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, Rupestres, Chlorostachyae, and Phaestoglochin, respectively), but not to A. misandreae, 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

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 cyperaceous 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. melanostachyaæ Denchev & T.T. Denchev from Iran and Tajikistan (Denchev and Denchev 2011b).

Carex koshewnikowii 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, Hissr 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 kosheknikowii subsp. chitralensis (Nelmes) Dickoré, an intranspecific taxon occurring in northeastern Afghanistan (Breckle et al. 2013). Carex koshewnikowii 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 koshewnikowii infected by the ovariicolous smut of the genus Anthracoidea were found in the Takob river valley of the Hissr Mts in 2012 and 2015. So far, Carex koshewnikowii has not been reported to harbour any Anthracoidea species nor any other smut fungus. Although Carex koshewnikowii 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 sempervirens Vâńky, a species originally described from Carex sempervirens Vill. (type host; see Vâńky 1979), and currently reported from 12 host sedges of the section Aulocystis Dumort. (= Frigidae Fr. ex Kük.) in Europe and East Asia (Vâńky 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 (Vâńky 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 koshewnikowii could be a species different to Anthracoidea sempervirens. Thus, this study aims to

resolve the systematic placement of Anthracoidea on Carex koshewnikowii 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 koshewnikowii 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 koshewnikowii 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. vankyii 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

A. koshewnikowii

A. cluster within a clade that included A. sempervirentis. A. baldensis all analyses, the Kukkonen globularis (Syd.) Kukkonen (fourth group after Hendrichs et al. 2005) as sister lineage (Castresana 2000):

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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 (A. caricis, A. irregularis, A. lasiocarpeae, A. hostiana, A. paniceae; 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...
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 koshewnikowii 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 koshewnikowii 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
hyaline mucilaginous sheath (Chlebicki 2002; Piątek 2012; Vánky 2012). In spore size range, Anthracoidea on Carex koshewnikowii is similar to A. misandrace and A. setosae, but both of them differ in having spores with more regular shape.

Fig. 3 Anthracoidea pamiralaica on Carex koshewnikowii (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
thinner spore walls (up to 1.5 μm thick), and a somewhat different ornamentation (Vánky 2012). In spore size and morphology, *Anthracoidea* on *Carex koshewnikowii* 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 koshewnikowii* 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 koshewnikowii* 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 misandrae* 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. misandrae* 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. vánkyi* (on *C. muricata* L.). Interestingly, all these species share a comparatively similar spore morphology, but infect host sedges in different *Carex* sections, *Baldenses* Tuck., *Ruprestes* (Tuck.) Meinh., *Chlorostachyae* Tuck. ex Meinh., and *Phaestoglochin* 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. koshewnikowii* 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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