

What is the type species of *Phanerochaete* (Polyporales, Basidiomycota)?

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Abstract *Phanerochaete velutina* and the closely related species *P. alnea*, *P. alnea* subsp. *lubrica*, and *P. rhodella* are identified as distinct species based on morphological criteria and molecular analyses. Besides differences in macroscopic and microscopic basidiocarp features, the taxa differ in distribution and ITS sequence. *Phanerochaete alnea* is widely distributed in Eurasia and North America, whereas *P. alnea* subsp. *lubrica* is limited to the Pacific Coast of North America. *Phanerochaete velutina* is known from Eurasia and Alaska, and *P. rhodella* is found in North America only. Nomenclatural problems with the name *Phanerochaete* P. Karst. are discussed, and type specimens for *Thelephora alnea* Fr., the generic type of *Phanerochaete*, and *Peniophora karstenii* Masee are selected. *Phanerochaete alnea*, *P. alnea* subsp. *lubrica*, and *P. velutina* are described and illustrated. In addition, the synonymy of *Phanerochaete robusta* and *P. aurantiobadia* is confirmed.

Keywords Corticioid fungi · Lectotype · *Phanerochaete* · Taxonomy

Introduction

Phanerochaete P. Karst. (1889) is a large genus of so-called corticioid fungi, encompassing over 100 species (Index Fungorum 2016). Its current concept was developed by Eriksson (1958, as *Membranicium*, nom. prov.), Donk (1962), Parmasto (1968), and Burdsall (1985). *Phanerochaete* includes resupinate, crust-like fungi with a monomitic hyphal structure of predominantly clampless hyphae, and thin-walled, variably shaped, inamyloid, smooth basidiospores. Many species possess cystidia, and their presence, as well as shape, size and encrustation, is important for species recognition (Eriksson et al. 1978b; Burdsall 1985). Recent phylogenetic studies show that *Phanerochaete* s.l. is polyphyletic, and several new genera have been introduced, some of them placed into different families, or even orders (Greslebin et al. 2004; Wu et al. 2010; Binder et al. 2013; Floudas and Hibbett 2015). Most *Phanerochaete* species are still retained in a monophyletic lineage (*Phanerochaetaceae* sensu Larsson 2007) within *Polyporales*, along with genera such as *Hyphodermella*, *Phlebiopsis*, and *Rhizochaete* (Larsson 2007; Wu et al. 2010; Floudas and Hibbett 2015; Miettinen et al. 2016).

Nomenclatural problems with *Phanerochaete* revolve around different opinions about the generic type (Donk 1957; Burdsall 1977; Eriksson et al. 1978a, b). Cooke (1953) designated *Thelephora alnea* Fr. as the lectotype for *Phanerochaete*. Recent authors, however, consider *Phanerochaete velutina* (DC.) P. Karst. as the generic type (Eriksson et al. 1978b; Burdsall 1985; Chamuris 1988; Bernicchia and Gorjón 2010). *Phanerochaete velutina* has a number of synonyms, including *Corticium decolorans* P. Karst., *Corticium rhodella* Peck, and *Peniophora karstenii* Masee (Burdsall 1985). Recently, Floudas and Hibbett (2015) resolved a clade called the “*Phanerochaete velutina* complex” that included *P. velutina*, *Phanerochaete*

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conifericola Floudas & Hibbett, and *P. rhodella* (Peck) Floudas & Hibbett. In this paper we explore the species of this clade in more detail using morphological and DNA data, and suggest a solution to the nomenclatural issues surrounding the name *Phanerochaete* by selecting a neotype for *Thelephora alnea* and reinstate it as the generic type species.

Material and methods

Type material and specimens from H, GB, S, CFMR, G, LY, OULU, LE, and K, as well as from the private herbarium of Elia Martini (Switzerland), were studied. Herbarium acronyms follow Thiers (2016). Microscopic methods are described in Spirin et al. (2016).

DNA extraction, amplification of the ITS1-5.8S-ITS2 region of the rDNA, and sequencing are described in Volobuev et al. (2015). The partial coding region of *tefl-α* was amplified and sequenced using the primer pair 983 F and 1567R (Rehner and Buckley 2005). In total, 15 ITS and 10 *tefl* sequences were prepared for this study and registered in GenBank or UNITE (Table 1).

Phylogenetic analyses Three datasets were constructed and analyzed. The ITS dataset includes all available ITS sequences from the *Phanerochaete velutina* group (46 sequences). Sequences were selected by performing a BLAST search against DDBJ/EMBL-EBI/GenBank databases. The *tefl* dataset includes 10 partial *tefl* sequences. The *tefl* and corresponding ITS sequences were combined into a third dataset.

We performed Bayesian inference with MrBayes 3.2 (Ronquist et al. 2012). Substitution models were determined with the aid of JModelTest (Darriba et al. 2012) and by comparing harmonic means of marginal probabilities of runs conducted with different settings. Models used were HKY + G for the ITS dataset (nst = 2, rates = gamma) and K80 (nst = 2, rates = equal, statfreqpr = fixed (equal)) for the *tefl* and partitioned combined datasets. In the analyses, three parallel runs with eight chains each, temp = 0.1, were run for 2 million generations. All chains converged to <0.01 average standard deviation of split frequencies. Burn-in of 25% was used in final analyses.

Specimens examined (sequenced specimens are marked by asterisk)

Phanerochaete alnea. Canada. Alberta: Woodlands Co., McLeod Lake, *Picea glauca* and *Populus* sp., 30.VI.1969 Eriksson 12390, 12392 (GB); Yellowhead Co., William A. Switzer Provincial Park, *Picea mariana*, 24.VII.2015 Spirin 8829a* (H). British Columbia: Columbia-Shuswap, Bugaboo Provincial Park, coniferous log, 19.VIII.1982 Hallenberg 6672 (GB); Comox Valley, Forbidden Plateau, *Abies amabilis*,

6.IX.1967 Eriksson 8679 (GB). Ontario: Leeds Co., Lawrence Nat. Park, *Pinus* sp., 2.X.1975 Ginns (H ex DAOM 152157); Nipissing Dist., Algonquin Provincial Park, *Thuja occidentalis*, 19.IX.1982 Hallenberg 7396 (GB); Renfrew Co., Petawawa, *Pinus banksiana*, 8.X.1967 Eriksson 8840 (GB). Finland. Etelä-Häme: Tammela, “ad lignum corticemque Alni, Betulae et Populi tremulae”, Karsten 828 (H), 829 (Rabenhorst-Winter, Fungi Europaei #3231) (H, lectotype of *Peniophora karstenii*), *Alnus* sp., 18.IX.1880 Karsten (H), *Betula* sp., 29.IX.1882 Karsten (H), *Juniperus communis*, 6.III.1882 Karsten 807 (H), *Populus tremula*, 20.IX.1883 Karsten 1588 (H); Vilppula, *Picea abies*, 1.X.2003 Miettinen 7749.7* (H, holotype of *Phanerochaete conifericola*); Somerniemi, *P. abies*, 17.X.2003 Miettinen 8083 (H), 19.X.2003 Miettinen 8110 (H). Pohjois-Karjala: Lieksa, *Pinus sylvestris*, 23.IX.2003 Penttilä 14627* (H). Satakunta: Eura, *P. abies*, 6.X.2012 Uimonen (H); Loimaa, *P. abies*, 13.IV.2009 Poso* (OULU F080062). Kainuu: Kajaani, deciduous tree, 21.IX.2006 Helo 1534* (OULU F079522); Suomussalmi, *P. abies*, 1.VII.2014 Miettinen 18345 (H); Perä-Pohjanmaa: Rovaniemi, *Betula* sp., 17.VIII.1957 Kujala (H), *P. abies*, 31.VII.1979 Niemelä 1562 (H), 7.VIII.1987 Kotiranta 6278 (H). France. Pyrénées Atlantiques: Sansanet, *Fagus sylvatica*, 20.VII.1986 Gilles 580 (LY 11985, holotype of *Phanerochaete binucleosporidida*). Germany. Nordrhein-Westfalen: Bielefeld, deciduous tree, 25.XI.2015 Miettinen 19852 (H). Schleswig-Holstein: Ahrensburg, bark of *Alnus* and *Betula*, 14.V.1908 Jaap (Fungi Selecti #899) (H). Italy. Trentino: Paneveggio, *Sorbus aucuparia*, VIII.1893 Bresadola (S F15720, lectotype of *Corticium cremeum*). Netherlands. Noord-Brabant: Breda, Zundert, *Salix* sp., 1.VII.1958 Bas 1471 (H ex L). Norway. Telemark: Nome, Mörkvasslia Nat. Res., *Betula* sp., 23.IX.2003 K.H. Larsson 12054* (GB). Poland. Mazovia: Siedlce, *Quercus robur*, 1900 Eichler (S F15722, lectotype of *Corticium eichlerianum*). Russia. Karelia: Medvezhiegorsk Dist., Vitska, *P. abies*, 1.VII.1942 Laurila 3262 (H). Leningrad Reg.: Boksitogorsk Dist., Shidrozero, *P. abies*, 13.VII.2014 Spirin 6932 (H); Podporozhie Dist., Nemzha, *P. abies*, 1.X.2010 Spirin 3367 (H), Oksozero, *P. abies*, 3.X.2013 Spirin 6820* (H). Nizhny Novgorod Reg.: Lukoyanov Dist., Sanki, *Q. robur*, 20.VIII.2015 Spirin 9695 (H); Pavlovo Dist., Vorsma, *Q. robur*, 16.VII.2016 Spirin 10288 (H). Oryol Reg.: Znamenskoe Dist., Elenka, *Q. robur*, 13.VII.2011 Volobuev* (LE 298547). Perm Reg.: Krasnovishersk Dist., Kvar Kush, *Abies sibirica*, 6.VIII.2005 Kotiranta 20848 (H), *Betula* sp., 6.VIII.2005 Kotiranta 20835 (H), Molebnyi Kamen, *Abies sibirica*, 12.VIII.2005 Kotiranta 20937* (H). Sweden. Östergötland, *Alnus* sp., 1891 Starbäck (herb. P. A. Karsten #675, H). Småland: Femsjö, *Alnus* sp., 27.VIII.1929 Nannfeldt 3408 (H, neotype of *Thelephora alnea*), *Ribes uva-crispa*, 25.VIII.1929 Nannfeldt 3382 (H); Ulhult, *Prunus padus* (?), 5.VIII.1929 Nannfeldt 2918 (H). Upland: Lena,

Table 1 ITS and *tef1* sequences used in this study

Species	Specimen / herbarium #	Geographic origin, host	ITS sequence (GenBank / UNITE #)	<i>tef1</i> sequence (GenBank #)	Source
<i>P. alnea</i>	Burdsall 15674 (CFMR)	USA (Alaska), <i>Picea</i>	KP135175	–	Floudas and Hibbett (2015)
	Burdsall FP-151125 (CFMR)	USA (Michigan), <i>Tsuga</i>	KP135177	–	Floudas and Hibbett (2015)
	Gilbertson 9919 (CFMR)	USA (Arizona), <i>Pinus</i>	KP135176	–	Floudas and Hibbett (2015)
	Helo 1534 (OULU)	Finland, hardwood	UDB 031214	–	This study
	Kotiranta 20937 (H)	Russia (Ural), <i>Abies</i>	KP135172	–	Floudas and Hibbett (2015)
	Larsson 12054 (GB)	Norway, <i>Betula</i>	KX538924	KX538926	This study
	Miettinen 7749.7 (H)	Finland, <i>Picea</i>	KP135173	–	Floudas and Hibbett (2015)
	Miettinen 8110 (H)	Finland, <i>Picea</i>	KP135171	–	Floudas and Hibbett (2015)
	Penttil 14627 (H)	Finland, <i>Pinus</i>	KP135174	–	Floudas and Hibbett (2015)
	Poso w/n (OULU)	Finland, <i>Picea</i>	UDB 031215	–	This study
	Spirin 6820 (H)	Russia (European), <i>Picea</i>	KU893877	KU893888	This study
	Spirin 8829a (H)	Canada (Alberta), <i>Picea</i>	KX538925	KX538927	This study
	Volobuev (LE 298547)	Russia (European), <i>Quercus</i>	KP994360	KU893885	Volobuev et al. (2015); this study
	Uncultured basidiomycete	Finland, house dust	AM902008	–	Ptik ranta et al. (2008)
	<i>P. alnea</i> ssp. <i>lubrica</i>	Burdsall 13733 (CFMR)	USA (Alaska), <i>Picea</i>	KP135178	–
Spirin 8229 (H)		USA (Washington), <i>Picea</i>	KU893876	KU893886	This study
Spirin 8333 (H)		USA (Washington), <i>Picea</i>	KU893875	–	This study
<i>P. rhodella</i>	Spirin 8779b (H)	USA (Washington), <i>Tsuga</i>	KU893874	KU893883	This study
	Burdsall 2879 (CFMR)	USA (North Carolina), <i>Acer</i>	KP135193	–	Floudas and Hibbett (2015)
	Floudas 18 (CFMR)	USA (Massachusetts), wood	KP135187	–	Floudas and Hibbett (2015)
	Floudas 286 (CFMR)	USA (Massachusetts), hardwood	KP135191	–	Floudas and Hibbett (2015)
	Floudas 329 (CFMR)	USA (Massachusetts), hardwood	KP135192	–	Floudas and Hibbett (2015)
	Floudas 482 (CFMR)	USA (New York), wood	KP135188	–	Floudas and Hibbett (2015)
	Floudas 486 (CFMR)	USA (New York), wood	KP135189	–	Floudas and Hibbett (2015)
	Floudas 522 (CFMR)	USA (Massachusetts), hardwood	KP135190	–	Floudas and Hibbett (2015)
	Miettinen 17278 (H)	USA (Massachusetts), <i>Quercus</i>	KU893882	–	This study
	Nakasone FP-150640 (CFMR)	USA (Wisconsin), <i>Castanea</i>	KP135194	–	Floudas and Hibbett (2015)
<i>P. robusta</i>	Parmasto (LE ex TAAAM 14125)	Russia (Far East), hardwood	KX512306	–	This study
	Lositskaya (LE 212721)	Russia (Karelia), <i>Pinus</i>	KP994367	–	Floudas and Hibbett (2015)
	Kotiranta 21402 (H)	Finland, <i>Quercus</i>	KP135179	–	Volobuev et al. (2015)
<i>P. sordida</i>	–	Japan	AB907603 (as “ <i>P. sordida</i> ”)	–	Floudas and Hibbett (2015)
	–	Japan	AB907611 (as “ <i>P. sordida</i> ”)	–	Fukusawa (unpublished)
<i>P. velutina</i>	–	Russia (Ural), <i>Ulmus</i>	KP994354	KU893884	Fukusawa (unpublished)
	Kotiranta 25567 (H)	Finland, <i>Alnus</i>	KP135181	–	Volobuev et al. (2015); this study
	Miettinen 14694.3 (H)	Finland, <i>Alnus</i>	KP135182	–	Floudas and Hibbett (2015)
	Miettinen 14735 (H)	Finland, <i>Alnus</i>	KP135180	–	Floudas and Hibbett (2015)
	Miettinen 15027 (H)	Finland, <i>Salix</i>	KP135184	–	Floudas and Hibbett (2015)
	Burdsall 15343 (CFMR)	USA (Alaska), <i>Populus balsamifera</i>	KP135183	–	Floudas and Hibbett (2015)
	Burdsall 15074 (CFMR)	USA (Alaska), <i>Populus tremuloides</i>	KP135185	–	Floudas and Hibbett (2015)
	Burdsall 17428 (CFMR)	USA (Alaska), <i>Populus trichocarpa</i>	KP135186	–	Floudas and Hibbett (2015)
	Floudas 346 (CFMR)	USA (Alaska), hardwood	KP135186	–	Floudas and Hibbett (2015)
	Ritel L86 (H)	Finland, <i>Betula</i>	UDB 031212	–	This study
	Spirin 3949 (H)	Russia (Far East), <i>Abies</i>	KU893879	KU893887	This study
	Spirin 5059 (H)	Russia (Far East), <i>Corylus</i>	KU893881	–	This study
	Spirin 7421 (H)	Russia (Far East), <i>Picea</i>	KU893880	KU893890	This study
	Spirin 9343	Russia (European), <i>Quercus</i>	KU893878	KU893889	This study
	Uncultured fungus	Germany	FJ820654	–	Fr hlich-Nowoisky et al. (2009)
<i>P. aff. velutina</i>	UC2022871	USA (California)	KP814202	–	Rosenthal & Bruns (unpublished)

P. sylvestris, V.1927 Lundell 331 (H). Hälsingland: Delsbo, *P. abies*, 25.VII.1986 Kotiranta 6028 (H). Switzerland. Fribourg: Corminboeuf, deciduous tree, 3.X.1998 Martini 6715 (EM, dupl. H). Ticino: Alpe Püschett, *Alnus viridis*, 24.VI.1995 Martini 4128, 4129, 4191, 4192 (EM, dupl. H); Besso, *Quercus* sp., 3.X.1992 Martini 3417 (EM, dupl. H); Broglio, coniferous tree, 4.VIII.1996 Martini 6055 (EM, dupl. H); Faedo, *Sarothamnus scoparius*, 13.X.1985 Martini 290 (EM, H); Mogno, deciduous tree, 4.VIII.1985 Martini 227 (EM, dupl. H); Mondada, deciduous tree, 5.IX.1987 Martini 2237 (EM, H). USA. Arizona: Pima Co., Coronado Nat. Forest, *Pinus* sp., 26.VIII.1968 Burdsall 1399 (CFMR). Wisconsin: Dane Co., Madison, *Pinus resinosa*, 21.VI.1978 Burdsall 10228 (GB).

Phanerochaete alnea subsp. *lubrica*. Canada. British Columbia: Cowichan, fallen branches, 8.IX.1967 Eriksson 7748, 7750 (H), *Alnus rubra*, 9.IX.1967 Eriksson 7809 (GB), 12–14.IX.1967 Eriksson 7957, 8014, 8118 (GB), 17.IX.1967 Eriksson 8211 (GB), 5.IX.1982 Hallenberg 7050 (GB), *Pseudotsuga menziesii*, 9.IX.1967 Eriksson 7826 (GB), 10.IX.1967 Eriksson 7891 (GB), 12–13.IX.1967 Eriksson 7791, 8032 (GB), 17–18.IX.1967 Eriksson 8208, 8264 (GB), 31.VIII.1982 Hallenberg 6917 (GB), drift wood, 27.IX.1967 Eriksson 8597 (GB); Squamish-Lillooet, Garibaldi Provincial Park, fallen log, 29.VIII.1982 Hallenberg 6877 (GB); Vancouver, fallen log of deciduous tree, 16.IX.1982 Hallenberg 7303 (GB). USA. Alaska: Chichagof Island, Pavlov Harbor, *Picea sitchensis*, 25.VII.1991 Burdsall 13753* (CFMR). Washington: Jefferson Co., Hoh River, *P. sitchensis*, 7.X.2014 Spirin 8229* (H), Spirin 8333* (H, holotype), *Tsuga heterophylla*, 20.X.2014 Spirin 8779b* (H), *Acer macrophyllum*, 20.X.2014 Spirin 8788 (H).

Phanerochaete martelliana. Iran. Golestan, Gorgan, dead hardwood twigs, 20.V.2008 Ghobad-Nejhad 1346 (H). Italy. Tuscany: Florence, *Quercus*, herb. Bresadola (H). Portugal. Trás-os-Montes e Alto Douro: Valpaços, *Cytisus* sp., 29.I.1991 Tellería 11358 (H ex LISU).

Phanerochaete rhodella. Canada. Alberta: Woodlands Co., McLeod Lake, *Populus* sp., 30.VI.1969 Eriksson 12346 (GB); Yellowhead Co., William A. Switzer Provincial Park, *Populus tremuloides*, 24.VII.2015 Spirin 8830 (H). Quebec: Cantley, deciduous branches, 10.VIII.1982 Hallenberg 6506 (GB); Outaouais, Gatineau National Park, *Fagus grandifolia*, 29.IX.1982 Hallenberg 7601 (GB). USA. Massachusetts: Worcester Co., Worcester, *Quercus* sp., 6.X.2013 Miettinen 17278* (H), Paxton, *Quercus* sp., 12.X.2013 Miettinen 17306 (H).

Phanerochaete robusta. Russia. Primorie: Khasan Dist., Kedrovaya Pad Nat. Res., angiosperm (fallen branch), IX.1961 Parmasto (LE 35895*, K ex TAAM 14125, isotypes).

Phanerochaete velutina. Finland. Varsinais-suomi: Tammisaari, *Q. robur*, 11.X.2006 Kotiranta 21402* (H).

Uusimaa: Helsinki, *Alnus glutinosa*, 5.IX.2011 Miettinen 14694.3* (H), *Betula* sp., 19.VIII.2013 Rätäl* (H), *Salix* sp., 30.X.2011 Miettinen 15027.1* (H). Etelä-Häme: Tammela, *Salix* sp., X.1879 Karsten 1405 (H, lectotype of *Corticium decolorans*). Pohjois-Karjala: Lieksa, *Alnus incana*, 25.VIII.1956 Kujala (H), *P. tremula*, 30.IX.2003 Penttilä 14759 (H). Russia. Bashkortostan: Burzyanskii Dist., Shulgan-Tash Nat. Res., *Ulmus glabra*, 8.VIII.2012 Kotiranta 25567* (H). Khabarovsk Reg.: Khabarovsk Dist., Bolshoi Khekhtsir Nat. Res., *Corylus mandshurica*, 5.IX.2013 Spirin 6671 (H), Malyi Niran, *Picea ajanensis*, 6.VIII.2012 Spirin 4986 (H), *C. mandshurica*, 8.VIII.2012 Spirin 5059* (H), Malyi Kukachan, *P. ajanensis*, 17.VIII.2012 Spirin 5344, 5353, 5357 (H), Povorotnaya, *Rhododendron dauricum*, 27.VIII.2012 Spirin 5740 (H), Ulun, *P. ajanensis*, 28.VIII.2012 Spirin 5765 (H); Solnechnyi Dist., Igdomi, *P. tremula*, 6.VIII.2011 Spirin 3854 (H), *Abies nephrolepis*, 7.VIII.2011 Spirin 3949* (H); Verkhnebureinskii Dist., Kyvyty, *P. ajanensis*, 17.VIII.2014 Spirin 7421* (H), Dublikan Nat. Res., *P. ajanensis*, 20.VIII.2014 Spirin 7666 (H). Krasnoyarsk Reg.: Turukhansk Dist., Mirnoe, *Alnus sibirica*, 19.VIII.2013 Kotiranta 26326 (H). Leningrad Reg.: Volkhov Dist., Zagubie, *P. tremula*, 3.X.2010 Spirin 3638 (H). Nizhny Novgorod Reg.: Lukoyanov Dist., Razino, *Q. robur*, 16.VIII.2015 Spirin 9343* (H), *Tilia cordata*, 16.VIII.2015 Spirin 9365 (H); Sharanga Dist., Kilemary Nat. Res., *Ulmus laevis*, 26.IX.1999 Spirin (LE 210942), *T. cordata*, 24.VIII.2000 Spirin (LE 210954). Switzerland. Jura, *Quercus* sp., 1813 Chaillet (G 00273767, lectotype of *Thelephora velutina*). Ukraine. Zakarpats'ka Reg.: Dilove, *Fagus sylvatica*, VIII.1938 Pilát (H ex PRM).

Results and discussion

Typification of *Thelephora alnea* Fr. and *Phanerochaete* P. Karst.

The genus *Phanerochaete* was introduced by Karsten (1889) with two species—*P. alnea* (Fr.) P. Karst. (= *Thelephora alnea* Fr.) and *P. odorata* (Fr.) P. Karst. (= *T. odorata* Fr.). For many years, *Phanerochaete* was considered a synonym of *Peniophora* when that genus included all corticioid species with cystidia. Cooke (1953) selected *P. alnea* as the generic type. Parmasto (1968), following Karsten (1898), Bresadola (1903), and Höhnelt and Litschauer (1906), considered *P. alnea* a synonym of *P. velutina*, and therefore listed the latter species as the type for *Phanerochaete*. However, the absence of type material for *Thelephora alnea* that could support the synonymy was not addressed.

Burdsall (1977), recognizing that the identity of *Thelephora alnea* was unclear, chose *Thelephora odorata* Fr. as a lectotype of the genus because its identity was

supported by an authentic material at UPS (see Hallenberg 1985). With this interpretation, *Phanerochaete* became an older name for *Scytinostroma*, and therefore Burdsall (1977) resurrected *Grandiniella* P. Karst. to replace *Phanerochaete* sensu Parmasto. A year later Eriksson et al. (1978a) made a counter proposal to preserve *Phanerochaete*. In their opinion, *T. alnea* could not be avoided as the generic type. In the protologue of *Phanerochaete*, Karsten (1889) included *Corticium decolorans* P. Karst. as a synonym of *Thelephora alnea*. *Corticium decolorans* was described 7 years earlier (Karsten 1882), and by listing it as a synonym of *T. alnea*, Karsten explained his interpretation of the latter name. By accepting *C. decolorans* as the lectotype of *Phanerochaete*, the modern concept of the genus could be preserved. Continuing in this vein, Eriksson et al. (1978b: 1038) selected a type specimen for *C. decolorans* from Karsten's herbarium that was conspecific with *T. velutina* Fr., in keeping with Karsten's 1893 intention for the genus. This specimen then also served as the lectotype for *Phanerochaete* (Eriksson et al. 1978b: 987). At this point, both *Thelephora alnea* and *T. velutina* were left non-typified, although the latter species was typified later by Burdsall (1985).

Our approach to typification of *P. alnea*, as well as the genus *Phanerochaete* in general, is based on the following arguments:

1. *Thelephora alnea* Fr. is considered the type species (lectotype) of the genus *Phanerochaete* P. Karst., in accordance with Art. 10.5 of the Code (2011), because the lectotypification of the genus by Cooke (1953) precedes those proposed by Burdsall (1977) and Eriksson et al. (1978a, b). Cooke's citation of the type species as "*Phanerochaete alnea* Karst.", without formal reference to Fries's *T. alnea*, is interpreted as an accidental omission and should not influence the validity of the lectotype selection.
2. The lectotype of *C. decolorans* designated by Eriksson et al. (1978b) does not preclude independent typification of *T. alnea* and *T. velutina* DC., according to Art. 9.16 of the Code (2011).
3. Only Karsten's original description of the genus (Karsten 1889) and his previous work (Karsten 1882) can be used to interpret his concept of *T. alnea*. A description of *T. alnea* first appeared in 1882 (Karsten 1882: 137) alongside a protologue of *C. decolorans* (ibid.: 144), suggesting that he considered these taxa to be different species. In a later description of *T. alnea*, Karsten (1889) used nearly identical language to describe a species with reddish-yellowish basidiocarps, tubular cystidia, and ellipsoid basidiospores that occurs on wood of pine and alder in southern and western parts of Finland. These diagnostic features fit well with specimens distributed by Karsten as *Corticium alneum* (Fr.) P. Karst. in Rabenhorst-Winter's

Fungi Europaei exsiccates (#3231), which, as Donk (1957) already noted, belong to a species closely related to *P. velutina*. Burdsall (1977), however, argued that these exsiccates cannot be used for neotypification of *T. alnea* Fr. because Fries (1821) never studied them nor collected in Finland. Furthermore, the original description gives no clear indication whether Fries' species is similar to Karsten's species concept. This problem is best resolved by selecting a neotype for *T. alnea* from Fries's home area in Sweden that also conforms to Karsten's (1882, 1889) descriptions. In this way, the current generic concept of *Phanerochaete* is preserved. In his later works, Karsten (1893, 1898) placed *T. alnea* and *C. decolorans* in synonymy under *P. velutina*. Although Eriksson et al. (1978b) considered these later works as an emendation to the protologue of *Phanerochaete*, we consider them not relevant for clarifying the identity of *Thelephora alnea*. Neither should we take into account Karsten's later decision to move *Phanerochaete velutina* to *Peniophora* (Karsten 1899) and to retain *Phanerochaete* for *Stereum karstenii* Bres. (\equiv *Dacryobolus karstenii* (Bres.) Oberw.).

Molecular phylogenetic analyses

DNA analyses confirm that *P. alnea* as defined herein is closely related to *P. rhodella* and *P. velutina*. The ITS dataset resolves four clades in the *Phanerochaete velutina* group: *P. velutina*, *P. alnea*, *P. rhodella* and *P. aff. velutina* from California (GenBank KP814202). In addition, *P. alnea* is composed of two subclades based on two nucleotide differences in the ITS sequence (Fig. 1). The *tefl* dataset analysis separated *P. alnea* from *P. velutina* (*P. rhodella* was not included) and grouped *P. alnea* samples slightly differently compared to the ITS tree (Fig. 2). The combined ITS-*tefl* dataset tree was similar to the ITS tree (Fig. 3).

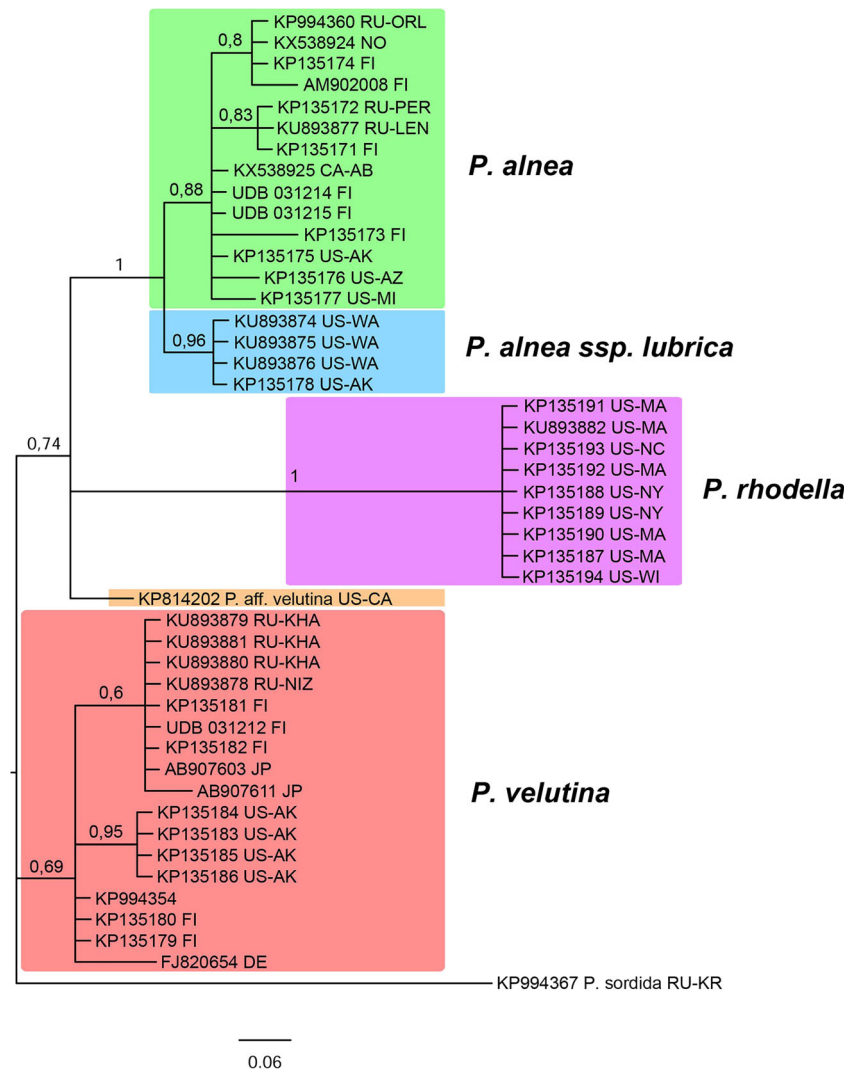
Phanerochaete aurantiobadia was recently introduced as a species belonging to the core *Phanerochaete* clade (Ghobad-Nejhad et al. 2015). Our analysis of ITS sequences confirms that this species belongs to *Phanerochaete* (as outlined by Floudas and Hibbett 2015) but also that it is distantly related to *P. alnea* and its allies (data not shown). *Phanerochaete robusta*, described from the same geographical region (Parmasto 1968), seems morphologically indistinguishable from *P. aurantiobadia*. ITS sequences from the types of *P. robusta* and *P. aurantiobadia* are identical.

Species descriptions

Phanerochaete alnea (Fr.) P. Karst., Bidr. Känned. Finlands Nat. Folk 48: 427, 1889. Figs. 4 and 7a, b

\equiv *Thelephora alnea* Fr., Systema Mycologicum 1: 446, 1821.

Fig. 1 Phylogenetic tree based on the ITS dataset – 619 nucleotide positions of 46 taxa. Bayesian inference: MrBayes 3.2, HKY+G substitution model, three runs with eight chains each, two million generations. 25% of trees discarded as burn-in



Neotype. Sweden. Småland: Femsjö, *Alnus* sp., 27.VIII.1929 Nannfeldt 3408 (H, selected here).

= *Peniophora karstenii* Masee, Bot. J. Linnean Soc. 25: 153, 1889.

Lectotype. Finland. Etelä-Häme: Mustiala, “ad lignum corticemque Alni, Betulae et Populi tremulae”, Karsten 829 (Rabenhorst-Winter, Fungi Europaei #3231) (H, selected here).

= *Corticium cremeum* Bres., Fungi Tridentini 2: 63, 1898.

Lectotype. Italy. Trentino: Paneveggio, *Sorbus aucuparia*, VIII.1893 Bresadola (S F15720, studied) (selected by Eriksson et al. 1978b).

= *Corticium eichlerianum* Bres., Ann. Mycol. 1: 95, 1903.

Lectotype. Poland. Mazovia: Siedlce, *Quercus robur*, 1900 Eichler (S F15722, studied) (selected by Eriksson et al. 1978b).

= *Phanerochaete velutina* (DC.) P. Karst. var. *cremicolor* Parmasto (pr. p.), Consp. Syst. Cort.: 222, 1968.

= *Phanerochaete binucleosporidida* Boidin, Lanq. & Gilles, Cryptogamie Mycologie 14: 195, 1993.

Holotype. France. Pyrénées Atlantiques: Sansanet, *Fagus sylvatica*, 20.VII.1986 Gilles 580 (LY 11985, studied).

= *Phanerochaete conifericola* Floudas & Hibbett, Fungal Biology 119: 705, 2015.

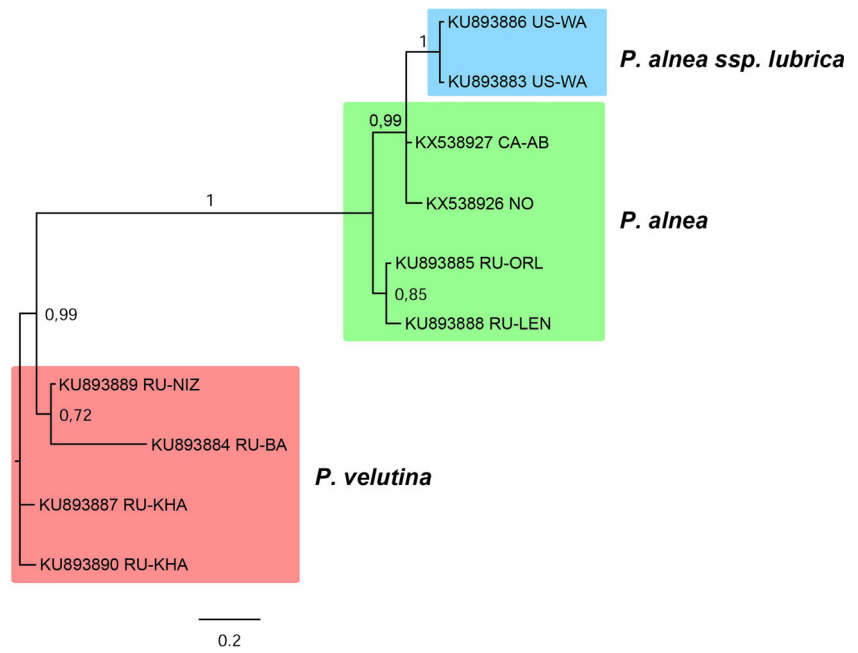
Holotype. Finland. Etelä-Häme: Vilppula, *Picea abies*, 1.X.2003 Miettinen 7749.7 (H, studied).

Basidiocarps resupinate, membranous, up to 20 cm in widest dimension, 0.2–0.5 mm thick. Margin first distinct, fibrillose, white, sometimes fimbriate with well-developed short hyphal strands, later more or less compact, thinning out, often paler than the hymenial surface, up to 1 mm wide. Hymenium ceraceous, pale pink to pale ochraceous, in vigorously growing specimens with reddish-vinaceous hues, in dry basidiocarps often darker, turning dark red in KOH, herbarium specimens stored for more than 20 years usually assume a yellowish-orange to bright orange colour.

Hyphal structure monomitic; hyphae mostly clampless.

Hyphae in strands parallel, with distinct (up to 2 µm thick) walls, clampless or with occasional clamps, 4–10 µm in diam.,

Fig. 2 Phylogenetic tree based on the *tef1* dataset – 581 nucleotide positions of 10 taxa. Bayesian inference: MrBayes 3.2, K80 substitution model, three runs with eight chains each, two million generations. 25% of trees discarded as burn-in



smooth or rarely covered by sparse angular crystals. Subicular hyphae parallel to interwoven, not adhering together, thin- to slightly thick-walled, mostly clampless but occasionally with large solitary or double clamps, branched at acute angles, (4.9–) 5.1–10.8 (–11.2) μm in diam. ($n = 80/4$), often easily collapsing, smooth or occasionally bearing small, irregularly arranged resinous grains or angular crystals. Subhymenial hyphae interwoven or more or less vertically arranged, clampless, mostly thin-walled, (3.1–) 3.2–5.1 (–5.2) μm in diam. ($n = 80/4$). Cystidia tubular to subfusiform, usually widened close to the base and more or less tapering towards the blunt or very rarely acute apex, (51.8–) 52.3–144.7 (–149) \times (6–) 6.2–11 (–11.4) μm ($n = 140/7$), projecting up to 80 μm beyond the hymenial layer, easily collapsing, walls first gradually thinning towards apex, later more or less equally thickened throughout,

up to 1.5 μm thick; encrustation irregularly present, often apical or located at the middle part of cystidia, crystals discrete, angular or very rarely aggregated to a solid sheath. Basidia long clavate, (20.8–) 21.4–49.4 (–50.1) \times (4.7–) 4.8–6.8 (–6.9) μm ($n = 92/6$). Basidiospores narrowly ellipsoid to broadly cylindrical, (4.8–) 4.9–7.5 (–8.1) \times (2.8–) 2.9–4 (–4.1) μm ($n = 270/9$), $L = 6.06$, $W = 3.20$, $Q = 1.68$ –2.14, ventral side flat or slightly convex, occasionally slightly concave; oil droplets often present in cytoplasm. Resinous substance present as variably shaped particles, abundant in older basidiocarps and herbarium specimens, golden yellow, covering subhymenial hyphae and hymenial elements.

Notes. In 1821, Fries described a pale-reddish corticioid fungus collected on wood of alder and indicated he saw a living specimen (“v.v.”), implying that it occurs in Femsjö,

Fig. 3 Phylogenetic tree based on the combined ITS+*tef1* dataset – 1327 nucleotide positions of 10 taxa. Bayesian inference: MrBayes 3.2, HKY+G substitution model for the ITS partition, K80 substitution model for the TEF1 partition. Three runs with eight chains each, two million generations. 25% of trees discarded as burn-in

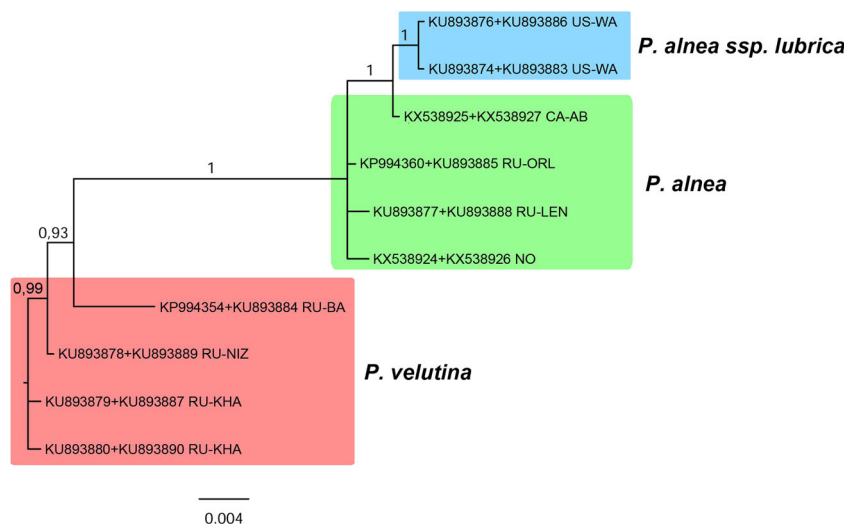




Fig. 4 *Phanerochaete alnea* (neotype): cystidia and basidiospores. Scale bar = 5 μm (basidiospores), 10 μm (cystidia)

Fries' primary collecting place in the southern part of Sweden. Since no authentic specimens of *T. alnea* exist, a neotype from Femsjö is designated here. The same species was distributed by Karsten in Rabenhorst-Winter's *Fungi Europaei* as *Corticium alneum* (Fr.) P. Karst. This exsiccati collection is the basis for *Peniophora karstenii* described by Masee (1890) and the lectotype of *P. karstenii* is designated above. We examined the type specimens of *Corticium cremeum* and *Corticium eichlerianum*, traditionally listed among the synonyms of *P. sordida* (P. Karst.) J. Erikss. & Ryvar den (Eriksson et al. 1978b; Volobuev et al. 2015). Both are conspecific with *P. alnea*. The more recent introductions of *Phanerochaete binucleosporidida* (Boidin et al. 1993) and *P. conifericola* (Floudas and Hibbett 2015) have extended the list of

synonyms further. Both species are morphologically identical to *P. alnea*. and in our phylogeny the type specimen sequence of *P. conifericola* clusters with *P. alnea* (Fig. 1).

Morphological identification of *Phanerochaete alnea* can be difficult. Herbarium specimens are often mislabelled as *P. sordida* or *P. velutina*, depending on the maturity of the basidiocarps. Young, thin basidiocarps of *T. alnea* lacking hyphal strands at the margin (e.g. types of *C. cremeum*, *C. eichlerianum* and *P. binucleosporidida*) are strongly reminiscent of *P. sordida*, and tubular, sparsely encrusted cystidia with walls thinning towards the apex also points to the latter species. Cystidia of *P. sordida* are on average narrower than in *P. alnea*, 4–8 μm in diam. versus 6–11 μm in *P. alnea*. Additionally, subicular hyphae of *P. sordida* are distinctly thick-walled, variably interwoven, 5–7.5 μm in diam., with exceptionally rare clamps (Volobuev et al. 2015). Mature and senescent basidiocarps of *P. alnea* (for example, types of *P. karstenii* and *P. conifericola*) can be mistaken for *P. velutina*. Microscopically, cystidia in *P. velutina* are wider and more heavily encrusted with fused, indistinct hyaline crystals. In addition, cystidia of *P. alnea* are typically narrower and basidiospores larger than in *P. velutina*, although these differences are not absolute (Tables 2 and 3). Moreover, subicular hyphae of *P. alnea* lack the dense crystalline encrustation so characteristic of *P. velutina*.

The most easily observed difference between these species is the ability of *P. alnea* to produce a dark red coloration in KOH (see Floudas and Hibbett 2015, as *P. conifericola*), whereas there is no color change in *P. velutina* or *P. sordida*. Another striking feature of *P. alnea* is the distinct, yellowish-orange or bright orange coloration of basidiocarps kept in herbarium for decades, which appears to be the result of accumulating yellow, resinous substances. All herbarium specimens of *P. velutina* studied had retained their original colour or developed greyish hues (Fig. 7c, d). Aged basidiocarps of *P. martelliana* (Bres.) J. Erikss. & Ryvar den also turn orange as in *P. alnea*. However, *P. martelliana* has much shorter, subulate cystidia and larger basidiospores compared to *P. alnea* (Eriksson et al. 1978b).

Phanerochaete alnea is widely distributed in the Northern Hemisphere and is the only holarctic species in the *P. velutina* group. Its distribution is in general more boreal than that of *P. velutina*. *Phanerochaete alnea* seems to be the most common species of *Phanerochaete* in the middle and northern taiga subzones. It inhabits mostly coniferous hosts but regularly occurs on wood of deciduous trees. Specimens of *P. alnea* from the Pacific coast of North America belong to a new subspecies, subsp. *lubrica*, due to small (2 bp) differences in ITS sequences and slightly deviating morphology as described below.

Phanerochaete alnea subsp. *lubrica* Spirin & Volobuev, subsp. nova – Fig. 5

Table 2 Basidiospore measurements of the core *Phanerochaete* species

Species / specimen	L'	L	W'	W	Q'	Q	n
<i>P. alnea</i>	(4.8) 4.9–7.5 (8.1)	6.06	(2.8) 2.9–4.0 (4.1)	3.20	(1.5) 1.6–2.4 (2.5)	1.90	270
Neotype	(5.3) 5.4–7.0 (7.1)	6.29	(2.9) 3.0–3.5 (3.6)	3.21	(1.8) 1.9–2.2 (2.3)	1.96	30
Karsten 829 ^a	(5.3) 5.4–7.5 (7.7)	6.01	(2.8) 3.0–3.3 (3.5)	3.17	(1.7) 1.8–2.1 (2.3)	1.90	30
Gilles 580 ^b	(5.9) 6.0–7.4 (8.1)	6.66	(2.8) 2.9–3.3	3.12	(1.9) 2.0–2.4 (2.5)	2.14	30
Miettinen 7749.7 ^c	(5.4) 5.6–7.0 (7.3)	6.18	(3.0) 3.1–4.0 (4.1)	3.33	(1.5) 1.6–2.1 (2.2)	1.87	30
Karsten 828	(5.2) 5.3–6.8 (7.1)	6.13	(2.9) 3.0–3.7 (3.8)	3.26	(1.6) 1.7–2.1 (2.2)	1.88	30
Larsson 12054	(5.2) 5.6–7.0 (7.1)	6.29	(3.0) 3.1–3.7 (3.8)	3.31	(1.6) 1.7–2.2 (2.3)	1.91	30
Martini 4192	(5.0) 5.1–7.0 (7.8)	5.82	(2.9) 3.0–3.4 (3.5)	3.15	(1.6) 1.7–2.0 (2.1)	1.85	30
Martini 6715	(5.1) 5.2–7.0 (7.3)	5.86	(2.9) 3.0–3.3 (3.5)	3.12	(1.5) 1.7–2.2 (2.3)	1.88	30
Spirin 3367	(4.8) 4.9–5.9 (6.3)	5.28	(2.9) 3.0–3.3 (3.5)	3.15	(1.5) 1.6–1.9 (2.0)	1.68	30
<i>P. alnea</i> ssp. <i>lubrica</i>	(4.2) 4.3–6.1 (6.2)	5.00	(2.3) 2.4–3.2 (3.3)	2.83	(1.4) 1.6–2.0 (2.1)	1.77	120
Holotype	(4.2) 4.3–5.5 (5.8)	4.96	(2.4) 2.5–3.1 (3.2)	2.78	(1.4) 1.6–2.0 (2.1)	1.79	30
Burdsall 13753	(4.6) 4.8–6.1 (6.2)	5.29	(2.3) 2.4–3.1 (3.2)	2.86	(1.5) 1.6–2.1 (2.2)	1.86	30
Spirin 8229	(4.2) 4.3–5.2 (5.3)	4.83	(2.3) 2.4–3.2 (3.3)	2.84	(1.5) 1.6–1.9 (2.0)	1.71	30
Spirin 8779b	(4.2) 4.3–5.4 (5.6)	4.91	(2.5) 2.6–3.2	2.83	(1.5) 1.6–1.8 (1.9)	1.73	30
<i>P. rhodella</i>	(4.2) 4.5–5.8 (6.2)	5.21	(2.6) 2.7–3.2 (3.3)	2.93	(1.5) 1.6–2.0 (2.1)	1.78	60
Miettinen 17278	(4.2) 4.5–5.8 (6.0)	5.26	(2.6) 2.7–3.2 (3.3)	2.97	(1.5) 1.6–1.8 (1.9)	1.77	30
Spirin 8830	(4.7) 4.8–5.8 (6.2)	5.16	(2.7) 2.8–3.2	2.88	(1.5) 1.7–2.0 (2.1)	1.79	30
<i>P. velutina</i>	(4.7) 4.8–7.2 (7.3)	5.55	(2.6) 2.7–3.6 (3.8)	3.05	(1.4) 1.5–2.3 (2.4)	1.83	340
Lectotype	(4.9) 5.0–6.0 (6.1)	5.38	(2.7) 2.8–3.1 (3.3)	2.94	(1.6) 1.7–2.0 (2.1)	1.83	30
Karsten 1405 ^d	(5.1) 5.2–6.6 (7.0)	5.74	(2.6) 2.7–3.2 (3.3)	2.95	(1.7) 1.8–2.2 (2.4)	1.95	40
Kotiranta 25567	(4.7) 4.8–5.7 (5.8)	5.04	(2.6) 2.7–3.0 (3.1)	2.85	(1.5) 1.7–2.1 (2.2)	1.77	30
Miettinen 14735	(4.8) 4.9–6.2 (6.7)	5.36	(2.6) 2.8–3.3 (3.6)	3.07	(1.5) 1.6–2.0 (2.2)	1.75	30
Miettinen 15027.1	(5.2) 5.3–7.1 (7.2)	6.09	(3.0) 3.1–3.5 (3.6)	3.20	(1.6) 1.7–2.2 (2.3)	1.91	30
Spirin 3854	(4.9) 5.0–6.3 (6.8)	5.47	(2.8) 2.9–3.3 (3.5)	3.09	(1.6) 1.7–2.0 (2.1)	1.77	30
Spirin 3949	(4.9) 5.0–7.2 (7.3)	5.92	(2.9) 3.0–3.2 (3.3)	3.08	(1.6) 1.7–2.3 (2.4)	1.92	30
Spirin 5059	(4.9) 5.0–6.3 (6.6)	5.61	(2.8) 2.9–3.2 (3.3)	3.02	(1.6) 1.7–2.0 (2.1)	1.86	30
Spirin 7421	(4.9) 5.0–5.8 (6.0)	5.23	(2.8) 2.9–3.6 (3.8)	3.12	(1.4) 1.5–1.8 (1.9)	1.68	30
Spirin 9343	(4.8) 5.0–6.2 (6.5)	5.53	3.1–3.6 (3.7)	3.32	(1.4) 1.5–1.8 (2.0)	1.67	30
Spirin 9365	(5.0) 5.1–6.2 (6.3)	5.66	(2.6) 2.7–3.0 (3.1)	2.86	(1.7) 1.8–2.2 (2.3)	1.98	30

^a Lectotype of *Peniophora karstenii*

^b Holotype of *Phanerochaete binucleosporidida*

^c Holotype of *Phanerochaete conifericola*

^d Lectotype of *Corticium decolorans*

Holotype. USA. Washington: Jefferson Co., Hoh River, *Picea sitchensis*, 7.X.2014 Spirin 8333 (H).

Etymology. “Lubricus” (Lat., adj.) – ticklish, critical; referring to the small morphological differences separating it from closely related species.

MB 818235

Basidiocarps resupinate, membranous, up to 5 cm large, 0.1–0.3 mm thick. Margin first distinct, whitish, arachnoid or rarely with hyphal strands, later more or less compact, thinning out, concolorous to or paler than hymenial surface, up to 0.5 mm wide. Hymenium ceraceous to gelatinous, pale grey, in dried basidiocarps pale ochraceous, turning faintly or

distinctly dark red in KOH, in specimens kept in herbarium for decades bright orange.

Hyphal structure monomitic; hyphae mostly clampless.

Hyphae in hyphal strands parallel, with distinct (up to 1 µm thick) walls, clampless or with occasional clamps, 4–14 µm in diam., often encrusted with densely arranged, angular crystals. Subicular hyphae parallel to interwoven, densely agglutinated, thin- to slightly thick-walled, mostly clampless but occasionally with large solitary or double clamps, branched at acute angles, (5.1–) 5.2–12.3 (–14.2) µm in diam. ($n = 60/3$), sometimes encrusted. Subhymenial hyphae interwoven or more or less vertically arranged, clampless, mostly thin-walled, (2.8–)

Table 3 Measurements of cystidia for the core *Phanerochaete* species

Species / specimen	L'	L	W'	W	Q'	Q	n
<i>P. alnea</i>	(51.8) 52.3–144.7 (149.0)	87.43	(6.0) 6.2–11.0 (11.4)	7.86	(6.6) 6.8–14.7 (14.8)	11.23	140
Neotype	(65.8) 69.7–99.8 (104.2)	80.08	(6.5) 6.8–8.4 (8.6)	7.66	(8.4) 8.8–12.4 (12.6)	10.49	20
Karsten 829	(61.2) 66.7–117.2 (120.4)	92.08	(6.2) 6.4–9.8 (11.6)	8.25	(9.0) 9.3–13.2 (14.0)	11.22	20
Gilles 580	(65.6) 69.3–101.2 (105.6)	83.25	(6.0) 6.2–9.2 (9.3)	7.51	(9.0) 9.3–13.2 (14.0)	11.26	20
Miettinen 7749.7	(51.8) 52.3–144.7 (149.0)	96.78	(7.0) 7.1–11.0 (11.4)	9.17	(6.6) 6.8–13.7 (14.2)	10.50	20
Larsson 12054	(65.2) 71.2–94.8 (97.4)	81.99	(6.0) 6.7–8.8 (9.8)	7.55	(7.7) 8.9–12.6 (13.7)	10.98	20
Martini 6715	(64.2) 83.7–104.4 (122.8)	92.41	(6.2) 6.3–8.3 (8.8)	7.19	(9.4) 9.5–14.7 (14.8)	12.98	20
Spirin 3367	(63.2) 63.7–104.3 (109.8)	85.40	(6.2) 6.3–9.2 (9.5)	7.69	(8.2) 8.3–14.1 (14.8)	11.20	20
<i>P. alnea</i> ssp. <i>lubrica</i>	(56.4) 59.6–104.2 (117.9)	82.05	(6.3) 6.5–10.8 (11.3)	8.27	(7.1) 7.5–14.3 (15.0)	10.09	60
Holotype	(65.8) 69.3–104.2 (107.4)	86.95	(6.3) 6.6–9.2 (9.3)	7.92	(8.1) 8.4–14.3 (15.0)	11.13	20
Spirin 8229	(56.4) 59.6–91.3 (107.8)	77.56	(6.5) 6.6–10.8 (11.2)	8.51	(7.4) 7.5–12.6 (12.7)	9.27	20
Spirin 8779b	(60.2) 66.2–102.5 (117.9)	81.64	(6.4) 6.5–9.4 (11.3)	8.37	(7.1) 7.7–12.5 (13.0)	9.86	20
<i>P. rhodella</i>	(41.6) 43.8–90.3 (109.0)	69.44	(5.9) 6.0–10.4 (11.8)	8.01	(5.3) 5.7–13.6 (16.5)	8.96	40
Miettinen 17278	(41.6) 43.8–80.0 (105.4)	64.80	(6.1) 6.4–10.4 (10.6)	8.28	(5.3) 5.7–11.1 (11.5)	8.04	20
Spirin 8830	(53.3) 60.4–90.3 (109.0)	74.07	(5.9) 6.0–10.4 (11.8)	7.74	(5.8) 7.0–13.6 (16.5)	9.88	20
<i>P. velutina</i>	(45.5) 55.1–142.3 (159.6)	91.01	(6.3) 6.6–15.8 (17.7)	10.29	(4.5) 5.0–14.1 (14.8)	8.97	200
Lectotype	(81.3) 82.0–142.3 (142.7)	106.99	(8.2) 8.3–13.2 (14.6)	9.61	(6.7) 7.4–11.8 (11.9)	9.61	20
Karsten 1405	(45.5) 55.1–100.4 (142.4)	77.58	(6.9) 7.0–14.3 (15.2)	10.04	(4.5) 5.9–10.0 (10.9)	7.82	20
Miettinen 14735	(67.5) 72.6–118.8 (128.6)	96.70	(7.6) 7.7–11.4 (11.7)	9.31	(6.2) 6.6–14.1 (14.8)	10.62	20
Miettinen 15027.1	(65.1) 66.4–108.9 (116.1)	86.34	(6.3) 6.6–11.6 (13.3)	8.65	(7.3) 7.8–13.2 (13.8)	10.26	20
Spirin 3854	(61.0) 65.2–111.3 (113.7)	87.22	(8.0) 8.8–13.1 (15.5)	11.01	(5.3) 5.5–10.0 (10.3)	8.06	20
Spirin 3949	(67.2) 74.8–115.8 (120.0)	91.25	(9.0) 9.6–13.0 (15.4)	11.32	(5.7) 6.6–10.9 (11.4)	8.17	20
Spirin 5059	(71.3) 74.8–124.2 (132.2)	94.75	(8.2) 8.9–13.7 (14.3)	11.13	(6.7) 6.8–11.0 (11.8)	8.63	20
Spirin 7421	(72.3) 76.0–112.0 (123.2)	87.04	(8.1) 8.2–13.7 (16.7)	11.44	(6.0) 6.1–11.0 (12.2)	7.85	20
Spirin 9343	(66.2) 66.8–126.4 (159.6)	92.65	(7.1) 7.2–10.3 (13.8)	9.16	(6.8) 7.2–11.8 (17.3)	10.22	20
Spirin 9365	(69.7) 72.9–118.0 (132.0)	90.42	(7.3) 8.2–15.8 (17.7)	11.25	(4.9) 5.0–11.5 (12.1)	8.40	20

2.9–4.7 (–4.8) μm in diam. ($n = 40/2$). Cystidia tubular, usually basally widened, tapering to a blunt or very rarely acute apex, (56.4–) 59.6–104.2 (–117.9) \times (6.3–) 6.5–10.8 (–11.3) μm ($n = 60/3$), projecting up to 70 μm beyond the hymenial layer, walls first gradually thinning out, later more or less equally thickened throughout, up to 1.5 μm thick; encrustation irregularly present, apical or scattered at the middle part of cystidia, rarely covering the whole cystidium, consisting of discrete angular crystals. Basidia clavate, (16.6–) 17.8–27.3 (–29.2) \times (4.3–) 4.4–5.2 (–5.3) μm ($n = 17/2$). Basidiospores broadly cylindrical to narrowly ovoid, (4.2–) 4.3–6.1 (–6.2) \times (2.3–) 2.4–3.2 (–3.3) μm ($n = 120/4$), $L = 5.00$, $W = 2.83$, $Q = 1.71$ –1.86, ventral side often flat or slightly convex, in some spores indistinctly concave; oil droplets often present. Resinous droplets rare or absent. Basidiospores in some older collections occasionally reaching 8 μm long; they are excluded from measurements given above.

Notes. The best features for recognizing *P. alnea* subsp. *lubrica* are more or less gelatinized hymenium and strongly agglutinated basal hyphae. Its basidiospores are narrower than in *P. alnea* s. str. (Table 2). *P. alnea* subsp. *lubrica* is widely

distributed along the Pacific Northwest coast, inhabiting fallen branches and logs of both conifer and hardwood trees.

Phanerochaete robusta Parmasto, Consp. Syst. Cort.: 220, 1968.

Holotype. Russia. Primorie: Khasan Dist., Kedrovaya Pad' Nat. Res., angiosperm (fallen branch), IX.1961 Parmasto (LE, K ex TAAM 14125 – isotypes, studied).

= *Phanerochaete aurantiobadia* Ghobad-Nejhad, S.L. Liu & E. Langer, Mycological Progress 14 (68): 4, 2015.

Holotype. China. Jilin: Antu Co., Changbai Nat. Res., angiosperm (stump), 7.IX.2011 Ghobad-Nejhad 2288 (BJFC) (not studied, see description in Ghobad-Nejhad et al. 2015).

Phanerochaete robusta is an East Asian species with reddish-orange basidiocarps that turn bright red in KOH. Microscopically, it is recognizable by enclosed cystidia and by cylindrical to narrowly ovoid basidiospores, (4.9–) 5.0–7.1 (–8.1) \times (2.1–) 2.2–3.0 (–3.1) μm ($n = 30/1$), $L = 5.98$, $W = 2.59$, $Q = 2.32$ (measured from the isotype in K). It was described from Primorie, Russian Far East (Parmasto 1968). *Phanerochaete aurantiobadia*, recently described from the

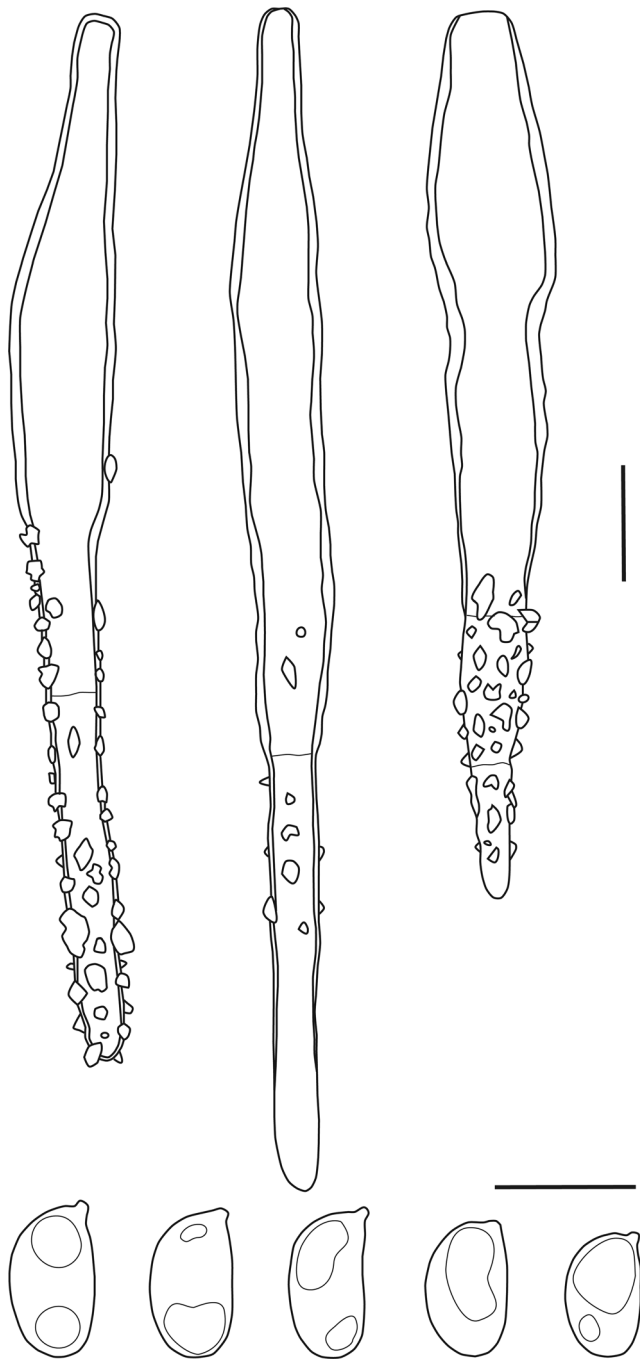


Fig. 5 *Phanerochaete alnea* subsp. *lubrica* (holotype): cystidia and basidiospores. Scale bar = 5 μ m (basidiospores), 10 μ m (cystidia)

adjacent part in China (Ghobad-Nejhad et al. 2015), shows no morphological differences when compared to *P. robusta* and is therefore considered its synonym. ITS sequences from the type specimens of *P. robusta* and *P. aurantiobadia* are identical.

Phanerochaete velutina (DC.) P. Karst., Kritisk Öfvers. Finlands Basidsvampar 3: 33, 1898. – Figs. 6 and 7c–d.

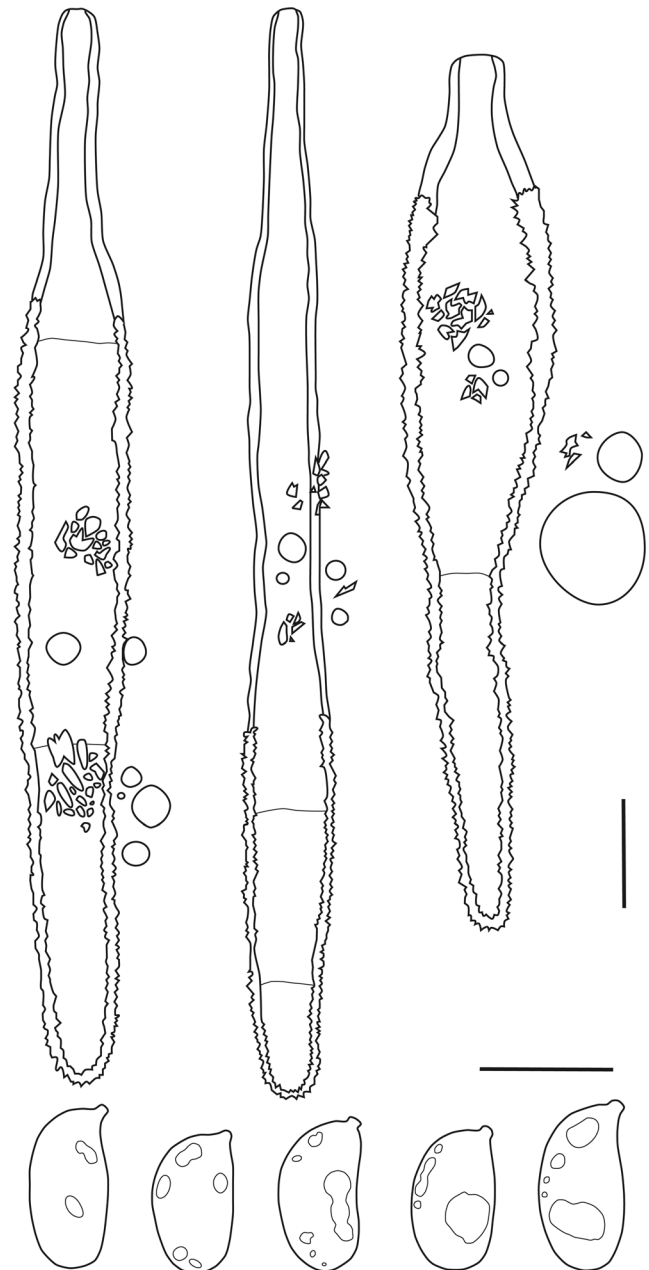


Fig. 6 *Phanerochaete velutina* (Spirin 9343): cystidia and basidiospores. Scale bar = 5 μ m (basidiospores), 10 μ m (cystidia)

\equiv *Thelephora velutina* DC., Flora Française 6: 33, 1815.

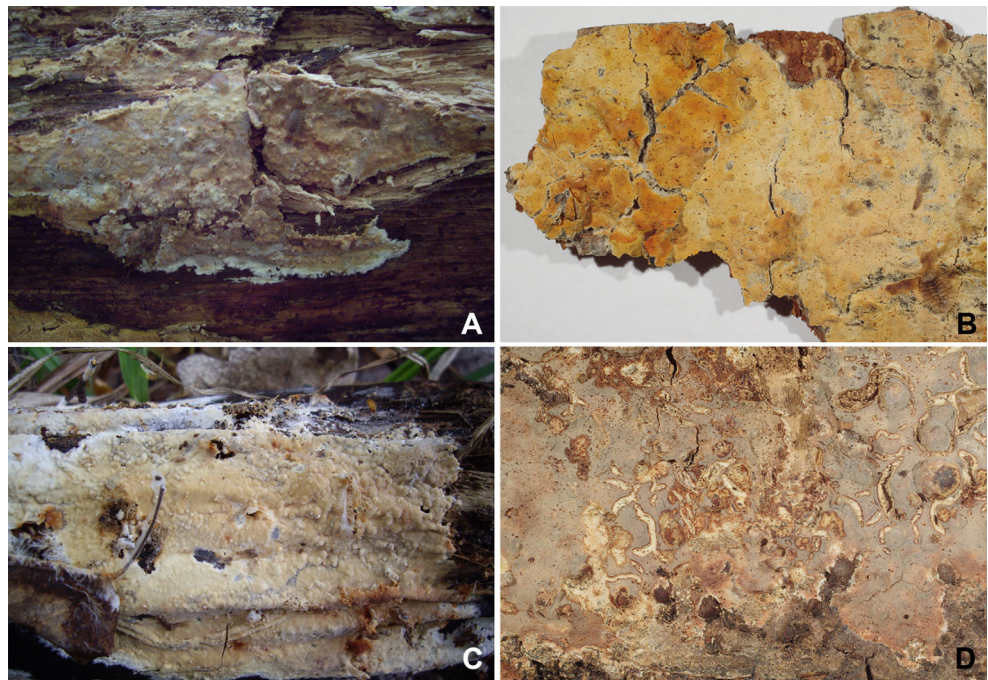
Lectotype. Switzerland. Jura, *Quercus* sp., 1813 Chaillet (G 00273767, studied) (selected by Burdsall 1985: 136, indicated as “holotype”).

= *Corticium decolorans* P. Karst., Bidr. Känned. Finlands Nat. Folk 37: 144, 1882.

Lectotype. Finland. Etelä-Häme: Tammela, *Salix* sp., X.1879 Karsten 1405 (H, studied) (selected by Eriksson et al. 1978b).

Basidiocarps resupinate, membranous, up to 20 cm large, 0.2–0.5 mm thick. Margin first distinct, fibrillose, white,

Fig. 7 Fresh basidiocarps (a, c) and herbarium specimens (b, d) of *P. alnea* (a – Spirin 10288, b – neotype of *T. alnea*) and *P. velutina* (c – Spirin 9343, d – Pilát VIII.1938)



sometimes fimbriate with well-developed short hyphal strands, later more or less compact, thinning-out, often paler than hymenial surface, up to 1 mm wide. Hymenium ceraceous, pale to bright pink, in vigorously growing specimens with scattered dark red dots, in dry basidiocarps pink to pinkish ochraceous, sometimes with greyish hues, almost unchanged in aged herbarium specimens, no color change in KOH.

Hyphal structure monomitic; hyphae mostly clampless.

Hyphae in hyphal strands parallel, with distinct (up to 2 µm thick) walls, clampless or with occasional clamps, 5–17 µm in diam., often densely encrusted with angular crystals. Subicular hyphae parallel to interwoven, densely packed but not agglutinated, with thickened walls, mostly clampless but occasionally with large solitary or double clamps, branched at acute angles, (4.6–) 5.3–11 (–12.2) µm in diam. ($n = 120/6$), often encrusted by tightly arranged angular crystals or bearing solid crystalline encrustation. Subhymenial hyphae interwoven or more or less vertically arranged, clampless, thin- to slightly thick-walled, (2.7–) 3–5.2 (–5.3) µm in diam. ($n = 100/5$). Cystidia tubular to obclavate, in most cases basally widened, tapering towards an obtuse apex, (45.5–) 55.1–142.3 (–159.6) × (6.3–) 6.6–15.8 (–17.7) µm ($n = 200/10$), projecting up to 100 µm beyond hymenium, walls more or less evenly thickened throughout, up to 3 µm thick; encrustation always present at apex, often covering the entire projecting part, first consisting of discrete angular crystals, later aggregated into a solid sheath. Basidia clavate, (19.4–) 21.2–40.8 (–41.0) × (4–) 4.4–6 (–6.2) µm

($n = 62/5$). Basidiospores ellipsoid, rarely broadly cylindrical (longest spores only), (4.7–) 4.8–7.2 (–7.3) × (2.6–) 2.7–3.6 (–3.8) µm ($n = 340/11$), $L = 5.55$, $W = 3.05$, $Q = 1.67$ –1.98, ventral side often slightly convex, rarely flat or somewhat concave; oil droplets often present. Resinous droplets usually abundant in mature specimens, brownish, found mostly on tramal and subhymenial hyphae, as well as on cystidia.

Notes. *P. velutina* was introduced by De Candolle (1815) as *Thelephora velutina* DC. The original specimen collected by Chaillet in Jura (G) was called holotype by Burdsall (1985) but is properly a lectotype. It is in perfect condition and agrees well with the species concept of *P. velutina* presented here. The protologue of *C. decolorans* P. Karst. was based on at least two collections so labelled by Karsten at H. One specimen is *P. alnea* and the other is *P. velutina* in the current sense. Eriksson et al. (1978) selected the latter specimen (Karsten 1405) as a lectotype of *C. decolorans*; therefore, *C. decolorans* is a later synonym of *P. velutina*.

Differences of *P. velutina* from *P. alnea* are discussed above. The North American *P. rhodella*, recently recognized as a distinct species (Floudas and Hibbett 2015), is similar to *P. velutina* macroscopically but has on average smaller cystidia and basidiospores (Tables 2 and 3).

The geographic distribution of *P. velutina* is uncertain because the name has been applied to several species. Most Canadian and US records of *P. velutina* on angiosperm hosts refer to *P. rhodella*; however, *P. velutina* occurs in Alaska based on three sequenced specimens (Floudas and Hibbett 2015). European and North American specimens of

P. velutina collected from conifers probably represent *P. alnea*. Verified records of *P. velutina* from coniferous hosts are known so far from the Russian Far East. These collections possess wider cystidia than specimens of *P. velutina* from Europe; however, there is no DNA evidence to support their recognition as a separate taxon.

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