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Cyphelloporia bialoviesensis (Fungi, Agaricales)—a new genus and species for a giant cyphelloid fungus from Białowieża virgin forest in Poland

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Abstract

A striking species of cyphelloid fungus tentatively identified as a *Henningsomyces* or *Rectipilus* was collected in Białowieża virgin forest in Poland since 1962. After search in literature, morphological studies and phylogenetic analyses based on LSU and ITS rDNA sequences, the species turned out to be unknown to science with ≥ 5% difference in LSU rDNA sequence from nearest representatives of both cyphelloid and agaricoid fungi. We describe it here as a new genus *Cyphelloporia* and new species *C. bialoviesensis*. The species is still known only from the Białowieża forest, where it produces large basidiomata consisting of a well developed subiculum and densely aggregated, tubular receptacles up to 10 mm long on decaying trunks of *Picea abies*. A detailed morphological description accompanied by line drawings and photographs is provided, and differences from similar *Rectipilus* and *Henningsomyces* species are discussed. Phylogenies based on LSU and ITS sequences show that *C. bialoviesensis* belongs to the lineage formed by *Rectipilus* species together with *Phyllotopsis nidulans* and *Pleurocybella porrigens*, whereas true *Henningsomyces* species belong to a highly unrelated lineage labelled Niaceae or Cyphellaceae. Family position of *C. bialoviesensis* is discussed showing that Phyllotopsidaceae is well justified.

Keywords: Basidiomycota, Europe, *Henningsomyces*, ITS, LSU, phylogeny, *Rectipilus*, taxonomy

Introduction

So-called "cyphellaceous" or "cyphelloid" fungi comprise mainly saprobic species of reduced agarics (Agaricales, Basidiomycota; see Hibbett *et al.* 2014) producing minute basidiomata, typically less than 2 mm in length and diameter, and sometimes resembling small discomycetes. They are cupulate, tubular, obconical, funnel- or barrel-shaped, sessile or pendant, sometimes stipitate, with smooth or somewhat wrinkled hymenophore covering their inner surface. They grow individually or gregariously; in the latter case the individual basidiomata are also called receptacles. In some species numerous basidiomata are crowded on a subiculum (Donk 1951, Bodensteiner *et al.* 2004).

Based on similar morphology, cyphelloid fungi were previously classified in the family Cyphellaceae. The name Porotheleaceae (Murrill 1916, as Porotheliaceae) was later created for this group and used for example by Cooke (1957, 1961). Today we know that placement of all cyphelloid fungi in one family is not justified phylogenetically. Recent molecular phylogenetic studies showed evolutionary affinities of cyphelloid forms to members of various lineages of the order Agaricales (Moncalvo *et al.* 2002, Bodensteiner *et al.* 2004, Binder *et al.* 2005, Thorn *et al.* 2005, Matheny *et al.* 2006, Baltazar *et al.* 2015, Lucas & Dentinger 2015, Moreno *et al.* 2017). Bodensteiner *et al.* (2004) found that there have been at least 8–12 independent origins of cyphelloid species from agaricoid ancestors, and cyphellization represents a striking case of convergent evolutionary reduction. Thus, cyphelloid fungi are polyphyletic and currently

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they are classified in a large number of families: Cyphellaceae or Niaceae (possible synonyms), Hymenogastraceae, Inocybaceae, Marasmiaceae, Schizophyllaceae and Tricholomataceae (Moreno *et al.* 2017; MycoBank, accessed 2022).

Shape of basidioma, spore morphology and anatomy of hyphae covering the external surface of basidiomata were traditionally used as characters delimiting cyphelloid species. In the past, contributions to the knowledge on diversity and taxonomy of the group based on macro- and micromorphology have been published e.g. by Burt (1914, 1924, 1926) in North America, Pilát (1924, 1925, 1926) and Bourdot & Galzin (1928) in Europe, Cunningham (1953) in New Zealand and Talbot (1956) in South Africa. Some more comprehensive works were published by Cooke (1961) and Reid (1964). Many questions related to the systematics, taxonomy and nomenclature of cyphelloid taxa have been discussed by Donk (1951, 1959, 1962, 1966) who firmly pointed out the heterogeneity of the group, and also introduced some new genera and combinations. A lot of new cyphelloid taxa were described by Agerer and co-authors (e.g. Agerer 1973, 1975, 1978, 1979, 1980a,b, 1983a,b; Agerer & Boidin 1981; Bodensteiner *et al.* 2001), often as a result of type studies or explorations in the tropics. New cyphelloid species are still being described, for example from Asia (Wei & Dai 2007, Wei & Qin 2009), Europe (Bodensteiner 2007, Lucas & Dentinger 2015, Moreno *et al.* 2017) and South America (Gorjón & de Jesus 2014, Trierveiler-Pereira *et al.* 2019).

Actually, more than 130 cyphelloid species accommodated in ca. 40 genera are described. However, their true diversity is still unknown. Bodensteiner *et al.* (2004) and Bodensteiner (2007) hypothesized that there could be as many as 400–500 species worldwide.

Since the early 1960s, a striking species of cyphelloid fungus tentatively identified as a *Henningsomyces* Kuntze (1898: 483) or *Rectipilus* Agerer (1973: 413) was sporadically collected in the Białowieża Forest in Poland. Probably the first documented record is from 5 August 1962 by Stanisław Domański preserved in Kraków herbarium (KRAM F-SD 2313). It was originally labelled as *Cyphella candida* (Persoon 1794: 116) Patouillard (1900: 55) but later supplemented by a handwritten note "*Henningsomyces* sp.". Domański's herbarium contains three more specimens of the fungus collected in 1962 and 1965, all labelled as *Henningsomyces* sp. Subsequently, this fungus was collected by Polish and Czech mycologists in various parts of the Białowieża National Park on wood of decayed *Picea abies* logs in the years 2009–2017 during their research projects in the area (see e.g. Karasiński & Wołkowycki 2015, Holec *et al.* 2019; unfortunately, it was not possible to visit the Belarusian part of the Białowieża forest). After search in literature (see above), morphological comparative studies and phylogenetic analyses we found that the species is unknown for science and differs quite considerably in LSU rDNA sequence from nearest representatives of both cyphelloid and agaricoid fungi. The aim of this study is to describe it as a new genus and species *Cyphelloporia bialoviesensis*.

Material & methods

Samples and morphological analyses

This study is based on specimens collected in the years 1962–2017 in the Białowieża virgin forest (NE Poland) deposited in KRAM, PRM and BRNU herbaria. Herbarium acronyms follow Index Herbariorum (http://sweetgum.nybg.org/ih/). The abbreviation KRAM F-SD refers to the collection of Stanisław Domański preserved in KRAM. Some collections are kept in the private herbarium of D. Karasiński (DK). The species description is based on fresh (macromorphology) and dry (micromorphology) specimens. All specimens were examined by light microscopy to verify their identification and some of them were studied in detail for description of microcharacters (KRAM F-59691; PRM 957089, 957093, 957095, 957099, 944786, 944799, 944810; BRNU 680032). For this purpose, free-hand sections of dry basidiomata were made under the stereomicroscope using a razor blade. Sections were mounted in Melzer's reagent, 0.1% Cotton Blue in 60% lactic acid, 3% KOH stained with phloxine (used by D. Karasiński: DK), 5% KOH unstained (J. Holec: JH), 1% solution of Congo Red in 10% aqueous ammonia solution (D. Dvořák: DD) and observed under Nikon Eclipse E-400 (DK), Olympus BX-43 (JH) and Olympus CX-41 (DD) light microscopes with magnifications up to ×1250. In the species description the spore size range is based on 30 spores per specimen measured in Melzer's reagent (DK, DD) or 5% KOH (JH). Twenty measurements were performed on the remaining anatomical elements. Q means quotient of length/width for each spore measured, Qav average value of Q. Line drawings were done free-hand (DK). MycoBank (https://www.mycobank.org/) and Index Fungorum (www.indexfungorum.org/) were consulted for nomenclature.

DNA extraction and PCR conditions

Collections analyzed by L. Nagy (LN). DNA was extracted using the Qiagen Plant Mini DNA kit following the manufacturer's instructions. The Internal Transcribed Spacer region (ITS1, 5.8S, ITS2) was PCR-amplified using the primer combination ITS1/ITS4 and sequenced commercially from both strands using the same primers. The first ~1500 bases of the ribosomal large subunit (28S) region was amplified and sequenced using the LROR/LR7 primer combination which delivered very good reads.

PRM collections analyzed by M. Kolařík (MK). DNA for the ITS (ITS1, 5.8S, ITS2) barcode sequencing was extracted as described in Holec & Kolařík (2013). PCR amplification of the ITS region sequence was done using the primers ITS1F-KYO2 and ITS4 as described in Kolařík & Vohník (2018). PCR products were bi-directionally sequenced using the same primers at the sequencing facility of the Institute of Microbiology, CAS (Prague).

Phylogenetic analyses tools and software

Two datasets, one for LSU and a second for ITS rDNA, were compiled from our sequences (Table 1), the most similar sequences from the NCBI GenBank (Sayers *et al.* 2019), UNITE database (Nilsson *et al.* 2019) and sequences representing major lineages of cyphelloid fungi selected from Bodensteiner *et al.* (2004) and members of the hydropoid clade sensu Matheny *et al.* (2006), where our preliminary analysis indicated that our species might belong there.

TABLE 1. Sequenced collections. Codes of Białowieża forest sections document that the collections originate from various parts of the forest. DK: collection by D. Karasiński, JH: collection by J. Holec, LN: sequenced by L. Nagy, MK: sequenced by M. Kolařík. For abbreviations of public herbaria see http://sweetgum.nybg.org/science/ih/.

Species	Voucher	Białowieża forest section, Date of collection	ITS accession no. (sequenced by)	LSU accession no. (sequenced by)
Cyphelloporia bialoviesensis	PRM 957089 (DK 3612)	319C, 28 Jul 2009	---	ON391556
Cyphelloporia bialoviesensis	KRAM F-59691 (DK 3715) **HOLOTYPE**	345A, 11 Aug 2009	ON350854	ON391555
Cyphelloporia bialoviesensis	PRM 957091 (DK 3723)	346, 11 Aug 2009	ON350856	---
Cyphelloporia bialoviesensis	PRM 957095 (DK 4291)	340, 20 Sep 2009	ON350857	MK278141* (LN) ON391557 (MK)
Cyphelloporia bialoviesensis	PRM 957097 (DK 12068)	374C, 23 Aug 2017	ON350855	---
Cyphelloporia bialoviesensis	PRM 957102 (DK 12159)	314, 28 Aug 2017	ON350858	---
Cyphelloporia bialoviesensis	PRM 944786 (JH 75/2016)	398B, 12 Sep 2016	ON350859	---
Cyphelloporia bialoviesensis	PRM 944799 (JH 96/2016)	402B, 13 Sep 2016	ON350860	ON391559
Cyphelloporia bialoviesensis	PRM 944810 (JH 107/2016)	373D, 13 Sep 2016	ON350861	ON391558
Henningsomyces puber	DK 8973	---	---	ON391561
Henningsomyces puber	PRM 923269	** CZ, Boubínský prales, 8 Oct 2013	---	ON391560

* sequence published in Varga *et al.* (2019) under name *Henningsomyces* sp.

** collection not from Białowieża

The dataset was enriched by our collections identified as *Henningsomyces puber* (Romell ex W.B. Cooke 1961: 26) D.A. Reid (1964: 119). Members of the Schizophyllaceae family, namely *Auriculariopsis ampla* (Léveillé 1848: 126) Maire (1902: 102) and *Schizophyllum radiatum* Fries (1851: 41), which is sister to the hydropoid clade (Matheny *et al.* 2006), were used as the outgroups. Sequence editing was done in Bioedit 7.09 (Hall 1999) and sequence alignment in MAFFT 6 (Katoh *et al.* 2009). To filter gaps and variable regions, we used Gblocks version 0.91b (Talavera & Castresana 2007) with less stringent selection, which allowed smaller final blocks and gap positions in the final blocks. The Gblocks curated LSU rDNA alignment had 86 sequences with 869 columns (26% of the original non-curated with 3330 positions) with 262 parsimony-informative, 70 singleton sites and 537 constant sites. The best model chosen according to Bayesian Information Criteria (BIC) using ModelTest v. 2.1.7 (Posada 2008) was GTR+I+G. For ITS rDNA the curated alignment had 22 sequences with 563 columns (55% of the original 781 positions), 282 parsimony-informative, 41 singleton sites and 239 constant sites. The best model chosen according to BIC was TIM2+F+I+G4.

Bayesian inference (MB) was conducted with MrBayes 3.0 (Ronquist & Huelsenbeck 2003) and 80 million generations were run together with the burn-in value in Tracer v1.5 (Drummond & Rambaut 2007). Maximum likelihood (ML) searches were conducted in IQ-TREE multicore version 1.4.1 with standard nonparametric bootstrap approximation ("-b 1000"), automated model selection ("-m TEST") and the FreeRate (+R) model, in which the site rates and proportions are inferred independently from the data. Parameters for MB were estimated in jModeltest 0.1.1 (Posada 2008). Three data partitions (ITS1, 5.8S and ITS2) were recognized in the ITS rDNA dataset. Datasets were deposited in the DRYAD repository (https://doi.org/10.5061/dryad.0gb5mkm5k).

The separated ITS1 and ITS2 sequences were searched against GlobalFungi Database release 3, which contains data from 36 684 samples, 367 studies and 582 264 149 ITS1 and 526 638 147 ITS2 sequences generated by environmental DNA-based studies (Větrovský *et al.* 2020).

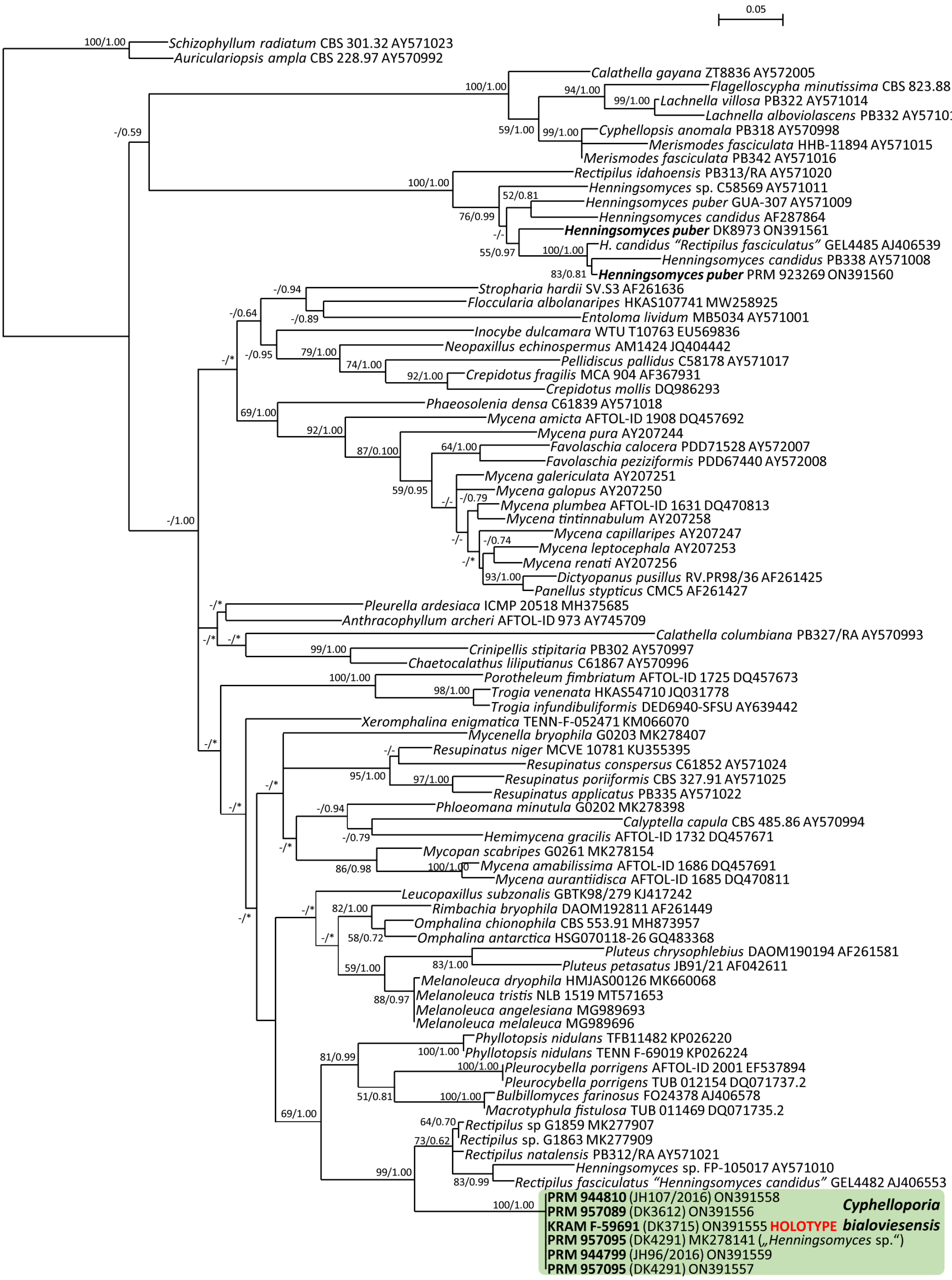

FIGURE 1. Phylogenetic placement of *Cyphelloporia bialoviesensis* based on LSU rDNA sequences. The topology is inferred from a ML phylogenetic analysis. Maximum likelihood bootrap support ≥ 50 followed by Bayesian posterior probabilities ≥ 0.60 are indicated. *Schizophyllum radiatum* and *Auriculariopsis ampla* were used as the outgroups. Sequences obtained by us are in bold.

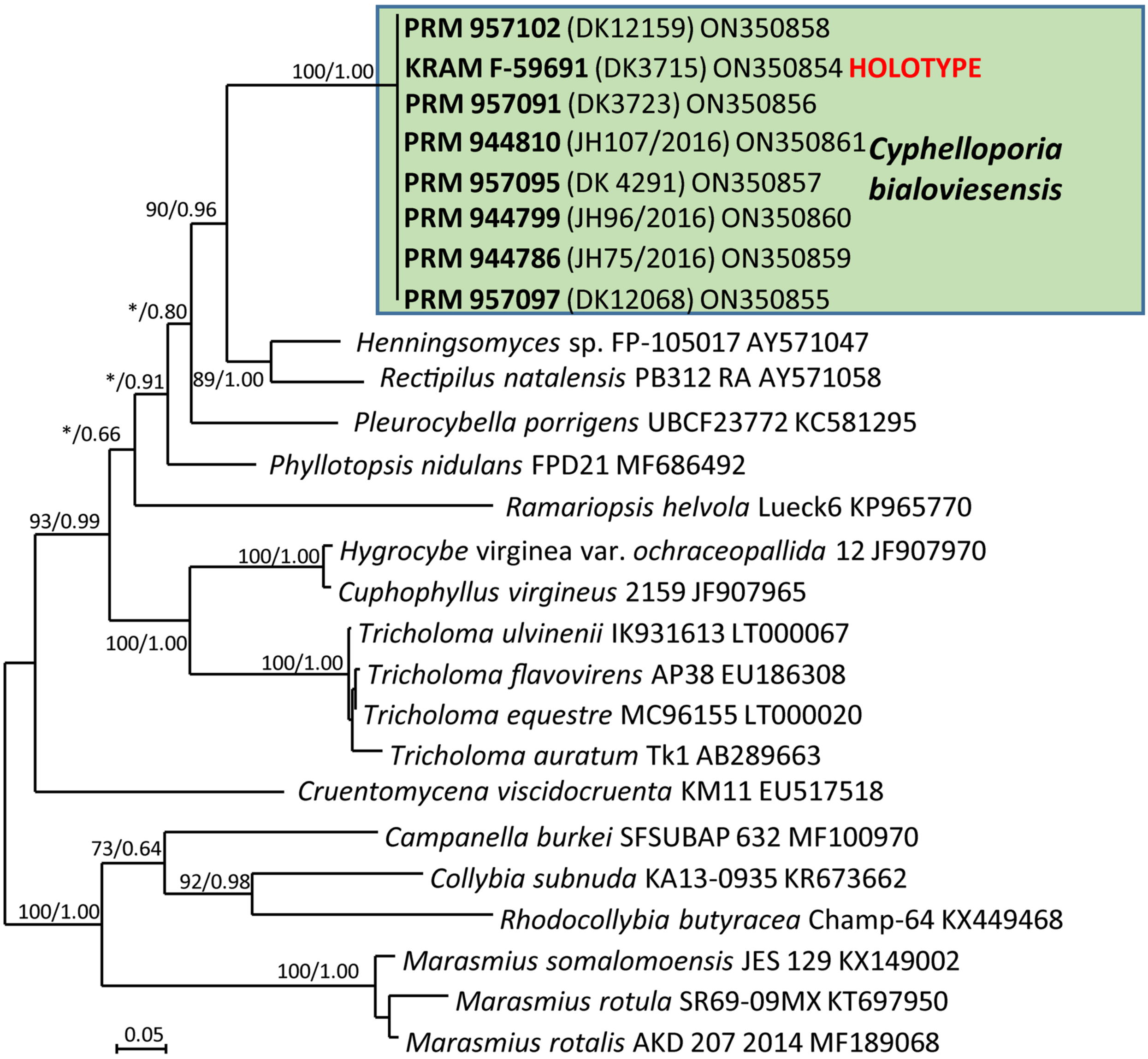

FIGURE 2. Phylogenetic placement of *Cyphelloporia bialoviesensis* based on ITS rDNA sequences. The topology is inferred from a ML phylogenetic analysis. Maximum likelihood bootrap support ≥ 50 followed by Bayesian posterior probabilities ≥ 0.60 are indicated. The tree is unrooted. Sequences obtained by us are in bold.

Results

For the LSU rDNA, all sequenced specimens of *Cyphelloporia bialoviesensis* were identical. The best BLASTn hit led to *Rectipilus natalensis* (W.B. Cooke in Talbot 1956: 481) Agerer (1973: 425) sequence AY571021 and other *Rectipilus* species with 95% identity, whereas other sequences exhibited identity of 93% or lower. For the ITS rDNA, all sequenced specimens of *C. bialoviesensis* were also identical. The best BLASTn hit led again to *Rectipilus natalensis* AY571058 and other *Rectipilus* species with 83% identity, whereas other species exhibited identity 73% or lower. In the phylogenetic analyses, LSU rDNA sequences of *C. bialoviesensis* formed a separate lineage sister to the clade *Henningsomyces*-*Rectipilus* B as defined by Bodensteiner *et al.* (2004), consisting of *R. natalensis*, *R. fasciculatus* (Persoon 1822: 325) Agerer (1973: 419), *Rectipilus* sp. G1859, *Rectipilus* sp. G1863 and "*Henningsomyces*" sp. (Fig. 1). This whole group clustered as sister group to a clade consisting of *Bulbillomyces farinosus* (Bresadola 1903: 105) Jülich (1974: 69), *Macrotyphula fistulosa* (Holmskjold 1790: 15) R.H. Petersen (1972: 140), *Phyllotopsis nidulans* (Persoon 1798: 19) Singer (1936: 76) and *Pleurocybella porrigens* (Persoon 1796: 54) Singer (1947: 81), representing the Phyllotopsidaceae sensu Olariaga *et al.* (2020). Phylogenetic analysis of the ITS region again showed the monophyly of the *Cyphelloporia bialoviesensis* lineage with "*Henningsomyces"* sp. and *Rectipilus natalensis* (Fig. 2). The closest relative to this clade, but with weak statistical support, was again the lineage containing *Phyllotopsis nidulans* and *Pleurocybella porrigens*.

Taxonomy

Cyphelloporia Karasiński, L. Nagy, Szarkándi, Holec & Kolařík, *gen. nov.* Figs. 3–6
MycoBank. MB843795

Etymology. *Cyphello-*: derived from the generic name *Cyphella*, formerly accommodating many cyphelloid fungi; *-poria*: resembling polypores with resupinate basidiomata, formerly classified in *Poria* Pers. sensu lato.

Type species. *Cyphelloporia bialoviesensis* Karasiński, Holec & Dvořák, see below.

Diagnosis. *Cyphelloporia* differs from the most related genus *Rectipilus* as well as from other cyphelloid fungi, especially *Henningsomyces*, by large basidiomata resembling some resupinate polypores and consisting of thousands of densely aggregated tubular receptacles that reach an unusual length of up to 10 mm and are crowded on distinct subiculum which is gelatinous when young. Genetically, *Cyphelloporia* belongs to the *Rectipilus* lineage but is very distant from *Rectipilus* in its LSU and ITS rDNA sequences.

Description. Basidiomata lignicolous on dead wood, cyphelloid, annual, resupinate, usually covering an area of several square decimeters, white to cream coloured when fresh, with individual receptacles initially sessile then short-stalked, densely packed, up to 10 mm long, arranged on a subiculum which is gelatinous when young. Hyphal system monomitic, generative hyphae with clamp connections, thin to slightly thick-walled. Hyphae on receptacle surface colourless, smooth, occasionally with short tuberculate to cylindrical or long flexuose outgrowths, hyphae of receptacles mouths cylindrical, unbranched, straight with flexuose ends. Basidia clavate with 4 sterigmata and basal clamp. Cystidia absent. Basidiospores principally ellipsoid to subglobose, hyaline, smooth, thin-walled, inamyloid, non-dextrinoid, acyanophilous.

Cyphelloporia bialoviesensis Karasiński, Holec & Dvořák, *sp. nov.* Figs. 3–6
MycoBank. MB843796

Etymology. The specific epithet represents the latinized version of the locality name, the Białowieża virgin forest in Poland, the only site where the species has been found so far. The same epithet has been used for *Dentipratulum bialoviesense* Domański (1965: 7).

Holotype. Poland, Podlasie Province, the Białowieża National Park, in mixed natural forest of primeval origin, forest section 345A, N52°44'31.5" E23°54'42.2", *Picea abies*: fallen big log ca. 65 cm in diameter, in advanced stage of decay, covered with mosses, 11 August 2009, leg. D. Karasiński 3715 (KRAM F-59691). Isotype in herbarium PRM (PRM 957105).

Diagnosis. *Cyphelloporia bialoviesensis* differs from other species of cyphelloid fungi by the following combination of characters: basidiomata large, covering area of several dm^2 on dead wood, consisting of thousands of tubular, finally short-stalked receptacles reaching a length of up to 10 mm and crowded on a distinct subiculum which is gelatinous when young, monomitic hyphal system with clamps, non-encrusted, colourless, mostly unbranched external hyphae, and mostly ellipsoid, broadly ellipsoid to subglobose basidiospores measuring (3.5–)4.0–5.0(–5.2) × (2.6–)3.0–3.5(–4.0) µm with Q = (1.00–)1.14–1.50(–1.71) and Qav = 1.40.

Description. Basidiomata annual, resupinate, widely effused, growing on dead wood, occupying an area up to 50 (–100) cm long and 30 cm wide, linear, circular or most often irregular in outline, consisting of densely aggregated individual receptacles, superficially resembling tubes of polypores, arranged on relatively thick (up to 100 µm, usually thinner), continuous, partially translucent subiculum which is clearly visible to the naked eye, very distinct especially in young basidiomata where it looks gelatinous-like, subhyaline or watery white, with fimbriate and radially arranged, short white strands on margin forming a sterile zone (without receptacles); in mature specimens subiculum less distinct and agglutinated, in senescent and old basidiomata present as an almost invisible subhyaline translucent coat on wood.

Receptacles (1.5–)3–8(–10) mm long and ca. 0.3–0.5 mm in diameter, initially cupulate to funnel- or barrel-shaped and sessile, then cylindrical to tubular and with short stipe-like base ca. 200–350 × 100–150 µm; white to cream, sometimes yellowish or even brownish in senescent fruitbodies, mouths white. In some well developed and large basidiomata, the receptacles sometimes have a cap-shaped, widely open apical part, but usually receptacle mouths have orifices equal to receptacle diameter or more often slightly folded inwards. Receptacle surface under lens with longitudinally arranged white fibrils. Smell faint, fungoid, taste at first acidulous, then bitterish.

FIGURE 3. Basidiomata of *Cyphelloporia bialoviesensis*.—a: Białowieża National Park in NE Poland, lowland primeval forest of the *Tilio-Carpinetum* association with *Picea abies*, large basidiomata on big fallen trunk of *Picea abies* in advanced stage of decay, photo D. Karasiński.—b: marginal part of basidioma with subiculum and sessile barrel-shaped young receptacles, photo D. Karasiński.—c: young basidioma with well visible subicular layer, photo D. Karasiński.—d: marginal part of mature basidioma with dry subicular layer, photo D. Dvořák (BRNU 680032).—e: mature basidioma with ± 1 cm long receptacles, photo D. Karasiński.

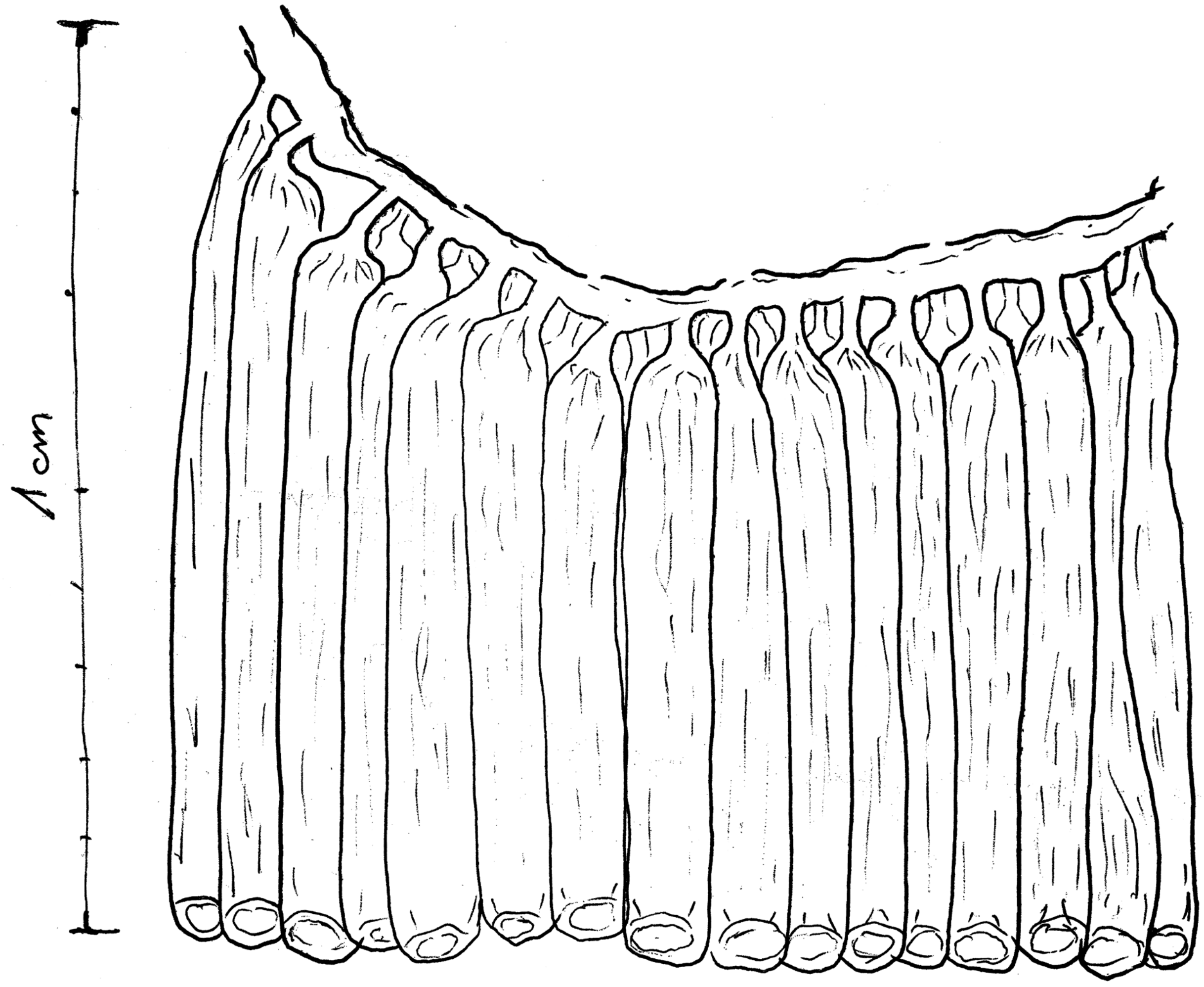

FIGURE 4. Receptacles of *Cyphelloporia bialoviesensis* (holotype: KRAM F-59691). Line drawing by D. Karasiński.

Hyphal system monomitic. Hyphae thin to slightly thick-walled, with clamp connections, hyaline, smooth, usually with long cells, not reacting in Melzer's reagent, 3% KOH and Cotton Blue. Subicular hyphae 1.5–4 µm wide, close to substrate forming dense and more or less agglutinated structure of richly branched interwoven hyphae, toward subicular surface hyphae are more loosely arranged, subparallel to interwoven, embedded in a gelatinous matrix which does not stain in Congo Red (while the hyphae wall does), with age collapsed and agglutinated as same as in basal part. Hyphae in a core of trama 2.5–4.5 µm wide, somewhat agglutinated, slightly thick-walled (or appearing so because they are slightly gelified), parallel, with long cells, usually straight or slightly flexuose, sparsely branched. External hyphae on receptacle surface 2–4 µm wide, thin-walled, colourless, densely to loosely interwoven, more or less projecting (trichoderm-like), some hyphal ends with short tuberculate to cylindrical or long flexuose outgrowths, occasionally with shortly forked tips. Hyphae of receptacle mouths of the same width, straight or slightly interwoven with more or less flexuose ends, unbranched, obtuse at apex, occasionally with shortly forked tips, colourless, smooth, without encrustations.

Cystidia and cystidioles absent.

Basidia 16–26 × 5–7 µm, clavate to narrowly clavate, sometimes constricted in middle part, with 4 sterigmata and basal clamp. Basidioles 12–22 × 4–5.5 µm, narrowly clavate.

Basidiospores (3.5–)4.0–5.0(–5.2) × (2.6–)3.0–3.5(–4.0) µm (270 spores from 9 specimens), mean length 4.5 µm, mean width 3.2 µm, Q = (1.00–)1.14–1.50(–1.71), Qav = 1.40, most of them ellipsoid, broadly ellipsoid to subglobose in front view, less frequently ovoid, rarely obovoid to globose, in side view some of them slightly inequilateral with flattened adaxial and convex abaxial side, hyaline, thin-walled, smooth, with small but distinct apiculus, inamyloid, non-dextrinoid, acyanophilous.

FIGURE 5. Microcharacters of *Cyphelloporia bialoviesensis* (holotype: KRAM F-59691), from left to right: external hyphae on receptacle surface, hyphae of receptacle mouth, basidiospores, hymenium. Scale bars = 10 µm (left: for external hyphae and hyphae of receptacle mouths; right: for basidiospores and hymenium). Line drawing by D. Karasiński.

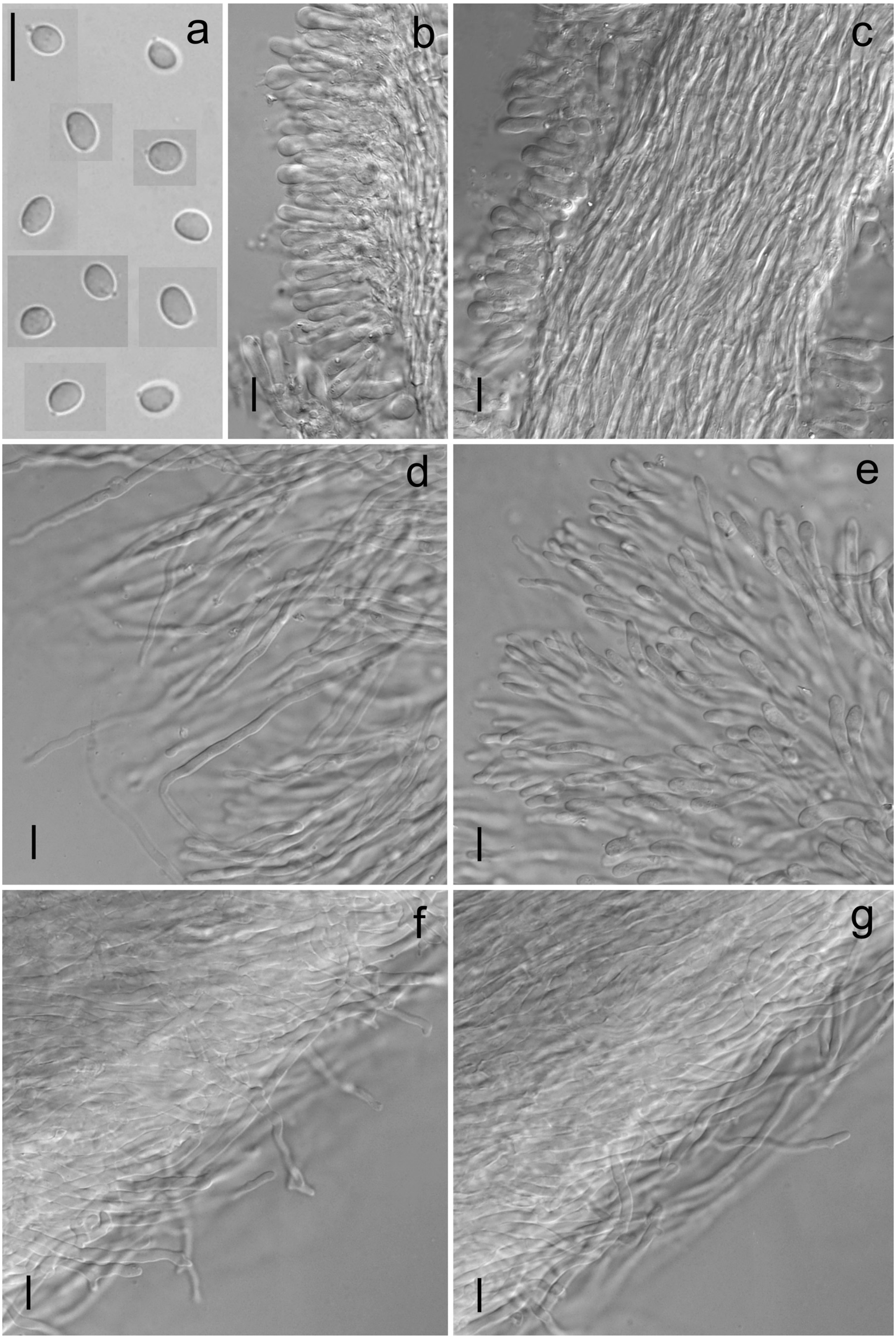

FIGURE 6. Microcharacters of *Cyphelloporia bialoviesensis* (PRM 944810).—a: basidiospores (grouped from different sites of the same microscopic mount).—b: hymenium.—c: hymenium with receptacle trama.—d, e: hyphae of receptacle mouth.—f, g: external hyphae on receptacle surface. Scale bars = 10 μm. Photos by J. Holec.

Ecology. *Cyphelloporia bialoviesensis* occurs in mixed lowland forests of primeval origin, most often in forest association *Tilio-Carpinetum* with admixed *Picea abies*. Basidiomata are mostly found on moderately to strongly decayed fallen trunks of *Picea abies* covered by mosses and less frequently on wood of barkless trunks in early stage of decay. Type of rot is unknown.

Distribution. So far, *C. bialoviesensis* is known only from the Białowieża virgin forest in northeastern Poland. The species is widely distributed there, which is documented by the high number of records and forest sections where it was found (see below). All records of our team originate from the strictly protected zone of the Białowieża National Park, mostly from its southern part near the village of Białowieża. However, we expect its occurrence also in well-preserved forest stands outside the strictly protected zone. The BLASTn search against GlobalFungi database (Větrovský *et al.* 2020) did not reveal any sequence with identity higher than 85%, which further documents that *C. bialoviesensis* is either a very rare species or has a very restricted distribution.

Additional specimens examined. All specimens were studied by us. The specimens are listed chronologically. Elevation range of all Białowieża collections is 150–170 m a.s.l., which corresponds to the range of the strictly protected zone of the Białowieża National Park (Faliński 1986). Ibid.: the same locality data as the previous record.—***Cyphelloporia bialoviesensis*, recent collections**. POLAND. Podlasie Province: Białowieża National Park, mixed natural forest of primeval origin, forest section 339B, *Picea abies*: fallen strongly decayed log covered with mosses, 5 July 2009 leg. D. Karasiński DK 3254 (PRM 957084).—Ibid., forest section 371D, *Picea abies*: fallen strongly decayed trunk, 5 July 2009 leg. D. Karasiński DK 3266 (PRM957085).—Ibid., forest section 340A, N52°44'13.8" E23°49'44.4", *Picea abies*: fragment of fallen strongly decayed trunk, 6 July 2009 leg. D. Karasiński DK 3286 (PRM 957086).—Ibid., forest section 340A, *Picea abies*: fallen log covered with mosses, 6 July 2009 leg. D. Karasiński DK 3297 (PRM 957087).—Ibid., forest section 346, N52°43'55.6" E23°56'17.3", *Picea abies*: fallen decayed trunk, 27 July 2009 leg. D. Karasiński DK 3578 (PRM 957088).—Ibid., forest section 319C, N52°44'39.3" E23°54'29.0", *Picea abies*: on wood of fallen trunk, 28 July 2009 leg. D. Karasiński DK 3612 (PRM 957089).—Ibid., forest section 370, N52°43'33.8" E23°50'45.7", *Picea abies*: decorticated fallen trunk, 10 August 2009 leg. D. Karasiński DK 3705 (PRM 957090).—Ibid., forest section 346, N52°44'29.8" E23°55'27.8", *Picea abies*: fallen decayed trunk, 11 August 2009 leg. D. Karasiński DK 3723 (PRM 957091).—Ibid., forest section 288D, N52°45'11.6" E23°54'20.9", *Picea abies*: fallen decayed big log, 12 August 2009 leg. D. Karasiński DK 3741 (PRM 957092).—Ibid., forest section 316, N52°46'39.1" E23°52'38.5", *Picea abies*: fallen trunk in advanced stage of decay, 14 August 2009 leg. D. Karasiński DK 3788 (PRM 957093).—Ibid., forest section 374, N52°43'33.1" E23°54'48.9", *Picea abies*: fallen trunk, 15 September 2009 leg. D. Karasiński DK 4160 (PRM 957094).—Ibid., forest section 340, N52°44'26.4" E23°49'49.2", *Picea abies*: fallen strongly decayed big log covered with mosses, 20 September 2009, leg. D. Karasiński DK 4291 (PRM 957095).—Ibid., N52°45'43.8" E23°54'25.7", *Picea abies*: fallen trunk, 22 September 2011 leg. D. Karasiński DK 6453 (PRM 957096).—Ibid., forest section 398B, N52°43.129 E23°50.461, *Picea abies*: fallen strongly decayed trunk covered with mosses, 12 September 2016 leg. J. Holec JH 75/2016 (PRM 944786).—Ibid., forest section 402B, N52°43.340 E23°53.015, *Picea abies*: fallen strongly decayed trunk covered with mosses, 13 September 2016 leg. J. Holec JH 96/2016 (PRM 944799; duplicate: PRM 956592, for herbarium processed by M. Kříž).—Ibid., forest section 373, *Picea abies*: upper part of lying mossy trunk, moderately decayed, 80 cm in diam., 13 September 2016 leg. D. Dvořák DD 160913-03 (BRNU).—Ibid., forest section 373D, N52°43.507 E23°54.468, *Picea abies*: fallen trunk in early stage of decay, without bark, 13 September 2016 leg. J. Holec JH 107/2016 (PRM 944810).—Ibid., forest section 374C, N52°43'28.0" E23°54'38.4", *Picea abies*: fallen decayed log covered with mosses, 23 August 2017 leg. D. Karasiński DK 12068 (PRM 957097).—Ibid., forest section 370C, N52°43'24.2" E23°51'06.4", *Picea abies*: fallen decayed log covered with mosses, 24 August 2017 leg. D. Karasiński DK 12100 (PRM 957098).—Ibid., forest section 399, N52°43'21.8" E23°51'26.6", *Picea abies*: fallen strongly decayed log, 24 August 2017 leg. D. Karasiński DK 12112 (PRM 957099).—Ibid., forest section 373D, N52°43'21.5" E23°54'11.7", *Picea abies*: fallen decayed big log covered with mosses, 27 August 2017 leg. D. Karasiński DK 12125 (PRM 957100).—Ibid., forest section 373D, N52°43'29.5" E23°54'06.4", *Picea abies*: fallen strongly decayed trunk covered with mosses, 27 August 2017 leg. D. Karasiński DK 12146 (PRM 957101).—Ibid., forest section 314, N52°45'03.4" E23°50'15.4", *Picea abies*: fallen decayed log, 28 August 2017 leg. D. Karasiński DK 12159 (PRM 957102).—Ibid., forest section 284, N52°45'19.4" E23°50'26.1", *Picea abies*: fallen decayed log covered with mosses, 28 August 2017 leg. D. Karasiński DK 12170 (PRM 957103).—Ibid., forest section 284, N52°45'17.6" E23°50'24.8", *Picea abies*: fallen decayed trunk, 28 August 2017 leg. D. Karasiński DK 12171 (PRM 957104).—Ibid., forest section 318D, N52°44.760' E23°54.384', *Picea abies*: fallen decayed trunk covered with mosses, 19 September 2017 leg. J. Holec (PRM 946078).—Ibid., forest section 318D, N52°44.710 E23°54.401, *Picea abies*: fallen trunk without bark of diameter 110 cm, 19 September 2017 leg. J. Holec (PRM 946149).—Ibid., forest section not given, on fallen decaying trunk of *Picea abies*, 22

September 2017 leg. M. Kříž (PRM 956593).—***Cyphelloporia bialoviesensis*****, old collections from Domański's herbarium KRAM F-SD** with annotations on labels. Exact sites of occurrence are unknown. Original texts from labels are given. POLAND. Podlasie Province: Białowieża, ad truncum emortuum *Piceae excelsae* in silva mixta virginea, 5.VIII.1962 leg. S. Domański (KRAM F-SD 2313 as *Cyphella candida*/*Henningsomyces* sp.).—Białowieża, distr. Hajnówka, ad caudicem *Piceae abietis*, 5.VIII.1962 leg. S. Domański (KRAM F-SD 5490 as *Henningsomyces* sp.).—Białowieża, distr. Hajnówka, ad caudicem putridum *Piceae abietis*, 6.VIII.1962 leg. S. Domański (KRAM F-SD 5493 as *Henningsomyces* sp.).—Białowieża, in silva mixta virginea, ad truncum putridum *Piceae excelsae*, 5.VIII.1965 leg. S. Domański (KRAM F-SD 4496 as *Henningsomyces* sp.).—***Henningsomyces puber*****, collections used for comparison**. POLAND. Podlasie Province: Białowieża, DK 8973.—CZECH REPUBLIC. South Bohemia: Boubínský prales virgin forest, fenced core area, 980 m a.s.l., on fallen decayed trunk of *Abies alba*, 8 October 2013 leg. et det. M. Kříž (PRM 923269).

Discussion

Taxonomy

Cyphelloporia bialoviesensis is characterized by large basidiomata often covering area of several dm^2 (Fig. 3a). They consist of thousands of tubular, finally short-stalked receptacles crowded on distinct subiculum (Figs. 3b, d) looking gelatinous-like when young (Fig. 3c). With their length up to 10 mm (Figs. 3e, 4), the receptacles seem to be the longest and whole basidiomata largest among cyphelloid species known to date (but some cyphelloid *Resupinatus* species come close). Basidiomata of *C. bialoviesensis* form aggregations reminiscent of some resupinate polypores, but, of course, with "tubes" (here receptacles) that are not grown together and stand densely but isolated (each receptacle with its own wall). *Cyphelloporia bialoviesensis* has monomitic hyphal system with clamps, clavate and slightly constricted basidia, mostly ellipsoid, broadly ellipsoid to subglobose basidiospores and non-encrusted, mostly unbranched external hyphae (Figs. 5, 6). However, some thin-walled hyphae covering external surface of receptacles have terminal cells with short tuberculate to cylindrical or long flexuose outgrowths (Fig. 6f), occasionally even moniliform or with shortly forked tips. Hyphae of receptacle mouths are unbranched, cylindrical, rather straight or slightly interwoven with more or less flexuose ends, obtuse at apex, occasionally with shortly forked tips, smooth and without encrustations (Figs. 6d, e).

Spores of *C. bialoviesensis* are rather variable in shape. Most of them are ellipsoid, broadly ellipsoid to subglobose, but rarely there are also ovoid, obovoid to globose ones in most of the collections studied (Fig. 6a). The situation is complicated by the fact that except for mature spores recognizable by their coloured content in stained microscopic mounts (Melzer'reagent, Congo Red), the immature ones are frequently present. They have „empty" content and slightly different shape (often more prolonged or inequilateral). Such spores were not taken into consideration for measurements.

Cyphelloporia bialoviesensis possesses some generic features of both *Rectipilus* Agerer (1973: 413) and *Henningsomyces* Kuntze (1898: 483). While the gelatinous consistency better fits the genus *Henningsomyces*, the unbranched and cylindrical external hyphae are very different from hairs present in *Henningsomyces* (that are highly branched and tapering at their tips) and resemble more those of *Rectipilus*. [Remark: Bodensteiner *et al.* (2004) published that collections with both ramified hairs ("*Henningsomyces*" type) and unbranched hairs ("*Rectipilus*" type) occur in both lineages containing their representatives. It suggests that the character of hair ramification might have no taxonomic value when phylogenetic generic concept is applied or, more likely, some of the sequenced collections were misidentified (see e.g. Thorn *et al.* 2005: 1146).]

The well developed subiculum is another crucial feature of the new genus *Cyphelloporia* (Figs. 3 b–d, 4). Among species assigned to *Rectipilus* and *Henningsomyces*, there are only a few having more or less developed subiculum. All of them clearly differ from *C. bialoviesensis* by their smaller size and the following characters:

Rectipilus fasciculatus (Persoon 1822: 325) Agerer (1973: 419) described from France is the closest one to our species (Fig. 1) by the tubular and densely aggregated receptacles. However, it has no or indistinct subiculum, receptacles only up to 2 mm long, and slightly longer spores measuring (4.5–)5–7(–7.5) µm.

Rectipilus natalensis (W.B. Cooke in Talbot 1956: 481) Agerer (1973: 425) described from South Africa has no or rudimentary subiculum, receptacles only up to 1 mm long, flexuose hyphae of receptacle mouths, and slightly smaller spores measuring 3.5–4.5 × 2.5–3.5 µm.

Rectipilus confertus (Burt 1924: 17) Agerer (1973: 417) described from the USA has a distinct subiculum but receptacles only up to 2.5 mm long, thick-walled hyphae of receptacle mouths and oval to ellipsoid spores measuring 4.5–6(–7.5) × 2.5–3.5 µm.

Rectipilus stromatoides Gorjón (in Gorjón & de Jesus 2014: 394) described from Brazil has receptacles embedded in a dense, and largely effused, vivid pink coloured "stroma" (subiculum?). Receptacles are very short, measuring 0.2–0.3(–0.6) mm, with external hyphae tortuose or spirally curved. The species has clavate to cylindrical cystidioles with elongated apical papilla. Its spores are broadly ellipsoid, measuring 5–5.5(–6) × 3–3.5 µm.

Henningsomyces subiculatus Y.L. Wei & W.M. Qin (2009: 226) described from China has about 100 µm thick subiculum but receptacles only up to 0.3 mm long. They are densely aggregated, white, becoming pinkish buff when bruised and drying, with branched, dendrohyphidia-like hyphae at receptacle mouths. Spores are subglobose, (3.9–) 4.8–5.7(–6) × (3.9–)4.3–5.1(–5.5) µm.

The phylogenetic position of the latter three species is unknown as they have not been sequenced yet.

Phylogeny

Based on ITS and LSU data (Figs. 1, 2), *C. bialoviesensis* belongs to the lineage which contains type species of the genus *Rectipilus* Agerer (1973: 413), namely *Rectipilus fasciculatus*, in our phylogram (Fig. 1) represented by sequence AJ406553 mistakenly labelled *Henningsomyces candidus* (Persoon 1794: 116) Kuntze (1898: 483) in GenBank, but in fact representing *Rectipilus fasciculatus* (see Thorn *et al.* 2005: 1146). Other representatives falling into this lineage are *R. natalensis*, two undescribed *Rectipilus* species, and a sample labelled *Henningsomyces* sp. (AY571010, AY571047; Bodensteiner *et al.* 2004) which certainly represents a *Rectipilus*. Purely on the basis of ITS and LSU phylogeny, *C. bialoviesensis* could be included within *Rectipilus*, but creating a genetically very broad genus. However, the genetic distance of our fungus from the above described *Rectipilus* group is large (5% for LSU rDNA), comparable to the distance separating other genera or even larger, which justifies the creation of a new genus. As shown above, such a classification is well supported morphologically by the presence of exceptionally large basidiomata with distinct subiculum and very long receptacles, a combination of characters unknown in other species and genera of cyphelloid fungi (see above).

The morphologically similar genus *Henningsomyces* Kuntze (1898: 483), with its type species *H. candidus*, belongs to a highly unrelated lineage (Fig. 1), a fact already known from previous studies (e.g. Thorn *et al.* 2005). Except for several representatives of *Henningsomyces* (with sequence AJ406539 mistakenly labelled *Rectipilus fasciculatus* in GenBank but representing *H. candidus*, see Thorn *et al.* 2005: 1146), this lineage also contains other cyphelloid fungi currently placed in the genera *Calathella* D.A. Reid (1964: 122), *Cyphellopsis* Donk (1931: 128), *Merismodes* Earle (1909: 406), *Flagelloscypha* Donk (in Singer 1951: 312), and *Lachnella* Fr. (1836: 343), and has been labelled the *Nia* clade (Bodensteiner *et al.* 2004), Niaceae (Handa & Harada 2005), Cyphellaceae (Vizzini *et al.* 2020), or Cyphellopsidaceae (Kalichman *et al.* 2020). Our newly obtained comparative sequences of *H. puber* from Białowieża forest and the Czech Republic belong to the group of samples labelled *H. candidus* and *H. puber*. Unfortunately, neither type specimen of *Rectipilus fasciculatus* (which exists in Leiden, see Agerer 1973), nor of *Henningsomyces candidus* (no type material existing) has been sequenced yet. It further contributes to the confusion in the proper generic placement of *Rectipilus* and *Henningsomyces* species, demonstrated e.g. by position of a sequence identified as *Rectipilus idahoensis* (W.B. Cooke 1961: 24) Agerer (1973: 424) (AY571057) close to the *Henningsomyces candidus/puber* group (Fig. 1). The same fact applies to the species *Rectipilus afibulatus* Al. Lucas & Dentinger (2015: 3).

If we discuss the family position of *C. bialoviesensis*, it must be said that the family classifications in this group of Agaricales are based on weakly supported phylogenies with a limited taxon sampling, and sometimes even on misidentified samples (see above). For example, the closest genus *Rectipilus* is classified as "incertae sedis" in Index Fungorum (www.indexfungorum.org) like some other genera in broader *Cyphelloporia*-*Rectipilus* lineage (Fig. 1), e.g. *Pleurocybella* and *Bulbillomyces* Jülich (1974: 69). *Rectipilus* represented by type species *R. fasciculatus* was recovered as a member of /phyllotopsis clade (Thorn *et al.* 2005, = *Henningsomyces/Rectipilus* clade B of Bodensteiner et al 2004). In the newest work on classification of this group of Agaricales, Vizzini *et al.* (2022) claim that *Rectipilus* and *Henningsomyces* belong to Cyphellaceae. In their phylograms, these two cyphelloid genera form a distinct lineage together with the corticioid *Acanthocorticium* Baltazar, Gorjón & Rajchenberg (in Baltazar *et al.* 2015: 456). However, Vizzini *et al.* (2022) have no true *Rectipilus* in their analyses as both samples used by them and labelled *R. fasciculatus* and *R. idahoensis* belong to the *Henningsomyces candidus/puber* clade (GEL4485—sequence AJ406539, PB313/RA—sequences AY571057 and AY571020; see Thorn *et al.* 2005: 1146). As shown above, this clade of true *Henningsomyces* species is very distant from the *Cyphelloporia*-*Rectipilus* lineage (Fig. 1). The unfortunate mistake in labelling these *R. fasciculatus* and *H. candidus* samples in GenBank (representing type species of these genera!) was discovered and corrected a long time ago (Thorn 2005, see above) but still makes confusion, causing both genera to be erroneously placed close to each other (e.g. Kalichman *et al.* 2020: Porotheleaceae s.l.).

The genera *Pleurocybella* and *Phyllotopsis*, which are very close to *Cyphelloporia* and *Rectipilus* (Fig.1), were classified to Typhulaceae by Kalichman *et al.* (2020). However, Olariaga *et al.* (2020) showed that *Pleurocybella* and *Phyllotopsis* are distant from Typhulaceae s.str. and validated the family Phyllotopsidaceae to accommodate *Macrotyphula*, *Phyllotopsis* and *Pleurocybella*. Based on our results, it can be said that *C. bialoviesensis* belongs to the Phyllotopsidaceae family.

Ecology and distribution

The Białowieża Forest is one of the last fragments of the ancient lowland forests of Europe. This UNESCO World Heritage Site, Biosphere Reserve, National Park and home of European bison represents a biodiversity-rich, natural mixed forest ecosystem, with *Picea abies* present in almost all forest habitats (Faliński 1986, Keczyński 2017, Kujawa *et al.* 2017). It is very surprising than none of the mycologists working in Białowieża in the past have reported such a striking species like *C. bialoviesensis*. When fructifying, it cannot be overlooked. We can speculate that the species has already been present in the form of non-fructifying or rarely fructifying mycelia (see records by Domański from the 1960s) and started to fructify more frequently in the 21st century. The possible driver could be the recent climatic change (global warming) which has led to the recent dieback of *Picea abies* in Białowieża (Boczoń *et al.* 2018) and the associated greater presence of its dead wood, a substrate of *C. bialoviesensis*. The migration via spore dispersal from other regions could be another possible explanation, however, we are of the opinion that such remarkable species would already have been described. In the current state of knowledge, we can consider *C. bialoviesensis* to be a rare relic tied to the exceptional ecosystems of the Białowieża virgin forest, like several other species living there and (almost) unknown from the rest of Europe (Karasiński & Wołkowycki 2015, Karasiński 2016), e.g. *Dentipratulum bialoviesense* (Holec & Zehnálek 2021).

As a species growing on dead wood of *Picea abies*, *C. bialoviesensis* is threatened by apparent retreat of this tree species in Białowieża forest (see e.g. Boczoń *et al.* 2018) caused by global warming, associated bark-beetle outbreak, and subsequent forestry measures like salvage logging and wood removal (not performed in strictly protected zone of the national park, but around it, decreasing amount of a potential substrate—naturally fallen and slowly rotting trees). As regards *Pinus sylvestris*, second conifer occurring in Białowieża forest, *C. bialoviesensis* was not found on its dead trunks indicating that the species is strictly bound to *Picea abies* wood, at least in this locality.

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