Phylogeny and taxonomy of the genera of Erysiphaceae, part 1: Golovinomyces

Michael J. Bradshaw, Uwe Braun, and Donald H. Pfister

Department of Organismic and Evolutionary Biology, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138; Department of Geobotany and Botanical Garden, Martin Luther University, Institute of Biology, Herbarium, Neuwerk 21, Halle (Saale) 06099, Germany

ABSTRACT
Powdery mildews are a monophyletic group of obligate plant pathogenic fungi in the family Erysiphaceae. Powdery mildews are economically important in that they cause damage to many agriculturally significant crops and plants in ecologically important habitats. In this contribution, we introduce a new series of publications focusing on the phylogeny and taxonomy of this group, with an emphasis on specimens collected from North America. The first part of the series focuses on the genus Golovinomyces and includes a section detailing the powdery mildew species concept. We conducted analyses of Golovinomyces spp. with available rDNA sequence data from GenBank and supplemented the data set with rDNA (ITS, 28S, IGS) as well as protein-coding (GAPDH) data from 94 North American collections. Many of the species evaluated are included in phylogenetic and morphological analyses for the first time, including the American species G. americanus, G. brunneopunctatus, G. californicus, G. greeneanus, G. hydrophyllacearum, and G. sparsus. A special emphasis was placed on acquiring ex-type or ex-epitotype sequences or presenting reference sequences for phylogenetic-taxonomic purposes. Three new species, G. eurybium, G. galorum, and G. malvacearum, are described, and the new combinations G. fuegianus, G. mutisiae, and G. reginae are introduced. Ex-holotype sequences of Erysiphe sparsa (= G. sparsus) reveal that it should be reduced to synonymy with G. ambrosiae, and ex-epitotype sequences of G. valerianae reveal that it should be reduced to synonymy with G. orontii. Multiple epitotypes are designated with ex-epitotype sequences.

INTRODUCTION
Powdery mildews (Erysiphaceae, Helotiales) represent a large group of obligate plant pathogenic ascomycetes occurring throughout the world on a range of angiosperm hosts. They cause disease on a variety of ecologically and agriculturally important plant species. The exact number of host species is unknown, but Amano (1986) listed up to 10,000 taxa and Bradshaw et al. (2022a) estimated ~16,000 taxa. In a worldwide treatment of powdery mildews, Braun and Cook (2012) outlined the history of the Erysiphaceae, from the first description of a powdery mildew, under the name Mucor erysiphe by Linné (1753), and the first monograph of this fungal group published by Salmon (1900) to Braun’s (1987) monograph. Braun and Cook’s (2012) treatment of the powdery mildews took into consideration phylogenetic information on powdery mildews in formulating both generic and species concepts (i.e., Saenz and Taylor 1999; Takamatsu et al. 1998, 1999; Mori et al. 2000a, 2000b; Takamatsu 2004). In the past 10 years, the number of phylogenetic-taxonomic treatments and revisions of genera and species complexes of the Erysiphaceae has increased substantially: Golovinomyces (Takamatsu et al. 2013); Erysiphe, Microsphaera lineage (Takamatsu et al. 2015a); Erysiphe, Uncinula lineage (Takamatsu et al. 2015b); Leveillula, Queirozia, Pleochaeta, and Phyllactinia (Takamatsu et al. 2016); Erysiphe on Papaveraceae (Pastirčáková et al. 2016); Golovinomyces biocellatus complex (Scholler et al. 2016); Golovinomyces chrysanthemi and allied species (Bradshaw et al. 2017); Erysiphe on Viburnum spp. (Bradshaw et al. 2020); phylogenetic complex (Bradshaw et al. 2021f); Erysiphe on Corylus spp. (Bradshaw et al. 2021a); Erysiphe on Lonicera spp. (Bradshaw et al. 2021b); Erysiphe on Lupinus spp. (Bradshaw et al. 2022b); Erysiphe on Cornus spp. (Meeboon and Takamatsu 2017); Golovinomyces cynoglossi complex (Braun et al. 2018); Golovinomyces orontii complex (Braun et al. 2019); Bulbomicroidium, gen. nov. (Marmolejo et al. 2018); Erysiphe gracilis complex on oaks (Siahana et al. 2018); Podosphaera on Prunus spp. (Moparthi et al. 2019); reintroduction of Salmonomyces (Kiss et al. 2020); Podosphaera tridactyla complex (Meeboon et al. 2020); Golovinomyces ambrosiae

CONTACT Michael J. Bradshaw mbradshaw@fas.harvard.edu

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complex (Qiu et al. 2020a); multilocus phylogeny on genus level (Shirouzu et al. 2020); *Erysiphe adunca* complex on Salicaeae (Darsarai et al. 2021); *Blumeria* (Liu et al. 2021); *Phyllactinia* on *Fraxinus* spp. (Maeda et al. 2021); and *Erysiphe* on *Fraxinus* spp. (Yamaguchi et al. 2021). Few of these papers deal with North American species, and as such our work is intended to characterize the powdery mildews in North America. Following modern conventions, many new species have been introduced supported by sequence data.

Beginning with this paper, we initiate a new series focusing on the phylogeny and taxonomy of powdery mildews, primarily dealing with North American species. In this first contribution, we focus on species of the genus *Golovinomyces*. The influx of new data on powdery mildews requires a broad-scale, systematic, phylogenetic-taxonomic approach. To set our studies on a firm foundation, we have produced sequences from type specimens or, if not possible, by designation of epitypes with ex-epitope sequences. Our intent is to provide reference sequences to document our work and provide a basis for future research dealing with this group. Only through a multipronged approach of sequencing and morphological studies can the Erysiphaceae be fully understood.

**MATERIALS AND METHODS**

**Sample collection.**—Specimens were primarily collected at the Arnold Arboretum, Boston, Massachusetts, USA, and the Harvard University main campus, Cambridge, Massachusetts, USA, in 2021. Additional collections were accomplished at various botanical gardens throughout the USA (TABLE 1) (Bradshaw et al. 2022a). Newly collected specimens were deposited in the Farlow Herbarium (FH), Harvard University. Previously collected herbarium specimens were evaluated from FH.

**Morphological examinations.**—Morphological examinations of the teleomorph were accomplished by transferring chasmothecia to a drop of distilled water on a microscope slide using a clean needle. Photographs were taken using a compound microscope equipped with an Olympus SC50 camera (Tokyo, Japan) and a Zeiss AX10 microscope (Oberkochen, Germany). Morphological examinations of the anamorph of recently collected samples were accomplished by placing clear adhesive tape over the powdery mildew colonies and mounting the tape on a slide with a drop of tap water. In studying dried specimens, examinations were done following the lactic acid protocol of Shin (1988).

**Sequencing.**—DNA extractions were done using the Chelex method (Hirata and Takamatsu 1996; Walsh et al. 1991). Polymerase chain reaction (PCR) was carried out for the internal transcribed spacer (ITS) and 28S regions using the primer pair PM10 (5’-GGCCGGAAAGTTGTCCAAAAC-3’)/PM28R (5’-ACG TTCACCTTTCATTCGCCG-3’) (Bradshaw and Tobin 2020). If PCR was unsuccessful, a nested approach was applied using the primer pair AITS (5’-CGATTGAATGGCTAAGTGAGG-3’) (Bradshaw and Tobin 2020)/TW14 (5’-GCTATCCTGAGGGAAAAC TTC-3’) (Mori et al. 2000a) followed by PM10/PM28R or AITS/PM11 (5’-TACCGTCTACCTCGCG TTC-3’) (Bradshaw and Tobin 2020) followed by PM10/PM2 (5’-TCACCTCGCCCTTAATGAGGT-3’) (Cunnington et al. 2003).

For the intergenic spacer (IGS) region, the primer pair IGS-12a (5’-AGTCTTGGAGTTAGTTGCCG-3’)/ NS1R (5’-GAGCAAGCATATGACT-3’) (Carbone and Kohn 1999) was used. For the *GAPDH* (glyceraldehyde-3-phosphate dehydrogenase) region, the primer pair PMGAPDH1 (5’-GGAATGGCTATGGCTACCATG-3’)/PMGAPDH3R (5’-CCCCATTCGTTGTCGTAC CATG-3’) (Bradshaw et al. 2022c) was used. All reactions were done with an annealing temperature of 57 C. DNA amplicons were sent to Eurofins (Luxembourg) to be purified and directly sequenced in the forward and reverse directions using the primer pairs above.

**Phylogenetic analyses.**—A phylogenetic tree was constructed from the concatenated *GAPDH*+*IGS*+*ITS*+28S sequences of selected *Golovinomyces* spp. (SUPPLEMENTARY FIG. 1). *Neoerysiphe galeopsis* was selected as an outgroup taxon based on Bradshaw et al. (2022c). In total, 148 of the 195 taxa were phylogenetically analyzed in the concatenated tree (species in the *G. ambrosiae* and *G. magnicellatus* complexes that only included ITS data were not included in the concatenated tree). For representative purposes, the SUPPLEMENTARY FIG. 1 tree was split into three trees, each with ~50 taxa (FIGS. 1–3). Nonconcatenated *ITS*+28S, IGS, and *GAPDH* trees are presented in SUPPLEMENTARY FIGS. 2–4 for comparative purposes. Sequences were aligned and edited using MUSCLE in MEGA11 (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 GAPDH+IGS+ITS+28S individually and combined using a Yule tree prior (Gernhard 2008) and a strict molecular clock, in BEAST 1.10.4 (Suchard et al. 2018). A single Markov chain Monte Carlo (MCMC) chain of 10⁶ steps was run, with a burn-in of 10%. Posterior probabilities were calculated from the remaining 9000 sampled trees. A maximum clade credibility tree was produced using TreeAnnotator 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 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

Phylogenetic analyses.—Amplicons for the specimens obtained were deposited in GenBank (TABLE 1). The phylogenetic analyses contained 195 sequences from powdery mildew specimens from around the world. Of these 195 sequences, 94 were obtained for the current study. The 101 sequences obtained from GenBank contained only ITS or ITS+28S data. A maximum clade credibility tree was constructed using Bayesian analyses from the combined GAPDH+IGS+ITS+28S sequences. Posterior probabilities ≥0.90 are displayed followed by bootstrap values greater than 70% for the maximum likelihood (ML) analyses conducted. The representative maximum clade credibility tree is illustrated in FIG. 1.

The overwhelming majority of species have been phylogenetically confirmed in the ITS+28S and concatenated analyses (FIGS. 1–3; SUPPLEMENTARY FIGS. 1–2). The following species form strongly supported species clades in both the ITS+28S and concatenated trees: Golovinomyces adenophorae, G. arabis, G. artemisiae, G. asperifolii, G. asperifloriourum, G. asterum, G. bolayi, G. calceolariae, G. californicus, G. chrysanthemi, G. cichoracearum (s. str.), G. circumfusus, G. cynoglossi, G. depressus, G. echinops, G. euphorbiicola, G. fischeri, G. fuggianus, G. galiorum, G. hieraciorum, G. inulae, G. ixodiae, G. leuceriae, G. malvacearum, G. macrocarpus, G. montagnei, G. monardae, G. mutisiae, G. neosalviae, G. ocimi, G. orontii, G. reginae, G. riedlianus, G. sonchicola, G. sordidus, G. tabaci, G. verbasci, G. verbenae, and G. vincae (FIGS. 1–3; SUPPLEMENTARY FIGS. 1–4). Golovinomyces ambrosiae, G. americanus, G. brunneopunctatus, G. eurybiorum, G. greeneanus, G. hydrophylacearum, G. latisporus, G. magnicellulatus, and the G. asterum varieties were confirmed in the concatenated tree, but not sufficiently resolved in the ITS analysis (FIGS. 1–3; SUPPLEMENTARY FIGS. 1–2).

The G. ambrosiae complex represents a special case in terms of phylogenetic analyses (this complex is resolved partially by IGS and GAPDH in single-locus analyses [SUPPLEMENTARY FIGS. 3–4] and in full in the concatenated analysis [FIG. 1]). However, it forms an insufficiently resolved complex in ITS+28S analyses (SUPPLEMENTARY FIG. 1). Solely IGS is able to differentiate G. eurybiorum from G. latisporus and G. ambrosiae (SUPPLEMENTARY FIG. 3). There is only one base difference between G. latisporus and G. ambrosiae in the IGS analysis (i.e., IGS does not fully differentiate these species in phylogenetic analyses), whereas in the GAPDH analysis there are enough differences to yield phylogenetic significant support levels between the two taxa (SUPPLEMENTARY FIG. 4). However, GAPDH solely cannot differentiate G. eurybiorum from G. latisporus and G. ambrosiae (G. eurybiorum falls in the G. latisporus clade in GAPDH analyses).

There are two unresolved complexes within Golovinomyces: one that consists of G. lycopersici and G. longipes and one that consists of G. salviae, G. biocellatus, and G. neosalviae (FIG. 3). These complexes do not have molecular data available for the IGS and GAPDH regions yet.

TAXONOMY

Species belonging in the genus Golovinomyces were previously treated under Erysiphe s. lat., which historically comprised species with chasmothecia characterized by having mycelium-like appendages and multiple asci (Braun 1987; Salmon 1900). Originally, the traits of the asexual morphs where not considered in species recognition. Braun (1978) introduced Erysiphe sect. Golovinomyces (type species: Erysiphe cichoracearum). This group was based on a combination of characters: almost inconspicuous to distinctly nipple-shaped hyphal appressoria, conidia in genuine chains without fibrosin bodies, and usually 2-spored ascis, which are developed in the current season. Heluta (1988) raised this section to genus rank. The recognition as a genus was confirmed by the first analyses of sequences retrieved from species of Erysiphe sect. Golovinomyces (Mori et al. 2000a; Saenz and Taylor 1999). Hence, Braun (1999, 52) recognized the genus Golovinomyces and placed it in a new subtribe, i.e., Erysipheae tribe Erysipheae subtribe Golovinomycetinae U. Braun.
Table 1. Lists of taxa, hosts, vouchers, collection localities, and GenBank accession numbers of the specimens examined in the current study.

| Taxon                          | Host                  | Voucher*                                      | Collection locality | ITS+LSU   | IGS     | GAPDH    | Notes                  |
|-------------------------------|-----------------------|-----------------------------------------------|---------------------|-----------|---------|----------|------------------------|
| Golovinomyces ambrosiae       | Acalypha rhomboidea   | FH00941205                                    | Massachusetts, USA  | ON073871  | ON361172| ON075624 |                        |
| Golovinomyces ambrosiae       | Acalypha rhomboidea   | FH00941206                                    | Massachusetts, USA  | ON073872  | ON361172| ON075624 |                        |
| Golovinomyces ambrosiae       | Acalypha virginica    | FH00965657                                    | Wisconsin, USA      | ON366996  | ON366713| ON360701 | Holotype of Erysiphe sparsa |
| Golovinomyces ambrosiae       | Actinomorpha alternifolia | FH01122006                                  | Kentucky, USA       | ON366977  |         |          |                        |
| Golovinomyces ambrosiae       | Ambrosiae artemisfloria | FH00941290                                   | North Carolina, USA | ON366998  |         |          |                        |
| Golovinomyces ambrosiae       | Asclepias syriaca     | FH00941223                                    | Massachusetts, USA  | ON073873  | ON361174| ON075625 |                        |
| Golovinomyces ambrosiae       | Aster exilis          | FH00941291                                    | North Carolina, USA | ON366999  |         |          |                        |
| Golovinomyces ambrosiae       | Aster simplex         | FH01122008                                    | Ontario, Canada     | ON367000  | ON361175| ON360702 |                        |
| Golovinomyces ambrosiae       | Bidens pilosa         | FH00941292                                    | North Carolina, USA | ON367001  |         |          |                        |
| Golovinomyces ambrosiae       | Cirsium altissimum    | FH01122009                                    | Wisconsin, USA      | ON367002  | ON361176| ON360703 |                        |
| Golovinomyces ambrosiae       | Coreopsis palmata     | FH01122010                                    | Wisconsin, USA      | ON367003  | ON361177| ON360704 |                        |
| Golovinomyces ambrosiae       | Cosmos bipinnatus     | FH00941267                                    | Colorado, USA       | ON367004  | ON361178| ON360704 |                        |
| Golovinomyces ambrosiae       | Dahlia “Knock Out”   | FH00941248                                    | Colorado, USA       | ON367381  | ON361179| ON075626 |                        |
| Golovinomyces ambrosiae       | Eupatorium maculatum  | FH01122011                                    | Ontario, Canada     | ON367005  | ON361180| ON360705 |                        |
| Golovinomyces ambrosiae       | Eutricium sp.         | FH00941257                                    | Massachusetts, USA  | ON367006  | ON361181|          |                        |
| Golovinomyces ambrosiae       | Eustrochium dumbium   | FH00941204                                    | Massachusetts, USA  | ON073874  | ON361182| ON075627 |                        |
| Golovinomyces ambrosiae       | Eustrochium fistulosum| FH00941289                                    | Delaware, USA       | ON367007  | ON361183|          |                        |
| Golovinomyces ambrosiae       | Helenium autumnale    | FH01122012                                    | Wyoming, USA        | ON367008  | ON361184| ON360706 |                        |
| Golovinomyces ambrosiae       | Lactuca spicata       | FH01122013                                    | Wisconsin, USA      | ON367009  | ON361185| ON360707 |                        |
| Golovinomyces ambrosiae       | Liatris spicata       | FH00941247                                    | Colorado, USA       | ON073875  | ON361186| ON075628 |                        |
| Golovinomyces ambrosiae       | Ratibida columnifera  | FH00941246                                    | Colorado, USA       | ON073842  | ON361187| ON075629 |                        |
| Golovinomyces ambrosiae       | Rudbeckia fulgida    | FH00941203                                    | Massachusetts, USA  | ON367010  | ON361188| ON075630 |                        |
| Golovinomyces ambrosiae       | Solanum carolinense   | FH01122023                                    | North Carolina, USA | ON367011  | ON361189| ON360708 |                        |
| Golovinomyces ambrosiae       | Symphyotrichum patens | FH00941234                                    | Minnesota, USA      | ON073876  | ON361190|          |                        |
| Golovinomyces ambrosiae       | Verbena alternifolia  | FH00941235                                    | Minnesota, USA      | ON073877  | ON361191|          |                        |
| Golovinomyces ambrosiae       | Vernonia fasciculata  | FH01122004                                    | Wisconsin, USA      | ON367012  | ON361192| ON360709 |                        |
| Golovinomyces ambrosiae       | Vernonia fasciculata  | FH00941293                                    | North Carolina, USA | ON367013  |         |          |                        |
| Golovinomyces ambrosiae       | Vernonia glauca       | FH00941278                                    | Delaware, USA       | ON367014  | ON361193|          |                        |
| Golovinomyces ambrosiae       | Zinnia elegans        | FH00941245                                    | Colorado, USA       | ON073878  | ON361194| ON075631 |                        |
| Golovinomyces ambrosiae       | Zinnia elegans        | FH00941258                                    | Massachusetts, USA  | ON367015  | ON361195|          |                        |
| Golovinomyces americanus      | Napaea dioica         | FH01122028                                    | Wisconsin, USA      | ON367016  | ON361196| ON360710 |                        |
| Golovinomyces asperifolii     | Amsinckia intermedia  | FH01122015                                    | Idaho, USA          | ON367017  |         |          |                        |
| Golovinomyces asperifolii     | Cryptantha aftnus     | FH01122016                                    | California, USA     | ON367018  |         |          |                        |
| Golovinomyces asperifolii     | Lappula california    | FH01122017                                    | California, USA     | ON367019  |         |          |                        |
| Golovinomyces asterum         | Aster “Woods Blue”    | FH00941271                                    | Washington, USA     | ON367020  |         |          |                        |
| Golovinomyces asterum         | Carthamus tinctorius  | FH00941264                                    | Massachusetts, USA  | ON367021  | ON361197|          |                        |
| Golovinomyces asterum         | Cinclidia integrifolia| FH00941285                                    | Washington, USA     | ON367022  |         | ON360713 |                        |
| Golovinomyces asterum var.    | Symphyotrichum georgianum | FH00941279                                | Delaware, USA       | ON367023  | ON361198| ON360714 |                        |
| Golovinomyces asterum var.    | Symphyotrichum nivae- angiae  | FH00941249                                  | Colorado, USA       | ON073879  | ON361199| ON075650 | Reference sequence     |
| Golovinomyces asterum var.    | Solidago canadensis   | FH00941272                                    | Washington, USA     | ON367024  |         |          |                        |
| Golovinomyces asterum var.    | Solidago sp.          | FH00941260                                    | Massachusetts, USA  | ON367025  |         |          |                        |
| Golovinomyces asterum var.    | Solidago sp.          | FH00941259                                    | Massachusetts, USA  | ON367026  | ON361200| ON360715 | Reference sequence     |
| Golovinomyces bolayi          | Lactuca serriola      | FH00941286                                    | Massachusetts, USA  | ON367027  |         |          |                        |
| Golovinomyces bruneopunctatus | Mimulus guttata       | FH00965643                                    | California, USA     | ON367028  |         | ON360716| Holotype               |
| Golovinomyces californicus    | Eriocanthera manifolium| FH00965644                                   | California, USA     | ON367029  |         | ON360717| Paratype               |

(Continued)
| Taxon | Host | Voucher* | Collection locality | ITS+LSU | IGS | GAPDH | Notes |
|-------|------|----------|---------------------|---------|-----|-------|-------|
| Golovinomyces cynoglossi | Rinderan lanata | WU-Myc 0043188 | Austria | ON367030 |     |       |       |
| Golovinomyces eurybiarum | Eurybia divaricata | FH00941281 | Delaware, USA | ON367031 | ON361201 |       | Holotype |
| Golovinomyces eurybiarum | Eurybia divaricata | FH00941263 | Massachusetts, USA | ON367032 | ON361202 | ON360718 |       |
| Golovinomyces eurybiarum | Eurybia schreberi | FH00941284 | Delaware, USA | ON367033 | ON361203 |       |       |
| Golovinomyces fischeri | Senecio vulgaris | FH00965646 | Switzerland | ON367034 |       | ON360719 | Lectotype |
| Golovinomyces galiorum | Galium aparine | FH0112200000 | Wisconsin, USA | ON367035 | ON361204 | ON360720 |       |
| Golovinomyces greenea | Galium bifolium | FH0112200001 | California, USA | ON367036 | ON361205 | ON360721 | Holotype |
| Golovinomyces greenea | Parietaria pennsylvaniaica | FH01122004 | Montana, USA | ON367037 | ON361206 | ON360722 |       |
| Golovinomyces greenea | Parietaria pennsylvaniaica | FH00965649 | Wisconsin, USA | ON367038 |       | ON360723 | Paratype |
| Golovinomyces holophyllum | Hydrophyllum macrophyllum | FH01122020 | Tennessee, USA | ON367039 | ON361207 | ON360724 |       |
| Golovinomyces holophyllum | Hydrophyllum tenuipes | FH01122021 | Oregon, USA | ON367040 | ON361208 | ON360725 |       |
| Golovinomyces holophyllum | Hydrophyllum virginianum | FH01122019 | Wisconsin, USA | ON367041 | ON361209 | ON360726 | Reference sequence |
| Golovinomyces holophyllum | Phlox paniculata | FH00941211 | Massachusetts, USA | ON367042 | ON361210 | ON360727 |       |
| Golovinomyces holophyllum | Helianthus annuus | FH00941224 | Germany | ON367043 |       | ON360728 |       |
| Golovinomyces holophyllum | Helianthus annuus | FH00941224 | California, USA | ON367044 | ON361211 | ON360732 |       |
| Golovinomyces holophyllum | Phlox paniculata | FH01122024 | Oregon, USA | ON367045 | ON361212 | ON360729 |       |
| Golovinomyces holophyllum | Phlox paniculata | FH00941265 | Massachusetts, USA | ON367046 |       | ON360730 |       |
| Golovinomyces holophyllum | Phlox paniculata | FH01122024 | Germany | ON367047 |       | ON360731 | Holotype |
| Golovinomyces malvacearum | Sidalcea hendersonii | FH00941273 | Washington, USA | ON367049 |       | ON360732 | Holotype |
| Golovinomyces monarade | Mentha arvensis | FH01122029 | Ontario, Canada | ON367050 | ON361214 | ON360733 |       |
| Golovinomyces monarade | Monarda dymon | FH00941280 | Delaware, USA | ON367051 | ON361215 | ON360734 |       |
| Golovinomyces monarade | Monarda fistulosa | FH00941287 | Minnesota, USA | ON367052 | ON361216 | ON360735 |       |
| Golovinomyces monarade | Monarda fistulosa | FH00941266 | Idaho, USA | ON367053 | ON361217 | ON360736 |       |
| Golovinomyces monarade | Monarda "Jacob Cline" | FH00941269 | Colorado, USA | ON367054 | ON361218 | ON360737 |       |
| Golovinomyces monarade | Monarda speciosa | FH00941288 | Massachusetts, USA | ON367055 | ON361219 | ON360738 |       |
| Golovinomyces montanei | Leueza carthamoides | FH00941274 | Colorado, USA | ON367056 |       |       |       |
| Golovinomyces orontii | Penstemon serrulatus | FH00941277 | Washington, USA | ON367057 |       |       |       |
| Golovinomyces salviae | Agastache scrophulariifolia | FH00941250 | Colorado, USA | ON367058 | ON361220 | ON360739 |       |
| Golovinomyces salviae | Salvia sp. | FH00941213 | Massachusetts, USA | ON367059 | ON361221 | ON360740 | Holotype |
| Golovinomyces sonchica | Sochclus oleraceus | FH00941275 | The Netherlands | ON367060 |       | ON360741 |       |
| Golovinomyces sonchica | Sonchus sp. | FH00941275 | Washington, USA | ON367061 |       | ON360742 |       |
| Golovinomyces sordidus | Plantago major | FH01122025 | Wisconsin, USA | ON367062 | ON361222 | ON360743 |       |
| Golovinomyces sordidus | Plantago major | FH00941262 | Massachusetts, USA | ON367063 |       | ON360744 | Reference sequence |
| Golovinomyces sordidus | Plantago major | FH01122025 | Wisconsin, USA | ON367064 |       | ON360745 |       |
| Golovinomyces sordidus | Plantago major | FH00941276 | Colorado, USA | ON367065 | ON361223 | ON360746 | Epitype of G. valeriae |
| Golovinomyces sp. | Artemisia arctica | FH01122031 | Canada | ON367066 | ON361224 | ON360747 |       |
| Golovinomyces sp. | Aster foliosa | FH01122007 | Wyoming, USA | ON367067 | ON361225 | ON360748 |       |
| Golovinomyces sp. | Hydrophyllum canadense | FH00941241 | Delaware, USA | ON367068 | ON361226 | ON360749 |       |
| Golovinomyces sp. | Mertensia paniculata | FH01122018 | Ontario, Canada | ON367069 | ON361227 | ON360750 |       |
| Golovinomyces sp. | Phacelia bipinnatifida | FH00941242 | Wisconsin, USA | ON367070 | ON361228 | ON360751 |       |
| Golovinomyces sp. | Scutellaria lateriflora | FH01122030 | Delaware, USA | ON367071 | ON361229 | ON360752 |       |
| Golovinomyces sp. | Asperugo procumbens | BP929818 | Russia | ON367072 | ON361230 | ON360753 |       |
| Golovinomyces orontii | Valeriana edulis | FH01122027 | Utah, USA | ON367073 | ON361231 | ON360754 |       |
| Golovinomyces orontii | Valeriana obovata | FH01122026 | Wyoming, USA | ON367074 | ON361232 | ON360755 |       |
| Golovinomyces orontii | Valeriana officinalis | HAL 1398 F | Germany | ON367075 | ON361233 | ON360756 |       |
Later, Braun and Takamatsu (2000, 32) treated this subtribe as tribe Golovinomyceteeae (U. Braun) U. Braun & S. Takam. This taxonomic conclusion was also supported by a particular pattern of the conidial germination in *Golovinomyces cichoracearum* and allied species (Euoidium type; see Cook and Braun 2009; Braun and Cook 2012, 22). Cook et al. (1997) divided the anamorph-typified genus *Oidium* into several subgenera, including subgenus *Reticuloidium* for asexual morphs of *Golovinomyces*. The anamorph subgenera phylogenetically align with the teleomorph genera.

Paul and Kapoor (1985) introduced the genus name *Euoidium*, with *Oidium erysiphoides* as type species. However, the exact application of this anamorph-typified name in terms of modern, phylogenetic generic concepts was unclear. Braun and Cook (2012) resolved the question when they neotypified *O. erysiphoides* with the asexual morph of *Golovinomyces biocellatus*. *Euoidium* can be treated as the asexual morph of *Golovinomyces*. However, with the discontinuation of the dual nomenclature for pleomorphic fungi in 2012 and the corresponding changes in the “International Code of Botanical Nomenclature” (now “International Code of Nomenclature for algae, fungi, and plants”), the separate naming of anamorphs and teleomorphs of powdery mildews became obsolete, i.e., *Euoidium* is now a heterotypic synonym of *Golovinomyces*. Unfortunately, the name *Euoidium*, described in 1985 (Paul and Kapoor 1985), takes priority over *Golovinomyces*, which was only introduced at genus rank in 1988 (Heluta 1988). Therefore, the name *Golovinomyces* needs to be conserved against *Euoidium*, which has been done in a proposal submitted to Taxon (Braun et al. 2022).

The first comprehensive phylogenetic examinations of the species of the genus *Golovinomyces* were published by Matsuda and Takamatsu (2003) and Takamatsu et al. (2006, 2013). Scholler et al. (2016) revised the *G. biocellatus* complex and divided it into several species. Bradshaw et al. (2017) introduced the name *G. chrysanthemi* and presented the phylogeny of the *Chrysanthemum* powdery mildews and allied species. Braun et al. (2018) published a phylogenetic revision of

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**Figure 1.** Bayesian maximum clade credibility tree of the concatenated (GAPDH+IGS+ITS+28S) sequences of the *Golovinomyces* taxa from group 1 of the SUPPLEMENTARY FIG. 1 tree. Posteriors 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; LT = ex-lectotype; NT = ex-neotype; PT = ex-paratype; RS = reference sequence(s). Quotations around taxa signify that the name is no longer current. Taxa in bold were sequenced for the current study.
Figure 2. Bayesian maximum clade credibility tree of the concatenated (GAPDH+IGS+ITS+28S) sequences of the Golovinomyces taxa from group 2 of the SUPPLEMENTARY FIG. 1 tree. 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; LT = ex-lectotype; NT = ex-neotype; PT = ex-paratype; RS = reference sequence(s). Quotations around taxa signify that the name is no longer current. Taxa in bold were sequenced for the current study.

G. cynoglossi and divided this taxon into several species. The complicated complex around the plurivorous G. orontii s. lat. was phylogenetically examined and split into multiple species by Braun et al. (2019). Another phylogenetically and taxonomically difficult complex around G. ambrosiae has recently been revised on the basis of a phylogenetic multilocus approach (Qiu et al. 2020a). In this work, the taxonomic status of the phytopathologically important sunflower powdery mildew was clarified, including the introduction of the name G. latisporus. The following results are contributions that improve the phylogenetic-taxonomic knowledge of Golovinomyces spp. This work has been performed within the framework of a project aiming to produce a monographic treatment of North American powdery mildews.

The monographic treatment of Golovinomyces spp. in Braun and Cook (2012) constitutes the basis for the morphological characterization and discrimination of recognized older species published up to that time. One of the main goals of the present paper is to clarify the phylogenetic status of the species from Braun and Cook (2012), and those additional species introduced after the publication of Braun and Cook (2012). We intend to give an overview of the recognized Golovinomyces spp., based on a combination of morphology, host range, and phylogenetic analyses. Molecular phylogenetic analyses have been performed using ITS, 28S, IGS, and GAPDH. Individual region analyses have been carried out and supplemented by a concatenated phylogenetic analysis.

Species concept applied in powdery mildews.—Species concepts should, in general, not be arbitrary. They should be clear, plausible, and uniform in classifying organisms. Therefore, the basic species concepts applied in the taxonomy of powdery mildews are briefly outlined as follows:

(i) New species should not be introduced without supporting sequence data, and an emphasis should be placed on having at least two collections of any newly described species.
All recognized species should form well-supported, monophyletic clades, separate from all other powdery mildew species.

In the case of assemblages of closely allied species or sister species, the species should be characterized by having unique morphologies and/or unique host ranges.

This allows the differentiation of populations from species. An example would be when two taxa groups are sister to each other and are monophyletic. If these organisms share the same host species, and are morphologically identical to each other, we will consider these separate populations of the same species.

Phylogenetically distant species (i.e., they are not sister to each other) may have similar morphologies and/or overlapping host ranges but would be considered distinct species.

When taxa are not phylogenetically separable but have clear morphological differences, we prefer to designate them as varieties, at least for the interim, until future multilocus analyses can be accomplished to resolve the taxa.

**Golovinomyces** (U. Braun) Heluta, Biol Zhurn Armenii 41(1):357. 1988, nom. cons. prop. (Braun et al. 2022).

≡ *Erysiphe* sect. Golovinomyces U. Braun, Feddes Repert 88:659. 1978 [type species: *Erysiphe cichoracearum* DC. (≡ *Golovinomyces cichoracearum* (DC.) Heluta)].

≡ *Euoidium* Y.S. Paul & J.N. Kapoor, Indian Phytopathol 38:761. 1985 [type species: *Oidium erysiphoides* Fr.], nom. rej. prop. (Braun et al. 2022).

≡ *Oidium* subgen. *Reticuloidium* R.T.A. Cook, A.J. Inman & C. Billings, Mycol Res 101(8):998. 1997.

≡ *Erysiphe* auct. p.p.

Type species: *Erysiphe cichoracearum* DC. (≡ *Golovinomyces cichoracearum* (DC.) Heluta).

References: Heluta (1989, 106), Simonyan (1994, 185), Braun (1999), Braun et al. (2002), Shin (2000, 73), Matsuda and Takamatsu (2003), Bolay (2005, 84), Schönbrunn et al. (2017a).
Takamatsu et al. (2006), Voytyuk et al. (2009, 148), Liu (2010, 142), and Braun and Cook (2012, 294).

Mycelium ectophytic, superficial, white, evanescent to persistent, effuse, forming patches or confluent, sometimes covering entire leaf blades. Hyphae thin-walled, mostly smooth or almost so, about (1.5–)2–10(–14) μm wide, usually colorless, old hyphae sometimes turning yellowish to brownish, forming pigmented secondary mycelium. Hyphal appressoria indistinct to usually nipple-shaped, occasionally with somewhat crenulate surface or slightly lobed, solitary or in opposite pairs. Asexual morphs belonging to the Euoidium type. Conidiophores arising from superficial hyphae, on the upper surface of mother cells or lateral, erect, unbranched, foot cells cylindrical or somewhat increasing in width from base to apex, straight or curved-sinuous, foot cell followed by 1–4 mostly shorter cells, occasionally by cells of the same length or longer. Conidia maturing gradually in short to long chains (cate- nescent), ellipsoid-ovoid, doliform, limoniform, subcy- lindrical, 1-celled, colorless, outline (margin) of young chains sinuous, surface (scanning electron microscope [SEM]) with “roughcast” outer wall in turgid conidia, drying into a more or less polygonal, reticulate pattern (Cook et al. 1997). Conidial germ tubes usually terminal or almost so, to moderately long (1–2.5 times as long as the conidial width), tips usually swollen, with a club-shaped appressorium [= Euoidium type (sect. Golovinomyces)] or almost terminal to lateral, on glass at 100% relative humidity (RH) mostly moderately long to very long (up to 10 times as long as the conidial width), narrow, filiform, without swollen apex, mostly aerial (negatively hydrotropic), unless in contact with glass surface then slightly swollen with an appressorium [= longitubus pattern of the Euoidium type]; sect. Depressi (dimorphic, some shorter tubes in contact with surface typical also of the Euoidium type). Chasma- thecia ±globose to depressed-globose or lentiform, about 70–160 μm diam, rarely larger, not distinctly dorsiventral; peridium multilayered, pigmented, dark, opaque, rarely semitransparent, cells of peridial walls polygonal, irregular in outline, but usually with curved to sinuous walls; chasmothecial appendages few to numerous, equatorial and in the lower half of the chasmothecium, occasionally in the upper half, ±mycelfloid, simple or occasionally irregularly branched, continuous to pluriseptate, hyaline to pigmented, walls thin to somewhat thickened, smooth to faintly rough; asci numerous, ellipsoid-obovoid to clavate-saccate, stalked or sessile, usually mature in the current season, 2(–4)-spored; ascospores ellipsoid-ovoid or almost globose, 1-celled, colorless to yellowish or greenish [mainly based on Braun and Cook (2012)].

**Survey of phylogenetically demonstrated Golovinomyces species, including taxonomic novelties, new records, and epitypifications.—**

Golovinomyces cichoracearum (DC.) Heluta, Ukarins’k Bot Zhurn 45(5):62. 1988, s. str. (emend.). [type species]

≡ Erysiphe cichoracearum DC., Fl franç 2:274. 1805.
≡ Alphitomorpha communis e cichoracearum (DC.) Wallr., Verh Ges Naturf Freunde Berlin 1(1):31. 1819.
≡ Erysibe communis var. cichoracearum (DC.) Link, Sp pl 4 6(1):107. 1824.
≡ Erysiphe communis o. cichoracearum (DC.) Fr., Syst mycol 3:241. 1829.
≡ E. horridula b. cichoracearum (DC.) Rabenh., Deutschl Krypt-FI 1:235. 1844.
≡ Uncinula cichoracearum (DC.) Fuss, Arch Vereins Siebenbürg Landesk N F 14(2):462. 1878.

Lectotype (designated by Braun 1987): FRANCE. On Scorzonera hispanica, “Erysiphe cichoracearum ad fl. fr. in Scorzonera hispanica”—herb. de Candolle (G 00298360). Epitype (designated here; MycoBank MBT10006874): GERMANY. SACHSEN-ANHALT: Saalekreis, Teutschenthal, Ortsteil Angersdorf, garden, on Scorzonera hispanica, 3 Aug 1977, U. Braun (VPRI 20383). Isotype: HAL 1173 F. Ex-epitype sequence: GQ183946 (ITS).

≡ Erysiphe scorzonerae Castagne, Cat pl Marseille:189. 1845.
≡ Erysiphe cichoracearum f. scorzonerae Jacz., Karm Opred Grib Vip 2 Muchn-roj griby:207. 1927.
≡ Erysiphe cichoracearum f. tragopogi Jacz., Karm Opred Grib Vip 2 Muchn-roj griby:212. 1927.

Notes: This is the type species of Golovinomyces. Previously, this species was recognized in a very broad sense, covering almost the complete host range of the currently recognized genus Golovinomyces (Blumer 1933, 1967; Homma 1937; Parmelee 1977; Salmon 1900). Braun (1987) made the first attempts to limit the circumscription of this species, confining it to diverse hosts of the Asteraceae, and added four varieties. Matsuda and Takamatsu (2003) demonstrated that the phylogeny of Golovinomyces spp. on Asteraceae hosts evolved along with the host subfamilies and tribes. Based on these results, Braun and Cook (2012) introduced a new concept and circumscription of G. cichoracearum and restricted this species to hosts belonging to tribe Cichorieae of fam. Asteraceae. However, this conclusion was not sustained. In comprehensive phylogenetic studies on Golovinomyces spp., Takamatsu et al. (2013) demonstrated that G. cichoracearum s. str. represents a species on Scorzonea and Tragopogon spp. (Asteraceae subtribe...
Scorzonerae). Sequences retrieved from infected species of these genera form a distinct, well-supported clade. The designated epitype is a collection on Scorzonera hispanica, the type host, from Germany (GQ183946).

*Golovinomyces adenophorae* (R.Y. Zheng & G.Q. Chen) Heluta, Ukrayins’k Bot Zhurn 45(5):62. 1988.

≡ *Erysipe adenophorae* R.Y. Zheng & G.Q. Chen, Sydowia 34:235. 1981.

**Holotype:** CHINA. HEBEI: Baihuashan, on *Adenophora tetraphylla*, 13 Sep 1978, *Han et al*. 70 (HMAS 38971).

≡ *E. cichoracearum* f. *adenophorae* Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:184. 1927.

≡ *E. cichoracearum* auct. p.p.

**Notes:** Two sequences retrieved from Japanese specimens on *Adenophora triphylla* group together and form a monophyletic clade separate from all other *Golovinomyces* spp., which confirms the status of *G. adenophorae* as a species of its own. However, it is still necessary to retrieve a sequence from the holotype or authentic material.

*Golovinomyces ambrosiae* (Schwein.) U. Braun & R.T.A. Cook, Mycol Res 113(5):628. 2009.

≡ *Erysiphe ambrosiae* Schwein., Trans Amer Philos Soc NS 4:270. 1834.

**Holotype:** USA. PENNSYLVANIA: Lehigh and Northampton counties, Bethlehem, on *Ambrosia* sp., 1826, *L. v. Schweinitz* (PH 62362). Epitype (designated by Qiu et al. 2020a): USA. IOWA: Guthrie County, Sheeder Prairie State Preserve, on *Ambrosia trifida*, 12 Aug 1997, L.H. Tiffany (ISC-F-0076753). Ex-epitype sequence: MK452568 (IGS).

≡ *Erysiphe spadicea* Berk. & M.A. Curtis, Grevillea 4:159. 1876.

≡ *Golovinomyces spadiceus* (Berk. & M.A. Curtis) U. Braun, in Braun & Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews):329. 2012.

≡ *Erysiphe cichoracearum f. ambrosiae* Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:186. 1927.

≡ *Erysiphe cichoracearum f. xanthii* Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:212. 1927.

≡ *Oidium acanthospermi* Chidd., Lloydia 18:46. 1955.

≡ *Acrorosporium acanthospermii* (Chidd.) Subram., Hyphomycetes (New Delhi):835. 1971.

≡ *Oidium lagascae* Chidd., Lloydia 18:47. 1955.

≡ *Acrorosporium lagascae* (Chidd.) Subram., Hyphomycetes (New Delhi):836. 1971.

≡ *Oidium parthenii* Satyapr. & Ushar., Curr Sci 50:1081. 1981.

≡ *E. cichoracearum* var. *transvaalensis* G.J.M. Gorter & Eicker, S Afr J Bot 2(2):130. 1983.

≡ *Golovinomyces cichoracearum* var. *transvaalensis* (G.J. M. Gorter & Eicker) U. Braun, Schlechtendalia 3:51. 1999.

≡ *Erysiphe sparsa* U. Braun, Mycotaxon 20:495. 1984, syn. nov. [Holotype: USA. WISCONSIN: Dane County, Madison, on *Acalypha virginica*, 17 Oct 1944, Greene (FH00965657). Ex-holotype sequences: ITS = ON366996; IGS = ON361173; GAPDH = ON360701.]

≡ *Golovinomyces sparsus* (U. Braun) Heluta, Ukrayins’k Bot Zhurn 45(5):63. 1988.

≡ *Oidium blainvillei* Bappamm., Hosag. & Udaian, New Botanist 22:117. 1995.

≡ *Erysiphe cichoracearum* auct. p.p.

≡ *Golovinomyces cichoracearum* auct. p.p.

**Notes:** Braun and Cook (2012) used the name *Golovinomyces ambrosiae* for the common sunflower powdery mildew, which is well characterized by having particular anamorphic traits, such as rather broad conidia with a special germination pattern. The common powdery mildew on a wide range of other hosts of the Heliantheae was referred to as *G. spadiceus* (type host *Xanthium* sp.). In phylogenetic analyses based on ITS sequences, *G. ambrosiae* and *G. spadiceus* could not be differentiated (Takamatsu et al. 2013). Therefore, Qiu et al. (2020a) carried out a multilocus analysis of this complex of *Golovinomyces* spp. and demonstrated that *G. ambrosiae* (= *G. spadiceus*) represents the correct name for the plurivorous powdery mildew on hosts of the Heliantheae. *G. ambrosiae* has also been confirmed in *GAPDH* and IGS analyses performed in the course of the present studies. This species occurs on a wide range of hosts of other families as well, including Fabaceae, Malvaceae, Polygonaceae, Solanaceae, and Verbenaceae (Qiu et al. 2020a). During the present studies, hosts of two additional families have been confirmed for *G. ambrosiae*, i.e., *Acalypha* (Euphorbiaceae) and *Asclepias* (Apocynaceae). Sequences retrieved from the holotype of *Erysiphe sparsa* (type host = *Acalypha virginica*) cluster within the *G. ambrosiae* clade, which led to the reduction of this taxon to synonymy with *G. ambrosiae*.

*Golovinomyces americanus* (U. Braun) Heluta, Ukrayins’k Bot Zhurn 45(5):62. 1988.

≡ *Erysiphe americana* U. Braun, Mycotaxon 18(1):124. 1983.

**Holotype:** USA. WISCONSIN: Green County, near Juda, on *Napaea dioica*, 12 Aug 1961, H.C. Greene.
(ARIZ-M-AN01117). Isotypes: BPI 560936, DAOM87575, RMS0003545, WIS-F-0015173, WSP52003.

= *E. cichoracearum* f. *napaeae* Jacz. [as 'napaeae'], Karm Opred Grib Vip 2 Muchn-rosj griby:218. 1927.

= *E. cichoracearum* auct. p.p.

Notes: A single sequence obtained from *G. americanus* has been added to the present tree (FIG. 1). It belongs to a little supported cluster composed of sequences from North American powdery mildews on different hosts, including *G. greeneanus*, adjacent to the *G. hydrophyllacearum* clade. A conclusion on the status of *G. americanus* and a satisfying interpretation of this complex is not yet possible. More sequence data are needed. It is possible that the taxa included cannot be sufficiently resolved based solely on ITS+28S sequence data, or that a plurivorous North American *Golovinomyces* species is involved.

**Golovinomyces arabisid** (R.Y. Zheng & G.Q. Chen) Heluta, Ukrayins’k Bot Zhurn 45(5):62. 1988.

= *Erysiphe arabisida* R.Y. Zheng & G.Q. Chen, Sydowia 34:256. 1981.

Holotype: CHINA. Beijing, Miaofengshan, on *Arabis pendula*, 15 Oct 1959, Wang et al. 599 (HMAS 39997). Reference sequences: KR048081 (ITS), KR048149 (28S); SHAA1X: On *Arabis pendula*, L. Bai (HMNWAFU-CF2009256, unpublished).

= *E. cichoracearum* auct. p.p.

Notes: Only a single unpublished sequence retrieved from the type host of *G. arabisid* in China is available. It clusters distant from all other *Golovinomyces* spp., which supports the status of *G. arabisid* as an independent species. The type material from 1959 might provide sequence data. Therefore, for the interim, we prefer to propose using the Chinese sequences cited above as a reference.

**Golovinomyces artemisiae** (Grev.) Heluta, Ukrayins’k Bot Zhurn 45(5):62. 1988.

= *Erysiphe artemisiae* Grev., Fl edin:459. 1824.

Lectotype (designated by Bradshaw et al. 2017): UK. SCOTLAND: Fife, Balmuto, on *Artemisia vulgaris*, in herb. Greville (E00456057). Epitype (designated by Bradshaw et al. 2017): UK. SCOTLAND: Edinburgh, Innocent Railway, 55°56′21.8″N, 3°09′47.5″W, on *Artemisia vulgaris*, 8 Oct 2016, S. Helfer (HAL 3172 F). Isoepitypes: TNS-F-88292, previously TSU-MUMH6849, and distributed as U. Braun, Fungi Sel Exs 230. Ex-epitype sequence: LC217864 (ITS+28S).

= *Alphitomorpha depressa* β *artemisiae* Wallr., Verh Ges Naturf Freunde Berlin 1(1):34. 1819.

= *A. artemisiae* Wallr., Ann Wetterauischen Ges Gesammte Naturk N F 4:240. 1819.

= *Erysiphe depressa* var. *artemisiae* (Wallr.) Link, Sp pl 4 6(1):110. 1824.

= *E. depressa* b. *artemisiae* (Wallr.) Rabenh., Deutsch Krypt-Fl 1:232. 1844.

= *E. artemisiae* (Wallr.) Fuss [as ‘(Link)’], Arch Vereins Siebenbürg Landesk N F 14(2):460. 1878, nom. illeg. (Art. 53.1).

= *E. cichoracearum* f. *artemisiae* Jacz. [as “(Fukkel) Jacz.”], Karm Opred Grib Vip 2 Muchn-rosj griby:186. 1927.

= *E. cichoracearum* auct. p.p.

Notes: Bradshaw et al. (2017) included *Golovinomyces artemisiae* in phylogenetic analyses, lecto- and epitypified this name, including ex-epitype sequences, and confirmed its status as an independent species. *Golovinomyces artemisiae* is widespread on *Artemisia vulgaris*, its type host. A collection on *A. arctica* from Canada has been sequenced and clusters adjacent to the *G. artemisiae* clade. This powdery mildew and many other collections on diverse *Artemisia* spp. worldwide require further examinations to clarify whether a single or additional *Golovinomyces* species are involved on hosts of this genus.

**Golovinomyces asperifolii** (Erikss.) U. Braun & H.D. Shin, Mycobiology 46(3):198. 2018.

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

Lectotype (designated by Braun et al. 2018): SWEDEN. Stockholm, Experimentalfaltet, on *Myosotis sylvatica* [M. “alpestris” hort.], 11 Jul 1882, J. Eriksson (Erikss., Fungi Paras Scand Exs 386) (S-F270062). Epitype (designated by Braun et al. 2018): GERMANY. SACHSEN: Görlitz-Bresnitz, on *Myosotis sylvatica*, 10 May 2007, H. Boyle (GLM-F079322). Ex-epitype sequence: MH189707 (ITS).

= *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).

Notes: *Golovinomyces asperifolii* was introduced in Braun et al. (2018) for a clade composed of sequences retrieved from a wide range of hosts of the Boraginaceae, which had previously been subsumed under *G. cynoglossi* s. lat. (Braun and Cook 2012). *Golovinomyces asperifolii* is a powdery mildew that occurs in Eurasia on hosts of the genera *Bothriospermum*, *Buglossoides*, *Cynoglossum*, *Echium*, *Myosotis*, and *Trigionotis*. In the course of the present...
examinations, sequences have been obtained from North American collections of *G. cynoglossi* s. lat. on *Amsinckia intermedia*, *Cryptantha affinis*, *Hackelia californica* (≡ *Lappula californica*), and *Mertensia paniculata*, all belonging to subfam. Cynoglossoideae, as is the case of *Myosotis*. They group close to the ex-epitope sequence of *G. asperifolii*. These North American powdery mildew samples are tentatively assigned to the latter species, but they require further examinations to eliminate the possibility of the presence of a cryptic North American *Golovinomyces* species closely related to *G. asperifolii*.

**Golovinomyces asperifoliorum** (Grev.) U. Braun & H.D. Shin, Mycobiology 46(3):196. 2018.

≡ *Erysiphe asperifoliorum* Grev., Fl edin:461. 1824.

Lectotype (designated by Braun et al. 2018): UK. SCOTLAND: Roslin, on *Symphytum* sp., undated, R.K. Greville (E 456091). Epitope (designated by Braun et al. 2018): GERMANY. SACHSEN-ANHALT: Roßlau, Ragösen, Rathbruch, on *Symphytum officinale*, 28 Aug 2004, A. Hoch (GLM-F073207). Ex-epitope sequence: MH189693 (ITS).

Notes: Braun et al. (2018) published results of a phylogenetic revision of the *Golovinomyces cynoglossi* s. lat. complex and split it into a number of species, including *G. asperifoliorum*, which forms a strongly supported clade composed of sequences obtained from European specimens on *Pulmonaria* spp. and *Symphytum* spp.

**Golovinomyces asterum** (Schwein.) U. Braun, in Braun & Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews):302. 2012, var. *asterum*.

≡ *Erysiphe asterum* Schwein., Trans Amer Philos Soc 4:270. 1834.

Holotype: USA. PENNSYLVANIA: Lehigh and Northampton counties, Bethlehem, on *Aster paniculatus* [Mill. non Lam.] (= *Symphyotrichum ×salignum*), 1826, L. von Schweinitz (PH00062363). Reference sequences: ON073879 (ITS+28S); ON361199 (IGS); ON075650 (GAPDH) (USA. COLORADO: Denver, on *Symphyotrichum novae-angliae*, FH00941249).

≡ *Erysiphe cichoracearum* f. *asteris* Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:188. 1927.

≡ *Oidium asteris-punicei* Peck, Bull New York State Mus Nat Hist 150:35. [“1910”] 1911.

≡ *O. astericum* I. Hino & H. Katoa, Bull Miyazaki Coll Agric 1:91. 1929.

≡ *Erysiphe cichoracearum* auct. p.p.

≡ *Golovinomyces cichoracearum* auct. p.p.

Notes: Sequences retrieved from *Golovinomyces* on *Aster* (s. lat.) and *Solidago* spp. form a well-supported clade. The two varieties of *G. asterum*, var. *asterum* and var. *solidaginis*, are not reflected in the ITS tree. The GAPDH and concatenated trees suggest that the two varieties might pertain to sister clades, but the number of included sequences retrieved from var. *solidaginis* is too small to reach a conclusion. Therefore, we prefer to maintain these varieties, for the interim until more sequences are available. Variety *asterum* is characterized by having conidiophores with straight foot cells, whereas the foot cells in var. *solidaginis* are curved to sinuous (Braun and Cook 2012). The phylogenetic and taxonomic status of *G. asterum* var. *moroczkovskii* (Heluta) U. Braun (≡ *Erysiphe moroczkovskii* Heluta, *Golovinomyces moroczkovskii* (Heluta) Heluta) is not yet clarified.

The exact identity of the type host of *Erysiphe asterum* is not clear. de Schweinitz (1834) cited “*Aster paniculatus*,” but without listing an author name. It can be assumed that he had applied the name *Aster paniculatus* Mill. A formal epitypification is postponed until corresponding sequenced North American collections are available. For the interim, we propose to use reference sequences (see above) for the phylogenetic characterization of *G. asterum*.

**Golovinomyces asterum** var. *solidaginis* U. Braun, in Braun & Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews):304. 2012.

Holotype: USA. COLORADO: Palmer Lake, on *Solidago canadensis*, 20 Sep 1913, Bartholomew & Bethel, Barthol., Fungi Columb 4226 (BPI 561572). Reference sequences: ON367026 (ITS+28S); ON361200 (IGS); ON360715 (GAPDH) (USA. MASSACHUSETTS: Boston, on *Solidago* sp., FH00941272).

≡ *Erysiphe cichoracearum* f. *solidaginis* Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:210. 1927.

**Golovinomyces biocellatus** (Ehrenb.) Heluta, Ukrayins’k Bot Zhurn 45(5):62. 1988.

≡ *Erysiphe biocellata* Ehrenb., Nova Acta Phys-Med Acad Caes Leop-Carol Nat Cur 10:211. 1821, nom. cons.

≡ *Erysibe biocellata* [“biocellaris”] (Ehrenb.) Link, Sp pl 4 6(1):109. 1824.

≡ *Erysibe communis* f. *biocellata* (Ehrenb.) Fr., Syst mycol 3:239. 1829.

Lectotype (designated by Braun 1987): Ehrenberg (1821:pl. 13, original drawing). Epitope (designated here; MycoBank MBT10006875): GERMANY. SCHLESWIG-HOLSTEIN: Lübeck, St. Gertrud, city
park, lakeside, on Lycopus europaeus, 14 Oct 2012, A. Schmidt (KR-M-0035027). Ex-epitype sequence: LC076832 (ITS+28S).

= Oidium erysiphoides Fr., Syst mycol 3:432. 1832, nom. rej. Neotype (designated by Braun and Cook 2012): GERMANY. SACHSEN-ANHALT: Halle (Saale), Dölauer Heide, near “Waldkater,” on Lycopus europaeus, 24 Oct 1976, U. Braun (HAL 1051 F).

= Euvoidium erysiphoides (Fr.) Y.S. Paul & J.N. Kapoor, Indian Phytothor 38(4):762. 1985, nom. inval. (Art. 33.3).

= Euvoidium erysiphoides (Fr.) Y.S. Paul & J.N. Kapoor, Indian J Mycol Pl Pathol 17(3):302. 1987, nom. inval. (Art. 33.3).

Notes: Golovinomyces biscellatus was previously applied in a broad circumscription, encompassing a wide range of hosts of the Lamiaceae (Braun 1987; Braun and Cook 2012). Scholler et al. (2016) published results of a comprehensive phylogenetic revision of the G. biscellatus complex and split this complex into multiple species. Scholler et al. (2016) showed that G. biscellatus s. str. is confined to Lycopus europaeus and to Glechoma hederacea.

Golovinomyces bolayi S. Takam., Lebeda & M. Götz, in Braun et al., Mycol Progr 18:341. 2019.

Holotype: HUNGARY. Eger, on Lactuca serriola f. serriola, Aug. 2014, B. Sedláková (OLM 35939). Ex-holotype sequence: LC417106 (ITS).

= Erysiphe lamprocarpa f. intybi Thüm., Fungi Austr Exs Cent XIII No. 1247. 1875.

= E. cichoracearum f. cichorii-intybi Jacz. (as “Lév.”), Karm Opred Grib Vyp 2 Muchn-roj griby:192. 1927.

= E. cichoracearum f. lactucae Jacz., Karm Opred Grib Vyp 2 Muchn-roj griby:201. 1927.

= E. cichoracearum auct. p.p.

= Golovinomyces cichoracearum auct. p.p.

Notes: Golovinomyces bolayi belongs to the G. orontii s. lat. complex, which has been reexamed and revised by Braun et al. (2019). This species is plurivorous. Collections on Lactuca spp. and other Asteraceae hosts were previously assigned to G. cichoracearum (Braun and Cook 2012). A sequence retrieved from a North American powdery mildew sample on Lactuca serriola clusters within the G. bolayi clade, which confirms the occurrence of this species in North America.

Golovinomyces brunneopunctatus (U. Braun) Heluta, Ukrayins’k Bot Zhurn 45(5):62. 1988.

≡ Erysiphe brunneopunctata U. Braun, Mycotaxon 20:494. 1984.

≡ E. cichoracearum f. mimuli Jacz., Karm Opred Grib Vyp 2 Muchn-roj griby:224. 1927.

≡ E. cichoracearum auct. p.p.

Holotype: USA. CALIFORNIA: Amador County, Eldorado National Forest, on Mimulus guttatus, 22 Sep 1954, Quick [Calif. Fungi 1025] (FH00965643). Isotypes: Calif. Fungi 1025, M-0014122 (ex herb. Petrak). Ex-holotype sequences: ON367028 (ITS); ON360716 (GAPDH).

Notes: In ITS analyses, the ex-holotype sequence of Golovinomyces brunneopunctatus groups next to sequences retrieved from G. magnicellulatus together with a sequence obtained from Golovinomyces sp. (G. biellulatus s. lat.) on Scutellaria lateriflora that needs further morphological and genetic examinations. Golovinomyces spp. are common in North America on a number of native Scutellaria spp. The position of G. brunneopunctatus in the concatenated tree indicates an independent species, but more sequence data are necessary to make a conclusion.

Golovinomyces calceolariae Havryl., S. Takam. & Heluta, Mycol Res 113(1):123. 2009.

Holotype: ARGENTINA. RIO NEGRO: Parque Nacional Nahuel Huapi, Cerro Challhuaco, on Calceolaria polyrrhiza, 18 Apr 2001, M. Havrylenko & S. Takamatsu (BCRU 4527). Isotypes: BCRU 4528, KW 34470, TNS-F-87765 (previously TSU-MUMH 1934). Ex-holotype sequence: AB430810 (ITS+28S).

Notes: This species is only known from Argentina on Calceolaria polyrrhiza and from Galium aparine (Rubioaceae). Previously, collections were likely confused with Golovinomyces riedlianaum and Neoerysiphe galeopsisidis (Braun and Cook 2012).

Golovinomyces californicus (U. Braun) Heluta, Ukrayins’k Bot Zhurn 45(5):62. 1988.

≡ Erysiphe californica U. Braun, Mycotaxon 20:492. 1984.

Holotype: USA. CALIFORNIA: Alameda County, Berkeley, court of Life Science Building, University of California, on Eriogonum ×bliissianum, 13 Sep 1944, Bonar [Calif. Fungi 630] (CUP, CaliforniaF.00630). Paratypes: I.c., on Eriogonum giganteum [Calif. Fungi 631] (CUP, CaliforniaF.00631); USA. CALIFORNIA: Mt. Shasta, near the Sisson Southern Trail, just below Horse Camp, on E. marifolium, 26 Jul 1939, W.B. Cooke (FH00965644). Ex-paratype sequences: ON367029 (ITS); ON360717 (GAPDH) (retrieved from the latter collection).

≡ E. cichoracearum auct. p.p.

Notes: In the ITS analysis and concatenated tree, a sequence retrieved from a paratype of Erysiphe californica clusters distantly from all other clades of Golovinomyces spp., which confirms the status of this
species. However, additional sequences are necessary to confirm this result.

Golovinomyces chrysanthei (Rabenh.) M. Bradshaw, U. Braun, J. Meeboon & S. Takam., Mycologia 109(3):512. 2017.

≡ Oidium chrysanthei Rabenh., Hedwigia 1:19. 1853.
≡ Acrosoriun chrysanthei (Rabenh.) Põldmaa, Fitopatogenyye Mikromitsyty Severnoj Estonii:83. Tallin 1967.
≡ A. chrysanthei (Rabenh.) Subram., Hyphomycetes (New Delhi):836. 1971, isonym (Art. 6, Note 2).
≡ Euoidium chrysanthei (Rabenh.) U. Braun & R.T. A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews):333. 2012.

Lectotype (designated by Bradshaw et al. 2017) GERMANY. SAXONY: Dresden, on chrysanthemum (= Chrysanthemum ×morifolium), Rabenh., Klotzschii Herb Viv Mycol Cent XVIII no. 1763 (HAL, s.n.). Epitype (designated by Bradshaw et al. 2017) GERMANY. LOWER SAXONY: Braunschweig, Julius Kühn Institute, greenhouse, on Chrysanthemum ×morifolium, Jan 2017, M. Götz (HAL 3189 F). Isoepitopes: U. Braun, Fungi Sel Exs 227 (e.g., BPI, HAL, M). Epitype sequence: LC217869 (ITS+28S).

Notes: Bradshaw et al. (2017) demonstrated that sequences retrieved from Asian, European, and North American specimens of the chrysanthemum powdery mildew form a well-supported clade within Golovinomyces, suggesting its status as an independent species. So far, G. chrysanthei is only known in its anamorphic state.

Golovinomyces circumfusus (Schltdl.) U. Braun, in Braun & Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews):309. 2012.
≡ Alphitomorpha circumfusus Schltdl., Verh Ges Naturf Freunde Berlin 1(1):49. 1819.
≡ Erysibe circumfusa (Schltdl.) Ehrenb., Nova Acta Phys-Med Acad Caes Leop-Carol Nat Cur 10:169. 1821.
≡ Erysiphe circumfusa (Schltdl.) Schltdl., Fl berol 2:169. 1824.
≡ Erysibe circumfusca (Schltdl.) Link, Sp pl 4 6(1):109. 1824.
≡ Erysiphe communis f. circumfusa (Schltdl.) Fr., Syst mycol 3:240. 1829.

Lectotype (designated by Dörfelt and Ali 1987) GERMANY. On Eupatorium cannabinum, ex herb. Schlechtendal, without further data (HAL 1423 F). Epitype (designated by Qiu et al. 2020a) GERMANY. BRANDENBURG: Spreewald, Briesensee, on Eupatorium cannabinum, 8 Oct 2016, V. Kummer (HAL 3300 F). Ex-epitype sequences: MK452628.1 (ITS); MK452701.1 (28S); MK452555 (IGS); MK452459 (TUB2); MK452455.1 (CHS1).

≡ E. cichoraeform auct. p.p.
≡ Golovinomyces cichoracearum auct. p.p.

Notes: Braun and Cook (2012) used the name Golovinomyces circumfusus for powdery mildews on Eupatorium spp. in Asia, Europe, and North America. However, the first phylogenetic examinations published by Takamatsu et al. (2013) raised doubts on this concept of G. circumfusus. A sequence obtained from G. "circumfusus" on Eupatorium chinense in Japan clustered together with sequences of G. spadiceus (now G. ambrosiae). To clarify the true status of G. circumfusus, Qiu et al. (2020a) performed a phylogenetic multilocus examination of this complex of species and confirmed the independent status of G. circumfusus as a species confined to Eupatorium cannabinum in Europe.

The affinity of E. cichoracearum f. euporitii Dearn. (in Rehm, Ascomyc Fasc 48, No. 1950, 1911, and Ann Mycol 9:290. 1911) is unclear. This form was based on Canadian material on Eupatorium perfoliatum. Another Canadian powdery mildew specimen on Eupatorium maculatum has been sequenced and groups within the G. ambrosiae clade, suggesting that E. cichoracearum f. euporitii is a synonym of G. ambrosiae.

Golovinomyces cynoglossi (Wallr.) Heluta, Ukrayins'k Bot Zhurn 45(5):62. 1988.
≡ Alphitomorpha cynoglossi Wallr., Ann Wetterauischen Ges Gesammte Natur F 4:240. 1819.
≡ Erysipe cynoglossi (Wallr.) U. Braun, Mycotaxon 15:136. 1982.
≡ E. artemisii var. cynoglossi (Wallr.) Ialongo, Mycotaxon 44(1):255. 1992, nom. inval. (Art. 41.3).

Lectotype (designated by Braun and Cook 2012) On Cynoglossum officinale, herb. Wallroth, without any further data (STR). Epitype (designated by Braun et al. 2018) GERMANY. NORDRHEIN-WESTFALEN: Kreis Soest, Erwitte, near Eikeloh, on Cynoglossum officinale, 16 Oct 1999, U. Raabe (GLM-F047442). Ex-epitype sequence: MH189701 (ITS).
≡ Erysipe horridula var. cynoglossi Sorok., Rev Mycol 11:147. 1889.

Notes: Braun and Cook (2012) used the name Golovinomyces cynoglossi (s. lat.) for Golovinomyces powdery mildews on hosts of the Borraginaceae. Based on results of phylogenetic sequence analyses, Braun et al. (2018) divided G. cynoglossi into a number of species. As a result, G. cynoglossi (s. str.) refers to a clade composed of sequences...
retrieved from Asian and European collections on Cynoglossum spp. and a single Australian sample on Myosotis sp., i.e., this specimen is likely the same powdery mildew as found on Cynoglossum. In the course of the current studies, a sequence was obtained from an Austrian Golovinomyces specimen on Rinderia lanata (≡ Cynoglossum lanatum) that groups within the G. cynoglossi clade.

**Golovinomyces depressus** (Wallr.) Heluta, Ukrayins`k Bot Zhurn 45(5):62. 1988.

≡ **Alphitomorpha depressa** Wallr., Verh Ges Naturf Freunde Berlin 1(1):34. 1819 (a bardanae).

Lectotype (designated by Braun and Cook 2012): On Arctium lappa, Oct, without any additional data, herb. Wallroth (STR). Epitype (designated here; MycoBank MBT10006876): HUNGARY. Budapest, on Arctium lappa, 7 Sep 1999, S. Takamatsu (TNS-F-87454). Ex-epitype sequences: AB077675 (ITS); AB077676 (28S).

≡ **Erysipe depressa** (Wallr.) Schltldl., Fl berol 2:169. 1824.

≡ **Erysibe depressa** (Wallr.) Link, Sp pl 4 6(1):110. 1824.

≡ **Erysipe communis f. depressa** (Wallr.) Fr., Syst mycol 3:240. 1829.

≡ **Alphitomorpha bardanae** Wallr., Ann Wetterauischen Ges Gesammte Naturk N F 4:239. 1819.

≡ **Erysipe bardanae** (Wallr.) Chev., Fl env Paris 1:381. 1826.

≡ **Erysiphe [Erysibe] depressa** var. *bardanae* (Wallr.) Link, Sp pl 6(1):110. 1824.

≡ **E. cichoraeacrum f. *bardanae*** (Wallr.) Jacz., Karm Opred Grib Vip 2 Muchn-rsøj griby:202. 1927.

≡ **E. arctii** Grev., Fl edin:460. 1824.

≡ **E. compositarum** Duby, Bot gall 2:870. 1830, nom. illeg. (nom. superfl., Art. 52.1), *E. depressa* was cited in the original description as synonym.

≡ **E. montagnei** Lév., Ann Sci Nat Bot 3 Sér 15:169. 1851, nom. illeg. (nom. superfl., Art. 52.1), *E. depressa* was included in the original circumscription.

≡ **E. cichoraeacrum f. centaureae-montanae** S. Blumer, Centrabl Bakteriol Abth II 57:45. 1922.

≡ **E. cichoraeacrum f. onopordonis** Jacz., Karm Opred Grib Vip 2 Muchn-rsøj griby:205. 1927.

**Notes:** Sequences obtained from **Golovinomyces depressus** form a well-supported clade in the ITS and concatenated analyses.

**Golovinomyces echinopis** (U. Braun) Heluta, Ukrayins`k Bot Zhurn 45(5):62. 1988.

≡ **Erysipe echinopis** U. Braun, Feddes Repert 92(7–8):504. 1981.

**Holotype:** GERMANY. SACHSEN-ANHALT: Kölln near Halle (Saale), on Echinops sphaerocephalus, Sep 1979, U. Braun (HAL 2339 F). Ex-holotype sequence: MT406368 (ITS+28S).

≡ **E. cichoraeacrum f. *echinopis*** Jacz., Karm Opred Grib Vip 2 Muchn-rsøj griby:196. 1927.

≡ **E. cichoraeacrum** auct. p.p.

**Notes:** Bradshaw et al. (2021f) published an ex-holotype sequence for *G. echinopis*, which confirmed its status as an independent species, and added a sequence from a North American collection on *Echinops*. This provides an unequivocal confirmation of the occurrence of *G. echinopis* in North America.

**Golovinomyces euphorbiicola** (Havryl.) U. Braun & Havryl., in Braun & Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews):313. 2012.

≡ **Erysipe sparsa** var. *euphorbiicola* Havryl., Nova Hedwigia 63(1–2):77. 1996.

≡ **Golovinomyces sparsus** var. *euphorbiicola* (Havryl.) U. Braun, Schlechtendalia 3:51. 1999.

**Holotype:** ARGENTINA. NEUQUÉN: Rio Pichi Trafal, on Euphorbia collina var. nahueluapina, Apr 1996, M. Havrylenko (HAL 1386 F). Isotype: BCRU 934. Ex-isotype sequence: AB769461 (ITS+28S).

**Notes:** This species is known on *Euphorbia collina* from Argentina and Brazil.

**Golovinomyces eurybiarum** M. Bradshaw, sp. nov.

**FIG. 4**

MycoBank MB843955

**Etymology:** Epithet derived from the name of the host genus in genitive plural.

**Diagnosis:** Morphologically barely distinguishable from *Golovinomyces ambrosiae* but confined to hosts of *Eurybia* and phylogenetically confirmed separate from *G. ambrosiae* in the IGS and concatenated analyses.

**Description:** Mycelium ectophytic, white, forming patches that sometimes cover the entire leaf surface. Hyphae thin-walled, septate, mostly smooth, hyaline, about 2–10 µm wide, colorless. Hyphal appressoria solitary, nipple-shaped, 4–6 µm diam. Conidiophores arising from the upper surface of mother cells, erect, unbranched, foot cells somewhat increasing in width from base to apex, straight, 32–93 × 7–11 µm (average = 53 × 8 µm), foot cell followed by 1–3 shorter cells forming catenescence conidia. Conidia ellipsoid-ovoid, doliiform, 24–33 × 11–18 µm (average = 29 × 15 µm)
with a length-to-width (L/W) ratio of 1.5–2.4 (average = 2). Conidial germ tubes short of the Euoidium type. Chasmothecia not observed.

Holotype: USA. MASSACHUSETTS: Boston, at the Arnold Arboretum beneath accession number 22898 on Eurybia divaricata, 26 Aug 2021 (FH00941263). Ex-holotype sequences: ON367032 (ITS+28S); ON361202 (IGS); ON360718 (GAPDH).

Notes: Golovinomyces eurybiarum pertains morphologically and phylogenetically to the G. ambrosiae complex. This species occurs on Eurybia spp. The genus Eurybia is a segregation of Aster (s. lat.) that mainly comprises North American species (Selliah and Brouillet 2008). Sequences of the new species cluster distantly from sequences of G. asterum, a species that was to be expected on Eurybia spp. ITS data are not sufficient for reliable resolutions within the G. ambrosiae complex. However, comparable to the case of G. latisporus, IGS proved to be a reliable marker for the differentiation on species level in this group (Qiu et al. 2020a) and confirmed G. eurybiarum as a species of its own. This is also evident in the concatenated tree. Specimen FH00941281 was infected with an Ampelomyces sp.

Golovinomyces fischeri (S. Blumer) U. Braun & R.T.A. Cook, Mycol Res 113(5):628. 2009.

= Erysiphe fischeri S. Blumer, Beitr Krypt-Fl Schweiz 7(1):262. 1933.

= E. cichoracearum var. fischeri (S. Blumer) U. Braun, Nova Hedwigia 34:695. 1981.

= Golovinomyces cichoracearum var. fischeri (S. Blumer) U. Braun, Schlechtendalia 3:51. 1999.

Lectotype (designated by Braun 1987): SWITZERLAND. BERN: Burgsdorf, Steinhof, on Senecio vulgaris, 12 Oct 1926, S. Blumer (FH0065646).

Ex-lectotype sequences: ON367034 (ITS); ON360719 (GAPDH).

= Erysiphe cichoracearum auct. p.p.

= Golovinomyces cichoracearum auct. p.p.

Notes: Sequences from Golovinomyces fischeri form a monophyletic clade separate from all other Golovinomyces spp. in the ITS, GAPDH, and concatenated phylogenetic analyses. G. fischeri occurs on hosts belonging to Senecio sect. Senecio, with S. vulgaris as its main host. The relationship of G. fischeri to G. senecionis, which mainly occurs on Senecio spp. of the S. nemorensis group in Eurasia, is not yet clear. The two species are easily distinguished by curved-sinuous (G. fischeri) vs. straight (G. senecionis) conidiophore foot cells. A sequence retrieved from Golovinomyces on Senecio doronicum clusters close to G. fischeri (only 1 bp difference from the ex-type sequence), but further studies are necessary to clarify the genuine affinity of this powdery mildew.

Golovinomyces fuegianus (Havryl. & U. Braun) U. Braun, M. Bradshaw & Pfister, comb. nov.

MycoBank MB843861

Basionym: Oidium fuegianum Havryl. & U. Braun, Nova Hedwigia 66:517. 1998.

= Euoidium fuegianum (Havryl. & U. Braun) U. Braun & Havryl., Taxonomic Manual of the Erysiphales (Powdery Mildews):334. 2012.

Holotype: ARGENTINA. TIERRA DEL FUEGO: Mt. Olivia, on Ranunculus peduncularis, Mar 1996,
M. Havrylenko (BCRU 01608). Ex-holotype sequence: AB769443 (ITS).

Notes: Takamatsu et al. (2013) provided an ex-holotype sequence of Oidium fuegianum. The type sequence of this species clusters within Golovinomyces distant from all other species clades. Oidium fuegianum is typified by a conidial state, but our results of sequence analyses justify the transfer of this species to Golovinomyces.

Golovinomyces galiorum M. Bradshaw, sp. nov. FIG. 5 MycoBank MB843956

Etymology: Epithet derived from Galium, the genus of the type host, in plural genitive.

Diagnosis: Differs from Golovinomyces riedlianus in having smaller chasmothecia and from G. calceolariae in having smaller asci. Additionally, contains fewer asci than both other taxa and forms a separate, distinct phylogenetic clade.

Description: No anamorph observed. Mycellium on both sides of the leaves. Chasmothecia scattered to gregarious, globose, about 80–140 µm diam (average = 116 µm), peridium multilayered, pigmented, dark, cells
of peridial walls polygonal, irregular in outline, but usually with curved to sinuous walls; chasmothelial appendages numerous, myceloid, thin-walled, septate, hyaline, variable length but tends to be shorter than the chasmothelial diam, 3–7 μm wide, interwoven with the mycelium and can be difficult to distinguish from mycelium; ascii numerous (6–14), immature, stalked, 25–55 × 20–35 μm (average = 39 × 28 μm); ascospores undeveloped.

Holotype: USA. CALIFORNIA: Tulame County, Sierra Nevada, south of Cow Creek, north of Pinecrest, 6200 feet alt., 6 Jul 1951, on Galium bifolium, C.R. Quick no. 51285-112 (FH011220001). Ex-holotype sequences: ON367036 (ITS+28S); ON361205 (IGS); ON360721 (GAPDH).

Paratype: USA. WISCONSIN: Dane County, Madison, 7 Jul 1942, on Galium aparine, H.C. Greene (FH011220000). Ex-paratype sequences: ON367035 (ITS); ON361204 (IGS); ON360720 (GAPDH).

Notes: Phylogenetically, G. galiurn has been confirmed as a species of its own in all analyses, including the ITS+28S, GAPDH, IGS, and concatenated trees. Originally the holotype and paratype of G. galiurn were annotated as “Neoerysiphe gali” at the Farlow Herbarium, likely due to the immature status of their chasmothecia (no ascospores had formed within the asci).

Golovinomyces greeneanus (U. Braun) Heluta, Ukrayinsk’sk Bot Zhurn 45(5):62. 1988.

≡ Erysiphe greeneana U. Braun, Mycotaxon 19:380. 1984.

Holotype: USA. KANSAS: Stockton, on Parietaria pensylvanica, 15 Aug 1892, Bartholomew [Ellis & Everh, Fungi Columb 1822] (CUP). Isotypes: Ellis & Everh., Fungi Columb 1822 (e.g., BPI 561275, BPI 561285).

Paratypes: USA. WISCONSIN: Columbia County, Gibraltar Rock, on Parietaria pensylvanica, 28 Jun 1938, H.C. Greene (BPI 561276, BPI 561280, CUP-033635, FH00965649, RMS0009391, UC680999, WIS-F-0015160); Dane County, Madison, on Parietaria pensylvanica, 30 Jul 1944, H.C. Greene (ARIZ-M-AN01021).

Ex-paratype sequences (ex FH00965649): ON367038 (ITS+28S); ON360723 (GAPDH).

≡ E. cichoracearum f. parietariae Jacz., Karm Opred Grib Vyp 2 Muchn-rosj griby:214. 1927.

≡ E. cichoracearum auct. p.p.

Notes: In ITS and IGS analyses, two sequences retrieved from G. greeneanus, including a paratype specimen, form a species complex composed of multiple species, including G. hydrophyllecearum, G. magnicellulatus, G. americanus, G. malvacearum, G. brunneopunctatus, and G. verbenae. However, the concatenated and GADPH analyses confirmed G. greeneanus as a distinct species.
G. hydrophyllacearum on Nemophila parviflora groups sister to the G. hydrophyllacearum clade and is tentatively referred to as Golovinomyces sp. until further collections on Nemophila spp. can be evaluated.

Golovinomyces inulæ U. Braun & H.D. Shin, in Braun & Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews):317. 2012.

Holotype: KOREA. Suwon, on Inula britannica var. chinensis, 21 Oct 2009, H.D. Shin & M.J. Park (HAL 2367 F). Isotype: KUS-F 24783.

≡ Sphaeroteca castagnei f. inulæ-hirtae Sacc., Mycoth Ven 630. 1876.
≡ Erysiphe cichoracearum auct. p.p.
≡ Golovinomyces cichoracearum auct. p.p.

Notes: Type material of G. inulæ has not yet been sequenced, but a sequence retrieved from a specimen on Inula salicina collected in Switzerland is available and forms a well-supported clade together with a German sequence from Golovinomyces sp. on Telekia speciosa. The morphology of the powdery mildew on Telekia agrees well with G. inulæ. Together with the results of the sequence analyses (ex HAL 3445 F), the Telekia powdery mildew can be assigned to the latter species. The genus Telekia belongs to the Asteraceae tribe Inuleae. These findings support the conclusions that there is coevolution among Golovinomyces spp. and tribes of the Asteraceae as suggested by the phylogenetic analyses of Golovinomyces spp. on Asteraceae carried out by Takamatsu et al. (2013). Golovinomyces inulæ on Telekia speciosa has spread in Germany in the last decades. The first record dates to Boyle et al. (2007). Currently, this powdery mildew is relatively common on Telekia speciosa in Germany.

Golovinomyces ixodiaæ (Cunningt., Beilharz & Pascoe) U. Braun & L. Kiss, in Kiss et al., Frontiers in Microbiology 11(no. 1571):22. 2020.
≡ Oidium ixodiaæ Cunningt., Beilharz & Pascoe, Australas PI Pathol 34:92. 2005.

Holotype: AUSTRALIA. SOUTH AUSTRALIA: Lenswood, on Ixodia achilleoides subsp. alata, 19 Sep 1995, B. Hall (VPRI 20703). Ex-holotype sequence: AY769954 (ITS).

Notes: Oidium ixodiaæ is an endemic powdery mildew species on Ixodia achilleoides, an indigenous Australian plant. This anamorphic species clusters within Golovinomyces, which justified its inclusion in the genus.

Golovinomyces latisporus (U. Braun) P.L. Qiu & S.Y. Liu, in Qiu, et al., BMC Microbiology 20(no. 51):11. 2020.
≡ Oidium latisporum U. Braun, Zentralbl Mikrobiol 137:315. 1982.

Holotype: GERMANY. SACHSEN-ANHALT: Greifenhagen, on Helianthus ×laetiflorus, 20 Sep 1981 (HAL 1434 F). Epitype (designated by Qiu et al. 2020a): SWITZERLAND. VAUD: Nyon, on Helianthus annuus, 17 Sep 2018, A. Bolay (HAL 3299 F). Ex-epitype sequences: MK452627 (ITS); MK452700 (28S); MK452552 (IGS); MK452497 (TUB2); MK452454 (CHS1).
≡ Erysiphe cichoracearum f. helianthi Jacz., Karm Opred Grib Vip 2 Muchn-roj griby;198. 1927.
≡ Erysiphe cichoracearum var. latispora U. Braun, Mycotaxon 18(1):117. 1983.
≡ Golovinomyces cichoracearum var. latisporus (U. Braun) U. Braun, Schlechtendalia 3:51. 1999.
≡ E. cichoracearum auct. p.p.
≡ Golovinomyces cichoracearum auct. p.p.

Notes: The history of the sunflower powdery mildew is intricate. Previously, this powdery mildew tended to be assigned to Erysiphe cichoracearum (Braun 1987). Braun (1982) introduced the name Oidium latisporum, based on anamorphs found in Germany. Later, Braun (1983) examined North American telemorphs and described Erysiphe cichoracearum var. latispora. Cook and Braun (2009) and Braun and Cook (2012) used the name Golovinomyces ambrosiae for this powdery mildew. Takamatsu et al. (2013) demonstrated that Golovinomyces spp. on hosts of the Asteraceae tribe Heliantheae forms a uniform ITS clade, including two morphologically differentiated powdery mildew species that were referred to as G. ambrosiae and G. spadicus in Braun and Cook (2012). However, in comprehensive phylogenetic multilocus examinations, Qiu et al. (2020a) revised this complex and showed that G. ambrosiae (syn. G. spadicus) is the correct name for the plurivorous Heliantheae Golovinomyces species and G. latisporus is the correct name for the sunflower powdery mildew, which occurs on hosts species of Helianthus, Zinnia, and probably additional genera. It is possible that G. latisporus might occur on Rudbeckia, but this still requires confirmation by sequencing. One specimen evaluated on R. fulgida in the present paper (FH00941203) fell in the G. ambrosiae clade. Additionally, Bradshaw et al. (2021d) conducted greenhouse trials and were unable to inoculate multiple Rudbeckia spp. with G. latisporus. The species of the following genera developed signs of disease caused by G. latisporus in greenhouse trials (Bradshaw et al. 2021d): Abelmochus, Ambrosia, Baccharis, Bebbia, Coreopsis, Encelia, Helianthus, Heliomeris, Melampodium, Parthenium, Ratibida, Sanvitalia, Vigulera, Xanthium, and Zinnia. It
should be noted that greenhouse experiments with powdery mildews are prone to contamination with non-target species (Bradshaw et al. 2021e).

_Golovinomyces leuceriae_ (Havryl.) U. Braun, Schlechtendal 3:51. 1999.

≡ _Erysiphe leuceriae_ Havryl., Nova Hedwigia 63(1–2):75. 1996.

_Holotype:_ ARGENTINA. RIO NEGRO: Bariloche, Mt. Tronador, on _Leuceria thermarum_, Apr 1996, M. Havrylenko (HAL 1387 F). Isotype: BCRU 00935. Reference sequence: AB246765 (ITS +28S) (ex TNS-F-87752, previously TSU-MUMH 1880).

_Notes:_ This species is confined to _Leuceria thermarum_ (Asteraceae [Carduoideae]) and is currently only known from Argentina (Chubut, Rio Negro). This species was phylogenetically examined by Takamatsu et al. (2006).

_Golovinomyces longipes_ (Noord. & Loer.) Kiss, in Braun et al., Mycol Progr 18(3):352. 2019.

≡ _Oidium longipes_ Noord. & Loer., Persoonia 14:53. 1989.

≡ _Euoidium longipes_ (Noord. & Loer.) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews):335. 2012.

_Notes:_ _Golovinomyces longipes_ occurs on tomato plants almost worldwide. Tomatoes are the most common host; thus, this widespread powdery mildew has special phytopathological relevance. It also occurs on other hosts of the Solanaceae (_Nicotiana, Petunia, and Solanum_ including _Lycopersicon_ [Braun and Cook 2012; Kiss et al. 2008; Toome et al. 2015]), and _Calibrachoa_ hybrids [Brielmaier-Liebetanz et al. 2015]). It has been recorded from Germany under glass house conditions on _Verbena xhybrida_, Verbenaceae (Brielmaier-Liebetanz et al. 2015), and on _Matricaria chamomilla_, Asteraceae (Göz and Braun 2022). The latter case was confirmed by sequence analyses. In the present phylogenetic analyses, sequences retrieved from _G. longipes_ and _G. lycopersici_ formed a species complex. Further studies are necessary to separate the taxa, including multilocus data (most importantly GAPDH sequences). Additionally, contaminations and misidentifications cannot be excluded. _G. longipes_ and _G. lycopersici_ are morphologically well distinguished and undoubtedly two different species.

_Golovinomyces lycopersici_ (Cooke & Massee) Kiss, in Braun et al., Mycol Progr 18(3):352. 2019.

≡ _Oidium lycopersici_ Cooke & Massee, in Cooke, Grevillea 16(80):114. 1888.

≡ _Euoidium lycopersici_ (Cooke & Massee) U. Braun & R.T.A. Cook, Taxonomic Manual of the _Erysiphales_ (Powdery Mildews):335. 2012.

_Holotype:_ AUSTRALIA. Upper Yarra (not preserved at K.). _Neotype_ (designated by Kiss et al. 2001): AUSTRALIA. VICTORIA: Timmering, on _Solanum lycopersicum_ (= _Lycopersicon esculentum_) cv. “Paycetter,” 1994, I. Pascoe (VPRI 19847). Ex-neotype sequence: AF229021 (ITS).

_Notes:_ The phylogeny and taxonomy of this powdery mildew was clarified by Kiss et al. (2001), who disentangled the confusing history of the tomato powdery mildew (see also _G. longipes_). _G. lycopersici_ is widespread in Australia and confined to tomato. See also notes under _G. longipes_.

_Golovinomyces macrocarpus_ (Speer) U. Braun, Taxonomic Manual of the _Erysiphales_ (Powdery Mildews):319. 2012.

≡ _Erysiphe macrocarpa_ Speer, Anz Österr Akad Wiss Math-Naturwiss Kl 106:245. [1969] 1970.

_Holotype:_ AUSTRIA. NIEDERÖSTERREICH: Zwerndorf, on _Tanacetum vulgare_, 14 Sep 1969, E.O. Speer (not preserved.) _Neotype_ (designated by Bradshaw et al. 2017): GERMANY. NORDHEIN-WESTFALEN: Regierungsbezirk Detmold, Kreis Höxter, Willebadessen, spa garden, on _Tanacetum vulgare_, 1 Sep 2016, U. Braun (HAL 3153 F). Isoneotype: TSU-MUMH6803. Ex-neotype sequence: LC217868 (ITS+28S).

_Notes:_ Bradshaw et al. (2017) included _Golovinomyces macrocarpus_ in phylogenetic analyses, neotypified this name, including ex-neotype sequences, and confirmed its status as an independent species. It occurs on hosts belonging to Asteraceae tribe Anthemideae, with _Tanacetum vulgare_ as a common, widespread host.

_Golovinomyces magnicellulatus_ (U. Braun) Heluta, Ukraiyns’k Bot Zhurn 45(3):63. 1988.

≡ _Erysiphe magnicellulata_ U. Braun, Feddes Repert 88 (9–10):656. 1978. nom. cons.

≡ _E. cichoracearum_ var. _magnicellulata_ (U. Braun) U. Braun, Nova Hedwigia 34:695. 1981.

_Holotype:_ GERMANY. BRANDENBURG: Rehefelde near Berlin, garden, on _Phlox paniculata_, 25 Sep 1976, U. Braun (HAL 1516 F). Isotypes: FH, HAL 1288 F, JE, K, LE, NY. Ex-holotype sequences: ON367047 (ITS +28S); ON360731 (GAPDH).

≡ _E. martii_ f. _phlogis_ Thüm., Mycoth Univ Cent 5 No. 449. 1876.

≡ _Oidium drummondii_ Thüm., Mycoth Univ Cent 12 No. 1177. 1878, nom. rej.

≡ _E. cichoracearum_ f. _phlogis_ Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:221. 1927.
Golovinomyces malvacearum M. Bradshaw, sp. nov.

**Notes:** North American sequences obtained from *G. magnicellulatus* cluster together with European sequences, including an ex-type sequence. This species was confirmed in the GAPDH and concatenated phylogenetic analyses. ITS and IGS analyses were not sufficient. Braun and Cook (2012) assigned diverse collections of Golovinomyces on *Polemonium* spp. (*Erysiphe cichoracearum* f. *polemonii* Jacz.) to *G. magnicellulatus*, which requires confirmation by sequence analyses. This also holds true for *G. magnicellulatus* var. *robustus* (R.Y. Zheng & G.Q. Chen) U. Braun (≡ *Erysiphe robusta* R.Y. Zheng & G.Q. Chen) on *Polemonium chinense* in China.

**Golovinomyces montagnei** U. Braun, in Braun & Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews):321. 2012.

**Holotype:** GERMANY. SAXONY: Pirna and Schandau, on *Cirsium oleraceum*, Oct 1892/Sep 1898, W. Krieger, Fungi Saxox Exs 1608 (HAL, s.n.). Epitype (designated by Bradshaw et al. 2021f): GERMANY. SAXONY: Vogtlandkreis, Pausa-Mühltroff, Ortsteil Mühltroff, on *Cirsium oleraceum*, 20 Aug 1976, U. Braun (WTU-F-072476). Isoepitype: HAL 954 F. Ex-epitype sequence: MT406369 (ITS).

**Notes:** Braun and Cook (2012) used the name *Golovinomyces montagnei* for a wide range of powdery mildews on hosts of the Asteraceae (Carduoideae), comprising *Carduus*, *Centaurea*, *Cirsium*, *Crupina*, *Saussurea*, *Serratula*, etc. This species is characterized by various morphological traits, including frequently 3-spored asci (Braun and Cook 2012). The available sequences from *G. montagnei* collections confirm the status of this taxon as an independent species. However, only few specimens
on few hosts have been sequenced. *G. montagnei* (sensu Braun and Cook 2012) undoubtedly encompasses some cryptic species.

**Golovinomyces mutisiae** (Havryl.) M. Bradshaw, U. Braun & Pfister, comb. nov.

*Basionym: Oidium mutisiae* Havryl., Mycotaxon 49:264. 1993.

≡ *Euoidium mutisiae* (Havryl.) U. Braun & Havryl., Taxonomic Manual of the Erysiphales (Powdery Mildews):336. 2012.

*Holotype:* ARGENTINA. RÍO NEGRO: Departamento Bariloche, Moreno Lake, near bridge, on *Mutisia spinosa*, 19 May 1991, M. Havrylenko (LPS 45139). Isotype: BCRU 330. Ex-isotype sequence: AB246762 (ITS+28S).

*Notes:* This species is confined to *Mutisia spinosa* (Asteraceae, Mutisieae) and, so far, only known from Argentina. Takamatsu et al. (2006) sequenced type material of this species.

**Golovinomyces neosalviae** M. Scholler, U. Braun & Anke Schmidt, in Scholler et al., Mycol Progr 15(no. 56):9. 2016.

*Holotype:* GERMANY. SCHLESWIG-HOLSTEIN: Lübeck, St. Gertrud, Grootkoppel 6, Flora nursery, two flower-pots, on *Salvia officinalis* “Purpurascens,” 4 Jun 2012, A. Schmidt (KR-M-0035013). Ex-holotype sequence: LC076824.

*Notes:* See under *Golovinomyces salviae*.

**Golovinomyces ocimi** (S. Naray. & K. Ramakr.) Meeboon & S. Takam., Trop Pl Pathol 43:203. 2017.

≡ *Oidium ocimi* S. Naray. & K. Ramakr., Madras Univ J 37–38:87. 1967.

*Lectotype* (designated by Meeboon et al. 2017): Narayanaswami & Ramakrishnan (1967:87, fig. 15). *Epitype* (designated by Meeboon et al. 2017): THAILAND. Chiang Rai, Wangpapao, on *Ocimum tenuiflorum*, 15 Dec 2015, J. Meeboon (TSU-MUMH6621). Ex-epitype sequence: LC306657 (ITS).

*Notes:* This species is known from Asia (India, Thailand) on *Ocimum tenuiflorum*. Braun and Cook (2012:305) cited *O. ocimi* as synonym under *Golovinomyces biocellatus*. Based on phylogenetic examinations, Meeboon et al. (2017) confirmed that sequences obtained from this powdery mildew form a separate species clade.

**Golovinomyces orontii** (Castagne) Heluta, Ukrayins’k Bot Zhurn 45(5):63. 1988 (emend. Braun et al. 2019:344).

≡ *Erysiphe orontii* Castagne, Suppl Cat pl Marseille:52. 1851.

[Holotype: FRANCE. Marseille, on *Misopates orontium* (≡ *Antirrhinum orontium*), herb. Castagne, not preserved.] *Neotype* (designated by Braun et al. 2019): SWITZERLAND: Geneva, Jardin botanique 3, on *Misopates orontium*, 13 Aug 2009, A. Bolay (G00295941). Ex-neotype sequence: GQ183950 (ITS).

≡ *E. communis* q. *violacearum* Rabenh., Deutschl Krypt-Fl 1:233. 1844.
＝ Oidium violae Pass., in Thüm., Mycoth Univ Cent 12 No. 1176. 1878.
＝ Euoidium violae (Pass.) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews):322. 2012.
＝ Erysiphe cichoracearum f. violarum Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:228. 1927.
＝ E. cichoracearum f. antirrhini Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:228. 1927.
＝ Erysiphe cichoracearum f. valeriana Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:227. 1927, syn. nov.

Lectotype (designated by Braun and Cook 2012:331): H.A. Dietr., Pl Fl Balt Crypt II 52, on Valeriana officialis (LEP). Epitype (designated here; MycoBank MBT10006877): GERMANY. SACHSEN-ANHALT: Landkreis Anhalt-Bitterfeld, Muldenstein, on Valeriana officialis, Oct 1977, U. Braun (HAL 1398 F). Ex-epitype sequences: ON367072 (ITS+28S); ON360749 (GAPDH).

＝ E. valeriana (Jacz.) S. Blumer, Beitr Krypt-Fl Schweiz 7(1):264. 1933.
＝ Golovinomyces valeriana (Jacz.) Heluta, Ukarayins’k Bot Zhurn 45(5):63. 1988.
＝ Erysiphe blumeri Mayor, Ber Schweiz Bot Ges 59:284. 1949.

Notes: Braun and Cook (2012) used the name Golovinomyces orontii in a very broad sense for a plurivorous powdery mildew on a very wide range of hosts. Based on results of molecular sequence analyses, Braun et al. (2019) demonstrated that sequences retrieved from specimens assigned to this species fall into several clades, including G. orontii s. str., G. bolayi, and G. tabaci. Golovinomyces valeriana is a new synonym of G. orontii. In phylogenetic ITS and concatenated trees, based on ex-epitype sequences, Golovinomyces on Valeriana clusters within the G. orontii clade. This synonymy is also reflected in the morphology of G. valeriana, which is characterized by having conidiophores with distinctly curved foot cells (Braun and Cook 2012, 331). Curved conidiophore foot cells are a basic characteristic of G. orontii (Braun et al. 2019). Other hosts of the Valerianaceae, such as Patrinia rupestris in China (see ITS and concatenated tree) and Valerianella spp., are also known to be hosts of G. orontii s. str. and s. lat. (Braun and Cook 2012), respectively. A Golovinomyces collection on Pentstemon serrulatum seems to belong to G. orontii s. str. This holds also true for the two North American samples involved, which have originally been identified as G. valeriana. Genetic differences among the different G. orontii specimens could be due to different geographic origins of the collections examined. For example, Golovinomyces on Valeriana from North America form a well-supported clade separate from the European samples, including the neotype of G. orontii and epitype of G. valeriana. However, this question is in need of further phylogenetic research.

Golovinomyces reginae (Havryl. & S. Takam.) M. Bradshaw, U. Braun & Pfister, comb. nov.
MycoBank MB843863
Basionym: Oidium reginae Havryl. & S. Takam., Mycol Res 110:1097. 2006.
＝ Euoidium reginae (Havryl. & S. Takam.) Havryl. & S. Takam., Taxonomic Manual of the Erysiphales (Powdery Mildews):337. 2012.

Holotype: ARGENTINA. RÍO NEGRO: Departamento Bariloche, Parque Nacional Nahuel Huapi, Slovenian trail to Mount Cathedral, on Mutisia decurrens, 8 Mar 2000, M. Havrylenko (BCRU 4645). Ex-holotype sequence: AB246759 (ITS+28S).

Notes: This species is confined to Mutisia decurrens (Asteraceae, Mutisieae) and is only known from Argentina.

Golovinomyces riedlianus (Speer) Heluta, Ukarayins’k Bot Zhurn 45(5):63. 1988.
＝ Erysiphe riedliana Speer, Anz Österr Akad Wiss Math-Nat Kl 106(1–4):244. [“1969”] 1970.
＝ E. cichoracearum var. riedliana (Speer) U. Braun, Mycotaxon 18(1):121. 1983.

Holotype: AUSTRIA. Near Herrnstein, “auf dem Hart,” on Galium verum, 17 Aug 1969, Riedl (W). Epitype (designated here; MycoBank MBT10006878): UKRAINE. KYIV REGION: Borodinskaya district, on Galium verum, 6 Sep 1979, V.P. Heluta (TFS-F-97932). Isoepitype: KW 11879. Ex-epitype sequence: AB430820 (ITS+28S).

＝ E. galii auct. p.p.
＝ E. cichoracearum auct. p.p.

Notes: Golovinomyces riedlianus is a common, widespread powdery mildew (Braun and Cook 2012, 326). The phylogeny and taxonomy of this species was examined by Takamatsu et al. (2009) in comprehensive phylogenetic analyses of powdery mildews on Galium spp. and other rubiaceous hosts.

Golovinomyces salviae (Jacz.) M. Scholler, U. Braun & Anke Schmidt, Mycol Progr 15(no. 56):8. 2016.
＝ Erysiphe labiatarum f. salviae Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:162. 1927.
＝ E. salviae (Jacz.) S. Blumer, Beitr Krypt-Fl Schweiz 7(1):273. 1933.

Lectotype (designated by Scholler et al. 2016): SWITZERLAND. VALAIS (WALLIS): Riddes, Ecône,
500 m alt., on Salvia pratensis, Sep 1893, Abbé Besse (LEP 130001 [ex herb. A. de Jaczewski 2214]). Epitype (designated here; MycoBank MBT10006879): GERMANY. BADEN-WÜRTTEMBERG: Owingen, NSG (Naturschutzgebiet; i.e., nature reserve) an der Eyach N Weilerkirche, dry grassland, south slope, on Salvia pratensis, 19 Aug 2005, M. Scholler (KR-M-0018634). Ex-epitype sequence: LC076803 (ITS+28S).

= Oidium verbenaceae Pass., in Thüms., Mycoth Cent 8 No. 789. 1877.

= Erysiphe simplex Heluta, Ukrayins’k Bot Zhurn 43-(5):53. 1986, nom. illeg. [nom. superfl.] (Art. 52.1).

= Golovinomyces simplex (Heluta) Heluta, Ukrayins’k Bot Zhurn 45(5):63. 1988 (Art. 6.10).

Notes: Scholler et al. (2016) revised the Golovinomyces biocellatus complex and showed that two species occur on Salvia spp., i.e., G. salviae on Salvia nemorosa, S. nutans, S. pratensis, S. verbenacea, and S. verticillata, and G. neosalviae on S. officinalis (main host), S. fruticosa, and S. lavandulifolia. Two sequences obtained from North American specimens on Agastache scrophulariifolia and Salvia sp. cluster in the G. salviae clade, which confirms that this species is also distributed in North America.

Scholler et al. (2016) cited Oidium verbenaceae as synonymy of G. salviae, but the status of this name is not clear, as sequences retrieved from powdery mildew on Salvia verbenacea are necessary. The identity of Erysiphe cichoracearum f. salviae Koshek. (Bot Mater Otd Sporov Rast Bot Inst Komarova Akad Nauk URSR 14:123. 1961; type: on Salvia virgata, LE 34536) is also unclear and requires morphological reexamination and genetic data of the powdery mildew on S. virgata.

Golovinomyces sonchicola U. Braun & R.T.A. Cook, in Cook & Braun, Mycol Res 113(5):629. 2009, nom. cons.

Holotype: THE NETHERLANDS. Utrecht, Oorspronck Park, on Sonchus oleraceus, 23 Jul 2008, U. Braun (HAL 2245 F). Ex-type sequences: ON367059 (ITS+28S); ON360740 (GAPDH).

= Erysiphe cichoracearum f. sonchi Jacz., Karm Opred Grib Vip 2 Muchn-rosj griby:210. 1927.

= Oidium sonchi-arnensis Sawada, Bull Dept Agric Gov Res Inst Formosa 24:34. 1927, nom. rej.

= Erysiphe cichoracearum auct. p.p.

= Golovinomyces cichoracearum auct. p.p.

Notes: Golovinomyces sonchicola is conserved against the older anamorph-typified name Oidium sonchi-arnensis (see Braun 2013). Sequences retrieved from G. sonchicola form a distinct clade in the ITS+28S and concatenated tree. The included sequence obtained from powdery mildew on Sonchus sp., USA, Washington, Seattle, University of Washington Medicinal Plant Garden (FH00941275), represents the first phylogenetic confirmation of this species for North America.

Golovinomyces sordidus (L. Junell) Heluta, Ukrayins’k Bot Zhurn 45(5):63. 1988.

= Erysiphe sordida L. Junell, Trans Brit Mycol Soc 48:544. 1965.

Holotype: SWEDEN. UPPLAND: Bondkyrka, Libron (near Uppsala), on Plantago major, 8 Sep 1942, Nannfeldt [Lundell & Nann., Fungi Exs Suec 1474] (UPS). Reference sequences: ON367063 (ITS); ON360743 (GAPDH) (GERMANY. On Plantago major, HAL 1032 F).

= Erysiphe artemisiae var. sordida (L. Junell) Ialongo, Mycotaxon 44(1):256. 1994.

= Erysibe lamprocarpa var. plantaginii Link, Sp. pl. 4 6(1): 109. 1824.

= E. lamprocarpa c. plantaginii (Link) Rabenh., Deutschl Krypt-Fl 1:232. 1844.

= Erysiphe plantaginii (Link) Fuss, Arch Vereins Siebenbürgen Landesk N F 14(2):460. 1878, nom. illeg. (Art. 53.1), non Castagne, 1845.

= E. plantaginii (Link) Sawada, Bull Dept Agric Govt Res Inst Formosa 24:47. 1927, nom. illeg., non Castagne, 1845.

= E. cichoracearum var. plantaginii (Link) U. Braun, Nova Hedwigia 34:659. 1981.

= E. communis v. plantaginearum Fr., Syst mycol 3:242. 1829.

= E. cichoracearum f. plantaginii Poteb., Gribnye parazity vysshikh rastenij Kharkovskoj i smezhnykh gubernij:233. 1915.

= E. lamprocarpa auct. p.p.

= E. cichoracearum auct. p.p.

Notes: Sequences obtained from Golovinomyces sor- didus form a well-supported clade. Several North American sequences are included, which confirms the occurrence of this species in the USA. For the time being, we prefer to propose reference sequences for this species. The holotype is not too old, i.e., attempts to get ex-type sequences are realistic.

Golovinomyces tabaci (Sawada) H.D. Shin, S. Takam. & L. Kiss, in Braun et al., Mycol Progr 18:347. 2019.

= Erysiphe tabaci Sawada, Bull Dept Agric Govt Res Inst Formosa 24:23. 1927.

Lectotype (designated by Braun et al. 2019): TAIWAN. Taichung, Fongyuan, on Nicotiana tabacum, 27 Mar 1920, H. Sawada (TNS-F-218387). Epitype (designated by Braun et al. 2019): HUNGARY. Budapest, glasshouse of the Plant Protection Institute
of the Hungarian Academy of Sciences, on Nicotiana tabacum cv. Samsun, 12 Sep 1998, L. Kiss (HAL 3270 F). Ex-epitype sequence: AF229013 (ITS).  
= ?E. cichoracearum f. cucurbitacearum Poterb., Gribnye parazity vysshikh rastenii Kharkovskoj i smezhnykh guberny:233. 1915.  
= Erysiphe cucurbitacearum R.Y. Zheng & G.Q. Chen, Sydowia 34:258. 1981. [Holotype: CHINA. XINJIANG UYGUR AUTONOMOUS REGION: Urumqi, on Cucumis sativus, 1954, Zhang et al. (HMAS 40016). Epitype (designated by Qiu et al. 2020b): CHINA. XINJIANG UYGUR AUTONOMOUS REGION: Altay Prefecture, on C. sativus, Sep 2014, Wen-Tao Jiang (HMJAU-PM91862). Ex-epitype sequences: MK937797 (ITS); MK937802 (LSU).]  
≡ Golovinomyces cucurbitacearum (R.Y. Zheng & G. Q. Chen) Vakal. & Kliron., Mycotaxon 80:490. 2001.  
≡ Erysiphe rubiae H.D. Shin & Y.J. La, Korean J Pl Pathol 4(3):243. 1988, nom. inval. (Art. 39.1).  
≡ E. rubiae H.D. Shin & Y.J. La, in Shin, Erysiphaceae of Korea [PhD thesis, Seoul National University, Korea]:84. 1988, not effectively published (Art. 30.8).  
≡ E. rubiae H.D. Shin & Y.J. La, Korean J Pl Pathol 5:182. 1989. [Holotype: KOREA. Suwon, on Rubia akane, 14 Oct 1987, H.D. Shin (KUS F-10080). Epitype (designated by Braun et al. 2019): KOREA. Hongcheon, Sutasama temple, on Rubia akane, 16 Jun 2017, H.D. Shin (KUS-F29804). Ex-epitype sequence: LC417101.]  
≡ Golovinomyces rubiae (H.D. Shin & Y.J. La) U. Braun, Schlechtendalia 3:51. 1999.  
Notes: Golovinomyces tabaci is a plurivorous powdery mildew species, which belongs to the G. orontii s. lat. complex. This complex recently has been phylogenetically revised and split into several species (Braun et al. 2019). The synonymy of G. cucurbitacearum has been proven by Qiu et al. (2020b, 32) on the basis of epitypification with an ex-epitype sequence. A sequence retrieved from a Russian collection on Asperugo procumbens (Russia, Rostov Region, Shakhty city district, Cotton Fabric urban microdistrict, block green belt, ruderal vegetation community under trees, T. Bulgakov, BP1929818) clusters in the G. tabaci clade. It is the second proven report of G. tabaci on a host of the Boraginaceae. Qiu et al. (2020b) demonstrated that this species may also occur on Trigonotis peduncularis in China. Powdery mildew on Boraginaceae was previously exclusively referred to as G. cynoglossi s. lat. (Braun and Cook 2012, 210). Recently, G. cynoglossi s. lat was phylogenetically and morphologically analyzed and split into several species (Braun et al. 2018). Previous findings of G. bolayi on Asperugo procumbens and Trigonotis peduncularis show that plurivorous Golovinomyces spp. must be considered with regard to boraginaceous hosts.  
Golovinomyces verbesi (Jacz.) Heluta, Ukrayins’k Bot Zhurn 45(5):63. 1988.  
≡ Erysiphe cichoracearum f. verbesi Jacz., Karm Opred Grib Vip 2 Muchn-rosh griby:224. 1927.  
≡ E. verbesi (Jacz.) S. Blumer, Beitr Krypt-Fl Schweiz 7(1):284. 1933.  
Lectotype (designated by Braun 1987): GERMANY. On Verbascum sp., Klotzsch, Herb. Viv. Mycol. 945 (HAL, s.n.). Epitype (designated here; MycoBank MBT10006880): Lithuania, on Verbascum densiflorum, 23 Aug 2000, B. Grigaliūnaitė (TNS-F-87561). Ex-epitype sequences: AB769468 (ITS); AB769469 (28S).  
≡ ?Oidium balsamii Mont., Ann Mag Nat Hist, 2 Sér 13:463. 1854.  
≡ E. verbesi Fuss, Arch Vereins Siebenbürg Landesk N F 14(2):460. 1878, nom. nud.  
≡ E. cichoracearum auct. p. p.  
Notes: Golovinomyces verbesi, a species of subsect. Depressi, is morphologically well distinguished from all other Golovinomyces spp. (Braun and Cook 2012). The European ex-epitype sequence, first published by Takamatsu et al. (2013), and a sequence retrieved from a North America collection form a well-supported clade in the ITS+28S and concatenated tree, distant from all other Golovinomyces clades, which supports the status of this taxon as species of its own.  
Golovinomyces verbesinae (Schwein.) Heluta, Ukrayins’k Bot Zhurn 45(5):63. 1988.  
≡ Erysiphe verbesinae Schwein., Trans Amer Phil Soc 4(2):270. [1832] 1834.  
Lectotype (designated by Bradshaw et al. 2021f, 101): USA. PENNSYLVANIA: Lehigh and Northampton counties, Bethlehem, on Verbena urticifolia, undated, herb. L.D. von Schweinitz (PH 62391). Isolectotype: PH 62392. Epitype (designated by Bradshaw et al. 2021f, 101): Wisconsin, Devils Lake, on Verbena urticifolia, 19 Jul 1941, C.G. Shaw (WSP13634). Ex-epitype sequence: MT162618 (ITS).  
≡ E. cichoracearum f. verbesinae Jacz., Karm Opred Grib Vip 2 Muchn-rosh griby:224. 1928.  
≡ Golovinomyces glandulariae L. Kiss & N. Vaghefi, in Kiss et al., Persoonia 43:433. 2019.  
≡ E. cichoracearum auct. p.p.  
Notes: Sequences obtained from Golovinomyces verbesinae form a well-supported clade in the ITS+28S and concatenated tree, clearly separated from all other clades within Golovinomyces. Based on results of sequence
analyses, Bradshaw et al. (2021f) reduced the recently described *G. glandulariae* to synonymy with *G. verbenae*.

*Golovinomyces vincae* U. Braun & S. Takam., in Braun et al., Mycol Progr 18(3):349. 2019.

= *Erysiphe cichoracearum* f. *vincae* Poteb., Gribine parazity vyssykh rastenij Khar’kovskoj i smezhnykh gubernij:232. Khar’kov 1915.

**Holotype:** GERMANY. SACHSEN-ANHALT: Freyburg (Unstrut), green area, on *Vinca major*, 25 Jun 2018, U. Richter (TSU-MUMH 7199). Isotype: HAL 3276 F. Ex-holotype sequence: LC417097 (ITS+28S).

**Notes:** The powdery mildew on *Vinca* spp. usually occurs as an anamorph and was previously assigned to *Erysiphe cichoracearum* s. lat. or *Golovinomyces orontii* (Braun and Cook 2012). The *G. orontii* (s. lat.) complex has recently been revised on the basis of sequence analyses (Braun et al. 2019). This study revealed that this powdery mildew represents an undescribed species of *Golovinomyces*, with *Vinca major* as the main host. *G. vincae* has been phylogenetically confirmed in the ITS+28S and concatenated analyses.

**Additional taxa.**—Multiple collections likely represent undescribed species but were preliminarily identified as *Golovinomyces* sp. (we refer that multiple collections are available for analyses prior to describing a new species). These collections include *Golovinomyces* sp. on *Artemisia arctica* FH01122031, *Golovinomyces* sp. on *Aster foliaecus* FH01122007, and *Golovinomyces* sp. on *Mertensia paniculata* FH01122018 (FIG. 1); *Golovinomyces* sp. on *Senecio dornicum* AB769450 labeled as “*Golovinomyces fischeri*” (FIG. 2); and *Golovinomyces* sp. on *Scutellaria lateriflora* FH01122030, *Golovinomyces* sp. on *Nemophila parviflora* FH01122022, *Golovinomyces* sp. on *Hydrophyllum canadense* FH00941241, and *Golovinomyces* sp. on *Phacelia bipinnatifida* FH00941242 (FIG. 3). Additionally, although the varieties of *G. asterum* are sufficiently resolved in the concatenated tree, we prefer to wait to move these taxa to the species rank until a wider collection effort with GAPDH sequences is undertaken.

**DISCUSSION**

The genus *Golovinomyces* encompasses a wide range of economically important plant diseases. A survey of phylogenetically proven *Golovinomyces* spp. is provided, with a special focus on North American powdery mildew collections. For multiple species of this genus, the first sequence data were retrieved, including *G. americanus*, *G. brunneopunctatus*, *G. californicus*, *G. greeneanus*, *G. hydrophyllacearum*, and *G. sparsus* (in some cases the generated sequences were ex-type sequences). The analyses presented were mainly based on ITS+28S sequences, as these markers represent the standard for powdery mildews. In addition to ITS+28S, GAPDH and IGS sequences were generated for various *Golovinomyces* spp., above all in cases of assemblages of species that are not sufficiently resolved in ITS+28S phylogenies. These sequences allowed a comprehensive, phylogenetic analysis of the whole genus *Golovinomyces*. The new sequences obtained from North American specimens included various first, unequivocal, phylogenetically confirmed records of *Golovinomyces* spp. for North America (e.g., *G. asperifoli and G. bolayi*). An ex-type sequence retrieved from *G. sparsus* clustered within the *G. ambrosiae* clade, which led to the reduction of this name to synonymy with the plurivorous *G. ambrosiae*. Similarly, an ex-epitype sequence of *G. valerianae* clustered within the *G. orontii* s. str. clade. This result, combined with the morphological similarity between the two species, resulted in the reduction *G. valerianae* to synonymy with *G. orontii*. These findings drastically emphasize the importance and necessity to sequence type collections and to designate epitypes with ex-epitype sequences when required.

The results of the present phylogenetic analyses of *Golovinomyces* collections have further confirmed the wide host ranges of several plurivorous species of this genus. Most new North American sequences that cluster within the *G. ambrosiae* clade expectantly originated from diverse Asteraceae hosts. However, other sequences belonging to this clade were obtained from *Golovinomyces* on hosts of other families, such as *Asclepias syriaca* (Apocynaceae) and *Solanum carolinense* (Solanaceae). Additionally, several new hosts of *G. ambrosiae* are unusual, since they belong to host genera that are usually infected by other *Golovinomyces* spp. For example, *Cirsium altissimum* [*Cirsium* spp. are common hosts of *G. montagnae*], *Eupatorium maculatum* [*Eupatorium* is also host genus for *G. circumfuscus*], *Lactuca spicata* [lettuce belongs to the host range of *G. bolayi*], and *Symphyotrichum patens* (= *Aster patens*) [asters are common hosts of *G. asterum*]. These findings underline that host identities should be used with caution in *Golovinomyces* because the occurrence of two or more species on a single host genus is not uncommon and should be considered. Morphological differences between various *Golovinomyces* spp. are often slight. Therefore, the most secure way to reach reliable identifications lies in the application of sequence analyses. It should be noted that many of the sequences from the
current study came from old herbarium specimens and previous host misidentifications or sequence contamination cannot be ruled out in outliers such as the Golovinomyces ambrosiae specimen on Solanum carolinnense. This is especially true for species within Golovinomyces that are morphologically similar and occur on a wide range of hosts.

For taxonomic-phylogenetic and for sequence-supported identifications of powdery mildew taxa, it is not sufficient to use sequence data arbitrarily. Sequences deposited in GenBank under certain names may be from various geographic origins and diverse hosts. Researchers should consider in their analyses that identifications on GenBank are not always reliable. As such, they should be critically evaluated. The nomenclature of names is, in general, ruled by types. Therefore, for final conclusions, it is necessary to use and compare ex-type sequence for taxonomic-phylogenetic purposes. This was the reason for our special emphasis on reference sequences for Golovinomyces spp., which were, whenever possible, retrieved from type collections.

The present contribution is the first step toward a comprehensive reexamination of Golovinomyces, based on phylogenetic analyses. A special focus was taken on North American species, as the current paper is in connection with a project to study the North American powdery mildews monographically. The provided phylogenetic analysis and phylogenetic-taxonomic overview are intended to serve as a phylogenetic “backbone” for future research on this powdery mildew genus. The phylogeny of numerous Golovinomyces spp. is still unknown, including Golovinomyces andinus, G. asterum var. moroczkovskii (= G. moroczkovskii), G. caulicola, G. franseriae, G. immersus, G. hyoscyami, G. laportaeae, G. poonensis, G. prenanthis, G. pseudosepultus, and G. rogeronii.

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ORCID

Michael J. Bradshaw http://orcid.org/0000-0002-7133-4679

LITERATURE CITED

Abadi S, Azouri D, Mayrose I, Pupko T. 2019. Model selection may not be a mandatory step for phylogeny reconstruction. Nat Commun. 10:1–11.
Amano (Hirata) K. 1986. Host range and geographical distribution of the powdery Mildew Fungi. Tokyo (Japan): Japan Scientific Societies Press. p. 741.
Blumer S. 1933. Die Erysipheaceen Mitteleuropas unter besonderer Berücksichtigung der Schweiz. Beiträge zur Kryptogamenflora der Schweiz. 7:1–483.
Blumer S. 1967. Echte Mehltäulilze (Erysiphaceae). Jena (Germany): G. Fischer Verlag. p. 436.
Bolay A. 2005. Les Oidiums de Suisse (Erysiphaceae). Cryptogam Helyv. 20:1–173.
Boyle H, Dietrich W, Brautigam S. 2007. First report of the powdery mildew Golovinomyces cichoreacarum on Telekia speciosa in Germany. Czech Mycol. 59(2):201–204.
Bradshaw M, Braun U, Elliott M, Kruse J, Liu SY, Guan G, Tobin P. 2021e. A global genetic analysis of herbarium specimens reveals the invasion dynamics of an introduced plant pathogen. Fungal Biol. 125(8):585–595.
Bradshaw M, Braun U, Götz M, Jurick W II. 2022b. Phylogeny and taxonomy of powdery mildew caused by Erysiphe species on Lupinus hosts. Mycologia. 114(1):76–88.
Bradshaw M, Braun U, Götz M, Meeboon J, Takamatsu S. 2017. Powdery mildew of Chrysanthemum × morifolium: phylogeny and taxonomy in the context of Golovinomyces species on Asteraceae hosts. Mycologia. 109:508–519.
Bradshaw M, Braun U, Götz M, Takamatsu S. 2021b. Taxonomy and phylogeny of the Erysiphe lonicerae complex (Helotiales, Erysiphaceae) on Lonicera spp. Fungal Syst Evol. 7:49–65.
Bradshaw M, Braun U, Götz M, Takamatsu S, Brand T, Cabrera MG, Dirchwolf P, Kummer V, Medina R, Moparthi S, et al. 2021f. Contributions to the phylogeny and taxonomy of the Erysiphaceae (powdery mildews)—part 1. Sydowia. 73:89–112.
Bradshaw M, Braun U, Meeboon J, Tobin PC. 2021a. Phylogeny and taxonomy of powdery mildew on Corylus species. Mycologia. 113:459–475.
Bradshaw M, Braun U, Wang S, Liu S, Feng J, Shin H-D, Choi YJ, Takamatsu S, Bulgakov TS, Tobin PC. 2020. Phylogeny and taxonomy of powdery mildew on Viburnum species. Mycologia. 112(3):616–632.
Bradshaw M, Goolsby E, Mason C, Tobin PC. 2021d. Evolution of disease severity and susceptibility in the Asteraceae to the powdery mildew Golovinomyces latisporus: major phylogenetic structure coupled with highly
variable disease severity at fine scales. Plant Dis. 105 (2):268–275.

Bradshaw M, Guan G-X, Nokes L, Braun U, Liu S-Y, Pfister D. 2022c. Secondary barcodes (GAPDH, RpB2, CAM and GS) to characterize species complexes and strengthen the powdery mildew phylony. Front Ecol Evol. 10. doi:10.3389/fevo.2022.918908

Bradshaw MJ, Quijada L, Tobin PC, Braun U, Newlander C, Potterfield T, Alford ER, Contreras C, Coombes A, Moparthi S, et al. 2022a. More than just plants: botanical gardens are an untapped resource of fungal diversity. HortScience. 57(10):1289–1293. doi:10.21273/HORTSCI16755-22

Bradshaw M, Tobin P. 2020. Sequencing herbarium specimens of a common detrimental plant disease (powdery mildew). Phytopathology. 110:1248–1254.

Braun U. 1978. Beitrag zur Systematik und Nomenklatur der Erysiphales. Feddes Repert. 88:655–665.

Braun U. 1982. Morphological studies in the genus Oidium (III). Zentralblatt für Mikrobiologie. 137:314–324.

Braun U. 1983. Descriptions of new species and combinations in Microsphaera and Erysipe (IV). Mycotaxon. 18:113–129.

Braun U. 1987. A monograph of the Erysiphales (powdery mildews). Beihete zur Nova Hedwigia. 89:1–700.

Braun U. 1999. Some critical notes on the classification and generic concept of the Erysiphales. Schlechtendalia. 3:49–55.

Braun U. 2013. (2210–2232) Proposals to conserve the teleomorphic-typified name Blumeria against the anamorphic-typified name Oidium and twenty-two teleomorph-typified powdery mildew species names against competing anamorph-typified names (Ascomycota: erysiphales). Taxon. 62:1328–1331.

Braun U, Bradshaw M, Pfister DH. 2022. Proposal to conserve the generic name Golovinomyces against Eiodium (Ascomycota: erysiphales). Taxon. 71(2):459. doi:10.1002/tax.12692

Braun U, Bradshaw M, Zhao -T-T, Cho S-E, Shin H-D. 2018. Taxonomy of the Golovinomyces cynoglossi complex (Erysiphales, Ascomycota) disentangled by phylogenetic analyses and reassessments of morphological traits. Mycobiology. 46:192–204.

Braun U, Cook RTA. 2012. Taxonomic manual of the Erysiphales (Powdery Mildews). CBS Biodivers Ser. 11:1–707.

Braun U, Cook RTA, Inman AJ, Shin HD. 2002. The taxonomy of the powdery mildew fungi. In: Bélanger R, Dick AJ, Bushnell WR, editors. The powdery mildews: a comprehensive treatise. St. Paul (USA): APS Press. p. 13–54.

Braun U, Shin H-D, Takamatsu S, Meeboon J, Kiss L, Lebeda A, Kittner M, Götz M. 2019. Phylogeny and taxonomy of Golovinomyces orontii revisited. Mycol Prog. 18:335–357.

Braun U, Takamatsu S. 2000. Phylogeny of Erysiphe, Microsphaera, Uncinula (Erysipehe) and Cystotheca, Podosphaera, Sphaerotheca (Cystothecae) inferred from rDNA ITS sequences – some taxonomic consequences. Schlechtendalia. 4:1–33.

Brielmaier-Liebetanz U, Field AE, Warfield CY, Braun U. 2015. Powdery mildew (Erysiphales) on Calibrachoa hybrids in Germany, Nicaragua and the USA. Plant Pathol Quar. 5(1):1–5.

Carbone I, Kohn LM. 1999. A method for designing primer sets for speciation studies in filamentous ascomycetes. Mycologia. 91:553–556.

Cook RTA, Braun U. 2009. Conidial germination patterns in powdery mildews. Mycol Res. 113:616–636.

Cook RTA, Inman AJ, Billings C. 1997. Identification and classification of powdery mildew anamorphs using light and scanning electron microscopy and host range data. Mycol Res. 101:975–1002.

Cunnington JH, Takamatsu S, Lawrie AC, Pascoe IG. 2003. Molecular identification of anamorphic powdery mildews (Erysiphales). Australas Plant Pathol. 32(3):421–428.

Darsaraei H, Khodaparast SA, Takamatsu S, Abbasi M, Asgari B, Sajedi S, Götz M, Liu SY, Feng J, Bradshaw M, et al. 2021. Phylogeny and taxonomy of the Erysiphe adunca complex (Erysiphales, Helotiales) on poplars and willows. Mycol Prog. 20(4):517–537.

de Schweinitz LD. 1834. Synopsis fungorum in America Boreali media ductemcntum. Trans Am Philos Soc N S. 4:141–316.

Dörfelt H, Ali N. 1987. Studien an Mehltauopilen des Herbariums von D.F.L. von Schlechtendal. Feddes Repert. 3(3–4):237–245.

Ehrenberg CG. 1821. De Mycetogenesi ad Acad. C.L.N.C. Praesidem Epistola. Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum. 10 (1):160–222.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution. 39:783e791.

Gernhard T. 2008. The conditioned reconstructed process. J Theor Biol. 253:769–778.

Götz M, Braun U. 2022. Golovinomyces longipes (Noordel. & Loer.) L. Kiss on Mattricia chamomilla L.: another host range expansion. J Plant Dis Prot. 129:201–205.

Guan G-X, Liu S-Y, Braun U, Qiu PL, Liu J, Zhao F-Y, Tang S-R, J-N L, Nguyen V-N. 2022. A cryptic powdery mildew species found on Hieracium and Pilosella spp. (Asteraceae) – Golovinomyces hieraciicorum sp. nov. Phytopathol Meditr. 61(1):107–117.

Heluta VP. 1988. Filogeneticheskie vzaimosvyazi mezhdyu rodami erizal'nykh gribov i nekotoroye voprosy sistematika poryadka Erysiphales. Biologicheskii Zhurnal Armenii. 41 (5):351–358.

Heluta VP. 1989. Flora Gribov Ukrainy. Muchnistorosyanye griby (Flora Fungorum RSS Ukrainice, Ascomycetes, Erysiphales). Kiev (Ukraine): Naukova Dumka. p. 256.

Hirata T, Takamatsu S. 1996. Nucleotide sequence diversity of rDNA internal transcribed spacers extracted from conidia and cleistothecia of several powdery mildew fungi. Mycocosience. 37:283–288.

Homma Y. 1937. Erysiphaceae of Japan. J Fac Agric Hokkaido Univ. 38:183–461.

Kiss L, Cook RTA, Saenz GS, Cunningham JH, Takamatsu S, Pascoe I, Bardin MB, Nicot PC, Sato Y, Rossman AY. 2001. Identification of two powdery mildew fungi, Oidium neolycopepisci sp. nov. and O. lycopersici, infecting tomato in different parts of the world. Mycol Res. 105(6):684–697.

Kiss L, Jankovics T, Kovacs GM, Daughtrey ML. 2008. Oidium longipes, a new powdery mildew fungus on Petunia in the
USA: a potential threat to ornamental and vegetable solanaceous crops. Plant Dis. 92(5):818–825.

Kiss L, Vaghefi N, Bransgrove K, Dearnaley JDW, Takamatsu S, Tan YP, Marston C, Liu S-Y, Jin D-N, Adorada DL, et al. 2020. Australia: a continent without native powdery Mildews? The first comprehensive catalog indicates recent introductions and multiple host range expansion events, and leads to the re-discovery of *Salomonomyces* as a new lineage of the Erysiphales. Front Microbiol. 11(1571):1–31.

Linné C von. 1753. Species plantarum. Tomus II. Stockholm (Sweden): Impensis Laurentii Salvii. p. 699. + [64].

Liu TZ. 2010. The Erysiphaceae of inner Mongolia. Chifeng (China): Inner Mongolia Science and Technology Press. p. 322.

Liu M, Braun U, Takamatsu S, Hambleton S, Shoukouhi P, Bisson KR, Hubbard K. 2021. Taxonomic revision of *Blumeria* based on multi-gene DNA sequences, host preferences and morphology. Mycoscience. 62(3):143–65.

Maeda M, Meeboon J, Heluta VP, Liu SY, Tang SR, Takamatsu S. 2021. Phylogeny and taxonomy of *Phyllactinia* species (powdery mildew: erysiphaceae) occurring on the ash trees (*Fraxinus* spp.). Mycoscience. 62(4):268–280.

Marmolejo J, Siahaan SAS, Takamatsu S, Braun U. 2018. Three new records of powdery mildews found in Mexico with one genus and one new species proposed. Mycoscience. 59 (1):1–7.

Matsuda S, Takamatsu S. 2003. Evolution of host–parasite relationship of *Golovinomyces* (Ascomycota: Erysiphaceae) inferred from nuclear rDNA sequences. Mol Phylogenet Evol. 27:314–327.

Meeboon J, Kokaew J, Takamatsu S. 2017. Notes on powdery mildews (Erysiphales) in Thailand. *Golovinomyces*. Trop Plant Pathol. 43(3):202–217.

Meeboon J, Takamatsu S. 2017. Phylogeny and taxonomy of *Erysiphe pulchra* (Erysiphales) and *E. cornicola* nom. nov. Mycoscience. 58(5):378–382.

Meeboon J, Takamatsu S, Braun U. 2020. Morphophylogenetic analyses revealed that *Podosphaera tridactyla* constitutes a species complex. Mycologia. 112 (2):244–246.

Moparthi S, Grove GG, Pandey B, Bradshaw MJ, Latham SR, Braun U, Meeboon J, Romberg M. 2019. Phylogeny and taxonomy of *Podosphaera cerasi*, sp. nov., and *Podosphaera prunicola* sensu lato. Mycologia. 111(4):647–659.

Mori Y, Sato Y, Takamatsu S. 2000a. Evolutionary analysis of the powdery mildew fungi using nucleotide sequences of the nuclear ribosomal DNA. Mycologia. 92:74–93.

Mori Y, Sato Y, Takamatsu S. 2000b. Molecular phylogeny and radiation time of Erysiphales inferred from the nuclear ribosomal DNA sequences. Mycoscience. 41:437–447.

Parmelee JA. 1977. The fungi of Ontario. II. Erysiphaceae (mildews). Can J Bot. 55(14):1940–1983.

Pastirčáková K, Jankovics T, Komáromi J, Pintye A, Pastirčák M. 2016. Genetic diversity and host range of powdery mildews on Papaveraceae. Mycol Prog. 15 (4):1–18.

Paul YS, Kapoor JN. 1985. Taxonomy of anamorphs of Erysiphaceae. Indian Phytopathol. 38(4):761–763.

Qiu P-L, Liu S-Y, Bradshaw M, Rooney-Latham S, Takamatsu S, Bulgakov TS, Tang S-R, Feng J, Jin D-N, Aroge T, et al. 2020a. Multi-locus phylogeny and taxonomy of an unresolved, heterogeneous species complex within the genus *Golovinomyces* (Ascomycota, Erysiphales), including *G. ambrosiae*, *G. circumfusus* and *G. spadiceus*. BMC Microbiol. 20(1):1–16.

Qiu PL, Qi X-F, Li Y, Braun U, Liu SY. 2020b. Epitypification and molecular confirmation of *Erysipe cucurbitacearum* as a synonym of *Golovinomyces tabaci*. Mycoscience. 61:30–36.

Rambaut A. 2009. Fig Tree ver. 1.3.1. http://tree.bio.ed.ac.uk/software/figtree.

Sanecz GS, Taylor JW. 1999. Phylogeny of the Erysiphales (powdery mildews) inferred from internal transcribed spacer (ITS) ribosomal DNA sequences. Can J Bot. 77:150–169.

Salmon E. 1900. A monograph of the Erysiphaceae. Mem Torrey Bot Club. 9:1–292.

Scholler M, Schmidt A, Siahaan SAS, Takamatsu S, Braun U. 2016. A taxonomic and phylogenetic study of the *Golovinomyces bicellatus* complex (Erysiphales, Ascomycota) using asexual state morphology and rDNA sequence data. Mycol Prog. 15(6):1–13.

Selliah S, Brouillet L. 2008. Molecular phylogeny of the North American eurybid calasters (Asteraeaceae, Astereae) based on the nuclear ribosomal internal and external transcribed spacers. Botany. 86(8):901–915.

Shin HD. 1988. Erysiphaceae of Korea [Thesis]. Department of Agricultural Biology, Graduate School of Seoul National University. p. 305.

Shin HD. 2000. Erysiphaceae of Korea. Plant Pathog Korea. 2:1–320.

Shirouzu T, Takamatsu S, Hashimoto A, Meeboon J, Ohkuma M. 2020. Phylogenetic overview of Erysiphaceae based on nrDNA and *MCMM* sequences. Mycoscience. 61 (5):249–258.

Siahaan SAS, Sakamoto H, Shinoda T, Takamatsu S. 2018. Morphophylogenetic study revealed that *Erysiphe gracilis* (powdery mildew of evergreen oaks, Erysiphales) is a species complex consisting of six different species. Mycoscience. 59(2):124–136.

Silvestro D, Michalak I. 2012. RaxmlGUI: a graphical front-end for RAxML. Org Divers Evol. 12:335–337.

Simonyan SA. 1994. Mikoflora Armenii. VII. Muchnistorosoyanye griby Armenii (por. Erysiphales). Yerevan (Armenia): Izdatel’stvo AN Armenii. p. 384.

Suchard MA, Lemey P, Baee G, Ayres DL, Drummond AJ, Rambaut A. 2018. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. Virus Evol. 4:vey016.

Takamatsu S. 2004. Phylogeny and evolution of the powdery mildew fungi (Erysiphales, Ascomycota) inferred from nuclear ribosomal DNA sequences. Mycoscience. 45:147–157.

Takamatsu S, Heluta V, Havrylenko M, Divarangkoon R. 2009. Four powdery mildew species with catenate conidia infect *Galium*: molecular and morphological evidence. Mycol Res. 113:117–129.

Takamatsu S, Hirata T, Sato Y. 1998. Phylogenetic analysis and predicted secondary structures of the rDNA internal transcribed spacers of the powdery mildew fungi (Erysiphales). Mycoscience. 39:441–453.
Takamatsu S, Hirata T, Sato Y, Nomura Y. 1999. Phylogenetic relationships of Microsphaera and Erysiphe sect. Erysiphe (powdery mildews) inferred from the rDNA ITS sequences. Mycoscience. 40:259–268.

Takamatsu S, Ito H, Shioya Y, Kiss L, Heluta V. 2015a. First comprehensive phylogenetic analysis of the genus Erysiphe (Erysiphales, Erysiphaceae) I. The Microsphaera lineage. Mycologia. 107:475–489.

Takamatsu S, Ito H, Shioya Y, Kiss L, Heluta V. 2015b. First comprehensive phylogenetic analysis of the genus Erysiphe (Erysiphales, Erysiphaceae) II: the Uncinula lineage. Mycologia. 107:903–914.

Takamatsu S, Matsuda S, Grigaliunaite B. 2013. Comprehensive phylogenetic analysis of the genus Golovinomyces (Ascomycota: Erysiphales) reveals close evolutionary relationships with its host plants. Mycologia. 105:1135–1152.

Takamatsu S, Matsuda S, Niinomi S, Havrylenko M. 2006. Molecular phylogeny supports a Northern Hemisphere origin of Golovinomyces (Ascomycota: Erysiphales). Mycol Res. 110:1093–1101.

Takamatsu S, Siahaan SAS, Moreno-Rico O, Cabrera de Álvarez MG, Braun U. 2016. Early evolution of endoparasitic group in powdery mildews: molecular phylogeny suggests missing link between Phyllactinia and Leveillula. Mycologia. 108:837–850.

Tamura K, Stecher G, Kumar S. 2021. MEGA11: molecular evolutionary genetics analysis version 11. Mol Biol Evol. 38 (7):3022–3027.

Toome M, Pearson HG, Alexander BJR. 2015. First report of Euoidium longipes, a new powdery mildew fungus on tamarillo (Solanum betaceum) in New Zealand. Plant Dis. 99(12):1863.

Voytyuk O, Heluta VP, Wasser SP, Nevo E. 2009. Biodiversity of the powdery mildew fungi (Erysiphales, Ascomycota) of Israel. Ruggell (Switzerland): Ganter Verlag. p. 290.

Walsh PS, Metzger DA, Higuchi R. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR–based typing from forensic material. Biotechniques. 10:506–513.

Yamaguchi Y, Meeboon J, Heluta VP, Liu SY, Feng J, Takamatsu S. 2021. Phylogeny and taxonomy of Erysiphe species (powdery mildew: erysiphaceae) occurring on the ash trees (Fraxinus spp.). Mycoscience. 62 (2):115–123.