

Entoloma sicoense, a new species in the subgenus *Cyanula* (Entolomataceae)

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Abstract

Entoloma sicoense, a bluish gray mushroom species belonging to section *Poliopodes*, is described as a new addition to the subgenus *Cyanula*. This study presents the phylogeny, taxonomy, and ecological significance of *Entoloma sicoense*, which inhabits mossy broad-leaved forests in the eastern North Atlantic region. The discovery of this new species expands our understanding of fungal diversity and highlights the ecological significance of the subgenus *Cyanula* in Serra de Sicó. *Entoloma sicoense* exhibits specific morphological characteristics, such as slate gray basidiomata, a smooth concolorous stipe, and a sterile gill edge rich in brilliant granules. This research underscores the importance of documenting and describing new species in Serra de Sicó for comprehensive cataloging, conservation efforts, and further exploration of its ecological role within the local ecosystem. The new species is presented with morphological, illustrated description as well as molecular work and comparison with similar species.

Keywords: Agaricales, Basidiomycota, European forests, Mediterranean mycobiota, Mutabilipedes, pink gills

Introduction

The genus *Entoloma* (Fr.) P. Kummer (1871: 97) is a large, and diversified genus within the order Agaricales. It also has a very wide ecological range, occurring from the Arctic to the tropical zones, in tundra, marshes and fens, (semi-natural) grasslands, shrubby vegetation, as well as in forests, from the boreal coniferous forest, temperate and thermophilic deciduous forest, to the tropical rain forest (Brandrud *et al.* 2023; Horak 2008; Horak 1980; Largent 1994; Noordeloos 1992, 2004; Noordeloos *et al.* 2022a; Noordeloos & Gates 2012). Within the genus, a wide range of trophic lifestyles can be encountered. Most commonly the species are supposedly saprotrophic, as litter or wood decomposers (Benucci *et al.* 2019; Holec 2008). Members of subgenus *Nolanea* (Fr.) P. Kummer (1871: 95) and subgenus *Cyanula* (Romagn.) Noordeloos (2012: 41), partly belonging to the so-called CHEGD species (Clavariaceae-Hygrocybe-Entoloma-Geoglossaceae-Dermoloma), do not behave as true saprotrophs, but might have a biotrophic or endophytic lifestyle (Halbwachs *et al.* 2018). A mycorrhizal lifestyle is reserved for the subgenus *Entoloma* (Fr.) P. Kummer (1871: 97) (Agerer & Waller 1993; Kasuya *et al.* 2010; Shishikura *et al.* 2021), while very few species have a parasitic lifestyle (Agerer & Waller 1993; Koch & Herr 2021; Xu *et al.* 2019). The CHEGD species as a whole might perform an important role as bioindicators for rare and vulnerable habitats (Arnolds 1992; Arnolds 1982; Jordal *et al.* 2016; Noordeloos *et al.* 2022b). Besides, species within this sensitive group are rather susceptible to human practices, being

readily disrupted if sufficiently pressed (Azul *et al.* 2011; Caboň *et al.* 2021). For these reasons, it is urgent to assess the diversity and ecological relevance of the genus before further habitat loss.

Within *Entoloma*, subgenus *Cyanula* stands out due to its captivating and distinctly colored basidiomata. It encompasses at least 200–300 species worldwide, with around 80–90 in Europe alone (Kibby 2023; Noordeloos *et al.* 2022a; Noordeloos *et al.* 2022c).

In this study we explored the karst massif of Serra de Sicó, a mountain range in West Portugal characterized by dense *Quercus faginea* Lamarck (1785: 725) forests and numerous water streams overlying a bedrock of limestones and dolomites (Cunha *et al.* 2020; Torres *et al.* 2011). This region is a known biodiversity hotspot when it comes to macrofungi but despite determined mycological efforts, many local species remain unidentified and potentially undescribed (Pereira 2015).

The objective of the present work is to add to the scientific knowledge by describing a new species within the subgenus *Cyanula* and to further characterize the mycobiota of the Sicó region. Using morphological and molecular study, we introduce the new species *Entoloma sicoense*, a pale bluish gray species inhabiting the broad-leaved forests of the western Iberian Peninsula and Macaronesia.

Material & Methods

Site description

The Serra de Sicó has a Mesomediterranean bioclimate, strongly influenced by both the Mediterranean and Atlantic climates. While the summers are characteristically hot, long, and dry, the winters on the other hand, are marked by significant rainfall and mild temperatures. The forests are dominated by *Quercus faginea*, *Arbutus unedo* Linné (1753: 395) and *Quercus coccinea* Linné (1753: 995) (Pereira 2015).

Field Work

The field surveys were conducted from November 2020 to December 2022. Two collections with numerous carpophores in different stages of maturation were made from different years. All macromorphological features were recorded from fresh basidiomata in each collection using a 5D Mark IV camera (Canon, Japan), equipped with a SP 1:2.5/90 mm objective (Tamron, Japan). Additionally, notes on ecology and organoleptic features were recorded. Processing of RAW image files was performed in RawTherapee (Horváth accessed 20 May 2023), while morphometry was carried in Fiji (Schindelin *et al.* 2012). The color codes are taken from Munsell (Munsell 1919) and the terminology follows Noordeloos (1992; 2004).

The fresh basidiomata were dried on a dehydrator at 40 °C (SilverCrest IAN 302447, Germany). Holotypes and paratypes were deposited in the PO Herbarium, at the Museum of Natural History of Porto University, Portugal.

Micromorphological Studies

The dehydrated specimens were hydrated with water before sectioning and examined under 5 % ammonium hydroxide (NH_4OH) and under Congo Red washed by NH_4OH . Microscopic features were studied using a BX50 BXFLA microscope (Olympus, Japan) coupled with a Axiocam 305 camera (Carl Zeiss, Germany), through FLUAR 40 \times /0.7 and UPlanFl 100 \times /1.30 oil objectives (Olympus, Japan).

The dimensions of all elements assessed are denoted as length \times width. The Q value is equivalent to the proportion of spore length to spore width, computed for each one of a total of 150 spores. The abbreviation av. and SD stand for 'average' and 'standard deviation', respectively.

Micrograph processing was done in Fiji (Schindelin *et al.* 2012) and CombineZP (Hadleys accessed 20 May 2023), while morphometry was carried out in Piximètre (Henriot & Cheype accessed 20 May 2023). Microscopic illustrations were drawn in Fiji (Schindelin *et al.* 2012) with the aid of a drawing tablet (Cadboy, NGS technologies, China).

DNA Sequencing

Total DNA was extracted from dried material in Eppendorf tubes containing sterilized glass beads and 600 µL of

CTAB buffer (CTAB 2 %, 1.4 M NaCl, 20 mM EDTA pH 8.0, 100 mM Tris-HCl pH 8.0). Samples were processed in the FastPrep-24 (MP Biomedicals, Inc.) lysis system. The mixture was incubated for 30 min at 65 °C, and then an equivalent volume of chloroform-isoamyl alcohol (24:1) was added. Samples were emulsified and centrifuged at 15,000 g for 5 min. and the upper phase transferred to a new tube. Next, DNA was precipitated with one volume of isopropanol and centrifuged for 20 min at 15,000 g at 4 °C.

Finally, the pellet was washed with cold 70 % ethanol (v/v), centrifuged again for 5 min., dried, and dissolved in ultrapurewater (50–100 µL). After dissolution, the quality and concentration of DNA were assessed by 1.5 % agarose electrophoresis. PCR reactions were performed using 20–50 ng of template genomic DNA, 2 × HS Mix (Bioline), and 500 nM each of the primers ITS1 and ITS4 for the ITS region (White *et al.* 1990), in a total volume of 15 µL. PCR conditions were: initial denaturation at 95 °C (2 min.), then 35 cycles of denaturation at 95 °C (30 s), annealing at 50 °C (30 s), elongation at 72 °C (2 min), and a final extension at 72 °C (10 min). The PCR products were checked on a 1 % agarose gel, and purified PCR amplicons were sequenced by STABVida (Portugal).

Phylogenetic analysis

Chromatograms were bidirectionally assembled and edited for ambiguities in MEGA X (Kumar *et al.* 2018). The remaining sequences completing the alignment were selected by BLASTing the previous against the GenBank and UNITE databases. The type sequences with high query cover and similarity (> 80 %, > 90 %, respectively) or from species of significant morphological relevance, were included in the alignment.

Additionally, we included all sequences belonging to the same UNITE 1 % species hypothesis (Nilsson *et al.* 2019) as the sequences produced in this study. The type sequence of *Entoloma incarnatofuscescens* (Britzelm.) Noordel. (1985: 461) (ON008496) was included in the alignment as an outgroup. All sequences used in this study are in Table 1. The alignment was made with MUSCLE in MEGA X (Kumar *et al.* 2018) and manually inspected for adjustments when necessary.

TABLE 1. Sequences used in this study. Vouchers in bold indicate type material. Under column 'Herbarium/source' the initials refer to herbaria according to Index Herbariorum, except when in italics (then referring to the isolation source).

UNITE classification	Country	Herbarium/ Source	Voucher/Sample	Sequence accession	Study reference
<i>E. caesiellum</i>	Austria	WU	25136	UDB0802175	(Krisai-Greilhuber <i>et al.</i> 2015)
<i>E. calceus</i>	Norway	O	F-259457	NR_182489	(Noordeloos <i>et al.</i> 2022c)
<i>E. cistocruentatum</i>	Spain	L	0607521	NR_182485	(Noordeloos <i>et al.</i> 2022c)
<i>E. consanguineum</i>	New Zealand	PDD	80751	MW775268	(Reschke <i>et al.</i> 2022)
<i>E. consanguineum</i>	New Zealand	PDD	112345	MW775252	Cooper&Park, unpubl.
<i>E. cyaneolilacinum</i>	Norway	O	F-252009	NR_176155	(Crous <i>et al.</i> 2021)
<i>E. cyanostipitum</i>	China	GDGM	31318	NR_154977	(He <i>et al.</i> 2017)
<i>E. exile</i>	Germany	?	Lueck8	KP965773	(Karich <i>et al.</i> 2015)
<i>E. exile</i>	UK	K	M157760	MF977951	Elsey, unpubl.
<i>E. incarnatofuscescens</i>	Germany	L	Dondl 2010-01	ON008496	(Noordeloos <i>et al.</i> 2022c)
<i>E. meridionale</i>	Greece	ACAM	2018-0151	NR_182477	(Lebeuf <i>et al.</i> 2022)
<i>E. mutabilipes</i>	Estonia	TUR	8788	LN850551	(Kokkonen 2015)
<i>E. mutabilipes</i>	Finland	TUR	610/12	LN850550	(Kokkonen 2015)
<i>E. nigrovelutinum</i>	Vietnam	LE	295077	MF898426	(Crous <i>et al.</i> 2017)
<i>E. olivaceomarginatum</i>	USA	PUL	00036174	ON561593	Russel, unpubl.
<i>E. palliodistriatum</i>	Spain	L	0607566	NR_177630	(Vila <i>et al.</i> 2021)
<i>E. perchalybeum</i>	Sweden	GB	0209474	NR_182490	(Noordeloos <i>et al.</i> 2022c)

.....continued on the next page

TABLE 1. (Continued)

UNITE classification	Country	Herbarium/ Source	Voucher/Sample	Sequence accession	Study reference
<i>E. poliopus</i>	Estonia	TUF	120259	UDB024650	Liiv, unpubl.
<i>E. pseudocoelestinum</i>	Germany	?	Lueck10	KP965774	(Karich <i>et al.</i> 2015)
<i>E. pseudocoelestinum</i>	UK	K	M132400	MF977966	Elsey, unpubl.
<i>E. pseudocruentatum</i>	Netherlands	L	0607915	MW934588	(Crous <i>et al.</i> 2021)
<i>E. rectangulum</i>	USA	SCL	SCL8524	KU574744	Gordon, unpubl.
<i>E. riparium</i>	Italy	L	0607563	NR_177632	(Vila <i>et al.</i> 2021)
<i>E. rivipollense</i>	Spain	L	0607585	NR_177634	(Vila <i>et al.</i> 2021)
<i>E. septentrionale</i>	Norway	O	F-254295	NR_174647	(Noordeloos <i>et al.</i> 2021)
<i>E. sicoense</i>	Portugal	PO	F2244	OR026624	this study
<i>E. sicoense</i>	Portugal	PO	F2252	OR026625	this study
<i>E. timidum</i>	Russia	LE	312480	MZ145197	(Dima <i>et al.</i> 2021)
<i>E. velutinum</i>	USA	TENN	070404	KY777376	Matheny <i>et al.</i> , unpubl.
<i>E. velutinum</i>	USA	TENN	070414	KY744172	(Alanbagi <i>et al.</i> 2019)
<i>Entoloma</i> sp.	Canada	soil	SG024 A12	KP889939	Guichon&Simard, unpubl.
<i>Entoloma</i> sp.	Portugal	soil	TUE003295	UDB05338481	(Tedersoo <i>et al.</i> 2014)
<i>Entoloma</i> sp.	Portugal	soil	TUE003295	UDB05338478	(Tedersoo <i>et al.</i> 2014)
<i>Entoloma</i> sp.	South Korea	KH	KA12-1295	KR673531	(Kim <i>et al.</i> 2015)
<i>Entoloma</i> sp.	USA	?	7	OM809180	Russel, unpubl.

The Tamura 3-parameter gamma model showed the lowest Bayesian information criterion score and was used for all three approaches: neighbor-joining (NJ), maximum likelihood (ML) using MEGA X (Kumar *et al.* 2018) and Bayesian inference (BI) using BEAST 2 (Bouckaert *et al.* 2014). For NJ and ML calculations, 10,000 bootstrap and 1,000 bootstrap replications (10 discrete categories) were used respectively. For BI, 10 discrete categories and the coalescent Bayesian skyline prior model were chosen to generate 100,000 trees from a 100 million length chain. From these, the last 75,000 trees were used to produce the final tree in FigTree 1.44 (Rambaut 2006–2018). The alignment and trees produced in study can be found in TreeBASE (study id TB2:S30312).

Results

Phylogeny

The tree in Figure 1 summarizes the relationship between the ITS sequences included in this study. In some cases, there were small discrepancies between the topologies of NJ, ML and BI, leading to low node support (*e.g.*, the position of *E. septentrionale* Noordel., Lorås, Eidissen & Dima (2021: 191) in relation to *E. consanguineum* E. Horak (2008: 191)).

However, for the purpose of this study, our tree demonstrates the unequivocal and well-supported placement of *E. sicoense* within subsection *Mutabilipedes* Dima & Noordel. (2022: 45), which in turn belongs to section *Poliopodes* Dima, Noordel., O.V. Morozova, Brandrud, & Reschke (2022: 45) (Fig. 1). As such, *E. sicoense* shows some affinity to *E. mutabilipes* Noordel. & Liiv (1992: 30) (=*E. caesiellum* Noordel. & Wölfel (1995: 185); see Noordeloos *et al.* 2022a) and a Canadian sequence (KP889939) from a likely undescribed species (Fig. 1). The differences between *E. sicoense* and *E. mutabilipes* amount to ~13.8 % or ~98 base pairs in the ITS region (see alignment in TB2:S30312).

The two *E. sicoense* sequences produced in this study sit well within UNITE's 0.5 % species hypothesis SH3797207.09FU, together with the environmental sequences UDB05338481 and UDB05338478, having a nearly identical ITS region and without any stable base pair differences (TB2:S30312).

subgen. *Cyanula*

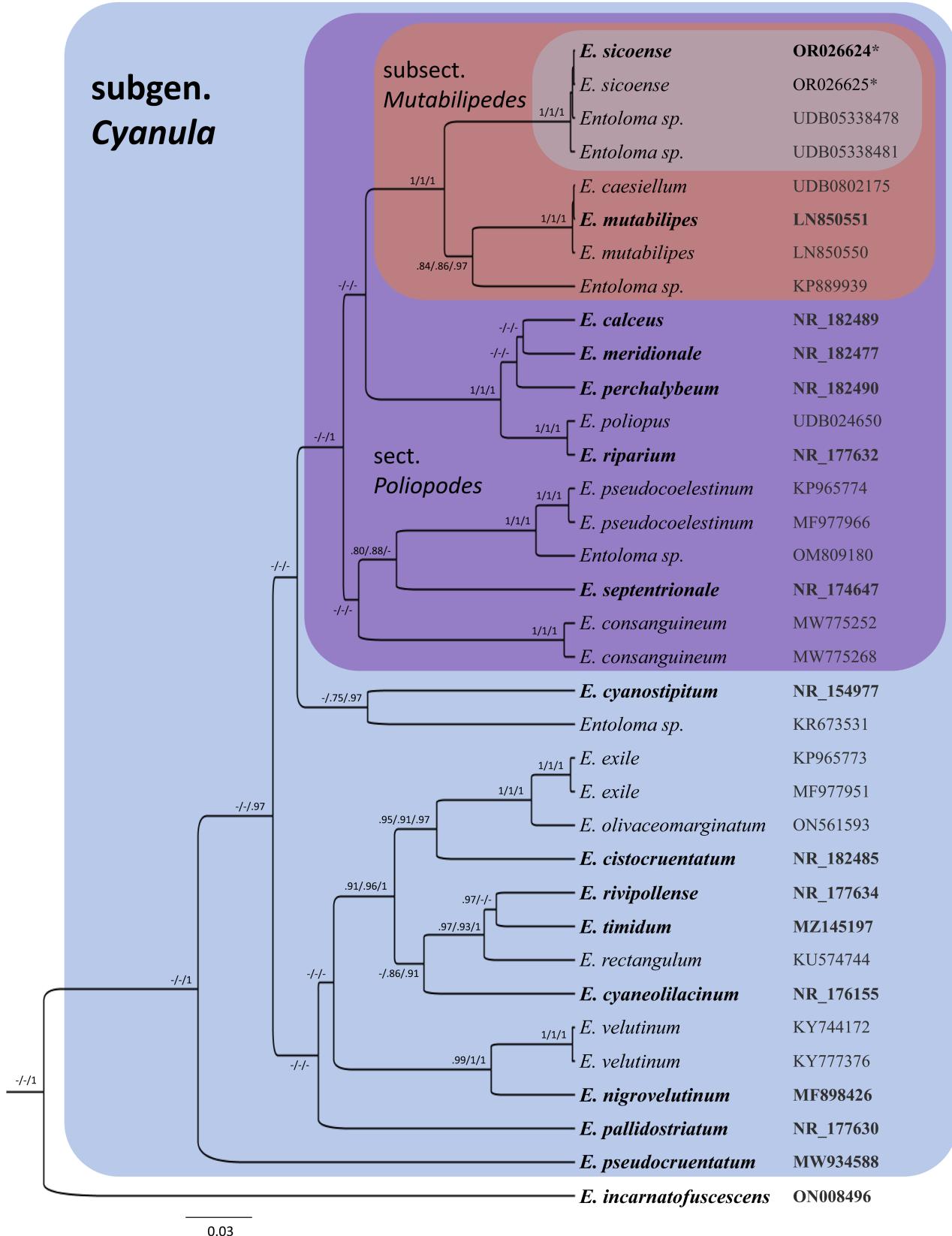


FIGURE 1. Phylogenetic tree built from ITS with topology derived from BI. The symbol # report node statistical support ($\geq 75\%$ for NJ bootstrap / $\geq 75\%$ for ML bootstrap / $\geq 90\%$ for BI posterior probability, respectively). Intraspecific ($\leq 0.5\%$ SH) node values are omitted. Type sequences are highlighted in boldface. Asterisks (*) symbolize the sequences produced in this study. Pale gray highlights the new species.

Taxonomy

Entoloma sicoense Fachada, Pedreiro, Raimundo, Noordel., Dima & Marques sp. nov. (Figs. 2, 3)
MycoBank: 848870

Diagnosis: *Entoloma sicoense* mostly produces slender basidiomata of a slate gray color, a concolorous smooth stipe, a sterile gill edge rich in brilliant granules and scattered intracellular blue pigment, which is often overtaken by brown pigment in maturation. It inhabits warm temperate broad-leaved forests. This combination of characters, together with the ITS region, sets it apart from other known *Entoloma* species.

Etymology: Refers to ‘Sicó’, the type locality.

Holotype:—PORTUGAL. Serra de Sicó, Ansião, Santiago da Guarda (WGS84 coordinates: 39.938305, -8.494221, elev. 254 m); 15 November 2020; on *Hypnum cupressiforme* Hedwig (1801: 291) covering calcareous rocks, in mixed dense forest composed mainly of *Arbutus unedo*, *Quercus faginea* and *Quercus coccinea*; plenty of *Ruscus aculeatus* Linné (1753: 1041) and *Smilax aspera* Linné (1753: 1028) also present, on alkaline soil; leg. *Vasco Fachada*. Holotype PO-F2244!; isotype priv. herb. V.F VF151120ES1!. GenBank ITS: OR026624.

Description:—*Basidiomata* mycenoid-collybioid. *Pileus* 10–40 mm convex soon expanding to plano-convex, later applanate, often eventually with wavy margin, with a depressed and somewhat umbilicate center, weakly hygrophanous, clearly translucently striate (often up to the center), frequently pale slate gray (Mu 2.5PB 7/2, 7/4, 6/4 to 2.5B 6/2) with faint dark violaceous tones (Mu 10PB 1/12) (Fig. 2a,b) less commonly dark brownish gray with violaceus brown tinges (10RP 4/2, 2/2) (Fig. 2e), almost always darker in the center, very finely fibrillose at the margin to subsquamulose, especially in the center (Fig. 2b). *Lamellae* L = 20–30, l = 1–5, adnate-emarginate or with short decurrent tooth, first whitish sometimes with soft blue tinge, soon becoming pinkish beige, edges mostly concolorous, sometimes marginated dark brownish blue, especially at maturity. *Stipe* 40–65 × 2–4 mm; relatively long and thin, slate gray with bluish tinge, usually rather pale, sometimes maturing to darker violaceus gray, rather concolorous with pileus, polished, sometimes lined dark blue to violaceus at the very apex where the decurrent gill meets the stipe as a continuation of the colored gill edges, base sometimes darker blue with white basal mycelium (Fig. 2c). *Context* concolorous or slightly paler than stipe surface. *Smell* pleasant and sweetish, *taste* not distinctive.

Basidiospores 8.4–12.5 × 5.3–8.7 µm (av. 9.0–10.8 × 6.5–7.4 µm, Q = 1.2–1.8, Qav = 1.3–1.6; with 5–7 (8) rather pronounced and sharp angles in profile view (Fig. 3d, f)). *Basidia* 20–32 × 7.5–13.5 µm), tetrasporic, claviform, clampless, hyaline but often pigmented light blue (Fig. 3c). *Lamella edge* mostly sterile but occasionally heterogeneous, consisting of clavate, often catenated (usually >1 septum) cheilocystidia, 27–100 × 8–14 µm, mostly with brown intracellular pigment (especially at maturation), rich in brilliant granules (Figs. 3a,f,g). *Hymenophoral trama* regular to subregular, made up of cylindrical hyphae, 3–13 µm wide, hyaline but often with very pale brown to light blue intracellular pigment (Fig. 3c). *Pileal trama* frequently with blue intracellular pigment. *Pileipellis* a cutis with transition to a trichoderm, composed of clavate to subglobose terminal elements, 40–90 × 10–30 µm, with variable intracellular pigment from blue (Fig. 3b) to strong brown at maturity. *Brilliant granules* common to abundant, especially in the cheilocystidia (Fig. 3e,g). *Clamp connections* not observed in any tissue.

Habitat and known distribution:—The two collections of *E. sicoense* were growing on mossy surfaces, covering large calcareous rocks and occasionally the soil (Fig. 4). This moss, *Hypnum cupressiforme*, is a species common to forests dominated by *A. unedo* and *Q. faginea* in Sicó and west mainland Portugal (Vieira et al. 2012).

Additional Portuguese records were found from environmental sequences (UDB05338481; UDB05338478) originating from the Madeira archipelago, in laurisilva forests dominated by *Laurus novocana-nariense* Rivas Mart., Lousã, Fern.Prieto, E.D'yas, J.C.Costa & C.Aguiar (2002: 703), *Clethra arborea* Aiton (1789: 73), *Picconia excelsa* (Aiton) Candolle. (1844: 288) together with the introduced *Quercus rubra* Linné (1753: 996).

To date, *E. sicoense* is only known from Portugal, ranging from the western Iberian Peninsula to southern Macaronesia.

Other material examined:—PORTUGAL. Serra de Sicó, Ansião, Santiago da Guarda (WGS84 coordinates: 39.939767, -8.492875, elev. 250 m); 03 Dec 2022; on *Hypnum cupressiforme* covering calcareous rocks, in mixed dense forest composed mainly of *Arbutus unedo*, *Quercus faginea* and *Quercus coccinea*; plenty of *Ruscus aculeatus* and *Smilax aspera* also present, on alkaline soil, exactly the same ecology as the holotype (Fig. 3d,f); leg. *Helder Pedreiro*. Paratype PO-F2252!; isoparatypic priv. herb. V.F VF031222EM1!. GenBank ITS: OR026625.



FIGURE 2. Macromorphology of *E. sicoense*. **a–c:** Basidiomata (holotype); **d–e:** Basidiomata (paratype). Photographs by Vasco Fachada.

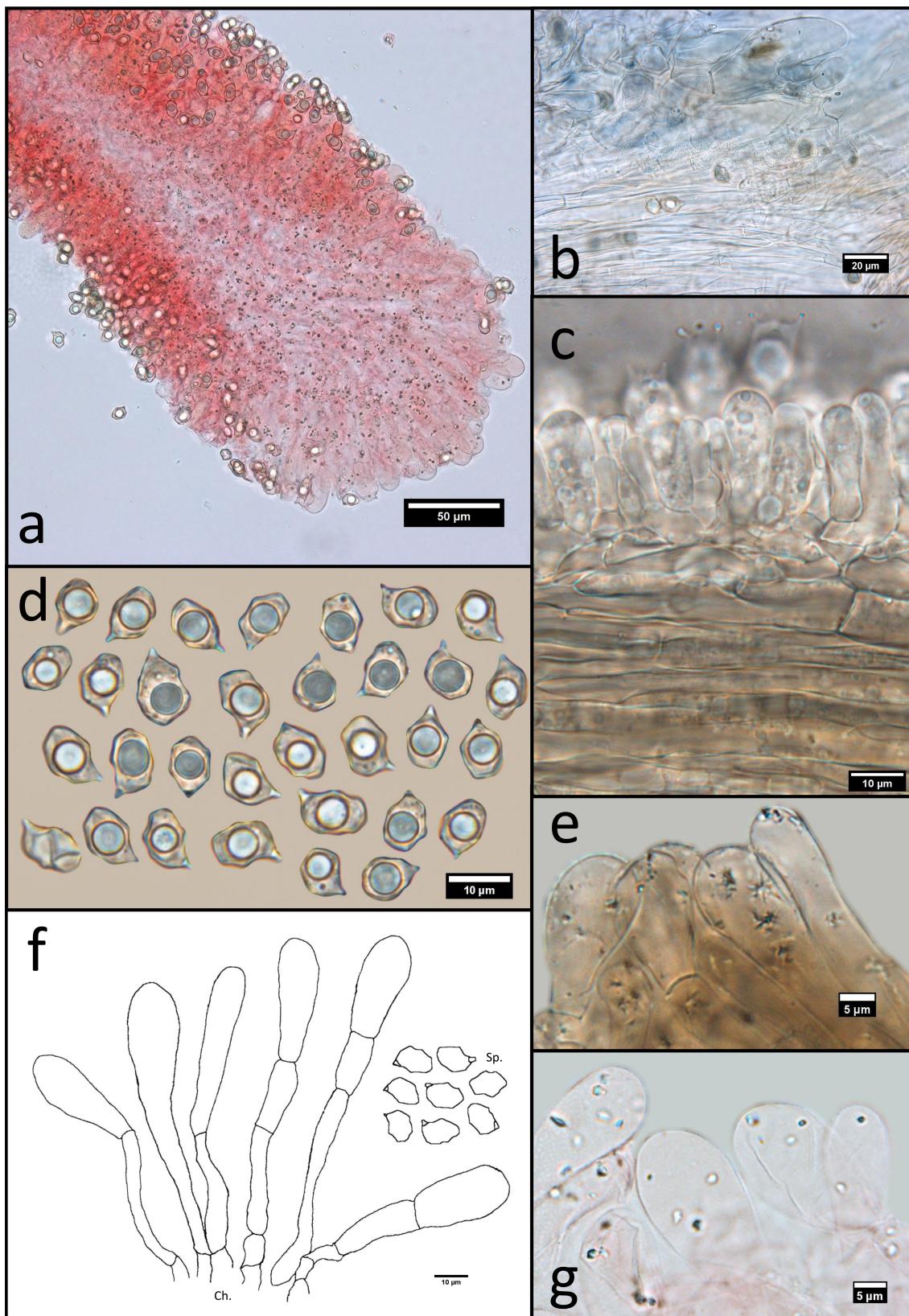


FIGURE 3. Micromorphology of *E. sicoense*. **a:** Lamellar cross-section near labial region under Congo Red, showing sterile edge (light pink) with abundant brilliant granules (holotype); **b:** Pileipellis radial section under NH_4OH , showing strong blue pigment in suprapellis of young basidiome (holotype); **c:** Mature lamellar pleura under NH_4OH , depicting unclamped hymenial cells and regular trama (paratype); **d:** Basidiospores under NH_4OH (paratype); **e:** Cheilocystidia from mature basidiome under NH_4OH , depicting crystal-like brilliant granules and strong brown pigment (paratype); **f:** Representative illustration of cheilocystidia (Ch.) and basidiospores (Sp.) (holotype); **g:** Cheilocystidia from young basidiome under Congo Red, depicting brilliant granules and weak brown pigment (holotype). Micrographs and microplate by Vasco Fachada.



FIGURE 4. Ecology of *E. sicoense*. **a:** Holotype collection site; **b:** Paratype collection site. Photographs by Helder Pedreiro.

Discussion

Entoloma sicoense has strong bootstrap and posterior probability support within subsection *Mutabilipedes* together with *E. mutabilipes* and is only the second species in this subsection known to date. Microscopically, the latter is nearly identical to *E. sicoense*, with comparable spore size, catenate cheilocystidia and abundance of brilliant granules. Nonetheless, *E. mutabilipes* may be macroscopically separated by the pinkish beige colors often present on the pileus and stipe surfaces. Furthermore, *E. mutabilipes* seems to prefer grassier subalpine and boreal forests (Brandrud *et al.* 2023; Kibby 2023; Noordeloos *et al.* 1995; Noordeloos & Liiv 1992), in contrast to the mossy and more Mediterranean–Macaronesian habitat of *E. sicoense*.

E. cyaneolilacinum Noordel., J.B. Jordal, Brandrud & Dima (2021: 449), *E. pseudocoelestinum* Arnolds (1982: 341) and the group of *E. cruentatum* (Quél.) Noordeloos (1984: 201), although phylogenetically distant, are reminiscent of *E. sicoense* in macromorphology. However, these species can be separated by their fertile lamellar edge (Crous *et al.* 2021; Noordeloos *et al.* 2022c).

E. pallidostriatum Vila, Noordel. & Dima (2021: 130), is also morphologically suggestive of species in subsect. *Mutabilipedes*, but it can be set apart by its poorly catenate cheilocystidia, somewhat thinner terminal elements in the pileipellis, apparent absence of brilliant granules, and phylogenetic distance (Vila *et al.* 2021).

Finally, less common darker forms of *E. sicoense* may bear some resemblance to *E. cyanulum* (Lasch) Noordel. (1984: 203) or *E. poliopus* (Romagn.) Noordel. (1979: 262). Yet, there are no mentions of brilliant granules in the cheilocystidia of these species, moreover, *E. cyanulum* has much longer spores (Noordeloos 1992, 2004).

Entoloma sicoense produced carpophores on thin layers of *Hypnum cupressiforme* covering solid rock, occasionally well above ground level (Fig. 4). This could suggest that this species' trophism is related to the moss.

The study of macrofungi in Serra de Sicó is an ongoing endeavor. Understanding the specific habitat preferences and potential functions of local species can provide valuable insights into the overall dynamics of ecosystems. Moreover, this knowledge may aid in the development of effective management strategies for biodiversity conservation.

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