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New taxa in *Aspergillus* section *Usti*

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Abstract: Based on phylogenetic analysis of sequence data, *Aspergillus* section *Usti* includes 21 species, incicluding two teleomorphic species *Aspergillus heterothallicus* (= *Emericella heterothallica*) and *Fennellia monodii*. *Aspergillus germanicus* sp. nov. was isolated from indoor air in Germany. This species has identical ITS sequences with *A. insuetus* CBS 119.27, but is clearly distinct from that species based on β-tubulin and calmodulin sequence data. This species is unable to grow at 37 °C, similarly to *A. keveii* and *A. insuetus*. *Aspergillus carlsbadensis* sp. nov. was isolated from the Carlsbad Caverns National Park in New Mexico. This taxon is related to, but distinct from a clade including *A. calidoustus, A. pseudodeflectus, A. insuetus* and *A. keveii* on all trees. This species is also unable to grow at 37 °C, and acid production was not observed on CREA. *Aspergillus californicus* sp. nov. is proposed for an isolate from chamise chaparral (*Adenostoma fasciculatum)* in California. It is related to a clade including *A. subsessilis* and *A. kassunensis* on all trees. This species grew well at 37 °C, and acid production was not observed on CREA. The strain CBS 504.65 from soil in Turkey showed to be clearly distinct from the *A. deflectus* ex-type strain, indicating that this isolate represents a distinct species in this section. We propose the name *A. turkensis* sp. nov. for this taxon. This species grew, although rather restrictedly at 37 °C, and acid production was not observed on CREA. Isolates from stored maize, South Africa, as a culture contaminant of *Bipolaris sorokiniana* from indoor air in Finland proved to be related to, but different from *A. ustus* and *A. puniceus.* The taxon is proposed as the new species *A. pseudoustus.* Although supported only by low bootstrap values, *F. monodii* was found to belong to section *Usti* based on phylogenetic analysis of either loci BLAST searches to the GenBank database also resulted in closest hits from section *Usti*. This species obviously does not belong to the *Fennellia* genus, instead it is a member of the *Emericella* genus. However, in accordance with the guidelines of the Amsterdam Declaration on fungal nomenclature (Hawksworth *et al.* 2011), and based on phylogenetic and physiological evidence, we propose the new combination *Aspergillus monodii* comb. nov. for this taxon. Species assigned to section *Usti* can be assigned to three chemical groups based on the extrolites. *Aspergillus ustus, A. granulosus* and *A. puniceus* produced ustic acid, while *A. ustus* and *A. puniceus* also produced austocystins and versicolorins. In the second chemical group, *A. pseudodeflectus* produced drimans in common with the other species in this group, and also several unique unknown compounds. *Aspergillus calidoustus* isolates produced drimans and ophiobolins in common with *A. insuetus* and *A. keveii*, but also produced austins. *Aspergillus insuetus* isolates also produced pergillin while *A. keveii* isolates produced nidulol. In the third chemical group, *E. heterothallica* has been reported to produce emethallicins, 5'-hydroxyaveranthin, emeheterone, emesterones, 5'-hydroxyaveranthin.

Key words: Ascomycetes, *Aspergillus* section *Usti,* ITS, calmodulin, extrolites, β-tubulin, polyphasic taxonomy.
Taxonomic novelties: *Aspergillus carlsbadensis* Frisvad, Varga & Samson sp. nov., *Aspergillus californicus* Frisvad, Varga & Samson sp. nov., *Aspergillus germanicus* Varga, Frisvad & Samson sp. nov. , *Aspergillus monodii* (Locquin-Linard) Varga, Frisvad & Samson comb. nov., *Aspergillus pseudoustus* Frisvad, Varga & Samson sp. nov., *Aspergillus turkensis* Varga, Frisvad & Samson sp. nov.

INTRODUCTION

Aspergillus ustus is a common filamentous fungus found in foods, soil and indoor air environments (Samson *et al.* 2004). This species was considered as a relatively rare human pathogen that can cause invasive infection in immunocompromised hosts (Weiss & Thiemke 1983, Stiller *et al.* 1994, Verweij *et al.* 1999, Nakai *et al.* 2002, Pavie *et al.* 2005, Panackal *et al.* 2006, Yildiran *et al.* 2006, Krishnan-Natesan *et al.* 2008, Florescu *et al.* 2008, Vagefi *et al.* 2008). However, recent studies clarified that infections attributed to *A. ustus* are caused in most cases by another species, *A. calidoustus* (Houbraken *et al.* 2007, Varga *et al.* 2008, Balajee *et al.* 2009, Peláez *et al.* 2010). This species is also common in indoor air (Houbraken *et al.* 2007, Slack *et al.* 2009) and is able to colonise water distribution systems (Hageskal *et al.* 2011). Other species related to *A. ustus* can also cause human or animal infections; *A. granulosus* was found to cause disseminated infection in a cardiac transplant patient (Fakih *et al.* 1995), while *A. deflectus* has been reported to cause disseminated mycosis in dogs (Jang *et al.* 1986, Kahler *et al.* 1990, Robinson *et al.* 2000, Schultz *et al.* 2008, Krockenberger *et al.* 2011).

Raper & Fennell (1965) classified *A. ustus* to the *Aspergillus ustus* species group (*Aspergillus* section *Usti* according to Gams *et al.* 1985) together with four other species: *A. panamensis, A. puniceus, A. conjunctus* and *A. deflectus*. Later, Kozakiewicz (1989) revised the taxonomy of the group, and included *A. ustus*, *A. pseudodeflectus, A. conjunctus, A. puniceus, A. panamensis* and *A. granulosus* in the *A. ustus* species group, and established the *A. deflectus* species group including *A. deflectus, A. pulvinus* and *A. silvaticus* based on morphological studies. Klich (1993) treated *A. granulosus* as member of section *Versicolores,* and found that *A. pseudodeflectus* is only weakly related to this section based on morphological treatment of section *Versicolores*. Peterson (2000) transferred *A. conjunctus, A. funiculosus, A. silvaticus, A. panamensis* and *A. anthodesmis* to section *Sparsi*. More recently, Peterson (2008) examined the relationships of the *Aspergillus* genus using phylogenetic analysis of sequences of four loci, and assigned 15 species to this section (see below).

We examined the evolutionary relationships among species assigned to section *Usti*. We have used a polyphasic taxonomic approach in order to determine the delimitation and variability of known and new species. For phenotypic analyses, macro- and micromorphology of the isolates was examined, and secondary

Table 1. Isolates in *Aspergillus* section *Usti* and related species examined in this study.

Species	Strain No.	Source
A. amylovorus	CBS 600.67[T] = NRRL 5813 = IMI 129961 = VKM F-906 = IBT 23158	Wheat starch, Ukraine
A. calidoustus	CBS 112452	Indoor air, Germany
	CBS 113228	ATCC 38849; IBT 13091
	CBS 114380	Wooden construction material, Finland
	CBS 121601; 677	Bronchoalveolar lavage fluid, proven invasive aspergillosis, Nijmegen, the Netherlands[†]
	CBS 121610; 91	Post-cataract surgery endophthalmitis, Turkey
A. californicus	CBS 123895[T] = IBT 16748	Ex chamise chaparral (*Adenostoma fasciculatum*), in the foothills of the San Gabriel Mountains on Baldy Mountain Road near Shinn Road Intersection, North of Claremont and near San Antonio Dam, California, USA, Jeff S. La Favre, 1978. A wildfire occurred here 31/8 1975.
A. carlsbadensis	CBS 123893 = IBT 16753	Soil, Galapagos Islands, Ecuador
	CBS 123894[T] = IBT 14493	Lechuguilla Cave, Carlsbad Caverns National Park, New Mexico, USA, D.E. Northup, 1992
	CBS 123903 =IBT 18616	Soil, Carthage, Tunesia
A. cavernicola	CBS 117.76[T] = NRRL 6327	Soil, cave wall, Romania
A. deflectus	CBS 109.55[T] = NRRL 2206 = IBT 24665	Soil, Rio de Janeiro, Brazil
	NRRL 4235 = IBT 25291	Potting soil
	NRRL 13131 = IBT 25254	Unknown
A. egyptiacus	CBS 123892 = IBT 16345 = RMF 9515	Soil, Iraq
	CBS 656.73[T] = NRRL 5920	Sandy soil, under *Olea europaea*, Ras-El-Hikma, Egypt
	CBS 991.72C	Bare ferruginous soil, Dahkla Oasis, Western desert, Egypt
	CBS 991.72A	Bare ferruginous soil, Dahkla Oasis, Western desert, Egypt
	CBS 991.72B	Bare ferruginous soil, Dahkla Oasis, Western desert, Egypt
	CBS 991.72F	Bare ferruginous soil, Dahkla Oasis, Western desert, Egypt
	CBS 991.72E	Bare ferruginous soil, Dahkla Oasis, Western desert, Egypt
A. elongatus	CBS 387.75[T] = NRRL 5176	Alkaline Usar soil, Lucknow, India
A. germanicus	CBS 123887[T] = DTO 27-D9 = IBT 29365	Indoor air, Stuttgart, Germany
A. granulosus	CBS 588.65[T]	Soil, Fayetteville, Arkansas, USA
	CBS 119.58	Soil, Texas, USA
A. heterothallicus	CBS 489.65[T]	Soil, Costa Rica
	CBS 488.65	Soil, Costa Rica
A. insuetus	CBS 107.25[T] = NRRL 279	South Africa
	CBS 119.27 = NRRL 4876	Soil, Iowa, USA
	CBS 102278	Subcutaneous infection, Spain
A. kassunensis	CBS 419.69[T] = NRRL 3752 = IMI 334938 = IBT 23479	Soil, Damascus, Syria
A. keveii	CBS 209.92	Soil, La Palma, Spain
	CBS 561.65 = NRRL 1974	Soil, Panama
	IBT 10524 = CBS 113227 = NRRL 1254	Soil, Panama
	IBT 16751	Soil at trail from Pelican Bay to inland, Isla Santa Cruz, Galapagos Islands, Ecuador, Tjitte de Vries and D.P. Mahoney, 1968
A. lucknowensis	CBS 449.75[T] = NRRL 3491	Alkaline Usar soil, Lucknow, India
A. monodii	CBS 434.93	Dung of *Procavia* sp. (daman), Darfur, Sudan
	CBS 435.93[T]	Dung of sheep, Ennedi, Chad
A. pseudodeflectus	CBS 596.65	Sugar, USA, Louisiana
	CBS 756.74[T]	Desert soil, Egypt, Western Desert
	NRRL 4846 = IBT 25256	Unknown
A. pseudoustus	ATCC 36063 = NRRL 5856 = CSIR 1128 = CBS 123904[T] = IBT 28161	Stored maize, South Africa
	MRC 096 = IBT 31044	Contaminant in a *Bipolaris sorokiniana* strain (MRC 093), South Africa

Table 1. (Continued).

Species	Strain No.	Source
A. pseudoustus	IBT 22361	Indoor air, Finland
A. puniceus	CBS 495.65^T	Soil, Zarcero, Costa Rica
	CBS 128.62	Soil, Louisiana, USA
A. subsessilis	CBS 502.65^T = NRRL 4905 = IMI 135820 = IBT 23160	Desert soil, Mojave desert, CA, USA
	CBS 988.72 = NRRL 4907 = IMI 335782 = IBT 23165	Desert soil, USA
A. turkensis	CBS 504.65^T = NRRL 4993 = WB 4993 = IBT 22553	Soil, Turkey
A. ustus	CBS 116057	Antique tapestries, Krakow, Poland
	CBS 114901	Carpet, The Netherlands
	CBS 261.67^T	Culture contaminant, USA
	CBS 133.55	Textile buried in soil, Netherlands
	CBS 239.90	Man, biopsy of brain tumor, Netherlands
	CBS 113233 = IBT 14495	Cave wall, Lechuguilla Cave, Carlsbad, New Mexico
	CBS 113232 = IBT 14932	Indoor air, Denmark

metabolite profiles were studied. For genotypic studies, partial sequences of the β-tubulin and calmodulin genes and the ITS region of the rRNA gene cluster were analysed.

MATERIALS AND METHODS

Isolates

The strains used in this study are listed in Table 1.

Morphological analysis

For macromorphological observations, Czapek Yeast Autolysate (CYA), Malt Extract Autolysate (MEA) agar, Yeast Extract Sucrose Agar (YES), Creatine Agar (CREA), and Oatmeal Agar (OA) were used (Samson *et al.* 2004). The isolates were inoculated at three points on each plate of each medium and incubated at 25 °C and 37 °C in the dark for 7 d. For micromorphological observations, microscopic mounts were made in lactic acid with cotton blue from MEA colonies and a drop of alcohol was added to remove air bubbles and excess conidia.

Extrolite analysis

The isolates were grown on CYA and YES at 25 °C for 7 d. Extrolites were extracted after incubation. Five plugs of each agar medium were taken and pooled together into same vial for extraction with 0.75 mL of a mixture of ethyl acetate/dichloromethane/methanol (3:2:1) (v/v/v) with 1 % (v/v) formic acid. The extracts were filtered and analysed by HPLC using alkylphenone retention indices and diode array UV-VIS detection as described by Frisvad & Thrane (1987), with minor modifications as described by Smedsgaard (1997).

Genotypic analysis

The cultures used for the molecular studies were grown on malt peptone (MP) broth using 1 % (w/v) of malt extract (Oxoid) and 0.1 % (w/v) bacto peptone (Difco), 2 mL of medium in 15 mL tubes. The cultures were incubated at 25 °C for 7 d. DNA was extracted from the cells using the Masterpure™ yeast DNA purification kit (Epicentre Biotechnol.) according to the instructions of the manufacturer. The ITS region and parts of the β-tubulin and calmodulin genes were amplified and sequenced as described previously (Houbraken *et al.* 2007, Varga *et al.* 2007, 2008).

Data analysis

DNA sequences were edited with the DNASTAR computer package. Alignments of the sequences were performed using MEGA v. 4 (Tamura *et al.* 2007). Phylogenetic analysis of sequence data was performed using PAUP v. 4.0b10 (Swofford 2000). Alignment gaps were treated as fifth character state, parsimony uninformative characters were excluded and all characters were unordered and equal weight. Maximum parsimony analysis was performed for all data sets using the heuristic search option. To assess the robustness of the topology, 1 000 bootstrap replicates were run by maximum parsimony (Hillis & Bull 1993). Other measures including tree length, consistency index and retention index (CI and RI, respectively) were also calculated. *Aspergillus versicolor* CBS 583.65^T was used as outgroup in these analyses. Sequences were deposited at GenBank under accession numbers FJ531124–FJ531191.

RESULTS AND DISCUSSION

Phylogenetic analysis

For the molecular analysis of the isolates, three genomic regions, the ITS region, and parts of the calmodulin and β-tubulin genes were amplified and sequenced. Phylogenetic analysis of the data was carried out using parsimony analysis. For the analysis of part of the β-tubulin gene, 589 characters were analysed, 197 of which were found to be parsimony informative. One of the 78 MP trees based on partial β-tubulin genes sequences is shown in Fig. 1 (tree length: 661 steps, consistency index: 0.6445, retention index: 0.8922). The calmodulin data set included 475 characters, with 266 parsimony informative characters. One of the 119 MP trees based on partial calmodulin gene sequences is shown in Fig. 2 (tree length:

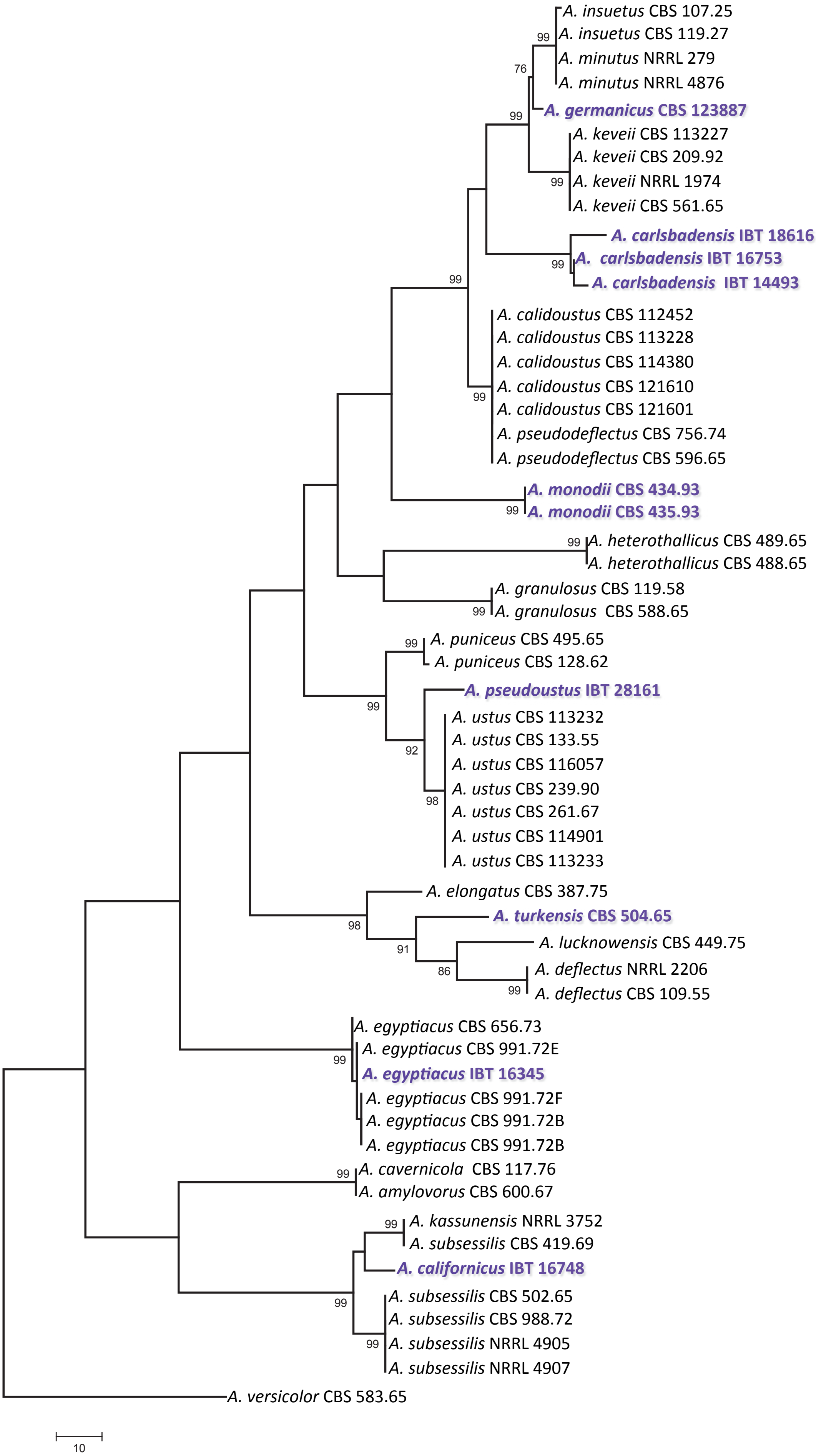

Fig. 1. The single MP tree obtained based on phylogenetic analysis of β-tubulin sequence data of *Aspergillus* section *Usti.* Numbers above branches are bootstrap values. Only values above 70 % are indicated.

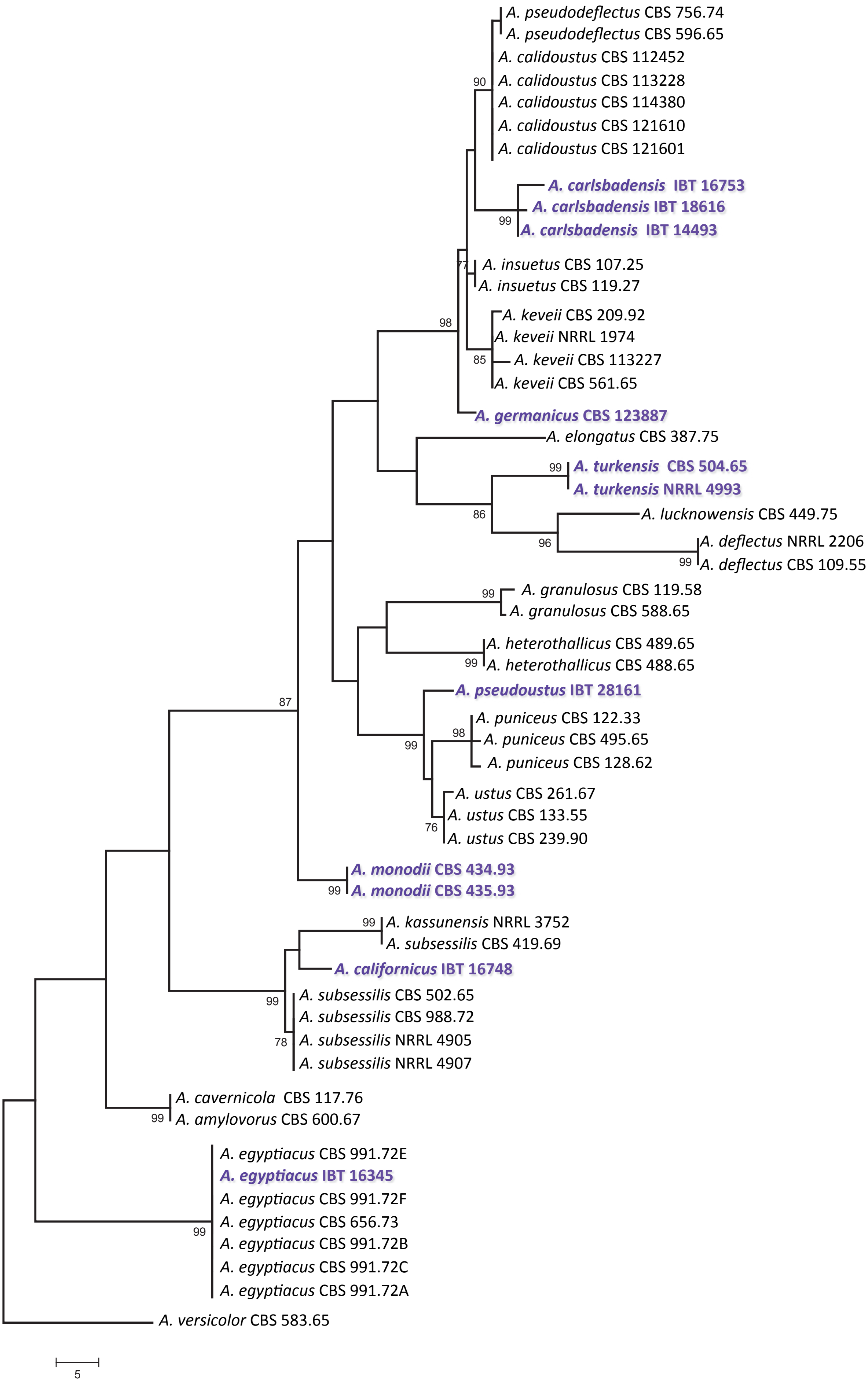

Fig. 2. One of the MP trees obtained based on phylogenetic analysis of calmodulin sequence data of *Aspergillus* section *Usti*. Numbers above branches are bootstrap values. Only values above 70 % are indicated.

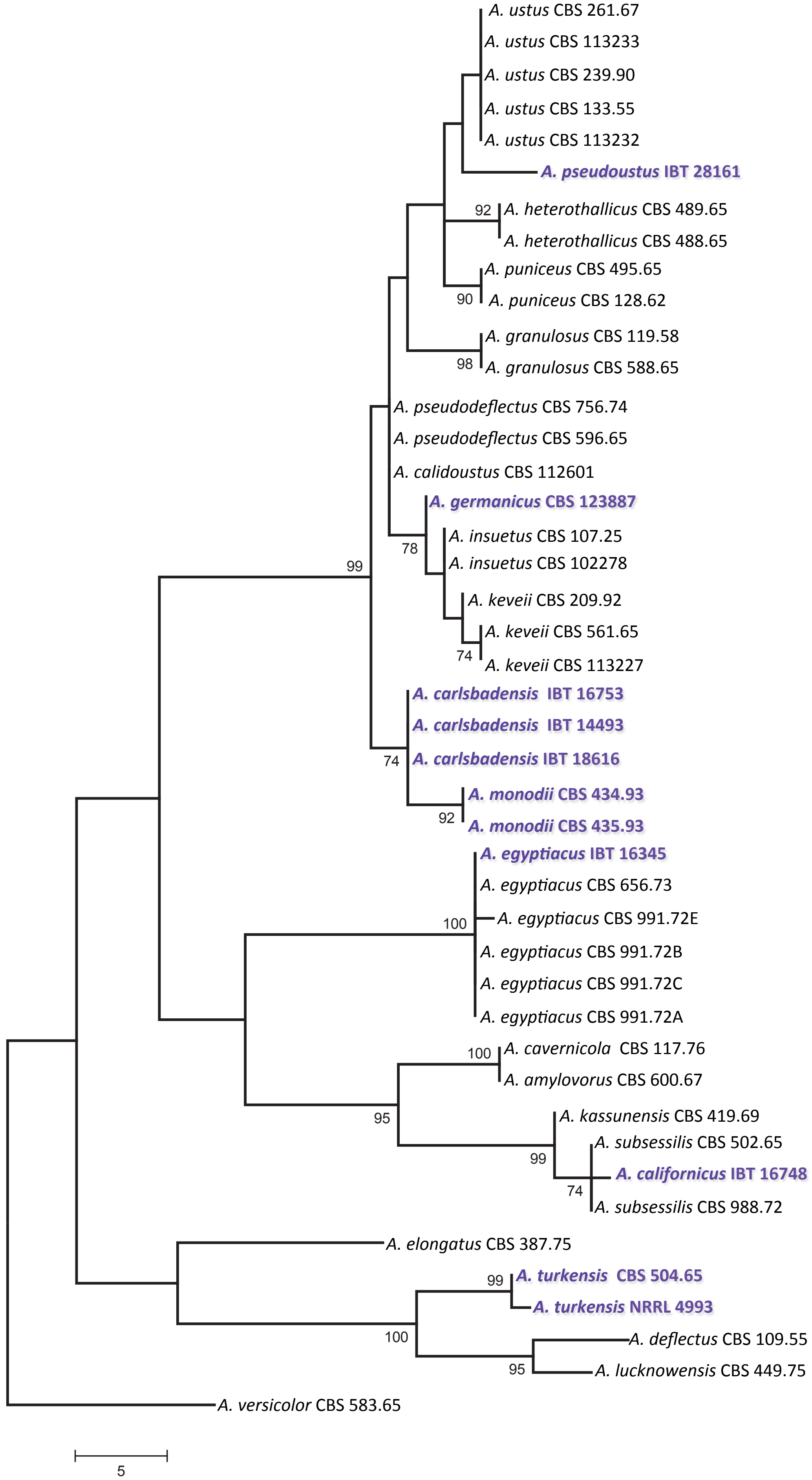

Fig. 3. One of the MP trees obtained based on phylogenetic analysis of ITS sequence data of *Aspergillus* section *Usti*. Numbers above branches are bootstrap values. Only values above 70 % are indicated.

890, consistency index: 0.5753, retention index: 0.8788). The ITS data set included 541 characters with 100 parsimony informative characters. One of the 8 MP trees is shown in Fig. 3 (tree length: 224, consistency index: 0.7366, retention index: 0.9230).

Based on phylogenetic analysis of sequence data, *Aspergillus* section *Usti* includes now 21 species, at least two of which are able to reproduce sexually: *Aspergillus heterothallicus* (=*Emericella heterothallica*) and *Fennellia monodii*. Although supported only by low bootstrap values, *F. monodii* was found to belong to section *Usti* based on phylogenetic analysis of either loci (Figs 1–3). BLAST searches to the GenBank database also resulted in closest hits from section *Usti* (*A. pseudodeflectus* and *A. calidoustus* for the ITS and calmodulin sequence data, and *A. ustus* and *A. insuetus* for the β-tubulin sequences). *Fennellia monodii* was described in 1990 by Locquin-Linard from dung of herbivores in Tchad and Sudan. This species is characterised by two-valved ascospores with low, wrinkled equatorial crests. The anamorph of this species has not yet been observed in spite of repeated attempts using various media (data not shown). This species obviously does not belong to the *Fennellia* genus, instead it is a member of the *Emericella* genus. However, in accordance with the guidelines of the Amsterdam Declaration on fungal nomenclature (Hawsksworth *et al.* 2011), and based on phylogenetic and physiological evidence, we propose the new combination *Aspergillus monodii* comb. nov. for this interesting species.

Another new species in this section was isolated from indoor air in Germany. This species has identical ITS sequences with *A. insuetus* CBS 119.27, but is clearly distinct from that species based on β-tubulin and calmodulin sequence data. This species is unable to grow at 37 °C, similarly to *A. keveii* and *A. insuetus*. We propose the name *A. germanicus* sp. nov. for this taxon.

Isolate IBT 16753 from Galapagos Islands, Ecuador, and IBT 14493 isolated from Lechuguilla Cave, Carlsbad Caverns National Park in New Mexico, USA were found to be related to, but clearly distinct from a clade including *A. calidoustus, A. pseudodeflectus, A. insuetus* and *A. keveii* on all trees. This species is also unable to grow at 37 °C, and acid production was not observed on CREA. We propose the name *A. carlsbadensis* sp. nov. for this taxon.

Isolate IBT 16748 was isolated from chamise chaparral (*Adenostoma fasciculatum)* in California, USA in 1978. It was found to be related to a clade including *A. subsessilis* and *A. kassunensis* on all trees. This species grew well at 37 °C, and acid production was not observed on CREA. We propose the name *A. californicus* sp. nov. for this taxon.

The "*A. deflectus*" isolate CBS 504.65 came from soil in Turkey is clearly distinct from the *A. deflectus* type strain on all trees, indicating that this isolate represents a distinct species in this section. This species grew, although rather restrictedly at 37 °C, and acid production was not observed on CREA. We propose the name *A. turkensis* sp. nov. for this taxon.

Another new species in this section, tentatively called *A. pseudoustus* sp. nov., is represented by NRRL 5856 = IBT 28161, which was found to be related to, but clearly different from *A. ustus* and *A. puniceus* on all trees (Figs 1–3). This isolate came from stored maize, South Africa. Other isolates belonging to this species include a culture contaminant of *Bipolaris sorokiniana* from South Africa (IBT 31044), and one isolate came from indoor air in Finland (IBT 22361).

Isolate IBT 16345 from soil, Iraq is a new isolate of *A. egyptiacus* based on all sequence data. The isolate grew well at 37 °C, and acid production was not observed on CREA. This is the first isolate of this species which was isolated outside Egypt.

In agreement with the data of Peterson (2008), *A. kassunensis*, which was treated as a synonym of *A. subsessilis* (Samson 1979, Samson & Moucchaca 2004), is also a valid species, related to *A. subsessilis* and *A. californicus* (Figs 1–3). *Aspergillus cavernicola* was treated as a synonym of *A. varians* by Samson (1979); however, based on sequence data, it is conspecific with *A. amylovorus* and belongs to section *Usti*, while the *A. varians* type strain belongs to *Aspergillus* section *Nidulantes* (data not shown). *Aspergillus amylovorus* was invalidly described (nom. inval., Art. 37) from wheat starch (Panasenko 1964), and subsequently validated by Samson (1979), while *A. cavernicola* was described in 1969 from cave wall from Romania. This species was validly described and hence is the correct name for *A. cavernicola* (= *A. amylovorus*).

Extrolites

The mycotoxins and other secondary metabolites found to be produced by the examined species in this study are listed in Table 2. Species assigned to section *Usti* could clearly be assigned to three chemical groups based on the extrolites produced by them. *Aspergillus ustus, A. granulosus* and *A. puniceus* produced ustic acids in common. *Aspergillus ustus* and *A. puniceus* also produced austocystins and versicolorins. In the second chemical group, *A. pseudodeflectus* produced drimans (Hayes *et al.* 1996) in common with the other species in this group, and also several unique unknown compounds. *Aspergillus calidoustus* isolates produced drimans and ophiobolins (Cutler *et al.* 1984) in common with *A. insuetus* and *A. keveii*, but also produced austins (Chexal *et al.* 1976) not identified in other species of section *Usti*. *Aspergillus insuetus* isolates also produced pergillin (Cutler *et al.* 1980), while *A. keveii* isolates produced nidulol. In the third chemical group, *E. heterothallica* has been reported to produce emethallicins A–F (Kawahara *et al.* 1989, 1990a, b), 5'-hydroxyaveranthin (Yabe *et al.* 1991), emeheterone (Kawahara *et al.* 1988), emesterones A & B (Hosoe *et al.* 1998), 5'-hydroxyaveranthin (Yabe *et al.* 1991), Mer-NF8054X (Mizuno *et al.* 1995). This latter compound, an 18,22-cyclosterol derivative, is closely related to the emesterones, and was also identified in an isolate identified as *A. ustus* (Mizuno *et al.* 1995). *Aspergillus deflectus* produces several antibiotics, including desferritriacetylfusigen, which inhibits the growth of bacteria (Anke 1977), and deflectins, angular azaphilons, which have antibiotic properties, and exhibit lytic activities against bacteria and erythrocytes (Anke *et al.* 1981). *Aspergillus egyptiacus* has been suggested to be more closely related to *E. nidulans* than to *A. versicolor* based on its biochemical behavior (Zohri & Ismail 1994). *Aspergillus egyptiacus* produces fumitremorgins and verruculogen, thus resembling *A. caespitosus* in that aspect. However *A. caespitosus* is placed within *Aspergillus* section *Nidulantes* (Peterson 2008, J. Varga, unpubl. data). *Aspergillus elongatus* CBS 387.75 produced fumitremorgin C, but other fumitremorgins and verruculogen could not be detected in that strain. The same strain also produced a member of the norgeamide / notoamide / aspergamide / stephacidin family of secondary metabolites (notoamide E). This type of compound has also been found in a strain of *A. versicolor* (Greshock *et al.* 2008).

Of particular interest is *A. pseudoustus* NRRL 5856 = CSIR 1128, which was originally identified as *A. ustus* and the first strain from which austamides, austdiols and austocystins (Table 2) were isolated (Steyn 1971, 1973, Steyn & Vleggaar 1974, 1976a, b, Vleggaar *et al.* 1974). This very toxic species has, however, only been isolated from maize in South Africa twice, and once in indoor

Table 2. Extrolites produced by species assigned to *Aspergillus* section *Usti*.

Species	Extrolites produced
A. amylovorus	An asperugin, monascorubramin-like extrolites, (CANO, SCYT, SENSTER, STARM)
A. calidoustus	Austins, drimans, ophiobolins G and H, TMC-120B, (ALTIN, FAAL, KNOF)
A. californicus	An arugosin, (CANDU, SAERLO, SCAM, SEND, XANXU)
A. carlsbadensis	Brevianamide A (only in IBT 14493), [An arugosin, DRI, TRITRA, TIDL (not in IBT 16753), GNI (only in IBT 18616), EMO (only in IBT 14493)]
A. deflectus	Desferritriacetylfusigen, deflectins A & B, emerin, a shamixanthone, (FUMU, RED2)
A. egyptiacus	Fumitremorgin A, fumitremorgin B, verruculogen, (FYEN, UTSCABI, TOPLA, FUMU, PRUD, HØJV)
A. elongatus	Fumitremorgin C, notoamide E, (DYK, SENT, TERRET)
A. germanicus	Drimans, (DRUL, KNAT, SLOT, SNOF)
A. granulosus	Asperugins, ustic acids, nidulol, drimans, (KMET, PUBO, SENSTER, SFOM)
A. heterothallicus	Emethallicins A, B, C, D, E & F, emeheterone, emesterones A & B and Mer-NF8054X, 5'-hydroxyaveranthin, stellatin, sterigmatocystin, (DRI, NIDU)
A. insuetus	Asperugins, drimans, ophiobolins G and H, pergillin-like compound, (AU, HETSCYT, INSU)
A. kassunensis	Asperugins, Mer-NF8054X, (FYRT, SAERLO, SENSCAB, SENSTER)
A. keveii	Asperugins, drimans, ophiobolins G and H, nidulol, (DRI, HETSCYT, INSU, PUBO, SENSTER, UP)
A. lucknowensis	An arugosin, (GULT, PULK, RED1)
A. monodii	Terrein, (DYVB, METK)
A. pseudodeflectus	Drimans, (DRI, DRUL, HUT, SLOT), asperugins in NRRL 4846
A. pseudoustus	Asperugins, austamide, prolyl-2-(1',1'-dimethylallyl) tryptophyldiketopiperazine, 12,13-dihydroaustamide, 12,13-dehydroprolyl-2-(1',1'-dimetylallyl)-tryptophyldiketopiperazine, 10,20-dehydro[12,13-dehydropropyl-2-1',1'-dimethylallyl)tryptophyldiketopiperazine], 12,13-dihydro-12-hydroxyaustamide, austdiol, dihydrodeoxy-8-epi-austdiol, austocystin A, B, C, D, E, F, G, H, I, norsolorinic acid, versicolorin C, averufin, (DRI, HETSCYT, SENSTER, UZ)
A. puniceus	Ustic acids, austocystins (and versicolorins), phenylahistin, nidulol, (SENSTER)
A. subsessilis	Mer-NF8054X, (SENSCAB, VIRO)
A. turkensis	An austocystin, deflectins, emerin, a shamixanthone, (RED2)
A. ustus	Ustic acids, austocystins (and versicolorins), austalides, nidulol, (SENSTER)

All designations in parenthesis with capital letters are secondary metabolites with characteristic chromophores (UV spectra) and retention-times, but their chemical structure is not yet known.

air in Finland. All three strains examined produced austamides, austdiol and austocystins. The austocystins have been found in *A. ustus, A. puniceus* and *A. pseudoustus* and one austocystin has also been found in *A. turkensis*. The austocystins seem to be another biosynthetic family of secondary metabolites that are derived from the versicolorins. In other species in sections *Aenei, Versicolores* and *Nidulantes*, versicolorins are precursors of sterigmatocystin and in few species, the aflatoxins (Frisvad *et al.* 2005, Varga *et al.* 2009). Sterigmatocystin has not yet been found in any species in section *Usti*, but a related metabolite, listed as SENSTER in Table 2 is common in this section, and may be related to sterigmatocystin, as it has a similar UV spectrum.

Comparing the secondary metabolite profiles of section *Usti* with other sections within subgenus *Nidulantes,* nidulol, and versicolorins are also produced by members of sections *Versicolores* and *Nidulantes* (Cole & Schweikert 2003). Interestingly, versicolorin, sterigmatocystin and 5'-hydroxyaveranthin are intermediates of the aflatoxin biosynthetic pathway and also produced by species assigned to *Aspergillus* sections *Flavi* and *Ochraceorosei* (Yabe *et al.* 1991, Frisvad *et al.* 2005). Other extrolites found in species in section *Usti* are also found in other sections in subgenus *Nidulantes*: arugosins, asperugins, austins and the metabolite DRI are present in species of the different sections. On the other hand, several metabolites have only been found in section *Usti*, including austamide, austdiol, austocystins, deflectins, drimans, emethallicins, emeheterones and ustic acids (Table 2). Two species produce red pigments, *A. amylovorus* produce a large number of monascorubramin like red pigments, while *A. turkensis* produce few monascorubramin-like extrolites.

Species descriptions

Aspergillus carlsbadensis Frisvad, Varga & Samson, **sp. nov**. MycoBank MB560399 Fig. 4.

Coloniis flavo-brunneis, cum caespitulis ex conglomerationibus cellularum obtegentium ("Hülle"). Cellulis obtegentibus ("Hülle") hyalinis, crassitunicatis, globosis vel late ellipsoideis, 15–30 µm. Conidiophoris biseriatis, stipitibus plerumque levibus, brunneis, 4–5 µm latis. Vesiculis globosis, 10–14 µm diam. Conidiis conspicue ornamentatis, echinulatis vel verrucosis, ellipsoideis, 2.5–3.0 × 3.0–3.5 µm.

Typus: **USA,** from soil, Lechuguilla Cave, Carlsbad Caverns National Park, New Mexico, isolated by D.E. Northup, 1992, (CBS H-30634 -- holotypus, culture ex-type CBS 123894).

CYA, 1 wk, 25 °C: 30–32 mm (poor to medium sporulation, cream yellow to dark brown reverse, Hülle cells), MEA, 1 wk, 25 °C: 7–29 mm (rather poor sporulation, light yellow to cream reverse), YES, 1 wk, 25 °C: 35–45 mm (no sporulation, yellow to curry yellow), OA, 1 wk, 25 °C: 25–32 mm (Hülle cells), CYA, 1 wk, 37 °C: no growth, CREA: good growth (18–22 mm) and no acid production.

Colonies yellow brown with white tufts of conglomerates of Hülle cells. Hülle cells hyaline, thick-walled, globose to broadly ellipsoidal, 15–30 µm. Conidiophores biseriate with typical smooth-walled, brown, 4–5 µm wide stipes. Vesicles globose, 10–14 µm in diam. Conidia, distinctly ornamented with spines or warts, ellipsoidal 2.5–3.0 × 3.0–3.5 µm.

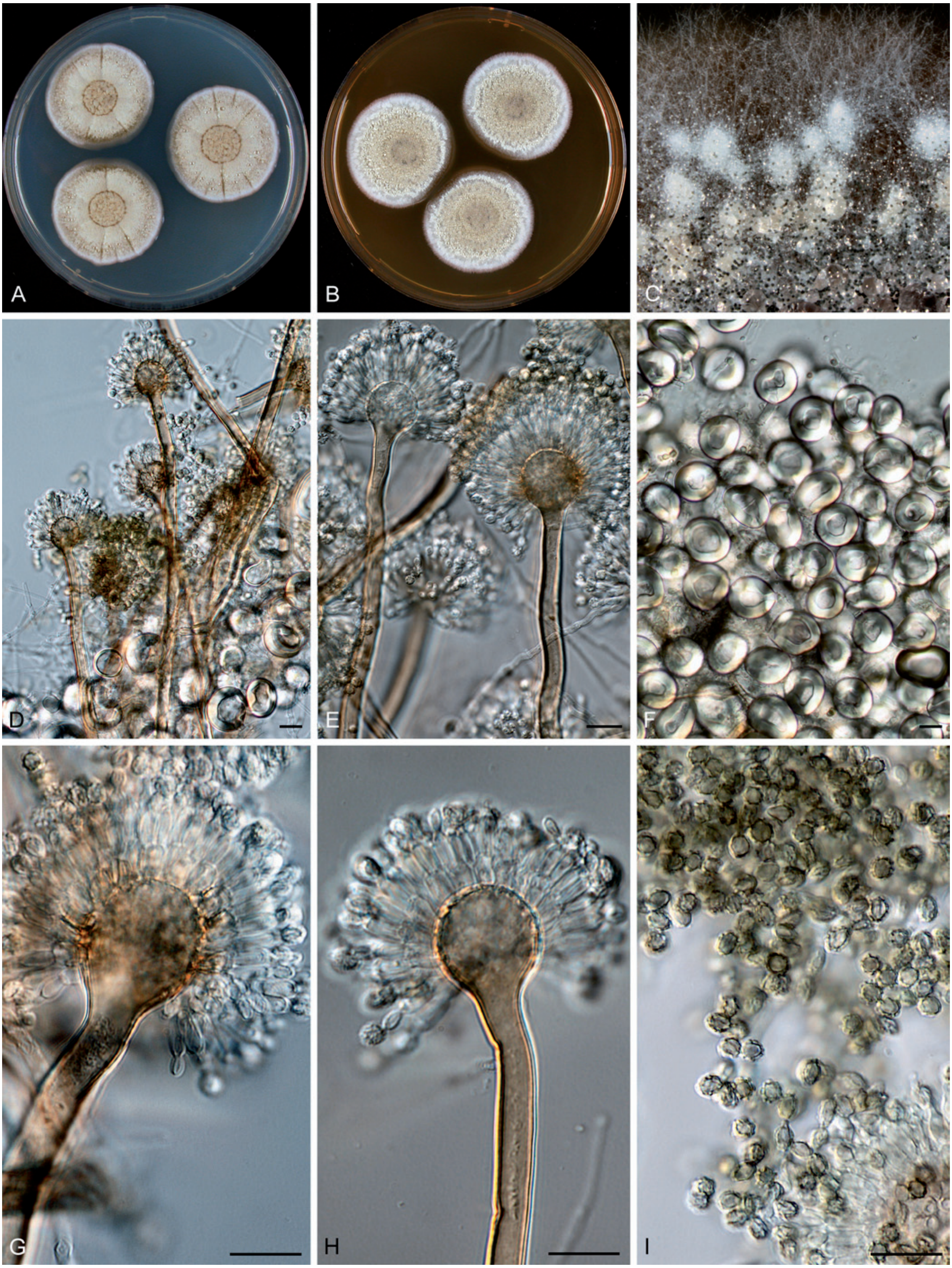

Fig. 4. *Aspergillus carlsbadensis* Frisvad, Varga & Samson sp. nov. A–C. Colonies incubated at 25 °C for 7 d, A. CYA, B. MEA, C. Tufts of Hülle cells. D–E, G–I. Conidiophores and conidia. F. Hülle cells. Scale bars = 10 µm.

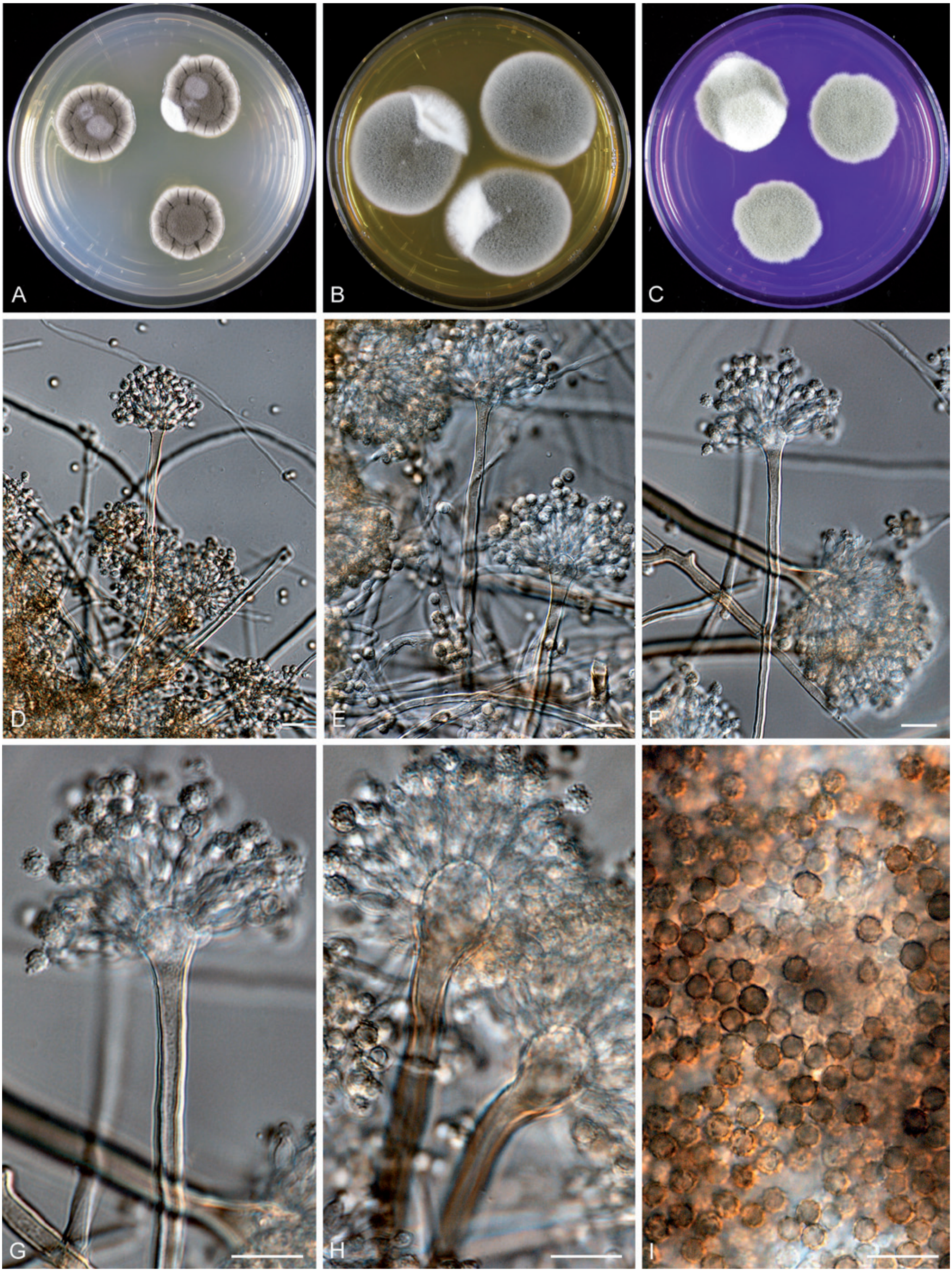

Fig. 5. *Aspergillus californicus* Frisvad, Varga & Samson sp. nov. A–C. Colonies incubated at 25 °C for 7 d, A. CYA, B. MEA, C. CREA, D–I. Conidiophores and conidia. Scale bars = 10 µm.

The taxon is related to, but clearly distinct from a clade including *A. calidoustus, A. pseudodeflectus, A. insuetus* and *A. keveii* on all trees. This species is also unable to grow at 37 °C, and acid production was not observed on CREA.

Aspergillus californicus Frisvad, Varga & Samson, **sp. nov.** MycoBank MB560400. Fig. 5.

Coloniis clare flavis, cum caespitulis albidis ex conglomerationibus cellularum obtegentium ("Hülle"). Cellulis obtegentibus ("Hülle") hyalinis, crassitunicatis, globosis vel late ellipsoideis. Conidiophoris biseriatis, stipitibus levibus, clare brunneis, 3.5–5 µm latis. Vesiculis globosis,. 11–16 µm in diam. Conidiis levibus vel subtiliter exasperates, subglobosis vel globosis, hyalinis vel viridibus, 2.5–3.0 µm.

Typus: **USA**, foothills of San Gabriel Mountains, California, ex chamise chaparral (*Adeonostoma fasciculatum*), Jeff S. La Favre, 1978 (CBS H-20635 -- holotypus, culture ex-type CBS 123895).

CYA, 1 wk, 25 °C: 18–20 mm (poor sporulation, yellow brown reverse, Hülle cells), MEA, 1 wk, 25 °C: 6–9 mm (rather poor sporulation, yellow brown reverse), YES, 1 wk, 25 °C: 23–26 mm (no sporulation, cream yellow reverse), OA, 1 wk, 25 °C: 18–21 mm (Hülle cells), CYA, 1 wk, 37 °C: no growth, CREA: good growth and no acid production.

Colonies light yellow with white tufts of conglomerates of Hülle cells. Hülle cells hyaline, thick-walled, globose to broadly ellipsoidal, 25–50 µm. Conidiophores biseriate with smooth-walled, light brown, 3.5–5 µm wide stipes. Vesicles globose, 11–16 µm in diam. Conidia, smooth to finely roughened, subglobose to globose, hyaline to greenish, 2.5–3.0 µm.

This species grew well at 37 °C, and acid production was not observed on CREA. It was found to be related to species in a clade including *A. subsessilis* and *A. kassunensis*.

Aspergillus germanicus Varga, Frisvad & Samson, **sp. nov.** MycoBank MB560401. Fig. 6.

Coloniis in agaro CYA brunneis et in agaro MEA griseo-brunneis, cellulis tectegentibus ("Hülle") nullis. Conidiophoris biseriatis, stipitibus plerumque levibus, brunneis, 6–9 µm latis. Vesiculis spathuliformibus, 14–22 µm diam. Conidiis conspicue echinulatis, globosis, brunneis, 3.5–5.0 µm diam.

Typus: **Germany**, ex indoor air, Stuttgart. Isolated by U. Weidner (CBS H-20636 -- holotypus, culture ex-type CBS 123887).

CYA, 1 wk, 25 °C: 22–26 mm (poor to medium sporulation, yellow brown to orange reverse, pigment diffusing, Hülle cells), MEA, 1 wk, 25 °C: 12–16 mm (good sporulation, light yellow to cream reverse), YES, 1 wk, 25 °C: 32–37 mm (some sporulation, yellow brown reverse), OA, 1 wk, 25 °C: 28–32 mm, CYA, 1 wk, 37 °C: 7–9 mm, CREA: good growth and no acid production.

Colonies on CYA brown, on MEA greyish brown. Hülle cells not observed. Conidiophores biseriate with typical smooth-walled, brown, 6–9 µm wide stipes. Vesicles spathulate, 14–22 µm diam. Conidia, distinctly echinulate, globose, brown, 3.5–5.0 µm.

This species has identical ITS sequences with *A. insuetus* CBS 119.27, but is clearly distinct from that species based on β-tubulin and calmodulin sequence data.

Aspergillus monodii (Locquin-Linard) Varga, Frisvad & Samson, **comb. nov.** MycoBank MB560402. Fig. 7.

Basionym: *Fennellia monodii* Locquin-Linard, *Mycotaxon* **39**: 10, 1990.

CYA, 1 wk, 25 °C: 2–21 mm (no sporulation, white to cream reverse), MEA, 1 wk, 25 °C: 6–8 mm (ascomata, light yellow reverse), YES, 1 wk, 25 °C: 8–23 mm (no sporulation, yellow to red brown reverse, yellow obverse), OA, 1 wk, 25 °C: 9–19 mm (ascomata), CYA, 1 wk, 37 °C: 0–2 mm, CREA: poor growth and no acid production.

Colonies producing an orange brown crusts of stromata with ascomata 200–350 µm in diam. Hülle cells forming the structure of the stromata, globose to ellipsoidal, 8–40 µm diam. Asci 8–10 × 10–13 µm. Ascospores 3.0–3.5 × 4.5–5.0 µm, hyaline, smooth-walled with two equatorial rings. *Aspergillus* anamorph not observed on various media and after cultivation at different temperatures.

This species occurs on dung and found on sheep dung in Chad and daman dung in Soudan.

Aspergillus pseudoustus Frisvad, Varga & Samson, **sp. nov.** MycoBank MB560403. Fig. 8.

Coloniis in agaro CYN cinnamomeo-brunneis et in agaro MEA flavo-brunneis, cellulis obtegentibus ("Hülle") nullis. Conidiophoris biseriatis, stipitibus plerumque levibus, brunneis, 3.5–5 µm latis. Vesiculis globosis, 10–14 µm diam. Conidiis levibus vel distinct echinulatis, globosis, brunneis vel viridibus, 2.5–3.0 µm.

Typus: **South Africa**, ex stored maize (CBS H-20637 -- holotypus, culture ex-type CBS 123904).

CYA, 1 wk, 25 °C: 30–32 mm (medium sporulation, yellow brown reverse), MEA, 1 wk, 25 °C: 15–25 mm (rather poor sporulation, light yellow reverse), YES, 1 wk, 25 °C: 35–45 mm (no sporulation, curry yellow to brown reverse), OA, 1 wk, 25 °C: 30–36 mm, CYA, 1 wk, 37 °C: no growth, CREA: 28–34 mm, no acid production.

Colonies on CYA cinnamon brown, on MEA yellow brown. Hülle cells not observed. Conidiophores biseriate with typical smooth-walled, brown, 3.5–5 µm wide stipes. Vesicles globose, 10–14 µm in diam. Conidia, smooth to distinctly echinulate, globose, brown to greenish, 2.5–3.0 µm.

Other strains: MRC 096 = IBT 31044, contaminant in *Bipolaris sorokiniana*, isolated from maize, South Africa; IBT 22361, indoor air, Finland

Aspergillus pseudoustus sp. nov., is related to, but clearly different from *A. ustus* and *A. puniceus* on all trees. This isolate came from stored maize, South Africa. Other isolates belonging to this species include a culture contaminant of *Bipolaris sorokiniana* from South Africa (IBT 31044), and one isolate came from indoor air in Finland (IBT 22361).

Aspergillus turkensis Varga, Frisvad & Samson **sp. nov.** MycoBank MB560404. Fig. 9.

Coloniis in agaro CYN clare brunneis et in agaro MEA flavo-brunneis, cellulis obtegentibus ("Hülle") nullis. Conidiophoris minute biseriatis, stipitibus plerumque levibus, clare brunneis, 2.5–3 µm latis. Vesiculis spathuliformibus, 5–8 µm diam. Conidiis levibus, globosis, hyalinis, 2.5–3.0 µm diam.

Typus: **Turkey**, ex soil isolated by K.B. Raper in 1950 (CBS H-20638 -- holotypus, culture ex-type CBS 504.65).

CYA, 1 wk, 25 °C: 13–18 mm (poor sporulation, red orange reverse), MEA, 1 wk, 25 °C: 4–10 mm (rather poor sporulation, cream yellow reverse), YES, 1 wk, 25 °C: 35–45 mm (no sporulation, orange

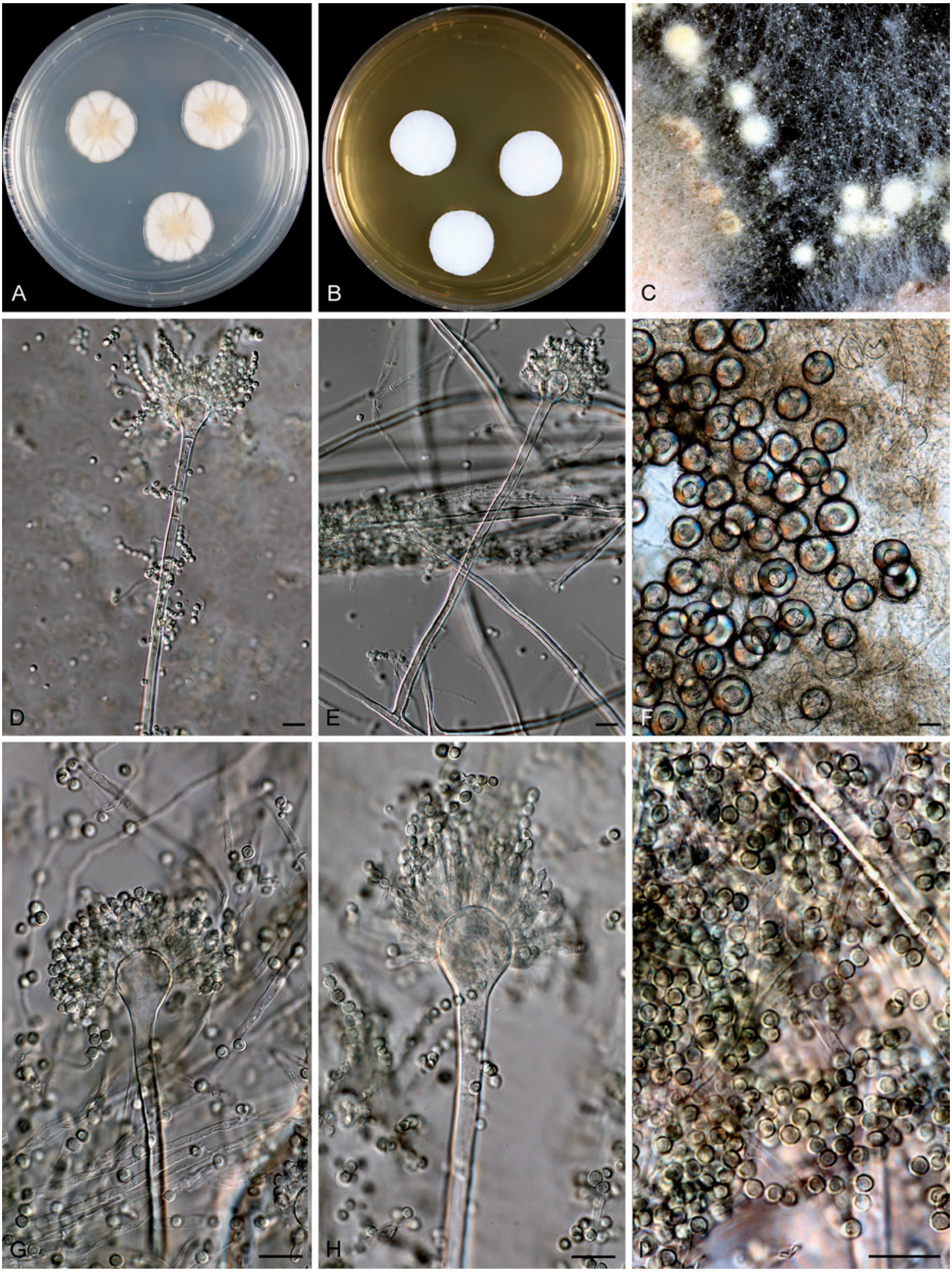

Fig. 6. *Aspergillus germanicus* Varga, Frisvad & Samson sp. nov. A–C. Colonies incubated at 25 °C for 7 d, A. CYA, B. MEA, C. Tufts of Hülle cells. D–E, G–I. Conidiophores and conidia. F. Hülle cells. Scale bars = 10 µm.

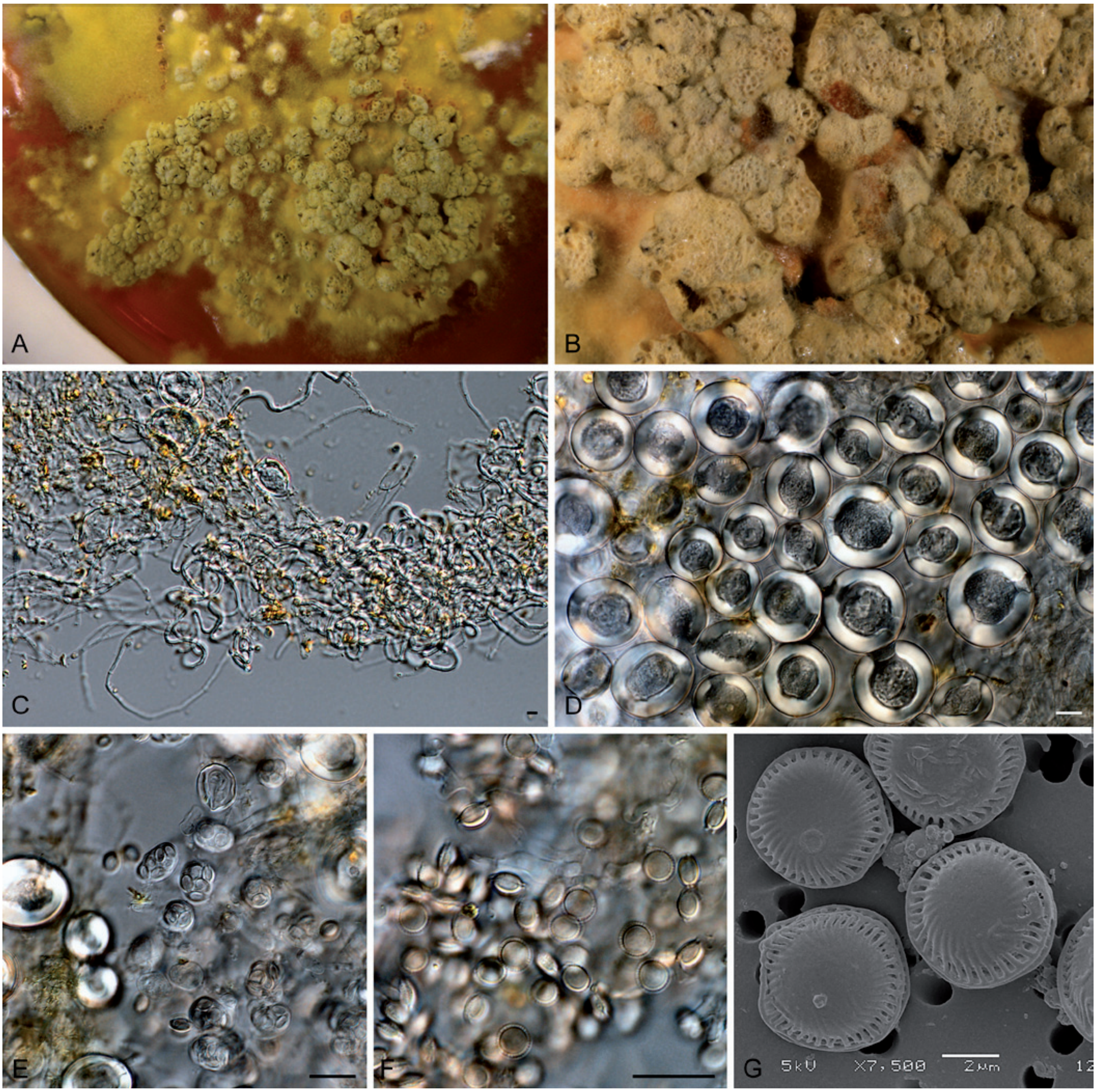

Fig. 7. *Aspergillus monodii* (Locquin-Linard) Varga, Frisvad & Samson comb. nov. A–B. Stromata containing ascomata, grown at 25 °C for 7 d, C. Mycelium with ascoma initials. D. Hülle cells, E–G. Asci and ascospores. Scale bars = 10 µm.

yellow reverse, yellow obverse), OA, 1 wk, 25 °C: 14–17 mm (yellow reverse and obverse), CYA, 1 wk, 37 °C: 6–14 mm, CREA: weak growth and no acid production.

Colonies on CYA light brown, on MEA pale yellow brown. Hülle cells not observed. Conidiophores small biseriate with typical smooth-walled, light brown, 2.5–3 µm wide stipes. Vesicles spathulate, 5–8 µm diam. Conidia, smooth-walled, globose, hyaline, 2.5–3.0 µm.

Isolate CBS 504.65 is distinct from the *A. deflectus* ex-type strain on all trees, indicating that this isolate represents a distinct species in this section. This species grew, although rather restrictedly at 37 °C, and acid production was not observed on CREA.

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Fig. 8. *Aspergillus pseudoustus* Frisvad, Varga & Samson sp. nov. A–C. Colonies incubated at 25 °C for 7 d, A. CYA, B. MEA, C. CREA, D–I. Conidiophores and conidia. Scale bars = 10 µm.

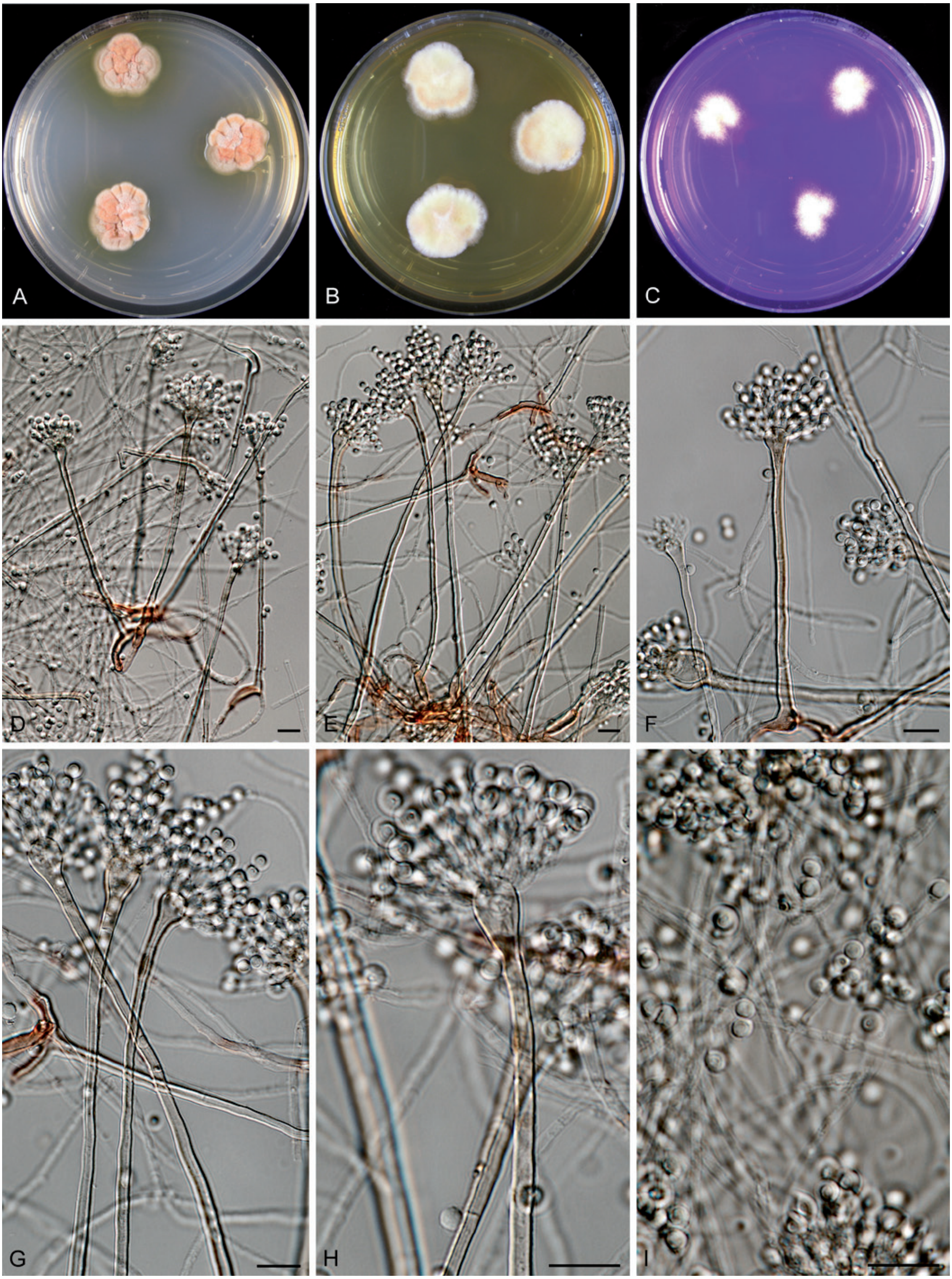

Fig. 9. *Aspergillus turkensis* Varga, Frisvad & Samson sp. nov. A–C. Colonies incubated at 25 °C for 7 d, A. CYA, B. MEA, C. CREA, D–I. Conidiophores and conidia. Scale bars = 10 µm.

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