

Phylogeny and morphology of *Anthracoidea pamiroalaica* sp. nov. infecting the endemic sedge *Carex koshewnikowii* in the Pamir Alai Mts (Tajikistan)

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Abstract A novel *Anthracoidea* species, *A. pamiroalaica* on the endemic sedge *Carex koshewnikowii*, is described and illustrated from the Pamir Alai Mts in Tajikistan (Central Asia). The new species is phenotypically nearly identical with *Anthracoidea sempervirentis*, but clearly divergent genetically. Phylogenetic analyses based on LSU sequences showed affinity of *Anthracoidea pamiroalaica* to *A. baldensis*, *A. rupestris*, *A. capillaris*, and *A. vankyi* infecting host sedges in different *Carex* sections (*Baldenses*, *Rupestris*, *Chlorostachyae*, and *Phaestoglochin*, respectively), but not to *A. misandrae*, and *A. sempervirentis*, two sequenced species parasitic on host species from the section *Aulocystis*. This phylogenetic placement is briefly discussed in the context of *Anthracoidea* evolution.

Keywords *Anthracoidea* · *Carex* · Central Asia · Cryptic species · Plant pathogens · Smut fungi · Ustilaginales

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Introduction

The genus *Anthracoidea* Bref., typified by *Anthracoidea caricis* (Pers.) Bref., includes smut fungi infecting host plants in the Cyperaceae (mostly species of *Carex* L.), forming globose sori in the ovaries and having spores produced directly on the outer surface of the reduced achenes (Kukkonen 1963; Vánky 2002). The species delimitation traditionally was based on comparative morphology and phenotypic differences between *Anthracoidea* species attacking host plants within a particular *Carex* section (Nannfeldt 1979; Vánky 1979, 2012). The first molecular phylogenetic study using LSU rDNA sequences including 28 *Anthracoidea* species (and two undescribed species), mainly from Europe, confirmed most of the analysed species (Hendrichs et al. 2005) and established a sound phylogenetic backbone for molecular work on *Anthracoidea*. The phylogenetic hypothesis presented by Hendrichs et al. (2005) can now be completed by the remaining described and potentially undescribed species. Since that study, only one additional *Anthracoidea* species was included in molecular phylogenetic analyses, namely the new species *A. caricis-meadii* K.G. Savchenko, M. Lutz & Piątek (Savchenko et al. 2013). The currently recognized biodiversity of *Anthracoidea* includes 110 species (Denchev and Denchev 2011a, b, 2012; He et al. 2011; Vánky and Abbasi 2011; Piątek 2012, 2013, 2014; Vánky 2012; Denchev et al. 2013; Savchenko et al. 2013), representing the largest species diversity among smut genera attacking cyperacean hosts.

The biodiversity of *Anthracoidea* species is, however, probably much higher than currently recognized. Novel species may be detected by disentangling polyphagous species that are likely species complexes, or they could be discovered on so far unknown host plants and in poorly surveyed ecoregions. The mountains of Central Asia are a promising area to search for unknown *Anthracoidea* species since they

are rich in potential host plants, the *Carex* species, and are relatively poorly surveyed for these smuts compared to, e.g., Europe. For example, the checklist of Tajik fungi (Korbonskaya 1990) contains seven *Anthracoidea* species that may, in most part, be wrongly identified considering the reported host plants. That this region may still hide undescribed species can be supported by the recent description of the new species *Anthracoidea mulenkoi* Piątek from Pakistan (Piątek 2006) or *A. melanostachyae* Denchev & T.T. Denchev from Iran and Tajikistan (Denchev and Denchev 2011b).

Carex koshevníkowi Litv. belongs to the section *Aulocystis* Dumort. subsect. *Lanatae* T.V. Egorova (1999). It is an endemic species with a small distribution area, occurring in Kyrgyzstan in the southwestern Tian Shan Mts (Egorova 1999; Lazkov and Sultanova 2011) and in Tajikistan in the Zeravshan Mts, Hissar Mts, Darvaz Mts, and Pamir Mts (Krachetovich 1963; Egorova 1999; Nobis et al. 2011). The south Pamirian specimens of that species need to be revised, to avoid intermingling with *Carex koshevníkowi* subsp. *chitralensis* (Nelmes) Dickoré, an intraspecific taxon occurring in northeastern Afghanistan (Breckle et al. 2013). *Carex koshevníkowi* is a member of the chasmophytic flora of the Pamir Alai and Tian Shan Mts, which in that area consists of many taxa of rock habitats that are geographically restricted to Tajikistan and its closest vicinities (Nobis et al. 2013; Nowak et al. 2014a, b, c, d).

In the course of systematic studies on vegetation and vascular plants of the Pamir Alai Mts in Tajikistan several specimens of *Carex koshevníkowi* infected by the ovariicolous smut of the genus *Anthracoidea* were found in the Takob river valley of the Hissar Mts in 2012 and 2015. So far, *Carex koshevníkowi* has not been reported to harbour any *Anthracoidea* species nor any other smut fungus. Although *Carex koshevníkowi* is very common in the Pamir Alai Mts, only one infected population was observed in the period of many years of field work. The collected specimens were phenotypically similar to *Anthracoidea sempervirentis* Vánky, a species originally described from *Carex sempervirens* Vill. (type host; see Vánky 1979), and currently reported from 12 host sedges of the section *Aulocystis* Dumort. (= *Frigidae* Fr. ex Kük.) in Europe and East Asia (Vánky 2012; Denchev et al. 2013). However, recent molecular studies revealed that many morphologically defined polyphagous smuts and false smuts in fact represent complexes of host-specific independent cryptic or pseudocryptic species (Vánky and Lutz 2007; Bauer et al. 2008; Lutz et al. 2005, 2008; Piątek et al. 2011, 2012, 2013a, b; Savchenko et al. 2014a, b; Vasighzadeh et al. 2014) and, therefore, *Anthracoidea* found on *Carex koshevníkowi* could be a species different than *Anthracoidea sempervirentis*. Thus, this study aims to

resolve the systematic placement of *Anthracoidea* on *Carex koshevníkowi* using light and scanning electron microscopy and phylogenetic analyses using LSU rDNA sequences.

Materials and methods

Morphological analyses

Sori and spore characteristics were studied using dried herbarium material. Specimens were examined by light microscopy (LM) and scanning electron microscopy (SEM). For LM, small pieces of sori were mounted in lactic acid, heated to boiling point and cooled, then examined under a Nikon Eclipse 80i light microscope. LM micrographs were taken with a Nikon DS-Fi1 camera. Spores were measured using NIS-Elements BR 3.0 (Nikon) imaging software. Spores were measured in plane view and measurements were adjusted to the nearest 0.5 µm. Spore size ranges were assigned to one of the three groups distinguished by Savile (1952): (1) small-sized spores—13–21(–23)×9–17(–20) µm; (2) medium-sized spores—15–25(–27)×10–21 µm; (3) large-sized spores—18–33×13–28 µm. For SEM, spores taken directly from dried herbarium samples were dusted onto carbon tabs and fixed to an aluminium stub with double-sided transparent tape. The stubs were sputter-coated with carbon using a Cressington sputter-coater and viewed under a Hitachi S-4700 scanning electron microscope, with a working distance of ca. 12 mm. SEM micrographs were taken in the Laboratory of Field Emission Scanning Electron Microscopy and Microanalysis at the Institute of Geological Sciences of Jagiellonian University (Kraków).

DNA extraction, PCR, and sequencing

Genomic DNA was isolated directly from the holotype specimen (KRA F-2012-146). For methods of isolation and crushing of fungal material, DNA extraction, amplification, purification of PCR products, sequencing, and processing of the raw data see Lutz et al. (2004) and Savchenko et al. (2013). The 5'-end of the nuclear large subunit ribosomal DNA (LSU) was amplified using the primer pair NL1 and NL4 (O'Donnell 1993). The LSU sequence obtained in this study was deposited in GenBank (accession number KT006854).

Phylogenetic analyses

In addition to the LSU sequence of *Anthracoidea* sp. on *Carex koshevníkowi* newly obtained in this study, sequences of all other species of *Anthracoidea* available in GenBank were used for molecular phylogenetic analyses (Hendrichs et al. 2005; Bauer et al. 2006; Begerow et al. 2007; Savchenko

et al. 2013). Methods of sequence alignment, handling of the alignment, and rooting of the trees followed Savchenko et al. (2013) with the following options for GBlocks 0.91b (Castresana 2000): “Minimum Number of Sequences for a Conserved Position” to 30, “Minimum Number of Sequences for a Flank Position” to 30, “Maximum Number of Contiguous Non-conserved Positions” to 8, “Minimum Length of a Block” to 5, and “Allowed Gap Positions” to “With half”. The resulting alignment was used for phylogenetic analyses using a Bayesian Approach (BA) and Maximum Likelihood (ML). For BA, a Markov chain Monte Carlo technique was used as implemented in the computer program MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). Four incrementally heated simultaneous Markov chains were run over 5,000,000 generations using the general time reversible model of DNA substitution with gamma distributed substitution rates and estimation of invariant sites, random starting trees and default starting parameters of the DNA substitution model as recommended by Huelsenbeck and Rannala (2004). Trees were sampled every 100th generation, resulting in an overall sampling of 50,001 trees. From these, the first 5001 trees were discarded (burn-in=5001). The trees sampled after the process had reached stationarity (45,000 trees) were used to compute a 50 % majority rule consensus tree in order to obtain estimates for the *a posteriori* probabilities of groups of species. This Bayesian approach to phylogenetic analyses was repeated five times to test the independence of the results from topological priors (Huelsenbeck et al. 2002). ML analysis (Felsenstein 1981) was conducted with the RAxML 7.2.6 software (Stamatakis 2006), using raxmlGUI (Silvestro and Michalak 2010), invoking the GTRCAT and the rapid bootstrap option (Stamatakis et al. 2008) with 1000 replicates.

Results

Phylogenetic analyses

The different runs of the BA that were performed and ML analyses yielded consistent topologies with respect to well-supported branches. To illustrate the results, the consensus tree of one run of the BA is presented (Fig. 1). In all analyses, the *Anthracoidea* specimen from *Carex koshevníkowi* clustered within a clade that included *Anthracoidea baldensis* Vánky, *A. capillaris* Kukkonen, *A. caricis*, *A. caricis-albae* (Syd.) Kukkonen, *A. globularis* Kukkonen, *A. irregularis* (Liro) Boidol & Poelt, *A. rupestris* Kukkonen, and *A. vankyi* Nannf. (fourth group after Hendrichs et al. 2005) as sister lineage of *A. baldensis* and *A. rupestris*, but with huge distance to *A. sempervirentis*.

Taxonomy

Anthracoidea pamiroalaica Piątek, M. Lutz & M. Nobis, **sp. nov.** Figs. 2d, e, and 3

MycoBank # MB 814814

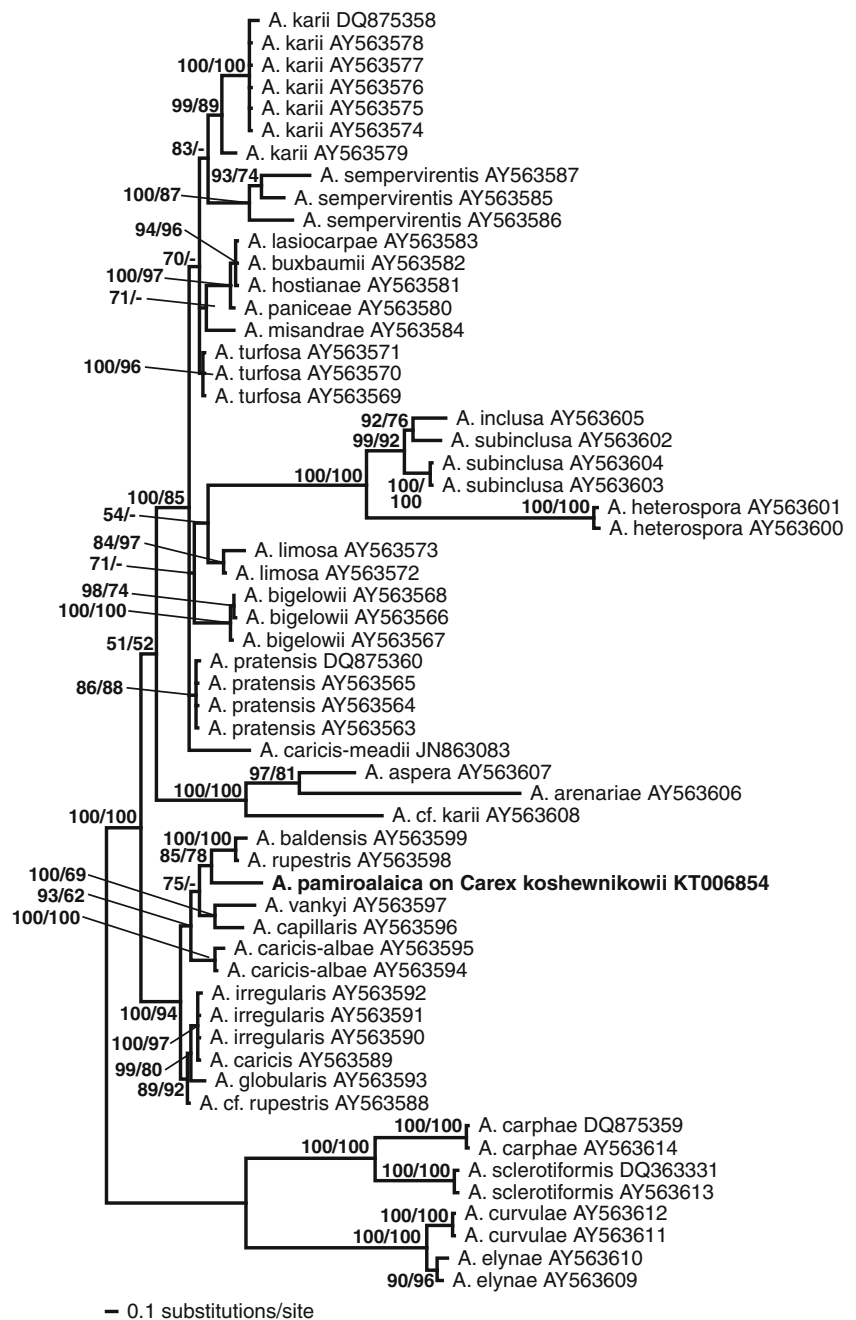
Etymology: In reference to the main Middle Asian Pamir Alai Mountain System, the type locality area of the new species, with abundant occurrence of the host plant *Carex koshevníkowi*.

Type: Tajikistan, Pamir Alai Mts: Hissar Mts, Takob river valley, on rocks, exp. SE, slope 80°, 38°49'57"N, 68°52'08"E, elev. ca. 1350 m a.s.l., on *Carex koshevníkowi*, 8 June 2012, M. Nobis & A. Nowak (holotype: KRA F-2012-146; GenBank: KT006854).—**Paratype:** Tajikistan, Pamir Alai Mts: Hissar Mts, Takob river valley, on rocks, exp. SE-E, slope 70–85°, 38°49'57"N, 68°52'08"E, elev. ca. 1350 m a.s.l., on *Carex koshevníkowi*, 31 May 2015, M. Nobis & A. Nowak (KRA F-2015-1, KRAM F-57734).

Description: Parasitic on *Carex koshevníkowi*. Sori in single ovaries of the inflorescences, usually one, but exceptionally two or three sori per inflorescence, forming black, globose bodies around achenes, about 2–4 mm in diameter, twice to three times as large as healthy achenes, enclosed by a whitish membrane (thin layer of host epidermis) that ruptures to reveal agglutinated spores, powdery on the surface, sori partly hidden by the perigynium. Spores medium-sized, irregularly flattened, yellow-brown, brown to reddish-brown, irregularly globose, subglobose, broadly ellipsoidal or polyangularly rounded, (15.0–)16.0–24.0(–25.0)×(13.0–)14.0–19.5(–21.0) μm, av.±SD, 19.4±2.2×16.6±1.6 μm, *n*=150/2 [(15.0–)16.0–23.5(–25.0)×(13.0–)14.0–19.5 μm, av.±SD, 18.9±2.1×16.4±1.6 μm, *n*=100, for the holotype; 17.0–24.0×(14.5–)15.0–18.5(–21.0) μm, av.±SD, 20.4±2.2×16.9±1.5 μm, *n*=50, for the paratype], rarely enclosed by a thin, hyaline, mucilaginous sheath; wall even, 1.0–2.5 μm thick, somewhat darker than the rest of spore, thicker at the angles, without internal swellings and protuberances, occasionally with light refractive spots; surface finely verruculose as seen by LM, spore profile almost smooth or finely wavy, surface finely verruculose as seen by SEM, with low warts up to 0.5 μm high (measured from SEM micrographs), warts usually single, rarely confluent, interspaces from almost smooth to finely punctate.

Ecology: At the type locality, *Anthracoidea pamiroalaica* grows abundantly on its host species *Carex koshevníkowi* in the Takob river valley, within the Hissar Mts (the western Hissaro-Darvasian geobotanical subregion). *Carex koshevníkowi* occurs there mainly in the association of *Dionysietum involucreatae* A. Nowak, M. Nobis, S. Nowak & A. Nobis (Nowak et al. 2014a). It grows on granite rocks of a relatively low cohesion index and acidity (pH 6.0 to 6.5) on rock faces, mainly on SW-S-SE-E aspects with almost

Fig. 1 Bayesian inference of phylogenetic relationships within the sampled *Anthracoidea* species: Markov chain Monte Carlo analysis of an alignment of LSU base sequences using the GTR+I+G model of DNA substitution with gamma distributed substitution rates and estimation of invariant sites, random starting trees, and default starting parameters of the DNA substitution model. A 50 % majority-rule consensus tree is shown computed from 45,000 trees that were sampled after the process had reached stationarity. The topology was rooted with sequences of *Anthracoidea carphae*, *A. curvulae*, *A. elynae*, and *A. sclerotiformis*. Numbers on branches before slashes are estimates for *a posteriori* probabilities, numbers on branches after slashes are ML bootstrap support values. Branch lengths were averaged over the sampled trees. They are scaled in terms of expected numbers of nucleotide substitutions per site. A. = *Anthracoidea*



vertical, or even overhanging, inclinations, the approximate mean being 100° (Fig. 2a, b, c).

Discussion

The phylogenetic relations between *Anthracoidea* species resolved in the current study are congruent with those resolved by the Bayesian Approach (BA) of Hendrichs et al. (2005), and, although based on sequences from only one rDNA region (LSU), most branches of the phylogenetic tree are well supported. Thus, in line with Hendrichs et al. (2005), this study

confirms that LSU is, in most cases, suitable to delimit *Anthracoidea* species and to a lesser extent to infer phylogenetic relations between species. Only a few species cannot be separated using LSU sequences (*Anthracoidea caricis* and *A. irregularis*, as well as *A. buxbaumii* Kukkonen, *A. hostianae* B. Lindeb. ex Nannf., *A. lasiocarpae* B. Lindeb. ex Kukkonen and *A. paniceae* Kukkonen; see also Hendrichs et al. 2005; Savchenko et al. 2013) and probably more sensitive genes should be sequenced to delimit those species pairs genetically though they still could be well separated phenotypically or ecologically (Piątek and Mułenko 2010; Vánky 2012). However, considering the predominance



Fig. 2 *Anthracoidea pamiroalaica* on *Carex koshevníkii*: **a** type locality area in the Takob river valley in the Hissar Mts (Tajikistan), **b–c** general habit of healthy *Carex koshevníkii*, **d–e** sori in the ovaries of *Carex koshevníkii*. Scale bars: **d–e**=5 mm

of LSU sequences (57 sequences) compared to ITS sequences (three sequences) or SSU sequences (two sequences) of *Anthracoidea* species deposited in GenBank (as checked on 6 June 2015), we recommend the LSU for molecular systematics and phylogeny of *Anthracoidea*.

The striking macroscopic character of the *Anthracoidea* specimens on *Carex koshevníkii* is the development of relatively large sori, which are twice or three times larger than healthy achenes, though this character alone may not be suitable to delimit the species. Considering micro-morphological

characters, *Anthracoidea* on *Carex koshevníkii* could be compared with other *Anthracoidea* species known on sedges from the section *Aulocystis* (sensu Egorova 1999): *A. altera* Nannf., *A. disciformis* (Liro) Piątek, *A. misandrae* Kukkonen, *A. sempervirentis*, *A. setosae* L. Guo, and *A. stenocarpae* Chleb. Of them, *A. altera*, *A. disciformis*, and *A. stenocarpae* have smaller spores (up to 21 μm long) with regular shape; additionally, *A. altera* and *A. stenocarpae* have weak internal swellings and thinner spore walls (up to 1.5 μm thick), and *A. disciformis* has papillate spores enclosed by a

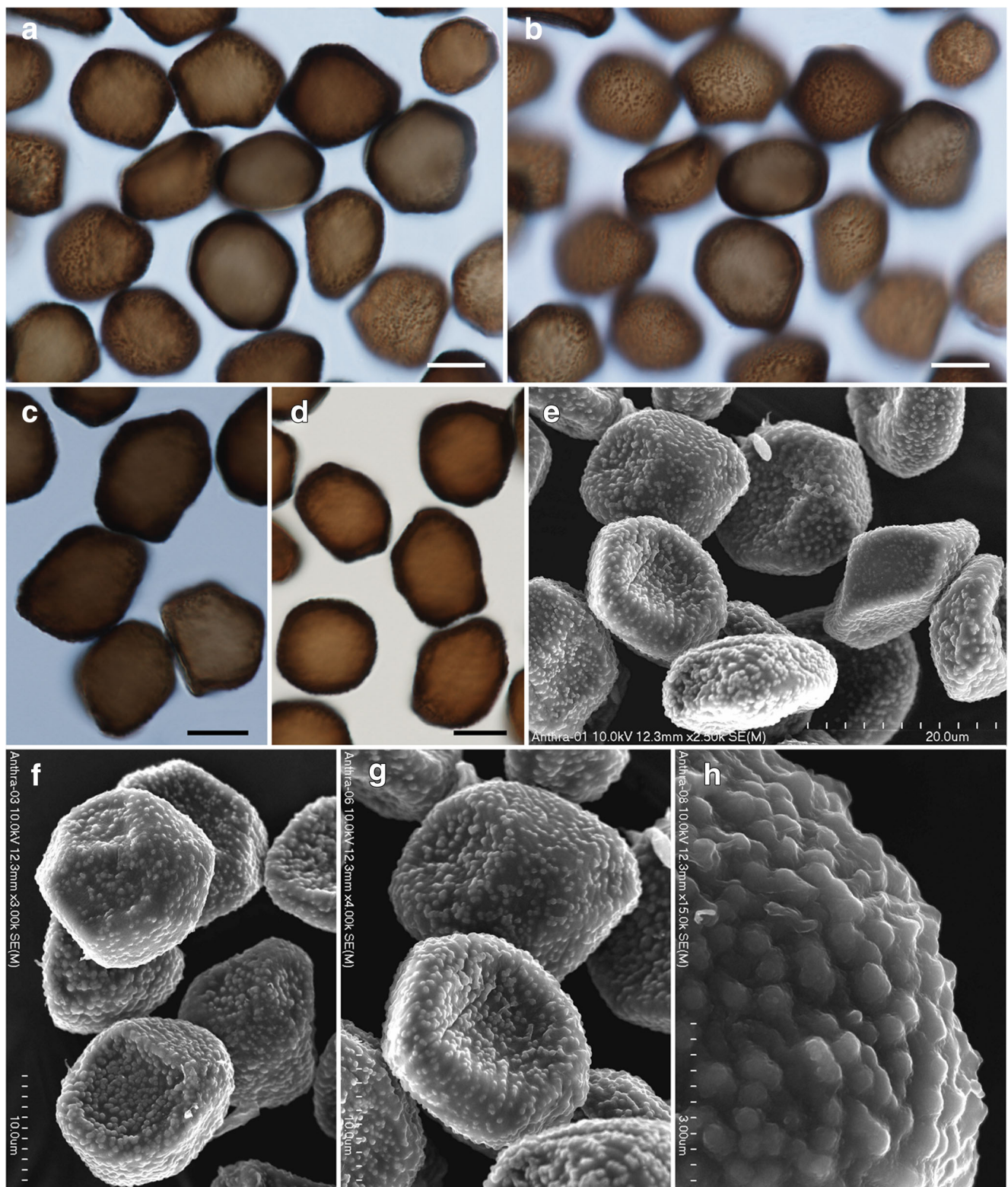


Fig. 3 *Anthracoidea pamiroalaica* on *Carex koshevníkowi* (all from KRA F-2012-146): **a–d** spores seen by light microscopy, median (**a**, **c–d**), and superficial (**b**) views, **e–g** spores seen by scanning

electron microscopy, **h** spore wall ornamentation seen by scanning electron microscopy. Scale bars: **a–d**, **f–g**=10 μm, **e**=20 μm, **h**=3 μm

hyaline mucilaginous sheath (Chlebicki 2002; Piątek 2012; Vánky 2012). In spore size range, *Anthracoidea* on *Carex*

koshevníkowi is similar to *A. misandreae* and *A. setosae*, but both of them differ in having spores with more regular shape,

thinner spore walls (up to 1.5 μm thick), and a somewhat different ornamentation (Vánky 2012). In spore size and morphology, *Anthracoidea* on *Carex koshevníkowi* is nearly identical with *A. sempervirentis*, and differs only in having a more distinctively developed ornamentation (for SEM illustrations of spore ornamentation of *A. sempervirentis* on type host *Carex sempervirens*, see Piątek 2005b; Piątek et al. 2005; Vánky 1994, 2012). More important, *Anthracoidea* on *Carex koshevníkowi* and *A. sempervirentis* are separated by a considerable genetic distance and cluster in two divergent *Anthracoidea* subclades (Fig. 1). This supports our initial hypothesis that, although phenotypically similar, the specimens on *Carex koshevníkowi* are not conspecific with *A. sempervirentis*, and are accordingly assigned to the novel species *Anthracoidea pamiroalaica*. The broad host spectrum reported for *Anthracoidea sempervirentis*, including 12 *Carex* species of the section *Aulocystis* in Europe, China, and Japan (Vánky 2012; Denchev et al. 2013) suggests that multiple species may be hidden within that species name. In the molecular studies of Hendrichs et al. (2005; confirmed here), *Anthracoidea sempervirentis* on *Carex ferruginea* Scop., *C. firma* Host, and *C. sempervirens* formed a monophyletic lineage, but with significant genetic divergence between (single) accessions on different hosts, indeed suggesting cryptic speciation within this species. Disentangling this complex is left open for future studies.

Genetic data are currently available for three of the seven recognized *Anthracoidea* species on sedges of the section *Aulocystis*. In the molecular phylogenetic analyses, *Anthracoidea sempervirentis* on *Carex ferruginea*, *C. firma*, and *C. sempervirens* form an independent lineage. *Anthracoidea misandreae* is a member of the same *Anthracoidea* subclade, but is not directly related to *A. sempervirentis*, indicating that they did not evolve from one and the same ancestral species. *Anthracoidea pamiroalaica* is, in turn, distantly related to *A. misandreae* and *A. sempervirentis* and additionally belongs to a different *Anthracoidea* subclade (Fig. 1). The closest phylogenetic relatives of *Anthracoidea pamiroalaica* resolved in the molecular analyses are *A. baldensis* (on *Carex baldensis* L.), *A. rupestris* (on *C. rupestris* All.), *A. capillaris* (on *C. capillaris* L.), and *A. vankyi* (on *C. muricata* L.). Interestingly, all these species share a comparatively similar spore morphology, but infect host sedges in different *Carex* sections, *Baldenses* Tuck., *Rupestris* (Tuck.) Meinsh., *Chlorostachyae* Tuck. ex Meinsh., and *Phaetoglochin* Dumort., respectively, predominantly in Europe (Nannfeldt 1979; Piątek 2005a; Vánky 2012), and the large inter-specific genetic distances support them as distinct species.

The placement of *Anthracoidea pamiroalaica* distantly to the remaining sequenced *Anthracoidea* species on *Carex* sect. *Aulocystis*, and the fact that these three *Anthracoidea* spp. do not form a monophyletic group could suggest that radiation of

Anthracoidea was (at least partly) realized in a different way than the hypothesized parallel fungus-host evolution (Kukkonen 1963). Alternatively, the traditional morphological classification of host sedges within the section *Aulocystis* (Egorova 1999) does not reflect evolutionary relations. Indeed, in the molecular studies of *Carex* subgenus *Carex* employing ITS sequences, the analysed sedges of the sect. *Aulocystis* were non-monophyletic and dispersed within the phylogenetic tree (Hendrichs et al. 2004), but *C. koshevníkowi* has not been included in molecular studies yet. Recent co-phylogenetic reconstructions of *Anthracoidea* spp. and host sedges suggested host-shift speciation in this smut genus (Escudero 2015); that study, however, included only 28 *Anthracoidea* (and two undescribed) species for which sequences were available (Hendrichs et al. 2005; Savchenko et al. 2013), i.e., only 25 % of all described species. Therefore, it is a challenge for future studies to include in molecular phylogenetic analyses the remaining described *Anthracoidea* spp., including those on host sedges in sect. *Aulocystis*, and to conduct similar co-phylogenetic analyses with as much smut and host species as possible.

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