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The identity of European and North American *Boletopsis* spp. (Basidiomycota; Thelephorales, Boletopsidaceae)

Roy Watling¹ and Jeremy Milne²

¹*Caledonian Mycological Enterprises, Edinburgh, EH4 3HU, Scotland, UK.* ²*Royal Botanic Garden, Edinburgh, EH3 5LR, Scotland, UK*

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Corresponding author: R. Watling, caledonianmyc@compuserve.com. Accepted for publication October 4, 2007. <http://pnwfungi.org> Copyright © 2008 Pacific Northwest Fungi Project. All rights reserved.

Abstract. The identity of *Boletopsis* collections from North America was compared with material from Europe using molecular techniques. Sequencing of the complete ITS region was conducted to see whether or not the European material could be correlated with that from North America as the presently accepted synonymy would suggest. It was found that the North American collections could be separated into two taxa. *Boletopsis grisea*, as previously reported for material from both Eastern and Western States of North America; and a second taxon, *B. perplexa*, a newly recognized species from the British Isles, and not European *B. leucomelaena*, as

the literature would suggest. There appears to be at least four distinct species of *Boletopsis* in North America: *B. grisea*; *B. perplexa* recently described from native *Pinus sylvestris* woodlands of Scotland; *B. smithii*; and an undetermined taxon. The latter requires further collections and analysis.

Key Words: *Boletopsis*, *B. grisea*, *B. perplexa*, *B. smithii*, Eastern North America, West Coast North America, biogeography, mycorrhiza

Dedication

It is a great pleasure to be able to offer a contribution to honour the work of Jack Rogers which has spanned many years. Although he rarely studied in depth members of the Basidiomycota we believe that this article is in the spirit of his understanding of how mycology should be conducted, that is to marry classical morphological and ecological methods with modern techniques. No method is better than any other and often one method answers questions spawned by others. Here we demonstrate this phenomenon amongst a group of terrestrial polypores known to occur in Jacks' own 'backyard'.

Introduction: *Boletopsis* world-wide is a rather small genus of ectomycorrhiza forming, stipitate poroid fungi characterised by irregularly polygonal, angular, hyaline to pale brown basidiospores. It is phylogenetically related to *Thelephora*, *Tomentella* and many of the stipitate hydroid fungi. It is comfortably accommodated in the Thelephorales albeit being the only poroid member, a feature which places it in the Boletopsidaceae. Three species are recognized in the literature, viz. *B. leucomelaena* (Pers.) Fayod, the type of the genus, *B. grisea* (Peck) Bond. & Sing. and *B. smithii* K. Harrison, the last a fungus based on a single collection from Washington State, USA. The nomenclature of the first two species has been hotly disputed over the years but the arguments clearly stated by Niemelä & Saarenoksa (1989) in their monograph of European members are now universally accepted.

Boletopsis leucomelaena is found with *Picea* throughout Scandinavia and beyond but is nowhere as frequent as the closely related and very similar *B. grisea*. The latter

although less restricted in its occurrence is always found with *Pinus*. It is recorded from the Canary Islands, France, Germany, Poland, Spain, Switzerland as well as the Nordic Countries. It appears to avoid the Atlantic fringe and apparently is more common northwards. In North America Overholts (1953) notes *B. grisea* from Alaska, New Hampshire, Massachusetts, Michigan, Montana, New Hampshire, New Jersey, New York, North Carolina, Pennsylvania, Tennessee and Washington. Gilbertson & Ryvarden (1986) may add other States in their listings under *B. subsquamosa* (Fr.) Kolt. & Pouzar, but only re-examination of the material would be able to confirm these sightings. From our own observations *B. leucomelaena* is also recorded from the Pacific Northwest and from Japan. In Europe it is known from Scandinavia but with few records from the west, Denmark (Vesterholt & Knudsen, 1990), Poland (Wojewoda & Lawrinowicz, 1986), the Netherlands (Arnolds, 1995), Scotland (Smith & Rea, 1907; see Coppins & Watling, 1997), Slovakia (Kotlaba, 1984) and Switzerland (Breitenbach & Kränzlin, 1986). Gilbertson & Ryvarden

(1986) supply further distributional data for Austria, Bulgaria, Estonia, Italy, Lithuania, Spain and the former Yugoslavia. Subsequent work by Watling & Milne (2007) has shown the Scottish collections of *B. leucomelaena* to represent a distinct entity and a sequence in GenBank based on Korean material of *B. leucomelaena* (Accession C.G. Harms) aligns with *B. grisea*. With such confusion it is essential to compare collections from Europe and other sites to ascertain their con-specificity and the present study is a preliminary approach to understanding members of the genus *Boletopsis* in North America.

Methods and Materials: Specimens used for morphological and molecular examination:

Boletopsis sp. - **United States**. Oregon. Wild Cat Mts. legit M. Rogers, 15 x 1995, E (Rec227609) – Genbank Accession EF547900; along Main Highway # 2, Diamond Lake, 25 miles from Crater Lake, with *Pinus contorta*, 5,000 ft., 13 x 2002, E (Rec227656) – Genbank Accession EF457903. New York State, Franklin Co., Slush Pond Road, Paul Smith's, legit S. Hopkins, under *Pinus sylvestris*, 14 ix 2004, E (Rec227653) - Genbank Accession EF457902.

Boletopsis grisea - **Finland**. Etelä-Savo, Kerimäki commune, Ruokojärvi, Keplakko, north of Lake Ylä-Kieluu, east side of road, Multamäki, between tracks in dry pine heath forest, alt. 90m. sm., 1 x 1994, coll. I. Kytövuori No. 94-1247, H with duplicates in E (Rec227607) – Genbank Accession DQ408768. St.Säkylä, Säkylänharju, NW side, in pine wood, 13 x 1997, coll. T. Niemelä (6166), Yu-Cheng Dai & I Pipponen, H with duplicates in E (Rec227608) – Genbank Accession DQ408769. Kniventtu, viii 2001, purchased at Dye conference viii 2001, coll.

K. & M. Palmen, legit S. Hopkins, E (Rec227609) - Genbank Accession DQ408770. **United States**. Washington. Wind River, Gifford Pinchot, 1 x 2004, coll. S. Hopkins, E (Rec227649) - Genbank Accession EF457898. Oregon: (Dark Top-*Boletopsis*) Oregon Mushroom Group, autumn show, legit Maggie Rogers, det. Judy Roger & L. Norvell as *B. grisea*, 22 x 2000, E (Rec227652) - Genbank Accession EF457901.

B. leucomelaena – **Finland**. Varsinais-Suomi, Karjaa commune, Mustio, NW of village, Kohagen, near waterside of Bruksträsket, between Bällbyströmmen, & 6677 grid boundary, rich grass-herb spruces forest with some pines and abundant hardwoods, e.g. *Corylus avellanea*, 20 viii 1988, coll. P. & I Kytövuori No. 88-669; duplicate collection, H with duplicates in E; U. Sippo, Hindsby, 9 x 1985, on soil humus, in grass-herb forest with *Corylus avellanea*, *Picea*, *Populus* and *Betula* in sloping grass-herb rich forest, coll. T. Niemelä (3325) & R. Saarenoksa, H with duplicates in E; Hameenlinna, Ahvenistonharju, 22 viii 2004, in spruce dominated wood, coll. T. Niemelä & M. Lahti, H with duplicates in E (Niemela7749) - Genbank Accession DQ408771.

Boletopsis perplexa – **United Kingdom**. Scotland. Aberdeenshire, Invery Wood, near Braemar, on gravel bank under *Pinus sylvestris*, 11 iv 2001, coll. E. Holden, Wat., E (Holden 150627) - Genbank Accession DQ408766; ditto 9 x 2004, legit L. Holden, Wat, E (Holden 077897) - Genbank Accession DQ408767; Inverness-shire, Aviemore near Free Church, Rothiemurchus, Aviemore, in fir wood, ix 1876 coll. J. Keith, K; Rothiemurchus Forest, 1901, coll. A. Grant; Rothiemurchus Forest, ix 1906, coll. A. Grant. Rothiemurchus Forest, Loch an Eilean, 11 x 1963, coll. D.A.Reid.

Boletopsis subsquamosa – **United States.** Connecticut. Big Low Hollow State Park, nr Sturbridge (Massachusetts), with Hemlock viz. *Tsuga canadensis*, legit S. Hopkins 23 ix 2000, E (Rec227658) - Genbank Accession EF457899.

Molecular studies: DNA was extracted from dried specimens following a modified version of the protocol in Gardes & Bruns (1993). 20-50mg of tissue were collected into separate 1.5 ml Eppendorf tubes, frozen in liquid nitrogen and then crushed and ground with a micro-pestle in the tubes. DNA was incubated with 2x CTAB lysis buffer, washed twice with chloroform: isoamyl alcohol (24:1), precipitated overnight at -20 °C in an equal volume of ice-cold isopropanol and resuspended in 50 µl of TE buffer.

The primers used for PCR-amplification were the fungal specific ITS1-F (Gardes & Bruns 1993) and universal ITS4 (White et al. 1990). A 1 µl aliquot of DNA was included in a final reaction volume of 25 µl consisting of the following components (given as final concentrations): 1x reaction buffer; 200µM dNTP's; 2.5mM MgCl₂; 0.3 µM primers; 0.025 units/µl Biotaq DNA polymerase (Bioline). The reaction mix was made up to final volume using sterile distilled water. The cycling parameters set for the PTC-200 Peltier DNA Thermal Cycler (MJ Research) were as follows: initial denaturation at 94 °C for 3 minutes; 30 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 60 s and extension at 72 °C for 90 s; final extension at 72 °C for 10 minutes; stored at 4 °C at end of reaction.

Prior to sequencing, PCR products were cleaned using Qiaquick purifying columns (Qiagen). The complete ITS region was sequenced using primers ITS1-F and ITS4. Sequencing reactions and clean-up of products were carried out according to the

protocols recommended for use with the CEQ 8000 (Beckman) sequencer.

Sequences were aligned in BioEdit v7.0 (Hall 1999) along with six sequences obtained from European *Boletopsis* material as part of another study (Watling & Milne, 2007). (See Table 1 for complete list of sequences included in the alignment). Inferences regarding the identity of the North American specimens were made from pair-wise sequence percentage similarity calculations and examination of informative sites in the alignment.

Results: ITS sequences were successfully obtained from six specimens of the North American material (Appendix 1). Two of the undetermined specimens labelled *Boletopsis* sp. (EF457902, EF457903) were found to be the same as the sample from Oregon labelled *Boletopsis grisea* (EF457901). The sequences of all three of these samples closely matched those of *Boletopsis grisea* specimens from Finland (DQ408768, DQ408769, DQ408770). Therefore it is now possible to say that North American collections of *Boletopsis grisea* are indeed con-specific with European collections so-named based on the monograph of Niemelä & Saarenkso (1989). Furthermore the results showed that the North American collection labelled *B. subsquamosa* (EF457899) was the same as the *B. grisea* specimens, thus supporting the literature researches previously carried out (Niemelä & Saarenoksa, 1989). *Boletopsis grisea* therefore appears to be a pine associate widely distributed throughout Scandinavia and across the breadth of North America, both the United States and Canada.

Boletopsis leucomelaena, a species originally described from Europe ('*in Hercynia*' ut *Polyporus leucomelas* Persoon, 1801, i.e.

Graz Mts. Germany), is also recorded from North America. Surprisingly, no collections agreeing with the European view, a concept which follows that developed in Scandinavia over the years, were located amongst the specimens available to us. However, what was of great interest was a partial sequence from one collection from the Wild Cat Mts., Oregon (15 x 1995) (EF457900) which agreed with the newly described *B. perplexa* Watl. & Milne from Scotland (DQ408766, DQ408767). This latter species had itself been confused for a century or more in Britain with *B. leucomelaena*. *B. perplexa* and *B. leucomelaena* are molecularly similar, their ITS sequences differing by just 2 % (Appendix 3, Watling & Milne 2007), and this based on a small number of samples. However, intra-specific variation in ITS sequences of *B. grisea* samples from Europe and N. America is consistently less than 1% (Appendix 3, Watling & Milne 2007) suggesting that the difference of 2% between *B. perplexa* and *B. leucomelaena* is informative. Furthermore, Watling & Milne (2007) erected *B. perplexa* as a new species on the strength of ecological and morphological evidence that was strongly supported by the available molecular data. In essence, *B. perplexa* is a pine associate that is clearly differentiated from the other European pine associate, *B. grisea*, by its DNA and morphology and moderately differentiated from *B. leucomelaena* in DNA and morphology but expressing a different ecological habit (*B. leucomelaena* associates with spruce) (Watling & Milne 2007). Though the sequence fragment presented here is only 159 base pairs, the American specimen agreed with the Scottish specimens of *B. perplexa* at crucial informative sites (see positions 44, 52, 53, 135, 142, 144, 145, 195 in Appendix 2). Unfortunately field data are sparse for this collection and more work is patently required as *B. leucomelaena* is

recorded from the West coastal United States; see Ryvarden & Gilbertson, 1993. Perhaps there has been confusion with this species in Oregon also. In the field notes that accompany Hopkins' specimen from which sequence EF457901 (Rec 227652) was obtained, there was an indication that two species of *Boletopsis* were at the show (i.e. Oregon Mushroom Group Show in October 2000). 'One, they call *B. 'grisea'* and had a light top and one (named 'Dark top *Boletopsis*' by Hopkins) with a dark top'. Although her material agrees with *B. grisea* perhaps she was actually noticing the other species represented by the earlier collection from the Wild Cat Mountains (Rec 227609) and now known to possess a major portion of its DNA sequence in common with *B. perplexa* from Scotland.

Finally a further distinct sequence was obtained from a collection labelled *Boletopsis grisea* from Wind River, Gifford Pinchat (1 x 2004) (EF457898). This was separate from all other *Boletopsis* spp. (Appendices 2 & 3) but sadly field notes are lacking. The collector had no difficulty apparently in recognizing this as *B. grisea* but the molecular data indicate that this may be another, as yet unidentified, species.

With one collection aligning with *B. perplexa* and the additional unique sequence it looks as if at least two more *Boletopsis* spp., excluding *B. smithii*, are to be found in North America than previously described. Overholts (1953) described *B. grisea* (*ut Polyporus*) as growing 'on the ground in coniferous or deciduous woods'. There is a vast literature on the often rather tight specificity of many ectomycorrhizal fungi with their hosts so one might interpret Overholts concept as possibly covering some of the unusual entities noted above. Except for the morphology unfortunately we know very little about *B. smithii* as it was brought into a Mushroom

Fair by an amateur collector presumably collected in conifer woodland but the putative tree host is unknown (Harrison, 1972). We could therefore not make any sensible comparisons.

Discussion: Pilát (1936-42) recognized an affinity of *Polyporus subsquamosus* (L) Fr., considering it a species of *Caloporus*, with *Boletopsis grisea*. He not only considered them the same but purely a form of *B. leucomelaena* and for this entity used the epithet f. *subsquamosa* (L.) Pilat. Subsequent European authors retained the autonomy of these two fungi but differed in their interpretation of Fries' *Polyporus subsquamosus*. Ryvar den & Gilbertson (1986) went further by reinstating 'subsquamosus' to full specific rank making both *B. grisea* and *B. leucomelaena* synonyms of it, along with *Polyporus earlei* Underw., a species described from pine-woods in Auburn, Alabama, North America (Underwood, 1897). Later these same authors (Ryvar den & Gilbertson, 1993) considered *P. subsquamosus* as probably not a species of *Boletopsis* at all but possibly representing *Albatrellus ovinus* (Schaeff.: Fr.) Maire, something maintained by Niemelä & Saarenoksa (1989). According to Ryvar den & Gilbertson (1993) *Boletopsis leucomelaena* is a component of the central spruce forests of Scandinavia (Finland, Norway, Sweden) and these same authors indicate the species is 'circumboreal in the conifer zone but everywhere rare'. It is apparently a southern continental species. *Boletopsis grisea*, in contrast, grows in continental Europe in dry forest type with *Pinus sylvestris*, indeed similar to the habitats in which *B. perplexa* has been found in Scotland. It is known in such communities in Scandinavia (Finland, Norway and Sweden). In its North American distribution it has even been reported on decaying *Pinus* from Montana (Weir, 1915).

This observation alone does not indicate *Boletopsis* is a wood-rotter, as many ectomycorrhizal fungi will fruit on old stumps, trunks etc. under favourable conditions.

Boletopsis grisea was originally described by Peck (*ut Polyporus*, 1874) from Copake, Columbia Co., New York State and apparently the molecular data from a collection within its eastern range in the United States agrees with the Scandinavian collections but is distinct from the most recent Scottish collection known only from dry pine-woods. The identity of Asiatic collections may also need some attention as the identification of the single Korean sample included in the study and named *B. leucomelaena* agreed with *B. grisea* (Watling & Milne 2007). This is contrary to the fact that *B. leucomelaena* is generally considered the species distributed in this part of the world (Imazeki et al, 1988) and certainly in Japan. The name *Polyporus earlei* Underw. is available for use and may in fact represent one of the additional entities recognised in this study; more critical studies in North America are undoubtedly required. Whatever the result of such studies the previous simplified approach adopted by some authors is no longer supported by our own studies.

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Appendix 1. Summary of DNA sequences included in the sequence alignment.

Genbank Accession No.	Specimen voucher (E)¹	Locality	Habitat	Specimen label	Identity after molecular analysis
EF457898	Rec 227649	Wind River, USA	Unknown	<i>Boletopsis grisea</i>	<i>Boletopsis sp.</i>
EF457899	Rec 227658	CT, USA	<i>Tsuga canadensis</i>	<i>Boletopsis subsquamosa</i>	<i>Boletopsis grisea</i>
EF457900	Rec 227609	OR, USA	Unknown	<i>Boletopsis sp.</i>	<i>Boletopsis sp.</i>
EF457901	Rec 227652	OR, USA	Unknown	<i>Boletopsis grisea</i>	<i>Boletopsis grisea</i>
EF457902	Rec 227653	NY, USA	<i>Pinus sylvestris</i>	<i>Boletopsis sp.</i>	<i>Boletopsis grisea</i>
EF457903	Rec 227656	OR, USA	<i>Pinus contorta</i>	<i>Boletopsis sp.</i>	<i>Boletopsis grisea</i>
DQ408766	Holden 150627	Scotland	<i>Pinus sylvestris</i>	<i>Boletopsis perplexa</i>	<i>Boletopsis perplexa</i>
DQ408767	Holden 077897	Scotland	<i>Pinus sylvestris</i>	<i>Boletopsis perplexa</i>	<i>Boletopsis perplexa</i>
DQ408768	Rec 227607	Finland	<i>Pinus sylvestris</i>	<i>Boletopsis grisea</i>	<i>Boletopsis grisea</i>
DQ408769	Rec 227608	Finland	<i>Pinus sylvestris</i>	<i>Boletopsis grisea</i>	<i>Boletopsis grisea</i>
DQ408770	Rec 227609	Finland	<i>Pinus sylvestris</i>	<i>Boletopsis grisea</i>	<i>Boletopsis grisea</i>
DQ408771	Niemelá 7749	Finland	<i>Picea</i>	<i>Boletopsis leucomelaena</i>	<i>Boletopsis leucomelaena</i>

¹ Royal Botanic Garden Edinburgh

Appendix 3. Pairwise percentage similarity of American *Boletopsis* DNA sequences with Scottish and European *Boletopsis* DNA sequences. Values in brackets represent the number of overlapping base pairs in each pairwise alignment. Sites with missing data and mutual gaps were ignored.

			<i>B. perplexa</i>	<i>B. perplexa</i>	<i>B. grisea</i>	<i>B. grisea</i>	<i>B. grisea</i>	<i>B. leucomelaena</i>
			Scotland	Scotland	Finland	Finland	Finland	Finland
			DQ408766	DQ408767	DQ408768	DQ408769	DQ408770	DQ408771
<i>B. grisea</i>	Wind River, USA	EF457898	94.4 (611)	94.8 (654)	93.5 (657)	93.5 (657)	93.2 (473)	95.0 (655)
<i>B. subsquamosa</i>	Connecticut, USA	EF457899	95.0 (602)	95.0 (602)	100 (600)	100 (600)	99.6 (456)	94.9 (603)
<i>B. sp.</i>	Oregon, USA	EF457900	98.7 (159)	98.7 (159)	93.2 (161)	93.2 (161)	88.1 (59)	96.2 (159)
<i>B. grisea</i>	Oregon, USA	EF457901	96.5 (457)	96.5 (457)	99.3 (457)	99.3 (457)	99.1 (341)	95.6 (458)
<i>B. sp.</i>	NY, USA	EF457902	95.1 (614)	95.4 (657)	100 (655)	100 (655)	99.6 (472)	95.3 (658)
<i>B. sp.</i>	Oregon, USA	EF457903	94.9 (613)	95.3 (656)	99.7 (655)	99.7 (655)	99.6 (472)	95.0 (657)
<i>B. leucomelaena</i>	Finland	DQ408771	97.9 (612)	98.0 (654)				

