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Disentangling the taxonomy of *Octospora meslinii* (*Pezizales*), a bryophilous ascomycete on *Grimmia pulvinata*

CSABA NÉMETH[1]*, JAN ECKSTEIN[2], MICHAL SOCHOR[3]

[1] Centre for Ecological Research, Institute of Ecology and Botany, Alkotmány u. 2-4, Vácrátót, H-2163, Hungary
[2] Arnoldiweg 20, Göttingen, D-37083, Germany
[3] Crop Research Institute, Centre of the Region Haná for Biotechnological and Agricultural Research, Šlechtitelů 29, Olomouc, CZ-78371, Czech Republic
*corresponding author: nemetcsaba@gmail.com

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The bryophilous ascomycete *Octospora meslinii* is a rarely reported species growing exclusively in cushions of the saxicolous moss *Grimmia pulvinata*. The taxon has been misunderstood in the past and hitherto reliably only reported from France and Germany.

Many recent collections from Hungary have made it possible to get a better understanding of *O. meslinii*, which is comprehensively described and illustrated in this paper. Because of the lack of original material, we designate an illustration in the protologue as the lectotype and one of the recent collections as the epitype of this fungus. *Octospora meslinii* is compared with other species of *Octospora* growing in the same type of habitat or having similar ascospores. The most closely related species to *O. meslinii* is *O. pseudoampezzana*. Both share apothecia with blackish pigmentation, a unique feature compared to bryophilous *Pezizales* as a whole, ellipsoid ascospores ornamented with isolated warts, moss hosts in the family *Grimmiaceae*, and the infection inducing galls on the rhizoids. A phylogenetic analysis using the EF1α, LSU and SSU rDNA loci confirms our morphological findings showing that *O. meslinii* forms a monophyletic clade with *O. pseudoampezzana*, whereas other species with which *O. meslinii* was confused in the past, e.g. *O. similis*, are related only distantly.

Key words: bryoparasitic fungi, EF1α, *Grimmia pulvinata*, LSU, SSU.

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Bryofilní vřeckovýtrusá houba *Octospora meslinii* je vzácně nalézaný druh rostoucí výhradně v trsech saxikolního mechu děrkavky poduškovité (*Grimmia pulvinata*). V minulosti byl taxon často chápán nesprávně; dosud byl věrohodně publikován pouze z Francie a Německa.

Četné recentní sběry z Maďarska umožnily druh lépe prozkoumat a pořídit detailní popis a fotodokumentaci. Z důvodu chybějící typové položky a autentického materiálu navrhujeme ilustraci v protologu jako lektotyp a jeden z recentních sběrů jako epityp druhu. *Octospora meslinii* je porovnána s dalšími druhy rodu *Octospora* rostoucími na stejných stanovištích nebo s podobnými výtrusy. Nejpříbuznějším druhem *O. meslinii* je *O. pseudoampezzana*. Oba druhy spojuje přítomnost černé pigmentace, což je mezi bryofilními zástupci řádu *Pezizales* unikátní znak, dále elipsoidní výtrusy ornamentované izolovanými bradavičkami, hostitelský mech z čeledi *Grimmiaceae* a infekce indukující tvorbu hálek na rhizoidech hostitele. Fylogenetická analýza založená na lokusech EF1α, LSU a SSU rDNA potvrdila, že *O. meslinii* a *O. pseudoampezzana* skutečně tvoří monofyletickou skupinu, zatímco jiné druhy, s nimiž byla *O. meslinii* zaměňována, např. *O. similis*, jsou jen vzdáleně příbuzné.

INTRODUCTION

Bryophilous *Pezizales* are known to be intimately associated with bryophytes. Most of these fungi are considered to be narrow specialists with a single moss or liverwort host plant (Benkert 1990, Vega et al. 2016, Egertová et al. 2018). A broad host spectrum with distantly related bryophyte species usually indicates an unresolved fungal species complex (Vega et al. 2017, 2019), although a seemingly broader host spectrum can sometimes stem from misidentification and confusion of similar species.

The latter is the case with *Octospora meslinii* (Le Gal) Svrček et Kubička, which was originally described to be growing in cushions of *Grimmia pulvinata* (Hedw.) Sm. (Le Gal 1939). Subsequently, along with *Grimmia pulvinata* (Dennis et Itzerott 1973, Itzerott 1981, Itzerott et Döbbeler 1982, Caillet et Moyne 1989) several other moss species have been reported as associated bryophytes or hosts, such as *Schistidium apocarpum* H.H. Blom (Itzerott 1981, Engel et Hanff 1985), *Campylopus subulatus* Schimp. ex Milde (Vivant 1998), *Tortula subulata* Hedw., and *Orthotrichum diaphanum* Schrad. ex Brid. (Caillet et Moyne 1989). Additionally, the taxonomic distinction of *Octospora meslinii* has long been disputed (Dennis et Itzerott 1973, Hohmeyer 1988), and in some cases this species is treated as a synonym of *Octospora similis* (Kirschst.) Benkert (Kirk on-line).

The aim of this study is to clarify the taxonomic status of *Octospora meslinii*, based mainly on recent collections from Hungary.

MATERIAL AND METHODS

Sample collection and observation. The description of *Octospora meslinii* is based on results of the examination of living collections (*) from Hungary collected between November 2017 and December 2020, as well as rehydrated herbarium specimens (†). Observations were made in tap water, while ascospore ornamentation was also studied after staining with Lactophenol Cotton Blue (LPCB), and non-amyloidity was checked in Lugol's solution. Macrographs were taken with an Olympus Tough TG-5 digital camera (Olympus Corporation, Tokyo, Japan). Microscopic photographs

were taken with a QImaging MicroPublisher 3.3 RTV camera (QImaging, Surrey, BC, Canada) attached to a Nikon Eclipse E200 microscope (Nikon Corporation, Tokyo, Japan). Spore size and other quantitative microscopic characters were measured by means of the AxioVision 4.8.2 (Carl Zeiss Microimaging, Jena, Germany) and QCapture Pro 7 software (QImaging, Surrey, BC, Canada). The length, width and Q value of ascospores are presented in the following form: (lowest measured value) 5% percentile value – *mean* – 95% percentile value (highest measured value). Scanning electron micrographs (SEM) were taken from air dried samples using a LEO-438 VP environmental scanning electron microscope (Carl Zeiss AG, Oberkochen, Germany).

A search for the type material of *Octospora meslinii* in the Muséum national d'Histoire naturelle in Paris (PC) failed, hence only the specimen labelled as *O. meslinii* in Le Gal's collection was studied. Additionally, we included five specimens collected and cited as *O. meslinii* by Mirko Svrček and Jiří Kubička (Svrček et Kubička 1961, 1963) from the Mycological Department of the National Museum in Prague (PRM), as well as two samples collected by Heinz Itzerott from the herbarium of the Botanische Staatssammlung München (M).

Vouchers of recently collected specimens are deposited in the Mycological Department of the National Museum in Prague as well as the private herbaria of the authors (Eckst. - personal herbarium of Jan Eckstein, CsN – personal herbarium of Csaba Németh).

DNA extraction and analyses. DNA was extracted from dried apothecia with the CTAB method as outlined by Doyle et Doyle (1987). Up to three apothecia were homogenised with a pestle, incubated in 300 µl extraction buffer at 65 °C for one hour; the extract was subsequently purified in a chloroform-isoamyl alcohol mixture, precipitated by isopropanol and finally dissolved in water and incubated with RNase for 30 min. at 37 °C. DNA quality was checked on agarose gel. Molecular sequence data were generated for three loci: the 28S subunit of ribosomal DNA (LSU) was amplified with primers LR0R and LR6 (Vilgalys et Hester 1990), the 18S subunit of rDNA (SSU) with primers NS1 and NS6 (White et al. 1990), and the translation elongation factor-1alpha (EF1α) with primers EF1-983F and EF1-1567R (Rehner et Buckley 2005). PCR was performed with Kapa polymerase (Kapa Biosystems, Wilmington, MA, USA), following a standard protocol with 37 cycles and annealing temperature of 55 °C. The PCR products were purified by precipitation with polyethylene glycol (10% PEG 6000 and 1.25M NaCl in the precipitation mixture) and sequenced in both directions using the Sanger method (Macrogen Europe, Amsterdam, The Netherlands). Sequences were edited and aligned in Geneious ver. 7.1.7 (Biomatters, Auckland, New Zealand). Sequences generated in this study were deposited in GenBank under the accession numbers listed in Tab. 1. Bayesian phylogeny inference for concatenated data (both newly generated and those available in GenBank; see Tab. 1) was computed in MrBayes ver. 3.2.4 (Ronquist et al. 2012) with 2×10^7 generations, sampling every 1000^{th} tree, in two independent runs, each with four chains. The first 50% (10^7) generations were excluded as burn-in. The most suitable substitution model (GTR+I+G) was determined for each locus in PartitionFinder 2.1.1 (Lanfear et al. 2017) using the corrected AIC (AICc) and a greedy search.

RESULTS

PHYLOGENETIC ANALYSES

Octospora meslinii was represented by four collections in the analysis. As a result, LSU, SSU and EF1α sequences showed that the studied collections form a well-supported monophyletic clade with only very little polymorphism among individual collections (Fig. 1). Sequences of three specimens (CsN 9194, CsN 9207, CsN 9250) are 100% identical in EF1α, the fourth one (CsN 9078) differs in

Tab. 1. Sequenced collections with voucher information and GenBank accession numbers. Sequences obtained in this study are highlighted in bold.

Species	Identification code in GenBank	Herbarium code	Country, collection date	Host	GenBank accession numbers		
					LSU	SSU	EF1α
Lamprospora dictydiola	ldic	PRM 945794	Czech Republic, 12 Feb 2014	*Tortula muralis*	MF754056	MK569365	MF754054
Lamprospora hispanica	MV2017012203	B 70 0100986	Spain, 22 Jan 2017	*Aloina ambigua*	MN394599	MW242827	MN366468
Lamprospora sylvatica	UA1	PRM 946415 (holotype)	Ukraine, 8 Jul 2017	*Dicranum montanum*	MG947604	MK569367	MK569290
Lamprospora verrucispora	MV15102504	HBG 1412 (holotype)	Germany, 25 Oct 2015	*Campylopus pyriformis*	MN994551	MN994527	MN990993
Neottiella vivida	NVZla	PRM 945797	Czech Republic, 22 Oct 2016	*Polytrichum piliferum*	MF066068	MK569337	MF754051
Octospora affinis	OAFZla	PRM 945798	Czech Republic, 22 Oct 2016	*Orthotrichum affine*	MF754075	MK569347	MF754045
Octospora americana	2055	S F43718 (holotype)	USA, 18 Feb 1981	*Forsstroemia trichomitria*	MN967346	MN994516	MT078729
Octospora axillaris	OAxi	PRM 954016	Czech Republic, 8 Nov 2016	*Phascum cuspidatum*	MW242829	MW242828	MW430761
Octospora bridei	bri	PRM 935151	Czech Republic, 18 Oct 2015	*Ephemerum minutissimum*	MF754061	MT001890	—
Octospora conidiophora	ZE48/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018	*Trichosteleum perchlorosum*	MK569321	MK569351	MK569297
Octospora doebbeleri	DEVh	PRM 954007 (holotype)	Czech Republic, 25 Dec 2019	*Dicranoweisia cirrata*	MW152148	MW152156	MW159137
Octospora erzbergeri	ERZ	PRM 945799	Czech Republic, 10 Dec 2016	*Pseudoleskeella nervosa*	MF754068	MK569340	MF754042
Octospora cf. *excipulata*	OExc	PRM 945800	Czech Republic, 16 Nov 2015	*Funaria hygrometrica*	MF754062	MK569369	MF754047
Octospora fissidentis	Fis	PRM 945801	Czech Republic, 13 Nov 2016	*Fissidens bryoides*	MF754073	MK569341	MF754044
Octospora gyalectoides agg.	49382	B 70 0100075	Germany, 22 Nov 2016	*Pottia lanceolata*	MT001891	MT001889	MN990995
Octospora humosa agg.	OHZla	PRM 945802	Czech Republic, 22 Oct 2016	*Polytrichum piliferum*	MF754074	MK569343	MF754043
Octospora hygrohypnophila	MV17082702	PRM 953064	France, 27 Aug 2017	*Hygrohypnum luridum*	MN994543	MN994520	MN990988
Octospora ithacaensis	OLOi	PRM 945803	Czech Republic, 6 May 2016	*Marchantia polymorpha*	MF754071	MK569346	MF754053
Octospora kelabitiana	oct-jat	PRM 945781	Malaysia, 3 Feb 2016	*Riccardia* sp.	MF754065	MK569372	MF754048
Octospora leucoloma	OLeu	PRM 945804	Czech Republic, 21 Oct 2016	*Bryum argenteum*	MF754063	MK569370	—
Octospora melina	DHP-04.552	DHP 04-552 (FH)	Iceland, 27 Jul 2004	unknown	KC012689	—	KC109259

Species	Identification code in GenBank	Herbarium code	Country, collection date	Host	GenBank accession numbers		
					LSU	SSU	EF1α
Octospora meslinii	CsN9078	PRM 954639	Hungary, 13 Dec 2017	*Grimmia pulvinata*	**MW507137**	**MW507001**	**MW526078**
Octospora meslinii	CsN9194	PRM 954637 (epitype)	Hungary, 7 Jan 2018	*Grimmia pulvinata*	MW152147	MW152158	MW159139
Octospora meslinii	CsN9207	PRM 954640	Hungary, 7 Jan 2018	*Grimmia pulvinata*	**MW507138**	**MW507002**	**MW526079**
Octospora meslinii	CsN9250	PRM 954638	Hungary, 26 Jan 2018	*Grimmia pulvinata*	**MW507139**	**MW507003**	**MW526080**
Octospora cf. *orthotrichi*	HR8	CNF 2/10561	Croatia, 2 Jan 2018	*Orthotrichum diaphanum*	MK569314	MK569342	MK569311
Octospora phagospora	PHG44	PRM 945805	Germany, 24 Oct 2015	unknown	MF754072	MK569344	MF754046
Octospora pseudoampezzana	OP1	PRM 935156	Czech Republic, 5 Mar 2016	*Schistidium crassipilum*	MF754069	MK569339	MF754050
Octospora rubens agg.	MV20181218-06	PRM 954641	Spain, 18 Dec 2018	*Ceratodon purpureus*	MW221931	MW206790	MW219144
Octospora similis agg.	LJDP45	PRC 4667	Slovakia, 26 Nov 2019	*Bryum* cf. *rubens*	MT766281	MT766280	MT759840
Octospora svrcekii	51959	PRM 954236	Albania, 8 Jul 2014	*Cratoneuron filicinum*	MN967347	MT065902	MN974531
Octospora wrightii	WRIG	PRM 945807	Czech Republic, 22 Apr 2017	*Amblystegium serpens*	MF754070	MK569345	MT078728
Octosporella perforata	PERF	PRM 945808	Czech Republic, 10 Dec 2016	*Porella platyphylla*	MF754060	MK569368	MF754052
Octosporopsis erinacea	DUM20/1	PRM 945774 (isotype)	Malaysia, 20 Jan 2017	*Dumortiera hirsuta*	MF754057	MK569338	MF754041
Octosporopsis nicolai	UL 151-13	pers. herb. U. Lindemann	Germany, 2 Feb 2013	*Lunularia cruciata*	KF771033	—	KF771042
Otidea leporina	KGOL	CNF 2/9962	Kyrgyzstan, 15 Jul 2016	—	MK569335	MK569371	MK569312

four nucleotides. In LSU, one specimen (CsN 9207) only differs in a single nucleotide from the other ones (CsN 9078, CsN 9194, CsN 9250). No variability was detected in SSU.

Based on the three markers, *O. meslinii* is most closely related to *O. pseudoampezzana* (pairwise identity 97.0–97.7% in EF1α, 99.5–99.6% in LSU, and 99.9% in SSU). Other species with ellipsoid and verrucose spores, i.e. *O. bridei*, *O. similis*, *O.* cf. *orthotrichi*, *O. fissidentis* and *O. phagospora* are related only distantly.

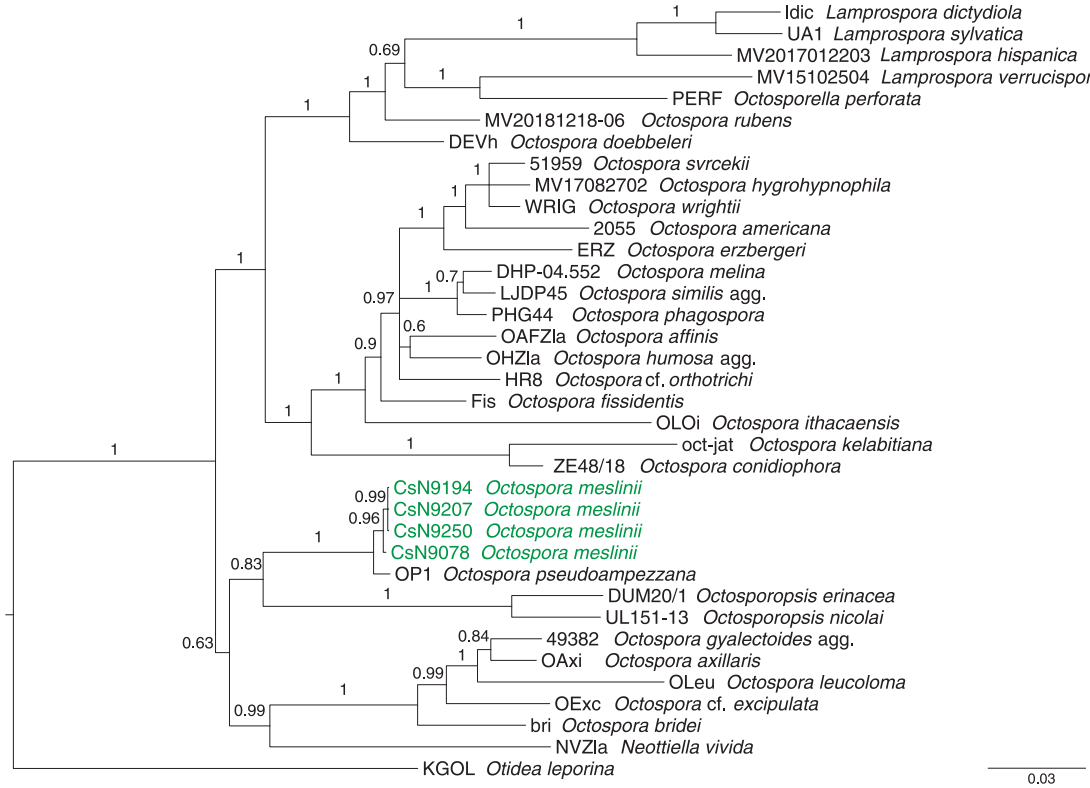


Fig. 1. Bayesian phylogeny inference based on concatenated alignment of EF1α, LSU and SSU sequences; Bayesian posterior probabilities are shown above the branches.

TAXONOMY

Octospora meslinii (Le Gal) Svrček et Kubička, Česká Mykol. 17(2): 67, 1963

Basionym: *Humaria meslinii* Le Gal, Rev. Mycol. (Paris) 4: 133, 1939

Etymology: named after its first known collector Roger Meslin.

Type: France, Calvados, Caen, 'parmi les coussinets de *Grimmia pulvinata* sur un mur de la venelle du Jardin des Plantes de Caen (Calvados)', Nov 1937, Dec 1938, Jan 1939 (the original material was not found in Le Gal's collection in PC and appears to be lost).

Typification

In agreement with ICN Art. 9.2 and Art. 9.7 (Turland et al. 2018), in lack of any original material, we herein designate one of the illustrations in the protologue as lectotype (Le Gal 1939: 135, Fig. 2; designated here, MycoBank MBT 10003657)

and one of the samples recently collected in Hungary as epitype (PRM 954637; designated here, MycoBank MBT 10003656) of *Octospora meslinii*. Data and characters from the original description are in agreement with those observed in our recent collections and our concept of *O. meslinii*. The lectotype illustration obviously depicts paraphyses in dead state and differs somewhat from our observations of living material (see details in the Discussion).

Description

Macroscopic features (Fig. 2d–l). Apothecia scattered or gregarious, embedded in cushions of the saxicolous moss *Grimmia pulvinata*; 1–3 mm in diam., finally thick and discoid, sessile; hymenium light orange to brownish orange depending on maturity, first with a whitish pubescent margin later becoming less conspicuous; first with scattered marginal blackish coloration later becoming gradually more pronounced, finally the whole apothecium turning black; with hyaline anchoring hyphae.

Microscopic features (Fig. 3). Hymenium 230–300 µm thick. Asci 220–280 × 20–24 µm, operculate, cylindrical, containing 8 ascospores arranged in a single row, pars sporifera 90–140 µm, inamyloid, shortly bifurcate at the base, arising from perforated croziers. Ascospores [only free ascospores considered, including ornamentation, n = 50] (18.2)18.3–*19.6*–21.9(22.1) µm long and (11.3)11.3–*12.5*–13.5(14.2) µm wide, Q = 1.5–*1.6*–1.7, hyaline, ellipsoid to broadly ellipsoid, always with a large lipid body situated slightly asymmetrically, (9.3)9.4–*10.1*–11.3(11.6) µm in diameter, accompanied by some small lipid bodies (0.9)1.2–*1.6*–1.7(3.3) µm in diameter. Ascospore ornamentation consisting of isolated, sometimes confluent warts of irregular shape up to 1 µm broad (long) and 0.3-0.4 µm high. Paraphyses filiform, straight or slightly curved, pluriseptate, sometimes forked, apically (or sometimes below the apex) slightly inflated, sometimes clavate, terminal cells 50–90 µm long, (4.5)5–6 µm wide in lower part, 6–9 µm wide in swollen (usually the uppermost) part; containing orange pigment. Hymenium of older apothecia also containing paraphyses with brownish-blackish coloration in addition to 'normally' pigmented ones.

Medullary excipulum composed of a dense *textura intricata*, 100–120 µm thick in the thickest part. Ectal excipulum 120–200 µm thick, formed by a *textura globulosa-angularis*, with an outer layer of dark brownish hyphae. Margo 150–250 µm wide, composed of a *textura porrecta* of elongated hyphae, with cells containing dark brown-black pigment.

Infection (Fig. 4). *Octospora meslinii* induces spherical galls 25–70 µm in diameter on the rhizoids of *Grimmia pulvinata*. The galls develop terminally or on short lateral ramifications of the rhizoids and usually form clusters.

Fig. 2. Habitat and apothecia of *Octospora meslinii* (PRM 955438 – a, i; PRM 955440 – b; PRM 955447 – c; PRM 954638 – d; PRM 955448 – e–f, l; PRM 954639 – g; PRM 955444 – h; PRM 955445 – j; PRM 955442 – k). **a, b** – habitat at Remete Valley, Börzsöny Mts; **c** – habitat at Mt Ördög, Börzsöny Mts; **d–g** – apothecia with the host *Grimmia pulvinata*; **h–l** – different stages of apothecial development. Photo C. Németh.

The rhizoid cells within these clusters are much shorter and have more ramifications than uninfected rhizoids. Galls are first partly and later completely covered by a layer of hyphae. This type of infection was first reported and illustrated by Itzerott et Döbbeler (1982).

Habitat, occurrence and distribution (Fig. 2a–c, Fig. 5)

In Hungary, *O. meslinii* occurs on dacite, andesite, granite and limestone rocks and rock outcrops usually deeply embedded in cushions of *Grimmia pulvinata*,

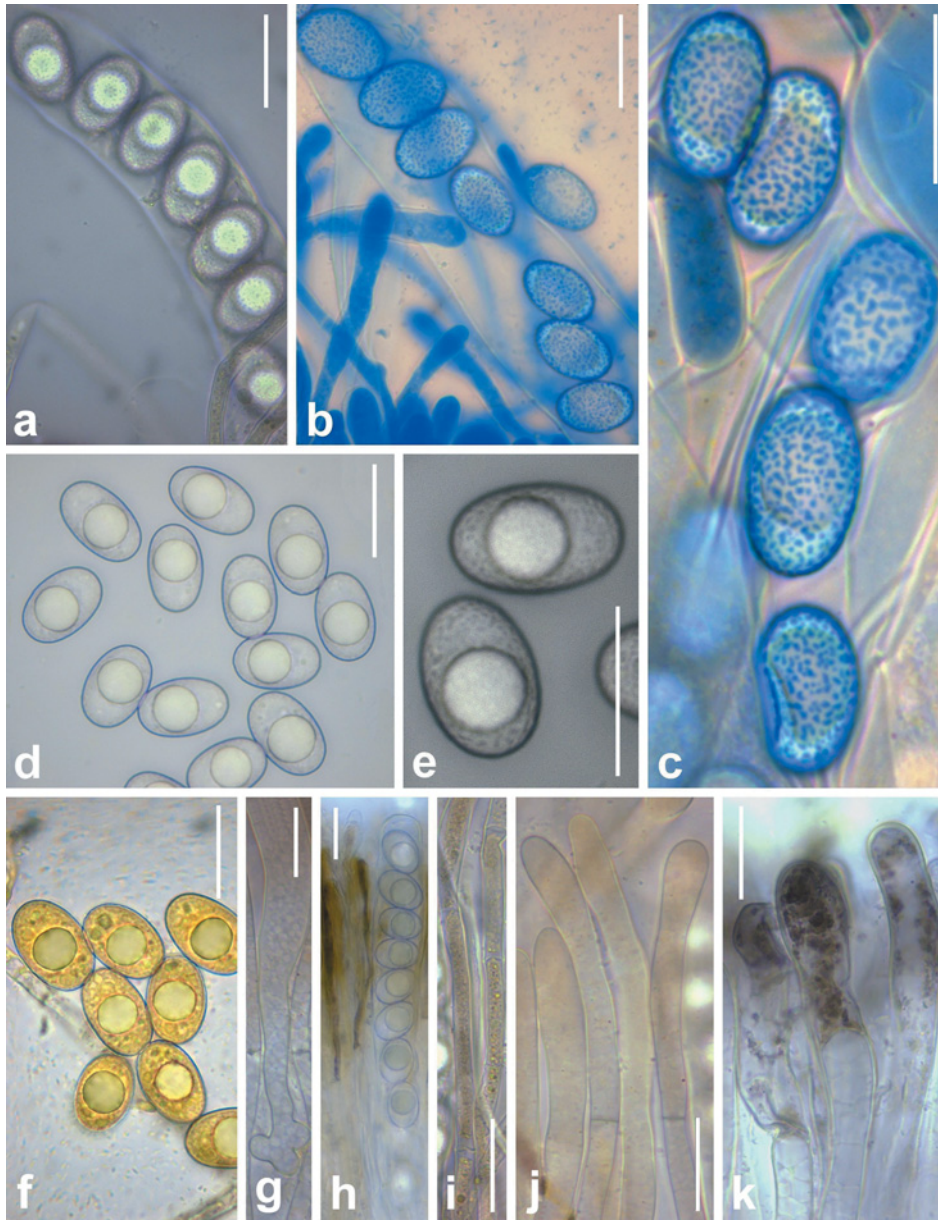


Fig. 3. Microcharacters of *Octospora meslinii* (PRM 955436 – a, i; PRM 955444 – b; PRM 955439 – c; PRM 955448 – d, e, g, j, k; PRM 955449 – f, h). **a** – ascus in tap water; **b** – ascus in LPCB; **c** – ascospores in LPCB; **d, e** – free ascospores in tap water; **f** – ascospores in Lugol's solution; **g** – hooked ascus base (crozier); **h** – hymenium in water showing blackish paraphyses and an ascus with ascospores; **i** – lower part of paraphyses in tap water; **j** – upper part of paraphyses in tap water; **k** – margin with blackish coloration in tap water. Scale bars = 20 µm. Photo C. Németh.

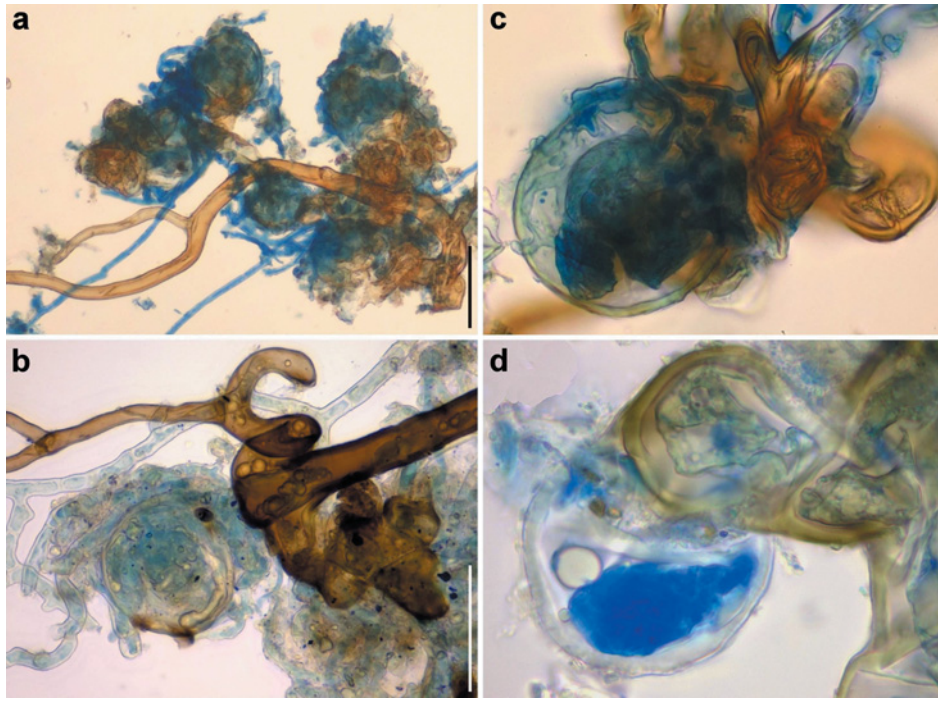


Fig. 4. Infections of *Octospora meslinii* (M 0258117 – a, c; PRM 955442 – b, d). **a** – rhizoids of *Grimmia pulvinata* with clustered galls stained with LPCB; **b, c** – infections stained with LPCB; **d** – haustorium inside a rhizoid gall stained with LPCB. Scale bars = 50 µm (a, b), 20 µm (c, d). Photos J. Eckstein (a, c), C. Németh (b, d).

more rarely attached directly to the rock. *Octospora meslinii* does not usually cause any visible damage to its host. However, in some cases it seems to destroy it (Fig. 2f), unless these kinds of damage have external causes (e.g. bird droppings). Other accompanying bryophytes included *Bryum argenteum* Hedw. var. *lanatum* (P. Beauv.) Hampe, *Homalothecium sericeum* (Hedw.) Schimp., *Hypnum cupressiforme* Hedw., *Grimmia laevigata* (Brid.) Brid., and *Schistidium flaccidum* (De Not.) Ochyra.

Hitherto, *O. meslinii* had reliably only been reported from France (Le Gal 1939) and Germany (Itzerott et Döbbeler 1982, Krieglsteiner 1999, Krieglsteiner et Markones 2007, Benkert 2009). Our collections are the first for Hungary. Records from the Czech Republic (Svrček et Kubička 1963) have been proved to be erroneous.

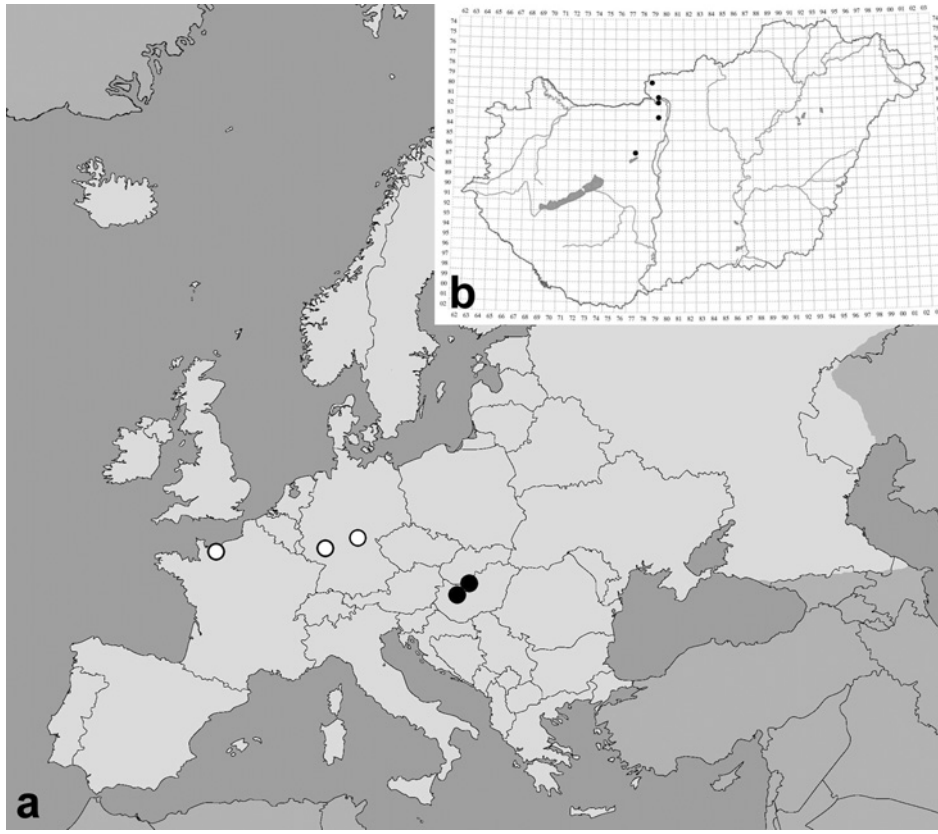


Fig. 5. European (a) and Hungarian (b) distribution of *Octospora meslinii*. Old localities: ○. Recent localities: ●.

Specimens examined

The original text of historical herbarium labels is written in German, Latin or French, whereas the herbarium data of current specimens are translated into English.

Octospora meslinii

The host is *Grimmia pulvinata* in all cases.

Germany. Rheinland-Pfalz, Naturpark Pfälzer Wald, Annaberg etwa 2 km nördlich Bad Dürkheim in Richtung Leistadt, 13 Jan. 1981, leg. H. Itzerott (M 0258117). – Leistadt, 22 Dec. 1980, leg. H. Itzerott (M 0258118).

Hungary. Velence Mts, Nadap, Mt János, 47°15'20.3" N, 18°37'09.3" E, 190 m a.s.l., on granite rock, 26 Jan. 2018, leg. et det. C. Németh (PRM 954638, CsN 9250). – Pilis Mts, Pomáz, Mt Majdán, 47°38'54.4" N, 18°59'48.7" E, 188 m a.s.l., on limestone rock, 13 Dec. 2017, leg. et det. C. Németh (PRM 954639, CsN 9078). – Börzsöny Mts, Kismaros, Mt Nagykőszikla, 47°50'09.3" N, 18°58'53.7" E, 310 m a.s.l., on dacite rock, 25 Nov. 2017, leg. J. Nagy, det. C. Németh (PRM 955444, CsN 8992). – Kismaros, Mt Kiskőszikla, 47°50'03.5" N, 18°58'21.9" E, 245 m a.s.l., on dacite rock, 12 Dec. 2017, leg. J. Nagy, det. C. Németh (PRM 955445, CsN 9090). – Nagymaros, Mt Nagykő, 47°47'20.5" N, 18°56'49.7" E, 210 m

a.s.l., on andesite rock, 8 Dec. 2017, leg. J. Nagy, det. C. Németh (PRM 955443, CsN 9087). – Nagymaros, Mt Rigó, 47°46'25.8" N, 18°56'18.8" E, 279 m a.s.l., on dacite rock, 7 Jan. 2018, leg. et det. C. Németh (epitype PRM 954637; isoepitypes PRM955442, CsN 9194); ibid., 47°46'26.7" N, 18°56'09.5" E, 259 m a.s.l., on dacite rock, 7 Jan. 2018, leg. et det. C. Németh (PRM 955446, CsN 9195); ibid., 47°46'24.0" N, 18°56'18.0" E, 257 m a.s.l., on dacite rock, 3 Jan. 2020, leg. et det. C. Németh (PRM 955448, CsN 9823). – Nagymaros, Mt Ördög, all collections on dacite rock, 7 Jan. 2018, leg. et det. C. Németh: 47°46'09.6" N, 18°55'57.4" E, 175 m a.s.l. (PRM 955447, CsN 9199); ibid., 47°46'09.0" N, 18°55'50.2" E, 184 m a.s.l. (PRM 955435, CsN 9200); ibid., 47°46'08.5" N, 18°55'48.4" E, 184 m a.s.l. (PRM 955436, CsN 9201); ibid., 47°46'07.9" N, 18°55'45.2" E, 187 m a.s.l. (PRM 955437, CsN 9202). – Nagymaros, Remete Valley, all collections on dacite rock, 7 Jan. 2018, leg. et det. C. Németh: 47°46'08.9" N, 18°55'24.1" E, 183 m a.s.l. (PRM 955438, CsN 9203); ibid., 47°46'09.7" N, 18°55'21.7" E, 177 m a.s.l. (PRM 955439, CsN 9204); ibid., 47°46'13.3" N, 18°55'15.5" E, 188 m a.s.l. (PRM 955440, CsN 9205). – Nagymaros, between Remete Valley and Mt Doboziorom, 47°46'23.3" N, 18°55'05.3" E, 265 m a.s.l., on dacite rock, 7 Jan. 2018, leg. et det. C. Németh (PRM 955441, CsN 9206). – Nagymaros, Mt Doboziorom, 47°46'29.8" N, 18°55'05.5" E, 330 m a.s.l., on dacite rock, 7 Jan. 2018, leg. et det. C. Németh (PRM 954640, CsN 9207). – Kemence, Mt Vadtető, 47°58'13.2" N, 18°53'29.7" E, 611 m a.s.l., on andesite rock, 29 Dec. 2020, leg. C. Németh et J. Nagy, det. C. Németh (PRM 955449, CsN 10389).

***Octospora similis* agg.**

In Czech specimens, the accompanied bryophyte (not mentioned on the label) is *Bryum* sp. in all cases. In German and Hungarian specimens, the host is *Bryum rubens* in all cases.

Czech Republic. Bohemia meridionalis: Ad piscinam "Dvořiště" prope vicum Dolní Slověnice, haud procul ab oppido Lomnice nad Lužnicí, ad terram muscosam, 1 June 1960, leg. et det. M. Svrček (PRM 620210; Svrček et Kubička 1961). – Ad piscinam "Dvořiště" prope vicum Smržov, haud procul ab oppido Lomnice nad Lužnicí, ad terram muscosam, 31 May 1960, leg. et det. M. Svrček (PRM 620213); ibid., ad terram nudam, 1 June 1960, leg. et det. M. Svrček (PRM 620217); ibid., ad terram, 24 June 1960, leg. et det. M. Svrček (PRM 620211; all collections cited in Svrček et Kubička 1961). – Ad piscinam "Dvořiště" prope Lomnice nad Lužnicí, ad terram arenosam musc, 14 June 1961, leg. J. Kubička, det. M. Svrček (PRM 616166; Svrček et Kubička 1963).

Germany. Thuringia, Nordhausen, 51°30'59" N, 10°47'29" E, 240 m a.s.l., on soil, 9 Sept. 2011, leg. et det. G. Eckstein (coll. No. 2833; Eckst. 23223).

Hungary. Pilis Mts, Pilisszántó, Mt Hosszú, 47°40'13.9" N, 18°54'39.6" E, 459 m a.s.l., on soil, 11 Nov. 2020, leg. et det. C. Németh (PRM 955433, CsN 10172). – Alsó-Kemeneshát Hills, Kám, Jeli Botanical Garden, 47°04'39.0" N, 16°53'04.0" E, 234 m a.s.l., on soil, 21 Nov. 2020, leg. et det. C. Németh (PRM 955434, CsN 10232).

Octospora pseudoampezzana

The host is *Schistidium crassipilum* in all cases.

Germany. Lower Saxony, Göttingen, 5 Jan. 2014, leg. et det. J. Eckstein (Eckst. 34609).

Hungary. Gerecse Mts, Bajót, Mt Öregkő, 47°43'24.9" N, 18°34'30.5" E, 365 m a.s.l., on limestone boulder, 12 Jan. 2015, 10 Jan. 2020, leg. et det. C. Németh (PRM 955453, CsN 7567, CsN 9836). – Cserhát Mts, Vác, Mt Naszály, 47°49'50.6" N, 19°08'56.4" E, 485 m a.s.l., on limestone boulder, 2 Jan. 2021, leg. et det. C. Németh (PRM 955451, CsN 10401). – Bükk Mts, Miskolc-Lillafüred, Szinva Valley, 48°05'09.9" N, 20°36'54.9" E, 391 m a.s.l., on limestone boulder, 4 Jan. 2021, leg. C. Németh et A. Schmotzer, det. C. Németh (PRM 955450, CsN 10411). – Vértes Mts, Oroszlány, Kő Valley, 47°24'36.9" N, 18°19'00.3" E, 388 m a.s.l., on limestone rock, 6 Jan. 2021, leg. C. Németh et A. Koszka, det. C. Németh (PRM 955452, CsN 10431).

Octospora* cf. *orthotrichi

The host is *Orthotrichum diaphanum* in all cases.

Hungary. Budapest, Buda Mts, Hűvösvölgy Valley, 47°32'34.4" N, 18°57'49.0" E, 221 m a.s.l., on limestone boulder, 23 Dec. 2017, leg. Z. Kiss, det. C. Németh (PRM 955431, CsN 9168). – Budapest-

Óbuda, Hunor St, 47°32'47.3" N, 19°02'06.4" E, 100 m a.s.l., on stone fence, 21 Dec. 2020, leg. et det. C. Németh (PRM 955432, CsN 10325).

Octospora musci-muralis

Hungary. Vértes Mts, Gánt, Horog Valley, 47°22'26.6" N, 18°20'24.8" E, 277 m a.s.l., on dolomite rock, bryophyte host: *Grimmia pulvinata*, 26 Dec. 2019, leg. C. Németh et A. Koszka, det. C. Németh (CsN 9807).

Octospora grimmiae

The host is *Grimmia pulvinata* in all cases.

Hungary. Buda Mts, Budapest, Mt Hármashatár, 47°33'09.4" N, 18°59'35.6" E, 455 m a.s.l., on dolomite rock, 22 Dec. 2017, leg. et det. C. Németh (CsN 9125). – Mezőföld region, Tárnok, Old Cemetery, 47°22'38.1" N, 18°50'19.4" E, 115 m a.s.l., on limestone frame of a grave, 26 Jan. 2018, leg. et det. C. Németh (CsN 9241).

***Octospora* sp.**

France. Carantec (Finistère): Parmi de petites mousses murales [bryophyte host: *Tortula muralis*], 23 Sept. 1950, leg. R. Meslin, det. M. Le Gal (PC 282).

DISCUSSION

Comparison of macro- and microscopic features of *Octospora meslinii* with the original description

The diagnosis of *O. meslinii* was given both in French and Latin, differing, however, in some details. The term '*tetrasporis*' in the Latin text may certainly be a misspelling, given that 8 spores are mentioned in the French description and the microscopic illustration displays 8-spored asci as well.

Le Gal (1939) reported paraphyses to have yellowish contents of a granular appearance. By contrast, paraphyses shown by the illustration appear to contain vacuoles of various sizes over their full length (Fig. 6a). We observed distinctive vacuoles almost exclusively in the lower parts, and only occasionally in the apical regions of living paraphyses (Fig. 3i, j). Nonetheless, floating vacuoles were observed throughout dead paraphyses (Fig. 6b). This and further differences between the protologue and our observations concerning size of asci, paraphyses and ascospores can presumably be ascribed to observations of dead vs. living material (Tab. 2; see Baral 1992).

Bryophilous *Pezizales* known to parasitise *Grimmia pulvinata*

In addition to *O. meslinii*, two other species of the genus *Octospora* are known to infect *Grimmia pulvinata*, namely *O. musci-muralis* Graddon and *O. grimmiae* Dennis et Itzerott.

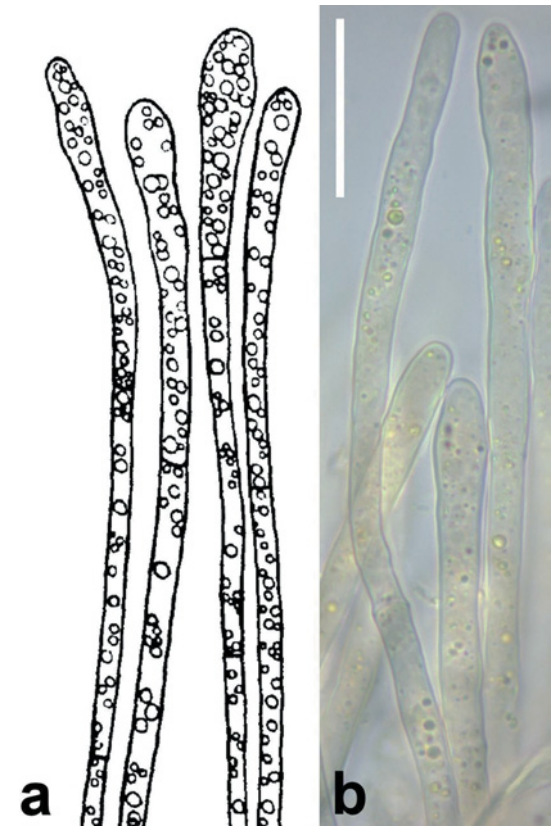


Fig. 6. Paraphyses of *Octospora meslinii*. **a** – drawings of paraphyses in Le Gal (1939); **b** – rehydrated dead paraphyses three years after drying (PRM 955442). Scale bar = 20 µm.
Photo C. Németh.

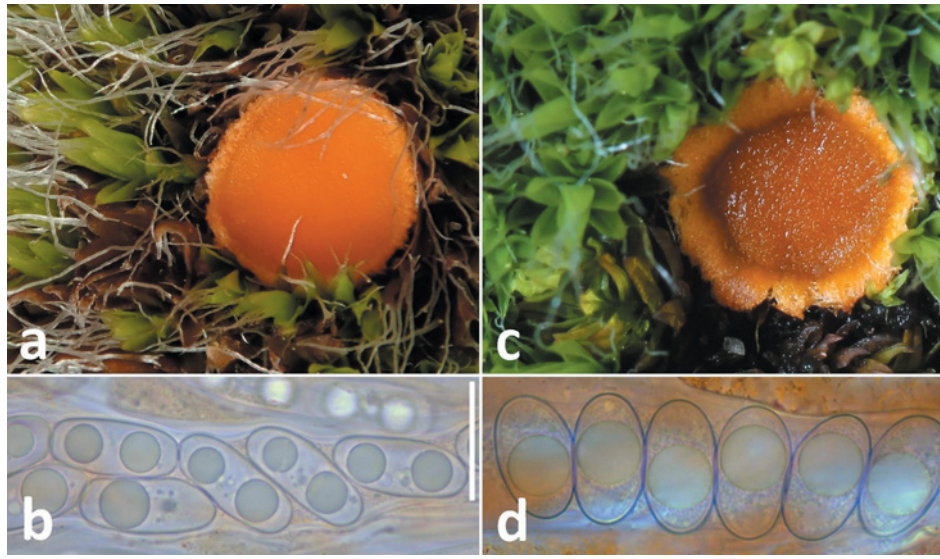


Fig. 7. Bryophilous *Pezizales* known to parasitise *Grimmia pulvinata* (CsN 9807 – a, b; CsN 9125 – c; CsN 9241 – d). **a** – apothecium of *Octospora musci-muralis*; **b** – ascus and ascospores of *Octospora musci-muralis* in tap water; **c** – apothecium of *Octospora grimmiae*; **d** – ascus and ascospores of *Octospora grimmiae* in tap water. Scale bars = 20 µm.
Photo C. Németh.

Tab. 2. Comparison of features of *Octospora meslinii* published in the protologue with our observations.

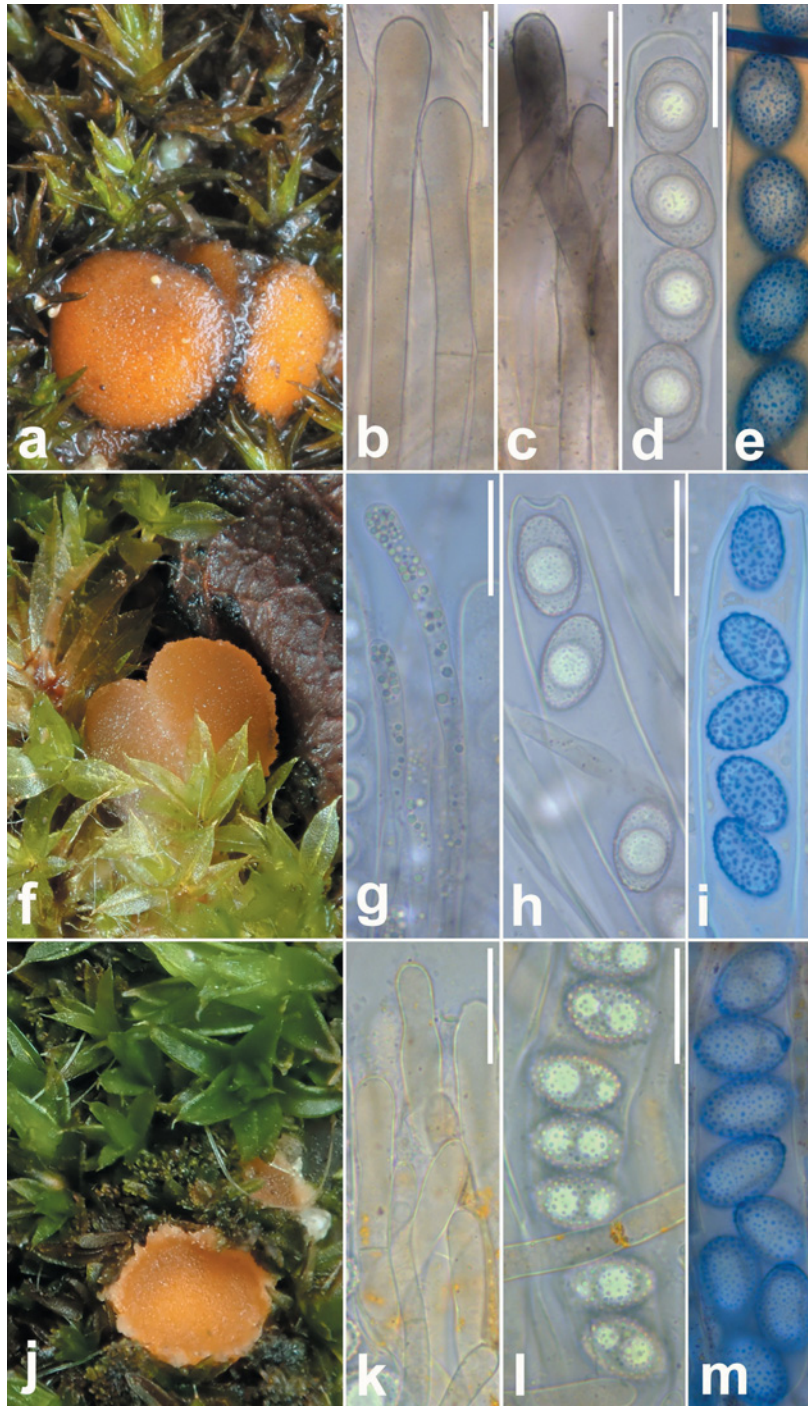
Character	Le Gal (1939)	Our observations
diameter of apothecia	1–3 mm	1–3 mm
colour of hymenium	orange	light orange to brownish orange, turning blackish when getting old
colour of margin	white, later becoming more or less brownish	first whitish pubescent, later turning less conspicuous; first with scattered blackish coloration which later becomes gradually more pronounced
size of asci	200–250(270) × 16–20 µm	*220–280 × 20–24 µm
size of ascospores	17–21 × 10–12.5 µm	*(18.2)18.3–*19.6*–21.9(22.1) × (11.3)11.3–*12.5*–13.5(14.2) µm; Q = 1.5–*1.6*–1.7 ††(17)18–21(24) × (10)11–12.5(13) µm †(18.0)18.4–*19.9*–21.5(21.9) × (11.9)12.15–*13.0*–13.8(14.5) µm; Q = 1.4–*1.6*–1.7
content of ascospores	1 large guttule accompanied by 1–3 small droplets (size not given)	*1 large lipid drop (9.3)9.4–*10.1*–11.3(11.6) µm in diameter, accompanied by some small oil droplets (0.9)1.2–*1.6*–1.7(3.3) µm in diameter †1 large lipid drop (9.5)9.5–*10.3*–11.1(11.1) µm in diameter accompanied by some small ones
shape of ascospores	elliptical	ellipsoid to broadly ellipsoid
paraphyses width	2–3 µm wide, in upper widened part up to 9 µm	*(4.5)5–6 µm in lower part, 6–9 µm wide in swollen (usually uppermost) part †3–4 µm in lower part, apically 5–8 µm wide
paraphyses content	– yellowish content of granular appearance (diagnosis) – many vacuoles throughout the paraphyses (illustration)	*granular orange pigment; vacuoles predominantly in lower part, only occasionally in upper part †numerous small oil drops over the entire length of the paraphyses

* living material; †† observations 35 years after drying (M 0258117, M 0258118); † observations 3 years after drying (PRM 955442)

Octospora musci-muralis has orange apothecia with a paler margin; ellipsoid to subcylindrical, smooth ascospores with parallel sides in the middle and broadly rounded ends, containing one or two large lipid bodies (Fig. 7a, b).

Octospora grimmiae has orange to reddish orange apothecia with conspicuous membranaceous, somewhat dentate margin, and ellipsoid, smooth ascospores containing one (or more rarely two) large lipid body (Fig. 7c, d).

Both species lack the characteristic blackish coloration of apothecia of *O. meslinii* and possess ascospores of totally different morphology. Furthermore, neither species form galls on the rhizoids of *Grimmia pulvinata* (Döbbeler 1980).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◀ **Fig. 8.** Bryophilous *Pezizales* with similar ascospores. *Octospora pseudoampezzana* (PRM 955450 – a; CsN 9836 – b–d; PRM 955453 – e): **a** – apothecia with the host *Schistidium crassipilum*; **b** – paraphyses in tap water; **c** – margin with blackish coloration in tap water; **d** – ascus and ascospores in tap water; **e** – ascus and ascospores in LPCB. *Octospora similis* (PRM 955434 – f, h, i; PRM 955433 – g): **f** – apothecia with the host *Bryum rubens*; **g** – paraphyses in tap water; **h** – ascus and ascospores in tap water; **i** – ascus and ascospores in LPCB. *Octospora* cf. *orthotrichi* (PRM 955432): **j** – apothecium with the host *Orthotrichum diaphanum*; **k** – paraphyses in tap water; **l** – ascus and ascospores in tap water; **m** – ascus and ascospores in LPCB. Scale bars = 20 µm. Photo C. Németh.

Bryophilous *Pezizales* historically confused with *Octospora meslinii*

Octospora pseudoampezzana is most similar to *O. meslinii* morphologically as well as genetically. The former species has orange to brownish orange apothecia with a whitish pubescent to fimbriate margin becoming dark brown to blackish with age. The ascospores are (19.0)19.1–*20.1*–21.5(22.0) µm long and (11.9)12.7–*14.0*–15.0(16.3) wide, Q = (1.2)1.4–*1.4*–1.6(1.6), with one lipid body (9.3)9.7–*10.8*–11.7(11.9) µm in diameter accompanied by some small ones. Spore ornamentation consists of dense, rounded, isolated warts up to 1 µm broad and 0.3–0.4 µm high. Paraphyses are (4)5–6 µm broad in their basal part, (7)9–10(11) µm in the apical part, straight or apically somewhat curved. Infection induces clusters of spherical galls on the rhizoids covered with hyphae. *Octospora pseudoampezzana* grows on *Schistidium crassipilum* occurring on stones or rocks (Eckstein et Eckstein 2009, Németh 2017b). In some cases, it is reported from *S. apocarpum* (Svrček 1969, Rubio et al. 2000, Benkert 2007, 2009) or simply *Schistidium* (Benkert 1976, Caillet et Moyne 1989). However, the name *Schistidium apocarpum* had long been used for a species complex which was later divided into several species including the common *S. crassipilum* (Blom 1996). It is therefore difficult to decide if the former reports on *S. apocarpum* refer in fact to *S. apocarpum* s.str. or to *S. crassipilum*. *Octospora pseudoampezzana* has once been reported from *Racomitrium heterostichum* (Hedw.) Brid. (Eckstein et al. 2020) but the taxonomic status of the collection in question is not yet resolved.

Octospora pseudoampezzana was first described as *Lachnea pseudoampezzana* by Svrček (1948) who later created the new genus *Hiemsia* Svrček (Svrček 1969) for it. Caillet et Moyne (1987) transferred this species to the species-rich genus *Octospora*. Subsequently, this classification has been followed by most of the recent authors, i.e. Benkert (1998, 2009), Rubio et al. (2000), Eckstein et Eckstein (2009), although *Hiemsia pseudoampezzana* is regarded as the current name in Species Fungorum (Kirk on-line). *Octospora meslinii* and *O. pseudoampezzana* share traits like general spore shape, spore ornamentation, development of dark pigmentation in apothecia, type of infection and host range in the family *Grimmiaceae*. Our molecular data indicate that the two taxa are closely

related but distinct species (Fig. 1). If one accepts the genus *Hiemsia* for *O. pseudoampezzana*, then *O. meslinii* would also have to be combined into *Hiemsia*. The molecular data indicate *Octospora* to be paraphyletic, and the genera *Lamprospora*, *Neottiella*, *Octosporella* and *Octosporopsis* all nested within *Octospora*. However, much additional work is required before *Octospora* can reliably be split into several smaller genera to better represent the phylogenetic relationships.

Due to the aforementioned similarities, *O. meslinii* can be easily confused with *O. pseudoampezzana*. Hohmeyer (1988) presumed both species as conspecific. Nevertheless, *O. pseudoampezzana* differs from *O. meslinii* by having broader ascospores with a somewhat larger lipid body, slightly broader paraphysis apices, and a different host moss (Fig. 8a–e, Fig. 9a, b).

Octospora similis agg. appears to be a species complex with hidden taxonomic diversity including several morphologically similar species. It was originally described as *Humaria similis* Kirschst. (Jaap 1922). Later, it was treated under several names such as *Humaria melina* Velen. (Velenovský 1934), *Octospora melina* (Velen.) Dennis et Itzerott (Dennis et Itzerott 1973), *Octospora similis* (Kirschst.) Benkert (Benkert 1996). Dennis et Itzerott (1973) regarded *O. meslinii* as a variety of *O. similis*. The holotype in B (herbarium of the Botanic Garden and Botanical Museum Berlin-Dahlem) is scant and only consists of one separated apothecium and one slide with hymenium as well as a few grains of sand with a few shoots of a glossy *Pohlia*, possibly *Pohlia nutans*. Ascospores measure 19–21 × 11.5–12.5 µm and are ornamented with coarse warts 0.5–1(2) µm wide and 0.5–1 µm high. The spore measurements given in the protologue deviate from our own data in being smaller (15–17 × 10–11 µm). The infection was not found in the type material. This, and the fact that the scant material is unavailable for molecular studies, makes it impossible to link the type with any of the recently collected lineages. Therefore, an epitype is needed for this name. Our description of *O. similis* is based on specimens associated with *Bryum rubens* Mitt. [*Ptychostomum rubens* (Mitt.) Holyoak et N. Pedersen] as the host.

Octospora similis has pale orange to orange apothecia with a finely fimbriate margin, paraphyses 5–7 µm broad, apically curved, containing many conspicuous vacuoles up to 4.9 µm in diameter. The ascospores are rather similar to those of *O. meslinii*, (16.4)16.7–*17.7*–18.6(18.6) µm long and (10.6)10.8–*11.3*–11.9(12.2) µm wide, Q = (1.5)1.5–*1.6*–1.7(1.7), with one [(7.8)8.1–*8.6*–9.1(9.2) µm in diameter] or sometimes two [both (5.6)5.9–*7.0*–7.4(7.4) µm in diameter] larger lipid bodies accompanied by some small ones (1–2 µm in diameter). Spore ornamentation consists of dense, rounded, isolated warts 0.5–1(1.5) µm wide and 0.5(1) µm high, sometimes connected to make short lines (Fig. 9c). Paraphyses 3–6.5 µm broad, apically more or less curved. Infectious structure includes appressoria on rhizoids covered by accompanying hyphae. Gall formation was reported from

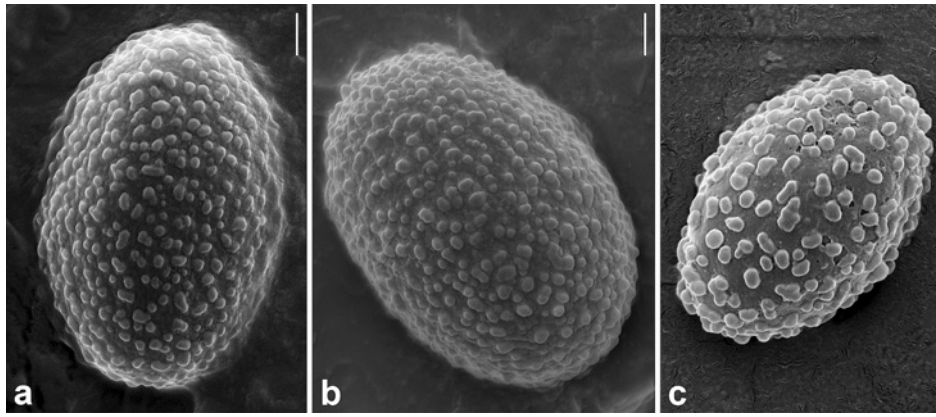

Fig. 9. SEM images of ascospores. **a** – *Octospora meslinii* (M 0258117); **b** – *Octospora pseudoampezzana* (herb. Eckst. 34609); **c** – *Octospora similis* (herb. Eckst. 23223). Scale bars = 2 µm. Photo J. Eckstein.

collections from Norway and Germany (Itzerott 1983) but could not be confirmed in our material on *Bryum rubens*, further indicating the presence of multiple lineages. *Octospora similis* agg. occurs on different species of *Bryum* s.l., including *Bryum* s.str. and *Ptychostomum* (Benkert 1996, Rubio et al. 2000, Vega 2017, Németh 2017b, Eckstein et al. 2020), and on *Pohlia* species (our data) on soil. Reports of *O. similis* agg. growing on other bryophytes (e.g. *Tortula* sp. in García et Conca 2016) may represent other, possibly undescribed species.

Octospora similis on *Bryum rubens* differs from *O. meslinii* by having many vacuoles in living paraphyses, by lacking blackening apothecia, by having smaller ascospores and lipid bodies inside, higher and coarser warts, a different infectious structure, as well as by its completely different habitat and host (Fig. 8f–i, Fig. 9a, c).

Octospora cf. *orthotrichi* is characterised by apothecia with a whitish fimbriate margin, and by ellipsoid, asymmetrical (often one side flattened), warted spores 16.5–19 × 11–13.5 µm in size with one or two larger lipid bodies accompanied by several small ones. Paraphyses are 3–6 µm broad, straight, containing orange pigment. The infection induces galls on the rhizoid tips which are completely covered with interwoven hyphae (Benkert 1998, Egertová et al. 2015). Our description of *O.* cf. *orthotrichi* is based on European material, which is exclusively associated with *Orthotrichum diaphanum*. The type from North America has an unidentified species of *Orthotrichum* not being *O. diaphanum* as a host. Therefore, the collections from Europe may belong to a separate, yet undescribed species. In Europe, *O.* cf. *orthotrichi* occurs on stones or on bark of trees among shoots of its host (Eckstein et Eckstein 2009, Egertová et al. 2015). It is readily

distinguished from *O. meslinii* by its apothecia lacking a blackish pigmentation, somewhat asymmetrical, slightly shorter spores and a different infectious structure, as well as by the identity of its host (Fig. 8j–m).

Further *Octospora* species with similar habitat preference

In addition to the abovementioned taxa, there are six other *Octospora* species growing exclusively or occasionally on saxicolous bryophytes: *O. hygrohypnophila* (host: *Hygrohypnum luridum*; Dissing et Sivertsen 1983), *O. guestfaliensis* (host: *Tortella tortuosa*; Benkert 2009), *O. musci-muralis* var. *neglecta* (host: *Schistidium* sp.; Németh 2017b, Eckstein et al. 2020), *O. doebbeleri* (host: *Dicranoweisia cirrata*; Sochorová et al. 2021), *O. svrcekii* (host: *Cratoneuron filicinum*; Benkert 1998, Sochorová et al. 2020), and *O. erzbergeri* (host: *Pseudoleskeella nervosa*; Benkert 2006, Németh 2017a). All these species differ from *O. meslinii* by, among others, the identity of their hosts and by apothecia not darkening with age.

Revision of specimens of *O. meslinii* in PC and PRM herbaria

Regrettably, the original material of *Humaria meslinii* has not been found in PC. The only specimen found under the name *O. meslinii* was also collected by Meslin in 1950 on a stone wall and was identified by Le Gal. However, it differs fundamentally from the type described and illustrated in the protologue in lacking the characteristic blackish coloration of the apothecium and by its host *Tortula muralis* instead of *Grimmia pulvinata*. As a matter of fact, this collection certainly represents a yet undescribed species (Fig. 10a–c). Because of the lack of type and authentic material in PC, a new lectotype and epitype are designated above (see Typification).

Svrček et Kubička (1961, 1963, 1968) published several finds of *O. meslinii* from the Czech Republic, all from sandy soil. They obviously had a broader taxonomic concept and included different taxa with similar spore morphology in *O. meslinii*, ignoring other important features (e.g. presence or absence of blackish coloration of apothecia, content of paraphyses) and ecology (host bryophyte, habitat requirements). All specimens studied by Svrček and Kubička in PRM proved to be *O. similis* agg. on *Bryum* spp. (Fig. 10d–f). Obviously, Svrček and Kubička did not know the true *O. meslinii*, otherwise they would have noticed the similarities to the genus *Hiemsia*, which was established by Svrček (1969).

Fig. 10. a–c – Specimen from Le Gal's collection associated with *Tortula muralis* and identified by Le Gal as *Humaria meslinii* (PC, Le Gal 282). **d–f** – Specimen of *Octospora similis* agg. associated with *Bryum* sp., collected and identified by Svrček as *Humaria meslinii* (PRM 620213). Scale bars = 20 µm. Photo N. Van Vooren (a), C. Németh (b–f).

CONCLUSIONS

The species closest to *O. meslinii* is *O. pseudoampezzana*, both morphologically and molecularly. *Grimmia pulvinata* and *Schistidium crassipilum*, the respective hosts of these two species, are also closely related, both belonging to the family *Grimmiaceae* (Hernández-Maqueda et al. 2008). It would be possible to use the generic name *Hiemsia* for both species, but we postpone the necessary new combination to a later study. We reject the synonymy of *O. meslinii* and *O. similis*.

Octospora meslinii always occurs on *Grimmia pulvinata*, a moss growing on exposed siliceous and calcareous rocks. Reports of *O. meslinii* observed to be associated with *Schistidium* (e.g. Itzerott 1981, Engel et Hanff 1985) and *Orthotrichum diaphanum* (see Plate II-1, Plate V-1, Fig. 6.8 in Caillet et Moyne 1987) may refer to *O. pseudoampezzana* and *O.* cf. *orthotrichi*, respectively. Reports from *Bryum* s.l. or *Pohlia* growing on soil probably represent *O. similis* agg. (Svrček et Kubička 1961, 1963, 1968, Itzerott 1981), whilst finds associated with other bryophytes (e.g. *Campylopus subulatus* in Vivant 1998; *Tortula* spp. in Caillet et Moyne 1987, García et Conca 2016) may represent undescribed species.

Since the whereabouts of the type collection of *O. meslinii* is unknown, we have designated an illustration in the protologue as the lectotype and one of the recent Hungarian collections as an epitype.

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