



Octospora tucumanensis (Pezizales), a new bryophilous ascomycete on *Dimerodontium balansae* (Bryophyta) from Argentina

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Abstract

Octospora tucumanensis, a new bryophilous ascomycete infecting rhizoids of the pleurocarpous moss *Dimerodontium balansae* (Fabroniaceae), is described and illustrated based on collections from Argentina. The new species has a unique set of morphological characters and is phylogenetically supported. Morphologically, *O. tucumanensis* is characterized by the globose to subglobose ascospores ornamented with warts of variable size and shape. Differences from other morphologically similar species of *Octospora* are discussed.

Keywords *Ascomycota* · New species · *Pyronemataceae* · *Pezizomycotina* · Phylogeny · Taxonomy

Introduction

The "bryophilous fungi" have their development linked to the dependence on mosses or liverworts, from which they take food to complete their development cycle (Calzada 2021). Due to their small size and special ecology, bryophilous fungi are often overlooked and somewhat

neglected by mycologists. Therefore, they are mostly spotted and collected by bryologists (Németh 2017).

Octospora Hedw. (*Ascomycota*, *Pezizales*) includes species known to be intimately associated with bryophytes, and most of them are narrow specialists having a single moss or liverwort species as host (Benkert 1990; Vega et al. 2016; Egertová et al. 2018b). The genus is characterized by sessile, discoid, saucer-shaped or turbinate apothecia, usually hairless, which are colored in orange, red or pink shades. At microscopic level, *Octospora* is characterized by operculate, inamyloid asci containing 8 or less commonly 4 ascospores, and by the content of carotenoid pigments, especially in paraphyses. Ascospores vary widely in shape (subglobose, ovoid, broadly to narrowly ellipsoid, cylindrical, fusoid or lemon-shaped), size, content of lipid bodies, and perispore ornamentation (smooth, warted, spiny or reticulate) (Sochorová et al. 2021).

Because of their difficult perceptibility, most bryophilous *Pezizales* are under-recorded worldwide and they have so far not been detected in many countries (Eckstein 2016). In Latin America, only a few species have been recorded based on work carried out at the beginning or middle of the last century (Cash 1957; Seaver 1914; Spegazzini 1918; Stevenson 1975). However, there were 10 species of bryophilous *Octospora* known from Argentina (Gamundí 1960; Gamundí et al. 2004): *O. argentina* (Speg.) Gamundí and *O. antarctica* (Speg.) Gamundí (now in *Humaria* Fuckel), *O. annulata* (Seaver) Yei Z. Wang and *O. macracantha* (Boud.) Caillet & Moyne (now in *Lamprospora* De Not.),

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O. citrina Hedw. (now in *Calycina* Nees ex Gray), *O. deformis* (P. Karst.) Gamundí and *O. fusispora* (Berk.) Brumm. (now in *Byssonectria* P. Karst.), *O. nivea* R. Hedw. (now in *Dasyscyphella* Tranzschel). *Octospora leucoloma* Hedw. and *O. humosa* (Fr.) Dennis are the only species that remain inside *Octospora*.

In 2020, an interesting *Octospora* species growing on the pleurocarpous moss *Dimerodontium balansae* Müll. Hal. was found on *Jacaranda mimosifolia* D. Don. In the following two years, more collections were found in the same host. Morphological and molecular analyses confirmed that these samples represented an undescribed species. Herein, we describe and illustrate *Octospora tucumanensis* sp. nov. and discuss its phylogenetic relationships.

Materials and methods

Specimens were collected over the years 2020–2022 in several points of San Miguel de Tucumán city and the Chaco Serrano forest in Tucumán province, Argentina. Fresh apothecia were photographed, measured, and macroscopically described using a stereoscope (Leica MZ6). Microscopic features were measured and illustrated under the light microscope (Olympus CX31). The material was mounted in tap water, potassium hydroxide solution (5% KOH), or lactophenol cotton blue (LPCB). At least 30 values of spore size and 10 values of other structures were measured in water and the Q values were calculated from the ratio between the average spore length and width. Staining with lactophenol cotton blue was used to study spore ornamentation and infection structure. The iodine reaction of the asci was checked with Melzer's solution. The material was also mounted in calcofluor (Romero and Minter 1988) for examination of the hymenium under epifluorescence (EF) microscopy (Olympus BX43F; camera Olympus Q color S, SMP). Ascospore ornamentation was also studied with scanning electron microscopy (SEM) (Cross-beam 340, Zeiss). The specimens used in this study are deposited and preserved in the LIL herbarium (Thiers 2023, updated continuously).

DNA extraction and analyses

Genomic DNA was extracted using the CTAB method described by Doyle and Doyle (1987). Three to five apothecia were homogenized with a pestle, and incubated in 300 µl extraction buffer at 65 °C for one hour; the extract was subsequently purified in a chloroform-isoamyl alcohol mixture, precipitated by isopropanol, dissolved in 30 µl bi distilled water and finally incubated overnight at 37 °C. Genomic DNA quality was

checked on agarose gel and the amount of DNA was determined by spectrophotometry at 260 nm absorbance using a Thermo Scientific™ Multiskan™ GO Spectrophotometer.

Three different regions were amplified and sequenced in this study. The first region (LSU), spans the ITS1, 5.8S, ITS2, and D1/D2 domain of the 28S rDNA. The sequence was amplified by using universal primers ITS1 and NL4 (White et al. 1990; O'Donnell et al. 1998). The second region, SSU, spans the 18S rDNA subunit and was amplified and sequenced with universal primers NS1 and NS8 (White et al. 1990). The third sequence, named *TEF1α*, includes a partial sequence of the translation elongation factor-1-alpha gene, specifically amplified by primers EF1-983F and EF1-1567R (Rehner and Buckley 2005).

PCR products were sequenced by Macrogen Inc., South Korea. The consensus sequences were edited with DNA Dragon 1.4.1 (Hepperle 2011) and compared in the GenBank database using the BLAST tool (Altschul et al. 1990) from the National Center for Biotechnological Information (NCBI).

The analyzed dataset includes sequences from *Octospora tucumanensis*, along with sequences from 65 pre-identified organisms from related species and genera selected from previous works (Sochorová et al. 2019; Eckstein et al. 2021; Németh et al. 2022). Sequences from two organisms (*Otidea concinna* and *Otidea leporina*) selected as outgroups, were also included in the final dataset. Selected organisms, along with the GenBank accession numbers are listed in Table 1. Datasets were aligned by using the MUSCLE algorithm implemented in MEGA11 (Tamura et al. 2021) and manually trimmed when necessary. Phylogenetic analyses were conducted in PhyloSuite (Zhang et al. 2020). Sequences were realigned using the MAFFT algorithm, and MACSE was used for codon usage optimization in sequences from *TEF1α*, using predefined parameters, as recommended by Xiang et al. (2023). Sequences from the three analyzed DNA fragments were trimmed with GBLOCKS and concatenated using BIC criterion in ModelFinder (Kalyaanamoorthy et al. 2017). The final dataset was submitted to TreeBase repository (<http://purl.org/phylo/treebase/phyloids/study/TB2:S29688?x-access-code=f8e234db12368538a92a5e94b0b1e13c&format=html>).

To explore the robustness of our data, three different approaches were employed to conduct the phylogenetic inference: maximum parsimony (MP), maximum likelihood (ML) and Bayesian Inference (BI). MP analysis was performed in TNT 1.5 (Goloboff and Catalano 2016) under equal weighting. Tree searches were conducted by using 100 Wagner trees as starting points, each subjected to 15 rounds of Tree Drifting, Sectorial Searches and 5 rounds of Fusing (Goloboff 1999). Support values were estimated with Bootstrapping using 100 replicates. ModelFinder (Kalyaanamoorthy et al. 2017), as implemented

Table 1 List of species and specimens used in the phylogenetic study together with their GenBank accession numbers. Sequences obtained in this study are in bold

Species	GenBank Id Code	Herbarium code	Geographic origin, collection date, collector	Host	LSU	SSU	<i>TEF1α</i>	References
<i>Lamprospora aneurae</i> Benkert		B 70 0005997 (holotype)	Germany, 28 Jun 1987, D. Benkert	<i>Aneura pinguis</i>	MZ343191	MZ343180	MZ336038	Eckstein et al. 2021
<i>Lamprospora campylopodis</i> W.D. Buckley	48633	HBG-024817	Germany, 3 Oct 2015, M. Vega	<i>Campylopus pyriformis</i>	MF066054	MK569364	MK569289	Egertová et al. 2018b, Eckstein et al. 2021, Sochorová et al. 2019
<i>Lamprospora dictydiala</i> Boud.	ldic	PRM 945794	Czech Republic, 12 Feb 2014, Z. Egertová	<i>Tortula muralis</i>	MF754056	MK569365	MF754054	Németh et al. 2022, Eckstein et al. 2021, Sochorová et al. 2019
<i>Lamprospora hispanica</i> Benkert	MV2017012203	B 70 0100986	Spain, 22 Jan 2017	<i>Aloina ambigua</i>	MN394599	MW242827	MN366468	Németh et al. 2022
<i>Lamprospora miniata</i> De Not. var. <i>parvispora</i> Benkert	LMSk				MF066065	MK569366	MF754055	Sochorová et al. 2019
<i>Lamprospora rehmi</i> Benkert		S F317032 (epitype)	Spain, R. Martínez-Gil	<i>Pleuridium acuminatum</i>	MH087070	MT792719		Vega et al. 2019, Eckstein et al. 2021, Vega et al. 2021
<i>Lamprospora sylvatica</i> Egertová & Eckstein	UA1	PRM 946415 (holotype)	Ukraine, 8 Jul 2017, Z. Egertová & M. Sochor	<i>Dicranum montanum</i>	MG947604	MK569367	MK569290	Egertová et al. 2018b, Németh et al. 2022, Eckstein et al. 2021, Sochorová et al. 2019
<i>Lamprospora verrucispora</i> M. Vega, Eckstein & Van der Kolk	MV15102504	HBG 1412 (holotype)	Germany, 25 Oct 2015, M. Vega	<i>Campylopus pyriformis</i>	MN994551	MN994527	MN990993	Sochorová et al. 2020, Németh et al. 2022, Eckstein et al. 2021
<i>Neottiella rutilans</i> (Fr.) Dennis	46853	B 70 0100473	Poland, J. Eckstein	<i>Oligotrichum hercynicum</i>	MK569313	MK569336	MK569288	Sochorová et al. 2019, Eckstein et al. 2021
<i>Neottiella vivida</i> (Nyl.) Dennis	NVZ1a	PRM 945797	Czech Republic, 22 Oct 2016, Z. Egertová	<i>Polytrichum piliferum</i>	MF066068	MK569337	MF754051	Egertová et al. 2018a, 2018b, Németh et al. 2022
<i>Octospora affinis</i> Benkert & L.G.Krieglst.	OAFZ1a	PRM 945798	Czech Republic, 22 Oct 2016, A. Polhorský, L. Janošik & Z. Egertová	<i>Orthotrichum affine</i>	MF754075	MK569347	MF754045	Egertová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octospora americana</i> Benkert	2055	S F43718 (holotype)	USA, 18 Feb 1981, G. Thor	<i>Forsstroemia trichomitria</i>	MN967346	MN994516	MT078729	Sochorová et al. 2020, Németh et al. 2022, Eckstein et al. 2021
<i>Octospora axillaris</i> (Nees) M.M. Moser	OAXi	PRM 954016	Czech Republic, 8 Nov 2016, Z. Egertová	<i>Phascum cuspidatum</i>	MW242829	MW242828	MW430761	Németh et al. 2022
<i>Octospora bridei</i> Caillet & Moyne		PRM 935151	Czech Republic, 18 Oct 2015, Z. Egertová	<i>Ephemereum minutissimum</i>	MF754061	MT001890		Egertová et al. 2018a, Sochorová et al. 2020, Németh et al. 2022

Table 1 (continued)

Species	GenBank Id Code	Herbarium code	Geographic origin, collection date, collector	Host	LSU	SSU	<i>TEF1α</i>	References
<i>Octospora conidiophora</i> Sochorová & Döbbele	ZE48/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569321	MK569351	MK569297	Sochorová et al. 2019, Németh et al. 2022
<i>Octospora conidiophora</i>	ZE23/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569324	MK569349	MK569294	Sochorová et al. 2019
<i>Octospora conidiophora</i>	ZE46/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569317	MK569350	MK569298	Sochorová et al. 2019
<i>Octospora conidiophora</i>	ZE57/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569318	MK569352	MK569295	Sochorová et al. 2019
<i>Octospora conidiophora</i>	ZE62/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569323	MK569354	MK569299	Sochorová et al. 2019
<i>Octospora conidiophora</i>	ZE63/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569319	MK569355	MK569292	Sochorová et al. 2019
<i>Octospora conidiophora</i>	ZE71/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569322	MK569356	MK569293	Sochorová et al. 2019
<i>Octospora conidiophora</i>	ZE75/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569320	MK569357	MK569300	Sochorová et al. 2019
<i>Octospora conidiophora</i>	ZE77/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569331	MK569353	MK569301	Sochorová et al. 2019
<i>Octospora conidiophora</i> agg. – lineage B	ZE37/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569325	MK569358	MK569302	Sochorová et al. 2019
<i>Octospora conidiophora</i> agg. – lineage B	ZE38/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569329	MK569359	MK569303	Sochorová et al. 2019
<i>Octospora conidiophora</i> agg. – lineage B	ZE51/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569327	MK569362	MK569306	Sochorová et al. 2019
<i>Octospora conidiophora</i> agg. – lineage B	ZE52/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569326	MK569360	MK569304	Sochorová et al. 2019

Table 1 (continued)

Species	GenBank Id Code	Herbarium code	Geographic origin, collection date, collector	Host	LSU	SSU	<i>TEF1α</i>	References
<i>Octospora conidiophora</i> agg. – lineage B	ZE53/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerťová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569328	MK569361	MK569307	Sochorová et al. 2019
<i>Octospora conidiophora</i> agg. – lineage B	ZE65/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerťová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569330	MK569363	MK569305	Sochorová et al. 2019
<i>Octospora conidiophora</i> agg. – lineage C	ZE44/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerťová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569332	MK569373	MK569308	Sochorová et al. 2019
<i>Octospora conidiophora</i> agg. – lineage C	ZE56/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerťová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569333	MK569374	MK569309	Sochorová et al. 2019
<i>Octospora conidiophora</i> agg. – lineage D	ZE69/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerťová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569334	MK569375	MK569310	Sochorová et al. 2019
<i>Octospora conidiophora</i>	ZE11/18	PRM 951743 (holotype)	South Africa, 2 Mar 2018, Z. Egerťová & M. Sochor	<i>Trichosteleum perchlorosum</i>	MK569315	MK569348	MK569291	Sochorová et al. 2019
<i>Octospora doebeleri</i> Sochorová & Eckstein	DEVh	PRM 954007 (holotype)	Czech Republic, 25 Dec 2019, Z. Sochorová & M. Sochor	<i>Dicranoweisia cirrata</i>	MW152148	MW152156	MW159137	Sochorová et al. 2021, Németh et al. 2022
<i>Octospora erzbergeri</i> Benkert	ERZ	PRM 945799	Czech Republic, 10 Dec 2016, Z. Egerťová	<i>Pseudoleskeella nervosa</i>	MF754068	MK569340	MF754042	Egerťová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octospora</i> cf. <i>excipitata</i> (Clem.) Benkert	OExc	PRM 945800	Czech Republic, 16 Nov 2015, Z. Egerťová	<i>Funaria hygrometrica</i>	MF754062	MK569369	MF754047	Egerťová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octospora fissidentis</i> Benkert & Brouwer	Fis	PRM 945801	Czech Republic, 13 Nov 2016, Z. Egerťová	<i>Fissidens bryoides</i>	MF754073	MK569341	MF754044	Egerťová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octospora gyalectoides</i> Svrček & Kubicka	49382	PRC 4694	Czech Republic, L. Janošik	<i>Tortula acaulon</i>	MZ343187	MZ343177	MZ336036	Eckstein et al. 2021
<i>Octospora gyalectoides</i> agg.	49382	B 70 0100075	Germany, 22 Nov 2016	<i>Pottia lanceolata</i>	MT001891	MT001889	MN990995	Németh et al. 2022
<i>Octospora humosa</i> (Fr.) Dennis agg.	OHZla	PRM 945802	Czech Republic, 22 Oct 2016, Z. Egerťová	<i>Polytrichum piliferum</i>	MF754074	MK569343	MF754043	Egerťová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octospora hygrophynophila</i> Dissing & Sivertsen	MV17082702	PRM 953064	France, 27 Aug 2017	<i>Hygrophynum luridum</i>	MN994543	MN994520	MN990988	Németh et al. 2022

Table 1 (continued)

Species	GenBank Id Code	Herbarium code	Geographic origin, collection date, collector	Host	LSU	SSU	<i>TEF1α</i>	References
<i>Octospora hygrophynophila</i>		PRM 953063	France, M. Vega	<i>Hygrophynum luridum</i>	MN994542	MN994522	MN990987	Sochorová et al. 2020, Eckstein et al. 2021
<i>Octospora ithacaensis</i> (Rehm) K.B.Khare	OLOi	PRM 945803	Czech Republic, 6 May 2016, Z. Egerťová	<i>Marchantia polymorpha</i>	MF754071	MK569346	MF754053	Egerťová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octospora kelabitiana</i> Egerťová & Döbbele	oct-jat	PRM 945781	Malaysia, 3 Feb 2016, Z. Egerťová & M. Sochor	<i>Riccardia</i> sp.	MF754065	MK569372	MF754048	Egerťová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octospora leucoloma</i> Hedw.	OLeu	PRM 945804	Czech Republic, 21 Oct 2016, Z. Egerťová	<i>Bryum argenteum</i>	MF754063	MK569370		Egerťová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octospora meslinii</i> (Le Gal) Svrček & Kubička	CsN9078	PRM 954639	Hungary, 13 Dec 2017	<i>Grimmia pubinata</i>	MW507137	MW507001	MW526078	Németh et al. 2022
<i>Octospora meslinii</i>	CsN9194	PRM 954637 (epitype)	Hungary, 7 Jan 2018	<i>Grimmia pubinata</i>	MW152147	MW152158	MW159139	Németh et al. 2022
<i>Octospora meslinii</i>	CsN9207	PRM 954640	Hungary, 7 Jan 2018	<i>Grimmia pubinata</i>	MW507138	MW507002	MW526079	Németh et al. 2022
<i>Octospora meslinii</i>	CsN9250	PRM 954638	Hungary, 26 Jan 2018	<i>Grimmia pubinata</i>	MW507139	MW507003	MW526080	Németh et al. 2022
<i>Octospora neerlandica</i> Benkert & Brouwer		PRC 4691	Germany, M. Vega & T. Richter	<i>Syntrichia ruralis</i> agg.	MZ343185	MZ343176	MZ336035	Eckstein et al. 2021
<i>Octospora</i> cf. <i>orthotrichi</i> (Cooke & Ellis) K.B.Khare & V.P.Tewari	HR8	CNF 2/10561	Croatia, 2 Jan 2018, Z. Egerťová & M. Sochor	<i>Orthotrichum diaphanum</i>	MK569314	MK569342	MK569311	Sochorová et al. 2019, Németh et al. 2022
<i>Octospora oscarii</i> Eckstein, Sochorová & Janošik		PRM 955619	Czech Republic, Z. Sochorová	<i>Pseudotaxiphyllum elegans</i>	MZ343189	MZ343179	MZ336037	Eckstein et al. 2021
<i>Octospora pannosa</i> T.Richter, M.Vega & D.Savić		PRC 4687	Czech Republic, L. Janošik & K. Daňková	<i>Brachytheciastrum velutinum</i>	MZ343193	MZ343181		Eckstein et al. 2021
<i>Octospora phagospora</i> (Flageolet & Lortton) Dennis & Izerott	PHG44	PRM 945805	Germany, 24 Oct 2015, M. Vega	<i>Pohlia lutescens</i>	MF754072	MK569344	MF754046	Egerťová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octospora pseudoampezzana</i> (Svrček) Caillet & Moyne	OP1	PRM 935156	Czech Republic, 5 Mar 2016, Z. Egerťová & M. Sochor	<i>Schistidium crassipilum</i>	MF754069	MK569339	MF754050	Egerťová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octospora rubens</i> (Boud.) M.M.Moser agg.	MV20181218-06	PRM 954641	Spain, 18 Dec 2018, M. Vega	<i>Ceratodon purpureus</i>	MW221931	MW206790	MW219144	Németh et al. 2022
<i>Octospora rustica</i> (Velen.) J. Moravec agg.		PRC 4690	Czech Republic, L. Janošik & K. Daňková	<i>Ceratodon purpureus</i>	MZ343184		MZ336034	Eckstein et al. 2021

Table 1 (continued)

Species	GenBank Id Code	Herbarium code	Geographic origin, collection date, collector	Host	LSU	SSU	<i>TEF1α</i>	References
<i>Octospora similis</i> (Kirschst.) Benkert agg.	LJDP45	PRC 4667	Slovakia, 26 Nov 2019	<i>Bryum cf. rubens</i>	MT766281	MT766280	MT759840	Németh et al. 2022
<i>Octospora svreckii</i> Benkert	51959	PRM 954236	Albania, 8 Jul 2014	<i>Cratoneuron filicinum</i>	MN967347	MT065902	MN974531	Németh et al. 2022
<i>Octospora svreckii</i> Benkert		PRM 951720	Croatia, Z. Egerová, N. Matošec & I. Kušan	<i>Cratoneuron filicinum</i>	MN967348	MN994518	MN974532	Sochorová et al. 2020, Eckstein et al. 2021
<i>Octospora tucumanensis</i>	APO1	LIL 159229	Argentina, 28 Apr 2021, G. Suárez	<i>Dimerodonitium balansae</i>	OP556111	OP458236	OP620770	This study
<i>Octospora wrightii</i> (Berk. & M.A. Curtis) J.Moravec	WRIG	PRM 945807	Czech Republic, 22 Apr 2017, Z. Egerová	<i>Amblystegium serpens</i>	MF754070	MK569345	MT078728	Egerová et al. 2018a, Sochorová et al. 2019, 2020, Németh et al. 2022
<i>Octosporella jungermanniarum</i> (P.Crouan & H.Crouan) Döb- beler		TUR 178050	Switzerland, P. Döb- beler	<i>Plagiochila asplen- ioides</i>	EU940133	EU940060		Stenroos et al. 2010, Eckstein et al. 2021
<i>Octosporella perforata</i> (Döbbeler) Döbbeler	PERF	PRM 945808	Czech Republic, 10 Dec 2016, Z. Egerová	<i>Porella platyphylla</i>	MF754060	MK569368	MF754052	Egerová et al. 2018a, Sochorová et al. 2019, Németh et al. 2022
<i>Octosporopsis erinacea</i> Egerová & Döbbeler	DUM20/1	PRM 945774 (isotype)	Malaysia, 20 Jan 2017, Z. Egerová & M. Sochor	<i>Dumortiera hirsuta</i>	MF754057	MK569338	MF754041	Egerová et al. 2018a, Sochorová et al. 2019, Eckstein et al. 2021
<i>Octosporopsis nicolai</i> (Maire) U.Lindemann, M.Vega & T.Richter	UL 151–13	pers. herb. U. Lindemann	Germany, 2 Feb 2013, M. Vega	<i>Lunularia cruciata</i>	KF771033		KF771042	Németh et al. 2022
<i>Oridea concinna</i> (Pers.) Sacc.		KH.09.183 (S) (epi- type)	Sweden, K. Hansen & I. Olariaga	—	NG_060279	NG_064990	KM823275	Hansen and Olariaga 2015, Schoch et al. 2012, Eckstein et al. 2021
<i>Oridea leporina</i> (Batsch) Fockel	KGOL	CNF 2/9962	Kyrgyzstan, 15 Jul 2016	—	MK569335	MK569371	MK569312	Németh et al. 2022

in Phylosuite, was used to select the best-fit model using BIC criterion. Maximum likelihood phylogenies were inferred using IQ-TREE (Nguyen et al. 2015) under the model automatically selected by IQ-TREE ('Auto' option in IQ-TREE) for 20000 ultrafast (Minh et al. 2013) bootstraps, as well as the Shimodaira–Hasegawa–like approximate likelihood-ratio test (Guindon et al. 2010). Bayesian Inference phylogenies were inferred using MrBayes 3.2.6 (Ronquist et al. 2012) under GTR + I + G + F model (2 parallel runs, 5000000 generations), in which the initial 25% of sampled data were discarded as burn-in. The visualization of the phylogenetic trees was carried out in iTOL v6 (Letunic and Bork 2007). Clades were considered strongly supported when either PP or BS \geq 0.95 (Hyde et al. 2013).

Results

Phylogenetic analysis

Three sequences were analyzed in this study: a 1374 bp sequence corresponding to the ITS1, 5.8S, ITS2, and D1/D2 domain of LSU rDNA, a 1719 bp sequence corresponding to the 18S subunit of rDNA (SSU), and a 561 bp sequence from the Translation Elongation Factor 1 α (*TEF1 α*). Pairwise alignment of the *O. tucumanensis* sequences with the closest matches in GenBank (all belonging to *O. americana*) showed high identities of 99.1% (1719 bp) in the SSU rDNA region and 97.9% (561 bp) in *TEF1 α* . The alignment of the LSU rDNA regions showed an identity of 99.4% when considering the full 1374 bp and 97.02% identity when considering exclusively the ITS1–5.8S–ITS2 region (over 538 bp compared).

Sequences from LSU, SSU, and *TEF1 α* corresponding to 67 taxa from the family *Pyronemataceae* were included in the phylogenetic analysis. After automatic trimming and manual curating, 223 bp were selected from the SSU region, with 29 positions resulted informatively. In the SSU, 631 characters remained after trimming and curating, with 63 considered informative. Sequences from the *TEF1 α* region produced an alignment of 103 bp with 35 informative sites. Overall, this concluded in a concatenated matrix of 957 characters (124 of which were parsimony informative).

In the section *Wrightioideae*, *Octospora tucumanensis* was strongly supported as the sister taxon to *O. americana* (Fig. 1A, B, and C). In all concatenated phylogenetic trees, the separation of the extended outgroup clade (*Otidea concinna* and *Otidea leporina*) was fully supported and the novel strain (*O. tucumanensis*) formed a distinct and separate lineage with *O. svrcekii*, *O. erzbergeri*, *O. hygrohypnophila*, and *O. americana*.

Taxonomy

Octospora tucumanensis Catania & G. M. Suárez, sp. nov. (Figs. 2, 3, 4, 5 and 6).

Mycobank: MB#848265.

Holotype: ARGENTINA. Tucumán, San Miguel de Tucumán, 26°49'31"S 65°13'24"W, 450 m asl., on *Dimerodontium balansae*, 28 Apr 2021, G. Suárez 1929 (LIL159229).

Etymology: “tucumanensis” in reference to the Tucumán province where the species was found.

Diagnosis: *Octospora tucumanensis* resembles *Octospora americana* but differs from it by the ascospores size, ornamentation consisting of regularly distributed warts (different size and morphology) with striate surface; and its ecology, only infecting the rhizoids of *Dimerodontium balansae*.

Host: *Octospora tucumanensis* was observed fruiting on *Dimerodontium balansae* Müll. Hal., an epiphytic moss species growing on *Jacaranda mimosifolia*, *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl. and *Fraxinus pennsylvanica* Marshall. Accompanying mosses: *Syntrichia laevipila* Brid., *Tricherpodium beccarii* (Müll. Hal.) Pursell and *Venturiella glaziovii* (Hampe) Pursell.

Macroscopic features: *Apothecia* scattered to gregarious, first spherical, later urceolate, rounded from the top view, sessile, (0.3)0.5–0.8 mm in diameter, hymenium orange, margin lacerate; receptacle and margin lighter, orange furfureous, covered by short hyaline hairs; at the base with numerous hyaline, branched hyphae; growing on stems of the host moss.

Microscopic features: *Asci* cylindrical, 107.5–130(137.5) \times 12.5–15 μ m, 8-spored, spores uniseriate, pars sporifera (85.5)90–115(125) μ m; apex operculate, non-amyloid; base arising from croziers. *Ascospores* subglobose, 11–12.5 (13) \times (10)10.5–11.5(12.5) μ m (ornamentation not included), Q = 1.06, hyaline, always with a large lipid body, 8–9 μ m diameter, accompanied by some small lipid bodies, 2–4.5 μ m in diameter. Ornamentation consisting of two types of warts: 1)- large warts with rounded ends, constricted in the basal or middle zone, 1.2–1.5 μ m high and 0.6–0.8 μ m broad; and 2)- small, regularly distributed, slightly conical warts, 0.3–0.4 μ m high and 0.25–0.3(0.35) μ m broad. Warts with striated surface. *Paraphyses* cylindrical, straight to slightly sinuous, sparsely branched (bifurcate), septate, last cell slightly inflated, with multiple yellow orange guttules; apical cells 21–27 \times 4.5–5.5 μ m, cells below narrower, 2.5–3.5 μ m wide. *Subhymenium* composed of *textura intricata-epidermoidea*, cells 3.5–4.5 μ m wide, thin-walled, hyaline, guttules containing orange pigment. *Medullary excipulum* of *textura intricata* with cells 6.0–8.0 μ m wide, thin-walled, hyaline. Subhymenium together with medullary excipulum contain orange pigment guttules. *Ectal excipulum* from base to flank of *textura*

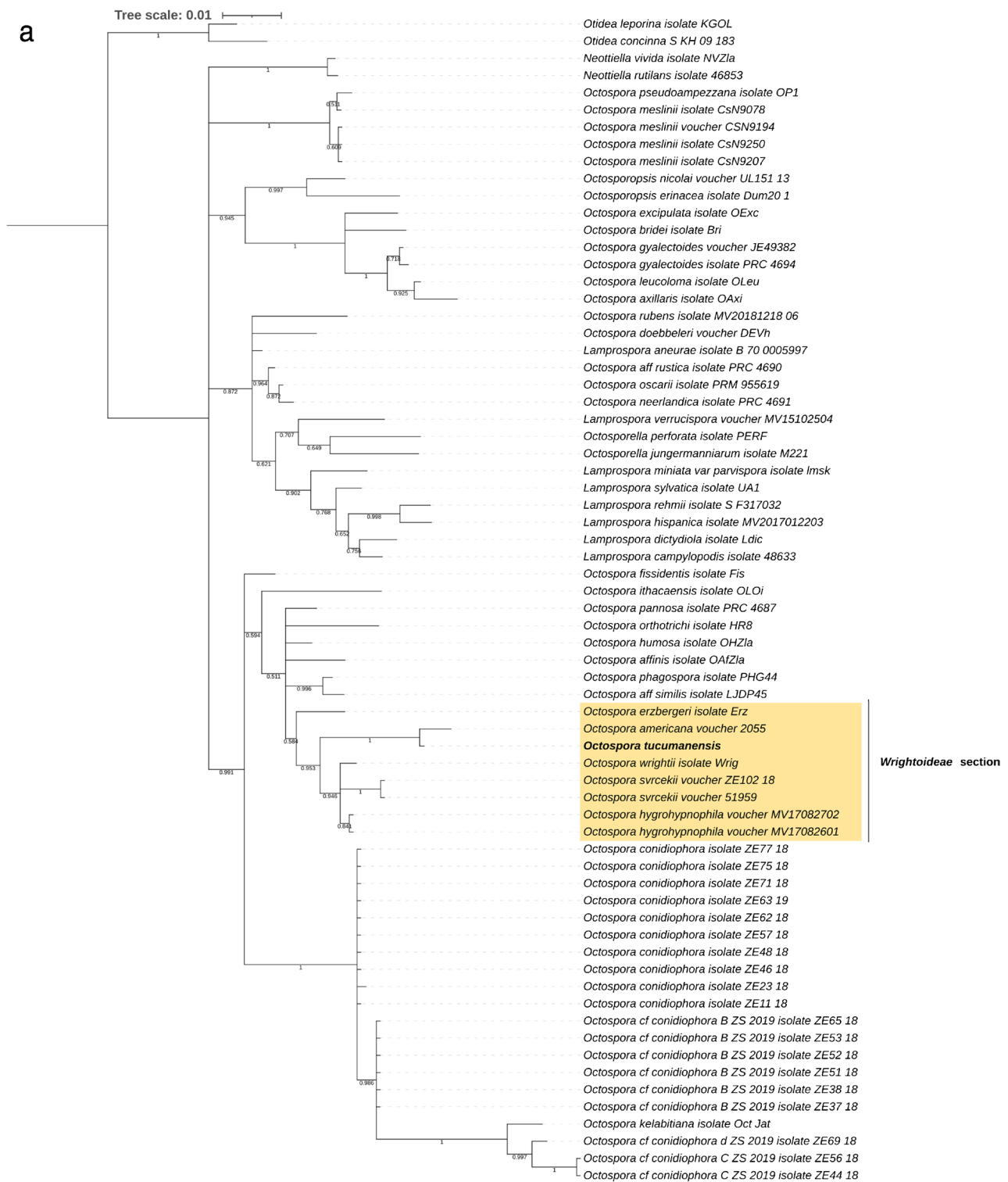


Fig. 1 a Bayesian phylogram based on the concatenated *TEF1α*, LSU and SSU rDNA sequences from *Octospora tucumanensis* and 67 related clades. Bayesian posterior probabilities (>0.50) are shown below the branches. **b** Maximum Likelihood phylogram based on the concatenated *TEF1α*, LSU and SSU rDNA sequences from *Octos-*

pora tucumanensis and 67 related clades. Bootstrap values (>0.75) are shown below the branches. **c** Maximum Parsimony phylogram based on the concatenated *TEF1α*, LSU and SSU rDNA sequences from *Octospora tucumanensis* and 67 related clades. Bootstrap values are shown below the branches

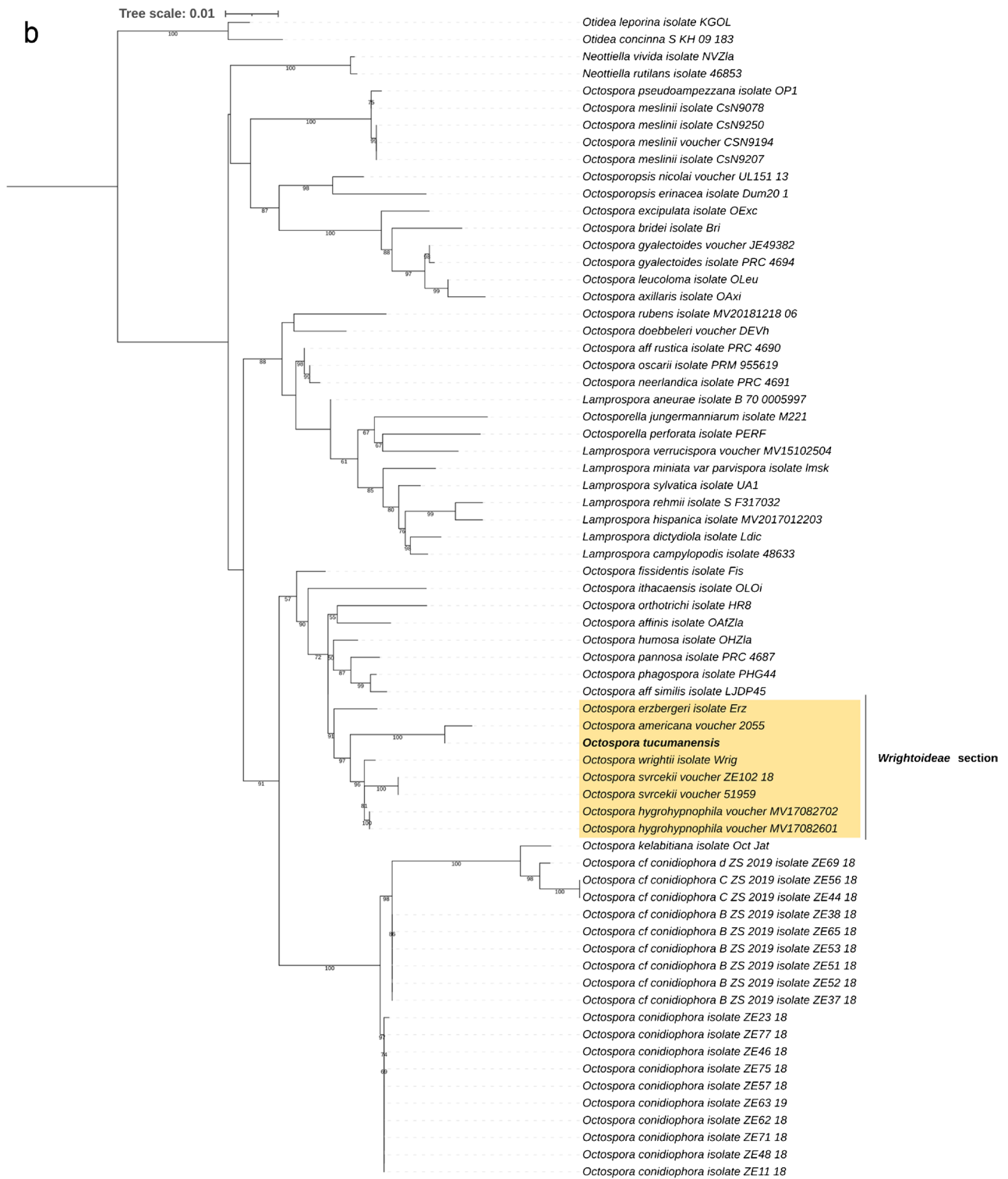


Fig. 1 (continued)

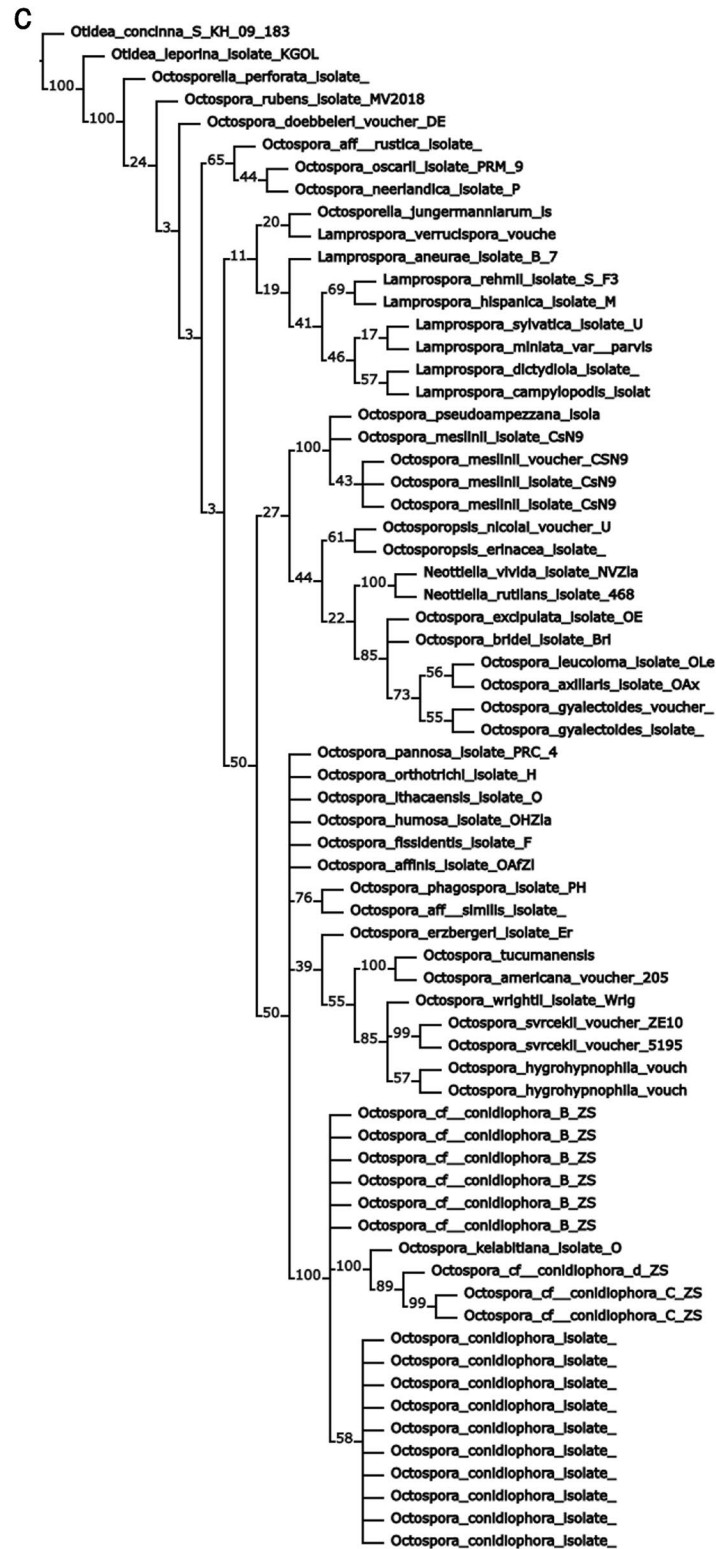


Fig. 1 (continued)



Fig. 2 Apothecia of *Octospora tucumanensis* growing on *Dimerodontium balansae*. (a, c LIL159234; b holotype; d LIL159230). Scale bar: a, b, c, d = 1 mm

angularis, cells 4.5–18 µm in diameter, hyaline, angular, subglobose or irregularly shaped. At the base of apothecia, hyphae growing from the outer cells of the ectal excipulum, 5–9 µm wide, hyaline, branched. *Margin* composed of hyphae arranged parallelly to form a *textura porrecta*, hyphal cells up to 10 µm in diameter, hyaline to pale yellow. Hairs 5–8.5 µm wide, thick-walled, hyaline, septate, with obtuse apices.

Infection. *Octospora tucumanensis* infects the rhizoids of the moss *Dimerodontium balansae*. The infection structure consists of appressoria connected to the terminal cell of rhizoid, which becomes a more or less spherical, one-celled gall 40–42.5 µm in diam. The galls are covered by thick-walled hyphae 3.5–5.5 µm wide. (Fig. 5).

Habitat and occurrence. The pleurocarpous moss *Dimerodontium balansae* (*Fabroniaceae*) is restricted to southern South Africa and South America: Argentina, Brazil, Paraguay, and Uruguay (O’Shea and Price 2008; Câmara and Magill 2009). It belongs to the order *Hypnales* and grows epiphytically, on trunks and exposed roots of trees. The Argentinian localities are in Tucumán in the northwest of the country, five of these points are in an urban place and one near to a rural zone in the Chaco Serrano forest.

Additional specimens examined (all samples were found growing on *Dimerodontium balansae* on different trees as indicated in each material): **ARGENTINA.** Tucumán, San Miguel de Tucumán, 26°49’29”S 65°12’56”W, 441 m asl., 20 Apr 2020, on *Jacaranda mimosifolia*, G. Suárez 1928 (LIL159230). Tucumán, San Miguel de Tucumán, 26°49’21”S 65°13’00”W, 458 m asl., 15 Oct 2021, on *J. mimosifolia*, M. Catania 4037 (LIL159231), Catania 4038 (LIL159232). Tucumán, Dpto. Trancas, San Pedro de Colalao, 26°15’05”S 65°31’16”W, 1141 m asl., 23 Jun 2022, on *Allophylus edulis*, G. Suárez 1930 (LIL159233). Tucumán, San Miguel de Tucumán, 26°49’18”S 65°13’53”W, 461 m asl., 28 Jun 2022, on *Fraxinus pennsylvanica*, G. Suárez 1931 (LIL159234).

Discussion

The ascomata of *Octospora* species are small and usually difficult to find in bryophyte collections, becoming more visible only upon rehydration of the samples. This study demonstrates the paucity of knowledge of bryophilous *Pezizales* in

Southern South America and it does not yet represent their real diversity in Argentina. Unlike the new species recorded here from Northwestern Argentina, the *Octospora* species mentioned for the country were collected at higher latitudes, in places with temperate to cold climate and rarely associated with mosses (Gamundí et al. 2004). According to Eckstein (2016), *Octospora tucumanensis* is currently the only species of bryophilous *Pezizales* known to infect *Dimerodontium balansae*. This moss grows epiphytically on native and exotic trees in Tucumán, Argentina. The finding of *Octospora tucumanensis* manifests that Argentine Northwest is still far from being satisfactorily explored and that future fieldwork will likely reveal novel bryophilous *Pezizales*.

From a phylogenetic viewpoint, *Octospora tucumanensis* is closely related to *O. americana* Benkert, however, the ascospores of *O. tucumanensis* in SEM have warts closer together with striated surface versus isolated warts without striated surface. The ascospores of both *O. tucumanensis* and *O. americana* are ornamented with warts, but they differ in size [$11\text{--}12.5(13) \times (10)10.5\text{--}11.5(12.5)$ µm vs $(12)13\text{--}15 \times (10)11\text{--}13$ µm], morphology (cylindrical, constricted in the middle zone versus conical) and size of the warts (large: $1.2\text{--}1.5 \times 0.6\text{--}0.8$ µm vs 1.0×1.0 µm; small: $0.3\text{--}0.4 \times 0.25\text{--}0.3$ µm vs 0.5×0.5 µm). Likewise, asci are smaller in *O. tucumanensis* ($107.5\text{--}130 \times 12.5\text{--}15$ µm long vs $150\text{--}200 \times 13\text{--}18$ µm) (Benkert 1998). In addition, *O. americana* grows on *Forsstroemia trichomitria* (Hedwig) Lindberg and *Cryphaea glomerata* Schimp. ex Sull., and is only known from temperate southeastern United States (Benkert 1998) while *O. tucumanensis* was found in subtropical, warm areas of Argentina.

The Bayesian, Maximum Parsimony, and ML trees obtained in this study closely reflect the topology of trees from previous studies, supporting the close relationship between *O. meslinii* and *O. pseudoampezzana* recently reported (Németh et al. 2022), the relationship between *O. oscarrii*, *O. rustica* and *O. neerlandica*—but excluding *L. aneurae* under MP (Eckstein et al. 2021), and the results obtained from the study and description of *O. conidiophora* (Sochorová et al. 2019). The section *Wrightoideae*, as described previously (Sochorová et al. 2019; Eckstein et al. 2021) is strongly supported in our ML analysis (BS 0.91), albeit weakly supported under BI (PP 0.59) and MP (<50) (Fig. 1B and C).

Octospora tucumanensis formed a well-supported monophyletic clade along with *O. hygrohypnophila*, *O. svrcekii*

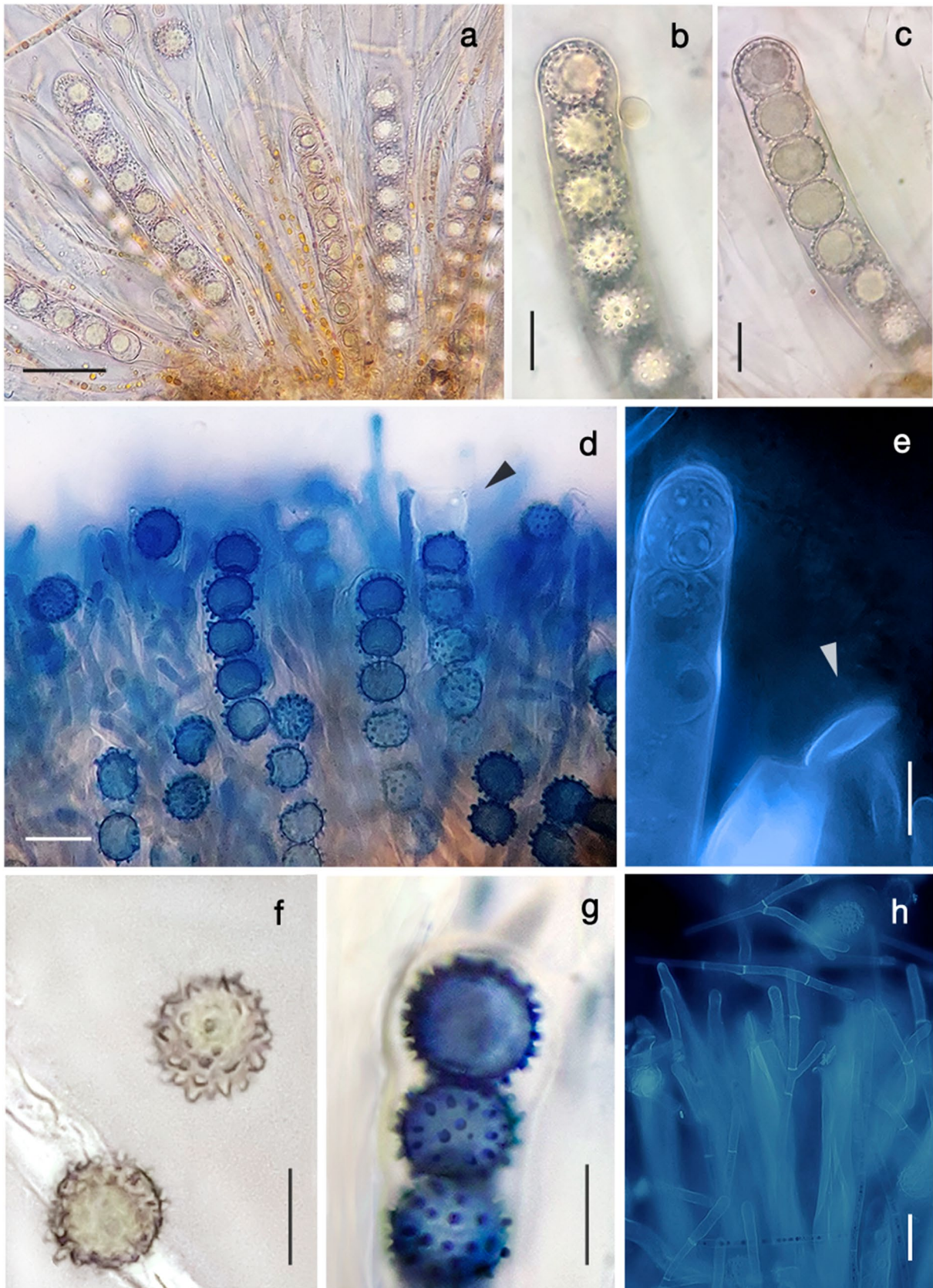


Fig. 3 Microscopic features of *Octospora tucumanensis* (holotype) **a** Asci and paraphyses, in water. **b, c** Ascospores inside ascus, ornamented with warts and ascospores with one large oil droplet, in water. **d** Asci and paraphyses in LPCB, the apex of the ascus open (arrow). **e** Young ascus: spores with a large lipid body and small lipid bodies. Ascus opens with an operculum (arrow) (EF). **f** Spores ornamented with warts, in water. **g** Spores ornamented with warts, in LPCB. **h** Paraphyses (EF). Scale bar: **a**=30 μm ; **b, c, e, f, g**=10 μm ; **d, h**=20 μm

and *O. wrightii*. The differences found in the pairwise alignment between *Octospora tucumanensis* and *O. americana* are small. Although this may suggest that both taxa could well be treated as synonyms, it shall be noticed that even minor differences have been described between two well established species (i.e. *O. meslinii* and *O. pseudoampezzana*; Németh et al. 2022). The small differences observed

do not prevent these organisms from being recognized as independent taxa.

Although our concatenated matrix consisted of 957 bp (124 parsimony informative sites), over 2600 bp obtained from the sequencing of LSU, and SSU rDNA and *TEF1 α* from *O. tucumanensis* had to be trimmed. Most of the trimmed sequences could be ascribed to the use of different primers for the amplification of target sequences. The relatively low support for the section *Wrightioideae* in our Bayesian analysis could be attributed mainly to the inclusion of partial *TEF1 α* sequences retrieved from GenBank. The exclusion of species on the basis of low-quality or partial *TEF1 α* sequences lead to a significant improvement in statistical support, explaining the differences between our results and those found in the literature (i.e. Eckstein et al. 2021; Sochorová et al. 2021; Németh et al. 2022).

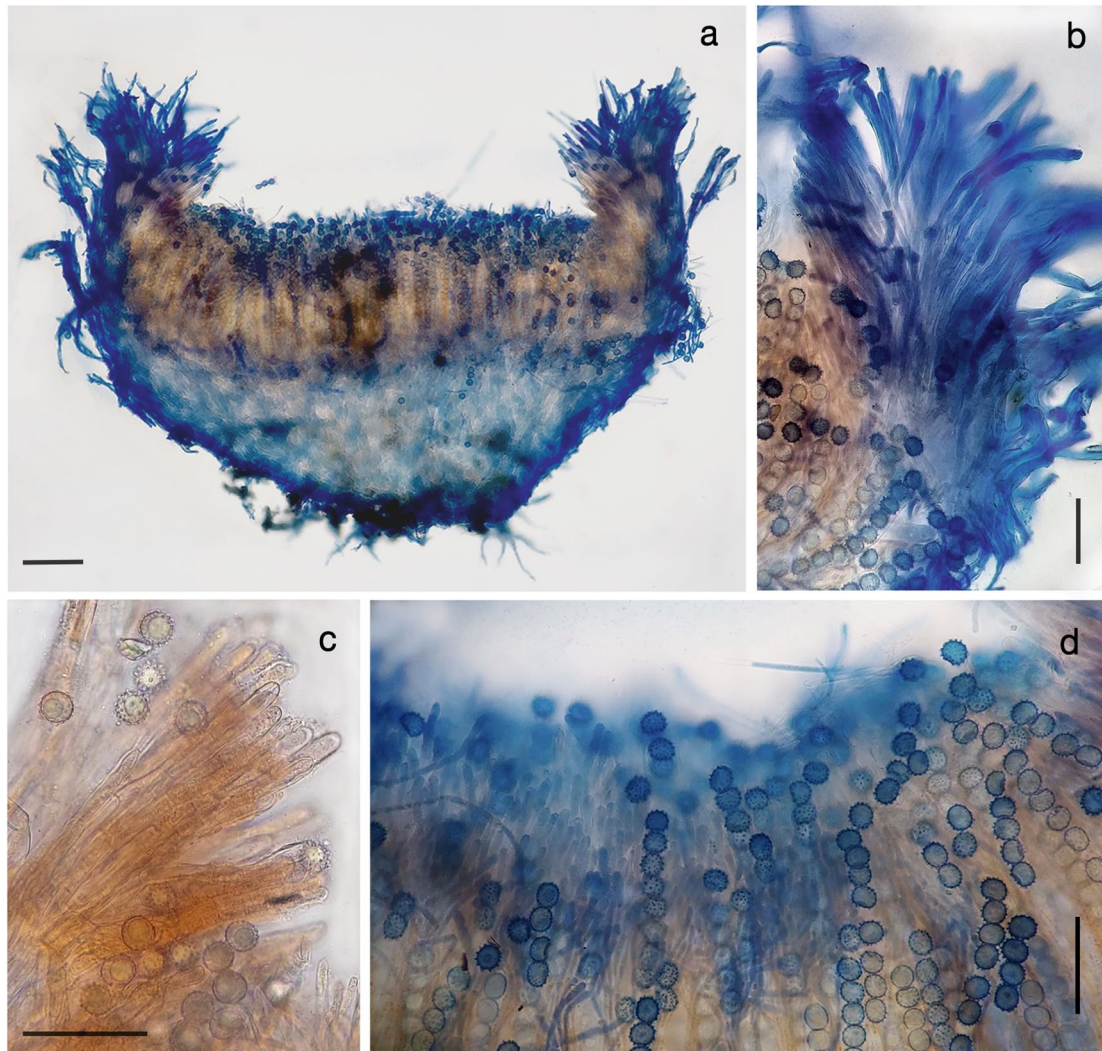


Fig. 4 Microscopic characters of *Octospora tucumanensis* (holotype) **a** Longitudinal section of an apothecium. **b** Detail of the hymenium and margin of apothecium, in LPCB. **c** Hymenium and margin of

apothecium, in water. **d** Asci and paraphyses, in LPCB. Scale bar: **a**=100 μm ; **b, c, d**=50 μm

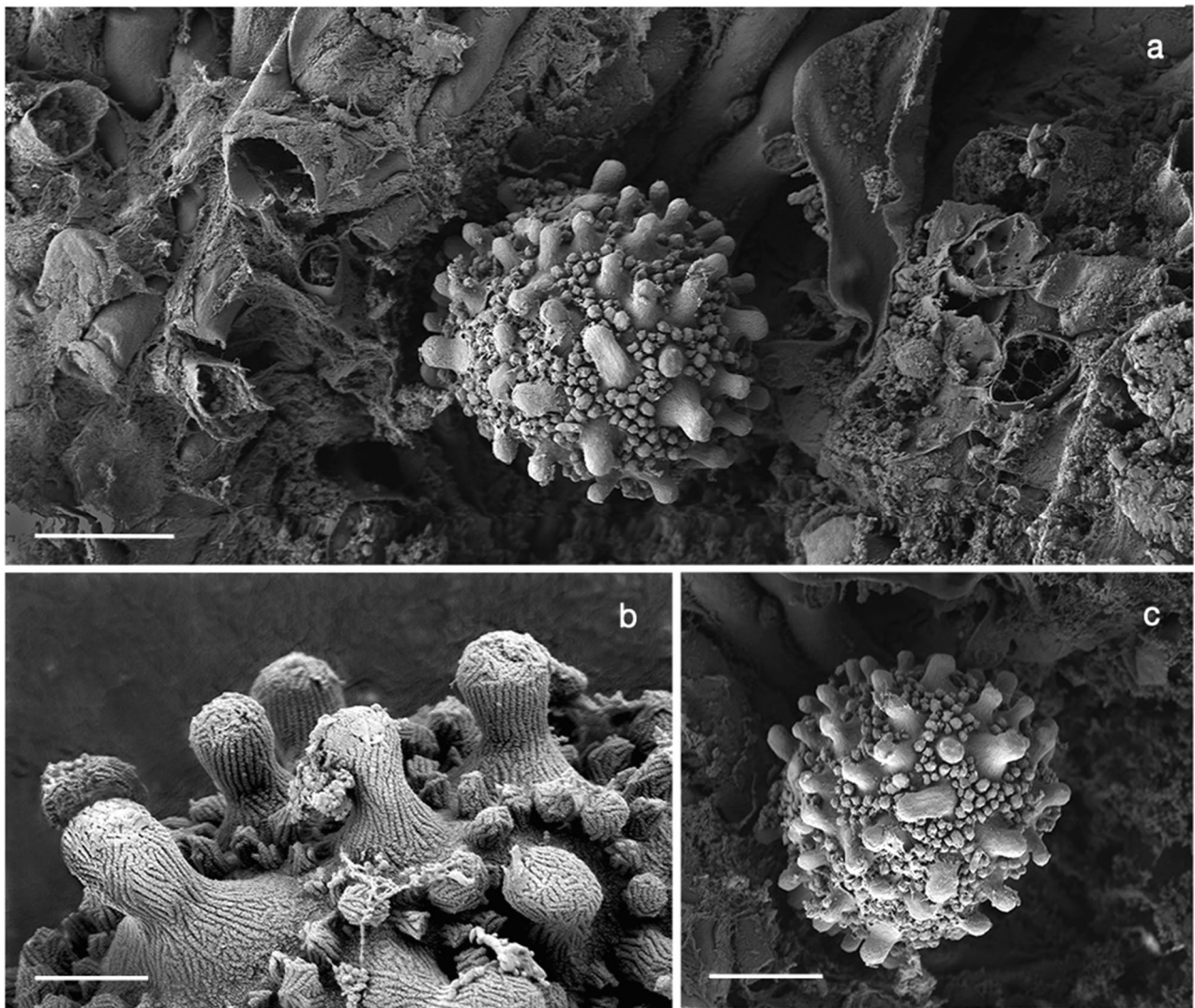
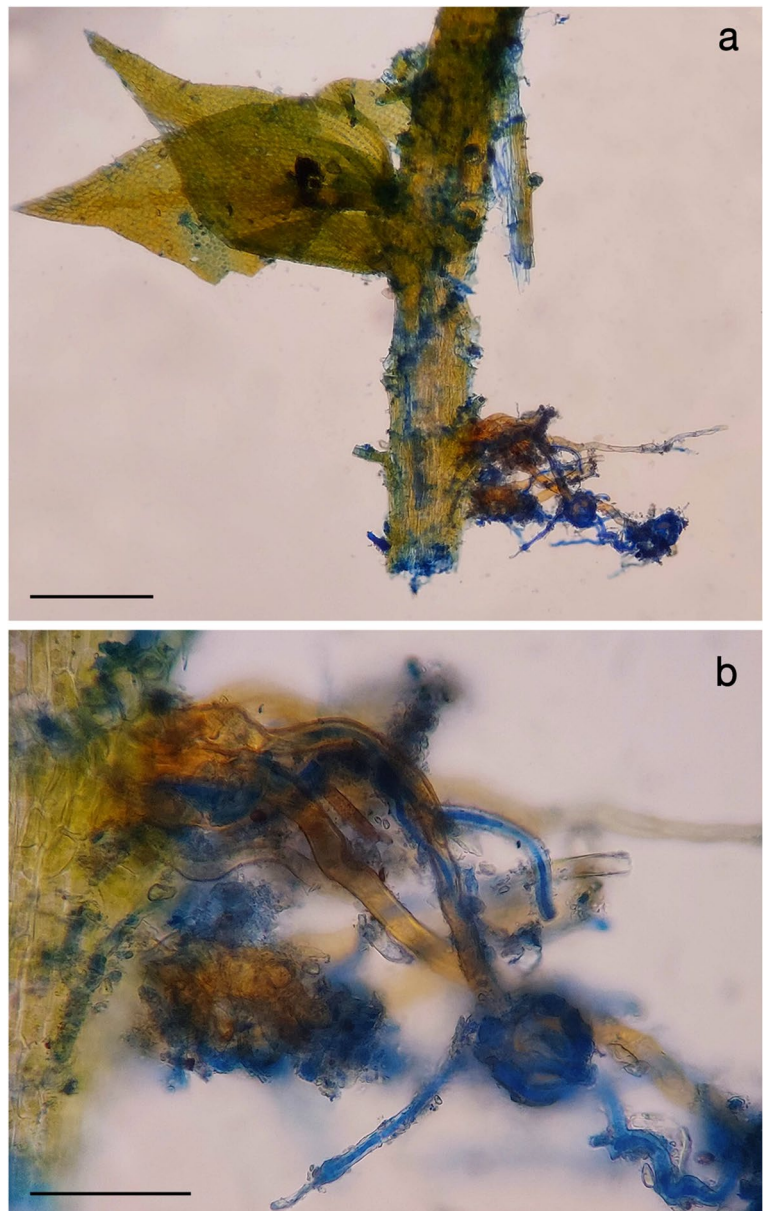


Fig. 5 SEM images of *Octospora tucumanensis* ascospores (holotype) **a**, **c** General view warts, **b** Detail showing the ornamented warts. Scale bar: **a**, **c** = 5 μm ; **b** = 1 μm

Octospora species that grow on pleurocarpic mosses are classified by Benkert (1998) in the section *Wrightoideae*, all of which induce gall formation on rhizoids of the host moss, except *O. affinis* (Sochorová et al. 2020). *Octospora hygrohypnophila* has larger ascospores than our new species, measuring 13.7–15 \times 11–12.5 μm , ornamentation consisting of isolated warts up 1 μm high. Its host is *Hygrohypnum luridum* (Hedw.) Jenn. (Dissing and Sivertsen 1983).

O. svrcekii also differs from *O. tucumanensis* in its larger ascospores, 14–16 \times 13–15 μm , and the ornamentation consisting of isolated, rounded warts; and infects *Cratoneuron filicinum* (Hedw.) Spruce (Benkert 1998). Finally, *Octospora wrightii* differs from our new species in having slightly larger ascospores, (11)12–14(15) \times 11–13(13.5) μm , and the host, *Amblystegium serpens* (Hedw.) Schimp. (Benkert 1998).

Fig. 6 Infections of *Octospora tucumanensis* on *Dimerodontium balansae* (holotype) **a** View of infected moss stem and rhizoids with hyphae. **b** Galls on rhizoid tips covered with interwoven hyphae stained with LPCB. Scale bar: **a**=200 μm ; **b**=100 μm



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Author contributions MC, GMS did the morphological analyses and assembled the descriptions; FD, HP and JF did the molecular data and phylogenetic analyses; all authors analyzed the results and wrote the manuscript. All authors read and approved the final manuscript.

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Data availability All data generated or analyzed during this study are included in this published article.

All sequence data generated in this study is available on GenBank (see Table 1).

The alignment files and original tree outputs are available in the TreeBase repository <http://purl.org/phylo/treebase/phylovs/study/TB2:S29688?x-access-code=f8e234db12368538a92a5e94b0b1e13c&format=html>.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interest The Authors declare that there is no conflict of interest and no competing interests.

Ethics approval Not applicable.

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