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Taxonomic revision of *Eurotium* and transfer of species to *Aspergillus*

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Abstract: *Aspergillus* section *Aspergillus* contains economically important, xerophilic fungi that are widely distributed in nature and the human environment and are known for their ability to grow on substrates with low water activity. The taxa were revised based on sequence data from four loci, PCR fingerprinting, micro- and macromorphology, and physiology. The number of taxa was reduced to 17 species, all of which can be distinguished with sequence data from either the *caM* or *RPB2* locus. The original description of *A. proliferans* was supplemented by a description of its teleomorph. This species seems to be relatively common and often has been confused with *A. glaucus*. In addition, green sporulating isolates of *A. niveoglaucus* isolated from food and several other substrates are indistinguishable in phenotype from *A. glaucus*. A dichotomous key based on ascospore size and ornamentation and the ability to grow at specific combinations of temperature and water activity is provided for identification of species. In response to recent changes in the botanical code, we transferred the *Eurotium* species to *Aspergillus* and selected one name for each species.

Key words: food spoilage, low water activity, multilocus sequence typing, scanning electron microscopy, stored grain, xerophilic species

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Introduction

Aspergillus section *Aspergillus* (Gams et al. 1985) comprises fungi referred to by Thom and Raper (1941) and Raper and Fennell (1965) as the ''*Aspergillus glaucus* group''. The section has been monographed and revised by several authors (Raper and Fennell 1965, Blaser 1975, Samson 1979, Kozakiewicz 1989), and its monophyly is supported by sequence data (Peterson 2000, 2008). Subgenus *Aspergillus* sects. *Aspergillus* and *Restricti* form a well supported basal clade within *Aspergillus* s. str. (Houbraken and Samson 2011). *Eurotium*, typified by Malloch and Cain (1972) with *E. herbariorum* as neotype, is the teleomorph genus associated with section *Aspergillus*. Only one species with a known *Eurotium* teleomorph, *A. halophilicus*, has been placed (with limited support) within the sister section *Restricti* (Peterson et al. 2008).

Species from section *Aspergillus* are usually characterized by having yellow cleistothecia (white only in *A. leucocarpus*), lenticular ascospores, uniseriate conidial heads in shades of green or blue, and often yellow-, orange- or red-encrusted hyphae. The members of section *Aspergillus* and its sister section *Restricti* typically grow on substrates with low water activity. These organisms are universally distributed in nature and usually are referred to as xerophilic or halophilic. Significant economic impact arises from their deterioration of stored grain, cereals and food products preserved by drying or high concentrations of salt or sugar. Other sources of isolates include dust, textiles, herbarium material, leather goods, softwood and building materials (Thom and Raper 1941, Raper and Fennell 1965, Pitt and Hocking 2009, Dovicicova 2010). Some species are used in food manufacturing (Dimici and Wada 1994).

These fungi are not considered to be important human pathogens, although cases of superficial infections and sporadic cases of invasive infections have been reported (summarized by de Hoog et al. 2009). The species are frequently isolated as saprotrophic fungi from clinical specimens, in particular from nails and skin (Hubka et al. 2012a). They can be confirmed uncommonly as etiologic agents of onychomycosis by repeated isolation (Summerbell et al. 2005).

Section *Aspergillus* species produce a rich spectrum of secondary metabolites, many of which exhibit biological activities or act as antioxidants. Possible health risks are associated with metabolites such as

echinulin (Umeda et al. 1974, Ali et al. 1989), physcion (Bachmann et al. 1979) and flavoglaucin (Nazar et al. 1984) whose toxicity has been demonstrated in animals. Reported production of aflatoxins, ochratoxins, gliotoxin and sterigmatocystin by section *Aspergillus* species is controversial and these reports have not been verified by subsequent studies using taxonomically well characterized isolates (Frisvad et al. 2002, 2007). More important, these organisms release metabolic water during their growth on substrates with low water activity and thereby create favorable conditions for less xerophilic fungi that can produce more hazardous mycotoxins.

In this study we revise the taxonomic position of all commonly accepted section *Aspergillus* species and include more recently described taxa whose position has not been determined. Fungal strains were characterized with sequence data from four loci (Peterson 2008), PCR fingerprinting, morphology and physiology. In addition we provide a necessary nomenclatural revision and transfer all *Eurotium* species to *Aspergillus*.

MATERIALS AND METHODS

Cultivation and study of morphology.—Strains were grown on malt extract agar (MEA), Czapek yeast autolysate agar with 20% (w/v) sucrose (CY20S) and Harrold's agar (M40Y) at 25 C (Raper and Fennell 1965, Klich 2002). When possible, micromorphology was examined with cultures on CY20S at 25 C. Color was based on the ISCC-NBS Centroid Color Charts (Kelly 1964). Growth at 37 C was tested on CY20S, M40Y and Harrold's agar with 60 and 70% (w/v) sucrose (M60Y and M70Y); experiments were conducted independently in two incubators and were repeated twice.

Scanning electron microscopy (SEM) was performed on a JEOL-6380 LV microscope (JEOL Ltd. Tokyo, Japan). Pieces of colonies (5 × 5 mm) that were grown 3 wk on CY20S and contained ascomata and conidiophores were fixed in osmium tetroxide vapors 2 wk at 5–10 C and gold-coated in Bal-Tec SCD 050 sputter coater. The specimens were observed with spot size 38–45 μm and accelerating voltage 15–20 kV.

Molecular studies and phylogenetic analysis.—DNA was isolated with ArchivePure DNA yeast and Gram−+ kit (5 PRIME Inc., Gaithersburg, Maryland) with modified time of incubation: lytic enzyme solution (2 h, 37 C) and cell lysis solution (4 h, 64 C). Alternatively the CTAB-chloroform method of Soares et al. (2012) was used. The ID region and partial sequences of *benA*, *caM* and *RPB2* were amplified with primer combinations described by Peterson (2008). The mixture composition and PCR reaction conditions followed the protocol described by Hubka et al. (2012a). The PCR products purification and sequencing were provided by Macrogen Europe, Amsterdam, the Netherlands. Both reverse and forward primers were used for sequencing. PCR fingerprinting was performed with the phage M13-core sequence as an oligonucleotide primer (5′–GAGGGTGGCGGTTCT) following the protocol and conditions described by Hubka and Kolarik (2012).

Sequencing errors were detected and corrected with Sequencher (Gene Codes Corp., Ann Arbor, Michigan). DNA sequences were aligned for phylogenetic analysis with Muscle as implemented in Mega5 (Tamura et al. 2011). PAUP* 4.0b10 (Swofford 2003) was used to conduct parsimony analysis and to generate phylogenetic trees for single gene alignments as well as for the combined alignment. Bootstrapping (bs) was performed in PAUP* with maximum parsimony criterion and TBR branch swapping for 1000 replicates. MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) was used to calculate Bayesian posterior probabilities (pp) of branches. *RPB2* datasets included only protein-coding sequences and were partitioned by codon position, whereas *benA* and *caM* loci included protein-coding and intronic regions and were partitioned into intron and exon regions. Markov chain Monte Carlo (MCMC) analysis was conducted for up to 5×10^6 generations until the chains converged. Genealogical concordance phylogenetic species recognition (GCPSR) concepts (Taylor et al. 2000, Dettman et al. 2003) were used for concordance analysis. Branches with 90% bs and 0.90 pp were considered strongly supported. The alignments were deposited in TreeBASE (submission ID 13673).

DNA sequences used for species identification and phylogenetic analysis include those obtained in this study and those deposited by Peterson (2008) and Hubka et al. (2012a). The sequences of the ex-type strain of *A. cibarius* were deposited by Hong et al. (2012). All isolates and accession numbers are provided (TABLE I).

RESULTS

DNA sequence analysis.—In phylogenetic analyses four regions were amplified and sequenced (TABLE I). The ID locus was uninformative for many of the species examined (SUPPLEMENTARY FIG. 1). *CaM* as well as *RPB2* locus alone (SUPPLEMENTARY FIGS. 2, 3) differentiated all accepted species recognized here on the basis of combining molecular data, morphology and physiology. An identical *benA* sequence is shared between *A. niveoglaucus* and *A. brunneus* (SUPPLEMENTARY FIG. 4). Seventeen distinct patterns were observed in PCR fingerprints with M13-core primer (TABLE I). The fingerprint patterns correlated well with the species boundaries inferred from sequence data and phenotypic features. M13 core primer was used for differentiating species of *Aspergillus* and other genera (Gadkar et al. 1997, Gräser et al. 1998, Zhou et al. 2001, Nováková et al. 2012).

Section *Aspergillus* contains 18 clades corresponding to species based on the genealogical concordance and phylogenetic species concept (GCPSC) (FIG. 1), 17 of which were supported by morphological and physiological data (see below). Six main clades were

TABLE I. *Aspergillus* strains from section *Aspergillus* examined in this study

Current species name	Strain no.[a]	Synonymized name associated with the ex-type strain[b]	Substrate; country	M13-core	GenBank/EMBL accession nos.			
					ID	*benA*	*caM*	*rpb2*
A. appendiculatus	**CBS 374.75^T**		smoked sausage; Switzerland	I	HE615132	HE801333	HE801318	HE801307
	CBS 101746	*A. aridicola*	sheep dung; China	I	HE615133	HE801334	HE801319	HE801308
A. brunneus	**NRRL 131^T**	*A. echinulatus*	fruit (*Ficus carica*); USA	II	EF652060	EF651907	EF651998	EF651939
	NRRL 133		unknown	II	EF652061	EF651908	EF651999	EF651940
	NRRL 124	*A. medius*	unknown	II	EF652056	EF651904	EF651997	EF651938
A. cibarius	**KACC 46346^T**		meju; Korea	—	JQ918177	JQ918180	JQ918183	JQ918186
	CCF 4098 = NRRL 62493		toenail; CR[c]	III	FR848828	FR837968	FR837973	FR837979
	CCF 4235 = NRRL 62492		toenail; CR	III	HE801341	HE801330	HE801324	HE801313
	CCF 4264		cave sediment; Spain	III	HE974462	HE974436	HE806186	HE974428
A. chevalieri	**NRRL 78^T**	*A. equitis*	coffee beans; USA	IV	EF652068	EF651911	EF652002	EF651954
	NRRL 79		unknown; USA	—[d]	EF652069	EF651912	EF652003	EF651955
	NRRL 4755		unknown	—	EF652071	EF651913	EF652004	EF651956
	CCF 1663		semolina; CR	IV				
	CCF 1676		semolina; CR	IV				
	CCF 3211		seeds of *Carum carvi*; CR	IV				
	CCF 3291		rice; CR	IV	FR727116	HE578085	HE578099	HE801314
A. costiformis	**CBS 101749^T**		moldy paper-box; China	V	HE615136	HE801338	HE801320	HE801309
	CCF 4097 = NRRL 62483		toenail; CR	V	FR837960	FR837970	FR837974	FR837978
A. cristatus	**NRRL 4222^T**	*A. cristatellus*	unknown; South Africa	VI	EF652078	EF651914	EF652001	EF651957
A. glaucus	**NRRL 116^T**		house lumber; USA	VII	EF652052	EF651887	EF651989	EF651934
	NRRL 117	*A. mangini*	house lumber; USA	VII	EF652053	EF651888	EF651990	EF651935
	NRRL 120	*A. umbrosus*	coffee beans; USA	VII	EF652054	EF651889	EF651991	EF651936
	NRRL 121		unknown	VII	EF652055	EF651890	EF651992	EF651937
A. intermedius	**NRRL 82^T**		cotton yarn; U.K.	VIII	EF652074	EF651892	EF652012	EF651958
	NRRL 84		unknown	—	EF652070	EF651893	EF652013	EF651959
	NRRL 4817		unknown	VIII	EF652072	EF651894	EF652014	EF651960
	NRRL 25823		soy protein; USA	—	EF652073	EF651895	EF652015	EF651961
	CBS 377.75	*A. spiculosus*	soil; Spain	VIII	HE974459	HE974432	HE974437	HE974425
	CCF 127		industrial material; China	VIII	HE578060	HE974431	HE578100	HE974426
A. leucocarpus	**NRRL 3497^T**		dried sausage; Germany	IX	EF652087	EF651925	EF652023	EF651972
A. montevidensis	**NRRL 108^T**		tympanic membrane; Uruguay	X	EF652077	EF651898	EF652020	EF651964
	NRRL 89		unknown	—	EF652075	EF651896	EF652016	EF651962
	NRRL 90	*A. hollandicus*	unknown	X	EF652076	EF651897	EF652017	EF651963
	NRRL 4716		candied grapefruit rind; USA	—	EF652079	EF651899	EF652018	EF651965
	NRRL 25850		refrigerated bread dough; USA	—	EF652082	EF651900	EF652021	EF651966
	NRRL 35696		nasal swab; USA	—	EF652083	EF651901	EF652019	EF651967
	NRRL 35697		nasal swab; USA	—	EF652084	EF651902	EF652022	EF651968
	NRRL A-13891	*A. heterocaryoticus*	rice; Mexico	—	EU021619	EU021670	EU021687	EU021659

TABLE I. Continued

Current species name	Strain no.[a]	Synonymized name associated with the ex-type strain[b]	Substrate; country	M13-core	GenBank/EMBL accession nos.			
					ID	*benA*	*caM*	*rpb2*
	CBS 651.74	*A. vitis*	*Vitis vinifera*; Kazakhstan	X	HE974460	HE974433	HE974441	HE974424
	CCF 1952		feed; CR	X	FR727111	FR775334		
	CCF 3998		neck skin; CR	X	FR727117	HE974434	FR751447	HE974418
	CCF 4069		heel skin; CR	X	FR839679	FR775356	HE974440	HE974419
	CCF 4070		fingernail; CR	X	FR848825	FR775335	FR751442	HE974420
	CCF 4071		thigh and neck skin; CR	X	FR839680	HE974435	FR751449	HE974421
	CCF 4248		window sill; CR	X	HE974461	HE801339	HE974442	HE974422
	CCF 4258		sputum; CR	X				
	CCF 4370		bronchoalveolar lavage; CR	X				
	CCF 4371		external auditory canal; CR	X				
A. neocarnoyi	**NRRL 126^T**	*E. carnoyi*	unknown	XI	EF652057	EF651903	EF651985	EF651942
A. niveoglaucus	**NRRL 127^T**	*A. glauconiveus*	unknown	XIIa[e]	EF652058	EF651905	EF651993	EF651943
	NRRL 128		unknown	—	EF652059	EF651906	EF651994	EF651944
	NRRL 136		unknown	XIIa	EF652062	EF651909	EF651995	EF651945
	NRRL 137		unknown	XIIa	EF652063	EF651910	EF651996	EF651946
	CBS 101750	*A. parviverruculosus*	soil; China	XIIb[e]	HE615135	HE801331	HE801323	HE801312
	CCF 4191		cave sediment; Spain	XIIa	HE801344	HE801332	HE974438	HE974427
	CCF 4388		cereals; CR	XIIa		HE801340		
	F-530		garlic; CR	XIIa	HE578069	HE578086	HE578092	HE578114
A. proliferans	**NRRL 1908^T**		cotton yarn; UK	XIII	EF652064	EF651891	EF651988	EF651941
	NRRL 71		leafhoppers; USA	XIII	EF652047	EF651885	EF651986	EF651932
	NRRL 114		unknown; USA	XIII	EF652051	EF651886	EF651987	EF651933
	CCF 4096 = NRRL 62482		palm skin; CR	XIII	FR848827	FR775375	HE650908	HE801303
	CCF 4115 = NRRL 62497		toenail; CR	XIII	FR851850	FR851855	HE578090	HE578107
	CCF 4146 = NRRL 62494		toenail; CR	XIII	HE578067	HE578076	HE650909	HE801304
	CCF 4192		cave sediment; Spain	XIII	HE615128	HE801328	HE801316	HE801305
	CCF 4232		stuffed bird; CR	XIII	HE615129	HE801329	HE801317	HE801306
	CCF 4263		toenail; CR	XIII				
A. pseudoglaucus	**NRRL 40^T**	*A. glaucoaffinis*	unknown	XIV	EF652050	EF651917	EF652007	EF651952
	NRRL 13	*A. reptans*; *E. repens*	*Prunus domestica*; France	XIV	EF652048	EF651915	EF652005	EF651950
	NRRL 17		wrist skin; USA	—	EF652049	EF651916	EF652006	EF651951
	NRRL 25865		unknown; Japan	—	EF652065	EF651918	EF652008	EF651953
	CBS 101747	*A. fimicola*	animal dung; China	XIV	HE615130	HE801335	HE801321	HE801310
	CBS 379.75	*A. glaber*	leaf; Switzerland	XIV	HE615131	HE801336	HE801322	HE801311
	CCF 1454		soil; Nepal	XIV	FR727113	FR775359		
	CCF 3283		mouldy sap; CR	XIV	FR727114	FR775360	HE974439	HE578110
	CCF 4011		back skin; CR	XIV	FR839678	FR775358	FR751446	HE578111
	CCF 4072		trunk skin; CR	XIV	FR839684			
	CCF 4372		toenail; CR	XIV				

TABLE I. Continued

Current species name	Strain no.[a]	Synonymized name associated with the ex-type strain[b]	Substrate; country	M13-core	GenBank/EMBL accession nos.			
					ID	*benA*	*caM*	*rpb2*
	CCF 4373		fingernail; CR	XIV				
	CCF 4374		toenail; CR	XIV				
A. ruber	**NRRL 52^T**		unknown	XV	EF652066	EF651920	EF652009	EF651947
	NRRL 76		unknown	—	EF652067	EF651921	EF652011	EF651948
	NRRL 5000	*A. athecius*; *A. atheciellus*	coffee beans; UK	—	EF652080	EF651922	EF652010	EF651949
	CBS 101748	*A. tuberculatus*	soil; China	XV	HE615134	HE801337	HE801325	HE801315
	CCF 2920		malt dust; CR	XV	FR727112	FR775357	FR751444	HE974430
	CCF 3464		textile; CR	XV	FR727115			
	CCF 4104		toenail; CR	XV	FR848826	FR848830		HE974429
	CCF 4377		toenail; CR	XV	HE578065	HE578087	HE578098	
	F-438		pepper; CR	XV	HE801343			
A. tonophilus	**NRRL 5124^T**		binocular lens; Japan	XVI	EF652081	EF651919	EF652000	EF651969
A. xerophilus	**NRRL 6131^T**		desert soil; Egypt	XVII	EF652085	EF651923	EF651983	EF651970
	NRRL 6132		desert soil; Egypt	XVII	EF652086	EF651924	EF651984	EF651971
A. halophilicus (*Restricti*)	**NRRL 2739^T**		stored wheat seed; USA	—	EF652088	EF651926	EF652034	EF651982
Hamigera avellanea (outgroup)	**NRRL 1938^T**		soil; USA	—	AF454075	EU021664	EU021682	EU021627
A. taklimakanensis	CBM-FA-876[f]		desert soil; China	—				

[a] Culture collection designations: CBS, Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands; NRRL, Agricultural Research Service Culture Collection, Peoria, Illinois, USA; KACC, Korean Agricultural Culture Collection, Suwon, South Korea; CCF, Culture Collection of Fungi, Prague, Czech Republic; F, Czech Collection of Microorganisms, Brno, Czech Republic; CBM-FA, dried holotype culture of *A. taklimakanensis* obtained from the Natural History Museum & Institute, Chiba, Japan. Ex-type strains shown in boldface.

[b] If there are identical epithets for both *Aspergillus* and *Eurotium*, only combination with *Aspergillus* is mentioned.

[c] Czech Republic.

[d] Not tested.

[e] Slight differences observed but general pattern of bands is shared.

[f] Type specimen; no living culture.

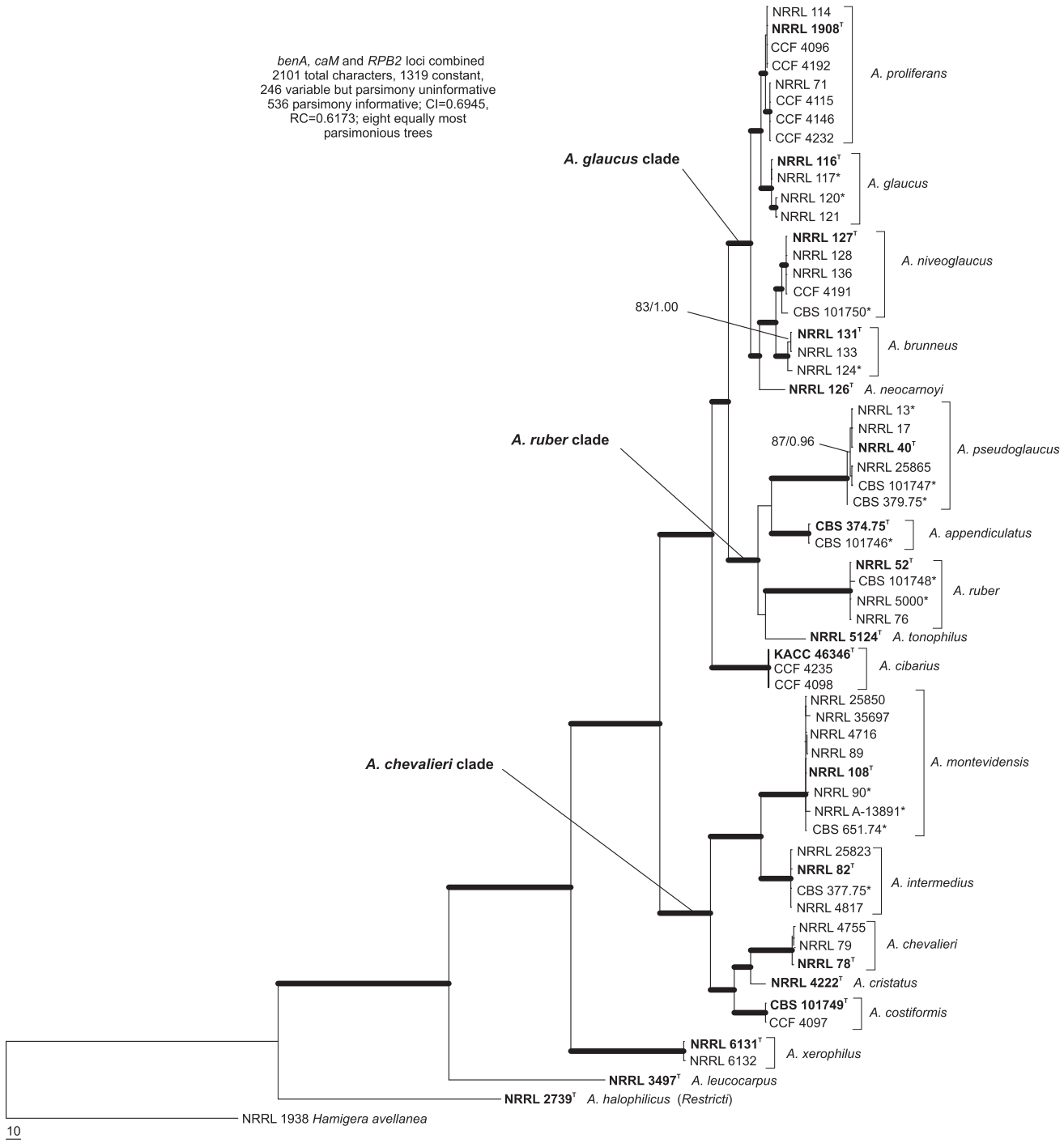

FIG. 1. Maximum parsimony tree showing the relationships of species in section *Aspergillus* based on the combined data from *benA*, *caM* and *RPB2* loci. Numbers on internodes are bootstrap proportions and Bayesian posterior probabilities. When bootstrap proportions were greater than 90% and Bayesian probabilities were greater than 0.90, the internode line is thick. Outgroup choice was based on Peterson (2008). The ex-type strains of synonymized species are designated with asterisks.

distinguished in the combined sequence datatree (FIG. 1) and are discussed below.

The *A. glaucus* clade (FIG. 1) contains six species by GCPSR, only five of which (*A. proliferans*, *A. glaucus*, *A. niveoglaucus*, *A. brunneus*, *A. neocarnoyi*) are differentiated here based on morphological and physiological data and are treated as valid species. The *A. proliferans* lineage is represented by the type isolate NRRL 1908 with defective development of ascomata, along with several isolates forming ascomata (TABLE I) that were

identified previously as *A. ruber* or *A. glaucus*. Two subclades within *A. proliferans* were supported only by *caM* and *RPB2* loci (SUPPLEMENTARY FIGS. 2, 3) but lacked the morphological and physiological support for separate species. The *A. glaucus* lineage includes two isolates, NRRL 120 and 121, that form a subclade supported by *caM* locus (SUPPLEMENTARY FIG. 2) and were treated as *A. umbrosus* by Raper and Fennell (1965). The *A. niveoglaucus* lineage includes the ex-type isolate of *A. parviverruculosus* CBS 101750, which is supported only by the *RPB2* locus (SUPPLEMENTARY FIG. 3). The sibling species relationship of *A. niveoglaucus* and *A. brunneus* is supported by three loci but not the *benA* locus (SUPPLEMENTARY FIG. 4). The interspecies relationships of all six species within *A. glaucus* clade are fully resolved, and the species branch together in single locus trees as well as the combined datatree.

The *A. ruber* clade (FIG. 1) includes four species by GCPSR (*A. pseudoglaucus*, *A. appendiculatus*, *A. ruber*, *A. tonophilus*). The *A. pseudoglaucus* lineage includes ex-type isolates of *A. glaber* CBS 379.75 (supported only by *RPB2* locus), *A. fimicola* CBS 101747 and *A. reptans* NRRL 13 (the name for teleomorphic state *E. repens* de Bary is not identical to *A. repens*; see below). The *A. appendiculatus* lineage includes the ex-type isolate of *A. aridicola* CBS 101746. The *A. ruber* lineage includes the ex-type isolates of *A. tuberculatus* CBS 101748 and *A. athecius* NRRL 5000. The relationships of the four species in the *A. ruber* clade are not fully resolved.

The *A. chevalieri* clade (FIG. 1) contains five species by GCPSR with fully resolved interspecies relationships (*A. montevidensis*, *A. intermedius*, *A. chevalieri*, *A. cristatus*, *A. costiformis*). The *A. montevidensis* lineage includes the ex-type isolates of *A. vitis* CBS 651.74, *A. hollandicus* NRRL 90 and *A. heterocaryoticus* NRRL A-13891. The *A. intermedius* lineage includes the ex-type isolate of *A. spiculosus* CBS 377.75, previously treated as synonymous to *A. cristatus* (Pitt 1985, Samson and Gams 1985, Pitt et al. 2000). *Aspergillus costiformis* is supported as a distinct species by all four loci (SUPPLEMENTARY FIGS. 1–4), and its closest relative is *A. cristatus*.

Aspergillus cibarius, *A. xerophilus* and *A. leucocarpus* each form a well supported single-species clade (FIG. 1). Whereas the position of *A. xerophilus* and *A. leucocarpus* is shared between single-locus trees (SUPPLEMENTARY FIGS. 1–4), the exact relationships of *A. cibarius* to other species remain unresolved because of weakly supported deeper branching. A similar ID region sequence is shared between *A. cibarius* and *A. pseudoglaucus* (SUPPLEMENTARY FIG. 1).

It was not possible to determine the position of *A. taklimakanensis* because the living culture is no longer available. The dried holotype was treated with formaldehyde and isolation of DNA was unsuccessful. Other phylogenetic relationships within section *Aspergillus* were discussed by Peterson (2008) and Peterson et al. (2008).

Ascospore morphology.—We sought reliable phenotypic markers for differentiating species defined a priori by the GCPSR concept (FIG. 1). The size and surface morphology of ascospores as viewed with the light microscopy and SEM and the ability to grow on CY20S and M60Y at 37 C (TABLE II, FIG. 2) were found to correlate most closely with the phylogenetic species concept.

The species from *A. glaucus* clade (FIG. 1) are characterized by having ascospores that are smooth or with convex surface roughened only near the equatorial area, have crests typically absent or very low and have mostly shallow but distinct furrows (FIG. 2). The ascospores of *A. neocarnoyi* are smooth and without crests, and only a trace of a furrow can be observed (FIG. 2). *Aspergillus neocarnoyi* ascospores resemble those of *A. pseudoglaucus* (FIG. 2) and *A. tonophilus* (FIG. 2) from *A. ruber* clade but are larger. The size is broad for ascospores in the *A. glaucus* clade (4.5–10.5 μm). In the *A. ruber* clade, ascospores are smooth, crests are absent or incomplete (*A. appendiculatus*; FIGS. 2, 3) and furrows are shallow or only a trace of a furrow is present (FIG. 2). The *A. chevalieri* clade (FIG. 1) includes species with rough ascospores having low to prominent crests (with exception of smooth ascospores in *A. chevalieri*) (FIGS. 2, 3). The ascospore body is relatively small, 3–7 μm (6–7 μm in *A. costiformis*, FIG. 3). The furrow is V-shaped in *A. montevidensis* (FIG. 2) and *A. costiformis* (FIG. 3) and absent in *A. chevalieri*, *A. intermedius* and *A. cristatus* (FIG. 2). *Aspergillus costiformis* (FIG. 3) and *A. montevidensis* (Kozakiewicz 1989) share lobate-reticulate ornamentation of ascospores, visible when examined with SEM. These two species can be separated easily by their ascospore sizes and conidial ornamentation (smooth in *A. costiformis*, FIG. 3). The ascospores of *A. intermedius* and *A. cristatus* are covered with echinulations (Kozakiewicz 1989). Three species, *A. cibarius*, *A. xerophilus* and *A. leucocarpus*, each form a separate single-species clade in phylogenetic analysis (FIG. 1). Ascospores of *A. cibarius* are relatively small and smooth or with convex surface slightly roughened near the equatorial area and have an obvious furrow and crests. The crests in isolates examined here (TABLE I) often were incomplete and consisted of petal-shaped projections. We present light microscope and SEM photos (FIG. 3) of this ascospore variety because it was not documented in the original description (Hong et al.

2012). The ascospores of *A. xerophilus* (FIG. 2) have a distinct furrow and are roughened near the equatorial region or over the entire surface and somewhat resemble ascospores of species from *A. glaucus* clade. The ascospores of *A. leucocarpus* (FIG. 2) resemble those of *A. chevalieri* in being smooth and having prominent crests, but the ascospores of *A. chevalieri* are smaller.

Phenotypic differentiation of *A. glaucus* and *A. niveoglaucus* is problematic (see below), but some minor differences in ascospore morphology can be found. The equatorial area of *A. niveoglaucus* ascospores is often ragged and consists of short projections or incomplete crests, and the convex surface near crests often is roughened markedly; these characters are less pronounced in *A. glaucus*. The ascospores of *A. niveoglaucus* CBS 101750 (the ex type of *A. parviverruculosus*) commonly had up to 2.5 μm long, thread-like appendages (FIG. 3). A significant number of ascospores with such appendages also were observed in *A. niveoglaucus* isolate F-530, supporting the classification of *A. parviverruculosus* as a synonym of *A. niveoglaucus*.

Intraspecific differences in ascospore size in section *Aspergillus* was typically 1.5–2 μm (TABLE II). In some cases, the morphology of ascospores differed within a single species, although the size remained unchanged. Two distinct types of ascospores were present in the ex type of *A. appendiculatus* CBS 374.75. Ascospores with incomplete equatorial crests composed of petaliform tips as well as those with filiform appendages flanking the equatorial area (FIG. 2) were documented with SEM by Kozakiewicz (1989). Blaser (1975) and Abliz et al. (2001) documented only the second type of ascospores. The ex-type isolate of *A. aridicola* CBS 101746 has ascospores with petal-shaped incomplete crests (FIG. 3) and is treated here as a synonym of *A. appendiculatus*, which is supported by the phylogenetic analysis (FIG. 1). In another example, *A. ruber* ascospores are smooth and a furrow is evident (Thom and Church 1926; FIG. 2), but the ascospores of CBS 101748 (ex type of *A. tuberculatus*) lack a furrow and the surface is coarsely tuberculate (FIG. 4). Similarly we isolated strain CCF 4248 with ascospores very similar to *A. tuberculatus* (FIG. 4) but with growth parameters and a colony phenotype identical to those of *A. montevidensis*. The molecular analysis supports the identification as *A. montevidensis*.

Colony morphology.—The features of the anamorph and macromorphology of colonies were of secondary importance in distinguishing many species but helpful in distinguishing some individual species. We noted that the isolates CCF 4191, F-530, AK 201/99 and CBS 101750 representing *A. niveoglaucus* have green conidial heads (SUPPLEMENTARY FIG. 5) in contrast to the white conidial heads in the species description (Thom and Raper 1941). White-spored isolates are apparently color mutants, and white conidial heads no longer can be used as a feature for distinguishing *A. niveoglaucus*. The differentiation of green sporulating *A. niveoglaucus* and *A. glaucus* also is problematic. These species have similar ascospore morphology and growth characteristics (FIG. 2, TABLE II), and we were not able to find a reliable phenotypic feature for their differentiation.

Based on our observations, orange to red colonies may occur at least in some isolates of *A. ruber*, *A. proliferans*, *A. glaucus*, *A. niveoglaucus*, *A. echinulatus* and *A. cibarius*. On the other hand, red hyphae were uniformly absent from species of the *A. chevalieri* clade (FIG. 1). Orange-red was observed also in some isolates of *A. pseudoglaucus*, in particular on media containing at least 20% sucrose. The orange-red to red shades were even more pronounced in *A. pseudoglaucus* CBS 379.75, the ex-type strain of *A. glaber*, and developed also on media with higher water activity such as MEA.

Growth on media with different water activities.—The ability of species to grow on media with different water activities at 37 C was useful in differentiating some species (TABLE II). The species from the *A. chevalieri* clade (see FIG. 1) in contrast to other species can consistently grow at 37 C on all media with low water activity (CY20S, M40Y, M60Y, M70Y). The ability to grow at 37 C on M60Y distinguished *A. ruber* from *A. glaucus*, *A. niveoglaucus* and *A. proliferans*, species that previously were confused with one another or were treated as one species (see below). Except for *A. glaucus* and *A. niveoglaucus*, section *Aspergillus* species can be distinguished by ascospore size and surface morphology, conidia ornamentation and ability to grow at 37 C on CY20S and M60Y (see TABLE II and KEY TO SPECIES).

Induction of asexual state.—The conidial heads of some species (*A. xerophilus*, *A. costiformis*, *A. cristatus*) usually were absent when using standard cultivation conditions (media containing 20–40% sucrose; 20–30 C) in contrast to other species from section *Aspergillus* that consistently produced conidial heads under these conditions. Only four species in section *Aspergillus*, including all three mentioned species and *A. intermedius*, have smooth-walled conidia (TABLE II). We found that the anamorph in *A. xerophilus*, *A. costiformis* and *A. cristatus* can be induced by decreasing the water activity of the medium and simultaneously raising the cultivation temperature. A conspicuous shift in macromorphology of colonies

TABLE II. Selected phenotypic features useful in differentiation of species in section *Aspergillus*

Species (No. of isolates examined)	37 C, 7 d				Ascospores[a]			Surface of conidia[b]	SEM of ascospores [c]
	CY20S	M40Y	M60Y	M70Y	Body (long axis, µm)	Equatorial region	Ornamentation[b]		
A. appendiculatus (2)	−	−	−	−	5–7	Crests incomplete (petal-shaped flanges or filiform projections); furrow shallow or absent	SM	RG	Abliz et al. (2001)[c], Blaser (1975)[c], Kozakiewicz (1989)[c], this study (ex-type of *A. aridicola*, FIG. 3e)
A. brunneus (3)	−	−	−	−	8.5–10(10.5)	Crests very low, irregular, incomplete, or absent; furrow shallow	SM, RGE[e]	RG	Kozakiewicz (1989)[c]
A. chavelieri (5)	+	+	+	+	4–5	Crests prominent, flexuous; furrow absent	SM	RG	Butinar et al. (2005), Gravesen et al. (1994), Hong et al. (2011), de Hoog et al. (2009)[c], Kozakiewicz (1989)[c], Tzean et al. (1990)
A. cibarius (3)	−	−	+/−[d]	+	3.5–5(5.5)	Crests low, sometimes irregular or incomplete, petal-shaped; furrow shallow	SM, RGE	RG	Hong et al. (2012)[c], this study (FIG. 3k)
A. costiformis (2)	+	+	+	+	6–7	Crests low, irregular; furrow V-shaped	RG	SM	This study[c] (FIG. 3b)
A. cristatus (1)	+	+	+	+	4.5–5.5(6)	Crests prominent; furrow absent	RG	SM	Abliz et al. (2001), Kozakiewicz (1989)[c], Tzean et al. (1990)
A. glaucus (4)	−	−	−	−	6–7.5(8.5)	Crests absent or very low; furrow shallow to V-shaped	SM, RGE	RG	Butinar et al. (2005), Kozakiewicz (1989)[c], Tzean et al. (1990)
A. intermedius (5)	+	+	+	+	3–4.5	Crests prominent; furrow absent	RG	SM	Blaser (1975)[c], Kozakiewicz (1989)[c]
A. leucocarpus (1)	−	−	+	+	4.5–6	Crests prominent, flexuous; furrow absent or shallow	SM	RG	Kozakiewicz (1989)[c]
A. montevidensis (10)	+	+	+	+	4–5	Crests low, irregular; furrow V-shaped	RG	RG	Butinar et al. (2005), Hong et al. (2011), Klich (2002), Kozakiewicz (1989)[c], Tzean et al. (1990), this study (atypical isolate CCF 4248, FIG. 4e)
A. neocarnoyi (1)	−	−	−	−	6.5–8.5	Rounded, trace of a furrow	SM	RG	Kozakiewicz (1989)[c]
A. niveoglaucus (6)	−	−	−	−	6.5–8(8.5)	Crests low, often incomplete and consisting of short finger-like projections, or absent; furrow shallow to V-shaped	SM, RGE	RG	Kozakiewicz (1989)[c], this study (ex-type of *A. parviverruculosus*, FIG. 3h)
A. proliferans (9)	−	−	−	+/−	4.5–6(6.5)	Crests absent; furrow shallow	SM	RG	Blaser (1975)[f], Butinar et al. (2005) [g], Klich (2002)[h], this study (isolate CCF 4096, FIG. 6f)
A. pseudoglaucus (10)	−	+/−	+	+	(4)4.5–5.5(6)	Counded or flattened; trace of a furrow	SM	RG	Butinar et al. (2005), Hong et al. (2011), Kozakiewicz (1989)[c], Tzean et al. (1990)

TABLE II. Continued

Species (No. of isolates examined)	37 C, 7 d				Ascospores[a]			Surface of conidia[b]	SEM of ascospores [c]
	CY20S	M40Y	M60Y	M70Y	Body (long axis, µm)	Equatorial region	Ornamentation[b]		
A. ruber (7)	−	−	+	+	(4.5)5–6(7)	Crests absent; furrow shallow to V-shaped	SM	RG	Butinar et al. (2005), Gravesen et al. (1994), Hong et al. (2011), Kozakiewicz (1989)[c], Tzean et al. (1990), this study (ex-type of *A. tuberculatus*, FIG. 4b)
A. tonophilus (1)	−	−	+/−	+	(4.5)5–6	Crests absent; furrow shallow or only a trace of furrow present	SM	RG	Hong et al. (2011), Kong and Qi (1995c)
A. xerophilus (2)	−	−	+/−	+/−	5–6.5(7)	Crests very low or absent; furrow shallow	RGE, R	SM	Kozakiewicz (1989)[c], Samson and Mouchacca (1975)[c]
A. taklimakanensis[i]					7–8	Incomplete crests (petal-shaped)	RG	SM	Abliz et al. (2001)[c]

[a] Dimensions based on at least 30 ascospores for each isolate; morphological ascospore features determined in this study using light microscopy.

[b] The ornamentation of ascospores and conidia was classified as smooth (SM), roughened (RG), or for ascospores, roughened in the area neighboring the equatorial region but elsewhere smooth (RGE).

[c] Type strain.

[d] Growth not consistent among isolates.

[e] Both ornamentation types are present.

[f] Published as *E. acutum*.

[g] Published as *E. halotolerans*.

[h] Published as *E. herbariorum*.

[i] Data given by Abliz et al. (2001); the body of ascospores from holotype examined in this study are 4.5–5.5 µm and resembled that of *A. cristatus*.

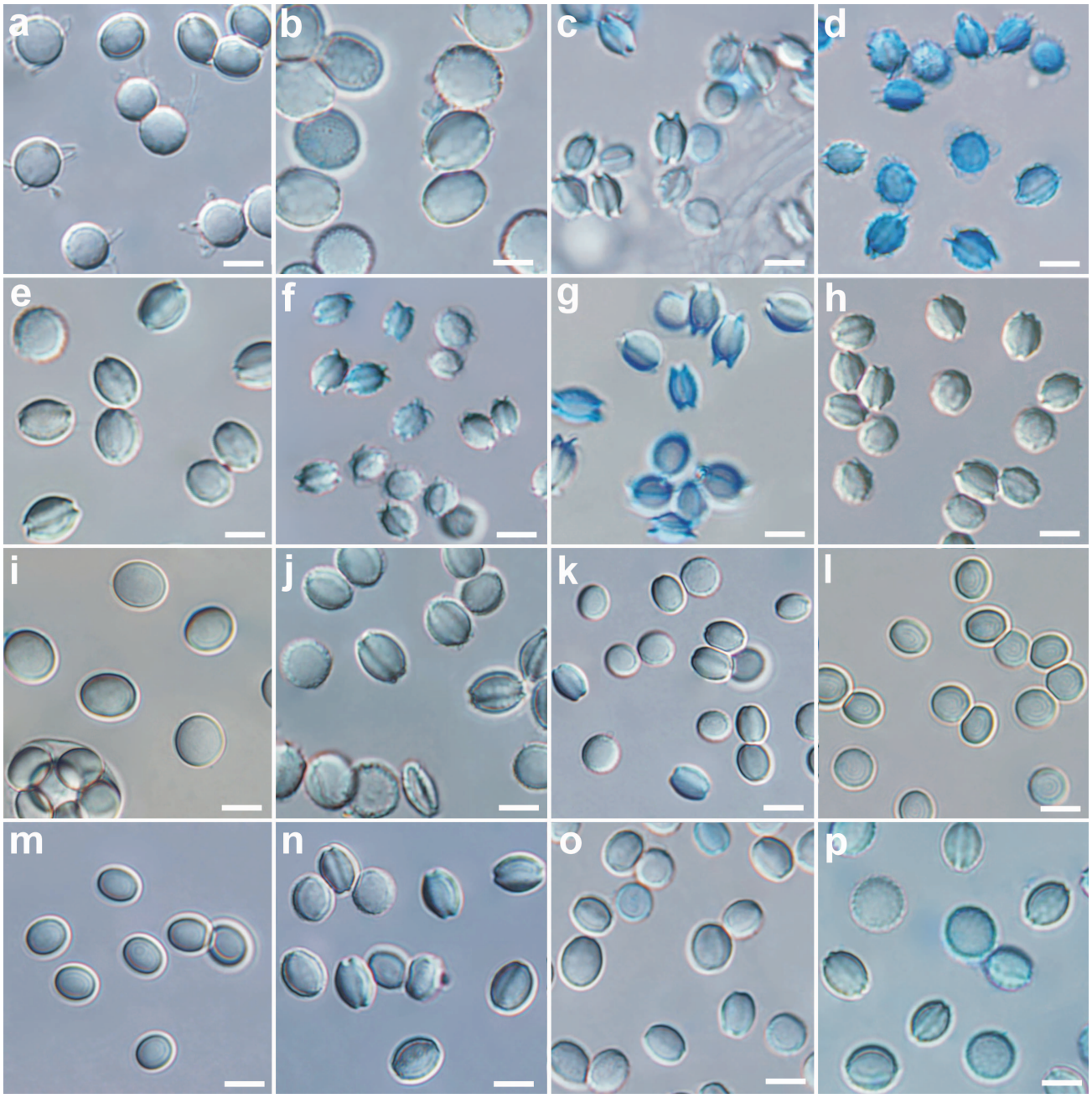

FIG. 2. Ascospores of species belonging to section *Aspergillus*, at same magnification. a. *A. appendiculatus* CBS 374.75 (ex type). b. *A. brunneus* NRRL 131 (ex type). c. *A. chevalieri* NRRL 78 (ex type). d. *A. cristatus* NRRL 4222 (ex type). e. *A. glaucus* NRRL 116 (ex type). f. *A. intermedius* NRRL 82 (ex type). g. *A. leucocarpus* NRRL 3497 (ex type). h. *A. montevidensis* NRRL 108 (ex type). i. *A. neocarnoyi* NRRL 126 (ex type). j. *A. niveoglaucus* NRRL 127 (ex type). k. *A. proliferans* CCF 4232. l. *A. pseudoglaucus* NRRL 40 (ex type). m. *A. pseudoglaucus* CBS 101747 (ex type of *A. fimicola*). n. *A. ruber* NRRL 52 (ex type). o. *A. tonophilus* NRRL 5124 (ex type). p. *A. xerophilus* NRRL 6131 (ex type). All Nomarski contrast. Scale bars, 5 µm. Ascospores of *A. cibarius* and *A. costiformis* are shown in FIG. 3.

(increase of the anamorph) occurred at a critical combination of temperature and water activity. For example, the optimal conditions for anamorph induction were 37 C on M60Y in *A. costiformis* and *A. cristatus* and 30 C on M70Y in *A. xerophilus* (FIG. 5). The diameter and shape of conidia are highly variable within species and generally not useful for species differentiation. The predominant shape of conidia is used here only as an additional characteristic for distinguishing *A. proliferans* and *A. ruber* (see below).

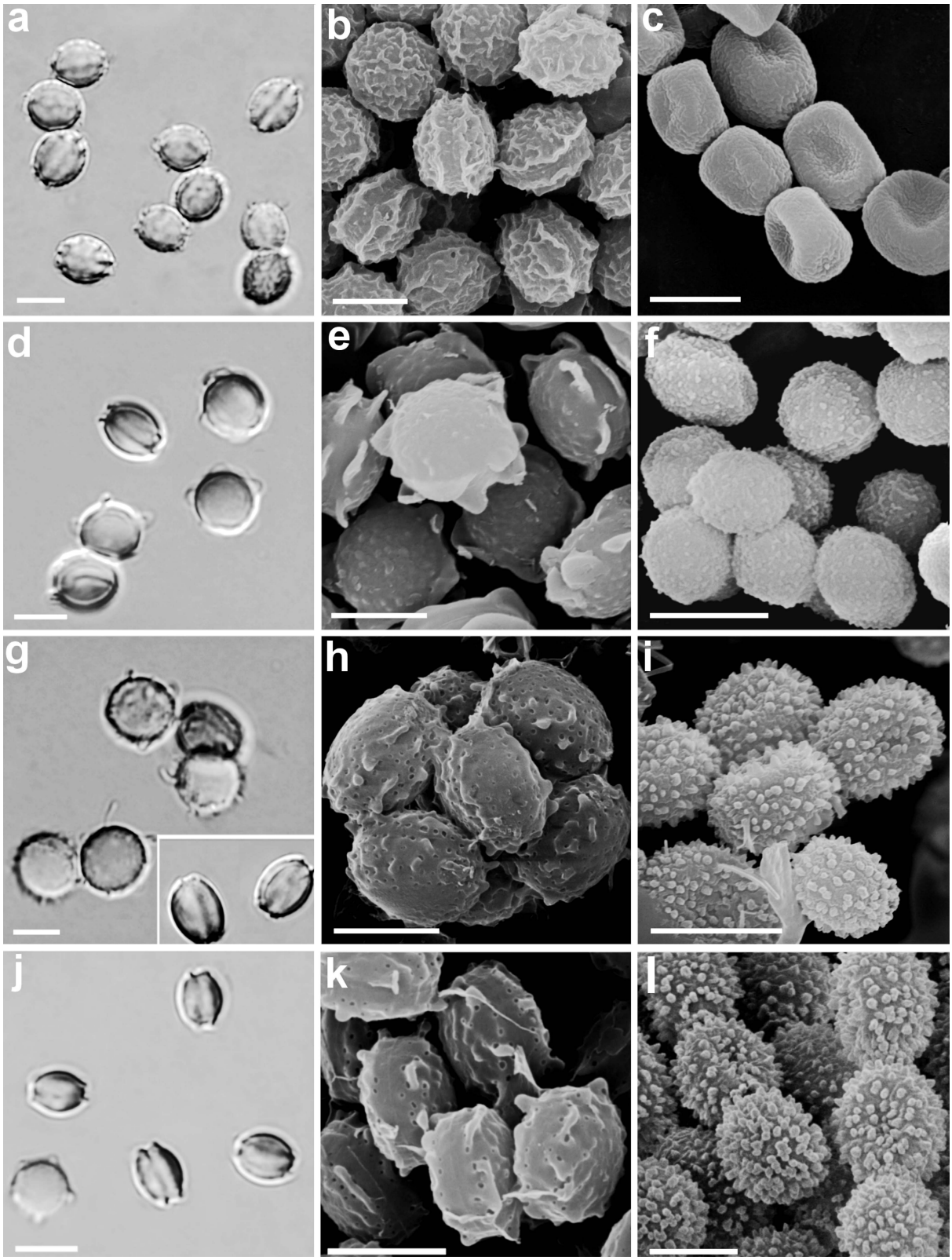

FIG. 3. Ascospores and conidia of some ex-type strains. a–c. *A. costiformis* CBS 101749 (ex type): a, b. ascospores, c. conidia. d–f. *A. appendiculatus* CBS 101746 (ex-type isolate of *A. aridicola*): d, e. ascospores , f. conidia. g–i. *A. niveoglaucus* CBS 101750 (ex-type isolate of *A. parviverruculosus*): g, h. ascospores, i. conidia. j–l. *A. cibarius* CCF 4098: j, k. ascospores, l. conidia. a, d, g, j. Nomarski contrast; remaining figures SEM. Bars = 5 μm.

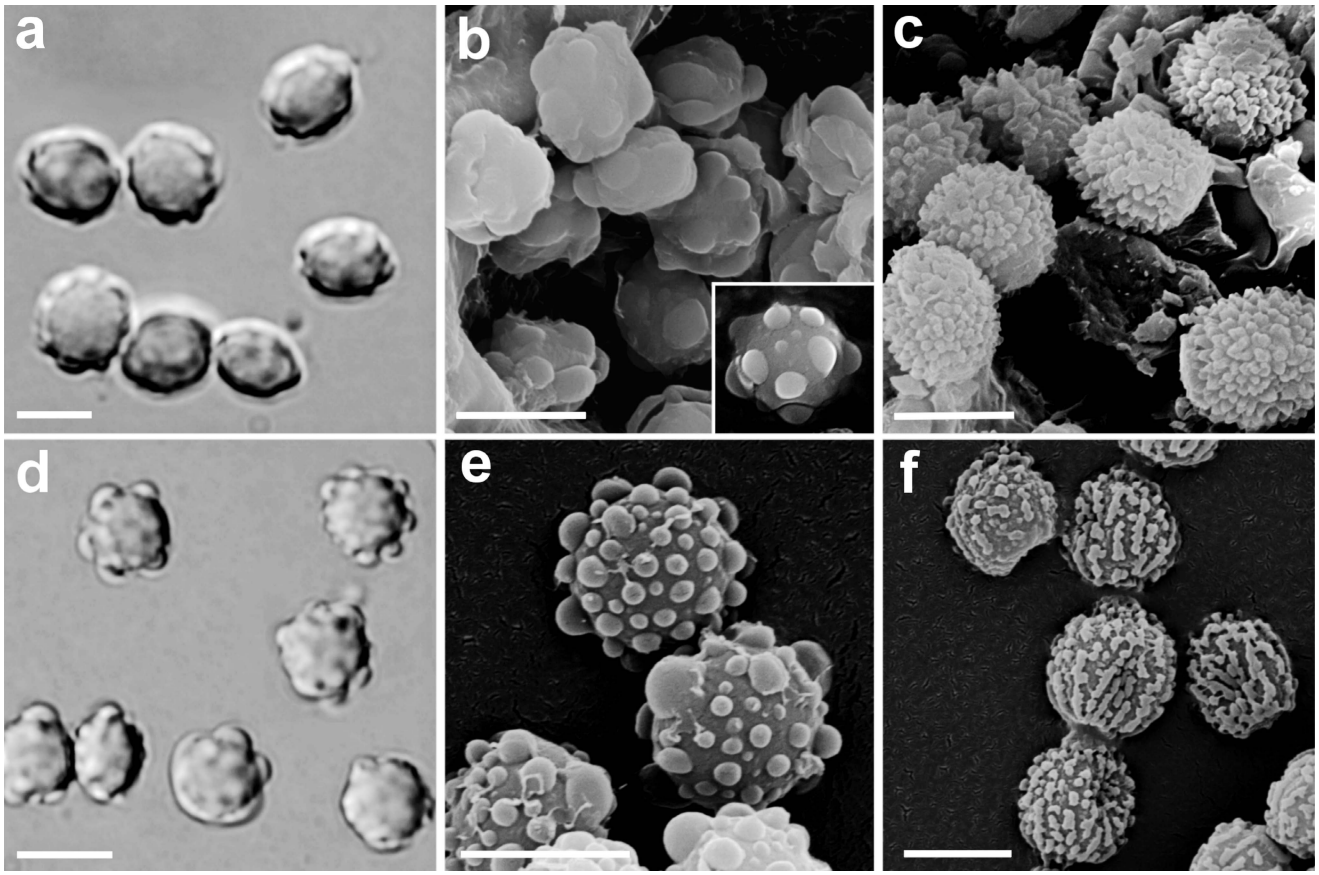

FIG. 4. Isolates with atypical morphology of ascospores. a–c. *A. ruber* CBS 101748 (ex-type isolate of *A. tuberculatus*): a, b. ascospores, c. conidia. d–f. *A. montevidensis* CCF 4248: d, e. ascospores, f. conidia. a, d Nomarski contrast; remaining figures SEM. Bars = 5 µm.

Species of uncertain position.—The phylogenetic position of *A. taklimakanensis* remained unresolved. The living culture of *A. taklimakanensis* is no longer available, and we examined only two plates of the dried herbarium specimens CBM-FA-876 treated with formaldehyde (both designated as holotype) (SUPPLEMENTARY FIG. 6). The morphology of the specimens resembled *A. cristatus* (ascospore body 4.5–5.5 µm, ascospores rough with distinct equatorial crests; conidia smooth to slightly echinulate) and differed from the original description of *A. taklimakanensis* with ascospore body 7–8 µm (Abliz et al. 2001). Because another fungal species possibly was deposited as the holotype and because multiple specimens were designated as a holotype, the species *A. taklimakanensis* is considered to be invalid.

TAXONOMY

The original description of *A. proliferans* based on strain NRRL 1908 lacked a teleomorph (Smith 1943), but the presence of hyphal coils and knots resembling cleistothecial initials suggests a defect in sexual development in that isolate. We identified eight cleistothecial strains that have an identical fingerprinting pattern with the ex-type NRRL 1908 (TABLE I) and form a clade strongly supported by phylogenetic analysis (FIG. 1). We therefore revise the description of *A. proliferans* to include the teleomorph.

Revised description of *Aspergillus proliferans* G. Sm. 1943, Trans. Brit. Mycol. Soc. 26:26. FIG. 6

Colonies on CY20S (25 C, 7 d) 15–22(–26) mm diam, 30–40 mm after 14 d, floccose to granulose due to abundant cleistothecia, red hyphae giving the colony vivid orange (F38400; Kelly 1964), strong orange (ED872D) to dark reddish orange (9E4732) appearance; reverse in red-brown shades, vivid reddish orange (E25822), deep orange yellow (C98500) or strong reddish brown (882D17). In ex type NRRL 1908 colonies brilliant greenish yellow (E9E450) in the center and moderate yellow green (8A9A5B) in marginal parts due to scattered pale green (8DA399) conidial heads and unpigmented vegetative hyphae; reverse deep yellow (AF8D13). Colonies on MEA (25 C, 7 d) 2–12 mm diam, 14–23 mm after 14 d, floccose,

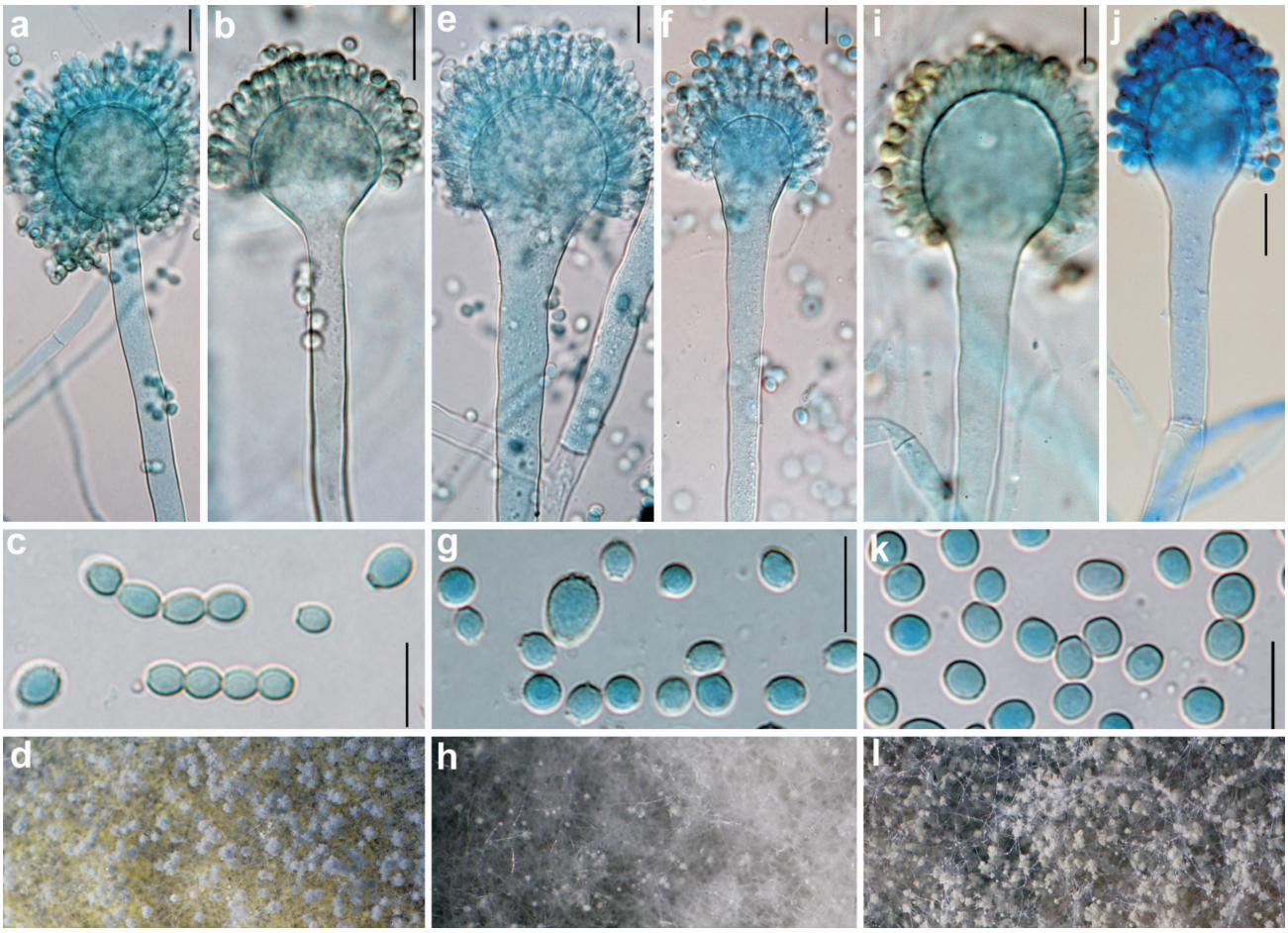

FIG. 5. Anamorphic state of *A. xerophilus*, *A. cristatus* and *A. costiformis* induced at 30 or 37 C on media with low water activity. a–d. *A. xerophilus* NRRL 6131 (ex type): a, b. conidiophores, c. conidia, d. conidial heads on M70Y at 30 C. e–h. *A. cristatus* NRRL 4222 (ex type): e, f. conidiophores, g. conidia, h. conidial heads on M60Yat 37 C. i–l. *A. costiformis* CBS 101749 (ex type): i, j. conidiophores, k. conidia, l. conidial heads on M60Y at 37 C. Bars = 10 µm.

colony color variable, most commonly moderate orange (D99058) to brownish orange (AE6938), in other strains pale greenish yellow (EBE8A4) or light yellow (F8DE7E), red-brown soluble pigment produced by some strains, reverse brownish orange (AE6938) to deep reddish orange (AA381E), strong yellow (D4AF37) in NRRL 1908; cleistothecia formed by only some strains, often small and sterile; conidiophores having atypical morphology, with reduced vesicles or branching, or with phialides proliferating into secondary heads. No growth at 37 C on CY20S, M40Y and M60Y after 7 d.

On CY20S, vegetative hyphae smooth, 2–4 µm diam, hyaline, later becoming encrusted, yellow or red to red-brown. Cleistothecia globose, yellow, naked, 80–200 µm diam; peridial wall consisting of one layer of yellow flattened cells; asci eight-spored, globose, ellipsoidal or pyriform, maturing after 14 d cultivation, 10.5–15(–16) × 9.3–11.8(–12.5) µm; ascospores hyaline to faintly yellow, lenticular, ascospore body 4.5–6(–6.5) × 3.7–5 µm, equatorial furrow mostly apparent but shallow, smooth under light microscope but with low tubercules and ribs when observed with SEM. Conidial heads loosely radiate to radiate, uniseriate; stipes smooth, hyaline or brown, nonseptate or with occasional septa, broadening toward the vesicle, usually 250–750 µm but up to 1000 µm long, 4.7–12.3(–14) µm wide in the middle third; vesicles globose, subglobose, ellipsoidal or clavate, 10–33.5 µm diam; phialides flask shaped, 6.5–10 × 3–5 µm, covering the upper half of the vesicle to entire surface; conidia globose to subglobose, echinulate, 3.7–7.2 µm.

Aspergillus proliferans often forms a significant number of short, reduced conidiophores (abundantly present particularly in isolates NRRL 1908, NRRL 71) with a few phialides that are commonly swollen and cover the end of the stipe without apparent vesicle or with only slightly swollen end. Globose conidia of *A. proliferans* can attain up to 15 µm diam, and such large conidia in particular are produced by reduced conidiophores.

FIG. 6. *Aspergillus proliferans* CCF 4096 (= NRRL 62482). a. conidiophore. b. colonies on MEA at 25 C after 21 d. c. colonies on CY20S at 25 C after 21 d. d. conidial heads and cleistothecia on CY20S. e. asci. f, g. ascospores. h. conidiophore. i–j. conidia. f, i = SEM. Bars: a = 50 µm, e–j = 5 µm.

Depending on the isolate, *A. proliferans* shows similarity in colony morphology on CY20S at 25 C to *A. glaucus*, *A. niveoglaucus*, *A. ruber* and *A. cibarius*. *Aspergillus glaucus* and *A. niveoglaucus* have larger ascospores than *A. proliferans*. Ascospores of *A. cibarius* have obvious crests. *Aspergillus ruber* but not *A. proliferans* is able to grow on M60Y at 37 C. Conidia of *A. ruber* and *A. cibarius* are usually ellipsoidal in contrast to globose conidia of *A. proliferans*.

KEY TO SPECIES

Features needed for identification.—Colony diameter on MEA and CY20S after 7 d at 25 C and abundance of conidial heads; ability to grow on CY20S and M60Y at 37 C after 7 d; color of cleistothecia; microscopic features (as viewed with the light microscope): ascospore size (body in long axis), presence of equatorial furrow, ridges or appendages, and ornamentation; ornamentation of conidia.

1a. cleistothecia in shades of yellow and orange 2
1b. cleistothecia white 16
2a. growth at 37 C on CY20S after 7 d 3
2b. no growth on CY20S at 37 C after 7 d 7
3a. conidial heads abundant on media with 20% (w/v) sucrose at 25 C 4
3b. conidial heads not present or extremely rare on media with 20% (w/v) sucrose at 25 C 6

4a. conidia smooth-walled . . . . . ***A. intermedius***
4b. conidia roughened 5
5a. ascospores smooth . . . . . ***A. chevalieri***
5b. ascospores distinctly roughened . . . ***A. montevidensis***
6a. ascospore bodies 6–7 µm . . . . . ***A. costiformis***
6b. ascospore bodies 4.5–5.5 µm . . . . . ***A. cristatus***
7a. ascospore body commonly 9–10 µm diam. . . . . ***A. brunneus***
7b. ascospore body smaller 8
8a. colonies on CY20S at 25 C lemon yellow; no growth on MEA at 25 C . . . . . ***A. tonophilus***
8b. Not as above 9
9a. conidia smooth-walled . . . . . ***A. xerophilus***
9b. conidia roughened 10
10a. ascospores predominantly with equatorial region rounded or flattened and without furrows and crests 11
10b. equatorial region otherwise (roughened, with crests, definite furrows, appendages) 12
11a. good growth (13–20 mm at 25 C after 7 d) and sporulation on MEA; ascospore body 4.5–5.5 µm . . . . . ***A. pseudoglaucus***
11b. growth on MEA 25 C extremely restricted (0–3 mm after 7 d), without sporulation; ascospore body 6.5–8.5 µm . . . . . ***A. neocarnoyi***
12a. ascospore body usually does not exceed 5 µm diam . . . . . ***A. cibarius***
12b. ascospore body usually exceeds 5 µm diam . . . 13
13a. equatorial crests incomplete, consisted of petal-shaped flanges or filiform projections (commonly longer than 2 µm); ascospore body 5–7 µm . . . . . ***A. appendiculatus***
13b. Not as above 14
14a. ascospore body mostly larger than 6 µm diam . . . . . ***A. glaucus*** and ***A. niveoglaucus***[a]
14b. ascospore body predominantly <6 µm diam . . . 15
15a. mature conidia predominantly globose, colony diam after 7 d on CY20S at 25 C <30 mm; no growth on M60Y at 37 C . . . . . ***A. proliferans***
15b. mature conidia predominantly ellipsoidal, colony diameter after 7 d on CY20S at 25 C >30 mm diam; growth on M60Y at 37 C . . . . . ***A. ruber***
16a. no growth on media with 20% (w/v) sucrose at 25 C . . . . . ***A. halophilicus*** (section *Restricti*)
16b. good growth on CY20S at 25 C (>20 mm diam) . . . . . ***A. leucocarpus***

DISCUSSION

Different approaches have been applied to the taxonomy of section *Aspergillus*. Raper and Fennell (1965) used light microscopy together with macromorphology of colonies. Kozakiewicz (1989) classified species using SEM of conidia and ascospores. Blaser (1975) implemented physiological characters in the taxonomy of the section. These species concepts resulted in conflicting taxonomy. DNA sequence data provided by Peterson (2000, 2008) helped to elucidate the intraspecific variability and objectively classify the species. This study revises section *Aspergillus* with all above-mentioned approaches, resulting in the recognition of 17 species.

Sequence-based identification.—The ID region showed the lowest variability among amplified loci and contained few informative positions; therefore this locus was not used for the combined phylogenetic analysis (FIG. 1). Only eight species had unique ID regions. However, analysis of the ID region is presented here (SUPPLEMENTARY FIG. 1) because of interest in bar-coding fungi. It has been shown that particular ITS genotypes do not uniquely identify species within sections of *Aspergillus* (Balajee et al. 2007, Jurjevic et al. 2012, Nováková et al. 2012, Hubka et al. 2012b, Peterson 2012) and use of more informative loci or multiple loci is necessary for exact species determination. The most suitable loci for identification of species in section *Aspergillus* in this study were *caM* and *RPB2*, which were able to uniquely determine all 17 species (SUPPLEMENTARY FIGS. 2, 3).

Phenotypic markers and variability.—The relatively frequent occurrence of isolates with abnormalities in ascomata formation (ex-type of *A. proliferans* NRRL 1908, ex-type of *A. athecius* NRRL 5000), colony color (ex-type of *A. niveoglaucus* NRRL 127, ex-type of *A. heterocaryoticus* NRRL A-13891), development of ascospores (ex-type of *A. tuberculatus* CBS 101748; *A. montevidensis* CCF 4248; see FIG. 4) or ornamentation of conidia (ex-type of *A. glaber* CBS 379.75, ex-type of *A. heterocaryoticus* NRRL A-13891, ex-type of *A. spiculosus* CBS 377.75) resulted in the description of a large number of species that in fact do not represent separate biological species. The genetic background for these changes in morphology is unknown, although the similarity in ascospore ornamentation among several atypical isolates representing different species (FIG. 4) suggests mutation in related genes. In species from other *Aspergillus* sections, conidial color mutants can be induced by in vitro UV mutagenesis, chemical treatment or agrobacterium. These changes in color often can be explained by a single mutation (Clutterbuck 1969, Cole et al. 1986, Jahn et al. 1997, Jackson et al. 2009). As was shown in *A. fumigatus*, altered conidial surface also might be the result of a single or few mutations (Jahn et al. 1997).

The macromorphology of colonies in this study was variable and correlated with cultivation conditions.

[a] White sporulating mutants have been reported in *A. niveoglaucus*. No reliable feature was found to differentiate green sporulating isolates of *A. glaucus* and *A. niveoglaucus*; sequences of all four loci examined unambiguously distinguish both species.

The abundance of cleistothecia and conidiophores and their proportions in culture depends strongly on water activity, nitrogen content and incubation temperature, and often shows large intraspecific variability (Blaser 1975, Raper and Fennell 1965, Butinar et al. 2005, Dovicicova 2010). Information about growth at 37 C without specification of cultivation medium (Sun and Qi 1994; Kong and Qi 1995a, b; Abliz et al. 2001) has only limited value because the ability of particular species to grow at 37 C depends on the water activity of the medium (TABLE II). The presence of orange- to red-pigmented hyphae has been an important characteristic for taxonomy. The red colonies were predominantly assigned to *A. ruber* and color was treated as a feature for distinguishing *A. ruber* from *A. glaucus* (Pitt 1985, Klich 2002). Some authors considered both species synonymous (Blaser 1975, Samson 1979, Domsch et al. 1980). As we showed here, red-pigmented hyphae are present in *A. ruber*, *A. glaucus* and several other species and cannot be used as a feature for differentiating these species.

The morphology of ascospores ranks among the most important morphological features in classification of taxa from section *Aspergillus*. In this study we used ascospore size in long axis, surface ornamentation and features of the equatorial region (FIG. 2, TABLE II) as important characters in species differentiation. Kozakiewicz (1989) classified taxa from section *Aspergillus* on the basis of ornamentation of conidia and ascospores observed by SEM; this resulted in recognition of a greater number of species compared with the species concepts proposed here. Nevertheless, SEM for taxonomy has value as a supplemental tool for species classification.

Based on ascospore size, phylogenetic analysis (distinguished by *benA*, *caM*, *RPB2* loci) and distinct fingerprint patterns, *A. glaucus* and *A. proliferans* are treated here as separate species. In past studies *A. proliferans* was likely missidentified or included within *A. glaucus* because the teleomorph of *A. proliferans* was not connected to the strictly anamorphic ex-type strain NRRL 1908 for *A. proliferans*. *Aspergillus glaucus*, as defined by some authors, has a wide range of ascospore sizes (e.g. 5–8 μm was listed by Pitt 1985 and 4–7.5 μm by Tzean et al. 1990), and it is possible that *A. glaucus* and *A. proliferans* were treated as one species. In contrast, Samson et al. (2004), Samson et al. (2010) and Klich (2002) listed ascospore size for *A. glaucus* as smaller than 6.5 μm and, according to the species concept presented here, these descriptions in fact may refer to *A. proliferans* (the type strain of *A. glaucus* was not included). Similarly, ascospore size of *A. acutus* (Blaser 1975), which has been treated as synonym of *A. glaucus* by Samson (1979), corresponds more closely to *A. proliferans*. Blaser's (1975) concept of *E. herbariorum* was based on strains of *A. proliferans* as well as *A. ruber*, most notably the strain CBS 530.65, later designated as type strain of *A. rubrobrunneus* by Samson and Gams (1985).

Ecology.—Species from section *Aspergillus* often cause spoilage of food. *Aspergillus montevidensis*, *A. pseudoglaucus*, *A. chevalieri*, *A. ruber*, *A. proliferans* and *A. glaucus* are the most significant species isolated from food. The occurrence of these species on food and food products was exhaustively elaborated by Pitt and Hocking (2009). However, taxonomic confusion exists because some authors have synonymized *A. ruber* with *A. glaucus* or *A. pseudoglaucus* with *A. glaucus*. Furthermore, *A. intermedius* was treated as synonymous with *A. cristatus* by Pitt (1985) and both mentioned species were probably also mistaken for *A. montevidensis*. Based on morphological characteristics, *A. cristatus* seems to be rare in contrast to *A. montevidensis* and *A. intermedius*. The colonies of *A. cristatus* on MEA and CY20S are almost brown and conidial heads are not present on these media. Colonies of *A. montevidensis* and *A. intermedius* are yellow to orange, and conidial heads are always present. Smooth conidia, small, roughened ascospores, and ability to grow at 37 C on all tested media (FIG. 2, TABLE II) unambiguously differentiate *A. intermedius* from all species in section *Aspergillus*. Recently described *A. cibarius* also has been isolated from food products, such as meju, black bean, bread and salami in Korea and the Netherlands (Hong et al. 2012). We examined two isolates of this species from human nails from Czech Republic and a third isolate from cave sediment (Sala de los Fantasmas, Spain). This species may be widely distributed in the environment and most probably has been confused with *A. ruber*. Another species important to the food industry is *A. niveoglaucus*. As mentioned above, green sporulating isolates are indistinguishable morphologically from *A. glaucus* and are probably commonly confused with it. Isolates of *A. niveoglaucus* from garlic and cereals were included in the dataset (TABLE I).

In our study none of the newly isolated strains belonging to *A. proliferans*/*A. glaucus*/*A. niveoglaucus* complex was *A. glaucus* (TABLE I), which is represented here by only authentic strains examined by Raper and Fennell (1965). *Aspergillus proliferans* is probably more widespread than *A. glaucus* and has been commonly misidentified. An additional isolate of *A. glaucus* identified by molecular methods was isolated from meju (Hong et al. 2011). Butinar et al. (2005) reported the isolation of a tentative new species from salterns, and they provisionally

designated the species as *E. halotolerans*. Based on deposited sequence data these isolates represent *A. proliferans* in the present study. Both *A. proliferans* and *A. glaucus/A. niveoglaucus* (based on ascospore size) were isolated from hypersaline waters of salterns together with *A. montevidensis*, *A. pseudoglaucus* and *A. ruber* (Butinar et al. 2005).

Human or animal infections due to members of section *Aspergillus* are rare. However, species are frequently isolated from clinical specimens collected from the surface of human body such as skin, nails and external auditory canal (Summerbell et al. 2005, Vennewald and Klemm 2010, Hubka et al. 2012a). This is probably due to the wide distribution of species in the environment and on substrates related to human activities. The clinical significance of these isolates is controversial and repeated sampling is necessary to verify their role as pathogens. The species associated with clinical specimens are also the most frequently isolated species in food products and indoor environment (Hubka et al. 2012a; TABLE I). Sporadic cases of invasive infection in man were mostly attributed to *A. glaucus* (Dreizen et al. 1985, Rippon 1988, Traboulsi et al. 2007), *A. montevidensis* (David et al. 1951, Young et al. 1972) and *A. chevalieri* (Naidu and Singh 1994).

Many section *Aspergillus* species are rarely isolated, and several of them (*A. leucocarpus*, *A. xerophilus*, *A. neocarnoyi*) are known only from the original taxonomic studies. *Aspergillus tonophilus* is known from binocular lens (Japan), soil (China) and meju (Korea) (Ohtsuki 1962, Kong and Qi 1995c, Hong et al. 2011). *Aspergillus appendiculatus* was regarded by Pitt (1985) as synonymous of *A. brunneus* and has been recorded from smoked sausage (Switzerland), sheep dung (China) and stored grain (Slovakia) (Blaser 1975, Kong and Qi 1995a, Dovicicova 2010). *Aspergillus costiformis* was known previously only from the ex-type isolate from moldy paper box (China); a second isolate was recorded recently from clinical material (Czech Republic) (Kong and Qi 1995b, Hubka et al. 2012a). Reliably identified isolates of *A. brunneus* are represented only by authentic strains examined by Raper and Fennell (1965) (see TABLE I).

Nomenclature: one name for one species.—Fungal names are subject to change in response to changes in the code of botanical nomenclature. This is true of pleomorphic fungi where rules were formulated for naming these fungi (Article 59, permitting the dual nomenclature of pleomorphic fungi). Pitt and Samson (1993) attempted to stabilize the names in the Trichocomaceae through the publication of a list of names in common usage (NCU), but the Tokyo Botanical Congress voted not to grant protection of the names (Greuter et al. 1994). In making the name changes herein we are responding to another revision of nomenclatural rules (Norvell 2011). Current nomenclature requires the use of only one name for a species, whereas previously two or more names could be applied to the same fungus. In anticipation of the new concept for naming pleomorphic fungi, our choice here is to take up the *Aspergillus* names over the *Eurotium* names in section *Aspergillus*. Several teleomorphic genera have been named that have *Aspergillus* anamorphs, but with only a few exceptions the *Aspergillus* species and their teleomorphs form a monophyletic clade (Peterson 2008, Houbraken and Samson 2011) and can be thought of as members of a single large genus. Arbitrarily choosing teleomorphic names would be a large inconvenience for the end users of the taxonomy. Medical mycologists are familiar with and use the name *A. fumigatus* for a human lung pathogen they work with, fungal geneticists are familiar with and use *A. nidulans* for the teleomorphic species some work with, plant pathologists and mycotoxicologists use the name *A. flavus* for an aflatoxin producing species in corn, peanuts and other crops and industrial mycologist are familiar with the many enzymes and chemicals produced by *A. niger*. The concept of naming teleomorph species as *Aspergillus* already has been applied in sections *Usti*, *Terrei*, *Aspergillus* and *Fumigati* (Samson et al. 2011a, b; Hong et al. 2012; Hubka et al. 2012b) and is also in agreement with the majority vote by the International Commission on *Penicillium* and *Aspergillus* (ICPA) in 2012. The treatment of *Eurotium* as a synonym of *Aspergillus* in itself does not prevent the use of Eurotiaceae and Eurotiales (Hawksworth 2012).

Following this precedent, we selected one name using the genus *Aspergillus* for each species in section *Aspergillus*. The priority rules were applied and the first validly published name for a species combined in *Aspergillus* is proposed as the correct name; all other names are listed as synonyms (TABLE III).

A somewhat similar concept designating all taxa across sections as *Aspergillus* species, irrespective of whether sexual state was known, was used by Raper and Fennell (1965) (see TABLE IV). The new botanical code enables the use of some well known names created by Thom and Church (1926) and Raper and Fennell (1965) who transferred some taxa into *Aspergillus* as holomorphs that were treated as illegitimate in the dual nomenclature system (Pitt 1985). The list of all accepted species and their synonyms along with designations of type and ex-type cultures is included herein (TABLE III).

TABLE III. List of current species names and common synonyms

Section *Aspergillus*	Type specimen/ex-type culture/MycoBank no.[a]
***Aspergillus appendiculatus* Blaser 1975, Sydowia 28:38.**	Holotype: ZT 8286
= *Eurotium appendiculatum* Blaser 1975	Ex-holotype culture: CBS 374.75 = IMI 278374 = FRR 2793 = JCM 1566
= *Aspergillus aridicola* H.Z. Kong et Z.T. Qi 1995	MycoBank: MB309209
= *Eurotium aridicola* H.Z. Kong et Z.T. Qi 1995	
***Aspergillus brunneus* Delacr. 1893, Bull. Soc. Mycol. Fr. 9:185.**	Lectotype designated here: FIG.III (Plate XI - not paginated) in Delacr., Bull. Soc. Mycol. Fr. 9: 184–188. 1909.[b]
= *Eurotium echinulatum* Delacr. 1893	Epitype designated here: Herb. IMI 211378
= *Aspergillus medius* R. Meissn. 1897	Ex-epitype culture: NRRL 131 = CBS 112.26 = ATCC 1021 = IMI 211378 = FRR 0131 = JCM 1570 = BCRC 33093 = UAMH 6592
= *Eurotium medium* R. Meissn. 1897	
= *Eurotium verruculosum* Vuill. 1918	
= *Aspergillus echinulatus* (Delacr.) Thom et Church 1926	MycoBank: MB204832
***Aspergillus chevalieri* L. Mangin 1909, Ann. Sci. Nat. Bot. 9:362.**	Lectotype designated here: FIG. 12 (As. χ) in L. Mangin, Ann. Sci. Nat. Bot. 9: 363. 1909.[b]
= *Eurotium chevalieri* L. Mangin 1909	Epitype designated here: Herb. IMI 211382
= *Aspergillus chevalieri* var. *multiascosporus* Nakaz. et al. 1934	Ex-epitype culture: NRRL 78 = CBS 522.65 = ATCC 16443 = FRR 2795 = IMI 211382 = JCM 1568 = UAMH 6583
= *Aspergillus allocotus* Bat. et H. Maia 1957	
= *Aspergillus equitis* Samson et W. Gams 1985	MycoBank: MB292839
***Aspergillus cibarius* S.B. Hong et Samson 2012, J. Micribiol. 50:713.**	Holotype: KACC 46346, culture preserved in a metabolically inactive state
	Ex-holotype culture: KACC 46346
	MycoBank: MB800861
***Aspergillus costiformis* H.Z. Kong et Z.T. Qi 1995, Acta Mycol. Sin. 14:10.**	Holotype: HMAS 62766
= *Eurotium costiforme* H.Z. Kong et Z.T. Qi 1995	Ex-holotype culture: CBS 101749 = CGMCC 3.4664 = AS 3.4664
	MycoBank: MB363444
***Aspergillus cristatus* Raper et Fennell 1965, Gen. *Aspergillus*:169.**	Neotype designated here: Herb. IMI 172280[c]
= *Eurotium cristatum* (Raper et Fennell) Malloch et Cain 1972	Ex-neotype culture: NRRL 4222 = CBS 123.53 = ATCC 16468 = IMI 172280 = FRR 1167 = JCM 1569 = BCRC 33090 = IHEM 5619
= *Aspergillus cristatellus* Kozak. 1989	MycoBank: MB326622
***Aspergillus glaucus* (L.) Link 1809, Mag. Ges. Naturf. Fr. Berl. 3:82.**	Neotype: Herb. DAOM 137960 (Gams and Samson 1985)
Basionym: *Mucor glaucus* L. 1753, Sp. pl., ed. 2: 1186.	Ex-neotype culture: NRRL 116 = CBS 516.65 = ATCC 16469 = IMI 211383 = FRR 0116 = JCM 1575 = BCRC 33091 = UAMH 6587
= *Mucor herbariorum* F.H. Wigg. 1780	MycoBank: MB161735
= *Eurotium herbariorum* (F.H. Wigg.) Link 1809	
= *Aspergillus herbariorum* (F.H. Wigg.) E. Fisch. 1897	
= *Eurotium herbariorum* var. *minor* L. Mangin 1909	
= *Aspergillus umbrosus* Bainier et Sartory 1912	
= *Aspergillus minor* (L. Mangin) Thom et Raper 1941	
= *Aspergillus testaceocolorans* Novobr. 1972	
= *Eurotium minus* (L. Mangin) Subram. 1972	
= *Eurotium testaceocolorans* Novobr. 1972	
= *Eurotium umbrosum* (Bainier et Sartory) Malloch et Cain 1972	
***Aspergillus intermedius* Blaser 1975, Sydowia 28:41.**	Neotype: Herb. IMI 89278 (Kozakiewicz 1989)[c]
= *Eurotium intermedium* Blaser 1975	Ex-neotype culture: NRRL 82 = CBS 523.65 = ATCC 16444 = IMI 89278 = FRR 0082 = JCM 1573 = BCRC 33088 = UAMH 6584 = CGMCC 3.4318
= *Aspergillus spiculosus* Blaser 1975	
= *Eurotium spiculosum* Blaser 1975	
	MycoBank: MB309226
***Aspergillus leucocarpus* Hadlok et Stolk 1969, Antonie Leeuwenhoek 35:9.**	Holotype: Herb. CBS 353.68
= *Eurotium leucocarpum* Hadlok et Stolk 1969	Ex-holotype culture: NRRL 3497 = CBS 353.68 = IMI 278375 = FRR 2799 = JCM 1574
	MycoBank: MB326642

TABLE III. Continued

Section *Aspergillus*	Type specimen/ex-type culture/MycoBank no.[a]
***Aspergillus montevidensis* Talice et J.A. Mackinnon 1931, Compt. Rend. Soc. Biol. 108:1007.** = *Aspergillus heterocaryoticus* C.M. Chr., L.C. López et C.R. Benj. 1965 = *Eurotium heterocaryoticum* C.M. Chr., L.C. López et C.R. Benj. 1965 = *Aspergillus vitis* Novobr. 1972 = *Eurotium montevidense* (Talice et J.A. Mackinnon) Malloch et Cain 1972 = *Eurotium vitis* Novobran. 1972 = *Aspergillus hollandicus* Samson et W. Gams 1985 = *Aspergillus vitis* var. *montevidensis* Kozak. 1989 = *Eurotium amstelodami* var. *montevidense* (Talice et J.A. Mackinnon) Kozak. 1989	Neotype designated here: BPI 884202, a dried specimen derived from the culture NRRL 108 Ex-neotype culture: NRRL 108 = CBS 491.65 = ATCC 10077 = IMI 172290 = FRR 0108 = JCM 1577 = BCRC 33131 = UAMH 6586 = CCRC 33131 = IHEM 3337 = CGMCC 3.4462 MycoBank: MB309231
***Aspergillus neocarnoyi* Kozak. 1989, Mycol. Pap. 161:61.** = *Eurotium carnoyi* Malloch et Cain 1972	Holotype: Herb. IMI 172279 Ex-holotype culture: NRRL 126 = CBS 471.65 = ATCC 16924 = IMI 172279 = FRR 0126 = JCM 1567 = BCRC 33095 = UAMH 6590 MycoBank: MB127756
***Aspergillus niveoglaucus* Thom et Raper 1941, Misc. Publ. U.S.D.A. 426:35.** (as ''*A. niveo-glaucus*'') = *Eurotium niveoglaucum* (Thom et Raper) Malloch et Cain 1972 = *Aspergillus glauconiveus* Samson et W. Gams 1985 = *Aspergillus parviverruculosus* H.Z. Kong et Z.T. Qi 1995 = *Eurotium parviverruculosum* H.Z. Kong et Z.T. Qi 1995	Neotype designated here: Herb. IMI 32050ii[c] Ex-neotype culture: NRRL 127 = CBS 114.27 = ATCC 10075 = IMI 32050 = FRR 0127 = JCM 1578 = BCRC 33096 = UAMH 6591 = CGMCC 3.4374 MycoBank: MB120985
***Aspergillus proliferans* G. Sm. 1943, Trans. Br. Mycol. Soc. 25:26.** = *Aspergillus acutus* Blaser 1975 = *Eurotium acutum* Blaser 1975	Lectotype designated here: Plate III (not paginated) in G. Sm., Trans. Br. Mycol. Soc. 25: 24–27. 1943.[b] Epitype designated here: Herb. IMI 16105iii Ex-type culture: NRRL 1908 = CBS 121.45 = ATCC 16922 = IMI 16105 = FRR 1908 = JCM 1729 = BCRC 33132 = CRC 33132 = IHEM 5219 = CGMCC 3.4465 MycoBank: MB284312
***Aspergillus pseudoglaucus* Blochwitz 1929, Ann. Mycol. 27:207.** = *Eurotium repens* de Bary 1870 = *Aspergillus scheelei* Bainier et Sartory 1912 = *Aspergillus glaber* Blaser 1975 = *Eurotium glabrum* Blaser 1975 = *Aspergillus glaucoaffinis* Samson et W. Gams 1985 = *Aspergillus reptans* Samson et W. Gams 1985 = *Eurotium pseudoglaucum* (Blochwitz) Malloch et Cain 1972 = *Eurotium repens* var. *pseudoglaucum* (Blochwitz) Kozak. 1989 = *Aspergillus fimicola* H.Z. Kong et Z.T. Qi 1995 = *Eurotium fimicola* H.Z. Kong et Z.T. Qi 1995	Neotype designated here: Herb. IMI 16122ii Ex-neotype culture: NRRL 40 = CBS 123.28 =ATCC 10066 = IMI 16122 = FRR 0042 = JCM 1579 = BCRC 33130 = UAMH 6581 = CCRC 33130 = IHEM 5618 MycoBank: MB275429
***Aspergillus ruber* (J. König, Spieck. et W. Bremer) Thom et Church 1926, The Aspergilli:112.** *Basionym: Eurotium rubrum* J. König, Spieck. et W. Bremer 1901, Z. Unters. Nahr. Genussm. 4: 726. = *? Aspergillus sejunctus* Bainier et Sartory 1911 = *Aspergillus athecius* Raper et Fennell 1965 = *Edyuillia athecia* (Raper et Fennell) Subram. 1972 = *Gymnoeurotium athecium* (Raper et Fennell) Malloch et Cain 1972 = *Eurotium athecium* (Raper et Fennell) Arx 1974 = *Aspergillus atheciellus* Samson et W. Gams 1985 = *Aspergillus rubrobrunneus* Samson et W. Gams 1985 = *Aspergillus tuberculatus* Z.T. Qi et Z.M. Sun 1994 = *Eurotium tuberculatum* Z.T. Qi et Z.M. Sun 1994	Neotype: Herb. CBS 530.65 (Samson and Gams 1985; for *E. rubrum*) Ex-neotype culture: NRRL 52 = CBS 530.65 = ATCC 16441 = IMI 211380 = JCM 22942 MycoBank: MB276893

TABLE III. Continued

Section *Aspergillus*	Type specimen/ex-type culture/MycoBank no.[a]
***Aspergillus tonophilus* Ohtsuki 1962, Bot. Mag. Tokyo 75:438.** = *Eurotium tonophilum* Ohtsuki 1962	Neotype: Herb. IMI 108299 (Pitt and Samson 2000) Ex-neotype culture: NRRL 5124 = CBS 405.65 = ATCC 16440 = IMI 108299 = FRR 1864 = JCM 1851 = BCRC 32879 = CGMCC 3.4468 MycoBank: MB326663
***Aspergillus xerophilus* Samson et Mouch. 1975, Antonie Leeuwenhoek 41:348.** = *Eurotium xerophilum* Samson et Mouch. 1975	Holotype: Herb. CBS 938.73 Ex-holotype culture: NRRL 6131 = CBS 938.73 = IMI 278377 = FRR 2804 = JCM 1583 MycoBank: MB309251
Section *Restricti*	
***Aspergillus halophilicus* C.M. Chr., Papav. et C.R. Benj. 1959, Mycologia 51:636.** = *Eurotium halophilicum* C.M. Chr., Papav. et C.R. Benj. 1959	Lectotype: BPI 566153; selected by Samson and Gams (1985) in accordance with Art. 40.2, Note 1[d] Ex-lectotype culture: NRRL 2739 = CBS 122.62 = ATCC 16401 = IMI 211802 = FRR 2739 = JCM 1571 = BCRC 33140 MycoBank: MB326633
Invalid and illegitimate names	
Aspergillus carnoyi Biourge ex Thom et Raper 1945, nom. inval. [Art. 39.1][d]	Published without Latin description.
Eurotium carnoyi (Thom et Raper) C.R. Benj. 1955, nom. inval. [Art. 39.1][d]	Basionym not validly published.
Aspergillus chevalieri (L. Mangin) Thom et Church 1926, nom. illeg. [Art. 52.1][d]	A later homonym of *A. chevalieri* L. Mangin 1909.
Aspergillus chevalieri var. *intermedius* Thom et Raper 1941, nom. inval. [Art. 39.1][d]	Published without Latin description.
Eurotium chevalieri var. *intermedium* (Thom et Raper) Malloch et Cain 1972, nom. inval. [Art. 39.1][d]	Basionym not validly published.
Aspergillus chevalieri var. *ruber* Sasaki 1950, nom. inval. [Art. 39.1][d]	Published without Latin description.
Aspergillus mangini Thom et Raper 1945, nom. illeg. [Art. 52.1][d]	A later homonym of *Aspergillus minor* (L. Mangin) Thom et Raper 1941
Aspergillus repens (de Bary) Fischer 1897, nom. illeg. [Art. 52.1][d]	A later homonym of *Aspergillus repens* (Corda) Sacc. 1882 referring to another species related or identical with *A. glaucus*.
Aspergillus taklimakanensis Abliz et Y. Horie 2001, nom. inval. = *Eurotium taklimakanense* Abliz et Y. Horie 2001, nom. inval.	A herbarium specimen CBM-FA-876 (holotype) include probably *A. cristatus* which morphology is in conflict with the protologue. Multiple specimens were selected as holotype. Ex-type culture is no longer available.
Names of uncertain position	
Aspergillus repens (Corda) Sacc. 1882, Michelia 2: 577. *Basionym*: *Aspergillus glaucus* var. *repens* Corda 1842, Icon. fung. 5:53.	Different from *E. repens* de Bary (see DISCUSSION).
Aspergillus amstelodami (L. Mangin) Thom et Church 1926, The Aspergilli:113. *Basionym*: *Eurotium amstelodami* L. Mangin 1909, Ann. Sci. Nat. Bot. 9: 360. = *Aspergillus repens* var. *amstelodami* (L. Mangin) Vuill. 1920	Different from *A. montevidensis* (see Discussion). The original description of *E. amstelodami* (Mangin 1909) was replaced by Thom and Raper (1941) with different incorrect description. Two subsequent neotypifications of *E. amstelodami* were also in error as they were in the conflict with the protologue of *E. amstelodami* L. Mangin (1909). [Art. 9.18][d] Lectotype designated here: Fig. 11 in L. Mangin, Ann. Sci. Nat. Bot. 9:360.

[a] Applies to the current species name in boldface.

[b] Original material represented by illustration is extant for the species; in this study, we designated a lectotype (iconotype) to supersede neotypes designated by Samson and Gams (1985) or Kozakiewicz (1989) and this ''neotypes'' are here designated as epitypes.

[c] Inappropriate type was designated by the original author (living culture), the neotypification of the species name should retain this well-known epithet.

[d] McNeil et al. (2012).

TABLE IV. Overview of the classifications of species from section *Aspergillus*; proposed epithets different from Raper and Fennell (1965) in boldface

Current study	Raper and Fennell (1965)	Samson and Gams (1985); teleomorph/anamorph	Pitt et al. (2000); teleomorph/anamorph
A. appendiculatus	—	*E. appendiculatum*/*A. appendiculatus*	*E. appendiculatum*/*A. appendiculatus*
A. brunneus	*A. echinulatus*	*E. echinulatum*/*A. brunneus*	*E. echinulatum*/*A. brunneus*
A. chevalieri	*A. chevalieri*	*E. chevalieri*/*A. equitis*	*E. chevalieri*/*A. chevalieri*
A. cibarius	—	—	—
A. costiformis	—	—	*E. costiforme*/*A. costiformis*
A. cristatus	*A. cristatus*	*E. cristatum*/*A. spiculosus*	*E. cristatum*/*A. cristatellus*
A. glaucus	*A. mangini*	*E. herbariorum*/*A. glaucus*	*E. herbariorum*/*A. glaucus*
A. intermedius	*A. chevalieri* var. *intermedius*	—	*E. intermedium*/*A. intermedius*
A. leucocarpus	—	*E. leucocarpum* / *A. leucocarpus*	*E. leucocarpum*/*A. leucocarpus*
A. montevidensis	*A. montevidensis*	—	—
A. neocarnoyi	*A. carnoyi*	*E. carnoyi*/*A. carnoyi*	*E. carnoyi*/*A. neocarnoyi*
A. niveoglaucus	*A. niveo-glaucus*	*E. niveoglaucum*/*A. glauconiveus*	*E. niveoglaucum*/*A. glauconiveus*
A. proliferans	*A. proliferans*	—/*A. proliferans*	—
A. pseudoglaucus	*A. pseudoglaucus*	*E. pseudoglaucum*/*A. glaucoaffinis*	*E. pseudoglaucum*/*A. glaucoaffinis*
A. ruber	*A. ruber*	*E. rubrum*/*A. rubrobrunneus*	*E. rubrum*/*A. rubrobrunneus*
A. tonophilus	*A. tonophilus*	*E. tonophilum*/*A. tonophilus*	*E. tonophilum*/*A. tonophilus*
A. xerophilus	—	*E. xerophilum*/*A. xerophilus*	*E. xerophilum*/*A. xerophilus*
Other accepted species:	*A. amstelodami*	*E. amstelodami*/*A. hollandicus*	*E. amstelodami*/*A. vitis*
	A. athecius	*Edyuillia athecia*/*A. atheciellus*	*E. athecium*/*A. atheciellus*
	—	*E. glabrum*/*A. glaber*	*E. glabrum*/*A. glaber*
	—	*E. heterocaryoticum*/*A. heterocaryoticus*	—
	A. medius	*E. medium*/*A. medius*	*E. medium*/*A. medius*
	A. repens	*E. repens*/*A. reptans*	*E. repens*/*A. reptans*
	A. umbrosus	—	—

Nomenclatural notes.—In a majority of cases, the most commonly used epithet is retained; other cases are discussed below. Only several section *Aspergillus* species epithets proposed here differ from those used by Raper and Fennell (1965) (TABLE IV). Delacroix (1893a, b) separately described anamorph and teleomorph of the same species as *A. brunneus* and *E. echinulatum*. Thom and Church (1926) used the name *A. echinulatus* for this species and, although widely used, it has always been a synonym of *A. brunneus*. Similarly, *A. mangini* (Thom and Raper 1945) has always been synonym of *A. glaucus*. Raper and Fennell (1965) considered the original descriptions of *A. glaucus* and *E. herbariorum* (Link 1809) as inadequate. Both species names were revised and neotypified (Malloch and Cain 1972, Gams and Samson 1985). *Eurotium carnoyi* Malloch and Cain was described first as *A. carnoyi* by Thom and Raper (1941). This description lacked the Latin diagnosis and is invalid. The name *A. neocarnoyi* proposed by Kozakiewicz (1989) is here considered the correct name for this species.

More complex problems exist in the species *E. rubrum*, *E. amstelodami* and *E. repens*. The earliest possible name that could correspond with the concept of *E. rubrum* is *A. sejunctus* (Bainier and Sartory 1911). However, the synonymy of *A. sejunctus* and *E. rubrum* was questionable in the view of Thom and Raper (1941). The lack of type material and difficulties of distinguishing *A. ruber* from *A. proliferans* by morphology (see revised description of *A. proliferans*) make the position of *A. sejunctus* even more uncertain. *Eurotium rubrum* later was transferred by Thom and Church (1926) into *Aspergillus* as the holomorphic species *A. ruber*, and we propose this name for use because there are no doubts about its phylogenetic position and the name is well known.

As noted by Pitt (1985), the ascospore morphology of the fungus described by Mangin (1909) as *E. amstelodami* differs from the current concept of *E. amstelodami*, and Magin's species is probably close to the current sense of *E. repens*. A similar description of Mangin's species under the name *A. amstelodami* also is listed by Thom and Church (1926). This description was replaced by Thom and Raper (1941) whose description fits the recent concept of *E. amstelodami* in having ascospores with prominent V-shaped equatorial furrow, broad irregular ridges and rough walls. This error was perpetuated (e.g. Raper and Fennell 1965, Blaser 1975) and both names, *E. amstelodami* and *A. amstelodami*, should be used no longer for this species.

The neotypification of *E. amstelodami* by Samson and Gams (1985) and Pitt and Samson (1993) was in error because they selected neotypes in conflict with protologue of *E. amstelodami* L. Mangin (1909). The description of *A. montevidensis* (Talice and Mackinnon 1931) is the first valid description of the species consistent with *E. amstelodami* sensu Thom and Raper (1941).

Eurotium repens was described by de Bary (1870). De Bary stated that his fungus is clearly different from that described by Corda (1842) under the name *A. glaucus* var. *repens* that is, according to size and globose shape of conidia, close to *A. glaucus*. Consequently the combination *A. repens* (Corda) Sacc. represents a fungus different from *E. repens* de Bary, and Corda's name cannot be treated as the basionym of *E. repens*. The combination *A. repens* (de Bary) Fischer (Fischer 1897) is illegitimate because the name *A. repens* was preoccupied by Saccardo's combination *A. repens* (Corda) Sacc. (Saccardo 1882). The first valid name identical to the concept of *E. repens* de Bary and combined in *Aspergillus* is *A. pseudoglaucus* Blochwitz (1929).

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