


Hidden treasures of herbaria - even small collections contain a wealth of diversity: the powdery mildews of the North Carolina State Larry F. Grand Mycological Herbarium

Scott LaGreca^{1,2}, Uma Crouch¹, Andrew Paul¹ , Jacklyn Thomas¹, Jake Thompson¹, Christian Shaw¹, Marc A. Cubeta¹, Uwe Braun³, Michael Bradshaw^{1,4} 

¹ Department of Entomology and Plant Pathology, Center for Integrated Fungal Research, North Carolina State University, Raleigh, NC, 27606, USA

² Sarah P. Duke Gardens, 420 Anderson Street, Duke University, Durham, NC, 27708-0341, USA

³ Department for Geobotany and Botanical Garden, Institute of Biology, Martin Luther University, Herbarium, Halle (Saale), 06108, Germany

⁴ Farlow Herbarium, Harvard University, 22 Divinity Avenue, Cambridge, MA 02138, USA

Corresponding author: Michael Bradshaw (mjbradsh@ncsu.edu)

Abstract

The occurrence of cryptic species is well documented in fungi but the extent of their diversity is not fully understood. This study assessed the fungal diversity within a part of the Larry F. Grand Mycological Herbarium (NCSLG), a small, well-maintained collection at North Carolina State University, with a focus on the powdery mildew fungi (*Erysiphaceae*). *Erysiphaceae* were selected due to their economic impact as plant pathogens and availability of extensive DNA sequence data for multiple barcode loci. Our research objectives included determining the number of phylogenetic species compared with those identified morphologically, and to identify undescribed species. We generated sequence data for 220 of the 299 powdery mildew specimens (73% success rate) in the herbarium, which represented 60 species in 10 genera, collected from 134 host plant species. Our analyses revealed that ~83% (183/220) of the sequenced specimens had identifications that were incorrect and/or outdated based on current genus/species concepts. Additionally, four new species are described: *Erysiphe ampicarpaicola*, *E. ulmi-alatae*, *E. quercus-virginianae*, and *Takamatsuella grandii*. A specimen deposited at NCSLG is designated as an epitype for *Phyllactinia liriodendri*, and a species of *Phyllactinia* identified on *Carpinus caroliniana*, as well as multiple species infecting *Quercus* spp., likely represent additional undescribed species that require more data. This research highlights the critical role of herbarium collections in uncovering fungal biodiversity, and underscores the importance of preserving these valuable resources, particularly with the growing trend to discard herbaria due to financial and space constraints.

Key words: Collection Based Research, *Erysiphaceae*, Fungarium, Museums, NCSLG

Introduction

Herbaria provide critical infrastructure for addressing key scientific research questions (Lavoie 2013; Dentinger et al. 2015; Verkley et al. 2015; James et al. 2018). Traditionally, they have served as a reference for biodiversity research, a field of biological inquiry that relies on accurate species



Academic editor: Marc Stadler

Received: 17 April 2025

Accepted: 21 May 2025

Published: 10 June 2025

Citation: LaGreca S, Crouch U, Paul A, Thomas J, Thompson J, Shaw C, Cubeta MA, Braun U, Bradshaw M (2025) Hidden treasures of herbaria - even small collections contain a wealth of diversity: the powdery mildews of the North Carolina State Larry F. Grand Mycological Herbarium. IMA Fungus 16: e156231. <https://doi.org/10.3897/ima fungus.16.156231>

Copyright: © Scott LaGreca et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

identification. Recent studies have demonstrated that herbarium specimens represent a rich yet underutilized resource to better understand fungal evolution (Staats et al. 2013; Dentinger et al. 2016; Tedersoo et al. 2016). More modern, non-traditional uses of herbaria include tracking species of fungi and plants through time and space to provide evidence of climate and environmental change as well as to understand host-pathogen interactions and disease spread (Lendemer et al. 2017; Willis et al. 2017; Meineke et al. 2018; Kido et al. 2019; Bradshaw et al. 2025c). Additionally, the increasing digitization of herbarium specimens has significantly enhanced their role in global biodiversity research, particularly through platforms like GBIF, which now serve as critical infrastructures for data accessibility (Knapp 2023; Park et al. 2023). Even though strides have been made to bring herbarium research into the 21st century (Staats et al. 2013; Dentinger et al. 2015; Yoshida et al. 2015; Buerki et al. 2016; Tedersoo et al. 2016; Forin 2018; Miller et al. 2022), their importance in research is broadly underutilized and undervalued (Andrew et al. 2018). Originally established to serve applied purposes—such as documenting medicinal plants—herbaria continue to hold untapped potential for addressing contemporary societal needs, including applications in public health, agriculture, education, and other translational research areas.

The influence of herbaria goes beyond scientific endeavors with herbarium specimens inspiring artwork as well as providing a unique resource for historians developing biographies of plant collectors (Flannery 2023). Another innovative use for herbaria is mining preserved specimens for DNA to study population genetics and reconstruct evolutionary relationships (Bradshaw and Tobin 2020; Bradshaw et al. 2021, 2023a, 2025c; Ristaino 2020; Folk et al. 2021). Recent technological advances have improved extraction, amplification, and sequencing of DNA from historic fungal material (Kistenich et al. 2019; Bradshaw et al. 2023a). Because of these advances, fungal herbaria (fungaria) represent an underutilized source of historical DNA that is now being used to explore many interesting research questions, from tracking the evolution and spread of plant disease-causing fungi and fungal-like organisms (Ristaino and Schmidt 2014; Bradshaw et al. 2021, 2025c), to revealing patterns of host adaptation and specialization of plant pathogens (Bradshaw et al. 2024, 2025c), to discovering undescribed fungal species (Bradshaw 2025a, 2025b).

The Larry F. Grand Mycological Herbarium (official acronym: NCSLG; NYBG Steere Herbarium 2024) is a small (c. 14,000 specimens) fungal herbarium located in Gardner Hall on the North Campus of North Carolina State University in Raleigh. The herbarium was established in 1970 by Professor Larry F. Grand (1940–2013), a mycologist who specialized in the study of wood decay, plant pathogenic, and ectomycorrhizal fungi. Professor Grand's research interests are strongly reflected in the fungarium. At the time of his retirement, wood decay fungi comprised over half the collections, followed by plant pathogenic and ectomycorrhizal mushroom forming fungi. Roughly, the collection consisted of 75% *Basidiomycota* and 25% *Ascomycota*, with a few specimens of zygomycetous fungi, *Oomycetes*, and slime molds. Geographically, most specimens were collected from the Southeastern United States. Unique North Carolina habitats of conservation concern (Schafale 2024) represented in the NCSLG collection include bald regions of the Southern Appalachian Mountains and Nags Head Woods, a remnant Coastal Plain longleaf pine ecosystem. NCSLG also houses

a substantial library of more than 1000 mycology books, scientific journals, illustrations, and reprints. Although Dr. Grand's mycological expertise was wood decay fungi, he had a major interest in plant pathogenic fungi such as the powdery mildew and rust fungi. During Grand's tenure as Director of the herbarium, he accumulated ~300 powdery mildew specimens.

Cryptic species represent morphologically indistinguishable, monophyletic species and are well-documented for fungi (Groenewald et al. 2006; Schubert et al. 2007; Bensch et al. 2010; Crous et al. 2012; Videira et al. 2016; LaGreca et al. 2020; U'Ren et al. 2024). Hawksworth and Lücking (2017) estimated that the Kingdom Fungi comprises between 2.2 and 3.8 million species, with a substantial number "hidden" as cryptic species. As a first step in exploring the hidden diversity present within a small, state university fungal herbarium, representative loci (Bradshaw et al. 2022) were sequenced for the powdery mildew (*Erysiphaceae*) specimens in NCSLG. The *Erysiphaceae* was chosen as our study group of fungi because of their economic importance as plant pathogens and the availability of DNA sequence data for multiple barcode loci (Bradshaw et al. 2022). Our primary research objective was to determine and compare the number of distinct phylogenetic species based on DNA analyses to the number of species names based on specimen collection labels. Given the large diversity of powdery mildew hosts in the herbarium, we hypothesized that our analyses of the powdery mildews in the herbarium would reveal multiple undescribed species.

Materials and methods

Morphological examination

Leaves and stems of each powdery mildew herbarium specimen were initially examined for mycelium, conidia and conidiophores, and appendages, asci, ascospores, and peridial cells of chasmothecia with a Nikon SMZ1270 dissecting microscope. To examine asexual structures, a 2 × 4 cm piece of 3M clear, adhesive tape was applied to the visible colonies of powdery mildew fungi on a diseased leaf, followed by placing the tape on a drop of distilled water or 3% KOH on a glass slide. The following measurements were taken: width of hyphae, length/width of conidiophores, and length/width of conidia (n = 20 for each structure, unless otherwise noted). To examine chasmothecia, a sterile dissecting needle was used to transfer c. 10 chasmothecia from diseased leaves (when possible) to a glass slide with a droplet of 10% KOH for a period of 5 minutes to allow for rehydration. The rehydrated chasmothecia were then transferred to a glass slide with a droplet of water followed by a glass cover slip. The following measurements were made: chasmothecium diameter, length/width of peridial cells, length/width of chasmothecial appendages, length/width of asci, length and width of asci, and length/width of ascospores (n = 20 for each structure, unless otherwise noted). Slides were examined with a Nikon Eclipse E600 compound microscope at 10×, 40× and 100× (= oil immersion) magnifications. Images were captured with a Nikon DSRi2 digital camera attached to the microscopes. All measurements were made using dedicated Nikon NIS-Elements 5.42.04 software. For the conidia of *E. ulmi-alatae* pen and ink hand illustrations were accomplished by the first author.

DNA sequencing

DNA extractions were performed using the Chelex method (Walsh et al. 1991; Hirata and Takamatsu 1996). The polymerase chain reaction (PCR) was used to amplify the ITS and LSU rDNA regions using the primer pairs PM10/PM28R (Bradshaw and Tobin 2020) for all specimens. If PCR was unsuccessful, a nested approach was applied using primers AITS (Bradshaw and Tobin 2020)/TW14 (Mori et al. 2000) followed by PM10/PM28R or AITS/PM11 (Bradshaw and Tobin 2020) followed by PM10/PM2 (Cunnington et al. 2003). For the undescribed species and for taxa that needed additional data for accurate identification, multiple loci were sequenced. For the calmodulin (*CAM*), Glyceraldehyde 3-Phosphate Dehydrogenase (*GAPDH*), Glutamine synthetase (*GS*), and RNA Polymerase II Subunit B2 (*RPB2*) region the primer pairs PMCAM1/PMCAM4R, PMGAPDH1/PMGAPDH3R, GSPM2/GSPM3R, and PMRpb2_4/PMRpb2_6R were used (Bradshaw et al. 2022). If these amplifications were unsuccessful for the *GS* and *RPB2* regions, the following primers from Bradshaw et al. (2023b) were used: EGS1/EGS2R and ERPB2_3/ERPB2_7R. For the β -tubulin (*TUB*) region the primers BT-F5b/BTR7a (Ellingham et al. 2019) were used followed by ETUB2 and ETUB2R (Bradshaw et al. 2023b). In reactions where *GAPDH* sequences were contaminated with DNA of *Ampelomyces* mycoparasites, EGAPDH1/EGAPDH2 primers (Bradshaw et al. 2025a) were used. To amplify the rDNA intergenic spacer (IGS) region, the primer pair IGS-12a/NS1R was used (Carbone and Kohn 1999).

Phylogenetic analysis

Phylogenetic trees were generated from analysis of concatenated ITS+28S+*CAM*+*GAPDH*+*GS*+IGS+*RPB2*+*TUB* sequences. Sequences were aligned and edited using Geneious Prime 2025.0.3. Taxa were chosen based on the analyses by Bradshaw et al. (2023b, 2025d). 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). The phylogeny was inferred using Bayesian analysis of the combined loci using a Yule tree prior (Gernhard 2008) and a strict molecular clock, in the program BEAST version 1.10.4 (Suchard et al. 2018). A single MCMC chain of 10^7 steps was run, with a burn-in of 25%. Posterior probabilities were calculated from the remaining 9000 sampled trees. A maximum clade credibility tree was produced using TreeAnnotator version 1.10.4 (part of the BEAST package). Stationarity was confirmed by running the analysis multiple times, which revealed convergence between runs. The resulting tree was visualized using FigTree ver. 1.3.1 (Rambaut, 2009). A maximum likelihood analysis was accomplished using raxmlGUI (Silvestro and Michalak 2012) under the default settings with a GTR+G+I evolutionary model. Bootstrap analyses were conducted using 1000 replications (Felsenstein 1985).

Results

DNA was successfully extracted, amplified, and sequenced from 219 of 299 (73% success rate) specimens (Suppl. material 1). All sequences were deposited in GenBank and all specimen data are now available on MycoPortal (Suppl. material 1). Based on sequence analyses, 60 species in 10 genera collected from 134 host

plant species were represented in the sample. Ninety-five percent of the specimens were collected from North Carolina (Fig. 1). Phylogenetic analyses resulted in new assignments and determinations for 84% of the specimens sequenced and revealed four undescribed species (Figs 2–7). Most sequenced specimens were collected between 1965 and 2012. An additional observation is that we extracted DNA from and sequenced the ITS+28S region of a *Brasiliomyces* specimen several

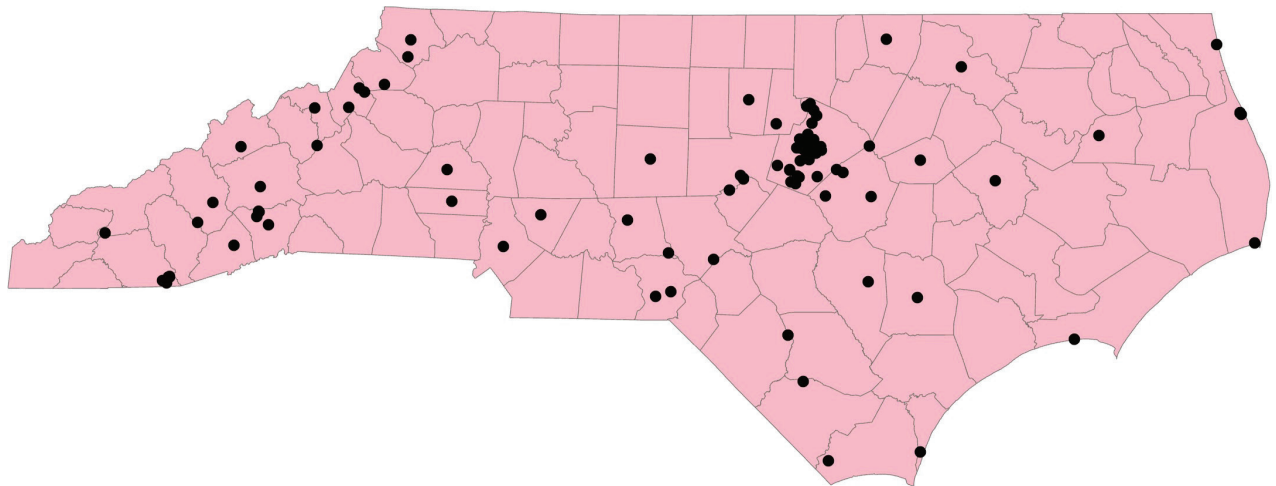


Figure 1. Map of North Carolina showing collection localities of *Erysiphaceae* specimens in the NCSLG herbarium. The cluster of collections in the middle of the state, representing ~66% of our specimens, is from the NCSU campus and surrounding Raleigh area.

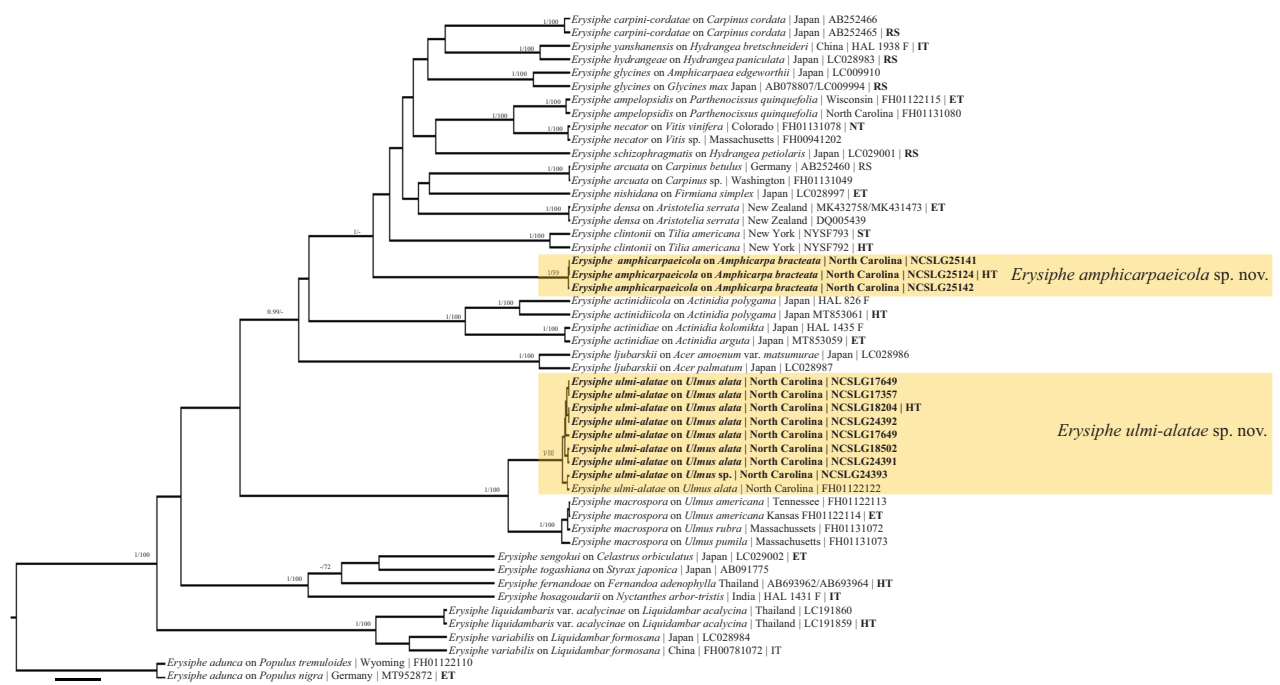


Figure 2. Bayesian maximum clade credibility tree of concatenated ITS+28S+CAM+GAPDH+GS+IGS regions of select taxa in the *Uncinula* lineage. The phylogenetic tree revealed two undescribed species. Fungal species are denoted and followed by the host, collection locality, and voucher number. Type status (HT: Holotype, IT: Isotype, ET: Epitype, NT: Neotype, ST: Syntype) of the specimens concerned is denoted as well as reference sequences for phylogenetic purposes (RS). Posterior probabilities ≥ 90 are displayed followed by bootstrap values greater than 70% for the maximum likelihood (ML) analyses. Taxa in bold were sequenced for the current study.

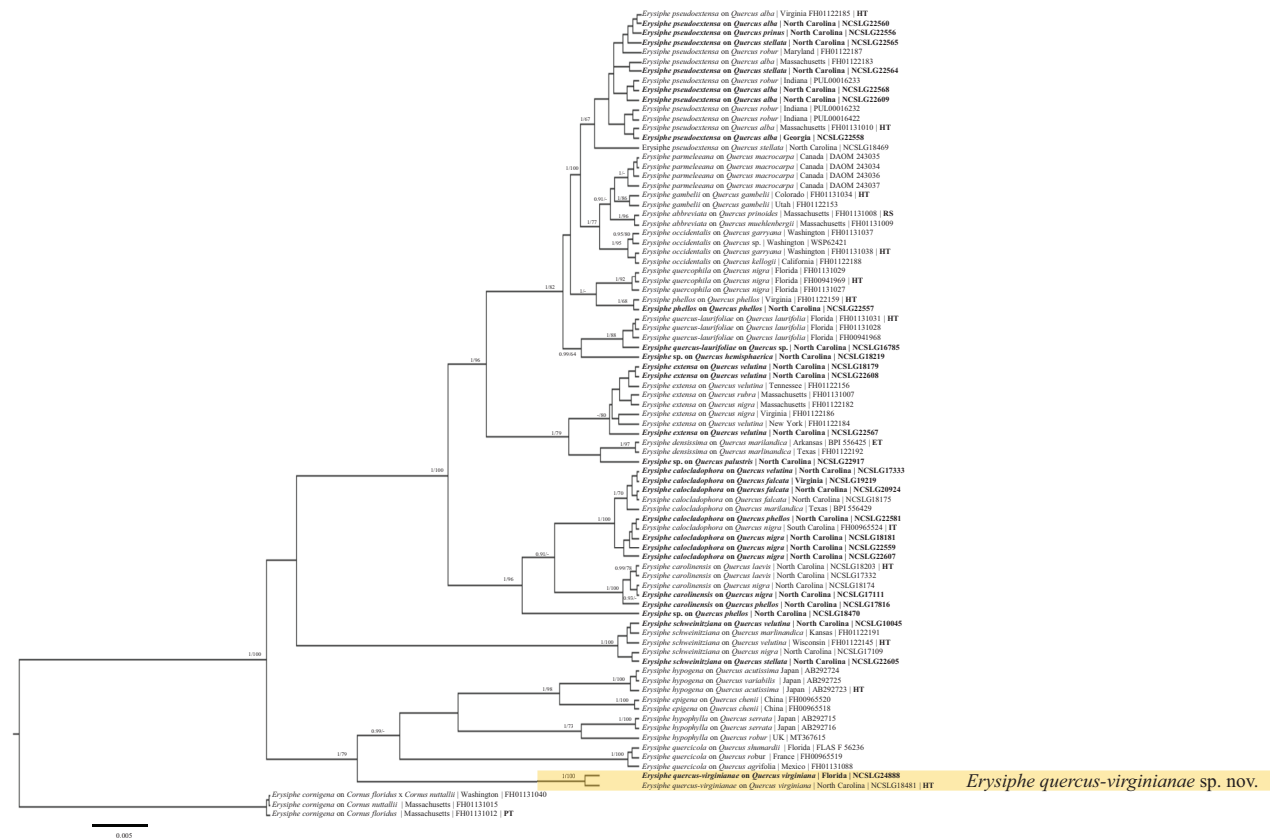


Figure 3. Bayesian maximum clade credibility tree of the concatenated ITS+28S+CAM+GAPDH+GS+IGS+RPB2+TUB regions of taxa in the North American *Quercus* lineage. The phylogenetic tree revealed one undescribed species as well as multiple, additional undescribed species, labeled as '*Erysiphe* sp.' Fungal species are denoted followed by the host, collection locality, and voucher number. Type status (HT, IT, ET) of the specimens concerned is denoted and reference sequences for phylogenetic purposes (RS). Posterior probabilities ≥ 90 are displayed followed by bootstrap values greater than 60% for the maximum likelihood (ML) analyses conducted. Taxa in bold were sequenced for the current study.

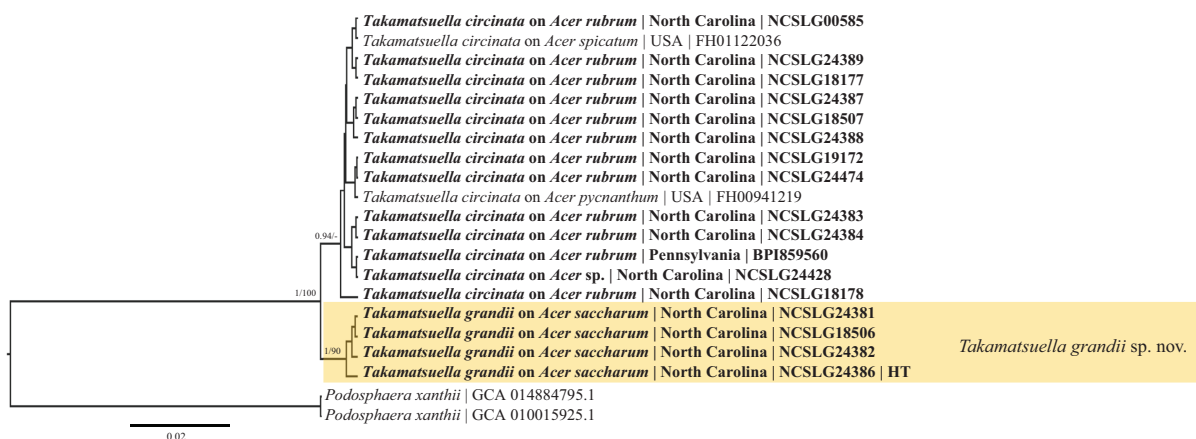


Figure 4. Bayesian maximum clade credibility tree of the concatenated ITS+28S+GAPDH+IGS+TUB regions of taxa in the genus *Takamatsuella*. Type status (HT, ET) of the specimens concerned is denoted. Posterior probabilities ≥ 90 are displayed followed by bootstrap values greater than 70% for the maximum likelihood (ML) analyses conducted. Taxa in bold were sequenced for the current study.

times due to uncertain results. The ITS region consistently displayed complex electropherograms with multiple bands in certain regions, likely resulting from intragenomic variation in this species (Bradshaw et al. 2023c).

Taxonomy

Erysiphe ampicarpaeicola M. Bradshaw, sp. nov.

MycoBank No: 858351

Fig. 5

Etymology. Epithet composed of the name of the host genus and the Latin-derived suffix “-cola” (dweller).

Diagnosis. Morphologically distinguished from *Erysiphe glycines* by having chasmothecia with shorter appendages, up to twice as long as the chasmothecial diameter (versus up to seven times as long as the diameter in *E. glycines*), and phylogenetically by forming a distant highly supported clade.

Type. USA • North Carolina, Ashe County, near West Jefferson, on leaves of *Ampicarpaea bracteata*, along Bluff Mountain logging road, 36°23'26.9"N, 81°33'21.2"W, 14 September 2024, J. Thompson (NCSLG 25124—holotype). Ex-holotype sequence: [PV416665](#) (ITS), [PV472002](#) (GAPDH), [PV471964](#) (GS).

Description. *Mycelium* amphigenous, forming effuse, arachnoid, whitish patches; *hyphae* branched, often at right angles, septate, hyaline, thin-walled, smooth, 3–5 µm wide; hyphal appressoria solitary, nipple-shaped to lobate, 4–10 µm wide; conidiophores 65–80 µm long, septate at base, foot cells 24–42 µm long and 6–8 µm wide, straight to usually somewhat flexuous, sinuous, followed by 1–2 shorter cells, about 15–20 × 7–8 µm *conidia* formed singly, cylindrical-doliform, 23–35 × 10–12 µm, germination not seen. *Chasmothecia* scattered, subglobose to globose, dark brown, 90–154 × 104–157 µm in diameter; *peridium* cells irregularly polygonal, 6–13 × 10–19 µm; *appendages* in the lower half of the chasmothecium, number variable, few to numerous, mycelioid, often interwoven with the mycelium and with each other, sometimes poorly developed and hard to distinguish from the mycelial hyphae, length variable (up to two times the diameter of the chasmothecium), thin-walled, smooth, narrow (up to 4 µm wide), septate, hyaline; *asci* 4–6 per chasmothecium, 63–70 × 38–45 µm, oblong-ellipsoid, short-stalked, 6-spored; *ascospores* ellipsoid-ovoid, 20–22 × 11–12 µm, colorless.

Additional specimens examined. (all on leaves of *Ampicarpaea bracteata*): USA • North Carolina, Macon County, Cashiers, along roadside, 35°00'59"N, 83°07'37"W, 2024, June 2024, J. Thompson 100 (NCSLG 25142); • Shortoff Mountain along trail, 35°00'59"N, 83°07'37"W, June 2024, J. Thompson 101. (NCSLG 25141); • Macon County, Highlands, on leaves of *Ampicarpaea bracteata* along roadside, 16 September 1975, L.F. Grand 2095 (NCSLG 22551).

Substrate/host. *Ampicarpaea bracteata*.

Distribution. North America (Canada, USA), probably widespread.

Notes. Amano (1986) listed *Ampicarpaea bracteata* as host of *Erysiphe communis* from Canada and the United States. Braun and Cook (2012) assigned North American *Erysiphe* specimens on *A. bracteata* to *E. glycines*, an Asian species that occurs on *Glycine* spp. and *Ampicarpaea edgeworthii*. This decision was based on the morphological similarity between Asian and North American specimens. Sequences retrieved from Asian collections on *Glycine* spp. and *Ampicarpaea edgeworthii* form a strongly supported species clade within the basal *Uncinula* lineage within *Erysiphe* (Bradshaw et al. 2023b). The North American *E. ampicarpaeicola* clade also clusters in the *Uncinula* lineage, far from *E. glycines* (Fig. 2). Based

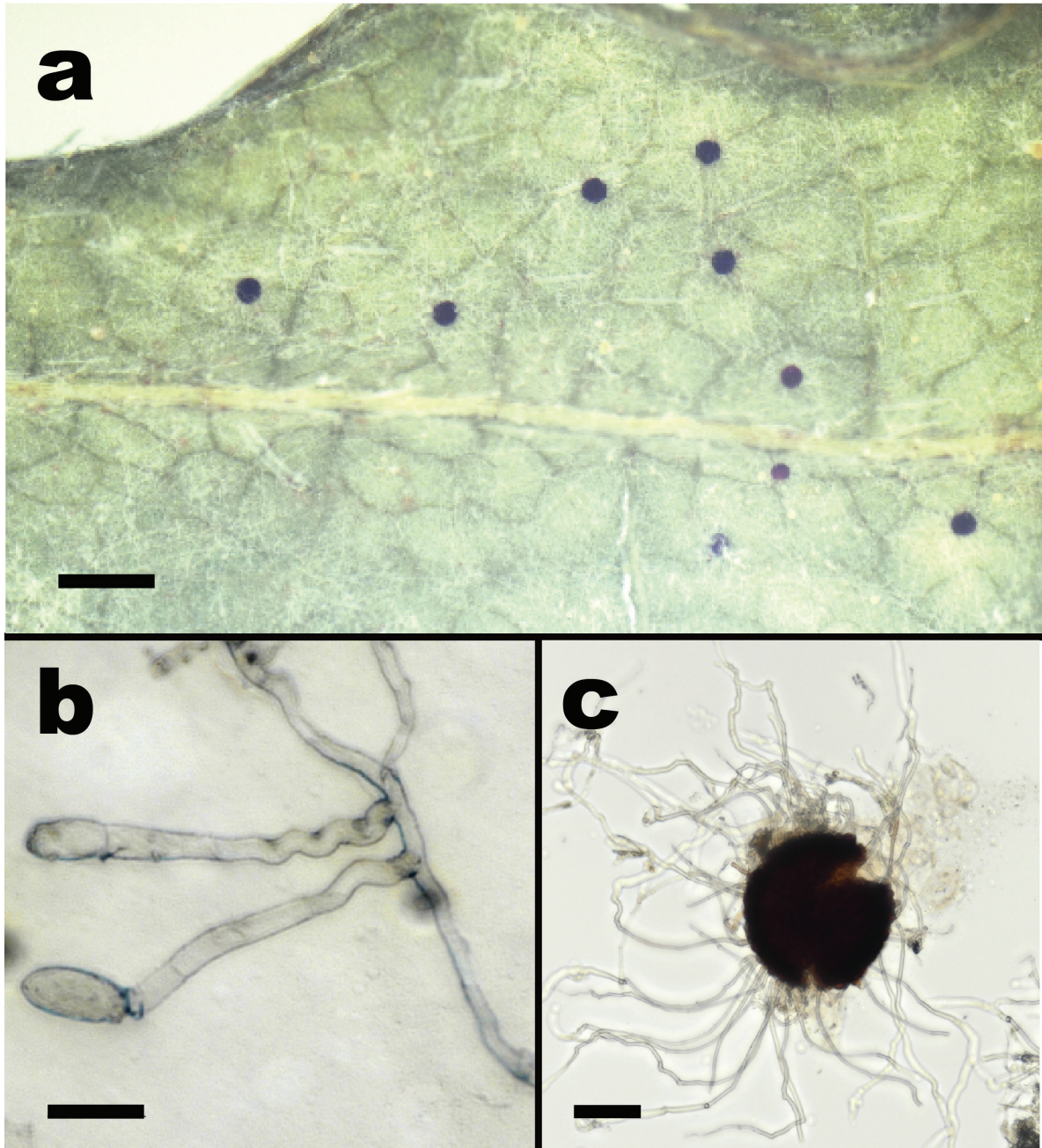


Figure 5. *Erysiphe amphicarpaicola* sp. nov. (**a**, **c** from NCSLG 22551 **b** from NCSLG25141) **a** habit, on leaves of *Amphicarpaea bracteata* **b** conidiophores with conidia **c** split chasmothecium showing mycelioid appendages. Scale bars: 0.5 mm (**a**); 25 µm (**b**); 30 µm (**c**).

on the examined specimens, chasmothecia on *A. bracteata* differ from *E. glycines* chasmothecia in having shorter appendages, up to twice as long as the chasmothecial diameter (versus up to seven times as long as the diameter).

***Erysiphe quercus-virginianae* M. Bradshaw, sp. nov.**

MycoBank No: 858352

Fig. 6

Etymology. Epithet derived from the name of the host plant, *Quercus virginiana*.

Diagnosis. Morphologically close to *Erysiphe abbreviata* s. lat., but differing by forming much larger chasmothecia, 116–159 μm diam., with up to 20 appendages, and 4–8-spored asci. Phylogenetically well-distinguished from *E. abbreviata* and all other North American *Erysiphe* spp. on oaks by forming a highly supported clade.

Type. USA • North Carolina, Wake County, J.C. Raulston Arboretum, NC State University, 4415 Beryl Road, Raleigh, on *Quercus virginiana* planted in the arboretum, 35°47.687.10'N, 78°41.97100'W, 149 m alt., 9 November 2011, L.F. Grand s.n. (NCSLG 18481—holotype). Ex-holotype sequence: [OR424987](#) (ITS+28S), [OR427493](#) (CAM), [OR427579](#) (GAPDH), [OR427663](#) (GS), [OR427727](#) (RPB2), [OR427793](#) (TUB).

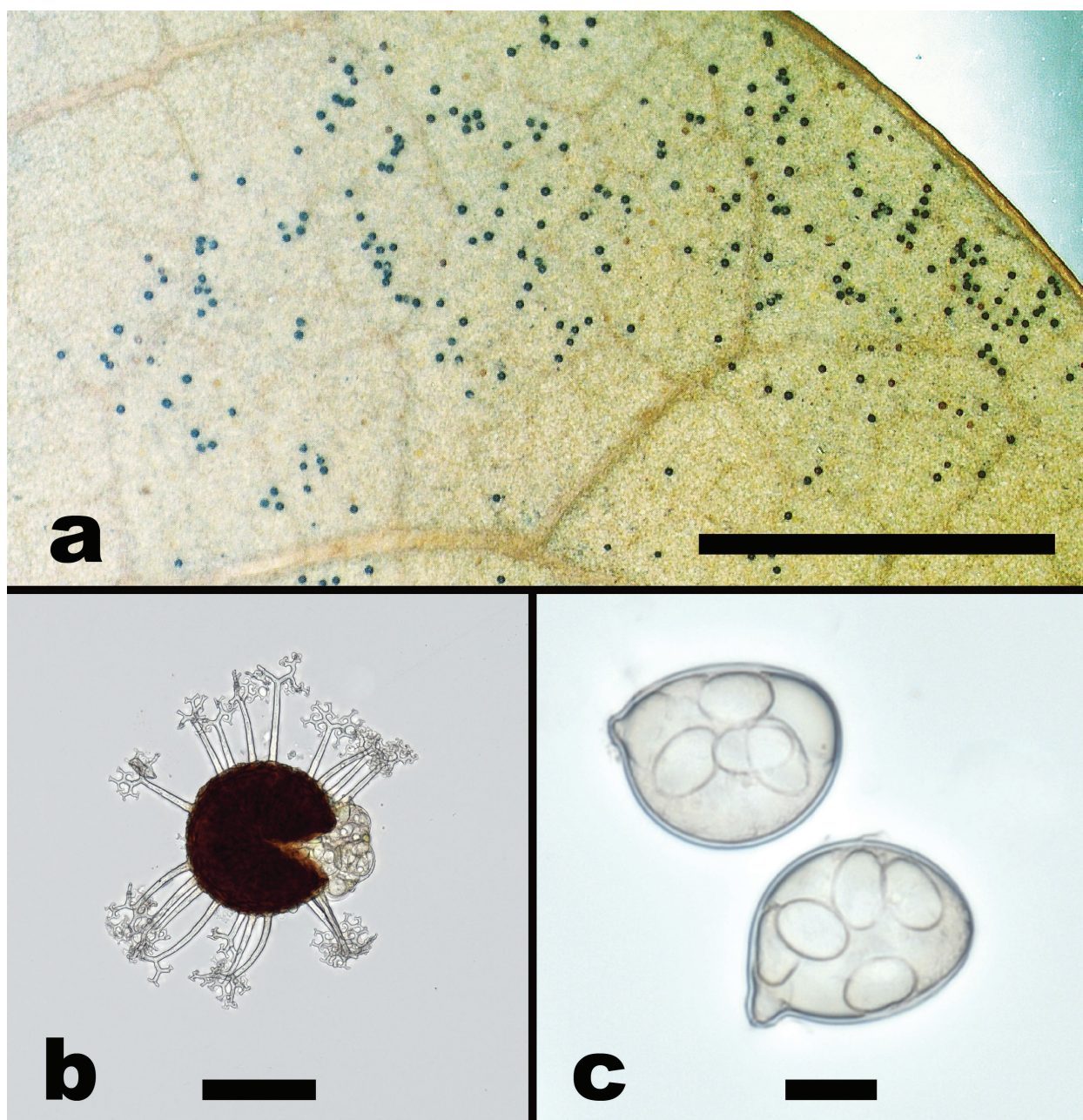


Figure 6. *Erysiphe quercus-virginianae* sp. nov. (based on NCSLG 18481) **a** habit, on leaves of *Quercus virginiana* **b** split chasmothecium showing apically branched appendages and emerging asci **c** close-up of asci with ascospores. Scale bars: 4 mm (**a**); 100 μm (**b**); 20 μm (**c**).

Description. *Mycelium* and *anamorph* not seen. *Chasmothecia* scattered to gregarious among trichomes on abaxial leaf surfaces, subglobose to globose, $116\text{--}159 \times 123\text{--}144\ \mu\text{m}$; *peridium* cells conspicuous, brown, irregularly polygonal, $12\text{--}21 \times 7\text{--}14\ \mu\text{m}$; *appendages* 8–20, equatorial, stiff, straight to somewhat curved, aseptate, hyaline, $60\text{--}125\ \mu\text{m}$ long, relative length usually about 0.5–1 times the chasmothecial diameter or somewhat shorter, $4\text{--}7\ \mu\text{m}$ wide [widest at base], *apices* 4–5 \times regularly dichotomously branched not strictly in one dimension, tips of the ultimate branchlets recurved; *asci* 5–8 per chasmothecium, obovoid, saccate, short-stalked, $55\text{--}75 \times 40\text{--}60\ \mu\text{m}$, walls up to $3\ \mu\text{m}$ thick, 4–8-spored; *ascospores* ellipsoid-ovoid, hyaline, $15\text{--}25 \times 8\text{--}13\ \mu\text{m}$.

Additional specimen examined. USA • Florida, Broward County, Fort Lauderdale, on *Quercus virginiana*, 2022, M.J. Bradshaw s.n. (NCSLG 24888).

Substrate/host. *Quercus virginiana* (*Quercus* subgen. *Quercus* sect. *Virentes*; Manos and Hipp 2021).

Distribution. North America (USA, Florida, North Carolina).

Notes. The new species, *Erysiphe quercus-virginianae*, is morphologically similar to the morphology-based circumscription of *E. abbreviata* in Braun and Cook (2012), especially with regard to the number and length of the chasmothecial appendages. However, *E. abbreviata* is characterized by having smaller chasmothecia, $70\text{--}110\ \mu\text{m}$ diam, with fewer, 3–6-spored, asci (3–6), and somewhat larger ascospores, $20\text{--}32 \times 13\text{--}21\ \mu\text{m}$ when mature. Bradshaw et al. (2025d) published a phylogenetic-taxonomic revision of North American *Erysiphe* spp. on oaks, including a re-assessment of *E. abbreviata*. A high degree of co-evolution between *Erysiphe* and *Quercus* species was revealed in that study and led to the introduction of multiple new species as well as emended circumscriptions of several species. Based on phylogenetic examination, *E. abbreviata* is confined to hosts of *Quercus* subgen. *Quercus* sect. *Quercus* subsect. *Prinoideae*. Hence, it is plausible that *E. quercus-virginianae*, on a host of another section (*Virentes*) represented another, undescribed species. *Quercus virginiana* and all other oak species assigned to sect. *Virentes* are to our knowledge not hosts of *E. abbreviata* (not listed as hosts in Braun and Cook 2012). Amano (1986) listed *Microsphaera alni* and *M. extensa* on *Q. virginiana* from North America. *Erysiphe extensa* is a morphologically distinct species with very long chasmothecial appendages (Braun and Cook 2012; Bradshaw et al. 2025d), whereas *E. quercus-virginianae* may be potentially hidden under reports of *M. alni* on *Q. virginiana*.

***Erysiphe ulmi-alatae* M. Bradshaw, sp. nov.**

MycoBank No: 858353

Fig. 7

Etymology. Epithet referring to the name of the type host, *Ulmus alata*.

Diagnosis. *Erysiphe ulmi-alatae* is morphologically barely distinguishable from *E. macrospora*, but can be distinguished by the host and the fact that it phylogenetically forms a separate, highly supported clade.

Type. USA • North Carolina: Wake County, Beaverdam Campground, Falls Lake, in upland hardwood-pine forest, on leaves of *Ulmus alata*, 3 November 2008, L.F. Grand 2095 and C.A. Vernia (NCSLG 18204 – holotype). Ex-holotype sequence: PV416510 (ITS), PV409586 (IGS).

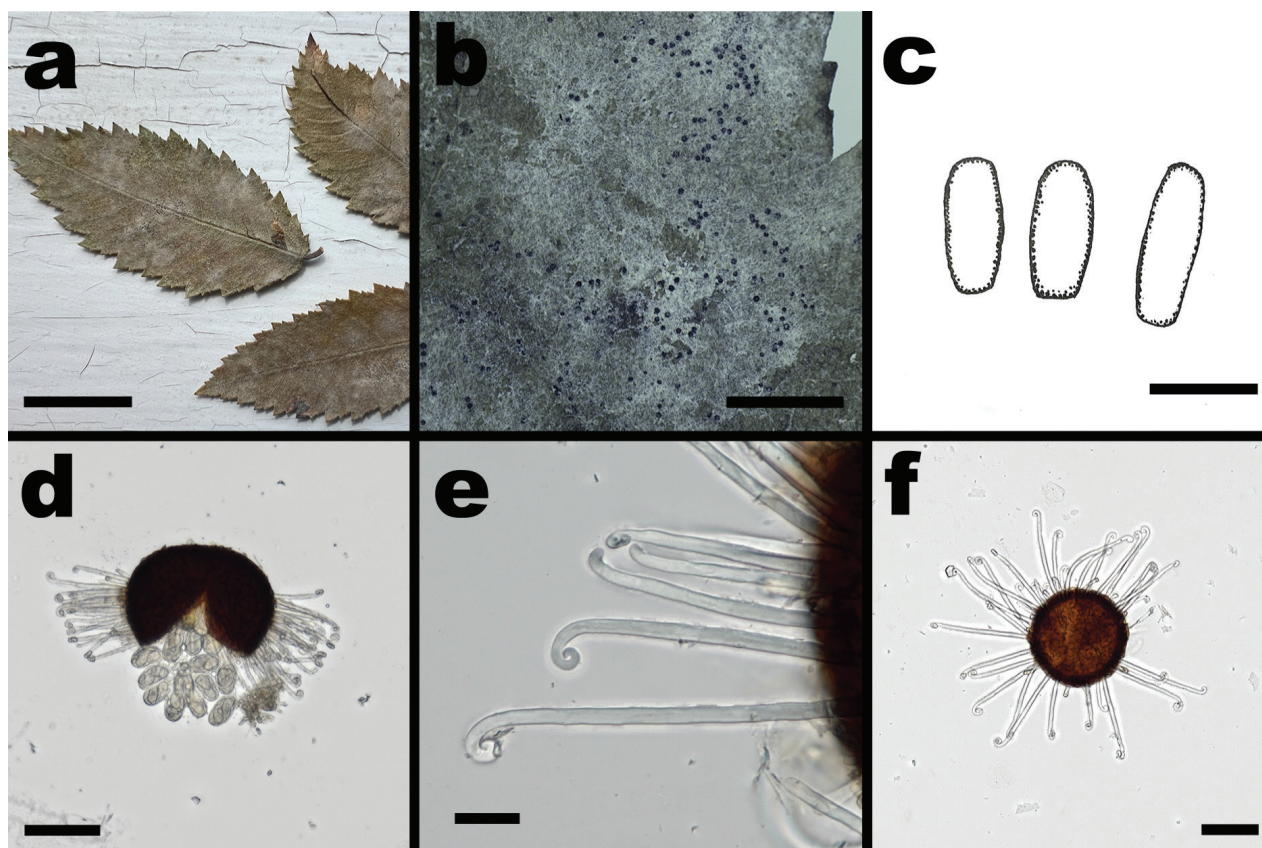


Figure 7. *Erysiphe ulmi-alatae* sp. nov. (a, b, d, f from NCSLG 18204 c from NCSLG 24391 e from NCSLG 24393) a mycelium on leaves of *Ulmus alata* b habit, on leaves of *Ulmus alata*, showing clustered chasmothecia c conidia (drawing by S. LaGreca) d split chasmothecium showing numerous appendages with circinate ends, and asci with ascospores e appendages, immature (top) and mature (bottom) f whole chasmothecium. Scale bars: 2 cm (a); 4 mm (b); 30 µm (c); 20 µm (b, e); 75 µm (f).

Description. *Mycelium* in persistent, creamy-white patches, almost entirely on adaxial leaf surfaces; *hyphae* branched, often at right angles, septate, hyaline, 3–5 µm wide; hyphal appressoria solitary or in opposite pairs, lobed; *conidia* formed singly, cylindrical-doliiform, 34–40 × 11–18 µm. *Chasmothecia* scattered to gregarious, dark brown, subglobose to globose, 130–178 µm in diameter; *peridium cells* irregularly polygonal, 7–13 × 10–21 µm; *appendages* numerous, number variable (40+), hyaline, aseptate, ± equatorial, 80–145 × 5–9 µm, mostly shorter than the chasmothecial diameter, width ± equal throughout, walls smooth, uniformly thickened from base to tip, *apices* uncinuate to circinate when mature, uncinuate-circinate apex not enlarged, circinate apices 10–15 µm across (appendages shorter, stiffer, and with pointed ends when immature); *asci* 10–25 per chasmothecium, obovoid, saccate, short-stalked, 48–70 × 23–24 µm, walls up to 3 µm thick, 2-spored; *ascospores* ellipsoid-ovoid to slightly teardrop-shaped, 22–30 × 11–17 µm, hyaline.

Additional specimens examined. (all on leaves of *Ulmus alata*): USA • North Carolina, Cabarrus County, Concord, 15 October 1972, R.L. Forster 63 (NCSLG 24392); • Wake County, Cary, 7 July 2008, Y. Weimin s.n. (NCSLG 17649); • NC State University campus, Raleigh, 27 September 1972, A.J. Julius s.n. (NCSLG 24393); • Miner Presbyterian Church, New Bern Avenue, Raleigh, 24 September 1978, R. Sohn s.n. and G. Emberger (NCSLG 24391).

Substrate/host. *Ulmus alata*.

Distribution. (based on specimens deposited in North American herbaria as '*Erysiphe macrospora*' or '*Uncinula macrospora*' on *Ulmus alata*): North America (USA: Alabama, Florida, Georgia, Illinois, Indiana, Mississippi, North Carolina, Oklahoma, South Carolina, Tennessee, Texas).

Notes. *Erysiphe* (*Uncinula* lineage) on *Ulmus alata* was previously assigned to *Uncinula macrospora* and *Erysiphe macrospora*, respectively (Salmon 1900; Braun 1987; Braun and Cook 2012). However, in the first phylogenetic examinations of *E. macrospora*, Bradshaw et al. (2023b) revealed the paraphyly of this species. Sequences obtained from the type host, *Ulmus americana*, as well as on *U. rubra* (= *U. fulva*) and *U. pumila*, formed a well-supported clade, with a sequence retrieved from *U. alata* clustering outside in sister position. Now, additional sequences are available and confirm the *Erysiphe* on *U. alata* as a distinct, cryptic, sister species. The genetic similarity between *E. macrospora* and *E. ulmi-alatae* in multiple loci is relatively low (~95%), which supports the description of a separate species. The two species are morphologically barely distinguishable, i.e., they can only be differentiated by their sequence differences and different hosts. The separation of *E. macrospora* s. lat. into two species, based on its host species, is not surprising. According to the current phylogenetic-taxonomic division of the genus *Ulmus* (Whittemore et al. 2021), the type species, *Ulmus americana*, pertains to *Ulmus* subgen. *Oreopteleae* sect. *Blepharocarpus*, whereas *U. alata* is assigned to *Ulmus* subgen. *Oreopteleae* sect. *Chaetoptelea*. *Ulmus crassifolia* and *U. thomasi* (= *U. racemosa*) are two additional elm species known to be hosts of *E. macrospora* s. lat. (Braun and Cook 2012) that belong to sect. *Chaetoptelea*. It can be assumed that these elm species also pertain to the host range of *E. ulmi-alatae*, which is, yet, unproven by means of sequence analyses. Additionally, *Ulmus rubra* (= *U. fulva*), a species pertaining to *Ulmus* subgen. *Ulmus* sect. *Ulmus*, is a proven host of *E. macrospora*, suggesting a wider host range of this species. The occurrence of *E. ulmi-alatae* on *U. alata* likely follows the distribution of its host species in the Southeastern and Central USA.

***Phyllactinia liriodendri* U. Braun, in Braun and Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews): 260. 2012.**

Type. USA • Pennsylvania, Centre County, State College Campus, on *Liriodendron tulipifera*, 1889, W.A. Buckhout (BPI 859705—holotype).

Epitype. (designated here, MycoBank, MBT10025444): USA • North Carolina, Wake County, Raleigh, on *Liriodendron tulipifera*, November 1972, L. Lazo s.n. (NCSLG22914). Ex-epitype sequences: [PQ585171](#) (ITS), [PQ589086](#) (*TUB*).

Notes. *Phyllactinia liriodendri* was included in phylogenetic-taxonomic studies recently published by Bradshaw et al. (2025b). The authors suggested that sequences from specimens of this species form highly supported species clades in concatenated, ITS+28S, and *TUB* analyses, confirming the status of *P. liriodendri* as a species within the morphologically poorly differentiated genus *Phyllactinia*, which requires sequence data for unequivocal identifications. *Ex typus* sequences are the best option to obtain and analyze reference

sequences for phylogenetic-taxonomic purposes. However, the type of *P. liriodendri* from 1889 is very old and sequencing was not attempted. In such cases, epitypification with ex-epitype sequences is the method of choice.

Phyllactinia* sp. on *Carpinus caroliniana

Fig. 8

Description. *Mycelium* amphigenous, mostly effuse but sometimes forming thin white patches; *hyphae* branched, septate, hyaline, thin-walled, smooth; *hyphal appressoria* not observed; anamorph not observed. *Chasmothecia* scattered, sphaeroid or nearly so, 180–200 µm in diameter; *peridium* cells large, light brown, irregularly polygonal, up to 30 µm long; *appendages* equatorial, between 4 and 10 per chasmothecium, aseptate, hyaline, up to 1.5 times the chasmothecial diameter, 5–7 µm wide, straight or almost so, rigid, acicular with bulbous swelling at the base (up to 40 µm wide); *asci* absent or poorly formed, indistinct, yellowish; *ascospores* not observed.

Specimen examined. USA • North Carolina, Carteret County, Theodore Roosevelt State Natural Area, Bogue Banks, town of Pine Knoll Shores, on leaves of *Carpinus caroliniana*, 26 November 2004, L.F. Grand and C.A. Vernia (NCSLG 17103).

Notes. Owing to the morphological similarity, Braun and Cook (2012) assigned *Phyllactinia* on *Carpinus caroliniana* in North America tentatively to *P. carpini*. The Asian *P. carpinicola* is morphologically readily distinguishable from *P. carpini* by having apiculate conidia (Braun and Cook 2012), and it is phylogenetically distinct (Takamatsu et al. 2008; Bradshaw et al. 2025b). Sequences obtained from the *Phyllactinia* specimen collected in North Carolina on *C. caroliniana* clearly showed that this powdery mildew fungus does not pertain to the European *P. carpini*. However, it is premature to introduce a new species for this *Phyllactinia*. There are only sequences obtained from a single immature specimen, without the anamorph and immature chasmothecia without mature asci and ascospores. Additional sequenced collections are needed. A further problem refers to *P. carpini*, from which there is only one sequence retrieved from *Carpinus orientalis* available (Bradshaw et al. 2025b) which is not the type host of this species. The North American *Phyllactinia* on *Carpinus caroliniana* is probably an undescribed species, but additional sequence data from mature specimens are needed, as well as an examination of European specimens on *Carpinus betulus*, the type host of *P. carpini*.

***Takamatsuella grandii* M. Bradshaw, sp. nov.**

MycoBank No: 858354

Fig. 9

Etymology. Epithet in honor of NCSU mycologist Larry F. Grand.

Diagnosis. *Takamatsuella grandii* differs morphologically from *T. circinata* in having appendages with walls uniformly 3 µm thick, and genetically by forming a highly supported clade.

Type. USA • North Carolina, Wake County, Ligon Street, Raleigh, on leaves of *Acer saccharum*, 5 November 1980, M. Daykin s.n. (NCSLG 24386—holotype). Ex-holotype sequences: [PV416651](#) (ITS), [PV409641](#) (IGS).



Figure 8. *Phyllactinia* sp. (based on NCSLG 17103) **a** habit, on leaves of *Carpinus caroliniana* **b** split chasmothecium showing peridium cells, emerging immature asci, and appendages with bulbous bases. Scale bars: 2 mm (**a**); 100 µm (**b**).

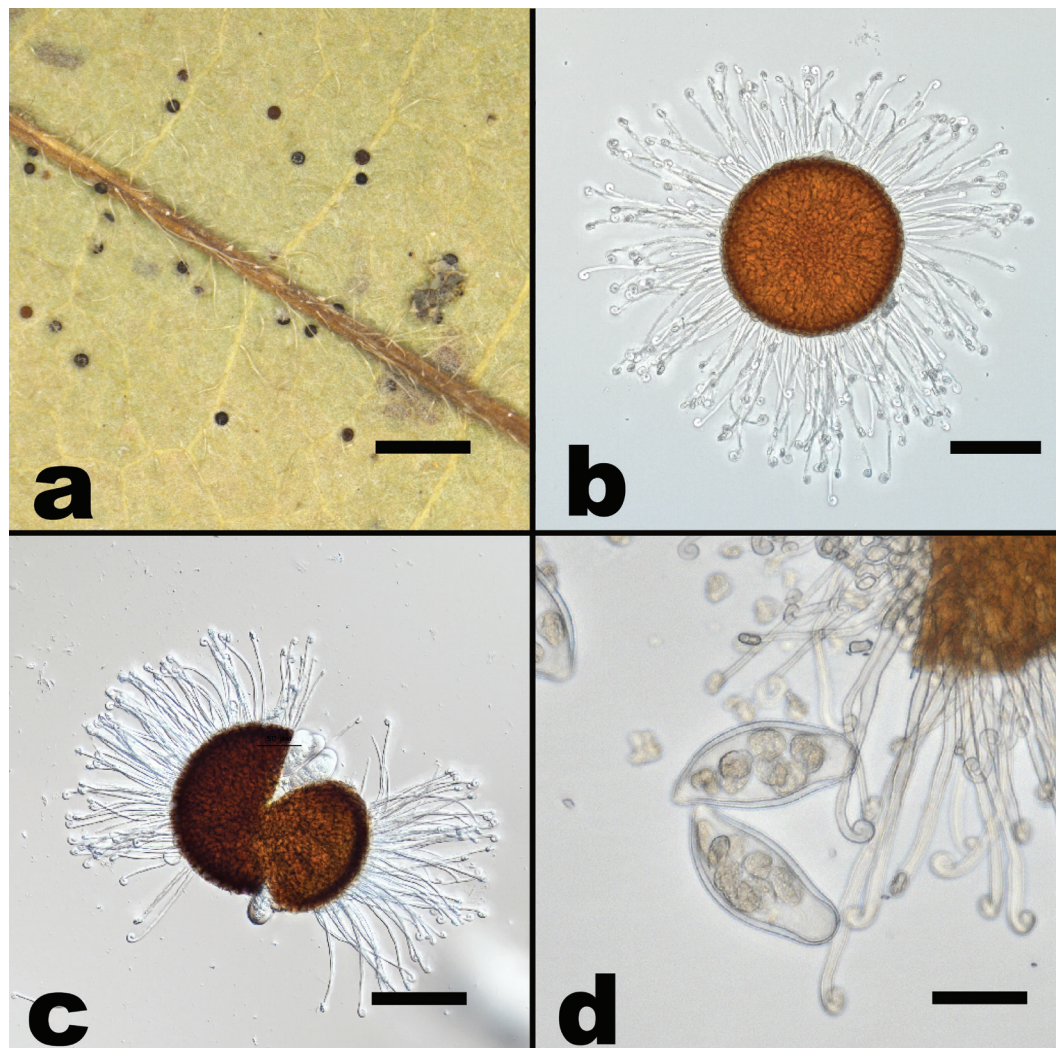


Figure 9. *Takamatsuella grandii* sp. nov. (**a** From NCSLG 18506 **b–d** from NCSLG 24386) **a** habit, on leaves of *Acer saccharum* **b** chasmothecium showing peridium cells and appendages with circinate ends **c** split chasmothecium showing appendages and emerging asci **d** close-up of asci with ascospores. Scale bars: 1 mm (**a**); 100 µm (**a**, **c**); 10 µm (**d**).

Description. *Mycelium* on abaxial surfaces of leaves, effuse, thin, arachnoid, grayish white; *hyphae* dichotomously branched, hyaline, thin-walled, smooth, septate; *hyphal appressoria* nipple-shaped; *anamorph* not seen. *Chasmothecia* scattered to +/- gregarious, depressed globose, 120–170 µm in diameter; *peridium cells* irregularly polygonal, light brown, 7–15 × 14–19 µm; *appendages* very numerous, up to 150 per chasmothecium, arising below the equator, stiff to flexuous, simple, apices tightly uncinuate to circinate, not enlarged, about 0.3–1 times as long as the chasmothecial diameter, uniformly 2–6 µm wide and walls uniformly 3 µm thick, hyaline, aseptate, smooth, thin-walled; *asci* up to 8 or more, clavate-saccate, 70–90 × 25–40 µm, usually stalked, wall uniformly 3 µm thick, 8-spored; *ascospores* ellipsoid-obovoid, 10–25 × 9–20 µm, hyaline.

Additional specimens examined. USA • North Carolina, Wake County, Schenck Research Forest, Raleigh, on leaves of *Acer saccharum*, in floodplain along stream, 35°48.958'N, 78°44.020'W, 165 m alt., 26 October 2011, L.F. Grand s.n. (NCSLG 18506); • Wake County, Schenck Research Forest, Raleigh, on leaves of *Acer saccharum* (= *A. barbatum*, ≡ *A. saccharum* var. *barbatum*, ≡ *A. saccharum* f. *barbatum*; = *A. dasycarpum*), 6 October 1998, G. Blosser 32 (NCSLG 24381).

Substrate/host. *Acer saccharum*.

Distribution (based on specimens on *Acer saccharum* deposited in North American herbaria): North America (USA: Indiana, New York, New Hampshire, North Carolina, Pennsylvania).

Notes. *Takamatsuella grandii* is an undescribed cryptic species infecting different *Acer* species to those of *T. circinata*. The host of the type specimen of *T. circinata* is *Acer spicatum* (*Acer* sect. *Spicata*) (Braun and Cook 2012). Additional *Acer* spp. cited as host species of *T. circinata* are *A. glabrum* (unresolved name), *A. nigrum* (*Acer* sect. *Acer* ser. *Saccharodendron*), *A. pensylvanicum* (*Acer* sect. *Macranthum*), *A. rubrum* (*Acer* sect. *Rubra*), *A. saccharum* (*Acer* sect. *Acer* ser. *Saccharodendron*), and *A. saccharinum* (*Acer* sect. *Rubra*); subgeneric affiliations according to Davis (2021). Phylogenetic analyses of specimens of *Takamatsuella* on *Acer saccharum* revealed the existence of a cryptic species on this host, now referred to as *T. grandii*. The new species presented here is morphologically very close to *T. circinata* but differs in having appendages with walls uniformly 3 µm thick (versus thin-walled or only thickened at the base). The affinity of *Takamatsuella* species on the other host species listed above remains unclear since they belong to different sections of *Acer*. Based on the currently available sequences, as well as the high degree of co-evolution within this group of powdery mildews, it can be assumed that the *Takamatsuella* species on *Acer nigrum* might be *T. grandii*, whereas specimens on *A. rubrum* and *A. saccharinum* (sect. *Rubra*) are expected to be part of the host range of *T. circinata*, pending molecular confirmation.

Discussion

Phylogenetic analyses of DNA from 220 herbarium specimens collected predominantly in central North Carolina from the 1970s through the early 2000s yielded four undescribed powdery mildew fungi, as well as multiple, additional, potentially undescribed species that require further, comprehensive examination. Three of the new species are in the genus *Erysiphe* (the most speciose genus in the *Erysiphaceae*), and one in *Takamatsuella*. We also detected a *Phyllactinia* sp. on *Carpinus caroliniana* and multiple *Erysiphe* spp. infecting *Quercus*

spp. that probably represent additional, undescribed species requiring further investigation. In total, approximately 84% of the powdery mildew holdings in NCSLG had to be re-determined at the species or genus rank based on our molecular phylogenetic analyses (Suppl. material 1).

All taxonomic novelties revealed by the molecular phylogenetic examinations presented here are cryptic species within known, long-recognized powdery mildew species. Specifically, for *Erysiphe amphicarpaeicola*, the host of the type specimen (*Amphicarpaea bracteata*) was thought to be within the host range of the Asian *E. glycines*; for *E. ulmi-alati*, the host of the type specimen (*Ulmus alata*) was thought to be within the host range of *E. macrospora*; and with regards to *Takamatsuella grandii*, the host of the type specimen (*Acer saccharum*) was assumed to be within the host range of *T. circinata* s. lat. (Braun and Cook 2012). Additionally, *E. quercus-virginianae* on *Quercus virginiana* agrees with the morphological species concept of *E. abbreviata* in Braun and Cook (2012). These results underscore the importance of revising previous morphological species concepts, primarily when broader host ranges and/or wider distributions, beyond continents, are involved. Furthermore, using ex type sequences of taxa as reference sequences for phylogenetic-taxonomic purposes is crucial. The application of sequences obtained from non-type specimens not confirmed by ex type sequences, may lead to erroneous conclusions in complexes of morphologically similar species or taxa with a high degree of cryptic speciation. However, type collections are sometimes too old to generate high-quality sequences for analyses, as exemplified by *Phyllactinia liriiodendri*. Designation of epitypes derived from recently collected material can help to mitigate such problems. In such cases, specimens deposited in herbaria can be valuable resources for helping to choose appropriate epitypes.

Conclusion

The trend of discarding or providing reduced support for herbarium collections has become increasingly prevalent. This is driven by a combination of financial constraints, space limitations, and shifting priorities within academic institutions (Davis 2024). Digitization is helpful but is not a solution for many issues—cryptic species, for example, cannot be detected through the use of an image. Despite their historical importance for conservation, education, and taxonomic research, many herbaria are facing obsolescence as both physical and digital management become more burdensome. The rise of digital herbarium initiatives and pressure to repurpose or downsize institutional spaces have led to the deaccessioning of valuable collections, posing significant risks to the continuity of plant biodiversity research and the preservation of historical botanical records (Thiers et al. 2024). The discovery of four undescribed powdery mildew species in the present study underscores the urgent need to safeguard these irreplaceable scientific resources by increasing both their accessibility and use. As exemplified in the present study, the possibility to sequence herbarium specimens highlights the enormous potential of preserved material for documentation of biodiversity. Previous identifications can be verified and corrected if found to be inaccurate, which is essential in the light of the high degree of outdated and

erroneous identifications in herbarium specimens, particularly for microscopic fungi. Furthermore, our results underline the importance of depositing herbarium specimens, and linking their sequence and annotated specimen data to repositories (i.e. GenBank and MycoPortal) (Conrad et al. 2014) and data networks (iDigBio and GBIF). Depositing voucher and reference specimens in officially recognized herbaria is a critical element for satisfying the “reproducibility” criterion, one of the key tenets of the scientific method, for results reported in peer-reviewed scientific journals.

Acknowledgements

We would like to thank James Mitchell at the Farlow Herbarium, Harvard University for extracting DNA from a specimen from BPI and the National Science Foundation, Award no. 2402193, for funding this research.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Adherence to national and international regulations

All the fungal strains used in this study have been legally obtained, respecting the Convention on Biological Diversity (Rio Convention).

Funding

National Science Foundation, Award no. 2402193. This work is supported by the Research Capacity Fund (HATCH), project award no. 7006142, from the U.S. Department of Agriculture's National Institute of Food and Agriculture.

Author contributions

MB brought together all the authors, collected a couple of specimens, conducted the phylogenetic analysis, and contributed to writing the first draft. SLG wrote the first draft, and conducted the majority of the morphological work as well as some of the curatorial work. UC and Jacklyn T accomplished all of the sequencing. AP contributed to the curatorial and morphological work. Jake T and CS extracted some of the specimens DNA. Jake T also collected a couple of specimens. UB assisted with writing the first draft and writing the taxonomy section. MC assisted with writing and organizing the manuscript. All authors contributed to the editing process.

Author ORCIDs

Andrew Paul  <https://orcid.org/0009-0000-3499-4080>

Michael Bradshaw  <https://orcid.org/0000-0002-7133-4679>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

- Abadi S, Azouri D, Mayrose I et al. (2019) Model selection may not be a mandatory step for phylogeny reconstruction. *Nature Communications* 10: 1–11. <https://doi.org/10.1038/s41467-019-08822-w>
- Amano K (1986) Host range and geographical distribution of the powdery mildew fungi. 2nd edn. Scientific Societies Press, Tokyo, 741 pp.
- Andrew C, Karakehian J, Raudabaugh DB et al. (2018) Fungarium specimens: a largely untapped source in global change biology and beyond. *Philosophical Transactions of the Royal Society, B*, 374(1763): 20170392. <https://doi.org/10.1098/rstb.2017.0392>
- Bensch K, Groenewald JZ, Dijksterhuis J et al. (2010) Species and ecological diversity within the *Cladosporium cladosporioides* complex (*Davidiellaceae*, *Capnodiales*). *Studies in Mycology* 67: 1–94. [https://doi.org/10.1016/S0166-0616\(14\)60026-9](https://doi.org/10.1016/S0166-0616(14)60026-9)
- Bradshaw M, Tobin P (2020) Sequencing herbarium specimens of a common detrimental plant pathogen (powdery mildew). *Phytopathology* 110: 1248–1254. <https://doi.org/10.1094/PHYTO-04-20-0139-PER>
- Bradshaw M, Braun U, Elliott M et al. (2021) A global genetic analysis of herbarium specimens reveals the invasion dynamics of an introduced pathogen. *Fungal Biology* 125: 585–595. <https://doi.org/10.1016/j.funbio.2021.03.002>
- Bradshaw MJ, Guan-Xiu G, Nokes L et al. (2022) Secondary DNA barcodes (CAM, GAPDH, GS, and RpB2) to characterize species complexes and strengthen the powdery mildew phylogeny. *Frontiers in Ecology and Evolution* 10: 918908. <https://doi.org/10.3389/fevo.2022.918908>
- Bradshaw MJ, Carey J, Liu M et al. (2023a) Genetic time traveling: sequencing old herbarium specimens, including the oldest herbarium specimen sequenced from kingdom Fungi, reveals the population structure of an agriculturally significant rust. *New Phytologist* 237: 1463–1473. <https://doi.org/10.1111/nph.18622>
- Bradshaw M, Braun U, Pfister DH (2023b) Phylogeny and taxonomy of the genera of *Erysiphaceae*, part 4, *Erysiphe* (the “*Uncinula* lineage”). *Mycologia* 115(6): 871–903. <https://doi.org/10.1080/00275514.2023.2230853>
- Bradshaw MJ, Aime MC, Rokas A et al. (2023c) Extensive intragenomic variation in the internal transcribed spacer region of fungi. *iScience* 26(8): 107317. <https://doi.org/10.1016/j.isci.2023.107317>
- Bradshaw MJ, Boufford D, Braun U et al. (2024) An in-depth evaluation of powdery mildew hosts reveals one of the world’s most common and widespread groups of fungal plant pathogens. *Plant Disease* 108: 576–581. <https://doi.org/10.1094/PDIS-07-23-1471-RE>
- Bradshaw M, Braun U, Mitchell JK et al. (2025a) Phylogeny and taxonomy of the genera of *Erysiphaceae*, part 6: *Erysiphe* (the “*Microsphaera* lineage” part 2). *Mycologia* 117: 110–165. <https://doi.org/10.1080/00275514.2024.2386230>
- Bradshaw M, Braun U, Khodaparast SA et al. (2025b) Phylogeny and taxonomy of the genera of *Erysiphaceae*, part 7, *Phyllactinieae*. *Mycologia Online First*. <https://doi.org/10.1080/00275514.2025.2476375>
- Bradshaw M, Ivors K, Broome JC et al. (2025c) An emerging fungal pathogen is spreading across the globe and affecting the blueberry industry. *New Phytologist* 246: 103–112. <https://doi.org/10.1111/nph.20351>
- Bradshaw M, Quijada L, Braun U et al. (2025d) Powdery mildews on North American oaks: high levels of diversity and pathogen-host coevolution. *Forest Pathology* 55: e70005. <https://doi.org/10.1111/efp.70005>

- Braun U (1987) A monograph of the *Erysiphales* (powdery mildews). Beihefte zur Nova Hedwigia. 89: 1–700.
- Braun U, Cook RTA (2012) Taxonomic Manual of the *Erysiphales* (Powdery Mildews). CBS Biodiversity Series 11: 1–707.
- Buerki S, Baker WJ (2016) Collections-based research in the genomic era. Biological Journal of the Linnean Society 117(1): 5–10. <https://doi.org/10.1111/bij.12721>
- Carbone I, Kohn LM (1999) A method for designing primer sets for speciation studies in filamentous ascomycetes. Mycologia 91: 553–556. <https://doi.org/10.2307/3761358>
- Crous PW, Braun U, Hunter GC et al. (2012) Phylogenetic lineages in *Pseudocercospora*. Studies in Mycology 75: 37–114. <https://doi.org/10.3114/sim0005>
- Cunnington JH, Takamatsu S, Lawrie AC et al. (2003) Molecular identification of anamorphic powdery mildews (*Erysiphales*). Australasian Plant Pathology 32(3): 421–428. <https://doi.org/10.1071/AP03045>
- Davis CC (2024) Collections are truly priceless. Science 383: 1035–1035. <https://doi.org/10.1126/science.ado9732>
- Davis E (2021) Systematic Classification of *Acer*. A Survey of the genus in accordance with The Maple Society Accepted Species Names. <https://maplesociety.org/wp-content/uploads/2021/07/classificationAcerMarch2021-vf2.pdf>
- Dentinger BTM, Gaya E, O'Brien H et al. (2016) Tales from the crypt: genome mining from fungarium specimens improves resolution of the mushroom tree of life. Biological Journal of the Linnean Society 117: 11–32. <https://doi.org/10.1111/bij.12650>
- Ellingham O, David J, Culham A (2019) Enhancing identification accuracy for powdery mildews using previously underexploited DNA loci. Mycologia 111(5): 798–812. <https://doi.org/10.1080/00275514.2019.1643644>
- Felsenstein J (1985) Confidence Limits on Phylogenies: An Approach Using the Bootstrap. Evolution 39: 783–791. <https://doi.org/10.1111/j.1558-5646.1985.tb00420.x>
- Flannery MC (2023) In the Herbarium: the Hidden World of Collecting and Preserving Plants. New Haven: Yale University Press, 325.
- Folk RA, Kates HR, LaFrance R et al. (2021) High-throughput methods for efficiently building massive phylogenies from natural history collections. Applications in Plant Sciences 9: e11410. <https://doi.org/10.1002/aps3.11410>
- Forin N (2018) A next generation sequencing approach for the study of ancient fungal specimens belonging to the Pier Andrea Saccardo collection preserved at the University of Padua. PhD Thesis, University of Padua, Italy.
- Gernhard T (2008) The conditioned reconstructed process. Journal of Theoretical Biology 253: 769–778. <https://doi.org/10.1016/j.jtbi.2008.04.005>
- Groenewald M, Groenewald JZ, Braun U et al. (2006) Host range of *Cercospora apii* and *C. beticola*, and description of *C. apiicola*, a novel species from celery. Mycologia 98: 275–285. <https://doi.org/10.3852/mycologia.98.2.275>
- Hawksworth DL, Lücking R (2017) Fungal Diversity Revisited: 2.2 to 3.8 Million Species. Microbiology Spectrum 5(4): 1–17. <https://doi.org/10.1128/microbiolspec.FUNK-0052-2016>
- Hirata T, Takamatsu S (1996) Nucleotide sequence diversity of rDNA internal transcribed spacers extracted from conidia and cleistothecia of several powdery mildew fungi. Mycoscience 37: 283–288. <https://doi.org/10.1007/BF02461299>
- James SA, Soltis PS, Belbin L et al. (2018) Herbarium data: global biodiversity and societal botanical needs for novel research. Applies Plant Science 6: 1–8.
- Kido A, Hood ME (2019) Mining new sources of natural history observations for disease interactions. American Journal of Botany 107(1): 3–5. <https://doi.org/10.1002/ajb2.1363>

- Kistenich S, Halvorsen R, Schröder-Nielsen A et al. (2019) DNA sequencing historical lichen specimens. *Frontiers in Ecology and Evolution* 7: 5. <https://doi.org/10.3389/fevo.2019.00005>
- Knapp S (2023) The past is a foreign country. *Nature Human Behaviour* 7: 1042–1043. <https://doi.org/10.1038/s41562-023-01622-9>
- LaGreca S, Lumbsch HT, Kukwa M et al. (2020) A molecular phylogenetic evaluation of the *Ramalina siliquosa* complex, with notes on species circumscription and relationships within *Ramalina*. *The Lichenologist* 52: 197–211. <https://doi.org/10.1017/S0024282920000110>
- Lavoie C (2013) Biological collections in an ever changing world: herbaria as tools for biogeographical and environmental studies. *Perspectives in Plant Ecology, Evolution and Systematics* 15: 68–76. <https://doi.org/10.1016/j.ppees.2012.10.002>
- Lendemer JC, Anderson Stewart CR, Besal B et al. (2017) The lichens and allied fungi of Mount Mitchell State Park, North Carolina: A first checklist with comprehensive keys and comparison to historical data. *Castanea* 82: 69–97. <https://doi.org/10.2179/17-126>
- Manos PS, Hipp AL (2021) An Updated Infrageneric Classification of the North American Oaks (*Quercus* Subgenus *Quercus*): Review of the Contribution of Phylogenomic Data to Biogeography and Species Diversity. *Forests* 12: 786. <https://doi.org/10.3390/f12060786>
- Meineke EK, Davis CC, Davies TJ (2018) The unrealized potential of herbaria for global change biology. *Ecological Monographs* 88: 505–525. <https://doi.org/10.1002/ecm.1307>
- Miller AN, Karakehian J, Raudabaugh DB (2022) Next-generation sequencing of ancient and recent fungarium specimens. *Journal of Fungi* 8(9): 932. <https://doi.org/10.3390/jof8090932>
- NYBG Steere Herbarium (2024) Index Herbariorum. <https://sweetgum.nybg.org/science/ih>
- Park DS, Feng X, Akiyama S, et al. (2023) The colonial legacy of herbaria. *Nature Human Behaviour* 7: 1059–1068. <https://doi.org/10.1038/s41562-023-01616-7>
- Rambaut A (2009) Fig Tree ver. 1.3.1. <http://tree.bio.ed.ac.uk/software/figtree>
- Ristaino JB (2020) The importance of mycological and plant herbaria in tracking plant killers. *Frontiers in Ecology and Evolution* 7: 521. <https://doi.org/10.3389/fevo.2019.00521>
- Ristaino JB, Schmidt SM (2014) Genetic diversity and historical distribution of *Phytophthora infestans* in herbarium specimens. *Phytopathology* 104: 158–169.
- Salmon E (1900) A monograph of the *Erysiphaceae*. *Memoirs of the Torrey Botanical Club*. 9: 1–292. <https://doi.org/10.5962/bhl.title.97215>
- Schafale M (2024) Classification of the Natural Communities of North Carolina—a Fourth Approximation. North Carolina Natural History Program, Raleigh. 1228 pp. https://doi.org/10.5149/9781469683904_Schafale
- Schubert K, Groenewald JZ, Braun U et al. (2007) Biodiversity in the *Cladosporium herbarum* complex (*Davidiellaceae*, Capnodiaceae), with standardisation of methods for *Cladosporium* taxonomy and diagnostics. *Studies in Mycology* 58: 105–156. <https://doi.org/10.3114/sim.2007.58.05>
- Schoch CL, Robbertse B, Robert V et al. (2014) Finding needles in haystacks: linking scientific names, reference specimens and molecular data for Fungi. *Database* 2014: bau061. <https://doi.org/10.1093/database/bau061>
- Silvestro D, Michalak I (2012) raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution* 12: 335–337. <https://doi.org/10.1007/s13127-011-0056-0>

- Staats M, Erkens RHJ, van de Vossenberg B et al. (2013) Genomic treasure troves: complete genome sequencing of herbarium and insect museum specimens. *PLoS ONE* 8(7): e69189. <https://doi.org/10.1371/journal.pone.0069189>
- Suchard MA, Lemey P, Baele G et al. (2018) Bayesian phylogenetic and phylodynamic data integration using BEAST. *Virus Evolution* 4(1): vey016. <https://doi.org/10.1093/ve/vey016>
- Takamatsu S, Inagaki M, Niinomi S et al. (2008) Comprehensive molecular phylogenetic analysis and evolution of the genus *Phyllactinia* (Ascomycota: *Erysiphales*) and its allied genera. *Mycological Research* 112(3): 299–315. <https://doi.org/10.1016/j.mycres.2007.11.014>
- Tedersoo L, Liiv I, Kivistik PA et al. (2016) Genomics and metagenomics technologies to recover ribosomal DNA and single-copy genes from old fruit-body and ectomycorrhiza specimens. *MycosKeys* 13: 1–20. <https://doi.org/10.3897/mycokeys.13.8849>
- Thiers B, Roberts TE, Rundell RJ et al. (2024) Duke's herbarium merits continued enhancement, not dissolution. *BioScience* 2024: biae031. <https://doi.org/10.1093/biosci/biae031>
- U'Ren JM, Oita S, Lutzoni F et al. (2024) Environmental drivers and cryptic biodiversity hotspots define endophytes in Earth's largest terrestrial biome. *Current Biology* 34: 1148–1156.e7. <https://doi.org/10.1016/j.cub.2024.01.063>
- Verkley GJM, Rossman A, Crouch JA (2015) The role of herbaria and culture collections. In: McLaughlin DJ, Spatafora JW (Eds) *The Mycota VII Part B, Systematics and Evolution*, 2nd edn. Springer-Verlag, Berlin, Heidelberg, 205–225. https://doi.org/10.1007/978-3-662-46011-5_8
- Videira SIR, Groenewald JZ, Braun U (2016) All that glitters is not *Ramularia*. *Studies in Mycology* 83: 49–163. <https://doi.org/10.1016/j.simyco.2016.06.001>
- 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.
- Whittemore AT, Fuller RS, Brown BH et al. (2021) Phylogeny, Biogeography, and Classification of the Elms (*Ulmus*). *Systematic Botany* 46(3): 711–727. <https://doi.org/10.1600/036364421X16312068417039>
- Willis CG, Ellwood ER, Primack RB et al. (2017) Old plants, new tricks: phenological research using herbarium specimens. *Trends in Ecology & Evolution* 32: 531–546. <https://doi.org/10.1016/j.tree.2017.03.015>
- Yoshida K, Sasaki E, Kamoun S (2015) Computational analyses of ancient pathogen DNA from herbarium samples: challenges and prospects. *Frontiers in Plant Science* 6: 771. <https://doi.org/10.3389/fpls.2015.00771>

Supplementary material 1

List of taxa, hosts, vouchers, collection localities, and GenBank accession numbers of the specimens examined in the current study

Authors: Scott LaGreca, Uma Crouch, Andrew Paul, Jacklyn Thomas, Jake Thompson, Christian Shaw, Marc A. Cubeta, Uwe Braun, Michael Bradshaw

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/ima fungus.16.156231.suppl1>