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RESEARCH ARTICLE

Identity of the subalpine–subarctic corticioid fungus *Megalocystidium leucoxanthum* (Russulales, Basidiomycota) and six related species

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Background and aims – To date, *Megalocystidium leucoxanthum*, a corticioid fungus originally described from the Italian Alps, was considered as a widely distributed species inhabiting numerous angiosperm hosts in the northern hemisphere. Its specimens collected in different geographic areas and from various host species revealed a high morphological variability and thus obfuscated differences from the closely related *M. luridum*. The objective of this study was to re-establish *M. leucoxanthum* based on newly collected and sequenced specimens and clarify the identity of morphologically deviating collections previously ascribed to this species.
Material and methods – In total, 87 specimens of *Megalocystidium* spp. (including two historical types) were studied by morphological methods. Their phylogenetic relations were investigated based on DNA sequences (nrITS, nrLSU, and *tef1*) of 29 specimens.
Key results – Based on morphological, ecological and DNA data, we showed *M. leucoxanthum* sensu typi is a rare species restricted to *Alnus alnobetula* in subalpine and subarctic zones. Consequently, records from other hosts (mostly representatives of *Salicaceae*) belong to three other species, *M. olens*, *M. perticatum*, and *M. salicis*, described as new to science. The fourth newly introduced species, *M. pellitum*, occurs on the same host tree as *M. leucoxanthum* but it can be separated from the latter due to distinctive morphological traits and DNA sequences. Additionally, *Aleurodiscus diffissus* is combined in *Megalocystidium* and the identity of *M. luridum* is clarified.

Keywords – Basidiomycetes; molecular systematics; *Russulales*; subalpine communities; taxonomy.

INTRODUCTION

Megalocystidium Jülich is a genus of corticioid fungi typified with *Corticium leucoxanthum* Bres. Initially introduced for three species, *Megalocystidium* currently embraces ten species (Jülich 1978; Ginns & Freeman 1994). As redefined in phylogenetic studies, it belongs to the family Stereaceae of the Russulales and encompasses crust-like fungi with clamped hyphae, long and deeply rooted gloeocystidia, as well as narrowly ellipsoid or cylindrical, smooth, strongly amyloid basidiospores (Larsson et al. 2004; Larsson 2007). The type species was described from the Italian Alps as growing on twigs of *Alnus alnobetula* subsp. *alnobetula* (= *Alnus viridis*) (Bresadola 1898).

Two European representatives of *Megalocystidium*, *M. leucoxanthum* (Bres.) Jülich, and *M. luridum* (Bres.) Jülich have been described in the literature as morphologically differentiated mainly due to the basidiospore length (above

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10 µm and under 10 µm, respectively) and host preferences (*Alnus* or *Salix* for *M. leucoxanthum* versus mainly *Fagus* for *M. luridum*) (Bourdot & Galzin 1927; Eriksson & Ryvarden 1975; Bernicchia & Gorjón 2010). However, identity of North European specimens collected mostly from wood of Salicaceae and having basidiospores of an intermediate size has been interpreted in two different ways. Litschauer (in herb.) was apt to associate *Corticium leucoxanthum* (as *Gloeocystidium leucoxanthum* (Bres.) Höhn. & Litsch.) with specimens found on *A. alnobetula* in the subalpine zone of Europe. In turn, he labelled the problematic North European material as *Gloeocystidium luridum* (Bres.) Höhn. & Litsch. (see Eriksson & Ryvarden 1975). Litschauer's viewpoint was accepted by Eriksson (1958). On the other hand, Parmasto (1968) and Eriksson & Ryvarden (1975) assigned the North European collections to *Gloeocystidiellum leucoxanthum* (Bres.) Donk (= *M. leucoxanthum*) although they stressed morphological variability of the latter species. No attempts to verify these hypotheses with the use of phylogenetic methods have so far been performed.

In the present paper, we revise the taxonomy of the *M. leucoxanthum–M. luridum* complex in temperate–boreal Eurasia based on morphological, ecological/geographic, and DNA data. Additionally, we provide new evidence on the taxonomic position of *Aleurodiscus diffissus* (Sacc.) Burt.

MATERIAL AND METHODS

Morphological study

Type material and specimens from herbaria H, S, O, GB, LE, PRM, TAAM, and OULU were studied. Herbarium acronyms are given according to Thiers (continuously updated). All measurements were made from microscopic slides mounted in Cotton Blue and Melzer's reagent (IKI), using phase contrast and oil immersion lens (Leitz Diaplan microscope, 1250× amplification). The following abbreviations are used in morphological descriptions: L – mean basidiospore length in the specimen measured, W – mean basidiospore width in the specimen measured, Q – mean length/width ratio in the specimen measured, n – number of measurements per specimens measured.

DNA extraction, amplification, and sequencing

DNA extractions were performed from small fragments of herbarium specimens using the NucleoSpin Plant II Kit (Macherey-Nagel GmbH and Co. KG, Düren, Germany) according to the manufacturer's protocols. The following primers were used for both amplification and sequencing: the primers ITS1F and ITS4B (Gardes & Bruns 1993) for the ITS1-5.8S-ITS2 region, primers EF1-983F and EF1-1567R (Rehner & Buckley 2005) for a part of the *tef1* region, and primers LROR-LR5 (White et al. 1990; Vilgalys & Hester 1990) for D1-D3 domains of the nrLSU region. Purification of the PCR products was done with the GeneJET PCR Purification Kit (Thermo Fisher Scientific, Lithuania). Sequencing was performed with an ABI model 3130 Genetic Analyzer (Applied Biosystems, CA, USA). The raw data were edited and assembled in MEGA v.7 (Kumar et al. 2016).

Phylogenetic analyses

For this study, 30 nrITS, six nrLSU, and 24 *tef1* sequences were generated. Additionally, four nrITS (containing ITS1, 5.8S, and ITS2 regions) and three nrLSU sequences of *Megalocystidium* spp. were retrieved from GenBank (table 1). We constructed four datasets: nrITS + nrLSU, nrITS, nrITS + *tef1*, and *tef1* datasets. Sequences were aligned with the MAFFT v.7 web tool (http://mafft.cbrc.jp/alignment/server/) using the Q-INS-i option and adjusted manually.

Phylogenetic reconstructions were performed with Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. Before the analyses, the best-fit substitution model for each alignment was estimated based on the Akaike Information Criterion (AIC) using the FindModel web server (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). The GTR model was chosen for all datasets. Maximum likelihood analysis was run on RAxML servers, v.0.9.0 (Kozlov et al. 2019) with 1000 rapid bootstrap replicates. Bayesian analyses was performed with MrBayes v.3.2.5 software (Ronquist et al. 2012), for two independent runs, each with 5 million generations, under described model, and four chains with sampling every 100 generations. To check for convergence of the MCMC analyses and to get estimates of the posterior distribution of parameter values, Tracer v.1.6 was used (Rambaut et al. 2014). We accepted the result where the ESS (Effective Sample Size) was 9782 for nrITS dataset, 11435 for nrITS + nrLSU dataset, 11303 for nrITS + *tef1* dataset, and 14736 for *tef1* dataset, and the PSRF (Potential Scale Reduction Factor) was close to 1.

Newly generated sequences have been deposited in GenBank with corresponding accession numbers (table 1). Sequenced specimens are marked in the Taxonomic Treatment by an asterisk.

RESULTS

Phylogeny

Four datasets were prepared and analyzed for the present study: (1) nrITS + nrLSU dataset for the family Stereaceae (Russulales), (2) nrITS only dataset, (3) *tef1* only dataset, and (4) combined nrITS + *tef1* dataset for defining species limits in the *Megalocystidium leucoxanthum* complex.

(1) nrITS + nrLSU dataset for ten genera accepted in Stereaceae (as outlined by Larsson et al. 2004 and Larsson 2007). The final alignment contained 1696 characters (including gaps). The overall topologies of the ML and BI trees were identical and recovered *Aleurodiscus diffissus* (Sacc.) Burt as a member of a strongly supported *Megalocystidium* clade (BS = 99, PP = 1) (fig. 1). The latter species was first introduced as *Peniophora diffissa* (Saccardo 1889) and then moved to *Aleurodiscus* due to the presence of acanthophyses, sterile hymenial cells with characteristic thorn-like outgrowths. However, this feature alone is not enough for justifying generic limits in Stereaceae because acanthophyses have been detected in almost all other genera of this family. Otherwise, *A. diffissus* is microscopically highly similar to *M. leucoxanthum* and *M. luridum*, and therefore we combine it in *Megalocystidium*.

Table 1 – Sequences of *Megalocystidium* spp. used in the present study.

Species	Specimen (herbarium) / culture	Origin (ISO 3166 code)	Host	GenBank numbers			Source
				nrLSU	nrITS	*tef1*	
M. diffissum	*Spirin 4244* (H)	RU-KHA	*Rhododendron dauricum*	MT477147	MT477147	–	this study
M. diffissum	*Spirin 5603* (H)	RU-KHA	*R. dauricum*	–	MT359925	MT366835	this study
M. leucoxanthum	*Boidin 1088* / CBS 269.54	FR	*Alnus alnobetula* subsp. *alnobetula*	MH868866	MH857325	–	Vu et al. (2019)
M. leucoxanthum	*Kotiranta 13164* (H)	IT	*A. alnobetula* subsp. *alnobetula*	–	MT359928	–	this study
M. leucoxanthum	*Spirin 7601* (H)	RU-KHA	*A. alnobetula* subsp. *fruticosa*	–	MT359923	MT366837	this study
M. leucoxanthum	*Kotiranta 26429a* (H)	RU-KRA	*Alnus hirsuta*	–	MT359931	MT366830	this study
M. leucoxanthum	*Spirin 13963* (H)	SI	*A. alnobetula* subsp. *alnobetula*	–	MW433691	MW448570	this study
M. luridum	*Boidin 771* / CBS 270.54	FR	–	MH868867	MH857326	–	Vu et al. (2019)
M. luridum	*Marstad 16/15* (O)	NO	hardwood	MT477150	MT477150	MT873029	this study
M. luridum	*Marstad 71/14* (O)	NO	hardwood	MT477149	MT477149	MT873028	this study
M. luridum	*Stalpers 161* / CBS 106.71	DE	*Quercus* sp.	–	MH860024	–	Vu et al. (2019)
M. olens	*Stalpers 1155* / CBS 454.86	BE	*Alnus* / *Corylus*	MH873677	MH861985	–	Vu et al. (2019)
M. olens	*Miettinen 14695.4* (H)	FI	*Salix caprea*	–	MT675934	MT892888	this study
M. olens	*Spirin 12456* (O)	NO	*Populus tremula*	MT477152	MT477152	MT873031	this study
M. olens	*Spirin 4701* (H)	RU-NIZ	*S. caprea*	–	MT359921	MT366839	this study
M. olens	*Spirin 10652* (H)	RU-NIZ	*S. caprea*	–	MT359933	–	this study
M. olens	*Spirin 11299* (H)	RU-NIZ	*Betula pendula*	–	MT675936	MT892887	this study
M. olens	*Spirin 11976* (H)	RU-NIZ	*Acer platanoides*	–	MT359935	–	this study
M. olens	*Volobuev s.n.* (LE286917)	RU-ORL	*A. platanoides*	–	MT359930	MT366831	this study
M. pellitum	*Kotiranta 26023* (H)	RU-KRA	*A. hirsuta*	–	MT359927	MT366833	this study
M. pellitum	*Spirin 7574* (H)	RU-KHA	*A. alnobetula* subsp. *fruticosa*	–	MT359926	MT366834	this study
M. perticatum	*Kotiranta 26667* (H)	RU-TY	*Salix* sp.	–	MT359924	MT366836	this study
M. perticatum	*Spirin 5474* (H)	RU-KHA	*Salix schwerinii*	–	MT359920	MT366840	this study
M. perticatum	*Spirin 11880* (H)	RU-LEN	*S. caprea*	–	MT359934	MT366828	this study
M. salicis	*Kulju 1/03* (OULU)	FI	*Salix* sp.	–	MT675935	–	this study
M. salicis	*Gabrielsen* 10.VIII.2018 (O)	NO	*Salix* sp.	–	MT359936	MT366827	this study
M. salicis	*Ryvarden 50314* (O)	NO	*Betula tortuosa*	MT477148	MT477148	–	this study
M. salicis	*Spirin 12098* (O)	NO	*Salix nigricans*	–	MT444030	MT444121	this study
M. salicis	*Spirin 10093* (H)	RU-LEN	*Salix myrsinifolia*	–	MT359929	MT366832	this study
M. salicis	*Spirin 10137* (H)	RU-LEN	*P. tremula*	–	MT359932	MT366829	this study
M. salicis	*Spirin 11883* (H)	RU-LEN	*S. caprea*	–	MT359938	MT366825	this study
M. salicis	*Spirin 11933* (H)	RU-LEN	*S. caprea*	–	MT359937	MT366826	this study
M. salicis	*Spirin 6512* (H)	RU-PRI	*Salix cardiophylla*	–	MT359922	MT366838	this study
M. salicis	*Westerberg* 6.XI.2017 (GB)	SE	*Salix* sp.	MT477151	MT477151	MT873030	this study

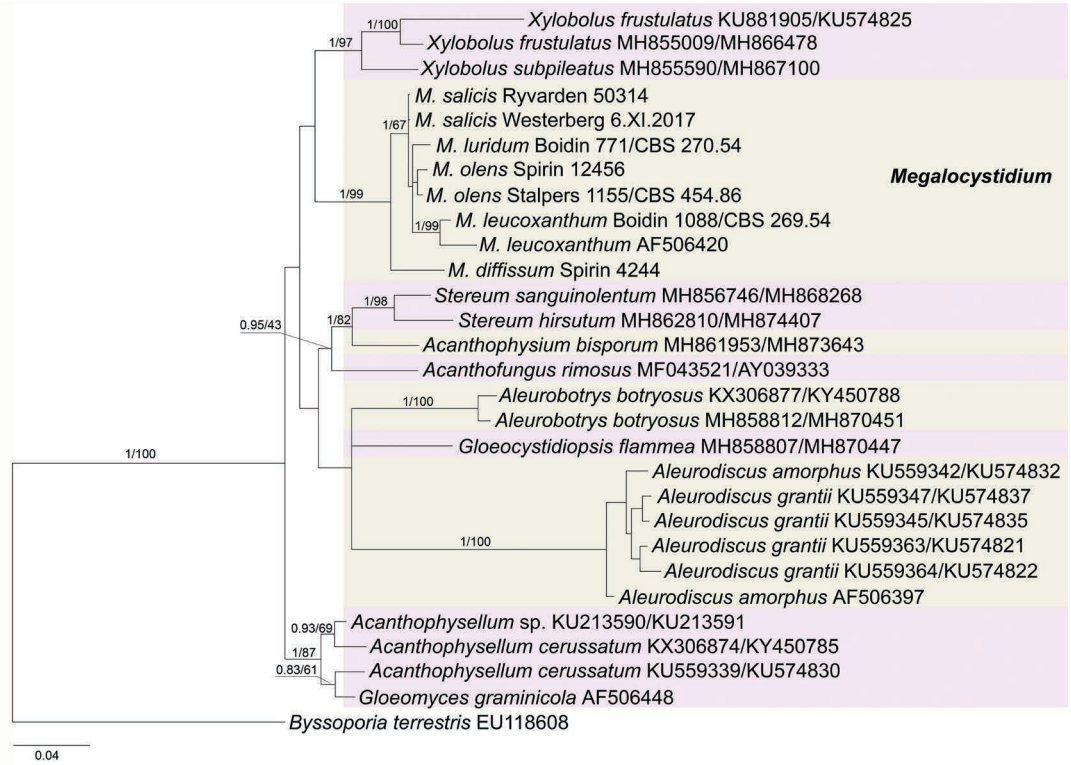

Figure 1 – Combined phylogenetic nrITS + nrLSU topology from Bayesian Inference showing main lineages within Stereaceae. GenBank accession numbers (or collection numbers of newly sequenced specimens) are given for all sequences. Support values (PP/BS) are given above the branches. Scale bar shows expected changes per site.

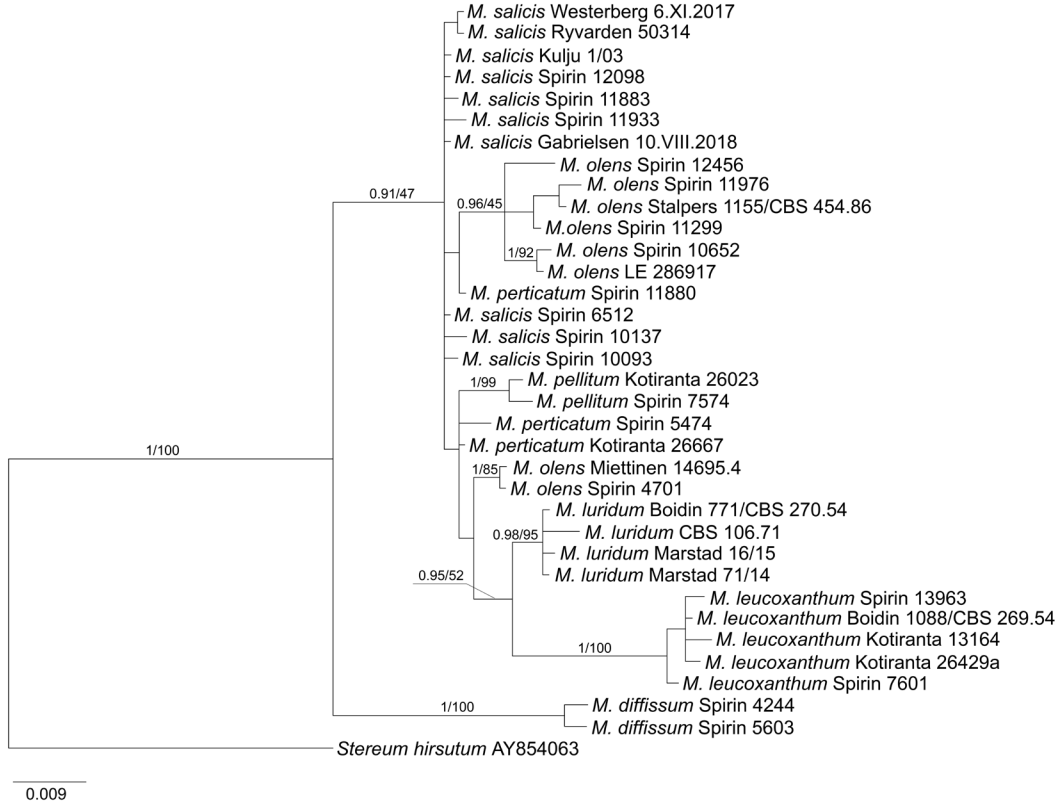

Figure 2 – Phylogenetic nrITS topology from Bayesian Inference showing main lineages within the *Megalocystidium* clade. Collection numbers of newly sequenced specimens are given for all sequences. Support values (PP/BS) are given above the branches. Scale bar shows expected changes per site.

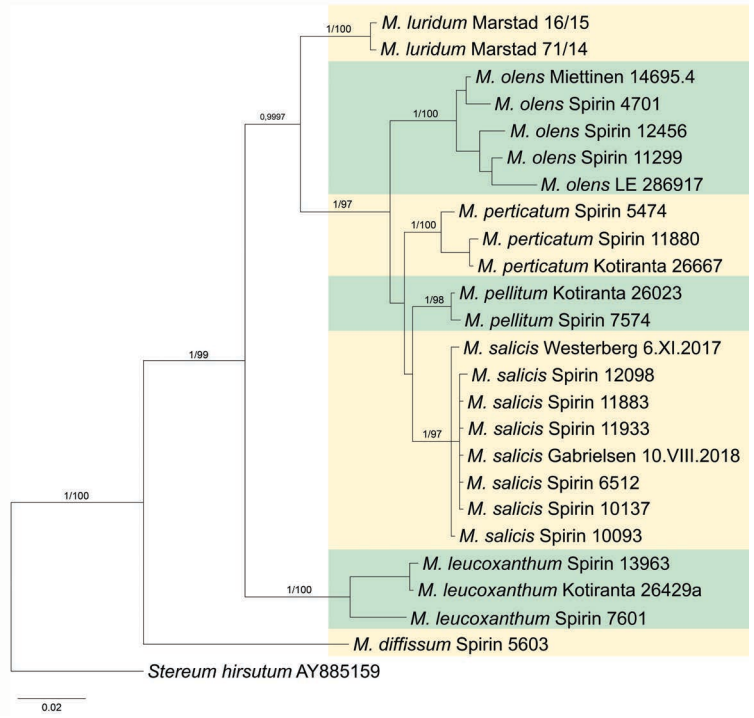

Figure 3 – Phylogenetic *tef1* topology from Bayesian Inference showing main lineages within the *Megalocystidium* clade. Collection numbers of newly sequenced specimens are given for all sequences. Support values (PP/BS) are given above the branches. Scale bar shows expected changes per site.

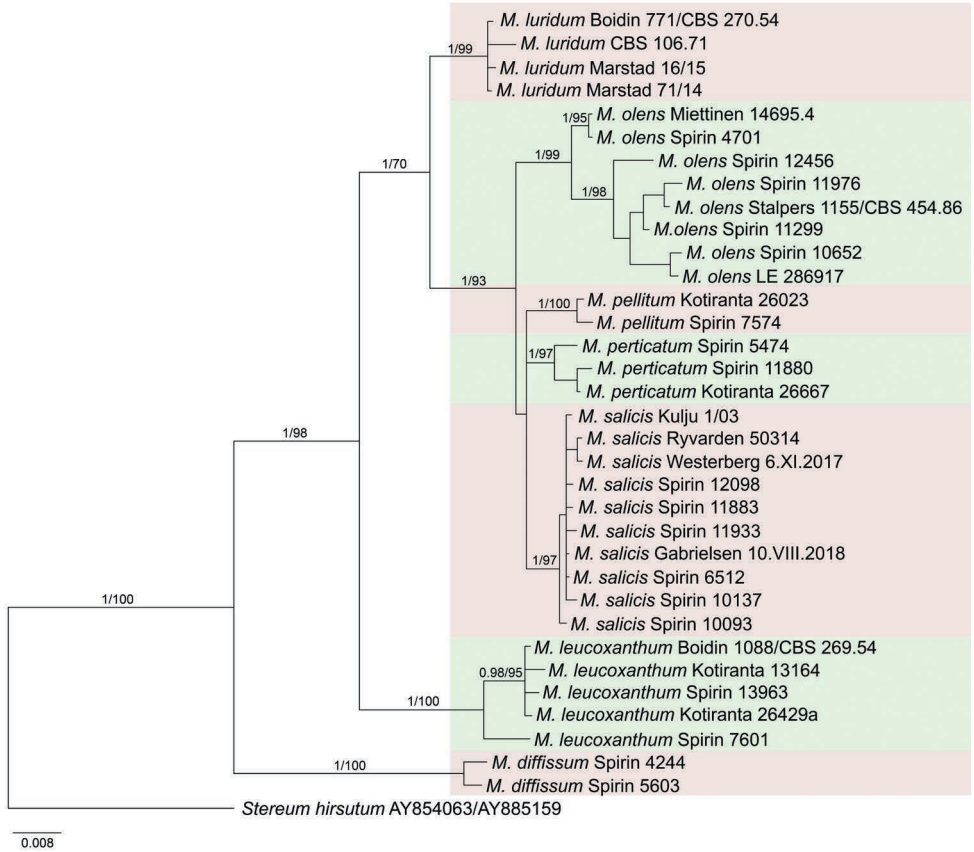

Figure 4 – Combined phylogenetic nrITS + *tef1* topology from Bayesian Inference showing main lineages within the *Megalocystidium* clade. Collection numbers of newly sequenced specimens are given for all sequences. Support values (PP/BS) are given above the branches. Scale bar shows expected changes per site.

(2) ITS only dataset for *Megalocystidium* spp. The final alignment contained 776 characters (including gaps). The overall topologies of the ML and BI trees clearly divided all included specimens in two strongly supported groups, i.e. *Megalocystidium diffissum* clade and *M. leucoxanthum–luridum* clade. Within the latter one, two strongly supported lineages corresponding to *M. leucoxanthum* s.s. (i.e. containing *Alnus*-dwelling specimens from subalpine or subarctic areas) and *M. luridum* were detected (fig. 2). However, the rest of ITS sequences derived mainly from specimens collected from *Salix* spp. do not group into well-supported clades. Morphological and genetic variability of this lineage prompted us to use one more marker (*tef1*).

(3) *tef1* only dataset for *Megalocystidium* spp. The final alignment contained 595 characters (including gaps). The overall topologies of the ML and BI trees were identical. They split the aforementioned *M. leucoxanthum–luridum* clade into six strongly supported lineages that we taxonomically interpret as separate species (fig. 3). This interpretation is supported by morphological (both macroscopic and anatomical), ecological (host specificity) and, to some degree, geographic data as discussed below. Four of these species (*M. olens*, *M. pellitum*, *M. perticatum*, and *M. salicis*) are described as new to science.

(4) combined nrITS + *tef1* dataset for *Megalocystidium* spp. The final alignment contained 1371 characters (including gaps). The overall topologies of the ML and BI trees were identical and they support our conclusions based on *tef1* only dataset (fig. 4).

Morphology, ecology, and geography

In the *M. leucoxanthum–luridum* complex, only one species, *M. luridum*, can without doubt be identified based on the single character, i.e. short basidiospores. Recognizing the other five species requires exact information about host tree species and meticulous morphological study. Two species presented below, *M. leucoxanthum* s.s. and *M. pellitum*, occur exclusively on wood of *A. alnobetula* in mountains and subarctic areas of Eurasia and subarctic zone of North-East Asia and North America – only exceptions in our material are one record for each species from *A. hirsuta* in Siberia. They possess rather thick basidiocarps with a well-developed subiculum, and long basidiospores when compared with other species in the complex. The three remaining species prefer to grow on wood of Salicaceae. Of them, *M. olens* produces insignificant, soft basidiocarps with a few gloeocystidia in the hymenial layer, and it certainly has a southern distribution (supplementary file 1). In turn, *M. perticatum* and *M. salicis* occur mainly in areas with cooler climate; they have more prominent and compact fructifications with easily detectable gloeocystidia, and they can be separated due to different basidiospore length.

TAXONOMIC TREATMENT

Megalocystidium diffissum (Sacc.) K.H.Larss. & Spirin, **comb. nov.** (figs 5–7) – *Peniophora diffissa* Sacc., *Bulletin de la Société Royale de Botanique de Belgique* 28: 79. 1889 (Saccardo 1889: 79) – Type: Table 4, figure 2 in *Bulletin de la Société Royale de Botanique de Belgique* 28, 1889; **designated here** (MBT395620).

MB838476

Aleurodiscus sajanensis Murashk. ex Pilát (Pilát 1931: 328) – Type: RUSSIA • 'Sayany'; *Rhododendron dauricum*; 11 Jul. 1927; *Murashkinsky*; holotype: PRM[PRM 650773].

Description – Basidiocarps perennial, resupinate, pulvinate-frustulate, gregarious, 1.5–4 mm in diam., 0.2–0.5 mm thick, tough. Margin abruptly delimited from the substrate, elevated, fuscous to black. Hymenial surface first cream-coloured or beige, later ochraceous to brownish, in senescent basidiocarps dark brown, in young basidiocarps more or less even, in older ones irregularly cracking and tuberculate. Hyphal structure monomitic; hyphae clamped, thin- to moderately thick-walled, 3.5–5 μm in diam., slightly dextrinoid. Gloeocystidia clavate to moniliform, thin- to distinctly thick-walled, 56–95 × 6–9.5 μm. Acanthophyses numerous, clavate, subulate to bottle-shaped, in upper part with abundant acute protuberances, thin- to moderately thick-walled, 43–68 × 6–10.5 μm (n = 10/1), slightly dextrinoid. Basidia clavate, 75–100 × 7–10 μm. Basidiospores hyaline, thin-walled, cylindrical, (12.3–)12.8–18.2(–18.4) × (4.5–)4.7–7.0(–7.3) μm (n = 90/3), L = 14.60–15.06, W = 5.56–5.68, Q = 2.64–2.68.

Distribution – Asia (Siberia, Russian Far East) (supplementary file 1).

Habitat and ecology – Dead, corticated, usually still attached branches of *Rhododendron dauricum.*

Additional material examined – RUSSIA – **Altai Republic** • Shebalino Dist., Ust-Sema; 13 Aug. 1985; *Alanko 52462*; H. – **Khabarovsk Region** • Khabarovsk Dist., Malyi Kukachan; 18–19 Aug. 2012; *Spirin 5368*, *5377*, *5417*; H • Khabarovsk Dist., Levyi Ulun; 22–25 Aug. 2012; *Spirin 5493*, *5603**, *5612*; H • Khabarovsk Dist., Ulun; 26 Aug. 2012; *Spirin 5677*; H • Komsomolsk Dist., Boktor; 18 Aug. 2013; *Spirin 6136*; H • Solnechnyi Dist., Suluk-Makit; 19–21 Aug. 2011; *Spirin 4220*, *4244**; H • Solnechnyi Dist., Sonakh; 15 Aug. 2014; *Spirin 7300*; H • Ulchsky Dist., Sofiisk; 7 Aug. 1982; *Parmasto*; H ex TAAM 104672. – **Primorie Region** • Krasnoarmeiskii Dist., Valinku; 26 Aug. 2013; *Spirin 6390*; H. All records on *Rhododendron dauricum*.

Notes – Saccardo (1889) described this species as *Peniophora diffissa* based on a single specimen collected by Nikolai Martiyanov in Siberia, seemingly in the present-day Krasnoyarsk Region. The collection was evidently sterile but its identity is doubtless due to the peculiar basidiocarp shape, presence of acanthophyses, and the specific host (*Rhododendron dauricum*). We could not trace any authentic material of *P. diffissa* in public herbaria, and therefore we select Saccardo's illustration as a lectotype of this species. The holotype of *Aleurodiscus sajanensis* (Pilát 1931) was collected in the same geographic area as *P. diffissa* and agrees perfectly with the protologue of the latter species and our newly collected specimens.

Megalocystidium diffissum is one of the most common species inhabiting dead but still attached branches of *Rhododendron dauricum* in the mountain regions of East Asia. Its basidiocarps die soon after branches are detached.

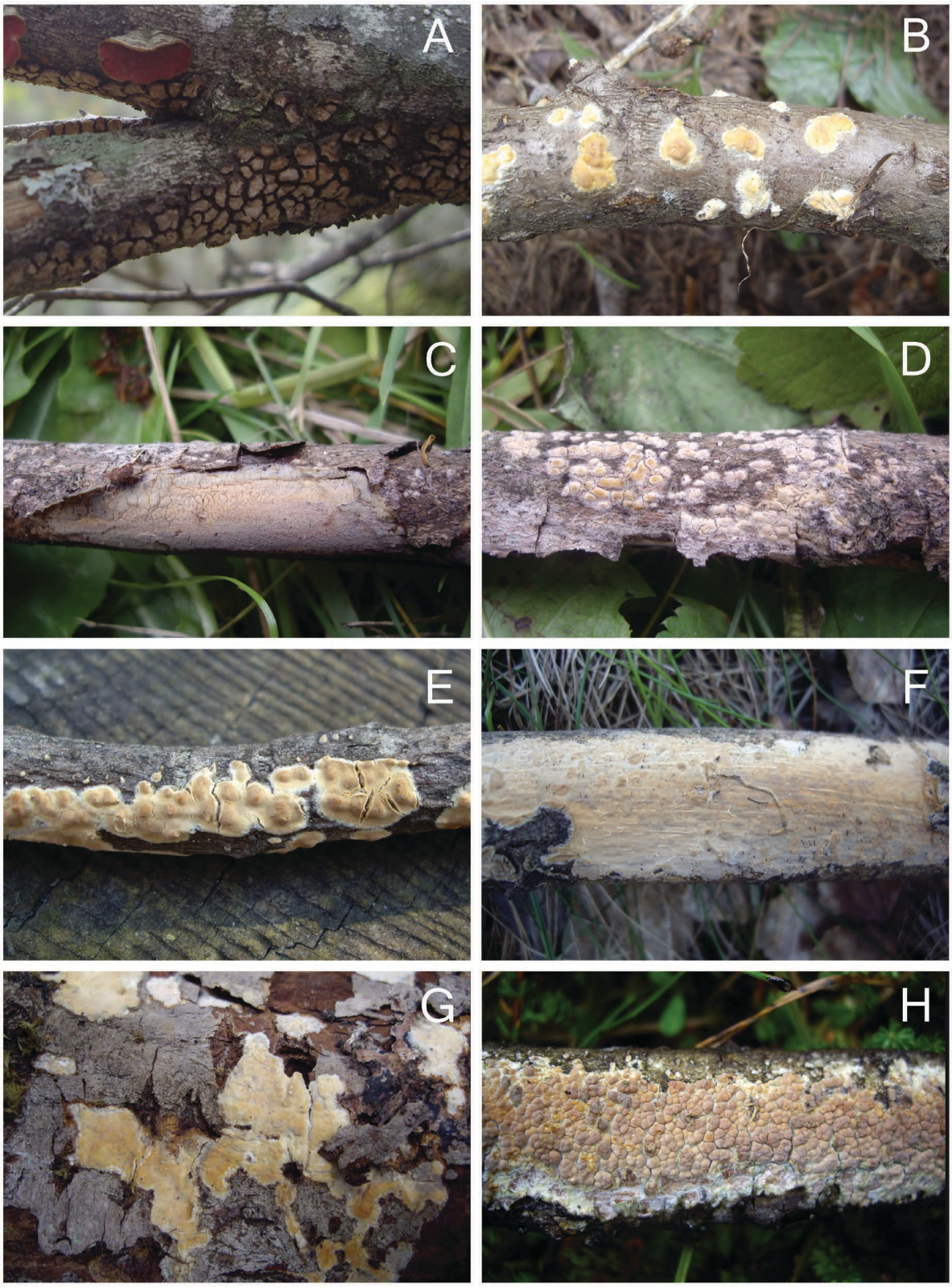

Figure 5 – Basidiocarps of *Megalocystidium* spp. **A**. *Megalocystidium diffissum* (with *Hymenochaete sphaericola*) (*Spirin 5493*). **B**. *Megalocystidium leucoxanthum* (*Spirin 12637*). **C**. *Megalocystidium olens* (*Spirin 12976*), continuous basidiocarp. **D**. *Megalocystidium olens* (*Spirin 12976*), frustulate basidiocarps. **E**. *Megalocystidium pellitum* (holotype). **F**. *Megalocystidium perticatum* (holotype). **G**. *Megalocystidium salicis* (*Spirin 11933*), mature basidiocarp. **H**. *Megalocystidium salicis* (*Spirin 12098*), senescent basidiocarp with strongly tuberculate hymenial surface.

It usually grows together with *Hymenochaete sphaericola* Lloyd, another primary decomposer of the *Rhododendron* wood. No verified records of *M. diffissum* exist from other hosts, and the identity of the North American collections so labelled deserve a closer study.

Megalocystidium leucoxanthum (Bres.) Jülich (Jülich 1978: 140) (figs 5–7) – Type: ITALY – **Trentino** – **Alto Adige** • Pejo; '*Alnus viridis*' [=*Alnus alnobetula* subsp. *alnobetula*]; Aug. 1892; *Bresadola s.n.*; lectotype: S[S F367903], **designated here**; isolectotype: GB (MBT395621).

Description – Basidiocarps annual or persistent, resupinate, first orbicular or frustulate, then fusing and producing crustaceous fructifications, 0.5–10 cm in widest dimension, 0.3–1 mm thick, leathery. Margin abruptly delimited from the substrate, adnate, 0.5–1 mm wide, first white, in older basidiocarps concolorous with the hymenial surface. Subiculum white, leathery, 0.1–0.2 mm thick. Hymenial surface cream-coloured to beige or ochraceous-brownish, often distinctly tuberculate, irregularly cracking with age. Smell weak, anise-like, or absent. Hyphal structure monomitic; hyphae clamped, 4–5(–5.5) µm in diam., thin- to moderately thick-walled in subhymenium, thick-walled (wall up to 2 µm thick) in subiculum. Gloeocystidia usually moniliform, rarely clavate, thin- to clearly thick-walled, 60–120 × 7–8.5 µm. Hyphidia simple or bi- or trifurcate, rare, embedded in or slightly projecting above the hymenial layer, 4–5.5 µm in diam. Basidia clavate, 45–68 × 8–11 µm. Basidiospores hyaline, thin-walled, cylindrical to narrowly ellipsoid, (12.8–)13.1–18.1(–18.2) × (4.7–)4.9–7.2(–8.0) µm (n = 120/4), L = 14.54–16.81, W = 5.66–6.51, Q = 2.47–2.61.

Distribution – Europe (Austria, France, Italy, Liechtenstein, Slovenia, Switzerland), Asia (Siberia, Russian Far East), North America (Canada) (supplementary file 1).

Habitat and ecology – Dead, corticated, usually still attached branches of *Alnus alnobetula* (once found on *Alnus hirsuta*) in subalpine or subarctic communities.

Additional material examined – AUSTRIA – **Tyrol** • Stubaier Alpen; *A. alnobetula* subsp. *alnobetula*; *Litschauer* (Kryptogamae Exsiccatae #3009); H.

CANADA – **Newfoundland and Labrador** • Newfoundland, White Bay; *A. alnobetula* subsp. *crispa*; 8 Sep. 2011; *Ryvarden 48774*; O[O F505487]. – **Quebec** • Nunavik, Poste-de-la-Baleine; *A. alnobetula* subsp. *crispa*; 23 Jul. 1982; *Niemelä 2513*, *2516*; H • Nunavik, Poste-de-la-Baleine; *A. alnobetula* subsp. *crispa*; 12 Aug. 1982; *Niemelä 2754*; H.

ITALY – **Trentino – Alto Adige** • Trento; *A. alnobetula* subsp. *alnobetula*; Aug. 1895; *Bresadola s.n.*; H • Trento, Bolzano; *A. alnobetula* subsp. *alnobetula*; 10 Sep. 1997; *Kotiranta 13164**; H.

LIECHTENSTEIN – **Triesen** • Lawena; deciduous tree (fallen twig); Aug. 1980; *Waldburger s.n.*; O[O F903111].

RUSSIA – **Chukotka** • Anadyr; *A. alnobetula* subsp. *fruticosa*; 8 Aug. 2009; *Kotiranta 26953*; H. – **Khabarovsk Region** • Verkhnebureinskii Dist., Dublikan Nat. Res.; *A. alnobetula* subsp. *fruticosa*; 20 Aug. 2014; *Spirin 7601**, *7703*; H • Verkhnebureinskii Dist., Hegdy, *A. alnobetula* subsp. *fruticosa*; 22 Aug. 2014; *Spirin 7843*; H. – **Krasnoyarsk Region** • Turukhansk Dist., Lebed'; *Alnus hirsuta*; 23 Aug. 2013; *Kotiranta 26429a**; H. – **Yakutia** • Anabar Dist., Saskylach; *A. alnobetula* subsp. *fruticosa*; 2 Aug. 1972; *Parmasto*; H ex TAAM[TAAM 56047, 56592] • Moma Dist., Honuu; *A. alnobetula* subsp. *fruticosa*; 23 Aug. 1972; *Parmasto*; H ex TAAM[TAAM 56720] • Nizhnekolymsk Dist., Cherski; *A. alnobetula* subsp. *fruticosa*; 18 Aug. 1972; *Parmasto*; H ex TAAM[TAAM 45832, 45835, 56629, 56634].

SLOVENIA – **Gorenjska** • Krnica, Lipanca; *A. alnobetula* subsp. *alnobetula*; 6 Jun. 2019; *Grebenc & Spirin 12637*; H • Krnica, Lipanca; *A. alnobetula* subsp. *alnobetula*; 29 Jul. 2020; *Spirin 13963**; H.

SWITZERLAND – **Schwyz** • Rigi; 3 Feb. 1979; *Baici*; O[O F903112].

Notes – According to our results, *M. leucoxanthum* is a species inhabiting dead, often still attached branches of *A. alnobetula* in subalpine and subarctic zones. It was found once on *A. hirsuta* but this record comes from an area where *A. alnobetula* is present, too. We interpret this finding as an accidental host change. Macroscopically, *M. leucoxanthum* is indistinguishable from *M. pellitum* but the latter species can be easily recognized due to clearly larger basidia and wider basidiospores. Microscopically, *M. leucoxanthum* is almost identical to *M. perticatum*. However, *M. perticatum* produces thinner basidiocarps with an indistinct subicular layer and it occurs on *Salix* spp.

Eriksson (in Eriksson & Ryvarden 1975) studied and depicted original material from the Bresadola collection at S but did not give any details on the specimen. From a fragment preserved in GB we know that the specimen Eriksson studied and called type specimen is the one we here select as lectotype. Ginns & Freeman (1994) referred to another specimen from herb S as the type but a specimen with the label information they reported ("Italy: Alpes, viii.1894, *G. Bresadola s.n.*") does not exist in S, neither in FH where an isotype should be stored according to them. It is not possible to decide what material Ginns & Freeman studied and we therefore regard their selected type as lost.

Megalocystidium luridum (Bres.) Jülich (Jülich 1978: 140) – Type: ITALY – **Tuscany** • Florence; hardwood; 1892; *Martelli s.n.*; lectotype: S[S F119263], designated by Burt (1926: 272).

Description – Basidiocarps annual or persistent, resupinate, crustaceous, up to 10 cm in widest dimension, 0.1–0.5 mm thick, compact. Margin abruptly delimited from the substrate, adnate, up to 0.5 mm wide, first white, in older basidiocarps concolorous with hymenial surface. Hymenial surface first cream-coloured to beige, smooth, then pale ochraceous to light brownish, tuberculate, sometimes irregularly cracking. No specific smell. Hyphal structure monomitic; hyphae clamped, 2–3.5 µm in diam., thin- to moderately thick-walled throughout. Gloeocystidia usually gradually tapering, rarely clavate, sometimes moniliform, thin- to slightly thick-walled, 57–112 × 7–14.5(–18) µm. Hyphidia simple or bi- or trifurcate, rare, embedded in or slightly projecting above hymenial layer, 1.5–2 µm in diam. Basidia clavate, 35–57 ×

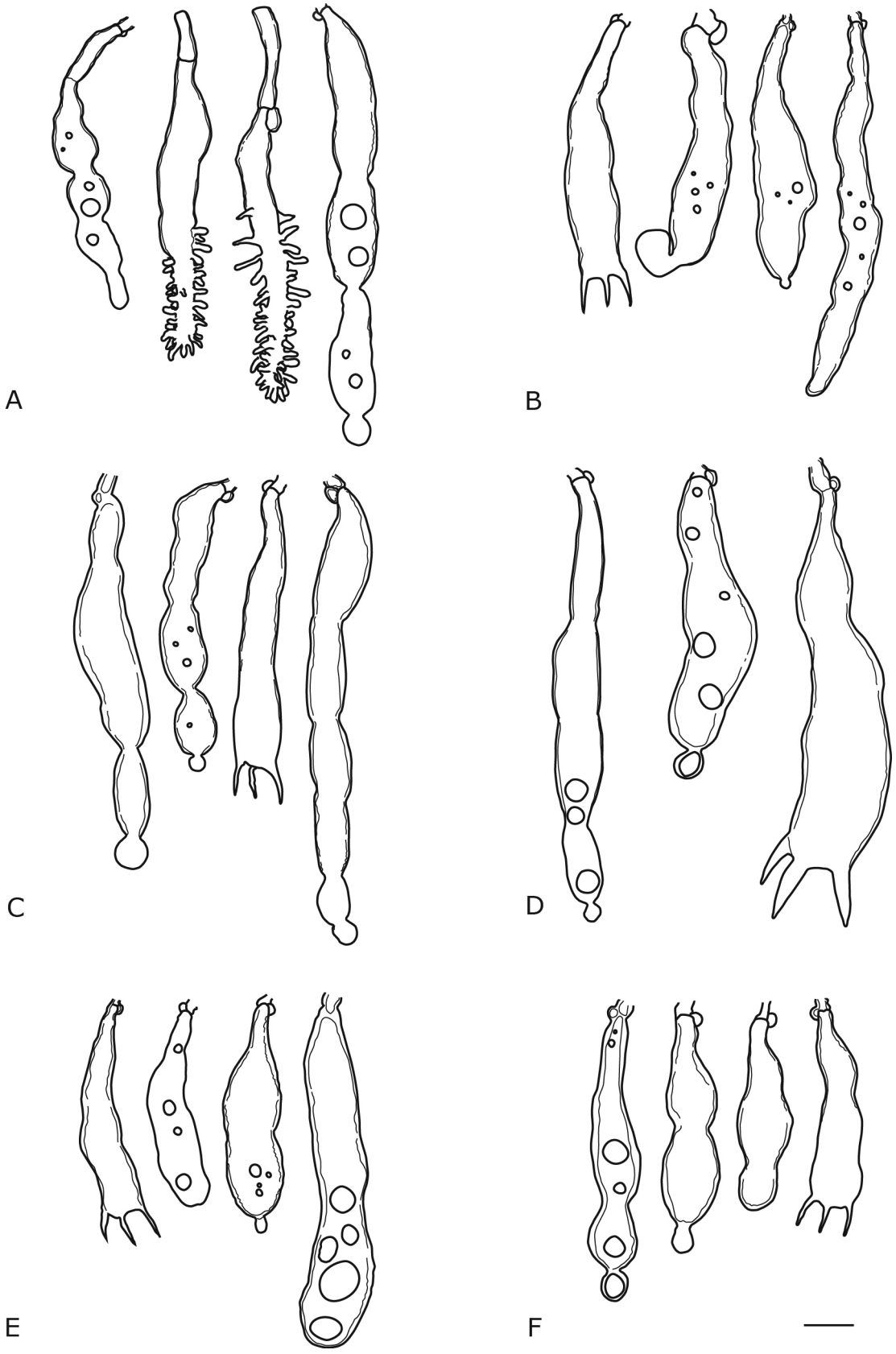

Figure 6 – Hymenial cells (acanthophyses, gloeocystidia, and basidia) of *Megalocystidium* spp. **A**. *Megalocystidium diffissum* (*Spirin 5603*). **B**. *Megalocystidium salicis* (holotype). **C**. *Megalocystidium perticatum* (holotype). **D**. *Megalocystidium pellitum* (holotype). **E**. *Megalocystidium olens* (holotype). **F**. *Megalocystidium leucoxanthum* (*Spirin 7601*). Scale bar = 10 µm.

6.5–9 µm. Basidiospores hyaline, thin-walled, cylindrical to ellipsoid, (7.0–)7.1–10.6(–10.7) × (3.9–)4.0–6.1(–6.2) µm (n = 150/5), L = 8.41–9.07, W = 4.56–5.35, Q = 1.61–1.85.

Distribution – Europe (France, Germany, Italy, Norway, Spain) (supplementary file 1).

Habitat and ecology – Dead wood of deciduous trees in temperate forests.

Additional material examined – FRANCE • *Prunus spinosa*; *Letendre 2029* (herb. *Karsten 1639*, as *Xerocarpus letendrei*); H.

NORWAY – **Vestfold** • Færder, Strengsdal; hardwood; 3 Mar. 2015; *Marstad 16/15**; O • Nøtterøy, Brattås; hardwood; 7 Apr. 2014; *Marstad 71/14**; O.

SPAIN – **Ávila** • Cillán; *Quercus rotundifolia*; 6 Mar. 1977; *Tellería 123/77MT*; H. – **Burgos** • Ordun; *Fagus sylvatica*; 12 Nov. 1977; *Ryvarden 15295*; O F3153, H.

Notes – *Megalocystidium luridum* is a southern species distributed in the temperate zone of Europe. It inhabits dead branches and fallen logs of various deciduous trees. From all other species treated here, it primarily differs in having much shorter, broadly cylindrical or ellipsoid basidiospores. Microscopic structures of *M. luridum* were illustrated in Eriksson & Ryvarden (1975).

Megalocystidium olens Spirin & Volobuev, **sp. nov.** (figs 5–7) – Type: RUSSIA – **Nizhny Novgorod Region** • Lukoyanov Dist., Razino; 54.9105°N, 44.2896°E; *Betula pendula* (fallen corticated branch); 31 Jul. 2017; *Spirin 11299**; holotype: H[H7009380].

MB838471

Diagnosis – Differs from *M. leucoxanthum* in having small-sized, soft basidiocarps, rare gloeocystidia and on average shorter basidiospores 12–16 × 4.5–7.5 µm.

Description – Basidiocarps annual or persistent, resupinate, first orbicular or frustulate, gregarious, a few mm in diam., then fusing to a continuous basidiocarp, membranous, a few cm in widest dimension, 0.3–1 mm thick, soft. Margin adnate, up to 0.5 mm wide, first white, arachnoid, in older basidiocarps compact and more or less concolorous with hymenial surface. Hymenial surface first cream-coloured to beige, smooth, then ochraceous to light reddish-brownish, smooth or indistinctly tuberculate, sometimes irregularly cracking. A distinct anise-like smell always present. Hyphal structure monomitic, clamps present; subicular hyphae loosely interwoven, with thickened walls, 3–5 µm in diam., subhymenial hyphae thin- or only slightly thick-walled, rather loosely arranged and well visible, 2.5–4.5 µm in diam. Gloeocystidia rather rare, normally embedded in the hymenial layer and thus poorly visible, gradually tapering or clavate, some moniliform, occasionally pleural, thin- to slightly thick-walled, 44–119 × (6.5–)7.0–13.5(–14) µm. Hyphidia simple or bi- to trifurcate, rare, embedded in the hymenial layer, 2–4 µm in diam. Basidia clavate, 35–79 × 7.5–11 µm. Basidiospores hyaline, thin-walled, cylindrical, (11.1–)11.8–15.8(–15.9) × (4.2–)4.4–7.7(–8.0) µm (n = 120/4), L = 12.81–14.59, W = 5.32–6.48, Q = 2.11–2.64.

Distribution – Europe (Belgium, Finland, Norway, Russia) (supplementary file 1).

Habitat and ecology – Dead, still attached or just fallen branches of various deciduous trees in temperate–hemiboreal forests.

Etymology – *olens* (Latin, adj.) – smelling, in reference to a distinct anise-like odour of basidiocarps.

Additional material examined – FINLAND – **Uusimaa** • Helsinki, Veräjämäki; *Salix caprea*; 5 Sep. 2011; *Miettinen 14695.4**; H.

NORWAY – **Akershus** • Asker, Esvika; *Populus tremula*; 28 Sep. 2018; *Spirin 12456**; O.

RUSSIA – **Nizhny Novgorod Region** • Lukoyanov Dist., Razino; *Acer platanoides*; 22 Jul. 2018; *Spirin 11976**; H • Lukoyanov Dist., Sanki; *S. caprea*; 14 Jul. 2012; *Spirin 4701** • Lukoyanov Dist., Sanki; *S. caprea*; 11 Aug. 2016; *Spirin 10652**; H. – **Oryol Reg.** • Novoderevenkovsky Dist., Mokhovoe; *A. platanoides*; 24 Jul. 2011; *Volobuev s.n.*; LE[LE286917*] • Znamenskoe Dist., Elenka; *Corylus avellana*; 13 Jul. 2011; *Volobuev s.n.*; LE[LE298532].

Notes – *Megalocystidium olens* produces small-sized, orbicular, gregarious basidiocarps later fusing but rarely exceeding one cm in widest dimension. Insignificant, soft, pale-coloured fructifications with a strong pleasant smell allow an identification already in the field. The species often occurs on thin, corticated, still attached branches of various deciduous trees (*Acer*, *Betula*, *Corylus*, *Populus*, *Salix*), and it seems to be restricted to nemoral and hemiboreal forests of Europe.

Megalocystidium pellitum Spirin & Kotiranta, **sp. nov.** (figs 5–7) – Type: RUSSIA – **Khabarovsk Region** • Verkhnebureinskii Dist., Dublikan Nat. Res.; 50.5173°N, 133.2551°E; *Alnus alnobetula* subsp. *fruticosa* (dead still attached branch); 19 Aug. 2014; *Spirin 7574**; holotype: H[H7009381]; isotype: LE.

MB838473

Diagnosis – Differs from *M. leucoxanthum* in having longer and wider basidiospores 12–21 × 8–12 µm.

Description – Basidiocarps persistent, resupinate, crustaceous, 5–40 mm in diam., 0.5–1 mm thick, leathery. Margin abruptly delimited from the substrate, adnate, 0.5–1 mm wide, first white, in older basidiocarps brownish to almost black. Subiculum white, leathery, 0.1–0.3 mm thick. Hymenial surface cream-coloured to beige or pale ochraceous, smooth or tuberculate, irregularly cracking with age. Young basidiocarps with faint pleasant smell, disappearing in herbarium specimens. Hyphal structure monomitic; hyphae clamped, 4–5(–5.5) µm in diam., thin- to moderately thick-walled in subhymenium, thick-walled (wall up to 2 µm thick) in subiculum. Gloeocystidia usually moniliform, rarely clavate, thin- to clearly thick-walled, 60–120 × 7–8.5 µm. Hyphidia simple or bi- to trifurcate, rare, embedded in or slightly projecting above hymenial layer, 4–5.5 µm in diam. Basidia clavate, 59–104 × 11–16.5 µm. Basidiospores hyaline, thin-walled, ellipsoid to cylindrical, (10.1–)12.3–20.8(–22.9) × (7.7–)8.0–11.8(–12.2) µm (n = 120/4), L = 14.82–18.59, W = 8.78–10.28, Q = 1.58–1.83.

Distribution – Asia (Siberia, Russian Far East), North America (Canada) (supplementary file 1).

Habitat and ecology – Dead, corticated, usually still attached branches of *A. alnobetula* (once found on *A. hirsuta*) in subalpine or subarctic communities.

Etymology – *pellitus* (Latin, adj.) – leathery; referring to the basidiocarp consistency.

Additional material examined – CANADA – **Quebec •** Nunavik, Poste-de-la-Baleine; *A. alnobetula* subsp. *crispa*; 23 Jul. 1982; *Niemelä 2607*; H.

RUSSIA – **Khabarovsk Region •** Khabarovsk Dist., Levyi Ulun; *A. alnobetula* subsp. *fruticosa*; 23 Aug. 2012; *Spirin 5545*, *5552*; H. – **Krasnoyarsk Region •** Evenk Autonomous Dist., Podkamennaya Tunguska; *A. hirsuta*; 7 Aug. 2013; *Kotiranta 26023**; H.

Notes – *Megalocystidium pellitum* is macroscopically identical to *M. leucoxanthum* and has the same host preferences (growing on *A. alnobetula* and exceptionally also on *A. hirsuta*). However, it is a much rarer species distributed in Asia and North America. Microscopically, *M. pellitum* can be easily identified due to the large basidia and basidiospores.

Megalocystidium perticatum Spirin & Volobuev, **sp. nov.** (figs 5–7) – Type: RUSSIA – **Leningrad Region •** Boksitogorsk Dist., Goryun; 59.251°N, 34.933°E; *Salix caprea* (dead corticated stem); 9 May 2018; *Spirin 11880**; holotype: H[H7009383]; isotype: LE.

MB838474

Diagnosis – Differs from *M. leucoxanthum* in having smooth, thin, tough basidiocarps and different host preferences (occurring on *Salicaceae*).

Description – Basidiocarps persistent, resupinate, crustaceous, a few cm in widest dimension, 0.1–0.3 mm thick, tough. Margin adnate, up to 0.5 mm wide, first whitish, pruinose, in older basidiocarps compact and more or less concolorous with hymenial surface. Hymenial surface first cream-coloured to beige, then pale ochraceous, smooth or indistinctly tuberculate, sometimes irregularly cracking. Smell anise-like, often faint, or absent. Hyphal structure monomitic, clamps present; subicular hyphae tightly interwoven or subparallel, with thickened walls, 3–5 µm in diam., subhymenial hyphae thin- or slightly thick-walled,

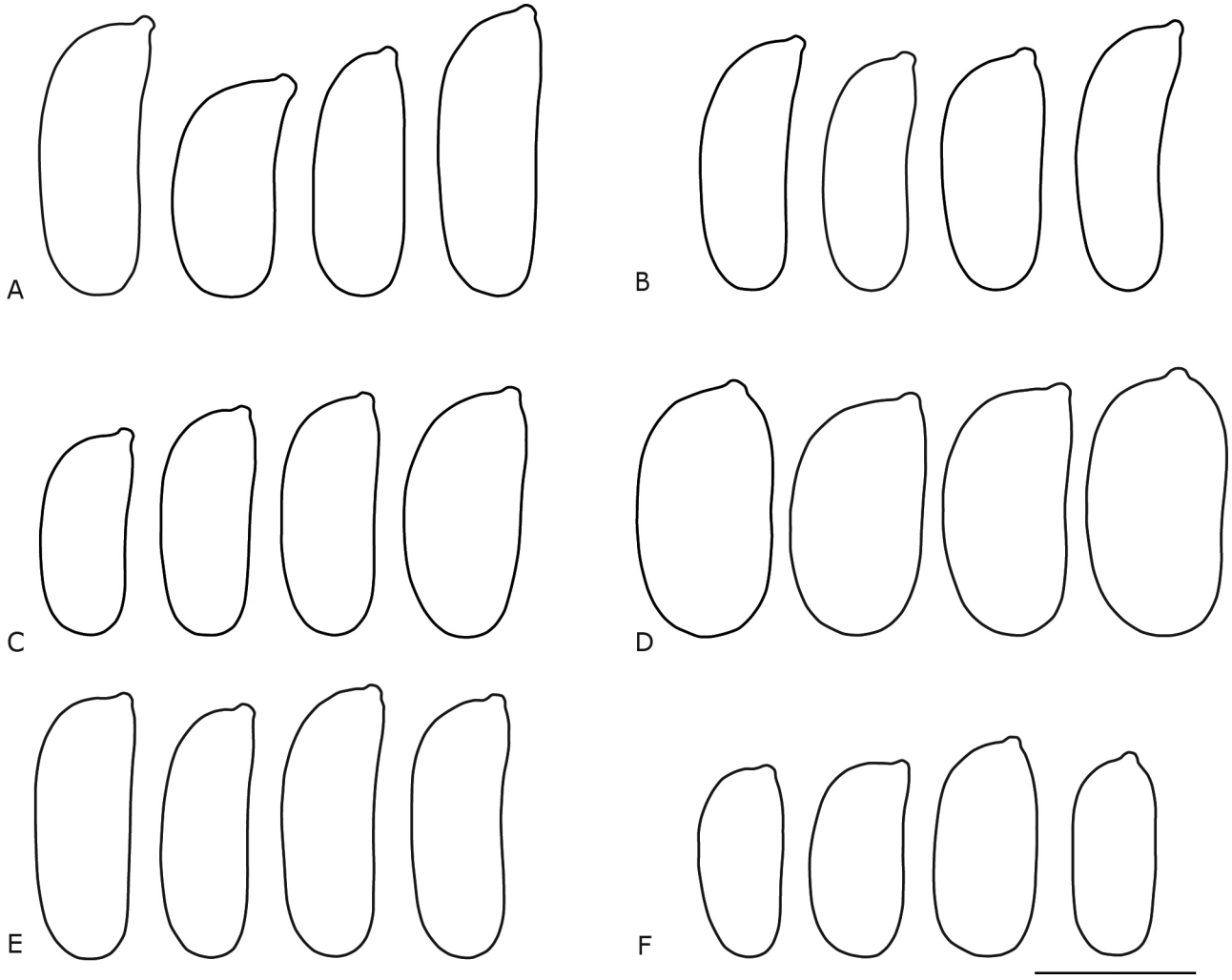

Figure 7 – Basidiospores of *Megalocystidium* spp. **A**. *Megalocystidium diffissum* (*Spirin 4244*). **B**. *Megalocystidium leucoxanthum* (*Spirin 7601*). **C**. *Megalocystidium olens* (holotype). **D**. *Megalocystidium pellitum* (holotype). **E**. *Megalocystidium perticatum* (holotype). **F**. *Megalocystidium salicis* (holotype). Scale bar = 10 µm.

rather tightly arranged, 2.5–4 µm in diam. Gloeocystidia abundant, embedded in or slightly projecting above hymenial layer, moniliform, with 2–3 clear constrictions at the apical part, more rarely tapering-fusiform, predominantly thin-walled, 65–150 × (7.0–)7.5–12(–14) µm. Hyphidia simple or rarely bi- to trifurcate, rare, embedded in hymenial layer, 2–3 µm in diam. Basidia clavate, 55–75 × 7–12 µm. Basidiospores hyaline, thin-walled, cylindrical, occasionally fusiform, (11.0–)11.2–19.2(–19.8) × (4.2–)4.3–7.6(–7.8) µm (n = 150/5), L = 13.72–15.70, W = 5.38–6.31, Q = 2.37–2.83.

Distribution – Europe (Finland, Russia), Asia (Siberia, Russian Far East) (supplementary file 1).

Habitat and ecology – Dead, corticated stems or still attached branches of *Salix* spp. (once found on *P. tremula*) in hemiboreal – boreal forests.

Etymology – *perticatum* (Latin, adj.) – growing on sticks.

Additional material examined – FINLAND – **Kainuu** • Suomussalmi, Juntusranta; *P. tremula*; 11 Nov. 1996; *Möttönen s.n.*; H[H6055539].

RUSSIA – **Khabarovsk Region** • Khabarovsk Dist., Levyi Ulun; *Salix schwerinii*; 21 Aug. 2012; *Spirin 5474**; H. – **Leningrad Region** • Boksitogorsk Dist., Radogoshch; *Salix cinerea*; 20 Aug. 2018; *Spirin 12198*; H. – **Tuva** • Erzin; *Salix* sp.; 14 Aug. 2014; *Kotiranta 26667**; H.

Notes – *Megalocystidium perticatum* is morphologically most similar to *M. salicis*, and it differs from the latter species mainly by thinner basidiocarps with smooth hymenial surface and longer basidiospores. However, senescent individuals of *M. salicis* may produce basidiospores with an average length almost approaching the lowermost limit of the average length in *M. perticatum*. In these critical cases, attention should be paid to macroscopic traits. The old basidiocarps of *M. salicis*, with basidiospores longer than average, are 1–2 mm thick, clearly tuberculate, strongly rimose, and with reddish or reddish-brownish colours. In turn, *M. perticatum* (even when old) has clearly thinner and paler, almost smooth basidiocarps. It seems that *M. perticatum* is much rarer than *M. salicis*, and it is reported here from North Europe (Finland and North-West Russia), Siberia and Russian Far East. It inhabits dead, still corticated branches and stems of *Salix* spp.

Megalocystidium salicis Spirin, Miettinen & K.H.Larss., **sp. nov.** (figs 5–7) – Type: RUSSIA – **Leningrad Region** • Podporozhie Dist., Vazhinka; 61.1426°N, 33.9958°E; *Populus tremula* (recently fallen decorticated branch); 22 May 2016; *Spirin 10137**; holotype: H[H7009382]; isotype: LE.

MB838475

Diagnosis – Differs from *M. leucoxanthum* in having tough, occasionally tuberculate basidiocarps and on average shorter basidiospores 10–16 × 4–7 µm, as well as different host preferences (occurring on Salicaceae).

Description – Basidiocarps persistent, resupinate, crustaceous, a few cm in widest dimension, 0.1–2 mm thick, rather tough, sometimes gelatinized. Margin adnate, up to 1 mm wide in mature basidiocarps, whitish or cream-coloured, compact. Hymenial surface first cream-coloured to greyish, sometimes with bluish tints, smooth, then pale to bright ochraceous-yellow, tuberculate, in senescent basidiocarps reddish, occasionally with brownish tints, tuberculate, strongly cracking. Distinct anise-like smell often present in mature or senescent, deep-coloured basidiocarps. Hyphal structure monomitic, clamps present; subicular hyphae tightly interwoven, with thickened walls, 3–5 µm in diam., subhymenial hyphae thin- or slightly thick-walled, tightly glued together, 2–4 µm in diam. Gloeocystidia present but usually rather rare, embedded in or slightly projecting above hymenial layer, tapering-fusiform or clavate, often with an apical schizopapilla, sometimes slightly moniliform, with 2–3 indistinct constrictions along the whole length, in senescent basidiocarps distinctly monilifrom, with 2–5 constrictions at the apical part, thin- to clearly thick-walled (walls up to 2 µm thick), 48–110 × (6.5–)7–13(–14) µm. Hyphidia simple or rarely bi- to trifurcate, rare, embedded in hymenial layer, 2–3 µm in diam. Basidia clavate, 45–75 × 7.5–12 µm. Basidiospores hyaline, thin-walled, cylindrical to narrowly ellipsoid, (10.1–)10.2–16.0(–16.8) × (4.1–)4.2–7.2(–7.7) µm (n = 300/10), L = 11.16–13.55, W = 4.87–6.30, Q = 2.00–2.52.

Distribution – Europe (Finland, Norway, Russia, Sweden), Asia (Siberia, Russian Far East) (supplementary file 1).

Habitat and ecology – Dead, usually corticated branches or small-sized, fallen logs of *Salix* spp. and *P. tremula* in hemiboreal–boreal forests, rarely on other angiosperms.

Etymology – *salicis* (Latin, adj.) – referring to the growth on wood of Salicaceae.

Additional material examined – FINLAND – **Varsinais-Suomi** • Turku, Ruissalo; *C. avellana*; 26 Aug. 1965; *Laine s.n.*; H. – **Uusimaa** • Helsinki, Toukola, Syyriankatu; *Philadelphus coronarius*; 3 Aug. 2002; *Saarenoksa 00202*; H • Helsinki, Veräjämäki; *P. tremula*; 19 Sep. 2011; *Miettinen 14920.2*; H. – **Etelä-Häme** • Hämeenlinna, Sudenpesänkangas; *Salix* sp.; 26 Sep. 2014; *Spirin 8104*; H. – **Kainuu** • Kuhmo, Teerisuo – Losonsuo; *P. tremula*; 9 Sep. 1990; *Penttilä 1710b*; H. – **Oulun Pohjanmaa** • Oulu, Selkäkari; *Salix* sp.; 22 Feb. 2003; *Kulju 1/03**; OULU[OULU29013].

NORWAY – **Finnmark** • Kautokeino, Øvre Anárjohka Nat. Park; *Betula tortuosa*; 24 Aug. 2017; *Ryvarden 50314**; O • Porsanger, Stabbursdalen Nat. Res.; *Salix phylicifolia*; 10 Aug. 2018; *Spirin 12095*; O, H • Porsanger, Čádjejohka; *Salix nigricans*; 11 Aug. 2018; *Spirin 12098**; O, H • Porsanger, Snekkernes; *Salix* sp.; 10 Aug. 2018; *Gabrielsen et al. s.n.**; O.

RUSSIA – **Khakassia** • Abakan, Erkagi; *Salix viminalis*; 15 Aug. 2011; *Kotiranta 25180*; H. – **Leningrad Region** • Boksitogorsk Dist., Ostrechka; *P. tremula*; 18 Aug. 2018; *Spirin 12164*; H • Boksitogorsk Dist., Kolp'; *Salix myrsinifolia*; 9 May 2016; *Spirin 10093**; H • Boksitogorsk Dist., Goryun; *S. caprea*; 9 May 2018; *Spirin 11883**; H • Boksitogorsk Dist., Radogoshch; *S. caprea*; 20 Aug. 2018; *Spirin 12196*; H • Podporozhie Dist., Oksozero; *P. tremula*; 3 Jun. 2018; *Spirin 11928*; H • Podporozhie Dist., Oksozero; *S. caprea*; 3 Jun. 2018; *Spirin 11933**; H • Podporozhie Dist., Vazhinka; *S. caprea*; 27 May 2017; *Spirin 11218*; H. – **Nizhny Novgorod Region** • Tonshaevo Dist., Okhtarskoe;

Key for the *M. leucoxanthum* complex in temperate–boreal Eurasia

1. Subicular layer of basidiocarps distinct (approximately of the same thickness as hymenial layer), white. On *Alnus* spp. in subalpine or subarctic zones **2**
1'. Subicular layer thin or indistinct. On various hosts except *Alnus* spp. **3**

2. Basidiospores 12.5–21 × 8–12 µm, W = 8.8–10.3. East Asia and North America ..... ***M. pellitum* Spirin & Kotiranta**
2'. Basidiospores 13–18 × 5–7 µm, W = 5.7–6.5. Holarctic species ..... ***M. leucoxanthum* (Bres.) Jülich**

3. Basidiospores broadly cylindrical to ellipsoid, 7–10.5 × 4–6 µm, L = 8.4–9.1. Temperate European species ..... ***M. luridum* (Bres.) Jülich**
3'. Basidiospores cylindrical to broadly cylindrical, L > 10 ..... **4**

4. Basidiocarps membranous, soft, always with a strong anise-like smell. Gloeocystidia embedded, rare and poorly visible. Temperate European species ..... ***M. olens* Spirin & Volobuev**
4'. Basidiocarps crustaceous, tough, anise-like smell present only in thick and deeply coloured basidiocarps. Gloeocystidia abundant or rare, at least some cystidia projecting. Hemiboreal–boreal Eurasian species **5**

5. Mature basidiocarps with a distinct smell. Basidiospores 10–15 × 4–7 µm, L = 11.2–13.6 ..... ***M. salicis* Spirin, Miettinen & K.H.Larss.**
5'. Smell faint or absent. Basidiospores 12–19 × 5–7.5 µm, L = 13.7–15.7 ..... ***M. perticatum* Spirin & Volobuev**

P. tremula; 30 May 2000; *Spirin s.n.*; LE[LE213678] • Vetluga Dist., Vetluga; *Salix* sp.; 19 Aug. 1999; *Spirin s.n.*; LE[LE222984]. – **Primorie Region** • Krasnoarmeiskii Dist., Valinku; *Salix cardiophylla*; 29 Aug. 2013; *Spirin 6512**; H. – **Sverdlovsk Region** • Olenii Ruchii Nat. Park, Bazhukovo; *P. tremula*; 20 Aug. 2002; *Kotiranta 19739*; H.

SWEDEN – **Norrbotten** • Luleå, Karlshäll; *Salix* sp.; 6 Nov. 2017; *Westerberg s.n.**; GB.

Notes – *Megalocystidium salicis* is one of three representatives of the genus occurring on wood of *Salicaceae* in temperate – boreal Eurasia (with a few records on host species from other families). Of them, *M. olens* has much softer and smaller basidiocarps than *M. salicis*, and it bears rare and often poorly differentiated gloeocystidia. Differences of *M. salicis* from *M. perticatum* are listed under the latter species. *Conferticium ravum* (Burt) Ginns & G.W.Freeman (= *Gloeocystidiellum karstenii* Donk) (Russulales) is macroscopically almost identical to *M. salicis* and it occurs mainly on dead branches of *Populus* and *Salix*. However, it can be easily separated from *M. salicis* by its clampless hyphae and much smaller, ornamented basidiospores (see Eriksson & Ryvarden 1975, under *G. karstenii*).

CONCLUSION

In the present paper, we re-described *M. leucoxanthum* as a species restricted to a particular host tree, *A. alnobetula*, and introduced six other taxa, four of them as new to science. These results were based on newly collected material from Eurasia studied by morphological and molecular methods. Using *tef1* region was crucial for the species delimitation in this group, and ecological and geographic data provided additional arguments for our species-level taxonomic conclusions. At the generic level, *Megalocystidium* was emendated to encompass one species with acanthophyses, *M. diffissum*.

However, the species diversity in *M. leucoxanthum* complex would be higher if the North American specimens are taken into account. We tentatively named a few Canadian collections available to us as belonging either to *M. leucoxanthum* s.s. or to *M. pellitum*. These specimens show no essential morphological differences from the Eurasian material so labelled but unfortunately our attempts to sequence them failed. Ginns & Lefebvre (1993) and Ginns & Freeman (1994) reported *M. leucoxanthum* from many geographic regions of North America. In these publications, the host list included not only various deciduous trees but also conifers (*Picea engelmannii*). This is a clear indication that the *M. leucoxanthum* complex in North America requires a closer look.

SUPPLEMENTARY FILE

Supplementary file 1 – Geographic distribution of *Megalocystidium* spp.

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