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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 |
|---|-------------------------------------|------------------------|------------------------------------|
| <i>Anthracoidea arenaria</i> (Syd.) Nannf. | <i>Carex arenaria</i> L. | AY563606 | Hendrichs & al. 2005 |
| <i>A. aspera</i> (Liro) Kukkonen | <i>C. chordorrhiza</i> L. f. | AY563607 | Hendrichs & al. 2005 |
| <i>A. baldensis</i> Vánky | <i>C. baldensis</i> L. | AY563599 | Hendrichs & al. 2005 |
| <i>A. bigelowii</i> Nannf. | <i>C. bigelowii</i> Schwein. | AY563566 | Hendrichs & al. 2005 |
| <i>A. bigelowii</i> | <i>C. bigelowii</i> | AY563567 | Hendrichs & al. 2005 |
| <i>A. bigelowii</i> | <i>C. bigelowii</i> | AY563568 | Hendrichs & al. 2005 |
| <i>A. buxbaumii</i> Kukkonen | <i>C. buxbaumii</i> Wahlenb. | AY563582 | Hendrichs & al. 2005 |
| <i>A. capillaris</i> Kukkonen | <i>C. capillaris</i> L. | AY563596 | Hendrichs & al. 2005 |
| <i>A. caricis</i> (Pers.) Bref. | <i>C. pilulifera</i> L. | AY563589 | Hendrichs & al. 2005 |
| <i>A. caricis-albae</i> (Syd.) Kukkonen | <i>C. alba</i> Scop. | AY563594 | Hendrichs & al. 2005 |
| <i>A. caricis-albae</i> | <i>C. alba</i> | AY563595 | Hendrichs & al. 2005 |
| <i>A. caricis-meadii</i> Savchenko & al. | <i>C. meadii</i> Dewey | JN863083 | Savchenko & al. 2013 |
| <i>A. carphae</i> (Speg.) Vánky | <i>Carpha alpina</i> R. Br. | AY563614 | Hendrichs & al. 2005 |
| <i>A. curvulae</i> Vánky & Kukkonen | <i>Carex curvula</i> All. | AY563611 | Hendrichs & al. 2005 |
| <i>A. curvulae</i> | <i>C. curvula</i> | AY563612 | Hendrichs & al. 2005 |
| <i>A. elynae</i> (Syd.) Kukkonen | <i>C. myosuroides</i> Vill. | AY563609 | Hendrichs & al. 2005 |
| <i>A. elynae</i> | <i>C. myosuroides</i> | AY563610 | Hendrichs & al. 2005 |
| <i>A. globularis</i> Kukkonen | <i>C. globularis</i> L. | AY563593 | Hendrichs & al. 2005 |
| <i>A. hallerianae</i> T. Denchev & al., sp. nov. | <i>C. halleriana</i> Asso | MT628657 | this study (SOMF 30201) |
| <i>A. hallerianae</i> | <i>C. halleriana</i> | MT628658 | this study (SOMF 30002) |
| <i>A. hallerianae</i> | <i>C. halleriana</i> | MT628659 | this study (SOMF 30001) |
| <i>A. hallerianae</i> | <i>C. halleriana</i> | MT628660 | this study (SOMF 30199) |
| <i>A. hallerianae</i> | <i>C. halleriana</i> | MT628661 | this study (SOMF 30000 [holotype]) |
| <i>A. heterospora</i> (B. Lindeb.) Kukkonen | <i>C. elata</i> All. | AY563600 | Hendrichs & al. 2005 |
| <i>A. heterospora</i> | <i>C. elata</i> | AY563601 | Hendrichs & al. 2005 |
| <i>A. hostianae</i> Nannf. | <i>C. hostiana</i> DC. | AY563581 | Hendrichs & al. 2005 |
| <i>A. inclusa</i> Bref. | <i>C. rostrata</i> Stokes | AY563605 | Hendrichs & al. 2005 |
| <i>A. irregularis</i> (Liro) Boidol & Poelt | <i>C. digitata</i> L. | AY563592 | Hendrichs & al. 2005 |
| <i>A. irregularis</i> | <i>C. ornithopoda</i> Willd. | AY563590 | Hendrichs & al. 2005 |
| <i>A. irregularis</i> | <i>C. ornithopoda</i> | AY563591 | Hendrichs & al. 2005 |
| <i>A. kariii</i> (Liro) Nannf. | <i>C. brunnescens</i> (Pers.) Poir. | AY563575 | Hendrichs & al. 2005 |
| <i>A. kariii</i> | <i>C. echinata</i> Murray | AY563576 | Hendrichs & al. 2005 |
| <i>A. kariii</i> | <i>C. echinata</i> | AY563577 | Hendrichs & al. 2005 |
| <i>A. kariii</i> | <i>C. echinata</i> | AY563578 | Hendrichs & al. 2005 |
| <i>A. kariii</i> | <i>C. lachenalii</i> Schkuhr | AY563579 | Hendrichs & al. 2005 |
| <i>A. kariii</i> | <i>C. paniculata</i> L. | AY563574 | Hendrichs & al. 2005 |
| <i>A. cf. kariii</i> | <i>C. davalliana</i> Sm. | AY563608 | Hendrichs & al. 2005 |
| <i>A. lasiocarpae</i> B. Lindeb. | <i>C. lasiocarpa</i> Ehrh. | AY563583 | Hendrichs & al. 2005 |
| <i>A. limosa</i> (Syd.) Kukkonen | <i>C. limosa</i> L. | AY563572 | Hendrichs & al. 2005 |
| <i>A. limosa</i> | <i>C. limosa</i> | AY563573 | Hendrichs & al. 2005 |
| <i>A. misandrae</i> Kukkonen | <i>C. atrofusca</i> Schkuhr | AY563584 | Hendrichs & al. 2005 |
| <i>A. pamiroalaica</i> Piątek & al. | <i>C. koshevníkovi</i> Litv. | KT006854 | Piątek & al. 2015 |
| <i>A. paniceae</i> Kukkonen | <i>C. panicea</i> L. | AY563580 | Hendrichs & al. 2005 |
| <i>A. pratensis</i> (Syd.) Boidol & Poelt | <i>C. flacca</i> Schreb. | AY563563 | Hendrichs & al. 2005 |
| <i>A. pratensis</i> | <i>C. flacca</i> | AY563564 | Hendrichs & al. 2005 |
| <i>A. pratensis</i> | <i>C. flacca</i> | AY563565 | Hendrichs & al. 2005 |
| <i>A. rupestris</i> Kukkonen | <i>C. rupestris</i> All. | AY563598 | Hendrichs & al. 2005 |
| <i>A. cf. rupestris</i> | <i>C. glacialis</i> Mack. | AY563588 | Hendrichs & al. 2005 |
| <i>A. sclerotiformis</i> (Cooke & Massee) Kukkonen | <i>C. punicea</i> K. A. Ford | AY563613 | Hendrichs & al. 2005 |
| <i>A. sempervirentis</i> Vánky | <i>C. ferruginea</i> Scop. | AY563587 | Hendrichs & al. 2005 |
| <i>A. sempervirentis</i> | <i>C. firma</i> Host | AY563585 | Hendrichs & al. 2005 |
| <i>A. sempervirentis</i> | <i>C. sempervirens</i> Vill. | AY563586 | Hendrichs & al. 2005 |
| <i>A. subinclusa</i> (Körn.) Bref. | <i>C. hirta</i> L. | AY563604 | Hendrichs & al. 2005 |
| <i>A. subinclusa</i> | <i>C. riparia</i> Curtis | AY563603 | Hendrichs & al. 2005 |

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

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

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

ports 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 Villagrana 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 μ l 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 (Kato & 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 \pm 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. pseudofetidae* 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.

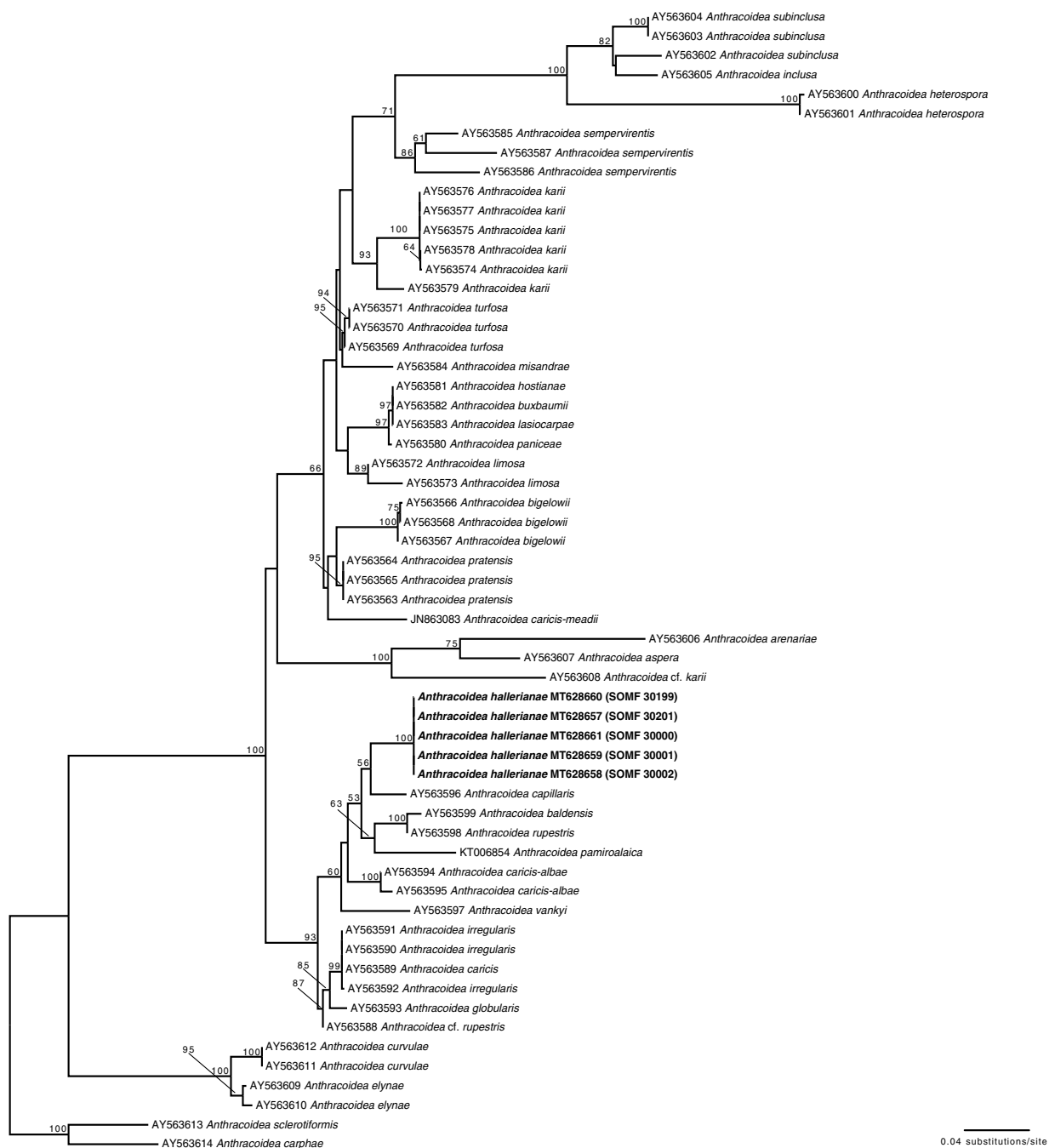


Fig. 1. Best tree of the RAxML analysis of species in the genus *Anthracoidea* based on a MAFIT alignment of partial LSU rDNA data. Bootstrap values ≥ 50 are depicted above the branches. The phylogeny is rooted with *A. sclerotiformis* and *A. carphae* according to Hendrichs & al. (2005).

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 sub-orbicular 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. Lindb.) 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*”);

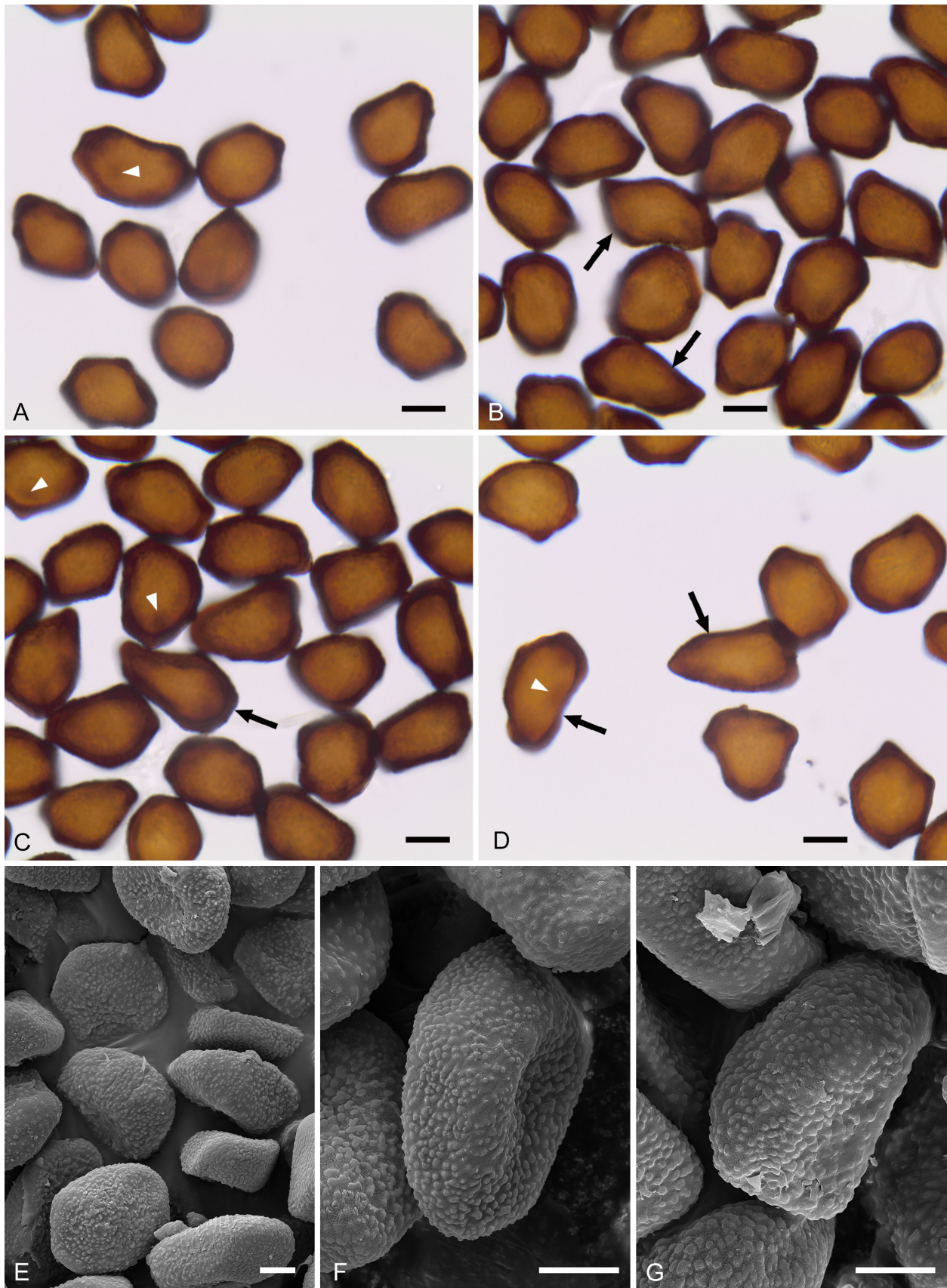


Fig. 3. *Anthracoidea hallerianae* on *Carex halleriana*. – A–D: spores in LM (A: holotype; B, C: SOMF 30202; D: SOMF 20359); arrows in B, C and D show irregularly elongated spores, arrowheads in A, C and D indicate internal swellings; E–G: spores in SEM (E, F: SOMF 30002; G: SOMF 30001). – Scale bars: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

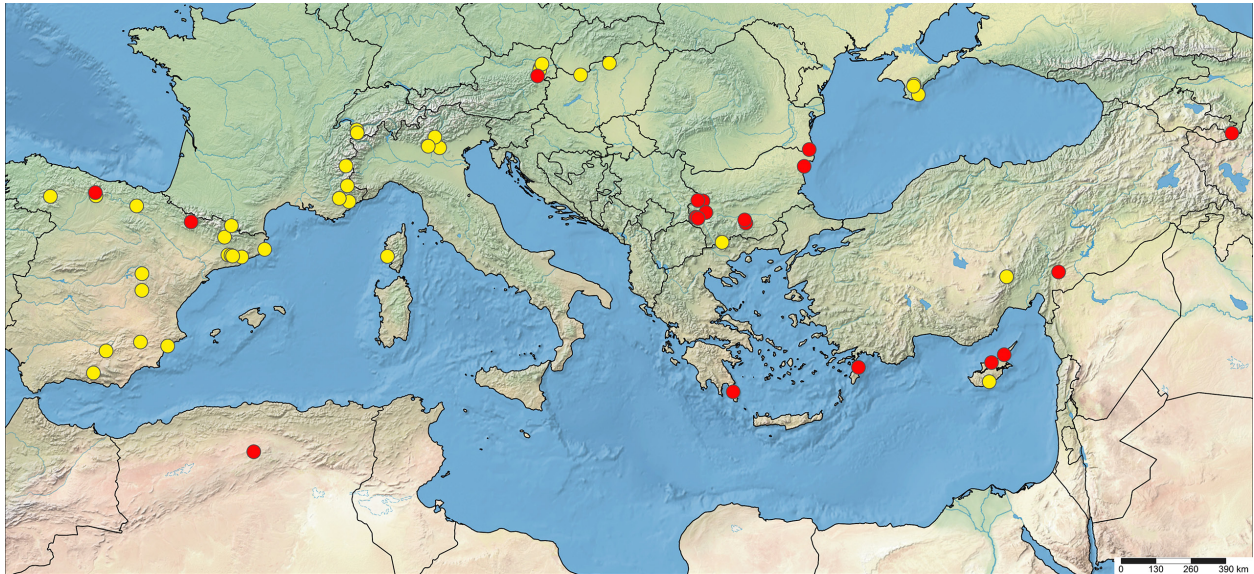


Fig. 4. Geographic distribution of *Anthracoidea hallerianae*. – Red circles = examined specimens; yellow circles = literature records. – Map generated with SimpleMappr (Shorthouse 2010).

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, Aseovgrad 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, Aseovgrad 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 Camporredondo 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. Carciá 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 (Kadzharan pass), 3 km N of Tashtun, 39°00'59"N, 46°12'38"E, 17 Jun 2016, alt. 1344, *H. Więclaw & J. Koopman s.n.* (SOMF 30201). — CYPRUS: Karpas (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 (CORSIKA): 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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References

- Almaraz T. 1999a: Nuevas aportaciones corológicas de *Ustilaginales*. – *Bol. Soc. Micol. Madrid* **24**: 95–102.
- Almaraz T. 1999b: Quelques *Ustilaginales* de l’Andalousie (Espagne). – *Cryptog. Mycol.* **20**: 5–10.
- Almaraz T. 2002: Bases corológicas de flora micológica ibérica. Numeros 1766–1932. – Pp. 11–124 in: Pando F. & Hernández J. C. (ed.), Cuadernos de trabajo de flora micológica ibérica **17**. – Madrid: Consejo Superior de Investigaciones Científicas, Real Jardín Botánico.
- Almaraz T. & Durrieu G. 1997: *Ustilaginales* from the Spanish Pyrenees and Andorra. – *Mycotaxon* **65**: 223–236.
- Castresana J. 2000: Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. – *Molec. Biol. Evol.* **17**: 540–552.
- Ciferri R. 1931: Quinta contribuzione allo studio degli *Ustilaginales*. – *Ann. Mycol.* **29**: 1–74.
- Denchev C. M. 1993: New data concerning Bulgarian smut fungi (*Ustilaginales*). 2. – *Fitologiya* **46**: 47–52.
- Denchev C. M. 2001: Class *Ustomycetes* (orders *Tilletiales*, *Ustilaginales*, and *Graphiiales*). – Pp. 1–286 in: Fakirova V. (ed.), *Fungi of Bulgaria* **4** [in Bulgarian with English summary]. – Sofia: Editio Academica “Prof. Marin Drinov” & Editio Pensoft.
- Denchev C. M. & Minter D. W. 2011: *Anthracoidea intercedens*. – In: IMI descriptions of fungi and bacteria **1862**. – Egham: CAB International.
- Denchev T. T. & Denchev C. M. 2016: *Anthracoidea caricis-reznicekii* (*Anthracoideaceae*), a new species on *Carex reznicekii*, and *A. eburneae*, a new record for the USA. – *Phytotaxa* **244**: 69–79.
- Denchev T. T., Denchev C. M., Michikawa M. & Kakishima M. 2013: The genus *Anthracoidea* (*Anthracoideaceae*) in Japan and some adjacent regions. – *Mycobiota* **2**: 1–125.
- Denchev T. T., Knudsen H. & Denchev C. M. 2020: The smut fungi of Greenland. – *MycKeys* **64**: 1–164.
- Durrieu G. 1968: *Micromycetes parasites de Grèce*. – *Biologia Gallo-Hellenica* **1**: 65–83.
- Egorova T. V. 1999: The sedges (*Carex* L.) of Russia and adjacent states (within the limits of the former USSR). – St. Petersburg: St. Petersburg State Chemical-Pharmaceutical Academy; St. Louis: Missouri Botanical Garden Press.
- Fischer de Waldheim A. 1877a: Aperçu systématique des *Ustilaginées*, leurs plantes nourricières et la localisation de leurs spores. – Paris: Lahure.
- Fischer de Waldheim A. 1877b [“1876”]: Les *Ustilaginées* et leurs plantes nourricières. – *Ann. Sci. Nat., Bot.*, ser. 6, **4**: 190–276.
- Fischer de Waldheim A. 1877c: Revue des plantes nourricières des *Ustilaginées*. – *Bull. Soc. Imp. Naturalistes Moscou* **52**: 312–331.
- González Fragoso R. 1923: Nueva serie de hongos del herbario del Museo de Ciencias Naturales de Barcelona. – *Butl. Inst. Catalana Hist. Nat.* **23**: 116–123.
- González Fragoso R. 1924: *Ustilagales* de la flora española existentes en el herbario del Museo Nacional de Ciencias Naturales de Madrid. – *Bol. Real Soc. Esp. Hist. Nat., Secc. Biol.* **24**: 116–127.
- Gouy M., Guindon S. & Gascuel O. 2010: SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. – *Molec. Biol. Evol.* **27**: 221–224.
- Hendrichs M., Begerow D., Bauer R. & Oberwinkler F. 2005: The genus *Anthracoidea* (*Basidiomycota*, *Ustilaginales*): a molecular phylogenetic approach using LSU rDNA sequences. – *Mycol. Res.* **109**: 31–40.

- Kabaktepe S., Akata I. & Karakuş Ş. 2018: A new *Anthracoidea* (*Ustilaginales*) record for Turkey. – *Hacettepe J. Biol. Chem.* **46**: 391–393.
- Katoh K. & Standley D. M. 2013: MAFFT multiple sequence alignment software version 7: improvements in performance and usability. – *Molec. Biol. Evol.* **30**: 772–780.
- Kravchuk E. A., Prosyannikova I. B., Repetskaya A. I. & Kadochnikova V. I. 2019: Obligate parasitic fungi of Bakla regional natural monument, Republic of Crimea, Russia [in Russian]. – *Uchen. Zap. Krymsk. Fed. Univ. V. I. Vernadskogo, Biol., Chimia* **5(1)**: 74–84.
- Kukkonen I. 1963: Taxonomic studies on the genus *Anthracoidea* (*Ustilaginales*). – *Ann. Bot. Soc. Zool.-Bot. Fenn.* “Vanamo” **34(3)**: 1–122.
- Kukkonen I. 1987: The genus *Carex* (*Cyperaceae*) in the Flora iranica area. – *Pl. Syst. Evol.* **155**: 27–43.
- Kukkonen I. 1998: *Cyperaceae*. – Pp. 1–307, t. 1–42 in: Rechinger K. H. (ed.), *Flora iranica* **173**. – Graz: Akademische Druck- und Verlagsanstalt.
- Llorens i Villagrasa I. 1984: Aportación al conocimiento de los *Uredinales*, *Ustilaginales* y *Fragmobasidiomicetos* de Espana. 1. – *Anales Biol., Fac. Biol., Univ. Murcia* **1**: 35–45.
- Losa-Quintana J. M. 1970: Contribución al estudio de los micromicetos españoles. – *Anales Inst. Bot. Cavanilles* **26**: 5–14.
- Luceño M. 2008 [“2007”]: *Carex* L. – Pp. 109–250 in: Castroviejo S., Luceño M., Galán A., Jiménez Mejías P., Cabezas F. & Medina L. (ed.), *Flora iberica* **18** (*Cyperaceae–Pontederiaceae*). – Madrid: Real Jardín Botánico, CSIC.
- Magnus P. 1926: Nachtrag zu: Die Pilze, bearbeitet von P. Magnus in der Flora der gefürsteten Grafschaft Tirol, des Landes Vorarlberg und des Fürstentums Liechtenstein von Prof. K. W. v. Dalla Torre und Ludw. Grafen v. Sarnthein: III. Band, Innsbruck, Wagner, 1905. – *Ber. Naturwiss.-Med. Vereins Innsbruck* **40**: 1–315.
- Maire R. 1905: Notes sur quelques champignons nouveaux ou peu connus. – *Bull. Soc. Mycol. France* **21**: 137–167.
- Maire R., Dumée P. & Lutz L. 1901: Prodrôme d'une flore mycologique de la Corse. – *Bull. Soc. Bot. France* **48**: clxxx–ccxlvii, t. 13, 14.
- Massalongo C. 1894: Nuova contribuzione alla micologia veronese. – *Malpighia* **8**: 97–130; 193–226, t. iii, iv.
- Moncalvo J.-M., Wang H.-H. & Hseu R.-S. 1995: Phylogenetic relationships in *Ganoderma* inferred from the internal transcribed spacers and 25S ribosomal DNA sequences. – *Mycologia* **87**: 223–238.
- Nannfeldt J. A. 1979: *Anthracoidea* (*Ustilaginales*) on Nordic *Cyperaceae–Caricoideae*, a concluding synopsis. – *Symb. Bot. Upsal.* **22(3)**: 1–41.
- Negrean G. 1993: New or rare host-plants for Romanian *Ustilaginales*. – *Rev. Roumaine Biol., Sér. Biol. Veg.* **38**: 139–148.
- Piątek M., Lutz M., Nobis M. & Nowak A. 2015: Phylogeny and morphology of *Anthracoidea pamiroalaica* sp. nov. infecting the endemic sedge *Carex koshevníkovićii* in the Pamir Alai Mts (Tajikistan). – *Mycol. Progr.* **14**: 120.
- Poelt J. 1978: Fungi. – Pp. 1–17 in: Poelt J. (ed.), *Plantae graecenses* **3**. – Graz: Institut für Systematische Botanik der Universität Graz. – Open access at https://www.zobodat.at/pdf/Plantae-Graecenses_PI_Graecenses_03_0001-0049.pdf [accessed 22 May 2020].
- Prosyannikova I. B., Kravchuk E. A., Repetskaya A. I. & Kadochnikova V. I. 2019: Inventarizatsiya vidovogo sostava fitotrofnikh obligatno-parazitnykh micromitsetov zapovednogo urochishcha “Lesnaya Dubovaya Roshcha ‘Levadki’”. – *Izv. S.-Peterburgsk. Lesotekhn. Akad.* **228**: 234–249.
- Rambaut A. 2012: FigTree v1.4. – Published at <http://tree.bio.ed.ac.uk/software/figtree/>
- Savchenko K. G., Lutz M., Piątek M., Heluta V. & Nevo E. 2013: *Anthracoidea caricis-meadii* is a new North American smut fungus on *Carex* sect. *Paniceae*. – *Mycologia* **105**: 181–193.
- Scholz H. & Scholz I. 1988: Die Brandpilze Deutschlands (*Ustilaginales*). – *Englera* **8**: 1–691.
- Shivas R., Tan Y. P. & Beasley D. 2020: Plant pathology herbarium. – Brisbane: Queensland Government, Department of Agriculture and Fisheries. – Published at <https://collections.daf.qld.gov.au/web/imu.php?request=search&page=herbarium> [accessed 19 May 2020].
- Shorthouse D. P. 2010: SimpleMappr, an online tool to produce publication-quality point maps. – Published at <https://www.simplemappr.net/> [accessed 19 May 2020].
- Stamatakis A. 2014: RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. – *Bioinformatics* **30**: 1312–1313.
- Thiers B. 2020+ [continuously updated]: Index herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden’s virtual herbarium. – Published at <http://sweetgum.nybg.org/science/ih/> [last accessed 26 May 2020].
- Tranzschel W. 1902: Contributiones ad floram mycologicam Rossiae. 1. Enumeratio fungorum in Tauria a. 1901 lectorum [in Russian]. – *Trudy Bot. Muz. Imp. Akad. Nauk* **1**: 47–75.
- Vánky K. 1979: Species concept in *Anthracoidea* (*Ustilaginales*) and some new species. – *Bot. Not.* **132**: 221–231.
- Vánky K. 1994: European smut fungi. – Stuttgart: Gustav Fischer Verlag.
- Vánky K. 2011 [“2012”]: Smut fungi of the world. – St. Paul: APS Press.
- Vánky K. 2013: Illustrated genera of smut fungi, ed. 3. – St. Paul: APS Press.
- Vánky K., Vánky C. & Denchev C. M. 2011: Smut fungi in Africa – a checklist. – *Mycol. Balcan.* **8**: 1–77.

- Vilgalys R. & Hester M. 1990: Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. – J. Bacteriol. **172**: 4238–4246.
- Voss W. 1877: Die Brand-, Rost- und Mehlthaupilze (*Ustilaginei*, *Uredinei*, *Erysiphei* et *Peronospori*) der Wiener Gegend. – Verh. K. K. Zool.-Bot. Ges. Wien **26**: 105–152.
- Winter G. 1880 [“1884”]: II. Ordnung *Ustilagineae*. – Pp. 79–131 in: Dr. L. Rabenhorst’s Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. Ed. 2. Band **1**. Pilze. Abt. **1**. Schizomyceten, Saccharomyceten und Basidiomyceten. – Leipzig: Eduard Kummer.
- Zogg H. 1986 [“1985”]: Die Brandpilze Mitteleuropas unter besonderer Berücksichtigung der Schweiz. – Cryptog. Helv. **16**: 1–277.
- Zwetko P. & Blanz P. 2004: Die Brandpilze Österreichs. *Doassansiales*, *Entorrhizales*, *Entylomatales*, *Georgefischeriales*, *Microbotryales*, *Tilletiales*, *Urocystales*, *Ustilaginales*. – In: Ehrendorfer F. (ed.) Catalogus florae Austriae **3(3)**, Biosystematics and Ecology Series **21**. – Wien: Verlag der Österreichischen Akademie der Wissenschaften.

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