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

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

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. halleriana*. 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

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-
| Species | Host | LSU rDNA accession no. | Reference |
|---------|------|------------------------|-----------|
| Anthracoida 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. caricis | C. caricis | AY563596 | 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 | 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) |
| A. heterospora (B. Lindeb.) Kukkonen | C. elata All. | AY563600 | Hendrichs & al. 2005 |
| A. heterospora | C. elata | AY563601 | Hendrichs & al. 2005 |
| A. hostiana 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. brunescens (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. lasiocarpeae 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. misandreae Kukkonen | C. atrofusca Schkuhr | AY563584 | Hendrichs & al. 2005 |
| A. pamiroalaica Piątek & al. | C. koshewnikowii Litv. | KT006854 | Piątek & al. 2015 |
| A. paniccae Kukkonen | C. panicca L. | AY563580 | Hendrichs & al. 2005 |
| A. pratensis (Syd.) Boidol & Poelt | C. flaccra Schreb. | AY563563 | Hendrichs & al. 2005 |
| A. pratensis | C. flaccra | AY563564 | Hendrichs & al. 2005 |
| A. pratensis | C. flaccra | 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. panicca 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
A. turfa (Syd.) Kukkonen
A. turfa
A. turfa
A. vankyi Nannf.

C. vesicaria L.
C. dioica L.
C. helaeonastes L. f.
C. parallelia (Laest.) Sommerf.
C. maricata L.

AY563602 Hendrichs & al. 2005
AY563571 Hendrichs & al. 2005
AY563569 Hendrichs & al. 2005
AY563570 Hendrichs & al. 2005
AY563597 Hendrichs & al. 2005

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

| 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. Halle rianae (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, Schizollena 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. cari - cis). Subsequently, this fungus was reported under different names: Cintractia urceolorum (DC.) Cif. (Ciferri 1931), Ustilago carici (Pers.) Fuckel (Voss 1877; Winter 1880; Massalongo 1894), Cintractia carici (Pers.) Magnus (Maire & al. 1901; Maire 1905; González Fragoso 1924; Magnus 1926), A. carici (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. halleriana. 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; Mon- calvo & 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,
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. pamirolaica*, *A. rapestris* 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.
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 (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 = 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. 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).

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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. kukkonensis Vánky on Carex distachya Desf. from Algeria and a dubious record of A. heterospora (B. Lindeberg) 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, Kostinbroad 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, Konyavsk planina, above Skakavitsa railway station, 6 Jun 1990, C. M. Denchev s.n. (SOMF 20357; in Denchev 1993 as “A. irregularis”).
Fig. 3. *Anthracoidea halleriana* 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.
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 V oden 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. Jagels n. (B 10 0427517); South Aegean, Rhodes, E of Astypalea, 17 Apr 1988, R. Böcker s.n. (B, as "A. irregularis"). — Romania: Dobrogea, Constanta county, Duranie Agiieni, 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 Camperdento da Alba, Espiguete, alt. 2180 m, 17 Jul 2003, R. Karl s.n. (W 2004-0008293); Huesca province, Mt. Oturia, alt. 1700 m, 3 Jun 1987, R. Carcia Adá & al. s.n. (MA-Fungi 37679, as "A. caricis"; ex MA 480029). — Turkey: prov. Kahramanmaras, distr. Pazaricik, between Narli and Karabiyikli, alt. 600–700 m, 11 May 1957, Davis & Hedge D 27796 (K). — Africa: Algeria: Mt. Djebel Touililla, 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): Ajaccio (Maire & al. 1901; Maire 1905, as "Cintractia caricis"; Kukkonen 1963, as "A. caricis"). — Greece: Peloponese, Laconia, Elafonisos island, 21 Apr 1991, A. Jugel 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 county, Pădurea Hagieni, 28 May 1981, G. Negrean s.n. (BUCM 59279; in Negrean 1993 as "A. caricis"). — Turkey: prov. Kahramanmaras, distr. Pazarcik, between Narli and Karabiyikli, alt. 600–700 m, 11 May 1957, Davis & Hedge D 27796 (K). — Africa: Algeria: Mt. Djebel Touililla, 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).
irregularis”). Gerona (González Fragoso 1923 – as “A. caricis”); Barcelona (González Fragoso 1924, as “C. caricis”); Almaraz 2002, as “A. caricis”). — Turkey: Niğde province (Kabaktepe & al. 2020, as “A. caricis”). — Switzerland: Valais (Zogg 1986, as “A. caricis”). — Spain: Navarra (Almaraz 1999b, as “A. caricis”); Alicante (Almaraz 1999a, 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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