



Golovinomyces inulae U. Braun & H.D. Shin is the causative agent of powdery mildew on *Telekia speciosa* L. in Germany

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Abstract

In central Europe, including Germany, *Telekia speciosa* (heart-leaved oxeye) is a synanthropic, non-native plant species commonly grown as an ornamental plant. A powdery mildew has recently been introduced on this host in Germany. This powdery mildew has previously been assigned to *Golovinomyces cichoracearum* (\equiv *Erysiphe cichoracearum*) sensu lato. Two German specimens of powdery mildew on *Telekia* have been sequenced and phylogenetically analysed. The analyses revealed that the German sequences obtained from the *Telekia* powdery mildew are identical with a sequence retrieved from *Golovinomyces inulae* on *Pentanema salicinum* (\equiv *Inula salicina*) collected in Switzerland. Furthermore, holotype material of *G. inulae*, described from Korea, has been sequenced, which confirmed *G. inulae* as causative agent of the *Telekia* powdery mildew. The current distribution of *G. inulae* in Germany is briefly discussed including a first report of this pathogen from Austria.

Keywords *Erysiphaceae* · Powdery mildew · *Golovinomyces* · Heart-leaved oxeye

Introduction

Telekia speciosa (Asteraceae) is an ornamental plant naturally distributed in south-east Europe, north-eastern Turkey and the Caucasus region, and it has also colonized Central Europe where it is considered a neophyte (Greuter 2006). There are previous records of powdery mildew on *T. speciosa*, referred to as *Erysiphe cichoracearum* (now *Golovinomyces cichoracearum*) s. lat., from its natural distribution area, including Armenia (Simonyan 1994), Bulgaria

(Fakirova 1991), Georgia (Amano 1986), Hungary (Amano 1986; Braun 1995), Romania (Sandu-Ville 1967; Eliade 1990), Slovakia (Paulech 1995), Ukraine (Heluta 1989), and the former Yugoslavia (Amano 1986; Braun 1995). A record from Estonia, listed in Amano (1986), is doubtful since *T. speciosa* is not cited as a host of *E. cichoracearum* for Estonia in Karis (1987). Bolay (2005) recorded *G. cichoracearum* on *T. speciosa* from Switzerland, Boyle et al. (2007) listed six German collections from Bavaria and Saxony, and Dietrich (2014) reported an additional location in Saxony. Since that time, the *T. speciosa* powdery mildew has quickly spread in southern parts of Germany. However, until the present manuscript the exact identification, proven by DNA analysis, of the causative agent of powdery mildew on *Telekia* from Germany is not yet clear. *G. cichoracearum* (\equiv *E. cichoracearum*) as circumscribed by previous authors, including Braun (1987, 1995) and Braun and Cook (2012), who used a narrower species concept for this taxon, was considered taxonomic “dust bin” which included a wide range of not closely allied powdery mildews. It was only until recently that Takamatsu et al. (2013) revealed through phylogenetic analyses that *G. cichoracearum* s. str., is confined to host species of the genera *Scorzonera* and *Tragopogon* (composite tribe *Cichorieae* subtribe *Scorzonerinae*). Bradshaw et al. (2022) epitypified *E. cichoracearum* with ex-epitypes sequences to provide an ex-type reference

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sequence for phylogenetic-taxonomic purposes. Included in their phylogenetic analyses was a sequence retrieved from a German sample of *Golovinomyces* sp. on *T. speciosa* which was identical genetically with a sequence obtained from *G. inulae* on *Pentanema salicinum* (\equiv *Inula salicina*) from Switzerland. However, the present publication aims at confirming the identity of the causative agent of this powdery mildew by sequencing the holotype of *G. inulae*, which was described on the basis type material from Korea. Additionally, the potential origin of this species and its current spread on *T. speciosa* in Germany is discussed.

Materials and methods

Morphological characterization

Morphological examinations were performed on the basis of specimens deposited at herbarium GLM and HAL (see collections examined). Most collections contained abundant mature chasmothecia, but the formation of the anamorph was already ceased. However, a few early collections with abundant formation of conidiophores and conidia allowed detailed examinations of the anamorph of this powdery mildew. Morphological characteristics covering size and shape of conidiophores, conidia, chasmothecia, including, peridial cells, appendages, asci and ascospores ($n = 30$), were assessed. Examinations and measurements were performed in distilled water, in the case of the anamorph mixed with aniline blue.

Molecular characterization

From specimen voucher HAL 2367 F (holotype), whole-cell DNA was extracted from infected leaves containing chasmothecia with the DNeasy plant mini kit (Qiagen, Germany), following the manufacturers recommendations. For the first PCR reaction, the primers AITS (Bradshaw & Tobin 2020)/TW14 were used followed by PM1 (Cunnington et al. 2003)/NLP2 (Mori et al. 2000). The reaction components were 2 μ l of total genomic DNA, 12.5 μ l MyFiTM Mix (Meridian Bioscience), 0.5 μ l each primer (10 μ M) and sterile ddH₂O up to a final volume of 25 μ l. PCR reactions included an initial predenaturation of 3 min at 94 °C, followed by 35 cycles of 30 s of denaturation at 94 °C, 45 s at 48 °C for annealing and 60 s at 72 °C for extension, and a final extension for 10 min at 72 °C. Amplicons were purified (ExoSAP-IT, Thermo Fisher Scientific) and sequenced in both directions (LGC Genomics GmbH, Germany) using the primers PM1/NLP2. Consensus sequences were generated and edited (CLC Main Workbench version 22.0.2, Qiagen Digital insights).

A phylogenetic tree was constructed from the ITS + 28S sequences.

Phylogeny

A phylogenetic tree was constructed from the ITS + LSU sequences of selected *Golovinomyces* spp. from Bradshaw et al. (2022) with *Golovinomyces echinopsis* and *Golovinomyces depressus* as outgroup taxa. Sequences were aligned and edited using MUSCLE in MEGA11: Molecular Evolutionary Genetics Analysis Version 11 (Tamura et al. 2021). A GTR + G + I evolutionary model was used for phylogenetic analyses as it is the most inclusive model of evolution and includes all other evolutionary models (Abadi et al. 2019). A fixed parameter-rich model (such as GTR + G + I) can be used in lieu of running a test to select the most suitable evolutionary model (Abadi et al. 2019). The phylogeny was inferred using Bayesian analysis of the ITS + LSU using a Yule tree prior (Gernhard 2008) and a strict molecular clock, in the program BEAST version 1.10.4 (Suchard et al. 2018). A single MCMC chain of 106 steps was run, with a burn-in of 10%. Posterior probabilities were calculated from the remaining 9,000 sampled trees. A maximum clade credibility tree was produced using TreeAnnotator version 1.10.4 (part of the BEAST package). Stationarity was confirmed by running the analysis multiple times, which revealed convergence between runs. The resulting tree was visualized using FigTree ver. 1.3.1 (Rambaut 2009). A maximum likelihood analysis was accomplished using raxmlGUI (Silvestro and Michalak 2012) under the default settings with a GTR + G + I evolutionary model. Bootstrap analyses were conducted using 1000 replications (Felsenstein 1985).

Results

Phylogeny

Owing to a preliminary result of a phylogenetic analysis of ITS + 28S sequences, published by Bradshaw et al. (2022), two German sequences currently generated from *Golovinomyces* sp. on *Telekia speciosa*, a sequence of *G. inulae* from Switzerland and a newly retrieved ex-holotype sequence, were included in a new phylogenetic analysis. All sequences cluster together in a well-supported species clade (Fig. 1), which confirms *G. inulae* as causative agent of the *T. speciosa* powdery mildew.

Taxonomy, morphology and distribution of *Golovinomyces inulae* on *Telekia speciosa*

Golovinomyces inulae U. Braun and H.D. Shin, in Braun and Cook, CBS Biodiversity Series 11: 317. 2012.

Fig. 1 Bayesian maximum clade credibility tree of the ITS + 28S sequences of selected *Golovinomyces* taxa, including *G. inulae*. Posterior probabilities ≥ 0.90 are displayed followed by bootstrap values greater than 70% for the maximum likelihood (ML) analyses conducted. ET = ex-epitype; HT = ex-holotype; IT = ex-isotype; PT = ex-paratype; RS = reference sequence. Taxa in bold were sequenced for the current study

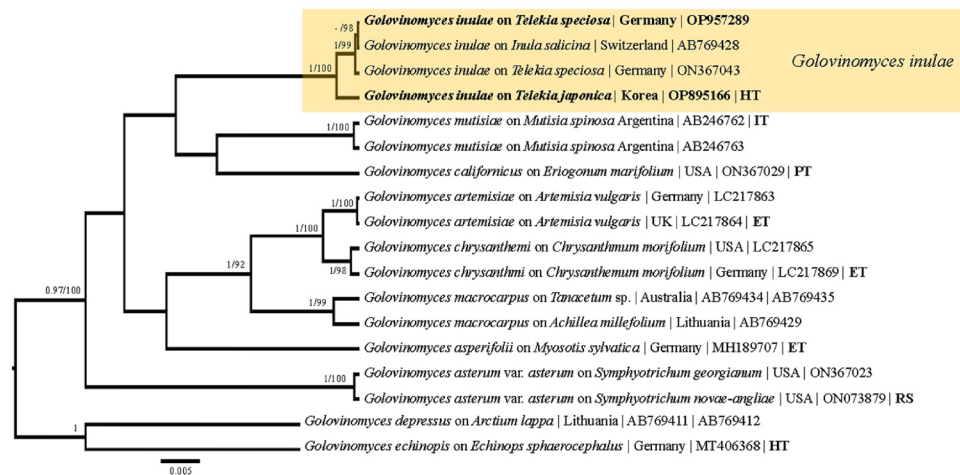


Illustration: Braun and Cook (2012; 318, Fig. 343).

Holotype: Korea, Suwon, on *Inula japonica* (= *I. britannica* var. *chinensis*), 21 Oct. 2009, H.D. Shin & M.J. Park (HAL 2367 F). Isotype: KUS-F 24,783. Ex-holotype sequence: OP895166.

Description based on collections of *G. inulae* on *Telekia speciosa*: Mycelium on leaves, amphigenous, but mainly epiphyllous, forming white to greyish white patches of variable shape and size, confluent, or effuse, finally covering almost the entire leaf surface, persistent (Fig. 2). Hyphae branched, septate, colourless, thin-walled, smooth, hyphal cells usually 40–70 μm long and 2–9 μm wide. Hyphal appressoria indistinct to nipple-shaped. Anamorph only formed in early developmental stages in June and early summer, formation immediately ceasing with the development of chasmothecium initials in July and thereafter. Conidiophores arising from superficial hyphae, on the upper surface, erect, straight, 90–160 μm long (without conidia), foot-cells cylindrical, rarely slightly curved or sinuous, 30–90 \times (8–)9–13(–15) μm , followed by 1–3 shorter cells, 12–32 μm long, basal septum at the junction with the supporting hypha, occasionally slightly elevated, 5–12 μm . Conidia catenescence, cylindrical, broad ellipsoid-doliiform to limoniform, 28–40 \times 12–18 μm , germ tubes perihilar to terminal, short to moderately long, aseptate, with a terminal swollen appressorium. Chasmothecia scattered to gregarious, subglobose, 87–145 μm diam.; peridial cells irregularly shaped, walls curved-sinuuous, 5–25 μm diam.; appendages in the lower half, mycelioid, unbranched, 0.5–1.5 times as long as the chasmothecial diam., at first colourless, later shorter ones brown throughout or brown below and paler towards the tip when longer, 3–9 μm wide, septate, thin-walled, smooth to rough-walled; asci 4–12 per chasmothecium, broad obovoid to saccate, 50–65 \times 30–40 μm , thin-walled, to 1 μm , terminal oculus not very conspicuous, subsessile to short-stalked,

2-spored; ascospores ellipsoid-ovoid, 15–25 \times 12–16 μm , colourless.

Austrian collection of *G. inulae* on *T. speciosa*: Kärnten, Bezirk Völkermarkt, Völkermarkt, northwest of Sittersdorf, Müllnern, Goritschach, wooden bridge, 13 Jul. 2015, J. Kruse (GLM-F130659).

German collections of *G. inulae* on *T. speciosa*: Bayern, Landkreis Garmisch-Partenkirchen, Isar floodplain to the south of Mittenwald, 11°15'E; 47°24'N, alt. 900 m, 22 July 2004, W. Dietrich (GLM-F078504 and Herb. W. Dietrich); Landkreis Coburg, Weitramsdorf, Ortsteil Weidach, Weidacher Forst, 24 Sep. 2015, A. Ulmer (herb. Ulmer); Landkreis Weilheim-Schongau, Bernried, Klosterhof, 9 Sep. 2016, J. Kruse (GLM-F130803); Regierungsbezirk Oberfranken, Coburg, Schloß Callenberg, 17 June 2017, J. Kruse (herb. Kruse); Regierungsbezirk Oberfranken, Coburg, Beiersdorf, 6 Oct. 2018, J. Götze (herb. Götze); Landkreis Pfaffenhofen, Wolnzach, Ortsteil Burgstall, 24 Oct. 2018, H. Ostrow (herb. Ostrow). Mecklenburg-Vorpommern, Landkreises Vorpommern-Rügen, Zingst, 20 Jul. 2020, F. Dämmrich (herb. Dämmrich). Nordrheinwestfalen, Hochsauerlandkreis, Brilon, Kurpark, 14 Aug. 2022, B. Sothmann (herb. Sothmann). Sachsen, Landkreis Sächsische Schweiz-Osterzgebirge, Rathen, Ortsteil Oberrathen, verge of a meadow adjacent to the river Elbe, 14°04'24"E; 50°57'31" N, alt. 125 m, 1 July 2006, S. Hoeflich (GLM-F074699); Erzgebirgskreis, Pockau-Lengefeld, road embankment at a lime quarry southwest of Lengefeld, 13°10'25"E; 50°42'03"N, alt. 625 m, 11 Jul. 2006, S. Brautigam (GLM-F074731); *ibid.*, 14 June 2009, H. Jage (GLM-F097207); Landkreis Sächsische Schweiz-Osterzgebirge, Altenberg, Ortsteil Schellerhau, verge of a road near the Botanical Garden, 13°42' E; 50°46'N, alt. 760 m, 16 August 2006, W. Dietrich (GLM-F078503, herb. W. Dietrich); Landkreis Bautzen, Kuppritz, Kuppritzer Park, 14°35'14"E; 51°09'07"N, alt. 240 m, 12 Sep. 2006, H. Boyle (GLM-F074972); *ibid.*,

Fig. 2 *Golovinomyces inulae* on *Telekia speciosa*. **A–E.** Macroscopic signs of infection, **A–B.** *Telekia speciosa* showing signs of powdery mildew, **C.** Mycelium on the leaf surface, **D–E.** Chasmothecia on the upper **D** and lower **E** leaf surfaces, **F–G.** Light microscope images of chasmothecia with asci. — Scale bars = 50 μ m



5 Nov. 2009, H. Boyle (GLM-F099588); Erzgebirgskreis, Schneeberg, path along the banks of the Filzteich pond, 12°36'48"E; 50°30'29"N, alt. 545 m, 30 Sep. 2006 S. Hoeflich (GLM-F078408); Landkreis Sächsische Schweiz-Osterzgebirge, Altenberg, Waldidyll, 7 Aug. 2007, H.J. Hardtke (herb. Hardtke); Landkreis Görlitz, Löbau, Äußere Bautzener Straße, 14 Jul. 2008, H. Boyle and S. Hoeflich (GLM-F090925); Landkreis Mittelsachsen, Augustusburg, Waldstraße, 25 Sep. 2009, H. Boyle (GLM-F099761); Landkreis Görlitz, Königshain, Schloßpark, Alpinum, 5 Nov. 2009, H. Boyle (GLM-F099580); Erzgebirgskreis, Oberwiesenthal, 18 Sep. 2012, W. Dietrich (herb. Dietrich, see also Dietrich

2014); Landkreis Sächsische Schweiz-Osterzgebirge, Altenberg, Ortsteil Fürstenwalde, Höllmühler-/Oberer Weg, 29 Jul. 2017, St. Zinke (herb. Zinke); Pirna, Mockethal, 8 Jul. 2016 and 1 June 2018, H. Wawrok (herb. Wawrok); Landkreis Sächsische Schweiz-Osterzgebirge, Bad Gottleuba, 26 Sep. 2019, H. Wawrok (herb. Wawrok); Landkreis Sächsische Schweiz-Osterzgebirge, Wehlen, Bastei, 1 Sep. 2019, F. Dämmrich (herb. Dämmrich); Landkreis Sächsische Schweiz-Osterzgebirge, Wehlen, Steinrücken Weg to Bastei, Steinerner Tisch, 19 Oct. 2020 (herb. Kruse/POLL 10,003, sequence – OP957289); Voglandkreis, Jägerswalde, between Lottengrün, Tirpsdorf and Bergen, 9 Oct. 2021, B. Gerischer

(HAL 3462 F), Dresden, Zoo, 3 Aug. 2022, J. Kruse and Roland (herb. Kruse/POLL 10,004). Sachsen-Anhalt, Burgenlandkreis, Bad Bibra, Steinburg, Park of the Castle, 31 Jul. 2021, U. Richter (HAL 3445 F, sequence – ON367043); *ibid.*, 8 Aug. 2021, U. Richter (herb. Richter); *ibid.*, 24 Jul. 2022, U. Richter (herb. Richter); *ibid.*, 21 Aug. 2022, U. Richter (herb. Richter).

Discussion

Powdery mildew on *Telekia speciosa* has previously been referred to as *Golovinomyces (Erysiphe) cichoracearum* (s. lat.). The latter species is nowadays confined to hosts of the genera *Scorzonera* and *Tragopogon* [Asteraceae tribe Cichorieae subtribe Scorzonerinae] (Takamatsu et al. 2013), and as such, the identity of the causative agent of *Golovinomyces* on heart-leaved oxeye was unclear. The present phylogenetic analyses revealed that this powdery mildew is caused by *G. inulae*, which has been confirmed by the inclusion of ex-holotype sequences obtained from the Korean holotype of this species. This result is expected as the genus *Telekia* pertains to the composite tribe *Inuleae*, in which it is phylogenetically very closely allied to *Inula* s. str. as currently circumscribed (Gutiérrez-Larruscain et al. 2018). Previously, the inclusion of *Telekia speciosa* into *Inula*, as *Inula telekia*, was proposed (see Krause 1905). However, further genetic examinations are necessary, above all in Asia. The ex-holotype sequence is ~99.5% similar to the sequences retrieved from European samples which are all identical to each other. This genetic difference might be explainable by the different host species and/or the different geographical origin of the collections. However, because the hosts all belong in the tribe *Inuleae*, and the powdery mildew from the Korean type specimen and from the European collections are nearly identical morphologically (see Braun and Cook (2012; 318, Fig. 343), we are, for the interim, in favour of a single species, *Golovinomyces inulae*.

There are previous records of *Golovinomyces (Erysiphe) cichoracearum* (s. lat.) from the native distribution zone of *T. speciosa*, including the Caucasus region and Eastern Europe, suggesting that *G. inulae* is widespread in the natural range of this host. Recently, *G. inulae* on *T. speciosa* has been found in Germany, i.e. from Bavaria in 2004 and Saxony in 2006 (Boyle et al. 2007). Since that time, powdery mildew on *Telekia* has become widespread in Germany, above all in Bavaria and Saxony. In these regions in the south of Germany, *G. inulae* occurs in natural synanthropic populations, but also on cultivated heart-leaved oxeyes in gardens and parks. A few collections have been made in other German regions, including Mecklenburg-Western Pomerania, North Rhine-Westphalia and Saxony-Anhalt (in all cases only on

cultivated *T. speciosa*). Besides Germany, the heart-leaved oxeye powdery mildew has also been detected in Austria.

G. inulae is widespread in the norther hemisphere (Asia, Caucasus, Europe, North America) on a wide range of *Inula* spp. and on *Pulicaria dysenterica* (Braun and Cook 2012). However, there are still open questions. Up to this point, there have been only a few phylogenetic examinations. Sequence analyses based on North American specimens are not yet available, and the identity of *Golovinomyces* on *Pulicaria dysenterica* is still unconfirmed.

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