μm. Asci 8 spored, stellate. Ascospores orange to reddish brown, in surface view stellate, 11–15 μm; spore bodies smooth, globose to subglobose, 3–4.5 × 3.5–4.5 μm, in side view broadly lenticular, with two stellate equatorial crests; undissected part of crests 1–1.5 μm broad, with 2–3 μm long extensions; crests ornamented with longitudinal, 0.3–0.4 μm wide pleats. Conidiophores with smooth stipes, pale brown, 300–410 × 4.5–6.5 μm; vesicles hyaline to pale brown, subclavate to subglobose, 12–17 μm wide, fertile over the upper half; metulae hyaline, 6–8 × 3–4.5 μm; phialides hyaline, flask-shaped, 6.5–10 × 3.5–4.5 μm. Conidia echinulate, globose to subglobose, 3.5–4.5 μm. (Anamorphic structures were observed from DG18).

**Extrólites:** a desertorin, eremicellin, 2-ω-hydroxyemodin, shamixanthones.

**Distinguishing characters:** Aspergillus dromiae resembles A. stella-maris and A. miraensis, however A. stella-maris produces wider (3.5–7 μm), septate conidiophores, while A. miraensis produces smaller conidia (2–3.5 μm).


**Typus:** CBM 10001. Culture ex-type: CBS 271.91 = IFM 4997 = NHL 2999 = ATCC 76117 = IBT 14808 = DTO 048-A2.

**ITS barcode:** KU866575. (Alternative markers: BenA = KU866815; CaM = KU866697; RP2B = KU866952).

**Colony diam.** 7 d (mm): CYA 30–40; CYA 37 °C 34–52; CYA 40 °C 30–45; MEA 34–45; MEA 37 °C 43–60; OA 33–48; YES 47–60; CREA 2–18; CYAS 2–20; DG18 2–24.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium light yellow and white; texture floccose; sporulation absent; soluble pigments absent; exudates light brown droplets; reverse reddish brown to brown. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium light yellow and white; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse pale yellow green; ascomata present after 1 wk. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium light yellow and white; texture velvety;
Fig. 23. *Aspergillus dromiae* CBS 140633T. A. 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, C. Conidiophores. D. Conidia. E. Ascomata. F. Hüll cells. G, H. Ascospores. Scale bars: B = 30 μm; C, D, F, G = 10 μm; E = 1000 μm; H = 2 μm.
Aspergillus falconensis CBS 271.91T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
sporulation moderately dense; conidia soluble pigments absent; exudates absent; reverse light yellow. OA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium yellow and white; texture floccose; sporulation moderately dense; conidia en masse greyish green; soluble pigments absent; exudates absent; reverse light yellow. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white and light yellow; texture velvety; sporulation sparse to moderately dense, conidia en masse yellow green; soluble pigments absent; exudates clear droplets; reverse light brown to cream yellow. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture velvety; sporulation dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse pale yellow green. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture granular due to ascomata production; sporulation absent; soluble pigments absent; exudates clear droplets; reverse pale brownish green. Ascomata present after 1 wk. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, reddish brown to dark brown, globose to subglobose, 300–700 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 14–25 μm. Ascii 8 spored, globose to subglobose. Ascospores orange to reddish brown, in surface view globose to subglobose, spore bodies smooth, 4–6 × 3.5 μm; in side view lenticular, with two equatorial crests measuring 1–2 μm wide; crests ornamented with longitudinal, 0.3–0.4 μm wide pleats. Conidiophores with smooth stipes, light brown, 75–240 × 4–6.5 μm; vesicles hyaline to pale brown, globose to subclavate, 8–10 μm wide, fertile over the upper half; metulae hyaline, 6–10 × 2–3.5 μm; phialides hyaline, flasks-shaped, 6–9 × 2–4 μm. Conidia echinulate, globose to subglobose, 2.5–4 μm, green in mass. (Anamorphic structures were observed from YES).

**Extrolites:**asperthecin, an austalide (tentatively identified), austinel, desertorins, falconensins, falconensons, shamixanthones, sterigmatocystin, versicolorins, violaceols, viridicatumtoxin.

**Distinguishing characters:** Aspergillus falconensis is characterized by ascospores with two conspicuously pleated crests up to 2 μm wide, which distinguish it from closely related A. fruticulosus and A. navahensis.

**Aspergillus filifer** Zalar, Frisvad & Samson, Mycologia 100: 787. 2008. MycoBank MB507357. Fig. 25.


**ITS barcode:** EU448277. (Alternative markers: BenA = EF428372; CaM = EU443973; RPB2 = KU866932).

**Colony diam.** 7 d (mm): CYA 32–40; CYA 37 °C 24–30; CYA 40 °C No growth; MEA 35–42; MEA 37 °C 23–30; OA 28–34; YES 40–48; CREA 6–13; CYAS 15–24; DG18 20–27.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white and pale olive; texture floccose; sporulation absent; soluble pigments absent; exudates clear to light brown droplets; reverse greyish brown at centre, buff at edge. Ascomata present after 1 wk. WEK 25 °C, 7 d: Colonies moderately deep, plane to slightly sulcate; margins entire; mycelium white and light yellow; texture floccose; sporulation absent; soluble pigments absent; exudates clear to light brown droplets; reverse dark brown at centre, yellowish brown at edge. Ascomata present after 1 wk. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white and light yellow; texture velvety; sporulation sparse to moderately dense, conidia en masse yellow green; soluble pigments absent; exudates clear droplets; reverse light brown to cream yellow.

**Notes:** Phylogenetically and morphologically Aspergillus appendiculatus (= Aspergillus chinensis) (Samson et al. 2014) is identical with A. filifer, and is considered a synonym of A. filifer as did Matsuzawa et al. 2012 and Hubka et al. 2016.


**Colony diam.** 7 d (mm): CYA 32–40; CYA 37 °C 24–30; CYA 40 °C No growth; MEA 35–42; MEA 37 °C 23–30; OA 28–34; YES 40–48; CREA 6–13; CYAS 15–24; DG18 20–27.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates clear to light brown droplets; reverse dark brown at centre, yellowish brown at edge. Ascomata present after 1 wk. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white and light yellow; texture velvety; sporulation sparse to moderately dense, conidia en masse yellow green; soluble pigments absent; exudates clear droplets; reverse light brown to cream yellow. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white and light yellow; texture velvety; sporulation dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse pale yellow green. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture granular due to ascomata production; sporulation absent; soluble pigments absent; exudates clear droplets; reverse pale brownish green. Ascomata present after 1 wk. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, greyish green to brown, globose to subglobose 220–660 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellow brown, globose to ovoid, 13–24 μm. Ascii 8 spored, stellate, globose to subglobose. Ascospores brown, in surface view globose to subglobose, spore bodies 3.5–4.5 × 3–4 μm; in side view broadly lenticular, with two equatorial crests measuring 0.5–1.2 μm wide; Crest bearing hyaline, filiform appendages, measuring 3–6 μm long with swollen tips. Convex surface tuberculate. Conidiophores with smooth stipes, yellowish brown, 120–250 × 3–5 μm; vesicles hyaline to pale yellow brown, subclavate to subglobose, 7–13 μm wide, fertile over the upper half to two thirds; metulae hyaline to pale yellow brown, 7–10 × 3–5 μm; phialides hyaline to pale yellow brown, flask-shaped, 7–11 × 2–4 μm. Conidia echinulate, globose to subglobose, 3–4 μm.

**Extrolites:**asperthecin, asperugins, asteltoxin, dihydroterrein, 2-μ-hydroemodin, emericellin, shamixanthones, terrein, a varitriol.

**Distinguishing characters:** Appended ascospores ornamented with capitale swellings. Morphologically this species is close to A. undulatus and A. qinqixianii, but can be easily distinguished from A. undulatus by filiform appendages and from A. qinqixianii by capitale swellings on convex surface of ascospores.
Fig. 25. Aspergillus filifer CBS 113636T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 \mu m; C,D,F,G = 10 \mu m; E = 1000 \mu m; H = 2 \mu m.
Fig. 26. Aspergillus foveolatus CBS 279.81T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
sporulation moderately dense, conidia en masse pale green; soluble pigments absent; exudates light brown droplets; reverse brown. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse greyish green to dark green; soluble pigments absent; exudates clear droplets; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulphate; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse pale green; soluble pigments absent; exudates clear droplets; reverse brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse pale green; soluble pigments absent; exudates absent; reverse brown. CREA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse greyish green to dark green; soluble pigments light brown; exudates absent; reverse cream white. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, superficial, dark brown, globose to subglobose, 100–280 μm, surrounded by numerous Hüle cells; Hüle cells hyaline, globose to ovoid, 7–21.5 μm. Asci 8 spored, globose to subglobose. Ascospor form to reddish brown, in surface view globose to subglobose, spore bodies finely pitted, 4–5 × 3.5–4.5 μm; in side view lenticular, with two equatorial crests measuring 0.5–1 μm wide. Conidiophores with smooth stipes, light brown to brown, 40–200 × 4.5–8.5 μm; vesicles light brown, subglobose to subclavate, 12–15 μm wide, fertile over the upper half to two thirds; metulae hyaline, 5–7 × 2–4 μm; phialides hyaline, flask-shaped, 6–8 × 2–3 μm. Conidial echinulate, globose to subglobose, 3.4–5 μm.

Extrolites: asperthecin, asperugins, 2-ω-hydroxyemodin, emercellin, emestrin, paxillin, shamixanthones, sterigmatocystin, versicolorins, violaceols.

Distinguishing characters: Aspergillus foveolatus can be easily recognized by pitted ascospores.

**Aspergillus fruticulosus** Raper & Fennell, Gen. Aspergillus: 506. 1965. MycoBank MB326630. Fig. 27.


**ITS barcode:** EF652483. (Alternative markers: BenA = EF652307; CaM = EF652395; RP2B = EF652219).

**Colony diam, 7 d (mm):** CYA 24–25; CYA 37 °C 35–36; CYA 40 °C 30–31; MEA 35–36; MEA 37 °C 50–51; OA 30–31; YES 46–47; CREA 3–5; CYAS 13–14; DG18 25–26.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, sulphate; margins slightly irregular; mycelium white and light yellow; texture floccose; sporulation moderately dense, conidia en masse pale green; soluble pigments absent; exudates light brown droplets; reverse dark brown. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white and light yellow; texture floccose; sporulation moderately dense, conidia en masse blue green; soluble pigments absent; exudates clear droplets; reverse reddish brown. YES 25 °C, 7 d: Colonies moderately deep, sulphate; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse blue green; soluble pigments absent; exudates absent; reverse brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse pale green; soluble pigments absent; exudates absent; reverse light yellow to centre, olive green at edge. OA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium yellow light; texture floccose; sporulation moderately dense, conidia en masse blue green; soluble pigments yellowish brown; exudates clear droplets; reverse yellowish brown. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, blackish to dark brown, globose to subglobose, 230–500 μm, surrounded by numerous Hüle cells; Hüle cells hyaline, globose to ovoid, 10–20 μm. Asci 8 spored, globose to subglobose. Ascospores orange to reddish brown, in surface view globose to subglobose, spore bodies smooth, 4.5–5.5 × 3–5 μm; in side view lenticular, with two equatorial crests measuring 0.8–1 μm wide; crests ornamented with longitudinal, 0.3–0.4 μm wide pleats. Conidiophores with smooth stipes, light brown, 40–200 × 4–6 μm; vesicles hyaline to pale brown, subglobose to subclavate, 8–12 μm wide, fertile over the upper half to two thirds; metulae hyaline, 5–6 × 3–4.5 μm; phialides hyaline, flask-shaped, 6–9 × 2–3.5 μm. Conidia echinulate, globose to subglobose, 3.5–4 μm, green in mass.

**Extrolites:** asperthecin, 2-ω-hydroxyemodin, falconensins, falconensons, sterigmatocystin, versicolorins, violaceols.

**Distinguishing characters:** Aspergillus fruticulosus is close to A. falconensis morphologically and phylogenetically, but the ascospore crests of A. falconensis (1–2 μm) are wider than in A. fruticulosus (0.8–1 μm).

**Aspergillus israelensis** A.J. Chen, Frisvad & Samson, sp. nov. MycoBank MB816091. Fig. 28.

**Etymology:** Name refers to its origin, isolated from evaporation pond, Ein Bokek, Dead Sea, Israel.

**Diagnosis:** Slow growth on CYA, MEA, OA and YES, narrow conidiophore stipes (3.5–4.5 μm), vesicles (7–10 μm) and globose, turbinate conidia measuring 2.5–3.5 μm.

**Typus:** Israel. Dead Sea, Ein Bokek, evaporation pond, 2002, isolated by L. Butinar (holotype CBS H-22491, culture ex-type: CBS 140627 = IBT 24293 = DTO 325-E2).

**ITS barcode:** KU866677. (Alternative markers: BenA = KU866915; CaM = KU866797; RP2B = KU867062).

**Colony diam, 7 d (mm):** CYA 10–19; CYA 37 °C No growth; CYA 40 °C No growth; MEA 15–20; MEA 37 °C No growth; OA 14–15; YES 14–22; CREA 8–9; CYAS 12–16; DG18 10–13.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, sulphate; margins entire; mycelium white, wood brown at edge;
Fig. 27. Aspergillus fruticulosus CBS 486.65. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Fig. 28. Aspergillus israelensis CBS 140627. A. 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. G. Conidia. Scale bars: B = 30 μm; C–E, G = 10 μm; F = 8 μm.
texture velvety; sporulation moderately dense, conidia en masse greyish green; soluble pigments absent; exudates absent; reverse dark brown. MEA 25 °C, 7 d: Colonies moderately deep, sulphate; margins entire; mycelium white; texture floccose at centre, velvety at edge; sporulation dense, conidia en masse dark green; soluble pigments absent; exudates absent; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulphate; margins entire; mycelium pale buff; texture velvety; sporulation moderately dense, conidia en masse pale green; soluble pigments absent; exudates absent; reverse light brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white and light buff; texture floccose; sporulation moderately dense, conidia en masse pale green; soluble pigments absent; exudates absent; reverse deep olive buff. OA 25 °C, 7 d: Colonies low, plane; margins entire; texture velvety to floccose; sporulation moderately dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse light greyish olive. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata not observed. Conidiophores with smooth stipes, pale brown, 90–160 × 3.5–4.5 μm; vesicles hyaline to pale brown, hemisphere to subclavate, 7–10 μm wide, fertile over the upper half; metulae hyaline to pale brown, 5–8 × 2.5–3.5 μm; phialides hyaline, flask-shaped, 6–8 × 2–2.5 μm. Conidia globose, tuberculate, 2.5–3.5 μm, green in mass.

**Extrolites:** an emindol (and many extrolites, of unknown chemical constitution, only found in this species).

**Distinguishing characters:** Compared to other non-ascosporic species, *A. israelensis* grows slower on most of the media (CYA, MEA, OA and YES), it resembles *A. unguis* and *A. asperescens*, but *A. unguis* produces echinulate conidia; *A. asperescens* produces subglobose to ellipsoidal conidia.

**Aspergillus jaipurensis** Samson, Visagie & Houbraken, Stud. Mycol. 78: 155. 2014. MycoBank MB809592. Fig. 29. 

**Typus:** IMI 378525. Culture ex-type: CBS 952.97 = IMT 1963

**ITS barcode:** KU866623. (Alternative markers: *BenA* = KU866761; *CaM* = KU866762; *RPB2* = KU867024).

**Colony diam., 7 d (mm):** CYA 25–33; CYA 37 °C 38–43; CYA 40 °C 34–36; MEA 32–36; MEA 37 °C 55–60; OA 31–34; YES 48–51; CREAS 5–6; CYAS 14–15; DG18 14–20.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, sulphate; margins slightly irregular; mycelium light brown at centre, white at edge; texture velvety; sporulation sparse; soluble pigments absent; exudates light brown droplets; reverse wood brown. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulphate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates light brown droplets; reverse wood brown to yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulphate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse light brown. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulphate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse cream white. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse pale green to yellow green; soluble pigments absent; exudates absent; reverse light brown. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, violet to dark brown, globose to subglobose, 150–500 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellowish brown, globose to ovoid, 14–25 μm. Ascii 8 spored, globose to subglobose. Ascosporules purplish red, in surface view globose to subglobose, spore bodies smooth, 6.7–7.5 × 5.6–6 μm; in side view lenticular, with two pleated equatorial crests measuring 0.8–1 μm; crests ornamented with longitudinal, 0.2 μm wide pleats. Conidiophores with smooth stipes, pale yellowish brown, 30–100 × 4–6 μm; vesicles hyaline to pale brown, subclavate to subglobose, 7–9 μm wide, fertile over the upper half; metulae hyaline to pale brown, 5–6.5 × 2.5–3.5 μm; phialides hyaline to pale brown, flask-shaped, 5–7 × 2–3.5 μm. Conidia verrucose to tuberculate, globose to subglobose, 4–6.5 × 3–4.5 μm. (Anamorphic structures were observed from OA).

**Extrolites:** asperugin, an austalide (tentatively identified), emestrin, emindols, shamixanthones, violaceols.

**Distinguishing characters:** *Aspergillus jaipurensis* is characterized by large, purplish red ascospores, which can easily distinguish it from other species in section Nidulantes.

**Notes:** In combination with the recent adoption of the one fungus one name concept, *Emicellula indica* was transferred to *Aspergillus*. Since the name *A. indicus* is already occupied, the new name *A. jaipurensis* was proposed (Samson et al. 2014), which was named after the city Jaipur in India, the origin of the type strain.

**Aspergillus latilabatus** A.J. Chen, Frisvad & Samson, sp. nov. MycoBank MB816093. Fig. 30.

**Etymology:** The name refers to the lip shaped crests of ascospores.

**Diagnosis:** Brown, smooth ascospores with two thick equatorial crests.


**ITS barcode:** KU866624. (Alternative markers: *BenA* = KU866684; *CaM* = KU866762; *RPB2* = KU867025).

**Colony diam., 7 d (mm):** CYA 22–23; CYA 37 °C 33–37; CYA 40 °C 25–28; MEA 27–28; MEA 37 °C 41–42; OA 22–23; YES 27–28; CREAS No growth; CYAS 16–17; DG18 1–4.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, slightly sulphate; margins slightly irregular; mycelium white; texture...
Fig. 29. Aspergillus jaipurensis CBS 952.97. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Aspergillus latiariatus CBS 426.93T. A. 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–C. Ascomata. D–H. Ascospores. E. Hüll cells. Scale bars: B = 30 μm; C–E = 10 μm; F–H = 2 μm.
textured floccose to velvety; sporulation absent; soluble pigments absent; exudates absent; reverse brown. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse light brown. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse cream white. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture absent; soluble pigments absent; exudates absent; reverse yellowish brown. CREA 25 °C, 7 d: No growth.

Micromorphology: Ascomata cleistothecial, superficial, blackish to dark brown, globose, 100–160 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 13–24 μm. Ascii 8 spored, globose to subglobose. Ascospores brown, in surface view globose to subglobose, spore bodies smooth, 5.5–7 × 4.5–6 μm; in side view lenticular, with two equatorial crests measuring 0.5–1 μm wide; crests smooth. Anamorph absent.

Aspergillus latus (Thom & Raper) A.J. Chen, Frisvad & Samson, comb. nov. MycoBank MB816100. Fig. 31.


Aspergillus latus var. sublatus. CBS 492.65 = ATCC 16848 = IMI 074181 = NRRL 200 = QM 7425 = WB 200 = IBT 22844 = DTO 047-H2.

ITS barcode: KF465768. (Alternative markers: BenA = AB248334; CaM = KU866693; RP2B = KU866946).

Colony diam, 7 d (mm): CYA 43–52; CYA 37 °C >60; CYA 40 °C 54–>60; MEA 38–51; MEA 37 °C >60; OA 33–46; YES 58–>60; CREA 12–46; CYAS 25–46; DG18 13–31.

Aspergillus miraensis (Zhang, Chen & Guo) Hubka, S.W. Peterson & M. Kolárík, Plant Syst. Evol. 302: 1288. 2016. Mycobank MB816283. Fig. 32.
Fig. 31. Aspergillus latus CBS 492.65T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.

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Fig. 32. *Aspergillus miraensis* CBS 140625T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
**Aspergillus miraensis** Sappa, Allionia 2: 87. 1954. MycoBank MB292849. Fig. 33.


**ITS barcode**: EF652477. (Alternative markers: BenA = EF652301; CaM = EF652389; RPB2 = EF652213).

Colony diam. 7 d (mm): CYA 39 – 40; CYA 37 °C 7 – 8; CYA 40 °C No growth; MEA 46 – 47; MEA 37 °C 5 – 6; OA 44 – 45; YES 55 – 56; CREA 8 – 12; CYAS 25 – 26; DG18 21 – 22.

**Colony characters**: CYA 25 °C, 7 d: Colonies moderately deep, slightly sulphate; margins entire; mycelium pink to purple drab; texture velvety; sporulation moderately dense, conidia en masse dull green to olive green; soluble pigments absent; exudates light brown droplets; reverse greyish olive. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulphate; margins entire; mycelium pink to purple drab; texture velvety; sporulation moderately dense, conidia en masse dull green to olive green; soluble pigments absent; exudates light brown droplets; reverse greyish olive. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulphate; margins entire; mycelium pink to purple drab; texture velvety; sporulation moderately dense, conidia en masse dull green to olive green; soluble pigments absent; exudates light brown droplets; reverse greyish olive. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulphate; margins entire; mycelium pink to purple drab; texture velvety; sporulation moderately dense, conidia en masse dull green to olive green; soluble pigments absent; exudates light brown droplets; reverse greyish olive.

**Micromorphology**: Ascomata cleistothecial, superficial, reddish brown, globose to subglobose, 320 – 600 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellowish brown, globose to ovoid, 14 – 22 μm. Ascii 8 spored, stellate to subglobose. Ascospores orange to reddish brown (violet in original description of Zhang et al. 2013), in surface view stellate, 8 – 10 μm; spore bodies smooth, ( verrucose in original description of Zhang et al. 2013) globose to subglobose, 2 – 4 × 2 – 3 μm; in side view broadly lenticular, with two stellate equatorial crests; undissected part of crests 0.7 – 1 μm broad, with 1.5 – 2.5 μm long extents; crests ornamented with longitudinal, 0.3 – 0.4 μm wide pleats. Conidiophores with smooth stipes, light brown, 300 – 500 X 5 – 6 μm; vesicles hyaline to pale green, subclavate to subglobose, 12 – 15 μm wide, fertile over the upper half to two thirds; metulae hyaline to pale green, 5 – 8 × 3 – 4 μm; phialides hyaline to pale green, flask-shaped, 6 – 8 × 2 – 3.5 μm. Conidia echinulate, globose to subglobose, 2 – 3.5 μm.

**Extrolites**: afatoxin B1, asperthecin, 2-hydroxyemodin, a desertorin, emericellin, shamixanthones, sterigmatocystin.

**Distinguishing characters**: Aspergillus miraensis is close to A. stellatus and A. stella-maris, but can be distinguished by smaller ascospores and conidia. In addition, A. miraensis grows faster on CYA, MEA, YES and OA plates.

**Aspergillus multicolor** Sappa, Allionia 2: 87. 1954. MycoBank MB292849. Fig. 33.


**Distinguishing characters**: The pink to purple drab mycelium and pink Hülle cells can easily distinguish A. multicolor from other related species. Brown Hülle cells were mentioned in Raper & Fennell (1965).
Fig. 33. Aspergillus multicolor CBS 133,54T. A. 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–E. Conidiophores and Conidia. F,G. Hüle cells. Scale bars: B = 30 μm; C–F = 10 μm; G = 1000 μm.
Fig. 34. Aspergillus mulundensis CBS 140610T. A. 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. G. Conidia. Scale bars: B = 30 μm; C–E,G = 10 μm; F = 8 μm.
ITS barcode: KU866604. (Alternative markers: BenA = KU866833; CaM = KU866729; RPB2 = KU866989).

Colony diam, 7 d (mm): CYA 22–23; CYA 37 °C 4–8; CYA 40 °C No growth; MEA 24–25; MEA 37 °C 5–6; OA 30–31; YES 36–37; CREA 6–11; CYAS 13–15; DG18 15–17.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white and buff; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse yellowish brown. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins slightly irregular; mycelium white and light yellow; texture velvety; sporulation moderately dense, conidia en masse blue green; soluble pigments absent; exudates light brown droplets; reverse reddish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white and light yellow; texture velvety; sporulation absent; soluble pigments absent; exudates absent; reverse saffron. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture cream white. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white and light yellow; texture velvety; sporulation moderately deep, conidia en masse pale green to blue green; soluble pigments light brown; exudates absent; reverse dark brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium light yellow and white; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse yellowish brown to brown. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium light yellow and white; texture floccose; sporulation moderately dense, conidia en masse pale green; soluble pigments light brown; exudates clear droplets; reverse yellow brown. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, superficial, blackish to dark brown, globose, 140–400 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 13–23 μm. Asci 8 spored, globose to subglobose. Ascospores orange to reddish brown, in surface view globose to subglobose, spore bodies smooth, 3.5–4.5 × 3–3.5 μm; in side view lenticular, with two equatorial crests measuring 0.7–1 μm wide, 0.4 μm thick; crests smooth. Conidiophores with smooth stipes, light brown, 35–150 × 2.5–3 μm; vesicles hyaline to pale brown, subclavate to globose, 6–8 μm wide, fertile over the upper half to two thirds; metulae hyaline, 6–9.5 × 3–4.5 μm; phialides hyaline, flask-shaped, 6–8 × 2.5–3 μm. Conidia echinulate, globose to subglobose, 3.5–4.5 μm, green in mass. (Anamorphic structures were observed from OA).

Extrólités: asperthecin, falconensins, cf. falconensins, gregatinis, sterigmatocystin, 6,7,8-hydroxy-3-methylsoucarmin, versiclorins, violaceols.

Distinguishing characters: Phylogenetically Aspergillus mulundensis is close to A. multicolor, but A. multicolor produces longer conidiophores (300–350 μm), larger vesicles (16–20 μm) and conidia (3.5–5.5 μm). Morphologically A. mulundensis resembles A. aurantiobrunneus, but A. mulundensis grows faster on all tested media.

Aspergillus navahoensis M. Chr. & States, Mycologia 74: 226. 1982. MycoBank MB110496. Fig. 35.


ITS barcode: EF652424. (Alternative markers: BenA = EF652248; CaM = EF652336; RPB2 = EF652160).

Colony diam, 7 d (mm): CYA 34–35; CYA 37 °C 30–33; CYA 40 °C 26–27; MEA 24–25; MEA 37 °C 35–38; OA 40–42; YES 34–35; CREA 2–8; CYAS 18–19; DG18 15–16.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium luteous; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse brown. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins slightly irregular; mycelium light yellow and white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse dark brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium light yellow; texture velvety; sporulation moderately dense, conidia en masse yellow green; soluble pigments light brown; exudates absent; reverse dark brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium luteous; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse yellowish brown to brown. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium light yellow and white; texture floccose; sporulation moderately dense, conidia en masse pale green; soluble pigments light brown; exudates light brown droplets; reverse yellow brown. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, superficial, blackish to dark brown, globose, 140–400 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 13–23 μm. Asci 8 spored, globose to subglobose. Ascospores orange to reddish brown, in surface view globose to subglobose, spore bodies smooth, 3.5–4.5 × 3–3.5 μm; in side view lenticular, with two equatorial crests measuring 0.7–1 μm wide, 0.4 μm thick; crests smooth. Conidiophores with smooth stipes, light brown, 35–150 × 2.5–3 μm; vesicles hyaline to pale brown, subclavate to globose, 6–8 μm wide, fertile over the upper half to two thirds; metulae hyaline, 6–9.5 × 3–4.5 μm; phialides hyaline, flask-shaped, 6–8 × 2.5–3 μm. Conidia echinulate, globose to subglobose, 3.5–4.5 μm, green in mass. (Anamorphic structures were observed from OA).

Extrólités: asperthecin, falconensins, cf. falconensins, gregatinis, sterigmatocystin, 6,7,8-hydroxy-3-methylsoucarmin, versiclorins, violaceols.

Distinguishing characters: Aspergillus navahoensis is close to A. fruticulosus, A. nidulans and A. pachycristatus, but can be easily distinguished by smooth, thick crests of ascospores, longer metulae and narrower vesicles.
Fig. 35. *Aspergillus navahoensis* CBS 351.81T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Fig. 36. Aspergillus nidulans CBS 589.65T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Fig. 37. Aspergillus nidulans CBS 114.63 (ex-type of A. dentatus). A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüllle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
**Typus: IMI 86806. Culture ex-type: CBS 589.65 = NRRL 187 = ATCC 10074 = IHM 3563 = IMI 126691 = IMI 86806 = QM 1985 = Thom 4640.5 = WB 187 = DTO 047-H9.**

**ITS barcode:** EF652427. (Alternative markers: *BenA* = EF652251; *CaM* = EF652339; *RPB2* = EF652163).

**Colony diam, 7 d (mm):** CYA 30–39; CYA 37 °C 47–58; CYA 40 °C 49–55; MEA 41–52; MEA 37 °C >60; OA 36–52; YES >60; CREA 5–10; CYAS 14–40; DG18 22–38.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation moderately dense, conidia en masse olive green; purple red soluble pigment produced after 2 wks; exudates clear droplets; reverse dark reddish brown. MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation dense, conidia en masse greyish green; soluble pigments absent; exudates clear droplets; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse pale green to yellow green; soluble pigments absent; exudates absent; reverse brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture velvety; sporulation dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse greyish green. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture velvety; sporulation dense, conidia en masse yellow green; soluble pigments absent; exudates clear droplets; reverse brown. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, violet to dark brown, globose to subglobe, 150–420 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 12–20 μm. Ascii 8 spored, globose to subglobe. Ascospores orange to reddish brown, in surface view globose to subglobe, 3.5–5 × 3–4.5 μm; in side view lenticular, with two pleated equatorial crests measuring 0.5–1 μm, crests entire or dentate. Conidiophores with smooth stipes, yellowish brown, 70–220 × 5–8 μm; vesicles pale brown, globose to subclavate, 6–14.5 μm wide, fertile over the upper half to two thirds; metulae hyaline, pale green to pale brown, 5–8 × 2.5–4.5 μm; phialides hyaline to pale green, flask-shaped, 6–8 × 2.5–3.5 μm. Conidia echinulate, globose to subglobe, 3–4 μm.

**Extralites:** asperthecin, asperugins, austinol, cordycepin, dehydroaustrol, 2-ω-hydroxyoxymid, diocinol, eremicillin, shamix-anthones, sterigmatocystin, versicolorins, violaceols. Asperugin was only detected on CYA with 5 % NaCl. Many further extralites have been found in this species (Nielsen et al. 2011) using different combinations of media, after biological interaction etc (Table 6).

**Distinguishing characters:** *Aspergillus nidulans* resembles *A. quadrilineatus*, but differs in two crests in contrast to four crests on the ascospores of *A. quadrilineatus*.

**Notes:** *Aspergillus nidulans* var. *dentatus* (CBS 114.63), isolated from diseased human fingernails, showed almost full phenotypic agreement with *A. nidulans* except for its dentate equatorial crests (Sandhu & Sandhu 1963), our observation confirms the original description (Figs 3C, D, 37). *Aspergillus dentatus* shares identical sequences (ITS, *BenA*, *CaM* and *RPB2*) and extralites with *A. nidulans*, therefore is considered a synonym here.

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**Aspergillus olivicola** Frisvad, Zalar & Samson, Mycologia 100: 781. 2008. MycoBank MB507362. Fig. 38.


**ITS barcode:** EU448268. (Alternative markers: *BenA* = AY339996; *CaM* = EU443986; *RPB2* = KU866923).

**Colony diam, 7 d (mm):** CYA 30–36; CYA 37 °C 0–14; CYA 40 °C No growth; MEA 33–42; MEA 37 °C 5–10; OA 30–35; YES 24–39; CREA 12–18; CYAS 27–30; DG18 20–25.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, plane to slightly sulcate; margins entire; mycelium gray to greyish violet; texture floccose; sporulation absent to moderately dense, conidia en masse olive green; soluble pigments absent; exudates absent; reverse dark violet to dark brown. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate to sulcate; margins entire; mycelium white; texture granular due to ascomata production; sporulation moderately dense, conidia en masse pale green; soluble pigments absent; exudates clear droplets; reverse yellowish brown to cream brown with brown dots, large amount of ascomata present after 1 wk. YES 25 °C, 7 d: Colonies moderately deep, plane to slightly sulcate; margins entire; mycelium smoke gray; texture floccose; sporulation sparse to moderately dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse dark brown at centre, cream white at edge. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse cream white. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture granular due to ascomata production; sporulation sparse; soluble pigments absent; exudates clear droplets; reverse white. Ascomata present after 1 wk. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, greenish brown, globose to subglobe, 400–770 μm, surrounded by numerous Hülle cells; Hülle cells brown, globose to ovoid, 15–28 μm. Ascii 8 spored, stellate to subglobe. Ascospores orange to reddish brown, in surface view stellate, 7.5–11 μm; spore bodies smooth, globose to subglobe, 3–4.5 × 3–4 μm; in side view broadly lenticular, with two stellate equatorial crests; undissected part of crests 0.4–0.7 μm broad, with 1–3 μm long extensions; crests ornamented with longitudinal, 0.3–0.5 μm wide pleats. Conidiophores with smooth stipes, yellowish brown, 150–340 × 4–5.5 μm; vesicles hyaline to pale brown, subglobe to subclavate, 8–15 μm wide, fertile over the upper half to two thirds; metulae hyaline, 7.5–10.5 × 2–3.5 μm; phialides hyaline to pale brown, flask-shaped, 7.5–12.5 × 1.5–3 μm. Conidia coarsely echinulate to tuberculate, globose to subglobe, 2–3.5 μm.
Aspergillus olivicola CBS 119.37T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Extrolites: aflatoxin B1 and B2, asperugin, astel toxin, desertorins, emericellin, shaminxanthone, sterigmatocystin, terrein, varirosi.

Distinguishing characters: Thin-walled Hülle cells, relatively long metulae (7.5–10.5 μm × 2–3.5 μm) and phialides (7.5–12.5 × 1.5–3 μm), coarsely echinulate conidia, these characters distinguish A. olivcola from other stellate ascosporous species.


**ITS barcode:** n.a. (Alternative markers: BenA = AB248347; CaM = AB524047; RPB2 = n.a.).

**Colony characters:** **Fide** Horie & Udagawa (1995) colonies on CZapek’s solution agar growing restrictedly, attaining a diameter of 25–26 mm in 14 days at 25 °C, more or less floccose, plane, consisting of a thin mycelial felt, producing scattered cleistothecia. Yellowish White (3A2 after Komor & Wanscher 1978) to pale Orange (6A3); conidial heads limited in number, not affecting the colony colour; reverse Brownish Orange (7C4) to Brown (7E6).

Colonies on MEA spreading broadly, attaining a diameter of 56–57 mm in 14 days at 25 °C, more or less floccose, plane, consisting of a thin mycelial felt, granular in appearance due to the production of abundant cleistothecia with Hülle cells, overgrown by loose network of aerial hyphae and numerous conidial heads, Greenish Gray (1C2) to Greyish Green (1D3); reverse Greyish Orange (5B3) to Brownish Orange (5C4).

**Micromorphology:** **Fide** Horie & Udagawa (1995), cleistothecia superficial, scattered or aggregated in a thin layer, globose to subglobose, 180–370 μm in diam, surrounded by a hyaline to pale yellowish brown layer of scattered hyphae bearing numerous globose to subglobose thick-walled Hülle cells measuring 10–35 μm in diam; peridium brown to dark brown, thin, of texture intricate, 2–3-layered; outermost layer consisting of hyphal cells measuring 3–17 μm wide. Ascii irregularly disposed, 8-spored, globose to subglobose or ovoid, 11–13.5 × 10–11 μm, evanescent. Ascospores at first hyaline to pale reddish brown, becoming brownish red, broadly lenticular, 4.5–5.5 × 4–4.5 μm including crests, with two conspicuously pleated equatorial crests measuring about 1 μm wide, with a tuberculate or verruculose convex wall. Conidial heads greyish green, short columnar to columnar, 70–190 μm long and 40–70 μm wide. Conidiophores arising mostly from aerial hyphae; stipes short, more or less sinuous, 50–120 × 4–7 μm, orange gray to brownish orange, smooth-walled; vesicles subglobose to subclavate, orange gray, 10–14 μm in diam, fertile over the upper half. Aspergilla biseriate; metulae greyish white to pale greyish green, 4–7 × 2–3 μm; phialides greyish white to pale greyish green, 5–8 × 2–4 μm. Conidia globose to subglobose, 4–5.5 μm in diam, verruculose.

**Extrolites:** Strain not available.

**Distinguishing characters:** Molecular analysis shows *A. omanensis* as a unique species. **Fide** Horie & Udagawa (1995) its morphology resembles that of *A. spinulosporus* and *A. desertorum*, but can be distinguished from *A. spinulosporus* by tuberculate or verruculose ornamentation on ascospore convex walls; and from *A. desertorum* by much smaller ascospores. Unfortunately, the type strain is unavailable and cannot be investigated during our study.

**Aspergillus pachycristatus** Matsuzawa, Y. Horie & Yaguchi, Mycoscience 53: 439. 2012. MycoBank MB580944. Fig. 39.


**ITS barcode:** n.a. (Alternative markers: BenA = AB375875; CaM = AB524062; RPB2 = n.a.).

**Colony characters:** **Fide** Horie & Udagawa (1995) colonies greatly branched, slightly sulcate; margins slightly irregular; mycelium white and rosy buff; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse dark reddish brown. MEA 25 °C, 7 d; Colonies moderately deep; slightly sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates light brown to purple droplets, large amount of purple droplets present on MEA at 37 °C after 1 wk; reverse dark reddish brown. Ascomata present after 2 wks. YES 25 °C, 7 d; Colonies moderately deep; sulcate; margins slightly irregular; mycelium white and light yellow; texture floccose; sporulation moderately dense, conidia en masse greyish green; soluble pigments absent; exudates absent; reverse reddish brown. DG18 25 °C, 7 d; Colonies moderately deep, slightly sulcate; margins slightly irregular; mycelium buff; texture floccose; sporulation moderately dense, conidia en masse greyish green; soluble pigments absent; exudates absent; reverse ochraceous buff. OA 25 °C, 7 d; Colonies large, plane; margins entire; mycelium white and light yellow; texture floccose to velvety; sporulation moderately dense, conidia en masse yellow green; soluble pigments light brown; exudates absent; reverse cream white to light brown. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, blackish to dark brown, globose to subglobose, 200–500 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 11–21 μm. Ascii 8 spored, globose to subglobose. Ascospores orange to reddish brown, in surface view globose to subglobose, spore bodies smooth, 4–5 × 3.5–4 μm; in side view lenticular, with two equatorial crests measuring 0.7–1 μm wide, 0.4 μm thick; crests ornamented with longitudinal, 0.3–0.4 μm wide pleats. Conidiophores with smooth stipes, light brown, 150–260 × 5–6 μm; vesicles hyaline to pale brown, subclavate, 8–12 μm wide, fertile over the upper half to two thirds; metulae hyaline, 5.5–7.5 × 2.5–4 μm; phialides hyaline, flask-shaped, 6–9 × 2.5–3.5 μm. Conidia echinulate, globose to subglobose, 3–4 μm. (Anamorphic structures were observed from OA).

**Extrolites:** asperugin, echinocandins, emecorrhugatin, sterigmatocystin, versicolorins, violaceols.
Fig. 39. Aspergillus pachycristatus NRRL 11440. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
**Distinguishing characters:** Morphologically, *Aspergillus pachycristatus* resembles *A. nidulans*, but the ascospore crests are thicker in *A. pachycristatus*. The smooth ascospore convex can distinguish it from phylogenetically related *A. rugulosus*.


**Typus:** FMR 5588; isotype IMI 370867. Culture ex-type: CBS 100523 = FMR 5588 = IMI 370867 = DTO 011-H1.

**ITS barcode:** KU866966. (Alternative markers: *BenA* = AY339989; *CaM* = EU443988; *RPB2* = KU866937).

**Colony diam, 7 d (mm):** CYA 20–25; CYA 40 °C No growth; CYA 40 °C No growth; MEA 31–32; MEA 37 °C No growth; OA 12–22; YES 28–30; CREA No growth; CYAS 1–2; DG18 1–2.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium pale pink to pale yellow at centre, white at edge; texture velvety; sporulation absent; soluble pigments absent; exudates clear droplets; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium pale pink to pale yellow at centre, white at edge; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse yellowish brown.

**Micromorphology:** *Fide* Stchigel & Guarro (1997) ascomata superficial, globose, nonostiolate, blackish, with green iridescence, 80–250 μm diam, produced very late, appearing after 2–3 months, surrounded by a felt of hyphae and Hülle cells and supported by masses of scattered hyphae and Hülle cells; Hülle cells pale yellowish to orange-brown, globose to irregularly shaped, thick-walled, 10–22 μm diam. Peridium 4–12 μm thick, pale to yellow-brown, semi-translucent to translucent, *textura intricate* to *epidermoidea*, 3–7 layered, cells of the outer layer measuring 3–14 μm diam. Asci 16 spored (8 sporulated according to Zalar et al. 2008), globose to broadly ellipsoidal, with several broad wall protrusions, 22–35 μm diam, evanescent. Ascospores one-celled, at first hyaline, becoming violet-brown, lenticular, 7–9 × 6–7 μm (crest not included), with two conspicuously pleated, stellate and striate equatorial crests, 4–8 μm wide; convex surface tuberculate under SEM. Anamorph absent.

**Extralites:** Dibenzofurans (asticolourins?), sclerotiorins (tentatively identified), violaceols.

**Distinguishing characters:** The large, violet stellate ascospores with tuberculate convex surface can distinguish *Aspergillus pluriseminatus* from other related species.

**Notes:** According to Stchigel & Guarro (1997), ascomata of *A. pluriseminatus* are produced very late, and only produced on PCA. Unfortunately, we could not find ascomata on several kinds of media including PCA after 3 months. Zalar et al. (2008) observed 8 spored instead of 16 spored asci in *A. pluriseminatus*.


**Typus:** CBS 754.74. Culture ex-type: CBS 754.74 = NRRL 6133 = IMI 334937 = LCP 82.3323 = DTO 047-H5.

**ITS barcode:** EF652506. (Alternative markers: *BenA* = EF652330; *CaM* = EF652418; *RPB2* = EF652242).

**Colony diam, 7 d (mm):** CYA 5–7; CYA 37 °C No growth; CYA 40 °C No growth; MEA 7–10; MEA 37 °C No growth; OA 5–7; YES 7–9; CREA No growth; DG18 7–8.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse rosy buff. MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse reddish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse reddish brown. MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse reddish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse reddish brown. MEA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse reddish brown. YES 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, blackish to dark brown, globose to subglobose, 90–200 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellowish brown, globose to ovoid, 8–20 μm. Ascii 8 sporous, globose to subglobose. Ascospores brown, in surface view globose to subglobose, spore bodies smooth, 6–7 × 4.5–5 μm; in side view lenticular, with two low crests measuring 0.3–0.6 μm wide. *Fide* Samson & Mouchacca (1975) conidial structures mostly absent on Czapek or MEA, but sometimes produced in old slant cultures on the glass surface; on Czapek agar with 20 % or more sucrose conidiophores are produced after one month. Conidial heads white, radiate, biseriate. Conidiophores hyaline, 40–50 × 2.5–5 μm. Vesicles ellipsoidal to clavate, 6–8 μm in diam. Metulae cylindrical, 3.5–6 × 2.5–3.5 μm bearing 2 to 3 phialides each. Phialides flask-shaped with short but distinct neck, 6–8 × 2.5–3 μm. Conidia ellipsoidal to cylindrical, hyaline, smooth, 3.5–5.5 × 1.5–2 μm.

**Extralites:** calbistrins, eremin, emindol PA, epurpurin A–C, nor-solorinic acid, shamixanthones, variecolins, versicolorins.
Fig. 40. Aspergillus purpureus CBS 754.74T. A. 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. Ascomata. C. Asci. D–F. Ascospores. E. Hüle cells. Scale bars: B = 1000 μm; C–E = 10 μm; F–H = 2 μm.
Fig. 41. Aspergillus qinxianii CBS 128788T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülfle cells. G.H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Aspergillus qinqixianii

Y. Horie, Abliz & R.Y. Li, Mycologia 41: 183. 2000. MycoBank MB464660. Fig. 41.

**Typus:** CBM FA-866. Culture ex-type: CBS 128788 = IFM 55020 = CMB-FA-866 = DTO 098-H6.

**ITS barcode:** KU866660. (Alternative markers: *BenA* = AB524360; *CaM* = AB524051; *RPB2* = KU866980).

**Colony diam, 7 d (mm):** CYA 40–42; CYA 37 °C 23–30; CYA 40 °C No growth; MEA 45–46; MEA 37 °C 26–28; OA 35–38; YES 54–55; CREA 16–17; CYAS 25–34; DG18 21–25.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white and gray; texture floccose; sporulation sparse; soluble pigments absent; exudates clear to light brown droplets; reverse dark olive green; Ascomata present after 1 wk. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white and light yellow; texture floccose; sporulation sparse; soluble pigments absent; exudates clear to light brown droplets; reverse dark brown at centre, yellowish brown at edge. Ascomata present after 1 wk. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia *en masse* yellow green; soluble pigments absent; exudates absent; reverse cream yellow to dark brown. Ascomata present after 1 wk. DG18 25 °C, 7 d: Colonies moderately deep; plane; margins entire; mycelium buff at centre, white at edge; texture floccose; sporulation dense, conidia *en masse* yellow green; soluble pigments absent; exudates absent; reverse pale yellow green. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture granular due to ascomata production; sporulation moderately dense; conidia *en masse* yellow green; soluble pigment absent; exudates clear to light brown droplets; reverse pale olive. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, greyish green to brown, globose to subglobose, 200–510 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellowish brown, globose to ovoid, 16–24 μm. Asci 8 spored, stellate. Ascospores brown, in surface view globose to subglobose, spore bodies smooth, 3.5–4.5 × 3–4 μm; in side view broadly lenticular, with two equatorial crests measuring 0.5 μm wide; Crest bearing hyaline, filiform appendages, measuring 3–7 μm long with swollen tips. Conidiophores with smooth stipes, yellowish brown, 120–280 × 3–5 μm; vesicles hyaline to pale yellowish brown, subglobose to subclavate, 7–12 μm wide, fertile over the upper half; metulae hyaline to pale yellowish brown, 4–8 × 3–5 μm; phialides hyaline to pale yellowish brown, flask-shaped, 7–8 × 2–4 μm. Conidia echinulate, globose to subglobose, 3–4 μm.

**Extriotics:** Asteltoxin, asperthecin, emericellin, 2-μ-hydroxy-yemodin, shammixanthones, terrein (CBS 128789 in addition produced curvularin and dehydrocurvularin).

**Distinguishing characters:** Aspergillus *qinqixianii* is close to *A. filifer*, they share identical *CaM*, but can be distinguished by small differences in *BenA* and *RPB2*. Morphologically these two species can be easily differentiated by the ornamentation on convex surface, the ascospores of *A. qinqixianii* have smooth ascospore convex in contrast with tuberculate convex in *A. filifer*.

**Aspergillus quadrilineatus** Thom & Raper, Mycologia 31: 660. 1939. MycoBank MB275888. Fig. 42.


**ITS barcode:** EF652433. (Alternative markers: *BenA* = EF652257; *CaM* = EF652345; *RPB2* = EF652169).

**Colony diam, 7 d (mm):** CYA 26–46; CYA 37 °C >60; CYA 40 °C >60; MEA 31–47; MEA 37 °C >60; OA 41–48; YES >60; CREA 8–11; CYAS 18–33; DG18 22–28.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium buff and white; texture floccose; sporulation sparse; light brown soluble pigments produced after 2 wks; exudates clear droplets; reverse dark brown. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium buff and white; texture floccose; sporulation sparse; soluble pigments absent; exudates clear droplets; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium buffy brown fading into white; texture floccose; sporulation sparse; soluble pigments absent; exudates clear droplets; reverse light brown. OA 25 °C, 7 d: Colonies morderately deep, plane; margins entire; mycelium buff; texture granular due to ascomata production; sporulation moderately dense; conidia *en masse* yellow green; soluble pigment absent; exudates clear to light brown droplets; reverse pale olive. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, greyish green to brown, globose to subglobose, 200–510 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellowish brown, globose to ovoid, 16–24 μm. Asci 8 spored, stellate. Ascospores brown, in surface view globose to subglobose, spore bodies smooth, 3.5–4.5 × 3–4 μm; in side view broadly lenticular, with two equatorial crests measuring 0.5 μm wide; Crest bearing hyaline, filiform appendages, measuring 3–7 μm long with swollen tips. Conidiophores with smooth stipes, yellowish brown, 120–280 × 3–5 μm; vesicles hyaline to pale yellowish brown, subglobose to subclavate, 7–12 μm wide, fertile over the upper half; metulae hyaline to pale yellowish brown, 4–8 × 3–5 μm; phialides hyaline to pale yellowish brown, flask-shaped, 7–8 × 2–4 μm. Conidia echinulate, globose to subglobose, 3–4 μm.

**Extriotics:** Asteltoxin, asperthecin, emericellin, 2-μ-hydroxy-yemodin, shammixanthones, terrein (CBS 128789 in addition produced curvularin and dehydrocurvularin).

**Distinguishing characters:** Aspergillus *qinqixianii* can be distinguished from other related species by large brown ascospores (Samson & Mouchaca 1975), but are not confirmed in this study.

**Aspergillus qinqixianii** Y. Horie, Abliz & R.Y. Li, Mycoscience 41: 183. 2000. MycoBank MB464660. Fig. 41.
100–700 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 10–24 μm. Ascii 8 spored, globose to subglobose. Ascospores orange to reddish brown, in surface view globose to subglobose, spore bodies smooth, globose to subglobose, 4–4.5 × 3–4.5 μm; in side view lenticular, with two plated equatorial crests about 0.5–1 μm in width paralleled by a secondary narrower pair which are sometimes indistinct, crests are entire, defective or with irregular protuberance. Conidiophores with smooth stipes, pale brownish, 50–150 × 4–5.5 μm; vesicles pale brown, globose, 10–13 μm wide, fertile over the upper half to two thirds; metulae hyaline, 5–7 × 2–4.5 μm; phialides hyaline, flask-shaped, 5–7 × 2–4 μm. Conidia echinulate, globose to subglobose, 3–4 μm.

Extrolites: asperhecin, asperuginis, echinocandins, emestrin, emericellin, emindols, quadrilineatin, shamixanthone, sterigmatocystin, violaceols.

**Distinguishing characters:** *Aspergillus quadrilineatus* is close to *A. nidulans* and *A. latus*, but can be distinguished by four crests.

**Notes:** Phylogenetically *Aspergillus acrisstatus*, *A. floriformis*, *A. parvathecius* and *A. miyajii* are identical with *A. quadrilineatus* and are considered as synonyms as did Hubka et al. (2016). Morphologically these species have minor differences in ascospore crests. *Aspergillus acrisstatus* was introduced as a crest-free variety of *A. nidulans* (Fig. 42I), Fennell and Raper (1955) suggested a close relationship between *A. acrisstatus* and *A. quadrilineatus*, because a number of *A. quadrilineatus* strains also show reduced four crests. *Aspergillus floriformis* was described as a anamorphic species, only Hülle cells were mentioned in the original description (Samson & Mouchacca 1975), but the ex-type (CBS 937.73) of *A. floriformis* is now regenerated and does not produce any anamorphic or teleomorphic structures. Also the ex-type (CBS 493.65) of *A. parvathecius* which was described with ascospores does not produce the teleomorph. Hubka et al. (2016) speculated that both *A. parvathecius* and *A. miyajii* represent atypical *A. quadrilineatus* strains characterized by smaller ascomata with delayed maturation in the first and ascospores with aberrant development and shape in the later. We agree with their opinion, one strain (CBS 853.96) collected from Spain further confirms the diversity of ascospore phenotype in *A. quadrilineatus*, the ascospore crests in this isolate are irregularly protuberate (Fig. 3G, H), phylogenetically it is identical in ITS, CaM and BenA with other *A. quadrilineatus* strains, but shows seven bp differences in RPB2 (99.2 % similarity, 907/914 bp).

**Aspergillus recurvatus** Raper & Fennell, Gen. *Aspergillus*: 529. 1965. MycoBank MB326653. Fig. 43.

**Typus:** IMI 36528. Culture ex-type: CBS 496.65 = NRRL 4902 = ATCC 16809 = IMI 136528 = O-566 = QM 7972 = WB 4902 = IBT 23271 = DTO 053-C8.

**ITS barcode:** EF652482. (Alternative markers: BenA = EF652306; CaM = EF652394; RPB2 = EF652218).
Colony characters: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse reddish brown. MEA 25 °C, 7 d: Colonies deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation absent to moderately dense, conidia en masse if present, olive green; soluble pigments absent; exudates absent to brown droplets; reverse reddish brown to yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation absent to moderately dense, conidia en masse if present, yellow green; soluble pigments absent; exudates absent to brown droplets; reverse brown to yellow brown. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse brown to light brown. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation absent to moderately dense, conidia en masse if present, greyish magenta; soluble pigments absent; exudates absent; reverse greyish brown. OA 25 °C, 7 d: Colonies low to moderately deep, plane; margins entire; mycelium olive buff and white; texture floccose; sporulation sparse to moderately dense, conidia en masse olive green; soluble pigments light brown; exudates absent to light brown droplets; reverse light brown. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, superficial, reddish brown to dark brown, globose to subglobose, 220–350 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellowish brown, globose to ovoid, 14–24 μm. Asci 8 spored, globose to subglobose. Ascospores orange, greyish violet, red-dish purple or brownish red, in surface view globose to subglobose, 4–4.5 × 3.5–4 μm; in side view lenticular, with two plaited equatorial crests with sinuate and entire margins measuring 0.5–0.6 μm wide. Conidiophores with smooth stipes, pale brown, 50–200 × 5–6 μm; vesicles pale brown, hemisphere to subclavate, 8–12 μm wide, fertile over the upper half to two thirds; metulae hyaline to pale brown, 7–8 × 3–3.5 μm; phialides hyaline to pale brown, flask-shaped, 6–7 × 2.5–3 μm. Conidia echinulate, globose to subglobose, 3–4 μm, green in mass.

Extróites: asperuginis, echinocandins, emecorragatin, emericillin, emestrin, sterigmatocystin, versicolorins, violaceols.

Distinguishing characters: Aspergillus rugulosus can be easily distinguished from other species by rugulose ornamentation on convex surface of ascospores.

Notes: The ascospore colour in A. rugulosus varies from greyish red to dark greyish red or reddish purple (Benjamin 1955, Raper & Fennell 1965). In this study, the type strain CBS 133.60 produces orange red ascospores, which turn to reddish purple after months. Emericella rugulosa var. laxulina was described based on its greyish magenta to greyish violet ascospores (Horie et al. 1996b), since it is identical in morphology (except the ascospores colour) and phylogeny with A. rugulosus, we treat it as a synonym as did Hubka et al. (2016). According to Mehrotra & Prasad (1969) Emericella cleistominuta differed from A. rugulosus in producing much smaller ascocoma (15–50 μm). However, we observed ascocoma measuring 200–300 μm in E. cleistominuta, the ascospores of these two species are identical too (Fig. 5E–H). Based on morphological and molecular results, E. cleistominuta is treated as a synonym.

Aspergillus savannensis A.J. Chen, Frisvad & Samson, sp. nov. MycoBank MB816096. Fig. 45.

Etymology: Name refers to its origin, isolated from A1 horizon soil, Halile Rest Camp south of Dolemile Hill, savanna.

Diagnosis: Moderately dense to dense sporulation on CYA, MEA, YES, OA and DG18, reddish brown, smooth ascospores, green conidia measuring 3.5–5 μm.


ITS barcode: KU866581. (Alternative markers: BenA = KU866818; CaM = KU866704; RP2B = KU86699).

Colonies diam, 7 d (mm): CYA 33–35; CYA 37 °C 55–56; CYA 40 °C 55–56; MEA 45–48; MEA 37 °C >60; OA 47–48; YES 64–65; CREA 6–7; CYAS 37–38; DG18 37–38.

Colonies characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium smoke gray; texture velvety; sporulation moderately dense, conidia en masse olive; soluble pigments absent; exudates light brown droplets; reverse dark reddish brown. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation absent at centre, velvety at edge; sporulation dense, conidia en masse dark green; soluble pigments absent; exudates clear droplets; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture velvety; sporulation moderately dense, conidia en masse pale green to yellow green; soluble pigments absent; exudates absent; reverse buff. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation dense, conidia en masse yellow green to dark green; soluble pigments absent; exudates absent; reverse pale green. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture velvety; sporulation dense, conidia en masse dark green; soluble pigments absent; exudates clear droplets; reverse pale yellow green. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, superficial, dark brown, globose to subglobose, 65–120 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to ovoid, 11–16.5 μm. Asci 8 spored, globose to subglobose. Ascospores orange to reddish brown, in surface view globose to subglobose, 4.5–3.5–4 μm; in side view lenticular, with two equatorial crests measuring 0.5–1 μm. Conidiophores with smooth stipes, pale brown, 85–190 × 5–7 μm; vesicles pale brown, globose to subclavate, 8–15.5 μm wide, fertile over the upper half to two thirds; metulae hyaline, 4.5–8 × 3.5–4.5 μm;...
Fig. 43. Aspergillus recurvatus CBS 496.65T. A. 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–E. Conidiophores and Conidia. F,G. Hüle cells. Scale bars: B = 30 μm; C–F = 10 μm; G = 1000 μm.
Aspergillus rugulosus CBS 133.60T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Fig. 45. Aspergillus savannensis CBS 140607T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Fig. 46. *Aspergillus speluncoeus* CBS 497.65<sup>T</sup>. A. 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. G. Conidia. Scale bars: B = 30 μm; C–G = 10 μm.
phialides hyaline, flask-shaped, 7.5–9 × 3–4 μm. Conidia echinulate, globose to subglobose, 3.5–5 μm, green in mass.

**Extrolites**: asperthecin, desertorins, emerins, epurpurins, paspalinine, paspalamine, paixillin.

**Distinguishing characters**: Phylogenetically Aspergillus savannensis clusters with A. desertorum, A. botwanensis and A. stercorarius, but the latter three species do not produce anamorph on any media, while A. savannensis sporulates well on CYA, MEA, YES, OA and DG18.

**Aspergillus speluncus** Raper & Fennell [as ‘speluneus’]. Gen. Aspergillus: 457. 1965. MycoBank MB326656. Fig. 46.


**ITS barcode**: EF652490. (Alternative markers: BenA = EF652314; CaM = EF652226; RPB2 = EF652402).

**Colony diam, 7 d (mm)**: CYA 18–19; CYA 37 °C No growth; CYA 40 °C No growth; MEA 22–23; MEA 37 °C No growth; OA 20–21; YES 18–19; CREA 11–12; CYAS 13–14; DG18 13–14.

**Colony characters**: CYA 25 °C, 7 d: Colonies deep, plane; margins entire; mycelium white and buff; texture floccose; sporulation sparse to moderately dense, conidia en masse pale green; soluble pigments absent; exudates absent; reverse dark brown at centre, buff at edge. MEA 25 °C, 7 d: Colonies deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation sparse to moderately dense, conidia en masse blue green; soluble pigments absent; exudates absent; reverse coral red at centre, yellowish brown at edge. YES 25 °C, 7 d: Colonies deep, slightly sulcate; margins entire; mycelium white; sporulation sparse; soluble pigments absent; exudates absent; reverse reddish brown. DG18 25 °C, 7 d: Colonies deep, plane; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse cream white. OA 25 °C, 7 d: Colonies deep, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse pale green to blue green; soluble pigments absent; exudates absent; reverse cream white. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology**: Ascomata not observed. Conidiophores with smooth stipes, yellowish brown, 130–300 × 4–6 μm; vesicles coloured as the conidiophores, globose to subglobose, 7–11 μm wide, fertile over the two thirds to whole surface; metulae hyaline, 4–6.5 × 2.5–3.5 μm; phialides hyaline, flask-shaped, 5.5–7.5 × 2–2.5 μm. Conidia globose to subglobose, tuberculate, 2.5–3.5 μm, green in mass.

**Extrolites**: cyclopenol, sterigmatocystin, versicolorins, viridicatin, viridicatol.

**Distinguishing characters**: Aspergillus speluncus is close to A. aureolatus morphologically and phylogenetically, but can be distinguished by its smaller, more roughened conidia.

**Note**: According to Emmons, Hülle cells were observed in the original isolation cultures grown on an agar medium containing 1 % neopeptone and 2 % glucose as nutrient. Raper & Fennell (1965) observed limited, degenerated terminal or intercalary cells that resemble Hülle cells. During our study, Hülle cells were not observed, the capacity to produce Hülle cells seems to have disappeared with continued laboratory cultivation.

**Aspergillus spinulosporus** Hubka, S.W. Peterson & M. Kolařík, Plant Syst. Evol. 302: 1290. MycoBank MB816282. Fig. 47.


**Typus**: IMI 061454, Culture ex-type CBS 120.55 = NRRL 2395 = ATCC 16825 = IMI 061454 = LCP 84.2557 = QM 1909 = WB 2395 = IBT 22841 = DTO 047-G9.

**ITS barcode**: EF652445. (Alternative markers: BenA = AY573553; CaM = EF652357; RPB2 = EF652181).

**Colony diam, 7 d (mm)**: CYA 33–38; CYA 37 °C >60; CYA 40 °C >60; MEA 44–50; MEA 37 °C >60; OA 42–48; YES 55–62; CREA 15–26; CYAS 22–36; DG18 5–19.

**Colony characters**: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium saffron and white; texture floccose; sporulation absent; soluble pigments absent; exudates brown droplets; reverse deep wood brown. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation sparse; soluble pigments absent; exudates brown droplets; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium saffron and white; texture floccose; sporulation sparse; soluble pigments absent; exudates brown droplets; reverse yellowish brown. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse cream white. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium saffron and white; texture velvety; sporulation sparse; soluble pigments light brown; exudates absent; reverse light yellowish brown. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology**: Ascomata cleistothecial, superficial, dark brown, globose to subglobose, 200–550 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 15–30 μm. Asci 8 spored, globose to subglobose. Ascospores orange to reddish brown, in surface view globose to subglobose, spore bodies echinulate, globose to subglobose, 3.5–4.5 × 3–4.5 μm; in side view lenticular, with two pleated equatorial crests measuring 0.8–1 μm. Conidiophores with smooth stipes, yellowish brown, 70–120 × 5–6 μm; vesicles yellowish brown, subclavate, 9–11 μm wide, fertile over the upper half; metulae pale brown to pale green, 6–8 × 3–4 μm; phialides hyaline to pale green, flask-shaped, 6–8.5 × 2–3 μm. Conidia echinulate, globose to subglobose, 3–4 μm, green in mass.
Fig. 47. Aspergillus spinulosporus CBS 120,55T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Fig. 48. *Aspergillus stella–maris* CBS 113638T. A. 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, C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G, H. Ascospores. Scale bars: B = 200 μm; C-D, F-G = 10 μm; E = 1000 μm; H = 2 μm.
Extrólitès: asperthecin, asperugins, shamixanthone, stergmatocystins, versicolorins, violaceols.

Distinguishing characters: Aspergillus spinulosporus can be easily distinguished by echinulate convex surface of ascospores.

Notes: This species was introduced as A. nidulans var. echinulatus (Fennell & Raper 1955). Molecular data show it as a unique species, which is also proved by its special ascospore ornamentation. Since the name A. echinulatus is already occupied, the new name A. delacroxi was proposed (Samson et al. 2014). Hubka et al. (2016) treated “A. delacroxi” as a correctable orthographical error and proposed a new name A. spinulosporus. In our study we also concur with this.


ITS barcode: EU448269. (Alternative markers: BenA = KU866886; CaM = EU443978; RBP2 = KU866929).

Colony diam, 7 d (mm): CYA 35–39; CYA 37 °C No growth; CYA 40 °C No growth; MEA 38–40; MEA 37 °C No growth; OA 33–35; YES 42–49; CREA 8–11; CYAS 29–32; DG18 23–25.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white and buff; texture granular due to ascomata production; sporulation sparse to moderately dense, conidia en masse olive green to dark green; soluble pigments absent; exudates clear droplets; reverse buff with radiate brown. Ascomata present after 1 wk. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate to sulcate; margins entire; mycelium white and buff; texture granular due to ascomata production; sporulation moderately dense, conidia en masse olive green to dark green; soluble pigments absent; exudates clear droplets; reverse dark brown at centre, yellowish brown at edge. Ascomata present after 1 wk. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white and buff; texture velvety; sporulation dense, conidia en masse olive green; soluble pigments absent; exudates absent; reverse dark brown at centre, cream white at edge. Ascomata present after 1 wk. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture velvety; sporulation dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse dark green at centre, olive buff at edge. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white and light yellow; texture velvety to granular; sporulation moderately dense, conidia en masse yellow green; soluble pigments absent; exudates clear to light brown droplets; reverse pale greyish green. Ascomata present after 1 wk. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, superficial, reddish brown, globose to subglobose, 370–770 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellowish brown, globose to ovoid, 16–22 μm. Asci 8 spored, stellate. Ascospores orange to reddish brown, in surface view stellate, 13–16 μm; spore bodies smooth, globose to subglobose, 3–4.5 × 2.5–4.5 μm; in side view broadly lenticular, with two stellate equatorial; undissected part of crests 1–1.5 μm broad, with 3–4.5 μm long extensions; crests ornamented with longitudinal, 0.3–0.4 μm wide pleats. Conidiophores with smooth stipes, yellowish brown, 300–800 × 3.5–7 μm; vesicles hyaline to pale green, globose to subclavate, 9–20 μm wide, fertile over the upper two thirds; metulae hyaline to pale green, 5–9 × 3–4 μm; phialides hyaline to green, flask-shaped, 6–9 × 2–3.5 μm. Conidia smooth to finely echinulate, globose to subglobose, 3–4 μm, green in mass.

Extrólitès: emericellin, shamixanthones, stergmatocystin, versicolorins.

Distinguishing characters: Until now stellate ascospores were described for A. pluriseminatus, A. venezuelensis, A. miraensis, A. stellatus, A. olivicola, A. dromiae and A. angustatus. Among these species, A. stella-maris is close to A. miraensis and A. stellatus in vesicle shape, but can be distinguished by septate conidiophores and larger ascospores and conidia.

Aspergillus stellatus Curzi, C.R. Accad. Lincei 19: 428. 1934. MycoBank MB254841. Fig. 49.

Typus: Bowenpilly near Secundarabad, s. coll., (K). Culture ex-type: CBS 598.65 = NNRRL 1858 = ATCC 16819 = IMI 136778 = QM 6835 = WB 1858 = IBT 32730 = DTO 327-F3.

ITS barcode: EF652426. (Alternative markers: BenA = EF652250; CaM = EF652338; RBP2 = EF652162).

Colony diam, 7 d (mm): CYA 26–35; CYA 37 °C 21–34; CYA 40 °C No growth; MEA 32–46; MEA 37 °C 18–35; OA 22–35; YES 38–53; CREA 7–10; CYAS 19–30; DG18 11–22.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white and buff; texture velvety; sporulation moderately dense, conidia en masse olive green; soluble pigments absent; exudates clear droplets; reverse dark olive fading into buff. Ascomata present after 1 wk. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture velvety; sporulation dense, conidia en masse yellow green to dark green; soluble pigments absent; exudates clear droplets; reverse yellowish brown with brown ring. Ascomata present after 1 wk. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture velvety to granular due to ascomata production; sporulation dense, conidia en masse dark green; soluble pigments absent; exudates absent; reverse brown at centre, yellowish brown at edge. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture velvety; sporulation dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse pale yellow green. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white and light yellow; texture floccose; sporulation moderately dense, conidia en masse yellow green; soluble pigments absent; exudates clear droplets; reverse yellowish brown. CREA 25 °C, 7 d: Acid production absent.
Fig. 49. Aspergillus stellatus CBS 598.65T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,G = 10 μm; E = 1000 μm; H = 2 μm.
Fig. 50. Aspergillus stercorarius CBS 428.93T. A. 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. Ascomata. C. Asci. D–H. Ascospores. E. Hülle cells. Scale bars: B = 1000 μm; C–E = 10 μm; F–H = 2 μm.
Aspergillus stercorarius
A.J. Chen, Frisvad & Samson

Ascomata cleistothecial, superficial, violet to reddish brown, globose to subglobose, 300–600 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellowish brown, globose to ovoid, 11.5–25.5 μm. Ascii 8 spored, subglobose to polygonal or stellate. Ascospores orange to reddish brown, in surface view stellate, 10–14 μm; spore bodies smooth, globose to subglobose, 3.5–4 × 3–4 μm; in side view broadly lenticular, with two stellate equatorial crests; undisectioned part of crests 0.5–1 μm broad, with 2.5–4 μm long extensions; crests ornamented with longitudinal, 0.3–0.4 μm wide pleats. Conidiophores with smooth stipes, yellowish brown, 320–610 × 4.5–6.5 μm; vesicles hyaline to pale yellowish brown, globose to subclavate, 13.5–18.5 μm wide, fertile over the upper half to two thirds; metulae hyaline, 4–7.5 × 3.5–4 μm; phialides hyaline, flask-shaped, 6–8.5 × 2.5–3.5 μm. Conidia echinulate, globose to subglobose, 2.5–3 μm.

Extrötils: asperthecin, calbistrins, desertorins, emindols, paspaline, paspalinine, paxillin, terrequinone A.

Distinguishing characters: The stellate ascospores of Aspergillus stellatus resemble those of A. stella-maris and A. dromiae, but it differs from A. dromiae by smaller conidia, differs from A. stella-maris by non-septate conidiophores.

Aspergillus stercorarius
A.J. Chen, Frisvad & Samson, sp. nov. MycoBank MB816094. Fig. 50.

Etymology: The name refers to the dung (from Uromastix acanthinurus) habitat.

Diagnosis: Brown, smooth ascospores measuring 4.5–6 × 3.5–4.5 μm, with two low equatorial crests measuring 0.3–0.4 μm wide.


ITS barcode: KU866625. (Alternative markers: BenA = KU866865; CaM = KU866763; RPB2 = KU87026).

Colony diam, 7 d (mm): CYA 30–40; CYA 37 °C 47–56; CYA 40 °C 47–48; MEA 42–46; MEA 37 °C >60; OA 35–42; YES 50–60; CYAS 5–7; CYAS 26–27; DG18 15–16.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white and buff; texture velvety; sporulation absent; soluble pigments absent; exudates clear droplets; reverse brown fading into yellowish brown. Ascomata present after 1 wk. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white and light yellow; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse orange brown fading into yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white and light yellow; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse orange brown fading into yellowish brown. DG18 25 °C, 7 d: Colonies deep, plane; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse light yellow.

Micromorphology: Ascomata cleistothecial, superficial, violet to reddish brown, globose to subglobose, 300–600 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale brown, globose to ovoid, 11.5–25.5 μm. Ascii 8 spored, subglobose to polygonal or stellate. Ascospores orange to reddish brown, in surface view stellate, 10–14 μm; spore bodies smooth, globose to subglobose, 3.5–4 × 3–4 μm; in side view broadly lenticular, with two stellate equatorial crests; undisectioned part of crests 0.5–1 μm broad, with 2.5–4 μm long extensions; crests ornamented with longitudinal, 0.3–0.4 μm wide pleats. Conidiophores with smooth stipes, yellowish brown, 320–610 × 4.5–6.5 μm; vesicles hyaline to pale yellowish brown, globose to subclavate, 13.5–18.5 μm wide, fertile over the upper half to two thirds; metulae hyaline, 4–7.5 × 3.5–4 μm; phialides hyaline, flask-shaped, 6–8.5 × 2.5–3.5 μm. Conidia echinulate, globose to subglobose, 2.5–3 μm.

Extrötils: asperthecin, calbistrins, desertorins, emindols, paspaline, paspalinine, paxillin, terrequinone A.

Distinguishing characters: Aspergillus stercorarius is close to A. latilabiatus and A. desertorum, but differs in smaller, smooth ascospores.

Aspergillus striatus


ITS barcode: EF652470. (Alternative markers: BenA = EF652294; CaM = EF652382; RPB2 = EF652206).

Colony diam, 7 d (mm): CYA 38–41; CYA 37 °C 47–60; CYA 40 °C 48–55; MEA 38–45; MEA 37 °C >60; OA 32–35; YES 50–60; CYAS 5–7; CYAS 12–22; DG18 11–15.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white and saffron; texture velvety; sporulation absent; soluble pigments absent; exudates clear droplets; reverse brown fading into saffron. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium saffron at centre, white at edge; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse yellowish brown to reddish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white and light yellow; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse yellowish brown.

DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium saffron at centre, white at edge; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse yellowish brown to reddish brown. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium saffron at centre, white at edge; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse yellowish brown to reddish brown. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, superficial, purple to dark brown, globose to subglobose, 70–150 μm, surrounded by numerous Hülle cells; Hülle cells hyaline, globose to ovoid, 8–14.5 μm. Ascii 8 spored, globose to subglobose. Ascospores brown, in surface view globose to subglobose, spore bodies smooth, 4.5–6 × 3.5–4.5 μm; in side view lenticular, with two low equatorial crests measuring 0.3–0.4 μm wide. Anamorph absent.

Extrötils: cf. asperthecin, calbistrins, desertorins, emindols, paspaline, paspalinine, paxillin, terrequinone A.
Fig. 51. Aspergillus striatus CBS 592.65\textsuperscript{T}. A. 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. Ascomata. C–G. Ascospores. D. Hülle cells. Scale bars: B = 1000 μm; C–D = 10 μm; E–G = 2 μm.
Fig. 52. Aspergillus sulphureoviridis CBS 140626T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüllle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
orange, in surface view globose to subglobose; spore bodies roughened, convex surface bearing simple or anastomosing thickenings arranged in more or less concentric rings, 6–7 × 5–5.5 μm; in side view broadly lenticular. Anamorph absent.

**Extrolites:** asperthecin, emericellin, emerin, emindol SA, paxillin, shanmikanthones, sterigmatocystin, versicolorins, violaceols.

**Distinguishing characters:** Morphologically this species is close to *A. rugulosus* and *A. violaceus*, but differs in orange ascospores with fingerprint like ornamentation.

**Aspergillus sulphureoviridis** A.J. Chen, Frisvad & Samson, sp. nov. MycoBank MB816097. Fig. 52.

**Etymology:** Name refers to its bluish green conidia mass.

**Diagnosis:** Large ascospores measuring 4.5–5.5 × 3.5–4.5 μm and bluish green conidia measuring 3.5–5 μm.

**Typus:** Denmark, factory, indoor air, 1999, isolated by J.C. Frisvad (holotype CBS H-22497, culture ex-type CBS 140626 = IBT 21868 = DTO 325-D1).

**ITS barcode:** KU866673. (Alternative markers: BenA = KU866911; CaM = KU866793; RPB2 = KU867058).

** Colony diam, 7 d (mm):** CYA 30–31; CYA 37 °C 55–56; CYA 40 °C 40–41; MEA 38–41; MEA 37 °C >60; OA 42–43; YES 43–45; CREA 12–13; CYAS 28–29; DG18 28–29.

** Colony characters:** CYA 25 °C, 7 d: Colonies deep, sulphate; margins slightly irregular; mycelium white and saffron; texture floccose; sporulation sparse; soluble pigments absent; exudates clear droplets; reverse brown. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulphate; margins entire; mycelium white; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse reddish brown fading into orange and yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulphate; margins entire; mycelium white; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse buff. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse yellow. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white and buff; texture floccose; sporulation sparse, conidia in masse pale green; soluble pigments light brown; exudates clear droplets; reverse buff. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata cleistothecial, superficial, dark reddish brown, globose, 300–500 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale brown, globose to ovoid, 10–22.5 μm. Ascii 8 spored, globose to subglobose. Ascospores orange to reddish brown, in surface view globose to subglobose, spore bodies smooth, 4.5–5.5 × 3.5–4.5 μm; in side view lenticular, with two equatorial crests measuring 0.8–1.2 μm. Conidiophores with smooth tapers, pale brown, 30–80 × 3–5 μm; vesicles pale brown, subglobose to subclavate, 7–10 μm wide, fertile over the upper half to two thirds; metulae hyaline, 6.5–8.5 × 2.5–3.5 μm; phialides hyaline, flask-shaped, 6.5–7.5 × 3–4 μm. Conidia echinulate, globose to subglobose, 3–4 μm.

**Extrolites:** a gregatin, a varitriol.

**Distinguishing characters:** The wave-crested ascospores with tuberculate convex can easily distinguish Aspergillus undulatus from other species.


**Typus:** HMAS 47644. Culture ex-type: CBS 261.88 = AS 3.4510 = IBT 28027 = DTO 011-H1.

**ITS barcode:** EU448275. (Alternative markers: BenA = EF428363; CaM = EU443989; RPB2 = KU866928).

** Colony diam, 7 d (mm):** CYA 13–14; CYA 37 °C 10–15; CYA 40 °C No growth; MEA 25–26; MEA 37 °C 14–18; OA 33–34; YES 29–30; CREA 3–5; CYAS 17–18; DG18 15–17.

** Colony characters:** CYA 25 °C, 7 d: Colonies deep, plane; margins entire; mycelium saffron and white; texture granular due to abundant ascocoma production; sporulation absent; soluble pigments absent; exudates absent; reverse dark brown at centre, fading into light brown. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture granular due to abundant ascocoma production; sporulation sparse; soluble pigments absent; exudates clear droplets; reverse dark brown. YES 25 °C, 7 d: Colonies moderately deep, plane; margins slightly irregular; mycelium white; texture granular due to abundant ascocoma production; sporulation absent; soluble pigments absent; exudates absent; reverse dark brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins slightly irregular; mycelium white; texture granular due to abundant ascocoma production; sporulation absent; soluble pigments absent; exudates absent; reverse dark brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture granular due to abundant ascocoma production; sporulation absent; soluble pigments absent; exudates absent; reverse dark brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture granular due to abundant ascocoma production; sporulation absent; soluble pigments absent; exudates absent; reverse dark brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture granular due to abundant ascocoma production; sporulation absent; soluble pigments absent; exudates absent; reverse dark brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture granular due to abundant ascocoma production; sporulation absent; soluble pigments absent; exudates absent; reverse dark brown.
Aspergillus undulatus CBS 261.88T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.

Fig. 53. Aspergillus undulatus CBS 261.88T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hülle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Aspergillus unguis CBS 132.55T. A. 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. G. Conidia. Scale bars: B = 30 μm; C–E, G = 10 μm; F = 8 μm.
Aspergillus unguis (Emile-Weill & L. Gaudin) Thom & Raper, Mycologia 31: 667. 1939. MycoBank MB255264. Fig. 54.


**ITS barcode:** EF652443. (Alternative markers: BenA = EF652267; CaM = EF652355; RP2B = EF652179).

**Colony diam,** 7 d (mm): CYA 22–35; CYA 37 °C 19–27; CYA 40 °C no growth or 1–2; MEA 23–35; MEA 37 °C 22–25; OA 30–35; YES 34–45; CREA 10–17; CYAS 32–35; DG18 18–22.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, plane to slightly sulcate; margins entire; mycelium white and light yellow; texture floccose to velvety; sporulation sparse to moderately dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse vinaceous buff. MEA 25 °C, 7 d: Colonies moderately deep to deep, plane to slightly sulcate; margins entire; mycelium white; texture floccose to velvety; sporulation moderately dense, conidia en masse greyish green; soluble pigments absent; exudates absent or clear droplets; reverse brown fading into yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, plane to sulcate; margins entire; mycelium white; texture velvety to floccose; sporulation sparse to moderately dense, conidia en masse greyish olive to olive green; soluble pigments absent; exudates absent; reverse light brown to vinaceous buff. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation sparse to moderately dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse light brown to vinaceous buff. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation sparse to moderately dense, conidia en masse dark green; soluble pigments absent; exudates absent; reverse pale green. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata not observed. Conidiophores with smooth stipes, pale brown, 600–1200 × 7–12 μm; vesicles hyaline, hemispherical to subclavate, 20–30 μm wide, fertile over the upper half to two thirds; metulae hyaline, 7–10 × 3.5–4.5 μm; phialides hyaline, flask-shaped, 8–12 × 3–4 μm. Conidia subglobose to ellipsoidal, smooth, 4–6 × 3.5–4 μm.

**Extrarites:** asperugin, nidulin, normidulin, unguisvin, unguisinol, ustilagionidi C.

**Distinguishing characters:** Aspergillus unguis is close to A. asperscens and A. aureolatus, but A. asperscens produces longer conidiophores (200–400 × 6–8 μm) and large, ellipsoidal conidia (4–7 × 3–5 μm); A. aureolatus is characterized by orange marginal zone of colonies. In addition A. asperscens and A. aureolatus cannot grow at 37 °C, while A. unguis grows well at this temperature.

Aspergillus varians Wehmer, Bot. Centralbl. 80: 460. 1899. MycoBank: MB172782. Fig. 55.

**Typus:** IMI 172297. Culture ex-type: CBS 505.65 = NRRL 4793 = ATCC 16836 = IFO 4114 = IMI 172297 = WB 4793 = IBT 22568 = DTO 073-B5.

**ITS barcode:** EF652479. (Alternative markers: BenA = EF652303; CaM = EF652391; RP2B = EF652215).

**Colony diam,** 7 d (mm): CYA 20–30; CYA 37 °C No growth; CYA 40 °C No growth; MEA 21–22; MEA 37 °C No growth; OA 25–26; YES 25–26; CREA 28–30; CYAS 24–25; DG18 14–15.

**Colony characters:** CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white and gray; texture floccose; sporulation moderately dense, conidia en masse greyish green; soluble pigments absent; exudates absent; reverse orange at centre, dark brown at edge. MEA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse glaucous; soluble pigments absent; exudates absent; reverse orange. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium yellow at centre, white at edge; texture floccose to velvety; sporulation moderately dense, conidia en masse dull green to greyish green; soluble pigments absent; exudates absent; reverse light yellow to light brown. DG18 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium light yellow; texture floccose; sporulation moderately dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse yellow ochre. OA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium white; texture floccose; sporulation moderately dense, conidia en masse yellow green; soluble pigments absent; exudates absent; reverse pale green. CREA 25 °C, 7 d: Acid production absent.

**Micromorphology:** Ascomata not observed. Conidiophores with smooth stipes, pale brown, 600–1200 × 7–12 μm; vesicles hyaline, hemispherical to subclavate, 20–30 μm wide, fertile over the upper half to two thirds; metulae hyaline, 7–10 × 3.5–4.5 μm; phialides hyaline, flask-shaped, 8–12 × 3–4 μm. Conidia subglobose to ellipsoidal, smooth, 4–6 × 3.5–4 μm.

**Extrarites:** 2-ω-hydroxyemodin, emerin, epurpurin A, B & C, shamanthanes, versicorlins.

**Distinguishing characters:** The long conidiophores (600–1200 μm) and wide vesicles (20–30 μm) can easily distinguish Aspergillus varians from other related species.


**ITS barcode:** AJ874119. (Alternative markers: BenA = AY339998; CaM = EU443977; RP2B = KU866931).

**Colony diam,** 7 d (mm): CYA 37–38; CYA 37 °C 3–5; CYA 40 °C No growth; MEA 42–43; MEA 37 °C No growth; OA 31–35; YES 49–50; CREA 18–19; CYAS 37–38; DG18 23–26.
Fig. 55. Aspergillus varians CBS 505.65T. A. 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. G. Conidia. Scale bars: B = 30 μm; C–G = 10 μm.
Fig. 56. Aspergillus venezuelensis CBS 868.97T. A. 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,C. Conidiophores. D. Conidia. E. Ascomata. F. Hüllle cells. G,H. Ascospores. Scale bars: B = 30 μm; C,D,F,G = 10 μm; E = 1000 μm; H = 2 μm.
Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, plane; margins entire; mycelium light yellow at centre, white at edge; texture floccose at centre, velvety at edge; sporulation absent; soluble pigments absent; exudates clear droplets; reverse light yellow fading into cream white; ascomata present after 1 wk. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium light yellow at centre, white at edge; texture floccose at centre, velvety at edge; sporulation absent; soluble pigments absent; exudates clear droplets; reverse dark brown at centre, yellowish brown at edge; ascomata present after 1 wk. CYA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium light yellow at centre, white at edge; texture floccose at centre, velvety at edge; sporulation absent; soluble pigments absent; exudates clear droplets; reverse cream white; ascomata present after 1 wk. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium light yellow at centre, white at edge; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse citron yellow; ascomata present after 1 wk. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium light yellow at centre, white at edge; texture floccose; sporulation absent; soluble pigments absent; exudates clear droplets; reverse cream white; ascomata present after 1 wk. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, superficial, violet to brown, globose to subglobose, 400–1000 μm, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellowish brown, globose to ovoid, 12–21.5 μm. Asci 8 spored, stellate. Ascospores orange to reddish brown, in surface view stellate, with two stellate equatorial; undissected part of crests 1–1.2 μm broad, with 2.5–4 μm long extensions; crests ornamented with longitudinal, 0.3–0.5 μm wide pleats. Conidiophores with smooth stipes, light yellowish brown, 65–130 × 2–3 μm; vesicles hyaline to pale yellowish brown, subclavate, 5.5–7 μm wide, fertile over the upper half to two thirds; metulae hyaline, 4–5 × 2.5–3.5 μm; phialides hyaline, flask-shaped, 6–7 × 2.5–3.5 μm. Conidia echinulate, globose to subglobose, 2.5–4 μm (Anamorphic structures were observed from CYA).

Extrolites: aflatoxin B1, B2, a desertorin, emericellin, an emerin, shamxanthones, sterigmatocystin, versicolin.

Distinguishing characters: Triangular flaps on the ascospore convex surface can distinguish this species from other stellate ascospored species.

Notes: The anamorph of A. venezuelensis occurs quite late (after 1 month) on unconventional media such as CREA, CYA + 40 % sucrose, while absent on conventional growth media (CYA, MEA, OA) (Frisvad & Samson 2004). During our study, sparse conidiophores are present on CYA after 2 months. The presented conidiophores show typical characters of section Nidulantes, but the vesicles are smaller (5.5–7 μm) compared with original description (7–10 μm).

Aspergillus violaceus Fennell & Raper, Mycologia 47: 75. 1955. MycoBank MB292863. Fig. 57.


ITS barcode: EF652438. (Alternative markers: BenA = EF652262; CaM = EF652350; RPBP2 = EF652174).

Colony diam, 7 d (mm): CYA 23–33; CYA 37 °C 45–56; CYA 40 °C 41–45; MEA 22–41; MEA 37 °C 58–70; OA 30–32; YES 38–53; CREA 5–13; CYAS 18–25; DG18 3–16.

Colony characters: CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse brown. MEA 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins slightly irregular; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, sulcate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse yellowish brown. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium white; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse yellowish brown. OA 25 °C, 7 d: Colonies low, plane; margins entire; mycelium white; texture velvety; sporulation absent; soluble pigments light olive to light brown; exudates clear droplets; reverse light yellowish brown. CREA 25 °C, 7 d: Acid production absent.

Micromorphology: Ascomata cleistothecial, blackish to dark brown, globose, 25–50 μm in CBS 138.55, up to 190 μm in CBS 293.93, surrounded by numerous Hülle cells; Hülle cells hyaline to pale yellowish brown, globose to ovoid, 6–26 μm. Asci 8 spored, globose to ovoid. Ascospores violet, in surface view globose to subglobose; spore bodies roughened, with reticulate intertwined ornamentation, 4–6.5 × 3–5 μm; in side view broadly lenticular, with two low equatorial crest, less than 0.3 μm wide. "Fide Fennell & Raper (1955) the conidial structures on hay-infusion agar scattered, small and commonly fractional, not affecting the colony appearance. Conidiophores arising primarily from aerial hyphae, smooth-walled, very short, 30–50 μm in length by 3–4 μm in diameter, somewhat sinuous, thin-walled, hyaline or nearly so, terminating in rounded and somewhat enlarged vesicular areas mostly 5–6 μm, metulaeae few in number, borne on the upper part of the vesicle only, variable in dimensions, mostly 6–7.5 × 3–3.5 μm; phialides about 5–6 × 2–2.5 μm, flask-shaped, bearing conidia in short chains; conidia globose or nearly so, light green in colour, smooth or delicately roughened, mostly 2.8–3.3 μm in diameter.

Extrolites: asperugin, emestrin, violaceols, emericellin, paxillin.

Distinguishing characters: Violet ascospores with reticulate intertwined ornamentation.

Notes: According to Fennell & Raper (1955), limited and generally minute conidial heads were produced on hay-infusion
Fig. 57. Aspergillus violaceus CBS 138.55T. A. 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. Conidiophores. C. Conidia. D. Hülle cells. E. Ascomata. F–H. Ascospores. Scale bars: B–D, F = 10 μm; E = 1000 μm; G–H = 2 μm.
Fig. 58. Aspergillus viridicatenatus CBS 140629T. A. 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. G. Conidia. Scale bars: B = 30 μm; C–G = 10 μm.
agard. During our observation, atypical conidiophores and much bigger conidia (3.5–4.5 μm) are produced quite late (after 2 months) on CYA. Aspergillus similis (ex-type CBS 293.93) is undifferentiated from A. violaceus in ascospore morphology (Fig. 5S, T) and multi-gene phylogeny, thus is considered a synonym of A. violaceus.

### Aspergillus viridicatenatus A.J. Chen, Frisvad & Samson, sp. nov.

**MycoBank**: MB816088. **Fig. 58.**

**Etymology**: Name refers to its long green conidial chains.

**Diagnosis**: Subglobose, ellipsoidal to cylindrical conidia measuring 3–5 × 2.5–4 μm, teleomorph not observed.

**Type**: **Denmark**, root of Gymnadenia conopsea, 2011, isolated by J.C. Frisvad (holotype CBS H-22498, culture ex-type CBS 140629 = IBT 31492 = DTO 325-F4).

**ITS barcode**: KU866682. (Alternative markers: **BenA** = KX423621; **CaM** = KU866802; **RPB2** = KU867067).

** Colony diam, 7 d (mm)**: CYA 15–16; CYA 37 °C No growth; CYA 40 °C No growth; MEA 21–23; MEA 37 °C No growth; OA 19–20; YES 20–21; CREA 10–11; CYAS 12–13; DG18 29–30.

** Colony characters**: CYA 25 °C, 7 d: Colonies deep, plane; margins entire; mycelium buff; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse pale green. DG18 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium buff; texture floccose; sporulation moderately dense, conidia en masse yellow green; reverse yellowish brown. YES 25 °C, 7 d: Colonies moderately deep, slightly sulcate; margins entire; mycelium buff; texture floccose; sporulation moderately dense, conidia en masse yellow green; reverse yellowish brown. OA 25 °C, 7 d: Colonies low, plane; margins entire; texture velvety to floccose; sporulation moderately dense, conidia en masse yellow green to dark green; soluble pigments absent; exudates absent; reverse pale green. CREA 25 °C, 7 d: Acid production absent.

** Micromorphology**: Ascomata not observed. Conidiophores with smooth stipes, yellowish brown to brown, 120–270 × 5–6 μm; vesicles hyaline to pale brown, globose to subglobose, 10–15 μm wide, fertile over the two thirds; metulae hyaline to pale brown, 6–9 × 2.5–3.5 μm; phialides hyaline to pale green, flask-shaped, 6–9.5 × 2.5–3.5 μm. Conidia subglobose, ellipsoid to cylindrical, echinulate, 3–5 × 2.5–4 μm, green in mass.

**Extrolites**: An unidentified extrolite in common with Penicillium bialowiezense, which has a UV spectrum with absorption maxima at 220 nm, 312 nm and 324 nm, was present. The extrolite with this UV spectrum has not been found in any other Aspergillus species yet.

**Distinguishing characters**: Aspergillus viridicatenatus is close to A. aureolatus and A. speluceus, but can be distinguished by its ellipsoid to cylindrical conidia.

### Aspergillus section Cavernicolus A.J. Chen, Frisvad & Samson, sect. nov.

**MycoBank**: MB816113.


**Description**: Conidial heads radiate to columnar, conidiophores biseriate, smooth, uncoloured or in brown shades. Vesicles globose to subglobose. Conidia smooth to rough. Hülle cells regularly present.

Five species previously assigned to section *Usti*, namely *A. amylovorus*, *A. californicus*, *A. cavernicola*, *A. egyptiacus*, *A. kassunensis* and *A. subsessilis* are included in this new section mainly based on multigene phylogeny (Fig. 1). Phylogenetically *A. amylovorus* is identical with *A. cavernicola*, although *A. amylovorus* was published at 1964, the name was not validated until 1979 (*Samson 1979*), thus *A. cavernicola* has priority based on its publication date. *A. amylovorus* is considered as a synonym.

### Doubtful Species List


ITS barcode: n.a. (Alternative markers: **BenA** = n.a.; **CaM** = n.a.; **RPB2** = n.a.). Type culture can be obtained at http://dx.doi.org/10.1016/j.simyco.2016.10.001.

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### APPENDIX A. SUPPLEMENTARY MATERIAL

Supplementary material related to this article can be found at http://dx.doi.org/10.1016/j.simyco.2016.10.001.

### REFERENCES


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