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A morphological and phylogenetic characterisation of *Inocybe similis* (Agaricales, Inocybaceae), a rare species described by Bresadola in 1905

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Abstract

Inocybe similis, a very rare smooth-spored species originally described from Italy by Bresadola, is illustrated. Based on sequence generated from the type specimen, freshly collected specimens from five sites, Grado in north-east Italy, Tolmin in Slovenia, Forchach and Rieden in Austria and Füssen in Gemany could be asigned to *I. similis* and a more detailed description is provided here.

The macro- and micromorphological features of *I. similis* suggest this species should be placed in *Inocybe* sect. *Splendentes* according to Singer´s classification. In contrast, our phylogenetic analyses support instead that *I. similis* belongs to *Inocybe* sect. *Marginatae*. From a morphological point of view, *I. similis* is close to *I. vulpinella,* but it is phylogenetically close to *I. flavobrunnescens* in sect. *Marginatae*.

Keywords: *Agaricomycetes*, *Basidiomycota, Inocybaceae*, taxonomy

Introduction

Inocybe similis Bres. (1905:161) is a rare and poorly known smooth-spored species originally described by Bresadola from Trento, Italy, collected under *Populus nigra*. From a morphological point of view, according to Singer´s classification (Singer 1986) this species should be placed in *Inocybe* subgen. *Inocibium* (Earle) Sing. that encompasses species with thick-walled, crystalliferous pleurocystidia, sect. *Splendentes* Sing. (1953:229) that include species with spores not nodulose, spiny-stellate or angular, stipe all over pruinose or at least pruinose from the apex down beyond the middle of it, often with marginate bulb and if the cortina is visible, it connects the margin of the pileus with the base of the stipe. Kuyper in his revision of the genus *Inocybe* in Europe (1986) placed *I. similis* in subg. *Inocybe* supersection *Cortinatae* which includes taxa characterised by presence of cortina in young specimens and absence of caulocystidia or only present in upper 1/3rd of the stipe. Twenty-five years after the description of Bresadola, Hruby (1930) described a new species of *Inocybe* with nodulose-spored named *Inocybe similis* Hruby (1930:280), but it is an illegitimate name. The aims of this paper are: 1) to study the type collection of *I. similis*, 2) to describe in detail recent collections and show coloured iconography of fresh collections of it, 3) to yield phylogenetic analyses in order to phylogenetically place *I. similis* within *Inocybe* and 4) to compare it morphologically to close species.

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Materials and methods

Morphology

The macroscopic descriptions are based on fresh material. Terminology follows Kuyper (1986). The micromorphological characters are based on the study of fresh and dried material; dry specimens were rehydrated in distilled water before observation. An electric dryer was used to dry freshly collected specimens. To calculate spore statistics, 20 basidiospores were measured, each from one specimen of each collection studied. The basidiospore dimensions are indicated with the following notations: (a–) = minimum value, b = (average – standard deviation), c = average, d = (average + standard deviation), and (–e) = maximum value. Voucher specimens were deposited in the Herbarium, Museo di Storia Naturale di Venezia, Venice, Italy (MCVE) and Germany (priv. herb. of D. Bandini, [DB]).

DNA extraction, PCR amplification and sequencing

Genomic DNA was isolated from dry fragments of four freshly collected specimens using the CTAB procedure by Doyle & Doyle (1987), or DNA extraction method using NaOH employed by Dovana *et al.* (2017). The type specimen of *I. similis* was extracted following the PTB DNA extraction Protocol described by Stielow *et al.* (2013). Primers ITS1F or ITS5, and ITS4 were used for the amplification of nrITS region (White *et al.* 1990, Gardes & Bruns 1993). Sequences were assembled and edited in Geneious v. 8.1.2 (Kearse *et al.* 2012) and then submitted to GenBank. Accession numbers are provided in Table 1.

TABLE 1. Samples sequenced for the present study.

Species	**GenBank acc. number** (nrITS)	**Source and country**
Inocybe similis	MT704951	S14475 (**holotype)**, Trento, ITALY
Inocybe similis	KY848219	MCVE28976, Grado, ITALY
Inocybe similis	KY848217	MCVE29287, Grado, ITALY
Inocybe similis	KY848218	MCVE29100, Tolmin, SLOVENIA
Inocybe similis	MT504413	DB11-9-18-1, Forchach, AUSTRIA

Phylogenetic Analyses

The nrITS dataset was constructed based on results of BLASTn queries and sequences came mainly from Ryberg *et al.* (2008), Vauras and Kokkonen (2009), Osmundson *et al.* (2013), Esteve-Raventós *et al.* (2015), Vauras & Larsson (2015), Esteve-Raventós *et al.* (2016) and Bandini *et al.* (2019). Two sequences of *Inocybe vulpinella* Bruyl. (1970: 341) and two of *Inocybe inodora* Velen. (1920: 373) were added for comparison. *Inocybe mixtilis* (Britzelmayr 1885: 152) Saccardo (1887: 780) was used as outgroup following Esteve-Raventós *et al.* (2015). The alignment of every DNA region was carried out using MAFFT v 7.017 (Katoh & Toh 2008) with default conditions for gap openings and gap extension penalties. In nrITS alignment gaps and phylogenetically uninformative positions were removed using Gblocks v. 0.91b (Castresana 2000) with options for a less stringent selection. The best-fit substitution model for each alignment was estimated by the Bayesian Information Criterion (BIC) with MEGA X (Kumar *et al.* 2018). In nrITS dataset: HKY+G was selected as the best-fit model for ITS1, JC for 5.8S and T92+G was selected for the ITS2 region. The datasets were analysed using Bayesian inference (BI) and Maximum Likelihood (ML) criteria. The BI was performed with MrBayes v.3.2 (Ronquist *et al.* 2012) in the CIPRES server (Miller *et al.* 2010) with four incrementally heated simultaneous Monte Carlo Markov Chains (MCMC) run for 10 million generations, under the selected evolutionary models. Trees were sampled every 1000 generations, resulting in overall sampling of 10001 trees; the first 2500 trees were discarded as "burn-in" (25%). For the remaining trees, a majority rule consensus tree showing all compatible partitions was computed to obtain estimates for Bayesian Posterior Probabilities (BPP). ML analyses was conducted with RAxML v. 8.2.7 (Stamatakis 2014) with one thousand bootstrap replicates (MLB) (Felsenstein 1985) under GTR GAMMA with estimate of proportion of invariable sites for each partition. Pairwise % identity values (P%iv) of the sequences were calculated using Geneious v. 11.1.5 (Kearse *et al.* 2012).

Results

The ITS-rDNA dataset consisted of 56 sequences and a total of 496 characters (gaps included). Both Bayesian and Maximum Likelihood analyses produced the same topology; therefore, only the maximum likelihood tree with both MLB and BPP values is shown (Figs. 1). The phylogenetic position of *I. similis* is highlighted in Figs.1. In the ITS-rDNA analysis (Fig. 1), the five collections of *I. similis* with an environmental sequence from Canada (GenBank Accession number KC840624) (P%iv = 99.3) form a strongly supported clade (MLB = 99 and BPP=1) sister to *Inocybe flavobrunnescens* Esteve-Rav., G. Moreno & Bizio in Esteve-Raventós *et al.* (2015: 5), a species described in the *Inocybe* section *Marginatae* (Kühner 1933: 81). The P%iv between the nrITS sequences of *I. similis* and *I. flavobrunnescens* range from 88% to 89%.

Taxonomy

***Inocybe similis* Bres.**, Annales Mycologici 3 (2): 161 (1905)

Description based on nine collections (see Fig. 2,4,5) and the holotype (Fig. 3)

Description

Pileus 20–35 mm, initially campanulate or hemispherical, then convex, finally plano-convex, with broad and low central umbo, pileus surface woolly-fibrillose, opaque, dry, from extremely fine to coarsely squamulose often with quadrangular, fringed squamules or fibre bundles, at margin not rimulose and not striate, ochraceous, yellowish brown to cinnamon-brown, generally lighter at the disk in younger specimens thanks to the presence of a white-greyish veil strongly sticking to the cuticle. *Cortina* not observed. *Lamellae* moderately crowded, adnate to emarginate, pale cream to ochraceous when young, finally brown to brown-olivaceous, edge fimbriate, whitish.

Stipe 50–65 × 4–5 mm, central, firm, solid, generally inserted in the sandy substrate for about one-third of its length, equal to subbulbous at base, sometimes ending in a small napiform bulb, usually completely pruinose, sometimes somewhat sparsely in the lower part, probably due to abrasion through sand, sometimes longitudinally striate, when young whitish, often with the middle part ochraceous, then concolorous with pileus. *Context* fibrous, compact, whitish in the cap, whitish to yellowish in the stipe, smell absent.

Spores (10.5–)11.3–12.1–12.9(–14.5) × (6.0–)6.7– 7.2–7.6(–8.0) µm, Q =(1.40–)1.60–1.69–1.79(–1.98) (n = 180); smooth, regular to subphaseoliform, with a largely obtuse apex, but in several collections also subangular spores present. *Basidia* 30–45 × 10–17 µm, 4-spored. *Pleurocystidia* 45–108 × 14–28 µm (n = 105), subcylindrical, bulgy (sub)fusiform or clavate, not lageniform, with a short neck and short pedicel, thick-walled (2.5–3 µm), up to 5.5 µm in the apex, bright yellow in NH3, generally crystalliferous at apex. *Cheilocystidia* 50–60 × 17–25 µm (n = 105), similar to pleurocystidia. *Paracystidia* up to 30 × 15 µm, abundant, clavate to pyriform. *Caulocystidia* present along the whole length of the stipe in coll. MCVE28976, MCVE29287 and MCVE29100, descending to about half-way stipe in coll. DB11-9-18-1 and to at least 3/4th of the stipe in the holotype, solitary or mainly in clusters, similar to the pleurocystidia but with more irregular forms and dimensions; in the lower part just a few cauloparacystidia can be found. *Pileipellis* a cutis of 7–15 µm wide, cylindric hyphae, with pigment ochraceous, parietal and intracellular, sometimes with a slightly encrusting membranous pigment. Terminal elements clavate. *Clamp-connections* present at septa of hyphae.

Collections examined:—SLOVENIA. *Goriška,* Tolmin, close to the levee of Isonzo river, on alluvial sandy-gravelly soil, near *Populus tremula* and *Salix* sp.*,* 11 October 2008, E. Bizio *and* A. Aiardi, MCVE29100 (MCVE!).—ITALY, Trentino Alto Adige, Trento, place called "desert" by Bresadola, May 1900, G. Bresadola, Holotype F-S14475 (S!). Friuli Venezia Giulia, Grado, Municipal park consisting of a flat sand ground, in the presence of *Populus tremula* and *Pinus halepensis*, 13 July 2014, G. Ferisin, MCVE 28976 (MCVE!); ibidem, 1 May 2014, MCVE29287 (MCVE!).—AUSTRIA, Tirol, Reutte, Forchach, bank of river Lech, in sand and gravel, with Willow tree (*Salix* sp.), 11 September 2018, D. Bandini (DB11-9-18-1) (DB!); ibidem, in some distance to former location, *Salix* sp., 11 September 2018, leg./det. D. Bandini (DB11-9-18-4) (DB!); Tirol, Reutte, Rieden, Lechaue, ÖK25V 2215-West, alt. 870 m, *Salix* sp., *Pinus sylvestris*, 19 September 2018, leg. D. Bandini; det. D. Bandini & B. Oertel (DB19-9-18-23) (DB!).—GERMANY Bayern, Schwaben, Ostallgäu, Füssen, TK25 8430/1, alt. 820 m, shore of river Lech with *Salix*

sp., 22 September 2016, leg. D. Bandini; det. D. Bandini & B. Oertel (DB22-9-16-18) (DB!); ibidem, in some distance to former location, alt. 820 m, shore of river Lech with *Salix* sp., 12 October 2016, leg. D. Bandini; det. D. Bandini & B. Oertel (DB12-10-16-19) (DB!); ibidem, in some distance to former location, alt. 800 m, shore of river Lech with *Salix* sp., 20 September 2018, leg./det. D. Bandini (DB20-9-18-9) (DB!).

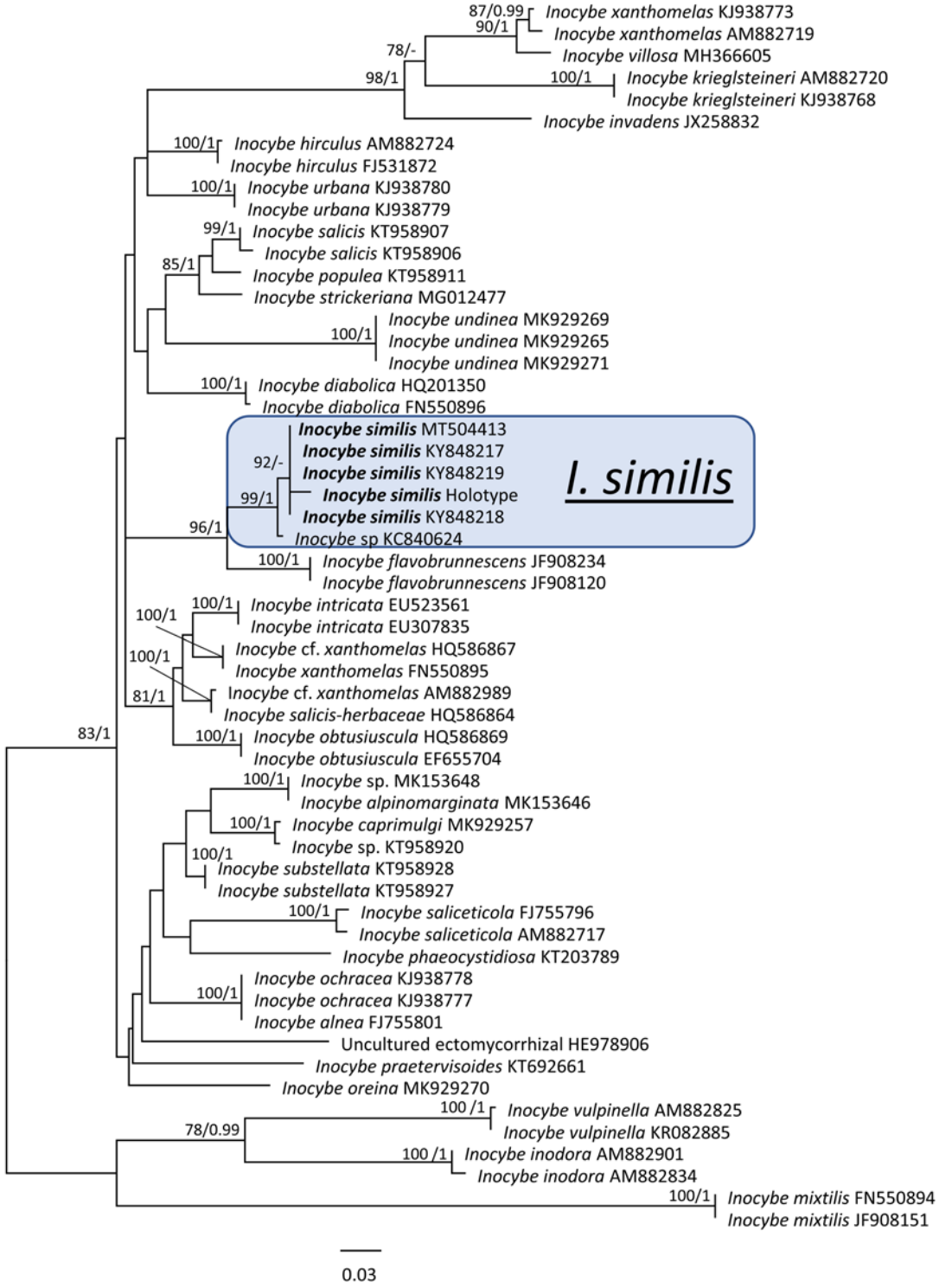

FIGURE 1. Best maximum likelihood (ML) tree produced by RAxML of the nrITS region from taxa closely related to *I. similis*. *I. mixtilis* was used as outgroup taxon. Support values (MLB ≥ 70 % / BPP ≥ 0.95) are given above branches. Newly generated sequences are in bold.

FIGURE 2. Macroscopic characters of *Inocybe similis*. **A-H** Fresh basidiomes *in situ*. **A** Coll. MCVE 28976. **B–D** Coll. MCVE29100. **E** Coll. DB11-9-18-1. **F** Coll. MCVE29100. **G** Coll. DB19-9-18-23. **H** Coll. DB20-9-18-0. Scale bars: 1 cm. Photos: **A–D** by G. Ferisin; **F** by E. Bizio; **E,G,H.** by D. Bandini.

FIGURE 3. *Inocybe similis*. **A** Holotype specimen (S-F14475). **B** Label of the holotype collection. Photos by F. Esteve-Raventós.

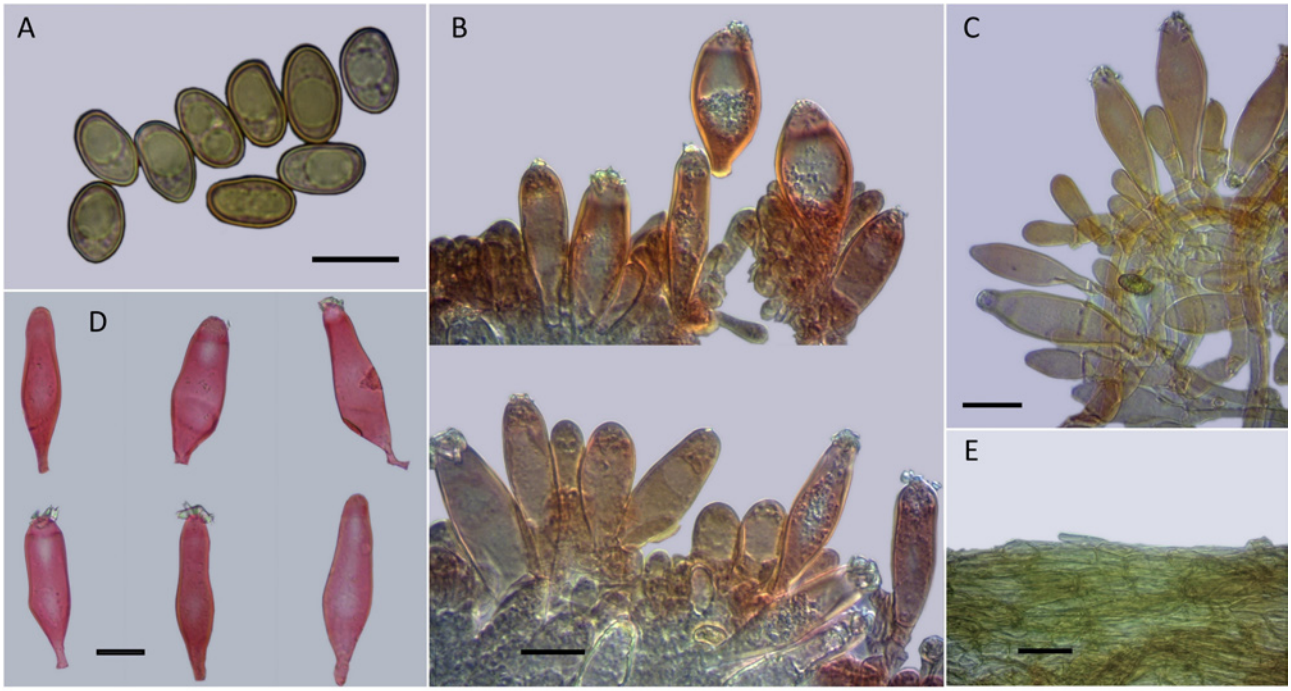

FIGURE 4. Microscopic characters of *I. similis* (MCVE 28976). **A** Basidiospores. **B** Cheilocystidia. **C** Caulocystidia. **D** Pleurocystidia. **E** Pileipellis. **A,C** in anionic Congo red. **B,D,E** in ammoniacal Congo red. Scale bars: **A** = 10 µm; **B-E**= 20 µm. Photos by G. Ferisin

Discussion

Despite the old holotype sample, the DNA extraction method used was able to provide an ITS sequence comprising 5.8s and ITS2 regions and partial ITS1. This result allowed to compare the sequence of the holotype with the other collections studied to confirm the morphological identification. Morphological data and phylogenetic analysis support recognition of *I. similis* as an independent species (Fig.1) in *Inocybe sensu stricto.* The phylogenetic analysis indicate that *I. similis* nests in section *Marginatae* together with nodulose-spored species. *Inocybe similis* shares with other species in *Inocybe* sect. *Marginatae* a more or less bulbous stipe and a pruinose stipe due to the presence of caulocystidia covering all or most of its surface (Esteve-Raventós *et al.* 2015), but it differs clearly from typical species in the section because of the presence of mostly smooth spores (though some spores may show a nearly imperceptible angular outline, especially at the apex), as for instance *I. diabolica* Vauras (1994: 122) that belongs also to the same clade (Fig.1). These results agree with other previous studies (Matheny *et al.* 2002, Matheny 2005, Ryberg *et al.* 2010) that showed the polyphyly of species with gibbous spores. *Inocybe similis* is morphologically characterised by:

(i) basidiomes small to medium in size, (ii) pileus ochraceus to cinnamon-brown, tomentose to squamulose surface, often with quadrangular squamules, generally with gray velipellis present on the disc and receding at the margin, (iii) stipe first whitish, then concolorous with pileus, with a small bulb, (iv) without distinct smell, (v) large spores mostly subphaseoliform, often with supra-apicular concavity, (vi) cystidia robust, variable in shape, with a short neck and big crystals, (vii) caulocystidia along the whole stipe or only along upper half. Our Italian collection of *I. similis* have been found on sandy ground in Grado, under *Pinus halepensis* and *Populus tremula,* while the one from Slovenia was collected by the shore of the river Soca in Tolmin in a gravelly-sandy area with constant presence of *Populus* spp. The Austrian and German collections were found on the bank of river Lech, in sand and gravel under *Salix* spp. A environmental sequence from Canada (KC840624) is 99% similar to our specimens of *I. similis*, and despite being associated with *Picea glauca*, represents probably the same species. According to this, *I. similis* could be a species with Holarctic-temperate distribution able to form mycorrhizal associations with Salicaceae and Pinaceae. According to Kuyper (1986) *I. similis* can also be associated with *Dryas octopetala* in the alpine zone, but this result is not supported by molecular analysis.

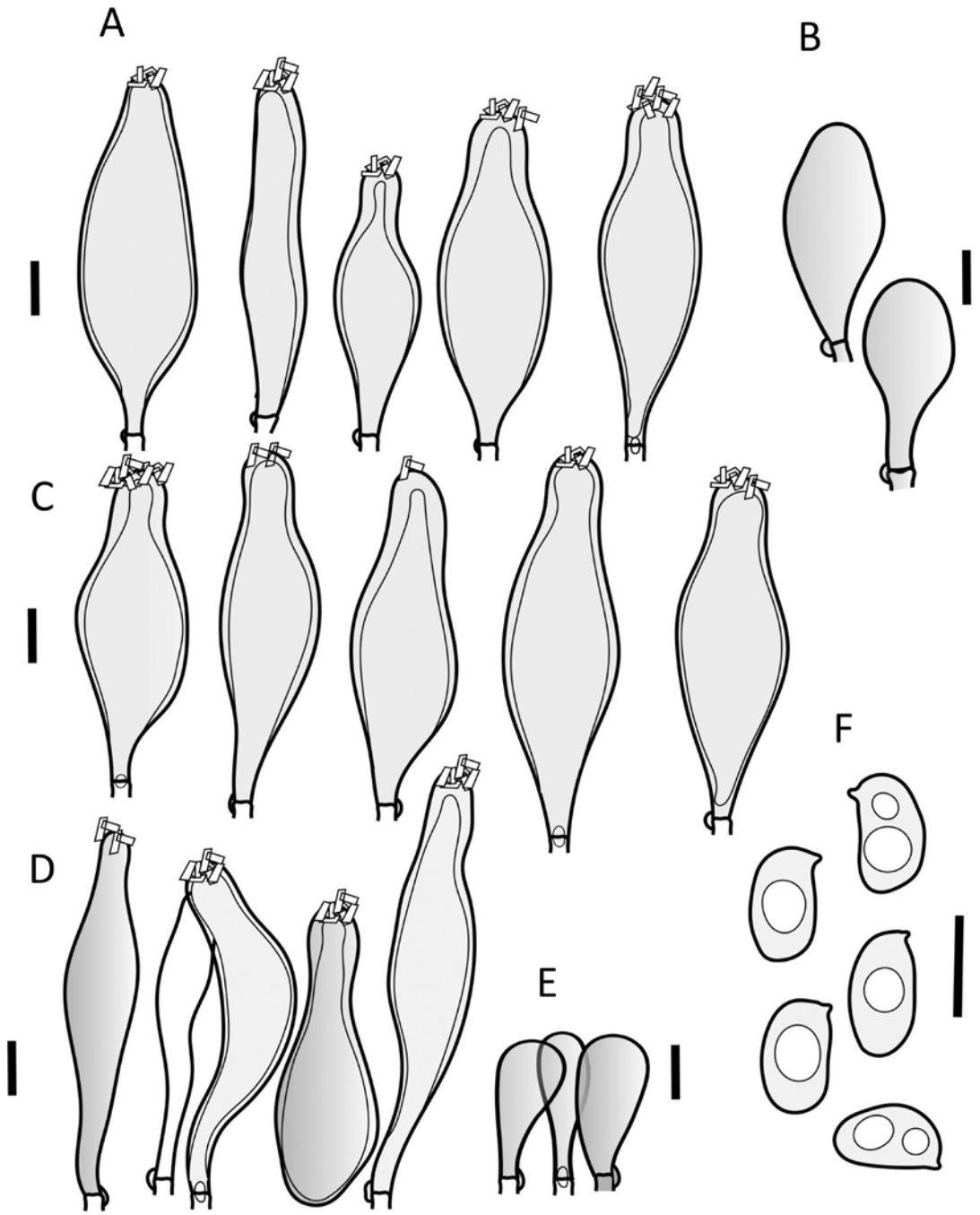

FIGURE 5. Microscopic characters of *I. similis*. (Holotype) **A**. Cheilocystidia **B.**. Paracystidia **C.** Pleurocystidia. **D.** Caulocystidia. **E.** Paracaulocystidia. **F.** Basidiospores. Scale bars: 10 μm.

After Bresadola described *I. similis* in 1905, very little information of it have become available. In 1978, Huijsman studied the holotype of *I. similis* and added a collection from the Netherlands. He summarised the diagnostic characteristics of *I. similis* as: large and phaseoliform spores, cystidia without distinct neck, pileus with quadrangular squamulae and bulbous stipe devoid of cystidia on its lower half. Kuyper (1986) described in his monograph macromorphological features of *I. similis* following Huijsman´s (1978) description. Even though Bresadola and Huijsman didn't mention the presence of a cortina, Kuyper placed *I. similis* in *Inocybe* subgen. *Inocybe*, Supersection *Cortinatae*. Probably following Kuyper (1986), Stangl (1989) included also *I. similis* in Supersection *Cortinatae*. Our observations did not confirm the presence of a cortina, and in contrast with Huijsman´s observations, we observed that caulocystidia are not restricted to the upper part of stipe.

Inocybe vulpinella is morphologically very similar to *I. similis* but differs by larger spores (11.5–)12.0–18.0(–18.5) × 7.0–9.0(–9.5) µm subapplanate towards apex, pleurocystidia with different shape and with thicker walls (Kuyper 1986). Also the quadrangular squamules on the pileus are missing. *Inocybe flavobrunnescens*, the sister species of *I. similis* in nrITS phylogenetic analysis (fig. 1), differs from it mainly by the cap with an opaque velvety cuticle, sometimes with small gold yellow scales and with a concentrically arranged fragile veil, thin lageniform caulocystidia and gibbous spores (Esteve-Raventós *et al.* 2015). In conclusion, even if *I. similis* ressembles morphologically *I. vulpinella*, genetically it has a particular affinity with a group of species that, according to Bon (1998), are included in the section *Marginatae* subsection *Praetervisae* Bon (1998: 10). *Inocybe similis* has in common with the species included in the subsection *Praetervisae* the colour of the stipe of the young basidiomes, ranging from white to chamois or yellowish and has never reddish colours, but it differs mainly for the generally smooth and not nodulous-gibbous spores.

Further research is necessary to seek for additional shared characteristics within this group.

Acknowledgments

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References

Bandini, D., Oertel, B., Moreau, P-A., Thines, M. & Ploch, S. (2019) Three new hygrophilous species of *Inocybe*, subgenus *Inocybe*. *Mycological Progress* 18: 1101–1119.
https://doi.org/10.1007/s11557-019-01509-y

Bon, M. (1998) Clé monographique du genre *Inocybe* (Fr.) Fr. (3ème partie: espèces gibbosporées = sous-genre Clypeus Britz., = Genre *Astrosporina* Schroet). *Doc Mycol* 28 (111): 1–45.

Bresadola, J. (1905) Hymenomycetes novi vel minus cogniti. *Annales Mycologici* 3 (2): 159–164.

Britzelmayr, M. (1885) Hymenomyceten aus Südbayern 4: *Cortinarius, Paxillus, Hygrophorus, Lactarius, Russula, Cantharellus, Marasmius, Lentinus, Panus, Trogia, Schizophyllum, Lenzites*. *Berichte des Naturhistorischen Vereins Augsburg* 28: 119–160.

Bruylants, J. (1970) *Inocybe vulpinella sp. nov. Bulletin de la Société Mycologique de France* 85: 340–344.

Castresana, J. (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17 (4): 540–552.
https://doi.org/10.1093/oxfordjournals.molbev.a026334

Dovana, F., Contu, M., Angeli, P., Brandi, A. & Mucciarelli, M. (2017) *Leucoagaricus ariminensis sp. nov.*, a lilac species from Italy. *Mycotaxon* 132: 205–216.
https://doi.org/10.5248/132.205

Doyle, J.J. & Doyle, J.L. (1987) A rapid DNA isolation procedure for small quantities of fresh leaf material. *Phytochem Bull* 19: 11–15.

Esteve-Raventós, F., Alvarado, P. & Olariaga, I. (2016) Unraveling the *Inocybe praetervisa* group through type studies and ITS data: *Inocybe praetervisoides sp. nov.* from the Mediterranean region. *Mycologia* 108 (1): 123–134.

https://doi.org/10.3852/15-053
Esteve-Raventós, F., Moreno, G., Bizio, E. & Alvarado, P. (2015) *Inocybe flavobrunnescens*, a new species in section *Marginatae*. *Mycological Progress* 14: 1–12.
https://doi.org/10.1007/s11557-015-1036-0
Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
https://doi.org/10.1111/j.1558-5646.1985.tb00420.x
Gardes, M. & Bruns, T.D. (1993) ITS primers with enhanced specificity for basidiomycetes–application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113–118.
https://doi.org/10.1111/j.1365-294X.1993.tb00005.x
Hruby, J. (1930) Beiträge zur Pilzflora Mahrens und Schlesiens. (Fortsetzung 1). *Hedwigia* 70: 234–358.
Huijsman, H.S.C. (1978) Notes on *Inocybe. Persoonia* 9 (4): 473–484.
Katoh, K. & Toh, H. (2008) Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* 9: 286–298.
https://doi.org/10.1093/bib/bbn013
Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentjies, P., & Drummond, A. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organisation and analysis of sequence data. *Bioinformatics* 28 (12): 1647–1649.
https://doi.org/10.1093/bioinformatics/bts199
Kühner, R. (1933) Notes sur le genre *Inocybe*: 1) Les Inocybes goniosporés (Fin). *Bulletin de la Société Mycologique de France* 49: 81–121.
https://doi.org/10.1080/00378941.1934.10833944
Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35: 1547–1549.
https://doi.org/10.1093/molbev/msy096
Kuyper, T.W. (1986) A revision of the genus *Inocybe* in Europe I. Subgenus Inosperma and the smooth-spored species of subgenus Inocybe. *Persoonia* 3 (Suppl.): 1–247.
Matheny, P.B. (2005) Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe;* Agaricales). *Molecular Phylogenetics and Evolution* 35 (1): 1–20.
https://doi.org/10.1016/j.ympev.2004.11.014
Matheny, P.B., Liu, Y.J., Ammirati, J.F. & Hall, B.D. (2002) Using RPB1sequences to improve phylogenetic inference among mushrooms(*Inocybe*, Agaricales). *American Journal of Botany* 89 (4): 688–698.
https://doi.org/10.3732/ajb.89.4.688
Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) "Creating the CIPRES Science Gateway for inference of large phylogenetic trees" in Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA pp. 1–8.
https://doi.org/10.1109/GCE.2010.5676129
Osmundson, T.W., Robert, V.A., Schoch, C.L., Baker, L.J., Smith, A., Robich G, Mizzan, L. & Garbelotto, M.M. (2013) Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. *PLoS ONE* 8 (4): E62419.
https://doi.org/10.1371/journal.pone.0062419
Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (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
Ryberg, M., Nilsson, R.H., Kristiansson, E., Topel, M., Jacobsson, S. & Larsson, E. (2008) Mining metadata from unidentified ITS sequences in GenBank: a case study in Inocybe (Basidiomycota). *BMC Evolutionary Biology* 8: 50.
https://doi.org/10.1186/1471-2148-8-50
Ryberg, M., Larsson, E. & Jacobsson, S. (2010) An evolutionary perspective on morphological and ecological characters in the mushroom family Inocybaceae. *Molecular Phylogenetics and Evolution* 55: 431–442.
https://doi.org/10.1016/j.ympev.2010.02.011
Saccardo, P.A. (1887) Sylloge Hymenomycetum, Vol. I. Agaricineae. *Sylloge Fungorum* 5: 1–1146.
Singer, R. (1953) The agarics of the Argentine sector of Tierra del Fuego and limitrophous regions of the Magallanes area. Part 2. The brown-spored genera (except *Cortinarius*). *Sydowia* 7 (1–4): 266–265.
Singer, R. (1986) *The Agaricales in modern taxonomy. 4th ed*. Koeltz scientific Books, Koenigstein, 977 pp.
Stamatakis, A. (2014) RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. *Bioinformatics* 30

(9): 1312–1313.
https://doi.org/10.1093/bioinformatics/btu033

Stangl, J. (1989) Die Gattung Inocybe in Bayern. – Hoppea, Denkschr. *Regensb. Bot. Ges.* 46: 5–388.

Stielow, B., Hensel, G., Strobelt, D., Makonde, H.M., Rohde, M., Dijksterhuis, J., Klenk, H.P. & Göker, M. (2013) Hoffmannoscypha, a novel genus of brightly coloured, cupulate Pyronemataceae closely related to *Tricharina* and *Geopora*. *Mycological Progress* 12: 675–686.
https://doi.org/10.1007/s11557-012-0875-1

Vauras, J. (1994) *Inocybe diabolica*, a new agaric from subarctic regions. *Mycologia Helvetica* 6 (2): 121–128.

Vauras, J. & Kokkonen, K. (2009) Finnish records on the genus *Inocybe*. The new species *Inocybe saliceticola*. *Karstenia* 48: 57–67.
https://doi.org/10.29203/ka.2009.429

Vauras, J. & Larsson, E. (2015) *Inocybe caprimulgi* and *I. lacunarum*, two new nodulose-spored species from Fennoscandia. *Karstenia* 55: 1–18.
https://doi.org/10.29203/ka.2015.465

Velenovský, J. (1920) *Ceské Houby II*. Ceské Botanické Společnosti, Prague, 224 pp.

White, T.J., Bruns, T., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In:* Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (Eds.) *PCR Protocols: a guide to methods and applications.* Academic Press, San Diego, California, pp. 315–322.
https://doi.org/10.1016/B978-0-12-372180-8.50042-1