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ORIGINAL ARTICLE

Studies in the *Basidiodendron caesiocinereum* complex (Auriculariales, Basidiomycota)

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Abstract

Taxonomy of *Basidiodendron caesiocinereum* complex is revised based on morphological and molecular methods (with the use of nc LSU rDNA, ITS and *TEF1* regions). The basidiospore ornamentation is justified as a key morphological character for the species recognition in the group. As redefined here, *B. caesiocinereum* is an angiosperm-dwelling species with smooth basidiospores. *Bourdotia cinerella* and *B. cinerella* var. *trachyspora* are proved to represent separate species with warted basidiospores; they are reintroduced as *Basidiodendron cinerellum* and *B. trachysporum*. Additionally, eight new species related to *B. caesiocinereum* are described based on material from Eurasia, North America and Africa, and identity of *B. spinosum* from Oceania is discussed.

Keywords Basidiospores · Heterobasidiomycetes · Phylogeny · Taxonomy

Introduction

For almost two centuries, the basidiospore features, e.g. their shape, size, colour and ornamentation, have remained among the main features for morphological recognition of the basidiomycetous taxa. Almost all members of the *Auriculariales* (Basidiomycota) have small or medium-sized, colourless (hyaline), smooth basidiospores and three species with ornamented (warted or spiny) basidiospores have been so far detected in the genus *Basidiodendron* Rick (Wojewoda 1981). Two of them, *Basidiodendron asperum* (L.S. Olive) Wojewoda and *B. spinosum* (L.S. Olive) Wojewoda, are known from their type localities in Tahiti, while the third one, *B. caesiocinereum* (Höhn. & Litsch.) Luck-Allen, was reported from different geographic areas of the world (Wells and Raitviir 1975).

As re-defined by Luck-Allen (1963), the genus *Basidiodendron* Rick embraces effused wood-inhabiting fungi with smooth or minutely warted hymenophore, prominent gloeocystidia and longitudinally septate, predominantly four-celled basidia. It differs from the morphologically similar genus *Bourdotia* (Bres.) Bres. & Torrend in having waxy or arid, non-hygroscopic basidiocarps and on average shorter basidia devoid of a basal stalk (Luck-Allen 1963, Wells and Raitviir 1975). Recent phylogenetic studies confirmed that *Basidiodendron* and *Bourdotia* should be treated as separate

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genera (Weiß and Oberwinkler 2001, Spirin et al. 2020). While re-describing *B. caesiocinereum*, Wells (1959) and Luck-Allen (1963) noted it may have smooth or ornamented basidiospores. McNabb (1969) and Gilbertson (1974) found this feature taxonomically insignificant. On the contrary, Oberwinkler (1963) designated warted-spored collections as *Bourdotia caesiocinerea* (Höhn. & Litsch.) Bourdot & Galzin var. *trachyspora* and clearly separated them from the smooth-spored *B. caesiocinerea* s. str. Based on nrLSU sequences, Weiß and Oberwinkler (2001) showed these taxa are not conspecific and they belong to *Basidiodendron*, although no explicit taxonomic conclusions were proposed. Finally, Roberts (2001) subsumed the warted-spored specimens of *B. caesiocinereum* under *B. spinosum*. To investigate this problem more closely, we examined type specimens of *Corticium caesiocinereum* Höhn. & Litsch. (= *Basidiodendron caesiocinereum*) and *Sebacina spinosa* L.S. Olive (= *B. spinosum*), as well as authentic material of *Bourdotia cinerella* Bourdot & Galzin (incl. var. *trachyspora*) (to date, a synonym of *B. caesiocinereum*) and a number of *B. caesiocinereum* s. lato specimens from boreal – temperate Eurasia, North America (USA and Mexico) and Africa (Malawi). Additionally, a DNA study based on three markers (nc LSU rDNA, ITS and *TEF1*) was conducted. Results of this study are presented below.

Material and methods

Morphological study

Type specimens and collections from herbaria H, O, GENT, LE, FH, PC, NY, TAAM, TU, CWU were studied. Herbarium acronyms are given according to Thiers (2020). Microscopic routine and terminology follow Spirin et al. (2020). All measurements were made from microscopic slides mounted in Cotton Blue, using phase contrast and oil immersion lens (Leitz Diaplan microscope, ×1250 magnification). At least 20 basidia, 10–20 gloeocystidia and 20–30 basidiospores were measured for each specimen studied. The following abbreviations are used in the taxonomic section: L, mean basidiospore length; W, mean basidiospore width; Q', L/W ratio; Q, mean L/W ratio; and n, number of measurements per specimens measured. Advances of phase contrast illumination versus bright-field microscopy are explained in Stein (1969). For microscopic study, we subjectively determined an accuracy of measurements as 0.1 µm. These measurements (including those for the basidiospore ornamentation elements, i.e. warts or spines) were subsequently calibrated with the scanning electronic microscope (SEM). For preparing SEM photos, basidiocarps were coated with a 25-mm layer of gold-palladium using an Eiko IB-3 sputter coater. Micrographs were taken using JSM-6380LA microscope at the Moscow State University (Russia) and JEOL JSM-7100FLV field emission microscope at Botanical Garden Meise (Belgium).

DNA study

In total, 80 specimens were selected for molecular sampling (Table 1). We performed PCR directly from small fragments of dried basidiocarps (without prior DNA extraction) using Phire Plant Direct PCR Kit (Thermo Scientific) according to the manufacturer's instructions. DNA extraction of Belgian and Dutch collections was done using the DNeasy Plant Mini kit (Qiagen).

The following primers were used for both amplification and sequencing: the primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990) for the nrITS1-5.8S-ITS2 region, primers EF1-983F and EF1-1567R (Rehner and Buckley 2005) for a part of the *TEF1* region and primers JS1 (Landvik 1996) and LR5 (Vilgalys and Hester 1990) for D1-D3 domains of nc LSU rDNA region. PCR products were purified applying the GeneJET Gel Extraction and DNA Cleanup Micro Kit (Thermo Scientific). Sequencing was performed with an ABI model 3500 Genetic Analyzer (Applied Biosystems). Raw data were edited and assembled in MEGA 7 (Kumar et al. 2018). Molecular studies were mostly carried out at the centre for collective use of scientific equipment "Cellular and molecular technology of studying plants and fungi" (Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg, Russia) and the centre for molecular phylogeny and evolution (CeMoFe) (Ghent University, Belgium).

For this study, 76 ITS, 30 *TEF1* and 35 nc LSU rDNA sequences were generated (Table 1). Additionally, 71 ITS and 61 nc LSU rDNA sequences, including the outgroup, were retrieved from GenBank and UNITE (www.ncbi.nlm.nih.gov/genbank/; https://unite.ut.ee/). Sequences were aligned with the MAFFT version 7 web tool (http://mafft.cbrc.jp/alignment/server/) with subsequent manual processing.

Three datasets were prepared for the present study: (1) ITS + nc LSU rDNA dataset (1647 characters including gaps) used to reconstruct a general topology of the *Auriculariales*, with special focus on *Basidiodendron* spp.; (2) ITS + nc LSU rDNA + *TEF1* (1884 characters including gaps); and (3) ITS only (628 characters including gaps) datasets for the *B. caesiocinereum* complex.

Phylogenetic reconstructions were performed with maximum likelihood (ML) and Bayesian (BI) analyses. Before the analyses, the best-fit substitution model for the alignment was estimated based on the Akaike Information Criterion (AIC) using FindModel web server (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). "K80 plus Gamma" model was chosen for ITS dataset, and "GTR

Table 1 DNA sequences generated for the present study

Species	Specimen/herbarium	Country (ISO code)	Host	GenBank / UNITE sequence numbers		
				nrITS	nrLSU	*TEF1*
Basidiodendron caesiocinereum	NS 18-172 (GENT)	BE	*Fagus sylvatica*	MW139272	-	-
B. caesiocinereum	NS 18-226 (GENT)	BE	*F. sylvatica*	MW139267	-	-
B. caesiocinereum	NS 18-625 (GENT)	BE	*F. sylvatica*	MW139268	-	-
B. caesiocinereum	NS 18-902 (GENT)	BE	*F. sylvatica*	MW139269	-	-
B. caesiocinereum	NS 18-925 (GENT)	BE	*F. sylvatica*	MW139270	-	-
B. caesiocinereum	NS 18-1050 (GENT)	BE	*F. sylvatica*	MW139266	-	-
B. caesiocinereum	NS 18-1051 (GENT)	BE	*F. sylvatica*	MW139271	-	-
B. caesiocinereum	OM 10608 (H)	CN	*Populus* sp. (?)	MW136071	-	-
B. caesiocinereum	VS 13663 (H)	IT	*Corylus avellana*	MW136105	MW136140	MW187110
B. caesiocinereum	VS 11764 (O)	NO	*Ulmus glabra*	MW136082	-	-
B. caesiocinereum	VS 11776 (O)	NO	*Betula pubescens*	MW136101	MW136136	MW187106
B. caesiocinereum	VS 12536 (O)	NO	*Tilia cordata*	MW136069	-	MW187084
B. caesiocinereum	VS 12500 (O)	NO	*C. avellana*	MW136061	-	-
B. caesiocinereum	VS 12502 (O)	NO	*U. glabra*	MW136084	-	MW187095
B. caesiocinereum	VS 12504 (O)	NO	*U. glabra*	MW136065	-	MW187082
B. caesiocinereum	VS 12511 (O)	NO	*U. glabra*	MW136083	-	MW187094
B. caesiocinereum	VS 12515 (O)	NO	*U. glabra*	MW136100	MW136135	MW187105
B. caesiocinereum	VS 12465 (O)	NO	*U. glabra*	MW136102	MW136137	MW187107
B. caesiocinereum	VS 11115 (O)	NO	*Alnus incana*	MW136103	MW136138	MW187108
B. caesiocinereum	SS 901 (O)	NO	*Picea abies*	MW259231	-	-
B. caesiocinereum	HK 26428 (H)	RU-KRA	*Alnus hirsuta*	MW136072	-	MW187085
B. cinerellum	VS 13485 (H)	BE	*Pinus sylvestris*	MW136088	MW136125	MW187097
B. cinerellum	VS 12337 (TU)	EE	*P. sylvestris*	UDB0754270	-	-
B. cinerellum	VS 12350 (TU)	EE	*C. avellana*	UDB0754279	-	-
B. cinerellum	VS 13681 (H)	IT	*P. abies*	MW136086	MW136123	MW187096
B. cinerellum	VS 11188 (O)	NO	*A. incana*	MW136104	MW136139	MW187109
B. cinerellum	VS 12449 (O)	NO	*U. glabra*	MW136064	-	MW187081
B. cinerellum	VS 13317 (H)	SI	*Pinus mugo*	MW136097	MW136131	MW187102
B. cinerellum	VS 13275 (H)	SI	*P. mugo*	MW136093	MW136130	MW187101
B. eyrei	ENZ 13-100 (GENT)	NL	*P. abies*	MW139273	-	-
B. eyrei	ENZ 18-101 (GENT)	NL	decayed wood	MW139274	-	-
B. eyrei	ENZ 18-103 (GENT)	NL	decayed wood	MW139275	-	-
B. eyrei	NS 19-411 (GENT)	NL	decayed wood	MW139277	-	-
B. glaucum	VS 11750 (O)	NO	*A. incana*	MW136085	-	-
B. glaucum	JN 9815 (O)	NO	*Picea abies*	MW259227	-	-
B. glaucum	JN 9920 (O)	NO	*P. abies*	MW259234	-	-
B. glaucum	JN 9858 (O)	NO	*P. abies*	MW259226	-	-
B. glaucum	SS 370 (O)	NO	*P. abies*	MW136079	MW136120	MW187091
B. glaucum	JN 9683 (O)	NO	*P. abies*	MW259233	-	-
B. glaucum	JN 9079 (O)	NO	*P. abies*	MW259232	-	-
B. glaucum	JN 9080 (O)	NO	*P. abies*	MW259228	-	-
B. glaucum	SS 11 (O)	NO	*P. abies*	MW259229	-	-
B. glaucum	SS 140 (O)	NO	*P. abies*	MW259235	-	-
B. glaucum	SS 144 (O)	NO	*P. abies*	MW136070	-	-
B. glaucum	SS 863 (O)	NO	*P. abies*	MW136078	MW136119	MW187090
B. glaucum	VS 7890 (H)	RU-KHA	*Picea ajanensis*	MW136063	-	-
B. groningae	GVA 20-040 (GENT)	BE	rotten wood	MW139280	-	-

Table 1 (continued)

Species	Specimen/herbarium	Country (ISO code)	Host	GenBank / UNITE sequence numbers		
				nrITS	nrLSU	*TEF1*
B. groningae	ENZ 18-001 (GENT)	NL	conifer	MW139278	MW136483	-
B. groningae	ENZ 19-073 (GENT)	NL	conifer	MW139276	MW136482	-
B. groningae	NS 18-1325 (GENT)	NL	*Hippophae rhamnoides*	MW139265	-	-
B. inconspicuum	VS 8171 (H)	US-WA	*Thuja plicata*	MW136098	MW136132	MW187103
B. mexicanum	LR 23131 (O)	MX	*Pinus patula*	MW136068	-	-
B. robenae	OM 16910.2 (H)	US-NY	hardwood	MW270998	MW271001	-
B. robenae	OM 19650 (H)	US-NY	hardwood	MW270997	MW271000	-
B. spiculosum	LR 23324 (O)	MX	*Cyathea* sp.	MW136076	MW136117	MW187088
B. trachysporum	TU 112986	EE	decayed wood	UDB016299	-	-
B. trachysporum	OM 22962.2 (H)	FI	*P. abies*	MW136096	-	-
B. trachysporum	ENZ 20-005 (GENT)	NL	*P. sylvestris*	MW139281	-	-
B. trachysporum	VS 11111 (O)	NO	*P. abies*	MW136089	MW136126	-
B. trachysporum	VS 12528 (O)	NO	*P. abies*	MW136067	MW136113	MW187083
B. trachysporum	VS 11801 (O)	NO	*P. abies*	MW136091	MW136129	MW187100
B. trachysporum	VS 11803 (O)	NO	*P. abies*	MW136090	MW136127	MW187098
B. trachysporum	VS 12508 (O)	NO	*P. abies*	MW136081	MW136122	MW187093
B. trachysporum	JN 9601 (O)	NO	*P. abies*	MW259230	MW136134	-
B. trachysporum	SS 608 (O)	NO	*P. abies*	MW136062	MW136111	-
B. trachysporum	HK 26387 (H)	RU-KRA	*Pinus sibirica*	MW136087	MW136124	-
B. trachysporum	VS 11886 (H)	RU-LEN	*P. abies*	MW152419	MW136128	MW187099
B. trachysporum	VS 9188a (H)	RU-NIZ	*P. sylvestris*	MW136080	MW136121	MW187092
B. trachysporum	VS 9481 (H)	RU-NIZ	*P. sylvestris*	MW136074	MW136115	MW187086
B. trachysporum	VS 9483 (H)	RU-NIZ	*U. glabra*	MW136077	MW136118	MW187089
B. trachysporum	HK 29616 (H)	RU-ZAB	conifer	MW270996	MW270999	-
B. trachysporum	VS 12548 (H)	SI	*Larix decidua*	MW136099	MW136133	MW187104
B. trachysporum	VS 12623 (H)	SI	*P. abies*	MW136095	-	-
B. trachysporum	VS 13147 (H)	SI	*P. abies*	MW136092	-	-
B. trachysporum	AS 72 (CWU)	UA	*Quercus robur*	MW136094	-	-
B. trachysporum	VS 8262 (H)	US-WA	*Pseudotsuga menziesii*	MW136060	-	-
B. trachysporum	VS 8740 (H)	US-WA	*Abies lasiocarpa*	MW136075	MW136116	MW187087
B. walleynii	WR 3081 (GENT)	BE	*Q. robur*	MW139279	-	-
B. walleynii	VS 9697 (H)	RU-NIZ	*Q. robur*	MW136066	MW136112	-
B. widdringtoniae	LR 11307a (O)	MW	*Widdringtonia whytei*	MW136073	MW136114	-

plus Gamma" model was chosen for nrITS + nc LSU rDNA + *TEF1* and ITS + nc LSU rDNA datasets.

Maximum likelihood analysis was run on RAxML servers, v.0.9.0 (Kozlov et al. 2019) with 1000 rapid bootstrap replicates. Bayesian analyses was performed with MrBayes 3.2.5 software (Ronquist et al. 2012), for two independent runs, each with 5 million generations (for ITS + nc LSU rDNA + *TEF1* dataset) and 10 million generations (for ITS and ITS + nc LSU rDNA datasets), under described models and four chains with sampling every 100 generations. To check for convergence of MCMC analyses and to get estimates of the posterior distribution of parameter values Tracer v1.6 was used (Rambaut et al. 2014). We accepted the result where the ESS (effective sample size) was above 200 and the PSRF (potential scale reduction factor) was close to 1.

The outgroup choice for the order-level phylogeny (*Sistotrema brinkmannii* (Bres.) J. Erikss., *Cantharellales*) was guided by the current JGI Basidiomycota tree ((https://mycocosm.jgi.doe.gov/mycocosm/species-tree/tree;_FJDxL?organism=basidiomycota) where *Cantharellales* were recovered close to *Auriculariales* and *Sebacinales*. ITS, nc LSU rDNA and *TEF1* sequences of *Bourdotia*, the sister genus of *Basidiodendron*, were selected as outgroups for the species-level analyses of the *B. caesiocinereum* complex.

Newly generated sequences have been deposited in GenBank with corresponding accession numbers (Table 1). Alignments have been deposited in TreeBASE (S27231).

Results

ITS + nc LSU rDNA dataset

The overall topologies of the ML and BI trees were nearly identical (Fig. 1). They uncovered all *B. caesiocinereum* s. lato specimens involved in the analyses in one strongly supported clade (bs =100, pp =1) with *B. luteogriseum* Rick (the generic type of *Basidiodendron*) and members of the *B. eyrei* complex (as defined by Spirin et al. 2020). Therefore, we interpreted all these taxa as belonging to one genus, *Basidiodendron*. In turn, the *Basidiodendron* clade was split into four strongly supported subclades. Two of them covered the *Basidiodendron eyrei* complex and contained fourteen species with smooth, ellipsoid or globose, usually small basidiospores. They all were dealt with in our previous publication (Spirin et al. 2020). Two remaining subclades encompassed the *B. caesiocinereum* complex. The larger subclade (designated in Fig. 1 as *B. caesiocinereum* group) contained sequences of specimens morphologically identical to the type material of *B. caesiocinereum* (smooth-spored) and *B. caesiocinereum* var. *trachysporum* (warted-spored). According to our results, these taxa should be accepted as two separate species; as a consequence, *B. caesiocinereum* var. *trachysporum* is raised to the species level. Additionally, five more lineages were detected in the *B. caesiocinereum* group. These are introduced as new species below. Two of them (*B. glaucum* and *B. robenae*) are smooth-spored, two species (*B. inconspicuum* and *B. walleynii*) have warted basidiospores, and in one species (*B. widdringtoniae*) the spore wall bears spines. The smaller subclade (labelled as *Basidiodendron cinerellum* group, Fig. 1) contained sequences of specimens identical to a lectotype of *Bourdotia cinerella*; the latter species is redescribed and combined in *Basidiodendron* below. Alongside *B. cinerellum* with warted spores, three new species (introduced as *B. groningae*, *B. mexicanum* and *B. spinulosum*) with spiny basidiospores were uncovered in the *B. cinerellum* group. Rather high variability of ITS sequences of some species (in particular, *B. caesiocinereum* s. str. and *B. trachysporum*) prompted us to investigate their identity with the use of an additional marker.

ITS + nc LSU rDNA + TEF1 dataset

The final alignment contained 1884 characters (including gaps). The overall topologies of the ML and BI trees were nearly identical and in a good correspondence with the ITS + LSU phylogeny (Fig. 2). Both *B. caesiocinereum* s. str. and *B. trachysporum* lineages are strongly supported and therefore interpreted by us as representing single species each.

ITS dataset

Twenty additional environmental ITS sequences related to *B. caesiocinereum* complex were retrieved from GenBank and UNITE and used in the phylogenetic analyses (Supplement). Seven of them belonged to *B. trachysporum* and confirmed this species is widespread in temperate—boreal forests of Eurasia and North America. *Basidiodendron caesiocinereum*, *B. cinerellum* and *B. walleynii* were represented by three, two and one environmental sequences, respectively. Seven remaining sequences potentially represent four more species in the *B. caesiocinereum* complex: two from Canada (British Columbia) (KP889384, KP889562), one from temperate Europe (Austria) (JF519252, JF519305) and possibly one more represented by sequences from UK, Estonia and Alaska (AF504871, KF297103, UDB0141409). However, we could not connect these sequences with available herbarium material, and therefore their identity remains unresolved.

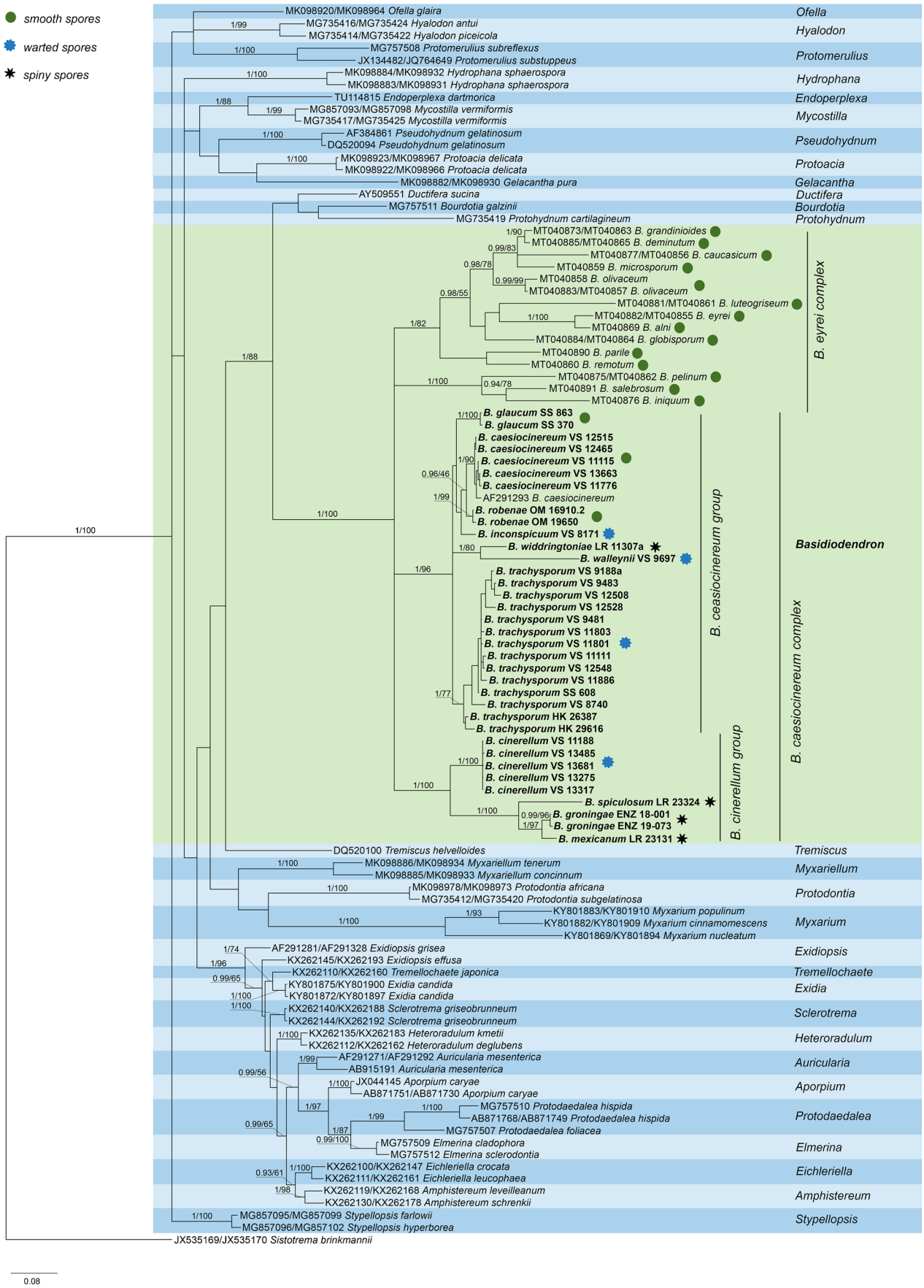
The morphology-based species identification in the *B. caesiocinereum* complex mainly relies on the presence and character of basidiospore ornamentation. As stated under "Material and methods," phase contrast illumination and Cotton Blue as a mountant are compulsory for this investigation. Of twelve species treated below, three species have completely smooth basidiospores and in nine species they are ornamented (Figs. 3, 4). Among the latter ones, four species possess warted and five have spiny outgrowths on the spore wall. Other morphological traits should also be considered for a correct species recognition. In particular, three species with warted basidiospores occurring in Europe (*B. cinerellum*, *B. trachysporum* and *B. walleynii*) are distinguishable due to differently looking basidiocarps and gloeocystidia, as well as specific arrangement of hymenial cells. Differentiating characters of *B. caesiocinereum* and related species are summarized in Table 2. Sequenced collections are marked by asterisk.

Taxonomy

***Basidiodendron caesiocinereum* (Höhn. & Litsch.) Luck-Allen**, Canadian J. Bot. 41: 1036, 1963. – Figs. 3, 4, 5 and 6

≡ *Corticium caesiocinereum* Höhn. & Litsch., Sitzungsb. Kaiserl. Akad. Wissenschaften, Math.-Naturw. Klasse Abt. 1, 117: 1116, 1908. Holotype. Germany. Nordrhein-Westfalen: Steinfurt, Lengerich, rotten hardwood, 1908 *Brinkmann* (FH 00304795, studied).

Basidiocarps effused, smooth, first waxy, pruinose or somewhat gelatinized, semitranslucent, greyish, then compact, greyish-bluish, older basidiocarps with a faint ochraceous-brownish tint, 0.02–0.03 (0.05) mm thick, up 3 cm in widest dimension, margin gradually thinning-out. Hyphal


smooth spores
warted spores
spiny spores
MK098920/MK098964 Ofella glaira
MG735416/MG735424 Hyalodon antui
MG735414/MG735422 Hyalodon piceicola
MG757508 Protomerulius subreflexus
JX134482/JQ764649 Protomerulius substuppeus
MK098884/MK098932 Hydrophana sphaerospora
MK098883/MK098931 Hydrophana sphaerospora
TU114815 Endoperplexa dartmorica
MG857093/MG857098 Mycostilla vermiformis
MG735417/MG735425 Mycostilla vermiformis
AF384861 Pseudohydnum gelatinosum
DQ520094 Pseudohydnum gelatinosum
MK098923/MK098967 Protoacia delicata
MK098922/MK098966 Protoacia delicata
MK098882/MK098930 Gelacantha pura
AY509551 Ductifera sucina
MG757511 Bourdotia galzinii
MG735419 Protohydnum cartilagineum
MT040873/MT040863 B. grandinioides
MT040885/MT040865 B. deminutum
MT040877/MT040856 B. caucasicum
MT040859 B. microsporum
MT040858 B. olivaceum
MT040883/MT040857 B. olivaceum
MT040881/MT040861 B. luteogriseum
MT040882/MT040855 B. eyrei
MT040869 B. alni
MT040884/MT040864 B. globisporum
MT040890 B. parile
MT040860 B. remotum
MT040875/MT040862 B. pelinum
MT040891 B. salebrosum
MT040876 B. iniquum
B. eyrei complex
B. glaucum SS 863
B. glaucum SS 370
B. caesiocinereum VS 12515
B. caesiocinereum VS 12465
B. caesiocinereum VS 11115
B. caesiocinereum VS 13663
B. caesiocinereum VS 11776
AF291293 B. caesiocinereum
B. robenae OM 16910.2
B. robenae OM 19650
B. inconspicuum VS 8171
B. widdringtoniae LR 11307a
B. walleynii VS 9697
B. trachysporum VS 9188a
B. trachysporum VS 9483
B. trachysporum VS 12508
B. trachysporum VS 12528
B. trachysporum VS 9481
B. trachysporum VS 11803
B. trachysporum VS 11801
B. trachysporum VS 11111
B. trachysporum VS 12548
B. trachysporum VS 11886
B. trachysporum SS 608
B. trachysporum VS 8740
B. trachysporum HK 26387
B. trachysporum HK 29616
B. ceasiocinereum group
B. cinerellum VS 11188
B. cinerellum VS 13485
B. cinerellum VS 13681
B. cinerellum VS 13275
B. cinerellum VS 13317
B. spiculosum LR 23324
B. groningae ENZ 18-001
B. groningae ENZ 19-073
B. mexicanum LR 23131
B. cinerellum group
Basidiodendron
B. caesiocinereum complex
DQ520100 Tremiscus helvelloides
MK098886/MK098934 Myxariellum tenerum
MK098885/MK098933 Myxariellum concinnum
MK098978/MK098973 Protodontia africana
MG735412/MG735420 Protodontia subgelatinosa
KY801883/KY801910 Myxarium populinum
KY801882/KY801909 Myxarium cinnamomescens
KY801869/KY801894 Myxarium nucleatum
AF291281/AF291328 Exidiopsis grisea
KX262145/KX262193 Exidiopsis effusa
KX262110/KX262160 Tremellochaete japonica
KY801875/KY801900 Exidia candida
KY801872/KY801897 Exidia candida
KX262140/KX262188 Sclerotrema griseobrunneum
KX262144/KX262192 Sclerotrema griseobrunneum
KX262135/KX262183 Heteroradulum kmetii
KX262112/KX262162 Heteroradulum deglubens
AF291271/AF291292 Auricularia mesenterica
AB915191 Auricularia mesenterica
JX044145 Aporpium caryae
AB871751/AB871730 Aporpium caryae
MG757510 Protodaedalea hispida
AB871768/AB871749 Protodaedalea hispida
MG757507 Protodaedalea foliacea
MG757509 Elmerina cladophora
MG757512 Elmerina sclerodontia
KX262100/KX262147 Eichleriella crocata
KX262111/KX262161 Eichleriella leucophaea
KX262119/KX262168 Amphistereum leveilleanum
KX262130/KX262178 Amphistereum schrenkii
MG857095/MG857099 Stypellopsis farlowii
MG857096/MG857102 Stypellopsis hyperborea
JX535169/JX535170 Sistotrema brinkmannii
Ofella
Hyalodon
Protomerulius
Hydrophana
Endoperplexa
Mycostilla
Pseudohydnum
Protoacia
Gelacantha
Ductifera
Bourdotia
Protohydnum
Tremiscus
Myxariellum
Protodontia
Myxarium
Exidiopsis
Tremellochaete
Exidia
Sclerotrema
Heteroradulum
Auricularia
Aporpium
Protodaedalea
Elmerina
Eichleriella
Amphistereum
Stypellopsis
0.08

◂**Fig. 1** Combined phylogenetic ITS + nc LSU rDNA topology from Bayesian analysis showing main lineages within the *Auriculariales*. Sequences generated for this study are indicated in bold. GenBank/UNITE or collection numbers (for newly generated sequences) are given for all sequences. Support values (BS/PP) are given above the branches. Scale bar shows expected changes per site

structure monomitic, hyphae clamped; subicular hyphae thin- or slightly thick-walled, subparallel, (2) 3–4 (5.5) µm diam, subhymenial hyphae thin-walled, easily collapsing, ascending or interwoven, 2–3 (3.5) µm diam. Gloeocystidia rather abundant to rare, tapering, slightly projecting, hyaline to yellowish, (13) 14–40 (41) × (4) 4.2–9.4 (10.0) µm (*n* = 86/11). Basidia four-celled, ovoid to suburniform, (11.8) 12.2–24.2 (26.8) × (7.0) 7.2–11.4 (12.3) µm (n = 339/20), occasionally with a distinct stalk-like base up to 10 × 3–5 µm, sterigmata gradually tapering, up to 15 × 2.5–3 µm; involucres poorly developed. Basidiospores smooth, thin-walled, compressed-subglobose or globose, (5.0) 5.1–7.8 (8.3) × (5.2) 5.3–8.1 (8.8) µm (n = 780/26), L = 5.57–6.93, W = 5.97–7.28, Q' = (0.8) 0.9–1.0, Q = 0.93–1.00, apiculus prominent, regular, sometimes slightly asymmetric, up to 2 × 2 µm.

Distribution and ecology. Europe (Belgium, Estonia, Finland, Germany, Italy, Norway), Asia (China, Russia – Siberia); almost exclusively on rotten wood of deciduous trees, as a rule in excessively humid habitats.

Remarks. Höhnel and Litschauer (1908) described *C. caesiocinereum* based on a single collection from Germany. They overlooked inner septation of basidia as well as the presence of cystidia, and this was a reason for them to assign the new species to the genus *Corticium* s. lato. Bourdot and Galzin (1927) restudied the type material of *C. caesiocinereum* and found that it has gloeocystidia and four-celled basidia. They concluded that *C. caesiocinereum* is an older name for *Bourdotia cinerella* Bourdot & Galzin. This viewpoint has persisted in the literature until the present day. However, we argue below that *B. cinerella* represents a warted-spored taxon, while the type specimen of *C. caesiocinereum* has smooth basidiospores. Therefore, the synonymy of *C. caesiocinereum* and *B. cinerella* should be abandoned.

As redefined here, *B. caesiocinereum* is most similar to *B. glaucum*. The two species are best separated by their ecological preferences. *Basidiodendron glaucum* is a northern species almost exclusively restricted to coniferous wood, while *B. caesiocinereum* is connected to angiosperm hosts, mainly in inundated habitats. However, *B. glaucum* may accidentally occur on deciduous trees, and one sequenced collection of *B. caesiocinereum* came from spruce. In these cases, *B. caesiocinereum* can be distinguished from *B. glaucum* due to longer basidia occasionally provided with a long stalk-like base. Basidiospores of *B. caesiocinereum* are on average larger than in *B. glaucum*, although their variation ranges are strongly overlapping. The distribution areas of both *B. caesiocinereum* and *B. glaucum* stretch along the northern part of Eurasia. No verified records of these species exist from North America. See *B. robenae* for further comments.

Specimens examined. Belgium. Vlaams-Brabant: Hoeilaart, Zoniënwoud, Kersselaerspleyn, *Fagus sylvatica*, X.2018 *Schoutteten 18-172**, *18-226**, *18-625**, *18-902**, *18-925**, *18-1050**, *18-1051** (GENT). China. Jilin: Antu Co., Huang Song Pu, *Populus* sp. (?), 28.VIII.2005 *Miettinen 10608** (H). Finland. Varsinaissuomi: Bromarv, Rilax, deciduous wood, 13.X.2000 *Saarenoksa 12100* (H). Uusimaa: Helsinki, Myllypuro – Puotinharju, *Betula* sp., 3.IX.1989 *Saarenoksa 18789* (H), Vanhakaupunki, *Alnus incana*, 10.IX.1989 *Saarenoksa 22889* (H), hardwood, 18.IX.1998 *Saarenoksa 17598* (H), Veräjämäki, *Salix caprea* (?), 19–21.X.2011 *Miettinen 14910.1, 14934.2* (H), *Betula* sp., 25.X.2019 *Miettinen 22920.1* (H); Porvoo, Stensböle, *S. caprea*, 1.XI.1990 *Kotiranta 9337* (H); Sipoo, Lilla Kummelberget Nat. Res., *Populus tremula*, 29.IX.2010 *Kotiranta 22735* (H). Enontekiön Lappi: Enontekiö, Kilpisjärvi, *Betula pubescens* spp. *tortuosa*, 2.IX.1983 *Kotiranta 4745a* (H). Germany. Bavaria: Bad Hindelang, Hinterstein, strongly decayed deciduous wood, 20.IX.1995 *Weiß 1995-320** (M.W.). Italy. Lombardy: Varese, Valganna, San Gemolo, *Corylus avellana*, 14.X.2019 *Spirin 13663** (H). Norway. Vest-Agder: Lyngdal, Skoland, *Ulmus glabra*, 1.XI.2017 *Spirin 11764** (O, H), rotten wood, 1.XI.2017 *Larsson 17730, 17733, 17735, 17737, 17751* (O); Mandal, Uføra, *Betula pubescens*, 2.XI.2017 *Spirin 11776** (O), *C. avellana*, 2.XI.2017 *Spirin 11780* (O). Aust-Agder: Grimstad, Sæveli, *C. avellana*, 2.XI.2017 *Spirin 11788* (O). Vestfold: Larvik, Jordstøyp i Kvelde, *Tilia cordata*, 30.IX.2018 *Spirin 12536** (O), *U. glabra*, 30.IX.2018 *Spirin 12538, 12539, 12542* (O), Vemannsås, *U. glabra*, 30.IX.2018 *Spirin 12523* (O). Telemark: Bamble, Rognsheia, *A. incana*, 3.XI.2017 *Spirin 11799* (O); Nome, Mørkvasslia, *A. incana*, 25.X.2016 *Spirin 11187* (O), *Picea abies*, 16.X.2011 *Svantesson 901** (O F253623). Buskerud: Lier, Asdøljuvet, *A. incana*, 29.IX.2018 *Spirin 12515** (O), *C. avellana*, 29.IX.2018 *Spirin 12500** (O), *U. glabra*, 29.IX.2018 *Spirin 12502*, 12504*, 12511** (O). Akershus: Asker, Esvika, *Acer platanoides*, 28.IX.2018 *Spirin 12462* (O), *U. glabra*, 28.IX.2018 *Spirin 12465** (O); Baerum, Kjaglidalen, *A. incana*, 16.IX.2016 *Spirin 11115*, 11121* (O), *C. avellana*, 16.IX.2016 *Spirin 11123, 11126* (O), *S. caprea*, 16.IX.2016 *Spirin 11129* (O). Oppland: Nord-Fron, Liadalane, *A. incana*, 12.IX.2016 *Spirin 11044* (O), 29.IX.2017 *Spirin 11636, 11649* (O), rotten wood, 29.IX.2017 *Larsson 17631* (O); Sel, Sagåa, *S. caprea*, 13.IX.2016 *Spirin 11069* (O). Møre og Romsdal: Nesset, Eikesdalen, *A. incana*, 27.IX.2017 *Spirin 11610* (O), rotten wood, 27–28.IX.2017 *Larsson 17548, 17558* (O). Russia. Krasnoyarsk Reg.: Turukhansk Dist., Lebed', *Alnus hirsuta*, 23.VIII.2013 *Kotiranta 26428** (H).

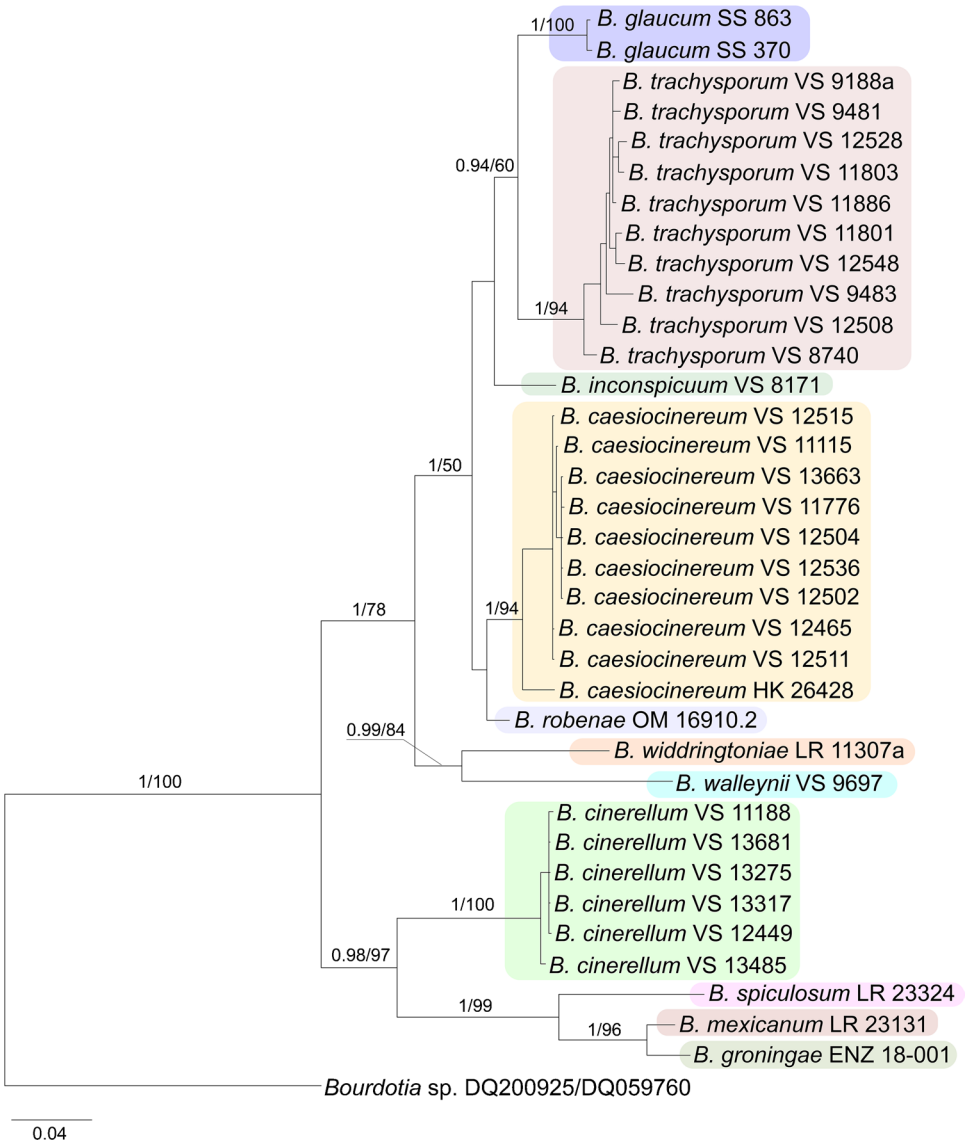


Fig. 2 Combined phylogenetic ITS + nc LSU rDNA + *TEF1* topology from Bayesian analysis showing phylogenetic relationships of the *Basidiodendron caesiocinereum* complex. GenBank/UNITE or collection numbers (for newly generated sequences) are given for all sequences. Support values (BS/PP) are given on the branches. Scale bar shows expected changes per site

Basidiodendron cinerellum **(Bourdot & Galzin) Spirin & V. Malysheva, comb. nov.** – Figs. 3, 4, 5 and 7

MB 838719

≡ *Bourdotia cinerella* Bourdot & Galzin, Bull. Soc. Mycol. France 36: 71, 1920. Lectotype (selected here, MBT395945). France. Aveyron: Causse Noir, *Pinus* sp., 20.XI.1913 *Galzin 14526* (herb. Bourdot 12419) (PC 0706677).

Basidiocarps effused, smooth, first waxy, pruinose-reticulate, greyish, then gelatinized, continuous, dirty-grey to pale ochraceous or brownish, occasionally tuberculate, often with irregularly scattered craters, 0.01–0.05 mm thick, covering a few cm, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, glued together; subicular hyphae thin-walled, subparallel, 2.5–4 µm diam, subhymenial hyphae thin-walled, ascending or interwoven, occasionally twisted, 1.5–3 µm diam, basidia-bearing hyphae distinct in older parts of hymenium, slightly thick-walled, up to 12 × 2–3.5 µm. Gloeocystidia abundant, more or less clearly tapering, slightly projecting, hyaline or yellowish to brownish, (13.5) 14–34 (35) × (3.4) 3.7–8.0 (9.0) µm (n = 75/8), solitary or in groups of 2–5. Basidia four-celled, ovoid to broadly suburniform, (8.8) 8.9–16.0 (17.0) × (6.3) 7.0–10.2 (10.3) µm (n = 70/7), sterigmata gradually tapering, up to 10 × 1.5–2 µm; involucres well-developed, often totally covering basidial cells (except sterigmata); basidia in mature specimens embedded in gelatinous matrix and glued together in large groups. Basidiospores warted, thin- or slightly thick-walled (wall up to 0.2 µm thick), compressed-subglobose or globose, (4.8–) 4.9–7.2 (–7.6) × (5.1–) 5.2–7.7 (–7.8) µm (n = 330/11), L = 5.48–6.43, W = 5.85–6.77, Q' = 0.9–1.0, Q = 0.94–0.97, apiculus prominent, regular, sometimes slightly asymmetric, up to 1.5 × 1.2 µm.

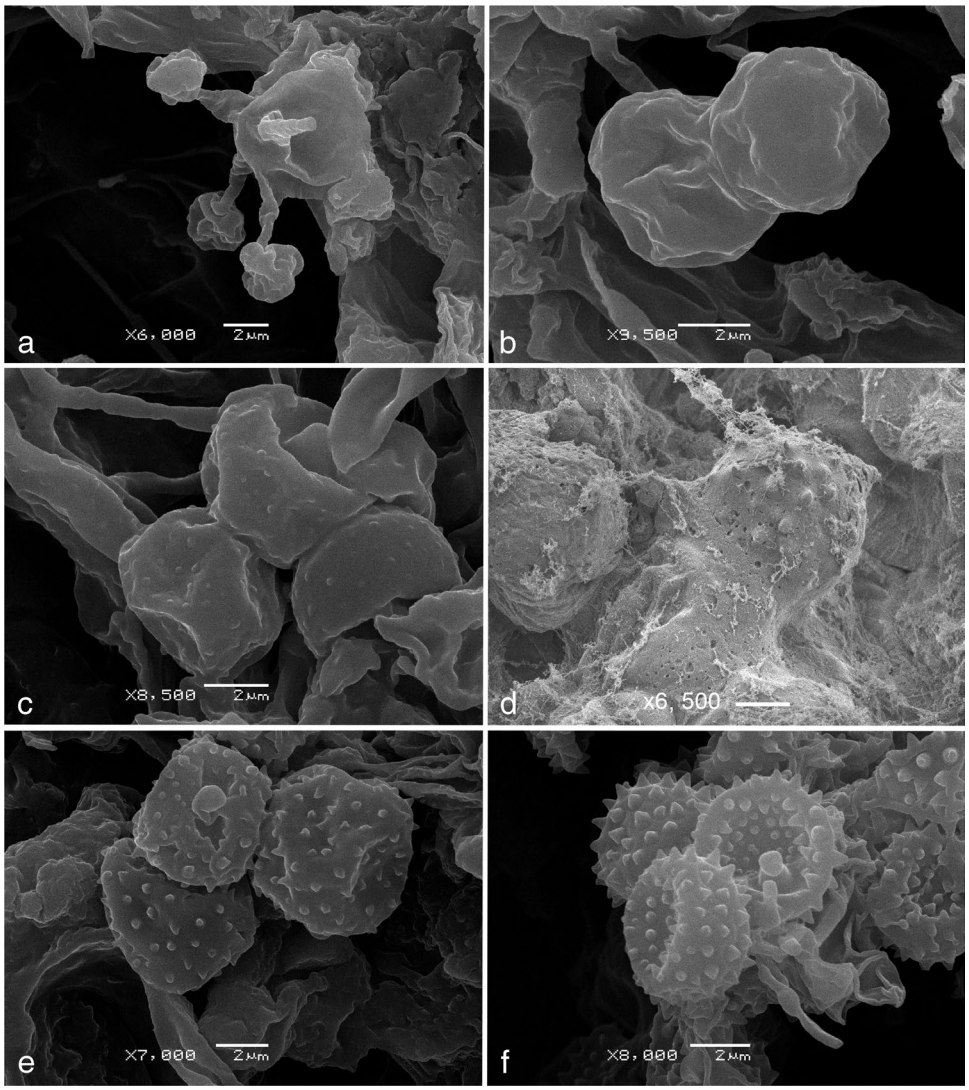


Fig. 3 Microscopic structures of *Basidiodendron* spp. as seen in scanning electron microscope. **a**, **b**: *B. caesiocinereum* (holotype of *Corticium caesiocinereum*), basidium and basidiospores; **c**: *B. cinerellum* (lectotype of *Bourdotia cinerella*), basidiospores; **d**: *B. groningae* (holotype), basidiospores; **e**: *B. spiculosum* (holotype), basidiospores; **f**: *B. spinosum* (holotype of *Sebacina spinosa*), basidiospores

Distribution and ecology. Europe (Belgium, Estonia, Finland, France, Germany, Italy, Norway, North-West Russia, Slovenia, Sweden); on tough, often still corticated branches and fallen logs in various stages of decay, predominantly of conifers.

Remarks. Bourdot and Maire (1920) introduced *B. cinerella* from a large set of specimens collected in the southern part of France. They described it as having smooth spherical basidiospores and later considered it a synonym of *C. caesiocinereum*. However, *B. cinerella* has remained untypified, and therefore its actual relation to *C. caesiocinereum* was obscure. We studied all (in total 29) specimens stored in Bourdot's herbarium (PC), which were labelled by him as '*Sebacina (Bourdotia) cinerella*'. Of them, two collections (*Bourdot 40882* and *9047*) belong to *B. cinereum* (Bres.) Luck-Allen s. lato, a species with cylindrical-ellipsoid spores; they do not fit to the protologue and cannot be used for typification. The rest of the specimens have globose spores, in good accordance with the original description, but they are warted, not smooth. Among them, two specimens represent *Bourdotia cinerella* var. *trachyspora* described seven years later (Bourdot and Galzin 1927) and considered here as a separate species. They certainly were not the main source for the *B. cinerella* description. Twelve remaining specimens were collected from coniferous (*Pinus*) and thirteen were from angiosperm hosts. However, both deciduous trees and conifers were mentioned as substrates in the protologue of *B. cinerella*, and therefore the host indication alone is insufficient for understanding the original idea of the species. Fortunately, Bourdot and Galzin provided a good description of macroscopic traits of *B. cinerella*: basidiocarps were described as 'whitish, whitish-grey, often glancing, pale ochraceous and crustaceous when old' ('blanchâtre, blanc-gris souvent brillant, subocracé et crustacé sur le vieux' – Bourdot and Galzin 1920: 71). These indications fit the pine-dwelling specimens and preclude collections from

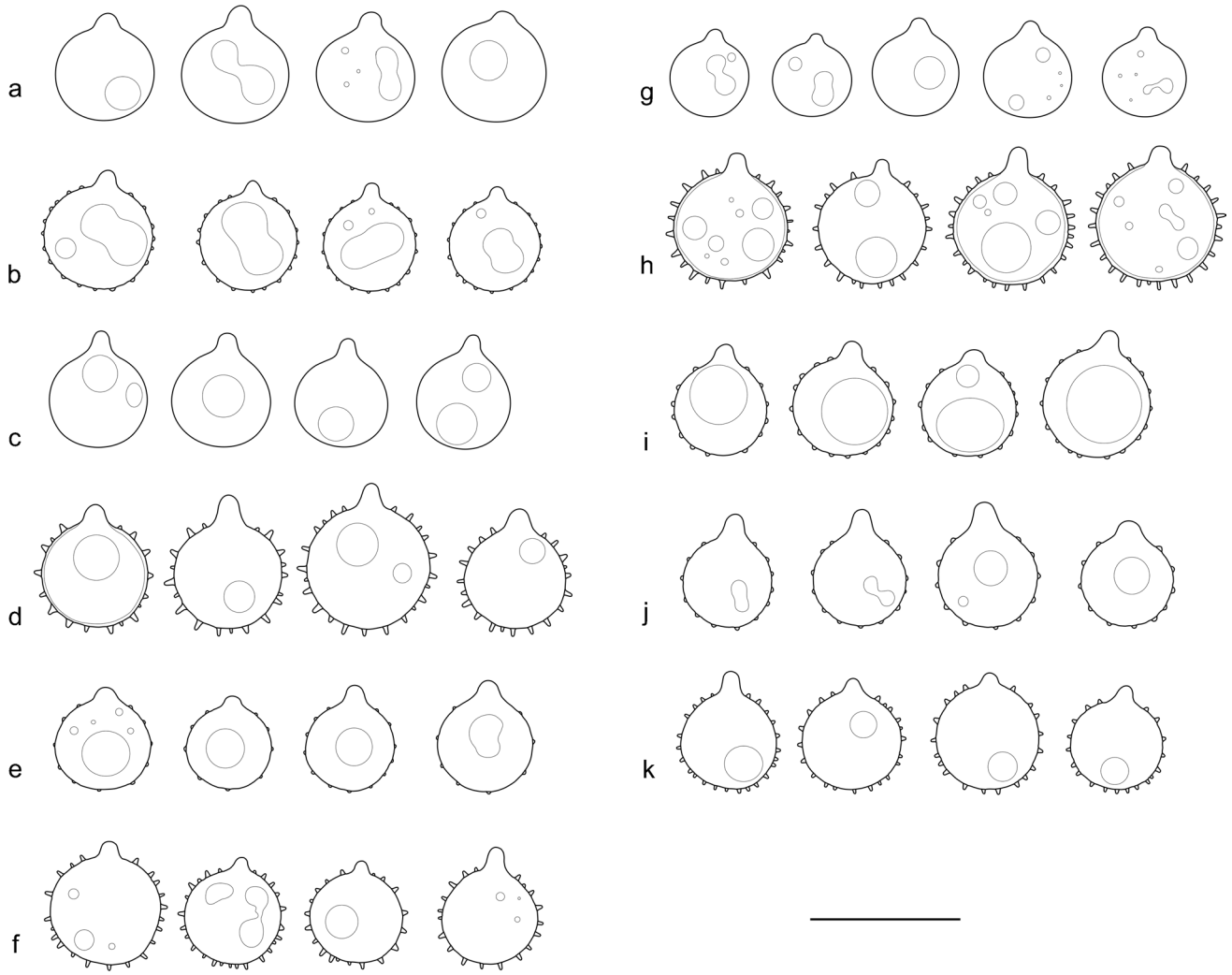


Fig. 4 Basidiospores of *Basidiodendron* spp. a: *B. caesiocinereum* (holotype of *C. caesiocinereum*); b: *B. cinerellum* (lectotype of *Bourdotia cinerella*); c: *B. glaucum* (holotype); d: *B. groningae* (holotype); e: *B. incospicuum* (holotype); f: *B. mexicanum* (holotype); g: *B. robenae* (holotype); h: *B. spiculosum* (holotype); i: *B. trachysporum* (Spirin 12548); j: *B. walleynii* (holotype); k: *B. widdringtoniae* (holotype). Scale bar = 10 µm

angiosperm hosts with arid, opaque basidiocarps. We assign the latter ones to a new species *B. walleynii* and select the best-developed specimen from *Pinus* (*Galzin 14526*, herb. *Bourdot 12419*) as a lectotype of *B. cinerella*.

Basidiodendron cinerellum is one of three species with warted basidiospores distributed in Europe. The most striking microscopic feature, differentiating *B. cinerellum* from two other species (i.e., *B. trachysporum* and *B. walleynii*), is the presence of a cyanophilous gelatinous matter covering basidial cells. In juvenile specimens, this matter is visible at least in some basidia as an essential (1–2 µm) thickening of the basidial wall. In mature, and especially in senescent basidiocarps, the gelatinous matrix covers basidia up to the very top and glues them together in large, easily detectable groups. Moreover, basidiocarps of *B. cinerellum* often have dirty-greyish or ochraceous-brownish tints and, at least in some parts, they are more or less clearly gelatinized. In contrast, basidiocarps of *B. walleynii* remain arid and normally pale, while in *B. trachysporum* they are usually very thin, constantly whitish-greyish and occasionally gelatinized only when old. No signs of hymenial gelatinous matter so characteristic for *B. cinerellum* were detected in *B. trachysporum* or *B. walleynii*.

Basidiodendron cinerellum and *B. trachysporum* inhabit mostly coniferous hosts and sometimes occur in the same habitats. Our data suggest, however, that they may have quite different ecological specialization. *Basidiodendron cinerellum* seemingly prefers tough, often still corticated wood—mainly thick, still hanging or just fallen branches or small- to medium-sized logs. In turn, *Basidiodendron trachysporum* mostly occurs on well-decomposed wood, often on rotten logs lying on the ground or inside old stumps,

Table 2 Geographic, ecological and morphological traits in *Basidiodendron caesiocinereum* complex

Species	Geographic distribution	Host	Basidia	Basidiospores
B. caesiocinereum	Eurasia, temperate – hemiboreal	Angiosperms	12–24 × 7–11.5 µm, exposed	smooth, 5.1–7.8 × 5.3–8.1 µm, Q = 0.93–1.00
B. cinerellum	Europe, temperate – boreal	Mostly gymnosperms	9–16 × 7–10 µm, glued in groups	warted, 4.9–7.2 × 5.2–7.7 µm, Q = 0.94–0.97
B. glaucum	Eurasia, boreal	Gymnosperms (predominantly *Picea*)	10–14.5 × 7.5–10.5 µm, exposed	smooth, 5.1–6.8 × 5.2–7.0 µm, Q = 0.96–0.98
B. groningae	Europe, temperate	Gymnosperms and angiosperms	13–18 × 9–12 µm, exposed	spiny, 6.0–7.9 × 6.2–8.2 µm, Q = 0.95–0.96
B. inconspicuum	North America (North West), temperate	Gymnosperms (*Thuja*)	10–13 × 7–9 µm, exposed	warted, 5.0–6.2 × 5.2–6.5 µm, Q = 0.95
B. mexicanum	North America, temperate	Gymnosperms (*Pinus*)	12–15.5 × 9.5–12 µm, exposed	spiny, 5.9–7.3 × 6.1–7.4 µm, Q = 0.96
B. robenae	North America, temperate	Angiosperms	12–18 × 7–9 µm, exposed	smooth, 5.1–6.4 × 5.2–6.9 µm, Q = 0.94–0.96
B. spiculosum	North America, subtropical	Fern remains	15–24 × 10–12 µm, exposed	spiny, 6.9–8.2 × 7.1–8.9 µm, Q = 0.96
B. spinosum	Oceania (Tahiti), tropical	Rotten wood	9–10 × 6–7.5 µm, exposed	spiny, 4.6–5.2 × 4.8–5.8 µm, Q = 0.96
B. trachysporum	Eurasia and North America (North-West), temperate – boreal	Mostly gymnosperms	8.5–16 × 7–11 µm, exposed	warted, 4.8–7.4 × 5.0–7.8 µm, Q = 0.94–0.98
B. walleynii	Europe, temperate	Angiosperms (mostly *Castanea* and *Quercus*)	11–15.5 × 7–11 µm, exposed	warted, 5.1–7.0 × 5.3–7.2 µm, Q = 0.96–0.98
B. widdringtoniae	South Africa, subtropical	Gymnosperms (*Widdringtonia*)	11.5–14 × 8–11 µm, glued in groups	spiny, 5.9–6.8 × 6.1–7.1 µm, Q = 0.96

although several records were made from small corticated coniferous branches.

Specimens examined. Belgium. Namur: Philippeville, Viroinval, Fondry des Chiens, *Pinus sylvestris*, 11.X.2019 *Spirin 13485*, 13494* (H). Estonia. Viljandimaa: Tipu, Kikepera, *P. sylvestris*, 16.IX.2018 *Spirin 12337** (H, TU114809), Lemmjõe, *C. avellana*, 17.IX.2018 *Spirin 12350** (H, TU114820). Finland. Varsinaissuomi: Lohja, Lohjansaari, *P. abies*, 28.VIII.2003 *Kotiranta 19980* (H); Tammisaari, Tenhola, *P. abies*, 1.IX.2004 *Kotiranta 20450* (H). Uusimaa: Helsinki, Kumpula, *P. abies*, 16.IX.2001 *Saarenoksa 04201* (H), Mölylä, *P. abies*, 4.XI.2017 *Miettinen 21459* (H), Veräjämäki, *P. abies*, 30.X.2019 *Viner 2019-195* (H), *P. sylvestris*, 3.VI.2019 *Spirin 12543* (H); Sipoo: Rörstrand, *P. abies*, 22.IX.2009 *Miettinen 14005* (H); Vantaa, Vestra, dead *Fomitopsis pinicola* on *P. abies*, 10.V.2014 *Spirin 6850* (H). Etelä-Häme: Hämeenlinna, Ahvenaistenjärvi, *P. abies*, 22.IX.2016 *Miettinen 20402* (H), Kotinen, *P. abies*, 25.IX.2014 *Spirin 8099* (H). Etelä-Karjala: Virolahti, Klamila, decorticated board (old house), 5.VI.2010 *Kotiranta 22704a* (H). Inarin Lappi: Utsjoki, Kevo, *Juniperus communis*, 20.IX.2009 *Kotiranta 23123* (H). France. Aveyron: Causse Noir, *Pinus* sp., 3.XI.1911 *Galzin 10147* (herb. Bourdot 9059) (PC 0706674), *Galzin 10190* (herb. Bourdot 9061) (PC 0084210), 20.XI.1913 *Galzin 14514* (herb. Bourdot 13962) (PC 0706665), *Galzin 14520* (herb. Bourdot 13963) (PC 0706676), *Galzin 14537* (herb. Bourdot 13964) (PC 0706673), 30.XI.1913 *Galzin 14775* (herb. Bourdot 13966) (PC 0706675), 17.V.1915 *Galzin 17703* (herb. Bourdot 20187) (PC 0706678), 5.XII.1915 *Galzin 18879* (herb. Bourdot 15695) (PC 0706666), *Galzin 18906* (herb. Bourdot 18566) (PC 0706660), *Galzin 18919* (herb. Bourdot 15733) (PC 0706681), 16.V.1919 *Galzin 24592* (herb. Bourdot 26851) (PC 0706682). Germany. Bavaria: Wertach, Jungholz, decayed *P.*

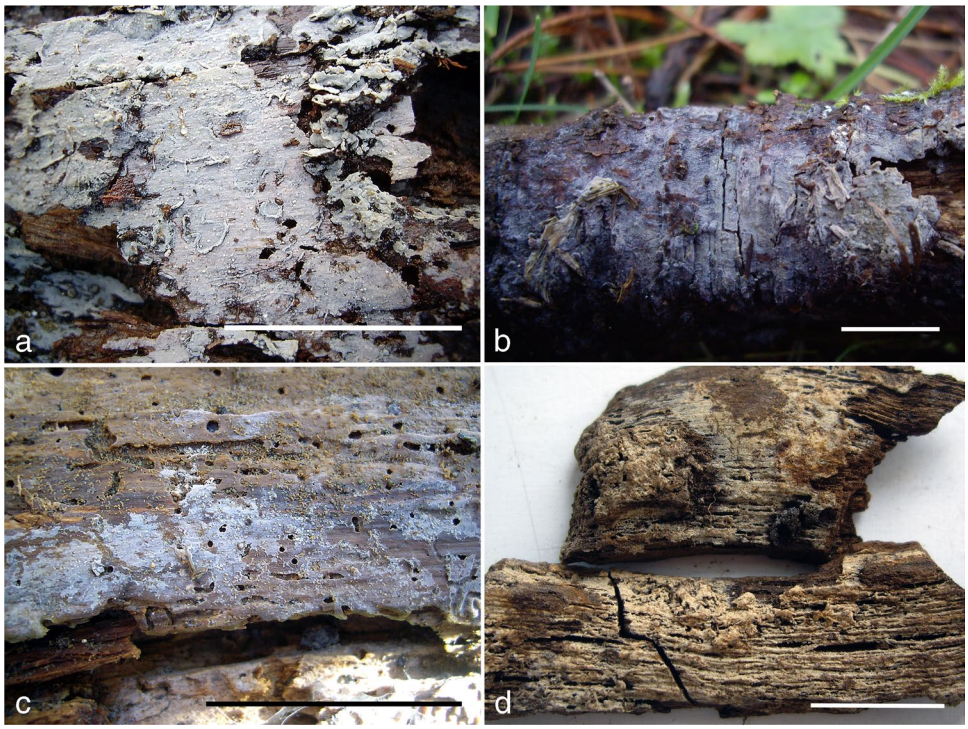


Fig. 5 Basidiocarps of *Basidiodendron* spp. **a**: *B. caesiocinereum* (Spirin 11764); **b**: *B. cinerellum* (Spirin 13317); **c**: *B. trachysporum* (Spirin 11801); **d**: *B. walleynii* (Bourdot 19447). Scale bar = 1 cm

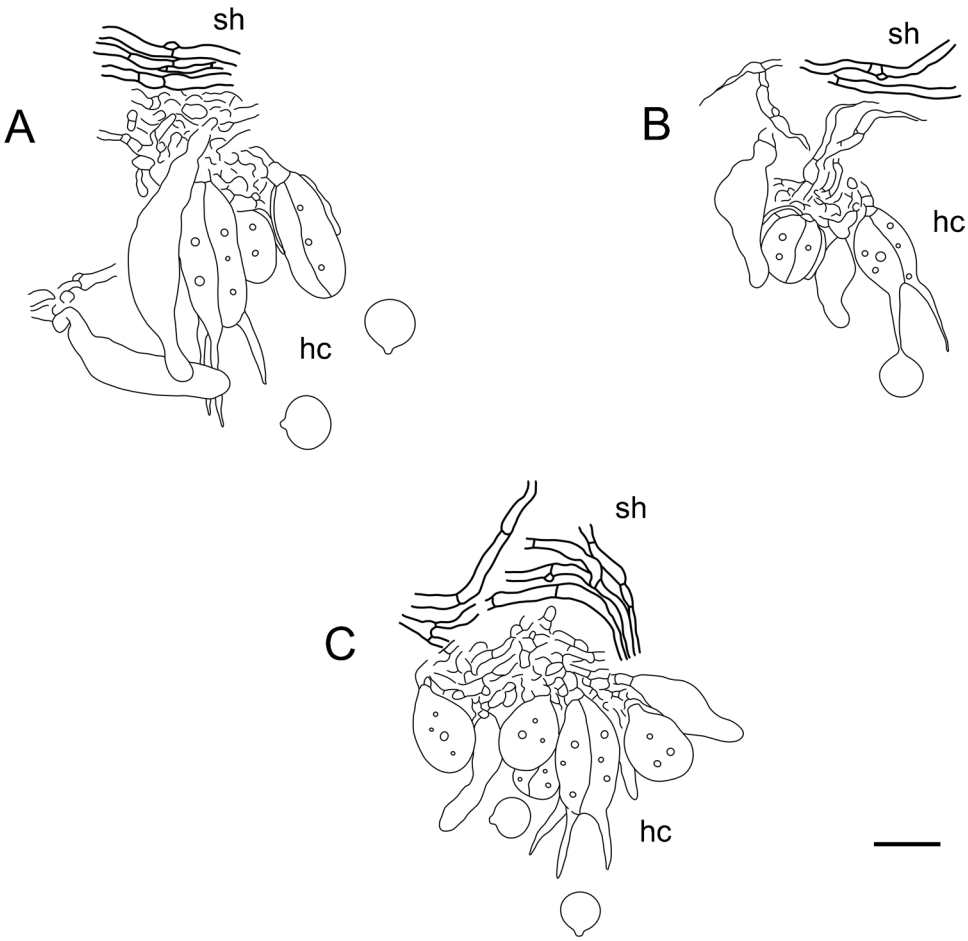


Fig. 6 Microscopic structures of smooth-spored *Basidiodendron* spp. **A**: *B. caesiocinereum* (holotype of *C. caesiocinereum*), **B**: *B. glaucum* (holotype), **C**: *B. robenae* (holotype); hc – hymenial cells, sh – subicular hyphae. Scale bar = 10 µm

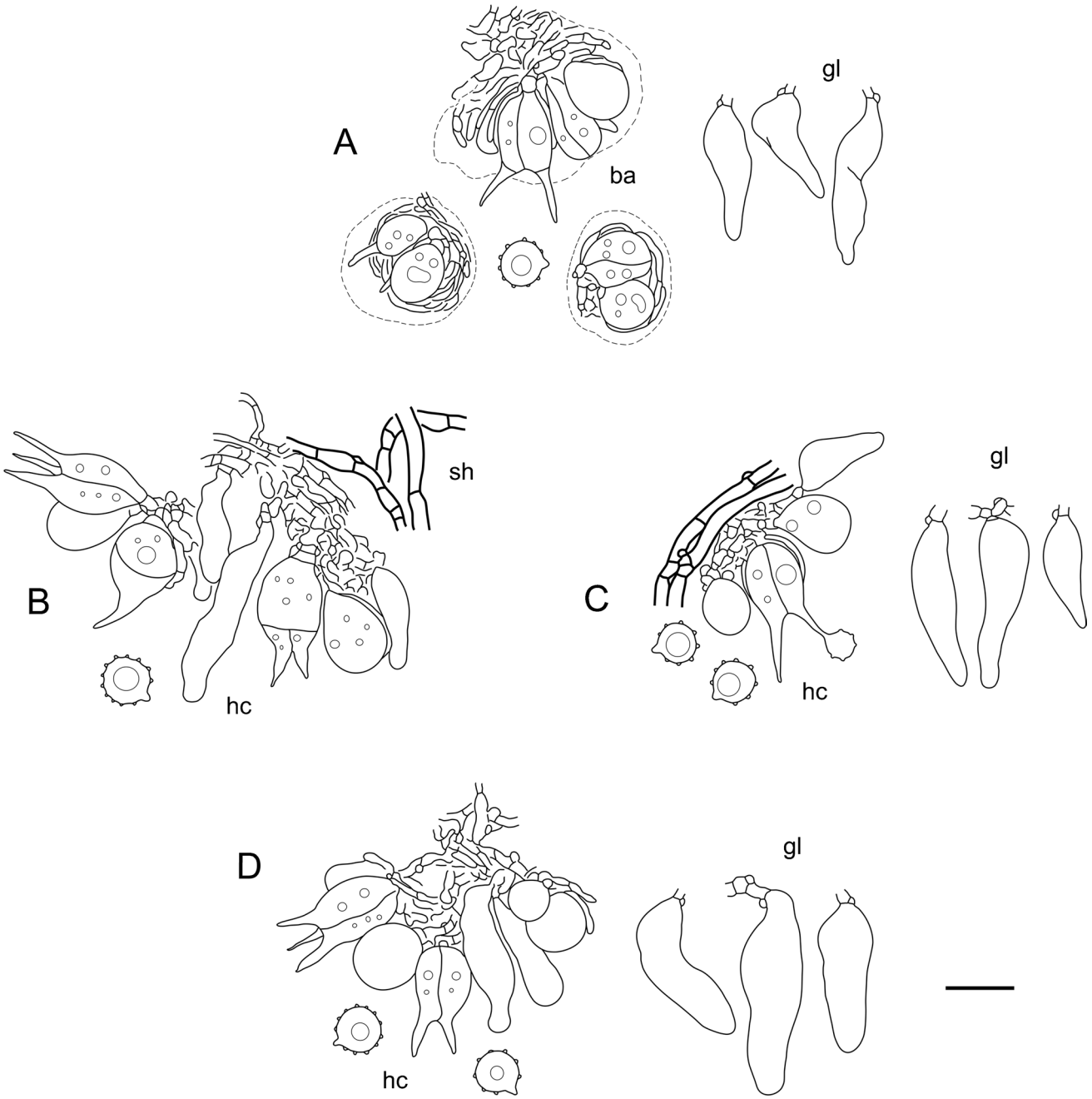


Fig. 7 Microscopic structures of European *Basidiodendron* spp. with ornamented spores. **A**: *B. cinerellum* (Spirin 12337), **B**: *B. groningae* (holotype), **C**: *B. trachysporum* (Spirin 11111), **D**: *B. walleynii* (hymenial cells from holotype, gloeocystidia from Walleyn 3081); ba – basidia embedded in gelatinous matrix, gl – gloeocystidia, hc – hymenial cells, sh – subicular hyphae. Scale bar = 10 μm

abies, 8.X.1996 *Weiß 1996-393** (M.W.). Italy. Lombardy: Varese, Bedero Valcuvia, Marteghetta, *P. abies*, 14.X.2019 *Spirin 13681** (H), *P. sylvestris*, 14.X.2019 *Spirin 13692* (H). Norway. Telemark: Bamble, Rognsheia, *P. abies* and dead *Phellinus ferrugineofuscus*, 3.XI.2017 *Larsson 17829* (O); Nome, Mørkvasslia, *A. incana*, 25.X.2016 *Spirin 11188** (O). Akershus: Asker, Stokkerelva at Åstaddammen, *U. glabra*, 28.IX.2018 *Spirin 12449** (O); Baerum, Kjaglidalen, *P. abies*, 4.V.2016 *Spirin 10019* (O). Oppland: Lunner, Rinilhaugen Nat. Res., *P. abies*, 17.IX.2016 *Spirin 11144* (O); Sel, Sagåa Nat. Res., *P. abies*, 13.IX.2016 *Spirin 11059* (O). Russia. Leningrad Reg.: Boksitogorsk Dist., Anisimovo, *P. abies*, 15.VII.2014 *Spirin 7004* (H), Vozhani, *P. abies*, 2.X.2016 *Spirin 11168* (H); Kirishi Dist., Klinkovo, *P. abies*, 7.VIII.2019 *Spirin 12872* (H); Podporozhie Dist., Vazhinka, *P. abies*, 16.IX.2017 *Spirin 11405* (H). Yamalo-Nenets

Autonomous Dist.: Priuralsky Dist., Sob', *Picea obovata*, 11.VIII.1969 *Parmasto* (TAAM 053842). Slovenia. Gorenjska: Kranjska Gora, Vršič, *Pinus mugo*, 5.VI.2019 *Spirin 12576* (H), 27.IX.2019 *Spirin 13317*, 13325, 13333, 13338, 13344* (H); Bohinj, Lipanca, *L. decidua*, 26.IX.2019 *Spirin 13290, 13303* (H), 29.VII.2020 *Spirin 13945* (H), *P. abies*, 6.VI.2019 *Spirin 12594, 12613, 12626* (H), 26.IX.2019 *Spirin 13229, 13237* (H), *P. mugo*, 26.IX.2019 *Spirin 13275*, 13281, 13287, 13293* (H), Mrežce, *P. abies*, 26.IX.2019 *Spirin 13221* (H), Mrzli Studenec, *P. abies*, 27.VII.2020 *Spirin 13879* (H), Ravne v Bohinju, *Abies alba*, 28.VII.2020 *Spirin 13888* (H), Studor, *P. abies*, 27.VII.2020 *Spirin 13852* (H); Mojstrana, Triglavska Bistrica, *P. abies*, 28.IX.2019 *Spirin 13418, 13422, 13471* (H). Sweden. Kalmar: Vimmerby, Norra Kvill, *P. abies*, 27.X.2010 *J. Nordén 7879* (O). Örebro: Lekeberg, Ugglehöjden, *P. abies*, 13.X.2010 *J. Nordén 7561* (O).

Basidiodendron glaucum **Spirin & K.H. Larss., sp. nov.** – Figs. 4 and 6

MB 838720

Holotype. Norway. Nord-Trøndelag: Snåsa, Blåfjella, 64.2939N 13.029E, *Picea abies* (decorticated log), 28.IX.2011 *J. Nordén 9683** (O F-248006, isotype – H).

Etymology: *Glaucus* (Lat., adj.) – bluish-grey, in reference to the basidiocarp's colour.

Basidiocarps effused, smooth, first waxy, pruinose, then continuous, arid, greyish, 0.02–0.06 (0.1) mm thick, up 6 cm in widest dimension, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped; subicular hyphae thin-walled, subparallel, 2–3 µm diam, subhymenial hyphae thin-walled, easily collapsing, ascending or interwoven, 1.5–2 (2.5) µm diam. Gloeocystidia rather rare, tapering, slightly projecting, hyaline to yellowish, (14) 14.5–34.0 (38.0) × (3.7) 4.0–8.2 (9.0) µm (n = 30/3). Basidia fourcelled, ovoid to broadly suburniform, (10.1) 10.2–14.3 (14.8) × (7.0) 7.7–10.3 (11.0) µm (n = 62/6), sterigmata gradually tapering, up to 13 × 2.5–3 µm; involucres poorly developed. Basidiospores smooth, thin-walled, compressed-subglobose or globose, (5.0) 5.1–6.8 (7.0) × (5.0) 5.2–7.0 (7.2) µm (n = 270/9), L = 5.53–6.24, W = 5.67–6.37, Q' = 0.9–1.0 (1.1), Q = 0.96–0.98, apiculus prominent, usually slightly asymmetric, up to 2 × 1.8 µm.

Distribution and ecology. Europe (France, Norway, North-West Russia, Sweden), Asia (Russian Far East); almost exclusively on rotten wood of conifers.

Remarks. *Basidiodendron glaucum* is distributed in boreal-subalpine coniferous forests of Eurasia. It seems to occur mostly in old-growth communities with abundant wood remnants. *Basidiodendron globisporum* Spirin & V. Malysheva has the same ecological preferences. It can be distinguished from *B. glaucum* by the smaller basidia (9–12 × 7–9 µm) and basidiospores (4.6–5.8 × 4.8–5.9 µm, L = 4.95–5.15, W = 5.10–5.33) with a less prominent apiculus (Spirin et al. 2020). Differences between *B. glaucum* and the look-alike *B. caesiocinereum* are listed above. *Basidiodendron robenae* is morphologically almost indistinguishable from *B. glaucum* but it was detected only on angiosperm hosts in North America.

Specimens examined (paratypes). France. Vosges: Saint-Dié-des-Vosges, Plainfaing, Col du Bonhomme, *A. alba*, 12.X.2019 *Spirin 13539* (H). Norway. Vest-Agder: Lyngdal, Fladstad, *A. incana*, 1.XI.2017 *Spirin 11750** (O). Akershus: Nannestad, Rudskampen, *P. abies*, 10.X.2011 *J. Nordén 9815** (O F-248007). Telemark: Drangedal, *P. abies*, 18.X.2011 *J. Nordén 9920** (O F253676); Nome, Mørkvasslia, *P. abies*, 16.X.2011 *J. Nordén 9858** (O F253666); Sandalslia, *P. abies*, 13.X.2011 *Svantesson 863** (O). Akershus: Nannestad, 8.X.2011 *J. Nordén 9760* (O). Sør-Trøndelag: Selbu, Råndalen, *P. abies*, 19–20.IX.2011 *J. Nordén 9313, 9326, 9339* (O), *Svantesson 351* (O); Tydal, Hilmo, *P. abies*, 22.IX.2011 *Svantesson 370** (O), 23.IX.2011 *J. Nordén 9573* (O). Nord-Trøndelag: Snåsa, Blåfjella, *P. abies*, 27.IX.2011 *J. Nordén 9605* (O), 28.IX.2011 *J. Nordén 9678, 9680* (O). Nordland: Hattfjelldal, Nordlia, *P. abies*, 9.IX.2011 *J. Nordén 9079** (O F253604), *J. Nordén 9080** (O F253638); Grane, Litltuva, *P. abies*, 5–6.IX.2011 *Svantesson 10* (O), *Svantesson 11** (O F253609), *Svantesson 52* (O), *Svantesson 140** (O F253677), *Svantesson 141, 144** (O). Russia. Khabarovsk Reg.: Verkhnebureinskii Dist., Dublikan Nat. Res., *Picea ajanensis*, 23.VIII.2014 *Spirin 7890** (H 7028622). Leningrad Reg.: Kirishi Dist., Shariya, *P. abies*, 10.VIII.2019 *Spirin 12922* (H). Sweden. Västra Götaland: Strömstad, Hästeskede, *P. abies*, 31.X.2011 *J. Nordén 10037* (O). Västerbotten: Lycksele, Altarliden, *P. abies*, 29.IX.2010 *J. Nordén 7152* (O).

Basidiodendron groningae **Schoutteten & Spirin, sp. nov.** – Figs. 3, 4 and 7

MB 838721

Holotype. Netherlands. Groningen: Lauwersoog, Ballastplaatbos, 53.402N 6.213E, *Hippophae rhamnoides* (dry corticated branch), 10.XI.2018 *Schoutteten 18-1325** (GENT, isotype – H).

Etymology: *Groninga* (Lat., noun) – a Latin name of Groningen, the type locality.

Basidiocarps effused, smooth, first waxy, pruinose-reticulate, greyish, then continuous, greyish to pale ochraceous, 0.02–0.04 mm thick, covering a few mm, in some portions slightly gelatinized, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped; subicular hyphae thin- or slightly thick-walled, interwoven, 2–3 µm diam, subhymenial hyphae thin- to slightly thick-walled, ascending or interwoven, 1.5–2 µm diam. Gloeocystidia abundant, distinctly tapering, slightly projecting, hyaline to yellowish, (14) 18–34 (41) × (4.0) 4.1–7.0 (7.5) µm (*n* = 20/1), solitary or in groups of 2–7. Hyphidia not observed.

Basidia normally four-celled, ovoid to broadly suburniform, (12.8) 12.9–17.8 (18.2) × (8.4) 9.0–12.0 (12.2) µm (*n* = 30/2), sterigmata gradually tapering, up to 14 × 2.5–3 µm; some basidia obliquely or even transversally septate, 1–2-sterigmatic, occasionally pleural; involucres indistinct. Basidiospores spiny (spines up to 0.3–0.6 µm long), thin-walled or with slightly thickened (up to 0.3 µm) walls, compressed-subglobose or globose, (5.9) 6–7.9 (9.1) × (6.1) 6.2–8.2 (9.4) µm (n = 90/3), L = 6.35–7.14, W = 6.68–7.40, Q' = 0.9–1.0, Q = 0.95–0.96, apiculus prominent, regular or eccentric, sometimes slightly asymmetric, up to 3 × 1.8 µm.

Distribution and ecology. Europe (Belgium, Netherlands); dead wood of unidentified conifers and deciduous trees (*Hippophae rhamnoides*).

Remarks. *Basidiodendron groningae* is the only species with spiny basidiospores so far detected in Europe. It was collected three times around Groningen in the Netherlands and once in Belgium, but its actual distribution is unknown. Four other species with spiny spores dealt with in this paper were found in North America (*B. mexicanum*, *B. spiculosum*), Africa (*B. widdringtoniae*) and Oceania (*B. spinosum*). In the type specimen of *B. groningae*, basidia occasionally bear oblique or even transversal septa, and then only one or two apical cells produce sterigmata. This feature illustrates morphological flexibility of basidial cells most likely caused by environmental conditions and seems to have no taxonomic importance.

Specimens examined (paratypes). Belgium. Antwerpen: Boeckhout, Den Turck, rotten wood, 6.II.2020 *Van Autgaerden 20-040** (GENT). Netherlands. Groningen: Lauwersoogbos, fallen corticated coniferous branch, 11.XI.2018 *Enzlin 18-001** (GENT); Oude Pekela, Pekelderbos, fallen corticated coniferous branch, 24.X.2019 *Enzlin 19-073** (GENT).

Basidiodendron inconspicuum **Spirin & V. Malysheva, sp. nov.** – Figs. 4 and 8

MB 838722

Holotype. USA. Washington: Clallam Co., Willoughby Creek, 47.8218N 124.1983W, *Thuja plicata* (very rotten decorticated log), 7.X.2014 *Spirin 8171** (H, isotype – LE).

Etymology: *Inconspicuus* (Lat., adj.) – inconspicuous, in reference to the hardly detectable basidiocarps of the species.

Basidiocarps effused, smooth, waxy, pruinose-reticulate, whitish or greyish, 0.01–0.02 mm thick, covering a few mm, hardly detectable. Hyphal structure monomitic, hyphae clamped; subicular hyphae slightly thick-walled, subparallel, 2–3 µm diam, subhymenial hyphae thin- or slightly thick-walled, ascending or interwoven, 1.5–3 µm diam. Gloeocystidia abundant, tapering, slightly projecting, hyaline to yellowish, (12) 13–27 (37) × (3.6) 3.8–7.8 (8.3) µm (*n* = 20/1), solitary. Basidia four-celled, ovoid to broadly suburniform, (9.8) 10.2–13.2 (13.7) × (6.8) 7.0–8.8 (9.2) µm (*n* = 20/1), sterigmata gradually tapering, up to 8 × 1.5 µm; involucres normally poorly developed, well-visible in senescent hymenium only. Basidiospores minutely warted, thin-walled, compressed-subglobose or globose, (4.8) 5.0–6.2 × (5.1) 5.2–6.5 (6.7) µm (n = 30/1), L = 5.49, W = 5.76, Q' = 0.9–1.0, Q = 0.95, apiculus regular, sometimes slightly asymmetric, up to 1.2 × 1.5 µm.

Distribution and ecology. So far known from the type locality; strongly decayed wood of conifers (*Thuja plicata*).

Remarks. *Basidiodendron inconspicuum* produces very thin, hardly detectable basidiocarps consisting of two–three subparallel basal hyphae and sparse subhymenial hyphae bearing hymenial cells. Morphologically, it is most similar to *B. trachysporum*. The latter species has on average larger basidiospores with more pronounced (up to 0.2–0.3 µm long) warts. In turn, the basidiospore ornamentation of *B. inconspicuum* is seen only under phase contrast as tiny (0.1–0.2 µm long) warts regularly arranged on the spore surface. Phylogenetically, *B. inconspicuum* is more closely related to the smooth-spored *B. caesiocinereum* than to *B. trachysporum*.

Basidiodendron mexicanum **Spirin & V. Malysheva, sp. nov.** – Figs. 4 and 8

MB 838723

Holotype. Mexico. Vera Cruz: Cofre de Perote, Mpio de Xico, El Revolcadera, 19.473N 97.154W, *Pinus patula* (rotten decorticated log), 18.IX.1985 *Ryvarden 23131** (O, isotypes – H, LE).

Etymology: *Mexicanus* (Lat., adj.) – after Mexico, where the species was collected.

Basidiocarps effused, smooth, first waxy, pruinose, whitish or greyish, then continuous, greyish to pale ochraceous, arid, 0.02–0.03 mm thick, covering a few cm, occasionally gelatinized and semitranslucent, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped; subicular hyphae slightly thick-walled, subparallel, 2–3.5 µm diam, subhymenial hyphae slightly thick-walled, ascending or interwoven, frequently anastomosing, 2–3.5 µm diam. Gloeocystidia abundant, distinctly tapering, slightly projecting, hyaline to yellowish or rarely brownish, (11) 17–34 (35) × (4.2) 4.3–6.2 (7.0) µm (*n* = 20/1), solitary or in groups of 2–3. Hyphidia occasionally present, mostly simple, 1–1.5 µm in diam. (apical part), projecting up to 15 µm. Basidia four-celled, ovoid to broadly suburniform, (11.5) 11.8–15.7 (16.0) × (9.2) 9.7–12.2 (12.3) µm (n = 20/1), sterigmata gradually tapering, up to 15 × 2–2.5 µm; involucres well-developed, often totally covering basidial cells (except sterigmata). Basidiospores spiny (spines up to 0.3–0.4 µm long), thin-walled, compressed-subglobose or globose, (5.8) 5.9–7.3 (7.6) × 6.1–7.4 (7.8) µm (n = 30/1), L = 6.45, W = 6.69, Q' = 0.9–1.0, Q = 0.96, apiculus prominent, regular, sometimes slightly asymmetric, up to 2 × 1.8 µm.

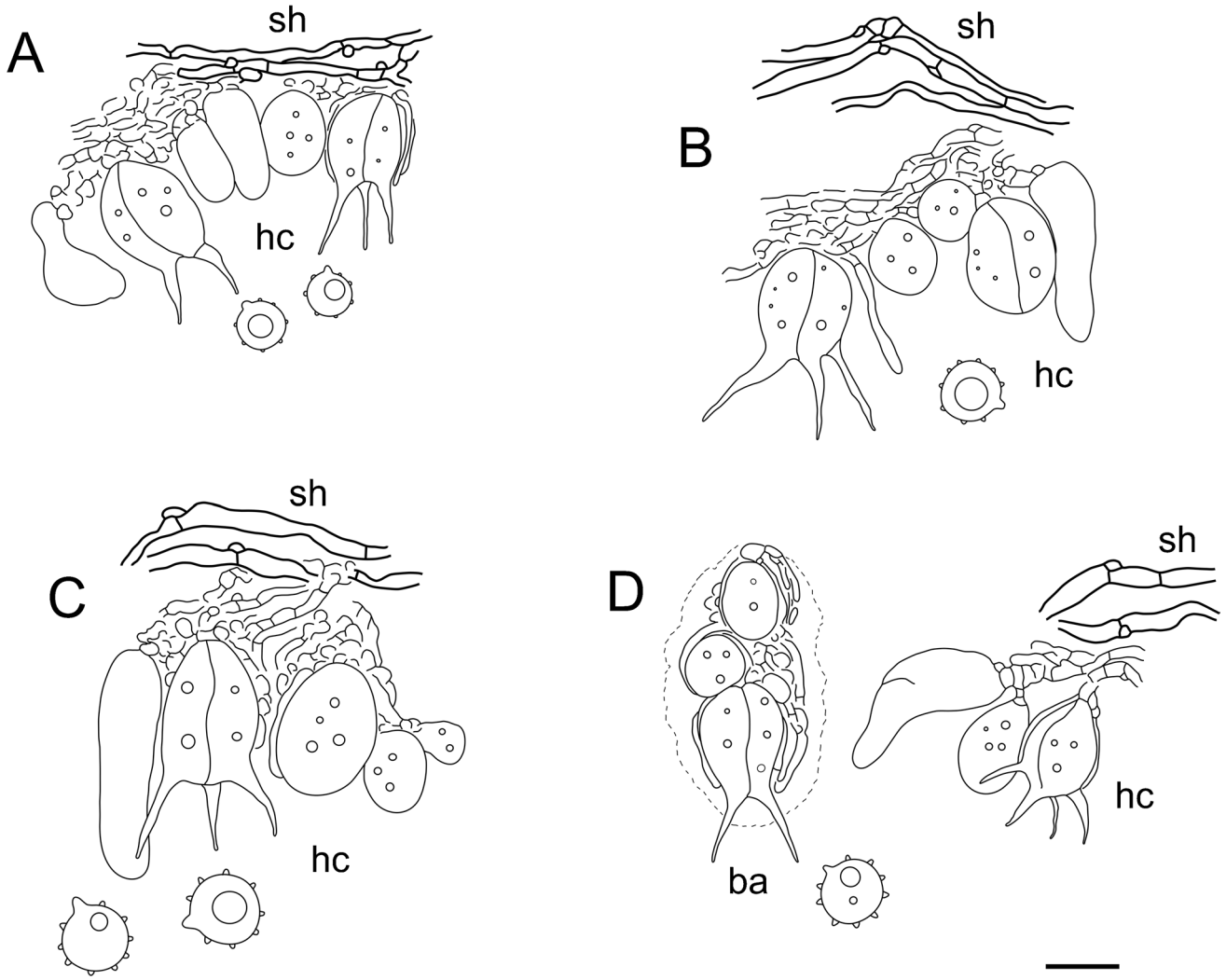


Fig. 8 Microscopic structures of extra-European *Basidiodendron* spp. with ornamented spores. **A**: *B. inconspicuum* (holotype), **B**: *B. mexicanum* (holotype), **C**: *B. spiculosum* (holotype), **D**: *B. widdringtoniae* (holotype); ba – basidia embedded in gelatinous matrix, gl – gloeocystidia, hc – hymenial cells, sh – subicular hyphae. Scale bar = 10 µm

Distribution and ecology. So far known from the type locality; decorticated coniferous wood in a highland forest.

Remarks. *Basidiodendron mexicanum* is one of the species with spiny basidiospores introduced here. It differs from *B. spiculosum*, also found in Mexico, in having thinner basidiocarps, shorter gloeocystidia and smaller basidiospores, as well as by the presence of hyphidia. Phylogenetically, *B. mexicanum* is closely related to *B. groningae* so far detected only in Europe (Figs. 1, 2). The latter species possesses basidiospores with more pronounced spines than in *B. mexicanum*, and it lacks hyphidia. ITS sequences of these species show 2.7–3.9% distance (the infraspecific differences within *B. groningae* are under 1.6%). Morphologically, *B. mexicanum* is most similar to *B. widdringtoniae* (see remarks under the latter species). *Basidiodendron widdringtoniae* is so far known from Malawi only and phylogenetically closer to *B. walleynii* than to *B. mexicanum* or *B. spiculosum*.

Basidiodendron robenae **Spirin & Miettinen, sp. nov.** – Figs. 4 and 6

MB 838725

Holotype: USA, New York, Essex Co., Arbutus Lake, 43.9836N 74.2354W, fallen angiosperm tree, 16.IX.2013 *Miettinen 16910.2** (H).

Etymology: After Robena Luck-Allen, the first monographer of the genus *Basidiodendron*.

Basidiocarps effused, smooth, waxy, continuous, pale ochraceous to greyish, 0.02–0.05 mm thick, covering a few cm in widest dimension, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped; subicular hyphae slightly thick-walled, subparallel, occasionally glued together, 2–3.5 µm diam, subhymenial hyphae thin- to slightly thick-walled, glued together, ascending or interwoven, 2–3 µm diam, basidia-bearing hyphae distinct in older parts of hymenium, slightly thick-walled, up to 10 × 2.5–3 µm. Gloeocystidia abundant, slightly or

distinctly tapering, projecting, hyaline to yellowish, (15) 16–32 (33) × (5.2) 5.6–8.8 (9.3) µm (n = 36/2). Basidia four-celled, ovoid to suburniform, (11.0) 12.2–18.2 (18.8) × (7.0) 7.1–9.2 (10.4) µm (n = 40/2), sterigmata gradually tapering, up to 10 × 1.5–2.5 µm; involucres occurring in senescent hymenium, covering basidia up to the very top. Basidiospores smooth, thin- or slightly thick-walled, compressed-subglobose or globose, (5.0) 5.1–6.4 × (5.1) 5.2–6.9 (7.2) µm (n = 90/3), L = 5.69–5.72, W = 5.95–6.03, Q' = 0.9–1.0, Q = 0.94–0.96, apiculus prominent, usually regular, up to 1.2 × 1.8 µm.

Distribution and ecology. North America (Canada – Ontario, USA – New York, Tennessee); rotten wood of deciduous trees.

Remarks. *Basidiodendron robenae* is a smooth-spored species distributed in the north-eastern part of North America. It is morphologically almost indistinguishable from the Eurasian species *B. glaucum*. In addition to separated distribution areas, these species have different substrate preferences: *B. robenae* has been detected on angiosperm hosts while *B. glaucum* occurs almost exclusively on coniferous wood, mainly on *Picea* spp.

Specimens examined (paratypes). Canada. Ontario: York Co., Nashville, *Fagus grandifolia*, 22.X.1955 *Cain* (H ex TRTC 31661). USA. Tennessee: Cocke Co., Cosby Creek, fallen angiosperm tree, 2.X.2015 *Miettinen 19650** (H), *Betula* sp., 2.X.2015 *Miettinen 19655* (H), Sevier Co., Ramsey Cascade Trail, *Quercus* sp., 30.IX.2015 *Miettinen 19562* (H).

Basidiodendron spiculosum **Spirin & Ryvarden, sp. nov.** – Figs. 3, 4 and 8

MB 838726

Holotype. Mexico. Vera Cruz: Xalapa, Botanical Garden, 19.514N 96.947W, *Cyathea* sp. (dry stem), 22.IX.1985 *Ryvarden 23324** (O, isotypes – H, LE).

Etymology: *Spiculosus* (Lat., adj.) – spiculate, in reference to the basidiospore ornamentation.

Basidiocarps effused, smooth, waxy, pruinose-reticulate, whitish or cream-coloured, then pale ochraceous, 0.02–0.04 mm thick, covering a few cm, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped; subicular hyphae slightly thick-walled, subparallel, 2–3 µm diam, subhymenial hyphae thin- or slightly thick-walled, interwoven, 1.5–2.5 µm diam, quickly collapsing. Gloeocystidia abundant, tapering or tubular-clavate, slightly projecting, hyaline to yellowish or brownish, (27) 28–51 (55) × (6.3) 6.8–10.0 (11.3) µm (n = 20/1), solitary of in groups of 2–3. Basidia four-celled, ovoid to broadly suburniform, (14.2) 14.8–24.2 (25.0) × (9.6) 9.8–12.0 (12.8) µm (n = 24/1), sterigmata gradually tapering, up to 10 × 2–2.5 µm; involucres well-developed, often covering basidial cells up to the middle part. Basidiospores spiny (spines up to 0.3–0.4 µm long), thin- or slightly thick-walled (wall up to 0.3 µm thick), compressed-subglobose or globose, (6.8) 6.9–8.2 (8.8) × (7.0) 7.1–8.9 (9.0) µm (n = 30/1), L = 7.62, W = 7.95, Q' = 0.9–1.0, Q = 0.96, apiculus prominent, regular, sometimes slightly asymmetric, up to 2 × 2 µm.

Distribution and ecology. So far known from the type locality; dry stem of a tree fern.

Remarks. Of the species dealt with herein, *B. spiculosum* is most similar to *B. mexicanum*; their differences are listed under the latter species. It seems the diversity of the spinose-spored *Basidiodendron* spp. in North America is not exhausted by two species only. Kisimova-Horovitz et al. (1997) reported *B. spinosum* from Costa Rica, and their description indicates the presence of one more, still unnamed species with spinose basidiospores.

Basidiodendron spinosum **(L.S. Olive) Wojewoda,** Mala Flora Grzybów 2: 91, 1981. – Fig. 3

≡ *Sebacina spinosa* L.S. Olive, Bull. Torrey Bot. Club 85: 27, 1958. Holotype. French Polynesia. Tahiti: Fautaua Valley, very rotten wood, 3.VII.1956 *Olive T398* (NY 01293275, studied).

Basidiocarps effused, smooth, waxy, pruinose-reticulate, whitish or greyish, 0.03–0.05 mm thick, covering a few cm, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, densely arranged; subicular hyphae thin- to slightly thick-walled, subparallel, 1.5–2.5 µm diam, subhymenial hyphae thin- to slightly thick-walled, ascending or interwoven, 1.5–2.5 µm diam. Gloeocystidia tapering or clavate, slightly projecting, hyaline or yellowish, 22–25 ×5.5–10 µm. Basidia four-celled, ovoid to broadly suburniform, widely collapsed, ca. 9–10 × 6–7.5 µm, sterigmata gradually tapering, up to 9 × 2–2.5 µm; involucres indistinct. Basidiospores spiny (spines up to 0.6 µm long), thick-walled (wall up to 0.7 µm thick), compressed-subglobose or globose, 4.6–5.2 × 4.8–5.8 µm (n = 30/1), L = 5.00, W = 5.22, Q' = 0.9–1.0, Q = 0.96, apiculus prominent, regular, sometimes somewhat asymmetric, up to 1.2 × 0.8 µm.

Distribution and ecology. So far known from the type locality; rotten wood of an unidentified tree.

Remarks. The only available material of this species is represented by the type specimen from Tahiti. *Basidiodendron spinosum* differs from other species of the *B. caesiocinereum* complex in having very prominent and densely arranged spines on the spore surface and clearly thick-walled basidiospores. Newly collected and sequenced specimens from the type locality are needed for clarifying phylogenetic relationships of *B. spinosum* with other representatives of the genus.

Basidiodendron trachysporum **(Bourdot & Galzin) Spirin, M. Weiß & Miettinen, comb. nov.** – Figs. 4, 5 and 7

MB 838727

≡ *Bourdotia cinerella* var. *trachyspora* Bourdot & Galzin, Hyménomycètes de France: 50, 1927. Lectotype (selected here, MBT395946). France. Aveyron: Causse Noir, *Pinus* sp., 8.V.1911 *Galzin 9106* (herb. Bourdot 9073) (PC).

Basidiocarps effused, smooth or indistinctly tuberculate, first waxy, pruinose, whitish or greyish, then continuous, greyish to pale ochraceous, arid, 0.01–0.03 mm thick, covering a few cm, occasionally gelatinized, semitranslucent and then almost invisible by a naked eye, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped; subicular hyphae thin- or slightly thick-walled, subparallel, (1.5) 2–3.5 µm diam, subhymenial hyphae thin- or slightly thick-walled, ascending or interwoven, 1.5–2.5 (–3) µm diam, basidia-bearing hyphae distinct in older parts of hymenium, slightly thick-walled, up to 15 × 2.5–3 µm. Gloeocystidia abundant, tapering, slightly projecting, hyaline to yellowish, (12) 13–45 (60) × (2.8) 3.0–7.8 (8) µm (n = 129/15), solitary or in groups of 2–6. Basidia four-celled, ovoid to broadly suburniform, (8.2) 8.3–15.8 (16.0) × (6.7) 6.9–11.0 (11.2) µm (*n* = 198/17), sterigmata gradually tapering, up to 10 × 1.5–2.5 µm; involucres normally poorly developed, well-visible in senescent basidiocarps only. Basidiospores warted, thin-walled, compressed-subglobose or globose, 4.8–7.4 (7.8) × (4.9) 5.0–7.8 (7.9) µm (*n* = 590/20), L = 5.26–6.58, W = 5.46–6.79, Q' = 0.9–1.0, Q = 0.94–0.98, apiculus prominent, regular, sometimes slightly asymmetric, up to 2 × 1.8 µm.

Distribution and ecology. Europe (Estonia, Finland, France, Netherlands, Norway, Russia, Slovenia, Sweden, Ukraine), Asia (Russia – Siberia and Far East), North America (USA – Washington); predominantly strongly decayed wood, mostly of conifers.

Remarks. This species was initially introduced as a warted-spored variety of *B. cinerella* (Bourdot and Galzin 1927), while the latter was erroneously described as a smooth-spored species (see discussion under *B. cinerellum*). The single authentic specimen labelled by Bourdot as '*Sebacina (Bourdotia) cinerella* f. *trachyspora*' is an extensive collection in good condition, and it is designated here as a lectotype. Morphological differences of *B. trachysporum* from *B. cinerellum* are listed under the latter species. Another similarly looking European species, *B. walleynii*, occurs on deciduous hosts and has thicker basidiocarps and differently shaped, wider and clearly projecting cystidia. *Basidiodendron trachysporum* is certainly the most common species of the genus in the middle- and north-boreal forests of North Europe.

The morphological variability of *B. trachysporum* deserves a closer look. In particular, one specimen collected in the North-American North-West (*Spirin 8262*) has unusually large basidia, 15–23 × 11.5–14.5 µm, and basidiospores, (8.6) 9.0–11.2 (11.7) × (9.1) 9.2–11.9 (12.3) µm (n = 30/1), L = 9.69, W = 10.00, Q' = 0.9–1.0 (1.1), Q = 0.97. However, the ITS sequence of this collection does not show any significant differences versus other ITS sequences of *B. trachysporum*, and our attempts to sequence additional markers were unsuccessful. For now, we treat the specimen under *B. trachysporum*.

Specimens examined. Estonia. Valgamaa: Otepää, Kääriku, decorticated decayed wood, 10.IX.2012 *Põldmaa* (TU 112986*), Välkjärve, *P. tremula*, 15.IX.2015 *Spirin 9848* (H). Finland. Ahvenanmaa: Geta, Getabergen, *P. abies*, 24.X.2001 *Kotiranta 19148* (H), Snäkö, small wooden planks, 24.X.2001 *Saarenoksa 18601* (H); Lumparland, Skag, *J. communis*, 23.X.2007 *Kotiranta 22098* (H). Varsinaissuomi: Salo, Orjanperä, *P. sylvestris*, 10.V.2010 *Kotiranta 22663* (H); Tammisaari, Tenhola, *P. abies*, 16.IX.2008 *Kotiranta 22418* (H). Uusimaa: Helsinki, Kumpula, coniferous wood, 13.XI.1999 *Saarenoksa 04699* (H), Patola, *A. incana*, 26.X.2011 *Miettinen 14981.3* (H), Veräjämäki, *P. abies*, 26.IX.2018 *Miettinen 21815* (H), 1.XI.2019 *Miettinen 22962.2** (H), *P. sylvestris*, 20.X.2019 *Miettinen 22899, 22906* (H), Viikki, *P. abies*, 1.X.2000 *Saarenoksa 07600* (H), 6.XI.2019 *Viner 2019-215* (H); Inkoo, Sommarö Nat. Res., *P. sylvestris* (old collapsed house), 22.V.2010 *Kotiranta 22695* (H); Kirkkonummi, Sundsberg, *P. sylvestris*, 17.V.2005 *Kotiranta 21261* (H), 20.X.2012 *Miettinen 15789.2* (H); Porvoo, Stensböle, *P. abies*, 1.XI.1990 *Kotiranta 9354* (H). Etelä-Häme: Hämeenlinna, Kotinen, *P. abies*, 25.IX.2014 *Spirin 8102* (H); Luhanka, Lempää, *J. communis*, 6.X.2010 *Kotiranta 22796, 22805* (H); Padasjoki: Koivukannonsuo, *P. abies*, 6–7.IX.2003 *Miettinen 7508.1* (H). France. Aveyron: L'Hospitalet, *Pinus* sp., 26.XI.1916 *Galzin 21134* (herb. Bourdot 20188) (PC 0706680); St. Sernin, *Cerasus* sp. and debris, 3.VI.1909 *Galzin 4250* (herb. Bourdot 20185) (PC 0706658). Netherlands. Groningen: Hoogezand, *P. sylvestris*, 7.II.2020 *Enzlin 20-005** (GENT). Norway. Vestfold: Larvik, Jordstøyp i Kvelde, *P. abies* (old collapsed building), 15.IX.2016 *Spirin 11111** (O), Vemannsås, *P. abies*, 30.IX.2018 *Spirin 12528*, 12530* (O). Telemark: Bamble, Rognsheia, *P. abies*, 3.XI.2017 *Spirin 11801*, 11803** (O), rotten wood, 3.XI.2017 *Larsson 17796* (O); Nome, Mørkvasslia, *P. abies*, 25.X.2016 *Spirin 11196* (O). Akershus: Nannestad, *P. abies*, 8.X.2011 *J. Nordén 9770* (O). Buskerud: Lier, Asdøljuvet, *P. abies*, 29.IX.2018 *Spirin 12508** (O), Stokkerinden, *P. abies*, 29.IX.2018 *Larsson 17910* (O). Hedmark: Åmot, Gravrusttjern, hardwood, 2.IX.1978 *Høgholen 832/78* (O 165333). Østfold: Aremark, Tjøstøl, *P. abies*, 24.X.2011 *Svantesson 1008* (O). Sør-Trøndelag: Tydal, Hilmo, *P. abies*, 22.IX.2011 *Svantesson 368* (O). Nord-Trøndelag: Snåsa, Blåfjella, *P. abies*, 26.IX.2011 *J. Nordén 9601** (O F-248016), *Svantesson 608** (O). Russia. Khabarovsk Reg.: Solnechnyi Dist., Igdomi, *Picea ajanensis*, 3.IX.2016 *Spirin 10856, 10916* (H). Krasnoyarsk Reg.: Turukhansk Dist., Mirnoye, *Pinus sibirica*, 20.VIII.2013 *Kotiranta 26387** (H). Leningrad Reg.: Boksitogorsk Dist., Chagoda, *P. abies*, 9.V.2018 *Spirin 11886** (H), Kolp', *P. abies*, 27.VII.2016 *Spirin 10376* (H), Vyalgozero, *P. abies*, 13.VII.2014 *Spirin 6936* (H); Kirishi Dist., Oblutskoye, dead *Trichaptum abietinum* on *P. abies*, 6.VIII.2019 *Spirin 12844* (H); Podporozhie Dist., Vazhinka, *P. abies*, 21.V.2016 *Spirin 10101, 10103, 10106, 10108* (H), 5.VI.2016 *Spirin 10182* (H). Nizhny Novgorod Reg.: Arzamas Dist., Pustynsky Nat. Res., *P. sylvestris*, 12.VIII.2015 *Spirin 9188a** (H); Lukoyanov

Dist., Panzelka, *P. sylvestris*, 17.VIII.2015 *Spirin 9481** (H), Razino, *U. glabra*, 18.VIII.2015 *Spirin 9483** (H); Sharanga Dist., Kilemary Nat. Res., *P. abies*, 23.VIII.2019 *Spirin 12972* (H), 24.VIII.2019 *Spirin 13046* (H). Tyumen Reg.: Yamalo-Nenets Autonomous Dist., W of Labytnangi, decorticated coniferous log, 24.VIII.1996 *Kotiranta 12721* (H). Zabaikalie: Duldurga Dist., Alkhanai, *Pinus* sp., 26.VIII.2010 *Kotiranta 29616** (H); Kyra Dist., Verkhnii Bukukun, decorticated coniferous log, 9.IX.2010 *Kotiranta 29923* (H). Slovenia. Gorenjska: Kranj, Njivica, *P. abies*, 25.IX.2019 *Spirin 13147** (H); Kranjska Gora, Vršič, *Larix decidua*, 5.VI.2019 *Spirin 12548** (H), Zelenci Spring, *P. abies*, 25.IX.2019 *Spirin 13190* (H); Bohinj, Lipanca, *L. decidua*, 26.IX.2019 *Spirin 13269* (H), *P. abies*, 6.VI.2019 *Spirin 12623** (H), 26.IX.2019 *Spirin 13244* (H), *P. mugo*, 6.VI.2019 *Spirin 12650* (H), Mrežce, *P. abies*, together with *Membranomyces delectabilis*, 26.IX.2019 *Spirin 13204* (H); Mojstrana, Triglavska Bistrica, *P. abies*, 28.IX.2019 *Spirin 13468* (H). Sweden. Västra Götaland: Strömstad, Hästeskede, *P. abies*, 31.X.2011 *J. Nordén 10035* (O). Ukraine. Kharkov Reg.: Krasnokutsky Dist., Slobozhansky Nat. Park, *Quercus robur*, 2.VII.2015 *Savchenko 72** (CWU 7558). USA. Washington: Clallam Co., Hurricane Ridge, *Abies lasiocarpa*, 19.X.2014 *Spirin 8740** (H), La Push, *Pseudotsuga menziesii*, 8.X.2014 *Spirin 8262** (H).

Basidiodendron walleynii **Spirin, V. Malysheva & Schoutteten, sp. nov.** – Figs. 4, 5 and 7

MB 838731

Holotype. Russia. Nizhny Novgorod Reg.: Lukoyanov Dist., Sanki, 54.841N 44.235E, *Quercus robur* (rotten stump), 20.VIII.2015 *Spirin 9697** (H, isotype – LE).

Etymology: After Ruben Walleyn, a Flemish mycologist and collector of the first modern specimen of this species.

Basidiocarps effused, smooth, first waxy, pruinose, whitish or greyish, then continuous, arid, rather soft, cream-coloured to pale ochraceous, opaque, 0.02–0.1 mm thick, covering a few cm, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, easily collapsing, freely spaced; subicular hyphae thin- or slightly thick-walled, subparallel, 2.5–3 µm diam, subhymenial hyphae thin- or slightly thick-walled, ascending, 2.5–3 µm diam. Gloeocystidia abundant, moderately tapering or tubular-clavate, rarely subcapitate, projecting up to 20 µm, hyaline to very pale yellowish or brownish, (14.5) 15–38 (39) × (4.6) 5.0–10.7 (11.2) µm (n = 67/5), often in groups of 3–5. Basidia four-celled, ovoid to broadly suburniform, (10.0) 10.8–15.7 (17.2) × (7.0) 7.2–11.1 (11.8) µm (n = 70/5), sterigmata gradually tapering, up to 10 × 2.5 µm; involucres indistinct. Basidiospores warted, thin-walled, compressed-subglobose or globose, (5.0) 5.1–7.0 × (5.2) 5.3–7.2 (7.3) µm (n = 120/4), L = 5.87–6.17, W = 6.07–6.38, Q' = 0.9–1.0, Q = 0.96–0.98, apiculus prominent, regular, sometimes slightly asymmetric, up to 2.5 × 2 µm.

Distribution and ecology. Europe (Belgium, France, Russia); decorticated wood of deciduous trees in temperate forests.

Remarks. *Basidiodendron walleynii* produces rather thick, opaque, soft basidiocarps reminiscent more of *Hyphoderma* or *Peniophorella* spp. than other *Basidiodendron* species. It differs from two other European *Basidiodendron* species with warted basidiospores, i.e., *B. cinerellum* and *B. trachysporum*, in having a non-gelatinized hymenium, a well-differentiated subhymenium consisting of ascending hyphae, and clearly projecting, variably shaped gloeocystidia. *Basidiodendron walleynii* is a temperate species; it occurs on rather tough, decorticated wood of deciduous trees (*Castanea*, *Erica*, *Quercus*).

Specimens examined (paratypes). Belgium. Vlaams-Brabant: Hoeilaart, Zoniënwoud, Kersselaerspleyn, *Q. robur*, 24.IX.2002 *Walleyn 3081** (GENT). France. Aveyron: Boutaran, dead *Inonotus dryadeus*, 12.V.1914 *Galzin 15320* (herb. Bourdot 13969) (PC 0706667); Forques, *Castanea sativa*, 20.IV.1912 *Galzin 11270* (herb. Bourdot 9068) (PC 0706671), *Galzin 11276* (herb. Bourdot 9067) (PC 0706662); Le Rec, *C. sativa*, XI.1922 *Galzin 27569* (herb. Bourdot 35049) (PC 0706663); Loubotis, *C. sativa*, 13.XI.1913 *Galzin 14136* (herb. Bourdot 12434) (PC 0706670); Matavalès, *C. sativa*, 20.IV.1912 *Galzin 11329* (herb. Bourdot 9069) (PC 0706664); Mazet Bas, *C. sativa*, 16.VII.1912 *Galzin 11650* (herb. Bourdot 9070) (PC 0084212), 5.IX.1912 *Galzin 11881* (herb. Bourdot 9071) (PC 0084223), 23.X.1915 *Galzin 18653* (herb. Bourdot 19447) (PC 0706659), XII.1915 *Galzin 19135* (herb. Bourdot 15528) (PC 0706661), 5.XI.1916 *Galzin 20597* (herb. Bourdot 19365) (PC 0706668), 24.XII.1916 *Galzin 21277* (herb. Bourdot 19356) (PC 0706669); Travès, *Erica arborea*, 12.II.1912 *Galzin 10712* (herb. Bourdot 9063) (PC 0084224).

Basidiodendron widdringtoniae **Spirin, V. Malysheva & Ryvarden, sp. nov.** – Figs. 4 and 8

MB 838732

Holotype. Malawi. Southern Prov.: Mulanje, Lichenya Plateau, 15.914S 35.589E, *Widdringtonia whytei* (rotten decorticated log), 9–10.III.1973 *Ryvarden 11307a** (O, isotypes – H, LE).

Etymology: After *Widdringtonia*, the host tree of the species.

Basidiocarps effused, smooth, waxy, pruinose-reticulate, whitish or greyish, 0.01–0.02 mm thick, covering a few cm, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, partly glued together; subicular hyphae thin- to slightly thick-walled, subparallel, 2.5–3 µm diam, subhymenial hyphae thin- to slightly thick-walled, ascending or interwoven, 2–3 µm diam. Gloeocystidia abundant, clearly tapering, slightly projecting, hyaline or yellowish to brownish, (12) 13.5–21 (24) × (3.4) 3.9–5.9 (6.0) µm (n = 14/1). Basidia two – four-celled, ovoid to broadly

suburniform, (10.2) 11.7–14.2 (14.8) × (8.1) 8.2–10.8 (12.0) µm (n = 20/1), sterigmata gradually tapering, up to 8 × 2–2.5 µm; involucres well-developed, often totally covering basidial cells (except sterigmata); basidia in older hymenium gluedin groups of 3–4 and occasionally embedded in gelatinous matrix. Basidiospores spiny (spines up to 0.3 µm long), thin-walled, compressed-subglobose or globose, (5.8) 5.9–6.8 × (6.0) 6.1–7.1 (7.2) µm (n = 30/1), L = 6.24, W = 6.48, Q' = 0.9–1.0, Q = 0.96, apiculus prominent, regular, sometimes asymmetric, up to 1.5 × 1.5 µm.

Distribution and ecology. So far known from the type locality; rotten wood of conifers (*Widdringtonia whytei*).

Remarks. *Basidiodendron widdringtoniae* is morphologically most similar to *B. mexicanum* occurring on coniferous wood in Mexico. It differs from the latter species mainly due to thinner basidiocarps and shorter gloeocystidia. However, our material is too scanty to assure these differences are not age-dependent. Therefore, the two species must for the time being be separated by different DNA sequences and distribution areas.

Discussion

In this study, we present the taxonomy of twelve species of the *B. caesiocinereum* complex of which eight are described as new to science. Our study focused mainly on temperate-boreal Europe, while sampling from North America and East Asia was occasional. More data may reveal other representatives of the *B. caesiocinereum* group in those areas, as well as in warm-temperate to Mediterranean regions of Europe. A few available environmental sequences support this suggestion. In fact, the species diversity in this complex could be even higher because *B. caesiocinereum* and *B. spinosum* s. lato were reported from Macaronesia (Roberts and Spooner 2004), North and Central Africa (Malençon 1954; Roberts 2001), the Caribbean (Roberts 2006, 2008), Central and South America (Kisimova-Horovitz et al. 1997; Roberts 2003), and New Zealand (McNabb 1969). This material awaits proper taxonomic revisions.

Despite rather uniform anatomical traits, members of the *B. caesiocinereum* complex are morphologically distinguishable, although microscopy requires the use of phase contrast illumination and Cotton Blue as mounting medium. Only this combination allows the verification of outgrowths on the basidiospore wall and an identification of their form (warts or spines). As stated above, the basidiospore ornamentation is a key morphological character in this group. Combined with other morphological features (basidiocarp colour and consistency, size of basidia and gloeocystidia, arrangement of hymenial cells), as well as ecological and geographic data, it facilitates the species recognition.

Key for species currently recognized in the *Basidiodendron caesiocinereum* complex

1. Basidiospores smooth.....2
1*. Basidiospores ornamented 4
2. Basidiospores 5.1–7.8 × 5.3–8.1 µm, basidia 12–24 × 7–11.5 µm, occasionally with a distinct stalk-like base. Eurasia, almost exclusively on ang iosperms.....*B. caesiocinereum*
2*. Basidiospores on average smaller, 5.1–6.8 × 5.2–7 µm, basidia 10–18 × 7–10.5 µm, devoid of stalk-like base 3
3. Eurasia, almost exclusively on gymnosperms (*Abies, Pic ea*)..... *B. glaucum*
3*. North America, exclusively on angiosperms..... .....*B. robenae*
4. Basidiospores warted..... 5
4*. Basidiospores spiny 8
5. Basidia glued in groups. Europe, mostly on gymnosperms ..... *B. cinerellum*
5*. Basidia exposed. On various hosts.....6
6. Basidiocarps arid, opaque. Subhymenial hyphae well-visible, ascending. Gloeocystidia tapering or tubular-clavate, 15–38 × 5–11 µm. Temperate Europe, exclusively on angiosperms (*Erica, Castanea, Quercus*) .....*B. walleynii*
6*. Basidiocarps waxy, hymenium often gelatinized. Subhymenium hyphae usually poorly discernible, glued together. Gloeocystidia tapering, 13–45 × 3–8 µm. Eurasia and North America, mostly on gymnosperms 7
7. Basidiospores distinctly warted, 4.8–7.4 × 5.0–7.8 µm. Eurasia and North America..... *B. trachysporum*
7*. Basidiospores minutely warted, 5.0–6.2 × 5.2–6.5 µm. North American North-West ..... *B. inconspicuum*
8. Basidia glued in groups. South Africa (Malawi), on gymnosperms.....*B. widdringtoniae*
8*. Basidia exposed. On various hosts.....9
9. Basidiospores with spines up to 0.6 µm long.....10
9*. Basidiospores with spines up to 0.4 µm long 11
10. Basidia 9–10 × 6–7.5 µm, basidiospores 4.6–5.2 × 4.8–5.8 µm. Oceania ..... *B. spinosum*
10*. Basidia 13–18 × 9–12 µm, basidiospores 6.0–7.9 × 6.2–8.2 µm. Europe ..... *B. groningae*
11. Basidia 12–15.5 × 9.5–12 µm, basidiospores 5.9–7.3 × 6.1–7.4 µm. Mexico (highlands), on gymnosperms .....*B. mexicanum*
11*. Basidia 15–24 × 10–12 µm, basidiospores 6.9–8.2 × 7.1–8.9 µm. Mexico (subtropical zone), on ferns (*Cyathea*)..... .....*B. spiculosum*

Additional specimens examined

Basidiodendron eyrei. Netherlands. Gelderland: Hoge Veluwe, decayed wood, 16.XI.2019 *Schoutteten 19-411** (GENT); Groningen: Nieuweschans, Houwingaham,

decayed wood, 24.X.2018 *Enzlin 18-101** (GENT); Oude Pekela, Emergobos, decayed wood, 7.X.2018 *Enzlin 18-103** (GENT); Ter Apel, Roelage Bos, *P. abies*, 22.X.2013 *Enzlin 13-100** (GENT).

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Author contribution All authors contributed to the study conception and design. Material preparation, data collection and analysis were initially performed by Viacheslav Spirin, Vera Malysheva, Otto Miettinen, Ilya Viner and Karl-Henrik Larsson. The authors Nathan Schoutteten, Jenni Nordén, Heikki Kotiranta, Leif Ryvarden, Annemieke Verbeken and Michael Weiß provided further important material and/or sequences. The first draft of the manuscript was written by Viacheslav Spirin and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability DNA sequences used in the present study are available in GenBank. Alignments were deposited in TreeBase. Fungal specimens are stored in public herbaria (as indicated under Specimens examined)

Declarations

Ethics approval Not applicable

Conflict of interests None.

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