DNA barcoding and phylogenetic analyses of the genus *Coleosporium* (Pucciniales) reveal that the North American goldenrod rust *C. solidaginis* is a neomycete on introduced and native *Solidago* species in Europe

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Abstract Recently, an unknown rust fungus of the genus *Coleosporium* appeared in Germany and Switzerland on giant goldenrod, *Solidago gigantea*, an invasive neophyte from North America, and on the indigenous European goldenrod, *S. virgaurea*. For identification, DNA barcodes were assembled in the course of the German Barcode of Life (GBOL) project and the investigation of neomycetes in Switzerland. Phylogenetic analyses were performed using ITS and LSU sequences of *Coleosporium* species representing various host plants and geographic regions. These analyses resulted in the first molecular evidence of the North American rust *Coleosporium solidaginis* in Europe. *Coleosporium solidaginis* is split into two subclades that are closely related to *Coleosporium asterum*, a species on *Aster* s.l., which was formerly synonymized with *C. solidaginis*. The genus is

divided into an American and a Eurasian clade. This phylogenetic pattern indicates that the geographic distribution, rather than the relationship with host plants, played a major role in the evolution of *Coleosporium* species. This finding particularly applies to the European species, which are genetically uniform according to the ITS and LSU sequences. Taxonomical consequences are discussed. *Coleosporium solidaginis* is fragmentarily distributed in Europe. The place of its introduction and host shift to *S. virgaurea* remains uncertain. Life cycle and propagation are mainly restricted to asexual urediniospores. Telia were found only once and the aecial stage was not observed at all on pine trees. The ecological impact of this neomycete is still unknown, but *C. solidaginis* has the potential to harm wild and cultivated goldenrods in Europe.

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Introduction

Neobiota, alien organisms, can have a large impact on the indigenous flora and fauna of the area where they have been introduced (e.g., Kowarik and Rabitsch 2010). In particular, plant parasitic neomycetes¹ can cause severe damage to forest trees and agricultural plants (e.g., Large 2003; Santini et al. 2013; Sieber 2014). Whereas these economically important alien fungi have been investigated thoroughly, current knowledge on other neomycetes and their influence on wild plants in

¹ Neomycetes were originally defined as introduced alien fungi that had established in a new area after 1492 (Kreisel and Scholler 1994). Other authors (e.g., Beenken and Senn-Irlet 2016; Klenke and Scholler 2015) have used the term in a broader sense, including also non-established ephemeral fungi.

natural ecosystems is insufficient (e.g., Beenken and Senn-Irlet 2016).

Rust fungi (Pucciniales) are an important group of plant parasitic fungi containing many neomycetes: 33 alien rust fungus species have been observed in Switzerland (Beenken and Senn-Irlet 2016) and around 40 have been found in Germany (Scholler, unpublished data). Most of these neomycete rust fungi occur only on their original host plants, which were also introduced to the area, as in the cases of *Phragmidium mexicanum* (Mains) H.Y. Yun, Minnis & Aime on *Potentilla indica* (Andrews) Th. Wolf [= *Frommeëlla mexicana* (Mains) J.W. McCain & J.F. Hennen on *Duchesnea indica* (Andrews) Focke] and *Puccinia komarovii* Tranzschel ex P. Syd. & Syd. on *Impatiens parviflora* DC. Several introduced rusts are known to occur almost exclusively on native plants; for example, *Melampsoridium hiratsukanum* S. Ito ex Hirats. has two indigenous major telial hosts in Europe, *Alnus incana* (L.) Moench and *A. glutinosa* (L.) Gaertn. (Hantula and Scholler 2013). Others infect introduced as well as indigenous plants, e.g., *Puccinia malvacearum* Bertol. ex Mont. occurs on several species of Malvaceae (Beenken and Senn-Irlet 2016; Klenke and Scholler 2015).

A *Coleosporium* species appeared on the introduced goldenrod, *Solidago gigantea* Ait. (Asteraceae), as well as on the indigenous *S. virgaurea* L. in southwest Germany in 2009 (Klenke and Scholler 2015) and in Switzerland in 2012 (Beenken and Senn-Irlet 2016; Brodtbeck 2017). There are numerous native *Coleosporium* species known to occur on several Asteraceae spp. in Europe, but none of these species had previously been found on *Solidago* spp. in this region (e.g., Gäumann 1959; Helfer 2013). Therefore, Klenke and Scholler (2015), who first reported occurrences of this *Solidago* rust in Central Europe, provisionally named it *Coleosporium asterum* (Dietel) Syd. & P. Syd., a species occurring on *Solidago* spp. in North America and Asia (e.g., Arthur 1962; Farr and Rossman 2017; Ginns 1986). Later, Beenken and Senn-Irlet (2016) and Brodtbeck (2017) reported further occurrences in Switzerland. In northern Spain, it was already found on *S. virgaurea* in 2007 (Menéndez and Rubio 2012).

The host plants

The genus *Solidago* (Asteraceae) includes ca. 100 species in North and Central America, Eurasia, and northernmost Africa (Wagenitz 1979). With more than 75 species occurring in North America, this region is the biodiversity hotspot of the genus (Flora of North America in <http://www.efloras.org>). In Europe and North Africa, only *S. virgaurea* is native; this species is also distributed throughout temperate Asia and is split into several subspecies (Wagenitz 1979). *Solidago virgaurea* is a medicinal plant used in urinary tract diseases

and is, therefore, cultivated in Germany and Switzerland (Kołodziej 2009; Schenk and Lück 2012; Vogel 2017). *Solidago gigantea*, like *S. canadensis* L., is native to North America. Both species have been introduced in many regions of the world, including Europe (Kowarik and Rabitsch 2010; Wagenitz 1979; Weber and Jakobs 2005). *Solidago gigantea* was introduced in England in 1758 as an ornamental plant and later on the European continent, where it soon grew wild. Since the mid-twentieth century, the species has become invasive in Central Europe (Kowarik and Rabitsch 2010; Weber and Jakobs 2005). Therefore, *S. gigantea* and *S. canadensis* are both on the “black list” of invasive neophytes in Switzerland (Weber 2013, <https://www.infoflora.ch>) and Germany (Nehring et al. 2013).

The genus *Coleosporium*

The pine needle rust genus *Coleosporium* (Coleosporaceae, Pucciniales) contains more than 100 species, which are mainly distributed in the temperate northern hemisphere but occur also in tropical regions (Farr and Rossman 2017; Kirk et al. 2008). Additionally, there have been multiple *Coleosporium* species introductions, e.g., in South America (Hennen et al. 2005), South Africa (Van Reenen 1995), Australia (Shivas et al. 2017), and New Zealand (McKenzie 1998), where host-alternating species often survive without an aecial host. Most species are heteroecious, with spermogonia and aecia on needles of *Pinus* spp. and uredinia and telia mainly on leaves of several dicot taxa (e.g., Helfer 2013; Kaneko 1981). In Europe, their native telial hosts belong to the families Asteraceae, Campanulaceae, Orobanchaceae, and Ranunculaceae (Gäumann 1959; Helfer 2013; Klenke and Scholler 2015). Outside Europe, *Coleosporium* species occur also on several other host plant families (Farr and Rossman 2017), such as Apocynaceae, Convolvulaceae, Lamiaceae, and Rutaceae (Table S1).

Depending on the authors and their species concept, one *Coleosporium* species with several *formae speciales* (Helfer 2013), 14 species (Gäumann 1959), or up to 20 species (Klenke and Scholler 2015) have been reported to exist in Europe. *Coleosporium* species are difficult to distinguish morphologically and, thus, are defined mainly by telial host taxonomy. Generally, one fungal species has been restricted to the plant species of a single genus or family (e.g., Gäumann 1959). Klebahn (1914) and Gäumann (1959), however, reported that several European *Coleosporium* species, mainly on Asteraceae, infect exotic plants of different families, namely *Schizanthus grahami* Gill. ex Hooker (Solanaceae) and *Tropaeolum* spp. (Tropaeolaceae). Thus, species identification of *Coleosporium* specimens on *Solidago* spp. has been challenging and the question has arisen as to whether it is really a neomycete or whether it is an indigenous *Coleosporium* species that jumped to *Solidago* spp. from non-related hosts. This

phenomenon happens quite frequently with plant parasitic fungi and has most recently been reported for powdery mildews in Switzerland (Beenken 2017).

The aim of this study was to identify the *Coleosporium* specimens on goldenrod species in Germany and Switzerland by molecular phylogenetic analyses and to resolve their relationships to other European, Asian, and American species on several host species.

Materials and methods

Fungal collections

To form a dataset that was as complete as possible for the phylogeny of the genus, samples of almost all host plant species infected by *Coleosporium* spp. in Europe were collected during numerous field trips in Germany (particularly SW Germany) and Switzerland or taken from herbarium specimens (Tables S1 and S2). German material was obtained in the course of the German Barcode of Life (GBOL) project. To find additional specimens of goldenrod rust in Switzerland, sites where alien and native *Solidago* spp. occur (according to <https://obs.infoflora.ch/app/neophytes/de/index.html>) were selected, and the plants at these sites were systematically checked for *Coleosporium* infections (Table S3; Beenken and Senn-Irlet 2016). From each location, one collected specimen of infected *S. gigantea* and/or of infected *S. virgaurea* was chosen for molecular analyses (Tables S1 and S2). The rust identification was confirmed by light microscopy, and each specimen was assigned to a species following the biological species concept of Gäumann (1959) and Klenke and Scholler (2015). Voucher specimens were deposited in KR and ZT (Tables S1 and S2).

Molecular analyses

Total DNA was extracted from small pieces of leaves (ca. 3×3 mm) with fungal infections, which were dried on silica gel, using the NucleoSpin Plant II extraction kit (Macherey-Nagel, Düren, Germany), following the manufacturer's standard protocol for plant tissue. The ITS1–5.8S–ITS2 and the neighboring part of the LSU region of the nrDNA were PCR-amplified and sequenced following the protocol described by Beenken et al. (2012) using the rust fungi-specific primer pairs ITS5u/ITS4rust and LRust1R/LR6 (Beenken et al. 2012; Pfunder et al. 2001; Vilgalys and Hester 1990). Sequences were deposited in GenBank (accession numbers are given in Table S1). The sequences of the rust fungi were compared with accessions deposited in GenBank by applying the Basic Local Alignment Search Tool (BLAST) using the nucleotide search option (blastn) (Altschul et al. 1990). The phylogenetic position of the collected *Solidago* rusts within the genus

Coleosporium was analyzed. For this purpose, sequences were combined with sequences of *Coleosporium* spp. from the GBOL project (<http://www.bolgermany.de>; Geiger et al. 2016). All *Coleosporium* spp. sequences available from GenBank, for which host plants and geographic origin were indicated, were included in the analyses. Thus, the datasets contained *Coleosporium* spp. occurring on different host plants and originating from different parts of the world (Table S1). Separate ITS and LSU alignments were created because neither the LSU nor the ITS were available for all species (Table S1). All alignments were performed using MAFFT v.7.017 (Kato et al. 2002; Kato and Standley 2013). Ambiguous regions within the resulting alignments were excluded from analyses with Gblocks v.0.91b (Castresana 2000).

The LSU alignment of 549 bp in length contained 58 sequences of *Coleosporium* spp., one sequence of a *Uredo* sp., and one of *Chrysomyxa rhododendri* (DC.) de Bary, the sister genus of *Coleosporium* (Maier et al. 2003). The closely related *Cronartium ribicola* J. C. Fisch (Maier et al. 2003) was used as the outgroup in the LSU analysis. The alignment of the ITS1–5.8S–ITS2 region (637 bp) included 71 sequences of *Coleosporium* spp. (Table S1), and the sequence of *Chrysomyxa rhododendri* was used as the outgroup (following the LSU analysis; Fig. 1). The eight sequences lacking the ITS1 region taken from GenBank (Table S1) were supplemented with unknown bases (N) in the ITS alignment. To validate this approach, the same ITS dataset but containing only the 5.8S–ITS2 region (270 bp) was used. Additionally, a combined alignment was created using 26 ITS1–5.8S–ITS2–LSU sequences and five 5.8S–ITS2–LSU sequences, with a total length of 1254 bp.

The datasets were analyzed using the maximum likelihood (ML) methods implemented in RAxML v.7.2.8 (Stamatakis 2006). Analyses were performed assuming a general time-reversible (GTR) model of nucleotide substitution and estimating a discrete gamma distribution (GTRGAMMA option in RAxML) with partitions according to the submatrices, which allowed multiple models of substitution. One thousand runs with distinct starting trees were completed using the rapid bootstrap (BS) algorithm of RAxML (Stamatakis et al. 2008). The resulting phylogenetic ML trees were rooted and visualized using the Dendroscope program (Huson et al. 2007).

Results

BLAST search

The ITS1–5.8S–ITS2 sequences of all *Coleosporium* samples found on *S. gigantea* and *S. virgaurea* in Germany and Switzerland were identical. The same result was found for the investigated LSU sequences. The 5.8S–ITS2 sequence of

Apocynaceae
Astereaceae
Campanulaceae
Convulvolaceae
Lamiaceae
Orobanchaceae
Rutaceae

Fig. 1 Phylogenetic positions of *Coleosporium solidaginis* and *C. asterum* within the genus *Coleosporium*, based on maximum likelihood (ML) analysis with RAxML v.7.2.6 recovered from LSU sequence data. The numbers at nodes indicate RAxML bootstrap support > 50%. Samples are given with species name, GenBank accession number (in parentheses) or voucher number, host plant, and origin (see also Table S1). Families of host plants are coded by color (see insert)

the European *Solidago* rust was nearly identical (> 99%) and the LSU sequence was 100% identical to the corresponding sequences of *Coleosporium solidaginis* (= *C. asterum*) on *Solidago* spp. from North America in GenBank (accession numbers: DQ354559, GU58009, and HQ317530).

Phylogenies

Figure 1 shows the tree resulting from the RAxML analysis of the LSU sequences, Fig. 2 of the ITS1–5.8S–ITS2 sequences, Fig. S1 of the 5.8S–ITS2 sequences, and Fig. S2 of the ITS1–5.8S–ITS2–LSU sequences. There were no mismatches between the topologies of these trees but the bootstrap supports of the clades were higher in the ITS1–5.8S–ITS2 analysis than in the other ITS analyses. In all phylogenetic analyses, the *Coleosporium* samples on *Solidago* spp. from Europe formed, together with the samples of *Coleosporium* spp. on *Solidago* spp. from North America and Asia, a single well-supported clade (*C. solidaginis* I clade in Figs. 1 and 2) that was well separated from the indigenous European *Coleosporium* species (Figs. 1, 2, S1, and S2). Two *Coleosporium* collections on *S. canadensis* from China appeared in a sister position to the clade in the LSU tree (*C. solidaginis* II clade in Fig. 1). The *C. asterum* samples on *Aster spathulifolius* Maxim., *Symphytotrichum pilosum* (Willd.) G.L. Nesom from South Korea, and on *S. ciliolatum* (Lindley) Á. Löve & D. Löve from Canada in the LSU analysis (Fig. 1, *C. asterum* clade), as well as the *Coleosporium* sample on *Eurybia macrophylla* (L.) Cass. (= *Aster macrophyllus* L.) from Canada in the ITS analyses (Figs. 2 and S1), appeared to be separated from the rusts on *Solidago* spp. All these *Coleosporium* samples formed, together with all other species of American origin [*C. apocynaceum* Cooke, *C. elephantopodis* Thüm., *C. ipomoeae* (Schwein.) Burrill, *C. plumeriae* Pat., and *Uredo* sp. on *Baccharis* sp.], a well-supported clade (Fig. 1). The European and Asian species appeared in the basal position to the clade of American species (Fig. 1).

With the exception of *C. inulae* Rabenh., all European *Coleosporium* species revealed more or less identical LSU sequences and appeared in one clade in the LSU tree (Fig. 1). In the ITS trees (Figs. 2 and S1), *C. inulae* was also well separated from all other European species that were monophyletic, with *C. pulsatillae* (F. Strauss) Fuckel and *C. pedicularis* F.L. Tai (from China) in the basal position to the remaining European species. The ITS region did not resolve the

European *Coleosporium* rusts occurring on Orobanchaceae [*C. euphrasiae* (Schumach.) G. Winter on the genera *Euphrasia*, *Odontites*, and *Rhinanthus*; *C. melampyri* (Rebent.) Kleb. on *Melampyrum* spp.], on Campanulaceae [*C. campanulae* (Pers.) Lév. on *Campanula* spp.], and on a part of Asteraceae [*C. cacaliae* G.H. Oth. on *Adenostyles alliariae* (Gouan) A. Kern., *C. senecionis* (Pers.) Fr. on native *Senecio* spp., as well as the introduced *S. inaequidens*, *C. sonchi* Lév. on *Sonchus* spp.]. *Coleosporium tussilaginis* (Pers.) Berk. on *Tussilago farfara* L. (Asteraceae) and *C. petasitis* Cooke on *Petasites hybridus* (L.) G. Gaertn., B. Mey. & Scherb. (Asteraceae) appeared together on a well-supported subclade nested within these European *Coleosporium* clades (Fig. 2) or in sister position to them (Fig. S2). The Asian species occurring on Asteraceae (*C. neocacaliae* Saho and *C. saussureae* Thüm.), on Lamiaceae (*C. plectranthi* Barclay and *C. phlomidis* Z.M. Cao & Z.Qi Li), on Orobanchaceae (*C. pedicularis*), on Ranunculaceae (*C. cimicifugatum* Thüm.), and on Rutaceae (*C. euodiae* Dietel, *C. phellodendri* Kom., and *C. zanthoxyli* Dietel & P. Syd.) were well separated from each other. They did not appear in a single clade but were intermixed with the European species (Figs. 1, 2, S1, and S2).

Discussion

Nomenclature and taxonomy

There is some confusion concerning the use of the two species names *C. asterum* and *C. solidaginis*. Therefore, the correct name of the goldenrod rust needs to be clarified before discussing our results in detail. Moreover, recent changes in nomenclatural rules (McNeill et al. 2012) and our phylogenetic results necessitate nomenclatural and taxonomical rearrangements.

In 1822, Schweinitz (see also Arthur and Bisby 1918) described *Uredo solidaginis* Schwein. on *Aster*, *Solidago*, and *Vernonia* species from North Carolina, USA. Thümen (1878) changed the name to *Coleosporium solidaginis* (Schwein.) Thüm. and listed *Solidago puberula* Nutt. and *S. gigantea* as hosts from the east coast of the USA. Later, Dietel (1900) described *Stichopsora*, a genus from Japan that is closely related to *Coleosporium* and consists of one species, *Stichopsora asterum* Dietel. As host plants, he listed *Callistephus chinensis* (L.) Nees, *Doellingeria scabra* (Thunb.) Nees (as *Aster scaber* Thunb.), *Aster tataricus* L.f., and *Kalimeris indica* (L.) Sch.Bip. (as *A. indicus* L.). Sydow and Sydow (1914) synonymized the genera by naming the species *Coleosporium asterum* (Dietel) Syd. & P. Syd. Finally, Cummins (1962) listed *C. solidaginis* as a synonym of *C. asterum* because *C. solidaginis* has been described only from uredinia. This approach was correct according to the

ITS1-5.8S-ITS2

Host families:

Apocynaceae
 Astereaceae
 Campanulaceae
 Convolvulaceae
 Lamiaceae
 Orobanchaceae
 Ranunculaceae
 Rutaceae

◀ **Fig. 2** Phylogenetic positions of *Coleosporium solidaginis* and *C. asterum* within the genus *Coleosporium*, based on ML analysis with RAXML v.7.2.6 recovered from ITS1–5.8S–ITS2 sequence data. The numbers at nodes indicate RAXML bootstrap support > 50%. Samples are given with species name, GenBank accession number (in parentheses) or voucher number, host plant, and origin (see also Table S1). Families of host plants are coded by color (see insert)

previous code of nomenclature (cf. McNeill et al. 2006). Consequently, authors (e.g., Klenke and Scholler 2015; Thite et al. 2016; Wang et al. 2017; Zhuang 1983, 2001; Index Fungorum 2017) called the *Coleosporium* rust on *Solidago* spp. *C. asterum*. According to the International Code of Nomenclature for algae, fungi and plants that has been in effect since 2011 (Melbourne Code, Article 59), the names of anamorphs and teleomorphs are to be “treated equally for the purposes of establishing priority, regardless of the life history stage of the type” (McNeill et al. 2012). *Uredo solidaginis* is the oldest valid description of the fungus and, consequently, the name *Coleosporium solidaginis* has priority. Additionally, our phylogenetic analyses show that *C. solidaginis* and *C. asterum* are not conspecific (see discussion below).

Consequently, the naming of the *Coleosporium* species on *Solidago* species is:

Coleosporium solidaginis (Schwein.) Thüm., Bull. Torrey Bot. Club 6: 216 (1878).

≡ *Uredo solidaginis* Schwein., Schr. naturf. Ges. Leipzig 1: 70 (1822) (basionym).

≡ *Stichopsora solidaginis* (Schwein.) Dietel, Hedwigia 42: 181 (1903)

= *Coleosporium asterum* s. auct., non (Dietel) Syd. & P. Syd., Ann. mycologici 12 (2): 109 (1914)

= *Peridermium acicola* Underw. & Earle, Bull. Torrey Bot. Club 23 (10): 400 (1896).

Coleosporium pini-asteris Orish. is a further species occurring on *Aster* and *Callistephus* species in Asia, but not on *Solidago* spp. (Kaneko 1981). *Coleosporium delicatulum* (Arthur & F. Kern) Hedgc. & Long is known from species of *Euthamia*, a genus closely related to *Solidago*, but it differs in the ornamentation of its urediniospores (Arthur 1962; Cummins 1978).

Phylogeny: biogeography versus host ranges

Our phylogenetic analyses of LSU data show that the *Solidago* rusts are split into two subclades (Fig. 1). Two *Coleosporium* samples from China occurring on the American *S. canadensis*, which is an invasive neophyte in China (Wang et al. 2017), form the sister group of the samples

on *S. gigantea*, *S. virgaurea*, and an unidentified *Solidago* species. In this context, it is conspicuous that, in one location, in the Blenio Valley, Ticino, Switzerland (Tables S2 and S3), *S. virgaurea* and *S. gigantea* were always infected, whereas the *S. canadensis* plants growing in close proximity to them were not. Also, in the remaining investigation areas, *Coleosporium* infection was not observed on *S. canadensis* prior to this study² (Brodbeck 2017; Table S3). This observation was surprising because the two introduced *Solidago* species are closely related and hybrids between them and hybrids of both species with *S. virgaurea* exist (Gudžinskas and Žalneravičius 2016; Pliszko and Zalewska-Gałosz 2016; Wagenitz 1979). Heath (1992) similarly described the host specificity of a *Coleosporium* strain obtained from *S. canadensis* based on infection experiments. Thus, it could be concluded that more than one *Coleosporium* species occurs on *Solidago* species.

The *Solidago* rusts are different from the *C. asterum* specimens on *Aster* s.l. species from Canada and South Korea (Figs. 1, 2, and S1). These results from molecular data support infection experiments conducted by Hedgecock and Hunt (1922). Also, Kaneko (1981) was not able to infect *Solidago virgaurea* var. *asiatica* Nakai with spores of *C. asterum* from *Aster* spp. and vice versa. Additionally, he described differences in telial and basidiospore morphology (Kaneko 1981). Dietel (1900) described *C. asterum* s. str. occurring on *Aster* s.l. from Japan, but *C. asterum* was also found on *Aster* s.l. in North America (Arthur 1962; Cummins 1978; Ginns 1986). Consequently, it remains unknown whether the American populations are conspecific with the Asian taxon. Five of six *C. asterum* samples used in our phylogenetic analyses were collected on *Eurybia macrophylla* (= *Aster macrophyllus*) and on *Symphytotrichum ciliolatum* (= *A. ciliolatus*) from Canada, as well as on *S. pilosum* (= *A. pilosus*), a species that was introduced from North America to South Korea (Table S1). Thus, they probably belong to the American *C. asterum* group. Sequencing Asian material—preferably from the type host of *C. asterum*, *Aster tataricus* (designated by Cummins 1978)—would be needed to barcode *C. asterum* s.str. This would be particularly important for a future revision of the *Coleosporium–solidaginis–asterum* complex in order to document species delimitation, host preferences, and distribution. Until then, the name “*Coleosporium asterum*” should only be used for specimens on *Aster* s.l., and “*Coleosporium solidaginis*” should be used for species on *Solidago* spp.

The *Coleosporium–solidaginis–asterum* complex belongs to a well-supported clade containing all species originally native to America (Fig. 1), including those (neomycete) specimens collected outside America (Table S1). Species native to Asia and Europe appear intermixed in the remaining clades. Two specimens of *C. senecionis* introduced in Australia (Walker and Priest 1984) and New Zealand (McKenzie 1998) appear in the European clade as well (Figs. 1 and 2, Table S1). The phylogenetic pattern within the genus follows the biogeographic

² The *S. canadensis* record from SW Germany by Klenke and Scholler (2015) was revised by one of the authors of the present study (M.S.) and was determined as *S. gigantea*.

distribution of the species rather than their host preferences. For example, species occurring on Asteraceae appear in different positions in the phylogenetic trees (Figs. 1 and 2). Thus, *C. solidaginis* and *C. asterum* are more closely related to species from America, which do not occur on Asteraceae, like the American *C. ipomoeae* on *Ipomea* spp. (Convolvulaceae) and *C. plumeriae* on *Plumeria* spp. (Apocynaceae) native to the Caribbean, than to Asian or European *Coleosporium* species on Asteraceae (Figs. 1 and 2). In conclusion, the relationship among the telial host plants is not always an indicator for the relationship within the genus *Coleosporium*. Therefore, we conclude that host jumps played a more important role than co-speciation in the evolution of *Coleosporium* species (cf. McTaggart et al. 2016). This particularly applies to the European *Coleosporium* species.

Most of the European species could not be distinguished in the present molecular analyses, even though they occur on different host families (Figs. 1, 2, S1, and S2). Neither the LSU nor the ITS sequences separate *C. cacaliae*, *C. campanulae*, *C. euphrasiae*, *C. melampyri*, *C. senecionis*, and *C. sonchi* from each other. These results are in contradiction to infection experiments that distinguished *C. euphrasiae* on *Euphrasia* and *Rhinanthus* spp. from *C. melampyri* on *Melampyrum* spp. (Gäumann 1959, and literature cited therein). Gäumann (1959) also split *C. campanulae* and *C. senecionis* into several *formae speciales* because of their preferences for specific *Campanula* and *Senecio* host species. Rusts from seven *Campanula* and four *Senecio* species were included in the present analyses, but the molecular data do not support a separation among them. In summary, the European *Coleosporium* spp., which occur on the distantly related families (orders) Asteraceae, Campanulaceae (both Asterales), and Orobanchaceae (Lamiales), are not distinguishable from each other using LSU and ITS sequence data. Indeed, the barcoding sequence of the ITS region cannot always discriminate among biologically well-separated species (e.g., Beenken et al. 2012; Schoch et al. 2012; Scholler et al. 2016). The morphological characteristics of these *Coleosporium* species are also uniform (Helfer 2013). Some authors, therefore, have questioned the species concept based mainly on telial host plant species (e.g., Gäumann 1959) and united all European species into one species, *C. tussilaginis*, with several host-specific *formae speciales* (f.sp.) (Boerema and Verhoeven 1972; Helfer 2013; Hylander et al. 1953; Majewski et al. 2008; Wilson and Henderson 1966; Index Fungorum 2017). However, the phylogenies presented in this study (Figs. 1, 2, S1, and S2) do not support this broad species concept in all cases. Four of the ten investigated European species were well separated (Figs. 1, 2, S1, and S2). *Coleosporium inulae*, which also differs morphologically from the other European species by the presence of a clearly thicker apical teliospore cell wall (e.g., Braun 1982), is well separated by its molecular phylogenetic position (Figs. 1, 2,

S1, and S2). The same applies to *C. pulsatillae* (Figs. 2 and S1). It is not resolved whether *C. tussilaginis* and *C. petasitis* are conspecific, because of the small differences in their sequences, but they are definitely not conspecific with other European species, from which they differ significantly in their ITS sequences (Figs. 2, S1, and S2). Thus, investigations of additional collections and further DNA regions with better resolution are needed to determine which European *Coleosporium* species are conspecific. In contrast, the Asian and American species are well separated from each other in all phylogenetic analyses (Figs. 1, 2, S1, and S2).

Distribution and spread

Coleosporium solidaginis is very common in North America and occurs on more than 50 *Solidago* spp. and several *Pinus* spp. native to this region (Arthur 1907, 1924, 1927, 1962; Farr and Rossman 2017; Ginns 1986; Hedgcock and Hunt 1922; Hunt 1926). The first reports of this rust species came from North Carolina (Schweinitz 1822), New Jersey, and New York (Thümen 1878). Outside of North America, *C. solidaginis* has been found only recently and often in association with introduced American *Solidago* species. Consequently, it can be assumed that *C. solidaginis* originated from North America (Hedgcock and Hunt 1922).

In East Asia, *C. solidaginis* (as *C. asterum*) was found in Japan on the indigenous *S. virgaurea* var. *asiatica* (Kaneko 1981), in South Korea on the indigenous *S. virgaurea* var. *gigantea* Nakai (Back et al. 2014), and in China, specifically in Jiangxi Province on *Solidago* sp. (Tai 1979), in Fujian Province on the indigenous *S. decurrens* Lour. (Zhuang 1983, 2001), and in Zhejiang Province on the introduced *S. canadensis* (Wang et al. 2017). In India, *C. solidaginis* was also found on *S. canadensis* (Thite et al. 2016). A finding of *C. solidaginis* on *S. virgaurea* in a pine forest in northeast Turkey is the observed occurrence located nearest to Europe (Bahecioglu and Kabaktepe 2012; Kabaktepe 2010). These recent reports of *C. solidaginis* in Asia suggest that the rust was also recently introduced to Asia and subsequently spread throughout that region. Because the rusts on *S. virgaurea* var. *gigantea* in South Korea and on *S. canadensis* in China belong to different subclades (Fig. 1), at least two introduction events in Asia may be postulated.

Menéndez and Rubio (2012)³ published and illustrated the first European record online as *C. asterum* on *S. virgaurea* from northern Spain, Asturias, near Lamuño, Cudillero, at the recreation area of Monte Valsera, observed in November 2007. The first report of *C. solidaginis* in Germany dates back to 2009

³ The record includes a photo of the infected plant and a photo of urediniospores viewed through a microscope. Therefore, we consider this a valid record and the first one from Europe, even though it was not published in a scientific journal.

(Klenke and Scholler 2015). It was collected from *S. gigantea* by P. Domes in Baden-Württemberg, Karlsruhe, close to the river Rhine (Table S2). Interestingly, the rust species was confirmed numerous times in the Upper Rhine Valley in Germany, but outside the valley, it could not be found, despite systematic searching. *Coleosporium solidaginis* was also observed on *S. gigantea* cultivated in the botanical garden of the University of Constance (Germany) in July 2016 (M. Tomowski, pers. communication). In Switzerland, the hot spot of infection of *S. virgaurea* and *S. gigantea* is in the Canton Ticino, where *C. solidaginis* was first found in 2012 (Brodtbeck 2017). North of the Alps, *C. solidaginis* seems to be scarcer and was found only in a few places close to the river Rhine and its tributary Töss in Switzerland (Table S2; Brodtbeck 2017). A continually updated distribution map for Switzerland is given by Senn-Irlet et al. (2017), and a worldwide map including the German records is located at the Global Biodiversity Information Facility (<http://www.gbif.org>).

Although potential host plants (*S. gigantea*, *S. virgaurea*) are widely distributed (Wagenitz 1979), the sudden appearance of *C. solidaginis* in Europe in places far away from each other raises the question as to the pathway of its introduction. One possibility is that *C. solidaginis* was introduced with living pine trees or goldenrods directly from North America or via Asia by human activities like plant trade (Palm and Rossman 2003). Alternatively, it may have been introduced through long-distance propagation by airborne spores (Brown and Hovmöller 2002; Kolmer 2005; Viljanen-Rollinson and Cromey 2002), possibly via Asia, with native as well as introduced *Solidago* and *Pinus* species as stepping stones. The current distribution of *C. solidaginis* in Europe may be the result of a combination of both mechanisms. For comparison, several other neomycetes have reached southern Switzerland via Italy (Beenken and Senn-Irlet 2016); for example, the North American powdery mildew of the plane tree, *Erysiphe platani* (Howe) U. Braun & S. Takam. (Beenken 2017) and, recently, *Favolaschia calocera* R. Heim (Spinelli 2016). Scholler et al. (2012) assumed that neomycetes enter Central Europe north of the Alps from the west via the Burgundian Gate (Belfort Gap). Examples of plant parasitic neomycetes that probably spread this way to Germany are the Australian Asteraceae rust *Puccinia lagenophorae* Cooke and the plane powdery mildew (Scholler et al. 2012). However, reports of *C. solidaginis* from the neighboring countries, such as Italy and France, are still lacking. Finally, knowledge of the distribution of *C. solidaginis* in Europe is quite limited and based mainly on accidental observations by a few rust specialists. Thus, it is difficult to determine when and where *C. solidaginis* first arrived in Europe.

Host shifts

It is widely accepted that host shifts or jumps of plant pathogenic fungi occur mainly between closely related plant species

(e.g., Bufford et al. 2016). Therefore, it was not surprising that *C. solidaginis* could infect the native *S. virgaurea*. When and where the host shift from an American *Solidago* species to the European *S. virgaurea* has happened is still not clear. This host shift could have already occurred in North America. Hunt (1926) listed two old records of *C. solidaginis* on introduced *S. virgaurea* plants from the New England states in the USA. Additional host shifts may have occurred in Asia, where *C. solidaginis* was found on introduced *Solidago* species, as well as on *S. virgaurea* (see above), or recently in Europe. Probably, the host shift to *S. virgaurea* has happened several times in several places.

A comparable host shift—but in the opposite direction—was verified by barcoding in the present study. *Coleosporium senecionis*, a native rust common on native *Senecio* spp., jumped to the invasive neophyte *Senecio inaequidens* from South Africa. Whereas the plant was introduced to Europe already at the end of the nineteenth century and became invasive in the second half of the twentieth century (Heger and Böhmer 2005; Weber 2013), the rust on *S. inaequidens* was first reported in Europe (Germany) in 2000 (Schmitz and Werner 2001). Nowadays, *C. senecionis* is quite common on *S. inaequidens* in Central Europe (e.g., Klenke and Scholler 2015). Interestingly, the European *C. senecionis* was also introduced to Australia and New Zealand (Fig. 1), where it occurs on introduced *Senecio* spp., as well as on native Asteraceae (Laundon 1978; McKenzie 1998; Walker and Priest 1984).

Life cycle

All collections of *C. solidaginis* investigated for the present study showed uredinia (Fig. 3a–d). Telia with basidia and basidiospores (Fig. 3e) were only found once, on *S. gigantea* in Switzerland (LB11178/ZT-Myc-58016), even though the rust fungi were mainly collected in the late autumn when telia are typically present (Tables S2 and S3). Like all other heteroecious *Coleosporium* species, *C. solidaginis* forms spermogonia and aecia on needles of *Pinus* spp., subgenus *Pinus* (Farr and Rossman 2017; Nicholls et al. 1968). Up to now, aecia, which were reported from North America as *Peridermium acicola* (Hedgcock and Hunt 1922), have not been documented in Europe, although a potential host, the native two-needle pine *Pinus sylvestris*, was observed at all locations where *C. solidaginis* was found. *Pinus sylvestris* was reported to be an aecial host of *C. solidaginis* (as *C. asterum*), even in Canada (Baranyay et al. 1962; Ziller 1974). Therefore, the infection of *P. sylvestris* and the formation of spermogonia and aecia on needles would be expected in Switzerland and Germany.

Telio- and basidiospores were reported only rarely in Central Europe, and, thus, *C. solidaginis* propagation in this region apparently occurs in most cases by asexual

Fig. 3 *Coleosporium solidaginis*: **a** flowering *Solidago virgaurea*, slightly infected by the rust fungus (Switzerland, Bellinzona, 31.08.2014); **b** rosette leaf of *S. virgaurea*, heavily affected by uredinia (Switzerland, Stadel, 13.11.2016); **c** urediniospore in face view; **d** urediniospore in optical section; **e** section through telium on *S. gigantea*, insert: basidiospore; (**c–e** from LB11178/ZT-Myc-58016)

urediniospores. Observations from North America (Mains 1916; Nicholls et al. 1968) and from Asia (Back et al. 2014) have demonstrated that *C. solidaginis* can overwinter without an aecial host, as urediniospores and mycelia on green leaves of *Solidago* plants, in mild winter climates where leaf rosettes can survive. In contrast, in our study, all leaves of *S. gigantea* and *S. virgaurea* died back and dried out during winter 2016/17 at all sites in Switzerland (Table S3). Thus, living mycelia and urediniospores were not observed on leaves in early spring. Clinton (1908), Mains (1916), and Nicholls et al. (1968) reported that mycelia of *C. solidaginis* were not perennial in the belowground organs of *Solidago* plants. However, it is possible that urediniospores survived in the leaf litter and soil and reinfected young leaves in spring, which would

explain why the rust occurred in several stands of *Solidago* spp. during five years of observations but disappeared at other locations (Table S3). Consequently, removing all infected aboveground parts of the plants in autumn may inhibit the reinfection of *Solidago* plants by *C. solidaginis* the next spring.

Impact

Some rust fungi are discussed as a biocontrol agent against invasive neophytes (e.g., Tanner et al. 2015). From that point of view, the reduction of the fitness of the invasive *S. gigantea* would be a positive effect of the *C. solidaginis* introduction. On the other hand, the indigenous *S. virgaurea* is potentially

threatened by this rust fungus. However, it is currently difficult to estimate the ecological and economic impact of *C. solidaginis* in Europe because little is known about its distribution and velocity of propagation. In the field, slightly infected plants of *S. virgaurea* (Fig. 3a) and *S. gigantea* flowered and produced seeds, but heavily infected plants of *S. virgaurea* were found to produce only sterile leaf rosettes (Fig. 3b). However, these field observations were not quantified. The presumed reduction of the fitness of host plants and the resulting impact of the alien pathogen on their competitiveness (Frantzen and Müller-Schärer 2006) need to be validated by experiments that quantify indicators of fitness, such as seed production per plant. In South Korea, Back et al. (2014) estimated that the productivity loss of the cultivated medicinal plant *S. virgaurea* var. *gigantea* due to rust disease is more than 10%. Similar loss rates could, therefore, be expected for cultures of *S. virgaurea* in Europe if *C. solidaginis* becomes more widespread. As a consequence, programs to control invasive *Solidago* species, which exist in several European countries (e.g., Weber 2013), should, as a preventive measure, emphasize areas where the native *S. virgaurea* occurs to protect it against *C. solidaginis* transmitted by non-native goldenrods. In cultures of goldenrods, the best phytosanitary treatment is to clean fields of all infected plant material (see above).

The powdery mildew *Golovinomyces asterum* var. *solidaginis* U. Braun, which is a North American neomycete as well (Beenken and Senn-Irlet 2016; Braun and Cook 2012; Klenke and Scholler 2015), was also found on all *Solidago* species in the present study, often associated with *C. solidaginis* on the same plant (Table S3). The extent to which the damage of the plants may be enhanced by such mixed infections is unknown. *Pinus sylvestris* is the second potential native host of *C. solidaginis* that could be affected. In North America, Ziller (1974) observed that the damage on pine needles by the aecial stage was mostly negligible, especially on older trees, but Mihail et al. (2002) observed a significant growth reduction of trees by infection with the pine needle rust *C. solidaginis* (as *C. asterum*).

In conclusion, *C. solidaginis* is a neomycete with origin in North America that has become established in several regions of Central Europe within a relatively short period and has the potential to spread across Europe and become invasive on indigenous plants.

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