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Research article

Pseudaleuria fibrillosa (Pezizales), a little-known and often confused species from the Umbria region (Italy)

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Abstract
The genus *Pseudaleuria* Lusk (Ascomycota, Pezizales, Pyronemataceae) comprises operculate discomycetes characterized by cupulate apothecia, distinctive apothecial hairs, and ornamented ascospores lacking conspicuous guttules. Among its species, *Pseudaleuria fibrillosa* is a rarely reported taxon that has often been confused with morphologically similar members of Pezizales. Because of this taxonomic complexity, well-documented collections integrating morphological and molecular data are essential to refine diagnostic characters and update its distribution. In this work we report the occurrence of *P. fibrillosa* for the first time in the Umbria region and for the third time in Italy. A detailed description of its macro- and micromorphological features and phylogenetic placement is provided, along with an updated distribution range for this species.

Keywords
Ascomycota, Pyronemataceae, *Pseudaleuria*, taxonomy, phylogeny

Introduction

The genus *Pseudaleuria* was established by Lusk (1987) introducing the description of *Pseudaleuria quinaultiana* Lusk. based on operculate asci, apothecial morphology, ascoma coloration, spore characteristics, and excipular structure, the genus was placed within the order Pezizales. Morphologically, *Pseudaleuria* shares structural similarities with the genus *Aleuria* Fuckel, particularly in ascus conformation, excipular organization, and paraphysis morphology. Ascoma size, shape, and coloration may also overlap with those observed in *Aleuria*. However, a distinctive combination of characters, including peculiar apothecial hairs, spore ornamentation patterns, and the general absence of guttules, clearly separates *Pseudaleuria* from *Aleuria* sensu Korf (1972), supporting its recognition as an independent genus within Pyronemataceae. The taxonomic position

of *Pseudaleuria fibrillosa* (Massee) J. Moravec has historically been controversial. Originally described as *Otidea fibrillosa* (Massee, 1895), it was subsequently combined into *Tricharina* by Yang and Korf (1985) based on non-holotype material. This reassignment relied on characters such as perispore behaviour in lactic acid, spore wall pigmentation changes in KOH, and the presence of fasciculate blunt marginal hairs (Moravec, 2003). However, later re-evaluations suggested that these features are variable and, in part, misinterpreted (Van Vooren et al., 2017; Saitta, 2019). In particular, the apothecial hairs of *P. fibrillosa* differ from those typical of *Tricharina*, the perispore appears separable, and spore pigmentation is influenced by maturity and environmental conditions, reducing its diagnostic value. Although Galán and Raitviir (1995) retained the species within *Tricharina*, they acknowledged morphological affinities with *Aleuria* and *Melastiza* (Cooke, 1876; Massee, 1895; Phillips, 1893). This persistent ambiguity highlights the atypical nature of the species and underscores the importance of integrative morphological and molecular approaches, as adopted in subsequent studies (Moravec, 2003; Van Vooren et al., 2017; Saitta, 2019). In Italy, *P. fibrillosa* has been rarely documented. The species was first reported from northern Italy by Jamoni (1997). A subsequent record from Sicily by Saitta (2019) provided detailed macro- and micromorphological descriptions, colour photographs, and molecular data. These studies emphasized the rarity and scattered occurrence of the species in Europe. To date, the genus *Pseudaleuria* comprises only two recognized species: *P. quinaultiana* Lusk, originally described from North America (Lusk, 1987), and *P. fibrillosa*, so far predominantly reported from European localities (Moravec, 2003; Van Vooren et al., 2017; Saitta, 2019). The present study reports the first occurrence of *P. fibrillosa* in the Umbria region and provides detailed morphological, ecological, and phylogenetic data aimed at clarifying the diagnostic features and regional distribution of this rarely recorded species.

Materials and Methods

Sampling and preservation

Ascomata were collected in October 2025 in the Umbria region, Sant'Anatolia di Narco (Province of Perugia, Italy), at 1153 m a.s.l. Specimens were found on very moist soil rich in organic matter and woody debris in a woodland area adjacent to a peat bog. Geographic coordinates were recorded as 42°40′51″ N, 12°54′30″ E. Soil pH was 7.2 (ISO, 2021). After examination, ascomata were dried at ≤ 40 °C for 8 h and stored with silica gel. Herbarium material is deposited at the mycological herbarium of the Associazione Gruppi Micologi Toscani (AGMT 15291).

DNA extraction, amplification, and sequencing

Genomic DNA was isolated from dried samples following a standard CTAB protocol (Palmer et al., 2008). The following primer pairs were used for PCR amplification and sequencing: ITS1F and ITS4 for the ITS1-5.8S-ITS2 region (White et al. 1990; Gardes and Bruns 1993); LR0R (Cubeta et al. 1991) and LR5 (Vilgalys and Hester 1990) for the D1–D3 domains of the nuclear 28S rDNA (nrLSU) and bRPB2-6F and bRPB2-7R2 for a fragment of the second largest subunit of RNA polymerase II (*rpb2*) (Liu et al. 1999; Matheny 2007). Sequencing was performed by the laboratory ALVALAB (Spain) using both forward and reverse primers. All GenBank/UNITE ITS sequences used to infer the phylogeny (ITS and LSU) together with voucher information and geographic origin, are listed in Supplementary Tables S1. Sequences were selected to maximize the representation of the currently available diversity within *Pseudaleuria* including all publicly accessible ITS and LSU accessions of

P. fibrillosa, P. quinaultiana, and *Pseudaleuria* sp. available in GenBank at the time of the study. Representative sequences of closely related genera within Pyronemataceae were included to provide phylogenetic context. Phylogenetic reconstructions were performed independently for the ITS and LSU datasets because only three previously published *P. fibrillosa* collections were represented by both markers generated from the same voucher specimens, namely those reported by Van Vooren et al. (2017), Saitta (2019), and Olariaga et al. (2020). Additional protein-coding loci, such as RPB2 were even scarcer and were available only for a single collection of *P. fibrillosa* (Saitta, 2019). Consequently, a combined multilocus phylogenetic analysis was not performed. Sequences generated in this study were deposited in GenBank database with the following accession numbers: PZ095248 (ITS), PZ098752 (LSU) and PZ148321 (*rpb2*).

Phylogenetic analysis

A total of 22 ITS sequences were included in the phylogenetic analysis. Sequences were aligned using the ClustalW algorithm (Thompson et al., 1994) implemented in MEGA v11 (Tamura et al., 2021) with default parameters. Maximum Likelihood (ML) phylogenetic reconstruction was performed using RAxML-NG v1.2.2 (Kozlov et al., 2019) under the GTR+G substitution model. Tree inference and bootstrap analysis were conducted using the *--all* algorithm with 1000 bootstrap replicates. Branch support values were estimated using the Felsenstein bootstrap proportion (FBP) method. The resulting best-scoring ML tree was rooted using *Cheilymenia stercorea* (Pers.) Boud. (MZ159404) as outgroup, selected based on its phylogenetic position within Pezizales and its clear morphological distinction from the taxa included in the ingroup (Moravec, 2003; Abdullah Kaya et al., 2016). The tree was visualized using FigTree v1.4.4. The same analytical pipeline was independently applied to a separate LSU dataset comprising 24 sequences.

Morphological study

Macroscopic and microscopic observations were performed on fresh and dried material. Thin hand-cut sections were mounted in water and cotton blue in lactic acid; dried specimens were rehydrated in water and 3% ammonia. Observations were conducted using an Olympus BH2 microscope with 20×, 40×, and 100× oil immersion objectives. Images were captured using a Canon R10 camera and measured with Piximètre software calibrated with a stage micrometer (Henriot, 2020). Spore measurements are expressed as: (minimum) mean − standard deviation – mean – mean + standard deviation (maximum), based on 45 measured ascospores (n = 45). Q values represent spore length/width ratios. Measurements of asci, paraphyses, and hair structures are given as minimum–maximum ranges with mean values.

Results

Phylogenetic analysis

The specimen examined in this study clustered within a well-supported clade (bootstrap = 94) together with three other European sequences of *P. fibrillosa* originating from Germany (KY364035; Van Vooren et al., 2017), Italy (MK720105; Saitta, 2019), and Spain (MW248487; Olariaga et al., 2020) (Fig. 1). Phylogenetic analysis of the ITS dataset grouped *P. fibrillosa*, *P. quinaultiana* as well as *Melastizia* and *Tricharina* species in the same lineage (bootstrap = 98) although several the internal nodes were not supported. Two environmental ITS sequences obtained from soil samples

(UDB05274559 – Colombia; UDB05275012 – Mexico) retrieved through GBIF and traceable to the UNITE as *Pseudaleuria* sp., did not cluster within either *P. fibrillosa* or *P. quinaultiana* clades but formed a distinct and unsupported clade outside the two currently recognized species of the genus. These sequences were conservatively treated as *Pseudaleuria* sp. in the present analysis, avoiding forced species- or genus-level assignment.

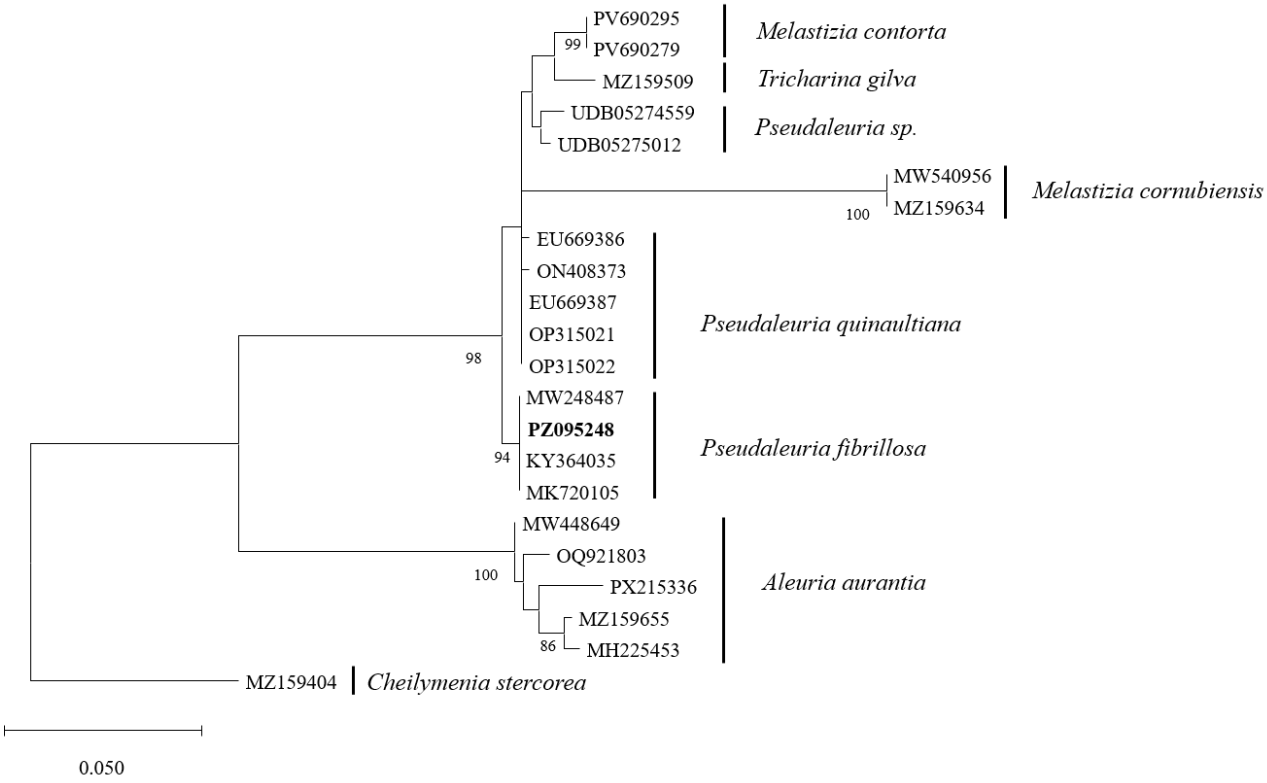

Fig. 1 - Maximum Likelihood phylogenetic tree based on ITS sequences (22 taxa). Bootstrap support values > 75 % are shown at the nodes. *Cheilymenia stercorea* was used as outgroup. Scale bar indicates substitutions per site.

LSU phylogenetic reconstruction (24 sequences; Supplementary Fig. S1) was performed using a dataset that only partially overlapped with the ITS dataset, as several specimens were represented by only one of the two markers in public databases. Despite these differences in taxon sampling, the LSU analysis confirmed the separation of the main *Pseudaleuria* lineages and supported the placement of the specimen within the *P. fibrillosa* clade, although with lower overall phylogenetic resolution compared to the ITS dataset.

The RPB2 sequence showed its best BLAST hit with *Pseudaleuria fibrillosa* voucher MCVE:30135 (MK722153; 97.53% identity, 94% query coverage), providing additional molecular support for the identification of the studied specimen as *P. fibrillosa*.

Biogeographic distribution

Pseudaleuria fibrillosa species fruits from summer to autumn and has been reported from lowland to montane areas. It is a terricolous taxon occurring on moist, humus-rich soils, often in mossy or marshy habitats. Based on published records and GBIF data, the species appears to be mainly distributed in the Atlantic biogeographical region of northern Europe, with fewer records from boreal, continental, alpine, or Mediterranean areas (Fig. 2). Nevertheless, only a limited number of these reports are supported by molecular data, as most records rely exclusively on morphological identification.

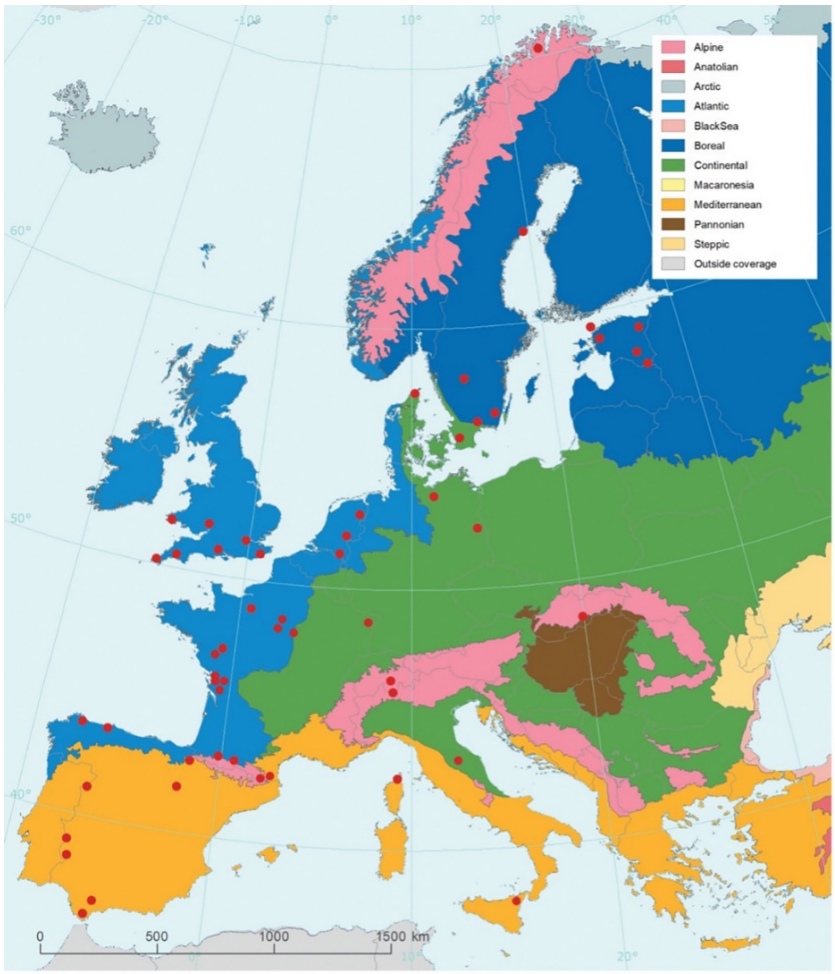

Fig. 2 - Known distribution of *Pseudaleuria fibrillosa* in Europe (red dots) overlaid on the main European biogeographical regions (European Environment Agency, 2016). Records are based on literature data and biodiversity platforms such as GBIF (Global Biodiversity Information Facility).

Taxonomy

Pseudaleuria fibrillosa (Massee) J. Moravec, Acta Musei Moraviae, Sci. biolog., 88 (1/2): 51 (2003).

Basionym: Peziza fibrillosa Currey, Trans. Linn. Soc. London 24: 153, 1863.

Synonyms: ≡ *Cheilymenia fibrillosa* (Currey) Le Gal, Ann. Sci. Nat. Bot. sÈr. 11, 8: 287, 1947.

≡ ***Tricharina fibrillosa*** (Currey) Yang et Korf, Mycotaxon 24: 487,1985.

≡ ***Otidea fibrillosa*** (Currey) Massee, Brit. Fung. Fl. 4: 449, 1895.

= ***Peziza campestris*** P. Crouan et H. Crouan, Fl. Finist. p. 53, 1867.

≡ ***Cheilymenia campestris*** (P. Crouan et H. Crouan) J. Moravec, Mycotaxon 44: 69, 1992.

Type: ex herb. F. Currey, Oct. 1861, K(M) – *Holotypus*

Fig. 3 - *Pseudaleuria fibrillosa*. Fresh apothecia in situ. (a) Close-up of a mature apothecium. (b) Side view. (c) Habitat showing scattered apothecia. (d) Cluster of apothecia on decaying wood. Scale bars = 0.5 cm. Voucher AGMT 15291 (photos by G. Guidi).

Original description

Peziza fibrillosa "Cup 1 inch broad, nearly sessile, irregular, orange, clothed externally with dingy-white downy fibrillae, which form a rather dense tomentose edging to the cup. Spores quite smooth, elliptical, without nuclei, 0.0006 to 0.0007 inch in length (that is 15.24–17.78 µm). Paraphyses filiform, enlarged spherically at the apex. Hanham Wood, near Bristol, October 1861. C. E. Broome, Esq. This species is allied to *P. aurantia*, from which it differs in the woolly external covering and smooth sporidia. In some of the asci I noticed a cupulate depression at the summit".

Macroscopic features

Ascomata 7–18 mm in diameter, 5–10 mm high, initially cup-shaped and regular, becoming expanded and irregular with lacerate margins at maturity. Attachment sessile or with a rudimentary stipe. Hymenial surface smooth, yellow to yellow orange. Outer surface concolorous, finely fibrillose near the margin, often paler. Flesh thin and fragile, without distinctive odor or taste (Fig. 3, Supplementary Figures S2 and S3).

Asci up to 240 × 11–14.5 µm, cylindrical, tapering basally, operculate, inamyloid, 8-spored, arising from croziers. Paraphyses cylindrical, multiseptate, 230–250 µm long, apices slightly to strongly capitate (4.6–8.1 µm), containing carotenoid pigments (Fig. 4; Supplementary Figures S4, S5 and S6).

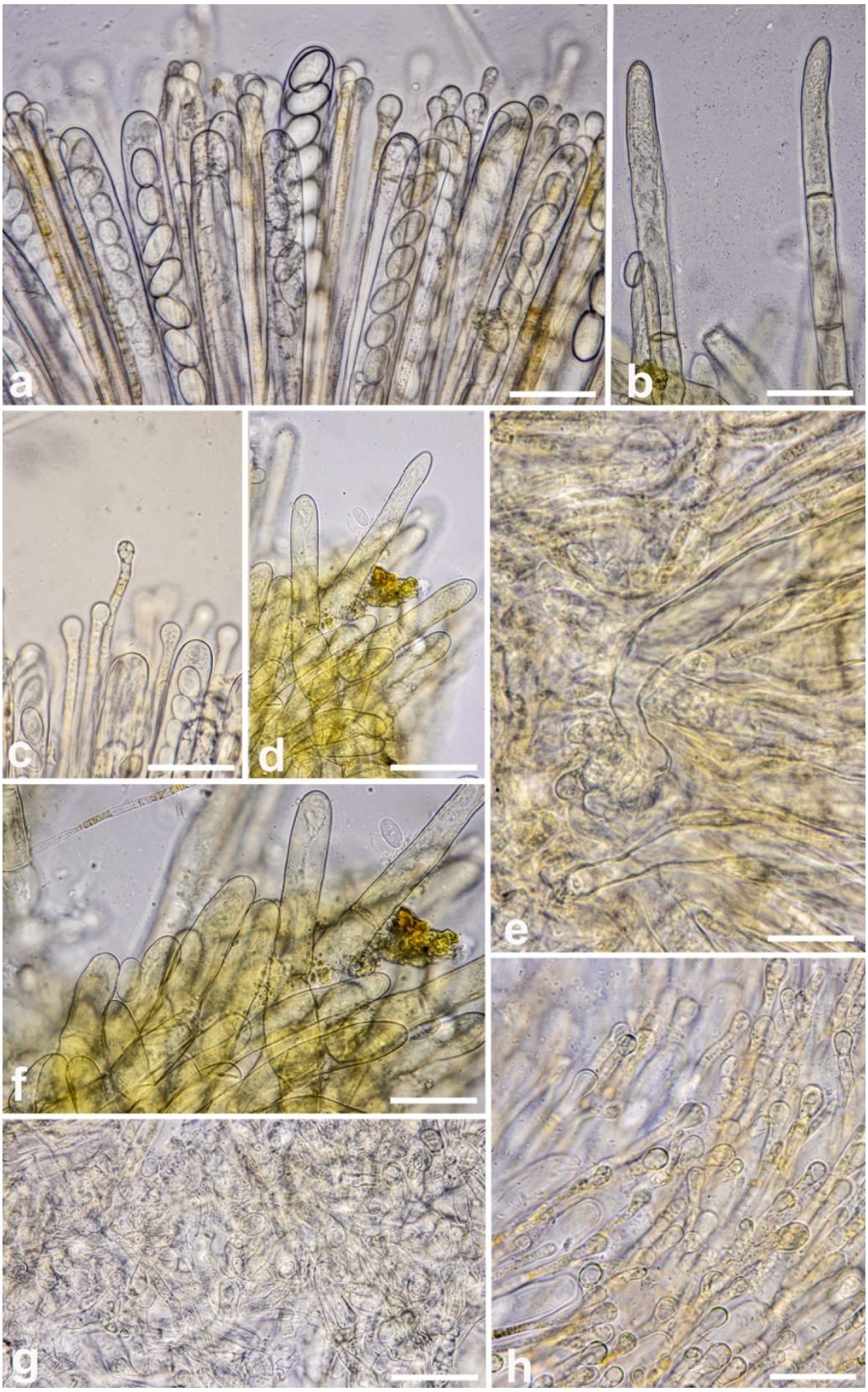

Fig. 4 - *Pseudaleuria fibrillosa*. Microscopic features. (a) Hymenial palisade with asci and paraphyses; (b) detail of an ascus; (c) capitate paraphyses; (d–f) developing and young apothecial hairs; (g) medullary excipulum; (h) palisade of paraphyses. All photographs taken in water. Scale bars = 50 µm. Specimen examined: AGMT 15291.

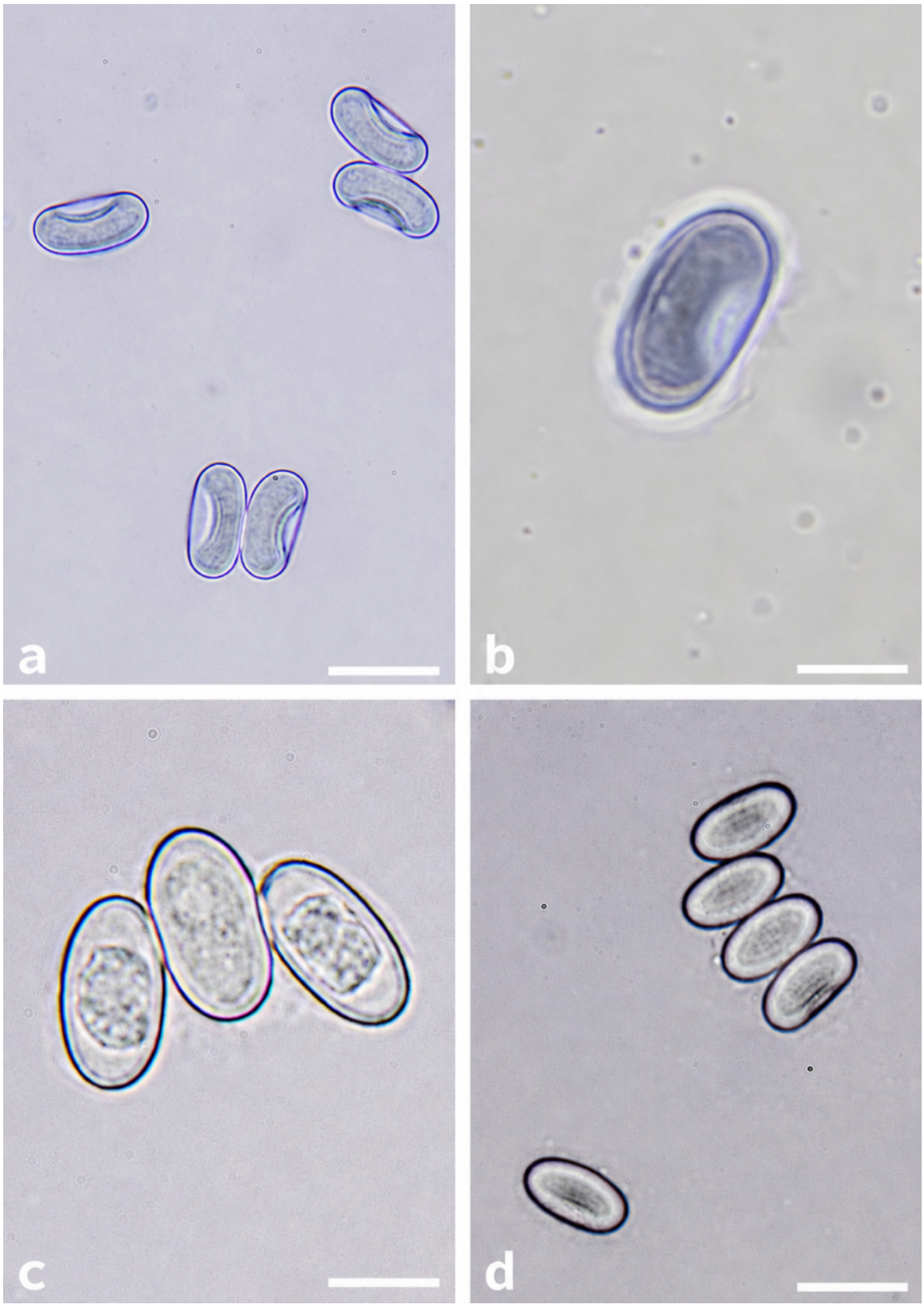

Fig. 5 - *Pseudaleuria fibrillosa*. Ascospores observed under light microscopy. (a–b) Collapsed ascospores in Cotton Blue in lactic acid; (c) ascospores showing collapsed cytoplasmic content; (d) smooth mature ascospores in water. Scale bars: 20 µm. Specimen examined: AGMT 15291**.**

Ascospores (n = 45): (14.8) 15.2–17.7–18.6 (19.3) × (8) 7.9–9.8–10.6 (11.0) µm (mean = 17.7 × 9.8 µm); Q = 1.7–1.8–1.9–2.0 (mean Q = 1.8), ellipsoid, hyaline, eguttulate, smooth. Subhymenium compact, of *textura intricata*. Medullary excipulum of *textura intricata*; ectal excipulum of *textura globulosa* with rounded cells, 28.5–60.1 µm diam. Apothecial hairs numerous, straw-yellow in colour, fasciculate, cylindrical to slightly pyriform basally, multiseptate, thin-walled, up to 350 µm long, and width 15–20 µm (Fig. 5).

Discussion

This study provides the first documented record of *P. fibrillosa* in the Umbria region and represents one of the few integrative contributions combining morphology and ITS-based phylogenetic analysis for this rarely reported species in Italy.

The *P. fibrillosa* lineage is clearly distinct from *P. quinaultiana*, originally described from North America (Lusk, 1987), although the LSU dataset provides only moderate support for the separation between the two lineages. Distribution data available through biodiversity platforms such as GBIF currently include 267 records attributed to *P. fibrillosa*, including 106 preserved specimens, 139 human observations, and 21 material samples. Since material samples generally lack associated fruiting body vouchers, these records may reflect automated ITS-based similarity assignments rather than confirmed species-level identifications. While *P. fibrillosa* appears consistently associated with European documented material, extra-European occurrences based exclusively on environmental ITS sequences should be interpreted with caution. ITS and LSU regions alone does not provide sufficient phylogenetic resolution to robustly infer relationships among *Pseudaleuria*, *Melastiza*, and *Tricharina*. Only a limited number of studies have generated ITS and LSU sequences from the same *Pseudaleuria* specimens (Van Vooren et al., 2017; Saitta, 2019; Olariaga et al., 2020). Furthermore, additional protein-coding loci, such as *tef1* and *rpb2*, are currently available only for a single collection of *P. fibrillosa* (Saitta, 2019). Consequently, the scarcity of comparable multilocus data hampers robust phylogenetic inference of the genus and the assessment of its relationships with allied genera such as *Melastiza* and *Tricharina*. Similar limitations have been reported for several genera of Pezizales, where single locus ITS phylogenies often fail to resolve deeper intergeneric relationships (Perry et al., 2007; De Mattheis et al., 2025). Nevertheless, these genera can be more reliably distinguished based on morphological characters. Species of *Tricharina* share non-guttulate ascospores and fasciculate hairs with blunt apices, but they are generally smaller, less brightly coloured, markedly sessile, and often partly embedded in the substrate (Van Vooren et al., 2017). Species of *Melastiza* are characterized by open cup-shaped or discoid ascomata and verrucose to subreticulate ascospores (Le Gal, 1958). In contrast, *Pseudaleuria* is distinguished by the presence of characteristic apothecial hairs and smooth ascospores lacking conspicuous guttules. In this study, the specimen was easily identified in situ using a magnifying glass by observing these apothecial hairs, which distinguish it from *Tricharina*, which generally has much smaller asci and markedly different colouration (Lindemann and Van Vooren, 2022). Subsequent microscopic examination confirmed the identification by revealing the typical apothecial hairs and smooth ascospores, and the molecular data further supported the assignment of the specimen to *P. fibrillosa*. To our knowledge, no molecular data are currently available from the holotype of *P. fibrillosa*, as a previous sequencing attempt on the historical material was unsuccessful (E. Hodgson, personal communication). However, the original description and morphology of the type specimen allow an unambiguous interpretation of

this species, and the designation of an epitype is therefore not considered necessary. Our collection morphologically agrees with the protologue of *P. fibrillosa* and our sequences provide new molecular data for the species. *Pseudaleuria quinaultiana*, although absent from Europe, differs in its bright red ascomata, and an ectal excipulum arranged in a *textura angularis* rather than the *textura globulosa* observed in *P. fibrillosa*. According to Saitta (2019), superficial identifications have likely led to an underestimation of the presence of this species in Italy. In conclusion, this study aims to expand current knowledge regarding the distribution, phenology, and macro- and micromorphological traits of the species, providing diagnostic characters to distinguish it from closely related taxa whose defining features have often been overlooked, leading to frequent misidentifications. Furthermore, the limited availability of multilocus datasets highlights the need for additional molecular data from well-documented voucher specimens to improve phylogenetic resolution and clarify the relationships within *Pseudaleuria* and among allied genera.

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Author Contributions

Conceptualization, G.G.; methodology, M.D.M.; software, M.D.M.; validation, G.G. and M.D.M.; formal analysis, M.D.M.; investigation, G.G. and M.D.M.; resources, G.G.; data curation, M.D.M.; writing—original draft preparation, G.G. and M.D.M.; writing—review and editing, G.G. and M.D.M.; visualization, M.D.M.; supervision, G.G. All authors have read and agreed to the published version of the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

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