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Peronosporaceae species causing downy mildew diseases of *Poaceae*, including nomenclature revisions and diagnostic resources

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Abstract: Downy mildew pathogens of graminicolous hosts (*Poaceae*) are members of eight morphologically and phylogenetically distinct genera in the *Peronosporaceae* (*Oomycota, Peronosporales*). Graminicolous downy mildews (GDMs) cause severe losses in crops such as maize, millets, sorghum, and sugarcane in many parts of the world, especially in tropical climates. In countries where the most destructive GDMs are not endemic, these organisms are often designated as high-risk foreign pathogens and subject to oversight and quarantine by regulatory officials. Thus, there is a need to reliably and accurately identify the causal organisms. This paper provides an overview of the *Peronosporaceae* species causing graminicolous downy mildew diseases, with a description of their impact on agriculture and the environment, along with brief summaries of the nomenclatural and taxonomic issues surrounding these taxa. Key diagnostic characters are summarized, including DNA sequence data for types and/or voucher specimens, morphological features, and new illustrations. New sequence data for *cox*2 and 28S rDNA markers are provided from the type specimens of three species, *Peronosclerospora philippinensis*, *Sclerospora iseilematis*, and *Sclerospora northii*. Thirty-nine species of graminicolous downy mildews are accepted, and seven previously invalidly published taxa are validated. Fifty-five specimens are formally designated as types, including lectotypification of 10 species, neotypification of three species, and holotype designation for *Sclerophthora cryophila*.

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INTRODUCTION

Graminicolous downy mildews (GDMs) are diseases caused by members of the *Peronosporaceae* (*Oomycota*, *Peronosporales*). GDM pathogens are obligate, biotrophic parasites of cultivated and wild cereals and other grasses in the *Poaceae* family (Kenneth 1981, Spencer & Dick 2002). In regions of the world where the most destructive GDM pathogens reside, these diseases can result in significant crop losses (60–100 %) of staple food and forage crops such as maize (*Zea mays*), pearl millet (*Pennisetum glaucum*), sorghum (*Sorghum* spp.), and sugarcane (*Saccharum* spp.) (Exconde & Raymundo 1974, Safeeulla 1976, Kenneth 1981, Rathore *et al.* 2002, Putnam 2007, Kumar *et al*. 2012, Li *et al.* 2020). In parts of the world where these organisms are not present, foreign GDM pathogens are often regulated as quarantine pests by governmental agencies and are subject to strict control measures to prevent their spread. For example, in the USA, the maize pathogens *Peronosclerospora philippinensis* and *Sclerophthora rayssiae* var. *zeae* pose such a significant potential threat to the country's agriculture that they are regulated as Select Agents. Designation of a plant pathogen as a Select Agent in the USA is a notable distinction, as there are only seven plant pathogenic organisms so named, and placement in this category subjects them to the same general oversight program that also deals with deadly human pathogens such as the plague bacterium *Yersinia pestis*, the smallpox virus, and the SARS-associated coronavirus (SARS-CoV).

As with all organisms capable of inciting plant diseases, reliable and accurate identification of the GDM pathogens is crucial, but identification is only possible when the characters that can be used to identify them are clearly known. Any taxonomic or nomenclatural confusion that would lead to the misidentification of species or misapplication of a name could hinder efforts to identify introduced species, detect emerging pathogen threats, and track the spread of disease (Thines & Choi 2016, Petrželová *et al*. 2017, Davis & Crouch 2022a). However, this group has never been monographed, and practical diagnosis of GDM pathogens is hindered by the absence of an updated, centralized treatment of the group. Key identification resources such as morphological descriptions, diagnostic traits, host associations, and molecular datasets for exemplary materials are currently spread across hundreds of papers spanning more than 100 years, sometimes in obscure and difficult to obtain publications. To our knowledge, one species – *Sclerospora farlowii* – has never been illustrated and several species are not formally typified. The most recent comprehensive taxonomic reviews of the *Peronosporaceae* pathogens of grasses were published more than four decades ago, harkening back to Kenneth's summary of the group in 1981 and Waterhouse's seminal review in 1964. Since Waterhouse's review, nineteen new species, one variety, and five new genera of GDM pathogens have been discovered, and molecular phylogenetic data has been used to study these organisms since 2002 (Riethmüller *et al*. 2002). Thus, the goal of this paper is to provide an annotated summary of the names applied to the *Peronosporaceae* species causing downy mildew diseases on *Poaceae*. We briefly discuss the impact of each species, and when possible, summarize resources and descriptions, provide new illustrations, address nomenclatural issues, and discuss possible research that could help clarify outstanding taxonomic issues.

MATERIALS AND METHODS

In compiling this treatment, Waterhouse (1964) and Shaw (1975, 1978) were used as starting points. A literature search was conducted online using Google Scholar, Index Fungorum, and MycoBank for publications dealing the nomenclature, taxonomy, and economic impacts of GDM pathogens. Herein, names of *Peronosporaceae* species causing downy mildew diseases of *Poaceae* are listed alphabetically by the genus they are currently assigned to. Given the similarity between host and pathogen epithets throughout this paper, all Latin binomials are given without abbreviation throughout the text to avoid confusion.

Host association

The USA National Fungus Collections (BPI) fungus/host databases were initially consulted for distribution and host information (Farr & Rossman 2021). BPI online databases are cited as Farr & Rossman (2021) to summarize reports of species listed in "checklist" type publications; relevant publications where identifications were reviewed and verified are directly cited. The Plant List (http://www.theplantlist.org), World Flora Online (http://www.worldfloraonline.org/), and the Germplasm Resources Information Network (GRIN, http://www.ars-grin.gov/) were used as sources for plant name synonymy, in that order. When there were disagreements among the three sources, preference was given to GRIN. Plant hosts from the original collection are listed as current name (synonym, subfamily, tribe) following Sorgen *et al.* (2015).

Typification and validation of names

Lectotypes or neotypes were designated for effectively published species when original materials and/or specimens consistent with the protolog were available, following the current International Code of Nomenclature for algae, fungi, and plants (ICNafp; Turland *et al.* 2018); these are summarized in Table 1. Names that were not validly described according to the rules of the ICNafp but representing distinct taxa are validated following the ICNafp (Turland *et al.* 2018). New taxa and typifications were registered with MycoBank and are cited as MB and MBT accession numbers, respectively. Fungarium abbreviations follow the New York Botanical Garden's Index Herbariorum (Verkeley *et al.* 2014).

Identification resources

Morphological features for asexual and sexual structures are summarized in Supplementary Table S1. Diagnoses are provided for some – but not all – species where sufficient traits were available to provide a reliable diagnosis, but it is important to note that morphological characteristics of *Peronosporaceae* are influenced by environment and host (Runge *et al.* 2012) and may therefore vary. Full descriptions from the species protologs and/or non-original sources are provided, with protolog descriptions taking precedence and other sources used when the protolog information was incomplete or determined by later authors as incorrect.

For *Peronosporaceae* fungarium specimens examined at BPI and the Canadian National Mycological Fungarium (DAOM) for this work, macroscopic images of the type specimens were obtained and are included in this paper as Supplementary Figs S1–S23.

Line drawings of microscopic features were prepared from published reference materials and new images of *Sclerospora farlowii* (Figs 1–11). Objects and scale bars from original sources were opened in Photoshop CS6, the contour of objects traced, then the illustrations were standardized to a uniform style, with a gray mottling representing cytoplasm and solid grays representing solid walls. Thick black lines represent significant boundries, such as the ones between cytoplasm and wall. Thin lines were used to represent delimitations of vesicles or zoospores, and dashed lines were used to delineate vacuoles. As much as possible, drawings were placed at the same scale to facilitate comparisons of the structures. New microscopic images were prepared from the type specimen of *Sclerospora farlowii*, as illustrations of this pathogen have never been published. Specimen material was rehydrated in 85 % lactic acid, stained with cotton blue, and visualized using a Zeiss Axio Imager M2 microscope (Carl Zeiss Microscopy, Thornwood, NY). Images were captured with an Axiocam 503 color digital camera using differential contrast illumination and processed with Zen 2 Pro v. 3.4 software (Carl Zeiss Microscopy).

DNA sequence data resources are summarized for types and/or voucher specimens when available. Accession numbers for nucleotide sequences of the barcode markers *cox*2 and 28S rDNA were obtained from the National Center for Biotechnology Information (NCBI) GenBank (https://www.ncbi.nlm.nih.gov/)

Table 1. Summary of type and exemplar materials for *Peronosporaceae* pathogens of *Poaceae*. Of the 66 total type specimens, 48 types are newly designated in the current paper (highlighted in bold text). Basionyms are given if different from the current name.

Current name	Basionym	Specimen	Specimen status	Year Collected	Host	Locale	*Cox*2 sequence	28S rDNA sequence	References
Baobabopsis donbarrettii R.G. Shivas *et al.*		BRIP 54675	Holotype	2011	*Perotis rara*	Australia, Western Australia	KT248948	KT248945	Thines *et al.* (2015)
Baobabopsis enneapogonis Thines *et al.*		BRIP 49822	Holotype	2007	*Enneapogon cylindricus*	Australia, Northern Territory	KT248946	—	Thines *et al.* (2015)
Baobabopsis marneyi R.G. Shivas *et al.*		BRIP 70341	**Holotype**	2019	*Enneapogon polyphyllus*	Australia, Queensland, Georgetown	OK336436	—	Ryley *et al.* (2022)
Eraphthora butleri (W. Weston) Telle & Thines	*Sclerospora butleri* W. Weston	BPI 187075	**Lectotype**	1927	*Eragrostis aspera*	Malawi (formerly Nyasaland), Bulaki	—	—	Weston (1933), this paper
		FH 965376	**Isotype**	1927	*Eragrostis aspera*	Malawi (formerly Nyasaland), Bulaki	—	—	Weston (1933), this paper
		BPI 187074	Might be isotype?	1927	Collection metadata incomplete	Collection metadata incomplete	—	—	Weston (1933), this paper
Eraphthora drenthii M. J. Ryley *et al.*		DAR 4201	Holotype	1950	*Eragrostis cilianensis*	Australia, New South Wales	HQ413338	—	Ryley *et al.* (2022)
Eraphthora occultata Y.P. Tan *et al.*		DAR 16237	Holotype	1967	*Eragrostis cilianensis*	Australia, New South Wales	OK391240	—	Ryley *et al.* (2022)
Graminivora graminicola (Naumov) Thines & Göker	*Bremia graminicola* Naumov	LEP4385	**Lectotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper
		BPI 786232	**Isotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper
		LEP4384	**Isotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper
		LEP4377	**Isotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper
		FH 01012075	**Isotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper
		E00297399	**Isotype**	1912	*Arthraxon hispidus*	Russia, South Ussuriysk region, Siberia	—	—	Naumov (1913), this paper

Table 1. (Continued).

Current name	Basionym	Specimen	Specimen status	Year Collected	Host	Locale	*Cox*2 sequence	28S rDNA sequence	References
		HUH 738	Voucher	2001	*Arthraxon hispidus*	China, Yunnan, A Zi Ying	KP965747	KP965742	Thines & Göker (2006)
Peronosclerospora aristidae J. Kruse *et al.*		BRIP 67069	Holotype	2018	*Aristida hygrometrica*	Australia, Queensland	OK336438	—	Ryley *et al.* (2022)
Peronosclerospora boughtoniae M.J. Ryley *et al.*		BRIP 14388	Holotype	1978	*Sorghum plumosum*	Australia, Queensland, Lizard Island	OK33649	—	Ryley *et al.* (2022)
Peronosclerospora dichanthiicola (Thirum. & Naras.) C.G. Shaw	*Sclerospora dichanthiicola* Thirum. & Naras.	Illustration	**Lectotype**	1952	*Dichanthium annulatum*	India, Bihar	—	—	Thirumalachar & Narasimhan (1952), this paper
Peronosclerospora eriochloae Ryley & Langdon		BRIP 13693	Holotype	1979	*Eriochloa pseudoacrotricha*	Australia, Upper Pilton, Queensland	—	—	Ryley & Langdon (200)1
		BRIP 13691	**Isotype**	1979	*Eriochloa pseudoacrotricha*	Australia, Upper Pilton, Queensland	—	—	Ryley & Langdon (2001)
		BRIP 13692	**Isotype**	1979	*Eriochloa pseudoacrotricha*	Australia, Upper Pilton, Queensland	—	—	Ryley & Langdon (2001)
		FR-0046005	**Isotype**	1979	*Eriochloa pseudoacrotricha*	Australia, Upper Pilton, Queensland	HQ261813	HQ261786	Telle *et al.* (2011)
Peronosclerospora heteropogonis Siradhana *et al.*		HOH 898	**Holotype**	2005	*Zea mays*	India: Rajasthan, Udaipur	EU116054	—	Thines *et al.* (2008), this paper
Peronosclerospora ischaemi M.J. Ryley *et al.*		BRIP 70369	Holotype	2019	*Ischaemum fragile*	Australia, Queensland	OK336443	OK350686	Ryley *et al.* (2022)
Peronosclerospora jamesiae R.G. Shivas *et al.*		BRIP 65234	Holotype	2016	*Sorghum intrans*	Australia, Northern Territory, Wagait Beach	OK336444	—	Ryley *et al.* (2022)
Peronosclerospora mactaggartii R.G. Shivas *et al.*		BRIP 57677	Holotype	2012	*Sorghum timorense*	Austrlia, Northern Territory, Dorat Rd., Robins Falls	OK336446	OK350687	Ryley *et al.* (2022)
Peronosclerospora maydis (Racib.) C.G. Shaw	*Peronospora maydis* Racib.	KRAM O-5859(J)	Lectotype	1897?	*Zea mays*	Indonesia, Java, Jawa Tengah	MW025835	—	Suharjo *et al.* (2020)
		BPI 789413	**Isotype**	1897?	*Zea mays*	Indonesia, Java, Jawa Tengah			This paper
Peronosclerospora miscanthi (T. Miyake) C.G. Shaw	*Sclerospora miscanthi* T. Miyake	BPI 187301	**Neotype**	1915	*Miscanthus sinensis*	Taiwan: Taipei	—	—	Miyake (1912), this paper
		Stevens 811[1]	Voucher	1930	*Miscanthus japonicus*	Philippines, Luzon	HQ261811	HQ261784	Telle *et al.* (2011)

Table 1. (Continued).

Current name	Basionym	Specimen	Specimen status	Year Collected	Host	Locale	*Cox2* sequence	28S rDNA sequence	References
Peronosclerospora noblei (W. Weston) C.G. Shaw	*Sclerospora noblei* W. Weston	DAR 1075	**Lectotype**	1928	*Sorghum leiocladum*	Australia, New South Wales	—	—	Weston (1929), this paper
		DAR 1076	**Isotype**	1928	*Sorghum leiocladum*	Australia, New South Wales	—	—	Weston (1929), this paper
		BPI 187306	**Isotype**	1928	*Sorghum leiocladum*	Australia, New South Wales	OK185343	OK255496	Weston (1929), this paper
		FH 965379	**Isotype**	1928	*Sorghum leiocladum*	Australia, New South Wales	—	—	Weston (1929), this paper
Peronosclerospora panici R.G. Shivas *et al.*		DAR 35733	**Holotype**	1980	*Panicum laevinode*	Australia, New South Wales, Narromine	HQ261814	HQ261787	Telle *et al.* (2011), Ryley *et al.* (2022)
Peronosclerospora philippinensis (W. Weston) C.G. Shaw	*Sclerospora philippinensis* W. Weston	BPI 187314	**Lectotype**	1919	*Zea mays*	Philippines, Los Banos	—	—	Weston (1920), this paper
		BPI 187044	**Isotype**	1919	*Zea mays*	Philippines, Los Banos	OK185341	OK181682	Weston (1920), this paper
		BPI 187311	**Isotype**	1919	*Zea mays*	Philippines, Los Banos	—	—	Weston (1920), this paper
		BPI 187313	**Isotype**	1919	*Zea mays*	Philippines, Los Banos	—	—	Weston (1920), this paper
		FH 965382	**Isotype**	1919	*Zea mays*	Philippines, Los Banos	—	—	Weston (1920), this paper
		FH 965383	**Isotype**	1919	*Zea mays*	Philippines, Los Banos	—	—	Weston (1920), this paper
Peronosclerospora sacchari (T. Miyake) Shirai & Hara	*Sclerospora sacchari* T. Miyake	BPI 187331	**Lectotype**	1910	*Saccharum officinarium*	Taiwan	—	—	Miyake (1927), this paper
		BRIP 44241A	Voucher	2004	*Saccharum* sp.	East Timor	EU116052	HQ261764	Telle *et al.* (2011)
Peronosclerospora sargae R.G. Shivas *et al.*		BRIP 27691	Holotype	2000	*Sorghum timorense*	Australia, Northern Territory	HQ261809	HQ261782	Shivas *et al.* (2012)
Peronosclerospora schizachyrii R.G. Shivas *et al.*		BRIP 67070	Holotype	2018	*Schizachyrium fragile*	Australia, Queensland	OK336452	OK350689	Ryley *et al.* (2022)
Peronosclerospora sehimatis M.J. Ryley *et al.*		BRIP 49806	Holotype	2006	*Sehima nervosum*	Australia, Northern Territory, Arnhem Highway, Jabira	OK336453	—	Ryley *et al.* (2022)
Peronosclerospora sorghi (W. Weston & Uppal) C.G. Shaw	*Sclerospora sorghi* (Kulk.) W. Weston & Uppal	BPI 187336	**Lectotype**	1915	*Sorghum vulgare*	India, Coimbatore	—	—	Weston & Uppal (1932), this paper
		HUH 897	Voucher	2005	*Sorghum bicolor*	India, Karnataka, Dharwad	EU116055	—	Thines *et al.* (2008)

Table 1. (Continued).

Current name	Basionym	Specimen	Specimen status	Year Collected	Host	Locale	*Cox*2 sequence	28S rDNA sequence	References
Peronosclerospora spontanea (W. Weston) C.G. Shaw	*Sclerospora spontanea* W. Weston	BPI 187043	**Lectotype**	1919	*Saccharum spontaneum*	Philippines, Los Banos	—	—	Weston (1921), this paper
		BPI 187073	**Isotype**	1919	*Saccharum spontaneum*	Philippines, Los Banos	—	—	Weston (1921), this paper
Peronosclerospora westonii J.A. Crouch & Thines		Illustration	**Holotype**	1961	*Iseilema prostratum*	India, Poona	—	—	Srinivasan *et al.* (1961), this paper
Poakatesthia penniseti (R.G. Kenneth & J. Kranz) Thines & Göker	*Plasmopara penniseti* R. G. Kenneth & Kranz	IMI 137328c	Holotype	1968	*Pennisetum glaucum*	Ethiopia, Bako/Shoa	EF426475	—	Thines & Göker (2007)
Sclerophthora cryophila W. Jones		DAOM 20643	**Holotype**	1948	*Dactylis glomerata*	Canada, British Columbia	—	—	Jones (1955), this paper
Sclerophthora lolii J.A. Crouch & Thines		Illustration	**Holotype**	1964	*Lolium rigidum*	Israel, Mikve	—	—	Kenneth (1964), this paper
Sclerophthora macrospora (Sacc.) Thirum. *et al.*	*Sclerospora macrospora* Sacc.	BPI 187265	**Neotype**	1895	*Phlaris arundinaceae*	Germany, Saxony, Königstein	—	—	This paper
		BPI 187266	**Isotype**	1895	*Phlaris arundinaceae*	Germany, Saxony, Königstein	—	—	This paper
		HUH 892	Voucher		*Zea mays*	China	KP965748	EU826119	Choi *et al.* (2015)
Sclerophthora rayssiae J.A. Crouch & Thines		Illustration	**Holotype**	1964	*Hordeum vulgare*	Israel, Valley of Esdraelon	—	—	Kenneth *et al.* (1964), this paper
Sclerophthora zeae J.A. Crouch & Thines		HCIO 29038	**Holotype**	1965	*Zea mays*	India, Pantnagar	—	—	Payak & Renfro (1967), this paper
Sclerospora farlowii Griffiths		BPI 187077	**Lectotype**	1900	*Chloris virgata*	United States of America, Arizona	—	—	Griffiths (1907), this paper
		BPI 187076	**Isotype**	1900	*Chloris virgata*	United States of America, Arizona			Griffiths (1907), this paper
		BPI 187078	**Isotype**	1900	*Chloris virgata*	United States of America, Arizona			Griffiths (1907), this paper
		FH 965329	**Isotype**	1900	*Chloris virgata*	United States of America, Arizona			Griffiths (1907), this paper
		FH 1093687	**Isotype**	1900	*Chloris virgata*	United States of America, Arizona			Griffiths (1907), this paper
Sclerospora graminicola (Sacc.) J. Schröt.	*Protomyces graminicola* Sacc.	Schneider 553[2]	Holotype	1886?	*Setaria viridis*	Poland: Legnica (Liegnitz), Waldau			Schröeter (1886)
		HV532	Voucher		*Pennisetum glaucum*	India, Gulbarga, Karnataka	DQ365768	AY035514, AY273987	Nayaka *et al.* (2017)

Table 1. (Continued).

Current name	Basionym	Specimen	Specimen status	Year Collected	Host	Locale	*Cox*2 sequence	28S rDNA sequence	References
Sclerospora iseilematis Thirum. & Naras.		BPI 187262	**Lectotype**	1947	*Iseilema prostratum*	India, Mysore	OK185342	OK255493	Thirumalachar & Narasimhan (1949), this paper
		IMI 38399	**Isotype**	1947	*Iseilema prostratum*	India, Mysore	—	—	Thirumalachar & Narasimhan (1949), this paper
Sclerospora northii W. Weston		BPI 187307	**Lectotype**	1924	*Saccharum maximum*	Fiji Islands, Suva	—	—	Weston (1929), this paper
		FH 965380	**Isotype**	1924	*Saccharum maximum*	Fiji Islands, Suva	—	—	Weston (1929), this paper
Sclerospora secalina Naumov		Not designated	—	1949?	*Secale cereale*	Former U.S.S.R.	—	—	Naumov (1949)
Viennotia oplismeni J.A. Crouch & Thines		GZU 335974	**Holotype**	1963	*Oplismeni hirtellus*	Guinea, near Kindia	—	AY035527, AY273977	Göker *et al.* (2003), this paper
		IMI 103944	**Isotype**	1963	*Oplismeni hirtellus*	Guinea, near Kindia	—	—	Göker *et al.* (2003), this paper
		BPI 784624	**Isotype**	1963	*Oplismeni hirtellus*	Guinea, near Kindia	—	—	Göker *et al.* (2003), this paper

[1] Stevens Philippine Fungi, Island of Luzon, No. 811.

[2] Herbarium Schlesischer Pilze: W. G. Schneider, No. 553.

for accessions that were associated with specimens lodged in reference collections and described in peer-reviewed literature. "Unpublished" NCBI nucleotide accessions with uncertain provenance and/or lacking association with a peer-reviewed scientific publication were not included in the summary. New *cox*2 and 28S rDNA sequence data was extracted from unpublished genome assemblies of three species: *Peronosclerospora philippinensis, Sclerospora iseilematis*, and *Sclerospora northii*. Genome data was generated using Illumina sequencing technology following the general protocols described in Fletcher *et al.* (2018); a full paper describing these genomes is forthcoming.

RESULTS

Including the six species described as part of this paper for validation purposes (see Taxonomy section, below), there are 39 distinct and validly published species that cause downy mildew diseases of *Poaceae* hosts. Three subfamilies in the *Poaceae*, the warm season (C4 photosynthesis) grass subfamilies *Chlorioideae*, *Panicoideae*, and the cool-season (C3 photosynthesis) grass subfamily *Pooideae*, are parasitized by these organisms. With the notable exception of the widespread pathogen *Sclerophthora macrospora*, all the most destructive, widespread, and economically important GDM pathogens parasitize cereals and other grasses in the *Panicoideae*. In contrast with the pathogens of the *Panicoideae*, the GDM species known from *Chlorideae* hosts (*Baobabopsis donbarretti*, *Baobabopsis enneapogonis*, *Eraphthora butleri*, *Sclerophthora farlowii*) have rarely been reported or were reported just once at the time of the original descriptions.

The species *Sclerospora magnusiana* (Sorokine 1889) is an uncertain member of the genus *Sclerospora*, given that its host – the spore-forming horsetail plant [*Equisetum* sp. (*Equisetaceae, Pterdophytes*)] – is not a member of *Poaceae*. Waterhouse (1964) suggested that the species might be a chytrid rather than a member of *Sclerospora*, but Sorokine's (1889) description and depiction of the formation of oospores appear to depict an oomycete. However, unlike *Sclerospora graminicola*, which produces oospores embedded in the host tissue, the mature oospores of *Sclerospora magnusiana* form a powder-like layer on the infected plants (Sorokine 1889). Sorokine did not specify a type, but LEP contains a specimen (LEP 9584) collected by N. Sorokine on *Equisetum arvense* from Orsk, Russia in 1894 that could serve as neotype for the species and should be examined, especially using molecular data. However, as *Sclerospora magnusiana* does not infect a grass, it is not included in our summary.

Taxonomy

Baobabopsis R.G. Shivas *et al.*, *IMA Fungus* **6**: 484. 2015.

Type species: *Baobabopsis donbarrettii* R.G. Shivas *et al.*, *IMA Fungus* **6**: 485. 2015.

Description: *Sporangiophores* evanescent, hyaline, cylindrical, 75–120 µm × 20–28 µm wide, unbranched, with 5–20 ampulliform to lageniform ultimate branchlets. *Sporangia* hyaline, deciduous. *Oogonia* subglobose, golden yellow, 27–45 × 25–39 µm; wall (including warts) uneven, verrucose with rounded warts, 3–11 µm thick. *Oospores* globose to broadly ellipsoidal, pale to golden yellow, 19–29 × 18–28 µm, one per oogonium; wall even, smooth, 1–3 µm thick (Thines *et al*. 2015).

Diagnosis: *Baobabopsis* is distinguished from all other *Peronosporaceae* genera in that it produces broad club-shaped to cylindrical sporangiophores bearing a cluster of terminal ampulliform projections that give rise to sporangia. The genus is also distinguished through its position in phylogenetic trees constructed using 28S rDNA and *cox*2 sequence data.

Note: *Baobabopsis* currently contains three species and is exclusively known from Australia as a parasite of *Chloridoideae* hosts (Thines *et al*. 2015, Ryley *et al.* 2021).

Baobabopsis donbarrettii R.G. Shivas *et al.*, *IMA Fungus* **6**: 485. 2015.

Typus: **Australia**, Western Australia, Kununurra, near Lake Kununurra, *Perotis rara* (*Chloridoideae*, *Cynodonteae*), 19 Apr. 2011, *R.G. Shivas & T.Y. Chi* (**holotype** BRIP 54675).

Description: *Sporangiophores* cylindrical, evanescent, hyaline, 75–120 × 20–28 µm, with 5–20 terminal ampulliform to lageniform branches with a narrow neck 7–14 × 3–7 µm. *Sporangia* broadly ellipsoidal, hyaline, narrowed slightly approaching base, 16–20 × 11–18 µm. *Oogonia* subglobose, golden yellow, (27–)32.5–36.0–39.5(–45) × (25–)28–31.7–36(–39) µm diam; wall (including warts) uneven, densely verrucose with rounded warts, 3–9 µm thick. *Oospores* globose to broadly ellipsoidal subhyaline to golden yellow, (19–)22–24.1–27(–29) × (18–)20–22.5–25(–28) µm diam; wall smooth, even, 1–3 µm thick (Thines *et al.* 2015; Fig. 1A).

Diagnosis: Produces broad club-shaped to cylindrical sporangiophores, a unique feature among the *Peronosporaceae*. Differs from *Baobabopsis enneapogonis* because of its parasitism of *Perotis rara*, the production of densely verrucose oogonia walls and its unique *cox*2 sequence, which shares 98.2 % nucleotide identity with *Baobabopsis enneapogonis*.

Reference sequence data: Ex-holotype nucleotide sequences KT248948 (*cox*2) and KT248945 (28S rDNA).

Host range: Known only from the type specimen on *Perotis rara*.

Notes: To our knowledge, this species has not been reported since its description in 2015 (Thines *et al.* 2015). The host is native to and widely distributed across Australia, and is also known from New Guinea, the Philippines, Thailand, and Vietnam. It is unknown if the range of *Baobabopsis donbarrettii* extends beyond the type locale or whether the species has any significant impact on host populations.

Baobabopsis enneapogonis Thines *et al.*, *IMA Fungus* **6**: 486. 2015.

Typus: **Australia**, Northern Territory, East MacDonnel Ranges, near Corroboree Rock turnoff, *Enneapogon cylindricus* (*Chloridoideae, Eragrostideae*), 21 Apr. 2007, *A.R. McTaggart, J. Liberato, M.D.E. & R.G. Shivas* (**holotype** BRIP 49822).

Description: *Oogonia* subglobose, golden yellow, (30–)32.5–36.3–40(–42) × (29–)30–33.1–36(–39) µm; wall moderately verrucose with rounded warts, 3–11 µm thick (including warts), uneven, remnants of antheridium often attached. *Oospores* globose to broadly ellipsoidal, pale to golden yellow, (20–) 21.3–23.0–24.7(–26) × (19–)20.5–21.9–23.5(–24) µm diam; wall even, smooth, (1–)1.5(–2) µm thick. Asexual morph not observed (Thines *et al*. 2015; Fig. 1B).

Diagnosis: Differs from *Baobabopsis donbarrettii* based on (1) the production of slightly less prominent warts, and moderately verrucose oogonial walls; (2) its unique *cox*2 sequence, which shares 98.2 % nucleotide identity with *Baobabopsis donbarrettii*; and (3) parasitism of *Enneapogon avenaceus* and *Enneapogon cylindricus.* Differs from *Baobabopsis marneyi* based on its unique *cox*2 sequence, which shares 96 % nucleotide identity.

Reference sequence data: Ex-holotype nucleotide sequence KT248946 (*cox*2).

Host range: *Enneapogon avenaceus*, *Enneapogon cylindricus* (*Chloridoideae*, *Eragrostideae*).

Notes: Sporangiophores have not been observed from *Baobabopsis enneapogonis*, so it is unknown whether this species shares the diagnostic broad club-shaped to cylindrical sporangiophores observed from *Baobabopsis donbarrettii*.

To our knowledge, this species has not been reported since its description in 2015 when four collections in Australia were made between 2007 to 2014 (Thines *et al*. 2015). *Enneapogon avenaceus* and *Enneapogon cylindricus* are endemic to Australia but are not known elsewhere in the world. Many members of the genus *Enneapogon* are globally distributed; however, it is not

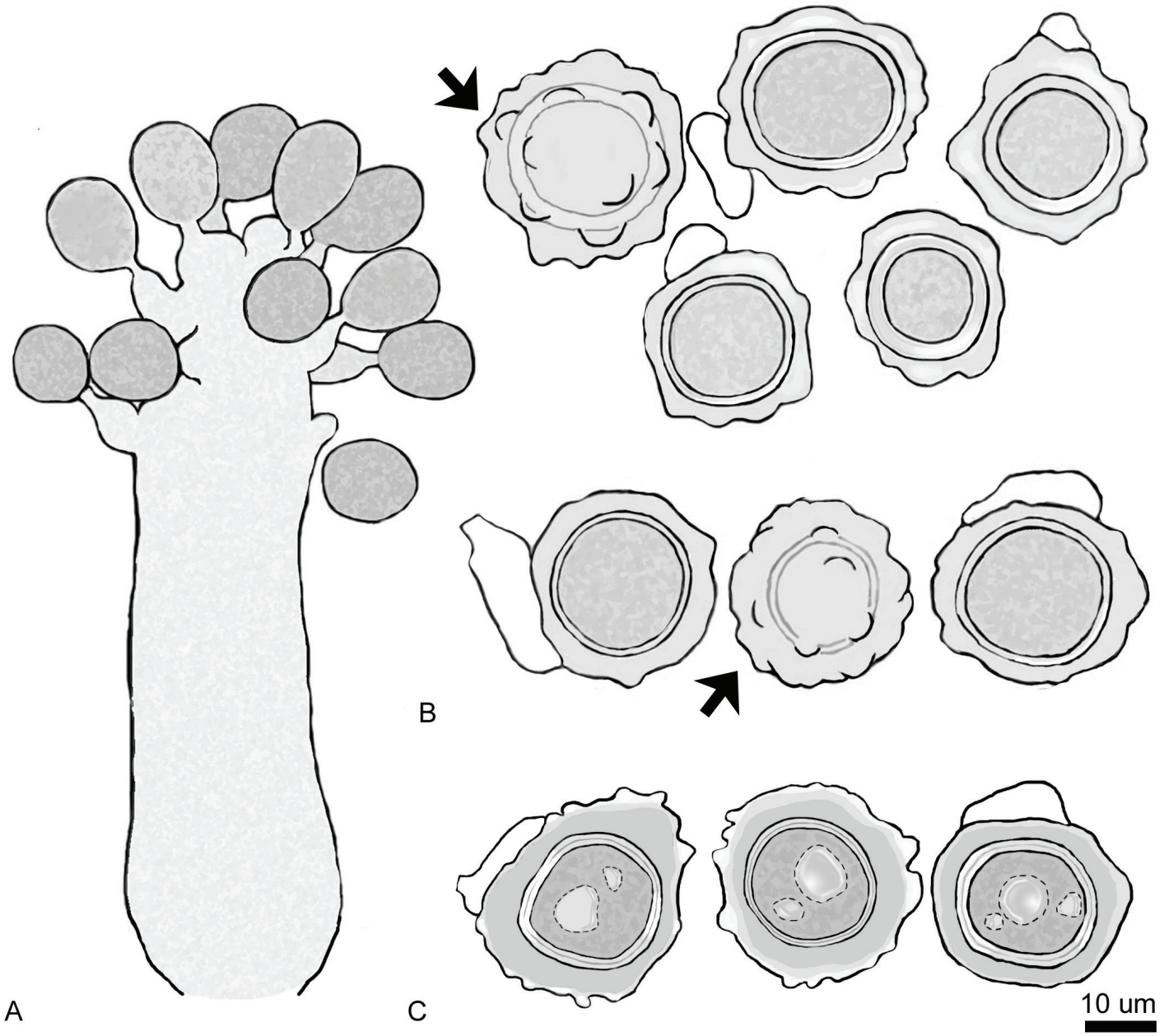

Fig. 1. A. *Baobabopsis donbarrettii*, sporangiophore (left) and oospores in cross-section, some with antheridia attached (upper right). One oospore is shown in surface view (arrow). **B.** *Baobabopsis enneapogonis*, oospores in cross-section, some with antheridia attached. One oospore is shown in surface view (arrow). **C.** *Baobabopsis marneyi*, oospores. Illustrations were prepared from published reference images found in Thines *et al.* (2015) and Ryley *et al.* (2022).

known if the host range of *Baobabopsis enneapogonis* extends beyond the two reported hosts or if the pathogen is distributed outside of Australia.

Because *Baobabopsis enneapogonis* parasitizes two of the same hosts and is similar in appearance to *Baobabopsis marneyi*, discrimination between these species should be confirmed using *cox*2 sequence data.

Baobabopsis marneyi R.G. Shivas *et al*., *Mycol. Progr*. **21**: 300. 2022.

Typus: **Australia**, Queensland, Georgetown, *Enneapogon polyphyllus* (*Chloridoideae, Eragrostideae*), 13 Apr. 2019, *J. Kruse, A.R. McTaggart, M.J. Ryley, M.D.E. & R.G. Shivas* (**holotype** BRIP 70341).

Description: *Oogonia* sub-globose to globose, golden brown, (24–)26–33(–35) µm diam; wall 3–8 µm thick (including warts), uneven, tuberculate, warts rounded 3–5 × 2–3 µm. *Oospores* globose to sub-globose, hyaline, (19–)21–24(–25) µm diam, adnate with oogonial wall; wall 1–2 µm thick, even, smooth (Ryley *et al.* 2021; Fig. 1C).

Diagnosis: *Baobabopsis marneyi* is distinguished from other species in the genus *Baobabopsis* through its unique *cox*2 sequence, which shares 92 % nucleotide identity with *Baobabopsis donbarrettii* and 96 % nucleotide identity with *Baobabopsis enneapogonis*. Differs from *Baobabopsis donbarrettii* by its parasitism of *Enneapogon* species.

Reference sequence data: Ex-holotype nucleotide sequence OK336436 (*cox*2).

Host range: *Enneapogon avenaceus*, *Enneapogon cylindricus, Enneapogon polyphyllus* (*Chloridoideae*, *Eragrostideae*).

Notes: *Baobabopsis marneyi* is recently documented from collections made on the foliage of three species of *Enneapogon* from three regions of Australia (Ryley *et al.* 2021). Infection results in the blades of grass splitting along the vascular strands, sometimes up to 20 cm in length. Given the overlapping host range and morphology of *Baobabopsis marneyi* and *Baobabopsis enneapogonis*, *cox*2 sequence data should be used to discriminate these two species.

Eraphthora Telle & Thines [as '*Erapthora*'], *Mycol. Progr*. **11**: 127. 2012.

Type species: *Eraphthora butleri* (W. Weston) Telle & Thines, *Mycol. Progr*. **11**: 127. 2012.

Diagnosis: Similar to *Basidiophora* and *Benua*, this species is unique among all other *Peronosporaceae* genera in possessing simple, club shaped sporangiophores. Differs from *Basidiophora* and *Benua* by the production of evanescent sporangiophores, oospores with thicker walls, and its parasitism of *Eragrostis* (Telle & Thines 2012).

Notes: The genus *Eraphthora* was established to accommodate the pathogen originally described as *Sclerospora butleri* based on the production of thick-walled oospores resembling those of *Sclerospora* (Weston 1921). Following the discovery that *Sclerospora butleri* produces unbranched, club-shaped sporangiophores and zoospores, these morphological characters were used to justify the transfer of the species to the genus *Basidiophora* (Thirumalachar & Whitehead 1952). However, Thirumalachar & Whitehead also noted that nocturnal sporangiospore production and host leaf shredding were not known from *Basidiophora* and suggested that the species might represent an intermediate form between *Basidiophora* and *Sclerospora* (Thirumalachar & Whitehead 1952). Subsequent authors rejected placement of *Sclerospora butleri* in *Basidiophora,* arguing that host preference, oogonial morphology, and the nocturnal production of evanescent sporangial structures were better aligned with the genus *Sclerospora* (Kenneth & Kranz 1973, Dick *et al*. 1984, Barreto & Dick 1991). In 2012, Telle & Thines erected the new genus *Erapthora* based on the unique combination of morphological characters and the *cox*2 phylogenetic distinctiveness that places it as the sister lineage of *Sclerophthora*.

The recent identification of two new species of *Eraphthora* parasitizing *Eragrostis cilianensis* (Ryley *et al*. 2021) introduces a new complication regarding members of the genus *Eraphthora*. Although the genus is typified by *Eraphthora butleri* (Telle & Thines 2012), the four specimens of this species that were examined when *Eraphthora* was erected were later identified as *Eraphthora drenthii* (Ryley *et al*. 2021). The two newly described species—*Eraphthora drenthii* and *Eraphthora occultata*—are sustantially different from generic type *Eraphthora butleri*, in that they produce substantially larger oospores, thicker oospore walls, and produce different symptoms in the host plant (Ryley *et al*. (2021). Additional molecular phylogenetic research incorporating type materials of *Eraphthora butleri* is recommended for further clarification of how these organisms are related to one another.

Eraphthora butleri (W. Weston) Telle & Thines, *Mycol. Progr*. **11**: 127. 2012.
Basionym: *Sclerospora butleri* W. Weston, *Phytopathol.* **21**: 125. 1933.
Synonyms: *Basidiophora butleri* (W. Weston) Thirum. & M. D. Whitehead *Amer. J. Bot*. **39**: 4. 1952.
'*Sclerophthora butleri*' (W. Weston) M. W. Dick, *Straminipilous Fungi* (Dordrecht): 147. 2001. [*nom. inval*., presumably *lapsus calami* (Telle & Thines 2012)].

Typus: **Malawi** (formerly Nyasaland), Bulaki, Evans tobacco estate, *Eragrostis aspera* (*Chloridoideae, Eragrostideae*), Mar. 1927, *E. J. Butler* [**lectotype** designated here, BPI 187075 (MBT 10002143); **isotype** designated here, FH 965376 (MBT 10002144)]. Supplementary Fig. S1 shows the lectotype BPI 187075.

Description: *Oogonia* spherical to irregularly subspherical, pallid golden to dark amber, 33–36.9 µm (up to 29–40.9 µm) diam, contents comprising a finely granular, hyaline or grayish matrix, with one or several oil droplets not arranged in any definite pattern; wall relatively even with numerous bluntly rounded, papillate to finger-like protrusions, 4–10 µm (excluding protrusions), protrusions hyaline, base 2–4 × 2–5 µm high. *Oospores* spherical, hyaline, 19–22.9 µm diam; wall 2–3 µm thick. Asexual morph not observed (Weston 1933; Fig. 2A).

Diagnosis: Except for *Basidiophora* and *Benua*, differs from all *Peronosporaceae* by its simple, unbranched, club-shaped sporangiophores. Differs from *Basidiophora* and *Benua* by

its parasitism of *Eragrostis* spp., thick-walled oospores and tuberculate oogonial wall, and nocturnal production of evanescent sporangiophores. *Eraphthora butleri* is distinguished from *Eraphthora drenthii* and *Eraphthora occultata* based on having smaller oospores, thinner oospore walls, and the symptoms produced in the parasitized host.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Eragrostis aspera*. Also reported from *Eragrostis amabilis* and *Eragrostis tremula* (*Chloridoideae*, *Eragrostideae*).

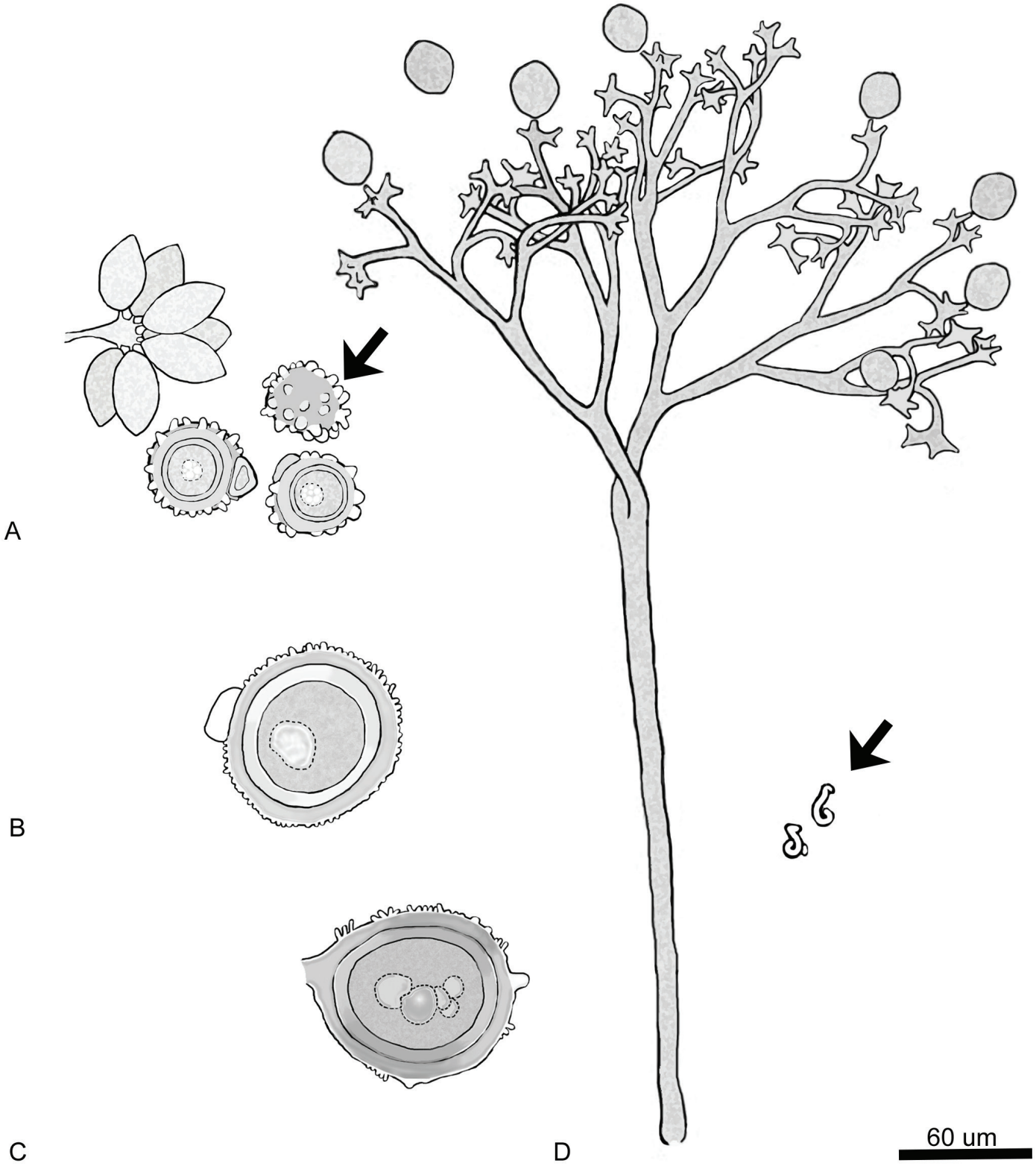

Fig. 2. A. *Eraphthora butleri*, sporangiophore and oospores in cross sections with antheridia attached. One oospore is shown in surface view (arrow). **B.** *Eraphthora drenthii*, oospores. **C.** *Eraphthora occultata*, oospores. **D.** *Graminivora graminicola*, sporangiophore and helical haustoria (arrow). Illustrations were prepared from published reference images found in Weston (1933), Thirumalchar & Whitehead (1952), Thines & Göker (2006) and Ryley *et al.* (2022).

Notes: *Eraphthora butleri* is reported on weedy species of *Eragrostis* from Africa, Australia, India, and Italy (Weston 1921, 1933, Patel 1949, Waterhouse 1964, Telle & Thines 2012, Farr & Rossman 2021). The type host, *Eragrostis aspera*, is a weedy grass distributed throughout Africa, India, and Malaysia in temperate and tropical regions. Natural infections of *Eragrostis aspera* by *Eraphthora butleri* result in disease symptoms such as chlorosis and malformed, shredded leaves (Weston 1921, 1933, Patel 1949, Telle & Thines 2012). As noted by Telle & Thines (2012) it is unknown whether *Eraphthora butleri* can infect agronomic species of *Eragrostis* such as *Eragrostis tef* (teff).

Reports prior to 2021 show *Eragrostis cilianensis* as a host of *Eraphthora butleri*, but new research shows that downy mildew on this host is attributable to at least two new species, *Eraphthora drenthii* and *Eraphthora occultata* but is not known from *Eraphthora butleri* (Ryley *et al.* 2021). To our knowledge, nucleotide sequence data from *bona fide* specimens of *Eraphthora butleri* are not currently available. Nucleotide sequences from specimens previously accepted as *Eraphthora butleri* parasitizing *Eragrotis cilianensis* are now known to be *Eraphthora drenthii* (DAR 4201: HQ413338; DAR 4200: HQ413337; DAR 4288: HQ413339; FR-0046004: HQ413336, KP965746, KT248944) (Ryley *et al.* 2021).

Weston did not designate a holotype, but specimens were accessioned at BPI and FH (BPI 187075, FH 965376). These specimens bear the published collection details and are annotated in Weston's handwriting; BPI 187075 is designated here as the lectotype for *Eraphthora butleri*.

Eraphthora drenthii M.J. Ryley *et al.*, *Mycol. Progr*. **21**: 301. 2022.

Typus: **Australia**, New South Wales, *Eragrostis cilianensis* (*Chloridoideae, Eragrostideae*), Apr. 1950, *P. Valder* (**holotype** DAR 4201).

Description: *Oogonia* globose to subglobose, light golden, (64–)68–84(–92) µm diam; wall uneven, 4–7 × 2–3 µm, with subhyaline, digitate, straight to curved projections measuring 7–8 µm thick. *Oospores* globose to sub-globose, (52–)56–67(–73) µm diam, adnate with oogonial wall, often with a single central vacuole; wall even, smooth 6–8 µm thick (Ryley *et al.* 2021; Fig. 2B).

Diagnosis: Differs from *Eraphthora butleri* on the basis of having larger oospores, thicker oospore walls, symptoms induced in the host, and parasitism of *Eragrostis cilianensis*. Differs from *Eraphthora drenthii* based on nucleotide sequence of the *Cox*2 marker. Differs from *Eraphthora occultata* based on nucleotide sequence of the *Cox*2 marker.

Reference sequence data: Ex-holotype nucleotide sequence HQ413338 (*cox*2).

Host range: Known only from the type host *Eragrostis cilianensis*.

Notes: The type host, *Eragrostis cilianensis*, is naturalized through most parts of the world, including Europe, Asia, Africa and North America. It is not yet known if *Eraphthora drenthi* is co-distributed with the host. To date, *Eraphthora cilianensis* is only known from from four specimens of *Eragrostis cilianensis* collected during the 1950s in Australia and from an unidentified species of *Eragrostis* collected in Italy. Unlike the generic type *Eraphthora butleri*, which induces leaf fraying in its hosts, *Eraphthora drenthii* parastism results in malformed inflorescences (Ryley *et al.* 2021).

Eraphthora occultata Y.P. Tan *et al.*, *Mycol. Progr*. **21**: 303. 2022.

Typus: **Australia**, New South Wales, Warren, *Eragrostis cilianensis* (*Chloridoideae, Eragrostideae*), Jan. 1967, *K. Brennan* (**holotype** DAR 16237).

Description: *Oogonia* globose to subglobose, light golden, (65–)71–90(–95) µm diam; wall uneven, 4–10 µm, with straight to curved, sub-hyaline, digitate projections measuring 4–7 × 3 µm thick. *Oospores* globose to sub-globose, (57–)60–71(–75) µm diam, adnate with oogonial wall, often with a single central vacuole; wall even, smooth, 5–6 µm thick. Asexual morph not observed (Ryley *et al.* 2021; Fig. 2C).

Diagnosis: Differs from *Eraphthora butleri* on the basis of having larger oospores, thicker oospore walls, symptoms induced in the host, and parasitism of *Eragrostis cilianensis*. Differs from *Eraphthora drenthii* based on nucleotide sequence of the *Cox*2 marker.

Reference sequence data: Ex-holotype nucleotide sequence OK392240 (*cox*2).

Host range: Known only from the type specimen on *Eragrostis cilianensis*.

Notes: *Eraphthora occultata* shares many features in common with its sister species, *Eraphthora cilianensis*, including morphology and parasitism of *Eragrostis cilianensis*. However, it has only been observed once from the type collection made in Australia in 1967.

Graminivora Thines & Göker, *Mycol. Res*. **110**: 651. 2006.

Type species: *Graminivora graminicola* (Naumov) Thines & Göker, *Mycol. Res.* **110**: 652. 2006.

Diagnosis: Differs from all other *Peronosporaceae* through differences in haustorium morphology, sporangiophore morphology and ultrastructure, and nucleotide sequences of rDNA.

Notes: The genus *Graminivora*, typified by *Graminivora graminicola*, was erected to accommodate the pathogen originally described as *Bremia graminicola*. The species was originally described as a *Bremia* based on features that were thought to be unique to the genus during the early 20th century. Specifically, *Bremia graminicola* produces lasting, dichotomously branched sporangiophores with inflated ends, multiple sterigmata and subglobose sporangia (Naumov 1913). Thines & Göker (2006) documented differences in haustorium and sporangiophore morphology and 28S rDNA sequences between the *Bremia* generic type and *Bremia graminicola*, resulting in the transfer of *Bremia graminicola* into the new genus *Graminivora*. *Graminivora* contains one species and is distributed in four Asian countries as a parasite of *Arthraxon hispidus*.

Graminivora graminicola (Naumov) Thines & Göker, *Mycol. Res*. **110**: 652. 2006.
Basionym: *Bremia graminicola* Naumov, *Bull. Soc. Mycol. France* **29**: 275. 1913.
Synonym: *Bremia graminicola* var. *indica* Patel, *Indian Phytopathol.* **1**: 106. 1949.

Typus: **Russia**, South Ussuriysk region, Siberia, *Arthraxon hispidus* (*Panicoideae, Andropogoneae*), 31 Jul. 1912, *N. Naumov* (**lectotype** designated here LEP 4385 [MBT 10002145]; **isotypes** BPI 786232, LEP 4377, LEP 4384, FH 01012075, E 00297399 [MBT 10002146]). Supplementary Fig. S2 shows the lectotype BPI 786232.

Description: *Sporangiophores* hyaline with inflated base above stomata; curved, dichotomous or irregular branching in the upper part, usually 4–6 times, after the last ramification inflated into a vesicle carrying four ultimate branchlets (sometimes two, as many as eight, typically in even numbers), up to 600 µm long × 9–10 µm wide at the base and 5–6 µm wide in the terminal ramifications. *Sporangia* globose to ovoid, hyaline, average diam 12 µm, with short basal and papilla at the slightly flattened apical end, mode of germination unknown. *Oospores* not observed (Naumov 1913, Thines *et al*. 2006; Fig. 2D).

Diagnosis: Differs from *Bremia* species in that it parasitizes *Arthraxon hispidus*, and produces hyphal haustoria that often form small spirals, with sporangiophores that usually show strong curving from the very start of ramifications, and swollen sporangiophore tips that typically carry 2–4 ultimate branchlets. Differs from other *Peronosporaceae* on the basis of lasting, dichotomously branched sporangiophores with inflated ends and its phylogenetic position based on *cox*2 and 28S rDNA sequences.

Reference sequence data: Sequence data not available from type materials. Ex-HUH 738 nucleotide sequences KP965747 (*cox*2), KP965742 (28S rDNA).

Host range: Known only from the type host *Arthraxon hispidus*.

Notes: *Graminivora graminicola* is known only from *Arthraxon hispidus* from China, India, Japan, and Russia (Togashi 1926, Ito 1936, Patel 1949, Novotel'nova & Pystina 1985, Tao 1998, Thines & Göker 2006). Parasitized leaves are discolored with variably sized yellow to reddish spots, often running parallel to the leaf veins, with leaves eventually withering and dying (Naumov 1913). The type host – a weedy grass commonly known as small carpetgrass—is native to the Asian continent where *Graminivora graminicola* has been reported. It is unknown if *Graminivora graminicola* also resides in North America, where *Arthraxon hispidus* is present as a highly invasive species thought to have been introduced to the continent in 1876. Although *Arthraxon hispidus* is widely distributed worldwide, there is no indication of any economic or ecological impact on the host when infected by this pathogen.

The Harvard Herbarium database lists the collection location of FH 01012075 as "Liberia, Africa," which appears to be a misreading of Naumov's handwriting. On the digitized version of the specimen label for FH 01012075 (http://storage.idigbio.org/fh/mycology/barcode-01012/FH01012075.jpg), one can see the ambiguity of the first letter (L/S) of the location. Naumov (1913) lists the location as "aux environs de Wladiwostok" and "Austro-Ussuriensi (Rossiae orient.)," which roughly translates to "around Wladiwostok" and "Ussurijsk region of eastern Russia." Both fall within the broad geographic area known as "Siberia"; therefore, "Liberia" is incorrect. Similarly, the online database of the Royal Botanical Garden of Edinburgh lists the location of E 00297399 as "Jaczewski, Poland," which is also an error in digitizing the specimen label. Both the FH and BPI specimens originated from "Herbario Instituti Mycol. et Phytopath. Jaczewski Petropolis," which is the former name of LEP. Assuming LEP also sent E their specimen, it seems likely "Jaczewski Petropolis" was incorrectly entered as the location of collection instead of the herbarium from which the material was sent.

Naumov did not designate a holotype, but materials from the original collection were found in BPI, E, FH, and LEP. LEP 4385 is designated here as the lectotype for *Graminivora graminicola*.

Peronosclerospora (S. Ito) Hara, in Shirai & Hara, List of Japanese Fungi hitherto unknown, 3rd Edn: 247 ['257']. 1927.
Basionym: *Sclerospora* subgen. *Peronosclerospora* S. Ito, *Bot. Mag., Tokyo* **27**: 218. 1913.
Peronosclerospora (S. Ito) C.G. Shaw, *Mycologia* **70**: 594. 1978. [*nom. illegit.*, Art. 53.1]

Type species: *Peronosclerospora sacchari* (T. Miyake) Shirai & Hara, *List of Japanese Fungi hitherto unknown*, **3rd edn**: 247 ['257'] (1927).

Description: No description was provided for the basionym *Sclerospora* subgen. *Peronosclerospora* or by Shirai & Hara when the genus *Peronosclerospora* was erected (Ito 1913; Shirai & Hara 1927). In his superfluous description of *Peronosclerospora*, Shaw (1978) provided a useful description of the genus, as follows: "*Mycelium* parasitic in higher plants, hyaline, coenocytic; imperfect state like *Sclerospora* except that conidia are always produced rather than sporangia. *Conidiophores* produced at night, erect, dichotomously branched two to five times; sterigmata conoid to subulate, usually two, but three or four in some species. *Conidia* ellipsoid, ovoid or cylindrical, wall of uniform structure, neither operculate or poroid, always germinating by a single germ tube. *Oogonia* subglobose to spherical. *Oospores* globose or subglobose, 25–55 µm in diam; oospore wall partially or completely fused to the wall of the oogonium, oospore wall of three layers: exosporium chestnut to reddish brown at maturity, irregularly ridged, 1.0–3.0 µm thick; mesosporium very thin, hyaline; endosporium hyaline, uniformly thick, 1.5–3.5 µm thick."

Notes: The distinction between what we now recognize as *Peronosclerospora* and the genus *Sclerospora* was first pointed out by Ito (1913), who split *Sclerospora* into two subgenera based on differences in asexual spore germination, which occurs directly by germ tubes in *Peronosclerospora* and indirectly by zoospores in *Sclerospora*. Ito recognized that two taxa would fall into the new subgenus *Sclerospora* subgen. *Peronosclerospora*; namely *Sclerospora sacchari* and *Sclerospora graminicola* var. *andropogonis-sorghi* (Ito 1913). *Sclerospora* subgen. *Peronosclerospora* was described as the genus *Peronosclerospora* in 1927 (Shirai & Hara 1927), with just one species (*Peronosclerospora sacchari*) transferred as the generic type (Shirai & Hara 1927). The original description of *Peronosclerospora* went unnoticed among some members of

the scientific community, resulting in the description of several non-zoosporic species in the genus *Sclerospora* rather than in *Peronosclerospora* (*Sclerospora dichanthiicola*, *Sclerospora philippinensis*, *Sclerospora sorghii*, *Sclerospora westonii*), and a second, superfluous description of the genus in 1978 (Shaw 1978, Shaw & Waterhouse 1980).

From a practical standpoint, discriminating between *Peronosclerospora* and *Sclerospora* based on differences in asexual structures is not a trivial matter. Development of asexual spores by members of both genera is nocturnal under natural conditions. In *Peronosclerospora*, structures persist for just a few hours in the early morning until they germinate under conducive environmental conditions (*e.g.*, Sriinivasan *et al*. 1961). After germination, the asexual spores and related structures rapidly collapse, leaving no trace behind. As a result, asexual structures are not well preserved on herbarium materials and other collections on non-living host material, hindering identification and taxonomic study. Structures of *Sclerospora* last longer, but within a few days can also vanish. The challenging application of asexual spore morphology for *Peronosclerospora* identification is further complicated by the impact of environmental effects, such as host species, variety, and climate, on spore size and shape (Delanie 1972, Leu 1973, Kimigafukuro 1979, Bock *et al.* 2000, Dudka *et al.* 2007, Runge & Thines 2011).

Peronosclerospora currently includes 12 species that are parasites of hosts in the subfamily *Andropogoneae*, including destructive pathogens of staple crops such as maize, sorghum, and sugarcane. The genus is widely distributed across the eastern hemisphere, including Africa, Australia, East Asia, and Oceania. Just one species of *Peronosclerospora* – *Peronosclerospora sorghi* – is well documented from the Western Hemisphere, following its introduction to Central America in the 1950s (Toler *et al.* 1959, Futtrell 1974, Frederickson & Renfro 1977). *Peronosclerospora eriochloae* (as *Peronosclerospora globosa*) was reported from Texas in a meeting abstract (Kubicek & Kenneth 1984), however those reports need further scrutiny to verify the identity of the pathogen.

Peronosclerospora aristidae J. Kruse *et al.*, *Mycol. Progr*. **21**: 303. 2022.

Typus: **Australia**, Queensland, in leaves of *Aristida hygrometrica* (*Poales*, *Poaceae*), 27 Apr. 2018, *J. Kruse, M.J. Ryley, S.M. Thompson, M.D.E. & R.G. Shivas* (**holotype** BRIP 67069).

Description: *Oogonia* globose to sub-globose, golden yellow, (30–)39–51(–53) µm diam; wall with sparse, low, irregular, truncate ridges, 6–14 µm thick. *Oospores* globose to sub-globose, golden yellow, (23–)27–31(–32) µm diam, adnate with oogonal wall, with a single vacuole; wall even, smooth, hyaline, 1–2 µm thick. Asexual morph not observed (Ryley *et al*., Fig. 3A).

Diagnosis: Differs from all other *Peronosclerospora* based on oogonial walls with irregular, low, truncate ridges, parasitisim of *Aristida hygrometrica*, and its phylogenetic position based on the *cox*2 nucleotide sequences.

Reference sequence data: Ex-holotype nucleotide sequence OK336438 (*cox*2).

Host range: Known only from the type specimen on *Aristida hygrometrica*.

Notes: The host of *Peronosclerospora aristidae*, *Aristida hygrometrica*, is an Australian native grass, and the only known member of the the subfamily *Aristidoide* associated with a downy mildew. Infection by *Peronosclerospora aristidae* results in splitting of the leaf blade into strands that can measure up to 50 cm long.

Peronosclerospora boughtoniae M.J. Ryley *et al.*, *Mycol. Progr*. **21**: 303. 2022.

Typus: **Australia**, Queensland, Lizard Island, in leaves of *Sorghum plumosum* (*Poales*, *Poaceae*), 7 May 1978, *V.H. Broughton* (**holotype** BRIP 14388).

Description: *Oogonia* globose to sub-globose, light golden brown, (25–)29–40(–50) µm in diam; wall smooth with occasional scabrid, flattened sides bordered by inconspicuous ridges, 1–12 µm thick. *Oospores* globose, hyaline, (22–)24–29(–31) µm diam; wall even, smooth, 1–2 µm thick. Asexual morph not observed (Ryley *et al*., Fig. 3B).

Diagnosis: Differs from *Peronosclerospora maydis* on the same host in that it has smaller oospores. Distinguished from *Peronosclerospora mactaggartii* on *Sorghum timorense* through its unique *cox*2 sequence (96 % nucleotide identity).

Reference sequence data: Ex-holotype nucleotide sequence OK33649 (*cox*2).

Host range: Known only from the type specimen on *Sorghum plumosum.*

Notes: Infection by *Peronosclerospora boughtoniae* results in splitting of the leaf blade into strands that can measure up to 15 cm long.

Peronosclerospora dichanthiicola (Thirum. & Naras.) C.G. Shaw, *Mycologia* **70**: 595. 1978.
Synonym: *Sclerospora dichanthiicola* Thirum. & Naras. [as '*dichanthicola*'], *Phytopathol.* **42**: 598. 1952.

Typus: Illustration in *Phytopathol.* **42**: 597, fig. 1, 1952 (**lectotype** designated here [MBT 10002147]) based on collection made in **India**, Bihar, in the culms of *Dichanthium annulatum* (*Panicoideae*, *Andropogoneae*), 18 Dec. 1951, *M. J. Thirumalachar*.

Description: *Conidiophores* evanescent, nocturnal, erect, 83–130 µm long × 13 µm wide at basal plug, 17–27 µm wide at main axis branching point; basal part isodiametric, 33 × 13 µm width with inconspicuous knob-like structure at the base; branches are dichotomous (rarely secondary and tertiary branches), 2–6 in number, 33–37 × 83–90 µm, usually with primary branches that give rise to 2–3 obconical tapering sterigmata with conidia. *Conidia* globose to obovoid, hyaline, thin-walled, 21–28 × 15–18 µm, germinating by germ tubes. *Oospores* unknown (Thirumalachar *et al*. 1952; Fig. 3D).

Reference sequence data: No sequence data available.

Host range: Known only from the type specimen on *Dichanthium annulatum*.

Notes: To our knowledge, reports of *Peronosclerospora dichanthiicola* are limited to a single observation on *Dichanthium annulatum*, an important perennial forage grass in India (Waterhouse 1964, Thirumalachar & Narasimhan 1952, Farr & Rossman 2021). *Dichanthium annulatum* infected with *Peronosclerospora dichanthiicola* exhibits leaves that are chlorotic with yellow streaks, but there is no indication as to the overall impact of the pathogen on plant health (Thirumalachar & Narasimhan 1952). Given the rarity of *Peronosclerospora dichanthiicola* and its inability to infect maize or sorghum

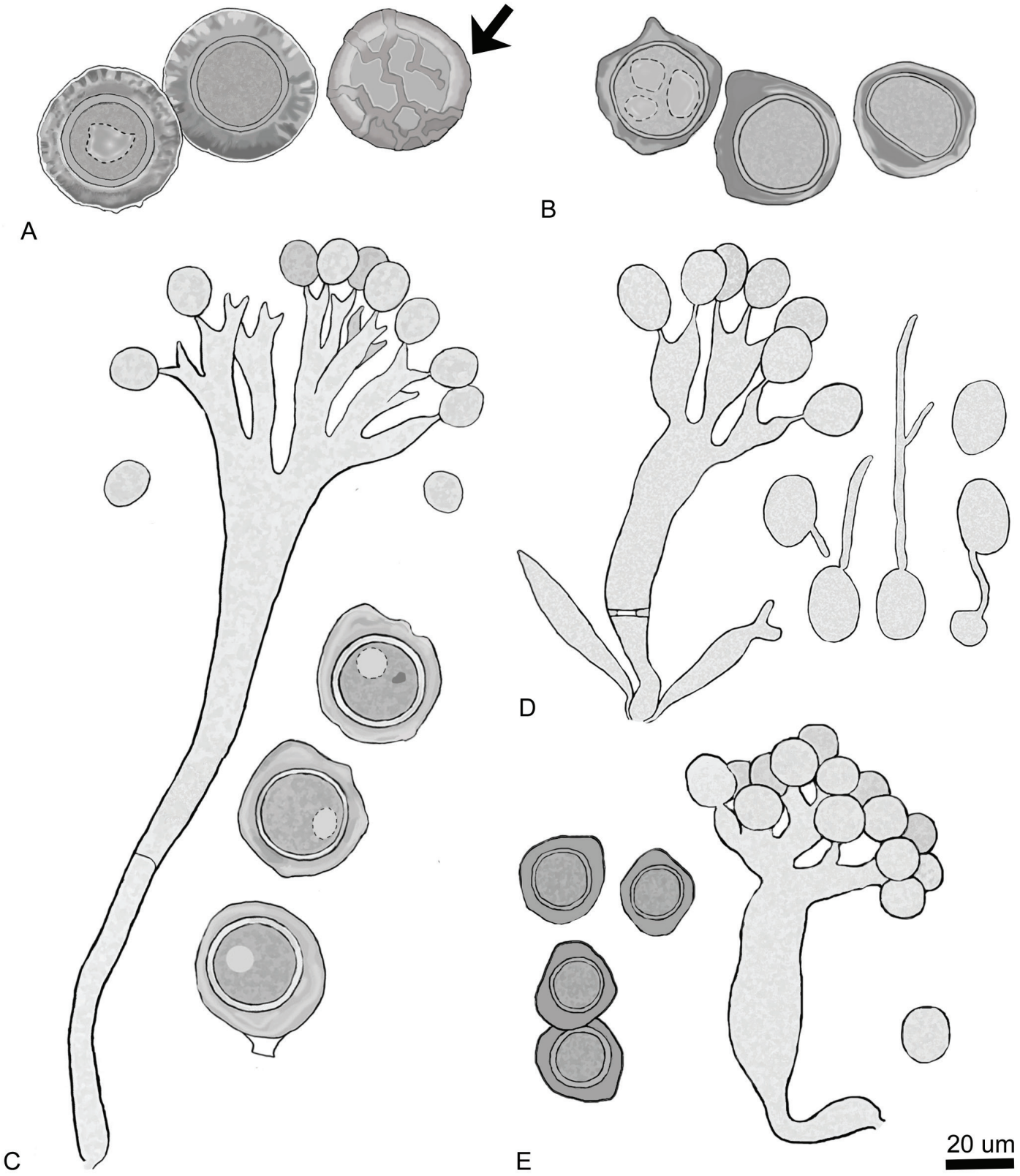

Fig. 3. A. *Peronosclerospora aristidae,* oospores in cross-section and one in surface view (arrow). **B.** *Peronosclerospora boughtoniae*, oospores. **C.** *Peronosclerospora eriochloae* sporangiophore and oospores. **D.** *Peronosclerospora dichanthicola*, mature and immature sporangiospores and germinating sporangia. **E.** *Peronosclerospora heteropogonis*, oospores and sporangiophore. Illustrations were prepared from published reference images in Thirumalachar & Narasimhan (1952), Siradhana *et al*. (1980), Ryley & Langdon (2001) and Ryley *et al.* (2022).

(Thirumalachar & Narasimhan 1952), the pathogen appears have little to no discernable impact on cultivated crops.

The species was described from material collected from India in 1951, but a type was not formally designated and it is unknown whether any materials from the study of Thirumalachar & Narasimhan (1952) were preserved in a reference collection. Although oospores were not observed, the asexual morph was well documented in the original publication, therefore an illustration from that publication is utilized as the lectotype.

Peronosclerospora eriochloae Ryley & Langdon, *Mycotaxon* **79**: 89. 2001.

Typus: **Australia**, Upper Pilton, Queensland, on tillers of *Eriochloa pseudoacrotricha* (*Panicoideae, Paniceae*), 9 Apr. 1979, *M.J. Ryley* [**holotype** BRIP 13693; **isotypes** BRIP 13691, BRIP 13692, FR-0046005 (MBT 10002148)].

Description: *Conidiophores* hyaline, 245–280 µm long with septum 90–115 µm above base; swollen base 6–13 µm wide decreasing to 6–9 µm wide at septum; above septum diam increases to 20–30 µm at the start of branching; dichotomously branched with secondary, tertiary, and quaternary branches 45–100 µm wide; sterigmata at tips of branches, conoid-subulate 4–9 µm long × 3–4 µm wide. *Conidia* globose to subglobose hyaline, (9–)13.3(–18) × (9–)12(–13.4) µm, without operculum or pore; germinating by one or two germ tubes. *Oogonium* globose to subglobose, orange to luteus, (33–)46.6(–70) µm diam; wall hyaline, confluent with oospore wall, 1.0–1.5 µm thick. *Oospores* globose, hyaline, 27–33.5(–46) µm diam, one per oogonium; wall in two layers with exosporium reddish brown, 2–15 µm thick; and endosporium hyaline, 2–3 µm thick. (Ryley & Langdon 2001; Fig. 3C).

Reference sequence data: Ex-isotype FR-0046005 nucleotide sequences HQ261813 (*cox*2), HQ261786 (28S rDNA).

Host range: *Eriochloa pseudoacrotricha*, *Eriochloa laevinode*, *Zea mays* (*Panicoideae*, *Andropogoneae*).

Notes: *Peronosclerospora eriochloae* has been identified from three hosts in Australia (Ryley & Langdon 2001, Telle *et al*. 2011), but it is unknown if the pathogen is distributed outside of that country. *Eriochloa pseudoacrotricha* is native to and widely distributed in Australia but also has been introduced across the southern USA (Texas) and South America. Based on similarities in morphological characteristics, Ryley & Langdon (2001) hypothesized that the invalidly published *Peronosclerospora globosa* described from *Eriochloa contracta* in Texas (Kubicek & Kenneth 1984) might represent the same species as *Peronosclerospora eriochloae*; see notes on *Peronosclerospora globosa* below.

The impact of *Peronosclerospora eriochloae* on host populations is not known. Infection of *Eriochloa pseudoacrotricha* results in tillers that do not produce inflorescences, and abnormally wide, chlorotic frayed leaves that eventually become necrotic (Ryley & Langdon 2001).

'***Peronosclerospora globosa***' Kubicek & R.G. Kenneth, *Phytopathol.* **74**: 792. 1984. [*nom. nud*, Art. 36.1, 39.1]

Typus: *non designates.*

Notes: Reported on *Eriochloa contracta* from the southern USA (Texas) and on *Eriochloa creba* (*Panicoideae, Paniceae*) from New South Wales, Australia (Kubicek & Kenneth 1984). Kubicek & Kenneth (1984) proposed the name *Peronosclerospora globosa* along with a short English description in a meeting abstract but never effectively published a Latin description or designated a holotype (Ryley & Langdon 2001). Based on morphology, Ryley & Langdon (2001) found their specimen of *Peronosclerospora eriochloae* on *Eriochloa pseudoacrotricha* similar to *Peronosclerospora globosa*, but deemed it sufficiently different to describe it as a new species rather than validate *Peronosclerospora globosa*. If specimens from the Texas collections referred to in Kubicek & Kenneth (1984) can be located, they should be further examined to see if they represent a distinct species. However, it is unknown if Kenneth's collections are extant, as a search of Mycoportal, BPI, and TAMU did not yield any specimens corresponding to the Texas collection.

Peronosclerospora heteropogonis J.A. Crouch ***sp. nov.*** MycoBank MB 840573.
Synonym: '*Peronosclerospora heteropogonis*' Siradhana *et al.* [as '*heteropogoni*'] *Curr. Sci*. **49**: 316. 1980. [*nom. inval*., Art. 40.1].

Typus: **India**, Rajasthan, Udaipur, Sisarma, on leaves of *Zea mays* (*Panicoideae*, *Andropogoneae*), 2005, *K. Mathur* (**holotype** designated here, HOH 898).

Description: *Conidiophores* evanescent, nocturnal, erect, with dichotomous branching and secondary and tertiary branches with a swollen base; from base to branching 81.6–142.8 × 14.3–255.5 µm with an average of 101.8 × 20.1 µm. *Conidia* globose, hyaline, thin-walled without operculum or pore, 14.3–22.4 × 14.3–20.4 (17.7 × 16.2) µm; germination by germ tubes. *Oospores* globose, tuberculate, persistent, 24.5–36.7 (29.0) µm diam, mostly fused to oogonial wall, contents granular, germination by zoospores (Siradhana *et al*. 1980; Fig. 3E).

Diagnosis: Similar morphology as *Peronosclerospora sorghi* but differs by its inability to infect sorghum and in oospore morphology, with *Peronosclerospora heteropogonis* producing tuberculate oospores and *Peronosclerospora sorghi* producing oospores that have an irregularly polygonally-angled ornamentation. Distinct on the basis of the nucleotide sequence of *cox*2.

Reference sequence data: Ex-holotype nucleotide sequence EU116054 (*cox*2).

Host range: *Heteropogon contortus*, *Zea mays* (*Panicoideae, Andropogoneae*).

Notes: *Peronosclerospora heteropogonis* causes Rajasthan downy mildew disease of *Heteropogon contortus* (spear grass) and maize on a regional basis in the Udaipur district of the state of Rajasthan in India (Siradhana *et al*. 1980, Yen *et al*. 2004). The disease can be quite destructive, leading to leaf chlorosis and shredding in both hosts, and causing as much as 60–80 % yield loss in susceptible hybrid corn lines depending on inoculum load and weather conditions (Dange *et al*. 1973, 1974, Rathore *et al.* 2002). However, research of this downy mildew is ranked as a low priority in India based on prevalence, incidence and acreage affected (Thakur & Mathur 2002).

This species was first reported as *Peronosclerospora sorghi* on *Heteropogon contortus* (Dange *et al.* 1973, Siradhana *et al.* 1980) and later described as *Peronosclerospora heteropogonis* based on morphology and the inability to infect sorghum, which distinguished the species from *Peronosclerospora sorghi* (Siradhana *et al*. 1980). However, Siradhana *et al.* (1980) did not designate a holotype, which means that *Peronosclerospora heteropogonis* Siradhana *et al.* was not validly published (Art. 40.1, Turland *et al.* 2018). In 2005, Thines *et al*. (2008) made a fresh collection of the pathogen from the Udaipur region of India from maize (HOH 898), where the original collections by Siradhana *et al*. (1980) were made. Thines *et al.* (2008) confirmed the distinctiveness of HOH 898 from *Peronosclerospora sorghi* and other members of the genus using a molecular phylogenetic analysis of *cox*2; this specimen is therefore designated the holotype for the newly validated species.

Peronosclerospora ischaemi M.J. Ryley *et al.*, *Mycol. Progr*. **21**: 304. 2022.

Typus: **Australia**, Queensland, on leaves of *Ischaemum fragile* (*Panicoideae*, *Andropogoneae*), 14 Apr. 2019, *J. Kruse, A.R. McTaggert, M.J. Ryley, M.D.E. & R.G. Shivas* (**holotype** BRIP 70369).

Description: *Oogonia* subglobose to irregular, golden brown, (55−)61−68(−70) × (49−)56−65(−68) µm diam; wall uneven, flattened, smooth, 5−20 µm thick. *Oospores* globose, hyaline, (35−)41−48(−50) diam, adnate with oogonium wall, with a single vacuole; wall µm thick, even, smooth, hyaline, 4−6 µm thick (Fig. 4A). Asexual morph not observed (Ryley *et al*. 2022).

Diagnosis: Distinct from other *Peronosporaceae* based on parasitisim of *Ischaemum fragile*. Distinguished from sister species *Peronosclerospora jamesiae* and *Peronosclerospora sehima* based on the nucleotide sequence of *cox*2 (98 % sequence similarity).

Reference sequence data: Ex-holotype nucleotide sequence OK336433 (*cox*2), OK350683 (28S rDNA).

Host range: Known only from the type specimen on *Ischaemum fragile*.

Notes: The host of *Peronosclerospora ischaemi, Ischaemum fragile*, a species distributed across parts of Australia and New Guinea, and is the only known member of the the genus *Ischaemum* associated with a downy mildew. Infection by *Peronosclerospora ischaemi* results in splitting of the leaf blade into tangled vascular strands that can measure up to 30 cm long.

Peronosclerospora jamesiae R.G. Shivas *et al.*, *Mycol. Progr*. **21**: 304. 2022.

Typus: **Australia**, Northern Territory, Wagait Beach, in leaves of *Sorghum intrans* (*Panicoideae*, *Andropogoneae*), 1 Apr. 2016, *R.S. James* (**holotype** BRIP 65234).

Description: *Oogonia* highly variable shape including sub-globose, ovoid and cuboid, dark golden brown, (40–)46–60(–80) µm in diam; wall smooth, rounded to flat, occasionally concave, 2–15 µm thick. *Oospores* sub-globose to ovoid sometimes with a flattened side, (30–)32–42(–55) µm diam, with prominent oil globule; wall hyaline, even, smooth, 1–2 µm thick (Fig. 4B). Asexual morph not observed (Ryley *et al*. 2022).

Diagnosis: Differs from other *Peronosporaceae* on *Sorghum* spp. by having larger oospores with a darker oogonial wall. Differes from sister species *Peronosclerospora ischaemi* and *Peronosclerospora sehima* based on the nucleotide sequence of *cox*2 (98 % nucleotide similarity) and parasitism of *Sorghum intrans*.

Reference sequence data: Ex-holotype nucleotide sequence OK336444 (*cox*2).

Host range: Known only from the type host *Sorghum intrans*.

Notes: The host of *Peronosclerospora jamesiae, Sorghum intrans*, is a wild annual grass species native to Northern regions of Australia. Infection by *Peronosclerospora jamesiae* results in splitting of the leaf blade into tangled vascular strands that can measure up to 30 cm long.

Peronosclerospora mactaggartii R.G. Shivas *et al.*, *Mycol. Progr*. **21**: 305. 2022.

Typus: **Australia**, Northern Territory, Dorat Rd., Robins Falls, in leaves of *Sorghum timorense* (*Panicoideae*, *Andropogoneae*), Apr. 2012, *A.R. McTaggart & R.G. Shivas* (**holotype** BRIP 57677).

Description: *Oogonia* sub-globose to globose, light golden brown, (30–)33–36(–40) µm diam; wall smooth, uneven, 1–8 µm thick. *Oospores* globose, (23–)25–27(–29) µm diam, with a single vacuole, adnate with oogonial wall; wall hyaline, even, smooth 1–2 µm thick. (Fig. 5A). Asexual morph not observed (Ryley *et al*. 2022).

Diagnosis: Distinguished from *Peronosporaceae* causing grass downy mildews based on the nucleotide sequence of *cox*2, which shares 96 % similarity with the most closely related taxon, *Peronosclerospora boughtoniae*.

Reference sequence data: Ex-holotype nucleotide sequence OK336446 (*cox*2), OK350687 (28S rDNA).

Host range: Known only from the type specimen on *Sorghum timorense*.

Notes: Infection by *Peronosclerospora mactaggartii* results in splitting of the leaf blade into tangled vascular strands that can measure up to 20 cm long.

Peronosclerospora maydis (Racib.) C.G. Shaw, *Mycologia* **70**: 595. 1978.
Basionym: *Peronospora maydis* Racib., *Ber. Deutsch. Bot. Ges.* **15**: 475. 1897.
Synonyms: *Sclerospora maydis* (Racib.) E. J. Butler, *Memoirs of the Dept. Agric. India. Bot. Ser.* **5**: 275. 1913.
Sclerospora javanica Palm, *Meded. Lab. Pl. Ziekt. Buitenz*. **32**: 18. 1918.
Peronosclerospora australiensis R.G. Shivas *et al.*, *Australas. Pl. Pathol*. **41**: 126. 2012.

Typus: **Indonesia**, Java, Jawa Tengah, Tengal, *Zea mays* (*Panicoideae, Andropogoneae*), *sine dat.* [**lectotype** KRA O-5859(J); **isotypes** BPI 789413 (MBT 10002149), in KRAM, and M. Raciborski, *Cryptogamae parasiticae* in Insula Java Lectae 7]. Supplementary Fig. S3 shows the isotype BPI 789413.

Description: *Mycelium* coenocytic, intercellular, parasitic throughout host (excluding roots), with many differentially shaped haustoria, and two kinds of hypha: straight and sparsely branched, and lobed and irregularly branched. *Conidiophores* robust, erect, 200–550 µm high × 20–25 µm wide, with septated basal cells 60–180 µm long, dichotomously branched 2–4 times, branchlets with two or more (generally 3–6) conical sterigmata (6–9 µm long) each bearing one individual sporangium. *Sporangia* hyaline, oval or spherical to subspherical, non-papillate, and 15–18 µm wide, direct germination by 1–2 germ tubes (Raciborski 1897; Fig. 4C). *Sexual structures* rare or unknown (Semangoen 1970), that have been described from the type specimen of what was originally described as *Peronosclerospora australiensis* but is now accepted as a synonym of *Peronosclerospora maydis* (Suharjo *et al*. 2020); that description is as follows: *Oogonia* golden orange to yellowish or reddish brown, globose, subglobose, broadly ellipsoidal to irregularly polyangular, 55–76 µm diam; exosporium 2–15 µm wide, uneven, smooth, convoluted. *Oospores* one per oogonium,

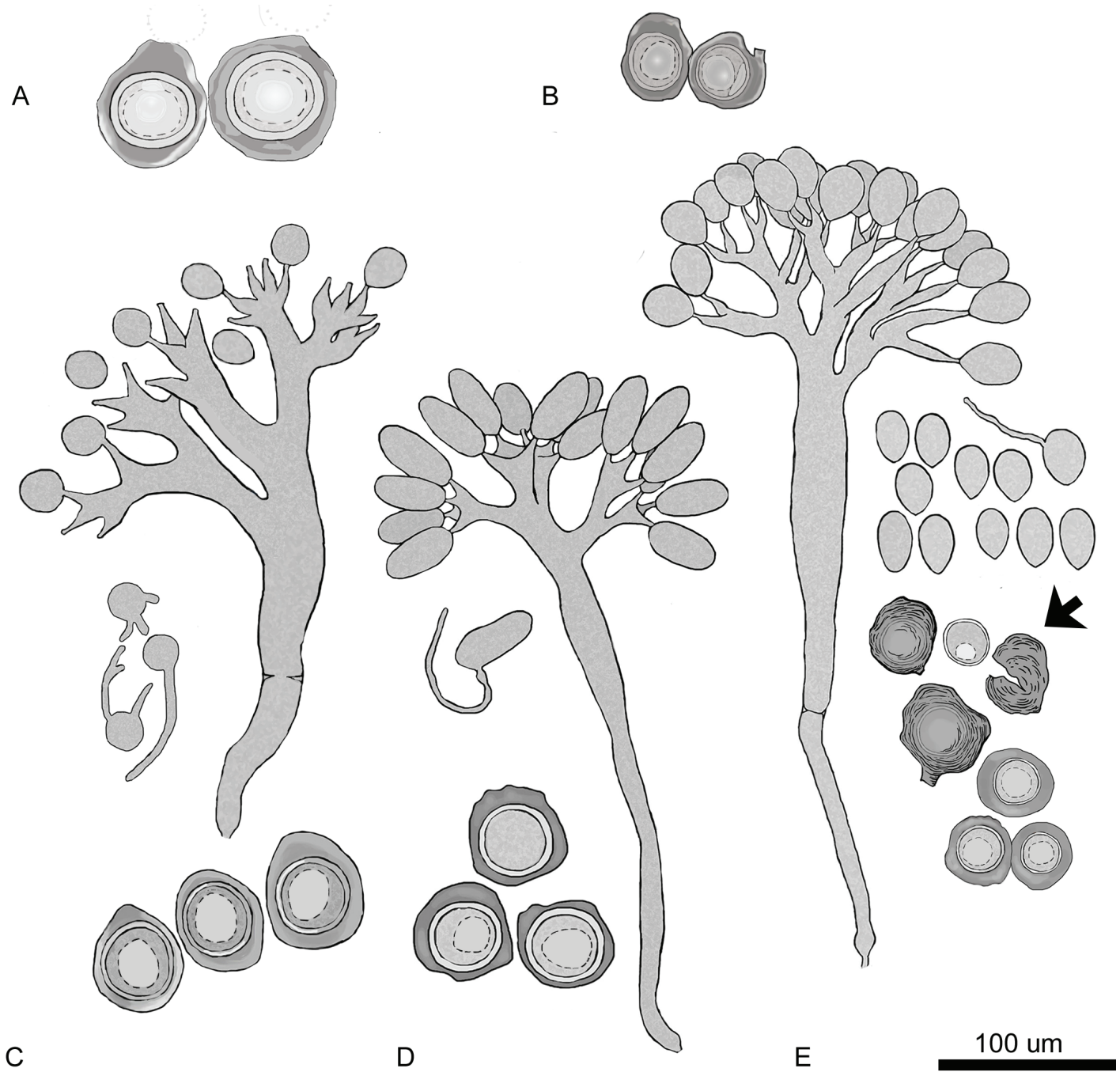

Fig. 4. A. *Peronosclerospora ischaemi*, oospores. **B.** *Peronosclerospora jamesiae*, oospores. **C.** *Peronosclerospora maydis*, sporangiophore, germinating sporangia, and oospores. **D.** *Peronosclerospora miscanthi*, sporangiophore, germinating sporangium, and oospores. **E.** *Peronosclerospora noblei*, sporangiophore, sporangia, and oospores. The top three oogonia are illustrated in surface view, including one oogonium that is one cracked open with an oospore released from oogonial wall (arrow). Illustrations were prepared from published reference images in Raciborski (1897), Weston (1929, 1942), Chu (1953), Shivas *et al.* (2012), Widiantini *et al*. (2015) and Ryley *et al.* (2022).

sub-hyaline to pale yellow, globose or broadly ellipsoidal, 39–55 µm diam, often with a large vacuole; endosporium 2.5–4.0 µm wide, even, smooth (Shivas *et al.* 2012; Fig. 4C).

Diagnosis: Sequence analysis of *cox*2 has been used to differentiate *Peronosclerospora maydis* from other *Peronosclerospora* spp. (Suharjo *et al.* 2020).

Reference sequence data: Ex-lectotype nucleotide sequence MW025835 (*cox*2).

Host range: *Saccharum spontaneum*, *Sorghum arundinaceum*, *Sorghum timorense*, *Zea mays*, *Zea mexicana*, *Zea mexicana* × *Zea mays* hybrids (*Panicoideae*, *Andropogoneae*).

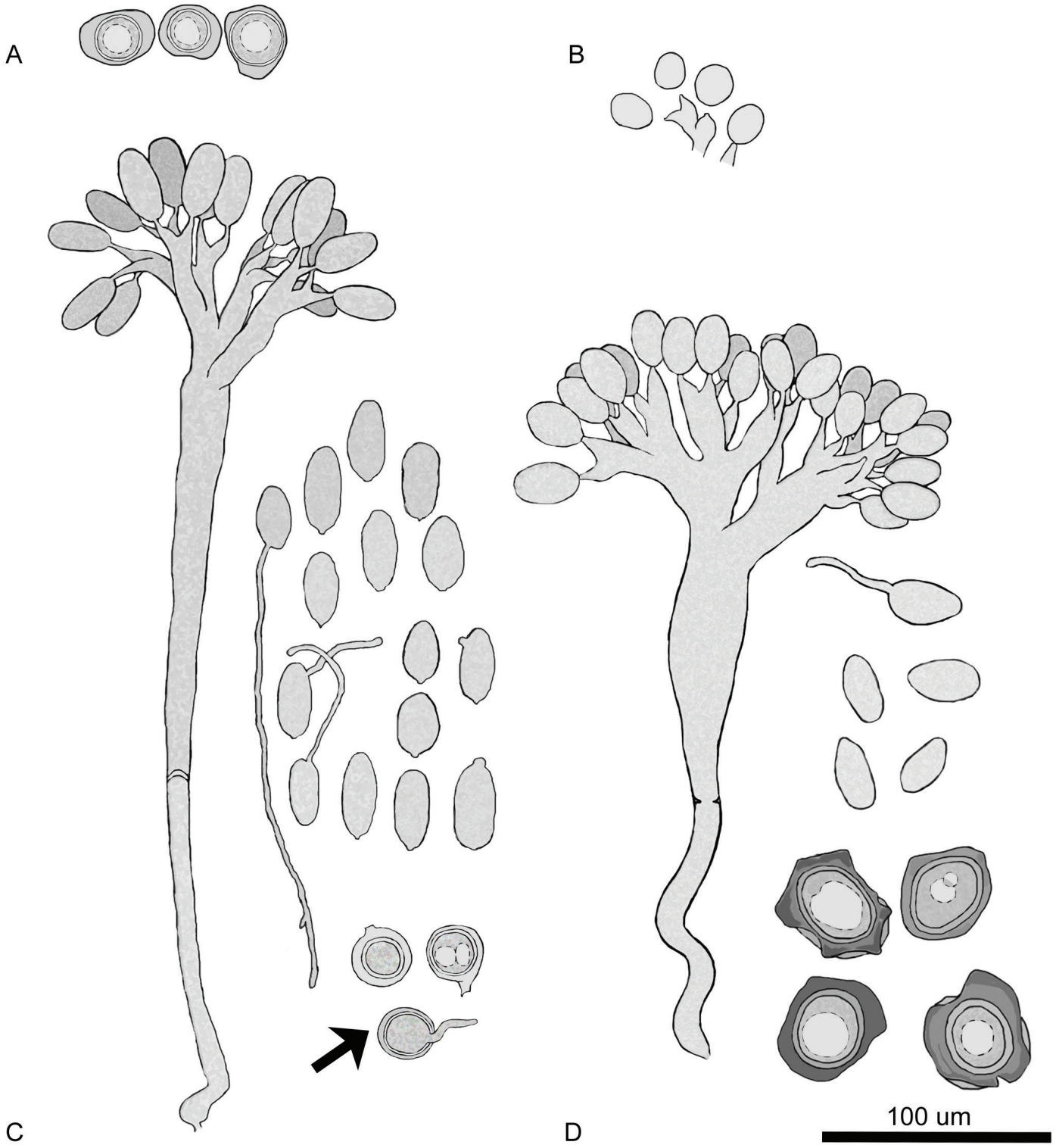

Fig. 5. A. *Peronosclerospora mactaggartii*, oospores. **B.** *Peronosclerospora panici*, sporangia and fragments of sporangiophore tips. **C.** *Peronosclerospora philippinensis*, sporangiophores, sporangia (including germinating sporangia), and oospores (including one germinating oospore, arrow). **D.** *Peronosclerospora sacchari*, sporangiophore, sporangia (including germinating sporangia), and oospores. Illustrations were prepared from published reference images in Miyake (1912), Weston (1920), Acedo & Exconde (1967), Elazegui & Exconde (1968), Singh & Chaube (1968), and photographs of *Peronosclerospora philippinensis* provided by Gary Peterson.

Notes: *Peronosclerospora maydis* is the causal agent of Java downy mildew and is one of the three most devastating downy mildew pathogens of maize (Lukman *et al.* 2016). In Indonesia, crop damages of 40–100 % have been recorded (Pudjiwati *et al.* 2013). Disease symptoms include severe chlorosis in the upper leaves, stunting, deformation, and lodging; infections by *Peronosclerospora maydis* may lead to death in susceptible maize varieties (Smith & Renfro 2016). The pathogen is widely distributed in the tropics of Australia, China, India, Indonesia, Jamaica, Taiwan, Thailand, and Venezuela. Reports of *Peronosclerospora maydis* in the Congo Democratic Republic and Argentina are considered possible misidentifications (Semangoen 1970, Kenneth 1976).

Sexual structures are rare or absent under natural or experimental conditions on the type host (Semangoen 1970, Suharjo *et al.* 2020), but were described from *Sorghum timorense* plants in Australia (Shivas *et al.* 2012). Oospores of *Peronosclerospora maydis* infecting maize originally described by Raciborski (1897) and Rutgers (1916) were later identified as *Pythium* spp. and *Paramecium* spp. (Palm 1918, Semangoen 1970).

Peronosclerospora miscanthi (T. Miyake) C.G. Shaw, Mycologia **70**: 596. 1978.
Basionym: *Sclerospora miscanthi* T. Miyake ex. Trotter [as '*mischanthi*'], in *Trotter, Syll. Fung. (Abellini)* **24**: 65. 1926.

Typus: **Taiwan**, Taipei, *Miscanthus sinensis* var. *formosanus*, 20 Jul. 1915, *K. Sawada* [**neotype** designated here BPI 187301 (MBT 10002150)]. Supplementary Fig. S4 shows the neotype BPI 187301.

Description: *Conidiophores* 97–300 (up to 438) × 12–37 µm, branched twice at the tip. *Conidia* elongately ovoid, (37.2–) 41.8(–48.6) × 14.3–22.9 µm (av. 41.8 × 18) µm diam, germinate directly by a germ tube. *Oogonia* reddish brown, mostly 58.3–63.5 × 51.5–56.9 (range 43.2–80 × 33.2–64.8) µm, walls unevenly thick from 3–8 µm to 12–24 µm thick, with small excrescences. *Oospores* 43.5–47.1 µm diam (Miyake 1912, Chu 1953; Fig. 4D).

Reference sequence data: Ex-NY: Stevens Philippine Fungi, Island of Luzon, No. 811 nucleotide sequences HQ261811 (*cox*2), HQ261784 (28S rDNA).

Host range: *Miscanthus japonicus*, *Miscanthus sinensis*, *Saccharum officinale*, *Saccharum robustum*, *Saccharum spontaneum* (*Panicoideae, Andropogoneae*).

Notes: Leaf splitting downy mildew disease caused by *Peronosclerospora miscanthi* was first identified in 1912 in Taiwan (Miyake 1912). The pathogen was subsequently reported from several species of *Miscanthus* and two species of *Saccharum* from China, Fiji, New Guinea, the Philippines, and Taiwan, with most reports of the pathogen presented in the form of checklists and surveys (Ito & Tokunaga 1935, Chu 1953, Waterhouse 1964, Telle *et al*. 2011). Inoculation experiments show that *Peronosclerospora miscanthi* has the ability to infect maize, but natural infections of this host are unknown (Shaw 1975). Infected *Miscanthus sinensis* leaves have white to yellowish white spots that eventually turn brown and are shredded (Ito & Tokunaga 1935, Waterhouse 1964). Pupipat (1975) considered the disease only a minor economic problem on sugarcane.

Miyake discovered this pathogen and made a report of it in the same publication in which *Peronosclerospora sacchari* is described (Miyake 1912). Although Miyake included a short discussion of the disease and briefly summarized the oospore morphology in that publication, he did not name the species at that time and no illustrations were included. In the 1914 English translation version of Miyake 1912, a note from Miyake was added (dated July 1913), stating that the pathogen would be described as a new species under the name of *Scelerospora* [sic] *miscanthus*, T. Miy. In 1926, Trotter validated the species, referring to Miyake 1912 for the description. Chu (1953) provided the first illustrations of the pathogen and a description of both the sexual and asexual morphology; Chu's description is consistent with the oospore morphology detailed in Miyake's text (1914). Therefore, the description provided above is primarily drawn from Chu (1953).

Further research is needed to address questions about whether or not *Peronosclerospora miscanthi* and *Peronosclerospora sacchari* are conspecific. Both species share similar oospore morphology (Chu 1935, Ito & Tokunaga 1935, Miyake 1914, Telle *et al*. 2011). Molecular phylogenetic analysis showed that a specimen of *Peronosclerospora miscanthi* and a *Peronosclerospora sacchari* voucher specimen (BRIP 44241) together a formed a distinct, highly supported clade (Telle *et al.* 2011), with the two species differing by just 0.92 % across two markers (1 426 nt).

The original description and validating publication for the species did not designate a holotype; BPI holdings include BPI 187301 dated 1915 from *Miscanthus sinensis* in Taiwan; this specimen is here designated as the species neotype.

Peronosclerospora noblei (W. Weston) C. G. Shaw, *Mycologia* **72**: 426. 1980.
Basionym: *Sclerospora noblei* W. Weston, *Phytopathol.* **19**: 1112. 1929.

Typus: **Australia**, New South Wales, Glenn Innes, *Sorghum leiocladum* (*Panicoideae, Andropogoneae*) Feb. 1928, *R. J. Noble* [**lectotype** designated here DAR 1075 (MBT 10002151); **isotypes** BPI 187306, DAR 1076, FH 965379 (MBT 10002152)]. Supplementary Fig. S5 shows the lectotype BPI 187306.

Description: *Oogonium* ovoid, ellipsoid, pyriform, or subspherical, 28–44 µm. Oogonial wall of variable thickness, typically 5–10 µm but ranging from 3–20 µm giving the appearance of bluntly rounded projections and sometimes the overall oogonia shape as gibbous and unsymmetrical; wall color dark, ranging from golden to rich brown; oogonial stalk fragments often retained. *Oospores* spherical, hyaline to pale golden, 23–28.9 (mode 25–26.9, range 20–34) µm in diam; wall 1–1.5 µm thick, contents comprising finely granular material with denser aggregations and oil drops, central to eccentric in position. Germination not observed (Weston 1929; Fig. 4E).

Diagnosis: In describing the species, Weston indicated that *Peronosclerospora noblei* is readily distinguishable from *Sclerospora graminicola* by the small size of the oospores, their thin walls, and the uniquely rounded exterior of the oogonium (versus flattened) with rounded surface prominences occurring due to the variable wall thickness and not due to out-bulgings.

Reference sequence data: Ex-isotype BPI 187306 nucleotide sequences, OK185343 (*cox*2), OK255496 (28S rDNA).

Host range: *Sorghum leiocladum*, *Sorghum plumosum* (*Panicoideae, Andropogoneae*).

Notes: *Peronosclerospora noblei* is only known from Australia (Weston 1929, 1942, Ryley & Langdon 2001, Thines *et al.* 2008, Farr & Rossman 2021). The type host, the wild sorghum *Sorghum leidocladum*, is indigenous to the northern tropical regions of Australia and not known from elsewhere in the world. *Sorghum leiocladum* infected by *Peronosclerospora noblei* show malformation, tillers mostly vegetative rather than flowering, and chlorotic, frayed leaves held in an abnormal bunch-like manner; infected leaves eventually become necrotic and die (Ryley 2001, 2002, Ryley & Langdon 2001). A second native Australian grass, *Sorghum plumosum* (as *Andropogon australis* or *Andropogon* sp.), is also listed as a host in checklists (Waterhouse 1964, Farr & Rossman 2021). However, the association of *Peronosclerospora noblei* with *Sorghum plumosum* bears further investigation, as molecular phylogenetic identity of a *Peronosclerospora* sp. specimen on *Sorghum plumosum* suggests that this organism is not conspecific with any known *Peronosclerospora* species and is not closely aligned with *Peronosclerospora noblei* (Thines *et al.* 2008).

As part of the description for *Sclerospora noblei*, Weston provided detailed collection data, but did not specify a holotype. Examination of Weston's collections at BPI, DAR, and FH identified specimens of *Sclerospora noblei* on *Sorghum leiocladum* with the outer envelopes both bearing the label of the *Herbarium of W. H. Weston* (BPI 187306, FH 965379). These specimens were annotated with the same collection data that was detailed in the protolog, written in Weston's hand. There can be no doubt that these are the original specimens described by Weston; DAR 1075 is therefore used to lectotypify the species.

Peronosclerospora panici R.G. Shivas *et al.*, *Mycol. Progr*. **21**: 306. 2022.

Typus: **Australia**, New South Wales, Narromine, on leaves of *Panicum laevinode* (as *Panicum whitei*) (*Panicoideae, Andropogoneae*), 4 Mar. 1980, *G. Stovold* (**holotype** DAR 35733).

Description: *Conidia* globose to sub-globose, rarely ovoid, hyaline, aseptate, (15–)15–17(–20) × (12–)13–16(–18) µm, thin walled without operculum or pore (Fig. 5B), germination by germ tube. Sexual morph not observed (Ryley *et al.* 2022)

Diagnosis: Differs from the sister taxon *Peronosclerospora erichloae* based on the nucleotide sequence of *cox2* (98 % sequence smiliarity with BRIP 22711).

Reference sequence data: Ex-holotype nucleotide sequence HQ261814 (*cox*2), HQ261787 (28S rDNA).

Host range: Known only from the type specimen on *Panicum laevinode*.

Notes: The host of *Peronosclerospora panici*, *Panicum laevinode*, is a forage species primarily restricted to Australia. Additional downy mildews have been reported from *Panicum* species globally (*Peronosclerospora sorghi*, *Sclerophthora macrospora, Sclerospora gramincola*).

Peronosclerospora philippinensis (W. Weston) C. G. Shaw, *Mycologia* **70**: 596. 1978.
Basionym: *Sclerospora philippinensis* W. Weston, *J. Agric. Res*., Washington **19**: 118. 1920.
Synonym: '*Sclerospora maydis*' Reinking, *Philipp. J. Sci, A* **13**: 1. 1918. [*nom. illegit*., Art. 53.1]
Possible synonym: *Sclerospora indica* E. J. Butler, *Fungi of India (Calcutta)*: 7. 1931.

Typus: **Philippines**, Laguna Province, Los Banos, *Zea mays*, 9 Feb. 1919, *W.H. Weston* [**lectotype** designated here BPI 187314 (MBT10002153); **isotypes** BPI 187044, BPI 187311, BPI 187313, FH 965382, FH 965383 (MBT10002154)]. Supplementary Fig. S6 shows the lectotype BPI 18731; Supplementary Figs S7–S9 show isotypes BPI 187044, BPI 187311, and BPI 187313, respectively.

Description: *Hyphae* intercellular throughout host (excluding root); branched, typically 8 µm diam, irregularly constricted and inflated; simple vesiculiform to subdigitate haustoria, 2 µm diam. *Conidiophores* evanescent, nocturnal, erect, 150–400 × 15–26 µm with basal cell, dichotomously branched two to four times; sterigmata conoid to subulate and slightly curved, 10 µm long. *Conidia* elongate ellipsoid, elongate ovoid, or rounded cylindrical, apex slightly rounded, hyaline, usually 17–21 × 17–39 µm with a minute apiculus at the base, episporium thin, contents minutely granular, germinating directly by a germ tube. *Oogonia* 22.9 µm diam, wall smooth, fragments of oogonial stalk or antheridia often adherent (Weston 1920). *Oospores* spherical, (15.3–)19.2(–22.6) µm diam, hyaline or straw-colored; wall smooth, 2.0–3.9 µm thick; contents finely granular with oil droplets, positioned central to eccentric; germination via single germ tube (Acedo & Exconde 1967; Fig. 5C).

Diagnosis: Efforts to discriminate *Peronosclerospora philippinensis* from related taxa with overlapping host ranges may not provide clear cut differentiation. *Peronosclerospora philippinensis* oospores are reported as smaller in size than those of *Peronosclerospora miscanthi*, *Peronosclerospora sacchari*, and *Peronosclerospora spontanea* (Sivanesan & Waller (1986). Conidial morphology distinguishes *Peronosclerospora philippinensis* from *Peronosclerospora spontanea*, which has more elongated and slender conidiophores and conidia (Waterhouse 1964), and from *Peronosclerospora sorghi*, which has conidiophores with a basal plug and smaller conidia (Weston & Uppal 1932, Janruang & Unartngam 2018), but these structures may be subject to variation depending on environmental conditions and host (Exconde *et al.* 1968, Leu 1973, Widiantini *et al.* 2015). Several authors have questioned whether or not *Peronosclerospora philippinensis* and *Peronosclerospora sacchari* are the same species based on morphological similarity, shared host range, and phenotypic profiles generated from isozyme analyses (Weston 1920, Bonde *et al.* 1984, Micales *et al.* 1988), but at present no conclusive data are available.

At the time of writing (February 2022), NCBI GenBank contained accessions for 26 sequences identified as *Peronosclerospora philippinensis*, but except for the sequences generated for this paper from the isotype BPI 187044, none of the sequences are associated with voucher specimens or type material. Twenty-four of the NCBI accessions are internal transcribed spacer (ITS) sequences. We recommend exercising caution in using these ITS accessions for identification, as the sequences are very diverse and share only 92.9–96.2 %

identity with one another, suggesting that either some are misidentified or that there are misassemblies of the sequences resulting from long stretches of repeat elements known to occur in some downy mildew genera (Thines *et al.* 2007). Readers are also cautioned that *cox*2 and rDNA 28S sequences have limited utility for identification of this species because these marker sequences share 99.2–100 % identity to sequence data from voucher materials of *Peronosclerospora miscanthi* and *Peronosclerospora sacchari*. DNA sequencing from type materials at additional loci may help resolve species boundaries and provide badly needed diagnostic resources for *Peronosclerospora philippinensis.*

Reference sequence data: Ex-isotype BPI 187044 nucleotide sequences OK185341 (*cox*2), OK181682 (28S rDNA).

Host range: *Miscanthus japonicus, Saccharum officinarum, Saccharum spontaneum, Sorghum arundinaceum, Sorghum bicolor, Sorghum halepense, Sorghum propinquum, Zea mays, Zea mexicana, Zea mexicana* × *Zea mays* hybrids (*Panicoideae*, *Andropogoneae*).

Experimental host range: *Peronosclerospora philippinensis* is capable of parasitizing several additional hosts under experimental conditions: *Andropogon* spp., *Botriochloa* spp., *Eulalia fulva, Miscanthus japonicus, Sorghum plumosum, Tripsacum* spp., *Zea diploperennis*, *Zea luxurians*, and *Zea perennis* (Bonde & Peterson 1983). Some of these plants are common perennial forage and wild prairie grasses in the USA and globally; therefore, they serve as inoculum reservoirs (Bonde & Peterson 1983).

Notes: *Peronosclerospora philippinensis*, causing Philippine downy mildew, is one of the most destructive and virulent pathogens infecting maize, with crop losses reaching as much as 80–95 % under favorable conditions (Exconde & Raymundo 1974, Exconde 1975, CABI 2021). Sugarcane crop losses are lower, ranging from 9–38 % (CABI 2021). The pathogen is recognized globally as a threat to plant health, with measures enacted in several parts of the world to restrict its movement. According to the European and Mediterranean Plant Protection Organization Global databases (EPPO 2021), *Peronosclerospora philippinensis* is a quarantine pest in Mexico and Morocco and is subjected to regulation in China and three EPPO regions due to its inclusion on the EPPO A1 invasive pest list. In the USA, *Peronosclerospora philippinensis* is included in the USDA Plant Protection and Quarantine Select Agents and Toxins list (www.selectagents.gov/sat/list.htm).

Symptoms of *Peronosclerospora philippinensis* infecting maize and sorghum are very similar to those of other downy mildews affecting *Poaceae*, including chlorotic streaks along the length of the leaf, tassel malformation, and seed sterility, which make diagnosis based on symptomology on this host difficult (Baer & Lalusin 2013, Smith & Renfro 2016). Sugarcane plants infected with *Peronosclerospora philippinensis* show discolorations at the base of the young leaves, chlorotic spots that turn brick red as leaves age, and thinner canes (Thompson *et al.* 2013). These symptoms are very similar to those caused by *Peronosclerospora sacchari* and *Peronosclerospora spontanea* infecting *Saccharum* but differ from those of *Peronosclerospora miscanthi*, which always causes leaf-splitting (Sivanesan & Waller 1986, Thompson *et al.* 2013).

The geographic distribution of *Peronosclerospora philippinensis* as reported in online resources (such as CABI, EPPO, and the BPI databases) at the time of writing were conflicted. Given the challenges associated with diagnosing the species using morphology and symptomology, readers are cautioned that in the absence of molecular data, the pathogen is easily misdiagnosed and some reports may be erroneous. Records indicate that *Peronosclerospora philippinensis* has been found in Bangladesh, the Democratic Republic of the Congo, India, Indonesia, Nepal, Pakistan, and the Philippines (Weston 1920, Doidge 1950, Gattani 1950, Ali 1959, Watson 1971, Bains & Jhooty 1982, Bonde *et al.* 1984, Farr & Rossman 2021; Faruq *et al.* 2014, Subedi 2015, Muis *et al.* 2016, Ekawati & Gusnawaty 2018, Pakki *et al.* 2019). Records of *Peronosclerospora philippinensis* in Japan and South Africa are not considered valid by CABI (CABI 2021). Janruang & Unartngam (2018) have recently suggested that *Peronosclerospora philippinensis* should be removed from the list of maize pathogens present in Thailand. Reports of the pathogen in the USA by EPPO (2021) and CABI are of uncertain origin but may be based on the existence of a specimen of *Peronosclerospora philippinensis* on maize held by herbarium WSP that is annotated as originating from Frederick, Maryland, USA (WSP60943). However, WSP60943 was taken from an experimental plant maintained within the USDA-ARS biosafety level 3 containment facilities on the Fort Detrick USA Army base. The *Peronosclerospora philippinensis* strain used to inoculate the WSP60943 specimen was originally collected by Ofelio R. Exconde from University of Philippines, Los Banos College, Laguna, Philippines in 1975 (M. Bonde, G. Peterson, pers. comm.).

Weston did not specify a holotype, but examination of his specimens at BPI and FH identified several specimens of *Sclerospora philippinensis* on *Zea mays* with the outer envelopes bearing the label of the *Herbarium of W. H. Weston* and annotated with the same collection data that was detailed in Weston's protolog. Labels for BPI 187314, BPI 187044 and FH 965383 are written in Weston's hand, and the two BPI specimens contain Weston's handwritten annotations together with his correspondence regarding the material (BPI 187314). There can be no doubt that these are the original specimens described by Weston; BPI 187306 is therefore used here to lectotypify the species.

Peronosclerospora sacchari (T. Miyake) Shirai & Hara, List of Japanese fungi hitherto unknown, **3rd edn**: 257. 1927.
Basionym: *Sclerospora sacchari* T. Miyake, *Rep. Sugar Exper. Stn, Gov. Formosa* **1**: 12. 1912.
Synonyms: *Sclerospora sorghi-vulgaris* Mundk. [as (Kulk.) Mundk.], *Indian J. Agric. Sci.* **20**: 138. [1950] 1951.
'Peronosclerospora sacchari' (T. Miyake) C.G. Shaw, *Mycologia* **70**: 595. 1978. [*nom. illegit.*, Art. 53.1]

Typus: **Taiwan**, *Saccharum officinarium* (*Panicoideae, Andropogoneae*) 8 Oct. 1910, *collector not specified* [**lectotype** designated here BPI 187331 (MBT 10002155)]. Supplementary Fig. S10 shows the lectotype BPI 187331.

Description: *Conidiophores* fugacious, erect, hyaline, 160–170 µm long; wall smooth, thin; base slightly narrower (10–15 µm broad), one or rarely two septate; middle part about two to three times broader than the base apex; two or three times branched two or three times each branch stocky and conical shaped. *Conidia* elliptical or oblong, hyaline, 25–41 × 15–23

µm, or 49–54 × 19–23 µm, apex rounded, base slightly apiculate or rounded, wall thin and smooth; direct germination by germ tubes. *Oogonium* irregularly elliptical, castanian brown, 49–58 × 55–73 µm; wall thickness unequal. *Oospores* globular, yellow, 40–50 µm diam, wall 3.8–5 µm thick; germination by germ tubes (Miyake 1912; Fig. 5D).

Diagnosis: *Peronosclerospora sacchari* shares similar morphology, host range, and induces similar symptoms in the parasitized host as *Peronosclerospora philippinensis* (Miyake 1912, Weston 1920, Ito & Tokunaga 1935, Chu 1953, Telle *et al.* 2011). Elazegui & Exconde (1968) reported size and shape differences from the conidiophores of *Peronosclerospora sacchari* and *Peronosclerospora philippinensis*, but these differences might be the result of interspecific variability and/or environmental influences (Leu 1973, Widiantini *et al.* 2015). Refer to *Diagnosis* section for *Peronosclerospora philippinensis* above for additional discussion.

Reference sequence data: Ex-BRIP 44241A nucleotide sequences EU116052 (*cox*2), HQ261764 (28S rDNA).

Host range: *Saccharum edule, Saccharum officinarum*, *Saccharum robustum*, *Saccharum spontanea*, *Tripsacum dactyloides, Sorghum vulgare* var. *technicum, Zea mays*, and *Zea mexicana* (*Panicoideae, Andropogoneae*).

Experimental host range: Bonde & Peterson (1981, 1983) showed that under experimental conditions, *Peronosclerospora sacchari* systemically infects 18 species of grasses in the genera of *Andropogon*, *Bothriochloa*, *Eulalia*, *Schizachyrium*, and *Sorghum* (Bonde & Peterson 1981), suggesting a possible role for these plants as alternate hosts.

Notes: *Peronosclerospora sacchari* causes sugarcane downy mildew on sugarcane or maize (also known as leaf stripe disease). This species is known from the Western-Pacific region of Asia and Oceania (Farr & Rossman 2021) where it has significant economic impact on the sugarcane industry (Sugarcane Research Australia 2019). The most characteristic symptoms of *Peronosclerospora sacchari* on sugarcane are chlorotic leaf stripes that turn red with age, brown lesions on external stalk surfaces, and stunting of infected stools.

The first sighting of *Peronosclerospora sacchari* causing a leaf splitting disease occurred in 1909 at the Sugar Experiment Station in Taiwan on sugarcane fields planted with canes of Australian origin (Miyake 1912). By 1912, the disease was so widespread and destructive that the Taiwanese government ordered destruction of all affected sugarcane cuttings across two cities and 18 villages (Miyake 1912). Severe epidemics on sugarcane occurred in Taiwan between 1962–1967 (Payak 1967). In India, *Peronosclerospora sacchari* was first recovered from maize from the Tarai area of Uttar Pradesh (where sugarcane was planted widely) in 1968 (Singh 1968). Since then, *Peronosclerospora sacchari* outbreaks on maize have been sporadic and natural infection of sugarcane has not been observed in India (Payak 1975a, b, Sugarcane Research Australia 2019). In the late 1950s the pathogen was introduced to Australia through infected sugarcane cuttings, producing severe economic losses (Pupipat 1975, Suma & Magarey 2000), but an aggressive eradication plan enacted by the government resulted in the eradication of *Peronosclerospora sacchari* from Australia by the mid-1960s (Suma & Magarey 2000, Shivas *et al.* 2012). Reports of *Peronosclerospora sacchari* from the Eastern hemisphere (Central America, South America and the USA) are unconfirmed as these reports are derived from checklist publications (Farr & Rossman 2021).

A holotype was not designated when the species was described, but the collection details for BPI 187331 match those described by Miyake (Miyake 1912); we therefore use this specimen to lectotypify *Peronosclerospora sacchari*.

Peronosclerospora sargae R.G. Shivas *et al.*, *Australas. Pl. Pathol.* **41**: 128. 2012.

Typus: **Australia**, Northern Territory, Florence Falls, *Sorghum timorense*, (*Panicoideae, Andropogoneae*), 13 Mar. 2000, *R.G. Shivas, I.T. Riley, C. & K. Vánky* (**holotype** BRIP 27691).

Description: *Oogonia* globose, subglobose to broadly ellipsoidal, occasionally irregularly polyangular, pale yellow to yellowish brown, (30–)37.9(–47) µm diam; wall 2–8 µm thick, smooth, uneven. *Oospores* globose, pale yellow, (24–)29.3(–34) µm diam, often containing large vacuole; wall (1.5–)2.1(–3.0) µm thick, even, smooth. Asexual morph not observed (Shivas *et al.* 2012; Fig. 6C).

Diagnosis: *Peronosclerospora sargae* shows similar morphological features to *Peronosclerospora noblei*; however, these species can by distinguished based on the thickness of the oospore wall, host range, and sequence of the *cox*2 and 28S rDNA loci (Shivas *et al.* 2012).

Reference sequence data: Ex-holotype nucleotide sequences HQ261809 (*cox*2) and HQ261782 (28S rDNA).

Notes: *Peronosclerospora sargae* has not been reported since its initial description (Farr & Rossman 2021) and is only known from the type specimen (Telle *et al.* 2011, Shivas *et al.* 2012). The host, *Sorghum timorense* (Down's sorghum), is endemic to tropical regions of Australia and several islands north of Australia; the impact of *Peronosclerospora sargae* on populations of this wild grass is unknown.

Peronosclerospora schizachyrii R.G. Shivas *et al.*, *Mycol. Progr.* **21**: 306. 2022.

Typus: **Australia**, Queensland, Mareeba Wetlands, *Schizachyrium fragile* (*Panicoideae, Andropogoneae*), 27 Apr. 2018, *J. Kruse, M.J. Ryley, S.M. Thompson, M.D.E. & R.G. Shivas* (**holotype** BRIP 67070).

Description: *Oogonia* globose to sub-globose, golden brown, (35–)41–55(–65) µm diam; wall 6–32 µm thick, uneven, polyangular, smooth. *Oospores* globose to sub-globose, hyaline, (26–)29–39(–47) µm in diam, adnate with oogonial wall, with a single vacuole; wall 1–4 µm thick, even, smooth. Asexual morph not observed. (Ryley *et al.* 2022; Fig. 6A).

Diagnosis: Differs from the sister taxon *Peronosclerospora erichloae* on the basis of the nucleotide sequence of *cox2* (98 % sequence smiliarity with BRIP 22711).

Reference sequence data: Ex-holotype nucleotide sequences OK336452 (*cox*2) and OK350689 (28S rDNA).

Host range: Known only from the type specimen on *Schizachyrium fragile*.

Notes: *Peronosclerospora schizachyrii* is the only known downy mildew from naturally infected hosts in the genus *Schizachyrium*, although experimental infection of *Schizachyrium* spp. by isolates identified as *Peronosclerospora* sacchari and *Peronosclerospora philippinensis* has been demonstrated (Bonde & Peterson 1983). Infection by *Peronosclerospora schizachyrii* results in splitting of the leaf blade into tangled vascular strands that can measure up to 10 cm long. The host, *Schizachyrium fragile*, is endemic to northern and central regions of Australia; the impact of *Peronosclerospora schizachyrii* on populations of this wild grass is unknown.

Peronosclerospora sehimatis M.J. Ryley *et al.*, *Mycol. Progr.* **21**: 307. 2022.

Typus: **Australia**, Northern Territory, Arnhem Highway, Jabiru, *Sehima nervosum*, (*Panicoideae, Andropogoneae*), 12 Apr. 2006, *M.J. Ryley & R.G. Shivas* (**holotype** BRIP 49806).

Description: *Oogonia* globose to sub-globose, light golden brown, (38–)45–58(–63) µm diam; wall 3–15 µm thick, smooth, uneven. *Oospores* one per oogonium, globose, (28–)34–42(–46) µm diam, adnate with oogonial wall, with a single vacuole; wall 2–4 µm thick, hyaline, even, smooth. Asexual morph not observed (Ryley *et al.* 2022; Fig. 6B).

Diagnosis: Differs from the related taxa *Peronosclerospora ischaemi* and *Peronosclerospora jamesiae* based on the nucleotide sequence of *cox2* (98 % sequence smiliarity); differs from other *Peronosporaceae* based on its parasitism of *Sehima nervosum*.

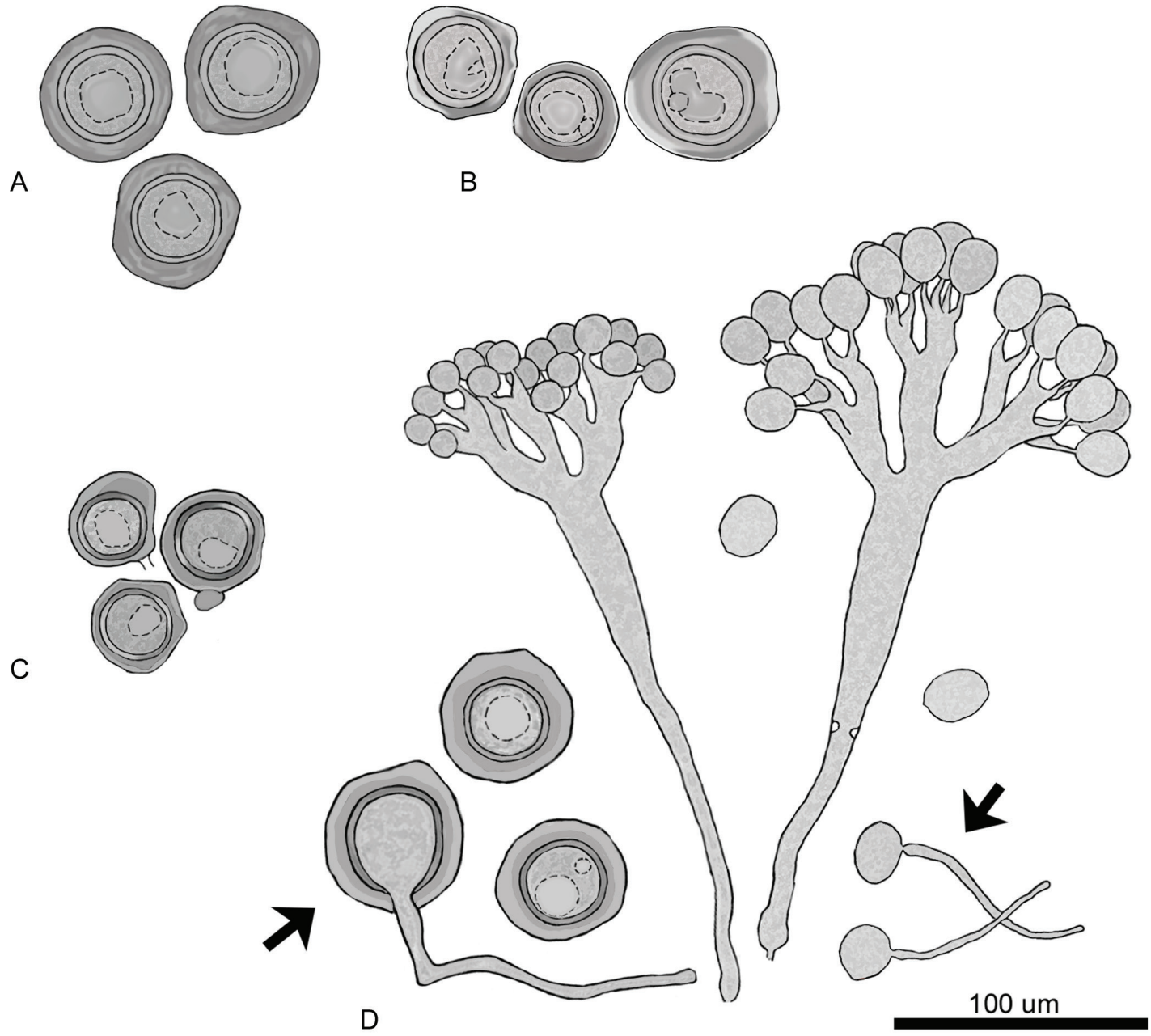

Fig. 6. A. *Peronosclerospora schizachyrii*, oospores. **B.** *Peronosclerospora sehimatis*, oospores. **C.** *Peronosclerospora sargae*, oospores. **D.** *Peronosclerospora sorghi*, sporangiophores at two stages (young and mature) and oospores. Arrows point to germinating oospores and sporangia. Illustrations were prepared from published reference images in Weston (1932), Shivas (2012), Ryley *et al.* (2021) and Ryley *et al.* (2022).

Reference sequence data: Ex-holotype nucleotide sequence OK336453 (*cox*2).

Host range: Known only from the type specimen on *Sehima nervosum*.

Notes: The host is widespread in Australia, tropical parts of Asia, and Africa, however *Peronosclerospora sehimatis* is the only known downy mildew from hosts in the genus *Sehima*. Infection by *Peronosclerospora sehimatis* results in splitting of the leaf blade into tangled vascular strands that can measure up to 10 cm long.

Peronosclerospora sorghi (W. Weston & Uppal) C.G. Shaw, *Mycologia* **70**: 596. 1978.
Basionym: *Sclerospora graminicola var*. *andropogonis-sorghi* Kulk., *Memoirs of the Dept. Agric. India, Bot. Ser*. **55**: 272. 1913.
Synonyms: *Sclerospora sorghi* (Kulk) W. Weston & Uppal, *Phytopathol.* **22**: 582. 1932.
Sclerospora sorghi W. Weston & Uppal, *Phytopathol.* **22**: 582. 1932.
Sclerospora andropogonis-sorghi (Kulk.) Mundk., *Indian J. Agric. Sci*. **20**: 138. 1951.
'Sclerospora andropogonis-sorghi' (Kulk.) Kulk. ex Safeeulla & Thirum. *Mycologia* **47**: 177. 1955. [*nom. nud.*, Art. 11.2]
Sorosporium andropogonis-sorghi S. Ito, *Trans. Sapporo Nat. Hist. Soc*. **14**: 93. 1935.

Typus: **India**, Coimbatore, *Sorghum bicolor* (*Panicoideae, Andropogoneae*), *collector not specified* [**lectotype** designated here BPI 187336 (MBT 10002156)]. Supplementary Fig. S11 shows the lectotype BPI 187336.

Description: *Conidiophores* erect, spreading, comprising basal cell, main axis more or less complex, usually dichotomously branched, expanded top; 100–150 µm length to the septum (rarely by a partial, ring-like thickening); main axis 15–25 µm diam; basal cell 7–9 µm wide, knobbed or bulbous at base. Branching comprising short, stout dichotomies usually with primary, secondary, and tertiary branches terminating in tapering sterigmata; sterigmata 13 µm long. *Conidia* suborbicular, hyaline, 21–24.9 × 19–22.9 µm (range 15–28.9 × 15–26.9 µm) diam, thin walled, germination direct by germ tubes. *Oogonia* with thick, irregularly polygonally-angled oogonial wall closely enveloping the oospore. *Oospores* spherical, hyaline, 31–36.9 µm (mode 35–36.9 µm, range 25–42.9 µm) diam; wall light Mars Yellow, 1.1–2.7 (range 0.3–4.3 µm) thick; contents finely granular with oil globules, positioned centrally or eccentric; germination direct by a branched, hyaline germ tube, 4.4 µm average width (range 2.5–8.3 µm) (Weston & Uppal 1932; Fig. 6D).

Diagnosis: Direct germination of conidia readily distinguishes *Peronosclerospora sorghi* from *Sclerospora graminicola* and other *Peronosporaceae* parasites of grasses with sporangia that germinate by means of zoospores. Distinguished from other *Peronosclerospora* species by molecular analyses including phylogenetic analysis of the *cox*2 marker, isozyme phenotypes, and SSR fragment analysis (Bonde *et al.* 1984, Micales *et al*. 1988, Thines *et al.* 2008).

Reference sequence data: Ex-HUH 897 (also referred to as "2ps001") nucleotide sequences EU116055 and HQ261790 (*cox*2), HQ261763 (28S rDNA).

Host range: *Sorghum bicolor* (*Andropogon sorghum*) *Sorghum* spp., *Zea mays*, *Zea mexicana* (*Panicoideae, Andropogoneae*). Possible reports from *Panicum maximum* and *Rottobellia exalta.*

Notes: *Peronosclerospora sorghi* is primarily associated with destructive global outbreaks of sorghum and maize downy mildew diseases. This species provides a textbook example of an invasive pathogen that moved from its endemic range in the Old World into the New World, first invading Central and South America during the 1950s and later the USA in the 1960s (Fredericksen & Renfro 1977). The pathogen quickly became widespread in the Americas after its introduction, causing heavy damages to sorghum and maize production. For example, in 1969 in the USA state of Texas, sorghum and maize losses due to *Peronosclerospora sorghi* were estimated at $2.5 million (Fredericksen *et al.*1969), the equivalent of $712.6 million in 2021 dollars.

The first known sighting of *Peronosclerospora sorghi* occurred in 1907, when Butler reported the pathogen infecting jowar (sorghum; *Sorghum bicolor*) in India (Butler 1907). Kulkarni provided the first name for the pathogen in 1913 when he described *Sclerospora graminicola* var. *andropogonis-sorghi,* primarily based on the observation that the conidia of the sorghum pathogen germinated by hyphae and not by zoospores, distinguishing it from *Sclerospora graminicola sensu stricto* (Kulkarni 1913). Weston & Uppal (1932) described *Sclerospora sorghi* in 1932 on the basis of *Sclerospora graminicola* var. *andropogonis-sorghi*. Given the parenthetical citation of Kulkarni and the fact that Weston & Uppal did not designate a type, their apparent intention was to make a new combination. But in naming the species, the replaced synonym did not supply the final epithet, and as a result some authors have treated *Sclerospora sorghi* as a replacement name (Shaw 1978) rather than a combination. However, the provisions of Art. 24.4 apply in this situation, allowing for the designation of a binary combination instead of an infraspecific epithet without change of authorship. Consequently, *Sclerospora sorghi* (Kulk.) W. Weston & Uppal was published as a new combination at a new rank (*comb. & stat. nov.*).

A holotype has not been designated for this species. BPI 187336 is part of the collection reported by Kulkarni (1913), and the specimen contains abundant, well preserved material, including both the conidial and oospore stages. We therefore designate BPI 187336 as the lectotype for *Peronosclerospora sorghi*.

Peronosclerospora spontanea (W. Weston) C.G. Shaw, *Mycologia* **70**: 597. 1978.
Basionym: *Sclerospora spontanea* W. Weston, *J. Agric. Res*, Washington **20**: 678. 1921.

Typus: **Philippines**, Laguna Province, Los Banos, Luzon, on leaves and shoots of *Saccharum spontaneum* (*Panicoideae, Andropogoneae*), 17 Aug. 1921, *W.H. Weston* [**lectotype** designated here BPI 187043 (MBT 10002157); **isotype** BPI 187073 (MBT 10002158)]. Supplementary Fig. S12 shows the lectotype BPI 187043; Supplementary Fig. S13 shows isotype BPI 187073.

Description: *Conidiophores* evanescent, nocturnal, erect, single or grouped, 350–550 µm length, basal cell 140–260 × 5–8 µm and usually exceeding or at least equaling in length the extent of the main axis from the septum to the primary branches;

more or less complex dichotomous branching system, and straight terminal sterigmata 13 µm long. *Conidia* elongately ellipsoid or cylindrical, hyaline, mostly 39–45 × 15–17 µm diam, finely granular content, thin wall, rounded apex lacking papilla, rounded base with apiculum of attachment, germination by germ tubes. *Oogonia* not observed (Weston 1921; Fig. 7A).

Diagnosis: *Sclerospora spontanea* is distinguished from *Peronosclerospora philippinensis* on maize hosts by having conidiophores that are more elongate and slenderer, with basal cells less knobbed and expanded at the base; branches longer, slenderer, less constricted at point of origin; sterigmata longer; slenderer and straighter conidia. However, cautious interpretation of asexual characters is recommended, as variation due to environmental factors may hinder accurate species discrimination.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Miscanthus japonicus, Saccharum spontaneum*, *Saccharum officinarum*, *Zea mays*, *Zea mexicana* (*Panicoideae*, *Andropogoneae*).

Experimental host range: *Peronosclerospora spontanea* can infect *Miscanthus japonicus* and *Zea mexicana* under experimental conditions (Weston 1921).

Notes: *Peronosclerospora spontanea* is known from the Philippines where it causes downy mildew disease of *Saccharum spontaneum* (bugang grass) and *Zea mays* (Weston 1921, Pupipat 1975) and has been documented once from cultivated sugarcane (*Saccharum officinarum*; Weston 1921). The pathogen may be limited to the Philippines, where Weston reported three sites with heavy natural infections of wild bugang grass and one natural infection of a single stand of sugarcane in the Visayas region (Weston 1921). However, a possible incidence of *Peronosclerospora spontanea* from Thailand during 1938 has been noted (Pupipat 1975, Shaw 1975, Farr & Rossman 2021).

The type host (*Saccharum spontaneum*) is a wild sugarcane native to India that has been introduced across tropical regions of Africa, Asia, and the Mediterranean, sometimes as an outcome of its widespread use in sugarcane breeding; it is often considered a noxious weed. *Saccharum sponteaneum* is not greatly damaged by infections of *Peronosclerospora spontanea*, exhibiting only minor chlorotic leaf striping and no deformation (Weston 1921). In contrast, *Peronosclerospora spontanea* is described as extremely debilitating to maize, with symptoms and damages to maize similar to those produced by *Peronosclerospora philippinesis* (Weston 1921).

In his description of the species, Weston did not designate a holotype. Weston's August 1921 collections of *Saccharum spontaneum* colonized by oogonia of *Sclerospora spontanea* are accessioned as BPI 187043 and BPI 187073 and match the published collection details; BPI 187043 is hereby used to lectotypify *Peronosclerospora spontanea*. One additional specimen of *Sclerospora spontanea* collected in December 1921, BPI 187342, consists of dried conidia scraped from the surface of diseased maize leaves that had been inoculated from conidia originally harvested from *Saccharum spontaneum*, and includes a typewritten note signed by Weston (Supplementary Fig. S14).

Peronosclerospora westonii J.A. Crouch & Thines ***sp. nov.*** MycoBank MB 840574.

Synonyms: '*Sclerospora westonii*' Sriniv. *et al*., *Bull. Torrey Bot. Club* **88**: 94. 1961. [*nom. inval.*, Art. 40.1]

'*Peronosclerospora westonii*' (Sriniv. *et al*.) C.G. Shaw, *Mycologia* **70**: 597. 1978. [*nom. inval.* Art. 35.1]

Typus: Illustration in *Bull. Torrey Bot. Club* **88**: 93, fig. 7, 1961 (**holotype** designated here) based on collection made in **India**, Poona, *Iseilema prostratum* (as *Iseilema laxum*; *Panicoideae, Andropogoneae*), Jul./Aug. 1960, *M.C. Srinivasan*, *M.J. Narasimhan*, *M.J. Thirumalachar*.

Description: *Conidiophores* 600–1 000 µm long, with single basal compartment; 9–11.5 µm broad at the basal compartment, 20–27 µm broad at main axis branching. Dichotomous branching, 20–25 µm high × 12–15 µm spread; typically limited to 2–4 primary branches with 2–3 obconical tapering sterigmata with conidia; rarely main axis producing secondary branches. *Conidia* globose to ovoid, hyaline 12–19 µm in diam, thin-walled, with granular contents at maturity, germinating by germ tubes. *Oogonia* spherical, subglobose, 40–50 µm diam, with granular contents. *Oospores* spherical, golden-brown, 23–29 µm diam, wall 6–9 µm thick, covered by the outer oogonial wall layer. (Srinivasan *et al.* 1961; Fig. 7B).

Diagnosis: In common with *Peronosclerospora dichanthiicola, Peronosclerospora westonii* has an aggregated, undifferentiated conidiophore branch structure, a feature that distinguishes the species from the well-developed branching structure of *Peronosclerospora noblei, Peronosclerospora philippinensis*, *Peronosclerospora sorghi,* and *Peronosclerospora spontanea*. However, conidia of *Peronosclerospora westonii* are smaller than those of *Peronosclerospora dichanthiicola*, measuring 12–19 µm diam versus 21–28 × 15–18 µm, respectively. *Peronosclerospora westonii* occurs on the same host species as *Peronosclerospora iseilematis*, but can be differentiated by differences in oospore size, with the spherical golden-brown oospores of *Peronosclerospora westonii* measuring 23–29 µm diam with thick endosporium walls of 6–9 µm thickness *vs*. the spherical, pale oospores of *Sclerospora iseilematis* measuring 38–50 µm diam with endosporium walls of 3.0–3.5 µm thickness.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Notes: To our knowledge, *Peronosclerospora westonii* has not been reported since the species was first diagnosed in 1961 (Srinivasan *et al.* 1961, Waterhouse 1964, Farr & Rossman 2021). The type host *Iseilema prostratum* (musal grass) is a common forage grass distributed in the waterlogged tropical regions of southern India and continental southeast Asia. The original report of *P. westonii* described leaves with chlorotic yellow streaking that became necrotic and eventually led to leaf shredding (Srinivasan *et al.* 1961).

Sclerospora westonii Sriniv. *et al*. is an invalid name, as Srinivasan *et al.* (1961) neglected to designate a type (Art. 40.1, Turland *et al.* 2018). The invalid status of *Sclerospora westonii* also renders *P. westonii* (Sriniv. *et al*.) C.G. Shaw invalid, as the name is based on an invalid basionym (Art. 35.1, Turland *et al.* 2018). It is unknown whether specimens utilized by Srinivasan *et al.* (1961) were formally lodged in a reference collection;

therefore, an illustration is utilized here as the holotype for the species, providing clear morphological features including conidiophores, sterigmata, conidia, oogonium, and oospores (Srinivasan *et al.* 1961).

'***Peronosclerospora zeae***' C. L. Yao, *Curr. Genet*. **22**: 415–420. 1992. [*nom. inval*., Art. 30.9, 36.1., 40.1]

Typus: *Non designatus*.

Notes: The first appearance of this name is found in Yao's (1991) dissertation; however, there was no description and a type was not designated. Yao *et al.* (1992) later applied this name and inaccurately referenced the dissertation as the effective publication. Later authors considered the strains used by Yao (1991) to be *Peronosclerospora maydis* (Perumal *et al.* 2008).

Poakatesthia Thines & Göker, *Mycol. Res.* **111**(12): 1381. 2007.

Type species: *Poakatesthia penniseti* (R.G. Kenneth & J. Kranz) Thines & Göker, *Mycol. Res.* **111**: 1381. 2007.

Notes: The genus *Poakatesthia* was designated to accommodate the pathogen originally described as *Plasmopara penniseti* based on the production of sporangiophores that are shaped similarly to those found in the genus *Plasmopara* (Kenneth & Kranz 1973). Thines & Göker (2007) designated the new genus *Poakatesthia* based on the unique morphology of the haustoria

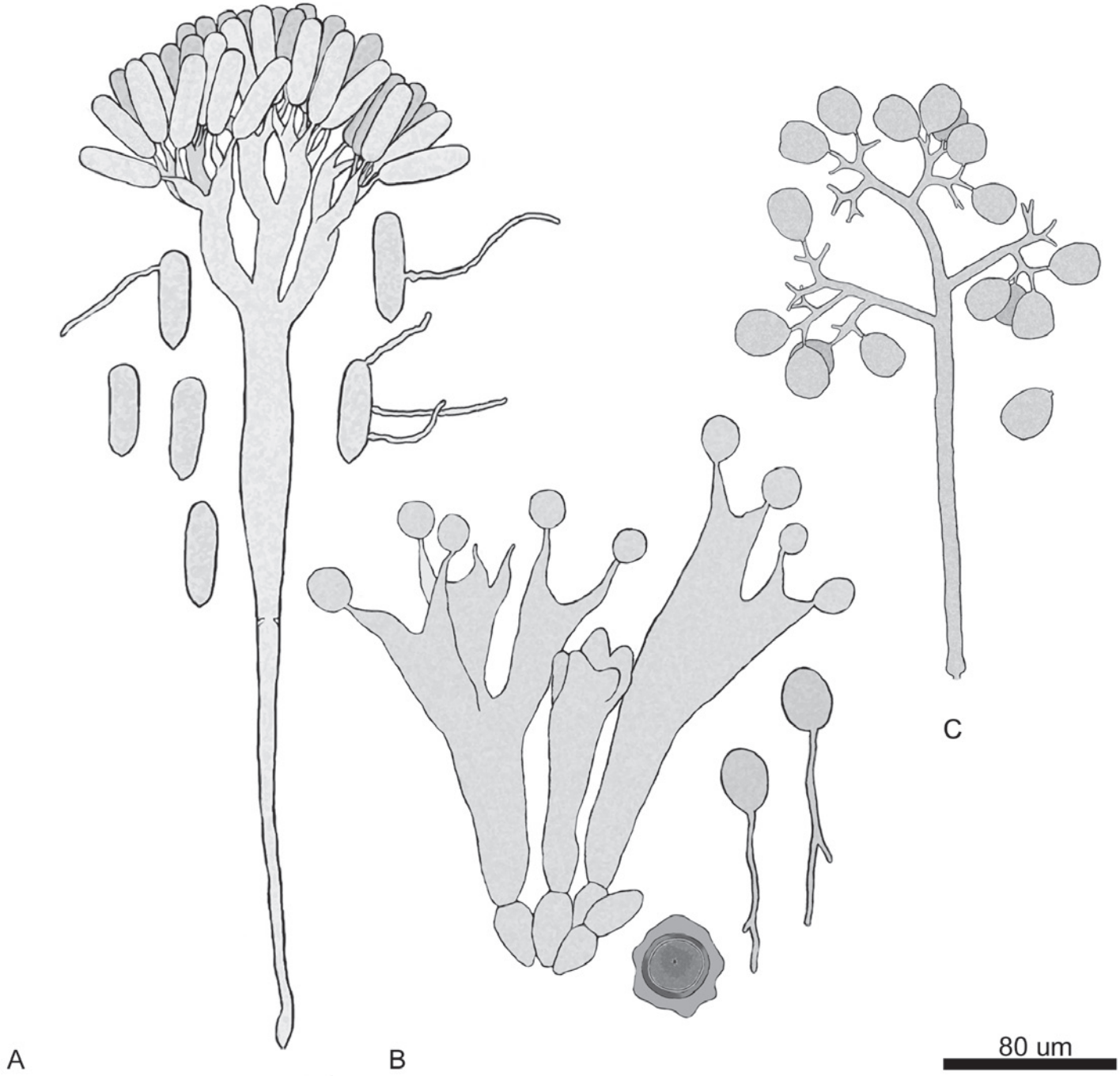

Fig. 7. A. *Peronosclerospora spontanea*, sporangiophore and sporangia (some germinating). **B.** *Peronosclerospora westonii*, sporangiophore, germinating sporangia and oospores. **C.** *Poakatesthia penniseti,* sporangiophore. Illustrations were prepared from published reference images in Weston (1921), Srinivasan *et al.* (1961), Titatarn & Syamanda (1978) and Thines *et al*. (2007).

and *cox2* sequence data that characterizes *Poakatesthia penniseti*. *Poakatesthia* contains one species and is known only from Ethiopia as a parasite of *Pennisetum glaucum*.

Poakatesthia penniseti (R.G. Kenneth & J. Kranz) Thines & Göker, *Mycol. Res.* **111**: 1381. 2007.
Synonym: *Plasmopara penniseti* R.G. Kenneth & Kranz, *Trans. Brit. Mycol. Soc*. **60**: 591. 1973.

Typus: **Ethiopia**, Bako/Shoa, *Pennisetum glaucum* (*Panicoideae, Paniceae*), Oct. 1968, *J. Kranz* (**holotype** IMI 137328c).

Description: *Sporangiophores* hyaline, amphigenous, erect, 300–580 µm high; trunk 0.55–0.77 of total height × 8–11 µm width; dichotomously branched once or twice, then branched irregularly monopodially to subdichotomously two or three times at right angles. Ultimate branchlets straight or slightly curved, usually two divaricate at apices of final branch, tapered with truncate tip, 4.7–9.5 µm long × 3.2 µm wide at base; 1–2 ultimate branchlets sometimes along sides on final branch, 4.7–12.6 µm long. *Sporangia* hyaline, wide obovoid with +/- flattened apical end and poroid papilla, base peducellate; 19–23.7 × 14.2–17 (19) µm. *Oogonia* not observed (Kenneth & Kranz 1973; Fig. 7C).

Diagnosis: Sporangiophore morphology similar to *Plasmopara* but differs based on obovoidal to egg shaped sporangia with flattened apex, intracellular mycelium and parasitism of *Pennisetum penniseti*. Uniquely diagnosed based on nucleotide sequence of *cox*2 that shares just 94.5 % identity with *Viennotia oplismeni*, its most closely related species.

Reference sequence data: Ex-holotype nucleotide sequence EF426475 (*cox*2).

Notes: *Poakatesthia penniseti* has not been reported since its initial description on pearl millet (*Pennistum glaucum*; Kenneth & Kranz 1973, Thines *et al.* 2007, 2008, Thines & Choi 2016, Farr & Rossman 2021), one of the most important staple food crops in India and several regions of Africa. Disease symptoms on infected plants were described as minor, and largely affected lower leaves of plants across an experimental plot in a remote region of the Ethiopian highlands (Kenneth & Kranz 1973). Initial symptoms are diffuse, small watersoaked spots or stripes that expand and coalesce to form irregular brown stripes between the veins leading to eventual necrosis (Kenneth & Kranz 1973). Since pearl millet was first introduced by seed to this isolated region of Ethiopia in 1966, Kenneth & Kranz speculated that the pathogen might have originated from one of several indigenous *Pennisteum* spp. growing in the area (Kenneth & Kranz 1973).

Sclerophthora Thirum., C.G. Shaw & Naras., *Bull. Torrey Bot. Club* **80**: 304. 1953.

Type species: *Sclerophthora macrospora* (Sacc.) Thirum. *et al*., *Bull. Torrey Bot. Club* **80**: 299. 1953.

Notes: *Sclerophthora* was erected by Thirumalachar *et al.* (1953) to accommodate *Sclerophthora macrospora*, a species that exhibits morphological characters typical of both *Sclerospora* (thick-walled oospores) and *Phytophthora* (hyphal sporangiophores, large, lemon-shaped phytophthora-like sporangia). The genus differs from all other *Peronosporaceae* genera, as it typically produces hardly differentiated sporangiophores, sporangia that germinate to produce biflagellate zoospores, and thick-walled oospores measuring 30–80 µm diam. It is unknown whether indirect oospore germination is a common trait for *Sclerophthora*, as oospore germination has not been described for the other five species currently assigned in the genus. It should be noted that the great variation in symptoms caused by the different species, as well as some morphological traits of the sporangia produced render it doubtful if the genus is monophyletic.

Sclerophthora cryophila W. Jones, *Canad. J. Bot*. **33**: 352. 1955.

Typus: **Canada**, British Columbia, Saanichton, *Dactylis glomerata* (*Pooideae, Poeae*), 1 Jun. 1948, *W. Jones* [**holotype** designated here DAOM 20643 (MBT 10002159)]. Supplementary Fig. S15 shows the holotype DAOM 20643.

Description: *Sporangiophores* short, sterigma-like, unbranched. *Sporangia* obpyriform, hyaline, (22.5–)30.5–38(–45.5) µm × (11.5–)15–19(–22.5) µm, apically poroid, pedicels persistent; nocturnal under natural conditions. *Oogonia* subglobose to spherical, sinuous, golden to amber-brown, (29.5–)38.5(–51.5) µm diam; wall 1.9-3.8 µm thick (average 3.7). *Antheridia* paragynous. *Oospores* spherical, (20–)31.8(–37.5) µm diam; wall (1.5–)2.6(–3.5) µm thick, confluent with oogonial wall (Jones 1955; Fig. 8A).

Diagnosis: Distinct from *Sclerophthora macrospora* in that it has smaller oospores, oogonia, and sporangia, and thinner oogonium walls.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Dactylis glomerata* (*Pooideae, Poeae*). Possible hosts: *Apluda mutica, Dichanthium annulatum, Digitaria marginata, Heteropogon contortus* (*Panicoideae*).

Notes: *Sclerophthora cryophila* was first reported on the cool-season grass *Dactylis glomerata* (orchard grass) from Canada (Jones 1955). Orchard grass infected by *Sclerophthora cryophila* in field plots produced symptoms described as similar to the effects of frost injury, with yellow/brown streaks on leaves and occasional pale brown to pale cream discoloration of inflorescence sheaths (Jones 1955). Although the type host is widely distributed across North America in stands of wild grown plants or cultivated as a high-quality forage grass, there have not been reports of *Sclerophthora cryophila* from orchard grass since the collection from the original outbreak (Jones 1955).

There have been reports of *Sclerophthora cryophila* from India affecting four hosts in the subfamily *Panicoideae* (Srinivasan & Thirumalachar 1962, Safeeulla *et al.* 1963). The morphology of the pathogen described from *Apluda mutica, Dichanthium annulatum, Digitaria marginata*, and *Heteropogon contortus* is consistent with *Sclerophthora cryophila* (Srinivasan & Thirumalachar 1962). Given the host range associated with these reports and our current understanding of downy mildew pathogens as mostly narrowly host-specific organisms (Thines & Choi 2016), the identification of *Sclerophthora cryophila* from

these warm-season grasses suggests that the species may be a complex of morphologically similar species. This is partially supported by the results of cross-inoculation experiments, where strains of *Sclerophthora cryophila* from *Digitaria marginata* and *Heteropogon contortus* were unable to infect each other's hosts (Srinivasan & Thirumalachar 1962).

Under natural conditions, *Sclerophthora cryophila* produces sporangiophores nocturnally for just a few hours in the early morning under conducive conditions, but sporangia collected from warm-season hosts exhibit no periodicity and can be readily induced by floating infected leaf sections on water (Srinivasan & Thirumalachar 1962), which is similar

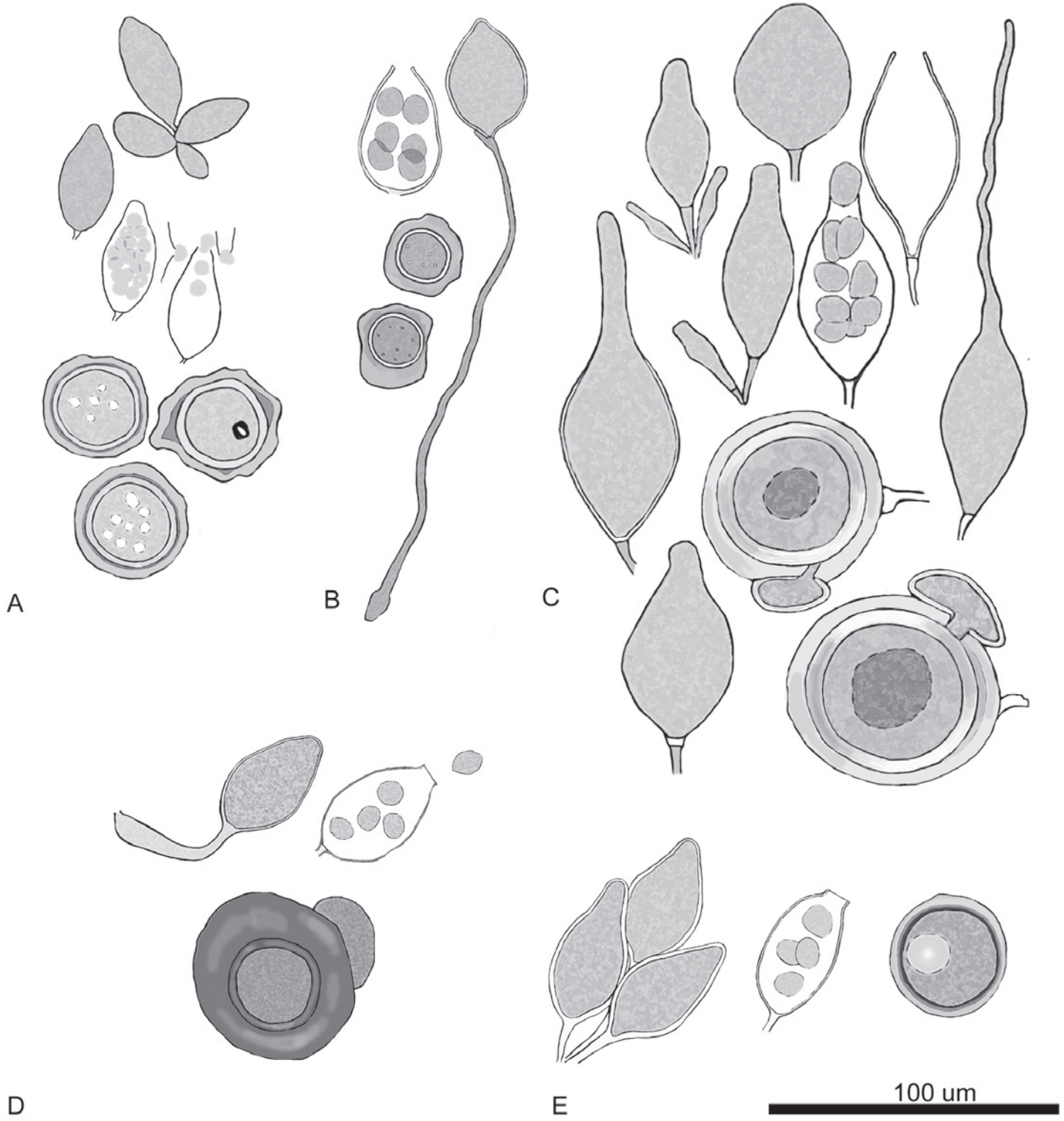

Fig. 8. A. *Sclerophthora cryophila*, sporangiophores, sporangia with zoospores, and oospores. **B.** *Sclerophthora lolii*, sporangiophores, sporangium with emerging zoospores, and oospores. **C.** *Sclerophthora macrospora*, sporangiophores (with sporangia filled with undifferentiated cytoplasm, empty, with emerging zoospores, or germinating), and oospores. **D.** *Sclerophthora rayssiae*, sporangiophore, sporangium with emerging zoospores, and oospores. **E.** *Sclerophthora zeae*, sporangiophore, sporangium with emerging zoospores, and oospore. Illustrations were prepared from published reference images in Jones (1955), Srinivasan & Thirumalachar (1962), Kenneth (1963), Waterhouse (1964), Payak & Renfro (1967) and Ryley *et al.* (2021).

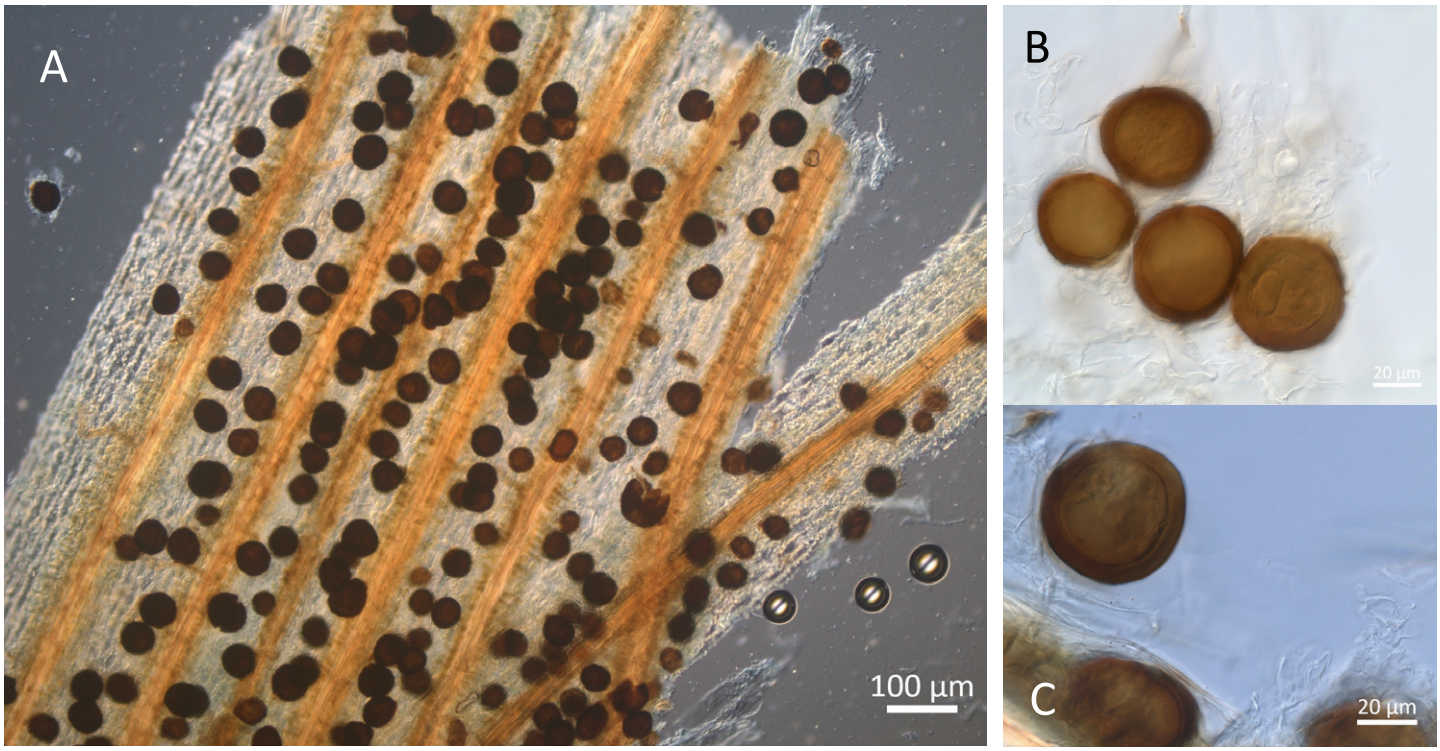

Fig. 9. *Sclerospora farlowii.* **A.** Oospores embedded in host tissue. **B, C.** Oospores.

to *Sclerophthora macrospora* (Thirumalachar *et al.* 1953), *Sclerospora graminicola*, and *Sclerospora sorghi* (Safeeulla & Thirumalachar 1956).

A holotype specimen was not formally designated for *Sclerophthora cryophila*. Jones indicated in the protolog that type materials were deposited in the herbarium of the Plant Pathology Laboratory, Saanichton, B.C.; the Saanichton collections were later transferred to DAOM. DAOM holdings of *Sclerophthora cryophila* include six specimens on *Dactylis glomerata*, but just one of these specimens (DAOM 20643) was collected on 1 Jun. 1948 by W. Jones, consistent with the species protolog. DAOM 20643 is clearly the sole specimen used to describe *Sclerophthora cryophila* and is therefore the holotype (Art. 9.1).

Sclerophthora lolii J.A. Crouch & Thines, ***sp. nov.*** MycoBank MB 840575.
Synonym: '*Sclerophthora lolii*' R.G. Kenneth, *Israel J. Bot.* **12**: 139. 1963. [*nom. inval.* Art. 40.1].

Typus: Illustration in *Israel J. Bot.* 12: 137–138, fig. 1–3, 1964 (**holotype** designated here) based on collection made in **Israel**, Mikve, *Lolium rigidum* (*Pooideae, Poeae*), Feb. 1962, *R.G. Kenneth*.

Description: *Sporangiophores* hyaline, slender, bearing sporangia. *Sporangia* lemon-shaped, 40.7–55.0(–63.7) × 25.2–35.0 µm; base with persistent peduncle, apex papillate, poroid, thin-walled; 10–15 pyriform *zoospores* produced within sporangium, 7.8–10.7 µm long, escaping through sporangial apex. *Oogonia* spherical to subspherical, sinuous, 25.2–28.8 µm diam. *Oospores* spherical, golden brown, 10.8–18.0 µm diam, smooth-walled, moderately thin-walled, centrally located within confluent thick oogonial walls (Kenneth 1963; Fig. 8B).

Diagnosis: Sporangia size and shape similar to *Sclerophthora cryophila* and *Sclerophthora raysiae*, but *Sclerophthora lolii* can be discriminated from these two species based on its smaller oogonia and oospore size. The length of the pyriform zoospores (7.8–10.7 µm), as with *Eraphthora butleri, Sclerophthora raysiae*, and *Sclerophthora zeae*, is distinctive among the *Peronosporaceae* (Kenneth 1963).

Reference sequence data: No sequence data available from type material or bona fide specimens.

Notes: Weedy, immature wild ryegrass (*Lolium rigidum*) infected with *Sclerophthora lolii* exhibit only mild disease symptoms, appearing as localized yellow patches on leaves that eventually necrotize without inducing leaf shredding (Kenneth 1964). To our knowledge, there have been no subsequent reports of this pathogen since the original 1962 discovery in Israel.

Sclerophthora lolii R.G. Kenneth was not validly published since a type specimen was not designated but was required at the time of publication (Art. 40.1; Turland *et al.* 2018). Kenneth's collection at HUJ, including his specimen of this species, appears to have been lost, but published illustrations of the original material clearly depict the diagnostic features of the organism and are therefore designated as the holotype for the newly validated species.

Sclerophthora macrospora (Sacc.) Thirum. *et al.*, *Bull. Torrey Bot. Club* **80**: 299. 1953.
Basionym: *Sclerospora macrospora* Sacc., *Hedwigia* **29**: 155. 1890.
Synonyms: *Sclerospora kriegeriana* Magnus, *Verh. Ges. Deutsch. Naturf.* **67**: 100. 1896.
Kawakamia macrospora (Sacc.) Hara, *Nôgyôkoku* [*Agriculturalist*] **9**: 24. 1915.
? *Nozemia macrospora* (Sacc.) Tasugi, 1931.
Phytophthora macrospora (Sacc.) S. Ito & Tanaka, *Ann. Phytopath. Soc. Japan* **10**: 138. 1940.

Possible synonyms: *Sclerospora oryzae* Brizi, *Natura, Milano* **10**: 168–180. 1919.
Phytophthora oryzae (Brizi) Hara, *Diseases of the rice plant* [*Ineno Byogai*], **Edn 2**: 57. 1939.

Typus: **Germany**, Saxony, Königstein, near the Königstein Fortress, *Phlaris arundinaceae (Pooideae*), 26 Aug. 1895, *P. Magnus* [**neotype** designated here BPI 187265 (MBT 10002160); **isotypes** BPI 187266 (MBT 10002161), MICH00010280]. Supplementary Fig. S16 shows the neotype BPI 187265; Supplementary Fig. S17 shows isotype BPI 187266.

Description: *Mycelium* hyaline, without septa, with haustoria, intercellular, aggregating near vascular bundles. *Sporangiophores* emerging from stomata, external hyphae (8–) 14(–28) µm long × 1–4 µm wide; undifferentiated from hyphae in the host, sympodial. *Sporangia* in clusters of 4–5, limoniform, obovate or ellipsoidal, hyaline to slightly purplish, moderately papillate; 58–98 × 30–65 µm (natural material) or (65–)87(–113) × (33–)44(–55) µm (in water). *Zoospores* at first ovate or irregularly kidney shaped, somewhat globose when motile, spherical at rest, (13–) 11(–16) × (10–)13(–14) µm, may produce zoosporangia (10–) 13(–16) µm diam with germ tubes 1.6–2.5 µm wide. *Oogonia* somewhat globose, light greenish to greenish brown, 50–95 × 55–100 µm (mostly 57–73 × 63–75 µm) and averaging 65 × 69 µm; wall 2.5–7.5 µm thick, commonly (3.8–)4.3(–5) µm thick. *Antheridia* laterally attached, hyaline to light yellow, obovate to ellipsoidal, wall slightly thickened, (13–)15(–23) × (23–)28(–41) µm, wall (1.8–)2.5(–3.8) µm thick. *Oospores* hyaline, somewhat globose, attached closely to the wall of the oogonium (43–) 57(–70) × (43–) 60(–73) µm; wall (3.8–)6.5(–10) µm thick, germinate indirectly by germ tube (Saccardo 1890, Tanaka 1940, Waterhouse 1964, Fig. 8C).

Diagnosis: The morphology of the asexual stage (short, unbranched, and undifferentiated sporangiophores) and the indirect germination of sporangia differentiate *Sclerophthora macrospora* from *Sclerospora* and all other *Peronosporaceae* genera. *Sclerophthora macrospora* can be distinguished from *Sclerospora graminicola* by its larger zoospores, and from *Sclerospora secalina* by its hyaline, larger oospores (Waterhouse 1964).

Reference sequence data: Ex-HUH 892 nucleotide sequences KP965748 (*cox*2), EU826119 (28S rDNA).

Host range: This species is reported from approximately 141 *Poaceae* hosts globally, comprising tropical and temperate cereals, forage grasses, turf grasses, and many weedy grasses (Pupipat 1975, Safeeulla 1976, Farr & Rossman 2021). However, it is possible that *Sclerophthora macrospora* is a species complex (Telle *et al.* 2011, Telle & Thines 2012, Thines *et al*. 2015). Molecular phylogenetic analyses of multiple isolates of *Sclerophthora macrospora* from different hosts resolved several distinct clades, with isolates collected from the same host species often falling within different clades (Telle & Thines 2012). Reported hosts include *Avena sativa (Pooideae, Poeae), Eleusine coracana (Chloridoideae*, *Cynodonteae*), *Festuca* spp. (*Pooideae, Poinae*), *Hordeum vulgare* (*Pooideae, Triticeae*), *Lolium* spp. (*Pooideae, Poinae*), *Pennisetum glaucum* (*Pooideae, Poeae*), *Oryza sativa* (*Oryzoideae, Oryzeae*), *Sorghum bicolor* (*Panicoideae, Andropogoneae*), *Triticum* spp. (*Pooideae, Panicoideae), Zea mays* (*Panicoideae, Andropogoneae*), and others (see *Notes*).

Notes: *Sclerophthora macrospora* causes diseases referred to as either downy mildew, crazy top, or witches' broom; on rice the pathogen causes yellow wilt, and on turfgrass it causes yellow tuft. The pathogen has a world-wide distribution in temperate and warm climate regions of Africa, Asia, Europe, the Americas, and Oceania. In Morocco and the USA, *Sclerophthora macrospora* is a quarantine pest. It is subjected to regulations in Egypt, Paraguay, Bahrain, and two EPPO regions due to its inclusion on the EPPO A1/A2 invasive pest list (EPPO 2021). The pathogen is considered of minor importance on maize, rice, sorghum, sugarcane, turfgrass, and wheat (Smith & Renfro 2016, Lee & Groth 2018, Sugarcane Research Australia 2019, CIMMYT 2021). However, because of high levels of disease incidence (> 50 %) and yield losses as high as 100 %, *Sclerophthora macrospora* has a significant economic impact on the production of finger millet (*Eleusine coracana*), pearl millet (*Pennisetum glaucum*), and other small millets in Africa and Asia, especially in India (Nagaraja & Das 2016, Nagaraja *et al.* 2016). The most characteristic symptoms induced by *Sclerophthora macrospora* are phyllody and the development of distorted, twisted, abnormally large panicles, tassels, or heads (Holliday 1980).

A holotype was not designated for *Sclerophthora macrospora* (Saccardo 1890), and no illustrations were published with the protolog. The protolog indicates that collections were made in Australia from living leaves of an unnamed species of *Alopecurus* (*Pooideae, Poodae*), a genus that currently comprises 45 species and also previously included species that are now members of at least 14 different genera. In the absence of original materials, we selected BPI 187265 to serve as the neotype for *Sclerophthora macrospora*. BPI 187265 is one of the original collections made by Magnus in 1895 when he described *Sclerospora kriegeriana* (Magnus 1896), a later synonym of *Sclerospora macrospora* published just a few years after Saccardo's work (Thirumalachar *et al.* 1953, Waterhouse 1964, Telle & Thines 2012).

Sclerophthora rayssiae J.A. Crouch & Thines ***sp. nov.*** MycoBank MB 840576.
Synonym: '*Sclerophthora rayssiae*' R.G. Kenneth *et al.*, *Bull. Torrey Bot. Club* **91**: 189. 1964. [*nom. inval.* Art. 40.1].

Typus: illustration in *Bull. Torrey Bot. Club* 91: 186, figs 1–4, 1964 (**holotype** designated here) based on a collection made in **Israel**, Valley of Esdraelon, Mishmar Ha-Emek, *Hordeum vulgare* (*Pooideae, Triticeae*), 24 Mar. 1958, *R.G. Kenneth*, *Y. Koltin*, & *I. Wahl*.

Description: *Sporangiophores* very short, hyphoid, nocturnal under natural conditions. *Sporangia* lemon shaped or ovate, hyaline 28.8–55.0 × 19.2–27.9 µm, base with wedge-shaped pedicel, apex poroid and sometimes protruding, granular, infrequently germinating directly but primarily germinating indirectly by 6–10 reniform zoospores through the apical pore. *Zoospores* biflagellate, 7.5 × 11.0 µm long. *Oogonia* usually sinuous, unevenly thickened, 44.4–59.2(–61.4) µm diam. *Antheridia* paragynous, closely appressed to oogonium. *Oospores* abundant throughout mesophyll within lesions, solitary, or in groups or clumped, not tending to congregate in any area of the blade. *Oospores* globular, occasionally subglobular, light golden amber, 29.6–44.4 (mostly 33.3) µm diam; wall deep golden brown, smooth and thin; usually eccentrically located within oogonial wall (Kenneth *et al.* 1964; Fig. 8D).

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Hordeum vulgare* (*Pooideae, Triticeae*).

Notes: *Sclerophthora rayssiae* was first identified in Israel in 1958 causing downy mildew disease in fields of *Hordeum vulgare* (barley). The disease recurred at the same site annually from 1961–1963 and was considered widespread throughout two regions of the country (Kenneth *et al.* 1964). Infected plants show symptoms such as minor leaf lesions and did not induce host deformation (Kenneth *et al.* 1964). Subsequently there have been limited reports of the pathogen (Farr and Rossman 2021). Barley downy mildew outbreaks that occurred in 2003–2004 and 2007–2008 in India were attributed to *Sclerophthora rayssiae*, but the pathogen identity cannot be readily confirmed, as the report was limited to an abstract (Singh *et al.* 2009) and did not detail the pathogen morphology. As such, we cannot rule out the possibility that the destructive symptomology (stunting, chlorosis, deformation leading to plant death) described in the 21st century Indian outbreaks might represent an outbreak of crazy top caused by *Sclerophthora macrospora* (Miles and Epps 1942, Oswald and Houston 1951) because the symptomology differs greatly from the descriptions of *Sclerophthora rayssiae* as a weak pathogen on the same host (Kenneth *et al.* 1964).

A type specimen was not designated but was required at the time of publication; therefore, *Sclerophthora rayssiae* R.G. Kenneth was not validly published (1964). Kenneth's collection at HUJ, including his specimen of this species, is thought to be lost. However published illustrations of the original material clearly depict the diagnostic features and are used as the holotype for the newly validated species.

Sclerophthora zeae J.A. Crouch & Thines, ***sp. nov.*** MycoBank MB 840577.
Synonym: '*Sclerophthora rayssiae* var. *zeae*' Payak & Renfro, *Phytopathol.* **57**: 395. 1967. [*nom. inval*. Art. 35.1].

Typus: **India**, Pantnagar (U. P.), *Zea mays* var. *indurate* (*Panidoideae, Andropogoneae*), 12 Oct. 1965, *M.M. Payak* & *B.L. Renfro* (**holotype** designated here, HCIO 29038).

Description: *Sporangiophores* short, hyphal. *Sporangia* ovate, obclavate, elliptic, hyaline, 29.0–66.5 × 18.5–26.0 µm, smooth-walled, poroid apex truncate or rounded, with a persistent, straight or curvate peduncle, producing 4–8 zoospores. *Zoospores* spherical, hyaline, 7.5–11.0 µm diam. *Oogonia* subglobose, hyaline to light straw-colored, 33–44.5 µm diam, thin-walled, with 1–2 paragynous antheridia. *Oospores* spherical or subspherical, hyaline, 29.5–37.0 µm diam; wall smooth and glistening, 4 µm thick, wall confluent with oogonial wall; contents include prominent oil globule; centrally located in the oogonium (Payak & Renfro 1967; Fig. 8E).

Diagnosis: The large size of *Sclerophthora zeae* zoospores (7.5–11.7 µm long), as with *Eraphthora butleri, Sclerophthora lolii*, and *Sclerophthora rayssiae*, is distinctive among the *Peronosporaceae* (Kenneth *et al*. 1964, Payak & Renfro 1967). Parasitic to *Zea mays*, which differentiates it from the host range of all other *Sclerophthora* species with the exception of *Sclerophthora macrospora.* Differs from *Sclerophthora rayssiae* based on the following morphological characters: smaller oogonia (33.0–44.5 µm *vs*. 44.4–59.2 µm for *Sclerophthora rayssiae*) with thin even walls (versus the sinuous, unevenly thickened walls of *Sclerophthora rayssiae*); the absence of the golden to amber brown oogonia and oospores exhibited by *Sclerophthora rayssiae*; a sporangial shape that is obovate, obclavate, or elliptic,

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Digitaria bicornis*, *Digitaria sanguinalis (Panicoideae, Panicodae*); *Zea mays* (*Panicoideae, Andropogoneae*).

Notes: Payak & Renfro (1967) first documented the causal agent of brown stripe downy mildew of maize as *Sclerophthora rayssiae* var. *zeae*, which was collected from severe disease outbreaks that occurred throughout several regions of India in the early 1960s. The pathogen is not known from outside India. Disease symptoms are distinct from those caused by *Sclerophthora macrospora,* in that leaf shredding and deformation are not observed (Payak & Renfro 1967). Only the leaves are infected and show narrow vein-delimited chlorotic stripes parallel to the vascular tissue with well-defined margins that eventually became reddish brown to purple (Galgóczy *et al*. 2014).

Brown stripe downy mildew can result in maize yield losses between 20–100 % depending on cultivar susceptibility and weather (Putnam 2007). In present day India, the disease is of minor importance compared to other maize diseases and is generally adequately controlled using cultivar resistance and chemical applications (B.M. Prassa and Sujay Rakshit, pers. comm.; Lal *et al.* 1980, Basadrai *et al.* 2002, Singh & Singh 2012). In the USA, this pathogen is regulated under strict quarantine protocols as a USDA-APHIS Select Agent because it is considered a significant potential threat to the country's agricultural security.

Sclerophthora rayssiae var. *zeae* Payak & Renfro was not validly published, as it was based on the invalid basionym *Sclerophthora rayssiae* R.G. Kenneth (Art. 35.1, Turland *et al.* 2018). This provides us with a unique opportunity to revisit the taxonomy of the organism from a modern perspective, given the narrow species concept that we now recognize as the primary evolutionary trajectory for downy mildew pathogens (Gäumann 1918, 1923, Gustavsson 1959). In their decision to describe the organism as a variety and not assign the rank of species, Payak & Renfro adopted a broad species concept in assigning a taxonomic rank that was consistent with the accepted practice of the time and in line with the approach of most applied plant pathologists (de Bary 1863, Yerkes & Shaw 1959). Payak & Renfro (1967) were of the opinion that the host differences between the two organisms were not sufficient evidence to warrant the delimitation of a new species. However, Payak & Renfro also acknowledged several morphological features and the differing host range of *Sclerophthora rayssiae*, parasitic of the cool-season grass *Hordeum vulgare* (*Pooideae*), and *Sclerophthora zeae*, which is parasitic of warm-season *Panidoideae* grasses. Based on diagnosable morphological differences and host range, we treat this organism as a separate species rather than a varietal form of *Sclerophthora rayssiae*.

Sclerospora J. Schröt., *Hedwigia* **18**: 86. 1879.
Synonyms: *Sclerospora* subgen. *Sclerospora*, *Hedwigia* **18**: 86. 1879.

'Sclerospora subgen. *Eusclerospora'*, *Bot. Mag.*, Tokyo **27**: 218. 1913. [*nom. nud.*, Art. 21.3, 22.2]
Sclerospora subgen. *Sclerospora* J. Schröt., *Hedwigia* **18**: 86. 1879. [*nom. nud.*, Art. 22.1]

Type species: *Sclerospora graminicola* (Sacc.) J. Schröt., in Cohn, *Krypt.-Fl. Schlesien (Breslau)* **3.1**(9–16): 236. 1886 [1889].

Description: *Sporangiophores* stiffly upright with sparse straight branches. *Sporangia* ovate, with a papilla at the apex, forming zoospores. *Oospores* spherical with very thick, multi-layered, brown wall that fuses with the skin of the oogonium (Schröter 1886).

Notes: *Sclerospora* was the first *Peronosporaceae* genus specifically erected to accommodate a grass parasite, and the type species *Sclerospora graminicola* was the first graminicolous downy mildew pathogen ever described, albeit three separate times (Shaw 1975). Members of the genus are diagnosed through their asexual structures – the sporangial production of zoospores, evanescent sporangiophores with multiple branches, and a sporangial papilla – morphological traits that uniquely distinguish members of the genus from other *Peronosporaceae*.

In practice, identification of the *Sclerospora* is difficult to achieve based on morphological features alone, given the evanescent nature of the diagnostic asexual stage. *Sclerospora* sporangial structures are formed nocturnally in the presence of dew on living host material, persist only for a few hours to days, and finally collapse, desiccate, and/or gelatinize after zoospore discharge (Kenneth 1970, Jeger *et al.* 1998). This means that asexual structures are often not preserved on herbarium materials or other dried specimens, limiting their value for identification and taxonomic study. Given the destructive nature of *Sclerospora graminicola* parasitizing the staple food crops pearl millet and foxtail millet (*Pennisetum glaucum, Setaria italica*) this fundamental limitation carries important implications for detecting, preventing, and quarantining downy mildew disease on millet crops globally.

Currently, *Sclerospora* contains five validly described species and is unique among the graminicolous downy mildew genera in that three different host subfamilies are parasitized. However, our understanding of *Sclerospora* species boundaries and host association within the genus is poorly defined. The generic identity of *Sclerospora farlowii*, *Sclerospora iseilematis*, *Sclerospora northii*, and *Sclerospora secalina* is not reliable at present, as these species were all described as members of the genus *Sclerospora* based on oogonial structures, in the absence of diagnostic asexual characters. However, the oogonial morph of these species shares common features: oogonia and oospores are generally dark colored, spherical to sub-globose, with thick, multi-layered oogonial walls fused to the oogonia (Schröter 1886).

For species-level discrimination of *Sclerospora*, a combination of morphological and host range characters is the only approach currently available. However, the globally distributed, broad-host-range type species *Sclerospora graminicola* appears to be a species complex, with 198 records of the pathogen reported from 20 species of *Poaceae* (Farr & Rossman 2021). It is conceivable that many graminicolous downy mildew outbreaks were attributed to *Sclerospora graminicola* based on insufficient evidence or simply because the species was one of just a few downy mildew pathogens known from *Poaceae* hosts during the late 19th and early 20th centuries.

Until the taxonomy of this genus can be further studied and resolved, it is clear that accurate diagnosis of *Sclerospora* species is a daunting task. Molecular phylogenetic research across host populations and incorporating type materials will be required to provide a basic framework to support identification, diagnostics, and taxonomic resolution of the *Sclerospora*.

Sclerospora farlowii Griffiths, *Bull. Torrey Bot. Club* **34**: 207. 1907.
Synonyms: '*Sclerophthora farlowii*' (Griffiths) R.G. Kenneth, *Israel J. Bot.* **12**: 139. 1963 [1964]. [*nom. nud.*, Art. 36.1, 39.1]
'*Sclerophthora farlowii*' (Griffiths) R. G. Kenneth, *Phytoparasitica* **7**: 50. 1964. [*nom. nud.*, Art. 36.1, 39.1]

Typus: **USA**, Arizona, Cochise, *Chloris virgata* (as *Chloris elegans*; *Chloridoideae, Cynodonteae*), Oct. 1900, *D. Griffiths* [**lectotype** designated here, BPI 187077 (MBT 10002162); **isotypes** BPI 187076, BPI 187078, FH 965329, FH 1093687 (MBT 10002163)]. Supplementary Fig. S18 shows the lectotype BPI 1187077. Supplementary Figs S19 and S20 show isotypes BPI 187076 and BPI 187078.

Description: *Oospores* sub-globose, deep dark reddish brown and often appearing black and opaque, 28–45 µm diam. Asexual morph not observed. (Griffiths 1907; Figs 9, 10A).

Diagnosis: *Sclerospora farlowii* produces sub-globose, deep dark reddish-brown oospores that often appear black and opaque and parasitizes *Chloris virgata*, which taken together are unique features for *Peronosporaceae* parasitizing hosts in the *Poaceae* family. *Peronosclerospora miscanthi* and *Peronosclerospora noblei* also produce dark reddish to amber brown oospores of similar diam to those of *Sclerospora farlowii,* but these species differ by their globose-shaped oospores versus the sub-globose oospores of *Sclerospora farlowii* and by their host range, which is limited to *Andropogoneae* hosts.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Chloris virgata (Chloridoideae, Cynodonteae)*; possible reports on *Cynodon dactylon (Chloridoideae, Cynodonteae*); *Deyeuxia* sp. (*Poaceae, Pooideae*).

Notes: Griffiths (1907) noted that *Sclerospora farlowii* was one of the most common "fungi" encountered in southern Arizona being locally abundant but with little to no discernable impact on the health of the infected host plants. The type host, *Chloris virgata* (feather fingergrass), is native to the Americas. It is most notable as a highly adaptable, prolific weed in numerous ecosystems and an aggressive invasive plant outside its native range.

The reports of *Sclerospora farlowii* on *Cynodon dactylon* and *Deyeuxia* sp. from checklist publications (Farr & Rossman 2021) need further investigation. Given that most *Peronosporaceae* species are highly specialized and their taxonomy follows a narrow species concept (*e.g.*, García-Blázquez *et al.* 2008, Thines & Choi 2016, Petrželová *et al.* 2017), it seems unlikely that these hosts from three different plant genera with different photosynthetic pathways are parasitized by *Sclerospora farlowii*. There are also several smuts that parasitize *Deyeuxia* species that could potentially be mistaken for the resting spores of a sclerospora-like species (Vánky & Guo 2001), as was the case when *Sclerospora graminicola* was mistakenly brought into

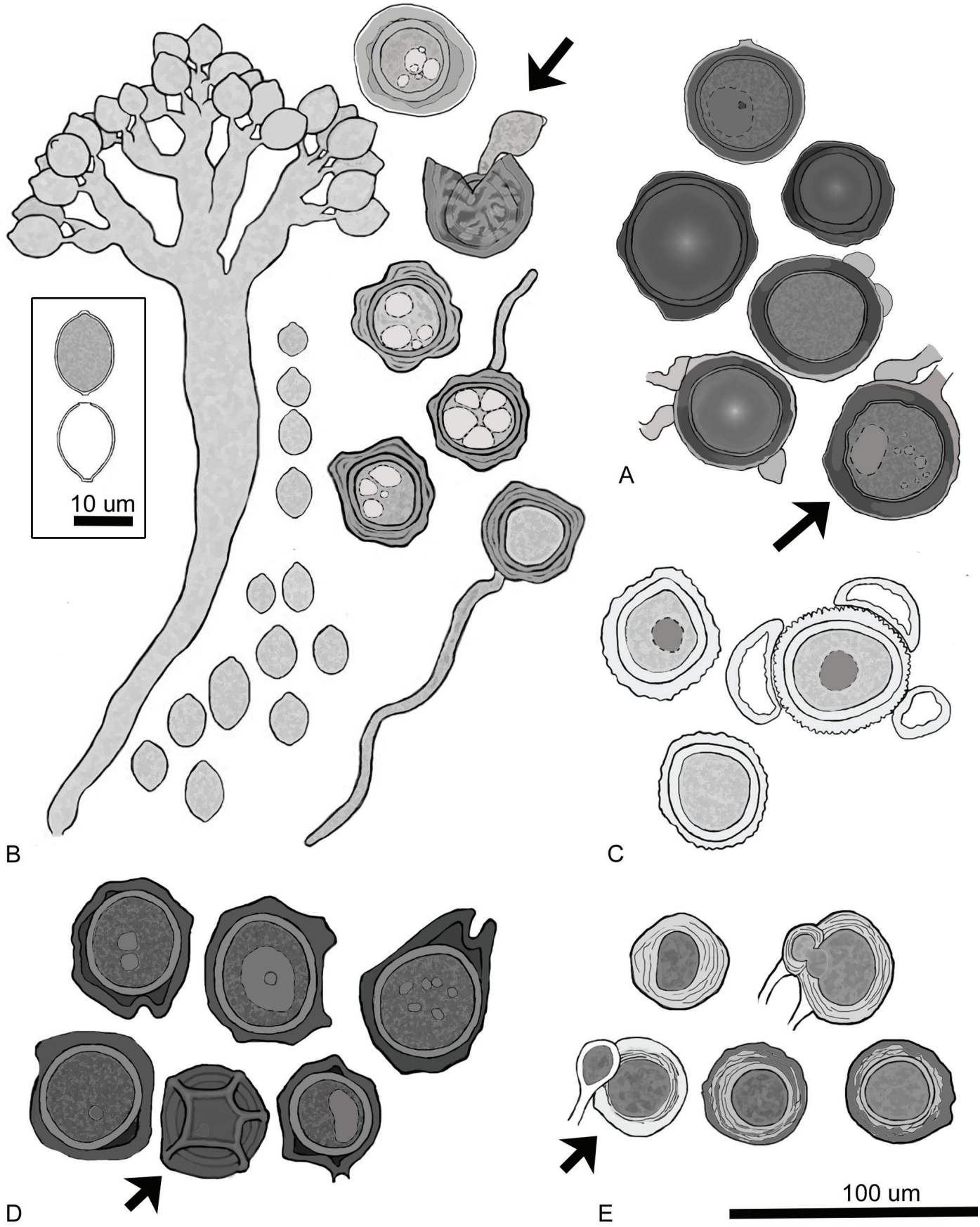

Fig. 10. A. *Sclerospora farlowii*, oogonium (arrow) and oospores **B.** *Sclerospora graminicola*, sporangiophore, sporangia, including a close-up of a cytoplasm-filled sporangium and an empty sporangium (inset); oospores, including an oospore germinating to produce a sporangium (arrow). **C.** *Sclerospora iseilematis*, oospores. **D.** *Sclerospora northii*, oospores, one in surface view (arrow). **E.** *Sclerospora secalina*, oogonium with antheridium (arrow) and oospores in various stages of maturity. Illustrations were prepared from published reference images in Weston (1924, 1929), Howe (1930), Naumov (1949), Thirumalachar & Narasimhan (1949), Pande (1972), and Thakur *et al*. (2011).

connection with the smut species *Ustilago urbani* (Waterhouse 1964, Shaw 1975).

In some publications, *Sclerospora farlowii* is listed under the name *Sclerophthora farlowii* (Griffiths) R.G. Kenneth (Kenneth 1981, Dick 2001, 2013, Spencer & Dick 2002). At the time of this writing (September 2021), MycoBank and Index Fungorum give the current name as *Sclerophthora farlowii* (Griffiths) R.G. Kenneth, *Israel J. Bot.*: 139. 1964. However, a publication by R.G. Kenneth in the *Israel Journal of Botany* from the year 1964 does not exist. A publication by R.G. Kenneth from 1963 in the *Israel Journal of Botany* does exist, and on page 139, one finds the diagnosis of *Sclerophthora lolii* R. G. Kenneth *sp. nov*., but not *Sclerophthora farlowii* (Griffiths) R. G. Kenneth *comb. nov*. The first published mention of *Sclerophthora farlowii* (Griffiths) R.G. Kenneth dates to 1979 (Kenneth 1979), in a scientific meeting abstract that states that examination of the *Sclerospora farlowii* herbarium material supports the hypothesis that the species should be transferred to *Sclerophthora*. Based on annotation labels in the Farlow Herbarium, these examinations took place in 1978. However, *Sclerophthora farlowii* (Griffiths) R. G. Kenneth is invalid under ICN Art. 36.1 and Art. 39.1 (Turland *et al.* 2018).

The original species description for *Sclerospora farlowii* is brief and limited to a description of oospore morphology. In Kenneth's 1979 meeting abstract, host range was cited as justification for transfer of *Sclerospora farlowii* to *Sclerophthora*, along with unspecified "sporangia and hyphoid sporangiophore" features, but host range is not a defining trait for the genus *Sclerophthora* and no details were provided about morphological characters. Overall, additional research is required to resolve any taxonomic uncertainty surrounding the generic identity of *Sclerospora farlowii*.

Griffiths did not designate a holotype for *Sclerospora farlowii*, although it was not required at the time of publication (Griffiths 1907). The original collections were distributed to BPI and FH, and in Griffith's personal herbarium (Griffiths 1907). Examination of the BPI collections identified specimen BPI 187077, BPI 18076, and BPI 187078 with the same collection details described by Griffith's, with notes written in W.H. Weston's handwriting that these were type material. BPI 187077 is herein used to lectotypify the species.

Sclerospora graminicola (Sacc.) J. Schröt., in Cohn, *Krypt.-Fl. Schlesien (Breslau)* **3.1**(9–16): 236. 1886.
Basionym: *Protomyces graminicola* Sacc., *Mycotheca Veneti* **5**: no. 496. 1876.
Synonyms: *Ustilago (?) urbanii* Magnus [as '*urbani*'], *Verh. Bot. Ver. Prov. Brandenb*. **20**: 52. 1878.
Sclerospora graminicola (Sacc.) J. Schröet., *Hedwigia* **18**: 86. 1879.
Peronospora setariae Pass., *Grevillea* **7**: 99. 1879.
Peronospora graminicola (Sacc.) Sacc., *Michella* **2**: 586. 1882.
Sclerospora graminicola var. setariae-italicae Traverso, *Boll. Soc. Bot. Ital.* **1902**: 1968. 1902.
Sclerospora graminicola var. graminicola Kulk*., Memoirs of the Dept. Agric. India, Bot. Ser*. **55**: 272. 1913.
'*Sclerospora graminicola*' Schröter *apud* Oudemans, *Enum. Syst. Fungi*. **1**: 719. 1919. [*nom. inval.* Art 32.1(c)]. A slip of the pen for *Peronospora graminicola* (Sacc.) Sacc.
'Sclerospora setariae-italicae' (Traverso) Cif. & Sousa da Câmara, *Quad. Ist. Bot. Uni. Pavia* **30**: 233. 1963. [*nom. inval.,* Art. 41.1]
Typus: **Poland**, Liegnitz, Waldau, Breslau, *Setaria viridis*, date unknown, *W.G. Schneider*, Herbarium Schlesischer Pilze: 553.

Description: *Sporangiophores* evanescent, nocturnal, erect, 100 × 12–15 µm; branched in the lower part but usually with a few short, thick branches that are dichotomously or trichotomously formed at the top and crowned with numerous ultimate branchlets on which sporangia are borne. *Sporangia* hyaline, subglobose to elliptical, slightly pointed at the free end, with a thin smooth wall; rapidly germinate in water, liberating zoospores in variable numbers, from three to four and up to a dozen or more zoospores per sporangium depending on size. *Zoospores* irregularly kidney shaped, unequal-sided, flattened bodies, 9–12 µm diam, forming two oppositely directed flagella on the concave side, and germinating via hyphae. *Oogonia* elliptical, angular or irregular shape due to irregularly thickened wall, tawny to brown or chestnut brown, (34–)42(–52) µm diam; wall irregular with thickened areas and conspicuous ridges, 4–11 µm, sometimes up to 17 µm thick, making the whole spore, thus, 33–45 µm (sometimes up to 50 µm) diam. *Oospores* spherical, yellow (Chromotaxia), (22.5–)32(–35) µm diam; wall evenly thickened, smooth. (Butler 1907, Schröeter 1886; Fig. 10B).

Diagnosis: Evanescent sporangiophores with multiple branches bearing sporangia uniquely distinguish *Sclerospora graminicola* from members of the *Peronosporaceae* outside of the genus *Sclerospora*. Differs from *Sclerospora iseilematis*, and *Sclerospora secalina* by having an oogonial wall with conspicuous ridges. Differs from *Sclerospora northii* by having smaller oogonia (41 µm diam versus 51–61 µm diam, respectively).

Reference sequence data: Ex-HV532 nucleotide sequences DQ365768 (*cox*2), AY035514 (28S rDNA D1/D2/D3), AY273987 (28S rDNA D7/D8).

Host range: *Setaria* spp. and *Pennisetum glaucum* (*Panicoideae, Paniceae*). Globally, the species is also reported as a parasite of 20 species of *Poaceae* in two subfamilies including 13 genera: *Beckeropsis, Digitaria, Echinochloa, Euchlaena*, *Panicum, Pennisetum*, *Setaria*, *Sorghum*, *Zea* (*Panicoideae*); *Alopecurus*, *Dactylis*, *Holcus*, and *Triticum* (*Pooideae*) (Weston & Weber 1928, Farr & Rossman 2021). As discussed in the Notes section below, the true host range and impact of this species may be limited to *Setaria* spp. or even the type host *Setaria viridis* (wild foxtail millet).

Notes: *Sclerospora graminicola* reportedly impacts production of two widely cultivated staple human food crops significantly: pearl millet (*Pennisetum glaucum*) and foxtail millet (*Setaria italica*; Safeeulla 1976, Francis & Williams 1983, Kumar *et al.* 2012). Pearl millet in Africa and Asia are the most affected by *Sclerospora graminicola*, with losses of 20–100 % reported (Kumar *et al*. 2012). Crop losses in foxtail millet can range between 20–70 % (Li *et al.* 2020). To date, pearl millet has not been reported as a host in the Americas (Francis & Williams 1983, Kumar *et al.* 2012, K.M. Devos, *pers. comm.*).

There are multiple lines of evidence that suggest *Sclerospora graminicola* is a species complex in need of careful taxonomic evaluation, particularly across host populations (M. Thines, unpubl. data). Broadly speaking, since most *Peronosporaceae* species are specialized to parasitism of a single or only a few host species, records of this species as a broad-host range pathogen of 13 different genera across two plant families are inconsistent with

expectations for the species (*e.g.*, Thines & Choi 2016, Petrželová *et al.* 2017). More specifically, most – but not all – experimental evidence from host range studies points to the distinction between *Sclerospora graminicola* strains that infect pearl millet from those that infect *Setaria* spp., including foxtail millet (Melhus *et al.* 1928, Safeeulla 1976, Francis & Williams 1983, Singh *et al*. 1993). Since *Sclerospora graminicola* isolates from pearl millet are heterothallic with two mating types (Michelmore *et al*. 1982, Idris & Ball 1984), the inability of strains from *Setaria* spp. to infect pearl millet could indicate that the lineage(s) on *Setaria* spp. are reproductively isolated from the lineages on pearl millet, which satisfies the separation of the two lineages into two species under a biological species concept. Molecular studies of *Sclerospora graminicola* are very limited, with only a few specimens from pearl millet analyzed using *cox*2 and 28S rDNA sequence data (Thines *et al.* 2008, Telle *et al.* 2011, Thines *et al.* 2015), although the availability of whole genome sequence data (Nayaka *et al*. 2017) may lead to new investigations of species diversity.

Sclerospora iseilematis Thirum. & Naras., *Indian Phytopathol*. **2**: 49. 1949.

Typus: **India**, Mysore, Nandi Hills, *Iseilema prostratum* (as *Iseilema laxum*; *Panicoideae, Andropogoneae*), 20 Jan. 1947, *M.J. Narasimhan* & *H.C. Govindu* [**lectotype** designated here BPI 187262 (MBT 10002239); **isotype** IMI 38399 (MBT 10002240)]. Supplementary Fig. S21 shows the lectotype BPI 187262.

Description: *Oogonia* sub-globose to spherical, pale golden-yellow, 43–61 µm diam; wall deeply folded, tuberculate, almost spiny, 5.5 µm thick. *Antheridia* 2–5, conoid to triangular, 27–40 × 15.5–27 µm, persistent in mature oospore. *Oospores* spherical, hyaline, 38–50 µm diam, plerotic, inner contents granular and enclosing a few droplets; wall 3–3.5 µm thick, confluent with the oogonial wall. Asexual morph not observed (Thirumalachar & Narasimhan 1949; Fig. 10C).

Diagnosis: Parasitizes the same host as *Peronosclerospora westonii*, but can be differentiated by oospore size, with the spherical, pale oospores of *Sclerospora iseilematis* measuring 38–50 µm diam with tuberculate endosporium walls 3.0–3.5 µm thick versus the spherical golden-brown oospores of *Peronosclerospora westonii* measuring 23–29 µm diam with smooth endosporium walls 6–9 µm thick. Differs from *Sclerospora graminicola, Sclerospora northii*, and *Sclerospora secalina* by having a tuberculate, almost spiny oogonial wall. Differs from *Sclerospora farlowii* by its parasitism of *Iseilema prostratum*.

Reference sequence data: Ex-lectotype nucleotide sequences OK185342 (*cox*2), OK255493 (28S rDNA).

Host range: Known only from the type host *Iseilema prostratum.*

Notes: *Sclerospora iseilematis* has not been reported since its original description in 1949, when a single field of *Iseilema prostratum* (musal grass) with downy mildew disease symptoms was documented in India (Thirumalachar & Narasimhan 1949). The type host is native to the Indian subcontinent and parts of South-East Asia, but the extent to which the pathogen is distributed with the host is unknown. *Sclerospora iseilematis* infections result in witches-broom-like inflorescences with reduced internodal elongation and excessive proliferation and branching of the spikelets. Although oogonia production is heavy within the mesophyll of infected leaves, no leaf shredding symptoms occur, and leaf symptoms are limited to chlorosis (Thirumalachar & Narasimhan 1949).

Since Thirumalachar & Narasimhan (1949) only observed the oogonial morph, it is impossible to conclude from morphological data alone that *Sclerospora iseilematis* is a member of the genus *Sclerospora*. The basic morphological features that define *Sclerospora* are only found in the sporangia: namely, through the evanescent production of sporangiophores with multiple branches, and the sporangial production of zoospores that escape through a pailla.

A holotype specimen was not designated in the protolog, although collection details were listed, followed by the word "type." BPI contains a specimen of *Sclerospora iseilematis* (BPI 187262) with collection details matching those given in the protolog and marked "type" on the outer envelope and as part of the enclosed handwritten annotations; we therefore use this specimen to lectotypify the species.

Sclerospora northii W. Weston [as '*nothi*'], *Phytopathol.* **19**: 965. 1929.
Synonym: *'Sclerophthora northii'* (W. Weston) Thirum. *et al.*, *Bull. Torrey Bot. Club* **80**: 300. 1953. [*nom. nud.*, Art. 36.1, 39.1]

Typus: **Fiji Islands**, Suva, Rarawai Estate, *Saccharum maximum* (as *Erianthus maximus* var. *seemanii*; *Panicoideae, Andropogoneae*), 23 Jun. 1924, *H.F. Clarke* [**lectotype** designated here BPI 187307 (MBT 10002241), **isotype** FH 965380 (MBT 10002242)]. Supplementary Fig. S22 shows the lectotype BPI 187307.

Description: *Oogonia* rounded polyhedral with several flattened faces bordered by ridges, occasionally irregular, elongate pyriform, or unequally rounded oblong, amber brown (sometimes raw sienna to argus brown), 40–70 µm (up to 57–60.9 µm × 51–56.9 µm) diam; wall with arched irregular, ridged prominences, 3–5 µm (occasionally to 10 µm); remains of oogonial stalk or antheridium rare. *Oogonia* spherical, hyaline to pale amber, 39–46.9 µm (mode 41–44.9 µm; up to 35–52 µm) diam, contents finely granular with denser aggregations, central area usually clear with occasionally one or more oil globules; wall dense, smooth, homogeneous to indistinctly lamellate, 2–4.5 µm thick. Asexual morph not observed. (Weston 1929b; Fig. 10D).

Diagnosis: Distinguished from *Peronosclerospora miscanthi, Peronosclerospora spontanea* and *Peronosclerospora sacchari,* which also parasitize *Saccharum* spp., due to the production of oospores each enclosed in a darkened, thickened oogonial wall with several flattened polyhedral faces. Differs from *Sclerospora iseiliematis* and *Sclerospora secalina* by having an oogonial wall with conspicuous ridges and by parasitism of *Saccharum maximum*. Differs from *Sclerospora graminicola* by having larger oogonia (51–61 µm diam *vs.* 41 µm diam, respectively). Differs from *Sclerospora farlowii* by parasitism of *Saccharum maximum*.
Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: Known only from the type host *Saccharum maximum Panicoideae*, *Andropogoneae*.

Notes: *Sclerospora northii* was reported as a pathogen of *Saccharum maximum*, a native reed-like grass common in Fiji

(Weston 1929). Infected plants were dried and brown with shredded leaves (Weston 1929). The pathogen has not been reported since the original 1924 sighting, and it is unknown what impact *Sclerospora northii* has on host populations.

At the time of writing (September 2021), Index Fungorum listed the current name for this species as *'Sclerophthora northii'* (W. Weston) Thirum. *et al*., *Bull. Torrey Bot. Club* **80**: 300. 1953. However, the correct name for this pathogen is *Sclerospora northii* W. Weston. The publication cited for *"Sclerophthora northii,"* in which the genus *Sclerophthora* was first described, did not make a new combination for *Sclerospora northii*, and the species was not mentioned at any point in the article.

As discussed by Shaw (1978), the asexual morph of this pathogen has not been observed. *Sclerospora northii* was one of five *Sclerospora* species that were not transferred to *Peronosclerospora* by Shaw (1978), as the absence of any record of asexual reproductive structures precluded assignment to either *Peronosclerospora* or *Sclerospora*.

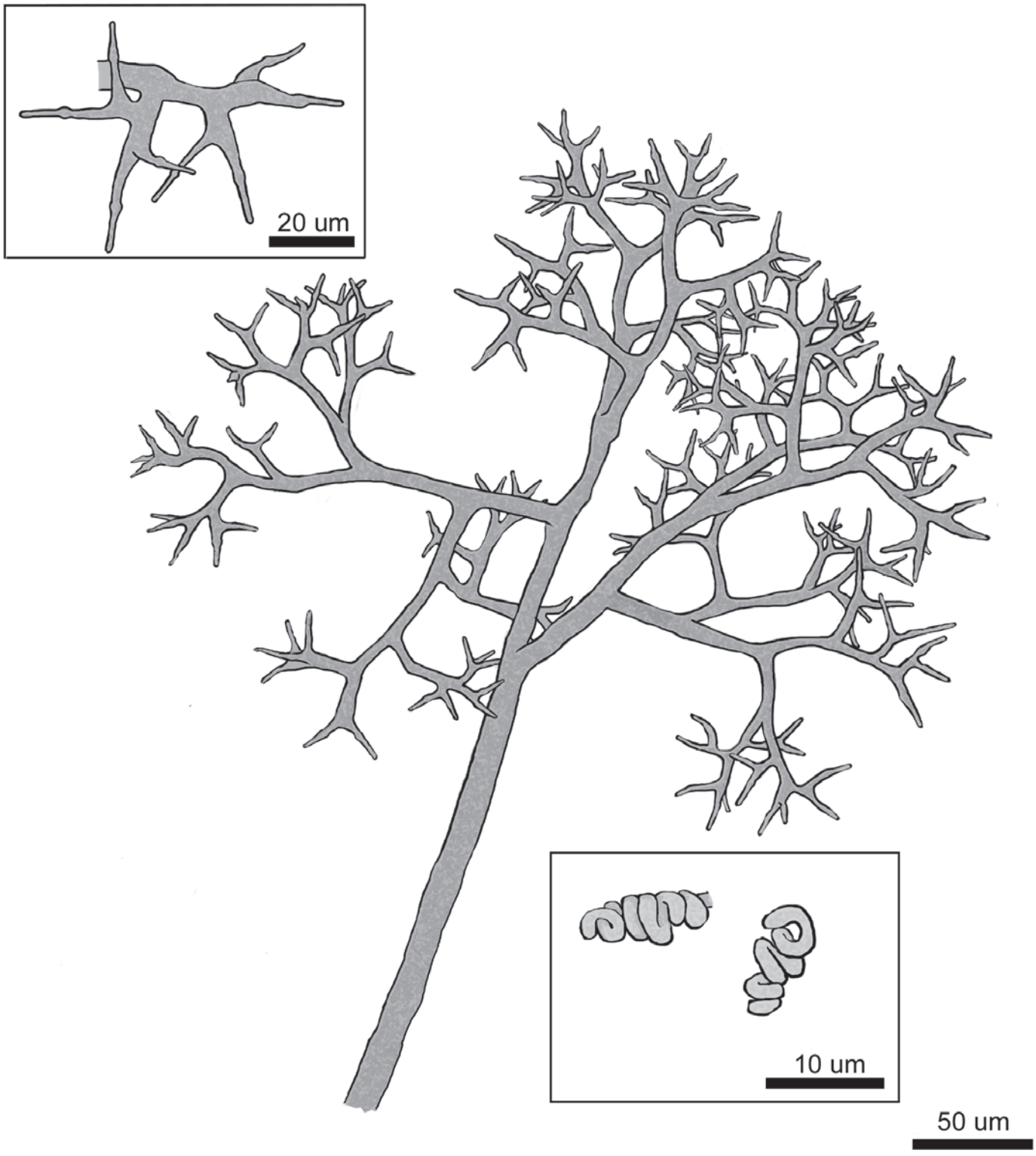

Fig. 11. *Viennotia oplismeni*, sporangiophore, with close-up of indeterminant sporangiophore tips (top inset) and helical haustoria (bottom inset). Illustrations were prepared from published reference images in Goker *et al*. (2007).

Weston did not designate a holotype for *Sclerospora northii*; however, he provided detailed collection data regarding his materials. BPI and FH holdings that originate from Weston's collections includes specimens BPI 187307 and FH 965380 with identical collection data as that which is communicated in the protolog, detailed in Weston's handwriting, and is written on a label from the *Herbarium of W. H. Weston*. These specimens are undoubtably part of Weston's original specimen collection used for describing the species; BPI 187307 is here used to lectotypify *Sclerophthora northii*.

Sclerospora secalina Naumov, *Notul. Syst. Sect. Cryptog. Inst. Acad. Sci. USSR* **6**: 79. 1949.

Typus: *Non designatus*.

Description: *Oogonia* sub-spherical, 33–38 [or 48] µm diam; wall smooth without tubercules or ridges. *Antheridia* 14.7 × 18 µm diam. *Oospores* spherical, deep ocher, then brown, 31–46 [or 36] µm diam at maturity; wall smooth. (Waterhouse 1964; Fig. 10E).

Diagnosis: Distinct from *Sclerophthora macrospora* parasitizing *Secale cereale* by oospore size and coloration, which are much smaller in *Sclerospora secalina* (versus a diam of 62.5 µm or more and hyaline oospores of *Sclerophthora macrospora*). Differs from *Sclerospora iseilematis*, *Sclerospora graminicola*, and *Sclerospora northii* by having a smooth oogonial wall without tubercules or ridges. Differs from *Sclerospora farlowii* by parasitism of *Secale cereale*.

Reference sequence data: No sequence data available from type material or *bona fide* specimens.

Host range: *Secale cereale* (*Pooideae*, *Triticaceae*).

Notes: According to Farr & Rossman (2021), this species has not been reported since its initial description as a parasite of *Secale cereale* (cereal rye) in the former USSR during 1942 (Waterhouse 1964). Since Naumov only observed the oogonial morph (Waterhouse 1964), the generic status of *Sclerospora secalina* is not clear. In the absence of sporangial features and/or molecular data, it is not possible to conclude with certainty that this species is a member of the genus *Sclerospora*.

Viennotia J.A. Crouch & Thines, ***gen. nov.*** MycoBank MB 840578.
Synonym: *'Viennotia'* Göker *et al.* [*nom. inval*. Art. 35.1]

Type species: *Viennotia oplismeni* J.A. Crouch & Thines

Description: *Canad. J. Bot*. **81**: 682. 2003. Haustoria hyaline, hyphoid, intracellular, long, often tightly coiled and slender. Sporangiophores hyaline, monopodially branched, with ultimate branches that are straight to slightly curved. Parasitic to members of the *Poaceae* (Göker *et al*. 2003).

Diagnosis: Differs from all other graminicolous downy mildews in sporangiophores that show recurrent outgrowth after sporangia have been shed (Thines 2009).

Notes: The genus *Viennotia* was based on an invalid basionym without type specimen (see notes on *Viennotia oplismeni*, below), rendering it invalid itself (Art. 40.1) Hence, the genus could not be described by reference to the type species (Art. 10.1), as it was not validly published, invalidating the genus description. Therefore, we validate the genus name and the type species here.

Viennotia oplismeni J.A. Crouch & Thines, ***sp. nov.*** MycoBank MB 840579.
Synonyms: *'Plasmopara oplismeni'* Vienn.-Bourg., *Bull. Soc. Mycol. France* **75**: 33. 1959. [*nom. inval*. Art. 40.1].
'*Viennotia oplismeni'* (Vienn.-Bourg.) Göker *et al.*, *Canad. J. Bot.* **81**: 682. 2003. [*nom. inval.* 35.1].

Typus: **Guinea**, near Kindia, on leaves of *Oplismeni hirtellus* (*Panicoideae, Panicodae*), 3 Nov. 1963, *J. Kranz* (**holotype** GZU 335974 designated here, **isotypes** BPI 784624, IMI 103944). Supplementary Fig. S23 shows the isotype BPI 784624.

Description: *Haustoria* intracellular, hyphoid, slender, long and often tightly coiled. *Sporangiophores* hyaline, monopodially branched, 180–230 × 6–8 µm; branching in the upper third into spreading branches; terminal branches straight to slightly curved divided at right angles into short ramifications with swellings typically carrying three sterigmata; sterigmata bloated and pinched, 14–23 µm long. *Sporangia* 14–28 × 11–17 µm. *Oogonia* not observed (Figs 11, S23).

Diagnosis: Differs from other *Peronosporaceae* by parasitizing *Oplismeni* spp. Differs from *Poakatesthia penniseti* by having globular citroform sporangia, shorter and dichotomously branched sporangiophores, and larger ultimate branchlets. Differs from *Graminivora graminicola* by 28S DNA sequences and, by successive outgrowth of the ultimate branchlets after sporangia have been shed, a feature that also distinguishes the species from all other graminicolous downy mildews.

Reference sequence data: Ex-holotype nucleotide sequences AY035527 (28S rDNA D1/D2/D3), AY273977 (28S rDNA D7/D8).

Host range: *Oplismeni hirtellus*, *Oplismeni compositus* (*Panicoideae, Panicodae*).

Notes: Reported just twice, on *Oplismeni hirtellus* (basketgrass) and *Oplismeni compositus* (running mountaingrass) from Guinea (Viennot-Bourgin 1959, Kranz 1965). The first report of the species did not list any symptoms associated with the host infection, but Kranz (1965) documented leaves that were streaked yellow and rapidly rotted. Although both hosts have a cosmopolitan distribution across most tropical and subtropical parts of the world, *Viennotia oplismeni* has not been reported since 1963 (Kranz 1965); therefore, it is unknown if the species has any impact on host populations.

Plasmopara oplismeni was not validly published, as a type was not designated as required at the time, meaning that *Viennotia oplismeni* (Vienn.-Bourg.) Göker *et al.* and the genus *Viennotia* Voglmayr *et al.* were not validly published (Art. 10.1, 40.1, Turland *et al.* 2018). It is unknown if Viennot-Bourgin's collections from 1955 are extant, and no illustrations of the species were provided (Viennot-Bourgin 1959). Duplicate collections of Kranz' materials are held at BPI, GZU, IMI (K) (det. G.M. Waterhouse, conf. H. Vogelmayr); these specimens were made from the same host in the same locale where Viennot-

Bourgin made collections. GZU 335974 was studied by Göker *et al.* (2003) when they designated the genus *Viennotia*, and it has been characterized through morphological and molecular analysis (Kenneth & Kranz 1973, Riethmüller *et al*. 2002, Göker *et al*. 2003, Thines *et al.* 2006, Thines 2009). This specimen is therefore designated as the holotype for *Viennotia oplismeni*.

DISCUSSION

Graminicolous downy mildews are predominantly tropical or subtropical, with only two of the seven genera, *Sclerophthora* and *Sclerospora*, extending into cool temperate climates (Spencer & Dick 2002, Davis & Crouch 2022a, b). As most tropical ecosystems are generally understudied, our current knowledge of the GDMs is restricted to species occurring on crops and some anecdotal reports from wild grasses (Waterhouse 1964, Shaw 1975, this paper). Interestingly, maize seems to be highly susceptible to a variety of GDM species (Kenneth 1989), and descriptions of some species, such as *Peronosclerospora maydis* and *Peronosclerospora philippinensis* are based on infections on this host. However, maize is not native to the natural range of *Peronosclerospora*, suggesting that the high susceptibility of maize is because of a naivity to downy mildew pathogens (Thines 2014), in line with the hypothesis that host susceptibility increases with increasing geographic distance from potential pathogens (Thines 2019). As maize is not native to Asia, the natural host reservoir may be in indigenous grasses. Because naturally occurring infections of wild and weedy grasses have not been systematically studied, the original source of inoculum is unknown for most species affecting maize, complicating phytosanitary measures. Only recently has a native host has been identified for *Peronosclerospora maydis* (Suharjo *et al.* 2020). Thus, studies of the GDMs in unmanaged habitats are highly warranted.

Although we treat the GDMs as a group in this review, it is unclear if the *Peronosporaceae* affecting grasses are monophyletic. So far, three potentially monophyletic groups have been identified from *Poaceae* hosts – the graminicolous downy mildews with lasting sporangiophores (*Graminivora*, *Poakatesthia*, and *Viennotia*), a group comprising *Eraphthora* and *Sclerophthora*, and the graminicolous downy mildews with evanescent sporangiophores (*Baobabopsis*, *Peronoscleropsora*, *Sclerospora*). The relationships of these groups remain unclear (Thines 2014), as well as how the other downy mildew genera are related to them. Thines (2009) hypothesized that, due to some plesiomorphic characters and a high degree of morphological variation, the evolution of downy mildews might have started out from graminicolous hosts, but as multigene phylogenetic data are lacking for most GDMs, this hypothesis has not yet been tested. In any case, the phytophthora-like species affecting sedges that are unculturable and have been placed in a genus of their own, *Kawakamia*, should be included in studies of these organisms, even though the independence of *Kawakamia* on the genus level was doubted in the most recent monograph of *Phytophthora* (Erwin and Ribeiro 1996). In addition, several sclerophthora-like species that share morphological similarities with *Kawakamia*, including *Sclerophthora zeae* and *Sclerophthora cryophila,* should be included in subsequent studies. Considering the often nonspecific and minor symptoms caused by the phytophthora/sclerophthora-like species affecting *Poales*, it seems likely that the few scattered reports of these organisms are only the tip of iceberg of their total diversity.

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Supplementary Material: http://fuse-journal.org/

Fig. S1. *Eraphthora butleri* lectotype BPI 187075.
Fig. S2. *Graminivora graminicola* lectotype BPI 786232.
Fig. S3. *Peronosclerospora maydis* isotype BPI 789413.
Fig. S4. *Peronosclerospora miscanthi* neotype BPI 187301.
Fig. S5. *Peronosclerospora noblei* lectotype BPI 187306.
Fig. S6. *Peronosclerospora philippinensis* lectotype BPI 18731.
Fig. S7. *Peronosclerospora philippinensis* isotype BPI 187044.
Fig. S8. *Peronosclerospora philippinensis* isotype BPI 187311.
Fig. S9. *Peronosclerospora philippinensis* isotype BPI 187313.
Fig. S10. *Peronosclerospora sacchari* lectotype BPI 187331.
Fig. S11. *Peronosclerospora sorghi* lectotype BPI 187336.
Fig. S12. *Peronosclerospora spontanea* lectotype BPI 187043
Fig. S13. *Peronosclerospora spontanea* isotype BPI 187073.
Fig. S14. *Peronosclerospora spontanea* BPI 187342.
Fig. S15. *Sclerophthora cryophila* holotype DAOM 20643.
Fig. S16. *Sclerophthora macrospora* neotype BPI 187265.
Fig. S17. *Sclerophthora macrospora* isotype BPI 187266.
Fig. S18. *Sclerospora farlowii* lectotype BPI 187077.
Fig. S19. *Sclerospora farlowii* isotype BPI 187076.
Fig. S20. *Sclerospora farlowii* isotype BPI 187078.
Fig. S21. *Sclerospora iseilematis* lectotype BPI 187262.
Fig. S22. *Sclerospora northii* lectotype BPI 187307.
Fig. S23. *Viennotia oplismeni* isotype BPI 784624.
Table S1. Summary of the primary features of the asexual and sexual structures produced by *Peronosporaceae* species that cause downy mildew diseases of *Poaceae* hosts.