Sowerbyella meridionalis (*Pezizales*), a new species from south-western Europe

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Abstract: *Sowerbyella meridionalis* is proposed as a new species from south-western Europe based on morphological and ecological studies. The spore size is similar to that of *Sowerbyella brevispora* Harmaja, from which it differs in spore ornamentation and its ecological features. Collections from western France, initially attributed to *S. brevispora*, are compared and also agree with this new species.
Keywords: *Ascomycota*, chorology, Mediterranean fungi, *Pyronemataceae*, taxonomy.

Resumen: En base a estudios morfológicos y ecológicos se propone *Sowerbyella meridionalis* como una nueva especie del sudoeste de Europa. Las dimensiones de las esporas son similares a las de *Sowerbyella brevispora* Harmaja, de la que se diferencia por la ornamentación esporal y por el hábitat meridional. Recolecciones del oeste de Francia, inicialmente atribuidas a *S. brevispora*, se corresponden también con esta nueva especie.
Palabras clave: *Ascomycota*, corología, hongos mediterráneos, *Pyronemataceae*, taxonomía.

Introduction

Sowerbyella Nannf. is a genus of ascomycetes that forms cupulate apothecia, almost discoid at extreme maturity, superficial, scattered, gregarious or caespitose, measuring up to 100 mm in diameter, stipitate or substipitate, with entire margins, rarely cleft, and not conspicuously hairy, with a smooth hymenophore of yellow, egg-yellow, ochraceous, brown or orange color, even with reddish hues and with a yellowish or ochraceous excipulum covered by an appressed and whitish tomentum. The stipes of the fruitbodies, very variable in length, are sometimes ribbed by mean of anastomosed ridges, covered by a whitish tomentum, and are usually buried in the substrate, so they can be easily broken when the ascomata are extracted from the soil.

From a microscopical point of view, the asci are inamyloid and the ascospores are ellipsoidal or subfusiform, contain 2 (-3) lipid bodies (LBs). They show a varied cyanophilic ornamentation consisting of a complete or incomplete reticulum, which sometimes forms deep alveoli, isolated warts or interconnected by ridges, grooves, or forming by more or less developed spines. The ectal excipulum is composed of a textura globulosa-angularis from which some more or less developed hyphoid hairs arise.

At present, the Index Fungorum database lists 16 species and 3 varieties. The species of this genus grow in both broad-leaved and coniferous forests, sometimes on ruderalised soils (Moravec, 1988a). They usually develop on plant remains (humus) of various trees (e.g. *Picea*, *Pinus*, *Cupressus*, *Fagus*, *Quercus*, *Fraxinus* and *Eucalyptus*). Many of them have ascospores ornamented by a well-formed reticulum, such as *Sowerbyella densireticulata* J. Moravec, *S. radiculata* (Sowerby) Nannf., *S. bauerana* (Cooke) Harmaja, a synonym of *S. radiculata* in the sense of Yao & Spooner (2006), *S. crassisculpturata* J. Moravec, *S. parvispora* (Trigaux) J. Moravec, *S. reguisii* (Quél.) J. Moravec or *S. rhenana* (Fuckel) J. Moravec. The spore ornamentation can also be formed by more or less anastomosed warts or ridges that can even form an incomplete reticulum, such as *Sowerbyella imperialis* (Peck) Korf (= *S. unicolor* (Gillet) Nannf.). In other species, the ornamentation consists of isolated warts, which can be fine (*Sowerbyella angustispora* J.Z. Cao & J. Moravec and *S. brevispora* Harmaja), more or less thick as in *S. fagicola* J. Moravec, very thick (*S. phlyctispora* (Lepr. & Mont.) Hohmeyer & J. Moravec) or spiny-pustulate (*S. polaripustulata* J. Moravec) [Moravec, 1985, 1986, 1988a, 1988b]. A species with smooth ascospores has also been described: *Sowerbyella laevispora* W.Y. Zhuang (Zhuang, 2009).

The genus is still taxonomically somewhat confused despite the studies of authors such as Moravec (1985, 1986, 1988a, 1988b), especially with regard to species with reticulate or subreticulate ascospores, because it is necessary to study fully mature ascospores to correctly evaluate such ornamentation, preferably obtained from a spore print.

In Spain, several species of *Sowerbyella* have been recorded, especially in mountain environments, such as *Sowerbyella fagicola* (Galán *et al.*, 2010; Ribes *et al.*, 2016; Rubio *et al.*, 2016), *S. imperialis* (Ribes *et al.*, 2016; Pancorbo *et al.*, 2017), *S. radiculata* (García Bona, 1991; Pérez-Butrón *et al.*, 2003; Rubio *et al.*, 2005, Calonge *et al.*, 2006), *S. rhenana* (Rocabruna & Tabarés, 2001; Becerra & Robles, 2011) and *S. reguisii* (Fernández & Undagoitia, 2005; Roqué & Pérez-de-Gregorio, 2011).

In this work, we describe three collections of a *Sowerbyella* morphologically close to *Sowerbyella brevispora* Harmaja, collected under *Cupressus* in Extremadura (in 2013 and 2021) and under *Pinus pinea*, *P. halepensis* and *Quercus ilex* in Catalonia (in 2010 and 2019). The Mediterranean climatic conditions and the habitat of these Spanish collections are significantly different from those of the type locality of *S. brevispora*, which was described in Finland under *Picea abies* (Harmaja, 1984), although Austrian collections under broad-leaved trees such as *Acer*, *Populus* and *Fraxinus* are cited (Klofac & Voglmayr, 2003). The existence of southern (or Mediterranean) species, analogous to similar to northern (or mountainous) species, is a fact verified among several discomycetes, for example, *Pseudoplectania ericae* Donadini vs. *Pseudoplectania nigrella* (Pers.) Fuckel, *Urnula mediterranea* (M. Carbone, Agnello & Baglivo) M. Carbone, Agnello & P. Alvarado vs. *Urnula craterium* (Schwein.) Fr. or *Legaliana (Peziza) badiofuscoides* (Donadini) Van Vooren vs. *Galactinia saniosa* (Schrad.) Sacc. We, therefore, felt it was important to compare our southern collections with the more northern specimens of *S. brevispora*, which has led us to propose *Sowerbyella meridionalis* as a new species.

Material and methods

Morphological study. — All specimens of *Sowerbyella meridionalis* have been studied fresh to avoid the loss or alteration of their vital characteristics although it has also been necessary to use non-vital agents such as Melzer's reagent or lactophenol blue for the study of the ascus tips and spore ornamentation. For the study of the holotype of *S. brevispora* and the French specimens determined under this name, it has been necessary to rehydrate them with the usual procedures. Scanning electron microscopy photographs of the spore ornamentation were taken with a Hitachi S-4100 microscope from the Serveis Tècnics de Recerca de la Universitat de Girona.

DNA extraction, amplification and sequencing. — Total DNA was extracted from dry specimens employing a modified protocol based on Murray & Thompson (1980). PCR reactions (Mullis & Faloona,

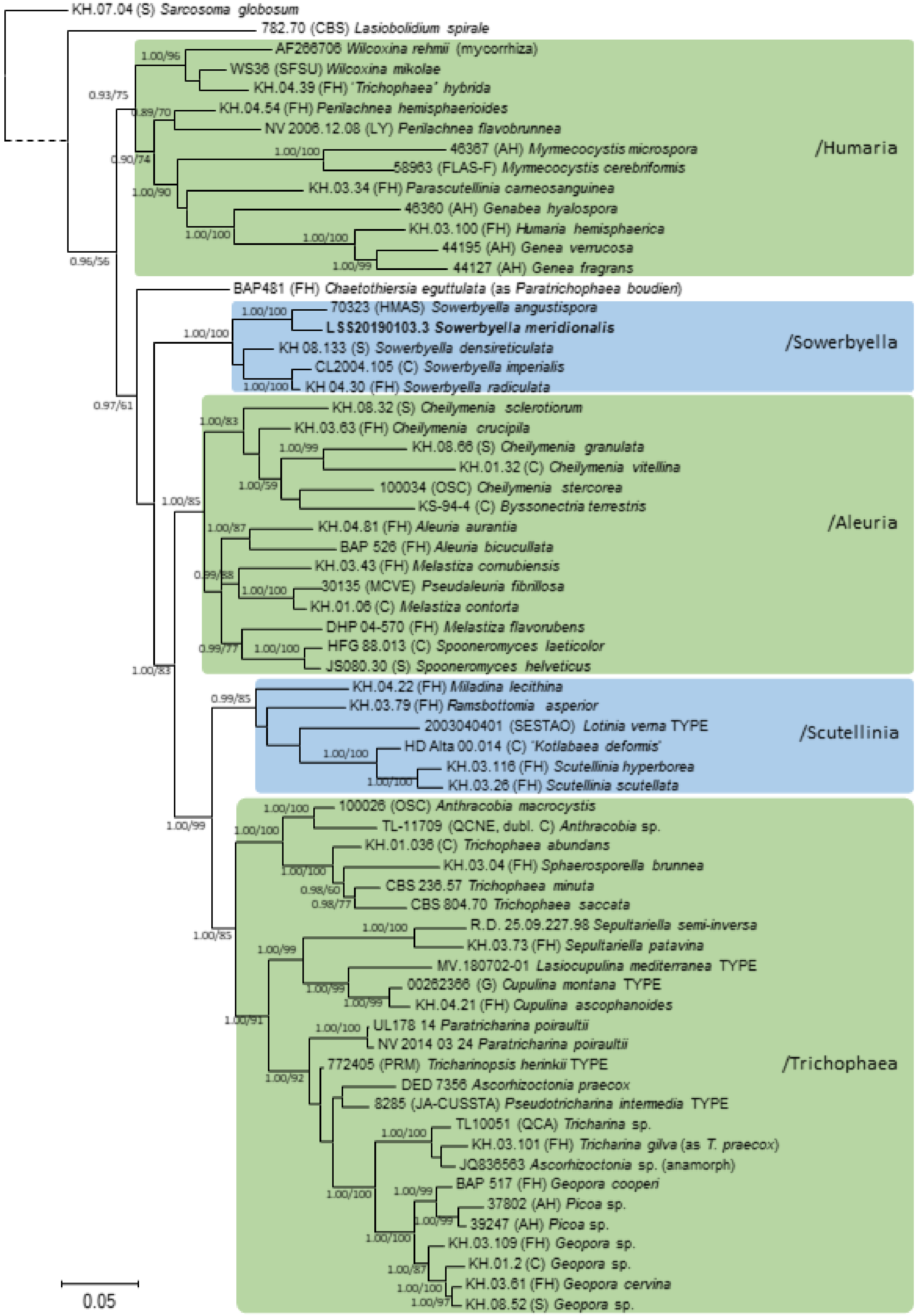

Plate 1 – 50% majority rule 28S rDNA- tef1- rpb2 consensus phylogram of the family *Pyronemataceae* (with *Sarcosoma globosum* from family *Sarcosomataceae* as outgroup) obtained using MrBayes from 2325 sampled trees. Nodes were annotated if they were supported by ≥ 0.95 Bayesian posterior probability (left) or ≥ 70% maximum likelihood bootstrap proportions (right). P. Alvarado (ALVALAB).

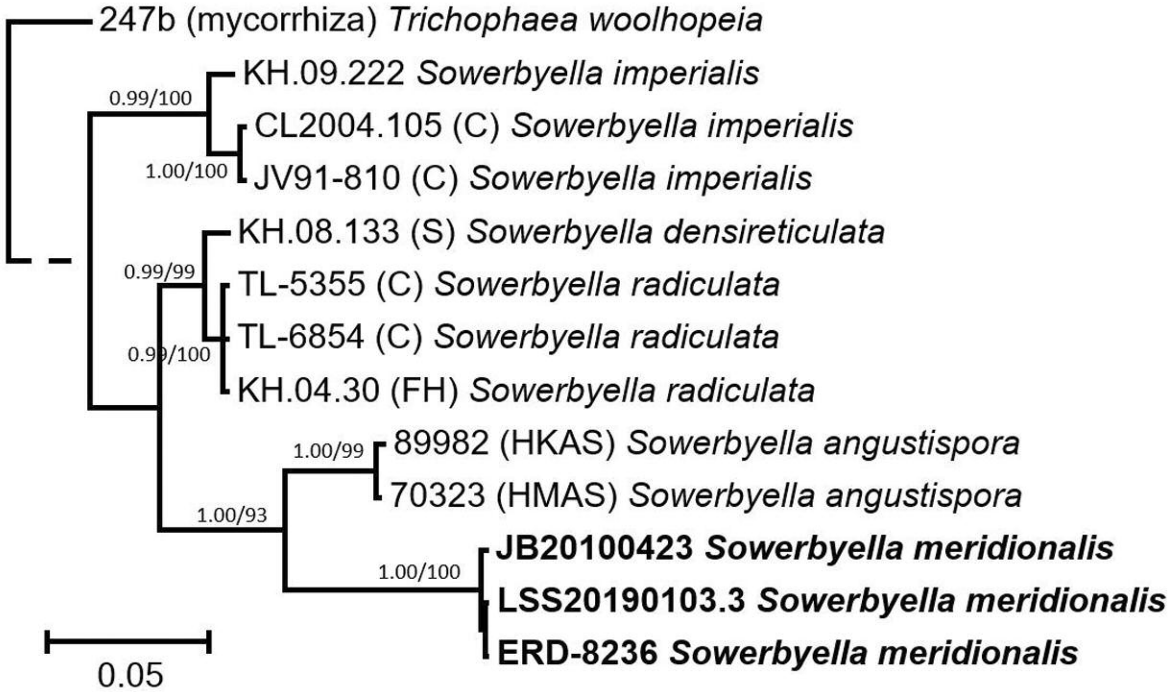

Plate 2 – 50% majority rule ITS-28S rDNA consensus phylogram of the genus *Sowerbyella* (with *Trichophaea woolhopeia* as outgroup) obtained using MrBayes from 30 sampled trees. Nodes were annotated if they were supported by ≥ 0.95 Bayesian posterior probability (left) or ≥ 70% maximum likelihood bootstrap proportions (right). P. Alvarado (ALVALAB).

1987) included 35 cycles with an annealing temperature of 54ºC. Primers ITS1F and ITS4 (White *et al.*, 1990; Gardes & Bruns, 1993) were employed to amplify the ITS rDNA region (ITS), while LR0R and LR5 (Vilgalys & Hester, 1990; Cubeta *et al*., 1991) were used for the 28S rDNA region (LSU), EF1-728F, EF1-983F and EF1- 2218R (Carbone & Kohn, 1999; Rehner & Buckley, 2005) for the translation elongation factor 1a (tef1) gene, as well as bRPB2-6F2 (reverse of bRPB2-6R2), and bRPB2-7R2 for the RNA polymerase II second largest subunit (rpb2) gene (Matheny *et al.*, 2007). PCR products were checked in 1% agarose gels, and positive reactions were sequenced with one or both PCR primers. Chromatograms were checked searching for putative reading errors, and these were corrected.

Unfortunately, due to failures in the PCR, it has been impossible to obtain genetic sequences for both the holotype and a topotype of *Sowerbyella brevispora*.

Phylogenetic analyses. — Two independent datasets were built: 1) a combined dataset of 28S rDNA, tef1 and rpb2 sequence from samples of several clades of the family *Pyronemataceae* related to genus *Sowerbyella*, using *Sarcosoma globosum* (*Sarcosomataceae*) as outgroup, and 2) another dataset combining ITS and 28S rDNA data from species of *Sowerbyella*, using *Trichophaea woolhopeia* as outgroup. BLAST (Altschul *et al*., 1990) was used to select the most closely related sequences from the International Nucleotide Sequence Database Collaboration (INSDC, Cochrane *et al*., 2011) public database. Sequences came mainly from Hansen & Pfister (2006), Perry *et al.* (2007), Hansen *et al.* (2013), Van Vooren *et al*. (2017), Alvarado *et al.* (2018) and Lindemann *et al.* (2019). Sequences first were aligned in MEGA 5.0 (Tamura *et al*., 2011) software with its Clustal W application and then corrected manually. Introns were excluded from tef1 and rpb2 datasets. The final alignment employed for the analysis of *Pyronemataceae* included 327/760 (LSU), 311/865 (tef1), and 299/589 (rpb2) variable/total sites. The final alignment employed for the analysis of *Sowerbyella* included 202/489 (ITS) and 135/756 (LSU) variable/total sites. The aligned loci were loaded in MrBayes 3.2.6 (Ronquist *et al*., 2012), where a Bayesian analysis was performed (data partitioned into different genes, GTR+G+I model, two simultaneous runs, four chains, temperature set to 0.2, sampling every 100th generation) until convergence parameters were met after 0.31 M (*Pyronemataceae*) and 0.04 M (*Sowerbyella*) generations, Standard deviation having fell below 0.01. Finally, a full search for the best-scoring maximum likelihood tree was performed in RAxML 8.2.12 (Stamatakis, 2014) using the standard search algorithm (data partitioned, GTRCAT (*Pyronemataceae*) or GTRGAMMA (*Sowerbyella*) model, 2000 bootstrap replications). Significance threshold was set above 0.95 for posterior probability (PP) and 70% bootstrap proportions (BP).

Taxonomy

Sowerbyella meridionalis E. Rubio, L. Sánchez, J. Bometón & C. Roqué, *sp. nov.* – MB 839027 – Pl. 3–9.

Diagnosis: Differs morphologically from *Sowerbyella brevispora* Harmaja mainly by the spore ornamentation formed by short interconnecting ridges rather than isolated obtuse warts, and by a Mediterranean ecology.

Holotype: Coll. LSS20190103-3.

Etymology: from Latin *meridionalis*, meaning “coming from” or “related to” the south.

Description: Ascomata gregarious, always in small numbers. **Apothecia** superficial, differentiated into a more or less deeply dome-shaped hymenophore, smooth or sometimes deeply umbilicate, (13.0–)18.0–20.0(–45.0) mm in diameter, mustard yellow, orange-yellow, more or less bright depending on its age (SYR6/12 or SYR7/12 of the Munsell color chart) and its hydration state. **Stipe** of the same color, up to 50 × 2(–5) mm, coarsely tomentose, whitish, subequal, sometimes anfractuous, widened or attenuated towards a deeply rooting base. The external surface of the apothecia is the same color as the whole, and much felted or finely pubescent. **Margin** undifferentiated, glabrous, usually not split, turning brown in the old specimens. **Context** pale yellowish, very scanty, without remarkable characteristics.

Plate 3 – *Sowerbyella meridionalis* (*holotypus*). Ascomata *in situ*. Photo L. Sánchez.

Hymenophore ca. 200-250 µm wide, composed of cylindrical **asci**, 172–210–240 × 8–9 µm, operculate, 8-spored, inamyloid, with the base arising from croziers, containing ellipsoidal, hyaline, biguttulate **ascospores**, with obtuse poles, (9.5–)10.5(–12.0) × (5.5–)6.0 (–6.5) µm, Q = (1.6–)1.7(–2.0), ornamented by very fine, obtuse, cyanophilic warts, 0.8–1 µm in height and 0.7–1 µm wide, which usually establish connections with short ridges, 10–35 µm in length, but never create a complete reticulum, although sometimes they can appear to form a very incomplete one. **Paraphyses** filiform, 1.5–2.0 µm wide, with the distal segments usually straight, slightly inflated up to 3–5 µm wide, filled with droplets of yellowish carotenoid pigment, becoming greenish in iodine. **Subhymenium** poorly differentiated, 35–40 µm thick, composed of a tight *textura globulosa-angularis* made of vesicular or polyhedral hyphal elements, 5–12 µm in diameter, without encrusting parietal pigment. **Medullar excipulum** 380–400 µm thick, composed of a loose *textura intricata* made of cylindrical hyphae, 5–11 µm in diameter, rarely inflated, with walls encrusted by a yellowish or yellowish-green pigment. **Ectal excipulum** comparatively thin, 50–75 µm thick, composed of a *textura globulosa-angularis* made of rounded, vesicular or more or less polyhedral cells, 9–25 µm in diameter. Numerous hyaline **hyphoid hairs** arise from vesicular cells of the ectal excipulum, 20–170 × 3.0–6.0 µm, septate, straight or wavy, with obtuse apices and walls up to 1 µm thick.

Studied collections: Spain. Barcelona, Dosrius (Canyamars), Can Rupit/Torrent de Rupit, 41° 36′ 40″ N 2° 29′ 10″ E, alt. 370 m, on siliceous soil (granite) and mediterranean environment, under *Pinus pinea* and *Quercus ilex*, 3 January 2019, *leg*. L. Sánchez, herb. LSS20190103-3; GenBank ITS MT741968, LSU MT741965, TEF1 MT741957 and RPB2 MT741958. Barcelona, Terrassa, Can Casanoves, 41° 32′ 18″ N 2° 1′ 39″ E, alt. 228 m, on siliceous soil (sandstone and clay) and mediterranean environment, under *Pinus halepensis* and *Quercus ilex*, 23 April 2010, *leg*. J. Bometón, herb. JB 20100423; GenBank ITS MT741969, LSU MT741966. Cáceres, Casas de Miravete, 39° 43′ 55″ N 5° 45′ 19″ W, alt. 451 m, on siliceous soil (slate and quartzite) under *Cupressus* sp., 30 November 2012, *leg*. C. Gelpi, J.A. Suárez & J. Muñoz, herb. ERD-5805. *Ibidem*, 27 February 2021, *leg*. J.A. Suárez, herb. ERD-8752. France. Côtes-d'Armor, Pleumeur-Bodou, Manoir de la Lande, chez Mme Paul à l'Ile-Grande, 5 March 1994, on siliceous soil (granite), in the litter of *Cupressus macrocarpa*, *leg*. Daniel Réaudin, herb. J.-P. Priou 10008, duplicate ERD-8235. *Ibidem*, 4 February 2020, herb. ERD-8236: GenBank ITS MT741970, LSU MT741967.

Additional studied collections: *Sowerbyella brevispora*: Finland, Etelä Häme, Hämeenlinna Lammi, Hauliala, south of Lamminjärvi, 8 September 1981, *leg*. K. Karttunen, H6010689 (holotype, Museum Botanicum Universitatis, Helsinki). *Ibidem*, 16 September 1981, *leg.* H. Harmaja & M. Olanen, H6075334 (topotype, Museum Botanicum Universitatis, Helsinki).

Discussion

Ascospores of our collections, stained with lactophenol blue, appear very similar in morphology and dimensions to those of *Sowerbyella brevispora*, of 9.0–12 × 5.0–6.5 µm (Harmaja, 1984), but the type of ornamentation is quite different and formed by small obtuse and isolated warts in this species, while it is formed by more or less long interconnected ridges in *S. meridionalis*. The scanning electron microscope also confirmed what we already recognized under the optical microscope: the spore ornamentation of our three collections of *Sowerbyella meridionalis* is formed by the same pattern of dense warts forming anastomosed ridges, very different from the spore ornamentation of the holotype of *Sowerbyella brevispora*, consisting of obtuse warts up to 0.3 µm in height and 0.2–0.4 µm wide,

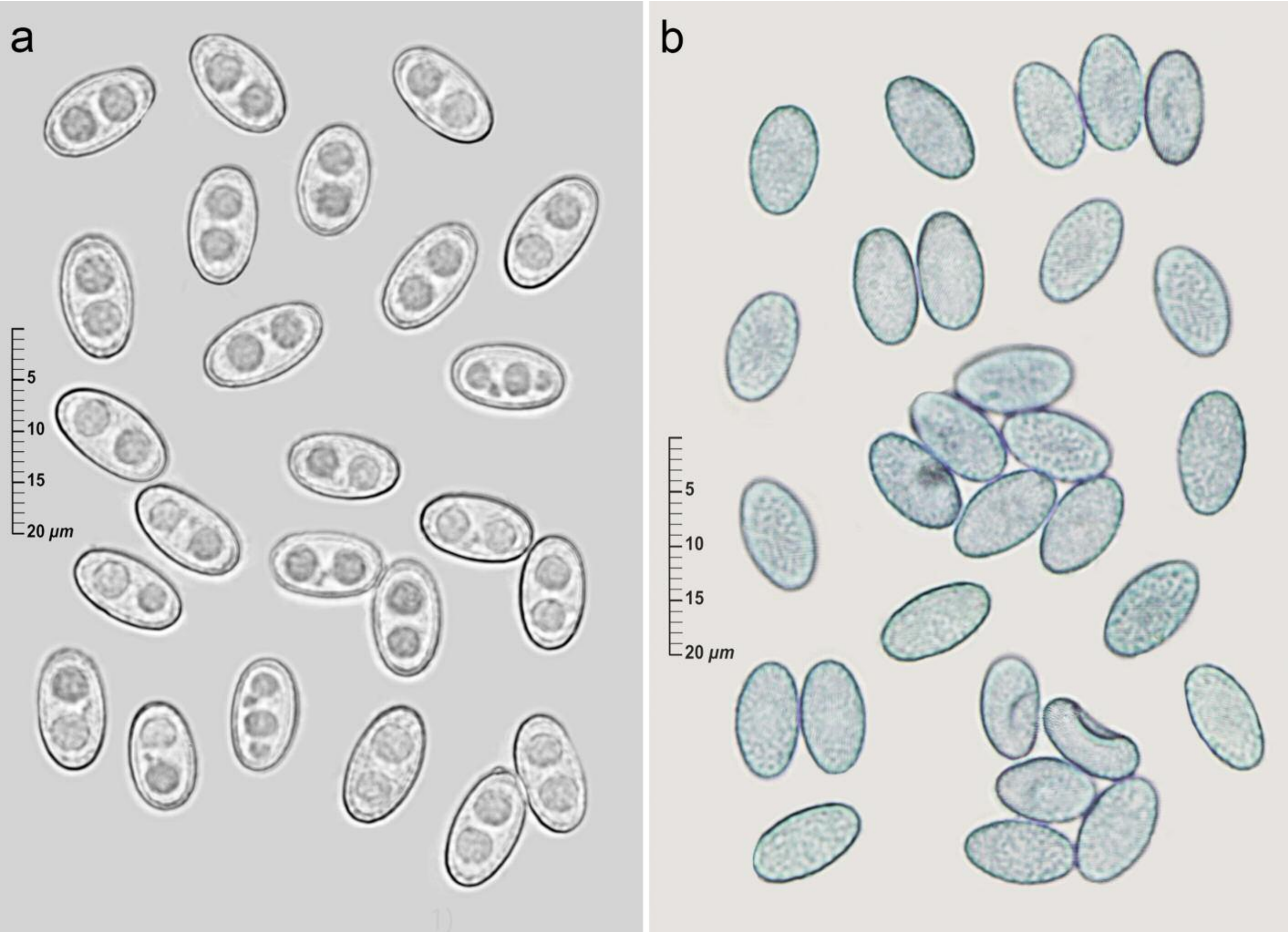

Plate 4 – *Sowerbyella meridionalis* LSS20190103-3 (*holotypus*). A: Ascospores in water. B: Ascospores in heated aqueous Cotton blue. Photos E. Rubio.

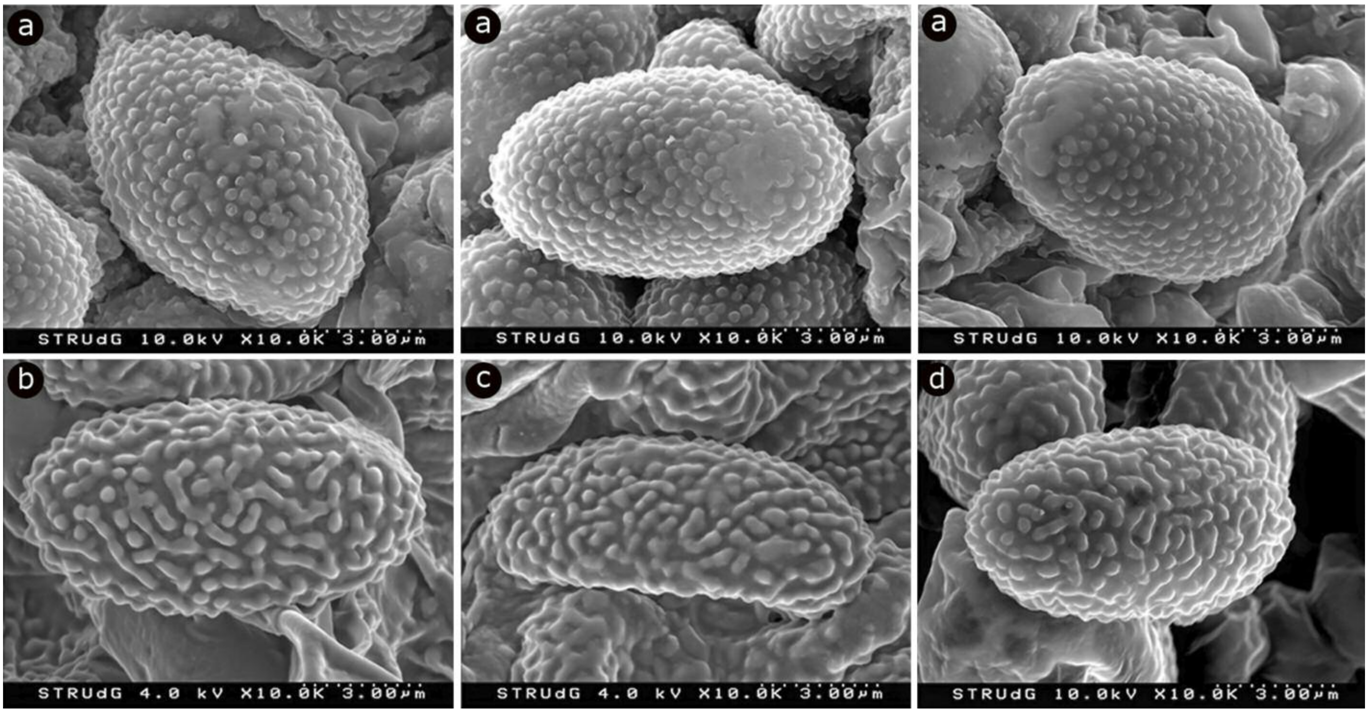

Plate 5 – SEM images, comparative. a. *Sowerbyella brevispora* H6010689 (*holotypus*). b. *Sowerbyella meridionalis* ERD-5805. c. *Sowerbyella meridionalis* JB 20100423. d. *Sowerbyella meridionalis* LSS20190103-3 (*holotypus*). All photos by Serveis Tècnics de Recerca de la Universitat de Girona

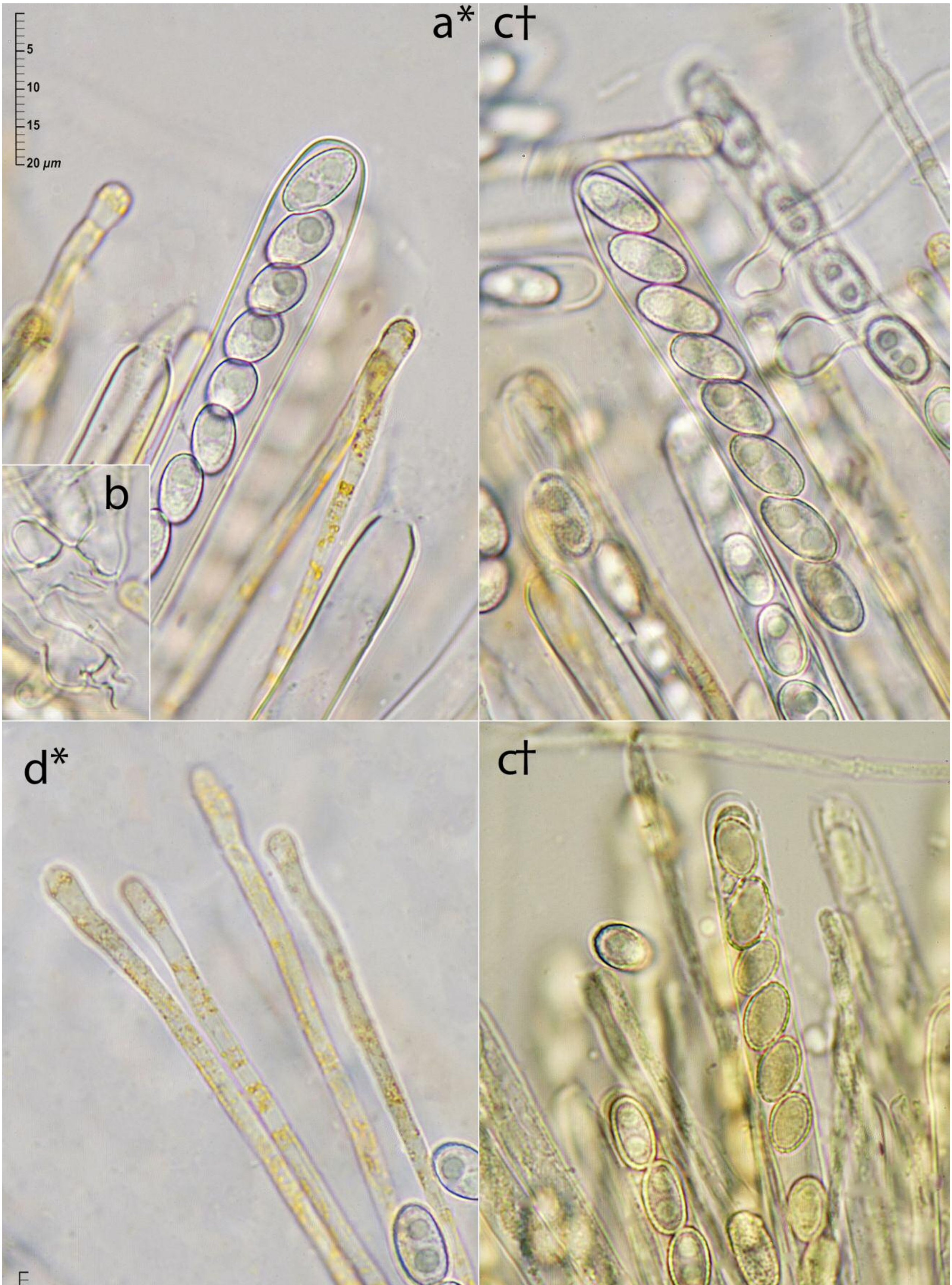

Plate 6 – *Sowerbyella meridionalis* LSS20190103-3 (*holotypus*). a. Fresh hymenium showing croziers (b). c. Hymenium in Melzer's reagent. d. Living paraphyses. (*) = Living state, (†) = Dead state. Photos E. Rubio.

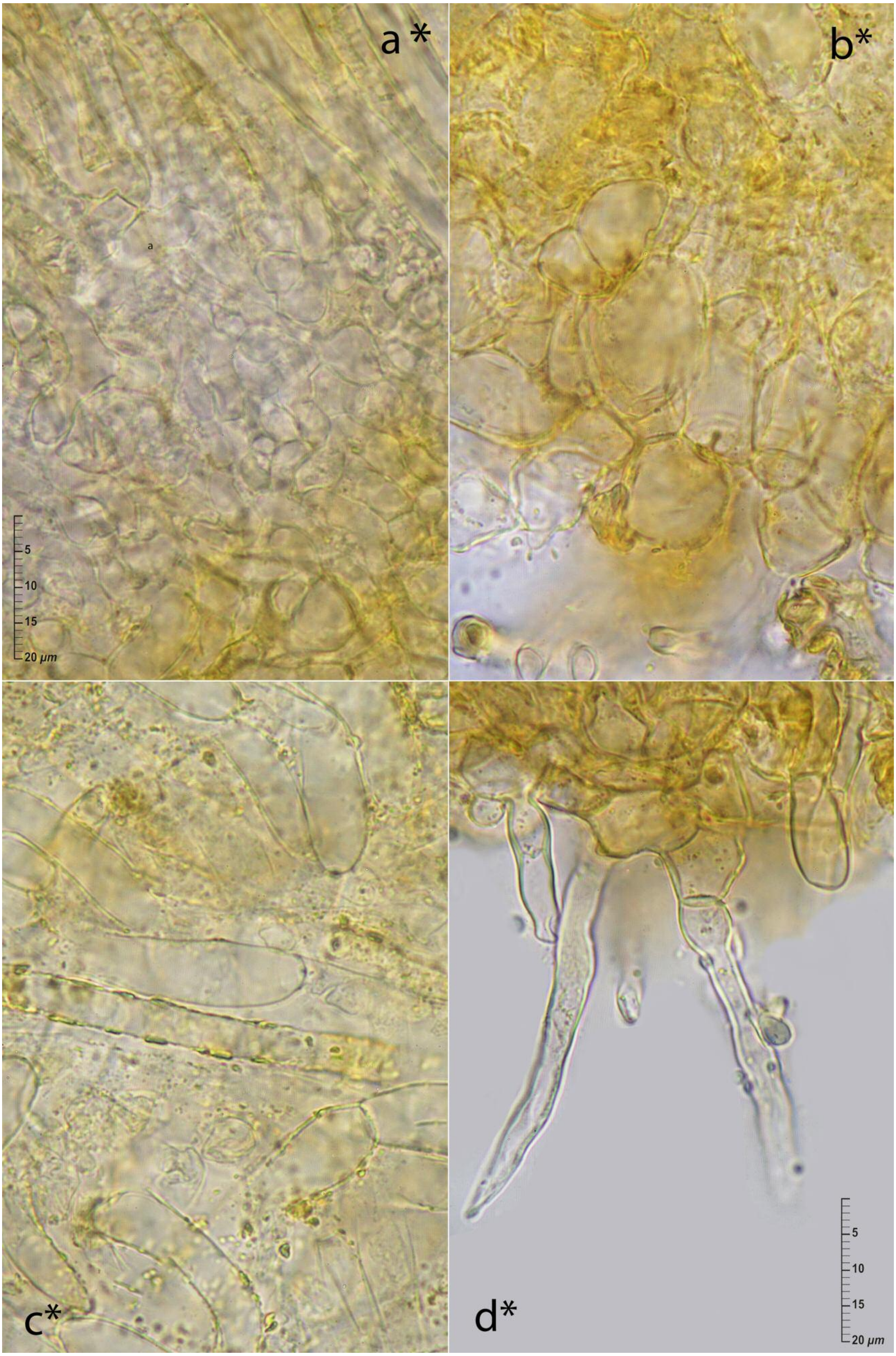

Plate 7 – *Sowerbyella meridionalis* LSS20190103-3 (*holotypus*). a. Subhymenium. b. Ectal excipulum. c. Medullary excipulum showing yellow exudates. d. Excipular hairs. (*) = Living state. Photos E. Rubio.

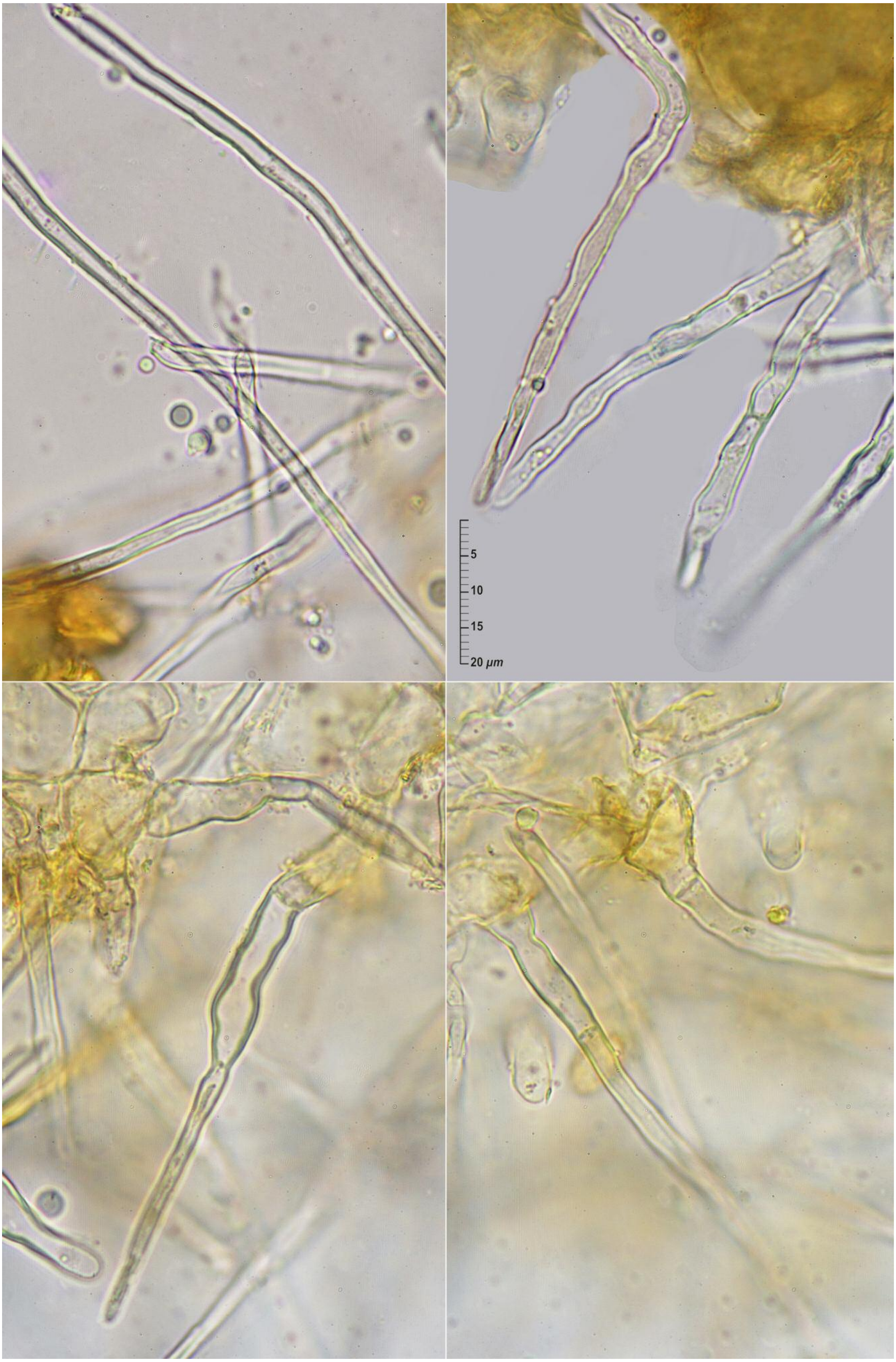

Plate 8 – *Sowerbyella meridionalis* LSS20190103-3 (*holotypus*). Excipular hairs from living material. Photos E. Rubio.

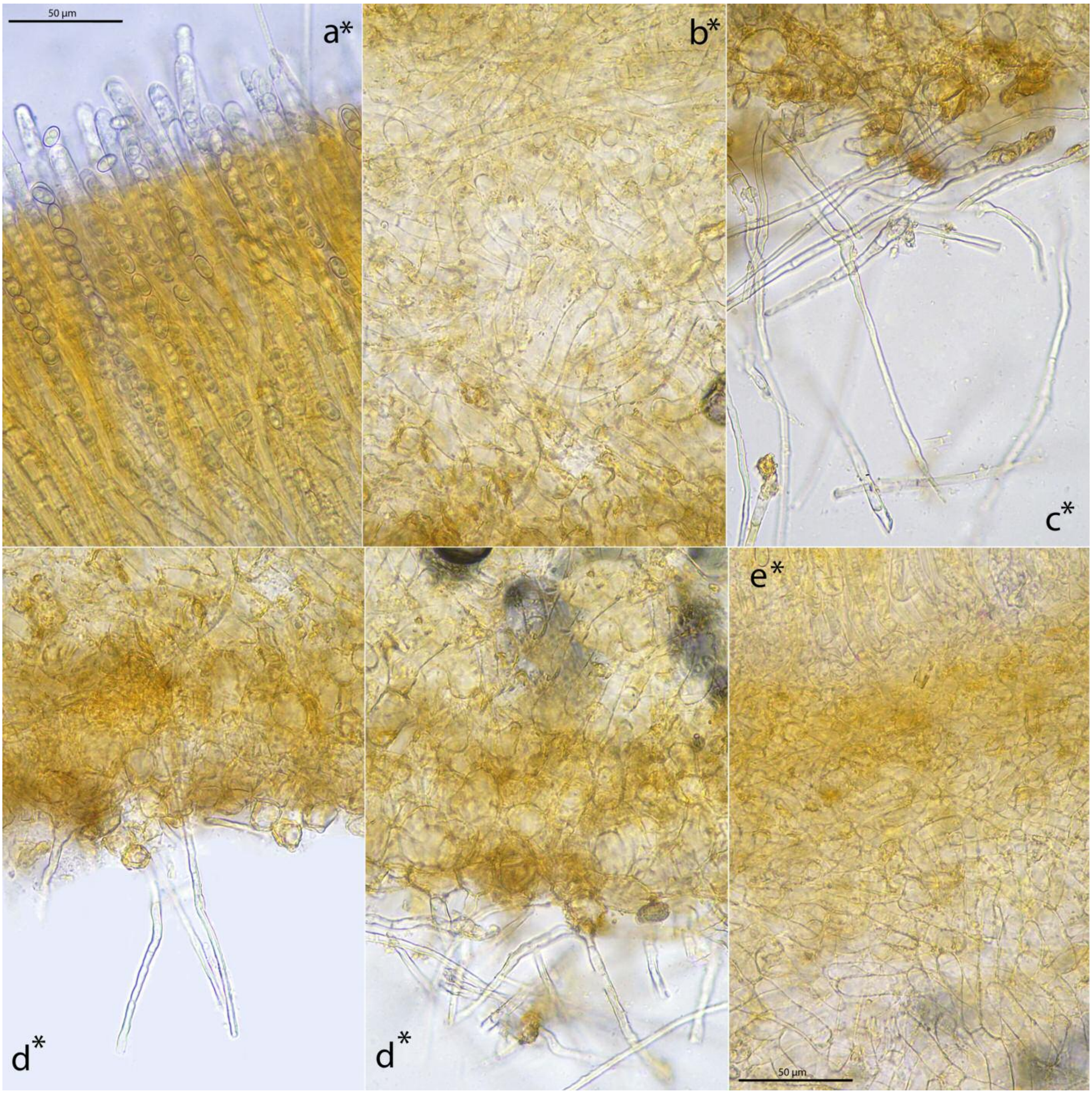

Plate 9 – *Sowerbyella meridionalis* LSS20190103-3 (*holotypus*). a. Hymenium. b. Medullary excipulum. c. Excipular hairs. d. Ectal excipulum. e. Subhymenium and upper medullary excipulum. (*) = Living state. Photos E. Rubio.

very rarely connected by ridges. On the other hand, while both species develop on siliceous soils, the ecology is very different: *Sowerbyella brevispora* grows in Nordic regions under *Picea abies*, whilst *S. meridionalis* grows in a Mediterranean environment, under *Pinus pinea*, *Quercus ilex* and *Cupressus* spp. However, there are also Austrian citations of *Sowerbyella brevispora* under broad-leaved trees (Klofac & Voglmayr, 2003) that agree with SEM images of *S. brevispora*. Priou & Réaudin (2010) report *Sowerbyella brevispora* on the coast of the "English Channel" or "La Manche", under *Cupressus*, a region which is much colder than the Atlantic coast, much less influenced by the Gulf Stream, but that has plants typical of warmer origins which could explain this distribution. This material, that we have been able to study, fits perfectly with the new species proposed here.

Unfortunately, we have not been able to genetically compare both species since the PCR has failed with the holotype and with a topotype of *Sowerbyella brevispora*, so it has not been possible to characterize the latter at the genetic level. However, we believe that the ecological, geographical and morphological differences, especially the spore ornamentation, justify the separation between the two species.

Sowerbyella meridionalis is part of the group of species with spore ornamentation that does not form a complete or partial reticulum. In comparison, *Sowerbyella phlyctispora* (Moravec, 1994) and *S. polaripustulata* have ascospores with much more prominent ornamentation (Moravec, 1985a), *S. angustispora* has larger ascospores with finer isolated warts (Moravec, 1988), and *S. fagicola* has larger ascospores with tapered ends and is associated with *Fagus* spp. (Moravec, 1973). *S. reguisii*, another Mediterranean species, differs from the new species by its longer, fusoid, reticulate ascospores (Moravec, 1985b).

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Authors' contributions

Enrique Rubio and Leandro Sánchez were responsible for the study conception, morphological studies and design. Carles Roqué financially contributed to the generation of rDNA sequences and SEM images. Leandro Sánchez, Javier Bometón and Juan Antonio Suárez provided voucher specimens. Molecular analyses and registrations in MycoBank were performed by Pablo Alvarado. All plates have been designed by Enrique Rubio, except pl. 1, 2 (Pablo Alvarado), 3 (Leandro Sánchez) and 5 (Carles Roqué). All authors read and approved the final manuscript.

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