Czech Mycology 73(2): 173–184, November 3, 2021 (online version, ISSN 1805-1421)

Triadelphia morgoensis, an enigmatic wood-associated hyphomycete: second record, updated description and molecular identification

Alena Kubátová, Vít Hubka

Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01 Praha 2, Czech Republic; kubatova@natur.cuni.cz, vit.hubka@gmail.com

Kubátová A., Hubka V. (2021): *Triadelphia morgoensis*, an enigmatic wood-associated hyphomycete: second record, updated description and molecular identification. – Czech Mycol. 73(2): 173–184.

Triadelphia (*Ascomycota*, *Microascales*) is a genus encompassing pleomorphic dematiaceous micromycetes occurring sporadically on rotting wood and other plant material, infrequently also on other substrates. In this study, we document a second record of *Triadelphia morgoensis*, found on a twig of *Populus nigra* near Prague (Czech Republic), after its original description from decaying wood in Hungary. This fungus is characterised by the production of three types of conidia. The identification was achieved by a combination of morphological, physiological and genetic traits. The description of the fungus is emended, and its differentiation from similar species is discussed. Multigene phylogeny showed that *T. morgoensis* is most closely related to *T. loudetiae* and *T. heterospora*. The DNA data from three loci generated in this study (ITS, LSU, *RPB2*) will facilitate identification of the species in the future. Our results add to the knowledge on the ecology and phylogeny of this understudied fungus, for which neither living type material nor a molecular sequence has been preserved.

Key words: microfungi, *Sordariomycetes*, *Triadelphiaceae*, multigene phylogeny.

Article history: received 19 June 2021, revised 22 September 2021, accepted 27 September 2021, published online 3 November 2021.

DOI: https://doi.org/10.33585/cmy.73205

Kubátová A., Hubka V. (2021): Enigmatický dřevní hyfomycet *Triadelphia morgoensis*: druhý nález, aktualizovaný popis a molekulární identifikace. – Czech Mycol. 73(2): 173–184.

Triadelphia (*Ascomycota*, *Microascales*) je rod zahrnující pleomorfní demaciové mikromycety, nacházené sporadicky na rozkládajícím se dřevě a jiném rostlinném materiálu či méně často na jiných substrátech. V této práci prezentujeme druhý nález houby *Triadelphia morgoensis*, objevené na větévce topolu černého poblíž Prahy; první nález pochází z Maďarska, odkud byl druh popsán. Tato houba je charakteristická tvorbou tří typů konidií. Byla identifikována na základě kombinace morfologických, fyziologických a genetických znaků. Je uveden její popis a diskutovány rozdíly oproti podobným druhům. Multigenová fylogeneze ukázala, že *T. morgoensis* je nejvíce příbuzná druhům *T. loudetiae* a *T. heterospora*. Údaje o DNA ze tří lokusů generovaných v této studii (ITS, LSU, *RPB2*) usnadní identifikaci tohoto druhu v budoucnosti. Výsledky této studie rozšiřují naše znalosti o ekologii a fylogenezi této málo prozkoumané houby, u které dosud neexistoval živý materiál ani dostupná molekulární sekvence.

Introduction

During a mycological field excursion in central Bohemia (Czech Republic) in 2004, poplar twigs were collected and a fungus with conspicuous conidia was isolated. Despite its characteristics, the fungus was not identified and was stored in the refrigerator. Surprisingly, it survived there on slope agar without any re-inoculation for 16 years. In 2020, when DNA sequences were analysed, the fungus was confirmed to belong to the genus *Triadelphia*.

The genus *Triadelphia* (*Ascomycota*, *Sordariomycetes*, *Microascales*, *Triadelphiaceae*) was described fifty years ago (Shearer et Crane 1971). The *Triadelphiaceae* family itself was introduced for the genus *Triadelphia* only recently (Luo et al. 2019). It is a small genus, currently comprising only eighteen species (according to Index Fungorum, www.indexfungorum.org, accessed on 11th August 2021). It encompasses pleomorphic dematiaceous micromycetes, some of which are able to form up to six conidial types (Constantinescu et Samson 1982); Réblová et al. (2016) even mentioned eight types of conidia.

Different species have been recorded worldwide (Africa, Asia, Australia, Europe, North America), more often in warmer regions, but relatively sporadically. For details, see the latest work by Chuaseeharonnachai et al. (2020). *Triadelphia* species are usually found on rotting wood or other plant material, often submerged in water. Three species represent exceptions in this aspect, namely *T. pulvinata* and *T. disseminata*, which were isolated from clinical material as opportunistic human pathogens (e.g. Al-Hedaithy 2001, Crous et al. 2015), and *T. moubasheri*, isolated from the gut of a red palm weevil in Egypt (Abdel-Sater et Soliman 2017).

In recent years, new species have been described (e.g. Crous et al. 2015, Li et Ye 2017, Chuaseeharonnachai et al. 2020) and the phylogeny of this group has been studied in more detail using DNA sequence data from rDNA (ITS, LSU and SSU regions) and the *RPB2* gene. Réblová et al. (2016) pointed to the polyphyly of the *Triadelphia* genus and reclassified *T. uniseptata* into the *Savoryellales*. In their phylogenetic study, Chuaseeharonnachai et al. (2020) transferred synnematic representatives to the new genus *Synnematotriadelphia*.

Despite the great increase in knowledge of the genus *Triadelphia*, our knowledge of the ecology of its species is very limited. Many species lack ex-type cultures and DNA data to facilitate identification of these fungi. One such example is *T. morgoensis*, which is only known from the original collection and herbarium specimen.

In this work, we document micro- and macroscopic features of this species based on living culture, revise and supplement its description, and publish valuable sequence data which can be used for identification of this species in future studies.

MATERIAL AND METHODS

Material studied

Locality: Czech Republic, central Bohemia, Bojov, ca 10 km SSW of Prague.

Substrate: Withered twig of a black poplar (*Populus nigra* var. *italica*), coll. A. Kubátová, 13 May 2004, isol. A. Kubátová (AK 106/04), July 2004.

Specimens: The living isolates are maintained at the Culture Collection of Fungi (CCF), Department of Botany, Faculty of Science, Charles University, Prague (Czech Republic) under accession number CCF 6437 and the Westerdijk Fungal Biodiversity Institute, Utrecht (The Netherlands) under accession number CBS 148471. The herbarium item (dried colony) is stored in the Herbarium of Charles University, Prague (PRC) under code PRC 4682.

Cultivation. The twig was incubated in a moist chamber for several weeks. The fungus was isolated on potato carrot agar (PCA). Colony diameters were measured after 14 days at 20, 25, 30, and 37 °C on PCA, oat agar (OA), malt extract agar (MEA) and potato dextrose agar (PDA) (according to Samson et al. 2010). Three replicates were used.

Micromorphology. Microscopic characters were examined after 5 weeks from colonies on MEA and mounted on slides with lactic acid including cotton blue. An Olympus BX51 microscope with a DP72 camera was used for observation (maximum magnification 1600×). Photomicrographs and measurements were made with the QuickPHOTO MICRO 3.0 and Helicon Focus 5.0 software. For each structure, 40 measurements were performed.

Molecular analyses. An ArchivePure DNA yeast and Gram2+ kit (5PRIME Inc., Gaithersburg, MD, USA) were used to isolate genomic DNA from 7-day-old colonies grown on MEA (Oxoid Ltd., Basingstoke, UK). The internal transcribed spacer regions (ITS1-5.8S-ITS2 cluster) and partial large subunit (LSU) ribosomal DNA region were amplified and sequenced with the primers ITS1 and NL4, and NL1 and LR6, respectively (Vilgalys et Hester 1990, White et al. 1990, O'Donnell 1993). The obtained sequences were subsequently assembled into one sequence containing both regions. The partial fragment of the *RPB2* gene, encoding the second largest RNA polymerase subunit, was amplified using the primers RPB2-5F2 (Sung et al. 2007) and fRPB2-7cR (Liu et al. 1999). The obtained DNA sequences were compared with those derived from the ex-type or reference strains and were deposited into the GenBank database under accession numbers MW429270 (region containing ITS and LSU rDNA) and MW411332 (*RPB2* gene).

Phylogeny. The sequences of ITS, LSU and *RPB2* of the *Triadelphiaceae* members were retrieved from previous studies (Réblová et al. 2016, Lu et al. 2018, Chuaseeharonnachai et al. 2020) and their accession numbers are listed in Tab. 1. Alignments of the regions were performed using the FFT-NS-i option implemented in MAFFT online (Katoh et al. 2019). The alignments were trimmed,

concatenated, and then analysed using the maximum likelihood (ML) and Bayesian inference (BI) methods. The dataset contained 13 taxa and a total of 2477 characters, of which 669 were variable and 525 parsimony-informative. Suitable partitioning schemes and substitution models (Bayesian information criterion) were selected using a greedy strategy implemented in PartitionFinder 2 (Lanfear et al. 2017). The partitioning scheme (3 partitions) and substitution models for the ML analysis were as follows: the TrNef+G model was proposed for the ITS region, the TrNef+I+G model for the LSU rDNA, and the K81+I+G model for the *RPB2* gene. The ML trees were constructed with IQ-TREE v. 1.4.4 (Nguyen et al. 2015) with nodal support determined by nonparametric bootstrapping (BS) with 1000 replicates. Bayesian posterior probabilities (PP) were calculated using MrBayes v. 3.2.6 (Ronquist et al. 2012). The optimal partitioning scheme and substitution models were as follows: the K80+G model was proposed for the ITS region, the SYM+I+G model for the LSU region, and the SYM+I+G model for the *RPB2* gene. The analysis ran for 10^7 generations using two parallel runs with four chains each, every 1000^{th} tree was retained, and the first 25% of trees were discarded as burn-in. The convergence of the runs and effective sample sizes was checked in Tracer v. 1.6 (http://tree.bio.ed.ac.uk/software/tracer). The trees were rooted with *Synnematotriadelphia stilboidea*.

Tab. 1. Accession numbers to DNA sequences used for phylogeny reconstruction.

Species	Strain No.*	GenBank/EMBL accession numbers		
		ITS	LSU	*RPB2*
Triadelphia disseminata	CBS 138592^T	MF434784	MF434788	MF434797
Triadelphia diversa	CBS 113.90^T	MF434782	MF434790	MF434799
Triadelphia fusiformis	MFLUCC 16-0231^T	MH777097	MH777098	—
Triadelphia heterospora	CBS 222.83^T	MF434779	MF434789	MF434798
Triadelphia hexaformispora	TBRC 9288^T	MK588842	MK588850	MK578528
Triadelphia loudetiae	CBS 589.77^T	MF434776	MF434785	MF434794
Triadelphia moubasheri	AUMC 10746^T	KY611849	—	—
Triadelphia moubasheri	CBS 744.84	MF434780	MF434787	MF434796
Triadelphia morgoensis	**CCF 6437**	**MW429270**	**MW429270**	**MW411332**
Triadelphia pulvinata	CBS 590.77^T	MF434777	MF434786	MF434795
Triadelphia romanica	CBS 162.79^T	MF434778	MF434791	MF434800
Synnematotriadelphia stilboidea	CBS 221.85^T	MF434781	MF434792	MF434801
Synnematotriadelphia stilboidea	CBS 101294	MF434783	MF434793	MF434802

* AUMC – Assiut University Mycological Centre, Egypt; CBS – Westerdijk Institute, Utrecht, The Netherlands; CCF – Culture Collection of Fungi, Czech Republic; MFLUCC – Culture Collection of Mae Fah Luang University, Thailand; TBRC – Thailand Bioresource Research Center, Thailand

^{T} ex-type strain

Sequences obtained in this study are marked in bold. References for other sequences: Lu et al. 2018 (strains from AUMC and MFLUCC), Chuaseeharonnachai et al. 2020 (other strains).

RESULTS AND DISCUSSION

Triadelphia morgoensis Révay, Stud. Bot. Hungar. 23: 63 (1993) [1992] Figs. 1–4

Characteristics in culture (isolate CCF 6437). Colonies (Fig. 1) growing slowly on all agar media (see Tab. 2), thin, velvet, dark grey-brown to brown-black, with whitish margins, abundantly sporulating. Colony reverse at first uncoloured, later grey-green to grey-brown. Sparse white tufts appearing on the colonies after two weeks. Optimal growth temperature obviously around 30 °C (according to observations presented in Tab. 2).

Tab. 2. Colony diameters (mm) of *Triadelphia morgoensis* CCF 6437 after 14 days on four agar media at different temperatures. For media abbreviations, see Material and methods.

Temperature / Medium	PCA	OA	MEA	PDA
20 °C	10–11	11–12	6	3–4
25 °C	14–15	12	6–9	6–7
30 °C	14–19	13–15	12–14	9–10
37 °C	12–13	9–10	7–9	6–9

Micromorphology (Figs. 2–3). Three conidial types were observed; codes of their types according to Constantinescu and Samson (1982) are given in parentheses: (a) dark cylindrical conidia, (c) long obclavate conidia, and (e) small allantoid conidia. Type 'a' prevailed. Conidiogenous cells were observed in type 'a' only. According to Révay (1993), the conidiogenous cells are similar in other types of conidia. They are hyaline, thin-walled, solitary or in clusters, ampulliform, 4–9 × 2–3.8 µm (mean ± standard deviation: 5.7 ± 1.2 × 2.6 ± 0.4 µm) (4.8–5.5 × 3–4 µm fide Révay 1993). Cylindrical 'a' conidia are smooth, 2-septate, 15–24 × 3.6–5.1 µm (mean ± SD: 18.7 ± 1.4 × 4.2 ± 0.4 µm) with an unpigmented truncate basal cell. Central and apical cells are brown, the apical cell rounded. They

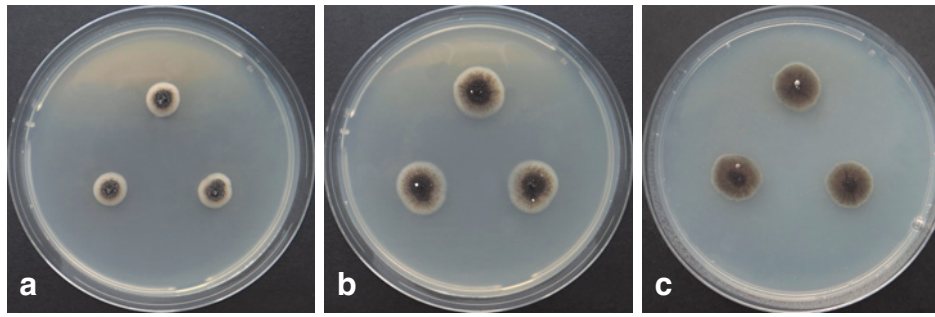


Fig. 1. *Triadelphia morgoensis* CCF 6437. Colonies on PCA after 14 days: **a** – at 20 °C, **b** – at 25 °C, **c** – at 30 °C. Photo A. Kubátová.

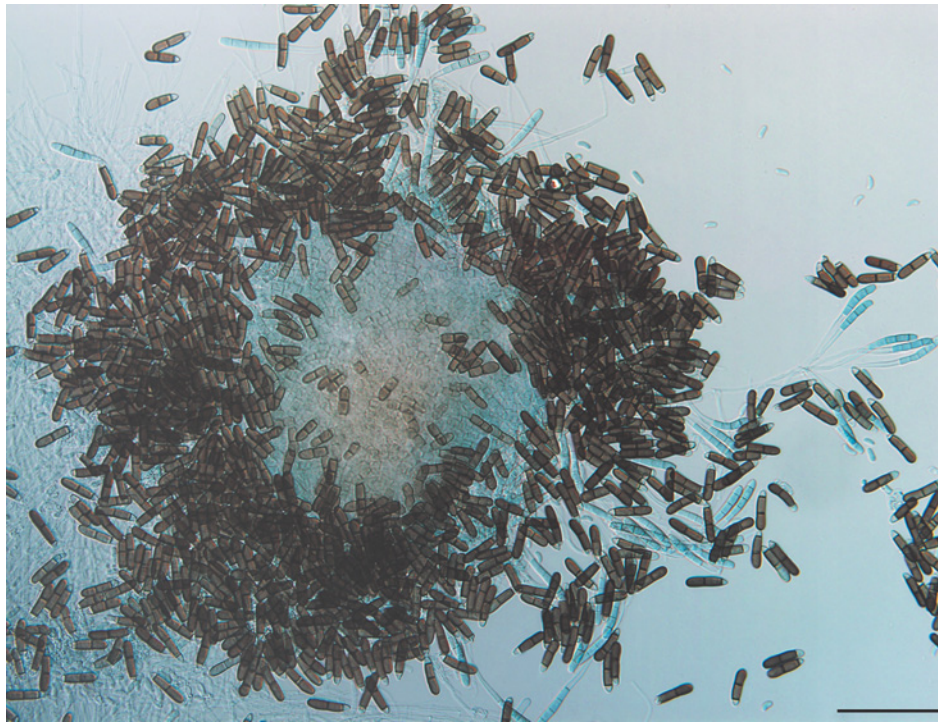
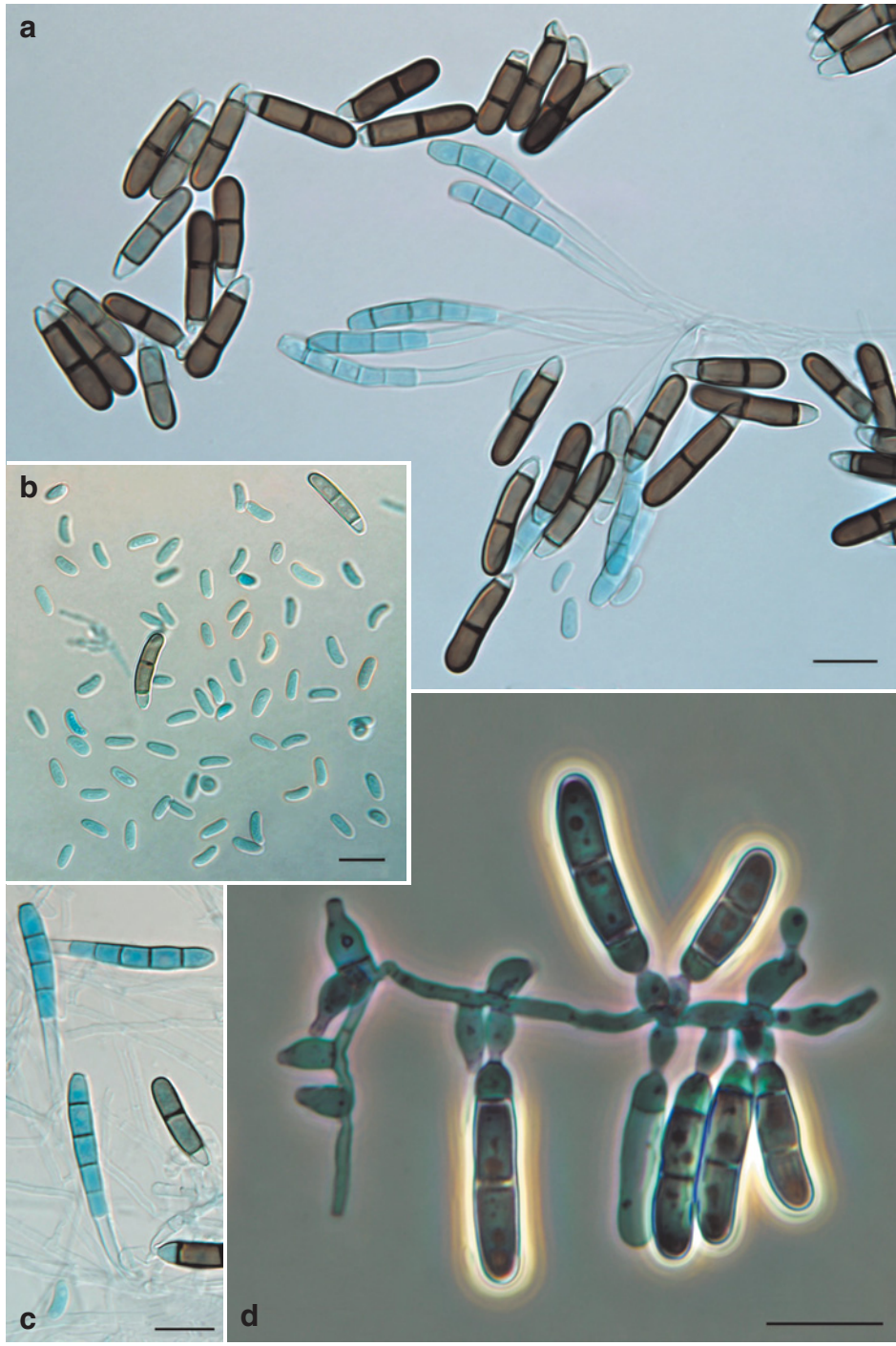


Fig. 2. *Triadelphia morgoensis* CCF 6437. Sporodochium-like cluster of cylindrical dark conidia type 'a'. Scale bar = 50 µm. Photo A. Kubátová.

are formed singly. Obclavate 'c' conidia are unpigmented, smooth, 4–5-septate, truncate at the base, gradually tapering into a long beak, 70–190 × 2.9–4.4 µm (mean ± SD: 122.5 ± 34.4 × 3.7 ± 0.3 µm) (40–57.6 × 3.2–4 µm fide Révay 1993). Allantoid 'e' conidia are hyaline, one-celled (sporadically with one septum), thin-walled, smooth, 4.7–7.7 × 2–3 µm (mean ± SD: 6.2 ± 0.6 × 2.5 ± 0.2 µm). A sexual state was not observed. These observations mostly correspond to the data given by Révay (1993) for the species *Triadelphia morgoensis*, however with one exception: in obclavate conidia, a longer thin terminal cell was observed. This may be due to differences in growth between the agar medium and the natural substrate. The type specimen was not obtained for comparison despite our efforts (type specimens are not sent on loan by the BP Herbarium).

Fig. 3. *Triadelphia morgoensis* CCF 6437. Three types of conidia. **a** – dark pigmented cylindrical conidia of type 'a' and long obclavate colourless conidia of type 'c', **b** – allantoid colourless conidia of type 'e' (and two conidia of type 'a'), **c** – long obclavate colourless conidia of type 'c' (and two conidia of type 'a'), **d** – dark pigmented cylindrical conidia of type 'a' on conidiogenous cells (phase contrast). Scale bars = 10 µm. Photo A. Kubátová. ▶


a
b
c
d

As Constantinescu et Samson (1982) stated, different forms of conidia may have a different ecological role. Darkly pigmented conidia are probably adapted to survive the winter, while thin-walled conidia could be important for dispersal.

Molecular studies. To achieve reliable identification and infer genus-wide phylogeny, we used sequences of three loci, i.e. ITS and LSU rDNA, and *RPB2*. The SSU rDNA region, which was also used by Chuaseeharonnachai et al. (2020), was omitted. This region contains only limited variability and is especially suitable for higher-level phylogenies.

At least some DNA sequences were available for nine of the eighteen *Triadelphia* species, and their accession numbers are listed in Tab. 1. Most species without sequences were described before 2001 (with three exceptions). Using the BLAST similarity search (blastn algorithm; Ye et al. 2006), the ITS rDNA region of isolate CCF 6437 showed that the highest similarity with the ex-type strain of *Triadelphia loudetiae* CBS 589.77 (GenBank accession number MF434776) was 93%. Other *Triadelphia* species with available sequence data showed similarities of 92% or lower. The LSU rDNA locus showed a sequence similarity of 97–98.5% to *Triadelphia* species deposited in GenBank. The species *T. disseminata* and *T. pulvinata* showed the highest degree of similarity (98–98.5%). Based on a BLAST search using the *RPB2* gene, *T. heterospora* (84%), *T. hexaformispora* (83%), *T. diversa* (83%) and *T. loudetiae* (82%) were the closest species, other species with available sequences showed similarities of 76–81%. No sequence designated as *T. morgoensis* was available in GenBank for comparison.

Phylogeny. In the best scoring maximum likelihood tree based on ITS, LSU and *RPB2* loci (Fig. 4), isolate CCF 6437 clustered with the species *T. loudetiae* and *T. heterospora* but with a low support (ML bootstrap support 61%). The topology of the phylogeny based on the Bayesian inference method was identical, and the statistical support for the mentioned clustering was high (posterior probability 0.99). The phylogeny also supported clustering of *T. pulvinata* and *T. disseminata* with *T. moubasheri* (79%/0.98), and of *T. hexaformispora* with *T. diversa* (100%/1.00). *Triadelphia romanica* was placed in a basal position towards the remaining species.

Identification. Significant micromorphological features of three types of conidia (dimensions, shape, number of cells, and colour of particular cells), together with the exclusion of species for which molecular data are available (as no sequence fits our specimen, see above), led us to identify the species as *T. morgoensis*. Our isolate originated from the same geographical area (Central Europe), thus physiological and ecological features are also important.

Similar species. *Triadelphia diversa* is morphologically most similar to *T. morgoensis*. Both species produce conidia of the type ‘a’ but with differently

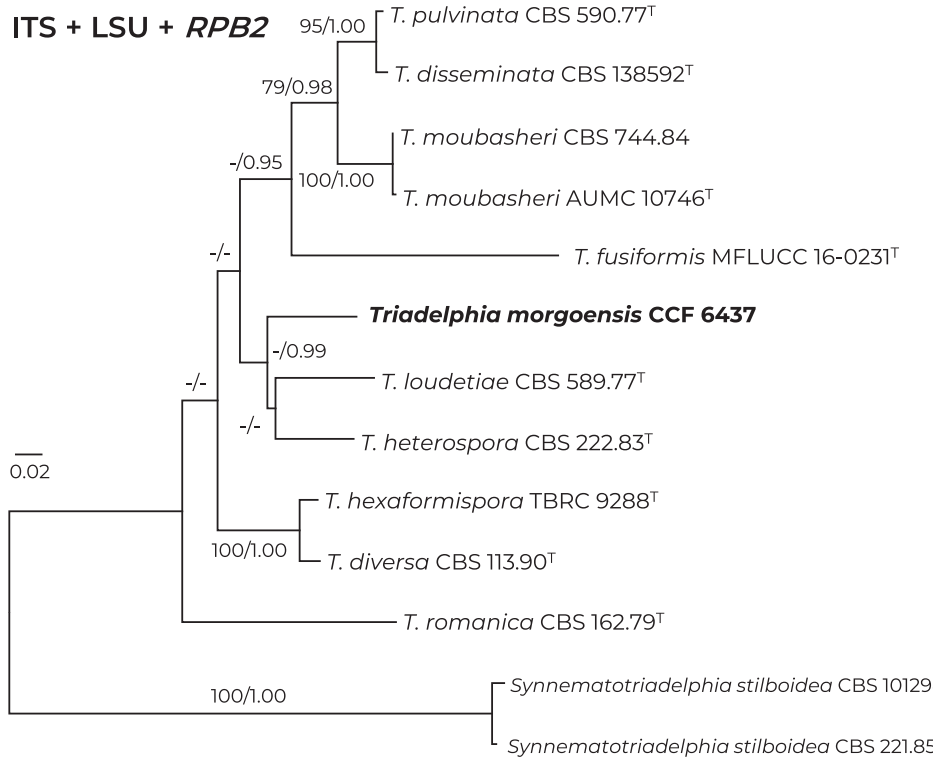


Fig. 4. Best scoring maximum likelihood tree calculated from ITS, LSU and *RPB2* sequences showing species relationships within the genus *Triadelphia* and the position of *T. morgoensis* CCF 6437. Maximum likelihood bootstrap supports and Bayesian posterior probabilities are appended to nodes; only values ≥ 70 % and ≥ 0.95, respectively, are shown; lower supports are indicated with a hyphen; ex-type strains are designated by a superscript ^{T}; the tree is rooted with *Synnematotriadelphia stilboidea*.

pigmented cells. The conidia of *T. diversa* are wider, and they have thick dark septa. This species also develops other conidial types, which are absent in *T. morgoensis*.

Triadelphia loudetiae and *T. heterospora* are the most closely related species to *T. morgoensis* based on the phylogeny. In *T. loudetiae*, conidia of type 'a' are mostly 2-septate just as in *T. morgoensis*. However, all three cells are brown, whereas the basal cell in *T. morgoensis* is unpigmented. Moreover, the conidia of type 'e' are two-celled in *T. loudetiae* compared to one-celled in *T. morgoensis*. Conidial types 'a' and 'd' of *T. heterospora* are characterised by conspicuously thick dark septa, whereas the septa in *T. morgoensis* are thick just as the conidial wall.

Identification keys to *Triadelphia* species are provided by Constantinescu et Samson (1982), Révay (1993), Li et Ye (2017) and Abdel-Sater et Soliman (2017).

Distribution. *Triadelphia morgoensis* was described by Révay (1993) from decaying wood in Hungary. No living culture has been retained. However, no further data on the occurrence of this species have been published. Consequently, no sequence data derived from this species have been deposited in GenBank. Our isolate is therefore the first documented record of this fungus for the Czech Republic and, to our knowledge, the second record ever. Optimal growth at 30 °C or above may indicate a preference for warmer regions. In addition to *T. morgoensis*, the following four species have been reported from Europe, i.e. *T. heterospora* from Hungary (Révay 1987) and Poland (Czeczuga et al. 2007), *T. inquinans* from Italy (Hughes et Pirozynski 1973), *T. romanica* from Romania (Constantinescu et Samson 1982), and *T. hungarica* from Hungary (Révay 1987, Gönczöl et Révay 2003).

Notes on etymology. The genus *Triadelphia* is named after the Triadelphia Reservoir on the Patuxent River in Maryland, USA (Shearer et Crane 1971). The reservoir was named after the town of Triadelphia and the town itself is said to be named after the three people who played a significant role in the town's early history (https://en.wikipedia.org/wiki/Triadelphia_Reservoir). The epithet *morgoensis* is derived from the name of the Morgó stream in Hungary, on the bank of which *T. morgoensis* was first found (Révay 1993).

ACKNOWLEDGEMENTS

We thank Lenka Zídková for assistance in the laboratory. The study was financed by the Institutional Support for Science and Research of the Ministry of Education, Youth and Sports of the Czech Republic.

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