


# Tenerife strikes again — *Lamprospora angularis* sp. nov.: another new member of the bryophilous *Pezizales* from a unique oceanic island

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**Abstract:** *Lamprospora angularis* sp. nov. is described and illustrated from finds in four different Tenerife localities. The new species is characterised by a combination of the following features: orange to reddish-orange apothecia with a conspicuous fimbriate to shaggy margin, globose ascospores with distinctive regular areolate ornamentation, and infection of the rhizoids of its bryophyte host *Campylopus pilifer*. Phylogenetic analysis of SSU, LSU and EF1- $\alpha$  gene sequences show that the studied collections of this species form a well-supported monophyletic clade and clearly differ from all other sequenced species of bryophilous *Pezizales*. Comparisons have been made with similar members of *Lamprospora* that infect species of *Campylopus*, namely *L. australis*, *L. campylopodis* and *L. verrucispora*.

**Keywords:** Ascomycota, bryophilous ascomycetes, *Campylopus pilifer*, ecology, Macaronesia, Pyronemataceae.

**Resumen:** *Lamprospora angularis* sp. nov. es descrita e ilustrada a partir de hallazgos en cuatro diferentes localidades de Tenerife. La nueva especie se define por la combinación de las siguientes características: apotecio naranja a rojizo-naranja con un conspicuo margen fimbriado a lanoso, ascosporas globosas con ornamentación areolada regular distintiva e infección de los rizoides de su briófito hospedador *Campylopus pilifer*. Los análisis filogenéticos de las secuencias de genes SSU, LSU y EF1- $\alpha$  muestran que las colecciones estudiadas de esta especie forman un clado monofilético bien soportado y difieren claramente de todas las demás especies secuenciadas de *Pezizales* briófilos. Se han realizado comparaciones con especies similares de *Lamprospora* que infectan especies de *Campylopus*, a saber, *L. australis*, *L. campylopodis* y *L. verrucispora*.

**Palabras clave:** Ascomycota, ascomicete briófilo, *Campylopus pilifer*, ecología, Macaronesia, Pyronemataceae.

## Introduction

The Canary Islands are hotspots for biodiversity and contain many interesting and endemic species, including bryophytes (mosses, liverworts, and hornworts), and the fungi associated with them. The bryophilous *Pezizales* represent a relatively conspicuous group of ascomycetes frequently found on or beside bryophyte host patches in a variety of habitats though these fungi are under-studied outside of Central Europe (VEGA *et al.*, 2021). QUINTERO *et al.* (2020) listed 15 species of bryophilous *Pezizales* from Tenerife, including the recently described *Octosporella microtricha* Döbbeler, Negrín & M. Vega, a parasite of the endemic leafy liverwort *Frullania polysticta* Lindenb. (DÖBBELER *et al.*, 2018).

In this article we describe a new species of a bryophilous ascomycete, *Lamprospora angularis*. *L. angularis* parasitises the rhizoids of the moss *Campylopus pilifer* Brid., causing asymptomatic infections, and appears to be host specific. We then compare the new species with other *Lamprospora* taxa on closely related host plants, highlighting points of distinction between the different species based on morphology, sequence data, and ecology.

## Material and methods

### Specimen collection and observation

The description of *Lamprospora angularis* is based on results of the examination of live structures of fresh collections. Most observations were made in tap water. Ascospore ornamentation was also studied after staining with Cotton Blue (CB), refractive vacuoles in the paraphyses were studied in aqueous Cresyl Blue, the absence of the iodine reaction of the asci was checked with Lugol's solution (IKI). Ascospores size was measured from free elements as well as from spore prints; at least 50 ascospores were measured. Ascospore dimensions include epispore ornamentation unless otherwise stated; this also applies to similar species treated. Q is used to indicate the length/width ratio of the ascospores. Nuclei were visualized

in apothecia upon staining with DAPI (4',6-diamidino-2-phenylindole). A piece of fresh hymenium was transferred to a 30  $\mu$ l drop of DAPI (2  $\mu$ g/ml) on a microscope slide and heated at 90 °C for 1 min on a hot plate. After at least 5 minutes at room temperature, the stained ascospores were observed using Olympus BX51 (excitation 360–370 nm and emission > 420 nm; Olympus, Tokyo, Japan). Micrographs were taken in tap water or CB using digital cameras mounted on microscopes and software for stacking pictures. Geographical coordinates are given in the WGS84 format. Vouchers have been deposited in the indicated public herbaria, using codes of Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>).

### DNA extraction, PCR amplification, and sequencing

Sequence data were generated for three regions: large subunit of ribosomal DNA (LSU); small subunit of rDNA (SSU); and elongation factor 1- $\alpha$  (EF1- $\alpha$ ). For further details of the analysis see VEGA *et al.* (2021).

### Phylogenetic analysis

Specimens used in the analysis and their GenBank accession numbers are listed in Table 1. Newly obtained sequences of LSU, SSU and EF1- $\alpha$  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 (KATO *et al.*, 2019). The ambiguously aligned regions of the alignments were removed with BMGE (CRISCUOLO & GRIBALDO, 2010) and the most suitable substitution model for each region 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 1000<sup>th</sup> 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 analysed as a partitioned dataset under the GTRCAT model with 1000 bootstrap iterations.

**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- $\alpha$	References
<i>Lamprospora angularis</i>	AH-44755	Spain, M. Vega & M. Ribes	<i>Campylopus pilifer</i>	<b>MZ190474</b>	<b>MZ190476</b>	<b>MZ189737</b>	
<i>L. angularis</i>	AH-44756 (holotype)	Spain, M. Vega	<i>Campylopus pilifer</i>	<b>MZ190473</b>	<b>MZ190475</b>	<b>MZ189736</b>	
<i>L. arvensis</i>	HBG-024465	Germany, M. Vega	<i>Ceratodon purpureus</i>	KY858950			VEGA <i>et al.</i> (2017)
<i>L. bulbiformis</i>	B 70 0100012 (holo-type)	Portugal, M. Vega	<i>Fissidens viridulus</i>	MT792684	MT792707	MT783993	VEGA <i>et al.</i> (2021)
<i>L. caillietii</i>	B 70 0100014	Switzerland, E. Stöckli	<i>Tortella tortuosa</i>	MN394604			ECKSTEIN <i>et al.</i> submitted
<i>L. campylopodis</i>	48632	Netherlands, H. van der Kolk	<i>Campylopus pyriformis</i>	MF066053			EGERTOVÁ <i>et al.</i> (2018b)
<i>L. campylopodis</i>	HBG-024817	Germany, M. Vega	<i>Campylopus pyriformis</i>	MF066054	MK569364	MK569289	EGERTOVÁ <i>et al.</i> (2018b); SOCHOROVÁ <i>et al.</i> (2019)
<i>L. carbonicola</i>	PRC 4118	Czech Republic, L. Janošik	<i>Funaria hygrometrica</i>	MH818440			VEGA <i>et al.</i> (2019)
<i>L. carbonicola</i>	PRC 4119	Spain, L. Janošik	<i>Funaria hygrometrica</i>	MH818441			VEGA <i>et al.</i> (2019)
<i>L. densireticulata</i>	HBG-024587 (para-type)	Germany, M. Vega & T. Richter	<i>Aloina ambigua</i>	MH818449			VEGA <i>et al.</i> (2019)
<i>L. densireticulata</i>	HBG-024591 (holo-type)	France, M. Vega	<i>Aloina ambigua</i>	MH818451			VEGA <i>et al.</i> (2019)
<i>L. dicranellae</i>	PRC 4619	Austria, L. Janošik	<i>Ditrichum heteromallum</i>	MT792686	MT792709	MT783995	VEGA <i>et al.</i> (2021)
<i>L. dictydiola</i>	PRC 4121	Czech Republic, L. Janošik	<i>Tortula muralis</i>	MH818446			VEGA <i>et al.</i> (2019)
<i>L. dictydiola</i>	PRM 945794	Czech Republic, Z. Egertová	<i>Tortula muralis</i>	MF754056	MK569365	MF754054	EGERTOVÁ <i>et al.</i> (2018a); SOCHOROVÁ <i>et al.</i> (2019)
<i>L. ditrichi</i>	PRC 4620	Czech Republic, L. Janošik	<i>Flexitrichum flexicaule</i>	MT792687	MT792710	MT783996	VEGA <i>et al.</i> (2021)
<i>L. ditrichi</i>	TRI: F- 10629	Norway, S. Sivertsen	<i>Flexitrichum flexicaule</i>	MG949140			
<i>L. ecksteinii</i>	B 70 0100007	Germany, G. Eckstein	<i>Microbryum curvicolium</i>	MT792688			VEGA <i>et al.</i> (2021)
<i>L. feurichiana</i>	B 70 0100471	Germany, G. Eckstein	<i>Ceratodon purpureus</i>	MF066038			EGERTOVÁ <i>et al.</i> (2018b)
<i>L. feurichiana</i>	B 70 0100472	Germany, J. Eckstein & G. Eckstein	<i>Ceratodon purpureus</i>	MF066039			EGERTOVÁ <i>et al.</i> (2018b)
<i>L. gibbosa</i>	B 70 0100017 (holo-type)	France, M. Vega	<i>Fissidens crassipes</i>	MT792691	MT792712	MT783997	VEGA <i>et al.</i> (2021)
<i>L. hispanica</i>	B 70 0100998	Spain, M. Vega	<i>Aloina aloides</i>	MN394607	MT792713	MT783998	ECKSTEIN <i>et al.</i> submitted; VEGA <i>et al.</i> (2021)
<i>L. kristiansenii</i>	33443	Germany, J. Eckstein	<i>Ceratodon purpureus</i>	MF066043			EGERTOVÁ <i>et al.</i> (2018b)
<i>L. kristiansenii</i>	PRM 946422	Czech Republic, Z. Egertová, L. Janošik & A. Polhorsky	<i>Ceratodon purpureus</i>	MF066045			EGERTOVÁ <i>et al.</i> (2018b)
<i>L. leptodictya</i>	ZT Myc 61079	Switzerland, E. Stöckli	<i>Aongstroemia longipes</i>	MN394610	MT792714		ECKSTEIN <i>et al.</i> submitted; VEGA <i>et al.</i> (2021)
<i>L. lubicensis</i>	HBG-024742	Germany, M. Vega & T. Richter	<i>Hennediella heimii</i>	MT792692			VEGA <i>et al.</i> (2021)
<i>L. lubicensis</i>	PRC 4622	Czech Republic, L. Janošik & Z. Egertová	<i>Hennediella heimii</i>	MT792693	MT792715	MT783999	VEGA <i>et al.</i> (2021)

Table 1 – (continued)

Species	Herbarium code	Geographic origin, collector	Host	LSU	SSU	EF1- $\alpha$	References
<i>L. lutziana</i>	MA-Fungi 90544	Spain, M. Vega, R. Martínez-Gil & J. De La Cruz	<i>Philonotis fontana</i>	MN434188	MT792716	MT784000	MARTÍNEZ-GIL et al. (2019); VEGA et al. (2021)
<i>L. miniata</i>	PRC 4122	Slovakia, L. Janošik	<i>Tortula protobryoides</i>	MH818444			VEGA et al. (2019)
<i>L. miniata</i> var. <i>parvispora</i>	PRM 945795	Slovakia, Z. Egertová	<i>Barbula unguiculata</i>	MF066065	MK569366	MF754055	EGERTOVA et al. (2018a, 2018b); SOCHOROVA et al. (2019)
<i>L. miniata</i> var. <i>ratisbonensis</i>	47528	Germany, D. Benkert	<i>Didymodon fallax</i>	MF066063			EGERTOVA et al. (2018b)
<i>L. miniata</i> var. <i>ratisbonensis</i>	PRM 946421	Croatia, Z. Egertová	<i>Didymodon luridus</i>	MF066064			EGERTOVA et al. (2018b)
<i>L. norvegica</i>	HBG-024743	Switzerland, M. Vega & B. Senn-Irlet	<i>Ditrichum pusillum</i>	MT792694	MT792717	MT784001	VEGA et al. (2021)
<i>L. paechnatzii</i>	B 70 0100018	Germany, T. Richter & M. Vega	<i>Bryum</i> sp.	MN394613			ECKSTEIN et al. submitted
<i>L. pseudoarvensis</i>	HBG-024462 (holotype)	Spain, M. Vega	<i>Pleuridium acuminatum</i>	NG_060353			VEGA et al. (2017)
<i>L. rehmi</i>	S F317032 (epitype)	Spain, R. Martínez-Gil	<i>Pleuridium acuminatum</i>	MH087070	MT792719		VEGA et al. (2018, 2021)
<i>L. seaveri</i>	B 70 0010018 (holotype)	Germany, D. Benkert	<i>Ceratodon purpureus</i>	MN394612			ECKSTEIN et al. submitted
<i>L. cf. spitsbergensis</i>	TRH:8581	Norway, H. Dissing & S. Sivertsen	<i>Hennediella heimii</i> var. <i>arctica</i>	MG949137			
<i>L. stellata</i> nom. prov.	HBG-024746	France, M. Vega	<i>Dicranella howei</i>	MT792696			VEGA et al. (2021)
<i>L. stellata</i> nom. prov.	PRC 4623	Slovakia, L. Janošik	<i>Dicranella howei</i>	MT792697	MT792720	MT784002	VEGA et al. (2021)
<i>L. sylvatica</i>	PRM 946415 (holotype)	Ukraine, Z. Egertová & M. Sochor	<i>Dicranum montanum</i>	MG947604	MK569367	MK569290	EGERTOVA et al. (2018b); SOCHOROVA et al. (2019)
<i>L. sylvatica</i>	PRM 946416	Slovakia, Z. Egertová & M. Sochor	<i>Dicranum montanum</i>	MF066051			EGERTOVA et al. (2018b)
<i>L. thelespora</i>	MA-Fungi 90701 (holotype)	Spain, R. Martínez-Gil	<i>Cheilothea chloropus</i>	MT792701	MT792724	MT784006	VEGA et al. (2021)
<i>L. tuberculata</i> agg.	PRC 4624	Slovakia, L. Janošik	<i>Pleuridium subulatum</i>	MT792703	MT792726	MT784008	VEGA et al. (2021)
<i>Neottiella albocincta</i>	PRM 945796	Slovakia, P. Včelička	<i>Atrichum undulatum</i>	MF754059			EGERTOVA et al. (2018a)
<i>N. vivida</i>	PRM 945797	Czech Republic, Z. Egertová	<i>Polytrichum piliferum</i>	MF066068	MK569337	MF754051	EGERTOVA et al. (2018a, 2018b); SOCHOROVA et al. (2019)
<i>Octospora affinis</i>	PRM 945798	Czech Republic, A. Polhorský, L. Janošik & Z. Egertová	<i>Lewinskya affinis</i>	MF754075	MK569347	MF754045	EGERTOVA et al. (2018a); SOCHOROVA et al. (2019)
<i>O. axillaris</i>	PRM 954016	Czech Republic, Z. Egertová	<i>Tortula acaulon</i>	MW242829	MW242828	MW430761	SOCHOROVA et al. (2021)
<i>O. humosa</i> agg.	PRM 945802	Czech Republic, Z. Egertová	<i>Polytrichum piliferum</i>	MF754074	MK569343	MF754043	EGERTOVA et al. (2018a); SOCHOROVA et al. (2019)
<i>O. leucoloma</i>	PRM 945804	Czech Republic, Z. Egertová	<i>Bryum argenteum</i>	MF754063	MK569370		EGERTOVA et al. (2018a); SOCHOROVA et al. (2019)
<i>O. wrightii</i>	PRC 4617	Czech Republic, L. Janošik	<i>Amblystegium serpens</i>	MN994534	MN994517	MN990994	SOCHOROVA et al. (2020)

Table 1 – (continued)

Species	Herbarium code	Geographic origin, collector	Host	LSU	SSU	EF1- $\alpha$	References
<i>Octosporella jungermannia-rum</i>	TUR 178050	Switzerland, P. Döbbeler	<i>Plagiochila asplenioides</i>	EU940133	EU940060		STENROOS <i>et al.</i> (2010)
<i>O. perforata</i>	PRM 945808	Czech Republic, Z. Egertová	<i>Porella platyphylla</i>	MF754060	MK569368	MF754052	EGERTOVÁ <i>et al.</i> (2018a); SOCHOROVÁ <i>et al.</i> (2019)
<i>Octosporopsis erinacea</i>	PRM 945774 (iso-type)	Malaysia, Z. Egertová & M. Sochor	<i>Dumortiera hirsuta</i>	MF754057	MK569338	MF754041	EGERTOVÁ <i>et al.</i> (2018a); SOCHOROVÁ <i>et al.</i> (2019)
<i>O. nicolai</i>	UL151-13	Germany, M. Vega	<i>Lunularia cruciata</i>	KF771033		KF771042	LINDEMANN <i>et al.</i> (2014)
<i>Otidea concinna</i>	KH.09.183 (S) (epi-type)	Sweden, K. Hansen & I. Olariaga	-	NG_060279	NG_064990	KM823275	HANSEN & OLARIAGA (2015); SCHOCH <i>et al.</i> (2012)

## Results

### Phylogenetic analysis

The two sequenced collections of *Lamprospora angularis* were identical in all three analyzed regions. They formed well-supported monophyletic clade and clearly differed from the other sequenced species of the genus *Lamprospora* in all three regions (Figs. 1, 6–8). The new species belongs to a group of *Lamprospora* species with complete, areolate reticula with fewer than eight meshes per diameter, and it is most closely related to the morphologically similar *L. campylopodis* W.D. Buckley.

### Taxonomy

***Lamprospora angularis*** M. Vega, Ribes & Janošík, *sp. nov.* – [MycoBank MB 840649]

**Diagnosis:** *Lamprospora angularis* differs from other species of *Lamprospora* by its globose ascospores, with a distinct regular areolate ornamentation, and infecting rhizoids of its bryophyte host *Campylopus pilifer*.

**Holotype:** SPAIN, Canary Islands, Tenerife, El Rosario, Camino Madroño Goteras, 28°26'17.8" N 16°23'17.1" W, 1195 m a.s.l., on banks alongside the forest road, 21 Dec. 2020, *leg.* M. Vega. Host *Campylopus pilifer* (AH-44756, *isotypus* PRC 4693).

**Etymology:** the epithet *angularis* comes from the Latin adjective *angūlaris* (= angular), referring to the ascospore ornamentation of angled meshes.

### Macroscopical features (Figs. 2A–F)

**Apothecia** scattered to gregarious, on soil, but also on stems and in leaf axils of *Campylopus pilifer*, 0.5–2 mm in diameter, spherical to turbinate to discoid, sessile; small fruitbodies in the leaf axils mostly with a fimbriate margin, bigger ones on soil with a rather broad shaggy margin, hymenium yellow-orange to light orange, margin whitish, outer surface orange.

### Microscopical features (Figs. 3–4A–F)

**Asci** 230–400(–480) × 21–30  $\mu$ m, cylindrical, 8-spored, operculate, inamyloid; bifurcate at the base, arising from perforated croziers. **Ascospores** globose, 18–22  $\mu$ m in diameter, hyaline, with a spherical drop of 10–13  $\mu$ m, uniseriate. Ornamentation areolate, consisting of ridges (0.5–)0.7–1.2  $\mu$ m wide and 0.8–1.5(–2)  $\mu$ m high, forming a complete regular reticulum of (3–)4–6(–7) pentagonal or hexagonal meshes/diameter, meshes 3–5(–6.5)  $\mu$ m wide, rarely with low warts. Ridges and occasionally also ascospore surface between ridges dotted. Ascospores in asci and free ascospores in hymenium uninucleate. Nuclei oblate and located close to the ascospore cell wall. **Paraphyses** slender, straight, mostly simple, rarely forked, pluriseptate, same length as the asci, apical cell not or only slightly inflated; apical cell 35–80 × 4–7  $\mu$ m, cells below narrower, 3  $\mu$ m in diam., containing orange pigment; when stained with IKI the content of the paraphyses turns olive-green; with only a few colourless refractive vacuolar bodies (VBs) of 1–2  $\mu$ m in diameter. **Margin** of *textura prismatica*, cells (17–)20–55(–70) × 7–21(–25)  $\mu$ m. **Ectal excipulum** 150–250(–270)  $\mu$ m thick, *textura angularis* at the base, at the margin rather a *t. prismatica*, cells (21–)24–37(–43) × (17–)19–28(–30)  $\mu$ m. **Medullary excipulum** of *textura intricata-angularis*, (72–)74–150(–174)  $\mu$ m thick. **Subiculum** with hyaline septate anchoring hyphae 3  $\mu$ m wide and a  $\pm$  bulbous base 8–10 × 6–8  $\mu$ m.

### Infection (Figs. 4G–H–5)

The infection structure of *L. angularis* occurs singly or in groups (up to three per infected cell) on the rhizoids of *Campylopus pilifer*. It consists of extracellular appressoria and intracellular haustoria. Both are connected by a short infection peg. Appressoria are usually covered

by a layer of connate hyphae and only visible in optical section. They are slightly kidney shaped in side view (in CB) 20–30 µm long, 12–18 µm high, 12–17 µm wide, and one-celled. The infection peg grows through a tube of host cell material, which is 3–5 µm wide and to 20 µm long. Haustoria usually occur as one per appressorium, forming a ramified and contorted filament with undulating thin walls. Infected cells show no growth modifications, and the host plant in general does not seem to be weakened by the infection.

**Habitat and occurrence of *Campylopus pilifer* (Figs. 2G–H)**

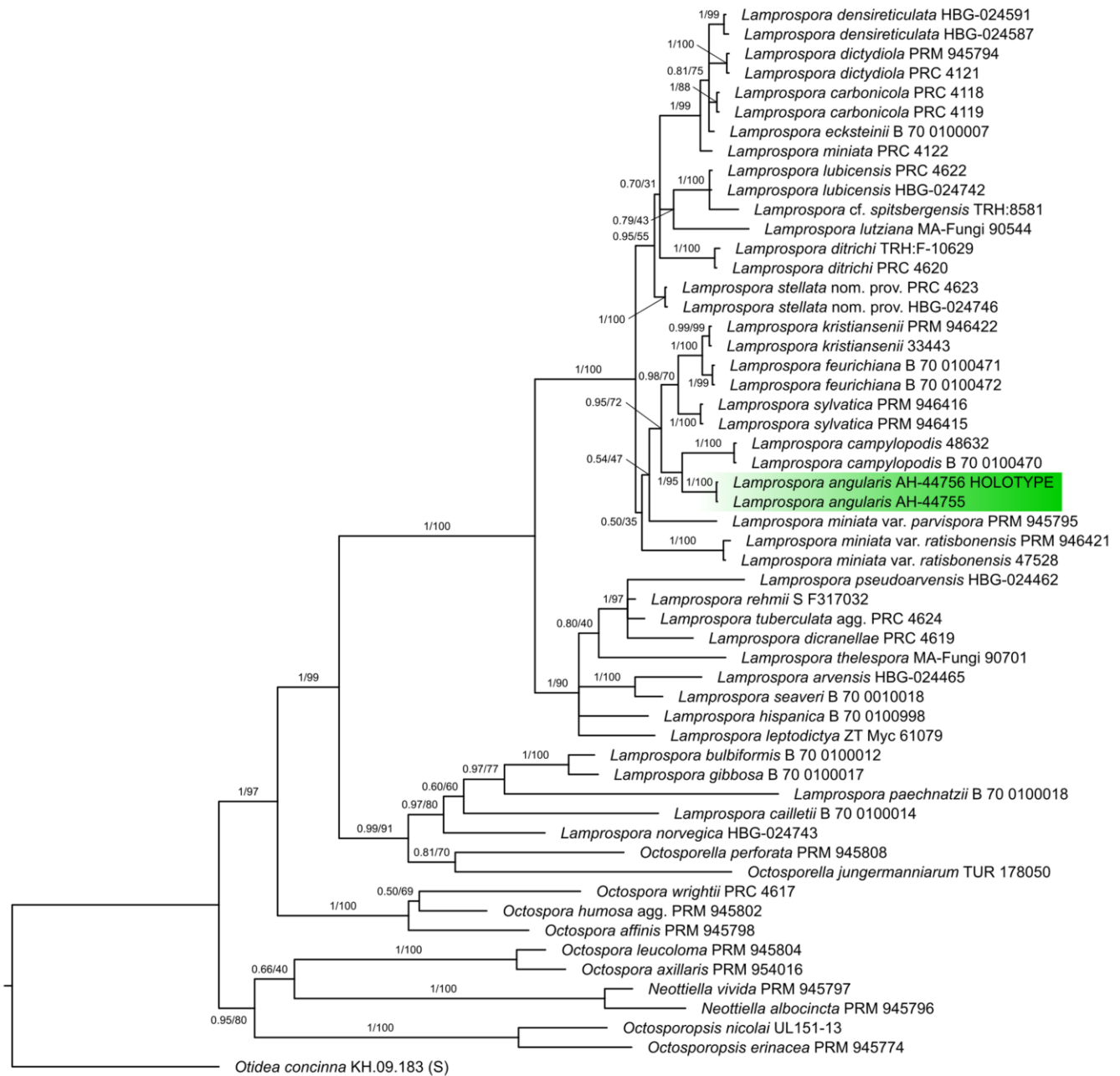
The bryophyte host could be found frequently in the lower Tenerife mountain region. It grows in arid, sun-exposed habitats on volcanic rock and boulders covered by a thin soil layer, preferably in localities like clearings, recreational areas, trails, or the sides of paths. Overall, *C. pilifer* is an oceanic Southern-temperate species occurring in coastal Europe north to Belgium and east to Greece, as well as in

Turkey, Macaronesia, Africa, India to Java, southern North America, Central America, Venezuela, and Galapagos Islands (SMITH, 2004; Ros *et al.*, 2013). FRAHM (2002) states that the occurrence in tropical America, tropical Africa, and Sri Lanka (but not other parts of Asia) suggests a Gondwanaland origin, from where the species had extended its range into warmer parts of North America and South-Western Europe, he gives an altitudinal distribution range from 50 to 1500 metres a.s.l.

**Additional specimens examined**

SPAIN, Tenerife, La Guancha, Barranco de la Gotera, 28°21'37.9" N 16°39'39.7" W, 710 m a.s.l., on banks alongside the forest road, 22 Dec. 2019, leg. M. Vega, M.A. Ribes, R. Negrín & D. Chavez. Host: *C. pilifer*, accompanying bryophyte: *Weissia* sp. Herb. AH-44753.

SPAIN, Tenerife, La Guancha, Camino El Lagar, 28°21'34.7" N 16°39'32.9" W, 740 m a.s.l., on banks alongside the forest road,



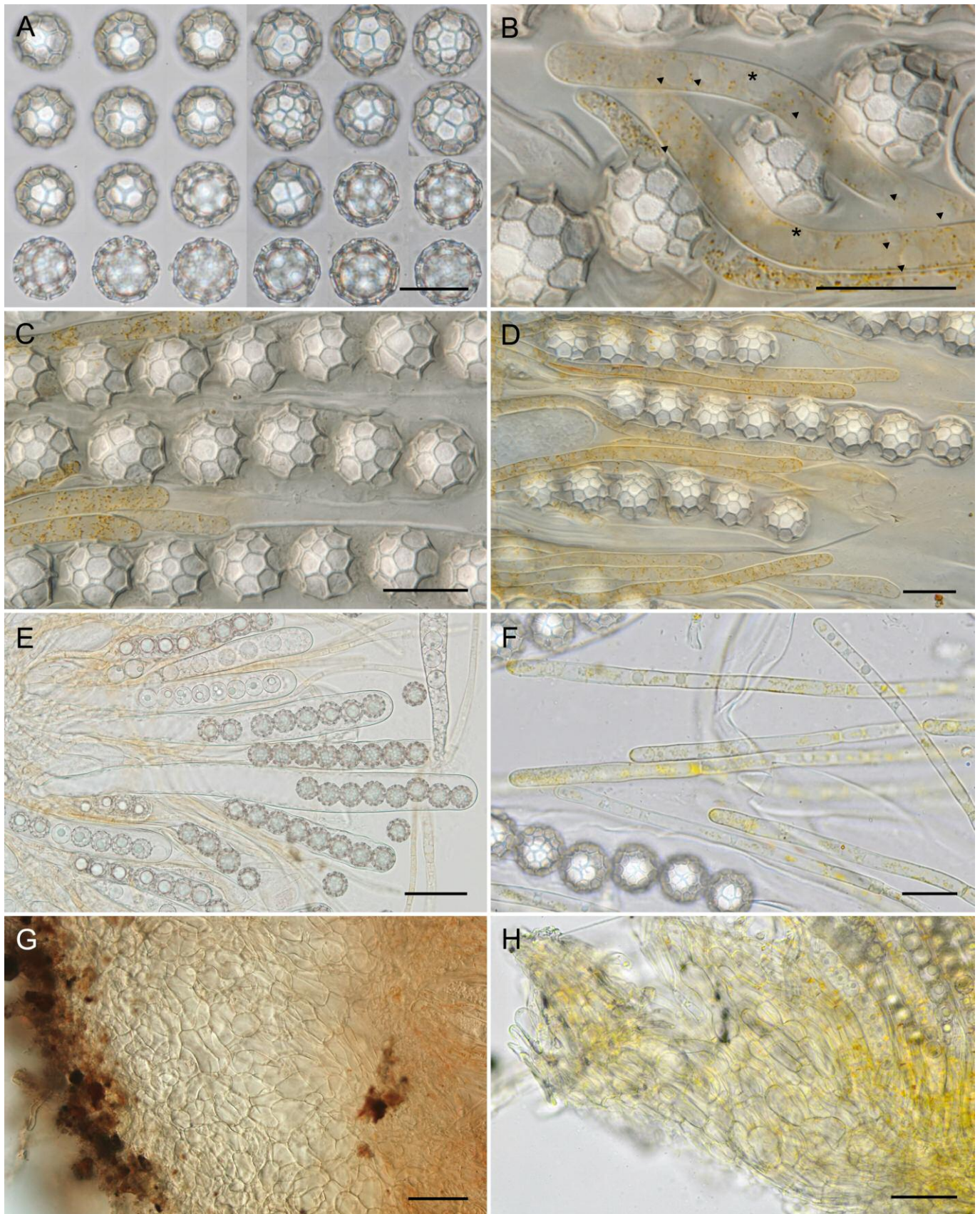
**Fig. 1** – Fifty percent majority rule Bayesian phylogram obtained from the concatenated LSU, SSU and EF1- $\alpha$  sequences showing the phylogenetic relationship of newly described *Lamprospora angularis* with other bryophilous Pezizales. Numbers above branches represent Bayesian posterior probability scores and RAxML bootstrap support values, respectively. GenBank accession numbers and additional collection information are indicated in Table 1.





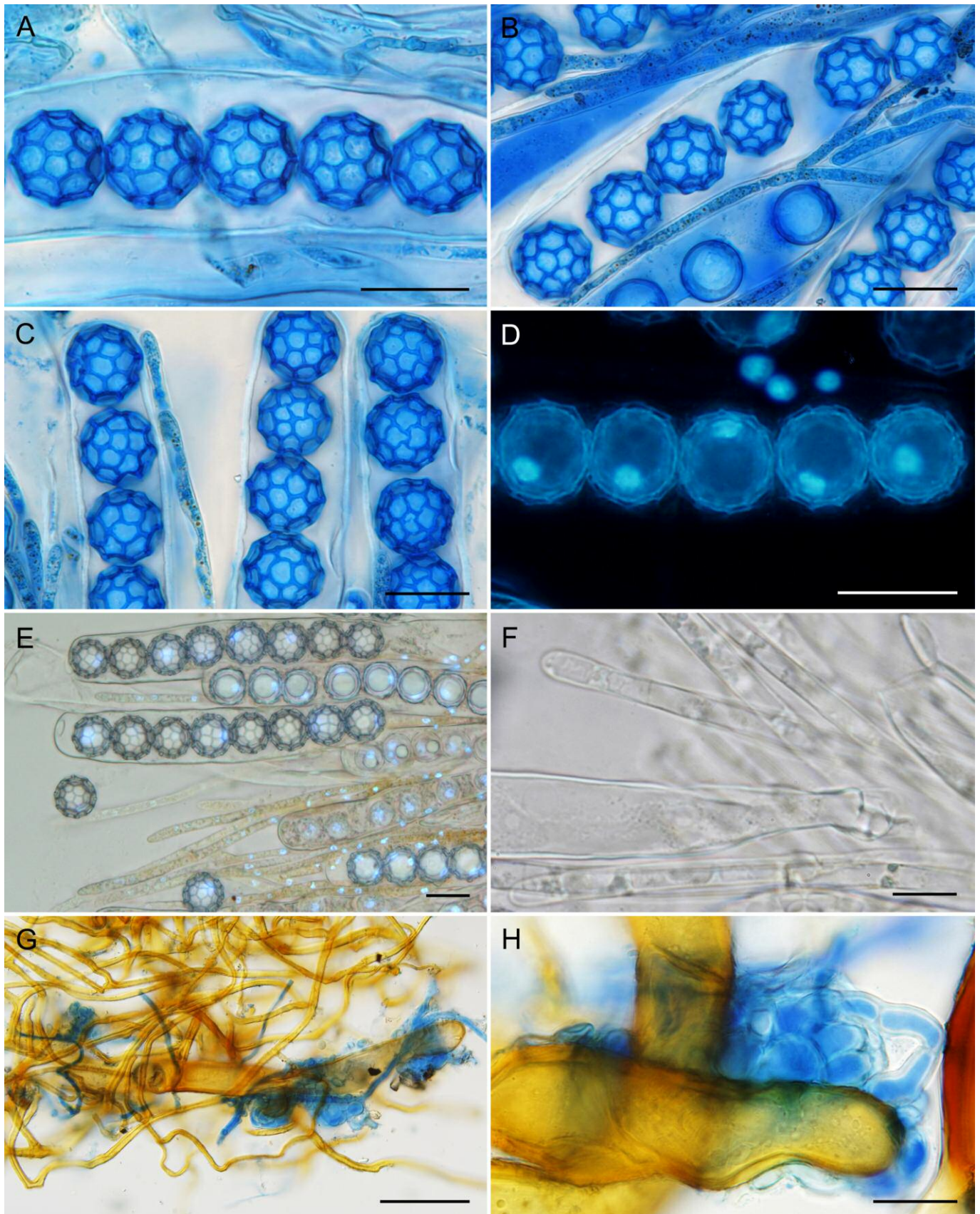
**Fig. 2** – *Lamprospora angularis* (A–D. AH-44755, E, F, H. Holotype AH-44756, G. AH-44753). A–F. Apothecia between shoots of *Campylopus pilifer*. G. Habitat of AH-44753. H. Habitat of AH-44756. Scale bars: A2, C, D = 2 mm; A1, B, F = 5 mm; E = 10 mm. Photos: A–D: M.A. Ribes, E–H: M. Vega.





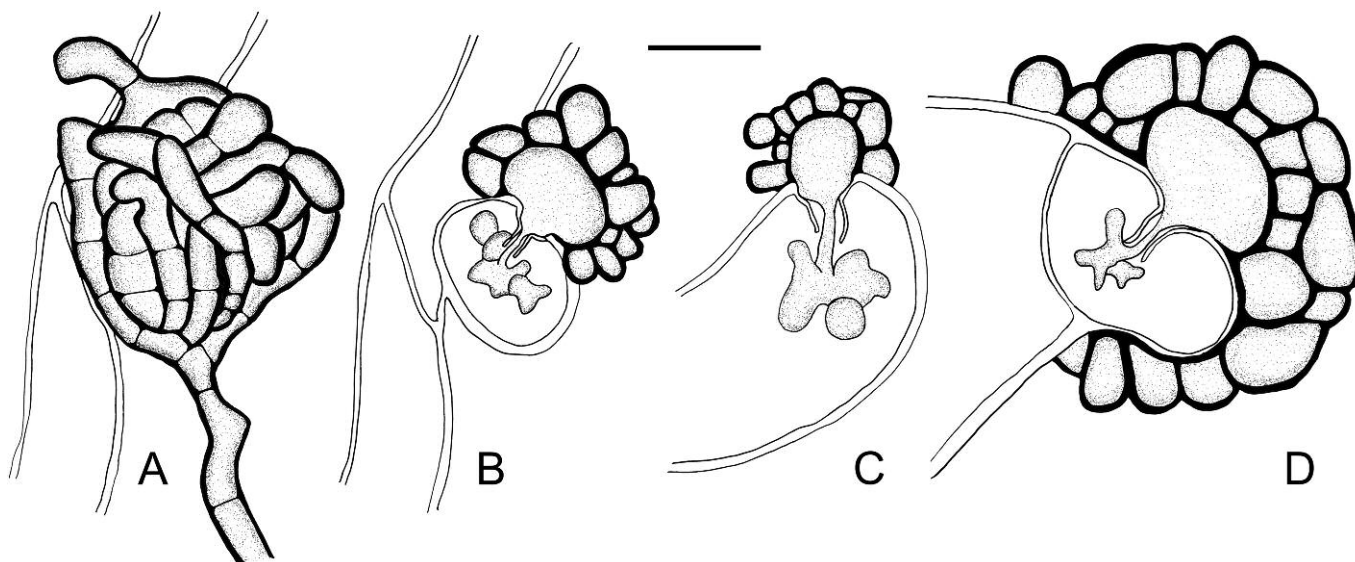
**Fig. 3** – *Lamprospora angularis*. Microscopical characters (A, F, H. Holotype AH-44756, B–E, G. Isotype PRC 4693). A. Free ascospores in water. B. Apical cells of paraphyses and ascospores in asci, weakly refractive vacuolar bodies are labeled with arrowheads and nuclei with asterisks. C–F. Ascospores inside asci and paraphyses in water. G. Cross section of an apothecium showing part of medullary and ectal excipulum in water. H. Cross section of an apothecium showing margin in water. Scale bars: A–D, F = 20  $\mu\text{m}$ ; E, G–H = 50  $\mu\text{m}$ . Photos: A, F, H: M.A. Ribes, B–E, G: L. Janošík.





**Fig. 4** – *Lamprospora angularis*. Microscopical characters (A, G–H. AH-44755, B–E. Isotype PRC 4693, F. Holotype AH-44756). A–C. Ascospores inside asci stained with CB. D–E. Ascospores inside asci and paraphyses with nuclei stained with DAPI. F. Crozier at the base of young ascus in water. G–H. Infection structures on rhizoids of *Campylopus pilifer* stained with CB. Scale bars: A–F, H = 20  $\mu$ m; G = 100  $\mu$ m. All photos by L. Janošík.





**Fig. 5** – *Lamprospora angularis*, drawings of infection structures on rhizoids of *Campylopus pilifer*, fungal cells dotted, (specimen). A. Infection in surface view. B. The same infection as in A in optical section. C–D. Further infections in optical section showing appressoria, haustoria and infection pegs. Scale bar = 20  $\mu\text{m}$ . Drawings: J. Eckstein.

27 Dec. 2019, leg. M. Vega & M.A. Ribes. Host: *C. pilifer*, accompanying bryophytes: *Gongylanthus ericetorum* (Raddi) Nees., *Didymodon* sp. Herb. AH-44754.

SPAIN, Tenerife, La Guancha, Camino El Lagar, 28°21'32.8" N 16°39'27.0" W, 765 m a.s.l., on banks alongside the forest road, 27 Dec. 2019, leg. M. Vega & M.A. Ribes. Host: *C. pilifer*, accompanying bryophytes: *G. ericetorum*, *Weissia* sp. Herb. AH-44755.

## Biogeographic background

The Canary Islands belong to the natural region of Macaronesia and are located northwest of the African coast. With distances of 95 km and 420 km from mainland Africa, Fuerteventura and El Hierro represent the closest and most remote Canary Islands respectively. The climate of the Canary Islands is characterised by three types of weather: the trade wind regime, unstable weather, and southern weather (MARZOL & MAYER, 2012). The trade wind regime is the predominant weather and provides a mass of humid air that forms a stratocumulus layer between 500 and 1500 metres a.s.l. on the northern face of the islands of greater relief, called “sea of clouds”. At higher elevations there is a thermal inversion that prevents the vertical development of clouds and precipitation, abruptly decreasing humidity and forming a layer of dry air that determines the type of vegetation present. A singular characteristic in this type of weather is the great difference between the warm temperatures of the coast and the much cooler temperatures of relatively close places, but with great altitude differences and exposure to the trade winds, more accentuated in winter than in summer (MARZOL & MAYER, 2015). The islands of Gran Canaria, Tenerife, La Palma, La Gomera

and El Hierro have enough altitude to retain the trade winds and take advantage of their humidity on the north side, but not Lanzarote, Fuerteventura, La Graciosa and other islets, which are much more arid by the absence of high mountains. On the other hand, the southern slopes of the mountainous islands share similar climatic characteristics with the latter mentioned, as it is impossible for the clouds to get over that mountainous barrier and thus these are retained on the north slope (FERNÁNDEZ-CALDAS *et al.*, 1978). Second, the climate is characterised by unstable weather, caused by storms from the polar front that cross the Atlantic and provide most of the rainfall on the islands. Last, but not least, there is the so-called southern weather, which usually brings suspended dust (haze), high temperatures and extremely low humidity, even accompanied by winds that seriously affect the vegetation.

The soils in the Canary Islands come from the evolution of geological materials of volcanic origin and are constituted mainly by alkaline basalts that form lava flows and pyroclastic products and by rocks formed by trachytes and phonolites, the phonolite being the most frequent acidic material (FERNÁNDEZ-CALDAS *et al.*, 1982). The different types of soils present on the islands are arranged in altitudinal bands, more or less coinciding with the different vegetation levels, although these sequences have notable differences due to the age of the geological materials that limit their degradation and evolution (MORA *et al.*, 2009).

Tenerife is located in the central western and it is the Canary Island with both the highest surface, 2034.38 km<sup>2</sup>, and the highest altitude, 3718 metres above sea level (a.s.l.). The different bioclimatic floors (DEL ARCO *et al.*, 2006) and an intricate orography maintain rich biodiversity and a large number of endemic species.

**Table 2** – *Lamprospora* species with a bryophyte host in the genus *Campylopus*

	<i>L. verrucispora</i>	<i>L. campylopodis</i>	<i>L. australis</i>	<i>L. angularis</i>
<b>Ascospore surface</b>	Isolated warts, densely covered	Regular areolate reticulum of pentagonal or hexagonal meshes	Regular areolate reticulum of pentagonal or hexagonal meshes	Regular areolate reticulum of pentagonal or hexagonal meshes
<b>Ascospores measurements (diam.)</b>	(13–)14–17 $\mu\text{m}$ ornamentation included	(17–)18–19 $\mu\text{m}$ ornamentation included	17–20 $\mu\text{m}$ ornamentation included	18–22 $\mu\text{m}$ ornamentation included
<b>Ridges or warts</b>	Warts (0.2–)0.4–0.9 $\mu\text{m}$ wide and 0.4–0.8 $\mu\text{m}$ high	Ridges 0.5–1 $\mu\text{m}$ wide and 1–1.6 $\mu\text{m}$ high	Ridges 0.6–1 $\mu\text{m}$ wide and 1.2–2.3 $\mu\text{m}$ high	Ridges (0.5–)0.7–1.2 $\mu\text{m}$ wide and 0.8–1.5(–2) $\mu\text{m}$ high
<b>Meshes / diameter</b>		4–6	3–4(–5)	(3–)4–6(–7)

All Tenerifan localities of *L. angularis* were banks beside forest roads. The fungus has been found on the northern face of the island, inside or very close to two areas with different protection levels: the Paisaje Protegido de Las Lagunetas (Las Lagunetas Protected Landscape), and the Parque Natural de la Corona Forestal (Corona Forestal Natural Park). Collections were from a strip located between 700 and 1200 a.s.l. that corresponds with the zone influenced by sea clouds and can be considered Tenerifan laurel forest (DEL ARCO *et al.*, 2006). However, the predominant habitats are mixed pine forest or humid pine forest, with temperate and humid climates, dry and hot summers, and average annual rainfall of beyond 500 mm (excluding horizontal rainfall). These habitats are characterised by the presence of *Pinus canariensis*, which effectively captures moisture in its needles from the sea fogs, thus adding extra water supply to the soil over and above seasonal rains (ARÉVALO & FERNÁNDEZ-PALACIOS, 2009). To a greater or lesser extent, laurel forest and fayal-heath species are present, such as *Laurus novocanariensis*, *Erica arborea*, *Morella faya*, *Ilex canariensis*, *Arbutus canariensis*, *Viburnum tinus* subsp. *rigidum*, *Cistus symphytifolius* and *Daphne gnidium*.

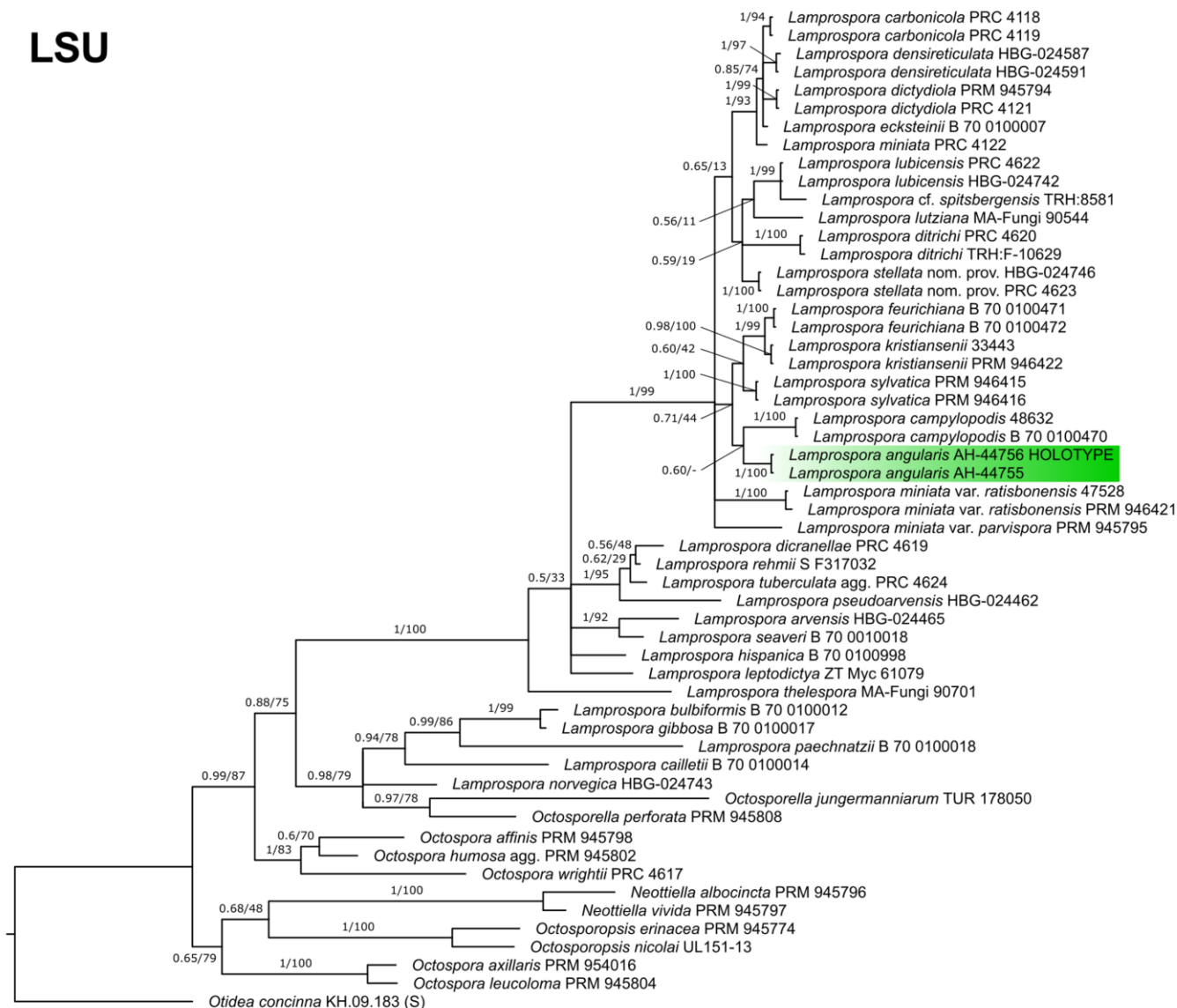
## Discussion

Three species of *Lamprospora* with a bryophyte host in the genus *Campylopus* Brid. have been described thus far, however none of them have been reported from Tenerife (QUINTERO *et al.*, 2020). These species are listed below and are compared with *L. angularis*.

1) *L. verrucispora* M. Vega, Eckstein & Van der Kolk infects *C. pyriformis* (Schultz) Brid., a moss not listed in the Tenerifan species inventory (GONZÁLEZ-MANCEBO *et al.*, 2008). *L. verrucispora* has ascospores with a surface densely covered with numerous isolated warts (VEGA *et al.*, 2016). This contrasts with the reticulate ornamentation of *L. angularis*, making confusion unlikely when specimens are examined microscopically.

2) *L. campylopodis* also has *C. pyriformis* as host. Information on its ascospore size and ornamentation are given below in paragraph 3.

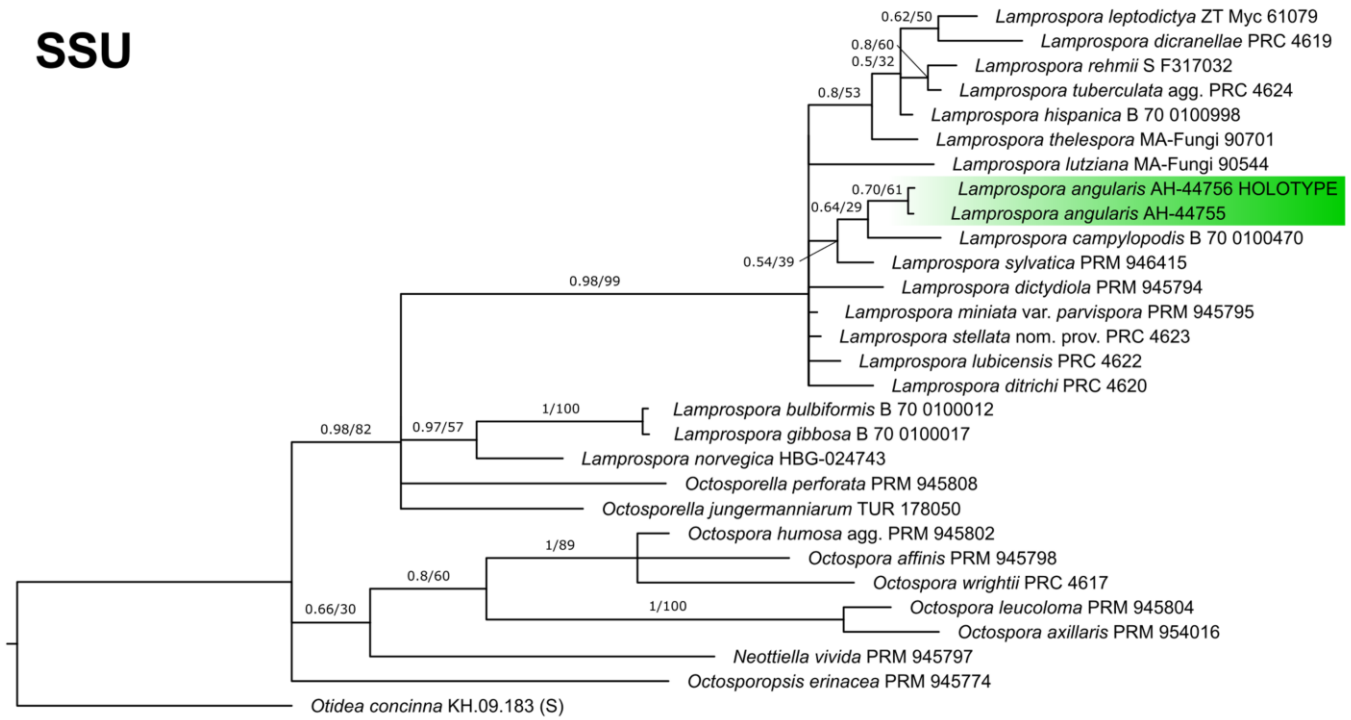
The identity of the host of the holotype collection of *L. campylopodis*, however, is not unequivocal. BUCKLEY (1923) described *L. campylopodis* and, rather unusually at the time as the relation between the ascomycete and its bryophyte host was not known,



**Fig. 6** – Fifty percent majority rule Bayesian phylogram obtained from the LSU sequences showing the phylogenetic relationship of newly described *Lamprospora angularis* with other bryophilous *Pezizales*. Numbers above branches represent Bayesian posterior probability scores and RAXML bootstrap support values, respectively. GenBank accession numbers and additional collection information are indicated in Table 1.

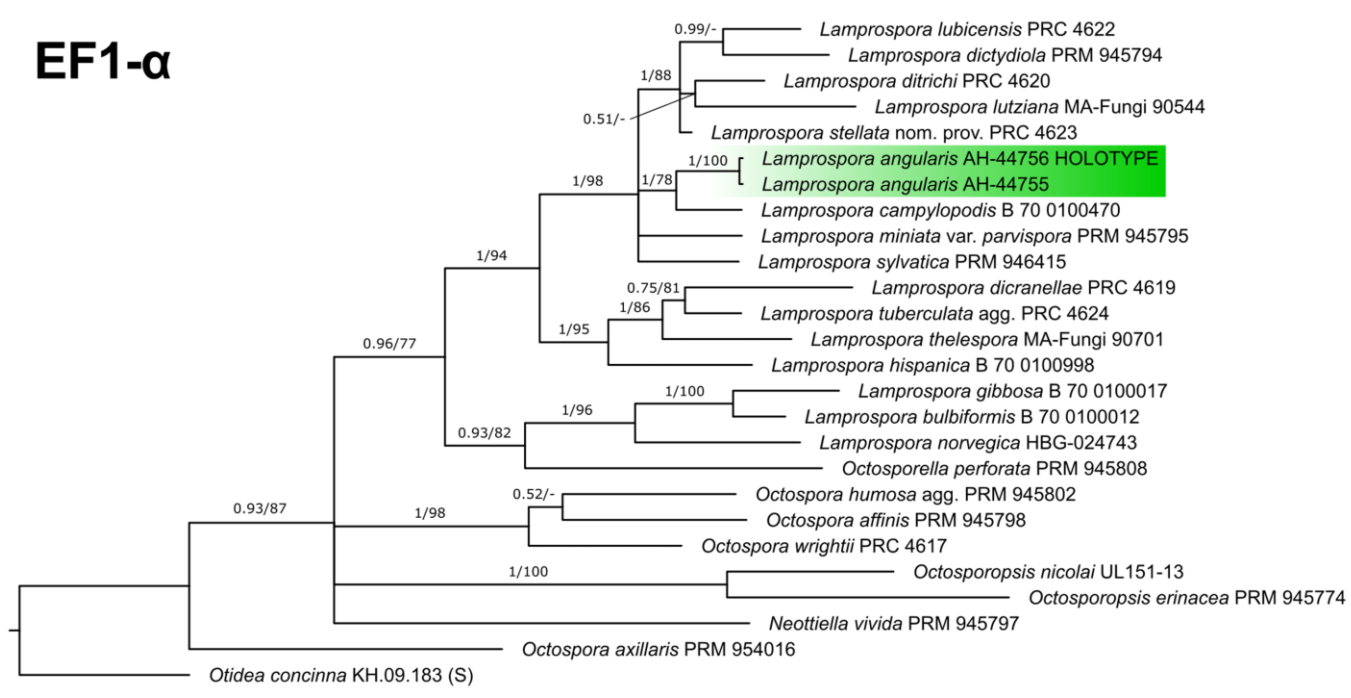


# SSU



**Fig. 7** – Fifty percent majority rule Bayesian phylogram obtained from the SSU sequences showing the phylogenetic relationship of newly described *Lamprospora angularis* with other bryophilous *Pezizales*. Numbers above branches represent Bayesian posterior probability scores and RAXML bootstrap support values, respectively. GenBank accession numbers and additional collection information are indicated in Table 1.

# EF1-α



**Fig. 8** – Fifty percent majority rule Bayesian phylogram obtained from the EF1-α sequences showing the phylogenetic relationship of newly described *Lamprospora angularis* with other bryophilous *Pezizales*. Numbers above branches represent Bayesian posterior probability scores and RAXML bootstrap support values, respectively. GenBank accession numbers and additional collection information are indicated in Table 1.

added information on bryophytes at the locality: "Hab. ad terram inter muscos (*Campylopus fragilis*) ad radices Pini truncorum in locis humidis." BENKERT (1987) informed that the type could not be found in K and that he had designated material collected by Broome in 1863 and being available in K as a neotype. The host of this collection is *C. pyriformis*. BENKERT (2007) reported a collection of *L. campylopodis* infecting *C. oerstedianus* (Müll.Hal.) Mitt. from Greece.

It is not unlikely that there could more than one taxon hidden behind the name *L. campylopodis* and that the different collections labelled with one and the same name effectively represent different species.

To our knowledge *L. campylopodis* could not be found again on *C. fragilis* (Brid.) Bruch & Schimp. or *C. oerstedianus*.

Available sequences from GenBank are from collections from Germany and Netherlands, all grew on *C. pyriformis* (EGERTOVÁ *et al.*, 2018b).

3) *L. australis* (McLennan & Cookson) Rifai grows on *C. introflexus* (Hedw.) Brid.

This *Lamprospora* had originally been described as *Lamprospora areolata* var. *australis* McLennan & Cookson from Australia in 1923, in the same year as *L. campylopodis*. It is true that the ascospores size and the ornamentation of *L. australis* and *L. areolata* Seaver are similar, McLENNAN & COOKSON (1923) emphasised: "It (= *Lamprospora areolata* var. *australis*) however, differs in its size, and in the possession of a well-marked fringe at the margin of the apothecium such a structure being entirely absent in the latter species. The differences, however, appear to be varietal rather than specific in character, and lead us to regard the Australian representatives of this species as a variety of the American type." RIFAI (1968) considered the differences to be important enough to combine the species to *L. australis*. BENKERT (1987) found the infection of *L. australis* on *C. introflexus* — the latter has been a neophyte in North America since 1975 only (FRAHM, 2002) and thus does not come into consideration as a host of *L. areolata* Seaver described in 1912 from the US. Recent studies of type material of *L. areolata* by J. Eckstein (unpublished) revealed its host is *Physcomitrium pyriforme* (Hedw.) Bruch & Schimp. When finding *L. angularis* for the first time, *L. australis* immediately came to our mind as we considered the moss at hand to be *C. introflexus*, a species which, as we soon found out, had been reported from Tenerife by BRULLO *et al.* (2004) only from fumaroles of the volcano Teide at an altitude of 3650–3700 metres. Thus, it was more likely that the host of *L. angularis* would be the commoner *C. pilifer*, and this was later confirmed by J. Eckstein. As for recent literature comparing *C. pilifer* with *C. introflexus* and dealing with their ecological niches, see GAMA *et al.* (2017) and HUGONNOT (2016).

GONZÁLEZ-MANCEBO *et al.* (2008) detail a total of 416 bryophyte species from Tenerife, four of them belong to the genus *Campylopus*: *C. fragilis*, *C. introflexus*, *C. flexuosus* (Hedw.) Brid. and *C. pilifer*.

*L. campylopodis* and *L. australis* both share two important morphological features with *L. angularis*, that is their apothecia have a conspicuous fimbriate to shaggy margin and their ascospore ornamentation consists of a fairly regular areolate reticulum of pentagonal or hexagonal meshes. In some of the references on the two described reticulate-spored species on *Campylopus* it is not indicated whether the ascospores measurements given are with or without ornamentation and whether they have been taken from live or dead material. Below, we state our own observations on vital material for a robust comparison.

*L. campylopodis*, according to ECKSTEIN & ECKSTEIN (2013) and unpublished notes by M. Vega (three collections examined; molecular data published in EGERTOVÁ *et al.*, 2018b), has ascospores measuring (17–)18–19 µm in diameter with ornamentation included, ridges 0.5–1 µm wide and 1–1.6 µm high, and ascospores with 4–6 meshes/diameter. The ascospores of *L. campylopodis* are smaller than those of *L. angularis*, whereas the ridges are slightly thinner.

The ascospores of *L. australis* (three Australian collections studied by L. Janošik; data unpublished) measure 17–20 µm in diameter, ridges 0.6–1 µm wide and 1.2–2.3 µm high, and the ascospores have 3–4(–5) meshes/diameter. *L. australis* has fewer meshes per diameter than *L. campylopodis* and *L. angularis*, its ridges are mostly higher than those of the latter two species, and its ascospores diameter is slightly smaller than has been reported for *L. angularis*.

As explained in VEGA *et al.* (2019), the species delimitation of bryophilous *Pezizales* frequently reflects host specificity and ecology. Our observations of *L. angularis* strictly occurring with *C. pilifer* supports this viewpoint, indicating the high likelihood that a tight symbiotic relationship exists between this pair of species.

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## Authors' contributions

The first draft of the manuscript was written by M. Vega and was subsequently completed and updated by the other authors. M. Vega, M.A. Ribes and L. Janošik undertook the species description, and provided macro- and micrographs, M. Vega wrote the part on bryophyte host distribution and the discussion. J. Eckstein identified the host, commented on its infection and drew a sketch of it, R. Negrín wrote the introduction and the part about the habitats, L. Janošik carried out the sequencing and upload of the sequences to GenBank, and outlined the phylogenetic analysis and results. Images are by M.A. Ribes, L. Janošik and M. Vega. All authors read and approved the final manuscript.

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