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Powdery Mildews on North American Oaks: High Levels of Diversity and Pathogen-Host Coevolution

Michael Bradshaw[1,2] | Luis Quijada[2,3] | Uwe Braun[4] | Matthew E. Smith[5] | Donald H. Pfister[2]

[1]Department of Entomology and Plant Pathology, Center for Integrated Fungal Research, North Carolina State University, Raleigh, North Carolina, USA | [2]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA | [3]Departamento de Botánica, Facultad de Farmacia, Ecología y Fisiología Vegetal, Avenida Astrofísico Francisco Sánchez, San Cristóbal de La Laguna, Canary Islands, Spain | [4]Department for Geobotany and Botanical Garden, Herbarium, Martin Luther University, Halle (Saale), Germany | [5]Department of Plant Pathology, University of Florida, Gainesville, Florida, USA

Correspondence: Michael Bradshaw (mjbradsh@ncsu.edu)

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ABSTRACT

Erysiphe species infecting oaks in North America are common and widespread, but compared to Asia and Europe, the taxonomy and phylogeny of North American species is unknown. The present study addresses this dispairity. Comprehensive multilocus phylogenetic analyses, including *CAM*, *GAPDH*, *GS*, ITS, *RPB2* and *TUB*, revealed a high degree of co-evolution between North American oaks and the *Erysiphe* spp. that infect them. A concatenated multilocus tree and individual trees based on single loci revealed many highly supported species clades. The clades are formally named to conform with the current taxonomic classification. Available names, such as *E. abbreviata*, *E. calocladophora* and *E. extensa*, are associated with corresponding clades, and are newly circumscribed supported by ex-type sequences or, if not available, by the designation of epitypes with ex-epitype sequences. *Erysiphe densissima* is reintroduced for a clade that corresponds to the old name '*E. extensa* var. *curta*'. Eight new species are described, including *Erysiphe carolinensis*, *E. gambelii*, *E. occidentalis*, *E. phellos*, *E. pseudoextensa*, *E. quercophila*, *E. quercus-laurifoliae* and *E. schweinitziana*. A new diagnostically and taxonomically relevant trait associated with the anamorphs of North American *Erysiphe* species on oaks has been assssed. This is a special conidiophore-like lateral outgrowth of the superficial hyphae, comparable to 'aerial hyphae,' which are also known for species of the powdery mildew genus *Cystotheca* which also infect *Quercus* species.

1 | Introduction

Quercus is a large, ecologically and taxonomically diverse genus in the family Fagaceae with ~470 currently recognised species (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:325819-2). These are deciduous and evergreen tree species distributed throughout the Northern Hemisphere with centers of diversity in southern North America and Eastern Asia (Nixon 2002, 2006; Hipp et al. 2020). The species of *Quercus* are split into two subgenera, *Quercus* and *Cerris*, and eight sections, including the monophyletic subgenus *Cerris* section. *Cyclobalanopsidis* (ring-cupped oaks), distributed in eastern and southeastern Asia, was previously recognised as a distinct genus or considered a subgenus of *Quercus* (Hipp et al. 2020; Yang et al. 2020). Manos and Hipp (2021) provided a comprehensive survey of North American oak species. Oaks

(*Quercus* species) are ecologically important components of forests in the whole northern hemisphere and many of them are economically important as a source of timber.

Quercus species are hosts to a wide range of powdery mildews within the genera *Cystotheca*, *Erysiphe* and *Parauncinula* throughout the world (Braun and Cook 2012). Interactions among oak trees and their powdery mildews are characterised by complex interactions between host defence mechanisms and pathogen effector systems, as well as long-term impacts on host growth (Desprez-Loustau et al. 2014; Bert et al. 2016; He et al. 2021; Li et al. 2020, 2022; Liang et al. 2018). *Cystotheca* is distributed in Eastern regions of Asia, ranging from Japan and China to India, and mainly southern parts of North America (Braun and Cook 2012). *Parauncinula* is a small East Asian genus that infects *Fagus* and *Quercus* species that is comprised of species formerly treated in *Uncinula*. *Parauncinula* species are phylogenetically positioned at the base of the Erysiphaceae, distant from the *Erysiphe* clade (Takamatsu, Braun, and Limkaisang 2005; Frantzeskakis et al. 2019). *Erysiphe* species are the most common and widespread causes of powdery mildew diseases and occur almost worldwide (Bhunjun et al. 2024). An estimated 23 *Erysiphe* species have been described on oak based on morphology and, in some cases through phylogenetic analyses (Takamatsu et al. 2007; Braun and Cook 2012; Siahaan et al. 2018). However, these phylogenetic revisions of *Erysiphe* species on oaks were mainly based on Asian and European specimens. The phylogenetic-taxonomic relationships of *Erysiphe* sect. *Microsphaera* on *Quercus* species in Asia and Europe are well-known (Takamatsu et al. 2007; Braun and Cook 2012), in contrast to North America where current data is lacking. Powdery mildews on oaks have attracted increased scientific attention in recent years due to their high infection rates and ecological impact (e.g., Desprez-Loustau et al. 2018; Gross et al. 2021; Faticov et al. 2022).

The knowledge of North American *Erysiphe* species is rudimentary with only a few recent studies. Braun et al. (2007) provided sequence data for a North American oak powdery mildew that was referred to as *E. abbreviata*. Bradshaw, Braun, and Pfister (2022) disentangled the intricate nomenclature and taxonomy of the *E. alphitoides*/*E. quercicola* complex, leading to a proposal to conserve *E. alphitoides* with a conserved type (Braun, Bradshaw, and Pfister 2022), and they confirmed the occurrence of the two species in North America by sequencing. These results confirmed the results of Gross et al. (2021) who examined the history of the introduction of *E. alphitoides*/*E. quercicola* in Europe, based on molecular examinations of herbarium samples.

Europe and Asia share a small number of powdery mildew species with North America but overall the two geographic areas are widely divergent. For example, Cho et al. (2018) recently demonstrated that Asian collections previously referred to as *Cystotheca lanestris* have to be assigned to a separate Asian species, for which they introduced the combination *C. kusanoi*, i.e., *C. lanestris* s. str. is now confined to North America. Eurasian and North American *Phyllactinia* species are also differentiated (Braun and Cook 2012). North America is rich in endemic *Erysiphe* species, which are not yet phylogenetically examined in detail. Thus, the aim of the present publication is to provide a comprehensive phylogenetic analysis of species of *Erysiphe* on oaks in North America, including genetic characterizations of all described species by means of ex-type sequences or, if not possible, epitypifications with ex-epitype reference sequences, and to detect cryptic speciation within this complex genus of powdery mildews.

2 | Materials and Methods

2.1 | Sample Collection and Morphological Examinations

Specimens were collected between 2018 and 2022 from throughout the United States. Newly collected specimens were deposited in the Farlow Herbarium (FH), Harvard University. Additional specimens were evaluated from the Farlow Herbarium and other American herbaria (Table 1).

Morphological examinations were accomplished following Bradshaw, Quijada et al. (2022). Morphological examinations of the asexual morph of recently collected samples were accomplished by placing clear adhesive tape on powdery mildew colonies and setting the tape onto a slide containing a drop of water, or by doing hand sections and mounting them onto a slide with potassium hydroxide (KOH), Melzer's reagent (MLZ), or Congo red. Examinations of the sexual morph were accomplished by using a clean needle to mount chasmothecia onto a microscope slide containing water, KOH, MLZ, or Congo red. Photographs were taken of the slides using a compound microscope with an Olympus SC50 camera (Tokyo, Japan) and a Zeiss AX10 microscope (Oberkochen, Germany) or an Olympus BX40 microscope (Tokyo, Japan).

2.2 | Sequencing

DNA extractions were done using the Chelex method (Hirata and Takamatsu 1996; Walsh, Metzger, and Higuchi 1991). Polymerase chain reaction (PCR) was carried out for the ITS and partial nuc 28S rDNA D1-D2 regions (28S) region using the primer pairs PM10/PM28R (Bradshaw and Tobin 2020). If PCR was unsuccessful, a nested approach was applied using the 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 *CAM*, *GAPDH*, *GS*, and *RPB2* region the primer pairs PMCAM1/PMCAM4R, PMGAPDH1/PMGAPDH3R, GSPM2/GSPM3R, and PMRpb2_4/PMRpb2_6R were used (Bradshaw, Guan et al. 2022). If these were unsuccessful for the *GS*, and *RPB2* regions, the following primers from Bradshaw, Braun, and Pfister (2023a) were used: EGS1 /EGS2R and ERPB2_3 / ERPB2_7R. If the GAPDH region was unsuccessful the following primers were used from Bradshaw et al. (2024): EGAPDH1 /EGAPDH2. For the *TUB* region the primers BTF5b/BTR7a (Ellingham et al. 2019) were used followed by ETUB2 and ETUB2R (Bradshaw, Braun, and Pfister 2023a).

TABLE 1 | Lists of taxa, hosts, vouchers, collection localities and GenBank accession numbers of the specimens examined in the current study.

Taxa	Host	Voucher[a]	Collection Locality	ITS (+LSU)	CAM	GAPDH	GS	RPB2	TUB	Notes
Erysiphe abbreviata	*Quercus muellenbergii*	FH01131009	USA: Massachusetts	OR424885	OR427399	OR427495	OR427583	OR427665	OR427763	
Erysiphe abbreviata	*Quercus prinoides*	FH01131008	USA: Massachusetts	OR424886	OR427400	OR427496	OR427584	OR427666	OR427762	Reference Sequence
Erysiphe calocladophora	*Quercus falcata*	NCSLG18175	USA: North Carolina	OR424900	OR427417	OR427511	OR427598	OR427678		
Erysiphe calocladophora	*Quercus falcata*	NCSLG19219	USA: North Carolina	OR424901	OR427418	OR427512				
Erysiphe calocladophora	*Quercus falcata*	NCSLG20924	USA: North Carolina	OR424902						
Erysiphe calocladophora	*Quercus marilandica*	BPI556429	USA: Texas	OR424903	OR427419	OR427513	OR427599		OR427739	
Erysiphe calocladophora	*Quercus nigra*	FH00965524	USA: South Carolina	OR424904	OR427416	OR427510			OR427746	Isotype
Erysiphe carolinensis	*Quercus laevis*	NCSLG17332	USA: North Carolina	OR424906	OR427421	OR427515	OR427600	OR427680		
Erysiphe carolinensis	*Quercus laevis*	NCSLG18203	USA: North Carolina	OR424907	OR427422	OR427516	OR427601	OR427681	OR427791	Holotype
Erysiphe carolinensis	*Quercus nigra*	NCSLG18174	USA: North Carolina	OR424908	OR427423	OR427517	OR427602	OR427682	OR427790	
Erysiphe densissima	*Quercus marilandica*	BPI556425	USA: Arkansas	OR424916	OR427429					Epitype
Erysiphe densissima	*Quercus marilandica*	BPI556426	USA: Texas	OR424917	OR427431	OR427521			OR427737	Isotype of *Erysiphe extensa* var. *curta*
Erysiphe densissima	*Quercus marilandica*	BPI556428	USA: Lousiana	OR424918	OR427430	OR427520			OR427738	
Erysiphe densissima	*Quercus marilandica*	FH01122192	USA: Texas	OR424915	OR427432	OR427522	OR427609		OR427760	
Erysiphe extensa	*Quercus nigra*	FH01122182	USA: Massachusetts	OR424925	OR427438	OR427528		OR427690	OR427752	

(Continues)

TABLE 1 | (Continued)

Taxa	Host	Voucher[a]	Collection Locality	ITS (+LSU)	CAM	GAPDH	GS	RPB2	TUB	Notes
Erysiphe extensa	*Quercus nigra*	FH01122186	USA: Virginia	OR424926	OR427439	OR427529	OR427615		OR427736	
Erysiphe extensa	*Quercus rubra*	FH01122181	USA: New Hampshire	OR424927	OR427441	OR427531	OR427617			
Erysiphe extensa	*Quercus rubra*	FH01122190_ Genotype 1	USA: Wisonsin	OR424928	OR427442	OR427532	OR427618		OR427731	
Erysiphe extensa	*Quercus rubra*	FH01131007	USA: Massachusetts	OR424929	OR427440	OR427530	OR427616	OR427691	OR427761	
Erysiphe extensa	*Quercus rubra*	FH01122190_ Genotype 2	USA: Wisonsin	OR424985	OR427492	OR427577	OR427661	OR427726	OR427758	
Erysiphe extensa	*Quercus rubra*	NYSf 1143.1	USA: New York	PQ105075						Holotype
Erysiphe extensa	*Quercus velutina*	FH01122156	USA: Tennessee	OR424930	OR427444	OR427534	OR427620	OR427693	OR427749	
Erysiphe extensa	*Quercus velutina*	FH01122184	USA: New York	OR424931	OR427443	OR427533	OR427619	OR427692	OR427754	
Erysiphe gambelii	*Quercus gambelii*	FH01122152	USA: Utah	OR424936						
Erysiphe gambelii	*Quercus gambelii*	FH01122153	USA: Utah	OR424937	OR427450	OR427538	OR427626	OR427699	OR427748	
Erysiphe gambelii	*Quercus gambelii*	FH01131034	USA: Colorado	OR424938	OR427449	OR427537	OR427625	OR427698	OR427769	Holotype
Erysiphe occidentalis	*Quercus garryana*	FH01131037	USA: Washington	OR424942	OR427454	OR427542	OR427630	OR427701	OR427771	
Erysiphe occidentalis	*Quercus garryana*	FH01131038	USA: Washington	OR424943	OR427455	OR427543	OR427632	OR427702	OR427772	Holotype
Erysiphe occidentalis	*Quercus kellogii*	FH01122188	USA: California	OR424944		OR427544	OR427631		OR427757	
Erysiphe occidentalis	*Quercus lobata*	FH01122146	USA: California	OR424945		OR427545				

(Continues)

TABLE 1 | (Continued)

Taxa	Host	Voucher[a]	Collection Locality	ITS (+LSU)	CAM	GAPDH	GS	RPB2	TUB	Notes
Erysiphe occidentalis	*Quercus* sp.	WSP62421	USA: Washington	OR424946	OR427456	OR427546	OR427633	OR427703	OR427732	
Erysiphe phellos	*Quercus phellos*	FH01122158	USA: North Carolina	OR424950	OR427460				OR427750	
Erysiphe phellos	*Quercus phellos*	FH01122159	USA: Virginia	OR424951	OR427461	OR427547	OR427635	OR427704	OR427751	Holotype
Erysiphe pseudoextensa	*Quercus alba*	FH01122183	USA: Massachusetts	OR424952	OR427462	OR427548			OR427753	
Erysiphe pseudoextensa	*Quercus alba*	FH01122185	USA: Virginia	OR424953	OR427463	OR427549			OR427755	Holotype
Erysiphe pseudoextensa	*Quercus alba*	FH01131010	USA: Massachusetts	OR424962	OR427472	OR427559	OR427642	OR427712	OR427764	
Erysiphe pseudoextensa	*Quercus robur*	FH01122187	USA: Maryland	OR424954	OR427464	OR427550			OR427756	
Erysiphe pseudoextensa	*Quercus robur*	PUL00016232	USA: Indiana	OR424965	OR427473	OR427560	OR427643	OR427713	OR427794	
Erysiphe pseudoextensa	*Quercus robur*	PUL00016233	USA: Indiana	OR424964	OR427474	OR427561	OR427644	OR427714	OR427795	
Erysiphe pseudoextensa	*Quercus robur*	PUL00016422	USA: Indiana	OR424963	OR427475	OR427562	OR427645	OR427715	OR427796	
Erysiphe quercicola	*Quercus agrifolia*	FH01131088	USA: Mexico	OR424960	OR427470	OR427556	OR427640	OR427709	OR427774	
Erysiphe quercicola	*Quercus robur*	FH00965519	France	OM436186	OR427471	OR427557	OR427641	OR427710	OR427745	
Erysiphe quercicola	*Quercus shumardii*	FLAS-F-56236	USA: Florida	OR424961		OR427558		OR427711		
Erysiphe quercophila	*Quercus nigra*	FH00941969	USA: Florida	OR424969	OR427476	OR427563	OR427646	OR427716	OR427730	Holotype
Erysiphe quercophila	*Quercus nigra*	FH01131026	USA: Florida	OR424968	OR427477		OR427647		OR427735	

(Continues)

TABLE 1 | (Continued)

Taxa	Host	Voucher[a]	Collection Locality	ITS (+LSU)	CAM	GAPDH	GS	RPB2	TUB	Notes
Erysiphe quercophila	*Quercus nigra*	FH01131027	USA: Florida	OR424966	OR427478	OR427564	OR427648	OR427717	OR427734	
Erysiphe quercophila	*Quercus nigra*	FH01131029	USA: Florida	OR424967	OR427479	OR427565	OR427649	OR427718	OR427765	
Erysiphe quercus-laurifoliae	*Quercus laurifolia*	FH00941968	USA: Florida	OR424935	OR427445	OR427535	OR427621	OR427694	OR427741	
Erysiphe quercus-laurifoliae	*Quercus laurifolia*	FH01131028	USA: Florida	OR424932	OR427446		OR427622	OR427695	OR427766	
Erysiphe quercus-laurifoliae	*Quercus laurifolia*	FH01131030	USA: Florida	OR424933	OR427447		OR427623	OR427696	OR427767	
Erysiphe quercus-laurifoliae	*Quercus laurifolia*	FH01131031	USA: Florida	OR424934	OR427448	OR427536	OR427624	OR427697	OR427768	Holotype
Erysiphe schweinitziana	*Quercus marilandica*	FH01122191	USA: Kansas	OR424977	OR427485	OR427571	OR427655		OR427759	
Erysiphe schweinitziana	*Quercus nigra*	NCSLG17109	USA: North Carolina	OR424978	OR427486	OR427572	OR427656			
Erysiphe schweinitziana	*Quercus velutina*	FH01122145	USA: Wisonsin	OR424979	OR427487	OR427573	OR427657		OR427747	Holotype
Erysiphe sp.	*Quercus stellata*	NCSLG18469	USA: North Carolina	OR424986		OR427578	OR427662		OR427792	
Erysiphe sp.	*Quercus virginiana*	NCSLG18481	USA: North Carolina	OR424987	OR427493	OR427579	OR427663	OR427727	OR427793	

[a] BPI = U.S. National Fungus Collections; FH = Farlow Herbarium; Harvard University; FLAS = University of Florida Herbarium, Florida Museum of Natural History; HAL = Martin-Luther-Universität Herbarium; NYCSLG = Larry F. Grand Mycological Herbarium; NYS = New York State Museum; WSP = Washington State University Plant Pathology Herbarium.

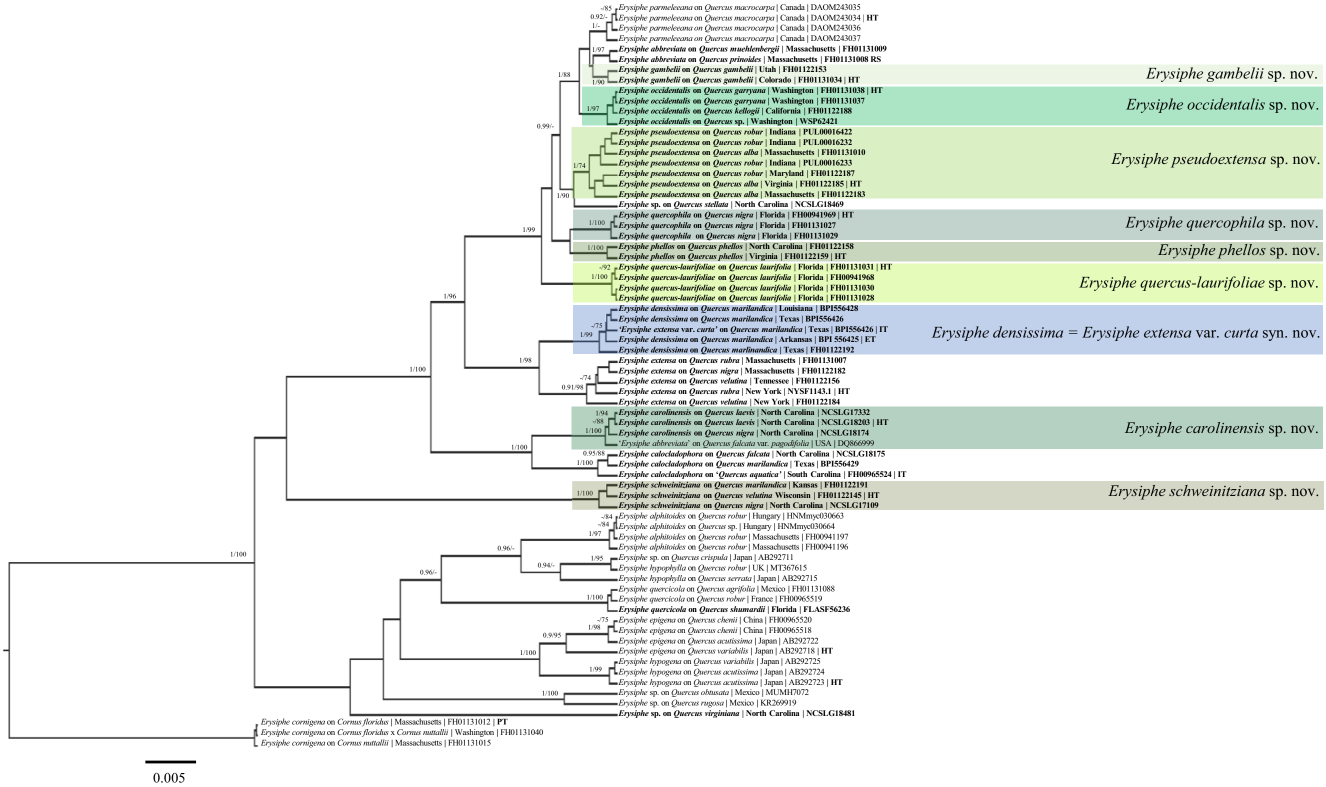

FIGURE 1 | Bayesian maximum clade credibility tree of the concatenated ITS+28S + *CAM* + *GAPDH* + *GS* + *RPB2* + *TUB* regions of *Erysiphe* taxa infecting *Quercus* species predominately from North America. Posterior probabilities ≥ 90 are displayed followed by bootstrap values greater than 70% for the maximum likelihood (ML) analyses conducted. ET = ex-epitype, HT = ex-holotype, IT = ex-isotype, RS = reference sequence. Quotations around taxa signify that the name is no longer current. Taxa in bold were sequenced for the current study.

2.3 | Molecular Phylogeny

A phylogenetic tree was constructed from the concatenated ITS+28S + *CAM* + *GAPDH* + *GS* + *RPB2* + *TUB* sequences (Figure 1). In addition, single loci trees were constructed from all the newly generated sequences (Figures S1–S6). Sequences were aligned and edited using MUSCLE in MEGA11: Molecular Evolutionary Genetics Analysis Version 11 (Tamura, Stecher, and Kumar 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 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 10%. 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 visualised 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).

3 | Results

3.1 | Molecular Phylogeny

Sequences obtained from the specimens were deposited in GenBank (Table 1). The phylogenetic analyses evaluated a total of 90 powdery mildew specimens collected on *Quercus* spp. Of these 90 specimens, 57 were sequenced for the current study. *Erysiphe cornigena* was selected as an outgroup taxon based on preliminary analysis. A maximum clade credibility tree was constructed using Bayesian analyses from the combined ITS+28S + *CAM* + *GAPDH* + *GS* + *RPB2* + *TUB* (Figure 1) sequences. Posterior probabilities ≥ 90 are displayed followed by bootstrap values > 70% for the maximum likelihood (ML) analyses conducted. The representative maximum clade credibility tree is illustrated in Figure 1.

High support is exhibited throughout the tree in both posterior and likelihood values for all of the *Erysiphe* on *Quercus* taxa from North America. A specimen on *Q. stellata* (NCSLG18469) and on *Q. virginiana* (NCSLG18481) likely represent two additional undescribed species. Only one specimen is currently available and as such we preliminarily label them as '*Erysiphe* sp.'

3.2 | Taxonomy

Taxonomic History of North America Oak Powdery Mildews

In the 19th Century, several *Erysiphe* and *Microsphaera* species had been described from oaks in North America, including *Erysiphe quercina*, *E. densissima*, *Microsphaera abbreviata*, *M. calocladophora*, and *M. extensa*. The history of the North American oak powdery mildews was controversial and confusing. von Schweinitz (1834) described *Erysiphe quercina* and *E. densissima* on North American oaks (host identities not specified) with brief, non-informative descriptions. Peck (1874) reassigned *E. densissima* to *Microsphaera* and regarded this species to be distinctive by forming characteristic white, dense, orbicular mycelial patches on host leaves, but he also failed to specify the identity of the host of the type. Burrill (in Burrill and Earle 1887) introduced the combination *Microsphaera quercina* and used this name in a very broad sense, i.e., for all North America oak powdery mildews, including *M. abbreviata* and *M. extensa*. Later, Atkinson (1891) added *M. calocladophora*, mainly based on trichotomously branched apices of the chasmothecial appendages. He cited *M. densissima* in the sense of certain North American authors as a synonym or as a synonym “pro parte.” In the first powdery mildew monograph, Salmon (1900) generally used extremely wide species concepts, including *M. alni* which he emended to include most species described at that time that are currently placed in *Erysiphe* sect. *Microsphaera*. This included all described North American oak powdery mildews. *Microsphaera calocladophora* and *M. extensa* were treated as varieties of *M. alni*. Griffon and Maublanc (1912a), the authors of *M. alphitoides*, discussed the North American oak powdery mildews and recognised *M. abbreviata* and *M. extensa*. Later, they introduced the combination *M. abbreviata* var. *calocladophora* (repeated in Griffon and Maublanc 1912b), reducing Atkinson's species to varietal status. Blumer (1933) discussed the North America oak powdery mildews in detail. Based on the examination of more than 100 samples, he recognised *M. abbreviata*, *M. densissima*, and *M. extensa*. *Microsphaera calocladophora* was a doubtful species to him. Furthermore, Blumer (l.c.) recommended the exclusion of *M. quercina* as a doubtful species name. Braun (1982, 1984, 1987) examined numerous collections of North American oak powdery mildews, including type specimens, and largely followed Blumer's (l.c.) taxonomic concept, except for recognition of *M. densissima*. Furthermore, he (Braun 1982) recognised *M. extensa* var. *curta*. Later, Braun and Takamatsu (2000) transferred all taxa, originally assigned to *Microsphaera*, to *Erysiphe*.

In the early 20th Century, a new oak powdery mildew emerged in Europe, which was later described as *Microsphaera alphitoides* (Griffon and Maublanc 1912a). Recently, this powdery mildew outbreak in Europe was determined to represent two allied species, viz., *E. alphitoides* and *E. quercicola* (detailed discussion, see Bradshaw, Braun, and Pfister 2022). However, in the early 20th Century, the European oak powdery mildews were confused by some authors with North American species. At the time, the origin of this powdery mildew outbreak in Europe was still not clear. Arnaud and Foex (1912) recognised a single North American oak powdery mildew species under the name *M. quercina* to which they also assigned the European oak powdery mildew. Săvulescu and Sandu-Ville (1929) accepted a single species, viz., *M. abbreviata*, including the European oak powdery mildew, *M. extensa*, and *M. quercina*.

These different species concepts and circumscriptions have their origin in a species concept based solely on morphology. However, the intricate taxonomy of the North American oak powdery mildews can only be reliably clarified by using phylogenetic methods. Therefore, the present work focussed on phylogenetic analyses of North American oak powdery mildews. The results of the present phylogenetic analyses of North America *Erysiphe* species on *Quercus* species were compared with the traditional morphology-based taxonomy of the species concerned, as outlined in Braun and Cook (2012). Our new phylogenetic evaluations yielded the following new taxonomic concepts, including the description of a several new species.

Identity and Application of *Erysiphe densissima*, *E. quercina* and *Microsphaera abbreviata*

Type material of *E. densissima* is preserved, but the identity of the type host was not specified in the original publication, and remains unclear. Blumer (1933) accepted the name *Microsphaera densissima* and gave a morphological description and included two host species. On the other hand, Blumer (l.c.) recommended the exclusion of *E. quercina* (type material is apparantly not preserved), which had been variously used, including in a very wide sense, covering all North American oak powdery mildews (Burrill and Earle 1887) and even including the European powdery mildews (Arnaud and Foex 1912). *Microsphaera abbreviata* is a similarly unclear name. The type is preserved and the morphology is rather characteristic (Braun 1987; Braun and Cook 2012), but the identity of the type host is unclear and results of sequence analyses have shown that sequences obtained from collections referred to *M. abbreviata* cluster in different clades.

Previous practices to exclude species by classifying them as “dubious names” (nom. dub.) or “ambiguous names” (nom. ambig.), a practice sanctioned by previous Codes, are no longer allowed. Names have to be clarified by typifications, including neotypes, when necessary, or they have to be excluded by proposals to reject the names concerned. In our work, we clarify the applications of these unclear names by neo- or epitypifications to present unambiguous species circumscriptions.

The Accepted *Erysiphe* Species on North American Oaks

Erysiphe abbreviata (Peck) U. Braun & S. Takam., Schlechtendalia **4**: 4, 2000, emend. Figure 2.

≡ *Microsphaera abbreviata* Peck, Rep. (Ann.) New York State Mus. Nat. Hist. **28**, 64, 1876.

Holotype. USA, New York, Buffalo, on *Quercus bicolor* [in the original publication as *Quercus* sp.], Oct.–Nov., G.W. Clinton (NYS). Reference sequence: OR424886 (ITS+28S); OR427400 (*CAM*); PP720294 (*GAPDH*); OR427584 (*GS*); OR427666

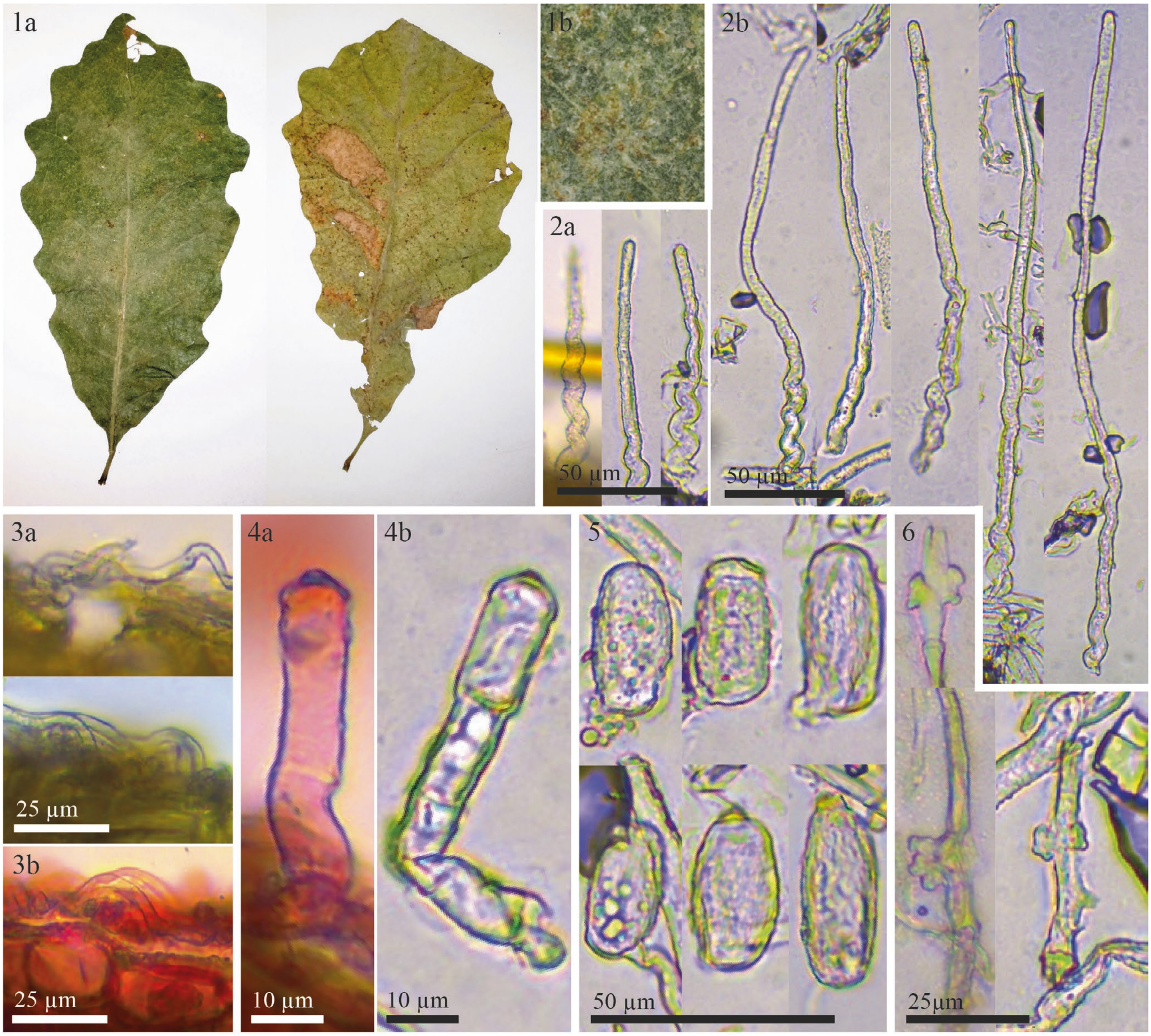

FIGURE 2 | Morphological details of the anamorph of *Erysiphe abbreviata*: 1a-b. Infected leaves and close-up of mycelia with the conidiophores; 2a-b. Immature and mature conidiophore-like hyphal outgrowths, 3a-b. Superficial hyphae over the leaf surface; 4a-b. Development of the conidiophores, 4a. Immature conidiophore, 4b. Mature conidiophore; 5. Different stages of development of the conidia, note the lipidic guttules inside the conidia, the ridged ornamentation of the walls, and the germination pattern; 6. Lobed appressoria on hyphae. All photos from H5. Reagents: KOH = 2a-b, 3a, 4b, 5, 6; KOH + CR = 3b, 4a.

(*RPB2*); OR427762 (*TUB*). [USA. MASSACHUSETTS: Suffolk County, Boston, Arnold Arboretum, on *Quercus prinoides*, Host Accession: 16865-MASS. 26 August 2021, *M. Bradshaw* (FH01131008).]

Descriptions and illustrations of the teleomorph based on type material: Braun (1987, 426, plate 191), Braun and Cook (2012, 420–430, figure 497).

Description. Mycelium epiphyllous, whitish, growing in dense patches on the adaxial leaf surface close to the leaf veins; hyphae sinuous, sometimes slightly helicoid, hyaline, cells 29–63 × 3–5 µm, irregularly branched, cell walls slightly ornamented with tiny yellowish warts, cells without content; hyphal appressoria nipple-shape to lobate (2–3 lobes), single or in opposite pairs, up to 10.8 µm wide; superficial hyphae forming "special aerial hyphae," i.e., conidiophore-like hyphal outgrowths, (92–)155–209(–271) × (4–)6.5–9(–10) µm, cylindrical and progressively tapering toward the apex, multiseptate, arising from closely septate and curved cells that form a ring-like structure, basal cell helicoid, (22–)34.5–38.5(–74.5) × (4–)7–8(–10) µm, following cells (36–)50–69.5(–102) × (4–)5.5–6.5(–7) µm, apex rounded or slightly clavate, walls slightly thickened and ornamented with warts, sometimes with sparse yellowish grains, ornamentation more prominent toward the base. Conidiophores insufficiently known (only observed detached and without foot-cells, few conidiophores with two following cells observed, 13–15 × 7–8.5 µm), forming conidia singly; conidia cylindrical to doliiform, (19–)28.5–33.5(–36.5) × (9–)14–17.5(–18) µm, conidial wall of dried conidia ornamented with yellowish warts or ridges connected like a reticulum, ornamentation lost in Melzer's reagent and wall became amyloid, scattered lipidic guttules present; germ tubes not observed. Chasmothecia usually hypophyllous and scattered, small, about 70–110 µm diam., rarely larger; peridium cells irregularly polygonal, 8–25 µm diam.; appendages 3–15, rarely more, equatorial, stiff and stout, 0.5–1(–1.25) times as long as the chasmothecial diam., mostly shorter than the diam., 7–10 µm wide at the base, 0–1-septate, hyaline or pigmented at the base, walls smooth and thin above to rough and thick toward the base, or moderately thick throughout, apices 4–6 times densely and regularly dichotomously branched, primary branches occasionally somewhat elongated, tips of the ultimate branchlets recurved; asci 3–6, broad ellipsoid-obovoid, subglobose, 50–65 × 35–55 µm, sessile or short-stalked, 3–6-spored; ascospores ellipsoid-ovoid (–subglobose), large, 20–32 × 13–21 µm, colourless, hyaline with sparse yellowish grey lipidic guttules.

Host range and distribution (see detailed discussion below under notes) on *Quercus* [sect. *Quercus* subsect. *Prinoideae*] (*bicolor*, *bicolor* × *michauxii*, *macrocarpa*, *macrocarpa* × *bicolor* [=×*schuettei*], *muehlenbergii* [= *acuminata*], *prinoides*). *Fagaceae*; North America (USA, central states, from Colorado and Kansas to Wisconsin, eastward and southeastward to New York, Tennessee and North Carolina).

Notes. Type material of *Microsphaera abbreviata* is preserved at NYS. The identity of the type host was not specified in the original publication. Braun (1987) examined type material and identified the host as *Quercus bicolor*. The identity of the host leaves has recently been confirmed by a botanist who is an expert in oak identification (personal communication). There are a few samples deposited at BPI (e.g., 558605, 558609, 558721) under the name *M. quercina*, which were collected at Buffalo, New York by G.W. Clinton, on *Quercus* sp. Given these were collected by the collector of the holotype it may be that one of these specimens could be isotype material of *M. abbreviata* but direct evidence is lacking.

Sequences retrieved from oak powdery mildews that morphologically agree with *Erysiphe abbreviata* as circumscribed and described by Braun (1987) and Braun and Cook (2012) are found in the phylogenetic trees in different clades, suggesting that *E. abbreviata* in the previous morphological sense has to be considered phylogenetically and taxonomically heterogenous. For instance, a North American specimen on *Quercus falcata*, agreeing well morphologically with the previous concept of *E. abbreviata*, has been sequenced (ITS+28S; Braun et al. 2007; Takamatsu et al. 2007). These sequences group in a clade together with an ex-type sequence retrieved from *E. calocladophora*. Hence, the application of the name *E. abbreviata* has to be determined by means of epitypification, including ex-epitype sequences. In the present case of North American *Erysiphe* species on oaks, a phylogenetic multilocus approach was necessary. Unfortunately, suitable collections of *E. abbreviata* on *Q. bicolor* are not available. Therefore, for the interim, we assign this name on the basis of morphology and host range, particularly noting the host specificity of North America powdery mildew species on oaks. *Quercus bicolor* and *Q. prinoides* are closely allied in *Quercus* subsect. *Prinoideae*. Both of these oak species are found in the eastern part of North America with overlapping distributions, and both occur in the New York region, where *E. abbreviata* was described. Therefore, we apply *E. abbreviata* to the clade composed of sequences obtained from *Q. muehlenbergii* and *Q. prinoides* and confine its host range to species from *Quercus* subsect. *Prinoideae*.

Braun and Cook (2012) listed hosts species of *E. abbreviata* as *Quercus bicolor*, *Q. bicolor* × *michauxii*, *Q. imbricata* [erroneously for *Q. imbricaria*], *Q. macrocarpa*, *Q. macrocarpa* × *bicolor* [=×*schuettei*], *Q. muehlenbergii* [= *acuminata*], *Q. prinoides*, *Q. prinus* [= *michauxii*], *Q. rubra*, and *Q. velutina*. However, *Q. imbricaria* [subsect. *Phellos*], *Q. michauxii* (= *prinus*) [subsect. *Albae*], *Q. rubra* [subsect. *Coccineae*], and *Q. velutina* [subsect. *Coccineae*] are doubtful records and seem to belong to other *Quercus* species. This is also the case of the powdery mildew *E. calocladophora* infecting *Q. falcata* [subsect. *Phellos*] (see above).

The *E. abbreviata* clade, as circumscribed in the present work, is highly supported in the concatenated tree, but also in the *RPB2* and *TUB* analyses. In the ITS tree, the reference sequence retrieved from *Q. prinoides* forms a single well supported clade together with sequences of *E. gambelii*.

Erysiphe alphitoides (Griff. & Maubl.) U. Braun & S. Takam., Schlechtendalia **4**: 5, 2000.

≡ *Microsphaera alphitoides* Griff. & Maubl., Bull. Soc. Mycol. France **28**: 103, 1912.

[Holotype: France, Gard, on *Quercus petraea* (= *Q. sessiliflora*, *Q. robur* p.p.), Dec. 1911, G. Arnaud (FH); ex-holotype sequence: OM436186.] Proposed conserved type (Braun, Bradshaw, and Pfister 2022): Switzerland, Neuchâtel, on *Quercus robur*, 4 Apr. 1999, S. Takamatsu (TNS-F87437 [previously MUMH 631]). Duplicate: HAL 1946 F. Ex-type sequence: AB292708.

= *Oidium alphitoides* Griff. & Maubl., Bull. Soc. Mycol. France **26**: 132, 1910.

= *M. dentatae* Liou, Contr. Lab. Bot. Natl. Acad. Peiping **1**: 19, 1931.

≡ *M. alni* var. *dentatae* (Liou) F.L. Tai, Bull. Chin. Bot. Soc. **1**: 22, 1935.

= *M. querci* Sawada, Bull. Gov. Forest Exp. Sta. Meguro **50**: 122, 1951.

Host range and distribution in North America: So far, there are only two phylogenetically confirmed collections on the introduced *Quercus robur*, *Fagaceae*, from Massachusetts (Bradshaw, Braun, and Pfister 2022). However, based on morphologically examined North American collections, Braun (1984) reported *E. alphitoides* on ornamental *Quercus robur* from the USA. He also cited an examined holomorphic specimen of *E. alphitoides* on *Quercus arizonica* from Arizona.

Erysiphe calocladophora (G.F. Atk.) U. Braun & S. Takam., Schlechtendalia **4**: 6, 2000.

≡ *Microsphaera calocladophora* G.F. Atk., J. Elisha Mitchell Sci. Soc. **7**: 73, 1891.

≡ *M. alni* var. *calocladophora* (G.F. Atk.) E.S. Salmon, Mem. Torrey Bot. Club **9**: 153, 1900.

≡ *M. abbreviata* var. *calocladophora* (G.F. Atk.) Griff. & Maubl., Bull. Soc. Mycol. France **28**: 97, 1912.

≡ *M. penicillata* var. *calocladophora* (G.F. Atk.) W.B. Cooke, Mycologia **44**: 572, 1952.

Lectotype (designated here, MycoBank, MBT10022127): USA, South Carolina, Richland County, Columbia, on *Quercus nigra* (= *Q. aquatica*), Oct. 1888, G.F. Atkinson 618 (CUP-A-000618(CS)). Isolectotype: FH 00965524. Ex-isolectotype sequence: OR424904 (ITS+28S); OR427416 (*CAM*); OR427510 (*GAPDH*); OR427746 (*TUB*).

Descriptions and Illustrations. Braun (1987, 377–378, plate 147), Braun and Cook (2012, 442–443, figure 517).

Host range and distribution (according to Braun and Cook 2012, based on morphology): on *Quercus* (*alba*, *gambelii*, *laurifolia*, *lyrata*, *marilandica*, *minor*, *nigra* [= *aquatica*], *phellos*, *rubra*, *stellata* [= *obtusiloba*], *velutina*), *Fagaceae*; North America (USA, Alabama, Arizona, Arkansas, Florida, Indiana, South Carolina).

Phylogenetically documented hosts: *Quercus* [sect. *Lobatae* subsect. *Phellos*] (*Q. falcata*, *marilandica*, *nigra*).

Notes. Braun (1987) and Braun and Cook (2012) cited a collection deposited at CUP as "holotype", but this is not correct. Atkinson (1891) neither designated a holotype nor listed a single collection. In addition to the sample from Columbia, South Carolina (no. 618), he cited "North Amer. Fungi 1538" and a collection from Alabama (Auburn, Dec. 1890). Therefore, it is necessary to designate a lectotype. A duplicate of the lectotype at CUP is deposited at FH (= isolectotype, no. 618 is cited, but the cited year, "1898," is incorrect and must be corrected to 1888). Asian records of *E. calocladophora* (e.g., Japan, on *Q. alba*; Amano 1986; Braun and Cook 2012) are doubtful. A record on *Quercus garryana* from Washington is also doubtful (Anonymous 1960).

The morphology of the anamorph of *E. calocladophora* is currently unknown. The *E. calocladophora* clade is strongly supported in the concatenated tree, but also in *GAPDH*, ITS, and *TUB* analyses. *E. calocladophora* is sister to *E. carolinensis* in the phylogenetic analyses. The morphology of the chasmothecia of *E. calocladophora* and *E. carolinensis* is very similar, except for shorter chasmothecial appendages [0.5–1(–1.25) times as long as the chasmothecial diam] in *E. carolinensis*, vs. (1–)1–1.5(–2) times as long as the chasmothecial diam in *E. calocladophora*, and 4–8-spored asci (vs. 3–6-spored in *E. calocladophora*).

Erysiphe carolinensis M. Bradshaw, U. Braun, & Quijada **sp. nov**. Figure 3.

MycoBank, MB855711.

Etymology. The epithet refers to North Carolina, the origin of the type material.

Holotype. USA, North Carolina, Carolina Beach State Park, *Quercus laevis* (*Quercus* sect. *Lobatae* subsect. *Phellos*), 28 November 2008, *L.F. Grand* and *C. Vernia* (NCSLG18203). Ex-holotype sequences: OR424907 (ITS+28S); OR427422 (*CAM*); OR427516 (*GAPDH*); OR427601 (*GS*); OR427681 (*RPB2*); OR427791 (*TUB*).

Additional collections examined: See Table 1.

Description and Illustration. Braun et al. (Braun et al. 2007, 658, 660; 660, Figure 3, anamorph; 661, Figure 4, teleomorph), anamorph as '*Erysiphe abbreviata*' on *Quercus falcata*.

Description. Mycelium epiphyllous or amphigenous, white, growing in dense patches on the adaxial leaf surface, hypophyllously thin and less conspicuous; hyphae straight, sinuous to sinuous-helicoid, septate, hyaline, thin-walled, cells (6–)21–40(–46) × (2.5–)4–5(–5.5) μm, irregularly branched, cell walls slightly ornamented with tiny yellowish warts; with conidiophore-like outgrowths (special aerial hyphae), (108–)220–356(–390) × 5–10 μm, cylindrical and progressively tapering toward the apex, multiseptate, arising from closely septate and curved hyphal cells that form a ring-like structure, basal cell helicoid (31.5–)34.5–38.5(–40.5) × (6.5–)7–8(–9) μm, following cells (44.5–)50–69.5(–111) × (4.5–)5.5–6.5 μm, apex rounded or slightly clavate, walls slightly thickened and ornamented with warts, ornamentation more prominent toward the base; hyphal appressoria nipple-shaped to moderately lobate, 3–8 μm diam, solitary; conidiophores (based on Braun et al. 2007) arising from the upper surface of mother cells, position between two septa more or less central, erect, straight, usually 60–120 μm long, occasionally somewhat longer, foot-cells subcylindrical, straight, somewhat curved to frequently sinuous-helicoid at the base, 40–70 × 3 5–10 μm, followed by 1–3 mostly shorter cells, occasionally following cells about as long as the foot cells, forming conidia singly, occasionally 2–3 conidia adhering in false chains; fresh conidia ellipsoid-ovoid, doliiform to cylindrical, 25–45 × 10–20 μm, length/width ratio 2.2–2.9, apex rounded to subtruncate, base subtruncate, germ tubes terminal or subterminal, short, straight to sinuous, terminating in a somewhat lobed appressorium or without any appressorium (old mature detached conidia observed in herbarium samples cylindrical to doliiform, (23–)28.5–33(–38) × (10.5–)12–15(–15.5) μm, conidial wall ornamented, less thickened in one of the poles, walls with yellowish warts and transverse/longitudinal ridges; germ tubes subterminal, up to 28 μm long, showing a *Pseudoidium* type morphology). Chasmothecia amphigenous, epiphyllous chasmothecia subgregrarious, globose, 129–157 μm diam, hypophyllous chasmothecia 70–130 μm diam; peridium made of textura angularis-prismatica, peridium cells 8–30 μm diam, thick-walled, shape irregularly rectangular-polygonal to sinous in outline, strong yellow-brown to deep brown, cell walls darker, 2–4.5 μm thick, with connections among cells where the wall becames thinner; appendages around the equatorial zone, number variable, 3–21, slightly to medium curved, appendages 50–160(–190) μm long and 7–10(–11) μm

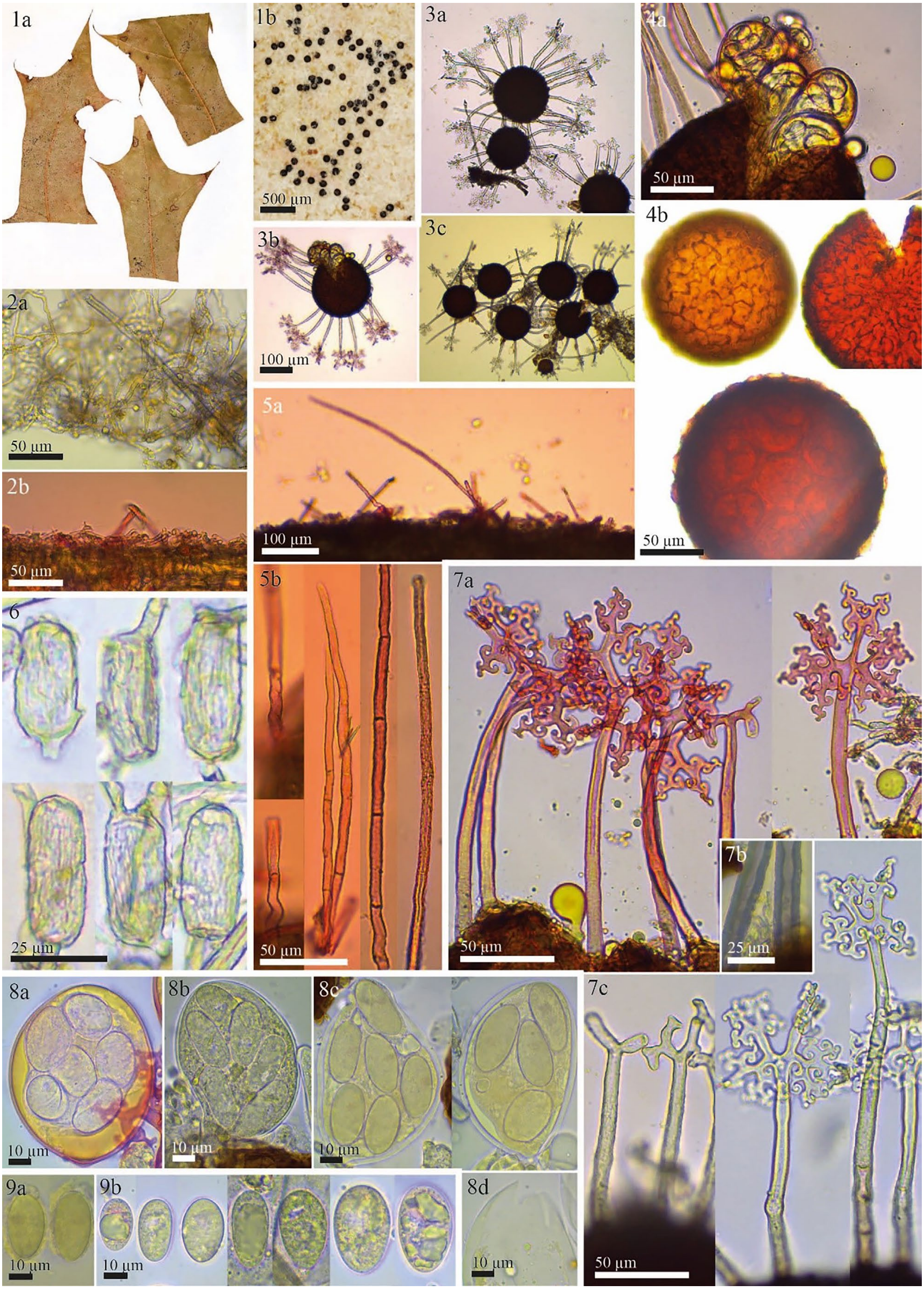

FIGURE 3 | Legend on next page.

FIGURE 3 | Morphological details of *Erysiphe carolinensis*: 1a-b. Infected leaves and close-up of mycelia with the chasmothecia; 2a-b. Free and attached hyphae over the leaves; 3a-c. Free immature and mature chasmothecia; 4. Open chasmothecia releasing the asci; peridium in immature and mature fruitbody, note the asci inside the chasmothecia in 4b; 5a-b. Immature and mature conidiophore-like hyphal outgrowths (special aerial hyphae); 6. Mature conidia, note the ridged ornamentation of the walls, and the germination pattern; 7a-c. Morphological variability of appendages, note the ornamented amyloid thick wall in 7b; 8a-b. Mature asci with 4–6 ascospores, note the ascus opening in 8d; 9a-b. Different stages of development of ascospores. Reagents: KOH = 3a, 4b, 6, 7c, 8b, 8d, 9b; KOH + CR = 3b, 4a, 5a-b, 7a, 8a; KOH + MLZ = 2a, 3c, 7b, 8c, 9a.

wide at the base, 0.5–1.25 times as long as the chasmothecial diam., hyaline, only light brownish close to the base, usually aseptate, rarely 1(–2)-septate close to the base, walls 1.5–3 µm wide, irregularly warted, amyloid in MLZ after KOH-pretreatment, apices regularly 3–6 times dichotomously branched, compact, primary branchlets occasionally slightly elongated, tips of the ultimate branchlets recurved; with 3–7 asci per chasmothecium, broad ellipsoid-ovoid to subglobose, 50–91.5(–104) × 35–66.5 µm, 3–6-spored, wall thickened, 1.5–3.5 µm throughout, except for the apical oculus which is about 20 to 25 µm wide, base with a short stalk; ascospores ellipsoid-obovoid, subglobose, 20–32 × 12–21 µm, hyaline, thin-walled, smooth, 75%–90% filled with yellowish grey lipidic guttules.

Host range and distribution on *Quercus* [*Quercus* sect. *Lobatae* subsect. *Phellos*] (*falcata*, *laevis*, *nigra*), *Quercus* subsect. *Phellos*, *Fagaceae*; North America (USA, North Carolina, Tennessee).

Notes. *Erysiphe carolinensis* is only known from North Carolina on *Quercus laevis* and *Q. nigra*, two oaks of *Quercus* subsect. *Phellos*. The sequences retrieved from these collections form a sister clade to the *E. calocladophora* clade, a species that also occurs on oaks of subsect. *Phellos*. The *E. carolinensis* clade is highly supported in all analyses (*CAM*, Concatenated, *GADPH*, ITS, *RPB2*, *TUB*), suggesting it is a separate species.

A North American specimen on *Quercus falcata*, morphologically identified as *Erysiphe abbreviata*, has been sequenced (ITS+28S; Braun et al. 2007; Takamatsu et al. 2007). These sequences group together in a clade with *E. carolinensis*, suggesting that this specimen is the latter species.

Erysiphe densissima Schwein., Trans. Amer. Philos. Soc., N. S., **4**: 269, 1834 Figure 4.

≡ *Microsphaera densissima* (Schwein.) Peck, Rep. (Ann.) New York State Mus. Nat. Hist. **26**: 80, 1874.

Holotype. USA, Pennsylvania, [Bethleham], on *Quercus* sp., undated, von Schweinitz (PH 01103545). Isotype: BPI 1052304. Epitype (designated here, MycoBank, MBT10022128): USA, Arkansas, Batesville, on *Quercus marilandica*, Arkansas, 5 October 1905, *E. bartholomew*, BPI556425. Ex-epitype sequences: OR424916 (ITS+28S); OR427429 (*CAM*).

= *Microsphaera extensa* var. *curta* U. Braun, Mycotaxon **15**: 130, 1982.

≡ *Erysiphe extensa* var. *curta* (U. Braun) U. Braun & S. Takam., Schlechtendalia **4**: 8, 2000.

Holotype. USA, Texas, Joaquin, on *Quercus marilandica*, 15 Oct. 1913, Barthol., Fungi Columb. 4238 (K(M) 169066). Isotypes: Barthol., Fungi Columb. 4238 (e.g., BPI 556426, FH, NY 2940490-2940492, WIS-F-24135, WSP3946). Ex-isotype sequences: OR424917 (ITS); OR427431 (*CAM*); OR427521 (*GAPDH*); OR427737 (*TUB*).

Description. Mycelium epiphyllous, white, growing scattered on the adaxial leaf surface; hyphae slightly to strongly sinuous, hyaline, cells (13.5–)18–32.5(–39) × 3.5–5.5 µm, irregularly branched, cell walls slightly ornamented with tiny yellowish warts, cells without content; hyphal appressoria lobed, in opposite pairs, (6–)7–9(–11) µm diam.; conidiophore-like hyphae outgrowths (special aerial hyphae) up to 222 µm long, cylindrical and progressively tapering toward a blunt apex, multiseptated, arising from helicoid cells, (32–)41–59.5(–65) × 8.5–10.5(–12.5) µm, following cells (33.5–)41–57(–60.5) × (4.5)5–7(–8) µm, walls slightly thickened and ornamented with warts, ornamentation more prominent toward the base. Single detached conidiophores observed, cell walls slightly thickened and ornamented with yellowish irregular warts, foot-cells cylindrical, straight to usually curved-helicoid, 36.5–46 × 10–13.5 µm, two following cells, shorter than foot-cells, 14.5–36 × 7.5–9 µm; forming conidia singly; conidia ellipsoid-doliiform, (19.5–)20–33 × (10–)14.5–22(–19.5) µm, conidial wall ornamented, walls with yellowish warts and transverse/longitudinal ridges in dried conidia; germ tubes subterminal, up to 22 µm long, showing a *Pseudoidium* type morphology. Chasmothecia subgregrarious, globose, (100–)145(–153) µm diam; peridium made of textura angularis-prismatica, cells (11.5–)15–19(–21) × (10–)10.5–14(–16) µm, thick-walled, irregularly rectangular-polygonal to sinous-shaped (interlocking-shape), strong yellow-brown to deep brown, cell walls with connections among cells where the wall became thinner; *appendages* above and below the equatorial zone, number variable, 7–13, straight to slightly curved, appendages (94.5–)110–126(–155) µm long and 6.5–8 µm wide at the base, about as long as the chasmothecial diam, hyaline or brownish close to the base, usually aseptate, rarely 1-septate close to the base, walls up to 2 µm width, irregularly warted, amyloid in MLZ after KOH-pretreatment, apices regularly 4–6 times dichotomously branched, tips of the ultimate branchlets recurved; asci broad ellipsoid-ovoid to subglobose, (45.–)52.5–61(–67) × (32.5–)40.5–46(–48.5) µm, 4–8 asci per chasmothecium, 2–4 (–6)-spored, wall thickened, 0.5–1.5 µm throughout, except for the apical oculus, base with a short stalk; ascospores ellipsoid-obovoid, (20.5–)22–24.5(–27.5) × (11.5–)12–13.5(–15.5) µm, hyaline, thin-walled, smooth, filled with yellowish grey lipidic guttules.

Host range and distribution: on *Quercus marilandica* [*Quercus* sect. *Lobatae* subsect. *Phellos*], *Fagaceae*; North America (central

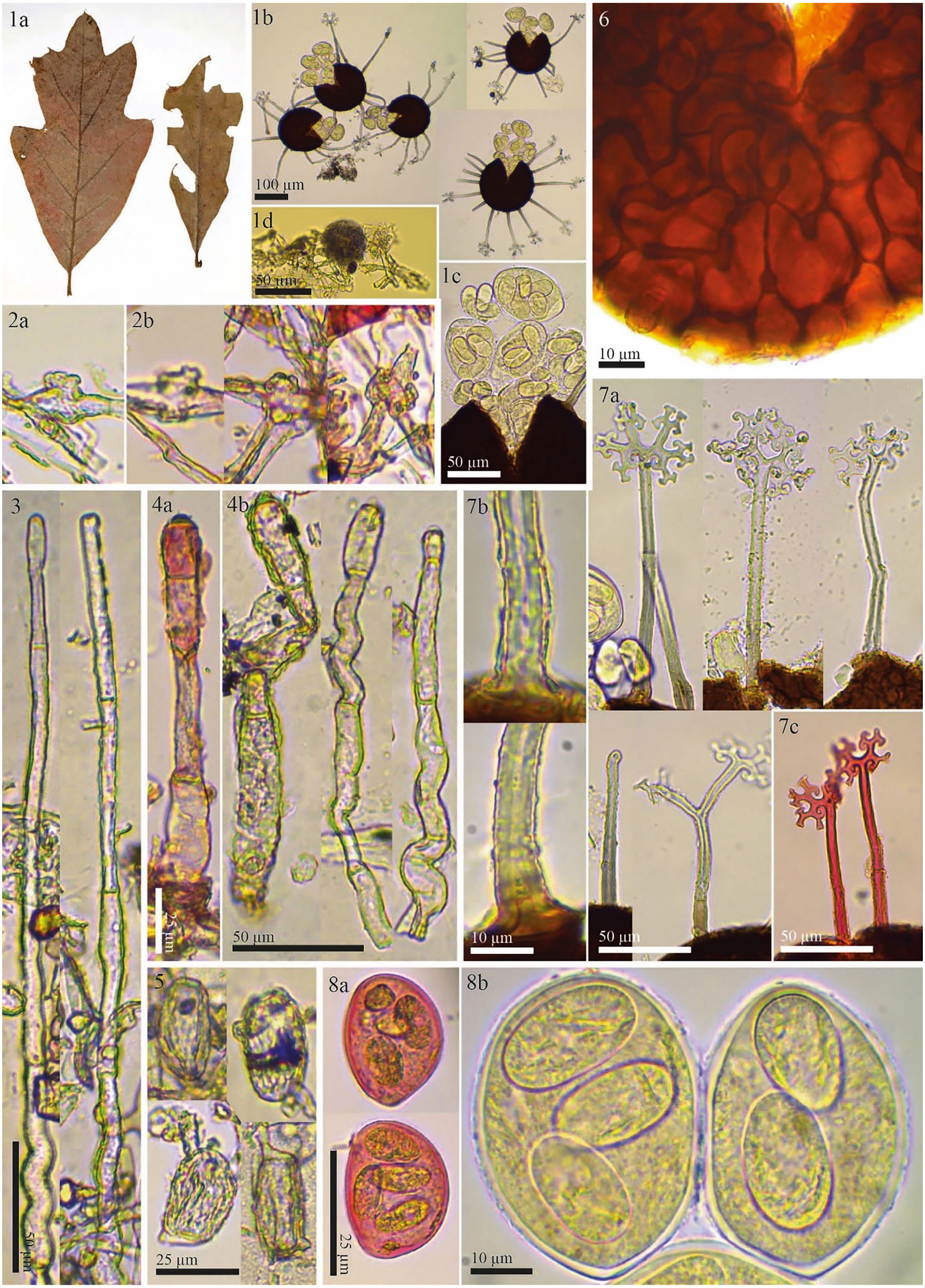

FIGURE 4 | Legend on next page.

FIGURE 4 | Morphological details of *Erysiphe densissima*: 1a-d. Infected leaves and close-up of mycelia with and chasmothecia; 2a-b. Hyphae with appressoria; 3. Mature conidiophore-like hyphal outgrowths (special aerial hyphae); 4a-b. Different developmental stages of conidiophores; 5. Mature conidia, note the ridged ornamentation of the walls, and the germination patterns; 6. Peridium cells; 7a-c. Morphological variability of appendages, note the ornamented thick wall in 7b; 8. Mature asci with 2–4 ascospores inside. Reagents: KOH = 2a, 3, 4b, 5, 6, 7b; KOH + CR = 2b, 4a, 7c, 8a; KOH + MLZ = 1b-d, 7a, 8b.

and easter USA). Probably also on *Quercus imbricaria*, *Q. rubra*, and *Q. velutina* (*Quercus* sect. *Lobatae* subsect. *Coccineae*).

Notes. Braun (1982) introduced *Microsphaera extensa* var. *curta* for a North American oak powdery mildew, which was considered morphologically close to *E. extensa*, but different in having shorter chasmothecial appendages. Braun (1987) and Braun and Cook (2012) assumed that Blumer's (1933) interpretation of *M. densissima* seemed to refer to *M. extensa* var. *curta*, with *Q. marilandica* as type host. The status and taxonomic affinity of *E. densissima* is unclear, and the host identity remains unclear as well. Braun (1987) mentioned that type material of *E. densissima* does not contain any ascomata (see also Braun and Cook 2012). Therefore, the application of the latter name has to be determined by epitypification. Peck (1876) recombined *E. densissima* in *Microsphaera* and emphasised that it is a "very distinct species, forming definite orbicular patches of dense white filaments," but the identity of the oak species of the type collection was not specified. Blumer (1933) discussed the North America oak powdery mildews in detail. He recognised *M. densissima* as a distinct species, well characterised by its special conspicuous symptoms, large chasmothecia, diameter > 100 μm (108–128 μm diam.), appendages 1–2 times as long as the chasmothecial diameter, asci usually 8-spored, rarely 5–7-spored, and cited *Quercus velutina* (= *Q. tinctoria*) and *Q. rubra* as hosts. The leaf fragments of the type material of *E. densissima* at PH are similar to these oak species, but they could belong to *Q. marilandica* as well. The leaves of the oak species involved are easily confused. *Q. rubra* and *Q. velutina* are two morphologically similar and phylogenetically closely allied species, both in *Quercus* subsect. *Coccineae*, which encompasses eastern North American lobe-leaved oaks (Manos and Hipp 2021). *Quercus marilandica* belongs to subsect. *Phellos*. However, according to the treatment of North American oak species in "Flora of North America, Vol. 3" (http://efloras.org/florataxon.aspx?flora_id=1&taxon_id=233501060), *Quercus marilandica* reportedly hybridises with numerous other oak species, including *Q. imbricaria* (subsect. *Phellos*), *Q. rubra* and *Q. velutina*. Braun (1984) cited *Quercus garryana*, *Q. imbricaria* (erroneously as "*Q. imbricata*"), *Q. kelloggii* and *Q. velutina* as additional hosts of var. *curta*. Braun and Cook (2012) excluded the first two oak species and listed only *Q. kellogii* and *Q. velutina* as additional hosts (*Q. garryana* is an oak of Western North America, and *Q. kelloggii* is confined to California and S.W. Oregon). The powdery mildews on *Q. garryana* and *Q. kelloggii* are undoubtedly other American *Erysiphe* species., but *Q. imbricaria*, *Q. rubra*, and *Q. velutina* have to be taken into consideration as hosts of this powdery mildew species, but host identifications remain difficult since these oak species are easily confused and hybrids cannot be excluded. In conclusion, it can be said that Blumer's (1933) interpretation of the name *E. densissima* and its assumed identity with *M. extensa* var. *curta* is reasonable and is supported by host range details and morphology. Therefore, we follow this interpretation and establish the name *E. densissima* in this sense by designating an epitype.

The phylogenetic position of the *E. densissima* (*E. extensa* var. *curta*) clade as sister to the *E. extensa* clade is not surprising. This result confirms the previously assumed close affinity of the two taxa that were previously considered varieties of a single species. However, the formation of two well-supported clades suggests the recognition of two separate species. The *E. densissima* clade is well supported in the concatenated tree and in addition in the *GAPDH*, ITS and *TUB* analyses.

Erysiphe extensa (Cooke & Peck) U. Braun & S. Takam., Schlechtendalia **4**: 8, 2000.

≡ *Microsphaera extensa* Cooke & Peck, J. Bot., N.S., **1**: 12, 1872.

≡ *Microsphaera quercina* var. *extensa* (Cooke & Peck) G.F. Atk., J. Elisha Mitchell Sci. Soc. **7**: 72, 1891.

≡ *Microsphaera alni* var. *extensa* (Cooke & Peck) E.S. Salmon, Mem. Torrey Bot. Club **9**: 152, 1900.

≡ *Microsphaera penicillata* var. *extensa* (Cooke & Peck) W.B. Cooke, Mycologia **44**: 572, 1952.

Lectotype (designated by Braun 1987): USA, New York, N. Greenbush, on *Quercus rubra*, undated, Peck (NYSf 1143.1). Isolectotypes: K(M) 169,067 (as Peck no. 157), NY 02941908 (as "*Microsphaera quercina*"). Ex holotype sequence: PQ105075 (ITS).

=? *Microsphaera extensa* var. *pseudoamericana* Klika, Acta Bot. Bohem. **3**: 21, 1924; type host—*Quercus laurifolia*.

Illustrations. Salmon (1900: plate 1, figure 18), Jaczewski (1927, 337, figure 90), Blumer (1933, 331, figure 131), Braun (1987, 359, pl. 129), Braun & Cook (2012, 463, figure 555).

Descriptions. Jaczewski (1927, 336), Blumer (1933, 331), Braun (1987, 358), Braun & Cook (2012, 463).

Host range and distribution (according to Braun and Cook 2012, based on morphology): on *Quercus* (*alba*, *coccinea*, *discolour*, ×*heterophylla*, *ilicifolia*, *laevis*, *laurifolia*, *macrocarpa*, *minor*, *muehlenbergiae*, *nigra*, *palustris*, *prinoides*, *prinus*, *pumila*, *robur*, *rubra*, *stellata*, *velutina* [= *tinctoria*], *virginiana*), *Fagaceae*; North America (Canada, USA, widespread).

Phylogenetically proven hosts: on *Quercus* (*nigra*, *robur*, *rubra*, *velutina*).

Notes. *Erysiphe extensa* is the only North America oak powdery mildew that can be readily identified based solely on morphology owing to the very long, flexuous appendages. Sequences retrieved from specimens of *E. extensa* on different hosts, including the type specimen from NYS form a well-supported clade in all trees, including the concatenated tree. These results support *E. extensa* as a morphologically and genetically differentiated species. The genetically examined specimens of *E. extensa* on *Q. nigra*, *Q. robur*, *Q. rubra*, and *Q. velutina*, belong to different subsections of *Quercus*, suggesting that *E. extensa* has a wide host range. *Quercus rubra*, the type host, belongs to sect. *Lobatae* subsect. *Coccineae*.

Erysiphe gambelii M. Bradshaw, U. Braun, & Quijada **sp. nov**. Figure 5.

MycoBank, MB855712.

Etymology. The epithet refers to the epithet of the host plant, *Quercus gambelii*.

Holotype. USA, Colorado, Denver Botanical Garden on *Quercus gambelii*, Host Accession from garden = 791954*3, 1 September 2021, *C. Newlander* (FH01131034). Ex-holotype sequences: OR424938 (ITS+28S); OR427449 (*CAM*); OR427537 (*GAPDH*); OR427625 (*GS*); OR427698 (*RPB2*); OR427737 (*TUB*). Additional collections examined: See Table 1.

Description. Mycelium epiphyllous, white, growing loosely or in dense patches close to the adaxial leaf surface veins; hyphae sinuous and curled-helicoid, hyaline or slightly yellowish, cells (30.5–)41.5–55(–69) × (4–)4.5–5.5(–7) μm, irregularly branched, cell walls slightly ornamented with yellowish sparse warts, cells without content; hyphal appressoria nipple-shaped and solitary or lobed in opposite pairs (2–5-lobate), 3.5–9 μm wide; conidiophore-like hyphal outgrowths (special aerial hyphae arising from superficial hyphae) sparse, 75–217 × 8–11 μm, cylindrical and progressively tapering toward the apex, sinuous-helicoid below, multiseptate, arising from long helicoid cells that arise from a ring-like structure, basal cell 45–95 × 8–9 μm, following cells 48.5–87 × 5.5–7 μm, apex rounded, walls slightly thickened and ornamented with warts, ornamentation more prominent toward the base; conidiophores arising from the upper surface of mother cells, straight to slightly curved, cell walls ornamented with yellowish irregular warts, foot cells cylindrical, straight or slightly curved, (21.5–)29.5–40(–56.5) × (6–)7–8.5(–9) μm, with 2–3 following cells, shorter than foot cells, (17–)20–23(–27) × (6–)7.5–9.5(–12) μm; conidia solitary, ellipsoid-obovoid, (24–)27–30(–33.5) × (11.5–)14–17(–17.5) μm, conidial wall ornamented, less thickened in the poles, walls with yellowish warts and transverse/longitudinal ridges when dry, ornamentation lost in Melzer's reagent and wall becoming amyloid, scattered lipidic guttules present; germ tubes subterminal, up to 31 μm long, showing a *Pseudoidium* type morphology. Chasmothecia epiphyllous, subgregrarious, globose, 92–144 μm diam; peridium made of textura angularis-prismatica, cells (16–)19–23(–29.5) × (10.5–)12–14.5(–167) μm, thick-walled, irregularly rectangular-polygonal to sinuous (interlocking-shape), strongly yellow-brown to deep brown, cell walls darker 1.5–2.5 μm thick, with connections among cells where the wall became thinner; appendages in the equatorial zone, usually 6–7, rarely with up to 14 appendages, slightly to medium curved, (42.5–)63.5–79.5(–94.5) μm long and (6.5–)7–7.5(–9) μm wide at the base, 0.4–1.5 times as long as the chasmothecial diam, hyaline, only light brownish close to the base, usually aseptate, rarely 1-septate close to the base, walls 1–2.5 μm thick, irregularly warted, amyloid in MLZ after KOH-pretreatment, apices regularly 1–2 times dichotomously branched (probably not fully mature), tips of the ultimate branchlets slightly recurved; asci 5–8 per chasmothecium, broad ellipsoid-ovoid to subglobose, (42.5–)48.5–53.5(–58) × (24.5–)30–34(–40) μm, wall thickened, up to 1.5 μm throughout, except for the apical oculus, base with a short stalk, 4–6-spored; ascospores ellipsoid-subglose, (14–)16–18(–21) × (8.5–)10–11(–13.5) μm, hyaline, thin-walled, smooth, 50%–75% filled with yellowish grey lipidic guttules.

Host range and distribution: on *Quercus* [sect. *Quercus* subsect. *Dumosae*] *gambelii*, *Fagaceae*; North America (USA, Colorado, Utah).

Notes. *Erysiphe gambelii* is confined to *Quercus gambelii* (*Quercus* subsect. *Dumosae*, previously subsect. *Gambelieae*). In the concatenated phylogenetic tree, the *E. gambelii* clade is strongly supported and sister to the *E. abbreviata* clade, as circumscribed in the present work. In addition, the *E. gambelii* clade is moderately supported in the RPB2 tree. In the ITS tree, sequences of *E. abbreviata* and *E. gambelii* form a single highly supported clade. *Erysiphe gambelii* is morphologically similar to *E. abbreviata*. The branched apices of the chasmothecial appendages in the examined specimens are undoubtedly immature and not fully developed. Nevertheless, it is interesting that such immature chasmothecial appendages in *E. gambelii* are found with mature asci and fully developed ascospores. This combination is unusual in species of *Erysiphe* sect. *Microsphaera*. Commonly, the ascospores become fully developed and mature when the chasmothecia, including apical ramification, are completely formed. *Erysiphe gambelii* differs from the phylogenetically closely allied *E. abbreviata* in having broader special aerial hyphae (hyphal outgrowths), 8–11 μm (vs. usually 6.5–9 μm broad in *E. abbreviata*), epiphyllous, subgregarious chasmothecia (vs. usually hypophyllous, scattered in *E. abbreviata*), 5–8 asci per chasmothecium (vs. 3–6 in *E. abbreviata*), and much smaller ascospores, (14–)16–18(–21) × (8.5–)10–11(–13.5) μm (vs. 20–32 × 13–21 μm in *E. abbreviata*).

Manos and Hipp (2021) assigned this oak species to *Quercus* subsect. *Dumosae* and discussed its phylogenetic affinity, which is still not quite clear. *Quercus gambelii* is distributed in the Western Central to South Central USA and northern Mexico.

Erysiphe occidentalis M. Bradshaw, U. Braun, & Quijada, **sp. nov**. Figure 6.

MycoBank, MB855713.

Etymology. Occidentalis, referring to the distribution of this species on oaks in western North America.

Holotype. USA, Washington, King Country, Washington State Arboretum on *Quercus garryana*, 12 October 2018, *M.*

Bradshaw (FH01131038). Ex-holotype sequences: OR424943 (ITS+28S); OR427455 (*CAM*); OR427543 (*GAPDH*); OR427632 (*GS*) ; OR427702 (*RPB2*); *OR427772* (*TUB*). Additional collections examined: See Table 1.

Description. Mycelium epiphyllous, white, growing in dense patches covering the whole adaxial leaf surface; hyphae sinuous and curled-helicoid, hyaline or slightly yellowish, cells (28–)32–48(–69.5) × 3.5–4.5 µm, irregularly branched, cell walls slightly ornamented with yellowish sparse warts, cells without content; hyphal appressoria nipple-shaped and solitary, 4–7.5 µm wide; conidiophore-like hyphae outgrowths (special aerial hyphae) sparse, 148–211 µm long, 8.5–10 µm wide at the base, cylindrical and progressively tapering toward the apex, sinuous-helicoid below, multiseptate, arising from a long helicoid cells that arise from a ring-like structure, basal cell 28–59 × 5–9.5 µm, following cells 30–39.5 × 7–8.5 µm, apex rounded, walls slightly thickened and ornamented with warts, ornamentation more prominent toward the base; conidiophores arising from the upper surface of the mother cell, straight to slightly curved, cell walls ornamented with yellowish irregular warts, foot-cells cylindrical, straight or slightly curved, cells 19–24.5 × 8–9 µm, with two following cells, similar in size, cells (13–)17.5–23(–25) × (7)8.5–12.5(–14) µm; forming conidia singly; conidia ellipsoid-cylindrical, (26–)29–32.5(–35) × (10.5)15–17.5(–20) µm, conidial wall ornamented, less thickened in the poles, walls with yellowish warts and transverse/longitudinal ridges when dry; germ tubes not observed. Chasmothecia subgregrarious, globose, 116–156 µm diam; peridium made of textura angularis-prismatica, cells (12–)14.5–18.5(–20.5) × (8.5–)10.5–13(–14.5) µm, thick-walled, irregularly rectangular-polygonal to sinuous-shaped (interlocking-shape), strongly yellow-brown to deep brown, cell walls darker 1.5–4.5 µm thick, with connections among cells where the wall became thinner; appendages in the equatorial zone, 6–13(–18) appendages, slightly to medium curved, (80–)110.5–143(–169) µm long, (5–)7–10(–12) µm wide at the base, (3.5–)4.5–7 µm wide at the apex before branching, about as long as chasmothecial diam, hyaline, usually aseptate, rarely 1-septate close to the base, walls 1.5–3 µm thick, irregularly warted, amyloid in MLZ after KOH-pretreatment, apices regularly 3–6 times dichotomously branched, branched part dense, compact to somewhat looser by somewhat longer branchlets, tips of the ultimate branchlets slightly to strongly recurved; asci 6, broad ellipsoid-ovoid to subglobose, (47.5–)54–60(–67.5) × (33–)36.5–40.5(–46.5) µm, 4–5-spored, wall thickened, up to 1.5 µm throughout, except for the apical oculus, base with a short stalk; ascospores ellipsoid-subglobose, (18.5–)21–24.5(–26.5) × (10–)11.5–12.5(–13.5) µm, hyaline, thin-walled, smooth, 50%–75% filled with yellowish grey lipidic guttules.

Host range and distribution: on *Quercus* [sect. *Quercus* subsect. *Dumosae*] *garryana* and *Q.* [sect. *Lobatae* subsect. *Agrifoliae*] *kellogii*, *Fagaceae*; North America, (PowUSA, California, Washington).

Notes. *Erysiphe occidentalis* is a North America oak powdery mildew that is cofined to western North America. *Quercus garryana* (*Quercus* sect. *Quercus* subsect. *Dumosae*) is found in western North America from British Columbia to Washington and California. *Quercus. kelloggii* (sect. *Lobatae* subsect. *Agrifoliae*) is confined to California and S.W. Oregon, i.e., the distribution areas of these oaks are overlapping. However, in the case of *Q. garryana* and *Q. kellogii*, two different *Quercus* sections are involved, viz., *Quercus* and *Lobatae*. *Q. garryana* is also distributed in California, so that a possible confusion between *Q. kelloggii* and *Q. garryana*, two species with deeply lobate leaves, should be taken into consideration.

The *E. occidentalis* clade is highly supported in the concatenated analysis and in the ITS, *RPB2* and *TUB* trees.

Erysiphe parmeleeana Hambl. & M. Liu, in Carey et al., Canad. J. Plant Pathol. 2024, in press.

Holotype. Canada, Ontario, Ottawa, Field at Fallowfield Bus station, on *Quercus macrocarpa*, 16 September 2013, *Tharcisse Barasubiye* (DAOM 243034). Ex-holotype sequences: OR940019 (ITS); OR914623 (*CAM*); OR914637 (*GAPDH*); OR914651 (*GS*); OR914665 (*RPB2*); OR935837 (*TUB*).

Description and illustration: see Carey et al. (2024).

Host range and distribution: on *Quercus* [*Quercus* subgen. *Quercus* sect. *Quercus*] (*macrocarpa*, *robur*), *Fagaceae*; North America, Canada (Manitoba, Ontario).

Notes. *Erysiphe parmeleeana*, described in Carey et al. (2024), is phylogenetically closely allied to *E. abbreviata* and *E. gambelii*, but sequences retrieved from this species on *Quercus macrocarpa* and *Q. robur*, which is exotic in North America, form a separate strongly supported clade in phylogenetic multilocus analyses. Furthermore, *E. parmeleeana* is morphologically distinguished from *E. abbreviata* by having longer chasmothecial appendages, up to 1.5 time as long as the chasmothecia diameter, occasionally even up to two times the diameter (vs. usually 0.5–1 time as long as the diameter in *E. abbreviata*) and up to 8-spored asci (vs. consistently 3–6-spored asci in *E. abbreviata*). In addition, *E. parmeleeana* forms epiphyllous mycelial colonies, in contrast to *E. abbreviata*, which is mostly strictly hypophyllous. Furthermore, *E. parmeleeana* is characterised by forming 'special aerial hyphae' (hyphal outgrowths) arising from common superficial hyphae that are distinctive from regular hyphae, resembling elongated, immature conidiophores, but they are flexuous, sinuous-helicoid toward the upper portion. Comparable structures are also known in *E. abbreviata*, but they are ony sinuous-helicoid below and arise from closely septate and curved cells that form a ring-like structure. *Erysiphe gambelii* forms similar hyphal outgrowths. The chasmothecia of *E. gambelii* and *E. parmeleeana* are barely different from each other, except for the apical ramifications of the chasmothecial appendages, which develop rather late in *E. gambelii*, i.e., they are not fully developed even when the ascospores are already mature.

All available sequences of *E. parmeleeana* have been retrieved from Canadian specimens collected on *Quercus macrocarpa* and the introduced *Q. robur*. However, *Q. macrocarpa* was cited by Braun and Cook (2012) within the host range of *E. abbreviata*. Therefore, a wider distribution of *E. parmeleeana* can be assumed, including USA.

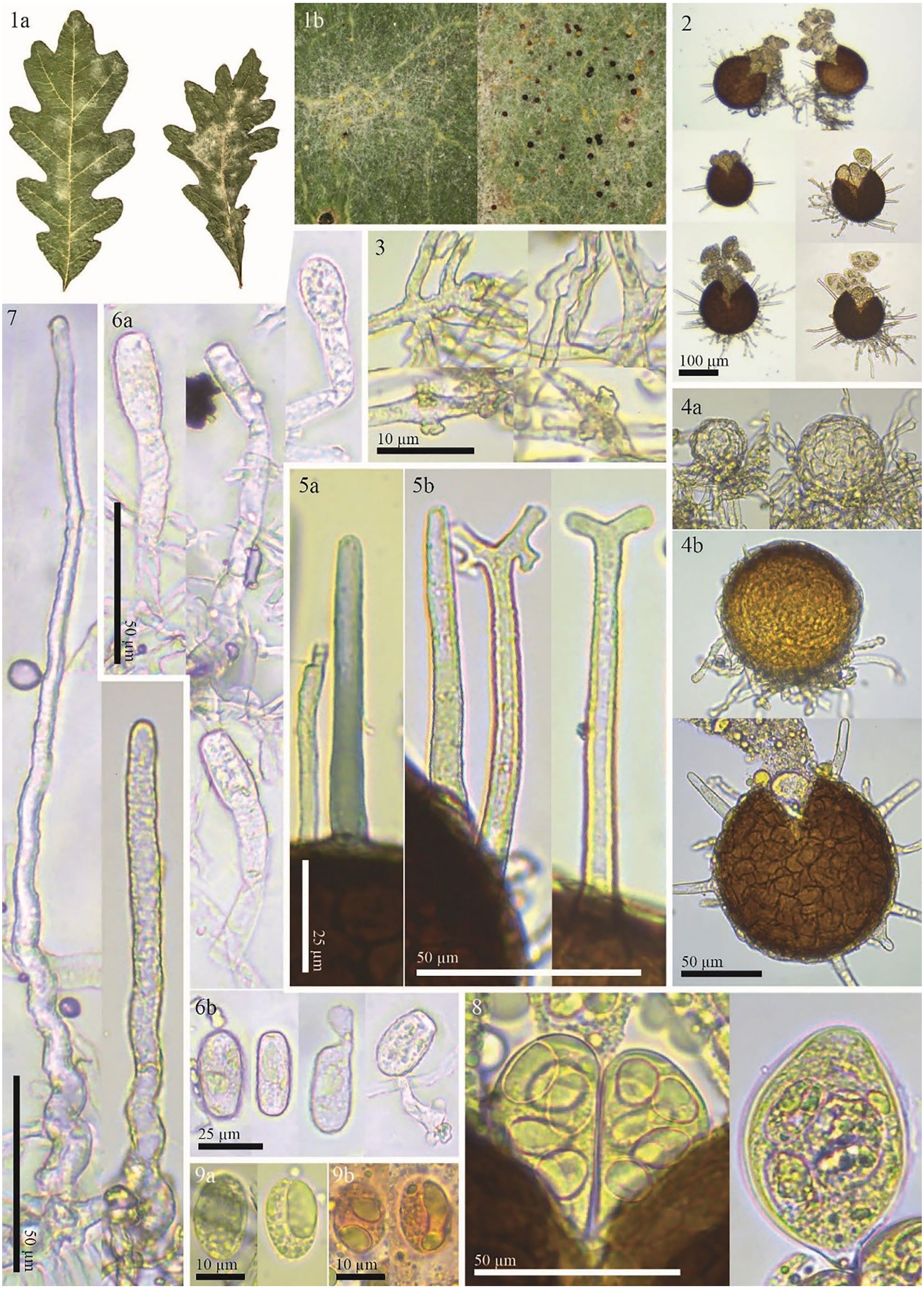

FIGURE 5 | Legend on next page.

FIGURE 5 | Morphological details of *Erysiphe gambelii*: 1a-b. Infected leaves and close-up of mycelia with and chasmothecia; 2. Chasmothecia releasing asci; 3. Hyphae with appressoria; 4. Development of chasmothecia, 4a. Hyaline immature chasmothecia, 4b. Melanized immature and mature chasmothecia; 5. Morphological variability of appendages, note the amyloid reaction in 5a; 6a-b. Different developmental stages of conidiophores and conidia; 7. Mature conidiophore-like hyphal outgrowths (special aerial hyphae); 8. Mature asci; 9a-b. Ascospores. Reagents: KOH = 2, 4a-b, 5b, 6a-b; KOH + MLZ = 5a, 7. KOH + MLZ = 3, 5a, 8, 9a; KOH + CR = 9b.

Erysiphe phellos M. Bradshaw, U. Braun & Quijada, **sp. nov**. Figure 7.

MycoBank, MB855714.

Etymology. The epithet refers to the epithet of *Quercus phellos*.

Holotype. USA, Virginia, Petersburg on *Quercus phellos*, 18 October 1936, *M.L. Fernald, B.H. Long & R. F. Smart* (FH01122159). Ex-holotype sequences: OR424951 (ITS+28S); OR427461 (*CAM*); OR427547 (*GAPDH*); OR427635 (*GS*); OR427704 (*RPB2*); OR427751 (*TUB*).

Additional collection examined: See Table 1.

Description. Mycelium epiphyllous, white, growing in dense patches; hyphae sinuous and curled-helicoid, hyaline or slightly yellowish, cells (22.5–)29–43.5(–51) × (3–)3.5–5.5(–6) µm, irregularly branched, cell walls slightly ornamented with yellowish sparse warts, cells without content; hyphal appressoria lobed in opposite pairs (2–6-lobate), 7–12.5 µm wide; conidiophores-like hyphae outgrowths (special aerial hyphae) frequent, (88.5)142–247(–279) µm long, at the base (4–)6.5–10(–10.5) µm wide, cylindrical and progressively tapering toward a blunt apex, up 1–4 µm, multiseptate, sinuous-helicoid below, arising from a long helicoid cells that arise from a ring-like structure, basal cell (16.5–)35.5–51.5(–55) × (4.5–)7–10.5(–11) µm, following cells (10–)20.5–50(–54) × (2–)4–7.5(–8.5) µm, apex rounded, walls slightly thickened and ornamented with warts and resinous granules, ornamentation more prominent toward the base. Conidiophores arising from the upper surface of the mother cell, straight to very slightly curved, cell walls ornamented with yellowish irregular warts, foot-cells cylindrical, slightly or medium helicoid, (29.5–)35.5–44(–46) × (8.5)9–12(12.5) µm, 1–3 following cells with similar size, cells (13–)25–35.5(–42.5) × (5–)7–10(–11) µm; forming conidia singly; conidia cylindrical-ellipsoid, (21.5–)26–31.5(–32) × (10.5–)12.5–17.5(–19.5) µm, conidial wall ornamented, walls with yellowish warts and transverse/longitudinal ridges when dry, without lipidic guttules present; germ tubes not observed. Chasmothecia subgregrarious or scattered, globose, 113–160 µm diam; peridium made of textura angularis-prismatica, cells (10.5–)14–17.5(–19) × (8.5–)10.5–13.5 µm, thick-walled, irregularly rectangular-polygonal to sinuous-shaped (interlocking-shape), strong yellow-brown to deep brown, cell walls darker, 1–2.5 µm thick, with connections among cells where the wall becames thinner; appendages in the equatorial zone, 5–9 appendages, slightly to medium curved, (109–)148.5–186.5(–229) µm long, (7–)8–9.5(–10) µm wide at the base, (4–)5–6.5(–7) µm wide at apex before branching, 0.9–1.4 times as long as the chasmothecial diam, hyaline, only medium to strongly brownish at the base, usually aseptate, rarely 1-septate close to the base, walls 1.5–3 µm thick, irregularly warted, amyloid in MLZ after KOH-pretreatment, apices regularly 4–6 times dichotomously branched, branched portion compact, dense to somewhat looser by somewhat longer branchlets, tips of the ultimate branchlets recurved; about four asci per chasmothecium, broad ellipsoid-ovoid to subglobose, (47–)61–70(–76) × (33–)46.5–56.5(–61.5) µm, 4 asci per chasmothecium, 4–6-spored, wall slightly thickened, up to 1 µm throughout, except for the apical oculus, base with a short stalk; ascospores ellipsoid-ovoid, (24.5–)27.5–31(–32) × (14–)16–17.5(–18) µm, hyaline, thin-walled, smooth, 50%–75% filled with yellowish grey lipidic guttules.

Host range and distribution: on *Quercus phellos* [*Quercus* sect. *Lobatae* subsect. *Phellos*], *Fagaceae*; North America (North Carolina, Virginia).

Notes. In the concatenated tree, sequences retrieved from powdery mildew on *Quercus phellos* form a highly supported group.

Erysiphe pseudoextensa M. Bradshaw, U. Braun, & Quijada **sp. nov**. Figure 8.

MycoBank, MB855715.

Etymology: *pseudoextensa*, referring to morphological similarity to *Erysiphe extensa*.

Holotype. USA, Virginia, Peterburg on *Quercus alba*, 18 October 1936, *M.L. Fernald, B.H. Long & R. F. Smart* (FH01122185), originally identified as *E. extensa*. Ex-holotype sequences: OR424953 (ITS+28S); OR427463 (*CAM*); OR427549 (*GAPDH*); OR427755 (*TUB*). Additional collections examined See Table 1.

Description. Mycelium epiphyllous, white, growing loosely or in dense patches close to the adaxial leaf surface veins; hyphae sinuous and curled-helicoid, hyaline or slightly yellowish, cells (12.5–)15–45(–55) × (3–)3.5–6.5(–7) µm, irregularly branched, cell walls slightly ornamented with yellowish sparse warts, cells without content; hyphal appressoria lobed in opposite pairs (2–6-lobate), 8–10 µm wide; conidiophores-like hyphae outgrowths (special aerial hyphae) sparse, (67)147–373(–481) µm long, at the base (4–)6.5–10(–11) µm wide, cylindrical and progressively tapering toward a blunt apex, up to 4 µm, multiseptate, sinuous-helicoid below, arising from a long helicoid cells that arise from a ring-like structure, basal cell (27–)35–47.5(–52.5) × (7.5–)8–10.5(–11.5) µm, following cells (10–)20.5–56(–61) × (5–)5.5–7.5(–8) µm, apex rounded, walls slightly thickened and ornamented with warts and resinous granules, ornamentation more prominent toward the base. Conidiophores arising from the upper

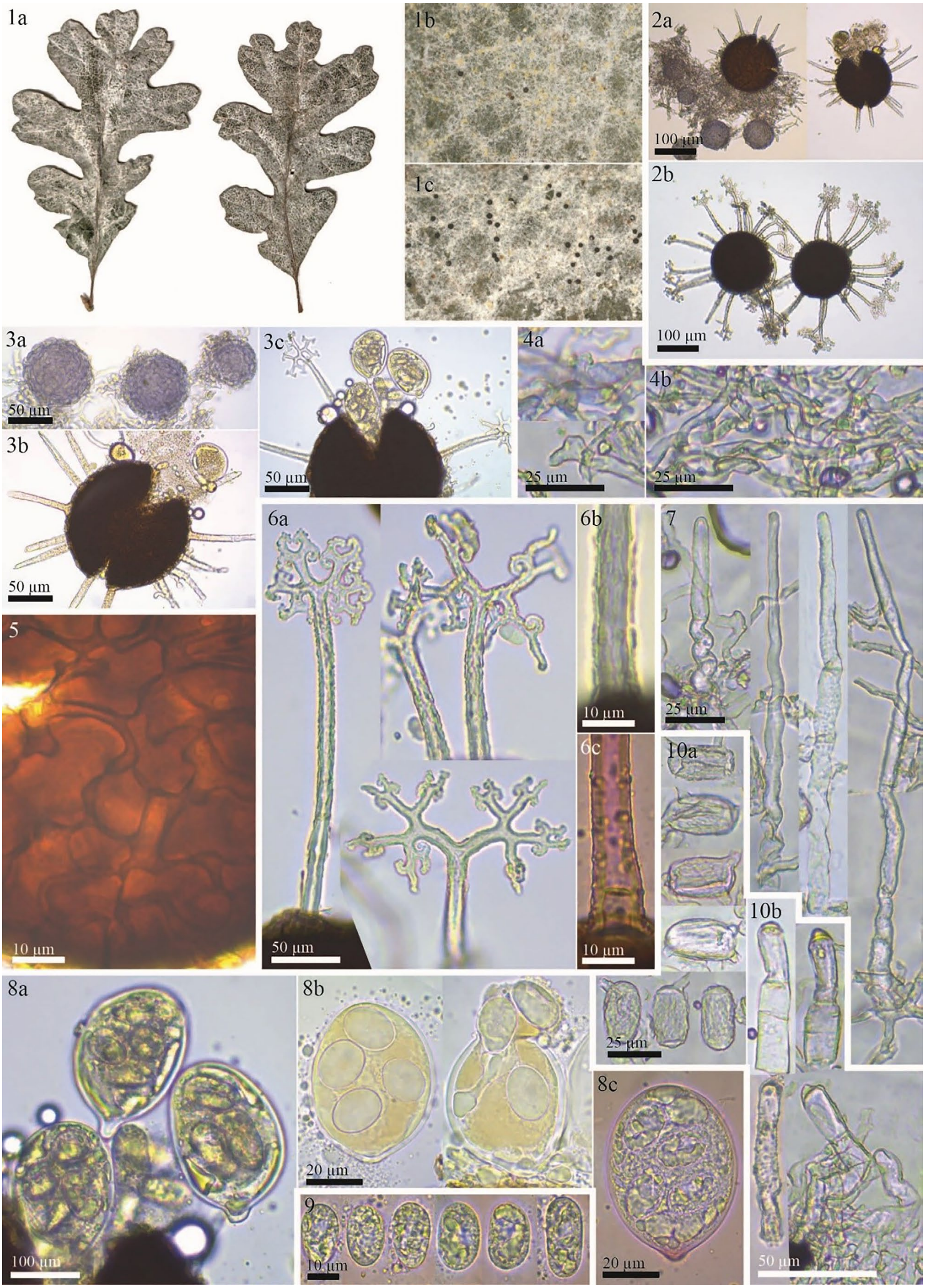

FIGURE 6 | Legend on next page.

FIGURE 6 | Morphological details of *Erysiphe occidentalis*: 1a-b. Infected leaves and close-up of mycelia with chasmothecia; 2a-b. Chasmothecia with immature and mature appendages; 3a-b. Immature amyloid chasmothecia in KOH + MLZ and mature opened chasmothecium releasing the asci; 3c. Mature, open chamothecium releasing asci; 4a-b. Hyphae with appressoria; 5. Peridium; 6a. Morphological variability of appendages, note the amyloid reaction in 6b. Amyloid appendage wall in KOH + MLZ; 6c. Ornamented appendage wall in CR; 7. Mature conidiophore-like hyphal; 8a-c. Mature asci; 9. Ascospores; 10. Different developmental stages of conidiophores and conidia. Reagents: KOH = 2a-b, 3b-c, 4a-b, 5, 6a, 7, 8a, 10a-b; KOH + CR = 6c, 8c, 9; KOH + MLZ = 3a, 6, 8b.

surface of the mother cell, straight to very slightly curved, cell walls ornamented with yellowish irregular warts, foot-cells cylindrical, straight or slightly curved, 17 × 8 µm, with 1–2following cells of similar size as the foot-cells, cells 11–28 × 9.5–10 µm; forming conidia singly; conidia ellipsoid, (22–)23–28 × (9)10.5–15 µm, conidial wall ornamented, walls with yellowish warts and transverse/longitudinal ridges when dry, without lipidic guttules present; germ tubes not observed. Chasmothecia subgregrarious or scattered, globose, 100–164 µm diam; peridium made of textura angularis-prismatica, cells (8.5–)14–22.5(–30.5) × (7–)10.5–15.5(–18.5) µm, thick-walled, irregularly rectangular-polygonal to sinuous-shaped (interlocking-shape), strong yellow-brown to deep brown, cell walls darker, 1–3 µm thick, with connections among cells where the wall becames thinner; appendages in the equatorial zone, (5–)8–18 appendages, slightly to medium curved, (109–)148.5–254.5(–281) µm long and (6.5–)7–9(–10) µm wide at the base or base somewhat inflated, 4–6.5(–7) µm wide at apex before branching, 0.9–1.9 times as long as the chasmothecial diam, hyaline, only medium to strongly brownish at the base, usually aseptate, rarely 1-septate close to the base, walls 1–3 µm thick, irregularly warted, amyloid in MLZ after KOH-pretreatment, apices regularly 3–6 times dichotomously branched, branched portion compact, dense to somewhat looser by somewhat longer branchlets, tips of the ultimate branchlets recurved; about four asci per chasmothecium, broad ellipsoid-ovoid to subglobose, (45–)51–77.5(–79.5) × (20–)27.5–54.5(–58) µm, 2–8-spored, wall slightly thickened, up to 1 µm throughout, except for the apical oculus, base with a short stalk; ascospores ellipsoid-subglobose, cylin drical-ovoid, (15.5–)19–23(–26) × (9–)10–13.5(–14.5) µm, hyaline, thin-walled, smooth, 50%–75% filled with yellowish grey lipidic guttules.

Host range and distribution: on *Quercus* [subgen *Quercus* sect. *Quercus* subsect. *Albae*] *alba* and *Q.* [subgen *Quercus* sect. *Quercus*] *robur*, *Fagaceae*, North America (USA, Indiana, Maryland, Massachussetts, Virginia).

Notes. The identity of the hosts originally referred to as *Quercus robur*, need to be proven. *Quercus alba* and *Q. robur* are allied species of *Quercus* sect. *Quercus*. They have similar leaves and are confusable. Alternatively, it cannot be excluded that *E. pseudoextensa* on *Q. alba* may also infect the allied *Q. robur* (subsect. *Albae* is sister to the roburoids in Europe) introduced to North America. In Bradshaw, Braun, and Pfister (2022) specimens collected on *Quercus robur* from North America were found to be *E. alphitoides* and *E. quercicola*. *Quercus alba* is native to North America whereas *Q. robur is* native to Europe however the latter is often planted in North America. The *E. pseudoextensa* clade is well supported in the concatenated and *GAPDH* trees.

Erysiphe quercicola S. Takam. & U. Braun, Mycol. Res. **111**: 819, 2007, nom. cons.

Holotype. Japan, Nara, Ikoma Mt., on *Quercus phillyraeoides*, 27 November 1999, *S. Takamatsu* (TNS-F87513 [previously MUMH 885]). Isotype: HAL 1969 F. Ex-holotype sequences: AB193591, AB237813.

= *Oidium anacardii* Noack, Bol. Inst. Estado São Paulo **9**(2): 77, 1898.

≡ *Pseudoidium anacardii* (Noack) U. Braun & R.T.A. Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 497, 2012.

= *Oidium mangiferae* Berthet, Bol. Agric. (São Paulo) **15**: 818, 1914.

≡ *Acrosporium mangiferae* (Berthet) Subram., Hyphomycetes (New Delhi): 834, 1971.

≡ *Oidium erysiphoides* f. *mangiferae* (Berthet) J.M. Yen & Chin C. Wang, Rev. Mycol. **37**(3): 138 "1972" 1973.

= *Microsphaera alni* var. *quercina* Neger, Naturwiss. Z. Forst-Landw. **8**: 3, 1915.

= *Oidium bixae* Viégas, Bragantia **4**(1–6): 19, 1944.

= *Oidium erysiphoides* f. *bixae* J.M. Yen, Cah. Pacifique **11**: 88, 1967.

= *Oidium erysiphoides* f. *citri* J.M. Yen, Cah. Pacifique **11**: 99, 1967.

≡ *Oidium citri* (J.M. Yen) U. Braun, Zentralbl. Mikrobiol. **137**: 323, 1982.

= *Oidium caesalpiniacearum* Hosag. & U. Braun, in Braun, Mycotaxon **25**(1): 267, 1986, **syn. nov**.

≡ *Pseudoidium caesalpiniacearum* (Hosag. & U. Braun) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews): 600, 2012.

= *Microsphaera alphitoides* auct. p.p.

= *Erysiphe alphitoides* auct. p.p.

Host range and distribution in North America: on *Quercus* (*agrifolia*, *robur*, *shumardii*), *Fagaceae*, Mexico, USA (Florida, Washington).

Notes. Bradshaw, Braun, and Pfister (2022) confirmed *Erysiphe quercicola* on *Quercus robur* in Washington. Holotype

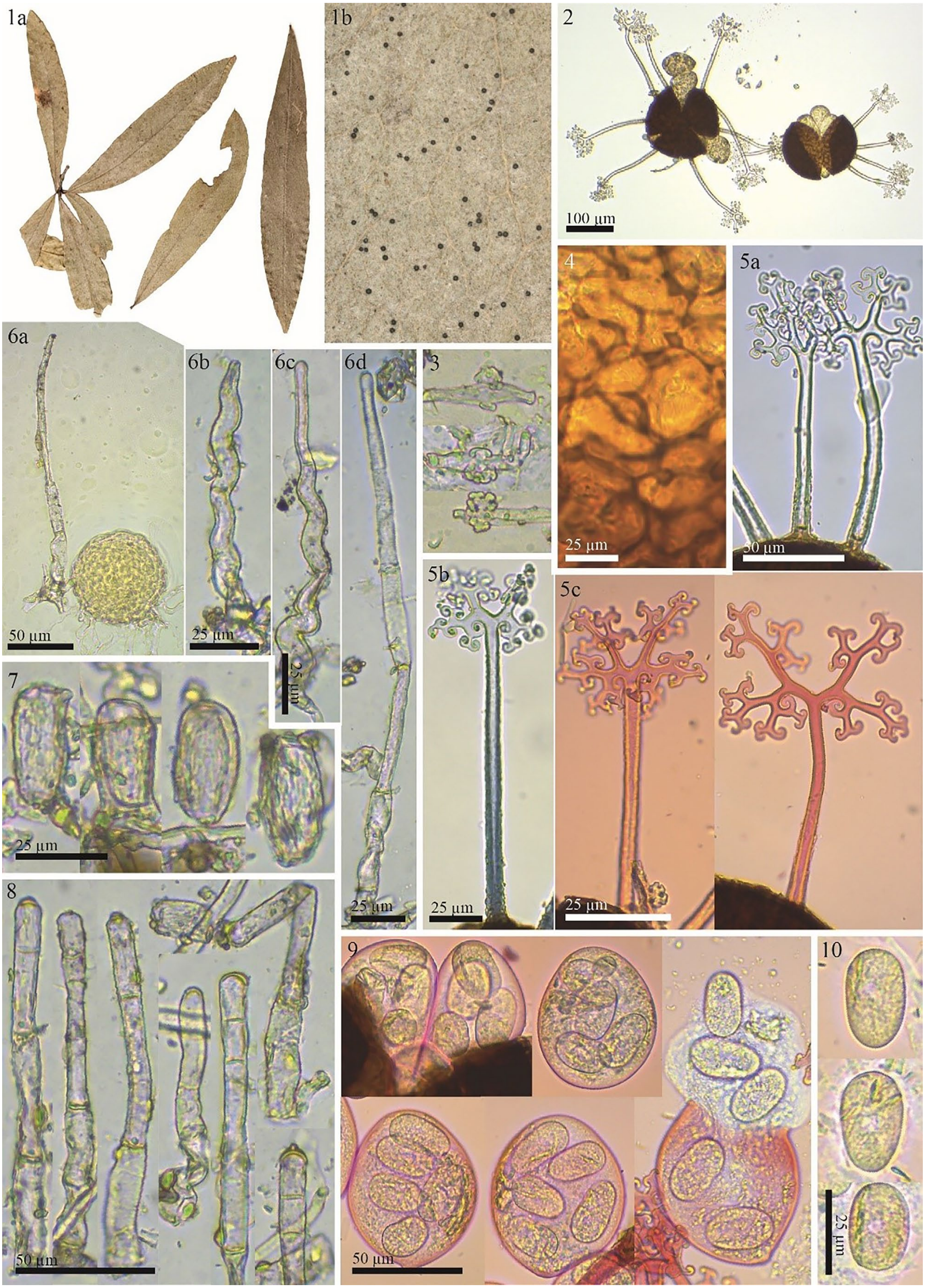

FIGURE 7 | Legend on next page.

FIGURE 7 | Morphological details of *Erysiphe phellos*: 1a-b. Infected leaves and close-up of mycelia with chasmothecia; 2. Chasmothecia with mature appendages; 3. Hyphae with appressoria; 4. Peridium; 5a-c. Morphological variability of appendages, note the amyloid reaction in 5b. Amyloid appendage wall in KOH + MLZ; 6a-d. Morphological variability of conidiophores-like hyphal; 7–8. Different developmental stages of conidiophores and conidia; 9. Mature asci; 10. Ascospores. Reagents: KOH = 2, 3, 4, 5a, 6a-d, 7, 8; KOH + CR = 5c, 9, 10; KOH + MLZ = 5b.

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material of *Oidium caesalpiniacearum* (India, Karnataka, Bangalore, on *Bauhinia* sp., 1984, V. B. Hosagodar, HAL 1430 F) has recently been sequenced. Based on analysis of the ex-type sequence, *O. caesalpiniacearum* must be reduced to synonymy with *E. quercicola*.

Erysiphe quercophila M. Bradshaw, U. Braun, & Quijada **sp. nov**. Figure 9.

MycoBank, MB855716.

Etymology. Epithet composed of the genus name, *Quercus*, + – phila (loving).

Holotype. USA, Florida, Gainsville, NW 93rd Avenue, on *Quercus nigra*, 17 December 2022, *M.E. Smith* (FH00941969). Ex-holotype sequences: Ex-holotype sequences: OR424969 (ITS+28S); OR427476 (*CAM*); OR427563 (*GAPDH*); OR427646 (*GS*); OR427716 (*RPB2*); OR427730 (*TUB*). Additional collections examined: See Table 1.

Description. Mycelium epiphyllous, white, growing in dense patches close to the adaxial leaf surface veins; hyphae sinuous and curled-helicoid, hyaline or slightly yellowish, cells (11.5–)29–63.5(–86) × (2–)3.5–6 µm, irregularly branched, cell walls slightly thickened with yellowish sparse warts, cells without content; hyphal appressoria lobate; conidiophores-like hyphal outgrowth (special aerial hyphae) sparse, up to 42 × 5.5 µm, cylindrical and progressively tapering toward a subclavate apex, multiseptate, arising from long helicoid cells that arise from a ring-like structure, basal cell 6.5–19 × 2.5–6 µm, following cells 16–24 × 2–6 µm, walls slightly thickened and ornamented with warts, ornamentation more prominent toward the base. Conidiophores arising from the upper surface of mother cells, straight to very slightly curved, cell walls ornamented with yellowish irregular warts, foot-cells cylindrical, straight or very slightly helicoid, cells (13–)15–20.5 × 3.5–4.5 µm, with 2–3 following cells, slightly shorter or longer than the foot-cells, (5.5–)8.5–17.5(–26.5) × (2.5–)3–3.5(–4.) µm; forming conidia singly; conidia ellipsoid-doliiform, (28)30–34(38) × (15)17–20 µm, conidial wall ornamented, walls with yellowish warts and tranverse/longitudinal ridges when dry, without lipidic guttules; germ tubes subterminal, up to 9.6 µm long, showing a Pseudoidium type morphology. Chasmothecia subgregrarious, globose, 96–150 µm diam; peridium made of textura angularis-prismatica, cells (9–)13.5–19(–23.5) × (6.5–)9.5–13(–14.5) µm, thick-walled, irregularly rectangular-polygonal to sinuous-shaped (interlocking-shape), strong yellow-brown to deep brown, cell walls darker 1–2.5 µm thick, with connections among cells where the wall became thinner; appendages in the equatorial zone, 4–10, slightly to medium curved, (118–)213.5–316(–332) µm long and (6.5–)7.5–10.5(–11.5) µm wide at the base, 0.8–2.2 times longer than chasmothecial diam, hyaline, brownish close to the base and up to ¼ of the length, aseptate or 1-septate, walls 2–3.4 µm thick, irregularly warted, amyloid in MLZ after KOH-pretreatment, apices regularly 5–6 times dichotomously branched, tips of the ultimate branchlets recurved; asci 3–5, broad ellipsoid-ovoid, (53–)56–62.5(–66) × (37–)42–51.5(–53) µm, (2–)4–6-spored, wall thickened, up to 3.5 µm throughout, except for the apical oculus, base with a short stalk; ascospores ellipsoid-ovoid, (14.5–)16.5–20.5(–21.5) × (8–)9.5–11.5(–13) µm, hyaline, thin-walled, smooth, 50%–75% filled with yellowish grey lipidic guttules.

Host range and distribution: on *Quercus* [*Quercus* sect. *Lobatae* subsect. *Phellos*] *nigra*, *Fagaceae*, North America (USA, Florida).

Notes. See discussion under *Erysiphe phellos*.

Erysiphe quercus-laurifoliae M. Bradshaw, U. Braun, & Quijada **sp. nov**. Figure 10.

MycoBank, MB855717.

Etymology. The epithet refers to the name of the host plant, *Quercus laurifolia*.

Holotype. USA, Florida, Melrose, Ordway Swisher Biological Station on *Quercus laurifolia*, 7 July 2021, *M. Bradshaw* (FH01131031). Ex-holotype sequences: OR424934 (ITS+28S); OR427448 (*CAM*); OR427536 (*GAPDH*); OR427624(*GS*); OR427697 (*RPB2*); OR427768 (*TUB*). Additional collection examined: See Table 1.

Description. Mycelium epiphyllous, white, growing on the adaxial leaf surface; hyphae straight, sinuous or slightly helicoid, hyaline, cells (25.5–)38.5–47.5(–112) × (4–)5.5–6.5(–9.5) µm, branched, cell walls slightly ornamented with yellowish warts, cells without content; hyphal appressoria strongly lobed (3–6-lobate) in opposite pairs, unequal-sided, i.e., one appressorium of each pair with more lobes and larger than the other, 8–13.5 µm width; conidiophore-like hyphae outgrowths (special aerial hyphae) present, 221–408 µm in length, cylindrical and progressively tapering toward the apex, sinuous-helicoid below, multiseptate, arising from helicoid cells, basal cell (52.5–)75–86.5(–113) × 10–11.5(–13.5) µm, following cells (47.5–)61.5–74.5(–82.5) × (5.5–)7–9(–9.5) µm, apex rounded, walls slightly thickened and ornamented with small warts, ornamentation more prominent toward the base. Conidiophores arising from the upper surface of mother cells, erect, solitary, straight to slightly curved or twisted, cell walls ornamented with yellowish irregular warts, foot-cells cylindrical, straight to usually curved at the base, cells (30–)46.5–59.5(–76) × (9–)10–11.5 µm, with 1–3 following cells, equal or shorter than foot-cells, (10–)17.5–25.5(–57) × (5.5–)8.5–10(–19) µm, forming conidia singly; conidia ellipsoid-cylindrical to doliiform, (31–)36–40.5(–44) × (13–)16.5–18.5(–20) µm, conidial wall ornamented with yellowish warts

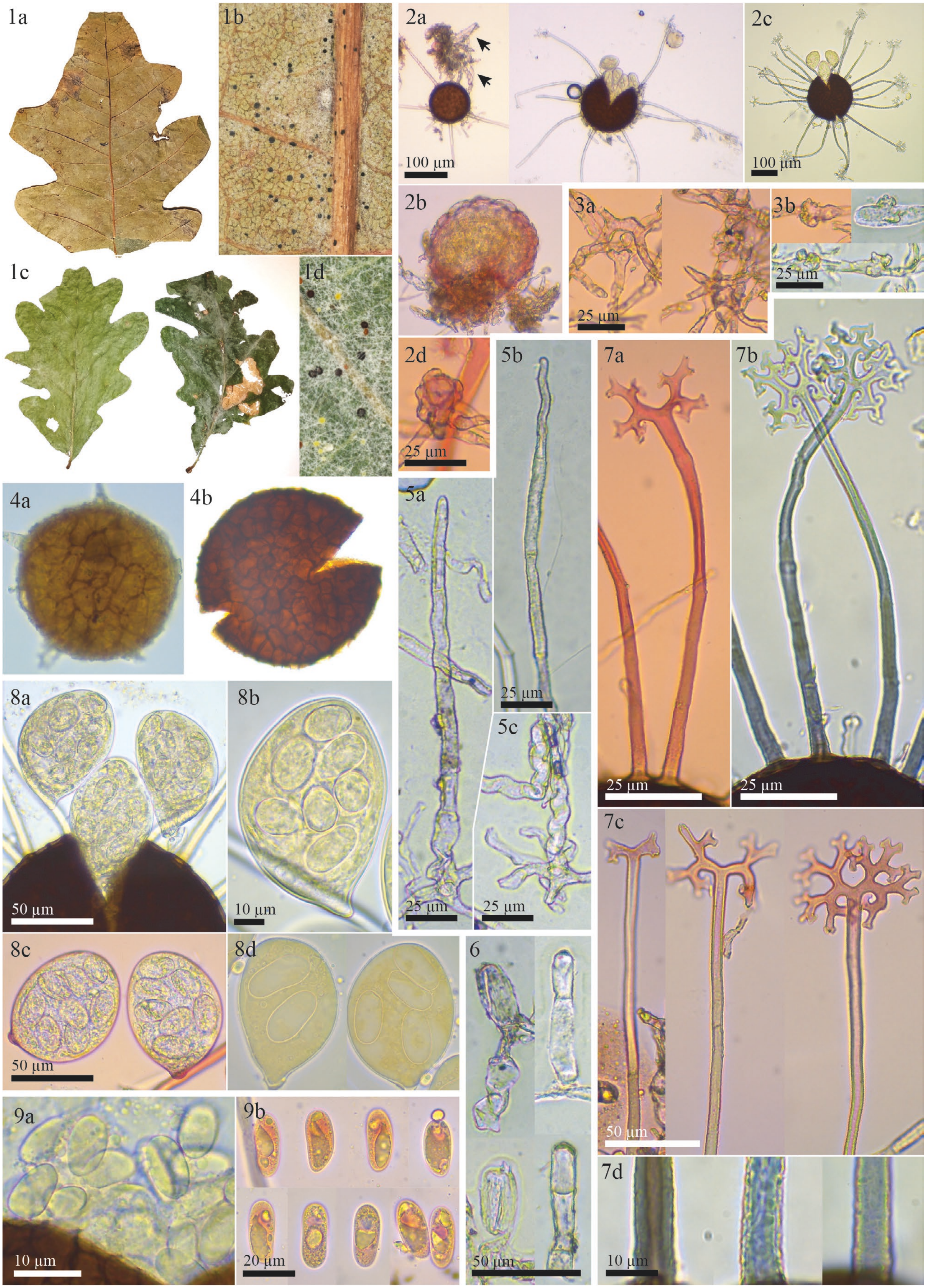

FIGURE 8 | Legend on next page.

FIGURE 8 | Morphological details of *Erysiphe pseudoextensa*: 1a-d. Infected leaves and close-up of mycelia with chasmothecia; 2a-d. Chasmothecial development, 2a. Chasmothecium with conidiophore-like hyphal outgrowth marked with black arrows, 2b. Immature chasmothecium, 2c. Chasmotheciium releasing asci, 2d. Chasmothecium initial; 3a-b. Hyphae with appressoria; 4a-b. Peridium; 5a-c. Mature conidiophore-like hyphal outgrowths; 6. Conidiophore development and conidia; 7a-d. Morphological variability of appendages, note the amyloid reaction in 7b, ornamented brownish amyloid appendage wall in 7d; 8a-d. Mature asci; 9a-b. Ascospores. Reagents: KOH = 2a, 2c, 4a-b, 5a-c, 6, 8a-b; KOH + CR = 2b, 2d, 3a-b, 7a, 7c, 8c, 9b; KOH + MLZ = 7b, 7d, 8d, 9a.

and transverse/longitudinal ridges when dry, ornamentation lost in Melzer's reagent and wall became amyloid, scattered lipidic guttules present; germ tubes subterminal, up to 53 μm long, showing a *Pseudoidium* type morphology. Chasmothecia scattered to subgregrarious, globose, 111–167 μm diam; peridium made of textura angularis-prismatica, cells (13.5–)17–20.5(–25) × (6.5–)9–12(–17) μm, thick-walled, irregularly rectangular-polygonal to sinuous (interlocking-shape), strongly yellow-brown to deep brown, cell walls darker, 1–2 μm thick, with connections among cells where the wall became thinner; appendages in the equatorial zone, 5–8(–9), slightly to medium curved, appendages (205–)252.5–295.5(–371) μm long and 6.5–7.5(–8.5) μm wide at the base, 1.8–2.2 times as long as the chasmothecial diam, hyaline, only light brownish close to the base, usually aseptate, rarely 1-septate close to the base, walls 1.5–2 μm width, irregularly ornamented with coarse warts, amyloid in MLZ after KOH-pretreatment, apices regularly 4–5(–7) times dichotomously branched, compact (branchlets of all levels short), sometimes branchings somewhat looser (primary or secondary branchlets somewhat elongated), tips of the ultimate branchlets recurved; asci 3–6 per chasmothecium, broad ellipsoid-ovoid to subglobose, (66–)68–72(–79) × (38–)43–50.5(–62) μm, (4–)6-spored, wall thickened up to 2 μm throughout, except for the apical oculus, base with a short stalk; ascospores ellipsoid-obovoid, (20–)22–24(–27) × (11)12–13.5(–14.5) μm, hyaline, thin-walled, smooth, 75%–95% filled with yellowish grey lipidic guttules.

Host range and distribution: on *Quercus* [*Quercus* sect. *Lobatae* subsect. *Phellos*] *laurifolia*, *Fagaceae*, North America (USA, Florida).

Notes. See discussion under *Erysiphe phellos*. The *E. quercus-laurifoliae* clade is highly supported in the concatenated tree, as well as in the *GADPH*, ITS and *RPB2* analyses.

Erysiphe schweinitziana M. Bradshaw, U. Braun, & Quijada **sp. nov**. Figure 11.

MycoBank, MB855718.

Etymology. The epithet commemorates L.D. von Schweinitz (1780–1835), the "patron saint" of North America mycology, who described the first North American oak powdery mildews.

Holotype. USA, Wisconsin, Dane County, Madison, *Quercus velutina*, 20 September 1944, *H.C. Greene* (FH01122145). Ex-holotype sequences: OR424979 (ITS); OR427487 (*CAM*); OR427573 (*GAPDH*); OR427657 (*GS*); OR427747 (*TUB*). Additional collections examined: See Table 1.

Description. Mycelium epiphyllous, white, growing loosely close to the adaxial leaf surface veins; hyphae sinuous and curled-helicoid, hyaline or slightly yellowish, cells (27–)32.5–46(–59) × 4–7 μm, irregularly branched, cell walls slightly ornamented with yellowish sparse warts, cells without content; hyphal appressoria lobed, in opposite pairs (2–6-lobate), 6–11 μm wide; conidiophore-like hypha outgrowths (special aerial hyphae) not observed. Conidiophores arising from the upper surface of the mother cells, straight to slightly curved, cell walls ornamented with yellowish irregular warts, foot-cells cylindrical, straight or slightly curved, up to 43 × 6.5 μm, with 2–3 following cells, shorter than the foot-cells, 17–36.5 × 7.5–9.5 μm; forming conidia singly; conidia ellipsoid-doliiform, 35–45.5 × 14.5–19 μm, conidial wall ornamented, less thickened in the poles, walls with yellowish warts and transverse/longitudinal ridges when dry, without lipidic guttules; germ tubes not observed. Chasmothecia hypophyllous, gregrarious, globose, 128–168 μm diam; peridium made of textura angularis-prismatica, cells (15–)17.5–21(–24.5) × (10–)13–16.5(–19) μm, thick-walled, irregularly rectangular-polygonal to sinuous-shaped (interlocking-shape), strong yellow-brown to deep brown, cell walls darker 1.1–2.5 μm thick, with connections among cells where the wall became thinner; appendages in the equatorial zone, 6–11 appendages, straight to slightly curved, (99–)105–146(–163) μm long and 7–10 μm wide at the base, relative length 0.7–1 times the chasmothecial diam, hyaline, only light brownish close to the base, aseptate, walls 1–3 μm thick, irregularly with long ridges, amyloid in MLZ after KOH-pretreatment, apices regularly 4–6 times dichotomously branched, tips of the ultimate branchlets recurved; asci 2–4 broad ellipsoid-ovoid, (42.5–)45.5–61(–65) × (33.5–)36.5–45(–50) μm, up to 6 asci per chasmothecium, wall thickened, up to 3.2 μm throughout, except for the apical oculus, base with a short stalk, 4–6-spored; ascospores ellipsoid-ovoid, (18.5–)21–26.5(–28.5) × (11.5–)13–17(–18.5) μm, hyaline, thin-walled, smooth, 50%–75% filled with yellowish grey lipidic guttules.

Host range and distribution: on *Quercus* [*Quercus* sect. *Lobatae* subsect. *Phellos*] (*marilandica*, *nigra*, *velutina*), *Fagaceae*, North America, USA (Kansas, North Carolina, Wisconsin).

Notes. Sequences retrieved from oak powdery mildews on *Quercus marilandica*, *Q. nigra* and *Q. velutina*, all belonging to *Quercus* subsect. *Phellos*, form a strongly supported species clade in all phylogenetic analyses (*CAM*, *GADPH*, ITS, *TUB*), except for *RPB2* which did not yield clear results. These results support this as an independent species.

Excluded and Doubtful Name

Erysiphe quercina Schwein., Trans. Amer. Philos. Soc., N. S., **4**: 270, 1834.

≡ *Microsphaera quercina* (Schwein.) Burrill, in Burrill & Earle, Bull. Illinois State Lab. Nat. Hist. **2**: 424, 1887.

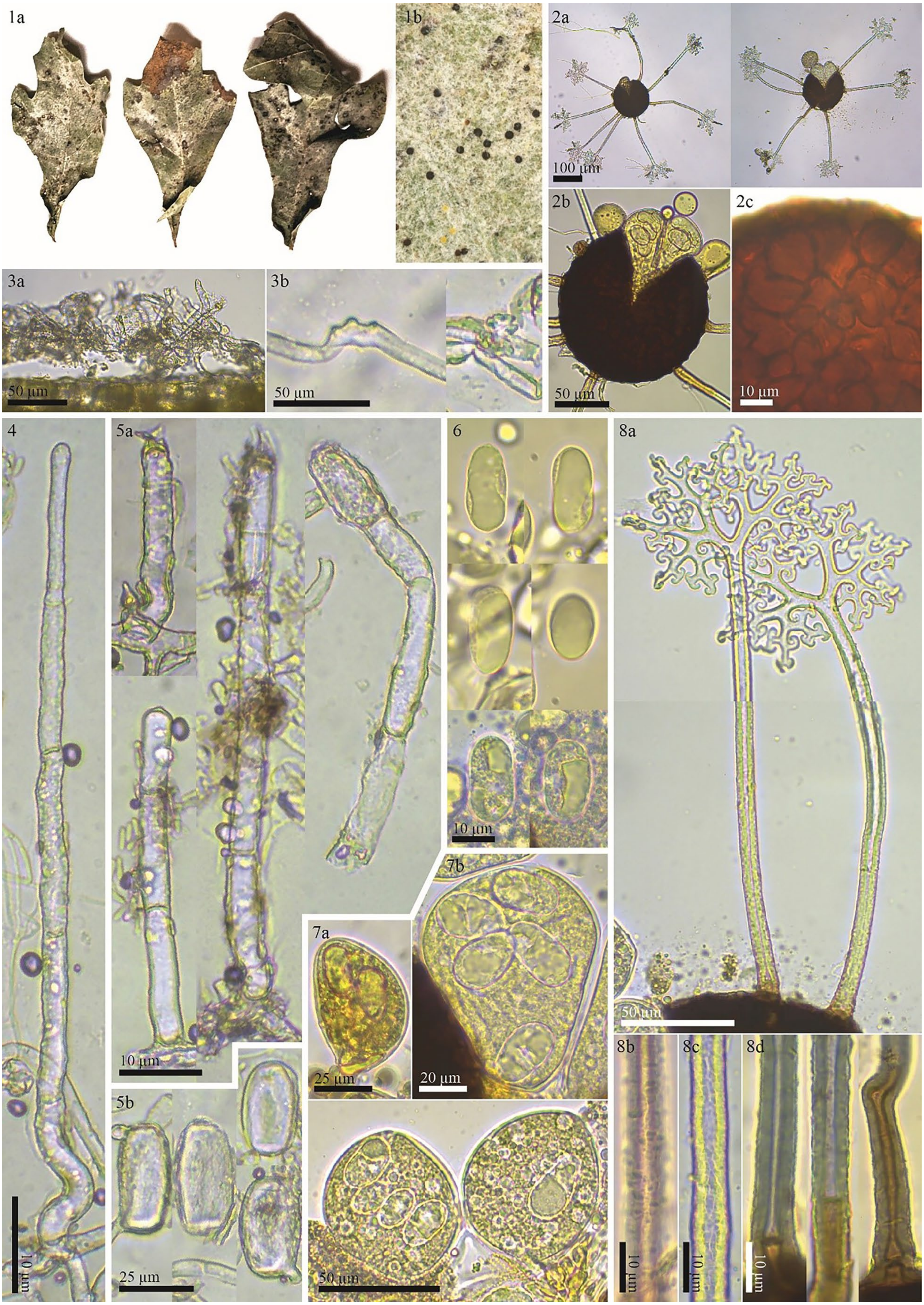

FIGURE 9 | Legend on next page.

FIGURE 9 | Morphological details of *Erysiphe quercophila*: 1a-b. Infected leaves and close-up of mycelia with and chasmothecia; 2a-c. Chasmothecia with mature appendages; 2c Peridium, close-up; 3a-b. Hyphae with appressoria; 4. Mature conidiophores-like hyphal outgrowth (special aerial hypha); 5a-b. Different developmental stages of conidiophores and conidia; 6. Morphological variability of ascospores; 7a-b. Immature and mature asci; 8a-d. Morphological variability of appendages, note the amyloid reaction in 8c-d, warted ornamented wall in CR in 8b. Reagents: KOH = 2a, 2c, 3a-b, 4, 5a-b, 8a, 8c; KOH + CR = 8b; KOH + MLZ = 2b, 6, 7a-b, 8d.

[Type: USA, Pennsylvania, on *Quercus* sp., undated, von Schweinitz (probably not preserved)].

Notes. The taxonomic status of this name is unclear. The original description (von Schweinitz, 1834) is not informative, and the host identity is unknown. The described scattered, minute ascomata and effuse, inconspicuous mycelium is in favour of what was later described as *M. abbreviata*. Type material could not be traced. This name had previously been applied broadly including all North American oak powdery mildews (Burrill and Earle 1887). Blumer (1933) argued that the application of this name is unclear and that it should be abandoned. Braun (1987) and Braun and Cook (2012) followed this proposal. However, previous practices of excluding species by classifying them simply as "dubious names" (nom. dub.) or "ambiguous names" (nom. ambig.), allowed by previous Codes, are now obsolete. Names have to be clarified by typifications, including neotypes, when necessary, or they have to be excluded by proposals to reject the names concerned. In any case, *E. quercina* should be rejected and its reintroduction is not advisable.

4 | Key to North American Species of *Erysiphe* Sect. *Microsphaera* on Oaks (*Quercus Species*) Based on Morphological Traits and Host Range

Whenever possible, identifications of *Erysiphe* species on oaks in North America should be confirmed by results of sequence analyses. Morphological identifications are difficult and require well-developed anamorphs and chasmothecia. Some groups of these species, such as *Erysiphe carolinensis*, *E. densissima* and *E. schweinitziana*, are morphologically very similar. Furthermore, examinations of North American *Erysiphe* species on oaks are still in a preliminary stage, so that the morphological variability of most of the species involved is insufficiently known.

1	Chasmothecia with 5–22 long, flexuous appendages, 2–6 times as long as the chasmothecial diam, on oaks of different sections of *Quercus*, widespread	*E. extensa*
1*	Chasmothecia with shorter appendages, 0.5–2 times as long as the chasmothecial diam	2
2	Chasmothecia rather small, 70–110 µm diam, usually ≤ 100 µm, with short appendages, 0.5–1(–1.25) the chasmothecial diam; on host species of *Quercus* [sect. *Quercus* subsect. *Prinoideae*] (*bicolor*, *bicolor* × *michauxii*, *macrocarpa*, *macrocarpa* × *bicolor* [= × *schuettei*], *muehlenbergii* [= *acuminata*], *prinoides*)	*E. abbreviata*
2*	Chasmothecia larger, 80–170 µm diam, Ø on average > 100 µm, when intermediate [chasmothecia (68–)73–124(–132) µm, appendages, (0.5–)0.8–1.5(–2.2) times as long as the chasmothecial diam] confined to hosts of *Quercus* subgen. *Quercus* sect. *Quercus* (*Q. macrocarpa*, *Q. robur*)	3
3	Introduced Eurasian species; special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] lacking	4
3*	North American species; special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] mostly developed	5
4	Appendages usually 1–1.5 times as long as the chasmothecial diam.; on *Quercus* spp., almost circumglobal, introduced in North America, on *Quercus robur*	*E. alphitoides*
4*	Appendages rather short, about as long as the chasmothecial diam. or somewhat shorter; on *Quercus* spp., introduced in North America, so far known from *Q. agrifolia*, *Q. robur*, and *Q. shumardii* (morphologically rather similar to *E. alphitoides* but genetically clearly distinct, identification by sequencing urgently recommended)	*E. quercicola*

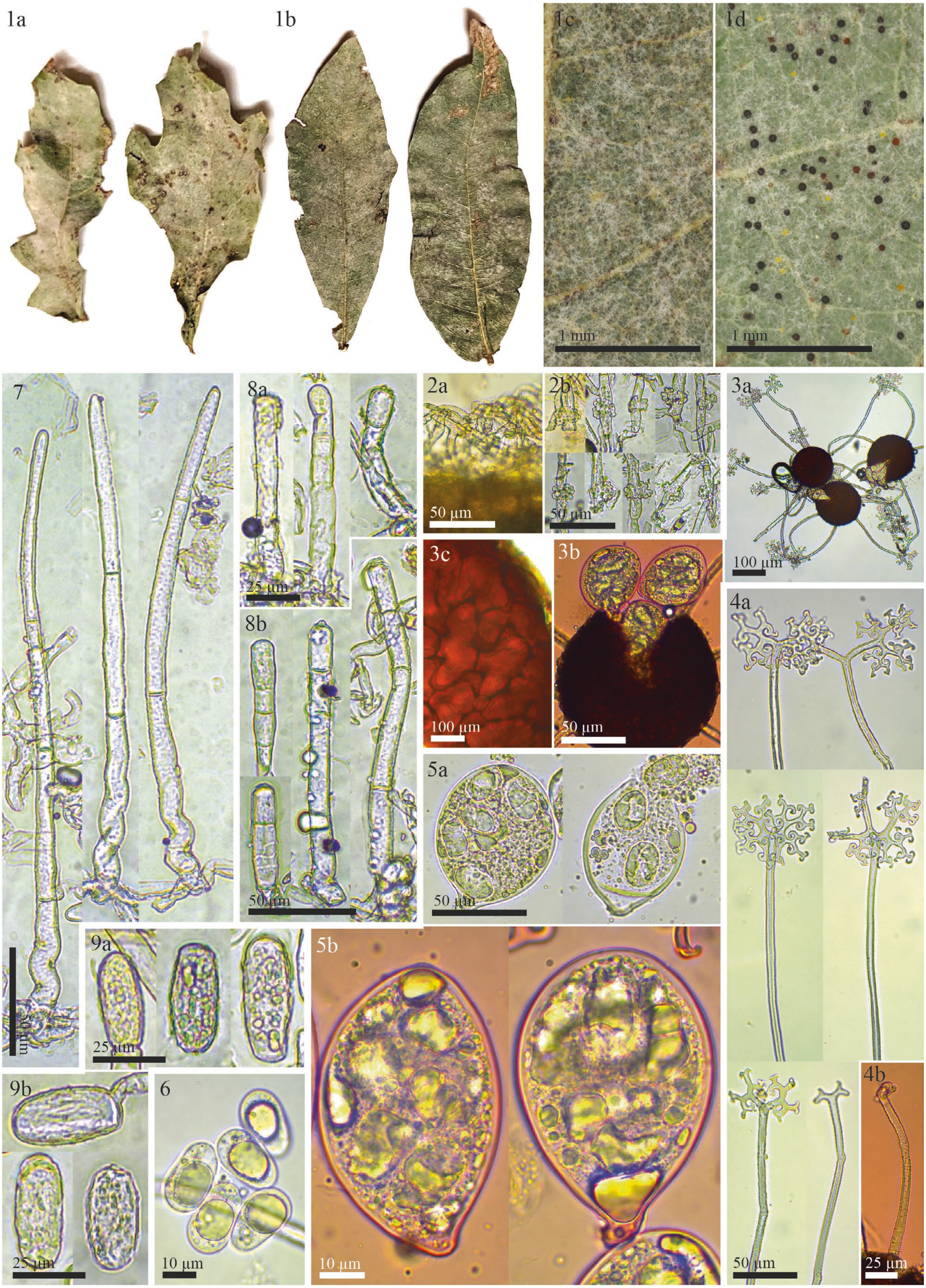

FIGURE 10 | Legend on next page.

FIGURE 10 | Morphological details of *Erysiphe quercus-laurifoliae*: 1a-d. Infected leaves and close-up of mycelia with and chasmothecia; 2a-b. Hyphae with appresoria; 3a-b. Details of chasmothecia and the peridium; 4a-b. Morphological variability of appendages, note the amyloid reaction in 4a; 5a-b. Mature asci; 6. Ascospores; 7. Mature conidiophore-like hyphal appendages; 8a-b. Different developmental stages of conidiophores; 9a-b. Mature conidia, note the warted ornamentation of the walls, guttules and the germination patterns. Reagents: KOH = 2b, 3a, 6, 7, 8a-b, 9a-b; KOH + CR = 3b-c, 4b, 5b; KOH + MLZ = 2a, 4a, 5a.

5	On white oaks (*Quercus* subgen. *Quercus* sect. *Quercus*)	6
5*	On red oaks (*Quercus* subgen. *Quercus* sect. *Lobatae*, subsect. *Phellos* and subsect. *Coccineae*)	9
6	Special aerial hyphae [conidiophore-like outgrowth of superficial hyphae] sinuous-helicoid to the upper half or even almost throughout; on *Q. macrocarpa* (may also infect introduced *Q. robur*)	*E. parmeleeana*
6*	Special aerial hyphae [conidiophore-like outgrowth of superficial hyphae] only sinuous-helicoid below	7
7	Chasmothecial appendages about 1–2 times as long as the chasmothecial diam; special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] rather long, 67–373(–481) μm long; on *Q. alba* (subsect. *Albae*), may possibly also infect introduced *Q. robur*	*E. pseudoextensa*
7*	Chasmothecial appendages shorter, about 0.5–1.5 times as long as the chasmothecial diam; special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] shorter, usually < 200 μm in length (on oaks of subsect. *Dumosae*)	8
8	Basal cell of the special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] 45–95 μm long; on *Q. gambelii*	*E. gambelii*
8*	Basal cell of the special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] shorter, 28–59 μm in length; on *Q. garryana*	*E. occidentalis*
9(5*)	Chasmothecial appendages long, 1–2 times as long as the chasmothecial diam	10
9*	Chasmothecial appendages short 0.5–1(–1.25) times the chasmothecial diam, usually about as long as the diam or shorter	12
10	Appendages 5–20(–28) per chasmothecium, terminal branching sometimes trichotomous; on *Q. falcata*, *Q. marilandica*, *Q. nigra*	*E. calocladophora*
10*	Appendages fewer, 4–10 per chasmothecium, trichotomous branching of the terminal part lacking	11
11	Chasmothecial appendages almost consistently two times as long as the chasmothecial diam; special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] well-developed, rather long, about 220–410 μm in length; conidia large, (31–)36–40.5(–44) × (13–)16.5–18.5(–20) μm, confined to *Quercus laurifolia*	*E. quercus-laurifoliae*
11*	Chasmothecia appendages 0.8–2.2 times as long as the chasmothecial diam; special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] sparingly developed, up to 42 μm long; conidia small, length < 20 μm, width < 10 μm; on *Q. nigra*	*E. quercophila*
12(9*)	Special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] not observed (lacking or perhaps very sparingly developed); on *Q. marilandica* and *Q. nigra*	*E. schweinitziana*

FIGURE 11 | Legend on next page.

FIGURE 11 | Morphological details of *Erysiphe schweinitziana*: 1a-b. Infected leaves and close-up of mycelia with and chasmothecia; 2a-d. Chasmothecia details, note in 2c the light erumpent brownish basal cells of appendages; 3. Hyphae with appresoria; 4. Conidiophores; 5. Conidia; 6a-d. Morphological variability of appendages, note the amyloid reaction in 6d, ornamented appendage wall in KOH in 6c; 7a-b. Mature asci with ascospores. Reagents: KOH = 2b, 2d, 3, 4, 5, 6a, 6c; KOH + CR = 2a, 6b, 7b; KOH + MLZ = 6d, 7a.

12*	Special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] well-developed	13
13	Special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] (108–)220–356(–390) µm long; conidia 25–45 µm long; on *Q. laevis* and *Q. falcata*	*E. carolinensis*
13*	Special aerial hyphae [conidiophore-like outgrowth of superficial hyphae with sinuous-helicoid base] shorter, up to 222 µm long; conidia c. 20–33 µm long; *Quercus marilandica* (probably also on *Quercus imbricaria*, *Q. rubra*, and *Q. velutina*)	*E. densissima*

5 | Discussion

A thorough understanding of the taxonomy and phylogeny of powdery mildews on *Quercus* is crucial due to the invasive nature of these organisms and the ecological damage they can inflict (Bebber, Holmes, and Gurr 2014; Bert et al. 2016; Kiss et al. 2020; Bradshaw et al. 2021). This is particularly significant for *Erysiphe* species infecting *Quercus*, which have spread across Europe over the past century, causing substantial ecological damage (Gross et al. 2021).

Salmon (1900) assigned all American oak powdery mildews to the misapplied name *Microsphaera alni* (now covering a wide range of species of *Erysiphe* sect. *Microsphaera*, including *M. calocladophora* and *M. extensa*, which he treated as varieties of *M. alni*). The first attempt to treat the American oak powdery mildew on a more refined morphological basis goes back to Blumer (1933). This was followed by Braun (1984, 1987), who applied a similar concept to Blumer's (1933), but with some modifications.

The present broad-scale approach to examine North American oak powdery mildews is the first attempt to treat this group employing phylogenetic methods. Initial analyses based on ITS data showed that this marker was not sufficient to resolve this complex of taxa, but that a multilocus approach was necessary. To overcome the shortcomings of ITS, *CAM*, *GAPDH*, *GS*, *RPB2* and *TUB* have been applied as additional markers. Analyses have been based on individual loci and concatenated analyses. Best resolutions of species clades were achieved in the concatenated analyses, but corresponding (supporting) results could also be obtained in single locus analyses, above all with *GAPDH*, *RPB2* and *TUB*. *CAM* turned out to be less useful. Some of the recognised species' clades are even well supported in the ITS tree alone.

Manos and Hipp (2021) summarised the most recent phylogenetic state of research on North American *Quercus* species, including next-generation DNA sequencing, and used this information in a formal classification, in which all subgenera, sections and subsections reflect well supported clades in the phylogenetic analyses. Their classification helped compare the evolutionary histories of American oak powdery mildews and their hosts. It became clear that there is a close co-evolution between North American oaks and their powdery mildew species, which is also reflected in the concatenated phylogenetic tree (Figure 1). *Erysiphe* species on hosts of sect. *Quercus* (white oaks), including *E. abbreviata*, *E. gambelii*, *E. occidentalis* and *E. pseudoextensa*, group together in the upper portion of the tree, whereas species on hosts of sect. *Lobatae* (red oaks), including *E. carolinensis*, *E. calocladophora*, *E. densissima*, *E. occidentalia*, *E. quercophila*, *E. quercus-laurifoliae* and *E. schweinitziana*, pertain to a group in the basal portion.

Ninety-two North American *Quercus* species are currently recognised. All of them belong to subgen. *Quercus*, which represents the North American oak clade. The North American oaks are placed in five sections (Manos and Hipp 2021). The North American *Erysiphe* species evolved in parallel with two sections, viz., sect. *Quercus* (white oaks) and sect. *Lobatae* (red oaks). Most species clades of oak powdery mildews are associated with specific subsections of *Quercus*: *E. abbreviata* is found on sect. *Quercus* subsect. *Prinoides*; *E. calocladophora* (emend.), *E. carolinensis*, *E. phellos*, *E. quercophila*, *E. quercus-laurifoliae*, and *E. schweinitziana* occur on sect. *Lobatae* subsect. *Phellos*; *E. gambelii* is on sect. *Quercus* subsect. *Dumosae*; *E. pseudoextensa* is on sect. *Quercus* subsect. *Albae*, *E. quercophila* on sect. *Lobatae* subsect. *Phellos*, *E. quercus-laurifoliae* on sect. *Lobatae* subsect. *Phellos*, and *E. schweinitziana* on sect. *Lobatae* subsect. *Phellos*. The host range of *E. densissima* comprises oaks of sect. *Lobatae* subsect. *Coccineae* and *Phellos*. *E. extensa* seems to have the widest host range covering hosts of different subsections. The association of *E. occidentalis* is not yet quite clear. The type host, *Quercus garryana*, is of sect. *Quercus* subsect. *Dumosae*, but the host of an additionally sequenced collection was identified as *Q. kelloggii* (sect. *Quercus* subsect. *Agrifoliae*). However, a possible misidentification of the host has be to taken into consideration.

During the course of the phylogenetic-taxonomic revision of North American *Erysiphe* species on oaks, a new morphological trait of the mycelium, produced by almost all species involved, has been detected. The superficial hyphae form special aerial hyphae, arising from the upper surface of the hyphal cells. These outgrowths are long, filiform, conidiophore-like and sinuous to spirally twisted in the lower portion, sometimes up to the upper half. These structures are characteristic for the North American oak powdery mildews, have yet to be observed in Asian or European *Erysiphe* spp. on *Quercus* spp. and thus undoubtedly constitute a synapomorphy. These special conidiophore-like outgrowths in North American *Erysiphe* species on oaks are comparable and probably homologous to the special aerial hyphae formed by species of the genus *Cystotheca*, which also occur on oak species (Braun and Cook 2012, 92; Bradshaw, Braun, and Pfister 2023b).

The highest degree of diversity of North America *Erysiphe* species on oaks occurs on *Quercus* sect. *Lobatae* subsect. *Phellos*, which seems to be a "hotspot" of diversification and radiation. This is interesting because the first phylogenetic split within the North America oak clade happened between sect. *Lobatae* and the remainder of the clade (Manos and Hipp 2021), suggesting that the *Erysiphe* species on oaks of subsect. *Phellos* are the most ancient species within this group. The phylogenetically most ancient powdery mildew species are found on sect. *Quercus*, *E. gambelii* and *E. occidentalis* on oaks of subsect. *Dumosae*, which represents the earliest branch within the phylogeny of white oaks.

Erysiphe species on North American oaks are common and widespread throughout the whole continent and have been reported on numerous *Quercus* species. However, only a limited number of collections on some of these oak species could be included in the present phylogenetic analyses. Therefore, the present studies is only the first step toward a phylogenetic-taxonomic revision of North American oak powdery mildews. The species diversity is probably much higher than reflected here, and the knowledge of the individual host ranges and distributions of the described species are still insufficient. To fill this gap, broad-scale investigations throughout North America are necessary. This must be accompanied by accurate identification of the hosts. The species diversity of oaks in North America is very high and proper identifications are challenging (Manos and Hipp 2021). Misidentifications have to be taken into consideration. In critical cases, it is recommendable to confirm the host identity by standard sequence analyses suitable for oaks. Oaks in Europe are less diverse, so that oak identification is easier in this region of the world, but the situation in Asia, most notably, eastern Asia, is complex and comparable with North America.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data associated with this research is available through GenBank.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.