Four novel Talaromyces species isolated from leaf litter from Colombian Amazon rain forests

Yilmaz, Neriman; López-Quintero, Carlos A.; Vasco-Palacios, Aída Marcela; Frisvad, Jens Christian; Theelen, Bart; Boekhout, Teun; Samson, Robert A.; Houbraken, Jos

Published in:
Mycological Progress

Link to article, DOI:
10.1007/s11557-016-1227-3

Publication date:
2016

Document Version
Publisher's PDF, also known as Version of record

Citation (APA):
Yilmaz, N., López-Quintero, C. A., Vasco-Palacios, A. M., Frisvad, J. C., Theelen, B., Boekhout, T., ... Houbraken, J. (2016). Four novel Talaromyces species isolated from leaf litter from Colombian Amazon rain forests. Mycological Progress, 15(10-11), 1041-1056. DOI: 10.1007/s11557-016-1227-3
**Four novel *Talaromyces* species isolated from leaf litter from Colombian Amazon rain forests**

Neriman Yilmaz1,2,3 · Carlos A. López-Quintero4 · Aída Marcela Vasco-Palacios1,5 · Jens C. Frisvad6 · Bart Theelen1 · Teun Boekhout1 · Robert A. Samson1 · Jos Houbraken1

Received: 29 April 2016 / Accepted: 7 September 2016 / Published online: 22 October 2016

© The Author(s) 2016. This article is published with open access at Springerlink.com

**Abstract** Various *Talaromyces* strains were isolated during a survey of fungi involved in leaf litter decomposition in tropical lowland forests in the Caquetá and Amacayacu areas of the Colombian Amazon. Four new *Talaromyces* species are described using a polyphasic approach, which includes phenotypic characters, extrolite profiles and phylogenetic analysis of the internal transcribed spacer region (ITS) barcode, and beta-tubulin (*BenA*) and calmodulin (*CaM*) gene regions. *Talaromyces amazonensis* sp. nov., *T. francoae* sp. nov. and *T. purgamentorum* sp. nov. belong to *Talaromyces* section *Talaromyces*, and *T. columbiensis* sp. nov. is located in section *Bacillispori*. The new species produce several bioactive compounds: *T. amazonensis* produces the potential anticancer agents duclauxin, berkelic acid and vermicillin, and *T. columbiensis* produces the effective anticancer agent wortmannin (together with duclauxin). In addition to the new species, *T. aculeatus* and *T. macrosporus* were isolated during this study on leaf litter decomposition.

**Keywords** Taxonomy · Phylogeny · Bioactive compounds · Plant biomass degradation

**Introduction**

Fungi play an important role in forest ecosystems, as they are involved in processes such as decomposition of leaf litter. Leaf decomposition contributes to nutrient cycling, in which a large proportion of nutrients from net primary production is returned to the forest floor (Maggs 1985). A number of papers have recently been published on fungal biodiversity in the Colombian Amazon region, reporting new species and new registers. Studies in this region revealed 248 species of macrofungi, but a large number of collections have remained unidentified (López-Quintero et al. 2012; Vasco-Palacios and Franco-Molano 2013). Several new taxa of micro- and macrofungi have been published—for instance, new species of *Penicillium* and *Trichoderma* (Houbraken et al. 2011; López-Quintero et al. 2013; Vasco-Palacios and Franco-Molano 2013; Vasco-Palacios et al. 2014). *Talaromyces* species have a worldwide distribution and are isolated from a wide range of substrates. The genus was initially described for teleomorphic species with a *Penicillium* or *Penicillium*-like anamorph that produces soft-walled ascomata covered by interwoven hyphae. Based on phylogenetic, phenotypic and extrolite data, and following the concept of single-name nomenclature, Samson et al. (2011) transferred all accepted species of *Penicillium* subg. *Biverticillium* to *Talaromyces*. The *Talaromyces* monograph of Yilmaz et al.
includes phenotypic characters, analysis of extrolites and mul-
pronomic status is the subject of this report. Four new species are
multiple gene phylogenies of internal transcribed spacer region
Barcoding using ITS sequences (Schoch et al. 2012) revealed
role in the regeneration process of tropical lowland forests.
litter as part of a project to investigate their diversity and their
Material and methods
The strains were isolated from leaf litter as described in
Houbraken et al. (2011). In short, small particles from fresh
or 4–6 month-old leaf litter were washed and placed on 2 %
water agar. The strains were obtained from three forests in
Colombia Amazonia, namely mature forests in Araracuara
(Middle Caquetá) and Amacayacu (Amazonas), and a
Psuedomonotes tropenbosii (Dipterocarpaceae) forest in Peña
Roja (Middle Caquetá). The litterbag studies were carried out
during February 2000 and July 2001 for the plots located in the
Caquetá region and between August 2003 and September 2004
in the plots located in the Amazonas. The newly obtained iso-
lates and strains used for comparison are listed in Table 1,
together with their origin, substrate information and GenBank
accession numbers for ITS, BenA and CaM genes. Strains of
the putative new Talaromyces species used in this study were
deposited in the culture collection of CBS-KNAW Fungal
Biodiversity Centre, Utrecht, the Netherlands; the Center for
Microbial Biotechnology at the Department of Systems
Biology, Technical University of Denmark, Lyngby, Denmark
(IBT); and the working collection of the Department of
Applied and Industrial Mycology (DTO), housed at CBS-
KNAW. The type material of the new taxa is preserved at the
herbarium of the University of Antioquia (HUA).

DNA extraction, PCR amplification and sequencing
DNA extractions were made from strains grown for 7–14 days
on MEA using the UltraClean® Microbial DNA Isolation Kit
(MO BIO Laboratories, Carlsbad, CA, USA), and extracted
DNA was stored at ~20 °C. ITS, CaM and BenA gene regions
were amplified and sequenced using previously described methods (Visagie et al. 2014; Yilmaz et al. 2014).

Phylogeny
Sequence contigs were assembled in SeqMan v. 9.0.4
(DNASTAR, Inc., Madison, WI, USA). The newly generated
sequences were included in a data set including sequences ob-
tained from Yilmaz et al. (2014) and supplemented with se-
quences of new species that were subsequently described
(Visagie et al. 2015; Wang et al. 2016; Yilmaz et al. 2016).
The dataset for each gene was aligned using the MUSCLE
software included in the MEGA v. 6.06 software package
(Tamura et al. 2013). The aligned ITS, BenA and CaM data
were analyzed using the maximum likelihood (ML) method.
The model for ML was selected based on the Akaike informa-
tion criterion (AIC) calculated in MEGA 6.06. The analysis
was performed by calculating an initial tree using BIONJ,
and the subsequent heuristic using Nearest-Neighbour-Interchange
(NDI). Bootstrap support was calculated using 1000 replicates.

Morphological analysis
Strains were morphologically studied on different media under
different growth conditions. Cultures were inoculated onto
Czapek yeast extract agar (CYA), CYA supplemented with
5 % NaCl (CYAS), yeast extract sucrose agar (YES), creatine
sucrose agar (CREA), dichloran 18 % glycerol agar (DG18),
oatmeal agar (OA) and malt extract agar (MEA; Oxoxyz)
at three points on 90-mm Petri dishes and incubated for 7 days at
25 °C in darkness. All media were prepared as described by
Visagie et al. (2014). Additional MEA and CYA plates were
incubated at 30 °C and 37 °C for 7 days in darkness. After
incubation, the diameters of the colonies on the various media
were measured. The density of sporulation, obverse and reverse
colony colours, and the production of soluble pigments were
noted. Colony colour codes refer to Kornerup and Wanscher
(1967). Colonies were photographed with a Canon EOS 400D
camera. Species were characterized microscopically by prepar-
ing slides from MEA. Lactic acid was used as mounting fluid,
and excess amounts of conidia were washed with ethanol.
Specimens were examined using a ZEISS AxioSkop 2 plus
microscope, and the Nikon NIS-Elements D software package
was used for capturing photographs and taking measurements.
Figure plates were prepared in Adobe® Photoshop® CS6.

Extralites
The strains isolated during this study were analyzed by high-
performance liquid chromatography (HPLC) with diode array
detection as described by Houbraken et al. (2012). Three agar
plugs from the Talaromyces isolates grown on CYA, MEA,
YES and OA at 25 °C for 7 days were extracted as described
by Smedsgaard (1997). The detected metabolites were identi-
ified by comparison with standards according to Kildgaard
et al. (2014) and Klitgaard et al. (2014).
| Species       | CBS number | Other collection numbers | Substrate and origin                                      | GenBank accession numbers |
|--------------|------------|--------------------------|-----------------------------------------------------------|---------------------------|
| *T. aculeatus* | 289.48T    | CBS 136670 = IMI 040588 = NRRL 2129 = NRRL A-1474 = IBT 14259 = IBT 4185 | Textile, USA              | KF741995 KF741929 KF741975 |
| *T. aculeatus* | IBT 23209 = DTO 093-F5 | Soil, Araracuara, dept. Amazonas, Colombia                  | KX011511 KX011491 NA     |
| *T. aculeatus* | IBT 23210 = DTO 093-F6 | Soil, Araracuara, dept. Amazonas, Colombia                  | KX011514 KX011492 NA     |
| *T. aculeatus* | IBT 23211 = DTO 093-F7 | Soil, Araracuara, dept. Amazonas, Colombia                  | KX011512 KX011493 NA     |
| *T. aculeatus* | IBT 23212 = DTO 093-F8 | Soil, Araracuara, dept. Amazonas, Colombia                  | KX011515 KX011494 NA     |
| *T. aculeatus* | DTO 276-H2  | Leaf litter, mature forest, Amacayacu, dept. Amazonas, Colombia | KX011513 KX011496 NA     |
| *T. amazonensis* | 140373T    | IBT 23215 = DTO 093-F9 | Leaf litter in from 6-month old litterbag in mature forest in Araracuara, dept. Amazonas, Colombia | KX011509 KX011490 KX011502 |
| *T. amazonensis* | DTO 276-H4 | Soil, Araracuara, dept. Amazonas, Colombia                  | KX011506 KX011495 NA     |
| *T. amazonensis* | DTO 276-H5 | Leaf litter, mature forest, Araracuara, dept. Amazonas, Colombia | KX011507 KX011497 NA     |
| *T. amestolkiae* | 132696T    | DTO 179-F5 | Leaf litter, 42-years old forest, Araracuara, dept. Amazonas, Colombia | JX315660 JX315623 KF741937 |
| *T. angelicus* | KACC 46611 | Dried root of Angelica gigas, Pyeongchang, Republic of Korea | JX183638 JX183640 KF885259 |
| *T. apiculatus* | 312.59T    | ATCC 18315 = FRR 635 = IMI 068239 = IBT 10894 = IBT 14261 | Soil, Japan              | KF741983 KF741916 KF741950 |
| *T. aurantiacus* | 314.59T    | IMI 099722 = NRRL 3398 | Soil, Georgia                | JN899380 KF741917 KF741951 |
| *T. australis* | 137102T    | DTO 273-F5 = IBT 4256 = FRR 2005 | Soil under pasture, Australia | KF741991 KF741922 KF741971 |
| *T. bacillisporus* | 296.48T    | IMI 040045 = NRRL 1025 | Leaf, New York, USA          | KM066182 AY753368 KJ885262 |
| *T. calidicanius* | 112002T    | DTO 038-B8 | Dried root of Oidium officinale, Chungbuk, Republic of Korea | JN899319 HQ156944 KF741934 |
| *T. cnidii* | KACC 46611T | Dried putrefaction of Nidularia rubra, Korea | KF183639 KF183641 KJ885266 |
| *T. colombiensis* | 113151T    | IBT 23206 = DTO 058-F3 | Fresh leaf litter in mature forest in Amacayacu National Park, Dept. Amazonas, Colombia | KX011503 KX011488 KX011499 |
| *T. derxi* | 412.89T    | NHL 2981 | Soil, Kurashiki, Japan          | JN899327 JX494305 KF741959 |
| *T. doulaxii* | 322.48T    | IMI 040044 = MUCL 28672 = MUCL 29094 = MUCL 29212 = NRRL 1030 | Soil, Kurashiki, Japan          | JN899342 JX091384 KF741955 |
| *T. emodensis* | 100536T    | IBT 14990 | Soil, Kathmandu, Nepal                  | JN899337 KJ865724 KJ885269 |
| *T. eucalorocarpus* | PF 1203T = DTO 176-B3 | Soil, Yokohama, Japan | AB176617 JX865733 KJ885271 |
| *T. flavofulvus* | 102801T    | IBT 27044 | Quercus suber leaf litter, Catalonia, Spain | JN899392 JX091376 KF741933 |
| *T. flavus* | 310.38T    | IMI 197477 = NRRL 2098 | Unknown source, New Zealand | JN899360 JX494302 KF741949 |
| *T. francoae* | 113134T    | IBT 23221 = DTO 056-D9 | Leaf litter from 4-month old litterbag in Pseudomonotes tropenhos (Dipterocarpaceae) forest in Pemba, Dept. Amazonas, Colombia | KX011510 KX011489 KX011501 |
| *T. fuscofuscius* | 272.86T    | IMI 193019 | Lagenaria vulgaris, India | JN899377 JX091383 KF741945 |
| *T. fuscofiltrum* | 193.69T    | IBT 14846 = IBT 32466 | Soil, the Netherlands | KF741979 KF741912 KF741942 |
| *T. galapagensis* | 751.74T    | IFO 31796 | Soil beneath Maytenus obovata, Galapagos Island, Ecuador | JN899338 JX091388 KF741966 |
| *T. hachiojensis* | 33024T    | IFM 53624 = PF 1174 | Soil, Hachijō-jima, Japan | AB176620 NA NA |
| *T. liani* | 225.66T    | IMI 098480 = NRRL 3380 = VKM F-301 | Soil, China              | JN899395 JX091380 KJ885257 |
| Species                  | CBS number | Other collection numbers     | Substrate and origin                                                     | GenBank accession numbers |
|--------------------------|------------|------------------------------|-------------------------------------------------------------------------|---------------------------|
| **T. intermedius**       | 152.65T    | IMI 100874                   | Alluvial pasture and swamp soil, Nottingham, England                    | JN899332 JX091387 KF741941 |
| T. kendrickii            | 13666T     | DTO 273-F4 = IBT 13593       | Forest soil, Canada                                                     | KF741987 KF741921 KF741967 |
| T. kendrickii            | 136669     | DTO 273-F8 = IBT 14128       | Soil from damping-off box, Nigeria                                     | KF741988 KF741925 KF741968 |
| T. macrosporus           | 317.63T    | FRR 404 = IMI 197478        | Apple juice, Stellaenbosch, South Africa                              | JN899333 JX091382 KF741952 |
| T. macrosporus           | 116297     | IBT 23205 = DTO 056-D8 = DTO 189-B9 Decomposing leaves after 4 months; Middle Caquetá, Araracuara, Colombia | KX011505 KX011486 NA |
| T. marnefei              | 388.87T    | CBS 334.59 = IMI 068794ii = IMI 068794ii Bamboo rat (Rhizomys sinensis), Vietnam | JN899344 JX091389 KF741958 |
| T. mimicus               | 659.80T    | FRR 1875 = IMI 223991       | Soil from creek bank, New South Wales                                  | JN899339 KJ865726 KJ885272 |
| T. muroi                 | 756.96T    | PF 1153                     | Soil, Chingpu, Taiwan                                                 | JN899351 KJ865727 KJ885274 |
| T. oumae-anae            | 138208T    | DTO 269-E8                  | House dust, Cape Town, South Africa                                    | KJ775720 KJ775213 KJ775425 |
| T. purpurogenes          | 286.36T    | IMI 091926                  | Leaf litter from 4-month old litterbag in Pseudomonotes tropenbosi (Dipterocarpaceae) forest in Peña Roja, Dept. Amazonas, Colombia | JN899372 JX315639 KF741947 |
| T. panamensis            | 128.89T    | IMI 297546                  | Parasitic on a culture of Aspergillus oryzae, Japan                    | JN899362 HQ149327 KF741936 |
| T. pauciolorus           | PF 1150T   | IFM 53616                   | Soil, Barro Colorado Island, Panama                                    | AB176603 NA NA |
| T. pinophilus            | 631.66T    | CECT 2809 = IMI 114933      | Soil, Aso-machi, Japan                                                | JN899382 JX091381 KF741964 |
| T. primulinus            | 321.48T    | FRR 1074 = IMI 040031 = MUCL Unknown source, USA | JN899317 JX494305 KF741954 |
| T. proteolyticus         | 303.67T    | NRRL 3378                   | Granite soil, Ukraine                                                 | JN899387 KJ865729 KJ885276 |
| T. ruber                 | 132704T    | DTO 193-H6 = IBT 10703      | Aircraft fuel tank, UK                                           | JX315662 JX315629 KF741938 |
| T. rubicans              | 342.59T    | IMI 099723 = NRRL 3400      | Soil, Georgia                                                        | JN899384 JX494309 KF741956 |
| T. sayulitensis          | 138204T    | DTO 245-H1                  | House dust, Sayulita, Mexico                                         | KJ775713 KJ775206 KJ775422 |
| T. siamensis             | 475.82T    | IMI 32204                   | Forest soil, Lampang, Tham District, Ban Daen Tham, Thailand         | JN899385 KJ865729 KF741960 |
| T. stellenboschii        | 135665T    | DTO 181-A2 = DAOM 241021 = IBT 32631 Soil, Stellenbosch, South Africa | JX091471 JX091605 JX140683 |
| T. stipitatus            | 375.48T    | IMI 039805 = NRRL 1006      | Decaying wood, Louisiana, USA                                        | JN899348 KM111288 KF741957 |
| T. stolii                | 408.93T    | DTO 060-E4                  | House dust, Sayulita, Mexico                                         | JX315674 JX315633 JX315646 |
| T. thailandensis         | 133147T    | KUFC 3399                   | AIDS patient, the Netherlands                                 | JX898041 JX494294 KF741940 |
| T. unicus                | 10053T     | CCRC 32703 = IBT 18385 = FRR 4436 Soil, Taiwan                            | JN899336 JX865735 KJ885283 |
| T. veerkampii            | 500.78T    | DTO 258-88 = IBT 14845 = IBT 32648 Soil, Dep. de Meta, Municipio de Villavicencio, Colombia | KF741984 KF741918 KF741961 |
| T. verruculosus          | 388.48T    | CBS 136671 = IMI 040039 = NRRL Soil, Texas, USA                           | KF741994 KF741928 KF741974 |
| T. viridis               | 114.72T    | NRRL 5575                   | Soil, Australia                                                      | AF285782 JX494310 KF741935 |
| T. viridulus             | 252.87T    | FRR 1863 = IMI 288716       | Soil, New South Wales, Australia                                    | JN899314 JX091385 KF741943 |

Newly generated sequences are marked in bold
Fig. 1 Phylogenies based on the ITS, BenA, CaM and combined data set showing the relationship between the new species described in the study and other members of Talaromyces sections Talaromyces and Bacillispori. Strains of known species (T. aculeatus and T. macrosporus) isolated in the course of this study are marked with asterisks in ITS and BenA phylograms. Strains belonging to new species are indicated by bold text. Support in nodes is indicated by thickened branches for bootstrap values ≥ 70, % and † indicates ex-type strains.
Fig. 1 continued.
Fig. 2 Morphological characters of *Talaromyces amazonensis* (CBS 140373T). a Colonies from left to right (top row) CYA, MEA, DG18 and OA; (bottom row) CYA reverse, MEA reverse, YES and CREA. b Colony texture and ascomata on OA after 2-week incubation. c–e Conidiophores. f Asci and ascospores. g Ascospores. h Conidia. Scale bar: h = 10 μm applies to c–h
Fig. 3 Morphological characters of *Talaromyces columbiensis*, CBS 113151T. a Colonies from left to right (top row) CYA, MEA, DG18 and OA; (bottom row) CYA reverse, MEA reverse, YES and CREA. b–d Conidiophores. e, f Asci and ascospores. g Conidia. Scale bar: \( f = 10 \mu m \) applies to b–g.
Fig. 4  Morphological characters of *Talaromyces francoae*, CBS 113134\(^T\). a Colonies from left to right (top row) CYA, MEA, DG18 and OA; (bottom row) CYA reverse, MEA reverse, YES and CREA. b–f Conidiophores. g Conidia. *Scale bar: g = 10 μm applies to b–g*. 
Fig. 5 Morphological characters of Talaromyces purgamentorum, CBS 113145T. a Colonies from left to right (top row) CYA, MEA, DG18 and OA; (bottom row) CYA reverse, MEA reverse, YES and CREA. b–f Conidiophores. g Conidia. Scale bar: g = 10 μm applies to b–g.
**Results**

**Diversity of Talaromyces species**

ITS barcoding of the isolated fungi revealed the presence of various *Talaromyces* species among the other fungi isolated from the litterbags. Two known species, *T. aculeatus* and *T. macrosporus*, were isolated from the samples, and several other isolates seemed to represent species unknown to science. They are further studied in detail below and described as new species *Talaromyces amazonensis*, *T. columbiensis*, *T. francoae* and *T. purgamentorum*.

**Phylogeny**

The phylogenies presented in Fig. 1 show that the isolates studied here are accommodated in *Talaromyces* section *Talaromyces* (i.e., *T. amazonensis*, *T. francoae* and *T. purgamentorum*) and section *Bacillispori* (*T. columbiensis*). The concatenated data set was 1348 bp in length (ITS 458 bp; *BenA* and *CaM* 445 bp). The Tamura 3-parameter (T92) with gamma distribution (+G) and invariant sites (+I) was found to be the most suitable model for the ML analysis of the combined tree (Fig. 1). For the single gene trees, the T92+G+I model was found to be the most suitable for the ML analysis of the ITS alignment, while the Kimura 2-parameter (K2)+G+I was the most suitable model for both *BenA* and *CaM* data sets. ML trees were used to present the phylogenetic data, with bootstrap values (bs) shown near the nodes of the phylogram (Fig. 1). The *BenA* and *CaM* data sets had sufficient discriminatory power to differentiate the new species from other recognized species. The ITS barcode of *T. francoae* (CBS 113134T) was identical to that of *T. apiculatus* (CBS 312.59T).

*Talaromyces columbiensis* (CBS 113151T) is located close to *T. unicus*, and *T. francoae* (CBS 113134T) is closely related to *T. kendrickii* in all phylogenies. Both *T. amazonensis* (CBS 140373T) and *T. purgamentorum* (CBS 113145T) shift their positions between phylogenies, making it difficult to determine their closest relatives.

**Morphology**

The new taxa share similarities with other known species, but can also be differentiated by various characters. Detailed descriptions of the new species are given in the Taxonomy section, and the differences from the other *Talaromyces* species are summarized in the Discussion. In short, *T. amazonensis* (CBS 140373T) produced yellow ascomata on OA at 25 and 30 °C after 1–2 weeks of incubation (Fig. 2), and its ascospores resembled those of *T. flavus*, *T. muroii*, *T. liani* and *T. thailandensis*. *Talaromyces columbiensis* (CBS 113151T) produced yellow ascomata on MEA, smooth ascospores with a single equatorial ridge, and has no growth at 37 °C (Fig. 3). No sexual state was observed in *T. francoae* (CBS 113134T) or *T. purgamentorum* (CBS 113145T). Both species produced ampulliform phialides with a tapering neck and spiny, globose conidia (Figs. 4 and 5). They were not able to grow at 37 °C and lacked acid production on CREA. *Talaromyces*

**Table 2** Production of extrolites by the *Talaromyces* species isolated in this study

| Species             | Culture collection numbers | Extrolites                                                                 |
|---------------------|-----------------------------|-----------------------------------------------------------------------------|
| *T. aculeatus*      | IBT 23209 = DTO 093-F5      | Altenusin, alternariol, an apolar dibenzofuran, mitorubrinic acid, penicillide, purpactin A, talaroderxines |
| *T. aculeatus*      | IBT 23210 = DTO 093-F6      | Alternariol, mitorubrinic acid, purpactin A, vermecillin                   |
| *T. aculeatus*      | IBT 23211 = DTO 097-F7      | Alternariol, mitorubrinic acid, purpactin A, vermecillin                   |
| *T. aculeatus*      | IBT 23212 = DTO 093-F8      | Alternariol, mitorubrinic acid, purpactin A, vermecillin                   |
| *T. amazonensis*    | CBS 140373T = IBT 23215 = DTO 093-F9 | berkelic acid, duclauxin, mitorubrinic acid, vermecillin                   |
| *T. amazonensis*    | IBT 23216 = DTO 276-H5      | Berkelic acid, duclauxin, mitorubrinic acid                                |
| *T. columbiensis*   | CBS 113151T = IBT 23206 = DTO 053-F3 | A corymbiferan lactone, duclauxin, mitorubrin, mitorubrinic acid, wortmannin |
| *T. francoae*       | CBS 113134T = IBT 23221 = DTO 056-D9 | Berkelic acid, mitorubrin, mitorubrinic acid, vermecillin                  |
| *T. macrosporus*    | CBS 116297 = IBT 23205 = DTO 189-B9  | A corymbiferan lactone, duclauxin                                          |
| *T. purgamentorum*  | CBS 113145T = IBT 23220 = DTO 056-E1 | A dibenzofuran, penicillide, purpactin A, a shamixanthone, a violaceol     |
purpamentorum exhibited restricted growth on DG18 and YES compared to T. francoae.

**Extrrolites**

The species described here produce various extrrolites, all of which are previously found in *Talaromyces* (Frisvad et al. 1990). Especially common are mitorubrinic acid, alternariol and the penicillides (Table 2). Details on the extrrolites found in each species are given in the species descriptions.

**Discussion**

This study focused on four novel *Talaromyces* species isolated from leaf litter in several Colombian lowland rain forests. The multiple gene phylogenies (ITS, *BenA* and *CaM*) resolved strains into four distinct lineages that represent species. Based on a multigene phylogeny (ITS, *BenA* and *RPB2*), Yilmaz et al. (2014) divided the genus into seven clades and provided a sectional classification. Three of the species from this study are located in *Talaromyces* section *Talaromyces*, whereas one species (T. colombiensis) falls in section *Bacilliospori*. Previous studies showed that ITS, which is the accepted DNA barcode for fungi (Schoch et al. 2012), is not sufficient to distinguish all *Talaromyces* species (Yilmaz et al. 2012; Frisvad et al. 2013; Manoeh et al. 2013; Yilmaz et al. 2014). As a result, Yilmaz et al. (2014) proposed the use of *BenA* as a suitable secondary barcode marker for identification of *Talaromyces* isolates. With the exception of *T. francoae*, however, all newly described species could be identified by using ITS alone. *BenA* and *CaM* data sets showed that all novel species are clearly distinct from previously described *Talaromyces* species.

Visagie et al. (2015) revised *Talaromyces* species producing ampulliform phialides and rough-walled, globose conidia, and recognized eight species. Except for *T. kendrickii*, all species could grow at 37 °C. In this study, *T. francoae* and *T. purpamentorum* have ampulliform phialides and rough-walled, globose conidia. Neither species grows at 37 °C, and neither produces acid on CREA. These two characters of the new species are shared with *T. kendrickii*. However, on CYA at 25 °C, *T. kendrickii* (25–31 mm) grows faster than *T. francoae* (8–10 mm) and *T. purpamentorum* (19–20 mm). *Talaromyces francoae* differs from *T. purpamentorum* by their growth rates on CYA and YES. The former species exhibits restricted growth on CYA (8–10 mm) and moderately fast growth on YES (20–22 mm), while *T. purpamentorum* attains a diameter on CYA of 19–20 mm and 10–12 mm on YES. *Talaromyces amazonensis* produces yellow ascomata with spiny, ellipsoidal ascospores, and these characters are common in the genus *Talaromyces*. Ascospores of *T. amazonensis* resemble those of *T. flavus*, *T. muroii*, *T. thailandensis*, and *T. liani*. Both *T. flavus* and *T. muroii* grow more restrictedly on CYA than *T. amazonensis* (9–16 mm vs. 30–38 mm). *Talaromyces amazonensis* differs from *T. thailandensis* by its ability to grow at 37 °C. The main difference between *T. liani* and *T. amazonensis* is the ascoma colour. *Talaromyces liani* has orange-red ascomata, whereas the ascomata of *T. amazonensis* are yellow. *Talaromyces columbiensis* produces abundant yellow ascomata and smooth-walled ascospores with a single ridge on MEA after 2 weeks of incubation at 25 °C. This species is phylogenetically closely related to *T. unicus*, which also produces ascospores with a single equatorial ridge. However, *T. unicus* differs by the production of ascospores with a very rough to spiny wall. *Talaromyces stipitatus* also produces ellipsoidal, smooth-walled ascospores with a single equatorial ridge. However, this species grows faster on standard agar media (CYA, MEA, OA and YES) and is able to grow on CYA incubated at 37 °C.

*Talaromyces* is an important genus in biotechnology and in medical and food mycology (Yilmaz et al. 2014). *Talaromyces* species are isolated worldwide from many kinds of substrates, including house dust, decaying leaves, soil, air, compost, food products, humans and animals. The fungi are considered key players in leaf litter decomposition because of their ability to produce a wide range of extracellular enzymes (de Boer et al. 2005), and some *Talaromyces* species also produce cellulose-degrading enzymes (Pol et al. 2012; Maeda et al. 2013; Fuji et al. 2014). In this study, we isolated six *Talaromyces* species from leaf litter in the Colombian Amazon region. Two of them, *T. aculeatus* and *T. macrosporus*, have been previously described. The other four species are new to the literature, and thus far found only in decomposed leaf litter in Amazonia, Colombia.

The new *Talaromyces* species were efficient producers of a series of anticancer compounds. *Talaromyces amazonensis* in particular produced three different anticancer compounds: duclauxin, berkelic acid and vermicillin. It would be interesting to determine whether these anticancer compounds have a synergistic effect when combined. Another interesting compound found in *T. columbiensis* was wortmannin, also an anticancer compound, with several additional biological activities.

**Taxonomy**

*Talaromyces amazonensis* Yilmaz, López-Quintero, Vascopal., Frisvad & Houbraken, sp. nov. Mycobank MB816230. Fig. 2.
**Etymology:** From Amazonas, the department from which the species was isolated.

**Diagnosis:** Moderately fast growth on CYA, MEA, YES and OA at 25 °C, restricted growth on DG18 at 25 °C, moderate acid production on CREA. Abundant yellow ascomata produced on MEA and OA after 1–2 weeks at 25 °C with broadly ellipsoidal, thick-walled, spiny ascospores.

**Typus:** Colombia, dept. Amazonas, Araracuara community in the Middle Caquetá, ex mixed leaves in litterbag, after 6 months of decomposition in a mature forest, isolated in July 2000, C. López-Quintero (holotype HUA 197223; culture ex-type CBS 140373 = IBT 23215 = DTO 093-F9).

**ITS barcode:** KX011509 (alternative markers: BenA = KX011490; CaM = KX011502).

**Colony diameter 7 days (mm):** CYA 30–38; CYA 30 °C 35–42; CYA 37 °C 19–22; MEA 40–45; MEA 30 °C 50–55; DG18 20–25; CYAS No growth; OA 30–45; CREA 12–18; YES 35–42.

**Colony characters:** CYA 25 °C, 7 days: Colonies slightly raised at centre, slightly sulcate; margins low, plane, entire (2 mm); mycelium white and in the centre brownish red due to the pigmentation in reverse; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse light yellow (4A4) with dark red (10C8) dots. MEA 25 °C, 7 days: Colonies slightly raised at centre, plane; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation sparse to moderately dense at centre, conidia en masse dull green (27D3); soluble pigments absent; exudates absent; reverse greyish orange (5B6–6B6). YES 25 °C, 7 days: Colonies sunken at centre, slightly sulcate; margins low, plane, entire (2–3 mm); mycelium white; in some parts pastel-red and in the centre yellowish brown (5E4) due to the reverse pigment; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse greenish yellow to greenish grey (28A2–28B2). OA 25 °C, 7 days: Colonies low, plane, yellow ascomata also at 30 °C abundant; margins low, plane, entire (4–5 mm); mycelium yellow; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse pastel-yellow. CREA 25 °C, 7 days: weak growth, moderate acid production.

**Micromorphology:** Conidiophores biverticillate, sometimes monoverticillate; stipes smooth-walled, 30–220 × 2–3 µm; metulae divergent, two to five, 7.5–12 × 2.4–3.8 µm; phialides acerose, two to five per metula, 8–13 × 2–3 µm; conidia smooth-walled, ellipsoidal, 2.5–4(–6) × 2–3 µm. Ascomata bright yellow, globose to subglobose, abundantly ripening within 1–2 weeks on OA at 25 °C, covered with a few layers of well-developed networks of yellow hyphae; asci broadly globose to subglobose, 9–13 × 8–12 µm; ascospores broadly ellipsoidal, thick-walled, spiny, 3–5.5 × 2–4 µm.

**Extracellular:** Talaromyces amazonensis produces berkelic acid, duclauxin, mitourubrinic acid and vermicillin. Berkelic acid was first found as an anticancer agent in *T. ruber* (Stierle et al. 2006). The anticancer agent duclauxin was first found in *T. duclauxii*, but this compound has also been reported from *T. macrosporus* (Shibata et al. 1965; Frisvad et al. 1990; Bryant et al. 1993). Duclauxin was also reported from *Penicillium herquei* and *P. manginii* (Bryant et al. 1993; Cao et al. 2015), but the strains used had been misidentified, and the producers were *Talaromyces* species as well. Vermicillin is the third anticancer agent from *T. amazonensis* (Fuska et al. 1979). Mitourubrinic acid is a common azaphilone metabolite in the genus *Talaromyces* (Frisvad et al. 1990).

**Talaromyces colombiensis** Yilmaz, López-Quintero, Vasco-Pal., Frisvad & Houbraken, *sp. nov*. Mycobank MB 816231. Fig. 3.

**Etymology:** From Colombia, the country where the species was isolated.

**Diagnosis:** Restricted growth on CYA, MEA, YES, OA and DG18 at 25 °C and no growth at 37 °C. Yellow ascomata abundant on MEA after 2 weeks at 25 °C with ellipsoidal, smooth, single equatorial ridge ascospores.

**Typus:** Colombia, Amazonia, Natural Park Amacayacu, ex litterbag containing fresh mixed leaves from mature forest, isolated in September 2004, C. López-Quintero (holotype HUA 197225; cultures ex-type CBS 113151 = IBT 23206 = DTO 058-F3).

**ITS barcode:** KX011503 (alternative markers: BenA = KX011488; CaM = KX011499).

**Colony diameter 7 days (mm):** CYA 15–17; CYA 30 °C 18; CYA 37 °C No growth; MEA 15–17; MEA 30 °C 16–17; DG18 5; CYAS 3; OA 15–17; CREA 8–10; YES 14–15.

**Colony characters:** CYA 25 °C, 7 days: Colonies low, sulcate; margins low, plane, entire (1 mm); mycelium white and yellow; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse yellowish brown (5F5) centre fading to brownish orange to yellowish brown (5C5–5D5–5E5). MEA 25 °C, 7 days: Colonies raised at centre, sulcate; margins low, plane, entire (1 mm); mycelium dominantly yellow, in the margins white; texture floccose; sporulation sparse, conidia en masse greyish green (28C5–28D5); soluble pigments pale red; exudates absent; reverse brownish orange (7B7) fading to reddish orange (7B7). YES 25 °C, 7 days: Colonies raised at centre, sulcate; margins low, plane, entire (1 mm); mycelium white, brownish orange to light brown (7C5–7D5); texture floccose; sporulation absent to sparse; soluble pigments absent; exudates absent; reverse brownish orange (5C5) centre fading to greyish orange (5B5). DG18 25 °C, 7 days: Colonies covered with sterile white mycelium; reverse yellowish white (4A2). OA 25 °C, 7 days: Colonies raised at centre, slightly
Talaromyces francoae Yilmaz, López-Q., Vasco-Pal. & Houbraken, sp. nov. Mycobank MB 816232. Fig. 4.

**Etymology:** named after the original substrate of the type strain, decomposed leaf litter debris.

**Diagnosis:** Conidiophores biverticillate with ampulliform phialides that taper to a very thin neck producing rough-walled, verrucose conidia. Lack of acid production on CREA and absence of growth on CYA at 37 °C. Restricted growth on YES (10–12 mm) and DG18 (5–6 mm) at 25 °C.

**Typus: Colombia,** Dept. Amazonas, Peña Roja, ex mixed leaf litter from 4 months old litterbag in Pseudomonotes tropenbosi (Dipterocarpaceae) forest, isolated in March 2000, C. López-Quintero (holotype HUA 197222; culture ex-type CBS 113145 = IBT 23220 = DTO 056-E1).

**ITS barcode:** KX011504 (alternative markers: BenA = KX011487; CaM = KX011501).

**Colony diameter 7 days (mm):** CYA 8–10; CYA 30 °C 29–30; CYA 37 °C No growth; MEA 20–21; MEA 30 °C 37–38; DG18 10–11; CYAS No growth; OA 35–37; CREA 5–9; YES 20–22.

**Colony characters:** CYA 25 °C, 7 days: Colonies raised at centre, slightly sulcate; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation moderately dense, conidia *en masse* dull to greyish green (25D4–25D5); soluble pigments absent; exudates absent; reverse pale orange (5A3–6A3). MEA 25 °C, 7 days: Colonies raised, slightly sulcate; margins low, plane, entire (2 mm); mycelium white; texture floccose and velvety; sporulation dense, conidia *en masse* dull to greyish green (26D4–27D4); soluble pigments absent; exudates absent; reverse greyish orange (5B6) with reddish brown (8D8) dots and circle. YES 25 °C, 7 days: Colonies raised at centre, sulcate; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation absent to sparse; soluble pigments absent; exudates absent; reverse brownish red (8C8) centre fading to light orange (5A4). DG18 25 °C, 7 days: Colonies sterile, raised, plane; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation moderately dense to dense, conidia *en masse* greyish green (26D5–26E5); soluble pigments absent; exudates absent; reverse pastel-red in centre fading to beige (at 30 °C violet red). CREA 25 °C, 7 days: weak growth, acid production absent.

**Mcromorphology:** Conidiophores biverticillate; stipes smooth-walled, (40–) 50–130 (–145) × 2.4–3 μm; metulae divergent, three to six, 8.5–11.5 × 2.4–3.5 μm; phialides acerose, sometimes atypical, two to six per metula, 7–9.5 × 1.5–2.5 μm; conidia smooth-walled, ovoid to ellipsoidal, 2.5–3 × (1.8–) 2–2.5 μm. Ascomata bright yellow, globose to subglobose, ripening within 1–2 weeks on OA at 25 °C, covered with layers of well-developed networks of yellow hyphae; ascospores broadly globose to subglobose, 7–9 × 7.5–10 μm; ascospores ellipsoidal, finely rough to spiny, usually with a single equatorial ridge, 2.5–4.2 (–5) × 2.5–3.5 μm.

**Extrolites:** Talaromyces colombiensis produced duclauxin and several related naphthalenones, but also mitorubrins and wortmannin. Wortmannin was originally discovered as an antifungal agent, but it is also a potent enzyme inhibitor of regulatory kinases and is thus an interesting anticancer drug candidate (Wipf and Halter 2005). Wortmannin was originally reported from *T. wortmannii* and *T. flavus* (Brian et al. 1957), but these two species are not able to produce wortmannin (Yilmaz et al. 2014). It is thus interesting that *T. colombiensis* can produce this compound. Wortmannin has also been mentioned as a hemorrhagic mycotoxin (Abbas and Mirocha 1998) and an inhibitor of aflatoxin biosynthesis (Lee et al. 2007).

**Talaromyces francoae** Yilmaz, López-Q., Vasco-Pal. & Houbraken, sp. nov. Mycobank MB 816232. Fig. 4.

**Etymology:** named after the family name of Dr. Ana Esperanza Franco-Molano, who made major contributions to Colombian mycology.

**Diagnosis:** Conidiophores biverticillate with ampulliform phialides that taper to a very thin neck producing rough-walled, verrucose conidia. Lack of acid production on CREA and absence of growth on CYA at 37 °C. Restricted growth on CYA at 25 °C (8–10 mm).

**Typus: Colombia,** Dept. Amazonas, Peña Roja, ex leaf litter from 4-month old litterbag in *Pseudomonotes tropenbosis* (Dipterocarpaceae) forest, isolated in March 2000, C. López-Quintero (holotype HUA 197222; culture ex-type CBS 113134 = IBT 23221 = DTO 056-D9).

**ITS barcode:** KX011510 (alternative markers: BenA = KX011489; CaM = KX011501).

**Colony diameter 7 days (mm):** CYA 30–100; CYA 30 °C 29–30; CYA 37 °C No growth; MEA 20–21; MEA 30 °C 37–38; DG18 10–11; CYAS No growth; OA 35–37; CREA 5–9; YES 20–22.

**Colony characters:** CYA 25 °C, 7 days: Colonies raised at centre, slightly sulcate; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation moderately dense, conidia *en masse* dull to greyish green (25D4–25D5); soluble pigments absent; exudates absent; reverse pale orange (5A3–6A3). MEA 25 °C, 7 days: Colonies raised, slightly sulcate; margins low, plane, entire (2 mm); mycelium white; texture floccose and velvety; sporulation dense, conidia *en masse* dull to greyish green (26D4–27D4); soluble pigments absent; exudates absent; reverse greyish orange (5B6) with reddish brown (8D8) dots and circle. YES 25 °C, 7 days: Colonies raised at centre, sulcate; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation absent to sparse; soluble pigments absent; exudates absent; reverse brownish red (8C8) centre fading to light orange (5A4). DG18 25 °C, 7 days: Colonies sterile, raised, plane; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation moderately dense to dense, conidia *en masse* greyish green (26D5–26E5); soluble pigments absent; exudates absent; reverse pastel-red in centre fading to beige (at 30 °C violet red). CREA 25 °C, 7 days: weak growth, acid production absent.

**Mcromorphology:** Conidiophores biverticillate; stipes smooth-walled, 125–450 × 2.2–3 μm; metulae divergent, 3–6, 8–13 × 2.5–4.5 μm; phialides ampulliform, tapering to a very thin neck, 3–6 per metula, 8.5–12 × 2.5–4 μm; conidia verrucose, rough-walled, globose, 2.5–4 × 2.5–4 μm.

**Extrolites:** Talaromyces francoae produces berkelic acid, mitorubrin, mitorubrinic acid and vermicillin.
velvety; sporulation dense, conidia en masse dull green (26D4–26E4); soluble pigments absent; exudates absent; reverse brown (6E7) centre reddish brown fading to greyish yellow (8D6 and 4B5). MEA 25 °C, 7 days: Colonies low, slightly sulcate; margins low, plane, entire (1–2 mm); mycelium white; texture velvety; sporulation dense, conidia en masse dull green (26D4–26E4); soluble pigments absent; exudates absent; reverse brownish orange (5C6–6C6). YES 25 °C, 7 days: Colonies slightly raised, sterile white aerial mycelium, slightly sulcate; margins low, plane, entire (<1 mm); mycelium white; texture floccose and funiculose; sporulation absent to sparse; soluble pigments absent; exudates absent; reverse bronze brown (5E5) centre fading to greyish orange (5B5). DG18 25 °C, 7 days: Colonies slightly raised, plane; margins low, plane, entire (<1 mm); mycelium white; texture velvety; sporulation dense, conidia en masse dull green (26D4–26E4); soluble pigments absent; exudates absent; reverse light brown (5D4–5D5). OA 25 °C, 7 days: Colonies low, plane; margins low, plane, entire (4–5 mm); mycelium white; texture velvety; sporulation moderately dense, conidia en masse dull green (28D4); soluble pigments absent; exudates absent; reverse pastel red. CREA 25 °C, 7 days: Weak growth, acid production absent.

**Micromorphology**: Conidiophores biverticillate; stipes smooth-walled, 170–300 × 2.8–4.2 μm; metulae divergent, 3–6, 7–11.5 × 3–4.5 μm; phialides ampulliform, tapering to a very thin neck, 3–6 per metulae, 7.5–12.5 × 3–4 μm; conidia rough-walled, globose to subglobose, 2–3.3 × 2–3 μm.

**Extrólites**: *Talaromyces purgamentorum* produces a dibenzofuran, penicillidine, purpactin A, a shamilpanthone and a violaceol. The dibenzofuran had the same UV spectrum as karnatakafurans A and B (Manniche et al. 2004), but was absent; reverse light brown (5D4–6E7) centre reddish brown fading to greyish orange (5B5). MEA 25 °C, 7 days: Colonies low, plane; margins low, plane, entire (4–5 mm); mycelium white; texture velvety; sporulation dense, conidia en masse dull green (28D4); soluble pigments absent; exudates absent; reverse pastel red. CREA 25 °C, 7 days: Weak growth, acid production absent.

**Acknowledgments** This research was supported in part by NWO-WOTRO grants 895.100.014 and WB 84-525. Aida Vasco received grants from The Netherlands Fellowship Programmes (NFP) of the Netherlands organization for international cooperation in higher education (NUFFIC), The Faculty for the Future of Schlumberger Foundation (FFTF Grant 2011–2013) and The International Foundation of Science (IFS Grant D:5052–1, 2011-2-130). Further financial support from the Studienstiftung Mykologie and the CBS-KNAW is greatly appreciated. Logistical support and collection permission was given by Tropenbos Colombia, and we thank Dr. Carlos Rodriguez for this. Uwe Braun is thanked for his advice on the new species names. Finally, we want to thank the indigenous people and the workers in the Parque Natural Nacional Amacayacu, Araracuara and Meta for their willingness to collaborate in this study.

**Open Access** This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

**References**

Abbas HK, Mirocha CJ (1998) Isolation and purification of hemorrhagic factor (wortmannin) from *Fusarium oxysporum* (N17B). Appl Environ Microbiol 54:1268–1274

Brian PW, Curtis PJ, Hemming HG, Norris GLF (1957) Wortmannin, an antibiotic produced by *Penicillium wortmannii*. Trans Br Mycol Soc 40:365–368

Bryant FO, Cutler HG, Jacyno JM (1993) Properties and cost-effective method for production of the antitumor agent duclauxin from sporation *Penicillum herquei*. J Pharm Sci 82:1214–1217

Cao P, Yang J, Miao C-P, Uan Y, Ma Y-T, Li X-N, Zhao L-X, Huang S-X (2015) New duclauxamides from *Penicillium manginii* YIM PH30375 and structure revision of the duclauxin family. Org Lett 17:1146–1149

Chung M-C, Lee H-J, Chun H-K, Kho Y-H (1998) Penicillidine, a nonpeptide calpain inhibitor, produced by *Penicillium* sp. F60760. J Microbiol Biotechnol 8:188–190

de Boer W, Folman LB, Summerbell RC, Boddy L (2005) Living in a fungal world: impact of fungi on soil bacterial niche development. FEMS Microbiol Rev 29:795–811

Frisvad JC, Filtenborg O, Samson RA, Stolk AC (1990) Chemotaxonomy of the genus *Talaromyces*. Antonie Van Leeuwenhoek 57:179–189

Frisvad JC, Yilmaz N, Thane U, Rasmussen KB, Houbrenker J, Samson RA (2013) *Talaromyces atraeous*, a new species efficiently producing industrially relevant red pigments. PLoS ONE 8:e84102

Fuji T, Hoshino T, Inoue H, Yano S (2014) Taxonomic revision of the cellulose degrading fungus *Acremonium cellulosidoticus* nomad nudum to *Talaromyces* based on phylogenetic analysis. FEMS Microbiol Lett 351:32–41

Fuska J, Nemec P, Fusková A (1979) Vermicillin, a new metabolite from *Penicillium verruculosum* inhibiting tumor cells in vitro. J Antibiot 32:667–669

Houbrenker J, López-Quintero CA, Frisvad JC, Boekhout T, Theelen B, Esperanza Franco-Molano A, Samson RA (2011) *Penicillium araracureannae* sp. nov., *Penicillium elleniae* sp. nov., *Penicillium penarjense* sp. nov., *Penicillium vanderhammii* sp. nov. and *Penicillium wotroi* sp. nov., isolated from leaf litter. Int J Syst Evol Microbiol 61:1462–1475

Houbrenker J, Spierenburg H, Frisvad JC (2012) *Rasamsonia*, a new genus comprising thermotolerant and thermophilic *Talaromyces* and *Geoosmithia* species. Antonie Van Leeuwenhoek 101:403–421

Kildgaard S, Mansson M, Dosen I, Kildgaard A, Frisvad JC, Larsen TO, Nielsen KF (2014) Accurate dereplication of bioactive secondary metabolites from marine-derived fungi by UHPLC-DAD-QTOFMS and MS/HRMS library. Mar Drugs 12:3681–3705

Kildgaard A, Iversen A, Andersen MR, Larsen TO, Frisvad JC, Nielsen KF (2014) Aggressive dereplication using UHPLC-DAD-QTOF-screening extracts for up to 3000 fungal secondary metabolites. Anal Bioanal Chem 406:1933–1943

Komerup A, Wanscher JH (1967) Methuen handbook of colour. Methuen & Co Ltd, Copenhagen

Lee J-W, Roze LV, Linz JE (2007) Evidence that a wortmannin-sensitive signal transduction pathway regulates aflatoxin biosynthesis. Mycologia 99:562–568
López-Quintero CA, Stratsma G, Franco-Molano AE, Boekhout T (2012) Macrofungal diversity in Colombian Amazon forests varies with regions and regimes of disturbance. Biodivers Conserv 21: 2221–2243

López-Quintero CA, Atanasova L, Esperanza Franco-Molano A, Gams W, Komon-Zelazowska M, Theelen B, Müller WH, Boekhout T, Druzhinina I (2013) DNA barcoding survey of Trichoderma diversity in soil and litter of the Colombian lowland Amazonian rainforest reveals Trichoderma strigosellum sp. nov. and other species. Antonie Van Leeuwenhoek 104:657–674

Maeda RN, Barcelos CA, Santa Anna LM, Pereira N Jr (2013) Cellulase production by Penicillium faniculosum and its application in the hydrolysis of sugar cane bagasse for second generation ethanol production by fed batch operation. J Biotechnol 163:38–44

Maggs J (1985) Litter fall and retranslocation of nutrients in a refertilized and prescribed burned Pinus elliottii plantation. For Ecol Manag 12: 253–268

Manniche S, Sprogøe K, Dalsgaard PW, Christophersen C, Larsen TO (2004) Karnatakafurans A and B: two dibenzofurans isolated from the fungus Aspergillus karnatakaensis. J Nat Prod 67:2111–2112

Manoch L, Dethoup T, Yilmaz N, Houbraken J, Samson RA (2013) Two new Talaromyces species from soil in Thailand. Mycoscience 54: 335–342

Pol D, Laxman RS, Rao M (2012) Purification and biochemical characterization of endoglucanase from Penicillium pinophilum MS 20. Indian J Biochem Biophys 49:189–194

Proksa B, Uhrin D, Adamcová J, Fuska J (1992) Vermixocins A and B, two novel metabolites from Penicillium verruculatum. J Antibiot 45:1268–1272

Romero SM, Romero AI, Barrera V, Comorio R (2016) Talaromyces systylos, a new synonymsatous species from Argentinean semi-arid soil. Nova Hedwigia 102:241–256

Samson RA, Yilmaz N, Houbraken J, Spierenburg H, Seifert KA, Peterson SW, Varga J, Frisvad JC (2011) Phylogeny and nomenclature of the genus Talaromyces and taxa accommodated in Penicillium subgenus Biverticillium. Stud Mycol 70:159–183

Sassa T, Niwa G, Unno H, Ikeda M, Miura Y (1974) Structure of penicillicide, a new metabolite produced by a Penicillium sp. Tetrahedron Lett 15:3941–3942

Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Lévesque CA, Chen W, Fungal Barcoding Consortium (2012) Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. PNAS 109:6241–6246

Shibata S, Ogihara Y, Tokutake N, Tanaka O (1965) Duclauxin, a metabolite of Penicillium duclauxii (Delacroix). Tetrahedron Lett 6:1287–1288

Smedsgaard J (1997) Micro-scale extraction procedure for standardized screening of fungal metabolite production in cultures. J Chromatogr A 760:264–270

Sterle AA, Sterle DB, Kelly K (2006) Berkelic acid, a novel spiroketal with selective anticancer activity from an acid mine waste fungal extremophile. J Org Chem 71:5357–5360

Suzuki K, Nozawa K, Usagawa S, Nakajima S, Kawai K (1991) Penicillide and dehydropenicillide from Talaromyces derxii. Phytochemistry 30:2096–2098

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. Mol Biol Evol 30:2725–2729

Tomoda H, Nishida H, Masuma R, Cao J, Okuda S, Omura S (1991) Purpactins, new inhibitors of acyl-CoA:cholesterol acyltransferase produced by Penicillium purpureogenum. I. Production, isolation and physico-chemical and biological properties. J Antibiot 44:136–143

Vasco-Palacios AM, Franco-Molano AE (2013) Diversity of Colombian macrofungi (Ascomycota–Basidiomycyte). Mycotaxon 121:499

Vasco-Palacios AM, López-Quintero C, Franco-Molano AE, Boekhout T (2014) Austroboletus amazonicus sp. nov. and Fistulinella campinaranae var. scrobiculata, two commonly occurring boletes from a forest dominated by Pseudomones tropenbosii (Dipterocarpaceae), in Colombian Amazonia. Mycologia 106: 1004–1014

Visagie CM, Houbraken J, Frisvad JC, Hong S-B, Klaassen CHW, Perrone G, Seifert KA, Varga J, Yaguchi T, Samson RA (2014) Identification and nomenclature of the genus Penicillium. Stud Mycol 78:343–371

Visagie CM, Yilmaz N, Frisvad JC, Houbraken J, Seifert KA, Samson RA, Jacobs K (2015) Five new Talaromyces species with amplyliform-like phialides and globose rough walled conidia resembling T. verruculosus. Mycosenctes 56:486–502

Wang QM, Zhang YH, Wang B, Wang L (2016) Talaromyces neofusisporus and T. qii, two new species of section Talaromyces isolated from plant leaves in Tibet, China. Sci Rep 6:18622

Wipf P, Halter RJ (2005) Chemistry and biology of wortmannin. Org Biomol Chem 3:2053–2061

Yilmaz N, Houbraken J, Hoekstra ES, Frisvad JC, Visagie CM, Samson RA (2012) Delimitation and characterisation of Talaromyces purpureogenum and related species. Persoonia 29:39–54

Yilmaz N, Visagie CM, Houbraken J, Frisvad JC, Samson RA (2014) Polyphasic taxonomy of the genus Talaromyces. Stud Mycol 78: 175–342

Yilmaz N, Visagie CM, Frisvad JC, Houbraken J, Jacobs K, Samson RA (2016) Taxonomic re-evaluation of species in Talaromyces section Islandici, using a polyphasic approach. Persoonia 36:37–56