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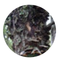

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Research

On some forgotten species of *Exidia* and *Myxarium* (Auriculariales, Basidiomycota)

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As shown by morphological and molecular (ITS, nrLSU and *tef1* sequences) evidence, the current concept of *Myxarium nucleatum* covers four species in the Nordic countries: *M. cinnamomescens*, *M. hyalinum*, *M. nucleatum* s.s. and *M. populinum*. These species are redescribed here, their nomenclature is discussed and all relevant names are typified. *Exidia cartilaginea* and *E. villosa* are typified and shown to be conspecific with the North American species *E. candida*. Based on morphological differences, *E. cartilaginea* is retained as a variety of *E. candida*. *Exidia subrepanda* is treated as a synomym of *E. saccharina*, and *Heterochaete europaea* as a synomym of *E. thuretiana*.

Introduction

The so-called jelly fungi (heterobasidiomycetes) is a poorly studied group, especially at the generic and species levels. This contribution deals with two genera, *Exidia* and *Myxarium*, currently considered members of the *Auriculariales* (Agaricomycetes). Despite certain morphological similarity, these genera are not closely related, and they belong to different lineages within the order (Weiss and Oberwinkler 2001, Hibbett et al. 2014). In the Nordic countries, Neuhoff's monograph (Neuhoff 1936) is the most recent systematic attempt to revise *Exidia* s.l. (incl. *Myxarium*). Therefore, a taxonomic revision based on modern methods and newly collected material is highly desirable. Here, we investigate the *Exidia*-like species with pale-coloured, orbicular or cerebriform basidiocarps, occurring on deciduous trees in northern Europe.

Microscopy-based studies of this group were first undertaken by Karsten. He regarded all pale-coloured exidioid fungi as belonging to one species, *Tremella albida* Huds. or *Exidia albida* (Huds.) Bref., and sequentially introduced f. *betulae* (Karsten 1866), subsp. *tuberculata* (Karsten 1889), var. *populina* and subsp. *subrepanda* (Karsten 1891). Oudemans (1919, 1920) accidentally raised the two latter taxa to the species rank, but they remained completely ignored by all subsequent mycologists. Neuhoff (1935)

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described two new species, *Exidia cartilaginea* S. Lundell & Neuhoff and *E. villosa* Neuhoff, and a year later, he accepted two other species, *E. albida* and *E. gemmata* (Lév.) Bourdot & Maire, and reported all of them from Sweden (Neuhoff 1936). Unfortunately, the type specimens of *E. cartilaginea* and *E. villosa* kept in Königsberg were destroyed at the end of the Second World War (Torkelsen 1968, Jahn 1971). While the first species was well-known and widely reported from northern Europe (Raitviir 1967, Torkelsen 1972, Hansen and Knudsen 1997), *E. villosa* was almost totally ignored. Donk (1966) replaced the name *E. gemmata* with the older name *Myxarium nucleatum* Wallr. and then synonymized the latter one with *Myxarium hyalinum* (Pers.) Donk (based on *Tremella hyalina* Pers.) (Donk 1966). However, this action resulted in a long-term controversy (Reid 1970, Roberts 1998). Although recent DNA-based studies have supported the independent generic status of *Myxarium* (Weiss and Oberwinkler 2001, Wells et al. 2004), the identity of both *M. hyalinum* and *M. nucleatum* has not been properly re-established. Competing or ambiguous names and ill-defined species concepts are the sources of the present ambiguosity concerning *Exidia* s.l. in northern Europe.

Here, we select type specimens for nine names. In total, five species and one variety are re-described and illustrated, and two new combinations in the genera *Exidia* and *Myxarium* are proposed (Fig. 1–6).

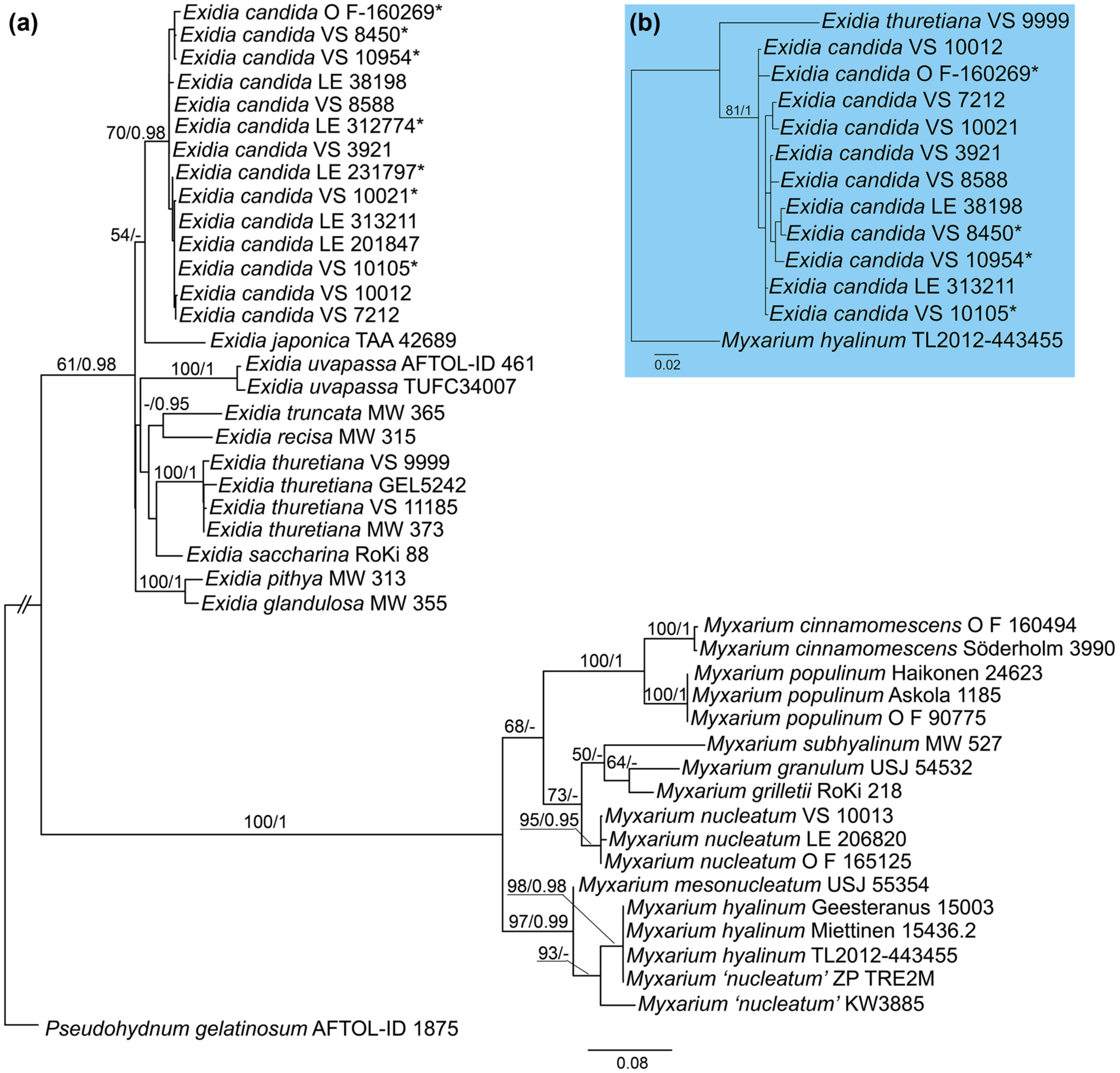

Figure 1. Phylogenetic reconstruction of *Exidia* and *Myxarium* species. Collections are indicated with the voucher number: (a) the best tree from the ML analyses of the combined dataset nrITS+nrLSU; (b) the best tree from the ML analyses of the *tef1* dataset. Support values (ML/BA) are given on the branches. Sequences of *Exidia candida* var. *cartilaginea* are marked by an asterisk.

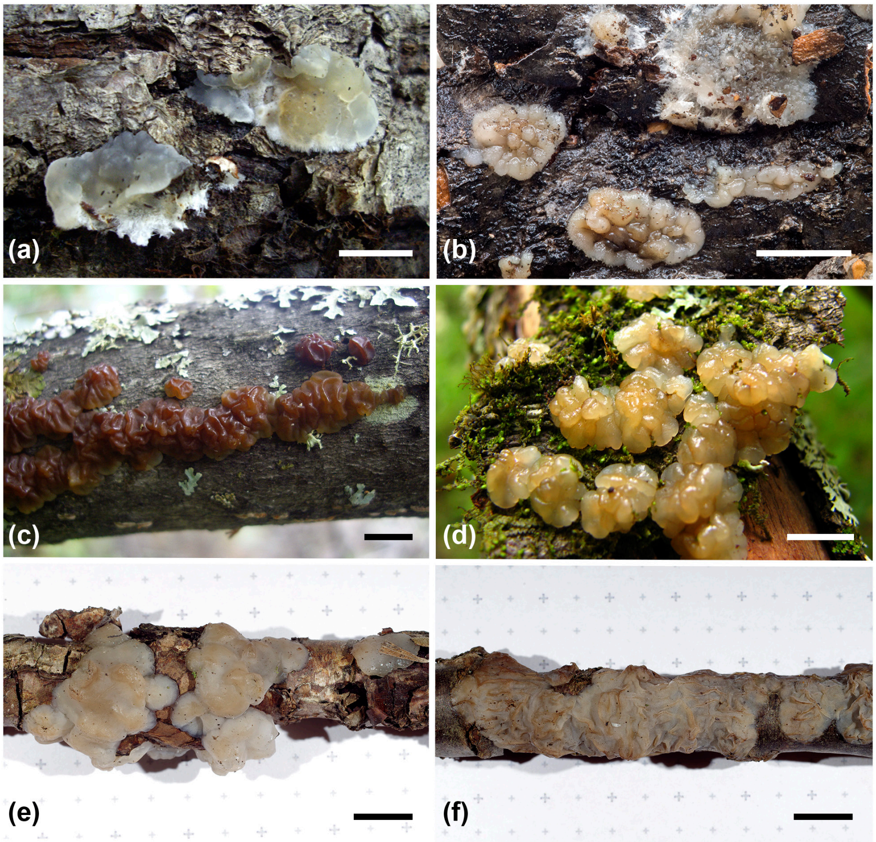

Figure 2. Basidiocarps: (a)–(b) *Exidia candida* (Spirin 9761, LE 313211); (c)–(d) *E. candida* var. *cartilaginea* (Spirin 10954, LE 231797); (e)–(f) *E. thuretiana* (Spirin 9999). Scale bar = 5 mm.

Material and methods

Type specimens and collections from herbaria H, O, LE, UPS, C, BPI, FH, TAAM, CWU were studied. The morphological methods follow Miettinen et al. (2012). The following abbreviations are used in the morphological descriptions: L = mean spore length, W = mean spore width, Q = length/width ratio, n = number of measurements per specimens.

DNA extraction and amplification

For DNA extraction, small fragments of dried basidiocarps were used. In total, 27 specimens were selected for molecular analyses (Table 1). The procedure of DNA extraction completely corresponded to the manufacturing protocol of the NucleoSpin Plant II Kit. The following primers were used for both amplification and sequencing: ITS1F-ITS4 (http://www.biology.duke.edu/fungi/mycolab/primers.htm) for the nuclear ribosomal internal transcribed spacer (ITS) region; primers JS1 (Landvik 1996) and LR5 (http://www.biology.duke.edu/fungi/mycolab/primers.htm) for the large ribosomal subunit (nrLSU) region; primers EF1-983F and EF1-1567R for approximately 500bp of translation elongation factor 1-α (*tef1*) region (Rehner and Buckley 2005). PCR products were purified applying the GeneJET Gel Extraction Kit. Sequencing was performed with an ABI model 3130 Genetic Analyzer. Raw data were edited and assembled in MEGA 6 (Tamura et al. 2013).

Phylogenetic analysis

For this study, 25 ITS, 26 nrLSU and 13 *tef1* sequences were generated (Table 1). An additional 11 ITS and 14 nrLSU sequences including the outgroups were retrieved from GenBank (www.ncbi.nlm.nih.gov/genbank/). Sequences were aligned with the MAFFT version 7 web tool (http://mafft.cbrc.jp/alignment/server/) using the Q-INS-i option for ITS and nrLSU. The final ITS+nrLSU alignment contained 1557 characters (including gaps). The final *tef1* alignment contained 523 characters (including gaps).

Phylogenetic reconstructions were performed with maximum likelihood (ML) and Bayesian (BA) methods. Before the analyses, the best-fit substitution models for the alignment were estimated for each dataset based on the Akaike Information Criterion (AIC) using the FindModel web server (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html).

For all datasets, the GTR model was selected. ML analysis was run in the PhyML server (http://www.atgc-montpellier.fr/phyml/), with one hundred rapid bootstrap replicates. BA

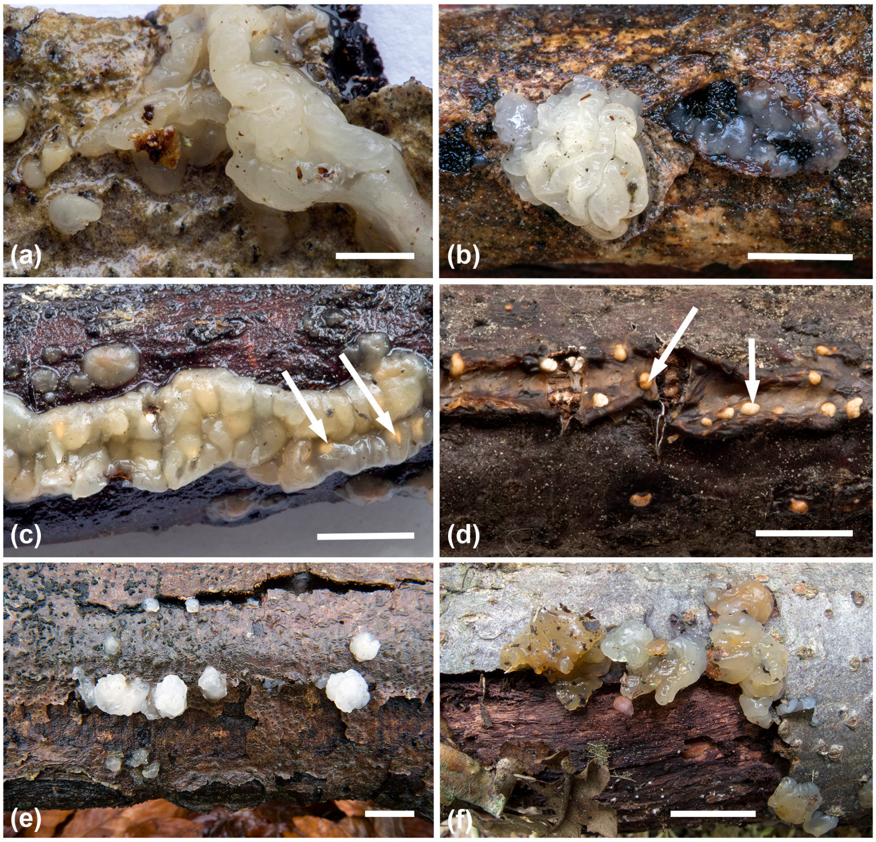

Figure 3. Basidiocarps: (a) *Myxarium populinum* (Haikonen 24623); (b) *M. cinnamomescens* (Hansen 595/72); (c) *M. nucleatum* (LE 206820) in fresh condition; (d) *M. nucleatum* (LE 206820) in dry condition; (e)–(f) *M. hyalinum* (Miettinen 19855, Miettinen 15436.2). Scale bar = 5 mm. Arrows point to white mineral grains.

was performed with the MrBayes software (Ronquist and Huelsenbeck 2003), for two independent runs, each with 5 million generations with sampling every 100 generations and four chains.

The newly generated sequences have been deposited in GenBank with corresponding accession numbers (Table 1).

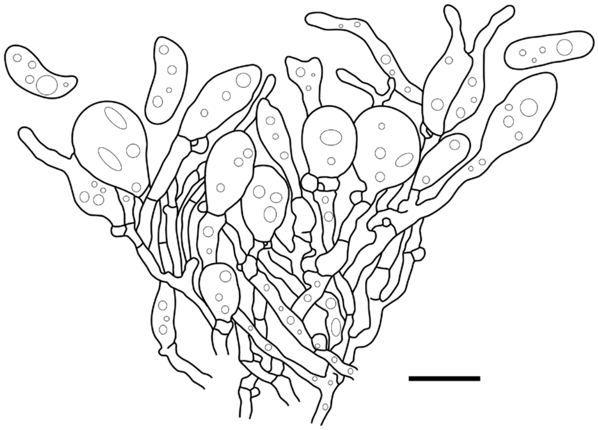

Figure 4. Microscopic structures of *Exidia candida* (Spirin 10012). Scale bar = 10 µm.

Results

ML and BA analyses produced almost the same topologies for the combined nrLSU – ITS dataset (Fig. 1). Specimens corresponding to the current concepts of *E. candida*, *E. cartilaginea* and *E. villosa* are only negligible different in their ITS and nrLSU sequences, and they should thus be considered conspecific. The *tef1* dataset for these taxa show more variation which is, however, not congruent to any morphological, ecological or geographic traits. Among the competing names for this species, *E. candida* has priority (below). *Exidia candida* is only rather distanly related to the similarly looking *E. thuretiana*, as well as to other *Exidia* species. A DNA-based revision of *Exidia* and *Exidiopsis* s.l. is desirable to properly define the limits of the genus.

All European collections of *Exidia*-like fungi with pedunculate basidia have so far been considered as belonging to one species, viz *Myxarium nucleatum*. However, our analyses show that four species are hidden under this name (Fig. 1). They are clearly different in their DNA sequences, as well as in morphology and, to some degree, host preferences and geographic distribution. In the phylogenetic trees, these species are intermixed with totally effused (corticioid), non-jelly *Myxarium* species (*M. grilletii*, *M. subhyalinum*). This

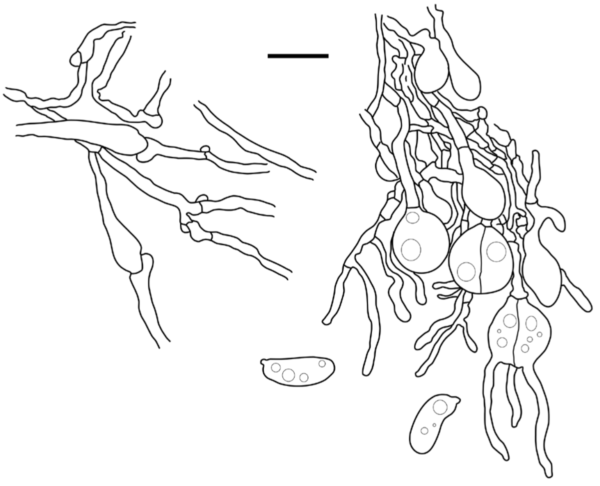

Figure 5. Microscopic structures of *Myxarium nucleatum* (Spirin 10013). Scale bar = 10 µm.

is, possibly, an indication that exidioid basidiocarps evolved independently in several lineages within this genus.

Species are re-described and commented in alphabetical order below.

Exidia candida Lloyd (1916, p. 620) (Fig. 2, 4, 6)

Type: USA. Washington: Clallam Co., Sequim, Grant (BPI 701884, lectotype designated here).

Taxonomic synonyms: *Exidia villosa* Neuhoff (1935, p. 22). Type: Norway. Oslo: Bygdøy, Dronningberget, *Tilia cordata*, 3.V.2016, Spirin 10012* (O, neotype designated here).

– *Tremella albida* f. *betulae* P. Karst. (1866, no. 317). Type: Finland. Etelä-Häme: Tammela, Mustiala, *Betula* sp., 'December', Karsten (Fungi Fenniae Exsiccati no. 317) (H, lectotype designated here).

– *Exidia albida* ssp. *tuberculata* P. Karst. (1889, p. 452). Type: Finland. Etelä-Häme: Tammela, Taipamala, *T. cordata*, 23.IX.1888, Karsten 2145 (H, lectotype designated here).

Description

Basidiocarps persistent, semitranslucent, gelatinous, easily cut by a razor blade, adpressed, orbicular, later pulvinate to cerebriform, fusing together, up to 20 cm in widest dimension and 2 cm thick. Margin first villose, white, detaching, later adnate, compact, more or less concolorous with hymenium. Hymenial surface pale to bright ochraceous, occasionally fading to almost white, indistinctly tuberculate or furrowed. Mineral inclusions often abundant, easily visible by the naked eye.

Hyphal structure monomitic; hyphae clamped (clamps often open), hyaline or brownish, often slightly thick-walled and 3–5 µm in diameter in deeper layers, more or less thin-walled and 2–4 µm in diameter in subhymenium, embedded in gelatinous matrix. Basidia four-celled, ellipsoid-ovoid, 11–16 × 8.5–11 µm. Hyphidia branched, thin- to slightly thick-walled, hyaline to brownish, 0.5–2 µm in diameter, spread among basidia and basidioles; epihymenial membrane absent. Cystidia-like cells abundant in vigorously growing basidiocarps, subfusiform or clavate, 15–25 × 5–7 µm. Basidiospores cylindrical, slightly or distinctly curved, (9.1–) 9.2–15.2 (–15.6) × (3.1–) 3.2–4.8 (–5.0) µm (n = 90/3), L = 11.41, W = 4.07, Q = 2.60–3.12.

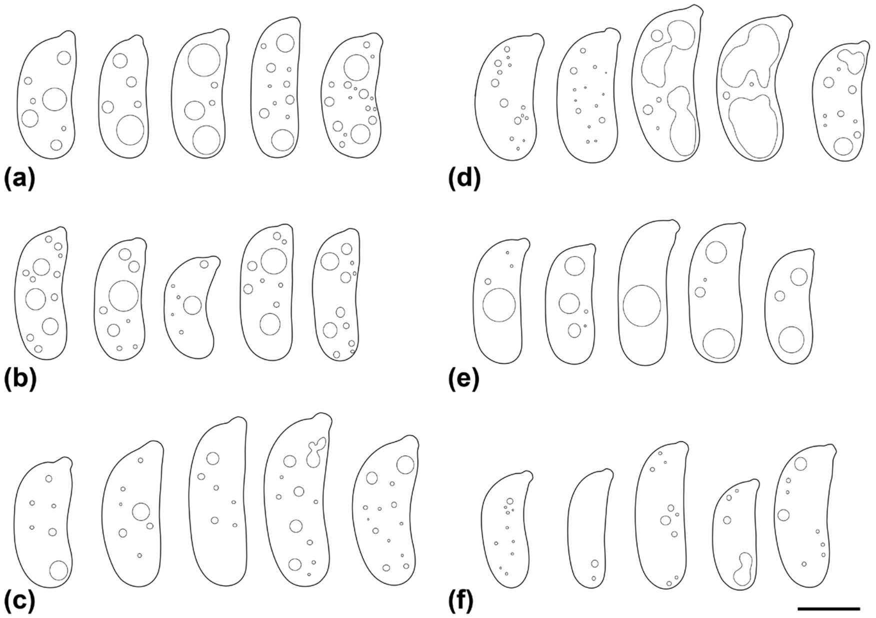

Figure 6. Basidiospores of *Exidia* and *Myxarium* spp. (a) *Exida candida* var. *cartilaginea* (Spirin 10021), (b) *E. candida* (Spirin 10012), (c) *Myxarium hyalinum* (Maas Geesteranus 15003), (d) *M. cinnamomescens* (Hansen 595/72), (e) *M. nucleatum* (Spirin 10013), (f) *M. populinum* (Karsten 1812). Scale bar = 5 µm.

Table 1. Data for ITS and LSU sequences used in the phylogenetic analyses. *=*Exidia candida* var. *cartilaginea*, **=Published as *M. nucleatum* (Weiss and Oberwinkler 2001).

Species	Collector/herbarium number	Origin (ISO code)	Host	LSU GenBank no.	ITS GenBank no.	*tef 1* GenBank #	Source
*Exidia candida**	O F160269	NO	*Tilia*	KY801897	KY801872	KY801922	this study
*E. candida**	Spirin 8450 (H)	US-WA	*Alnus*	KY801900	KY801875	KY801925	this study
*E. candida**	Spirin 10954 (H)	RU-KHA	*Alnus*	KY801901	KY801876	KY801926	this study
E. candida	LE 38198	CA-BC	–	KY801896	KY801871	KY801921	this study
E. candida	Spirin 8588 (H)	US-WA	*Corylus*	KY801895	KY801870	KY801920	this study
*E. candida**	LE 312774	RU-KYA	*Alnus*	KY801902	KY801877	–	this study
E. candida	Spirin 3921 (H)	RU-KHA	*Betula*	KY801892	KY801867	KY801918	this study
*E. candida**	LE 231797	RU-AL	–	KY801904	–	–	this study
*E. candida**	Spirin 10021 (O)	NO	*Alnus*	KY801899	KY801874	KY801924	this study
E. candida	LE 313211	RU-MO	*Tilia*	KY801893	KY801868	KY801919	this study
E. candida	LE 201847	RU-LEN	*Alnus*	KY801903	–	–	this study
*E. candida**	Spirin 10105 (H)	RU-LEN	*Betula*	KY801898	KY801873	KY801923	this study
E. candida	Spirin 10012 (O)	NO	*Tilia*	KY801890	KY801865	KY801916	this study
E. candida	Spirin 7212 (H)	RU-NIZ	*Tilia*	KY801891	KY801866	KY801917	this study
Exidia japonica	TAAM 42689	RU-PRI	–	AF291320	AF291274	–	Weiss and Oberwinkler (2001)
Exidia uvapassa	AFTOL-ID 461		–	AY645056	DQ241776	–	GenBank
E. uvapassa	TUFC 34007	JP	–	AB871843	AB871863	–	GenBank
E. truncata	MW 365	DE	–	AF291325	AF291279	–	Weiss and Oberwinkler (2001)
E. recisa	MW 315	DE	–	AF291322	AF291276	–	Weiss and Oberwinkler (2001)
E. thuretiana	Spirin 9999 (H)	FI	*Ribes*	KY801905	KY801878	KY801927	this study
E. thuretiana	GEL 5242	DE	–	AF291278	AF291278	–	GenBank
E. thuretiana	Spirin 11185 (O)	NO	*Ulmus*	KY801914	KY801889	–	this study
E. thuretiana	MW 373	DE	–	AF291324	AF291278	–	Weiss and Oberwinkler (2001)
Exidia saccharina	RoKi 88	DE	–	AF291323	AF291277	–	Weiss and Oberwinkler (2001)
Exidia pithya	MW 313	DE	–	AF291321	AF291275	–	Weiss and Oberwinkler (2001)
Exidia glandulosa	MW 355	DE	–	AF291319	AF291273	–	Weiss and Oberwinkler (2001)
Myxarium cinnamomescens	O F160494	NO	*Populus*	KY801909	KY801882	–	this study
M. cinnamomescens	Söderholm 3990 (H)	FI	*Padus*	KY801912	KY801886	–	this study
Myxarium populinum	Haikonen 24623 (H)	FI	*Populus*	KY801910	KY801883	–	this study
M. populinum	Askola 1185 (H)	FI	*Populus*	KY801911	KY801885	–	this study
M. populinum	O F90775	NO	*Populus*	–	KY801888	–	this study
Myxarium subhyalinum	MW 527	DE	–	AF291352	–	–	Weiss and Oberwinkler (2001)
Myxarium granulum	USJ 54532	CR	–	AF291348	–	–	Weiss and Oberwinkler (2001)
Myxarium grilletii	RoKi 218	DE	–	AF291349	–	–	Weiss and Oberwinkler (2001)
Myxarium nucleatum	Spirin 10013 (O)	NO	*Tilia*	KY801906	KY801879	–	this study
M. nucleatum	LE 206820	RU-LEN	*Tilia*	KY801894	KY801869	–	this study
M. nucleatum	O F165125 (H)	NO	*Tilia*	–	KY801884	–	this study
Myxarium mesonuclearum	USJ 55354	CR	–	AF291350	–	–	Weiss and Oberwinkler (2001)
M. hyalinum	Geesteranus 15003 (H)	NL	*Acer*	KY801908	KY801881	–	this study
M. hyalinum	Miettinen 15436.2 (H)	DE	–	KY801913	KY801887	–	this study
M. hyalinum	TL2012-443455 (C)	DK	*Tilia*	KY801907	KY801880	KY801928	this study
*M. hyalinum***	ZP TRE2M	PT	–	AF291351	–	–	Weiss and Oberwinkler (2001)
M. hyalinum	Miettinen 19855 (H)	DE	*Fagus*	KY801915	–		this study
M. nucleatum s.l.	KW 3885	US-CA	–	AY509554	AY509554	–	Wells et al. (2004)

Remarks

Exidia candida was first introduced as *Tremella albida* f. *betulae* (Karsten 1866). Later Karsten (1889) described it as *Exidia albida* ssp. *tuberculata*. Both of these names are typified here. Mussat (in Saccardo 1901) published a new combination, *E. tuberculata* (P. Karsten) Mussat, but he evidently did not accept it because this species epithet was treated as a synonym of Karsten's subspecies. Therefore, the species name *E. tuberculata* is considered invalid (ICN Art. 36.1) (McNeill et al. 2012).

Lloyd (1916) described *E. candida* based on a single collection from Washington, USA. His description was amended by Burt (1921). The authentic specimen formally designated here as the lectotype is identical to three recent collections from the same region used in the present study. *Exidia villosa* was described from East Prussia (Neuhoff 1935) and needs to be typified since original material is lacking. Fortunately, the protologue provides an excellent description of morphology and ecology of this taxon which is sufficient for selecting a neotype (indicated above). *Exidia candida* and *E. villosa* are morphologically indistinguishable, and our DNA study confirms that they are conspecific. Donk (1966) assumed that *Heterochaete europaea* Höhn. could be conspecific with *E. villosa*. We studied the single original specimen of *H. europaea* (FH, selected here as a lectotype), and it certainly belongs to *Exidia thuretiana*.

Morphologically, *E. candida* is recognizable by its rather soft and often light-coloured basidiocaprs, lack of epihymenial membrane and numerous mineral inclusions in the hymenial layer. *Exidia thuretiana* is macroscopically similar but often totally white, and it can be distinguished by much larger basidiospores, (12.2–) 13.8–18.2 (–18.7) × (4.8–) 5.2–7.5 (–8.2) µm (n = 60/2), L = 15.81, W = 6.27, Q = 2.35–2.74. *Myxarium cinnamomescens* and *M. hyalinum* possess the same colours as *E. candida* but their basidiocarps are as a rule smaller and thinner; additionally, basidia of *Myxarium* spp. have a prononunced enucleate stalk.

In Europe, *E. candida* has a more southern distribution than *E. candida* var. *cartilaginea*. It often occurs on just fallen branches of lime (*Tilia cordata*), and can easily be detected on this substrate after strong winds. Some records were made on recently fallen lime logs. A few collections from other hosts exist, too. In North America, it has been found on *Corylus*.

Exidia candida var. *cartilaginea* (S. Lundell & Neuhoff) Spirin & V. Malysheva comb. et stat. nov. (Fig. 2, 6)

Basionym: *Exidia cartilaginea* S. Lundell & Neuhoff (in Neuhoff 1935, p. 19).

Type: Sweden. Uppland: Bondkyrka, Vårdsätra, *Betula* sp., 18.X.1932, Lundell (Fungi Exsiccati Suecici no. 263) (UPS F-010986, lectotype designated here).

MycoBank 821860.

Description

Basidiocarps persistent, semitranslucent, though gelatinous, often hardly cut by a razor blade, adpressed, orbicular, later pulvinate to somewhat cerebriform, fusing together, up to 5 cm in widest dimension and 1 cm thick. Margin first villose, white, detaching, later adnate, compact, paler than or more or less concolorous with hymenium. Hymenial surface pale ochraceous to bright ochraceous-brown, then fading to almost white, indistinctly tuberculate to more or less clearly ridged. Mineral inclusions rare, seen as white grains under lens, or often absent.

Hyphal structure monomitic; hyphae clamped (clamps usually open), hyaline or brownish, often slightly thick-walled and 2.5–4.5 µm in diameter in deeper layers, more or less thin-walled and 2–3 µm in diameter in subhymenium, embedded in gelatinous matrix. Basidia four-celled, ellipsoid-ovoid, 11–17 × 8–12 µm. Hyphidia branched, thin- to slightly thick-walled, hyaline to brownish, 1.0–2.5 µm in diameter, densely arranged and glued together, producing firm layer on hymenial surface (epihymenial membrane). Cystidia-like cells abundant in vigorously growing basidiocarps, subulate or bottle-shaped, 15–25 × 3–6 µm, sometimes producing simple or branched apical outgrowth. Basidiospores cylindrical, slightly to distinctly curved, (9.9–) 10.2–14.2 (–14.3) × (3.8–) 4.0–5.1 (–5.2) µm (n = 60/2), L = 11.90, W = 4.44, Q = 2.58–2.81.

Remarks

Exidia cartilaginea was described by Neuhoff (1935) based on several collections from Sweden. The type specimen is lost, and therefore we select another collection mentioned in the protologue (paratype) as a lectotype. As indicated above, *E. cartilaginea* should be considered merely a variety of *E. candida*.

One of two authentic specimens of *E. albida* subsp. *subrepanda* (Karsten 2142, on *Betula*, H) belongs to *E. candida* var. *cartilaginea*. This subspecies was raised to the species rank by Oudemans (1919, p. 398) but its identity remained obscure. In the protologue, Karsten (1891) stated that *E. albida* subsp. *subrepanda* occurs on *Picea*. Therefore, we select another original specimen collected from *Picea* (Karsten 2143, H) as a lectotype of this taxon. This collection belongs to *Exidia saccharina* (Alb. & Schwein.) Fr., and thence we place *E. subrepanda* as a synonym of the latter species.

Exidia candida var. *cartilaginea* differs from *E. candida* s.s. in having darker, sturdier basidiocarps with firm epihymenial membrane, and wider basidiospores. Most collections of *E. candida* var. *cartilaginea* are sterile or contain just a few mature basidiospores. Fertile specimens are collected mostly in spring when the epihymenial membrane partly degrades and exposes basidia embedded in a dense, gelatinized layer of hyphidia.

This variety has a predominantly boreal distribution. It is often collected on dead but still attached branches of *Alnus* and *Betula* but found rarely also on other host species

(*Acer*, *Salix*, *Tilia*). Here we confirm its presence in east Asia (Russian Far East) and the American northwest.

Myxarium cinnamomescens (Raitviir) Raitviir (1971, p. 113) (Fig. 3, 6)

Basionym: *Exidia cinnamomescens* Raitviir (1963, p. 208).

Type: Russia. Komi Rep.: Syktyvdinsky Dist., Graddor, *Populus tremula* (fallen log), 8.VIII.1957, Põldmaa (Holotype: TAAM 5995!).

Description

Basidiocarps persistent, gelatinous, first semitranslucent, pustulate, about 1 mm in diameter, then fusing together, cerebriform or adpressed-orbicular, finally opaque, up to 8 mm in widest dimension and 1–3 mm thick. Margin detaching, later adnate, compact, more or less concolorous with hymenium. Hymenial surface hyaline with light yellowish tints, then almost white, indistinctly furrowed to more or less smooth, in herbarium specimens pale ochraceous or brownish. Mineral inclusions usually absent or, if present, very small, embedded in hymenial layer and thus seen only under lens.

Hyphal structure monomitic; hyphae clamped (clamps often open), hyaline, thin- or slightly thick-walled and 3–6 µm in diameter in deeper layers, at some septa swollen up to 9 µm in diameter, thin-walled and 1.0–2.5 µm in diameter in subhymenium. Basidia four-celled, ellipsoid-ovoid to subglobose, 11.0–17.5 × 7–13 µm, with enucleate stalk up to 65 × 3.5 µm. Hyphidia branched, thin-walled, hyaline, 1–2 µm in diameter, covering hymenial surface. Cystidia absent. Basidiospores cylindrical to broadly cylindrical, slightly to distinctly curved, (9.3–) 10.2–14.0 (–14.5) × (4.0–) 4.1–5.7 (–5.8) µm (n = 132/4), L = 11.96, W = 4.82, Q = 2.43–2.53.

Remarks

Myxarium cinnamomescens was first described from Komi (European part of Russia) as *Exidia cinnamomescens* (Raitviir 1963), but the species was later moved to *Myxarium* (Raitviir 1971). Roberts (1998) suggested its synonymy with *Exidia nucleata* (= *Myxarium nucleatum*). However, as we show in this study, the older concept of *M. nucleatum* covers at least four species. The type of *M. cinnamomescens* has been studied by us, and it is morphologically identical to two sequenced collections from Finland and Norway.

Macroscopically, *M. cinnamomescens* is most similar to *M. populinum*, and the only reliable character to separate them is their different basidiospores size (especially width). *Myxarium hyalinum* has more deeply coloured and larger basidiocarps that in the end of the growing season show abundant mineral inclusions, well visible through the almost translucent hymenial surface. In turn, *M. cinnamomescens* never produces inclusions detectable by the naked eye, and its senescent basidiocarps become completely white and opaque. Moreover, basidiospores of *M. hyalinum* are on average wider than in *M. cinnamomescens* although attention should be paid to the age of basidiocarps: younger specimens of *Myxarium* spp. tend to produce basidiospores somewhat narrower than in well developed fruitbodies.

Myxarium cinnamomescems is distributed in the hemiboreal zone of Europe. As a rule, it inhabits still attached or just fallen branches of various deciduous trees. Its basidiocarps typically occur in ruptures of the bark, especially in those produced by stromatic pyrenomycetes. The other three gelatinous *Myxarium* species treated below usually grow on still corticated branches and logs. Here *M. cinnamomescens* is reported from Finland, Norway and northwest Russia.

Myxarium hyalinum (Pers.) Donk (1966, p. 233) (Fig. 3, 6)

Basionym: *Tremella hyalina* Pers. (1822, p. 105).

Type: Netherlands. Zuid-Holland: Leiden, *Acer* sp., 20.XI.1966, Maas Geesteranus 15003* (H) (neotype, designated here).

Description

Basidiocarps persistent, semitranslucent, gelatinous, first adpressed-orbicular, often cerebriform, 2–5 mm in diameter, then fusing together, up to 3 cm in widest dimension and 3 mm thick. Margin detaching, later adnate, compact, more or less concolorous with hymenium. Hymenial surface ochraceous to brownish, then fading to whitish (but staying translucent), indistinctly furrowed to more or less smooth, in herbarium specimens dark amber to brown. Mineral inclusions appearing only in coalescent basidiocarps, abundant, up to 1 mm in diameter.

Hyphal structure monomitic; hyphae clamped (clamps often open), hyaline, thin- or slightly thick-walled and 2–4 µm in diameter in deeper layers, at some septa swollen up to 9 µm in diameter, thin-walled and 1.0–2.5 µm in diameter in subhymenium. Basidia four-celled, ellipsoid-ovoid to subglobose, 11–18 × 9–12 µm, with enucleate stalk up to 60 × 3.5 µm. Hyphidia branched, thin-walled, hyaline, 1–2 µm in diameter, covering hymenial surface. Basidiospores cylindrical to broadly cylindrical, slightly or distinctly curved, (9.0–) 9.2–15.7 (–16.7) × (4.0–) 4.1–6.0 (–6.2) µm (n = 90/3), L = 12.01, W = 5.01, Q = 2.38–2.45.

Remarks

The protologue of *T. hyalina* (Persoon 1822) is very concise and thus provides opportunities for different interpretations. Bourdot and Galzin (1909, 1928) were seemingly the first authors who adopted Persoon's species name for collections of *E. gemmata* (at that time a collective name for all gelatinous *Myxarium* species) lacking mineral inclusions. Neuhoff (1935) accepted this treatment, albeit with some reservations. Following this line, Donk (1966) recombined *T. hyalina* in *Myxarium* in order to replace *M. nucleatum* with an older name. Reid (1970) argued that Persoon's description is so inexact that it could hardly be applied to any specific species. Roberts (1998) disagreed with both Donk's synonymy and his elimination of *M. nucleatum* from *Exidia*. However, Mycobank (www.mycobank.org) lists *M. hyalinum* as having priority over *M. nucleatum*.

We agree that Persoon's description is open to various interpretations, and our solution to this problem is merely pragmatical – to avoid as many name changes as possible. We studied and sequenced four morphologically identical collections including one identified by Donk as *M. hyalinum* (Maas Geesteranus 15003). Three of them lack mineral stuff while the specimen labelled by Donk represents senescent, coalescent basidiocarps with numerous, well-visible inclusions. Since the central European species is dealt with, we decided apply the name *Myxarium hyalinum* to this taxon. Our solution at least partly corresponds to the idea of the species developed by Bourdot and Galzin and their followers. A neotype of *T. hyalina* from the Netherlands is designated here.

Normally developed basidiocarps of *M. hyalinum* differ from other *Myxarium* species in being more robust and having deeper, ochraceus or brownish colours. Basidiospores and basidia of *M. hyalinum* are on average larger than those of *M. nucleatum* and *M. populinum*. Differences between *M. hyalinum* and *M. cinnamomescens* are discussed under remarks to the latter species.

Myxarium hyalinum is a southern species distributed mainly in the nemoral zone. We have studied specimens from Denmark, Germany, the Netherlands, Norway and Ukraine.

Myxarium nucleatum Wallr. (1833, p. 260) (Fig. 3, 5, 6)

Type: Norway. Oslo: Bygdøy, Dronningberget, *Tilia cordata*, 3.V.2016, Spirin 10013* (O, neotype designated here).

Description

Basidiocarps persistent, translucent, gelatinous, easily cut by a razor blade, adpressed-orbicular, 1–5 mm in diameter, often in gregarious groups, partly fusing together, 0.1–0.5 mm thick, drying to almost invisible vernicose films. Margin adnate, compact, more or less concolorous with hymenium. Hymenial surface whitish or faintly yellowish to pale ochraceous, more or less smooth. Mineral inclusions always present, abundant, 0.4–0.8 mm in diameter.

Hyphal structure monomitic; hyphae clamped (clamps often open), hyaline, thin- or slightly thick-walled and 2.0–3.5 µm in diameter in deeper layers, at some septa swollen up to 7 µm in diameter, thin-walled and 1–2 µm in diameter in subhymenium. Basidia four-celled, ellipsoid-ovoid to subglobose, 10.5–13 × 8–10.5 µm, with enucleate stalk up to 30 × 2.5 µm. Hyphidia branched, thin-walled, hyaline, 1–2 µm in diameter, covering hymenial surface. Basidiospores cylindrical, slightly or distinctly curved, (7.9–) 8.5–13.8 (–14.0) × (3.2–) 3.5–5.2 (–5.4) µm (n = 130/4), L = 10.88, W = 4.26, Q = 2.38–2.70.

Remarks

Wallroth (1833) described *Myxarium* as monotypic, with *M. nucleatum* as the only accepted species. His description contains a reference to the North American *Tremella nucleata* Schwein. (as '*Nematelia nucleata* Fr.'). However, as Donk (1966) correctly noted, Wallroth's *M. nucleatum* is not a simple recombination of Schweinitz's species to the new genus but a new species name referring to a different species. No type material exists for *M. nucleatum*, and therefore we designate a neotype here. In our opinion, pale-coloured, adpressed, coalescent basidiocarps with numerous, distinctive mineral inclusions are rather clear indications of what species was considered in the protologue.

Basidiocarps of *M. nucleatum* are hardly visible in dry condition and detectable mainly due to a presense of white mineral grains. This feature makes *M. nucleatum* different from the microscopically similar *M. populinum*, as well as from *M. cinnamomescens*. The latter species also possesses larger basidia and basidiospores. Senescent basidiocarps of *M. hyalinum* may also bear mineral inclusions, but the latter species has more deeply coloured basidicarps, well visible in dry condition, and bigger basidiospores.

Tremella gemmata Lév. was described from Crimea (Demidov 1842), and it is often considered a synonym of *M. nucleatum*. The protologue points towards the latter species as accepted here. However, this synonymy should be re-confirmed. *Exidia alboglobosa* Lloyd was listed among the synonyms of *M. nucleatum* by Reid (1970) but its identity should be re-considered. White globose basidiocarps are untypical for *M. nucleatum* s.s., and they may well represent the senescent, discoloured specimen of *M. cinnamomescens* or *M. hyalinum*. This problem, however, can be solved with newly collected and sequenced material from France.

Myxarium nucleatum seems to be widely distributed in the temperate zone although its distribution area stretches up to the Arctic Circle, with the northernmost locality in Kuusamo (Finland). The favorite host of *M. nucleatum* in North Europe is *Tilia cordata*. Here the species is reported from Denmark, Finland, Norway, northwest Russia and Sweden.

Myxarium populinum (P. Karst.) Spirin & V. Malysheva comb. nov. (Fig. 3, 6)

Basionym: *Exidia albida* var. *populina* P. Karst. (1891, p. 73).

Type: Finland. Etelä-Häme: Tammela, Mustiala, *Populus tremula*, XI.1890, Karsten 1812 (H, lectotype designated here).

MycoBank 821861.

Description

Basidiocarps persistent, gelatinous, first semitranslucent, adpressed-orbicular, about 3 mm in diameter, then fusing together, up to 15 mm in widest dimension and 0.5–1.0 mm thick. Margin detaching, compact, more or less concolorous with hymenium. Hymenial surface whitish, sometimes with light yellowish tints, indistinctly furrowed to more or less smooth, in herbarium specimens pale ochraceous or brownish. Mineral inclusions usually absent or, if present, very small, embedded in hymenial layer and thus seen only under lens.

Hyphal structure monomitic; hyphae clamped (clamps often open), hyaline, thin- or slightly thick-walled and 2.5–5.5 µm in diameter in deeper layers, at some septa swollen up to 8 µm in diameter, thin-walled and 1.0–2.5 µm in diameter in subhymenium. Basidia four-celled, ellipsoid-ovoid to subglobose, 10.5–13.0 × 9.0–12.0 µm, with enucleate stalk up to 50 × 2.5 µm. Hyphidia branched, thin-walled, hyaline, 1–2 µm in diameter, covering hymenial surface. Basidiospores cylindrical to narrowly cylindrical, slightly or distinctly curved, (8.7–) 9.0–13.8 (–16.2) × (3.0–) 3.1–4.9 (–5.0) µm (n = 150/5), L = 11.08, W = 3.94, Q = 2.72–2.95.

Remarks

This species was initially described as *E. albida* var. *populina* (Karsten 1891). Oudemans (1920, p. 94) raised this variety to species rank. Karsten's single original collection is designated here as the lectotype. It is morphologically identical to a number of specimens collected in northern Europe, of which three have been sequenced. From macroscopically similar *M. cinnamomescens* and *M. hyalinum*, this species differs in having considerably narrower basidiospores. *Myxarium nucleatum* possesses basidiospores of almost the same size as *M. populinum* but its basidiocarps look different.

Myxarium populinum seems to be rather common in northern Europe. All but one collections studied by us came from aspen (*Populus tremula*).

Specimens examined (sequenced specimens are marked by asterisk)

Exidia candida. Canada. British Columbia: Vancouver, deciduous tree, 15.IV.1968 Bandoni* (LE 38198). Finland. Uusimaa: Helsinki, Käpylä, *Tilia cordata*, 30.IV.2015 Miettinen 19135 (H). Etelä-Häme: Tammela, Mustiala (H, lectotype of *Tremella albida* f. *betulae*, above), Taipamala (H, lectotype of *T. albida* subsp. *tuberculata*, above). Norway. Oslo: Bygdøy (O, neotype of *Exidia villosa*, see above). Vest-Agder: Flekkefjord, Hidra, *T. cordata*, 16.IV.1973 Gulden 439/73 (O F-179584). Russia. Khabarovsk Reg.: Solnechnyi Dist., Igdomi, *Betula platyphylla*, 7.VIII.2011 Spirin 3921* (H). Leningrad Reg.: Lodeinoe Pole Dist., Nizhnesvirsky Nat. Res., *Alnus incana*, 18.IX.1996 Zmitrovich* (LE 201847). Mordovia: Temnikov Dist., Mordovsky Nat. Res., *T. cordata*, 2.X.2014 Bolshakov* (LE 313211). Nizhny Novgorod Reg.: Lukoyanov Dist., Razino, *T. cordata*, 6.VIII.2013 Spirin 5999 (H), 7–8.VIII.2014 Spirin 7212*, 7263 (H), 19–21.VIII.2015 Spirin 9595, 9761 (H), Srednii, *T. cordata*, 18.VIII.2006 Spirin 2600 (H). USA. Washington: Clallam Co. (lectotype of *E. candida*, above); Pend Oreille Co., Lime Creek, *Corylus cornuta*, 15.X.2014 Spirin 8584*, 8588* (H).

Exidia candida var. *cartilaginea*. Finland. Etelä-Häme: Tammela, Mustiala, *Betula* sp., 18.XII.1890 Karsten 2142 (H, as *E. albida* subsp. *subrepanda*). Norway. Baerum: Kjaglidalen, *A. incana*, 4.V.2016 Spirin 10021* (O); Lysakerelven, *Acer pseudoplatanus*, 16.X.1964 Torkelsen 159/4 (O F160479). Hordaland: Kvinnherad, Stonganeset, *T. cordata*, 27.XII.1984 Flatabø* (O F-160269). Russia. Khabarovsk Reg.: Solnechnyi Dist., Igdomi, *Alnus hirsuta*, 2.IX.2016 Spirin 10762* (H), 3.IX.2016 Spirin 10906 (H), *Alnus (Duschekia) fruticosa*, 4.IX.2016 Spirin 10954* (H), Suluk-Makit, *Salix* sp., 17.VIII.2011 Spirin 4159 (H); Verkhnebureinskii Dist., Hegdy, *A. fruticosa*, 22.VIII.2014 Spirin 7833 (H). Krasnoyarsk Reg.: Ermakovskoe Dist., Sayano-Shushensky Nature Reserve, *Alnus* sp., 17.VIII.2015 Malysheva* (LE 312774). Leningrad Reg.: Podporozhie Dist., Vazhinka, *Betula pubescens*, 21.V.2016 Spirin 10105* (H). Republic of Altai: Ulagan Dist., Altai Nature Reserve, 18.VIII.2008 Malysheva* (LE 231797). Sweden. Uppland: Bondkyrka, Vårdsätra, (UPS F-010986, lectotype of *E. cartilaginea*, above). USA. Washington: Pend Oreille Co., Sullivan Creek, *Alnus rubra*, 13.X.2014 Spirin 8450* (H).

Exidia saccharina. Finland. Etelä-Häme: Tammela, Mustiala, *Picea abies*, 15.XI.1890 Karsten 2143 (H, lectotype of *E. subrepanda*).

Exidia thuretiana. Bosnia and Herzegovina. Jaize, *Fagus sylvatica*, 14.IV.1901 Höhnel (FH – lectotype of *Heterochaete europaea*). Finland. Uusimaa: Helsinki, Viikki, *Ribes nigrum*, 28.IV.2016 Spirin 9999* (H). Norway. Akershus: Baerum, Kjaglidalen, *Ulmus glabra*, 16.IX.2016 Spirin 11128 (O). Telemark: Nome, Mörkvasslia Nat. Res., *U. glabra*, 25.X.2016 Spirin 11185* (O). Russia. Leningrad Reg.: Podporozhie Dist., Grishino, *Ribes* sp., 26.V.2017 Spirin 11207 (H).

Myxarium cinnamomescens. Finland. Etelä-Häme: Kangasala, Vihtinen, *Padus avium*, 7.IX.2008 Söderholm 3990* (H). Norway. Aust-Agder: Arendal, Tromøy, *T. cordata*, 25.XII.1972 Pedersen (O F160483). Akershus: Ås, Ved Høyskolen, *Populus tremula*, 10.XII.1972 Hansen and Gulden 595/72* (O F160494); Bærum, Eikeli, *Betula* sp., 26.X.1971 Schumacher (O F160499), Sandvikselva, garden shrub, 22.V.1972 Schumacher (O F160498). Oslo: Bygdøy, *T. cordata*, 9.XI.1969 Eftenstøl (O F160490). Buskerud: Hole, Vik, *Betula* sp., 13.IX.1965 Torkelsen (O F160489), 30.IX.1967 Torkelsen (O F160484). Hedmark: Hamar, Domkirkeodden, *Betula pubescens*, 19.IX.1965 Torkelsen 135/5 (O F160491). Hordaland: Ulvik, Osa, *Betula* sp., 3.VII.1951 Stordal (O F160502). Oppland: Etnedal, Bruflat i Valdres, *P. tremula*, Blytt (O F160503). Russia. Komi Rep. (holotype, above).

Myxarium hyalinum. Denmark. Sjælland: Slagelse, Borreby, *T. cordata*, 14.IV.2012 Læssøe TL2012-443455* (C, dupl. H). Germany. Bremen: Botanical Garden, deciduous tree, 28.VI.2012 Miettinen 15436.2* (H). Nordrhein-Westfalen: Bielefeld, Ochsenburg, *Fagus sylvatica*, 25.XI.2015 Miettinen 19855* (H). Netherlands. Zuid-Holland: Leiden (neotype, above). Norway. Vest-Agder: Flekkefjord, Hidra, *Quercus robur*, 16.IV.1973 Gulden 431/73 (O F160501). Akershus: Bærum, Evje, *Fraxinus excelsior*, 27.VII.1952 Stordal

(O F160485). Ukraine. Kharkov Reg.: Kharkov, Forest Park, *Acer platanoides, Q. robur*, 25.IX.2013 Akulov (CWU).

Myxarium nucleatum. Denmark. Jylland: Horsens, Hansted skov, *F. sylvatica*, 19.IX.1972 Torkelsen (O F160480). Finland. Etelä-Häme: Lahti, Ritamäki, *T. cordata*, 26.X.1998 Haikonen 19456 (H). Koillismaa: Kuusamo, Liikasenvaara, *Ribes* sp., 23.VIII.1978 Ryvarden (O F160841). Norway. Vestfold: Tønsberg, Slagentangen, *T. cordata*, 24.I.1993 Marstad (O F160504), 25.I.1993 Marstad 42-93* (O F165125). Akershus: Baerum, Lysakerelven, *A. pseudoplatanus*, 16.X.1964 Torkelsen 158/4 (O F160478). Oslo: Bygdøy, Dronningberget (neotype, above). Aust-Agder: Grimstad, Reddalskollen, *T. cordata*, 11.IV.2005 Fonneland 05-01 (O F157942); Bygland, Fånefjell, *T. cordata*, 1.X.2006 Fonneland 06-144 (O F282994). Møre og Romsdal: Averøy, Mellom Bodalen og Hoset, *Corylus avellana*, 4.VIII.1974 Torkelsen 779/74 (O F160477). Russia. Leningrad Reg.: Tosno Dist., *T. cordata*, 2.X.1997 Zmitrovich* (LE 206820). Sweden. Uppland: Bondkyrka, Hällby, *P. tremula*, 15.X.1944 Nannfeldt 7532 (O F160508).

Myxarium populinum. Finland. Uusimaa: Nurmijärvi, Kirkonkylä, *P. tremula*, 21.XI.1982 Askola 1185* (H). Etelä-Häme: Nastola, Villähde, *P. tremula*, 13.XI.2005 Haikonen 24623* (H); Tammela, Mustiala (lectotype of *Exidia albida* var. *populina*, above). Norway. Vestfold: Larvik, Jordstøyp i Kvelde, *P. tremula*, 6.IX.1995 Andersen* (O F90775). Akershus: Nannestad, Hurdalssjøen, *P. tremula*, 28.IX.1969 Gulden (O F160506). Buskerud: Kongsberg, Fulsebakkåsen i Jondalen, *P. tremula*, 21.VIII.1999 Winter (O F63156); Nes, Eidal i Rukkedalen, *Salix caprea*, 2.X.1965 Torkelsen 151/5 (O F160500). Hedmark: Ringsaker, Veldre, *P. tremula*, 19.IX.1965 Torkelsen 136/5 (O F160507).

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