

Emendation of the genus *Tricharina* (Pezizales) based on phylogenetic, morphological and ecological data

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Abstract: *Tricharina* is one of the most difficult genera of *Pezizales* because it is hard to distinguish morphologically among species. To provide a more robust taxonomy, new investigations on the genus were conducted, both morphologically and phylogenetically. This study focuses on the four key species of the genus: *T. ascophanoides*, *T. gilva*, *T. ochroleuca* and *T. praecox*. The type material of these species was reviewed. In the literature, *T. gilva* is considered to be close or even identical to *T. ochroleuca*. The phylogenetic analysis shows that all recent collections identified as *T. ochroleuca* appear to be *T. gilva*. Furthermore, the morphological study of the type material of *T. ochroleuca* leads to the conclusion that the name is a *nomen dubium*. The presence of several endophytes sequences in the *Tricharina*-core clade suggests that this genus has an endophytic lifecycle. The confusion between *T. gilva* and *T. praecox*, both considered as pyrophilous species, is now resolved thanks to phylogenetic analyses and new data based on vital taxonomy. In contrast to *T. gilva*, which can occasionally grow on burnt places, *T. praecox* is a strictly pyrophilous taxon and belongs genetically to a different clade than *T. gilva*. In agreement with art. 59 of ICN, the anamorphic genus *Ascorhizoctonia* is used to accommodate the species belonging to the “*T. praecox* clade”. *T. ascophanoides*, an extra-limital species, is excluded from the genus *Tricharina* and combined in the genus *Cupulina* based on the phylogenetic results. The genetic exploration of some other tricharinoid species, i.e. *Leucoscypha semiimmersa* and *L. patavina*, confirms they do not belong to the genus *Leucoscypha* in its original sense, and deserve their own genus. The name *Sepultariella* is validated to accommodate the latter.

Keywords: *Ascorhizoctonia*, *Cupulina*, *Leucoscypha*, *Pseudaleuria fibrillosa*, *Pyronemataceae*, ribosomal DNA, *Scutellinia-Trichophaea* lineage, *Sepultariella*, taxonomy.

Introduction

The genus *Tricharina* is a member of *Pezizales* and was proposed as a new name by ECKBLAD (1968: 60) replacing *Tricharia* Boud., an illegitimate name. The latter was first published by BOUDIER (1885) in his “tribu Cupulés, groupe Lachnés” for species with short, stiff, brown hairs, longer at the margin, with a sharp top, and smooth, eguttulate ascospores (“sans sporidioles”). *Peziza gilva* Boud. and *Lachnea fimbriata* Qué. were designated to belong to this genus. BOUDIER (1907a) partially emended this genus: it contains species with smooth ascospores or rarely verrucose without oil drops or only with some minute granules, sometimes organized in small groups (“quelques petites granulations parfois réunies en groupes”). These small inclusions are named “bipolar spore granules”, BSG, by KUŠAN *et al.* (2015). Twenty species were listed.

The type-species, *Peziza gilva*, was designated by CLEMENTS & SHEAR (1931: 329), followed by ECKBLAD (1968) and KORF (1972). Due to the rather similar characters of the *Tricharina* species, numerous confusions appeared in the literature and misinterpretations were frequent. For example, the concept of *Tricharina gilva* by BRUMMELEN (1983) was reevaluated as *Wilcoxina mikolae* (Chin S. Yang & H.E. Wilcox) Chin S. Yang & Korf (see YANG & KORF, 1985b). Recently LINDEMANN (2013) tried to clarify some taxonomical aspects and proposed a new key to the 12 accepted taxa.

The genus was monographed by YANG & KORF (*op. cit.*) who proposed a more accessible taxonomy, although the species were studied exclusively from herbarium material. In their work, the genus *Wilcoxina* was erected to segregate *Tricharina mikolae* Chin S. Yang & H.E. Wilcox due to morphological differences and a different type of asexual stage.

Since that publication, two species were combined in *Tricharina*, *T. flava* (Fuckel) J. Moravec (MORAVEC, 1990) and *T. herinkii* (Svrček) Benkert (BENKERT, 2010), and three additional new species were published: *T. tophiseda* Matočec & I. Kušan (KUŠAN *et al.*, 2015), *T. glabra* U. Lindemann & Böhning (LINDEMANN & BÖHNING, 2016) and *T. aethiopicica* U. Lindemann (LINDEMANN, 2017).

One species has been excluded from the genus: *Tricharina fibrillosa* (Currey) Chin S. Yang & Korf was transferred to the genus *Pseudaleuria* as *P. fibrillosa* (Currey) J. Moravec (MORAVEC, 2003). In the present work, our phylogenetic analysis of *P. fibrillosa* confirms the placement in *Pseudaleuria* (cf. Fig. 1 and 2).

Phylogenetic studies on the family *Pyronemataceae* (PERRY *et al.*, 2007; HANSEN *et al.*, 2013) revealed that *Tricharina* was paraphyletic.

Molecular analyses conducted in the course of the study of some tricharinoid species (VAN VOOREN *et al.*, 2015a, 2015b) confirmed the paraphyly. The present work is a contribution to serve the reevaluation of the genus *Tricharina* in the light of new molecular analyses, the review of type material, and new morphological data based on vital taxonomy methods (BARAL, 1992).

Materials and methods

Morphology and cytology. — The observations were made both on fresh and dried material. For dried samples, some small pieces of specimen were rehydrated for about twelve hours in tap water or in potassium hydroxide (5% KOH). The following mounts were used to observe microscopic characters: tap water, cotton blue (CB) both in lactophenol and lactic acid, aqueous solution of cresyl blue (CRB), 5% potassium hydroxide (KOH), and Lugol's solution (IKI) or Melzer (MLZ) to test the amyloid reaction. Measurements were made on 20 to 30 ascospores from each collection, mounted in water, under the 100× oil immersion lens of transmission light microscopes, excluding the ornamentation. “X” represents the average value of spore dimensions, and “Q” the ratio between spore length and width. Macro photographs were made *in situ* using digital cameras, while micrographs were taken using digital cameras mounted directly on microscopes. Line drawings were made freehand to scale.

Abbreviations: † is used to annotate observations from dead rehydrated material.

DNA extraction, amplification and sequencing. — DNA was extracted using the same method as described in VAN VOOREN *et al.* (2015a). Loci that were amplified included the ITS (ITS1, 5.8S and ITS2 rDNA) and LSU (D1, D2 and D3 of the 28S rDNA). Sequences obtained during this study were deposited in GenBank under the accession numbers listed in Table 4.

Phylogenetic analyses. — BLAST® was used to select the most closely related ITS and LSU sequences from the International Nucleotide Sequence Database Collaboration (INSDC) public databases. These were downloaded and aligned with the sequences obtained during this study using MAFFT v. 7.187 (KATO & TOH, 2010), followed by manual adjustment of obviously misaligned columns in SeAL v. 2.0a11 (RAMBAUT, 2007). The final ITS alignment had 80 sequences and 475 sites. The LSU alignment had 94 sequences and 847 sites. *Ascobolus* served as the outgroup for the LSU analyses, while the ITS tree was midpoint rooted. Both alignments were analyzed with Maximum likelihood (ML) using RAXML 8.1.24 (STAMATAKIS,

2014) with 1000 bootstrap iterations, and the Mr. Bayes (MB) program (HUELSENBECK & RONQUIST, 2001) using 20,000,000 generations sampled at every 1000 generations with the first 25% of samples discarded as burn in. Priors were estimated in jModelTest 0.1.1 (POSADA, 2008) using the Akaike information criterion. Tracer v1.4 (RAMBAUT & DRUMMOND, 2007) was used to inspect the completeness of the mixing of chains, whether stationarity was reached, and the adequacy of sampling. The programs MAFFT, RAxML and MB were run on XSEDE on the CIPRES Science Gateway v. 3.3 (MILLER *et al.*, 2010). Branch supports that are considered meaningful are shown where RAxML bootstrap percentages are $\geq 70\%$, and MB posterior probabilities are ≥ 0.95 .

Nomenclature. — All the references to articles of ICN come from the Melbourne Code (MCNEILL *et al.*, 2012). New nomenclatural determinations were registered in the MycoBank Database (<http://www.mycobank.org>).

Results

The molecular analyses based on the LSU and ITS loci confirmed that the genus *Tricharina* is paraphyletic, with species grouped in three distinct well-supported clades (Fig. 1 and 2), in the Scutellinia-Trichophaea-lineage (HANSEN *et al.*, 2013). The core clade of *Tricharina*, which includes the type species *Tricharina gilva*, is well supported in analyses of both ITS and LSU alignments. The core group includes the following species: *T. aethiopica*, *T. gilva*, *T. glabra*, *T. groenlandica*, *T. hiemalis*, and *T. striispora*. The sequences from the neotype of *T. ochroleuca* matched those from the holotype of *T. groenlandica*. The *Tricharina*-core group is sister to the Geopora lineage.

The ITS analyses also revealed the existence of a complex of species around *T. gilva*. This phylogenetic diversity does not appear in the LSU analyses and we did not find morphological differences in the studied collections to clearly delimit species in this complex. Therefore, *T. gilva* is here described and illustrated based on its morphological concept. We expect that analyses on other loci could help us to clarify the taxonomic delimitations of these collections.

A second clade comprises the *Tricharina* species around *T. praecox* and is distinctly outside the *Tricharina*-core group. The sequenced collections we used — either from GenBank or obtained during this study — suggest that all species belonging to the clade with *T. praecox* share the same ecology: a habitat on burnt ground. Based on these results and supported by morphological characters, we accept the emendation of MATOČEČ & KUŠAN, in KUŠAN (2015: 55) of the genus *Ascorhizoctonia* — previously known as an anamorphic genus — for taxa in the *T. praecox* clade (see discussion in chapter “The *Ascorhizoctonia*/*Tricharina*-*praecox* clade”).

A third distinct clade comprised *T. ascophanoides* and *Cupulina montana*. We here transfer *T. ascophanoides* to the genus *Cupulina* (see discussion in the chapter “The *Cupulina*-*Tricharina*-*ascophanoides* clade”). A new species of *Pseudotracharina* from Argentina was included in these analyses, and will be described in a forthcoming paper.

The *Tricharina*-Core group

In this chapter, we focus on the clade containing the type species of the genus *Tricharina*, *Peziza gilva*, and allied species. Comparisons between the type materials and modern collections gave us the opportunity to better circumscribe some of these species. The ITS and LSU sequences extracted from the type material of *P. gilva* were essential to the circumscription of the genus *Tricharina sensu stricto*, which is now strongly supported by molecular evidence. We here provide a description based on all studied and sequenced collections that we recognize as the “true” *T. gilva*.

Re-examination of type-material of *Peziza gilva*

Peziza gilva Boud., in COOKE (1879), is typified by the collection PC 0167813 which contains a single apothecium, in poor condition. The Boudier’s label indicates “*Lachnea* = *Tricharia gilva* Boud. Montmancy, terra culta.”

Contrary to YANG & KORF (1985b: 492) who designated this collection as the holotype, there is no evidence in the protologue (COOKE, 1879) or in the description provided by Boudier in his *Icones* (BOUDIER, 1907b) that can justify the designation as holotype. In our opinion, it seems highly improbable that this taxon was published on the basis of only one element (ICN Art. 9.1). In the text accompanying plate 347 of *Icones mycologicae*, Boudier writes “Cette espèce, qui n’est pas commune, croît surtout au printemps et en automne [...]” which means “This species, which is uncommon, grows mostly in spring and autumn [...]”. This suggests that he collected it several times. Cooke’s drawing was reproduced from the illustration used by Boudier for his plate 347, based on Boudier’s find from Montmancy. Therefore we consider that this sample is only a part of the protologue and can be only designated as a lectotype.

Description (t) of microscopic characters:

Excipulum composed of two layers: **Medullary excipulum** of *textura intricata*, with hyaline to light yellowish hyphae; **Ectal excipulum** of *textura angularis*, composed of brown-yellow cells. **Marginal hairs** superficial, more or less fasciculate, (80) 115–225 \times 9–14 μm , pale brownish, straight, thick-walled, apically obtuse or sharp, with a simple, enlarged base, sometimes subbulbous, septate, wall refractive, 1.2–2 μm thick. **Asci** cylindrical, about 180–200 μm long, 8-spored, base not seen distinctly. **Paraphyses** not seen. **Ascospores** uniseriate, ellipsoid, (14.5) 15–17 \times 9–10.5 μm [$X = 16 \times 9.8 \mu\text{m}$, $n = 40$], $Q = 1.5$ –1.8 [$Q_m = 1.6$], sometimes slightly truncate at the poles, smooth, wall up to 0.5 μm thick, without oil drops but containing sometimes bipolar spore granules which merge in KOH forming small drops; the wall appears refractive in CB.

Comments: BOUDIER (1907b) gave a spore size of 13–16 \times 9–11 μm which is more in conformity with our re-examination than the dimensions given by COOKE (1879), i.e. 14–16 \times 7.5 μm , in the protologue. The spores shown on fig. g, plate 347 (BOUDIER, *op. cit.*) are well represented (see Fig. 3 and Pl. 3, fig. A–D for comparison), as well as the marginal hairs. Indeed, the hair size given by Boudier is, after the scale, between 178 and 244 μm in length versus 80–225 μm after our own measurements.

Re-examination of type-material of *Peziza fimbriata*

Peziza fimbriata Quélet, in COOKE (1879), is typified by the collection K(M) 101314 containing two apothecia, in poor condition. The Cooke’s label indicates “*Peziza* (*Sarc*¹) *fimbriata* C&Q. On the ground, Vosges. France. Quelet”. This collection is undoubtedly the holotype of *Peziza fimbriata*.

Description (t) of microscopic characters:

The structure of the excipulum is not clearly discernable, but the **ectal excipulum** consists of a *textura globulosa*, with cells 10–32 μm in diam., more elongated in the marginal area, becoming a *textura subprismatica*. **Marginal hairs** superficial, fasciculate, 40–137 \times 8–14 μm , brownish, straight, apically obtuse or almost sharp, with a simple, slightly enlarged base, septate, wall not refractive, 1–1.5 μm thick. **Excipular hairs** superficial, more or less flexuous, 102–355 \times 5–6 μm , subhyaline to brownish, with a simple, bulbous base, up to 22 μm wide, 1.5–2 μm thick-walled. **Asci** 8-spored. **Paraphyses** not seen. **Ascospores** uniseriate, ellipsoid, 15–17 \times 9–10 (10.2) μm [$X = 15.7 \times 9.6 \mu\text{m}$, $n = 22$], $Q = 1.6$ –1.8 [$Q_m = 1.6$], sometimes slightly truncate at the poles, hyaline to pale yellowish, smooth, without oil drops, nor BSG, thin-walled, wall refractive in CB.

¹ Means “*Sarcoscypha*”, the subgenus where Cooke placed this species.

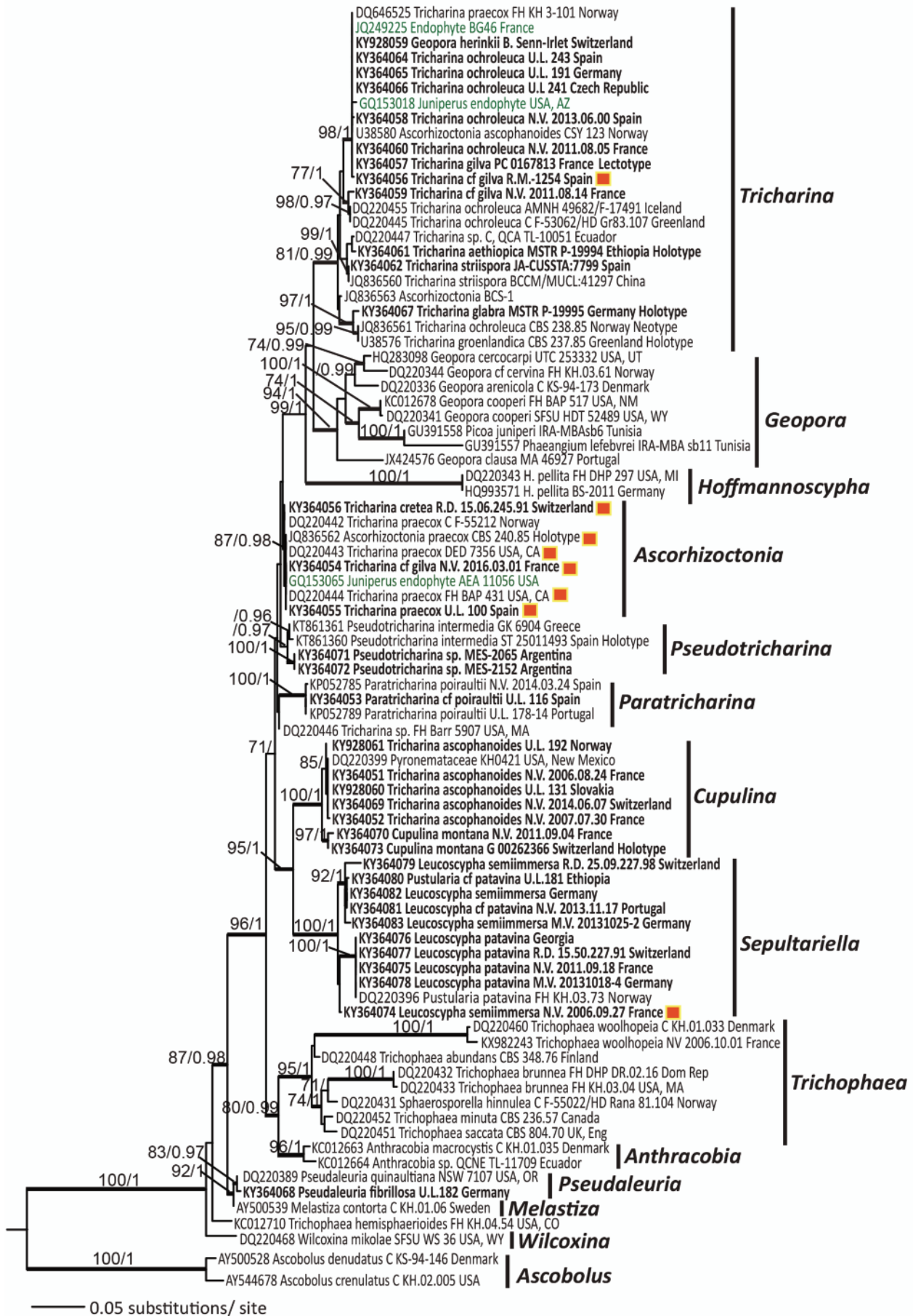


Fig. 1 – RAxML consensus phylogram from analysis of LSU alignment of *Tricharina* and related species, rooted with *Ascobolus*. Meaningful supports shown at branch nodes, with ML bootstrap support on the left and MB posterior probability on the right. Branches are thickened where both supports are meaningful: RAxML bootstrap support is $\geq 70\%$ and MB posterior probability is ≥ 0.95 . Endophyte sequences are green, fruitbody sequences are black. Bolded terminals are newly generated sequences. Red boxes outlined in yellow indicate pyrophilous fruitbodies.

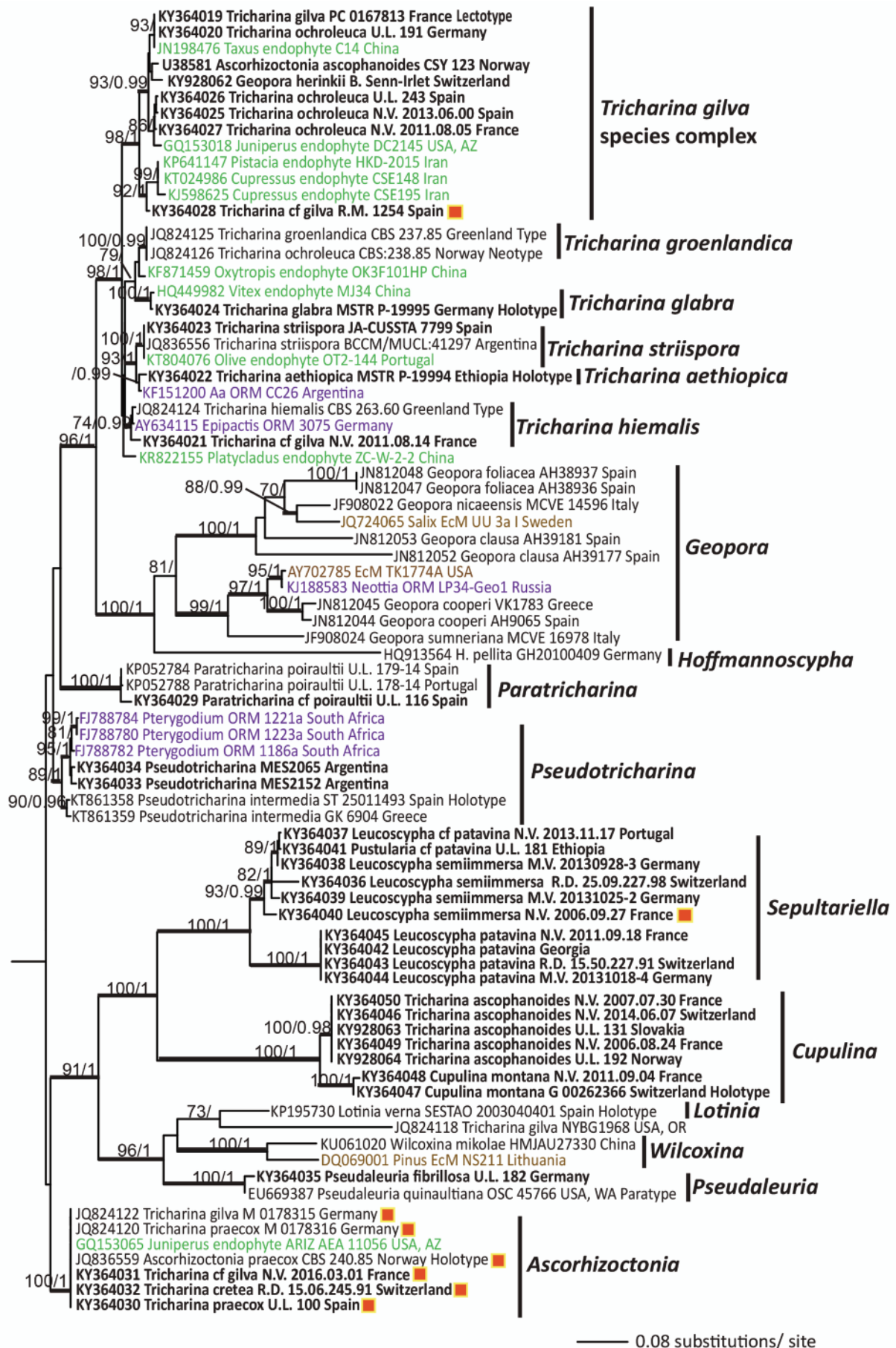


Fig. 2 – RAxML consensus phylogram of analysis of ITS alignment of *Tricharina* and related species, midpoint rooted. Meaningful supports shown at branch nodes, with ML bootstrap support on the left and MB posterior probability on the right. Branches are thickened where both supports are meaningful: RAxML bootstrap support is $\geq 70\%$ and MB posterior probability is ≥ 0.95 . Endophyte sequences are green, ectomycorrhizal sequences are brown, orchid mycorrhizal sequences are purple, fruitbody sequences are black. Bolded terminals are newly generated sequences. Red boxes outlined in yellow indicate pyrophilous fruitbodies.

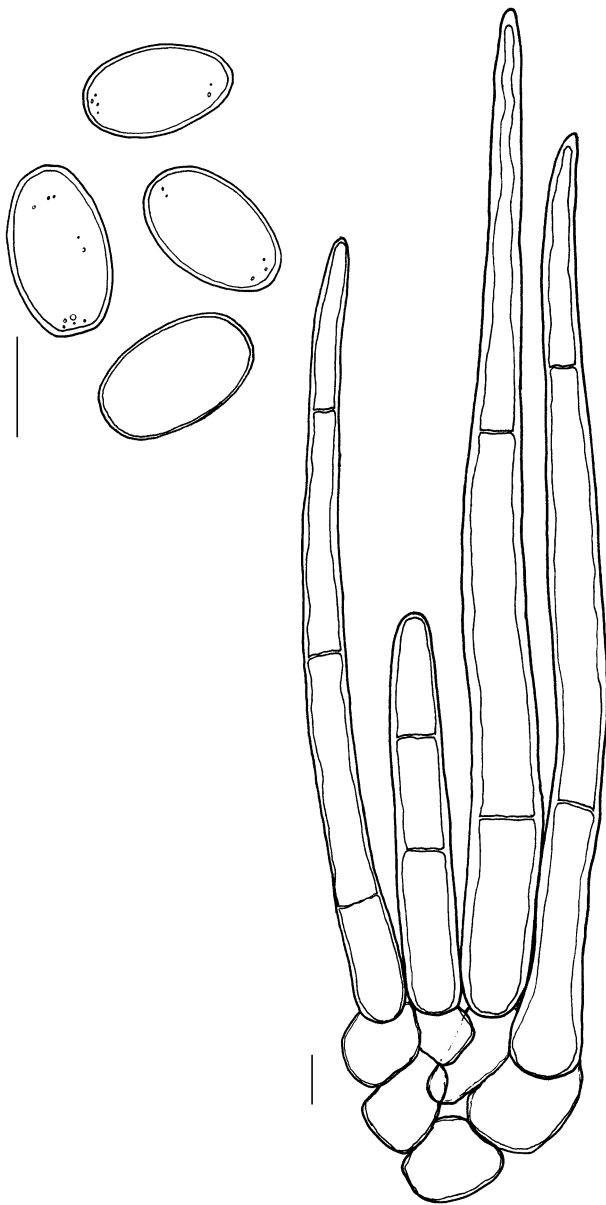


Fig. 3 – *Peziza gilva*. Lectotype PC 0167813. Micro-characters. A. Ascospores, in water. B. Marginal hairs. Scale bars = 10 μm .

Comments: *Peziza fimbriata* Quél., *nom. illeg.*², is the second species cited by BOUDIER (1885, under the name *Lachnea fimbriata*) belonging to the original genus *Tricharina*. YANG & KORF (1985b) synonymized it to *Tricharina gilva* despite some microscopic differences, especially the length of marginal hairs. The species was described as having marginal hairs reaching about 500 μm in length (COOKE, 1879), and ascospores size of 17–18 \times 8 μm , although QUÉLET (1879) gave only 15 μm .

After our re-examination, the spore size does not reach the dimensions given by Cooke and is closer to the “length” given by Quélet. As noted by YANG & KORF (1985b), Cooke probably measured overmature ascospores. We did not find any long hair on the sample but it is in poor condition. The hairs observed were short and not different from those seen on the type specimen of *T. gilva*.

BOUDIER (1907b) also illustrated this species under the name *Tricharina fimbriata* with another collection from eastern France with hairs reaching 290 μm in length and spore size 16–17 \times 10 μm .

Based on our own experience, marginal hairs of *T. gilva* can reach exceptionally 300 μm in length, so the Boudier’s collection of *T. fimbriata* could represent *T. gilva*. On the other hand, we studied a collection from the French Jura (coll. N.V. 2011.08.04) resembling *T. gilva* but with hairs reaching 420 μm in length, with ascospores 15–16 (17) \times 9.8–10.5 μm . This collection appears phylogenetically different from the *T. gilva* clade and very close or identical to *T. hiemalis* based on ITS sequences. In this context, the question remains open to know if *Peziza fimbriata* in its original sense is distinct or not from *T. gilva*.

Another interpretation of *Peziza fimbriata* comes from DENNIS (1978) who suggested this species could be a synonym of *Tricharina cretea* (Cooke) J. Moravec. This opinion is shared by MORAVEC (1974). We don’t think that this hypothesis is correct because of the shape of ascospores drawn by COOKE (1878, fig. 362, as *Peziza cretea*) which is clearly fusoid contrary to the shape of *P. fimbriata* which is ellipsoid. Later MORAVEC (pers. comm.) examined the type collection of this fungus and revised his position, considering that it is identical with *Tricharina gilva*.

Re-examination of type-material of *Peziza ochroleuca*

Peziza ochroleuca Bres. is lectotypified by the collection S-F190915 which is considered as part of the type material but contains very little material (mostly substrate), in poor condition, and we were unable to locate any portion of an apothecium. The Bresadola’s label indicates “*Lachnea ochroleuca* Bres.³ In silva conifera Tertiolasii. Sp. 15-18 = 10-12. G. Bresadola”. This mention agrees with the protologue in BRESADOLA (1887).

YANG & KORF (1985b: 500) examined this collection (“we use the characters associated with that apothecium as a basis for a concept for Bresadola’s name”), but surprisingly decided to designate a neotype from a more abundant Norwegian collection. This is not in accordance with the current nomenclatural rules concerning the typification of names (ICN Art. 9). After examining the collection S-F190915 we consider this lectotype as totally “unusable”. In this context, the plate CIV, fig. 2 in Bresadola’s *Fungi tridentini novi*, cited in the protologue (BRESADOLA, 1887) should serve as a lectotype.

Another little packet is present in the envelope and contains a single apothecium glued to a slip of paper. It was separated by YANG & KORF (1985b) and considered to be a *Cheilymenia* species. The examination of this sample reveals ellipsoid ascospores, with tapered ends, eguttulate, measuring 15–18 \times 10–11 μm . In CB, spores show a yellow refractive content — which is typical of the genus *Cheilymenia* — and are finely ornamented with low warts, partially elongated and connected, sometimes mixed with pustulate warts, as some species of the section *Pseudoscutellinae* (MORAVEC, 2005: 171). Unfortunately we did not see any hair.

Strangely the spores drawn by BRESADOLA (1887, Pl. CIV, fig. 2) look like those we observed in this *Cheilymenia* sample⁴ and the hairs also resemble to hairs of this genus. YANG & KORF (1985b) indicated about this drawing: “His hairs are clustered but too sharp for *Tricharina*.” So it seems that Bresadola mixed up two species.

At the same time, our phylogenetic analyses show that ITS sequence JQ824126 from a culture based on this neotype of *Tricharina ochroleuca* (YANG & KORF, 1985b) is identical to the ITS sequence JQ824125 from a culture based on the holotype of *T. groenlandica*. The LSU sequences (JQ836561 and U38576) are also identical. These results suggest that the neotype designated by YANG & KORF (*op. cit.*) for *T. ochroleuca* must be rejected.

For all these reasons, we propose to consider *Peziza ochroleuca* Bres. as a *nomen dubium* and to abandon the name *Tricharina*

² Not *Peziza fimbriata* Chaillat ex Fr., *Syst. mycol.*, 2 (2): 511 (1823). The name *Lachnea fimbriata* Quél. (1879) is considered as a *nomen novum*.

³ This name was not retained in BRESADOLA’S (1887) original description. The name *P. ochroleuca* chosen by Bresadola is illegitimate due to *Peziza ochroleuca* Bolton (1789), an older valid name. The name *Lachnea ochroleuca* proposed by SACCARDO (1889) has to be considered as a *nomen novum* (ICN Art. 58.1).

⁴ In his diagnosis, Bresadola qualifies the spores as “subhyalinae”, maybe due to an effect of refractiveness.

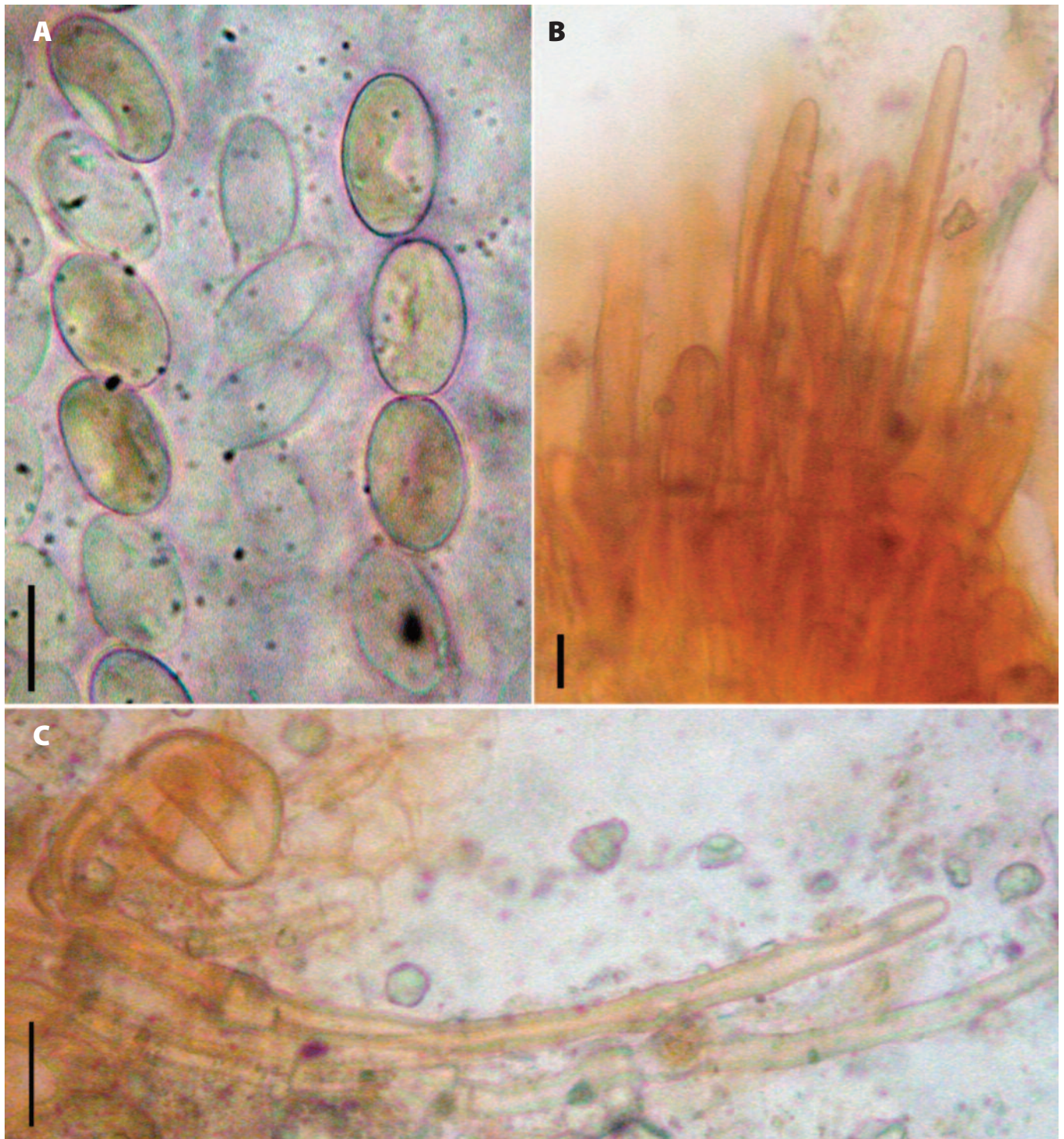


Plate 1 – *Peziza fimbriata*. Holotype K(M) 101314. Micro-characters.

A. Ascospores in 5% KOH. B. Marginal hairs, in water. C. Bulbous hairs from the excipular surface, in water. Scale bars = 10 μ m.

ochroleuca (Bres. ex Sacc.) Eckblad because the concept introduced by YANG & KORF (*op. cit.*) is doubtful.

Other species in the *Tricharina*-Core group

Other species that share the well-supported clade with *Tricharina gilva* are:

- *Tricharina aethiopica* U. Lindemann, a well-defined species collected in Ethiopia which has many similarities with *T. gilva* but differs in very long hairs and the bright yellowish-brown color of the hymenium (LINDEMANN, 2017). For the time being it is only known from the type locality.
- *T. glabra* U. Lindemann & Böhning, a well-defined species, characterized by very short hairs, broad ellipsoid spores with many fine

oil droplets inside and a positive iodine reaction (greenish) of the orange-brown content of the paraphyses. In regard to the morphology, this species differs the most from the generic concept of *Tricharina* as outlined by YANG & KORF (1985b). Until now, this species was known only from the type locality on the island Fehmarn in the Baltic Sea.

- *T. groenlandica* Dissing, Chin S. Yang & Korf, characterized by excipular and marginal short hairs, intermixed with undifferentiated brown cells fide YANG & KORF (1985b), distributed in Northern Europe and Northern America; until now there is no collection of these species known which was described using methods of vital taxonomy. Therefore morphological studies of fresh material are required to have a more complete image of this taxon.

• *T. hiemalis* Chin S. Yang & Korf is a widespread but rare species, known from North America (WHITNEY & PARMETER, 1964) and Europe (YANG & KORF, 1985b). It is very close to *T. gilva* but the spore shape is slightly different, the marginal hairs are distinctly longer than those of *T. gilva* (reaching up to 460 µm), and the apothecia of *T. hiemalis* are generally more hairy than those of *T. gilva*. Because of the slight differences with *T. gilva* (as far as we know them), further morphological studies of fresh material are required.

• *T. striispora* Rifai, Chin S. Yang & Korf, a well-defined species, characterized by striate ascospores (YANG & KORF, 1985b; ARGAUD, 2008; GALÁN *et al.*, 2010; IVALDI & FOUCHIER, 2014; SAMMUT, 2016). This is a widespread species known from Australia (type locality), Southern Europe (Portugal, Spain, France, Greece, Malta) and South America; it is often found in or near to plantations of *Olea europaea*.

The phylogenetic positions of *T. japonica* Chin S. Yang & Korf and *T. tophiseda* Matočec & I. Kušan are unknown. Based on the morphology and ecology of these species we predict that they are most closely affiliated with species in the *Tricharina*-core group. The same could be stated for *T. pallidisetosa* (E.K. Cash) K.S. Thind & S.C. Kaushal and *T. flava* (Fuckel) J. Moravec which are known only from their type localities. Descriptions of *T. herinkii* (Svrček) Benkert in SVRČEK (1949) and BENKERT (2010) morphologically situate this species between *Tricharina s. str.* and *Geopora* Harkn. *s. l.* Our review of Senn-Irlet's collection of *Geopora herinkii* (SENN-IRLET, 1989) proved to be *T. gilva*, both morphologically and phylogenetically. Further studies are required, especially in regard to the phylogenetic positions of these three taxa.

Taxonomy

Tricharina gilva (Boud.) Eckblad, *Nytt Mag. Bot.*, 15 (1-2): 60 (1968).

Basionym: *Peziza gilva* Boud., in Cooke, *Mycographia*, 6: 240 (1879). Lectotype here designated: PC 0167813; MBT 204678; GenBank KY364019 (ITS) and KY364057 (LSU).

Homotypic synonyms: *Humaria gilva* (Boud.) Sydow, *Mycoth. march.* no. 775 (1884); *Lachnea gilva* (Boud.) Sacc., *Syll. fung.*, 8: 184 (1889); *Scutellinia gilva* (Boud.) Kuntze, *Rev. gen. pl.*, 2: 869 (1891); *Tricharia gilva* (Boud.) Boud., *Icon. Mycol., liste prelim.*: 3 (1904); *Patella gilva* (Boud.) Seaver, *N. Amer. Cup-Fungi (Operculates)*: 166 (1928); *Trichophaea gilva* (Boud.) Gamundí, *Rev. Mus. La Plata*, 10: 60 (1967).

Taxonomic synonyms: *Ascorhizoctonia gilva* Chin S. Yang & Korf, *Mycotaxon*, 23: 472 (1985).

For other putative synonyms, see YANG & KORF (1985b).

Apothecia cupulate, 5–6.5 mm in diam., partially buried in the substrate, sessile, hymenium pale greyish to ochraceous grey, dull orange; external surface concolorous or darker, finely pustulate, covered by scattered, hyaline hairs. **Margin** eroded, covered by small brown hairs, often fasciculate.

Excipulum composed of two layers, a thin **medullary excipulum**, of *textura intricata*, composed of hyaline hyphae, and an **ectal excipulum** of *textura globulosa* to *subangularis*, with cells 10–40 µm wide, hyaline to yellowish brown in the outer part. **Excipular hairs** superficial, scattered, more or less flexuous, 150–370 (550) × 5–6.5 µm, brownish yellow at the base, hyaline in the upper part, with a simple base, septate, wall up to 0.5 µm thick. **Marginal hairs** superficial, straight, 60–260 (300) × 9–10 µm, pale brownish, often sub-hyaline at the top, apically obtuse for the smallest ones, more or less sharp for the other, with a simple base, septate, wall up to 1 µm thick. **Asci** cylindrical, 160–190 × 12–16 µm, with crozier, 8-spored, inamyloid. **Paraphyses** not enlarged at the top, 3–5 µm in diam., hyaline, septate, without vacuoles. **Ascospores**⁵ ellipsoid with rounded ends, 14–17.5 (18.1) × (8) 8.5–11 (11.5) µm [$X = 16 \times 9.9 \mu\text{m}$], $Q = 1.4\text{--}1.8$ [$Q_m = 1.6$], † (14) 14.5–17 × (8.5) 9–10.5 µm [$X = 15.8 \times 9.7 \mu\text{m}$], † $Q = 1.5\text{--}1.8$ [$Q_m = 1.6$], sometimes very slightly truncate (mostly in rehydrated exsiccates, when stained in cotton blue with lactic acid [see Plate 3, A2] or when fresh but a bit overmature [see Plate 3, D1], hyaline, smooth, thin-walled when mature, slightly thick-walled when unripe or overmature, mature without oil drops but when overmature with many very minute droplets due to the process of germination (LINDEMANN, 2013, Fig. 5), rarely with bipolar spore granules.

Studied collections: CZECH REPUBLIC – Central Bohemia, Prague, 50.084444° N 14.423888° E, alt. 197 m, in a huge flowerpot among *Tagetes*, *leg.* Z. Egertova, 17 Jul. 2014, pers. herb. U.L. 241. FRANCE – Doubs, Levier, route forestière de Ravonnet, 46.929224° N 6.080289° E, alt. 750 m, on soil, in a rut, *leg.* N. Van Vooren, 17 Aug. 2011, pers. herb. N.V. 2011.08.05. Bouches-du-Rhône, Marseille, parc Longchamp, 43.30575° N 5.397855° E, alt. 63 m, on soil, *leg.* M. Vega, 20 Mar. 2014, pers. herb. N.V. 2014.03.11. GERMANY – Erbach/Donau, 48.326091° N 9.898097° E, alt. 480 m, on sandy, clay-like soil within bark mulch at a parking place of a supermarket, *leg.* R. Seibert, 26 Apr. 2014, pers. herb. U.L. 191. SPAIN – La Rioja, Sojuela, 42.356389° N -2.55° E, alt. 805 m, on sandy and moist soil on the bank of a river, between *Corylus avellana*, *Castanea sativa*, *Populus* sp. and *Quercus* sp., with *Verpa conica*, *Peziza depressa* and *Pachyella violaceonigra*, *leg.* Rubén Martín Gil, 23 Apr. 2016, pers. herb. U.L. 243. Asturias, Pola de Somiedo, near the school, 43.090328° N -6.257085° E, alt. 718 m, on soil, *leg.* G. Moyne, 2 Jun. 2013, pers. herb. N.V. 2013.06.00. La Rioja, San Millán, río Cárdenas, 42.275555° N -2.921944° E, alt. 940 m, on an old burnt site, *leg.* Rubén Martín Gil, 6 Dec. 2012, pers. herb. R.M.-1254. SWITZERLAND – Valais, massif of Great St. Bernard, Bourg-Saint-Pierre, Valsorey, Sander des Glaciers de Valsorey, 45.917722° N 7.259806° E, ca. alt. 2390 m., *leg.* and det. B. Senn-Irlet, 27 Aug. 1983, Herbarium Helveticum B. Irlet no. 83/168, under the name *Geopora herinkii*.

Table 1 – Range of spore size and marginal hair size of the collections of *Tricharina gilva* sequenced during this study

Coll. Number	Spore size (µm)	Mean spore size (µm)	Q value	Mean Q value	Marginal hair size (µm)
PC 0167813 (lectotype)	† (14.5) 15–17 × 9–10.5 (n = 40)	16 × 9.8	1.5–1.8	1.6	up to 225
N.V. 2011.08.05	14–16.5 × (8.5) 9–10.5 (n = 20)	15.2 × 9.6	1.5–1.8	1.6	up to 155
N.V. 2013.06.00	15–17 × 9–10 (n = 20)	15.9 × 9.5	1.5–1.8	1.7	up to 170
R.M.-1254	14.5–18 × 9.3–11.9 (n = 36)	16.3 × 10.6	1.4–1.7	1.6	up to 300
U.L. 191	15.5–17.3 (18.1) × 9.1–10.5 (n = 24)	16.7 × 9.9	1.6–1.8	1.7	up to 260
U.L. 241	15.8–17.8 × 10.1–11 (11.5) (n = 15)	16.6 × 10.9	1.4–1.6	1.5	up to 280
U.L. 243	15–17.5 (18.4) × (8.6) 9.3–11 (n = 49)	16.3 × 10.2	1.5–1.7	1.6	up to 200
Herb. Helveticum no. 83/168	† (14) 15–16.3 × 8.5–9.6 (9.9) (n = 14)	15.4 × 9.2	1.6–1.7 (1.8)	1.7	up to 280

⁵ For the data of the all sequenced collections see Table 1.



Plate 2 – *Tricharina gilva*. Macroscopic aspects.

A. Coll. U.L. 191. B. Coll. N.V. 2013.06.00. C. Coll. N.V. 2011.08.05. D. Coll. U.L. 241. E. U.L. 243. F. Boudier's drawing of *Tricharia gilva* adapted from his *Icones* pl. 347. G. Coll. R.M.-1254.

Discussion

In the light of our results, *Tricharina gilva* must be regarded as mostly non-pyrophilous contrary to the opinion of several authors (ECKBLAD, 1968; MAAS GEESTERANUS, 1969; DENNIS, 1978; DISSING *et al.*, 2000; MEDARDI, 2006; BEUG *et al.*, 2014; VAN VOOREN, 2014). Although *T. gilva* may exceptionally occur on burnt ground (see collection R.M.-1254), all other studied collections that were collected from a fire place and initially identified as *T. gilva* were phylogenetically inferred in the *T. praecox* clade. The misinterpretation of *T. gilva* as a pyrophilous taxon (strictly or occasionally) can be explained by the confusion over species and generic delimitation, as apparent in the “*Ascorhizoctonia/Tricharina-praecox*” clade of the phylogenetic trees (Fig. 1 and 2) where extra-generic species have been determined under this name. The ecology of the species in the *Tricharina* clade appears to include an endophytic habit. There is also evidence that some species play a role in orchid mycorrhizae in both hemispheres.

The subtle morphological differences between *T. gilva* and *T. praecox* has led to many misidentifications. The color of living apothecia can possibly be used to differentiate the species. It seems that apothecia of *T. praecox* are more “yellowish” to “orange” in the fresh state (see Plate 5), probably due to a yellowish pigment present in the paraphyses, which is more or less dense and visible in the living state; this pigment is always lacking in *T. gilva*. Microscopically, the main difference comes from the spore shape: in *T. gilva*, the ascospores are mainly ellipsoid with rounded ends; in *T. praecox*, they are mainly ellipsoid with tapered ends (looking more fusoid, see Plate 3, E-I).

Tricharina ochroleuca (Bres. ex Sacc.) Eckblad is another name often used for collections corresponding in fact to *T. gilva*. As *T. gilva* was generally accepted as a pyrophilous species in modern literature, we think that many mycologists named their collections of brownish or ochraceous *Tricharina* growing on soil under the epithet *ochroleuca*. Although BOUDIER (1907b), ECKBLAD (1968) and YANG & KORF (1985b) considered this taxon as a good species, their interpretations seem different. As shown in our phylogenetic analyses, the neotype of *T. ochroleuca*, chosen by the latter authors, is in reality conspecific with *T. groenlandica*. As previously said, we consider *Peziza ochroleuca* Bres. (and the subsequent homotypic synonyms) as a *nomen dubium*.

In the literature, the range of spore size of *T. gilva* is heterogeneous (see Table 2). Surprisingly REHM (1895, as *Lachnea gilva*) gives 10–12 × 7–8 µm, a range value too small to fit *T. gilva*. The revision of this collection by YANG & KORF (1985b) demonstrated this was a new species, published by them as *Wilcoxina rehmi*. SEEVER (1928, as *Patella gilva*) was the first author who described a collection on an

old burnt site determined as *T. gilva*. GRELET (1939) gives a description in accordance with the Boudier’s description, except for the larger marginal hairs that reach 400 µm in length. His collection may represent “*Tricharia fimbriata* (see discussion below). The cited Grelet’s collection from Nov. 1924 was also revised by YANG & KORF (1985b: 527) and identified as *Trichophaea gregaria* (Rehm) Boud. SVRČEK (1948) described two collections on burnt places, and the description and the spore drawing (*opt. cit.*, Pl. I, fig. 10) fit for *T. gilva*, but we cannot exclude the possibility that this represents *T. praecox*. Note that the max length value of 19.5 µm was probably measured on ascospores which are ready to germinate and are starting to swell (cf. LINDEMANN, 2013: 33, fig. 5). As a general matter, we think that a spore size over 18 µm indicates probably these swollen ascospores. This could be also the case for the collection(s) studied and illustrated by MAAS GEESTERANUS (1969). DENNIS (1977) described *T. gilva* after a collection on a burnt site, but there are few differences with his description of *T. praecox*, except larger spores for *T. gilva*. The collection illustrated by BREITENBACH & KRÄNZLIN (1984) represents undoubtedly *T. praecox* due to the substrate and spore shape; YANG & KORF (1985b) who revised the material depicted in Breitenbach & Kränzlin considered it as *T. praecox* var. *cretea*. CETTO (1987) illustrates also a collection on a fire place which could be *T. praecox* (general aspect and narrow spores). In *Nordic Macromycetes* (DISSING *et al.*, 2000), *T. gilva* is noted as a pyrophilous species with hair length reaching 600 µm! It seems that *T. gilva* is given here in a very broad sense. A collection from Argentina on a burnt site, provided by GAMUNDÍ & LORENZO (2001), is not illustrated but the authors refer to BRUMMELEN (1983) to compare with their fungus. It should be noted, however, that Brummelen’s interpretation of *T. gilva* was reevaluated as a *Wilcoxina* species (YANG & KORF, 1985b). We suppose that the collections illustrated by MEDARDI (2006) and BEUG *et al.* (2014) on pure charcoal, with narrow ascospores might also represent *T. praecox* instead of *T. gilva*. After revision, the collection identified by VAN VOOREN (2014) as *T. gilva* corresponds also to *T. praecox*.

The *Ascorhizoctonia/Tricharina-praecox* clade

As shown in the phylogenetic analyses, *Tricharina praecox* s. lato belongs to a distinct clade outside the *Tricharina-Geopora*-lineage. Therefore, a new genus name is required for the species in this clade. Although no sequence of the type material of *Peziza praecox* P. Karst. is available, the asexual stage of *Tricharina praecox* var. *praecox* has been identified as *Ascorhizoctonia praecox* Chin S. Yang & Korf (YANG & KORF, 1985a) and chosen as the type-species of the anamorphic

Table 2 – Range of spore size and marginal hair size found in the literature for collections named *Tricharina gilva*

Reference	Correct name	Ascospores size (µm)	Hairs (µm)
REHM (1895)	<i>Wilcoxina rehmi</i>	10–12 × 7–8	150–200 × 6–10
SEEVER (1928)		14–18 × 8–10	up to 200 × 8
GRELET (1939)	<i>Trichophaea gregaria</i>	15–17 × 10–11	100–400 × 8–12
SVRČEK (1948)	<i>Tricharina gilva</i> ?	15–19.5 × 9–11	80–200 × 5.5–8.5
MOSER (1963)		13–16 × 9–11	?
MAAS GEESTERANUS (1969)	<i>Tricharina gilva</i> ?	17.7–18.5 × 9.5–11	up to 265 × 4–10
DENNIS (1978)	<i>Tricharina gilva</i> ?	14–19 × 9–10	up to 200 × 10
BREITENBACH & KRÄNZLIN (1984)	<i>Tricharina praecox</i>	14–16 × 8–10	150–190 × 3–5 (10)
CETTO (1987)	<i>Tricharina praecox</i> ?	14–16 × 8–10	?
DISSING <i>et al.</i> (2000)	Wide concept of <i>T. gilva</i>	16–17 × 8.5–10	200–600
GAMUNDÍ & LORENZO (2001)	<i>Tricharina</i> sp.	14–15.5 × 9.5–10	110–230 × 5–7.5
MEDARDI (2006)	<i>Tricharina praecox</i> ?	14–14.5 × 8.5–10	~ 200
BEUG <i>et al.</i> (2014)	<i>Tricharina praecox</i> ?	14–19 × 8–10	150–200 × 3–5
VAN VOOREN (2014)	<i>Tricharina praecox</i>	14–16.5 (17) × (8) 9–10.2	130–280 × 5–10

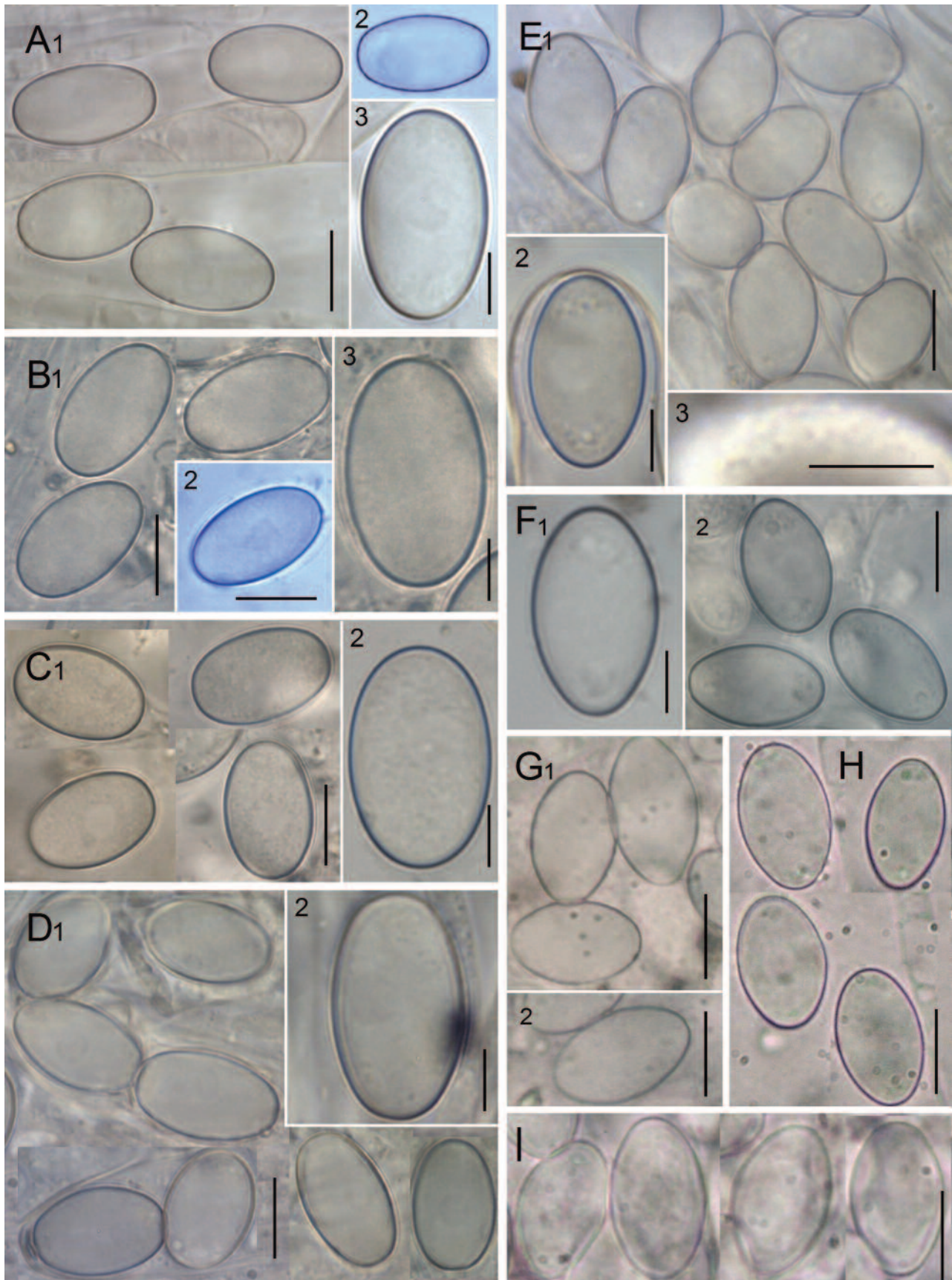


Plate 3 – Ascospores of *Tricharina gilva* (left column: A-D) versus *T. praecox* (right column: E-I)

A: *T. gilva*: coll. U.L. 191; A1 + A3: ascospores in H₂O (in the living state); A2: ascospore (with slightly truncate poles), stained in CB in lactic acid. B: *T. gilva*: coll. U.L. 243; B1 + B3: ascospores in H₂O (in the living state); B2: ascospore, stained in CB in lactic acid. C: *T. gilva*: coll. U.L. 241; C1 + C2: ascospores in H₂O, slightly thick-walled (in the living state); D: *T. gilva*: coll. R.M.-1254; D1 + D2: ascospores in H₂O (in the living state), slightly overmature. E: *T. praecox*: coll. U.L. 100; E1 + E2: ascospores in H₂O (in the living state) E3: Ornamentation of the ascospores; F: *T. praecox*: coll. N.V. 2016.03.01: F1: ascospores in H₂O (in the living state), F2: idem, slightly overmature. G: *T. praecox*: coll. N.V. 2010.05.32; G1 + G2: (rehydrated) ascospores in H₂O (in the dead state). H: *T. praecox*: coll. DED 7356 (SFSU); H: (rehydrated) ascospores in H₂O (in the dead state). I: *T. praecox*: lectotype, collection P.A. Karsten no. 1176 (H); Scale = 10 µm (except for A3, B3, C2, D2, E2, E3 + F1: scale = 5 µm).

genus *Ascorhizoctonia* Chin S. Yang & Korf. In this context, the ICN Art. 59 leads the choice for a new name of the genus: *Ascorhizoctonia* must be used following the principle of nomenclatural priority after the recommendations made by ROSSMAN (2014). The same conclusion was retained by MATOČEC & KUŠAN (in KUŠAN, 2015: 55). Consequently, all other taxa with similar morphological characters belonging to this clade must be combined in this genus.

Re-examination of type-material of *Peziza praecox*

Peziza praecox P. Karst. was lectotypified by YANG & KORF (1985b) with the collection P.A. Karsten no. 1176 housed in the University of Helsinki botanical herbarium. It contains some apothecia embedded in black ashes, in rather good condition. The label indicates "*Peziza praecox* Karst. Fennia. Tavastia australis. Tammela, Mustalia. In carbonario versus Haarakorpi." This agrees with one of the localities cited in the protologue (KARSTEN, 1869).

Description (†) of microscopic characters:

Excipulum rather thin, about 150 µm thick, bilayered, with an **ectal excipulum** of *textura angularis/subglobulosa*, with yellowish cells 10–22 µm wide, and a **medullary excipulum** of *textura intricata*, with hyaline hyphae. **Anchor hyphae** present, 4–6 µm wide, hyaline, septate, with a refractive wall, 0.5–1 µm thick, enlarged at the base or subbulbous. **Marginal hairs** superficial, dense, 112–340 × 9–13 µm, yellow-brown to subhyaline, straight, apically sharp, more rarely obtuse, with a simple, slightly enlarged base, septate, wall not refractive, 1–1.2 µm thick. **Asci** 8-spored, inamyloid. **Paraphyses** cylindrical, 2.5–3.5 µm in diam., hyaline. **Ascospores** uniseriate, ellipsoid, with somewhat tapered poles, (14) 14.5–16.5 (17) × (7.5) 8.7–10 µm [$X = 15.7 \times 9.4 \mu\text{m}$, $n = 40$], $Q = 1.5\text{--}1.9$ [$Q_m = 1.7$], sometimes slightly truncate at the poles, hyaline, smooth, without oil drops, nor BSG, but with a spumous content, wall thin, up to 0.5 µm, appearing refractive in CB.

Comments: The re-examination of this type-collection confirms the main micro-characters we observed on fresh collections, especially the spore shape, the most important element to distinguish *Ascorhizoctonia praecox* from *Tricharina gilva*. The spore length is a bit longer than reported by YANG & KORF (1985b: 504). The hairs can reach 340 µm in length. It is also important to note that the ascospores are totally smooth.

Taxonomy

Ascorhizoctonia praecox Chin S. Yang & Korf, *Mycotaxon*, 23: 475 (1985).

Holotype: CUP 61609, ex type culture CBS 240.85; GenBank JQ836562 (28S) and JQ836559 (ITS).

Taxonomic synonyms: *Peziza praecox* P. Karst., *Not. Sällsk. Fauna Fl. Fenn. Förhandl.*, 10: 124 (1869); *Lachnea praecox* (P. Karst.) Sacc.,

Syll. fung., 8: 183 (1889); *Scutellinia praecox* (P. Karst.) Kuntze, *Rev. gen. pl.*, 2: 869 (1891); *Tricharia praecox* (P. Karst.) Boud., *Icon. Mycol., liste prélim.*: 3 (1904); *Tricharina praecox* (P. Karst.) Dennis, *Kew Bull.*, 25 (2): 338 (1971).

Apothecia cupulate, 2–5 mm in diam., sessile, spread at the end, hymenium first greyish on very young specimens, then ochraceous yellow, sometimes with dull orange tinges, sometimes bright yellow, often with some olivaceous tinges; external surface concolorous, covered by small brown hairs, scattered. **Margin** darker by the presence of small hairs.

Excipulum thin, 80–200 µm wide, bilayered, with a **medullary excipulum** of *textura ± intricata* to *subprismatica*, composed of pale orange hyphae, becoming a *textura prismatica* in the marginal area, and an **ectal excipulum** of *textura subglobulosa*, with roundish or widely clavate cells, 15–43 × 15–26 µm, hyaline. **Anchor hyphae** present, more or less flexuous, 5–8 µm wide, hyaline, smooth, septate, ~1 µm thick-walled, with a simple, bulbous base. **Marginal hairs** superficial, 150–270 (340) × 7–10 (12) µm, often fasciculate, straight, apically obtuse, with a simple subbulbous base, subhyaline to pale brown, septate, wall refractive, up to 1 (2) µm thick. **Asci** cylindrical, 200–220 × 11–14 µm, slightly narrowed at the base, with crozier, 8-spored, inamyloid. **Paraphyses** hyaline, septate, more or less constricted at the septa, not or slightly enlarged at the top or sometimes with a sort of lateral protuberance, 4–5 µm in diam., frequently forked at the apex, containing non-refractive vacuoles, sometimes also a slightly yellowish pigment, partially staining in CRB, without reaction in Lugol. **Ascospores** uniseriate, ellipsoid with somewhat tapered poles, 14–18 (19) × (8) 9–11.5 (12.5) µm [$X = 16.0 \times 10.1 \mu\text{m}$], $Q = 1.5\text{--}1.8$ [$Q_m = 1.6$], † (14.5) 15–17 (18) × (8.7) 9–10.5 (11) µm [$X = 15.9 \times 9.7 \mu\text{m}$], † $Q = 1.5\text{--}1.9$ [$Q_m = 1.7$], rarely truncate at the poles, hyaline, without oil drops, but with bipolar spore granules, one or two bigger than the others, not staining in CRB, disappearing in KOH, smooth or very finely warted (coll. U.L.100) or sometimes distinctly verrucose (coll. R.D. 15.06.245.91), wall up to 0.5 µm thick, appearing refractive in CB.

Studied collections: FRANCE – Ardennes, Givet, Fort Condé, 50.13772° N 4.80067° E, alt. 170 m, on a burnt place, under *Pinus nigra*, leg. B. Clesse, 9 Mar. 2016, pers. herb. N.V. 2016.03.01. Savoie, Méribel-les-Allues, near the "altiport", 45.4104851° N 6.5788434° E, alt. 1760 m, on a recent burnt place, with *Peziza lobulata*, under *Picea abies*, leg. N. Van Vooren, 23 May 2010, pers. herb. N.V. 2010.05.32. Doubs, Gevresin, carrefour du Roi de Rome, 46.9626° N 6.063534° E, alt. 690 m, on a burnt place, leg. G. Moyno & N. Van Vooren, 30 Aug. 2006, pers. herb. N.V. 2006.08.27. Haute-Savoie, Saint-Jean-de-Sixt, forêt des Traversiers, 45.9163471° N 6.4045474° E, alt. 1010 m, on a burnt place, leg. N. Van Vooren, 23 Sept. 2006, pers. herb. N.V. 2006.09.21. Loire, Écoche, bois du Châtelet, 46.161544° N 4.3099131°

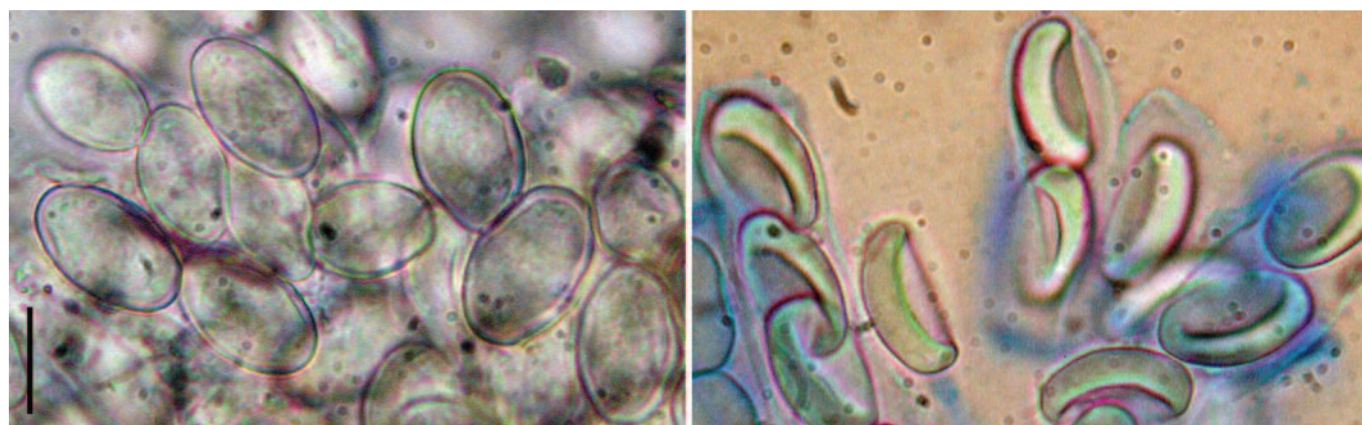


Plate 4 – *Peziza praecox* H 6055460 lectotype. Ascospores.

A. Ascospores, in water. B. Ascospores in CB, showing their refractiveness. Scale bar = 10 µm.



Plate 5 – *Ascorhizoctonia praecox*. Macroscopic aspects.

A. Coll. N.V. 2016.03.01. B. Coll. R.D. 15.07.245.91. C. Coll. Fellmann 2007. D. Coll. N.V. 2010.05.32. E. U.L.100. F. Boudier's drawing of *Tricharia praecox* adapted from his *Icones* pl. 349.

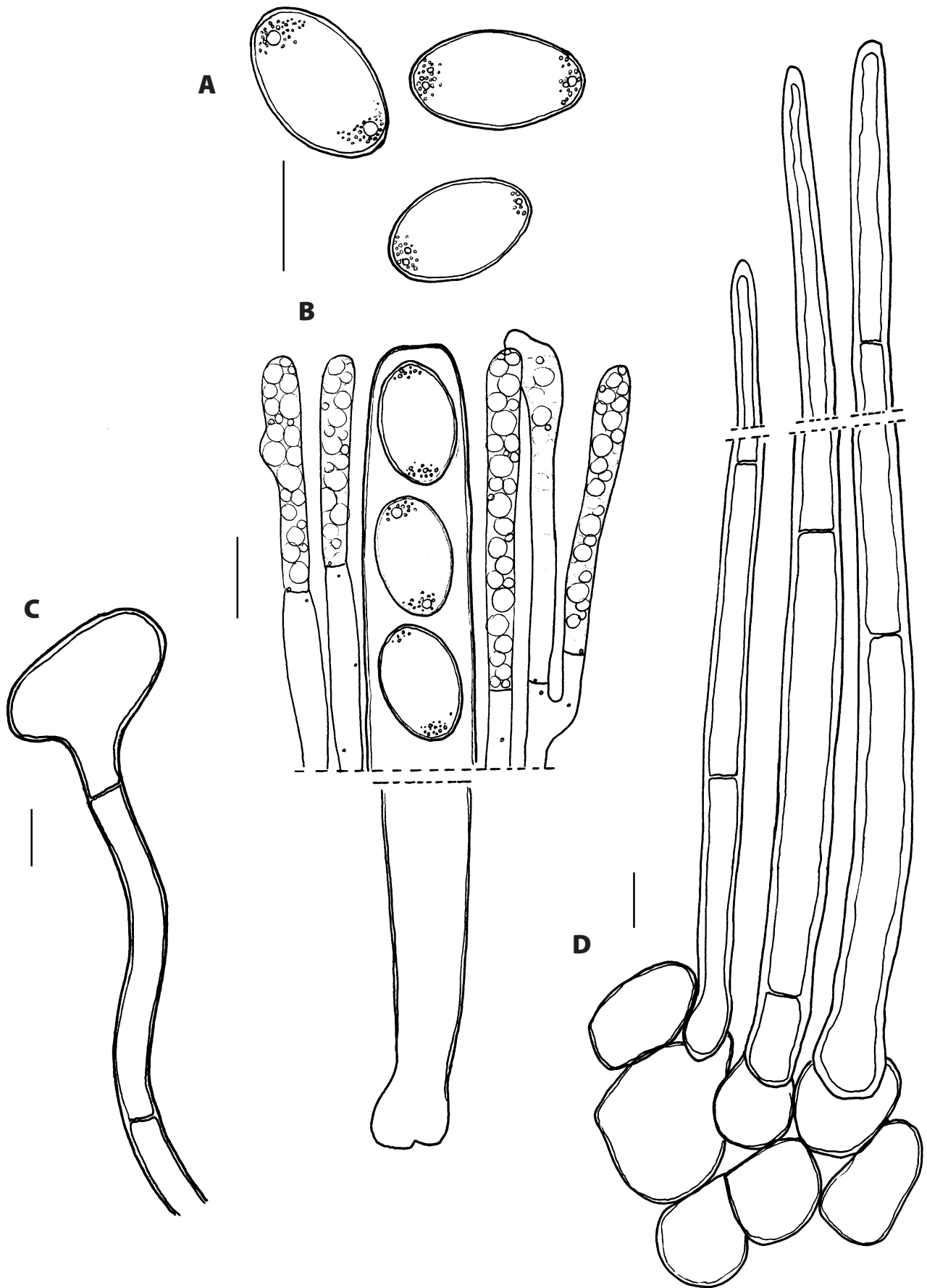


Fig. 4 – *Ascorhizoctonia praecox*. Coll. N.V. 2016.03.01. Micro-characters.

A. Ascospores, in water. B. Top of ascus and paraphyses. C. Anchor hypha, with bulbous base. D. Marginal hairs. Scale bars = 10 μm.

E, alt. 600 m, on a 1-year old burnt area, with *Peziza lobulata* and *P. echinospora*, leg. N. Van Vooren, 18 Oct. 2003, pers. herb. N.V. 2003.10.12. FINLAND – Tavastia australis⁶, Tammela, Mustalia, near Haarankorpi {estimated coordinates: 60.8540451° N 23.7764637° E, alt. 120 m}, in ash on burnt ground, leg. P.A. Kärten, 1 Jun. 1868, H 6055460, ex herb. P.A. Karsten no. 1176, lectotype of *Peziza praecox*. Tavastia australis, Tammela, Letku, on burnt ground, leg. P.A. Kärten, 22 Jun. 1868, H 6055461, ex herb. P.A. Karsten no. 2501, syntype of *Peziza praecox*. SPAIN – Canary Islands, La Gomera, Las Hayas, Valle Gran Rey, 28.12720723° N -17.2825993° E, alt. 1100 m, in a very wet place, recently burned site, “fayal-brezal” habitat (*Myrica fayae-Ericion arborea*), with *Ascobolus carbonarius* and *Peziza* sp., 13. Feb. 2013, leg. R. Negrín, det. M. Ribes, conf. U. Lindemann, pers. herb. U.L.100. GERMANY – Munich, Waldperlach, 48.091415° N 11.675750° E, alt. 550 m, on an old burnt site, leg. B. Fellmann, 04. Jun. 2007 (only macro- and micropictures, no exsiccate). SWITZERLAND – Fribourg, Bulle, Cabane d’Inson, 46.584153° N 7.0010782° E, alt. 1020 m, on a 2-years old burnt site, leg. N. Van Vooren, 5 Jun. 2015, pers. herb. N.V. 2015.06.09. Fribourg, Montagny, forêt de la Chanéaz, 46.80083° N 7.004722° E, alt. 590 m, on a burnt place, leg. R. Dougoud, 29 Apr. 1991, pers. herb. R.D. 15.06.245.91, under the name *Tricharina praecox* var. *cretea*. USA – California, Calaveras county, near Big Trees State Park, 38.277573° N -120.308335° E, alt. 1435 m, on burnt soil under conifers, leg. D.E. Desjardin, rev. N. Van Vooren, 20 Apr. 2002, coll. DED 7356 (SFSU) as *Tricharina gilva*.

Discussion

As shown previously, a great confusion exists between *Tricharina gilva* and *Ascorhizoctonia praecox* due to their similar morphology and the suggestion by the older literature that both species should grow in the same habitat: burnt site or charcoal. Contrary to *A. praecox* which seems strictly pyrophilous, *T. gilva* grows only occasionally on burnt sites and we think on old ones. A review of numerous herbarium collections should validate these hypotheses. The distinction between *T. gilva* and *A. praecox* is easily observed in their different spore shapes, which offer a quick means of identification (see Plate 3). At the same time, this distinction is generally not correctly indicated or drawn in the literature, e.g. DENNIS (1971), so we encourage the readers to review their own material to check their previous determinations.

Note that *A. praecox* is probably one of the most common tricharinoid discomycetes on recent fire places (up to 2 years old).

The *Ascorhizoctonia* clade contains collections with multiple determinations. Two of these collections correspond to *Tricharina gilva* (coll. HD Rana 81.118 from herb. C, on “moist soil”), and *T. cretea* (coll. RD 15.06.245.91, on burnt place). The latter has been revised and corresponds to the fungus called *T. praecox* var. *cretea* by YANG & KORF (1985b). This taxon differs mainly from *T. praecox* var. *praecox* by its distinctly verrucose fusoid ascospores. But phylogenetically, this collection appears to be the same as the collections of *A. praecox* sequenced during this study. If the DNA data from the type collection of *Peziza cretea* Cooke confirm this result, *T. cretea* should be considered as a synonym of *A. praecox*.

YANG & KORF (1985b) proposed another variety of *T. praecox* called *T. praecox* var. *intermedia* Egger, Chin S. Yang & Korf, based on some North American collections. This taxon is distinguished by Yang & Korf from *T. praecox* var. *praecox* by its smooth ascospores, a different asexual state and its geographical distribution. Our phylogenetic analysis shows that a collection from California (DED 7356), initially determined as *T. gilva*, was in fact genetically identical to *A. praecox* (see Fig. 1). Our study of the sample of DED 7356 confirmed this observation also in regard to the microcharacters of this collection: the ascospores were smooth with tapered poles (see Plate 3, fig. H). Contrary to the opinion of YANG & KORF (1985b) who suggested that *A. praecox* var. *praecox* was not present in North

America, we think that the situation is more complex. Further investigations using the methods of vital taxonomy and phylogeny with additional genetic loci are required to evaluate whether *Ascorhizoctonia intermedia* could be distinguished by its morphological characters from *A. praecox* or not.

The *Cupulina-Tricharina-ascophanoides* clade

Among the species of the genus *Tricharina*, *T. ascophanoides* (Boud.) Chin S. Yang & Korf is quite atypical because of the absence of true marginal hairs. On the other hand, its eguttulate ascospores contain bipolar spore granules, a character that agrees well with the typical spore-morphology of the genus as defined by BOUDIER (1885) and others. But despite this, the phylogenetic analyses show definitely that *T. ascophanoides* does not belong to the *Tricharina*-core clade.

Re-examination of type-material of *Tricharia ascophanoides*

Tricharia ascophanoides Boud. is typified by the collection PC 0167814, considered as the holotype. It contains some apothecia in rather good condition embedded in the substrate. The Boudier’s label indicates “*Tricharia ascophanoides* B. vid. Icones n° 586. Arbois augusto 1902 ad corium putridum legit Dr Hetier.” These data agree with the protologue (BOUDIER, 1903).

Description (†) of microscopic characters:

The excipulum is bilayered, with a **medullary excipulum** of *textura intricata*, composed of hyaline to light yellowish hyphae, and a thin ectal excipulum of *textura angularis*. **Hairs** not seen but anchor hyphae present, hyaline, 6–9 µm wide, more or less obtuse at the top, septate, with refractive wall, 1–1.2 µm thick, arising from a bulbous basal cell, 17–26 µm wide. **Asci** cylindrical, 8-spored, inamyloid. **Paraphyses** not seen. **Ascospores** uniseriate, ellipsoid or ellipsoid with somewhat tapered poles, 17–20 × 10–12 (12.7) µm [$X = 18.8 \times 11.3 \mu\text{m}$, $n = 30$], $Q = 1.5\text{--}1.9$ [$Q_m = 1.7$], sometimes slightly inequilateral, hyaline, without oil drops but with bipolar spore granules that merge in KOH, smooth, thin-walled, wall sometimes refractive and pale yellow in CB.

Comments: These characters are in conformity with the description published by BOUDIER (1903), especially the spore size which is evidently larger than indicated by YANG & KORF (1985b: 486) who gave 14.6–16.1 (16.8) × 9.5–11 µm based on the study of only two collections of *T. ascophanoides*. Such a difference is difficult to explain but probably caused by the medium used to observe the small number of examined material, including the type-collection. Our own collections, studied in living state (as Boudier did), show that these dimensions are clearly underestimated. We measured (16) 16.5–22.5 (24) × (9.5) 10–13 (14.5) µm with a mean value of 18.7 µm in length and of 11.3 µm in width. YANG & KRISTIANSEN (1989) obtained an anamorph in culture — named *Ascorhizoctonia ascophanoides* by the authors — based on Kristiansen’s collection (RK 82.146), with spores measured to 14–16 × 9–11 µm after KRISTIANSEN (2014). Molecular analyses based on ITS and LSU sequences of the type-material of *A. ascophanoides* show clearly that this species belongs to the *Tricharina gilva* species complex and is different from *T. ascophanoides* in the sense of Boudier. In contrast to this result, our re-examination of the collection RK 82.146 (teleomorph) revealed that it is morphologically highly similar to *T. ascophanoides* in the sense of Boudier. In the light of this result, we also sequenced apothecia from RK 82.146. Based on the LSU and ITS loci, this confirmed the result of our morphological study. The sequences of RK 82.146 and of CSY 1237 — the anamorph culture of RK 82.146 — are different!

⁶ Historical province, see [https://en.wikipedia.org/wiki/Tavastia_\(historical_province\)](https://en.wikipedia.org/wiki/Tavastia_(historical_province))

⁷ Sequenced by EGGER (1996).

Tricharina ascophanoides is a rather common species in mountainous areas in Central Europe (also at lower elevation in Nordic countries), often collected in forest along paths at anthropogenic influenced areas. Its determination is quite easy. Illustrations of this species can be found in BOUDIER (1907b, pl. 351), ENGEL & HÄFFNER (1986), DOUGOUD (2002) and VAN VOOREN (2014). It mainly differs from the other *Tricharina* species by the absence of true marginal hairs. Only short hyphoid and hyaline hairs can be observed at the margin. On the outer surface, hyphoid hairs, typically with a bulbous base, are present. This type of hair is very similar to the type found on colored species "*Leucoscypha*", i.e. *L. patavina* or *L. semi-immersa*. Recent phylogenetic analyses inferred that *T. ascophanoides* is affiliated with colored "*Leucoscypha*", but in a sister clade together with *Cupulina montana* Dougoud, Van Vooren & M. Vega. *Cupulina* is a recently described monotypic genus with *C. montana* as type species (see DOUGOUD *et al.*, 2015). Since molecular phylogenetic analyses and morphological characters provide strong evidence that *T. ascophanoides* is closely allied with *C. montana*, we here exclude it from the genus *Tricharina s. str.* and transfer *T. ascophanoides* to *Cupulina*.

Taxonomy

Cupulina ascophanoides (Boud.) Van Vooren, *comb. nov.* – MB 819489

Basionym: *Tricharia ascophanoides* Boud., *Bull. Soc. mycol. Fr.*, 19 (3): 195 (1903).

Homotypic synonyms: *Lachnea ascophanoides* (Boud.) Sacc. & D. Sacc., *Syll. fung.*, 18: 37 (1905); *Tricharina ascophanoides* (Boud.) Chin S. Yang & Korf, *Mycotaxon*, 23: 485 (1985).

Misapplication: *Ascorhizoctonia ascophanoides* Chin S. Yang & R. Kristiansen, *Mycotaxon*, 35 (2): 314 (1989), which represents a member of the genus *Tricharina s. str.* as circumscribed in this paper.

Apothecia 1–4 mm diam., discoid or weakly cupulate, hymenium plan or a bit depressed, pale beige to ochraceous beige, or dull orange; external surface concolor, looking alike glabrous. **Margin** sometimes a bit eroded, without hairs.

Ectal excipulum up to 500 µm thick, of *textura globulosa/angularis*, with cells 6–40 µm wide, intermixed with some piriform or cla-

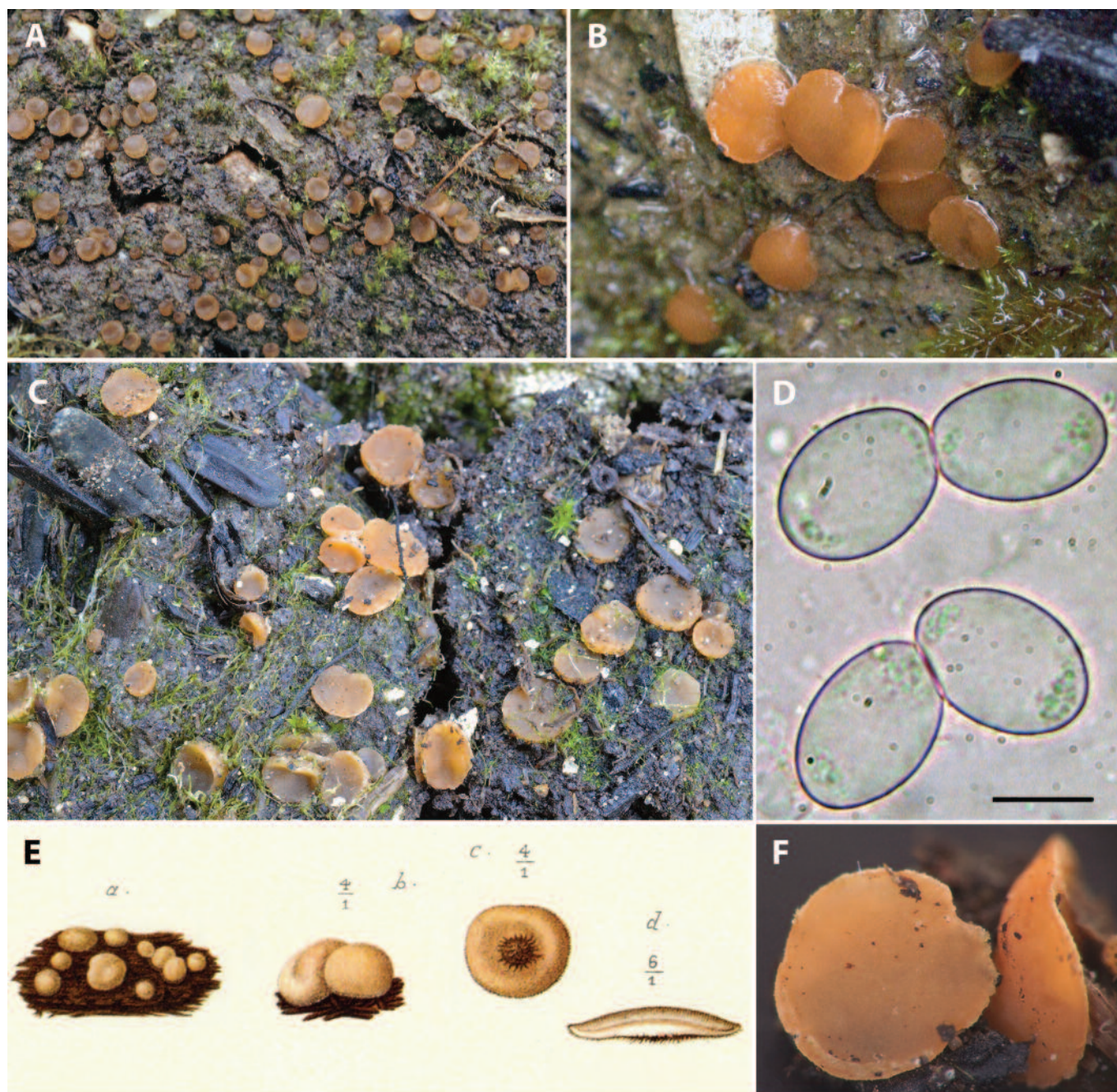


Plate 6 – *Cupulina ascophanoides*.

A. Coll. N.V. 2006.08.24. B. Coll. N.V. 2007.07.30. C. Coll. N.V. 2015.06.04. D. Ascospores from coll. N.V. 2007.07.30, in water (Scale bar = 10 µm). E. Figures of *Tricharia ascophanoides* adapted from Boudier's plate 351 in his *Icones*. F. Coll. U.L. 131.

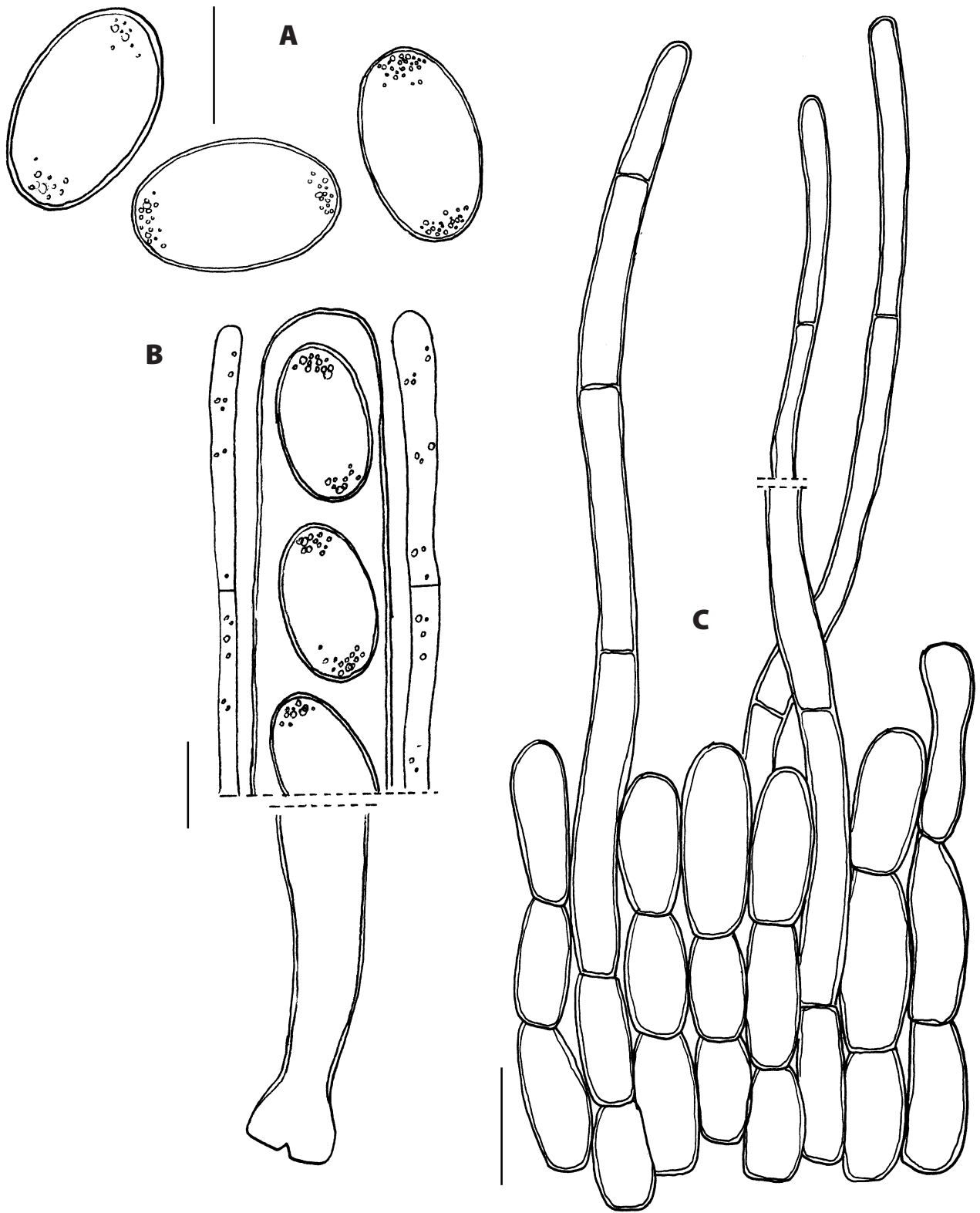


Fig. 5 – *Cupulina ascophanoides*. Micro-characters.

A. Ascospores, in water. B. Top of ascus and paraphyses. C. Marginal cells and hyphoid hairs. Scale bars = 10 μ m. A-B from coll. N.V. 2014.06.07, C from coll. N.V. 2015.06.14.

Table 3 – Comparison between *Cupulina montana* and *C. ascophanoides*

	<i>Cupulina montana</i>	<i>Cupulina ascophanoides</i>
Macroscopic habit	Apothecia sessile, cupulate to hemispherical, sometimes plane, Ø (1) 2–4 mm, ochraceous yellow to orange	Apothecia sessile, hemispherical, rarely cupulate, Ø 1–4 mm, ochraceous beige to orange beige
Ascospore shape	Fusoid, often inequilateral	Ellipsoid, sometimes a bit tapered at the poles
Ascospore size	27–35 (36) × 12–13.6 (14) µm, Qm = 2.5	16.5–22.5 (24) × (9.5) 10–13 (14.5) µm, Qm = 1.7
Ascospore content	Filled with oil drops	Without oil drops, but with BSG
External surface	Anchor hyphae present, with a bulbous base, reaching 1000 µm in length	Hyphoid hairs present, with an enlarged or subbulbous base, reaching 450–500 µm in length
Ecology	In mountainous area, on calcareous soil, on naked or mossy ground	In mountainous area, on naked ground
Phenology	From July to September	From June to September

vate hyphae. **Medullary excipulum** and **subhymenium** not distinct, rather thin, about 120–130 µm thick, of *textura intricata*, with hyaline or slightly pale orange hyphae. **Marginal cells** organized in a *textura prismatica*, the terminal cell often clavate, 10–11 µm wide, with some scattered, hyaline, hyphoid hairs emerging, 80–120 × 5–8 µm, with a simple base, up to 0.5 µm thick-walled, apically obtuse or tapered. **Excipular hairs** present, hyphoid, 70–240 × 3–6 µm, hyaline, more or less flexuous, septate, with an enlarged to subbulbous base, up to 1 µm thick-walled, usually sharp at the top. **Asci** cylindrical, 160–220 × 14–21 µm, with crozier, 8-spored, operculate, inamyloid. Paraphyses not or only a few enlarged at the top, 3–5 (8) µm wide, septate, hyaline, without vacuoles but with some small inclusions, not reacting in MLZ. **Ascospores** uniseriate, ellipsoid, sometimes a bit tapered at the poles, (16) 16.5–22.5 (24) × (9.5) 10–13 (14.5) µm [X = 18.7 × 11.3 µm], Q = 1.3–1.9 [Qm = 1.7], hyaline, thin-walled or slightly thick-walled, without oil drops but containing bipolar spore granules, smooth, partially refractive in CB.

Studied collections: FRANCE – Doubs, Levier, route forestière de Ravonnet, 46.929224° N 6.080289° E, alt. 750 m, *leg.* G. Moyne, on soil, under *Picea abies*, 30 Aug. 2006, pers. herb. N.V. 2006.08.24. Doubs, Levier, route forestière du Pont de la Marine, 46.9480952° N 6.0671202° E, alt. 705 m, *leg.* N. Van Vooren, on soil, under *Picea abies*, 20 Jul. 2007, pers. herb. N.V. 2007.07.30. Jura, La Pesse, forêt de Chapuzieux, 46.27027° N 5.827954° E, alt. 1185 m, *leg.* N. Van Vooren, on soil, in a mixed forest, 18 Sept. 2009, pers. herb. N.V. 2009.09.24. Hautes-Alpes, Allos, Digue d'Allos, 44.2226786° N 6.6350181° E, alt. 1365 m, *leg.* N. Van Vooren, on soil, 6 Jun. 2010, pers. herb. N.V. 2010.06.37. Savoie, Beaufort, la Tétraz, 45.707127° N 6.615065° E, alt. 1000 m, *leg.* N. Van Vooren, on soil, 28 Aug. 2013, pers. herb. N.V. 2013.08.53. Isère, Lans-en-Vercors, bois de Chabaud, route forestière de Servagnet, 45.1159° N 5.5488° E, alt. 1258 m, *leg.* N. Van Vooren, on soil, 26 Sept. 2013, pers. herb. N.V. 2013.09.31. Savoie, Bonneval-sur-Arc, Pont de la Neige, 45.40652° N 7.02843° E, alt. 2520 m, *leg.* N. Van Vooren, on soil, in alpine grassland, 24 Aug. 2015, pers. herb. N.V. 2015.08.15. SWITZERLAND – Fribourg, Bulle, Cabane d'Inson, 46.584153° N 7.0010782° E, alt. 1025 m, *leg.* N. Van Vooren, on soil, 23 Jun. 2012, pers. herb. N.V. 2012.06.20. *Idem*, 20 Jun. 2014, pers. herb. N.V. 2014.06.07. *Idem*, 5 Jun. 2015, pers. herb. N.V. 2015.06.04. AUSTRIA – Carinthia, Weißensee (Ostufer), 46.704189° N 13.413577° E, alt. 940 m, *leg.* and det. B. Wergen, at a wayside on soil between mosses within a *Picea*-forest, 8 Jun. 2013, pers. herb. U.L. 85. ITALY – South Tyrol, Sesto, 46.685679° N 12.375881° E, alt. 1420 m, *leg.* and det. U. Lindemann, at a wayside on soil, 16 Aug. 2009, pers. herb. U.L. 33. SLOVAKIA – Vysoké Tatry, Siedmich Valley, 49.21651° N 20.290085° E, alt. 1010 m, *leg.* and det. U. Lindemann, on soil, 10 Sept. 2012, pers. herb. U.L. 131. Vysoké Tatry, near Ždiar, 49.26941° N 20.270406° E, alt. 880 m, *leg.* and det. U. Lindemann, on soil at the

edge of a burnt site, 14 Sept. 2012 (only macro- and micropictures, no exsiccate). NORWAY – Østfold county, Fredrikstad community, Borge, Torp, 59.240630° N 11.007230° E, alt. 13 m, *leg.* M. Pettersen, det. R. Kristiansen, rev. U. Lindemann, closed paper mill area, on artificial calcareous ground with few mosses, created by man, 2 Jun. 2014, pers. herb. U.L. 192. *Idem*, *leg.* and det. R. Kristiansen, rev. U. Lindemann and N. Van Vooren, on balls of cellulose, partially burnt, 3 Jul. 1982, pers. herb. R.K. 82.146.

Distribution: North and Central Europe – Austria (our data), Czech Republic (YANG & KORF, 1985b), France (BOUDIER, 1903; our data), Germany (ENGEL & HÄFFNER, 1986), Italy (our data), Norway (KRISTIANSEN, 2014, *pro parte*⁸; our data), Slovakia (YANG & KORF, 1985b; our data), and Switzerland (DOUGOUD, 2002; our data).

Comments: Although *Cupulina montana* and *C. ascophanoides* are in some aspects morphologically similar, the taxonomic position of the latter was a bit surprising due to the different ascospore structure of each species. Table 3 gives a comparison of them.

Two attempts to sequence the holotype of *Tricharia ascophanoides* failed due to a fungal contamination, but we think that Boudier's protologue, our re-examination of type-material and the characters consistent with the species description for *T. ascophanoides* coming from the numerous collections we studied are sufficient to circumscribe this species without ambiguity.

The *Sepultariella* clade

PERRY *et al.* (2007) showed that some tricharinoid species attached to *Pustularia* (as "*P. patavina*") or *Leucoscypha* (as *L. semiimmersa*) do not belong to either of these genera. Our own analyses confirm that *Pustularia patavina* cannot be retained because the name *Pustularia* is illegitimate (ICN Art. 53.1), and *L. semiimmersa* does not belong to the same clade as the type species of *Leucoscypha*, *L. leucotricha* (Alb. & Schwein.) Boud. They were included in *Leucoscypha* by SVRČEK (1974), following the enlarged concept of this genus proposed by SACCARDO (1889), LE GAL (1957), RIFAI (1968), ECKBLAD (1968), PANT & TEWARI (1977) and many others. Thus *Leucoscypha* became a heterogeneous assemblage of species, not supported by phylogenetic analyses. KUTORGA (2000) used the name *Sepultariella* for this group but unfortunately the publication of this name is invalid (ICN Art. 39.1). As it is registered in well-known fungal nomenclature databases (Index Fungorum and MycoBank), we think that it is better to validate *Sepultariella* than to create another name. We therefore propose the newly validated genus *Sepultariella* to accommodate *P. patavina* and *L. semiimmersa*, the first two species included in this genus. We choose *Peziza patavina* as type species because *S. semiimmersa* could represent a species complex.

⁸ The collection R.K. 82.146 that we re-examined corresponds to *C. ascophanoides*, but the fungus illustrated by KRISTIANSEN (2014: 50) does not look like the latter and is probably another *Tricharina* species.

Sepultariella Van Vooren, U. Lindemann & Healy, *gen. nov.* – MB 819861

Diagnosis: Differs from *Leucoscypha* Boud. by pigmented apothecia and smooth ascospores.

Type species: *Peziza patavina* Cooke & Sacc.

Etymology: From Latin *sepultus* that means buried.

Sepultariella patavina (Cooke & Sacc.) Van Vooren, U. Lindemann & Healy, *comb. nov.* – MB 819862

Basionym: *Peziza patavina* Cooke & Sacc., in Saccardo, *Michelia*, 1: 70 (1877).

Homotypic synonyms: *Neottiella patavina* (Cooke & Sacc.) Sacc., *Syll. fung.*, 8: 193 (1889); *Humaria patavina* (Cooke & Sacc.) Rehm, *Rabenh. Kryptog.-Fl.*, 1 (3): 957 (1894); *Pustularia patavina* (Cooke & Sacc.) Boud., *Icon. mycol., liste prélim.*: 3 (1904); *Leucoscypha patavina* (Cooke) Svrček, *Česká Mykol.*, 28 (3): 132 (1974); *Leucoscypha patavina* (Cooke) Pant & V.P. Tewari, *Trans. Brit. Mycol. Soc.*, 68 (3): 441 (1977), *illeg.*

Sepultariella semi-immersa (P. Karst.) Van Vooren, U. Lindemann & Healy, *comb. nov.* – MB 819863

Basionym: *Peziza semi-immersa* P. Karst., *Notis. Sällsk. Fauna Fl. Fenn. Förhandl.*, 10: 117 (1869).

Homotypic synonyms: *Humaria semi-immersa* (P. Karst.) Sacc., *Syll. fung.*, 8: 143 (1889); *Sepultaria semi-immersa* (P. Karst.) Masee, *Brit. Fung.-Fl.*, 4: 391 (1895); *Humarina semi-immersa* (P. Karst.) Seaver, *N. Amer. Cup-Fungi (Operc.)*: 130 (1928); *Leucoscypha semi-immersa* (P. Karst.) Svrček, *Česká Mykol.*, 28 (3): 133 (1974); *Octospora semi-immersa* (P. Karst.) K.B. Khare & V.P. Tewari, *Canad. J. Bot.*, 56 (17): 2118 (1978); *Byssonectria semi-immersa* (P. Karst.) Benkert, *Gleditschia*, 15 (1): 181 (1987).

Outlook

Here we focused on the four key species of *Tricharina* and the delimitation of the most closely allied genera. In an upcoming manuscript, we will focus on the other species of the genus which are until now not sufficiently known in regard to their taxonomic position, that include: *T. flava*, *T. groenlandica*, *T. herinkii*, *T. hiemalis*, *T. japonica*, *T. pallidisetosa*, *T. striispora*, and *T. tophiseda*. These species will be also analyzed morphologically and phylogenetically based on type studies and recent findings. On the basis of the results, a key will be provided with which it will be possible to distinguish the morphologically often very similar species of *Tricharina* and those of closely allied genera.

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Appendix

This appendix contains the list of sequences used during our study to release the phylotrees (Fig. 1 and 2).

Table 4 – List of collections of *Tricharina* and other genera sequenced during this study

Original name (identified as...)	Correct name (if different)	Voucher or Strain Number	Country	Collector(s)	GenBank Number	
					ITS	LSU
<i>Cupulina montana</i>		N.V. 2011.09.04	France	N. Van Vooren	KY364048	KY364070
<i>Cupulina montana</i>		G 00262366 (holotype)	Switzerland	R. Dugoud	KY364047	KY364073
<i>Geopora herinkii</i>	<i>Tricharina gilva</i> complex	(HH) 83/168	Switzerland	B. Senn-Iilet	KY928062	KY928059
<i>Leucoscypha patavina</i>	<i>Sepultariella patavina</i>	N.V. 2011.09.18	France	N. Van Vooren	KY364045	KY364075
<i>Leucoscypha patavina</i>	<i>Sepultariella patavina</i>	N.V. 2013.08.71	Georgia	Z. Egertova	KY364042	KY364076
<i>Leucoscypha patavina</i>	<i>Sepultariella patavina</i>	R.D. 15.50.227.91	Switzerland	R. Dugoud	KY364043	KY364077
<i>Leucoscypha patavina</i>	<i>Sepultariella patavina</i>	M.V. 2013.10.18-4	Germany	M. Vega	KY364044	KY364078
<i>Leucoscypha cf. patavina</i>	<i>Sepultariella patavina</i>	N.V. 2013.11.17	Portugal	N. Van Vooren	KY364037	KY364081
<i>Leucoscypha semi-immersa</i>	<i>Sepultariella semi-immersa</i>	R.D. 25.09.227.98	Switzerland	R. Dugoud	KY364036	KY364079
<i>Leucoscypha semi-immersa</i>	<i>Sepultariella semi-immersa</i>	NV 2006.09.27	France	N. Van Vooren	KY364040	KY364074
<i>Leucoscypha semi-immersa</i>	<i>Sepultariella semi-immersa</i>	M.V. 2013.09.28-3	Germany	M. Vega	KY364038	KY364082
<i>Leucoscypha semi-immersa</i>	<i>Sepultariella semi-immersa</i>	M.V. 2013.10.25-2	Germany	M. Vega	KY364039	KY364083
<i>Paratracharina cf. poirauii</i>	<i>Paratracharina poirauii</i>	U.L. 116	Spain	F. Hampe & J. Kleine	KY364029	KY364053
<i>Pseudoleuria fibrillosa</i>		U.L. 182	Germany	M. Vega	KY364035	KY364068
<i>Pseudotracharina sp.</i>		MES-2152	Argentina	R. Healy	KY364033	KY364072
<i>Pseudotracharina sp.</i>		MES-2065	Argentina	D. Torres Acuna	KY364034	KY364071
<i>Pustularia cf. patavina</i>	<i>Sepultariella semi-immersa</i> complex	U.L. 181	Ethiopia	U. Lindemann	KY364041	KY364080
<i>Tricharina aethiopica</i>		MSTR P-19994 (holotype)	Ethiopia	U. Lindemann	KY364022	KY364061
<i>Tricharina ascophanooides</i>	<i>Cupulina ascophanooides</i>	N.V. 2014.06.07	Switzerland	N. Van Vooren	KY364046	KY364069
<i>Tricharina ascophanooides</i>	<i>Cupulina ascophanooides</i>	N.V. 2006.08.24	France	N. Van Vooren	KY364049	KY364051
<i>Tricharina ascophanooides</i>	<i>Cupulina ascophanooides</i>	N.V. 2007.07.30	France	N. Van Vooren	KY364050	KY364052
<i>Tricharina ascophanooides</i>	<i>Cupulina ascophanooides</i>	U.L. 131	Slovakia	U. Lindemann	KY928063	KY928060
<i>Tricharina ascophanooides</i>	<i>Cupulina ascophanooides</i>	U.L. 192	Norway	M. Pettersen	KY928064	KY928061
<i>Tricharia gilva</i>	<i>Tricharina gilva</i>	PC 0167813 (lectotype)	France	E. Boudier	KY364019	KY364057
<i>Tricharina cf. gilva</i>	<i>Tricharina hiemalis</i>	N.V. 2011.08.14	France	N. Van Vooren	KY364021	KY364059
<i>Tricharina cf. gilva</i>	<i>Ascorhizoctonia praecox</i>	N.V. 2016.03.01	France	B. Clesse	KY364031	KY364054
<i>Tricharina cf. gilva</i>		R.M.-1254	Spain	R. Martínez Gil	KY364028	KY364063
<i>Tricharina glabra</i>		MSTR P-19995 (holotype)	Germany	T. Böhring	KY364024	KY364067
<i>Tricharina ochroleuca</i>	<i>Tricharina gilva</i> complex	N.V. 2011.08.05	France	N. Van Vooren	KY364027	KY364060
<i>Tricharina ochroleuca</i>	<i>Tricharina gilva</i>	U.L. 191	Germany	R. Seibert	KY364020	KY364065
<i>Tricharina ochroleuca</i>	<i>Tricharina gilva</i> complex	U.L. 241	Czech Republic	Z. Egertova	-	KY364066
<i>Tricharina ochroleuca</i>	<i>Tricharina gilva</i> complex	U.L. 243	Spain	R. Martínez Gil	KY364026	KY364064
<i>Tricharina cf. ochroleuca</i>	<i>Tricharina gilva</i> complex	N.V. 2013.06.00	Spain	G. Moyne	KY364025	KY364058
<i>Tricharina praecox</i>	<i>Ascorhizoctonia praecox</i>	U.L. 100	Spain	R. Negrin	KY364030	KY364055
<i>Tricharina praecox var. cretea</i>	<i>Ascorhizoctonia praecox</i>	R.D. 15.06.245.91	Switzerland	R. Dugoud	KY364032	KY364056
<i>Tricharina striispora</i>		JA-CUSSTA: 7799	Spain	S. Tello	KY364023	KY364062

Table 4 – List of collections of *Tricharina* and other genera sequenced during this study

Original name (identified as...)	Correct name (if different)	Voucher or Strain Number	Country	Collector(s)	GenBank Number	
					ITS	LSU
<i>Cupulina montana</i>		N.V. 2011.09.04	France	N. Van Vooren	KY364048	KY364070
<i>Cupulina montana</i>		G 00262366 (holotype)	Switzerland	R. Dugoud	KY364047	KY364073
<i>Geopora herinkii</i>	<i>Tricharina gilva</i> complex	(HH) 83/168	Switzerland	B. Senn-Ilet	KY928062	KY928059
<i>Leucoscypha patavina</i>	<i>Sepultariella patavina</i>	N.V. 2011.09.18	France	N. Van Vooren	KY364045	KY364075
<i>Leucoscypha patavina</i>	<i>Sepultariella patavina</i>	N.V. 2013.08.71	Georgia	Z. Egertova	KY364042	KY364076
<i>Leucoscypha patavina</i>	<i>Sepultariella patavina</i>	R.D. 15.50.227.91	Switzerland	R. Dugoud	KY364043	KY364077
<i>Leucoscypha patavina</i>	<i>Sepultariella patavina</i>	M.V. 2013.10.18-4	Germany	M. Vega	KY364044	KY364078
<i>Leucoscypha cf. patavina</i>	<i>Sepultariella patavina</i>	N.V. 2013.11.17	Portugal	N. Van Vooren	KY364037	KY364081
<i>Leucoscypha semi-immersa</i>	<i>Sepultariella semi-immersa</i>	R.D. 25.09.227.98	Switzerland	R. Dugoud	KY364036	KY364079
<i>Leucoscypha semi-immersa</i>	<i>Sepultariella semi-immersa</i>	NV 2006.09.27	France	N. Van Vooren	KY364040	KY364074
<i>Leucoscypha semi-immersa</i>	<i>Sepultariella semi-immersa</i>	M.V. 2013.09.28-3	Germany	M. Vega	KY364038	KY364082
<i>Leucoscypha semi-immersa</i>	<i>Sepultariella semi-immersa</i>	M.V. 2013.10.25-2	Germany	M. Vega	KY364039	KY364083
<i>Paratracharina cf. poirauii</i>	<i>Paratracharina poirauii</i>	U.L. 116	Spain	F. Hampe & J. Kleine	KY364029	KY364053
<i>Pseudoleuria fibrillosa</i>		U.L. 182	Germany	M. Vega	KY364035	KY364068
<i>Pseudotracharina sp.</i>		MES-2152	Argentina	R. Healy	KY364033	KY364072
<i>Pseudotracharina sp.</i>		MES-2065	Argentina	D. Torres Acuna	KY364034	KY364071
<i>Pustularia cf. patavina</i>	<i>Sepultariella semi-immersa</i> complex	U.L. 181	Ethiopia	U. Lindemann	KY364041	KY364080
<i>Tricharina aethiopica</i>		MSTR P-19994 (holotype)	Ethiopia	U. Lindemann	KY364022	KY364061
<i>Tricharina ascophanooides</i>	<i>Cupulina ascophanooides</i>	N.V. 2014.06.07	Switzerland	N. Van Vooren	KY364046	KY364069
<i>Tricharina ascophanooides</i>	<i>Cupulina ascophanooides</i>	N.V. 2006.08.24	France	N. Van Vooren	KY364049	KY364051
<i>Tricharina ascophanooides</i>	<i>Cupulina ascophanooides</i>	N.V. 2007.07.30	France	N. Van Vooren	KY364050	KY364052
<i>Tricharina ascophanooides</i>	<i>Cupulina ascophanooides</i>	U.L. 131	Slovakia	U. Lindemann	KY928063	KY928060
<i>Tricharina ascophanooides</i>	<i>Cupulina ascophanooides</i>	U.L. 192	Norway	M. Pettersen	KY928064	KY928061
<i>Tricharia gilva</i>	<i>Tricharina gilva</i>	PC 0167813 (lectotype)	France	E. Boudier	KY364019	KY364057
<i>Tricharina cf. gilva</i>	<i>Tricharina hiemalis</i>	N.V. 2011.08.14	France	N. Van Vooren	KY364021	KY364059
<i>Tricharina cf. gilva</i>	<i>Ascorhizoctonia praecox</i>	N.V. 2016.03.01	France	B. Clesse	KY364031	KY364054
<i>Tricharina cf. gilva</i>		R.M.-1254	Spain	R. Martínez Gil	KY364028	KY364063
<i>Tricharina glabra</i>		MSTR P-19995 (holotype)	Germany	T. Böhnig	KY364024	KY364067
<i>Tricharina ochroleuca</i>	<i>Tricharina gilva</i> complex	N.V. 2011.08.05	France	N. Van Vooren	KY364027	KY364060
<i>Tricharina ochroleuca</i>	<i>Tricharina gilva</i>	U.L. 191	Germany	R. Seibert	KY364020	KY364065
<i>Tricharina ochroleuca</i>	<i>Tricharina gilva</i> complex	U.L. 241	Czech Republic	Z. Egertova	-	KY364066
<i>Tricharina ochroleuca</i>	<i>Tricharina gilva</i> complex	U.L. 243	Spain	R. Martínez Gil	KY364026	KY364064
<i>Tricharina cf. ochroleuca</i>	<i>Tricharina gilva</i> complex	N.V. 2013.06.00	Spain	G. Moyne	KY364025	KY364058
<i>Tricharina praecox</i>	<i>Ascorhizoctonia praecox</i>	U.L. 100	Spain	R. Negrin	KY364030	KY364055
<i>Tricharina praecox var. cretea</i>	<i>Ascorhizoctonia praecox</i>	R.D. 15.06.245.91	Switzerland	R. Dugoud	KY364032	KY364056
<i>Tricharina striispora</i>		JA-CUSSTA: 7799	Spain	S. Tello	KY364023	KY364062

Table 5 – List of other sequences from the INSDC public databases also used in phylogenetic analyses

Original name (identified as...)	Correct name (if different)	Voucher or Strain number	Country	Collector(s)	GenBank Number	
					ITS	LSU
<i>Anthracobia macrocystis</i>		C KH.01.035	Denmark	K. Hansen		KC012663
<i>Anthracobia</i> sp.		QCNE TL-11709	Ecuador			KC012664
<i>Ascorhizoctonia ascophanooides</i>	<i>Tricharina gilva</i> complex	CSY 123 (holotype)	Norway	R. Kristiansen	U38581	U38580
<i>Ascorhizoctonia praecox</i>		CBS 240.85 (holotype)	Norway	H. Dissing & S. Sivertsen	JQ836559	JQ836562
<i>Ascorhizoctonia</i> sp. (culture)	<i>Tricharina</i> sp.	BCS-1	China ?	Z.L. Yuan	JQ836557	JQ836563
<i>Ascorhizoctonia</i> sp. (endophyte)		23 HKD-2015	Iran	H.K. Dolatabad et al.	KP641147	
<i>Ascorhizoctonia</i> sp. (endophyte)		CSE195	Iran	J. Soltani et al.	KJ598625	
<i>Ascorhizoctonia</i> sp. (endophyte)		CSE148	Iran	J. Soltani & S. Pakvaz	KT024986	
<i>Ascorhizoctonia</i> sp. (endophyte)	<i>Tricharina</i> sp.	ZC-W-2-2	China	F. Bu & Z. Yu	KR822155	
<i>Ascorhizoctonia</i> sp. (endophyte)	<i>Tricharina gilva</i> complex	23 HKD-2015	Iran	H.K. Dolatabad et al.	KP641147	
Fungal sp. (endophyte)	<i>Tricharina gilva</i> complex	BG46	France	A. Langenfeld et al.		JQ249225
Fungal sp. (orchid mycorrhiza)	<i>Tricharina</i> sp.	CC26	Argentina	S. Fracchia et al.	KF151200	
<i>Geopora arenicola</i>		C KS-94-173	Denmark	K. Hansen & S.K. Sandal		DQ220336
<i>Geopora cercocarpi</i>		Kropp2	USA	D. Southworth & J.L. Frank		HQ283098
<i>Geopora cervina</i> (EcM)		UU_3a_1	Sweden		JQ724065	
<i>Geopora cf. cervina</i>		FH KH.03.61	Norway	K. Hansen		DQ220344
<i>Geopora clausa</i>		AH39177	Spain		JN812052	
<i>Geopora clausa</i>		AH39181	Spain		JN812053	
<i>Geopora clausa</i>		MA 46927	Portugal			JX424576
<i>Geopora cooperi</i>		SFSU HDT 52489	USA	J. Ammarati		DQ220341
<i>Geopora cooperi</i>		AH9065	Spain		JN812044	
<i>Geopora cooperi</i>		VK1783	Greece	V. Kaounas	JN812045	
<i>Geopora cooperi</i>		FH BAP 517	USA			KC012678
<i>Geopora foliacea</i>		AH38936	Spain		JN812047	
<i>Geopora foliacea</i>		AH38937	Spain		JN812048	
<i>Geopora nicaensis</i>		MCVE 14596	Italy	E. Campo	JF908022	
<i>Geopora summeriana</i>		MCVE 16978	Italy	A. Montecchi	JF908024	
<i>Hoffmannoscypha pellita</i>		FH DHP 297	USA	D.H. Pfister		DQ220343
<i>Hoffmannoscypha pellita</i>		M GH20100409	Germany	D. Strobel & G. Hensel	HQ913564	HQ993571
<i>Lotinia verna</i>		SESTAO 2003040401 (holotype)	Spain	J.L. Pérez-Butrón	KP195730	KP195729
<i>Melastiza contorta</i>		C KH.01.06	Sweden	K. Hansen		AY500539
<i>Paratracharina poiraultii</i>		U.L. 179-14	Spain	T. Illescas et al.	KP052784	KP052785
<i>Paratracharina poiraultii</i>		U.L. 178-14	Portugal	M. Vega	KP052788	KP052789
<i>Pezizaceae</i> sp. (endophyte)	<i>Tricharina gilva</i> complex	C14	China	L.W. Shang	JN198476	
<i>Pezizomyces</i> sp. (endophyte)	<i>Tricharina gilva</i> complex	ARIZ AEA DC2145	USA	B. Klein et al.	GQ153018	GQ153018
<i>Pezizomyces</i> sp. (endophyte)	<i>Ascorhizoctonia praecox</i>	ARIZ AEA 11056	USA	M. Hoffman	GQ153065	GQ153065
<i>Pezizomyces</i> sp. (endophyte)	<i>Tricharina glabra</i>	MJ34	China	F. Huang et al.	HQ449982	
<i>Pezizomyces</i> sp. (endophyte)	<i>Tricharina gilva</i> complex	DC2145	USA	B. Klein et al.	GQ153018	

Table 5 – (continued)

Original name (identified as...)	Correct name (if different)	Voucher or Strain Number	Country	Collector(s)	GenBank Number	
					ITS	LSU
<i>Phaeangium lefebvrei</i>		IRA-MBA sb11	Tunisia	I. Sbissi <i>et al.</i>		GU391557
<i>Picoa juniperi</i>		IRA-MBA sb6	Tunisia	I. Sbissi <i>et al.</i>		GU391558
<i>Pseudaleuria quinaulfiana</i>		OSC 45766 (paratype)	USA	D. Lusk-Newman	EU669387	
<i>Pseudaleuria quinaulfiana</i>		NSW 7107	USA	N.S. Weber		DQ220389
<i>Pseudotrifarina intermedia</i>		ST 25011493 (holotype)	Spain	S. Tello	KT861358	KT861360
<i>Pseudotrifarina intermedia</i>		GK 6904	Greece	G. Konstantinidis	KT861359	KT861361
<i>Pustularia patavina</i>	<i>Sepultariella patavina</i>	FH KH.03.73	Norway	K. Hansen & C. Lange		DQ220396
<i>Pyronemataceae</i> sp.	<i>Cupulina ascophanoides</i>	FH KH.04.21	USA	N. Weber & K. Hansen		DQ220399
<i>Sphaerosporella brunnea</i>	<i>Trichophaea brunnea</i>	FH DHP DR.02.16	Dominican Republic	D.H. Pfister		DQ220432
<i>Sphaerosporella brunnea</i>	<i>Trichophaea brunnea</i>	FH KH.03.04	USA	K. Hansen		DQ220433
<i>Sphaerosporella hinnulea</i>		C F-55022	Norway	H. Dissing		DQ220431
<i>Tricharina gilva</i>	<i>Ascorhizoctonia praecox</i>	C F-55212	Norway	H. Dissing		DQ220442
<i>Tricharina gilva</i>	<i>Ascorhizoctonia praecox</i>	DED 7356	USA	D.E. Desjardin		DQ220443
<i>Tricharina gilva</i>	<i>Ascorhizoctonia praecox</i>	FH BAP 431	USA	B.A. Perry		DQ220444
<i>Tricharina gilva</i>	Not a <i>Tricharina</i> species	NY NYBG 1968	USA	F.A. Wolf	JO824118	
<i>Tricharina groenlandica</i>		CBS 237.85 (holotype)	Greenland	H. Dissing	JO824125	U38576
<i>Tricharina hiemalis</i> (culture as <i>Rhizoctonia hiemalis</i>)		CBS 263.60	Canada	H.K. Saksena	JO824124	
<i>Tricharina ochroleuca</i>	<i>Tricharina hiemalis</i> (?)	C F-53062	Greenland	H. Dissing		DQ220445
<i>Tricharina ochroleuca</i>	<i>Tricharina groenlandica</i>	CBS 238.85 (neotype)	Norway	S. Silvertsen & H. Dissing	JO824126	JO836561
<i>Tricharina ochroleuca</i> (EcM? Endophyte?)		OK3F101HP	China	X. Yang <i>et al.</i>	KF871459	
<i>Tricharina praecox</i>	<i>Tricharina gilva</i>	FH KH.03.101	Norway	K. Hansen	DQ646552	DQ646525
<i>Tricharina praecox</i>	<i>Ascorhizoctonia praecox</i>	M 0178315	Germany	T. Kupka	JO824122	
<i>Tricharina praecox</i>	<i>Ascorhizoctonia praecox</i>	M 0178316	Austria	M. Moser	JO824120	
<i>Tricharina</i> sp.	Not a <i>Tricharina</i> species	Barr 5907	USA	M.E. Barr		DQ220446
<i>Tricharina</i> sp.		C TL-10051	Ecuador	J. Salazar & T. Laessøe		DQ220447
<i>Tricharina striispora</i> (culture)		BCCM/MUCL 41297	Argentina	Z.L. Yuan	JO836556	JO836560
<i>Tricharina striispora</i> (endophyte)	<i>Tricharina striispora</i>	OT2-144	Portugal	T. Gomes <i>et al.</i>	KT804076	
<i>Trichophaea abundans</i>		CBS 348.76	Finland	V. Hintikka		DQ220448
<i>Trichophaea hemisphaeroides</i>		FH KH.04.54	USA	K. Hansen		KC012710
<i>Trichophaea hybrida</i>	<i>Tricharina hiemalis</i> (?)	AMNH-49682	Iceland			DQ220455
<i>Trichophaea minuta</i>		CBS 236.57 (isotype)	Canada	R.F. Cain & N.A. Hastings		DQ220452
<i>Trichophaea saccata</i>		CBS 804.70 (type)	UK	H.C. Evans		DQ220451
<i>Trichophaea woolhopeia</i>		N.V. 2006.10.01	France	N. Van Vooren	KX982244	KX982243
<i>Trichophaea woolhopeia</i>		KH-01.033	Denmark	K. Hansen		DQ220460
Uncultured <i>Ascorhizoctonia</i> clone (soil sample, ginger rhizosphere)		BDR3C10	India	H. Thakur <i>et al.</i>	KJ591759	
Uncultured <i>Geopora</i> (orchid mycorrhiza)	<i>Geopora</i> sp.	LP34-Geo1	Russia	T. Tesitelova <i>et al.</i>	KJ188583	
Uncultured Pezizaceae (orchid mycorrhiza)	<i>Pseudotrifarina</i> sp.	1221a	South Africa	R.J. Waterman <i>et al.</i>	FJ788784	

Table 5 – (continued)

Original name (identified as...)	Correct name (if different)	Voucher or Strain Number	Country	Collector(s)	GenBank Number	
					ITS	LSU
Uncultured <i>Pezizaceae</i> (orchid mycorrhiza)	<i>Pseudotrifarina</i> sp.	1223a	South Africa	R.J. Waterman <i>et al.</i>	FJ788780	
Uncultured <i>Pezizaceae</i> (orchid mycorrhiza)	<i>Pseudotrifarina</i> sp.	1186a	South Africa	R.J. Waterman <i>et al.</i>	FJ788782	
Uncultured <i>Pyronemataceae</i> (orchid mycorrhiza)	<i>Trifarina hiemalis</i>	3075	Germany	M.I. Bidartondo	AY634115	
<i>Wilcoxina mikolae</i>		SFSU WS 36	USA	W. Stoll		DQ220468
<i>Wilcoxina mikolae</i>		HMJAU27330	China	C.H. Shi & T. Bau	KU061020	
<i>Wilcoxina rehmsii</i> (ECM)		NS211	Lithuania	A. Menkis <i>et al.</i>	DQ069001	



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