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Pyropezia, a new genus to accommodate *Peziza rifaii* (*Pezizaceae, Ascomycota*)

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Abstract

Recent collections of the rare *Peziza rifaii* J. Moravec & Spooner made in Italy and France, as well as examination of historical collections from Australia and Panama, allowed for a re-evaluation of its distribution and taxonomic position within *Pezizaceae* (*Pezizomycota, Ascomycota*), based on morphological and newly generated molecular data. The new genus *Pyropezia* is proposed to accommodate *Peziza rifaii*.

Keywords: *Ascomycota*, cup-forming fungi*, Pezizomycota*, pyrophilous discomycetes, taxonomy.

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Introduction

Peziza rifaii is a dark brown, cup-forming ascomycete that is typically found on burnt soil. It was described by Moravec & Spooner (1988) based on New Zealand material originally identified as *P. retiderma* Cooke by Rifai (1968). Compared to *P. retiderma*, Moravec & Spooner (1988) noted the smaller spores with a different ornamentation bearing more isolated ridges, despite an otherwise similar morphology with respect to size, colour and habit of the apothecia. Interestingly, they did not record any association of *P. rifaii* with burning or soil sterilization. This rare species was later cited in Madagascar (Le Gal, 1953, under *P. retiderma*), Japan (Nagao & Fukiharu, 2000) and France (Priou & Delannoy, 2006). The phylogenetic placement of *P. rifaii* within *Pezizaceae* remains unresolved to date and no DNA genetic material has been extracted from the species until now (Pfister *et al*., 2022).

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Methods

Specimens studied. — The European specimens were collected in the field and exsiccata were deposited in the herbarium of Université Claude Bernard Lyon, France (LY) and the Museo Civico di Storia Naturale Giacomo Doria, Genoa, Italy (GDOR). The Australian specimen, initially identified as *Peziza repanda* Wahlenb. ex Fr., was found during our investigation of *Pezizaceae* from the fungal collections of the Western Australian Herbarium (PERTH 09367233). The Panamanian specimens, deposited in the herbarium of the New York Botanical Garden, USA (NY), were originally identified questionably as *Peziza retiderma* Cooke by Pfister.

Morphological study. — For the European specimens, the description and study of macroscopic and micromorphological characters were performed on both fresh and dried material. Ascoma were photographed in the field with digital cameras equipped with macro lens. Micromorphological characters were examined using a Leica DM 750 microscope, equipped with Leica planachromatic objectives 10×, 40×, 63× and 100× oil immersion, for the Italian collection, and using an Olympus CX-31 microscope for the French collection. Sections of apothecia were mounted in tap water to observe pigmentation and measure micromorphological characters. The following reagents were used: Melzer's reagent to observe the amyloid reaction of asci, anionic Congo red to observe cellular structures, 5% KOH to assess any colour changes, and cotton blue to observe ascospore ornamentation. Spores, paraphyses and asci measurements were recorded in water using 1000× magnification with oil immersion.

Micromorphological characters of the Australian dried voucher specimen were examined by cutting sections of apothecia that were then rehydrated in water or 5% KOH, as specified, before adding Melzer's reagent. Microscopic features were measured at 400× or 1000× magnification in water, and photographed in water, 5% KOH, and Melzer's reagent using an Olympus BX51 microscope with differential interference contrast (Olympus, Tokyo, Japan) and an Olympus DP-73 camera attachment. Measurements were recorded using the Olympus cellSens standard software (v1.16). Dried specimens collected in Panama were rehydrated in water and examined with an Olympus BX50 microscope. Measurements were made using an ACCU-SCOPE Excelis MPX-20RC camera unit (Commack, New York) with the CaptaVision+ interface software.

In the species description, measurements are presented under the following format: (min) d1–d9 (max), where d1 and d9 represent the 1st and 9th decile, followed by Me for the mean value and Md for the median value (Fannechère, 2006). Q represents the ratio between the ascospore length and width.

DNA extraction, amplification and sequencing. — The sequences generated during this study were deposited in GenBank and are listed in Table 1. Methods follow Pfister *et al.* (2024) and Van Vooren *et al.* (2018) except for the Australian specimen (PERTH 09367233). In the latter, genomic DNA was isolated from dried apothecial tissue using a modified 2% CTAB extraction method (Fauchery *et al.*, 2018). Polymerase chain reactions (PCR) were conducted to amplify the internal transcribed spacer (ITS) region of nuclear ribosomal RNA (rDNA) and domains D1-D2 of the large subunit (LSU) of rDNA, using primer pairs ITS1F/ITS4 (White *et al*., 1990; Gardes & Bruns, 1993) and LROR/LR3 (Vilgalys & Hester, 1990), respectively. PCRs were performed in 20 µl reactions consisting of 10 µl MyTaq™ Red Mix (Meridian Bioscience, UK), 0.8 µl forward primer, 0.8 µl reverse primer, 7.4 µl sterile water, and 1 µl genomic DNA diluted to 2:25, with the following thermocycling protocol: 95°C for 3 min, 35 cycles at 95°C for 15 sec, 50°C for 30 sec, and 72°C for 30 sec, with final extension at 72°C for 5 min. Successful amplifications were assessed by gel electrophoresis. Sanger sequencing was undertaken by the Australian Genome Research Facility (AGRF, Melbourne, Australia). Resultant chromatograms of forward and reverse sequence strands were aligned and manually edited using Geneious Prime v2021.0.3 to generate consensus sequences.

The RNA polymerase II gene (RPB2) sequence for the Australian specimen (PERTH 09367233) was extracted from a de novo genome assembly that was included in an ongoing genome sequencing project focusing on *Pezizomycetes* (Lemmond *et al*., in prep.), following methods outlined in Pfister *et al.* (2024). Genomic DNA extracted from PERTH 09367233 was sequenced with a 150bp paired-end sequencing protocol on the Illumina NovaseqX platform by Macrogen (Oceania).

Phylogenetic analyses. — A combined LSU – RPB2 – β-tubulin alignment was built using sequences from O'Donnell *et al.* (1997), Hansen *et al.* (2001, 2005), Cabero *et al.* (2016), Van Vooren *et al.* (2018), Van Vooren (2020), Albanese *et al*. (2022), Paz *et al.* (2022), and Pfister *et al*. (2024) retrieved from the International Nucleotide Sequence Database Collaboration (INSDC) public database (Arita *et al*., 2021), and new sequences obtained in this study (Table 1). Sequences for each locus were aligned in MEGA v5.0 (Tamura *et al.*, 2011) using its Clustal W application (Thompson *et al*., 1994) and corrected manually. Preliminary maximum likelihood analyses were conducted for each locus to check for incongruence. The loci were then concatenated after conflicts were not detected, producing a final alignment that included 124 LSU sequences, 94 RPB2 sequences and 62 β-tubulin sequences. Bayesian analyses were performed on a local computer in MrBayes v3.2.6 (Ronquist *et al*., 2012) using a GTR+G+I model and data manually partitioned into LSU, RPB2 exons and β-tubulin exons. Two simultaneous runs were performed with four chains, temperature set to 0.2 and sampling every 100th generation, until convergence parameters were

Table 1 – DNA sequences of *Pyropezia rifaii* and *Velenovskya vacini* generated for this study.

Name	Coll. Ref.	Country	GenBank accession numbers		
			ITS	28S	RPB2
P. rifaii	LY NV 2022.10.32	France	PV165883	PV165881	PV167295
P. rifaii	GDOR 5078	Italy	PV165882	PV165880	PV167294
P. rifaii	PERTH 09367233	Australia	PX401659	PX401660	PX505737
P. rifaii	NY 03638397	Panama	PV433200	PV433247	PV437275
V. vacini	NY 03638399	Panama	PV433199	PV433246	PV437274

met after 2.18 M generations and standard deviation had fallen below 0.01. Additionally, a tree search for the best-scoring maximum likelihood tree was performed in RAxML v8.2.12 (Stamatakis, 2014) using the standard search algorithm (data partitioned, 2000 bootstrap replications and the GTRGAMMA substitution model). Significance threshold was set above 0.95 for posterior probability (PP) and 70% bootstrap proportions (BP). These analyses were conducted by ALVALAB (Spain).

A second phylogenetic analysis, focusing on closely related taxa, was conducted on a combined ITS – LSU – RPB2 alignment to examine the relationship of '*Peziza*' *rifaii* with *Phaeopezia* and putatively related genera. Sequence alignments for each locus were conducted individually with MAFFT, through the CIPRES Science Gateway (Miller *et al*., 2010) and checked in Geneious Prime. Ambiguously aligned sites were removed from the ITS alignment using Gblocks v0.91.1 (https://ngphylogeny.fr/tools/tool/276/form) with the more relaxed settings (minimum 50% + 1 sequence for a flanking position; minimum block length of 5 bp; allowing gap positions with half). The final alignments included 28 ITS sequences, 28 LSU sequences and 28 RPB2 sequences. Maximum Likelihood (ML) phylogenetic analyses were performed for each locus separately to check for incongruence before concatenating the loci, applying the GTRGAMMA substitution model, default parameters and 1000 bootstrap replicates using the online version of RAxML-HPC2 on XSEDE v8.2.12 (CIPRES, Miller *et al*., 2010; Stamatakis, 2014). When no conflicts were detected, the same ML methods were applied for the concatenated ITS – LSU – RPB2 dataset.

Results

The combined LSU – RPB2 – β-tubulin phylogeny of the main clades of the *Pezizaceae* family, including the European collections of *P. rifaii,* produced a topology (Fig. 1) similar to recently published phylogenies (Van Vooren, 2020; Pfister *et al*., 2024). The two sequences from *Pyropezia rifaii* formed a clade with strong support (1.00 PP, 100 BP) and this clade placed within a larger lineage with significant support (0.99 PP, 75 BP) containing species with ornamented ascospores from the genera *Legaliana* Van Vooren, *Rugosporella* Pfister, Healy & LoBuglio, *Velenovskya* Albanese, Boragine, M. Carbone & P. Alvarado, *Galactinia* (Cooke) Boud., and multiple truffle-forming genera. The clade of *Pyropezia* and other genera with ornamented ascospores is sister to a clade comprising species of *Phaeopezia* and *Purpureodiscus*. These species are devoid of characters shared with *P. rifaii*, except for the tendency of ascospores to become brownish at maturity, a feature also observed in *Phaeopezia* (Van Vooren, 2020; Paz *et al*., 2022). This tendency of ascospores to become brownish is not considered by the authors to be a synapomorphic character.

The combined ITS – LSU – RPB2 phylogeny (Fig. 2), including the newly generated sequences from Australia and Panama, confirm that all *Pyropezia rifaii* specimens form a highly supported clade (100 BP, Fig. 2). The topology is the same as in the LSU – RPB2 – β-tubulin phylogeny (Fig. 1) with strong support (96 BP) for the clade of *Phaeopezia* as sister to the clade containing *Pyropezia* and other genera with ornamented ascospores. *Velenovskya vacini* shows micromorphological and ecological similarities to *P. rifaii*, with similar spore ornamentation, ascospores becoming brownish with age, the same type of amyloid reaction, and a tendency to grow on burnt ground. However, some of these characters are also shared by some other genera (see paragraph above), and the shape of apothecia of *V. vacini* and *P. rifaii* are very different. *Velenovskya vacini* are small, pulvinate to disciform apothecia, rarely exceeding 20 mm diam., and *P. rifaii* are large, deeply cupuliform apothecia, reaching 45 mm diam. Moreover, *Velenovskya* consistently placed in a separate lineage to *Pyropezia* in both combined phylogenetic analyses (Fig. 1, Fig. 2), though the support for the relationship remains uncertain. The phylogenetic relatedness between the genera within *Pezizaceae* needs further investigation in a phylogenomic framework (Lemmond *et al*., in prep.). The strong support for the *Pyropezia rifaii* clade, combined with its morpholog-

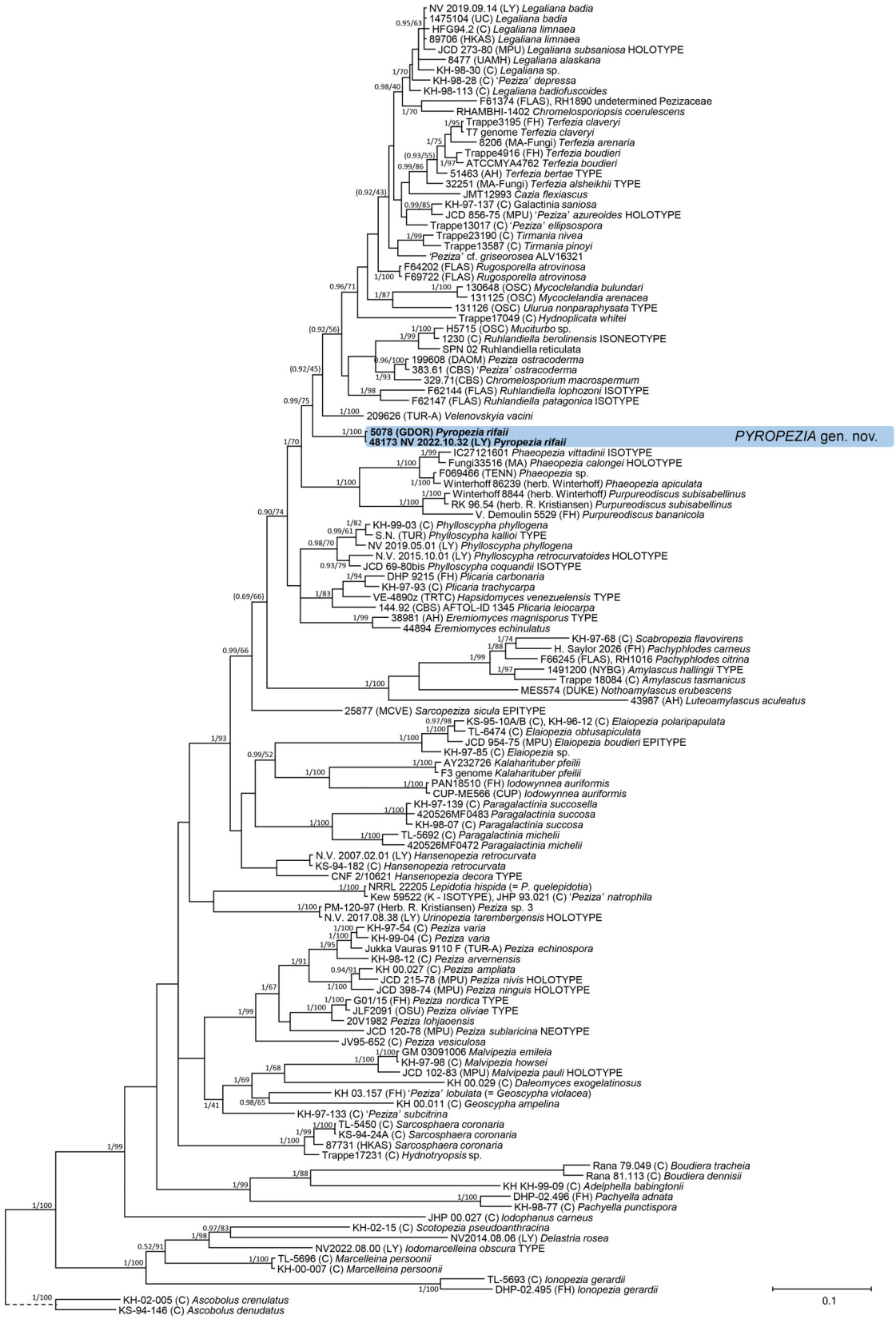

Fig. 1 – Bayesian 50% majority rule LSU – RPB2 – β-tubulin consensus phylogeny of the family *Pezizaceae,* with selected *Ascobolus* Pers. ex J.F. Gmel. species as the outgroup. Nodes were annotated if they were supported by ≥ 0.95 Bayesian posterior probability (left) or ≥ 70% bootstrap proportions (right) reported from the maximum likelihood tree search in RAxML. The *P. rifaii* specimens sequenced in this study are indicated in bold and cluster into the newly described genus *Pyropezia* with high support.

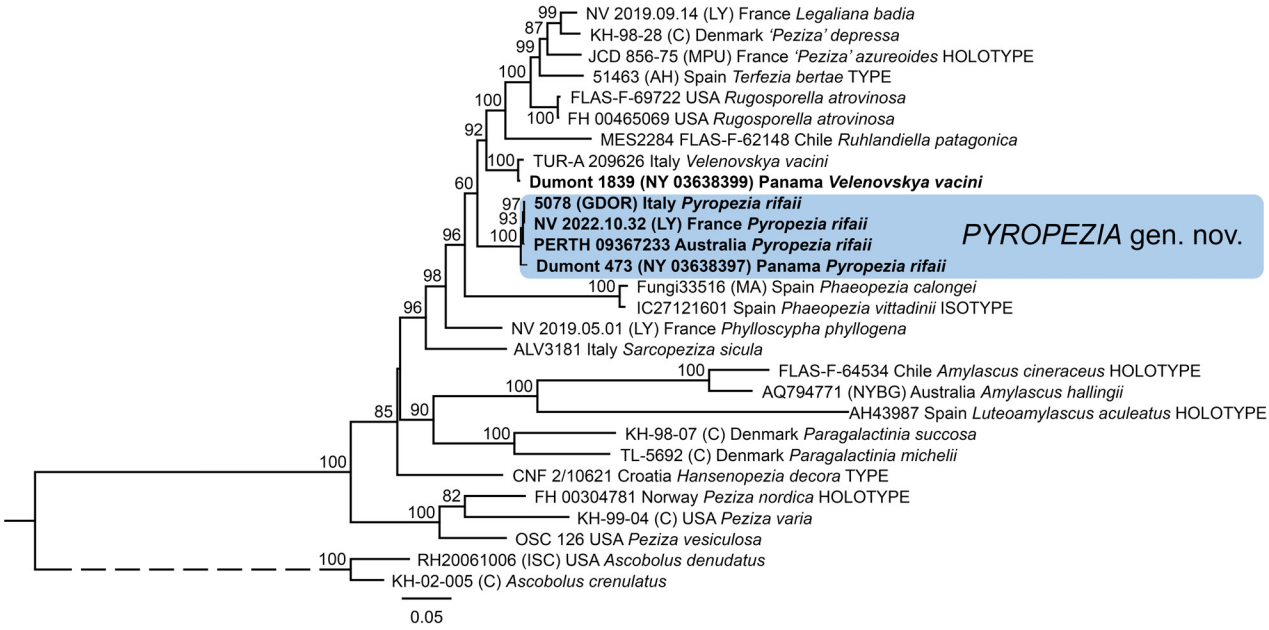

Fig. 2 – Maximum Likelihood phylogeny based on the concatenated ITS – LSU – RPB2 alignment from *Pyropezia rifaii* and selected genera in the *Pezizaceae,* with *Ascobolus crenulatus* and *A. denudatus* as the outgroup. Bootstrap proportions are shown at nodes. *Pyropezia rifaii* and *Velenovskya vacini* specimens sequenced in this study are indicated in bold.

ical and ecological characters, leads us to propose the new genus *Pyropezia* to accommodate this species.

Taxonomy

Pyropezia **Van Vooren, Albanese, Boragine & Lezzi, *gen. nov*.**

MB860797

Type: *Peziza rifaii* J. Moravec & Spooner

Etymology: From ancient Greek πῦρ (*pûr*) meaning fire, and πέζις (*pezis*) meaning "fungus without stipe", referring to the colours of apothecia and preferential habitat.

Description: Ascomata epigeous, cupulate or discoid, sessile, beige, yellow to yellowish orange, to reddish grey. Flesh without juice. Asci operculate, 8-spored, with crozier, wall diffusely amyloid in an iodine solution except at the top where the reaction is more intense (WT–WT+ type after Van Vooren, 2020). Paraphyses containing non-refractive vacuoles. Ascospores biguttulate, ornamented with cyanophilous, thick, more or less elongated or pustulate warts, forming short crests. Ectal excipulum of *textura globulosa* with medium-sized cells. Species saprobic. Asexual morph unknown.

Notes: Among the pezizalean species growing preferentially on burnt substrates (see Dougoud, 2023), *Pyropezia rifaii* is easily distinguished from any other species based on its spore characters. The ascospore ornamentations of *Pyropezia* are more rounded, form longer crests and are generally of lower profile than those of morphologically similar *Velenovskya*, which form short, high pyramidal warts or ridges (Moravec & Spooner, 1988; Albanese *et al.*, 2022).

Other known species in the clade of *Pezizaceae* containing *Pyropezia* and other species with ornamented ascospores can also be distinguished from *Pyropezia. Rugosporella atrovinosa* has pigmented ascospores but the ornamentations form a reticulum, and apothecia are found directly on soil rather than in burnt habitats (Pfister *et al.,* 2024). Ascospores of *Legaliana badia* typically form similar reticulate ornamentation but apothecia are not found in burnt habitats (Van Vooren, 2020). Several genera in the larger clade containing *Pyropezia* are hypogeous and are easily distinguished by macroscopic characters.

Pyropezia rifaii **(J. Moravec & Spooner) Van Vooren, Albanese, Boragine, Lezzi, L.J. Vaughan & Truong, *comb. nov*.**

MB860798

Basionym: *Peziza rifaii* J. Moravec & Spooner, *Trans. Br. mycol. Soc*., 90 (1): 45 (1988).

Typification: New Zealand, ad terram, s. dat., Colenso b 664 (Holotype, K).

Misapplied name: *Peziza retiderma* Cooke, *sensu* Le Gal (1953) and Rifai (1968) [not in the original sense of Cooke, which is a synonym of *Rugosporella atrovinosa* (Cooke) Pfister, Healy & LoBuglio according to Pfister *et al*. (2024)].

Fig. 3–5

Description:

Macromorphology (Fig. 3A–B)

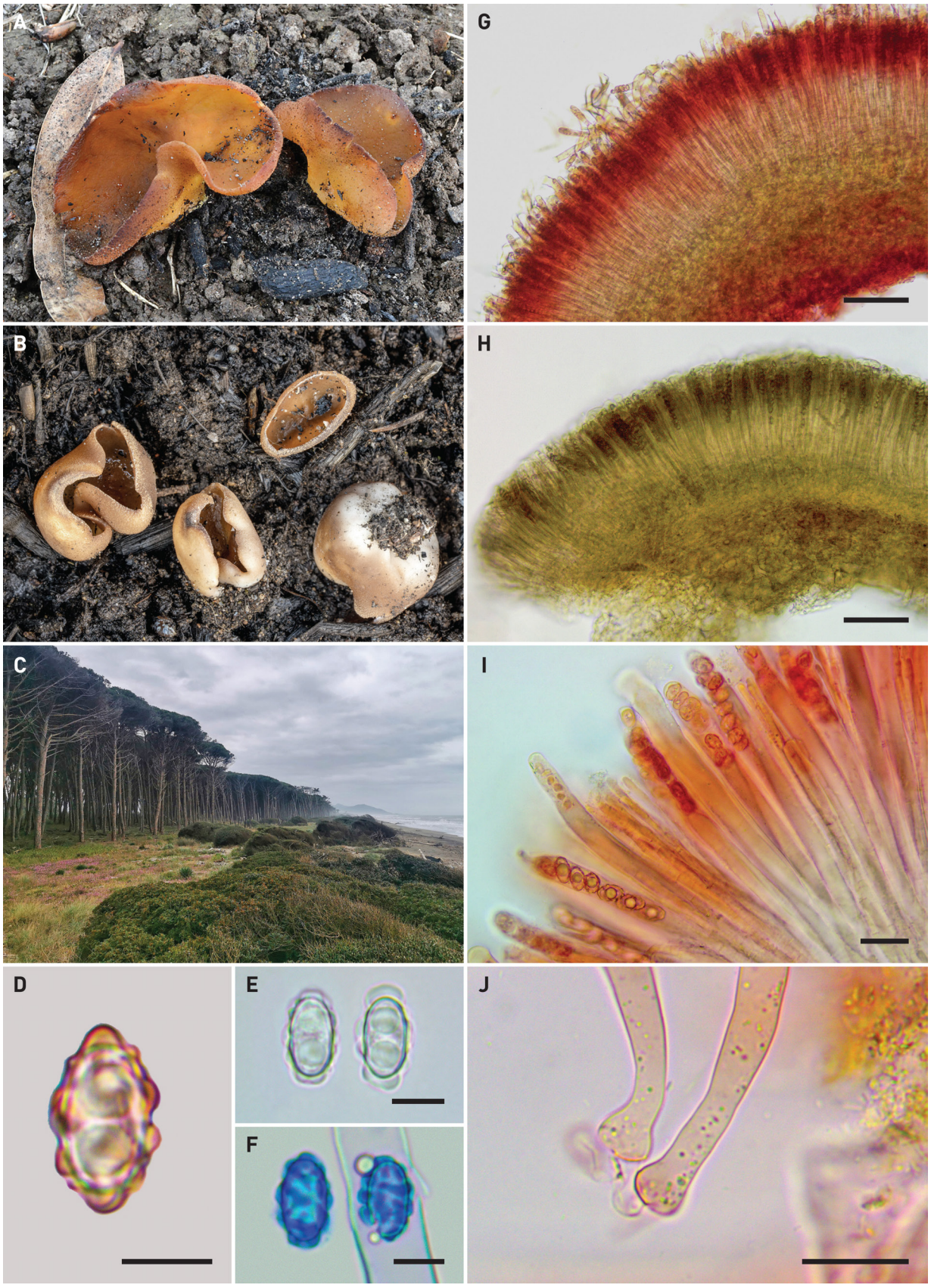

Fig. 3 – *Pyropezia rifaii*. A. Coll. LY NV2022.10.32, photo N. Van Vooren; **B–J.** Coll. GDOR 5078, photos A. Albanese; **C.** Habitat; **D.** Ascospore in Congo red; **E.** Ascospores in KOH; **F.** Ascospores in cotton blue; **G.** Section of the apothecium in Congo red; **H.** Section of the apothecium in 5% KOH; **I.** Asci, paraphyses and ascospores in Congo red; **J.** Ascus base in Congo red. Scale: D = 10 µm; E, F = 5 µm; G, H = 100 µm; I, J = 20 µm.

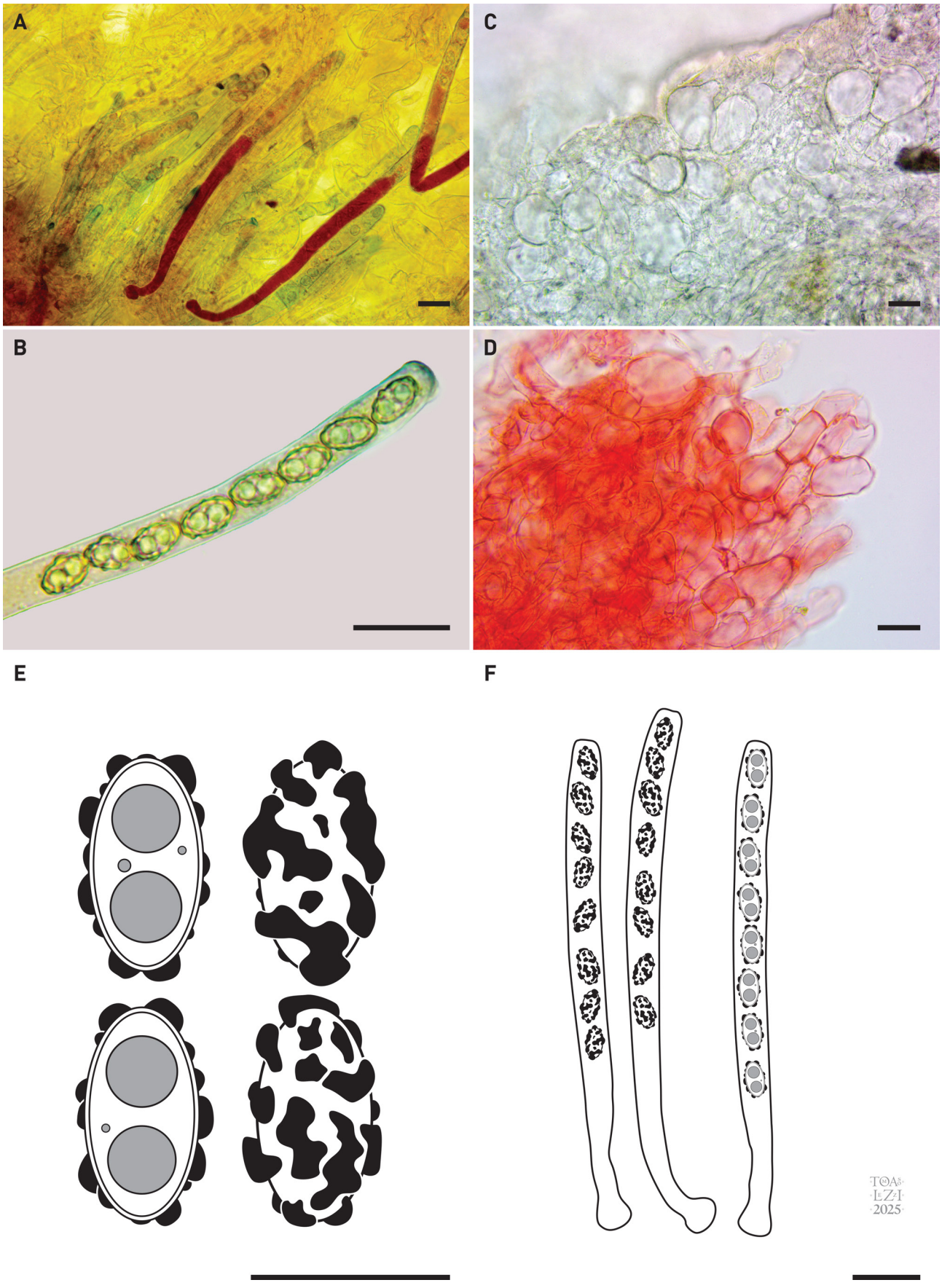

Fig. 4 – *Pyropezia rifaii*. Coll. GDOR 5078; **A–B.** Asci in Melzer's reagent. **C.** Ectal excipulum in water; **D.** Medullary excipulum in Congo red; **E.** Ascospores; **F.** Asci and ascospores. Scale: A, B, C, D, F = 20 µm; E = 10 µm. Photos A–D by A. Albanese, drawings E–F by T. Lezzi.

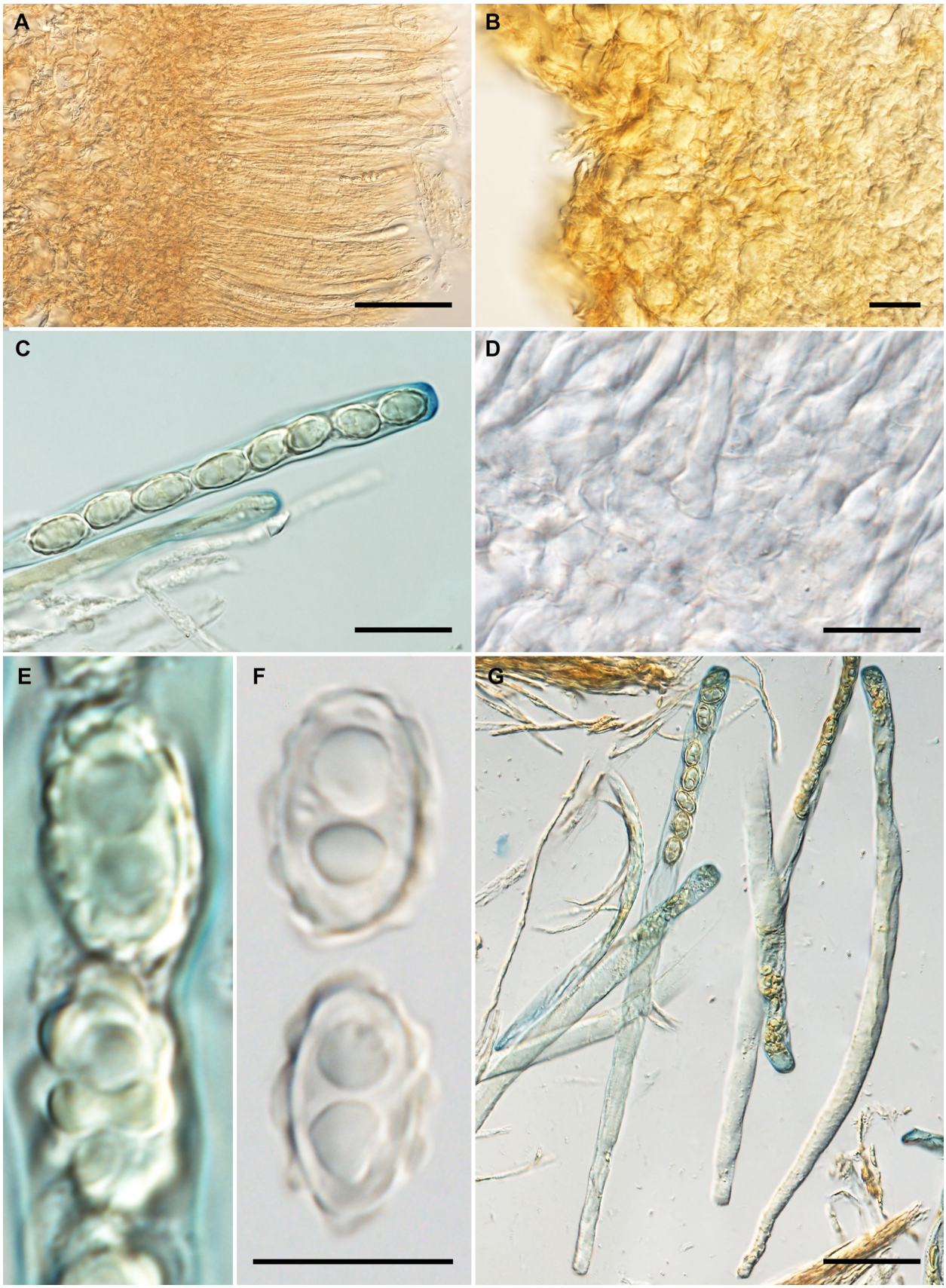

Fig. 5 – *Pyropezia rifaii*. Coll. PERTH 09367233; **A.** Section of apothecium in water; **B.** Ectal excipulum in water; **C.** Ascus pretreated in 5% KOH, in Melzers reagent; **D.** Subhymenium and ascus base in 5% KOH. **E.** Ascospores pretreated with 5% KOH, in Melzers reagent; **F.** Ascospores in 5% KOH. **G.** Asci pretreated with 5% KOH, in Melzers reagent. Scale: A = 100 µm; B, G = 40 µm; C, D = 20 µm; E, F = 10 µm.

Ascomata gregarious. **Apothecia** (20) 40–50 mm diam., 30–45 mm high, sessile, initially spheroidal or sub-globose, becoming deeply cup-shaped, spreading with age. Disc smooth then slightly wrinkled, at first beige then ochre or yellowish orange, finally reddish-brown to dark brown. External surface finely granular, sub-concolorous. Margin irregular, inrolled and partly lobed, becoming reddish brown. Flesh thin, soft, not lactescent, sub-concolorous to the external surface. Presence of a basal sulphur yellow **mycelial tomentum**. **Spore print** white.

Micromorphology (Fig. 3–5)

Ascospores (9.5–) 10–12.5 (–14) × (5.5–) 6–7.5 (–8) µm, Me = 11.2 × 6.8 µm, Md = 11 × 6.9 µm, Q = (1.38–) 1.50–1.80 (–2.00), Qm = 1.62 {n = 138}, initially hyaline then yellow-brownish, ellipsoid, biguttulate, more rarely uniguttulate, thick-walled, ornamented with large irregular warts, measuring up to 2.5 µm diam. and 1–1.5 µm high, with rounded apex, and thick rounded crests, isolated or slightly interconnected (Fig. 3D–F, 4E, 5E–F). **Paraphyses** 162–196 × 4–5.5 µm, filiform, septate, not or slightly widened at the top, containing small vacuolar bodies. **Asci** 229–268 × 10.5–12.5 µm on coll. GDOR 5078, 300–350 × 11–14 µm on coll. LY NV 2022.10.32 and 200–294 × 10.5–11.5 µm on coll. PERTH 09367233, cylindrical, amyloid (WT–WT+ type after Van Vooren, 2020), operculate, 8-spored, with croziers (Fig. 3G–L, 4A–B, 5C–D, 5G). **Subhymenium** thin, composed of dense, interwoven hyphae. **Medullary excipulum** of *textura globulosa-subglobulosa*, in the upper part, with brownish cells "in mass", 8–30 (–40) µm diam.; lower part of *textura intricata*, with various types of cells, including elongated hyphae, clavate, sometimes subglobose cells, 9–36 µm wide (Fig. 4C). **Ectal excipulum** of *textura globulosa*, with yellow-brown cells, 8–50 µm diam., in the marginal zone organised in small pyramidal clusters, made of brown cells, ± arranged in a *textura prismatico-angularis* (Fig. 4D, 5B).

Studied collections: France. Haute-Corse, Aghione, near Maison Pieraggi, 42.091712° N 9.388293° E, 94 m a.s.l., on soil, in a burnt *Eucalyptus* plantation, *leg*. S. Biancardini, *det*. N. Van Vooren, 24-X-2022, LY NV 2022.10.32. Italy. Caserta, Sessa Aurunca, near Cellole, "Domitio" coast, 41.223194° N 13.766611° E, 10 m a.s.l., on sandy soil, among burnt debris, with *Pinus halepensis* Mill., *Cistus salviifolius* L., *Juniperus communis* L., *Smilax aspera* L. and *Olea europaea* L., *leg*. A. Albanese, 8-XII-2022, GDOR 5078 and pers. herb. AA221208-01. Australia. Western Australia, Dombakup, Nineteen Road, 34.581389° S 115.949722° E, 23 m a.s.l., on burnt soil in *Eucalyptus* forest, *leg*. J. Fielder [RR 983 WA, as *Peziza repanda*], 10-V-2007, PERTH 09367233. Panama. Balboa Heights, Canal Zone, Summit Gardens, 92 m a.s.l., on burned site, *leg*. K. P. Dumont (PA 473), S. E. Carpenter & S. A. Mori, 12-VI-1975, NY 03638397; as above, *leg.* K. P. Dumont (PA 478), NY 03638400.

Ecology, phenology and distribution

The Italian specimens (GDOR 5078, duplicate AA221208-01) were collected in winter, along the 'Domitio' coast near Cellole (Fig 3C). The temperature was 13 °C (85% humidity) and the soil was very wet due to the abundant rainfall in previous days. The soil was acidic, sandy and siliceous. Specimens of *V. vacini* (Velen.) Albanese, Boragine, M. Carbone & P. Alvarado (Albanese *et al*., 2022) were found half a meter away but were not collected. The Corsican collection (LY NV2022.10.32) was made at the end of October, in a burnt area (about 0.5 ha) within a small forest mainly composed of exotic *Eucalyptus spp.*, accompanied with *Erica arborea* and *Arbutus unedo*, about 13 weeks after the fire event. The temperature was around 24 °C, with dry conditions (no rainfall during the past month). The Western Australian specimen (PERTH 09367233) was collected in May 2007, on burnt soil in *Eucalyptus* forest following wildfires during the Australian summer of 2006-2007. Both specimens from Panama were found on burnt ground in a bamboo and oak forest. They were collected in July, corresponding to the rainy season in Panama.

This species is apparently rare but is distributed worldwide. Originally described from New Zealand (Rifai, 1968, under *Peziza retiderma*) and later formally named by Moravec & Spooner (1988), it has been cited in Madagascar (Le Gal, 1953, under *P. retiderma*), and France (Priou & Delannoy, 2006), and is confirmed here for Australia, Panama, France and Italy. It may also be present in Argentina according to Gamundí (1966, under *P. retiderma*), although Pfister *et al*. (2022) noted that the ascospore measurements Gamundi provides were smaller than those given by Moravec & Spooner. Finally, *Pyropezia rifaii* was cited from Japan (Nagao & Fukiharu, 2000), but we consider these records as doubtful because of the larger spore size (mean 16.6 × 8.2 µm) and distinct spore ornamentation that does not correspond to our current concept of *P. rifaii.*

In Australia, three iNaturalist observations (86246926, 87957376, 88906836) by observer Peter Zuidland (iNat: peterzuidland), recorded in 2021 from the Gippsland region of the state of Victoria, are likely records of *P. rifaii* based on the morphology of apothecia, ascospores and ascospore ornamentation shown in accompanying photographs. Although specimens were not preserved to confirm the species identity with molecular data, those Gippsland observations were also found on burnt soil in a sclerophyllous forest, within six months of controlled hazard reduction burns performed in early 2021.

Taxonomy notes

As explained in Moravec & Spooner (1988), *Peziza rifaii* was previously included within the taxonomic concept of *Peziza retiderma* Cooke that however shows a distinct spore ornamentation of reticulate ridges. Indeed, Le Gal (1953) described and illustrated this fungus from Madagascar under Cooke's epithet. Le Gal's misidentification

was based on examination of the poorly preserved type specimen of *P. retiderma*. Interestingly, she noted that the specimens she studied from Madagascar were different from *Peziza atrovinosa* Cooke based on their spore ornamentation, which did not form a reticulum. We now know that *P. retiderma* is a later synonym of *P. atrovinosa*, now *Rugosporella atrovinosa* (Pfister *et al*., 2024). This confusion was followed by Rifai (1968) who revised Australasian collections of *Pezizales* housed in the Herbarium of the Royal Botanic Gardens, Kew, using the same justifications as Le Gal (1953). Finally, Moravec & Spooner (1988), in their study of brown-spored species of *Peziza*, highlighted these misinterpretations and clarified the taxonomy of these species, separating the 'true' *Peziza retiderma* from the species they named '*Peziza' rifaii*.

Disclosures

No conflicts to declare.

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