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Host specialization and molecular evidence support a distinct species of smut fungus, *Anthracoidea hallerianae* (*Anthracoideaceae*), on *Carex halleriana* (*Cyperaceae*)

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Abstract: The species of *Anthracoidea* on *Carex* are host-specific smut fungi restricted to sedges belonging to the same or closely related sections. They are characterized by sori that form black, hard bodies around aborted nuts of their hosts. In *Carex* sect. *Hallerianae*, only one species, *C. halleriana*, is known as a host of *Anthracoidea*. The taxonomic status of this smut fungus was problematic due to a lack of molecular data. It has been reported under different names, mainly as "*A. caricis*" or "*A. irregularis*". A comparative morphological study and molecular phylogenetic analysis, using LSU (large subunit) nuclear rDNA sequences, supported the recognition of a distinct species, *A. hallerianae*. The new species is described and illustrated based on material from Central Europe, the Iberian Peninsula, the Balkan Peninsula, the Mediterranean area and Transcaucasia.

Key words: *Anthracoidea*, *Anthracoideaceae*, *Carex halleriana*, *Cyperaceae*, new species, phylogeny, smut fungi, taxonomy

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Introduction

The smut fungi in the genus *Anthracoidea* Bref. are characterized by sori that form globose to broadly ellipsoidal or ovoid, black, hard bodies around aborted nuts of cyperaceous plants. In *Carex* L. (*Cyperaceae*), the sori are scattered in female spikes or in female flowers of mixed spikes, depending on the *Carex* species. The sori are covered initially by a thin peridium, which later ruptures to expose the spore mass. This spore mass is firmly agglutinated at first, at maturity becoming powdery on the surface of the sorus. A few species of *Anthracoidea* have mature sori with an agglutinated spore mass, which cracks into small, irregular pieces. The spores are formed singly and are usually flattened. Mature spores are liberated and dispersed by the wind after the peridium ruptures. At an early stage of host flowering, spores germinate to produce basidiospores that may infect flowers. The infection is local and confined to individual flowers (Kukkonen 1963; Vánky 1979, 2013; Denchev & al. 2013; Denchev & Denchev 2016).

Currently, 111 species are recognized in *Anthracoidea* (Denchev & Denchev 2016; Denchev & al. 2020), the largest genus of smut fungi on host plants in the *Cy-*

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Table 1. *Anthracoidea* NCBI nucleotide database accession numbers used for the phylogenetic analysis (newly generated sequences indicated in boldface). For corresponding herbarium specimens, see the study cited in the Reference column.

Species	Host	LSU rDNA accession no.	Reference
Anthracoidea arenaria (Syd.) Nannf.	*Carex arenaria* L.	AY563606	Hendrichs & al. 2005
A. aspera (Liro) Kukkonen	*C. chordorrhiza* L. f.	AY563607	Hendrichs & al. 2005
A. baldensis Vánky	*C. baldensis* L.	AY563599	Hendrichs & al. 2005
A. bigelowii Nannf.	*C. bigelowii* Schwein.	AY563566	Hendrichs & al. 2005
A. bigelowii	*C. bigelowii*	AY563567	Hendrichs & al. 2005
A. bigelowii	*C. bigelowii*	AY563568	Hendrichs & al. 2005
A. buxbaumii Kukkonen	*C. buxbaumii* Wahlenb.	AY563582	Hendrichs & al. 2005
A. capillaris Kukkonen	*C. capillaris* L.	AY563596	Hendrichs & al. 2005
A. caricis (Pers.) Bref.	*C. pilulifera* L.	AY563589	Hendrichs & al. 2005
A. caricis-albae (Syd.) Kukkonen	*C. alba* Scop.	AY563594	Hendrichs & al. 2005
A. caricis-albae	*C. alba*	AY563595	Hendrichs & al. 2005
A. caricis-meadii Savchenko & al.	*C. meadii* Dewey	JN863083	Savchenko & al. 2013
A. carphae (Speg.) Vánky	*Carpha alpina* R. Br.	AY563614	Hendrichs & al. 2005
A. curvulae Vánky & Kukkonen	*Carex curvula* All.	AY563611	Hendrichs & al. 2005
A. curvulae	*C. curvula*	AY563612	Hendrichs & al. 2005
A. elynae (Syd.) Kukkonen	*C. myosuroides* Vill.	AY563609	Hendrichs & al. 2005
A. elynae	*C. myosuroides*	AY563610	Hendrichs & al. 2005
A. globularis Kukkonen	*C. globularis* L.	AY563593	Hendrichs & al. 2005
A. hallerianae **T. Denchev & al., sp. nov.**	*C. halleriana* Asso	**MT628657**	this study (SOMF 30201)
A. hallerianae	*C. halleriana*	**MT628658**	this study (SOMF 30002)
A. hallerianae	*C. halleriana*	**MT628659**	this study (SOMF 30001)
A. hallerianae	*C. halleriana*	**MT628660**	this study (SOMF 30199)
A. hallerianae	*C. halleriana*	**MT628661**	this study (SOMF 30000 [holotype])
A. heterospora (B. Lindeb.) Kukkonen	*C. elata* All.	AY563600	Hendrichs & al. 2005
A. heterospora	*C. elata*	AY563601	Hendrichs & al. 2005
A. hostianae Nannf.	*C. hostiana* DC.	AY563581	Hendrichs & al. 2005
A. inclusa Bref.	*C. rostrata* Stokes	AY563605	Hendrichs & al. 2005
A. irregularis (Liro) Boidol & Poelt	*C. digitata* L.	AY563592	Hendrichs & al. 2005
A. irregularis	*C. ornithopoda* Willd.	AY563590	Hendrichs & al. 2005
A. irregularis	*C. ornithopoda*	AY563591	Hendrichs & al. 2005
A. karii (Liro) Nannf.	*C. brunnescens* (Pers.) Poir.	AY563575	Hendrichs & al. 2005
A. karii	*C. echinata* Murray	AY563576	Hendrichs & al. 2005
A. karii	*C. echinata*	AY563577	Hendrichs & al. 2005
A. karii	*C. echinata*	AY563578	Hendrichs & al. 2005
A. karii	*C. lachenalii* Schkuhr	AY563579	Hendrichs & al. 2005
A. karii	*C. paniculata* L.	AY563574	Hendrichs & al. 2005
A. cf. *karii*	*C. davalliana* Sm.	AY563608	Hendrichs & al. 2005
A. lasiocarpae B. Lindeb.	*C. lasiocarpa* Ehrh.	AY563583	Hendrichs & al. 2005
A. limosa (Syd.) Kukkonen	*C. limosa* L.	AY563572	Hendrichs & al. 2005
A. limosa	*C. limosa*	AY563573	Hendrichs & al. 2005
A. misandrae Kukkonen	*C. atrofusca* Schkuhr	AY563584	Hendrichs & al. 2005
A. pamiroalaica Piątek & al.	*C. koshewnikowii* Litv.	KT006854	Piątek & al. 2015
A. paniceae Kukkonen	*C. panicea* L.	AY563580	Hendrichs & al. 2005
A. pratensis (Syd.) Boidol & Poelt	*C. flacca* Schreb.	AY563563	Hendrichs & al. 2005
A. pratensis	*C. flacca*	AY563564	Hendrichs & al. 2005
A. pratensis	*C. flacca*	AY563565	Hendrichs & al. 2005
A. rupestris Kukkonen	*C. rupestris* All.	AY563598	Hendrichs & al. 2005
A. cf. *rupestris*	*C. glacialis* Mack.	AY563588	Hendrichs & al. 2005
A. sclerotiformis (Cooke & Massee) Kukkonen	*C. punicea* K. A. Ford	AY563613	Hendrichs & al. 2005
A. sempervirentis Vánky	*C. ferruginea* Scop.	AY563587	Hendrichs & al. 2005
A. sempervirentis	*C. firma* Host	AY563585	Hendrichs & al. 2005
A. sempervirentis	*C. sempervirens* Vill.	AY563586	Hendrichs & al. 2005
A. subinclusa (Körn.) Bref.	*C. hirta* L.	AY563604	Hendrichs & al. 2005
A. subinclusa	*C. riparia* Curtis	AY563603	Hendrichs & al. 2005

Anthracoidea subinclusa	*C. vesicaria* L.	AY563602	Hendrichs & al. 2005
A. turfosa (Syd.) Kukkonen	*C. dioica* L.	AY563571	Hendrichs & al. 2005
A. turfosa	*C. heleonastes* L. f.	AY563569	Hendrichs & al. 2005
A. turfosa	*C. parallela* (Laest.) Sommerf.	AY563570	Hendrichs & al. 2005
A. vankyi Nannf.	*C. muricata* L.	AY563597	Hendrichs & al. 2005

Table 2. Comparative morphological spore measurements (mean ± 1 standard deviation) of herbarium specimens of *Anthracoidea hallerianae*.

Country	Specimen	M ± 1 σ
Austria	GZU 222890	21.4 ± 3.2 × 16.4 ± 1.3
Bulgaria	SOMF 30244	22.1 ± 2.9 × 16.1 ± 1.4
Bulgaria	SOMF 20359	22.5 ± 2.9 × 17.2 ± 1.6
Bulgaria	SOMF 30202	22.4 ± 3.1 × 17.1 ± 1.5
Bulgaria	SOMF 30000 (holotype)	22.2 ± 2.7 × 17.2 ± 1.7
Bulgaria	SOMF 20357	21.6 ± 2.0 × 17.9 ± 1.2
Bulgaria	SOMF 30001	20.8 ± 2.6 × 16.3 ± 1.2
Bulgaria	SOMF 30002	21.6 ± 2.2 × 17.0 ± 1.2
Bulgaria	SOMF 30199	20.9 ± 2.3 × 17.0 ± 1.3
Bulgaria	SOMF 30245	22.2 ± 2.4 × 17.3 ± 1.4
Greece	B 10 0427517	21.4 ± 2.2 × 16.8 ± 1.4
Greece	B (*R. Böcker s.n.*)	20.9 ± 2.2 × 16.0 ± 1.2
Romania	BUCM 59279	21.5 ± 2.2 × 17.0 ± 1.3
Spain	W 2004-0008293	21.4 ± 2.0 × 17.5 ± 1.5
Spain	MA 480029	21.9 ± 2.3 × 18.2 ± 1.3
Armenia	SOMF 30201	20.8 ± 2.2 × 16.2 ± 1.3
Cyprus	P00283665	22.1 ± 2.6 × 17.4 ± 1.3
Cyprus	L (*E. C. Vellinga 903*)	21.4 ± 2.2 × 16.7 ± 1.6
Turkey	K (*Davis & Hedge D 27796*)	21.5 ± 2.7 × 15.5 ± 1.3
Algeria	P01998567	21.9 ± 2.1 × 18.5 ± 1.5
Algeria	P01832709	21.7 ± 2.4 × 17.7 ± 1.5

peraceae. It is a cosmopolitan genus, but more widely distributed in the northern hemisphere. The most comprehensive taxonomic treatments of *Anthracoidea* are the monographs by Kukkonen (1963, where the genus *Anthracoidea* was re-established), Nannfeldt (1979, mainly species occurring in Fennoscandia), Vánky (1994, 2011, species distributed in Europe and at global scale, respectively), Denchev & al. (2013, species distributed in Japan and the Korean Peninsula) and Denchev & al. (2020, species distributed in Greenland). Individual *Anthracoidea* species are considered to be restricted to host plants belonging to the same or closely related sections of *Carex*, whereby host specificity of *Anthracoidea* species is regarded to be a result of homothallism and cospeciation with their hosts (Kukkonen 1963; Vánky 1979).

Carex halleriana Asso (syn.: *C. gynobasis* Vill., *C. alpestris* All.) belongs to a small section, *C.* sect. *Hallerianae* (Asch. & Graebn.) Rouy (Egorova 1999; Luceño 2008), which contains five species. Five smut fungi have been reported to infect this sedge: *Moreaua aterrima* (Tul. & C. Tul.) Vánky, *Schizonella cocconii* (Morini) Liro, *S. melanogramma* (DC.) J. Schröt., *Urocystis fischeri* Körn. and a species of *Anthracoidea* (Vánky 2011). The taxonomic treatments of the *Anthracoidea* species on *C. halleriana* vary considerably. The first reports of this smut fungus were published by Fischer de Waldheim (1877a, 1877b, 1877c, as "*Ustilago urceolorum* Tul.", i.e. *A. caricis*). Subsequently, this fungus was reported under different names: *Cintractia urceolorum* (DC.) Cif. (Ciferri 1931), *Ustilago caricis* (Pers.) Fuckel (Voss 1877; Winter 1880; Massalongo 1894), *Cintractia caricis* (Pers.) Magnus (Maire & al. 1901; Maire 1905; González Fragoso 1924; Magnus 1926), *A. caricis* (Pers.) Bref. (Tranzschel 1902; González Fragoso 1923; Kukkonen 1963; Durrieu 1968; Vánky 1994; Almaraz & Durrieu 1997; Almaraz 1999a, 1999b, 2002; Prosyannikova & al. 2019; Shivas & al. 2020), *A. irregularis* (Liro) Boidol & Poelt (Poelt 1978; Nannfeldt 1979; Zogg 1986; Scholz & Scholz 1988; Denchev 1993, 2001; Denchev & al. 2013) or *A. pratensis* (Syd.) Boidol & Poelt (*Cintractia pratensis* Syd.) (Llorens i Villagrasa 1984).

The aim of the present study is to clarify the taxonomic status of the *Anthracoidea* species on *Carex halleriana*. A combined approach, using host specialization and molecular data, revealed a new smut fungus, *A. hallerianae*. This species is described and illustrated herein and its phylogenetic placement and affinities in *Anthracoidea* are analysed.

Material and methods

DNA extraction, PCR amplification, and sequencing — For DNA extraction, one sorus per infected *Carex halleriana* was removed. The samples were milled in the Fastprep-24™ Sample Preparation Instrument (MP Biomedicals), 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 combination LR0R/LR6 (Vilgalys & Hester 1990; Moncalvo & al. 1995) was performed to amplify the LSU (large subunit) of nuclear rDNA, which is the standard molecular marker for *Anthracoidea* (e.g. Hendrichs & al. 2005; Piątek & al. 2015). Standard thermal cycling conditions with an annealing temperature of 52°C were used for amplification. Five μl of PCR products were purified using ExoSAP (1:5 diluted in ddH2O; New England Biolabs, U.S.A.). Amplicons were sequenced in both directions with the BigDye™ Terminator Cycle Sequencing Kit V3.1 (Applied Biosystems) on an ABI 3130xl Genetic Analyser at the Faculty of Chemistry and Biochemistry, Ruhr-Universität Bochum, Germany. Subsequently, forward and reverse read were quality controlled individually and merged in Sequencher 5.1 (Gene Codes Corporation, Ann Arbor). Sequences were deposited in the NCBI nucleotide database (see Table 1 for accession numbers).

Phylogenetic analysis — The newly generated *Anthracoidea* sequences and representative sequences downloaded from GenBank (Table 1) were aligned using the e-ins-i option in MAFFT v7.450 (Katoh & Standley 2013). Ambiguous alignment regions 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. The alignments are available in fasta format (see Supplemental content online; https://doi.org/10.3372/wi.51.51105). A Maximum Likelihood phylogeny was inferred in RAxML 8.2.11 (Stamatakis 2014) under the GTRGAMMA model and applying 1000 bootstrap replicates using the rapid bootstrap option. The resulting phylogeny was visualized in FigTree v1.4.3 (Rambaut 2012).

Morphological examination — Dried specimens from B, BUCM, GZU, K, L, MA, P, SOMF and W (herbarium codes according to Thiers 2020+) were examined under 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 total number of spores (*n*) from all collections (x) measured are given in the form "(*n*/x)". The spore length range is assigned to one of the groups distinguished by Denchev & al. (2020: 11): very small-sized, small-sized, medium-sized and large-sized. For SEM, spores were attached to specimen holders by double-sided adhesive tape and coated with gold in an ion sputter. The surface structure of spores was observed and photographed at 10 kV accelerating voltage using a ZEISS SIGMA VP scanning electron microscope. The description of spore ornamentation is in accordance with Denchev & al. (2013). The description below is based on the specimens examined. The shapes of spores are arranged in descending order of frequency.

Results

Phylogenetic analysis — Phylogenetic relationships between different *Anthracoidea* species in our analysis corroborated those inferred in previous studies (Hendrichs & al. 2005; Piątek & al. 2015). The specimens recovered from *Carex halleriana* formed a statistically well-supported monophyletic group. This group formed the sister species to *A. capillaris*, but this phylogenetic relationship had low statistical support. Together they clustered within a clade that also contained *A. baldensis*, *A. caricis-albae*, *A. pamiroalaica*, *A. rupestris* and *A. vankyi*. Importantly, specimens of *Anthracoidea* parasitizing *C. halleriana* clustered neither with the clade containing specimens of *A. caricis* and *A. irregularis* nor with *A. pratensis*, the three *Anthracoidea* species previously reported on *C. halleriana* (Fig. 1).

Morphology — The *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 and *A. subinclusa* (Körn.) Bref.; Denchev & Minter 2011; Vánky 2011; Denchev & al. 2020). The most important characteristics are spore-based: sizes, shape (in plane view, since most species have flattened spores), wall thickness and wall 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.

The morphological description of the studied smut fungus on *Carex halleriana* was based on the examination of 21 specimens from Central Europe, the Iberian Peninsula, the Balkan Peninsula, the Mediterranean area and Transcaucasia. The specimens were characterized by irregularly rounded to angular or elongated to irregularly elongated spores (as seen in plane view), with an unevenly thickened, 1–3.3(–3.7) μm thick spore wall, that was minutely to moderately verruculose (warts up to 0.4(–0.5) μm high). The mean values of the spore length and width of the examined specimens fell into a range of 20.8–22.5 μm and 15.5–18.5 μm, respectively (Table 2). Spores longer than 26 μm were usually with elongated or irregularly elongated shape. As an exception, single spores with a length up to 31 μm were observed. The spores often had light-refractive areas and 1(–3) protuberances and sometimes had 1 or 2(–4) internal swellings.

Taxonomy

Based on the host specialization and molecular data, we propose a new species of *Anthracoidea* on *Carex halleriana*.

Anthracoidea hallerianae T. Denchev, Denchev, Begerow & Kemler, **sp. nov.** – Fig. 2, 3.
Index Fungorum number: IF 557794.

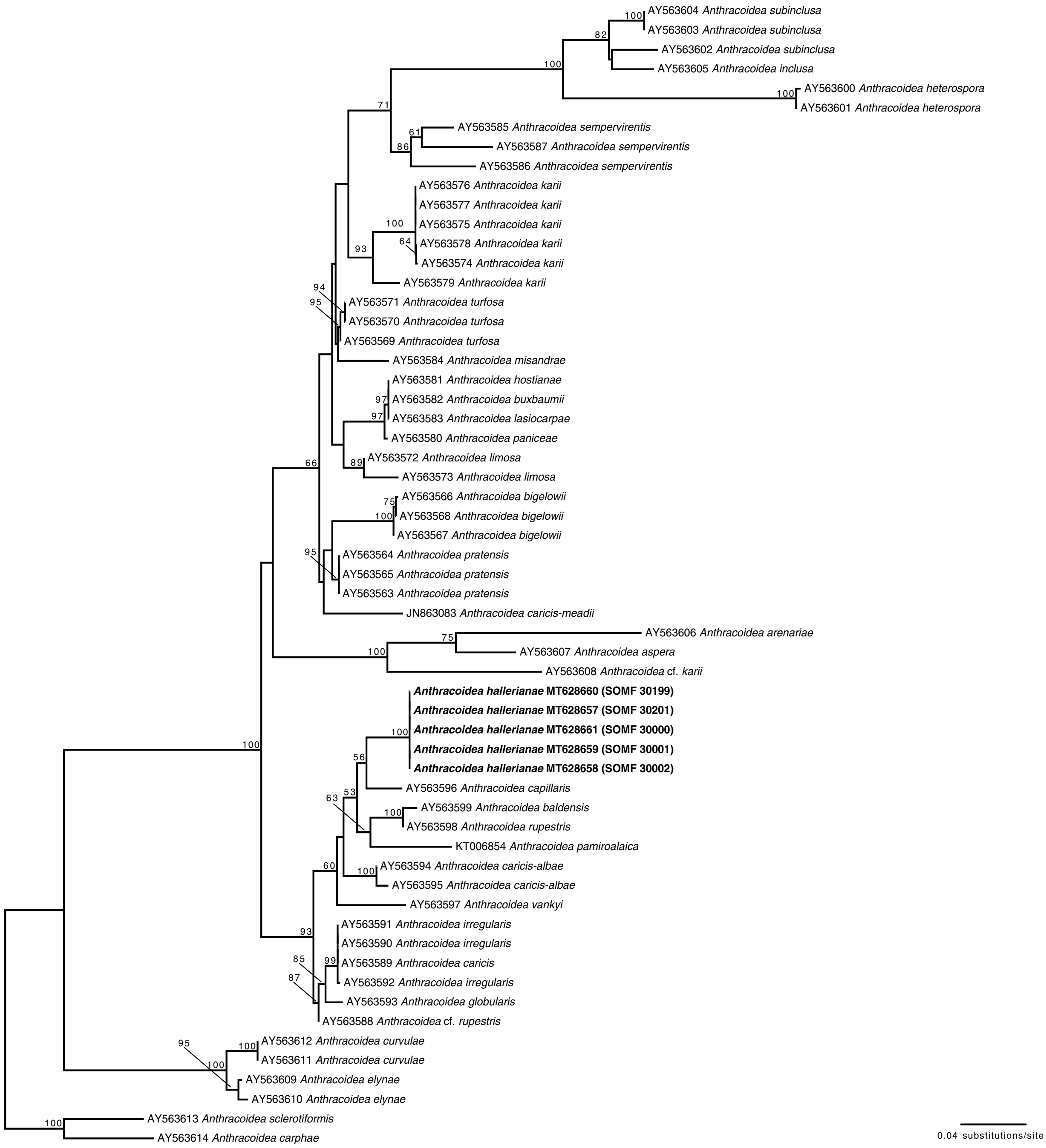

Fig. 1. Best tree of the RAxML analysis of species in the genus *Anthracoidea* based on a MAFFT alignment of partial LSU rDNA data. Bootstrap values ≥ 50 are depicted above the branches. The phylogeny is rooted with *A. sclerotiformis* and *A. carphae* according to Hendrichs & al. (2005).

Holotype: on *Carex halleriana* Asso, Bulgaria, Pernik Province, Mt. Vitosha, above the entrance of Douhlata cave near Bosnek village, 42°29'46"N, 23°11'45"E, alt. 930 m, 13 Jun 2019, *T. T. Denchev & C. M. Denchev 1918* (SOMF 30000).

Diagnosis — Differs from other *Anthracoidea* species by specialization on sedges in *Carex* sect. *Hallerianae*.

Description — *Infection* local. *Sori* in some female flowers, around aborted nuts as ovoid, ellipsoidal or broadly ellipsoidal, hard bodies, 2.2–3 × 1.2–1.8 mm, initially covered by a thin, greyish peridium that later flakes away exposing a black spore mass, powdery on surface. *Spores* medium- to large-sized, slightly flattened, in plane view usually irregularly rounded to angular or elongated to irregularly elongated, sometimes broadly elliptic or suborbicular in outline, often with 1(–3) protuberances, (15.5–)17–26.5(–29) × (13–)14.5–19.5(–21.5) (21.5 ± 2.4 × 17 ± 1.4) µm ($n/_{21}$ = 2100), in side view 10–14 µm thick, medium to dark reddish brown; wall unevenly thickened, 1–3.3(–3.7) µm thick, thickest at angles and

Fig. 2. *Anthracoidea hallerianae* on *Carex halleriana*. – A: infected plant; B: close-up of infected female spike. – Photographs: Bulgaria, type locality, 13 Jun 2019, T. T. Denchev.

protuberances (up to 5 µm thick), sometimes with 1 or 2(–4) internal swellings (variable in conspicuousness), light-refractive areas often present; minutely to moderately verruculose, warts up to 0.4(–0.5) µm high, spore profile not affected to slightly affected. In SEM, warts sometimes partly confluent, forming short rows or small groups. *Spore germination* unknown.

Host plant and distribution — On *Cyperaceae*: *Carex* sect. *Hallerianae*: *C. halleriana*, Europe (Spain, Corsica, Alps, Lower Austria, Hungary, Balkan Peninsula, Aegean Islands, Crimea), Mediterranean Asia (Turkey, Cyprus), Transcaucasia (Armenia), Mediterranean Africa (Algeria) (Fig. 4).

Etymology — The epithet is derived from the host plant, *Carex halleriana*.

Remarks — The examined specimens share the same morphology, with only small variations. The Austrian specimen (GZU 222890) has spores with more regular shape and lower ornamentation, but the other characteristics match well with the morphology of the new species. Some specimens (like SOMF 30199; *R. Böcker s.n.*, B; P00283665) possess spore walls with common and well-visible internal swellings, while most of the studied specimens have spore walls with uncommon and inconspicuous internal swellings. When numerous specimens of a particular species are examined, it may turn out that the presence and conspicuousness of internal swellings can vary considerably (cf. the case of *Anthracoidea eburneae* Denchev & T. Denchev; Denchev & Denchev 2016: 77). Internal swellings are more visible in the lightly coloured immature spores.

It was found that spores longer than 26 µm usually had an elongated or irregularly elongated shape (Fig. 3F). As an exception, single spores with length up to 31 µm were also observed.

Carex halleriana is distributed from C and S Europe, the Mediterranean area and Crimea to the Caucasus and W Asia (to Afghanistan) (Kukkonen 1987, 1998; Egorova 1999; Luceño 2008). It is a lowland to montane species, usually occurring on dry mountain slopes or in dry broad-leaved mountain forests, usually on limestone (Egorova 1999; Luceño 2008). Based on the available distribution data, it can be assumed that *Anthracoidea hallerianae* is coextensive with its host.

Recording a new species of *Anthracoidea* for Africa is noteworthy, as currently only two species of this genus have been reported from this continent: *A. kukkonenii* Vánky on *Carex distachya* Desf. from Algeria and a dubious record of *A. heterospora* (B. Lindeb.) Kukkonen from Nigeria (Vánky & al. 2011).

Additional specimens examined (*paratypes*) — On *Carex halleriana*. — **Europe:** Austria: Lower Austria, Thermenalpen, Fischauer Berge, Emmerberg, 9 Jun 1966, *coll. ? s.n.* (GZU 222890). — Bulgaria: Varna province, near Zlatni Pyasutsi resort (Golden Sands), 19 May 1994, *A. Petrova 1626* (SOMF 30244); Sofia province, Kostinbrod municipality, Beledie Han, 21 May 1991, *D. Stoyanov s.n.* (SOMF 20359; in Denchev 1993 as "*Anthracoidea irregularis*"); Sofia province, Mt. Chepun, near Dragoman, 42°56'33"N, 22°56'04"E, alt. 814 m, 10 Jun 2016, *T. T. Denchev & C. M. Denchev 1618* (SOMF 30202); Kyustendil province, Konyavska planina, above Skakavitsa railway station, 6 Jun 1990, *C. M. Denchev s.n.* (SOMF 20357; in Denchev 1993 as "*A. irregularis*");

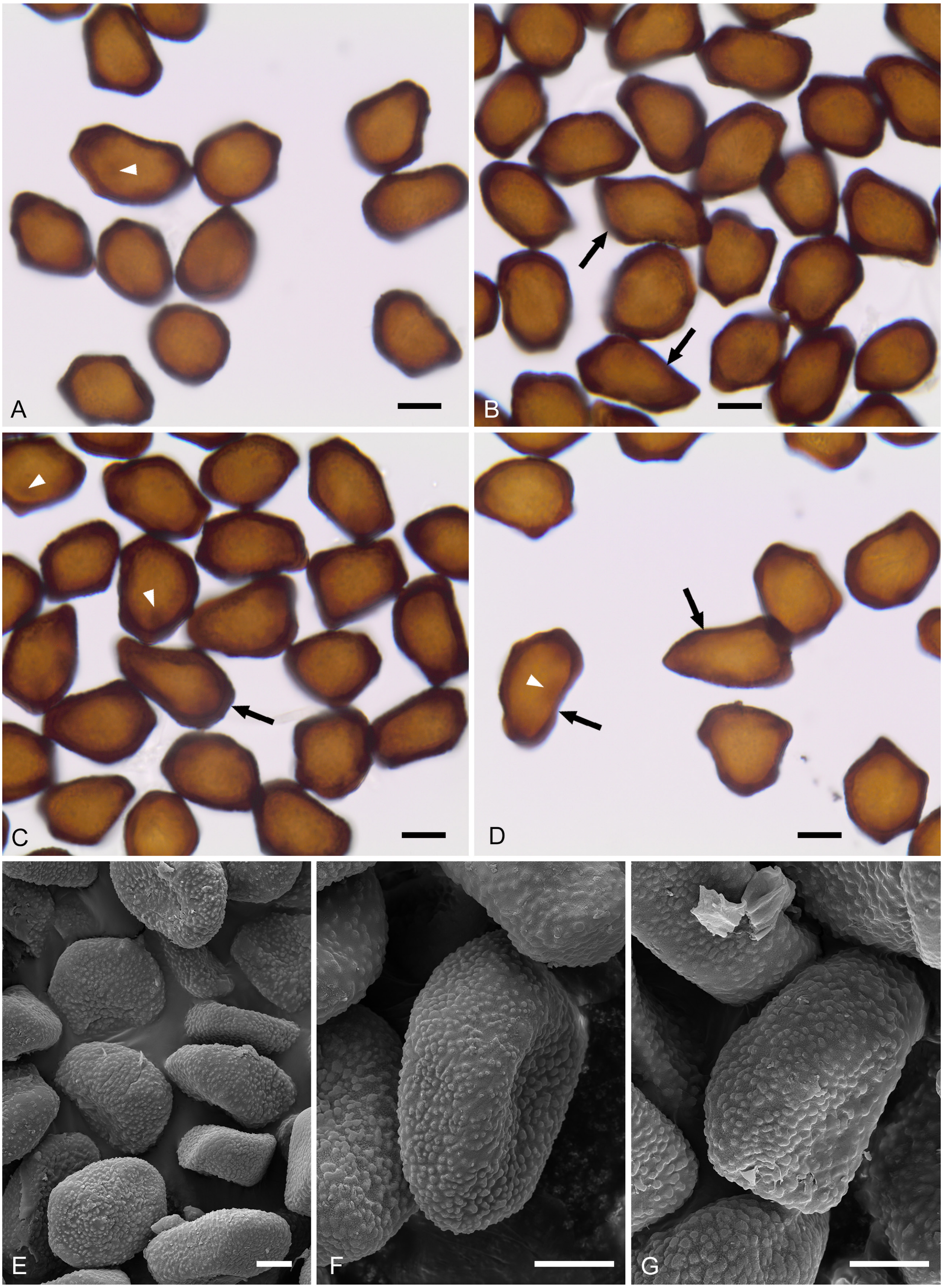

Fig. 3. *Anthracoidea hallerianae* on *Carex halleriana*. – A–D: spores in LM (A: holotype; B, C: SOMF 30202; D: SOMF 20359); arrows in B, C and D show irregularly elongated spores, arrowheads in A, C and D indicate internal swellings; E–G: spores in SEM (E, F: SOMF 30002; G: SOMF 30001). – Scale bars: A–D = 10 µm; E–G = 5 µm.

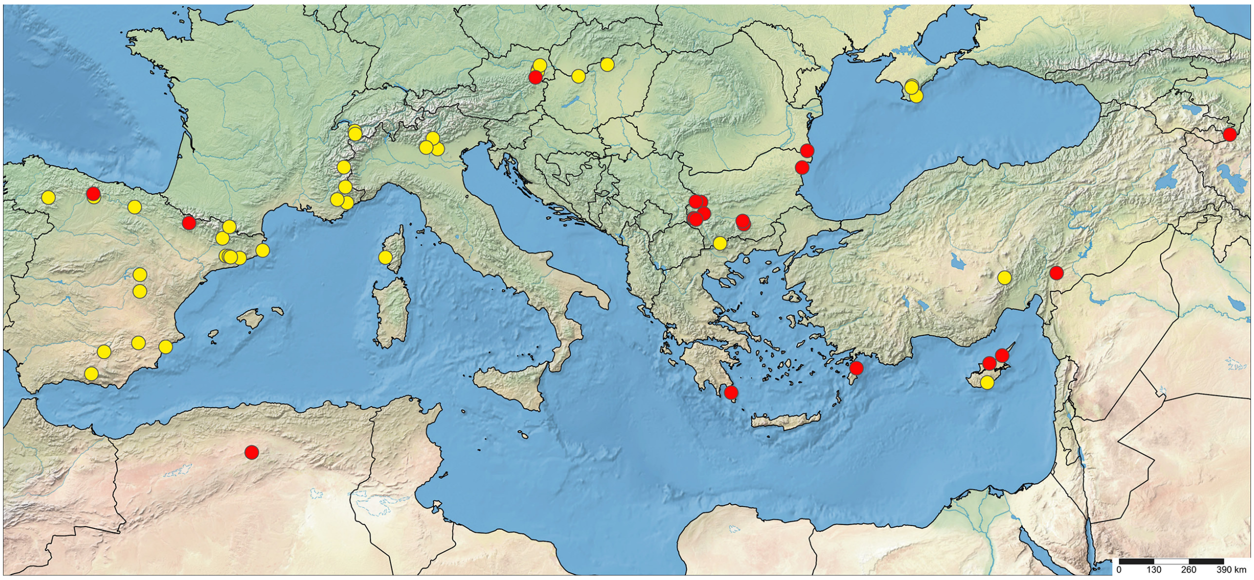

Fig. 4. Geographic distribution of *Anthracoidea hallerianae*. – Red circles = examined specimens; yellow circles = literature records. – Map generated with SimpleMappr (Shorthouse 2010).

Kyustendil province, Kyustendil municipality, Konyavska planina, valley of Shegava river near Ruzhdavitsa village, 42°23'54"N, 22°43'35"E, alt. 593 m, 10 May 2014, *T. T. Denchev & C. M. Denchev 1415* (SOMF 30001); Kyustendil province, Kyustendil municipality, Konyavska planina, near Tsurvenyano village, 42°21'08"N, 22°48'00"E, alt. 920 m, 10 May 2014, *T. T. Denchev & C. M. Denchev 1419* (SOMF 30002); Plovdiv province, Asenovgrad municipality, Rhodopes, near Gorni Voden monastery St. Kirik and St. Yulita, 41°59'59"N, 24°50'58"E, alt. 636 m, 21 May 2014, *T. T. Denchev & C. M. Denchev 1411* (SOMF 30199); Plovdiv province, Asenovgrad municipality, Rhodopes, near Martsiganitsa hut, above Dobrostan village, 41°53'27"N, 24°52'31"E, alt. 1336 m, 26 Jul 2019, *T. T. Denchev & C. M. Denchev 1977* (SOMF 30245). — Greece: Peloponnese, Laconia, Elafonisos island, 21 Apr 1991, *A. Jagel s.n.* (B 10 0427517); South Aegean, Rhodes, E of Pastida, pine forest, 17 Apr 1988, *R. Böcker s.n.* (B, as "*A. irregularis*"). — Romania: Dobrogea, Constanța district, Pădurea Hagieni, 28 May 1981, *G. Negrean s.n.* (BUCM 59279; in Negrean 1993 as "*A. caricis*"). — Spain: Palencia province, "Reserva Nacional de Fuentes Carrionas", c. 7 km NNW Camporredonto de Alba, Espigüete, alt. 2180 m, 17 Jul 2003, *R. Karl s.n.* (W 2004-0008293); Huesca province, Mt. Oturia, alt. 1700 m, 3 Jun 1987, *R. Carcía Adá & al. s.n.* (MA-Fungi 37679, as "*A. caricis*"; ex MA 480029). — **Asia:** Armenia: Syunik province, slope in forest along Kajaran (Kadzharan) to Meghri road, Tashtun pass (Kadjaran pass), 3 km N of Tashtun, 39°00'59"N, 46°12'38"E, 17 Jun 2016, alt. 1344, *H. Więcław & J. Koopman s.n.* (SOMF 30201). — Cyprus: Karpass (Karpasia, Karpaz) peninsula, Mt. Kantara, Apr 1880, *P. E. E. Sintenis & Rigo 356* (P00283665); Kyrenia Mts (Beşparmak Mts), W of Bellapais, alt. c. 300 m, 31 Mar 1986, *E. C. Vellinga 903* (L, as "*A. caricis*"). — Turkey: prov. Kahramanmaraş, distr. Pazarcik, between Narli and Karabiyikli, alt. 600–700 m, 11 May 1957, *Davis & Hedge D 27796* (K). — **Africa:** Algeria: Mt. Djebel Touilila, N of Zahrez Chergui salt lake, maquis, 1300 m, 27 Apr 1938, *A. Dubuis s.n.* (P01998567); "in collibus, Algeria", 6 Apr 1836, *C. Martius 504* (P01832709).

Literature records (*specimens not seen*) — On *Carex halleriana*. — **Europe:** Andorra: Almaraz (1999a, 2002, as "*Anthracoidea caricis*"). — Austria: Lower Austria (Voss 1877, as "*Ustilago caricis*"; Zwetko & Blanz 2004, as "*A.* sp."); Vienna (Zwetko & Blanz 2004, as "*A.* sp."). — Bulgaria: Blagoevgrad province, Mt. Slavyanka (Shivas & al. 2020, as "*A. caricis*"). — France (mainland): Hautes-Alpes (French Alps) (Kukkonen 1963, as "*A. caricis*"); Alpes-de-Haute-Provence (Shivas & al. 2020, as "*A. caricis*"); Alpes-Maritimes (Kukkonen 1963, as "*A. caricis*"; Fungi 105 in Poelt 1978, as "*A. irregularis*"). — France (Corsica): Aiaccio (Maire & al. 1901; Maire 1905, as "*Cintractia caricis*"; Kukkonen 1963, as "*A. caricis*"). — Greece: Durrieu (1968, as "*A. caricis*"). — Hungary: Nógrád county (Shivas & al. 2020, as "*A. caricis*"); Komárom-Esztergom county (Shivas & al. 2020, as "*A. caricis*"). — Italy: Trentino-Alto Adige/Südtirol, province of Trentino (Magnus 1926, as "*C. caricis*"); Lombardia, province of Brescia (Shivas & al. 2020, as "*A. caricis*"); Veneto, province of Verona (Massalongo 1894, as "*U. caricis*"). — Russia: Crimea, Simferopol rayon (Prosyannikova & al. 2019, as "*A. caricis*"); Bakhchysarai rayon (Kravchuk & al. 2019, as "*A. heterospora*"); Yalta (Tranzschel 1902, as "*A. caricis*"). — Spain: León (Almaraz 1999a, 2002, as "*A. caricis*"); Palencia (Almaraz 1999a, 2002, as "*A. caricis*"); Álava (Almaraz 2002, as "*A. caricis*"); Huesca (Almaraz 2002, as "*A. caricis*"); Lérida (Almaraz & Durrieu 1997; Almaraz 2002, as "*A.*

caricis"); Gerona (González Fragoso 1923 – as "*A. caricis*"; González Fragoso 1924, as "*C. caricis*"; Almaraz 2002, as "*A. caricis*"); Barcelona (González Fragoso 1924, as "*C. caricis*"; Ciferri 1931, as "*C. urceolorum*"; Losa-Quintana 1970, as "*C. caricis*"; Llorens i Villagrasa 1984, as "*C. pratensis*"; Almaraz 2002, as "*A. caricis*"); Cuenca (Almaraz 1999a, 2002, as "*A. caricis*"); Albacete (Almaraz 1999a, 2002, as "*A. caricis*"); Alicante (Almaraz 1999a, 2002, as "*A. caricis*"); Jaén (Almaraz 1999b, 2002, as "*A. caricis*"); Granada (Almaraz 2002, as "*A. caricis*"). — Switzerland: Valais (Zogg 1986, as "*A. irregularis*"). — **Asia:** Cyprus: Limassol (Shivas & al. 2020, as "*A. caricis*"). — Turkey: Niğde province (Kabaktepe & al. 2018, as "*A. irregularis*").

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