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FULL PAPER

Vuilleminia erastii sp. nov. (Corticiales), an amphi-Beringian species and revision of the occurrence of *Vuilleminia comedens* in North America

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Abstract *Vuilleminia* is a basidiomycete genus the species of which have resupinate, corticioid fruiting bodies. It is apparently a North Hemisphere genus, and the majority of its species are distributed in Europe and western Asia. In North America, there are two reports of *Vuilleminia comedens*. Detailed study of North American specimens and comparisons with additional collections led to the conclusion that they belong to a new lineage named *Vuilleminia erastii* sp. nov., whose distribution extends from western North America to East Asia, Siberia, and Finland. The species is recognized by the decorticating fruiting bodies with preference for species of Betulaceae in the boreal zone, relatively small allantoid basidiospores, and little-developed cystidia with apical appendix.

Keywords Corticioid Agaricomycotina · Fungal taxonomy · Molecular systematics · Resupinate hymenophore · Vuilleminiaceae

Introduction

The corticioid basidiomycete genus *Vuilleminia* Maire (Vuilleminiaceae, Agaricomycotina) is a wood-inhabiting (lignicolous) member of the order Corticiales. Its species predominantly occur in Europe and western Asia (Ghobad-Nejhad et al. 2009, 2010). Species of *Vuilleminia* produce strictly resupinate and smooth fruiting bodies on (usually decorticated) surfaces of dead and weak branches and twigs of angiosperms. The species have large clavate basidia and large allantoid basidiospores, except for one species with fusoid-ellipsoid spores. The application of the genus name was recently safeguarded through conserving the generic type *Thelephora comedens* Nees for which a conserved type specimen was designated (Ghobad-Nejhad and Hallenberg 2010). The occurrence of *Vuilleminia* in North America has been limited to the rare finds of *V. comedens* (Nees) Maire in western Canada (Ginns 1989; Ghobad-Nejhad et al. 2010). Regarding the total absence of *Vuilleminia* in eastern North America, Ghobad-Nejhad et al. (2010) speculated that the presence of *V. comedens* in western Canada might have been the result of recent expansions from Eurasia through Beringia. We show here that this is not the case, however.

Ginns (1989), in the first report of *V. comedens* in North America, noted that the basidiospore sizes in the Canadian collection were smaller than the range described for the European samples. Accordingly, Ghobad-Nejhad et al. (2010) reported that "smaller spores (in *V. comedens*) can be seen in material from East Asia and western North America." Because of the variability of spore size in *Vuilleminia*, the small spores of Canadian material were first attributed to size variation within the species. Nevertheless, detailed morphological study of North American and East Asian specimens showed that they differ from *V. comedens* in some other characters. This finding, combined with the analyses of nuclear internal transcribed spacer (ITS) and large subunit (LSU) sequences, led us to describe these specimens as belonging to a new species.

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Materials and methods

Morphology and taxon sampling

Specimens were studied from the following herbaria: DAOM, H, TAA (acronyms from Index Herbariorum, http://sweetgum.nybg.org/ih/), and the Ghobad-Nejhad ref. coll. Observations were made under a binocular and light microscope, using bright-field and phase-contrast optics. Squash mounts were prepared in 5% potassium hydroxide (KOH), cotton blue in lactic acid (CB), and Melzer's reagent (IKI). Measurements were made in CB. At least 30 spores were measured per collection. In the description, Q is the variation in length:width ratios. Spore volume (V) was calculated from the equation of a revolution ellipsoid: $4\pi/3$ $(L/2) \times (W/2)^2$ (Gross 1972).

Samples for molecular analyses were chosen from herbarium material as follows: specimens with a clean and healthy-looking hymenophore were examined microscopically, and mature, spore-rich samples were selected for DNA work. Under a binocular and with a sterilized razor blade, a piece of hymenophore surface at least 5 mm^2 was carefully removed from the wood beneath and put into a new 1.5-ml Eppendorf tube. *Vuilleminia* samples are usually not so recalcitrant to DNA extraction. If clean and spore rich, herbarium materials up to 31 years old have also been positive. Taxon sampling for molecular study was improved by incorporating GenBank sequences (http://www.ncbi.nlm.nih.gov).

DNA extraction, amplification, and sequencing

All DNA samples obtained in this study were isolated from herbarium specimens. Total DNA extraction was performed using the DNeasy Plant Mini Kit (Qiagen, Sweden). Basidiomycete-specific primers ITS1F and ITS4B were used for amplifying nuclear ribosomal internal transcribed spacer regions (ITS1, 5.8S, and ITS2) (Gardes and Bruns 1993). Partial nuclear LSU region was amplified with LR0R and LR7 (Vilgalys Lab; http://www.biology.duke.edu/fungi/mycolab/primers.htm). The PCR amplifications were carried out using Ready-To-Go PCR Beads kits (Amersham Pharmacia Biotech, Uppsala) following the manufacturer's recommendations. PCRs were run on a MBS 0.2 G Thermal Cycler (Thermo Hybaid, Germany) with thermal cycling parameters as described by Ghobad-Nejhad and Hallenberg (2011). DNA concentration of the PCR products was measured with a Thermo Scientific NanoDrop 1000 spectrophotometer. Purification and sequencing of PCR products were performed by Macrogen (Macrogen, Seoul, Korea). The primers used for sequencing were the same as used for the PCR reactions. The obtained sequences were assembled in SeqMan NGen II version 4.0 (DNASTAR, USA) or Sequencher v. 4.1 (GeneCodes, Ann Arbor, MI, USA), and were submitted to GenBank (Table 1).

Alignment and model selection

The ITS and LSU datasets by Ghobad-Nejhad et al. (2010) were modified with emphasis on the members of Vuilleminiaceae and Punctulariaceae (sensu Ghobad-Nejhad et al. 2010). Sequences were aligned in MUSCLE (Edgar 2004) through the Web server version (http://www.ebi.ac.uk/Tools/msa/muscle/) and adjusted in PhyDE v. 0.995 (Müller et al. 2005). Rather than being hand cut, ambiguous parts of alignments were cut using Gblocks v. 0.91b (Castresana 2000). Outgroups were selected after Ghobad-Nejhad et al. (2010). Nucleotide models were estimated separately for ITS and LSU using MrModeltest v. 2.2 (Nylander 2004), implementing the Akaike information criterion. The best fitting models were SYM + invariant sites + gamma for ITS and GTR + invariant sites + gamma for LSU.

Phylogenetic analyses

Bayesian and maximum likelihood (ML) analyses were performed for inferring phylogenetic relationships. Bayesian searches were conducted with MrBayes v. 3.0B4 (Ronquist and Huelsenbeck 2003). The ITS dataset was analyzed using four independent runs, each with eight MC^3 chains running for 10 million generations with tree and parameter sampling every 5,000 generations. Burn-in was set to discard 50% of samples, and majority-rule consensus trees were assembled from post-burn-in tree samples. For combined ITS and LSU dataset, searches were done with four independent runs and 40 million generations with tree and parameter sampling every 4,000 generations, with other parameters as for ITS. Bayesian analyses were performed on processors at the Finnish IT Center for Science, CSC (Espoo, Finland).

The ML analyses were performed for both datasets in RAxML (Stamatakis 2006) implemented in raxmlGUI v.0.93 (Silvestro and Michalak 2010), with the search strategy set to rapid bootstrapping and the GTRGAMMAI model of nucleotide substitution. The *stopping* criterion automatically inferred the number of replicates (Pattengale et al. 2009).

Results

The final ITS dataset covered 47 taxa and 526 bp, including 343 constant and 134 informative positions. All samples belonging to the new species reported here

Table 1 Specimens used in the molecular analyses and their GenBank (ITS, LSU) accession numbers

Species	Voucher	GenBank accession no.	
		ITS	LSU
Australovuilleminia coccinea Ghobad-Nejhad & Hallenb.		HM046875	HM046930
A. coccinea		HM046876	HM046931
Cytidia salicina (Fr.) Burt		–	DQ915478
C. salicina		GU590881	HM046921
Dendrocorticium polygonioides (P. Karst.) M.J. Larsen & Gilb.	Iran, East Azerbaijan, Oshtobin, on *Quercus*, 10.X.2006, Ghobad-Nejhad 504 (Ghobad-Nejhad ref. coll.); isolate MG27	**JN388011**	U80646
D. polygonioides		HM046877	AJ406531
D. roseocarneum (Schwein.) M.J. Larsen & Gilb.		–	AF393053
Dendrothele maculata (H.S. Jacks. & P.A. Lemke) P.A. Lemke		–	AY586652
Gloeophyllum abietinum (Bull.) P. Karst.		–	AJ583431
G. sepiarium (Wulfen) P. Karst.		–	AY333806
Punctularia strigosozonata (Schwein.) P.H.B. Talbot		DQ398958	AY586702
P. strigosozonata		–	AF518642
Punctulariopsis obducens (Hjortstam & Ryvarden) Ghobad-Nejhad		HM046918	HM046933
P. subglobispora (Hallenb. & Hjortstam) Ghobad-Nejhad		HM046917	HM046932
Veluticeps abietina (Pers.) Hjortstam & Tellería		–	EU118619
Vuilleminia comedens (Nees) Maire		HM046882	AF518666
V. comedens		HM046881	AJ406515
V. comedens		HM046898	AY586725
V. comedens		HM046880	–
V. comedens		HM046891	–
V. coryli Boidin, Lanq. & Gilles		HM046908	–
V. coryli		HM046903	–
V. coryli		HM046901	–
V. coryli		FJ820638	–
V. coryli		HM046906	–
V. coryli		HM046907	–
V. coryli		FJ481052	–
V. coryli		FJ481021	–
V. coryli	Turkmenistan, Kara-Kala, on *Acer turcomanicum*, 22.IV.1971, Parmasto 54967 (TAA); isolate MG135	**JN387995**	–
V. coryli		HM046884	–
V. coryli		HM046904	–
V. coryli		HM046902	–
V. coryli		HM046883	–

Table 1 continued

Species	Voucher	GenBank accession no.	
		ITS	LSU
V. coryli	Turkmenistan, Kara-Kala, on *Crataegus pontica*, 22.IV.1971, Parmasto 54999 (TAA); isolate MG136	**JN387996**	**JN388005**
V. cystidiata Parmasto		HM046909	HM046923
V. cystidiata		HM046911	HM046924
V. cystidiata		HM046912	HM046925
V. cystidiata		–	HM100715
V. erastii Ghobad-Nejhad	Russia, Primorsky, on *Corylus* sp., 28.IX.1979, Järva (TAA 93312); isolate MG121	**JN387997**	**JN388006**
V. erastii	Canada, Yukon, on *Betula glandulosa*, 1.VIII.1980, Ginns 5238 & Cody (DAOM 199025); isolate MG97	**JN387998**	**JN388007**
V. erastii	Finland, Pohjois-Savo, on *Betula pendula*, 8.VII.2004, Haikonen 23446 (H); isolate MG139	**JN387999**	**JN388008**
V. erastii	Canada, Yukon, on *Betula occidentalis*, 11.VII.1984, Ginns 8168 (DAOM 221371); isolate MG96	**JN388000**	**JN388009**
V. erastii	Russia, Primorsky, on *Betula dahurica*, 18.V.1983, Parmasto 105367 (TAA); isolate MG100	**JN388001**	–
V. erastii	Russia, Primorsky, on *Corylus* sp., 22.IX.1979, Järva (TAA 93228); isolate MG98	**JN388002**	–
V. erastii	Canada, British Columbia, on *Betula occidentalis*, 5.VI.2006, Ginns 11612 (DAOM 241443, Ex in H); isolate MG95	**JN388003**	**JN388010**
V. macrospora (Bres.) Hjortstam		–	AY586726
V. macrospora		HM046885	HM046927
V. megalospora Bres.		HM046913	–
V. megalospora		HM046914	–
V. megalospora		HM046886	–
V. megalospora		HM046887	HM046926
V. pseudocystidiata Boidin, Lanq. & Gilles	Armenia, Idzhevan, on *Cornus mas*, 16.X.1962, Parmasto 15670 (TAA); isolate MG87	**JN388004**	–
V. pseudocystidiata		FJ820499	–
V. pseudocystidiata		HM046915	–
V. pseudocystidiata		HM046916	–
V. pseudocystidiata		HM046888	HM046928

Numbers in bold were generated for this study. Voucher data are given for the new sequences

appeared in a distinct and well-supported clade (Fig. 1; PP = 1.00, ML = 92). The ML analysis of ITS dataset used 1,000 bootstrap replicates and yielded a tree topologically similar to the Bayesian phylogram, with the likelihood value ln = −2,591.689784. The ML branch support values are marked on the Bayesian tree in Fig. 1.

The combined ITS + LSU alignment covered 56 taxa and 1,226 bp, with 885 constant and 239 informative positions. The unknown *Vuilleminia* samples (Fig. 2) found a place within Vuilleminiaceae, on a well-supported clade (PP = 1.00, ML = 99). The ML analysis of the combined dataset used 500 bootstrap replicates and yielded a tree topologically similar to the Bayesian phylogram, with the likelihood value ln = −5,215.163618. The ML bootstrap values are marked on the phylogram in Fig. 2.

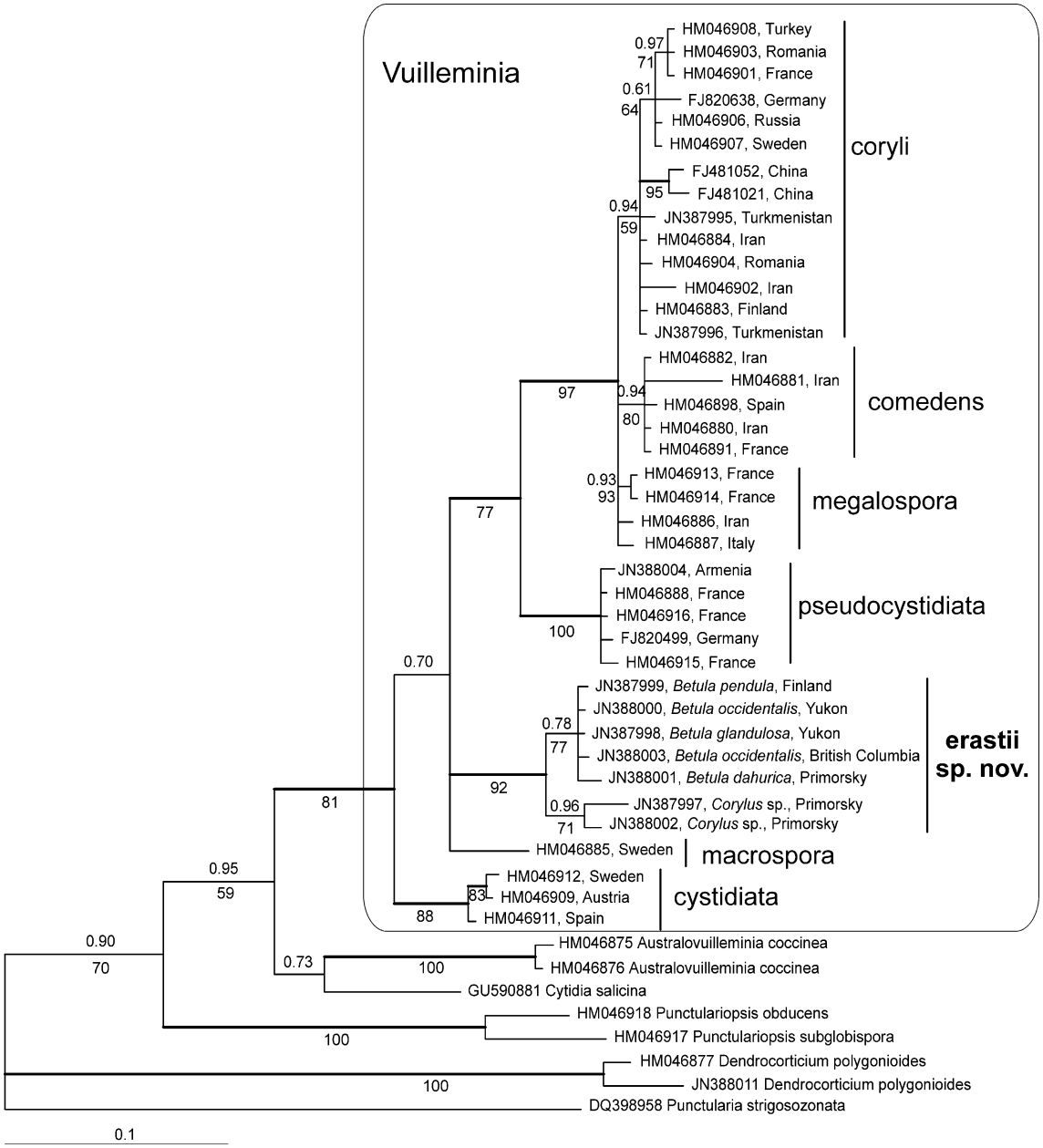

Fig. 1 Bayesian phylogram representing the phylogenetic relationships of *Vuilleminia* and the placement of *Vuilleminia erastii* sp. nov. inferred from internal transcribed spacer (ITS) sequences. *Numbers above branches* indicate Bayesian posterior probabilities (PP). *Branches in bold* indicate PP ≥0.99. *Numbers below branches* are ML bootstrap values ≥50. The tree is rooted with *Punctularia strigosozonata*

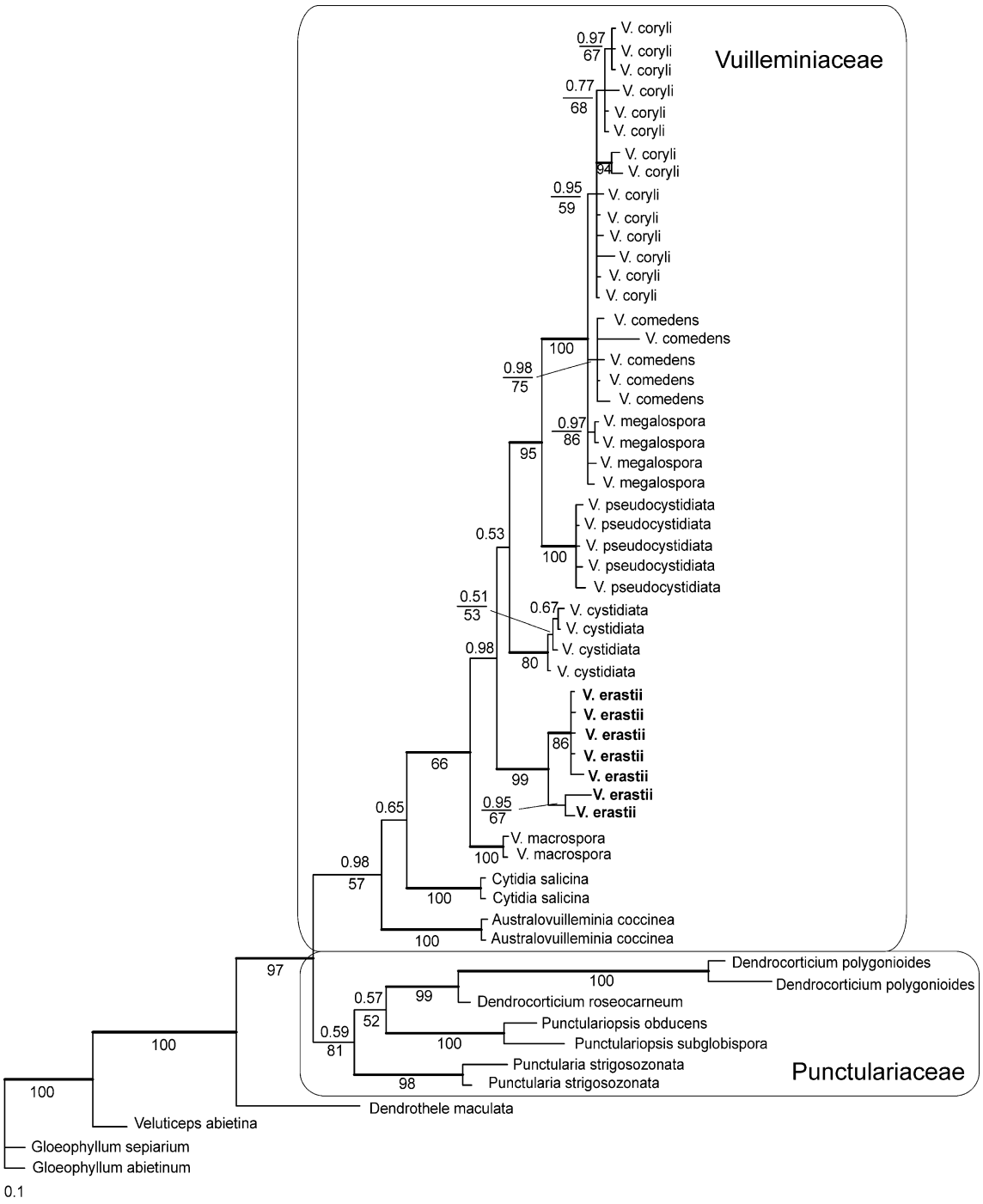

Fig. 2 Bayesian phylogram showing the placement of *Vuilleminia erastii* sp. nov. within Vuilleminiaceae. Tree inferred from analysis of combined ITS + LSU sequence datasets. *Numbers above branches* indicate Bayesian posterior probabilities (PP). *Branches in bold* have PP ≥0.99. *Numbers below branches* are ML bootstrap values ≥50. The tree is rooted with *Gloeophyllum sepiarium*

Taxonomy

Vuilleminia erastii Ghobad-Nejhad, sp. nov. Fig. 3

MycoBank no.: MB 561933

Basidiocarpium resupinatum, effusum, erumpens, ochraceum, gelatinosum, in sicco ceraceum, adnatum, ~200 µm crassum. Systema hypharum monomiticum; hyphae fibulatae. Basidia elongata, clavata, 4-sterigmata, flexuosa, 65–88(–100) × 7.5–8.5 µm. Cystidia debiliter evoluta, breviter clavata vel cylindrica, apicibus ramosis, 33–40 × 5–7.5(–12.5) µm. Dendrohyphidia praesentia. Basidiosporae allantoideae, laeves, (11.8–)12.0–15.5(–16.2) × 3.0–4.6(–5.2) µm, CB−, IKI−.

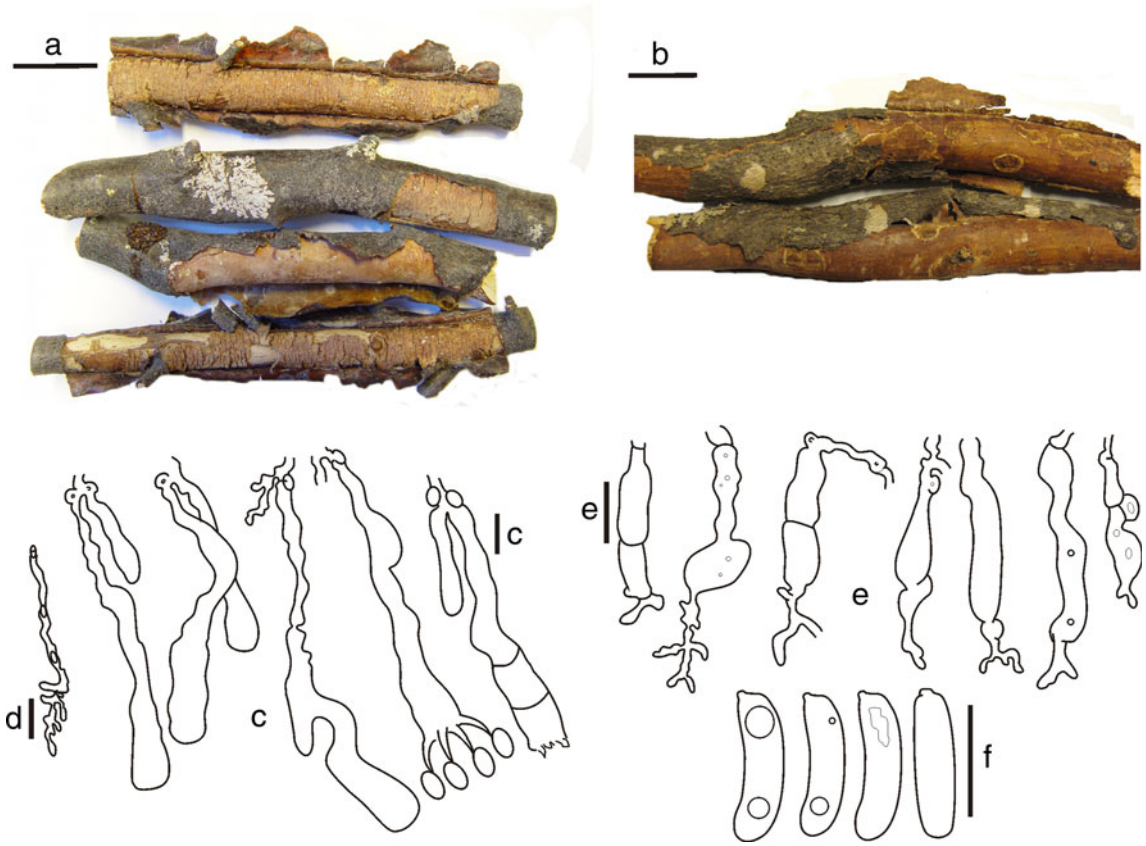

Fig. 3 Fruiting body of *Vuilleminia erastii* sp. nov. **a**, **b** Basidiocarps. **c** Basidia in different stages of development. **d** Dendrohyphidia. **e** Cystidia. **f** Basidiospores. **a**, **c–f** from holotype, **b** from paratype TAA 93228. *Bars* **a**, **b** 2 cm, **c–f** 10 μm

Typus: Canada, Yukon, South Canol Road km 12, 60°33′N, 133°12′W, on dead standing stem of *Betula glandulosa*, 1.VIII.1980, Ginns 5238 & W.J. Cody (holotypus, DAOM 199025).

rDNA sequence ex holotype: GenBank nos. JN387998 (ITS) and JN388007 (LSU).

Etymology: *erastii*, to honor the eminent Estonian mycologist Prof. Erast Parmasto, for his significant and long-term contributions to the knowledge of corticioid fungi.

Basidiocarp resupinate, erumpent, closely adnate, ochraceous, gelatinous when fresh, ceraceous when dry, ~200 μm thick; hymenium surface smooth, pruinose when young, cracking when old; margin indistinct. Hyphal system monomitic, hyphae thin-walled, CB−, not changing in KOH, with clamps at all septa, usually containing oil drops, interwoven, nodulose, sinuous, 2–3 μm wide. Subiculum indistinct.

Basidia first tubular or developing from rounded probasidia, arising at different levels of the hymenophore, becoming elongate, long clavate, thin walled, with a basal clamp, flexuose, with percurrent proliferation, 65–88(–100) × 7.5–8.5 μm, with four stout sterigmata 5–7 × 1.5–2.5 μm, contents granular, old basidia may develop 1–2 transverse septa. Cystidia rare, little developed, short clavate to cylindrical with a moderately branched apical appendix, 33–40 × 5–7.5(–12.5) μm, thin walled, contents usually lacking. Dendrohyphidia uncommon to frequent, 2.0–3.5 μm wide, smooth, thin walled, with clamps, contents granular.

Basidiospores allantoid, contents usually guttulate especially when seen in CB, (11.8–)12.0–15.5(–16.2) × 3.0–4.6(–5.2) μm, 13.8 × 4.0 μm on average, $Q = 2.55$–4.35, log $V = 1.74$–2.35, walls smooth, thin, CB−, IKI−, some old spores develop a transverse septum, typically germinating from the apiculus.

Paratypes: Canada, British Columbia, Naramata, Turnbull Creek, alt. ~633 m, 49°33′29″N, 119°33′23″W, on dead twigs 1.0–1.5 cm in diameter of *Betula occidentalis*, 23.XI.1999, Ginns 10970 (DAOM 241441), 8.XII.1999, Ginns 10982 (DAOM 241442, Ex in H), 5.VI.2006, Ginns 11612 (DAOM 241443, Ex in H) and 28.III.2010, Ginns 11853 (DAOM 241444). Yukon, Hwy. 9, km 15, NW of Dawson, 64°06′N, 139°34′W, on *Betula occidentalis* (as *B. fontinalis*), 11.VII.1984, Ginns 8162 (DAOM 221370) and Ginns 8168 (DAOM 221371). Finland, Pohjois-Savo, Kangaslampi, Rauhamäki, Rauhajärvi, mixed forest, on *Betula pendula*, 8.VII.2004, Haikonen 23446 (H). Russia, Primorsky, Terney Distr., Reservatum Sichote-Alinicum,

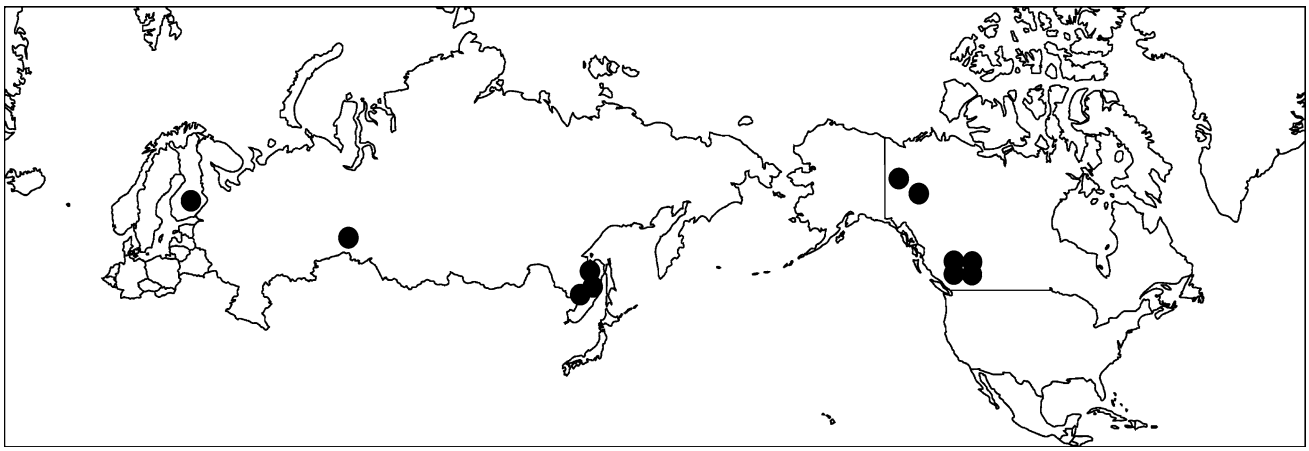

Fig. 4 Known distribution of *Vuilleminia erastii* sp. nov. based on specimens examined in this study

on branch of *Corylus* sp., 28.IX.1979, Järva (TAA 93312); Primorsky, Terney Distr., Reservatum Sichote-Alinicum, Kuruma, on branch of *Corylus* sp., 22.IX.1979, Järva (TAA 93228); Primorsky, Partizanski Distr., Sergeyevka, *Quercus* forest, on branch of *Betula dahurica*, 18.V.1983, Parmasto (TAA 105367); Siberia, Tyumen Province, Surgut Distr., at the river Bolshoy Yugan, Kayakovo, on very thin twig of *Betula* sp., 13.VI.1987, Saar (TAA 148631).

Habitat and distribution: On dead attached branches and twigs of *Betula* and *Corylus*: in western North America found on American dwarf birch (*Betula glandulosa*) and water birch (*Betula occidentalis*), a native species of western North America; in the Russian Far East found on *Betula dahurica* and *Corylus* sp. (cf. *C. heterophylla* or *C. sieboldiana* var. *mandshurica*); in western Siberia found on *Betula* sp.; and in Finland on *Betula pendula*. An amphi-Beringian species apparently confined to the boreal zone of the Northern Hemisphere, currently known from Yukon and British Colombia in Canada, Primorsky, western Siberia, and Finland (Fig. 4).

Discussion

Vuilleminia erastii is distinguished from *V. comedens* by its smaller basidia and spores and the presence of weakly developed cystidia. It is the only *Vuilleminia* species occurring on both sides of the North Pacific Ocean in the boreal zone of the Northern Hemisphere. The form of cystidia in *V. erastii* is unique in the genus. Other cystidiate *Vuilleminia* species have elongated cylindrical (lepto-) cystidia with rounded (*V. coryli* Boidin, Lanq. & Gilles, *V. macrospora* (Bres.) Hjortstam, and *V. pseudocystidiata* Boidin, Lanq. & Gilles) or pointed (*V. cystidiata* Parmasto) apices, whereas in *V. erastii* the cystidia are short cylindrical to short clavate and develop an apical appendix.

Regarding spore size (*V* values), *V. erastii* seems to have the smallest spores among *Vuilleminia* species, most comparable to those of *V. pseudocystidiata* (Fig. 5). Concerning the shape (*Q* values), spores of *V. erastii* resemble most of other *Vuilleminia* species, only differing from *V. macrospora* and *V. megalospora* Bres. (Fig. 5).

In their phylogenetic study, Ghobad-Nejhad et al. (2010) recognized a well-supported clade comprising *V. comedens*, *V. coryli*, *V. megalospora*, and *V. pseudocystidiata*, referred to as the 'core *Vuilleminia*' clade. One synapomorphy of the core *Vuilleminia* species is the presence of a unique 13-bp-long insertion at the 5′-end of their ITS2 alignment positions 34–46: TGTGCGGCTTGGA. It is here shown that the rest of the *Vuilleminia* species each have their specific base pair arrangement in this region, differing from the core *Vuilleminia* in one or two nucleotides (Table 2). *Vuilleminia erastii* is distinguished from the core *Vuilleminia* by its peculiar cystidia and by its order of nucleotides at the 5′-end of ITS2, with a C replaced with A: TGTG**A**GGCTTGGA. The genetic distances (ITS) between *Vuilleminia erastii* and other *Vuilleminia* species as well as with *Australovuilleminia coccinea* Ghobad-Nejhad & Hallenb. and *Cytidia salicina* (Fr.) Burt are shown in Fig. 6.

Recently, Ghobad-Nejhad et al. (2011) provided the first large-scale comparison of the composition of corticioid fungi in the Northern Hemisphere. In contrast to Europe where several monographic studies have been done on corticioid fungi (Eriksson and Ryvarden 1973, 1975, 1976; Eriksson et al. 1978, 1981, 1984; Hjortstam et al. 1987, 1988; Bernicchia and Gorjón 2010), no such comprehensive studies are available for corticioids in North America and especially in Asia. However, Ginns and Lefebvre (1993) provided a detailed synopsis of the systematics, geographic distribution, and ecology of more than 1,000 species of corticioid fungi in North America, and as an aid

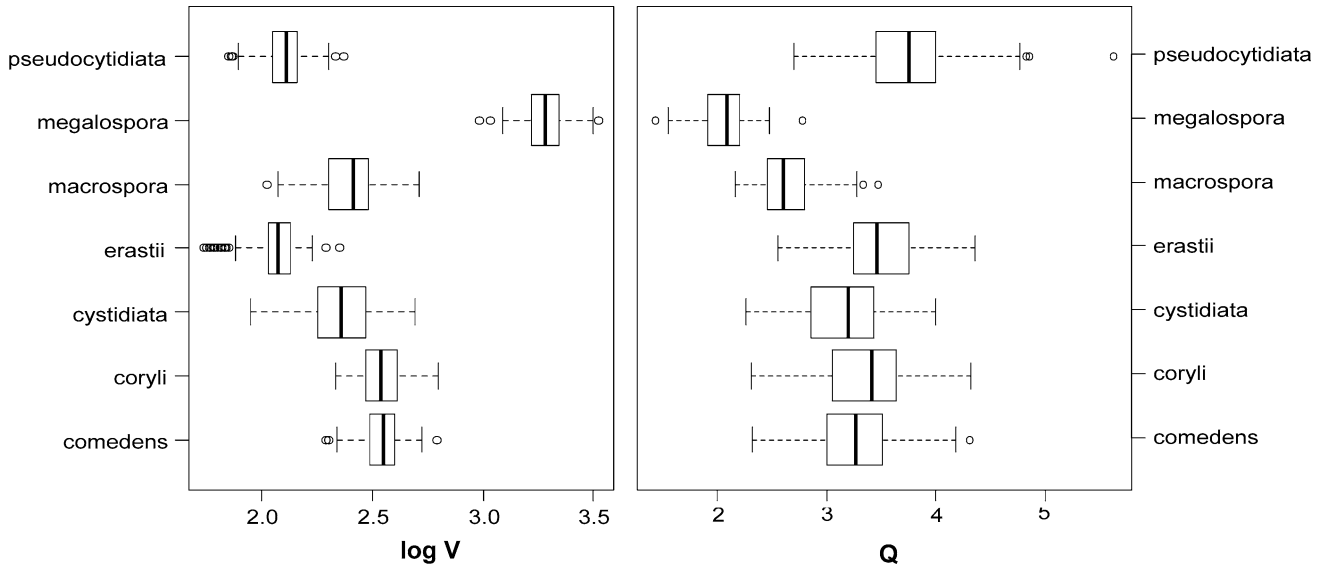

Fig. 5 *Box plots* representing the spore volume (log *V*) on the *left* and spore length:width ratio (*Q*) on the *right* for *Vuilleminia* species, measured from 150 spores of five collections per species. *Thick bars* are mean values

Table 2 A 13 bp long portion of ITS2 sequence in *Vuilleminia* species

Species differ from the core *Vuilleminia* in the nucleotides marked in bold. *Numbers in brackets* are the available observations

Species	Nucleotides in ITS2 alignment positions 34–46 (5′ → 3′)
Core *Vuilleminia* including *V. comedens*, *V. coryli*, *V. megalospora*, *V. pseudocystidiata* (48)	TGTGCGGCTTGGA
Vuilleminia cystidiata (6)	**C**GTG**A**GGCTTGGA
Vuilleminia erastii (7)	TGTG**A**GGCTTGGA
Vuilleminia macrospora (1)	TGTG**T**GGCTTGGA

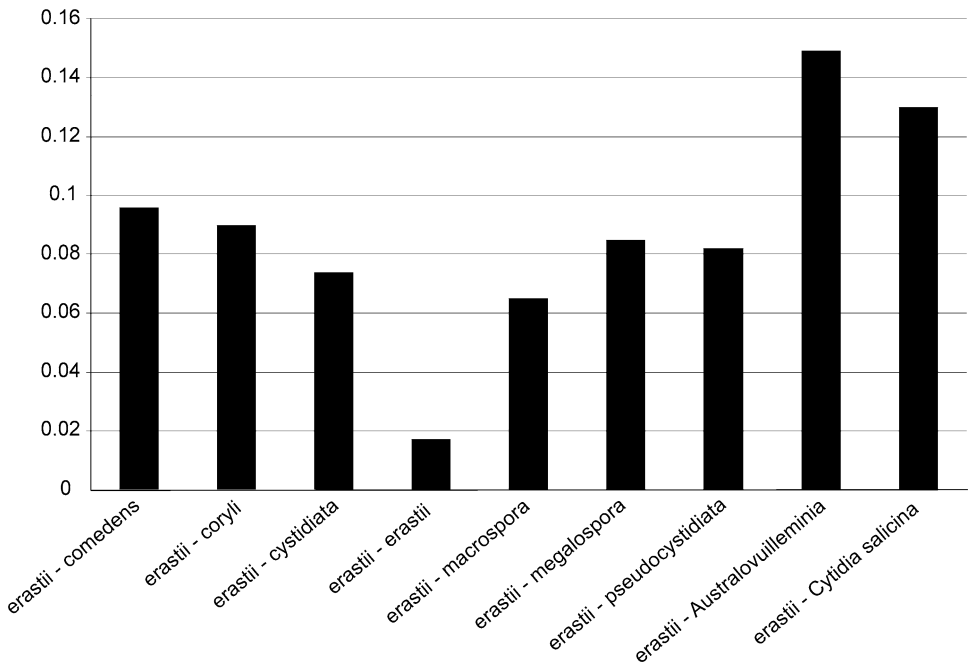

Fig. 6 Mean values of pairwise ITS genetic distances (uncorrected 'p', 5.8 s excluded) between *Vuilleminia erastii* and other *Vuilleminia* species as well as *Australovuilleminia coccinea* and *Cytidia salicina*

in the identification of specimens, Ginns (1998) gave the distinctive features of 165 genera, including keys to species and diagnostic features of the species.

The first report of the genus *Vuilleminia* from North America (Ginns 1989) was based upon a collection (Ginns 5238) from Yukon, Canada. This material and several other *Vuilleminia* collections from British Columbia and Yukon have been included in the present study. Their morphological characters and molecular data distinguish these collections from both *V. comedens* and other species of *Vuilleminia*, and we have named them *V. erastii*. As a result, the presence of *V. comedens* in North America could not be confirmed, and the name should be deleted from its mycota.

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Conflict of interest The authors have no conflict of interest and declare that the experiments comply with the current laws of Finland and Canada.

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