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 gleocystidia 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
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 *Basidiодendron*, 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. (= *Basidiодendron 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. lat 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 *Basidiодendron* 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 |
|---------|--------------------|--------------------|------|----------------------------------|
| B. 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 |
| B. caesiocinereum | VS 11764 (O) | NO | Ulmus glabra | MW136082 |
| B. caesiocinereum | VS 11776 (O) | NO | Betula pubescens | MW136101 |
| B. caesiocinereum | VS 12536 (O) | NO | Tilia cordata | MW136069 |
| B. caesiocinereum | VS 12500 (O) | NO | C. avellana | MW136061 |
| B. caesiocinereum | VS 12502 (O) | NO | U. glabra | MW136084 |
| B. caesiocinereum | VS 12504 (O) | NO | U. glabra | MW136065 |
| B. caesiocinereum | VS 12511 (O) | NO | U. glabra | MW136083 |
| B. caesiocinereum | VS 12515 (O) | NO | U. glabra | MW136100 |
| B. caesiocinereum | VS 12465 (O) | NO | U. glabra | MW136102 |
| B. caesiocinereum | VS 11115 (O) | NO | Alnus incana | MW136103 |
| B. caesiocinereum | VS 11115 (O) | NO | Alnus incana | MW136104 |
| B. caesiocinereum | VS 12337 (TU) | EE | Pinus sylvestris | MW136088 |
| B. caesiocinereum | VS 12350 (TU) | EE | C. avellana | MW136064 |
| B. caesiocinereum | VS 12368 (H) | IT | P. abies | MW136086 |
| B. caesiocinereum | VS 11188 (O) | NO | A. incana | MW136104 |
| B. caesiocinereum | VS 12449 (O) | NO | U. glabra | MW136064 |
| B. caesiocinereum | VS 13317 (H) | SI | Pinus mugo | MW136097 |
| B. caesiocinereum | VS 13275 (H) | SI | P. mugo | MW136093 |
| 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 |
| 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 |
| B. glaucum | VS 7890 (H) | RU-KHA | Picea ajanensis | MW136063 |
| B. groningae | GVA 20-040 (GENT) | BE | rotten wood | MW139280 |
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/mycocos/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).

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              | Thuya 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 23234 (O)     | MX                 | Cryathea 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 -              |
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 taxa involved in the analyses in one strongly supported clade (bs =100, pp =1) with *B. luteostrigillum* 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 *Basidiocerebrum 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. walleyii*) have warted basidiospores, and in one species (*B. widdringtoniae*) the spore wall bears spines. The smaller subclade (labelled as *Basidiocerebrum cinerellum* group, Fig. 1) contained sequences of specimens identical to a lectotype of *Bourdotia cinerella*; the latter species is redescribed and combined in *Basidiocerebrum* 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. *Basidiocerebrum caesiocinereum*, *B. cinerellum* and *B. walleyii* 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. walleyii*) are distinguishable due to differently looking basidiocarps and gleo-cystidia, 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**

*Basidiocerebrum caesiocinereum* (Höhn. & Litsch.) Luck-Allen, Canadian J. Bot. 41: 1036, 1963. – Figs. 3, 4, 5 and 6
eq Corticium caesiocinereum Höhn. & Litsch., Sitzungsbl. Kaiscr. 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
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 C. cinerella represents a warted-spored taxon, while the type specimen of C. caesiocinereum has smooth basidiospores. Therefore, the synonymy of C. caesiocinereum and C. 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 accidently 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, Zoniënwood, Kersselaerspleyn, Fagus sylvatica, X.2018 Schoutetten 18-172*, 18-226*, 18-625*, 18-902*, 18-925*, 18-1050*, 18-1051* (GENT). China. Jiilin: Antu Co., Huang Song Pu, Populus sp. (?), 28.VIII.2005 Miettinen 10608* (H). Finland. Varvinsaissuomu: Bromarv, Rilax, deciduous wood, 13.X.2000 Saarenokska 12100 (H). Uusimaa: Helsinki, Myllypuro – Puotinharju, Betula sp., 3.IX.1989 Saarenokska 18789 (H), Vanhakaupunki, Alnus incana, 10.IX.1989 Saarenokska 22889 (H), hardwood, 18.IX.1998 Saarenokska 17598 (H), Veräjämiäki, Salix caprea (?), 19–21.X.2011 Miettinen 14910.1, 14934.2 (H), Betula sp., 25.X.2019 Miettinen 22920.1 (H); Porvoo, Stensbøle, S. caprea, 1.XI.1990 Kotiranta 9337 (H); Sipoo, Lilla Kummelberget Nat. Res., Populus tremula, 29.IX.2010 Kotiranta 22735 (H). Enontekkio Lappi: Enontekkiö, 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 (H); 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, Rognshei, A. incana, 3.XI.2017 Spirin 11799 (O); Nome, Mørkvasslia, A. incana, 25.X.2016 Spirin 11187 (O), Picea abies, 16.X.2011 Svanesson 901* (O F253623). Buskerud: Lier, Asdøljuvet, A. incana, 29.X.2018 Spirin 12515* (O), C. avellana, 29.X.2018 Spirin 12500* (O), U. glabra, 29.X.2018 Spirin 12502*, 12504*, 12511* (O). Akershus: Asker, Esivika, Acer platanoides, 28.XI.2018 Spirin 12462 (O), U. glabra, 28.XI.2018 Spirin 12465* (O); Baerum, Kjøglidalen, A. incana, 16.X.2016 Spirin 11115*, 11121 (O), C. avellana, 16.X.2016 Spirin 11123, 11126 (O), S. caprea, 16.X.2016 Spirin 11129 (O). Oppland: Nord-Fron, Liadalane, A. incana, 12.X.2016 Spirin 11044 (O), 29.XI.2017 Spirin 11636, 11649 (O), rotten wood, 29.XI.2017 Larsson 17631 (O); Sel, Sagåa, S. caprea, 13.X.2016 Spirin 11069 (O). Møre og Romsdal: Nesset, Eikesdalene, A. incana, 27.X.2017 Spirin 11610 (O), rotten wood, 27–28.X.2017 Larsson 17548, 17558 (O). Russia. Krasnoyarsk Reg.: Turukhansk Dist., Lebed’, Alnus hirsuta, 23.VIII.2013 Kotiranta 26428* (H).
**Basidiodendron cinerellum** (Bourdot & Galzin) Spirin & V. Malysheva, comb. nov. – Figs. 3, 4, 5 and 7
MB 838719

≡ *Bourdota 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 broad-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.

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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 *Bourdotia (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 warty, 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. 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.
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 warded 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.

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**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
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 Saarenkoska 04201 (H), Mölylä, P. abies, 4.XII.2017 Miettinen 21459 (H), Veräjämäki, P. abies, 30.X.2019 Vinter 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).

Table 2 Geographic, ecological and morphological traits in Basidiidendron 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 (Thuya)      | 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 |
Fig. 5 Basidiocarps of *Basidiiodendron* 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 *Basidiiodendron* 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
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

Fig. 7 Microscopic structures of European *Basidiodendron* spp. with ornamented spores. A: *B. cinerellum* (Spirin 12337), B: *B. gronin-gae* (holotype), C: *B. trachysporum* (Spirin 11111), D: *B. walleynii* (hymenial cells from holotype, gloeocystidia from Walley 3081); ba – basidia embedded in gelatinous matrix, gl – gloeocystidia, hc – hymenial cells, sh – subicular hyphae. Scale bar = 10 µm.
Autonomous Dist.: Priuralsky Dist., Sob’. *Picea obovata*, 11.VIII.1969 Parmasto (TAAM 053842), Slovenia. Gorenska: Kranjska Gora, Vršič, *Pinus mugo*, 5.VI.2019 Spirin 12576 (H), 27.IX.2019 *Spirin 13317* (H), 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, Triglavská Bistrica, *P. abies*, 26.IX.2019 *Spirin 13418*, 13422, 13471 (H), Sweden. Kalmar: Vimmerby, Norra Kvill, *P. abies*, 27.X.2010 *J. Nordén 7879* (O), Örebro: Lekeberg, Ugglehöjd, *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, 27.IX.2019 *Sprit 13561* (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, easily collapsing, ascending or interwoven, 1.5–2 (2.5) μm diam. Gloeocystidia rather rare, tapering, slightly projecting, hyaline to 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.

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. Basidiiodendron 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 *Sprit 13539* (H). Norway. Vest-Agder: Lyngdal, Fladstad, *A. incana*, 1.XI.2017 *Sprit 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, Merkvaslia, *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, Liltuva, *P. abies*, 5–6.IX.2011 *Svantesson 10* (O), *Svantesson 11* (O F253609), *Svatesson 52* (O), *Svantesson 140* (O F253677), *Svantesson 141, 144* (O), Russia. Khabarovsky: Verkhnebureinskii Dist., Dublikan Nat. Res., *Picea ajanensis*, 23.VIII.2014 *Sprit 7890* (H 702862). Leningrad Reg.: Kirishi Dist., Shariya, *P. abies*, 10.VIII.2019 *Sprit 12922* (H). Sweden. Västra Götaland: Strömstad, Hästeskede, *P. abies*, 13.X.2011 *J. Nordén 10037* (O), Västerbotten: Lycksele, *P. abies*, 29.IX.2010 *J. Nordén 7152* (O).

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

MB 838721

Holotype. Netherlands. Groningen: Lauwersoog, Ballastplaatbos, 53.402N 6.213E, 28.IX.2011 *Schoutteten & Spirin, sp. nov.* – Figs. 4 and 6

Holotype. Norway. Nord-Trøndelag: Snåsa, Blåfjella, 64.2939N 13.029E, 28.IX.2011 *J. Nordén 9683* (O F-248006, isotype – H). Etymology: *Glaucus* (Lat., noun) – a Latin name of Groenlandia, the type locality.

Basidiocarps effused, smooth, first waxy, pruinose-reticulate, greyish, then continuous, greyish to pale ochraceous, 0.02–0.04 mm thick, 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.

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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. So far known from the type locality; strongly decayed wood of conifers (Thuja plicata). Remarks. 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. Gloecystidia abundant, distinctly tapering, slightly projecting, hyaline to yellowish or rarely brownish, (11) 17–34 (35) × (4.2) 4.3–6.2 (7.0) μm (m = 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.

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. Gloecystidia abundant, distinctly tapering, slightly projecting, hyaline to yellowish or rarely brownish, (11) 17–34 (35) × (4.2) 4.3–6.2 (7.0) μm (m = 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.
Distribution and ecology. So far known from the type locality; decorticated coniferous wood in a highland forest.

Remarks. Basidiomycetaceae 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 basidiocarps 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). Basidiomycetaceae widdringtoniae is so far known from Malawi only and phylogenetically closer to B. wallevii than to B. mexicanum or B. spiculosum.

Basidiomycetaceae 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 Basidiomycetaceae.

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 thinner 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

Fig. 8 Microscopic structures of extra-European Basidiomycetaceae 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.
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 globbose, (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 196590* (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, Cytathea sp. (dry stem), 22.IX.1985 Ryvarden 23324* (O, isotypes – H, LE).

Etymology: Spiculosus (Lat., adj.) – spiculate, in reference with other representatives of the genus.

Basidiocarps effused, smooth, waxy, bruinose-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 globbose, 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; 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 spino-seored 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 spino basidiospores.

Basidiodendron spinosum (L.S. Olive) Wojewoda, Mala Flora Grzybów 2: 91, 1981. – Figs. 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 globbose, 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 (Bourdut & Galzin) Spirin, M. Weiß & Miettinen, comb. nov. – Figs. 4, 5 and 7
MB 838727
≡ Bourdotia cinerella var. trachyspora Bourdut & Galzin, Hyménomycètes de France: 50, 1927. Lectotype (selected here, MBT395946). France. Aveyron: Causse Noir, Pinus sp., 8.V.1911 Galzin 9106 (herb. Bourdut 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, semi-transparent and then almost invisible by a naked eye, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped; subicular hyphes 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, Sweden, Denmark, 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. cinerella*). The single authentic specimen labelled by Bourdot as ‘Sebacina (Bourdota) 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. Basidiocadron 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. Valguma: Otepää, Kääriku, decorticated decayed wood, 10.IX.2012 Pöldmaa (TU 112986*), Väljärve, *P. tremula*, 15.IX.2015 Spirin 9848 (H). Finland. Ahvenanmaa: Geta, Getaberger, *P. abies*, 24.X.2001 Kotiranta 19148 (H), Snäsö, small wooden planks, 24.X.2001 Saarenkoska 18601 (H); Ljumpearl, Skag, *J. communis*, 23.X.2007 Kotiranta 22098 (H). Varsinaisuuomi: 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 Saarenkoska 04699 (H), Patola, *A. incana*, 26.X.II.2011 Miettinen 14981.3 (H), Veräjämäki, *P. abies*, 26.IX.2018 Miettinen 21815 (H), 1.XI.2007 Miettinen 22962.2* (H), *P. sylvestris*, 20.X.2019 Miettinen 22899, 22906 (H), Viikki, *P. abies*, 1.X.2000 Saarenkoska 07600 (H), 6.XI.2019 Vinner 2019-215 (H), Inkoo, Sommaro Nat. Res., *P. sylvestris* (old collapsed house), 22.V.2010 Kotiranta 22695 (H); Kirkkonummi, Sandsberg, *P. sylvestris*, 17.V.2005 Kotiranta 21261 (H), 20.X.2012 Miettinen 15789.2 (H); Porvoo, Stensböle, *P. abies*, 1.XL990 Kotiranta 9354 (H). Etelä-Häme: Hämeenlinna, Kotinen, *P. abies*, 25.IX.2014 Spirin 8102 (H); Luhanka, Lempiälä, *J. communis*, 6.XI.2010 Kotiranta 22796, 22805 (H); Padasjoki: Koivukannonsuo, *P. abies*, 6–7. IX.2003 Miettinen 7508.7 (H), France. Aveyron: L’Hospital, *Pinus sp.*, 26.XI.1916 Galian 21134 (herb. Bourdot 20188) (PC 0706680); St Sernin, *Cerasus sp.* and debris, 3.VI.1909 Galian 4250 (herb. Bourdot 20185) (PC 0706658). Netherlands. Groningen: Hoogezand, *P. sylvestris*, 7.II.2020 Ensln 20-005* (GENT), Norway. Vestfold: Larvik, Jordstyp i Kvelde, *P. abies* (old collapsed building), 15.IX.2016 Spirin 111111* (O), Vemmansås, *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, Gravstsjern, hardwood, 2.IX.1997 Høgholmen 832/78 (O 165333). Østfold: Aremark, Tjøstøl, *P. abies*, 24.XI.2011 Svantesson 1008 (O); Sør-Trøndelag: Tydal, Hilimo, *P. abies*, 22.IX.2011 Svantesson 368 (O). Nord-Trøndelag: Snåsa, Blåfjella, *P. abies*, 26.IX.2011 J. Nordén 9601* (O 248016), Svantesson 608* (O). Russia. Khabarovsk Reg.: Solnechny Dist., Igdomi, *Picea ajanensis*, 3.XI.2016 Spirin 10856, 10916 (H). Krasnoyarsk Reg.: Turukhansk Dist., Mirmooy, *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., Vazhinaka, *P. abies*, 21.V.2016 Spirin 10101, 10103, 10106, 10108, 5.V.2016 Spirin 10182 (H). Nizhny Novgorod Reg.: Arzamas Dist., Pustynsky Nat. Res., *P. sylvestris*, 12.VIII.2015 Spirin 9188a* (H); Lukoyanov
Basidiocarps effused, smooth, waxy, pruinose-reticulate, 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 subbiform, (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, thick-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.
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 Macaronia (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 angiosperms..............................................2. *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, Pinus).............................................................3. *glaucum*
   3*. North America, exclusively on angiosperms...... .............................................................3. *walleynii*
   3*. South America, exclusively on gymnosperms......8
   3*. South America, exclusively on angiosperms......8
4. Basidiospores warted.............................................5
   4*. Basidiospores spiny..........................................8
5. Basidia glued in groups. Europe, mostly on gymnosperms ..................................................5. *cinerellum*
   5*. Basidia exposed. On various hosts.........................6
   6. Basidiocarps arid, opaque. Subhymenial hyphae visible, ascending. Gloeocystidia tapering or tubular-clavate, 15–38 × 5–11 μm. Temperate Europe, exclusively on angiosperms (Erica, Castanea, Quercus).................................6. *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...............................7. *trachysporum*
   7*. Basidiospores minutely warted, 5.0–6.2 × 5.2–6.5 μm. North American North-West ......................8. *inconspicuum*
8. Basidia glued in groups. South Africa (Malawi), on gymnosperms..............................................8. *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 ...........................................10. *pinus*
10*. Basidia 13–18 × 9–12 μm, basidiospores 6.0–7.9 × 6.2–8.2 μm. Europe ..............................10. *caesiocinereum*
11. Basidia 12–15.5 × 9.5–12 μm, basidiospores 5.9–7.3 × 6.1–7.4 μm. Mexico (highlands), on gymnosperms ..............................................11. *mexicanum*
11*. Basidia 15–24 × 10–12 μm, basidiospores 6.9–8.2 × 7.1–8.9 μm. Mexico (subtropical zone), on ferns (Cyathea)......................................................11. *spiculosum*

Additional specimens examined

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

Bourd'H, Galzin A (1927) Hyyménomyctes de France. Hetérobasidiés – Homobasidiés gymnoacées. Sceaux
Bourd'H, Maire L (1920) Notes critiques sur quelques Hyménomyctes nouveaux ou peu connus. Bull Soc Mycol France 36:69–85
Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes – applications to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118
Gilbertson RL (1974) Fungi that decay ponderosa pine. University of Arizona Press, Tucson
Höhnle F, Litschauer V (1908) Beiträge zur Kenntnis der Corticieen. III. Sitzungsb. Kais. Akad. Wissenschaften Wien, Mat – Nat Klasse Abt. I, 117:1081–1124
Kisimova-Horovitz L, Oberwinkler F, Gómez LD (1997) Basidiomycetes resupinados de Costa Rica. Exidiaceae (Tremellales). Rev Biol Trop 45:1325–1347
Kozlov AM, Darriba D, Flouri T, Morel B, Stamatakis A (2019) RAxML-NG: A fast, scalable, and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics btz305. https://doi.org/10.1093/bioinformatics/btz305
Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Mol Biol Evol 35:1547–1549
Landvik S (1996) Neolepta, a fruit-body producing genus of the basal ascomycetes, as shown by SSU and LSU rDNA sequences. Mycol Res 100:199–202
Luck-Allen R (1963) The genus Basidiodendron. Can J Bot 41:1025–1052
Malençon G (1954) Prodrome d’une Flore Mycologique du Moyen Atlas. 2e Contribution. Bull Soc Mycol France 70:117–156
McNabb RFR (1969) New Zealand Tremellales – III. N Z J Bot 7:241–261
Oberwinkler F (1963) Niedere Basidiomyceten aus Südbayern. III. Die Gattung Sebacina. Tul. s.1. Ber Bayerischen Bot Gen 36:41–55
Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6. http://tree.bio.ed.ac.uk/software/tracer/ Accessed 20 Dec 2020
Rehner SA, Buckley E (2005) A Beauveria phylogeny inferred from nuclear ITS and EF1-alpha sequences: evidence for cryptic diversification and links to Cordyceps teleomorphs. Mycologia 97:84–98
Roberts P (2001) Heterobasidiomycetes from Korup National Park, Cameroon. Kew Bull 56:163–187
Roberts P (2003) Heterobasidiomycetes from Rancho Grande, Venezuela. Mycotaxon 87:25–41
Roberts P (2006) Caribbean heterobasidiomycetes: 2 Jamaica. Mycotaxon 96:83–107
Roberts P (2008) Caribbean heterobasidiomycetes: 3 British Virgin Islands. Mycotaxon 105:137–147
Roberts P, Spooner B (2004) Heterobasidiomycetes from the Azores. Kew Bull 59:95–101
Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 61:539–542
Stein F (1969) Particle size measurements with phase contrast microcopy. Powder Technol 2:327–334
Spirin V, Malysheva V, Mendes-Alvarenga RL, Kotiranta H, Larsson KH (2020) Studies in Basidiodendron eyrei and similar-looking taxa (Auriculariales, Basidiomycota). Botany 98:623–638
Thiers B (2020) Index Herbariorum: a global directory of public herbaria and associated stuff [continuously updated]. New York Botanical Garden’s Virtual Herbarium. http://sweetgum.nybg.org/ih. Accessed 20 Dec 2020
Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Crypto-
coccus species. J Bacteriol 172:4238–4246
Weiβ M, Oberwinkler F (2001) Phylogenetic relationships in Auricu-
lariales and related groups – hypotheses derived from nuclear ribosomal DNA sequences. Mycol Res 105:403–415
Wells K (1959) Studies of some Tremellaceae III. The genus Boardotia. Mycologia 51:540–563
Wells K, Raitviir A (1975) The species of Boardotia and Basidioden-
dron (Tremellaceae) of the USSR. Mycologia 67:904–922
White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and sequenc-
ing of fungal ribosomal RNA genes for phylogenetics. In: Innis
MA et al (eds) PCR protocols A guide to methods and applica-
tions. Academic Press, San Diego, pp 315–322
Wojewoda W (1981) Mała flora grzybów. Tom 2. Krakow, Państwowe Wydawnictwo Naukowe Warsaw

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