Peronosclerospora australiensis is a synonym of *P. maydis*, which is widespread on Sumatra, and distinct from the most prevalent Java maize downy mildew pathogen

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Abstract
This study was performed to identify *Peronosclerospora* species found in Indonesia based on sequence analysis of the *cox2* gene. In addition, sequence data in total, 26 isolates of *Peronosclerospora* were investigated in this study. They were obtained from 7 provinces in Indonesia, namely Lampung, Jawa Timur, Jawa Barat, Sumatera Utara, Jawa Tengah, Yogyakarta, and Sulawesi Selatan. Sequence analysis of *cox2* and phylogenetic inference were performed on all the 26 isolates. A set of primers developed in this study, PCOX2F and PCOX2R, was used for PCR amplification. Phylogenetic analyses showed that all the Indonesian isolates were divided into two groups. Group I contained 13 isolates; 9 isolates obtained from Lampung, 3 isolates from Sumatera Utara, and 1 isolate from Jawa Barat. Group II consisted of 13 isolates; 7 isolates from Jawa Timur, 2 isolates from Jawa Tengah, 1 isolate from Yogyakarta, and 3 isolates from Sulawesi Selatan. All the members of group I clustered with the ex-type sequence of *P. australiensis*. Meanwhile, all members of Group II formed the sister clade of isolates obtained from Timor-Leste and may represent *P. maydis*.

Keywords Biosecurity · *cox2* · Genetic variation · Graminicolous downy mildews · Phylogeny

Introduction
Downy mildew of *Zea mays* (maize, corn) caused by *Peronosclerospora* spp. is one of the most important diseases in this crop, causing severe economic losses worldwide (Bonde 1982; Singh et al. 1987; Telle et al. 2011). Eleven species of *Peronosclerospora* have been reported until a decade ago, namely *P. dichanthiicola*, *P. eriochloae*, *P. heteropogonis*, *P. maydis*, *P. miscanthi*, *P. noblei*, *P. phillipinensis*, *P. sacchari*, *P. sorghi*, and *P. spontanea*, and *P. westonii*. In 2012, Shivas et al. (2012) described two new species of *Peronosclerospora*, namely *P. australiensis* and *P. sargae*. Three species have been reported as the causal agent of downy mildew on maize in Indonesia namely *P. maydis*, *P. philippinensis*, and *P. sorghi* (Bonde 1982; Muis et al. 2013; Rustiani et al. 2015; Muis et al. 2016). Interestingly, Telle et al. (2011) found that maize is infected by *P. eriochloae* and Shivas et al. (2012) revealed that their newly described species, *P. australiensis*, infects both native grasses and maize.

Species of *Peronosclerospora* in Indonesia have mainly been identified on the basis of host identity and morphological characteristics (Hikmahwati et al. 2011; Widiantini et al. 2015; Muis et al. 2016). This approach has limitations, and may cause unreliable identification results, as conidia, which serve as a key structure for identification, are very similar between some species (Telle et al. 2011). In addition, it has been reported for other downy mildews that conidal dimensions may vary depending on host, organ affected, and humidity (Runge and Thines 2011, Delanoe 1972, Dudka et al. 2016).
Peronosclerospora investigate the identity of from the continent. It was the aim of this study to P. maydis Peronosclerospora cox of partial sequence analysis is essential (Telle et al. 2011; Shiva et al. 2011). Sequence analysis of Cytochrome C Oxidase subunit II (cox2) has been widely performed to identify species of oomycetes, including Peronosclerospora (Telle et al. 2011; Thines et al. 2015; Choi et al. 2015). Using sequence analysis of partial cox2 and nLSU (nuclear ribosomal large subunit), Telle et al. (2011) could distinguish groups of Australian Peronosclerospora species and confirmed the absence of P. maydis from the continent. It was the aim of this study to investigate the identity of Peronosclerospora species found in Indonesia, including sequence analysis of the cox2 gene.

Materials and methods

Specimens of Peronosclerospora

For DNA extraction, samples of infected maize plants with downy mildew symptoms were collected throughout Indonesia. In total, 27 isolates of Peronosclerospora from 7 provinces in Indonesia were analyzed in this study (Table 1). Twenty-three specimens (CX1 – 3, KM, PRS, MK2, KD3SG, KD4SG, MDR, NGK, CK, MC, TR, DS, BY, KL, Y, ER5, L2, P2, TGM, BJR and BJS) were received as infected leaves and for 3 isolates (Ppr, Smbh, Jnu) cox2 sequences were obtained directly from DNA extracts, the type specimen has been obtained from KRAM (Table 1). DNA of most specimens has been deposited in the Herbarium Senckenbergianum (FR) under the accession number B001-1 to B001-23 (Table 1).

Molecular identification

DNA extraction The infected leaves of fresh specimens were cut to pieces (1 cm²) and 10 pieces per sample were placed into a cold mortar. For the grinding of the material, 500 μl extraction buffer (1 M Tris-HCL (tris (hydroxymethyl) aminomethane-HCL) pH 8.0, 10% SDS, 5 M NaCl (Natrium chloride), 2% CTAB (cetyltrimethyl ammonium bromide)) was added into the mortar and the leaves were disrupted using a grinding pestle. After the sample was ground to a suspension, the mortar was covered using aluminum foil and incubated at −40 °C overnight. Afterwards, before melting, the plant material was ground again until it became suspension. In total, 600 μl of the suspension was transferred to a 1.5 mL tube, 400 μl of 2% CTAB was added, and the tube incubated at 65 °C for 1 h. After incubation, 500 μl phenol:chloroform:isoamyl alcohol (25:24:1) was added, and the tubes vigorously shaken by hand. Subsequently, tubes were centrifuged at 14,000 rpm in a microcentrifuge (Microspin12, Biosan, Latvia) for 10 min. The supernatant was transferred to a new 1.5 mL tube and chloroform:isoamyl alcohol (24:1) was added with the same volume as the supernatant, the tube shaken by hand, and then centrifuged at 14,000 rpm for 10 min. The supernatant was transferred to a new 1.5 mL tube, and cold isopropanol (60% of volume) was added. After this, tubes were vigorously mixed by hand and incubated at −40 °C for 10 min and then centrifuged at 14,000 rpm for 10 min. The supernatant was removed and 500 μl cold ethanol 70% was added into the tube. After this, it was centrifuged at 14,000 rpm for 5 min. The supernatant was removed and the pellet air-dried overnight. After this, 30–50 μl 1× TE buffer (pH 8.0) (1st Base, Malaysia) was added. DNA extraction from the type specimen of P. maydis was done as described in Telle et al. (2008) and also PCR was done according to that publication.

PCR amplification PCR was performed using a thermal cycler (Sensoquest Thermal Cycler, Sensoquest, Germany). In this study, a set of primer was developed from available oomycete sequences of cytochrome C oxidase subunit II (cox2) that were used for PCR amplification, namely PCOX2F (TCCAGCAA CTCCAGTTATGG) and PCOX2R (ACCTGGACAAGCAT CTAATT). This primer pair produces an amplicon of 529 bp. PCR was performed using MyTaq™ HS RedMix (Bioline, USA) PCR Kit according to the instructions of the manufacturer. As for DNA amplification, initial denaturation was carried out at 95 °C for 5 min, continued with 30 cycles of denaturation at 95 °C for 1 min; primer annealing at 48–52 °C for 1 min, primer extension at 72 °C for 1 min, and a final elongation at 72 °C for 5 min. PCR products were evaluated using a DigiDoc UV trans illuminator (UVP, USA) after electrophoresis through an 0.5% agarose gel (w/v using 1× Tris Boric Acid EDTA (TBE) pH 8.0, 1st Base, Malaysia), containing 1 μL ethidium bromide (1 μg/mL) at 50 V for 70 min.

Sequencing and sequence analyses The PCR product from the cox2 amplification was sent to 1st Base Malaysia for bi-directional sequencing, using the primers used in PCR. The resulting chromatograms were edited using BioEdit for windows ver 7.2.6 (Hall 1999). Reference sequences used in this study were those from Telle et al. 2011, with some additional sequences obtained from NCBI using the TrEase webserver (Mishra et al. (unpublished), http://www.thines-lab.senckenberg.de/trease) with standard settings. Alignments were generated using muscle (Edgar 2004) as implemented on the TrEase webserver. Leading
and trailing gaps were removed from the final alignment, which did not contain internal gaps. Phylogenetic inference for Minimum Evolution was done using MEGA7 (Kumar et al. 2016) using the Tamura-Nei substitution model and 1000 bootstrap replicates. Maximum likelihood analysis was done using RAxML (Stamatakis 2014) as implemented on the TrEase webserver, using the GTRGAMMA1 substitution model. Bayesian inference was done using MrBayes (Ronquist et al. 2012) as implemented on the TrEase webserver, running 5 million generations and discarding the first 30% of the sampled trees for ensuring a sampling from the stationary phase. The resulting trees were visualized and edited using MEGA7. Sequences were submitted to GenBank and the corresponding accession numbers are given in Table 1.

### Table 1 Peronosclerospora isolates from Zea mays used in this study

| Isolate name | Island | Province | County | Year | GenBank accession (cox2) | Herbarium accession number for DNA extracts |
|--------------|--------|----------|--------|------|--------------------------|--------------------------------------------|
| CX-1         | Sumatra| Lampung  | Metro  | 2015 | MT506921                 | DNA used up                                |
| CX-2         | Sumatra| Lampung  | Negeri Sakti | 2015 | MT506920                 | DNA used up                                |
| CX-3         | Sumatra| Lampung  | Bintang | 2015 | MT506919                 | DNA used up                                |
| Ppr          | Java   | Jawa Timur | Kediri | 2016 | MT506927                 | DNA used up                                |
| Smbh         | Java   | Jawa Timur | Probolinggo | 2016 | MT506926                 | DNA used up                                |
| Jnu          | Java   | Jawa Timur | Tuban  | 2016 | MT506935                 | DNA used up                                |
| KM           | Sumatra| Lampung  | Kota Metro | 2016 | MT506917                 | FR B001-1                                  |
| PRS          | Sumatra| Lampung  | Pringsewu | 2016 | MT506914                 | FR B001-2                                  |
| MK2          | Sumatra| Lampung  | Metro  | 2016 | MT506915                 | FR B001-3                                  |
| KD3SG        | Java   | Jawa Timur | Kediri | 2016 | MT506934                 | FR B001-4                                  |
| KD4SG        | Java   | Jawa Timur | Tuban  | 2016 | MT506935                 | DNA used up                                |
| MDR          | Java   | Jawa Timur | Madura | 2016 | MT506930                 | FR B001-6                                  |
| NGK          | Java   | Jawa Timur | Madura | 2016 | MT506929                 | FR B001-7                                  |
| CK           | Java   | Jawa Barat | Cikampek | 2016 | MT506922                 | FR B001-8                                  |
| MC           | Sumatra| Sumatera Utara | Mincirim | 2017 | MT506916                 | FR B001-9                                  |
| TR           | Sumatra| Sumatera Utara | Tungguron | 2017 | MT506912                 | FR B001-10                                 |
| DS           | Sumatra| Sumatera Utara | Diski  | 2017 | MT506918                 | FR B001-11                                 |
| BY           | Java   | Jawa Tengah | Boyolali | 2017 | MT506937                 | FR B001-12                                 |
| KL           | Java   | Jawa Tengah | Klaten  | 2017 | MT506932                 | FR B001-13                                 |
| Y            | Java   | Yogyakarta | Bantul  | 2017 | MT506925                 | FR B001-14                                 |
| ER5          | Sulawesi| Sulawesi Selatan | Enrekang | 2017 | MT506936                 | FR B001-15                                 |
| L2           | Sulawesi| Sulawesi Selatan | Lamasai | 2017 | MT506931                 | FR B001-16                                 |
| P2           | Sulawesi| Sulawesi Selatan | Pinnang | 2017 | MT506928                 | FR B001-17                                 |
| TGM          | Sumatra| Lampung  | Tanggamus | 2018 | MT506913                 | FR B001-18                                 |
| BJR          | Sumatra| Lampung  | Banjar Rejo | 2019 | MT506924                 | FR B001-19                                 |
| BJS          | Sumatra| Lampung  | Banjar Sari | 2019 | MT506923                 | FR B001-20                                 |
| TYPE         | Java   | Jawa Tengah | Tegal s.d | 2017 | MW025835                 | KRAM O-5859(J)                              |
Results

From 2015 to 2019, several collections of maize downy mildew were done throughout Indonesia, to clarify their phylogenetic diversity and taxonomic identity. For this, also the type specimen of *P. maydis* deposited in KRAM was requested and obtained on loan (Table 1). Phylogenetic inference (Fig. 1) revealed that the isolates were divided into two groups. The first group contained 13 isolates; 9 from Lampung (CX 1-3, KM, PRS, MK2, TGM, BJR, and BJS), 3 from Sumatera Utara (MC, TR, and DS), and 1 isolate from Jawa Barat (CK). The second group consisted of 13 isolates; 7 from Jawa Timur (Ppn, Smbh, Jnu, KD3SG, KD4SG; MDR, NGK), 2 from Jawa Tengah (KL, BY), 1 from Yogyakarta (Y), and 3 from Sulawesi Selatan (ER5, L2, and P2). These isolates were identical or less than 1% divergent from the ex-type sequence of *P. australiensis* reported by Shivas et al. (2012), but three isolates showed some divergence. Interestingly, also the type specimen of *Peronospora maydis* (Indonesia, Java, Java Tengah, Tegal, leg. Marjan Raciborski, likely 1897, KRAM O-5859(J), lectotypus hic designatus (MBT394155), as this specimen fits the site mentioned in the protologue to the description of the species (Raciborski 1897) and is the only specimen of the species preserved in KRAM). All members of the first group were revealed as the sister to the isolates obtained from Timor-Leste that was previously thought to probably represent *P. maydis* (clade 4) (Telle et al. 2011). While this grouping received moderate to strong support, no other.

Discussion

Identification by morphological characteristics (Shaw 1978) is still often applied for *Peronosclerospora* species in Indonesia (Hikmahwati et al. 2011; Widiyantini et al. 2015; Muis et al. 2016). Based on morphological characteristics, three *Peronosclerospora* species have been reported from Indonesia, namely *P. maydis* (Bonde 1982; Rustiani et al. 2015; Muis et al. 2016), *P. sorgii* (Rustiani et al. 2015; Muis et al. 2016), and *P. philippinensis* (Bonde 1982; Rustiani et al. 2015; Muis et al. 2016). However, morphological investigations in *Peronosclerospora* are complicated by the evanescent conidiophores, which quickly vanish after the ripening of conidia. Due to this nature, conidiophores and conidia are not well-preserved in herbarium specimens, which renders comparative analyses difficult. At the same time, there is the high risk to harvest not fully mature conidiophores on which the conidia are not fully developed. In addition, conidial dimensions have been reported to be affected by environmental conditions (Dudka et al. 2007), rendering morphology-based identification difficult. Long-lasting oospores that could serve as an alternative means of identification are not produced in maize, further complicating identification of maize downy mildew.

Thus, since morphology-based identification has many constraints (Telle et al. 2011; Spencer and Dick 2002), molecular identification is crucial. In Indonesia, molecular investigation on *Peronosclerospora* has also been performed (Lukman et al. 2003; Muis et al. 2016). On the basis of simple sequence repeat (SSR) and amplified ribosomal DNA restriction analysis (ARDRA), Lukman et al. (2003) differentiated *Peronosclerospora* found in Java, Sumatra, and Sulawesi into three clusters—two from Java (cluster I and II) and one from Sumatra and Sulawesi (cluster III). Also based on SSR, Muis et al. (2016) divided *Peronosclerospora* that was obtained from Sulawesi Selatan, Sulawesi Tengah, Jawa Timur, Jawa Barat, Lampung, Sumatera Utara, Aceh, and Kalimantan Barat into 5 clusters. In neither case a morphological determination was carried out and no sequencing was done, so it remains unclear, which species the clusters could be attributed to.

Cytochrome C oxidase subunit II (*cox2*) has been reported as well-suited tool to differentiate species of oomycetes including *Peronosclerospora* (Telle et al. 2011; Thines et al. 2015; Choi et al. 2015). Telle et al. (2011) reported that specimens of *Peronosclerospora* from maize and sorghum formed four distinct phylogenetic groups different from the known *Peronosclerospora* species included in the phylogeny. Those isolates were placed in clades 4, 5, 6, and 8. In 2012, Shivas et al. (2012) introduced *P. sargae* as the name of the isolates placed in clade 5 and *P. australiensis* as the name of the isolates within clade 8. Meanwhile, the members of clade 4 and 6 were still undetermined. The members of clade 4 have been reported to infect maize in Timor-Leste and were tentatively assigned to *P. maydis* (Telle et al. 2011).

Except for one, all sequences obtained from infected maize from Sumatra investigated in this study grouped together with the ex-type sequence of *P. australiensis* with strong to maximum support, up to 100% identical to some Australian specimens. Interestingly, the type of *P. australiensis* is identical in *cox2* sequence to the type of *P. maydis*, rendering the former a synonym of the latter. However, it is also conceivable that the species is indigenous, with some species of *Sorghum*, such as *Sorghum timorense*, from which it is also known in Australia, as natural host. Whether *P. australiensis* occurs in Indonesia naturally or has been imported from Australia, probably by infested seeds, needs to be clarified in future studies.

Using partial *cox2* sequences, several Indonesian isolates of *Peronosclerospora* from Jawa Timur (KD3SG, KD4SG, Ppr, Smbh, Jnu), Jawa tengah (BY), Yogyakarta (Y, KL), and Sulawesi (ER5, L2, P2) were grouped with *Peronosclerospora* sp. (Telle et al. 2011) that was speculated to probably represent...
P. maydis, an assumption refuted in the present study. However, as the sequences reported in Telle et al. (2011) showed only around 98% homology to this group and were consistently forming a group of its own. This suggests that the specimens found on Timor-Leste might represent an undescribed species, closely related to the unidentified Peronosclerospora species from Java. Peronosclerospora maydis was the first Peronosclerospora species reported from Indonesia (Raciborski 1897), infecting maize in the island of Java (Semangun 2008). Peronosclerospora maydis contr has been reported from Australia (Morschel 1980; Ramsey and Jones 1988) and their attribution to P. australiensis (Shivas et al. 2012) cannot be upheld anymore, suggesting that care should be taken not to spread the disease from Australia to other parts of the world. Future studies including the type specimens of other Peronosclerospora species will be needed to clarify the identity of other species occurring in Indonesia.

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