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## **Studies in the *Phaeotremella foliacea* group (Tremellomycetes, Basidiomycota)**

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3 Studies in the *Phaeotremella foliacea* group (Tremellomycetes, Basidiomycota)  
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11

12 Abstract

13 Taxonomy of the *Phaeotremella foliacea* group is revised based on morphological, ecological, geographic and DNA  
14 data. The name *P. foliacea* is retained for the gymnosperm-dwelling species associated with *Stereum sanguinolentum* in  
15 Eurasia and North America. *Tremella neofoliacea* and *Cryptococcus skinneri* are considered synonyms of *P. foliacea*  
16 s.str. Three other species in the complex inhabit deciduous trees. Of them, *Phaeotremella fimbriata*, comb. nov., is  
17 associated with *Stereum rugosum*; this species possesses blackening basidiocarps and small basidiospores, and it occurs  
18 in Europe. Its close relative is the East Asian *Phaeotremella eugeniae*, sp. nov., inhabiting *Quercus mongolica* and  
19 having larger basidiospores. The third species, *Phaeotremella frondosa*, comb. nov., produces the largest basidiospores  
20 in the genus and is associated either with *S. rugosum* (mainly in North Europe) or with other *Stereum* species (temperate  
21 Eurasia and North America). Additionally, *T. nigrescens* is typified and placed in the synonyms of *P. frondosa*, and two  
22 species, *T. fuscusuccinea* and *T. roseotincta*, are combined to *Phaeotremella*.

23  
24 Key words: heterobasidiomycetes, mycoparasite, phylogeny, typification

25  
26 Introduction

27 *Tremella foliacea* Pers. (= *Phaeotremella foliacea* (Pers.) Wedin et al.) is one of the most common jelly fungi well  
28 known to both professional mycologists and amateur collectors. It produces large, foliaceous, light brown to almost  
29 black basidiocarps on fallen logs of conifers and deciduous trees and is known to parasitise crust fungi of the genus  
30 *Stereum* (Russulales, Agaricomycotina, Basidiomycota) (Roberts 1999, Pippola & Kotiranta 2008). Due to four-celled  
31 basidia and subglobose basidiospores, *T. foliacea* has been placed among true *Tremella* species. Several characteristics  
32 such as septal pore structure, formation of haustoria and presence of haploid yeast stage, suggested that the genus  
33 *Tremella* is heterogeneous and its delimitation from allied heterobasidiomycetes (e.g. *Filobasidium* L.S. Olive,  
34 *Holtermannia* Sacc. & Traverso, *Sirobasidium* Lagerh. & Pat., *Sirotrema* Bandoni, *Tetragoniomyces* Oberw. &  
35 Bandoni, *Trimorphomyces* Bandoni & Oberw.) is problematic (Bandoni 1987; Oberwinkler 1987).

36 Based on DNA and morphological evidences, Chen (1998) separated *T. foliacea* and some other species into the *T.*  
37 *foliacea* group. Sequencing of nuclear ribosomal DNA loci (small and large subunits, internal transcribed spacer)  
38 showed that the genus *Tremella* is polyphyletic (Fell et al. 2000; Fell et al. 2001; Scorzetti et al. 2002). In agreement  
39 with the study of Chen (1998), the Foliacea clade in Tremellales has been recognized by Fell et al. (2000) and Scorzetti  
40 et al. (2002). These studies, however, have analyzed about 10% of the estimated 200 species in the Tremellales (cf.  
41 Bandoni 1987).

42 The study of Tremellomycetes by Millanes et al. (2011) almost tripled the number of sequenced taxa in this class. The  
43 phylogenetic analysis, still based on nrDNA loci, confirmed that the genus *Tremella* in its traditional scope is  
44 polyphyletic. In agreement with previous studies, the *T. foliacea* clade was resolved as a separate lineage within  
45 Tremellales, together with *T. neofoliacea* Chee J. Chen, *T. simplex* H.S. Jacks. & G.W. Martin, *T. mycophaga* G.W.  
46 Martin, *T. mycetophiloides* Kobayasi and also the yeast species *Cryptococcus skinneri* Phaff & Carmo Souza. In spite of  
47 the well-documented taxonomic complexity in Tremellales, several attempts have been performed to restrict taxonomic  
48 genera to the clades comprising the respective type species. As a result, several new genera have been proposed to  
49 accommodate species in a few monophyletic clades previously classified in the polyphyletic genera *Cryptococcus* Vuill.  
50 and *Bullera* Derx (e.g. Wang & Bai 2008; Wuczkowski et al. 2011).

51 Liu et al. (2015a) produced first a comprehensive seven-gene phylogeny that can be used as a solid background for the  
52 re-classification of Tremellomycetes. They constructed their dataset from living cultures, which left out many  
53 teleomorphic taxa. To address this problem, Liu et al. (2015b) undertook an expanded nrLSU-based analysis with  
54 constrained topology to place species known from LSU sequences in the clades previously recognized in the analysis of  
55 the seven-gene dataset. These analyses were used to revise the classification of anamorphic and teleomorphic  
56 Tremellomycetes. As a consequence, several clades comprising *Tremella* species were transferred into newly described  
57 or reintroduced genera, such as *Carcinomyces* Oberw. & Bandoni, *Naematelia* Fr., *Phaeotremella* Rea, and  
58 *Pseudotremella* X.Z. Liu et al.

59 Liu et al. (2015b) resurrected the older generic name *Phaeotremella* for the *T. foliacea* clade. The genus is typified by  
60 *P. pseudofoliacea* Rea, and Liu et al. (2015b) transferred six further species to the genus: *Cryptococcus fagi*  
61 Middelhoven & Scorzetti, *C. skinneri*, *T. neofoliacea*, *T. mycetophiloides*, *T. mycophaga*, and *T. simplex*. A new family  
62 *Phaeotremellaceae* was also introduced to accommodate the genus *Phaeotremella* and the newly described monotypic  
63 genus *Gelidatrema* Yurkov et al. Although this proposal was supported by the phylogenetic analyses, the emendation of  
64 the genus *Phaeotremella* was performed without reconsidering available specimens of the type species *Phaeotremella*  
65 *pseudofoliacea* from different geographical localities and hosts. Moreover, the history of the species and present  
66 taxonomic synonyms were not addressed. In the absence of molecular data for reference specimens, the strain CBS  
67 6969 (= MUCL 31979) sampled in British Columbia by R.J. Bandoni was chosen to serve as a reference for  
68 *Phaeotremella pseudofoliacea*.

69 *Phaeotremella pseudofoliacea* has been regarded as a synonym of *T. foliacea* (Donk 1966, Roberts 1999), a much older  
70 species described more than two hundred years ago (Persoon 1799). Identity of the latter species, however, is  
71 controversial. Donk (1966) recognized *T. foliacea* alongside with two other, similarly looking species, *T. frondosa* Fr.

72 and *T. intumescens* Sowerby (= *T. nigrescens* Fr.) sensu auct. Reaching a different conclusion, Neuhoﬀ (1936) and  
73 Torkelsen (1968) re-introduced *T. foliacea* in a wide sense while recognizing its morphological variability and wide  
74 host range. With some reservations, Chen (1998) accepted the latter viewpoint. However, he used two Taiwanese  
75 collections as a source of his concept of *T. foliacea* and described four new allied species, *T. griseobrunnea* Chee J.  
76 Chen, *T. vasifera* Chee J. Chen (from Europe), *T. neofoliacea* and *T. fuscossuccinea* Chee J. Chen (from East Asia).  
77 None of the numerous presumable synonyms of *T. foliacea* from Europe were mentioned by him, and therefore the  
78 species concepts in the whole complex became even more obscure. Finally, Wedin et al. (2016) formally recombined *T.*  
79 *foliacea* into *Phaeotremella*, without revising the species concept and delimiting it from morphologically sibling species  
80 and putative taxonomic synonyms.

81 In the present paper, we revise taxonomy of the *Phaeotremella foliacea* complex using morphological characters,  
82 information about species ecology, geographic distribution, and nucleotide sequence data. This study comprises 72  
83 specimens and 11 cultures sampled mostly in temperate and boreal Eurasia. In order to facilitate species identification  
84 in the future, a comprehensively sampled set of specimens was accompanied with DNA-barcodes using ITS (Schoch et  
85 al. 2012) and *tef1* (Stielow et al. 2015) genetic markers. Phylogenetic analyses were performed using ribosomal ITS and  
86 LSU, and partial *tef1* gene sequences. Based on these results, four new taxonomic combinations are proposed in the  
87 genus *Phaeotremella*, and one species is described as new.

88

## 89 Material and methods

90 Specimens from herbaria H, O, LE, K were studied. Herbarium acronyms are given according to Thiers (2017).

91 Morphological study follows Miettinen et al. (2012). The following abbreviations are used in morphological  
92 descriptions and tables: L – mean spore length, W – mean spore width, Q' – length/width ratio, Q – mean length/width  
93 ratio, n – number of measurements per specimens.

94 Yeast cultures were isolated from fresh dried fruiting bodies on solid yeast extract–malt extract (YM) medium  
95 supplemented with 200 mg/L chloramphenicol using the spore-fall method.

96 *DNA extraction and amplification.* In total, 30 specimens and 11 living cultures were selected for molecular sampling  
97 (Table 1). DNA extraction was done with NucleoSpin Plant II Kit (Macherey-Nagel GmbH & Co. KG) following  
98 manufacturer's protocol. The following primers were used for both amplification and sequencing of the ITS region and  
99 28S rRNA gene (LSU): ITS1F-ITS4 (White et al. 1990; Gardes & Bruns 1993) for the ITS region, and JS1 (Landvik  
100 1996) and LR5 (Vilgalys & Hester 1990) for the D1/D2 domains of the LSU region. Partial sequences of the gene  
101 coding translation elongation factor 1 alpha (*tef1*) were amplified and sequenced using primers EF1-983F and EF1-  
102 1567R (Rehner & Buckley 2005). PCR products were purified applying the GeneJET Gel Extraction Kit (Thermo  
103 Scientific, Thermo Fisher Scientific Inc., MA, USA).

104 Cultures were obtained from the fungal collection of the Leibniz Institute DSMZ – German Collection of  
105 Microorganisms and Cell Cultures (Braunschweig, Germany). Some of these cultures were included previously in the  
106 phylogenetic analysis by Liu et al. (2015b). Cultures were cultivated on malt extract (MA) or potato dextrose (PDA,  
107 Difco BD) agars for 7 days at room temperature. Their DNA was extracted using MasterPure Yeast DNA Purification  
108 Kit (Epicentre, WI, USA) following manufacture's instructions. Amplification of the ITS and partial LSU regions were  
109 performed with primers ITS1F and LR5, while internal primers ITS4 and NL4 were used for sequencing. Partial  
110 sequences of the gene coding translation elongation factor 1 alpha (*tef1*) were amplified and sequences using primers  
111 EF1-728F (Carbone and Kohn 1999) and EF1-1620R (Stielow et al. 2015).

112 The assembly and editing of sequence data were performed using Sequencher 5.3 (Gene Codes, USA) and MEGA 6  
113 (Tamura et al. 2013). Sequences were compared with sequences deposited in the NCBI ([www.ncbi.nih.gov](http://www.ncbi.nih.gov)) and CBS  
114 ([www.cbs.knaw.nl](http://www.cbs.knaw.nl)) databases. Nucleotide sequences were deposited in NCBI/EMBL under the accession numbers,  
115 which are provided in Table 1.

116 *Phylogenetic analyses.* A total of 32 ITS, 23 LSU and 24 *tef1* sequences were generated in this study (Table 1). The  
117 additional sequences were retrieved from NCBI GenBank, MycoBank and public catalogues of several service culture  
118 collections. Sequence alignments were performed with the genomic sequences using online version of MAFFT  
119 algorithm using the Q-INS-i option with the default parameters. The following four datasets were used in phylogenetic  
120 analyses:

- 121 (i) a 2-loci dataset (ITS and LSU) was used to analyse members of the *Phaeotremella* clade from older studies;
- 122 (ii) a 3-loci dataset (ITS+LSU and *tef1*) was used to analyse the *Phaeotremella foliacea* specimens, including the  
123 potential novel species;
- 124 (iii) a 2-loci (ITS and *tef1*) dataset was used to analyse the *Phaeotremella foliacea* specimens in two sub-clades;
- 125 (iv) a ITS dataset was used to place available ITS sequences into the topology inferred from the analysis of the three  
126 DNAloci.

127 The final LSU, ITS and *tef1* alignments contained 583, 546 and 523 characters, respectively. The three datasets  
128 contained 41, 53 and 22 sequences. Phylogenetic relationships were inferred by the maximum likelihood (ML) method  
129 based on the general time reversible (GTR) model with RaxML (version 7.4.2) using raxmlGUI 1.31 and the  
130 GTRGAMMA option with 1,000 rounds of bootstrap replicates (Silvestro and Michalak 2012).

131

132 Specimens examined (sequenced specimens are marked by asterisk)

133 *Phaeotremella eugeniae*. **Russia**. Primorie: Khanka Dist., Novokachalinsk, *Quercus mongolica*, 27.VII.1985 *Lelei* (LE

134 303434\*); Ternei Dist., Sikhote-Alin Nature Reserve, *Q. mongolica*, 23.VIII.2011 *Malysheva* (LE 262894\*),

135 7.VIII.2012 *Malysheva* (LE 303429\* – holotype).

136 *Phaeotremella fimbriata*. **Finland**. Etelä-Savo: Valkeala, Repovesi, *Alnus incana*, 16.IX.2004 *Niemelä* 7897\* (H).

137 **Norway**. Akershus: Bærum, Kjaglidalen, *Corylus avellana* + *Stereum rugosum*, 16.IX.2016 *Spirin* 11114\* (O),

138 Dælivannet, 22.III.1989 *Torkelsen* 2/89 (O F149407), Ullensaker, *A. incana*, 25.V.1979 *Torkelsen* 141/79 (O F149405).

139 Østfold: Skiptvet, Svartedal, *A. incana*, 7.IX.1997 *Løfall* (O F63256). Oppland: Lunner, Rinilhaugen, *A. incana* + *S.*

140 *rugosum*, 17.IX.2016 *Spirin* 11139\* (O).

141 *Phaeotremella foliacea*. **Finland**. Pohjois-Häme: Saarijärvi, *Picea abies*, 14.VIII.2008 *Miettinen* 13267\* (H), *P.*

142 *sylvestris* (?), 14.VIII.2008 *Miettinen* 13270, 13271, 13273.1, 13274.1 (H), *P. sylvestris* (?) + *S. sanguinolentum*,

143 16.VIII.2008 *Miettinen* 13291.1 (H). Kainuu: Hyrynsalmi, Paljakka, *P. abies* + *S. sanguinolentum*, 24.IX.2010

144 *Miettinen* 14170 (H). **Germany**. Baden-Württemberg: Schwarzwald, *Picea* sp., 25.X.1987 *Laber* (O). **Norway**.

145 Vestfold: Re, Reggestad, *P. abies*, 27.VII.1950 *Stordal* 4414 (O F149518). Vest-Agder: Mandal, Furulunden, *P.*

146 *sylvestris* + *S. sanguinolentum* + *Naematelia encephala*, 19.IX.2006 *Fonneland* 06-12 (O F282970). Akershus: Asker,

147 Bak Skaugum, *P. abies*, 30.IX.1966 *Lauritzen* (O F149419); Hurdal, Brustadkolen, *P. abies*, 24.V.1979 *Torkelsen*

148 118/79 (O F149406); Opegård, Hvitebjørn, *P. abies*, 20.XI.1950 *Eftestøl* (O F149397). Oslo: Oslo, Rektorhaugen, *P.*

149 *abies*, 30.VIII.1953 *Bratsberg* (O F149467), Sognsvann, *P. abies* + *S. sanguinolentum*, 9.IV.2005 *Hanssen* (O F67636).

150 Buskerud: Nes, Hallingdal, *P. abies*, 3.X.1965 *Torkelsen* (O F149513); Ringerike, Veienmoen, *P. abies*, 23.VIII.1953

151 *Eckblad* (O F149505). Rogaland: Sandnes, Espeland, *P. abies*, 21.X.1992 *Torkelsen* 272/92 (O F149553). Østfold:

152 Fredrikstad, Heieren, *P. abies*, 17.IV.1931 *Jørstad* (O F149383). Telemark: Bø, Oredalen, *P. sylvestris*, 3.IX.1971

153 *Hovda* (O F149532). Oppland: Sør-Fron, Hundorp, *P. abies*, 14.V.1989 *Torkelsen* 93/89 (O F149500). Sør-Trøndelag:

154 Meldal, *P. abies*, 28–29.IX.1991 *Høiland* 8-57, 32-84 (O F149977, 149958). Hedmark: Grue, Ulvika vid Skasen, *P.*

155 *sylvestris*, 12.X.1974 *Ryvarden* 13340 (O F149496); Åmot, Rena, *P. abies*, 5.IX.1992 *Ryvarden* 32035 (O F104117).

156 Nordland: Hemnes, Kangsen, conifer, 27.VIII.1969 *Ryvarden* (O F149605); Rana, *P. abies*, 11.IX.1976 *Torkelsen*

157 738/76 (O F149614). **Russia**. Leningrad Reg.: Boksitogorsk Dist., Vozhani, *P. abies* + *S. sanguinolentum* + *N.*

158 *encephala*, 2.X.2016 *Spirin* 11170\* (H). Khabarovsk Reg.: Solnechnyi Dist., Igdomi, *Pinus pumila*, 2.IX.2016 *Spirin*

159 10814\* (H), *Picea ajanensis* + *S. sanguinolentum*, 3.IX.2016 *Spirin* 10865\* (H); Verkhnebureinskii Dist., Dublikan, *P.*

160 *ajanensis* + *S. sanguinolentum*, 21.VIII.2014 *Spirin* 7721\* (H). Primorie: Ternei Dist., Sikhote-Alin Nature Reserve,

161 *Abies nephrolepis*, 23.VIII.2012 *Malysheva* (LE 303430\*), *Pinus koraiensis*, 23.VIII.2011 *Malysheva* (LE 303431\*).

162 **Sweden**. Jämtland: Berg, Viksjöbacken, *P. abies* + *S. sanguinolentum*, 18.VIII.2011 *Miettinen* 14610\* (H). **USA**.

163 Massachusetts: Worcester Co., Holden, *Pinus strobus* + *S. sanguinolentum*, 26.IX.2011 *Miettinen* 14812.2\* (H). New

164 York: Essex Co., Harris Lake, *Abies* sp. + *S. sanguinolentum*, 23.IX.2013 *Miettinen* 17173 (H).

165 *Phaeotremella frondosa*. **Czech Republic**. South Moravia: Brno, Tišnov, fallen log + *Stereum gausapatum*, VIII.1942

166 *Šmarda* (O), Řečkovický les, deciduous tree, 24.VIII.1962 *Valkoun* (O). **Finland**. Uusimaa: Kirkkonummi, Sundsberg,

167 *Betula pubescens* + *Stereum hirsutum*, 20.X.2012 *Miettinen* 15774, 15844\* (H); Helsinki, Pasila, *C. avellana*,

168 11.IV.2008 *Miettinen* 12406\* (H); Porvoo: Sannainen, *Alnus glutinosa*, 9.IX.1999 *Salo* 5889 (H); Sipoo, Gillerberget,

169 *Salix caprea* (?) + *S. rugosum*, 20.XII.2015 *Miettinen* 19896\* (H), Hindsby, *A. incana* + *Stereum subtomentosum*,

170 13.X.1984 *Saarenoksa* 46984 (H). Etelä-Häme: Hämeenlinna, Lammi, *Padus avium*, 20.XII.2015 *Miettinen* 19406\*

171 (H). Pohjois-Häme: Jyväskylä, Vuoritsalo, *S. aucuparia* + *S. rugosum*, 13.VII.2011 *Miettinen* 14498 (H). **Norway**.

172 Akershus: Asker, Syverstadvannet, 23.IV.1972, *Alnus* sp., 23.IV.1972 *Torkelsen* 13/72 (O F149411). Oslo: Oslo,

173 Holmlia, *Betula* sp., X.1980 *Wischmann* (O F149446). Telemark: Nome, Mørkvasslia, *A. incana* + *S. rugosum*,

174 25.X.2016 *Spirin* 11194\*, 11202\* (O). Østfold: Fredrikstad, Femdal, *Sorbus aucuparia*, 8.XII.1979 *Kristiansen* 30 (O

175 F149415); Sarpsborg, Bjørnland, *A. incana*, 18.IV.2003 *Løfall* (O F66427). **Russia**. Leningrad Reg.: Podporozhie Dist.,

176 Vachozero, *Populus tremula* + *S. hirsutum*, 15.X.2017 *Spirin* 11747 (H); Vsevolozhsk Dist., Vaskelovo, fallen log,

177 with *S. hirsutum*, 16.IX.1993 *Zmitrovich* (LE 206897\*). St. Petersburg: Muzhestva sq., *Tilia cordata*, 22.XI.2016 *Spirin*

178 11204\* (H). Karachayevo-Circassian Republic: Karachaevska Dist., Teberda Nat. Res., *Betula* sp., 12.VIII.2009 *V.*

179 *Malysheva* (LE 253852\*). Khabarovsk Reg.: Solnechnyi Dist., Igdomi, *Alnus* (*Duschekia*) *fruticosa* + *Peniophora*

180 *aurantiaca*, 4.IX.2016 *Spirin* 10969\* (H). **United Kingdom**. England: Somerset, Staple Park, 20.IX.1911 *Rea*

181 (lectotype of *P. pseudofoliacea*, see below).

182 *Phaeotremella fuscisuccinea*. **Russia**. Khabarovsk Reg.: Verkhnebureinsky Dist., Kyvyty, *P. ajanensis* + *S.*

183 *sanguinolentum*, 17.VIII.2014 *Spirin* 7337\*, 7429 (H), Dublikan Nat. Res., *P. ajanensis* + *S. sanguinolentum*,

184 23.VIII.2014 *Spirin* 7905\* (H).

185 *Phaeotremella roseotincta*. **Russia**. Primorie: Khasan Dist., Kedrovaya Pad Nat. Res., deciduous tree (fallen log),

186 15.VIII.1994 *Govorova* (LE 303436\*); Ternei Dist., Sikhote-Alin Nat. Res., *Betula* sp., 12.VIII.2012 *V. Malysheva* (LE

187 303428\*).

188 *Phaeotremella* sp. **USA**. North Carolina: Transylvania Co., Pisgah National Forest, 26.IX.2015 *Infanzon*\* (H).

189

190 Results

191 Specimens examined in this study corresponded to the broad concept of *Phaeotremella foliacea* (Neuhoff 1936, Pippola  
192 and Kotiranta 2008) with fruiting bodies varying in colour from pale brown to totally black, originating from about 50  
193 different localities in Eurasia and North America, and associated either with *Stereum sanguinolentum* (Alb. &  
194 Schwein.) Fr. on conifers (7 species) or with *S. hirsutum* (Willd.) Pers. / *S. rugosum* Pers. on deciduous trees (10  
195 species).

196 Our phylogenetic analyses cover taxa included in Liu et al. (2015a, b) and closely related sequences obtained from  
197 public repositories. The selection of studied sequences is thus based on the delimitation of the genus *Phaeotremella*  
198 provided in Liu et al. (2015b). Additionally, cultures derived from specimens collected by Franz Oberwinkler  
199 (University of Tübingen) were analyzed to serve as a reference to earlier molecular studies. The results of the three-  
200 gene analysis confirmed that all species and specimens analyzed in the present study belong to the genus  
201 *Phaeotremella*. *Phaeotremella fagi* (Middelhoven & Scorzetti) Yurkov & Boekhout, *P. simplex* (H.S. Jackson & G.W.  
202 Martin) Millanes & Wedin and *P. mycetophiloides* (Kobayasi) Millanes & Wedin branched separately from *P. foliacea*  
203 s.l. and *T. fuscusuccinea* (Fig. 1). Specimens corresponding to the broad concept of *P. foliacea* were placed in two large  
204 subclades:

205 1. The first subclade (ML: 100%) encompasses large-spored specimens collected on deciduous wood in Eurasia and  
206 North America and associated with *Stereum rugosum* (nigrescent collections from North Europe – *Miettinen 19896*,  
207 *Spirin 11194* etc.) or other *Stereum* species, mainly with *S. hirsutum* (rather light-coloured, non-blackening specimens  
208 from more southern geographic areas – LE 206897, LE 253852, *Miettinen 15844*; one specimen, *Spirin 10969*, was  
209 detected on the same host with *Peniophora aurantiaca*). This group also contains the reference strain (CBS 6969) of  
210 *Phaeotremella pseudofoliacea* (Liu et al. 2015b) (Fig. 1, 2). There is 2 bp difference in ITS region between nigrescent  
211 and light-coloured morphotypes. However, *tefl* sequences do not allow to separate them, and thus they are considered  
212 conspecific (Fig. 3). The name *Tremella frondosa* is applied to this group, and a new combination, *Phaeotremella*  
213 *frondosa*, is proposed below.

214 2. The second subclade (ML: 91%) includes both angiosperm- and gymnosperm-dwelling specimens, mostly with  
215 smaller basidiospores than those in the first subclade, as well as cultures obtained from specimens collected in  
216 Germany, plus the type strain of *C. skinneri* (Fig.1). This subclade was also resolved in the ITS analysis (ML: 89%) and  
217 additionally accommodated specimens of *T. foliacea* sensu Chen (1998) and *T. neofoliacea* from Asia (Fig. 2). The  
218 analysis of the combined ITS–*tefl* dataset revealed two lineages (ML: 79% and 88%) in this subclade (Fig. 3):

219 A) *P. foliacea* s.str. lineage embraces specimens from coniferous wood from Eurasia (*Miettinen 14610*, *Spirin 11170*  
220 etc.) and North America (*Miettinen 14812.2*). The host species (if documented) is always *S. sanguinolentum*. In both  
221 ITS and ITS–*tefl* phylogenies (Fig. 2, 3), sequences from type collections of *C. skinneri* and *T. neofoliacea* end up in  
222 this subclade, and therefore they are considered taxonomic synonyms of *P. foliacea*.

223 B) *P. fimbriata* lineage encompasses blackening collections from deciduous hosts. Its sequences are placed as a sister  
224 taxon of *P. foliacea* s.str. in the three-gene analysis (Fig. 1). In the combined ITS–*tefl* dataset, two species are detected  
225 in this lineage (Fig. 3). The first species is represented by small-spored European collections from inundated habitats  
226 (*Niemelä 7897*, *Spirin 11114*, *11139*) and it is coined here with an older name *T. fimbriata* (the appropriate combination  
227 in *Phaeotremella* is proposed below). The host species of *T. fimbriata* is *S. rugosum*. The second species covers  
228 nigrescent specimens collected on *Quercus mongolica* in temperate East Asia (LE 303429), and it is introduced below  
229 as *Phaeotremella eugeniae*, sp. nov. This new species differs from the European *P. fimbriata* in having larger and  
230 differently shaped basidiospores (Table 2, Fig. 5). There are seemingly more unnamed species in the *T. fimbriata*  
231 lineage. The first one is represented by the single collection CCJ 1396 (GenBank AF042417). This specimen was  
232 collected in Taiwan on *Abies kawakamii*, and it is a source of the *T. foliacea* description in Chen's monograph of  
233 *Tremella* s. lato (Chen 1998). However, host species and basidiospore measurements given in the description do not fit  
234 to either species known in the *P. fimbriata* complex. The second potential species is represented by the North-American  
235 collection *Infanzon 26.IX.2015* (*Phaeotremella* sp. in Specimens examined section) with nigrescent basidiocarps and  
236 small basidiospores (Table 2). More collections and *tefl* sequences are needed to establish these taxa properly.  
237 *Phaeotremella roseotincta* (LE 303428, 303436) was placed as a sister taxon to *P. frondosa*, together with two  
238 specimens of *P. fuscusuccinea* (*Spirin 7429*, *7905*) from East Asia (Fig. 2). Among taxa only known from rRNA  
239 sequences, two lineages represent potential novel asexual species of the genus *Phaeotremella*. The corresponding  
240 nucleotide sequences in GenBank refer to yeast (originally *Cryptococcus* spp.) cultures GT-159, 338, GT-178 and CBS  
241 11775 (Fig. 2).

#### 242 Taxonomy

243 By 1822, five legitimate species names later synonymized with *T. foliacea* s. lato had been published, i.e. *Tremella*  
244 *verticalis* (Bulliard 1786), *T. undulata* (Hoffmann 1787), *Merulius lichenoides* Schrank (1789), *T. foliacea* and *T.*  
245 *fimbriata* (Persoon 1799). Of them, Fries (1822) accepted and sanctioned only *T. fimbriata* Pers. and *T. foliacea* Pers.,  
246 and introduced a third one, *T. frondosa* Fr. In addition, *T. nigrescens* Fr. was later described as one more member of the  
247 *T. foliacea* group (Fries 1849). Since no original type material survived for any of them and their descriptions were  
248 merely macroscopic, we will discuss their identity based on indications in protologues and Fries's sanctioning work  
249

250 (under Code Art. 9.2, 9.10 – McNeill et al. 2011), as well as on our current knowledge of morphological and ecological  
251 features of these species and available DNA data.

252 1. *T. fimbriata*. Persoon's (1799) original diagnosis gives no specific features which would help to recognize a certain  
253 species. Later, however, Persoon (1801) provided more detailed description, especially concerning ecology of his  
254 species: it was described as growing 'in ramis dejectis ad marginem fluviorum' (on fallen branches by forest streams).  
255 Fries (1822) evidently knew this species because his description of *T. fimbriata* refers to a fungus with blackening, thin,  
256 deeply incised lobes, inhabiting mainly branches of *Alnus* in humid localities. Consequently, we apply this name for a  
257 nigrescent species associated with *S. rugosum* and occurring on deciduous trees in inundated habitats.

258 2. *T. foliacea*. The protologue (Persoon 1799) describes a fungus with folded or undulate, first reddish, then brownish to  
259 dark brown fruit bodies. The host is indicated as rotten logs, mostly those of *Corylus*. The description includes some  
260 uncertain elements; in particular, 'forma pezizoidea' of fructifications is noted. This seemingly implies that Persoon's  
261 description came from mixed source. The subsequent redescription of the species (Persoon 1801) mainly repeats the  
262 protologue but lacks any host indication. As opposed to the description of *T. fimbriata* on the previous page ('color  
263 nigrescens'), Fries's (1822) treatment of *T. foliacea* deals with a species whose basidiocarps show no colour changes  
264 ('color constanter obscure rufus') and which grows on both conifers and deciduous trees. However, as already  
265 mentioned above, there are no hitherto known species in the *T. foliacea* complex having such a wide host range.

266 Therefore, Fries's description of *T. foliacea* most likely contains two elements, and it may be typified with either a  
267 conifer-dwelling or an angiosperm-dwelling specimen. We prefer the first opportunity for the following reasons:

268 A) There are no indications of the basidiocarp's nigrescence in descriptions of *T. foliacea* in Fries's Systema (1822) and  
269 his subsequent works. In particular, while describing *T. nigrescens*, Fries (1849) listed it after *T. foliacea* and directly  
270 distinguished it from the latter based on black basidiocarps, namely as 'praecedenti similis, sed lobi crassiores et color  
271 Exidia glandulosae'. From three North European species of the *T. foliacea* group found on deciduous wood and  
272 accepted by Fries (1849), two species, *T. fimbriata* and *T. nigrescens*, do have blackening basidiocarps. The third one,  
273 *T. frondosa*, was described by Fries (1822) alongside *T. fimbriata* and *T. foliacea*, and it was certainly recognized as a  
274 separate species. Results of phylogenetic analyses performed in the present study suggest *T. frondosa* and *T. nigrescens*  
275 are conspecific, being merely colour varieties of one species (Fig. 1–3). Thus, the angiosperm-dwelling element of *T.*  
276 *foliacea* sensu Fries 1822 has two potentially suitable names, of which *T. frondosa* has a priority. According to the  
277 Code Recommendation 9A4 (McNeill et al. 2011), we can apply the name *T. foliacea* to another element of the  
278 description, i.e. the gymnosperm-dwelling, non-blackening species associated with *S. sanguinolentum*.

279 B) *Tremella foliacea* was mentioned as common on conifer wood in Sweden by Fries himself (1874), Neuhoff (1936)  
280 and Lundell & Nannfeldt (1941). This implies that collections from coniferous hosts seemed to be the main source in  
281 Fries's interpretation of this species.

282 3. *T. frondosa*. In the protologue, Fries (1822) stressed high similarity of this species to *T. foliacea* whose description is  
283 coming next ('sequenti proxima'). Larger ('triplo major') and fading ('luteo-pallescens') basidiocarps are mentioned as  
284 characters differentiating *T. frondosa* from *T. foliacea*. There are different opinions on the identity of *T. frondosa*. Donk  
285 (1966) accepted it as a good species. Neuhoff (1936) and Torkelsen (1968) pointed towards possible synonymy with *T.*  
286 *foliacea*. Roberts (1995, 1999) suggested that *T. frondosa* may be conspecific with *T. aurantia*. We cannot agree with  
287 the latter opinion because *T. aurantia* is a brightly coloured species, not known from North Europe. In our opinion,  
288 Fries's description fits to specimens of the *P. foliacea* complex with large, rather light-colored and fading (non-  
289 blackening) basidiocarps. These specimens are associated mainly with *S. hirsutum*, a common inhabitant of fallen oak  
290 logs which are indicated as a host in the protologue of *T. frondosa*. Fries's reference to Buillard's drawing (selected  
291 below as a lectotype) depicting pale brown (not yellow or orange) species confirms our view on identity of *T. frondosa*.

292 4. *T. nigrescens*. Our concept of this taxon is discussed above. Here we apply this name to specimens of *P. frondosa*  
293 with blackening and thick lobes, associated with *S. rugosum* in North Europe.

294 Because original type material did not survive for any of the aforementioned species and because species descriptions  
295 are merely macroscopic, lectotypes (iconotypes) for *T. fimbriata*, *T. foliacea* and *T. frondosa* are selected below in  
296 accordance with Code Art. 9.2, 9.12 and Recommendation 9A2 (McNeill et al. 2011), and epitypes are indicated to  
297 support our choices. Additionally, a neotype for *T. nigrescens* is designated. Additionally, living cultures from epitype  
298 and neotype material were obtained and deposited to serve a reference for future studies.

#### 300 Species descriptions

301 **Phaeotremella eugeniae** V. Malysheva, sp. nov. – Figs. 4e–f, 5d.

302 Holotype. Russia. Primorie: Ternei Dist., Sikhote-Alin Nature Reserve, *Quercus mongolica*, 7.VIII.2012 Malysheva  
303 (LE 303429).

304 MB 821825

305 Etymology: named in honour of Dr. Eugenia M. Bulakh, an indefatigable researcher of the Russian Far East.

306 Basidiocarps foliaceous, 1.5–3 cm high, 1–5 cm in diam., blackish brown with rusty shade in fresh condition,

307 completely black when dried. Lobes arising directly from the point of attachment, entire, rotund, strongly undulate, up  
308 to 1–1.5 cm wide, 0.2–0.6 mm thick. Hyphae clamped, at the basal part of basidiocarps distinctly thick-walled, 3–5 µm  
309 in diam., brownish, bearing strongly inflated, globose or bladder-shaped segments 5–10 µm in diam., subhyemial

310 hyphae slightly thick-walled, anastomosing, 2–5 µm in diam., hyaline to brownish, occasionally covered by brownish-  
311 black amorphous matter. Basidia four-celled, varying in shape (ovoid, subglobose, pyriform), 10–19 × 7–10 µm,  
312 longitudinally or obliquely septate, with brownish content. Basidiospores ovoid, broadly ellipsoid or subglobose,  
313 hyaline, (6.2–) 6.4–8.5 (–8.9) × (4.7–) 4.9–6.7 (–7.0) µm (n = 80/3), L = 7.63, W = 5.84, Q = 1.31.

314 Remarks. *Phaeotremella eugeniae* differs from the closely related species *P. fimbriata* in having thinner lobes of  
315 basidiocarps and predominantly ovoid or ellipsoid, larger basidiospores (Table 2). Moreover, these species have  
316 different geographical distribution (East Asia versus Europe) and host preferences (Fagaceae versus Betulaceae). The  
317 fungal host species of *P. eugeniae* is still unknown.

318  
319 ***Phaeotremella fimbriata*** (Pers.) Spirin & V. Malysheva, comb. nov. – Figs. 4d, 5a.

320 ≡ *Tremella fimbriata* Pers., *Observationes Mycologicae* 2: 97, 1799.

321 Lectotype. Plate 272 (*Tremella verticalis*) in Bulliard's *Herbier de la France* 6, 1786 (cited as 'Bull. Champ. t. 272.  
322 optime' by Fries 1822: 212) (selected here).

323 Epitype. Norway. Oppland: Lunner, Rinilhaugen, *Alnus incana* + *Stereum rugosum*, 17.IX.2016 Spirin 11139 (O)  
324 (selected here). Ex-epitype culture DSM 105659 (*Spirin 11139.c*) is preserved in a metabolically inactive state in the  
325 German Collection of Microorganisms and Cell Cultures (Braunschweig, Germany).

326 MB 821826

327 Basidiocarps foliaceous, 1.5–2.5 cm high, 1–4 cm in diam., first brownish black, quickly turning completely black.  
328 Lobes arising directly from the point of attachment, first entire, rotund, then distinctly undulate, up to 1.5 cm wide, 0.5–  
329 0.8 mm thick. Hyphae clamped, at the basal part of basidiocarps distinctly thick-walled, 4–7 µm in diam., brownish,  
330 bearing strongly inflated, globose or bladder-shaped segments 7–15 µm in diam., subhymenial hyphae slightly thick-  
331 walled, anastomosing, 2–5 µm in diam., hyaline to brownish, occasionally covered by brownish-black or violet-black  
332 amorphous matter. Basidia four-celled, ovoid to subglobose, 9–14 × 9–12 µm, slightly thick-walled, with hyaline or  
333 brownish content. Swollen cells often present on basal lobes, broadly ellipsoid to globose, slightly to distinctly thick-  
334 walled, up to 18 µm in diam., producing ellipsoid or subglobose conidial cells, 4–8 × 3–6 µm. Basidiospores broadly  
335 ellipsoid to subglobose, hyaline to brownish or blackish, (5.2–) 5.3–8.1 (–8.2) × (4.3–) 4.5–6.6 (–7.2) µm (n = 150/5), L  
336 = 6.60, W = 5.57, Q = 1.19.

337 Remarks. *Phaeotremella fimbriata* has the smallest basidiospores in the whole species complex (Table 2), and it  
338 produces rather small-sized basidiocarps turning completely black when aged or dried. However, nigrescent specimens  
339 of *P. frondosa* occurring mainly in inundated habitats can be mistaken for *P. fimbriata*. The latter species produces on  
340 average larger basidiospores.

341 Fries (1822) listed *Tremella undulata* Hoffm. among synonyms of *T. fimbriata*. The original description and illustration  
342 of *T. undulata* (Hoffmann 1787) seemingly agree with our interpretation of *T. fimbriata*. Nevertheless, we designated  
343 Bulliard's illustration as a lectotype of *T. fimbriata* because it reflects Fries' concept of this species better (marked by  
344 him as 'optime'). Identity of another possible synonym of *P. fimbriata*, *T. tinctoria* Pers., must be re-established after  
345 studying authentic material in Leiden. In addition, Donk (1966) restored *T. intumescens* Smith and referred it to the  
346 black-coloured *Tremella* species described by Bourdot and Galzin (1928) as *T. nigrescens*. Wojewoda (1981) accepted  
347 Donk's proposal. However, it is impossible to prove that the latter authors dealt with *T. intumescens* sensu orig. Roberts  
348 (1999) considered *T. intumescens* a *nomen dubium*, and we agree with his viewpoint. The protologue of *Tremella*  
349 *griseobrunnea* (Chen 1998), especially small basidiospores, points towards *P. fimbriata*, although its basidiocarps were  
350 characterized as 'grayish brown to brownish black'. This may also imply a small-spored specimen of *P. frondosa*.

351  
352 ***Phaeotremella foliacea*** (Pers.) Wedin, J.C. Zamora & Millanes, *Mycosphere* 7: 296, 2016. – Figs. 4a–b, 5b.

353 ≡ *Tremella foliacea* Pers., *Observationes Mycologicae* 2: 98, 1799.

354 Lectotype. Plate 406, figures A, a (*Tremella mesenteriformis*) in Bulliard's *Herbier de la France* 9, 1789 (cited by  
355 Fries 1822: 213) (selected here).

356 Epitype. Sweden. Jämtland: Berg, Viksjöbacken, *Picea abies* + *Stereum sanguinolentum*, 18.VIII.2011 Miettinen 14610  
357 (H 7005546) (selected here). Ex-epitype culture DSM 105660 (*Miettinen 14610.b*) is preserved in a metabolically  
358 inactive state in the German Collection of Microorganisms and Cell Cultures (Braunschweig, Germany).

359 = *Tremella neofoliacea* Chee J. Chen, *Bibliotheca Mycologica* 174: 135, 1998.

360 = *Cryptococcus skinneri* Phaff & Carmo Souza, *Antonie van Leeuwenhoek* 28: 205, 1962.

361 Basidiocarps foliaceous, 1–3 cm high, 1–5 cm in diam., brown, darkening (but not blackening) in herbarium specimens.  
362 Lobes arising for the common base, entire, rotund, even to undulate, up to 1.5 cm wide, 0.5–1 mm thick. Hyphae  
363 clamped, at the basal part of basidiocarps slightly to distinctly thick-walled, 2–7 µm in diam., brownish, bearing  
364 strongly inflated, globose or bladder-shaped segments 8–16 µm in diam., subhymenial hyphae thin- to slightly thick-  
365 walled, anastomosing, 2–4 µm in diam., hyaline to brownish. Basidia four-celled, ovoid to subglobose, 12–18 × 10–14  
366 µm, slightly thick-walled, with hyaline or brownish content. Swollen cells often present on basal lobes, broadly  
367 ellipsoid to globose, slightly to very thick-walled, up to 25 µm in diam., producing ellipsoid or subglobose conidial  
368 cells, 4–10 × 3–7 µm. Basidiospores broadly ellipsoid to subglobose, hyaline to brownish, (5.2–) 5.3–9.1 (–10.2) ×  
369 (4.6–) 4.7–8.5 (–9.5) µm (n = 280/9), L = 7.32, W = 6.36, Q = 1.16.

370 Remarks. As understood here, *P. foliacea* is recognizable primarily due to its growth on conifers where it often occurs  
371 together with its host species *S. sanguinolentum*. Basidiospores of *P. foliacea* are on average larger than in *P. fimbriata*  
372 and smaller than in *P. frondosa* (Table 2). However, their variation range in both *P. foliacea* and *P. frondosa* is wide,  
373 and therefore the basidiospore size only is not a stable character to distinguish these two species.  
374 Neuhoff (1936) adopted *Tremella succinea* Pers. to encompass conifer-dwelling collections of *T. foliacea* s.l. from  
375 Sweden. However, as Donk (1966) correctly pointed out, Persoon's description contained no host indication and,  
376 therefore, the identity of *T. succinea* is vague.

377  
378 **Phaeotremella frondosa** (Fr.) Spirin & V. Malysheva, comb. nov. – Figs. 4c, 5c.

379 ≡ *Tremella frondosa* Fr., Systema Mycologicum 2: 212, 1822.

380 Lectotype. Plate 499, figure T ('Tremelles') in Bulliard's Herbarium de la France 11, 1791 (cited by Fries 1822: 212)  
381 (selected here).

382 Epitype. Russia. Leningrad Reg.: Vsevolozhsk Dist., Vaskelovo, fallen log, with *Stereum hirsutum*, 16.IX.1993

383 Zmitrovich (LE 206897) (selected here).

384 = *Merulius lichenoides* Schrank, Baiersche Flora 2: 575, 1789.

385 = *Tremella nigrescens* Fr., Summa Vegetabilium Scandinaviae 2: 341, 1849.

386 Neotype. Norway. Telemark: Nome, Mørkvasslia, *Alnus incana* + *Stereum rugosum*, 25.X.2016 Spirin 11202 (O)

387 (selected here). Ex-neotype culture DSM 105661 (*Spirin 11202.c*) is preserved in a metabolically inactive state in the  
388 German Collection of Microorganisms and Cell Cultures (Braunschweig, Germany).

389 = *Phaeotremella pseudofoliacea* Rea, Trans. British Mycol. Soc. 3: 377, 1912.

390 Lectotype. United Kingdom. Somerset: Staple Park, 20.IX.1911 Rea (K(M) 56574, studied) (selected by Roberts 1999:  
391 130).

392 MB 821827

393 Basidiocarps foliaceous, 1–5 cm high, 1–7 cm in diam., often fusing together, ochraceous-brown to dark brown,  
394 darkening (sometimes blackening) in herbarium specimens. Lobes arising for the common base, entire, rotund, even to  
395 undulate, up to 2 cm wide, 0.5–1 mm thick. Hyphae clamped, at the basal part of basidiocarps slightly to distinctly  
396 thick-walled, 2–10 µm in diam., brownish, bearing strongly inflated, globose or bladder-shaped segments 8–18 µm in  
397 diam., subhymenial hyphae thin- to slightly thick-walled, anastomosing, 2–8 µm in diam., hyaline to brownish,  
398 occasionally covered by brownish amorphous matter. Basidia four-celled, ovoid to subglobose, 13–18 × 12–16 µm,  
399 slightly thick-walled, with hyaline or brownish content. Swollen cells often present on basal lobes, broadly ellipsoid to  
400 globose, slightly to very thick-walled, up to 25 µm in diam., producing ellipsoid or subglobose conidial cells, 4–10 × 4–  
401 7 µm. Basidiospores broadly ellipsoid to subglobose, hyaline to brownish, (6.1–) 6.2–10.2 (–10.8) × (5.0–) 5.1–8.7 (–  
402 9.0) µm (n = 240/8), L = 8.12, W = 6.70, Q = 1.22.

403 Remarks. In most cases, *P. frondosa* produces large, often rather light-colored basidiocarps on deciduous trees.

404 However, its blackening, small-sized basidiocarps associated with *S. rugosum* can be mixed up with *P. fimbriata*. In this  
405 case, microscopic study is necessary. *Phaeotremella frondosa* has been detected throughout temperate and boreal zones  
406 of Eurasia. In North America, the verified records known so far come only from British Columbia (Bandoni's  
407 collections). Coker (1920) reported *T. frondosa* from North Carolina, and his description more or less corresponds with  
408 our concept of the species. However, this problem should be solved by sequencing newly collected material from that  
409 area.

410 Roberts (1999) stated that the original material of *P. pseudofoliacea* is identical to *T. foliacea* sensu auct. from  
411 deciduous hosts (= *P. frondosa* in the current sense), and we accept his opinion. Chen (1998) described a new species,  
412 *Tremella vasifera*, based on a single collection from Germany. In the protologue, the presence of swollen cells and  
413 vessel-like conidiophores was stressed as a main diagnostic feature of *T. vasifera*. However, these two kinds of cells  
414 occur also in *P. fimbriata*, *P. foliacea* s.str. and *P. frondosa*, and therefore they cannot be used for separating species in  
415 this complex. The description of *P. vasifera* strongly suggests it is conspecific with *P. frondosa*. The original  
416 description of *Merulius lichenoides* (Schrank 1789) points towards *P. frondosa*, too.

417  
418 **Phaeotremella fuscusuccinea** (Chee J. Chen) Spirin & Yurkov, comb. nov.

419 ≡ *Tremella fuscusuccinea* Chee J. Chen, Bibliotheca Mycologica 174: 124, 1998.

420 MB 821828

421 This species was described and illustrated based on one collection from the highland forest in Taiwan (Chen 1998).

422 Three specimens studied in the present work have been collected in Russian Far East. They agree well with the  
423 protologue, and two of them were included in our phylogenetic analyses.

424 *Phaeotremella fuscusuccinea* inhabits fallen spruce logs and is associated with *S. sanguinolentum*. Thus it shares similar  
425 ecology with *P. foliacea*. Macroscopically, these species are rather different, however, because terminal lobes of *P.*

426 *fuscusuccinea* are pinkish-ochraceous and normally much paler than the dark-colored (vinaceous-brown) basal part of  
427 the basidiocarps. There are no so striking colour differences in basidiocarps of *P. foliacea*. Moreover, basidiospores of

428 *P. fuscusuccinea* are more clearly ellipsoid, with higher Q values than in *P. foliacea* (Table 2).

429

430 **Phaeotremella roseotincta** (Lloyd) V. Malysheva, comb. nov.  
431 ≡ *Tremella roseotincta* Lloyd, Mycol. Writings 7 (70): 1229, 1923.  
432 MB 821829  
433 A modern description and illustrations of *P. roseotincta* are given in Malysheva et al. (2015). This species is  
434 morphologically very similar to *P. fuscusuccinea* and differs primarily by its growth on deciduous trees. Ecological  
435 preferences of *P. roseotincta* deserve further study as there is still no information about its fungal host species.  
436  
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444  
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534   Legends  
535   Fig. 1. Phylogenetic analysis of the genus *Phaeotremella* inferred from the ML analysis of ITS, LSU and *tef1* nucleotide  
536   sequences. The numbers given at the branches are frequencies (>50%) with which a given branch appeared in 1000  
537   bootstrap replications. The scale bar indicates the numbers of expected substitutions accumulated per site. The tree is  
538   rooted with *Gelidatrema spencermartinsiae*. Accession numbers of nucleotide sequences are provided in Table 1.  
539   Fig. 2. Phylogenetic analysis of the genus *Phaeotremella* inferred from the ML analysis of ITS sequences. Tree  
540   topology was constrained with the well-supported (>80%) bipartitions of the topology of the tree presented in Figure 1.  
541   The numbers given at the branches are frequencies (>50%) with which a given branch appeared in 1000 bootstrap  
542   replications. The scale bar indicates the numbers of expected substitutions accumulated per site. The tree is rooted with  
543   *Gelidatrema spencermartinsiae*. Accession numbers of nucleotide sequences are provided in Table 1.  
544   Fig. 3. Phylogenetic analysis of the genus *Phaeotremella* inferred from the ML analysis of ITS and *tef1* nucleotide  
545   sequences. The numbers given at the branches are frequencies (>50%) with which a given branch appeared in 1000  
546   bootstrap replications. The scale bar indicates the numbers of expected substitutions accumulated per site. The tree is  
547   rooted with *Gelidatrema spencermartinsiae*. Accession numbers of nucleotide sequences are provided in Table 1.  
548   Fig. 4. Basidiocarps of *Phaeotremella* spp.: a – *P. foliacea* (LE 303431); b – *P. foliacea* (*Spirin 11170*); c – *P. frondosa*  
549   (LE 253852); d – *P. fimbriata* (*Spirin 11114*); e – *P. eugeniae* (LE 262894); f – *P. eugeniae* (LE 303429).  
550   Fig. 5. Basidiospores of *Phaeotremella* spp.: a – *P. fimbriata* (*Spirin 11139*); b – *P. foliacea* (*Miettinen 14610*); c – *P.*  
551   *frondosa* (*Spirin 11202*); d – *P. eugeniae* (LE 303429). Scale bar = 5 µm.