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REVIEW

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Current status of *Phytophthora* in Australia

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Abstract Among the most economically relevant and environmentally devastating diseases globally are those caused by *Phytophthora* species. In Australia, production losses in agriculture and forestry result from several well-known cosmopolitan *Phytophthora* species and infestation of natural ecosystems by *Phytophthora cinnamomi* have caused irretrievable loss to biodiversity especially in proteaceous dominated heathlands. For this review, all available records of *Phytophthora* in Australia were collated and curated, resulting in a database of 7 869 records, of which 2 957 have associated molecular data. Australian databases hold records for 99 species, of which 20 are undescribed. Eight species have no records linked to molecular data, and their presence in Australia is considered doubtful. The 99 species reside in 10 of the 12 clades recognised within the complete phylogeny of *Phytophthora.* The review includes discussion on each of these species' status and additional information provided for another 29 species of concern. The first species reported in Australia in 1900 was *Phytophthora infestans.* By 2000, 27 species were known, predominantly from agriculture. The significant increase in species reported in the subsequent 20 years has coincided with extensive surveys in natural ecosystems coupled with molecular taxonomy and the recognition of numerous new phylogenetically distinct but morphologically similar species. Routine and targeted surveys within Australian natural ecosystems have resulted in the description of 27 species since 2009. Due to the new species descriptions over the last 20 years, many older records have been reclassified based on molecular identification. The distribution of records is skewed toward regions with considerable activity in high productivity agriculture, horticulture and forestry, and native vegetation at risk from *P. cinnamomi.* Native and exotic hosts of different *Phytophthora* species are found throughout the phylogeny; however, species from clades 1, 7 and 8 are more likely to be associated with exotic hosts. One of the most difficult challenges to overcome when establishing a pest status is a lack of reliable data on the current state of a species in any given country or location. The database compiled here for Australia and the information provided for each species overcomes this challenge. This review will aid federal and state governments in risk assessments and trade negotiations by providing a comprehensive resource on the current status of *Phytophthora* species in Australia.

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INTRODUCTION

Plant diseases caused by *Phytophthora* species are among the most economically and environmentally devastating globally (Erwin & Ribeiro 1996, Hansen et al. 2012). In Australia, these diseases cause loss of production in pastures, annual and perennial crops, orchards, ornamental and forestry industries (Irwin et al. 1995). Due to the large number of diseases caused by many *Phytophthora* species in a wide range of different crops in different plant-based industries, the overall impact, and the annual cost to control them, is challenging to estimate. The production of several plant species relies on sustained *Phytophthora* disease management (Bradshaw et al. 2021). However, while the cost of disease control in agriculture and horticulture is high, the impact on natural ecosystems are incalculable and permanent as the impacted landscapes are forever changed. For example, ongoing impact of *P. cinnamomi* in the natural ecosystems of Australia is devastating (Cahill et al. 2008). The infestation has resulted in an irretrievable loss of biodiversity, especially in proteaceous dominated heathlands (Shearer et al.

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2004). Dieback mapping in West Australian forests and woodlands is an ongoing activity of the Department of Biodiversity Conservation and Attractions (DBCA).

Anton de Bary described the genus *Phytophthora* in 1886, and the type isolate of the species, *Phytophthora infestans*, was the causal agent of the potato famine in the mid-19th century. Over the next 110 years, approximately 60 additional species were recognised, most of which caused diseases on cultivated plant species of economic importance (Erwin & Ribeiro 1996). Most of these species have global distributions. With limited morphological features, there were several attempts to produce tabular keys to distinguish species. The Waterhouse (1963) classification divided *Phytophthora* into six groups depending on whether the sporangia were papillate, semi-papillate or non-papillate, and whether the antheridial attachment was amphigynous or paragynous. Additional features, such as colony morphology, sporangiophore branching, the presence of hyphal swellings and chlamydospores, caducity of sporangia, the size and shape of sporangia and oogonia, colour, ornamentation, cardinal temperatures and host preferences, were used for species differentiation (Erwin & Ribeiro 1996). The seminal paper by Cooke et al. (2000) on the molecular phylogeny of *Phytophthora* based on the ITS sequence divided the genus into eight phylogenetic clades. These clades have remained robust as additional nuclear and mitochondrial genes have been added into the phylogenies (Blair et al. 2008, Martin et al. 2014, Robideau et al. 2011, Yang et al. 2017), although, through the inclusion of basal species, the number of recognised clades in these later manuscripts increased to 10. Molecular systematics led to the description of numerous new taxa, many of which were morphologically indistinct but phylogenetically distant (Brasier et al. 2003a, Burgess et al. 2009). While historically new species recovery and descriptions were from agricultural settings, since 2000 most new species have been from natural ecosystems. Except for a few species causing unique disease symptoms (such as *P. infestans*) or having unique morphological features (such as the coralloid hyphae of *P. cinnamomi*), most records predating 2000 or post-2000, without accompanying molecular identifications, should be considered as unsubstantiated records.

Oomycetes are ancient organisms diverging from brown algae about 1 billion years ago (Berbee et al. 2017). Relatives of *Phytophthora* probably moved onto land with the first plants (Krings et al. 2011) and, as such, representatives can be expected to occupy all favourable niches, and over time, geographic isolation and reproductive barriers would have led to speciation (Hansen 1987). Humans have been migrating for over 100 000 years and have taken food plants with them, especially since the birth of agriculture 12 000 years ago (Santini et al. 2018). However, many non-native plant pathogens would have been introduced with fruit and vegetables accompanying Europeans as they colonised new countries over the past six centuries (Santini et al. 2018, Saville & Ristaino 2021). These human activities in providing pathways for pathogen movement have introduced non-native *Phytophthora* to new regions. Depending upon the suitability of the environment, non-native pathogens either fail to establish, remain on the hosts with which they were introduced or find new hosts (Hansen et al. 2012, Paap et al. 2020). Plants-for-Planting is the primary pathway for the introduction of *Phytophthora* (Brasier 2008). Current phytosanitary regulations for Australia are among the strictest in the world with a well-developed program, including the need for phytosanitary certificates, import permits, import inspections, pathway risk analysis, pre-export treatments and, when required, post-entry quarantine (Eschen et al. 2015). Australia is an island, and since the *Quarantine Act* of 1908 (Fish 1970) it has aimed to adhere to stringent quarantine regulations; thus, it is likely that most *Phytophthora* introductions are historical. Good evidence for this comes from the population genetics of *P. infestans;* diversity in Australia is very low, and only old genotypes are found (Dyer et al. 1993). The risk of new *Phytophthora* introductions may shift from agricultural to natural systems in the future as nature-based tourism grows. Travellers inadvertently carry large numbers of propagules on their clothing, footwear and luggage (Huiskes et al. 2014). Dispersal of *Phytophthora* species within Australia is therefore inevitable because there are no phytosanitary measures for tourists at State borders. The risk is lower for international tourists but not negligible, as the country promotes its natural assets to the world.

This review documents the species within the genus *Phytophthora* recorded, to date, in Australia. Records have been collected from Australian and international databases and collections and include host and location data, where possible, to provide a definitive baseline. All molecular records available from NCBI and various culture collections have been gathered and identities validated using a curated reference sequence database based on the type isolates or authenticated isolates designated by Abad et al. (2019). The distribution and pathology of each species are discussed, including several species whose presence in Australia is in doubt. Guidelines for the interpretation of results obtained from environmental DNA are provided. Access to these data will aid new species descriptions and direct sampling efforts for newly emerging species or where there has been little sampling previously. Most importantly, the data compiled here can be used to facilitate declarations of species status in Australia for trade purposes.

Sources of Phytophthora records

Records of *Phytophthora* in Australia were obtained from the following sources:

1 Australian Plant Pest Database (APPD) using '*Phytophthora'* as a search term. Records from the BRIP, DAR, DNAP, VPRI and WAC collections are included, but it does not contain recent records.
2 Queensland Plant Pathology Herbarium (BRIP), Department Agriculture and Fisheries, Queensland.
3 Victorian Plant Pathology Herbarium (VPRI), Agriculture Victoria, Department of Jobs, Precincts and Regions, Victoria.
4 New South Wales Plant Pathology and Mycology Herbarium (DAR), Orange, NSW Department of Primary Industries.
5 Royal Botanic Gardens Culture Collection (W), Sydney, NSW.
6 West Australian Plant Pathology Reference Culture Collection (WAC), Department of Primary Industries and Regional Development, Perth, WA.
7 Northern Territory Plant Pathology Herbarium (DNAP), Berrimah, Northern Territory.
8 Vegetation Health Service Collection (VHS), DBCA, WA. The VHS database in WA has over 20 000 records for *Phytophthora*, predominately from natural ecosystems. The majority of these records are of *P. cinnamomi.* Records for *P. cinnamomi* from the VHS database were excluded from the complete Australian dataset unless the isolate had been sequenced. All data can be viewed in DIDMS (Dieback Information Delivery and Management System) and is available upon request from the VHS.
9 The personal collection of Dr Roz Hart many of which are now held at the VHS.
10 Phytophthora Science and Management Collection (CPSM), Murdoch University, WA.
11 University of Queensland Oomycete Collection (UQ).

12 World Phytophthora Collection (WPC), University of California, Riverside using the search term 'Australia'.
13 International Mycological Institute (IMI) culture collection, Kew Royal Botanical Gardens, UK (now subsumed into CABI) using the search term 'Australia', and then scrolling to the *Phytophthora* section – this cannot be downloaded.
14 Westerdijk Fungal Biodiversity Institute culture collection (CBS). Searches were done for each *Phytophthora* species.
15 Publication records, where possible, for additional information.

Once compiled in Excel and data formatted to the same style, accessions from the different sources were cross-referenced and duplicates removed where possible, retaining the different collection codes with each isolate. The data collection, while exhaustive, may not include records from private collections or from government departments where records have not been digitised or made publicly available. A record was considered unsubstantiated if no supporting molecular data was available.

Molecular data sources

A search was conducted on GenBank using the search terms 'Phytophthora' and 'Australia', accessions downloaded, and duplicate isolates were discarded. Each accession was checked to ensure it was an accurate record from Australia, and thus records submitted by an author with an Australian affiliation but with the isolate from another country were removed (approximately 400 final records). Publications linked to the GenBank accession were then acquired to obtain host and location data. Additional molecular data were obtained from the CPSM database. Molecular data for some accessions were also provided from the BRIP, DNAP, RBG and VPRI collections. All hybrid isolates were excluded. For most isolates, sequence from the Internal Transcribed Spacer (ITS) gene region was available. All sequences were uploaded into Geneious Prime® v. 2019.2.3 (Biomatters Ltd). A curated database was generated, including the sequence of all type isolates identified in the IDphy online resource (Abad et al. 2019) and the type isolates of all species described since 2019. All ITS sequences were assigned to a species in a two-step process. Firstly, a Custom Blast search against the curated database identified the most closely related species and placed the isolates into one of the phylogenetic clades known for *Phytophthora*. Secondly, isolates were aligned based on phylogenetic clade using MAFFT, Neighbour Joining Trees generated using the HKY distance model, and 1 000 bootstrap replicates using Genious Tree Builder. An isolate was assigned to a species based on these phylogenies. The final database includes 7 869 records, of which 2 957 have a molecular-based identity (Supplementary material S1). 649 records, mostly predating 2000, are not assigned to species, and 85 records, mainly from IMI or WPC, are not linked to a jurisdiction.

A representative phylogenetic tree to show the placement of all species recorded in Australia was generated from 194 described *Phytophthora* species and an additional 20 undescribed taxa identified from Australian collections. *Phytopythium vexans* and a *Northophytophthora* species were used as outgroup taxa. A maximum likelihood tree was inferred from ITS rDNA using IQTREE 2.1 (Nguyen et al. 2015). Support values shown are bootstrap replicate percentages of 60 and above from the IQTREE ultrafast bootstrap (Hoang et al. 2018); the analysis was otherwise conducted as described by Trouillas et al. (2021).

Cumulative reports

Except for a few records obtained from International databases, most records have an associated date (year of record). According to the database (Supplementary material S1), 99 *Phytophthora* species have been reported from Australia, including 20 undescribed taxa. The first species, reported in 1900, was *P. infestans*, followed by *P. citrophthora* in 1919, *P. hibernalis* in 1925, *P. cinnamomi* in 1930 and *P. cactorum* in 1938 (Fig. 1). By 1950, nine species had been reported, which had risen to 27 species by 2000 (Supplementary material S2). All these species were first reported from diseases of orchards or crops and were mostly already described before they were reported in Australia (Supplementary material S2). *Phytophthora hibernalis*, *P. vignae* and *P. macrochlamydospora* are exceptions as they were all first described from Australia.

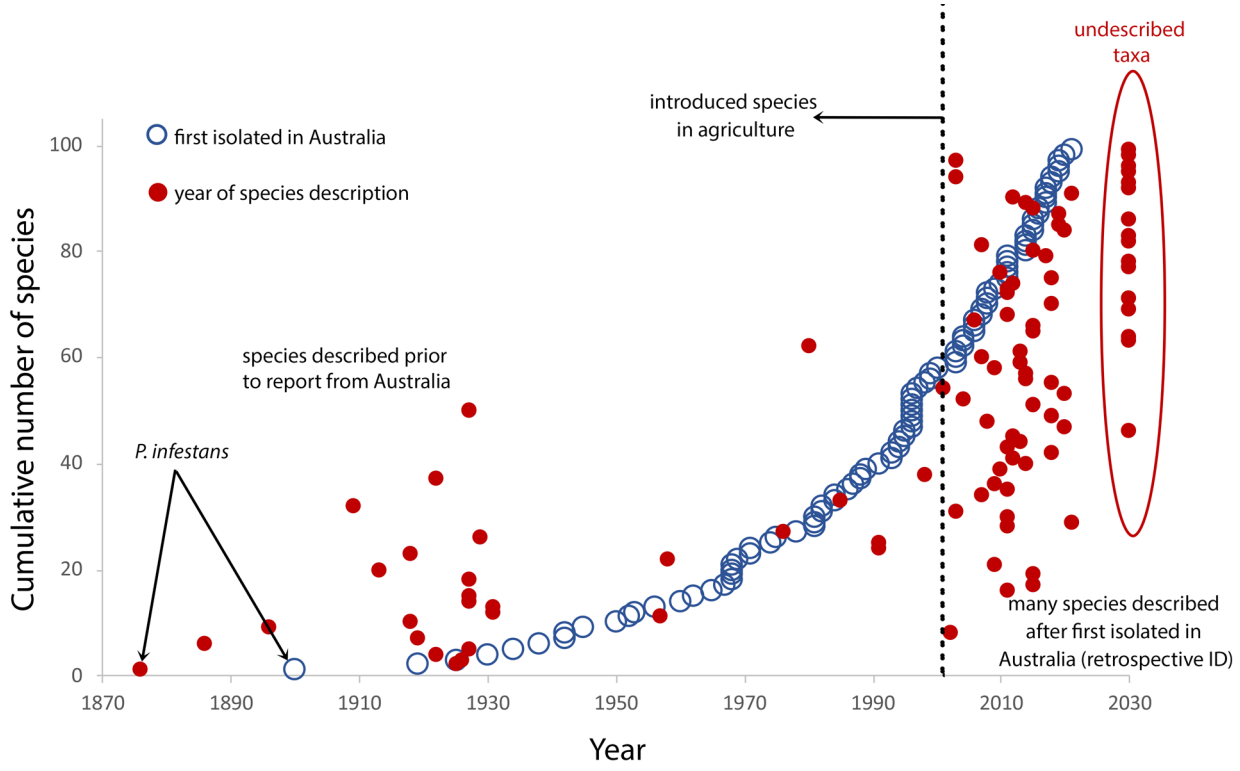


Fig. 1 Cumulative number of *Phytophthora* species reported from Australia.

Table 1 Records of the 99 *Phytophthora* species and taxa and their distribution within Australian jurisdictions; New South Wales (NSW), Northern Territory (NT), Queensland (QLD), Tasmania (TAS), South Australia (SA), Victoria (VIC), Western Australia (WA). Values in brackets are the number of records with a molecular identification. Shaded rows indicate species where records in Australia are not linked to molecular data and whose status in Australia is therefore in doubtful.

Species	Clade	Sub-Clade	Year[1]	NSW[2]	NT	QLD	SA	TAS	VIC	WA	Australia[3]
Phytophthora cactorum	1	1a	1938	32(13)		33(1)	5(2)	6(2)	37(8)	22(4)	136(31)
Phytophthora hedraiandra	1	1a	1996				1(1)		1(1)		1(1)
Phytophthora clandestina	1	1b	1984	57			15		50(2)	48(9)	174(13)
Phytophthora infestans	1	1c	1900	16		28	14	12	46	1	120(2)
Phytophthora nicotianae	1	1	1945	140(7)	35(13)	193(18)	17(5)	3	40(2)	231(153)	664(201)
Phytophthora citrophthora	2	2a	1919	57		15(4)	18(1)		7(1)	60(4)	159(10)
Phytophthora insulinativitatica	2	2a	2017								3(3)
Phytophthora meadii	2	2a	1971			9					9
Phytophthora capsici	2	2b	1988	2		6					8
Phytophthora mengei	2	2b	2000			1(1)					1(1)
Phytophthora siskiyouensis	2	2b	2003						2(1)		2(1)
Phytophthora sp. AUS2F	2	2b	2019			2(2)					2(2)
Phytophthora tropicalis	2	2b	1997			5(5)					5(5)
Phytophthora acerina	2	2c	2017	1(1)							1(1)
Phytophthora citricola	2	2c	1934	10(1)		2	8	1	14	63(9)	99(10)
Phytophthora multivora	2	2c	1968	19(14)		21(16)	4(4)		30(29)	634(631)	712(698)
Phytophthora bishii	2	2d	1996			2(2)			1(1)	2(2)	5(5)
Phytophthora elongata	2	2d	1989	28(28)				1(1)	8(8)	163(163)	200(200)
Phytophthora frigida	2	2d	2014	1(1)		4(3)					5(4)
Phytophthora multivesiculata	2	2	1988	1(1)						2(1)	3(2)
Phytophthora sp. AUS2E	2	2d	2004							6(6)	6(6)
Phytophthora arenaria	4	4	1986							129(129)	129(129)
Phytophthora boodjera	4	4	2006	2(2)						85(85)	87(87)
Phytophthora cathayensis	4	4	2015	2(2)							2(2)
Phytophthora palmivora	4	4	1950	5(1)	21	288(13)			3(3)	25(18)	350(41)
Phytophthora sp. AUS4A	4	4	2018							1(1)	1(1)
Phytophthora sp. AUS4B	4	4	2021							2(2)	2(2)
Phytophthora castanae	5	5	1978			2					2
Phytophthora cocois	5	5	2014			4(4)					4(4)
Phytophthora heveae	5	5	1975	2(2)	18(8)	2(2)					23(13)
Phytophthora aquae-cooljarloo	6	6a	1996							4(4)	4(4)
Phytophthora balyanboodja	6	6a	2001							3(3)	3(3)
Phytophthora condilina	6	6a	2008							14(14)	14(14)
Phytophthora cooljarloo	6	6a	1996							3(3)	3(3)
Phytophthora inundata	6	6a	1982			1(1)			3(2)	100(98)	106(101)
Phytophthora kwongonina	6	6a	1993							3(3)	3(3)
Phytophthora oreophila	6	6a	2015	1(1)						2(2)	3(3)
Phytophthora personensis	6	6a	1996	1(1)					3(3)	4(4)	8(8)
Phytophthora pseudorosacearum	6	6a	1998							8(8)	8(8)
Phytophthora rosacearum	6	6a	1987	1(1)					1(1)	16(16)	18(18)
Phytophthora sp. AUS6E	6	6a	2007							1(1)	1(1)
Phytophthora sp. walnut	6	6a	2018						2(2)		2(2)
Phytophthora amnicola	6	6b	1993			1(1)			9(9)	38(38)	48(48)
Phytophthora bilorbang	6	6b	2010							10(10)	10(10)
Phytophthora chlamydospora	6	6b	2006	2(2)					7(7)		9(9)
Phytophthora crassamura	6	6b	1968	6(6)			4(4)			17(17)	29(29)
Phytophthora fluvialis	6	6b	1994							25(25)	25(25)
Phytophthora gibbosa	6	6b	2009							4(4)	4(4)
Phytophthora gonapodyides	6	6b	1996	9(2)		4		2(2)	4(4)	13	32(8)
Phytophthora gregata	6	6b	1965	13(13)				6(6)	6(6)	11(11)	36(36)
Phytophthora litoralis	6	6b	2007							17(17)	17(17)
Phytophthora megasperma	6	6b	1953	24		7	7	5	7	26	78
Phytophthora moyootj	6	6b	1999						1(1)	21(21)	22(22)
Phytophthora ornamentata	6	6b	2016							3(3)	3(3)
Phytophthora thermophila	6	6b	1981	1(1)			2(2)		22(22)	103(103)	128(128)
Phytophthora sp. paludosa	6	6b	2008						1(1)		1(1)
Phytophthora sp. raspberry	6	6b	2019							1(1)	1(1)
Phytophthora sp. AUS6G	6	6b	2017							7(7)	7(7)
Phytophthora sp. AUS6H	6	6b	1995							2(2)	2(2)
Phytophthora lacustris	6	6c	1994						6(6)	9(9)	15(15)
Phytophthora asparagi	6	6	1995						13(11)	4(4)	17(15)
Phytophthora cambivora	7	7a	1968	2(1)		1	7(4)	1	3(1)	22(1)	43(10)
Phytophthora rubi	7	7a	1984	1			1	1	21(2)	3(3)	28(6)
Phytophthora niederhauserii	7	7b	1991	1(1)	3	7(5)	3(3)		10(8)	19(18)	43(35)
Phytophthora sojae	7	7b	1969	137(6)		46(3)	1		4(1)	4	196(10)
Phytophthora vignae	7	7b	1952	27		38(6)			1		68(8)
Phytophthora cinnamomi	7	7d	1930	1013(83)	12(1)	577(50)	55(4)	115(3)	121(34)	276(175)	2181(351)
Phytophthora parvispora	7	7d	1999	2(2)	1(1)	12(12)				11(11)	26(26)

Table 1 (cont.)

Species	Clade	Sub-Clade	Year[1]	NSW[2]	NT	QLD	SA	TAS	VIC	WA	Australia[3]
Phytophthora sp. AUS7A	7	7d	2020			1(1)				1(1)	2(2)
Phytophthora cryptogea	8	8a	1942	108(14)		25	16(2)	3	41(3)	52(4)	264(28)
Phytophthora drechsleri	8	8a	1956	66	7	16	1	8	7	28	136
Phytophthora erythroseptica	8	8a	1968	10		1	4(1)	11(2)	10	2	41(3)
Phytophthora kelmanii	8	8a	1981	12(12)		4(4)				3(3)	21(21)
Phytophthora medicaginis	8	8a	1971	52(2)		37(3)			1		95(7)
Phytophthora pseudocryptogea	8	8a	1967	40(40)		2(2)		2(2)	5(5)	165(165)	225(225)
Phytophthora dauci	8	8b	2003						1(1)	1(1)	2(2)
Phytophthora porri	8	8b	1942	8			1			1	10
Phytophthora sp. parsley	8	8b	2003	1(1)					1(1)		2(2)
Phytophthora hibernalis	8	8c	1925	4			1			3(1)	8(1)
Phytophthora syringae	8	8d	1982	1(1)			5(2)		3(1)	1(1)	11(6)
Phytophthora aquimorbida	9	9a	2017							2(2)	2(2)
Phytophthora hydropathica	9	9a	2011						3(3)	1(1)	4(4)
Phytophthora sp. AUS9A	9	9a	2008			2(2)			1(1)	4(4)	7(7)
Phytophthora sp. AUS9B	9	9a	2015	1(1)		1(1)					2(2)
Phytophthora sp. AUS9E	9	9a	2004							3(3)	3(3)
Phytophthora sp. AUS9F	9	9a	2019			1(1)					1(1)
Phytophthora insolita	9	9b	2004							4(4)	4(4)
Phytophthora macrochlamydospora	9	9c	1947	57(11)		9(7)					68(20)
Phytophthora richardiae	9	9c	1960	1							1
Phytophthora cacuminis	9	9d	2016					2(2)			2(2)
Phytophthora constricta	9	9d	1981							49(49)	49(49)
Phytophthora fallax	9	9d	2006	4(4)				4(4)	6(6)		14(14)
Phytophthora sp. AUS9C	9	9d	2011							14(14)	14(14)
Phytophthora sp. AUS9D	9	9d	2011							1(1)	1(1)
Phytophthora sp. AUS9G	9	9d	2014			1(1)					1(1)
Phytophthora sp. AUS9H	9	9d	2014							2(2)	2(2)
Phytophthora boehmeriae	10	10	1962	3		2			1		6
Phytophthora gondwanense	10	10	1996	6(6)		19(19)			1(1)	1(1)	27(27)
Phytophthora versiformis	12	12	2011							39(39)	39(39)
Phytophthora sp.				259	6	221	30	10	70	41	649
Total				2247(283)	103(23)	1653(190)	230(34)	193(24)	639(199)	2697(2148)	7869(2957)
Number of species				48(35)	7(4)	41(29)	21(12)	17(9)	45(37)	71(64)	99(91)

[1] Year first recorded in Australia.
[2] Includes a few records for the Australian Capital Territory.
[3] Includes (a) Lord Howe Island and Christmas and Cocos Islands and (b) records from international databases reported only by country.

A collaboration between Drenth in Queensland and Cooke in Scotland brought together species from temperate and tropical climes and resulted in the first comprehensive molecular phylogeny of *Phytophthora* (Cooke et al. 2000). Subsequently, an increased interest in *Phytophthora* in natural ecosystems (Hansen et al. 2012) and a molecular basis for species description has resulted in numerous new species; 127 species have been described since 2000. In Australia alone, 27 species have been described from natural ecosystems since 2009. Thus, while species described before 2000 were mainly known elsewhere before they were reported from Australia, since 2000, most species were isolated in Australia before their formal species description. Consequently, many isolates were first assigned to a known species and their identity was later updated based on molecular data; i.e., the identifications are retrospective. In particular, 1 326 isolates from the VHS collection have been identified using molecular taxonomy, resulting in the reassignment of many isolates, especially those previously identified as *P. megasperma*, *P. gonapodyides*, *P. drechsleri* and *P. citricola* (Burgess et al. 2009). For example, an isolate recovered in 1981 and reported as *P. drechsleri* has now been reclassified as *P. kelmanii*, a species only described in 2021. Similarly, *P. multivora* was described in 2009 and now accommodates isolates recovered as far back as 1968 originally reported as *P. citricola.* An isolate of *P. megasperma* from 1968 has been reclassified as *P. crassamura*, a species described in 2015. Numerous species from clade 6 were originally recorded as *P. gonapodyides* including *P. amnicola* (first isolated in 1993, described in 2012), *P. thermophila* (first isolated in 1981, described in 2011) and *P. gregata* (first isolated in 1968, described in 2011).

Distribution of Phytophthora records in Australia

Using the location data (nearest town), every record was assigned to a state jurisdiction; New South Wales (NSW), Northern Territory (NT), Queensland (QLD), South Australia (SA), Tasmania (TAS), Victoria (VIC), Western Australia (WA). Records for the Australian Capital Territory (ACT) were included with NSW as the ACT surrounded by NSW. Records for Australian Islands in the Pacific and Indian Oceans were included in the records for Australia, but not with the individual state jurisdiction records (Table 1).

The heat map of *Phytophthora* distribution reflects the sampling effort (Fig. 2). Effort is skewed toward regions with considerable activity in high productivity agriculture, horticulture and forestry, and native vegetation at risk from *P. cinnamomi.* Consequently, this map may not give an accurate picture of the *Phytophthora* distribution in Australia. In particular, tropical Australia is underrepresented. Records are uneven across jurisdictions (Table 1); the majority of records (34.3 %) and most of the molecular records (72.7 %) are from WA. Most of the remaining records (57.7 %) are from eastern Australia; QLD, NSW and VIC. Records from NT, SA, and TAS are limited (6.6 %), and these regions are undersampled (Table 1).

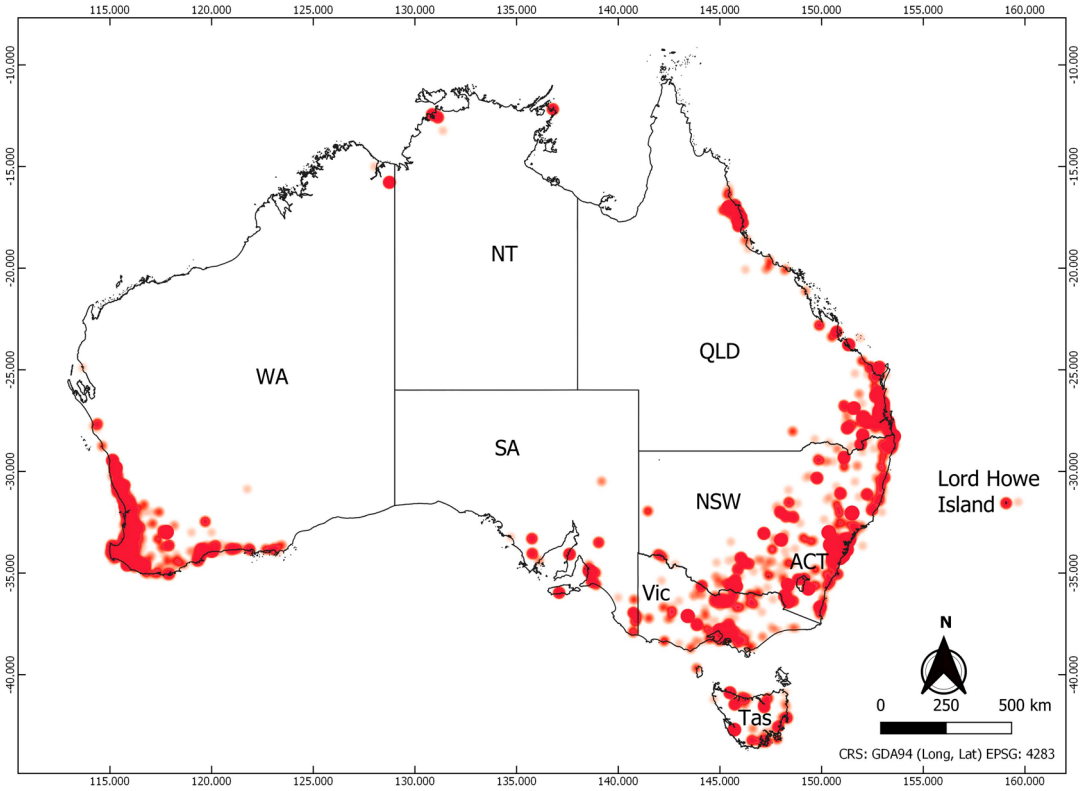


Fig. 2 Heat map of the distribution of *Phytophthora* records within Australia.

Host association of Phytophthora species

Where available, host data were included. All host data were checked for current taxonomy (World Flora Online), and the family and order data were added (Supplementary material S1). All hosts were recorded as native or exotic to Australia. Of these, 7 384 records contained host information, 43.7 % of records are from native hosts, 46.2 % from exotic hosts, 3.9 % of records were recovered directly from water and for 6.1 % of records there is no host information (Supplementary material S1). The proportion of isolates from native or exotic hosts differed between jurisdictions. Over 75 % of the isolates in NT, QLD, SA and VIC were recovered from exotic hosts, for NSW this was 53 %, 33.1 % for TAS and for WA only 20.7 % of isolations were from exotic hosts. Once again the proportion of isolates recovered from different environments is a reflection of sampling effort. In WA there is considerable effort within the native forest in order to map the distribution of *P. cinnamomi.* While native and exotic hosts have been reported for *Phytophthora* species across the phylogeny, clades 1, 7 and 8 species are more likely to be associated with exotic hosts (Fig. 3). Additionally, species from clades 2a–c and clades 9a–b are also usually associated with exotic hosts. Species in clade 2d, clade 6a and clade 9d are more likely to be associated with native hosts.

Forty-seven host Orders, 130 host Families, 416 host Genera are recorded in the database (Supplementary material S1). Common genera of exotic hosts with more than 50 records are, in order of most to least common (with number of different *Phytophthora* species isolates from each host genera in brackets), *Solanum* (tomato and potato, 12 spp.), *Glycine* (soybean, 3 spp.), *Trifolium* (clover, 6 spp.), *Citrus* (citrus, 11 spp.), *Persea* (avocado, 11 spp.), *Ananas* (pineapple, 2 spp.), *Carica* (papaya, 3 spp.), *Malus* (apple, 12 spp.), *Fragaria* (strawberries, 10 spp.), *Vigna* (cowpea, 4 spp.), *Rubus* (raspberry, blackberry, 11 spp.), *Pinus* (pines, 14 spp.), *Prunus* (almonds, cherry, 16 spp.), *Cicer* (chickpeas, 8 spp.), *Durio* (durian, 3 spp.), *Medicago* (lucerne, 6 spp.) and *Nicotiana* (tobacco, 2 spp.). Common genera of native hosts with more than 50 records are, in order of most to least common (with number of different *Phytophthora* species isolates from each host genera in brackets), *Eucalyptus* (35 spp.), *Banksia* (34 spp.), *Xanthorrhoea* (21 spp.), *Corymbia* (15 spp.), *Patersonia* (8 spp.), *Chamalaucium* (10 spp.), *Wollemia* (2 spp.) and *Auracaria* (6 spp.).

SPECIES PRESENT IN AUSTRALIA

Of the 99 species recorded in Australia, eight are unsubstantiated and will be discussed in the 'Doubtful Records' section. *Phytophthora cinnamomi* is the most commonly reported species because of extensive sampling within natural ecosystems (Table 1). Other common species, with over 100 records, are (in descending order) *P. multivora*, *P. nicotianae*, *P. palmivora*, *P. cryptogea*, *P. pseudocryptogea*, *P. elongata*, *P. sojae*, *P. clandestina*, *P. citrophthora*, *P. cactorum*, *P. drechsleri*, *P. arenaria*, *P. thermophila*, *P. infestans*, *P. inundata* and *P. citricola.* Forty-one species have fewer than five records; many of these are undescribed taxa. The described species with fewer than five records, although rare, have identities based on molecular data; *P. aquae-cooljarloo*, *P. gibbosa*, *P. hydropathica*, *P. insolita*, *P. balyanboodja*, *P. bishii*, *P. cocois*, *P. insulinativitatica*, *P. kwongonina*, *P. multivesiculata*, *P. oreophila*, *P. ornamentata*, *P. tropicalis*, *P. aquimorbida*, *P. cacuminis*, *P. cathayensis*, *P. cooljarloo*, *P. dauci*, *P. siskiyouensis*, *P. acerina* and *P. hedraiandra.*

We consider 91 species to be confidently present in Australia. Species distribution and host association are based on records from the database (Supplementary material S1), summarised by the jurisdiction in Table 1 and host in Fig. 3. Species are discussed in order of the clade to which they have been assigned in the *Phytophthora* phylogeny (Fig. 4). Species clusters are discussed together. The authority, original publication phylogenetic clade, MycoBank number and IDPhy link are provided for each species. For undescribed taxa, the date they were first isolated in Australia is provided. For cosmopolitan, widely distributed species described before 1996, data on global distribution are taken from IDPhy. For less common species,

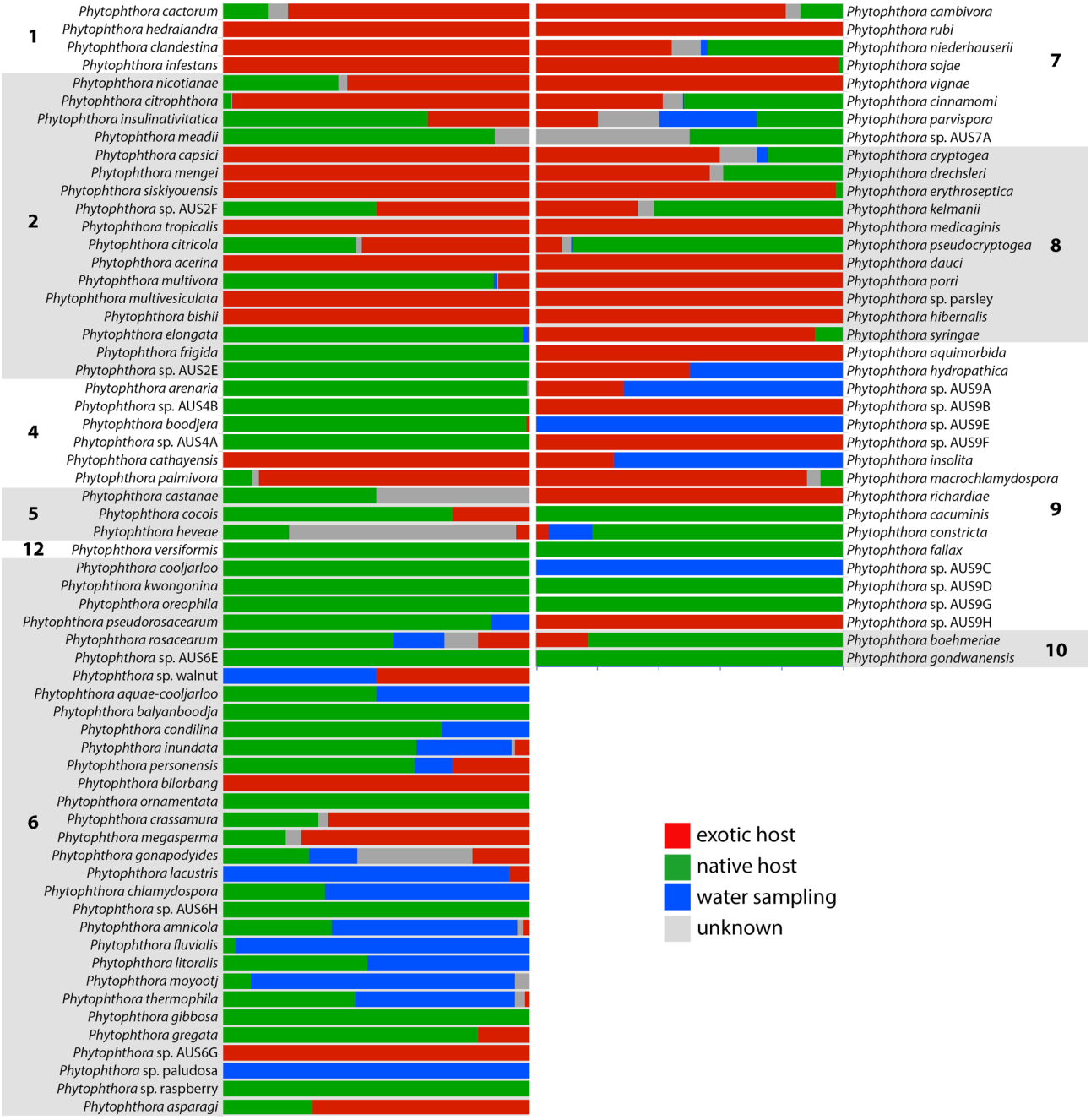


Fig. 3 Relative proportion of native and exotic hosts for each *Phytophthora* species in Australia as determined from Appendix S1. Species are grouped by phylogenetic clades as indicated by the number next to the names.

hosts and distribution data were based on GenBank records only, not from published reports without supporting molecular data. To do this, a blastn search was run in GenBank based on the ITS sequence of the type isolate, and all accessions were downloaded into Geneious. A MAFFT alignment and distance tree using Geneious tree builder was done to confirm identity. This process identified numerous misnamed accessions on GenBank (Supplementary material S3).

CLADE 1 — Fig. 4

Phytophthora cactorum (Lebert & Cohn) J. Schröt., in Cohn, Krypt.-Fl. Schlesien (Breslau): 3.1: 236. 1886

Clade 1a, MycoBank MB 199322; IDPhy

Phytophthora cactorum has been recovered from all jurisdictions, except NT, predominantly from apples, stone fruit and strawberries, but it has also been found in natural ecosystems, including in alpine areas (Khaliq et al. 2019). Crown rot of strawberry is a significant disease caused by *P. cactorum*, and based on Amplified Fragment Length Polymorphism (AFLP) genetic analysis, isolates causing this disease from multiple countries, including Australia, are genetically distinct to isolates causing disease on other hosts (Eikemo et al. 2004).

Phytophthora hedraiandra de Cock & Man in 't Veld, Stud. Mycol. 50: 486. 2004

Clade 1a, MycoBank MB 539092; IDPhy

Phytophthora hedraiandra is a rarely encountered species related to *P. cactorum*, first described from a *Viburnum* sp. in the Netherlands (De Cock & Lévesque 2004). This species has now been reported from various ornamental hosts in Italy, Japan, the Netherlands, Spain, UK and the USA (Supplementary material S3). Additionally, records on GenBank listed as *P. cactorum* from Europe, China, Pakistan and Taiwan have 100 % identity with the type isolate of *P. hedraiandra* (Supplementary material S3). Globally, there are no reports from natural ecosystems

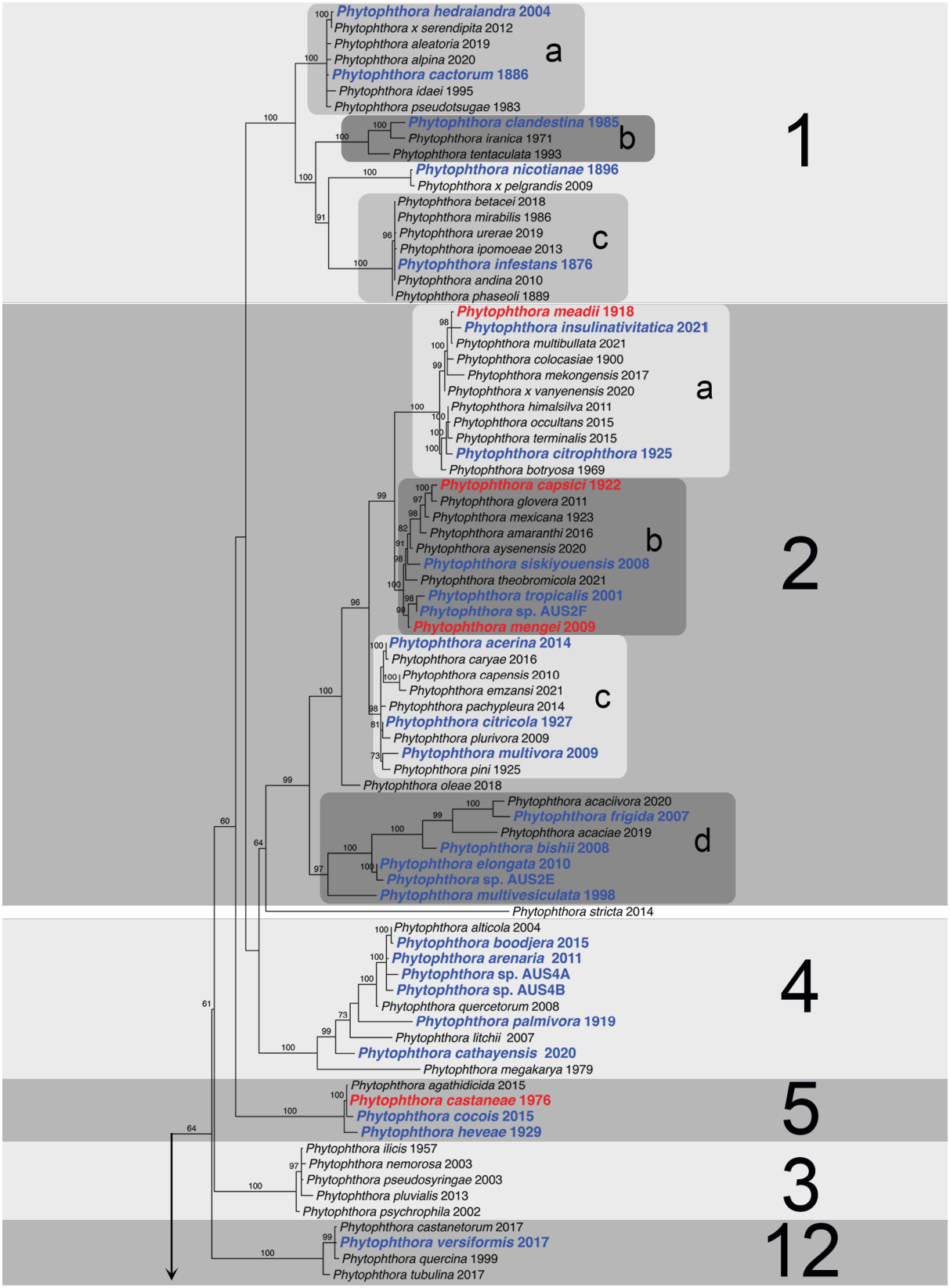


Fig. 4 Maximum likelihood best tree inferred from the ITS rDNA locus of 215 *Phytophthora* species and taxa. Numbers on top of branches represent maximum likelihood bootstrap values. Species highlighted in blue have been recorded in Australia, species in red have been recorded in Australia but their status is doubtful. *Phytopythium vexans* and a *Northophytophthora* species were used as outgroup taxa (not shown).

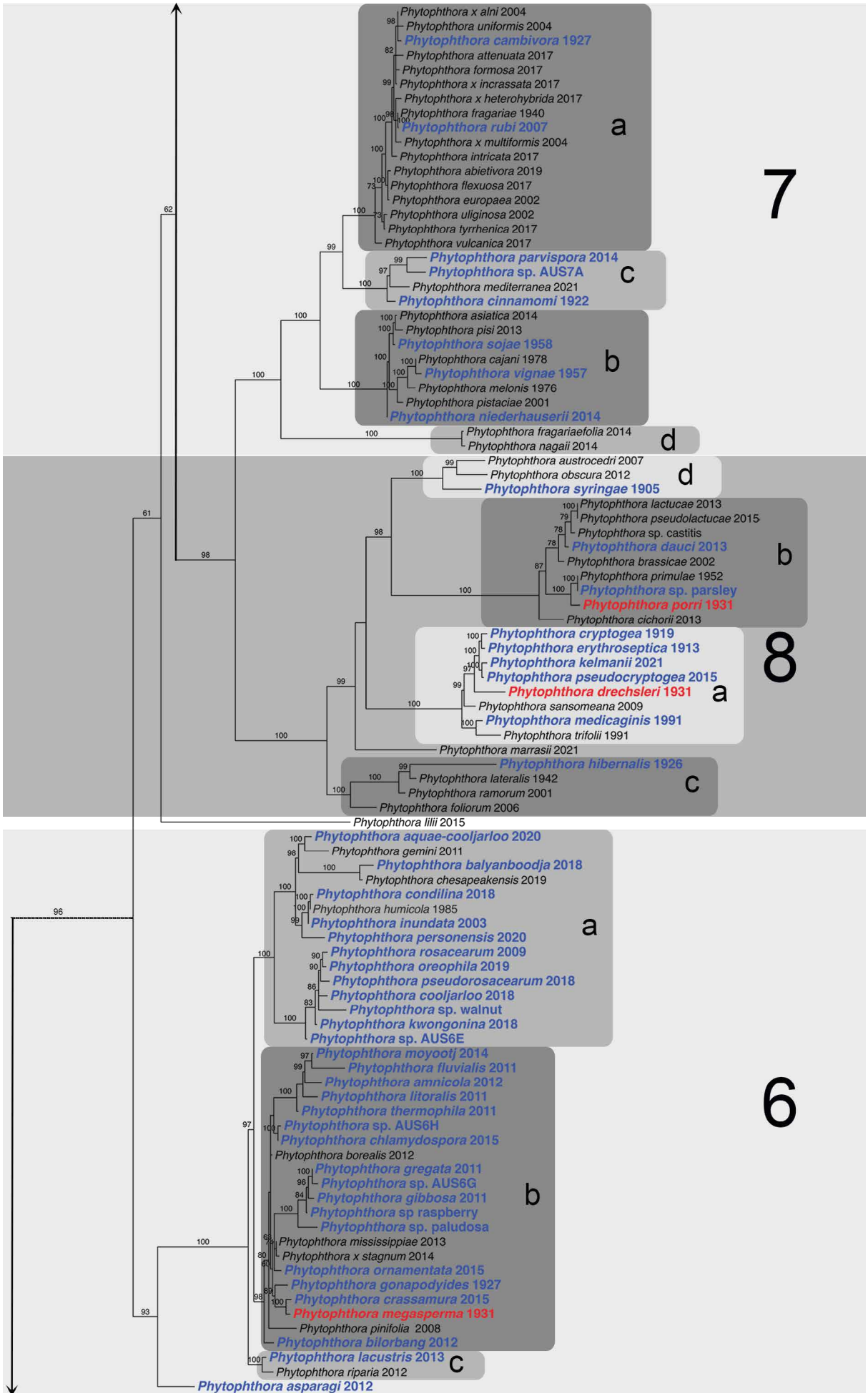

Phytophthora x alni 2004
Phytophthora uniformis 2004
Phytophthora cambivora 1927
Phytophthora attenuata 2017
Phytophthora formosa 2017
Phytophthora x incrassata 2017
Phytophthora x heterohybrida 2017
Phytophthora fragariae 1940
Phytophthora rubi 2007
Phytophthora x multiformis 2004
Phytophthora intricata 2017
Phytophthora abietivora 2019
Phytophthora flexuosa 2017
Phytophthora europaea 2002
Phytophthora uliginosa 2002
Phytophthora tyrrhenica 2017
Phytophthora vulcanica 2017
a
Phytophthora parvispora 2014
Phytophthora sp. AUS7A
Phytophthora mediterranea 2021
Phytophthora cinnamomi 1922
c
Phytophthora asiatica 2014
Phytophthora pisi 2013
Phytophthora sojae 1958
Phytophthora cajani 1978
Phytophthora vignae 1957
Phytophthora melonis 1976
Phytophthora pistaciae 2001
Phytophthora niederhauserii 2014
b
Phytophthora fragariaefolia 2014
Phytophthora nagaii 2014
d
7
Phytophthora austrocedri 2007
Phytophthora obscura 2012
Phytophthora syringae 1905
d
Phytophthora lactucae 2013
Phytophthora pseudolactucae 2015
Phytophthora sp. castitis
Phytophthora dauci 2013
Phytophthora brassicae 2002
Phytophthora primulae 1952
Phytophthora sp. parsley
Phytophthora porri 1931
Phytophthora cichorii 2013
b
Phytophthora cryptogea 1919
Phytophthora erythroseptica 1913
Phytophthora kelmanii 2021
Phytophthora pseudocryptogea 2015
Phytophthora drechsleri 1931
Phytophthora sansomeana 2009
Phytophthora medicaginis 1991
Phytophthora trifolii 1991
a
8
Phytophthora marrasii 2021
Phytophthora hibernalis 1926
Phytophthora lateralis 1942
Phytophthora ramorum 2001
Phytophthora foliorum 2006
c
Phytophthora lilii 2015
Phytophthora aquae-cooljarloo 2020
Phytophthora gemini 2011
Phytophthora balyanboodja 2018
Phytophthora chesapeakensis 2019
Phytophthora condilina 2018
Phytophthora humicola 1985
Phytophthora inundata 2003
Phytophthora personensis 2020
Phytophthora rosacearum 2009
Phytophthora oreophila 2019
Phytophthora pseudorosacearum 2018
Phytophthora cooljarloo 2018
Phytophthora sp. walnut
Phytophthora kwongonina 2018
Phytophthora sp. AUS6E
a
Phytophthora moyootj 2014
Phytophthora fluvialis 2011
Phytophthora amnicola 2012
Phytophthora litoralis 2011
Phytophthora thermophila 2011
Phytophthora sp. AUS6H
Phytophthora chlamydospora 2015
Phytophthora borealis 2012
Phytophthora gregata 2011
Phytophthora sp. AUS6G
Phytophthora gibbosa 2011
Phytophthora sp raspberry
Phytophthora sp. paludosa
Phytophthora mississippiae 2013
Phytophthora x stagnum 2014
Phytophthora ornamentata 2015
Phytophthora gonapodyides 1927
Phytophthora crassamura 2015
Phytophthora megasperma 1931
Phytophthora pinifolia 2008
Phytophthora bilorbang 2012
b
6
Phytophthora lacustris 2013
Phytophthora riparia 2012
c
Phytophthora asparagi 2012

Fig. 4 (cont.)

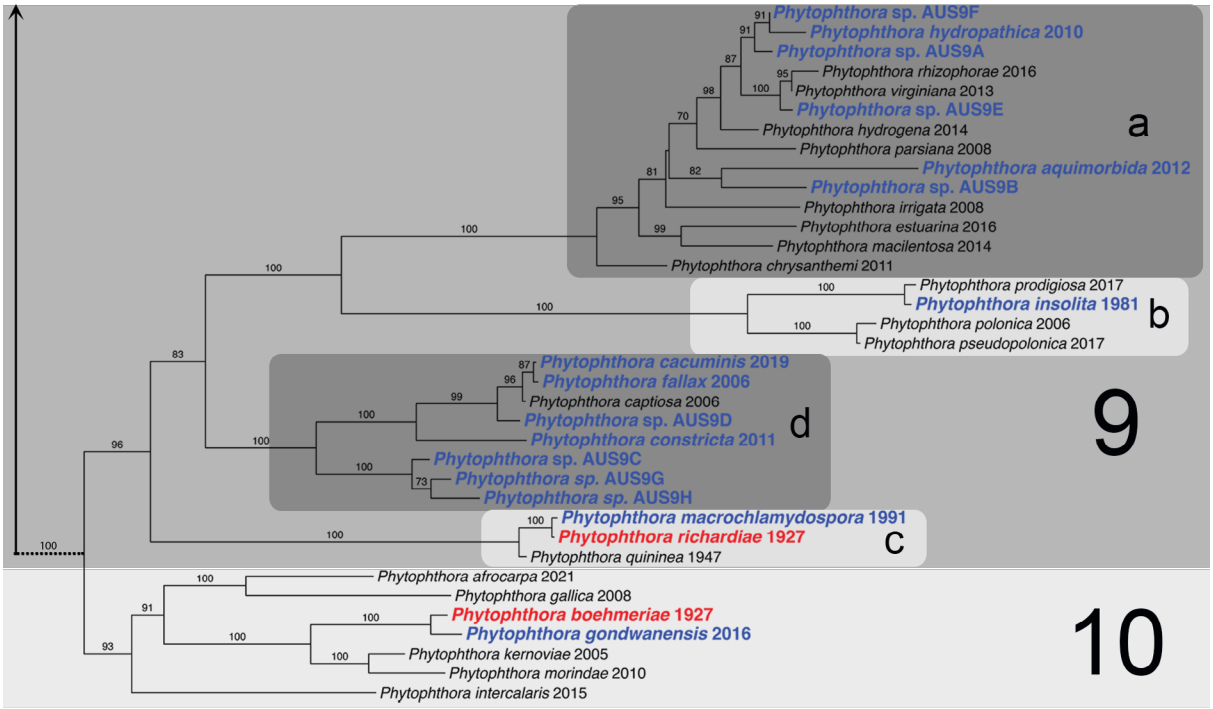


Fig. 4 (cont.)

except for the isolate recovered from *Pleione formosana*, an orchid, in Taiwan submitted to GenBank as *P. cactorum.* Within Australia, a single isolate was recovered in 1996 from soil next to horticulture polyhouses in Werribee, VIC (Cunnington et al. 2006). More recently, an isolate recovered from almonds in SA, originally identified as *P. cactorum*, has been reclassified as *P. hedraiandra.* As only 25 % of *P. cactorum* isolates have a molecular identification, *P. hedraiandra* may possibly be more common in Australia than currently known.

Phytophthora clandestina P.A. Taylor et al., Mycotaxon 22: 80. 1985

Clade 1b, MycoBank MB 105695; IDPhy

Phytophthora clandestina was described from Australia in 1985 and associated solely with root rot and decline of subterranean clover in pastures (Taylor et al. 1985). It was first isolated in VIC but subsequently recovered from pastures in NSW, SA and WA. It can reduce the annual production of subterranean clover, especially in wet or irrigated areas. Genetic studies have identified several races within Australia based on restriction fragment length polymorphisms (RFLP) (Purwantara et al. 2001) and single-strand conformation polymorphisms (SSCP) (Ma et al. 2009). Phylogenetically, this species is closely related to *P. iranica*, known only from Iran, and *P. tentuculata* found in China, Germany, Italy, Spain and the USA (California). To date, *P. clandestina* has only been reported from Australia. However, its only host, *Trifolium subterraneum*, is an exotic plant species naturally distributed in the Mediterranean basin and the Middle East but widely cultivated globally. As no other clade 1 species are considered native to Australia, likely, *P. clandestina* is also an introduced species.

Phytophthora infestans (Mont.) de Bary, J. Roy. Agric. Soc. England, 12: 240. 1876

Clade 1c, MycoBank MB 232148; IDPhy

Except for NT, *Phytophthora infestans* has been reported from all jurisdictions, predominantly from potatoes and a few records from tomatoes in NSW and QLD. *Phytophthora infestans* has been present in Australia since 1900, and it was the first *Phytophthora* species reported for the country. However, disease outbreaks in Australia are sporadic, localised, and easily controlled. In comparison with other countries, the impact of *P. infestans* in Australia is minimal (Drenth et al. 2001). The first and only report for WA was in 1909, and it has not been detected since. Interestingly, there are no supporting molecular sequence data. Forbes et al. (1998) conducted a global genetic study of *P. infestans* whereby RFLP fingerprints were used to classify the isolates. The Australian isolates included were identical and grouped with the 'old' genotypes. A recent study of the original *P. infestans* pandemic based on herbarium samples included two specimens from Australia collected in 1911 and 1917 (Saville & Ristaino 2021). Both isolates belonged to the first genotype (FAM-1) which was detected in all former British colonies spread there from European sources. These two studies can be considered to provide molecular confirmation of *P. infestans* in Australia.

Phytophthora nicotianae Breda de Haan, Meded. Lds Plantentuin Batavia 15: 57. 1896

Clade 1, MycoBank MB 194443; IDPhy

First described as the causal agent of black shank of tobacco, *Phytophthora nicotianae* (synonym *Phytophthora parasitica*) is now known from numerous hosts and has a global distribution. Within Australia, it is widespread, commonly reported, and recovered from all jurisdictions and a range of hosts, both exotic and native.

CLADE 2 — Fig. 4

Phytophthora citrophthora (R.E. Sm. & E.H. Sm.) Leonian, Amer. J. Bot. 12: 445. 1925

Clade 2a, MycoBank MB 251464; IDPhy

Phytophthora citrophthora was one of the first described species and has a global distribution. It has been recovered from numerous hosts, especially in orchards and nurseries in regions with sub-tropical and Mediterranean climates (Erwin & Ribeiro 1996). It is best known as the cause of gummosis of citrus trees and has been extensively studied (Graham & Feichtenberger

2015). In Australia, *P. citrophthora* has been recovered from all jurisdictions, except NT and TAS, and most of these records are from *Citrus* and *Malus* species in production orchards.

Phytophthora insulinativitatica Q.N. Dang et al., Mycol. Progr. 20: 117. 2021

Clade 2a, MycoBank MB 836442

This recently described species from clade 2a has only been recovered from disturbed natural vegetation on Christmas and Cocos Islands (Dang et al. 2021). It is not known from mainland Australia. Species in clade 2a are thought to have their origin in South-East Asia (Jung et al. 2020).

Phytophthora multivesiculata Ilieva et al., Eur. J. Pl. Pathol. 104: 683. 1998

Clade 2, MycoBank MB 445238; IDPhy

Phytophthora siskiyouensis Reeser & E.M. Hansen, Mycologia 99: 640. 2008

Clade 2b, MycoBank MB 505953; IDPhy

Phytophthora tropicalis Aragaki & J.Y. Uchida, Mycologia 93: 139. 2001

Clade 2b, MycoBank MB 467732; IDPhy

***Phytophthora* sp. AUS 2F** 2019. Supplementary material S3

Four rarely encountered species with limited global distribution from clade 2 have been reported in Australia. They are all known pathogens, and further work is required within the agricultural setting to determine their status in Australia.

Phytophthora multivesiculata was first described as causing root rot of *Cymbidium* in the Netherlands. The only other records of this species are from the same host in Australia and Vietnam (Supplementary material S3). *Cymbidium* spp. are native to tropical and subtropical Asia and Australia (Cunnington et al. 2009). However, the records for Australia (one each in NSW and WA) were from cultivated orchids. The existence of this host-specific species in Australia is intriguing.

Phytophthora siskiyouensis was described from the forest of southwest Oregon, USA (Reeser et al. 2007), predominantly from water and occasionally from stem cankers. To date, the distribution has only been extended to Australia and UK (Supplementary material S3). The record from the UK was from grey alder, and the only records for Australia were from riparian soil associated with exotic alder trees in VIC.

Isolates collected in 1997 from the garden vine *Mandevilla* in far north QLD, which were initially identified as *P. capsici*, have recently been reassigned to *P. tropicalis*, a species often confused with *P. capsici. Phytophthora tropicalis* is differentiated from *P. capsici* based on morphological features and weak virulence toward *Capsicum* (Aragaki & Uchida 2001). It is known from Colombia, India, Italy, Mexico, Pakistan, Tahiti, Taiwan, South Africa, the USA, Vietnam (Supplementary material S3) and a couple of records from northern Europe. All reports are from Mediterranean or tropical regions, except the northern European records, where it has been found in greenhouses, causing wilt of cyclamen. *Phytophthora* sp. AUS 2F is closely related to *P. tropicalis* and has been isolated twice in QLD. These records are very recent, and their recognition is indicative of the increasing accessibility to molecular identification. There are sequences on GenBank for isolates incorrectly submitted as *P. capsici* and *P. tropicalis* from various hosts in Brazil, China, Costa Rica, Mexico, Taiwan and Vietnam (Supplementary material S3 as *P.* aff. tropicalis).

Phytophthora citricola Sawada, Special Bull. Agric. Exp. Sta. Formosa 27: 21. 1927

Clade 2c, MycoBank MB 260970; IDPhy

Phytophthora multivora P.M. Scott & T. Jung, Persoonia 22: 6. 2009

Clade 2c, MycoBank MB 512497; IDPhy

Phytophthora acerina B. Ginetti et al., Plant Pathology 63: 866. 2014

Clade 2c, MycoBank MB 804019; IDPhy

Phytophthora citricola was originally described causing fruit rot of *Citrus* in Taiwan, and it has since been reported as having a global distribution and numerous hosts (Erwin & Ribeiro 1996). However, many older records of *P. citricola* may correspond to other morphologically similar species in the '*P. citricola* complex' described after 2009, such as *P. multivora* (Scott et al. 2009), *P. pini* (Hong et al. 2011), *P. plurivora* (Jung & Burgess 2009) and *P. acerina* (Ginetti et al. 2014). Based on the available sequences in GenBank, the correct distribution for *P. citricola* s.str. is in Argentina, Australia, Canada, China, Japan, South Africa, Spain, Taiwan and USA (California) and the only hosts are *Citrus* and *Verbena* (Abad et al. 2019). Within Australia, *P. citricola* has been reported from every state, except NT, with molecular confirmation for a few isolates recovered from a *Citrus* orchard in NSW and from *Citrus* and *Persea americana* (avocado) in WA. Four of these isolates, recovered from *Citrus*, and included in the isozyme study of Oudemans et al. (1994), clustered with the group of isolates later confirmed to represent *P. citricola* s.str. (Jung & Burgess 2009). These confirmed isolates from Australia extend the host range of *P. citricola* to include avocado. Thus, while many of the earlier records for *P. citricola* in Australia, especially those from native vegetation, are likely to be incorrect, it is present but with restricted host associations.

Phytophthora acerina was first recovered from the severe dieback of a native tree, *Acer pseudoplatanus*, in plantations of Northern Italy in 2010 (Ginetti et al. 2014). It has since been reported with dying *Alnus* and olives in Italy (Linaldeddu et al. 2020, Seddaiu & Linaldeddu 2020), and from beneath *Populus fremontii* in California, USA. In addition, two sequences submitted to GenBank as *P. citricola*, one from a stream in Tennessee and another from *Prunus persica* in Taiwan, have 100 % identity with *P. acerina* (Supplementary material S3). Within Australia, a single isolate has been recovered from an almond orchard in NSW.

Phytophthora multivora was first described from WA to accommodate many isolates originally classified as *P. citricola* (Scott et al. 2009). Subsequent molecular re-evaluation of numerous '*P. citricola*' isolates from WA has led to their reclassification as *P. multivora.* After being described from dying native plants in Australia, *P. multivora* was discovered to be widespread in asymptomatic wild forests in South Africa. *Phytophthora multivora* has now been reported on five continents. However, in the northern hemisphere it is usually associated with horticulture or nurseries and is rarely encountered in natural settings. *Phytophthora multivora* is more likely to be found in Mediterranean climates, while the morphologically similar and closely related species *P. plurivora* is more common in temperate climates. Like *P. cinnamomi*, *P. multivora* causes root and collar rot with a growing number of woody hosts in orchards, gardens and native ecosystems and has now been reported from NSW, QLD, SA and VIC. In WA, *P. multivora* is much more likely to be recovered than *P. cinnamomi* from urban gardens and parks (Migliorini et al. 2019).

Phytophthora bishii Z.G. Abad et al., Mycologia 100: 103. 2008

Clade 2d, MycoBank MB 505876; IDPhy

Phytophthora bishii was described initially as a pathogen of *Rosaceae* isolated from roots of strawberry, roots of young rose cuttings, and roots of raspberry in Australia, Netherlands and USA (North Carolina) (Abad et al. 2008). This is a rarely encountered species, and while the distribution has been extended to Brazil, Spain, and Taiwan, and the hosts to ginger and rhododendron, there are only sequences of 11 isolates available on GenBank (Supplementary material S3). The only records from Australia are from VIC (isolate in the original species description), WA (raspberry) and QLD from an unknown host.

Phytophthora elongata A. Rea et al., Australas. Pl. Pathol. 39: 483. 2010

Clade 2d, MycoBank MB 515142; IDPhy

Phytophthora frigida Maseko et al., Mycol. Res. 111: 1325. 2007

Clade 2d, MycoBank MB 511178; IDPhy

***Phytophthora* sp. AUS 2E** 2004. Supplementary material S1

Since 1992, isolates described, at the time, as *P. citricola*, have been recovered from dead and dying *Eucalyptus marginata* at rehabilitated bauxite mine pits in the northern jarrah forest of WA. Later molecular re-evaluation of these isolates maintained by VHS led to the description of a new species, *P. elongata* (Rea et al. 2010). Further examination of the VHS collection has revealed that this species is widespread within the natural ecosystems in WA and is also present in NSW, TAS and VIC. In eastern Australia, the recovery of *P. elongata* has been from asymptomatic native vegetation. *Phytophthora elongata* is only known from Australia and may be naturally distributed in eastern Australia and subsequently introduced to WA. Several isolates related to, but distinct from, *P. elongata* from WA have been designated as *Phytophthora* sp. AUS 2E.

Phytophthora frigida was described in South Africa as a root pathogen of cold-tolerant eucalypts in plantations (Maseko et al. 2007). It has since been associated with gummosis in trunks of *Acacia mearnsii* in Brazil (Alves et al. 2016), and from a river in Sicily (Jung et al. 2019). Within Australia, it has been recovered from rhizosphere soil in native forests in both NSW and QLD. Thus, while first isolated in South Africa, given its association with native Australian tree species and its presence in Australia with asymptomatic vegetation, *P. frigida* is probably native to Australia.

CLADE 4 — Fig. 4

Phytophthora arenaria Rea et al., Pl. Pathol. 60: 1061. 2011

Clade 4, MycoBank MB 518792; IDPhy

Phytophthora boodjera A.V. Simamora & T.I. Burgess, IMA Fungus 6: 326. 2015

Clade 4, MycoBank MB 809223; IDPhy

***Phytophthora* sp. AUS4A** 2018. Supplementary material S1

***Phytophthora* sp. AUS4B** 2021. Supplementary material S1

Phytophthora arenaria was first isolated in WA in 1986, but only described in 2011 (Rea et al. 2011). This species is only known from the proteaceous kwongan vegetation of the WA sandplains. The disease it causes has only been observed on rare occasions, usually following excessive summer rain (Rea et al. 2011). *Phytophthora boodjera* was described in WA following observations of extensive death of seedlings in a native plant production nursery (Simamora et al. 2015); its distribution in WA was thought to be limited to nurseries and urban gardens (Simamora et al. 2018). However, it has since been isolated in a remote, isolated region, Forrestania, in the Great Western Woodlands of WA. *Phytophthora boodjera* has also been recovered from NSW. *Phytophthora arenaria* is pathogenic toward *Banksia* spp., and *P. boodjera* is pathogenic toward some *Eucalyptus* spp. (Belhaj et al. 2018, Simamora et al. 2018). *Phytophthora* sp. AUS4A and AUS4B denote a few isolates from WA related to, but distinct from, *P. arenaria* and *P. boodjera.* These species are all found in remote dry regions of WA and are all thought to be native.

Phytophthora boodjera was described because although it was phylogenetically similar to *P. alticola*, a species described from cold tolerant eucalypts in South Africa, it was morphologically distinct (Simamora et al. 2015). Subsequently, after new isolates of *P. alticola* were recovered from South Africa, it was realised that the original species description was based on mixed species. The species description was amended, and a neotype was proposed (Bose et al. 2017). However, the morphological features of *P. alticola* and *P. boodjera* now overlap, and across several gene regions, the neotype of *P. alticola* and ex-type of *P. boodjera* are phylogenetically very similar. We believe they could represent lineages within a single species rather than separate species.

Phytophthora cathayensis C. Morales-Rodríguez et al., Fungal Syst. Evol. 7: 102. 2021 (2020)

Clade 4, MycoBank MB 834619

Phytophthora cathayensis was recently described to encompass several isolates from clade 4, originally designated as *Phytophthora* sp. pecan (Morales-Rodríguez et al. 2021). The known hosts are *Carya cathayensis* (Chinese hickory) and *Carya illinoinensis* (pecan). Two isolates have been recovered in NSW from rhizosphere sil beneath pecans. A more detailed survey of pecan orchards may uncover more infestations.

Phytophthora palmivora (E.J. Butler) E.J. Butler, Science Rep. Agric. Res. Inst. Pusa: 82. 1919

Clade 4, MycoBank MB194605; IDPhy

Phytophthora palmivora is a species with a global distribution and a broad host range, commonly associated with disease of roots, stems and fruits of numerous tropical species. Reflecting this, the distribution of *P. palmivora* in Australia is predominantly tropical, recovered from a wide range of plant species, including durian and papaya. One record from VIC comes from the fruit growing area around Mildura and the other two from the suburbs of Melbourne.

CLADE 5 — Fig. 4

Phytophthora cocois B.S. Weir et al., Phytotaxa 205: 32. 2015

Clade 5, MycoBank MB 550519; IDPhy

Phytophthora heveae A.W. Thomps., Malay. Agric. J. 17: 77. 1929

Clade 5, MycoBank MB 252580; IDPhy

Clade 5 consists of only four described species. *Phytophthora castanae* is mainly known for causing trunk rot of chestnut and fruit and heart rot of coconut and has a pan-tropical distribution (Supplementary material S3). *Phytophthora cocois* also

causes fruit and heart rot of coconut and to date has only been recovered from Hawaii and the Ivory Coast (Weir et al. 2015). *Phytophthora heveae* is responsible for several diseases of tropical tree crops, including black stripe of rubber and bud rot and nut fall of coconut with a distribution predominantly in Asia and South America, but with reports from North Carolina and Tennessee in the USA. The fourth species, *Phytophthora agathidicida*, causes dieback in kauri (*Agathis australis*) trees and is only known from New Zealand (Weir et al. 2015).

A few isolates of three of the four species from clade 5 have been reported from NSW and QLD in natural ecosystems. However, only two of the four isolates of *P. castanae* have been sequenced (BRIP 41017a and BRIP 41220a) and these have identical sequence to *P. cocois*, and thus the status of *P. castanae* in Australia is doubtful (Supplementary material S3). *Phytophthora heveae* was recovered from an unknown host in the NT and was also reported widely from tropical rainforests in north Queensland during surveys by Brown from 1975–1982, but these records have never been verified. Given the pan pacific distribution of clade 5 species and their association with native vegetation in northern Australia, it is likely that these species are naturally distributed within Australia's tropics and could tentatively be considered native.

CLADE 6 — Fig. 4

Phytophthora cooljarloo T.I. Burgess, Persoonia 41: 11. 2018

Clade 6a, MycoBank MB 822011; IDPhy

Phytophthora kwongonina T.I. Burgess, Persoonia 41: 11. 2018

Clade 6a, MycoBank MB 822012; IDPhy

Phytophthora oreophila I. Khaliq & T.I. Burgess, Fungal Biol. 123: 33. 2019

Clade 6a, MycoBank MB 825252

Phytophthora pseudorosacearum T.I. Burgess, Persoonia 41: 12. 2018

Clade 6a, MycoBank MB 822013; IDPhy

Phytophthora rosacearum E.M. Hansen & Wilcox, Mycologia 101: 130. 2009

Clade 6a, MycoBank MB 499442; IDPhy

***Phytophthora* sp. AUS 6E** 2007. Supplementary material S1

***Phytophthora* sp. walnut** 2018. Supplementary material S1

Phytophthora rosacearum was one of the species recovered from rosaceous fruit trees in North America originally classified as *P. megasperma* (Hansen et al. 2009). Since its description, *P. rosacearum* has been recovered from several locations in Europe and the USA (California) (Supplementary material S3). Within Australia, there are verified records from chickpeas in NSW (1988), olives in VIC (2005), and *Pinus radiata* in WA (1987), and in WA this species has been frequently isolated from asymptomatic plants in native ecosystems. Phylogenetically, the closest relatives to *P. rosacearum* are *P. cooljarloo*, *P. kwogonina* and *P. pseudorosacearum*, all of which have a restricted distribution within natural ecosystems of WA (Burgess et al. 2018), and have not been associated with disease. *Phytophthora oreophila*, another closely related species, has been recovered from asymptomatic natural vegetation in the Kosciusko National Park, NSW, and in Perth, WA (Khaliq et al. 2019). In addition to NSW, *Phytophthora* sp. walnut has been recovered from Italy, Tunisia, Turkey and the USA (California) (Supplementary material S3). *Phytophthora* sp. AUS6E has been isolated once from rhizosphere soil beneath *Banksia grandis* in WA. Given the close phylogenetic relationship and evidence for recent radiation, all these species, including *P. rosacearum*, may be native to Australia and may be evolving within the south-western WA biodiversity hotspot (Burgess et al. 2018).

Phytophthora aquae-cooljarloo Mostowf. & T.I. Burgess, Persoonia 45: 377. 2020

Clade 6a, MycoBank MB 835165

Phytophthora balyanboodja T.I. Burgess, Persoonia 41: 8. 2018

Clade 6a, MycoBank MB 822009; IDPhy

Phytophthora condilina T.I. Burgess, Persoonia 41: 8. 2018

Clade 6a, MycoBank MB 822010; IDPhy

Phytophthora inundata Brasier et al., Mycol. Res. 107: 480. 2003

Clade 6a, MycoBank MB 373599; IDPhy

Phytophthora personensis Z.G. Abad et al., Persoonia 44: 441. 2020

Clade 6a, MycoBank MB 834875

Phytophthora inundata was described in 2003 to accommodate isolates from a variety of riparian habitats and tree crops in Europe with similarity to *P. gonapodyides*, but with distinctive colony morphology and higher temperature optima (Brasier et al. 2003b). Since then, *P. inundata* has been reported from Argentina, Chile, Iran, Tunisia, Turkey, and the USA, and despite its ability to grow in high temperatures, it has also been recovered from Norway (Supplementary material S3). *Phytophthora inundata* species is widespread in WA in waterways (Hüberli et al. 2013), but is also associated with disease of riparian vegetation. *Phytophthora condilina* is closely related to *P. humicola*, a species described from citrus orchard soil in Taiwan (Ko & Ann 1985), but also known from Japan, and a single record from Tuscany, Italy. *Phytophthora condilina*, known only from WA, is difficult to distinguish from *P. humicola* based only on the ITS barcode, but in multilocus phylogenies, it resides in its own strongly supported terminal clade (Burgess et al. 2018). *Phytophthora balyanboodja* and *Phytophthora aquae-cooljarloo* are also confined to WA. *Phytophthora gemini* and *P. chesapeakensis*, known only from seagrass in the northern hemisphere, are closely related to *P. aquae-cooljarloo and P. balyanboodja*, respectively. *Phytophthora personensis* has been recovered from various hosts in NSW, VIC, and WA and is also known from North America. The association of these species with the natural ecosystems in southwest WA and its patchy distribution elsewhere globally suggests they may be native to the region, or at least significant radiation has occurred in the region.

Phytophthora amnicola T.I. Burgess & T. Jung, Persoonia 28: 141. 2012

Clade 6b, MycoBank MB 863549; IDPhy

Phytophthora fluvialis T. Jung & T.I. Burgess, Persoonia 26: 147. 2011

Clade 6b, MycoBank MB 561042; IDPhy

Phytophthora litoralis T. Jung et al., Persoonia 26: 25. 2011

Clade 6b, MycoBank MB 518765; IDPhy

Phytophthora moyootj T.I. Burgess, Persoonia 33: 279. 2014

Clade 6b, MycoBank MB 809152; IDPhy

Phytophthora thermophila T. Jung et al., Persoonia 26: 28. 2011

Clade 6b, MycoBank MB 518766; IDPhy

Species in clade 6b of the *Phytophthora* phylogeny are predominantly aquatic specialists. Several related species have been recovered from rivers, streams and ponds in WA; *P. amnicola*, *P. fluvialis*, *P. litoralis*, *P. moyootj* and *P. thermophila* (Crous et al. 2011, 2012, 2014, Jung et al. 2011). Of these, *P. thermophila* has the broadest distribution and has also been recovered from rhizosphere soil in riparian vegetation. All these species can reduce the growth of native WA hosts in pathogenicity trials (Belhaj et al. 2018). These species can also readily hybridise, which led to the hypothesis that they may have evolved in isolation in different water catchments and have been reunited by anthropogenic activities (Burgess 2015). *Phytophthora fluvialis* and *P. litoralis* are only known from WA; *P. amnicola* and *P. moyootj* have also been isolated in VIC; and *P. thermophila* has been recovered in NSW, SA and VIC. There are reports of *P. thermophila* from Italy and California, USA. All these species are considered native to Australia.

Phytophthora gregata T. Jung et al., Persoonia 26: 24. 2011

Clade 6b, MycoBank MB 518764; IDPhy

Phytophthora gibbosa T. Jung et al., Persoonia 26: 22. 2011

Clade 6b, MycoBank MB 518763; IDPhy

***Phytophthora* sp. paludosa** T. Jung et al., Persoonia 26: 28. 2011

Clade 6b, Supplementary material S1

***Phytophthora* sp. raspberry**. 2019. Supplementary material S1

***Phytophthora* sp. AUS6G**. 2017. Supplementary material S1

Phytophthora gibbosa and *P. gregata* were described in 2011 to accommodate strains collected by VHS in WA as far back as 1981 and originally classified as *P. megasperma* (Burgess et al. 2009). *Phytophthora gregata* has since been recovered from eastern Australia, where it is present in sub-alpine regions (Khaliq et al. 2019), and is responsible for severe dieback of a native shrub, *Pimelea bracteata* (McDougall et al. 2018). *Phytophthora gregata* has also been recovered from China, Japan, Vietnam, and the USA (Oregon) (Supplementary material S3). *Phytophthora* sp. paludosa refers to a single isolate recovered from native vegetation in VIC; a very similar isolate has been recovered from Christmas trees in Sweden (Supplementary material S3). *Phytophthora* sp. raspberry is an undescribed species related to *P. gregata*, first recovered from Sweden in 1994 (Brasier et al. 2003a). In GenBank, isolates with identical sequences to *P.* sp. raspberry have been recovered from China, California, and several countries in Europe (Supplementary material S3). *Phytophthora* sp. AUS6G is another related species recovered from pasture in WA; a similar isolate has also been recovered in Austria (Supplementary material S3).

Phytophthora bilorbang Aghighi & T.I. Burgess, Eur. J. Pl. Pathol. 133: 848. 2012

Clade 6b, MycoBank MB 563863; IDPhy

Phytophthora bilorbang was first described from WA as a pathogen associated with blackberry decline (Aghighi et al. 2012). To date, no further records exist for Australia. Based on sequence data for several gene regions, *P. bilorbang* is identical to *P.* taxon Oaksoil, a species widely distributed in waterways of the Pacific northwest (Reeser et al. 2011). The only difference is that *P. bilorbang* is homothallic, and *P.* taxon Oaksoil is sterile. *Phytophthora bilorbang* is well established in Europe (records from Italy, Poland, Ukraine and the UK) and has been reported as a pathogen of olives in Italy (Santilli et al. 2020). Although first described from Australia, *P. bilorbang* is likely an introduced species.

Phytophthora chlamydospora Brasier & Hansen, N. Amer. Fungi 10: 3. 2015

Clade 6b, MycoBank MB 809175; IDPhy

Phytophthora gonapodyides (H.E. Petersen) Buisman, Root rots caused by Phycomycetes: 7. 1927

Clade 6b, MycoBank MB 252402; IDPhy

Phytophthora lacustris Brasier et al., Pl. Pathol. 62: 365. 2013

Clade 6c, MycoBank MB 564262; IDPhy

***Phytophthora* sp. AUS 6H** 1995.Supplementary material S1

Phytophthora gonapodyides, *P. chlamydospora* (= *P.* taxon PgChlamydo) and *P. lacustris* (= *P.* taxon Salixsoil) are widely distributed aquatic specialists from clade 6b, found commonly in rivers, streams, lakes and ponds in the northern hemisphere. Reports of these species in the southern hemisphere are less common, as other species seem to dominate the aquatic environment in these regions. *Phytophthora chlamydospora* has been isolated in NSW and VIC, *P. lacustris* in VIC and WA, and *P. gonapodyides* in NSW, TAS and VIC. Two isolates from WA initially reported as *P. chlamydospora* have been placed in *Phytophthora* sp. AUS6H; in multiple gene phylogenies, they are closely related but reside in their own strongly supported terminal clade. There are unsubstantiated records of *P. gonapodyides* in water samples collected from WA before 2000. However, it is now known there are numerous other morphologically similar species in the waterways of WA (Hüberli et al. 2013), and thus *P. gonapodyides* can be considered absent from WA.

Phytophthora crassamura Scanu et al., PLoS One 10: 24. 2015

Clade 6b, MycoBank MB 814006; IDPhy

There are numerous records of *P. megasperma* associated with a wide range of annual and perennial crops from all jurisdictions in Australia, except NT. Of these, none have accompanying molecular data. *Phytophthora crassamura* was described in 2015 from Sardinia, Italy, and is common in restoration sites in California (Sims et al. 2019). It is closely related to *P. megasperma*, and many isolates submitted to GenBank as *P. megasperma* will require reclassification (Supplementary material S3). Re-evaluation of sequence data of '*P. megasperma'* isolates recovered from NSW, SA and WA has resulted in their reclassification as *P. crassamura.* Several isolates of *P. megasperma* s.lat. from Australia clustered together in the genetic study of Förster & Coffey (1993). This cluster includes isolates now considered to be *P. crassamura.*

Phytophthora ornamentata Scanu et al., PLoS One 10: 24. 2015

Clade 6b, MycoBank MB 814009; IDPhy

Phytophthora ornamentata is a recently described species recovered from *Pistacia lentiscus* in Sardinia, Italy; most isolates recovered were from wetlands or ponding water (Scanu et al. 2015). The recovery of this species in WA from within a genetics trial site of *Corymbia calophylla* planted on an ex-pasture site was unexpected. The isolates were from trees with poor growth on a water gaining area of the trial site. To date, these are the only isolates of *P. ornamentata* in Australia.

Phytophthora asparagi Saude & Hausbeck, Persoonia 28: 147. 2012

Clade 6c, MycoBank MB 511931; IDPhy

Phytophthora asparagi was described as a pathogen causing spear and root rot of asparagus in Michigan, USA (Saude et al. 2008). GenBank includes accessions of *P. asparagi* from Japan, South Africa, Switzerland, and sequences with 100 % match from China (submitted as *P. infestans*) (Supplementary material S3). In Australia, *P. asparagi* has been recovered in VIC from asparagus and other *Asparagaceae* and is associated with native vegetation in WA. *Phytophthora asparagi* is basal to clade 6 in the *Phytophthora* phylogeny and is quite distant from other species in the clade.

CLADE 7 — Fig. 4

Phytophthora cambivora (Petri) Buisman, Meded. Phytopath. Labor. Willie Commelin Scholten Baarn 11: 4. 1927

Clade 7a, MycoBank MB 251211; IDPhy

Phytophthora cambivora has a global distribution causing root and canker disease of numerous woody hosts. Distribution in Australia is mostly in temperate regions associated with fruit tree orchards, although it has recently been recovered from dying plants of a native alpine shrub, *Nematolepis ovatifolia* (Green 2016). Although widespread, there are fewer records for *P. cambivora* than other common agriculture tree pathogens, such as *P. nicotianae* and *P. palmivora.*

Phytophthora rubi (Wilcox & Duncan) Man in 't Veld, Mycologia 99: 226. 2007

Clade 7a, MycoBank MB 505721; IDPhy

Phytophthora rubi (= *Phytophthora fragariae* var. *rubi*) causes red raspberry root rot. It has only one known host and a cosmopolitan distribution. This species has been reported from NSW, SA, TAS, WA and VIC, with molecular confirmation for VIC and WA. There is also a single sequence on GenBank linked to Australia (AY129196) included in the phylogenetic study of Martin & Tooley (2003) for which there is no location data. However, the disease symptoms are considered unique; the pathogen is fastidious and requires a specially prepared medium for isolation. *Rubus* cultivars have been tested for resistance to Australian isolates of *P. rubi* (Brinson & Edwards 2008). Additionally, this species has been detected from raspberry roots in WA through the sequencing of amplicons obtained with *Phytophthora* specific primers (Supplementary material S1).

Phytophthora niederhauserii Z.G. Abad & J.A. Abad, Mycologia 106: 440. 2014

Clade 7b, MycoBank MB 515114; IDPhy

Although only recognised as a new species in 2014, *Phytophthora niederhauserii*, has a broad host range and distribution. The original description included isolates from 13 countries on 5 continents (Abad et al. 2014). Since the description, additional records have been reported from the Canary Islands and China. It is predominantly a pathogen of ornamentals and fruit trees. In Australia, it has often been recovered from all states except TAS in orchards, home gardens and natural ecosystems.

Phytophthora sojae Kaufm. & Gerd., Phytopath. 48: 207. 1958

Clade 7b, MycoBank MB 303624; IDPhy

Phytophthora sojae causes root and stem rot of soybeans and other *Fabaceae* and is found in Asia, New Zealand, and North and South America. Within Australia, almost all records are from soybeans in most jurisdictions, except NT and TAS. Records of *P. sojae* from non-*Fabaceae* hosts in WA are unsubstantiated. As *P. sojae* exhibits strong hosts specificity, these records are most likely incorrect, and therefore, distribution is likely to be restricted to eastern Australia.

Phytophthora vignae Purss, Queensland J. Agric. Anim. Sci. 14: 141. 1957

Clade 7b, MycoBank MB 303625; IDPhy

Phytophthora vignae is a species with a limited host range (*Vigna* spp.) and distribution, described originally as causing stem rot of cowpeas (*Vigna unguiculata*) in Australia (Purss 1957). More recently, it has been identified as causing the same disease in adzuki (*V. angularis*) and mung beans (*V. radiata*) in China (Sun et al. 2021) (Supplementary material S3). While *P. vignae* is known from *Vigna* spp. in Australia, it is not the only *Phytophthora* species isolated from these hosts as *P. cinnamomi* and *P. mengei* have also been recovered. *Phytophthora vignae* is unlikely to be native to Australia as it resides in clade 7, and all other species from this clade are considered exotic.

Phytophthora cinnamomi Rands, Meded. Inst. Plantenziekt. 54: 1. 1922

Clade 7d, MycoBank MB 320473; IDPhy

Phytophthora parvispora Scanu & Denman, For. Pathol. 44: 6. 2014

Clade 7d, MycoBank MB 803239; IDPhy

***Phytophthora* sp. AUS7A** 2020. Supplementary material S1

More than any other species, *Phytophthora cinnamomi* has had a considerable disease impact in Australia, both in agriculture and natural ecosystems. Unlike other *Phytophthora* species, *P. cinnamomi* has distinctive coralloid mycelial growth on agar, and it is easy to diagnose in culture, and as such, records without accompanying molecular data can be considered accurate records. *Phytophthora cinnamomi* is the most frequently isolated and widely distributed *Phytophthora* species in Australia. The disease is routinely managed in many agriculture crops, in both perennial tree crops, such as avocado and chestnut, and annual crops such as pineapple. However, it is in natural ecosystems where the most significant impact has been observed; many native plant species, especially the megadiverse and iconic species within the *Proteaceae*, are very susceptible to *P. cinnamomi.* Impact on these ecosystems leads to irreversible changes in ecosystem structure and function. Monitoring native ecosystems to map the extent of *P. cinnamomi* infection by state departments is the main reason why so much is known about *Phytophthora* in native ecosystems in Australia.

Confirmed records for *P. parvispora* (formerly *P. cinnamomi* var. *parvispora*) are relatively uncommon in Australia although this could be due to previous identification as *P. cinnamomi.* Recoveries of this species are limited to warmer climates, including from irrigation water in northern WA. A single isolate

from a native *Hardenbergia* plant in WA, *Phytophthora* sp. AUS7A, appears to be a closely related species based on ITS sequence data; this warrants further investigation.

CLADE 8 — Fig. 4

Phytophthora cryptogea Pethybr. & Laff., Scientific Proc. R. Dublin Soc. NS. 15: 498. 1919

Clade 8a, MycoBank MB 231743; IDPhy

Phytophthora erythroseptica Pethybr., Scientific Proc. R. Dublin Soc., NS. 13: 547. 1913

Clade 8a, MycoBank MB 231826; IDPhy

Phytophthora kelmanii Z.G. Abad et al., Persoonia 46: 497. 2021

Clade 8a, MycoBank MB 838760

Phytophthora medicaginis E.M. Hansen & D.P. Maxwell, Mycologia 83: 377. 1991

Clade 8a, MycoBank 127932; IDPhy

Phytophthora pseudocryptogea Safaief. et al., Mycol. Progr. 14: 5. 2015

Clade 8a, MycoBank MB811590; IDPhy

Phytophthora cryptogea is a well-known cosmopolitan species with numerous hosts (predominantly annual and perennial crops and ornamentals) and a global distribution (Erwin & Ribeiro 1996). Within Australia, it has been reported from all jurisdictions, except the NT. *Phytophthora erythroseptica*, the causal agent of pink rot of potato tubers, is very closely related *to P. cryptogea*, but differs because it is homothallic. Within Australia, *P. erythroseptica* has been found in all states, except the NT. While only a two records have molecular data, and other related species also cause the pink rot symptoms (*P. cryptogea*, *P. drechsleri* and *P. pseudocryptogea*), *P. erythroseptica* is the only homothallic species, and therefore, the records can be considered accurate.

The species boundaries between *P. cryptogea*, *P. drechsleri* and *P. erythroseptica* have long been controversial, and this was only resolved by multilocus phylogeny (Mostowfizadeh-Ghalamfarsa et al. 2010). Five groups were recognised, *P. cryptogea* s.str., *P. drechsleri* and *P. erythroseptica*, and two groups were subsequently described as *P. kelmanii* (Crous et al. 2021) and *P. pseudocryptogea* (Safaiefarahani et al. 2015). All records of *P. kelmanii* and *P. pseudocryptogea* within Australia are based on molecular identification, often for isolates previously classified as *P. cryptogea* or *P. drechsleri.* Isolates of *P. cryptogea* from Australia considered in the global genetic study of Mills et al. (1991) were classified as group C and have been reclassified as *P. pseudocryptogea*. *Phytophthora pseudocryptogea* is now recognised from NSW, QLD, TAS, VIC and WA and is primarily associated with native vegetation. *Phytophthora kelmanii* is now recognised from NSW, QLD and WA, also commonly associated with native vegetation. Many records listed as *P. cryptogea* and *P. drechsleri*, especially those from native vegetation, may, in fact, be records for other related species (Supplementary material S1). There are numerous records for *P. drechsleri* from all jurisdictions, however all that have been sequenced have been reallocated to another species and there are no substantiated records for *P. drechsleri.*

Phytophthora medicaginis is one of the species previously confused with *P. megasperma* (Hansen & Maxwell 1991). It causes root and stem rot of several annual crop species in *Fabaceae* (chickpeas and alfalfa), and has a global distribution. Distribution in Australia is restricted to the eastern states, predominantly NSW and QLD, with a single unconfirmed record for VIC. Several isolates have associated molecular data. (Liew et al. 1998) sequenced three isolates of *P. medicaginis*, developed specific primers based on the IGS2 region and used these primers to confirm the identity of 29 additional isolates from eastern Australia. However, one of these isolates, BRIP 40475a (UQ250) from chickpea, has subsequently been sequenced and identified as *P. rosacearum;* hence the identity of the remaining isolates is in doubt.

Phytophthora dauci Bertier et al., Persoonia 31: 69. 2013

Clade 8b, MycoBank MB 803103; IDPhy

***Phytophthora* sp. parsley** Bertier et al., Persoonia 31: 75. 2013

Clade 8b, Supplementary material S1

Phytophthora dauci and *P.* sp. parsley were both described in 2013 based on a collection of isolates from winter grown vegetable crops (Bertier et al. 2013). Two isolates from Australia, reported initially as *P. porri*, were included in the collection. One isolate, corresponding to *P. dauci*, was intercepted in WA on carrots imported from VIC and is the only known isolate of *P. dauci* from Australia. The other isolate from parsley in VIC corresponds to *P.* sp. parsley. Another isolate of *P.* sp. parsley collected from onion in NSW is available from the WPC, although there is no reference to this isolate within Australian collections (Supplementary material S1).

Phytophthora hibernalis Carne, J. Royal Soc. West. Aust. 12: 36. 1925

Clade 8c, MycoBank MB 267110; IDPhy

Phytophthora hibernalis is a pathogen primarily of *Citrus* sp., responsible for brown rot of fruit, leaf and twig blight. While first described from WA (Carne 1925), this species has a global distribution and was likely introduced to Australia with *Citrus* germplasm. To date, there are only records within Australia for NSW, SA and WA. The reports from SA and NSW do not have molecular data and are therefore unconfirmed. As several other pathogens can cause brown rot of *Citrus* fruit additional surveys will be required to confirm its presence in NSW.

Phytophthora syringae (Kleb.) Kleb., Krankh. Flieders (Berlin): 18. 1909

Clade 8d, MycoBank MB 194524; IDPhy

Phytophthora syringae was first described from Germany as the species causing post-harvest *Phytophthora* fruit rot of apples due to contamination with infected soil. Globally, *P. syringae* is widely distributed and has been associated with root and collar diseases from numerous hosts but is not considered a significant pathogen. There are only a few records for Australia, all from fruit and nut trees in SA, NSW and VIC, except for an isolate recovered from a disturbed forest in the Perth Hills, WA.

CLADE 9 — Fig. 4

Phytophthora aquimorbida C.X. Hong, Mycologia 104: 1101. 2012

Clade 9a, MycoBank MB 513049; IDPhy

Phytophthora hydropathica C.X. Hong & Gallegly, Pl. Pathol. 59: 916. 2010

Clade 9a, MycoBank MB 514043; IDPhy

***Phytophthora* sp. AUS 9A** 2008. Supplementary material S1

***Phytophthora* sp. AUS 9B** 2015. Supplementary material S1

***Phytophthora* sp. AUS 9E (= *Phytophthora* sp. kunnunurra)** 2003. Supplementary material S1

***Phytophthora* sp. AUS 9F** 2019. Supplementary material S1

Species in clade 9a of the *Phytophthora* phylogeny have an aquatic lifestyle similar to species in clade 6b but tend to be associated with warmer water. Many of these species were first described from irrigation water in eastern USA. Within Australia, *P. aquimorbida* has been isolated from irrigation water in northern WA, *P. hydropathica* from orchard soil and water in VIC, and a farm stream in WA. Additional four undescribed species have been recovered from orchard soil or water at various locations around Australia. As these species are only known from Australia, they could be considered native. However, in GenBank, numerous sequences of related undescribed species for many countries have been submitted, and it seems that, like clade 6, these aquatic specialists from clade 9 are widespread in rivers and streams and may readily hybridise (Supplementary material S3). Much more work needs to be done to resolve the species boundaries within this clade, their pathogenicity and origin.

Phytophthora insolita Ann & W.H. Ko, Mycologia 72: 1180. 1981

Clade 9b, MycoBank MB 112569; IDPhy

Phytophthora insolita was described from Taiwan and has mainly been recovered from irrigation water and nursery soil. On GenBank, there are reports from a citrus orchard in India and from pomelo in Vietnam However, the isolates from Vietnam match the type isolate of a closely related species *P. prodigiosa*, a species known to cause brown rot of pomelo in southern Vietnam (Supplementary material S3). The isolates from Australia are all from northern WA, three from irrigation water and one from an invasive woody weed, *Parkinsonia aculeata*.

Phytophthora macrochlamydospora J.A.G. Irwin, Mycologia 83: 517. 1991

Clade 9c, MycoBank MB 355271; IDPhy

Phytophthora macrochlamydospora presents a conundrum. Until recently, it was known only as a soybean pathogen in Australia but has recently been recovered in the rainforests of northern NSW and far north QLD. The discovery of this species within asymptomatic natural vegetation suggests it is most likely native to Australia. Reports on GenBank of *P. macrochlamydospora* in India recovered from mandarin are incorrect as the sequence submitted is a poor match (Supplementary material S3). However, there is a single sequence submitted from Vietnam recovered by water baiting that warrants further investigation (Jung et al. 2020).

Phytophthora cacuminis I. Khaliq & T.I. Burgess, Fungal Biol. 123: 34. 2019

Clade 9d, MycoBank MB 825231

Phytophthora constricta A. Rea et al., Pl. Pathol. 60: 1064. 2011

Clade 9d, MycoBank MB 518793; IDPhy

Phytophthora fallax Dobbie & M.A. Dick, Mycol. Res. 110: 398. 2006

Clade 9d, MycoBank MB 357172; IDPhy

***Phytophthora* sp. AUS9C** 2011. Supplementary material S1

***Phytophthora* sp. AUS9D** 2011. Supplementary material S1

***Phytophthora* sp. AUS9G** 2014. Supplementary material S1

***Phytophthora* sp. AUS9H** 2014. Supplementary material S1

Phytophthora captiosa and *P. fallax*, the first species described in clade 9b, were, at the time, known only from leaves of eucalypts in New Zealand (Dick et al. 2006). This report was a cause for concern in Australia as it was seen as a possible biosecurity threat and initiated a flurry of activity to determine if the species were present. *Phytophthora fallax* was first found in Victoria in 2007, isolated from water gauges placed under the canopy of *Eucalyptus regnans*, and was considered to be a foliar *Phytophthora* (Cunnington et al. 2010). It has since been recovered from soil from beneath asymptomatic vegetation in sub-alpine regions of NSW, TAS and VIC (Khaliq et al. 2019). A related species, *P. cacuminis*, was described from the soil beneath sub-alpine vegetation in TAS (Khaliq et al. 2019). To date, *P. captiosa* has not been recovered in Australia, but given its close relationship to other species within this clade, it is expected to be native to Australia. *Phytophthora constricta* is widespread within proteaceous heathland in WA; it has been associated with episodic dieback following extreme rain events (Rea et al. 2011). *Phytophthora* sp. AUS9D corresponds to a single isolate found in the *Eucalyptus marginata* forest of WA. The remaining undescribed species have been recovered from waterways south of Perth WA (AUS9C), Kununurra, in northern WA (AUS9H), and Cairns, QLD (AUS9G). It is expected that more species within this clade will be discovered in Australia.

CLADE 10 — Fig. 4

Phytophthora gondwanensis L.A. Shuttlew. et al., Persoonia 35: 299. 2015

Clade 10, MycoBank MB 812576; IDPhy

Phytophthora gondwanensis was initially isolated from rhizosphere soil collected in Gondwana Rainforest in NSW; it has and has since been found in the rhizosphere of Macadamia in NSW and *Araucariaceae* and *Proteaceae* hosts in QLD rainforest. *Phytophthora boehmeriae* was described from a leaf of *Boehmeria nivea* in Taiwan, and has been reported from Japan and Korea, and is responsible for a severe blight of capsicum in southern India (Chowdappa et al. 2014) and cotton boll blight in China. On GenBank, there are also the accessions of *P. boehmeriae* from *Citrus* in Argentina, *Ficus* in Papua New Guinea, *Zanthoxylum piperitum* (pepper tree) in China, in *Eucalyptus smithii* in South Africa, and *Acacia mearnsii* in Brazil (Supplementary material S3). However, these records are doubtful as the sequence available has 100 % identity with the newly described *P. gondwanensis*. Isolates from VIC and WA, identified initially as *P. boehmeriae* have also been reclassified as *P. gondwanensis.* This species is aptly named as it is found across the southern hemisphere, predominantly on Australian native hosts.

CLADE 12 — Fig. 4

Phytophthora versiformis T. Paap & T.I. Burgess, Australas. Pl. Pathol. 46: 373. 2017

Clade 12, MycoBank MB 820727; IDPhy

Phytophthora versiformis has only been recovered from WA from a single host, *Corymbia calophylla*. It is very slow-growing, challenging to isolate, and has not been associated with disease

(Paap et al. 2017), nor is it pathogenic toward *C. calophylla* or any other plant species tested to date (Croeser et al. 2018, Khdair et al. 2020). All these are characteristics of a native organism. However, closely related species, *P. castanetorum*, *P. quercina*, and *P. tubulina* (Jung et al. 2017) are found in Europe and the undescribed species *P.* sp. ohioensis in the USA. *Phytophthora quercina* is pathogenic in soil infestation trials, although considerably less so than other *Phytophthora* species such as *P. cinnamomi* (Delatour et al. 2000). Further work needs to be conducted to better understand the natural distribution of this cluster of species.

DOUBTFUL RECORDS

For the following species, the records for Australia are not linked to molecular data. In the absence of other compelling characteristics, the presence of these species in Australia is considered doubtful.

Phytophthora meadii McRae, J. Bombay Nat. Hist. Soc. 25: 760. 1918

Clade 2a, MycoBank MB 120866; IDPhy

Phytophthora meadii is a pathogen of *Hevea brasiliensis* (rubber trees) causing disease on the leaves, fruit and stems (McRae 1918). There are no reliable records of this species in Australia. Brown (1999) reports a species as 'near' *P. meadii* at 23 sites within tropical rainforest in QLD and submitted some of these isolates to IMI (IMI 224620 – IMI 244627). IMI has another record from the same region in the period (IMI 213912). The VPRI also has a single record for an isolate collected in QLD during the same timeframe. None of these records are associated with live isolates, and there are no subsequent collections from anywhere else in Australia. This species was the subject of a pest report to FAO, IPPC in 2014, where it was declared that *P. meadii* is considered to be absent from Australia (FAO 2014).

Phytophthora capsici Leonian, Phytopathol. 12: 403. 1922

Clade 2b, MycoBank MB 259718; IDPhy

The database includes a few reports for *P. capsici* associated with exotic hosts, mainly pineapple, from NSW and QLD. Isolates recovered from pineapple and the non-native vine, *Mandevilla*, in QLD were compared with an isolate of *P. capsici* from IMI. The ITS sequence similarity was > 98 %, and they were reported as *P. capsici* (Weinert et al. 1999). However, the molecular data was not deposited, and 98 % similarity is insufficient for species identification. Subsequently, isolates from the same collections have been analysed and since identified as *P. tropicalis.* Therefore, *P. capsici* may be absent from Australia.

Phytophthora mengei Browne et al., Mycologia 101: 836. 2009

Clade 2b, MycoBank MB 513047; IDPhy

Phytophthora mengei is only known as a pathogen of avocado in southern California, USA, where it infects the trunks, structural roots and fruit. The species had been previously misidentified as *P. citricola*. During the data gathering process for this project, all isolates from Australia from the WPC were examined, including an isolate (P1825) from cowpeas collected in QLD, recorded as *P. siskiyouensis.* However, during the data verification, the sequence (GU258661) was found to have 100 % identity with the type isolate of *Phytophthora mengei* (Supplementary material S3). This is the only record for Australia, and the provenance of this isolate requires further investigation.

Phytophthora castanae Katsura & K. Uchida, Trans. Mycol. Soc. Japan 17: 241. 1976

Clade 5, MycoBank MB 283626; IDPhy

Four isolates of this species have been reported in Australia from Queensland between 1978 and 2000. Sequence data is not available for three isolates. Sequence data is available for two isolates (BRIP 41017a and BRIP 41220a), and molecular reevaluation places this isolate in a strongly supported terminal clade with *P. cocois*, a species only described in 2015. Thus, there are no substantiated reports of *P. castanae* in Australia.

Phytophthora megasperma Drechsler, J. Wash. Acad. Sci. 21: 524. 1931

Clade 6b, MycoBank MB 270758; IDPhy

Phytophthora megasperma s.lat. was described in 1931 as a pathogen on hollyhock (*Althaea rosea*). However, the morphology accommodated numerous other records from a range of hosts, including isolates from alfalfa, clover, and soybean, which resulted in the use of varieties or forma speciales to differentiate groups showing host specificity (Hansen et al. 1986). An examination of a large number of isolates resulted in the recognition of six distinct types; *P. megasperma* s.str., the legume pathogens *P. medicaginis*, *P. sojae* and *P. trifolii* (Hansen & Maxwell 1991), and two species subsequently described as *P. rosacearum* and *P. sansomeana* (Hansen et al. 2009). There are numerous records of *P. megasperma* associated with a wide range of annual and perennial crops from all jurisdictions in Australia, except NT. All records with accompanying sequence data have been reclassified as *P. crassamura* (see above). Molecular re-examination of this species complex has resulted in the description of several new species, and therefore records from Australia could all be incorrect, and *P. megasperma* may be absent from Australia.

Phytophthora drechsleri Tucker, Bull. Mississ. Agric. Exp. Stn. 153: 158. 1931

Clade 8a, MycoBank MB 251892; IDPhy

There are reports of *P. drechsleri* from every jurisdiction in Australia on a range of cultivated and native hosts. However, all these reports cannot be confirmed as there are no living cultures and no molecular data associated with this species in Australia. With non-papillate sporangia and amphigynous antheridia, *P. drechsleri* is placed in taxonomic group VI, along with many common species, such as *P. cambivora*, *P. cinnamomi*, *P. cryptogea* and *P. gonapodyides.* In fact, *P. drechsleri* can only be separated from *P. cryptogea* by its ability to grow at 35 °C, a criterion too variable to be definitive (Bumbieris 1974). Shepherd & Pratt (1973) recognised northern and southern ecotypes among 70 Australian isolates of *P. drechsleri.* Unfortunately, other than four isolates submitted to IMI, they did not provide isolate codes. A single isolate from the paper, IMI 129907, was subsequently send to the WPC and has now been identified as *P. pseudocryptogea.* Pratt et al. (1974) conducted pathogenicity trials with 34 of those isolates, but again no codes were provided. Isolates of *P. drechsleri* from Australia considered in the global genetic study of Mills et al. (1991) were classified as group E which has now been described as *P. kelmanii*. Molecular re-examination of isolates initially considered to be *P. drechsleri* held within the VHS collection resulted in the identification and description of several new species in clade 6, *P. amnicola*, *P. litoralis* and *P. thermophila* (Burgess et al. 2009). Similarly, a re-examination of *P. drechsleri* isolates at RGB led them to be reassigned to *P. cryptogea* and two isolates from BRIP correspond to *P. kelmanii.* Given that no living cultures are available for historical collections, and no new records have

been recorded since molecular identification became routine, it is likely that *P. drechsleri* is absent from Australia.

Phytophthora porri Foister, Trans. Bot. Soc. Edinb. 30: 277. 1931

Clade 8b, MycoBank MB 275104; IDPhy

Since 1942, sporadic reports of *P. porri* associated with onion in NSW have been documented, and there is a report from lettuce in SA in 1980. The report from WA in 2004 is associated with an interception of imported onion in Kununurra. None of these records has associated living specimens. There are three living specimens recorded in herbaria as *P. porri.* The first, an intercept in WA on carrots imported from VIC, has subsequently been described as *P. dauci* (Bertier et al. 2013). The remaining isolates, one from NSW and one from VIC, have been described as *Phytophthora* sp. parsley (Bertier et al. 2013). Based on these observations, *P. porri* can be considered absent from Australia.

Phytophthora richardiae Buisman, Proef. Univ. Utrecht: 19. 1927

Clade 9c, MycoBank MB 276520; IDPhy

DAR contains a single record for *P. richardiae* isolated from asparagus in NSW in 1960. The specimen is non-viable, and there have been no other records in Australia. Since its description in 1927 from calla lily (*Zantedeschia aethiopica*), there have been few records of this species globally and all are from calla lily. The nine records on GenBank (Supplementary material S3) come from the Netherlands (the type isolate), Japan and the USA. Based on these observations, *P. richardiae* can be considered absent from Australia.

Phytophthora boehmeriae Sawada, Bull. Agric. Exp. Station Formosa 27: 10. 1927

Clade 10, MycoBank MB 258590; IDPhy

Phytophthora boehmeriae is distributed in East and South Asia. All other records on GenBank (Supplementary material S3) are likely to be incorrect (see above under *P. gondwanensis*). Sequenced isolates from Australia have been reclassified as *P. gondwanensis.* All other isolates of *P. boehmeriae* in Australia without molecular data are unconfirmed, and therefore, this species may be absent.

SPECIES OF CONCERN

Many of the *Phytophthora* species frequently associated with agriculture in other parts of the world are already found in Australia. Most of these species were likely introduced to Australia with known European fruits and vegetables during early colonisation. Australian forests and woodlands, especially in regions with a Mediterranean climate, have been irreversibly altered by the biological invasion of *P. cinnamomi* (Cahill et al. 2008). However, *Phytophthora* species responsible for other devastating diseases of natural ecosystems elsewhere in the world have not been discovered in Australia. As a result, it is critical to regulate commodities or pathways via which these species could be introduced. Monitoring of urban parks and gardens is also recommended as a likely establishment pathway for non-native pathogens (Hulbert et al. 2019). Except for *P. richardiae*, all of the species listed above as doubtful can be considered pathogens of concern to agriculture production. Additionally, listed below, are several species currently absent from Australia whose introduction could impact existing crops, commodities, parks and gardens, and natural ecosystems. Many of these species were listed as species of concern during the 2009 *Phytophthora* prioritization project conducted by USDA APHIS PPQ CPHST PERAL (Abad et al. 2019).

Another issue of concern is new and more virulent variants of species already present in Australia and/or the introduction of the alternate mating type. This scenario took place in Europe where, after 150 years of managing late blight, the disease suddenly became more difficult to control due to the introduction of new strains from Mexico of both mating types, enabling genetic recombination and survival as oospores, replacing the archetypal A1 mating type population (Drenth et al. 1993).

Phytophthora aleatoria P.M. Scott et al.. Australas. Pl. Pathol. 48: 317. 2019

Clade 1a, MycoBank MB 363440

Phytophthora aleatoria is known from New Zealand where it sporadically causes disease in *Pinus radiata* including root and collar damage, stem bleeding cankers, discoloured foliage and sometimes mortality in small seedlings (Scott et al. 2019b). It is related to other clade 1 species that have an association with *Pinaceae* including *P. pseudotsugae* and *P. cactorum*. This pathogen is a concern to Australia due to the potential impact to the significant forestry species, *Pinus radiata.*

Phytophthora idaei **Kennedy,** Mycol. Res. 99: 67. 1995

Clade 1a, MycoBank MB 363440; IDPhy

Phytophthora idaei is a root pathogen only found in Europe with a single host, *Rubus idaeus* (raspberry) (Kennedy & Duncan 1995). It can cause moderate root damage especially in conjunction with *P. rubi.*

Phytophthora tentaculata Kröber & Marwitz, Z. Pflanzenk. Pflanzen. 100: 251. 1993

Clade 1b, MycoBank MB 360186; IDPhy

Phytophthora tentaculata was first described as a root and stem rot pathogen of ornamentals in Europe (Kröber & Marwitz 1993) and has since been recorded in Asia and the USA from a variety of ornamental hosts. More recently, it has been recovered as a serious invasive pathogen in Californian natural ecosystems, especially at restoration sites, and it is thought to have been introduced to these sites with planting stock (Rooney-Latham et al. 2019). These observations confirm the ability of this pathogen to be introduced, establish and spread within a natural ecosystem.

Phytophthora oleae Schena et al., Pl. Pathol. 67: 1367. 2018

Clade 2, MycoBank MB 824218; IDPhy

Phytophthora oleae has very recently been described as a pathogen of olive fruit (drupes) in southern Italy (Ruano-Rosa et al. 2018) and then a little later as a root pathogen of wild olives in Spain (González et al. 2019) and Italy (Riolo et al. 2020). This pathogen is of concern to the expanding olive industry in Australia.

Phytophthora botryosa Chee, Trans. Brit. Mycol. Soc. 52: 428. 1969

Clade 2a, MycoBank MB 336993; IDPhy

Phytophthora colocasiae Racib., Parasit. Alg. Pilze Java's (Jakarta) 1: 9. 1900

Clade 2a, MycoBank MB 232219; IDPhy

Phytophthora clade 2a currently contains 11 species, of which only *P. citrophthora* is known from mainland Australia. The other well-known pathogens from this clade are *P. coloca-*

siae, *P. meadii* and *P. botryosa*. *Phytophthora colocasiae* is a significant pathogen of *Colocasia esculenta* (taro), causing leaf spot symptoms (Raciborski 1900). *Phytophthora meadii* has been considered above as a species reported from Australia, but further investigation deemed this species absent. *Phytophthora botryosa*, like *P. meadii*, also causes various diseases of rubber trees (Chee 1969). Notably, species from clade 2a are commonly found in tropical climates and are pathogens of tropical trees in orchards and plantations.

Phytophthora theobromicola Pinho et al., Front. Microbio. 12: e537399 (6). 2021

Clade 2b, MycoBank MB 833783

Phytophthora theobromicola is a new species causing black pod disease on cacao in Brazil (Decloquement et al. 2021) where it appears to be outcompeting *P. palmivora*.

Phytophthora plurivora Jung & T.I. Burgess, Persoonia 22: 102. 2009

Clade 2c, MycoBank MB 512914; IDPhy

Globally, many records previously ascribed to *P. citricola* have now been reassigned to other species within the complex, predominantly *P. plurivora* and *P. multivora*. *Phytophthora plurivora* is a widespread pathogen of ornamental plants in nurseries and gardens and temperate forests and the northern hemisphere, where it is frequently associated with root and stem disease (Jung & Burgess 2009, Schoebel et al. 2014). *Phytophthora plurivora* was introduced to North America from Europe, according to microsatellite population genetic studies; however, moderate genetic diversity and lack of genetic population structure in the European population suggested it is also introduced (Schoebel et al. 2014). While *P. multivora* is widespread and present in Australian forests, there are currently no confirmed reports of *P. plurivora*. This is an invasive forest pathogen of concern.

Phytophthora acaciae dos Santos et al., Mycologia 111: 448. 2019

Clade 2d, MycoBank MB 823684

Phytophthora acaciivora T.Q. Pham et al., Fungal Syst. Evol. 6: 246. 2020

Clade 2d, MycoBank MB 834471

Phytophthora acacia and *P. acaciivora* have recently emerged as pathogens of Australian *Acacia* spp. in Brazil and Vietnam, respectively (Alves et al. 2019, Burgess et al. 2020). Phylogenetically, they are closely related to *P. frigida*, a species first found as a pathogen of eucalypts in South Africa (Maseko et al. 2007) but later also recovered from *Acacia mearnsii* in Brazil (Alves et al. 2016). Pathogens of *Acacia* spp. are of concern as, if introduced, they could quickly disperse into natural ecosystems in Australia. *Phytophthora frigida* has recently been recovered from asymptomatic vegetation in eastern Australia (Supplementary material S3), and other species in clade 2d appear to be native to Australia. Further exploration of Australian forests may uncover other species from this clade, including *P. acacia* and *P. acaciivora*.

Phytophthora pluvialis Reeser et al., North American Fungi 8: 2. 2013

Clade 3, MycoBank MB 803172; IDPhy

Phytophthora pluvialis is the most consistently isolated pathogen associated with red needle cast of *Pinus radiata* in New Zealand, although it is known to have originated in mixed Douglas fir-tanoak forests of the U.S. Pacific Northwest (PNW) (Tabima et al. 2021). In the PNW, *P. pluvialis* is a minor pathogen. Due to an extensive *P. radiata* plantation industry in Australia, *P. pluvialis*, *P. aleatoria* and *P. pinifolia*, all needle blight pathogens of *P. radiata*, are serious pathogens of concern.

Phytophthora megakarya Brasier & Griffin, Trans. Brit. Mycol. Soc. 72: 137. 1979

Clade 4, MycoBank MB 320483; IDPhy

Phytophthora megakarya was long confused with a related species, *P. palmivora* (Brasier & Griffin 1979). It has only been associated with one disease, black pod disease in Theobroma cacao (cacao) and its distribution is currently restricted to west Africa (Akrofi 2015). *Phytophthora megakarya* is considered the most aggressive of the *Phytophthora* species causing black pod disease which includes *P. capsisci*, *P. citrophthora*, *P. heveae*, *P. palmivora* and *P. theobromicola*.

Phytophthora agathidicidia B.S. Weir et al., Phytotaxa 205: 32. 2015

Clade 5, MycoBank MB 550518; IDPhy

Phytophthora agathidicida, causes dieback in kauri (*Agathis australis*) trees and is only known from New Zealand (Weir et al. 2015). It is a species of concern to Australia given our proximity to New Zealand and the diversity of native *Araucariaceae*.

Phytophthora pinifolia Durán et al., Pl. Pathol. 57: 722. 2008

Clade 6b, MycoBank MB 511870; IDPhy

Phytophthora pinifolia causes the disease known as Daño Foliar del Pino (a pine needle blight) in Chile on the important plantation species, *Pinus radiata* (Durán et al. 2008). The population on *P. radiata* is clonal (Durán et al. 2010), however, the species has not yet been detected anywhere else. Interestingly, it is a non-caducous species causing a foliar disease, although disease development is linked to heavy fog. Its biology is intriguing as *P. pinifolia* belongs to clade 6b clustering with species mostly known to be aquatic specialists.

Phytophthora* × *alni Brasier & Kirk, Mycol. Res. 108: 1174. 2004

Clade 7a, MycoBank MB 496769; IDPhy

Phytophthora* × *multiformis Brasier & Kirk, Mycol. Res. 108: 1177. 2004

Clade 7a, MycoBank MB 488623; IDPhy

Phytophthora uniformis Brasier & Kirk, Mycol. Res. 108: 1175. 2004

Clade 7a, MycoBank MB 488624; IDPhy

Alder dieback in Europe is caused by *Phytophthora* × *alni* and related species (Brasier et al. 2004). *Phytophthora* × *alni* is a hybrid with *P.* × *multiformis* and *P. uniformis* as parents, all reside in clade 7a and are closely related to *P. cambivora* and *P. fragariae*. The parents of the hybrid *P. x multiformis* are unknown (Ioos et al. 2006). Of these three species, only *P. uniformis* has been recovered outside Europe, in Alaska and Oregon (Aguayo et al. 2013). European and North American populations were compared using polymorphic microsatellite markers. There is no indication of gene flow between the populations; European isolates have extremely little genetic diversity, whereas the North American population is thought to be native (Aguayo et al. 2013). While alder is not native to Australia, introduction of this species alter the urban and peri-urban landscape in temperate regions.

Phytophthora fragariae Hickman, J. Pomology Hort. Soc. 18: 2. 1940

Clade 7a, MycoBank MB 289688; IDPhy

Phytophthora fragariae only causes one disease; red core root disease of strawberry. It has been reported infrequently in Australia based on morphological features (Wicks 1982), however, there is no supporting molecular data. An isolate, DAR 42005a, originally classified as *P. fragariae* by Wicks (1982) was subsequently sequenced and reassigned to *P. citrophthora* (Supplementary material S3). This pathogen does not appear to have established and is considered absent from Australia (Anonymous 2020a).

Phytophthora cajani Amin et al., Mycologia 70: 174. 1978

Clade 7a, MycoBank MB 289688; IDPhy

Phytophthora pisi Heyman, Plant Dis. 97: 466. 2013

Clade 7b, MycoBank MB 801280; IDPhy

Phytophthora pistaciae Mirabolfathy, Mycol. Res. 105: 1173. 2001

Clade 7b, MycoBank MB 474113; IDPhy

Phytophthora melonis Katsura**,** Trans. Mycol. Soc. Jpn. 17: 238. 1976

Clade 7b, MycoBank MB 320484; IDPhy

Clade 7b contains several important pathogens, mostly of field crops in the *Fabaceae* (*P. asiatica*, *P. cajani*, *P. melonis*, *P. pisi*, *P. sojae* and *P. vignae*), but also of orchard trees (*P. niederhauserii* and *P. pistaciae*). *Phytophthora niederhauserii*, *P. sojae* and *P. vignae* are already established in Australia. The field crop pathogens cause leaf and stem blights; *P. asiatica* on kudzu (*Peuraria lobata*) (Rahman et al. 2014), *P. cajani* on pigeon pea (Cajanus cajani) (Amin et al. 1978) and *P. pisi* on common pea (*Pisum sativum*) (Heyman et al. 2013). *Phytophthora melonis* is a pathogen of peas (*Fabaceae*) but is better known as a significant pathogen of cucumber (*Cucurbitaceae*) (Ho et al. 2007). *Phytophthora pistaciae*, like *P. niederhauserii*, causes stem cankers and gummosis (Mirabolfathy et al. 2001), unlike *P. niederhauserii*, it has only been found on a single host genus, *Pistacia.*

Phytophthora mediterranea Bregant et al., Forests 12: 8. 2021

Clade 7c, MycoBank MB 839612

Surveys of symptomatic seedlings in Italian nurseries have uncovered a new species *P. mediterranea*, closely related to *P. cinnamomi. Phytophthora mediterranea* was recovered from root and collar rot of *Myrtus communis*, one of the few species in the *Myrtaceae* found in the northern hemisphere (Linaldeddu et al. 2020). Given the huge array of native *Myrtaceae* in Australia this pathogen is of major concern.

Phytophthora primulae Toml., Trans. Brit. Mycol. Soc. 35: 233. 1952

Clade 8b, MycoBank MB 303623; IDPhy

Phytophthora primulae is only known as a pathogen of *Primula* spp., common garden flowers, in Europe. Reports of this species from New Zealand are unsubstantiated as there are no molecular records. Several other species in clade 8b, also with a narrow host range, are pathogens of annual crops in Europe.

Phytophthora lateralis Tucker & Milbrath, Mycologia 34: 97. 1942

Clade 8c, MycoBank MB 289691; IDPhy

Phytophthora ramorum Werres et al., Mycol. Res. 105: 1164. 2001

Clade 8c, MycoBank MB 474485; IDPhy

Sudden oak death (SOD) caused by *P. ramorum* and Port Orford Cedar root disease caused by *P. lateralis* are two particularly devastating diseases in the forests of the United States' Pacific coast. Although first described as a pathogen of ornamental *Rhododendron* and *Viburnum* in Europe (Werres et al. 2001), *P. ramorum* was already well established in California where it was causing the death of oaks and tanoaks (Grünwald et al. 2012). Interestingly the diseases expresses as bleeding stem lesions on the oaks (terminal host) but is a foliar pathogen of bay laurel and several other species (sporulating host). In Europe, *P. ramorum* is still mostly confined to nurseries and gardens, although in the UK, it has emerged as a pathogen of plantation Japanese larch (Brasier & Webber 2010). Host screening, conducted in the USA, has already identified several Australian native plant species as potential hosts if the pathogen where to enter Australia (Ireland et al. 2012).

Phytophthora lateralis has been established and causing a disease of *Chamaecyparis lawsoniana* (Port Orford Cedar) in the Pacific northwest of the USA for over 100 years (Hansen et al. 2000). Since 1999, it has also been known from Europe (Hansen et al. 1999), where it has affected *C. lawsoniana* trees and plantations in the United Kingdom, Ireland and France. The origin of *P. ramorum* and *P. lateralis* is thought to be East Asia, and the recovery of these species from asymptomatic forests in the region appear to confirm this hypothesis (Brasier et al. 2010, Jung et al. 2021).

Phytophthora austrocedri Greslebin & Hansen, Mycol. Res. 111: 312. 2007

Clade 8d, MycoBank MB 530225; IDPhy

Phytophthora austrocedri has been identified as the primary pathogen causing the disease known as Mal del ciprés in Patagonian Andes forests which causes mortality of *Austrocedrus chilensis* (Greslebin et al. 2007). The pathogen has been introduced to the United Kingdom, probably through the nursery trade. It is found in nurseries and has been introduced into native *Juniperus communis* habit through restoration plantings (Donald et al. 2021). Ancient Gondwanan vegetation, *Arthotaxis* spp. and *Callitris* spp., could be at risk from this pathogen.

Phytophthora captiosa Dick & Dobbie, Mycol. Res. 110: 395. 2006

Clade 9d, MycoBank MB 356996; IDPhy

Phytophthora captiosa, while described from New Zealand as a pathogen of Australian *Eucalyptus* spp. at the same time as *P. fallax*, has not been recovered in Australia. Surprisingly for a non-caducous species, *P. captiosa* causes crown disease in eucalypts with symptoms including leaf spots, petiole infection, and twig and small branch lesions (Dick et al. 2006). Targeted surveys in Australia have discovered *P. fallax* but have failed, to date, to uncover *P. captiosa.* However, all other species in clade 9d, including several undescribed species, have an Australian origin.

Phytophthora kernoviae Brasier et al., Mycol. Res. 109: 855. 2005

Clade 10, MycoBank MB 305803; IDPhy

During *P. ramorum* surveys in the United Kingdom, *P. kernoviae* was first isolated and described from bleeding stem lesions on mature *Fagus sylvatica* and foliar and stem necrosis of *Rhododendron ponticum* (Brasier et al. 2005). Subsequently, isolates recovered from New Zealand were identified as *P. kernoviae* and isolates recovered from pine plantations in the 1970s are now thought to be *P. kernoviae* (Scott & Williams 2014). This species is also found in Chile (Sanfuentes et al. 2016). A Gondwanan origin for this species has been suggested, but it has not been recovered in Australia to date.

Environmental DNA

Extraction of DNA from environmental samples and parallel mass sequencing has transformed biological surveys (Deiner et al. 2017, Van der Heyde et al. 2020). This methodology has been applied to *Phytophthora* surveys on several continents. The most relevant of these to the status of *Phytophthora* in Australia is the extensive survey of Burgess et al. (2017), in which metabarcoding using *Phytophthora* specific primers for the ITS1 gene region was used to detect *Phytophthora* in approximately 600 soil samples collected from across Australia. In this study, several new species not known from culture were detected and designated codes based on the phylogenetic clade (e.g., *P.* sp. AUS 9A). Subsequently, several of these species have been isolated and are included in the current review as undescribed species. However, several other species not known from Australia were detected, including *P. brassicae*, *P. capensis*, *P. europea*, *P. litchi*, *P. primulae* and *P. trifoli* (Burgess et al. 2017). These detections were mostly limited to 1–2 locations, and the read numbers were relatively low (Burgess et al. 2019). To date, none of these species has been isolated. In the absence of isolations, their detection raises an important issue; should these species be reported as present in Australia?

Metabarcoding environmental DNA (eDNA), a powerful new tool, is not without its flaws, namely laboratory contamination, false positives and mixed sequences (Calderón-Sanou et al. 2020). Riddell et al. (2019), using control reactions with known *Phytophthora* species and the same primers as Burgess et al. (2017), has demonstrated the generation of false-positive sequences, although generally with low read numbers. Careful curation of the data, basing identification on phylogenetics, and removing amplicon sequence variants (ASVs) with low read numbers reduce the chance of detecting false positives. However, while eDNA and metabarcoding are valuable tools, we strongly recommend that the detection of a species in an environmental sample must be followed up with traditional isolation methods to be considered an accurate record. Thus, without cultures, and therefore proof that the living organism was present, it is recommended that under ISPM8 (Anonymous 2017) these detected species are still considered absent from Australia.

Management within Australia

The Vegetation Health Service (VHS) laboratory at DBCA maintains the largest *Phytophthora* database in Australia. The database holds records for over 55 000 samples that have been analysed since 1982, which includes over 20 000 samples from which a *Phytophthora* spp. was isolated. As a partner in the Western Australian NRM funded Project Dieback, the department makes the VHS data available to the Dieback Information and Delivery Management System (DIDMS) a web based platform for storage, viewing, basic mapping and sharing of spatial *Phytophthora* dieback information. DIDMS is an important public communication and education tool. The department has had a dieback interpretation and mapping program since the early 1980s and, it is a requirement that on lands managed by the department, it undertaken by a suitably trained individual called an 'interpreter'. The interpreters assess the signs and symptoms of dieback in the landscape and for known susceptible (or indicator) species and undertake targeted sampling of soil and plant tissues to support their assessment. Samples are sent for analysis to VHS. Interpretation and mapping underpin 'dieback management plans', which are developed to reduce the risk of dieback introduction and spread associated with disturbance activities (e.g., mining, harvesting, road construction and maintenance).

The database compiled for this review (Supplementary material S1), as summarised in Table 1, provides a valuable baseline resource for all Australian jurisdictions. Some common species have been detected in all jurisdictions, but other species are absent, and a restriction in the movement of plants-for-planting between states could prevent their introduction. Several major crop pathogens, *P. macrochlomydospora*, *P. medicaginis*, *P. sojae* and *P. vignae*, are absent from WA. Regulation of the movement of their host species between States can help to ensure they do not get introduced. For example, WA requires soybean seed to be treated with metalaxyl to prevent introducing *Phytophthora sojae* from the eastern states (Anonymous 2020b); however, perhaps other commodities should also be regulated. Conversely, 28 newly described species and undescribed taxa, predominantly isolated from natural ecosystems in WA, have not been found in eastern Australia. Very little is known about these taxa's pathogenicity and host range, and care should be taken to avoid their introduction into eastern Australia. Regulation of plants-for-planting (trade in living plants and germplasm) would be the most effective way to prevent their movement.

Managing risk of new Phytophthora introductions

The unified framework for biological invasions recognises four stages; transport, introduction, management and spread (Blackburn et al. 2011, Robertson et al. 2020). The cost of controlling or managing pathogens increases as an organism moves along the stages. The cheapest and most effective option is at the transport phase and involves prevention. Early detection at the arrival stage can allow eradication, while only containment and asset protection are practicable for later stages. Transportation pathways for *Phytophthora* would be translocation with the host plant (including soil) and soil adhering to luggage (including hiking boots), equipment, or machinery. Many *Phytophthora* species produce resistant resting structures, such as oospores, which can survive without a living host for some time. However, to establish, the resting structures must germinate in the presence of a host. As a result, regulations governing the transportation of living plants and the inspection of imported goods for soil adhering to them can help to prevent their introduction.

Managing invasive pathogen risk associated with international trade has three major hurdles. The first is the conundrum of name-based biosecurity; many invasive pathogens were unknown until they were introduced into a naïve environment and caused disease (Hortal et al. 2015); that is, it is difficult to stop the import of organisms that are unknown or not known to be a threat. The second is estimating the danger of various diseases due to the uncertainty associated with the likelihood of an outbreak occurring. This is based on the biology of the pathogen, the presence of suitable hosts and a conducive environment. The third hurdle is regulatory, based on the parameters of multilateral agreements that handle international trade hazards (Perrings 2016).

Name-based biosecurity

Name-based biosecurity relies on robust and accepted taxonomy, but for many microorganisms, the presence of morphologically identical species and lack of information on biogeography hinders timely identification and assignment of alien status (McTaggart et al. 2016). Named-based biosecurity is helpful for species with a limited host range as it is possible to control the trade in a few commodities; however, this is more problematic for species with a broad host range. Even when an organism is known, one of the most perplexing impediments in declaring a species native or introduced to a particular country is a definitive understanding of its native range (or centre of origin). One of the few ways to unravel this is to conduct population genetic studies based on extensive collections of isolates. Various genetic markers have been used with *Phytophthora*, such as isozymes, RFLPs, AFLP, microsatellite markers and SNPs (Grover & Sharma 2016). Using markers, the Andes mountain range in South America was determined as the centre of origin of *P. infestans* (Fry et al. 1992) and South-East Asia the native range for *P. palmivora* (Mchau & Coffey 1994). However, admixture was observed among a global collection of *P. nicotianae* from a wide range of hosts (Mammella et al. 2013, Biasi et al. 2016). Using SNPs, the introduction of *P. pluvialis* to New Zealand from the northwestern USA was confirmed (Brar et al. 2018). Many of the earlier studies investigating intraspecific variability have subsequently turned out to be investigations of species complexes. For example, Oudemans et al. (1994) identified five isozyme groups within the *P. citricola* complex; each group was subsequently described as a new species. Similarly, Förster & Coffey (1993) identified four groups within the *P. megasperma* complex, now separate species. One of the biggest obstacles to overcome when declaring a pest status is the lack of reliable data on the present status of a species in any specific country or location (Hortal et al. 2015). The database compiled for this review and the information provided for each *Phytophthora* species does this for Australia.

Estimating risk

In the absence of knowledge on the centre of origin, the best alternative is to compare presence and absence data between countries and assess risk. Two recent studies have addressed this. Firstly, (Scott et al. 2019a) collated a global database of approximately 12 500 *Phytophthora* disease reports to benchmark genus-wide distribution and invasiveness. Countries with diverse ecosystems, diversified agriculture and forestry, and intensive research programs had reported the most diseases. Consequently, most countries, especially in the developing world, had lower than predicted species numbers. Thus, while the database has been used to generate a tool whereby the species present in two countries could be compared, the absence of a *Phytophthora* species in one country could reflect a lack of reporting rather than genuine absence. Secondly, Barwell et al. (2021) used host range, habitat and morphological and physiological traits of known *Phytophthora* species to predict the risk and future global impacts of *Phytophthora* species. Informative traits for horizon scans and risks assessments were identified as the disease symptom, growth rate, minimum temperature for growth and the wall thickness of resting structures. Root pathogens were more widely distributed and found on more hosts than foliar pathogens. Host generalists tended to have thicker resting structures and faster growth rates. In both these approaches, information already gathered from well-known species can be extrapolated to newly described species to predict their potential behaviour.

The assignment of risk and the management response for species within Australia has traditionally been made on whether they are native or introduced. As we have shown, the global origin of most *Phytophthora* species is uncertain. However, the distribution of most species within Australia is also poorly known, making decisions about which to prevent or manage complex. Good phytosanitary practices in production systems and natural ecosystems will be necessary for limiting dispersal and preventing new disease outbreaks for introduced *Phytophthora* species. Rew et al. (2020) argue that, with native species also moving to new areas because of the changing climate, the most important consideration for management should be whether they cause impacts regarded as negative when they arrive rather than from where they came. Careful monitoring of plant health will be essential for the early detection of such negative impacts.

Regulations

Plant and plant product transportation has frequently been shown to be the primary avenue for introducing plant pathogens (Schrader & Unger 2003, Santini et al. 2018, Sikes et al. 2018). The International Plant Protection Convention (IPPC) and the World Trade Organization Agreement on the Application of Sanitary and Phytosanitary Measures (SPS) both have phytosanitary laws in place to avoid the accidental introduction of plant pathogens. However, the General Agreement on Tariffs and Trade (GATT) makes it challenging to balance the nett gains from trade and the costs of infectious disease risks of trade by limiting both the range of measures available for dealing with infectious disease risks and the scope for coordinating international action (Perrings 2016). The WTO agreement on applying sanitary and phytosanitary measures (SPS Agreement) excludes many of the measures known to be most effective at the national level by limiting permissible options to those that cannot be characterised as protectionist or discriminatory.

The increasing volume and diversity of traded plants present a significant challenge (Schrader & Unger 2003), as, in most countries, only a small percentage (estimated 2–3 %) of consignments are subject to standard inspections (Eschen et al. 2015). In a recent review of managing biological invasions and international trade, Epanchin-Niell et al. (2021) identified five biosecurity interventions to manage the risk of introducing new pathogens.

1 Pest risk assessments (PRAs) evaluate the likelihood of a species arriving and establishing itself, as well as the potential for damage. The limitation here is that the organism being assessed needs to be a known pathogen.
2 Pre-border biosecurity interventions include phytosanitary treatments (such as fumigating imported plant material), pre-export clearance inspections, and risk-reducing procedures deployed during production and transport to reduce the risk of alien invasive pathogens from trade before arrival in a recipient port.
3 Incentive-based options for minimising alien invasive pathogens risk include tariffs, tradeable risk permits, liability insurance, and environmental performance bonds.
4 Border inspections targeted toward high-risk commodities.
5 Combined inspections, pre-interventions and SPS measures have been more cost-effective than solo interventions.

CONCLUSIONS

Based on the extensive database compiled for this review, there are 99 *Phytophthora* species reported from Australia, of which eight are unsubstantiated and can be considered absent. Additionally, several *Phytophthora* species, currently absent from Australia, were identified as high risk; these species are all well-known pathogens in agriculture or forestry or cause severe damage to natural ecosystems. Restricting the introduction of

pathogens with few hosts, for example, several *Phytophthora* species in clades 1, 7 and 8, is relatively easy to manage as only a few commodities need to be considered. Restriction of unknown species is almost impossible within regulatory systems limited to name-based biosecurity. Unknown species can only be managed by controlling pathways.

Most introductions of *Phytophthora* into Australia are probably historical, as regulations on the trade of soil and live plants have been in place since the *Quarantine Act* of 1908. Australian import conditions for plant-for-planting are more stringent than most countries (Eschen et al. 2015). Most whole imported plants must undergo a post-entry quarantine period for 3–12 months in an approved facility, and 100 % of tissue cultures are inspected at the border (Bicon). This is an enviable position; management of existing introduced *Phytophthora* species within man-managed agricultural systems can be accomplished without the added complication of new genotypes constantly arriving. However, the spread of serious pathogens such as *P. cinnamomi* within our natural ecosystems still needs to be limited.

The lack of trustworthy data on the current condition of a species in any specific country or place is one of the most difficult challenges to overcome when establishing a pest status. For Australia, the database compiled for this assessment and the information supplied for each species accomplishes this. As such, it is hoped that this review will help facilitate risk assessments and trade negotiations by federal and state governments by providing a comprehensive resource on the current status of *Phytophthora* species in Australia. Such uses would include international trade in plants and plant products and the domestic movement of plants-for-planting and soil or other natural products.

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