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Research article

Breaking a 128-year silence: new records of *Cyphella digitalis* (Alb. & Schwein.) Fr. in Italy

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Abstract
Cyphella digitalis develops small, distinctly campanulate basidiomata exclusively on *Abies alba*. While its presence has been well documented north of the Alps, only a singular record has been reported from Italy almost 128 years ago with no further findings until now. In 2024, *C. digitalis* was recorded on several *A. alba* individuals in the relict population of Monte Nero (Emilian-Ligurian Apennines, SIC IT4010003) along with few specimens from the broader *A. alba* populations in Trento Province. Consistent with the hardly mistakable morphology, molecular barcode confirmed the basidiomata identity. Unfortunately, very few nucleotide sequences of this species have been deposited in repositories to date, making it impossible to reconstruct a robust intraspecific phylogeny. No differences have been pointed out between samples from the Apennines and the Alps based on either the ITS region or morphology, nor with regard to other European regions according to the literature. This study suggests that *C. digitalis* may have been overlooked in both Italian sides of the Alps as well as in the relict *A. alba* populations of the Apennines. Since *C. digitalis* is monophagous, these findings highlight the importance of conserving relict habitats including *A. alba* in the Apennines, especially from a fungal conservation perspective.

Keywords
Abies alba, Cyphellaceae, disjunction, monophagous fungi, relict population, spore metrics

Introduction

Cyphella digitalis is a saproxylic species in Cyphellaceae Burnett (Agaricales Underw.) developing small, campanulate basidiomata. Despite "it can hardly be mistaken" according to Breitenbach and Kränzlin (1986), its taxonomic history is rather complex. In 1822, Fries moved the species from *Peziza* Fr. to the novel genus *Cyphella* Fr. describing it as an easily recognizable basidiomycete "in Pino picea satis frequens" (Fries, 1822). To date, *C. digitalis* has been reliably and consistently documented from *Abies alba* Mill. only, which is the accepted name and exact synonym of *Pinus picea* L. (Kew-Royal Botanic Gardens, https://powo.science.kew.org/, accessed on 28, April 2025).

It is well known that *A. alba* does not naturally form monospecific stands, normally forming mixed stands with broadleaves, such as *Fagus sylvatica* L. at lower altitudes, and conifers like *Picea abies* (L.) H. Karst. at higher altitudes (Grossoni et al., 2018). Accordingly, Roberts (2003) linked *C. digitalis* to mixed fir-beech forests as well as spruce-beech forests containing scattered firs, particularly in the Baden-Württemberg (south-western Germany), a view consistently supported by more recent observations by Wilhelm (2018). Karasch (2024) reviewed the available records in Europe and referred them to France (Vosges), Central Switzerland and Jura, Liechtenstein, Austria and Germany - mainly Bavaria and Baden-Württemberg, while suggesting may be the species extinct in Oberlausitz. Raillere (1996) also reported *C. digitalis* from the Loire and Savoie regions of France, whereas Holec et al. (2022) provided one of the very few publications on this species, examining its habitat preferences in the Bohemian and Carpathian regions, that resulted in substantiating Roberts' thesis. Overall, Karasch (2024) defines *C. digitalis* distribution as European or Carpathic-Alpic, with no known records from the southern regions of the *A. alba* distribution area, such as the Southern Balkans. Global Biodiversity Information Facility (GBIF) records (https://www.gbif.org/species/2532923, accessed on 9, August 2025) are mainly clustered in Switzerland and broadly align with the above-mentioned literature. However, GBIF also includes scattered records from Slovenia and a significant population in the Pyrenees (both in Spanish and French sides).

As for Italy, the only known record dates to 1896, when Bresadola and Cavara reported *C. digitalis* from the Vallombrosa forest (province of Florence) (Bresadola and Cavara, 1901). It is worth noting that the Vallombrosa forest has been managed by Benedictine monks for several centuries, and the presence of *A. alba* had not been documented until the late XIV Century. Later, *A. alba* spread from small stands close the Abbey and its presence was promoted by the monks for forestry purposes. *Abies alba* stands in Vallombrosa reached their widest range between XVII and XIX Centuries coinciding with the Little Ice Age maximum (https://rgpbio.it/riserva/vallombrosa/, accessed on 9, august 2025). In summary, Vallombrosa firs and its inhabitant fungi are non-native to the area, although they are currently included within the "Apennine beech forests with *Abies alba* and beech forests with *Abies nebrodensis*", i.e. habitat 9220* according to Directive 92/43/EEC (http://vnr.unipg.it/habitat/cerca.do).

Based on morphological and molecular identification, the aim of this work was to present the first records of *C. digitalis* in Italy since 1896 and the very first ever documented in Italy from native *A. alba* populations, highlighting the necessity to protect and conserve this relict tree stand that hosts a unique fungal community including the case of *C. digitalis*.

Materials and Methods

Sampling area

The main focus of this study was the relict population of *Abies alba* on Monte Nero (top 9.509317 E, 44.562917 N, 1753 m asl), located across the border between Ferriere and Bedonia municipalities in northern Apeninnes, Italy (https://geoportale.regione.emilia-romagna.it/mappe/geo-viewer; accessed on 9, August 2025). This *A. alba* population includes several old individuals, up to almost 270 years old (Carrer et al., 2010). As far as known, the *A. alba* population on Monte Nero represents a never managed, native relict in the Apennine Subprovince disjuncted from the main Alpic corpus and other

Apennine cores, i.e. it represents an “effective refugium” which contributed to the post-glacial recolonization (Piotti et al., 2017).

As a whole, the area is part of IT4010003-ZSC-ZPS- Monte Nero, Monte Maggiorasca, La Ciapa Liscia managed by Regione Emilia-Romagna within Rete Natura 2000 (Bassi et al., 2015; https://ambiente.regione.emilia-romagna.it/it/parchi-natura2000/rete-natura-2000/siti/it4010003, accessed on 9, August 2025) and hosts, among others, Habitat 9220*I Apennine beech forests with *A. alba* and beech forests with *Abies nebrodensis* as a spot in contact with Habitat 9110 Luzulo-Fagetum beech forests - subtype 41.171 (http://vnr.unipg.it/habitat/cerca.do). Unlikely the 9110 areas, Monte Nero is underlain by ultramafic bedrck and belongs to the Mt. Aiona Element of the External Ligurian Units (https://www.isprambiente.gov.it/Media/carg/215_BEDONIA/Foglio.html, accessed on 9, August 2025). The ultramafic substrate severely constraints beech colonization, allowing *A. alba* to escape the competition enhanced by human-driven forestry. Notwithstanding, *A. alba* is in turn replaced by *Pinus mugo* Turra in the cacuminal belt and across the ridge (Ubaldi, 2003; https://dryades.units.it/floritaly/index.php?procedure=taxon_page&tipo=all&id=159, accessed on 9, August 2025). In summary, the *A. alba* in Monte Nero is divided into two cores: one occupying the steep northern slope and the other located on the debris layer at the base of the southern slope (Fig. 1).

Most accessible *A. alba* individuals from both the slopes of Monte Nero were surveyed, with particular attention given to the decaying, still-attached branches in the lower portions of the crown. Surveys were conducted on October 6th and November 6th-7th, 2024. Approximately 43,900 m^2 were surveyed on the northern slope, and 62,750 m^2 on the southern slope as measured by web GIS tools (https://geoportale.regione.emilia-romagna.it/mappe/geo-viewer). Consistently with Girometta et al. (2023), specimens found on a single branch were considered as single individual.

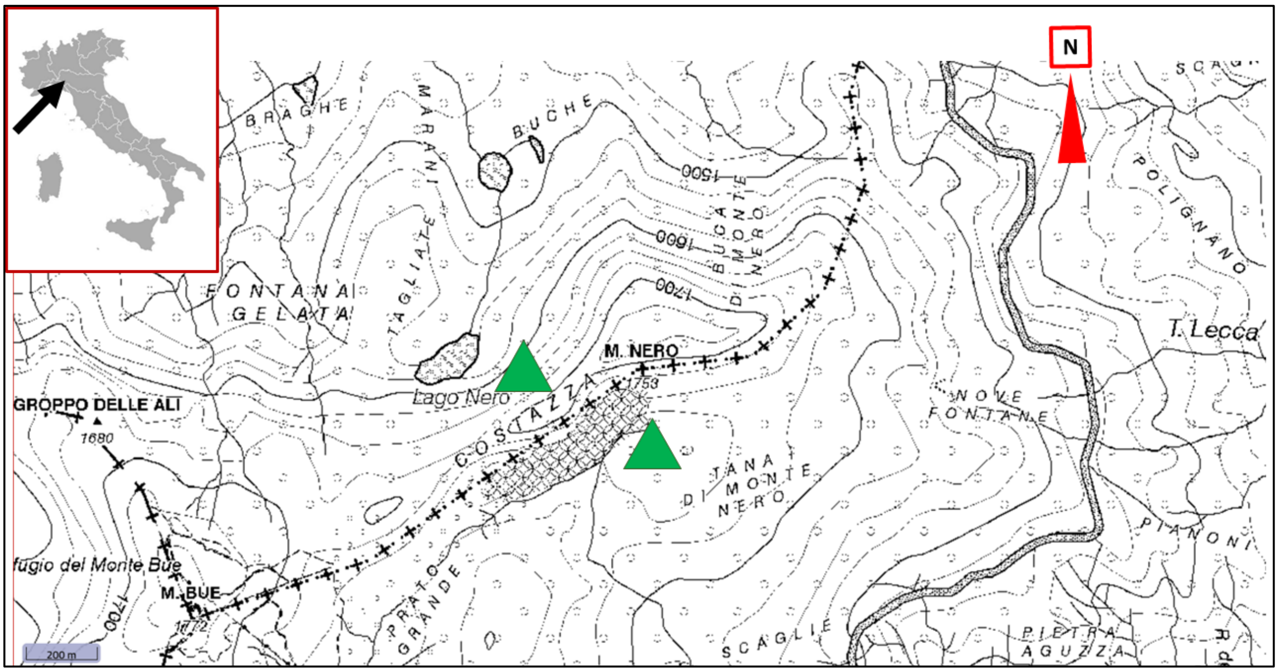

Fig. 1 – Sampling area on Monte Nero, Northern Apennines (Italy). Geographic (true) North and a scale bar are shown. The locations of northern and southern cores of *A. alba* population are indicated by the green triangles. Modified from CTR – Regional Technical Map.

In order to provide a broader ecological and geographical context, very preliminary surveys were also conducted in two outgroup localities in the province of Trento: Magrè (Lavarone municipality) and Val Noana (Mezzano municipality). A single survey was carried out in each locality in November 2024. Based on data from the Portale Geocartografico Trentino (https://webgis.provincia.tn.it/, accessed on 9, August 2025), about 1.92 km^2 and 26 trees were surveyed in Magrè (approximate centroid 11.285330 E, 45.95027 N), while 1 km^2 and 16 trees were examined in Val Noana (approximate centroid 11.856029 E, 46.1383076 N). Both of the sampling areas included mixed forests with a prevalence of *P. abies* with scattered *A. alba* individuals; however, neither area falls within habitats in Council Directive 92/43/EEC.

Morphological identification

Macro- and micromorphology from fresh and dried samples were examined and cross-checked in the laboratories of DSTA-Unipv and Annarosa Bernicchia. At DSTA-Unipv, observations were performed using a Zeiss KL200 stereomicroscope and Zeiss Axiostar Plus phase contrast optical microscope. In order to test the possible spore deformation, slides were separately mounted in: KOH (3%); diluted Congo Red (1%) + KOH (3%); water; acid lattofuchsin. In Annarosa Bernicchia's laboratory, observations were carried using Optech SZ-NT stereomicroscopes and Leitz Vialux 22FB optical microscopes equipped with Optika 4083.13 H camera; slides were mounted in diluted Congo Red (1%) + KOH (3%). Morphometric data were analyzed using Microsoft Excel 2016 and IBM SPSS Statistics version 26.

Exsiccata

Basidiomata of different size were dried at 30 °C, then preserved at -18 °C for one month and subsequently stored in sealed collection tubes. Exsiccata are partly conserved at the University of Pavia and partly in the private herbarium of Annarosa Bernicchia.

Molecular barcode

Total genomic DNA was directly extracted from basidiomata without preliminary surface disinfection. DNA extraction, amplification, purification and sequencing were carried out following Girometta et al. (2020). The following nuclear DNA regions were amplified using the corresponding primers: ITS (ITS1-ITS4); LSU (LR0R-LR7); SSU (NS1-NS8); RPB2 (5F-7CR). Primer sequences are available at Hibbett's Laboratory (https://www2.clarku.edu/faculty/dhibbett/Protocols_Folder/Primers/Primers.pdf, accessed on 9, August 2025), a resource referenced by several authors, such as Liu et al. (2023) and Spirin et al. (2023) for Polyporales. Sequence data were processed by Sequencher 5.0. The newly generated sequences were deposited in GenBank under the following codes: PV388090–PV388094 (ITS), PV383446–PV383451 (LSU), PV383452–PV383459 (SSU); PX584497 (RPB2).

Results and discussion

Morphological description

Basidiomata were consistently reported on living and standing *A. alba* individuals. They occurred gregariously in dense groups often composed by basidiomata of very different sizes, attached to the lower, decaying branches of the tree crown. No specimens were found on the trunk bark. The basidiomata are pendant downward, campanulate to thimble-shaped (collapsed when dried), pseudostipitate (stipe < 2 mm in largest specimens), and with dimensions ranging from 0.5 to 1 cm in length and less than 0.7 cm in width, with many specimens growing smaller. Fresh samples are membranous to elastic, becoming rigid and quite brittle when dried. The outer surface is light brown, with dark brown fibrils which are visible when fresh (resembling the "pubescent-pruinose" appearance in according to Fries). These dark fibrils are arranged in festoon-like tufts. The overall aspect is cocoa powder brown when dried. Margins are roughly crenate in fresh samples, while the inner surface is smooth, and hazelnut cream coloured in fresh samples. The basidia are tetrasporic with large sterigmata and granular content (Fig. 2).

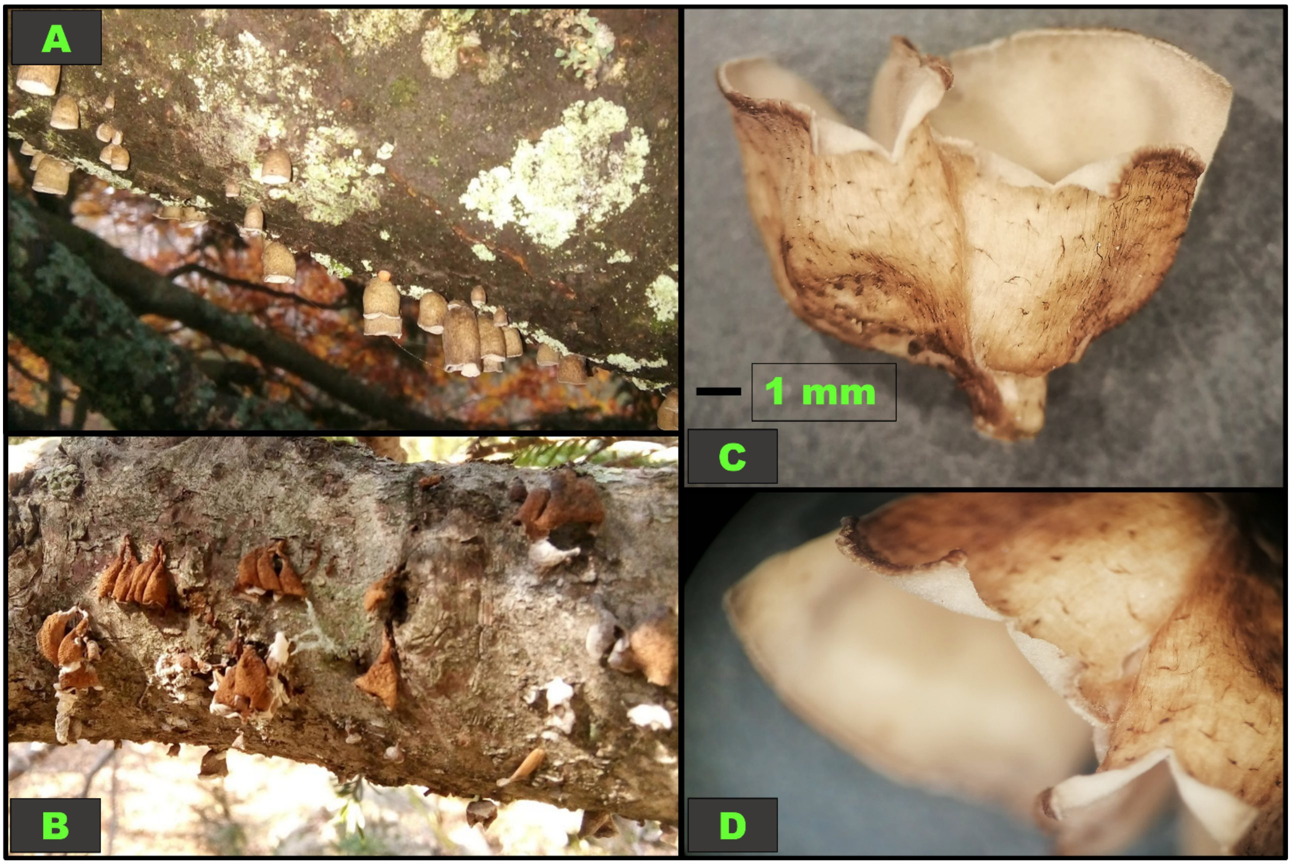

Fig. 2 – *Cyphella digitalis* in the southern slope of Monte Nero, October 2024 (A); specimens in field in the same locality in November 2024 (B); details of basidiomata at about 36× (C, D).

The hyphal system is monomitic, composed of hyphae thin-walled with abundant clamps. Cystidia are absent, but pseudo-moniliform to capitate elements were observed. Spores are subglobose, thin walled, hyaline and apiculate, often appearing guttulate. They are white in mass and are massively expelled in dried specimens. In some cases, spores appeared glued to the basidioma margin and external surface, forming beard-like or lump-like accumulations (Fig. 3).

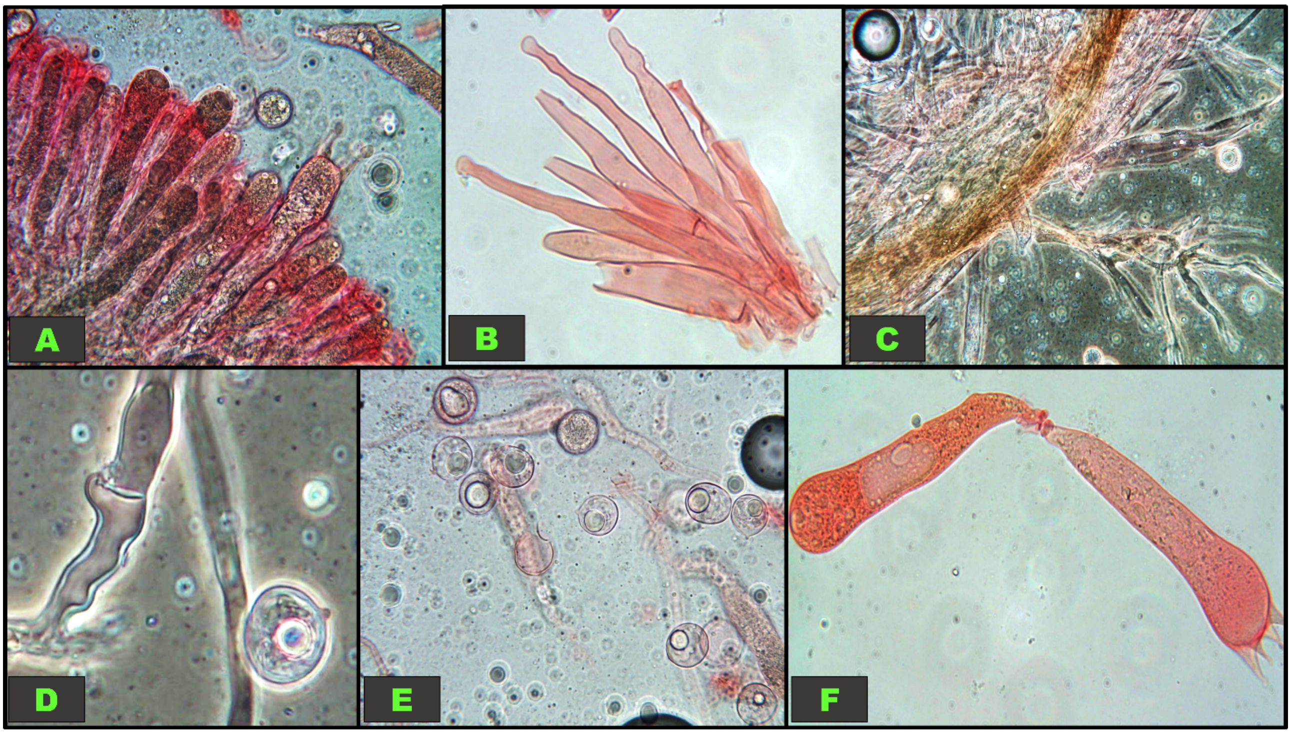

Fig. 3 – Micromorphological features of *C. digitalis*. Ripe and unripe basidia with spore (A); pseudo-moniliform to capitate, non-fertile bodies (B); tramal hyphae (C); hypha with clamp and spore (D); spores (E); basidia with basal clamp (F).

Table 1 – Spore metrics in diluted Congo Red (left) and asymptotic H_0 significance (%) of the median test for k independent samples with Bonferroni's correction (right). L = length, W = width, Q = L/W, avg = average, sd = standard deviation, N = 30, significance threshold = 5%. H_0 = the medians are not significantly different. Statistics details are explained in Soliani et al. (2003).

Site	Character	avg	%$_{sd/avg}$	median	N	M.N. north	M.N. south	Magrè	Val Noana
M.N. north	L (µm)	21.33	6.0%	21.3		-	18.20	10.40	10.40
	W (µm)	19.88	7.3%	20.0	30	-	0.00	100.00	61.10
	Q	1.08	5.8%	1.1		-	0.00	71.00	15.10
M.N. south	L (µm)	20.83	5.7%	20.0			-	0.00	0.00
	W (µm)	18.13	6.0%	17.5	30		-	0.00	33.80
	Q	1.15	3.6%	1.1			-	0.00	2.40
Magrè	L (µm)	19.79	2.4%	20.0				-	100.00
	W (µm)	17.81	4.2%	17.5	30			-	11.40
	Q	1.11	4.1%	1.1				-	27.00
Val Noana	L (µm)	19.79	7.7%	20.0					-
	W (µm)	18.54	8.2%	17.5	30				-
	Q	1.07	9.7%	1.1					-

Regarding the spore size, it is noteworthy that northern and southern slopes of Monte Nero seem to differ with each other more than Magrè and Val Noana do with Monte Nero (Table 1). Namely, the median test yielded a complex frame of similarities between Monte Nero and the Alpic localities; the two slopes of Monte Nero are similar in spore length (18.2% of the H_0 significance), whereas spore width and Q ratio didn't show any similarity. On the other hand, spores from the northern side resulted in higher similarity with both Magrè and Val Noana concerning length, width as well as Q ratio. Spore morphology (subglobose in this species) was expected to be conserved in different samples, although length and width are primitive quantities whereas Q is a derivative one (i.e. derived from length and width) and this could introduce an autocorrelation error (Bandyopadhyay and Forster, 2011) when making comparisons. However, Q ratio in the southern slope of Monte Nero is not similar to any other. The median test in fact relies on the data distribution with respect to the median itself, and such a distribution is clearly downshifted in the southern slope of Monte Nero (Fig. 4). As Q = L/W, this is consistent with the fact that length is more variable than width in this locality, despite the outliers (see asterisks in the boxplot). On the other hand, the medians of length and width in Magrè, Val Noana and the northern slope of Monte Nero are clearly downshifted with respect to the southern slope of Monte Nero. This furtherly confirms that the sample from the southern slope of Monte Nero has bigger spores.

A possible explanation of such differences in spore metrics could be the local microclimate, rather than the overall phytoclimate or the spatial disjunction, influences spore metrics, i.e. the northern slope of Monte Nero could have temperature, humidity and insulation conditions similar to Magrè and Val Noana ones, where *A. alba* occurs in north-east aspects. If confirmed by further studies, this result could be consistent with an adaptation (either epigenetic or ecotypic) to different dehydration and day-night variation in temperature. Thus, larger spores in the southern slope could reduce the dehydration damage.

As mentioned above, the spore size was obtained from the slides mounted in Congo Red (1%), and the present work also suggests to avoid both fuchsin and water mounting as they respectively resulted in spore collapse and fuzzy visualization. The spores analyzed in the present study lay in the same size range reported in literature. The German references (Roberts, 2003; Wilhelm, 2018; Karasch, 2024) agree in indicating 14–20 (22) × 14–17 (20) µm, whereas Terra (1966) assumes the sphericity of the spores and indicates 15-18 µm in diameter, consistently with Raillére (1996), who reports (16) 17–18 (20) × (14) 16–18 µm; Breitenbach and Kränzlin (1986) and Knudsen (2008) also assumes sphericity and report 16–19 µm and 16–21 µm, respectively. As a whole – and lacking details on the examined samples and localities - the mentioned ranges cannot point out any size correlation with latitude nor longitude. Notwithstanding, it is clear that the new data in the present study reflect dissimilarities in the spore metrics depending on the study area and probably due to the associated microclimatic conditions, also rejecting the perfect sphericity of the spores; this is important since these are the southernmost data published so far.

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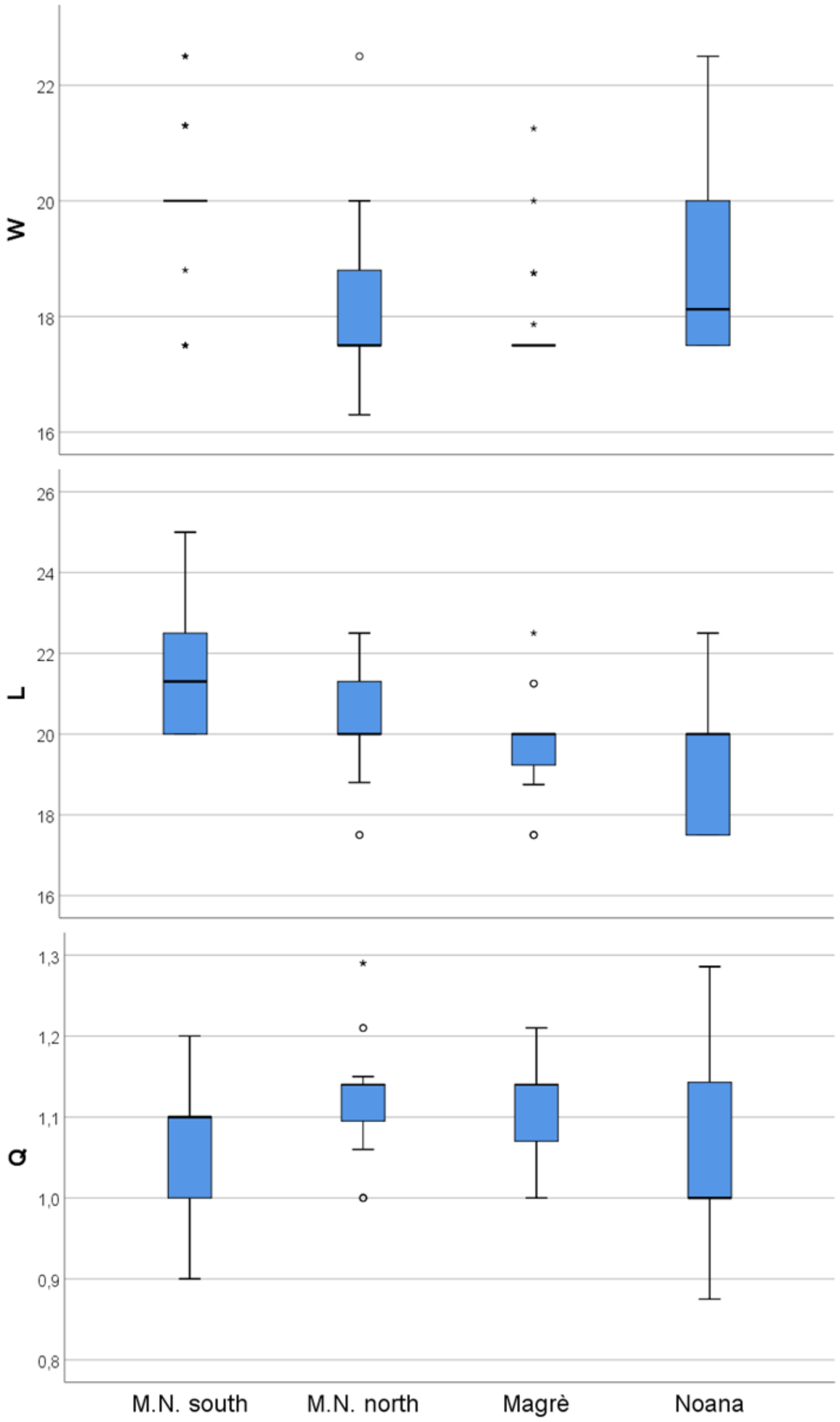

Fig. 4 – Data distribution supporting the median test for k independent samples for spores in diluted Congo Red. Each locality was treated as a sample. L = spore length (µm); W = spore width (µm); Q = L/W. Asterisks and empty circles indicate outliers.

Thus, accordingly to the possible scenario of local adaptation against dehydration, Roberts (2003) clearly remarks that *C. digitalis* prefers northern aspects, as well as Karasch (2024) and Raillére (1996) do regarding significant air humidity and shadow. Similar environmental preferences are reported by Holec et al. (2022) too, who confirm the need of cool and humid conditions. Altogether, this is perfectly consistent with the host needs, as *A. alba* is typically related to broadly defined oceanic climates in the temperate European region and in the Mediterranean mountains. This is also why *A. alba* adaptation to climate change is of major concern for the conservation of habitats such as 9220*I in southern areas (Ducci et al., 2021). This habitat is often associated to very peculiar fungal communities including rare monophagous and oligophagous species (Bernicchia et al., 2007), and provides unique insights on the host-fungus coevolution especially in the case of native fir stands and relict populations which have not been significantly altered or shaped by human activities.

Molecular barcoding

The ITS sequences of the specimens from Val Noana, Magrè and Monte Nero confirmed the morphological identification, showing similarities > 97% (up to 100%) with accessions of *C. digitalis* from both Mycobank and NCBI. The samples from Magrè were analyzed twice as they first resulted contaminated by *Panellus violaceofulvus* (Fr.) Singer growing on the same tree branch. It should be noted that while both primers performed equally well in *P. violaceofulvus*, the ITS4 primer has a better performance than the ITS1 primer in both PCR and subsequent sequencing for *C. digitalis*. Notably, only two sequences of the complete ITS region (DQ486698 and OM837174) are currently available in public repositories. Similarly, the LSU region confirmed the identification using both the LR7 and LR0R primers, although only one accession (AY635771) is available. PCR and sequencing of the SSU region using the NS1-NS8 primers were successful, but misleading matches were found from the repositories because no SSU sequences from *C. digitalis* have been deposited to date. Moreover, the region SSU itself appears to be a poor discriminant marker, as it shows > 98% similarity with other species such as *Laetiporus portentosus* (Berk.) Rajchenb. and *Baeospora myosura* (Fr.) Singer. Analogously, no matches with *C. digitalis* were found when analyzing the RPB2 subregion amplified using 5F-7CR primers, since no RPB2 sequences from *C. digitalis* have been deposited so far.

In general, the lack of reference sequences deposited in public repositories is a major issue in several fields of taxonomy and feeds a negative loop especially when dealing with neglected or poorly known taxa just like *Cyphella* species. Based on the available data, it is not currently possible to reconstruct a robust phylogeny for this species or related taxa. Regarding the present work, all newly generated sequences have been deposited in Genbank.

In conclusion, the present work has revealed the hitherto undetected presence of *C. digitalis* in both Alpine and Apennine *A. alba* populations in Italy. Moreover, spore metrics seem to suggest that adaptation to local microclimatic conditions may have occurred to mitigate dehydration particularly in the southern slopes of Monte Nero. Further studies and comparisons with a broader range of European populations are necessary to validate this phenotypic plasticity and its molecular basis. Finally, this study contributes to furtherly highlight the importance of *A. alba* populations for the conservation of fungal diversity, as this tree species is well known to host several monophagous or oligophagous wood-inhabiting fungi (Bernicchia et al., 2007; Bernicchia and Gorjón, 2010; Bernicchia and Gorjón, 2020).

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