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RESEARCH ARTICLE

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Taxonomy of the *Golovinomyces cynoglossi* Complex (*Erysiphales, Ascomycota*) Disentangled by Phylogenetic Analyses and Reassessments of Morphological Traits

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ABSTRACT

The name *Golovinomyces cynoglossi s. lat.* is traditionally applied to a complex of morphologically similar powdery mildews on hosts of the plant family *Boraginaceae*. The current species-level taxonomy within this complex is ambiguous due to the lack of phylogenetic examinations. The present study applied phylogenetic methods to clarify the taxonomy of *G. cynoglossi s. lat.* Phylogenetic analysis of rDNA ITS sequences retrieved from Asian, European and North American specimens revealed that *G. cynoglossi s. lat.* collections from different hosts involved several species in five clearly separated lineages. Clade I consists primarily of *Golovinomyces cynoglossi s. str.* on *Cynoglossum*. Clade III consists of *Golovinomyces* sequences retrieved from the host genera *Symphytum* and *Pulmonaria*. The taxa within clade III are now assigned to *G. asperifoliorum* comb. nov. Clade V encompasses *G. cynoglossi s. lat.* on the host genera *Bothriospermum*, *Buglossoides*, *Echium*, *Myosotis*, and *Trigonotis*. The taxa within clade V are now assigned to *G. asperifolii* comb. nov. The species concerned in this study were lecto- and epitypified to stabilize their nomenclature.

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1. Introduction

Boraginaceae is a large angiosperm family encompassing around 2740 species in 148 to 156 genera, depending on the recognized generic concept. The highest diversity within this prominent plant family resides in the Mediterranean region, Central Asia, the Near East, and Pacific North America (http://www.spektrum.de/lexikon/biologie-kompakt/boraginaceae/1818; http://data.kew.org/cgi-bin/vpfg1992/genlist.pl?BORAGINACEAE). Numerous boraginaceous species are vulnerable to powdery mildew infections [1,2], from species in the genera *Erysiphe*, *Golovinomyces*, *Leveillula*, and *Phyllactinia*. Powdery mildew infections from the genus *Golovinomyces* on *Boraginaceae* have been traditionally attributed to a single widespread species, *G. cynoglossi* [2]. Thus, *G. cynoglossi* is known to exhibit a wide host range of 31 genera belonging to the subfamilies *Boraginoideae* and *Cordioideae* [2,3]. Although comprehensive inoculation tests with powdery mildew on *Boraginaceae* [4] revealed a high degree of biological specialization, the taxonomic unity and status as a single species have not yet been evaluated. Recent molecular phylogenetic analyses of *Golovinomyces* spp. including *G. cynoglossi s. lat.* casted doubts on the monophyly of this species. Takamatsu et al. [5] found that a sequence of *Golovinomyces* on *Myosotis* sp. (VPRI20429, Australia) did not cluster with other sequences of *G. cynoglossi*. The morphology of *Golovinomyces* sp. on *Bothriospermum tenellum* and *Trigonotis peduncularis* collected in Korea was recently examined and revealed minimal differences with *G. cynoglossi* on other hosts. *T. peduncularis* has been reported as a host of *G. cynoglossi* in China, Japan, and Korea [1, 6, 7] and *B. tenellum* has been reported as a host in Japan [1]. Recently, Meeboon and Takamatsu [8] identified the powdery mildew on *T. peduncularis* as *Euoidium* sp., due to the lack of the sexual morph. In Korea, asexual and sexual morphs of powdery mildew were first reported on *T. peduncularis* in 1989 and on *B. tenellum* in 1999. The initial point of these examinations was to conduct phylogenetic analyses on collections of *G. cynoglossi s. lat.* and its synonyms on a wide range of hosts and from Europe (the origin of the type localities). The main objectives of these examinations were to (1) clarify the species concept of *G. cynoglossi*, i.e., to determine whether this species represents a single taxon or a complex of cryptic species, (2) to identify

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Table 1. List of herbarium specimens of powdery mildew fungi used for nucleotide sequence analysis in this study.

Host plant	Location and year of collection	Herbarium specimen no.	GenBank accession no.
Borageineae			
Pulmonaria officinalis	Sachsen, Germany; 2010	GLM-F100040	MH189691
Symphytum officinale	Vladivostok, Russia; 2015	KUS-F28744	MH189692
S. officinale	Sachsen, Germany; 2004	GLM-F073207	MH189693
S. officinale	Sachsen, Germany; 2006	GLM-F079060	MH189694
Cynoglosseae			
Asperugo procumbens	Sachsen, Germany; 2001	GLM-F056808	MH189695
Bothriospermum tenellum	Seoul, Korea; 1999	KUS-F15866	MH189696
B. tenellum	Seoul, Korea; 2010	KUS-F24884	MH189697
B. tenellum	Namyangju, Korea; 2016	KUS-F29208	MH189698
B. tenellum	Osan, Korea; 2007	KUS-F22651	MH189699
Cynoglossum officinale	Sachsen-Anhalt, Germany; 2005	GLM-F075252	MH189700
C. officinale	Nordrhein-Westfalen, Germany; 1999	GLM-F047442	MH189701
C. officinale	Glenwood, Washington, USA; 2017	KUS-F30414	MH189702
C. officinale	Missoula, Montana, USA; 2010	WSP71856	MH189703
Myosotis arvensis	Sachsen, Germany; 2007	GLM-F079306	MH189704
M. arvensis	Sachsen, Germany; 2007	GLM-F079292	MH189705
Myosotis sylvatica	Sachsen, Germany; 2007	GLM-F079458	MH189706
M. sylvatica	Sachsen, Germany; 2007	GLM-F079322	MH189707
Trigonotis peduncularis	Seoul, Korea; 2016	KUS-F29281	MH189708
T. peduncularis	Gapyeong, Korea; 2016	KUS-F29517	MH189709
T. peduncularis	Seoul, Korea; 2016	KUS-F29189	MH189710
T. peduncularis	Seoul, Korea; 2008	KUS-F23263	MH189711
T. peduncularis	Namyangju, Korea; 2016	KUS-F29206	MH189712
Lithospermeae			
Buglossoides arvensis	Sachsen-Anhalt, Germany; 2005	GLM-F073217	MH189713
B. arvensis	Saxony, Germany; 2007	GLM-F079145	MH189714
Cerinthe minor	Sachsen-Anhalt, Germany; 2000	GLM-F093819	MH189715
Echium vulgare	Rheinland-Pfalz, Germany; 2005	GLM-F070123	MH189716
E. vulgare	Sachsen, Germany; 2006	GLM-F070465	MH189717

GLM: Senckenberg Gesellschaft für Naturforschung: Senckenberg Museum für Naturkunde Görlitz, Görlitz, Germany; KUS: Korea University, Seoul, Korea; WSP: Washington State University, Pullman, Washington, USA.

the powdery mildews on *Trigonotis* and *Bothriospermum* in Korea, and (3) to elucidate parasite–host relationships and the co-evolutionary aspects of *Golovinomyces* and its hosts.

2. Materials and methods

2.1. Molecular analyses

Genomic DNA was extracted using Chelex 100 resin (Bio-Rad Laboratories, Hercules, CA) as described by Hirata et al. [9]. The internal transcribed spacer (ITS) regions were amplified with the primers PMITS1/PMITS2 [10]. The PCR products were sequenced with the same primers by Macrogen, a sequencing service company in Seoul, Korea. The sequences were edited by DNASTAR Lasergene software package 7.0 (DNASTAR, Madison, WI). New sequences obtained from the present study were deposited in GenBank under the accession numbers MH189691–189717 (Table 1). These sequences were aligned with the reference sequences of *Golovinomyces* species used in Takamatsu et al. [5] by MUSCLE implemented in MEGA 7.0 [11]. Phylogenetic trees were constructed by neighbor joining (NJ) and maximum likelihood (ML) methods in MEGA 7.0, and evaluated with 1000 bootstrap (BS) values [12]. All positions containing gaps and missing data were eliminated.

2.2. Morphology

In order to take micrographs, fresh samples were mounted in sterile water, and dried specimens in lactic acid [13]. Measurements of asexual and sexual structures were performed by means of an Olympus BX51 microscope (Olympus, Tokyo, Japan) under bright-field. Micrographs were acquired using a Zeiss AX10 microscope equipped with an AxioCam MRc5 camera (Carl Zeiss, Göttingen, Germany) under differential-interference contrast microscopy. Each structure was measured at least 30 times at magnifications of 400× and 1000×.

3. Results

3.1. Phylogenetic analyses

In total, 27 ITS sequences were analyzed in this study (Table 1). Each sequence was aligned with 25 *Golovinomyces* sequences. A sequence of *Arthrocladiella mougeotii* was retrieved from GenBank and used as outgroup according to Takamatsu et al. [5]. Two trees constructed by NJ and ML methods were consistent with each other, except for minor branch orders and branch lengths. The NJ tree with BS values higher than 50% is shown in Figure 6. In the phylogenetic trees, the *G. cynoglossi* complex is separated into five distinct clades. Clade I consists of four sequences, including three powdery mildew collections on *Cynoglossum* from Germany and Japan, and an

Figure 1. *Golovinomyces cynoglossi s. str.* examined from GLM-F047442 ex *Cynoglossum officinale*. (A–E) Conidiophores. (F–K) Conidia. (L–M) Primary conidia. (N–O) Conidia in germination. (P) Appressorium. (Q) Surface of a conidium. Scale bar =100 µm for A–D, 30 µm for E–O, and 10 µm for P–Q.

Australian specimen on *Myosotis*. However, it should be noted that the BS value of this clade is low. Clade III is composed of sequences of five specimens on *Pulmonaria* and *Symphytum* and is supported with a high BS value (BS =94). Clade II and IV contain only a single sequence originated from *Asperugo* and *Cerinthe*, respectively. Clade V encompasses 21 samples from *Bothriospermum*, *Buglossoides*, *Cynoglossum*, *Echium*, *Myosotis*, and *Trigonotis*, and is highly supported with a BS value of 100.

3.2. Taxonomy

The phylogenetic and morphological analyses reveal that powdery mildew collections on *Cynoglossum* within clade I represent *G. cynoglossi s. str.*, whereas *G. cynoglossi s. lat.* on *Pulmonaria* and *Symphytum* (clade III) constitutes a species of its own for which the name *G. asperifoliorum* comb. nov., based on *Erysiphe asperifoliorum*, is introduced. Powdery mildews on the genera *Bothriospermum*, *Buglossoides*, *Cynoglossum* [only in the USA, i.e., outside the natural range], *Echium*, *Myosotis*, and *Trigonotis* within clade V represent an additional species of *Golovinomyces* that occurs on a wider range of boraginaceous plants. *Myosotis* species are common hosts of this taxon in Europe for which the name *G. asperifolii* comb. nov., based on *Oidium asperifolii*, is introduced. Identification and application of *G. cynoglossi*, *G. asperifoliorum*, and *G. asperifolii* by means of phylogenetic methods are supported by epitypifications and ex-epitype reference sequences.

It is too early to settle the identification and taxonomic status of the single specimens of *Asperugo* and *Cerinthe* in clades II and IV. Broader sampling is needed to clarify the taxonomy of these clades.

The three species constituting the former *G. cynoglossi* complex are characterized as follows:

Golovinomyces cynoglossi (Wallr.) Heluta, Ukrayins'k. Bot. Zhurn. 45(5): 62, 1988, *emend.* (*s. str.*) (Figure 1)

Figure 2. *Golovinomyces asperifoliorum* examined from GLM-F079060 ex *Symphytum officinale*. (A–E) Conidiophores. (F–K) Conidia. (L–M) Primary conidia. (N) Conidium in germination. (O) Surface of a conidium. (P) Appressorium. Scale bar =20 µm for A–E and 10 µm for F–P.

≡*Alphitomorpha cynoglossi* Wallr., Ann. Wetterauischen Ges. Gesammte Naturk., N. F., 4: 240, 1819.
≡*Erysiphe cynoglossi* (Wallr.) U. Braun, Mycotaxon 15: 136, 1982.
=*Erysiphe horridula* var. *cynoglossi* Sorok., Rev. Mycol. 11: 147, 1889.
=*Erysiphe horridula* f. sp. *cynoglossi* S. Blumer, Jahrb. Philos. Fakult. II, Univ. Bern 2: 30, 1922.
=*Erysiphe horridula* f. sp. *cynoglossi* S. Blumer, Centralbl. Bakteriol., 2. Abth., 55: 291, 1922.

Illustrations: Braun and Cook (2002: 311, fig. 333, upper chasmothecium with short appendages) [2], Chen et al. (1987: 80, Figure 27) [14].

Mycelium amphigenous, on stems and sepals, dense, forming irregular white patches or effuse; hyphae hyaline, thin-walled, smooth, 4–7 µm wide; hyphal appressoria nipple-shaped, 4–8 µm diam; conidiophores erect, arising from the upper surface of hyphal mother cells and always towards one end of the cell, i.e., not centrally positioned, 130–250 µm long, foot-cells straight, cylindrical, subcylindrical or slightly increasing in width from base to top, 55–200 × 9–15 µm, basal septum of the foot-cell raised above the junction with the hyphal mother cell, 5–25 µm, rarely directly at the branching point, followed by 1–3 shorter cells, forming catenescent conidia; conidia ellipsoid-ovoid to doliiform, 25–40 × 15–20 µm, length/width ratio 1.4–2.0; primary conidia apically rounded and basally subtruncate; germ tubes perihilar, short, apex with somewhat swollen appressorium (*Euoidium* type). Chasmothecia amphigenous, scattered to gregarious, often immersed in mycelial patches, 85–150 µm diam; peridium cells rounded, irregular to daedaleoid in shape, (5–)10–25(–30) µm diam; appendages usually numerous, equatorially arising and in the lower half, mycelioid, usually unbranched, 0.5–1.5(–2) times as long as the chasmothecial diam (gregarious chasmothecia immersed in dense mycelial patches often with very short appendages),

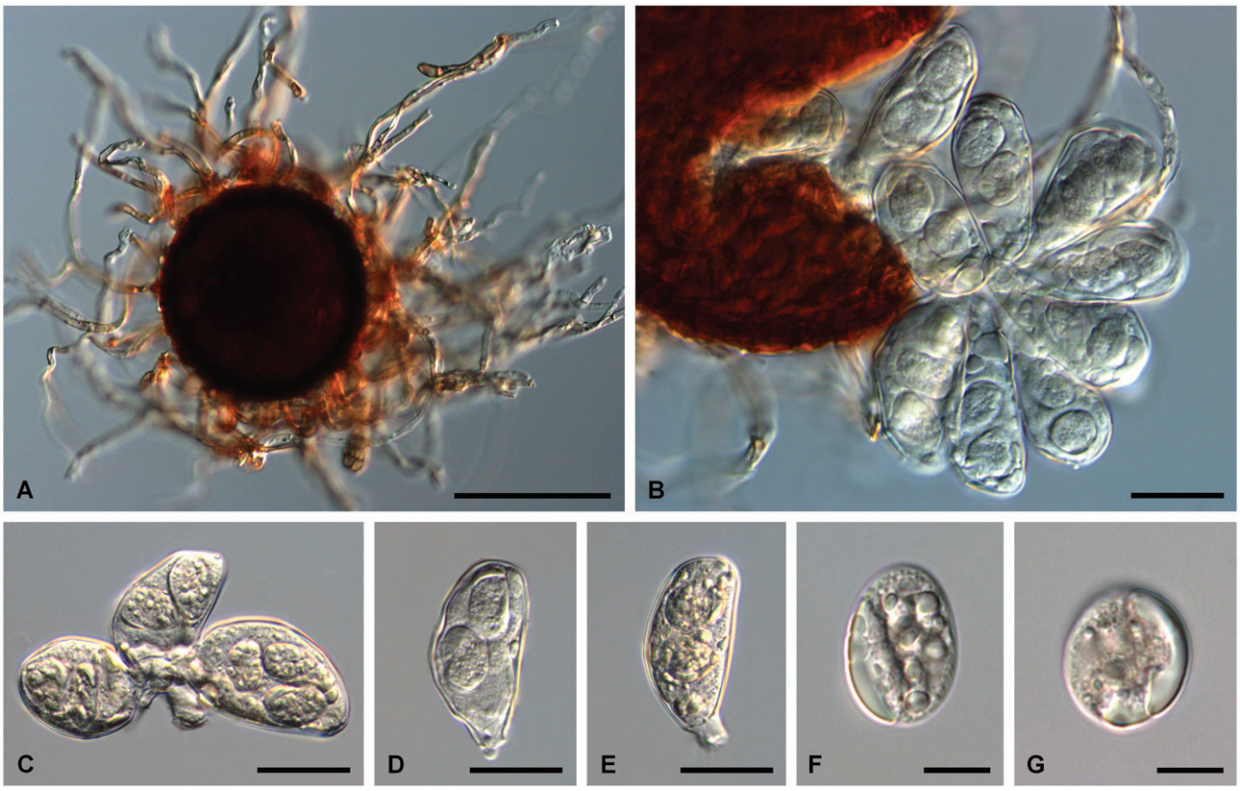

Figure 3. *Golovinomyces asperifoliorum* examined from GLM-F079060 ex *Symphytum officinale*. (A) Chasmothecium with mycelioid appendages. (B) Cluster of asci containing 2 ascospores each. (C–E) Asci containing 2 or 3 ascospores. (F–G) Ascospores. Scale bar =100 µm for A, 30 µm for B–E, and 10 µm for F–G.

3.5–8 µm wide, at first hyaline, subhyaline to yellowish, later pale to medium brown throughout or paler towards the tip, septate, wall thin, 1–1.5(–2) µm, smooth or almost so; asci 8–16, subglobose-ovoid, saccate to clavate, stalked, 45–75 × 25–40 µm, apex rounded to frequently subtruncate, wall thin, 1–1.5(–2) µm, terminal oculus not very conspicuous, 8–18 µm wide, 2-spored, rarely with 3 spores; ascospores broad ellipsoid-ovoid, 15–24 × 10–15 µm, colorless.

Lectotype (designated in Braun and Cook 2012): Germany, on *Cynoglossum officinale*, herb. Wallroth, without any further data (STR). **Epitype** (designated here, MycoBank, MBT381246): Germany, Nordrhein-Westfalen, Kreis Soest, Erwitte, near Eikeloh, on *Cynoglossum officinale*, October 16 1999, U. Raabe (GLM-F047442).

Additional specimens examined: On *Cynoglossum officinale* – Armenia, Megrinskij Rajon, 2300–2600 m alt., July 15 1958, M. Manukyan & R. Bagalyan (HAL 870 F). Germany, Sachsen-Anhalt, Halle (Saale), September 1976, U. Braun (HAL 882 F), Halle (Saale), Dölauer Heide, Heidesee, November 4 1977, U. Braun (HAL 883 F), Merseburg, Buna stockpile, August 9 1978, S. Klotz (HAL 878 F), Saalekreis, Niemberg, October 18 2005, H. Jage 3223/05 (GLM-F075252). Russia, Bashkortostan, 10 km west of Starye Bogdaly, July 17 1977, U. Braun (HAL 881 F). On *Cynoglossum* sp. – China, Xingjian Uyghur Autonomous Region, July 3 1959, H.-Y. Liu & R. Liu 674 (HAL 871 F).

Golovinomyces asperifoliorum (Grev.) U. Braun & H.D. Shin, **comb. nov.** (Figures 2 and 3)

Basionym: *Erysiphe asperifoliorum* Grev., Fl. Edin.: 461, 1824.

MycoBank, MB 824901

=*Erysiphe horridula* f. sp. *pulmonariae* S. Blumer, Jahrb. Philos. Fakult. II, Univ. Bern 2: 30, 1922.

=*Erysiphe horridula* f. sp. *symphyti* S. Blumer (l.c.).

=*Erysiphe horridula* f. sp. *pulmonariae* S. Blumer, Centralbl. Bakteriol., 2. Abth., 55: 491, 1922.

=*E. horridula* f. sp. *symphyti* S. Blumer (l.c.: 490).

Illustration: Braun and Cook (2002: 311, Figure 333, lower chasmothecium and asexual morph) [2].

Mycelium amphigenous, on stems and sepals, dense, forming regular or irregular white patches, effuse; hyphae hyaline, thin-walled, smooth, 3.5–7 µm wide; hyphal appressoria nipple-shaped, 4–7 µm diam; conidiophores erect, arising from the upper surface of hyphal mother cells, always towards one end of the cell, i.e., not centrally positioned, 80–165 µm long; foot-cells straight, cylindrical or subcylindrical, 40–120 × 8–14 µm, basal septum of foot-cell at the junctions with the mother cells or only slightly raised, 2.5–5 µm, foot-cell followed by 1–3 shorter cells, forming catenescent conidia;

Figure 4. *Golovinomyces asperifolii* examined from GLM-F79292 ex *Myosotis arvensis*. (A–H) Conidiophores. (I) Surface of a conidium. (J) Appressorium. (K–Q) Conidia. (R–T) Primary conidia. (U–X) Conidia in germination. Scale bar =30 µm for A–H, 10 µm for I–T, and 30 µm for U–X.

conidia ovoid-oblong to doliiform, 27–40 × 15–20 µm, length/width ratio 1.5–2.3, primary conidia apically rounded and sub-truncate at the base; germ tubes perihilar, short, apex with somewhat swollen appressorium (*Euoidium* type). Chasmothecia gregarious or somewhat scattered, often densely aggregated and immersed in the mycelial felt, forming brown patches composed of ascomata, appendages and hyphae that may become pigmented with age, sub-globose, 70–145 µm diam; peridium cells polygonal to daedaleoid, 8–25 µm diam; appendages equatorial and in the lower half of the chasmothecia, numerous, mycelioid, simple, interlaced with each other and with the mycelium, 0.5–2(–3) times as long as the chasmothecial diam, 4–10 µm wide, sometimes up to 12 µm at the very base, septate, walls thin, smooth, pale to medium dark brown throughout or brown below and paler towards the tips; asci 5–15, ellipsoid-obovoid, clavate-saccate, apex rounded to truncate, 50–80 × 20–35 µm, stalked, wall 1–2 µm wide, terminal oculus not very conspicuous, 10–18 µm diam, 2-spored, rarely with 3 spores; ascospores ellipsoid-ovoid to almost globose, 13–28 × (10–)12–18 µm, colorless.

Lectotype (designated here, MycoBank, MBT381247): Scotland, Roslin, on *Symphytum* sp., undated, R.K. Greville (E 456091). **Epitype** (designated here, MycoBank, MBT381248): Germany, Sachen-Anhalt, Roßlau, Ragösen, Rathsbruch, *S. officinale*, August 28 2004, A. Hoch (GLM-F073207).

Additional specimens examined: On *Pulmonaria angustifolia* – Germany, Thuringia, Steinach, Holzberg, July 21 1979, St. Rauschert (HAL 850 F). On *Pulmonaria mollis* – Russia, Bashkortostan, Pavlovaka, water reservoir, July 14 1977, U. Braun (HAL 849 F). On *Pulmonaria obscura* – Germany, Sachen-Anhalt, Bad Düben, cemetery, 25 Aug. 1977, U. Braun (HAL 846 F); Russia, Bashkortostan, Yumatovo, July 3 1977, U. Braun (HAL 861 F), Pavlovaka, water reservoir, 14 Jul. 1977, U. Braun (HAL 879 F). On *Pulmonaria officinalis* – Germany,

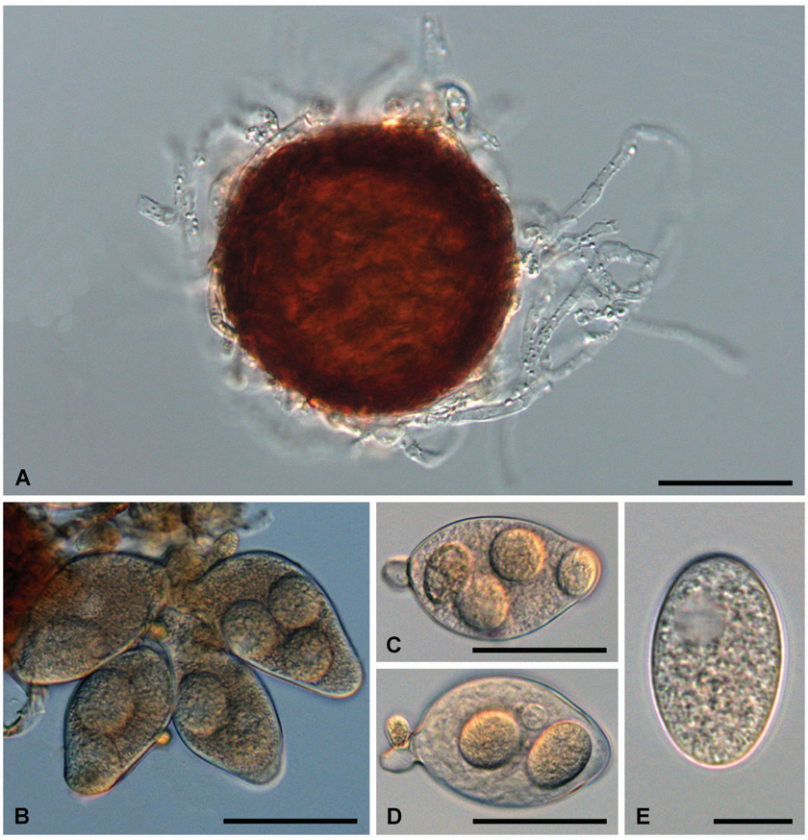

Figure 5. *Golovinomyces asperifolii* examined from KUS-F29281 ex *Trigonotis peduncularis*. (A) Chasmothecium. (B–D) Asci containing 2–4 ascospores. (E) Ascospore. Scale bar =50 µm for A, 30 µm for B–D, and 10 µm for E.

Saxony, Königshain, Schloßpark, May 22 2010, S. Hoeflich (GLM-F100040). On *Symphytum officinale* – Germany, Sachsen-Anhalt, Halle (Saale), Dölauer Heide, August 17 1975, U. Braun (HAL 860 F), Ziegelrodaer Forst, Jägerhof, August 28 1976, U. Braun (HAL 880 F), Greifenhagen, Aug. 1980, U. Braun (HAL 851 F), Grimmen, September 14 1982, U. Braun (HAL 853 F), Saxony, Westerzgebirge, Annaberg-Buchholz, June 1986, W. Dietrich (HAL 868 F), Görlitz-Biesnitz, Kunnewiter Grund, Reiherweiher, October 31 2006, S. Hoeflich (GLM-F079060); Russia, Bashkortostan, Ufa, Belaja, Kalinin Park, July 4 1977, U. Braun (HAL 864 F), Tujmazinskij Rayon, Lake Kandrykul, July 12 1977, U. Braun (HAL 845 F), Vladivostok, Skver Imeni K. Sukhanova, July 18 2015, B.S. Kim (KUS-F28744); Scotland, Stirlingshire, road ascending to Wallace Monument, July 1 2008, R. Watling (E 278591).

Notes: The name *Erysiphe asperifoliorum* is available for clade III, which comprises European *Golovinomyces* collections on *Pulmonaria* and *Symphytum* spp. Greville [15] described *Erysiphe asperifoliorum* from Scotland ("*Symphytum tuberosum*, *Lycopsis arvensis*, & c., about Edinburgh, Autumn"). Junell [16] discovered in Edinburgh (herb. E) a single original specimen examined by R.K. Greville and cited it as "type" of this species, which did not constitute a formal lectotypification and cannot be corrected as "lectotype" according to Art. 9.9 of the Code. Therefore, a formal lectotypification in the sense of Junell is designated herein. In order to fix and establish the application of the name *G. asperifoliorum*, epitypification with German material on *S. officinale* is proposed, including an ex-epitype sequence serving as a reference sequence. Attempts to retrieve DNA from the Scottish material (E 278591, see collections examined) failed for unknown reasons and prevented to designate this material as an epitype. However, since this species is common in Europe on *Symphytum* spp., an epitype from Germany is reasonable and undoubtedly acceptable.

Golovinomyces asperifolii (Erikss.) U. Braun & H.D. Shin, **comb. nov.** (Figures 4 and 5)

Basionym: *Oidium asperifolii* Erikss., Fungi Paras. Scand. Exs., Fasc. 8, no. 386, 1891.

=*Oidium myosotidis* Rabenh., Fungi Eur. Exs., Ed. Nov., Ser. Sec., Cent. 26, no. 2558, 1881, nom. inval. (Art. 36.1).

≡*Oidium myosotidis* Rabenh. ex Jacz., Karm. Opred. Grib., Vip. 2, Muchn.-rosj. Griby (Leningrad): 460, 1927, nom. illeg. (Art. 52.1).

=*Erysiphe horridula* f. sp. *echii-myosotidis* S. Blumer, Jahrb. Philos. Fakult. II, Univ. Bern 2: 30, 1922.

=*Erysiphe horridula* f. sp. *echii-myosotidis* S. Blumer, Centralbl. Bakteriol., 2. Abth., 55: 491, 1922.

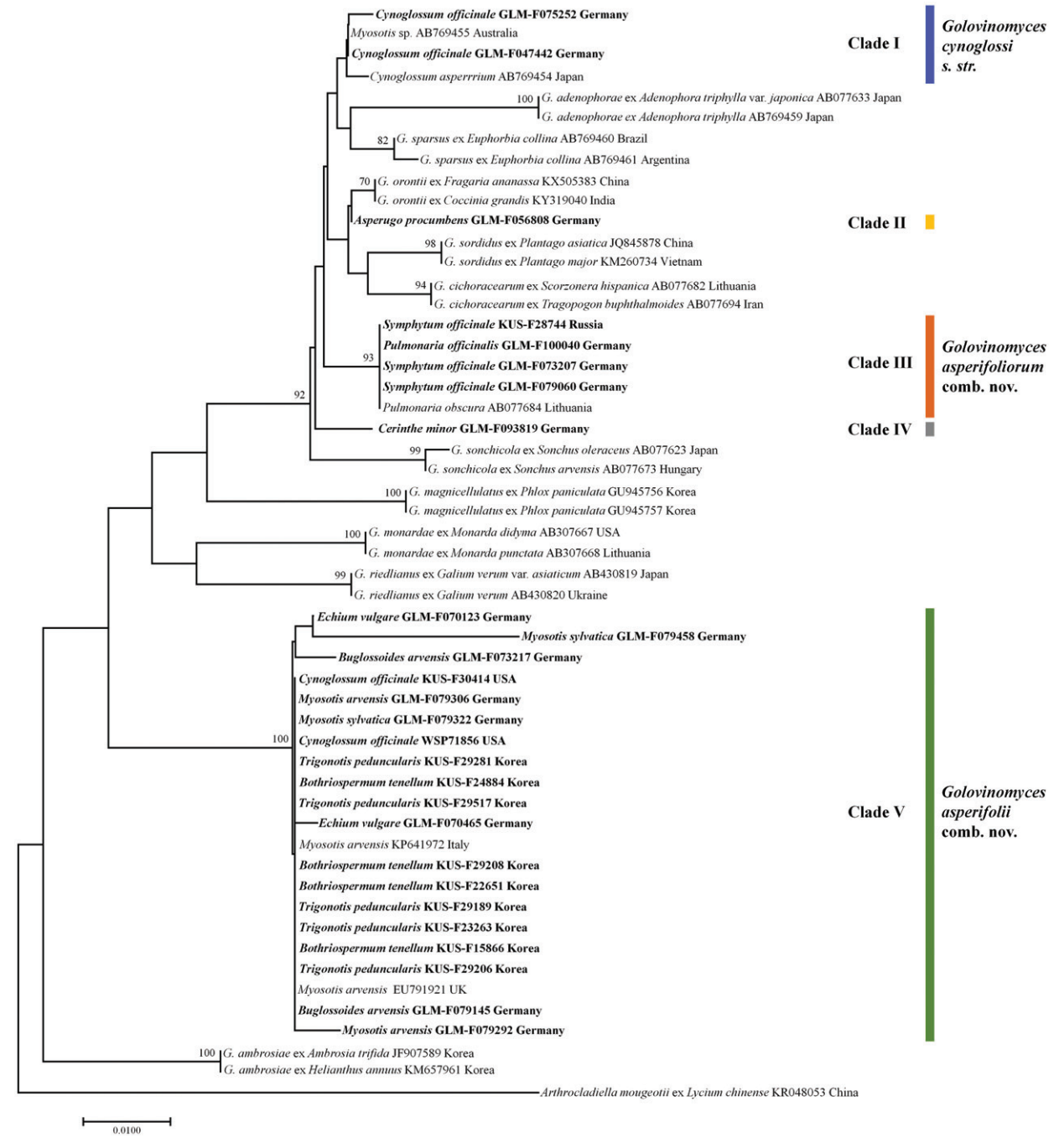

Figure 6. Phylogenetic relationship between *Golovinomyces cynoglossi, G. asperifoliorum,* and *G. asperifolii* isolates and some reference isolates retrieved from GenBank, inferred by maximum likelihood method using the internal transcribed spacer regions. Bootstrap values based on 1000 replications are indicated above the branches. The scale bar represents 0.01 nucleotide substitutions per site. The isolates presented in this study are indicated in bold.

Illustration: Liu (2010: 156, Figure 74 A, based on a collection on *Trigonotis peduncularis*) [6].

Mycelium amphigenous, on stems and sepals, dense, persistent, forming regular or irregular white patches, effuse; hyphae hyaline, thin-walled, smooth, 3.5–7 µm wide; hyphal appressoria nipple-shaped, 3.5–7 µm diam; conidiophores erect, arising from upper surface of hyphal mother cells and always towards one end of the cell, i.e., not centrally positioned, 100–250 µm long; foot-cells straight, cylindrical, 40–130 × 8–14 µm, basal septum of the foot-cell somewhat raised, 5–25 µm above the junction with the hyphal mother cells, foot-cells followed by 1–3 shorter cells, forming catenescent conidia; conidia ovoid to doliiform, 22–38 × 12–20 µm, length/width ratio 1.4–2.4, primary conidia apically rounded and sub-truncate at the base; germ tubes perihilar, short, apex with somewhat swollen appressorium (*Euoidium* type). Chasmothecia gregarious to somewhat scattered, usually gregarious and immersed in dense mycelial patches, sub-globose to globose, 80–140 µm diam; peridium cells irregularly

polygonal to daedaleoid, 10–25 µm diam; appendages more or less equatorial and in the lower half of the chasmothecia, always numerous, mycelioid, simple, interlaced with each other and with the mycelium, 0.5–2.5 times as long as the chasmothecial diam, 4–8 µm wide, septate, walls thin, smooth or almost so, hyaline or brown below and paler or colorless towards the tips; asci 5–15, with oil drops, ellipsoid-obovoid, clavate-saccate, 38–65 × 22–35 µm, short-stalked, 2–4-spored; ascospores ellipsoid-ovoid to almost globose, 10–20 × 10–18 µm, colorless.

Lectotype (designated here, MycoBank, MBT381249): Sweden, Stockholm, Experimentalfältet, on *Myosotis sylvatica* [*M.* "*alpestris*" hort.], July 11 1882, J. Eriksson [Erikss., Fungi Paras. Scand Exs. 386] (S-F270062). Isolectotypes: Erikss., Fungi Paras. Scand Exs. 386, e.g., BPI 409301, HAL. Epitype (designated here, MycoBank, MBT381250): Germany, Saxony, Görlitz-Bresnitz, on *Myosotis sylvatica*, May 10 2007, H. Boyle (GLM-F079322).

Additional specimens examined: On *Bothriospermum tenellum* – Korea, Seoul, Forestry Research Institute, April 27 1999, H.D. Shin (KUS-F15700), Seoul, Korea University, May 1 1999, H.D. Shin (KUS-F15715), Seoul, Korea University, May 25 1999, H.D. Shin (KUS-F15866), Jinju, Southern Forest Resources Research Center, May 28 2003, H.D. Shin (KUS-F19530), Cheongju, Chungbuk National University, May 1 2004, H.D. Shin (KUS-F20150), Osan, Mulhyanggi Botanical Garden, May 30 2007, H.D. Shin (KUS-F22651), Suwon, Seodun-dong, 8 May 2009, H.D. Shin (KUS-F24054), Seoul, Korea University, May 8 2010, H.D. Shin (KUS-F24884), Namyangju, Chukryeongsan Recreational Forest, June 8 2016, H.D. Shin (KUS-F29208). On *Buglossoides arvensis* – Armenia, Martuninsij Rayon, 2700–2800 m alt., August 12 1980, S. Simonyan (HAL 876 F); Germany, Sachsen-Anhalt, Merseburg, south of Klötzschen, June 16 2005, H. John (GLM-F073217), Saxony, Kringelsdorf, May 6 2007, leg. H. Boyle (GLM-F079145), Görlitz-Tauchitz, July 6 2006, leg. H. Boyle (GLM-F079081); Ukraine, Altagir, May 31 1984, U. Braun (HAL 852 F). On *Cynoglossum officinale* – USA, Montana, Missoula, August 29 2010, unknown collector (WSP71856), Washington, Glenwood, October 24 2017, M. Bradshaw (KUS-F30414). On *Echium vulgare* – Germany, Rheinland-Pfalz, Koblenz, Knappenrode, July 21 2005, S. Hoeflich (GLM-F070123), Sachsen, Sproitz, May 31 2006, H. Boyle & S. Hoeflich (GLM-F070465). On *Myosotis arvensis* – Germany, Sachsen-Anhalt, Greifenhagen, September 1981, U. Braun (HAL 848 F), Saxony, Westerzgebirge, Annaberg-Buchholz, August 26 1981, W. Dietrich (HAL 869 F), Olbersdorf, May 17 2007, S. Höflich (GLM-F079292), Olbersdorf, May 10 2007, H. Boyle (GLM-F079306). On *Myosotis sylvatica* – Germany, Saxony, Görlitz, May 6 2007, R. Franke (GLM-F079458). On *Myosotis* sp., Bulgaria, Rila Mts., Sokolvec, July 27 1978, U. Braun (HAL 847 F). On *Trigonotis peduncularis* – Korea, Gangneung, Ponam-dong, May 17 1989, H.D. Shin (KUS-F10143), Gangneung, Ponam-dong, May 30 1991, H.D. Shin (KUS-F10748), Gangneung, Ponam-dong, May 17 1992, H.D. Shin (KUS-F11590), Gangneung, Gangneung National University, April 23 1994, H.D. Shin (KUS-F12759), Gangneung, Eoheul-ri, May 22 1994, H.D. Shin (KUS-F12783), Seoul, Korea University, May 17 1997, H.D. Shin (KUS-F13776), Seoul, Korea University, October 11 1997, H.D. Shin (KUS-F14397), Seoul, Korea University, March 27 1999, H.D. Shin (KUS-F15668), Seoul, Korea University, April 3 1999, H.D. Shin (KUS-F15671), Seoul, Korea University, April 5 1999, H.D. Shin (KUS-F15673), Seoul, Korea University, April 24 1999, H.D. Shin (KUS-F15688), Chuncheon, Udu-dong, May 13 1999, H.D. Shin (KUS-F15783), Namyangju, Deokso Farm, May 28 1999, H.D. Shin (KUS-F15889), Seoul, Forestry Research Institute, May 31 1999, H.D. Shin (KUS-F15926), Samcheok, Miro-myeon, May 11 2000, H.D. Shin (KUS-F17290), Seoul, Forestry Research Institute, May 19 2000, H.D. Shin (KUS-F17338), Hongcheon, Bukbang-myeon, November 4 2005, H.D. Shin (KUS-F21629), Seoul, Forestry Research Institute, November 1 2006, H.D. Shin (KUS-F22434), Gimhae, Inje University, November 25 2006, H.D. Shin (KUS-F22503), Seoul, Korea University, April 7 2008, H.D. Shin (KUS-F23263), Suwon, Seodun-dong, May 8 2009, H.D. Shin (KUS-F24053), Seoul, Korea University, June 6 2016, T.T. Zhao (KUS-F29189), Namyangju, Chukryeongsan Recreational Forest, June 8 2016, H.D. Shin & S.E. Cho (KUS-F29206), Seoul, Seoul National University, June 30 2016, H.D. Shin & S.E. Cho (KUS-F29281), Gapyeong, Homyeongsan, September 29 2016, H.D. Shin & S.E. Cho (KUS-F29517).

Notes: Clade V encompasses powdery mildew collections occurring on a wider range of boraginaceous genera, including *Myosotis* spp. This powdery mildew species is common on *Myosotis* spp. in Europe. All sequences based on European powdery mildew samples on *Myosotis* spp. cluster within clade V for which teleomorph-typified names are not available. However, names based on asexual morphs on *Myosotis* have to be taken into consideration. The oldest name, *Oidium myosotidis*, proposed in Rabenhorst, Fungi Eur. Exs., Ed. Nov., Ser. Sec., Cent. 26, no. 2558, 1881, is invalid due to it was not being accepted by Rabenhorst, i.e., it was designated as "ad int." (Art. 36.1). Rabenhorst (l.c.) failed to describe *O. myosotidis*, only stating: "Die Konidien unterscheiden sich von den *O. ruborum* etc.

in keiner Weise" [the conidia differ from those of *O. ruborum* etc. not at all]. Jaczewski [17] took up the name *O. myosotidis* and added a brief description of the conidia. Jaczewski [17] failed to validate this name due to his citation of the valid name *O. asperifolii* as synonym. By doing so, he made *O. myosotidis* Rabenh. ex Jacz. a superfluous name (nom. illeg.). *O. asperifolii*, introduced in Eriksson, Fungi Paras. Scand. Exs., Fasc. 8, no. 386, 1891 (with brief description of the conidia), for a powdery mildew collected in an experiment field near Stockholm, Sweden, on *Myosotis* "*alpestris*" [hort.] (= *M. sylvatica*, see Junell 1967: 23), refers to clade V and has to be utilized for the taxon involved. A new specimen on *M. sylvatica* collected in Sweden, suitable for phylogenetic analyses, was not available for epitypification purposes. Therefore, a German powdery mildew sample on *M. sylvatica* is designated as epitype to establish the application of *G. asperifolii*. There is a certain degree of genetic variation within clade V. Most sequences in this clade are identical or almost so, however, some of them retrieved from the German samples on *Buglossoides arvensis* (GLM-F073217), *E. vulgare* (GLM-F070123, 070405), and *Myosotis* spp. (GLM-F079458, 079292) are genetically deviating and need a further investigation. Currently we prefer to maintain all collections and corresponding sequences of clade V in *G. asperifolii*, at least tentatively.

Key to three recognized species of *Golovinomyces cynoglossi* complex based on morphological characteristics:

1 Conidiophores 80–165 µm long, basal septum at the junction with the mother cell or only slightly elevated (2.5–5 µm); on *Pulmonaria* and *Symphytum* spp. as principal hosts ..... *G. asperifoliorum*

1* Conidiophores longer, up to 250 µm, basal septum usually 5–25 µm above the junction with the mother cell 2

2 Conidia 25–40 × 15–20 µm, length/width ratio 1.4–2.0; chasmothecial appendages pale to medium brown throughout or paler towards the tip; asci usually 2-spored; on *Cynoglossum* spp. as principal hosts, widespread in the natural range of the species ..... *G. cynoglossi*

2* Conidia 22–38 × 12–20 µm, length/width ratio 1.4–2.4; chasmothecial appendages hyaline or brown below and paler or colorless towards the tip, asci 2–4-spored; on various hosts, including *Bothriospermum*, *Buglossoides*, *Echium* (only outside of the range in North America), *Myosotis*, and *Trigonotis* spp. ..... *G. asperifolii*

4. Discussion

Golovinomyces cynoglossi, previously known as *Erysiphe asperifoliorum* and *E. horridula*, is the most common and widespread powdery mildew on hosts of the *Boraginaceae* [1,2,7,18]. Other powdery mildews on hosts of this family pertain to the genera *Erysiphe*, *Leveillula*, and *Phyllactinia*. Species of the genus *Podosphaera*, including *Sphaerotheca*, which are common on hosts of many other plant families, are not known to infect hosts within *Boraginaceae*. *Sphaerotheca lappulae* [19], introduced as a powdery mildew on *Lappula heteracantha* in China, is an excluded and doubtful species (incorrect host identification and description of the sexual morph based on chasmothecia deposited as contamination) [2]. Almost all host species of *G. cynoglossi s. lat*. belong to genera of the subfamily *Boraginoideae*, which is currently split into four tribes, i.e., *Boragineae*, *Cynoglosseae*, *Echiochilieae*, and *Lithospermeae* [3]. Of the 31 boraginaceous genera recorded as hosts of this species [1,2], 17 are in tribe *Cynoglosseae*, six are in tribe *Lithospermeae*, and nine are in tribe *Boragineae*. Blumer [4,20] performed comprehensive inoculation tests and morphological examinations on powdery mildew referred to as *Erysiphe horridula*. Blumer's [4,20] research dictated the current wide concept of *G. cynoglossi*. He revealed a high degree of biological specialization and proposed to split this species into seven taxonomic entities for which he used the category "forma specialis", i.e., he introduced informal taxa not regulated by the Code (ICN): *Erysiphe horridula* f. sp. *anchusae*, f. sp. *asperuginis*, f. sp. *cerinthes*, f. sp. *cynoglossi*, f. sp. *echii-myosotidis*, f. sp. *pulmonariae*, and f. sp. *symphyti* [20]. On the basis of his own results and inoculation experiments carried out by Neger [21] and Hammarlund [22], Blumer [18] provided the following classification and overview: (1) *Erysiphe asperifoliorum* f. sp. *anchusae*, on *Anchusa officinalis* as principal host, ascus 2–5-spored, conidia formed singly [unrelated to *G. cynoglossi* and corresponding to *Erysiphe lycopsidis*]. Ascus 2–3-spored, conidia formed in chains (catenescent), corresponding to *G. cynoglossi s. lat*.: (2) *E. asperifoliorum* f. sp. *echii-myosotidis*, on *Echium* and *Myosotis* spp. as principal hosts, and *Borago officinalis*, *Omphalodes linifolia*, *Cerinthe major*, and *C. glabra* as secondary hosts, appendages thin, short, almost hyaline, conidia 33–38 µm long. Appendages thicker, more or less brown: (3) *E. asperifoliorum* f. sp. *lithospermi*, mainly on *Lithospermum arvense*, conidia 33–38 µm long. (4) *E. asperifoliorum* f. sp. *asperuginis*, on *Asperugo procumbens* and *Cerinthe major*, conidia 38–41 µm long. (5) *E. asperifoliorum* f. sp. *cynoglossi*, on *Cynoglossum officinale*, conidia 38–41 µm long. (6) *E. asperifoliorum* f. sp. *symphyti*, mainly on *Symphytum* spp., secondary hosts *Lappula echinata*, *Cerinthe major*, *C. glabra*, *Lycopsis arvensis* and *Anchusa azurea,* conidia 40–45 µm long. (7) *E. asperifoliorum* f. sp. *pulmonariae*, mainly on

Pulmonaria spp., secondary hosts *Symphytum officinale*, and *Cerinthe major*, conidia 40–45 µm long. The biological heterogeneity of *G. cynoglossi s. lat*., the slight morphological differences between collections from different host genera and the first molecular sequence analyses raised serious doubts as to the monophyly of this species. Phylogenetic analyses recently performed on the basis of specimens from Asia, Europe and North America clearly showed that *G. cynoglossi s. lat*. is genetically divided into several clades which are in concordance with Blumer's [18] concept of *formae speciales*, at least to a certain degree.

Clade I consists of three sequences retrieved from powdery mildew on *Cynoglossum* (*Cynoglosseae*) in Germany and Japan, and a single sequence of *Golovinomyces* on *Myosotis* from Australia. Although ITS sequences are commonly and widely used for powdery mildews, they are often not sufficiently reliable for final taxonomic conclusions on the species level [23,24]. However, in this scenario, sequence data are indispensable for the clarification of the *G. cynoglossi* complex. All sequences obtained from *Golovinomyces* on *Cynoglossum* in Europe and Asia cluster together, and in spite of a low BS value and a limited number of included sequences, the results from clade I corroborated with the epitypification of a German collection and an ex-epitype sequence (due to the original description of this species from Germany on the Eurasian host species, *Cynoglossum officinale*), allows the position and circumscription of *G. cynoglossi s. str*. to be fixed. The type material for the *G. cynoglossi* complex is old and is thus inappropriate for phylogenetic analyses. Because of this, epitypification with appropriate material for analyses is the currently preferred method. A single sequence in clade I originates from *Golovinomyces* on *Myosotis* in Australia which raises the assumption that *G. cynoglossi* may cause accidental infections on other hosts, including those outside of this powdery mildew species' natural range. Otherwise, Blumer [4,18,20] found a strict specialization of the *C. officinale* powdery mildew, without any secondary hosts. On the other hand, it is worth noting that a sequence obtained from *Golovinomyces* on *Cynoglossum* in Montana, USA, clustered in clade V. The *Golovinomyces* within clade V represent *G. asperifolii*, a distinct, not closely allied species with a wider host range amongst boraginaceous genera. This suggests that the genus *Cynoglossum* may be infected by at least two *Golovinomyces* species, with *G. cynoglossi* as the principal powdery mildew species within the natural range of *Cynoglossum* spp. However, many questions remain open. Seventeen genera of tribe *Cynoglosseae* were listed as hosts of *G. cynoglossi s. lat*. [1,2,7], including *Amsinkia*, *Cryptantha*, *Lindefolia*, and *Plagiobotrys*, which are considered as phylogenetically closely allied to *Cynoglossum* [3]. The identity of *Golovinomyces* on hosts of these genera is still unclear and needs to be morphologically and phylogenetically re-examined.

Clade III contains sequences of powdery mildews from two genera, *Symphytum* and *Pulmonaria*, which belong to tribe *Boragineae*. This clade is well supported, is clearly distinct from *G. cynoglossi s. str*., and corresponds to Blumer's *E. horridula* f. sp. *pulmonariae* and f. sp. *symphyti* which were classified to have identical morphology and overlap in their host range (*S. officinale* was listed as a secondary host for f. sp. *pulmonariae*) [18]. *Golovinomyces* species within clade III constitutes a species of its own, *Golovinomyces asperifoliorum*, which is also morphologically distinguished from the powdery mildews of clade I (*G. cynoglossi s. str*.) and clade V (*G. asperifolii*). The conidiophores are relatively short, 90–165 µm, and the basal septum of the conidiophores is located at the junction with the mother hypha or only slightly elevated, 2.5–5 µm (vs. conidiophores longer, up to 250 µm, basal septum 5–25 µm elevated in *G. cynoglossi* and *G. asperifolii*). The chasmothecial appendages in *G. asperifoliorum* are usually pigmented throughout and the asci are 2-spored, rarely 3-spored, in contrast to appendages pigmented below and paler or hyaline towards the tip and asci 2–4-spored in *G. asperifolii*.

E. asperifoliorum was introduced as powdery mildew on *Symphytum tuberosum*, *Lycopsis arvensis* and other boraginaceous hosts [15], which necessitates a lectotypification to define the application of this name. A collection on *Symphytum* sp. is the only original material examined by Greville that is maintained in the herbarium in Edinburgh (E). This specimen is designated as lectotype and enables the application of this name for clade III.

Anchusa, *Borago*, *Brunnera*, *Nonea*, *Pectocarya*, *Rindera*, and *Solenanthus* are additional host genera belonging in tribe *Boragineae*. Species of these genera are known to be hosts of *G. cynoglossi s. lat*. [1,2,7]. Morphological re-examinations and phylogenetic analyses are necessary to clarify the affinity of the powdery mildews on the hosts concerned.

Clade II and IV comprise *Golovinomyces* on *Asperugo* and *Cerinthe*, respectively. The two clades contain a single genus and, in each case, only one sequence. The positions of the two clades suggest the possible involvement of additional species on *Boraginaceae*, but the examined collections were not sufficient for final taxonomic conclusions. A larger sampling is necessary to discern the involvement of additional species. *Cerinthe* belongs to tribe *Lithospermeae*, but sequences retrieved from

Golovinomyces on hosts of two other genera belonging to tribe *Lithospermeae*, i.e., *Echium* and *Buglossoides*, are located in clade V. *Alkanna* and *Onosma* spp. are common, widespread hosts of *Golovinomyces* reported from many European countries [1,7,25]. However, the identity of *Golovinomyces* on hosts of these genera is unclear and needs to be examined on the basis of molecular and morphological methods. Although *Asperugo* belongs to tribe *Cynoglosseae* and contains a close phylogenetic relationship to *Trigonotis* and *Bothriospermum* [3], a sequence obtained from *Golovinomyces* on *Asperugo procumbens* collected in Germany clusters separately from clade I (*G. cynoglossi s. str.*), as well as from clade V (*G. asperifolii*), which includes powdery mildew on *Trigonotis* and *Bothriospermum*. Other genera, such as *Mertensia* and *Omphalodes*, which have close phylogenetic relationships to *Asperugo*, *Trigonotis* and *Bothriospermum*, are also host plants of *G. cynoglossi s. lat.* [1,7,25], but have not yet been included in phylogenetic analyses.

Clade V is the largest clade with the broadest host range, consisting of host species belonging to genera of the tribes *Cynoglosseae* (*Bothriospermum*, *Myosotis,* and *Trigonotis*) and *Lithospermeae* (*Echium* and *Buglossoides*), suggesting a plurivorous, widespread species. All sequences of *Golovinomyces* on *Myosotis* ssp. from various European countries belong to clade V. Hence, the name *Oidium asperifolii*, described from Sweden on *Myosotis sylvatica*, can be used for this clade and its application is determined by a corresponding epitypification. A sequence retrieved from *Golovinomyces* on *Myosotis* in Australia clustering in clade I seems to be the results of an unusual infection, under exotic conditions, outside of the natural range of *G. cynoglossi*. Clade V is well supported and clearly distinct from clade I and III, i.e., the treatment of this clade as species of its own, *G. asperifolii*, is fully justified. In addition, there are some morphological peculiarities such as longer conidiophores with distinctly raised basal septum (in comparison with *G. asperifoliorum*) and paler chasmothecial appendages as well as 2–4-spored asci (compared to *G. cynoglossi*).

In conclusion, it can be stated that the three species, *G. cynoglossi s. str.*, *G. asperifoliorum,* and *G. asperifolii*, discovered and substantiated within the course of the present examinations, are phylogenetically and morphologically distinct. Differences in the characters of the conidiophores have been found for the first time. Previous analyses of asexual characters just focused on the conidial size [4,18,26]. The germ tubes within *G. cynoglossi s. lat.* are rather uniform (short, subclavate, apex somewhat swollen, occasionally twined), which was already stated in Neger [21] for powdery mildew on *Cerinthe*, *Echium*, *Buglossoides* (*Lithospermum*), *Pulmonaria*, and *Symphytum*. Blumer [4,18,26] and Junell [16] discussed morphological differences in the sexual morphs of boraginaceous powdery mildews, which could be confirmed in the course of our own examinations. These differences are, however, gradual and difficult to discern, and thus are only applicable in combination with characters of the asexual morphs and phylogenetic data.

G. cynoglossi s. lat. has a wide host range covering host species of numerous genera. Only powdery mildew on hosts of a limited number of these genera could be included in our analyses, i.e., the present work is just a first step in the revision of this species complex and should be seen as a basis for further analyses and taxonomic examinations. The splitting of the *G. cynoglossi* (*s. lat.*) complex into three species, *G. cynoglossi s. str.*, *G. asperifoliorum* and *G. asperifolii*, is reasonable and supported by sequence analyses, biological aspects and morphological differences. The initial question regarding the identity of powdery mildew on *Trigonotis* and *Bothriospermum* in Korea could also be answered, i.e., it does not belong to *G. cynoglossi s. str.*, but to *G. asperifolii*, a species with a wide host range and distribution. In general, it can be stated that the particular clades and corresponding *Golovinomyces* species on boraginaceous host genera are not aligning confidently with the phylogenetic-taxonomic affinity of the host genera to tribes of the *Boraginaceae*. However, they reflect to a certain extent, previous biological analyses and classifications into *formae speciales* [4,21,22].

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