



Peronosclerospora neglecta sp. nov.—a widespread and overlooked threat to corn (maize) production in the tropics

Amran Muis¹ · Malcolm J. Ryley² · Yu Pei Tan^{2,3} · Radix Suharjo⁴ · Nurnina Nonci¹ · Yanuar Danaatmadja⁵ · Iman Hidayat⁶ · Ani Widiastuti⁷ · Sri Widinugraheni⁸ · Roger G. Shivas² · Marco Thines⁹ 

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Abstract

Downy mildew is a serious threat to corn (maize) production in the tropics and subtropics. Corn is native to Central America, and was introduced into South-East Asia by the Spanish colonisers in the 1700s. Corn is evolutionarily naïve to downy mildews of the genus *Peronosclerospora*. Consequently, corn monocultures are particularly susceptible to a variety of *Peronosclerospora* species, which spread to the crop from local grasses. Globally, corn is one of the most important crops for both humans and livestock. Several downy mildews of corn have been identified as potential threats to global food security, and trade with corn seeds is strictly regulated to avoid spreading the pathogens. Despite their importance, little is known about the biodiversity of graminicolous downy mildews, because their identification has often relied on variable morphological features, such as conidial dimensions. DNA barcodes for most species have become available only recently. During surveys for downy mildews on corn in Indonesia, a previously unrecognised species of *Peronosclerospora* was found and investigated using a combination of morphological characters and molecular phylogenetic analyses. The new species, introduced here as *Peronosclerospora neglecta*, is widely distributed in South-East Asia from Thailand to eastern Indonesia. The impact of this downy mildew can be severe, with complete crop losses in heavily affected fields. Given the aggressiveness of the species, close surveillance is warranted to restrict its further spread.

Keywords Downy mildew · Phylogeny · *Poaceae* · Tropics · One new species

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✉ Roger G. Shivas
roger.shivas@usq.edu.au

✉ Marco Thines
marco.thines@senckenberg.de

¹ Research Center for Food Crops, Research Organization for Agriculture and Food, National Research and Innovation Agency, Bogor, Indonesia

² Centre for Crop Health, University of Southern Queensland, Toowoomba, QLD 4350, Australia

³ Queensland Plant Pathology Herbarium, Department of Agriculture and Fisheries, Dutton Park, QLD 4102, Australia

⁴ Department of Plant Protection, Faculty of Agriculture, University of Lampung, Jl. Prof. Sumantri Brojonegoro I, Bandar Lampung, Indonesia 35145

⁵ PT Syngenta Indonesia, Jl. TB Simatupang No.2 RT 001 RW 005, Cilandak Timur, Pasar Minggu, South Jakarta 12560, Indonesia

⁶ Research Organization for Life Sciences and Environment, National Research and Innovation Agency, Bogor, Indonesia

⁷ Department of Plant Protection, Faculty of Agriculture, Universitas Gadjah Mada, Yogyakarta, Indonesia 55281

⁸ Universitas Nusa Cendana, Kupang, NTT, Indonesia 85118

⁹ Institute of Ecology, Evolution and Diversity, Department of Biological Sciences, Goethe University, Max-Von-Laue-Str. 13, 60439 Frankfurt Am Main, Germany

Introduction

Corn (maize, *Zea mays*) was first domesticated from the wild grass teosinte (*Z. mays* subsp. *parviglumis*) in central America about 9000 years ago (Ramos-Madrigal et al. 2016; Wang et al. 2017; Stitzer and Ross-Ibarra 2018). It has become one of the most important crops globally, for both humans and livestock, due to its fast growth and high yield (Nuss and Tanumihardjo 2010). Graminicolous mildews of the genus *Peronosclerospora* are naturally absent in Central America, the native range of maize and teosinte, and consequently, specific resistance to *Peronosclerospora* spp. is lacking in commercial cultivars and most current corn cultivars are susceptible to several *Peronosclerospora* spp. (Kenneth 1981; Thines 2014). *Peronosclerospora* spp. are characterised by the production of conidia that form germ tubes to infect host plants (Shaw 1978). The centre of origin of the genus is likely to be South-East Asia or parts of the Australasian realm (Spencer and Dick 2002; Thines 2014), where it parasitises a wide range of C4 grasses, such as sugarcane and sorghum species (Telle et al. 2011; Suharjo et al. 2020; Ryley et al. 2022). The grasses parasitised by *Peronosclerospora* are largely unrelated, even though most of them are members of the tribe *Andropogonoideae*. It can be assumed that *Peronosclerospora* spp. have colonised this tribe by host jumps and subsequent radiation, as described for other genera of downy mildew (Thines 2019). The pathogenicity effectors that triggered the successful radiation within *Andropogonoideae* likely also enable parasitism of corn, which has been observed for most species described in *Peronosclerospora* (Kenneth 1981; Shivas et al. 2012).

Downy mildew of corn caused by *Peronosclerospora* spp. has been reported in many countries in South-East Asia and Australasia (Sharma et al. 1993; Spencer and Dick 2002; Suharjo et al. 2020; Crouch et al. 2022). The native grass species that serve as the primary host for most of the *Peronosclerospora* species that infect corn are known. Some examples are *Eriochloa pseudoacrotricha* parasitised by *P. eriochloae* (Telle et al. 2011); *Heteropogon contortus* parasitised by *P. heteropogonis* (Siradhana et al. 1980); *Sorghum spontaneum* parasitised by *P. spontanea* (Weston 1921); and *Sorghum timorense* parasitised by *P. maydis* (Suharjo et al. 2020), which was first described from corn (Raciborski 1897). The native host grass for corn downy mildew caused by *P. philippinensis* remains unknown (Weston 1920). Recently, Suharjo et al. (2020) reported a potentially undescribed downy mildew on corn in Indonesia. However, due to the absence of specimens, the species could not be morphologically compared to the known species of *Peronosclerospora* and was not formally introduced. More recently, ex-type sequences of additional *Peronosclerospora* species have been made available (Crouch et al. 2022), but none of them

matched the new lineage found in Indonesia. It was the aim of the current study to clarify the identity of this *Peronosclerospora* species using the *cox2* gene sequence barcode (Choi et al. 2015) and specimen morphology.

Materials and Methods

Plant material and microscopy

Downy mildew specimens were collected from corn fields in Indonesia during 2018–2019, and deposited in the internationally recognised herbaria at the Research Centre for Biology, Cibinong, Indonesia (BO) and the Queensland Plant Pathology Herbarium (BRIP), Dutton Park, Australia. Detailed information on the specimens is given in the Taxonomy section. Microscopy was done as described in Ryley et al. (2022), using specimen pieces rehydrated in hot lactic acid. Due to the evanescent nature of the asexual morph of the newly discovered corn downy mildew, only the maximum and minimum dimensions of 25 conidia were recorded from the type specimen.

DNA extraction PCR, sequencing, and phylogenetic reconstruction

DNA extraction, PCR, and sequencing methods followed Ryley et al. (2022), using the AnalyticJena plant DNA extraction kit (AnalyticJena, Germany) and the *cox2* amplification procedure described in Telle et al. (2011). The sequences obtained were added to the dataset of Suharjo et al. (2020), to which additional sequences with high similarity to the new lineage identified by Suharjo et al. (2020) were added, as identified by BLAST (Altschul et al. 1990) searches against sequences deposited in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). Alignments were done in MUSCLE (Edgar 2004) as implemented in MEGA7 (Kumar et al. 2016), which resulted in an alignment without internal gaps. Leading and trailing gaps were removed before phylogenetic analyses, and the final alignment is available as Supplemental File 1. Phylogenetic reconstruction using the Minimum Evolution algorithm was done in MEGA7, with 500 bootstrap replicates and default settings, except for choosing the Tamura-Nei substitution model (Tamura and Nei 1993), which is the most complex standard model offered by the programme. The phylogenetic reconstructions using Bayesian Inference and Maximum Likelihood were done using MrBayes (Ronquist et al. 2012) and RAxML (Stamatakis 2014), respectively, as implemented on the TrEase webserver (<http://thines-lab.senckenberg.de/trease>), using default settings.

Results

Morphology

Plants infected by downy mildew exhibited chlorotic streaks and were stunted (Fig. 1). Evanescent conidiophores protruded from stomata, predominantly on the abaxial leaf surface. The morphology of conidiophores and conidia was typical for *Peronosclerospora*. The conidiophores were often intertwined on the abaxial surface of leaf blades, up to 180 µm long, swollen at the base, and dichotomously branched 2–4 times. The ultimate ramification gave rise to 2–3 (mostly 2) ultimate branchlets which were 5–11 µm long and 2–4 µm broad. Conidia were hyaline, sub-globose to ovoid, 23–30 µm long and 13–19 µm broad and thin-walled. Conidia germinated by producing germ tubes. Oospores were not found.

Phylogeny

In the phylogenetic reconstruction based on partial *cox2* sequences (Fig. 2), all five genera of graminicolous downy mildews were resolved as monophyletic with high to maximum support. Within the genus *Peronosclerospora*, the monophyly of all species represented by more than one sequence received moderate to strong support. None of the infrageneric splits received significant support. Both *P. maydis* and the corn-parasitic lineage reported by Suharjo et al. (2020) were represented by samples from several different regions. Within *P. maydis*, some variation was present, but no clear-cut association of the variants within a specific

region was found. Samples of *P. maydis* were obtained from both *Z. mays* and *Sorghum timorense*, but no strict correlation between genotype and host was found. The lineage reported by Suharjo et al. (2020) was genetically uniform, despite being sampled throughout a wide geographic range. It included samples from Thailand and Indonesia, where the pathogen was found on three different islands. All samples of this lineage originated from *Z. mays*.

Taxonomy

Peronosclerospora neglecta Muis, Ryley, Suharjo, Y.P. Tan, Thines and R.G. Shivas, **sp. nov.**, MycoBank MB 846809.

Etymology: from Latin *neglecta* meaning neglected, overlooked.

Classification: *Peronosporaceae*, *Peronosporales*, *Oomycota*.

Description: *Asexual sporulation* on abaxial surfaces of leaf blades. *Conidiophores* emerging from stomata, evanescent, up to 180 µm long, swollen base, dichotomously branched, ultimate branchlets 5–11 × 2–4 µm. *Conidia* hyaline, sub-globose or ovoid, 23–30 × 13–19 µm, thin-walled, germination by a germ tube. *Oospores* not seen.

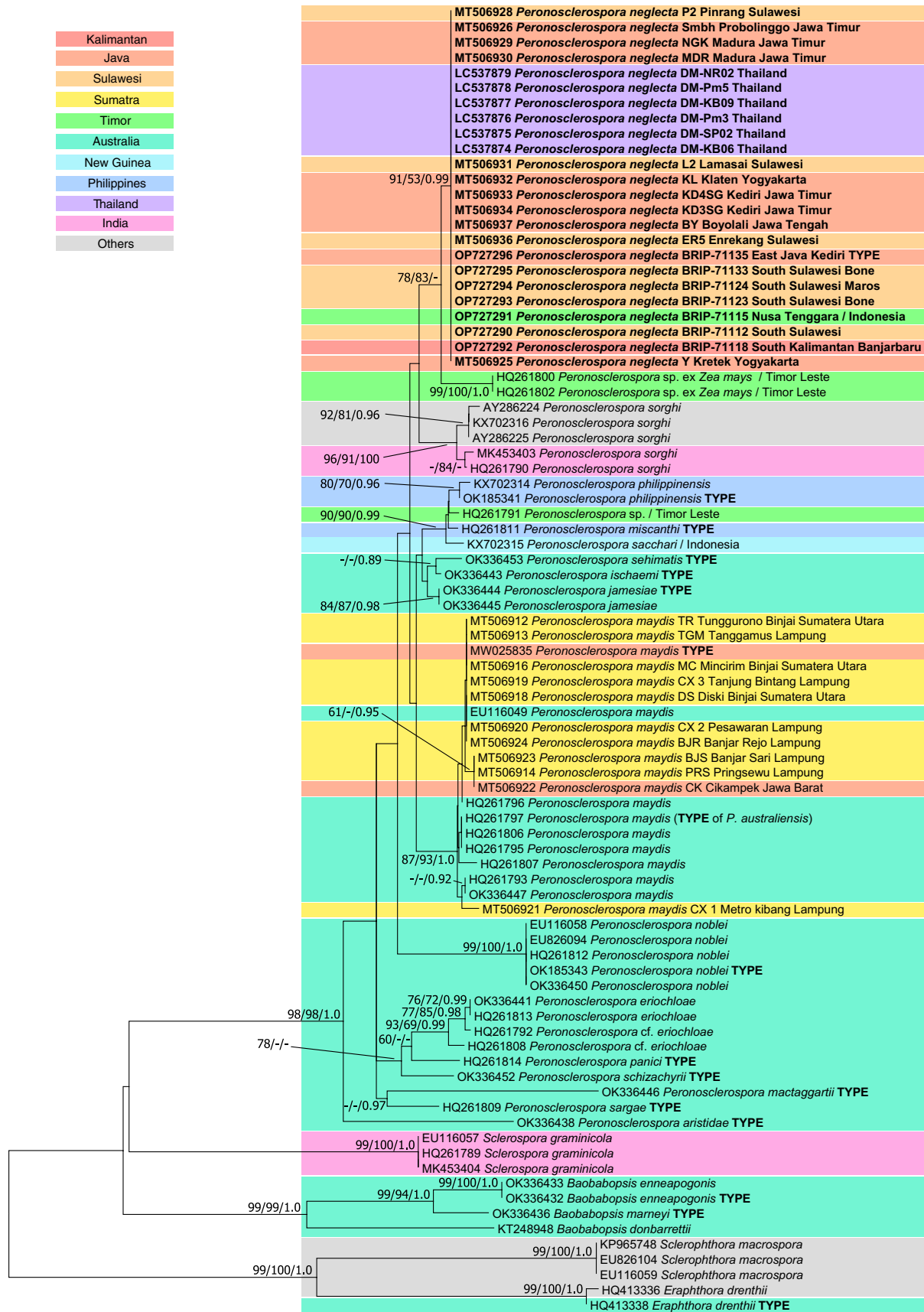
Typus: Indonesia, East Java, Grogol, Kediri, 07° 49' 01" S, 111° 58' 12" E, on leaves of *Zea mays*, 18 Jan. 2019, A. Muis, N. Nonci, S.H. Kalqutny, Aminah, M.J. Ryley, M.D.E. Shivas and R.G. Shivas (holotype BO 24212, isotype BRIP 71135; *cox2* sequence GenBank OK336429).

Additional specimens examined: Indonesia, East Java, Kediri, 07° 45' 13" S, 111° 58' 20" E, on leaves of *Z. mays*, 18 Jan. 2018, A. Muis, N. Nonci, S.H. Kalqutny, Aminah (BRIP 71133, BO 24210, *cox2* sequence GenBank



Fig. 1 Symptoms and morphological features of *Peronosclerospora neglecta* on maize. **A** stunted maize plant with chlorotic streaks. **B** close-up of symptoms, with whitish conidiophores emerging from

stomata on the abaxial leaf surface. **C** conidia and ultimate branchlets. Scale bars equal to 10 mm in **B** and 10 µm in **C**



0.02

Fig. 2 Phylogenetic reconstruction in Minimum Evolution, based on partial *cox2* sequences. Numbers on branches denote support from Minimum Evolution bootstrapping, Maximum Likelihood bootstrapping, and Bayesian posterior probabilities, in the respective order. A minus sign denotes a lack of support for the topology (bootstrap support < 50%, posterior probabilities < 0.8)

OK336427); East Nusa Tenggara, Timor, 10° 08' 01" S, 123° 41' 37" E, on leaves of *Z. mays*, 09 May 2018, *A. Muis*, *N. Nonci* (BRIP 71115, BO 24192, *cox2* sequence GenBank OK336428); South Kalimantan, Banjarbaru, 03° 26' 11" S, 114° 48' 00" E on leaves of *Z. mays*, 16 Oct. 2018, *Suriani* (BRIP 71118, BO 24195, *cox2* sequence GenBank OK336430); South Sulawesi, Indonesian Cereals Research Institute, Bajeng Experimental Station, 05° 18' 34" S, 119° 30' 26" E, on leaves of *Z. mays*, 23 Aug 2018, *A. Muis* (BRIP 71112, BO 24189, *cox2* sequence GenBank OK336425); Bone, 04° 32' 08" S, 119° 57' 18" E, on leaves of *Z. mays*, 29 Dec. 2018, *Suriani* (BRIP 71123, BO 24200, *cox2* sequence GenBank OK336426); Maros, 04° 58' 55" S, 119° 34' 32" E, on leaves of *Z. mays*, 14 Jan. 2018, *S.H. Kalqutny* (BRIP 71124, BO 24201, *cox2* sequence GenBank OK336431).

Known distribution: Indonesia and Thailand.

Notes: Based on a BLASTn search, *P. neglecta* differed from *P. maydis* (ex-type specimen KRAM O-5859(J)) in *cox2* (GenBank MW025835; Identities 580/594 (98%), 0 gaps); from *P. miscanthi* sensu Telle et al. (2011) in *cox2* (GenBank HQ261811; Identities 532/541 (98%), 0 gaps); from *P. philippinensis* (specimen Pp04, Telle et al. (2011)) in *cox2* (GenBank KX702314 Identities 518/528 (98%), 0 gaps); and from *P. sorghi* sensu Telle et al. (2011) (specimen HUH 897) in *cox2* (GenBank EU116055; Identities 251/257 (98%), 0 gaps). A summary of the morphological features of the species known to affect maize is given in Table 1.

Discussion

Peronosclerospora neglecta causes a serious disease of corn (maize) in Indonesia, especially in Java and South Sulawesi. The symptoms of infection are chlorotic leaf lesions, leaf distortion, and stunted plants, which can lead to complete crop loss. The conidia of *P. neglecta* differ in shape and size from those recorded for *P. maydis*, *P. philippinensis*, *P. sorghi*, and *P. spontanea*, which have been previously recorded on maize in South-East Asia (Weston 1921; Suharjo et al. 2020). The subglobose to ovoid conidia of *P. neglecta* are larger than those of *P. maydis* (Raciborski 1897) and smaller than the conidia of *P. sorghi* (Weston and Uppal 1932), *P. spontanea* (Weston 1921), and *P. philippinensis* (Weston 1920). Sequence data must be obtained for unambiguous identification of *P. neglecta* and other

Peronosclerospora spp., as it is known that morphology can be unreliable for identification, because the dimensions of downy mildew conidia may be influenced by environmental conditions (Dudka et al. 2007) and host (Runge and Thines 2011).

In contrast to *P. maydis*, no variation in the *cox2* sequences was observed in *P. neglecta*, which hints at a rather uniform metapopulation. An explanation for this uniformity might be that the downy mildew only recently spread throughout South-East Asia with infested corn seeds. The potential of seed infection and spread by other *Peronosclerospora* species is well known (Advincula and Exconde 1975; Sommartaya et al. 1975; Adenle and Cardwell 2000). *Peronosclerospora neglecta* appears to be the dominant downy mildew of corn in Java (Suharjo et al. 2020, this study), which raises the possibility that Lukman et al. (2016) and Sommartaya et al. (1975) detected *P. neglecta* in corn seeds rather than *P. maydis* or *P. sorghi*. Sequences available on GenBank showed that *P. neglecta* occurs in Thailand, reported as *P. maydis* (Janruang and Unartngam 2018).

Corn is alien to Asia and cannot be the primary host for *Peronosclerospora* species, which likely evolved in South-East Asia (Spencer and Dick 2002). *Peronosclerospora* spp. are absent from the native range of maize and its wild progenitor, teosinte. In addition, the high virulence potential of *P. sacchari* is noteworthy. A Taiwanese isolate of *P. sacchari* was able to infect eight genera of *Andropogonoideae* (*Andropogon*, *Bothriochloa*, *Eulalia*, *Saccharum*, *Schizachyrium*, *Sorghum*, *Tripsacum*, and *Zea*) at different levels of susceptibility under laboratory conditions (Bonde 1981). The susceptibility of corn is likely due to the long-standing evolutionary interaction of *Peronosclerospora* with grasses of the tribe *Andropogonoideae* that leads to a high virulence potential, coupled with the absence of corn varieties that have high resistance to downy mildew (Thines 2014). Apart from *P. neglecta* and *P. philippinensis*, the primary hosts of all graminicolous downy mildews infecting corn are known (Kenneth 1981; Spencer and Dick 2002; Telle et al. 2011; Suharjo et al. 2020). Oospores on corn are rarely formed or not at all (Kenneth 1981). It should follow that infections of corn result from the spread of the pathogen into the crop population from native grass host(s). For some species, e.g. *P. eriochloae*, this might be the case as only sporadic outbreaks have been reported (Telle et al. 2011). However, vertical transmission by seeds might explain a wider distribution and occurrence than expected through the spread from primary to secondary hosts. For example, the downy mildew *Bremia lactucae* on cultivated lettuce has been known to often spread from infected populations of wild lettuce (Runge et al. 2021), which has resulted in the pathogen becoming widely distributed in cultivated lettuce (e.g. Trimboli and Nieuwenhuis 2011; Marin et al. 2020).

Table 1 Key morphological features of *Peronosclerospora* species recorded on maize

Species	Oogonium wall	Oospore diam. (µm)	Conidium shape	Conidium dimensions (µm)	Reference
<i>P. eriochloae</i>	Smooth	(27–)30.4–36.6(–46)	Globose-subglobose	(9–)12.2–14.4(–18) × (9–)10.6–13.4(–16) ^A	Ryley and Langdon (2001)
<i>P. heteropogoni</i>	Tuberculate	(24–)29(–36.7)	Globose	(14.3–)17.7(–22.4) × (14.3–)16.2(–30.4) ^B	Siradhana et al. (1980)
<i>P. maydis</i>	Absent	Absent	Globose	15–18 ^C	Raciborski (1897)
<i>P. miscanthi</i>	Smooth	(40–55)	Glongate-ovoid	(37–)41.4(–48.5) × (14–)18(–23) ^B	Waterhouse (1966)
<i>P. neglecta</i>	None observed	None observed	Subglobose	(23–)24.3–27.7(–30) × (13–)14.8–18(–19) ^A	This study
<i>P. philippinensis</i>	Smooth	22.6	Elongate ellipsoidal-ovoid	(27–39) × (17–21) ^D	Weston (1920)
<i>P. sacchari</i>	Smooth	40–50	Elliptical-oblong	(25–41) × (15–23) ^D	Ito (1913)
<i>P. sorghi</i>	Smooth	(25–)31.6–36.9(–42.9)	Subglobose	(15–)21–24.9(–28.9) × (15–)19–22.9(–26.9) ^E	Weston and Uppal (1932)
<i>P. spontanea</i>	Smooth	15–23	Elongate ellipsoidal-cylindrical	(25–)39–45(–65) × (11–)15–17(–21) ^E	Weston (1921)

^A(Minimum–)mean–standard deviation–mean + standard deviation(–maximum) × (minimum–)mean– standard deviation—mean + standard deviation(–maximum)

^B(Minimum–)mean(–maximum) × (minimum–)mean(–maximum)

^Cminimum–maximum

^D(Minimum–maximum) × (minimum–maximum)

^E(Minimum–)most frequent range(–maximum) × (minimum–)most frequent range(–maximum)

Fungicide-containing seed cover is frequently applied for disease management, but its long-term usage might also lead to the emergence of fungicide-tolerant strains (Pakki and Jainuddin 2019). Apart from fungicide treatments, the removal of weedy and proximal primary hosts could be an important measure to prevent disease spread into crops. Knowledge of the primary host(s) and the frequency of the spread of downy mildew to cultivated corn crops is a prerequisite for understanding the epidemiology of these diseases. Considering the potential damage *P. neglecta* can inflict, it is advisable to maintain vigilance by monitoring the distribution of the species and to further develop diagnostic tools (Lukman et al. 2016) for standardised detection in seed lots and soil.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11557-022-01862-5>.

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Author contribution AM, MR, RS, and MT conceived the study; AM and NN provided plant material; AM, MR, and RS did the morphological examination; YPT did the molecular biology work; MT conducted the phylogenetic reconstructions; MT wrote the manuscript with major contributions from AM, MR, and RS, as well as contributions from the other authors; all authors discussed the findings and contributed to the final draft.

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Data availability Sequence data have been deposited in GenBank.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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