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New records of *Anthracoidea pseudofoetidae* (Anthracoideaceae) from Russia, and *Microbotryum* (Microbotryaceae) from Greece and Morocco

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Abstract. A rare smut fungus, *Anthracoidea pseudofoetidae*, is reported for the first time from Russia, based on a specimen from the Altai Republic, and *Carex enervis* is reported as a new host. Two new records for Greece, *Microbotryum duriaeanum* and *M. moenchiae-manticae,* and one for Morocco, *Microbotryum moehringiae,* are also presented. *Microbotryum moehringiae* is recorded for the first time from Africa. *Cerastium brachypetalum* subsp. *roeseri* is a new host record for *Microbotryum duriaeanum*. New molecular data are provided for these smut fungi. Updated phylogenetic trees for *Anthracoidea* and *Microbotryum* are also presented.

Keywords. Phylogenetic analyses, smut fungi.

Resumen. *Anthracoidea pseudofoetidae*, un raro hongo tizón, se cita por primera vez para Rusia, a partir de un espécimen de la República de Altai, and *Carex enervis* se reporta como un nuevo hospedador. Se presentan dos nuevos registros para Grecia, *Microbotryum duriaeanum* y *M. moenchiae-manticae*, y uno para Marruecos, *Microbotryum moehringiae*. *Microbotryum moehringiae* se registra por primera vez en África. *Cerastium brachypetalum* subsp. *roeseri* es un nuevo hospedador de *Microbotryum duriaeanum*. Se aportan nuevos datos moleculares sobre estos hongos. También se presentan árboles filogenéticos actualizados de *Anthracoidea* y *Microbotryum*.

Palabras clave. Análisis filogenéticos, hongos tizón.

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INTRODUCTION

Smut fungi are plant parasites. They are characterized by a specific life cycle that alternates between a dikaryotic, plant-parasitic stage and a haploid, saprobic yeast phase, and by the presence of thick-walled teliospores. Smut fungi represent a phylogenetically heterogeneous group that has evolved three times independently in the Ustilaginomycotina, Microbotryales (Pucciniomycotina), and Entorrhizomycota (Begerow & al. 2014; He & al. 2022). They are mostly found on herbaceous plants, very rarely on woody hosts. More than 1900 species of smut fungi are currently known. The highest species diversity is reported from the northern hemisphere, with most species found in Europe and Asia (He & al. 2022).

The species of *Anthracoidea* Bref. (Anthracoideaceae, Ustilaginomycotina) have as hosts plants the genera *Carex* L., *Carpha* R.Br., *Fuirena* Rottb., *Schoenus* L., and *Trichophorum* Pers. (Cyperaceae). *Anthracoidea* form sori in female flowers around aborted nuts as ovoid, ellipsoidal or broadly ellipsoidal hard bodies (Denchev & al. 2021). The species of *Microbotryum* Lév. (Microbotryaceae, Pucciniomycotina) are parasites on hosts in ten dicot families. They form sori in various organs of the infected plants (flowers, anthers, ovules, filaments of stamina, branches of inflorescences, capitula, stems or leaves), filing them with single, subhyaline to dark reddish brown or dark purple, variously ornamented spores (Vánky 2011; Denchev & al. 2020; Kemler & al. 2020).

The aim of this study was to increase the knowledge about the geographical distribution and host specialization of *Anthracoidea pseudofoetidae* L. Guo and three seed-destroying species of *Microbotryum* (*M. duriaeanum* (Tul. & C. Tul.) Vánky, *M. moehringiae* (Togashi & Y.Maki) Vánky, and *M. moenchiae-manticae*) (Lindtner) Vánky, as well as to provide new molecular data for these smut fungi.

MATERIAL AND METHODS

The new records are based on collections that were discovered during a visit of two of the authors (T.T.D. & C.M.D.) to the herbarium at the Botanic Garden and Botanical Museum Berlin (B) in March 2022. Dried specimens from B were examined with a light microscope (LM) and scanning electron microscope (SEM). For LM observations and measurements, spores were mounted in lactoglycerol solution (w : la : gl = 1 : 1 : 2) on glass slides, gently heated to boiling point for rehydration, and then cooled. The measurements of spores are given in the form: min–max (extreme values) (mean ± 1 standard deviation). For SEM, spores were attached to specimen holders by double-sided adhesive tape and coated with gold in an ion sputter. SEM images were taken with a Hitachi FE SEM 8010. Information on shapes of spores is arranged in descending order of frequency. The descriptions of spore length range and spore ornamentation of *Anthracoidea pseudofoetidae* are in accordance with Denchev & al. (2020: 11) and Denchev & al. (2013), respectively. The descriptions given below are based entirely on the specimens examined.

Genomic DNA of the herbarium specimens was isolated using the myBudget Plant DNA KitTM (Bio-Budget Technologies GmbH, Germany) using the SLS protocol according to the manufacturer's instructions. PCR of the ITS and/or the large subunit (LSU) region of the rDNA was performed using the primer pairs ITS1F/ITS4 and LR0R/LR6, respectively. Amplicons were purified using a modified ExoSAP (1:5 diluted in ddH_2O; New England Biolabs, USA) protocol and subsequently sequenced using the respective forward and reverse primers with the BigDyeTM Terminator Cycle Sequencing Kit V3.1 (Applied Biosystems) on an ABI3130xl Genetic Analyser at the Faculty of Biochemistry of the Ruhr-Universität Bochum, Germany. Forward and reverse reads were quality checked and assembled in Geneious 10.2.6 (Biomatters Ltd, New Zealand).

Multiple alignments were inferred using the online version of MAFFT 7 (Katoh & Standley 2013) with either the E-INS-i (*Microbotryum* ITS and *Anthracoidea* LSU) or L-INS-i option (*Microbotryum* LSU). Leading and trailing gaps, as well as ambiguous sites were removed using GBlocks (Castresana 2000) implemented in SeaView (Gouy & al. 2010), whereby smaller final blocks, gap positions, and less strict flanking positions were allowed. For *Microbotryum* the ITS and LSU regions were concatenated before phylogenetic analysis. RAxML-NG (Kozlov & al. 2019) implemented in raxmlGUI 2.0 (Edler & al. 2021) was used for phylogenetic inference and bootstrapping (1000 replicates). Before phylogenetic analyses, ModelTest-NG (Darriba & al. 2020) was used to select the most appropriate nucleotide substitution model (*Anthracoidea*: GTR+I+G; *Microbotryum*: GTR+I+G). Bootstrap values ≥ 50 are shown above branches.

RESULTS AND DISCUSSION

Taxonomic treatment

Anthracoidea pseudofoetidae L. Guo, Fungal Diversity 21: 84, 2006. Type: China, Xizang, Gégyai Xian, Alingshan, alt. 5200 m, in ovaries of *Carex pseudofoetida* Kük., 15 August 1976, Qinghai-Xizang expedition 13486 (HMAS 130321, holotype; isotype HUV 20091). Fig. 1.

Infection local. Sori in some female flowers, around aborted nuts as broadly ellipsoidal, subglobose or ovoid hard bodies, 1.0–1.7 mm long, initially covered by a thick, blackish brown peridium that later flakes away exposing a blackish brown, powdery on the surface spore mass. Spores very small-sized, irregularly rounded, subglobose, broadly ellipsoidal, ovoid or ellipsoidal, (8.5–)9–11.5(–12.5) × (8–)8.5–10.5(–11.5) (10.2 ± 0.7 × 9.3 ± 0.6) µm (n = 100), medium reddish brown; wall unevenly thickened, 0.9–1.5 µm thick, with a few paler, rounded areas with thinner wall (0.5–0.9 µm thick); internal swellings, light refractive areas, and protuberances absent; spore surface minutely verruculose, spore profile not affected. In SEM, spore wall depressed on 3–6 places, ornaments up to 0.15

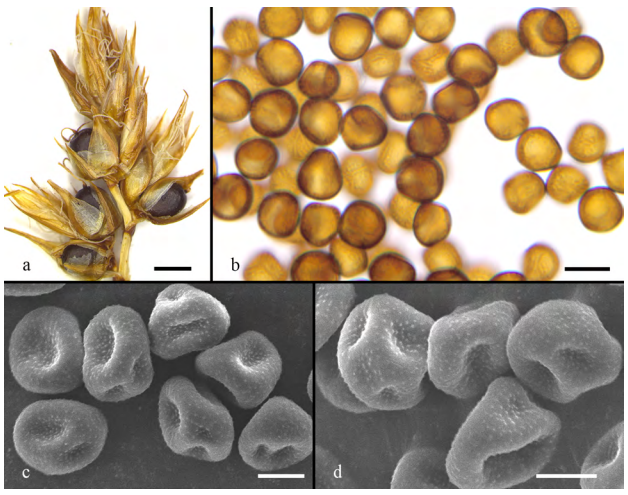

Fig. 1. *Anthracoidea pseudofoetidae* on *Carex enervis* (B 10 0240205): **a,** habit; **b,** spores in LM; **c, d,** spores in SEM. Scale bars: a = 1 mm, b = 10 µm, c, d = 5 µm.

Fig. 2. Maximum Likelihood phylogeny inferred using RAxML-NG based on LSU sequence data representing the species of Anthracoideaceae. The phylogeny was rooted using *Anthracoidea carphae* and *A. sclerotiformis* according to Hendrichs & al. (2005). Values above branches indicate bootstrap values inferred by 1000 replicates; only values ≥ 50% are shown.

µm high, usually solitary and sparsely spaced, occasionally partly confluent, forming short rows or small groups.

Specimen examined.—Russia, Altai Republic, Kosh-Agachskiy District, 20 km ENE Kosh-Agach, valley of the Kokorya River, 50°05′30″N, 88°53′57″E, alt. 2080 m, on *Carex enervis* C.A.Mey., 9 Aug 2008, leg. L. Martins 2476, fungus comm. & det. T.T. Denchev & C.M. Denchev (B 10 0240205; GenBank LSU OQ067238).

Hosts and Distribution.—On Cyperaceae: on *Carex enervis*, *C. maritima* Gunnerus, and *C. pseudofoetida*. Known from Asia (China and Russia) and North America (Greenland).

Comments.—*Anthracoidea pseudofoetidae* was recovered as a sister species to a group of *A. aspera*, *A. arenaria*, and *A.* cf. *karii*, however with low bootstrap support (Fig. 2, Table 1).

Anthracoidea pseudofoetidae is recorded for the first time from Russia, on a new host plant species, *Carex enervis*. This smut fungus is an Arctic-alpine species with a restricted distribution (Denchev & al. 2020). It has been

Table 1. *Anthracoidea* specimens, plant hosts, vouchers, and NCBI Genbank accession numbers of the large subunit (LSU) of nuclear ribosomal DNA sequences used in the phylogenetic analysis. The single newly generated sequence is shown in bold.

Species	Host	Voucher	Accession
Anthracoidea arenaria	*Carex arenaria*	PUL F916	AY563606
A. aspera	*C. chordorrhiza*	HMH 2774	AY563607
A. baldensis	*C. baldensis*	HMH 2861	AY563599
A. bigelowii	*C. bigelowii*	HMH 2733	AY563566
A. bigelowii	*C. bigelowii*	HMH 927	AY563567
A. bigelowii	*C. bigelowii*	HMH 2736	AY563568
A. buxbaumii	*C. buxbaumii*	HMH 2744	AY563582
A. capillaris	*C. capillaris*	HMH 2769	AY563596
A. caricis	*C. pilulifera*	HMH 3364	AY563589
A. caricis-albae	*C. alba*	HMH 2869	AY563594
A. caricis-albae	*C. alba*	HMH 2873	AY563595
A. caricis-meadii	*C. meadii*	ISC 428408	JN863083
A. carphae	*Carpha alpina*	M-40218	AY563614
A. curvulae	*Carex curvula*	HMH 3912	AY563611
A. curvulae	*C. curvula*	HMH 2380	AY563612
A. elynae	*C. myosuroides*	HMH 3958	AY563609
A. elynae	*C. myosuroides*	M 6794	AY563610
A. globularis	*C. globularis*	HMH 2422	AY563593
A. hallerianae	*C. halleriana*	SOMF 30199	MT628660
A. hallerianae	*C. halleriana*	SOMF 30201	MT628657
A. heterospora	*C. elata*	HMH 2438	AY563600
A. heterospora	*C. elata*	HMH 921	AY563601
A. hostianae	*C. hostiana*	HeRB 4706	AY563581
A. inclusa	*C. rostrata*	HMH 2883	AY563605
A. irregularis	*C. ornithopoda*	HMH 3480	AY563590
A. irregularis	*C. ornithopoda*	HMH 3520	AY563591
A. irregularis	*C. digitata*	HMH 933	AY563592
A. karii	*C. brunnescens*	HMH 2777	AY563575
A. karii	*C. echinata*	HMH 3892	AY563576
A. karii	*C. echinata*	HMH 3676	AY563577
A. karii	*C. echinata*	HMH 3414	AY563578
A. karii	*C. lachenalii*	HMH 2644	AY563579
A. karii	*C. paniculata*	HMH 3890	AY563574
A. **cf.** *karii*	*C. davalliana*	HMH 3898	AY563608
A. lasiocarpae	*C. lasiocarpa*	HMH 972	AY563583
A. limosa	*C. limosa*	HMH 2428	AY563572
A. limosa	*C. limosa*	HMH 2790	AY563573
A. misandrae	*C. atrofusca*	HMH 2653	AY563584
A. pamiroalaica	*C. koshewnikowii*	KRA F-2012-146	KT006854
A. paniceae	*C. panicea*	HMH 2818	AY563580
A. pratensis	*C. flacca*	HMH 3599	AY563563
A. pratensis	*C. flacca*	HMH 1164	AY563564
A. pratensis	*C. flacca*	HMH 3870	AY563565
A. pseudofoetidae	*C. enervis*	B 10 0240205	**OQ067238**
A. rupestris	*C. rupestris*	HMH 3948	AY563598
A. cf. *rupestris*	*C. glacialis*	HMH 3692	AY563588
A. sclerotiformis	*C. punicea*	M 4946	AY563613
A. sempervirentis	*C. firma*	HMH 3612	AY563585
A. sempervirentis	*C. ferruginea*	HMH 3616	AY563587
A. sempervirentis	*C. sempervirens*	HMH 3950	AY563586
A. subinclusa	*C. hirta*	HMH 3700	AY563604
A. subinclusa	*C. riparia*	PUL F915	AY563603
A. subinclusa	*C. vesicaria*	HMH 2809	AY563602
A. turfosa	*C. dioica*	HMH 2797	AY563571
A. turfosa	*C. heleonastes*	HMH 2662	AY563569
A. turfosa	*C. parallela*	HMH 2523	AY563570
A. vankyi	*C. muricata*	HMH 1305	AY563597

previously known only on *Carex pseudofoetida* from the type locality in China (Xizang) (Guo 2006), and on *C. maritima* from two localities in the High Arctic of Greenland (Denchev & al. 2020). The species of *Anthracoidea* on *Carex* are host-specific smut fungi restricted to sedges belonging to the same or closely related sections (Denchev & al. 2021). All three hosts of *A. pseudofoetidae* were traditionally placed in *Carex* sect. *Foetidae* (L.H. Bailey) Kük. (Egorova 1999; Reznicek 2002). Currently, these sedges are considered belonging to the Disticha clade that includes 27 species (Roalson & al. 2021). Most species in this clade are distributed in North America and temperate Eurasia. *Carex pseudofoetida* and *C. enervis* are Central Asiatic species while *C. maritima* has a bipolar distribution (Egorova 1999; Reznicek 2002). *Anthracoidea pseudofoetidae* can be easily distinguished from other *Anthracoidea* species by a suite of distinctive features that includes: (i) sori covered by a thick, dark brown peridium; (ii) very

small-sized spores; and (iii) a characteristic spore wall, depressed on 3–6 places where the wall is paler and thinner (Denchev & al. 2020).

Microbotryum duriaeanum (Tul. & C. Tul.) Vánky, Mycotaxon 67: 43, 1998; *Ustilago duriaeana* Tul. & C. Tul., Ann. Sci. Nat., Bot., Sér. 3, 7: 105, 1847. Type: ALGERIA, Tlemcen, on *Cerastium glomeratum* Thuill., 30 May 1842, M.C. Durieu de Maisonneuve (PC s.n., holotype). Fig. 3a–c.

Infection systemic. Sori destroying the seeds, filling the capsules initially with a semi-agglutinated, later powdery, dark sepia (based on Rayner 1970) or dark purplish date (based on the Color identification chart of Anonymous 1969) spore mass. Spores subglobose, globose or broadly ellipsoidal, sometimes ovoid, (12–)13–16(–17) × (11.5–)12.5–14.5(–15.5) (14.4 ± 0.9 × 13.3 ± 0.8) µm (n = 100), light to medium reddish brown; wall reticulate, 1.9–2.5 µm thick (including reticulum), meshes (5–)6–8(–9) per spore diameter, polyhedral or irregular, 0.6–2.7(–3.5) µm wide, muri (0.8–)1.0–1.4(–1.7) µm high. In SEM, the meshes smooth, often with a hemispherical protuberance at the bottom. The description is based on the infected specimen of *Cerastium brachypetalum* subsp. *roeseri* (Boiss. & Heldr.) Nyman.

Specimens examined.—GREECE. **Western Macedonia Region**: Grevena, W of Kallithea, 39°51′01″N, 21°19′14″E, alt. 1050 m, on *Cerastium brachypetalum* subsp. *roeseri*, 16 May 2012, leg. R. Willing & E. Willing 219.396, fungus comm. & det. T.T. Denchev & C.M. Denchev (B 10 1224088; GenBank ITS OQ096632, LSU OQ067234). **Western Macedonia Region**: Grevena, Milea, 40°11′00″N, 21°28′22″E, alt. 670 m, on *Cerastium semidecandrum* L., 24 May 2012, leg. R. Willing & E. Willing 221.910, fungus comm. & det. T.T. Denchev & C.M. Denchev (B 10 0499209; GenBank ITS OQ096633, LSU OQ067235).

Hosts and Distribution.—On *Cerastium* spp. (Caryophyllaceae). Known from Europe, North Africa, Asia, and North America.

Comments.—Both specimens of *Microbotryum duriaeanum* from this study fell into a clade with all other *M. duriaeanum* specimens sequenced up to date. The specimen on *Cerastium brachypetalum* subsp. *roeseri* emerged sister to all other *M. duriaeanum* specimens, whereas the specimen on *C. semidecandrum* formed a polytomy with the other specimens (Fig. 4, Table 2).

Microbotryum duriaeanum is reported here as a new record for Greece, on two host plants, among which *Cerastium brachypetalum* subsp. *roeseri* is recorded for the first time.

Microbotryum moehringiae (Togashi & Y.Maki) Vánky, Mycotaxon 67: 46, 1998; *Ustilago moehringiae* Togashi & Y.Maki, Ann. Phytopathol. Soc. Japan 10: 139, 1940. Type: Japan, Fukuoka Pref., Yoshikawa-mura, on *Moehringia trinervia* var. *platysperma* (Maxim.) Makino, 7 May 1938, Y. Maki (TNS s.n., holotype). Fig. 3d–f.

Infection systemic. Sori destroying the seeds, filling the capsules initially with a semi-agglutinated, later powdery, dark bay (based on Rayner 1970) or bay (based on the Color identification chart of Anonymous 1969) spore mass. Spores subglobose, globose or broadly ellipsoidal, sometimes ovoid, (10.5–)11.5–13.5(–14.5) × (10–)11–12.5(–13.5) (12.8 ± 0.6 × 11.8 ± 0.6) µm (n = 100), light to medium reddish brown; wall reticulate, 1.4–2.2 µm thick (including reticulum), meshes (4–)5–6(–7) per spore diameter, polyhedral or irregular, (0.7–)1.0–2.7(–3.3) µm wide, muri 0.6–1.1(–1.3) µm high. In SEM, meshes smooth, often with a hemispherical protuberance at the bottom.

Specimen examined.—MOROCCO. **Fès-Meknès Region**: Foret de Jaba, ca 15 km from El Hajeb, road to Ifrane, 33°36′N, 5°17′W, alt. 1400 m, on *Moehringia trinervia* (L.) Clairv., 9 Jun. 1992, leg. B. Valdés & al., 5th Iter Mediterraneum of OPTIMA, Morocco, Jun. 1992, 04-0237, fungus comm. & det. T.T. Denchev & C.M. Denchev (B 10 0298453; GenBank ITS OQ096635, LSU OQ067237).

Hosts and Distribution.—On *Moehringia* spp. (Caryophyllaceae). Known from Europe, North Africa, and Asia.

Comments.—The specimen of *M. moehringiae* from this study formed a well-supported clade with the only other specimen of *M. moehringia* (on *Moehringia trinervia*) sequenced so far, indicating that *M. moehringiae* is indeed a distinct species (Fig. 4, Table 2).

Microbotryum moehringiae is recorded for the first time from Africa. It has been previously reported for Asia (Japan, on *Moehringia trinervia* var. *platysperma*; Denchev & al. 2006) and Europe (Spain, on *M. pentandra* J.Gay; Almaraz 1999, as '*Ustilago duriaeana*', and France, on *M. trinervia*; Kemler & al. 2020).

Microbotryum moenchiae-manticae (Lindtner) Vánky, Mycotaxon 67: 46, 1998; *Ustilago moenchiae-manticae* Lindtner, Bull. Mus. Hist. Nat. Serbe, Ser. B 3–4: 33, 1950. Type: Serbia, Rudnik near Milanovac, on *Moenchia mantica* Bartl., 15 Jun. 1946, V. Lindtner (HUV 4123, lectotype; Ustilag. Jugosl., no. 3, isolectotypes). Fig. 3g–i.

Infection systemic. Sori destroying the seeds, filling the capsules initially with a semi-agglutinated, later powdery, sepia (based on Rayner 1970) or date brown (based on the Color identification chart of Anonymous 1969) spore mass. Spores subglobose, globose, broadly ellipsoidal or ovoid, (11–)12–15.5(–16.5) × (10–)11–14(–15) (13.8 ± 1.1 × 12.6 ± 1.1) µm (n = 100), medium reddish brown; wall reticulate, 1.4–2.2 µm thick (including reticulum), meshes (5–)6–9 per spore diameter, polyhedral or irregular, 0.7–2.5(–3.0) µm wide, muri 0.7–1.2(–1.5) µm high. In SEM, meshes

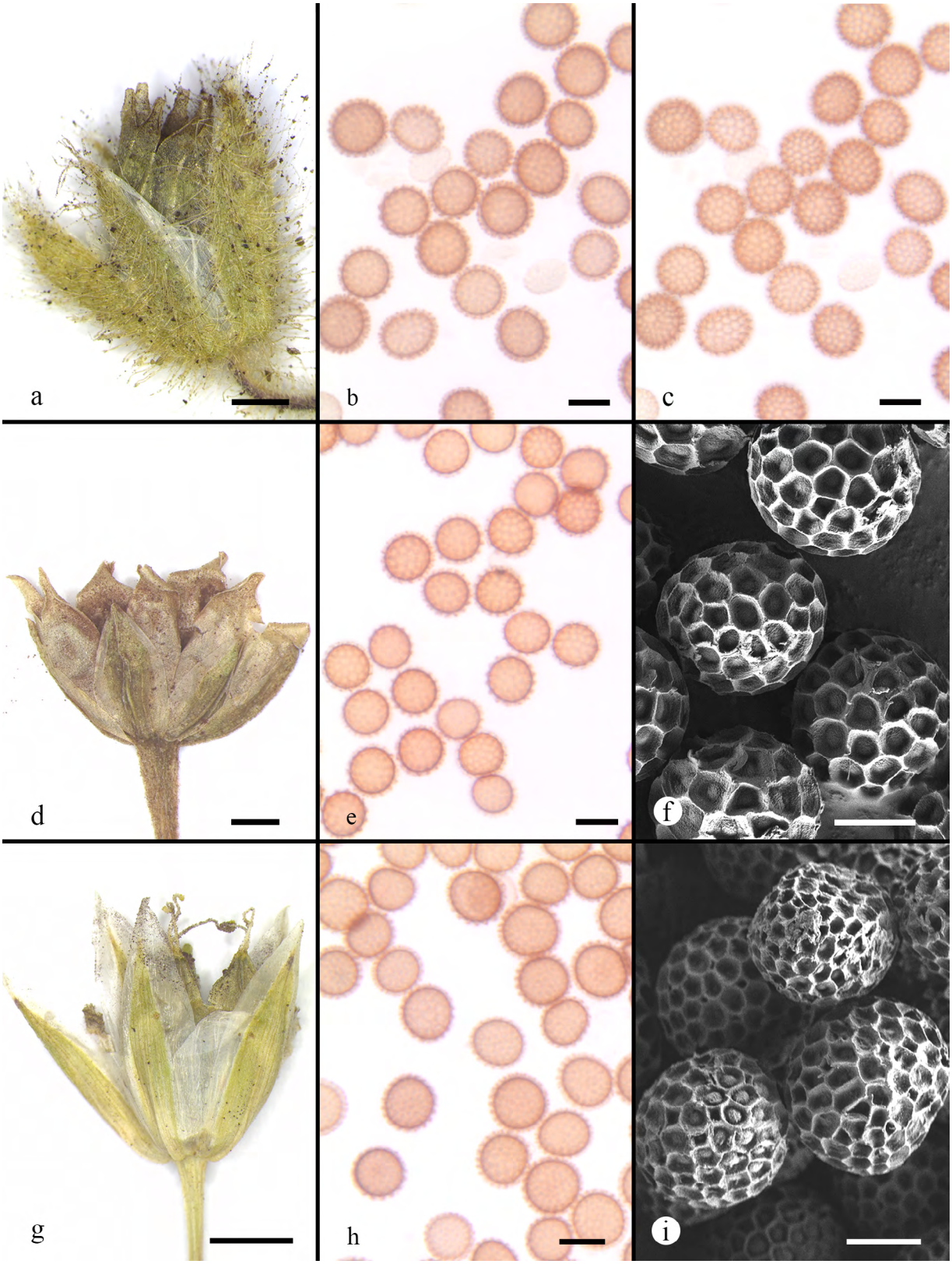

Fig. 3. *Microbotryum duriaeanum* on *Cerastium brachypetalum* subsp. *roeseri* (B 10 1224088): **a,** capsule filled with spores; **b, c,** spores in LM (in median and surface view, respectively). *Microbotryum moehringiae* on *Moehringia trinervia* (B 10 0298453): **d,** capsule filled with spores; **e,** spores in LM; **f,** spores in SEM. *Microbotryum moenchiae-manticae* on *Moenchia mantica* (B 10 0255208): **g,** capsule filled with spores; **h,** spores in LM; **i,** spores in SEM. Scale bars: a, d, g = 1 mm, b, c, e, h = 10 µm, f, i = 5 µm.

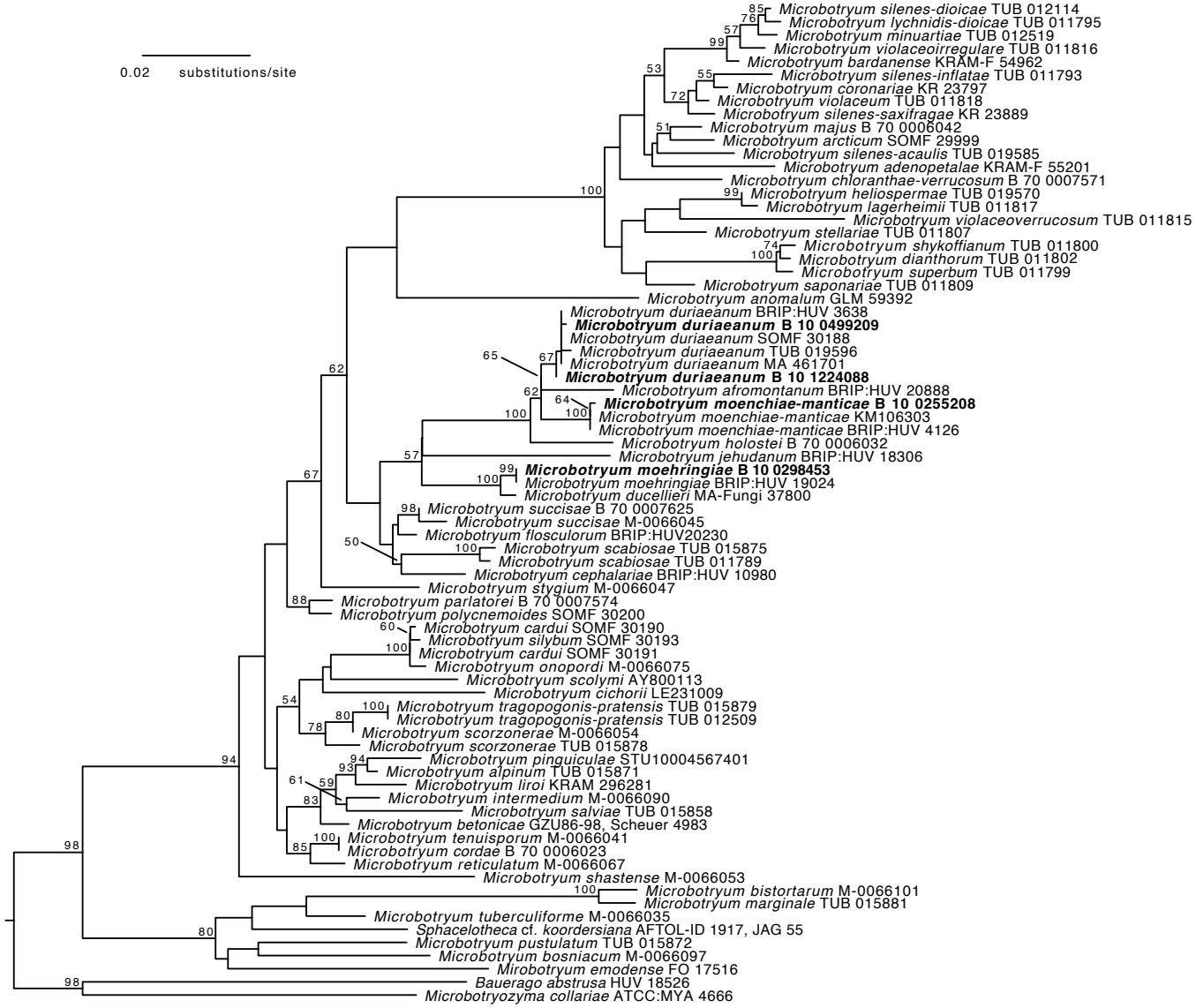

Fig. 4. Maximum Likelihood phylogeny inferred using RAxML-NG based on combined LSU and ITS sequence data representing the species of Microbotryaceae. The tree is rooted with *Microbotryozyma collariae* and *Bauerago abstrusa*. Values above branches indicate bootstrap support inferred by 1000 replicates; only values ≥ 50% are shown.

smooth or rugulose, often with a hemispherical protuberance at the bottom.

Specimens examined.—GREECE. **Thessaly**: Karditsa, near Kryoneri, 39°19′39″N, 21°42′00″E, alt. 785 m, on *Moenchia mantica*, 29 May 2005, leg. R. Willing & E. Willing 140.865, fungus comm. & det. T.T. Denchev & C.M. Denchev (B 10 0255208; GenBank ITS OQ096634, LSU OQ067236). **Western Greece Region**: Aetolia-Acarnania, Ep. Nafpaktias, 1 km SE of Ano Hora, 38°35′N, 21°55′30″E, alt. 1020 m, on *M. mantica*, 15 Jun. 1991, leg. R. Willing 15.741, fungus comm. & det. T.T. Denchev & C.M. Denchev (B 10 1224076).

Hosts and Distribution.—On *Moenchia* spp. (Caryophyllaceae). Known from Europe and North Africa.

Comments.—The sequence of the specimen B 10 0255208 formed a well-supported clade with two sequences from this species (Fig. 4, Table 2).

Microbotryum moenchiae-manticae is recorded for the first time from Greece. It has been previously reported from Europe – Bulgaria, Spain, and UK, on *Moenchia erecta* G.Gaertn., B.Mey. & Scherb. subsp. *erecta* (Denchev 1997; Denchev & al. 2010; Denchev & Denchev 2017), and Romania and Serbia, on *M.*

Table 2. Smut fungi specimens, plant hosts, vouchers, and NCBI accession numbers of the sequences used in the phylogenetic analysis of *Microbotryum*. Newly generated sequences are shown in bold. LSU: large subunit of the nuclear ribosomal DNA.

Species	Host	Voucher	ITS	LSU
Bauerago abstrusa	*Juncus* sp.	HUV18526	DQ238719	EF621955
Microbotryozyma collariae	n/a	ATCC:MYA-4666	JN849458	JN849460
Microbotryum adenopetalae	*Silene adenopetala*	KRAM F 55201	DQ366848	DQ366876
M. afromontanum	*Cerastium afromontanum*	BRIP: HUV 20888	MN657185	MN657208
M. alpinum	*Pinguicula alpina*	TUB 015871	EF621944	EF621995
M. anomalum	*Fallopia convolvulus*	GLM 59392	EF621921	EF621960
M. arcticum	*Silene uralensis* subsp. *arctica*	SOMF 29999	MK474659	MK474658
M. bardanense	*S. moorcroftiana*	KRAM F 54962	DQ366856	DQ366877
M. betonicae	*Stachys alopecuros*	GZU 86-98, Scheuer 4983	EF621927	EF621967
M. bistortarum	*Bistorta vivipara*	M-0066101	DQ238709	EF621969
M. bosniacum	*Koenigia alpina*	M-0066097	DQ238740	EF621977
M. cardui	*Carduus acanthoides*	SOMF 30191	MN657187	MN657210
M. cardui	*C. crispus*	SOMF 30190	MN657188	MN657211
M. cephalariae	*Cephalaria humilis*	BRIP: HUV 10980	MN657203	MN657212
M. chloranthae-verrucosum	*Silene chlorantha*	B 70 0007571	AY877404	DQ366878
M. cichorii	*Cichorium intybus*	LE 231009	MN657189	MN657213
M. cordae	*Persicaria hydropiper*	B 70 0006023	DQ238726	EF621978
M. coronariae	*Silene flos-cuculi*	KR 23797	KC684887	KC684886
M. dianthorum	*Dianthus monspessulanus*	TUB 011802	AY588080	DQ366871
M. ducellieri	*Arenaria leptoclados*	MA-Fungi 37800	MN657190	MN657214
M. duriaeanum	*Cerastium brachypetalum*	BRIP: HUV 3638	MN657192	MN657216
M. duriaeanum	*C. brachypetalum*	TUB 019596	MN657191	MN657215
M. duriaeanum	*C. brachypetalum*	MA 461701	MN657194	–
M. duriaeanum	*C. brachypetalum* subsp. *roeseri*	B 10 1224088	**OQ096632**	**OQ067234**
M. duriaeanum	*C. gracile*	SOMF 30188	MN657193	MN657217
M. duriaeanum	*C. semidecandrum*	B 10 0499209	**OQ096633**	**OQ067235**
M. emodense	*Persicaria chinensis*	FO17516/DB1037	DQ238743	AY512858
M. flosculorum	*Knautia arvensis*	BRIP: HUV 20230	MN657195	MN657218
M. heliospermatis	*Heliosperma pusillum*	TUB 019570	HQ832086	HQ832087
M. holostei	*Holosteum umbellatum*	B 70 0006032	DQ238722	EF621981
M. intermedium	*Scabiosa lucida*	M-0066090	DQ238723	EF621982
M. jehudanum	*Silene colorata*	BRIP: HUV 18306	MN657196	MN657219
M. lagerheimii	*Atocion rupestre*	TUB 011817	AY588100	DQ366874
M. liroi	*Pinguicula villosa*	KRAM 296281	KY421500	KY421502
M. lychnidis-dioicae	*Silene latifolia*	TUB 011795	AY588096	DQ366886
M. majus	*S. otites*	B 70 0006042	AY877419	DQ366858
M. marginale	*Bistorta officinalis*	TUB 015881	EF621940	EF621989
M. minuartiae	*Minuartia recurva*	TUB 012519	DQ366853	DQ366862
M. moehringiae	*Moehringia trinervia*	BRIP: HUV 19024	MN657197	MN657220
M. moehringiae	*M. trinervia*	B 10 0298453	**OQ096635**	**OQ067237**
M. moenchiae-manticae	*Moenchia erecta*	K(M) 106303	MN657198	MN657221
M. moenchiae-manticae	*M. mantica*	BRIP: HUV 4126	MN657199	MN657222
M. moenchiae-manticae	*M. mantica*	B 10 0255208	**OQ096634**	**OQ067236**

Table 2. Cont'd.

Species	Host	Voucher	ITS	LSU
M. onopordi	*Onopordum bracteatum*	M-0066075	DQ238735	EF621990
M. parlatorei	*Rumex maritimus*	B 70 0007574	DQ238736	EF621991
M. pinguiculae	*Pinguicula vulgaris*	STU 10004567401	KY421498	KY421501
M. polycnemoides	*Polygonum polycnemoides*	SOMF 30200	MN989380	MN989381
M. pustulatum	*Bistorta officinalis*	TUB 015872	EF621947	EF621998
M. reticulatum	*Persicaria lapathifolia*	M-0066067	DQ238730	EF621999
M. salviae	*Salvia pratensis*	TUB 015858	EF621922	EF621962
M. saponariae	*Saponaria officinalis*	TUB 011809	AY588089	DQ366887
M. scabiosae	*Knautia arvensis*	TUB 011789	AY588083	DQ366861
M. scabiosae	*K. longifolia*	TUB 015875	EF621950	EF622003
M. scolymi	n/a	n/a	AY800113	–
M. scorzonerae	*Scorzonera humilis*	M-0066054	DQ238731	EF622006
M. scorzonerae	*S. humilis*	TUB 015878	EF621953	EF622007
M. shastense	*Polygonum shastense*	M-0066053	DQ238739	EF622008
M. shykoffianum	*Dianthus sylvestris*	TUB 011800	AY588082	DQ366857
M. silenes-acaulis	*Silene acaulis*	TUB 019585	JN223408	JN223413
M. silenes-dioicae	*S. dioica*	TUB 012114	AY877416	DQ366868
M. silenes-inflatae	*S. vulgaris*	TUB 011793	AY588105	DQ366884
M. silenes-saxifragae	*S. saxifraga*	KR 23889	JN000073	JN000079
M. silybum	*Silybum marianum*	SOMF 30193	MN657200	MN657224
M. stellariae	*Stellaria graminea*	TUB 011807	AY588109	DQ366872
M. stygium	*Rumex acetosa*	M-0066047	DQ238737	EF622009
M. succisae	*Succisa pratensis*	M-0066045	MN657204	MN657225
M. succisae	*S. pratensis*	B 700007625	MN657201	MN657226
M. superbum	*Dianthus superbus*	TUB 011799	AY588081	DQ366867
M. tenuisporum	*Persicaria glabra*	M-0066041	DQ238727	EF622011
M. tragopogonis-pratensis	*Tragopogon pratensis*	TUB 015879	EF621954	EF622014
M. tragopogonis-pratensis	*T. pratensis*	TUB 012509	DQ238733	EF622012
M. tuberculiforme	*Polygonum runcinatum*	M-0066035	DQ238744	EF622015
M. violaceoirregulare	*Silene vulgaris*	TUB 011816	AY588104	DQ366875
M. violaceoverrucosum	*S. viscosa*	TUB 011815	AY588103	DQ366882
M. violaceum	*S. nutans*	TUB 011818	AY588099	DQ366880
Sphacelotheca cf. *koordersiana*	n/a	JAG 55 AFTOL-ID 1917	DQ832221	DQ832219

mantica subsp. *mantica* (Lindtner 1950; Vánky 1985), and Africa–Algeria and Morocco, on *M. erecta* subsp. *octandra* (Ziz ex Mert. & W.D.J.Koch) Gürke ex Cout. (Denchev & Denchev 2017).

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