IJM - Italian Journal of Mycology
ISSN 2531-7342 - Vol. 54 (2025): 19 - 31
Journal homepage: https://italianmycology.unibo.it/

Research article

Leucocoprinus idae-fragum in a cypress alley nearby lake Bracciano in Latium

Arnold Knijn[1], Amalia Ferretti[1], Irja Saar[2]

[1]Via Arno 36, 00198 Roma, Italy
[2]Institute of Ecology and Earth Sciences, University of Tartu, J. Liivi 2, 50409 Tartu, Estonia

Corresponding author e-mail: knijn_roma@hotmail.com

ARTICLE INFO
Received 09/11/2024; accepted 29/01/2025
https://doi.org/10.6092/issn.2531-7342/20651

Abstract
In the area of the Italian town Trevignano Romano, within the Bracciano-Martignano Regional Natural Park, we have found several rare *Leucocoprinus* specimens belonging to section *Piloselli*. In the same cypress alley in precedence, we have reported the presence of the two uncommon species *Myriostoma coliforme* and a still undefined *Battarrea* sp. Specifically, in the winter period of recent years, we have found *Leucocoprinus pseudopilatianus*, *Leucocoprinus gaillardii*, *Leucocoprinus marginatus* and particularly, *Leucocoprinus idae-fragum*. The taxonomic identities of the specimens were confirmed through molecular and phylogenetic analyses. Because information on the extremely rare *L. idae-fragum* is still limited, a description of these specimens is presented including their peculiar growth environment which seems now under threat of human intervention.

Keywords
Bracciano-Martignano Regional Natural Park; conservation; *Cupressus sempervirens*; habitat; *Piloselli*

Introduction

In a previous article (Ferretti et al., 2020), we highlighted the presence of the two uncommon species *Myriostoma coliforme* (Dicks.) Corda and a *Battarrea* (Dicks.) Pers. species belonging to clade A (as defined in Martín et al., 2013), in an alley of cypress trees (*Cupressus sempervirens* L.) that extends towards the shores of Lake Bracciano, in the Trevignano Romano area, part of the Bracciano-Martignano Regional Natural Park in Lazio. In the winter months of recent years (2022–2024) in the same cypress alley, we have collected specimens of several uncommon or very rare *Leucocoprinus* species of section *Piloselli* (Kühner ex Singer) Migl. & Donato, particularly, *Leucocoprinus pseudopilatianus* Migl., (Migl., Rocabruna & Tabarés) Migl. & Donato (Migliozzi et al., 2001), *Leucocoprinus gaillardii* (Bon & Boiffard) M. Asif, Saba & Vellinga, *Leucocoprinus marginatus* (Burt.) Migl. & Donato (Boisselet, 2002) and *Leucocoprinus idae-fragum* (Guinb., Boisselet & G.

Dupuy) M. Asif, Saba & Vellinga (Guinberteau et al., 1998). The *Piloselli* section includes species whose basidiomata context stain orange-red or turquoise-green when bruised and which turn green on contact with KOH or ammonia; with white then pink lamellae, basidiospores without germ pore (Singer, 1986; Vellinga, 2010; Latha et al., 2020). The molecular studies by Vellinga (2010) showed that section *Piloselli* is polyphyletic.

Recently, nomenclatural novelties have been introduced with respect to many species previously classified as belonging to the genus *Leucoagaricus* Locq. ex Singer and now as *Leucocoprinus* Pat. (Redhead, 2023; Asif et al., 2024; Migliozzi and Donato, 2024) to obtain a well-supported monophyletic molecular clade for the combined genera (Justo et al., 2021). The merging process is in progress as for instance *Leucocoprinus subvolvatus* (Malençon & Bertault) M. Asif, Saba & Vellinga has been renamed but *Leucoagaricus volvatus* Bon & A. Caball. not yet and still several *Lepiota* species occur in the present *Leucocoprinus* clade such as *Lepiota decorata* Zeller. Pending the consolidation of the merge, in this article we have classified the specimens according to the present state of art as defined in Index Fungorum (November 2024).

The specimen of *L. marginatus* found in the Trevignano Romano cypress alley had a diffracted, brown pileus with a darker brown and sooty centre. It had white context that quickly turned red, discoloured and then turned brown. White, cream lamellae and white coloured stem with redding annulus. The morphology is similar to specimens described in literature (Boisselet et al., 2002; Migliozzi, 2022). Basidiomata of *L. marginatus* have been found under *Hesperocyparis macrocarpa* (Hartw. ex Gordon) Bartel in Point Lobos, California. Recently, *L. marginatus* specimens, found under *Cupressus* sp. in the Castel di Guido area in Lazio, have been identified and morphologically and molecularly fully described (Migliozzi, 2022).

The specimens of *L. gaillardii* had a convex cap, brown to finely dotted reddish-brown in colour. The pileus turned red-dark red if rubbed, such as the context. The whitish lamellae as the stem turned red over time. Stem with a poorly developed ring, and with a marginate base. The species is described to be rare, its habitat located in sandy areas on the litter of old cypress trees and in dune thickets and to appear only after heavy rains in early autumn (Bon and Boiffard, 1974; Gennari et al., 1995).

The species *L. idae-fragum* is even more rare, initially described in France in 1998 to be present in the Atlantic dunes among tamarisk groves on the Ile d'Oleron and some slimmer shaped specimens under cypresses (*H. macrocarpa*) on the Ile de Ré (Guinberteau et al., 1998; Guinberteau, 2011). Another *L. idae-fragum* specimen collected in France in Nogent-sur-Vernisson under *Juniperus thurifera* L., is present in the Global Biodiversity Information Facility GBIF (occurrence 4150510803). The fungus is described as a particularly beautiful species, with a raspberry-coloured pileus, an elongated white to bright pink stem, with the typical leucoagaric ring, edged in pink, with a flattened basal bulb (Guinberteau, 2011). *Leucocoprinus idae-fragum* was synonymised with the north American species *L. decorata*, based on morphology (Vellinga, 2006), from which it differs in the presence of a universal veil, a green ammonia reaction on pileus and lamellae, and differently shaped cheilocystidia (Vizzini et al., 2017). However, in 2017 the validity of *L. idae-fragum* with respect to *L. decorata* was demonstrated, by molecular analysis (Vizzini et al., 2017).

Further specimens of *L. idae-fragum* were found later in some areas of Italy: in the Botanical Garden of Cagliari in Sardinia under *Phytolacca dioica* L. and *Ficus* Tourn. & L. sp., on the Polvese island in Umbria and along the famous Cypress Avenue (*C. sempervirens*) of Bolgheri in Tuscany,

with species' determination confirmed through molecular and phylogenetic analyses (Vizzini et al., 2017). Another occurrence was found in 1990 and 2015 in a pinewood in the province of Ragusa in Sicily (Brugaletta, 2018). This pinewood is a Nature Reserve overlooking the sea and is part of the State Forestry Property. The habitat consists of sandy soil with *Pinus halepensis* Mill., and *Pinus pinea* L. In 2021, a finding was reported in the sea dunes (Amsterdamse Waterleidingduinen, AWD) of The Netherlands (Somhorst et al., 2022). The AWD is a Natura 2000 Reserve of herbaceous dunes where since 1853 water is filtered for the drinking water supply of the city of Amsterdam.

We present the description of our findings of *L. idae-fragum* because of its extreme rarity to obtain further characteristics of this species. Their peculiar growth environment is shared by other interesting and uncommon fungal species but is currently endangered by urban expansion, highlighting the importance of conservation.

Materials and Methods

Area of study and collection of samples

The area of study (42°09'36" N 12°13'44" E, 173 m asl) is located in Trevignano Romano, a small town, municipality of the Metropolitan City of Rome Capital, on the north coast of the volcanic Lake Bracciano and part of the Bracciano-Martignano Regional Natural Park. Trevignano Romano has a Mediterranean climate, the average annual maximum temperature is 20 °C. In December/January maximum temperatures range from 4 °C to 11 °C. The climate is dry with November statistically the wettest month (data obtained from https://it.weatherspark.com/).

The site of the mycological findings is a 140 meters long alleyway perpendicular to the lake's coast, connecting the lake front with an interior road and composed exclusively of densely planted *C. sempervirens* trees. The trail is historical, but the trees have been planted in the late 50s or early 60s of the twentieth century. In some parts, *Phytolacca* plants grow among the cypresses and *Hedera* helix L. covers some trees. The alleyway is a sandy soil path covered by cypresses' debris, grassy at the sides (Fig. 1). It is privately owned but freely accessible and intensively transited by pedestrians with dogs and bicyclists. Adjacent to the cypress alley are currently uncultivated fields and an area used for dog training.

In the last days of December 2022, we have collected specimens of *L. pseudopilatianus* (TUF137358, TUF137359), *L. gaillardii* (TUF137356) and *L. idae-fragum* (TUF137362). *Leucocoprinus gaillardii* (TUF137945) and *L. idae-fragum* (TUF137946) were also found in the first days of January 2024 along with *L. marginatus* (TUF137944). The collected specimens are conserved as a part of the Mycological Collections of the Natural History Museum and Botanical Garden of the University of Tartu, Estonia (acronym TUF).

Morphological analyses

Photographs and notes were taken from fresh basidiomata. Microscopic characters were observed on fresh and dried material; dried basidiomata were studied using a light microscope Leica DM750 with Leica Application Suite v4.13 at ×1000. Measurements of basidiospores were made in 3% KOH and stained in Congo Red. Melzer's reagent, Cotton Blue and Cresyl Blue were used to test dextrinoid, cyanophilous and metachromatic reactions, respectively. Dimensions of the microscopic elements are given as "(minimum value)–average value–(maximum value) of length × (minimum value)–average

value–(maximum value)" of width. Q is the spore quotient (length/width ratio). The terminology for descriptive terms is based on several studies (Vellinga, 1988; Vizzini et al., 2017; Asif et al., 2024).

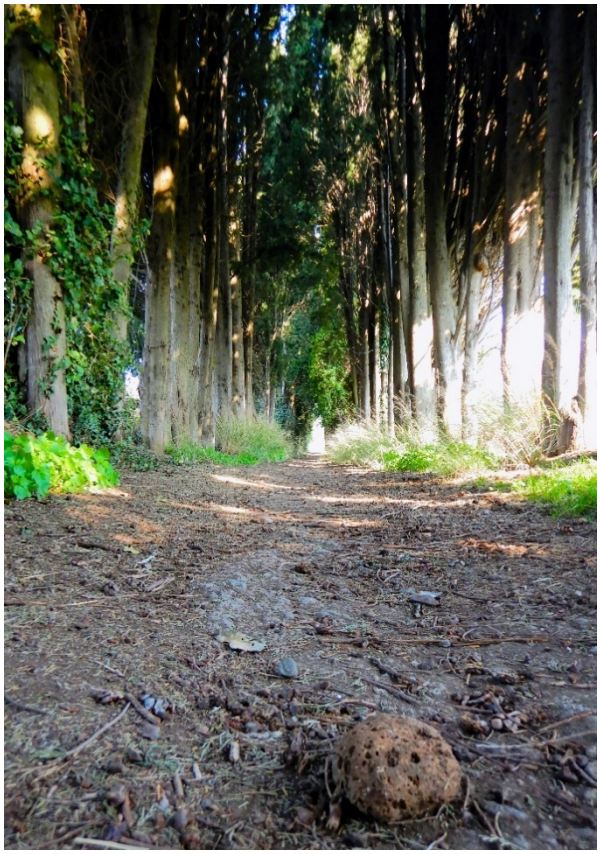

Fig. 1 – The cypress alley.

Molecular analyses

Ribosomal DNA-based analysis was performed on the specimens in the frame of the UNITE project (Kõljalg et al., 2013). DNA extraction, PCR amplification of SSU partial, ITS1, 5.8S, ITS2, LSU partial regions and sequencing were performed as in Voitk et al. (2018). Together with the thirteen new sequences obtained from *Leucocoprinus/Leucoagaricus* species in this (seven) and our previous studies (six), the sequences after Vizzini et al. (2017) integrated with closely matching sequences obtained through a BLAST 2.13.0+ (Camacho et al., 2009) alignment against the updated Full UNITE+INSD v9.0 dataset for Fungi (Abarenkov et al., 2022) were used (Table S1). Thus, a total of ninety-seven sequences were aligned using the L-INS-I method of the MAFFT v7.520 algorithm (Katoh and Standley, 2013) in Aliview 1.28 (Larsson, 2014). The ITS1, 5.8S and ITS2 regions of ribosomal RNA gene were determined by ITSx v1.1.3 software (Bengtsson-Palme et al., 2013).

Maximum Likelihood (ML) and Bayesian inference were applied with HKY+I+G4 as the model for nucleotide evolution as suggested by ModelTest-NG v0.1.7 (Flouri et al., 2014; Darriba et al., 2020) using RAxML-NG v1.2.0 (Kozlov et al., 2019) and MrBayes 3.2.7a (Ronquist et al., 2012), respectively. Otherwise, K3Pu+F+I+G4 was applied as suggested by ModelFinder (Kalyaanamoorthy et al., 2017) integrated in the IQ-TREE2 v2.3.4 software (Minh et al., 2020). In IQ-TREE2 Nearest Neighbour Interchange was set up as topology research, with 20 initial trees obtained applying RapidNJ and 148 iterations for bootstrap analysis. An all-in-one analysis (ML tree

search and non-parametric bootstrap) was performed with RAxML-NG using 10 randomised parsimony starting trees and 200 bootstrap replicates. In the parallel version of MrBayes, the Markov Chain Monte Carlo algorithm was run using four chains (three hot, one cold), a temperature of 0.1, a stop value of 0.01 on two trees with a diagnose frequency every 100 generations and a 25% burn-in. The Bayesian consensus phylogenetic tree was visualised using FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree) and annotated manually to include results from the various analyses. To further investigate the *L. idae-fragum* clade, an alignment was performed on 706 overlapping bases of the six existing sequences of this species only and their Single-Nucleotide Variants were highlighted by the snipit software (O'Toole et al., 2024).

The sequences of the new specimens are publicly available in the UNITE database (https://unite.ut.ee/): *L. gaillardii* (UDB07674349, UDB07675666), *L. pseudopilatianus* (UDB07674351, UDB07674352), *L. marginatus* (UDB07675665), *L. idae-fragum* (UDB07674355, UDB07675667).

Results

Mycological findings in the study area

Concomitantly with the various specimens belonging to section *Piloselli* (*L. pseudopilatianus*, *L. gaillardii*, *L. marginatus* and *L. idae-fragum*), specimens of various other fungal species appeared in December after some days of rain and in January: *Lepista* sp. (TUF137357, TUF137388), *Limacella* sp. (TUF137387), *Agaricus bisporus* (J.E. Lange) Imbach (TUF137361), *Agaricus cupressicola* Bon & Grilli (TUF137360). Specimens of *Battarrea* sp. were stably observed even in the winter period. Contrarily, the presence of *M. coliforme* was no longer ascertained within the cypress alley since spring 2019.

Morphological description of the L. idae-fragum *specimens*

Pileus up to 6 cm in diameter campanulate, convex to plano-convex, with umbo. Margin sometimes exceeding lamellae. Surface felted, smooth in the centre, squamulose on the perimeter of colour raspberry pink, purplish mauve, vinaceous pink, darker at the centre and paler towards the margin, on whitish background. In some but not all specimens, velar patch on the pileus was present. Lamellae rather dense (crowded), free, white but tending towards light pink, with darker, greyish brown, fringed edge (Fig. 2).

Stem 6–10 × 0.5–1.0 cm, cylindrical, protruding into the pileus, flexuous, equal or longer than the pileus diameter, widening towards the base. Base with oblong or globose bulb. Felted, whitish under the lamellae to a pink concolor with pileus towards the base, but often raspberry pink coloured. Decorated by a membranous and/or fibrillose annulus placed towards the base, sometimes turned inside out like a cuff, white in the inner upper side, raspberry pink or concolor with pileus in the external side or underside and dark pink at the rim. Context white, rather thick and without relevant smell.

Fig. 2 – *Leucocoprinus idae-fragum* basidiomata on *Cupressus sempervirens* needles litter.

Microscopy

Spores: (5.5)–6.7–(7.8) × (3.3)–4.1–(4.6) µm, Q = (1.2)–1.6–(2.2) (n = 42) (Fig. 3). Ellipsoid, with apiculum, hyaline, smooth, with thick wall, a part with one large lipid droplet other with several little lipid droplets inside, strongly dextrinoid and cyanophilous, faintly metachromatic. Basidia 22–30 × 7.5–9 µm, clavate, usually 4-spored sometimes 2-spored. Cheilocystidia (23.6)–30.0–(37.9) × (8.8)–13.0–(15.8) µm, thin-walled, colourless, variable in shape and size, clavate to pyriform. Clamp-connections absent.

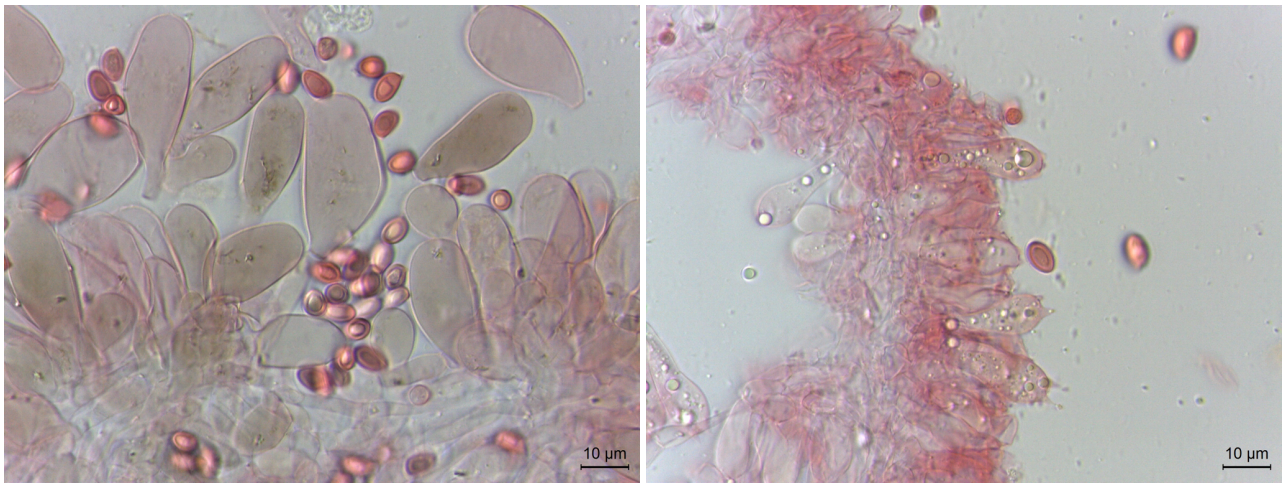

Fig. 3 – *Leucocoprinus idae-fragum* a) cheilocystidia and basidiospores in Congo Red; b) basidia and basidiospores in Congo Red.

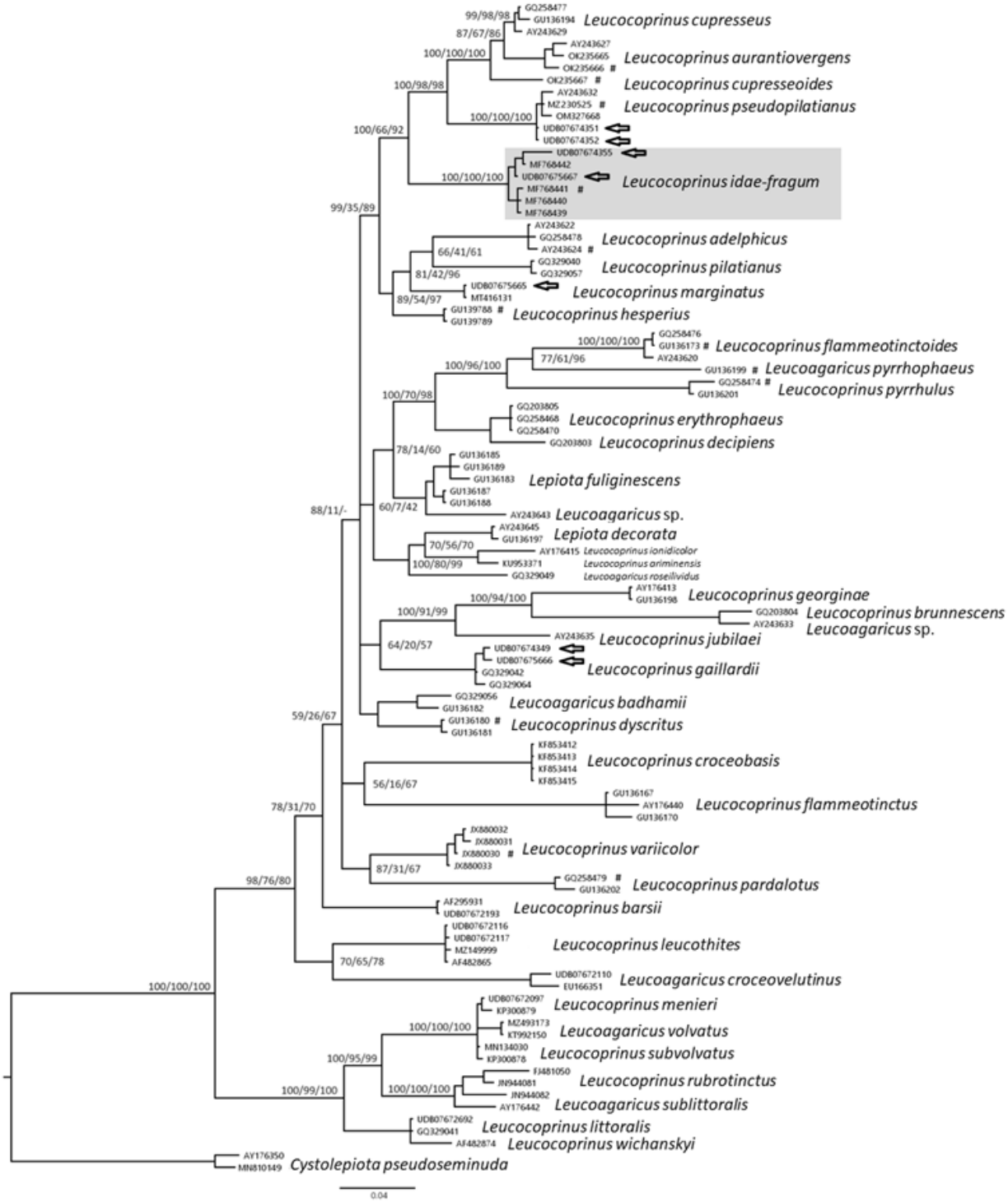

Fig. 4 – Phylogenetic tree upon alignment of the nuclear ribosomal ITS sequences of *Leucocoprinus/Leucoagaricus* species, identified by their UNITE/GenBank accession number and associated species. The sequences AY176350 and MN810149 from *Cystolepiota pseudoseminuda* were used as outgroup to root the tree. The new samples described in the article are indicated by arrows and sequences from holotype/isotype material by hashes. Bayesian posterior probabilities and Maximum likelihood bootstrap support values are reported as MrBayes/RAxML/IQ-TREE on the main branches.

Molecular analyses

Phylogenetic inference (Fig. 4) gave comparable results for Bayesian and ML analyses. The taxonomies of the *Leucoagaricus* and *Leucocoprinus* genera are currently being merged (Redhead 2023; Asif et al., 2024; Migliozzi and Donato, 2024), a process which is still ongoing as can be seen from Fig. 4 where not all species have yet been reclassified as *Leucocoprinus*. Regardless, no monophyletic definition has been found for section *Piloselli*. Despite these uncertainties for the backbone, the three analyses were confidently overlapping at the species' level and allowed for the identification of the *Leucocoprinus* specimens under study, in particular, two specimens were confirmed to be *L. idae-fragum*. These sequences from the Trevignano specimens were closely aligned to the sequence from the specimen found on the Polvese island (MCVE29342). The branching between these three sequences and those obtained from the French holotype specimen (LIP97113001) and the other Italian specimens from Bolgheri (MCVE29362) and Cagliari on the Sardinia Island (CAGP.12_9/8.38) was present in all evaluated trees in the ML analysis and with a 100% posterior probability in the Bayesian inferred tree.

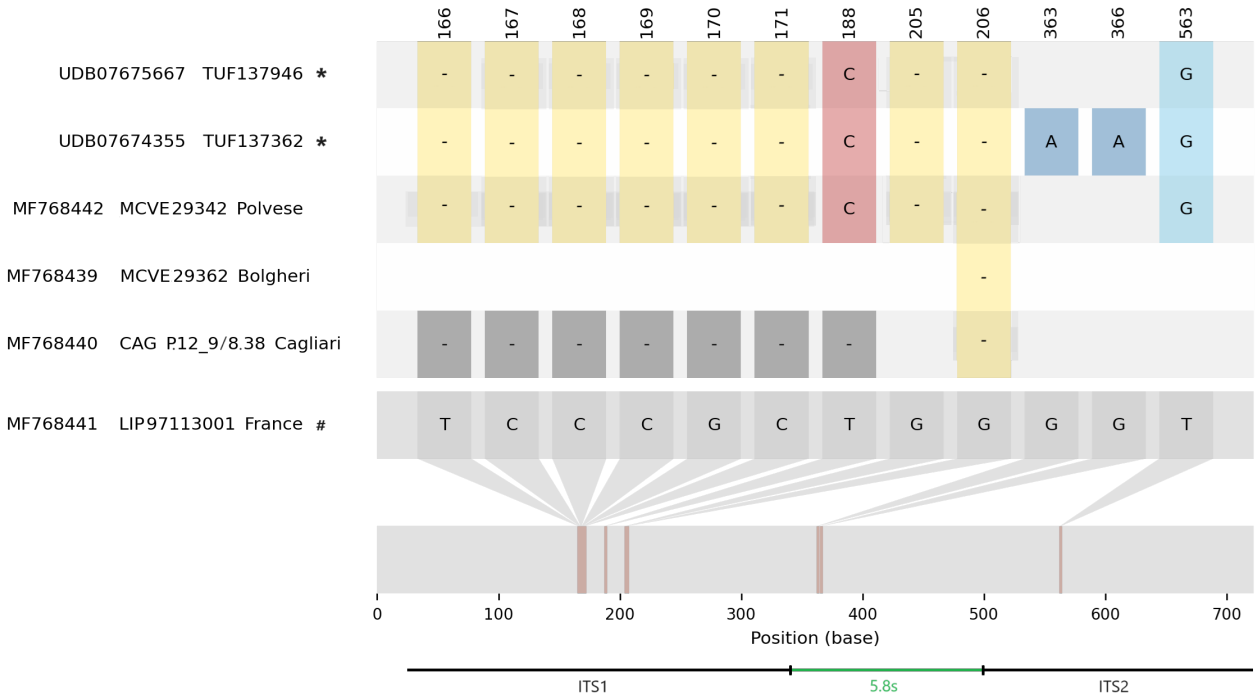

Fig. 5 – Single-Nucleotide Variants of the sequences from *Leucocoprinus idae-fragum* are shown with respect to the holotype MF768441 sequence at the lower row. The hyphen indicates gaps, also intra-sequence gaps are indicated (yellow boxes). The new samples described in the article are indicated by asterisks and the hash indicates the holotype specimen. The barcode regions are annotated at the bottom.

A Single-Nucleotide Variant analysis (Fig. 5) was performed, to further investigate the origin of this ramification. The only mutations in common between the Trevignano+Polvese specimens with respect to the holotype clade, were a C in position 188 bp of ITS1 (tctCggt) against a T (tctTggt) and a G in position 563 bp of ITS2 (gtcGgct) against a T (gtcTgct) (Fig. 5). Furthermore, in ITS1 six consecutive nucleotides (TCCCGC) were missing (positions 166-171 bp) in the Trevignano+Polvese clade with respect to the holotype. These six nucleotides seem to be insertions in the holotype

complex because all other *Leucocoprinus*/*Leucoagaricus* species analysed in this study do not have them.

Discussion

We report the findings of rare fungal species *L. marginatus*, *L. gaillardii*, and the very rare *L. idae-fragum* specimens inside a short cypress alley in the Bracciano-Martignano Natural Regional Park. The *C. sempervirens* alley was planted about seventy years ago in proximity of the Lake Bracciano shore, with a vegetation of *Phytolacca* sp. and ivy growing at the edges. The soil is sandy, covered by cypresses needles debris, and since it is a busy pedestrian crossing, it is often dirty. Bracciano-Martignano Natural Regional Park is a volcanic area affected by the ancient Sabatino volcano. The climate of the area is sunny and mild, due to constant ventilation from the sea. Rain is mainly concentrated in the autumn months. Comparing with other sites of *L. idae-fragum* findings in Italy, the presence of the lake would yield the environment not dissimilar to that of the *C. sempervirens* area of the Polvese Island in the Trasimeno Lake in Umbria, although geologically the latter has a tectonic origin (Gasperini et al., 2010). Interestingly, on the Polvese Island the same concomitance of the two species *M. coliforme* and *Battarrea* sp. clade A (Bistocchi et al., 2001; Angelini et al., 2016) was found as in the area of study (Ferretti et al., 2020). The Bolgheri area, comprising the bicentenary *C. sempervirens* Avenue, shows a similar climate trend (data obtained from https://it.weatherspark.com/). Regarding weather conditions during fungal growth, *L. idae-fragum* specimens were found in winter after several days of rain, in the coldest period of Lake Bracciano. Likewise, in literature, the specimens have been found in late autumn/winter (Guinberteau, 2011; Vizzini et al., 2017; Brugaletta, 2018; Somhorst et al., 2022). Single exception are the specimens found on the Polvese Island in June 2016 which was a particularly rainy month in Umbria (data obtained from https://it.weatherspark.com/). Therefore, the current climatic changes producing drought could reduce their proliferation and represent a threat to this species. Notably, in December 2024 and the beginning of January 2025, no specimens of *L. idae-fragum* have been observed.

It was reported *L. idae-fragum* basidiomata show morphological variability (Guinberteau, 2011; Vizzini et al., 2017). The specimens found in Trevignano Romano appeared to be more slender and smaller in size than those described in the literature (ibidem). It has been hypothesised that the different position of the annulus on the stem evidenced in the specimens from the Bolgheri cypress alley compared with these from the Polvese Island, was due to an asynchronous elongation of parts of the stem which could be in relation with ecological factors (Vizzini et al., 2017). Presumably, fungi with a basal annulus on the stem present an early opening of the pileus related to the development of the hymenophore compared to the elongation of the stipe. In the specimens found in Trevignano Romano, the position of the annulus on the stem is basal like the collection from the Bolgheri cypress avenue. Consequently, the involved ecological factors should be similar in these two sites and different from the Polvese Island. One ecological factor that could be involved is the soil composition. It was reported that greater nitrogen availability together with soil temperature rise can influence the development and the growth of some species of fungi (Solly et al., 2017; Treseder et al., 2021). The soil in the Trevignano Romano cypress alley is rich of organic matter with a large amount of nitrogen and phosphorus due to the presence of dog excrements. The specimens therefore could have humicolous and nitrophilic properties. Instead, the environment of the Polvese Island, which is only inhabited seasonally and is a scientific-educational park, is much less influenced by anthropic agents

(Ricci, 2015) with a different effect on soil composition. Another factor is the distance from the sea of the three locations, where the Polvese Island is inland with the greatest distance from the sea. The combination of soil and environmental characteristics could be responsible for the variable maturation of basidiomata.

The microscopic analyses revealed basidiospores, basidia and cheilocystidia with comparable dimensions of that reported for the other various collections. The basidiospores generally contain one lipid droplet inside, but some have many small lipid droplets. Lipid droplets presence in the spores is not reputed a relevant characteristic for the taxonomic classification of fungal species, but their different composition entails various roles in metabolism, signalling and development in fungi (Murphy, 2001; Knijn et al., 2019; Kameoka and Gutjahr, 2022).

A molecular definition of section *Piloselli* is still challenging due to its polyphyletic origin. Some authors include *Leucoagaricus croceovelutinus* (Bon & Boiffard) Bon in section *Piloselli* (Muñoz et al., 2014), which falls within a branch together with *Leucocoprinus leucothites* which is part of section *Annulati*. Although molecular analyses not always support the branches within the *Piloselli* section, probably due to missing sequences of species able to polarise and better define the branches, at the leaf level the separations are generally clear. For instance, the *L. idae-fragum* clade is well defined. Interestingly, phylogenetic inference shows that the specimens from Trevignano Romano cluster together with the sequence from the specimen found on the Polvese island in Umbria. The morphological differences between these two collections seem therefore effectively caused by ecological factors. With the addition of further sequences of this species, it will become clear if the differences with the sequence from the holotype specimen are indicative of stable nucleotide variations. In fact, based on these preliminary results one could hypothesise the existence of two sister species, although further data will be needed to obtain the necessary resolution to confute or confirm this hypothesis.

Because fungi are generally not considered with respect to habitat preservation plans, it is of great importance to document the mycological richness of this cypress alley. In fact, the land comprising the alley is considered a building area. The area is categorised as a Zone for general and local public services in the General Urban Plan of 2019. East of the alley, facing south towards the lake, a station of the "Protezione Civile" is present. However, the area facing north has been sold with a permit to build a condominium and here construction works will soon begin. This will have an impact on this interesting and peculiar natural environment. It is noteworthy that already in the last five years disturbing factors have interfered with the presence of *M. coliforme*, a rare species considered threatened (Ferretti et al., 2020). The mycological diversity in this short alley is truly astonishing and deserves due attention to preserve its peculiar microhabitat.

Acknowledgements

IS was supported by the Estonian Research Council grant (PRG1170).

References

Abarenkov K, Zirk A, Piirmann T, Pöhönen R, Ivanov F, Nilsson RH, Kõljalg U (2022) Full UNITE+INSD dataset for Fungi. Version 18.07.2023. UNITE Community. https://doi.org/10.15156/BIO/2938065

Angelini P, Arcangeli A Bistocchi G, Padula R, Venanzoni R (2016) I funghi: un tesoro dell'Isola Polvese. Micron 33:42–47.

Asif M, Saba M, Raza M, Vellinga EC (2024) Molecular insights into fungal diversity reveal three novel species of *Leucocoprinus* from southern Punjab, Pakistan. Mycologia 116:601–620. https://doi.org/10.1080/00275514.2024.2351769

Bengtsson-Palme J, Veldre V, Ryberg M, Hartmann M, Branco S, Wang Z, Godhe A, Bertrand Y, De Wit P, Sanchez M, Ebersberger I, Sanli K, de Souza F, Kristiansson E, Abarenkov K, Eriksson KM, Nilsson RH (2013) ITSx: Improved software detection and extraction of ITS1 and ITS2 from ribosomal ITS sequences of fungi and other eukaryotes for use in environmental sequencing. Methods in Ecology and Evolution, 4:914–919. https://doi.org/10.1111/2041-210X.12073

Bistocchi G, Le Roy V, Mariotti L (2001) I funghi del parco scientifico didattico Isola Polvese. Provincia di Perugia, Circolo Micologico Naturalistico Perugino, Perugia, Italy.

Boisselet P (2002) *Leucoagaricus marginatus* comb. nov., espèce d'origine californienne retrouvée en France. Bulletin de la Société mycologique de France 117:183–192.

Bon M, Boiffard J (1974) Lépiotes de Vendée et de la cote Atlantique française. Bulletin de la Société Mycologique de France 90:287–306.

Brugaletta E (2018) *Leucoagaricus idae-fragum*, an interesting find from the pinewood of Randello, Sicily. Micologia e vegetazione mediterranea 33:105–110.

Camacho C, Coulouris G, Avagyan V, Ma N, Papadopoulos J, Bealer K, Madden TL (2009) BLAST+: architecture and applications. BMC Bioinformatics 10:421–429. https://doi.org/10.1186/1471-2105-10-421

Darriba D, Posada D, Kozlov AM, Stamatakis A, Morel B, Flouri T (2020) ModelTest-NG: a new and scalable tool for the selection of DNA and protein evolutionary models. Molecular Biology and Evolution 37:291–294. https://doi.org/10.1093/molbev/msz189

Ferretti A, Saar I, Knijn A (2020) On two endangered species (*Myriostoma coliforme* and *Battarrea* sp.) sharing the same microhabitat. Italian Journal of Mycology 49:1–7. https://doi.org/10.6092/issn.2531-7342/10039

Flouri T, Izquierdo-Carrasco F, Darriba D, Aberer AJ, Nguyen LT, Minh BQ, von Haeseler A, Stamatakis A (2014) The phylogenetic likelihood library. Systematic Biology 64:356–362. https://doi.org/10.1093/sysbio/syu084

Gasperini L, Barchi MR, Bellucci LC, Bortoluzzi G, Ligi M, Pauselli C (2010) Tectonostratigraphy of Lake Trasimeno (Italy) and the geological evolution of the Northern Apennines. Tectonophysics, 492:164–174. https://doi.org/10.1016/j.tecto.2010.06.010

Gennari A, Migliozzi V, Siquier Virgós JL (1995) Tre interessanti Leucocoprinae sabulicole. *Leucoagaricus gaillardii* Bon & Boiffard, *Sericeomyces subvolvatus* (Malençon & Bertault) Contu fo. *subvolvatus* e *S. subvolvatus* fo. *pictus* (Malençon & Bertault) Bon. Micologia e Vegetazione Mediterranea 10:9–21.

Guinberteau J (2011) Le petit livre des champignons des dunes. Ed. Confluences, Bordeaux, France.

Guinberteau J, Boisselet P, Dupuy G (1998) *Leucoagaricus idae-fragum*, sp. nov., un nouveau *Leucoagaricus* des dunes atlantiques françaises de coloration rose framboise. Bulletin de la Société Mycologique de France 114:1–18.

Justo A, Angelini C, Bizzi A (2021) The genera *Leucoagaricus* and *Leucocoprinus* in the Dominican Republic. Mycologia 113:348–389. https://doi.org/10.1080/00275514.2020.1819142

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14:587–589. https://doi.org/10.1038/nmeth.4285

Kameoka H, Gutjahr C (2022) Functions of lipids in development and reproduction of arbuscular mycorrhizal fungi. Plant Cell Physiology 63:1356–1365. https://doi.org/10.1093/pcp/pcac113

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30:772–780. https://doi.org/10.1093/molbev/mst010

Knijn A, Saar I, Ferretti A (2019) Biological characteristics of *Punctularia atropurpurascens* through morphological and molecular analyses during development. Italian Journal of Mycology 48:39–49. https://doi.org/10.6092/issn.2531-7342/9574

Kõljalg U, Nilsson RH, Abarenkov K, Tedersoo L, Taylor AFS, Bahram M, Bates ST, Bruns TD, Bengtsson-Palme J, Callaghan TM, Douglas B, Drenkhan T, Eberhardt U, Dueñas M, Grebenc T, Griffith GW, Hartmann M, Kirk PM, Kohout P, Larsson E, Lindahl BD, Lücking R, Martín MP, Matheny PB, Nguyen NH, Niskanen T, Oja J, Peay KG, Peintner U, Peterson M, Põldmaa K, Saag L, Saar I, Schüßler A, Scott JA, Senés C, Smith ME, Suija A, Taylor DL, Telleria MT, Weiß M, Larsson KH (2013) Towards a unified paradigm for sequence-based identification of fungi. Molecular Ecology 22:5271–5277. https://doi.org/10.1111/mec.12481

Kozlov AM, Darriba D, Flouri T, Morel B, Stamatakis A (2019) RAxML-NG: A fast, scalable, and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics 35:4453–4455 https://doi.org/10.1093/bioinformatics/btz305

Larsson A (2014) AliView: a fast and lightweight alignment viewer and editor for large datasets. Bioinformatics 30:3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Latha K, Raj K, Manimohan P (2020) *Leucoagaricus callainitinctus* – a new species of *Leucoagaricus* section *Piloselli* (Agaricaceae) from tropical India. Phytotaxa 442:111–120. https://doi.org/10.11646/phytotaxa.442.2.6

Martín MP, Rusevska K, Dueñas M, Karadelev M (2013) *Battarrea phalloides* in Macedonia: genetic variability, distribution and ecology. Acta Mycologica 48:113–122. https://doi.org/10.5586/am.2013.013

Migliozzi V (2022) Contributo allo studio del genere *Leucoagaricus*, sezione *Piloselli*. 1. Prima segnalazione per il territorio italiano di *Leucoagaricus marginatus*. Bollettino del Gruppo Micologico «G. Bresadola» - Nuova Serie 55-56:103–114.

Migliozzi V, Donato G (2024) Nuove combinazioni per ritrovamenti italiani del genere *Leucoagaricus* ora *Leucocoprinus*. Errotari 21:60–69.

Migliozzi V, Rocabruna A, Tabares M. (2001) *Leucoagaricus pseudopilatianus*, una nueva especie de la sección *Piloselli*. Revista Catalana de Micologia 23:67–74.

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R (2020) IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37:1530–1534. https://doi.org/10.1093/molbev/msaa015

Muñoz G, Caballero A, Contu M, Ercole E, Vizzini A (2014) *Leucoagaricus croceobasis* (*Agaricales*, *Agaricaceae*), a new species of section *Piloselli* from Spain. Mycological Progress 13:649–655. https://doi.org/10.1007/s11557-013-0947-x

Murphy DJ (2001) The biogenesis and functions of lipid bodies in animals, plants and microorganisms. Progress in Lipid Research 40:325–438. https://doi.org/10.1016/S0163-7827(01)00013-3

O'Toole Á, Aziz A, Maloney D (2024) Publication-ready single nucleotide polymorphism visualization with snipit. Bioinformatics 40:btae510 https://doi.org/10.1093/bioinformatics/btae510

Redhead SA (2023) Nomenclatural novelties. Index Fungorum 551:1.

Ricci S (2015) I Parchi dell'Umbria. Guida alla diversità. Giunti Progetti Educativi, Florence, Italy.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61:539–542. https://doi.org/10.1093/sysbio/sys029

Singer R (1986) The Agaricales in Modern Taxonomy. 4th edn. Koeltz Scientific Books, Königstein, Germany.

Solly EF, Lindahl BD, Dawes MA, Peter M, Souza RC, Rixen C, Hagedorn F (2017) Experimental soil warming shifts the fungal community composition at the alpine treeline. New Phytologist 215:766–778. https://doi.org/10.1111/nph.14603

Somhorst I, Noordeloos M, Eenshuistra P, Verweij R, Vaessen A (2022) Ecological Monitoring Newsletter − 25. Coolia 65:184−200.

Treseder KK, Alster CJ, Anh Cat L, Gorris ME, Kuhn AL, Lovero KG, Hagedorn F, Kerekes JF, McHugh TA, Solly EF (2021) Nutrient and stress tolerance traits linked to fungal responses to global change: Four case studies. Elementa: Science of the Anthropocene 9:00144. https://doi.org/10.1525/elementa.2020.00144

Vellinga EC (1988) Glossary. In Flora Agaricina Neerlandica 1 (Kuyper TW, Noordeloos ME, Vellinga EC, eds). AA Balkema, Rotterdam, pp. 54–64.

Vellinga EC (2006) Lepiotaceous fungi in California, U.S.A. – 3. Pink and lilac species in *Leucoagaricus* sect. *Piloselli*. Mycotaxon 98:213–224. https://doi.org/10.5248/112.393

Vellinga EC (2010) Lepiotaceous fungi in California, U.S.A. *Leucoagaricus* sect. *Piloselli*. Mycotaxon 112:393–444. https://doi.org/10.5248/112.393

Vizzini A, Lezzi T, Tatti A, Iannotti M, Filippa M, Dovana F (2017) Molecular confirmation of *Leucoagaricus idae-fragum* (Agaricales, Agaricaceae), and notes on its morphological variability. Phytotaxa 332:157–171. https://doi.org/10.11646/phytotaxa.332.2.3

Voitk A, Saar I, Trudell S, Spirin V, Beug M, Kõljalg U (2018) *Polyozellus multiplex* (Thelephorales) is a species complex containing four new species. Mycologia 109:975–992. https://doi.org/10.1080/00275514.2017.1416246