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Molecular phylogeny and a new Iranian species of *Caudospora* (Sydowiellaceae, Diaporthales)

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Abstract

For the first time, molecular phylogenetic data on the peculiar diaporthalean genus *Caudospora* are available. Macro- and microscopic morphology and phylogenetic multilocus analyses of partial nuc SSU-ITS-LSU rDNA, *cal*, *ms204*, *rpb1*, *rpb2*, *tef1* and *tub2* sequences revealed two distinct species of *Caudospora*, which are described and illustrated by light and scanning electron microscopy. *Caudospora iranica* is described as a new species from corticated dead twigs of *Quercus* sp. collected in Iran. It differs from the generic type, *C. taleola*, mainly by coarsely verrucose ascospores. The asexual morph of *C. taleola* on natural substrate is described and illustrated. *Caudospora taleola* is neotyped, and it is recorded from Iran for the first time. Phylogenetic analyses of a multigene matrix containing a representative selection of Diaporthales from four loci (ITS, LSU rDNA, *rpb2* and *tef1*) revealed a placement of *Caudospora* within Sydowiellaceae.

Keywords

Ascomycota; Diaporthales; new species; phylogenetic analysis; Sydowiellaceae; taxonomy

Starbäck (1889) introduced the genus *Caudospora* for a single peculiar species, *C. taleola*, which is characterized by perithecia immersed in a brown corticolous pseudostroma delimited by a distinct blackish zone, a whitish ectostromatic disc bearing few converging dark ostioles, cylindrical asci and hyaline, two-celled ascospores with an appendage at each end and 2–3 median appendages. The single known species, *C. taleola*, is confined to various species of *Quercus* spp., where it is widely distributed in Europe and North America (Rogers 1984). Ecologically, *C. taleola* is a saprotroph or weak pathogen of oaks, which can cause canker diseases (Phillips & Burdekin 1992).

Whereas morphological features clearly place *C. taleola* within Diaporthales, its generic as well as familial affiliation within the order remained controversial. Munk (1957) provided a detailed morphological description, noted that the genus is very distinct and found a high similarity of its centrum to that of *Sydowiella fenestrans* (Sydowiellaceae). Wehmeyer

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(1933) included *Caudospora* in the genus *Diaporthe*, whereas Müller & Arx (1962) transferred it to *Hercospora*. This generic classification was accepted by Kobayashi (1970) and Barr (1978). Rogers (1984) re-examined *C. taleola* from natural substrate and characterized the anamorph in pure culture. He concluded that *Caudospora* should not be considered synonymous with *Hercospora* because of its verrucose ascospores and appendages. Moreover, the anamorph of *H. tiliae*, the type species of *Hercospora*, is rabenhorstia-like whereas that of *C. taleola* is phomopsis-like. Rogers (1984) concluded that *C. taleola* is related to certain species of *Diaporthe* (*D. leiphaemia* var. *raveneliana*) based on the verrucose ascospores and anamorph. However, this connection has never been proven in molecular studies, and it is also doubtful whether *D. leiphaemia* var. *raveneliana* really belongs to *Diaporthe*. Until now, in the lack of sequence data the phylogenetic position of *Caudospora* within Diaporthales is uncertain.

During a survey of diatrypaceous fungi in Iran, a collection resembling *Caudospora* was revealed from dead corticated twigs of *Quercus* sp., which markedly differed from *C. taleola* in coarsely verrucose ascospores. Several fresh collections of *C. taleola* from Austria, France and Iran provided the opportunity for pure culture isolation and sequencing to clarify the phylogenetic affinities of *Caudospora* and the species status of the Iranian collection with verrucose ascospores, the results of which are here presented.

Materials and methods

Isolates and specimens

All isolates used in this study originated from ascospores of fresh specimens. Numbers of strains including NCBI GenBank accession numbers of gene sequences generated in the present study are listed in Tables 1 and 2. Strain acronyms other than those of official culture collections are used here primarily as strain identifiers throughout the work. Details of the specimens used for morphological investigations are listed in the Taxonomy section under the respective descriptions. In addition, the following strain of *Hapalocystis berkeleyi* was sequenced as outgroup taxon: UK, England, London, Royal Botanic Gardens Kew (RGB), on corticated branches of *Platanus × hispanica*, 11 November 2008, H. Voglmayr D84 (WU 39959, living culture CBS 124568). Isolates were deposited in the Iranian Fungal Culture Collection of the Iranian Research Institute of Plant Protection (IRAN...C) and at the Westerdijk Fungal Biodiversity Centre, Utrecht, The Netherlands (CBS culture collection), and dry specimens in the Herbarium of Iranian Research Institute of Plant Protection (IRAN...F) and the Fungarium of the Department of Botany and Biodiversity Research, University of Vienna (WU).

Light microscopy

Dead corticated branches were examined with the aid of an Olympus SZH or a Nikon SMZ 1500 stereomicroscope. Microscopic observations were made in tap water except where noted. Sections were cut manually with a sterilized razorblade and microscope mounts were examined with a Nikon 80i equipped with a Canon digital camera or a Zeiss Axio Imager.A1 equipped with a Zeiss Axiocam 506 colour digital camera. Measurements were taken with the help of DinoCapture 2.0 or Zeiss ZEN Blue Edition softwares. Measurements are

reported as maxima and minima in parentheses and the range representing the mean plus and minus the standard deviation of a number of measurements given in parentheses; in addition, the means (\bar{x}) are given.

Scanning electron microscopy (SEM)

For SEM of ascospores, perithecial contents were re-hydrated in a drop of distilled water on a cover slide and thoroughly cleaved with a fine forceps and preparation needles to release the ascospores from the asci. After evaporation of the water at room temperature, the cover slides were mounted on Cambridge stubs, sputter coated with gold, and examined in a Jeol JSM-6390 scanning electron microscope at 10 kV.

Pure culture isolation

Single ascospore isolates were made by spreading ascospores on 1.5 % potato dextrose agar (PDA, Difco), or on 2 % corn meal agar (CMA, Sigma-Aldrich) plus 2 % w/v dextrose (CMD) supplemented with 200 mg/l penicillin G and streptomycin sulphate (Sigma-Aldrich). Germinated ascospores were then transferred to PDA or CMD plates, sealed with laboratory film and incubated at room temperature. Colony morphology, colour (Rayner, 1970) and growth rate were determined on PDA at 24 °C.

DNA extraction, PCR and sequencing

Growth of liquid cultures and extraction of genomic DNA was done according to Voglmayr & Jaklitsch (2011), using the DNeasy Plant Mini Kit (QIAgen GmbH, Hilden, Germany). The following loci were sequenced for phylogenetic analyses: The complete ITS region and D1 and D2 domains of 28S nuc rDNA region (ITS-LSU) were amplified with primers V9G (Hoog & Gerrits van den Ende 1998) and LR5 (Vilgalys & Hester 1990); a ca 0.6–0.7 kb fragment of the calmodulin (*cal*) gene with primers CAL-228F (Carbone & Kohn 1999) and CAL2Rd (Groenewald et al. 2013); a ca 1 kb fragment of the guanine nucleotide-binding protein subunit beta (*ms204*) gene with primers MS-E1F1n1 (5' AAGGGNACYCTSGAGGGCCAC 3') and MS-E5R2n (5' CCASAGCATGGTGGTRCCRT 3'); a ca 1.1 kb fragment of the RNA polymerase II subunit 1 (*rpb1*) gene with primers RPB1-6R1asc (Hofstetter et al. 2007) and RPB1-Af (Stiller & Hall 1997); a ca 1.1 kb fragment of the RNA polymerase II subunit 2 (*rpb2*) gene with primers dRPB2-5f and dRPB2-7r (Voglmayr et al. 2016a); a ca 1.3–1.5 kb fragment of the translation elongation factor 1- α (*tef1*) gene with primers EF1728F (Carbone & Kohn 1999) and TEF1LLErev (Jaklitsch et al. 2005) or EF1-2218R (Rehner & Buckley 2005); and a ca 1.5 kb fragment of the beta tubulin (*tub2*) gene with primers T1 and T22 (O'Donnell & Cigelnik 1997). PCR products were purified using an enzymatic PCR cleanup (Werle et al. 1994) as described in Voglmayr & Jaklitsch (2008). DNA was cycle-sequenced using the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit v. 3.1 (Applied Biosystems, Warrington) and the PCR primers; in addition, the following primers were used: ITS-LSU region: ITS4 (White et al. 1990), LR3 (Vilgalys & Hester 1990); *tub2*: BtHV2r (Voglmayr et al. 2016b, 2017) and BtHVf (5' AACTGGGCMAAGGGYCAYTACAC 3'). Sequencing was performed on an automated DNA sequencer (ABI 3730xl Genetic Analyzer, Applied Biosystems). GenBank accession numbers of the newly generated sequences are given in Tab. 1.

Phylogenetic analyses

All alignments were produced with the server version of MAFFT (<http://mafft.cbrc.jp/alignment/server/>), the E-INS-i iterative refinement method and a gap opening penalty of 1.4 for the ITS-LSU and *tef1*, and with default settings for the other loci. All alignments were checked and refined using BioEdit version 7.0.9.0 (Hall 1999).

To reveal the phylogenetic position of *Caudospora* within Diaporthales, ITS-LSU, *rpb2* and *tef1* sequences of two accessions of *C. taleola* and of the new Iranian species sequenced in the present study were aligned to representative sequences of Diaporthales selected and downloaded from GenBank according to the phylogeny of Senanayake et al. (2017a). The final matrix contained 75 representatives of Diaporthales, with *Kohlmeyeriopsis medullaris* and *Gaeumannomyces graminis* (Magnaportheales) selected as outgroups (Voglmayr et al. 2017); the strain details and GenBank accession numbers of sequences are given in Tab 2. The resulting combined four-loci sequence matrix contained 5188 nucleotide positions (2148 from ITS-LSU, 1210 from *rpb2*, 1830 from *tef1*).

For phylogenetic relationships within *Caudospora*, a combined matrix of nine loci was produced, containing 8683 nucleotide positions (1665 from SSU-ITS-LSU, 710 from *cal*, 1017 from *ms204*, 1151 from *rpb1*, 1160 from *rpb2*, 1433 from *tef1*, 1547 from *tub2*). According to the results of phylogenetic analyses of the four-loci matrix, *Hapalocystis berkeleyi* was selected as outgroup.

Maximum likelihood (ML) analyses were performed with RAxML (Stamatakis 2006) as implemented in raxmlGUI 1.3 (Silvestro & Michalak 2012), using the ML + rapid bootstrap setting and the GTRGAMMA substitution model with 1000 bootstrap replicates. The matrix was partitioned for the individual gene regions, and substitution model parameters were calculated separately for them.

Maximum parsimony (MP) analyses were performed with PAUP v. 4.0a157 (Swofford 2002). All molecular characters were unordered and given equal weight; analyses were performed with gaps treated as missing data; the COLLAPSE command was set to MINBRLEN. For the combined four-loci matrix, a parsimony ratchet approach was applied. A nexus file was prepared using PRAP v. 2.0b3 (Müller 2004), implementing 1000 ratchet replicates with 25 % of randomly chosen positions upweighted to 2, which was then run with PAUP. The resulting best trees were subsequently loaded in PAUP and subjected to heuristic search with TBR branch swapping (MULTREES option in effect, steepest descent option not in effect). Bootstrap analysis with 1000 replicates was performed using 5 rounds of replicates of heuristic search with random addition of sequences and subsequent TBR branch swapping during each bootstrap replicate, with each replicate limited to 1 million rearrangements. MP analysis of the combined nine-loci matrix was done using 1 000 replicates of heuristic search with random addition of sequences and subsequent TBR branch swapping. Bootstrap analyses with 1 000 replicates were performed in the same way, but using 10 rounds of random sequence addition and subsequent TBR branch swapping during each bootstrap replicate.

Results

Molecular phylogeny

Of the 5188 nucleotide positions included in the four-loci sequence matrix, 1838 were parsimony informative (590 from ITS-LSU, 566 from *rpb2*, 682 from *tef1*). The best ML tree ($\ln L = -48924.555$) revealed by the RAxML analysis is shown as phylogram in Fig. 1. Maximum parsimony analyses revealed 12 MP trees 9903 steps long (not shown). In both ML and MP analyses, *Caudospora* is placed within the Sydowiellaceae with high support, but its closest relatives remain uncertain due to lack of bootstrap support of most nodes within Sydowiellaceae.

Of the 8683 nucleotide positions included in the nine-loci sequence matrix, 72 were parsimony informative (6 from SSU-ITS-LSU, 5 from *cal*, 15 from *ms204*, 9 from *rpb1*, 14 from *rpb2*, 15 from *tef1*, 8 from *tub2*). The MP analysis revealed a single tree 1559 steps long (Fig. 2); it is identical in topology to the best ML tree ($\ln L = -18010.352$) revealed by RAxML. Sister group relationship of *Caudospora iranica* to *C. taleola* received maximum and high (93 %) bootstrap support in MP and ML analyses (Fig. 2), respectively, confirming their status as distinct species.

Taxonomy

Caudospora iranica Mehrabi & Voglmayr, sp. nov. – Figs. 3, 5a, b, e.

MycoBank no.: MB 823458

Type. – IRAN. East Azerbaijan Province, Arasbaran, on dead branches of *Quercus* sp., 11 July 2015, leg. M. Mehrabi (IRAN 16716 F holotype; WU 39950 isotype; ex-holotype culture IRAN 2552 C, ex-isotype culture CBS 143507).

Description. – Pseudostromata 1–3.5 mm diam., immersed in the bark of dead branches (ca. 1.5 cm thick), erumpent, circular to irregular, separate, scattered, sometimes confluent, delimited from surrounding bark by a black line, the latter visible on the bark surface. Ectostromatic discs white, convex, circular to oval, tissue between ostiolar necks distinctly gray to dark grey, powdery. Central column whitish to grey. – Ostioles dark, at the same level as the disc surface, rarely projecting, opening separately. – Perithecia 2–7 per stroma, 300–700 µm diam., subglobose to ovoid, black, monostichous, arranged circinately in brown entostromata, with long ostiolar necks converging towards the ectostromatic disc. – Paraphyses elongate, hyaline, filiform, septate, evanescent. – Ascii (170)181–211(230) × 15–18 µm ($\bar{x} = 196 \times 16.7$ µm; n=20), cylindrical, with short or obsolete stalks and a conspicuous apical ring, containing eight uniseriate ascospores. – Ascospores (18)21–27(32) × (8)10.5–13(15) µm ($\bar{x} = 23.7 \times 11.7$ µm; n=42), l/w = (1.6)1.8–2.3(2.5), broadly ellipsoid, two-celled, constricted at the septum, hyaline or pale yellowish, coarsely verrucose, in SEM with isolated warts 0.4–1 µm diam., with a tubular gelatinous appendage 10–17 × 1–1.3 µm long at each end and 2–3 (rarely 4) similar median tubular gelatinous appendages arising from near the septum.

Cultural characteristics. – Colonies felty, with irregular margins, first white, later primrose (23,,b) at the surface, often deeply immersed into the agar, reverse primrose, becoming olivaceous black (27,,,m) in the dark at 24 °C, reaching the margin of a 30 mm Petri-dish after 30 days at 24 °C. No asexual morph seen.

Etymology. – Referring to its origin from Iran.

Habitat. – On dead corticated twigs of *Quercus* sp.

Distribution. – Only known from the type collection in Iran.

Notes. – *Caudospora iranica* resembles *C. taleola* in stroma and ascoma morphology and ascospore appendages. However, there are pronounced differences between these species in the ascospore ornamentation. In *C. iranica*, the surface of the ascospore wall is covered with prominent isolated warts up to 1 µm diam. that are easily visible by light microscopy, whereas in the latter a finely verruculose ornamentation is scarcely visible in light microscopy without staining; the much smaller (up to 0.4 µm diam.) and densely disposed warts are clearly revealed only in SEM. In addition, ascii (196 × 16.7 vs. 162 × 12.1 µm on average) and ascospores (23.7 × 11.7 vs. 23.9 × 9 µm on average) of *C. iranica* are wider than those of *C. taleola*.

Caudospora taleola (Fr.) Bih. K. Svenska Vetensk Akad. Handl., Afd. 15(2): 11 (1889). – Figs. 4, 5c, d, f–m.

Basionym. – *Sphaeria taleola* Fr., Syst. mycol. (Lundae) 2(2): 391 (1823).

Synonyms. – *Aglaospora taleola* (Fr.) Tul. & C. Tul., Select. fung. carpol. (Paris) 2: 168 (1863).

Chorostate taleola (Fr.) Traverso, Fl. ital. crypt. 1(2): 212 (1906).

Diaporthe taleola (Fr.) Sacc., Atti Soc. Veneto-Trent. Sci. Nat., Padova, Sér. 4 4: 112 (1875).

Hercospora kornhuberi Bäumler, Annln K. K. naturh. Hofmus. Wien 13: 440 (1898).

Hercospora taleola (Fr.) E. Müll., in Müller & von Arx, Beitr. Kryptfl. Schweiz 11(no. 2): 728 (1962).

Melanconis taleola (Fr.) Speg., Atti Soc. Crittogram. Ital., Série 2 3(1): 54 [no. 77] (1881).

Valsa taleola (Fr.) Fr., Summa veg. Scand., Sectio Post. (Stockholm): 391 (1849).

Type. – AUSTRIA. Oberösterreich, Raab, Wetzlbach, on dead branches of *Quercus robur*, 24 December 2015, leg. H. Voglmayr (WU 39951, **neotype here designated**, MBT381444; ex-neotype culture D185 = CBS 143508)

Description. – Pseudostromata 1–4 mm diam., immersed in the bark of dead branches (1–3 cm diam.), flat or erumpent, circular to irregular, separate, scattered, sometimes confluent, delimited from surrounding bark by a black line. Ectostromatic discs white, flat, circular to

ovoid, tissue between ostiolar necks distinctly gray to dark grey, powdery. Central column whitish to grey. – Ostioles dark, at the same level as the disc surface, rarely projecting, opening separately, sometimes necks of perithecia united below the disc and discharging through a single ostiole. – Perithecia 2–16 per stroma, 300–700 µm diam., subglobose to ovoid, black, monostichous, arranged circinately in brown entostromata, with long ostiolar necks converging towards the ectostromatic disc. – Paraphyses elongate, hyaline, filiform, septate, evanescent. – Ascii (140)145–180(207) × 10–13 µm ($\bar{x} = 163 \times 12.1$ µm; n = 20), cylindrical, with short or obsolete stalks and a conspicuous apical ring, containing eight uniseriate ascospores. – Ascospores (17)20–28(31) × (6.5)8–10(11) µm ($\bar{x} = 23.9 \times 9$ µm; n = 30), l/w = (2.1)2.3–3.0(3.4), ellipsoid, two-celled, constricted at the septum, hyaline, appearing smooth in light microscopy but distinctly verrucose in SEM with densely disposed warts 0.1–0.4 µm diam., with a hyaline tubular gelatinous appendage 6–17 × 1–1.5 µm long at each end and 2–3 (rarely 4) similar median tubular gelatinous appendages arising from near the septum.

Asexual morph on natural substrate acervular, phomopsis-like. – Conidiomata ca. 1 mm diam., visible as darker spots in surface view, showing the same organisation as the sexual morph, i.e. a central whitish stromatic column with a white ectostromatic disc and a brown pseudostroma delimited from surrounding bark by a black line, preceding the sexual morph; conidiogenous region in section pale olivaceous green. – Conidiophores branched, hyaline, septate, formed on the upper margin of the central column. – Conidiogenous cells phialidic, (6.5)11.5–18.5(26) × (1.4)1.7–2.5(3.5) µm ($\bar{x} = 14.8 \times 2.1$ µm; n = 70), hyaline, smooth. – Conidia (15)17–25 (32) × 0.7–1.1(1.6) µm ($\bar{x} = 21 \times 0.9$ µm; n=50), l/w = (14.8)18.2–29.7(37.2), filiform with variable shape from more or less straight, sigmoid, falcate, semicircular to circular, unicellular, hyaline, smooth.

Cultural characteristics. – Colonies felty, irregular, often deeply immersed into the agar, white at the surface and primrose (23,,b) to olivaceous black (27,,,m) at the reverse in the dark at 24 °C, reaching the margin of 30 mm Petri-dish after 30 days at 24 °C.

Habitat. – On dead corticated twigs of *Quercus* sp.

Distribution. – Widely distributed in Europe, Asia, North America.

Other specimens examined. – AUSTRIA. Oberösterreich, St. Willibald, Gr. Sallet, on dead branches of *Quercus robur*, 26 December 2015, leg. H. Voglmayr (WU 39952, culture D186); St. Willibald, Geitzedt, on dead branches of *Quercus robur*, 31 December 2015, leg. H. Voglmayr (WU 39953, culture D187); Niederösterreich, Mannersdorf im Leithagebirge, Schweingraben, on dead branches of *Quercus petraea*, 12. March 2016, leg. H. Voglmayr (WU 39957, culture D216). FRANCE. Ardèche (07), Saint-Jean-Roure, Mandon, on dead branches of *Quercus robur*, 27 December 2015, leg. A. Gardiennet A.G. 15171 (WU 39955, culture D197); Saint-Jean-Roure, Grange de Sagne, on dead branches of *Quercus robur*, 28 December 2015, leg. A. Gardiennet A.G. 15173 (WU 39956, culture D198). IRAN. East Azerbaijan Province, Arasbaran, on dead branches of *Quercus* sp., 11 July 2015, leg. M. Mehrabi (IRAN 16715 F, WU 39954, culture IRAN 2551 C).

Notes. – No type specimen of *Sphaeria taleola* is preserved in the Fries collection at UPS (A. Kruys, pers. comm.), which necessitates neotypification. We here select a well-developed, abundant Austrian collection from the most likely original host, *Quercus robur*, as neotype, for which a culture and sequence data are available.

To our knowledge, *C. taleola* has not been previously been recorded from Iran; it is not listed in Ershad (2009). For comparison with *C. iranica*, see Notes there.

Discussion

Although morphologically undoubtedly a member of Diaporthales (Kirk et al. 2008), the phylogenetic affiliation and familial classification of *Caudospora* remained unclear up to now in the lack of DNA sequence data. Based on similarities in stromata and perithecia, Müller & Arx (1962) classified *Caudospora* in *Hercospora* (Lamproconiaceae), which was challenged by Rogers (1984), who recognized it to be substantially different from *Hercospora* in verrucose ascospores and a phialidic phomopsis-like asexual morph, vs. the holoblastic conidiation of the rabenhorstia-like asexual morph in *Hercospora*. However, although Rogers (1984) noted some similarities to the quercicolous *Diaporthe leiphaemis* var. *raveneliana* in verrucose ascospore ornamentation, he considered taxonomic rearrangements premature due to insufficient data. In our phylogenies, *Caudospora* is clearly revealed as a member of Sydowiellaceae (Fig. 1). Remarkably, already Munk (1957) noted a high similarity of centrum morphology of *Caudospora* to that of *Sydowiella fenestrans*, to which it is closely related.

After transfer of several lineages originally classified in other families of Diaporthales (e.g. Gnomoniaceae, Melanconidaceae), the Sydowiellaceae have in recent years become a rather heterogeneous assemblage which is difficult to define morphologically (Rossman et al. 2007). It currently comprises about 15 genera occurring as saprotrophs, endophytes and parasites of various herbaceous and woody hosts (Senanayake et al. 2017b). Most genera and species are characterized by reduced, poorly developed stromata containing few to a single perithecium, but there are few exceptions like *Sillia* and *Chapeckia* with well-developed multiperitheciate stromata. Also *Caudospora* has well-developed pseudostromata, which are delimited from the surrounding host tissue by a conspicuous black line, which is so far unique in Sydowiellaceae.

The molecular data reveal that *Caudospora iranica* and *C. taleola* are closely related, and they share a similar ecology and the same host genus, *Quercus*. However, they can be easily separated by ascospore morphology. *Caudospora iranica* has coarsely verrucose ascospores with isolated warts (Figs. 3h–j, 5a, b, e), whereas the ascospores of *C. taleola* appear smooth in light microscopy (Fig. 4g, h) but are shown to be finely verrucose in SEM (Fig. 5c, d, f). Ascospore ornamentation of *C. taleola* revealed by SEM in our investigations matches that illustrated in Rogers (1984: fig. 5) from a North American collection.

To our knowledge, the asexual morph of *C. taleola* is here described and illustrated for the first time in detail from natural substrate. We did not observe an asexual morph in our cultures, but Rogers (1984) obtained a phomopsis-like asexual morph on oatmeal agar, with

unicellular, sigmoid to falcate hyaline conidia ($5)10\text{--}17 \times 1\text{--}1.5 \mu\text{m}$ in size produced on phialides. He compared it with the descriptions of *Myxosporium taleola* and *Libertella taleola*, which were formally described by Saccardo (1884) as putative asexual morphs of *C. taleola*, based on data reported by Tulasne & Tulasne (1863) and Fuckel (1871) from associations of sexual and asexual morphs on natural substrate. Rogers (1984) found some differences of his strain in conidial size; especially conidial width was substantially narrower in his isolate than that reported for *Myxosporium taleola* ($16 \times 8 \mu\text{m}$) and *Libertella taleola* ($20\text{--}30 \times 4 \mu\text{m}$). However, he was unable to resolve whether these differences related to strain differences, differences caused by conidiation in pure culture vs. on natural substrate, or erroneous connections of asexual morphs of species other than *C. taleola*. The asexual morph from natural substrate investigated by us agrees well with that reported by Rogers (1984) in its phialidic conidiogenous cells produced on short, branched conidiophores, conidial shape and conidial width, but our conidia are somewhat longer (15–32 vs. (5)10–17 μm in Rogers 1984), which may be caused by the different substrate. It therefore seems likely that the erroneous conidial width reported by Tulasne & Tulasne (1863) and Fuckel (1871) is due to misidentification.

Acknowledgements

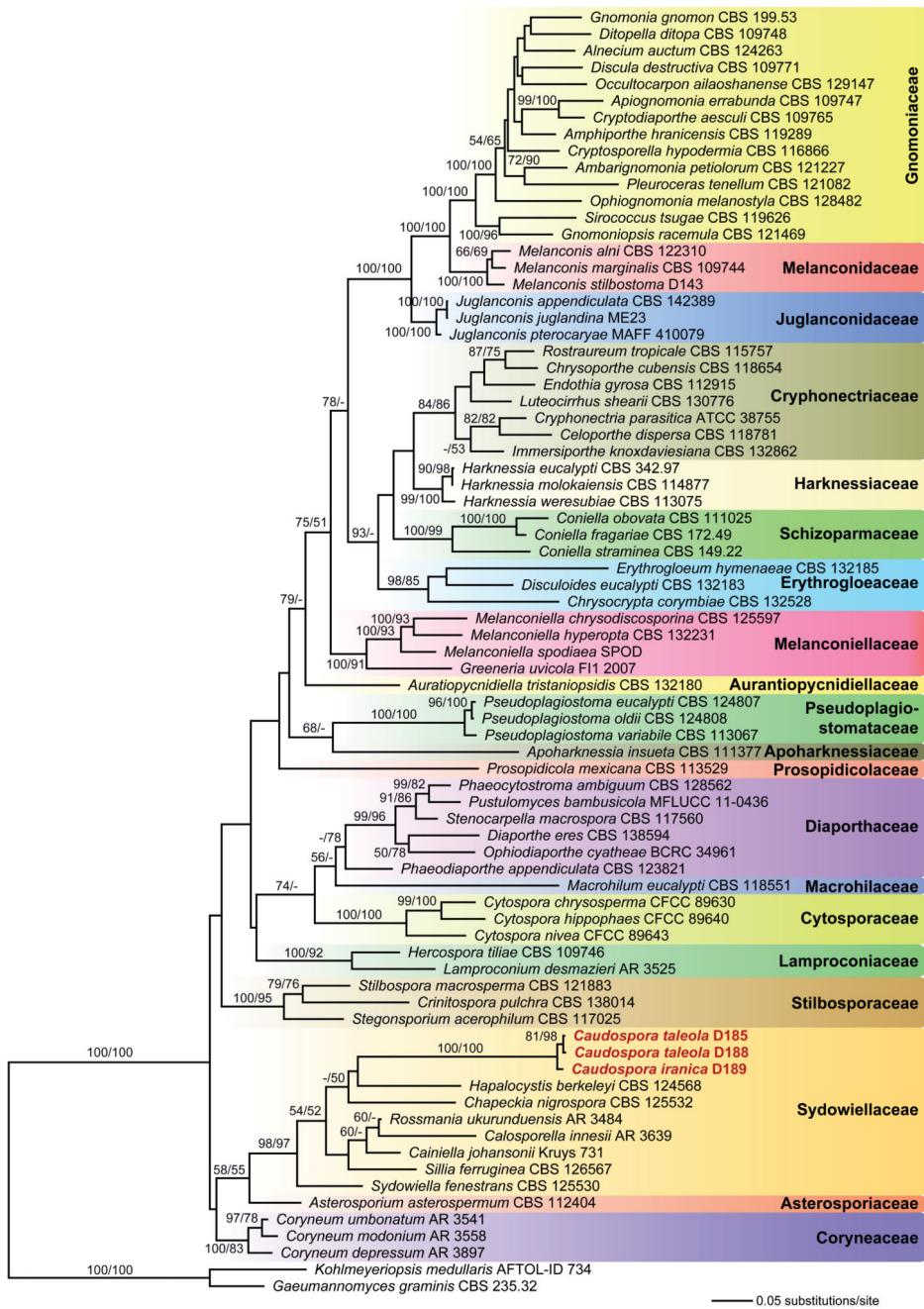
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**Fig. 1.**

Phylogram of the best maximum likelihood tree ($\ln L = -48924.555$) revealed by RAxML from an analysis of the combined ITS-LSU-*rpb2-tef1* matrix of 75 selected members of Diaporthales, with two members of Magnaportheaceae (*Gaeumannomyces graminis*, *Kohlmeyeriopsis medullaris*) selected as outgroup. Familial classification follows Senanayake et al. (2017a). **Caudospora** (bold) is revealed as a member of Sydiowilliaceae with high support. ML and MP bootstrap support above 50 % are given above or below the branches.

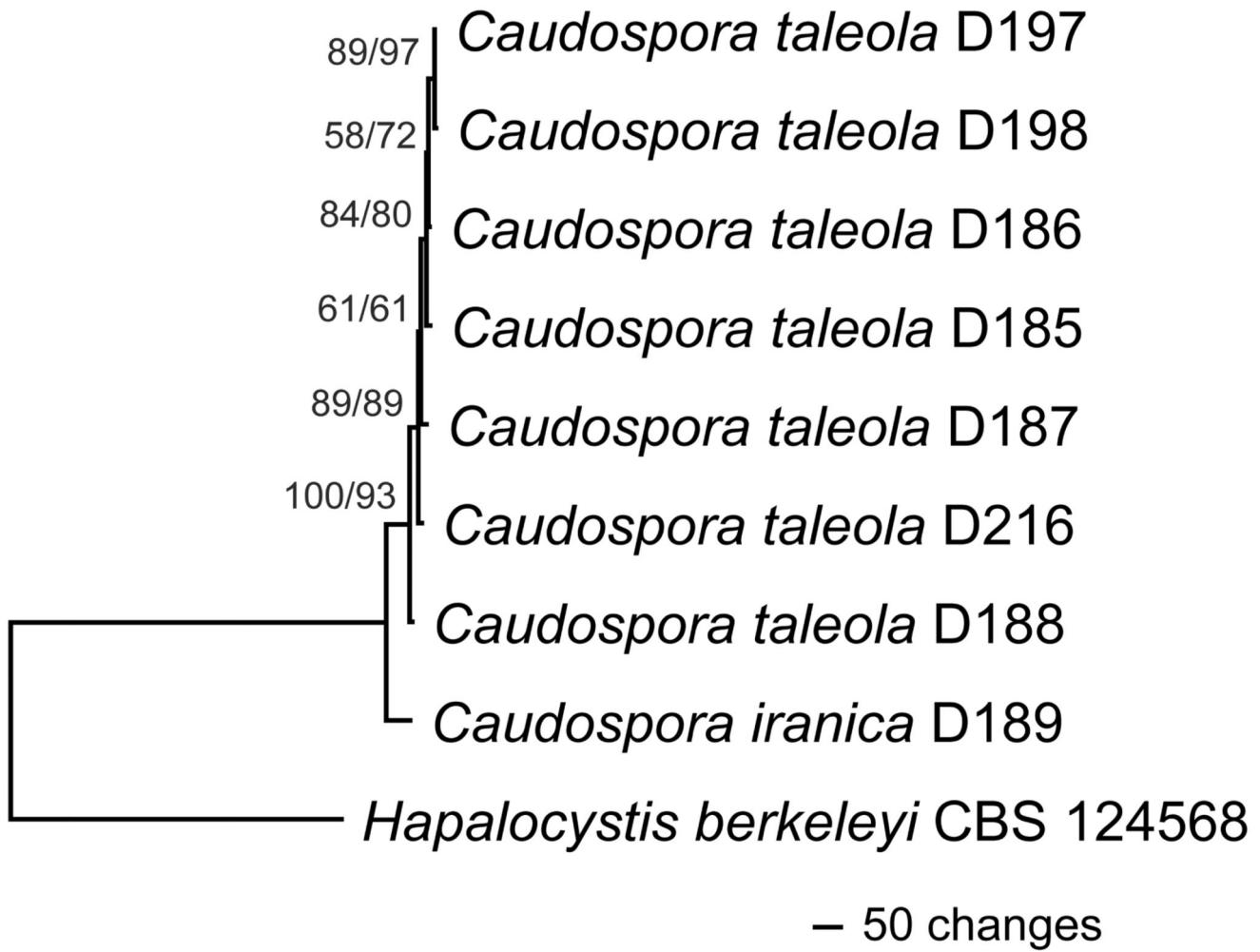


Fig. 2.

Phylogram of the single MP tree 1559 steps long, obtained by PAUP from an analysis of the combined nine-loci matrix (SSU-ITS-LSU, *cal*, *ms204*, *rpb1*, *rpb2*, *tef1*, *tub2*) of *Caudospora*, with *Hapalocystis berkeleyi* selected as outgroup according to Fig. 1. MP and ML bootstrap support above 50 % are given at the first and second position, respectively, above or below the branches.

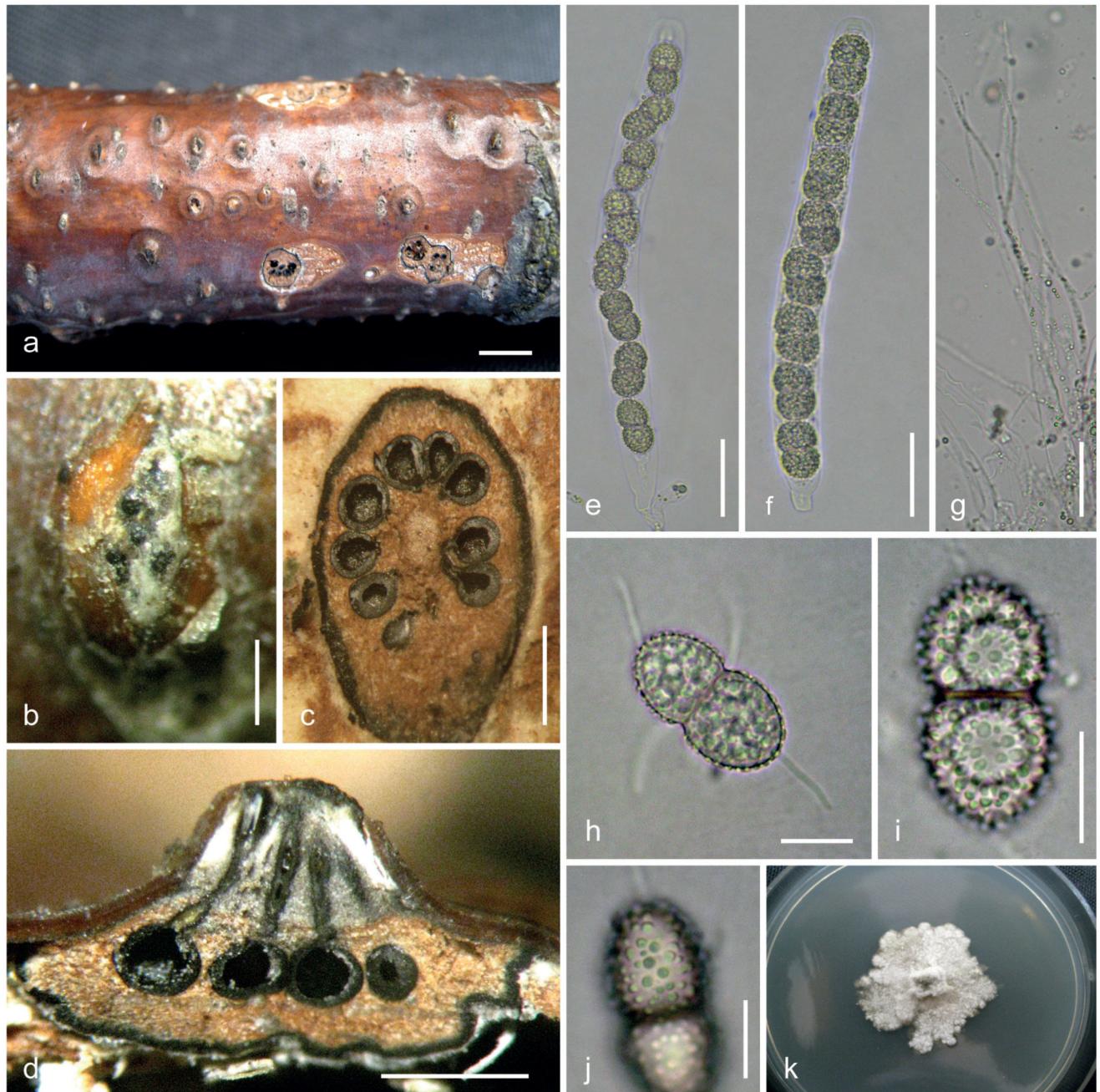


Fig. 3.
Caudospora iranica (IRAN 16716 F, holotype). **a.** stromata on dead branch of *Quercus* sp.; **b.** ectostromatic disc; **c.** transverse sections of a pseudostroma; **d.** vertical section of a pseudostroma; **e, f.** ascii; **g.** paraphyses; **h–j.** ascospores, showing coarsely verrucose ornamentation; **k.** culture on PDA. Bars: a 3 mm; b 300 µm; c, d 1 mm; e–g 30 µm; h–j 10 µm.

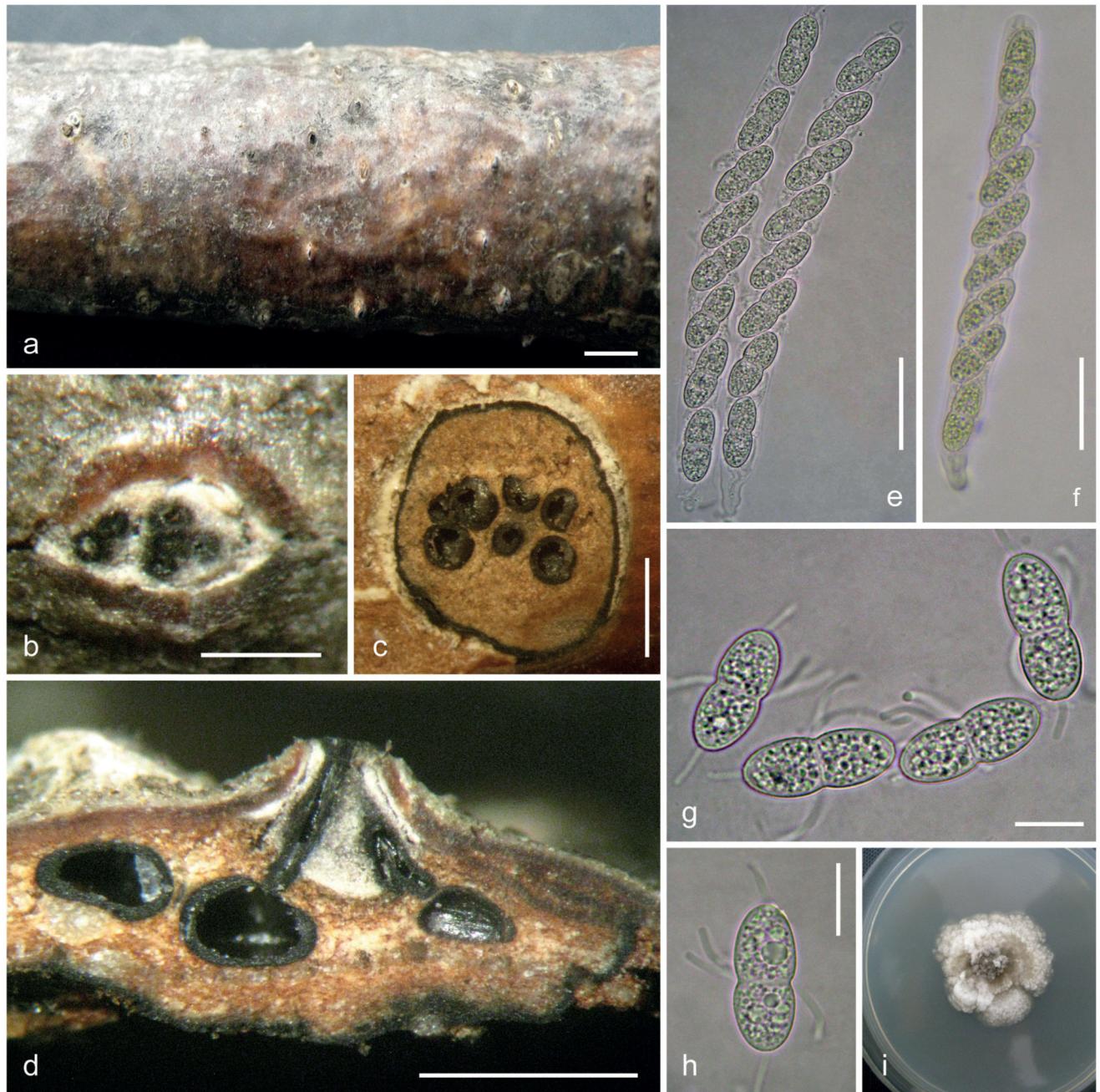
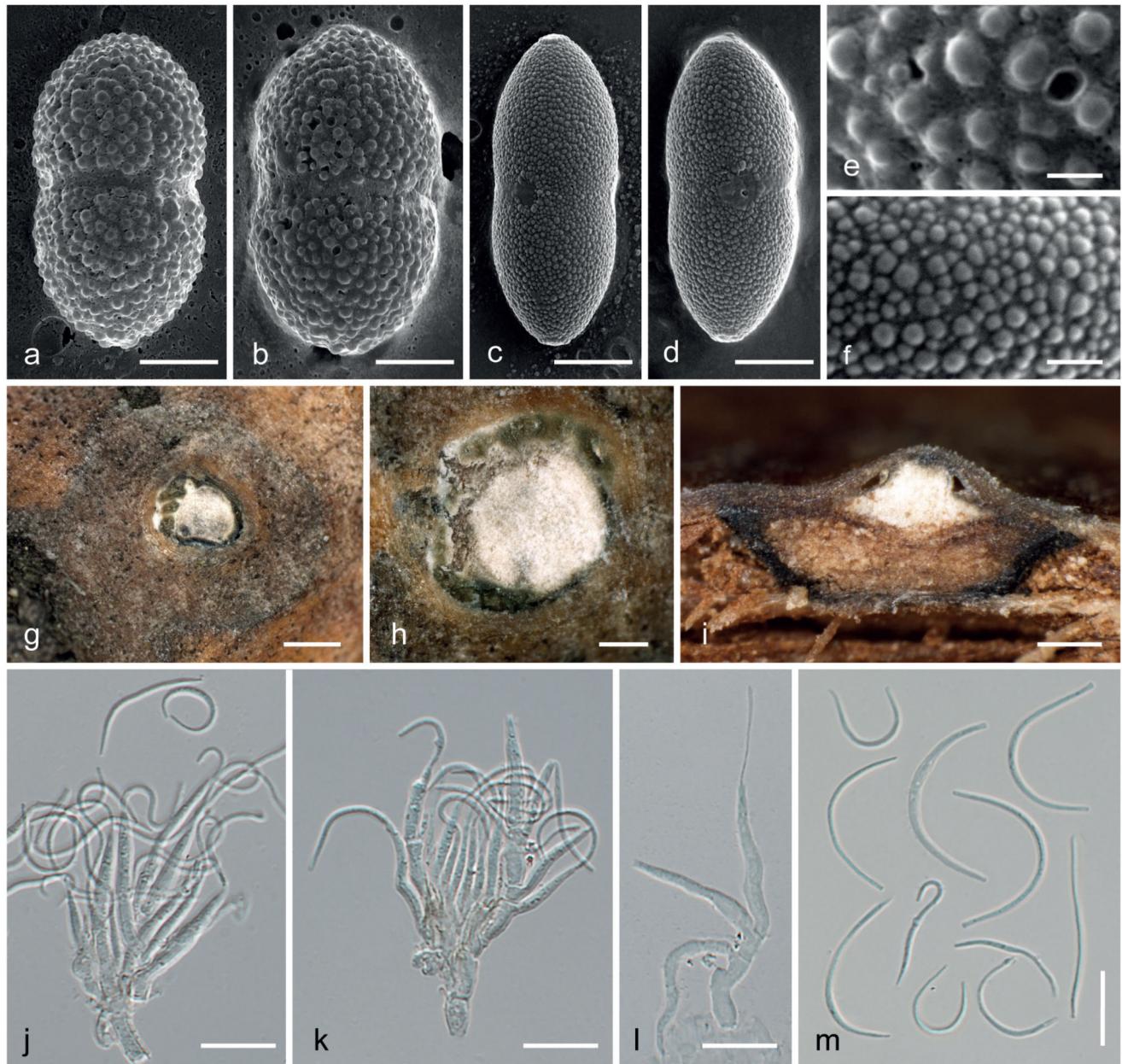


Fig. 4.

Caudospora taleola (IRAN 16715 F). **a.** stromata on dead branch of *Quercus* sp.; **b.** ectostromatic disc; **c.** transverse sections of a pseudostroma; **d.** vertical section of a pseudostroma (showing two united necks under ectostromatic disc); **e, f.** ascospores; **g, h.** ascospores; **i.** culture on PDA. Bars: a 3 mm; b 300 µm; c, d 1 mm; e, f 30 µm; g, h 10 µm.

**Fig. 5.**

a-f. SEM pictures of ascospores of *Caudospora iranica* (**a, b, e**) and *C. taleola* (**c, d, f**), showing the coarsely and finely verrucose ascospore ornamentation in *C. iranica* and *C. taleola*, respectively; the median smooth circular areas in **c, d**. represent the scars of median gelatinous appendages. **g-m.** Asexual morph of *C. taleola*. **g, h.** conidiomata in transverse section, showing the central stromatic column and olive-green conidial masses; **i.** conidiomata in vertical section, showing pseudostromata delimited by a black line, the central stromatic column and the olive-green conidial masses produced on the stromatic column; **j-l.** branched conidiophores with phialides producing filiform conidia (in **j**. with released elongate and circular conidia); **m.** conidia. **a, b, e.** IRAN 16716 F (holotype of *C.*

iranica). c, d, f–m. WU 39951 (neotype of *C. taleola*). Bars: a–d 5 µm; e, f 1 µm; g 500 µm; h, i 200 µm; j–m 10 µm.

Tab. 1

Strains and NCBI GenBank accessions used in the phylogenetic analyses of the combined SSU-ITS-LSU-*cal-ms204-rpb1-rpb2-tef1-tub1* matrix. All sequences were generated during the present study.

Taxon	Strain	Voucher	Country	Host/substrate	GenBank accession numbers						
					<i>SSU-ITS-LSU</i>	<i>cal</i>	<i>ms204</i>	<i>rpb1</i>	<i>rpb2</i>	<i>tef1</i>	<i>tub2</i>
<i>Caudospora iranica</i>	D189 = IRAN 2552 F, IRAN 2552 C = CBS 143507	IRAN 16716 F, WU 39950	Iran	<i>Quercus sp.</i>	MG495960	MG495951	MG495970	MG495979	MG495988	MG495997	MG496004
<i>C. taleola</i>	D185 = CBS 143508	WU 39951	Austria	<i>Quercus robur</i>	MG495961	MG495952	MG495971	MG495980	MG495989	MG495998	MG496005
<i>C. taleola</i>	D186	WU 39952	Austria	<i>Quercus robur</i>	MG495962	MG495953	MG495972	MG495981	MG495990	MG495999	MG496006
<i>C. taleola</i>	D187	WU 39953	Austria	<i>Quercus robur</i>	MG495963	MG495954	MG495973	MG495982	MG495991	MG496000	MG496007
<i>C. taleola</i>	D188 = IRAN 16715 F, IRAN 2551 C WU 39954	IRAN 16715 F, WU 39954	Iran	<i>Quercus sp.</i>	MG495964	MG495955	MG495974	MG495983	MG495992	MG496001	MG496008
<i>C. taleola</i>	D197	WU 39955	France	<i>Quercus robur</i>	MG495965	MG495956	MG495975	MG495984	MG495993	MG496002	MG496009
<i>C. taleola</i>	D198	WU 39956	France	<i>Quercus robur</i>	MG495966	MG495957	MG495976	MG495985	MG495994	–	MG496010
<i>C. taleola</i>	D216	WU 39957	Austria	<i>Quercus petraea</i>	MG495967	MG495958	MG495977	MG495986	MG495995	–	MG496011
<i>Hapalocystis berkeleyi</i>	D84 = CBS 124568	WU 39959	UK	<i>Platanus x hispanica</i>	MG495968	MG495959	MG495978	MG495987	MG495996	MG496003	MG496012

Tab. 2

Strains and NCBI GenBank accessions used in the phylogenetic analyses of the combined ITS-LSU-*tpb2-tef1* matrix. Sequences in bold were generated during the present study.

Taxon	Strain	Voucher	Host/substrate	GenBank accession numbers			
				ITS	LSU	<i>tpb2</i>	<i>tef1</i>
<i>Ahnfeltium auctum</i>	CBS 124263	WU 30206	<i>Ahnetia glutinosa</i>	KF570154	KF570170	KF570200	
<i>Ambarignomonia petiolorum</i>	CBS 121227	BPI 844274	<i>Liquidambar styraciflua</i>	EU254748	EU255070	EU211898	
<i>Amphiphorthe iranicensis</i>	CBS 119289	BPI 843515	<i>Tilia platyphyllos</i>	EU199178	EU199122	EU199137	–
<i>Apignomonia errabunda</i>	CBS 109747	AR 2813	<i>Fagus sylvatica</i>	DQ313525	NG_027592	DQ862014	DQ313565
<i>Apothanknessia insuta</i>	CBS 111377	CPC 1451	<i>Eucalyptus pellita</i>	JQ706083	AY720814	–	–
<i>Asterosporium asterospermum</i>	CBS 112404	–	<i>Fagus sylvatica</i>	–	AB553745	–	–
<i>Auratiopycnidella tristaniopsis</i>	CBS 132180	CBS H-20932	<i>Tristaniopsis laurina</i>	JQ685516	JQ685522	–	–
<i>Caniella johnsonii</i>	Kruys 731	UPS F-567263	<i>Dryas octopetala</i>	JF701922	JF701920	–	–
<i>Caudospora iranica</i>	D189 = IRAN 2552 C	IRAN 16716 F	<i>Quercus</i> sp.	MG495960	MG495988	MG495997	
<i>Caudospora taleola</i>	D185	WU 39951	<i>Quercus robur</i>	MG495961	MG495961	MG495989	MG495998
<i>Caudospora taleola</i>	D188 = IRAN 2551 C	IRAN 16715 F	<i>Quercus</i> sp.	MG495964	MG495964	MG495992	MG496001
<i>Calosporella innesii</i>	AR 3639	BPI 840945	<i>Acer pseudoplatanus</i>	JF681965	EU683071	–	–
<i>Celoporthis dispersa</i>	CBS 118781	PREM 58897	<i>Syzygium cordatum</i>	AY214316	HQ730854	–	HQ730841
<i>Chapeckia nigrospora</i>	CBS 125532	BPI 863766	<i>Betula</i> sp.	JF681957	EU683068	–	–
<i>Chrysoscypha corymbiae</i>	CBS 132528	CPC 19279	<i>Corymbia</i> sp.	JX069867	JX069851	–	–
<i>Chrysosporthe cubensis</i>	CBS 118654	PREM 58788	<i>Eucalyptus</i> sp.	JN942342	JN940856	–	GQ290137
<i>Coniella fragariae</i>	CBS 172.49	CBS H-10697	Forest soil	AY339317	AY339322	KX833472	KX833663
<i>Coniella obovata</i>	CBS 111025	CBS H-22703	Leaf litter	AY339313	KX833497	KX833692	
<i>Coniella straminea</i>	CBS 149.22	STE U 3932	<i>Fragaria</i> sp.	AY339348	AY339348	KX833506	KX833704
<i>Coryneum deppressum</i>	AR 3897	BPI 843585	<i>Quercus cerris</i>	–	EU683074	–	–
<i>Coryneum modonium</i>	AR 3558	BPI 749131	<i>Castanea sativa</i>	–	EU683073	–	–
<i>Coryneum umbonatum</i>	AR 3541	BPI 872021	<i>Quercus cerris</i>	–	EU683072	–	–
<i>Criniospora pulchra</i>	CBS 138014	CBS H-21729	<i>Mangifera indica</i>	KJ710466	KJ710443	–	–
<i>Cyphonectria parasitica</i>	ATCC 38755	–	<i>Castanea dentata</i>	AY141856	EU199123	–	EU222014
<i>Cryptodiaporthe aesculi</i>	CBS 109765	BPI 748430	<i>Aesculus hippocastanum</i>	EU199179	AF408342	EU199138	–
<i>Cryptosporella hypodermia</i>	CBS 116866	BPI 748432	<i>Ulmus minor</i>	EU199181	AF408346	EU199140	–

Taxon	Strain	Voucher	Host/substrate	GenBank accession numbers		
				TTS	LSU	rpb2
<i>Cytopspora chrysosperma</i>	CFCC 89630	BIFC-3978	<i>Salix psammophila</i>	KF765674	KF765690	KF765706
<i>Cytopspora hippophaes</i>	CFCC 89640	—	<i>Hippophae rhamnoides</i>	KF765682	KF765698	KF765714
<i>Cytopspora nivea</i>	CFCC 89643	—	<i>Salix psammophila</i>	KF765685	KF765701	KP310865
<i>Diaporthe eres</i>	CBS 138594	BPI 892912	<i>Ulmus</i> sp.	KJ210529	—	KJ210550
<i>Discula destructiva</i>	CBS 109771	BPI 1107757	<i>Cornus nuttallii</i>	EU199186	AF408359	EU199144
<i>Disculoides eucalypti</i>	CBS 132183	CBS H-20935	<i>Eucalyptus</i> sp.	JQ685517	JQ685523	—
<i>Ditopella diopae</i>	CBS 109748	BPI 748439	<i>Alnus glutinosa</i>	DQ323526	EU199126	EU199145
<i>Endothia gyrosa</i>	CBS 112915	—	<i>Quercus palustris</i>	AF046905	AY194114	—
<i>Erythrgleum hymenaceae</i>	CBS 132185	CBS H-20937	<i>Hymenaea courbaril</i>	JQ685519	JQ685525	—
<i>Gaeumannomyces graminis</i>	CBS 235.32	—	<i>Oryza sativa</i>	JX134669	JX134681	JX134695
<i>Gnomonia gnomon</i>	CBS 199.53	—	<i>Corylus avellana</i>	DQ491518	AF408361	EU219295
<i>Gnomoniopsis racemula</i>	CBS 121469	BPI 871003	<i>Epilobium angustifolium</i>	EU254841	EU255122	EU219241
<i>Greeneria uvicola</i>	FTI 2007	—	<i>Vitis</i> sp.	HQ586009	GQ870619	—
<i>Hapalocystis berkeleyi</i>	CBS 124568	WU 39959	<i>Platanus × hispanica</i>	MG495668	MG495996	MG496003
<i>Harknessia eucalypti</i>	CBS 342.97	—	<i>Eucalyptus regnans</i>	AY720745	AF408363	—
<i>Harknessia molokaiensis</i>	CBS 114877	—	<i>Eucalyptus robusta</i>	AY720749	AY720842	—
<i>Harknessia wexsobiae</i>	CBS 113075	CBS H-9903	<i>Eucalyptus</i> sp.	AY720741	AY720835	—
<i>Hercospora tiliæ</i>	CBS 109746	BPI 748440	<i>Tilia tomentosa</i>	—	AF408365	—
<i>Immersiporthe knoxdaviesiana</i>	CBS 132862	PREM 60740	<i>Rapanea melanophloeos</i>	JQ862770	JQ862760	—
<i>Juglanconis appendiculata</i>	CBS 142389	WU 35960	<i>Juglans nigra</i>	KY427145	KY427195	KY427214
<i>Juglanconis juglandina</i>	ME23	WU 35965	<i>Juglans nigra</i>	KY427150	KY427150	KY427222
<i>Juglanconis pterocaryaæ</i>	MAFF 410079	TFM FPH 3373	<i>Pterocarya rhoifolia</i>	KY427155	KY427155	KY427224
<i>Kohlmeyeriopsis medullaris</i>	CBS 117849	—	<i>Juncus roemerianus</i>	KM484852	FJ176854	—
<i>Lamproconium desmazeri</i>	AR 3525	BPI 748445	<i>Tilia</i> sp.	—	AF408372	—
<i>Luteocinthus shearrii</i>	CBS 130776	PERTH 08439362	<i>Banksia baxteri</i>	KC197021	KC197019	—
<i>Macrothilum eucalypti</i>	CBS 118551	—	<i>Eucalyptus</i> sp.	DQ195781	DQ195793	—
<i>Melanconella chrysodiscosporina</i>	CBS 125597	WU 31859	<i>Carpinus betulus</i>	JQ926238	JQ926310	JQ926376
<i>Melanconella hyperopae</i>	CBS 132231	WU 31836	<i>Carpinus betulus</i>	JQ926285	JQ926351	JQ926418
<i>Melanconella spodiacea</i>	SPOD	WU 31854	<i>Carpinus betulus</i>	JQ926300	JQ926366	JQ926433
<i>Melanconis alni</i>	CBS 122310	BPI 872035	<i>Alnus viridis</i>	EU199195	EU199130	EU199153

Taxon	Strain	Voucher	Host/substrate	GenBank accession numbers			
				TTS	LSU	rpb2	tfl
<i>Melanconis marginalis</i>	CBS 109744	BPI 748446	<i>Alnus rubra</i>	EU199197	AF408373	EU219301	EU221991
<i>Melanconis stilbostoma</i>	D143	WU 35970	<i>Betula pendula</i>	KY427156	KY427206	KY427225	
<i>Occultocarpon ailaooshanense</i>	CBS 129147	BPI 879254	<i>Alnus nepalensis</i>	JF779848	JF779852	JF779857	JF779862
<i>Ophiodiaporthe cyathaeae</i>	BCRC 34961	HAST 1364	<i>Cyathea lepifera</i>	JX570889	JX570891	JX570893	KC465406
<i>Ophiognomonia melanostyla</i>	CBS 128482	BPI 879257	<i>Tilia cordata</i>	JF779850	JF779854	JF779858	—
<i>Phaeocyttorina ambiguum</i>	CBS 128562	—	<i>Zea mays</i>	FR748042	FR748101	—	FR748074
<i>Phaeodiaporthe appendiculata</i>	CBS 123821	WU 32449	<i>Acer campestre</i>	KF570156	KF570156	—	—
<i>Pleuroceras tenellum</i>	CBS 121082	BPI 871059	<i>Acer rubrum</i>	EU199199	EU255202	EU199155	EU221907
<i>Prosopidiola mexicana</i>	CBS 113529	CBS-H 7948	<i>Prosopis glandulosa</i>	AY720709	—	—	—
<i>Pseudoplagiostoma eucalypti</i>	CBS 124807	CBS H-20303	<i>Eucalyptus urophylla</i>	GU973512	GU973606	—	GU973542
<i>Pseudoplagiostoma oldii</i>	CBS 124808	CBS H-20300	<i>Eucalyptus camaldulensis</i>	GU973534	GU973609	—	GU973564
<i>Pseudoplagiostoma variabile</i>	CBS 113067	CBS H-20304	<i>Eucalyptus globulus</i>	GU973536	GU973611	—	GU973566
<i>Pustulomyces bambuscola</i>	MFLUCC 11-0436	MFLU 13-0369	<i>Bambusa</i> sp.	KF806752	KF806753	—	KF806755
<i>Rossmania ukurunduensis</i>	AR 3484	BPI 747566	<i>Acer ukurunduense</i>	—	EU683075	—	—
<i>Rostrareum tropicale</i>	CBS 115757	PREM 57519	<i>Terminalia ivorensis</i>	AY167436	AY194092	—	—
<i>Silbia ferruginea</i>	CBS 126567	BPI 843619	<i>Corylus avellana</i>	JF681959	EU683076	—	—
<i>Siroccoccus tsugae</i>	CBS 119626	BPI 871167	<i>Tsuga mertensiana</i>	EU199203	EU199136	EU199159	EF512534
<i>Siegonsporium acerophilum</i>	CBS 117025	WU 28050	<i>Acer saccharum</i>	EU039982	EU039993	KF570173	EU040027
<i>Stenocarpella macrospora</i>	CBS 117560	MRC 8615	<i>Zea mays</i>	FR748048	EU754219	—	—
<i>Stilbospora macrosperma</i>	CBS 115073	WU 24708	<i>Carpinus betulus</i>	EU039965	MG49969	KF570195	EU039999
<i>Syadowiella fenestrans</i>	CBS 125530	BPI 843503	<i>Chamereion angustifolium</i>	JF681956	EU683078	—	—