

# An expanded phylogeny for the genus *Phytophthora*

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**Abstract:** A comprehensive phylogeny representing 142 described and 43 provisionally named *Phytophthora* species is reported here for this rapidly expanding genus. This phylogeny features signature sequences of 114 ex-types and numerous authentic isolates that were designated as representative isolates by the originators of the respective species. Multiple new subclades were assigned in clades 2, 6, 7, and 9. A single species *P. lillii* was placed basal to clades 1 to 5, and 7. *Phytophthora stricta* was placed basal to other clade 8 species, *P. asparagi* to clade 6 and *P. intercalaris* to clade 10. On the basis of this phylogeny and ancestral state reconstructions, new hypotheses were proposed for the evolutionary history of sporangial papillation of *Phytophthora* species. Non-papillate ancestral *Phytophthora* species were inferred to evolve through separate evolutionary paths to either papillate or semi-papillate species.

**Key words:**  
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## INTRODUCTION

The genus *Phytophthora* has had profound impacts on human history by causing agriculturally and ecologically important plant diseases (Erwin & Ribeiro 1996). Among the most notorious *Phytophthora* species is *P. infestans*, cause of the late blight disease, which was the primary cause of the Irish potato famine from 1845 to 1852 in which approximately one million people died and 1.5 million emigrated from Ireland (Turner 2005). Another example is the sudden oak death pathogen, *P. ramorum*, that has killed millions of coast live oak, tanoak and Japanese larch trees, and has permanently altered the forest ecosystems in California and Oregon, USA (Goheen *et al.* 2002, Rizzo *et al.* 2002, Rizzo *et al.* 2005). Other species, such as *P. cinnamomi*, *P. nicotianae*, and *P. sojae*, can also cause highly destructive plant diseases (Erwin & Ribeiro 1996). The impact caused by *Phytophthora* species has continued to increase with the emergence of new pathogens and diseases. The number of species known in the genus has doubled during the past decade due to extensive surveys in previously unexplored ecosystems such as natural forests (Jung *et al.* 2011, 2017, Rea *et al.* 2010, Reeser *et al.* 2013, Vettraino *et al.* 2011), streams (Bezuidenhout *et al.* 2010, Brazee *et al.* 2017, Reeser *et al.* 2007, Yang *et al.* 2016), riparian ecosystems (Brasier *et al.* 2003a, 2004, Hansen *et al.* 2012), and irrigation systems (Hong *et al.* 2010, 2012, Yang *et al.* 2014a, b). The total number of formally named species in the genus was about 58 in 1996 (Erwin & Ribeiro 1996), but now is more than 150. In addition, some provisionally or informally named species are also expected to be formally described in the near future.

A sound taxonomic system is foundational for correctly identifying *Phytophthora* species and safeguarding agriculture, forestry, and natural ecosystems. Traditionally, taxonomy of the genus was based on morphological characters. A fundamental morphology-based classification of *Phytophthora* species was established by Waterhouse (1963) who classified the species into six groups based on the morphology of sporangia, homothallism, and configuration of antheridia. However, plasticity in morphological characters amongst isolates of individual species is significant, so is homology or homoplasy among different species. For example, isolates of *P. constricta* (Rea *et al.* 2011), *P. gibbosa* (Jung *et al.* 2011), *P. lateralis* (Kroon *et al.* 2012), *P. mississippiiae* (Yang *et al.* 2013), and *P. multivesiculata* (Ilieva *et al.* 1998) all produce a mixture of semi-papillate and non-papillate sporangia. Many non-papillate species recovered from irrigation water such as *Phytophthora hydropathica* (Hong *et al.* 2010) and *P. irrigata* (Hong *et al.* 2008) were morphologically inseparable from *P. drechsleri*, while sequence analyses demonstrated that they are distinct species. Also, production of many morphological structures and physiological features needs specific environmental conditions, while observation of these features requires substantial training and expertise. Difficulty in obtaining important morphological data can impair accurate species identification.

With the advent of DNA sequencing, the taxonomic concept for the genus has evolved from morphology to molecular phylogeny-based (Blair *et al.* 2008, Cooke *et al.* 2000, Kroon *et al.* 2004, Lara & Belbahri 2011, Martin *et al.* 2014, Martin & Tooley 2003, Robideau *et al.* 2011, Villa *et al.* 2006). In particular, the availability of whole genome

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sequences from *P. sojae*, *P. ramorum* (Tyler *et al.* 2006) and *P. infestans* (Haas *et al.* 2009) enabled the identification of genetic markers useful for multi-locus phylogenies (Blair *et al.* 2008).

Cooke *et al.* (2000) developed the first molecular phylogeny for the genus by analyzing sequences of the internal transcribed spacer region (ITS) of 51 species. Kroon *et al.* (2004) constructed a phylogeny based on sequences of four nuclear and mitochondrial genes of 48 species, and Blair *et al.* (2008) produced a sophisticated phylogeny based on sequences of seven nuclear genetic markers. That multi-locus phylogeny divided 82 *Phytophthora* species into 10 phylogenetically well-supported clades. Martin *et al.* (2014) analyzed sequences of seven nuclear and four mitochondrial genes of 90 formally named and 17 provisional species and provided phylogenies including 10 clades, almost identical to that of Blair *et al.* (2008), except that *P. quercina* and *P. sp. ohioensis* were excluded from clade 4 and grouped into a potentially new clade.

A comprehensive molecular phylogeny is required to understanding the evolution of *Phytophthora* species. Although discordance has been found between the molecular phylogeny and the morphology-based taxonomy (Cooke *et al.* 2000, Ersek & Ribeiro 2010), correlations have been observed between molecular phylogenies and individual morphological and physiological traits. Recent studies indicated that species in individual clades or subclades are mostly identical in sporangial papillation, and optimum and maximum growth temperatures (Cooke *et al.* 2000, Kroon *et al.* 2012, Martin *et al.* 2012, Yang 2014). However, there was limited to no correlation between phylogeny and the morphology of sexual organs, such as antheridial configuration (Cooke *et al.* 2000, Kroon *et al.* 2012, Martin *et al.* 2012, Yang 2014). These studies have implied that divergence in sporangial morphology and variation in environmental specialization may be the keys in the evolutionary history of *Phytophthora* species. Nevertheless, these hypotheses need to be further tested and the exact evolutionary history of the genus *Phytophthora* warranted more investigation.

In this study, an expanded phylogeny, including more than 180 *Phytophthora* taxa, many not included in any previous phylogeny, was constructed. Sequences of seven nuclear genetic markers were used for construction of the phylogeny. In light of this phylogeny, ancestral state reconstructions were conducted on the sporangial papillation of *Phytophthora* species. Important evolutionary divergence events and associated changes in the sporangial morphology of *Phytophthora* species are discussed.

## MATERIALS AND METHODS

### Isolate selection

A total of 376 *Phytophthora* isolates representing 142 described and 43 provisionally named species, plus one isolate of each *Elongisporangium undulatum* (basonym: *Pythium undulatum*), *Halophytophthora fluviatilis*, and *Phytophthora vexans* (basonym: *Pythium vexans*) as outgroup taxa were included (Table 1). These included 114 ex-types (Table 2). Also included were 164 authentic isolates

that were designated as representative isolates by the originators of the respective species names (Table 1). The majority of these isolates were provided by the originators of the respective species, while the rest were purchased from the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, The Netherlands.

### DNA extraction

To extract genomic DNA (gDNA), an approximately 5 × 5 mm culture plug of each isolate was taken from the actively growing area of a fresh culture. This was then grown in 20 % clarified V8 broth (lima bean broth for growing a *P. infestans* isolate 27A8) at room temperature (ca. 23 °C) for 7–14 d to produce a mycelial mass. The mass was then blot-dried using sterile tissue paper and then lysed in liquid nitrogen or using a FastPrep®-24 system (MP Biomedicals, Santa Ana, CA). gDNA was extracted using the DNeasy® Plant Mini kit (Qiagen, Valencia, CA) or the Maxwell® Plant DNA kit in combination with a Maxwell® Rapid Sample Concentrator (Promega, Madison, WI).

### DNA amplification and sequencing

A set of primers for seven genetic markers were used for DNA amplification including 60S Ribosomal protein L10 (60S), beta-tubulin (Btub), elongation factor 1 alpha (EF1α), enolase (Enl), heat shock protein 90 (HSP90), 28S ribosomal DNA (28S), and tigA gene fusion protein (TigA) as indicated in Blair *et al.* (2008). PCR reaction mixtures were prepared with the Takara *Taq* DNA polymerase (Takara Shuzo, Shiga, Japan) according to the manufacturer's instructions. The PCR cycling protocol was the same as indicated by Blair *et al.* (2008), except that the Eppendorf® Mastercycler® Pro thermal cycler (Eppendorf, Hamburg) was used in this study. All PCR products were evaluated for successful amplification using agarose gel electrophoresis. Unsuccessful PCR amplifications were repeated using a modified protocol to attempt successful amplifications by optimizing annealing temperature using gradient PCR (typically with lower annealing temperatures) or using the GoTaq® Flexi DNA Polymerase (Promega, Madison, WI) PCR mixture system.

Prior to sequencing, excess primer and dNTPs were removed from successful PCR products with shrimp alkaline phosphatase and exonuclease I (USB Catalog # 70092Y and 70073Z). One unit of each enzyme was added to 15 µL PCR product, incubated at 37 °C for 30 min, followed by heat inactivation at 65 °C for 15 min. Sequencing was performed with both amplifying primers as well as internal primers, if any, for individual genetic markers at the University of Kentucky Advanced Genetic Technologies Center (Lexington, KY). Derived sequencing files were visualized with FinchTV version 1.4.0 (Geospiza, Seattle, WA). Sequences of each isolate with all primers for individual genetic markers were aligned with Clustal W (Larkin *et al.* 2007) and edited manually to correct obvious sequencing errors and code ambiguous sites according to the International Union of Pure and Applied Chemistry (IUPAC) nucleotide ambiguity codes to produce a consensus sequence. All sequences produced in this study have been deposited in GenBank (Supplementary Table 1).

Among 379 isolates (including three isolates of the outgroup taxa) in the following phylogenetic analyses,

**Table 1.** Information regarding isolates used in this study. GenBank accession numbers are listed in Table S1.

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>						Isolate origins						
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference		
1a	<i>P. cactorum</i>	P	22E6				P10194	p25		<i>Rhododendron</i> sp.	Ohio, USA	n.a. <sup>f</sup>	(Schröter 1886)		
			22E7		16693	21168	P0715	p6		n.a.	UK	n.a.			
			22E8		16694, MYA-3653	50470	P10193	p7		<i>Malus</i> sp.	Zimbabwe	n.a.			
	<i>P. hedraiandra</i>	P	33F3		MYA-4165			p225		<i>Rhododendron</i> sp.	Minnesota, USA	2002	(de Cock & Lévesque 2004)		
			38C2							Irrigation water	Virginia, USA	2006			
	<i>P. idaei</i>	P	62A5	111725			P19523		T	<i>Viburnum</i> sp.	The Netherlands	2001			
			34D4	971.95	MYA-4065	313728	P6767	p220	T	<i>Rubus idaeus</i>	Scotland, UK	1987	(Kennedy & Duncan 1995)		
	<i>P. pseudotsugae</i>	P	62A1	968.95					A	<i>Rubus idaeus</i>	Scotland, UK	1985			
					52938	331662	P10339		T	<i>Pseudotsuga menziesii</i>	Oregon, USA	n.a.	(Hamm & Hansen 1983)		
		<i>P. aff. hedraiandra</i>	P	33F4						<i>Rhododendron</i> sp.	Minnesota, USA	2003	n.a.		
	<i>P. aff. pseudotsugae</i>	P	29B3						<i>Pseudotsuga menziesii</i>	Oregon, USA	1975	n.a.			
1b	<i>P. clandestina</i>	P	32G1	347.86	58713, 60438	278933	P3943	p200	T	<i>Trifolium subterraneum</i>	Australia	1985	(Taylor <i>et al.</i> 1985)		
			33D8		MYA-4064	287317			p215	A	<i>Trifolium subterranea</i>	Australia	1985		
			38D4					p304		n.a.	Australia	n.a.			
	<i>P. iranica</i>	P	61J4	374.72	60237	158964	P3882	p218	T	<i>Solanum melongena</i>	Iran	1969	(Ershad 1971)		
	<i>P. tentaculata</i>	P	29F2	552.96						<i>Chrysanthemum leucanthemum</i>	Germany	n.a.	(Kröber & Marwitz 1993)		
			30D5							<i>Bacopa</i> sp.	The Netherlands	2004			
			30G8		MYA-3655					<i>Argyranthemum frutescens</i>	Germany	2004			
	1c	<i>P. andina</i>	SP	60A2						p460	A	<i>Solanum betaceum</i>	Ecuador	n.a.	(Oliva <i>et al.</i> 2010)
60A3									p461	A	<i>Solanum betaceum</i>	Ecuador	n.a.		
							P13365			T	<i>Solanum brevifolium</i>	Ecuador	2001		
<i>P. infestans</i>		SP	27A8								<i>Solanum tuberosum</i>	Mexico	1992	(De Bary 1876)	
<i>P. ipomoeae</i>		SP	31B4				P10650					<i>Solanum tuberosum</i>	Mexico	n.a.	
			31B5	109229			P10226			A	<i>Ipomoea longipedunculata</i>	Mexico	n.a.	(Flier <i>et al.</i> 2002)	
			31B6				P10225			T	<i>Ipomoea longipedunculata</i>	Mexico	1999		
			31B6				P10227			A	<i>Ipomoea longipedunculata</i>	Mexico	n.a.		
<i>P. mirabilis</i>		SP	30C1		64069, MYA-4062		P3006	p145	A	<i>Mirabilis jalapa</i>	Mexico	n.a.	(Galindo-A & Hohl 1985)		
<i>P. phaseoli</i>		SP	30C2		64070, MYA-4063		P3007	p153	A	<i>Mirabilis jalapa</i>	Mexico	n.a.			
	23B4							p106		<i>Phaseolus lunatus</i>	Delaware, USA	2000	(Thaxter 1889)		
	35B6									<i>Phaseolus</i> sp.	Delaware, USA	2000			
						P10145				<i>Phaseolus lunatus</i>	Delaware, USA	n.a.			
						P10150				<i>Phaseolus lunatus</i>	Delaware, USA	n.a.			

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>						Isolate origins						
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference		
1	<i>P. nicotianae</i>	P	22F9		15410, MYA-4037				p23		<i>Nicotiana tabacum</i>	North Carolina, USA	n.a.	(Breda de Haan 1896)	
			22G1		15409, MYA-4036				p22		<i>Nicotiana tabacum</i>	North Carolina, USA	n.a.		
2a	<i>P. botryosa</i>	P	22H8		MYA-4059				p44		<i>Metrosideros excelsa</i>	California, USA	2002		
			46C2		26481				p384	A	<i>Citrus</i> sp.	California, USA	n.a.		
			62C6	581.69			136915	P3425		T	<i>Hevea brasiliensis</i>	Thailand	n.a.	(Chee 1969)	
	<i>P. citrophthora</i>	P	03E5						p132		Irrigation water	Virginia, USA	2000	(Smith & Smith 1906)	
			26H3						p31		n.a.	n.a.	n.a.		
	<i>P. colocasiae</i>	SP	22F8		MYA-4159				p47		<i>Colocasia esculenta</i>	n.a.	1992	(Raciborski 1900)	
			35D3						p276		<i>Colocasia esculenta</i>	Hawaii, USA	2005		
	<i>P. himalsilva</i>	P	61G2	128767						T	<i>Quercus leucotricophora</i>	Nepal	2005	(Vettraino <i>et al.</i> 2011)	
			61G3	128753						A	<i>Quercus leucotricophora</i>	Nepal	2005		
	<i>P. meadii</i>	P	22G5		MYA-4043				p75		<i>Citrus</i> sp.	India	1992	(McRae 1918)	
			61J9	219.88			129185				<i>Hevea brasiliensis</i>	India	1987		
	<i>P. occultans</i>	SP	65B9	101557						T	<i>Buxus sempervirens</i>	The Netherlands	1998	(Man In't Veld <i>et al.</i> 2015)	
	<i>P. terminalis</i>	SP	65B8	133865						T	<i>Pachysandra terminalis</i>	The Netherlands	2010	(Man In't Veld <i>et al.</i> 2015)	
	<i>P. aff. citrophthora</i>	P	26H4						p32	A	n.a.	n.a.	n.a.	n.a.	
	<i>P. aff. himalsilva</i>	P	61G4	128754				342898	P10341		A	<i>Syringa</i> sp.	England, UK	1990	
<i>P. sp. 46C3</i>			n.a.	46C3		66767			P6713	p385	A	<i>Castanopsis</i> sp.	Nepal	2005	n.a.
<i>P. sp. P6262</i>			n.a.						P6262		A	<i>Hevea brasiliensis</i>	Malaysia	n.a.	n.a.
<i>P. sp. P6310</i>			n.a.						P6310		A	<i>Hevea brasiliensis</i>	India	n.a.	n.a.
<i>P. sp. P6310</i>			n.a.								A	<i>Theobroma cacao</i>	Indonesia	n.a.	n.a.
2b	<i>P. capsici</i>	P	22F4		15399, MYA-4034				p8	A	<i>Capsicum annum</i>	New Mexico, USA	1948	(Leonian 1922)	
					46012							<i>Theobroma cacao</i>	Mexico	1964	
	<i>P. glovera</i>	SP	31E5		121656				P0253		<i>Cucumis sativus</i>	Michigan, USA	1997		
			62B4	121969					P10386			<i>Nicotiana tabacum</i>	Brazil	n.a.	(Abad <i>et al.</i> 2011)
	<i>P. mingei</i>	SP	42B2			MYA-4554				p340	T	<i>Nicotiana tabacum</i>	Brazil	1995	
			42B3			MYA-4555				p341	A	<i>Persea americana</i>	California, USA	n.a.	(Hong <i>et al.</i> 2009)
<i>P. mexicana</i>	P	45G4	554.88	46731		92550	P0646	p355		<i>Persea americana</i>	California, USA	n.a.			
										<i>Solanum lycopersicum</i>	Argentina	n.a.	(Hotson & Hartge 1923)		

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>						Isolate origins					
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference	
2c	<i>P. siskiyouensis</i>	SP	41B7	122779	MYA-4187		P15122		T	Stream water	Oregon, USA	2003	(Reeser <i>et al.</i> 2007)	
			41B8						A	Soil	Oregon, USA	2003		
	<i>P. tropicalis</i>	P	22H5					p27		<i>Vanilla</i> sp.	Tahiti	n.a.	(Aragaki & Uchida 2001)	
				35C8	434.91	76651, MYA-4218			p272	T	<i>Macadamia integrifolia</i>	Hawaii, USA	n.a.	
	<u><i>P. aff. capsici</i></u>	P	22F5			15427, MYA-4035			p9		<i>Nicotiana tabacum</i>	North Carolina, USA	n.a.	n.a.
	<i>P. sp. brasiliensis</i>	n.a.				46705		P0630		A	<i>Theobroma cacao</i>	Brazil	1969	(Oudemans & Coffey 1991)
	<i>P. acerina</i>	SP	61H1	133931						T	<i>Acer pseudoplatanus</i>	Italy	2010	(Ginetti <i>et al.</i> 2014)
				61H2						A	Soil	Italy	2010	
	<i>P. capensis</i>	SP	62C1	128319				P1819		T	<i>Curtisia dentata</i>	South Africa	n.a.	(Bezuidenhout <i>et al.</i> 2010)
				62C2	128320			P1822		A	Stream water	South Africa	n.a.	
				62C3	128321			P1823		A	<i>Olea campensis</i>	South Africa	1986	
	<i>P. citricola</i>	SP	33H8	221.88	60440		21173	P0716	p396	T	<i>Citrus sinensis</i>	Taiwan	1987	(Sawada 1927)
				33J2	295.29				p375	A	<i>Citrus</i> sp.	Japan	1929	
	<i>P. multivora</i>	SP	55C5	124094						T	Soil	Western Australia, Australia	2007	(Scott <i>et al.</i> 2009)
	<i>P. pachypleura</i>	SP	61H6							A	Soil	UK	2006	(Henricot <i>et al.</i> 2014)
				61H7			502404			T	<i>Acuba japonica</i>	UK	2008	
				61H8						A	Soil	UK	2009	
	<i>P. pini</i>	SP	22F1			MYA-3656			p53	A	<i>Rhododendron</i> sp.	West Virginia, USA	1987	(Hong <i>et al.</i> 2011)
				45F1		64532			p343	T	<i>Pinus resinosa</i>	Minnesota, USA	1925	
	<i>P. plurivora</i>	SP	22E9			MYA-3657			p101		<i>Kalmia latifolia</i>	Western Australia, Australia	1998	(Jung & Burgess 2009)
			22F2					p52		<i>Rhododendron</i> sp. cv. "Olga Mezitt"	New York, USA	n.a.		
			33H9	379.61						<i>Rhododendron</i> sp.	Germany	1958		
<u><i>P. sp. 22F3</i></u>	SP	22F3						p33	A	n.a.	Ohio, USA	n.a.	n.a.	
<u><i>P. sp. 28D1</i></u>	SP	28D1						p119	A	<i>Fagus sylvatica</i>	New York, USA	n.a.	n.a.	
			28D3					p121	A	<i>Fagus sylvatica</i>	New York, USA	n.a.		
<u><i>P. sp. citricola VIII</i></u>	SP	27D9							A	Unidentified leaf	Hainan, China	n.a.	n.a.	
<u><i>P. sp. pini-like</i></u>	SP	56G1							A	<i>Taxus</i> sp.	Pennsylvania, USA	2011	n.a.	
<i>P. taxon emzansi</i>	SP	61F2							A	<i>Agathosma betulina</i>	South Africa	2005	(Bezuidenhout <i>et al.</i> 2010)	

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>							Isolate origins					
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference		
2d	<i>P. bisheria</i>	SP	61F3							A	<i>Agathosma betulina</i>	South Africa	2005		
			29D2									<i>Rubus idaeus</i> cv. Canby	Wisconsin, USA	1989	(Abad <i>et al.</i> 2008)
			31E6	122081					P10117	T		<i>Fragaria ×ananassa</i>	North Carolina, USA	1999	
	<i>P. elongata</i>	SP							P1620			<i>Rhododendron</i> sp.	North Carolina, USA	n.a.	
			33J3							A	n.a.	Australia	1995	(Rea <i>et al.</i> 2010)	
			33J4							A	n.a.	Australia	1995		
<i>P. frigida</i>	P									T	Soil	Western Australia, Australia	2004		
		47G6							A		<i>Eucalyptus smithi</i>	South Africa	n.a.	(Maseko <i>et al.</i> 2007)	
		47G7							A		<i>Eucalyptus smithi</i>	South Africa	n.a.		
2e	<i>P. multivesiculata</i>	SP to NP	29E3	545.96						T	<i>Cymbidium</i> sp.	South Africa	2001		
			30D4					P10410	T		<i>Cymbidium</i> sp.	The Netherlands	n.a.	(Ilieva <i>et al.</i> 1998)	
3	<i>P. taxon aquatilis</i>	SP	38J5		MYA-4577					A	Stream water	Virginia, USA	2006	(Hong <i>et al.</i> 2012)	
	<i>P. ilicis</i>	SP	23A7		56615, MYA-3897			P3939	p113		<i>Ilex</i> sp.	Canada	n.a.	(Buddenhagen & Young 1957)	
	<i>P. nemorosa</i>	SP									T	<i>Quercus</i> sp.	Germany	1999	
			34D6									<i>Ilex aquifolium</i>	The Netherlands	n.a.	
			62A7	114348								<i>Umbellularia californica</i>	California, USA	n.a.	(Hansen <i>et al.</i> 2003)
	<i>P. pluvialis</i>	SP				MYA-4061				p141			California, USA	n.a.	
			41C4			MYA-2948				p320	T	<i>Lithocarpus densiflorus</i>	California, USA	n.a.	
	<i>P. pseudosyringae</i>	SP				MYA-4930					T	Rainwater	Oregon, USA	2008	(Reeser <i>et al.</i> 2013)
			30A8	111772	MYA-4222					p284	T	<i>Quercus robur</i>	Germany	1997	(Jung <i>et al.</i> 2003)
	<i>P. psychrophila</i>	SP								Pp285	A	<i>Quercus robur</i>	Germany	1997	
30B1										T	<i>Quercus robur</i>	Germany	1995	(Jung <i>et al.</i> 2002)	
4	<i>P. alticola</i>	P	29J5	803.95						T	<i>Quercus robur</i>	Germany	1995	(Jung <i>et al.</i> 2002)	
			29J6		MYA-4083					p288	A	<i>Quercus ilex</i>	France	1996	
	<i>P. arenaria</i>	P	47G5	121939							A	<i>Eucalyptus dunnii</i>	South Africa	n.a.	(Maseko <i>et al.</i> 2007)
			55C2	127950							T	Soil	Western Australia, Australia	2009	(Rea <i>et al.</i> 2011)
<i>P. megakarya</i>	P									A	Soil	Western Australia, Australia	2009		
		62B7	125800												
			22H7		MYA-4040				p42		<i>Theobroma cacao</i>	Africa	n.a.	(Brasier & Griffin 1979)	

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>						Isolate origins				
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference
5	<i>P. palmivora</i>	P	61J5	238.83	42100	202077			T	<i>Theobroma cacao</i>	Cameroon	n.a.	
			61J6	239.83	42099	106327			A	<i>Theobroma cacao</i>	Nigeria	n.a.	
			22G8		MYA-4039		P10213	p65		<i>Citrus</i> sp.	Florida, USA	n.a.	(Butler 1910)
			22G9		MYA-4038			p26		<i>Theobroma cacao</i>	Costa Rica	n.a.	
	<i>P. quercetorum</i>	P	15C7							Soil	South Carolina, USA	1997	(Balci <i>et al.</i> 2008)
			15C8							Soil	South Carolina, USA	1997	
	<i>P. quercina</i>	P	30A4	783.95					A	<i>Quercus robur</i>	Germany	1995	(Jung <i>et al.</i> 1999)
			30A5	784.95	MYA-4084				T	<i>Quercus robur</i>	Germany	1995	
			30A7							<i>Quercus</i> sp.	Serbia	2003	
	<i>P. sp. ohioensis</i>	n.a.					P16050	A	Soil	Ohio, USA	2006	n.a.	
<i>P. agathidicida</i>	P	67D5						T	<i>Agathis australis</i>	New Zealand	2006	(Weir <i>et al.</i> 2015)	
<i>P. castaneae</i>	P	22H6		MYA-4060				p45	<i>Castanea</i> sp.	Japan	n.a.	(Katsura 1976)	
		30E7							Soil	Hainan, China	n.a.		
<i>P. cocois</i>	P	61J7	587.85	36818	325914			T	Soil	Taiwan	n.a.		
		67D6						T	<i>Cocos nucifera</i>	Hawaii, USA	1990	(Weir <i>et al.</i> 2015)	
<i>P. heveae</i>	P	22J1			180616			p28	<i>Heaveae</i> sp.	Malaysia	n.a.	(Thompson 1929)	
		22J2		16701, MYA-3895				p17	soil	Tennessee, USA	1964		
6a	<i>P. gemini</i>	NP	46H1	123382					A	<i>Zostera marina</i>	The Netherlands	1999	(Man in't Veld <i>et al.</i> 2011)
			46H2	123383					A	<i>Zostera marina</i>	The Netherlands	1999	
<i>P. humicola</i>	NP	32F8	200.81	52179, MYA-4080			P3826	p198	T	Soil	Taiwan	1976	(Ko & Ann 1985)
		32F9					P6702	p199	A	<i>Phaseolus vulgaris</i>	Taiwan	n.a.	
<i>P. inundata</i>	NP	30J3			390121			p291	T	<i>Olea</i> sp.	Spain	1996	(Brasier <i>et al.</i> 2003b)
		30J4			389751			p298	T	<i>Salix matsudana</i>	UK	1972	
<i>P. rosacearum</i>	NP	22J9		MYA-3662				p82	A	<i>Prunus</i> sp.	California, USA	1987	(Hansen <i>et al.</i> 2009)
		41C1						p321	A	<i>Prunus</i> sp.	California, USA	n.a.	
<i>P. sp. 48H2</i>	NP	47J1		MYA-4456					T	<i>Malus domestica</i>	California, USA	n.a.	
		48H2							A	Stream water	Virginia, USA	2008	n.a.
<i>P. sp. 62C9</i>	NP	62C9							A	Stream water	Taiwan	2013	n.a.
		<i>P. sp. personii</i>	n.a.					P11555	A	<i>Nicotiana tabacum</i>	North Carolina, USA	n.a.	n.a.
<i>P. taxon walnut</i>	NP	40A7							A	Irrigation water	Virginia, USA	2006	(Brasier <i>et al.</i> 2003a)
		43G1							A	Irrigation water	Virginia, USA	2007	
6b	<i>P. amnicola</i>	NP	61G6	131652					T	Stream water	Western Australia, Australia	2009	(Crous <i>et al.</i> 2012)

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>							Isolate origins					
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference		
	<i>P. bilorbang</i>	NP	62C5	133867							<i>Pachysandra</i> sp.	The Netherlands	n.a.		
			61G8	131653					T	Soil	Western Australia, Australia	2010	(Aghighi <i>et al.</i> 2012)		
	<i>P. borealis</i>	NP	60B2	132023	MYA-4881					T	Stream water	Alaska, USA	2008	(Hansen <i>et al.</i> 2012)	
	<i>P. crassamura</i>	NP	66C9							A	<i>Picea abies</i>	Italy	2012	(Scanu <i>et al.</i> 2015)	
	<i>P. fluvialis</i>	NP	66D1	140357						T	Soil	Italy	2011		
			55B6	129424					T	Stream water	Western Australia, Australia	2009	(Crous <i>et al.</i> 2011)		
	<i>P. gibbosa</i>	NP to SP	55B7							A	Soil	Western Australia, Australia	2009	(Jung <i>et al.</i> 2011)	
			62B8	127951					T	Soil	Western Australia, Australia	2009			
	<i>P. gonapodyides</i>	NP	21J5		46726					p117	Water	England, UK	n.a.	(Buisman 1927, Petersen 1910)	
	<i>P. gregata</i>	NP	34A8	554.67	60351						Reservoir water	n.a.	1967		
			55B8					P6872		A	Soil	Western Australia, Australia	2009	(Jung <i>et al.</i> 2011)	
	<i>P. lacustris</i>	NP	62B9	127952							Soil	Western Australia, Australia	2009		
			61D6							A	Soil	Germany	2003	(Nechwatal <i>et al.</i> 2013)	
			61D8							A	Soil	Germany	2003		
	<i>P. litoralis</i>	NP	61E1								Soil	Germany	2006		
			55B9	127953				389725	P10337	T	<i>Salix matsudana</i>	England, UK	1972		
	<i>P. megasperma</i>	NP	62C7	402.72	58817		32035	P3599		T	<i>Althaea rosea</i>	Washington DC, USA	1931	(Drechsler 1931)	
	<i>P. mississippiae</i>	NP to SP	57J1								Irrigation water	Mississippi, USA	2012	(Yang <i>et al.</i> 2013)	
			57J2								A	Irrigation water	Mississippi, USA	2012	
			57J3			MYA-4946					T	Irrigation water	Mississippi, USA	2012	
			57J4								A	Irrigation water	Mississippi, USA	2012	
	<i>P. ornamentata</i>	NP	66D2	140647						T	Soil	Italy	2012	(Scanu <i>et al.</i> 2015)	

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>						Isolate origins				Reference	
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year		
			66D3							A	Soil	Italy	2012	
	<i>P. pinifolia</i>	NP	47H1	122924						T	<i>Pinus radiata</i>	Chile	2007	(Duran <i>et al.</i> 2008)
			47H2	122922						A	<i>Pinus radiata</i>	Chile	2007	
	<i>P. riparia</i>	NP	60B1	132024	MYA-4882					T	Stream water	Oregon, USA	2006	(Hansen <i>et al.</i> 2012)
	<i>P. thermophila</i>	NP	55C1	127954						T	Soil	Western Australia, Australia	2004	(Jung <i>et al.</i> 2011)
	<i>P. ×stagnum</i>	NP	36H8							A	Irrigation water	Virginia, USA	2006	(Yang <i>et al.</i> 2014c)
			36J7							A	Irrigation water	Virginia, USA	2006	
			43F3		MYA-4926					T	Irrigation water	Virginia, USA	2007	
			44F9							A	Irrigation water	Virginia, USA	2007	
	<u><i>P. sp. 26E1</i></u>	NP	26E1						p116	A	<i>Malus domestica</i>	New York, USA	n.a.	n.a.
	<i>P. sp. canalensis</i>	n.a.						P10456		A	Canal water	California, USA	2002	n.a.
	<u><i>P. sp. delaware</i></u>	NP	63H4							A	Pond water	Delaware, USA	2014	n.a.
			63H7							A	Pond water	Delaware, USA	2014	
	<u><i>P. sp. gregata-like</i></u>	NP	22J5		16698				p16	A	n.a.	n.a.	n.a.	n.a.
	<u><i>P. sp. megasperma-like</i></u>	NP	23A1						p81	A	<i>Prunus sp.</i>	California, USA	n.a.	n.a.
			23A3		MYA-3660				p79	A	<i>Actinidia chinensis</i>	California, USA	1987	
6	<i>P. asparagi</i>	NP	33D7				384046			A	<i>Asparagus officinalis</i>	New Zealand	1980	(Crous <i>et al.</i> 2012)
			62C4	132095	MYA-4826					T	<i>Asparagus officinalis</i>	Michigan, USA	2006	
	<i>P. sp. sulawesiensis</i>	n.a.						P6306		A	<i>Syzygium aromaticum</i>	Indonesia	1989	n.a.
7a	<i>P. attenuata</i>	NP	67C5							T	Soil	Taiwan	2013	(Jung <i>et al.</i> 2017)
	<i>P. europaea</i>	NP	30A3								<i>Quercus sp.</i>	France	1998	(Jung <i>et al.</i> 2002)
			34C2								<i>Quercus sp.</i>	Germany	1999	
			62A2	109049						T	Soil	France	1998	
	<i>P. flexuosa</i>	NP	67C3							T	Soil	Taiwan	2013	(Jung <i>et al.</i> 2017)
	<i>P. formosa</i>	NP	67C4							T	Soil	Taiwan	2013	(Jung <i>et al.</i> 2017)
	<i>P. fragariae</i>	NP	22G6		11374			P3570	p114		<i>Fragaria ×ananassa</i>	Maryland, USA	n.a.	(Hickman 1940)
			30C5								<i>Fragaria ×ananassa</i>	Virginia, USA	n.a.	
			61J3	209.46			181417	P6231		T	<i>Fragaria ×ananassa</i>	England, UK	n.a.	
	<i>P. intricata</i>	NP	67B9							T	Soil	Taiwan	2013	(Jung <i>et al.</i> 2017)
	<i>P. rubi</i>	NP	30D7						p186	A	<i>Rubus sp.</i>	Australia	n.a.	(Man in 't Veld 2007)
			41D5								<i>Rubus sp.</i>	Norway	2005	
			46C7		90442				p389	T	<i>Rubus idaeus</i> cv. "Glen Clova"	Scotland, UK	n.a.	
	<i>P. uliginosa</i>	NP	62A3	109054				P10413		T	Soil	Poland	1998	(Jung <i>et al.</i> 2002)

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>						Isolate origins				Reference			
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year				
7b	<i>P. xalni</i>	NP	62A4	109055				P10328	A	Soil	Germany	1998	(Brasier <i>et al.</i> 2004, Husson <i>et al.</i> 2015)			
			32J6	392317	MYA-4081				p205	A	<i>Alnus glutinosa</i>	France		1996		
			32J7	392318					p206	A	<i>Alnus</i> sp.	Austria		1996		
			47A7			392314				T	<i>Alnus</i> sp.	UK		1994		
			47A8							A	<i>Alnus</i> sp.	The Netherlands		n.a.		
	<i>P. xCambivora</i>	NP	22F6		46719, MYA-4076				p64	<i>Abies</i> sp.	Oregon, USA	n.a.		(Buisman 1927, Jung <i>et al.</i> 2017)		
			26F8		MYA-4075				p38	n.a.	New York, USA	n.a.				
			67C1							T	Stream water	Taiwan		2013		
	<i>P. xheterohybrida</i>	NP	67C2						T	Stream water	Taiwan	2013		(Jung <i>et al.</i> 2017)		
	<i>P. xincrassata</i>	NP	33F7					p229	A	Soil	West Virginia, USA	2005		n.a.		
	7c	<i>P. asiatica</i>	NP	45G1		90455				p352	A	<i>Robinia pseudoacacia</i>		Jiangsu, China	n.a.	(Rahman <i>et al.</i> 2014a)
				46C6		56194				p388	A	<i>Robinia pseudoacacia</i>		Jiangsu, China	n.a.	
				61H3	133347						T	<i>Pueraria lobata</i>		Japan	2005	
		<i>P. cajani</i>	NP	33D9						p214		<i>Cajanus cajani</i>		India	n.a.	(Amin <i>et al.</i> 1978)
				45F6		44389				p348	A	<i>Cajanus cajani</i>		India	n.a.	
45F7					44388			P3105	p349	T	<i>Cajanus cajani</i>	India	n.a.			
<i>P. melonis</i>		NP	32F6		MYA-4079			P1371	p196	A	<i>Cucumis sativus</i>	China	n.a.	(Katsura 1976)		
			41B4						p318	A	<i>Cucumis sativus</i>	Iran	n.a.			
			45F3	582.69	52854					T	<i>Cucumis sativus</i>	Japan	n.a.			
<i>P. niederhauserii</i>		NP	01D5						p312	A	Irrigation water	Virginia, USA	2000	(Abad <i>et al.</i> 2014)		
			23J6		MYA-4163				p57	A	Unknown ornamental	Israel	n.a.			
			31E7					P10617	p169	A	<i>Thuja occidentalis</i>	North Carolina, USA	2001			
<i>P. pisi</i>		NP	60A4							T	Pea	Sweden	2009	(Heyman <i>et al.</i> 2013)		
			60A5							A	Pea	Sweden	2009			
<i>P. pistaciae</i>		NP	33D6		MYA-4082		386658		p216	T	<i>Pistacia vera</i>	Iran	1986	(Mirabolfathy <i>et al.</i> 2001)		
	41A9							p314	A	<i>Pistacia vera</i>	Iran	n.a.				
<i>P. sojae</i>	NP	22D8	312.62	16705, MYA-3899	131375			p19		<i>Glycine max</i>	Ontario, Canada	1959	(Kaufmann & Gerdemann 1958)			
		28F9						p236		<i>Glycine max</i>	Mississippi, USA	1970				
		45G6		46735				p357	A	<i>Glycine max</i>	n.a.	n.a.	(Purss 1957)			
<i>P. vignae</i>	NP	45G9		64832		316196	P3420	p379		<i>Vigna unguiculata</i>	Sri Lanka	n.a.				
		46C1	112.76	64129				p380		<i>Vigna sinensis</i>	n.a.	n.a.				
		23B1		15400, MYA-4057				p10		<i>Camellia japonica</i>	South Carolina, USA	n.a.	(Rands 1922)			

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>						Isolate origins					
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference	
			23B2		15401, MYA-4058				p11		<i>Persea americana</i>	Puerto Rico	1960	
			61J1	144.22	46671		22938	P2110		T	<i>Cinnamomum burmannii</i>	Indonesia	1922	
	<i>P. parvispora</i>	NP	30G9		MYA-4078				p178	A	<i>Beaucarnea</i> sp.	Germany	1991	(Scanu <i>et al.</i> 2014)
			46F6							A	<i>Beaucarnea</i> sp.	Germany	1992	
			66C7	132771						A	<i>Arbutus unedo</i>	Italy	2008	
			66C8	132772						T	<i>Arbutus unedo</i>	Italy	2011	
	<i>P. sp. ax</i>	NP	46H5							A	<i>Ilex glabra</i> cv. "Shamrock"	Virginia, USA	2008	n.a.
7d	<i>P. fragariaefolia</i>	NP	61H4	135747						T	<i>Fragaria xananassa</i>	Japan	2005	(Rahman <i>et al.</i> 2014b)
	<i>P. nagaii</i>	NP	61H5	133248						T	<i>Rosa</i> sp.	Japan	1968	(Rahman <i>et al.</i> 2014b)
8a	<i>P. cryptogea</i>	NP	61H9	113.19			180615	P1738		T	<i>Solanum lycopersicum</i>	Ireland	n.a.	(Pethybridge & Lafferty 1919)
	<i>P. drechsleri</i>	NP	15E5								Soil	South Carolina, USA	1997	(Tucker 1931)
			15E6								Soil	South Carolina, USA	1998	
			23J5	292.35	46724			P1087	p41	T	<i>Beta vulgaris</i> var. <i>altissima</i>	California, USA	n.a.	
								P10331			<i>Gerbera jamesonii</i>	New Hampshire, USA	2003	
	<i>P. erythroseptica</i>	NP	61J2	129.23			34684	P1693		T	<i>Solanum tuberosum</i>	Ireland	n.a.	(Pethybridge 1913)
	<i>P. medicaginis</i>	NP	23A4		MYA-3900				p37		<i>Medicago sativa</i>	Ohio, USA	n.a.	(Hansen & Maxwell 1991)
			28F1		44390			P1057	p124		<i>Medicago sativa</i>	California, USA	1975	
	<i>P. pseudocryptogea</i>	NP			52402			P3103			<i>Solanum marginatum</i>	Ecuador	n.a.	(Safaiefarahani <i>et al.</i> 2015)
	<i>P. richardiae</i>	NP	31E8					P10355	p170		<i>Zantedeschia</i> sp.	Japan	1989	(Buisman 1927)
			45F5	240.30	60353, 46734		325930		p347	T	<i>Zantedeschia aethiopica</i>	USA	n.a.	
								P10811			<i>Zantedeschia aethiopica</i>	Japan	1989	
	<i>P. sansomeana</i>	NP	47H3		MYA-4455					T	<i>Glycine</i> sp.	Indiana, USA	n.a.	(Hansen <i>et al.</i> 2009)
			47H4							A	<i>Glycine</i> sp.	Indiana, USA	n.a.	
			47H5							A	<i>Glycine</i> sp.	Indiana, USA	n.a.	
	<i>P. trifolii</i>	NP	29B2		MYA-3901				p142	A	<i>Trifolium vesiculosum</i>	Mississippi, USA	1978	(Hansen & Maxwell 1991)
			62A9	117687						T	<i>Trifolium</i> sp.	Mississippi, USA	n.a.	
	<i>P. aff. cryptogea</i>	NP	22G2	308.62	15402, MYA-4161		325907		p12		<i>Aster</i> sp.	California, USA	n.a.	n.a.

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>							Isolate origins					
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference		
8b	<i>P. aff. erythroseptica</i>	NP	22J4		MYA-4041				p50		n.a.	Ohio, USA	n.a.	n.a.	
			33A1						p207		<i>Solanum tuberosum</i>	Maine, USA	2004		
	<i>P. sp. kelmania</i>	NP	24A7		MYA-4162				p102	A	<i>Abies concolor</i>	West Virginia, USA	1998	n.a.	
			31E4						P10613	p166	A	<i>Abies fraseri</i>	North Carolina, USA	2002	
	<i>P. brassicae</i>	SP	29D8	686.95							A	<i>Brassica oleracea</i>	The Netherlands	1995	(Man in't Veld <i>et al.</i> 2002)
			61J8	179.87					P7517, P19521		T	<i>Brassica oleracea</i>	The Netherlands	1986	
	<i>P. cichorii</i>	SP	62A8	115029							T	<i>Cichorium intybus</i> var. <i>foliosum</i>	The Netherlands	2004	(Bertier <i>et al.</i> 2013)
	<i>P. dauci</i>	SP	61E5	127102							T	<i>Daucus carota</i>	France	2009	(Bertier <i>et al.</i> 2013)
			32E5									<i>Daucus carota</i>	France	2004	
			32E6						P10728			<i>Daucus carota</i>	France	2004	
			32E7							p194		<i>Daucus carota</i>	France	2004	
	<i>P. lactucae</i>	SP	61F4								T	<i>Lactuca sativa</i>	Greece	2001	(Bertier <i>et al.</i> 2013)
			61F7								A	<i>Lactuca sativa</i>	Greece	2002	
			61F8								A	<i>Lactuca sativa</i>	Greece	2003	
	<i>P. primulae</i>	SP	29E9	620.97						p286		<i>Primula acaulis</i>	Germany	1997	(Tomlinson 1952)
			29F1							p287		<i>Primula</i> sp.	The Netherlands	1998	
	<i>P. aff. brassicae-2</i>	n.a.		112968					P6207		A	<i>Allium cepa</i>	Switzerland	n.a.	n.a.
	<i>P. aff. cichorii</i>	SP	61E3	133815							A	<i>Cichorium intybus</i> var. <i>foliosum</i>	UK	1999	n.a.
	<i>P. sp. 29E7</i>	SP	29E7								A	<i>Allium porrum</i>	The Netherlands	n.a.	n.a.
<i>P. taxon castitis</i>	SP	61E7	131246							A	<i>Fragaria ×ananassa</i>	Sweden	1995	(Bertier <i>et al.</i> 2013)	
<i>P. taxon parsley</i>	SP	61G1								A	<i>Petroselinum crispum</i>	Greece	2006	(Bertier <i>et al.</i> 2013)	
8c	<i>P. foliorum</i>	SP	49J8	121655	MYA-3638				P10974		T	<i>Rhododendron</i> sp.	Tennessee, USA	2004	(Donahoo <i>et al.</i> 2006)
	<i>P. hibernalis</i>	SP	22H1	270.31	60352	36906	P6871	p115				<i>Citrus sinensis</i>	Portugal	1931	(Carne 1925)
			32F7	114104	56353, MYA-3896	134760	P3822	p197				<i>Citrus sinensis</i>	Western Australia, Australia	1958	
	<i>P. lateralis</i>	NP to SP	22H9		MYA-3898				p51	A	<i>Chamaecyparis lawsoniana</i>	Oregon, USA	n.a.	(Tucker & Milbrath 1942)	
			29A9		201856				p128			<i>Chamaecyparis lawsoniana</i>	California, USA	1997	
<i>P. ramorum</i>	SP	32G2									<i>Camellia japonica</i>	South Carolina, USA	n.a.	(Werres <i>et al.</i> 2001)	

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>							Isolate origins				
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference	
8d	<i>P. austrocedrae</i>	SP	33F2								<i>Quercus agrifolia</i>	California, USA	n.a.	
			41B5		MYA-4073				A	<i>Austrocedrus chilensis</i>	Argentina	n.a.	(Greslebin <i>et al.</i> 2007)	
	<i>P. obscura</i>	SP	41B6	122911	MYA-4074				T	<i>Austrocedrus chilensis</i>	Argentina	2005		
			60E9	129273					T	Soil	Germany	1994	(Grünwald <i>et al.</i> 2012)	
8	<i>P. syringae</i>	SP	60F1						A	<i>Pieris</i> sp.	Oregon, USA	2009		
			60F2						A	<i>Kalmia latifolia</i>	Oregon, USA	n.a.		
	<i>P. stricta</i>	NP	21H9		34002		P0649	p187		<i>Citrus</i> sp.	California, USA	n.a.	(Klebahn 1905)	
			23A6		MYA-3659			p35		n.a.	New York, USA	n.a.		
9a (cluster 9a1)	<i>P. aquimorbida</i>	NP	58A1		MYA-4944				T	Irrigation water	Mississippi, USA	2012	(Yang <i>et al.</i> 2014a)	
			58A2						A	Irrigation water	Mississippi, USA	2012		
			58A3						A	Irrigation water	Mississippi, USA	2012		
			58A4						A	Irrigation water	Mississippi, USA	2012		
	<i>P. chrysanthemi</i>	NP	40A6		MYA-4578				T	Irrigation water	Virginia, USA	2006	(Hong <i>et al.</i> 2012)	
			40E3						A	Irrigation water	Virginia, USA	2006		
			44G9						A	Irrigation water	Virginia, USA	2007		
	<i>P. hydrogena</i>	NP	61E9						A	<i>Chrysanthemum</i> sp.	Japan	1998	(Naher <i>et al.</i> 2011)	
			61F1	123163					T	<i>Chrysanthemum ×morifolium</i>	Japan	2000		
			44G8						A	Irrigation water	Virginia, USA	2007	(Yang <i>et al.</i> 2014b)	
	<i>P. hydropathica</i>	NP	46A3		MYA-4919				T	Irrigation water	Virginia, USA	2007		
			46A4						A	Irrigation water	Virginia, USA	2007		
05D1				MYA-4460			p366	T	Irrigation water	Virginia, USA	2000	(Hong <i>et al.</i> 2010)		
<i>P. irrigata</i>	NP	5C11		MYA-4459				A	Irrigation water	Virginia, USA	2000			
		04E4		MYA-4458			p335	A	Irrigation water	Virginia, USA	2000	(Hong <i>et al.</i> 2008)		
<i>P. macilentosa</i>	NP	23J7		MYA-4457				p108	T	Irrigation water	Virginia, USA	2000		
		44E4						A	Stream water	Virginia, USA	2007			
		58A5						A	Irrigation water	Mississippi, USA	2012	(Yang <i>et al.</i> 2014a)		
		58A6						A	Irrigation water	Mississippi, USA	2012			
<i>P. parsiana</i>	NP	58A7		MYA-4945				T	Irrigation water	Mississippi, USA	2012			
		58A8						A	Irrigation water	Mississippi, USA	2012			
		47C3				395329		T	<i>Ficus carica</i>	Iran	1991	(Mostowfizadeh-Ghalamfarsa <i>et al.</i> 2008)		

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>							Isolate origins							
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference				
9a (cluster 9a2)	<i>P. virginiana</i>	NP	40A9							A	Irrigation water	Virginia, USA	2006	(Yang & Hong 2013)			
			44G6							A	Irrigation water	Virginia, USA	2007				
			46A2		MYA-4927					T	Irrigation water	Virginia, USA	2007				
	<i>P. aff. parsiana G1</i>	NP	47C7							A	<i>Pistacia vera</i>	Iran	n.a.	n.a.			
			47C8							A	<i>Pistacia vera</i>	Iran	n.a.				
	<i>P. aff. parsiana G2</i>	NP	47C5				395328	P8618		A	<i>Pistacia vera</i>	Iran	1992	n.a.			
			47C6				395330			A	<i>Pistacia vera</i>	Iran	1992				
	<i>P. aff. parsiana G3</i>	NP	47D5							A	<i>Pistacia vera</i>	Iran	n.a.	n.a.			
			47D8							A	<i>Pistacia vera</i>	Iran	n.a.				
			47E1							A	<i>Pistacia vera</i>	Iran	n.a.				
<i>P. sp. 35G4</i>	NP	35G4							A	Irrigation water	Virginia, USA	2005	n.a.				
<i>P. sp. 38D9</i>	NP	38D9							A	<i>Dianthus caryophyllus</i>	Taiwan	n.a.	n.a.				
<i>P. sp. 40J5</i>	NP	40J5							A	Unknown leaf in seawater	Hainan, China	n.a.	n.a.				
	<i>P. sp. cuyabensis</i>	n.a.								P8213	A	n.a.	Ecuador	1993	n.a.		
9a (cluster 9a3)	<i>P. sp. lagoariana</i>	NP	60B4							P8220	A	n.a.	Ecuador	n.a.	n.a.		
			60B5							P8217	T	n.a.	Ecuador	n.a.			
											P8223	A	n.a.	Ecuador	1993		
											P10264			<i>Glycine max</i>	New South Wales, Australia	n.a.	(Irwin 1991)
	<i>P. macrochlamydospora-G1</i>	SP	33E1							P10267			<i>Glycine max</i>	New South Wales, Australia	1994		
9a (cluster 9a3)	<i>P. macrochlamydospora-G2</i>	SP	31E9				351473	P8017	p171				<i>Glycine max</i>	Queensland, Australia	n.a.	(Irwin 1991)	
			33D5	240.30	60353		340618						<i>Zantedeschia aethiopica</i>	The Netherlands	1927		
			45F2	406.48	56964					p344	A	<i>Cinchona officinalis</i>	Peru	n.a.	(Crandall 1947)		
			46C4	407.48	46733					p386	T	<i>Cinchona officinalis</i>	Peru	n.a.			
9a (cluster 9a3)	<i>P. insolita</i>	NP	327E1			MYA-4077				p123			Waterfall water	Hainan, China	n.a.	(Ann & Ko 1980)	
			38E1	691.79	38789		288805					T	Soil	Taiwan	1980		
											P6703	A	Soil	Taiwan	n.a.		
9b	<i>P. polonica</i>	NP	40G9										Irrigation water	Virginia, USA	2006	(Belbahri <i>et al.</i> 2006)	
			43F9											Irrigation water	Virginia, USA	2007	
			49J9								P15005	A	Soil	Poland	2006		
			46H6									A	<i>Eucalyptus saligna</i>	New Zealand	1999	(Dick <i>et al.</i> 2006)	
			46H7								P10719	T	<i>Eucalyptus saligna</i>	New Zealand	1992		
	46H8									A	<i>Eucalyptus saligna</i>	New Zealand	2000				

Table 1. (Continued).

(Sub)clade <sup>a</sup>	Species <sup>b</sup>	Papilla <sup>c</sup>	Isolate identification <sup>d</sup>						Isolate origins						
			CH	CBS	ATCC	IMI	WPC	MG	Type <sup>e</sup>	Host or Substrate	Location	Year	Reference		
10	<i>P. constricta</i>	NP to SP	55C3	125801				P10721		A	<i>Eucalyptus saligna</i>	New Zealand	1998	(Rea <i>et al.</i> 2011)	
											Soil	Western Australia, Australia	2006		
	<i>P. fallax</i>	NP	46J2	46J3	46J5				P10722		T	<i>Eucalyptus delegatensis</i>	New Zealand	1997	(Dick <i>et al.</i> 2006)
	<i>P. boehmeriae</i>	P	45F9	291.29				180614	P10725		A	<i>Eucalyptus fastigata</i>	New Zealand	2004	
	<i>P. gallica</i>	NP	50A1	111474					P6950		T	<i>Boehmeria nivea</i>	Taiwan	1927	(Sawada 1927)
									P16826						
	<i>P. gondwanensis</i>	P	61D5 22G7	111475		MYA-3893			P16827		A	<i>Phragmites australis</i>	Germany	2004	(Crous <i>et al.</i> 2015)
												n.a.	Ohio, USA	n.a.	
<i>P. intercalaris</i>	NP	45B7 48A1	140632	TSD-7						T	Stream water	Virginia, USA	2007	(Yang <i>et al.</i> 2016)	
<i>P. kernoviae</i>	P	49A7 46C8	140631							A	Stream water	Virginia, USA	2009		
<i>P. morindae</i>	P	46J6 46J8	121982					P10956		p390	<i>Rhododendron ponticum</i>	England, UK	2004	(Brasier <i>et al.</i> 2005)	
n.a.	<u><i>P. sp. boehmeriae-like</i></u>	P	45F8	357.52	60173					A	<i>Annona cherimola</i>	New Zealand	2002		
outgroup	<i>P. lillii</i>	NP	135746					P10681		T	Soil	New Zealand	2003		
								P10671							
outgroup	<i>Elongisporangium undulatum</i>	P	101728							T	<i>Morinda citrifolia</i> var. <i>citrifolia</i>	Hawaii, USA	2005	(Nelson & Abad 2010)	
outgroup	<i>Phytophthora vexans</i>	P	340.49	12194						T	<i>Citrus sinensis</i>	Argentina	1939	n.a.	
outgroup	<i>Halophytophthora fluviatilis</i>	P	57A9		MYA-4961					T	<i>Lilium</i> sp.	Japan	1987	(Rahman <i>et al.</i> 2015)	
outgroup	<i>Phytophthora vexans</i>	P	340.49	12194						T	<i>Larix</i> sp.	Scotland, UK	1989	(Uzuhashi <i>et al.</i> 2010)	
outgroup	<i>Phytophthora vexans</i>	P	340.49	12194						T	n.a.	n.a.	n.a.	(de Cock <i>et al.</i> 2015)	
outgroup	<i>Halophytophthora fluviatilis</i>	P	57A9		MYA-4961					T	Stream water	Virginia, USA	2011	(Yang & Hong 2014)	

<sup>a</sup> Molecular (sub)clade as designated in Fig. 1

<sup>b</sup> Names of taxa informally designated for the first time in this study are underlined.

<sup>c</sup> Sporangial papillation: NP = non-papillate, P = papillate, and SP = semi-papillate.

<sup>d</sup> Isolate identification abbreviations: CH, Chuanxue Hong laboratory at Virginia Polytechnic Institute and State University, Virginia Beach, VA, USA; CBS, Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; ATCC, American Type Culture Collection, Manassas, VA, USA; IMI, CABI Biosciences, UK; WPC, the World Phytophthora Genetic Resource Collection at University of California, Riverside, USA; MG, Mannon E. Gallegly laboratory at West Virginia University, USA. Local identifications of respective isolates are provided in Table S1.

<sup>e</sup> Ex-types (T) or authentic (A) isolates (designated as representative isolates by the originators of the respective species).

<sup>f</sup> n.a.= not available.

**Table 2.** Numbers of species and ex-types included in phylogenies for the genus *Phytophthora* in previous studies and this study.

Phylogeny in	Number of species		Number of ex-types
	Formal	Provisional	
Cooke <i>et al.</i> (2000)	49	2	9
Kroon <i>et al.</i> (2004)	46	2	18
Blair <i>et al.</i> (2008)	72	10	16
Martin <i>et al.</i> (2014)	90	17	31
This study	142	43	114

all seven phylogenetic markers from 321 isolates were sequenced in this study. Sequences of all markers from 49 isolates by Blair *et al.* (2008) were also included in the analyses. Additionally, for seven isolates, sequences of one or two genes were newly produced in this study while the remaining gene sequences were from Blair *et al.* (2008). Sequences from *P. lillii* (CBS 135746) and *P. sp. ohioensis* (ST18-37) were obtained from Rahman *et al.* (2015) and from the Phytophthora Database (Park *et al.* 2013), respectively.

### Phylogenetic analyses

Concatenated sequences of all isolates were aligned using Clustal X version 2.1 (Larkin *et al.* 2007). The alignment was edited in BioEdit version 7.2.5 (Hall 1999) to trim aligned concatenated sequences to an equal size and set missing data to question marks. The edited alignment was then analyzed in jModelTest version 2.1.7 (Posada 2008) to select the most appropriate model for the following phylogenetic analyses. Maximum likelihood (ML) analysis was performed using RAxML version 8.2.0 (Stamatakis 2014) with the selected model and 1000 bootstrap replicates. Maximum parsimony (MP) analysis was conducted using PAUP version 4.0a147 (Swofford 2002) with 1000 bootstrap replicates. Bayesian analysis (BA) was performed using MrBayes version 3.2.6 (Ronquist *et al.* 2012) for two million generations with the selected model. Phylogenetic trees were viewed and edited in FigTree version 1.4.2. Alignment and phylogenetic trees from all methods have been deposited in TreeBASE (S19303).

### Ancestral character state reconstructions of sporangial papillation

Information on the sporangial papillation of individual species was compiled from the literature (Erwin & Ribeiro 1996, Gallegly & Hong 2008, Kroon *et al.* 2012, Martin *et al.* 2012) with emphasis given to their respective original descriptions (Table 1). Both likelihood and parsimony ancestral state reconstructions were performed on the ML tree from the phylogenetic analyses using Mesquite version 3.03 (Maddison & Maddison 2017).

## RESULTS

### Sequences, alignment, and phylogenetic model

PCR amplification and sequencing was successful for almost all isolates and seven genetic markers. Failure to obtain sequences only occurred occasionally for a few isolates,

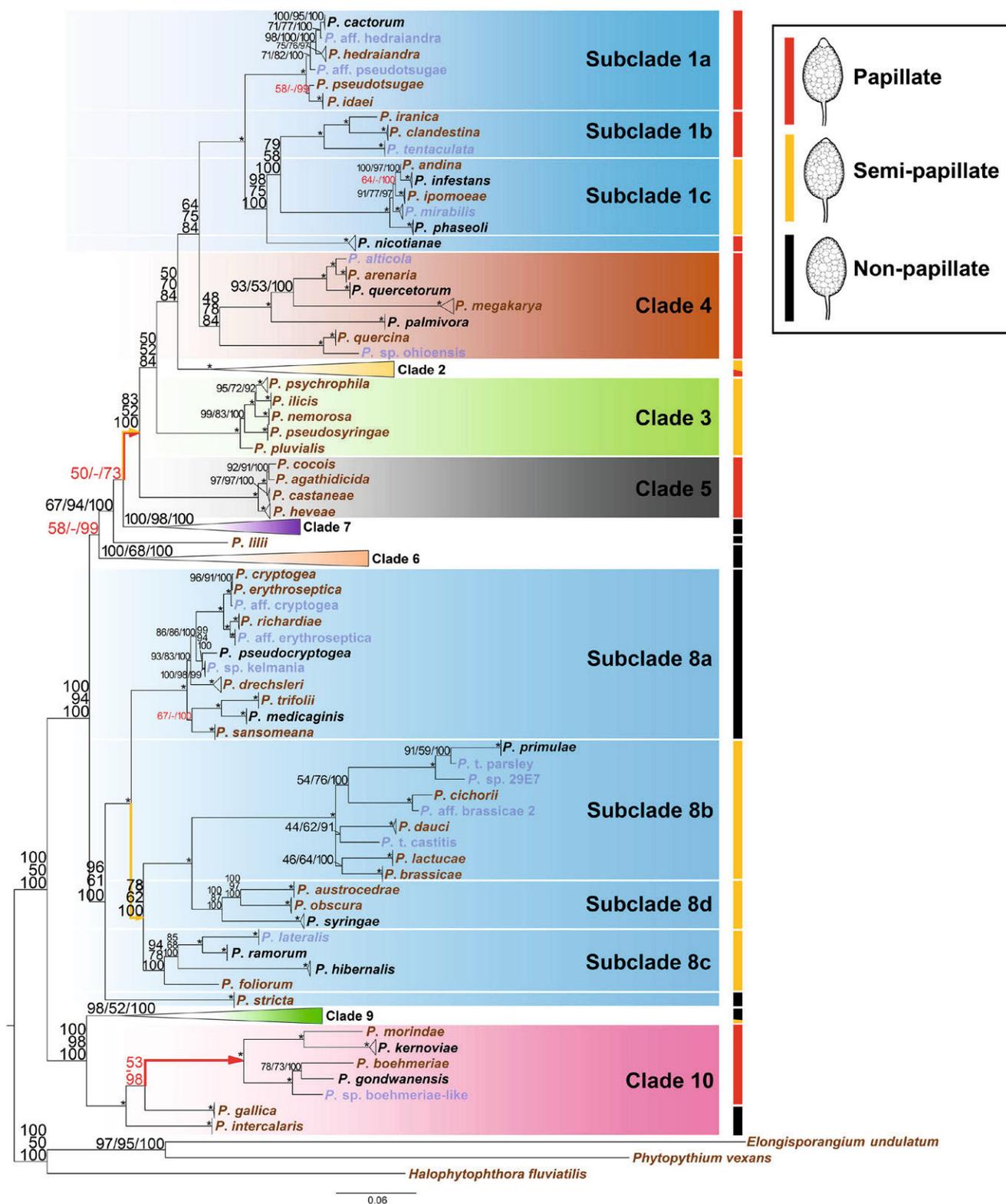
such as the EF1 $\alpha$  gene of *Phytophthora bilobang* (61G8), the Enl gene of *P. macrochlamyospora* (33E1, 31E9, and 33D5), and *P. quininea* (45F2), and TigA of *P. megasperma* (62C7) (Supplementary Table 1). These failures were set as missing data in the alignment. After trimming, each isolate was represented by an 8435-bp concatenated sequence in the alignment including gaps and missing data. This included 496 bp for 60S, 1136 bp for Btub, 965 bp for EF1 $\alpha$ , 1169 bp for Enl, 1758 bp for HSP90, 1270 bp for 28S, and 1641 bp for TigA (TreeBASE S19303). The general time reversible nucleotide substitution model with gamma-distributed rate variation and a proportion of invariable sites (GTR+I+G) was identified by jModelTest as the most appropriate model for the phylogenetic analyses.

### An expanded phylogeny including 10 clades and basal taxa

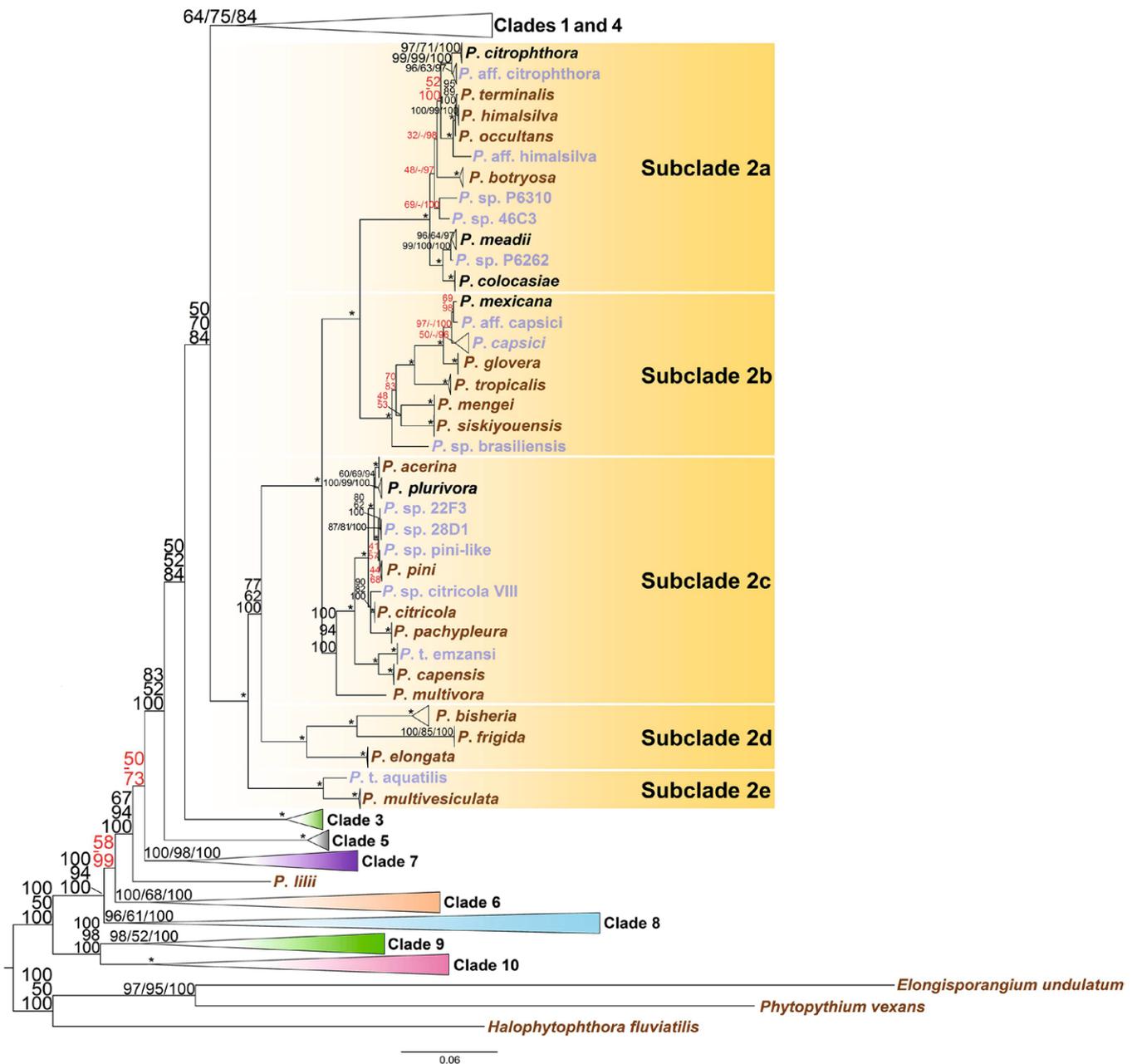
The three phylogenetic analysis methods, including ML, MP, and BA analyses (TreeBASE S19303), resulted in similar tree topologies. The topology and branch lengths of the ML inference are shown in Fig. 1. The monophyly of each of the previously recognized 10 clades was generally well supported with a few exceptions. Specifically, all clades except for clade 4 were highly supported by > 95 % bootstrap values in ML analysis and 100 % posterior probability (PP) in BA analysis (Fig. 1). Clades 1–3, 5, 7, and 10 were also highly supported by > 95 % bootstrap values in the MP analysis (Fig. 1). However, clades 6, 8, and 9, were only moderately supported with bootstrap numbers of 68, 61, and 52 in the MP analysis, respectively (Fig. 1).

As nearly half of all taxa included in this phylogeny were recently described, all clades in this phylogeny are expanded here to various extents compared to previously published phylogenies. The general structure of clades 1, 3, 5, 8 and 10 remained as previously assigned by Blair *et al.* (2008) and Martin *et al.* (2014) with additions of new species. For example, clade 1 was divided into three well-supported subclades and *P. nicotianae* was placed basal to subclades 1b and 1c (Fig. 1). Clade 8 was divided into four generally well-supported subclades, except *P. stricta*, which was placed basal to all clade 8 species (Fig. 1). New subclades were assigned to clade 2 (Fig. 2), clade 6 (Fig. 3), clade 7 (Fig. 4) and clade 9 (Fig. 5).

Several species were placed basal to other species in their respective clades. First, the cluster of *P. quercina* and *P. sp. ohioensis* was placed basal to other species of clade 4 in all three analyses. The bootstrap supports of the ML and MP analyses, and PP (percentage) for the separation of this cluster from that of *P. alticola*, *P. arenaria*, *P. megakarya*, *P. palmivora*, and *P. quercetorum* in clade 4 were only 48, 78, and 84, respectively (Fig. 1). Second, *P. lillii* was excluded from all known clades; it was placed basal to clades 1–5 and 7 (Fig. 1). Third, in clade 6, bootstrap support for the ML and MP analyses, and PP for all species except *P. asparagi* and *P. sp. sulawesiensis* were 100/100/100 (Fig. 3). This set of support numbers decreased to 99/92/100 when *P. sp. sulawesiensis* was included, and to 100/68/100 when further including *P. asparagi* (Fig. 3). Fourth, the support numbers for clade 8 species excluding *P. stricta* was 100/100/100, but 96/61/100 when *P. stricta* was included (Fig. 1). Fifth,



**Fig. 1.** A phylogeny for the genus *Phytophthora* based on concatenated sequences of seven nuclear genetic markers. Topology and branch lengths of maximum likelihood analysis are shown. Bootstrap values for maximum likelihood and maximum parsimony, and Bayesian posterior probabilities (percentages) are indicated on individual nodes and separated by a forward slash. An asterisk is used in place of nodes with unambiguous (100 %) support in all three analyses. A dash is used in place of a topology from an analysis ambiguous to the other two analyses and these sets of numbers with ambiguity in one analysis are also highlighted in red. Detailed structures of clades 2, 6, 7, and 9 are shown in Figs 2–5, respectively. Species represented by ex-types and authentic isolates are written in brown and blue, respectively. Branches indicating three hypothesized evolutionary paths with all species producing papillate or semi-papillate sporangia are drawn in red or orange, respectively. Scale bar indicates number of substitutions per site.



**Fig. 2.** Structure of *Phytophthora* clade 2 in a genus-wide phylogeny for the genus *Phytophthora* based on concatenated sequences of seven nuclear genetic markers. Topology and branch lengths of maximum likelihood analysis are shown. Bootstrap values for maximum likelihood and maximum parsimony, and Bayesian posterior probabilities (percentages) are indicated on individual nodes and separated by a forward slash. An asterisk is used in place of nodes with unambiguous (100 %) support in all three analyses. A dash is used in place of a topology from an analysis ambiguous to the other two analyses and these sets of numbers with ambiguity in one analysis are also highlighted in red. Species represented by ex-types and authentic isolates are written in brown and blue, respectively. Scale bar indicates number of substitutions per site.

all papillate species in clade 10 (Table 1) formed a well-supported main cluster, while two more recently described non-papillate species, *P. gallica* and *P. intercalaris*, were placed basal to the main cluster (Fig. 1).

### New subclades in clades 2, 6, 7, and 9

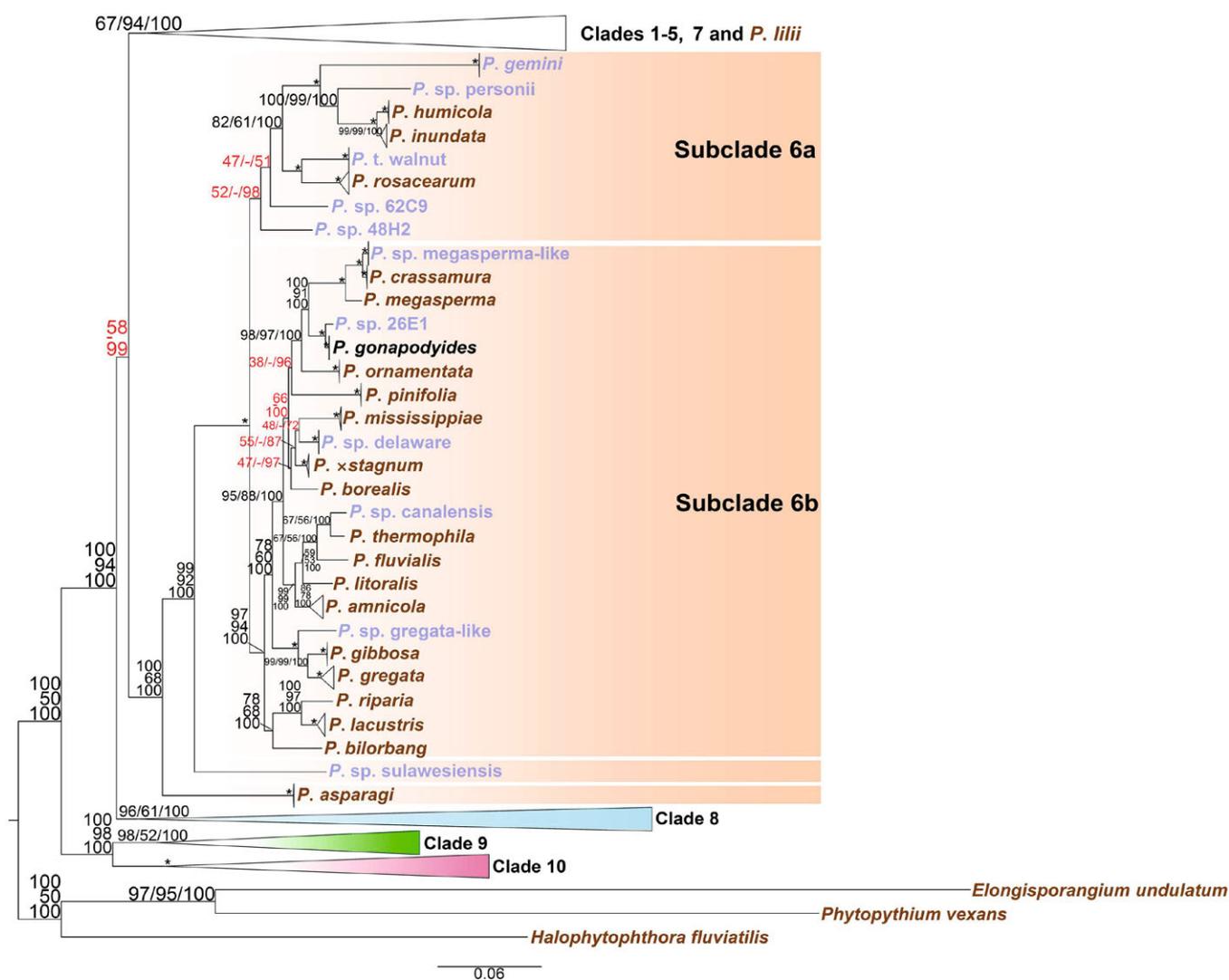
#### (a) Clade 2

In addition to the previously recognized subclades 2a and 2b, many species, such as *P. acerina*, *P. capensis*, *P. citricola*, *P. multivora*, *P. pachypleura*, *P. plurivora*, and *P. pini* in the commonly referred to “*Phytophthora citricola*-complex”

defined a new subclade 2c (Fig. 2). Furthermore, *P. bisheria*, *P. frigida*, and *P. elongata* formed new subclade 2d and the cluster of *P. multivesiculata* and *P. taxon aquatilis* formed new subclade 2e, with maximum support values in each case (Fig. 2).

#### (b) Clade 6

Subclade 6a included *P. gemini*, *P. humicola*, *P. inundata*, *P. rosacearum*, *P. sp. personii*, *P. sp. 48H2*, *P. sp. 62C9* and *P. taxon walnut*. The cluster of *P. rosacearum* and *P. taxon walnut* could not be separated from that represented by *P. gemini* with only moderate support values for separation



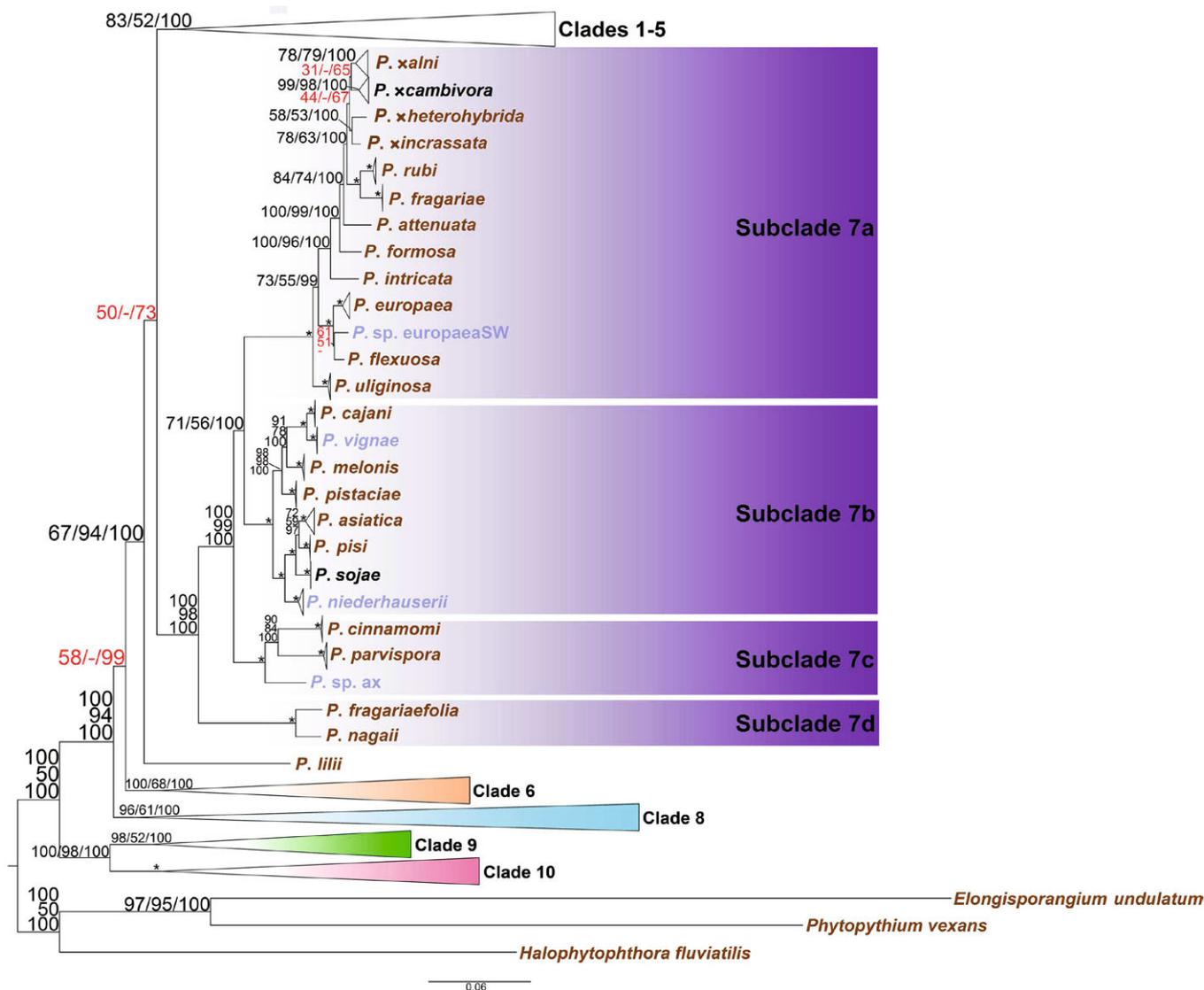
**Fig. 3.** Structure of *Phytophthora* clade 6 in a genus-wide phylogeny for the genus *Phytophthora* based on concatenated sequences of seven nuclear genetic markers. Topology and branch lengths of maximum likelihood analysis are shown. Bootstrap values for maximum likelihood and maximum parsimony, and Bayesian posterior probabilities (percentages) are indicated on individual nodes and separated by a forward slash. An asterisk is used in place of nodes with unambiguous (100 %) support in all three analyses. A dash is used in place of a topology from an analysis ambiguous to the other two analyses and these sets of numbers with ambiguity in one analysis are also highlighted in red. Species represented by ex-types and authentic isolates are written in brown and blue, respectively. Scale bar indicates number of substitutions per site.

(82/61/100) (Fig. 3). Isolates 62C9 and 48H2, belonging to two new species, had ambiguous placements within subclade 6a among the three analyses (Fig. 3). With approximately 20 species newly included in the present phylogeny, the previously recognized “*P. megasperma*-*P. gonapodyides* complex” (Brasier *et al.* 2003a), subclade II of clade 6 (Jung *et al.* 2011), or subclade 6b (Kroon *et al.* 2012) expanded and its separation from subclade 6a was well-supported by 100/100/100 values (Fig. 3). Within subclade 6b, separation of the cluster of *P. bilorbang*, *P. lacustris*, and *P. riparia* from the other subclade 6b species was highly supported by 97/94/100 (Fig. 3), indicating that these three species may define a new subclade, although this is not done in this study. *Phytophthora* sp. *sulawesiensis* was placed basal to other clade 6 species except for *P. asparagi*, while *P. asparagi* was basal to all other species in clade 6 (Fig. 3). *Phytophthora asparagi* was previously assigned as subclade 6c (Kroon *et al.* 2012) and subclade III of clade 6 (Jung *et al.* 2011);

considering that the support value of MP analysis was only moderate (68 %) when this single taxon was included (Fig. 3), this previous assignment as a subclade was not adopted here. In addition, in order to be consistent with subclade names in other clades, subclades 6a and 6b were used here instead of subclades I and II by Jung *et al.* (2011).

### (c) Clade 7

Four subclades were distinguished in clade 7. Separation of the previously assigned subclades 7a and 7b was only moderately supported by values 71/56/100 (Fig. 4). The general structure of subclade 7a remained the same even with the addition of seven new taxa. Six of these new species, including *P. attenuata*, *P. flexuosa*, *P. formosa*, *P. intricata*, *P. xheterohybrida*, and *P. xincrassata* were recently recovered from forest soils and streamwater in Taiwan (Jung *et al.* 2017). On the other hand, *P. cinnamomi* and *P. parvispora* were separated from subclade 7b. They,



**Fig. 4.** Structure of *Phytophthora* clade 7 in a genus-wide phylogeny for the genus *Phytophthora* based on concatenated sequences of seven nuclear genetic markers. Topology and branch lengths of maximum likelihood analysis are shown. Bootstrap values for maximum likelihood and maximum parsimony, and Bayesian posterior probabilities (percentages) are indicated on individual nodes and separated by a forward slash. An asterisk is used in place of nodes with unambiguous (100 %) support in all three analyses. A dash is used in place of a topology from an analysis ambiguous to the other two analyses and these sets of numbers with ambiguity in one analysis are also highlighted in red. Species represented by ex-types and authentic isolates are written in brown and blue, respectively. Scale bar indicates number of substitutions per site.

along with a provisional species, *P. sp. ax* from Virginia, USA (Table 1), formed a distinct new subclade 7c (Fig. 4). The new subclade 7d, including two recently described species from Japan (Rahman *et al.* 2014b), *P. fragariaefolia* and *P. nagaii*, was placed basal to other subclades in clade 7 (Fig. 4).

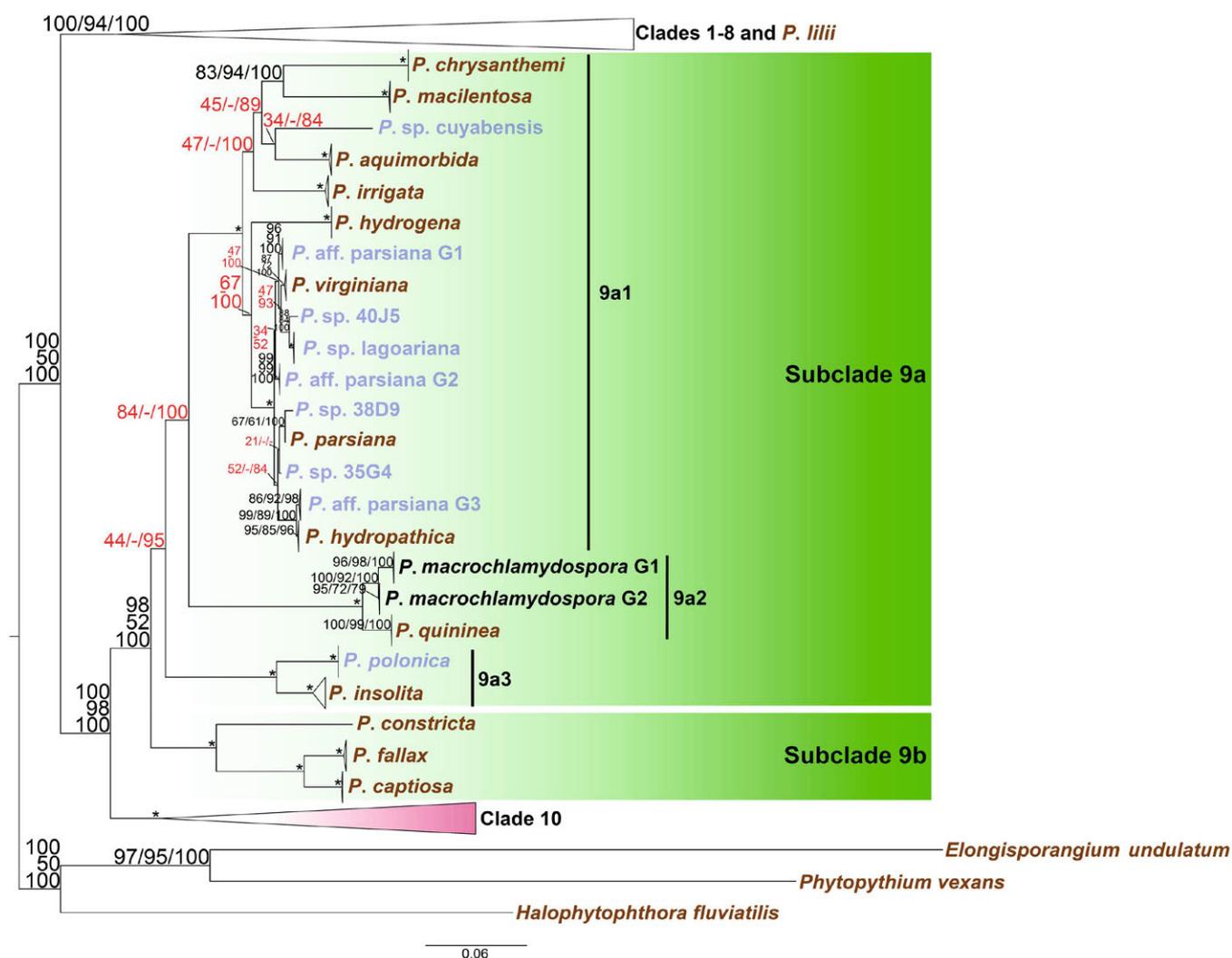
#### (d) Clade 9

The split of clade 9 into two subclades 9a and 9b was highly supported in ML (98 %) and BA (100 %) analyses and moderately supported in the MP (52 %) analysis (Fig. 5). However, monophyly was highly supported for subclade 9b (100/100/100) but not for subclade 9a (44/-/95) (Fig. 5). Within subclade 9a, three monophyletic clusters were formed: 9a1, 9a2, and 9a3. However, support for the separation of these three clusters was moderate or ambiguous. In particular, the MP results did not produce any consistent separation of the three clusters (Fig. 5). Cluster 9a1 included many

recently described high-temperature tolerant species, such as *P. aquimorbida*, *P. chrysanthemi*, *P. hydropathica*, *P. macilentosa*, *P. parsiana*, and *P. virginiana*). The cluster of *P. macrochlamydospora* (two lineages with two isolates in each lineage, Table 1) and *P. quininea* constituted 9a2 (Fig. 5). The cluster of two other high-temperature tolerant species *P. insolita* and *P. polonica* constituted 9a3 (Fig. 5). The well-supported cluster of *P. captiosa*, *P. constricta*, and *P. fallax* was assigned as subclade 9b (Fig. 5).

#### Evolutionary history of sporangial papillation inferred from ancestral character state reconstructions

Sporangial papillation of individual species is indicated in Table 1 and Fig. 6. Due to the size of the cladograms, clusters including species with the same sporangial papillation within each (sub)clade were compressed in Mesquite. Both



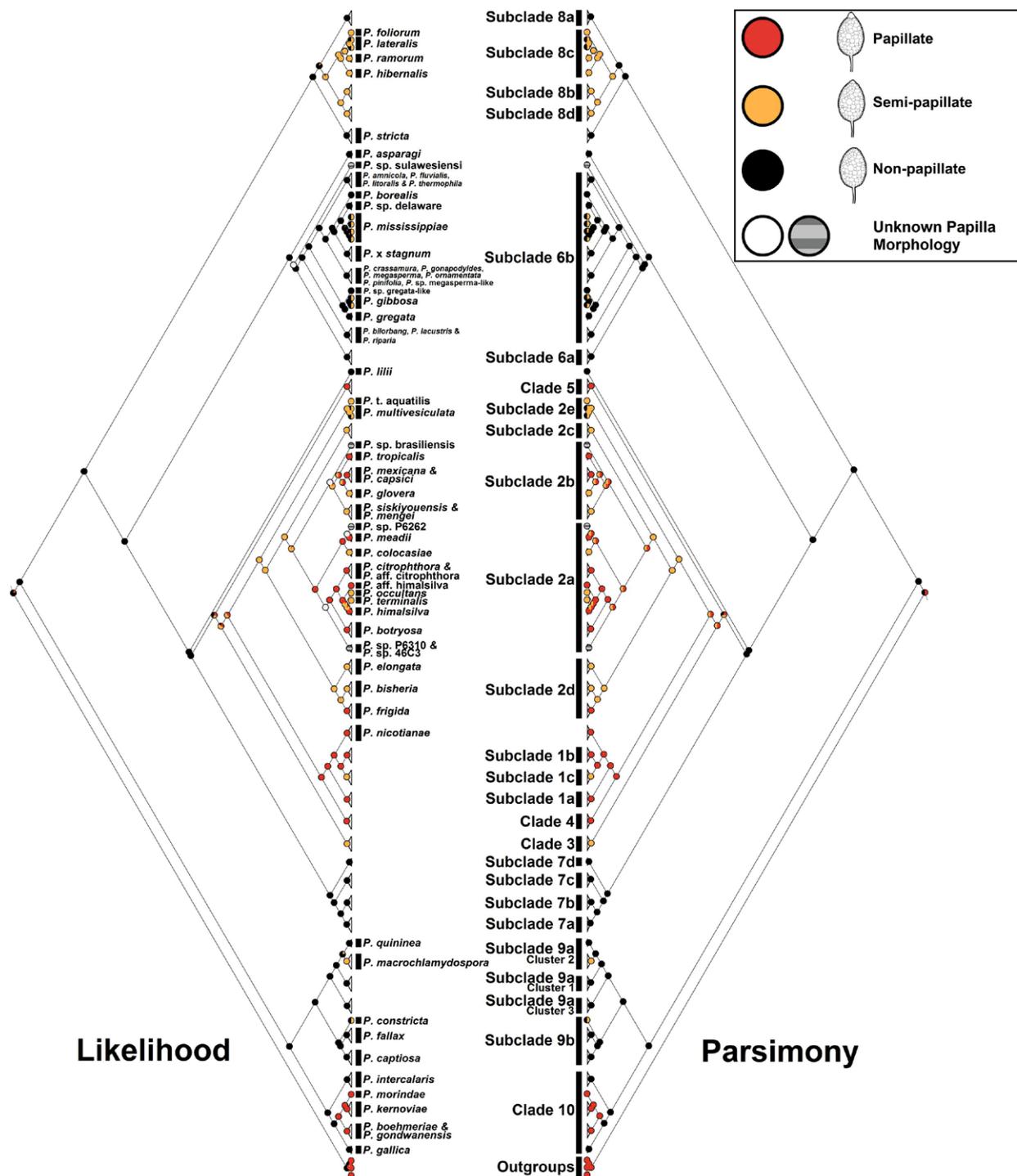
**Fig. 5.** Structure of *Phytophthora* clade 9 in a genus-wide phylogeny for the genus *Phytophthora* based on concatenated sequences of seven nuclear genetic markers. Topology and branch lengths of maximum likelihood analysis are shown. Bootstrap values for maximum likelihood and maximum parsimony, and Bayesian posterior probabilities (percentages) are indicated on individual nodes and separated by a forward slash. An asterisk is used in place of nodes with unambiguous (100 %) support in all three analyses. A dash is used in place of a topology from an analysis ambiguous to the other two analyses and these sets of numbers with ambiguity in one analysis are also highlighted in red. Species represented by ex-types and authentic isolates are written in brown and blue, respectively. Scale bar indicates number of substitutions per site.

likelihood and parsimony methods suggested that non-papillate is the progenitor state of *Phytophthora* species, and that semi-papillate and papillate types were derived from the non-papillate. The analyses indicated three major clusters of semi-papillate and (or) papillate species diverged from the non-papillate ancestors. First, species in clades 1 to 5 (semi-papillate or papillate) diverged from non-papillate species in clade 7 and *P. lillii* (Fig. 6). Second, species in subclades 8b to 8d (semi-papillate) diverged from non-papillate subclade 8a species (Fig. 6). Third, papillate clade 10 species including *P. boehmeriae*, *P. gondwanensis*, *P. kernoviae*, and *P. morindae* diverged from the non-papillate *P. gallica* and *P. intercalaris* (Fig. 6). Several species such as *P. macrochlamydospora*, *P. mississippiiae*, *P. gibbosa*, and *P. constricta* also evolved to produce partially semi-papillate sporangia (Fig. 6).

## DISCUSSION

Here we presented an expanded phylogeny for the genus *Phytophthora*, encompassing 142 formally named and 43 provisionally recognized species (Table 2). In addition to this comprehensive coverage, this expanded phylogeny features over 1500 signature sequences generated from 278 ex-type and authentic isolates of 162 *Phytophthora* taxa (Supplementary Table 1). Furthermore, this study provided new insights into the evolutionary history of sporangial papillation in *Phytophthora*.

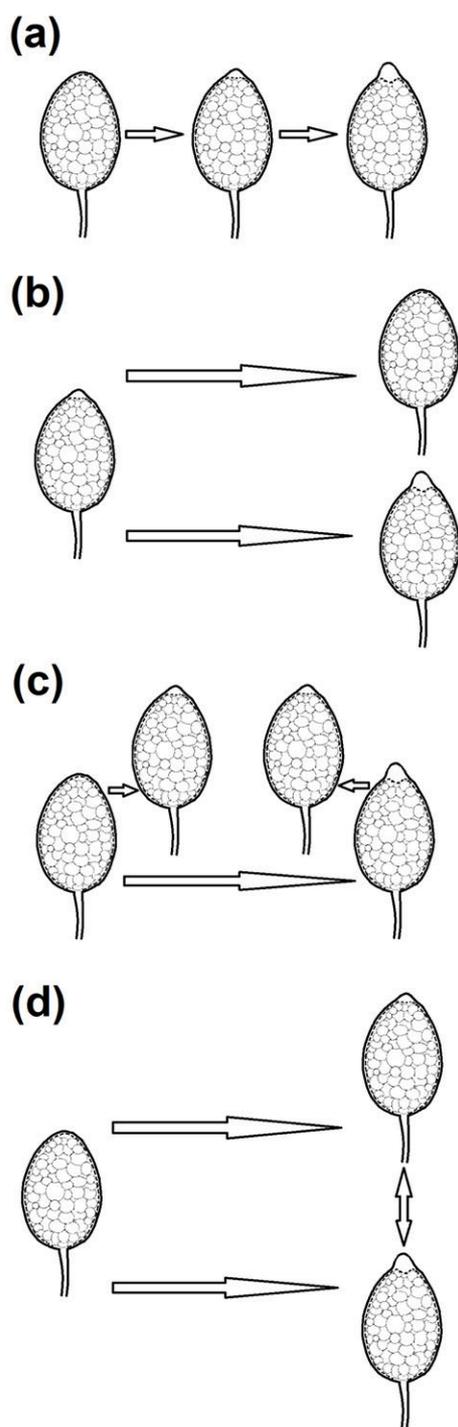
The expanded phylogeny provides a sound taxonomic framework for this agriculturally and ecologically important genus. One hundred and fourteen ex-types were included, representing 80 % of the 142 formally named species in this phylogeny. The majority of the 29 species not represented by ex-types, such as *P. gonapodyides*, *P. infestans*, *P. meadii*, *P. mexicana*, and *P. nicotianae*, were described long ago without



**Fig. 6.** Ancestral state reconstructions of sporangial papillation for the genus *Phytophthora* based on likelihood (left cladogram) and parsimony (right cladogram). Trace character history analyses were performed on the maximum likelihood phylogeny in Mesquite. Clusters including species of uniform sporangial papillation within individual (sub)clades were compressed in Mesquite.

designation of an ex-type culture. Likewise, almost all the 43 provisional species in this phylogeny were represented by authentic isolates from the originators of the respective species (Table 1 and Supplementary Table 1). This new framework will facilitate identification of new taxa in the future. As the genus continues to rapidly expand, some recently described species were not included in this study: *P. mekongensis* in subclade 2a (Puglisi et al. 2017), *P. amaranthi* in subclade 2b (Ann et al. 2016), *P. boodjera* in clade 4 (Simamora et al. 2015), *P. chlamydospora* in subclade 6b (Hansen et al.

2015), *P. uniformis* (basynonym: *P. alni* subsp. *uniformis*) and *P. ×multiformis* (basynonym: *P. alni* subsp. *multiformis*) in subclade 7a (Brasier et al. 2004, Husson et al. 2015), *P. pseudolactucaea* in subclade 8b (Rahman et al. 2015), and *P. prodigiosa* (Puglisi et al. 2017) and *P. pseudopolonica* (Li et al. 2017) in subclade 9a. Likewise, some informally designated species also were not included: such as *P. taxon humicola*-like, *P. taxon kwongan*, and *P. taxon rosacearum*-like in subclade 6a (Jung et al. 2011). These and other emerging species are yet to be incorporated in the overall phylogeny of the genus.



**Fig. 7.** Illustration of hypotheses on evolution of *Phytophthora* and associated changes in sporangial papillation: (a) species producing papillate sporangia evolved from non-papillate ancestors. Semi-papillation is considered as intermediate between non-papillation and papillation (Blackwell 1949, Cooke *et al.* 2000, Erwin & Ribeiro 1996); (b) some semi-papillate species, exemplified by *P. primulae* in the group III of Waterhouse (1963), are primitive and evolved to be non-papillate and papillate through two evolutionary paths, by Brasier (1983); (c) papillate species evolved from non-papillate ancestors. Semi-papillate species have been considered as morphological variants of papillate or non-papillate species, by Cooke *et al.* (2000); (d) a new hypothesis developed in this study that non-papillate ancestors evolved directly to either papillate or semi-papillate species. Some semi-papillate species further evolved to be papillate, or vice versa.

The generation of over 1500 signature sequences from ex-types and authentic isolates in this study will aid researchers and first responders in correctly identifying *Phytophthora* cultures to the species level. DNA sequencing of selected genetic markers has become common practice in the identification of *Phytophthora* cultures (Kang *et al.* 2010). However, it is recognized that the accuracy of culture identity determined by this approach depends on the quality of the reference sequences used – and currently many sequence deposits are erroneously identified in public repositories, including GenBank (Kang *et al.* 2010). These errors originated in sequence deposits of cultures that were identified by morphological characters alone, and compounded by those identified through sequence matches to erroneous reference sequences or by single DNA markers (Kang *et al.* 2010). In this study, 29 isolates were found associated with an erroneous or modified identity (Supplementary Table 2). For instance, isolate 29B3 in clade 1 was identified as *P. pseudotsugae* and used as a key isolate for this species by Gallegly & Hong (2008). However, its sequences were distinct from those of the *P. pseudotsugae* ex-type (ATCC 52938). In the phylogenetic tree, it was basal to the cluster of *P. cactorum* and *P. hedraiaandra*, thus its species identity was changed to *P. aff. pseudotsugae* (Fig. 1). In clade 2, isolate 26H4 was identified as *P. citrophthora* (Gallegly & Hong 2008) but sequences and phylogeny showed that it was close to but distinct from *P. citrophthora* isolates 03E5 and 26H3. It formed a cluster with isolate IMI 342898 (P10341), which was coded as *P. sp. aff. colocasiae-1* by Martin *et al.* (2014). The identity of both isolates was then changed to *P. aff. citrophthora* (Fig. 2). Similarly, in clade 8, isolate 22G2 had been identified as *P. cryptogea*, although it was distinct from the *P. cryptogea* ex-type 61H9 (CBS 113.19). In the phylogenetic tree, it was basal to the cluster of *P. cryptogea* and *P. erythroseptica*, and the species identity was consequently changed to *P. aff. cryptogea* (Fig. 1). Changes in the identifications of these isolates, including the new and original names used, are indicated in Supplementary Table 2. The changes in the naming of these isolates highlights the importance of using signature sequences from ex-type or authentic isolates as references in future culture identification. In order to facilitate this practice, the signature sequences generated from ex-types or authentic isolates in the present study are marked as '(ex-type)' or '(authentic)', respectively, under the 'isolate' section in the 'feature' table of GenBank deposits. The research, diagnostic and regulatory communities are encouraged to use these sequences as references in future culture identification.

This study provided new insights into the evolutionary history of sporangial morphology in the genus *Phytophthora*, a subject that has fascinated generations of mycologists and plant pathologists. There have been three major hypotheses regarding the development of papillation, as illustrated in Fig. 7a, b, and c, respectively. First, papillate species were considered as descendants of *Pythium*-like, non-papillate ancestors and semi-papillation has been considered as intermediate between non-papillation and papillation (Blackwell 1949, Cooke *et al.* 2000, Erwin & Ribeiro 1996). Second, some semi-papillate species, exemplified by *P. primulae* in the group III of Waterhouse (1963) are

primitive; they were suggested to have evolved to papillate and non-papillate species through two distinct evolutionary lines (Brasier 1983). Third, semi-papillate sporangia are morphological variants of papillate and non-papillate types (Cooke *et al.* 2000). Here we suggest that the non-papillate type is ancestral, and that non-papillate species could have evolved directly into either semi-papillate or papillate species (Fig. 7d). The evolution to semi-papillate species is exemplified by those in subclades 8b–d (Fig. 1), while evolution to papillate species is illustrated by *P. boehmeriae* and other papillate species in clade 10 (Fig. 1). The relationship between semi-papillate and papillate species appears to be more complicated (Fig. 7d). We also hypothesize that some semi-papillate species, such as those in subclade 1c, may have diverged from papillate ancestors, while some papillate species such as *P. frigida* may have evolved from semi-papillate ancestors of subclade 2d (Fig. 6).

These new hypotheses are supported by the results from phylogeny and ancestral state reconstructions that suggest three major evolutionary paths in sporangial papillation of *Phytophthora* species (Fig. 1). First, the ancestor of modern species in clades 1–5 evolved to be papillate or semi-papillate (Figs 1, 6) while diverging from the common non-papillate ancestor of clade 7 species (Figs 1, 6). Second, the common ancestor of species in subclades 8b–d diverged from that of subclade 8a species while acquiring semi-papillation (Figs 1, 6). Third, the common ancestor of five clade 10 species in the main cluster including *P. boehmeriae*, *P. gondwanensis*, *P. kernoviae*, *P. morindae*, and *P. sp. boehmeriae*-like, acquired papillate sporangia while diverging from two non-papillate clade 10 species, *P. gallica* and *P. intercalaris* (Figs 1, 6). Besides these three major groups of papillate or semi-papillate species, a few species may have evolved to acquire semi-papillation independently, such as *P. macrochlamydospora* in clade 9 (Fig. 6). This evolutionary process may be underway for some other species including *P. constricta*, *P. gibbosa*, and *P. mississippiiae*, which all produce both semi-papillate and non-papillate sporangia (Fig. 6). Furthermore, evolutionary reversion to partial production of non-papillate sporangia may have occurred in *P. multivesiculata* and *P. lateralis* in two semi-papillate subclades 2e and 8c, respectively (Fig. 6). However, that conclusion is uncertain due to limited and ambiguous data from species in these two subclades. Specifically, *P. lateralis* was ambiguously reported as non-papillate (Erwin & Ribeiro 1996, Gallegly & Hong 2008, Martin *et al.* 2012, Tucker & Milbrath 1942) or non- to semi-papillate (Kroon *et al.* 2012) in different studies. In subclade 2e, the only sister taxon of *P. multivesiculata*, *P. taxon aquatilis*, was provisionally described as semi-papillate, but only based on a single isolate (Hong *et al.* 2012). Evolutionary reversion in the sporangial papillation of these two species requires validation in the future. Also, more studies are warranted to analyze additional characters based on phylogenies with better clade-to-clade resolutions and provide a more comprehensive picture on the evolutionary history of *Phytophthora* species.

That a number of species were placed basal to other species in their respective clades in this expanded phylogeny presents a significant challenge to the monophyly of their

respective clades and the current 10-clade system. First, *P. stricta* was initially placed close to other species in subclade 8a based on sequences of the cytochrome *c* oxidase 1 (*cox1*) gene, but was not grouped in any ITS clade (Yang *et al.* 2014a). This species was grouped in clade 8 in our expanded phylogeny by ML and BA analyses (Fig. 1); the monophyly of this clade was only moderately supported (61 %) in the MP analysis (Fig. 1). Second, the monophyly of clade 6 including *P. asparagi* was only moderately supported (68 %) in the MP analysis (Fig. 3). Third, although the inclusion of *P. intercalaris* in clade 10 was supported with maximum values, the exact positions of this species and *P. gallica* were still unresolved since the next node was only moderately supported (53 %) in the ML analysis and ambiguous in the MP analysis (Fig. 1). Fourth, similar to the finding of Blair *et al.* (2008), support for the monophyly of clade 4 including *P. quercina* and *P. sp. ohioensis* was only moderate (48/78/84). Also, similar ambiguity in the placement of the '*P. quercina* – *P. sp. ohioensis*' cluster was observed among different phylogenetic approaches, and using different datasets including nuclear, mitochondrial, and combined nuclear and mitochondrial sequences (Martin *et al.* 2014). Fifth, this phylogeny confirmed the finding by Rahman *et al.* (2015) that *P. lillii* was not grouped in any clade of the current 10-clade system (Fig. 1). This species was not assigned as a distinct clade in our study, due to the relatively low clade-to-clade resolutions (Fig. 1). Further analyses are warranted to determine whether this unique species should be assigned as a new clade.

Although many branches in the expanded phylogeny have consistent maximum support in all three methods, some have only moderate to low or inconsistent support. These results highlight the challenges of correctly inferring the evolutionary separation of many closely related *Phytophthora* species, even when concatenated sequences from seven phylogenetic markers were used. It can be expected that as the cost of gene sequencing drops further, it will become possible to increase phylogenetic resolution among *Phytophthora* species by using concatenations of much larger numbers of genes. For example, Ye *et al.* (2016) used 293 concatenated housekeeping proteins to infer a robust phylogeny of seven fully sequenced *Phytophthora* species and confirmed that downy mildews (represented by three genome sequences) are nested within the genus *Phytophthora*, close to *Phytophthora* clade 4 (Ye *et al.* 2016). However, even with full genome sequences, ambiguity may not be completely resolved in cases where speciation has involved large populations of sexually reproducing individuals, for example, as a result of geographic separation. In these cases, there may be many sequence polymorphisms shared among separated species and these may confound the inference of a reliable phylogeny. Resolution of this level of ambiguity may require sequencing the whole genome of many isolates from the species of interest as well as using improved phylogenetic and coalescent methods.

With the number of described *Phytophthora* species increasing, recent studies have raised an important concern in the accurate detection of species boundaries using phylogenetic data (Jung & Burgess 2009, Pánek *et al.* 2016,

Safaiefarahani *et al.* 2015). One example is the status of *P. hedraiaandra* as a distinct species in subclade 1a (Pánek *et al.* 2016). As evidenced by the amplified fragment length polymorphism (AFLP) and phylogenetic analysis based on sequences of ITS, phenolic acid decarboxylase, and *cox1* genes, a recent study concluded that *P. hedraiaandra* was just one lineage of *P. cactorum*, while morphological data provided only limited information to delimitate these two species (Pánek *et al.* 2016). Also, phylogenetic analyses in this study indicated that *P. cactorum* and *P. hedraiaandra* cluster with strong support (98/100/100), and *P. aff. hedraiaandra* isolate 33F4 (previously identified as *P. hedraiaandra* Supplementary Table 2), was clustered with *P. cactorum* (Fig. 1). Phylogenies based on nuclear sequences prior to this study also supported *P. hedraiaandra* as closely related to *P. cactorum* (Blair *et al.* 2008, Martin *et al.* 2014). However, in the phylogenies based on concatenated sequences of four mitochondrial loci, and combined seven nuclear and four mitochondrial loci, *P. hedraiaandra* was basal to the cluster of *P. cactorum* and *P. pseudotsugae*, and clustered with *P. idaei*, respectively (Martin *et al.* 2014). *Phytophthora cactorum* and *P. hedraiaandra* also have very distinctive single-strand-conformation polymorphism patterns (Gallegly & Hong 2008). Apparently, more investigations are warranted to resolve the *P. cactorum* complex. Likewise, indistinct boundaries are present among species in other subclades, such as the '*P. citricola* complex' or subclade 2c (Brazee *et al.* 2017, Jung & Burgess 2009), the '*P. cryptogea* complex' in subclade 8a (Safaiefarahani *et al.* 2015, 2016) and cluster 9a1 in subclade 9a including *P. hydropathica* (Hong *et al.* 2010), *P. parsiana* (Mostowfizadeh-Ghalamfarsa *et al.* 2008), *P. virginiana* (Yang & Hong 2013) and other provisionally designated species. Accurately delimiting these closely related species within the genus remains an important task.

This expanded phylogeny has highlighted the importance and difficulty of accurately interpreting the position of hybrid *Phytophthora* species. As exemplified by *P. ×alni* (Brasier *et al.* 2004, Husson *et al.* 2015), many hybrid species have been identified among emerging plant pathogens (Jung *et al.* 2017, Man in't Veld *et al.* 2012, Nirenberg *et al.* 2009). Due to the presence of multiple alleles originated from parent species in their nuclear genes, phylogenetic analysis of these hybrids based on nuclear sequences alone may not produce a robust placement. As illustrated in this phylogeny, the placement of hybrid species may be ambiguous. Specifically, in subclade 6b, support values for the placement of *P. ×stagnum* and its closely related species, *P. mississippiiae*, *P. borealis*, and *P. sp. delaware* were moderate in the ML and BA analyses and ambiguous in the MP analysis (Fig. 3). Similarly, in subclade 7a, the placement of *P. ×alni*, *P. ×cambivora*, *P. ×heterohybrida*, and *P. ×incrassata* cluster was not well resolved due to ambiguous placement in the MP analysis and moderate support values in the other two analyses (Fig. 4). Adding mitochondrial sequences into the phylogenetic analyses may be a solution to this problem. However, due to the uniparental inheritance of mitochondria, the hybrids and their maternal parents are inseparable by mitochondrial sequences and their placements could conflict with nuclear analyses (Martin *et al.* 2014).

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