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Exploring the European *Trichophaea*-like discomycetes (*Pezizales*) using morphological, ecological and molecular data

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Abstract: Recent collections of unknown *Trichophaea*-like discomycetes made in Europe enabled the authors to explore the taxonomy of *Trichophaea* and allies, based on morphological, ecological and molecular data. Our 3-gene phylogeny confirms the paraphyly of the genus *Trichophaea* and designs a new systematics for this group of cup-fungi. Three new genera are published to accommodate several species previously assigned to *Trichophaea* or morphologically close genera: *Perilachnea* gen. nov. with *Lachnea hemisphaerioides* as type-species, *Aurantiolachnea* gen. nov. with *Lachnea solsequia* as type-species, and *Parawilcoxina* gen. nov. with *P. inexpectata* sp. nov. as type-species. Some species of the genus *Paratrichophaea* belong to the cleistothecial genus *Lasiobolidium*, and furthermore two new species, *L. trachysporum* and *L. coprophilum*, are described. *Paratrichophaea macrocystis* is also combined in *Lasiobolidium*. Finally, three new species of *Chaetothiersia*, *C. laricina*, *C. cupressicola* and *C. eguttulata* are described. A new species of *Perilachnea*, *P. ochraceoflava*, is outlined from Italy, and a new species of *Trichophaeopsis*, *T. asturiensis*, is described from Spain. A total of 15 species are described and illustrated herein. Keys are provided.
Keywords: *Ascomycota*, *Pyronemataceae*, rDNA, phylogeny, taxonomy, 3 new genera, 8 new species, 2 new typifications.

Introduction

Under the term "*Trichophaea*-like" discomycetes we designate an informal group of hairy cup-fungi belonging to the *Pyronemataceae* Corda, having a light-coloured hymenium, i.e. white, pale grey to pale brown, and showing a strong contrast between dark marginal hairs and this light-coloured hymenium. Besides the genus *Trichophaea* Boud. itself, this group mainly encompasses the genera *Paratrichophaea* Trigaux (Trigaux, 1995; Bronckers, 2003), *Trichophaeopsis* Korf & Erb (Korf & Erb, 1972), *Chaetothiersia* B.A. Perry & Pfister (Perry & Pfister, 2008), some *Wilcoxina* species (Yang & Korf, 1985), and *Humaria* Fuckel, but some genera like *Tricharina* Eckblad (Yang & Korf, 1985; Van Vooren *et al*., 2017, 2019), *Pseudotricharina* Van Vooren, Tello & M. Vega (Van Vooren *et al.*, 2015), *Tricharinopsis* U. Lindem., Van Vooren & Healy (Van Vooren *et al.*, 2019) and *Lotinia* Pérez-Butrón, Fern.-Vic. & P. Alvarado (Pérez-Butrón *et al*., 2015) may also have some morphological affinities. The latter are not treated here because they have been treated in detail in recent articles (see previous references) and belong to the */Geopora-Tricharina* clade (see "Molecular results" chapter). However, they are cited in the main key published at the end of this paper. The genus *Geopora* Harkn. is excluded because of its mode of semi-hypogeous or hypogeous development. Some other extralimital species have been explored during this study because of their current systematic position inside the */Humaria* clade (see "Molecular results" chapter), e.g. *Humaria solsequia* (Quél.) Van Vooren & Moyne, *Parascutellinia* spp. and yellow-coloured *Chaetothiersia* spp.

From a historical point of view, the hairy operculate discomycetes had been treated by Fries (1822) in his tribe *Sarcoscyphae*, series *Lachnea*, of the genus *Peziza*. This group was a heterogeneous assemblage of 30 species. Karsten (1861) partially followed Fries but placed the species previously assigned to *Sarcoscyphae* in a new subgenus, *Hystricina* P. Karst., and in the subgenus *Lachnea*, the latter being composed of operculate discomycetes (*Sarcoscyphae*) as well as inoperculates (*Dasyscyphae*). Later, Karsten (1869) changed his system: he only kept the inoperculate species in *Lachnea* (as a section of *Peziza*), whereas he transferred other species to a section *Aleuria*. Fuckel (1870) proposed another system to classify these species and defined the genus *Humaria* to accommodate most of them. Cooke (1879), using the Friesian classification, divided the series *Lachnea* into 5 subgenera: *Sarcoscypha* Fr., *Sepultaria* Cooke, *Rhizopodella* Cooke, *Scutellinia* Cooke and *Neottiella* Cooke. Gillet (1880) also followed Fries but raised *Lachnea* to the rank of genus. No difference between operculate and inoperculate hairy discomycetes was made in his publication. Saccardo (1884) adopted the genus *Lachnea* but also used the name *Humaria* in the sense of Fuckel, as a subgenus, to accommodate these species. Saccardo (1889) partly changed his classification, *Humaria s.* Fuckel being there treated as a simple synonym of *Lachnea*. Boudier (1885) proposed a more natural classification in which the dehiscence of asci was the first criterion to separate the discomycetes in two distinct groups (operculate and inoperculate discomycetes). He classified the hairy operculate discomycetes having a cupulate shape in his family Pezizés, group Lachnés, genera *Leucoscypha*, *Tricharia*, *Lachnea*, *Hydnocystis* and *Sepultaria*, whilst the discoid hairy species had been placed in his family Ciliariés, genera *Trichophaea*, *Ciliaria*, *Cheilymenia*, *Melastiza*, *Anthracobia* and *Pseudombrophila*. Later Boudier (1907) partially amended or completed his system: the family Pezizés became Pezizacées and Ciliariés became Humariacées, but the previously defined genera did not change. Phillips (1887) adopted Cooke's system, as did Massee (1895), both using the name *Lachnea* at the rank of genus for accommodating these species, instead of the genus *Peziza* as Cooke had done. Rehm (1896) proposed his own system where operculate discomycetes are classified in his family *Eupezizeae*. The hairy species had been placed in an amended definition of the genus *Lachnea s*. Fries and in *Sepultaria*.

In the first part of the 20th Century, the classification proposed by Boudier was variously admitted. It was mainly accepted by French authors like Grelet (1935) or Le Gal (1947), but, for this group of species, Lagarde (1906a, 1906b), Velenovský (1933) and Svrček (1948) used the genus *Lachnea* (Fr.) Gillet, following the Friesian tradition. Seaver (1928) and Snyder (1938) placed them in the genus *Patella* F.H. Wigg. Denison (1959) pointed out that *Lachnea* (Fr.) Gillet was illegitimate due to the existence of *Lachnea* L. 1753. Denison (1959) also designated *Peziza hemisphaerica* F.H. Wigg. as lectotype of the genus *Humaria*. Following the works of Kanouse (1958), Batra & Batra (1963) and Korf (1972), as well as subsequent authors, adopted Boudier's circumscription of *Trichophaea* and related genera, with the exception of Eckblad (1968) who considered it as a later synonym of *Humaria* Fuckel.

The recent discoveries of *Trichophaea*-like species made by the authors offered the opportunity to evaluate the taxonomy of this group of *Pyronemataceae* fungi in detail, in the light of their morphological, ecological and molecular data. Our results are presented in this article.

Material and methods

Morphological study. — The microscopic studies were based on both fresh and dried specimens, and made with optical microscopes with plan-achromatic objectives. For dried specimens, a small piece was placed in water for about two hours before the observation. The following main reagents were used: iodine solution (Melzer's reagent or Lugol solution), Cotton blue (CB), Congo red, and 5% KOH. Water mounts were used for the observation of the pigmentation and measurements; photographs of microscopical characters shown in our plates are made from water mounts, unless another medium is mentioned. At least 30 to 50 ascospores naturally discharged from the asci were measured from studied material. Ascospore measurements are given including ornamentation, using an ocular micrometer or the softwares Piximètre (www.piximetre.fr/) and Micam (science4all.nl/? Microscopy_and_Photography).

Note that the term "free croziers" is applied to asci having a particular pleurorynchous development as defined by Chadefaud (1943) that forms a horseshoe-shaped base. This type of crozier is well represented in the genus *Pulvinula* Boud. (Pfister, 1976).

Table 1 – Collections sequenced for this study

Name	Type	Collection ref.	Country	GenBank Accession Numbers			
				ITS	LSU	RPB2	TEF1
Anthracobia rehmii		FV2017052101	France	MW476530	MW476531	-	-
Aurantiolachnea solsequia		TUR-A 208919	Italy	MW546578	MW546543	MW544613	MW544628
Aurantiolachnea solsequia	E	LY NV 2016.10.11	France	MW546579	MW546544	MW544614	MW544629
Chaetothiersia laricina	H	TUR-A 208918	Italy	MW546580	MW546545	MW544615	MW544630
Chaetothiersia cupressicola	P	LY NV 2020.01.04	Spain	MW546581	MW546546	MW544616	-
Chaetothiersia eguttulata	H	MSTR:P-25015	Spain	MW546582	MW546547	-	-
Lasiobolidium boudieri		L.D. 31.08.04	France	MW546583	MW546548	MW544617	MW544631
Lasiobolidium coprophilum	H	MAAS RB 01127	Netherlands	MW546584	MW546549	-	-
Lasiobolidium coprophilum	P	R.B. 01123	Netherlands	-	MW546550	-	-
Lasiobolidium coprophilum	P	JA-CUSSTA 9525	Spain	MW546585	MW546551	-	-
Lasiobolidium parvisporum		E.R.D. 7668	Spain	MW546586	MW546552	MW544618	MW544632
Lasiobolidium trachysporum	I	LY NV 2019.04.14	Spain	MW546587	MW546553	-	-
Lasiobolidium spirale	P	TRTC 41596	USA	MW546588	MW546554	-	-
Lasiobolidium spirale	P	TRTC 41942	USA	MW546589	MW546555	-	-
Perilachnea hemisphaerioides		LY NV 2010.07.02	France	MW546590	MW546556	-	MW544633
Perilachnea hemisphaerioides		LY NV 2014.06.12	France	MW546591	MW546557	MW544619	MW544634
Perilachnea hemisphaerioides		ERD-4327	Spain	MW546592	MW546558	-	-
Perilachnea flavobrunnea cf.		TUR-A 208921	Italy	MW546593	MW546559	MW544620	MW544635
Perilachnea flavobrunnea		TUR-A 208916	Hungary	MW546594	MW546560	MW544621	MW544636
Perilachnea ochraceoflava	H	TUR-A 208917	Italy	MW546595	MW546561	MW544622	MW544637
Parascutellinia carneosanguinea		MSTR P04365	Germany	MW546596	MW546562	-	-
Parascutellinia fuckelii		U.R. 1000-1016	Switzerland	MW546597	MW546563	MW544623	MW544638
Parawilcoxina inexpectata	I	LY NV 2019.09.17	Spain	MW546598	MW546564	MW544624	MW544639
Sphaerosporella sp.		FV2014071601	France	MW476527	MW546565	-	-
Sphaerosporella hinnulea		G RD 25.31.242.98	France	MW476529	-	-	-
Trichophaea pseudogregaria		LY NV 2013.08.71	France	MW546599	MW546566	-	-
Trichophaea contradicta		G.M. 2019 07 01	France	MW546600	-	-	-
Trichophaea contradicta		G RD 27.03.246.02	Switzerland	MW476528	MW546567	MW544625	MW544640
Trichophaea paludosa		LY NV 2011.08.35	France	-	MW546568	-	-
Trichophaea woolhopeia		LY NV 2013.08.51	France	MW546601	MW546569	-	MW544641
Trichophaea woolhopeia		TUR-A208920	Italy	MW546602	MW546570	MW544626	MW544642
Trichophaea woolhopeia		K(M) 46543	Great Britain	MW546603	MW546571	-	-
Trichophaeopsis asturiensis	H	LY NV 2013.06.19	Spain	MW546604	MW546572	-	-
Trichophaeopsis bicuspis		LY NV 2012.05.04	France	MW546605	MW546573	-	-
Wilcoxina sp. 1		G.M. 20160801	France	MW546606	MW546574	-	-
Wilcoxina sp. 2		LY NV 2016.09.01	Belgium	MW546607	MW546575	-	-
Pyrometaceae sp. UR		ETH ZT Myc 61122	Switzerland	MW546608	MW546576	MW544627	MW544643
Pyrometaceae sp. UR		ETH ZT Myc 61123	Switzerland	MW546609	MW546577	-	-

Type values: H=holotype, I=isotype, E=epitype, P=paratype.

DNA extraction, amplification and sequencing. — Total DNA has been extracted from dry specimens employing a modified protocol based on Murray & Thompson (1980). PCR reactions (Mullis & Faloona, 1987) included 35 cycles with an annealing temperature of 54 °C. Primers ITS1F and ITS4 (White *et al.*, 1990, Gardes & Bruns, 1993) were employed to amplify the ITS rDNA region, while LR0R and LR5 (Vilgalys & Hester, 1990; Cubeta *et al.*, 1991) were used for the 28S rDNA region, EF1-728F, EF1-983F and EF1- 2218R (Carbone & Kohn, 1999; Rehner & Buckley, 2005) for the translation elongation factor 1α (tef1) gene, and bRPB2-6F2 (reverse of bRPB2-6R2), and bRPB2-7R2 for the RNA polymerase II second largest subunit (rpb2) gene (Liu *et al.*, 1999; Matheny *et al.*, 2007). PCR products have been checked in 1% agarose gels, and positive reactions have been sequenced with one or both PCR primers. Chromatograms have been checked searching for putative reading errors, and these have been corrected.

Phylogenetic analyses. — The system BLAST (Altschul *et al.*, 1990) was used to select the most closely related sequences from the International Nucleotide Sequence Database Collaboration (INSDC) public database (Cochrane *et al.*, 2011). Sequences came mainly from Hansen *et al.* (2005, 2013), Perry *et al.* (2007), Van Vooren *et al.* (2017), Alvarado *et al.* (2018) and Lindemann *et al.* (2019). Sequences were first aligned in MEGA 5.0 (Tamura *et al.*, 2011) software with its Clustal W application and then corrected manually. The final alignment included 445/798 (LSU, 156 sequences), 389/865 (tef1, 103 sequences) and 331/589 (rpb2, 99 sequences) variable/total sites. Final alignments have been loaded in MrBayes 3.2.6 (Ronquist *et al.*, 2012), where a Bayesian analysis has been performed (3 partitions (LSU, tef1, rpb2), two simultaneous runs, four chains, temperature set to 0.2, sampling every 100th generation) until convergence parameters were met after 4.41 M generations, standard deviation having fallen 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 (same partitions, GTRCAT model, 2000 bootstrap replications). Significance threshold was set above 0.95 for posterior probability (PP) and 70% bootstrap proportions (BP).

Nomenclature, terminology. — The taxonomic novelties were registered in the MycoBank database (www.mycobank.org), including typifications (MBT number). The nomenclature follows the current version of ICN (Turland *et al.*, 2018). The herbarium acronyms are in conformity with the Index Herbariorum (sweetgum.nybg.org/science/ih/). For specimens housed in personal herbaria, the term "pers. herb." is used, followed by the author's reference.

Locations. — Locations of studied collections are given by countries, in alphabetical order, then region (or province or department), town, more precise location (in native language). The coordinates are given in decimal WGS84 format.

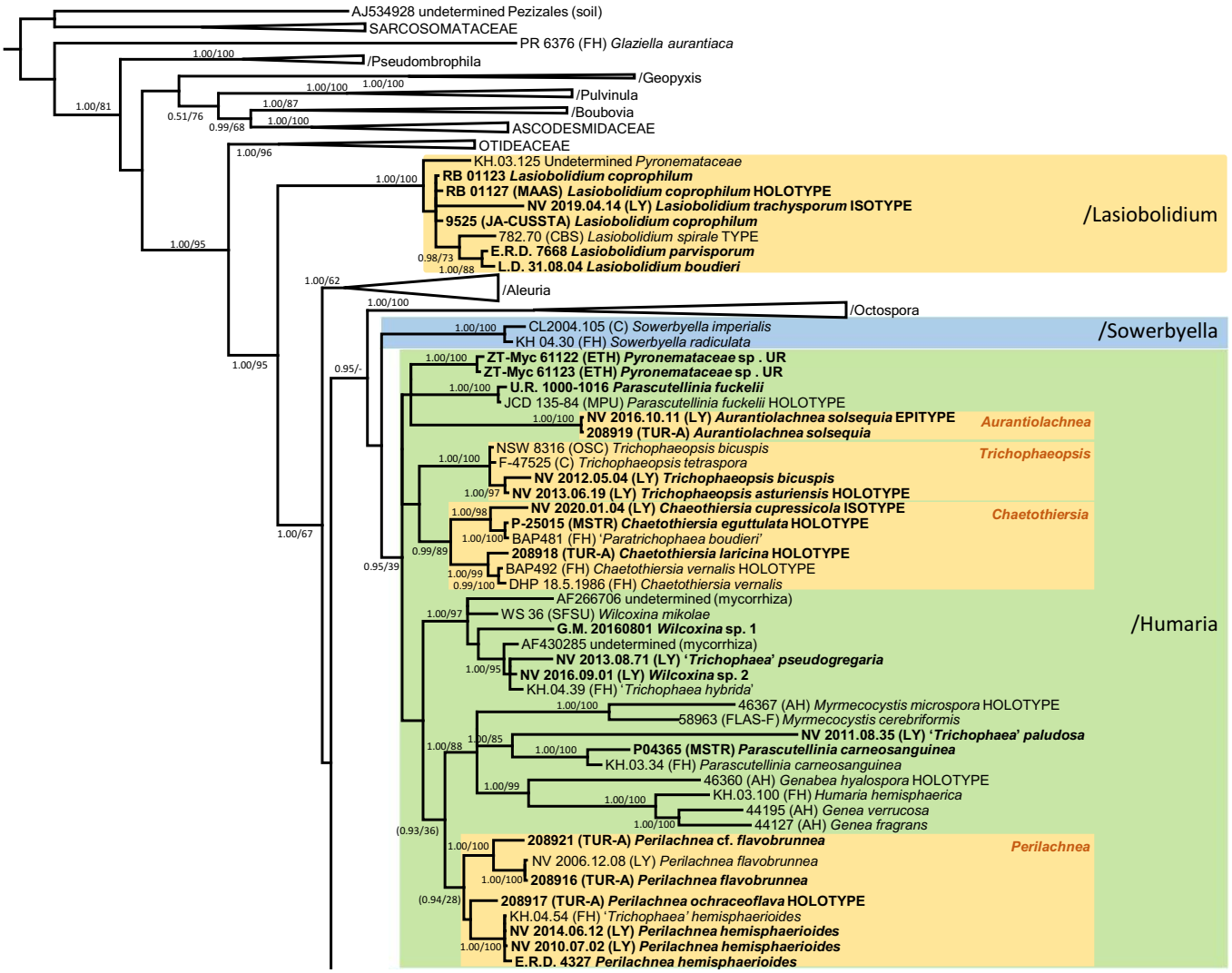

Fig. 1 – 50% majority rule 28S rDNA-tef1-rpb2 consensus phylogram of the family *Pyronemataceae* (*Pezizales*) and related clades (with family *Sarcosomataceae* as outgroup) obtained in MrBayes from 36900 sampled trees. Nodes were annotated if supported by ≥ 0.95 Bayesian PP (left) or ≥ 70% ML BP (right). Nonsignificant support values are exceptionally represented inside parentheses. Nodes in bold come from sequences obtained during this study.

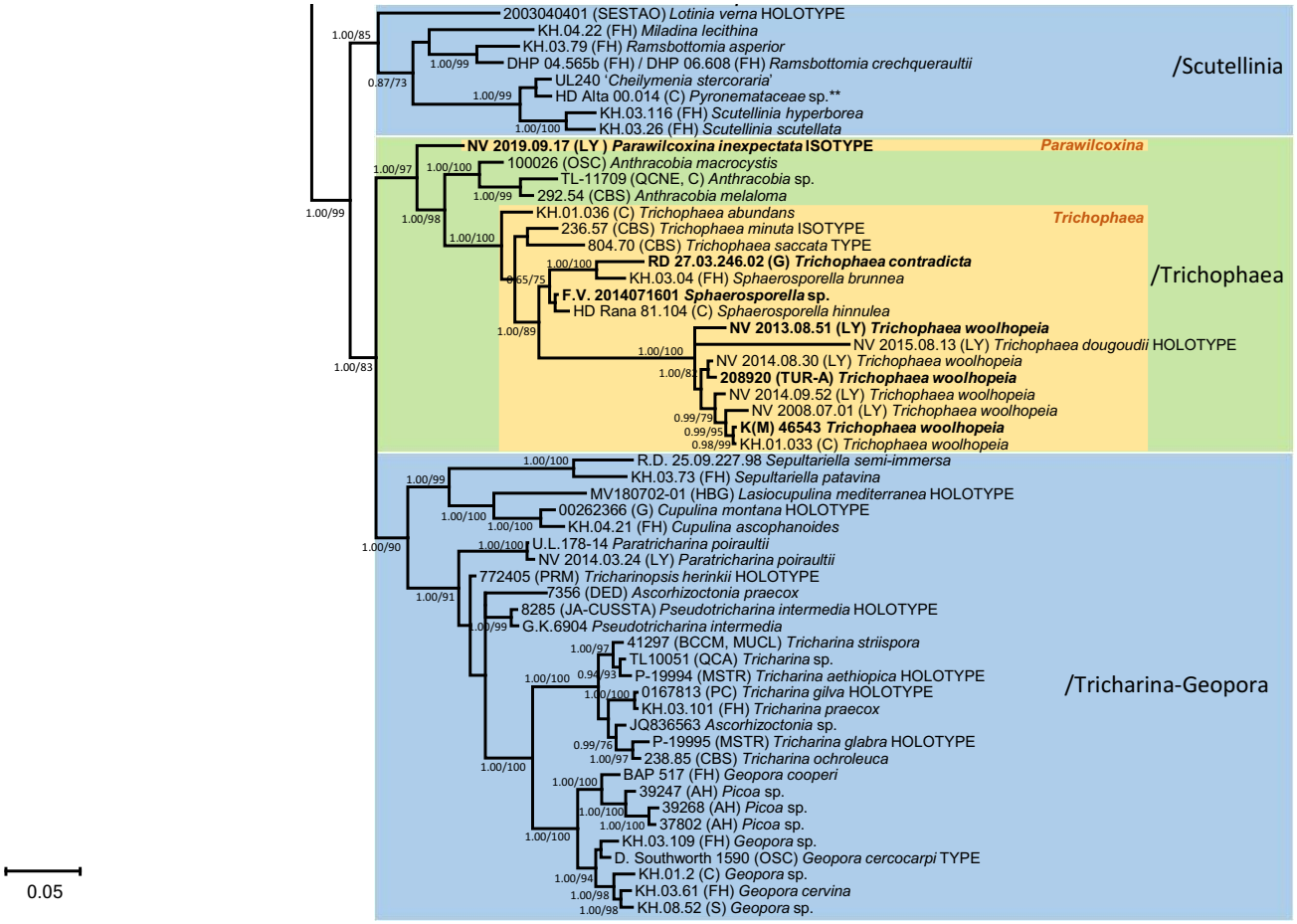

Fig. 1 (continued). ** In GenBank this sequence has been registered under the erroneous name *Kotlabaea deformis*. See Lindemann *et al.* (2015).

Molecular results

Our 3-gene phylogeny was initially focused on the */Scutellinia*, */Trichophaea* and */Humaria* lineages as delineated by Hansen *et al.* (2013). It contains sequences of species belonging to *Trichophaea* as circumscribed by classical systematics (Korf, 1972; Dennis, 1978; Dissing *et al*., 2000; Bronckers, 2003). Our results confirm the paraphyly of *Trichophaea* which must be used only for smooth-spored species belonging to the *T. woolhopeia* complex (see Van Vooren, 2016) and to a group of species having a *Dichobotrys*-like asexual morph, i.e. *T. abundans* (P. Karst.) Boud., *T. minuta* (Cain) Korf, *T. saccata* (H.C. Evans) Korf, *T. contradicta* (Seaver) H.J. Larsen, *T. brunnea* (Alb. & Schwein.) L.R. Batra, etc. (see Fig. 1). *Trichophaea* belongs to a super clade also containing the genus *Anthracobia* Boud. but we believe that merging these two genera into one single "super" genus would be unsatisfactory from a morphological point of view, *Anthracobia* having excipular pseudo-hairs and paraphyses containing carotenoid pigments.

All other known and sequenced species of *Trichophaea* do not belong to the */Trichophaea* lineage. Thus, *Trichophaea hemisphaerioides* (Mouton) Graddon and *T. flavobrunnea* (Richon) Priou, B. Perić, Van Vooren & Hairaud belong to a clade in the */Humaria* lineage that deserves a new genus, namely *Perilachnea* nov. gen. (see description below). Furthermore, another new species *Perilachnea ochraceoflava* is described.

As previously shown in Perry *et al*. (2007) and Hansen *et al.* (2013), the species of *Trichophaea gregaria – hybrida* complex — characterised by pluriguttulate fusoid ascospores — belong to the *Wilcoxina* clade. The other known species of *Wilcoxina* have eguttulate ascospores. All the species of this genus possess hairs arising from a chain of roundish thick-walled brown cells (Yang & Korf, 1985). *Trichophaea paludosa* (Boud.) Boud., another warted-spored species of *Trichophaea s.l.*, belongs to its own clade, sister of *Parascutellinia*. Other species ornamented with large, irregular or tuberculous warts such as *T. livida* (Schumach.) Boud. or *T. tuberculata* (Seaver) Kanouse need to be evaluated.

Among the *Trichophaea*-like genera, *Trichophaeopsis* Korf & Erb and *Paratrichophaea* Trigaux were tested with new sequenced collections. *Trichophaeopsis* belongs to the */Humaria* lineage. A new species *T. asturiensis* is described from north-western Spain.

Several species previously belonging to *Paratrichophaea* appear to be nested in the */Lasiobolidium* lineage, containing fimicolous and soil-inhabiting hairy cleistothecial species. This result strongly suggests that *Paratrichophaea* is a later synonym of *Lasiobolidium* Malloch & Cain that requires to be amended to include apothecial species. The sequence of *Paratrichophaea boudieri* (Grelet) Bronckers [coll. BAP 481 (FH) from USA] proved to belong to the genus *Chaetothiersia* as amended in this article, and is described as a new species, *C. eguttulata*. The revision of this collection also proved that its morphological characters are different from the known European collections of *P. boudieri*. Two other new species of *Chaetothiersia* are described in the present paper, *C. cupressicola* and *C. laricina*.

Lotinia verna Pérez-Butrón, Fernández-Vicente & P. Alvarado which resembles some brown species of *Trichophaea* belongs to the */Scutellinia* lineage in an isolated position. As this species had already been described and illustrated in detail in Pérez-Butrón *et al*. (2015) and Van Vooren & Vega (2018), we do not present this species in the current paper. However, it is important to note that in the latter paper the asci were described without croziers which is a mistake because they are present.

Although *Humaria solsequia* (Quél.) Van Vooren & Moyne belongs to the */Humaria* lineage, it occupies an isolated position and the new genus *Aurantiolachnea* is proposed to accommodate it.

Finally, *Humaria hemisphaerica* (F.H. Wigg.) Fuckel considered as a *Trichophaea*-like species by some authors (Eckblad, 1968; Bronckers,

2003) is actually related to the hypogeous genus *Genea* Vittad. (Alvarado *et al*., 2018) and has to be considered as a species complex. It will be not treated in the present paper.

We briefly summarise the taxonomic groups in the table 2.

The genus *Trichophaea*

The genus *Trichophaea* was published by Boudier (1885) to accommodate some operculate discomycetes having "des poils du réceptacle longs et aigus, [à] spores le plus souvent garnies de gouttelettes intérieures, [à] hyménium blanchâtre ou glauque" that is "long and sharp hairs of receptacle, spores often containing droplets, a whitish to glaucous hymenium." The type species is *Peziza woolhopeia* Cooke & W. Phillips, the only species designated by Boudier (*op. cit*.) in the original publication (Art. 9.1 ICN). The genus was amended by Boudier (1907) who confirmed that the apothecia were not cupulate but thick and lenticular. A list of 22 species was given in this publication. Afterward, based on morphological criteria, some species were transferred to new genera, *Trichophaeopsis* (Korf & Erb, 1972) and *Paratrichophaea* (Bronckers, 2003).

The molecular works by Perry *et al.* (2007) dealing with the *Pyronemataceae* demonstrated that the genus *Trichophaea* was paraphyletic but did not provide much more than a first step. Van Vooren (2016) produced a phylogeny based on the LSU locus that confirmed this result and showed that *T. woolhopeia* (Cooke & W. Phillips) Arnould represents a species complex.

As a starting point of our study, we propose to amend the definition of the genus *Trichophaea*:

Trichophaea Boud. – MB 5574

Type species: *Trichophaea woolhopeia* (Cooke & W. Phillips) Arnould, *Bull. Soc. mycol. Fr*., 9: 112 (1893).

Synonyms: *Sphaerosporella* (Svrček) Svrček & Kubička; *Dichobotrys* Hennebert.

Amended description: Ascomata epigeous, apothecial, sessile, subglobose, discoid or cupuliform, hymenium whitish, pale grey to grey-brown, brown or blackish, with an external surface covered by superficial brown hairs. Margin hairy. Excipulum two-layered: medullary layer thick, of *textura intricata* and ectal layer of *textura subglobulosa/angularis*. Hairs superficial, septate, with a simple base. Asci operculate, arising from croziers, inamyloid, 8-spored. Paraphyses slender, equal to enlarged (sometimes capitate) at the top, hyaline. Ascospores uniseriate, ellipsoid or spherical, hyaline, uniguttulate, more rarely biguttulate, thick-walled, smooth. Species forming ectomycorrhizas. Asexual morph of *Dichobotrys* type (Hennebert, 1973).

Contains the other following European species: *T. abundans*, *T. brunnea*, *T. contradicta*, *T. dougoudii*, *T. hinnulea*, *T. minuta*, *T. paraphysincrustata*, and *T. saccata*.

As the genus *Anthracobia* appears closely related to *Trichophaea* from a molecular point of view, we also propose an amended definition:

Anthracobia Boud. – MB 228

Type species: *Anthracobia melaloma* = *Peziza melaloma* Alb. & Schwein., *Consp. fung*.: 336 (1805), *nom. sanct*.

Amended description: Ascomata epigeous, apothecial, sessile, first cupuliform then discoid or flattened, hymenium yellow-orange to dull orangish, with an external surface covered by superficial light umber brown to brown pseudo-hairs, i.e. brown clavate or obtuse elongated cells. Margin hairy. Excipulum two-layered: medullary layer of *textura intricata* and ectal layer of t*extura subglobulosa/angularis*. Asci operculate, arising from croziers, inamyloid, 8-spored. Paraphyses slender, enlarged to capitate at the top, hyaline. Ascospores uniseriate, ellipsoid, hyaline, biguttulate, thick-walled, smooth. Species saprobic on burnt soil. Asexual morph of *Scytalidium* type (Larsen, 1976).

Contains the other following species: *A. macrocystis*, *A. nitida*, *A. tristis* (syn. *A. muelleri*), and *A. uncinata*. Based on the LSU gene, Perry *et al.* (2007) suggested *A. subatra* to be a *Trichophaea* species (as also suggested by Boudier, 1907). However, the type of "hairs" of *A. subatra* (the same as in *Anthracobia*) and the ascospore content are rather different from a true *Trichophaea*. Another problematic species is *A. uncinata* (Velen.) Spooner which does not have carotenoid pigments in its paraphyses. Finally, *A. rehmii* Brumm. is also a species which could be excluded from *Anthracobia*, because it possesses true hairs and does not have carotenoid pigments. A molecular analysis with several genes is required to resolve these questions.

These two genera will be treated in a forthcoming article.

Taxonomy

This chapter provides a detailed description of a series of *Trichophaea*-like genera, including the European species that belong to them. For existing genera an amended definition is given. A dichotomous key to the species included is proposed after the description of each plurispecific genus.

Aurantiolachnea Van Vooren, *gen. nov.* – MB 836267

Diagnosis: Differs from *Humaria* by the orange-coloured hymenium, smooth or finely dotted ascospores, its saprobic trophic status and genetic profile.

Type species: *Lachnea solsequia* Quél., *C. R. Assoc. Fr. Avancem. Sci*., 20 (2): 464 (1892).

Etymology: From Latin *aurantio* meaning "orange" and ancient Greek λάχνη *(lákhnê)* meaning "down, hairs". *Lachnea* is also the original genus to which the type species had been referred (considered now as a later synonym of *Humaria*).

Table 2 – Taxonomic groups treated in our phylogeny. The new genera are marked with *

Lineage	Genera	Synonyms	References
/*Humaria*	*Aurantiolachnea**		
	Chaetothiersia		Perry & Pfister (2008)
	Humaria	*Mycolachnea*	Denison (1959)
	*Perilachnea**		
	Trichophaeopsis		Korf & Erb (1972)
	Wilcoxina		Yang & Korf (1985)
/*Lasiobolidium*	*Lasiobolidium*	*Paratrichophaea*	Malloch & Benny (1973), Trigaux (1985)
/*Scutellinia*	*Lotinia*		Pérez-Butrón *et al.* (2015)
/*Trichophaea*	*Anthracobia*		Larsen (1976)
	*Parawilcoxina**		
	Trichophaea	*Sphaerosporella, Dichobotrys*	Bronckers (2003)

Description: Ascomata epigeous, apothecial, sessile, orange-coloured, with an external surface and margin covered by brown hairs. Excipulum two-layered: medullary layer of *textura intricata*, ectal layer of *textura subglobulosa/angularis*. Hairs simple, superficial, septate, with a simple base. Ascospores uniseriate, ellipsoid, hyaline, biguttulate, smooth or very finely dotted. Asci operculate, narrowing towards the base, arising from croziers, inamyloid, 8-spored. Paraphyses slender, not enlarged at the top, containing carotenoid pigments. Trophic status probably saprobic. Asexual morph unknown.

Comments: For a long time, mycologists named this rarely reported fungus *Humaria aurantia* (Clem.) Häffner, Benkert & Krisai until Van Vooren & Moyne (2010) resurrected Quélet's epithet *solsequia*. This species until now had been placed in the genus *Humaria* because of its appearance, resembling *H. hemisphaerica*, except for the orange colour and smooth ascospores. Molecular data suggest that this species deserves its own genus (Fig. 1) and we propose to name it *Aurantiolachnea*. It is also interesting to note that we did not find any correspondence with some EcM sequences using the ITS gene, suggesting the species to be saprobic, another difference with *H. hemisphaerica* which forms ectomycorrhizas (Tedersoo *et al*., 2006).

Aurantiolachnea solsequia (Quél.) Van Vooren, *comb. nov.* – MB 836268 – Pl. 1

Basionym: *Lachnea solsequia* Quél., *C.R. Assoc. fr. avanc. sci*., 20 (2): 464 (1892).

Homotypic synonym: *Humaria solsequia* (Quél.) Van Vooren & Moyne, *Bull. mycol. bot. Dauphiné-Savoie*, 197: 47 (2010).

Other synonyms: *Sepultaria aurantia* Clem., *in* Pound & Clem., *Bot. Survey Nebraska*, 4: 12 (1896); *Lachnea aurantia* (Clem.) Sacc. & P. Sydow., *Syll. fung*., 14: 757 (1899); *Scutellinia aurantia* (Clem.) Waraitch, *Trans. Br. mycol. Soc*., 68 (1): 37 (1977); *Humaria aurantia* (Clem.) Häffner, Benkert & Krisai, *Österr. Z. Pilzk*., 3: 84 (1994).

Misinterpretations: *Lachnea hybrida* (Sow.) W. Phillips, in the sense of Boudier (1905-1910), non Sowerby (1803); *Scutellinia hybrida* (Sow.) M. M. Moser, *Kl. Kryptog*., IIa: 106 (1963), *nom. inval.*

Original diagnosis: Peridium ovoïde puis hémisphérique (0m,005-15), céracé-coriace, mince, paille, hérissé de poils courts, fauves, plus longs et bais au bord. Hyménium souci. Spore ellipsoïde (0mm,012-015), sublancéolée, biocellée (Pl. II, fig. 5.)

Été. – En troupe sur l'humus mêlé de charbon, dans les bois, Jura. Décrit sous le nom de *Humaria hybrida*, Sow. *Enchir. Fungorum*, p. 284, lequel est une forme de *crinita*, Bull. Il est affine à *carneorufa*.

Typification: Lectotype here designated: fig. 5, pl. II, in Quélet (1892); MBT 393136. Epitype here designated: France, coll. LY:NV 2016.10.11; MBT 393137.

Apothecia 5–25 mm diam., sessile, first subglobular then deeply cupuliform, hymenium first reddish orange, then orange, apricot, or yellow orangish; external surface ochraceous yellow, densely covered with brown short hairs on young specimens, more sparsely with age. **Margin** densely hairy with dark brown hairs. **Flesh** thin.

Subhymenium and **medullary excipulum** not distinguished, of *textura intricata*, with hyaline hyphae. **Ectal excipulum** of *textura subglobulosa/angularis* with yellow-brown cells, up to 40 µm diam. **Excipular hairs** superficial, straight, 70–540 × 11–20 µm, brown, septate, 1.5–2.5 µm thick-walled, sharp or obtuse at the top, with a simple enlarged or bulbous base, up to 30 µm wide. **Marginal hairs** similar but longer, up to 850 µm on average, but sometimes reaching 2000 µm. **Ascospores** uniseriate, ellipsoid, 15–16.5 (–17) × (6.5–) 8–9 µm, X = 15.7 × 8.3 µm, Q = 1.8–2.1, Qm = 1.9, hyaline, rather thick-walled, biguttulate, but often accompanied by smaller droplets, smooth or very finely verrucose in CB. **Asci** cylindrical, 220–260 × 10–12 µm, arising from free croziers, operculate, 8-spored. **Paraphyses** filiform, septate, not enlarged at the top, 3–4 µm diam., containing an orange granular pigment (carotenoids).

Studied collections: France. Haut-Rhin, Blotzheim, Am Liesbachberg, 47.58382° N 7.498834° E, alt. 288 m, on soil, under *Fagus sylvatica*, *Quercus*, *Carpinus*, 19 Oct. 2016, *leg*. M. Wilhelm, *rev*. N. Van Vooren, herb. LY:NV 2016.10.11 (epitype) and pers. herb. MW 52421865; GenBank ITS MW546579, LSU MW546544, RPB2 MW544614, TEF1 MW544629. Italy. Emilia-Romagna, Ferrara, Sant'Agostino, Bosco della Panfilia, 44.78257° N 11.376526° E, alt. 37 m, on the ground under broadleaves trees, 11 Jun. 2016, *leg*. A. Testoni, *rev*. M. Carbone, herb. TUR-A 208919; GenBank ITS MW546578, LSU MW546543, RPB2 MW544613, TEF1 MW544628. Moldova. Străşeni District, Lozova, Nature Reserve of Codru, ~47.092332° N 28.423519° E, alt. 300 m, on a decaying trunk of *Populus* sp., 1 Oct. 2005, *leg*. S. Manic, *det*. P. Chapon & P. Roux, *rev*. N. Van Vooren, pers. herb. P. Roux 4316.

Comments: The history of this taxon was reviewed in detail by Van Vooren & Moyne (2010). The lectotype designated here is an illustration by Quélet (1892). Boudier (1905-1910) also represented well this species in his *Icones*, pl. 356, but under the erroneous name of *Lachnea hybrida*, a misinterpretation of *Peziza hybrida* as figured by Sowerby (1803, pl. 369, fig. 1).

Distribution: Seemingly rare but widely distributed in Europe: Austria, France, Germany, Italy, Latvia, Moldova, Switzerland (Van Vooren & Moyne, 2010; Wilhelm, 2011; Tanchaud, 2020), and based on Internet ressources (GBIF): Poland, Serbia, and Slovakia. Outside Europe: India (Waraitch, 1977) and USA (Pound & Clements, 1896). The collections reported from Spain by García-Blanco *et al.* (2008) is a misinterpretation for *Chaetothiersa cupressicola* (see under this name). The Turkish collection presented by Kaya *et al*. (2016), on litter of *Cupressus sempervirens*, is doubtful based on the morphology of the presented specimens and may also represent *C. cupressicola*, but their description is much too vague to propose a correct determination.

Chaetothiersia B.A. Perry & Pfister – MB 510434

Type species: *Chaetothiersia vernalis* B.A. Perry & Pfister, *Fungal Divers*., 28: 69 (2008).

Amended description: Ascomata epigeous, apothecial, sessile, cupuliform, pale grey to whitish-coloured or yellow to orangish yellow, with an external surface covered by brown hairs. Margin hairy. Excipulum two-layered: medullary layer thick, of *textura intricata*, and ectal layer of *textura globulosa/angularis*. Hairs superficial, simple, septate, with a simple ± swollen base. Ascospores uniseriate, ellipsoid, hyaline, guttulate or not, smooth. Asci operculate, narrowing toward base, arising from free croziers, inamyloid, 8-spored. Paraphyses slender, equal to enlarged (sometimes subcapitate) at the top, hyaline or containing a sparse granular yellow pigment. Species saprobic on the litter and woody debris of conifers. Asexual morph unknown.

Comments: The monotypic genus *Chaetothiersia* was originally described to accommodate *Chaetothiersia vernalis* B.A. Perry & Pfister, a vernal species growing on bark of Red Fir (*Abies magnifica* A. Murray) in the High Sierra Nevada, California, USA (Perry & Pfister, 2008). Known only from the type locality, the distribution of *Chaetothiersia vernalis* has been recently widened by eight confirmed locations in a high-elevation forest of the northern central Sierra Nevada, near the Cascades, in California (Siegel *et al*., 2019).

Upon a single parsimony phylogenetic analysis inferred from nLSU sequence data, the genus was genetically confirmed as sister to *Paratrichophaea* and morphologically distinguished from the latter mainly by brown, non-rooting, stiff superficial excipular and marginal hairs with obtuse apices, and larger apothecia (Perry & Pfister, 2008). But this result is based on an erroneous determination of the specimen named *P. boudieri*. We revised this collection and con-

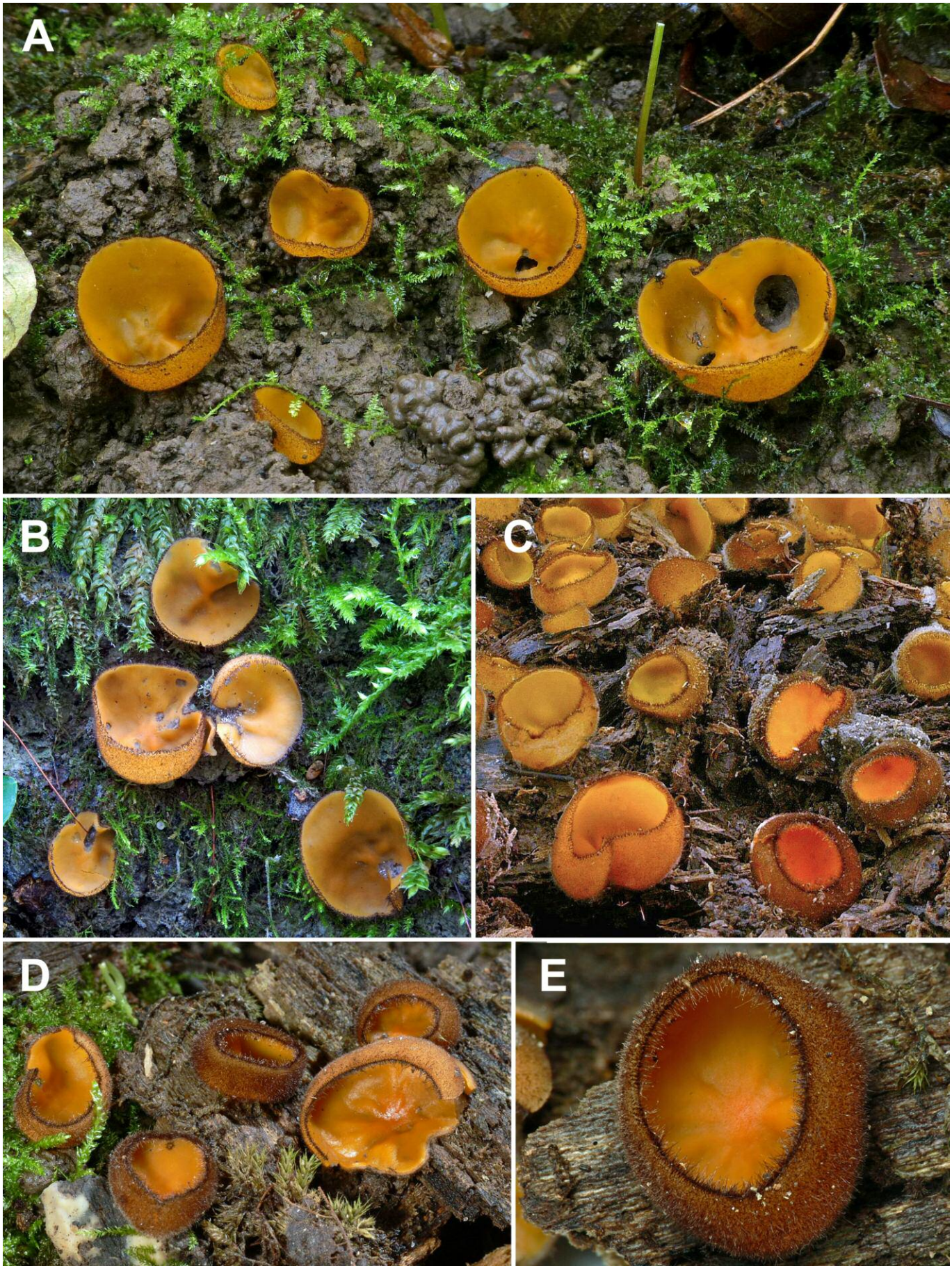

Plate 1 – *Aurantiolachnea solsequia*

Various collections *in situ*. A. Coll. NV 2016.10.11, photo M. Wilhelm. B. Coll. TUR-A 208919, photo A. Testoni. C. Coll. PR 4316, photo P. Roux. D–E. Coll. MW 3685, photos M. Wilhelm.

Key to the species of *Chaetothiersia*

1. Apothecia with a whitish to pale grey hymenium **2**
1. Apothecia with a yellow to orangish yellow hymenium **3**
2. Ascospores 15.5–17 × 9–9.5 µm; on woody debris of *Larix decidua* ..... ***C. laricina***
2. Ascospores 16.8–18.4 × 10–11.2 µm; on woody debris of *Abies* [USA] ..... ***C. vernalis***
3. Ascospores 18–19.1 (20.1) × 10.5–11.7 (12.3) µm, biguttulate; on wood of *Cupressus* ..... ***C. cupressicola***
3. Ascospores 17–18.7 (19.5) × 11.2–12.2 (12.9) µm, eguttulate; on wood of *Abies* ..... ***C. eguttulata***

cluded it was a new species, very different from *P. boudieri*, and we named it *Chaetothiersia eguttulata*. Thus, the species of *Paratrichophaea* are far from *Chaetothiersia* in our own 3-gene phylogeny, but nested in the */Lasiobolidium* clade.

Two other new species of *Chaetothiersia*, the first one growing in the litter of *Larix decidua* and the second one on dead branches of *Cupressus*, are decribed and illustrated in the following.

Chaetothiersia laricina M. Carbone & Alvarado, *sp. nov*. – MB 837596 – Pl. 2–3

Diagnosis: Besides its genetic profile it differs morphologically from *C. vernalis* mainly by its shorter asci and smaller ascospores, 15.5–17 × 9–9.5 µm vs. 16.8–18.4 × 10–11.2 µm, a thinner wall to the hairs and by a different ecology, i.e. debris of *Larix*.

Type: Coll. TUR-A 208918 (holotype).

Etymology: From *Larix*, the host-tree.

Apothecia 5–25 mm diam, cupulate to discoid and tending to become slightly convoluted. Hymenium pale gray to whitish with some very pale yellowish hues, smooth; external surface concolorous, but appearing darker due to the brown appressed hairs. **Margin** distinct and covered with brown hairs.

Medullary excipulum of *textura intricata*, composed of densely woven hyaline hyphae, 2–7 µm wide, sometimes constricted at the septa, slightly thick-walled. **Ectal excipulum** of *textura globulosa/subangularis*, with hyaline cells up to 25 µm diam. **Excipular hairs** 70–380 × 5–8 µm, superficial, pale brown to almost hyaline, septate, thick-walled (up to 1.5 µm), apically rounded, bulbous at the base or enlarged and slightly swollen, arising from cells of the ectal excipulum. **Marginal hairs** similar. **Ascospores** (15–) 15.5–17 (–18) × 9–9.5 (–10), Qm = 1.7, ellipsoid, smooth, eguttulate, hyaline, with granular cytoplasmic content, slightly thick-walled. **Asci** 260–300 × 11–12 µm, cylindrical, arising from free croziers, operculate, 8-spored. **Paraphyses** narrow, 1.5–2 µm diam., apically enlarged up to 3.5 µm, straight, multiseptate, simple, hyaline.

Studied collection: Italy. Piemonte, Cuneo, Pontechianale, Chianale, 44.64975° N 6.985944° E, alt. 1800 m, on the edge of a track in a pure *Larix decidua* forest, on mossy soil with debris, 10 Jun. 2018, *leg*. M. Carbone, herb. TUR-A 208918; GenBank ITS MW546580, LSU MW546545, RPB2 MW544615, TEF1 MW544630.

Comments: *Chaetothiersia laricina* is macroscopically very similar to its sister American species *C. vernalis* but it clearly differs from the

Plate 2 – *Chaetothiersia laricina*. Coll. TUR-A 208918 (photo M. Carbone)

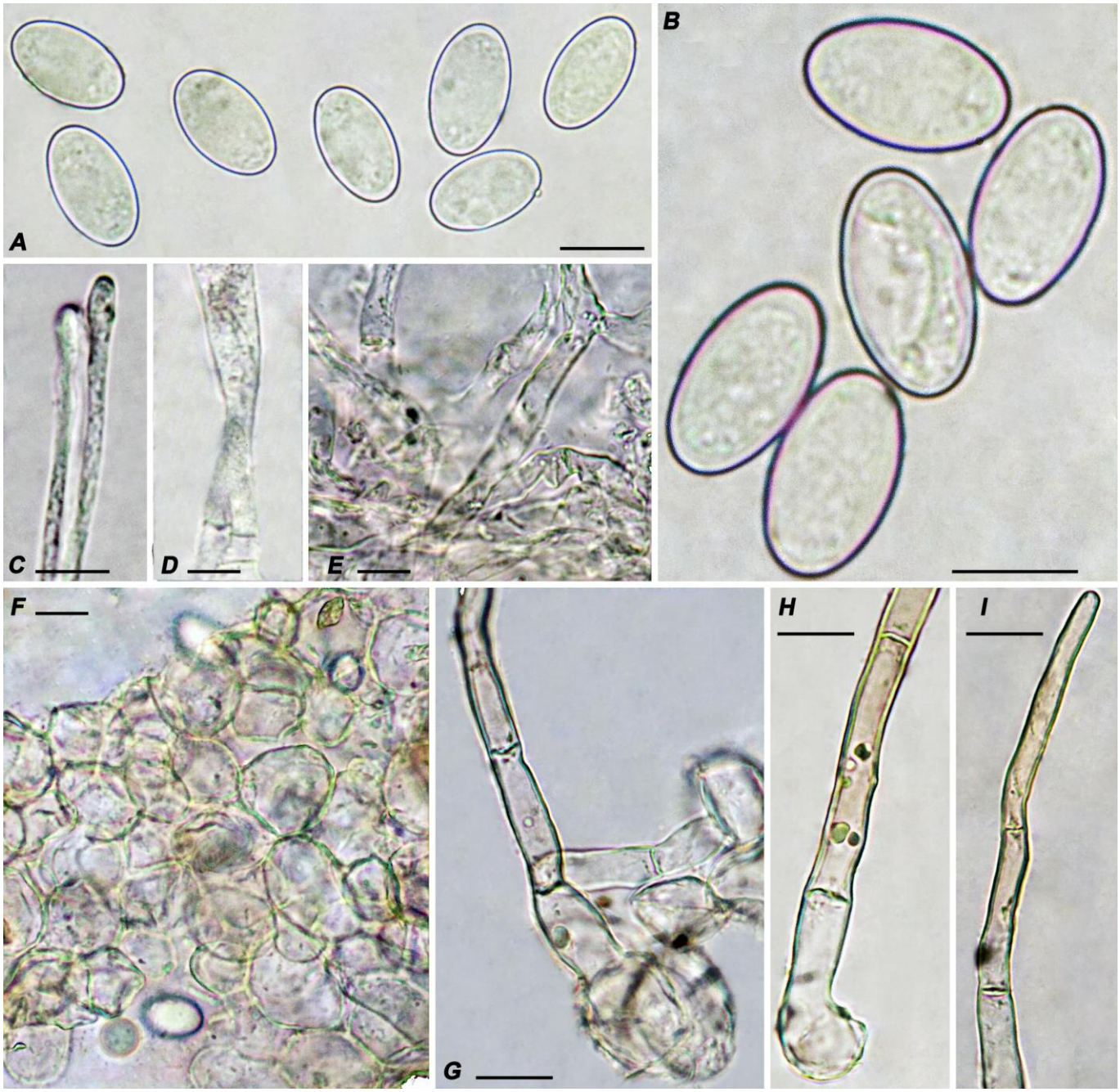

Plate 3 – *Chaetothiersia laricina*. Microscopical characters
A–B: Ascospores; C: Paraphyses tips; D: Ascus base; E: Medullary excipulum; F: Ectal excipulum; G–H: Basal part of external hairs; I: Excipular hair tip. All mounted in water. Scale bars = 10 µm. Photos M. Carbone.

latter by its shorter asci and smaller ascospores. Compared to the protologue of the latter, the excipular hairs seem to show some morphological difference as they have thinner walls, up to 1.5 µm in laricina and 2.4 µm in vernalis. The two species show a different ecology: *C. laricina* is so far known to be associated with *Larix decidua*, whilst *C. vernalis* had been reported to be related to *Abies magnifica*.

Trichophaea laricina (Velen.) Svrček was described from rotten wood of *Larix* and is mainly characterised by very small apothecia (2–3 mm diam.) having hairs with pointed tips (Velenovský, 1934, under *Lachnea laricina*). Bronckers (2003) regarded this species as a *nomen dubium*.

In the Italian Alps, another species has been found under *Larix*, it is described herein as *Perilachnea ochraceoflava* (see description for the differences).

Distribution: Only known from the type locality in Northern Italy.

Chaetothiersia cupressicola Valencia, Van Vooren & M. Vega, *sp. nov.* – MB 837944 – pl. 4–5

Diagnosis: Differs from *C. eguttulata* by its guttulate ascospores, longer marginal hairs, and its growth on woody debris and dead branches of *Cupressus*.

Type: Coll. JA-CUSSTA:9527 (holotype).

Etymology: From *Cupressus*, the host-tree, and Latin suffix *–cola* meaning "living on".

Misinterpretation: *Humaria aurantia* s. García-Blanco *et al.* (2008).

Apothecia 3.5–10 mm diam., sessile, at first slightly obconical, then cupulate or discoid, barely depressed in the centre, hymenium yellow to glaucous yellowish; external surface subconcolorous or paler, with brown hairs at the margin and numerous anchoring hyphae at the base.

Subhymenium of *textura intricata/subglobulosa*, made of narrow hyphae mixed with subglobular elements. **Medullary excipulum** of *textura intricata*, thick, with hyaline hyphae, 4–8 µm wide. **Ectal**

excipulum thin, of *textura angularis/subglobulosa*, (15.5–) 20–21.5 (–26) × (12–) 14–15 (–18) µm, with hyaline cells, but with a yellowish wall in the outermost part. **Marginal cells** of *textura prismatica*, pale brown, the emerging article being clavate. **Marginal hairs** dense, pale brown, sometimes subhyaline at the top, straight or ± flexuous, (150–) 223–1093 × 8–15 µm, septate, 0.8–1.5 µm thick-walled, sharp at the top, more rarely obtuse, regular or subventricose, with a simple and often narrowed base, sometimes showing a hyaline amorphous matter in the lower part. **Excipular hairs** similar, but shorter, 40–450 × 8–12.5 µm, pale brown, more rarely subhyaline, sharp at the top, but the shortest being clavate. **Anchoring hyphae** present, up to 470 µm in length, 5–10 µm wide, flexuous, arising from a bulbous base, with a yellowish wall. **Ascospores** uniseriate, ellipsoid, (17–) 18–19.1 (–20.1) × (9.5–) 10.5–11.7 (–12.3) µm, X = 19 × 11.5 µm, Q =1.5–1.7 (–1.8), Qm = 1.6, hyaline, rather thick-walled, smooth, containing two large lipid drops, measuring 5–7 µm diam., accompanied by smaller droplets. **Asci** cylindrical, 255–300 (–317) × (10.5–) 11–15 (–15.5) µm, arising from free croziers, operculate, 8-spored. **Paraphyses** straight, slender, hyaline, septate, not or slightly enlarged at the top, 2.5–4 µm diam., diffusely yellow-pigmented, with sparse minute granular dark yellow pigments, without vacuolar bodies.

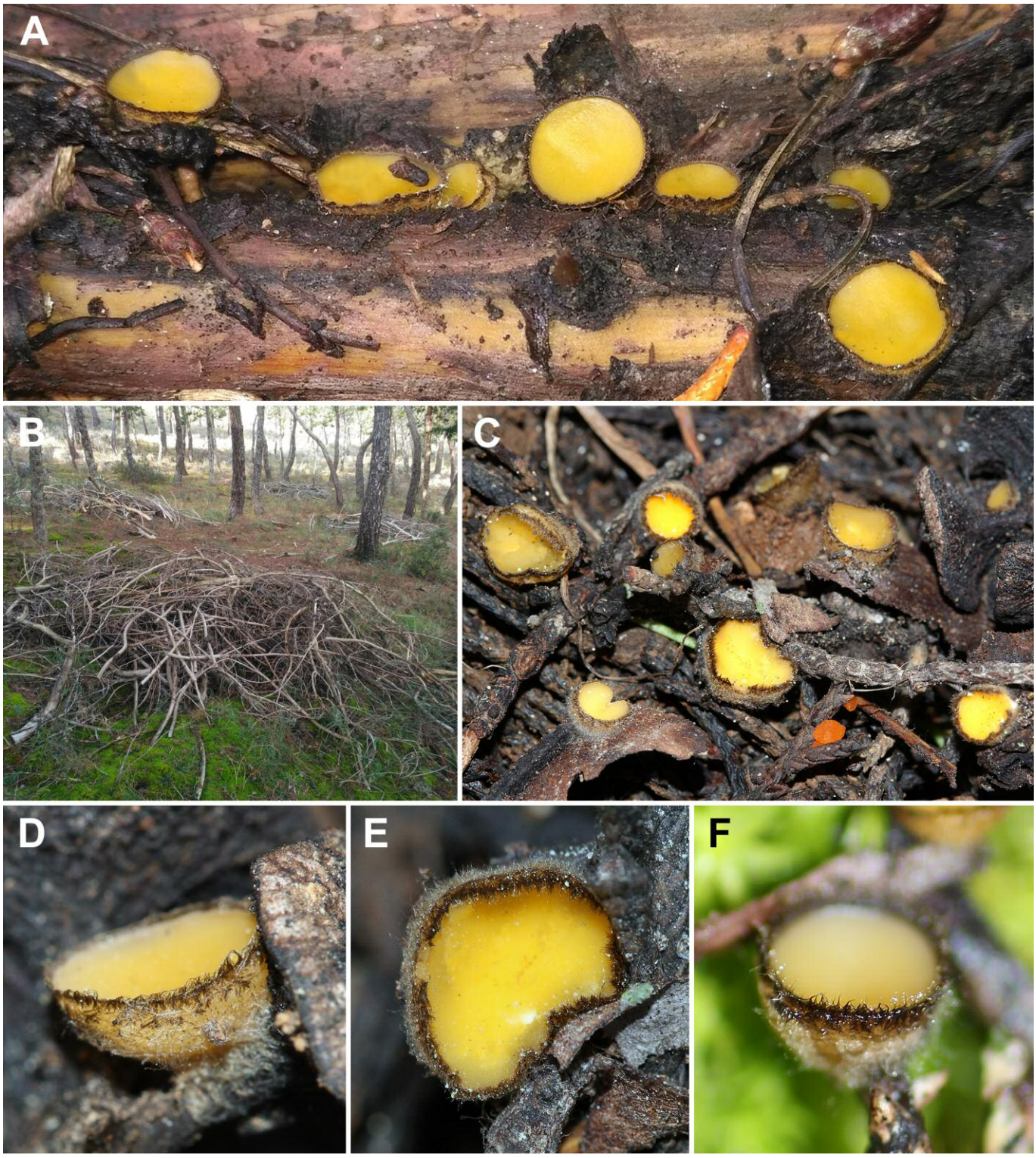

Plate 4 – *Chaetothiersia cupressicola*

A. View *in situ* of coll. CVL271219(1). B. Habitat of coll. CVL271219(1). C. View of coll. CVL100120(1). D–F. Close-up views. All photos by F.J. Valencia.

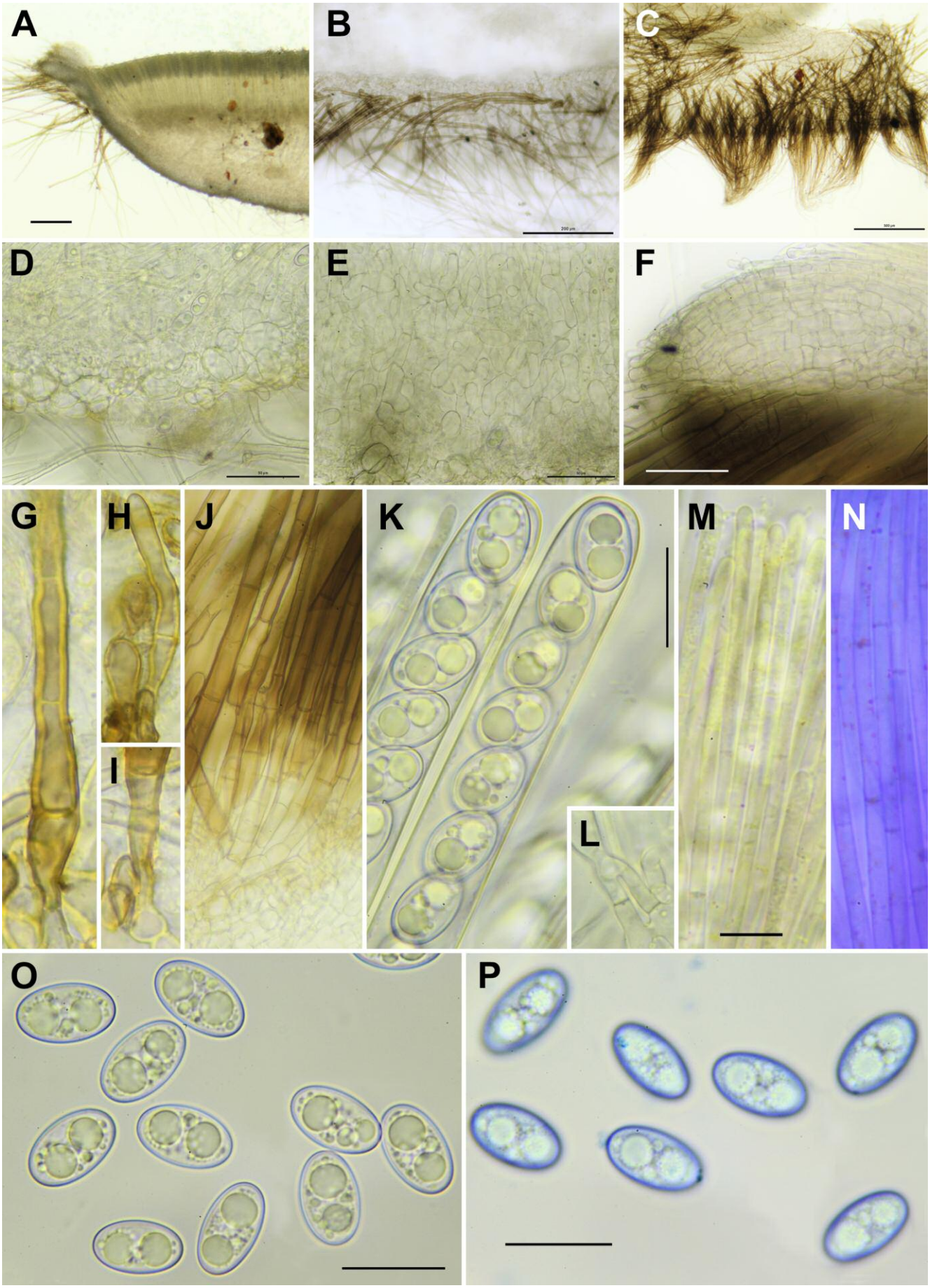

Plate 5 – *Chaetothiersia cupressicola*. Microscopical characters

A. Section of an apothecium. B. Excipular hairs. C. Marginal hairs. D. Ectal excipulum and base of anchoring hyphae. E. Medullary excipulum. F. Marginal cells. G–I. Different types of excipular hairs base. J. Marginal hairs base. K. Asci. L. Ascus base. M. Paraphyses. N. Paraphyses in aqueous Cresyl blue. O. Ascospores in water. P. Ascospores in Cotton blue. Scale bars: A–B = 200 µm, C = 500 µm, D–F = 50 µm, K, M, O–P = 20 µm. All photos by F.J. Valencia.

Studied collections: Spain. Palencia, Villamuriel de Cerrato, Monte Palentino, 41.9697° N 4.54467° W, alt. 820 m, in a plantation of *Pinus* sp. and *Cupressus* sp., on dead branches and debris of *Cupressus* sp., 27 Dec. 2019, *leg*. F.J. Valencia, ex herb. CVL271219(1), JACUSSTA:9527 (holotype). *Idem*, 3 Jan. 2020, *rev*. N. Van Vooren herb. LY:NV 2020.01.04; GenBank ITS MW546581, LSU MW546546, RPB2 MW544616. Málaga, Ronda, Paraje del Pilar de Coca, 36.76629° N 5.10867° W, alt. 735 m, along a path, on woody debris of *Cupressus arizonica*, 10 Jan. 2020, *leg*. F.J. Valencia, ex herb. CVL100120(1), JACUSSTA:9528.

Comments: Based on collections made in two different localities in Spain, *Chaetothiersia cupressicola* seems to be clearly associated to woody debris of *Cupressus* spp. Although this fungus shows a bright yellow hymenium, it seems that mycologists have not discovered this species before. This is even more curious because *Cupressus* trees are widespread in the Mediterranean basin and Western Atlantic coast. *C. cupressicola* could be confused with another species growing on dead twigs of *Cupressus*, *Strobiloscypha cupressina* B. Perić & Pfister. The latter usually has apothecia with a greyish to glaucous hymenium but some collections are yellowish-coloured (Perić *et al*., 2014). Microscopically, *S. cupressina* has ascospores with a different shape and content, and its hairs arise from an enlarged to bulbous base and have rounded apices.

García-Blanco *et al.* (2008) reported and illustrated this species, under *Humaria aurantia*, from collections growing on dead branches of *Cupressus arizonica* var. *glabra*.

Distribution: Only known from Spain. See also our remark under *Aurantiolachnea solsequia* concerning the latter in Kaya *et al.* (2016).

Chaetothiersia eguttulata Valencia, U. Lindemann & Van Vooren, *sp. nov.* – MB 837945 – pl. 6–7.

Diagnosis: Differs from *C. cupressicola* by its yellowish colour with slightly more orange tints, eguttulate ascospores, shorter marginal hairs and its growth on debris of *Abies*.

Type: Coll. MSTR:P-25015 (holotype).

Etymology: From Latin prefix *e-* meaning "without" and *guttula* meaning "droplet" (derived from Latin *gutta* "drop of liquid").

Plate 6 – *Chaetothiersia eguttulata*

A. Coll. CVL 050417(3) *in situ*. B. Close-up view of the external surface and margin. C. Close-up view of an apothecium. All photos by F.J. Valencia.

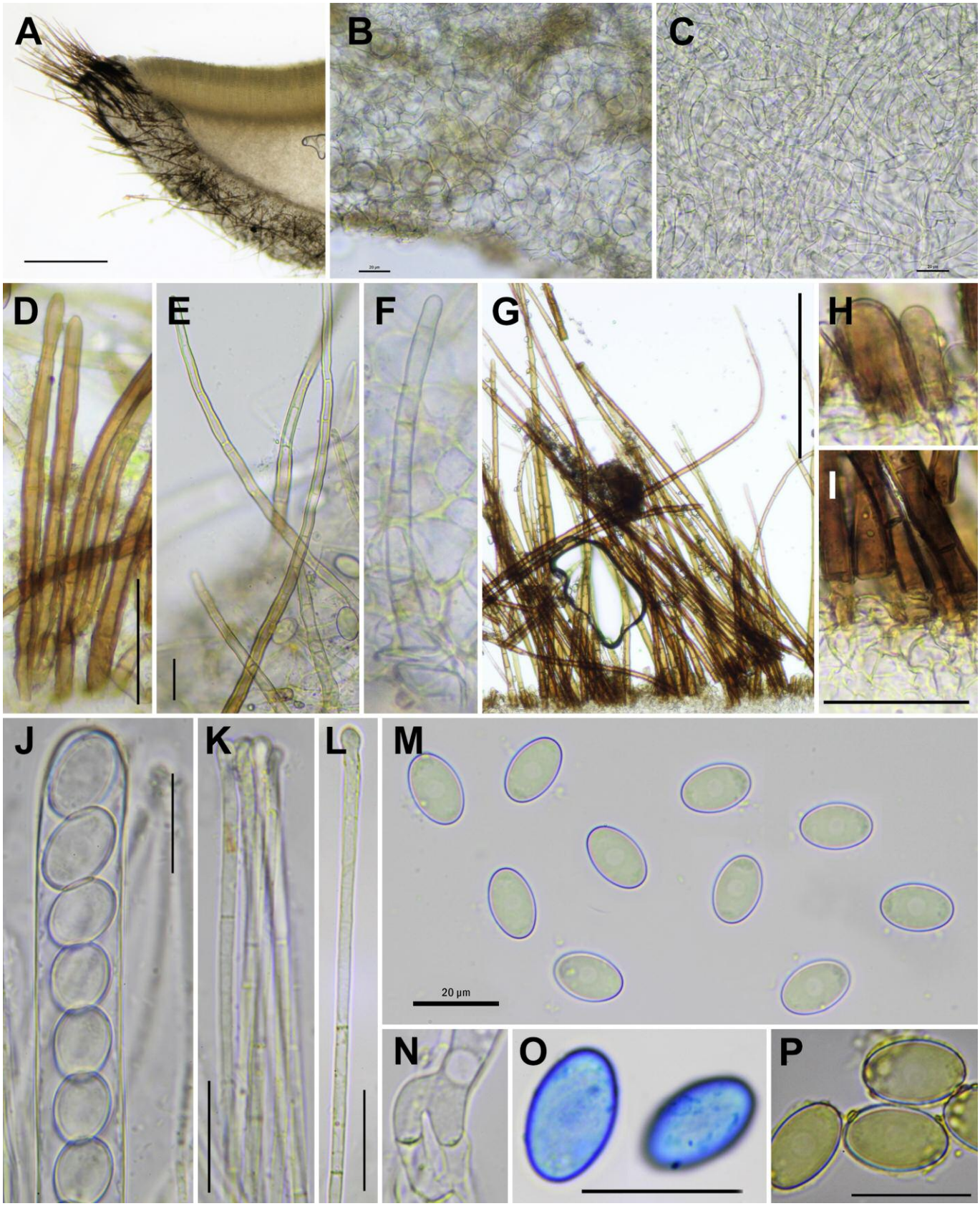

Plate 7 – *Chaetothiersia eguttulata*. Microscopical characters
A. Section of an apothecium. B. Ectal excipulum. C. Medullary excipulum. D. Brown excipular hairs. E. Light brown excipular hairs. F. Hyaline excipular hairs. G. Marginal hairs. H. Marginal micro-hairs. I. Base of marginal hairs. J. Ascus. K–L. Paraphyses. M. Ascospores in water. N. Ascus base. O. Ascospores in Cotton blue. P. Ascospores in Lugol's solution. Scale bars: A = 500 µm, B–C, J–P = 20 µm, D, I = 50 µm, E = 20 µm, G = 200 µm. All photos by F.J. Valencia.

Apothecia up to 6 mm diam., sessile, cupulate, hymenium yellowish orange; external surface concolorous. **Margin** densely covered by straight brown hairs, much less on the external surface.

Subhymenium and **medullary excipulum** not distinguished, of *textura intricata*, composed of hyaline thin-walled hyphae. **Ectal excipulum** of *textura angularis/subglobulosa*, composed of thin-walled hyaline cells, (7.5–) 12–28 (–33) × (7.3–) 10.3–20.7 (–26) µm diam. **Margin** composed of cylindrical to clavate hyaline cells with a brownish wall. **Marginal hairs** 195–735 × 9–17.6 µm, superficial, light brown to brown, 1.3–2.8 µm thick-walled, multi-septate, straight or ± flexuous, not sharply pointed, with a simple, sometimes slightly swollen, base. **Excipular hairs** 18.5–670 × 7–12.4 µm, similar to those of the margin, light brown to hyaline, intermingled with short cylindrical light brown to hyaline hairs. **Ascospores** uniseriate, ellipsoid, (16.7–) 17–18.7 (–19.5) × (10.9–) 11.2–12.2 (–12.9) µm, X = 17.7 × 11.7 µm, Q = 1.4–1.6, Qm = 1.5, thin-walled, hyaline, smooth, without lipid drops but with some polar granules, uninucleate, with cell plasma not staining in Cotton Blue or Lugol's solution; ascospores in the ascus, when unripe, have a sheath, loosening when ripe. **Asci** cylindrical, 290–354 × 12.8–16.5 µm, operculate, 8-spored, arising from free croziers, inamyloid. **Paraphyses** filiform, hyaline, septate, slightly enlarged at the top, 3–4.3 µm diam., without vacuolar bodies, forked near the base.

Studied collections: Spain. Málaga, Parauta, monumento natural Pinsapo de las Escaleretas, Parque natural Sierra de las Nieves, 36.66559° N 5.03168° W, alt. 1176 m, in a clump of branches, on litter and woody debris of *Abies pinsapo*, 5 Apr. 2017, *leg*. F.J. Valencia, *rev*. U. Lindemann, ex herb. CVL 050417(3), MSTR:P-25015 (holotype); GenBank ITS MW546582, LSU MW546547. USA. California, Placer Co., French Meadows Reservoir, west end of reservoir, ~39.105225° N 120.475587° W, alt. 1620 m, on woody debris and needles of *Abies concolor* under burned log (2-year old burn), with also *Pinus ponderosa* around, 28 May 2003, *leg*. B.A. Perry, *rev*. N. Van Vooren, herb. FH:BAP 481, under *Paratrichophaea boudieri*; GenBank LSU DQ220402, RPB2 JX943820, TEF1 KC109267.

Comments: *Chaetothiersia eguttulata* is easily distinguished from its sister taxon *C. cupressicola* by several morphological features (cf. diagnosis). Due to the eguttulate ascospores, some other species of *Pyronemataceae* could be confused with *C. eguttulata*: smooth-spored species of *Cheilymenia* but the latter can be delimited by their different hair type; species of *Tricharina* should also be considered but these species lack carotenoids in the paraphyses (except *T. glabra*), and therefore they can never be as bright yellow-orange as *C. eguttulata*. The other known operculate discomycetes with bright yellow hymenium and long brown marginal hairs always have ascospores containing lipid droplets and/or have ornamented ascospores.

As far as we know, *C. eguttulata* is saprobic and seems restricted to needles and woody debris of *Abies* spp. It is very surprising that this species has not been described before, as it has a very striking appearance.

Distribution: Known from the type locality in Spain and from the USA, California.

Perilachnea Van Vooren, *gen. nov.* – MB 836269

Diagnosis: Differs from *Trichophaea s. str.* by deeply cupulate apothecia (at least in young state), mainly with a *Humaria*-like appearance, bi- or pluriguttulate ascospores, paraphyses containing small lipid bodies, a saprobic status, and genetic profile.

Type species: *Lachnea hemisphaerioides* Mouton

Etymology: From ancient Greek περί *(perí)* meaning "around to" and λάχνη *(lákhnê)* meaning "down, hairs". *Lachnea* is also the original genus where the type species had been placed.

Description: Ascomata epigeous, apothecial, sessile, deeply cupuliform or discoid, whitish, yellowish or orange, with an external surface covered by sparse brown hairs. Margin hairy. Excipulum two-layered: medullary layer of *textura intricata* and ectal layer of *textura globulosa/angularis*. Hairs superficial, septate, with a simple base. Asci operculate, narrowing toward base, arising from croziers, inamyloid, 8-spored. Paraphyses slender, containing small lipid bodies. Ascospores uniseriate, ellipsoid, hyaline, bi- or pluriguttulate, smooth or very finely dotted. Species saprobic, growing on the litter and woody debris of conifers or on enriched or burnt soil. Asexual morph unknown but germinating ascospores observed in *P. hemisphaerioides* (Webster *et al*., 1964) and *P. flavobrunnea* (Perić *et al*., 2015).

Comments: Based on morphological, ecological and molecular data, we propose the new genus *Perilachnea* to accommodate a group of saprobic species characterised by their deep cup (at least in young state), resembling *Humaria hemisphaerica*, and having bi- or pluriguttulate ascospores, with a smooth surface or very finely dotted in some species (only visible at a high magnification in CB). Contrary to species of the genus *Trichophaea s. str.*, all *Perilachnea* species have paraphyses containing small lipid bodies (mainly in the top cell). Two previously known species are integrated in this genus: *Trichophaea hemisphaerioides* and *T. flavobrunnea*. A new species *P. ochraceoflava* is also described and illustrated.

Perilachnea hemisphaerioides (Mouton) Van Vooren, *comb. nov.* – MB 836270 – Pl. 8

Basionym: *Lachnea hemisphaerioides* Mouton, *Bull. Soc. Roy. Bot. Belgique*, 36 (2): 21 (1897).

Homotypic synonyms: *Trichophaea hemisphaerioides* (Mouton) Graddon, *Trans. Brit. Mycol. Soc*., 43 (4): 689 (1960); *Humaria hemisphaerioides* (Mouton) Eckblad, *Nytt Mag. Bot*., 15 (1-2): 58 (1968).

Original diagnosis: *Cupula urceolata dein hemisphaerico-concava, 5-15 mm. diam., extus praesertim marginem versus pilis simplicibus, rectis, fuscis, pluriseptatis, sursum sensim attenuatis,* 10 *µ crassis,* ¼–½ *mm. longis, vestita. Hymenium concavum albo-glaucescens ; asci cylindracei, iodo non coerulescentes,* 8*-spori,* 200 = 10. *Paraphyses hyalinae, lineares,* 2 *µ, septatae, apice vix incrassatae, ascos aequantes. Sporidia monosticha, elliptica, levia* 13-15 = 7-8, *utrinque guttula oleosa mediocri praedita.*

Hab. In terra carbonata, praesertim in pinetis. Beaufays, Gomzé, etc., *prope* Liège.

Aliquando e causis externis pili decolorati evadunt et tunc totus fungillus albidus. Lachn. hemisphaericae adspectus, sed statura minore, pilis minus densis et dilutioribus sporidiis que omnino diversa. Tab. A, fig. 10. *Pili* × 500. — *Sporidia* × 800.

Key to the species of *Perilachnea*

1. Ascospores biguttulate in living state; on burnt soil ..... ***P. hemisphaerioides***
1. Ascospores pluriguttulate in living state; on different substrate **2**
2. Ascospores 19–21 (21.5) × 9.5–10.5 (11) µm; on litter of *Cupressus* or *Juniperus*, more rarely on dead wood ..... ***P. flavobrunnea***
2. Ascospores 24–26 (27) × 10.5–11.5 µm; on litter of *Larix*..... ***P. ochraceoflava***

Type: BR5020088910584 in Meise Botanic Garden (BR) herbarium (lectotype).

Misinterpretation: *Lachnea abundans* in the sense of Velenovský (1934: 310), not P. Karst.

Apothecia 2.5–6 mm diam., sessile, first globular then deeply cupuliform, spreading with age, hymenium whitish to pale greyish; external surface concolorous but covered with brownish short hairs. **Margin** hairy by dense brown hairs organised in small tufts.

Subhymenium and **medullary excipulum** not distinguished, of *textura intricata*, with hyaline hyphae. **Ectal excipulum** of *textura angularis/subglobulosa* with hyaline cells, 10–22 µm diam., becoming brownish yellow in the outermost part, with a brown intercellular pigment. **Excipular hairs** superficial, straight, 45–380 × 5–13 µm, pale brown, septate, 1–2 µm thick-walled, sharp at the top, with a simple base, slightly enlarged. **Marginal hairs** similar but more dense and longer, 400–680 × 10–12 µm, sometimes lighter at the top, often slightly ventricose in the low part. **Ascospores** uniseriate, ellipsoid, 12–13.5 (–15) × 6.5–8.2 µm, X = 13 × 7.4 µm, Q = 1.6–2.0, Qm = 1.8, hyaline, biguttulate, rather thick-walled, smooth or very finely verrucose in CB. **Asci** cylindrical, 170–190 × 8–10.5 µm, arising from croziers, operculate, 8-spored. **Paraphyses** filiform, septate, not or slightly enlarged at the top, 2–4 µm diam., containing some non-refractive small bodies in the top article.

Studied collections: France. Rhône, Lyon, Botanical Garden, 45.77314° N 4.854895° E, alt. 165 m, in a greenhouse, on enriched soil, 16 Sept. 1966, *leg*. P. Berthet, *rev*. N. Van Vooren [May 2012], herb. LY:PB 710, under *Trichophaea* sp. *Idem*, 6 Jun. 1969, herb. LY:PB 856. Haute-Savoie, Saint-Jean-de-Sixt, forêt des Traversiers, 45.9163471° N 6.4045474° E, alt. 1010 m, on burnt soil, under conifers, 23 Sept. 2006, *leg*. N. Van Vooren, herb. LY:NV 2006.09.20. Loire, Chalmazel, Bois Chapouilloux, 45.6902272° N 3.8217423° E, alt. 1035 m, on burnt soil, 31 Jul. 2010, *leg*. N. Van Vooren, herb. LY:NV 2010.07.02; GenBank ITS MW546590, LSU MW546556, TEF1

Plate 8 – *Perilachnea hemisphaerioides*

Various collections *in situ*. A. Coll. Levier 11/09/2007, photo G. Moyne. B. Coll. ERD-4327, photo E. Rubio. C. Coll. NV 2014.06.12, photo N. Van Vooren.

MW544633. Germany. Niedersachsen, Undeloh, 53.182148° N 9.968788° E, alt. 90 m, on a fireplace, 11 Sept. 2011, *leg*. M. Vega, herb. LY:NV 2011.09.40. Niedersachsen, Neu Wulmstorf, Große Kieskuhle, 53.453884° N 9.777496° E, alt. 10 m, in an ancient gravel pit, 25 Oct. 2012, *leg*. M. Vega, herb. LY:NV 2012.10.30. Spain. Asturias, La Tejera, 43.565761° N 6.208241° W, alt. 115 m, on burnt soil with *Funaria hygrometrica*, 21 Dec. 2007, *leg*. E. Rubio, *rev*. M. Carbone, pers. herb. ERD-4327; GenBank ITS MW546592, LSU MW546558. Switzerland. Fribourg, Bulle, Cabane d'Inson, 46.584153° N 7.0010782° E, alt. 1025 m, on burnt soil, 20 Jun. 2014, *leg*. N. Van Vooren, herb. LY:NV 2014.06.12; GenBank ITS MW546591, LSU MW546557, RPB2 MW544619, TEF1 MW544634.

Other collection (not studied, but well documented): France. Doubs. Levier, forêt de Levier, route forestière de la Géline, ~46.923348° N 6.103849° E, alt. 750 m, on burnt soil with *Funaria hygrometrica*, 11 Sept. 2007, *leg*. G. Moyne, not kept.

Comments: As many other *Trichophaea*-like species, *Perilachnea hemisphaerioides* has initially been described in the genus *Lachnea* by Mouton (1897). Strangely enough it had been ignored by Boudier (1907). It was combined in the genus *Trichophaea* by Graddon (1960). It can be easily identified thanks to its habitat on old burnt soil, charcoals, etc. (nevertheless it can also be found on enriched soil, see the collections studied) and its biguttulate ascospores. As in other members of the new genus *Perilachnea*, the apothecia are densely hairy at the margin, contrasting with the external surface.

Svrček (1949) described a variety *tenuipilosa* differing from the type by shorter hairs of different shape and larger ascospores, 16.5–17.5 × 8–9 µm. Svrček (1981) placed this variety in synonymy with *Trichophaea abundans*.

Distribution: Based on literature, rather common on burnt soil and charcoals, sometimes also on enriched soil (Van Vooren, 2014), and widely distributed in Europe, especially in mountainous areas. Outside Europe it has been reported from Canada (Huhtinen, 1984), Israel (Nemlich & Avizohar-Hershenzon, 1975), Kazakhstan (Dissing & Raitviir, 1973), Turkey (Doğan & Aktaş, 2010), and USA (Beug *et al*., 2014).

Perilachnea flavobrunnea (Richon) Van Vooren, M. Carbone & Valencia, *comb. nov*. – MB 836271 – Pl. 9–10

Basionym: *Peziza flavobrunnea* Richon, *Descr. dess. pl. crypt. nouv*.: 551 (1879).

Homotypic synonyms: *Lachnea flavobrunnea* (Richon) Sacc., *Syll. fung*., 8: 171 (1889); *Lachnella juniperi* Richon, *Catalogue raisonné des champignons qui croissent dans le département de la Marne*: 212 (1889), *nom. illeg*.; *Scutellinia flavobrunnea* (Richon) Kuntze, *Rev. Gen. Plant*., 2: 869 (1891); *Trichophaea flavobrunnea* (Richon) Priou, B. Perić, Van Vooren & Hairaud, *Mycol. Monten*., 17: 68 (2015).

Original diagnosis: *Peziza flavo-brunnea. (Lachnea) Cupula sessilis, sub-hemisphaerica, extus brunnea, pilis fuscis, tenuibus, densis. septatis obsessa. Disco sicco, concavo, subochraceo; udo tumescente sordide pallido — 4-5 mil. lat. Ascis cylindricis, longis* 0mm,18, *octosporis. Sporis* 0mm,015, *ellipticis, oblique in asci apice monostichis. Paraphysibus filiformibus, continuis. Habitat in ramis muscosis Juniperi communis humi jacentibus — prope* Aulnay-l'Aître, 20 novembre 1878.

Typification: Lectotype here designated, fig. 1–6, pl. II, in Richon (1879); MBT 393138.

Apothecia 5–20 mm diam., sessile, cupuliform, spreading with age, hymenium whitish to pale cream; external surface subconcolorous, but densely covered with short brown hairs, mainly appressed. **Margin** densely hairy by amber brown hairs organised in small tufts.

Subhymenium and **medullary excipulum** not distinguished, of *textura intricata*, with hyaline hyphae, 3–8 µm wide, mixed with some inflated or roundish articles, up to 15 µm wide. **Ectal excipulum** of *textura globulosa/angularis* with hyaline cells, 12–27 µm diam., becoming brownish in the outermost part, mixed with some elongated or subfusoid articles. **Marginal hairs** superficial, straight, 60–800 × 7–12 µm, brown, septate, 0.5–1 µm thick-walled, sharp at the top, with a simple enlarged base. **Excipular hairs** similar but slightly shorter. **Anchoring hyphae** present, dense, hyaline, septate, 3–5 µm wide. **Ascospores** uniseriate, ellipsoid with tapering ends to subfusoid, sometimes inequilateral, (18–) 19–21 (–21.5) × (9–) 9.5–10.5 (–11) µm, X = 19.9 × 10.0 µm, Qm = 2.0, hyaline, smooth, rather thick-walled, containing several lipid droplets, with 2–4 drops larger than the others. **Asci** cylindrical, 310–340 × 10–13 µm, arising from croziers, operculate, 8-spored. **Paraphyses** filiform, hyaline, septate, sometimes forked, not or slightly enlarged at the top, 1.5–3 µm diam., containing numerous small yellowish bodies.

Studied collections: France. Charente-Maritime, Saint-Clément-des-Baleines, forêt du Lizay, 46.247059° N 1.526005° W, alt. 7 m, on dead, decaying branches of *Cupressus*, 15 Dec. 2006, *leg*. M. Hairaud & N. Van Vooren, *det*. J.-P. Priou, herb. LY:NV 2006.12.08, duplicate pers. herb. MH 31206; GenBank ITS KY024697, LSU KY024698. Hungary. Pusztavám, Vértes-hegység, 47.408258° N 18.281986° E, alt. 280 m, on litter of *Juniperus communis*, 28 Dec. 2019, *leg*. A. Koszka, *det*. M. Carbone & N. Van Vooren, herb. TUR-A 208916; GenBank ITS MW546594, LSU MW546560, RPB2 MW544621, TEF1 MW544636. Italy. Sicilia, Siracusa, Buccheri, Bosco della Contessa, on wood of *Cupressus sempervirens*, 37.109156° N 14.857673° E, alt. 910 m, 18 Jan. 2020, *leg*. V. Avola, *det*. M. Carbone, herb. TUR-A 208921; GenBank ITS MW546593, LSU MW546559, RPB2 MW544620, TEF1 MW544635. Spain. Málaga, Ronda, Partido Rural Navares y Tejares, 36.73465° N 5.1405103° W, alt. 685 m, along a cypress hedge (*Cupressus sempervirens*), on the ground with decaying remains, with *Strobiloscypha cupressina*, *Pithya cupressina* and *Pulvinula* sp., 14 Jan. 2017, *leg*. F.J. Valencia, pers. herb. CVL140117(1).

Other collections (not studied, but well documented): France. Morbihan, Plouharnel, Bois d'Amour, 47.592222° N 3.130277° W, alt. 9 m, on woody debris of *Cupressus*, 29 Nov. 2000, *leg*. J.-P. Priou, pers. herb. JPP 20196. *Idem*, on litter of *Cupressus*, 27 Dec. 2014, pers. herb. JPP 14224.

Comments: *Perilachnea flavobrunnea* has rarely been cited since its discovery by Richon (1879). Perić *et al.* (2015) highlighted this species thanks to new collections that allowed a deep study of living characters and molecular data. It has been provisionally combined in the genus *Trichophaea* although phylogenetic results proved it was not a *Trichophaea s. stricto*. *P. flavobrunnea* can grow on either *Juniperus* or *Cupressus* litter, more rarely on wood, as with some other cup-fungi such as *Smardaea planchonis* (Dunal ex Boud.) Korf & W.Y. Zhuang and *Pseudopithyella minuscula* (Boud. & Torrend) Seaver.

It is interesting to note that the collection TUR-A 208921 (from Sicily) grew on dead wood of *Cupressus*, not on litter, and genetically deviates from the other sequenced collections even if microscopical characters do not seem to do so. We are waiting for further collections also growing on wood to evaluate if this divergence is taxonomically valuable.

Distribution: Rarely reported, it has to be searched for in its particular habitat, in littoral areas or in higher elevations in natural habitats of *Juniperus* or *Cupressus*. Known from France, Montenegro (Perić *et al*., 2015), Spain (Rubio & Tena, 2016; this paper), Bosnia and Herzegovina (Jukić, 2018), and Hungary (this paper).

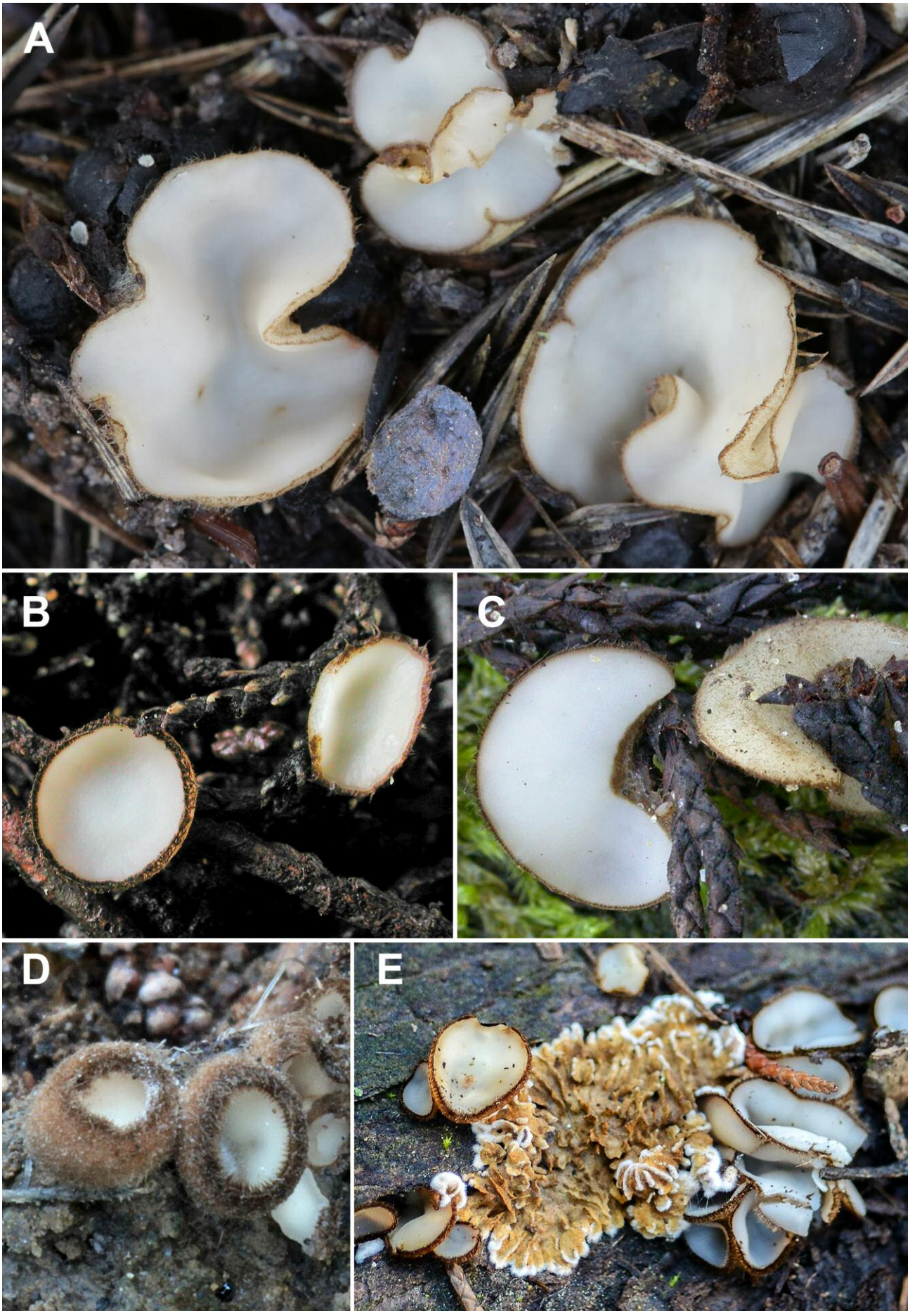

Plate 9 – *Perilachnea flavobrunnea*

Various collections *in situ*. A. Coll. TUR-A:208916, photo A. Kuszka. B. Coll. JPP 22141, photo J.-P. Priou. C. Coll. NV 2006.12.08, photo M. Hairaud. D. Coll. CVL140117(1), young specimens, photo F.J. Valencia. E. *Perilachnea* cf. *flavobrunnea* Coll. TUR-A 208921, photo V. Avola.

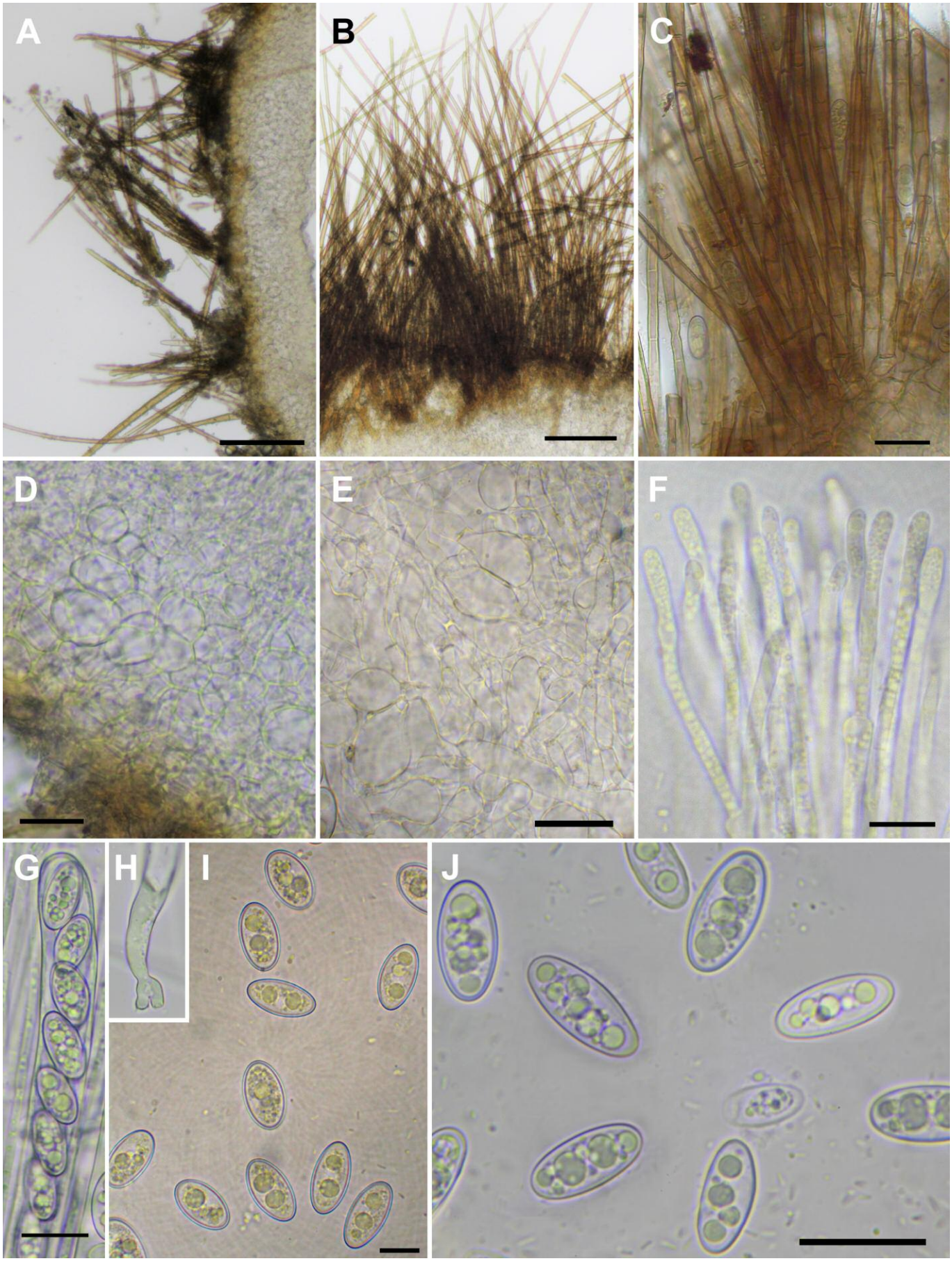

Plate 10 – *Perilachnea flavobrunnea*. Microscopical characters

A–B, D, G–H, J: Coll. CVL140117(1); C, E, I: Coll. MH 31206. A. Outer part of ectal excipulum with excipular hairs. B. Marginal hairs. C. Basal part of marginal hairs. D. Ectal excipulum. E. Medullary excipulum. F. Top of paraphyses. G. Ascus. H. Base of ascus. I–J. Ascospores in water. Scale bars: A–B = 100 µm; C–E, J = 20 µm; G, I = 10 µm. Photos A–B, D, G–H, J by F.J. Valencia, C, E, I by Michel Hairaud.

Perilachnea ochraceoflava M. Carbone, Cartabia & P. Alvarado, *sp. nov.* – MB 837946 – Pl. 11–12

Diagnosis: Besides its unique genetic profile, it differs from the closely similar *P. flavobrunnea* by larger ascospores with a slightly higher Q ratio, apothecia that are more yellowish-ochraceous-coloured and its growth under *Larix decidua*.

Type: Coll. TUR-A 208917 (holotype).

Etymology: From Latin *ochraceus* meaning "ochre-coloured" and *flavus* meaning "yellow" referring to the colour of the species.

Apothecia 5–20 mm diam., sessile, cupuliform, hymenium whitish-cream to pale ochraceous; external surface subconcolorous, but densely covered with short brown hairs, mainly appressed. **Margin** densely hairy with brownish hairs organised in small tufts.

Subhymenium and **medullary excipulum** not distinguished, of *textura intricata*, with hyaline hyphae, septate, (3–) 4–6 µm wide. **Ectal excipulum** of *textura globulosa/angularis* with hyaline cells, up to 35 µm diam., wall yellowish, 1.5–2 µm thick. **Marginal hairs** superficial, straight, up to 700 × 8–10 µm, pale brown, septate, up to 1.5 µm thick-walled, slightly blunt to sharper at the top, with a simple enlarged base. **Excipular hairs** similar but slightly shorter. **Ascospores** uniseriate, ellipsoid with tapering ends to subfusoid, sometimes inequilateral, (22–) 24–26 (–27) × (9.5–) 10.5–11.5 µm, Qm = 2.3, hyaline, smooth, 0.5–0.8 µm thick-walled, containing several lipid droplets, with 2–4 drops larger (5–7 µm diam.) than the others (1.5–3 µm diam.), all merged into a large ellipsoid drop in dead ascospores. **Asci** cylindrical, 270–310 × 12–15 µm, arising from croziers, operculate, 8-spored. **Paraphyses** filiform, hyaline, septate, 2–2.5 µm wide, enlarged at the top up to 3.5–4 (–5) µm, containing very small bodies.

Studied collections: Italy. Piemonte, Baceno, Alpe Devero, 46.308944° N 8.260555° E, alt. 1600 m, on the side of a track, on *Larix decidua* litter, 31 Aug. 2019, *leg*. M. Carbone & M. Cartabia, herb. TUR-A 208917; GenBank ITS MW546595, LSU MW546561, RPB2 MW544622, TEF1 MW544637.

Comments: Microscopically, *Perilachnea ochraceoflava* is well distinguished from *P. hemisphaerioides* and *P. flavobrunnea* by the definitely larger ascospores. Compared to *P. flavobrunnea* some other minor microscopical differences could be found, i.e. the enlarged paraphyses tips and the thicker wall of the external hairs. Due to its growth among *Larix decidua* litter, it could be confused with *Chaetothiersia laricina*, which however has a different microscopy (see the description above).

Distribution: Only known from the type locality in Northern Italy.

Lasiobolidium Malloch & Cain – MB 2648

Type species: *Lasiobolidium spirale* Malloch & Cain, *Can. J. Bot*., 49 (6): 853 (1971).

Synonym: *Paratrichophaea* Trigaux (see comments below).

Amended description: Ascomata cleistothecial or apothecial, small, sessile, subglobose, slightly cupuliform or discoid, whitish, pale greyish or yellow-brown, with an external surface covered by brown hairs. Margin hairy on the apothecial species. Ectal excipulum of *textura globulosa/angularis*. Hairs ± superficial or deeply rooted, septate, with a simple base, sometimes multifurcate, long, upward-pointing, straight or helically coiled. Ascospores ellipsoid, hyaline, eguttulate, but sometimes containing small granules usually disappearing in mature ascospores, smooth or verrucose with isolated warts. Asci operculate, narrowing toward base, arising from croziers, inamyloid, 4- or 8-spored. Species saprobic, coprophilous or not. Asexual morph unknown.

Plate 11 – *Perilachnea ochraceoflava*. Coll. TUR-A 208917 (photo M. Carbone)

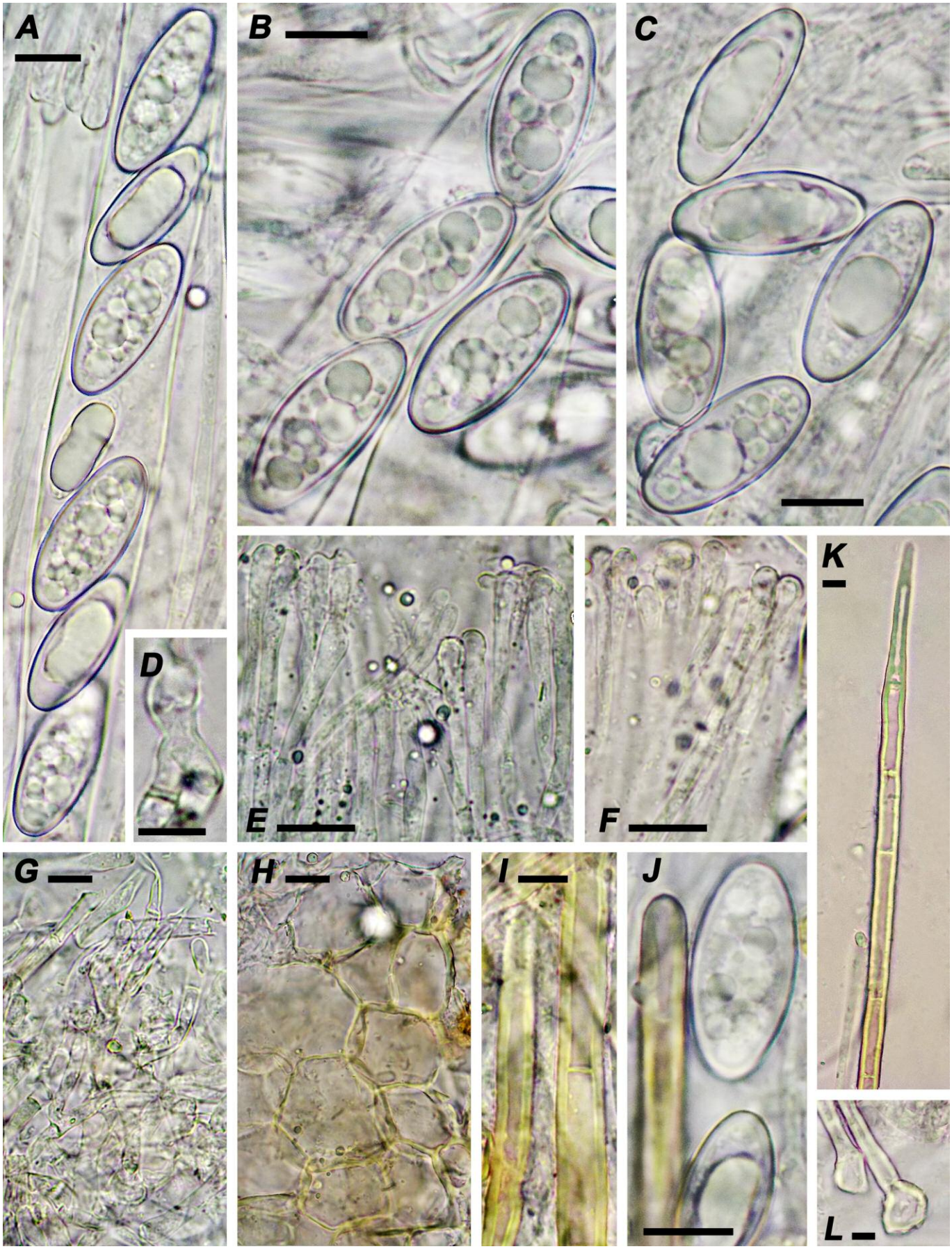

Plate 12 – *Perilachnea ochraceoflava*. Microscopical characters
A–C. Ascospores; D. Ascus base; E–F. Paraphyses tips; G. Medullary excipulum; H. Ectal excipulum; I. Walls and septa of excipular hairs; J–K. Excipular hair tip; L. Basal part of excipular hairs. All mounted in water. Scale bars = 10 µm. Photos M. Carbone.

Comments: The genus *Lasiobolidium* was published by Malloch & Cain (1971) for a cleistothecial fimicolous species, *L. spirale*, ressembling a *Lasiobolus* species but with helically coiled hairs. Several species have been described in this genus since its publication: *L. orbiculoides* Malloch & Benny (Malloch & Benny, 1973), *L. fallax* Locq.-Lin., *L. helicoideum* Locq.-Lin., *L. recurvatum* Locq.-Lin. (Locquin-Linard, 1983), *L. aegyptiacum* Moustafa & Ezz-Eldin (Moustafa & Ezz-Eldin, 1989) and *L. gracile* Yaguchi, Someya & Udagawa (Yaguchi *et al.*, 1996). A key to the cleistothecial species of *Lasiobolidium* is available in Guarro *et al.* (2012). Only *L. spirale*, the type-species, and *L. orbiculoides* have been evaluated with molecular data. The works of Hansen *et al.* (2005) and Perry *et al.* (2007) demonstrated that the latter belongs to the *Pseudombrophila* lineage and has to be excluded from *Lasiobolidium*. The type of hairs of *L. helicoideum* and *L. recurvatum*, as well as their coloured ascospores do not fit very well with the initial definition of *Lasiobolidium*.

It was a bit surprising to see that two of our new species and two others which previously had been placed in the genus *Paratrichophaea* Trigaux (Trigaux, 1985), i.e. *P. boudieri* (Grelet) Bronckers and *P. parvispora* Benkert, where nested in the same clade as *L. spirale*. However, except for the cleistothecial shape of ascomata and the type of hairs, all these species have many other characters in common. As the sequence "GenBank NG_057747" of *L. spirale* is based on a culture obtained from the holotype, we decided to sequence material coming from cleistothecia of this species. Thus, two paratypes (see Table 1) were selected among the revised type-collections of *L. spirale*. The LSU results obtained were 100% identical to the sequence used in our phylogeny. A deeper revision of these type-collections will be presented in a forthcoming paper. Based on these results, the question of the synonymy of *Paratrichophaea* with *Lasiobolidium* has been raised. Unfortunately, we were unable to locate the type collection of *P. macrocystis* Trigaux, the type-species. The discovery of *Lasiobolidium coprophilum* sp. nov. (see under this name) gave us the opportunity to observe the same marginal macrocells — called "pseudopoils" by Trigaux (1985) that means "pseudohairs"— described and illustrated for *Paratrichophaea macrocystis*. Based on this observation and the other characters of these species, we are convinced that *Paratrichophaea* is a later synonym of *Lasiobolidium*. Thus, we propose the following new combination:

Lasiobolidium macrocystis (Trigaux) Van Vooren, *comb. nov.* – MB 836354

Basionym: *Paratrichophaea macrocystis* Trigaux, *Doc. mycol.*, 16 (61): 6 (1985).

Lasiobolidium boudieri (Grelet) Van Vooren & Valade, *comb. nov.* – MB 836273 – Pl. 13–14

Basionym: *Trichophaea boudieri* Grelet, *Bull. Soc. mycol. France*, 33 (3-4): 95 (1917).

Homotypic synonym: *Paratrichophaea boudieri* (Grelet) Bronckers, *Sterbeekia*, 23: 20 (2003).

Original diagnosis: *Gregaria vel subsparsa, sessilis, carnosa, ex hemisphaerico applanata*, 1–4 *mm. lata, extus pilis erectis, brunneis, vestita, hymenio albido vel pallido, margine ciliato. Thecae cylindraceo-clavatae, ad basim attenuatae, operculatae, octosporae*, 200–280 *µ longae*, 15–20 *µ latae, iodo non tinctae. Paraphyses graciles, septatae, hyalinae, ad basim ramosae, ad apicem haud incrassatae,* 2–3 *µ crassae. Sporae monostichae, ovato-ellipticae, hyalinae, leaves, intus minute sed ad maturitatem vix perspicue granulosae,* 18–21 *µ longae,* 12–13 *µ crassae. Pili marginales simplices, brunnei, rigiduli, apice acuti vel obtuse, parce septati vel continui,* 200–900 *µ circiter longi,* 13–18 *µ crassi. Pili inferi breviores, saepe bulbosi (basi bulbosa* 17–35 *µ circiter crassa). Quidam alii intermixti longissimi, flexuosi, pallidi aut pallidefusci, pluri-septati, hyphaeformes,* 2–3 *µ crassi, praesertim ad basim receptaculi interdum perspiciuntur.*

Aspecti externo Trichophaeam Woolhopeiam Cooke *et* Phill. *sat simulat sed notis micrologicis, praesertim sporis, omnino distincta. Trichophaeae bulbo-crinitae* Phill. *Disco pallidiore, pilis et loco diversa.*

Hanc speciem eximiam dilecto magistro E. Boudier *libenter dicamus. Aestate. Prope* Savigné (Vienne), *ad terram uliginosam in umbrosis.*

Type: *ex* herb. Grelet in herbarium PC (herbier général), s.n.

Apothecia 2–4 mm diam., sessile, first cupulate then discoid to pulvinate with age, hymenium whitish to pale greyish; external surface subconcolorous, covered with brown hairs. **Margin** hairy with long upward-pointing dark brown hairs.

Subhymenium of *textura globulosa-angularis*, with hyaline cells, 5–12 µm diam. **Medullary excipulum** thin, of *textura ± intricata*, with hyaline hyphae. **Ectal excipulum** of *textura globulosa/angularis* with hyaline cells, 10–30 µm diam., slightly becoming a *textura prismatica* near the margin. **Margin** composed of clavate cells, 23–39 × 10–15.5 µm, hyaline. **Marginal hairs** deeply rooted in the excipulum, straight, 600–850 (–1300) × 14–20 (–30) µm, brown, septate, 5–6 (8) µm thick-walled, sharp at the top, with a simple or bifurcate base. **Excipular hairs** shorter, pale brown, 100–290 × 6.5–13 µm, septate or not, 2.5–5 µm thick-walled, with a simple enlarged or typical bulbous base, up to 35 µm wide. **Anchoring hyphae** present, up to 80 µm in length, 4–6 µm wide. **Ascospores** uniseriate, ellipsoid, 15–20 (–21) × (9–) 10–12 µm, X = 18.7 × 11.2 µm, Q = 1.6–2.1, Qm = 1.9, hyaline, smooth or sometimes very finely dotted, rather thick-walled, containing numerous polar granules when immature, disappearing in mature ascospores, sometimes showing a spore

Key to the European species of *Lasiobolidium*

1. Ascomata cleistothecial, subglobose, less than 1 mm diam., with helically coiled hairs ..... ***L. spirale***
1. Ascomata apothecial, hairs upward-pointing **2**

2. Ascospores smooth **3**
2. Ascospores ornamented by low and minute warts ..... ***L. trachysporum***

3. Apothecia growing on dung ..... ***L. coprophilum***
3. Apothecia growing on other substrates **4**

4. Clavate macrocells present at the margin, up to 180 µm long, hairs often multifurcate; on wood ..... ***L. macrocystis***
4. Clavate macrocells absent or shorter **5**

5. Asci 8-spored **6**
5. Asci 4-spored ..... ***Paratrichophaea michiganensis***

6. Ascospores 15–20 × 10–12 µm, containing bipolar small granules, disappearing at maturity; marginal hairs reaching 850 µm long or sometimes more ..... ***L. boudieri***
6. Ascospores 16.2–17.7 × 10.6–12.2 µm, containing persistent small granules; marginal hairs reaching 500 µm long .. ***L. parvisporum***

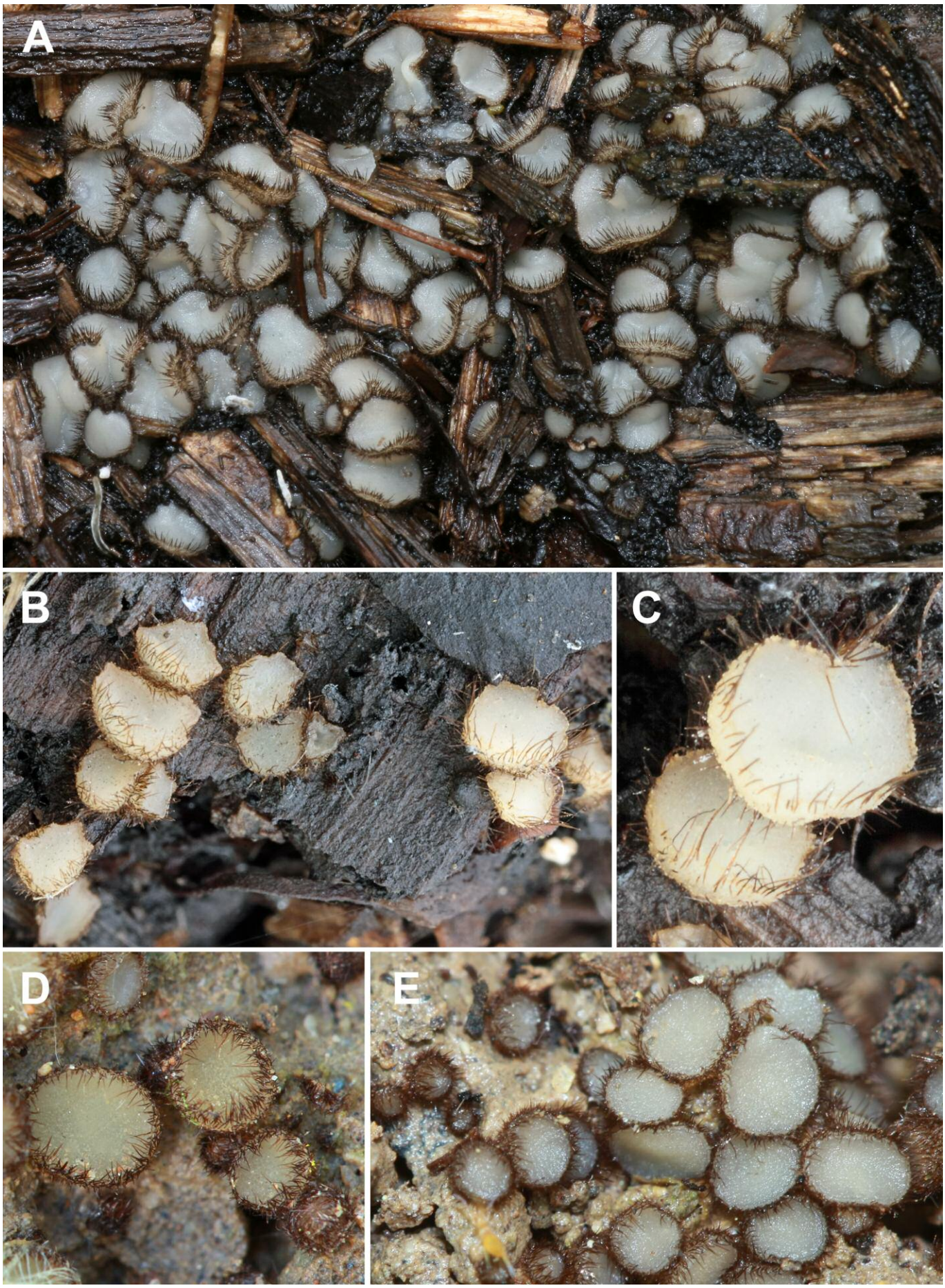

Plate 13 – *Lasiobolidium boudieri*

Various collections *in situ*. A. Coll. GM 20091101, photo G. Eyssartier. B–C. Coll. FV2016111501, photos F. Valade. D–E. Coll. CVL130417, photos F.J. Valencia.

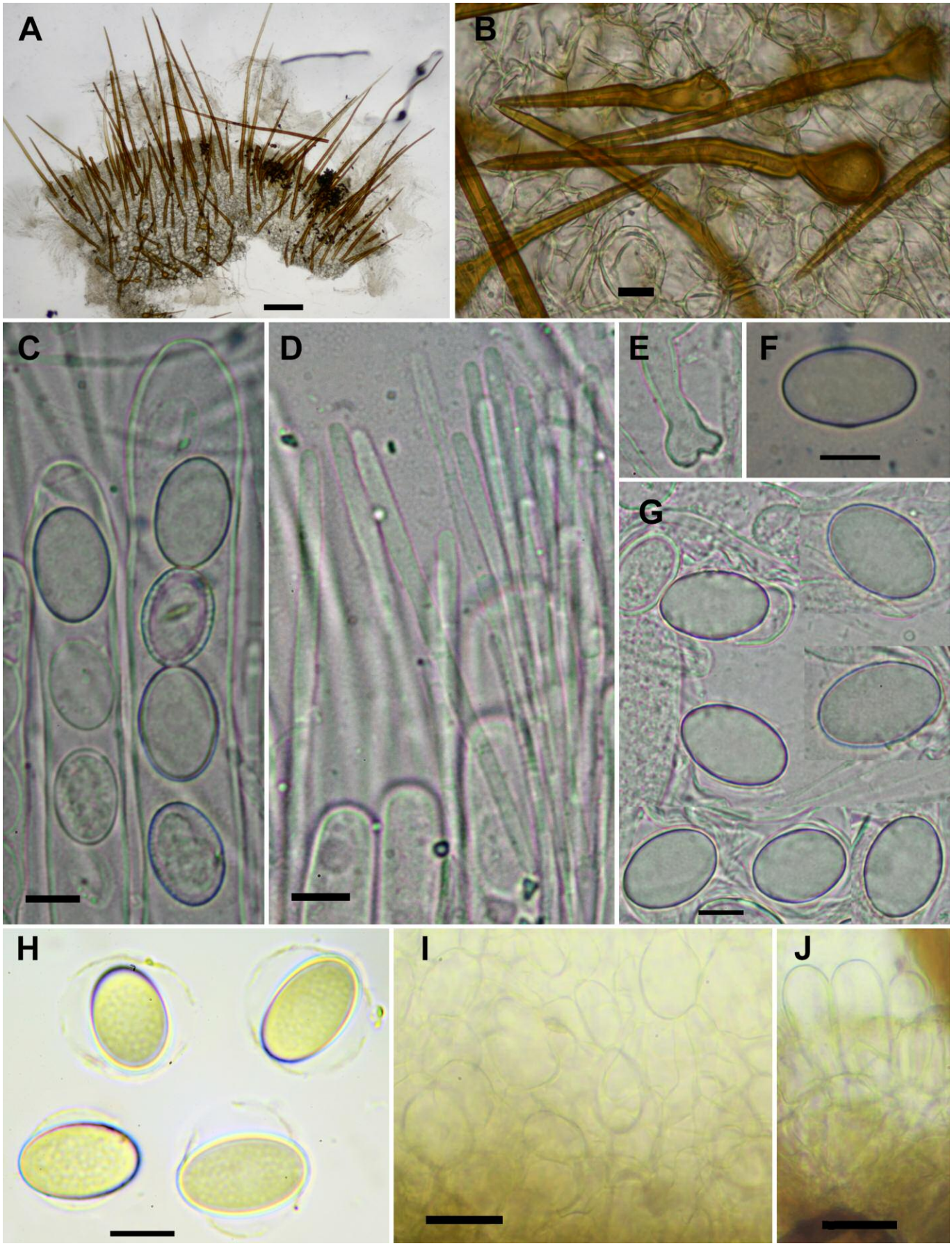

Plate 14 – *Lasiobolidium boudieri*. Microscopical characters

A–G: Coll. FV2016111501; H–J: Coll. CVL130417. A. Outer part of excipulum showing excipular and marginal hairs. B. Detail of hairs. C. Top of asci. D. Top of paraphyses. E. Base of ascus. F. Ascospore in Cotton blue. G. Ascospores in water. H. Ascospores in IKI showing the spore sheath. I. Ectal excipulum. J. Marginal macrocells. Scale bars: A = 100 µm; B, I–J = 20 µm; C–D, F– H = 10 µm. Photos A–G by F. Valade, H–J by F.J. Valencia.

sheath. **Asci** cylindrical, 220–250 × 12–16 µm, arising from croziers, operculate, 8-spored. **Paraphyses** filiform, hyaline, septate, slightly enlarged at the top, 4–4.5 µm wide.

Microscopical description of the type-collection (see below): **Medullary excipulum** of *textura intricata*, with hyaline hyphae. **Ectal excipulum** rather thin, of *textura globulosa/angularis* with amber brown cells, 15–30 µm wide. **Margin** with clavate cells, 21–31 × 10–14 µm, hyaline. **Marginal hairs** rooted in the excipulum, straight, 250–600 × 14–20 µm, brown, septate, 3–5 µm thick-walled, sharp at the top, with a simple non-bulbous base. **Excipular hairs** superficial, brown, 90–220 × 9–12 µm, septate, 1.5–2 µm thick-walled, sharp at the top, more rarely obtuse, with a simple enlarged or bulbous base, up to 30 µm wide. **Anchoring hyphae** present, hyaline, 4–5 µm wide. **Ascospores** uniseriate, ellipsoid, 17–19.5 (–20) × 11–12.5 (–13) µm, X = 18.4 × 11.9 µm, Q = 1.4–1.7, Qm = 1.6, hyaline, smooth, rather thick-walled, with polar granules ± merged. **Asci** cylindrical, ~220–250 µm long, 8-spored. **Paraphyses** filiform, too much collapsed for a decent description.

Studied collections: France. Vienne, Savigné, on marshy soil, 6 Aug. 1917, *leg*. L.-J. Grelet, *rev*. N. Van Vooren [Sept. 2020], herb. PC:s.n. (type). Haute-Savoie, Loisin, marais Décrey, ~46.290146° N 6.30016° E, alt. 445 m, on peaty soil, in a mesotrophic marsh, under *Alnus* sp., 31 Aug. 2003, *leg*. L. Deparis, *det*. N. Van Vooren, pers. herb. L.D. 31.08.04; GenBank ITS MW546583, LSU MW546548, RPB2 MW544617, TEF1 MW544631. Charente, Cognac, Chateaubernard, 45.6779444° N 0.330999° W, alt. 20 m, in a private garden, on wood chips under *Rubus idaeus*, 15 Nov. 2016, *leg*. F. Valade, pers. herb. FV2016111501. Spain. Málaga, Ronda, area of Navares-Tejares, near the river Guadalevín, 36.73576° N, 5.14613° W, alt. 673 m, on sandy soil under *Populus nigra*, *Equisetum ramosissimum* and gramineous plants, 13 Apr. 2020, *leg*. F.J. Valencia, pers. herb. CVL130417, JACUSSTA:9518. *Idem*, 26 Apr. 2020 {soc. *Lasiobolidium trachysporum*}. Switzerland. Bern, Dürrenroth, 47.06655° N 7.799341° E, alt. 850 m, by the side of a path, on soil and wooden debris, under *Tussilago* sp. and other plants, 11 Aug. 1995, *leg*. H. Aeberhard & J. Gilgen, *det*. R. Dougoud, *rev*. N. Van Vooren, herb. G:RD 22.02.240.95.

Other collections (not studied but well documented): France. Seine-Saint-Denis, Aulnay-sous-Bois, parc départemental du Sausset, ~48.963491° N 2.50484° E, alt. 70 m, on chipped wood chips, 17 Nov. 2009, *leg*. G. Eyssartier, *det*. G. Moyne, pers. herb. GM 20091101.

Comments: This species was published by Grelet (1917) who provided a detailed description. It was also presented and illustrated in detail by Van Vooren *et al.* (2005). It is characterised by its growth on wooden debris, its numerous hairs with a bulbous base and eguttulate ascospores, only containing small bipolar granules when immature. Bronckers (2003) synonymised *Paratrichophaea macrocystis*, now *Lasiobolidium macrocystis*, with *L. boudieri* but the latter can be distinguished by the absence of large marginal macrocells and hairs having a simple base.

Two other species are supposed to be close to or synonymised with *L. boudieri*: *Paratrichophaea albescens* (Dissing & Raitviir) T. Schumach. and *Tricharina bisetosa* K.S. Thind & S.C. Kaushal. The first one was originally described as *Cheilymenia albescens* Dissing & Raitviir and tentatively placed in this genus because of the eguttulate ascospores (Dissing & Raitviir, 1973). It was combined in the genus *Paratrichophaea* by Schumacher (1988), a coherent choice based on the characters of this species. The perisporial sheath described by Dissing & Raitviir (1973) was not observed by Schumacher (1988). Based on the original description the species seems intermediate between *L. macrocystis* and *L. boudieri*, therefore more investigations are required to rule the correct position of this taxon.

The second one, *Tricharina bisetosa* K.S. Thind & S.C. Kaushal, was excluded from this genus by Yang & Korf (1985), a decision in agreement with the amended definition of *Tricharina* by Van Vooren *et al.* (2017), but its combination in the genus *Cheilymenia*, as *C. bisetosa* Wang & Korf, is rather curious, mainly based on the eguttulate ascospores being refractive in Cotton blue. Based on the original description (Thind & Kaushal, 1979), including the substrate given as "decaying twigs", the characters of this species fit well with *Lasiobolidium* as amended herein. The presence of hairs with a bulbous base and the absence of marginal macrocells point to *L. boudieri*, but the ascospores seem to be slightly larger. As it is an extra-European species, we refrain for accepting a synonymy with *L. boudieri*. Molecular investigations are required to evaluate the correct position of this taxon.

Pfister (1988) described two American species of *Paratrichophaea*, *P. pygmea* (Clem.) Pfister and *P. michiganensis* (Kanouse) Pfister. They should be revised based on our results. *P. michiganensis* has been reported twice from Europe. The first collection, from the Netherlands (Bronckers, 2002b), is described herein as a new species, *Lasiobolidium coprophilum*. The second one, from Sweden (Olariaga & Hansen, 2011) is rather in conformity with the original description by Kanouse (1958) and the revision by Pfister (1988), including the substrate.

Distribution: Uncommon, but widely distributed in Europe: France, Spain, Switzerland (Van Vooren *et al.*, 2005; Sierra López *et al.*, 1995), and based on Internet resources: Austria, Denmark, Germany, Netherlands, Poland, and Slovakia. It seems there are many misidentifications, often associated to species of *Tricharina* or other species (e.g. Blanco-Dios & Castro González, 2012). The occurrences outside Europe need to be revised, e.g. the Israelian collection cited with doubts by Nemlich & Avizohar-Hershenzon (1975) is clearly another species based on ascospore shape and content.

Lasiobolidium parvisporum (Benkert) Van Vooren, M. Carbone & Rubio, *comb. nov.* – MB 836274 – Pl. 15–16

Basionym: *Paratrichophaea parvispora* Benkert, *Z. Mykol.*, 76 (1): 31 (2010).

Original diagnosis: *Apothecia* 0,5–2 *mm lata, anguste- vel late-obconica, postea paene applanata, solitaria. Hymenium album. Superficies exterior alba, dissociate tecta cum paucis rigidis et brunneo-parietalibus pilis et piliformiter serpentibus hyphis. Pili rigidi, acuti, usque ad* 325 *µm longi, crasse-parietales* (2–3 *µm*), *cum* 3–5 *septis, basaliter plurimum quasi ampullariter dilatati, infra denuo coartati et radicantes. Ektoexcipulum ex textura globulosa-angulari. Asci cylindracei, octospori,* 200–220 × 10–12 *µm. Sporae uniseriatae, ellipsoideae, laeves,* 14–16(17) × 8–10 *µm, in statu immaturo diffuse granulariter impletae, in statu matura sine guttulis. Paraphysae rectae, filiformes,* 2–3(4) *µm latae.*

Type: Germany, Wemigerode, 27 Aug. 1988, *leg*. E. Oemler (B), holotype.

Apothecia 0.5–2 mm diam., sessile, discoid, hymenium whitish to pale greyish; external surface subconcolorous, covered with sparse brown hairs. **Margin** hairy with upward-pointing dark brown hairs.

Medullary excipulum of *textura* ± *intricata*, with hyaline hyphae, 2–5 µm wide, mixed with globose or subglobose cells, up to 10 µm diam. **Ectal excipulum** of *textura globulosa/subangularis*, with hyaline cells, 8–27 (45) µm diam., becoming light yellow-brown in the outermost part. **Margin** composed of clavate cells, 30–70 × 13–38 µm, hyaline, thick-walled. **Marginal hairs** superficial or sometimes more deeply rooted in the excipulum, straight, up to 500 µm in length, 17–19 µm wide, brown, septate, 2–3 µm thick-walled, sharp at the top, with a simple base. **Excipular hairs** shorter, 54–130 × 6–9 µm, septate, 1.5–3 µm thick-walled, with a simple base, sometimes enlarged or bulbous, up to 20 µm wide. **Ascospores** uniseriate, ellipsoid, 16.2–17.7 × 10.4–12.2 µm, X = 16.9 × 11.5 µm, Q = 1.4–1.5, hyaline, smooth, rather thick-walled, containing numerous granules, mainly positioned at the poles, partly disappearing on

mature spores. **Asci** cylindrical, 200–212 × 12–13 µm, arising from croziers, operculate, 8-spored. **Paraphyses** filiform, hyaline, septate, not enlarged at the top, 2–4 µm diam.

Studied collections: Spain. Asturias, Pravia, Puente de Quinzanas, near Veygañán, 43.4673944° N 6.117486° W, alt. 12 m, on muddy soil, periodically flooded, under *Alnus lusitanica* and *Salix alba*, 20 Sept. 2018, *leg*. E. Rubio, *rev*. M. Carbone, pers. herb. ERD 7668; GenBank ITS MW546586, LSU MW546552, RPB2 MW544618, TEF1 MW544632. Málaga, Ronda, area of Navares-Tejares, along the river Guadalevin, 36.735778° N 5.145972° W, alt. 676 m, on lime, under *Populus nigra*, *Salix alba* and plants (*Equisetum ramosissimum* and *Typha* sp.), 1 Sept. 2020, *leg*. F.J. Valencia, *det*. N. Van Vooren, pers. herb. CVL010920(1).

Plate 15 – *Lasiobolidium parvisporum*

A. Coll. ERD 7668, ascomata *in situ* ; photo E. Rubio. B–C. Coll. CVL010920(1), B: Ascomata *in situ*, C: Location of this collection, photos F.J. Valencia.

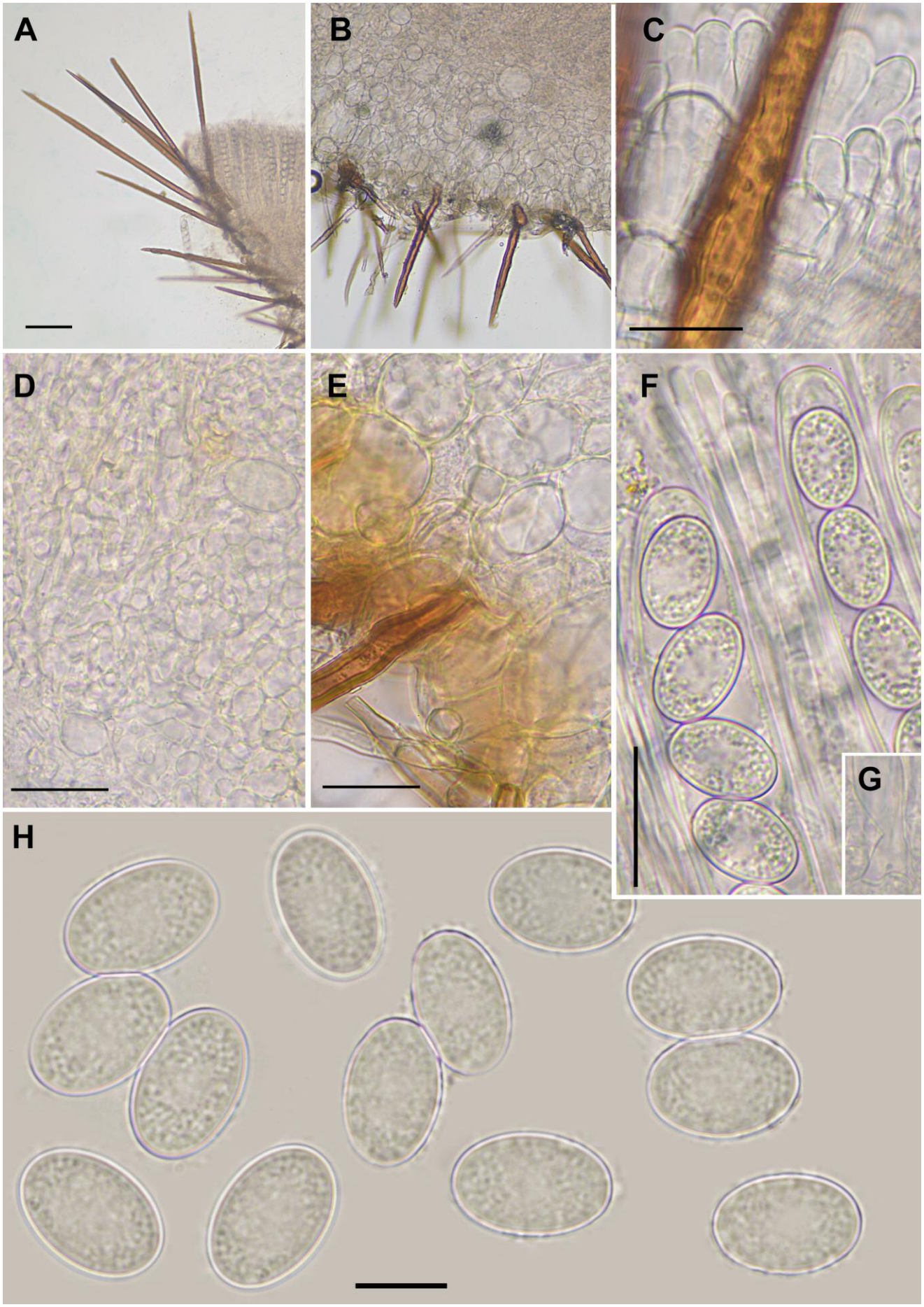

Plate 16 – *Lasiobolidium parvisporum*. Microscopical characters
Coll. ERD 7768. A. Marginal hairs. B. Excipular hairs. C. Marginal cells between the hairs. D. Medullary excipulum. E. Ectal excipulum. F. Top of asci and paraphyses. G. Ascus base. H. Ascospores. All elements in water. Scale bars: A = 100 µm, C = 50 µm, D–F = 20 µm, H = 10 µm. Photos E. Rubio.

Comments: Initially published as a *Paratrichophaea*, our molecular data placed it in the genus *Lasiobolidium*, close to *L. boudieri*. The two species are morphologically close but *L. parvisporum* is distinguished by its shorter ascospores (in average), with a lower Q ratio, its spore content, and its shorter marginal hairs. Unfortunately the type collection of *P. parvispora* was unavailable for a loan, but we think that these Spanish collections fit well with the protologue.

Distribution: Very rarely reported, only known from Germany (Benkert, 2010) and Spain (this paper). The report from France of a collection on cow dung (Courtecuisse *et al.*, 2020) is doubtful and may be more related to *L. coprophilum* (see under this name).

Lasiobolidium trachysporum Valencia, M. Vega & Van Vooren, *sp. nov.* – MB 836276 – Pl. 17–19

Diagnosis: Differs from the other known *Lasiobolidium* by its distinctly warted ascospores.

Type: Coll. JA-CUSSTA:9520 (holotype).

Etymology: From ancient Greek, τραχυ'ς *(trakus)*, meaning "rough", and σπορά *(sporá)* meaning "seed(ing)" = spores.

Ascomata gregarious. **Apothecia** 1–10 (20) mm diam., sessile, discoid, barely depressed in the centre, hymenium livid white or pale greyish; external surface subconcolorous, densely covered with brown short hairs, mainly upward-pointing, more densely set at the margin.

Subhymenium and **medullary excipulum** not distinguished, of *textura intricata*, with hyaline hyphae, 5–7 µm wide, mixed with enlarged or ampullaceous articles. **Ectal excipulum** of *textura globulosa/angularis* with hyaline cells, 14–24 µm diam. or (8–) 11–37 (–50) × (6–) 9–28 (–37) µm. **Marginal cells** clavate, ± organised in a *textura subprismatica*. **Excipular hairs** deeply rooted, straight, more rarely curved, (67–) 72–290 × (8–) 12–17 µm, brown, septate (1–2) or non-septate, up to 3 µm thick-walled, sharp at the top, with a simple, enlarged or bulbous base, 15–22 µm diam. **Marginal hairs** similar but all septate, with a simple or more rarely bifurcate, non-bulbous base, (135–) 165–590 (–650) × (12–) 14–20 (–22) µm, 2.5–4.1 µm thick-walled. **Anchoring hyphae** present, hyaline or slightly yellowish, septate, 3–5 (–6) µm wide, with a bulbous base. **Ascospores** uniseriate, ellipsoid to broadly ellipsoid, (14.7–) 15.8–17.6 (–18.1) × (9.9–) 10.5–11.7 (–12.2) µm, X = 16.9 × 11.1 µm, Q = 1.4–1.6, Qm = 1.5, hyaline, containing granules of various size often concentrated at the poles, with two polar larger guttules (mainly visible in asci), measuring 4–5 µm diam., appearing thick-walled due to the perispore which occasionally is loosening when spores are ejected, ornamented by low and minute warts, angular or slightly stretched, cyanophilous, up to ~1 µm diam., sometimes coalescent and forming small plates. **Asci** cylindrical, (185–) 210–275 (–287) × (12.5–) 13–17.1 (–19) µm, arising from croziers, operculate, 8-spored. **Paraphyses** filiform, straight or slightly curved at the top, hyaline, septate, not enlarged at the top but sometimes sublanceolate, 2.5–4.3 µm wide, no vacuolar bodies seen.

Studied collections: Spain. Málaga, Ronda, Dehesa del Mercadillo, 36.76355° N 5.17545° W, alt. 585 m, on wet soil and woody debris of *Populus nigra* and other plants (*Ranunculus ficaria*, *Arum italicum*, *Scirpus holoschoenus*, *Mentha suaveolens*, etc.), 10 Apr. 2019, *leg*. F.J. Valencia, ex herb CVL100419(1), JA-CUSSTA:9520 (holotype) and herb. NV 2019.04.14 (LY, isotype); GenBank ITS MW546587, LSU MW546553. Málaga, Pujerra, Bentomiz, nature reserve of "Valle del Genal", near the stream Bolage, 36.6174° N 5.14859° W, alt. 595 m, on soil and woody debris of *Populus nigra* (other plants around: *Salix alba*, *Lamium flexuosum*, *Rubia peregrina*, *Rubus ulmifolius*, *Dorycnium rectum*, *Ranunculus ficaria*, *Vinca difformis*), 8 Nov. 2019, *leg*. F.J. Valencia, pers. herb. CVL081119(1). Málaga, Ronda, Navares/Tejares, near the river Guadalevin, 36.73554° N 5.14619° W, alt. 675 m, on soil with woody debris of *Populus nigra* and also on decorticated wood of *P. nigra*, associated with *Lasiobolidium boudieri*; other plants around: *Salix alba*, *Rubus ulmifolius*, *Hedera helix* and *Ficaria verna*, 9 Apr. 2020, *leg*. F.J. Valencia, ex herb. CVL090420(1), JA-CUSSTA:9521.

Comments: Based on its morphology, especially its upward-pointing hairs, this species may resemble *Trichophaeopsis bicuspis*, a species which regularly grows on decaying wood and debris of *Populus* spp., but neither the typical bifurcate hairs of *Trichophaeopsis*, nor the typical *textura prismatica* of the ectal excipulum were observed, except in the marginal area were the cells are more or less organised in such a way. The habitat and presence of the bulbous excipular hairs are also similar to *Lasiobolidium boudieri* but the latter has smooth ascospores with a different content and longer marginal hairs on average.

Distribution: Only known from Southern Spain.

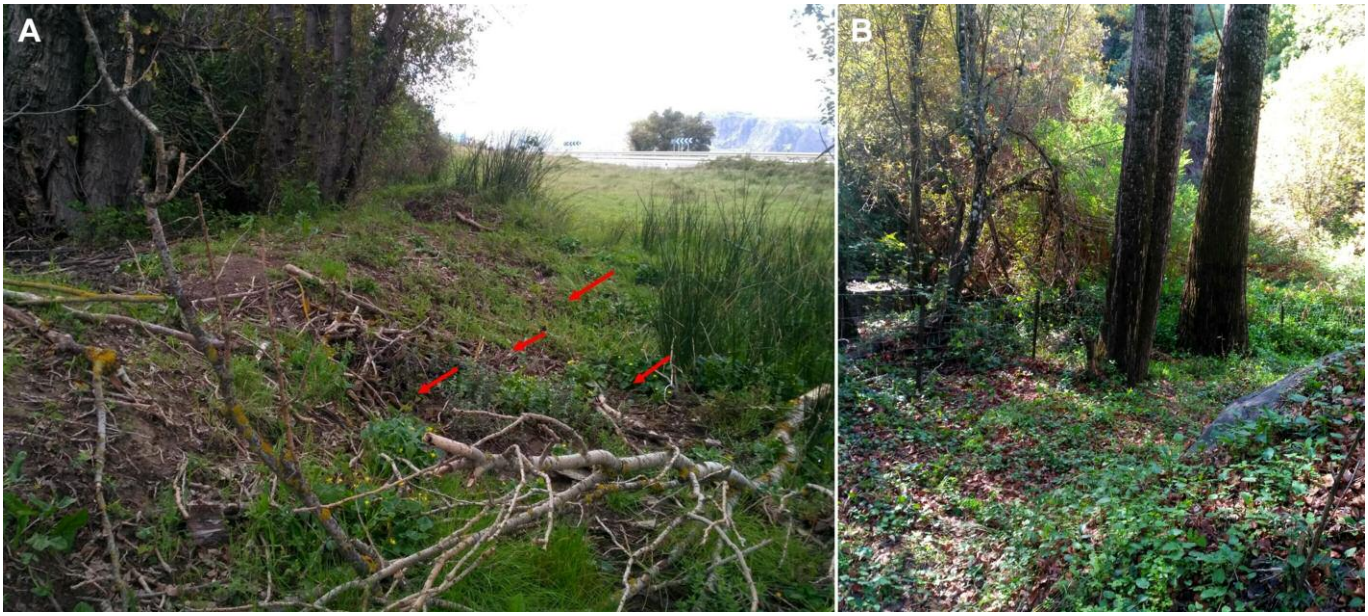

Plate 17 – Habitats of *Lasiobolidium trachysporum*
A. Ronda, Dehesa del Mercadillo (red arrows mark the location of specimens). B. Pujerra, Bentomiz. Photos F.J. Valencia.

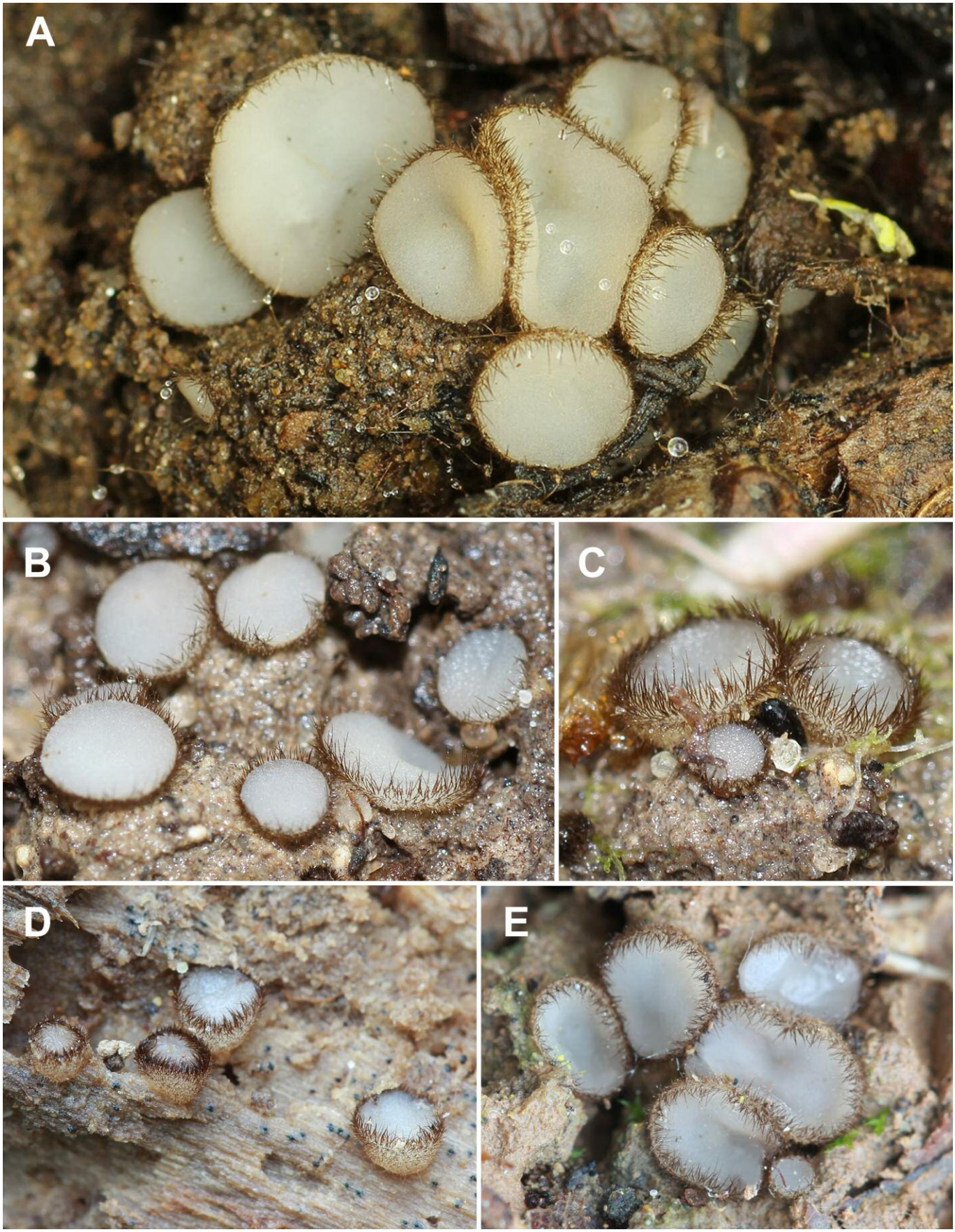

Plate 18 – *Lasiobolidium trachysporum*
Various collections *in situ*. A. Coll. CVL081119(1). B–C. Coll. CVL100419(1). D–E. Coll. CVL090420(1). Photos F.J. Valencia.

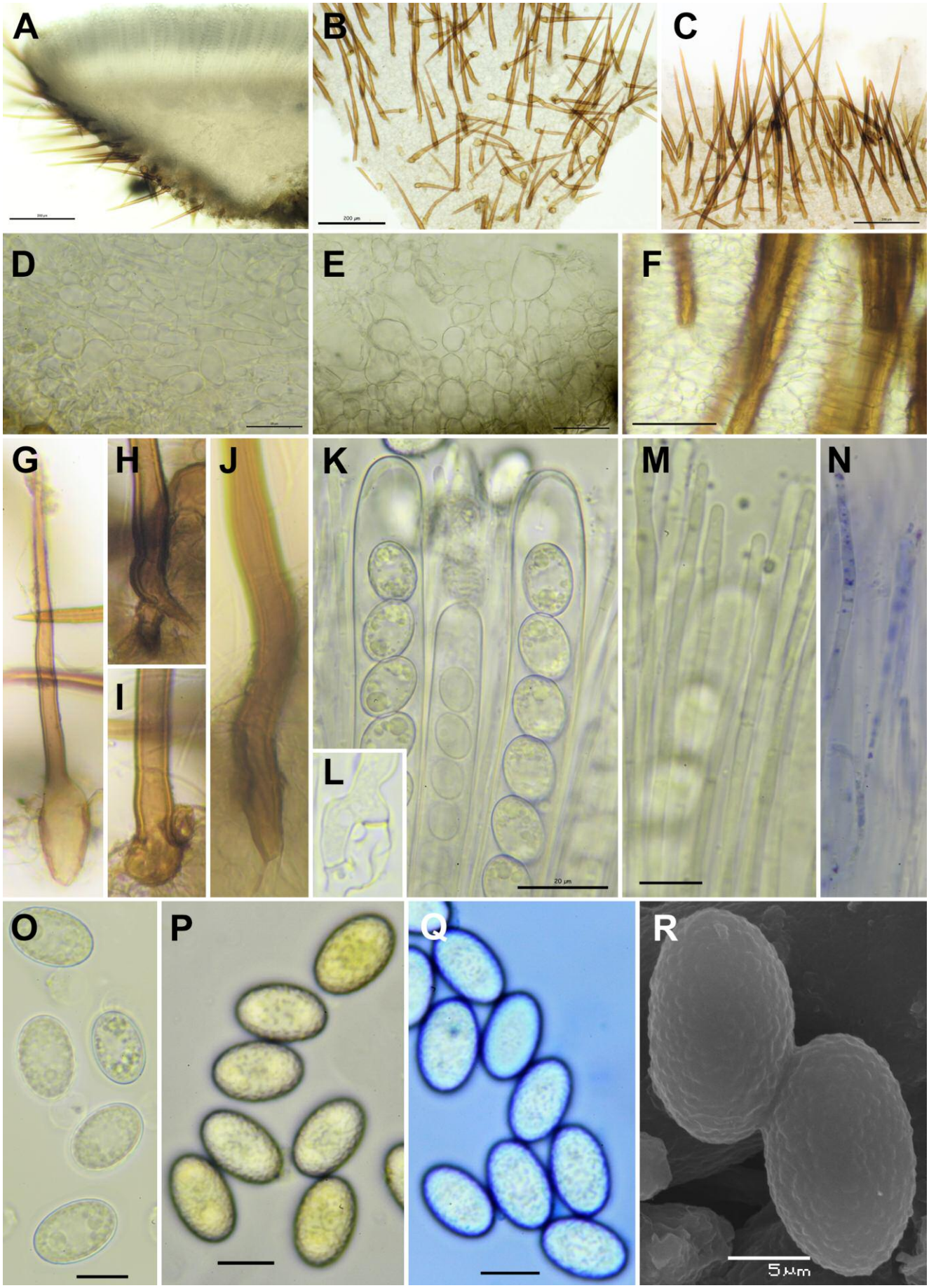

Plate 19 – *Lasiobolidium trachysporum*. Microscopical characters

A. Section of an apothecium. B. Excipular hairs. C. Marginal hairs. D. Medullary excipulum. E. Ectal excipulum. F. Marginal cells. G–J. Different types of excipular hairs. K. Asci. L. Ascus base. M. Top of paraphyses. N. Paraphyses in aqueous Cresyl blue. O. Ascospores in water. P. Ascospores in Lugol's solution. Q. Ascospores in Cotton blue. R. Ascospores under SEM. Scale bars: A–C = 200 µm, D, K, M = 20 µm, E–F = 50 µm, O–Q = 10 µm. All photos by F.J. Valencia, except R, L. Janošík.

Lasiobolidium coprophilum Van Vooren, Bronckers & Valencia, *sp. nov*. – MB 836355 – Pl. 20–22

Diagnosis: Differs from other apothecial species of *Lasiobolidium* by its growth on dung.

Type: Coll. MAAS:RB01127 (holotype).

Etymology: From ancient Greek κόπρος *(kópros)* meaning "dung", and φίλος *(phílos)* meaning "beloved, loving" because of the lifestyle of this species.

Misinterpretations: *Paratrichophaea boudieri*, in the sense of Bronckers (2003) *pro parte*.

Apothecia up to 2 mm diam., sessile, first obconical then discoid, barely depressed in the centre, hymenium pale greyish; external surface subconcolorous, densely covered with brown hairs, mainly upward-pointing, more densely set at the margin.

Subhymenium made of subglobular hyaline cells, mixed with more elongated hyphae. **Medullary excipulum** of *textura intricata*, with hyaline hyphae, 2.5–7.5 µm wide, mixed with some clavate cells, up to 11 µm wide. **Ectal excipulum** of *textura globulosa/angularis* with hyaline cells, 12–30 µm diam., becoming a *textura prismatica* near the margin. **Excipular hairs** rather deeply rooted, straight, (66–) 140–390 × 13–18 µm, amber brown or pale brownish, septate, 3–4 µm thick-walled, sharp at the top, with a simple, enlarged or bulbous base, up to 40 µm diam. **Marginal hairs** similar but longer, with a simple or more rarely bifurcate, non-bulbous base, (250–) 400–900 (–1000) × 19–33 (–37) µm, 3.5–6 µm thick-walled, sharp,

Plate 20 – *Lasiobolidium coprophilum*
A–B. Coll. JA-CUSSTA 9525. C. Coll. MAAS:RB01127. Photos A–B by F.J. Valencia, C by N. Van Vooren.

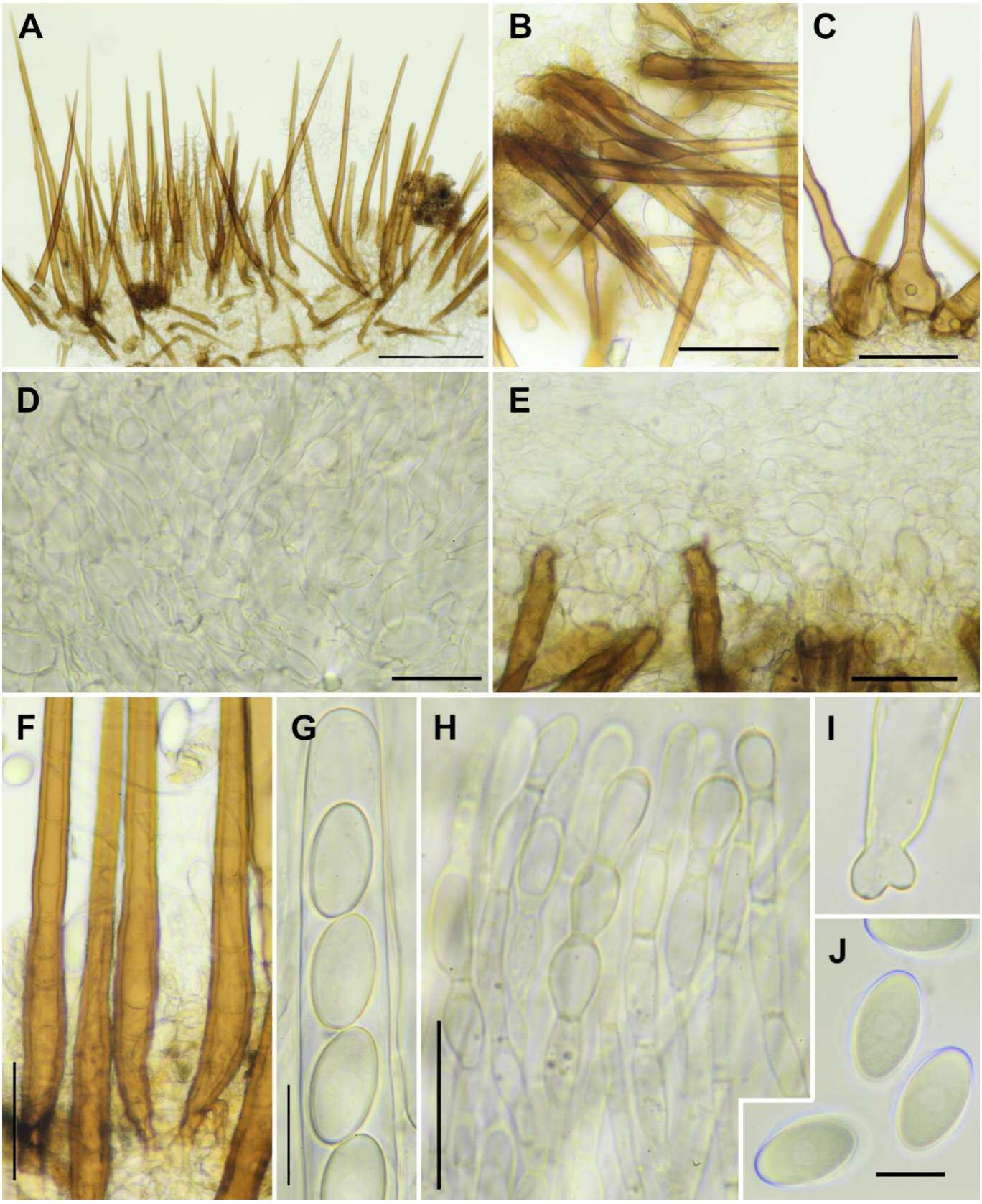

Plate 21 – *Lasiobolidium coprophilum*. Microscopical characters
Coll. JA-CUSSTA 9525. A. Marginal hairs. B. Excipular hairs. C. Excipular hairs with a bulbous base. D. Medullary excipulum. E. Ectal excipulum. F. Basal part of marginal hairs. G. Ascus top. H. Paraphyses. I. Ascus base. J. Ascospores. All in water. Scale bars: A = 200 µm; B–C, E–F = 50 µm; D, G–H, J = 20 µm. All photos by F.J. Valencia.

Table 3 – Comparison between the collections of *L. coprophilum*

Collections	Asci	Ascospores size (µm)	Marginal hairs dim. (µm)
MAAS:RB01127	8-spored	16.5–18 (–18.2) × (9–) 9.5–10.5	(250–) 400–760 × 19–33 (–37)
RB01123	4-spored	19–23.5 (–25) × (10–) 11–13 (–14)	270–580 × 15–23
JA-CUSSTA:9525	4-spored	23.6–25.9 (–28.5) × (12.8–) 13.2–14.1 (–14.7)	170–550 × 10–23
Welt & Heine (2006) under *P. boudieri*	8-spored	18–20 (–20.5) × 10.5–11.5 (–12)	300–910 × 25

more rarely obtuse. Margin composed of clavate cells, 35–40 × 5–10 µm, and macrocells (pseudohairs), ± clavate, 18–90 (–100) × 10–30 µm, hyaline, 1–3 µm thick-walled. **Anchoring hyphae** present, hyaline, septate, 3–3.5 µm wide, arising from a bulbous base. **Ascospores** uniseriate, ellipsoid, (17–) 18–20 (–22) × (9–) 10–12 (–13) µm, † (16–) 16.5–18 (–18.2) × (9–) 9.5–10.5 µm, X = 17.2 × 9.8 µm, Q = 1.6–1.9, Qm = 1.8, hyaline, eguttulate, smooth; in 4-spored asci, ascospores measure: 19–25.9 (–28.5) × (10–) 11–14.1 (–14.7) µm [X = 24.7 × 13.6, n = 40], † 21–23 (–24) × 11.5–12.5 (–13) µm, X = 21.8 × 12 µm, Q = 1.7–2.0, Qm = 1.8. **Asci** cylindrical, 195–275 × 13–18 µm, arising from croziers, operculate, 4- or 8-spored. **Paraphyses** slender, 1.5–2 µm diam., slightly enlarged at the top, up to 3 µm wide, hyaline, sometimes with moniliform articles.

Studied collections: The Netherlands. Zuid-Limburg, Bemelen, Groeve't Rooth, ~50.837596° N 5.776368° E, alt. 140 m, in a quarry, on old horse dung (Konik breed), on calcareous soil between some grasses and litter of a vegetation with *Salix caprea* and *Betula pendula*, 22 Sept. 2001, *leg*. R. Bronckers, *rev*. N. Van Vooren, pers. herb. RB01123 under *Paratrichophaea michiganensis*; GenBank LSU MW546550. Zuid-Limburg, Fauquemont, Ingendael, ~50.868793° N 5.806111° E, alt. 130 m, on old horse dung (Konik breed), in a deciduous forest (*Carpinion betuli*), 27 Sept. 2001, *leg*. R. Bronckers, *rev*. N. Van Vooren, herb. MAAS:RB01127 (holotype) under *Paratrichophaea boudieri*; GenBank ITS MW546584, LSU MW546549. Spain. Málaga, Parauta, Parque Natural Sierra de las Nieves, monumento natural Pinsapo de las Escaleretas, 36.667278° N 5.035972° W, alt. 1167 m, on cow dung, in a wood of *Abies pinsapo*, *Pinus pinaster* and *Quercus* sp., 15 Apr. 2019, *leg*. F.J. Valencia, *rev*. N. Van Vooren, pers. herb. CVL150419(1) under *Trichophaeopsis tetraspora*, JA-CUSSTA:9525, duplicate LY:NV 2019.04.00; GenBank ITS MW546585, LSU MW546551.

Comments: Initially described as *Paratrichophaea macrocystis* by Bronckers (2002b) for 8-spored collections, then synonymised with *P. boudieri* (Bronckers, 2003), the revision of the collection and molecular data proved the originality of this taxon. Unlike *Lasiobolidium boudieri*, *L. coprophilum* possesses very distinct marginal clavate macrocells (or pseudohairs). The substrate is also clearly different. *Lasiobolidium macrocystis* also presents such marginal macrocells (*inde nomen*) but reaching a length of 180 µm, grows on decorticated wood, and its marginal hairs are mainly multifurcate, whereas *L. coprophilum* has marginal hairs with a simple or more rarely bifurcate base. The collection with 4-spored asci named *Paratrichophaea michiganensis* by Bronckers (2002b) appeared to be the same species. It is interesting to note that the ascospores in 4-spored asci collections show an important variability in size (Fig. 21) and are larger than the other collections (see Table 3), probably because they have more "space" to develop. We think that the collection of *Paratrichophaea boudieri* described from Germany by Welt & Heine (2006) on cow dung is probably *L. coprophilum*. *Paratrichophaea michiganensis* has been described with 4-spored asci, hairs reaching 700 µm in length and ascospores 19–22 (–24) × 10–12 µm (Pfister, 1988) or 16–18 × 8–10 µm (Kanouse, 1958). Macrocells are also present at the margin based on the description and illustration of the original collection (Kanouse, 1958). As it grows on wet leaf litter and has been described from North America, we expect it is different from the species presented here.

Trichophaeopsis tetraspora Dissing & M.D. Paulsen (see under this name) is very similar with 4-spored asci, and a coprophilous lifestyle, but it shows a different type of hairs and the outerpart of the ectal excipulum is entirely composed of *textura prismatica*.

Interestingly *Cheilymenia pallida* Bell & Dennis, growing on dung of opossum in New Zealand, shows morphological affinities with *L. coprophilum*: greyish white ascomata, upward-pointing marginal hairs rather deeply rooted in the ectal excipulum, eguttulate smooth ascospores, and marginal cells forming a *textura prismatica* as depicted by Moravec (2005: 138). The multifurcate hairs base also resembles that of the hairs of *L. macrocystis*. The size of ascospores, less than 12 µm long, excludes a link with the latter or with *L. coprophilum*, but the other characters question the position of *C. pallida* in the genus *Cheilymenia*.

Finally we noted that *L. coprophilum* may be considered as paraphyletic based on molecular data (Fig. 1). More collections are required to improve the taxonomy of coprophilous *Lasiobolidium*.

Distribution: Known from the Netherlands, Spain and probably Germany (but see our previous comments).

Parawilcoxina Van Vooren, *gen. nov*. – MB 836719

Diagnosis: Differs from *Wilcoxina* by the presence of vacuolar bodies in paraphyses, its saprobic status, and its genetic profile.

Type species: *Parawilcoxina inexpectata*

Etymology: From ancient Greek παρά *(pará)*, "close to", and *Wilcoxina*, the closest genus.

Description: Ascomata epigeous, apothecial, sessile, slightly cupuliform, disciform to discoid, whitish to pale greyish, with an external surface covered by small brown hairs. Excipulum two-layered: medullary layer of *textura intricata* and ectal layer of *textura globulosa/angularis*. Hairs superficial, straight, septate, with a simple base, sometimes arising from a chain of rounded cells. Ascospores uniseriate or irregularly biseriate, ellipsoid to narrow ellipsoid, hyaline, guttulate, smooth. Asci operculate, narrowing toward base, arising from croziers, inamyloid, 8-spored. Paraphyses containing vacuolar bodies. Species saprobic[1]. Asexual morph unknown.

Comments: *Parawilcoxina* is proposed as a new genus to accommodate a species discovered in southern Spain which morphologically resembles a minute *Wilcoxina* or *Trichophaea* species. Its isolated position in the /*Trichophaea* clade had been unexpected.

Parawilcoxina inexpectata Valencia, Van Vooren & M. Vega, *sp. nov*. – MB 836721 – Pl. 23–24

Diagnosis: Differs from guttulate-ascospored *Wilcoxina* by shorter marginal hairs, vacuolar bodies in paraphyses, its saprobic status, and genetic profile.

Type: Coll. JA-CUSSTA:9522 (holotype).

Etymology: From Latin *inexpectatus* meaning "unexpected".

[1] There is no correspondence between rDNA data obtained from the type species and EcM sequences registered in GenBank, this is why we hypothesize the genus to be saprobic.

Ascomata gregarious or isolated. **Apothecia** 1–3.5 mm diam., sessile, first subglobose then discoid, hymenium whitish to greyish; external surface concolorous or slightly darker, covered with appressed brown short hairs, upward-pointing, more densely set at the margin.

Subhymenium and **medullary excipulum** not distinguished, of *textura intricata*, with hyaline narrow hyphae, 3–6 µm wide, mixed with some subgloblose cells near the margin. **Ectal excipulum** of *textura globulosa/angularis* with hyaline cells, 9–22 µm diam. or (15–) 28–33 (–46) × (14–) 21–23 (–29.5) µm. **Marginal hairs** dense, straight, (45–) 75–125 (–150) × 6–10 (–15) µm, superficial, pale brown, septate, sharp at the top or apically rounded, ± ventricose, with a simple base, 0.5–1.4 µm thick-walled, often arising from a chain of rounded cells. **Excipular hairs** superficial, slightly shorter, straight or curved, (50–) 78–94 (–122) × (5.5–) 6–7 (–7.5) µm. **Anchoring hyphae** present, 200–237 (–245) × (5.5–) 7–15 (–17) µm,

Plate 23 – *Parawilcoxina inexpectata*
A, C. Different views *in situ* of coll. CVL170919(1). B. Habitat. D–E. Close-up views. All photos by F.J. Valencia.

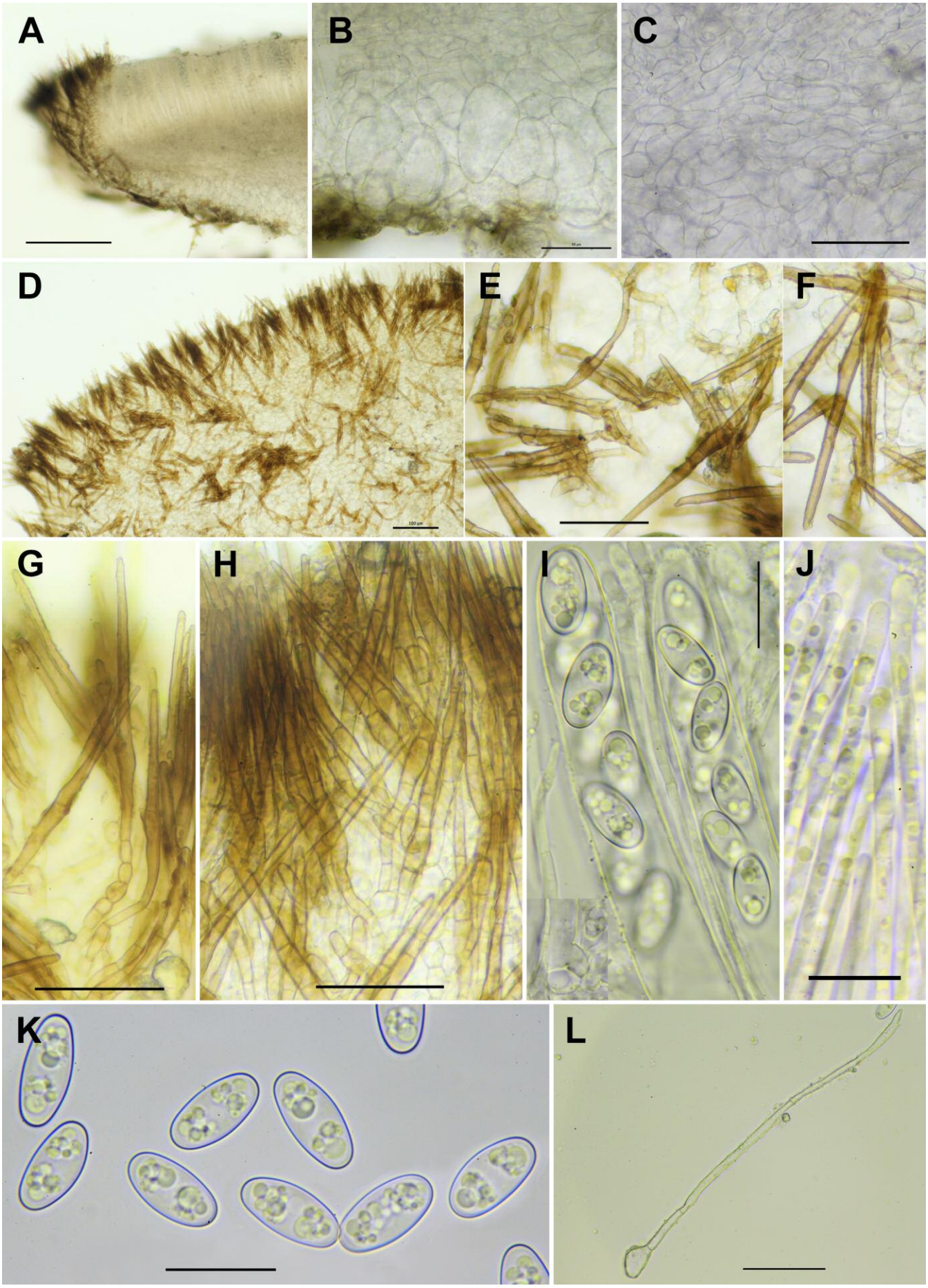

Plate 24 – *Parawilcoxina inexpectata*. Microscopical characters

A. Section of an apothecium. B. Ectal excipulum. C. Medullary excipulum. D. Hairs on the excipular surface. E–F. Excipular hairs. G–H. Marginal hairs. I. Asci. J. Paraphyses. K. Ascospores in water. L. Anchoring hypha. Scale bars: A = 200 µm, B–C, E–H, L = 50 µm, D = 100 µm, I–K = 20 µm. All photos by F.J. Valencia.

with a rather thick yellowish wall, rounded or slightly sharp at apex, arising from a bulbous base. **Ascospores** uniseriate or irregularly biseriate, ellipsoid or narrow ellipsoid, at times flattened on one side, (17.3–) 18.6–19 (–20.2) × 9–9.5 (–9.9) µm µm, X = 18.8 × 9.4 µm, Q = 1.8–2.2, Qm = 2.0, hyaline, smooth, containing two polar lipid drops, measuring 0.5–3 µm diam., accompanied by smaller droplets. **Asci** cylindrical, 215–270 × 15–17 µm, arising from croziers, operculate, 8-spored. **Paraphyses** filiform, hyaline, septate, sometimes slightly enlarged at the top, 3.5–4 µm diam., sometimes bifurcate at the top, containing small yellowish vacuolar bodies, up to 0.8 µm diam. and, in the middle or down part, small refractive bodies bluing in aqueous Cresyl blue.

Studied collection: Spain. Málaga, Ronda, Arroyo de la Ventilla, 36.79388° N 5.11151° W, alt. 717 m, on wet soil, in a riparian forest, among small bryophytes, with *Populus nigra*, *Ficas carica*, *Hedera helix*, *Equisetum telmateia*, *Carex pendula*, *Berula erecta* and *Clematis vitalba*, 17 Sept. 2019, *leg*. F.J. Valencia, ex herb. CVL170919(1), JACUSSTA:9522 (holotype) and LY:NV 2019.09.17 (isotype); GenBank ITS MW546598, LSU MW546564, RPB2 MW544624, TEF1 MW544639.

Comments: Based on its morphology, we first supposed this species could be associated with the genus *Trichophaea* or eventually *Wilcoxina*, especially because of the presence of some hairs having a basal chain of rounded cells (Fig. 24G), but the molecular data unexpectedly revealed it was nested in the same clade as *Anthracobia*/*Trichophaea* but in an isolated branch. Such a result offered the opportunity to propose the creation of the genus *Parawilcoxina*.

Distribution: Only known from the type locality in Spain.

Trichophaeopsis Korf & Erb – MB 5575

Type species: *Ciliaria bicuspis* Boud., *Bull. Soc. mycol. France*, 12: 11 (1896).

Amended description: Ascomata epigeous, apothecial, sessile, pale greyish, with an external surface and margin covered by upward-pointing brown hairs. Excipulum three-layered: medullary layer of *textura intricata*, ectal layer of *textura globulosa/angularis* and the outermost part of ectal excipulum of *textura prismatica*. Hairs simple or bifurcate, deeply inserted in the excipulum, septate, mainly with a simple base. Ascospores uniseriate, ellipsoid, hyaline, eguttulate, but sometimes containing small granules that can merge into two lipid drops in overmature or dead ascospores, smooth or verrucose. Asci operculate, narrowing toward base, arising from croziers, inamyloid, 8-spored, more rarely 4-spored. Paraphyses slender, not enlarged at the top. Species saprobic, on soil, woody debris or organic matter. Asexual morph unknown.

Comments: This genus was published by Korf & Erb (1972) to separate *Trichophaea bicuspis* from the other *Trichophaea* species because of the excipulum structure, the particular type of bifurcate hairs and ascospores lacking true lipid drops. Later, based on these characters, the coprophilous *T. tetraspora* was published by Dissing & Paulsen (1975) and *T. latispora* by Moravec (1979), although the latter has warted ascospores. Häffner & Krieglsteiner (1991) combined *Trichophaea paludosa* (Boud.) Boud. and *T. tuberculata* (Seaver) Kanouse into *Trichophaeopsis* but their arguments are far from being clear, as they are just referring to the similarity of hairs because they are forked as in *Scutellinia*, and evoke other morphological and ecological similarities without developing this point. Based on their descriptions, illustrations, and our own experience of these species, we disagree with this combination in *Trichophaeopsis* because the ectal excipulum structure is not a *textura prismatica*, no specific bifurcate hairs have been observed and the ascospores are biguttulate. A preliminary rDNA result based on a personal collection of *Trichophaea paludosa* confirms that it does not belong to *Trichophaeopsis* (Fig. 1).

A new species, collected in Spain during the Ascomycota foray 2013 in Somiedo, is described and illustrated.

Trichophaeopsis bicuspis (Boud.) Korf & Erb, *Phytologia*, 24: 18 (1972) – Pl. 25–26

Basionym: *Ciliaria bicuspis* Boud., *Bull. Soc. mycol. France*, 12: 11 (1896).

Homotypic synonyms: *Lachnea bicuspis* (Boud.) Sacc. & P. Syd., *Syll. fung.*, 11: 616 (1895); *Trichophaea bicuspis* (Boud.) Boud., *Icones mycologicæ, liste prélim.*: 3 (1904).

Other synonyms: *Lachnea eichlerii* Bres., *Ann. Mycol*., 1 (2): 119 (1903), *fide* Korf & Erb (1972); *Tricharia eichlerii* (Bres.) Boud., *Hist. classif. Discom. Eur.*: 57 (1907); *Lachnella setiformis* Rehm, *Ann. Mycol*., 12 (2): 174 (1914), *fide* Korf & Erb (1972).

Original diagnosis: *Sparsa aut aggregata minuta,* 1–3 *mm. lata, albido-glauca, extus pilis sparsis fuscis inferne productis vestita. Receptaculum hemisphaericum, marginalum, pallidum, extus pilis longis, sparsis, intense fuscis, acutissimis, septalis continuisve, ad basim saepius longe et acute productis, ad marginem membranaceum longioribus,* 200–600 *µ sine appendiculo,* 300–800 *cum,* 13–16 *µ crassis, hymenium planum aut in adultis parum convexum albido caesium, paraphyses graciles, ramosae, ad apicem non crassiores* 3 *µ crassae. Thecae operculatae, octosporae, ad basim paululum attenuatae,* 250–300 *µ longae,* 16–17 *spissae. Sporae ellipticae, intus primo granulosae, dein evidenter biguttulatae, sed guttulis crassis tamen subobliteratis,* 16–18 *µ longae* 12–13 *crassae.*

Ad terram glareosam, locis umbrosis humidiusculis in sylvis. Montmorency *Augusto* 1895 *et etiam ante reperi*.

Type: *ex* herb. Boudier in herbarium PC, s.n. (lectotype) [not revised, material available too poor].

Apothecia 1–2 mm diam., sessile, first urn-shaped then discoid, hymenium pale greyish; external surface concolorous but covered with sparse long brown hairs, mainly upward-pointing, more densely set at the margin.

Subhymenium thin, of *textura intricata*, with hyaline hyphae. **Medullary excipulum** of *textura globulosa/subglobulosa*, with hyaline cells 10–30 µm wide. **Ectal excipulum** of *textura prismatica* with cells hyaline or pale brown-coloured. **Excipular hairs** straight, 330–850 × 11–20 µm, amber brown, simple or bifurcate, septate, sharp

Key to the European species of *Trichophaeopsis*

1. Ascospores smooth **2**
1. Ascospores ornamented ..... ***T. latispora***
2. Apothecia growing on dung; asci 4-spored ..... ***T. tetraspora***
2. Apothecia growing on other substrates **3**
3. Ascospores 16–20 (–22) × 11–13.2 (–14) µm; hairs often bifurcate, reaching 850 µm long; often with woody debris of *Populus* ..... ***T. bicuspis***
3. Ascospores 16–18 (–18.5) × 11–12 (–12.2) µm; hairs simple, reaching 470 µm long; on soil ..... ***T. asturiensis***

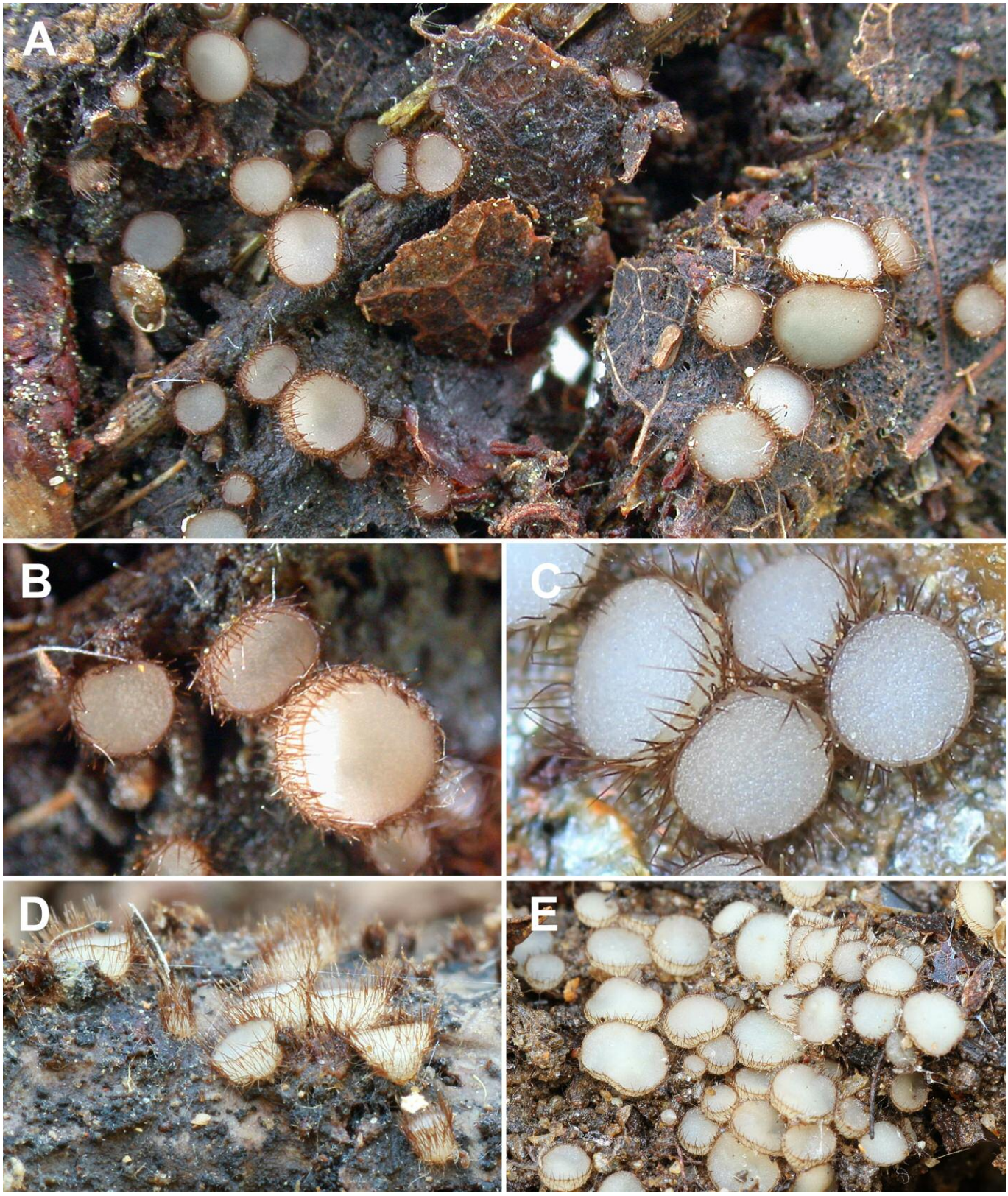

Plate 25 – *Trichophaeopsis bicuspis*

Various collections *in situ*. A–B. Coll. NV 2012.05.04. C. Close-up view. D. Coll. CVL141116(1). E. Coll. CVL061117. All photos by F.J. Valencia, except A–B by N. Van Vooren.

at the top, with a simple base, inserted in the ectal excipulum. **Anchoring hyphae** present, 300–400 × 5–6 µm, hyaline or pale brown, septate, with a bulbous base. **Ascospores** uniseriate, ellipsoid, (15.8–) 16–20 (–22) × (10.5–) 11–13.2 (–14) µm, X = 17.6 × 11.8 µm, Q = 1.3–1.6 (–1.7), Qm = 1.5, hyaline, smooth, rather thick-walled, containing bipolar lipid droplets of various size that often merge at the end into two lipid drops[2]. **Asci** cylindrical, (200–) 220–260 × 12–16 µm, arising from croziers, operculate, 8-spored. **Paraphyses** filiform, sometimes forked, hyaline, septate, not enlarged at the top, 2–2.5 µm diam.

[2] Contrary to the opinion of Korf & Erb (1972), the content of these drops is oleaginous and stainable, for example, with aqueous Cresyl blue (Baral, 1992).

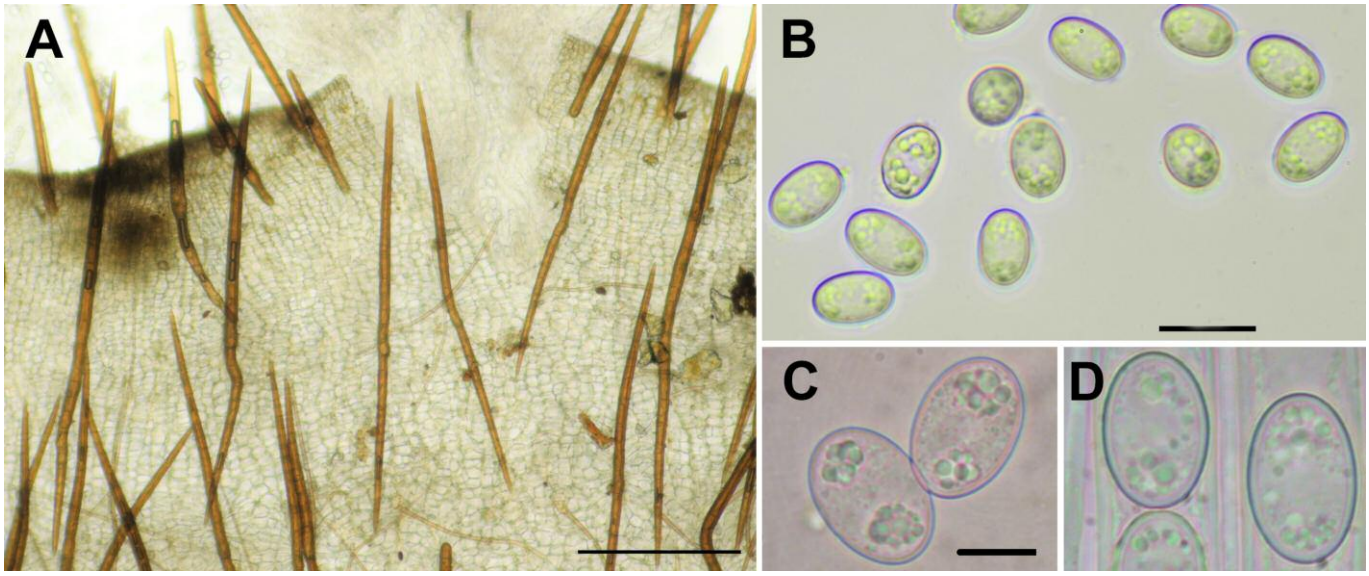

Plate 26 – *Trichophaeopsis bicuspis*. Microscopical characters
A. Ectal excipulum and excipular hairs. B. Ascospores (coll. CVL061117). C. Ascospores (coll. NV 2007.04.07). D. Ascospores in asci (coll. NV 2012.05.04). Scale bars: A = 200 µm, B = 20 µm, C = 10 µm. Photos A–B by F.J. Valencia, C–D by N. Van Vooren.

Studied collections: France. Rhône, Sérézin-du-Rhône, île de la Table Ronde, 45.6406648° N 4.819367° E, alt. 158 m, on decayed wood of *Populus nigra*, 6 Apr. 2007, *leg*. N. Van Vooren, herb. LY:NV 2007.04.07. Vendée, Barbâtre, île de Noirmoutier, 46.907122° N 2.157848° W, alt. 2 m, on decaying litter of *Cupressus macrocarpus* and *Populus* sp., 10 May 2012, *leg*. G. Moyne & N. Van Vooren, herb. LY:NV 2012.05.04; GenBank ITS MW546605, LSU MW546573. Spain. Málaga, Pujerra, Valle del Genal, near the stream Arroyo Bolage, 36.6174° N 5.14859° W, alt. 596 m, on soil with woody debris of *Populus nigra*, 14 Nov. 2016, *leg*. F.J Valencia, pers. herb. CVL141116(1). Málaga, Pujerra, Valle del Genal, near the stream Arroyo Bolage, 36.615556° N 5.145833° W, alt. 622 m, on soil on decaying remains of *Populus nigra*, 6 Nov. 2017, *leg*. F.J. Valencia, pers. herb. CVL061117.

Comments: This species is easily recognised by the presence of bifurcate hairs and its habitat on decaying wood or plant debris (Boudier, 1896), especially from *Populus* spp. The spore content is also characteristic with numerous lipid droplets of various size, sometimes merged into two polar drops. Korf (1977) combined *Trichophaea eguttulispora* Gamundí, a species discovered in Patagonia (Gamundí, 1973; 1975) as a subspecies of *T. bicuspis* because of the few differences with the typical collections of the latter. This raises doubts as the biogeographical characters of this taxon may be sufficient to keep it as a "good" species but molecular data are required to validate this hypothesis.

Based on our phylogeny (Fig. 1), the American collection of *T. bicuspis* seems to be a different species from the European one. More collections need to be sequenced and studied to evaluate the taxonomic value of this preliminary result.

Distribution: Based on literature, uncommon but widely distributed in Europe. Outside Europe, known from Kazakhstan (Dissing & Raitviir, 1973), Turkey (Kaya *et al*., 2016), USA (Kanouse, 1958; Korf & Erb, 1972; Beug *et al*., 2014) and based on Internet resources, Canada and Eastern Russia.

Trichophaeopsis tetraspora Dissing & M.D. Paulsen, *Bot. Tidsskr*., 70: 147 (1975) – Pl. 27

Original diagnosis: *Carposomata* 0.5–1 *mm lata, turbinata vel disciformia, regulariter orbicularia, solitaria vel gregaria. Hymenium albidum, planum vel paulum cavum. Margo laevis, elevatus. Superficies exterior carposomatis fuscida, pilis longis rigidis fuscidis obsita, summis simplicibus sursum directis, pilis mediae partis saepe bifidis, ramo breviore deorsum directo. Excipulum exterius in parte superiore textura angulata,* 50–56 *µm crassum, in inferiore textura angulata vel globosa, 53–66 µm crassum. Cellulae eius in parte superiore* 8.3–14.5 × 6.6–9.9 *µm, in inferiore* 6.6–16.5 × 6.6–13.2 *µm magnae, in ipso margine minores, claviformes,* 3.3–8.3 × 5.0–8.3 *µm magnae, superficiales totius excipuli in series verticales dispositae* (Fig. 1)*, membranis fuscidis, valde cyanophilis. Pili e cellulis excipuli exterioris orti ad* 580 *µm longi* 23 *µm crassi fuscidi acuti septis ad* 15 *divisi, membranis ad* 3.3 *µm crassis. Rami inferiores pilorum bifidorum ad* 400 *µm longi. Pars inferior excipuli pilis flexuosis instructa hyphoidibus hyalinis septatis ad* 400 *µm longis* 3.3–3.5 *µm crassis, membranis tenuibus. Excipulum medullare e cellulis hyalinis membranis tenuibus formatum, aliis hyphoidibus* 3.3–6.6 *µm latis, aliis angulatis* 9.9–16.5 × 8.3–16.5 *µm magnis. Subhymenium paulum manifestum. Hymenium* 170–190 *µm altum; asci tetraspori* 13–14 *µm crassi cylindrici operculati iodo non mutati, basibus pleurorhynchis; paraphyses supra paulum incrassatae, ad 3 µm crassae, rectae vel subcurvae septatae. Sporae* 18.2–19.5–20.5 × 10.9–12.2–13.2 *µm magnae ovales uniseriatae hyalinae laeves uninucleatae, guttulis nullis, nonnullae vagina gelatinosa indutae, nonnullae unam vel duas bullulas debaryanas exhibentes.*

Type: Denmark, Møen, Ulfshale, 28 Sept. 1974, *leg*. M.D. Paulsen, N. Tams & H. Dissing, holotype (C).

Apothecia 0.3–0.5 mm, sessile, first urn-shaped then discoid, hymenium whitish to pale greyish; external surface concolorous, but covered with dense and long hairs, brown, mainly upward-pointing, more densely set at the margin.

Subhymenium thin, of *textura intricata*, with hyaline hyphae. **Excipulum** of *textura globulosa/subangularis*, with hyaline cells, 9–15 µm diam., rather thick-walled, becoming a *textura prismatica* in the outermost part. **Hairs** straight, up to 550 µm in length, 9–15 µm wide, brown, septate, thick-walled, sharp at the top, with a simple or more rarely forked base, enlarged or sometimes bulbous at the base; bifurcate hairs not observed in this collection. **Ascospores** uniseriate, ellipsoid, sometimes tapering at the ends, 17.5–20 × (9.8–) 10–10.5 µm, X = 18.6 × 10.3 µm, Q = 1.7–2.0, Qm = 1.8, hyaline, rather thick-walled, eguttulate but with sparse small granules in young spores, smooth or very finely dotted (only visible in CB at immersion). **Asci** cylindrical or slightly clavate, 130–160 × 15–17 µm, arising from croziers, operculate, 4-spored. **Paraphyses** filiform, hya-

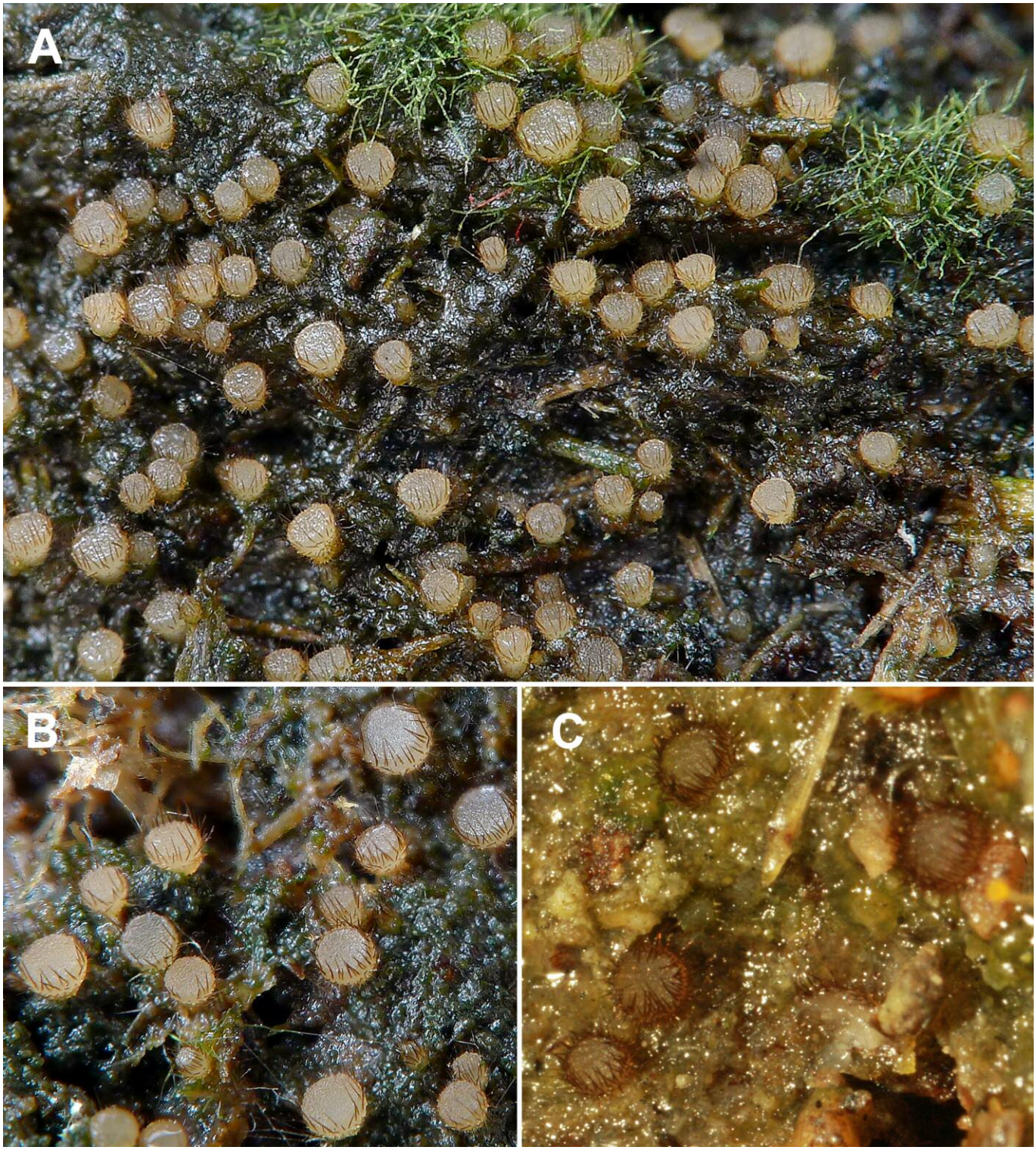

Plate 27 – *Trichophaeopsis tetraspora*
A–B. Different views of Bender's coll., photos by H. Bender. C. Coll. NV 2009.10.07, photo by P. Roux.

line, septate, often constricted at the septa, not enlarged at the top, 2–3 µm diam.

Studied collection: France. Haute-Corse, Morosaglia, Ponte Leccia, ~42.4634571° N 9.209948° E, alt. 300 m, on old cow dung, 12 Oct. 2009, *leg*. and *det*. B. Senn-Irlet, *rev*. N. Van Vooren, herb. LY:NV 2009.10.07.

Other collection (not studied but well documented): Germany. Nordrhein-Westfalen, Brüggen, NSG Brachter Wald, 51.27745° N 6.152463° E, alt. 60 m, on cow manure, 19 Sept. 2015, *leg*. H. Bender, pers. herb. Bender.

Comments: Although being very rarely reported, this typical *Trichophaeopsis* species is easy to recognise due to its 4-spored asci and growth on old cow dung. It has been scarcely cited in mycological literature since its publication by Dissing & Paulsen (1975), even though the literature on coprophilous fungi is abundant. As the species is widely distributed, it suggests a lifestyle requiring particular conditions of growth. *Lasiobolidium coprophilum*, described in this paper, is close to *T. tetraspora* because some collections present 4-spored asci, but it has a different structure of ectal excipulum and hairs of a different type.

Distribution: Seems very rare, known only from Denmark (Dissing & Paulsen, 1975), France (Donadini, 1985; Van Vooren, 2010), Germany

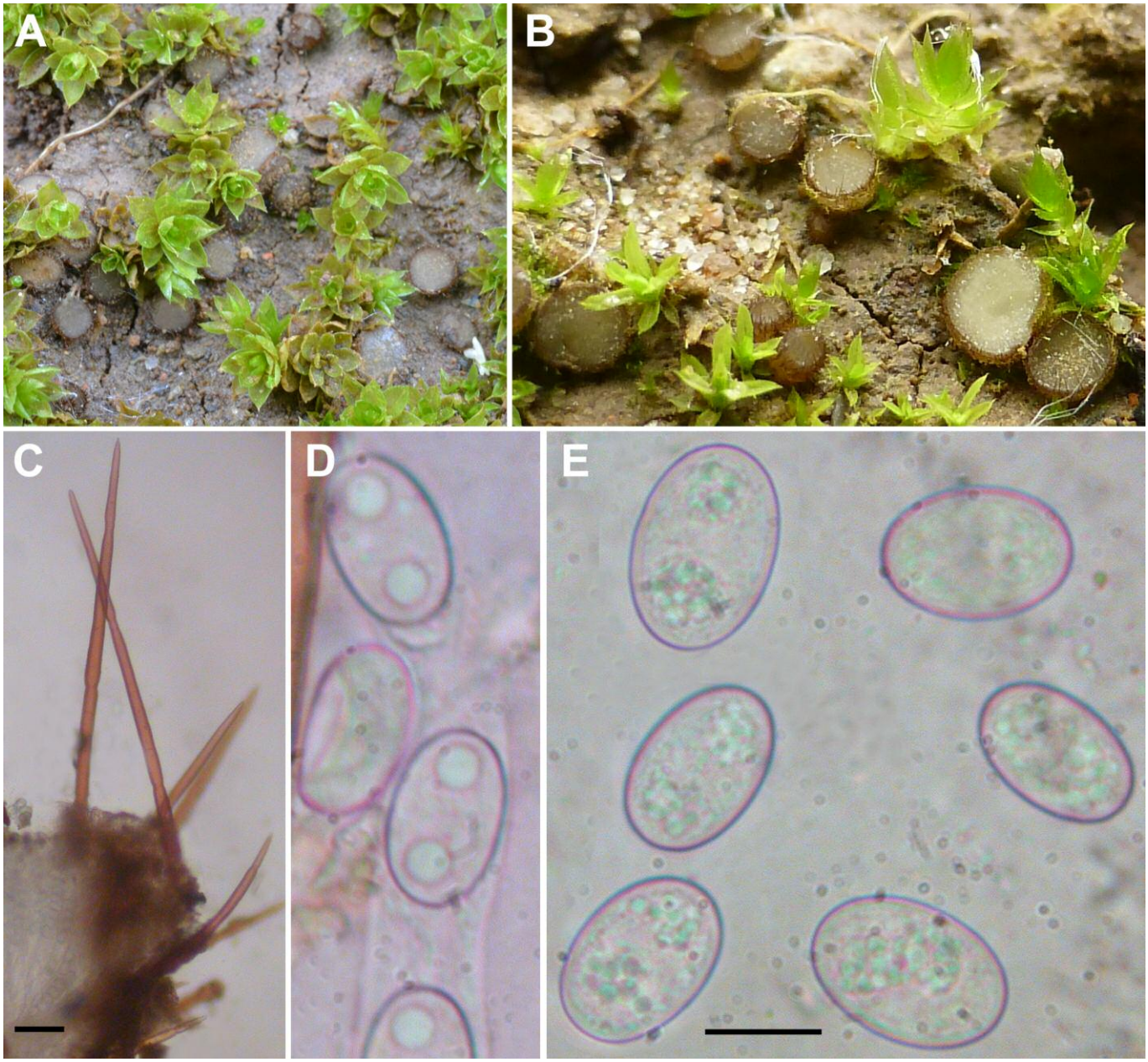

Plate 28 – *Trichophaeopsis asturiensis*

A–B. Different views of coll. NV 2013.06.19. C. Hairs. D. Dead ascospores. E. Living ascospores. Scale bars: C = 50 µm, E = 10 µm. All photos by N. Van Vooren, except B, M. Vega.

(this paper), Netherlands (Bronckers, 2002a), Spain (Ortega & Galán, 1984; this paper) and based on Internet resources also Belgium. Outside Europe, the species has been found in Canada.

Trichophaeopsis asturiensis Van Vooren & M. Vega, *sp. nov.* – MB 836275 – Pl. 28

Diagnosis: Differs from *T. bicuspis* by its simple shorter hairs and ascospores slightly shorter on average, as well as a terricolous habitat.

Type: Coll. LY:NV 2013.06.19 (holotype).

Etymology: From Asturias, the Spanish autonomous community where the species was first collected.

Apothecia 1–2 mm diam., sessile, discoid or slightly pulvinate, hymenium pale greyish; external surface concolorous but covered with sparse small brown hairs, mainly upward-pointing, more densely set at the margin.

Subhymenium thin, of *textura intricata*, with hyaline hyphae, 10–15 µm wide. **Medullary excipulum** of *textura intricata* in the upper part, then of *textura angularis* in lower part, with hyaline cells, 10–25 µm wide. **Ectal excipulum** of *textura prismatica*. **Hairs** straight, 110–470 × 15–18 µm, amber brown, septate, with wall 1–2 µm thick, sharp at the top, with a simple base, deeply inserted in the excipulum, often constricted in the middle part. **Ascospores** uniseriate, ellipsoid to broadly ellipsoid, (15–) 16–18 (–18.5) × (10.5–) 11–12 (–12.2) µm, X = 16.7 × 11.5 µm, Q = 1.4–1.6 (–1.7), Qm = 1.5, hyaline, ~0.5 µm thick-walled, smooth, containing small bipolar granules; these granules can merge into two drops in overmature or dead ascospores. **Asci** cylindrical, 200–220 × 12–14 µm, arising from croziers, operculate, 8-spored. **Paraphyses** filiform, flexuous, hyaline, septate, not enlarged at the top, 1.5–3.5 µm diam.

Studied collection: Spain. Asturias, Pola de Somiedo, 43.095127° N 6.256286° W, alt. 685 m, on soil, among small mosses, 6 Jun. 2013, *leg*. M. Vega, herb. LY:NV 2013.06.19 (holotype); GenBank ITS MW546604, LSU MW546572.

Comments: Genetically very close to *Trichophaeopsis bicuspis*, this new taxon is well characterised by its rather short excipular and marginal hairs, upward-pointing, and its terricolous habitat. As in

the other species of this genus, the ectal excipulum is made of a *textura prismatica*. The spore content is similar to that of *T. bicuspis*, with numerous droplets that merge into polar lipid drops in dead or rehydrated ascospores.

Distribution: Only known from the type locality in Spain.

Key to the European *Trichophaea-like* and similar genera

The key is divided in three parts and proposes the colour of hymenium as first criterion. These keys are based on characters observed in living state.

Apothecia with a bright coloured hymenium (yellow, orangish or pink-red) ..... **Key A**
Apothecia with a whitish-cream, white- to pale grey-coloured, or yellow-brown hymenium ..... **Key B**
Apothecia with a dark-coloured hymenium (brown, grey-brown or blackish) ..... **Key C**

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KEY A: Apothecia with a bright coloured hymenium (yellow, orangish or pink-red)

1. Apothecia only with excipular hairs or without true hairs **2**
1. Apothecia with both marginal and excipular hairs **3**
2. Excipular hairs absent but coloured clavate cells present. Hymenium dull orange, orange to orangish brown, more rarely yellow ..... ***Anthracobia***
2. Excipular true hairs present. Hymenium bright orange. Ascospores ellipsoid ..... ***Pyronemataceae* sp. UR**
3. Hymenium reddish pink to vinaceous red ..... ***Parascutellinia***
3. Hymenium differently coloured **4**
4. Hairs base simple, arising from a chain of thick-walled excipular roundish cells ..... ***Wilcoxina***
4. Hairs base different **5**
5. Asci arising from free croziers; hymenium yellow-coloured; on conifers debris ..... ***Chaetothiersia***
5. Asci arising from croziers; hymenium often more orangish; on other substrates **6**
6. Paraphyses containing vacuole bodies ..... ***Paratricharina***
6. Paraphyses without vacuole bodies **7**
7. Ascospores eguttulate but containing small bipolar granules; on burnt soil ..... ***Ascorhizoctonia***
7. Ascospores guttulate **8**
8. Ascospores containing numerous refractive droplets; apothecia discoid or slightly convex ..... ***Tricharina glabra***
8. Ascospores biguttulate; apothecia deeply cupuliform ..... ***Aurantiolachnea solsequia***
8. Ascospores bi- or pluriguttulate; apothecia discoid ..... ***"Parascutellinia" fuckelii***

KEY B: Apothecia with a whitish-cream, white- to pale grey-coloured, yellow-brown hymenium

1. Outer part of the ectal excipulum fully of *textura prismatica* ..... ***Trichophaeopsis***
1. Outer part of the ectal excipulum of *textura globulosa* to *angularis*, sometimes of *textura prismatica* but only at the margin **2**
2. Hairs base simple, arising from a chain of thick-walled excipular roundish cells ..... ***Wilcoxina***
Note: See also *Parawilcoxina inexpectata* which shows some similar hairs.
2. Hairs base simple, with shortened articles in the lower part and typically constricted septae ..... albino collections or pale species of ***Spooneromyces***
2. Hairs base different **3**
3. Ascospores spherical; apothecia subglobose, ≤ 1 mm diam. ..... ***Trichophaea minuta***
3. Ascospores not spherical **4**
4. Hairs superficial **5**
4. Hairs distinctly rooted in the excipulum, upward pointing; ascospores eguttulate, sometimes with small bipolar granules, rarely ornamented ..... ***Lasiobolidium***
4. Hairs distinctly rooted in the excipulum; ascospores multiguttulate and always ornamented ..... albino collections of ***Scutellinia***
5. Ascospores guttulate **6**
5. Ascospores eguttulate **11**

Key B (continued)

6. Ascospores smooth or very finely dotted (CB in high magnification) **7**
6. Ascospores distinctly ornamented **9**

7. Ascospores uniguttulate ..... ***Trichophaea****
7. Ascospores bi- or pluriguttulate **8**

8. Marginal hairs < 150 µm in length ..... ***Parawilcoxina inexpectata***
8. Marginal hairs mainly longer ..... ***Perilachnea***

9. Hymenium whitish to light grey **10**
9. Hymenium cream white, yellowish, yellow-brown, nut-brown or pale orangish ..... ***Pseudotricharina***

10. Ascospores ornamented with rather small, regular warts ..... ***Humaria hemisphaerica*** complex
10. Ascospores ornamented with large, irregular or tuberculous warts ..... ***Pseudotrichophaea*** nom. prov.**

11. Excipular hairs long and flexuous, hyaline or light brown ..... ***Tricharinopsis***
11. Excipular hairs different, brown-coloured **12**

12. Asci arising from free croziers; on litter of conifers or woody debris ..... ***Chaetothiersia***
12. Asci arising from croziers; mainly on soil, more rarely on wood ..... ***Tricharina***

* Includes *Trichophaea woolhopeia* complex and *T. dougoudii*.
** Includes *Trichophaea paludosa*, *T. tuberculata* and *T. livida*.

KEY C: Apothecia with a dark-coloured hymenium (brown, grey-brown or blackish)

1. Hymenium dark grey-brown to blackish **6**
1. Hymenium of brown shades **2**

2. Ascospores eguttulate ..... ***Lotinia verna***
2. Ascospores pluriguttulate, fusoid ..... ***Anthracobia rehmii***
2. Ascospores uni- or biguttulate **3**

3. Ascospores spherical **4**
3. Ascospores ellipsoid ..... ***Trichophaea contradicta***

4. On burnt soil **5**
4. Not on burnt soil ..... ***Trichophaea hinnulea*** complex

5. Apothecia subglobose, < 500 µm diam. ..... ***Trichophaea saccata***
5. Apothecia discoid, 2–10 mm diam. ..... ***Trichophaea brunnea***

6. Ascospores mainly uniguttulate, very thick-walled ..... ***Trichophaea paraphysincrustata***
6. Ascospores mainly biguttulate, with or without droplets **7**

7. Marginal hairs sharp; ascospores subfusoid, 13.5–15.5 × 6.5–7 µm ..... ***Trichophaea abundans***
7. Marginal hairs obtuse; ascospores ellipsoid, 18–21 × 10–11 µm ..... ***Anthracobia subatra***

Authors' contributions

Nicolas Van Vooren was responsible for the study conception and design. Nicolas Van Vooren, Matteo Carbone, Uwe Lindemann and François Valade financially contributed to the generation of rDNA sequence. All authors provided voucher specimens. Morphological analyses were performed by the authors on their collections; on other collections, they are mentioned as "rev.". Molecular analyses were performed by Pablo Alvarado (ALVALAB). The first draft of the manuscript was written by Nicolas Van Vooren and was subsequently updated by all authors. All plates have been designed by Nicolas Van Vooren, except pl. 2, 3, 11 and 12 by M. Carbone. All authors read and approved the final manuscript.

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