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The *Talaromyces pinophilus* species complex

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ABSTRACT

A sample of isolates from *Talaromyces pinophilus* (55 isolates) and closely related species (76 isolates) was sequenced at four loci, the data were analyzed using maximum likelihood analysis and the GCPSR. The isolates were subjected to growth studies on the recommended media for description of *Talaromyces* species. On the basis of the combined data, five new species were segregated out of *T. pinophilus* and placed in newly described species. The *T. pinophilus* species complex contains ten species. The three other new species, *Talaromyces argentinensis, T. californicus and T. louisianensis* were not a part of the *T. pinophilus* species complex but occurred in *Talaromyces* sect. *Talaromyces*. *T. argentinensis* produces a teleomorphic state and is phylogenetically and morphologically distinct from other *Talaromyces* species.
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1. Introduction

The number of species in *Talaromyces* sect. *Talaromyces* has rapidly increased in recent years (Raper and Thom, 1949; Pitt, 1979; Samson et al., 2011; Yilmaz et al., 2014; Barbosa et al., 2018; Cerullo et al., 2018; Jiang et al., 2018; Su and Niu, 2018; Varriale et al., 2018) leading to a new understanding of the diversity of the genus (Tsang et al., 2018). The treatments of the new species have not included *Talaromyces pinophilus* and closely related species with one exception (Jiang et al., 2018).

In addition to the inherent interest in knowing the diversity of these fungi, there are useful aspects of some *Talaromyces* species in plant protection (Abdel-Rahim and Abo-Elyousr, 2018), pharmacology (Salvatore et al., 2018; Xu et al., 2018) and an ongoing interest in human infection caused by *Talaromyces marneffei* (Castro-Lainez et al., 2018; Lei et al., 2018; Ellett et al., 2018).

Over the past several years we have been collecting *Talaromyces* isolates from different substrates including air from the built environment, maize seeds and various soils. We have worked on understanding the species identity and phylogenetic placement of the species (Peterson and Jurjević, 2013). Sequences were obtained for *BenA*, *CaM*, ITS, and *RPB2* gene sequences and were analyzed in light of the genealogical concordance phylogenetic species recognition model (GCPSR) (Taylor et al., 2000; Dettman et al., 2003). We amassed a sampling of *T. pinophilus* and other related *Talaromyces* spp., and provide our interpretation of the species in the *T. pinophilus* species complex.

2. Materials and methods

2.1. Cultures and growth

The cultures used here are available from the ARS Culture Collection (https://nrrl.ncaur.usda.gov), or the sequences may be downloaded from GenBank. The provenance of the individual isolates is given in Table 1. Culture were grown for diagnostics on CYA, MEAbl, CY20, PDA, OA, DG18, CYAS, and CREA. Media formulations followed Visagie et al. (2014) or Pitt (1979). Seven d old MEA cultures were used for microscopic examination. Bits of mycelium were teased apart in a small drop of lactic acid (85 %) and viewed using a Zeiss axioskope fitted with a Nikon D7100 camera, or a Leica 250 microscope and camera. Other preparations were made by touching a 15 × 5 mm piece of clear tape to the culture to lift spores and associated structures. Individual photographs were optimized for contrast and fitted into composite plates using Photoshop Elements 10.

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2.2. DNA techniques

Fungal isolates were grown in 125 mL flasks containing 25 mL of ME broth kept on a rotary shaker (200 rpm) at 25 °C. Mycelium was separated from medium using filter paper and a vacuum funnel. The mycelium was freeze-dried and was ground to a powder in a 1.5 mL centrifuge tube. DNA was isolated using the CTAB method (Peterson et al., 2015) or using a DNeasy Ultraclean Microbial kit (Qiagen). DNA was stored in distilled water at −20 °C until used.

Individual gene locus amplification used the primers and conditions listed by Peterson (2008). The loci were the partial β-tubulin sequence *BenA*, the partial calmodulin sequence *CaM*, the nuclear ITS1-5.8S rDNA-ITS2 repeat ITS, and the partial sequence of DNA dependent RNA polymerase *RPB2*. Sequencing the genes was accomplished using the techniques and reagents of Peterson et al. (2015). Amplicons were sequenced in both directions and were viewed and harmonize using Sequencher 5.1 (Gene Codes, Ann Arbor, MI).

Homologous sequences were aligned using MAFFT 7.217 (Katoh and Standley, 2013) and the alignments were analyzed using IQtree 1.6.10 (Nguyen et al., 2015), SH-alrt (Guindon et al., 2010) and ultrafast bootstrap (Hoang et al., 2018). Trees were viewed using TREEVIEW (Page, 1996) and redrawn for publication using CorelDraw. Sequences were deposited in GenBank and accession numbers are provided in Supplementary Table 1.

The data sets were analysed using the model finding function in IQtree (Kalyaanamoorthy et al., 2017). The data were partitioned essentially by separating the intron from the exon data for *CaM* and *BenA*, the ITS regions from the 5.8s sequence in the ITS locus and positions 1, 2, and 3 were treated as separate data sets in the data for the *RPB2* data. Best-fit model according to BIC: K2P + G4:part1(*BenA* intron), TNe + G4:part2 (*BenA* exon), TIM3e + G4:part3 (*CaM* intron), TNe + G4:part4 (*CaM* exon), TN + F + R2:part5 (ITS1 and ITS2), K2P:part6 (5.8s rRNA), TIM + F + R2:part7 (*RPB2* first position), K2P:part8 (*RPB2* second position), and TN + F + G4:part9 (*RPB2* third position). For Fig. 1 IQtree was run using partitions and the preferred models in an edge-linked analysis (Chernomor et al., 2016). The combined data set included 79 taxa, 2474 characters-sites and were partitioned into 9 rate categories. The ultrafast bootstrap and SH-alrt tests were run for 1000 iterations.

3. Results

3.1. Phylogeny of Talaromyces sect. Talaromyces

The phylogenetic relationships of the species from *Talaromyces* sect. *Talaromyces* were determined using IQtree, sequences produced in this study, and a set of sequences from GenBank. To reduce the number of species in the tree, *Talaromyces beijingensis* was chosen as a suitable outgroup on the basis on the initial analysis of all sect. *Talaromyces* spp. (tree not shown). The phylogenetic analysis was performed using the smaller group of species with multiple isolates of each (Fig. 1). The individual locus trees (Supplemental Figs. 1–4) do not have the resolution afforded by the composite tree and resolve little of the deeper branching but show the grouping of isolates into putative species.

3.2. Talaromyces pinophilus

The set of 55 *T. pinophilus* isolates spanned collection dates from 1928 to 2009 and geographically the isolates came from SE Asia and the Indian subcontinent, Africa, North America, South America, and Europe, with the greatest proportion coming from maize in the central U.S. The isolates are variable at the four loci sampled displaying 8 haplotypes at *BenA*, 19 haplotypes at *CaM*, 3 haplotypes at ITS, and 13 haplotypes at *RPB2* (Fig. 2, Supplementary Figs. 5–7). By comparison with the closely related *Talaromyces mae*, *Talaromyces adpressus* and *Talaromyces lentulus* there is a substantial gap between the intraspecific variation in *T. pinophilus* and the other three species. The *T. pinophilus* species complex includes the new species *T. soli, T. tumuli, T. malicola, T. domesticus* and *T. pratensis* and the described species *T. mae, T. lentulus, T. adpressus* and *T. pinophilus* sensu stricto.

3.3. GCPSR

At the *BT2* locus (Supplemental Fig. 1) *Talaromyces sayulitensis, T. lentulus, T. adpressus, T. tumuli, T. domesticus, T. soli, T. malicola, T. californicus, T. louisianensis and T. argentinensis* were supported in species clades. *Talaromyces pratensis* isolates formed two groups. Many groups were statistically supported but no statistically supported clade united these species with *T. pinophilus*. At the CaM locus (Supplemental Fig. 2) all of the isolates grouped into species clades with *T. sayulitensis* and *T. domesticus* distinct from the *T. pinophilus* clade and no statistically supported clade showing the relationship between the two. At the ITS locus (Supplemental Fig. 3) there was little statistical support but the isolates of *T. sayulitensis, T. domesticus, T. adpressus and T. californicus* all displayed a single ITS genotype. *Talaromyces tumuli, T. louisianensis, T. soli, T. pratensis* and *T. pinophilus* all showed mixed, sometimes overlapping ITS sequences. At the *RPB2* locus (Supplemental Fig. 4) clades that contain *T. soli, T. pratensis, T. lentulus, T. tumuli, T adprssus, T. sayulitensis, T. domesticus, T. pinophilus, T. mae* and *T. malicola* and those species are statistically part of a larger group defining the *T. pinophilus* clade. *Talaromyces californicus, T. louisianensis* and *T. argentinensis* isolates are united into species clades.

3.4. Other Talaromyces species

Talaromyces argentinensis, T. louisianensis and *T. californicus* are located in a clade that is distinct from *T. pinophilus* but is within the larger clade defined by *T. beijingensis* (Fig. 1). In addition to the previously mentioned species, *T. sayulitensis* was a common and abundant species, often isolated from maize. *Talaromyces domesticus* was separated from isolates of *T. sayulitensis* by small consistent differences. *Talaromyces fuscoviridis* and *Talaromyces veerkampii* were identified based on the sequence identity of the ex type isolate and the isolates used in this study.

Concordance of the gene trees was established from viewing the trees (Supplemental Figs. 1–4). Isolates assigned to a species were so assigned because of their placement into a branch with or without significant support. Only when the isolates were placed in the same branch of all three protein coding loci they were considered to be a species.

3.5. Taxonomy

Colony descriptions are made from colonies grown 7d at 25 °C except where noted.

Talaromyces pinophilus Mycobank MB560662. Fig. 3.

Medium dependent growth, in mm. CYA 16–31, MEA 37–45, PDA 38–43, CY20S 12–35, DG18 8–17, OA 30–40, CYAS 0–4, CREA 22–31.

Temperatures dependent growth in mm: CYA/MEA 20 °C 10–20/20–31; 30 °C 26–41/50–61; 35 °C 30–45/41–54; 37 °C 24–40/39–48. On CYA at 20 °C, resembles colony at 25 °C, at 30 °C, poor to moderate sporulation, conidial area deep green-blue gray

Table 1
Provenance of the isolates used in this study.

NRRL	Provenance
Talaromyces adpressus	
6014	USA, Georgia, isol ex peanut, *RJ Cole*, 1974.
62299	USA, Oklahoma, isol ex peanut, *P Jatala*, 1991.
62466	USA, Georgia, isol ex peanut, *BW Horn*, 2001.
Talaromyces argentinensis	
28750	Ghana, isol ex soil, 1950.
28758	Argentina, isol ex soil, *RW Jackson*, 1956.
Talaromyces californicus	
58168	USA, Calilfornia, isol ex air sampler, *Z Jurjevic*, April 2008.
58207	USA, Calilfornia, isol ex air sampler, *Z Jurjevic*, April 2008.
58221	USA, Calilfornia, isol ex air sampler, *Z Jurjevic*, April 2008.
58661	USA, Calilfornia, isol ex air sampler, *Z Jurjevic*, April 2008.
Talaromyces domesticus	
58121	USA, Pennsylvania, isol ex floor swab, *Z Jurjevic*, July 2008
62132	USA, New Mexico, isol ex untreated cotton cloth, *WD Gray*, 1953.
Talaromyces lentulus	
62119	Portugal, Canary Is., isol ex volcanic soil, *F Bustinza*, 1950.
62143	unknown provenance, *RD Goos*, 1959.
Talaromyces liani	
1009	derived from Biourge 368
1014	=1009
1015	=1009
1019	USA, Arizona, isol ignotae, *KD Butler*, 1936.
3380	China, isol ex soil, =CBS 225.66
28759	USA, Illinois, isol ex waste-water, *WB Cooke*, 1956
28771	USA, Illinois, isol ex amoniated corn, 1974
28778	Brazil, isol ex soil, *RW Jackson*, 1956.
28834	India, isol ignotae.
Talaromyces louisianensis	
35823	USA, Louisiana, isol ex air sample, *Z Jurjevic*, Sep 2007
35826	USA, California, isol ex air sampler, *Z Jurjevic*, Oct 2007
35928	USA, Louisiana, isol ex air sampler, *Z Jurjevic*, Feb 2008
58410	USA, New York, isol ex air sampler, *Z Jurjevic*, June 2008.
Talaromyces malicola	
3724	Italy, Milan, isol ex apple rhizosphere, *R. Locci*, 1967.
Talaromyces pinophilus	
1060	Malaysia, isol ex seed, *JR Weir*, 1928.
2126	USA, Maryland, isol ex mercury treated cloth, *WL White*, 1945.
3503	Papua New Guinea, isol ex radio, *M Downing*, 1953.
3647	USA, Maryland, isol ex mercury treated cloth, *WL White*, 1945.
5200	ex type isolate *Penicillium korosum*
5837	India, isol ignotae, *SM Batrabet*, 1973.
13016	USA, Texas, isol ex dung ball, *DT Wicklow*, 1982.
13037	Egypt, isol ex sugar cane baggasse, 1979
13038	Egypt, isol ex sugar cane baggasse, 1979
13039	Egypt, isol ex sugar cane baggasse, 1979
13040	Egypt, isol ex sugar cane baggasse, 1979
13041	Egypt, isol ex sugar cane baggasse, 1979
13042	Egypt, isol ex sugar cane baggasse, 1979
13043	Egypt, isol ex sugar cane baggasse, 1979
22961	USA, Illinois, isol ex *A. flavus* sclerotium, *DT Wicklow*, 1994.
25743	USA, Illinois, isol ex soil, *DT Wicklow*, 1996.
29068	India, *AK Sarbhoy*, 1975.
31483	Mexico, Chiapas, isol ex coffee borer feces, *F Infante*, 2001.
35251	USA, Colorado, isol ex house dust, *SP Abbott*, 2003.
58022	USA, NJ, isol ex air sampler, *Z Jurjevic*, May 2008.
58422	USA, Virgin Is., isol ex air sampler, *Z Jurjevic*, June 2008.
58691	USA, Illinois, isol ex corn, *DT Wicklow*, 2009
62103	New Guinea, isol ex cloth, *EA Kostopoulus*, 1944
62107	USA, Florida, isol ex nylon cloth on ground, *WH Weston*, 1946
62118	Ghana, isol ex soil, 1950.
62135	USA, Ohio, isol ex sewage scum, *WB Cooke*, 1954.
62136	India, isol ignotae, *BK Bakshi*, 1955.
62140	USA, Alabama, isol ignotae, *U Diener*, 1957.
62144	Peru, Clipperton Is., isol ex soil, 1959.
62145	Peru, Clipperton Is., isol ex soil, 1959.
62153	USA, Georgia, isol ignotae, *CR Jackson*, 1964.
62162	USA, Georgia, isol ex peanut, *RT Hanlin*, 1968.
62167	Canada, Quebec, isol ex buried electrical cables, 1969
62168	Canada, Quebec, isol ex buried electrical cables, 1969
62172	USA, isol ex wheat seed, *DI Fennell*, 1971.
62173	USA, isol ex wheat sample, *DI Fennell*, 1971.
62176	SE Asia, isol ex paper product, *GF Orr*, 1973.

(*continued on next page*)

Table 1 (*continued*)

NRRL	Provenance
62178	India, isol ignotae, *Kamal*, 1973
62182	USA, SC, isol ex corn, 1973.
62183	USA, SC, isol ex corn, *CW Hesseltine*, 1974
62195	USA, SC, isol ex corn, *CW Hesseltine*, 1974.
62197	India, isol ignotae, *KS Bhargana*, 1974.
62200	USA, Missouri, isol ex corn, *RJ Bothast*, 1974.
62201	USA, Missouri, isol ex corn, *RJ Bothast*, 1974.
62233	USA, NC, isol ex corn, *R Rogers*, 1978
62251	USA, Arizona, isol ex *Larea tridentata* seed, *GL Adams*, 1978.
62256	USA, Georgia, isol ex peanut soldier, *RJ Cole*, 1979.
62267	USA, Texas, isol ex beetle dung ball, *WT Chan*, 1981.
62275	USA, Texas, isol ex rodent burrow seed, *G Melaik*, 1982.
62281	Jamaica, isol ex corn, *D Johns*, 1984.
62282	Jamaica, isol ex corn, *D Johns*, 1984.
62285	USA, isol ex corn, *RF Vesonder*, 1988.
62287	USA, Oklahoma, isol ex wheat, *P Jatala*, 1991.
62288	USA, Oklahoma, isol ex peanut, *P Jatala*, 1991.
62297	USA, Georgia, isol ex *A. flavus* sclerotium, *DT Wicklow*, 1990.
62415	ex neotype isolate = CBS 631.66
62461	USA, Georgia, isol ex peanut seed, *BW Horn*, 1999.
Talaromyces pratensis	
13548	USA, NC, isol ex corn seed, *R Rogers*, 1978.
62126	USA, Ohio, isol ex river water, *WB Cooke*, 1952.
62170	ignotae, *WB Cooke*, 1969.
62240	USA, Illinois, isol ex *Bouteloua* seed, 1978.
Talaromyces sayulitensis	
1064	USA, Virginia, isol ex corn, *C Thom*, 1912, type isolate of *P. purpurogenum* var *rubrisclerotium*.
6420	USA, NC, isol ex corn, *DT Wicklow*, 1978.
25074	USA, Georgia, isol ex corn, *DT Wicklow*, 1995.
35430	USA, Illinois, isol ex corn, *DT Wicklow*, 2004.
35431	USA, Illinois, isol ex corn, *DT Wicklow*, 2004.
35432	USA, Illinois, isol ex corn, *DT Wicklow*, 2004.
58690	USA, Arizona, isol ex corn, *DT Wicklow*, 2009.
62120	USA, Colorado, isol ex soil, *JG Zoril*, 1950.
62139	Brazil, isol ex sandy soil, *RW Jackson*, 1956.
62166	USA, Georgia, isol ex corn, 1969.
62174	USA, Missouri, isol ex white corn, 1972.
62184	USA, SC, isol ex corn, *CW Hesseltine*, 1974.
62185	USA, SC, isol ex corn, *CW Hesseltine*, 1974.
62194	USA, SC, isol ex corn, *CW Hesseltine*, 1974.
62202	USA, SC, isol ex weavil bored corn seed, 1975.
62203	USA, SC, isol ex weavil bored corn seed, 1975.
62204	USA, SC, isol ex weavil bored corn seed, 1975.
62205	USA, SC, isol ex weavil bored corn seed, 1975.
62206	USA, SC, isol ex corn, 1975.
62220	USA, NC, isol ex corn, *R Rogers*, 1978.
62265	USA, Georgia, isol ex corn, *BW Horn*, 1981.
62266	USA, Georgia, isol ex corn, *BW Horn*, 1981.
62269	USA, Georgia, isol ex lodged corn, *BW Horn*, 1981.
62272	USA, Texas, isol ex seed from rodent burrow, *G. Melaik*, 1982
Talaromyces soli	
1768	Unknown, isol ex soil, *CW Hesseltine,* 1941.
62104	Nicaragua, isol ex soil, 1945.
62122	USA, Loiusiana, isol ignotae, *HH Luke*, 1952.
62142	USA, NH, isol ignotae, *RA Kilpatrick*, 1958.
62152	USA, Indiana, isol ex sand dune soil, RW Tuveson, 1963.
62160	USA, Indiana, *P Mislivec*, 1967.
62163	USA, Georgia, isol ignotae, *RT Hanlin*, 1968.
62165	USA, Michigan, isol ignotae, *G Rall*, 1969.
62171	USA, NC, Ignotae, isol *CS Hodges,* 1971.
62221	USA, NC, isol ex corn, *R. Rodgers*, Apr 1978.
62227	USA, NC, isol ex corn seed, *R Rogers*, 1978.
62237	USA, Illinois, isol ex *Andropogon* sp. seed, 1978.
62261	USA, Michigan, isol ex cow dung, *S Crabtree*, 1980.
62298	USA, Oklahoma, isol ex peanut seed, *P Jatala*, 1991.
62470	USA, Georgia, isol ex peanut seed, *BW Horn*, 2010.
Talaromyces tumuli	
6013	USA, Georgia, isol ignotae, *RJ Cole*, 1974.
62151	USA, Indiana, isol ex *Andropogon* sp. rhizosphere, *RW Tuveson*, 1963.
62459	USA, Georgia, isol ex peanut, *BW Horn*, 1999.
62469	USA, Georgia, isol ex peanut, *BW Horn*, 2010.
62471	USA, Georgia, isol ex peanut, *BW Horn*, 2010.
62693	USA, Georgia, isol ex peanut solder, *R J Cole*, Jan 1979.
Talaromyces veerkampii	
6095	Japan.
62286	USA, Oklahoma, isol ex wheat flour, *P Jatala*, 1991.

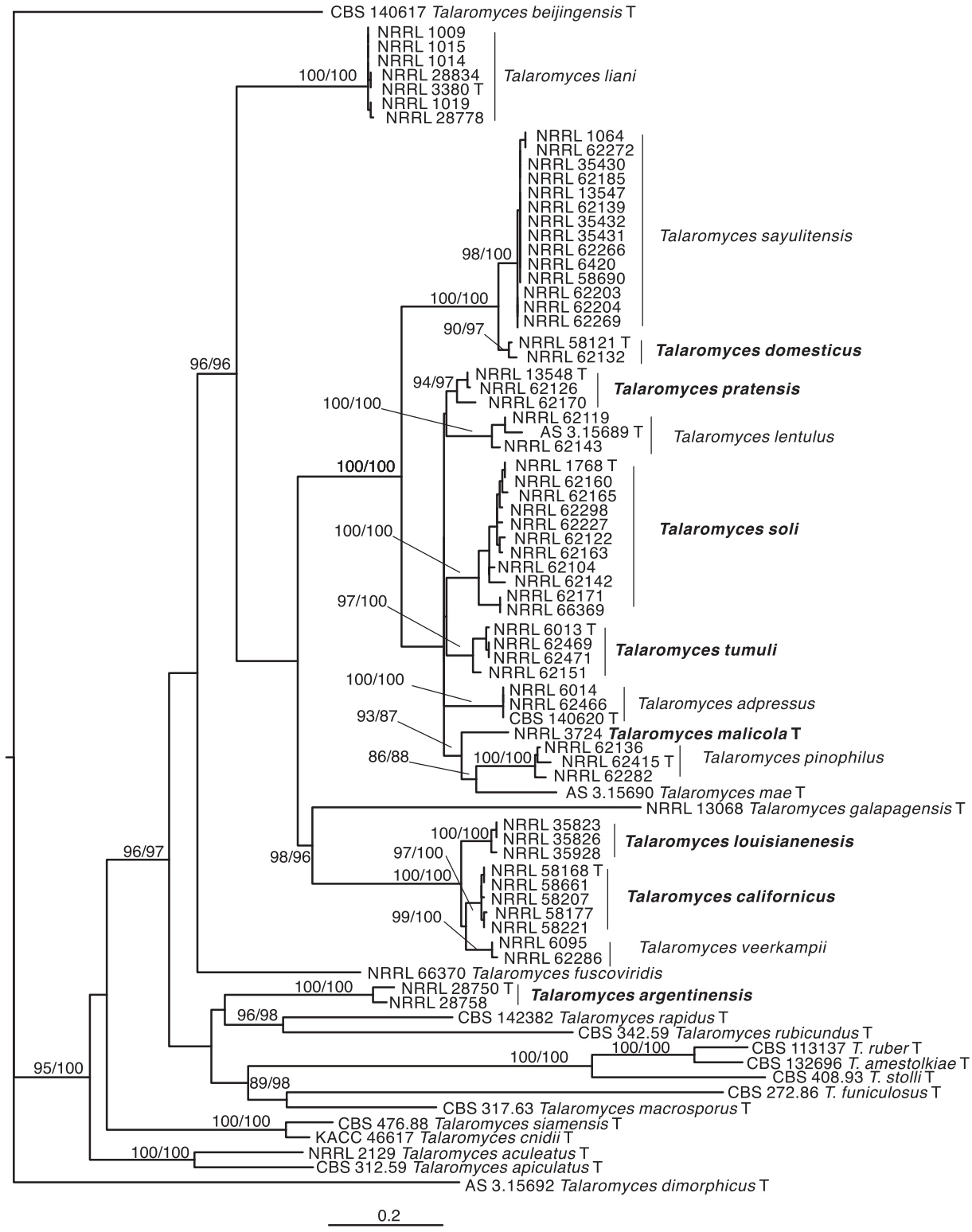

Fig. 1. Phylogram of part of section *Talaromyces* based on maximum likelihood analysis of concatenated *BenA*, *CaM* and *RPB2* and using multiple isolates of each species where possible. The polytomy of *T. soli, T. tumuli, T. adpressus, T. pinophilus, T. mae, T. pratensis, T. lentulus, T. domesticus, T. sayulitensis, T. malicola and T. mae* make the informal group the *T. pinophilus* species complex. Numbers on nodes are SH-alrt value/ultrafast bootstrap values greater than 80 % SH-alrt and greater than 95 % UF bootstrap.

(R48; Ridgway, 1912), resembles colony at 25, at 35 and 37 °C, resembles colony at 25 °C; On MEA at 20, 30, 35 and 37 °C resembles colony at 25 °C.

CYA colonies floccose to funiculose, mycelium white, to amber yellow, primuline yellow (R16) near yellow ocher (R15), subsurface at margins ca 2–5 mm, rising ca 3–4 mm, occasionally lightly radially sulcate, poor sporulation, inconspicuous, exudate when present clear to mustard yellow, abundant to sparse, no soluble pigments, reverse cream-buff to chamois (R30), yellow ocher, Mars yellow (R3), occasionally with deep red shades; **MEA**

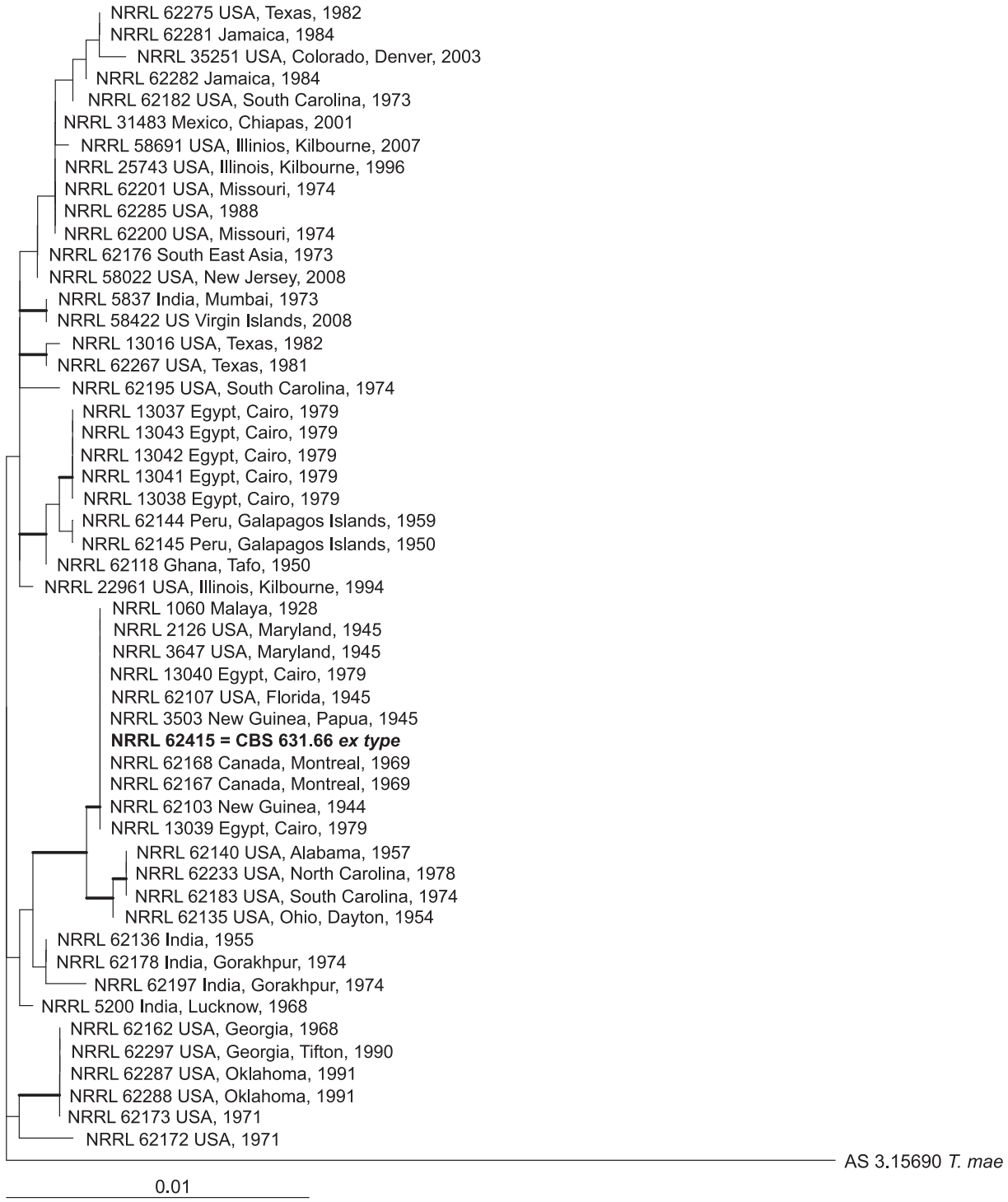

Fig. 2. Phylogram of *Talaromyces pinophilus*, using *T. mae* as outgroup and based on maximum likelihood analysis of *BenA, CaM,* ITS and *RPB2* sequences concatenated into a single file. Nodes supported by >80 % SH-alrt and >95 % UF bootstrap value are shown in bold lines.

colonies plane, floccose to funiculose, moderate sporulation, conidial area artemisia green (R47) to deep green-blue gray (R48), commonly overgrown with mycelium white to antimony yellow near yellow ocher (R15), amber yellow (R16), occasionally with pale vinaceous pink shades, occasionally radially sulcate, exudate when present, clear to orange-yellow, embedded in the mycelium, no soluble pigments, reverse apricot orange (R14), antimony yellow near yellow ocher (R15), to colonial buff (R30); **PDA** colonies floccose to funiculose, mycelium white to antimony yellow (R15), amber yellow, mustard yellow (R16), occasionally with pale vinaceous pink shades, occasionally radially sulcate, poor to moderate sporulation, conidial area artemisia green (R47) to deep green-blue gray (R48), exudate when present capucine yellow to clear, no soluble pigments, reverse cadmium orange to pale orange yellow (R4), antimony yellow (R15), colonial buff to crème-buff (R30); **CY20S** colonies low, mycelium white, with pale

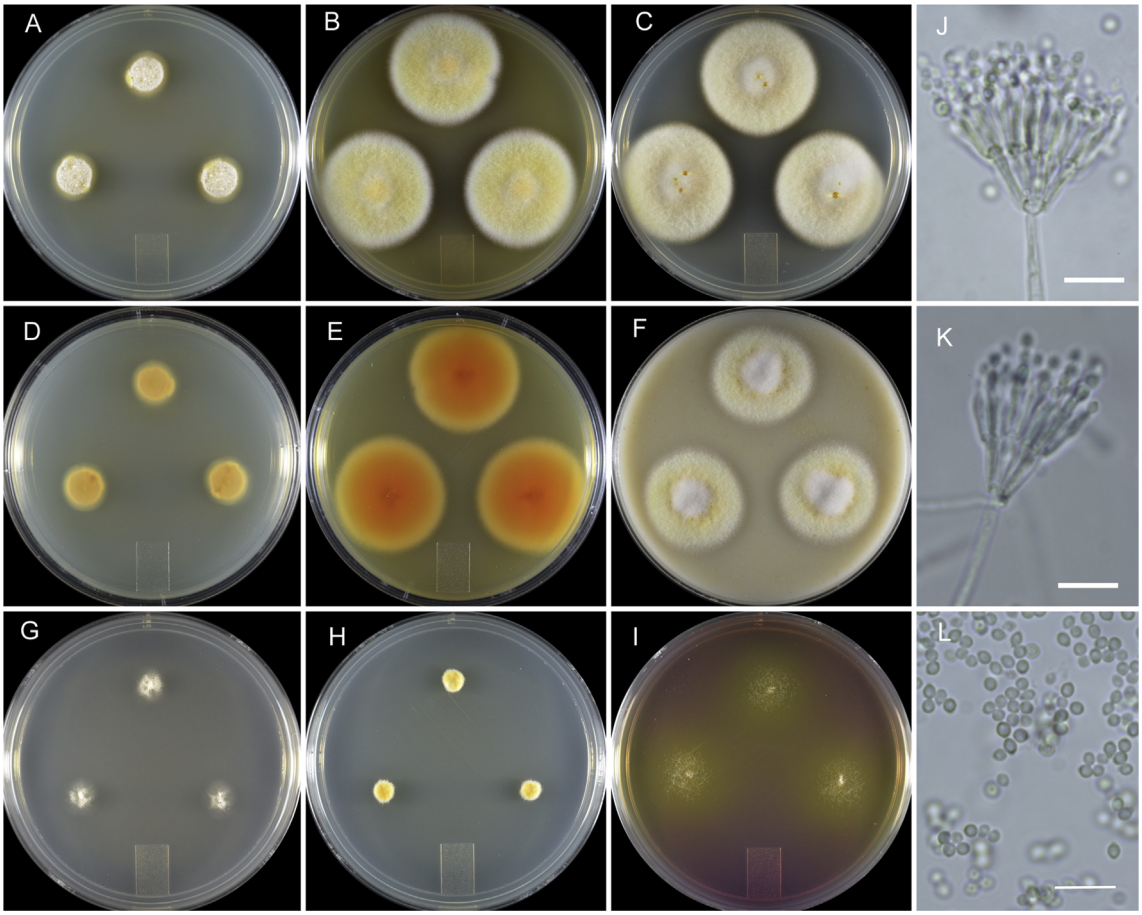

Fig. 3. *Talaromyces pinophilus* NRRL 62415. (A) CYA. (B) MEA. (C) PDA. (D) CYA reverse. (E) MEA reverse. (F) OA. (G) CY20S. (H) DG18. (I) CERA. (J, K) Conidiophores and phialides. (L) Conidia. Bar = 10 μm.

buff-yellow shades, largely subsurface, poor to moderate sporulation, sporulating area artemisia green (R47) to deep green-blue gray (R48); reverse uncolored to pale yellow shades; **DG18** colonies loose, floccose to funiculose, mycelium white to primuline yellow, amber yellow (R16), occasionally with pale purplish shades, occasionally radially sulcate, poor to moderate sporulation, conidial area indistinct to artemisia green (R47) to deep green-blue gray (R48), no exudate, no soluble pigments, reverse cartridge buff to cream-buff to chamois (R30), mustard yellow (R16); **OA** colonies floccose to lightly funiculose, mycelium white to primuline yellow or wax yellow (R16), poor to moderate sporulation, conidial area indistinct to artemisia green (R47) to deep green-blue gray (R48), exudate clear to cadmium yellow (R3), no soluble pigments, reverse uncolored occasionally English red; **CREA** colonies thin, hyphae largely submerged, very weak to moderate acid production.

Conidiophores commonly borne from aerial hyphae, occasionally rope like hyphal aggregations (10–)40–200(–300) × 2.5–4(–5) μm, smooth, rarely finely roughened with age, bearing terminal biverticillate, occasionally monoverticillate, or more complex penicilli (Fig. 3J, K), *metulae* 8–12(–14) × 2.5–3.5(–4) μm, in verticils of 4–11(–14), *phialides* 9–11(–16) × 2–3(–4) μm, acerose with gradually tapering collula, (3–)5–7(–9), per metula; *conidia* (Fig. 3L) subglobose, occasionally broadly ellipsoidal or ellipsoidal (large spore), 2.5–3.5(–9) × 2.5–3(–5) μm, with smooth to finely roughened walls, born in short disordered chains or loose columns.

Talaromyces argentinensis Jurjević & S. W. Peterson **sp. nov.** Mycobank MB827826. Fig. 4.

Etym.: The species is named for Argentina where it was once isolated.

Holotype: Ghana, Tafo, West Africa Cacao Research Institute, isolated from soil, 1950, culture dried and deposited in the U.S. National Herbarium, Beltsville, MD, under accession number BPI-910716. Culture ex type NRRL 28750; ITS barcode = MH793045; alternative markers BenA = MH792917; CaM = MH792981; RPB2 = MH793108.

Medium dependent growth in mm: CYA 24–31, MEA 50–52, PDA 47–52, CY20S 20–25, DG18 11–14, OA 38–40, CYAS 0, CREA 43–58.

Temperature dependent growth in mm: On CYA/MEA 20 °C 6–9. 30 °C 31–40/50–62, 35 °C 12–34/13–33, 37 °C 7–25/0–32. On CYA at 20 °C, moderate sporulation, conidial area artemisia green (R47), resembles colony at 25 °C, at 30, 35 and 37 °C, light to moderately deep sulci, no sporulation, mycelium predominately white, resemble colonies grown at 25 °C. On MEA at 20 °C moderate sporulation, conidial area artemisia green (R47), resembles colony at 25 °C, at 30, 35 and 37 °C light to moderately deep sulci, resembles colony at 25 °C.

CYA colonies floccose to funiculose, mycelium white, to mustard yellow (R16), to vinaceous pink (R28), subsurface at margins ca 3 mm, rising ca 3 mm, very poor sporulation, no exudate, no soluble pigments, reverse cream-buff to chamois near honey yellow (R30); **MEA** colonies plane, floccose to funiculose, mycelium white to amber yellow, wax yellow (R16), poor sporulation, no exudate, no soluble pigments; reverse colonial buff to deep colonial buff (R30), with pale orange-reddish shades; **PDA** colonies floccose to

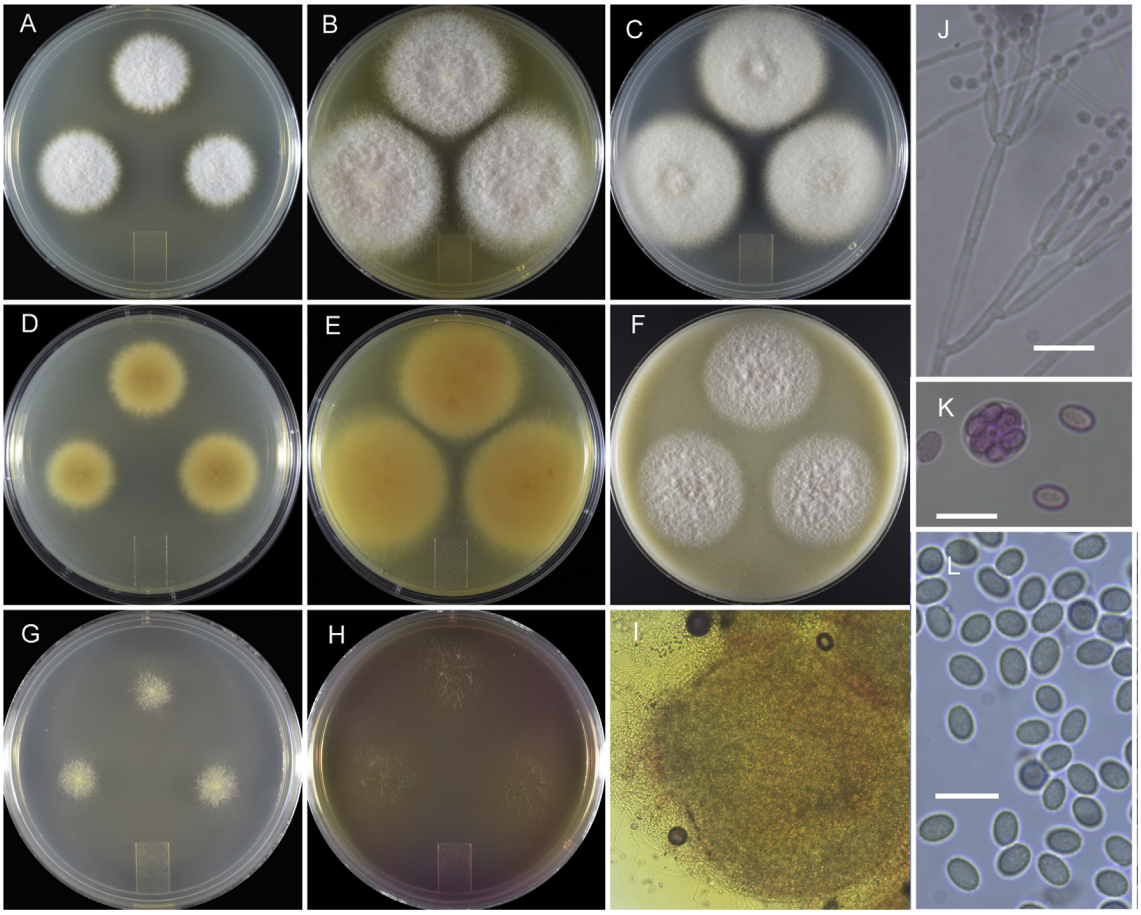

Fig. 4. *Talaromyces argentinensis* NRRL 28758. (A) CYA. (B) MEA. (C) PDA. (D) CYA reverse. (E) MEA reverse. (F) OA. (G) CY20S. (H) CREA. (I) Ascoma. (J) Conidiophores, phialides and conidia. (K) Ascus and ascospores. (L) Slightly roughened ascospores. Bar = 10 μm.

funiculose, mycelium white to mustard yellow (R16), pinkish vinaceous (R27) shades, poor sporulation, no exudate, no soluble pigments, reverse colonial buff (R15), to deep colonial buff (R30); **CY20S** colonies ropy, low, mycelium white to pale buff-yellow shades, largely subsurface, poor to moderate sporulation, not strongly colored to celandine green color (R47), reverse uncolored to pale buff shades; **DG18** colonies loose, plane, funiculose to floccose, mycelium white to mustard yellow (R16), poor to moderate sporulation, not strongly colored to celandine green color (R47), exudate when present apricot yellow (R4), no soluble pigments; reverse light buff to warm yellow (R15); **OA** colonies funiculose to floccose, mycelium white to mustard yellow (R16), with pinkish vinaceous (R27) shades centrally, very poor sporulation, ascomata, abundant, yellow, not fully mature after 7 d, exudate clear to apricot yellow (R4), no soluble pigments; **CYAS** no growth; **CREA** colonies thin, hyphae submerged, moderate acid production.

Ascomata on MEA and OA abundant, covering almost entire colony, globose to subglobose, commonly 250–500 μm diam (Fig. 4I), maturing in 20 d; asci globose to subglobose, 10–12 μm uncolored; ascospores ellipsoidal, occasionally subglobose, pale yellow, (4–)5–7 × 4–5 μm, with spinose walls; *Conidiophores* (Fig. 4J) commonly borne from aerial rope like hyphal aggregations (8–)15–65(–130) × (2–)2.5–3.5(–4) μm, smooth, occasionally finely roughened, bearing terminal biverticillate, monoverticillate, or occasionally more complex penicilli, occasionally irregular branching, *metulae* 7–12(–18) × 2.5–3.5(–4.5) μm, *phialides* 9–12(–16) × 2.5–3(–3.5) μm, acerose with long gradually tapering collula, in whorls of 2–7 per metula; *conidia* (Fig. 4J) subglobose to ellipsoidal, occasionally fusiform, 2.5–3(–4.5) × 2.5–3.5 μm, with smooth to finely roughened walls, born in short disordered chains or loose columns.

Comments. Other isolate examined: NRRL 28758. The DNA sequences of *T. argentinensis* show a high similarity to the undescribed species #12 MGS-2017 (GenBank), with little high similarity to other *Talaromyces* species. On the basis of morphology *T. argentinensis* stands apart from other described species on the basis of ascospore production and the growth characteristics.

Talaromyces californicus Jurjević & S. W. Peterson **sp. nov.**
Mycobank MB827827. Fig. 5.

Etym.: named for California where the type was isolated.

Holotype: USA, California, isol ex air sampler, *Željko Jurjević*, Apr 2008, culture dried down and deposited in the U.S. National Herbarium, Beltsville, MD as BPI 910714. Culture ex type NRRL 58168; ITS barcode = MH793056, alternative markers *BenA* = MH792928; *CaM* = MH792992; *RPB2* = MH793119.

Medium dependent growth in mm: CYA 25–40, MEA 40–51, PDA 32–50, CY20S 17–28, DG18 13–19, OA 29–60, CYAS 0, CREA 28–40.

Temperatures dependent growth in mm: CYA/MEA 20 °C 19–25/29–35; 30 °C 39–53/44–67; 35 °C 38–48/39–59; 37 °C 30–40/26–50.

On CYA at 20 °C resembles colony at 25 °C but no sulcation, at 30, 35 and 37 °C resemble colonies grown at 25 °C; On MEA at 20, 30, 35 and 37 °C resembles colony at 25 °C.

CYA colonies floccose to funiculose, mycelium white to primuline yellow (R16) to dark vinaceous (R27), radially sulcate in some

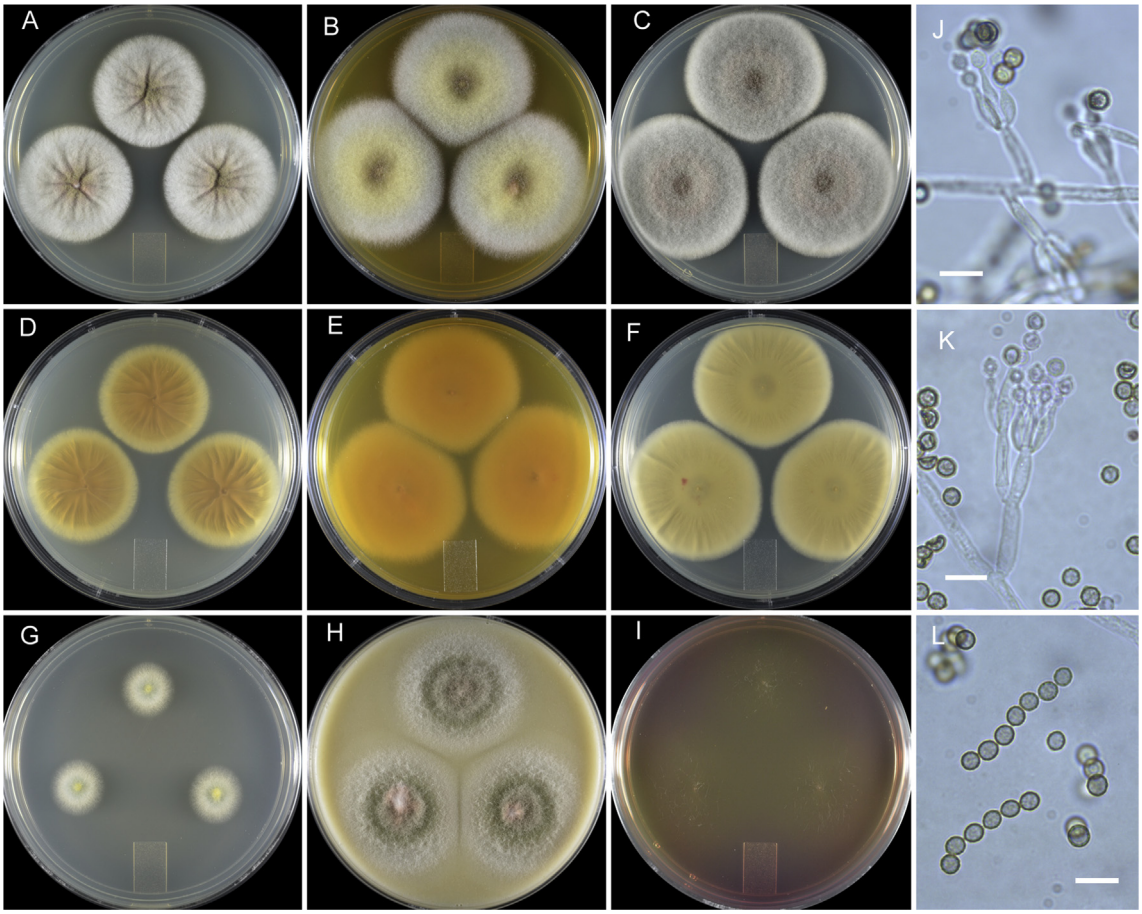

Fig. 5. *Talaromyces californicus* NRRL 58168. (A) CYA. (B) MEA. (C) PDA. (D) CYA reverse. (E) MEA reverse. (F) PDA reverse. (G) DG18. (H) OA. (I) CREA. (J, K) Conidiophores phialides and conidia. (L) Conidia. Bar = 10 μm.

isolates, sporulation varies from none (NRRL58661), to very poor (NRRL58207), to very good (NRRL58168 and NRRL58221), conidial area artemisia green (R47); exudate clear to buff to dark vinaceous near hydrangea red (R27), sparse to moderate, no soluble pigments, reverse warm buff (R30), cinnamon-buff to vinaceous-cinnamon (R29) or chamois to near honey yellow (R30); **MEA** colonies floccose to funiculose, mycelium white, mustard yellow to strontian yellow (R16) occasionally with vinaceous shades, occasionally subsurface at margins ca 5–10 mm (NRRL58661); occasionally fermentation-like odor (NRRL58661), very poor to heavy sporulation, conidial area not strongly colored to artemisia green (R47), no exudate, no soluble pigments, reverse warm buff (R30), to chamois to near honey yellow (R30), occasionally with vinaceous shades; **PDA** colonies floccose to funiculose, mycelium white with Naples yellow (R16) to orange vinaceous near dark vinaceous shades (R27), or pinkish vinaceous (R27) to yellow ocher to ochraceous-orange (R15), white at margins (NRRL58661), poor to heavy sporulation, conidial area not strongly colored, puritan gray to andover green (R47), no exudate, soluble pigments carrot red (NRRL58661); reverse cream-buff (R30), naples yellow to straw yellow (R16), or brick red, apricot yellow to salmon-buff at margins (R8); **CY20S** colonies thin, low, mycelium white, submerged, occasionally poor sporulation, reverse uncolored; **DG18** colonies loose, floccose to funiculose, rising ca 3–4 mm, mycelium white to apricot yellow (R4), to amber yellow (R16), poor to moderate sporulation, occasionally inconspicuous, not strongly colored to artemisia green (R47), exudate clear to apricot yellow (R4), no soluble pigments, reverse maize yellow to apricot yellow (R4) to orange (R3) centrally, or cream color to straw yellow (R16); **OA** colonies floccose to funiculose, mycelium mycelium white to primuline yellow (R16) to dark vinaceous (R27), occasionally submerged at margins ca 5–16 mm, poor (NRRL58661) to very good sporulation, conidial area puritan gray, tea green to andover green (R47), exudate clear to reddish-pink, small droplets, embedded into mycelium, no soluble pigments; reverse in brownish shades, mustard yellow NRRL 58207; **CYAS** no growth; **CREA** colonies thin, hyphae submerged in agar, poor growth, week acid production.

Conidiophores (Fig. 5J) borne from aerial hyphae, or rope like hyphal aggregations (5–)10–50(–85) × (2.5–)3–4(–5) μm, smooth to finely roughened walls, bearing irregular terminal to subterminal monoverticillate or biverticillate penicilli (Fig. Fig. 5J, K), occasionally more complex structures, occasionally pigmented, reddish-orange; *metulae* 8–14(–22) × 2.5–4 μm, *phialides* 9–12(–17) × 3–4(–5) μm, (2–)3–7(–9) per metula, acerose with long gradually tapering collula, occasionally mono-phialides up to 22 × 4 μm; *conidia* (Fig. 5L) globose to subglobose, occasionally broadly ellipsoidal or pyriform (large spores), 4–6 (–11) × 4–7(–8) μm, with finely rough to rough walls, born in short columns to disordered chains.

Comments. The five isolates of *T. californicus* are identical in sequence at the *Bena*, *CaM* and ITS sequences with small variation in the *RPB2* locus. High similarity (98–99 %) was observed toward two non-type isolates of *T. veerkampii*. There is a high proportion of monoverticillate penicilli that range from single phialides sessile on vegetative hyphae to vesiculate monoverticillate conidial structures. This feature is unusual among the species of *T.* sect. *Talaromyces* and is diagnostic of the species.

Talaromyces domesticus Jurjević & S. W. Peterson **sp. nov.**
Mycobank MB827828. Fig. 6.

Etym.: isolated from the home environment.

Holotype: USA, Pennsylvania, isol ex a floor swab, *Ž. Jurjević*, Feb 2008, dried down and deposited in the U.S. National Herbarium, Beltsville, MD, as BPI 910711. Culture ex type NRRL 58121; ITS barcode = MH793055; alternative markers *BenA* = MH792927; *CaM* = MH792991; *RPB2* = MH793118.

Medium dependent growth in mm: CYA 22–25, MEA 43–49, PDA 41–48, CY20S 22–25, DG18 7–14, OA 30–38, CYAS 0, CREA 28–31.

Temperature dependent growth in mm: on CYA/MEA 20 °C 15–18/29–30, 30 °C32–37/49–62, 35 °C 30–38/47–51, 37 °C 30–38/35–42. On CYA at 20 °C resembles colony at 25 °C, at 30 °C moderate to heavy sporulation, conidial area celandine green (R47) to grayish blue-green (R48), radially sulcate, resembles colony at 25 °C**,** at 35 and 37 °C similar to 30°C, exudate clear to Apricot yellow (R4), large droplets; reverse orange vinaceous (R27), walnut brown, to pale greenish yellow (R5) at margins. On MEA at 20 °C resembles colony at 25 °C, at 30, 35 and 37 °C occasional exudate at 35 °C and 37 °C, apricot yellow (R4); reverse occasionally dark Indian red near black, ocher red centrally, resembles colony at 25 °C.

CYA colonies floccose to funiculose, mycelium white to antimony yellow, ochraceous-buff (R15), occasionally with light vinaceous shades, subsurface at margins ca 3–4 mm; rising ca 4 mm, lightly to moderate sulcate, poor sporulation, mainly at margins; exudate when present clear, sparse, no soluble pigments; reverse yellow ocher, ochraceous-tawny to warm buff at margins (R15); **MEA** colonies funiculose to floccose, mycelium white to wax yellow or mustard yellow (R16), subsurface at margins ca 3–5 mm; moderate to heavy sporulation, conidial area celandine green (R47) to grayish blue-green (R48), no exudate, no soluble pigments; reverse warm buff (R15), to chamois near honey yellow (R30), occasionally centrally vinaceous-brown; **PDA** colonies floccose to funiculose, occasionally radially sulcate, mycelium white to wax yellow to primuline yellow (R16), subsurface at margins ca 3–5 mm; centrally rising ca 3 mm, moderate to abundant sporulation, conidial area celandine green to artemisia green (R47), no exudate, no soluble pigments; reverse variable straw yellow to amber yellow (R16) or deep colonial buff (R30) to dark Maroon-purple near black (R26) centrally; **CY20S** colonies thin, low, mycelium white to Ivory yellow (R30), largely subsurface, poor sporulation, reverse uncolored to pale buff shades (R15); **DG18** colonies loose, floccose to funiculose, rising ca 2–3 mm, mycelium white to mustard yellow (R16), moderate sporulation, no exudate, no soluble pigments, reverse warm buff (R15), to primuline yellow (R16); **OA** colonies funiculose to floccose, mycelium white to amber yellow to primuline yellow (R16), moderate sporulation, conidial area artemisia green (R47), to pale green-blue gray (R48), exudate variable clear to apricot-yellow (R4), to orange-vinaceous (R27), no soluble pigments; **CYAS** no growth; **CREA** colonies thin, hyphae submerged, moderate acid production.

Conidiophores (Fig. 6J, K) commonly borne from aerial rope like hyphal aggregations (20–)50–300(–450) × (2.5–)3–4 μm, smooth, occasionally finely roughened, bearing terminal biverticillate, occasionally more complex penicilli, *metulae*

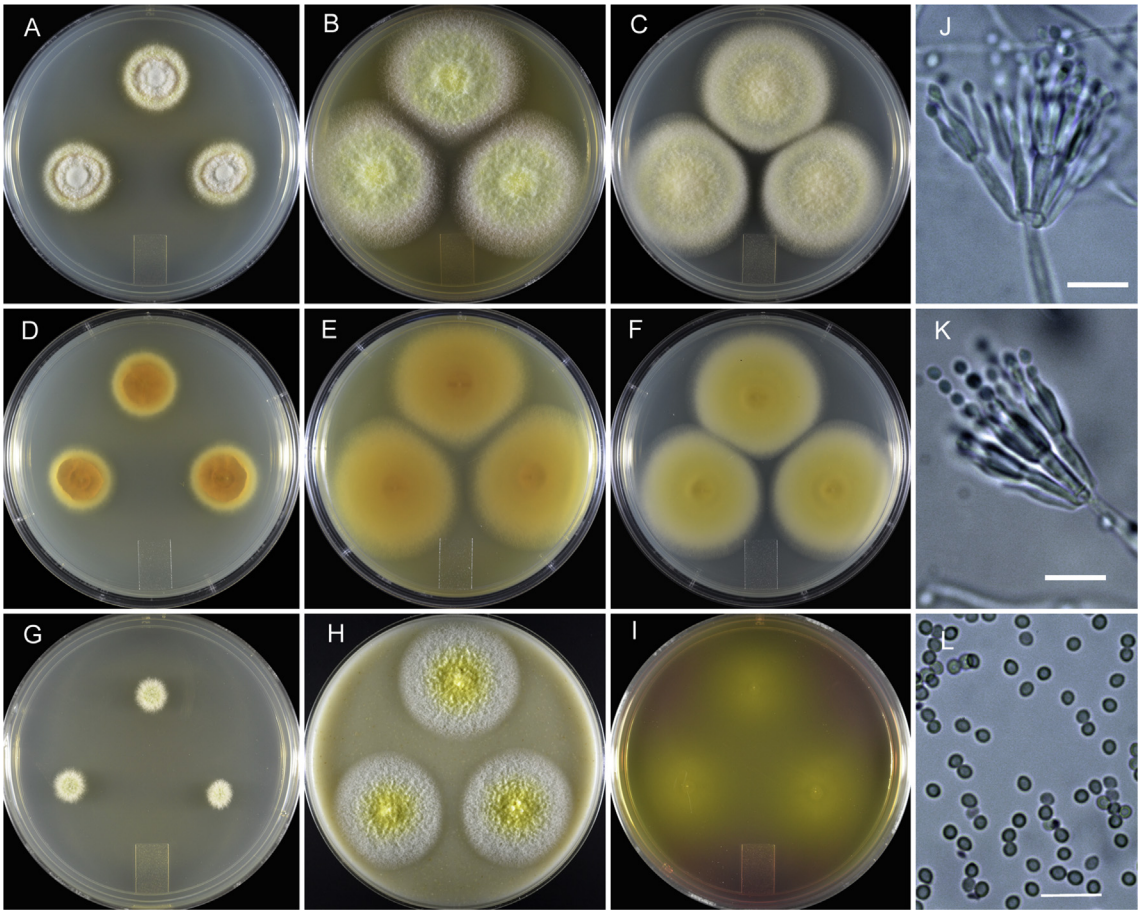

Fig. 6. *Talaromyces domesticus* NRRL 58121. (A) CYA. (B) MEA. (C) PDA. (D) CYA reverse. (E) MEA reverse. (F) PDA reverse. (G) CY20S. (H) OA. (I) CREA. (J, K) Conidiophores and phialides. (L) Conidia. Bar = 10 μm.

8–12(–18) × 2.5–3.5(–4) µm, in verticils of (3–)5–11(–13), *phialides* 9–11(–16) × 2.5–3(–4) µm, acerose with long gradually tapering collula, (3–)5–9(–11) per metula; *conidia* (Fig. 6L) subglobose to broadly ellipsoidal, 2.5–3.5(–5) × 2.5–3(–3.5) µm, with smooth to finely rough walls, born in short disordered chains or loose columns.

Comments. The DNA sequences at each locus are distinct from *T. sayulitensis*. The *BenA* locus is 98 % similar to non-type isolates of *T. sayulitensis*; the *CaM* locus is 99 % similar to *T. sayulitensis* DTO 245-H1; and the *RPB2* locus is 99 % similar to *T. pinophilus ex type.* The difference is consistent and sufficient to call *T. domesticus* a distinct species. The growth on MEA is higher, on DG18 is higher, and CREA is significantly higher making the species identifiable.

Talaromyces louisianensis Jurjević & S. W. Peterson **sp. nov.**
Mycobank MB827829. Fig. 7.

Etym.: named for the state of Louisiana where it was isolated.

Holotype: USA, Louisiana, isol ex air sampler, *Željko Jurjević*, Sept 2007, culture dried down and deposited in the U.S. National Herbarium, Beltsville, MD as BPI 910715. Culture ex type NRRL 35823; ITS barcode = MH793052; alternative markers *BenA* = MH792924; *CaM* = MH792988; *RPB2* = MH793115.

Medium dependent growth in mm. CYA 35–39, MEA 45–55, PDA 47–52, CY20S 17–29, DG18 15–19, OA 38–42, CYAS 0–3, CREA 39–42.

Temperature dependent growth in mm. Colonies on CYA/MEA 20 °C 21–26/30–40; 30 °C 47–51/60–73; 35 °C 41–57/40–67; 37 °C 37–43/39–55. On CYA at 20C, 30C, 35C and 37 °C resembles colony at 25 °C, exudate pale brown (orange-buff R3) to red-orange (Mars–orange R2) at 30 °C and moderately abundant, at 35 °C occasionally clear, sparse, no exudate observe on 20 °C and 37 °C; On MEA at 20, 30, 35 and 37 °C resembles colony at 25 °C, at 37 °C exudate clear, moderately abundant.

CYA colonies floccose to funiculose rudiments, low, sporulation heavy, conidial area grayish-blue green (light medici blue to deep green-blue gray R48), mycelium amber yellow to primuline yellow (R16), white at margins ca 3–6 mm, rising ca 3 mm, radially sulcate, no exudate, no soluble pigments; reverse brown (yellow ocher to Dresden brown R15); **MEA** colonies floccose to funiculose, sporulation heavy, conidial area artemisia green (R47) to colonial buff (R30) centrally, mycelium mustard yellow to primuline yellow (R16), white at margins, no exudate, no soluble pigments, reverse warm buff to Dresden brown (R15) or ochraceous tawny (R15); **PDA** colonies floccose to funiculose, low, mycelium white to mustard yellow near primuline yellow (R16), subsurface at margins ca 3–4 mm, heavy sporulation, conidial area celandine green to artemisia green (R47), exudate clear to brown (ochraceous-tawny R15) or red-orange (Mars–orange R2), largely embedded in the mycelium, no soluble pigments; reverse reddish-orange (Mars–orange near burnt sienna (R2)), to capucine buff (R3); **CY20S** colonies low, mycelium white, largely subsurface or submerged in agar, thin, poor sporulation in artemisia green (R47); reverse uncolored; **DG18** colonies loose, floccose to funiculose, mycelium white to warm buff, antimony yellow (R15), subsurface at margins ca 3–5 mm, occasionally lightly sulcate, moderate sporulation, conidial area artemisia green (R47), no exudate, no soluble pigments, reverse uncolored at margins to colonial buff, to olive

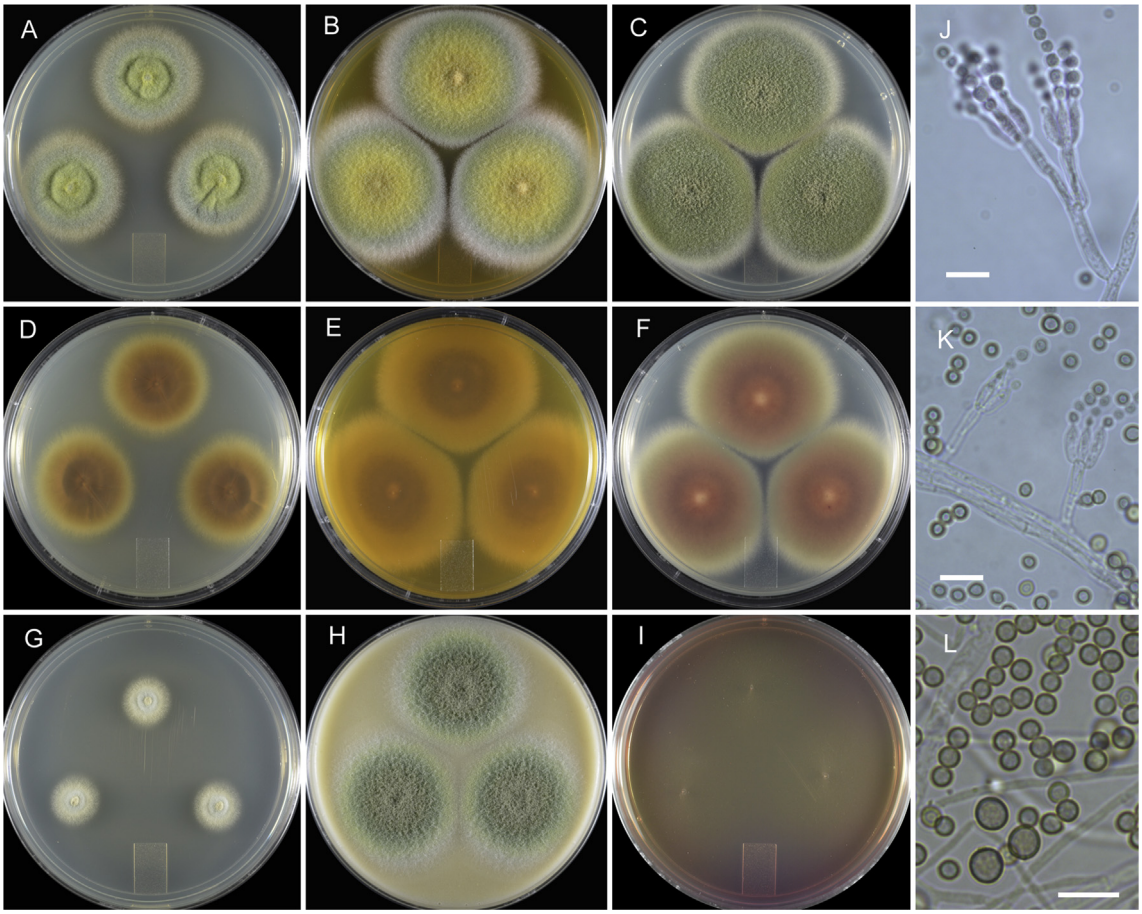

Fig. 7. *Talaromyces louisianensis* NRRL 35823. (A) CYA. (B) MEA. (C) PDA. (D) CYA reverse. (E) MEA reverse. (F) PDA reverse. (G) DG18. (H) OA. (I) CREA. (J, K) Conidiophores and conidia. (L) Conidia. Bar = 10 µm.

yellow (R30); **OA** colonies floccose to lightly funiculose, mycelium white to mustard yellow near primuline yellow (R16), heavy sporulation, conidial area celandine green to artemisia green (R47), exudate clear to brown, small droplets embedded in mycelium, no soluble pigments; reverse in brownish shades; **CYAS** no growth to 3 mm; **CREA** colonies thin, poor growth, hyphae largely submerged, weak acid production.

Conidiophores (Fig. 7J, K) commonly borne from aerial hyphae, occasionally rope-like hyphal aggregations (3–)10–75(–120) × (2.5–)3–4(–5) μm, smooth, occasionally finely roughened with age, bearing terminal biverticillate, occasionally mono-verticillate, or more complex penicilli, *metulae* (8–)9–12(–18) × (2.5–)3–4(–5) μm, in verticils of (2–)5–9(–11), *phialides* 9–12(–24) × (2.5–)3–4(–5) μm, acerose with gradually tapering in long collula, (2–)5–9(–11), per metula; *conidia* (Fig. 7L) globose to subglobose, to broadly ellipsoidal, occasionally nearly pyriform or fusiform (large spore), (3–)3.5–5 (–11) × (3–)3.5–5(–8.5) μm, with smooth to finely roughened to rough walls, born in short disordered chains.

Comments. *Talaromyces louisianensis* is 98 % similar to *T. veerkampii* at the *BenA* locus, with similar values for *CaM* and *RPB2*. The cultures differ in the growth rates and in the grayish color of *T. veerkampii* versus the white to yellow color of *T. louisianensis*. Also *T. louisianensis* produces acid on CREA and has relatively longer metulae and *T. veerkampii* does not make acid and has short metulae.

Talaromyces malicola Jurjević & S. W. Peterson **sp. nov.**

Mycobank MB827830. Fig. 8.

Etym.: isolated from the rhizosphere of apple tree.

Holotype: Italy, isol ex rhizosphere of an apple tree, *R. Locci*, April 1970, culture dried down and deposited in the U.S. National Herbarium, Beltsville, MD as BPI 910712. Culture ex type NRRL 3724; ITS barcode = MH909513; alternative markers *BenA* = MH909406; *CaM* = MH909459; *RPB2* = MH909567.

Medium dependent growth in mm. CYA 24–25, MEA 29–31, PDA 34–35, CY20S 15–16, DG18 3–4, OA 37–39, CYAS 0, CREA 25–26.

Temperature dependent growth in mm. On CYA/MEA at 20 °C 9–11/19–20, 30 °C 29–30/29–30, 35 °C18–19/22–24, 37 °C 9–10/6–7. On CYA at 20 °C, mycelium white to amber yellow (R16), very poor sporulation, at 30 °C, moderately sulcate, reverse warm buff (R15), resembles colony at 25C, at 35 and 37 °C colonies white, sulcate, no sporulation. On MEA at 20 and 30 °C resembles colonies at 25 °C, at 35 °C mycelium white with pale orange-yellow shades, radially moderate or deeply sulcate, no sporulation, at 37 °C, mycelium white.

CYA colonies floccose to lightly funiculose, mycelium white with pale vinaceous-lilac to light vinaceous purple (R44) shades centrally, ivory yellow to deep colonial buff (R30) marginally, radial sulcate, poor sporulation, inconspicuous, no exudate, no soluble pigments, reverse vinaceous to orange vinaceous (R27), or vinaceous purple (R28), cream-buff to chamois (R30) marginally; **MEA** colonies floccose to funiculose, mycelium white to light vinaceous-cinnamon (R29), to deep colonial buff near chamois (R30), moderate sporulation, conidial area gnaphalium green (R47), no exudate, no soluble pigments, reverse light ochraceous–buff to ochraceous-orange (R15); **PDA** colonies floccose to funiculose, mycelium white to mustard yellow (R16), to vinaceous shades (R27), centrally rising ca 3 mm, moderate sporulation, conidial area artemisia green (R47), overgrown with hyphae, no exudate, no soluble pigments; reverse deep vinaceous (R27), to light ochraceous-buff to ochraceous-buff (R15); **CY20S** colonies ropy, thin, low, mycelium white to Naples yellow (R16), occasionally subsurface, moderate sporulation in celandine green color (R47), reverse uncolored or light buff shades (R15); **DG18** colonies loose, floccose to lightly funiculose, mycelium white to pale buff shades, moderate sporulation, no exudate, no soluble pigments; reverse light (R15); **OA** colonies floccose to funiculose, mycelium white to antimony yellow (R15), moderate sporulation, conidial area buff to gnaphalium green (R47), centrally rising ca 3 mm, exudate clear, sparse, no soluble pigments; **CYAS** no growth; **CREA** colonies hyphae largely submerged, weak to moderate acid production.

Conidiophores commonly borne from aerial rope-like hyphal aggregations (15–)25–100(–130) × 3–4 μm, smooth, occasionally finely roughened, bearing terminal biverticillate, rarely mono-verticillate penicilli (Fig. 8J, K), *metulae* 8–12(–14) × 2.5–4 μm, in appressed verticils of (2–)5–9(–11), *phialides* 9–11(–16) × 2.5–3(–3.5) μm, acerose with long gradually tapering collula, (2–)5–7(–9) per metula; *conidia* (Fig. 8L) globose to ellipsoidal 2.5–3(–4) × 2–5.5 μm, with walls thick and finely roughened, occasionally pyriform to elongate large conidia, 9 × 5.5 μm, born in short columns.

Comments. *T. malicola BenA* is 97 % similar to *T. sayulitensis*, CaM is 98 % similar to *T. adpressus* and *T. pinophilus*, and RPB2 is 99 % similar to *T. pinophilus* and *T. lentulus*. *T. malicola* makes acid on CREA which *T. adpressus* does not. The colors of T. *malicola* tend to be white or brownish while *T. lentulus* is a definite yellow. Growth on CYA is much less for *T. malicola* than *T. pinophilus*.

Talaromyces pratensis Jurjević & S. W. Peterson **sp. nov.**

Mycobank MB827831. Fig. 9.

Etym.: named for the prairie meadowlands where many isolates originated.

Holotype: USA, Ohio, isolated from effluent of water treatment plant near Cincinnati, *W. B. Cooke*, date unknown, dried down and deposited in the U.S. National Herbarium, Beltsville, MD, as BPI 910710. Culture ex type NRRL 62170; ITS barcode = MH793075; alternative markers *BenA* = MH792948; *CaM* = MH793012; *RPB2* = MH793139.

Medium dependent growth in mm. CYA 20–22, MEA 34–36, PDA 34–35, CY20S 16–17, DG18 7–8, OA 30–31, CYAS 3–4, CREA 24–25.

Temperature dependent growth in mm. On CYA/MEA 20 °C 11–16/14–27, 30 °C30–34/45–55, 35 °C 30–35/44–51, 37 °C 25–30/34–40. On CYA at 20 °C mycelium more yellow than at 25 °C, on 30 °C, exudate clear, sparse resembles colony at 25 °C, at 35 °C colony funiculose, exudate clear, on 37 °C, colony funiculose, mycelium white, exudate clear; On MEA at 20 °C resembles colony at 25 °C, on 30 °C, funiculose, exudate clear to apricot yellow resembles colony at 25 °C, at 35 °C colony nearly white, funiculose, radially moderate deep sulcate, exudate clear to pale yellow, abundant, at 37 °C, no sulci, resembles colony at 25 °C.

CYA colonies funiculose to floccose, mycelium white to apricot yellow (R4), cadmium yellow (R3), radially and concentrically sulcate, poor sporulation, exudate clear to apricot yellow (R4), sparse, no soluble pigments, reverse honey yellow to crème-buff (R30); **MEA** colonies floccose to funiculose, centrally lightly sulcate, mycelium white to amber-yellow near mustard yellow (R16), subsurface at margins ca 3–4 mm, moderate sporulation, conidial area artemisia green (R47), no exudate, no soluble pigments; reverse warm buff to yellow-ocher (R15); **PDA** colonies funiculose to floccose, centrally lightly sulcate, mycelium white to amber-yellow (R16), to strontian-yellow (R16), subsurface at margins ca 4 mm, moderate to abundant sporulation, conidial area artemisia green (R47), no exudate, no soluble pigments, reverse colonial buff to deep colonial buff (R30); **CY20S** colonies thin, low, mycelium white to buff-yellow (R4), largely subsurface, very poor to moderate sporulation not strongly colored to celandine green (R47), reverse uncolored to pale buff shades (R15); **DG18** colonies loose, floccose to funiculose, moderately deeply sulcate, commonly masked with white to amber yellow, near mustard yellow (R16) mycelium,

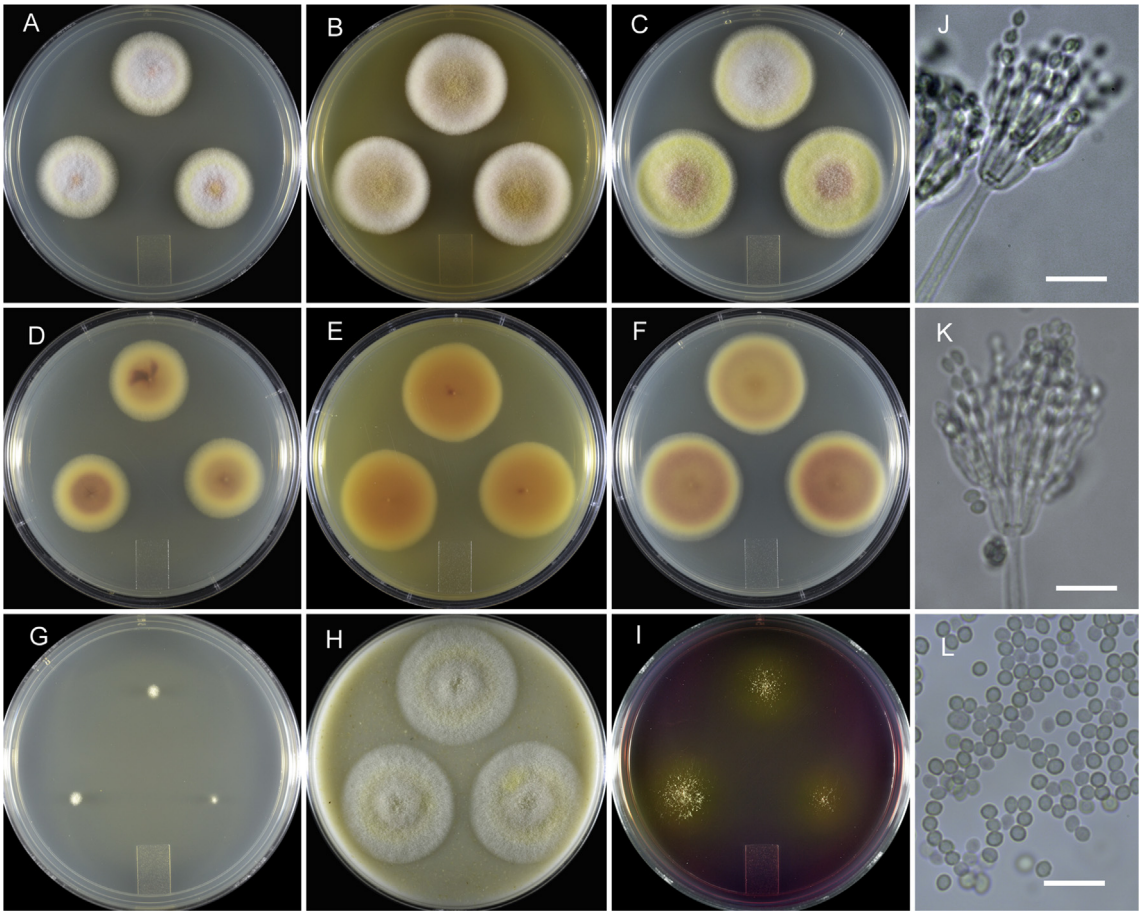

Fig. 8. *Talaromyces malicola* NRRL 3724. (A) CYA. (B) MEA. (C) PDA. (D) CYA reverse. (E) MEA reverse. (F) PDA reverse. (G) CY20S. (H) OA. (I) CREA. (J, K) Conidiophores and phialides. (L) Conidia. Bar = 10 μm.

conidial area artemisia green (R47), no exudate, no soluble pigments, reverse warm buff to antimony yellow (R15); **OA** colonies funiculose, mycelium pale lemon yellow to empire-yellow (R4), white at margins, sporulation heavy, conidial area artemisia green (R47) to pale green-blue gray (R48), exudate variable clear to orange-buff (R3), sparse, no soluble pigments; **CYAS** colonies lightly floccose, mycelium white, very poor sporulation; **CREA** colonies thin, hyphae submerged, moderate acid production.

Conidiophores commonly borne from aerial rope like hyphal aggregations (5–)25–250(–420 rare) × 2.5–4(–4.5) μm, smooth, occasionally finely roughened, bearing terminal biverticillate, occasionally monoverticillate penicilli (Fig. 9J, K), *metulae* 8–12(–16) × 2.5–4 μm, in verticils of (3–)5–11(–14), *phialides* 9–11(–18) × 2.5–3(–4) μm, acerose with long tapering collula, (3–)5–9(–13) per metula; *conidia* (Fig. 9L, M) globose to subglobose, occasionally broadly ellipsoidal, 2.5–3 (–7) × 2.5–3.5(–4.5) μm, with smooth to finely roughened walls, born in short columns to disordered chains.

Comments. *T. pratensis BenA* is 98 % similar to *T. adpressus*, the *CaM* locus is 98 % similar to *T. adpressus* and *T. pinophilus*, *RPB2* is 99 % similar to *T. pinophilus* and *T. lentulus*. *T. pratensis* makes acid on CREA which distinguishes it from *T. adpressus.* Sporulation of *T. lentulus* on MEA is grayish olive, while *T. pratensis* makes artemisia green conidia. *T. pinophilus* cultures are not funiculose on OA medium while *T. pratensis* cultures are intensely funiculose.

Talaromyces soli Jurjević & S. W. Peterson **sp. nov.**
Mycobank MB827832. Fig. 10.
Etym.: isolated from soil.

Holotype: USA, Michigan, isol ex soil, *Gloria Rall*, 1969, culture dried down and deposited in the U. S. National Herbarium, Beltsville, MD, as BPI 910709. Culture ex type NRRL 62165; ITS barcode = MH793074; alternative markers *BenA* = MH792947; *CaM* = MH793011; *RPB2* = MH793138.

Medium dependent growth in mm. CYA 20–26, MEA 37–42, PDA 34–45, CY20S 14–26, DG18 7–14, OA 23–43, CYAS 0–3, CREA 21–31.

Temperature dependent growth in mm. On CYA/MEA 20 °C 12–18/21–29, 30 °C 25–35/39–56, 35 °C 25–36/41–50, 37 °C 23–38/25–43. On CYA at 20 °C resembles colony at 25 °C, but smaller, at 30 °C colony is slightly darker, commonly soluble pigment in yellowish-orange to brown shades, or brown, very intense, exudate when present, clear to mustard yellow (R16) to ochraceous-tawny (R15), moderate to abundant, at 35 and 37 °C colonies in some isolates are more white and resemble colonies grown at 25 °C, exudate clear to pale yellow, sparse to abundant, soluble pigments when present in shades of brown; On MEA at 20 °C hyphae straw yellow to white, resembles colony at 25 °C, at 30, 35 and 37 °C sporulation is abundant, exudate clear to apricot yellow (R4), or brown, colony is mealy, buff-yellow (R4) to Capucine-orange (R3), nearly white in some isolates, resemble colonies grown at 25 °C, occasionally produce odor similar to grape fermentation (NRRL 1768).

CYA colonies funiculose to floccose, mycelium white to Apricot yellow (R4) or cadmium yellow (R3), occasionally with vinaceous shades, subsurface at margins ca 2–4 mm, rising ca 3 mm, radially sulcate, poor to moderate sporulation, conidial area celandine

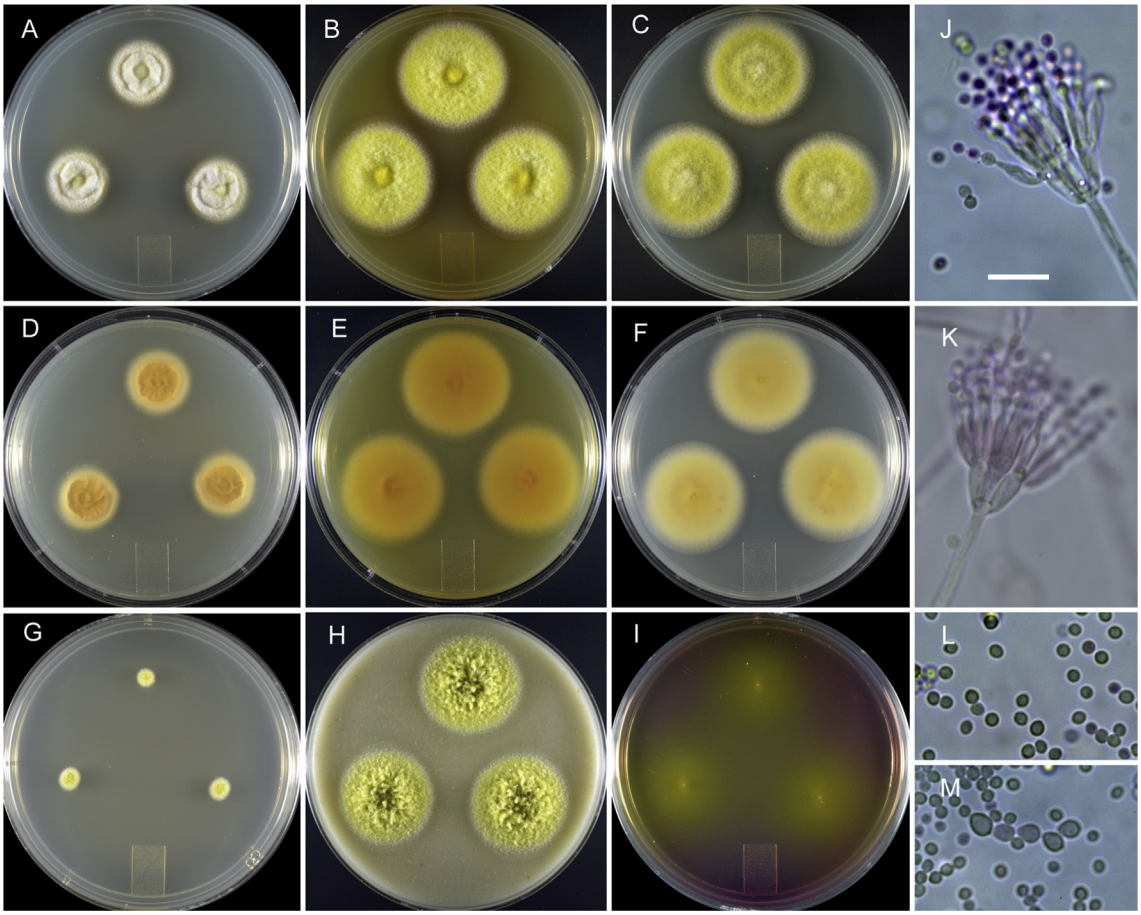

Fig. 9. *Talaromyces pratensis* NRRL 62170. (A) CYA. (B) MEA. (C) PDA. (D) CYA reverse. (E) MEA reverse. (F) PDA reverse. (G) CY20S. (H) OA. (I) CREA. (J, K) Conidiophores, and phialides. (L, M) Conidia. Bar = 10 μm.

green to artemisia green (R47), or deep bluish gray–green (R42), occasionally with vinaceous shades, exudate clear to apricot yellow (R4) sparse, no soluble pigments, reverse honey yellow (R30), light ochraceous-salmon to ochraceous-tawny (R15), or sayal brown (R29); **MEA** colonies funiculose to floccose makes appearance mealy, occasionally radially sulcate, mycelium white to straw yellow near mustard yellow (R16), subsurface at margins ca 3–5 mm, moderate sporulation, conidial area pea-green to artemisia green (R47) or near light Medici blue (R48), exudate clear to apricot yellow (R4) sparse, no soluble pigments, reverse warm buff to buckthorn brown (R15) or orange rufous (R2); **PDA** colonies funiculose to floccose, lightly radially sulcate, mycelium white to straw yellow (R16) or antimony yellow (R15), occasionally with deep vinaceous-lavender shades (R44), subsurface at margins ca 3–5 mm, centrally rising ca 3 mm, moderate to abundant sporulation, conidial area artemisia green (R47), exudate clear to deep orange, or vinaceous-orange, sometime embedded in hyphae, no soluble pigments, reverse deep colonial buff (R30) to warm buff (R15) or orange rufous (R2) occasionally with rusty spots; **CY20S** colonies ropy, thin, low, mycelium white to buff-yellow (R4), largely subsurface, poor to moderate sporulation, not strongly colored to celandine green (R47), reverse uncolored to pale buff shades (R15); **DG18** colonies loose, funiculose to floccose, occasionally lightly sulcate, rising ca 2–3 mm, mycelium white to amber yellow, to mustard yellow (R16), poor sporulation, exudate when present clear to orange, commonly embedded in mycelium, no soluble pigments, reverse warm buff to antimony yellow (R15); **OA** colonies funiculose to floccose, mycelium amber yellow near mustard yellow (R16), white and subsurface at margins ca 3–4 mm, heavy sporulation, conidial area artemisia green (R47), to pale green-blue gray (R48), exudate variable clear to pale yellow, to orange-buff (R3), no soluble pigments; **CYAS** no growth to 3 mm; **CREA** colonies thin, hyphae submerged, moderate acid production.

Conidiophores commonly borne from aerial rope like hyphal aggregations (5–)30–200(–320 rare) × (2.5–)3–4(–4.5) μm, smooth, occasionally finely roughened, bearing terminal biverticillate, rarely monoverticillate penicilli (Fig. 10J, K), *metulae* 8–12(–14) × 2.5–4 μm, in verticils of (3–)5–9(–11), *phialides* 9–11(–20) × 2.5–3(–3.5) μm, acerose with long gradually tapering collula, in verticils of (3–)5–9(–11); *conidia* (Fig. 10L) subglobose to broadly ellipsoidal, 2.5–3.5(–5.5) × 2.5–3.5(–4.5) μm, with walls thick, and finely roughened to roughened, born in short disordered chains or loose columns.

Comments: On the basis of 100 % ITS match to sequences in GenBank, *Talaromyces soli* been isolated from ant nest in Texas (Rodrigues et al., 2011), endophytes of beans in Columbia (Parsa et al., 2016), *Elodia bifoliata* in China (Wang and Shang, GenBank) and aquatic macrophytes in Arizona (Sandberg et al., 2014). The *BenA* of *T. soli* 98 % similar to *T. adpressus*, the *CaM* is 97 % similar to *T. adpressus*, and the *RPB2* locus is 98 % similar to *T. adpressus* and *T. pinophilus*. *T. soli* makes acid on CREA and the cultures have a yellow green coloration whereas *T. adpressus* does not make acid on CREA and the culture coloration is bluish green. *T. soli* is much more funiculose on all media than *T. pinophilus*.

Talaromyces tumuli Jurjević & S. W. Peterson **sp. nov.**
Mycobank MB827833 Fig. 11.

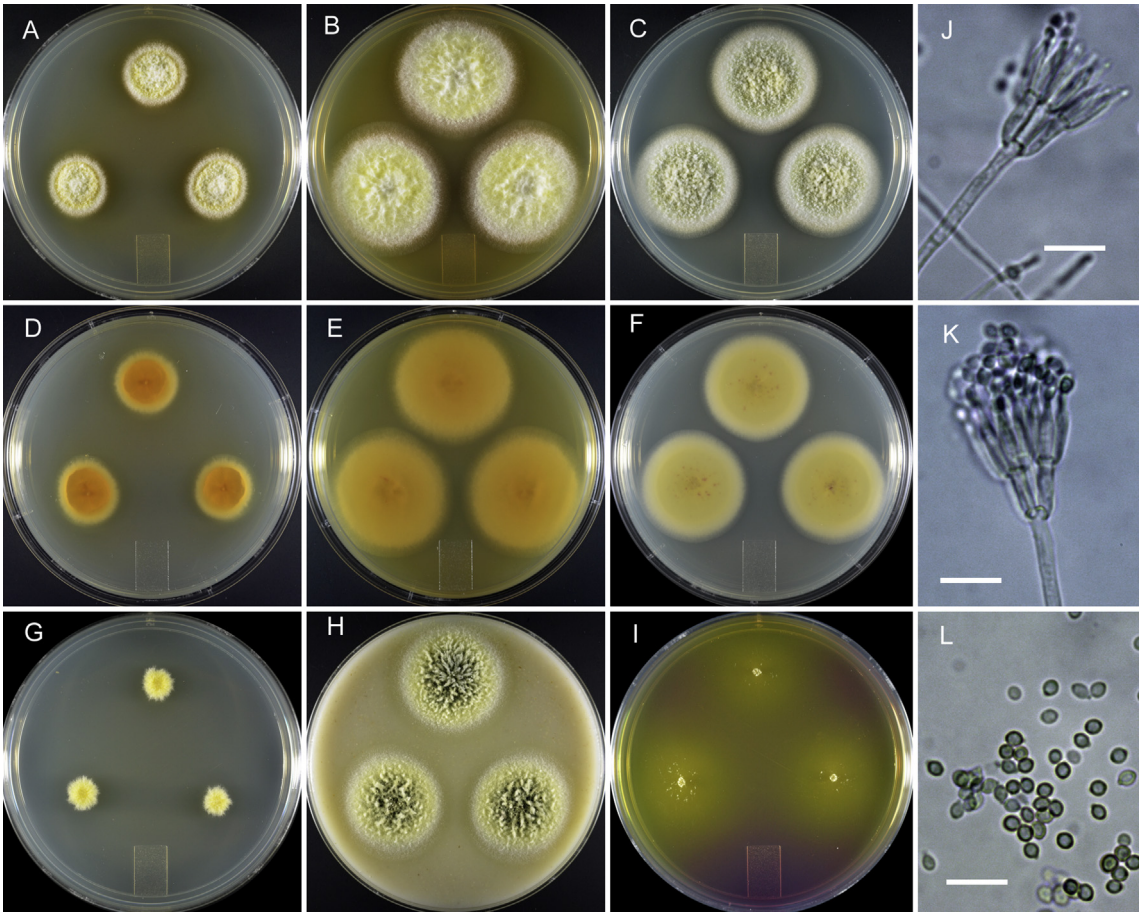

Fig. 10. *Talaromyces soli* NRRL 62165. (A) CYA. (B) MEA. (C) PDA. (D) CYA reverse. (E) MEA reverse. (F) PDA reverse. (G) CY20S. (H) OA. (I) CREA. (J, K) Conidiophores and phialides. (L) Conidia. Bar = 10 μm.

Etym.: commemorates the rolling hills of the prairie where many isolates originated.

Holotype: USA, Indiana, Dunes State Park, isol ex soil from the big bluestem prairie, Apr 1963, R. W. Tuveson, culture dried down and deposited in the U.S. National Herbarium, Beltsville, MD as BPI 910713. Culture ex type NRRL 62151; ITS barcode = MH793071; alternative markers *BenA* = MH792944; *CaM* = MH793008; *RPB2* = MH793135.

Medium dependent growth in mm. CYA 19–27, MEA 36–42, PDA 35–43, CY20S 12–25, DG18 10–15, OA 30–37, CYAS 0–3, CREA 19–29.

Temperature dependent growth in mm. On CYA/MEA 20 °C 9–15/21–30, 30 °C 28–41/35–52, 35 °C 24–45/35–43, 37 °C 21–35/34–50. On CYA at 20 °C resembles colony at 25 °C, but smaller, at 30 °C colony is darker, commonly heavy sporulation, exudate when present clear to apricot yellow (R4), reverse warm buff to yellow-ocher (R15), to primuline yellow (R16), to walnut brown (R28), at 35 and 37 °C colony resembles colonies grown at 30 °C; On MEA at 20, 30, 35 and 37 °C resembles colony at 25 °C.

CYA colonies funiculose to floccose, mycelium white to mustard yellow near primuline yellow, to wax yellow (R16), rising ca 3–4 mm, occasionally radially sulcate, moderate to abundant sporulation, conidial area artemisia green (R47), near light Medici blue (R48); exudate clear to apricot yellow (R4), sparse, no soluble pigments, reverse honey yellow to deep colonial buff (R30); **MEA** colonies funiculose to floccose, occasionally radially sulcate, mycelium white to mustard yellow or wax yellow (R16), subsurface at margins ca 5 mm, moderate to abundant sporulation, conidial area artemisia green (R47), to light Medici blue (R48), exudate, clear to buff, no soluble pigments, reverse colonial buff to olive-ocher (R30); **PDA** colonies funiculose to floccose, occasionally radially sulcate, mycelium white to Naples yellow near mustard yellow (R16), occasionally with very pale pinkish shades, subsurface at margins ca 5 mm, centrally rising ca 3 mm, abundant sporulation, conidial area artemisia green (R47), to light Medici blue (R48), exudate clear occasionally in pale yellow to vinaceous shades, no soluble pigments, reverse colonial buff to olive-ocher (R30); **CY20S** colonies ropy, thin, low, mycelium white to pale-buff, largely subsurface, poor to moderate sporulation, celandine green (R47), reverse uncolored to pale buff shades (R15); **DG18** colonies funiculose to floccose, occasionally lightly sulcate, mycelium white to mustard yellow shades (R16), moderate sporulation, conidial area artemisia green (R47), to light Medici blue (R48), exudate sparse, clear to pale yellow, commonly embedded in mycelium, no soluble pigments, reverse cream color to primuline yellow (R16); **OA** colonies funiculose to floccose, mycelium white, occasionally with pale yellowish or purplish shades, white at margins, subsurface at margins ca 3–4 mm, heavy sporulation, conidial area green-blue gray to dark green-blue gray (R48), exudate variable clear to vinaceous (R27), commonly abundant, no soluble pigments; **CYAS** no growth to 3 mm; **CREA** colonies thin, hyphae largely submerged, weak to moderate acid production.

Conidiophores commonly borne from aerial rope like hyphal aggregations (8–)30–250(–300) × (2.5–)3–4(–4.5) μm, smooth, occasionally finely roughened, bearing terminal biverticillate, occasionally monoverticillate penicilli (Fig. 11J, K), *metulae*

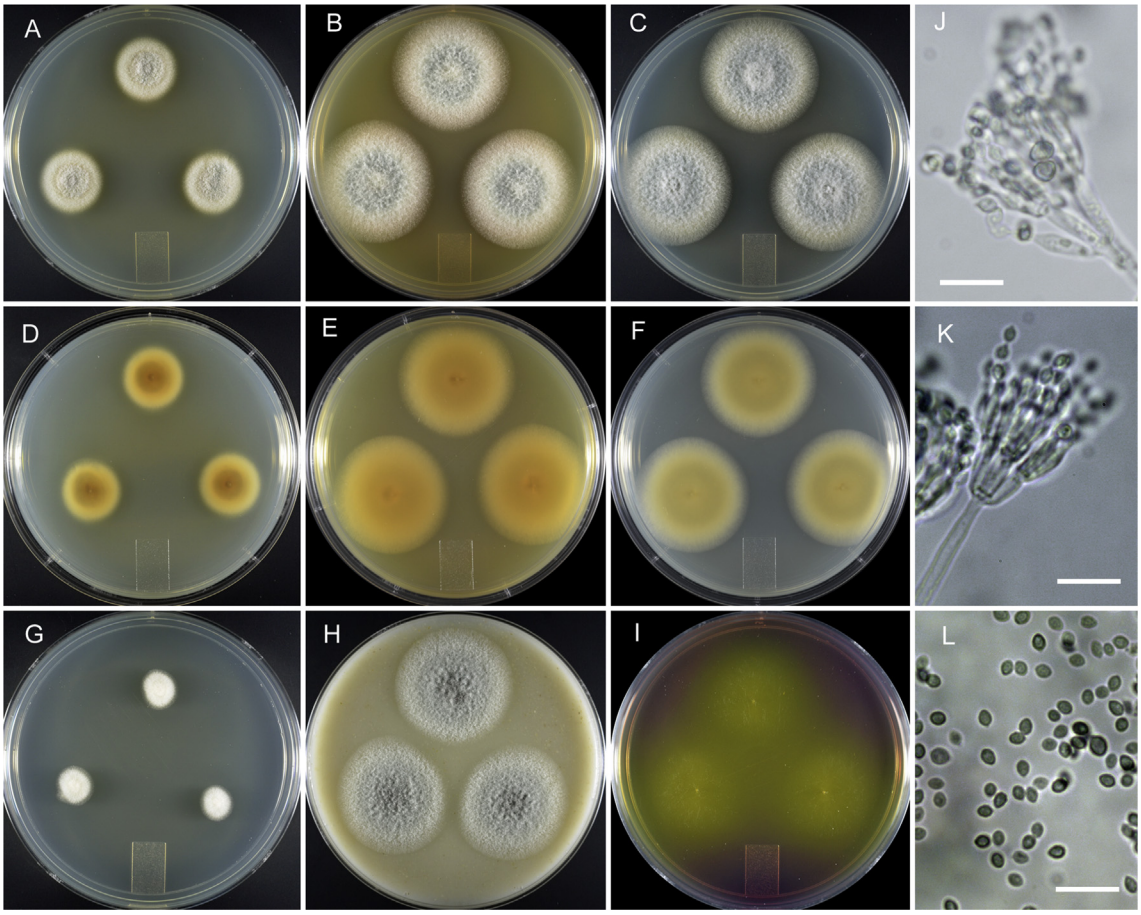

Fig. 11. *Talaromyces tumuli* NRRL 62151. (A) CYA. (B) MEA. (C) PDA. (D) CYA reverse. (E) MEA reverse. (F) PDA reverse. (G) CY20S. (H) OA. (I) CREA. (J, K) Conidiophores and phialides. (L) Conidia. Bar = 10 μm.

8–12 × 2.5–3.5(– 4) μm, in verticils of (3–)5–11(–13), *phialides* 9–11(–16) × 2.5–3 μm, acerose with gradually tapering collula, (2–)5–9(–11) per metula; *conidia* (Fig. 11L) subglobose to broadly ellipsoidal, 2.5–3.5(–7) × 2.5–3.5(–4.5) μm, with smooth to finely rough walls, born in short columns or short disordered chains.

Comments. *T. tumuli BenA* is 98 % similar to *T. adpressus* and *T. sayulitensis*. At the *CaM* locus *T. tumuli* is 97 % related to *T. adpressus* and *T. pinophilus*. At the *RPB2* locus the similarity is 99 % to *T. pinophilus*, and 98 % to *T. adpressus, T. lentulus* and *T. mae*. *T. tumuli* produces acid on CREA while *T. adpressus* does not. *T. tumuli* makes smaller colonies on CYA and MEA than does *T. lentulus*. *T. mae* makes smaller colonies on CYA than does *T. tumuli* and while *T. tumuli* makes colony colors in blue-green shades, *T. mae* produces yellow-green colors. *T. pinophilus* colonies are yellowish, the CYA reverse is an orange shade, while *T. tumuli* forms bluish-green colony colors and the CYA reverse is a shade of brown.

Other comments. *T. adpressus* isolates were also found in the survey. The three isolates were all from peanuts in Oklahoma and Georgia. All three isolates had the adpressed penicilli that Chen et al. (2016) noted in the species description. One isolate (NRRL 6014) made acid on CREA medium. Two isolates of *T.lentulus* were found in this study. The growth was similar, the reverse color on CYA was close to cinnamon cited by Jiang et al. (2018) and in other respects fit the description of *T. lentulus*. *T. veerkampii* isolates in this study produced weak acid on CREA, produced the blue-green to gray green colony color characteristic of the species. In other respects our isolates fit well with the species description (Visagie et al., 2015).

4. Discussion

T. pinophilus sensu lato is a broad and difficult concept to put into practice. In the ongoing study of *Talaromyces* species from maize, most isolates were placed in *Talaromyces funiculosus* for consistency because Raper and Thom (1949) believed that *T. pinophilus* was a synonym of *T. funiculosus*. The characters that were applied to species identification were the characters that unite large numbers of species rather than those that separate. It is clear at first glance that *T. funiculosus* and *T. pinophilus* are phylogenetically distinct species in *Talaromyces* section *Talaromyces* (Fig. 1). In looking at more detailed level there are a number of other distinct species around *T. pinophilus*. The analysis of the four loci by GCPSR (Taylor et al., 2000) maps out the species phylogenetically and the morphological features are such that the groups can be distinguished by appearance of the cultures and micromorphology. Thus the descriptions of the new species is acceptable under the ICN (Turland et al., 2018) rules.

Fifty-five isolates of *T. pinophilus* sensu stricto were sequenced for this study (results shown as Supplementary Figs. 5–7). There are a number of polymorphisms in the data (*BenA* 8 haplotypes, CaM 19 haplotypes, ITS 3 haplotypes, *RPB2* 13 haplotypes), suggesting that the array of haplotype arose as a result of mixis because the haplotypes do not co-vary. There are also a number of genotypes repeated in the data set that suggests that there is a proportion of clonal reproduction involved in this species. This species is not known to have a teleomorphic state, but the data suggest that it does or did have a teleomorph (Lopez-Villavicencio et al., 2010)

with infertile ascospores being formed in the cross of two *T. pinophilus* isolates. This is much the same situation as found by Geiser et al. (1998) for the plant pathogenic *Aspergillus flavus*. That study found evidence of clonality and cryptic mictic reproduction. Later (Horn et al., 2009), discovered a teleomorph in *A. flavus* and showed that it occurs naturally in maize (Horn et al., 2014). They also found complete incongruence of some isolates from the typical *A. flavus* pattern of genes that they argued was evidence of a separate species among the morphologically similar isolates.

In examining the *T. pinophilus* species complex we find that it consists of ten species. These species are shown to be distinct by the complete non-concordance of the haplotypes at each of the loci examined (Supplemental Figs. 1–4).

Sampling of the isolates from a wide geographical range can make the difference between describing new species (Sugui et al., 2014) and understanding the level of intraspecific variation present in the species (O'Donnell et al., 1998; Hubka et al., 2018). The largest sample of isolates possible always is more informative than a limited sample. However, an infinitely large sample size is not possible but using a diversity of techniques can lead to the description of novel species represented by one or only a few isolates (Sugui et al., 2012; Peterson and Jurjevic, 2015; Jurjevic and Peterson, 2016). The four loci used in this study have been used in successful studies previously (Peterson, 2008; Yilmaz et al., 2014). It is possible that the four genes will by random chance not pick up on all the variation present and lead to an under appreciation of the species present or interpreted in a limited data set lead to over interpretation of the species present (Sugui et al., 2014). When whole genomes are sampled and the number of genes is increased we will have a more stable and reliable taxonomy.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funbio.2019.06.007.

References

Abdel-Rahim, I.R., Abo-Elyousr, K.A.M., 2018. *Talaromyces pinophilus* strain AUN-1 as a novel mycoparasite of *Botrytis cinerea*, the pathogen of onion scape and umbel blights. Microbiol. Res. 212–213, 1–9.

Barbosa, R.N., Bezerra, J.D.P., Souza-Motta, C.M., Frisvad, J.C., Samson, R.A., Oliveira, N.T., Houbraken, J., 2018. New penicillium and talaromyces species from honey, pollen and nests of stingless bees. Antonie Van Leeuwenhoek. https://doi.org/10.1007/s10482-018-1081-1.

Castro-Lainez, M.T., Sierra-Hoffman, M.L., Lompart-Zeno, J., Adams, R., Howell, A., Hoffman-Roberts, H., Fader, R., Arroliga, A.C., Jinadatha, C., 2018. *Talaromyces marneffei* infection in a non-HIV non-endemic. IDCases 12, 21–24.

Cerullo, G., Houbraken, J., Granchi, Z., Pepe, O., Varriale, S., Ventorino, V., Chin, A., Woeng, T., Meijer, M., de Vries, R.P., Faraco, V., 2018. Draft genome sequence of *Talaromyces adpressus*. Genome Announc. 6 https://doi.org/10.1128/genomeA.01430-17.

Chen, A.J., Frisvad, J.C., Sun, B.D., Varga, J., Kocsube, S., Dijksterhuis, J., Kim, D.H., Hong, S.-B., Houbraken, J., Samson, R.A., 2016. *Aspergillus* section *Nidulantes* (formerly *Emericella*): Polyphasic taxonomy, chemistry and biology. Stud. Mycol. 84, 1–184.

Chernomor, O., von Haeseler, A., Minh, B.Q., 2016. Terrace aware data structure for phylogenomic inference from supermatrices. Syst. Biol. 65, 997–1008.

Dettman, J.R., Jacobson, D.J., Taylor, J.W., 2003. A multilocus genealogical approach to phylogenetic species recognition in the model eukaryote *Neurospora*. Evolution 57, 2703–2720.

Ellett, F., Pazhakh, V., Pase, L., Benard, E.L., Weerasinghe, H., Azabdaftari, D., Alasmari, S., Andrianopoulos, A., Lieschke, G.J., 2018. Macrophages protect *Talaromyces marneffei* conidia from myeloperoxidase-dependent neutrophil fungicidal activity during infection establishment in vivo. PLoS Pathog. 14, e1007063.

Geiser, D.M., Pitt, J.I., Taylor, J.W., 1998. Cryptic speciation and recombination in the aflatoxin-producing fungus *Aspergillus flavus*. Proc. Natl. Acad. Sci. U.S.A. 95, 388–393.

Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W., Gascuel, O., 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Syst. Biol. 59, 307–321.

Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q., Vinh, L.S., 2018. UFBoot2: improving the ultrafast bootstrap approximation. Mol. Biol. Evol. 35, 518–522.

Horn, B.W., Moore, G.G., Carbone, I., 2009. Sexual reproduction in *Aspergillus flavus*. Mycologia 101, 423–429.

Horn, B.W., Sorensen, R.B., Lamb, M.C., Sobolev, V.S., Olarte, R.A., Worthington, C.J., Carbone, I., 2014. Sexual reproduction in *Aspergillus flavus* sclerotia naturally produced in corn. Phytopathology 104, 75–85.

Hubka, V., Barrs, V., Dudova, Z., Sklenar, F., Kubatova, A., Marsuzawa, T., Yaguchi, T., Horie, Y., Novakova, A., Frisvad, J.C., Talbot, J.J., Kolarik, M., 2018. Unravelling species boundaries in the *Aspergillus viridinutans* complex (section *Fumigati*): opportunistic human and animal pathogens capable of interspecific hybridization. Persoonia 41, 142–174.

Jiang, X.-Z., Yu, Z.-D., Ruan, Y.-M., Wang, L., 2018. Three new species of *Talaromyces* sect. *Talaromyces* discovered from soil in China. Sci. Rep. 8, 4932.

Jurjevic, Z., Peterson, S.W., 2016. *Aspergillus asper* sp. nov. and *Aspergillus collinsii* sp. nov., from *Aspergillus* section *Usti*. Int. J. Syst. Evol. Microbiol. 66, 2566–2572.

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A., Jermiin, L.S., 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nat. Methods 14, 587–589.

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. Evol. 30, 772–780.

Lei, H.L., Li, L.H., Chen, W.S., Song, W.N., He, Y., Hu, F.Y., Chen, X.J., Cai, W.P., Tang, X.P., 2018. Susceptibility profile of echinocandins, azoles and amphotericin B against yeast phase of *Talaromyces marneffei* isolated from HIV-infected patients in Guangdong, China. Eur. J. Clin. Microbiol. Infect. Dis. 37, 1099–1102.

Lopez-Villavicencio, M., Aguileta, G., Giraud, T., de Vienne, D.M., Lacoste, S., Couloux, A., Dupont, J., 2010. Sex in *Penicillium*: combined phylogenetic and experimental approaches. Fungal Genet. Biol. 47, 693–706.

Nguyen, L.-T., Schmidt, H.A., von Haeseler, A., Minh, B.Q., 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Mol. Biol. Evol. 32, 268–274.

O'Donnell, K., Cigelnik, E., Nirenberg, H.I., 1998. Molecular systematics and phylogeography of the Gibberella fujikuroi species complex. Mycologia 90, 465–493.

Page, R.D.M., 1996. TREEVIEW: an application to display phylogenetic trees on personal computers. Comput. Appl. Biosci. 12, 357–358.

Parsa, S., García-Lemos, A.M., Castillo, K., Ortiz, V., López-Lavalle, L.A.B., Braun, J., Vega, F.E., 2016. Fungal endophytes in germinated seeds of the common bean, *Phaseolus vulgaris*. Fungal Biol. 120, 783–790.

Peterson, S.W., 2008. Phylogenetic analysis of *Aspergillus* species using DNA sequences from four loci. Mycologia 100, 205–226.

Peterson, S.W., Jurjević, Ž., 2013. *Talaromyces columbinus* sp. nov., and genealogical concordance analysis in *Talaromyces* clade 2a. PLoS One 8, e78084.

Peterson, S.W., Jurjevic, Z., Frisvad, J.C., 2015. Expanding the species and chemical diversity of *Penicillium* section *Cinnamopurpurea*. PLoS One 10, e0121987.

Pitt, J.I., 1979. The Genus *Penicillium* and its Teleomorphic States *Eupenicillium* and *Talaromyces*. Academic Press, New York.

Raper, K.D., Thom, C., 1949. A Manual of the Penicillia. Williams and Wilkins, Baltimore.

Ridgway, R., 1912. Color Standards and Color Nomenclature. Published by the author: Washington, DC.

Rodrigues, A., Mueller, U.G., Ishak, H.D., Bacci, M., Pagnocca, F.C., 2011. Ecology of microfungal communities in gardens of fungus-growing ants (Hymenoptera: Formicidae): a year-long survey of three species of attine ants in Central Texas. FEMS Microbiol. Ecol. 78, 244–255.

Salvatore, M.M., DellaGreca, M., Nicoletti, R., Salvatore, F., Vinale, F., Naviglio, D., Andolfi, A., 2018. Talarodiolide, a new 12-membered macrodiolide, and GC/MS investigation of culture filtrate and mycelial extracts of *Talaromyces pinophilus*. Molecules. https://doi.org/10.3390/molecules23040950.

Sandberg, D.C., Battista, L.J., Arnold, A.E., 2014. Fungal endophytes of aquatic macrophytes: diverse host-generalists characterized by tissue preferences and geographic structure. Microb. Ecol. 67, 735–747.

Samson, R.A., Yilmaz, N., Houbraken, J., Spierenburg, H., Seifert, K.A., Peterson, S.W., Varga, J., Frisvad, J.C., 2011. Phylogeny and nomenclature of the genus *Talaromyces* and taxa accommodated in *Penicillium* subgenus *Biverticillium*. Stud. Mycol. 70, 159–183.

Su, L., Niu, Y.C., 2018. Multilocus phylogenetic analysis of *Talaromyces* species isolated from cucurbit plants in China and description of two new species, *T. cucurbitiradicus* and *T. endophyticus*. Mycologia 110, 375–386.

Sugui, J.A., Peterson, S.W., Clark, L.P., Nardone, G., Folio, L., Riedlinger, G., Zerbe, C.S., Shea, Y., Henderson, C.M., Zelazny, A.M., Holland, S.M., Kwon-Chung, K.J., 2012.

Aspergillus tanneri sp. nov., a new pathogen that causes invasive disease refractory to antifungal therapy. J. Clin. Microbiol. 50, 3309–3317.
Sugui, J.A., Peterson, S.W., Figat, A., Hansen, B., Samson, R.A., Mellado, E., Cuenca-Estrella, M., Kwon-Chung, K.J., 2014. Genetic relatedness versus biological compatibility between *Aspergillus fumigatus* and related species. J. Clin. Microbiol. 52, 3707–3721.
Taylor, J.W., Jacobson, D.J., Kroken, S., Kasuga, T., Geiser, D.M., Hibbett, D.S., Fisher, M.C., 2000. Phylogenetic species recognition and species concepts in fungi. Fungal Genet. Biol. 31, 21–32.
Tsang, C.C., Tang, J.Y.M., Lau, S.K.P., Woo, P.C.Y., 2018. Taxonomy and evolution of *Aspergillus, Penicillium* and *Talaromyces* in the omics era - past, present and future. Comput. Struct. Biotechnol. J. 16, 197–210.
Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J., Smith, G.F. (Eds.), 2018. International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code) Adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books.
Varriale, S., Houbraken, J., Granchi, Z., Pepe, O., Cerullo, G., Ventorino, V., Chin, A., Woeng, T., Meijer, M., Riley, R., Grigoriev, I.V., Henrissat, B., de Vries, R.P., Faraco, V., 2018. *Talaromyces borbonicus*, sp. nov., a novel fungus from biodegraded *Arundo donax* with potential abilities in lignocellulose conversion. Mycologia 110, 316–324.
Visagie, C.M., Hirooka, Y., Tanney, J.B., Whitfield, E., Mwange, K., Meijer, M., Amend, A.S., Seifert, K.A., Samson, R.A., 2014. *Aspergillus, Penicillium* and *Talaromyces* isolated from house dust samples collected around the world. Stud. Mycol. 78, 63–139.
Visagie, C.M., Yilmaz, N., Frisvad, J.C., Houbraken, J., Seifert, K.A., Samson, R.A., Jacobs, K., 2015. Five new *Talaromyces* species with ampulliform-like phialides and globose rough walled conidia resembling *T. verruculosus*. Mycoscience 56, 486–502.
Wang, R., Shang, Q.. GenBank entry KU375466. https://www.ncbi.nlm.nih.gov/nucleotide/KU375466.1?report=genbank&log$=nuclalign&blast_rank=5&RID=PKKUAX8701R accessed August 7, 2018.
Xu, Y., Feng, X., Jia, J., Chen, X., Jiang, T., Rasool, A., Lv, B., Qu, L., Li, C., 2018. A novel beta-glucuronidase from *Talaromyces pinophilus* Li-93 precisely hydrolyzes glycyrrhizin into glycyrrhetinic acid 3-O-mono-beta-d-glucuronide. Appl. Environ. Microbiol. 2018.
Yilmaz, N., Visagie, C.M., Houbraken, J., Frisvad, J.C., Samson, R.A., 2014. Polyphasic taxonomy of the genus *Talaromyces*. Stud. Mycol. 78, 175–341.