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Phylogenetic analyses, morphological characteristics, and host specificity reveal *Anthracoidea koopmanii sp. nov.* (Anthracoideaceae, Ustilaginales) on *Carex oreophila* (Cyperaceae) from Armenia

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Abstract

Anthracoidea species are highly specialized parasitic fungi on *Carex*. Their host range is restricted to a single sedge species or sedge species belonging to the same or closely related sections. The present study reports for the first time the finding of an *Anthracoidea* species on sedge in *Carex* sect. *Capituligerae*, based on a recent collection from Armenia. We employed an integrative systematic approach combining molecular (based on LSU rDNA sequences) and morphological data with host-specificity to elucidate the taxonomic status of this *Anthracoidea* species. The phylogenetic analyses indicate that it differs from the *Anthracoidea* species with available molecular data. Additionally, this species possesses morphological characters, by which it can be easily distinguished from all *Anthracoidea* species recognized on sedges in the former Capitata Clade sensu Roalson *et al.* It differs from *Anthracoidea obtusatae* on *Carex obtusata* by its larger spores and lack of internal swellings, from *A. rupestris* on *Carex rupestris* by its thinner spore walls and lack of protuberances, internal swellings, and light refractive areas, from *A. nardinae* on *Carex nardina* by having punctate to minutely verruculose spore wall ornamentation (as seen in SEM), and from the other *Anthracoidea* species by specialization on *Carex oreophila*. Based on molecular and morphological evidence, and host specialization, a new species, *Anthracoidea koopmanii*, is described and illustrated. The phylogenetic placement and affinities of the new species in *Anthracoidea* are analyzed.

Key words: *Anthracoidea*, Armenia, *Carex* sect. *Capituligerae*, new species, phylogeny, smut fungi, taxonomy

Introduction

Anthracoidea was introduced by Brefeld (1895) with the type species *A. caricis* (Pers.) Bref. Currently, 120 species of *Anthracoidea* are recognized worldwide (Denchev *et al.* 2025). It is the largest genus of the Anthracoideaceae, and at the same time, the largest genus of smut fungi on host plants belonging to the Cyperaceae (Vánky 2011, Denchev & Denchev 2016, Denchev *et al.* 2020, 2021, 2023a). *Anthracoidea* is a cosmopolitan genus, but more widely distributed in Temperate, Subarctic, and Arctic regions of the Northern Hemisphere (Denchev *et al.* 2020). Their sori form globose, broadly ellipsoidal or ovoid, black, hard bodies around aborted nuts of cyperaceous plants, mainly on *Carex*. Initially, the sori are covered by a thin peridium, which later ruptures exposing the spore mass. The spore mass is initially firmly agglutinated, later powdery on the surface; less often the mature sori are agglutinated on the surface, breaking into small, irregular pieces. Spores are formed singly, surrounded by a gelatinous sheath, which breaks down at maturity (Vánky 2013, Denchev *et al.* 2020, 2021, 2023a). Spore germination results in a two-celled aerial basidium

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forming one or more basidiospores on each cell. The basidiospores may infect flowers. Infection is local and confined to individual flowers (Kukkonen 1964a, b, Ingold 1989).

Anthracoidea species are highly specialized parasitic fungi on *Carex*. Their host range is restricted to a single sedge species or sedge species belonging to the same or closely related sections (Vánky 1979, Denchev & Denchev 2016, Denchev *et al.* 2021, 2023a, b, Kemler *et al.* 2024, Cao *et al.* 2025).

In the course of an investigation of specimens of *Anthracoidea* collected in Armenia, as part of our ongoing study of the smut fungi on Cyperaceae, an infected specimen of *Carex oreophila* C.A. Mey. was examined. This fungus was considered to represent an unknown species of *Anthracoidea*.

Carex oreophila has been traditionally included in a small section, *C.* sect. *Capituligerae* Kük. of *Carex* subgen. *Psyllophora* (Degl.) Peterm. (Egorova 1999), containing five species. *Carex oreophila* is a Western Asiatic floristic element (Egorova 1999), distributed in rocky alpine meadows in the North Caucasus, Transcaucausus, Turkey, N. Iraq, and N. Iran (Egorova 1999, Koopman *et al.* 2021, Koopman 2022). A recently proposed classification of *Carex* places this sedge within the Capitata Clade of *Carex* subgen. *Euthyceras* Peterm. (Roalson *et al.* 2021). The Capitata Clade is an informal group of species that includes 11 carices with a single, terminal androgynous spike: *C. arctogena* Harry Sm., *C. argunensis* Turcz. ex Trevir., *C. capitata* Sol., *C. microglochin* Wahlenb., *C. monostachya* A. Rich., *C. motuoensis* Y.C. Yang, *C. nardina* (Hornem.) Fr., *C. obtusata* Lilj., *C. oreophila* C.A. Mey., *C. runssoroensis* K. Schum., and *C. rupestris* All. (Roalson *et al.* 2021). At the time of publication of this informal group, however, its authors considered the inclusion of some species problematic (Roalson *et al.* 2021: 735). Three *Anthracoidea* species have been previously reported on carices in the Capitata Clade: *A. rupestris* Kukkonen on *Carex rupestris*, *A. obtusatae* T. Denchev *et al.* on *C. obtusata*, and *A. nardinae* (Kukkonen) Nannf. on *C. nardina* (Vánky 2011, Denchev *et al.* 2020, 2023a). In the most recently published system of sections in the genus *Carex* (Jiménez-Mejías *et al.* 2025), significant changes were proposed in the Capitata Clade sensu Roalson *et al.*, which changed the position of *Carex oreophila*. As a result of a reassessment of the relationships between species in this lineage, *Carex* sect. *Capituligerae* was reclassified as a distinct section typified by *C. capitata* L. Although only the type species of the sections are listed in this upgraded infrageneric classification, molecular data indicates that *C. oreophyla* should be assigned to *C.* sect. *Capituligerae* (cf. Jiménez-Mejías *et al.* 2016: Fig. 2). In the new system, the traditional sectional placement of the carices of interest for this study was restored as follows: *Carex rupestris* as type species of *C.* sect. *Petraeae* (O. Lang) Kük., and *C. obtusata* and *C. nardina* as type species of *C.* sect. *Obtusatae* (Tuck.) Mack. and *C.* sect. *Nardinae* (Tuck.) Mack., respectively. None of the currently recognized species in *Anthracoidea* is known to infect carices in *C.* sect. *Capituligerae*.

The aim of the present study was to elucidate the taxonomic status of the *Anthracoidea* species on *Carex oreophila*. An integrative systematic approach combining molecular (based on LSU rDNA sequences) and morphological data with a host-specificity analysis revealed a new smut fungus, *A. koopmanii*. This species is described and illustrated herein and its phylogenetic placement and affinities in *Anthracoidea* are analyzed.

Material and methods

Materials

This study is based on phylogenetic and morphological analyses of *Anthracoidea* specimens on hosts in *Carex* sect. *Capituligerae*, *C.* sect. *Petraeae*, *C.* sect. *Obtusatae*, and *C.* sect. *Nardinae*.

DNA extraction, PCR amplification, and sequencing

For DNA extraction, sori of *Anthracoidea* were used. The sample was milled in the Bead Ruptor 12™ homogenizer (Omni International), using two steel beads. Genomic DNA was isolated using the my-Budget Plant DNA Kit™ (Bio-Budget Technologies GmbH, Germany), according to the manufacturer's protocol (protocol 1: "Isolation of DNA from plant material using lysis buffer SLS"). PCR using GoTaq™ Master Mix (Promega, U.S.A.) with the primer combinations M-ITS1/ITS4 (Stoll *et al.* 2003, White *et al.* 1990) and LR0R/NL4 (Moncalvo *et al.* 1995, O'Donnell 1992) was performed to amplify the LSU rDNA region, which is the standard molecular marker for *Anthracoidea* (e.g., Denchev *et al.* 2021, 2023a, b). Standard thermal cycling conditions with an annealing temperature of 53 °C were used for amplification. Five µl of PCR products were purified using a modified ExoSAP protokol (1 : 5 diluted in ddH_2O; New England Biolabs, USA). Amplicons were sequenced in both directions at Macrogen Europe (Macrogen Inc.)

using the same primers as in the respective PCRs. Forward and reverse reads were checked for quality and assembled in Geneious 10.2.6 (Biomatters Ltd, New Zealand). Molecular work was conducted at the Mycology Laboratory at the Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences. Sequences were deposited in the NCBI nucleotide database (see Table 1 for accession numbers).

TABLE 1. Specimens and NCBI nucleotide database accession numbers used for phylogenetic analysis (newly generated sequence indicated in boldface).

Species	Host	Country	Voucher	LSU	Reference
Anthracoidea arenariae	*Carex arenaria*	Germany	PUL F916	AY563606	Hendrichs *et al.* 2005
A. arenariae	*C. brizoides*	Austria	SOMF 31457	PP476615	Denchev *et al.* in Cao *et al.* 2025
A. arenariae	*C. praecox*	France	SOMF 31454	PP476616	Denchev *et al.* in Cao *et al.* 2025
A. aspera	*C. chordorrhiza*	Sweden	HMH 2774	AY563607	Hendrichs *et al.* 2005
A. aspera	*C. chordorrhiza*	Canada	SOMF 31456	PP476614	Denchev *et al.* in Cao *et al.* 2025
A. baldensis	*C. baldensis*	Switzerland	HMH 2861	AY563599	Hendrichs *et al.* 2005
A. bigelowii	*C. bigelowii*	Sweden	HMH 2733	AY563566	Hendrichs *et al.* 2005
A. buxbaumii	*C. buxbaumii*	Sweden	HMH 2744	AY563582	Hendrichs *et al.* 2005
A. capillaris	*C. capillaris*	Sweden	HMH 2769	AY563596	Hendrichs *et al.* 2005
A. caricis	*C. pilulifera*	Switzerland	HMH 2364	AY563589	Hendrichs *et al.* 2005
A. caricis-albae	*C. alba*	Switzerland	HMH 2869	AY563594	Hendrichs *et al.* 2005
A. carphae	*Carpha alpina*	Australia	M 40218	AY563614	Hendrichs *et al.* 2005
A. caryophylleae	*Carex caryophyllea*	Bulgaria	SOMF 30793	OQ801114	Denchev *et al.* in Crous *et al.* 2023
A. curvulae	*C. curvula*	Switzerland	HMH 3912	AY563611	Hendrichs *et al.* 2005
A. elynae	*C. myosuroides*	Switzerland	HMH 3958	AY563609	Hendrichs *et al.* 2005
A. ferrugineae	*C. ferruginea*	Austria	SOMF 29700	OR960710	Kemler *et al.* 2024
A. firmae	*C. firma*	Italy	SOMF 29701	OR960711	Kemler *et al.* 2024
A. globularis	*C. globularis*	Finland	HMH 2422	AY563593	Hendrichs *et al.* 2005
A. hallerianae	*C. halleriana*	Bulgaria	SOMF 30000	MT628661	Denchev *et al.* 2021
A. heterospora	*C. elata*	Russia	HMH 921	AY563601	Hendrichs *et al.* 2005
A. hostianae	*C. hostiana*	Austria	HeRB 4706	AY563581	Hendrichs *et al.* 2005
A. inclusa	*C. rostrata*	Austria	HMH 2883	AY563605	Hendrichs *et al.* 2005
A. irregularis	*C. digitata*	Slovenia	HMH 933	AY563592	Hendrichs *et al.* 2005
A. irregularis	*C. ornithopoda*	Germany	HMH 3480	AY563590	Hendrichs *et al.* 2005
A. karii	*C. brunnescens*	Sweden	HMH 2777	AY563575	Hendrichs *et al.* 2005
A. karii	*C. echinata*	Switzerland	HMH 3892	AY563576	Hendrichs *et al.* 2005
A. kitaibelianae	*C. kitaibeliana*	Bulgaria	SOMF 30152	OR960745	Kemler *et al.* 2024
A. koopmanii	***C. oreophila***	**Armenia**	**SOMF 31200**	**PX634062**	**this study**
A. lasiocarpae	*C. lasiocarpa*	Finland	HMH 972	AY563583	Hendrichs *et al.* 2005
A. limosae	*C. limosa*	Finland	HMH 2428	AY563572	Hendrichs *et al.* 2005

......*continued on the next page*

TABLE 1. (Continued)

Species	Host	Country	Voucher	LSU	Reference
A. misandrae	*C. atrofusca*	Sweden	HMH 2653	AY563584	Hendrichs *et al.* 2005
A. obtusatae	*C. obtusata*	Russia	SOMF 30400	OQ679943	Denchev *et al.* 2023a
A. pamiroalaica	*C. koshewnikowii*	Tajikistan	KRA F-2012-146	KT006854	Piatek *et al.* 2015
A. paniceae	*C. panicea*	Switzerland	HMH 2818	AY563580	Hendrichs *et al.* 2005
A. pratensis	*C. flacca*	Germany	HMH 1164	AY563564	Hendrichs *et al.* 2005
A. pseudofoetidae	*C. enervis*	Russia	B 10 0240205	OQ067238	Denchev *et al.* 2023b
A. rupestris	*C. rupestris*	Switzerland	HMH 3948	AY563598	Hendrichs *et al.* 2005
A. sclerotiformis	*C. punicea*	New Zealand	M 4946	AY563613	Hendrichs *et al.* 2005
A. sempervirentis	*C. sempervirens*	Austria	SOMF 31196	OR960718	Kemler *et al.* 2024
A. siccatae	*C. siccata*	Canada	SOMF 31455	PP476613	Denchev *et al.* in Cao *et al.* 2025
A. subinclusa	*C. hirta*	France	HMH 3700	AY563604	Hendrichs *et al.* 2005
A. subinclusa	*C. riparia*	Germany	PUL F915	AY563603	Hendrichs *et al.* 2005
A. subinclusa	*C. vesicaria*	Germany	HMH 2809	AY563602	Hendrichs *et al.* 2005
A. turfosa	*C. dioica*	Sweden	HMH 2797	AY563571	Hendrichs *et al.* 2005
A. turfosa	*C. heleonastes*	Sweden	HMH 2662	AY563569	Hendrichs *et al.* 2005
A. turfosa	*C. parallela*	Sweden	HMH 2523	AY563570	Hendrichs *et al.* 2005
A. umbrosae	*C. umbrosa*	Bulgaria	SOMF 30500	OQ801120	Denchev *et al.* in Crous *et al.* 2023
A. vankyi	*C. muricata*	Switzerland	HMH 1305	AY563597	Hendrichs *et al.* 2005
Cintractia amazonica	*Rhynchospora barbata*	-	MP 2008	AJ236142	Piepenbring *et al.* 1999
C. axicola	*Fimbristylis tetragona*	India	BRIP: HUV 17460	AF009847	Begerow *et al.* 2007
C. tangensis	-	Cuba	HAJB 10488	DQ645506	Matheny *et al.* 2007

Phylogenetic analysis

The sequence of *Anthracoidea koopmanii* generated in this study, as well as representative sequences downloaded from GenBank (Table 1) were aligned using the g-ins-i option in MAFFT 7 in the server version (Katoh *et al.* 2019). The best nucleotide substitution model was determined using ModelTest-NG (Darriba *et al.* 2020) implemented in raxmlGUI 2.0 (Edler *et al.* 2021). RaxML-NG (Kozlov *et al.* 2019), also implemented in raxmlGUI, was used for inferring a maximum likelihood phylogeny with 1000 thorough bootstrap replicates. The phylogeny was visualized in iTOL 5 (Letunic & Bork 2021).

Morphological examination

Dried specimens of *Anthracoidea* were examined using 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 to rehydrate the spores, and then cooled. The measurements of spores are given as min–max (extreme values) (mean ± 1 standard deviation). The spore length range is assigned to one of the groups distinguished by Denchev *et al.* (2020: 11): very small-sized, small-sized, medium-sized, and large-sized. For SEM, spores were attached to a specimen stub by double-sided adhesive tape and coated with gold in an ion sputter. The surface structure of spores and sterile cells was observed and photographed at 10 kV accelerating voltage using a JCM-7000 Benchtop scanning electron microscope. The description of spore ornamentation is in accordance with

Denchev *et al.* (2013). The description below is based on the specimen examined. The shapes of spores are arranged in descending order of frequency.

Results

Phylogenetic analysis

The best substitution model determined by ModelTest-NG was GTR+I+G. Similar phylogenetic relationships within *Anthracoidea* were inferred as in previous studies. All *Anthracoidea* species formed a well-supported clade. The *Anthracoidea* specimen on *Carex oreophila* clustered together with *A. obtusatae* on *C. obtusata*. This clade formed a sister clade to all other *Anthracoidea* species (Fig. 1).

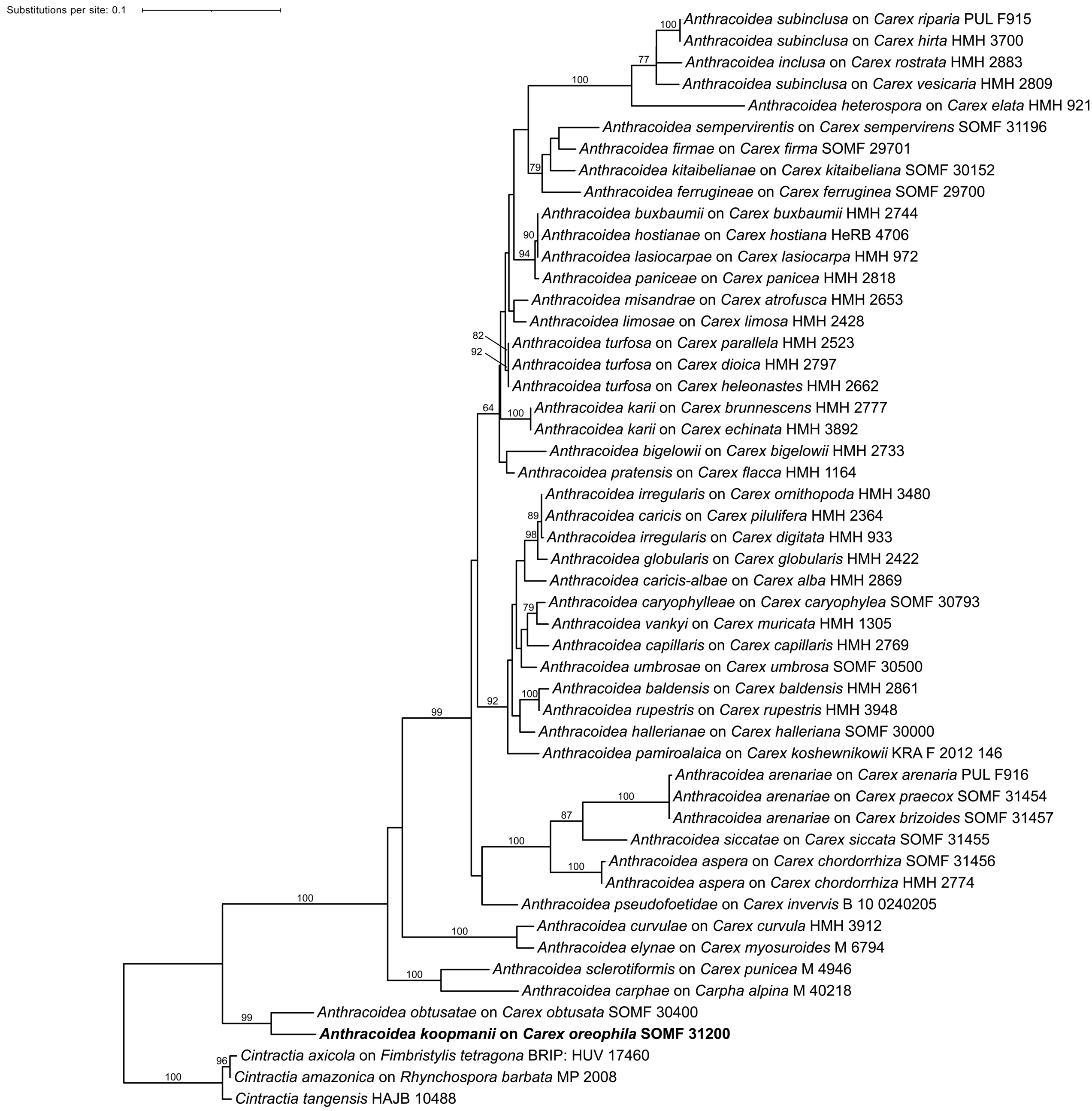


FIGURE 1. RAxML phylogeny of species in the genus *Anthracoidea* based on a MAFFT g-ins-i alignment of LSU rDNA sequences. Bootstrap values ≥ 60 are shown above branches. The phylogenetic tree was rooted with *Cintractia amazonica* Syd. & P. Syd., *C. axicola* (Berk.) Cornu, and *C. tangensis* Henn.

Morphology

Anthracoidea species have very few diagnostic morphological characteristics. The morphology of the sori bears no diagnostic value, with the exception of very few species (e.g., *A. intercedens* Nannf., *A. pseudofoetidae* L. Guo, *A. subinclusa* (Körn.) Bref.; Vánky 2011, Denchev *et al.* 2020). The most important characteristics are spore-based: sizes, shape (in plane view, since most species have flattened spores), and wall thickness and ornamentation (pattern and height). Characteristics of less taxonomic significance include internal swellings, light-refractive areas, and protuberances. Their presence and frequency may vary between different collections of one species, but due to the scarcity of morphological characteristics, their careful examination and use in combination with the diagnostic morphological features is still very important (Denchev *et al.* 2021, 2023a).

The morphological description of the studied smut fungus on *Carex oreophila* was based on examination of a specimen from Armenia. The specimen was characterized by small- to medium-sized spores (15.5–22 µm long), irregularly rounded, suborbicular, broadly elliptical or ovate in outline (as seen in plane view), with an unevenly thickened, 0.8–1.8(–2.3) µm thick spore wall, without internal swellings, light refractive areas, and protuberances. The wall was smooth to minutely verruculose; in SEM punctate to minutely verruculose.

Taxonomy

Based on the host specialization, morphology, and phylogenetic data, we propose a new species of *Anthracoidea* on *Carex oreophila*.

Anthracoidea koopmanii T. Denchev, Denchev, Więcław, Mišek & Kemler, *sp. nov.* (Figs 2–8)
Index Fungorum number: IF 904622

Holotype:—On *Carex oreophila* C.A. Mey. (Cyperaceae). Armenia, Gegham Mts, 40°15′42.9″N, 44°55′55.9″E, 25 August 2023, leg. V. Mišek *s.n.*, fungus comm. & det. T.T. Denchev & C.M. Denchev (SOMF 31200).

LSU rDNA GenBank accession no.:—PX634062.

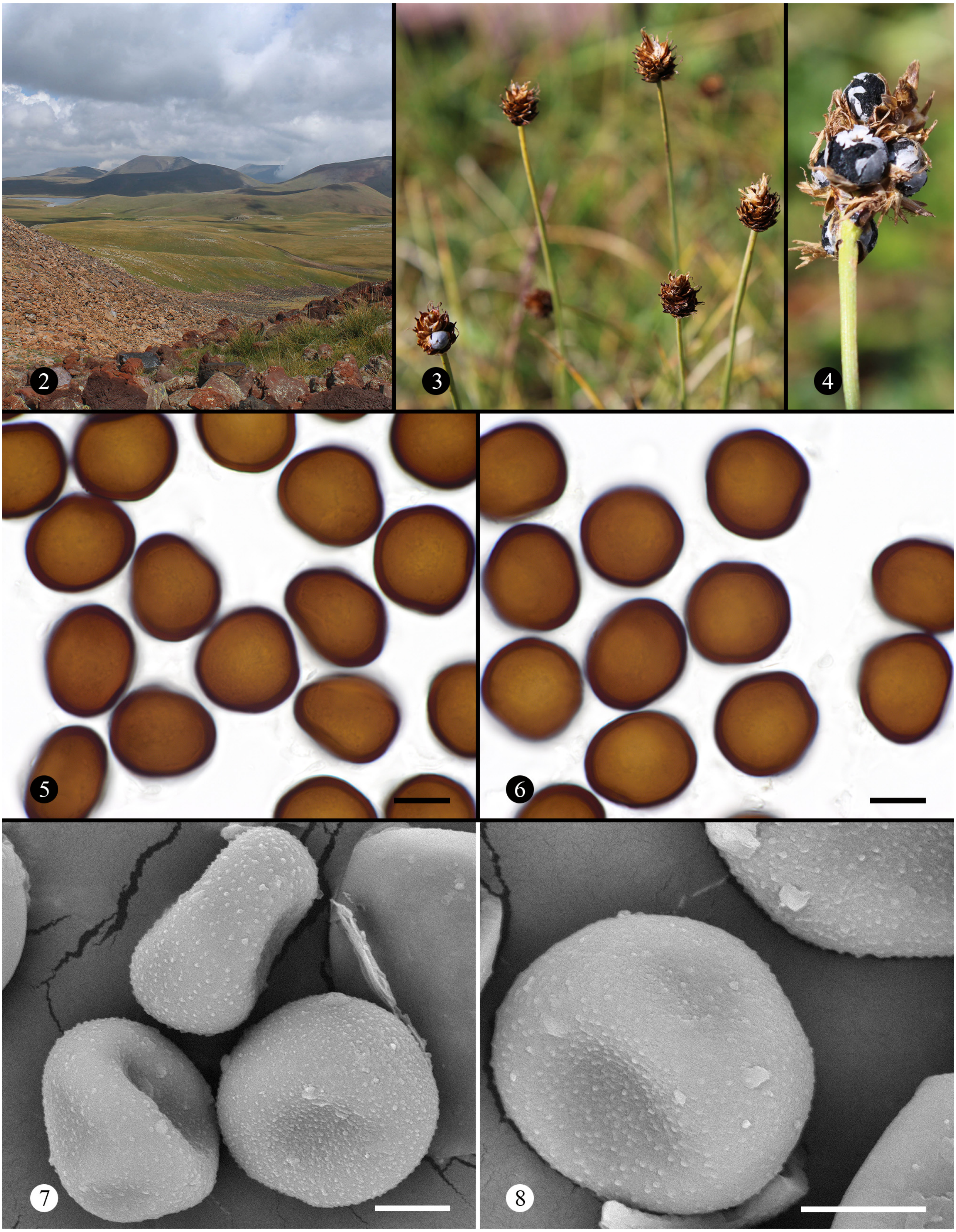
Diagnosis:—Differs from *Anthracoidea obtusatae* by its larger spores and lack of internal swellings, from *A. rupestris* by its thinner spore walls and lack of protuberances, internal swellings, and light refractive areas, from *A. nardinae* by having punctate to minutely verruculose spore wall ornamentation (as seen in SEM), and from the other *Anthracoidea* species by specialization on *Carex oreophila*.

Etymology:—Named after Dr. Jacob Koopman (Choszczno, Poland), in recognition of his contributions to the taxonomy of the genus *Carex* in Europe and the Transcaucasia.

Description:—*Infection* local. *Sori* in some female flowers, around aborted nuts as subglobose, ovoid or broadly ellipsoidal hard bodies, 2.0–3.0 mm long, initially covered by a thin, greyish peridium that later flakes away exposing a black spore mass, powdery on the surface. *Spores* small- to medium-sized, flattened, in plane view irregularly rounded, suborbicular, broadly elliptical or ovate in outline, in plane view (15.5–)16.5–21(–22) × (13.5–)14.5–19(–20) (19.0 ± 1.2 × 17.0 ± 1.1) µm (n = 300), in side view 8–12 µm thick, medium to dark reddish brown; wall unevenly thickened, 0.8–1.8(–2.3) µm thick, internal swellings, light refractive areas, and protuberances absent; smooth to minutely verruculose, spore profile not affected. In SEM spore wall punctate to minutely verruculose, warts up to 0.15 µm high, usually solitary (Figs 7, 8). *Spore germination* unknown.

Known host and distribution:—On Cyperaceae: *Carex* sect. *Capituligerae*: *Carex oreophila*, Asia (Armenia).

Comments:—As mentioned above, three *Anthracoidea* species have been reported on hosts in the Capitata Clade sensu Roalson *et al.*: *A. obtusatae* on *Carex obtusata*, *A. rupestris* on *C. rupestris*, and *A. nardinae* on *C. nardina* (Vánky 2011, Denchev *et al.* 2020, 2023a). *Anthracoidea koopmanii* differs from *A. obtusatae* by (i) its larger spores, (15.5–)16.5–21(–22) (19.0 ± 1.2) µm long, versus (12.5–)13.5–19(–20) (15.7 ± 1.3) µm long for *A. obtusatae*, and (ii) lack of internal swellings (spores of *A. obtusatae* have 1–3(–4), well visible internal swellings) (after Denchev *et al.* 2023a); from *A. rupestris* by (i) its thinner spore walls, 0.8–1.8(–2.3) µm thick, versus 1–3(–3.8) µm thick for *A. rupestris*, and (ii) lack of protuberances, internal swellings, and light refractive areas (spores of *A. rupestris* on *C. rupestris* have protuberances, usually have 1–4, well visible internal swellings, and light refractive areas often present) (data for *A. rupestris* based on a study of Greenlandic specimens in C-Greenland herb., conducted by TMD & CMD, Denchev *et al.* 2020); and from *A. nardinae* by having punctate to minutely verruculose spore wall ornamentation (as seen in SEM) versus smooth spore walls of *A. nardinae* (after Denchev *et al.* 2020). *Anthracoidea koopmanii* differs from the other *Anthracoidea* species by specialization on *Carex oreophila*, and it is the only known *Anthracoidea* species on a host plant in *Carex* sect. *Capituligerae* sensu Jiménez-Mejías *et al.* (2025).



FIGURES 2–8. *Anthracoidea koopmanii sp. nov.* on *Carex oreophila* (from holotype). 2. Armenia, Gegham Mts—habitat. 3, 4. Habit. 5, 6. Spores in LM. 7, 8. Spores in SEM. Scale bars: 5, 6 = 10 µm, 7, 8 = 5 µm.

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