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Coniochaeta fodinicola (*Fungi*: *Sordariomycetes*) from a sulphurous spring in Poland

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Abstract. *Coniochaeta fodinicola* is an acidophilic fungus which has been isolated only several times from extremely acidic environments. In this study, *Coniochaeta fodinicola* was isolated from a sulphurous spring with slightly acidic, nearly neutral pH water (pH = 6.8) in Poland. The identification of this fungus was conducted based on sequencing and phylogenetic analyses of ITS and LSU rDNA regions. Detailed morphological characteristics were provided for the isolated strain. The finding of *C. fodinicola* in a slightly acidic environment indicates that the species may occur in a broader range of conditions than previously known.

Key words: acid tolerance, acidophilic fungi, *Coniochaeta fodinicola*, *Coniochaetaceae*, extremophiles, morphology, phylogeny

Introduction

The fungal genus *Coniochaeta* belongs to the family *Coniochaetaceae* in the order *Coniochaetales* within the class *Sordariomycetes* (García et al. 2006). Members of the genus *Coniochaeta* represent a broad spectrum of lifestyles. They are known mainly as lignicolous, humicolous, coprophilous or parasitic species isolated from living and decaying plants, plant debris, wood, soil, dung and humans (Checa et al. 1988; de Hoog et al. 2000; Weber 2002; Damm et al. 2010; Guarro et al. 2012; Khan et al. 2013). However, one species – *Coniochaeta fodinicola* represents a unique lifestyle in this genus – the species is an extremophile (Vázquez-Campos et al. 2014). *C. fodinicola* was described from process waters of a uranium mine in Australia (Vázquez-Campos et al. 2014). The species was also isolated from hyperacidic water from the São Domingos mine in Portugal (Gadanho et al. 2006), acidic wastewater from a tin mine in China (Zhao et al. 2010), acidic water from a volcanic environment in Argentina (Russo et al. 2016), acidic soils in the Czech Republic (Hujslová et al. 2017), an acidic river in Argentina (Bernardelli et al. 2021) and from wood in the mining camp of Sewell in Chile (GenBank, https://www.ncbi.nlm.nih.gov/genbank/, see Table 1). Adaptation to low or extremely low pH is observed in species of the genera *Aspergillus*, *Epicoccum*, *Fusarium*, *Hypholoma*, *Mortierella*, *Mucor*, *Penicillium*, *Talaromyces*, *Trichoderma* and others (Gross & Robbins 2000; López-Archilla et al. 2004; Hujslová et al. 2017). Many of them are classified as acid-tolerant fungi because of their ability to live in highly acidic environments, as well as a capability to live under neutral or even alkaline pH (Gross & Robbins 2000). In turn, true acidophiles are organisms for which optimal pH for growth is at, or below 3–4 (Horikoshi & Bull 2011). Acidophilic fungi are specialized to live in acidic habitats and are mainly or exclusively isolated from them. They constitute an extremely rare ecological group of fungi represented by only a few species, of which the best known members belong to genera *Acidea* (*A. extrema*), *Acidiella* (*A. bohemica*, *A. polonica*), *Acidomyces* (*A. acidophilus*, *A. acidothermus*), *Acidothrix* (*A. acidophila*), *Neohortaea* (*N. acidophila*), *Soosiella* (*S. minima*), and *Coniochaeta* – represented by the isolated strain in this study, *Coniochaeta fodinicola* (Hujslová et al. 2019). To date, *C. fodinicola* was exclusively isolated from acidic habitats (Hujslová et al. 2019, see Table 1). Moreover, the species reaches optimal growth at pH 4 (Vázquez-Campos et al. 2014). Therefore *C. fodinicola* is considered to be a truly acidophilic species. To date, studies on acidophiles have primarily been focused on prokaryotes (Johnson 1998). Taxonomical studies on acidophilic fungi were conducted during the 20th century, but they more rapidly developed in the 21th century (Sigler & Carmichael 1974; Hölker et al. 2004; Selbmann et al. 2008; Yamazaki et al. 2010; Hujslová et al. 2013, 2014, 2017, 2019; Vázquez-Campos et al. 2014; Kolařík et al. 2021). Consequently, fungal diversity and their ecological role in acidic environments is still not fully understood. However, initial research indicated that acid-tolerant and acidophilic fungi may play an important role in such ecosystems by taking part

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Table 1. List of species, strains, isolation source, country of origin and GenBank accession numbers of sequences used for phylogenetic analyses. Data on analyzed strain with newly generated sequences are indicated in bold. T – ex-type strain.

Species	Strain	Isolation source	Country	GenBank accession numbers	
				ITS	LSU
Coniochaeta canina	CBS 133243 T (= UTHSC 11-2460)	USA	bone aspirate of dog	NR_120211	NG_042720
Coniochaeta cateniformis	CBS 131709 T (= UTHSC 01-1644)	USA	aspirate of canine bone marrow	NR_111517	HE610329
Coniochaeta discospora	CBS 168.58 T	Canada	dung of horse	MH857740	MH869278
Coniochaeta fodinicola	CBS 136963 T (= FRL)	Australia	uranium mine process waters	JQ904603	KF857172
Coniochaeta fodinicola	CBS 136964 (= BS)	Australia	uranium mine process waters	JQ904604	KF857174
Coniochaeta fodinicola	CBS 136965 (= NFR)	Australia	uranium mine process waters	JQ904605	KF857176
Coniochaeta fodinicola	CBS 136966 (= YoF)	Australia	uranium mine process waters	JQ904607	KF857178
Coniochaeta fodinicola	CGMCC 3329	China	acidic wastewater of a tin mine	GU082377	–
Coniochaeta fodinicola	MH 1062	Czech Republic	acidic soil	LN901096	LN901096
Coniochaeta fodinicola	MH 1232	Czech Republic	acidic soil	LN901097	LN901097
Coniochaeta fodinicola	MH 1234	Czech Republic	acidic soil	LN901098	LN901098
Coniochaeta fodinicola	MH 1290	Czech Republic	acidic soil	LN901099	LN901099
Coniochaeta fodinicola	MH 1303	Czech Republic	acidic soil	LN901100	LN901100
Coniochaeta fodinicola	MH 1315	Czech Republic	acidic soil	LN901101	LN901101
Coniochaeta fodinicola	**P26**	**Poland**	**sulphurous spring**	**OR671200**	**OR671202**
Coniochaeta fodinicola	RA2-15-H-e	Argentina	acidic water	–	MN519399
Coniochaeta fodinicola	SDY 295	Portugal	acidic water	–	AY731809
Coniochaeta fodinicola	SW5	Chile	wood	KU321538	–
Coniochaeta fodinicola	SW6	Chile	wood	KU321539	–
Coniochaeta fodinicola	SW14	Chile	wood	KU342662	–
Coniochaeta hansenii	CBS 885.68	Netherlands	rabbit dung	OP962072	AJ875223
Coniochaeta hoffmannii	CBS 245.38 T	Switzerland	butter	NR_167688	MH867452
Coniochaeta luteorubra	CBS 131710 T	USA	human leg wound	MH865901	MH877339
Coniochaeta simbalensis	NFCCI 4236 T	India	soil	NR_164024	MG917738
Paragaeumannomyces garethjonesii	MFLUCC 15-1012 T	Thailand	seed pod of *Fabaceae*	NR_154840	NG_059017
Zanclospora jonesii	MFLUCC 15-1015 T	Thailand	wood	NR_154841	NG_067549

Abbreviations: CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, Netherlands; CGMCC: China General Microbiological Culture Collection Center, Beijing, China; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; MH: personal culture collection of M. Hujslová; NFCCI: National Fungal Culture Collection of India, Pune, India; UTHSC, Fungus Testing Laboratory, University of Texas Health Science Center at San Antonio, San Antonio, USA. P26: strain analyzed in this study, deposited in W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland.Other strain numbers – personal numbers or unknown abbreviation: BS, FRL, NFR, RA2-15-H-e, SDY, SW, YoF.

in transformations of sulphur and sulphates, the sulphur cycle, being decomposers of organic matter or playing an important role in the remediation of acid mine drainage, the degradation of environmental pollutants and the formation of microbial biofilm (Das et al. 2009; Aguilera & González-Toril 2019; Hujslová et al. 2019; Gao et al. 2021). Acid-tolerant and acidophilic fungi occur in many kinds of acidic environments, which may have a natural or anthropogenic origin and may vary in acidic level from slightly to extremely acidic (pH < 3) (Gross & Robbins 2000). Most acidophilic fungal species were detected from extremely acidic environments such as acidic waste water from mines, acid mine drainage, acidic soils, polluted areas or acidic springs and rivers (Hujslová et al. 2019). Studies on mycobiota from slightly acidic environments were conducted with less attention. Slightly acidic environments or environments with near-neutral pH where different acids may occur are also a reservoir of acidophiles (Cadillo-Quiroz et al. 2009). In this study, the acidophilic fungus – *Coniochaeta fodinicola* was isolated from a sulphuric spring (Napoleon spring in Swoszowice, Kraków) in Poland that is an example of such a habitat.

Materials and methods

A water sample was collected in March 2018 from Napoleon spring (49°59′44.6″N, 19°56′00.9″E) in Swoszowice, the administrative district of Kraków. Water of the Napoleon spring is characterized by having hydrogen sulfide (H_2S = 61.1 mg/dm^3) and is slightly acidic, near neutral pH (pH = 6.8) (Rajchel et al. 2002). The sample was collected in a sterile container. In the laboratory, under sterile conditions, 15 water drops were sprinkled into a Petri dish (Ø 90 mm) containing Rose Bengal Chloramphenicol (RBC) agar (Carl Roth, Germany) and incubated at 12°C until fungal colonies appeared. One representative of each morphotype was transferred to a Petri dish with Malt Extract Agar (MEA) (Carl Roth, Germany) in order to obtain pure cultures which were used for molecular analyses. One distinctive white-colored morphotype (strain P26) is studied here. It is preserved as a dried specimen

in the fungal collection (KRAM F-59984) and as a living culture stored under paraffin oil in the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.

DNA was extracted using a slightly modified CTAB protocol (Owczarek-Kościelniak & Sterflinger 2018). Amplification reactions were prepared for nuc rDNA ITS1-5.8S-ITS2 (ITS) and nuc rDNA 28S D1–D2 (LSU). PCR mixture for both loci was performed in a 25 ml volume containing final concentration of 0.05 U/µl Taq DNA Polymerase (Sigma Aldrich, Germany), 1× PCR Buffer, 2.5 mM Mg^{2+}, 200 µM of each dNTP and 0.2 µM of each primer – ITS1 and LR5. PCR reaction was conducted with an initial denaturation at 94°C for 3 min, followed by 35 cycles of denaturation in 94°C for 45 s, annealing in 50°C for 45 s, elongation in 72°C for 2 min and the final extension in 72°C for 10 min. Amplicons containing ITS and LSU were enzymatically purified using Exo-BAP Mix (EURx, Poland) and sequenced by Macrogen Europe B.V. (Amsterdam, the Netherlands) with primer pairs – ITS1-ITS4 for ITS and LSU1Fd-LR5 for LSU (Vilgalys & Hester 1990; White et al. 1990; Crous et al. 2009).

Forward and reverse sequences were assembled and trimmed in Geneious Prime® 2020.0.4. Newly obtained sequences were deposited in NCBI's GenBank nucleotide database under accession numbers: OR671200 (ITS), OR671202 (LSU) (Table 1). Megablast queries of the GenBank nucleotide database (Zhang et al. 2000) were used to find the closest taxonomic affinities of obtained sequences. Subsequently, a dataset containing concatenated ITS and LSU sequences was prepared. The dataset included newly generated sequences and reference sequences of the species closely related to *Coniochaeta fodinicola*. Selected members of the family *Chaetosphaeriaceae* – *Paragaeumannomyces garethjonesii* and *Zanclospora jonesii* were used as an outgroup. Details of sequences used in the phylogenetic analyses are given in Table 1. The dataset contained concatenated alignments of ITS and LSU sequences of 26 species (including outgroup) with a total length of 1,388 characters (ITS: 552, LSU: 836), including alignment gaps. The maximum likelihood (ML) analysis was performed with TrN+G4 substitution model for ITS and LSU. The Bayesian inference (BI) analysis was performed with SYM+G4 substitution model for ITS and K80+G4 for LSU.

Micromorphology was studied using 2-week-old culture grown on MEA medium at 25°C. Additionally, 2-week-old cultures grown at 15°C and 25°C were measured and characterized. Mycelium was scraped from the edge of culture, placed in 80% lactic acid and examined under a Nikon Eclipse 80i light microscope at a magnification of 1000×. Microscopic structures were measured and photographed using NIS-Elements BR 3.0 imaging software.

The growth of fungal mycelium at different pH levels was tested in MEA medium from pH ranging between 2–8. The pH of the medium was adjusted by HCl/NaOH supplement after sterilization. Diameters of colonies were measured after 7 days. Tests were duplicated for each pH level. Average colony diameters for each pH level were calculated.

Results and discussion

Colonies on MEA and PDA after 2 weeks at 15°C were nearly identical, flat to slightly convex with radial furrows from the colony center toward margin, creamy, with fimbriate margin, reaching 24 mm diam. on MEA or 25 mm diam. on PDA, with creamy reverse. Colonies on MEA and PDA after 2 weeks at 25°C were nearly identical, flat, creamy, with fimbriate margin, reaching 40 mm diam. on MEA or 43 mm diam. on PDA, with creamy reverse. The mycelium of the examined strain consisted of branched, septate, hyaline, smooth, 2–3.5 µm diam., hyphae, with occasionally formed characteristic hyphal coils and spirally intertwined hyphae. Conidiophores were reduced to conidiogenous cells. Conidiogenous cells were ampulliform, cylindrical, hyaline, smooth, aseptate, intercalary or terminal on hyphae, 5.5–10.5 × 1.5–3.5 µm. Conidia were cylindrical, hyaline, smooth, aseptate, 4–7.5 × 1.5–2.5 µm. The morphology of examined material was nearly identical to the type of *C. fodinicola* with the exception that strain P26 formed characteristic spirally intertwined hyphae, which were not observed in the type specimen. Moreover, rarely formed chlamydospores were observed in the type material (Vázquez-Campos et al. 2014), but not in strain P26 from Poland (Fig. 1). Sequences of the analyzed strain clustered together with the type specimen of *Coniochaeta fodinicola* (Fig. 2). Sequences of the analyzed strain together with all sequences of *C. fodinicola* available in GenBank formed an independent and highly supported clade in the phylogenetic tree containing sampled *Coniochaeta* species (Fig. 2).

In this study, *Coniochaeta fodinicola* was isolated from sulphuric spring in Poland. To date, the species has been previously isolated and phylogenetically studied from only six localities in the world: Argentina, Australia, Chile, China, Czech Republic, Portugal and a locality in Poland (Table 1). Interestingly, an isolation from Poland was the first from an environment characterized by slightly acidic, nearly neutral pH (pH = 6.8) (Rajchel et al. 2002) in contrast to the remaining strains, where pH was highly acidic (pH < 3) (Gadanho et al. 2006; Zhao et al. 2010; Vázquez-Campos et al. 2014; Hujslová et al. 2017; Bernardelli et al. 2021). Detection of *C. fodinicola* from the Napoleon spring indicates that extremely acidic conditions are not required for the occurrence of this species. It is consistent with results of experiments conducted on the type specimen of *C. fodinicola* (Vázquez-Campos et al. 2014) and the strain P26 (Fig. 3). Both strains exhibited optimal growth at acidic pH (with the peak growth at pH 4 for both strains), but they also grew on medium with neutral or even alkaline pH. It is worth noting that the shape of the growth curve and pH preferences of both strains were nearly identical, even though the strains were isolated from environments with different pH. The results of both tests confirmed the acidophilic nature of *C. fodinicola* even for a strain from a non-extremely acidic environment, but simultaneously show that the species may also live in non-acidic conditions. The isolation and phylogenetic examination of *C. fodinicola* from Napoleon spring shed a new light into the biology of this species

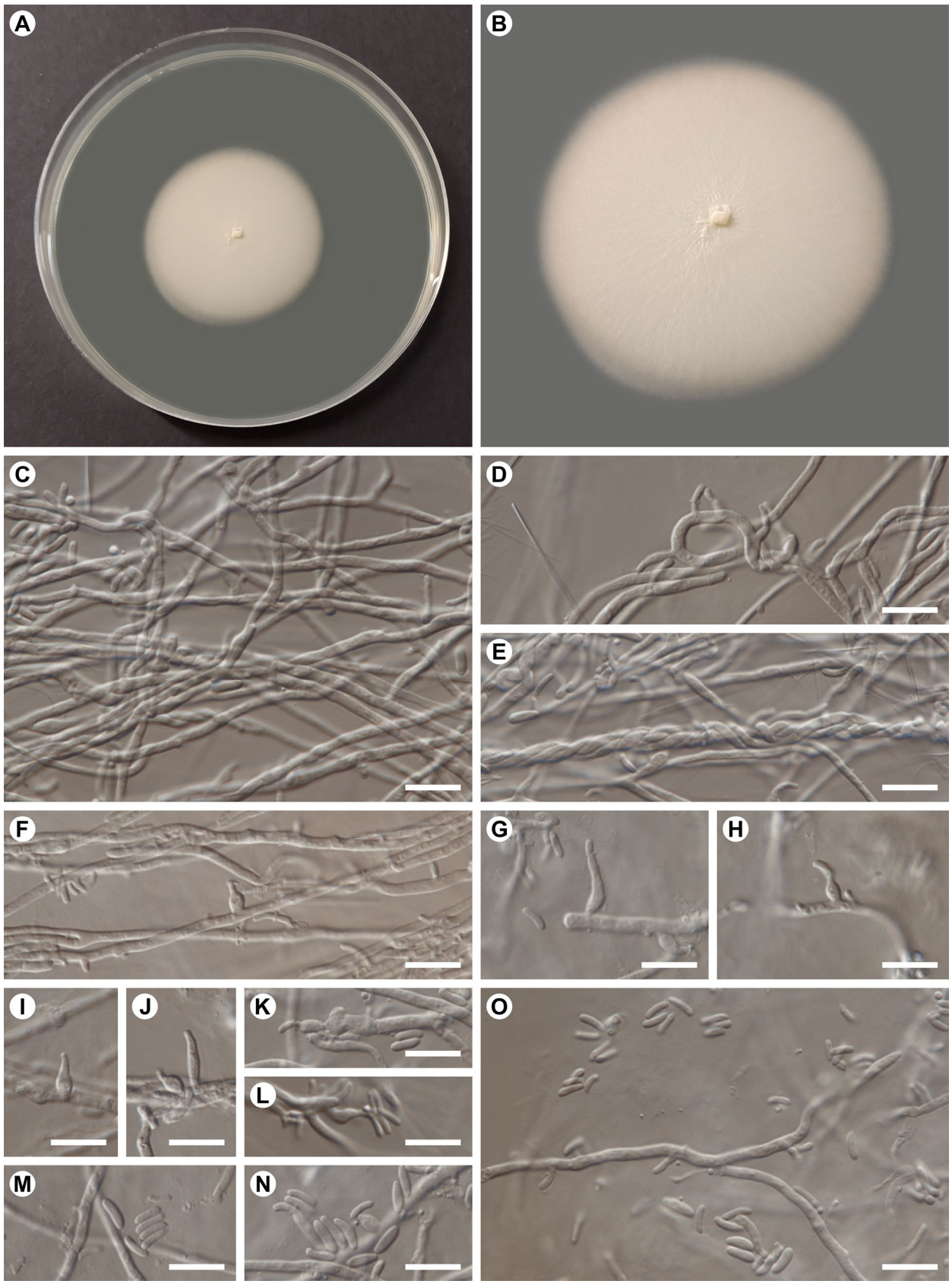

Figure 1. Morphology of *Coniochaeta fodinicola* (strain P26). A, B – general view and detailed view of upper side of colony on MEA after 2 weeks of growth at 25°C; C – hyphae; D – hyphae and hyphal coil with conidiogenous cells and conidia; E – spirally intertwined hyphae; F – hyphae with conidiogenous cells; G–L – conidiogenous cells and conidia; M–O – conidia. Scale = 10 μm.

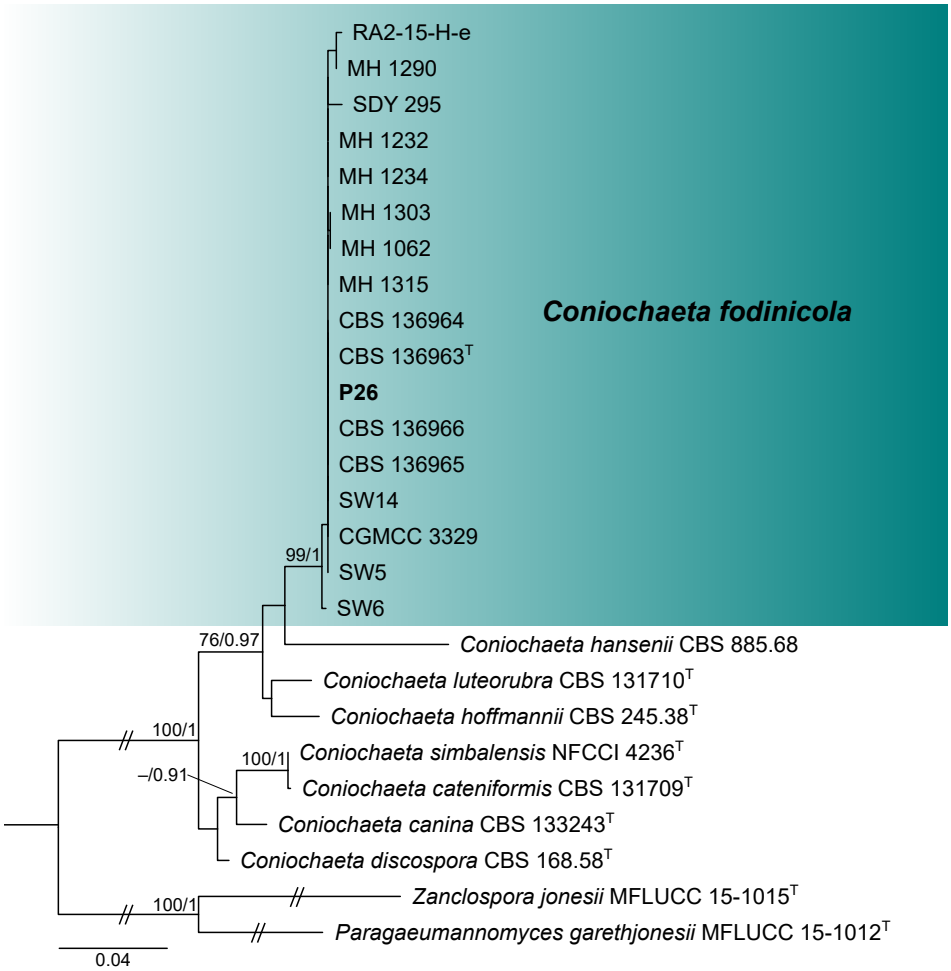

Figure 2. Phylogenetic placement of *Coniochaeta fodinicola* within closely related *Coniochaeta* species, inferred with maximum likelihood analysis using combined ITS and LSU sequences. Maximum likelihood bootstrap (MLB) support values ≥70% and Bayesian posterior probabilities (BPP) ≥0.9 are given above branches (MLB/BPP). The positions of analyzed strain is indicated in bold. The scale bar represents the expected changes per site. The branch lengths denoted by a double slash (//) have been shortened to a half of their length to improve visualization. The superscript T refers to ex-type cultures.

by being the first phylogenetically confirmed report of *C. fodinicola* from non-extremely acidic environment, but where acids occur. It is worth noting, that the Napoleon spring, despite a nearly neutral pH, is characterized by the relatively high concentration of H_2S (61.1 mg/dm^3), as well as being inhabited by sulphur bacteria (Rajchel et al. 2002). Sulphur bacteria take a part in transformations of sulphur and hydrogen sulfide in such habitats (Rajchel et al. 2002). Fungi are also known from their participation in the sulphur cycle. It cannot be ruled out that *C. fodinicola*, similarly to other fungal taxa living in such environments, take a part in transformations of sulphur and sulphates (Wainwright 1988; Das et al. 2009; Aguilera & González-Toril 2019), but this hypothesis needs a further investigation.

An interesting issue for a discussion about the biology of *C. fodinicola* consists of environmental studies of areas where the species was detected. Based on the GlobalFungi database (https://globalfungi.com, Větrovský et al. 2020), *C. fodinicola* was reported in 82 samples mainly from dead wood and soil. This could indicate that the species may occur more frequently, even in non-acidic habitats. However, interestingly, 64 out of 82 samples have pH between highly to slightly acidic (4.1–6.7 pH) and only 18 samples had neutral, near-neutral or alkaline pH. Moreover, Szewczyk et al. (2017) reported *C. fodinicola* as an inhabitant of knots of *Pinus sylvestris* affected by the polypore *Porodaedalea pini*. Their study was also based on environmental sequencing using Illumina sequencing technology, but the resulting sequences are not available in the GenBank database, which makes it impossible to compare and verify them in the phylogenetic context. In fact, reports of *C. fodinicola* from dead wood and soil (https://globalfungi.com) or on *Pinus sylvestris*

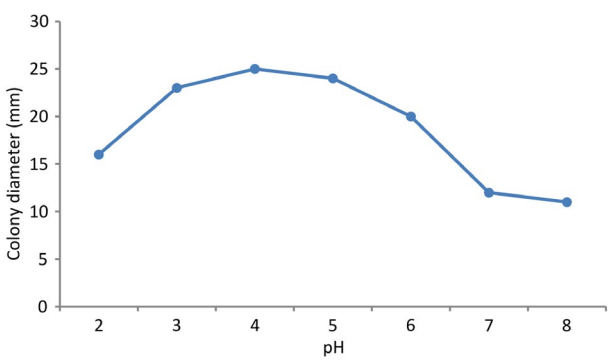

Figure 3. The growth of *Coniochaeta fodinicola* (strain P26) on MEA at different pH values after 1 week at 25°C.

(Szewczyk et al. 2017) are interesting reports which may indicate new ecological niches for this species. Environmental studies may lead to a conclusion that the species prefers acidic environments, but it may also live in non-acidic conditions. However, it is worth noting that conclusions about the precise identification of fungal taxa from untypical habitats investigated by environmental sequencing should be considered with caution. Especially, when *C. fodinicola* was exclusively isolated from acidic environments or those where acids occur (Table 1). It is not excluded that *C. fodinicola* reported from environmental samples belongs to undescribed *Coniochaeta* species, because short ITS fragments obtained with the Illumina sequencing technology may be insufficient to identify them at species level. Such misidentifications may happen in cryptic fungal species (Balasundaram et al. 2015). The best practice in such cases is the isolation of strains from such environments, then conducting phylogenetic studies using sequences obtained by Sanger sequencing. The results obtained in this study are such an example, where *C. fodinicola* was isolated from an untypical habitat – not an extremely acidic environment, but simultaneously where some typical elements – the occurrence of H_2S, are present. It sheds a new light into the discussion about the biology of this interesting and poorly known species.

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