



Description of three widespread new *Peronospora* species parasitising *Caryophyllales*

Man Mu^{1,2} · Young-Joon Choi³ · Marco Thines^{1,2}

Received: 31 July 2024 / Revised: 20 August 2024 / Accepted: 21 August 2024 / Published online: 28 September 2024
© The Author(s) 2024

Abstract

Downy mildews are cosmopolitan obligate biotrophic parasites of flowering plants. They are fungus-like eukaryotes of the kingdom *Straminipila*, and most species are highly specialised, often parasitising only a single host species. Due to the prevalence of a broad species concept before the advent of molecular phylogenetics and the paucity of differentiating characteristics in some groups, many widespread species are still undescribed. This is also the case for some downy mildews in the clade containing the type species of *Peronospora*, *Peronospora rumicis*. Spurred by the discovery of the undescribed species parasitising *Rumex acetosa* at the Blávík research station in East Iceland, three new widespread species of *Peronospora* are introduced in this article: *Peronospora blauvikensis* parasitic to *Rumex acetosa*, *P. boylei* parasitic to *Rumex thyrsiflorus*, and *P. spergulariae* parasitic to *Spergula marina*. As the species are morphologically highly similar, a set of diagnostic bases is given for each species, allowing a quick identification via molecular barcoding.

Keywords Cryptic species · Diagnostic bases · Downy mildews · Evolution · Phylogeny · *Peronospora effusa* · *Peronospora rumicis* · *Peronosporaceae* · *Polygonaceae* · Three new species

Introduction

The genus *Peronospora* is the largest of the genera of oomycetes, comprising more than 400 known species (Thines and Choi 2016). Similar to powdery mildews and rust fungi, downy mildews are obligate biotrophs but have evolved fungus-like characteristics independently from true fungi, belonging to the kingdom *Straminipila* (Beakes and Thines 2017). The genus *Peronospora* is cosmopolitan and has been reported from all continents except Antarctica. Despite being the most species-rich genus of oomycetes, only a fraction of the species in the

genus have likely been described so far (Thines and Choi 2016). Due to the pioneering work of Gäumann (e.g. 1918a, b, c, 1923), it became clear that the broad species concept used until then was no longer tenable, leading to the description of a plethora of new species in the years after that (e.g. Săvulescu and Rayss 1930; Gustavsson 1959). However, the increasingly influential publication of Yerkes and Shaw (1959), who advocated for a broad species concept, led to the decline of new species descriptions in *Peronospora* in the following years and the widespread belief that most *Peronospora* species were only specialised on the host genus or even host family level.

The first phylogenetic investigations with a larger array of downy mildews (Riethmüller et al. 2002; Voglmayr 2003) revealed that the taxonomic view of Gäumann (1923) mirrored the phylogenetic diversity of *Peronospora* much better and suggested that specialisation might be even higher than suggested by him. Over the past 20 years, host-specific evolutionary lineages were revealed for most groups of *Peronospora* (e.g. Choi et al. 2007, 2009, 2015; García-Blázquez et al. 2008; Thines et al. 2009, 2019; Thines and Kummer 2013; Voglmayr et al. 2014, Voglmayr and Korytnianska 2015; Mu et al. 2024a, b).

Due to implications for the security of the production of economically important hosts, species descriptions in the genus have mostly focussed on species infecting important

Section Editor: Tanay Bose

✉ Marco Thines
m.thines@thines-lab.eu

¹ Department of Biological Sciences, Institute of Ecology, Evolution and Diversity, Goethe University, Max-Von-Laue-Str, 13, 60439 Frankfurt Am Main, Germany

² Senckenberg Biodiversity and Climate Research Centre, Senckenberganlage 25, 60325 Frankfurt Am Main, Germany

³ Department of Biological Science, College of Ocean, Natural Sciences, and Engineering, Kunsan National University, 54150 Gunsan, South Korea

ornamentals (Thines et al. 2019; Hoffmeister et al. 2020; Mu et al. 2024a), culinary herbs (Thines et al. 2009; Choi et al. 2009), and crops (Voglmayr et al. 2014). While this prioritising is understandable, it neglects the vast majority of undescribed species. An example is the downy mildew specimens related to the type of the genus, *Peronospora rumicis*. While the phylogeny of the group was resolved almost a decade ago, with the important finding that downy mildew on spinach, *Peronospora effusa*, and downy mildew of beet, *Peronospora schachtii*, are distinct species (Choi et al. 2015), the undescribed lineages in that study have not been described to date, as the focus was laid on economically more important species. However, some of the undescribed species found in that study are rather widespread, so their description would be a significant contribution towards acknowledging the diversity of *Peronospora* and achieving a taxonomic framework reflecting evolutionary distinctiveness.

One of these species is the undescribed lineage parasitising *Rumex acetosa*, which is a common species throughout Europe. Its discovery near the research station Blávík in East Iceland has led to the recognition that it is high time to start with the description of the neglected diversity of downy mildews and thereby motivated this study to characterise and describe three widespread species of *Peronospora* in the clade containing also the downy mildew pathogens of beet and spinach.

Materials and methods

Plant and oomycete material

The plant specimens investigated are those previously used for the phylogenetic reconstruction of the *Peronospora rumicis* clade (Choi et al. 2015). To these, the plant specimen that triggered this study was added, which was collected in Iceland, Fáskrúðsfjörður, Blávík, on the 4th of July 2024 by Marco Thines (Table 1).

DNA extraction, PCR, and sequencing

DNA extraction, PCR, and sequencing for the specimens apart from the one newly sampled were described in Choi et al. (2015). The newly sampled specimen from Blávík, Iceland was extracted using the AnalyticJena Plant DNA extraction kit (AnalyticJena, Jena, Germany) according to the instructions of the manufacturer. The other steps followed Choi et al. (2015).

Phylogenetic analyses

The sequences obtained in this study were edited and assembled using Geneious v5.6 (Biomatters, Auckland, New

Zealand) and added to the dataset used in Choi et al. (2015). Alignments were done as described there, using Mafft v7 (Katoh and Standley 2013) and employing the Q-INSi algorithm (Katoh and Toh 2008). Phylogenetic analyses in this study followed the methods described by Mu et al. (2024a). In short, RAxML v7 (Stamatakis 2006) was used for Maximum Likelihood inference (ML), MEGA v7 (Kumar et al. 2016) for Minimum Evolution inference (ME), and MrBayes v3.1.6 (Ronquist et al. 2012) for Bayesian Inference (BI). The alignments used in this study have been deposited in Zenodo (concatenated alignment, <https://doi.org/10.5281/zenodo.12996089>; ITS alignment, <https://doi.org/10.5281/zenodo.12997752>; *HSP90* alignment, <https://doi.org/10.5281/zenodo.12996843>; *COX2*/cox2-1 spacer/*COX1* alignment, <https://doi.org/10.5281/zenodo.12997540>; *NAD1* alignment, <https://doi.org/10.5281/zenodo.12997959>; *RPS10* alignment, <https://doi.org/10.5281/zenodo.12998055>).

Morphology

Morphological characteristics of conidiophores, conidia, and oospores were investigated using dried herbarium specimens, as described in Mu et al. (2024a). Mycelia with reproductive structures was scraped from symptomatic plant tissue using a sterile scalpel into a drop of lactic acid solution on a slide. The sample was briefly heated, covered with a coverslip, and visualised using a Zeiss Imager M2 (Zeiss, Oberkochen, Germany) microscope with differential interference contrast and equipped with a 5-megapixel colour camera (M5c, Zeiss, Oberkochen, Germany). Measurements are reported as (minimum–) standard deviation towards the minimum–mean–standard deviation towards the maximum(–maximum). All measured values were rounded to the nearest 0.5 µm.

Results

Phylogenetic analyses

The phylogenetic relationships based on a concatenated alignment from two nuclear loci (ITS, *HSP90*) and four mitochondrial loci (*COX2*, cox2-1 spacer, *COX1*, *NAD1*, and *RPS10*) revealed no supported conflicting topologies with the trees based on individual genes. The concatenated alignment contained a total of 86 specimens, each with all loci amplified included, resulting in an overall alignment length of 4378 sites. Phylogenetic reconstructions using ME, ML, and BI methods showed no significant conflicts in the topologies. The tree from the ML inference is presented in Fig. 1 and is fully congruent with the tree previously reported by Choi et al. (2015). The specimen from Iceland was identical in all loci sequenced to

Table 1 GenBank accession numbers in this study

Species	Herb. No.	Host	Geographic origin	Year	GenBank accession number				Reference
					ITS	HSP90	COX2S/I	NADHI	RPS10
<i>Peronospora blauvikensis</i>	FR-0214054	<i>Rumex acetosa</i>	Iceland, Fáskrúðsfjörður	2024	PQ095908	PQ094561	PQ094562	PQ094563	PQ094564 This study
<i>Peronospora blauvikensis</i>	GLM75948	<i>Rumex acetosa</i>	Germany, Sachsen-Anhalt	2005	KP330806	KP330716	KP330626	KP330896	KP330986 Choi et al. 2015
<i>Peronospora blauvikensis</i>	WU32786	<i>Rumex arifolius</i>	Austria, Kärnten	2000	KP330818	KP330728	KP330638	KP330908	KP330998 Choi et al. 2015
<i>Peronospora blauvikensis</i>	UPS25	<i>Rumex acetosa</i>	Sweden, Härjedalen	1975	KP330807	KP330717	KP330627	KP330897	KP330987 Choi et al. 2015
<i>Peronospora blauvikensis</i>	WU34310	<i>Rumex acetosa</i>	Austria, Oberösterreich	2011	KP330808	KP330718	KP330628	KP330898	KP330988 Choi et al. 2015
<i>Peronospora blauvikensis</i>	WU33730	<i>Rumex acetosa</i>	Germany, Baden-Württemberg	2001	KP330813	KP330723	KP330633	KP330903	KP330993 Choi et al. 2015
<i>Peronospora blauvikensis</i>	WU34347	<i>Rumex acetosa</i>	England, South Yorkshire	2011	KP330810	KP330720	KP330630	KP330900	KP330990 Choi et al. 2015
<i>Peronospora blauvikensis</i>	WU35780	<i>Rumex arifolius</i>	Italy, Lombardia	2012	KP330817	KP330727	KP330637	KP330907	KP330997 Choi et al. 2015
<i>Peronospora blauvikensis</i>	BPI790739	<i>Rumex acetosa</i>	Finland, Nyländia	1970	KP330802	KP330712	KP330622	KP330892	KP330982 Choi et al. 2015
<i>Peronospora blauvikensis</i>	UPS27	<i>Rumex acetosa</i>	Finland, Nyländia	1960	KP330801	KP330711	KP330621	KP330891	KP330981 Choi et al. 2015
<i>Peronospora blauvikensis</i>	JKF0513	<i>Rumex arifolius</i>	Italy, Valle d'Aosta	2013	KP330815	KP330725	KP330635	KP330905	KP330995 Choi et al. 2015
<i>Peronospora blauvikensis</i>	HMR2940	<i>Rumex arifolius</i>	Romania, Harghita	1980	KP330816	KP330726	KP330636	KP330906	KP330996 Choi et al. 2015
<i>Peronospora blauvikensis</i>	WU22925	<i>Rumex acetosa</i>	Austria, Oberösterreich	2001	KP330812	KP330722	KP330632	KP330902	KP330992 Choi et al. 2015
<i>Peronospora blauvikensis</i>	WU33899	<i>Rumex acetosa</i>	Austria, Wien	2004	KP330809	KP330719	KP330629	KP330899	KP330989 Choi et al. 2015
<i>Peronospora blauvikensis</i>	GLM62941	<i>Rumex acetosa</i>	Germany, Sachsen-Anhalt	2004	KP330803	KP330713	KP330623	KP330893	KP330983 Choi et al. 2015
<i>Peronospora rumicis</i>	BPI790753	<i>Rumex acetosella</i>	Denmark, Ulvshale	1913	KP330814	KP330724	KP330634	KP330904	KP330994 Choi et al. 2015
<i>Peronospora boylei</i> s.l.	JKF0051	<i>Rumex aff. thyrsiflorus</i>	Germany, Niedersachsen	2009	KP330824	KP330734	KP330644	KP330914	KP331004 Choi et al. 2015
<i>Peronospora boylei</i> s.l.	GLM74313	<i>Rumex aff. thyrsiflorus</i>	Germany, Sachsen	2003	KP330819	KP330729	KP330639	KP330909	KP330999 Choi et al. 2015
<i>Peronospora boylei</i> s.l.	GLM74510	<i>Rumex aff. thyrsiflorus</i>	Germany, Sachsen-Anhalt	2003	KP330823	KP330733	KP330643	KP330913	KP331003 Choi et al. 2015
<i>Peronospora boylei</i>	GLM73428	<i>Rumex thyrsiflorus</i>	Germany, Sachsen-Anhalt	2003	KP330821	KP330731	KP330641	KP330911	KP331001 Choi et al. 2015
<i>Peronospora boylei</i>	GLM64100	<i>Rumex thyrsiflorus</i>	Germany, Sachsen-Anhalt	2004	KP330820	KP330730	KP330640	KP330910	KP331000 Choi et al. 2015
<i>Peronospora boylei</i>	WU35760	<i>Rumex thyrsiflorus</i>	Austria, Niederösterreich	2012	KP330811	KP330721	KP330631	KP330901	KP330991 Choi et al. 2015
<i>Peronospora boylei</i>	GLM73434	<i>Rumex thyrsiflorus</i>	Germany, Sachsen-Anhalt	2003	KP330822	KP330732	KP330642	KP330912	KP331002 Choi et al. 2015
<i>Peronospora boylei</i>	GLM90812	<i>Rumex thyrsiflorus</i>	Germany, Sachsen	2008	KP330804	KP330714	KP330624	KP330894	KP330984 Choi et al. 2015
<i>Peronospora boylei</i>	GLM90995	<i>Rumex thyrsiflorus</i>	Germany, Sachsen	2008	KP330805	KP330715	KP330625	KP330895	KP330985 Choi et al. 2015
<i>Peronospora sp.</i>	VK 0471/2	<i>Rumex spinosus</i> (syn. <i>Emex spinosa</i>)	Greece, Tsambika	2011	KP330799	KP330709	KP330619	KP330889	KP330979 Choi et al. 2015
<i>Peronospora sp.</i>	VK 0471/1	<i>Rumex spinosus</i> (syn. <i>Emex spinosa</i>)	Greece, Tsambika	2012	KP330798	KP330708	KP330618	KP330888	KP330978 Choi et al. 2015
<i>Peronospora schachtii</i>	DML17	<i>Beta vulgaris</i>	USA, California	2012	KP330797	KP330707	KP330617	KP330887	KP330977 Choi et al. 2015
<i>Peronospora schachtii</i>	DML4	<i>Beta vulgaris</i>	USA, California	2012	KP330790	KP330700	KP330610	KP330880	KP330970 Choi et al. 2015
<i>Peronospora schachtii</i>	DML38	<i>Beta vulgaris</i>	USA, California	2012	KP330791	KP330701	KP330611	KP330881	KP330971 Choi et al. 2015
<i>Peronospora schachtii</i>	BPI790781	<i>Beta vulgaris</i>	unknown	1931	KP330796	KP330706	KP330616	KP330886	KP330976 Choi et al. 2015
<i>Peronospora schachtii</i>	DML3	<i>Beta vulgaris</i>	USA, California	2012	KP330789	KP330699	KP330609	KP330879	KP330969 Choi et al. 2015

Table 1 (continued)

Species	Herb. No.	Host	Geographic origin	Year	GenBank accession number					Reference
					ITS	HSP90	COX2/S/I	NADHI	RPS10	
<i>Peronospora schachtii</i>	HMAS57033	<i>Beta vulgaris</i>	China, Yunnan	1979	KP330794	KP330704	KP330614	KP330884	KP330974	Choi et al. 2015
<i>Peronospora schachtii</i>	HMAS57030	<i>Beta vulgaris</i>	China, Sichuan	1979	KP330793	KP330703	KP330613	KP330883	KP330973	Choi et al. 2015
<i>Peronospora schachtii</i>	BPI790777	<i>Beta vulgaris</i>	Germany, Nossen	1888	KP330795	KP330705	KP330615	KP330885	KP330975	Choi et al. 2015
<i>Peronospora schachtii</i>	RD864	<i>Beta vulgaris</i>	Argentina, Bahía Blanca	1991	KP330792	KP330702	KP330612	KP330882	KP330972	Choi et al. 2015
<i>Peronospora lepigoni</i>	GLM77927	<i>Spergularia rubra</i>	Germany, Sachsen	1998	KP330838	KP330748	KP330658	KP330928	KP331018	Choi et al. 2015
<i>Peronospora lepigoni</i>	GLM68688	<i>Spergularia rubra</i>	Germany, Sachsen-Anhalt	1991	KP330840	KP330750	KP330660	KP330930	KP331020	Choi et al. 2015
<i>Peronospora lepigoni</i>	GLM76298	<i>Spergularia rubra</i>	Germany, Sachsen-Anhalt	2002	KP330842	KP330752	KP330662	KP330932	KP331022	Choi et al. 2015
<i>Peronospora lepigoni</i>	GLM75718	<i>Spergularia rubra</i>	Germany, Sachsen	2005	KP330837	KP330747	KP330657	KP330927	KP331017	Choi et al. 2015
<i>Peronospora lepigoni</i>	GLM64180	<i>Spergularia rubra</i>	Germany, Sachsen-Anhalt	2004	KP330839	KP330749	KP330659	KP330929	KP331019	Choi et al. 2015
<i>Peronospora lepigoni</i>	GLM73623	<i>Spergularia rubra</i>	Germany, Sachsen-Anhalt	2001	KP330841	KP330751	KP330661	KP330931	KP331021	Choi et al. 2015
<i>Peronospora spergulariae</i>	GLM73809	<i>Spergularia marina</i>	Germany, Sachsen-Anhalt	2001	KP330834	KP330744	KP330654	KP330924	KP331014	Choi et al. 2015
<i>Peronospora spergulariae</i>	GLM75894	<i>Spergularia marina</i>	Germany, Sachsen-Anhalt	2005	KP330835	KP330745	KP330655	KP330925	KP331015	Choi et al. 2015
<i>Peronospora spergulariae</i>	WU33808	<i>Spergularia marina</i>	Austria, Burgenland	2001	KP330836	KP330746	KP330656	KP330926	KP331016	Choi et al. 2015
s.l.										
<i>Peronospora polycarponis</i>	WU33676	<i>Polycarpon diphyllum</i>	France, Montpellier	2001	KP330800	KP330710	KP330620	KP330890	KP330980	Choi et al. 2015
<i>Peronospora obovata</i>	WU32858	<i>Spergula arvensis</i>	Germany, Sachsen-Anhalt	2002	KP330832	KP330742	KP330652	KP330922	KP331012	Choi et al. 2015
<i>Peronospora obovata</i>	WU22914	<i>Spergula arvensis</i>	Austria, Oberösterreich	2000	KP330833	KP330743	KP330653	KP330923	KP331013	Choi et al. 2015
<i>Peronospora obovata</i>	WU34372	<i>Spergula arvensis</i>	Austria, Niederösterreich	2011	KP330831	KP330741	KP330651	KP330921	KP331011	Choi et al. 2015
<i>Peronospora obovata</i>	GLM73791	<i>Spergula arvensis</i>	Germany, Sachsen-Anhalt	2001	KP330826	KP330736	KP330646	KP330916	KP331006	Choi et al. 2015
<i>Peronospora obovata</i>	GLM76717	<i>Spergula arvensis</i>	Germany, Sachsen-Anhalt	2002	KP330829	KP330739	KP330649	KP330919	KP331009	Choi et al. 2015
<i>Peronospora obovata</i>	GLM76830	<i>Spergula arvensis</i>	Germany, Sachsen-Anhalt	2000	KP330830	KP330740	KP330650	KP330920	KP331010	Choi et al. 2015
<i>Peronospora obovata</i>	GLM73399	<i>Spergula arvensis</i>	Germany, Sachsen-Anhalt	2003	KP330825	KP330735	KP330645	KP330915	KP331005	Choi et al. 2015
<i>Peronospora effusa</i>	KUS-F15680	<i>Spinacia oleracea</i>	Germany, Sachsen-Anhalt	1999	KP330852	KP330762	KP330672	KP330942	KP331032	Choi et al. 2015
<i>Peronospora effusa</i>	BPI788361	<i>Spinacia oleracea</i>	Korea, Namyangju	1932	KP330866	KP330776	KP330686	KP330956	KP331046	Choi et al. 2015
<i>Peronospora effusa</i>	BPI791055	<i>Spinacia oleracea</i>	USA, Virginia	1943	KP330865	KP330775	KP330685	KP330955	KP331045	Choi et al. 2015
<i>Peronospora effusa</i>	UPS20	<i>Spinacia oleracea</i>	USA, Oklahoma	1896	KP330862	KP330772	KP330682	KP330952	KP331042	Choi et al. 2015
<i>Peronospora effusa</i>	DML40	<i>Spinacia oleracea</i>	USA, Kingston	2012	KP330860	KP330770	KP330680	KP330950	KP331040	Choi et al. 2015
<i>Peronospora effusa</i>	DML5	<i>Spinacia oleracea</i>	USA, California	2012	KP330861	KP330771	KP330681	KP330951	KP331041	Choi et al. 2015
<i>Peronospora effusa</i>	DM65	<i>Spinacia oleracea</i>	Japan, Shiga	2000	KP330851	KP330761	KP330671	KP330941	KP331031	Choi et al. 2015
<i>Peronospora effusa</i>	DM22	<i>Spinacia oleracea</i>	Japan, Gifu	unknown	KP330848	KP330758	KP330668	KP330938	KP331028	Choi et al. 2015
<i>Peronospora effusa</i>	BPI788300	<i>Spinacia oleracea</i>	USA, Maryland	1958	KP330863	KP330773	KP330683	KP330953	KP331043	Choi et al. 2015
<i>Peronospora effusa</i>	BPI788309	<i>Spinacia oleracea</i>	USA, Maryland	1951	KP330864	KP330774	KP330684	KP330954	KP331044	Choi et al. 2015
<i>Peronospora effusa</i>	BPI788314	<i>Spinacia oleracea</i>	Mexico, Nogales	1949	KP330856	KP330766	KP330676	KP330946	KP331036	Choi et al. 2015
<i>Peronospora effusa</i>	BPI788308	<i>Spinacia oleracea</i>	Mexico, Nogales	1953	KP330855	KP330765	KP330675	KP330945	KP331035	Choi et al. 2015

Table 1 (continued)

Species	Herb. No.	Host	Geographic origin	Year	GenBank accession number					Reference
					ITS	HSP90	COX2S/I	NADH1	RPS10	
<i>Peronospora effusa</i>	UPS19	<i>Spinacia oleracea</i>	Sweden, Gästrikland	1942	KP330857	KP330767	KP330677	KP330947	KP331037	Choi et al. 2015
<i>Peronospora effusa</i>	DML39	<i>Spinacia oleracea</i>	USA, California	2012	KP330859	KP330769	KP330679	KP330949	KP331039	Choi et al. 2015
<i>Peronospora effusa</i>	KUS-F18808	<i>Spinacia oleracea</i>	Korea, Seoul	2001	KP330853	KP330763	KP330673	KP330943	KP331033	Choi et al. 2015
<i>Peronospora effusa</i>	DM34	<i>Spinacia oleracea</i>	Japan, Shiga	unknown	KP330850	KP330760	KP330670	KP330940	KP331030	Choi et al. 2015
<i>Peronospora effusa</i>	VPRI22523	<i>Spinacia oleracea</i>	Australia, Turna	2000	KP330844	KP330754	KP330664	KP330934	KP331024	Choi et al. 2015
<i>Peronospora effusa</i>	VPRI31625	<i>Spinacia oleracea</i>	Australia, V.I.C.	2003	KP330845	KP330755	KP330665	KP330935	KP331025	Choi et al. 2015
<i>Peronospora effusa</i>	DM81	<i>Spinacia oleracea</i>	Japan, Hokkaido	2004	KP330849	KP330759	KP330669	KP330939	KP331029	Choi et al. 2015
<i>Peronospora effusa</i>	KUS-F18809	<i>Spinacia oleracea</i>	Korea, Sinan	2001	KP330854	KP330764	KP330674	KP330944	KP331034	Choi et al. 2015
<i>Peronospora effusa</i>	HMAS57074	<i>Spinacia oleracea</i>	China, Sichuan	1958	KP330846	KP330756	KP330666	KP330936	KP331026	Choi et al. 2015
<i>Peronospora effusa</i>	DM68	<i>Spinacia oleracea</i>	Japan, Fukui	2000	KP330847	KP330757	KP330667	KP330937	KP331027	Choi et al. 2015
<i>Peronospora effusa</i>	DML2	<i>Spinacia oleracea</i>	USA, California	2012	KP330858	KP330768	KP330678	KP330948	KP331038	Choi et al. 2015
<i>Peronospora effusa</i>	VPRI30202	<i>Spinacia oleracea</i>	Australia, Leppington	2002	KP330843	KP330753	KP330663	KP330933	KP331023	Choi et al. 2015
<i>Peronospora littoralis</i>	BPI789214	<i>Arriplex littoralis</i>	Sweden, Oland	1959	KP330778	KP330688	KP330598	KP330868	KP330958	Choi et al. 2015
<i>Peronospora atriplicis-hastatae</i>	JK-F0359	<i>Arriplex prostrata</i>	Germany, Schleswig-Holstein	2012	KP330783	KP330693	KP330603	KP330873	KP330963	Choi et al. 2015
<i>Peronospora atriplicis-hastatae</i>	GLM73408	<i>Arriplex prostrata</i>	Germany, Sachsen-Anhalt	2003	KP330784	KP330694	KP330604	KP330874	KP330964	Choi et al. 2015
<i>Peronospora atriplicis-hastatae</i>	GLM67010	<i>Arriplex prostrata</i>	Germany, Sachsen-Anhalt	1990	KP330785	KP330695	KP330605	KP330875	KP330965	Choi et al. 2015
<i>Peronospora minor</i>	UPS29	<i>Arriplex patula</i>	Sweden, Västergötland	1962	KP330779	KP330689	KP330599	KP330869	KP330959	Choi et al. 2015
<i>Peronospora minor</i>	GLM68024	<i>Arriplex patula</i>	Germany, Sachsen	1993	KP330780	KP330690	KP330600	KP330870	KP330960	Choi et al. 2015
<i>Peronospora minor</i>	GLM77764	<i>Arriplex patula</i>	Germany, Sachsen	1999	KP330781	KP330691	KP330601	KP330871	KP330961	Choi et al. 2015
<i>Peronospora minor</i>	GLM73462	<i>Arriplex patula</i>	Germany, Sachsen-Anhalt	2003	KP330782	KP330692	KP330602	KP330872	KP330962	Choi et al. 2015
<i>Peronospora boni-henrici</i>	GLM51002	<i>Chenopodium bonus-henricus</i>	Austria, Tirol	1991	KP330867	KP330777	KP330687	KP330957	KP331047	Choi et al. 2015

ME/ML/BI

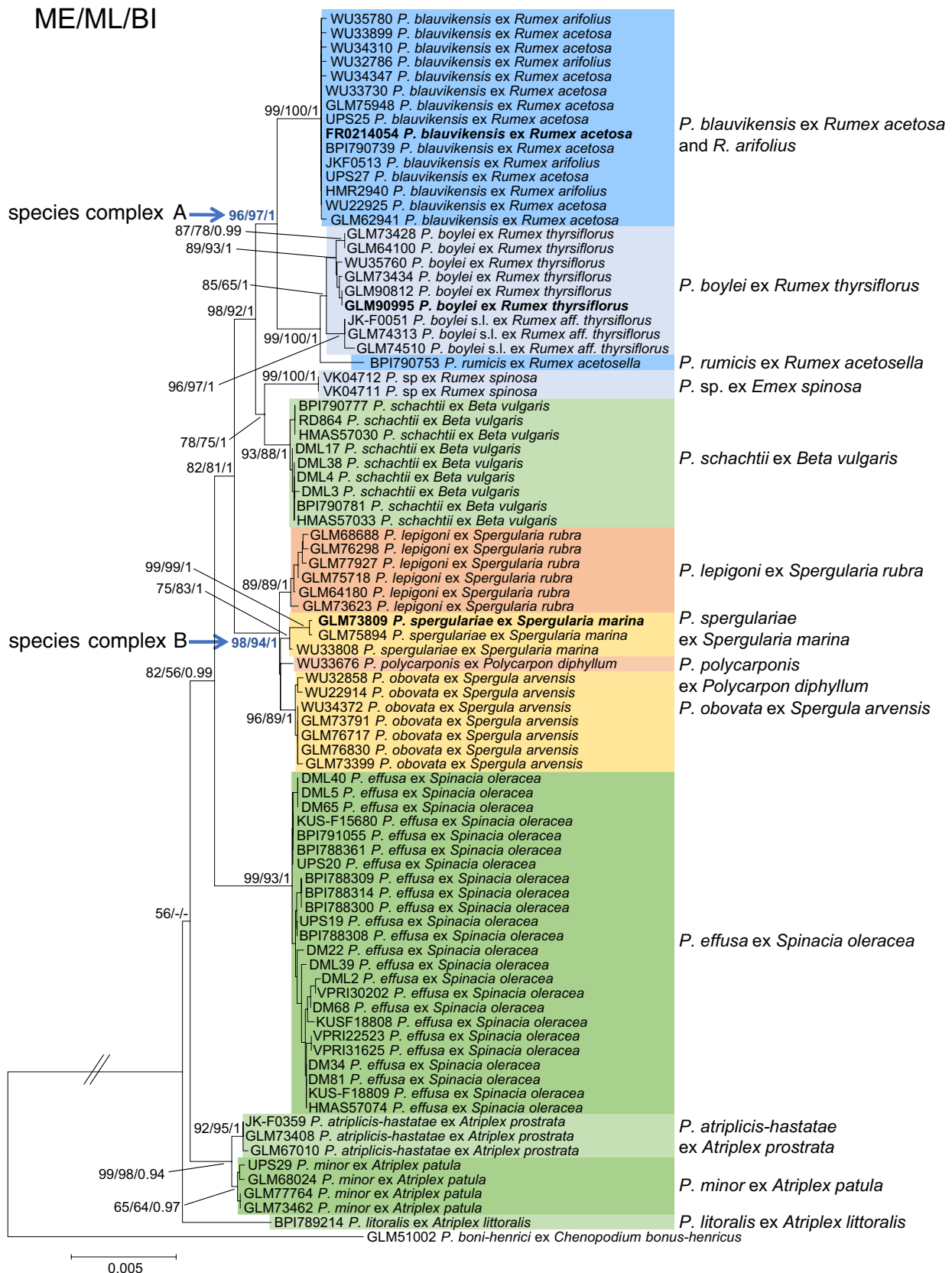


Fig. 1 Phylogenetic tree inferred from Maximum Likelihood analysis of a concatenated alignment of two nuclear loci (ITS and *HSP90*) and five mitochondrial (*COX2*, *cox2/1spacer*, *COX1*, *NAD1*, *RPS10*). Bootstrapping support values of Maximum Likelihood and Minimum Evolution methods, as well as Bayesian posterior probabilities are indicated along branches, in the respective order. The scale bar denotes the number of nucleotide substitutions per site

specimens from Austria, Finland, Germany, Romania, and Sweden. The divergence within the group of *Peronospora* specimens on *Rumex acetosa* was very low, with more than 99.9% identity. The clade with these specimens received high to maximum support in all analyses and was resolved as the sister to the other clades of species complex A (Fig. 1). The second subclade of species complex A also received high to maximum support in all analyses. In line with the high host specificity of *Peronospora* within this subclade, *Peronospora rumicis* on the type host *Rumex acetosella* was set apart from *Peronospora* on *Rumex thrysiflorus*. Specimens from *Rumex thrysiflorus* were divided into two groups, which were clustered together with low (ML, ME) to maximum (BI) support. Also within species complex B, specimens grouped by host species, and the specimens of *Peronospora* from *Spergula arvensis*, *Spergularia marina*, and *Spergularia rubra* were each grouped with maximum support in BI, moderate to high support in ME, and low to moderate support in ML. Higher-level relationships among the specimens could mostly not be resolved, in line with the results of Choi et al. (2015).

Morphology

The morphology of the species within the *Peronospora rumicis* clade is rather uniform, as can be seen from the measurements detailed in Table 2 and Figs. 2, 3 and 4. All species in the two species complexes investigated had sporangiophores of short to intermediate length, averaging between 200 and 300 µm. The average conidial length varied from 27 to 29 µm and the conidial breadth from 19 to 21 µm and the length/breadth ratios from 1.31 to 1.48. Thus, it is almost impossible to distinguish the species investigated in this study from each other and several other species in the *Peronospora rumicis* clade based on their morphology. Consequently, we refrained from doing detailed morphological comparisons but only give our measurements as a reference for future studies (see also the discussion section) and provide diagnostic alignment positions for molecular identification by barcoding.

Taxonomy

Typification of *Peronospora rumicis*

When Corda (1837) described *Peronospora rumicis*, he provided a single illustration for the species in plate 5,

Fig. 273. Thus, this figure could be considered to be the type of the species (ICNafp, Art. 9.1, Note 1; Turland et al. 2018). However, as he did not explicitly state that the figure would be the type and because additional information, such as the colour of the sporangia and the sampling location, are given in the description, it needs to be concluded that he based those observations on a specimen he had in his hands.

In 1991, Constantinescu (1991) gave the specimen PRM 155590 as the type (cited as “holotype”) of the species and stated the host to be *Rumex acetosella*, in line with Corda (1837). Some years later, Constantinescu (in Constantinescu and Fatehi 2002) changed his previous opinion and stated that the host was *Rumex acetosa* instead, without giving a rationale for this. A re-examination of the specimen PRM 155590 from the collection of Corda showed that the host is undoubtedly *Rumex acetosella*, as the ochrea of the herbarised plant with downy mildew infection is white, with entire margins and not tightly attached to the stem. In addition, the lower stem leaves are stalked and not sitting directly on the stem, and do not show the characteristic arrow-shaped base of *Rumex acetosa*. Furthermore, the upper stem leaves are widest above the median, typical for *Rumex acetosella* (Fig. 5).

The type designation of Constantinescu (1991) would need to be followed if it is the earliest type designation compliant with the ICNafp. However, the specimen preserved as PRM 155590 cannot be the material Corda based the description upon, as the developmental stage of that specimen is advanced and the host plant is already forming nuts. Even if the drawing in plate 5, Fig. 273 is sketchy for both the host and the pathogen, it seems obvious that an earlier developmental stage of the host is depicted, suggesting that PRM 155590 had been collected by Corda at a later date, even if probably from the same location. Thus, while it is authentic material investigated and identified by Corda, it cannot be considered to be part of the material that he based his description on. Therefore, the type designation by Constantinescu (1991) cannot be upheld and would need to be considered a neotype, which is not compliant with the current ICNafp, as the illustration needs to be considered part of the original material (Art. 9.2, Note 2a).

While there is no reason to doubt that Corda used a specimen from *Rumex acetosella* to describe *Peronospora rumicis*, it is likely that the original specimen is lost or destroyed, as no additional specimens were found in PRM that could have been the specimen on which Corda based his description. However, the illustration of Corda (1837) remains as original material.

To resolve this uncertainty and to stabilise the taxonomy of *Peronospora rumicis* in the sense of Corda (1837), a lectotype and an epitype are designated here. Even though the

Table 2 Morphological details for the species of *Peronospora* described in this study

Species	Host	Conidiophores (<i>n</i> = 50)		Trunks (<i>n</i> = 50)		Ratio conidiophore/ trunk length	Branch- ing orders	Ultimate branchlets (UB) (<i>n</i> = 50)				Conidia (<i>n</i> = 50)			
		Length (μm)	Base (μm)	Length (μm)	Breadth (μm)			Length of the longer UB (μm)	Length of the shorter UB (μm)	Longer/ shorter ratio	Breadth (μm)	Length (μm)	Breadth (μm)	Length-to- breadth ratio	
<i>Peronospora blauvikensis</i>	<i>Rumex acetosa</i>	(151–)	5–11–16	(68–)90–143– 195(–258)	(3–)7–9– 10.5(–12.5)	(1.1–)1.5–1.9– 2.2(–3.3)	3–8	(7–)9–11.5– 13.5(–15)	(6–)8–10–12 (–15)	(1.00–)1.03– 1.11–1.20 (–1.28)	(2)2.5–3– 3.5(–4)	(23.5–)25– 27–29.5 (–31)	(17–)19–21– 23(–24.5)	(1.01–)1.17– 1.31–1.45 (–1.52)	
		174–261– 348(–502)													
<i>Peronospora boylei</i>	<i>Rumex thyrsiflorus</i>	(179–)199– 240–282 (–338)	9–13–18	(89–)107–131– 155(–167)	(5.5–)7.5–9– 10.5(–11.5)	(1.6–)1.7–1.9– 2.0(–2.1)	4–7	(7–)8.5–11.5– 14(–17.5)	(6–)7–9–11 (–14.5)	(1.00–)1.10– 1.29–1.48 (–1.73)	(2.5–)2.5–3– 3.5(–4)	(19.5–)24.5– 27–29.5 (–34)	(15–)17–19– 21(–24.5)	(1.19–)1.31– 1.42–1.53 (–1.67)	
<i>Peronospora spergulariae</i>	<i>Spergularia marina</i>	(127–)158– 200–241 (–279)	11–14–18	(54–)78–102– 126(–145)	(8–)9–10– 11(–11.5)	(1.4–)1.6–2.0– 2.4(–2.8)	3–6	(5–)7.5–9.5– 12(–14)	(3.5–)6–8– 10(–12)	(1.01–)1.09– 1.24–1.39 (–1.56)	(1.5–)2–2.5– 3.5(–3.5)	(24–)26.5– 29–31.5 (–33.21)	(17.5–)18.5– 20–21.5 (–23)	(1.20–)1.34– 1.45–1.56 (–1.61)	

figure of Corda is variously cited, e.g. in Dick (2001), to our knowledge, there is no unambiguous type designation for the figure of Corda (1837). Thus, the conidiophore in Fig. 273 of plate 5 of Corda (Icon. fung. 1 (Prague), agreeing to the description on page 20 of the same work from 1837) is designated as a lectotype here (MBT 10021875). Even though the entire drawing represents the original material, the restriction to the conidiophore is done as it cannot be excluded that the other drawings were taken from additional host individuals, thereby representing more than one specimen.

The chosen epitype is deposited in the USDA United States National Fungus Collections under the accession number BPI 790753 (epitype designated here, MycoBank typification number MBT 10021530) and has been collected by J. Lind in 1913 in the South of Denmark, less than 500 km away from Bohemia, from where the specimen used by Corda originated. This choice is made as the specimen is part of the exsiccate collection *Phycomyceten et Protomyceten* of P. Sydow (as number 310), which has been distributed worldwide in many copies. Especially considering the complications arising from the current international regulations with respect to the shipment of plant pathogens and the access to genetic resources, as well as increasingly strict loan policies, a specimen already widely distributed is preferable over a specimen present in only a single herbarium. Furthermore, as the host is widely distributed over several thousand kilometres, and it has been shown that the other species parasitic to *Rumex* also have a wide distribution with their host plants, a distance of less than 500 km between the collection localities seems acceptable. Another advantage of the designated epitype is that the *Phycomyceten et Protomyceten* series is exceptionally well-preserved, reflected by the possibility of obtaining several loci for multigene phylogenies from the epitype specimen, even if it is more than 100 years old. The designation of a sequenced epitype specimen also ends the debate regarding the conspecificity of *Peronospora rumicis* and *Peronospora effusa*, the economically important pathogen infecting spinach (Choi et al. 2007, 2015).

Description of new species of *Peronospora* parasitic to *Caryophyllales*

Based on host preference and phylogenetic distinctiveness, three widespread new species of *Peronospora* from the *Peronospora rumicis* clade are introduced here.

Peronospora blauvikensis Thines & M. Mu, sp. nov. (Fig. 2).

MycoBank: MB 855031.

Etymology: Referring to the locality (Blávík, Fáskrúðsfjörður, Iceland) where the specimen that prompted this study was collected.

Description: Lesions on leaves pale green or chlorotic, mostly systemic, sporulation mostly diffuse but sometimes vein-delimited in local infections *Rumex acetosa*. Down present on the lower leaf surface, purplish or grey, consisting of scattered to dense felt-like conidiophore outgrowth. *Conidiophores* hyaline, straight to curved, thin-walled, 174–348 µm long, av. 261 µm; trunk 90–195 µm long, av. 143 µm, 7–9.5 µm broad, sometimes slightly swollen up to 16 µm at the base, the ratio of the total length to trunk length 1.5–2.2, callose plugs absent. *Branching* subdichotomous in 3–8 orders, with sub-straight to curved branches, gradually attenuate, often at right angles. *Ultimate branchlets* straight to substraight, rarely curved, paired branchlets differing in length, with the longer ones 9–13.5 µm long, the shorter ones 8–12 µm long, with a ratio of the longer to the shorter ultimate branchlet of 1.0–1.2, base 2.5–3.5 µm broad. *Conidia* ellipsoid to ovate with a pale brown colour, 25–29.5 µm long, 19–23 µm broad, length-to-breadth ratio 1.2–1.5. *Oospores* not observed.

Diagnosis: Differs from *Peronospora rumicis* by having a C instead of a T at position 240 in the *RPS10* alignment. Differs from all other species in species cluster 1 (see Fig. 1) in the *NAD1* alignment by having a G instead of an A at position 64, an A instead of a G at position 124, a G instead of T at position 390, and a G instead of an A at position 430. Differs from all other species in species cluster 1 in the *COX2-cox2/1spacer-COX1* alignment by having a G instead of a T at position 99, an A instead of a G at positions 216, 555, and 1415, a G instead of an A at position 1526, as well as an A instead of a C at position 1569.

Habitat: Living leaves of *Rumex acetosa* and *Rumex arifolius*.

Distribution: Austria, Czech Republic, Denmark, England, Finland, Germany, Iceland, Ireland, Italy, Poland, Portugal, Romania, Russia, Spain, Sweden, Switzerland, United Kingdom.

Typus: Iceland, Fáskrúðsfjörður, Blávík, on living leaves of *Rumex acetosa*, 4 Jul. 2024, Thines M, deposited in the Herbarium Senckenbergianum under the accession number FR-0214054.

Additional specimens examined: Austria, Kärnten, on living leaves of *Rumex arifolius*, 2000, WU32786; Oberösterreich, on living leaves of *Rumex acetosa*, 2001, WU22925; Oberösterreich, on living leaves of *Rumex acetosa*, 2011, WU34310; Wien, on living leaves of *Rumex acetosa*, 2004, WU33899. England, South Yorkshire, on living leaves of *Rumex acetosa*, 2011, WU34347; Finland, Nylandia, on living leaves of *Rumex acetosa*, 1960, UPS27; Nylandia, on living leaves of *Rumex acetosa*, 1970, BPI790739. Germany, Baden-Württemberg, on living leaves of *Rumex acetosa*, 2001, WU33730; Saxony-Anhalt, Querfurter Platte, on living leaves of *Rumex acetosa*, 6 May 2005, H. Jage, GLM75948. Germany, Saxony-Anhalt, Helme-Unstrut

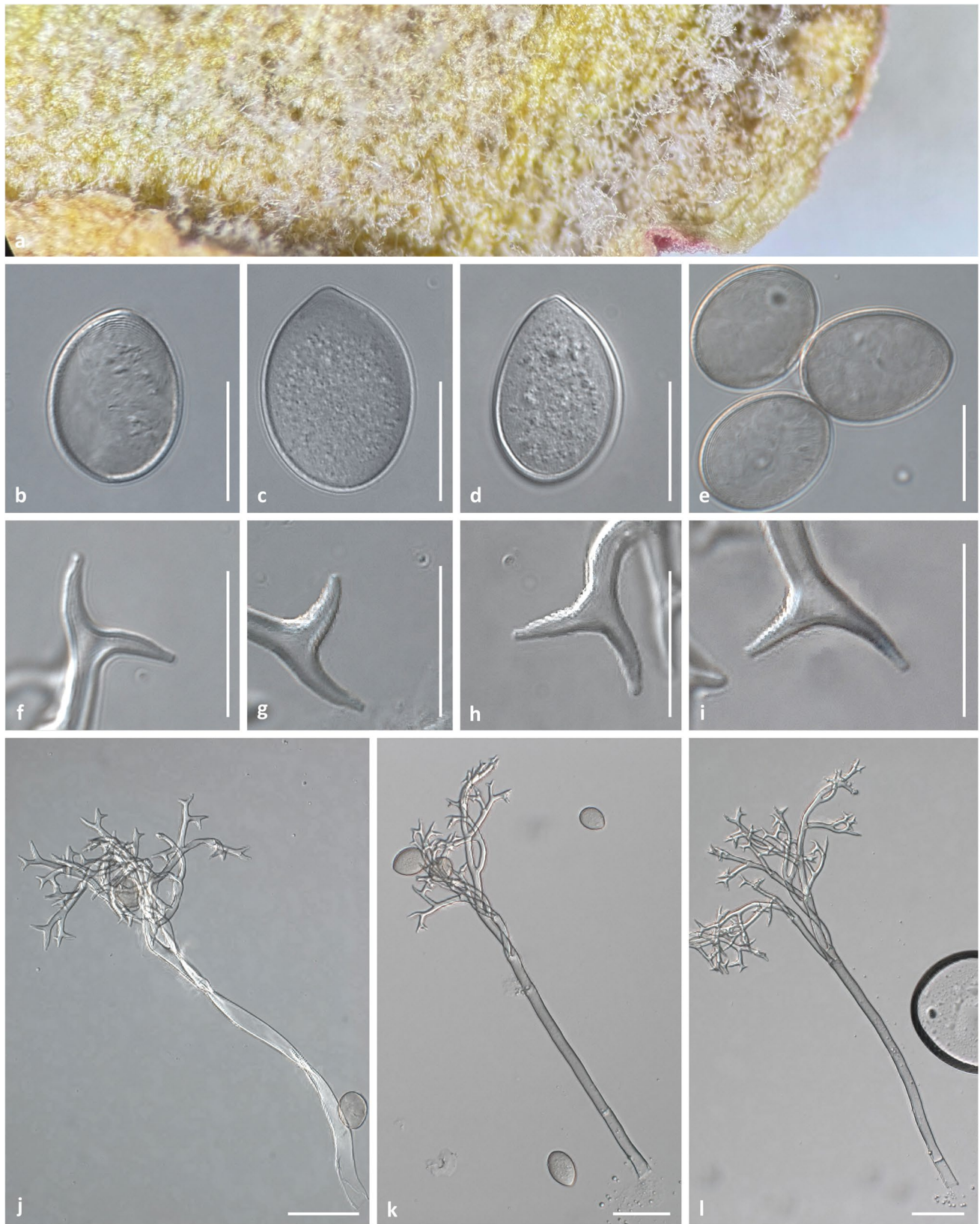


Fig. 2 Symptoms and morphology of *Peronospora blauvikensis* parasitic on *Rumex acetosa* (FR-0214054). **a** Down on the leaf surface. **b–e** Conidia. **f–i** Ultimate branchlets. **j–l** Conidiophores. Bars: **b–i** = 20 µm; **j–l** = 50 µm

Buntsandsteinland, on living leaves of *Rumex acetosa*, 30 May 2004, H. Jage, holotype GLM62941. Italy, Lombardia, on living leaves of *Rumex arifolius*, 2012, WU35780; Valle d'Aosta, on living leaves of *Rumex arifolius*, 2013, JKF0513. Romania, Harghita, on living leaves of *Rumex arifolius*, 1980, HMR2940. Sweden, Härjedalen, on living leaves of *Rumex acetosa*, 1975, UPS25.

Peronospora boylei M. Mu & Thines, sp. nov. (Fig. 3).

Mycobank: MB 855032.

Etymology: Named to honour the collector of the type specimen, Herbert Boyle, who has been a long-term curator of the herbarium GLM and contributed numerous collections of phytopathogens to it.

Description: Lesions on leaves yellow–brown, diffuse to vein-delimited in *Rumex thyrsiflorus*. Down present on the lower leaf surface, beige, consisting of scattered to dense felt-like conidiophore outgrowth. *Conidiophores* hyaline, straight to curved, thin-walled, 199–282 µm long, av. 240 µm; trunk 107–155 µm long, av. 131 µm, 7.5–10.5 µm broad, sometimes slightly swollen to up to 18 µm at the base, ratio of the total length to trunk length 1.7–2.0, callose plugs absent. *Branching* subdichotomous in 4–7 orders, with straight to sub-straight branches, gradually attenuate, often at right angles. *Ultimate branchlets* straight to sub-straight, rarely curved, paired branchlets differing in length, with the longer ones 8.5–14 µm long, the shorter ones 7–11 µm long, with a ratio of the longer to the shorter ultimate branchlet of 1.1–1.5, base 2.5–3.5 µm broad. *Conidia* ellipsoid to ovoid with a pale grey colour, 24.5–29.5 µm long, 17–21 µm broad, length-to-breadth ratio 1.3–1.5. *Oospores* not observed.

Diagnosis: Differs from *Peronospora rumicis* by having a C instead of a T at position 240 in the *RPS10* alignment. Differs from *Peronospora rumicis* in the *NAD1* alignment by having a C instead of a T at position 120, and a C instead of an A at position 448 and from *Peronospora blauvikensis* by having a G instead of an A at position 64, an A instead of a G at position 124, a G instead of T at position 390, and a G instead of an A at position 430. Differs from *Peronospora rumicis* in the *COX2-cox2/1spacer-COX1* alignment by having an A instead of a C at position 12, a G instead of an A at position 92, a G instead of a T at position 725, a C instead of a T at position 1454, a T instead of a G at position 1568, and a T instead of a C at position 1576. At the same locus, it differs from *Peronospora blauvikensis* by having a G instead of a T at position 99, an A instead of a G at positions 216, 555, and 1415, a G instead of an A at position 1526, as well as an A instead of a C at position 1569.

Habitat: Living leaves of *Rumex thyrsiflorus*.

Distribution: Austria, Germany, Kazakhstan, Mongolia, Russia.

Typus: Germany, Saxony, Östliche Oberlausitz, on living leaves of *Rumex thyrsiflorus*, 5 Jun. 2008, H. Boyle, holotype GLM90995.

Additional specimens examined: Austria, Niederösterreich, on living leaves of *Rumex thyrsiflorus*, 2012, WU35760. Lausitzer Grenzwall, on living leaves of *Rumex thyrsiflorus*, 22 May 2008, H. Boyle GLM90812; Sachsen-Anhalt, Dessauer Elbetal, on living leaves of *Rumex thyrsiflorus*, 30 Aug. 2003, H. Jage, GLM73434; Dübener Heide, on living leaves of *Rumex thyrsiflorus*, 9 May 2004, H. Jage, GLM64100; Mosigkau Heide, on living leaves of *Rumex thyrsiflorus*, 1 Sept. 2003, H. Jage, GLM73428; specimens of *Peronospora boylei* s.l. investigated: Ländchen im Elbe-Havel-Winkel, on living leaves of *Rumex aff. thyrsiflorus*, 1 Oct. 2003, H. Jage, GLM74510; Germany, Niedersachsen, on living leaves of *Rumex aff. thyrsiflorus*, 21 Sept. 2009, J. Kruse, JKF0051; Sachsen, Düben-Dahlener Heiden, on living leaves of *Rumex aff. thyrsiflorus*, 24 May 2003, H. Jage, GLM74313.

Peronospora spergulariae M. Mu & Thines, sp. nov. (Fig. 4).

Mycobank: MB 855033.

Etymology: Derived from the host genus *Spergularia*.

Description: Lesions on leaves yellow–brown, diffuse to vein-delimited in *Spergularia marina*. Down present on the lower leaf surface, white to beige, consisting of scattered to dense felt-like conidiophore outgrowth. *Conidiophores* hyaline, straight, thin-walled, 158–241 µm long, av. 200 µm; trunk 78–126 µm long, av. 102 µm, 9–11 µm broad, sometimes slightly swollen to up to 18 µm at the base, ratio of the total length to trunk length 1.6–2.4, callose plugs absent. *Branching* subdichotomous in 3–6 orders, with straight to sub-straight branches, gradually attenuate, often at right angles. *Ultimate branchlets* straight, paired branchlets differing in length, with the longer ones 7.5–12 µm long, the shorter ones 6–10 µm long, with a ratio of the longer to the shorter ultimate branchlet of 1.1–1.4, base 2–3.5 µm broad. *Conidia* ellipsoid to oval with a pale grey colour, 26.5–31.5 µm long, 18.5–21.5 µm broad, length-to-breadth ratio 1.3–1.6. *Oospores* not observed.

Diagnosis: Differs from *P. lepidoni* in having broader conidia, shorter conidiophores and trunks, broader trunks and conidiophore bases, as well as shorter ultimate branchlets.

Habitat: Living leaves of *Spergularia marina*.

Distribution: Austria, Germany, United Kingdom.

Typus: Germany, Saxony-Anhalt, Magdeburger Börde, on living leaves of *Spergularia marina*, 4 Nov. 2005, H. Jage, holotype GLM75894.

Additional specimens examined: Germany, Sachsen-Anhalt, on living leaves of *Spergularia marina*, 7 Oct. 2001, H. Jage, GLM73809; specimen of *Peronospora spergulariae* s.l. investigated: Austria, Burgenland, on living leaves of *Spergularia marina*, 2001, WU33808.



Fig. 3 Symptoms and morphology of *Peronospora boylei* parasitic on *Rumex thyrsiflorus* (GLM90995). **a** Down on the leaf surface. **b–e** Conidia. **f–i** Ultimate branchlets. **j–l** Conidiophores. Bars: **b–i** = 20 μ m; **j–l** = 50 μ m



Fig. 4 Symptoms and morphology of *Peronospora spargulariae* parasitic on *Spergularia marina* (GLM75894). **a** Down on the leaf surface. **b–d** Conidia. **e–g** Ultimate branchlets. **h–j** Conidiophores. Bars: **b–g** = 20 μ m; **h–j** = 50 μ m

Discussion

The downy mildew genus *Peronospora* is the largest oomycete genus, with more than 400 species described. However, this is only the tip of the iceberg, as recent studies have shown

that the host specificity of the genus is mostly very high, with each species infecting only a single or very few closely related host species (García-Blázquez et al. 2008; Choi et al. 2007, 2009, 2015; Thines et al. 2009, 2019; Voglmayr et al. 2014; Hoffmeister et al. 2020; Davis et al. 2021; Mu et al. 2024a, b).

Fig. 5 Herbarium specimen designated as type by Constantinescu (1991). **a** Label of the capsule. **b–e** Fragments of the specimen. The scale bar equals 5 mm in (**b**)–(**e**). The figure is based on photographs provided by the staff of PRM with the kind permission to reproduce them in this article



The careful revision of *Peronospora* species complexes is therefore warranted, also for economically less important groups.

The present study is the first step towards this in the clade of *Peronospora* containing several closely related species parasitising *Chenopodiaceae* and *Polygonaceae*, which had been phylogenetically investigated by Choi et al. (2015). Apart from the economically important species *P. effusa* and *P. schachtii*, which parasitise spinach and beet, respectively, this group also contains the type of *Peronospora*, *P. rumicis*, and several other species on wild plant hosts. The finding of downy mildew on *Rumex acetosa* at the Blávk research station in East Iceland reminded the first author of this study of the non-mended threads of the earlier publication (Choi et al. 2015), explicitly with respect to resolving the typification of the type species of *Peronospora*.

While epitypification should be used with caution, as it can only be superseded by conservation according to the current ICNafp (Turland et al. 2018), it seemed warranted in this case, as neither the plate provided by Corda (1837) provides sufficient information for unambiguous identification of the species, nor is it doubtless that PRM 155590 is

the exact specimen Corda had based his description of *P. rumicis* on. Thus, the only unambiguous fact remaining is that the type host of *P. rumicis* is *Rumex acetosella*, and accordingly an epitype was chosen of which duplicates are widely present in herbaria throughout the world.

The study of Choi et al. (2015) already demonstrated that *Peronospora* on *Rumex acetosella* and *Rumex acetosa* are distinct and cannot be considered the same species, necessitating the description of *Peronospora* on *Rumex acetosa* as a new species. However, as Choi et al. (2015) did not pursue the description of the species, this matter remained unresolved until the description of *P. blauvikensis* in this study. The two additional species described in this study are much more closely related to species already described but belong to phylogenetic lineages that cannot be attributed to other species in the *P. effusa* clade. As species in this clade seem to be highly host-specific, similar to the situation in other *Peronospora* groups (García-Blázquez et al. 2008; Voglmayr et al. 2014; Mu et al. 2024a, b), the description of *P. boylei* on *Rumex thyrsiflorus* and *P. spergulariae* on *Spergularia marina* seems justified.

While Gümman (1919, 1923) found clear-cut differences for various host–pathogen–associations in line with later

phylogenetic investigations, he listed several *Rumex* species as hosts for *P. rumicis* that have been demonstrated to host different species of the genus. The reason for this is that many species parasitising *Polygonaceae* are highly similar in their morphology, so their morphological differentiation is less than the plasticity likely incited by environmental factors (Dudka et al. 2007). In line with this, no clear-cut morphological differences were found in the current study, even though the species were distinct in terms of their molecular phylogeny. So far, oospores have only been found in *P. rumicis-rosei* (Rayss 1945), further complicating species differentiation based on morphology.

Even though the current study is a first step towards resolving the downy mildew pathogens in the *P. effusa* clade, there will be several more steps necessary to resolve it, such as performing a broader sampling of *Peronospora* on *Rumex thyrsiflorus* and *Spergularia marina*, to clarify, if the specimens now designated as *P. boylei* s.l. and *P. spergulariae* s.l., respectively, can still be included in the natural spectrum of variation of these species or need to be considered independent from them.

Acknowledgements We thank the curator of GLM at the Senckenberg Institute in Görlitz for allowing access to specimens deposited in the herbarium. In addition, we are grateful to the curators of PRM for providing pictures of the specimen PRM 155590 designated as type by Ovidiu Constantinescu and allowing the use of them in this article. This study was enabled by a stay at the Blávik Arctic Research Station in Blávik on Fáskrúðsfjörður, Fjarðabyggð, Iceland and partly conducted there.

Author contribution MT conceived the study. MM conducted laboratory work and performed morphological investigations. MT and MM wrote this manuscript with contributions from YJC. All authors agreed with the submission of the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. A special gratitude is extended to the China Scholarship Council (CSC) for supporting the first author through a doctoral fellowship in Germany (No. 202108530140).

Data availability Specimens are deposited in the Herbarium Senckenbergianum at the Senckenberg Museum für Naturkunde in Görlitz (GLM) and Frankfurt am Main (FR). Sequence data are submitted to GenBank. The names of *Peronospora* species have been submitted to MycoBank.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests MT is the Editor-in-Chief of Mycological Progress but was not involved in the editorial processes associated with handling this manuscript.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated

otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Beakes GW, Thines M (2017) *Hypochytriomycota* and *Oomycota*. In: Archibald J, Simpson A, Slamovits C (eds) Handbook of the Protists. Springer International Publishing, Cham, pp 435–505. https://doi.org/10.1007/978-3-319-28149-0_26
- Choi Y-J, Hong S-B, Shin H-D (2007) Re-consideration of *Peronospora farinosa* infecting *Spinacia oleracea* as distinct species *Peronospora effusa*. Mycol Res 111:381–391. <https://doi.org/10.1016/j.mycres.2007.02.003>
- Choi Y-J, Klosterman SJ, Kummer V, Voglmayr H, Shin H-D, Thines M (2015) Multi-locus tree and species tree approaches toward resolving a complex clade of downy mildews (*Straminipila*, *Oomycota*) including pathogens of beet and spinach. Mol Phylogenet Evol 86:24–34. <https://doi.org/10.1016/j.ympev.2015.03.003>
- Choi Y-J, Shin H-D, Thines M (2009) Two novel *Peronospora* species are associated with recent reports of downy mildew on sages. Mycol Res 113:1340–1350. <https://doi.org/10.1016/j.mycres.2009.08.010>
- Constantinescu O (1991) An annotated list of *Peronospora* names. Thunbergia 15:1–110
- Constantinescu O, Fatehi J (2002) *Peronospora*-like fungi (*Chromista*, *Peronosporales*) parasitic on *Brassicaceae* and related hosts. Nova Hedwigia 74:291–338
- Corda ACJ (1837) Icones Fungorum Hucusque Cognitorum 1:1–32
- Davis WJ, Ko M, Ocenar JR, Romberg MK, Thines M, Crouch JA (2021) *Peronospora kuwae*, sp. nov., a new downy mildew species infecting the endangered Hawaiian plant *Plantago princeps* var. *princeps*. Mycologia 113:643–652
- Dick MW (2001) Straminipilous Fungi. Kluwer, Netherlands
- Dudka IO, Anishchenko IM, Terent'eva NG (2007) The variability of *Peronospora alta* Fuckel conidia in dependence on the ecological conditions. In: Lebeda A, Spencer-Phillips PTN (eds) Advances in Downy Mildew Research, vol 3. Palacký University in Olomouc and JOLA, Kostelec na Hané, pp 39–46
- García-Blázquez G, Göker M, Voglmayr H, Martín MP, Tellería MT, Oberwinkler F (2008) Phylogeny of *Peronospora* parasitic on *Fabaceae* based on ITS sequences. Mycol Res 112:502–512. <https://doi.org/10.1016/j.mycres.2007.10.007>
- Gäumann E (1918a) Über die Formen der *Peronospora parasitica* (Pers.) Fries. Beih Bot Centralbl 35:395–533
- Gäumann E (1918b) Über die Spezialisierung der *Peronospora* auf einigen Scrophulariaceen. Ann Mycol 16:189–199
- Gäumann E (1918c) Zur Kenntnis der Chenopodiaceen bewohnenden *Peronospora*-Arten. Mitt Naturf Ges Bern 1918:45–66
- Gäumann E (1919) Les espèces de *Peronospora* sur les Euphorbiacées et les Polygonacées. Ann Conservât Bot Genève 21:1–23
- Gäumann E (1923) Beiträge zu einer Monographie der Gattung *Peronospora* Corda. Beiträge Zur Kryptogamenflora der Schweiz 5:1–360
- Gustavsson A (1959) Studies on Nordic *Peronosporas*. I. Taxonomic revision. Opera Botanica 3:1–271
- Hoffmeister M, Ashrafi S, Thines M, Maier W (2020) Two new species of the *Peronospora belbahrii* species complex *Pe. choii* sp. nov. and *Pe. salviae-pratensis* sp. nov. and a new host for *Pe. salviae-officinalis*. Fungal Syst Evol 6:38–52. <https://doi.org/10.3114/fuse.2020.06.03>

- Katoh K, Standley DM (2013) MAFFT Multiple sequence alignment software version 7: improvements in performance and usability. *Mol Biol Evol* 30:772–780. <https://doi.org/10.1093/molbev/mst010>
- Katoh K, Toh H (2008) Improved accuracy of multiple ncRNA alignment by incorporating structural information into a MAFFT-based framework. *BMC Bioinformatics* 9:212. <https://doi.org/10.1186/1471-2105-9-212>
- Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Mol Biol Evol* 33:1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Mu M, Choi Y-J, Kruse J, Crouch JA, Ploch S, Thines M (2024a) Single host plant species may harbour more than one species of *Peronospora* – a case study on *Peronospora* infecting *Plantago*. *Persoonia* 52:94–118. <https://doi.org/10.3767/persoonia.2024.52.04>
- Mu M, Choi Y-J, Thines M (2024b) *Peronospora* species on *Myosotis* – a showcase for the uncharted diversity of a highly diverse and specialised downy mildew genus. *Mycol Prog* 23:51. <https://doi.org/10.1007/s11557-024-01984-y>
- Rayss T (1945) Nouvelle Contribution à l'étude de la Mycoflore de Palestine (Troisième partie). *Palestine J Bot Jerusalem Ser* 3:151–166
- Riethmüller A, Voglmayr H, Göker M, Weiß M, Oberwinkler F (2002) Phylogenetic relationships of the downy mildews (*Peronosporales*) and related groups based on nuclear large subunit ribosomal DNA sequences. *Mycologia* 94:834–849. <https://doi.org/10.1080/15572536.2003.11833177>
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst Biol* 61:539–542. <https://doi.org/10.1093/sysbio/sys029>
- Săvulescu T, Rayss T (1930) Contribution to the knowledge of the *Peronosporaceae* of Romania. *Ann Mycol* 28:297–320
- Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690. <https://doi.org/10.1093/bioinformatics/btl446>
- Thines M, Choi Y-J (2016) Evolution, diversity and taxonomy of the *Peronosporaceae* with focus on the genus *Peronospora*. *Phytopathol* 106:6–18. <https://doi.org/10.1094/PHYTO-05-15-0127-RVW>
- Thines M, Denton GJ, Beal EJ, Kilty A, Denton JO, Shin H-D, Choi Y-J (2019) *Peronospora aquilegiicola* sp. nov., the downy mildew affecting columbines in the UK is an invasive species from East Asia. *Eur J Pl Pathol* 155:515–525. <https://doi.org/10.1007/s10658-019-01787-y>
- Thines M, Kummer V (2013) Diversity and species boundaries in floricolous downy mildews. *Mycol Prog* 12:321–329. <https://doi.org/10.1007/s11557-012-0837-7>
- Thines M, Telle S, Ploch S, Runge M (2009) Identity of the downy mildew pathogens of basil, coleus, and sage with implications for quarantine measures. *Mycol Res* 113:532–540. <https://doi.org/10.1016/j.mycres.2008.12.005>
- Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herednden PS, Knapp S, Kuser W-F, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code). *Regnum Vegetabile* no. 159. Koeltz Botanical Books, Glashütten, Germany
- Voglmayr H (2003) Phylogenetic relationships of *Peronospora* and related genera based on nuclear ribosomal ITS sequences. *Mycol Res* 107:1132–1142. <https://doi.org/10.1017/S0953756203008438>
- Voglmayr H, Korytnianska V (2015) *Peronospora odessana* sp. nov. a downy mildew pathogen of a Tertiary relict species *Gymnospermium odessanum*. *Mycol Prog* 14:1–7. <https://doi.org/10.1007/s11557-015-1059-6>
- Voglmayr H, Montes-Borrego M, Landa BB (2014) Disentangling *Peronospora* on *Papaver*: phylogenetics, taxonomy, nomenclature, and host range of downy mildew of opium poppy (*Papaver somniferum*) and related species. *PLoS One* 9
- Yerkes WD, Shaw CG (1959) Taxonomy of the *Peronospora* species on *Cruciferae* and *Chenopodiaceae*. *Phytopathology* 49:499–507

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.