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Warts galore – on three new *Lamprospora* De Not. species (Pezizales) from Southern Europe and Macaronesia and a type revision of three species described from the US by F. J. Seaver in the 1910s

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ABSTRACT
Lamprospora bulbiformis M.Vega & Janošík, sp. nov., *L. gibbosa* M.Vega & Janošík, sp. nov. and *L. thelespora* Martínez-Gil, M.Vega & E.Rubio, sp. nov. are described and illustrated based on live collections from Cyprus, France, Portugal and Spain. Phylogenetic analyses of the concatenated LSU, SSU and EF1-α gene sequences show the studied collections of the three species form well supported monophyletic clades. *Lamprospora bulbiformis* sp. nov. infects *Fissidens viridulus* (Sw. ex anon.) Wahlenb., *L. gibbosa* sp. nov. has *F. crassipes* Wilson ex Bruch & Schimp. as host and *L. thelespora* sp. nov. grows on *Cheilothela chloropus* (Brid.) Broth. Three *Lamprospora* De Not. species namely *L. tuberculata* Seaver, *L. tuberculatella* Seaver and *L. spinulosa* Seaver with a slightly similar ascospore ornamentation were described by Seaver from US collections. Results of our studies of their types and additional material collected by Seaver are presented. The host of *L. tuberculata* is *Pleuridium subulatum* (Hedw.) Rabenh., that of *L. tuberculatella* is a species of *Weissia* Hedw. and that of *L. spinulosa* is *Physcomitrium pyriforme* (Hedw.) Bruch & Schimp. It has yet to be proven that species of *Lamprospora* described from North America also occur in Europe. European collections assigned to any *Lamprospora* described from North America require revision. It is not unlikely that many or even all of them represent taxa yet to be described. A considerable part of existing literature on bryophilous Pezizales needs to be reevaluated.

KEY WORDS
Ascomycota,
bryoparasitic fungi,
Pyronemataceae,
ecology,
new species.

RÉSUMÉ

Verrues à foison – sur trois nouvelles espèces de Lamprospora *De Not. (Pezizales) de l'Europe du Sud et de Macaronésie et une révision des types de trois espèces décrites des États-Unis par F. J. Seaver dans les années 1910.*

Lamprospora bulbiformis M.Vega & Janošík, sp. nov., *L. gibbosa* M.Vega & Janošík, sp. nov. et *L. thelespora* Martínez-Gil, M.Vega & E.Rubio, sp. nov. sont décrites et illustrées à partir de récoltes vivantes provenant de Chypre, France, Portugal et Espagne. Des analyses phylogénétiques des séquences concaténées des gènes LSU, SSU et EF1-α montrent que les récoltes étudiées des trois espèces forment des clades monophylétiques robustes. *Lamprospora bulbiformis* sp. nov. infecte *Fissidens viridulus* (Sw. ex anon.) Wahlenb., *L. gibbosa* sp. nov. a pour hôte *F. crassipes* Wilson ex Bruch & Schimp. et *L. thelespora* sp. nov. pousse sur *Cheilothela chloropus* (Brid.) Broth. Trois espèces de *Lamprospora* De Not. avec une ornementation sporale un peu ressemblante, notamment *L. tuberculata* Seaver, *L. tuberculatella* Seaver et *L. spinulosa* Seaver, ont été décrites par Seaver à partir de récoltes américaines. Les résultats de nos études de leurs types et de matériel supplémentaire récolté par Seaver sont présentés. L'hôte de *L. tuberculata* est *Pleuridium subulatum* (Hedw.) Rabenh., celui de *L. tuberculatella* est une espèce de *Weissia* Hedw. et celui de *L. spinulosa* est *Physcomitrium pyriforme* (Hedw.) Bruch & Schimp. Il reste à démontrer que des espèces de *Lamprospora* décrites d'Amérique du Nord apparaissent aussi en Europe. Les récoltes européennes attribuées à toutes espèces de *Lamprospora* décrites d'Amérique du Nord doivent être révisées. Il est assez probable qu'un grand nombre, voire toutes, représentent des taxons qui restent encore à décrire. Une part considérable de la littérature existante sur les Pézizales bryophiles doit donc être réévaluée.

MOTS CLÉS
Ascomycota,
champignons bryoparasitaires,
Pyronemataceae,
écologie,
espèces nouvelles.

INTRODUCTION

Species belonging to the bryophilous Pezizales – these comprise the genera *Octospora* Hedw., *Lamprospora* De Not., *Neottiella* (Cooke) Sacc., *Octosporopsis* U.Lindem. & M.Vega, *Octosporella* Döbbeler and *Filicupula* Y.J.Yao & Spooner – often occur with their small-sized bryophyte hosts in ecological niches not or not yet colonized by the more competitive vascular plants. Sites such as stones and rocks, the bark of trees and ± disturbed soil attract diverse bryophytes and ascomycetes attached on their leaves, stems, or thalli. Benkert (1995) pointed out that a considerable number of collections of bryophilous Pezizales come from habitats with high anthropogenic disturbance, however a few species are described and reported from unspoiled or inaccessible natural habitats only. Surprisingly high species diversity has been shown from studies in urban areas. Németh (2020) presents 150 occurrences of 12 bryophilous Pezizales from Hungarian graveyards, Vega (2017) lists 28 species and varieties for the City of Hamburg, Eckstein & Eckstein (2009) detail 18 species and varieties from the Old Botanical Garden, Göttingen, an area of 5 hectares. Finally – though the locality is not within an urban area but exposed to regular human exploitation – we would like to mention that Vega *et al.* (2013) report seven species of bryophilous Pezizales from a sand pit which barely measures 1 hectare.

Bryophilous Pezizales have been documented from all continents and from diverse climatic zones, from the temperate zone to the tropics to regions with tundra or boreal climate. Results from both morphological and phylogenetic studies indicate that the diversity of species of bryophilous Pezizales and the number of bryophytes suitable as their hosts are more numerous than first thought. Field studies carried out by us in Southern Europe and Macaronesia and numerous collections and documentations received from colleagues show that there is still a hidden treasure of numerous unknown taxa to uncover. In this paper we describe three new representatives of the genus *Lamprospora* infecting mosses belonging to the genera *Fissidens* Hedw. and *Cheilothela* Broth. In order to provide an updated picture of three United States species with a slightly similar ascospore ornamentation but different bryophyte hosts – *L. tuberculata* Seaver, *L. tuberculatella* Seaver and *L. spinulosa* Seaver – we summarise results of our type studies.

MATERIAL AND METHODS

Specimen collection and observation

The descriptions of the new species are based on results of the examination of live structures of fresh collections from several localities in Southern Europe and Macaronesia. Most observations were made in tap water. Ascospore ornamentation was also studied after staining with Cotton Blue (CB), the absence of the iodine reaction of the asci was checked with Lugol's solution (IKI). The (non-)existence of refractive vacuolar bodies (VBs) was verified with aqueous Brilliant Cresyl Blue (CRB) and Potassium Hydroxide 3% (KOH). With the exception of the etymology-section and the diagnoses we refer to ascospores as "spores" for brevity, no conidia have been observed. Spore size of the three new species was measured from free spores as well as from spore prints, at least 50 spores were measured. Spore dimensions are always indicated including ornamentation unless otherwise stated; this also applies to spore dimensions

of similar species mentioned in the discussion. Q is used to indicate the length/width ratio of the spores. Scanning electron microscopy (SEM) was performed on air-dried and gold-coated samples. A LEO-438 scanning electron microscope with 15 kV accelerating voltage and about 10 mm working distance was used. All images are by the authors except Figures 5B, C and 6D-F by Andgelo Mombert and Figure 14I by Elisabeth Stöckli, infection sketches are by Jan Eckstein. Collections are listed in alphabetical order by country and from north to south within each country, geographical coordinates are given in the WGS 84 format. Vouchers have been deposited in the public or private herbaria indicated.

DNA extraction, PCR amplification, and sequencing

DNA was extracted from fresh, dried or CTAB-stored apothecia using the Quick-DNA™ Fungal/Bacterial Miniprep Kit (Zymo Research, Irvine, California, United States). Sequence data were generated for three loci: large subunit of ribosomal DNA (LSU) was amplified with primers NL1 and NL4 (O'Donnell 1993) or in combination with primers LSU-octoF (5'-CAACAGGGATTGCCTYAGTAACT-3') and LSU-octoR (5'-GGTCCGTGTTTCAAGACGGGT-3') designed in this study; small subunit of rDNA (SSU) with primers NS1 and NS6 (White *et al.* 1990); and elongation factor 1-alpha (EF1-α) with primers EF1-983F and EF1-1567R (Rehner & Buckley 2005) or in combination with primers EF1-octoF (5'-GCYGAGCGTGARCGTGGWAT-3') and EF1-octoR (5'-GGTGCATYTCMACRGACTTG-3') designed in this study. PCR products were purified with Agencourt AMPure XP beads (Beckman Coulter, Massachusetts, United States) and both strands of the PCR fragments were sequenced with the primers used for amplification at the Sequencing Laboratory of the OMICS Core Facility, BIOCEV (Vestec, Czech Republic). Obtained sequences were checked and edited in Geneious 9.1 (Biomatters, Auckland, New Zealand) and deposited in GenBank.

Phylogenetic analyses

Specimens used in the analysis and their GenBank accession numbers are listed in Table 1. Newly obtained sequences of LSU, SSU and EF1-α together with other sequences of bryophilous Pezizales, as well *Otidea concinna* (Pers.) Sacc., serving as an outgroup, were aligned with MAFFT (online version 7) using the E-INS settings (Katoh *et al.* 2019). The most suitable substitution model for each locus and codon position of the concatenated dataset was determined in PartitionFinder 2.1.1 (Lanfear *et al.* 2017), using the BIC and a greedy search. Bayesian analysis (BI) was conducted using MrBayes 3.2.3 (Ronquist *et al.* 2012), with two independent runs of five million generations and four chains, sampling every 1000th generation, the first 25% of samples were discarded as burn-in. Maximum likelihood analysis (ML) was performed using raxmlGUI 2.0 (Edler *et al.* 2021; Stamatakis 2014) and analyzed as a partitioned dataset under the GTRCAT model with 1000 bootstrap iterations. Trees based on analysis of each locus are shown in Appendices 1-3.

RESULTS

Phylogenetic analyses

The total length of the concatenated alignment was 2968 bp (1056 bp from LSU, 1311 bp from SSU, 601 from EF1-α, including gaps), of which 654 were parsimony informative and 844 were variable. Sequenced collections of the individual new species were identical in all sequenced regions and did not show any polymorphism within species. All three new species formed well-supported monophyletic lineages and clearly differed from analysed collections of the other species (Fig. 1). *Lamprospora rehmii* Benkert, *L. pseudoarvensis* M.Vega, Eckstein, Friebes & R.Tena, *L. dicranellae* Benkert and *L. tuberculata* agg. (PRC 4624) were identified as the closest relatives of *L. thelespora* sp. nov. *Lamprospora bulbiformis* sp. nov. and *L. gibbosa* sp. nov. clustered together and formed a strongly supported lineage with *L. cailletii* Benkert, *L. tuberculatella* agg., *L. benkertii* ined. (to be published by Eckstein *et al.*), *L. paechnatzii* Benkert, *L. tuberculata* agg. (ZT Myc 61081) and *L. norvegica* Benkert, Aas & R.Kristiansen.

Interestingly other species with globose spores and ornamentation consisting of warts or tubercles (Figs 13-14) occur in several different lineages within the tree, suggesting changes in the ornamentation type are frequent among bryophilous Pezizales. Furthermore, the two sequenced collections of *L. tuberculata* agg. associated with the same host species, but differing in their infection apparatus, did not cluster together and formed two distinct lineages.

TAXONOMY

Lamprospora bulbiformis M.Vega & Janošík, sp. nov.

MycoBank number. — MB835293.

Etymology. — *bulbiformis* refers to the bulbous warts of the ascospore ornamentation.

Diagnosis. — *Lamprospora bulbiformis* sp. nov. differs from other species of *Lamprospora* by its ascospores with an ornamentation of coarse bulbous warts together with an infection on the rhizoids of *Fissidens viridulus* (Sw. ex anon.) Wahlenb.

Holotype. — **Portugal**, Funchal (Madeira), Jardim Botânico da Madeira, 32°39'43"N, 16°53'43"W, 290 m alt., under trees in a mixed orchard. 17.XII.2014, leg. MV. Host: *Fissidens viridulus*, accompanying bryophytes: *Leptophascum leptophyllum* (Müll.Hal.) J.Guerra & M.J.Cano, *Didymodon* sp. (holotypus B 70 0100012, isotypus PO_F2128).

Additional specimens examined. — **Spain**, Málaga (Málaga), Camino del Jardín Botánico, 36°45'41"N, 4°25'30"W, 60 m alt., on soil in a roadside ditch, 03.I.2017, leg. MV. Host: *F. viridulus*, accompanying mosses: *Aloina* sp., *Didymodon* sp. (paratypus B 70 0100013).

Macroscopic features (Fig. 2A-E)

Apothecia gregarious on soil among shoots of *F. viridulus* and other bryophytes, sessile, 0.5-1 mm in diameter, first spherical, becoming cup-shaped, finally discoid with an inconspicuous

TABLE 1. — List of specimens used in the phylogenetic study together with their GenBank accession numbers. Sequences obtained in this study are highlighted in **bold**.

Species	Herbarium code	Geographic origin, collector	Host	LSU	SSU	EF1-α	References
Lamprospora arvensis	HBG-024465	Germany, M. Vega	*Ceratodon purpureus*	KY858950	–	–	Vega *et al.* (2017)
L. benkertii ined.	PRC 4580	Slovakia, L. Janošík	*Trichostomum crispulum*	MN394614	**MT792706**	**MT783992**	Eckstein *et al.* in press
L. bulbiformis sp. nov.	B 70 0100012 (holotype)	Portugal, M. Vega	*Fissidens viridulus*	**MT792684**	**MT792707**	**MT783993**	–
L. bulbiformis sp. nov.	B 70 0100013 (paratype)	Spain, M. Vega	*F. viridulus*	**MT792685**	**MT792708**	**MT783994**	–
L. cailletii	B 70 0100014	Switzerland, E. Stöckli	*Tortella tortuosa*	MN394604	–	–	Eckstein *et al.* in press
L. campylopodis	HBG-024817	Germany, M. Vega	*Campylopus pyriformis*	MF066054	MK569364	MK569289	Egertová *et al.* (2018b); Sochorová *et al.* (2019)
L. carbonicola	PRC 4118	Czech Republic, L. Janošík	*Funaria hygrometrica*	MH818440	–	–	Vega *et al.* (2019)
L. densireticulata	HBG-024591 (holotype)	France, M. Vega	*Aloina ambigua*	MH818451	–	–	Vega *et al.* (2019)
L. dicranellae	PRC 4619	Austria, L. Janošík	*Ditrichum heteromallum*	**MT792686**	**MT792709**	**MT783995**	–
L. dictydiola	PRM 945794	Czech Republic, Z. Egertová	*Tortula muralis*	MF754056	MK569365	MF754054	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
L. ditrichi	PRC 4620	Czech Republic, L. Janošík	*Ditrichum flexicaule*	**MT792687**	**MT792710**	**MT783996**	–
L. ecksteinii	B 70 0100007	Germany, G. Eckstein	*Phascum curvicolle*	**MT792688**	–	–	–
L. esterlechnerae	PRC 4621	Germany, L. Janošík & M. Vega	*Dicranodontium denudatum*	**MT792689**	–	–	–
L. feurichiana	23168	Germany, J. & G. Eckstein	*Ceratodon purpureus*	MF066039	–	–	Egertová *et al.* (2018b)
L. gibbosa sp. nov.	B 70 0100016 (paratype)	France, M. Vega	*Fissidens crassipes*	**MT792690**	**MT792711**	–	–
L. gibbosa sp. nov.	B 70 0100017 (holotype)	France, M. Vega	*F. crassipes*	**MT792691**	**MT792712**	**MT783997**	–
L. gibbosa sp. nov.	PRC 4665	France, A. Mombert	*F. crassipes*	**MW354921**	–	–	–
L. hispanica	B 70 0100998	Spain, M. Vega	*Aloina aloides*	MN394607	**MT792713**	**MT783998**	Eckstein *et al.* in press
L. kristiansenii	PRM 946422	Czech Republic, Z. Egertová, L. Janošík & A. Polhorský	*Ceratodon purpureus*	MF066045	–	–	Egertová *et al.* (2018b)
L. leptodictya	ZT Myc 61079	Switzerland, E. Stöckli	*Aongstroemia longipes*	MN394610	**MT792714**	–	Eckstein *et al.* in press
L. lubicensis	HBG-024742	Germany, M. Vega & T. Richter	*Hennediella heimii*	**MT792692**	–	–	–
L. lubicensis	PRC 4622	Czech Republic, L. Janošík & Z. Egertová	*H. heimii*	**MT792693**	**MT792715**	**MT783999**	–
L. lutziana	MA-Fungi 90544	Spain, M. Vega, R. Martínez-Gil & J. De La Cruz	*Philonotis fontana*	MN434188	**MT792716**	**MT784000**	Martínez-Gil *et al.* (2019)
L. miniata	PRC 4122	Slovakia, L. Janošík	*Protobryum bryoides*	MH818444	–	–	Vega *et al.* (2019)
L. miniata var. *parvispora*	PRM 945795	Slovakia, Z. Egertová	*Barbula unguiculata*	MF066065	MK569366	MF754055	Egertová *et al.* (2018a, 2018b); Sochorová *et al.* (2019)
L. miniata var. *ratisbonensis*	PRM 946421	Croatia, Z. Egertová	*Didymodon luridus*	MF066064	–	–	Egertová *et al.* (2018b)
L. norvegica	HBG-024743	Switzerland, M. Vega & B. Senn-Irlet	*Ditrichum pusillum*	**MT792694**	**MT792717**	**MT784001**	–
L. paechnatzii	B 70 0100018	Germany, T. Richter & M. Vega	*Bryum* sp.	MN394613	–	–	Eckstein *et al.* in press
L. pseudoarvensis	HBG-024462 (holotype)	Spain, M. Vega	*Pleuridium acuminatum*	NG_060353	–	–	Vega *et al.* (2017)
L. rehmii	S F317032 (epitype)	Spain, R. Martínez-Gil	*P. acuminatum*	MH087070	**MT792719**	–	Vega *et al.* (2018)
L. rehmii	HBG-024745	Spain, R. Martínez-Gil	*P. acuminatum*	MH087069	**MT792718**	–	Vega *et al.* (2018)
L. seaveri	PRC 4581	Montenegro, L. Janošík	*Ceratodon purpureus*	**MT792695**	–	–	–
L. cf. *spitsbergensis*	TRH:8581	Norway, H. Dissing & S. Sivertsen	*Hennediella heimii* var. *arctica*	MG949137	–	–	–
L. stellata ined.	HBG-024746	France, M. Vega	*Dicranella howei*	**MT792696**	–	–	–
L. stellata ined.	PRC 4623	Slovakia, L. Janošík	*D. howei*	**MT792697**	**MT792720**	**MT784002**	–
L. stellata ined.	ZT Myc 61080	Switzerland, E. Stöckli	*D. varia*	**MT792698**	**MT792721**	**MT784003**	–
L. sylvatica	PRM 946415 (holotype)	Ukraine, Z. Egertová & M. Sochor	*Dicranum montanum*	MG947604	MK569367	MK569290	Egertová *et al.* (2018b); Sochorová *et al.* (2019)
L. thelespora sp. nov.	B 70 0100020 (paratype)	Cyprus, M. Vega & C. Hobart	*Cheilothela chloropus*	**MT792699**	**MT792722**	**MT784004**	–
L. thelespora sp. nov.	ERD-5763	Spain, C. Gelpi	*C. chloropus*	**MT792700**	**MT792723**	**MT784005**	–
L. thelespora sp. nov.	MA-Fungi 90701 (holotype)	Spain, R. Martínez-Gil	*C. chloropus*	**MT792701**	**MT792724**	**MT784006**	–

Table 1. — Continuation.

Species	Herbarium code	Geographic origin, collector	Host	LSU	SSU	EF1-α	References
L. thelespora sp. nov.	VIT-Micoteca 9734	Spain, R. Martínez-Gil	*C. chloropus*	**MT792702**	**MT792725**	**MT784007**	–
L. tuberculata agg.	PRC 4624	Slovakia, L. Janošík	*Pleuridium subulatum*	**MT792703**	**MT792726**	**MT784008**	–
L. tuberculata agg.	ZT Myc 61081	Switzerland, E. Stöckli	*P. subulatum*	**MT792704**	**MT792727**	–	–
L. tuberculatella agg.	PRC 4625	Slovakia, L. Janošík	cf. *Trichostomum crispulum*	**MT792705**	**MT792728**	**MT784009**	–
L. verrucispora	HBG-1412 (holotype)	Germany, M. Vega	*Campylopus pyriformis*	MN994551	MN994527	MN990993	Sochorová *et al.* (2020)
L. verrucispora	PRM 953062	Germany, M. Vega	*C. pyriformis*	MN994550	MN994526	MN990992	Sochorová *et al.* (2020)
L. verrucispora	PRM 953061	Netherlands, H. van der Kolk	*C. pyriformis*	MN994549	–	–	Sochorová *et al.* (2020)
Neottiella albocincta	PRM 945796	Slovakia, P. Včelička	*Atrichum undulatum*	MF754059	–	–	Egertová *et al.* (2018a)
N. rutilans	46853	Poland, J. Eckstein	*Oligotrichum hercynicum*	MK569313	MK569336	MK569288	Sochorová *et al.* (2019)
N. vivida	PRM 945797	Czech Republic, Z. Egertová	*Polytrichum piliferum*	MF066068	MK569337	MF754051	Egertová *et al.* (2018a, 2018b); Sochorová *et al.* (2019)
Octospora affinis	PRM 945798	Czech Republic, A. Polhorský, L. Janošík & Z. Egertová	*Orthotrichum affine*	MF754075	MK569347	MF754045	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
O. americana	S F43718 (holotype)	United States, G. Thor	*Forsstroemia trichomitria*	MN967346	MN994516	MT078729	Sochorová *et al.* (2020)
O. bridei	PRM 935151	Czech Republic, Z. Egertová	*Ephemerum minutissimum*	MF754061	MT001890	–	Egertová *et al.* (2018a); Sochorová *et al.* (2020)
O. conidiophora	PRM 951743 (holotype)	South Africa, Z. Egertová & M. Sochor	*Trichosteleum perchlorosum*	MK569321	MK569351	MK569297	Sochorová *et al.* (2019)
O. erzbergeri	PRM 945799	Czech Republic, Z. Egertová	*Pseudoleskeella nervosa*	MF754068	MK569340	MF754042	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
O. cf. *excipulata*	PRM 945800	Czech Republic, Z. Egertová	*Funaria hygrometrica*	MF754062	MK569369	MF754047	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
O. gyalectoides agg.	B 70 0100075	Germany, J. Eckstein	*Pottia lanceolata*	MT001891	MT001889	MN990995	Sochorová *et al.* (2020)
O. humosa agg.	PRM 945802	Czech Republic, Z. Egertová	*Polytrichum piliferum*	MF754074	MK569343	MF754043	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
O. hygrohypnophila	PRM 953063	France, M. Vega	*Hygrohypnum luridum*	MN994542	MN994522	MN990987	Sochorová *et al.* (2020)
O. ithacaensis	PRM 945803	Czech Republic, Z. Egertová	*Marchantia polymorpha*	MF754071	MK569346	–	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
O. kelabitiana	PRM 945781	Malaysia, Z. Egertová & M. Sochor	*Riccardia* sp.	MF754065	MK569372	MF754048	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
O. leucoloma	PRM 945804	Czech Republic, Z. Egertová	*Bryum argenteum*	MF754063	MK569370	–	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
O. cf. *orthotrichi*	CNF 2/10561	Croatia, Z. Egertová & M. Sochor	*Orthotrichum diaphanum*	MK569314	MK569342	MK569311	Sochorová *et al.* (2019)
O. pannosa	PRC 4124 (isotype)	Germany, T. Richter & M. Vega	*Brachytheciastrum velutinum*	MN994529	–	–	Sochorová *et al.* (2020)
O. phagospora	PRM 945805	Germany, M. Vega	*Pohlia lutescens*	MF754072	MK569344	MF754046	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
O. pseudoampezzana	PRM 935156	Czech Republic, Z. Egertová & M. Sochor	*Schistidium crassipilum*	MF754069	MK569339	MF754050	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
O. splachnophila	O74755 (paratype)	Norway, R. Kristiansen	*Splachnum vasculosum*	MH886392	–	–	–
O. svrcekii	PRC 4125	Slovakia, L. Janošík	*Cratoneuron filicinum*	MN994537	MN994525	MN990991	Sochorová *et al.* (2020)
O. svrcekii	PRM 951720	Croatia, Z. Egertová, N. Matočec & I. Kušan	*C. filicinum*	MN967348	MN994518	MN974532	Sochorová *et al.* (2020)
O. svrcekii	PRM 953067	Spain, M. Vega & R. Martínez-Gil	*C. filicinum*	MN994538	MN994524	MN990990	Sochorová *et al.* (2020)
O. wrightii	PRC 4617	Czech Republic, L. Janošík	*Amblystegium serpens*	MN994534	MN994517	MN990994	Sochorová *et al.* (2020)
O. wrightii	PRC 4618	Czech Republic, L. Janošík	*A. serpens*	MN994535	–	–	Sochorová *et al.* (2020)
O. wrightii	PRM 945807	Czech Republic, Z. Egertová	*A. serpens*	MF754070	MK569345	MT078728	Egertová *et al.* (2018a); Sochorová *et al.* (2019, 2020)
Octosporella erythrostigma	TUR 178060	Denmark, S. Huhtinen	*Frullania dilatata*	EU940108	EU940035	–	Stenroos *et al.* (2010)
O. perforata	PRM 945808	Czech Republic, Z. Egertová	*Porella platyphylla*	MF754060	MK569368	MF754052	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
Octosporopsis erinacea	PRM 945774 (isotype)	Malaysia, Z. Egertová & M. Sochor	*Dumortiera hirsuta*	MF754057	MK569338	MF754041	Egertová *et al.* (2018a); Sochorová *et al.* (2019)
O. nicolai	UL151-13	Germany, M. Vega	*Lunularia cruciata*	KF771033	–	KF771042	Lindemann *et al.* (2014)
Otidea concinna	KH.09.183 (S) (epitype)	Sweden, K. Hansen & I. Olariaga	-	NG_060279	NG_064990	KM823275	Hansen & Olariaga (2015); Schoch *et al.* (2012)

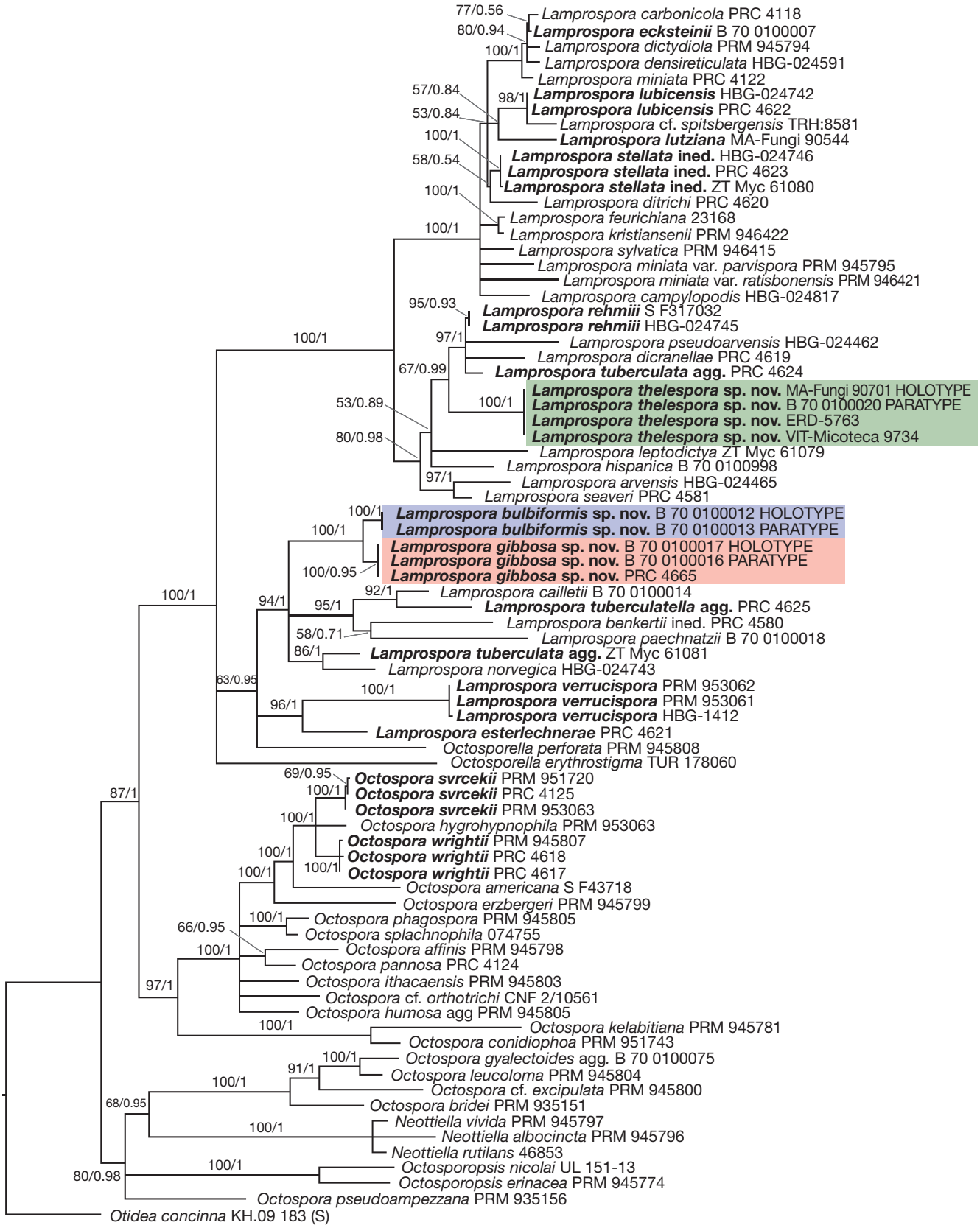

Fig. 1. — RAxML phylogram obtained from the combined LSU, SSU and EF1-α sequences showing the phylogenetic relationship of the three new *Lamprospora* De Not. species among bryophilous Pezizales. Numbers above branches represent RAxML bootstrap support values and Bayesian posterior probability scores, respectively. Nodes for which RAxML bootstrap support values were below 50 were collapsed. GenBank accession numbers are indicated in Table 1. New species described in this study are highlighted in color. Species with globose or subglobose ascospores (Q < 1.1) and ornamentation consisting of isolated warts or tubercles are highlighted in **bold**.

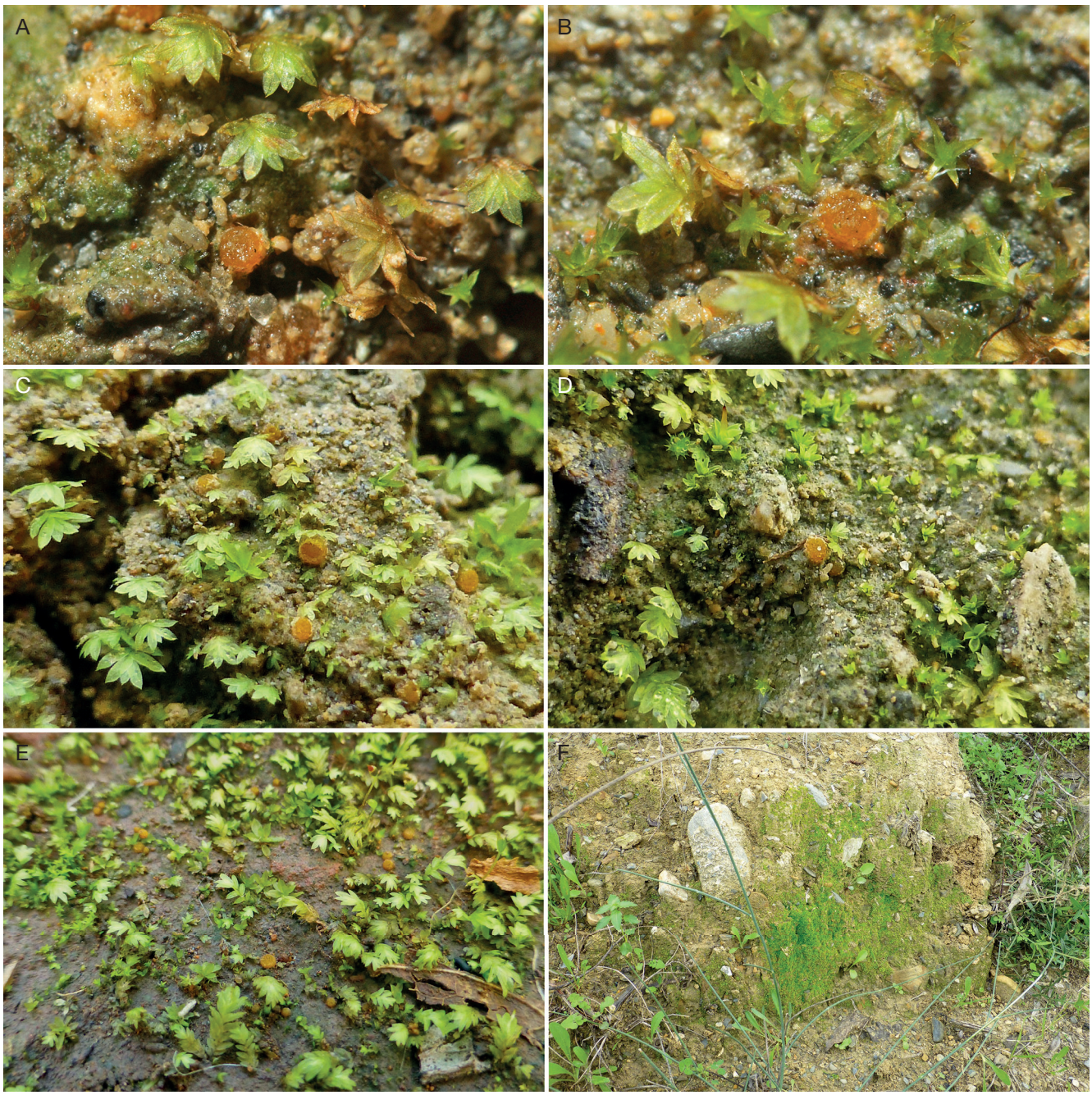

Fig. 2. — *Lamprospora bulbiformis* M.Vega & Janošík, sp. nov. (**A**-**D**, **F**, paratype B 70 0100013; **E**, holotype B 70 0100012) **A**-**E**, apothecia between shoots of *Fissidens viridulus* (Sw. ex anon.) Wahlenb.; **F**, habitat.

fimbriate margin; hymenium pale-orange to orange, margin and outer surface slightly paler than the hymenium; subiculum present, whitish *en masse*.

Microscopic features (Figs 3-4)

Asci

Straight, cylindrical, narrowing toward base, 180-310 × 18-23 µm, operculate, IKI-, arising from perforated croziers, 8-spored.

Spores

Uniseriate, hyaline, globose, (15)16-17(18) µm diam., with an excentric lipid drop 9-11 µm in diameter. Spore surface generally covered with isolated warts of different sizes, remaining space between the warts showing either no ornamentation or appearing slightly asperulate in SEM. Larger warts in side view mostly hemispherical, bulbous, knobbly and rarely acute; in face view rounded, oval, onion-shaped, dacryoid or pyriform, occasionally also elongated or con-

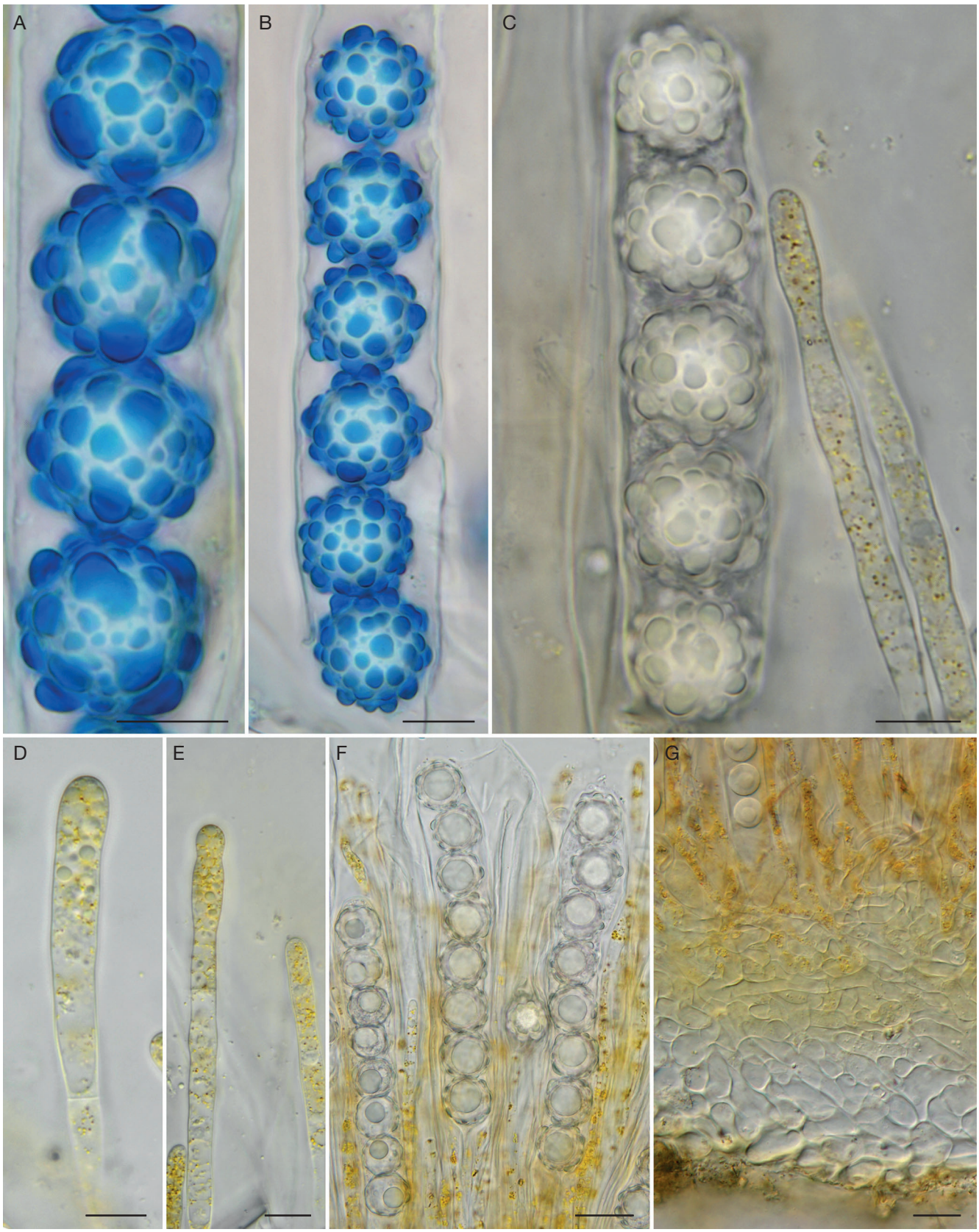

Fig. 3. — *Lamprospora bulbiformis* M.Vega & Janošík, sp. nov. (**A**-**G**, paratype B 70 0100013) **A**, **B**, ascospores inside asci stained with CB; **C**, **F**, ascospores inside asci in water; **D**, **E**, paraphyses in water; **G**, cross-section of an apothecium showing subhymenium, medullary and ectal excipulum in lactic acid. Scale bars: A-E, 10 µm; F-G, 20 µm.

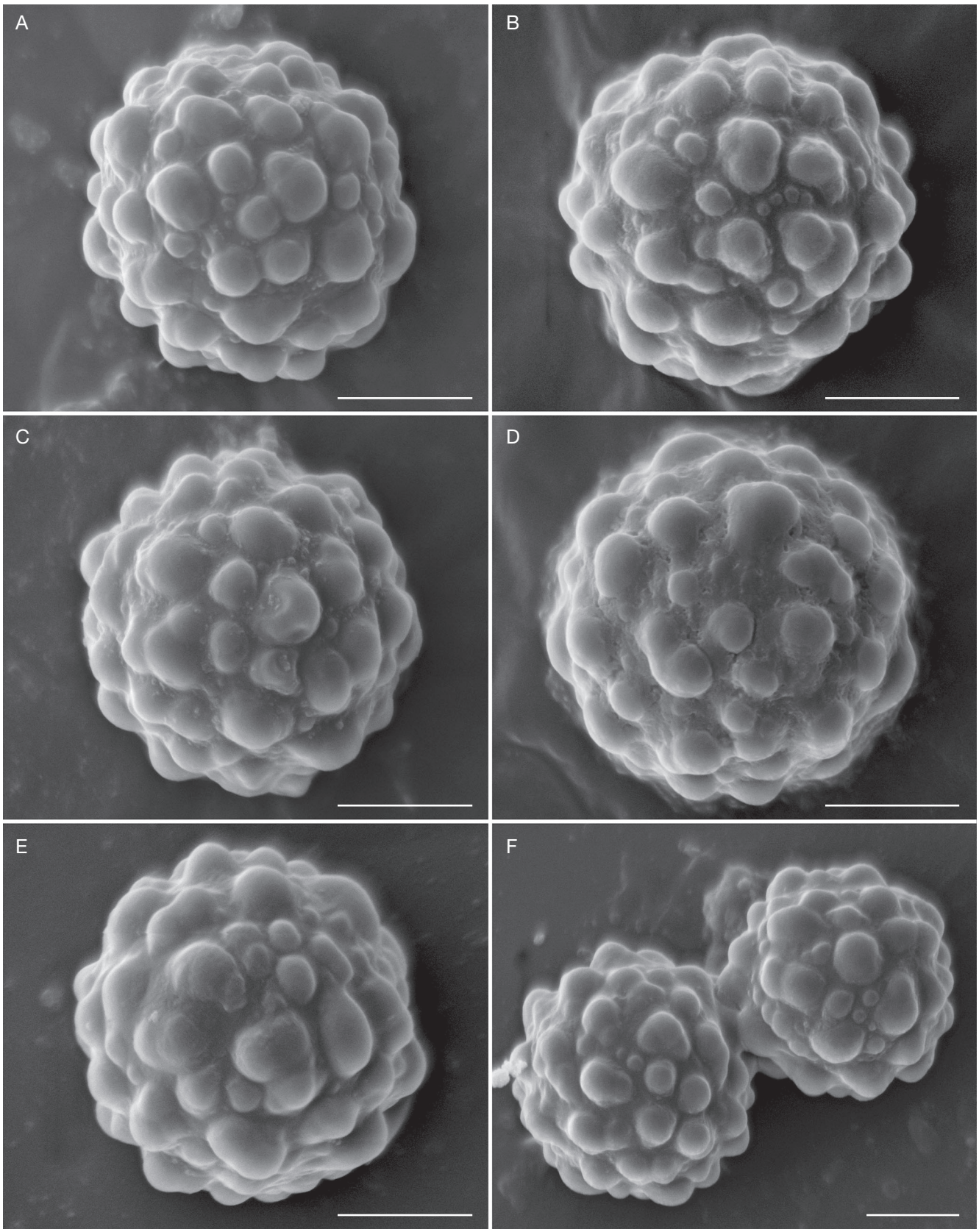

Fig. 4. — *Lamprospora bulbiformis* M.Vega & Janošík, sp. nov. (**A**-**F**. holotype B 70 0100012) SEM photos of ascospores. Scale bars: A-F, 5 µm.

fluent, rarely with subtle interconnections between warts. Larger warts wider than high, 2-4(6.5) µm wide and 1-2.5 µm high. Smaller warts usually ± hemispherical, 0.5-1(1.5) µm wide and 0.4-1 µm high.

Paraphyses
Filiform, cylindrical, straight, 3.5-5.5 µm wide, multiseptate, at times branched at the base, with abundant orange carotenoid pigment, mostly in lipid bodies (LBs), carotenoids occasionally form larger crystals (iridescent in polarised light), pigment turns green in IKI, apical cell slightly thickened, 35-90 × 5-7 µm with colourless slightly refractive vacuolar bodies (VBs) of 1-3 µm in diameter.

Structure of the apothecium
Ectal excipulum consisting of a *textura angularis-intricata* of mostly thin-walled cells 10-30 × 7-20 µm, cells of the outer edge thick-walled, with cell walls 1.5-2.5 µm thick. Medullary excipulum consisting of a *textura intricata* with thin-walled cells 14-40 × 6-10 µm. Margin consisting of a *textura porrecta* with cells 22-54 × 5-12 µm. Subiculum with numerous hyaline septate anchoring hyphae.

Infection (Fig. 8A, B)
Lamprospora bulbiformis sp. nov. infects the rhizoids of the moss *Fissidens viridulus*; no growth modifications of the infected cells were observed. An infection structure consists, as in all other bryophilous Pezizales, of appressorium, infection peg and haustorium. The ellipsoid appressoria are 20-43 × 10-25 µm in side-view and are single-celled or sometimes with a thin septum. They are mostly free and not covered by accompanying hyphae. From the appressorium an infection peg grows through the rhizoid wall forming a ramified haustorium inside the host cell. The penetration point is surrounded by a circular thickening of the rhizoid cell wall.

Habitat and occurrence (Fig. 2F)
The site of the Portuguese holotype collection is situated in the 'Plantas Agro-Industriais'-section of Funchal's Jardim Botânico da Madeira in a mixed orchard of mainly tropical and subtropical fruit trees. Apothecia grew below them on soil among different mosses.

The Spanish locality is a roadside-ditch with pioneer mosses alongside the road leading to Málaga's botanical garden Jardín Botánico-Histórico La Concepción. Several plants of the host moss near the apothecia showed brown leaves, suggesting the host could be weakened by the infection.

Fissidens viridulus grows on basic to slightly acidic soil in mostly open situations such as banks, grasslands, amongst rocks and also in woodlands. It has a wide-temperate circumpolar distribution occurring in most of Europe, Macaronesia, Africa, Asia, North and Central America as well as in Australia (Smith 2004; Ros *et al.* 2013). In North America it was synonymized with *F. bryoides* Hedw. (Pursell 2007) but most European floras treat it as distinct species, a concept supported by sequencing results (Hassel *et al.* 2013).

Lamprospora gibbosa M.Vega & Janošík, sp. nov.

MycoBank number. — MB835294

Etymology. — *gibbosa* refers to the gibbous warts of the ascospore ornamentation.

Diagnosis. — *Lamprospora gibbosa* sp. nov. differs from other species of *Lamprospora* by its ascospores with an ornamentation densely covered with gibbous warts together with an infection on rhizoids of its host *Fissidens crassipes* Wilson ex Bruch & Schimp.

Holotype. — **France**, Vergons (Alpes-de-Haute-Provence), L'Iscle, torrent La Galange, 43°55'54"N, 6°38'44"E, 900 m alt., on rocks in a mountain brook, 13.X.2017, leg. MV. Host: *Fissidens crassipes*, accompanying bryophytes: *Hygrohypnum luridum* (Hedw.) Jenn., *Pohlia melanodon* (Brid.) A.J.Shaw. (holotypus B 70 0100017, isotypus PRC 4626).

Additional specimens examined. — **France**, Vergons (Alpes-de-Haute-Provence), L'Iscle, torrent La Galange, 43°55'54"N, 6°38'44"E, 900 m alt., on rocks in a stream. 13.X.2017, leg. MV. Host: *F. crassipes* (paratypus, B 70 0100015); France, Ubraye (Alpes-de-Haute-Provence), ruisseau La Bernade, 43°55'37"N, 6°40'0"E, 820 m alt., on rocks in a stream. 03.X.2017, leg. MV. Host: *F. crassipes* (paratypus B 70 0100016); France, Cléron (Doubs), ravin de Valbois, 47°05'32"N, 6°04'52"E, 330 m alt., on rocks in a stream. 05.X.2020, leg. Andgelo Mombert. Host: *F.* cf. *crassipes* (PRC 4665). Add. collection: 10.X.2020 (personal herbarium Gilbert Moyne, GM-20200901); France, Amancey (Doubs), source de Comboyer, 47°02'36"N, 6°05'05"E, 550 m alt., on banks of a stream, 06.X.2020, leg. Andgelo Mombert. Host: *Fissidens* sp. (no material preserved); France, Amondans (Doubs), cascade de l'Adhuy, 47°03'55"N, 6°23'59"E, 330 m alt., on banks of a stream. 10.X.2020, leg. Andgelo Mombert & Gilbert Moyne. Host: *F. crassipes* (GM-20200902). Add. collection: 22.X.2020, leg. Andgelo Mombert (PRC 4666).

Macroscopic features (Fig. 5A-D)
Apothecia gregarious on *F. crassipes* growing on rocks, sessile, 0.5-1.5(2) mm in diameter, first spherical, becoming cup-shaped, finally discoid with an inconspicuous fimbriate margin or no raised margin at all; hymenium bright-orange, outer surface slightly paler than the hymenium.

Microscopic features (Figs 6, 7)
Asci
Straight, cylindrical, narrowing toward base, 200-350 × 16-28 µm, operculate, IKI-, arising from perforated croziers, 8-spored.

Spores
Hyaline, uniseriate, globose, (14)15-17 µm diam., with an excentric lipid drop 9-11 µm in diameter. Spore surface densely covered with isolated warts of varying size. Warts in side view hemispherical, gibbous, in face view also pyriform, packed, elongated or confluent, few warts with a punctiform cavity visible after staining in CB. Larger warts wider than high, 2-3(4) µm wide and 0.6-1(1.2) µm high; smaller warts ± hemispherical, approx. 0.5 µm wide and 0.5 µm high.

Paraphyses
Filiform, cylindrical, straight, 3-5 µm wide, multiseptate, occasionally branched at the base, with sparse carotenoid pale-orange pigment, mostly in lipid bodies (LBs), pigment turns green in

Fig. 5. — *Lamprospora gibbosa* M.Vega & Janošík, sp. nov. (**A**, **F**, holotype B 70 0100017; **B**, **C**, PRC 4665; **D**, **E**, paratype B 70 0100016). **A**-**D**, apothecia between shoots of *Fissidens crassipes* Wilson ex Bruch & Schimp.; **E**, **F**, habitat.

IKI, apical cell slightly thickened, 40-80 × 4-7 µm with colourless slightly refractive vacuolar bodies (VBs) of 1-2.5 µm in diameter.

Structure of the apothecium

Ectal excipulum consisting of a *textura angularis* of mostly thin-walled cells 20-40 × 17-30 µm, cells of the outer edge thick-walled, with cell walls 1-1.5 µm thick. Medullary excipulum consisting of a *textura intricata* with thin-walled cells 10-40 × 5-8 µm. Margin consisting of a *textura prismatica*.

Infection (Fig. 8C, D)

Lamprospora gibbosa sp. nov. infects the rhizoids of the aquatic moss *Fissidens crassipes*, infected cells appear swollen and shorter than uninfected ones. The ellipsoid single-celled appressoria are 13-22 × 6-14 µm in side view. They are mostly free and only weakly differentiated from adjacent hyphae. From the appressorium an infection peg grows through the rhizoid wall forming a ramified haustorium inside the host cell.

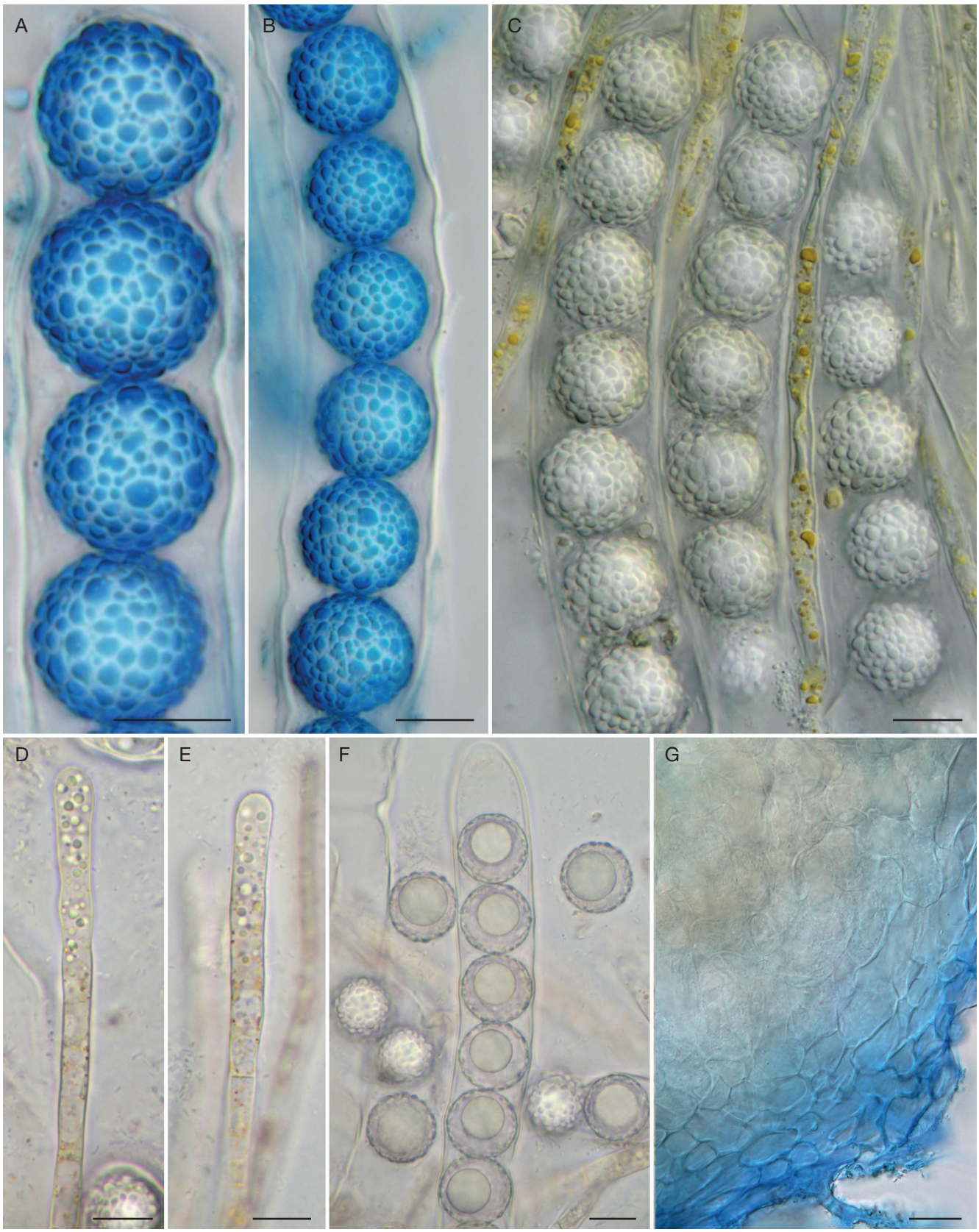

Fig. 6. — *Lamprospora gibbosa* M.Vega & Janošík, sp. nov. (**A**-**C**, **G**, isotype PRC 4626; **D**-**F**, PRC 4666). **A**, **B**, ascospores inside asci stained with CB; **C**, **F**, ascospores inside asci and free ascospores in water; **D**, **E**, paraphyses in water; **G**, cross-section of an apothecium showing part of medullary and ectal excipulum in CB. Scale bars: A-F, 10 µm; G, 20 µm.

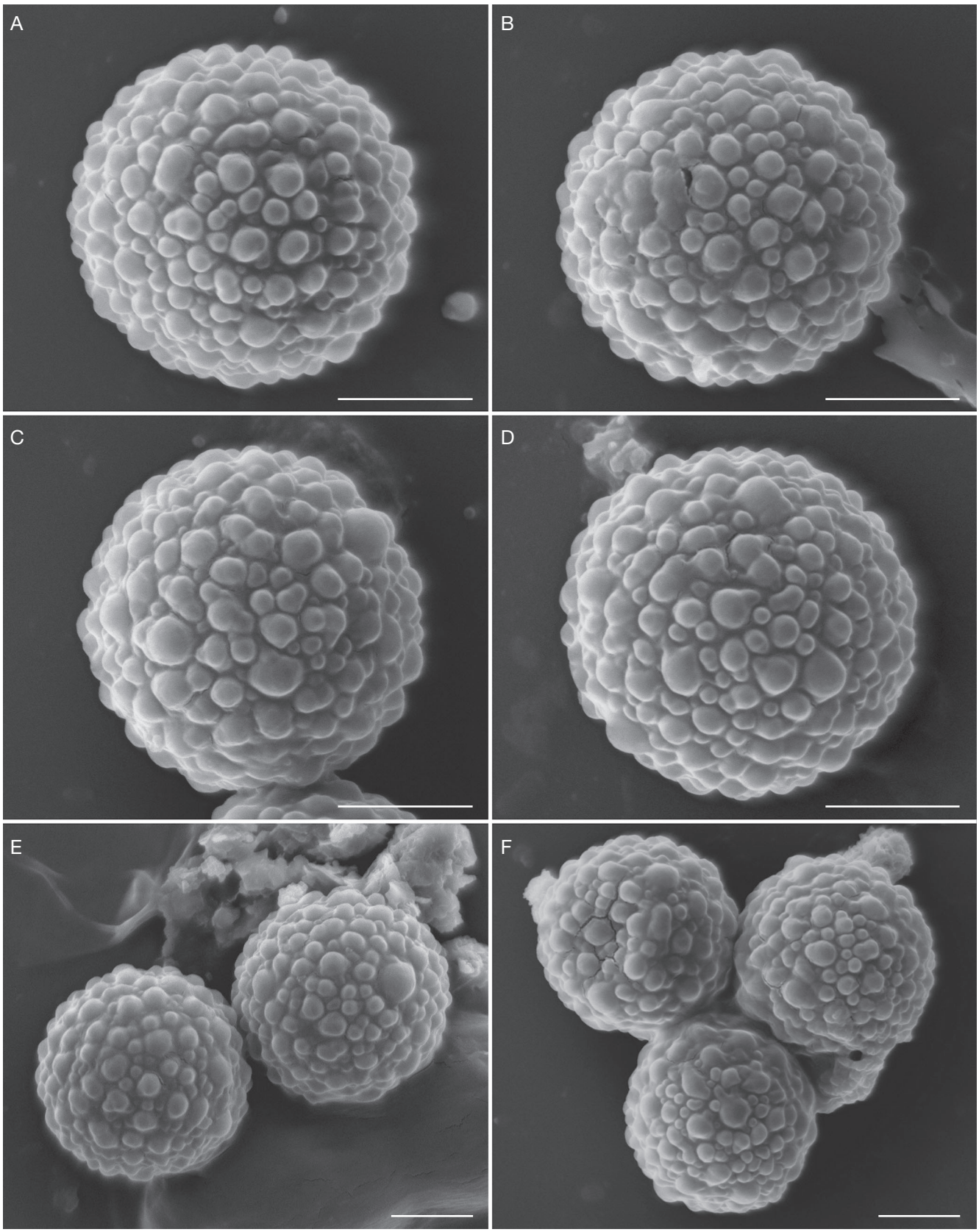

Fig. 7. — *Lamprospora gibbosa* M.Vega & Janošík, sp. nov. (**A**-**F**, holotype B 70 0100017). SEM photos of ascospores. Scale bars: A-F, 5 µm.

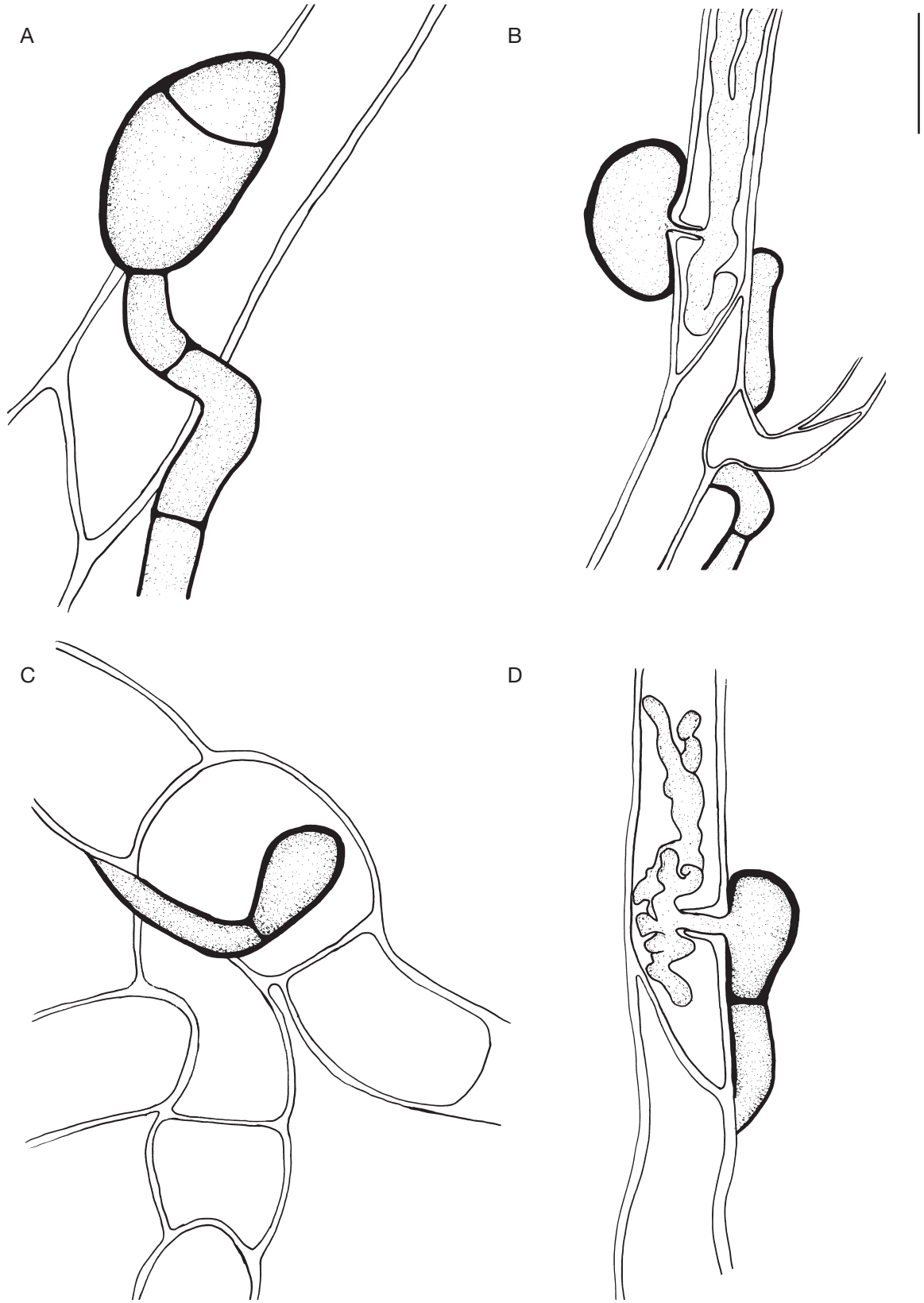

Fig. 8. — Infection structures. *Lamprospora bulbiformis* M.Vega & Janošík, sp. nov. (**A**, **B**, paratype B 70 0100013). **A**, appressorium on a rhizoid in surface view; **B**, appressorium, infection peg and haustorium on a rhizoid in optical section. *Lamprospora gibbosa* M.Vega & Janošík sp. nov. (**C**, **D**, holotype B 70 0100017). **C**, appressorium on a rhizoid in surface view; **D**, appressorium, infection peg and haustorium on a rhizoid in optical section. Scale bar: 20 µm.

Habitat and occurrence (Fig. 5E, F)
All collections of *L. gibbosa* sp. nov. were found on *F. crassipes* colonizing siliceous rocks in streams shaded by the riparian vegetation. Infected moss plants grew at or below water level and often were densely coated with lime. On the occasion of an excursion to the localities in southern France nine months later in May 2018, the boulders inhabited by *F. crassipes* were entirely submerged.

Fissidens crassipes occurs on rocks and walls in or alongside streams and rivers with a preference for basic and calcareous bases. It is somewhat pollution resistant and can even live in canals, irrigation channels or fountains. *Fissidens crassipes* is frost-sensitive (Florschütz *et al.* 1972) and, in Europe, has a southern-temperate distribution with southern Scandinavia as the northern limit. It further occurs in Macaronesia, Asia, North and Central Africa and Australia but is missing in North America (Smith 2004; Pursell 2007; Ros *et al.* 2013).

Lamprospora thelespora
Martínez-Gil, M.Vega & E.Rubio, sp. nov.

MycoBank number. — MB835295

Etymology. — *thelespora* refers to the warts of the ascospores reminiscent of the teats on a cow's udder.

Diagnosis. — *Lamprospora thelespora* sp. nov. differs from other species of *Lamprospora* by its ascospores with an ornamentation of ± elongated warts together with an infection on the rhizoids and stems of its host *Cheilothela chloropus* (Brid.) Broth.

Holotype. — **Spain**, Ventosa (La Rioja), 42°25'10"N, 2°37'38"W, 690 m alt., a mossy area in a copse of *Quercus ilex* L., 8.III.2018, leg. RM. Host: *Cheilothela chloropus*, accompanying bryophytes*: Barbula convoluta* Hedw., *Dicranella howei* Renault & Cardot, *Didymodon vinealis* (Brid.) R.H.Zander, *Pleurochaete squarrosa* (Brid.) Lindb., *Riccia sorocarpa* Bisch., *Trichostomum brachydontium* Bruch, *Gongylanthus ericetorum* (Raddi) Nees. (holotypus MA-Fungi 90701, isotypus personal herbarium Rubén Martínez-Gil, RM-2445).

Additional specimens examined. — **Cyprus**. Agios Nikolaos (Paphos), 34°53'7"N, 32°45'19"E, 500 m alt., on banks alongside a road, 1.III.2019, leg. MV & Carol Hobart. Host: *C. chloropus*, accompanying mosses: *Didymodon vinealis*, *Dicranella howei*, *Barbula convoluta*, *Pleurochaete squarrosa* (paratypus B 70 0100020). — **Spain**. Fontecha (Álava), 42°44'29"N, 3°2'10"W, 485 m alt., mossy area amongst *Q. ilex*, 7.XII.2018, leg. RM. Host: *C. chloropus* (RM-2509). Add. collection: 14.XII.2019, leg. Antonio Ezquerro, Asier Ayala and RM (RM-2581); Ventosa (La Rioja), 42°25'10"N, 2°37'40"W, 680 m alt., mossy area under *Q. ilex*, 4.III.2018, leg. RM. Host: *C. chloropus*, accompanying bryophytes: *P. squarrosa*, *Gongylanthus ericetorum*, *Riccia* sp., *Bryum* sp., *Syntrichia* sp. (RM-2444). Add. collection: 5.I.2019 (RM-2533), 16.II.2019, accompanying bryophytes: *G. ericetorum*, *Trichostomum brachydontium*, *Hypnum lacunosum* (Brid.) Bertsch, *Bryum* sp., *Riccia sorocarpa* (RM-2534); Ventosa (La Rioja), 42°25'12"N, 2°37'36"W, 695 m alt., a mossy area in a *Q. ilex* forest, 10.III.2018, leg. RM. Host: *C. chloropus*, accompanying bryophytes: *P. squarrosa*, *Riccia* sp. (VIT-Micoteca 9734). Add. collection: 6.XII.2018 (RM-2512); Almaraz (Cáceres), El Sierro, 39°46'41"N, 5°38'3"W, 360 m alt., among mosses in an old olive grove, 25.I.2013, leg. Celestino Gelpi. Host: *C. chloropus* (ERD-5763). Add. collections: 26.I.2014, 3.I.2015 (no material conserved); Alcaraz (Albacete), Cortijo Palomar, 38°38'43"N, 2°38'11"W, 805 m alt., mossy area under *Q. ilex* near a road, 7.III.1986, leg. R. Ros. Host: *C. chloropus* (MA-Fungi 45890); Parauta (Málaga), Área Recreativa Conejeras, 36°39'41"N, 5°05'45"W, 1160 m alt., mossy area in green space used as pastureland for sheep and goats, 7.II.2020, leg. MV. Host: *C. chloropus* (personal herbarium Marcel Vega, MV200207-01).

Additional specimen, not examined by us. — **Spain**. Villa del Prado (Madrid), 40°15'06"N, 4°16'46"W, 470 m alt., mossy area among oaks, 5.XII.2020, leg. Jorge Hernanz. Host: *C. chloropus* (AH-56109).

Macroscopic features (Fig. 9A-D)
Apothecia scattered, sometimes packed, on soil among shoots of *C. chloropus* and other bryophytes, sessile, 0.7-2.5 mm in diameter, broadly turbinate with a conspicuous fimbriate to shaggy margin up to 350-500 µm; hymenium slightly convex or flattened, bright orange, margin and outer surface paler than the hymenium; subiculum present, whitish.

Microscopic features (Figs 10, 11)
Asci
Straight, cylindrical, narrowing toward base, 225-480 × 22-40 µm, operculate, IKI-, arising from perforated croziers, usually with eight spores, at times also with four normal and four aborted spores.

Spores
Uniseriate, hyaline, globose, (17)18-20(22) µm diam., with an excentric lipid drop (10)11-14 µm in diameter. Spore ornamentation of isolated warts of irregular shape and size, 1-2.5 µm wide and 1-3 µm high, number and distribution of warts on the spore surface varies from one spore to the next but coverage of the surface is rather low. Warts in side view hemispherical, nodulose or rarely acute, but mostly blunt or truncate, the contours of some warts reminiscent of a baby's dummy others resemble a light bulb, especially those with a constricted base. Warts in face view rounded, oval, pyriform or uncinate, but also lenticular, elongated or cuneiform. Warts mostly isolated but also sometimes packed and occasionally confluent, only rarely anastomosing. Spore surface between coarse warts ± rugose or slightly gibbose and often covered with tiny applanate warts, with pustules, in some spores there were short and very thin crests approx. 0.5 µm wide, occasionally anastomosing.

Paraphyses
Filiform, cylindrical, straight, 3-6 µm wide, multiseptate, not branched, with abundant orange carotenoid pigment which turns green in IKI, pigment also occurs in lipid bodies (LBs), apical cell slightly thickened, 40-100 × 5-8 µm with refractive vacuolar bodies (VBs) of 2-5 µm in diameter.

Structure of the apothecium
Ectal excipulum consisting of a 30-70 µm thick layer of *textura angularis-intricata*, a mixture of elongate and isodiametric cells 10-40 × 6-14 µm, with VBs, with walls up to 3 µm thick. Medullary excipulum 180-200 µm thick, consisting of a *textura intricata* of large and wide irregular almost vesiculose hyphae with cells 25-90 × 15-30 µm.

Fig. 9. — *Lamprospora thelespora* Martínez-Gil, M.Vega & E.Rubio, sp. nov. (**A**, RM-2534; **B**, VIT-Micoteca 9734; **C**, RM-2533; **D**, **F**, paratype B 70 0100020; **E**, holotype MA-Fungi 90701). **A**-**D**, apothecia between shoots of *Cheilothela chloropus* (Brid.) Broth; **E**, **F**, habitat.

Within the hardly differentiated subhymenium of cylindrical cells 3.5-6 µm wide these hyphae reduce in size and appear more or less rounded. Anchoring hyphae of the subiculum are 4.5-9.5 µm wide, septate, with cell walls 1-2.5 µm thick, apex rounded or obtuse.Margin prominent consisting of chains of hyaline cells, with walls 2 µm thick, at the base parallel to the paraphyses, later abruptly changing direction and oriented perpendicular to the paraphyses. At the same time cells gradually become shorter and thicker and end in claviform or pyriform elements of 20-45 × 11-21 µm, the latter contain VBs up to 5 µm.

Infection (Fig. 12)

Lamprospora thelespora sp. nov. infects the rhizoids and cortical cells of subterranean stems – for information on this growth form see Porley (1992) – of the moss *Cheilothela chloropus*; no growth modifications of the infected cells were observed. Appressoria are 40-70 × 20-40 µm in side-view with mostly two septa and sometimes with additional oblique walls. They are first partly, and later completely covered, by a layer of accompanying hyphae. From the middle cell of an appressorium an infection peg grows through the moss cell wall forming a numerously ramified haustorium inside the infected cell. The

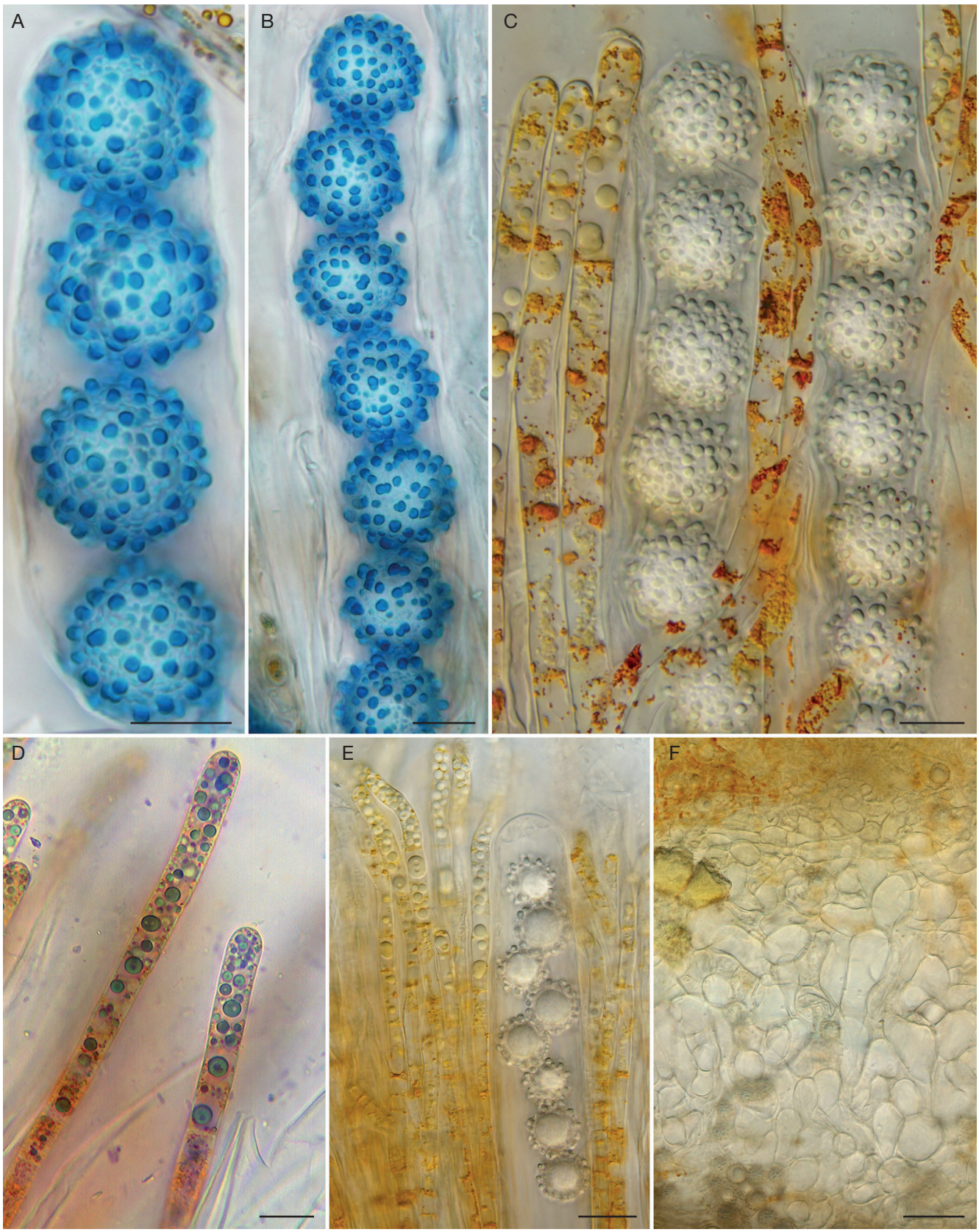

Fig. 10. — *Lamprospora thelespora* Martínez-Gil, M.Vega & E.Rubio, sp. nov. (**A**, **B**, **E**, **F**, paratype B 70 0100020; **C**, VIT-Micoteca 9734; **D**, RM-2533). **A**, **B**, ascospores inside asci stained with CB; **C**, **E**, ascospores inside asci and paraphyses in water; **D**, paraphyses in CRB; **F**, cross-section of an apothecium showing subhymenium, medullary and part of ectal excipulum in water. Scale bars: A-D, 10 µm; E, 20 µm; F, 50 µm.

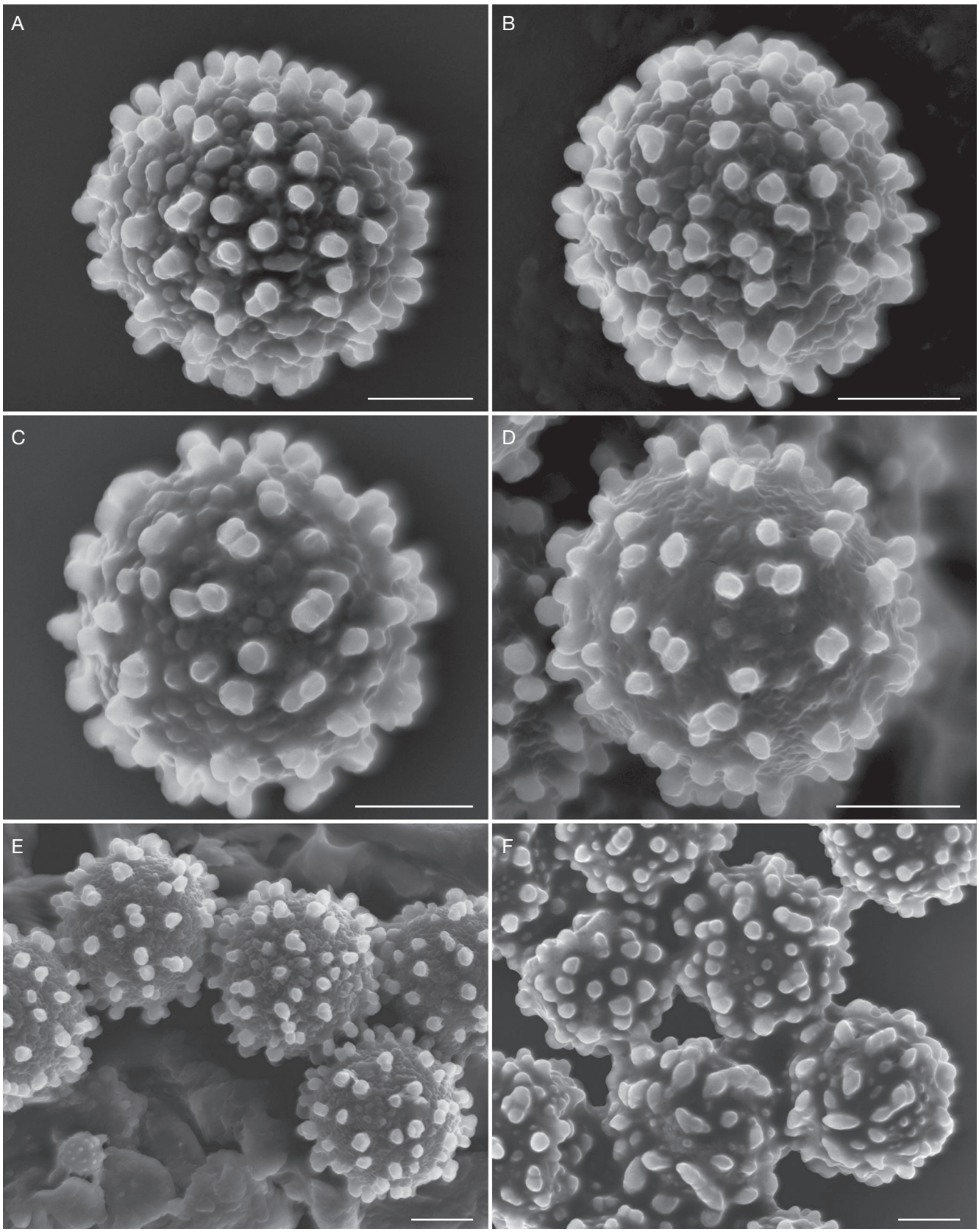

FIG. 11. — *Lamprospora thelespora* Martínez-Gil, M.Vega & E.Rubio, sp. nov. (**A**-**F**. RM-2534). SEM photos of ascospores. Scale bars: A-F, 5 µm.

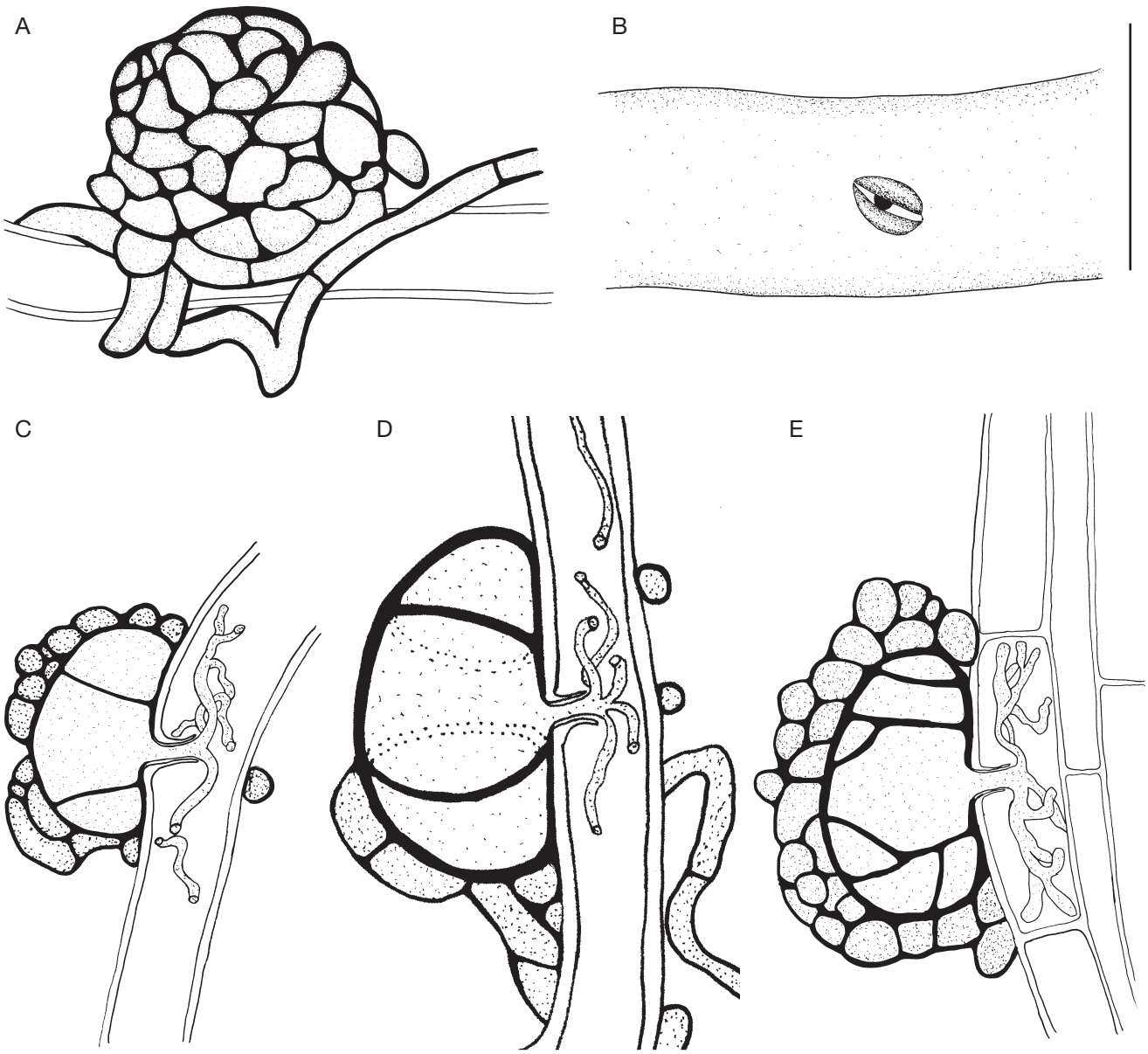

Fig. 12. — *Lamprospora thelespora* Martínez-Gil, M.Vega & E.Rubio, sp. nov. infection structures, RM-2534: **A**, appressorium with a cover of accompanying hyphae on a rhizoid in surface view; **B**, infected rhizoid with removed appressorium showing the penetration point in surface view; **C**, **D**, infection structures on rhizoids in optical section; **E**, infection structures on a cortical cell of subterranean stem in optical section. Scale bar: 50 µm.

penetration point is flanked by two parallel thickenings of the rhizoid cell wall resulting in a slit-like structure.

Habitat and occurrence (Fig. 9E, F)

The site of the Spanish holotype collection is situated in an oak forest with *Quercus ilex* subsp. *ballota* (Desf.) Samp. as the main species, other vascular plants are *Q. coccifera* L., *Cistus albidus* L., *C. salviifolius* L., *Erica cinerea* L., *Genista scorpius* (L.) DC., *Asparagus acutifolius* L., *Ononis tridentata* L. The soil is not excessively acidic. The rocks are conglomerates of siliceous gravels embedded in matrix or cement, a little calcareous and marls with some lime and even plaster in some areas.

The Cypriot locality is in the Paphos Forest south of the Troodos Mountains, the vegetation is dominated by *Pinus brutia* Ten. and *P. halepensis* Mill. growing on calcareous rendzina soil. There were numerous patches of *C. chloropus* on banks alongside a road leading to Tzelefos Bridge, several plants' rhizoids were infected by *L. thelespora* sp. nov. Differing from the Spanish collections, apothecia not only grew exposed on the soil among moss plants but often were hidden and embedded in host moss cushions at the bases of the stems.

Cheilothela chloropus, the host of *L. thelespora* sp. nov., is a pioneer species that occurs in open habitats such as clearings, on rocky ground and in grasslands. It develops an intricate system of underground axes that is a unique feature among

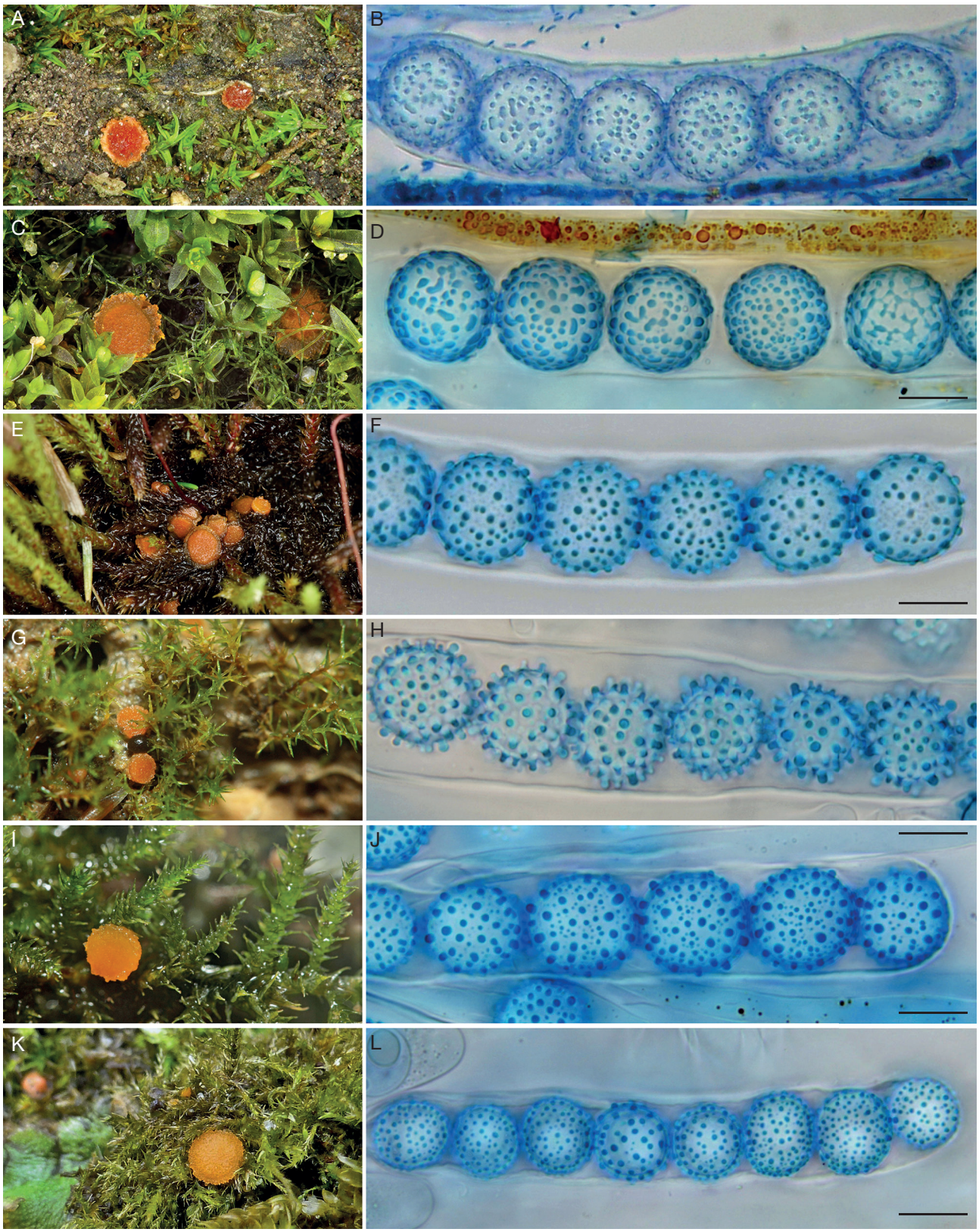

Fig. 13. — Similar species of bryophilous Pezizales with globose or subglobose ascospores (Q < 1.1) and an ornamentation consisting of isolated warts **A**, **B**, *Lamprospora ecksteinii* Benkert (B 70 0100007): **A**, apothecia between shoots of *Microbryum curvicollum* (Hedw.) R.H.Zander (host) and *Weissia* sp.; **B**, ascospores stained with CB; **C**, **D**, *L. lubicensis* Benkert: **C**, apothecia between shoots of *Hennediella heimii* (Hedw.) R.H.Zander (personal herbarium Jan Eckstein, JE-11609); **D**, ascospores stained with CB (PRC 4622); **E**, **F**, *L. lutziana* Boud: **E**, apothecia on shoots of *Philonotis fontana* (Hedw.) Brid. (MA-Fungi 90544); **F**, ascospores stained with CB (NML 2208-10 KM 1); **G**, **H**, *L. stellata* ined. (PRC 4623): **G**, apothecia between shoots of *Dicranella howei* Renault & Cardot; **H**, ascospores stained with CB; **I**-**J**, *Octospora svrcekii* Benkert (PRC 4125): **I**, apothecium on shoots of *Cratoneuron filicinum* (Hedw.) Spruce; **J**, ascospores stained with CB; **K**, **L**, *O. wrightii* (Berk. & M.A.Curtis) J.Moravec; **K**, apothecium on shoots of *Amblystegium serpens* (MV20160306-01); **L**, ascospores stained with cotton blue (PRC 4606). Scale bars: 10 µm.

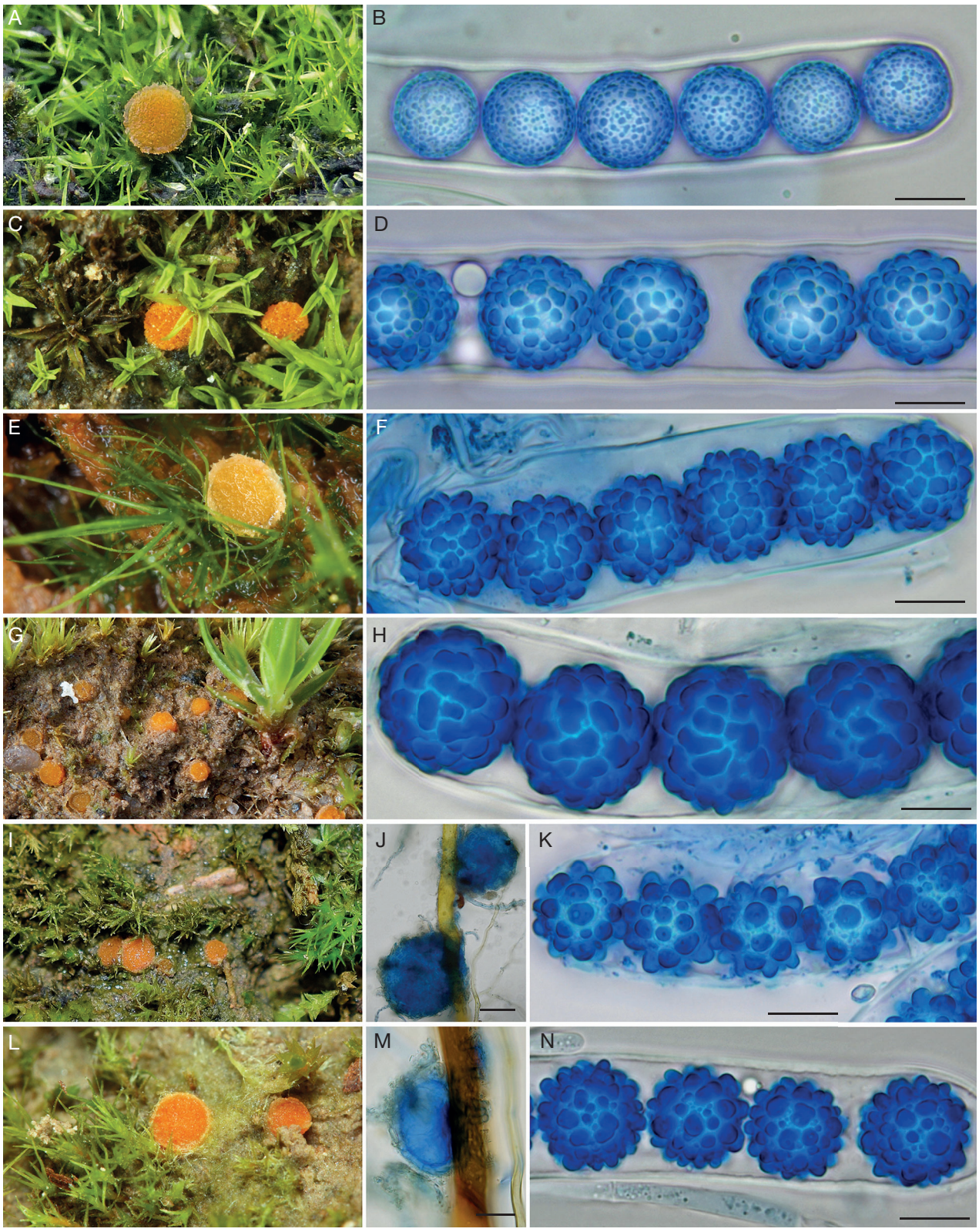

FIG. 14. — Similar species of bryophilous Pezizales with globose ascospores and ornamentation consisting of isolated warts or tubercles **A**, **B**, *Lamprospora verrucispora* M.Vega, Eckstein & Van der Kolk: **A**, apothecium between shoots of *Campylopus pyriformis* (Schultz) Brid. (MV20151107-01); **B**, ascospores stained with CB (isotype PRC 4608); **C**, **D**, *L. tuberculatella* agg. (PRC 4625): **C**, apothecia between shoots of cf. *Trichostomum crispulum* Bruch; **D**, ascospores stained with CB; **E**, **F**, *L. esterlechnerae* Benkert ex F. Hampe & Kleine (PRC 4621): **E**, apothecium between shoots of *Dicranodontium denudatum* (Brid.) E.Britton; **F**, ascospores stained with CB; **G**, **H**: *L. rehmii* Benkert; **G**, apothecia between shoots of *Pleuridium acuminatum* Lindb. (RM-2367); **H**, ascospores stained with CB (S F317032); **I**-**K**, *L. tuberculata* agg. (ZT Myc 61081): **I**, apothecia between shoots of *P. subulatum* (Hedw.) Rabenh.; **J**, hyphae-covered galls stained with CB, **K**, ascospores stained with CB; **L**-**N**, *L. tuberculata* agg. (PRC 4125): **L**, apothecia between shoots of *P. subulatum*; **M**, appressorium covered by a layer of accompanying hyphae stained with CB; **N**, ascospores stained with CB. Scale bars: B, D, F, H, K, N, 10 µm; J, 50 µm; M, 20 µm.

members of the Dicranales (Porley 1992). As a xerophilous and highly dessication-tolerant species (Proctor & Pence 2002) it is widespread in Spain including the Balearic Islands and the Canary Islands on both basic and acidic soils (pers. communication R. M. Ros). It has been detected in most countries of the Mediterranean region (Ros *et al.* 2013), as well as in Northern France and Brittany (Gaume 1956; Werner 1994). According to Porley (2013), *C. chloropus* is a rare species in southern United Kingdom and has also been found in South Africa. Further occurrences from the rest of the world are not known so far.

DISCUSSION

The three new species and their bryophyte hosts

1) Bryophilous Pezizales on Fissidens

Lamprospora bulbiformis sp. nov. and *L. gibbosa* sp. nov. are the first *Lamprospora* species reported having hosts that belong to the moss genus *Fissidens*. So far this has only been known for members of the genus *Octospora* namely *Octospora fissidentis* Benkert & Brouwer and *O. nemoralis* Benkert & Brouwer both infecting *Fissidens bryoides* Hedw. (Benkert & Brouwer 2004). Though *F. bryoides* and *F. viridulus* might occur in the same habitat it would be impossible to confuse the two species of *Octospora,* with ellipsoid spores, with the globose-spored *L. bulbiformis* sp. nov.

2) Bryophilous Pezizales on Cheilothela

No other representative of the bryophilous Pezizales has been reported to infect species of the genus *Cheilothela* so far.

The three new species and other species of Lamprospora with a ± similar spore ornamentation

1) Species with a spore ornamentation similar to L. bulbiformis *sp. nov.*

Lamprospora bulbiformis sp. nov. can be recognised by its spore ornamentation of mostly coarse and scattered small warts. One species with an ornamentation of coarse warts or tubercles is *L. esterlechnerae* Benkert ex F. Hampe & Kleine with spores measuring 14-17 µm diam. However the greater part of its ornamentation consists of conical-truncate tubercles 1-4 µm wide and 1-4 µm high which densely cover the spore surface (Benkert 2011, pers obs.) and not of bulbous warts more loosely spread over the spore surface as in *L. bulbiformis* sp. nov. *Lamprospora esterlechnerae* infects *Dicranodontium denudatum* (Brid.) E.Britton, a moss often occurring in woodlands growing on rotting logs, stumps or similar substrata, it cannot be confused with plants of *Fissidens*.

Other species with a spore ornamentation of coarse warts – though quite different from those of *L. bulbiformis* sp. nov. – are *L. rehmii* and *L. maireana* Seaver both of which have much larger spores and different hosts (Seaver 1914; Benkert 1987, 1994b, 2002; Vega *et al.* 2018).

Last but not least, *Lamprospora tuberculata* has to be considered. Seaver (1912) described *L. tuberculata* based on United States collections and in later works (Seaver 1914, 1928) added further information. We reexamined the type which was from a locality near Yonkers (New York) as well as further contemporary material by Seaver from New York and West Virginia. Contrary to reports by Benkert (1987) and Wang & Kimbrough (1992) we observed *Pleuridium subulatum* (Hedw.) Rabenh. as the host. Astonishingly, a few plants have large irregular shaped rhizoidal tubers which had not been reported for *P. subulatum* in North America but are known from Scandinavia (Jensen 1939; Hallingbäck 2006). Our spore measurements are 15-17 µm diam. with larger tubercles 2-4 µm wide and up to 2.5 µm high. Whereas the host is the same in North American and European collections, there are differences in the spore ornamentation. The tubercles in Seaver's samples are more hemispherical and not so irregularly shaped as in European collections examined in this study or in those documented in Eckstein *et al.* (2014) and Egertová *et al.* (2015). Furthermore, one of the collections presented here as *L. tuberculata* agg. (ZT Myc 61081) and the collection in Egertová *et al.* (2015) induce large galls (60-125 µm in case of ZT Myc 61081) on the rhizoids of the bryophyte host while no galls could be found in the United States material. New collections of *L. tuberculata* from Northern America are needed for DNA analysis to resolve the question whether United States and European collections of *L. tuberculata* represent the same taxon. Coming back to *L. bulbiformis* sp. nov. after the digression on *L. tuberculata* it should be emphasised that members of the moss genus *Fissidens* are easy to recognise even if one is not acquainted with mosses and completely different than species of *Pleuridium* Rabenh.

2) Species with a spore ornamentation similar to L. gibbosa *sp. nov.*

Lamprospora gibbosa sp. nov. is well characterised by its particular spore ornamentation of ± regular, mid-sized hemispherical warts densely covering the spore.

Though the spore ornamentation of *L. tuberculatella* is different than that of *L. gibbosa* sp. nov. – warts of the former are more loosely spread out over the spore surface. We would like to comment on this species, as its concept is far from comprehensible, with differing information available from Seaver (1914, 1928), Wang & Kimbrough (1992) and Benkert (1987, 2002) concerning spore size and bryophyte hosts of the type and other United States collections. Our measurements of Seaver's material (six vouchers) are 16-18 µm diam., which corresponds to the measurements 16-18(20) µm diam. reported by Wang & Kimbrough (1992), and though identification of the bryophyte host to species level was not possible due to a lack of sporophytes, the host of *L. tuberculatella* belongs to the genus *Weissia* Hedw.

Having said this the differences between the numerous diverse collections from different continents assigned to *L. tuberculatella* (Benkert 1987, 2002; Eckstein 2014) and the new *L. gibbosa* sp. nov. are: 1) the spore ornamentation of ± regular mid-sized warts densely covering the spore surface of *L. gibbosa* sp. nov.; 2) its host, *F. crassipes,* belongs to the genus *Fissidens* the plants of which do not resemble any of the moss

species previously suspected to be the host of *L. tuberculatella* (Benkert 2002). *Fissidens crassipes* is not related to them; and 3) the habitat on periodically or permanently flooded rocks.

3) Species with a spore ornamentation similar to L. thelespora *sp. nov.*

Lamprospora thelespora sp. nov. is distinguished from other species of the genus *Lamprospora* by its spore ornamentation of ± elongated warts.

One *Lamprospora* with a spore ornamentation of ± elongated warts or rather spines, hence the species' name, is *L. spinulosa* described from a collection from the New York Botanical Garden (Seaver 1914). Later Seaver (1928) corrects the measurements given in the protologue: spores 18-20 µm diam. and spines up to 1 µm wide and 2 µm high. Wang & Kimbrough (1992) as an outcome of their study of several collections by Seaver give somewhat differing measurements, they describe the species as having "blunt spines densely distributed on spore surface" (Wang & Kimbrough 1992: 49) and mention that *L. spinulosa* is missing in the work of Benkert (1987). They provide a SEM-picture of one spore (Wang & Kimbrough 1992: 15 fig. 21) unfortunately no indication is given in their paper as to which collection the SEM-picture relates. The spore surface on this image is rugose to rough. The spines are visibly higher than wide and apically not only blunt but rounded off, some of them are slightly enlarged to capitate. As far as the host or accompanying mosses are concerned, Wang & Kimbrough (1992) named *Funaria* sp. without specifying voucher numbers. Our revision of the holotype, as well as nine additional collections by Seaver, revealed that spores measure 16-18 µm and the bryophyte host is *Physcomitrium pyriforme* (Hedw.) Bruch & Schimp. This moss also occurs in Europe, however no species of *Lamprospora* has been recorded on it yet. Interestingly *Cheilothela chloropus*, the host of *L. thelespora* sp. nov., has not been recorded in North America so far (Seppelt 2007). Returning to the differences between *L. spinulosa* and the new *L. thelespora* sp. nov. with regard to the spore ornamentation these are as follows: The warts of *L. thelespora* sp. nov. do not cover the spore surface as densely as in *L. spinulosa*, they are less numerous, and leave space for additional small applanate warts or thin and low ridges between the larger warts. Though warts are often elongate they are more or less the same height and width whilst the ratio of height to width is smaller than those of *L. spinulosa*. Warts in *L. thelespora* sp. nov. are more sturdy and not as slender as in *L. spinulosa* and their base is narrower or even constricted whereas the base of the spines *L. spinulosa* in some cases appears to be broad.

To our knowledge no collection of *L. spinulosa* on *Physcomitrium pyriforme* has been published from Europe. The collection assigned to *L. spinulosa* infecting *Dicranella howei* listed in Capoen (2017) does not represent *L. spinulosa* but a new species which will be described in a future paper and is referred to under *Lamprospora stellata* ined. This name is also used in the comparative table and the phylogenetic tree of this paper.

We would like to conclude with the fact that Thind & Batra (1957) described *Lamprospora spinulosa* var. *magnispora* K.S.Thind & L.R.Batra from the Mussoorie Hills, India, with spores measuring 20-24 µm diam. without ornamentation and spines up to 4 µm long. They indicate it had been collected on soil but do not mention any accompanying bryophytes. This fact together with their spore sketch (Thind & Batra 1957: 429 fig. 1C) and the spore size suggest this species could belong to the genus *Ramsbottomia* W.D.Buckley. We can exclude that this species is conspecific with *L. thelespora* sp. nov.

4) Other species with globose or subglobose spores (Q < 1.1) and an ornamentation consisting of isolated warts

Six additional species with rather small warts, all infecting bryophyte hosts different from those of the three newly described species should briefly be mentioned here to make the picture comprehensive (see also Figs 13, 14):

Spores of *L. lubicensis* Benkert measure (14)15-17(18) µm diam., warts are (0.5)1-1.5 µm high and often elongated and/or confluent. *Lamprospora lubicensis* infects *Hennediella heimii* (Hedw.) R.H.Zander (Benkert 1994a).

Lamprospora lutziana Boud. occurs on *Philonotis fontana* (Hedw.) Brid., its spore ornamentation is formed by hemispherical warts 0.5-1.7 µm high, spores measure 15.7-20.3 µm diam. (Boudier 1917, Martínez-Gil *et al.* 2019).

Spores of *L. verrucispora* M.Vega, Eckstein & Van der Kolk measure (13)14-17 µm diam.; they are densely covered with numerous small warts (0.4-0.8 µm high), occasionally some bigger warts (0.8-1.6 µm high) can occur, its host is *Campylopus pyriformis* (Schultz) Brid. (Vega *et al.* 2016).

The spores of the following three species are not globose but subglobose or broadly ellipsoid:

Lamprospora ecksteinii Benkert shows spores that are slightly subglobose, warts are irregularly spread over the spore surface, and the host is *Microbryum curvicollum* (Hedw.) R.H.Zander (Benkert 2009).

Octospora svrcekii Benkert grows on *Cratoneuron filicinum* (Hedw.) Spruce whereas *O. wrightii* (Berk. & M.A.Curtis) J.Moravec infects *Amblystegium serpens* (Hedw.) Schimp., both have subglobose to broadly ellipsoid spores (Benkert 1998, Sochorová *et al.* 2020).

Consequences of the outcome of the type study of Seaver's US species

As a conclusion from our studies of Seaver's type collections we would like to stress that care should be taken when applying names of species of the bryophilous Pezizales described from one continent to collections of another.

- For the time being we are not in a position to judge whether collections from Europe assigned to *L. tuberculata* are conspecific with the United States species or whether they represent new species.

- The diverse United States collections of *L. tuberculatella* on hosts other than *Weissia* sp. mentioned in Benkert (1987, 2002) likely represent different taxa. Further studies are necessary to clarify the identity of any collection from Europe and Australia infecting species of the genus *Weissia*. Collections filed under *L. tuberculatella* occurring on mosses belonging

to other genera require revision, several new species have to be described in the future.

-It has still to be proven that species of *Lamprospora* described from North America also occur in Europe. Therefore, European collections assigned to any *Lamprospora* described from North America require revision as most of them lack information on their bryophyte hosts and the infection mode. It is not unlikely that many or even all of them represent taxa yet to be described. The key in Vega *et al.* (2016) has to be considered as void and should not be used any longer as information on spore measurements and hosts had been merged from literature referring to United States collections as well as from papers dealing with European collections. A considerable part of existing literature on bryophilous Pezizales needs to be reevaluated.

Following the study of available types, we must emphasise the importance of bryophyte host determination and the study of infection modes, in conjunction with spore features and measurements to be crucial for species determination. This is obviously even more true when it comes to numerous easily confused species of *Octospora* lacking spore ornamentation.

The host should always be one of the first characters to consider. Nevertheless, as we have shown in the case of European collections of *L. tuberculata* agg. (Figs 1; 14) even collections from the same host species and with very similar spore ornamentation can sometimes represent distinct species.

As outlined in the introduction bryophilous Pezizales and their hosts appear in diverse habitats many of which are created or marked by human impact. Though the above-mentioned type localities of the three Seaver species might have been deteriorated or destroyed during the more than hundred years since description it would be worth a try to visit the New York Botanical Garden. All three species had been collected there by Seaver and it still is on the same spot. It is not unlikely that new material of these species could be encountered there, this would enable us to complete the species concepts and to gain sequences. We would thus warmly welcome any cooperation-offers from the United States.

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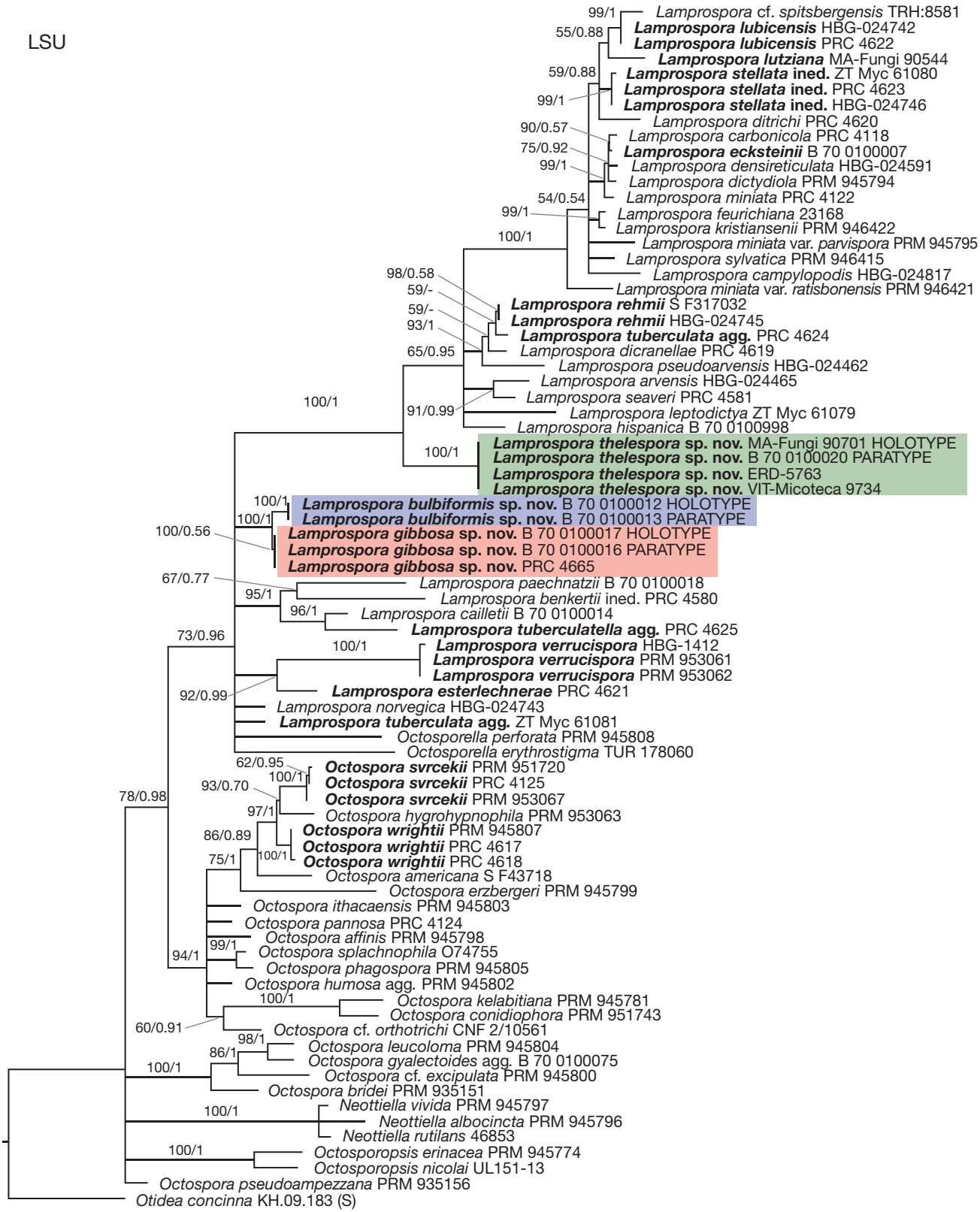
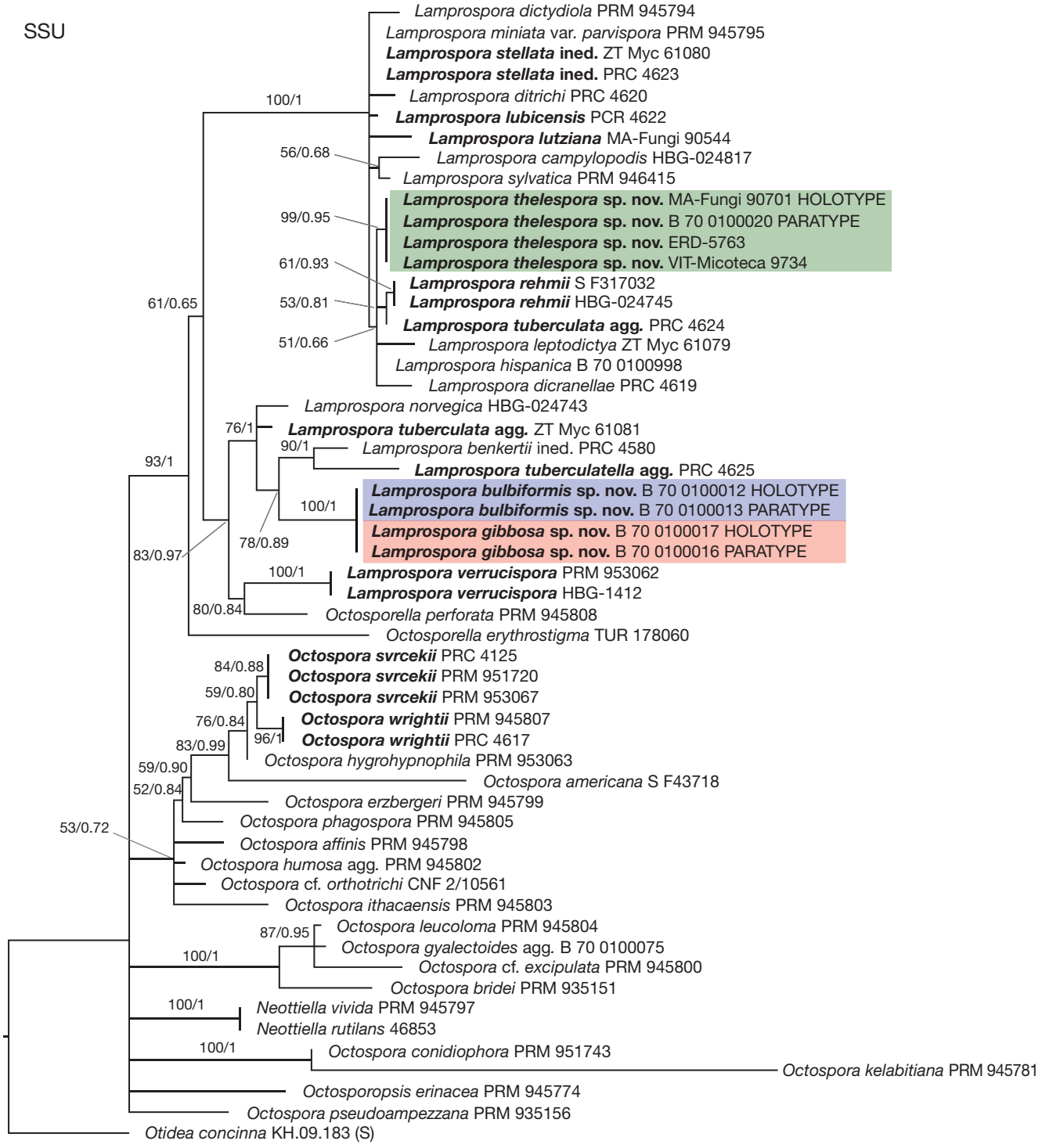
APPENDICES

Appendix 1. — RAxML phylogram obtained from the LSU sequences showing the phylogenetic relationship of the three new *Lamprospora* De Not. species among bryophilous Pezizales. Numbers above branches represent RAxML bootstrap support values and Bayesian posterior probability scores, respectively. Nodes for which RAxML bootstrap support values were below 50 were collapsed. GenBank accession numbers are indicated in Table 1. New species described in this study are highlighted in color. Species with globose or subglobose ascospores (Q < 1.1) and ornamentation consisting of isolated warts or tubercles are highlighted in **bold**.



Appendix 2. — RAxML phylogram obtained from the SSU sequences showing the phylogenetic relationship of the three new *Lamprospora* De Not. species among bryophilous Pezizales. Numbers above branches represent RAxML bootstrap support values and Bayesian posterior probability scores, respectively. Nodes for which RAxML bootstrap support values were below 50 were collapsed. GenBank accession numbers are indicated in Table 1. New species described in this study are highlighted in color. Species with globose or subglobose ascospores (Q < 1.1) and ornamentation consisting of isolated warts or tubercles are highlighted in **bold**.



Appendix 3. — RAxML phylogram obtained from the EF1-α sequences showing the phylogenetic relationship of the three new *Lamprospora* De Not. species among bryophilous Pezizales. Numbers above branches represent RAxML bootstrap support values and Bayesian posterior probability scores, respectively. Nodes for which RAxML bootstrap support values were below 50 were collapsed. GenBank accession numbers are indicated in Table 1. New species described in this study are highlighted in color. Species with globose or subglobose ascospores (Q < 1.1) and ornamentation consisting of isolated warts or tubercles are highlighted in **bold**.