The genus *Delastria* (*Pezizaceae*), a worldwide revision

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Abstract: We propose a monographic revision of the genus *Delastria*, with the description of four new species (*Delastria evae* sp. nov., *D. faustiniana* sp. nov., *D. javieri* sp. nov. and *D. liebanensis* sp. nov.) and the revision of two published ones (*D. rosea* and *D. supernova*).
Keywords: Ascomycota, *Pezizaceae*, phylogeny, taxonomy.

Résumé : nous proposons une révision monographique du genre *Delastria*, avec la description de quatre nouvelles espèces (*Delastria evae* sp. nov., *D. faustiniana* sp. nov., *D. javieri* sp. nov. et *D. liebanensis* sp. nov.) et la révision de deux taxons publiés (*D. rosea* et *D. supernova*).
Mots-clés : Ascomycota, *Pezizaceae*, phylogénie, taxinomie.

Resumen: Nosotros proponemos una revisión monográfica del género *Delastria*, con la descripción de cuatro nuevas especies (*Delastria evae* sp. nov., *D. faustiana* sp. nov., *D. javieri* sp. nov. y *D. liebanensis* sp. nov.) y la revisión de dos taxones publicados (*D. rosea* y *D. supernova*).
Palabras clave: Ascomycota, *Pezizaceae*, filogenética, taxonomía.

Introduction

The genus *Delastria* Tul. & C. Tul. (Ascomycota, *Pezizomycetes*) was created by the Tulasne brothers (Tulasne & Tulasne, 1843), to honour the French botanist Charles Jean Louis Delastre (1792-1859), author of an influential opus "Flore analytique et descriptive du département de la Vienne" (1842) and wide-ranging naturalist who provided to the Tulasne brothers a number of important collections from the Poitiers area. *Delastria* was defined as monotypic, based on *Delastria rosea* Tul. & C. Tul collected by themselves in two localities in Western France (at Lignières near Tours, and Nintré-les-Barres), along the Vienne River in sandy ground and under pines. Their description was completed later, with coloured illustrations and a detailed microscopy plate (Tulasne & Tulasne, 1851: 178), based on more collections from Southwestern France (la Teste-de-Buch and Villandraut, Gironde), and others sent to them from Nérac, Lot-et-Garonne, by the painter Maurice Lespiault in 1843. *Delastria rosea* remained the only known species in the genus until the recent publication of a second species from Spain, *D. supernova* A. Paz & Lavoise (Paz & Lavoise, 2013).

The genus was originally included in the family *Terfeziaceae* E. Fisch. (Tulasne & Tulasne, 1843), a morphology-based position followed by most authors such as Trappe (1979) and Montecchi & Sarasini (2000), while Castellano *et al*. (2004) included it in the family *Tuberaceae* Dumort. The first molecular analyses of *D. rosea* by Alvarado *et al*. (2011), revealed that this species was related to both pezizoid (*Marcelleina* Brumm. *et al*.) and tuberoid (*Hydnobolites* Tul. & C. Tul.) lineages in the *Pezizaceae*, underlining the autonomy of the genus *Delastria* within this family.

In 2007, we encountered our first collection of *Delastria supernova*. Picking it out from the ground was enough to make us suspect a new species distinct from the "usual" *Delastria rosea*, so far the only species described in the genus, due to its pruinose peridium and remarkably spiny-areolate spores. This was the starting point of a ten-year project. In 2013, this new species was finally officially published (Paz & Lavoise, 2013), supported by ITS and LSU DNA sequences of the paratype collection. Molecular data revealed that various sequences were already deposited in the public sequence database GenBank, corresponding to this genus, suggesting a greater diversity than initially inferred. Our attention was especially caught by two sequences identified as "*Delastria rosea*": JN048883 and JN102449 published in Alvarado *et al*. (2011), and Healy *et al*. (2013), respectively. These two sequences differed by much more than the 3% of differences usually admitted for intraspecific variability (70% of similarity only on a pairwise alignment of the ITS2 region, 343 positions) and thus were likely to represent two distinct species, only one of them, if any, belonging to the Tulasne's species. In 2015 again, during a visit to the "Jardín Micológico de la Trufa" at Córdoba, we collected a species morphologically and microscopically distinct from all previous ones. In addition, several collections have been provided by collaborators in Spain and France.

This accumulation of collections and sequence data, prompted us to propose a worldwide revision of the genus. The aim of this study is to revise the species concepts in *Delastria*, based on ITS sequences as well as ecological, macroscopical and microscopical features.

Material and methods

Morphology and microscopy. — The methods used for our research and identification of hypogeous fungi are as described in previous publications (Paz *et al.*, 2012). Microscopical observations of fresh collections were made in water, Hoyer's medium, and phenolic Methylene blue. Sections from exsiccata were revived in chloral hydrate before mounting in the same media. Macrophotographs were made with a Nikon D7100 DSLR camera with an objective AF micro-Nikkor 60 mm. Microscopic observations and microphotographs were made under a microscope Nikon Eclipse E800 coupled with a Nikon D5000 or D7100 camera; pictures were captured using the software Helicon Remote (Helicon Soft Ltd), then stacked using Helicon Focus (Helicon Soft Ltd), and refined using Photoshop (Adobe Systems Software Ireland Ltd). All spore measurements include ornamentations.

Studied collections were air-dried and deposited in A. Paz's personal herbarium (cited below as "IC"), and partly in the herbarium of the Faculty of pharmacy, University of Lille, France (LIP).

Extraction, amplification and sequencing. — Nine collections of *Delastria* from France, Morocco and Spain were targeted for sequencing in this study. Sequences from the complete ITS regions were generated by Alvalab (Oviedo, Spain), IDforest (Palencia, Spain) and the CEFE-CNRS (Montpellier, France), as described, respectively, in Alvarado *et al.* (2011), http://www.idforest.es/es, and Richard *et al*. (2015), using the primers ITS1F and ITS4 (White *et al*., 1990; Gardes & Bruns, 1993). Sequences were edited and assembled using Codon Code Aligner v. 4.1.1 (CodonCode Corp., Centerville, MA USA). Sequences generated for the present study as well as that of the holotype of *Delastria supernova* generated earlier (Paz & Lavoise, 2013) but not published yet, have been deposited in GenBank under the accession numbers listed in Table 1.

Phylogenetic analyses. — The analysed dataset includes the 9 ITS sequences generated for this study, the unpublished sequence produced in Paz & Lavoise (2013), as well as 10 published GenBank sequences (www.ncbi.nlm.nih.gov/genbank), selected by BLAST and taxonomic requests, and 3 *Hydnobolites* sequences, as outgroup (Table 1 and Fig. 1). Phylogenetic analyses were performed online at www.phylogeny.lirmm.fr (Dereeper *et al*., 2008) and on the CIPRES

Table 1 – Specimens included in the phylogenetic analysis.
* Sequences generated for the present study or unpublished are highlighted in bold.

Species	Voucher id	Voucher original annotation	Collection year	Host(s)	Country	GenBank ITS accession *
Delastria evae sp. nov.	IC6021501 (isotype)	*Delastria evae*	2015	*Quercus*, *Cistus*, *Tuberaria*	Spain	**MH469536**
	IC25031126	*Delastria evae*	2011	*Quercus*	Spain	**MH469537**
	AH39235	*Delastria rosea*	2011	*Cistus*, *Pinus*	Spain	JN048883
	17003	*Hydnocystis piligera*	1998	Unknown	Italy (Sardinia ?)	JF908767
Delastria faustiana sp. nov.	IC19051301 (holotype)	*Delastria supernova* (paratype)	2013	*Quercus*, *Tuberaria*	Spain	KF604908
	Clone R217	Uncultured fungus (ectomycorrhizal root tip)	2008	*Pinus*	Spain	JQ976001
Delastria javieri sp. nov.	IC06121503 (isotype)	*Delastria javieri*	2015	*Cistus*	Spain	**MH469545**
	AH39200	*Delastria* sp.	Unknown	Unknown	Unknown	JN048884
Delastria liebanensis sp. nov.	IC15051606 (holotype)	*Delastria liebanensis*	2016	*Quercus*, *Cistus*	Spain	**MH469544**
	IC16011801	*Delastria liebanensis*	2018	*Quercus*, *Cistus*	Spain	**MH469539**
Delastria rosea	IC17091307	*Delastria rosea*	2013	*Pinus*, *Tuberaria*	France	**MH469543**
	IC20020901	*Delastria rosea*	2009	*Quercus*, *Cistus*	France (Corsica)	**MH469540**
	IC06081601	*Delastria rosea*	2011	*Helianthemum*	Morocco	**MH469538**
	IC15061407	*Delastria rosea*	2011	*Pinus*, *Cistus*	Spain	**MH469542**
	OSC:JT17961	*Delastria rosea*	1995	Unknown (truffle fruitbody)	Spain (Canary Isl.)	JN102449
	Isolate ML62	Uncultured fungus (ectomycorrhizal root tip)	2004	*Pinus*	Spain	DQ386141
	Clone OT-66	Uncultured fungus (ectomycorrhizal root tip)	Unknown	*Pinus*	Spain	FJ013057
	Clone R174	Uncultured fungus (ectomycorrhizal root tip)	2008	*Pinus*	Spain	JQ975997
Delastria supernova	IC14040701 (holotype)	*Delastria supernova*	2007	*Quercus*	Spain	**MH469541**
Delastria sp1	Clone MB-3c	Uncultured fungus (ectomycorrhizal root tip)	2009	*Halimium* or *Cistus*	Portugal	HQ625455
Delastria sp2	Clone OT-70	Uncultured fungus (ectomycorrhizal root tip)	Unknown	*Pinus*	Spain	FJ013076
Hydnobolites sp. (outgroup)	MIN:RH164	*Hydnobolites* sp. 10 RH-2012	2010	Unknown (woodland soil)	USA	JX414185
Hydnobolites sp. (outgroup)	OSC:JT11013	*Hydnobolites* sp. 17 RH-2012	1988	Unknown (truffle fruitbody)	Mexico	JN102460
Hydnobolites sp. (outgroup)	FLAS:MES446	*Hydnobolites* sp. 18 RH-2012	2010	Unknown (truffle fruitbody)	China	JN102461

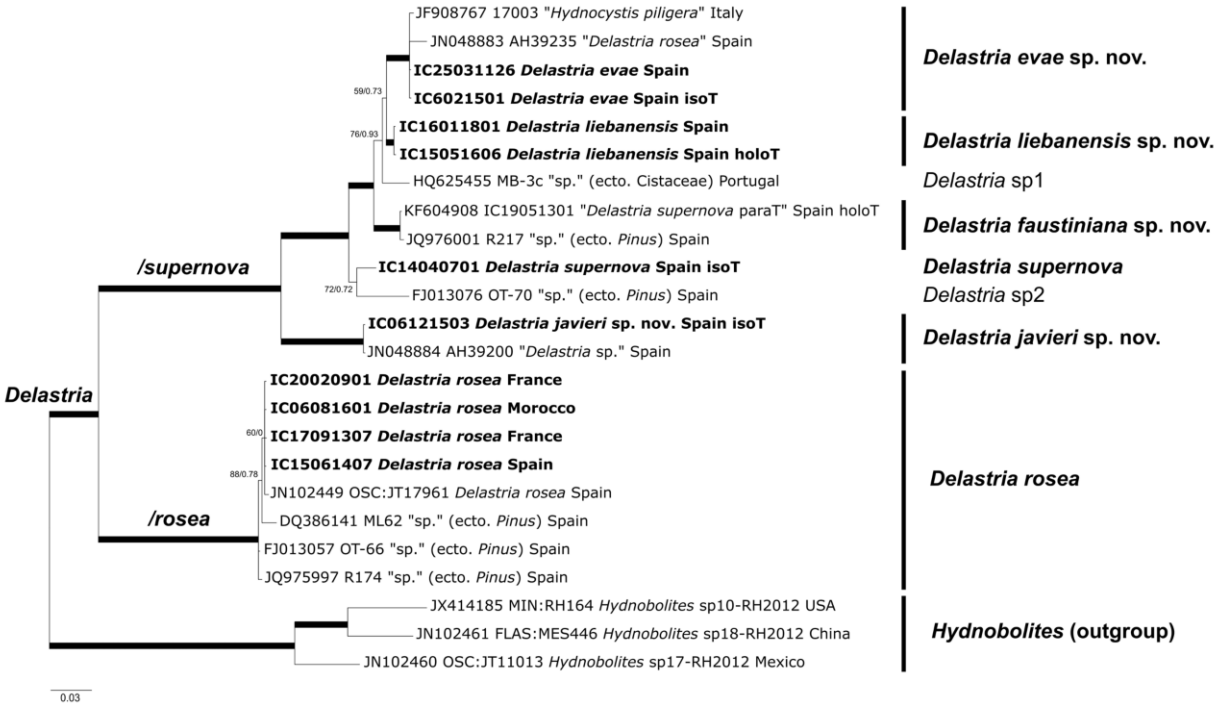

Fig. 1 – ITS phylogeny of *Delastria*. Bayesian 50 % majority-rule consensus tree inferred from the analysis of 21 ITS sequences belonging in *Delastria*, plus 3 Hydnobolites sequences chosen as outgroup. Branches with significant statistical support (BPP ≥ 95% and SH-aLRT > 0.8) are highlighted as thick lines, others display support values as % BPP/SH-aLRT. Sequences generated for the present study or so far unpublished are highlighted in bold.

Science Gateway (www.phylo.org/index.php). Multiple sequence alignment was carried out with MUSCLE v. 3.7 (Edgar, 2004). Alignments were edited with Gblocks 0.91b, set to lowest stringency in the selection of conserved blocks (Castresana, 2000; Talavera & Castresana, 2007). Maximum likelihood (ML) phylogenetic analysis was performed with PhyML v. 3.0 (Guindon *et al.*, 2010), using the GTR + I + Γ model of evolution and the Shimodaira-Hasegawa version of the approximate likelihood-ratio test (SH-aLRT) of branch support (Anisimova *et al.*, 2011). Bayesian inference of phylogeny was assessed using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck, 2003). Eight Markov Chain Monte Carlo (MCMC) were performed in two separate runs of 1,000,000 generations, with stationarity convergence estimated by the Potential Scale Reduction Factor = 1 (Gelman & Rubin, 1992). Trees and parameters were sampled every 1000 generations (1000 trees), with an initial burn-in set to 25% (250 trees). A 50% majority-rule consensus phylogram was computed from the remaining trees and branch support was estimated by Bayesian posterior probabilities (BPP). Trees were built using TreeDyn 198.3 (Chevenet *et al.*, 2006) or FigTree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree) and edited with Inkscape 0.91 (https://inkscape.org/fr).

Taxonomy

Delastria rosea Tul. & C. Tul., *Ann. Sci. Nat. Bot., ser. 2*, 19: 380 (1843) – Fig. 2, 3, 9A-B.

Synonym: *Terfezia rosea* (Tul. & C. Tul.) Torrend, *Bull. Soc. Port. Sci. Nat.*, 1: 178 (1908).

Original diagnosis of the genus *Delastria* (Tulasne & Tulasne, 1843: 379): *Peridium tenuissimum byssaceum, candidum, arenae immistum; substantia carnosa, molliuscula, humida, in glebulis versiformibus septis mollibus albis immutabilibus (peridii filamentis stipatis intropulsis aequiparandis) dissecta; sporangia ovato-oblonga, obtusa saepius incurvato-subreniformia, in glebulis nidulantia, sporas* 3 *(rarius* 4*) sphaericas reticulato-echinatas foventia; guttula (?) in quaque spora subconcentrica. Fungus basi absorbenti patentissima eradicata donatus.*

Original diagnosis of *D. rosea* (Tulasne & Tulasne, 1843: 380): *In sylvis arenosis Pictonum prope Heraldi Castrum (*Barres de Nintré*), necnon et pinetis Turoniae (*Lignières*), octobri-februario, copiosè. Fung. nucis magnit. et ultrà, intùs maturus amoene roseus dein lutescens et tandem fuscatus; peridio è niveo sordido; odore debili; sapore ingrato.*

Description: Ascomata subglobose, slightly gibbose, 20–50 mm diam. **Peridium** when young embedded in a thin white coating to which debris and sand adhere, loosening with age; when mature more or less intensely pinkish, turning brownish at full maturity. **Gleba** compact, white when young, with broad bright pinkish spots between thin white sterile veins when mature. **Odour** fruity.

Peridium very thin and loosening, white, formed by aseptate ("skeletoid") hyphae 6–12 µm wide, thin-walled, branched, pigmented towards surface and colourless, slightly enlarged towards gleba. **Sterile veins** of gleba made of gelatinized hyphae, colourless, hooked. **Asci** kidney-shaped to cylindrical, slightly pear-shaped, measuring 100–180 × 30–60 µm. **Ascospores** spherical, 28–35 µm diam., reticulate, with dimples more or less regular, at maturity forming spines only on the top of the dimples, conical with acute apex, 1.32 (width) × 4.5 µm (height).

Ecology: All reported localities are on sandy, siliceous soils with pines (*Pinus pinaster*, *P. pinea*, etc.), often along with *Cistaceae* (*Cistus ladanifer*, *C. monspeliensis*, *Tuberaria guttata*, etc.).

Observations: The interpretation of this species has been commented upon in Paz & Lavoise (2013). Original collections of *D. rosea* have been extensively tracked in the herbarium PC (Paris), where only two collections were located, in the patrimonial herbarium of Camille Montagne. One of them, not dated, was labelled "Turonia" (latin name of Tours), *leg*. Tulasne, and matches the indications of the protologue, although it cannot be ascertained wether this collection was collected prior to the publication. The second, from Nérac, *leg*. Lespiault, is cited by Tulasne & Tulasne (1851: 178) without date, but not in the protologue (1843). A third collection, from the Tulasnes and from Lignières, France, 1 Oct 1842, has been traced in

H.M. Gilkey's collections at OSC (#131355, http://oregonstate.edu/dept/botany/herbarium) but unfortunately, it could not be made available to us for study. Because this collection would be the only one dated and eligible as a lectotype, we refrained from neotypifying *D. rosea* with the Nérac collection. Should OSC#131355 turn out to match the protologue and be designated as lectotype, the recent and sequenced IC17091307 collection from the same area and matching all microscopic features of the two collections kept in PC, may be designated as epitype to support our interpretation with molecular data. The species is also represented by four additional published sequences, all from Spain (incl. Canary Islands) and mostly from ectomycorrhizal root tips of *Pinus* spp. (Fig. 1).

Material studied (sequenced material marked with *): France. "Turonia" [Touraine], not dated, *leg*. Tulasne, coll. C. Montagne n° MC4373, PC0723300. Lot-et-Garonne, Nérac, landes sablonneuses, "décembre-janvier, commune", *leg*. M. Lespiault, coll. C. Montagne n° MC4374, PC0723301. Charente-Maritime, Sainte-Gemme, la Petite Vergne, N 45° 46′ 2.6″ W 0° 55′ 12.6″, 32 m elev., under *Pinus* sp. and *Tuberaria guttata*, 17 Sept 2013, *leg*. P. Chautrand, pers. herb. A. Paz IC17091307* and LIP 0001436. Corse du Sud, Pietrosella, Mare e Sol, E 8° 46′ 44″ N 41° 48′ 44″, 10 m elev., *Quercus suber* and *Cistus* sp., 20 Feb 2009, *leg*. C. Lavoise, pers. herb. A. Paz IC20020901*. Spain. Badajoz, Zalamea de la Serena, Finca las Morenillas, N 38º 35.381′ W 5º 38.204′, 608 m elev., under *Pinus pinea* with *Cistus ladanifer*, 27 Dec 2011, *leg*. M. Romero, pers. herb. A. Paz IC15061407*. Cáceres, Jaraíz de la Vera, N 40º 03′ 35.22″ W 5º 46′ 08.60″, 729 m elev., under *Cistus ladanifer* and *Pinus pinaster*, 15 Dec 2012, *leg*. A. Paz & C. Lavoise, pers. herb. A. Paz IC15121213. Morocco. Rabat, forêt de la Mâmora, with *Helianthemum guttatum*, 9 Apr 2011, *leg*. A. Zambonelli, herb. CMI-UNIBO 4240, pers. herb. A. Paz IC6081601*.

Delastria supernova Paz & Lavoise, *Bol. Micol. FAMCAL*, 8: 72 (2013), *emend*. MycoBank MB804699 – Fig. 4, 9C

Original diagnosis (Paz & Lavoise, 2013): Ascomata globose, irregular, 1,5–3 cm wide, with protuberances. Cortex white very pubescent when young, then silky white with pinkish shades, not staining when bruised, smooth. Peridium cream white with light pink tones, thin, persistent when mature. Gleba hymenioid made of irregular whitish veins, stained light pink by mature spores. Asci subglobose to pyriform with short peduncle, measuring 105–130 × 65–90 µm, containing 1–3 elliptical to subglobose spores measuring 24–26 × 20–22 µm, reticulate-alveolate at first then aculeolate with 2–3 µm high spines. Holotype: Spain, Cáceres, Parque Nacional de Monfragüe, 14-IV-2007, IC14040701 (LIP). Isotype deposited in A. Paz' private herbarium.

Description: Ascomata globose, irregular, 1.5-3 cm diam., with protrusions. Surface when young densely pubescent and white, later silky white with slight pinkish tones, smooth and unchanging when bruised. **Gleba** compact, with distinct hymenium forming light pink irregular spots, marbled by thin white sterile veins. **Odour** pleasant, faint, reminiscent of bitter almonds.

Peridium 180–250 µm thick, two-layered: outer layer with colourless, thin-walled branched hyphae; inner layer made of strongly thick-walled globose cells. **Sterile veins** of gleba gelatinized, made of colourless slender hyphae. **Asci** subglobose to pear-shaped, shortly pedunculate, 105–130 × 65–90 µm, 1- to 3-spored. **Ascospores** broadly ellipsoidal to subglobose, 33–41 × 28–36.4 µm, with a reticulate ornamentation made of very irregular dimples, topped by vertical spines 1.49 µm broad, 4.59 µm high, intercalated with smaller ones (1.08 × 2.14 µm) all along the crest, which cover the surface of the spores at full maturity.

Ecology: All collections studied by us were made under *Quercus ilex*, sometimes accompanied by *Tuberaria guttata*.

Observations: In the original publication of *Delastria supernova* (Paz & Lavoise, 2013), were cited two ITS-sequenced collections, one from the isotype (IC14040701) on which the description was based, and a second "paratype" (IC19051301) collection considered as conspecific in spite of a slightly divergent ITS sequence (5.86% of divergence, Table 2). With more data from new collections analysed for the present study, it becomes clear that two distinct species were originally confused under the name *D. supernova*. To fix this issue, we propose here: 1) an emendation of *D. supernova* with exclusion of the former paratype collection, and 2) the recognition of the latter as a new species, described below as *D. faustiniana* sp. nov., that is distinguished from *D. supernova* by a combination of micromorphological and molecular features detailed below (see Observations under *D. faustiniana*).

Material studied: Spain. Cáceres, Parque Nacional de Monfragüe, N 39º 49.019′, O 6º 0.512′, 370 m elev., under *Quercus ilex*, 14 Apr 2007, *leg*. A. Paz, LIP 0001298 (holotype), herb. pers. A. Paz IC14040701 (isotype)*. Cataluña, Girona, Foixà, N 42º 2′ 42.66″ E 2º 59′ 0.59″, 140 m elev., under *Cistus monspeliensis*, 12 Dec 1990, *leg*. J. M. Vidal, pers. herb. A. Paz JMV901212-6. Castilla y León, Valladolid, Rábano, N 41º 28′ 49.92″ O 4º 3′ 48.54″, 779 m elev., under *Quercus faginea* in sandy soil, 29 Sept 2001, *leg*. F. García, pers. herb. J.M. Vidal JMV20010929-1.

Delastria evae M. Romero, A. Paz & Lavoise, *sp. nov.* – MycoBank MB 826768 – Fig. 5, 9D

Diagnosis: Differs from *Delastria rosea* by a pubescent and persistent peridium, a gleba with broader spots between thin white sterile veins, and smaller ascospores. Holotype: LIP 0001435.

Etymology: The epithet is dedicated to Eva Cabeza Romero, Manuel Romero's granddaughter.

Description: Ascomata subglobose, 2–6 cm diam., with many protrusions, covered by thin yellowish-cream pubescence when young, when maturing staining cinnamon-brown, strongly adherent, persistent but brittle and disappearing easily when touched, washed or brushed, and then making the outer gleba visible, which is light brown with pinkish tones. **Peridium** thin, colourless, persistent. **Gleba** compact, white when young, when mature with a distinct hymenium appearing as small subcircular spots, originally light pink-brown, turning pinkish brown as spores mature, separated by thin white sterile veins. **Odour** faint, pleasant.

Peridium thin, two-layered: outer layer made of "skeletoid" hyphae 5-12 µm wide, septate, branched, incrusted, thin-walled, light brown; inner layer made of thickened colourless "skeletoid" hyphae, enlarging towards gleba, gradually forming a thin layer of thick-walled subglobose cells measuring 22–34 × 20–27 µm along the gleba. **Gleba** with sterile veins made of colourless gelatinized hyphae, septate, 7–6 µm wide. **Asci** kidney-shaped to subspherical, sometimes slightly pear-shaped, 100–135 × 70–95 µm, usually 3-spored. **Ascospores** spherical, 29–36 µm diam., with dimples regular with irregular vertical aculei on their walls, the highest measuring 1.95 (width) × 4.5 µm (height), intercalated by much smaller ones, isolated and brittle, all along the crests, measuring 0.63 × 2.09 µm.

Ecology: All studied collections grew under *Quercus ilex*, *Q. rotundifolia* or *Q. pyrenaica*, *Pinus pinaster*, with many *Cistaceae* (*Cistus ladanifer*, *C. monspeliensis*, *Tuberaria guttata* or *Helianthemum* spp.), usually under the litter, half-buried in siliceous, sandy ground.

Observations: *Delastria evae* has probably been collected, studied and published multiple times as "*Delastria rosea*". Both species are easily confused in the field, even though they clearly represent distinct lineages, distant by more than 25% of ITS sequence diver-

Fig. 2 – *Delastria rosea* Tul. & C. Tul. A, C, E: Authentic collection (PC 43733), herbarium label, ascomata, and ascospores; B: Authentic collection (PC 4374), herbarium label and ascomata. Photos: A. Paz & C. Lavoise

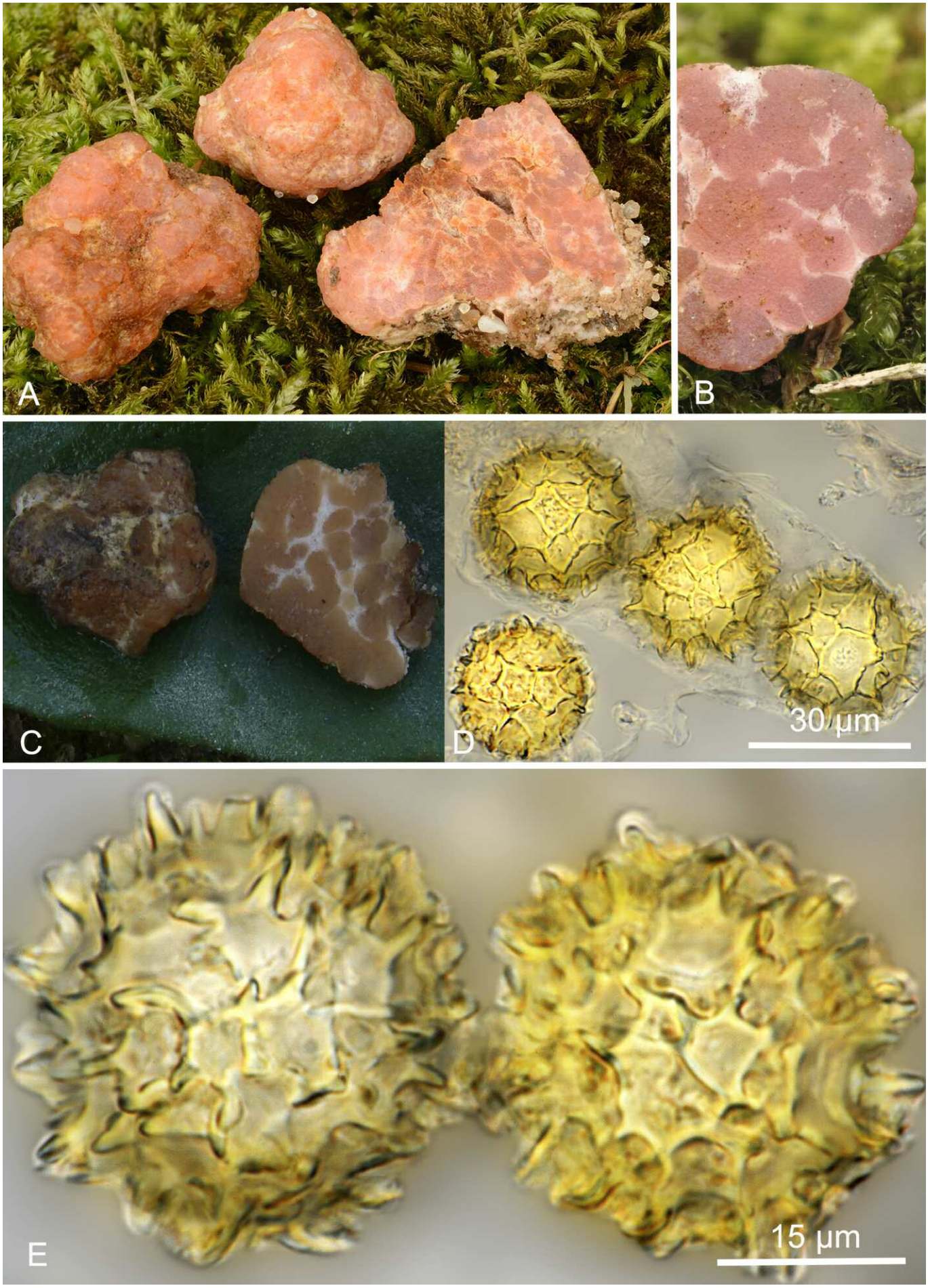

Fig. 3 – *Delastria rosea* Tul. & C. Tul. (LIP 0001436). A, B, C: Ascomata; E, F: Ascospores. Photos: A. Paz & C. Lavoise

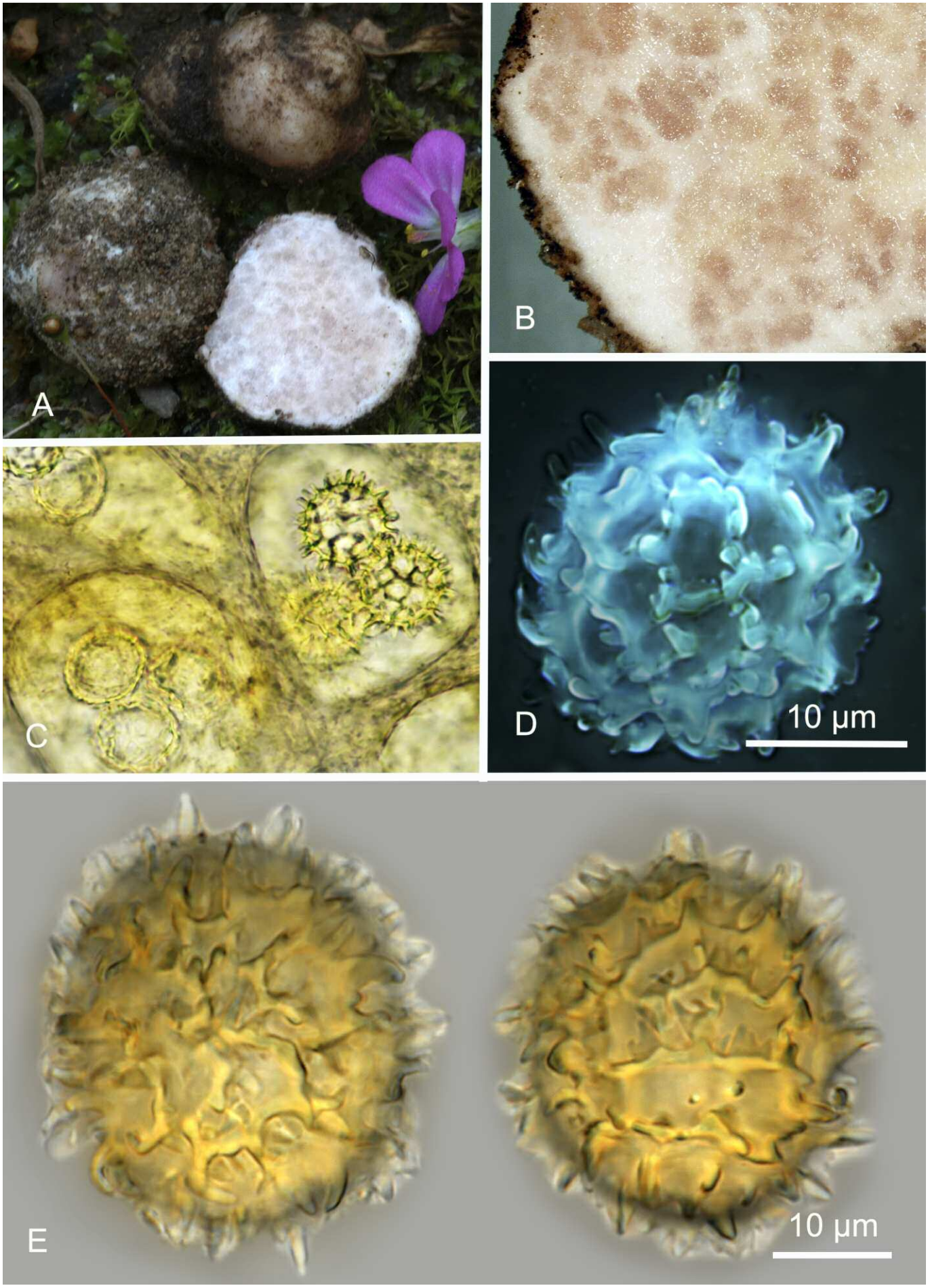

Fig. 4 – *Delastria supernova* A. Paz & Lavoise. Holotype (IC14040711). A, B, C: Ascomata; D, E: Ascospores. Photos: A. Paz & C. Lavoise

gence (Fig. 1 and Table 2). As redefined here, *Delastria rosea* displays a white pubescence, a brighter pink colour, a gleba with broader spots between thin white sterile veins, and smaller ascospores ornamented by spines only arising from wall sides of the dimples. The species is also represented by two published fruitbody sequences, from Spain and Italy and identified, respectively, as *D. rosea* and *Hydnocystis piligera* (Fig. 1).

Material studied: Spain. Badajoz, Quintana de la Serena, Sierra Agalla, N 38º 44.922´ W 5º 45.229´ 504 m elev., under *Quercus ilex* with *Cistus ladanifer* and *Tuberaria guttata*, 1 Feb 2015, *leg*. M. Romero, LIP 0001435 (holotype), pers. herb. A. Paz IC6021501 (isotype)*. Castilla y León, Zamora, Peleagonzalo, Toro, N 41º 28' 49.92" W 5º 29' 56.69", 722 m elev., woods of *Quercus rotundifolia* in sandy soil, 25 Mar 2011, *leg*. J. Cabero, pers. herb. A. Paz IC25031126*. Cataluña, Barcelona, La Roca del Vallès, Can Company de Dalt, N 41º 34' 30.86" E 2º 20' 1.18", 230 m elev., under *Pinus pinaster*, *Cistus monspeliensis*, *Rosmarinus officinalis* and *Erica arborea*, sandy soil, 19 Nov. 2017, *leg*. L. Sánchez & C. Magrasó, pers. herb. L. Sánchez LSS 20171119-2 and A. Paz IC19111701; Girona, Torroella de Montgrí, Sobrestany, N 42º 4' 33.72" E 3º 7' 50.31", 22 m elev., under *Cistus ladanifer*, 23 Mar 1996, *leg*. J.M. Vidal, pers. herb. J.M. Vidal JMV960323-2. Castilla y León, Valladolid, Aldealbar, N 41º 29' 44.60" W 4º 21' 45", 877 m elev., under *Helianthemum* sp. in sandy soil, 4 Apr 2000, *leg*. F. García, pers. herb. J.M. Vidal JMV20000604-4. Castilla y León, Zamora, Peleagonzalo, Toro, N 41º 28' 49.92" W 5º 29' 56.69", 722 m elev., woods of *Quercus rotundifolia* in sandy soil, 21 Jun 2007, *leg*. J. Cabero, pers. herb. J.M. Vidal JMV20070621-2. Castilla y León, Zamora, Tabara, N 41º 48' 53.22" W 5º 57' 35.59", 747 m elev., under *Quercus pyrenaica* and *Cistus ladanifer*, 25 May 2010, *leg*. J. Cabero, pers. herb. J.M. Vidal JMV20100509-2.

Delastria faustiniana A. Paz, Lavoise & P. Juste, *sp. nov.* – MycoBank MB 826769 – Fig. 6, 9E.

Diagnosis: Differs from *Delastria supernova* by spherical ascospores ornamented by truncate aculei. Holotype: LIP 0001434.

Etymology: Dedicated to the great mycologist Faustino García, a precursor in the collection, study and sharing of hypogeous fungi in the Spanish Plateau.

Misapplied name: *Delastria supernova* A. Paz & Lavoise, *pro parte*, *in* Paz & Lavoise, *Bol. Micol. FAMCAL*, 8 : 71-86 (2013).

Description: Ascomata subglobose, 1.5–3.5 cm diam., irregular with protrusions, firm, compact, evoking some *Tuber* species. **Surface** when young embedded in a dense white pubescent coating strongly adhering to sand and soil debris; with age silky white with faint pinkish tones, unchanging when bruised. **Gleba** originally white, with a distinct hymenium appearing as very small, irregular spots, turning cinnamon pink with age while spores become mature, marbled by thin white sterile veins. **Odour** pleasant, faint.

Peridium 140–210 µm thick, 2-layered: outer layer made of parallel branched, colourless thin-walled hyphae, encrusted by soil particles, 6–12 µm wide; inner layer made of subglobose, thick-walled (1.5–2 µm thick) colourless cells measuring 23–36 × 20–28 µm. **Gleba** with very thin sterile veins made of colourless, septate gelatinized slender hyphae 7–16 µm thin. **Asci** originally pear-shaped, becoming subspherical while spores mature, shortly pedunculate, 95–130 × 63–98 µm, 1–3(–4)-spored. **Ascospores** spherical, 26–33 µm diam., ornamented first as a reticulum with irregular dimples, forming cylindrical aculei on wall sides during maturation, usually truncate at apex (exceptionally rounded or acute), 1.9 µm wide, 4 µm high; progressively the crests of the dimples also form small cylindrical aculei with rounded apex, which finally coat the whole spore.

Ecology: The only finding was made under *Quercus ilex* with *Tuberaria guttata* present.

Observations: The unique collection on which this new species is based was formerly included within the delimitation of *D. supernova* (Paz & Lavoise, 2013), in spite of less than 95% of similarity between ITS sequences of the two collections analysed. The diversity of the genus *Delastria*, monospecific at that time, was not suspected, but the accumulation of collections and observations in recent years led us to consider these collections as specifically distinct. The species is also represented by a published sequence originating from a *Pinus pinaster* root tip, in the Guadalajara region of Spain (Fig. 1 and Rincon *et al*., 2014). Macroscopically, *D. supernova* and *D. faustiniana* are very similar, of hard consistence and evoke *Tuber* species. Microscopically however, they are morphologically diagnosable: *D. supernova* has unique ellipsoidal ascospores, with some conical aculei which ultimately entirely cover the spore.

Material studied: Spain. Segovia, Carbonero el Mayor, N 41º 9.48', W 4º 14.128', 852 m elev., under *Quercus ilex* and *Tuberaria guttata*, 19 Apr 2013, *leg*. F. García and P. Juste, LIP 0001434 (holotype), pers. herb. A. Paz IC19051301 (isotype)*.

Delastria javieri A. Paz, Lavoise & R. Molina, *sp. nov.* – MycoBank MB 826770 – Fig. 7, 9F.

Diagnosis: Differs from the other *Delastria* spp. by its nodulose ascomata, looking like a *Hydnobolites* species, and especially from *D. liebanensis* by its multiple hymenial chambers. Holotype: LIP 0001433.

Etymology: Dedicated to the great mycologist Javier Gomez, another precursor in the collection, study and sharing of hypogeous fungi in the Spanish Plateau.

Description: Ascomata irregular, strongly lobulate, of cerebriform shape, 1–3 cm diam. **Surface** when young pubescent, dirty white, adhering to much debris and sand and forming a continuous coating around the ascoma; when mature glabrescent and yellowish cream maculated by purple- to pink-brown spots from the underlying hymenium. **Gleba** compact, with a hymenium forming chambers and septa, appearing as irregular spots of vinaceous to purplish pink tones, marbled by thin sterile cream-colour veins. **Smell** sweet, fungoid.

Peridium thin, translucid, waxy, yellowish cream, 2-layered: outer layer an epicutis of 7–11 µm wide "skeletoid" hyphae, septate, branched, incrusted, thin-walled; inner layer pseudoparenchymatous, formed by irregularly globose, thick-walled cells 20–32 × 7–26 µm. **Ascospores** spherical, 26–32 µm diam., with a regularly reticulate ornamentation, with aculei developing on the edges, very small and isolate, 0.9 µm wide, 1.5 µm high, larger on the sides (2.4 × 3.5 µm).

Ecology: Under *Cistus ladanifer*, on sandy bare ground.

Observations: We collected this species only once, but another collection (AH39200 "*Delastria* sp.") is represented in public databases, without any precision of locality or ecology (Fig. 1 and Alvarado *et al*., 2011). Morphologically, *D. javieri* evokes a *Hydnobolites* species, but all species in this genus have 8-spored asci. Within *Delastria*, it can only be confused with *D. liebanensis* (cf. below), which also displays lilac tones on its surface, but the latter is subglobose and possesses a single hymenial chamber.

Material studied: Spain. Córdoba, Priego de Córdoba, Zagrilla, Mycological garden "la Trufa", N 37º 28' 57.23" W 4º 14' 3.77", 552 m elev., under *Cistus ladanifer*, 6 Dec 2015, *leg*. A. Paz, LIP 0001433 (holotype), pers. herb. A. Paz IC06121503 (isotype)*.

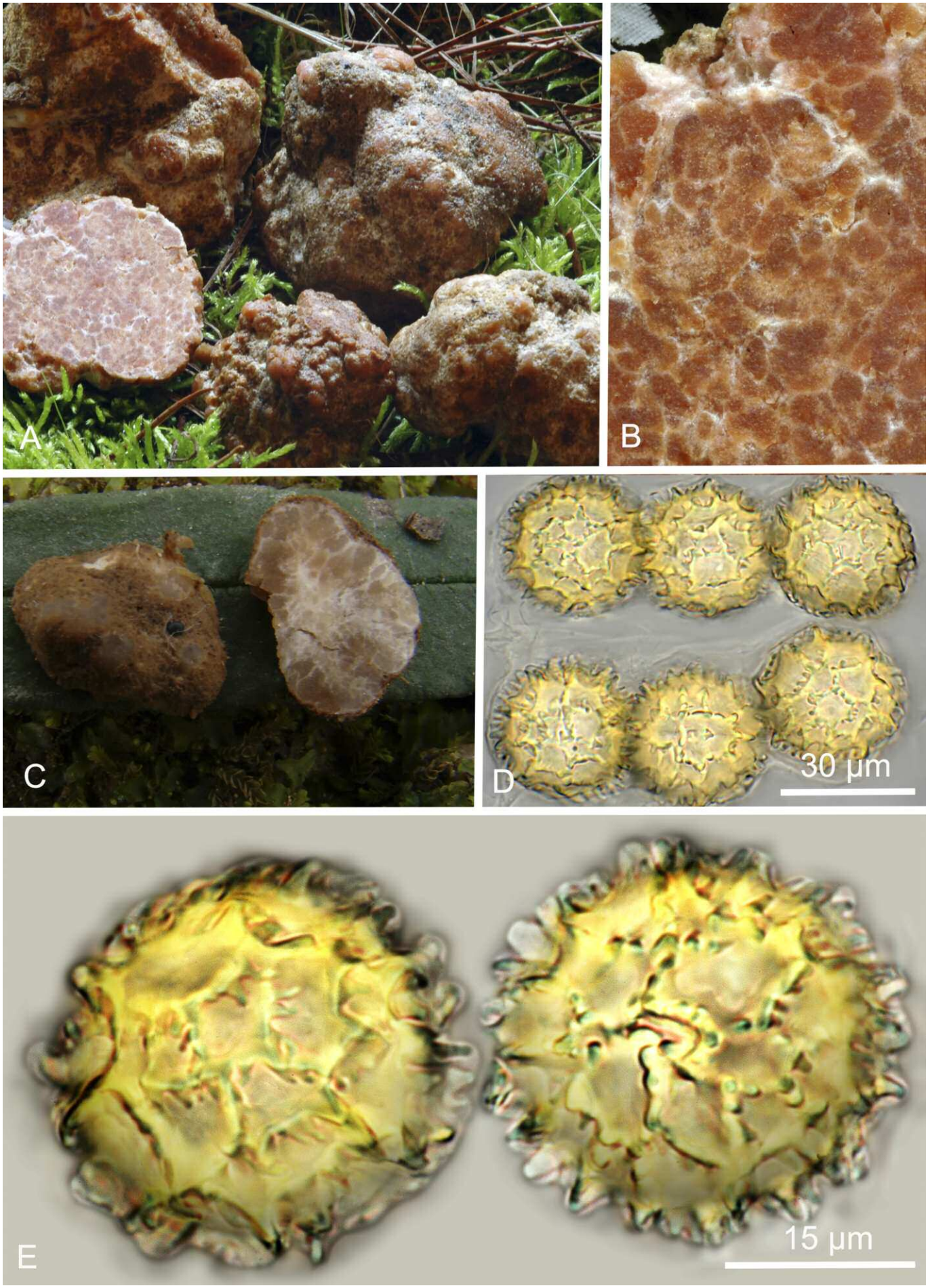

Fig. 5 – *Delastria evae*. Holotype (LIP 0001435). A, B, C: Ascomata; E, F: Ascospores. Photos: A. Paz & C. Lavoise

Fig. 6 – *Delastria faustiniana*. Holotype (LIP 0001434). A, B: Ascomata; C: Gleba; D: Ascospores. Photos: A. Paz & C. Lavoise

Delastria liebanensis A. Paz, F. Rodríguez & Lavoise, *sp. nov*. – MycoBank MB 826771 – Fig. 8, 9G.

Diagnosis: Differs from *Delastria evae* by its regular globose ascomata and its gleba with thick lilac-grey veins. Holotype: LIP 0001432.

Etymology: The epithet refers to Liébana (Spain), the place where the species was discovered.

Description: Ascomata globose, 1.5–2.5 cm diam. **Surface** when young embedded in a thick but brittle cream then light brown pubescence with light lilac tones, strongly aggregating particles of sand and debris; peridium persistent, very thin, colourless and unchanging where bruised. **Gleba** compact, originally white, at first with a hymenium appearing as small subcircular to ellipsoidal, light pink spots, with reddish brown tones between thick sterile, lilac-grey veins when mature. **Odour** fungoid.

Peridium 96–160 µm thick, 2-layered: outer layer a cutis of parallel thin-walled, branched hyphae 5–12 µm wide, encrusted by soil particles; inner layer made of subglobose, colourless thick-walled (1.5–2 µm thick) cells measuring 22–34 × 18–26 µm. **Gleba** made of thick sterile veins made of colourless, thin-walled gelatinized hyphae 6-4 µm wide, septate. **Asci** originally pear-shaped, becoming subspherical at maturity, shortly pedunculate, 95–115 × 65–100 µm, usually 3–spored. **Ascospores** spherical, 28–39 (–42) µm diam., with a reticulate ornamentation of irregular dimples, during maturation with long and thin conical aculei formed on wall sides, 1.3 µm wide, 5.5 µm high, smaller and thicker on crests, 1.8 × 3.2 µm.

Ecology: All collections were found in late spring, under *Quercus suber* and with many *Cistaceae* (*Cistus ladanifer* and *C. monspeliensis*).

Observations: This species displays an ITS sequence distinct from all others in the genus by at least 2.7% of divergence (*D. evae*, Table 2). *Delastria evae* is distinct by its irregularly nodulose ascomata and thin white veins in gleba, whilst *D. liebanensis* is remarkable by its globose, almost regular ascomata and thick, lilac-grey veins. Both species are characterized in the genus by a cinnamon-coloured peridial coating.

Material studied: Spain. Cantabria, Camaleño, Tanarrio, N 43º 9′ 27.23″ W 4º 42′ 11.23″, 715 m elev., under *Quercus suber* and *Cistus ladanifer*, 15 May 2016, *leg*. A. Paz, LIP 0001432 (holotype), pers. herb. A. Paz IC15051606 (isotype)*; *ibid*., 13 Apr 2011, *leg*. A. Paz, pers. herb. A. Paz IC13041113; *ibid*., 7 May 2014, pers. herb. A. Paz IC07051407. Cataluña, Girona, Selva, Santa Coloma de Farners, Sant Miquel de Cladells, N 41º 51′ 33.31″ E 2º 33′ 48.12″, 464 m elev., under *Quercus suber* and *Cistus monspeliensis*, 16 Jan 2018, *leg*. F. Rodríguez & A. Paz, pers. herb. A. Paz IC16011801*; *ibid*., 13 Mar. 2018, *leg*. F. Rodríguez, pers. herb. A. Paz IC13031801.

Results and discussion

The phylogenetic analysis of our ITS dataset reveals a well-supported monophyletic /Delastria lineage, encompassing two main clades (/rosea and /supernova), quite distant from each other (Fig. 1 and Table 2). The limited number of sequences in most clades prevents intraspecific polymorphism to be estimated but based on that of *D. rosea* (Dintra = 1.2%, Table 2), all *Delastria* species described in this study should display Dintra < Dinter and thus be resolved by ITS DNA barcoding.

The first clade (/rosea) so far includes the sole *D. rosea*. With ca 25% of sequence divergence at the ITS locus (Table 2), relative to species in the /supernova clade, *D. rosea* has an evolutionary history quite distinct from, and older than, that of the other species in the genus. Perhaps, linked to an ancient origin, this species displays the widest biogeographical distribution in the genus, from North Morocco to the middle of France along a S–N axis, and from Canary Islands to Corsica along a W–E axis. From a morphological point of view, *D. rosea* is characterized by ascomata wrapped in a very fragile white pubescence, gradually fading and exposing the outside of the gleba, which is intensely pink.

The second clade (/supernova) includes seven lineages, two of them so far known only by a single ectomycorrhizal sequence each and referred to as *D.* sp1 and *D.* sp2 on Fig. 1. Further taxon sampling is needed to formally describe them. The remaining five species, all but one described here as new to science, diverge from *D. rosea* by a persistent peridium consisting of an encrusted cream-cinnamon pubescence and a gleba marbled in small-sized patches. Our phylogenetic analysis unveiled crypticism within the previously published *D. supernova*, leading to the introduction of *D. faustiniana* as a new species. The two species look very similar (reminding white truffles) but differ by 37 differences along their ITS sequences (5.86% of sequence length, Table 2). In its narrower limits, *D. supernova* can be distinguished from its cryptic sibling and from all other known species in the genus, by its unique broadly ellipsoidal spores (Fig. 9). Additional collections of *D. faustiniana* will help better circumscribing its taxonomic borders. *Delastria javieri* occupies the most basal branch of the phylogram and thus represents the most ancient lineage within the genus, after *D. rosea* (Fig. 1). It differs from its closest relative *D. supernova* by 71 nucleotide differences at the ITS locus, representing more than 11% of sequence divergence (Table 2). Morphologically, the species is easily recognized by its typical cerebriform ascomata, with the gleba divided in septate chambers. *Delastria evae* and *D. liebanensis* constitute the two most derived, and likely latest, lineages in the /supernova clade, but this distal phylogenetic position, as well as their sister clade relationships, are only weakly supported (Fig. 1). This species pair is, however, the most closely related one in the genus, with only 18 differences at the ITS locus, representing 2.74% of sequence divergence (Table 2). The former is morphologically very similar to *D. rosea* but can be distin-

Table 2 – Pairwise phylogenetic distances within *Delastria*.*

	D. evae	*D. liebanensis*	*D. faustiana*	*D.* sp1	*D. supernova*	*D.* sp2	*D. javieri*	*D. rosea*
D. evae	2/0.3%	2.74%	3.66%	4.12%	5.34%	6.4%	13.26%	25.83%
D. liebanensis	18	na	3.17%	4.01%	4.68%	5.1%	14.84%	26.28%
D. faustiana	24	20	0/0%	5.23%	5.86%	6.03%	14.42%	25.83%
***D.* sp1**	27	25	33	na	5.94%	6.49%	14.45%	32.02%
D. supernova	35	29	37	37	na	4.95%	11.45%	24.77%
***D.* sp2**	42	33	39	42	32	na	11.75%	24.62%
D. javieri	87	92	91	90	71	76	0/0%	25.08%
D. rosea	171	174	171	212	164	163	166	8/1.2%

* Maximal intraspecific distances (Dintra, diagonal) and minimal interspecific distances (Dinter), expressed as absolute number of differences (lower matrix, light grey) and percent difference relative to the longest paired sequence (upper matrix, dark grey). Values include indels but exclude polyN length polymorphisms and nucleotide changes located at distal ends of sequences for which no trace file is available. na: not applicable (single sequence).

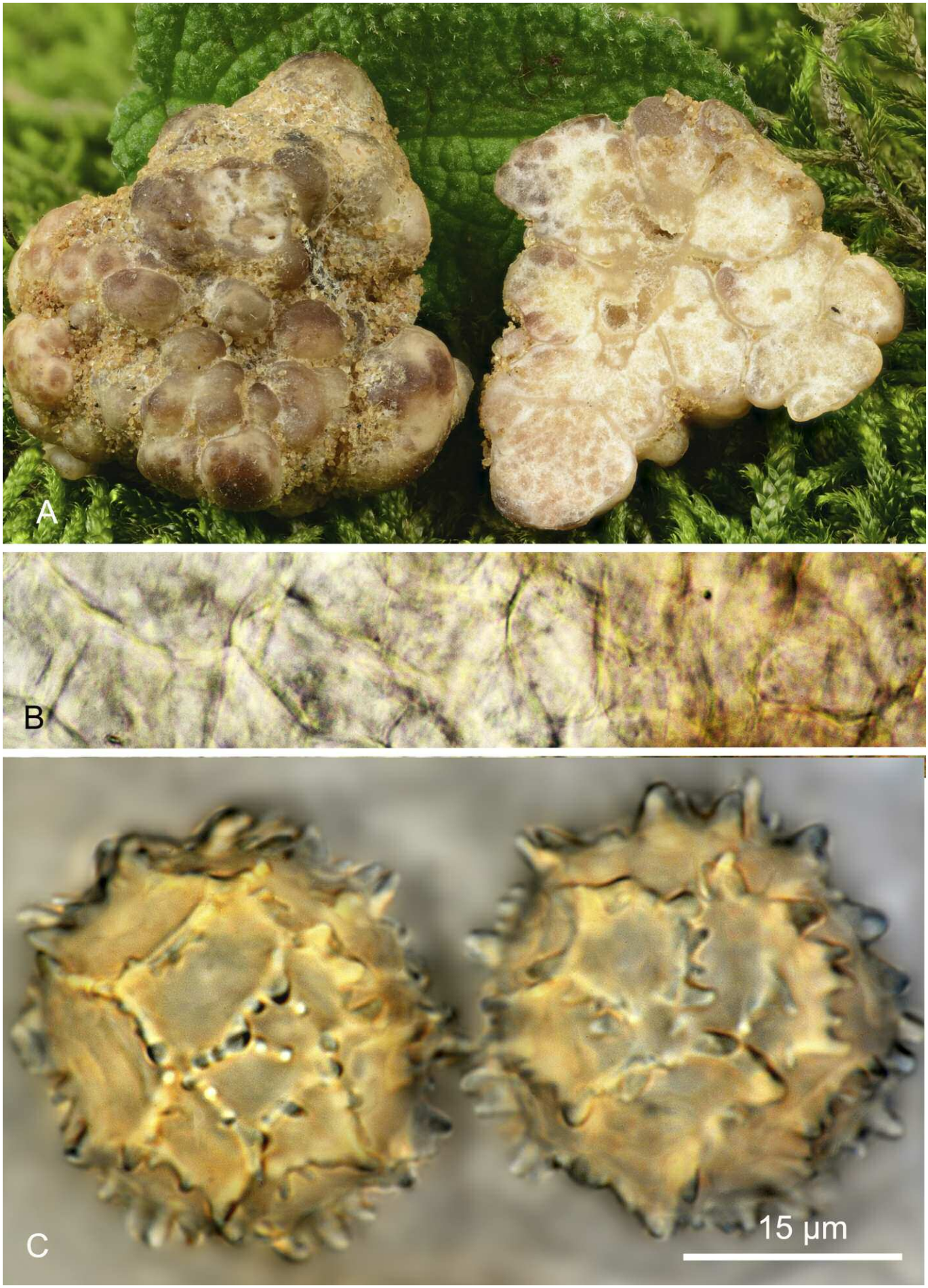

Fig. 7 – *Delastria javieri*. Holotype (LIP 0001433). A: Ascomata; B: Peridium; C: Ascus and ascospores; D: Ascospores. Photos: A. Paz & C. Lavoise

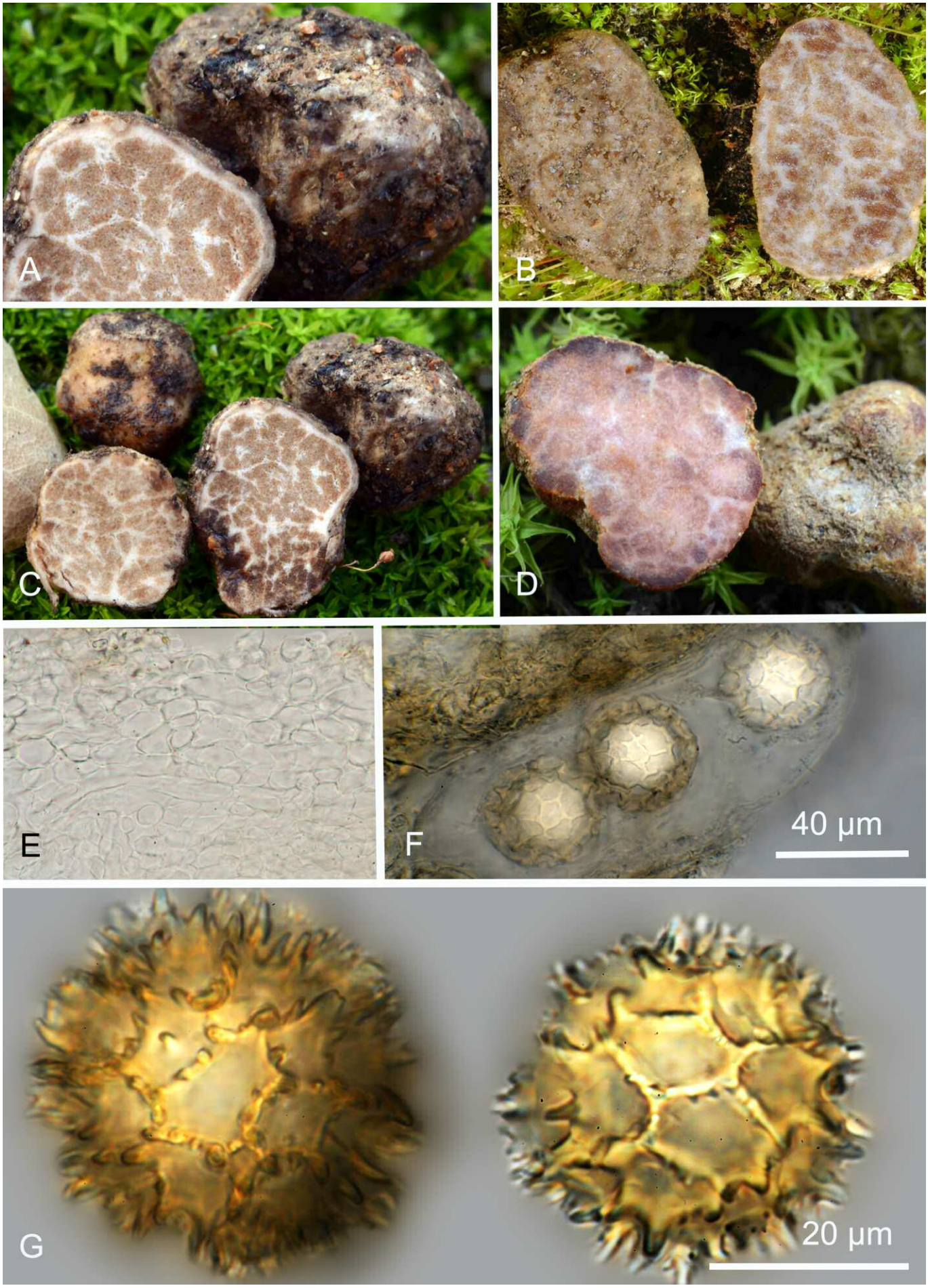

Fig. 8 – *Delastria liebanensis*. Paratype (IC05071801). A, C: Ascomata. Holotype (LIP 0001432). B, D: Ascomata. E: Peridium. F: Ascus and ascospores. G: Ascospores. Photos: A. Paz & C. Lavoise

guished from it by, in addition to the persistent peridium, a cream pubescence, a less intensely pink colour, a gleba with smaller spots and slightly larger spores differently ornamented. It occurs in various regions of Spain and is also reported from Italy, likely Sardinia (Table 1 and Osmundson *et al*., 2013). The latter, so far known from Cantabria and Cataluña, produces globose ascomata with very persistent cream-brown pubescence with lilac tinges and the largest spores in the genus.

In its currently known worldwide content, the genus *Delastria* is mostly represented within a relatively small area centered on Spain. Considering that 1) underground fungi are not so intensively collected nor studied as their more visible relatives, and 2) one of us (A. Paz) is an internationally recognized expert in the field and lives in the North of Spain, an obvious "mycologist bias" may be responsible for this narrow biogeography. However, although we do not contest this bias in general, we don't believe *Delastria* biogeography can be explained just by its overlap with home and field trips of one of its taxonomic specialists. First, even though underground fungi are less thoroughly studied than epigeous taxa, other experts of these truffle-like mushrooms exist in the world and none of them so far published a sequence belonging in this lineage, that did not originate from Spain, Portugal, Morocco, Italy or France. Second, the increasing number of molecular studies aiming at describing soil or ectomycorrhizal fungal communities, fill public databases with thousands of fungal ITS sequences and so far, the only ones nesting in the *Delastria* lineage are from the Iberian Peninsula. Third, other underground genera are represented in Spain, without displaying such a restricted distribution range. This is the case for *Elaphomyces* for instance, which has been studied by A. Paz for decades but is present all over the world (Paz *et al*., 2017).

Thus, the current West Mediterranean distribution of *Delastria* is likely not artefactual and may reflect a genuine regional endemism. However, the report of *D. rosea* in California (Harkness, 1899; Gilkey, 1916; Parks, 1921, and Gilkey, 1954) and Mexico (Gómez-Reyes *et al*., 2017), despite not confirmed by molecular data, challenges this view and raises two competing hypotheses to account for the presence of the genus in North America. First, a late introduction of *D. rosea* from its original Mediterranean range to North America, may have occurred, potentially through anthropogenic activities. This hypothesis is, however, not strongly supported by the reported ecology of the Mexican collections, quite distinct from that of Mediterranean collections of this species (*Carpinus caroliniana* vs *Cistaceae* and *Pinus* spp., respectively). Alternatively, an early split from a common Euramerican ancestor, may have segregated two old lineages that would have subsequently undergone asymmetric radiation, yielding one (or a few) *D. rosea*-like species in North America and the bunch of species reviewed here in the Mediterranean area. Sequencing the recent Mexican material would sort these two hypotheses out and will be crucial to unveil the evolutionary history of the genus. Ecological drivers of such a biogeography remain to be identified but the biotrophic association of most species with *Pinus* and *Cistaceae* members, evidenced by several ectomycorrhizal sequences, certainly constitutes a first clue to be investigated further.

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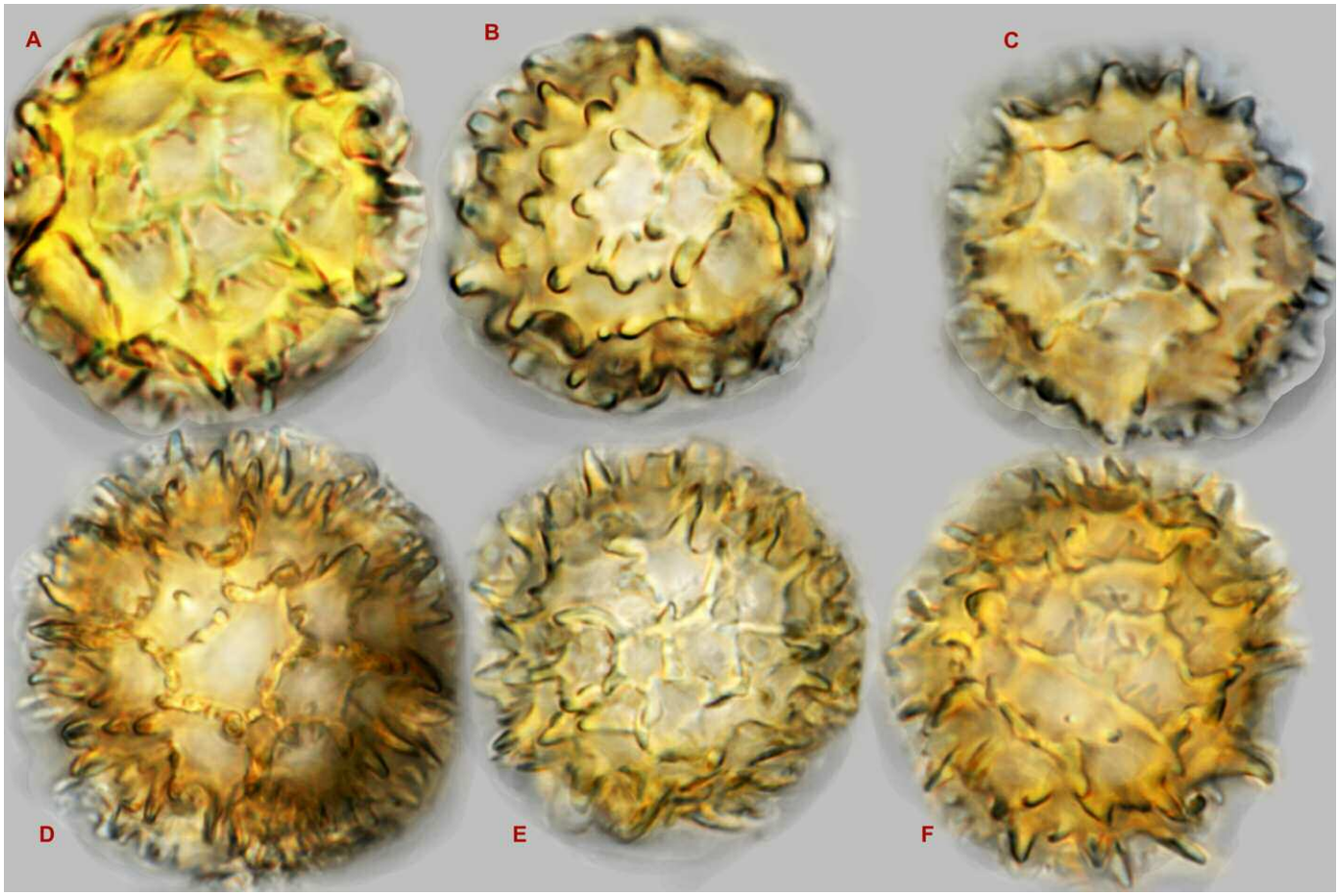

Fig. 9 – *Delastria* spp., ascospores. A, B: *D. rosea*; C: *D. supernova*; D: *D. evae*; E: *D. faustiniana*; F: *D. javieri*; G: *D. liebanensis*. Photos: A. Paz & C. Lavoise

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