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

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Abstract

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

Key words: heterobasidiomycetes, mycoparasite, phylogeny, typification

Introduction

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

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

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

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

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

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

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

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

Material and methods

Specimens from herbaria H, O, LE, K were studied. Herbarium acronyms are given according to Thiers (2017). Morphological study follows Miettinen et al. (2012). The following abbreviations are used in morphological descriptions and tables: L – mean spore length, W – mean spore width, Q' – length/width ratio, Q – mean length/width ratio, n – number of measurements per specimens.

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

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

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

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

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

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

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

Specimens examined (sequenced specimens are marked by asterisk)

Phaeotremella eugeniae. **Russia.** Primorie: Khanka Dist., Novokachalinsk, *Quercus mongolica*, 27.VII.1985 *Lelei* (LE 303434*); Ternei Dist., Sikhote-Alin Nature Reserve, *Q. mongolica*, 23.VIII.2011 *Malysheva* (LE 262894*), 7.VIII.2012 *Malysheva* (LE 303429* – holotype).

Phaeotremella fimbriata. **Finland.** Etelä-Savo: Valkeala, Repovesi, *Alnus incana*, 16.IX.2004 *Niemelä 7897** (H). **Norway.** Akershus: Bærum, Kjaglidalen, *Corylus avellana + Stereum rugosum*, 16.IX.2016 *Spirin 11114** (O), Dælivannet, 22.III.1989 *Torkelsen 2/89* (O F149407), Ullensaker, *A. incana*, 25.V.1979 *Torkelsen 141/79* (O F149405). Østfold: Skiptvet, Svartedal, *A. incana*, 7.IX.1997 *Løfall* (O F63256). Oppland: Lunner, Rinilhaugen, *A. incana + S. rugosum*, 17.IX.2016 *Spirin 11139** (O).

Phaeotremella foliacea. **Finland.** Pohjois-Häme: Saarijärvi, *Picea abies*, 14.VIII.2008 *Miettinen 13267** (H), *P. sylvestris* (?), 14.VIII.2008 *Miettinen 13270, 13271, 13273.1, 13274.1* (H), *P. sylvestris* (?) + *S. sanguinolentum*, 16.VIII.2008 *Miettinen 13291.1* (H). Kainuu: Hyrynsalmi, Paljakka, *P. abies + S. sanguinolentum*, 24.IX.2010 *Miettinen 14170* (H). **Germany.** Baden-Würtemberg: Schwarzwald, *Picea* sp., 25.X.1987 *Laber* (O). **Norway.** Vestfold: Re, Reggestad, *P. abies*, 27.VII.1950 *Stordal 4414* (O F149518). Vest-Agder: Mandal, Furulunden, *P. sylvestris + S. sanguinlentum + Naematelia encephala*, 19.IX.2006 *Fonneland 06-12* (O F282970). Akershus: Asker, Bak Skaugum, *P. abies*, 30.IX.1966 *Lauritzen* (O F149419); Hurdal, Brustadkolen, *P. abies*, 24.V.1979 *Torkelsen 118/79* (O F149406); Oppegård, Hvitebjørn, *P. abies*, 20.XI.1950 *Eftestøl* (O F149397). Oslo: Oslo, Rektorhaugen, *P. abies*, 30.VIII.1953 *Bratsberg* (O F149467), Sognsvann, *P. abies + S. sanguinolentum*, 9.IV.2005 *Hanssen* (O F67636). Buskerud: Nes, Hallingdal, *P. abies*, 3.X.1965 *Torkelsen* (O F149513); Ringerike, Veienmoen, *P. abies*, 23.VIII.1953 *Eckblad* (O F149505). Rogaland: Sandnes, Espeland, *P. abies*, 21.X.1992 *Torkelsen 272/92* (O F149553). Østfold: Fredrikstad, Heieren, *P. abies*, 17.IV.1931 *Jørstad* (O F149383). Telemark: Bø, Oredalen, *P. sylvestris*, 3.IX.1971 *Hovda* (O F149532). Oppland: Sør-Fron, Hundorp, *P. abies*, 14.V.1989 *Torkelsen 93/89* (O F149500). Sør-Trøndelag: Meldal, *P. abies*, 28–29.IX.1991 *Høiland 8-57, 32-84* (O F149977, 149958). Hedmark: Grue, Ulvika vid Skasen, *P. sylvestris*, 12.X.1974 *Ryvarden 13340* (O F149496); Åmot, Rena, *P. abies*, 5.IX.1992 *Ryvarden 32035* (O F104117). Nordland: Hemnes, Kangsen, conifer, 27.VIII.1969 *Ryvarden* (O F149605); Rana, *P. abies*, 11.IX.1976 *Torkelsen 738/76* (O F149614). **Russia.** Leningrad Reg.: Boksitogorsk Dist., Vozhani, *P. abies + S. sanguinlentum + N. encephala*, 2.X.2016 *Spirin 11170** (H). Khabarovsk Reg.: Solnechnyi Dist., Igdomi, *Pinus pumila*, 2.IX.2016 *Spirin 10814** (H), *Picea ajanensis + S. sanguinolentum*, 3.IX.2016 *Spirin 10865** (H); Verkhnebureinskii Dist., Dublikan, *P. ajanensis + S. sanguinolentum*, 21.VIII.2014 *Spirin 7721** (H). Primorie: Ternei Dist., Sikhote-Alin Nature Reserve, *Abies nephrolepis*, 23.VIII.2012 *Malysheva* (LE 303430*), *Pinus koraiensis*, 23.VIII.2011 *Malysheva* (LE 303431*). **Sweden.** Jämtland: Berg, Viksjöbacken, *P. abies + S. sanguinolentum*, 18.VIII.2011 *Miettinen 14610** (H). **USA.** Massachusetts: Worcester Co., Holden, *Pinus strobus + S. sanguinolentum*, 26.IX.2011 *Miettinen 14812.2** (H). New York: Essex Co., Harris Lake, *Abies* sp. + *S. sanguinolentum*, 23.IX.2013 *Miettinen 17173* (H).

Phaeotremella frondosa. **Czech Republic.** South Moravia: Brno, Tišnov, fallen log + *Stereum gausapatum*, VIII.1942 *Šmarda* (O), Řečkovický les, deciduous tree, 24.VIII.1962 *Valkoun* (O). **Finland.** Uusimaa: Kirkkonummi, Sundsberg, *Betula pubescens + Stereum hirsutum*, 20.X.2012 *Miettinen 15774, 15844** (H); Helsinki, Pasila, *C. avellana*, 11.IV.2008 *Miettinen 12406** (H); Porvoo: Sannainen, *Alnus glutinosa*, 9.IX.1999 *Salo 5889* (H); Sipoo, Gillerberget, *Salix caprea (?) + S. rugosum*, 20.XII.2015 *Miettinen 19896** (H), Hindsby, *A. incana + Stereum subtomentosum*, 13.X.1984 *Saarenoksa 46984* (H). Etelä-Häme: Hämeenlinna, Lammi, *Padus avium*, 20.XII.2015 *Miettinen 19406** (H). Pohjois-Häme: Jyväskylä, Vuoritsalo, *S. aucuparia + S. rugosum*, 13.VII.2011 *Miettinen 14498* (H). **Norway.** Akershus: Asker, Syverstadvannet, 23.IV.1972, *Alnus* sp., 23.IV.1972 *Torkelsen 13/72* (O F149411). Oslo: Oslo, Holmlia, *Betula* sp., X.1980 *Wischmann* (O F149446). Telemark: Nome, Mørkvasslia, *A. incana + S. rugosum*, 25.X.2016 *Spirin 11194*, 11202** (O). Østfold: Fredrikstad, Femdal, *Sorbus aucuparia*, 8.XII.1979 *Kristiansen 30* (O F149415); Sarpsborg, Bjørnland, *A. incana*, 18.IV.2003 *Løfall* (O F66427). **Russia.** Leningrad Reg.: Podporozhie Dist., Vachozero, *Populus tremula + S. hirsutum*, 15.X.2017 *Spirin 11747* (H); Vsevolozhsk Dist., Vaskelovo, fallen log, with *S. hirsutum*, 16.IX.1993 *Zmitrovich* (LE 206897*). St. Petersburg: Muzhestva sq., *Tilia cordata*, 22.XI.2016 *Spirin 11204** (H). Karachayevo-Circassian Republic: Karachaevsk Dist, Teberda Nat. Res., *Betula* sp., 12.VIII.2009 *V. Malysheva* (LE 253852*). Khabarovsk Reg.: Solnechnyi Dist., Igdomi, *Alnus (Duschekia) fruticosa + Peniophora aurantiaca*, 4.IX.2016 *Spirin 10969** (H). **United Kingdom.** England: Somerset, Staple Park, 20.IX.1911 *Rea* (lectotype of *P. pseudofoliacea*, see below).

Phaeotremella fuscosuccinea. **Russia.** Khabarovsk Reg.: Verkhnebureinsky Dist., Kyvyty, *P. ajanensis + S. sanguinolentum*, 17.VIII.2014 *Spirin 7337*, 7429* (H), Dublikan Nat. Res., *P. ajanensis + S. sanguinolentum*, 23.VIII.2014 *Spirin 7905** (H).

Phaeotremella roseotincta. **Russia.** Primorie: Khasan Dist., Kedrovaya Pad Nat. Res., deciduous tree (fallen log), 15.VIII.1994 *Govorova* (LE 303436*); Ternei Dist., Sikhote-Alin Nat. Res., *Betula* sp., 12.VIII.2012 *V. Malysheva* (LE 303428*).

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

Results

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

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

1. The first subclade (ML: 100%) encompasses large-spored specimens collected on deciduous wood in Eurasia and North America and associated with *Stereum rugosum* (nigrescent collections from North Europe – *Miettinen 19896*, *Spirin 11194* etc.) or other *Stereum* species, mainly with *S. hirsutum* (rather light-coloured, non-blackening specimens from more southern geographic areas – LE 206897, LE 253852, *Miettinen 15844*; one specimen, *Spirin 10969*, was detected on the same host with *Peniophora aurantiaca*). This group also contains the reference strain (CBS 6969) of *Phaeotremella pseudofoliacea* (Liu et al. 2015b) (Fig. 1, 2). There is 2 bp difference in ITS region between nigrescent and light-coloured morphotypes. However, *tef1* sequences do not allow to separate them, and thus they are considered conspecific (Fig. 3). The name *Tremella frondosa* is applied to this group, and a new combination, *Phaeotremella frondosa*, is proposed below.
2. The second subclade (ML: 91%) includes both angiosperm- and gymnosperm-dwelling specimens, mostly with smaller basidiospores than those in the first subclade, as well as cultures obtained from specimens collected in Germany, plus the type strain of *C. skinneri* (Fig.1). This subclade was also resolved in the ITS analysis (ML: 89%) and additionally accommodated specimens of *T. foliacea* sensu Chen (1998) and *T. neofoliacea* from Asia (Fig. 2). The analysis of the combined ITS–*tef1* dataset revealed two lineages (ML: 79% and 88%) in this subclade (Fig. 3):

A) *P. foliacea* s.str. lineage embraces specimens from coniferous wood from Eurasia (*Miettinen 14610*, *Spirin 11170* etc.) and North America (*Miettinen 14812.2*). The host species (if documented) is always *S. sanguinolentum*. In both ITS and ITS–*tef1* phylogenies (Fig. 2, 3), sequences from type collections of *C. skinneri* and *T. neofoliacea* end up in this subclade, and therefore they are considered taxonomic synonyms of *P. foliacea*.

B) *P. fimbriata* lineage encompasses blackening collections from deciduous hosts. Its sequences are placed as a sister taxon of *P. foliacea* s.str. in the three-gene analysis (Fig. 1). In the combined ITS–*tef1* dataset, two species are detected in this lineage (Fig. 3). The first species is represented by small-spored European collections from inundated habitats (*Niemelä 7897*, *Spirin 11114*, *11139*) and it is coined here with an older name *T. fimbriata* (the appropriate combination in *Phaeotremella* is proposed below). The host species of *T. fimbriata* is *S. rugosum*. The second species covers nigrescent specimens collected on *Quercus mongolica* in temperate East Asia (LE 303429), and it is introduced below as *Phaeotremella eugeniae*, sp. nov. This new species differs from the European *P. fimbriata* in having larger and differently shaped basidiospores (Table 2, Fig. 5). There are seemingly more unnamed species in the *T. fimbriata* lineage. The first one is represented by the single collection CCJ 1396 (GenBank AF042417). This specimen was collected in Taiwan on *Abies kawakamii*, and it is a source of the *T. foliacea* description in Chen's monograph of *Tremella* s. lato (Chen 1998). However, host species and basidiospore measurements given in the description do not fit to either species known in the *P. fimbriata* complex. The second potential species is represented by the North-American collection *Infanzon* 26.IX.2015 (*Phaeotremella* sp. in Specimens examined section) with nigrescent basidiocarps and small basidiospores (Table 2). More collections and *tef1* sequences are needed to establish these taxa properly.

Phaeotremella roseotincta (LE 303428, 303436) was placed as a sister taxon to *P. frondosa*, together with two specimens of *P. fuscosuccinea* (*Spirin 7429*, *7905*) from East Asia (Fig. 2). Among taxa only known from rRNA sequences, two lineages represent potential novel asexual species of the genus *Phaeotremella*. The corresponding nucleotide sequences in GenBank refer to yeast (originally *Crytococcus* spp.) cultures GT-159, 338, GT-178 and CBS 11775 (Fig. 2).

Taxonomy

By 1822, five legitimate species names later synonymized with *T. foliacea* s. lato had been published, i.e. *Tremella verticalis* (Bulliard 1786), *T. undulata* (Hoffmann 1787), *Merulius lichenoides* Schrank (1789), *T. foliacea* and *T. fimbriata* (Persoon 1799). Of them, Fries (1822) accepted and sanctioned only *T. fimbriata* Pers. and *T. foliacea* Pers., and introduced a third one, *T. frondosa* Fr. In addition, *T. nigrescens* Fr. was later described as one more member of the *T. foliacea* group (Fries 1849). Since no original type material survived for any of them and their descriptions were merely macroscopic, we will discuss their identity based on indications in protologues and Fries's sanctioning work (under Code Art. 9.2, 9.10 – McNeill et al. 2011), as well as on our current knowledge of morphological and ecological features of these species and available DNA data.

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

2. *T. foliacea*. The protologue (Persoon 1799) describes a fungus with folded or undulate, first reddish, then brownish to dark brown fruit bodies. The host is indicated as rotten logs, mostly those of *Corylus*. The description includes some uncertain elements; in particular, 'forma pezizoidea' of fructifications is noted. This seemingly implies that Persoon's description came from mixed source. The subsequent redescription of the species (Persoon 1801) mainly repeats the protologue but lacks any host indication. As opposed to the description of *T. fimbriata* on the previous page ('color nigrescens'), Fries's (1822) treatment of *T. foliacea* deals with a species whose basidiocarps show no colour changes ('color constanter obscure rufus') and which grows on both conifers and deciduous trees. However, as already mentioned above, there are no hitherto known species in the *T. foliacea* complex having such a wide host range. Therefore, Fries's description of *T. foliacea* most likely contains two elements, and it may be typified with either a conifer-dwelling or an angiosperm-dwelling specimen. We prefer the first opportunity for the following reasons:

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

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

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

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

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

Species descriptions

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

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

MB 821825

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

Basidiocarps foliaceous, 1.5–3 cm high, 1–5 cm in diam., blackish brown with rusty shade in fresh condition, completely black when dried. Lobes arising directly from the point of attachment, entire, rotund, strongly undulate, up 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 in diam., brownish, bearing strongly inflated, globose or bladder-shaped segments 5–10 μm in diam., subhymenial hyphae slightly thick-walled, anastomosing, 2–5 μm in diam., hyaline to brownish, occasionally covered by brownish-black amorphous matter. Basidia four-celled, varying in shape (ovoid, subglobose, pyriform), 10–19 × 7–10 μm, longitudinally or obliquely septate, with brownish content. Basidiospores ovoid, broadly ellipsoid or subglobose, 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.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Remarks. As understood here, *P. foliacea* is recognizable primarily due to its growth on conifers where it often occurs together with its host species *S. sanguinolentum*. Basidiospores of *P. foliacea* are on average larger than in *P. fimbriata* and smaller than in *P. frondosa* (Table 2). However, their variation range in both *P. foliacea* and *P. frondosa* is wide, and therefore the basidiospore size only is not a stable character to distinguish these two species.

Neuhoff (1936) adopted *Tremella succinea* Pers. to encompass conifer-dwelling collections of *T. foliacea* s.l. from Sweden. However, as Donk (1966) correctly pointed out, Persoon's description contained no host indication and, therefore, the identity of *T. succinea* is vague.

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

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

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

Epitype. Russia. Leningrad Reg.: Vsevolozhsk Dist., Vaskelovo, fallen log, with *Stereum hirsutum*, 16.IX.1993 *Zmitrovich* (LE 206897) (selected here).

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

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

Neotype. Norway. Telemark: Nome, Mørkvasslia, *Alnus incana + Stereum rugosum*, 25.X.2016 *Spirin 11202* (O) (selected here). Ex-neotype culture DSM 105661 (*Spirin 11202.c*) is preserved in a metabolically inactive state in the German Collection of Microorganisms and Cell Cultures (Braunschweig, Germany).

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

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

MB 821827

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

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

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

Phaeotremella fuscosuccinea (Chee J. Chen) Spirin & Yurkov, comb. nov.

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

MB 821828

This species was described and illustrated based on one collection from the highland forest in Taiwan (Chen 1998). Three specimens studied in the present work have been collected in Russian Far East. They agree well with the protologue, and two of them were included in our phylogenetic analyses.

Phaeotremella fuscosuccinea inhabits fallen spruce logs and is associated with *S. sanguinolentum*. Thus it shares similar ecology with *P. foliacea*. Macroscopically, these species are rather different, however, because terminal lobes of *P. fuscosuccinea* are pinkish-ochraceous and normally much paler than the dark-colored (vinaceous-brown) basal part of the basidiocarps. There are no so striking colour differences in basidiocarps of *P. foliacea*. Moreover, basidiospores of *P. fuscosuccinea* are more clearly ellipsoid, with higher Q values than in *P. foliacea* (Table 2).

Phaeotremella roseotincta (Lloyd) V. Malysheva, comb. nov.
≡ *Tremella roseotincta* Lloyd, Mycol. Writings 7 (70): 1229, 1923.
MB 821829

A modern description and illustrations of *P. roseotincta* are given in Malysheva et al. (2015). This species is morphologically very similar to *P. fuscosuccinea* and differs primarily by its growth on deciduous trees. Ecological preferences of *P. roseotincta* deserve further study as there is still no information about its fungal host species.

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Legends

Fig. 1. Phylogenetic analysis of the genus *Phaeotremella* inferred from the ML analysis of ITS, LSU and *tef1* nucleotide sequences. The numbers given at the branches are frequencies (>50%) with which a given branch appeared in 1000 bootstrap replications. The scale bar indicates the numbers of expected substitutions accumulated per site. The tree is rooted with *Gelidatrema spencermartinsiae*. Accession numbers of nucleotide sequences are provided in Table 1.

Fig. 2. Phylogenetic analysis of the genus *Phaeotremella* inferred from the ML analysis of ITS sequences. Tree topology was constrained with the well-supported (>80%) bipartitions of the topology of the tree presented in Figure 1. The numbers given at the branches are frequencies (>50%) with which a given branch appeared in 1000 bootstrap replications. The scale bar indicates the numbers of expected substitutions accumulated per site. The tree is rooted with *Gelidatrema spencermartinsiae*. Accession numbers of nucleotide sequences are provided in Table 1.

Fig. 3. Phylogenetic analysis of the genus *Phaeotremella* inferred from the ML analysis of ITS and *tef1* nucleotide sequences. The numbers given at the branches are frequencies (>50%) with which a given branch appeared in 1000 bootstrap replications. The scale bar indicates the numbers of expected substitutions accumulated per site. The tree is rooted with *Gelidatrema spencermartinsiae*. Accession numbers of nucleotide sequences are provided in Table 1.

Fig. 4. Basidiocarps of *Phaeotremella* spp.: a – *P. foliacea* (LE 303431); b – *P. foliacea* (*Spirin 11170*); c – *P. frondosa* (LE 253852); d – *P. fimbriata* (*Spirin 11114*); e – *P. eugeniae* (LE 262894); f – *P. eugeniae* (LE 303429).

Fig. 5. Basidiospores of *Phaeotremella* spp.: a – *P. fimbriata* (*Spirin 11139*); b – *P. foliacea* (*Miettinen 14610*); c – *P. frondosa* (*Spirin 11202*)*;* d – *P. eugeniae* (LE 303429). Scale bar = 5 μm.