



Taxonomy, biogeography and evolution of thirty-four taxa in *Phytophthora* Clade 7a including eleven new species from natural forests and updated descriptions for *P. fragariae*, *P. rubi* and the '*P. ×alni* hybrid complex'

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Abstract: Over the past three decades, surveys in natural and managed ecosystems, driven mainly by forest biosecurity issues, have greatly expanded knowledge of the global diversity and biogeography of the plant pathogen genus *Phytophthora*. In *Phytophthora* subclade 7a alone, 16 new species were described raising the number of validly described species in this subclade to 18. Recently, in further surveys conducted in natural forests of Japan, Vietnam, Europe and North America, 11 more new Clade 7a species and one other 7a taxon have now been identified. All are considered to be endemic to the surveyed sites. They are formally described here, including their morphological properties, colony and temperature-growth characteristics and their phylogenetic relationships. Informal, updated descriptions without nomenclatural act are also presented for the known species *P. fragariae*, *P. rubi*, *P. uniformis*, *P. ×alni* and *P. ×multiformis*. With now 34 taxa including hybrids, Clade 7a is currently the largest *Phytophthora* subclade. It is essentially a Northern Hemisphere subclade, with a disjunct distribution in North America, Europe and Asia which probably reflects an original Laurasian ancestral distribution ~90–80 Mya and subsequent post-Laurasian migrations and radiations. It is comprised of predominantly soilborne and aquatic species with non-papillate non-caducous sporangia, though some may have facultative adaptations to a degree of aerial dispersal. The largest diversity hotspots are in Southeast and East Asia, and both adaptive sympatric and non-adaptive radiations are indicated in the data. All 22 'pure' or non-hybrid species are self-fertile and exhibit relatively low nuclear heterozygosity levels. In contrast, high heterozygosity levels, relatively high numbers of tri- and partly tetra-allelic sites and maternal lines partly shared with other Clade 7a taxa are consistent with ten of the taxa (30 %) originating via interspecific hybridisation. Of these five are self-fertile, but unusually, given their likely self-fertile parents, the other five, including the '*P. ×cambivora* hybrid complex', have an A1/A2 or outcrossing breeding system. Some of the hybrids, such as the '*P. ×alni* hybrid complex', are known to have emerged as a result of anthropogenic disturbance events. Numerous *Phytophthora* species, including several in Clade 7a, have become highly damaging pathogens of trees and agricultural crops as a result of historical introductions via global plant trade. However, for the 11 new species described here, no symptoms were observed at the natural sample sites and their natural and potential hosts are unknown. The same applies to well over 150 *Phytophthora* species in other Clades and subclades, representing a significant plant health evidence gap. It is recommended that the biosecurity risk to forests, natural ecosystems and agriculture posed by these previously scientifically unknown taxa be actively investigated.

Key words: allopatric speciation, biodiversity, breeding systems, hybrids, Laurasia, novel taxa, pathogens, phylogeny, plant biosecurity, sympatric species radiation.

Taxonomic novelties: New species: *Phytophthora algida* T. Jung, N.M. Chi, I. Milenković & M. Horta Jung, *Phytophthora arta* T. Jung, K. Kageyama, C.M. Brasier, Z.Á. Nagy & M. Horta Jung, *Phytophthora facultativa* T. Jung, T. Corcobado, Z.Á. Nagy & S. Raghuwinder, *Phytophthora grandoogonia* T. Jung, N.M. Chi, Z.Á. Nagy & M. Horta Jung, *Phytophthora infundibuliformis* T. Jung, T. Májek, I. Milenković & M. Ferreira, *Phytophthora irregularis* T. Jung, K. Kageyama, S. Uematsu, J.F. Webber & M. Horta Jung, *Phytophthora laevigata* I. Milenković, T. Jung, Z. Tomić & Z. Stanivuković, *Phytophthora sessilis* T. Jung, N.M. Chi, I. Milenković & M. Horta Jung, *Phytophthora ×grandisporangia* T. Jung, N.M. Chi, I. Milenković & M. Horta Jung, *Phytophthora ×leptopleura* T. Jung, H. Masuya, K. Kageyama, A. Hieno & M. Horta Jung, *Phytophthora ×nodosa* T. Jung, A. Hieno, H. Masuya, K. Kageyama, & S. Uematsu

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INTRODUCTION

The oomycete genus *Phytophthora* is one of the most environmentally and economically damaging genera of plant pathogens, responsible for diseases of many horticultural and agricultural crops, forest trees, ornamentals and native plants. Severe damage occurs primarily when *Phytophthora* species are introduced to new environments or when naïve and susceptible hosts are introduced to their natural ranges (Erwin & Ribeiro 1996, Lamour 2013, Jung *et al.* 2018a, Brasier *et al.* 2022, Chen *et al.* 2022). In contrast, many globally damaging *Phytophthoras*, such as *P. cinnamomi*, *P. infestans*, *P. lateralis*, *P. ramorum* and *P. ×cambivora*, apparently cause little damage to natural hosts within their centres of origin (Niederhauser 1991, Brasier *et al.* 2010, 2012, Goss *et al.* 2014, Jung *et al.* 2017a, 2020, 2021, 2024, Shakya *et al.* 2021, Mullett *et al.* 2023). Outbreaks can reach epidemic levels on susceptible hosts when conditions are conducive for rapid sporangial or zoospore spread. Host ranges can be highly species- or genus-specific, or range from ferns and conifers to monocots and dicots, as in the case of *P. cinnamomi* (Hardham & Blackman 2018).

The scale of the threats posed by introduced *Phytophthoras* means that understanding the biodiversity of the genus is critical for effective food and ecosystem biosecurity. Over the past 25 years, largely through targeted diversity surveys, the number of described *Phytophthora* species has increased exponentially (cf. Brasier *et al.* 2022). Currently the genus comprises nearly 270 culturable necrotrophic or hemibiotrophic species exhibiting mainly soil-, water- or airborne lifecycles (Chen *et al.* 2022, Jung *et al.* 2022, 2024, Abad *et al.* 2023, Brasier *et al.* 2025, Abad & Abad 2026, Crous *et al.* 2026, Paap *et al.* 2026, Wang *et al.* 2026) and seven validly described and accepted, near-obligate biotrophic species, i.e., *P. cyperi*, *P. cyperi-bulbosi*, *P. leporinae*, *P. leersiae*, *P. oryzae*, *P. polygoni* and *P. verrucosa* (e.g., Brasier *et al.* 2022, 2025, Abad *et al.* 2023, Bourret *et al.* 2025, Abad & Abad 2026). Due to the many new species descriptions, the ten *Phytophthora* evolutionary clades identified in the first genus-wide ITS rDNA sequence-based phylogeny of Cooke *et al.* (2000) have now been expanded to 16 phylogenetic clades with numerous subclades (Brasier *et al.* 2022, Chen *et al.* 2022, Abad *et al.* 2023, Seidl & Bourret 2024).

Within this structure, the highly specialised, obligate biotrophic downy mildews reside as two separate clades (one including also *P. podocarp*), having apparently rapidly evolved at least twice from *Phytophthora* ancestors (e.g., Cooke *et al.* 2000, Thines & Choi 2016, Jung *et al.* 2017a, Brasier *et al.* 2022, Abad *et al.* 2023, Seidl & Bourret 2024). This led to some proposals to split major *Phytophthora* evolutionary clades into multiple genera (Runge *et al.* 2011, Thines 2023, Thines *et al.* 2023 and cf. Brasier *et al.* 2022). In response, the global scientific community has voted overwhelmingly in favour of preserving and protecting the current, long standing generic concept, for reasons ranging from the absence of salient character differences between the clades to the genus' immense communication value (Brasier *et al.* 2025).

In the original Cooke *et al.* (2000) phylogeny, subclade 'a' of major Clade 7 (hereafter Clade 7a) comprised only two host-specific varieties of *P. fragariae* and two wide-host range pathogens, *P. cambivora* and *P. cinnamomi*. Since then, *P. cinnamomi* has been resolved into a new subclade, 7c; *P. fragariae* var. *rubi* has been designated as a separate species *P. rubi*; and Clade 7a has expanded to a current 18 described species and two informally designated taxa (Jung *et al.* 2017a, b, Chen *et al.* 2022, Abad *et al.* 2023, Crous *et al.* 2024). Apart from *P. abietivora* (Li *et al.* 2019), all 15 Clade 7a species formally or informally described since 2000 have been

isolated exclusively or predominantly from natural ecosystems (Jung *et al.* 2002, 2017a, b, Brasier *et al.* 2004, Crous *et al.* 2024). Some Clade 7a species, such as the host-specific *P. fragariae* and *P. rubi* and the wide-host range pathogen *P. ×cambivora*, have long been known for causing severe damage to horticultural crops and forest trees (Wilcox *et al.* 1993, Milholland 1994, Erwin & Ribeiro 1996, Jung *et al.* 2018a). Since the 1990s, the host-specific species from the '*P. ×alni* complex' have killed high numbers of *Alnus* trees in riparian ecosystems and swamps across Europe (Gibbs *et al.* 2003, Brasier *et al.* 2004, Jung *et al.* 2018a). Most other Clade 7a species, in contrast, have only been found associated with healthy native trees or streams in natural forests of Taiwan (Jung *et al.* 2017a, b) and healthy or, at most, mildly declining forest trees in Europe (Jung *et al.* 2002, 2017c). Further, six of the 20 known Clade 7a taxa (~30 %) show evidence of interspecific hybridisation, underlining the evolutionary importance of this process in emergence or continuing adaptation of *Phytophthoras* (Brasier 1995, Brasier *et al.* 1999, May *et al.* 2003, Donahoo & Lamour 2008, Bertier *et al.* 2013, Nagel *et al.* 2013, Burgess 2015, Husson *et al.* 2015, Jung *et al.* 2017a, c, 2024).

Over the past two decades we have sampled widely for *Phytophthoras* in relatively unsurveyed natural ecosystems, in particular in Asia, Europe and the Americas. These surveys are aimed at advancing understanding of the diversity and evolutionary history of the genus; identifying the geographic origins of damaging *Phytophthora* species; and assessing the scale of the biosecurity threats posed to forests globally by 'scientifically unknown' *Phytophthoras* (cf. Brasier 2008, Jung *et al.* 2016). In these surveys 12 putative new Clade 7a taxa were preliminarily identified, distributed among 400 *Phytophthora* isolates. Some of these have already been informally designated, e.g., as *P. taxon attenuata*-like 1, 2 and 3 (Jung *et al.* 2020), *P. ×attenuata*-related and *P. ×heterohybrida*-related (Van Poucke *et al.* 2021). In the present study, morphological criteria, temperature-growth rate data and DNA sequence data from eight nuclear and three mitochondrial gene regions were used to characterise the 12 new taxa and compare them to existing Clade 7a species. Here we formally characterise and describe 11 of them as new species and discuss the implications of our broader findings for the evolution and biogeography of Clade 7a and for global plant biosecurity.

TERMINOLOGY

Use of the terms *Phytophthora* taxon x and *Phytophthora* sp. x

The informal term '*Phytophthora* taxon x' (cf. Brasier *et al.* 2003) was developed to cover situations where it was clear that a novel entity of some taxonomic level had been identified, but formal description was likely to be delayed pending further analysis to determine the level of taxonomic distinction (e.g., species, subspecies, variety etc; cf. Brasier & Rayner 1987) and because of the often considerable time required to produce the appropriate publication. This situation has arisen more frequently as more and more novel *Phytophthora* taxa are being discovered.

In this context, we do not concur with the use of the informal terminology '*Phytophthora* sp. x'. A putative new taxon is not a species (or a 'sp.') until its correct hierarchical status has been determined (as far as is reasonable), and its proposed name has been formally designated under the ICNafp (International Code of Nomenclature for algae, fungi, and plants; <https://www.iaptglobal.org>).

org/ncn) guidelines. On this basis, we consider that informal use of the term '*Phytophthora* sp. x' in the case of a putative but only partially characterised new taxon is essentially prejudicial to its eventual ranking. We have therefore confined ourselves to using the term '*Phytophthora* taxon x' or '*Phytophthora* t. x' throughout this manuscript.

Definitions of 'homothallism', 'heterothallism' and sterility

Homothallism and heterothallism are somewhat archaic, quasi-morphological terms used more to describe whether gametangia are formed in single or paired *Phytophthora* cultures rather than the biological strategy this represents. We prefer a more Darwinian process-related definition that implies the organism's underlying breeding system or breeding strategy.

However, because historically these terms have been used routinely in species descriptions, we have also used them occasionally here, but with the following qualification. By *homothallic* we mean intrinsically self-fertile in a single culture and therefore often inbreeding, but this process does not preclude outbreeding in nature as a result of the fusion between antheridia and oogonia of different genotypes of the species. We will more often refer to these taxa in the text as 'self-fertile'. By *heterothallic* we mean that two mating or compatibility types (A1 and A2) are typically required to initiate gametogenesis between bisexual, largely self-incompatible individuals; but while this process promotes outcrossing, once initiated it can also lead to a significant frequency of self-fertilisation (selfing). We will refer to this breeding system in the text as A1/A2 outcrossing, or just 'A1/A2'. By *sterile* we mean an apparent lack of the intrinsic ability to form gametangia whether in a single culture or pairings with A1 or A2 isolates; but this does not exclude the possibility that an isolate or taxon may act as a 'silent' A1 or A2, inducing gametangial formation by selfing in an A2 or an A1 isolate of another species (cf. *P. gonapodyides*, Brasier *et al.* 2003).

SPECIES DELIMITATION AND HYBRID DESIGNATION

'Species concept'

As the number of known *Phytophthora* taxa has grown, the methods and criteria used to assess the structure of *Phytophthora* populations have also increased. As a result, the range of genetic and phenotypic structure accepted as representing 'conspecific' *Phytophthora* populations is now remarkably diverse. This situation is compounded by the potential conflict between attempting to define species boundaries at the population level and the need to apply useful 'species labels' in scientific communication. There are no fixed criteria — species are necessarily proscribed by combinations of behavioural, morphological and molecular variables; and species may be shapeshifting (Brasier 1983), especially in the context of introductions. The 'species concept' we have applied here aims to be holistic and population-based in terms of criteria (cf. Brasier 1991), and to be in line with the vast majority of *Phytophthora* species descriptions published since molecular tools began to be used in *Phytophthora* taxonomy. While this broadly applies to both pure (non-hybrid) taxa and hybrid taxa, it is accepted that hybrid taxa are a special category, and that they may not even 'breed true', especially hybrid taxa of recent origin.

To be formally described here as a novel species, a taxon

needs in particular to be well supported in multi-locus nuclear and mitochondrial phylogenetic analyses including — as a minimum — the accepted 'barcode genes' for the genus (cf. Chen *et al.* 2022, Abad *et al.* 2023). In addition, it must have synapomorphies, i.e., morphological, physiological (cardinal temperatures, growth rates) or behavioural (e.g., breeding system, reproductive strategy, lifestyle, ecology, host range) characters or combinations of characters that distinguish it from related species.

In our view, on current evidence there is no specific threshold of sequence differences in *Phytophthora* that determines whether or not a taxon constitutes a distinct species, i.e., we do not concur with a purely phylogenetic species concept. As a consequence, some taxa will be described as species where there is a both a unique and well supported phylogenetic position and clear distinguishing synapomorphies, despite comparatively small sequence differences to related species. In cases where there is considerable genetic variability or substructure across a taxon population but no associated variation in synapomorphies we will not, for now, assign specific or subspecific epithets.

Hybrid designation

As in other recent investigations (e.g., Nagel *et al.* 2013, Burgess 2015, Jung *et al.* 2017a, 2024) the conclusion that a taxon is a species hybrid is based mainly on high levels of nuclear heterozygosity. This has recently been characterised as ca > 0.3 % heterozygosity (Jung *et al.* 2024). High similarity of different mitochondrial gene sequences to another *Phytophthora* taxon is taken as an indication that the latter is a potential 'maternal parent'. Unusually high oogonial and oospore abortion rates, including chromosome pairing failures during meiosis, are also taken as possible evidence of interspecific hybridity, especially heteroploidy (cf. Brasier *et al.* 1995, 1999). So too is the failure to differentiate sporangial cytoplasm into zoospores, resulting in multi-nucleate, multi-flagellate structures. Where possible, allopolyploidy may be confirmed by genome sequencing, nuclear genotyping-by-sequencing (GBS) and flow cytometry, although the latter is not diagnostic for hybrids with diploid genomes (cf. Jung *et al.* 2017a, Van Poucke *et al.* 2021, Mullett *et al.* 2023). A probable hybrid taxon is considered a confirmed hybrid if allelic phasing in genome sequencing or GBS studies demonstrates the presence of tri-allelic or tetra-allelic sites (cf. Van Poucke *et al.* 2021, Mullett *et al.* 2023).

MATERIAL AND METHODS

Phytophthora isolates

Details of all isolates used in the phylogenetic, morphological and temperature-growth studies are given in Table 1. Sampling and isolation methods from forest soil and river systems were according to Jung *et al.* (1996, 2017c, 2020) and Pérez-Sierra *et al.* (2022). Necrotic baiting leaves, necrotic leaves attached to plants or naturally fallen leaves collected from streams were plated onto selective PARPNH-agar (Jung *et al.* 1996, 2020). The isolates of the 11 new Clade 7a species were recovered during oomycete surveys between 2016 and 2020 from streams, rhizosphere soil and, rarely, necrotic leaves in subtropical montane cloud forests and humid evergreen forests in Vietnam; a subtropical lowland forest in Louisiana, USA; warm-temperate forests in Japan; and cool-temperate forests in Bosnia-Herzegovina and Japan (Table 1, Fig. 1). One isolate was obtained in 2022 from a horticultural *Corylus avellana* plantation



Table 1. Details of isolates from *Phytophthora* major Clade 7 included in the phylogenetic, morphological, growth-temperature and biogeography studies. GenBank accession numbers are given in Table S2.

<i>Phytophthora</i> taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. abietivora</i>	7a	NRRL 6889, RC2017-1, TJ1652, ET	SF	P, T	<i>Abies fraseri</i> christmas tree	USA, Connecticut, 2017, R. Cowles	Li <i>et al.</i> (2019)
		062_E, OPT2019_014	SF	P	<i>Abies balsamensis</i> christmas tree, rhizosphere soil	Canada, Quebec, Chaudière-Appalaches, 2019, G. Charron	Charron <i>et al.</i> (2024)
		170_B, OPT2019_030	SF	P	<i>A. fraseri</i> christmas tree, rhizosphere soil	Canada, Quebec, Estrie, 2019, G. Charron	Charron <i>et al.</i> (2024)
		33F7 ⁵ , p229, BM416 ⁶	SF	B	<i>Quercus</i> sp., rhizosphere soil	USA, West Virginia, 2005, Y. Balci	Balci <i>et al.</i> (2007), Yang <i>et al.</i> (2017)
		HK09	SF	B	<i>Iris ensata</i> var. <i>ensata</i> ; basal rot	Japan, Fukuoka, 2011, n/a	Amemiya <i>et al.</i> (2011a, b)
		KM09	SF	B	<i>Iris ensata</i> var. <i>ensata</i> ; basal rot	Japan, Shizuoka, 2011, n/a	Amemiya <i>et al.</i> (2011a, b)
		SW09 ⁷	SF	B	<i>Iris ensata</i> var. <i>ensata</i> ; basal rot	Japan, Chiba, 2011, n/a	Amemiya <i>et al.</i> (2011a, b)
<i>P. algid</i> ⁸	7a	YZ09 ⁷	SF	B	<i>Iris ensata</i> var. <i>ensata</i> ; basal rot	Japan, Yamagata, 2011, n/a	Amemiya <i>et al.</i> (2011a, b)
		CBS 153095, VN029, ET	SF	P, M, T	<i>Acer oblongum</i> , rhizosphere soil	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	Amemiya <i>et al.</i> (2011a, b) This study
		VN031	SF	P, M, T, G	<i>A. oblongum</i> , rhizosphere soil	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	Jung <i>et al.</i> (2017b)
		VN304	SF	P, M, T, G	<i>A. oblongum</i> , rhizosphere soil	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	This study
		VN568	SF	P, M, T, G	<i>Castanopsis chinensis</i> , rhizosphere soil	Vietnam, Ba Vi National Park, 2016, T. Jung & N.M. Chi	This study
		CBS 153092, JP032, ET	SF	P, M, T, G	Baiting stream R20, montane mixed forest	Japan, Kyushu, Shiiba area, 2017, T. Jung & S. Uematsu	This study
		JP055	SF	P, M	Baiting stream R20, montane mixed forest	Japan, Kyushu, Shiiba area, 2017, T. Jung & S. Uematsu	This study
<i>P. arta</i>	7a	JP066	SF	P, M, T	Baiting stream R13, <i>laurosilva</i> forest	Japan, Shikoku, Ichinomata, 2017, T. Jung & K. Kageyama	This study
		JP418	SF	P, M, T	Baiting stream R20, montane mixed forest	Japan, Kyushu, Shiiba area, 2017, T. Jung & S. Uematsu	This study
		JP425	SF	P, M	Necrotic <i>Pteris japonica</i> leaf, montane mixed forest	Japan, Kyushu, Shiiba area, 2017, J. Webber & C.M. Brasier	This study
		JP720	SF	P, M, T, G	Necrotic leaf floating in stream R15, <i>laurosilva</i> forest	Japan, Shikoku, Ichinomata, 2017, T. Jung & M. Horta Jung	This study
		JP821	SF	P, M, T, G	Necrotic leaf floating in stream R20, montane mixed forest	Japan, Kyushu, Shiiba area, 2017, T. Jung & H. Masuya	This study
		JP974	SF	P, M, T	Necrotic leaf floating in stream R21, montane mixed forest	Japan, Kyushu, Shiiba area, 2017, T. Jung & H. Masuya	This study
		CBS 141199, TW129, ET	SF	P, T, G	<i>Castanopsis carlesii</i> , rhizosphere soil	Taiwan, Sheipa National Park, 2013, T. Jung	Jung <i>et al.</i> (2017a)



Table 1. (Continued).

Phytophthora taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. cinnamomi</i>	7c	CBS 141200, TW118	SF	P, T, G	<i>Chamaecyparis formosensis</i> , rhizosphere soil	Taiwan, Sheipa National Park, 2013, T. Jung	Jung et al. (2017a)
		VN026	SF	P, M, T, G	<i>A. oblongum</i> , rhizosphere soil	Vietnam, Hoàng Liễn National Park, 2016, T. Jung & N.M. Chi	This study
		CBS 144.22, ATCC 1407, IMI 022938, WPC P2110, TJ082, 61J1, P61/04, Pc 110, P 724, ET	A1/A2 (A2)	P	<i>Cinnamomum burmannii</i> , bark canker	Indonesia, Sumatra, 1922, Rands	Rands (1922), Scanu et al. (2014), Jung et al. (2017a)
		TW012	A1/A2 (A1)	MA	<i>Cinnamomum micranthum</i> , rhizosphere soil	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a, c)
		MP74, TJ1123	A1/A2 (A2)	MA	n/a	Australia, Western Australia, n/a, n/a	Hüberli (1995), Jung et al. (2017a)
<i>P. europaea</i>	7a	TJ1244	A1/A2 (A2)	M	<i>Banksia</i> sp., bark canker	Australia, Western Australia, 2009, T. Jung	This study
		CBS 109049, TJ1621, EUR2, ET	SF	P	<i>Quercus robur</i> , rhizosphere soil	France, Amance, 1998, T. Jung	Jung et al. (2002)
		CBS 109051, 2AE2, EUR3, TJ321	SF	P, T, G	<i>Quercus</i> sp., rhizosphere soil	France, Amance, 1998, E.M. Hansen	Jung et al. (2002)
		CBS 109053, TJ1822, EUR1, JKI-BBA 12/02-3, ILVO SW37	SF	T, G	<i>Q. robur</i> , rhizosphere soil	Germany, Lübeck, 1995, T. Jung	Jung et al. (2002, 2017a)
		SFB021, SB1265	SF	T	<i>Q. robur</i> , rhizosphere soil	Serbia, Srem Forest Area, 2011, I. Milenkovic	This study
<i>P. facultativa</i>	7a	CBS 153101, LU410, ET	SF	P, M, T	<i>Rubus</i> sp. leaf floating in forest stream	USA, Louisiana, 2020, T. Corcobado & T. Májek	This study
		LU060	SF	P, M, T	<i>Rubus</i> sp. leaf floating in forest stream	USA, Louisiana, 2020, T. Corcobado & T. Májek	This study
		LU409	SF	P, M, T	<i>Rubus</i> sp. leaf floating in forest stream	USA, Louisiana, 2020, T. Corcobado & T. Májek	This study
		LU411	SF	P, M, T	<i>Rubus</i> sp. leaf floating in forest stream	USA, Louisiana, 2020, T. Corcobado & T. Májek	This study
<i>P. fagacearum</i>	7a	CBS 150432, PDA2233, ET	SF	P	<i>Fagus grandifolia</i> , necrotic leaf	USA, Pennsylvania, Lancaster County, 2020, D.S. Bily	Crous et al. (2024)
<i>P. flexuosa</i>	7a	CBS 141201, TW078, ET	SF	P, T, G	<i>Fagus hayatae</i> , rhizosphere soil	Taiwan, Taiping Mountain, 2013, T. Jung	Jung et al. (2017a)
		CBS 141202, TW108	SF	P, T, G	<i>F. hayatae</i> , rhizosphere soil	Taiwan, Taiping Mountain, 2013, T. Jung	Jung et al. (2017a)
		JP219	SF	P, M, T, G	Baiting stream R06, montane forest	Japan, Honshu, Takayama, 2017, T. Jung & K. Kageyama	This study
		JP722	SF	P, M, T	<i>Pterocarya rhoifolia</i> , rhizosphere soil	Japan, Honshu, Takayama, 2017, T. Jung & S. Uematsu	This study

Table 1. (Continued).

Phytophthora taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. formosa</i>	7a	JP803	SF	P, M, T, G	<i>Chamaecyparis pisifera</i> , rhizosphere soil	Japan, Honshu, Takayama, 2017, T. Jung & A. Hieno	This study
		JP819	SF	P, M, T, G	Baiting stream R07, montane forest	Japan, Honshu, Takayama, 2017, T. Jung & H. Masuya	This study
		JP1053	SF	P, M, T	<i>Chamaecyparis obtusa</i> , rhizosphere soil	Japan, Shikoku, Ichinomata, 2017, T. Jung & C.M. Brasier	This study
		JP1058	SF	P, M, T	<i>C. obtusa</i> , rhizosphere soil	Japan, Shikoku, Ichinomata, 2017, T. Jung & J.F. Webber	This study
		CBS 141203, TW107, ET	SF	P, T	<i>Araucaria cunninghamii</i> , rhizosphere soil	Taiwan, Lenchuachih, 2013, T. Jung	Jung et al. (2017a)
		TW013	SF	P, T	<i>Quercus glandulifera</i> , rhizosphere soil	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a)
		JP343	SF	P, M, T	Baiting stream R15, <i>Quercus-Chamaecyparis-Tsuga-Abies</i> forest	Japan, Shikoku, Ichinomata, 2017, T. Jung & K. Kageyama	This study
		JP440	SF	P, M, T, G	Baiting stream R17, <i>laurosilva</i> forest	Japan, Kyushu, Aya, 2017, T. Jung & S. Uematsu	This study
		JP639	SF	P, M, T	Streambed soil, <i>laurosilva</i> forest	Japan, Kyushu, Takakuma, 2017, T. Jung & H. Masuya	This study
		JP968	SF	P, M, T, G	<i>Machilus thunbergii</i> , rhizosphere soil, <i>laurosilva</i> forest	Japan, Shikoku, Satayama, 2017, T. Jung & M. Horta Jung	This study
<i>P. fragariae</i>	7a	JP2357	SF	M	Baiting stream R15, <i>Quercus-Chamaecyparis-Tsuga-Abies</i> forest	Japan, Shikoku, Ichinomata, 2017, T. Jung & C.M. Brasier	This study
		JP2358	SF	M	Baiting stream R15, <i>Quercus-Chamaecyparis-Tsuga-Abies</i> forest	Japan, Shikoku, Ichinomata, 2017, T. Jung & J.F. Webber	This study
		CBS 309.62, NRRL 64315, ATCC 11107, Hickman R-4, CPHST BL 213, EPT	SF	B, G	<i>Fragaria</i> × <i>ananassa</i>	UK, Scotland, n.a., n.a.	Abad et al. (2023)
		CBS 209.46, 61J3, IMI 181417, WPC P6231, WPC P19539, CPHST BL 18	SF	P	<i>F. × ananassa</i>	UK, Cornwall, 1946, C.J. Hickman?	Jung et al. (2017a), Yang et al. (2017), Chen et al. (2022)
		BBA L1, TJ011, LSM 773, ILVO JA06, ILVO SW38	SF	P, T, G	<i>F. × ananassa</i>	Germany, 1983, JKI	Jung et al. (2017a)
		BBA 11/94, TJ012, K018, ILVO SW39	SF	P, T, G	<i>F. × ananassa</i> 'Eisanta'	Germany, 1994, JKI	Jung et al. (2017a)
		CBS 153094, VN556, ET	SF	P, M, T, G	<i>Dysoxylum juglans</i> & <i>C. chinensis</i> , rhizosphere soil	Vietnam, Ba Vi National Park, 2016, T. Jung & N.M. Chi	This study
		VN574	SF	P, M, T, G	<i>Castanopsis</i> sp., rhizosphere soil	Vietnam, Ba Vi National Park, 2016, T. Jung & N.M. Chi	This study
<i>P. grandoogonia</i> ⁸	7a						



Table 1. (Continued).

Phytophthora taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. infundibuliformis</i>	7a	VN581	SF	P, M, T, G	<i>C. chinensis</i> , rhizosphere soil	Vietnam, Ba Vi National Park, 2016, T. Jung & N.M. Chi	This study
		VN616	SF	P, M, T, G	<i>C. chinensis</i> , rhizosphere soil	Vietnam, Ba Vi National Park, 2016, T. Jung & N.M. Chi	This study
		VN618	SF	P, M, T, G	<i>Vernicia montana</i> & <i>Antidesma</i> sp., rhizosphere soil	Vietnam, Ba Vi National Park, 2016, T. Jung & N.M. Chi	This study
		VN623	SF	P, M, T, G	<i>Quercus glauca</i> & <i>Meliosma arnottiana</i> , rhizosphere soil	Vietnam, Ba Vi National Park, 2016, T. Jung & N.M. Chi	This study
		CBS 153100, LU258, ET	SF	P, M, T	<i>Acer</i> sp., rhizosphere soil	USA, Louisiana, Liberty Creek, 2020, T. Corcobado & T. Majek	This study
		LU257	SF	P, M, T	<i>Acer</i> sp., rhizosphere soil	USA, Louisiana, Liberty Creek, 2020, T. Corcobado & T. Majek	This study
<i>P. intricata</i>	7a	LU259	SF	P, M, T	<i>Acer</i> sp., rhizosphere soil	USA, Louisiana, Liberty Creek, 2020, T. Corcobado & T. Majek	This study
		LU260	SF	P, M, T	<i>Acer</i> sp., rhizosphere soil	USA, Louisiana, Liberty Creek, 2020, T. Corcobado & T. Majek	This study
		CBS 141211, TW259, ET	SF	P, T, G	<i>Quercus tarokoensis</i> , rhizosphere soil	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a)
		CBS 141210, TW007	SF	P, T, G	<i>Q. tarokoensis</i> , rhizosphere soil	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a)
<i>P. irregularis</i>	7a	TW016	SF	P	<i>Q. tarokoensis</i> , rhizosphere soil	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a)
		CBS 153091, JP1056, ET	SF	P, M, T	<i>Castanopsis cuspidata</i> , rhizosphere soil	Japan, Kyushu, Aya, 2017, T. Jung & K. Kageyama	This study
		JP095	SF	P, M, T, G	<i>Castanopsis sieboldii</i> , rhizosphere soil	Japan, Shikoku, Satayama, 2017, T. Jung & S. Uematsu	This study
		JP421	SF	P, M, T, G	<i>C. sieboldii</i> , <i>M. thunbergii</i> & <i>Quercus acuta</i> , rhizosphere soil	Japan, Shikoku, Satayama, 2017, T. Jung & S. Uematsu	This study
<i>P. laevigata</i>	7a	JP574	SF	P, M, T, G	<i>C. sieboldii</i> , rhizosphere soil	Japan, Kyushu, Takakuma, 2017, T. Jung & H. Masuya	This study
		JP745	SF	P, M, T, G	<i>Zelkova serrata</i> , rhizosphere soil	Japan, Kyushu, Takakuma, 2017, T. Jung & H. Masuya	This study
		JP853	SF	P, M, T	<i>C. sieboldii</i> , <i>M. thunbergii</i> & <i>Q. acuta</i> , rhizosphere soil	Japan, Shikoku, Satayama, 2017, T. Jung & S. Uematsu	This study
		JP964	SF	P, M, T, G	<i>C. sieboldii</i> , rhizosphere soil	Japan, Kyushu, Takakuma, 2017, T. Jung & H. Masuya	This study
		CBS 153102, BN333, ET	SF	P, M, T	<i>F. sylvatica</i> , rhizosphere soil	Bosnia and Herzegovina, Kneževo, 2019, I. Milenković	This study
		BN300	SF	P, M, T	<i>F. sylvatica</i> , rhizosphere soil	Bosnia and Herzegovina, Kneževo, 2019, I. Milenković	This study



Table 1. (Continued).

<i>Phytophthora</i> taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. rubi</i>	7a	BN301	SF	P, M, T	<i>F. sylvatica</i> , rhizosphere soil	Bosnia and Herzegovina, Knežev, 2019, I. Milenković	This study
		BN321	SF	P, M, T	<i>F. sylvatica</i> , rhizosphere soil	Bosnia and Herzegovina, Knežev, 2019, I. Milenković	This study
		BN332	SF	P, M, T	<i>F. sylvatica</i> , rhizosphere soil	Bosnia and Herzegovina, Knežev, 2019, I. Milenković	This study
		TJ1684, PLIO22	SF	P, M, T	<i>Corylus avellana</i> recently died, rhizosphere soil	Croatia, Čačinci, 2022, Z. Tomić	This study
		ATCC 90442, CBS 967.95, IMI 355974, WPC P15596, WPC P16899, FVR 11, SCRP333, R49, ET	SF	M, T, G	<i>Rubus idaeus</i> cane	UK, Scotland, 1985, SCRI	Wilcox et al. (1993), Jung et al. (2017a)
		CBS 109892, WPC P15596, FVR 67, SCRP324, P823, TJ015	SF	M	<i>R. idaeus</i>	UK, 1991, D. Kennedy	Brasier et al. (1999), Jung et al. (2017a)
	7a	CH106, TJ323	SF	P, M	<i>R. idaeus</i>	Sweden, n/a, C. Olsson	Jung et al. (2017a)
		BBA93, TJ013	SF	P, T, G	<i>R. idaeus</i>	Germany, n/a, JKI	Jung et al. (2017a)
		BBA390, TJ014	SF	P, T	<i>R. idaeus</i>	Germany, 1990, JKI	Jung et al. (2017a)
		5005038, TJ322	SF	M, G	<i>R. idaeus</i>	Netherlands, 2010, K. Rosendahl	Jung et al. (2017a)
<i>P. sessilis</i> ¹⁰	7a	9A9, P714, CC947, TJ1103	SF	M	<i>R. idaeus</i>	UK, n/a, n/a	Jung et al. (2017a)
		PHRM 09, P718, TJ010	SF	M, T	<i>R. idaeus</i>	Croatia, 2009, Z. Tomić	Jung et al. (2017a)
		230553, TJ320	SF	M	<i>R. idaeus</i>	Norway, 2006, M.-L. Herrero	Jung et al. (2017a)
		CBS 153096, VN059, ET	SF	P, M, T, G	<i>Rhododendron arboreum</i> , rhizosphere soil	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	This study
		VN253	SF	P, M, T, G	<i>Betula alnoides</i> & <i>Elaeocarpus japonicus</i> , rhizosphere soil	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	This study
		VN266	SF	P, M, T	<i>Neolitsea pollanai</i> , rhizosphere soil	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	This study
	7b	VN272	SF	P, M, T, G	Streambed soil in a swampy depression, cloud forest	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	This study
		VN273, ILVO TJ105	SF	M, T	Streambed soil in a swampy depression, cloud forest	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	Van Poucke et al. (2021)
		WPC P6497, 28F9, p236	SF	P	<i>Glycine max</i>	USA, Mississippi, 1970, n/a	Yang et al. (2017)
		CBS 142301, PH154, TJ1153, ET	SF	P, T, G	<i>Quercus ilex</i> , rhizosphere soil	Italy, Sardinia, 2012, B. Scanu	Jung et al. (2017b)
<i>P. sojajae</i>	7b						
<i>P. tyrthenica</i>	7a						
		CBS 142302, TJ533, TYR1	SF	P, T, G	<i>Q. ilex</i> , rhizosphere soil	Italy, Sicily, 2015, T. Jung	Jung et al. (2017b)



Table 1. (Continued).

<i>Phytophthora</i> taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. uliginosa</i>	7a	TJ537, TYR5, 20-6 K10e	SF	P	<i>Q. ilex</i> , rhizosphere soil	Italy, Sicily, 2015, T. Jung	Jung et al. (2017b)
		CBS 109054, WPC P10413, TJ1622, PD_00157, Pulig_OSU-2014, UL11, ET	SF	P, T, G	<i>Q. robur</i> , rhizosphere soil	Poland, Krotoszyn, 1998, T. Jung	Jung et al. (2002), Kronmiller et al. (2023)
		CBS 109055, WPC P10328, PD_00012, TJ1821, UL12	SF	P, T	<i>Quercus petraea</i> , rhizosphere soil	Germany, 1998, T. Jung	Jung et al. (2002)
		BD550	SF	B	<i>Quercus suber</i> , rhizosphere soil	Portugal, Beja, 2010, T. Jung & M. Horta Jung	Horta Jung et al. (2025)
<i>P. uniformis</i>	7a	CBS 149409, WPC P16206, CPHST BL 3, IMI 392315, NRRL 64373, P875, CH161, SCRP 9, ET	SF	P	<i>Alnus glutinosa</i> , bark canker	Sweden, 1996, C. Olsson	Brasier et al. (2004)
		TJ002, ALN58, P705, ILVO TJ007	SF	P, M, T, G	<i>A. glutinosa</i> , bark canker	Germany, Bavaria, Vilsbiburg, 1998, T. Jung	Jung et al. (2017a)
		250001, TJ027, P707	SF	P, M, T, G	<i>A. glutinosa</i> , bark canker	Norway, 2012, G.M. Strømeng	Jung et al. (2017a)
		WPC P10565, 155c, PAU 98, TJ0139, ILVO TJ009	SF	M	<i>A. glutinosa</i> , bark canker	Hungary, Hanság, 1999, I. Szabó	Nagy et al. (2003), Iosos et al. (2007), Jung et al. (2017a)
<i>P. vulcanica</i>	7a	ALN 222, P706, TJ004	SF	M	<i>A. glutinosa</i> , bark canker	Germany, Bavaria, Rott, 2001, T. Jung	Jung et al. (2017a)
		PAU 60, TJ017	SF	M	<i>A. glutinosa</i> , bark canker	France, 1999, J.C. Streito	Jung et al. (2017a)
		P887, CH166, TJ104, ILVO TJ008	SF	M, G	<i>A. glutinosa</i> , bark canker	Sweden, Save River, 1997, C. Olsson	Brasier et al. (1999), Jung et al. (2017a)
		TJ1358	SF	M, T	<i>A. glutinosa</i> , bark canker	Czechia, Svratka River, 2020, T. Jung	This study.
<i>P. xalni</i>	7a	CBS 141216, TJ229, x3a, ET	SF	P, T, G	<i>F. sylvatica</i> , rhizosphere soil	Italy, Sicily, Mount Etna, 2013, T. Jung	Jung et al. (2017b)
		CBS 141217, TJ230, x/3b Fagus TJ231, x3c	SF	P, G	<i>F. sylvatica</i> , rhizosphere soil	Italy, Sicily, Mount Etna, 2013, T. Jung	Jung et al. (2017b)
		IMI 403468, IMI 392314, WPC P16203, CBS 148927, CPHST BL 1, P772, 47A7, P155, P4/00, TJ1623, ET	SF	P	<i>Alnus</i> , bark canker	UK, Yorkshire, Doncaster, 1994, G. MacAskill	Brasier et al. (2004), Jung et al. (2017a)
		TJ1160, MAL5, P689, ILVO TJ003	SF	M, T, G	<i>A. glutinosa</i> , bark canker	Spain, Galicia, Miño River, 2009, T. Jung	Solla et al. (2010), Jung et al. (2017a)
		WPC P10568, Héviz9, PAA 93, TJ326, ILVO TJ002	SF	P, M, T, G	<i>A. glutinosa</i> , rhizosphere soil	Hungary, Héviz, 2001, Z.Á. Nagy	Nagy et al. (2003), Jung et al. (2017a)
		WPC P10569, H-5/02, TJ143	SF	M, T	<i>A. glutinosa</i> , bark canker	Hungary, Teskánd, 2002, J. Bakonyi	Bakonyi et al. (2006), Jung et al. (2017a)

Table 1. (Continued).

Phytophthora taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. ×cambivora</i> DAPC1	7a	ALN45, TJ001, ILVO TJ001	SF	M, T	<i>A. glutinosa</i> , bark canker	Germany, Bavaria, Dachau, 1999, A. Schlenzig	Jung et al. (2017a)
		TJ003, ALN144	SF	G	<i>A. incana</i> , bark canker	Rott am Inn, Bavaria, Germany, 2001, T. Jung	This study
		TJ023, Reis2, P691	SF	M, T	<i>A. glutinosa</i> , bark canker	Germany, Bavaria, Reischenhart, 2014, T. Jung	Jung et al. (2017a)
		TJ006, ALN402	SF	M	<i>A. glutinosa</i> , bark canker	Germany, Bavaria, Zolling, 2003, C. Clemenz	Jung et al. (2017a)
		2303, TJ140	SF	M, T	<i>Alnus incana</i> , bark canker	Belgium, 2002, A. Chandelier	De Merlier et al. (2005), Jung et al. (2017a)
		TJ030, DE1	A1/A2 (A1)	P, T	<i>F. sylvatica</i> , rhizosphere soil in nursery	Germany, Schleswig-Holstein, 2013, T. Jung	Jung et al. (2017a), Mullett et al. (2023)
		TJ540, 3399H, ILVO AC08	A1/A2 (A1)	P, T	<i>F. sylvatica</i> , bark canker	Belgium, Aubain, 2005, A. Chandelier	Jung et al. (2017a), Van Poucke et al. (2021), Mullett et al. (2023)
		TJ543, resi75, ILVO AC12	A1/A2 (A1)	P, T	<i>F. sylvatica</i>	Belgium, 2014, A. Chandelier	Jung et al. (2017a), Van Poucke et al. (2021), Mullett et al. (2023)
		TJ836, W1846, P771, ILVO TJ090	A1/A2 (A1)	P, T	Forest soil	Australia, New South Wales, Mt. Kosciansho National Park, 2013, n/a	Jung et al. (2017a), Van Poucke et al. (2021), Mullett et al. (2023)
		JP117	A1/A2 (A1)	P, M, T	Baiting stream R16, laurosilva forest	Japan, Shikoku, Ichinomata, 2017, T. Jung & H. Masuya	Mullett et al. (2023)
<i>P. ×cambivora</i> DAPC2	7a	JP118	A1/A2 (A1)	M, T	Baiting stream R16, laurosilva forest	Japan, Shikoku, Ichinomata, 2017, T. Jung & H. Masuya	Mullett et al. (2023)
		JP123	A1/A2 (A2)	P, M, T, G	Baiting stream R12, laurosilva forest	Japan, Shikoku, Satayama, 2017, T. Jung & K. Kageyama	Mullett et al. (2023)
		JP182	A1/A2 (A1)	P, M, T	Baiting stream R12, laurosilva forest	Japan, Shikoku, Satayama, 2017, T. Jung & K. Kageyama	Mullett et al. (2023)
		JP361	A1/A2 (A1)	P, M, T	Baiting stream R18, laurosilva forest	Japan, Kyushu, Aya, 2017, T. Jung & S. Uematsu	Mullett et al. (2023)
		JP429	A1/A2 (A2)	M, T	Baiting stream R18, laurosilva forest	Japan, Kyushu, Aya, 2017, T. Jung & S. Uematsu	Mullett et al. (2023)
		JP927	A1/A2 (A2)	M, T	Baiting stream R12, laurosilva forest	Japan, Shikoku, Satayama, 2017, T. Jung & K. Kageyama	Mullett et al. (2023)
		TJ1331, JKI-148-10-13-00-00-00, P588	A1/A2 (A1)	P, T	River	Poland, 2008, n/a	Mullett et al. (2023)



Table 1. (Continued).

Phytophthora taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. ×cambivora</i> DAPC4	7a	TJ1332, JKI-149-10-13-00-00, P589	A1/A2 (A2)	T	River	Poland, 2008, n/a	Mullett et al. (2023)
		TJ1333, JKI-145-10-00-00-00, P590	A1/A2 (A1)	P, T	<i>Castanea sativa</i>	Poland, 2008, n/a	Mullett et al. (2023)
		JP263	A1/A2 (A1)	T	Baiting Mya River	Japan, Honshu, Takayama, 2017, T. Jung & A. Hieno	Mullett et al. (2023)
		JP930	A1/A2 (A1)	T	Baiting Tamagawa River, <i>F. crenata</i> forest	Japan, Honshu, Tose, 2017, T. Jung & C.M. Brasier	Mullett et al. (2023)
		JP996	A1/A2 (A2)	P, T	<i>Fagus crenata</i> , rhizosphere soil	Japan, Honshu, Komagatake, 2017, T. Jung & M. Horta Jung	Mullett et al. (2023)
		JP1027	A1/A2 (A1)	T	<i>F. crenata</i> , rhizosphere soil	Japan, Honshu, Komagatake, 2017, T. Jung & M. Horta Jung	Mullett et al. (2023)
		JP1051	A1/A2 (A2)	P, T	<i>F. crenata</i> , rhizosphere soil	Japan, Honshu, Komagatake, 2017, T. Jung & M. Horta Jung	Mullett et al. (2023)
<i>P. ×cambivora</i> DAPC4 mixed	7a	JP257	A1/A2 (A2)	T	Baiting stream R01, montane <i>Alnus hirsuta</i> forest	Japan, Honshu, Takayama, 2017, T. Jung & C.M. Brasier	Mullett et al. (2023)
		ATCC 38811, IMI 229178, TJ035, P 9/04, ILVO TJ075	A1/A2 (A1)	T	<i>Malus pumila</i>	Japan, n/a, n/a	Van Poucke et al. (2021), Mullett et al. (2023)
		CBS 111329, TJ048, P115, ILVO TJ079, KACC 40159	A1/A2 (A1)	T	<i>Malus pumila</i> var. <i>dulcissima</i>	South Korea, Adong, 1996, H.-J. Jee	Jee et al. (1997); Jung et al. (2017a), Van Poucke et al. (2021), Mullett et al. (2023)
		CBS 376.61, TJ1288, P114	A1/A2 (A2)	T	<i>Andromeda floribunda</i>	Poland, 1961, n/a	Mullett et al. (2023)
		TJ1314, 4080R1	A1/A2 (A2)	T	<i>Pseudotsuga menziesii</i> , rhizosphere soil	USA, Oregon, Linn County, n/a	Saavedra et al. (2007), Mullett et al. (2023)
		BD150	A1/A2 (A2)	P, T	Baiting forest stream R06	Portugal, Parque Nacional da Peneda-Gerês, 2014, T. Jung & M. Horta Jung	Mullett et al. (2023), Horta Jung et al. (2025)
		TJ500	A1/A2 (A2)	T	<i>Thuja occidentalis</i> , rhizosphere soil	Germany, Bavaria, 2013, T. Jung	Mullett et al. (2023)
<i>P. ×cambivora</i> DAPC5	7a	TJ542, 4557H, ILVO AC09	A1/A2 (A2)	P, T	<i>F. sylvatica</i> , bark canker	Belgium, Morte-han, 2014, A. Chandelier	Jung et al. (2017a), Van Poucke et al. (2021), Mullett et al. (2023)
		TJ1006	A1/A2 (A2)	T	<i>Prunus serotina</i> 'Shiro-fugen', rhizosphere soil in nursery	Germany, Schleswig-Holstein, 2013, T. Jung	Mullett et al. (2023)
		TJ1263, P3037, PH130	A1/A2 (A2)	P, T	<i>F. sylvatica</i> , bark canker	UK, England, 2015, Forest Research	Mullett et al. (2023)
		JP952	A1/A2 (A1)	T	<i>F. crenata</i> , rhizosphere soil	Japan, Honshu, Komagatake, 2017, T. Jung & M. Horta Jung	Mullett et al. (2023)
		JP953	A1/A2 (A1)	P, T, G	<i>F. crenata</i> , rhizosphere soil	Japan, Honshu, Komagatake, 2017, T. Jung & M. Horta Jung	Mullett et al. (2023)



Table 1. (Continued).

Phytophthora taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. ×cambivora</i> DAPC7	7a	JP989	A1/A2 (A1)	T	Baiting stream R28, <i>F. crenata</i> forest	Japan, Honshu, Tazawako highland, 2017, T. Jung & H. Masuya	Mullett et al. (2023)
		JP1022	A1/A2 (A2)	T	Baiting stream R28, <i>F. crenata</i> forest	Japan, Honshu, Tazawako highland, 2017, T. Jung & H. Masuya	Mullett et al. (2023)
		JP1035	A1/A2 (A1)	P, T	Baiting stream R28, <i>F. crenata</i> forest	Japan, Honshu, Tazawako highland, 2017, T. Jung & H. Masuya	Mullett et al. (2023)
		JP031	A1/A2 (A1)	T	Baiting stream R21, laurosilva forest	Japan, Kyushu, Shiiba, 2017, T. Jung & S. Uematsu	Mullett et al. (2023)
		JP058	A1/A2 (A1)	P, T	Baiting stream R19, laurosilva forest	Japan, Kyushu, Shiiba, 2017, T. Jung & K. Kageyama	Mullett et al. (2023)
		JP194	A1/A2 (A1)	T	Baiting stream R20, laurosilva forest	Japan, Kyushu, Shiiba, 2017, T. Jung & M. Horta Jung	Mullett et al. (2023)
		JP277	A1/A2 (A1)	P, T	<i>Quercus crispula</i> , rhizosphere soil	Japan, Honshu, Takayama, 2017, T. Jung & K. Kageyama	Mullett et al. (2023)
<i>P. ×cambivora</i> DAPC8	7a	JP420	A1/A2 (A1)	T	Necrotic leaf floating in forest stream R20	Japan, Kyushu, Shiiba, 2017, T. Jung & J.F. Webber	Mullett et al. (2023)
		JP090	A1/A2 (A1)	T	Baiting stream R08, montane forest	Japan, Honshu, Takayama, 2017, T. Jung & A. Hieno	Mullett et al. (2023)
		JP152	A1/A2 (A1)	P	<i>Magnolia obovata</i> , rhizosphere soil	Japan, Honshu, Takayama, 2017, T. Jung & K. Kageyama	Mullett et al. (2023)
		JP215	A1/A2 (A1)	T	Baiting stream R06, montane forest	Japan, Honshu, Takayama, T. Jung & H. Masuya	Mullett et al. (2023)
		JP248	A1/A2 (A1)	P, T	Baiting stream R01, montane <i>A. hirsuta</i> forest	Japan, Honshu, Takayama, 2017, T. Jung & C.M. Brasier	Mullett et al. (2023)
		JP828	A1/A2 (A1)	T	<i>Aesculus turbinata</i> , rhizosphere soil	Japan, Honshu, Takayama, 2017, T. Jung & S. Uematsu	Mullett et al. (2023)
		CBS 141218, TJ197, IT5-3, NT	A1/A2 (A2)	P, T, G	<i>Quercus pubescens</i> , rhizosphere soil	Italy, Sicily, 2013, T. Jung	Jung et al. (2017a), Mullett et al. (2023)
<i>P. ×cambivora</i> DAPC9	7a	BD001, ILVO TJ085	A1/A2 (A2)	T	<i>C. sativa</i> , rhizosphere soil	Portugal, Parque Natural Montesinho, 2014, T. Jung & M. Horta Jung	Van Poucke et al. (2021), Mullett et al. (2023), Horta Jung et al. (2025)
		BD004, ILVO TJ150	A1/A2 (A2)	P	<i>C. sativa</i> , rhizosphere soil	Portugal, Parque Natural Montesinho, 2014, T. Jung & M. Horta Jung	Van Poucke et al. (2021), Mullett et al. (2023), Horta Jung et al. (2025)
		CL001, ILVO TJ081	A1/A2 (A2)	T	<i>F. sylvatica</i> , rhizosphere soil	Chile, Valdivia, 2014, T. Jung & M. Horta Jung	Jung et al. (2017a), Van Poucke et al. (2021), Mullett et al. (2023)

Table 1. (Continued).

Phytophthora taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. ×cambivora</i> DAPC10	7a	TJ029, SK 9, ILVO TJ067	A1/A2 (A2)	T	<i>F. sylvatica</i> , rhizosphere soil	Slovakia, Marianka, 2013, T. Jung	Jung et al. (2017a), Van Poucke et al. (2021), Mullett et al. (2023)
		TJ1342, SCRP86, CAM3, Ried 1/1, P154	A1/A2 (A2)	T	<i>Q. petraea</i> , rhizosphere soil	Germany, Bavaria, Riedenburg, 1996, T. Jung	Jung et al. (2000), Mullett et al. (2023)
		TJ066, 4044.1, P513, ILVO TJ077	A1/A2 (A1)	T	<i>Chrysopsis chrysophylla</i> , basal canker	USA, Oregon, Jackson County, 2001, A. Saavedra	Saavedra et al. (2007), Van Poucke et al. (2021), Mullett et al. (2023)
		TJ331, TJ1309, 4044.7, P514, ILVO TJ080	A1/A2 (A1)	P	<i>C. chrysophylla</i>	USA, Oregon, Jackson County, 2001, A. Saavedra	Mullett et al. (2023)
		TJ068, 403101, P526, ILVO TJ076	A1/A2 (A1)	P, T	<i>C. chrysophylla</i> , rhizosphere soil	USA, Oregon, Jackson County, 2001, A. Saavedra	Saavedra et al. (2007), Van Poucke et al. (2021), Mullett et al. (2023)
<i>P. ×cambivora</i> DAPC11	7a	TJ1310, 9706, P519	A1/A2 (A1)	T	<i>Notholithocarpus densiflorus</i>	USA, 2006, Oregon State University	Mullett et al. (2023)
		TJ1311, 9709.1, P520	A1/A2 (A1)	T	<i>N. densiflorus</i>	USA, 2006, Oregon State University	Mullett et al. (2023)
		BD177	A1/A2 (A1)	T	<i>Quercus pyrenaica</i> , rhizosphere soil	Portugal, 2014, T. Jung & M. Horta Jung	Mullett et al. (2023), Horta Jung et al. (2025)
		BD212	A1/A2 (A1+A2)	P, T	<i>Q. suber</i> , rhizosphere soil	Portugal, 2014, T. Jung & M. Horta Jung	Mullett et al. (2023), Horta Jung et al. (2025)
		TJ1257, P2165	A1/A2 (A1)	P, T	<i>F. sylvatica</i> , xylem	UK, England, Landue Estate, 2009, Forest Research	Mullett et al. (2023)
<i>P. ×grandisporangia</i> ¹¹	7a	TJ1298, PC643, P448	A1/A2 (A1)	T	<i>C. sativa</i> , soil	France, 2000, LNPV-UMAF	Mullett et al. (2023)
		TJ1316, PC98-1116, P531	A1/A2 (A1)	T	<i>Phorinia</i> sp.	USA, 1981, Oregon State University	Mullett et al. (2023)
		CBS 153093, VN074, ILVO TJ109, ET	A1/A2 (A1sf)	P, M, T	Baiting stream R01 in montane laurosilva forest	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	Van Poucke et al. (2021)
		VN081, ILVO TJ106	A1/A2 (A1sf)	P, M, T, G	Baiting stream R01 in montane laurosilva cloud forest	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	Jung et al. (2020), Van Poucke et al. (2021)
		VN082	A1/A2 (A1)	P, M, T, G	Baiting stream R01 in montane laurosilva cloud forest	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	This study
<i>P. ×heterohybrida</i>	7a	VN093	A1/A2 (A1)	P, M, T, G	Baiting stream R04 in montane laurosilva cloud forest	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	This study
		VN279	A1/A2 (A1)	P, M, T, G	Baiting stream R01 in montane laurosilva cloud forest	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	This study
		VN406	A1/A2 (A1)	P, M, T, G	Baiting stream R07 in montane laurosilva cloud forest	Vietnam, Hoàng Liên National Park, 2016, T. Jung & N.M. Chi	This study
		CBS 141207, TW030, 67C1, ILVO TJ038, ET	A1/A2 (A2)	P, T, G	Stream baiting; tributary of Ha-pen River in subtropical evergreen forest	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a)



Table 1. (Continued).

Phytophthora taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. ×incrassata</i>	7a	TW028, ILVO TJ036	A1/A2 (A2)	MA, G	Stream baiting; tributary of Ha-pen River in subtropical evergreen forest	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a)
		TW038	A1/A2 (A2)	P, T, G	Stream baiting; tributary of Ha-pen River in subtropical evergreen forest	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a)
		TW056	A1/A2 (A2)	P	Stream baiting; Cukeng River in subtropical evergreen forest	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a)
		CBS 141209, TW269, ILVO TJ061, ET	A1/A2 (A1)	P, T, G	Stream baiting; tributary of Ha-pen River in subtropical evergreen forest	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a), Van Poucke et al. (2021)
		TW043	A1/A2 (A1)	P, T	Stream baiting; tributary of Ha-pen River in subtropical evergreen forest	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a)
<i>P. ×leptopleura</i>	7a	TW347, 67C2, ILVO TJ065	A1/A2 (A1)	P, T	Stream baiting; tributary of Ha-pen River in subtropical evergreen forest	Taiwan, Fushan, 2013, T. Jung	Jung et al. (2017a)
		CBS 153090, JP859, ET	A1/A2 (A1)	P, M, T, G	Baiting stream R10, laurosilva forest	Japan, Shikoku, Satayama, 2017, T. Jung & H. Masuya	This study
		JP077	A1/A2 (A1)	P, M, T, G	Baiting stream R09, laurosilva forest	Japan, Shikoku, Satayama, 2017, T. Jung & K. Kageyama	This study
		JP204	A1/A2 (A1)	P, M, T, G	Baiting stream R10, laurosilva forest	Japan, Shikoku, Satayama, 2017, T. Jung & S. Uematsu	This study
		JP375	A1/A2 (A2)	M	Baiting stream R09, laurosilva forest	Japan, Shikoku, Satayama, 2017, T. Jung & M. Horta Jung	This study
		JP591	A1/A2 (A2)	M, G	Baiting stream R12, laurosilva forest	Japan, Shikoku, Satayama, 2017, T. Jung & J.F. Webber	This study
		JP673	A1/A2 (A2)	P, M, T, G	Baiting stream R11, laurosilva forest	Japan, Shikoku, Satayama, 2017, T. Jung & C.M. Brasier	This study
		JP702	A1/A2 (A2)	P, M, T, G	Baiting stream R11, laurosilva forest	Japan, Shikoku, Satayama, 2017, T. Jung & A. Hieno	This study
<i>P. ×multiformis</i>	7a	IMI 392316, WPC P16202, CPHST BL 2 P770, TJ1625, ET	SF	P	A. glutinosa, bark canker	Netherlands, 1994, H. van Kesteren	Brasier et al. (2004), Jung et al. (2017a)
		TJ008, PHAKO 12, P696	SF	P, M, T	A. glutinosa, bark canker	Croatia, 2012, Z. Tomić	Jung et al. (2017a)
		TJ009, PHAPI 12, P694	SF	P, M, T, G	A. glutinosa, bark canker	Croatia, 2012, Z. Tomić	Jung et al. (2017a)
		PAM 396, TJ022, ILVO TJ004	SF	M, G	A. glutinosa, bark canker	France, 2007, T. Scordia	Husson et al. (2015), Jung et al. (2017a)
		IMI 392321, P889, ALN1, TJ332, ILVO TJ005	SF	M, T	A. incana, bark canker	Germany, Freising, 1995, T. Jung	Brasier et al. (2004), Jung et al. (2017a)
		PH055, TJ0239	SF	M, T	A. glutinosa, bark canker	Italy, Sardinia, 2010, B. Scanu	Jung et al. (2017a)
		TJ1460, LI109	SF	M	A. lusitanica, bark canker	Portugal, Lima River, 2020, I. Gomes Marques	Gomes Marques et al. (2025)



Table 1. (Continued).

Phytophthora taxon	Sub-clade	Isolate codes ^{1,2}	Breeding system (mating type) ³	Use in this study ⁴	Host, substrate or ecosystem	Location, year, collector	References
<i>P. x nodosa</i>	7a	CBS 153088, JP761, ET	SF	P, M, T, G	<i>Lithocarpus edulis</i> , rhizosphere soil, laurosilva forest	Japan, Kyushu, Takakuma, 2017, T. Jung & A. Hieno	This study
		JP532	SF	P, M, T, G	Baiting stream R22, laurosilva forest	Japan, Kyushu, Takakuma, 2017, T. Jung & K. Kageyama	This study
		JP577	SF	P, M, T, G	Baiting stream R24, laurosilva forest	Japan, Kyushu, Takakuma, 2017, T. Jung & H. Masuya	This study
		JP923	SF	P, M, T, G	<i>L. edulis</i> , rhizosphere soil, laurosilva forest	Japan, Kyushu, Takakuma, 2017, T. Jung & M. Horta Jung	This study
<i>P. taxon cadmea</i>	7a	SCVWD235	n/a	P	<i>Juncus</i> sp., rhizosphere soil	USA, California, Santa Clara County, 2015, T.B. Bourret & S.N. Fajardo	Bourret et al. (2023)
<i>P. taxon cadmea-like</i>	7a	WPC P15554	n/a	B	<i>Quercus rubra</i> , rhizosphere soil	USA, West Virginia, n/a, n/a	n/a
<i>P. taxon europaea-like</i> ¹²	7a	P1385	n.a.	B	<i>Fagus sylvatica</i> , seedling cotyledon and stem	Poland, Klucze, 2021, R. Jankowiak, H. Stepniewska & S.J. Taerum	Jankowiak et al. (2023)
<i>P. taxon xalni-like</i>	7a	TJ005, ALN 268, P692	SF	P, M, T	<i>A. incana</i> , bark canker	Germany, Bavaria, Fischbachau, 2001, T. Jung	Jung & Blaschke (2004), Jung et al. (2017a)
<i>P. taxon xmultiformis-like</i>	7a	TJ028, 4971496	SF	P, T, G	<i>A. glutinosa</i> , bark canker	Netherlands, 2011, K. Rosendahl & W. Man In 't Veld	Jung et al. (2017a)

n/a = not available.

¹ ATCC and MYA: American Type Culture Collection, Manassas, VA, USA, BBA and JKI: Julius-Kühn Institute, Braunschweig, Germany; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; BD, CL, TJ and TW: Dr Thomas Jung's personal culture collection, housed at Mendel University in Brno, Czech Republic and the University of Algarve, Faro, Portugal; BN, JP, LU and VN: Culture collection of Mendel University in Brno, Czech Republic; CPHST BL: Dr. Gloria Abad, USDA-APHIS-PPQ-Center for Plant Health, Science & Technology-Beltsville Laboratory, Beltsville, MD, USA; ILVO: Flanders Research Institute for Agriculture, Fisheries and Food, Mellebeke, Belgium; IMI: CABI Biosciences, UK; NRRL: ARS Culture Collection, Peoria, IL, USA; SCRP: The James Hutton Institute, Dundee, UK; WPC: The World Phytophthora Genetic Resource Collection at University of California, Riverside, USA; all other codes are as given by the collectors and on GenBank, respectively.

² ET, EpT and NT denote ex-type, ex-epitype and ex-neotype strains, respectively.

³ SF denotes isolates with a self-fertile (homothallic) breeding system; A1/A2 denotes a self-sterile (heterothallic) breeding system showing A1 or A2 mating type in parenthesis; A1sf denotes weakly self-fertile isolates forming gametangia abundantly in pairings with A2 isolates; A1+A2 denotes self-sterile (heterothallic) isolates forming gametangia in pairings with both A1 and A2 mating types.

⁴ P, M and T denote isolates used in the phylogenetic, morphological and temperature-growth studies; MA denotes isolates used only for mating tests; all isolates were used for the biogeography studies; B denotes isolates used only for the Notes on biogeography and host and habitat associations; G denotes isolates used in the genotyping-by-sequencing study of Mullet et al. (2023) whose results were not published but are presented together with *P. x cambivora* isolates CBS 141218, JP123 and JP954 in Fig. S7 of the present study.

⁵ Previously designated as *P. sp. europaea*SW (Yang et al. 2017).

⁶ Previously designated as *P. europaea* (Balci et al. 2007).

⁷ Previously designated as *Phytophthora* sp. (Amemiya et al. 2011a, b).

⁸ Previously designated as *P. sp. attenuata-like* 2 (Jung et al. 2020).

⁹ Previously designated as *P. sp. attenuata-like* 3 (Jung et al. 2020).

¹⁰ Previously designated as *P. sp. attenuata-like* 1 (Jung et al. 2020).

¹¹ Previously designated as *P. x heterohybrida* (Jung et al. 2020) and *P. x heterohybrida*-related (Van Poucke et al. 2021).

¹² Previously designated as *P. europaea* (Jankowiak et al. 2023).

in Croatia (Table 1, Fig. 1). For comparative studies isolates of 17 described species and one designated taxon from Clade 7a were sourced from the culture collections of the authors or kindly provided by colleagues (Table 1). In addition, isolates from four described Clade 7a species were obtained during oomycete surveys conducted in 2016 and 2017: *P. flexuosa*, *P. formosa* and *P. ×cambivora* from rhizosphere soil and streams of temperate forests in Japan; and *P. attenuata* from rhizosphere soil in a subtropical montane cloud forest in Vietnam (Table 1, Fig. 1). For all isolates, single hyphal tip cultures were produced under the dissecting microscope at ×20 from the margins of fresh cultures on V8-juice agar (V8A; 16 g agar from Sigma-Aldrich/Merck Life Science in Prague, Czech Republic, 3 g CaCO₃, 100 mL organic vegetable juice from the company DM in Karlsruhe, Germany, 900 mL distilled water; Jung *et al.* 2002). Stock cultures were maintained on V8A and carrot juice agar (CA; 20 g agar, 3 g CaCO₃, 100 mL organic carrot juice from the company DM, 900 mL distilled water; Scanu *et al.* 2014) at 10 °C in the dark. All isolates of the 11 new *Phytophthora* spp. are preserved in the culture collection maintained at Mendel University in Brno. Ex-type cultures were deposited at the CBS Culture Collection (CBS) at the Westerdijk Fungal Biodiversity Institute, Utrecht, Netherlands (Table 1). Dried V8A cultures of the 11 ex-type isolates were deposited as holotypes in the CBS Fungarium (CBS H).

DNA isolation, amplification and sequencing

For all *Phytophthora* isolates from Clade 7a obtained in this study or sourced from the culture collections of the authors or colleagues and for the ex-type isolate CBS 144.22 of *P. cinnamomi* from Clade 7c, DNA was extracted from ca 15–100 mg of mycelium scraped from 1–3-wk-old V8A cultures using the same protocol, consumables and equipment as in Jung *et al.* (2024) and preserved at -80 °C for long-term storage.

Eight nuclear gene regions, i.e., the internal transcribed spacer region (ITS1–5.8S–ITS2) of the ribosomal RNA gene (ITS), the 5' terminal domain of the large subunit (28S-LSU) of the nuclear ribosomal RNA, heat shock protein 90 (*hsp90*), β -tubulin (*β tub*), 60S ribosomal protein L10 (*rpl10*), *TGA* gene fusion protein (genes encoding triose-phosphate isomerase (TPI) and glyceraldehyde-3-phosphate dehydrogenase (GAPDH) fused and forming a single transcriptional unit: *tigA*), translation elongation factor 1 alpha (*tef-1 α*), enolase (*enl*), and the three mitochondrial genes cytochrome-c oxidase 1 (*cox1*), subunit 1 of NADH dehydrogenase (*nadh1*), and 40S ribosomal protein S10 (*rps10*) were amplified and sequenced using the same PCR conditions, primers, annealing temperatures and equipment as in Jung *et al.* (2024) (Table S1). All primers were synthesized by Elizabeth Pharmacon spol. s.r.o. (Brno, Czech Republic).

Amplification products were visualised by gel electrophoresis (300 V; 5 min) using 2 % agarose gel stained by DNA Stain G (SERVA, Heidelberg, Germany). All amplicons were purified and sequenced in both directions by Eurofins Genomics GmbH (Cologne and Ebersberg, Germany) using the amplification primers, except for the LSU and *tigA* amplicons which required two additional primers each (Jung *et al.* 2024). Electropherograms were quality-checked and forward and reverse reads were compiled using Geneious Prime® v. 2026.0.2 (Biomatters Ltd., Auckland, New Zealand). Pronounced double peaks were considered as heterozygous positions and labelled according to the IUPAC (International Union of Pure and Applied Chemistry; <https://iupac.org>) coding system. All sequences generated in this study were deposited in GenBank INSDC

(International Nucleotide Sequence Databases Collaboration) and accession numbers are given in Table S2.

Phylogenetic analysis

For phylogenetic analyses, the sequences obtained in this study were complemented with publicly available sequences of isolates from *Phytophthora* Clade 7 sourced from the GenBank Nucleotide Collection, and GenBank Whole-Genome Shotgun contigs (Table S1). The sequences of all loci used in the analyses were aligned using the MAFFT v. 7 (Katoh & Standley 2013) plugin within Geneious Prime® 2026.0.2 (<https://www.geneious.com>) by the E-INS-I strategy (ITS) or the G-INS-I strategy (all other loci). The ITS alignments in this study were manually edited and adjusted.

The phylogenetic structure of Clade 7a and the relative phylogenetic positions of the 11 new species were studied using a mitochondrial 3-partition (*cox1*, *nadh1*, *rps10*), a nuclear 8-partition (LSU, ITS, *β tub*, *hsp90*, *tigA*, *rpl10*, *tef-1 α* , *enl*) and a combined 11-partition (LSU, ITS, *β tub*, *hsp90*, *tigA*, *rpl10*, *tef-1 α* , *enl*, *cox1*, *nadh1*, *rps10*) dataset of 122 type and other key isolates from the 11 new and 18 previously described species and three informally designated taxa within Clade 7a with *P. cinnamomi* from Clade 7c and *P. sojae* from Clade 7b as outgroup taxa.

For Maximum Likelihood (ML) analyses, tree reconstruction for the three datasets was carried out using two different programs, namely IQ-TREE version v. 2.3.6 (Minh *et al.* 2020) and RAXML-NG v. 1.1.0 (Kozlov *et al.* 2019), with slightly different settings. For the IQ-TREE analyses, coding loci were partitioned by codon position. An internal PartitionFinder (Lanfear *et al.* 2016) step, unlinked partitioning, the greedy algorithm and the ultrafast bootstrap approximation (Minh *et al.* 2013) were used. For the RAXML-NG analyses, coding loci were not partitioned by codon position. The best-fitting substitution (evolutionary) models with site-rate heterogeneity were selected using PartitionFinder v. 2 (Lanfear *et al.* 2016) based on the corrected Akaike Information Criterion (AICc). Each locus was treated as a separate partition (i.e., the choice of whether branch lengths were linked or unlinked across partitions was irrelevant). All 84 available evolutionary models were used, including those with base frequencies estimated by maximum likelihood (the parameter models = allx;). The number of bootstrap replicates was determined automatically using the bootstopping method based on the extended majority rule (MRE, also known as greedy consensus) (Pattengale *et al.* 2010) with the cut-off value 0.03 (–bs-cutoff 0.03). To calculate branch support values, the Transfer Bootstrap Expectation method (TBE; Lemoine *et al.* 2018) was selected. The presented ML trees from both IQ-TREE and RAXML-NG represent the best-scoring trees.

Bayesian Inference (BI) analyses were performed using two different programs, BEAST v. 2.6.7 (Bouckaert *et al.* 2014) and MrBayes v. 3.2.7 (Ronquist *et al.* 2012). For the BEAST BI analyses, Metropolis coupled MCMC (MC3) implemented in the CoupledMCMC package (Müller & Bouckaert 2019) was used with four chains – three heated and one cold. The chain length was initially set to 20 M and every 5000th state was sampled. The target switch probability was set to the recommended value of 0.234 (Kone & Kofke 2005, Atchadé *et al.* 2011). The substitution (evolutionary) models with site-rate heterogeneity were selected automatically for each individual locus via model averaging implemented in the bModelTest package (Bouckaert & Drummond 2017). All analyses were conducted under the optimised relaxed clock (Douglas *et al.* 2021), a performance-optimised version of the uncorrelated log-



Fig. 1. Habitats of known and new *Phytophthora* species from phylogenetic Clade 7a. **A.** Submontane natural *Fagus sylvatica* forest in the Bavarian Alps, Germany with severe chlorosis, dieback and mortality due to root and collar rot caused by *P. ×cambivora* lineage DAPC9. **B.** Natural, healthy cool-temperate forest of *Fagus crenata*, *Quercus crispula* and *Aesculus turbinata* in the Iwate region in the North of Honshu Island, Japan (*P. ×cambivora* lineages DAPC4 and 6). **C.** Natural, warm-temperate diverse laurosilva forest in the Satayama region on Shikoku Island, Japan (*P. formosa*, *P. irregularis*, *P. ×cambivora* lineage DAPC2, *P. ×leptopleura*). **D.** Natural, warm-temperate diverse laurosilva forest in the Takakuma region on Kyushu Island, Japan (*P. irregularis*, *P. ×nodosa*). **E.** Diverse montane cloud forest at the Fansipan in northern Vietnam (*P. alvida*, *P. attenuata*, *P. sessilis*, *P. ×grandisporangia*). **F.** Diverse, subtropical, humid evergreen forest in Ba Vi National Park in northern Vietnam (*P. alvida*, *P. grandisporangia*). **G.** Flooded swamp forest near Archie in Louisiana, USA (*P. facultativa*). **H.** Acute wilting and mortality of a *Corylus avellana* tree (left) in a horticultural plantation in Croatia (*P. laevigata*).



normal relaxed molecular clock model (Drummond *et al.* 2006). Substitutions per site were used as the unit of branch lengths of the sampled trees. The first 25 % of MCMC samples were discarded as burn-in. Posterior trees were summarized as a maximum clade credibility tree using TreeAnnotator v. 2.6.0 (part of BEAST v. 2.6.7). The posterior estimates of the parameters were summarised with Tracer (Rambaut *et al.* 2018). The quality of the parameter estimates was assessed based on Effective Sample Size (ESS) values and visual analysis of the trace plots. Convergence of the MCMC was assessed by ensuring that ESS values for the likelihood and posterior parameters exceeded 200. When convergence was not achieved, the MCMC chain was repeatedly extended by 20 M generations until convergence was reached. In the final analyses, the vast majority of other parameters also had ESS values greater than 200. The nuclear dataset reached convergence after 40 M generations, the mitochondrial dataset after 20 million generations, and the combined dataset after 60 M generations. The MrBayes BI analyses differed from the BEAST BI analyses mainly in that coding loci were partitioned by codon position; schemata produced with standalone PartitionFinder (Lanfear *et al.* 2016) using linked partitions and a fixed clock model were implemented; and analyses were run at least 10 M generations or until runs were observed to converge.

All final ML and BI trees were visualised in TreeGraph2 v. 2.15.0-887 beta (Stöver & Müller 2010) and/or MEGA v. 11.0.11 (Tamura *et al.* 2021) and edited in figure editor programs. Bipartitions with support values below 50 (ML) or 0.5 (BI) were collapsed. All datasets and trees deriving from BI and ML analyses were deposited in the Mendeley Data Repository, V1, doi: [10.17632/md2pvx2vk.1](https://doi.org/10.17632/md2pvx2vk.1).

Morphology of asexual and sexual structures

Morphological features of sporangiophores, sporangia, chlamydospores, oogonia, oospores, antheridia, hyphal swellings and aggregations of all isolates of the 11 new species and selected isolates of related species from Clade 7a were compared with each other.

To induce the formation of sporangia, two 12–15 mm square discs were cut from the growing edge of a 3–7-d-old colony on V8A and flooded in a 90-mm-diam. Petri dish with non-sterile soil extract (50 g of filtered oak forest soil in 1 000 mL of distilled water, filtered after 24 h) just above the surface of the aerial mycelium (Jung *et al.* 1996). The Petri dishes were incubated at 20 °C and natural daylight near a window and the soil extract changed after ca 6 h. Shape, type of apex, caducity and special features of sporangia, sporangiophore branching patterns and the formation of hyphal swellings and aggregations were recorded after 24–48 h. For each isolate 50 sporangia were measured at $\times 400$ using a compound microscope (Zeiss Imager.Z2), a digital camera (Zeiss Axiocam ICc3) and a biometric software (Zeiss ZEN).

The formation of chlamydospores, gametangia (oogonia and antheridia) and their characteristic features were examined on V8A (self-fertile or 'homothallic' species) or on clarified carrot agar prepared from fresh grated organic carrots (fgCA) (A1/A2 outcrossing or 'heterothallic' species; Brasier 1967) after 21–30 d growth at 20 °C in the dark. Self-sterile isolates of the *P. ×cambivora* Discriminant Analysis of Principal components (DAPC) 2 lineage (Mullett *et al.* 2023), *P. ×grandisporangia* and *P. ×leptopleura* were paired on V8A with A1 and A2 mating type tester strains of *P. cinnamomi* (A1: TW012; A2: MP74) and *P. ×cambivora* (A1: TJ030; A2: TJ029) and examined after 4 wk incubation at 20 °C in the dark to determine their mating type (Jung *et al.* 2017c). For those species

with the presence of both mating types (*P. ×cambivora* DAPC2 and *P. ×leptopleura*) isolates from opposite mating types were paired with each other while isolates from *P. ×grandisporangia* which all belonged to the A1 mating type were paired with A2 tester strains of *P. cinnamomi* (MP74) and *P. ×heterohybrida* (TW028) using a polycarbonate membrane (Whatman Nuclepore™ Track-Etched Membranes, Sigma-Aldrich, St. Louis, MO, USA) test (Scanu *et al.* 2021). For each isolate each 50 oogonia, oospores and antheridia chosen at random were measured under a compound microscope at $\times 400$ as described before. The oospore wall index was calculated according to Dick (1990).

Colony morphology, growth rates and cardinal temperatures

Colony growth patterns of all 11 new Clade 7a species, one new and one known informally designated Clade 7a taxon, and, excepting *P. fagacearum*, all 18 described Clade 7a species were described from 10-d-old or 14-d-old (slow growing species) cultures grown at 20 °C in the dark on V8A, CA and potato-dextrose agar (PDA; HiMedia, Mumbai, India). Colony morphologies were described according to patterns observed previously (Erwin & Ribeiro 1996, Jung *et al.* 2002, 2017a, b, 2021, 2022, 2024).

For temperature-growth relationships, representative isolates of all 11 new Clade 7a species, one new and one known informally designated Clade 7a taxon, and the 17 described Clade 7a species included in the colony morphology studies (Table 1) were sub-cultured onto 90 mm V8A plates and incubated for 24 h at 20 °C to stimulate onset of growth (Jung *et al.* 2002). Then three replicate plates per isolate were transferred to 10, 15, 20, 25, 27.5, 30, 32.5 and 35 °C. Radial growth was recorded after 4–14 d, before colonies reached the margin of the Petri dishes, along two lines intersecting the centre of the inoculum at right angles and the mean growth rates (mm/d) were calculated. Plates showing no growth at 25, 27.5, 30, 32.5 or 35 °C were returned to 20 °C to determine the lethal temperatures.

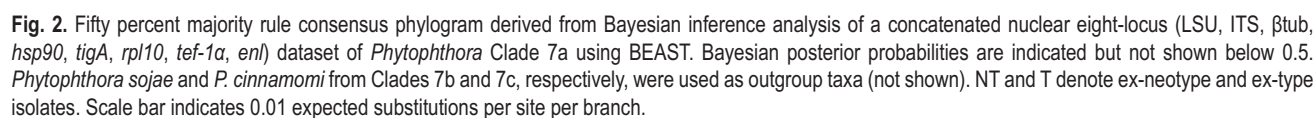
RESULTS

Phylogenetic results

The relative phylogenetic positions of the 11 new Clade 7a species and the phylogenetic structure of Clade 7a were studied using a mitochondrial 3-locus (*cox1*, *nadh1*, *rps10*), a nuclear 8-locus (LSU, ITS, β tub, *hsp90*, *tigA*, *rpl10*, *tef-1a*, *enl*) and a combined 11-locus dataset of 122 type and other key isolates from the 11 new and 18 previously described species and three informally designated taxa within Clade 7a with *P. cinnamomi* from Clade 7c and *P. sojiae* from Clade 7b as outgroup taxa.

Due to the high number (47) of hybrid isolates from 10 taxa in the dataset, in addition to the trees from the combined analyses, the trees from the mitochondrial-only and the nuclear-only analyses are also presented separately to show the maternal lines of the hybrids and potential mito-nuclear discordances.

With all datasets, the ML analyses were performed using both RAXML and IQ-TREE whereas for the BI analyses both MrBayes and BEAST were used. The ML bootstrap best trees produced by RAXML and IQ-TREE shared similar but not identical topologies. The same applied to the BI 50 % majority consensus rule trees derived from MrBayes and BEAST. Here, the ML bootstrap best trees derived from IQ-TREE and the BI 50 % majority consensus



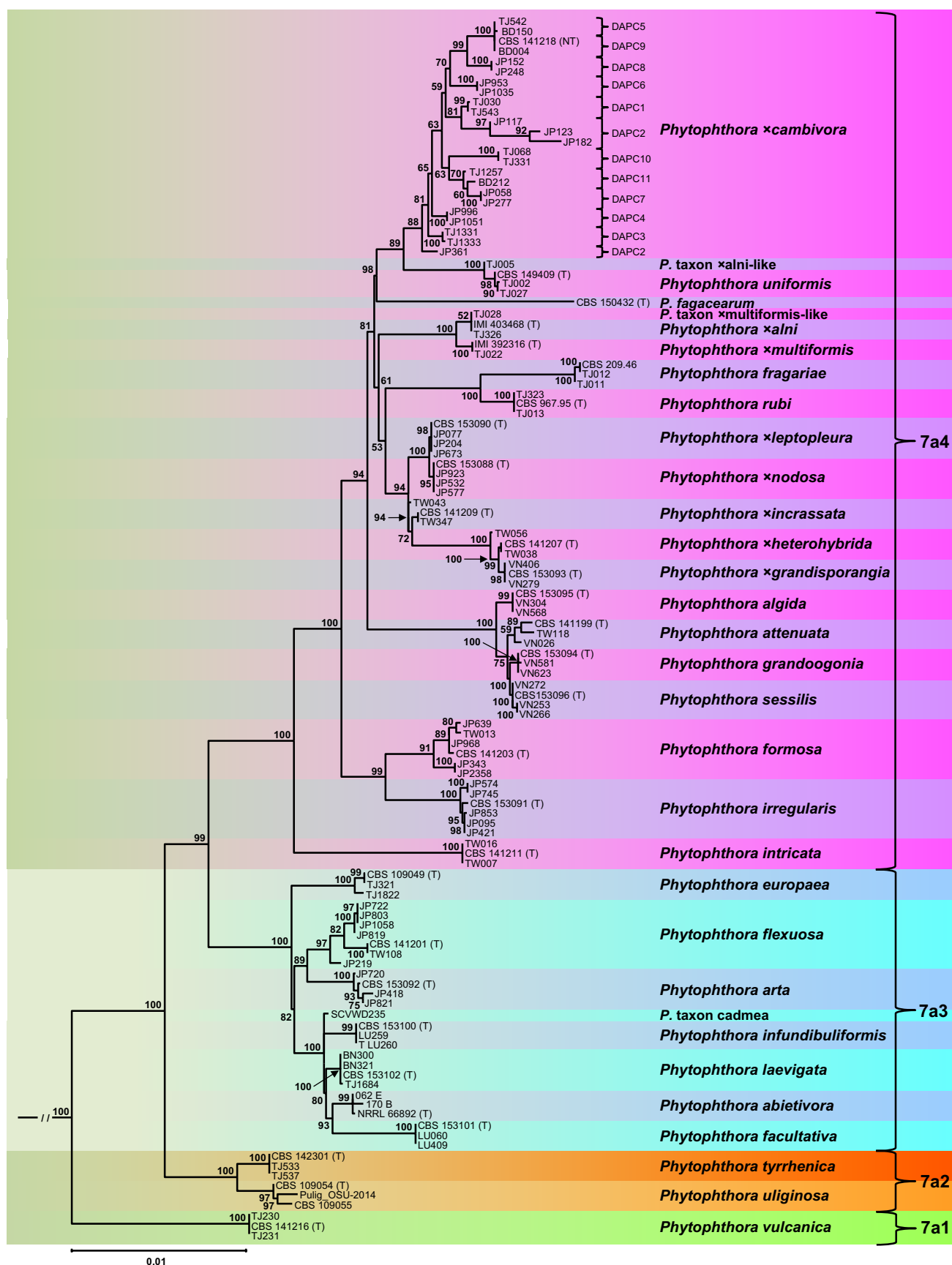


Fig. 3. ML bootstrap best tree derived from Maximum Likelihood analysis of a concatenated nuclear eight-locus (LSU, ITS, *βtub*, *hsp90*, *tigA*, *rpl10*, *tef-1α*, *enl*) dataset of *Phytophthora* Clade 7a using IQ-TREE. Bootstrap values are indicated but not shown below 50 %. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 expected substitutions per site per branch.

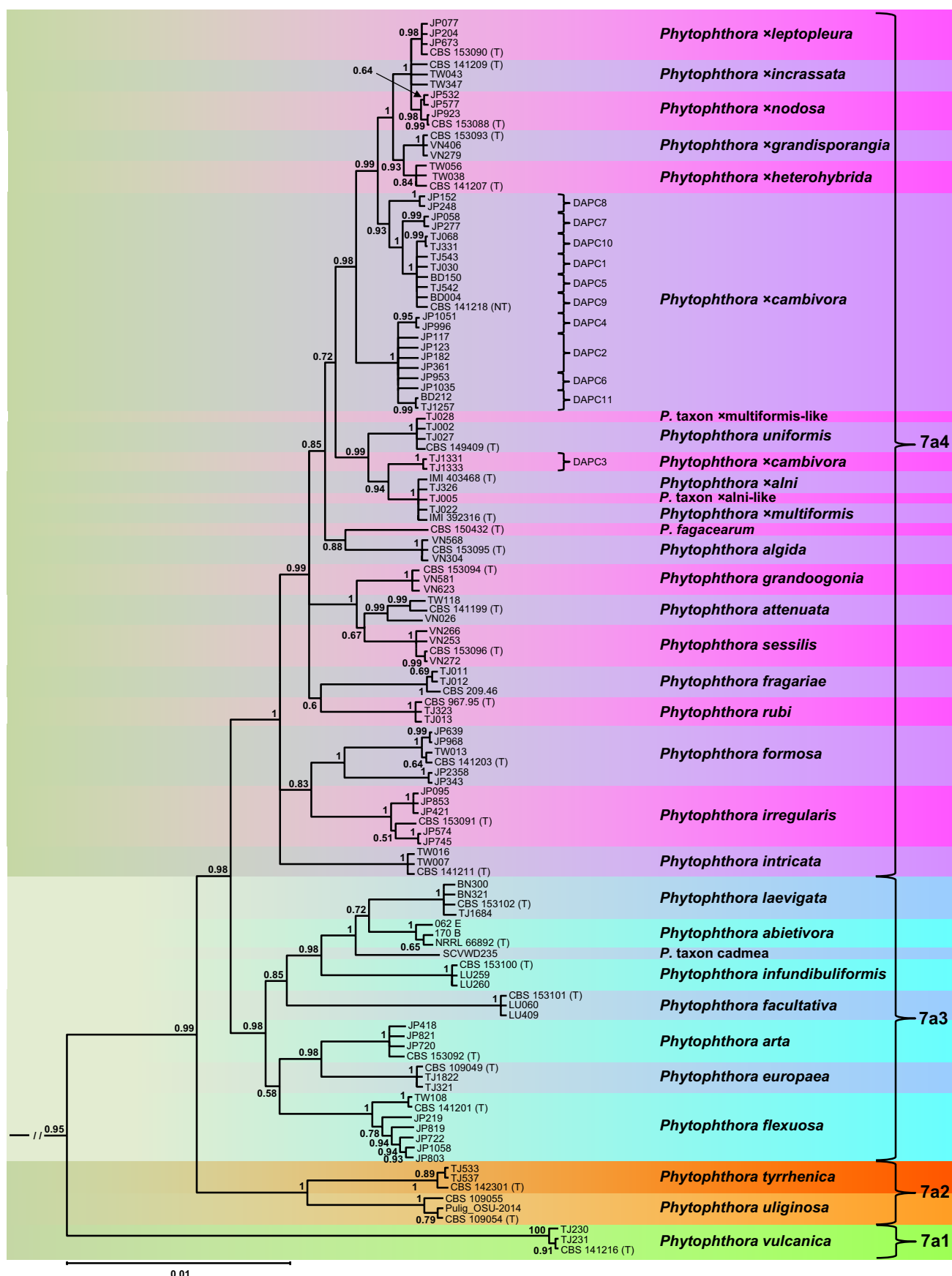


Fig. 4. Fifty percent majority rule consensus phylogram derived from Bayesian inference analysis of a concatenated mitochondrial three-locus (*cox1*, *nadh1*, *rps10*) dataset of *Phytophthora* Clade 7a using BEAST. Bayesian posterior probabilities are indicated but not shown below 0.5. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 expected substitutions per site per branch.



Fig. 5. ML bootstrap best tree derived from Maximum Likelihood analysis of a concatenated three-locus (*cox1*, *nadh1*, *rps10*) dataset of *Phytophthora* Clade 7a using IQ-TREE. Bootstrap values are indicated but not shown below 50 %. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 expected substitutions per site per branch.

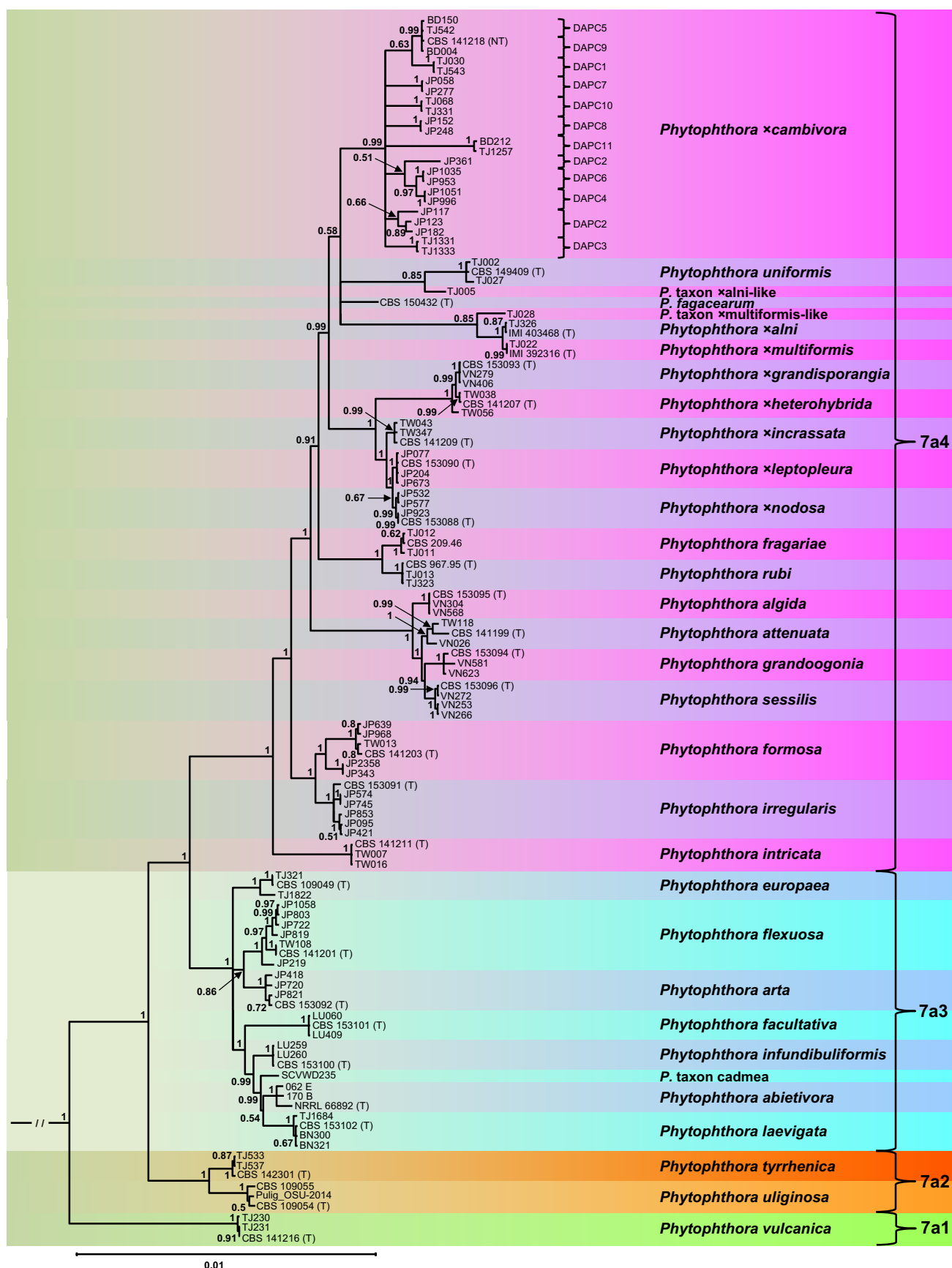


Fig. 6. Fifty percent majority rule consensus phylogram derived from Bayesian inference analysis of a concatenated nuclear and mitochondrial eleven-locus (LSU, ITS, *βtub*, *hsp90*, *tigA*, *rpl10*, *tef1α*, *enl*, *cox1*, *nadh1*, *rps10*) dataset of *Phytophthora* Clade 7a using BEAST. Bayesian posterior probabilities are indicated but not shown below 0.5. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 expected substitutions per site per branch.



Fig. 7. Maximum Likelihood (ML) bootstrap best tree derived from ML analysis of a concatenated eleven-locus (LSU, ITS, *βtub*, *hsp90*, *tigA*, *rpl10*, *tef-1α*, *enl*, *cox1*, *nad1*, *rps10*) dataset of *Phytophthora* Clade 7a, using IQ-TREE. Bootstrap values are indicated but not shown below 50 %. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 substitutions changes per site per branch.

rule trees derived from BEAST are presented (Figs 2–7). The ML bootstrap best trees derived from RAXML and the BI 50 % majority consensus rule trees derived from MrBayes are provided as supplementary figures (Figs S1–S6). Differences between the respective RAXML and IQ-TREE trees as well as between the respective MrBayes and BEAST trees are discussed in detail in the supplementary phylogenetic results (Mendeley Data Repository, V1, doi: 10.17632/md2pvgx2vk.1).

Across the alignments of 8 205 nuclear and 2 469 mitochondrial characters pairwise sequence differences between the Clade 7a taxa

were 0.1–2.7 % (8–220 bp) and 0–5.6 % (0–137 bp), respectively. Excluding hybrid taxa with identical maternal line, mitochondrial pairwise sequence differences were 0.04–5.6 % (1–137 bp).

Nuclear phylogeny: The resolution was generally good at terminal clades. The ML bootstrap best trees and the BI 50 % majority consensus rule trees resolved within Clade 7a 31 discrete lineages (Figs 2, 3, S1, S2). The deeper phylogeny was fully or well supported. In both the BI and ML analyses, the evolutionary history of Clade 7a was characterised by the early divergence of the *P. vulcanica* lineage, designated here as Clade 7a1, followed

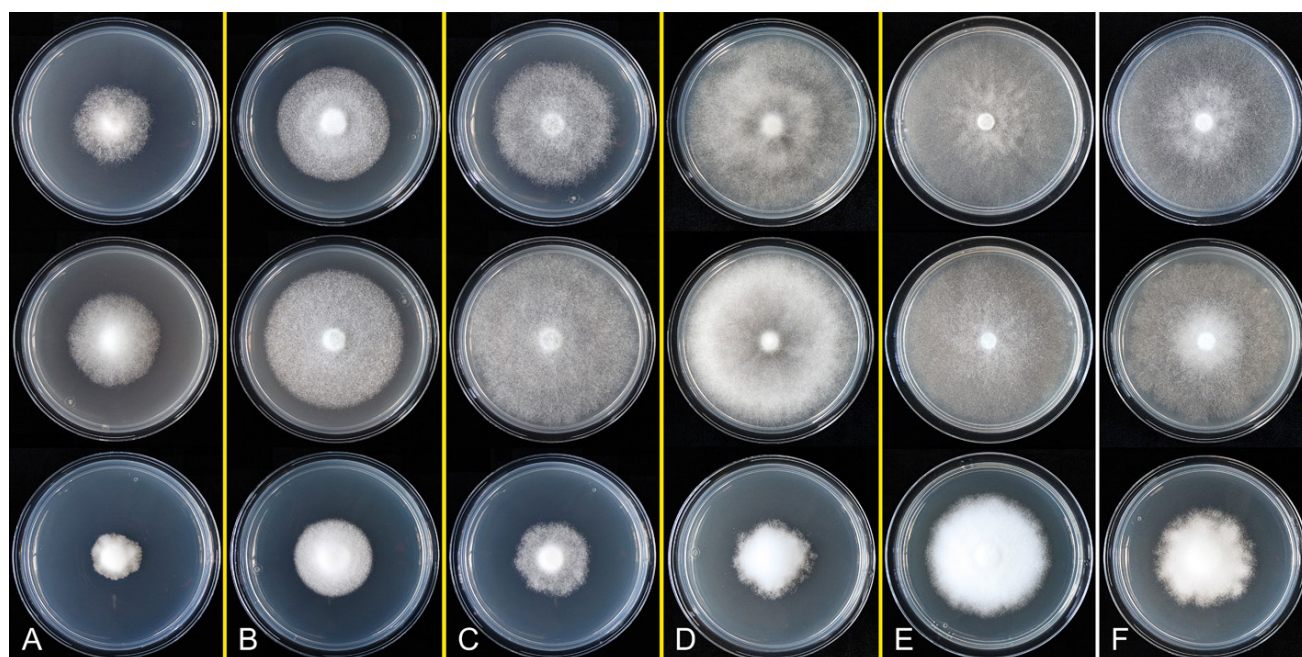


Fig. 8. Colony morphology of *Phytophthora* species from Clades 7a1–a3 after 14 d (A–C) or 10 d (D–F) growth at 20 °C on V8-agar, carrot juice agar and potato-dextrose agar (from top to bottom). **A.** *Phytophthora vulcanica* (ex-type CBS 141216). **B.** *Phytophthora tyrrenica* (ex-type CBS 142301). **C.** *Phytophthora uliginosa* (CBS 109055). **D.** *Phytophthora abietivora* (ex-type NRRL 6689). **E, F.** *Phytophthora laevigata* (E. ex-type CBS 153102; F. TJ1684). Yellow lines separate different taxa.

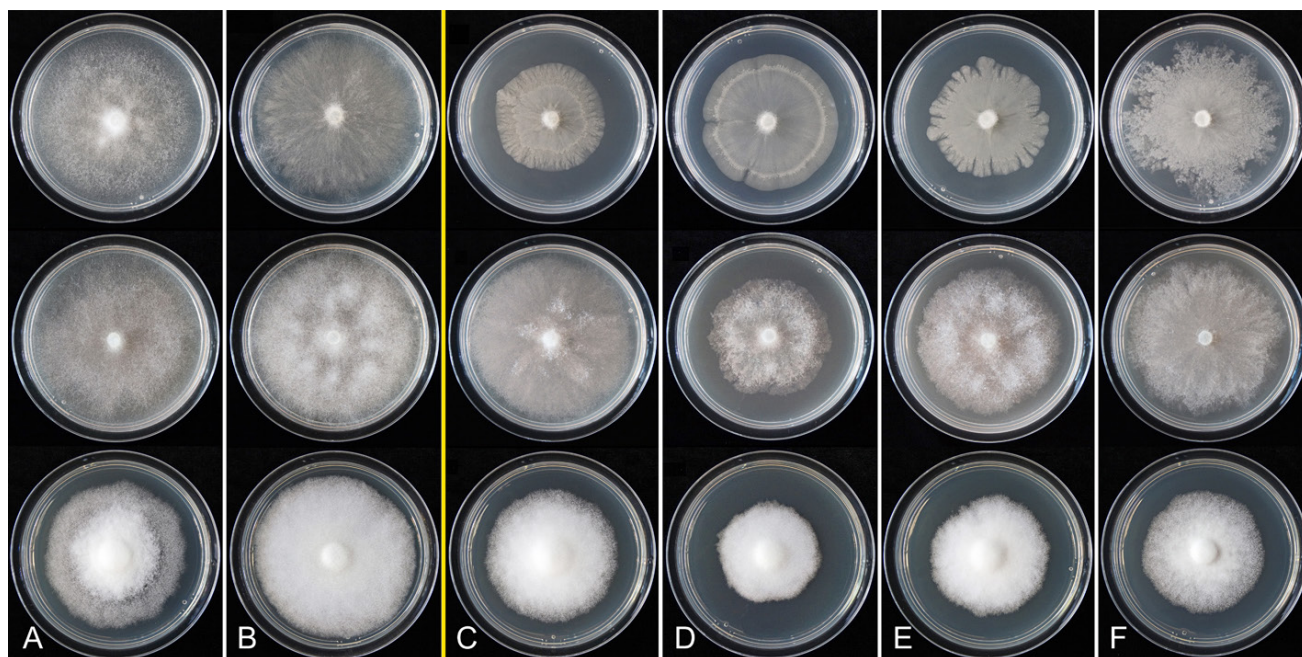


Fig. 9. Colony morphology of *Phytophthora* species from Clade 7a3 after 10 d growth at 20 °C on V8-agar, carrot juice agar and potato-dextrose agar (from top to bottom). **A, B.** *Phytophthora flexuosa* (A. ex-type CBS 141201; B. JP1053). **C–F.** *Phytophthora arta* (C. ex-type CBS 153092; D. JP418; E. JP720; F. JP821). Yellow lines separate different taxa.

by the divergence of the lineage leading to the sister species *P. tyrrenica* and *P. uliginosa*, designated as Clade 7a2. These self-fertile European lineages were basal to two large clusters, Clade 7a3 and Clade 7a4, which included all other Clade 7a taxa. In Clade 7a3, comprising exclusively self-fertile taxa, *P. europaea* resided in a fully supported basal position to two smaller clusters. One of them contained the East Asian sister species *P. arta* and *P. flexuosa* and the second one four North American taxa, *P. abietivora*, *P. facultativa*, *P. infundibuliformis* and *P. t. cadmea*, and *P. laevigata* from the

European Balkans residing in a basal position to the North American sister species *P. abietivora* and *P. facultativa* (Figs 2, 3). In Clade 7a4, which included both self-fertile and A1/A2 (self-sterile) taxa, the early divergence of the self-fertile *P. intricata* from Taiwan is followed by the subsequent divergences of a cluster containing the self-fertile sister species *P. formosa* and *P. irregularis* from Japan and Taiwan and the self-fertile '*P. attenuata* complex' which includes besides *P. attenuata*, three new species from Vietnam, *P. algida*, *P. grandoogonia* and *P. sessilis*. The next major evolutionary event

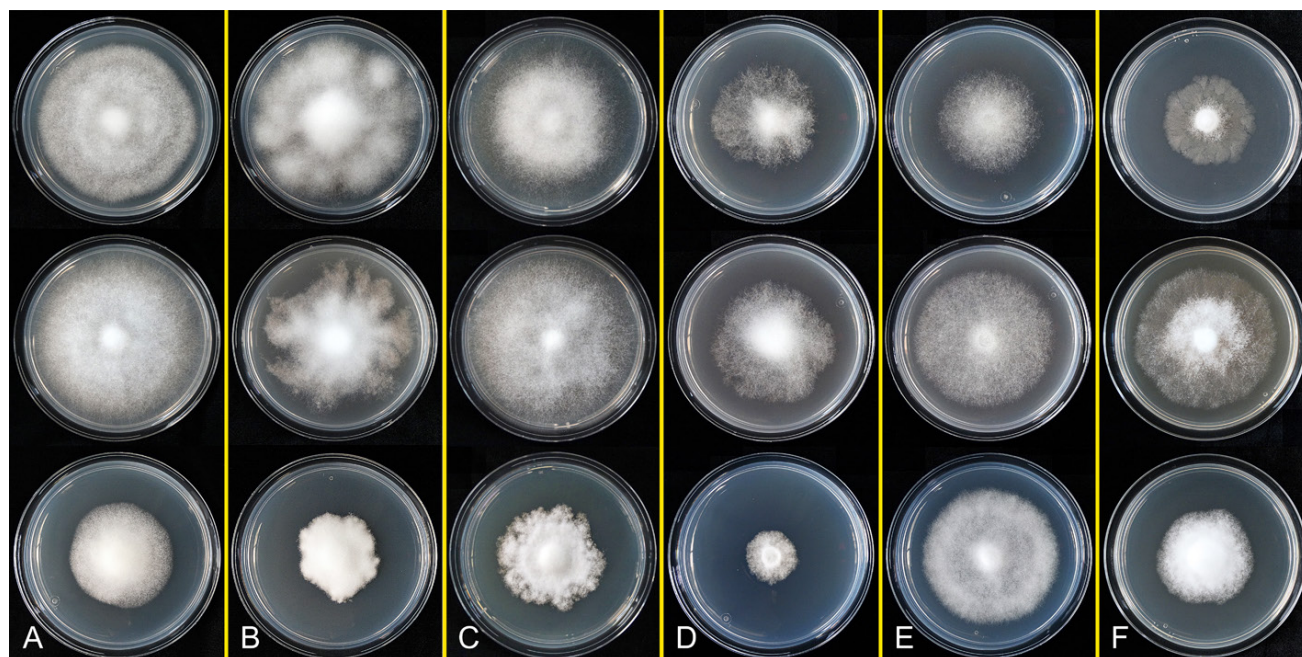


Fig. 10. Colony morphology of *Phytophthora* species from Clade 7a3 and 7a4 after 10 d (A–C, F) or 14 d (D–E) growth at 20 °C on V8-agar, carrot juice agar and potato-dextrose agar (from top to bottom). **A.** *Phytophthora europaea* (CBS 109051). **B.** *Phytophthora facultativa* (ex-type CBS 153101). **C.** *Phytophthora infundibuliformis* (ex-type CBS 153100). **D.** *Phytophthora fragariae* (TJ011). **E.** *Phytophthora rubi* (TJ015). **F.** *Phytophthora algida* (ex-type CBS 153095). Yellow lines separate different taxa.

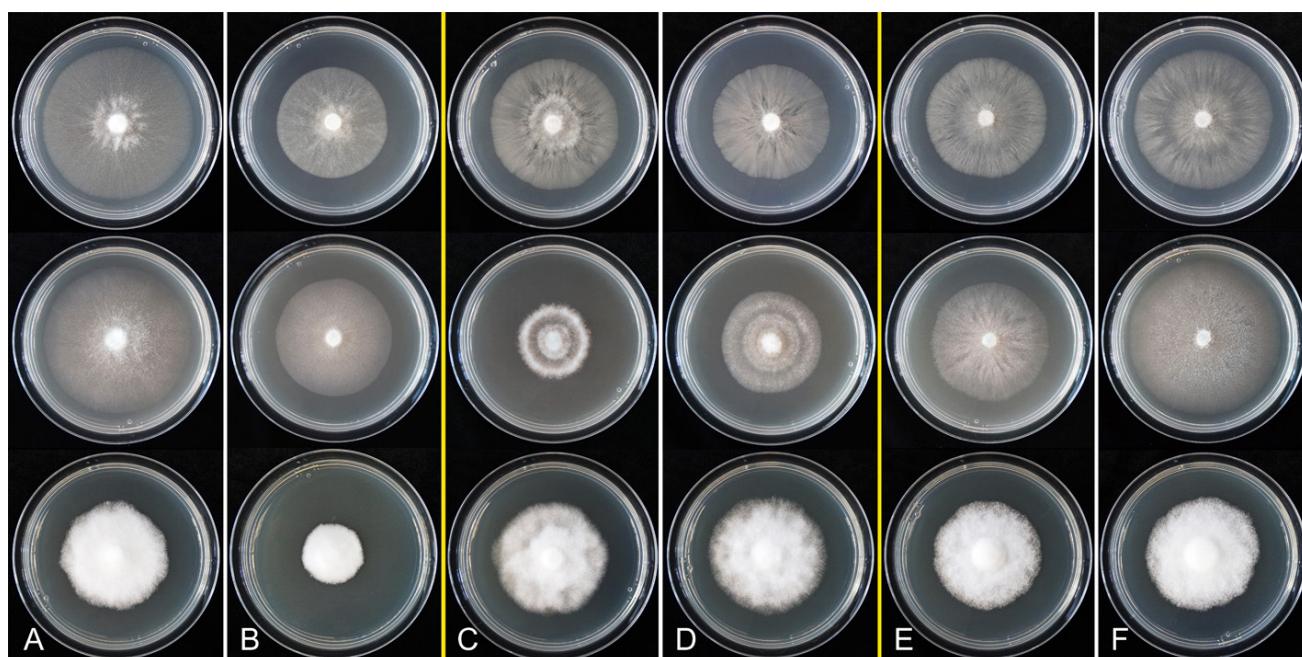


Fig. 11. Colony morphology of *Phytophthora* species from the '*Phytophthora attenuata* complex' in Clade 7a4 after 10 d growth at 20 °C on V8-agar, carrot juice agar and potato-dextrose agar (from top to bottom). **A, B.** *Phytophthora attenuata* (A. ex-type CBS 141199; B. VN026). **C, D.** *Phytophthora grandoogonia* (C. ex-type CBS 153094; D. VN618). **E, F.** *Phytophthora sessilis* (E. ex-type CBS 153096; F. VN266). Yellow lines separate different taxa.

in Clade 7a4 was the divergence of a large cluster containing the self-fertile sister species *P. fragariae* and *P. rubi*, both of unknown geographical origin, the self-fertile *P. fagacearum* from North America and several hybrid complexes: The self-fertile '*P. xalni* complex' with *P. uniformis* from the Pacific Northwest, *P. xmultiformis* of unknown origin and their interspecific hybrids *P. xalni*, *P. t. xmultiformis*-like and the new *P. t. xalni*-like from Europe; the A1/A2 *P. xcambivora* with 11 DAPC lineages (Mullett *et al.* 2023) from diverse origins; a cluster with the A1/A2 sister species *P. xgrandisporangia* from

Vietnam and *P. xheterohybrida* from Taiwan, two closely related sister species from Japan, the self-fertile *P. xnodosa* from Kyushu Island and the A1/A2 *P. xleptopleura* from Shikoku Island, and the A1/A2 *P. xincrassata* from Taiwan residing in a weakly supported, hence, ambiguous basal position. The topology of Clade 7a4 was similar in the BI and ML analyses with slight rearrangements among weaker supported nodes.

Mitochondrial phylogeny: Both the BI 50 % majority consensus rule tree (Fig. 4) and the ML bootstrap best tree (Fig. 5) resolved

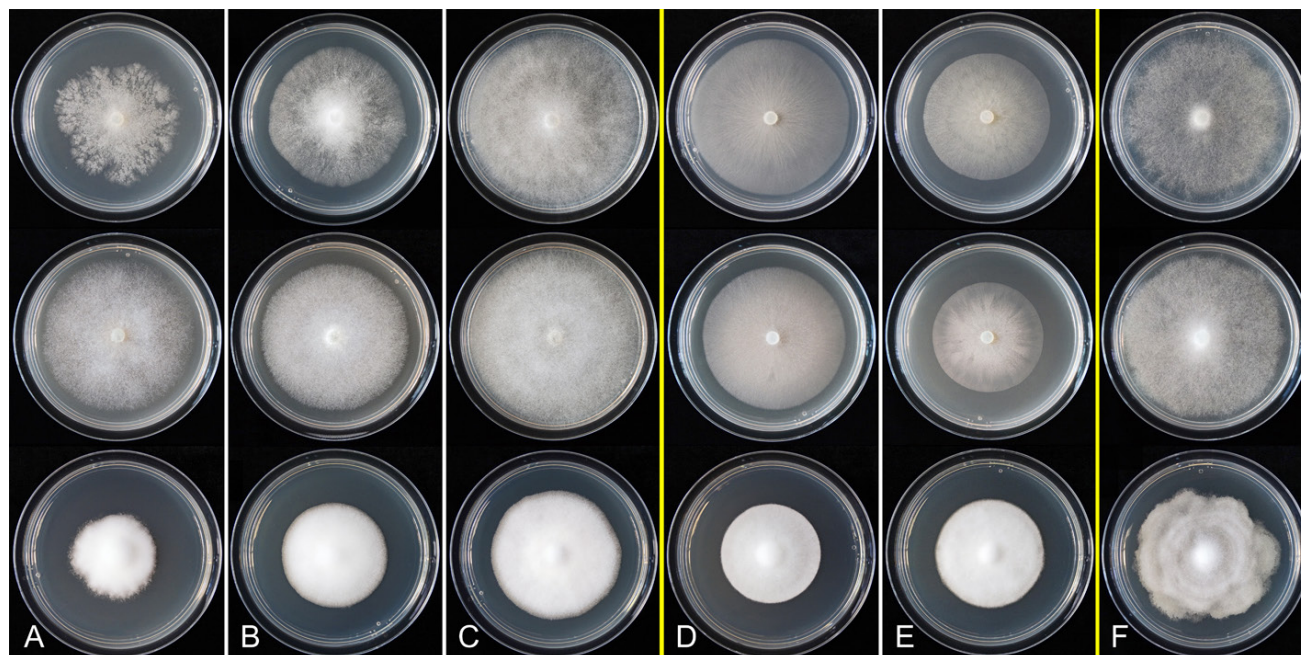


Fig. 12. Colony morphology of *Phytophthora* species from Clade 7a4 after 10 d growth at 20 °C on V8-agar, carrot juice agar and potato-dextrose agar (from top to bottom). **A–C.** *Phytophthora formosa* (A. ex-type CBS 141203; B. JP968; C. JP440). **D, E.** *Phytophthora irregularis* (D. ex-type CBS 153091; E. JP745). **F.** *Phytophthora intricata* (ex-type CBS 141211). Yellow lines separate different taxa.

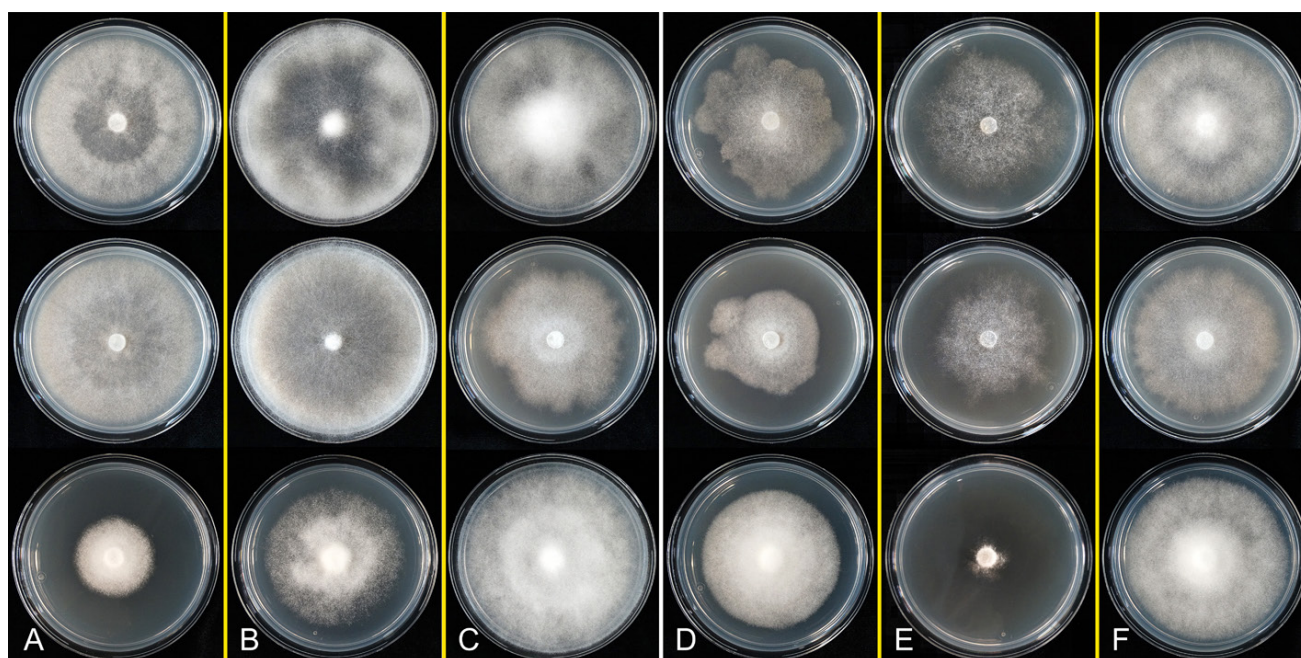


Fig. 13. Colony morphology of species from the '*Phytophthora xalni* complex' in Clade 7a4 after 10 d growth at 20 °C on V8-agar, carrot juice agar and potato-dextrose agar (from top to bottom). **A.** *Phytophthora uniformis* (TJ002). **B.** *Phytophthora xalni* (TJ1160). **C, D.** *Phytophthora xmultiformis* (D. TJ008; E. TJ009). **E.** *Phytophthora* taxon *xalni*-like (TJ005). **F.** *Phytophthora* taxon *xmultiformis*-like (TJ028). Yellow lines separate different taxa.

Table 2. Relationship between level of heterozygosity across eight nuclear genes (LSU, ITS, *βtub*, *hsp90*, *tigA*, *rpl10*, *tef-1α*, *enl*), breeding system and interspecific hybridity in *Phytophthora* Clade 7a.

Taxon	No. of isolates	Mean nuclear heterozygosity (%)	Nuclear heterozygosity range (%)	Breeding system	Hybrid status ¹
<i>P. t. cadmea</i> ²	1	0 ³	n/a	Unknown	Pure
<i>P. fagacearum</i> ⁴	1	0 ³	n/a	Self-fertile	Pure
<i>P. abietivora</i>	3	0.004	0–0.01	Self-fertile	Pure
<i>P. tyrrhenica</i>	3	0.01	0–0.02	Self-fertile	Pure
<i>P. facultativa</i> ⁵	3	0.01	0–0.01	Self-fertile	Pure
<i>P. attenuata</i>	3	0.01	0.01–0.03	Self-fertile	Pure
<i>P. formosa</i>	5	0.02	0–0.05	Self-fertile	Pure
<i>P. fragariae</i>	3	0.02	0.01–0.04	Self-fertile	Pure
<i>P. intricata</i> ⁵	3	0.02	0.01–0.05	Self-fertile	Pure
<i>P. vulcanica</i> ⁵	2	0.02	0.02–0.02	Self-fertile	Pure
<i>P. uliginosa</i>	1	0.03	0 ³ –0.1	Self-fertile	Pure
<i>P. sessilis</i>	4	0.03	0.01–0.05	Self-fertile	Pure
<i>P. infundibuliformis</i> ⁵	3	0.03	0.03–0.05	Self-fertile	Pure
<i>P. flexuosa</i>	7	0.04	0–0.1	Self-fertile	Pure
<i>P. irregularis</i>	6	0.04	0–0.1	Self-fertile	Pure
<i>P. arta</i>	4	0.04	0.01–0.1	Self-fertile	Pure
<i>P. europaea</i>	3	0.05	0.03–0.05	Self-fertile	Pure
<i>P. algida</i>	3	0.07	0.06–0.08	Self-fertile	Pure
<i>P. grandisporangia</i>	3	0.09	0.09–0.1	Self-fertile	Pure
<i>P. rubi</i>	3	0.09	0.06–0.1	Self-fertile	Pure
<i>P. laevigata</i>	4	0.1	0.07–0.11	Self-fertile	Pure
<i>P. uniformis</i>	3	0.11	0.09–0.15	Self-fertile	Pure
<i>P. t. ×multiformis</i> -like	1	0.38	n/a	Self-fertile	Confirmed
<i>P. ×multiformis</i>	2	0.38	0.26–0.5	Self-fertile	Confirmed
<i>P. ×heterohybrida</i> ⁵	3	0.42	0.39–0.48	A1/A2	Confirmed
<i>P. ×cambivora</i> DAPC6 ⁶	2	0.46	0.46–0.46	A1/A2	Confirmed
<i>P. ×grandisporangia</i>	3	0.55	0.47–0.64	A1/A2	Confirmed
<i>P. ×cambivora</i> DAPC3 ⁶	2	0.57	0.57–0.57	A1/A2	Confirmed
<i>P. ×cambivora</i> DAPC2 ⁶	4	0.60	0.44–0.91	A1/A2	Confirmed
<i>P. ×cambivora</i> DAPC1, 4, 5, 7–11 ⁷	18	0.71	0.56–0.9	A1/A2	Confirmed
<i>P. ×alni</i>	3	0.72	0.63–0.76	Self-fertile	Confirmed
<i>P. t. ×alni</i> -like	1	0.80	n/a	Self-fertile	Probable
<i>P. ×leptopleura</i>	4	0.95	0.91–1.06	A1/A2	Confirmed
<i>P. ×nodosa</i>	4	0.95	0.92–1.01	Self-fertile	Confirmed
<i>P. ×incrassata</i> ⁵	3	0.97	0.95–1.01	A1/A2	Confirmed

n/a = not available.

¹ Pure: isolate genotypes assumed to be representative of a near pure species.

Confirmed: based on nuclear genotyping-by-sequencing (Van Poucke et al. 2021; Mullett et al. 2023; Fig. S7); a high level of nuclear heterozygosity and in some species mitochondrial profile corresponds closely to that of another (presumed maternal) Clade 7a species.

Probable: high level of nuclear heterozygosity consistent with isolates examined being some form of interspecific hybrid. In addition the following can apply: mitochondrial profile shows high similarity to one or more other Clade 7a taxa; different mitochondrial genes show high similarity to different other Clade 7a taxa; multiple mitochondrial genotypes.

² LSU, *hsp90*, *rpl10*, *tigA* and *tef-1α* not available³ Most likely due to the use of automated sequence editing.⁴ *enl*, *rpl10* and *tef-1α* not available.⁵ Isolates examined could be genetically identical or closely related due to local asexual reproduction.⁶ Diploid genome (Mullett et al. 2023).⁷ Polyploid genome (Mullett et al. 2023).

within Clade 7a 29 discrete lineages. The overall topology of both trees was similar to each other and to the nuclear trees supporting the grouping into the four clusters Clade 7a1–a4 and their subsequent divergences. Both the BI and ML tree contained multiple polytomies which might indicate true species radiations or phylogenetic conflicts caused by reticulation events, recombination events or homoplasy (Bandelt *et al.* 1999, Posada & Crandal 2001, Cassens *et al.* 2005) which will be discussed in the ‘Notes on the phylogeny of Clade 7a’. Both analyses resolved nine different mitochondrial

genotypes within *P. ×cambivora* with the DAPC3 lineage consistently residing in sister position to the shared maternal line of *P. ×alni*, *P. ×multiformis* and *P. t. ×alni*-like (Figs 4, 5). Also *P. uniformis* and *P. t. ×multiformis*-like share an identical maternal line. The phylogenetic distinctiveness of both sister pairs *P. ×leptopleura*/*P. ×nodosa* and *P. ×heterohybrida*/*P. ×grandisporangia* received full or strong support. In both analyses, *P. formosa* displayed high genetic variability with two Japanese isolates, JP343 and JP2358, grouping on a separate branch in considerable genetic distance (21 bp = 0.9 %) from other

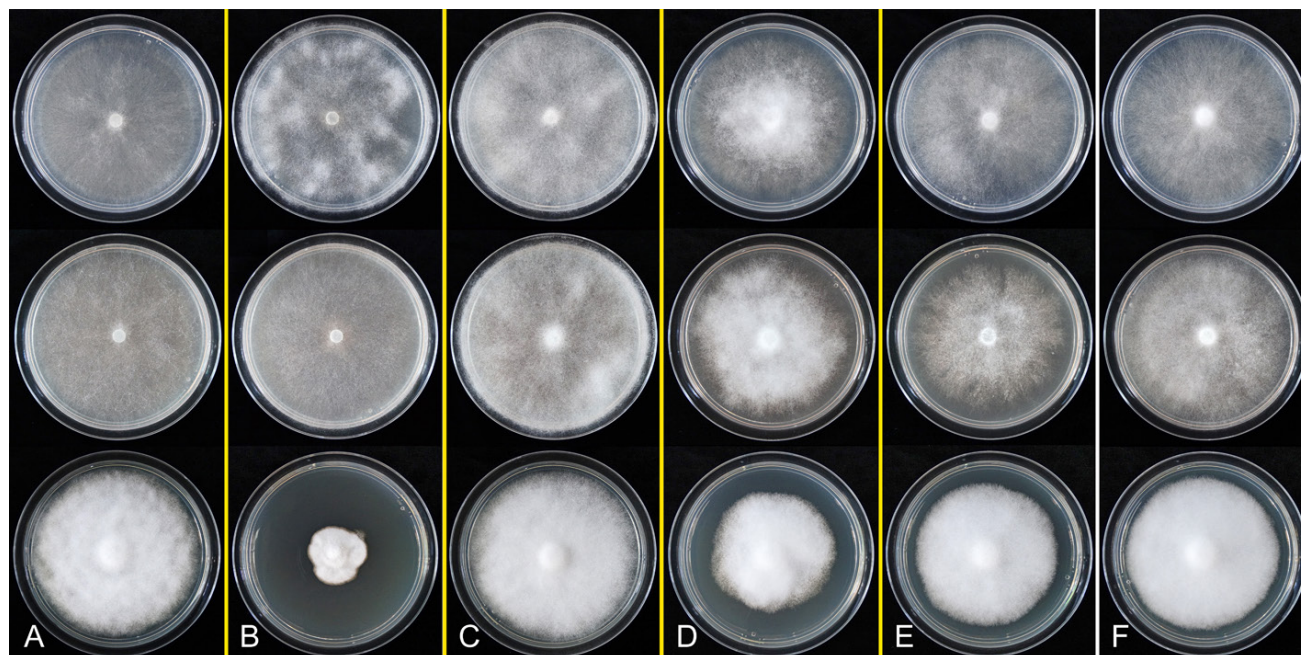


Fig. 14. Colony morphology of *Phytophthora* species from Clade 7a4 after 10 d growth at 20 °C on V8-agar, carrot juice agar and potato-dextrose agar (from top to bottom). **A.** *Phytophthora ×grandisporangia* (ex-type CBS 153093). **B.** *Phytophthora ×heterohybrida* (ex-type CBS 141207). **C.** *Phytophthora ×incrassata* (ex-type CBS 141209). **D.** *Phytophthora ×leptopleura* (ex-type CBS 153090). **E, F.** *Phytophthora ×nodosa* (E. JP532; F. ex-type CBS 153088). Yellow lines separate different taxa.

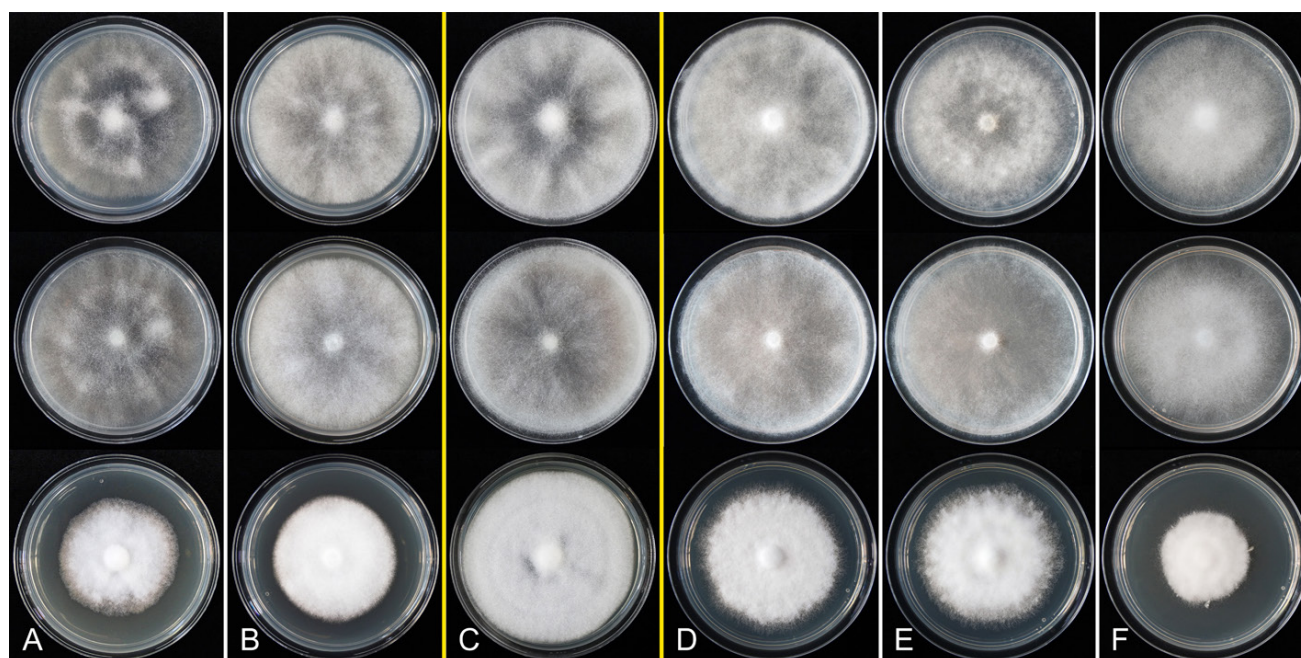


Fig. 15. Colony morphology of different DAPC lineages of *Phytophthora ×cambivora* from Clade 7a4 after 10 d growth at 20 °C on V8-agar, carrot juice agar and potato-dextrose agar (from top to bottom). **A, B.** DAPC9 (A. ex-neotype CBS 141218; B. TJ1342). **C.** DAPC10 (TJ066). **D–F.** DAPC2 (D. JP182; E. JP361; F. JP429). Yellow lines separate different taxa.

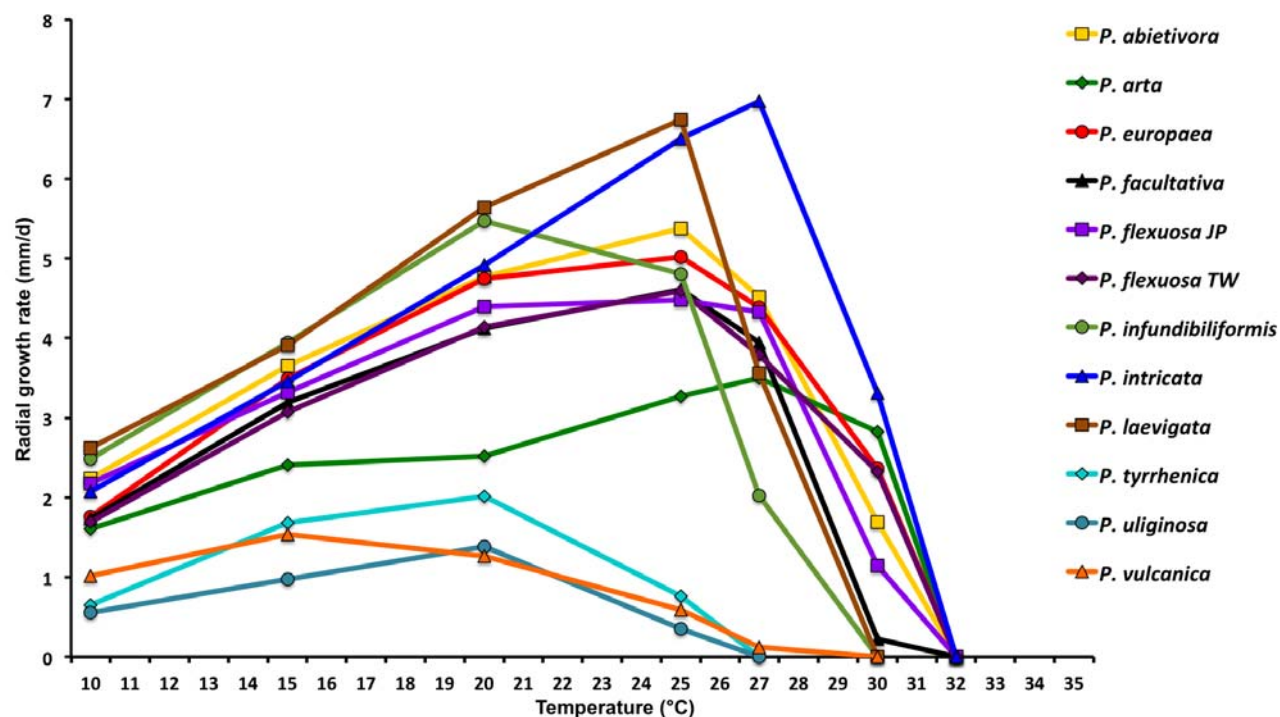


Fig. 16. Mean radial growth rates of seven known and four new *Phytophthora* species from Clade 7a1: *P. vulcanica* (2 isolates); Clade 7a2: *P. tyrrhenica* (2 isolates); *P. uliginosa* (2 isolates); Clade 7a3: *P. abietivora* (1 isolate); *P. arta* (6 isolates); *P. europaea* (3 isolates); *P. facultativa* (4 isolates); *P. flexuosa* (2 isolates from Taiwan - TW; 6 isolates from Japan - JP); *P. infundibuliformis* (4 isolates); *P. laevigata* (6 isolates); and Clade 7a4: *P. intricata* (2 isolates) on V8-agar at different temperatures.

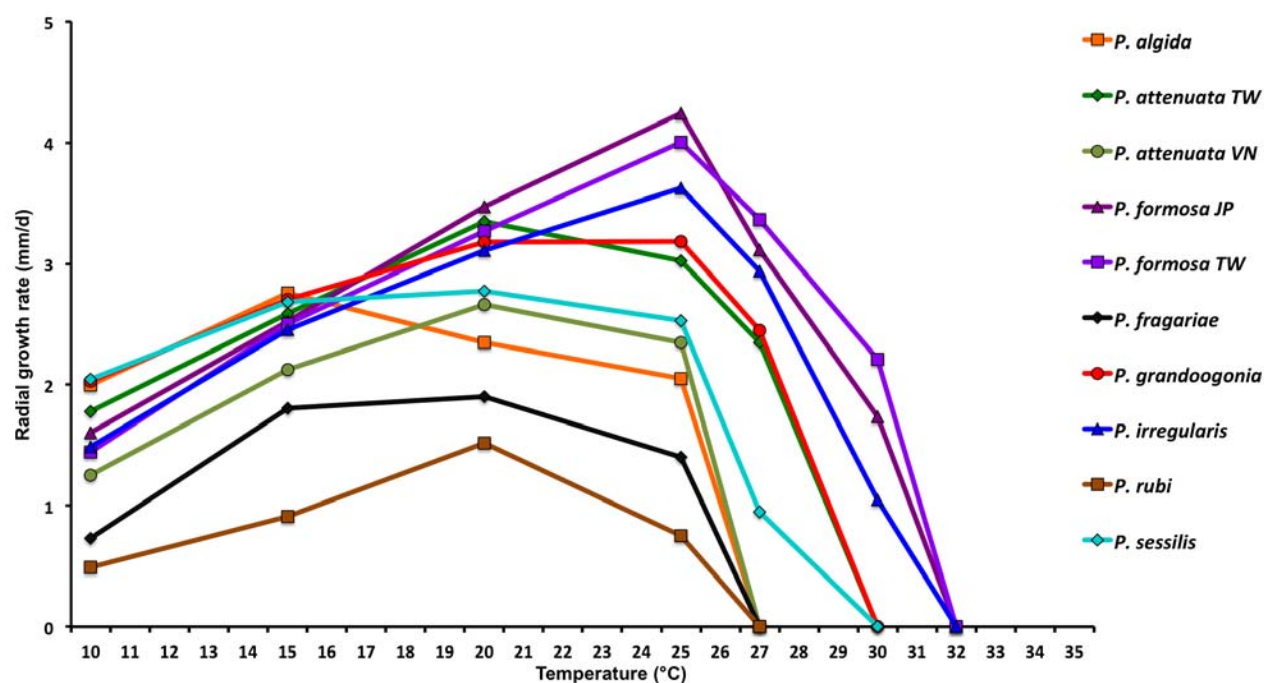


Fig. 17. Mean radial growth rates of four known and four new *Phytophthora* species from Clade 7a4 on V8-agar at different temperatures: *P. algida* (4 isolates); *P. attenuata* (2 isolates from Taiwan - TW; 1 isolate from Vietnam - VN); *P. formosa* (4 isolates from Japan - JP; 2 isolates from TW); *P. fragariae* (2 isolates); *P. grandoogonia* (6 isolates); *P. irregularis* (7 isolates); *P. rubi* (4 isolates); *P. sessilis* (5 isolates).

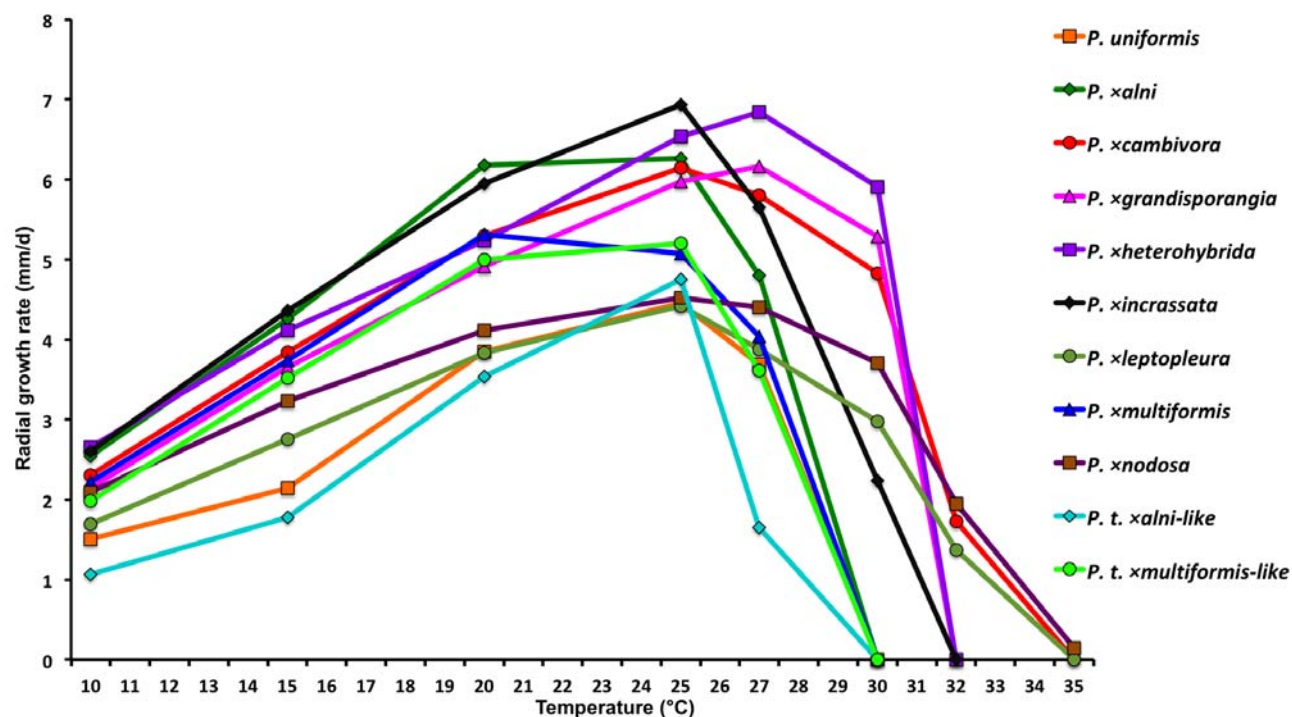


Fig. 18. Mean radial growth rates of seven known taxa and four new *Phytophthora* taxa from hybrid complexes in Clade 7a4 on V8-agar at different temperatures: *P. uniformis* (3 isolates); *P. xalni* (6 isolates); *P. xcombivora* (57 isolates from all 11 DAPC lineages); *P. xgrandisporangia* (6 isolates); *P. xheterohybrida* (2 isolates); *P. xincrassata* (3 isolates); *P. xleptopleura* (5 isolates); *P. xmultiformis* (4 isolates); *P. xnodosa* (4 isolates); *P. taxon xalni-like* (1 isolate); and *P. taxon xmultiformis-like* (1 isolate).

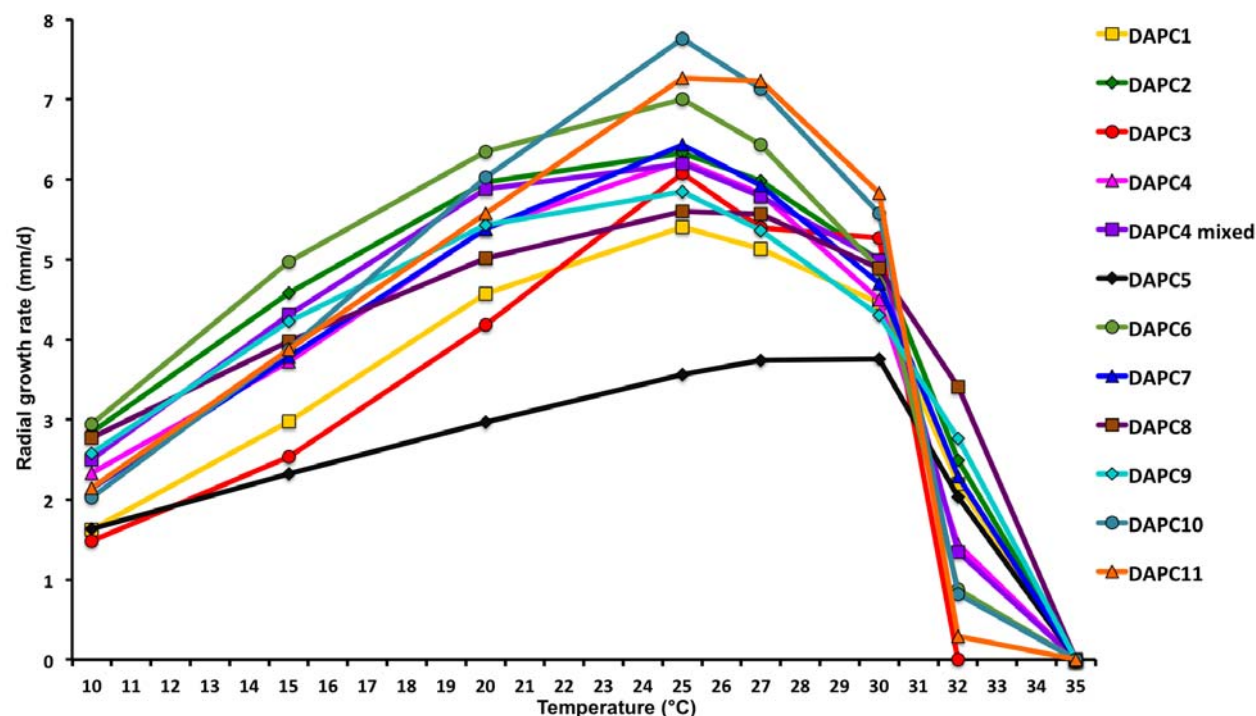


Fig. 19. Mean radial growth rates of 11 DAPC lineages of *Phytophthora xcombivora* from Clade 7a4 on V8-agar at different temperatures: DAPC1 (4 isolates); DAPC2 (7 isolates); DAPC3 (3 isolates); DAPC4 (5 isolates); DAPC4mixed (5 isolates); DAPC5 (5 isolates); DAPC6 (5 isolates); DAPC7 (5 isolates); DAPC8 (4 isolates); DAPC9 (5 isolates); DAPC10 (4 isolates); DAPC11 (5 isolates).

Japanese and Taiwanese isolates of the species. Also *P. attenuata*, *P. flexuosa* and *P. irregularis* showed intraspecific variability (Figs 4, 5).

Combined nuclear and mitochondrial phylogeny: The phylogenetic analyses of the combined dataset of nuclear and mitochondrial sequences resolved several phylogenetic conflicts of the separate nuclear and mitochondrial analyses. Both the BI 50 % majority consensus rule tree and the ML bootstrap best tree resolved within Clade 7a 32 discrete lineages discriminating all 18 described species, the two informally designated taxa, the 11 new species and the new informally designated taxon *P. t. xalni*-like (Figs 6, 7). Almost all nodes in the deeper phylogeny had full or high support values. The structuring of Clade 7a into the four clusters 7a1–7a4 was strongly supported. Since the nuclear dataset outnumbered the mitochondrial dataset by loci (8 vs 3), concatenated sequence length (8205 vs 2469) and parsimony-informative sites (577 vs 263), the topology of the combined 11-loci trees resembled more closely the respective nuclear (Figs 4, 5) than the respective mitochondrial trees (Figs 3, 5).

Within *P. xambivora*, in both analyses all 11 DAPC lineages grouped separately from each other except for DAPC2 isolate JP361 which resided apart from the other three DAPC2 isolates and DAPC5 and 9 which are identical across the 11 loci. In the cluster comprising *P. fagacearum*, *P. xambivora* and the '*P. xalni* complex', all deeper nodes had only weak support due to the high number of hybrid taxa (5 out of 7) and maternal lines in *P. xambivora* causing discordances between the nuclear and the mitochondrial phylogenies, as highlighted by the maternal line of DAPC3 residing outside of *P. xambivora* in sister position to the maternal line of *P. xalni*, *P. xmultiformis* and *P. t. xalni*-like (Figs 4, 5).

Mito-nuclear discordance: A significant level of discordance was observed in nuclear and mitochondrial phylogenetic placement among several hybrid taxa, i.e., the DAPC lineages of *P. xambivora*, *P. t. xalni*-like and *P. t. xmultiformis*-like, but also among several 'pure' species, in particular *P. algida*, *P. europaea* and *P. fagacearum* (Figs 2–5).

Nuclear gene heterozygosity: In contrast to the homozygous mitochondrial three-loci (*cox1*, *nadh1*, *rps10*) alignment, the eight-loci nuclear (LSU, ITS, *βtub*, *hsp90*, *tigA*, *rpl10*, *tef-1α*, *enl*) alignment of Clade 7a contained numerous heterozygous positions. Among the 32 taxa mean heterozygosity varied widely from zero or close to zero to 0.97 % (Table 2). In some isolates of *P. xleptopleura* nuclear heterozygosity reached 1.06 %. Further, within a few taxa and lineages wide variations in heterozygosity also occurred (Table 2). For instance, the two isolates of *P. xmultiformis* tested had heterozygosity levels of 0.26 and 0.5 %, respectively; and in the four isolates from the DAPC2 lineage of *P. xambivora* heterozygosity varied between 0.44 and 0.91 % (Table 2). Relationships between nuclear heterozygosity and interspecific hybridity are considered in detail in the 'Notes on heterozygosity, breeding systems and hybridity of Clade 7a' and the Discussion. Heterozygosity levels together with other data like shared maternal lines with other Clade 7a species and results from genotyping-by-sequencing (GBS) studies demonstrating high numbers of tri-allelic loci and in some taxa even occurrence of tetra-allelic loci (Van Poucke et al. 2021; Fig. S7) formed the basis for deciding whether a new taxon would be formally designated a hybrid.

TAXONOMY

For all Clade 7a species included in this study colony morphologies on CA, PDA and V8A and temperature-growth relations on V8A are presented in Figs 8–19. Morphological and physiological characters and morphometric data of the 11 newly described and 18 known species and two informally designated taxa in Clade 7a are comprehensively recorded in Tables 3–8. To enable detailed comparisons between Clade 7a species described here and previously (Jung et al. 2002, 2017a, b, Li et al. 2019, Crous et al. 2024) and the known species *P. fragariae*, *P. rubi*, *P. uniformis*, *P. xalni* and *P. xmultiformis* updated taxonomic descriptions of the latter five species without nomenclatural act, based on morphometric data from Jung et al. (2017a), additional morphometric measurements and our present temperature-growth studies, are given below after the descriptions of new species. To enable comparisons between the original descriptions of *P. attenuata*, *P. flexuosa* and *P. formosa* from Taiwan (Jung et al. 2017a) and new isolates of these species from Vietnam and Japan, respectively, morphological, morphometric and temperature growth data of these isolates are provided in Tables 3–5 and Figs 16–17, and their structures are shown in Figs 21, 28 and 30. Morphological and physiological comparisons between closely related Clade 7a species are provided in the 'Notes on the taxonomy of Clade 7a taxa'.

Clade 7a3

Phytophthora arta T. Jung, K. Kageyama, C.M. Brasier, Z.Á. Nagy & M. Horta Jung, **sp. nov.** MB 857770. Fig. 20.

Etymology: The name refers to the crowded conditions occurring in some sporangia during internal simultaneous proliferation with two new sporangia in either a nested or in both a nested and extended way (*arta* Latin = crowded).

Typus: **Japan**, Kyushu, Shiiba, isolated from a stream flowing through a montane, temperate mixed forest, May 2017, *T. Jung* & *S. Uematsu* [**holotype** CBS H-25673, dried culture on V8A, ex-holotype living culture CBS 153092 = JP032; GenBank accession nos. PX606952 (LSU), PX607124 (ITS), PX580959 (*βtub*), PX581619 (*hsp90*), PX581939 (*tigA*), PX581092 (*rpl10*), PX581263 (*tef-1α*), PX581440 (*enl*), PX581758 (*cox1*), PX580828 (*nadh1*), PX580656 (*rps10*)].

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or rarely in lax sympodia of 2–3 sporangia (Fig. 20L); mostly ovoid, broad-ovoid or elongated ovoid (53.7 %; Fig. 20A, B, K), ellipsoid to elongated ellipsoid (26.4 %; Fig. 20D, E, L), obpyriform to elongated-obpyriform (12.8 %; Fig. 20C), less frequently limoniform to elongated limoniform (3.9 %), cigar-shaped (1.3 %; Fig. 20F), pyriform (1.3 %; Fig. 20H), obovoid (0.3 %) or ampulliform (0.3 %); sporangial apices non-papillate (Fig. 20A–F, H, I, K, L); sporangial proliferation internal in both a nested and extended way, occasionally with 2 sporangia or one sporangium and one additional sporangiophore arising simultaneously (Fig. 20H–K), rarely external; sporangial dimensions averaging $67.2 \pm 9.7 \times 37.2$

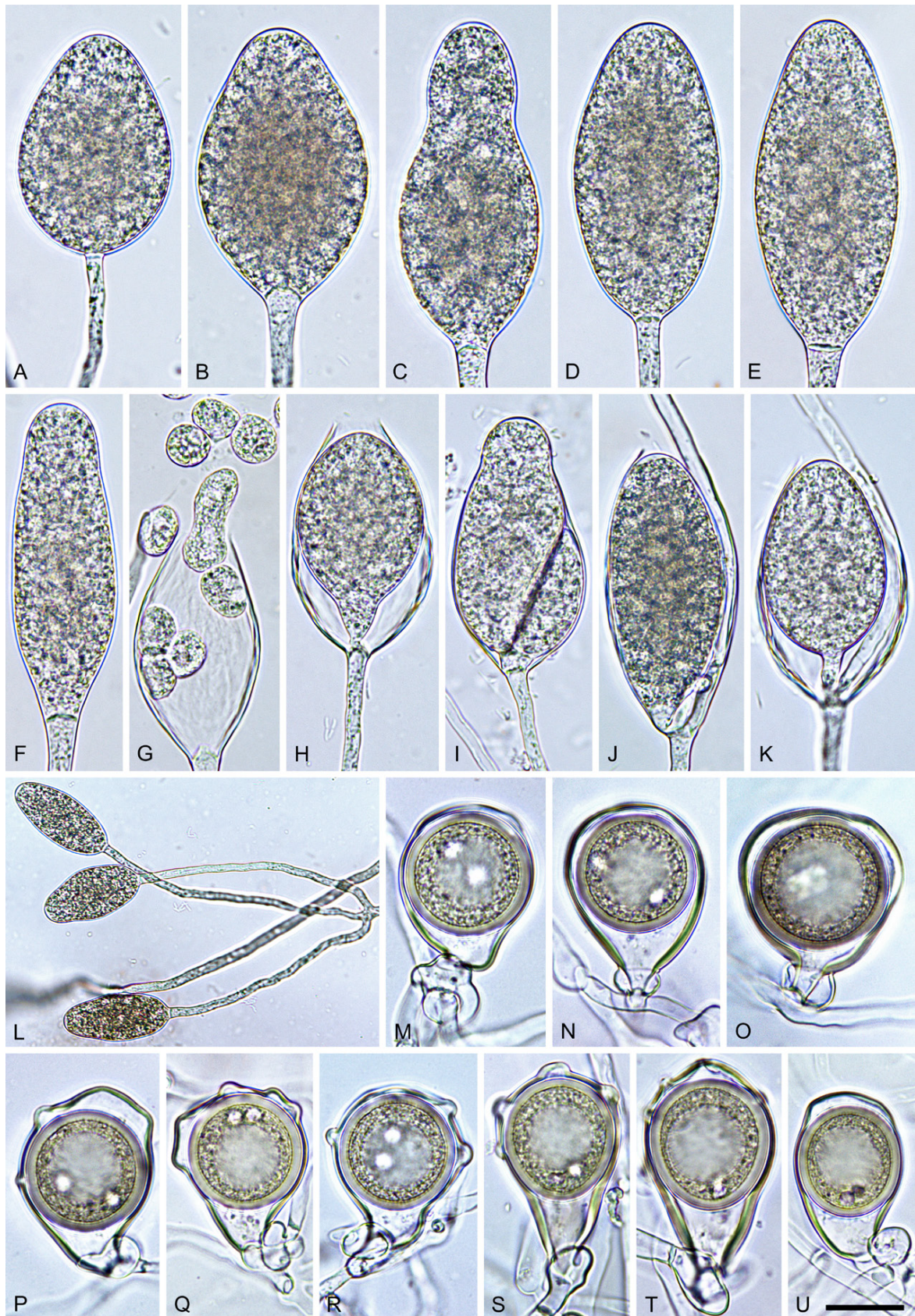


Fig. 20. *Phytophthora arta*. **A–L.** Persistent sporangia formed on V8-agar (V8A) in soil extract. **A–F, H, K, L.** Ovoid, ellipsoid, obpyriform, cigar-shaped or pyriform non-papillate sporangia. **G.** Sporangium releasing zoospores. **H.** Internal nested proliferation. **I.** Internal nested proliferation with two sporangia simultaneously. **J, K.** Internal nested and extended proliferation simultaneously. **L.** Sympodium with three sporangia. **M–U.** Oogonia with predominantly tapering bases and plerotic oospores, sessile or on short stalks, formed in single culture in solid V8A. **M–O, U.** Smooth oogonial walls. **P–T.** Ornamented walls. **M, R.** Globose to subglobose oogonia. **N, P, S–U.** Elongated oogonia. **O–Q.** Excentric oogonia. **M, P–U.** Paragnathous antheridia. **N–O.** Amphigynous unicellular antheridia. Images: **B, I, R, S.** CBS 153092; **M–O.** JP066; **G.** JP418; **P, T.** JP425; **A, H, J, K.** JP720; **C–F, L, Q, U.** JP821. Scale bar = 20 µm in **A–K, M–U**, and 50 µm in **L**.

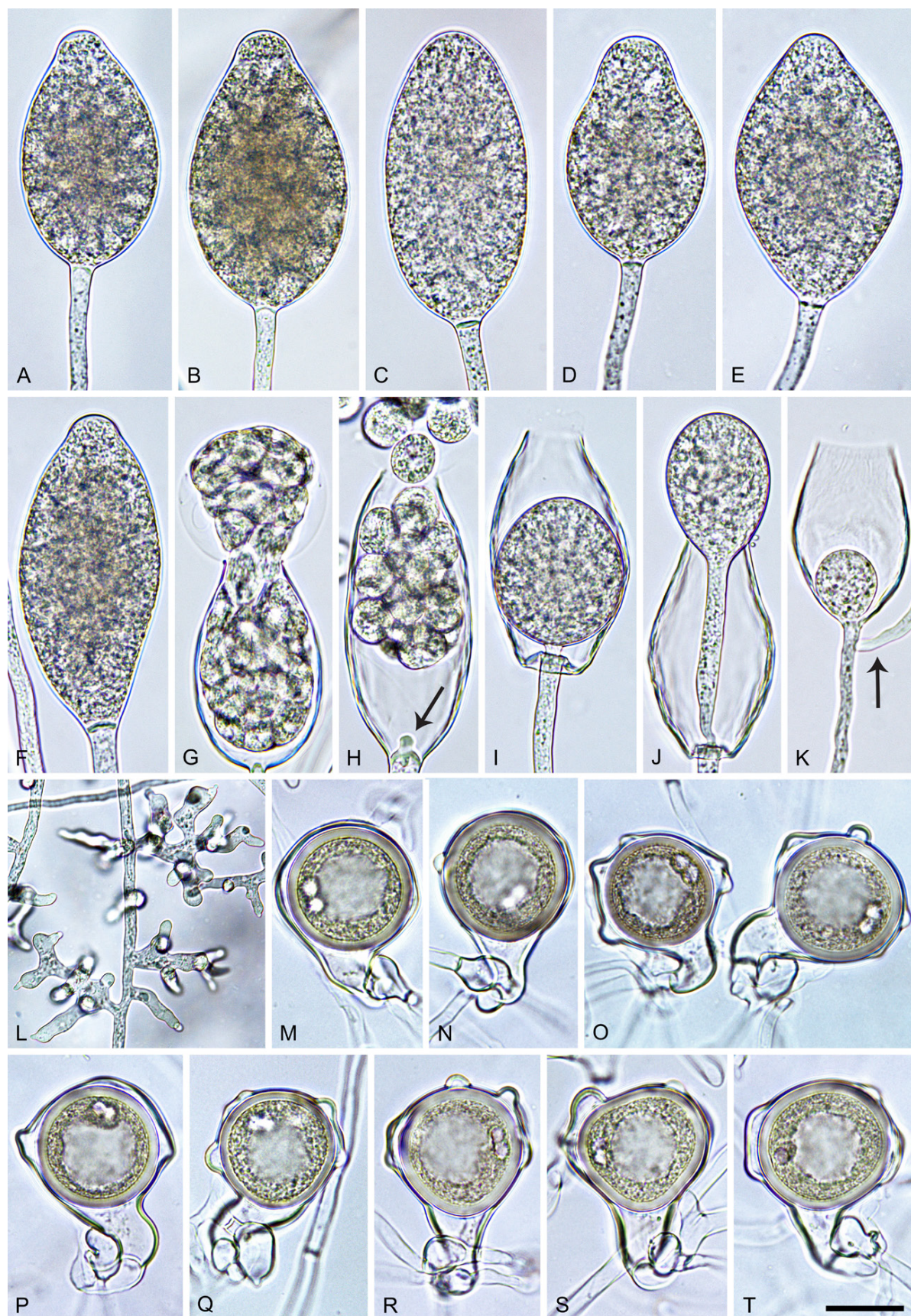


Fig. 21. *Phytophthora flexuosa* from Japan. **A–K.** Persistent sporangia formed on V8-agar (V8A) in soil extract. **A–F.** Ovoid, ellipsoid, obpyriform or limoniform non-papillate sporangia. **G–H.** Sporangia releasing zoospores. **H.** Conspicuous basal plug. **I.** Internal nested proliferation. **J.** Internal extended proliferation. **K.** Internal nested and external (arrow) proliferation. **L.** Coralloid lateral hyphae. **M–T.** Oogonia with tapering bases,plerotic oospores and paragynous antheridia, sessile or on short stalks, formed in single culture in solid V8A. **M.** Globose oogonium with smooth wall. **N.** Globose oogonium with slightly ornamented wall. **O–T.** Flexuose oogonia with ornamented walls. Images: A, B, D, E, G, J, K. JP722; C, H, L. JP219; F, I, N–P, R, T. JP1053; M. JP803; Q, S. JP819. Scale bar = 20 µm in A–K, M–T, and 50 µm in L.

$\pm 4.4 \mu\text{m}$ (overall range $38.7\text{--}95.2 \times 24.8\text{--}46.4 \mu\text{m}$; range of isolate means $55.3\text{--}77.3 \times 32.5\text{--}39.3 \mu\text{m}$) with a length/breadth ratio of 1.82 ± 0.26 (overall range $1.3\text{--}3.0$); sporangial germination indirect with zoospores discharged through an exit pore $8.2\text{--}18.7 \mu\text{m}$ wide (av. $12.3 \pm 2.3 \mu\text{m}$) (Fig. 20G). Zoospores limoniform to reniform whilst motile (Fig. 20G), becoming spherical (av. diam. $12.0 \pm 1.5 \mu\text{m}$) on encystment; cysts germinating directly by forming a hypha or a microsporangium or indirectly by releasing a secondary zoospore (diplanetism). Hyphal swellings not observed. Chlamydospores not observed. Oogonia abundantly formed in single culture (self-fertile 'homothallic' breeding system); globose to subglobose (24.4 %; Fig. 20M, R), elongated (28.9 %; Fig. 20N, P, S–U) or excentric (36.7 %; Fig. 20O–Q); predominantly with short or long tapering bases (83.1 %; Fig. 20M, N, P–U) or less frequently with round bases (16.9 %; Fig. 20O); smooth-walled (47.3 %; Fig. 20M–O, U) or ornamented (52.7 %; Fig. 20P–T), often flexuose (25.4 %; Fig. 20P, Q); mostly sessile or on short stalks (Fig. 20M–U); oogonial diam. $34.2 \pm 3.7 \mu\text{m}$ (overall range $18.1\text{--}48.3 \mu\text{m}$; range of means $32.1\text{--}35.4 \mu\text{m}$); nearly plerotic to plerotic (83.2 %; Fig. 20M, N, P–U) or infrequently slightly aplerotic (16.8 %; Fig. 20O). Oospores usually globose (Fig. 20M–R) or slightly elongated in elongated oogonia (Fig. 20S–U), with one large lipid globule; diam. $29.5 \pm 3.4 \mu\text{m}$ (overall range $14.7\text{--}37.5 \mu\text{m}$; range of means $26.7\text{--}31.8 \mu\text{m}$); wall thickness $2.1 \pm 0.5 \mu\text{m}$ (overall range $0.87\text{--}3.69 \mu\text{m}$); oospore wall index 0.36 ± 0.06 (overall range $0.22\text{--}0.55$); low abortion rate of 8.1 % (2–25 %) after 4 wk. Antheridia predominantly paragynous and club-shaped, ovoid or subglobose and unicellular (av. 98 %; Fig. 20M, P–U) or rarely amphigynous unicellular and cylindrical, subglobose or irregular (Fig. 20N, O); dimensions $12.8 \pm 2.6 \times 9.5 \pm 1.5 \mu\text{m}$.

Culture characteristics: Colonies variable between isolates; on V8A submerged to appressed, uniform or with faint radiate to striate pattern, with irregular dendroid or tongue-shaped margins, in several isolates with a concentric ring behind the advancing margin; on CA submerged to appressed with limited aerial mycelium, uniform or with faint radiate to striate pattern; on PDA uniform and woolly-cottony (Fig. 9).

Cardinal temperatures and growth rates: On V8A optimum at 27.5°C with $3.5 \pm 0.88 \text{ mm/d}$ radial growth; maximum 30 to $< 32.5^\circ\text{C}$; minimum $< 10^\circ\text{C}$ (Fig. 16), lethal temperature 32.5°C . At 20°C on V8A, CA and PDA $2.52 \pm 0.64 \text{ mm/d}$, $3.22 \pm 0.37 \text{ mm/d}$ and $2.61 \pm 0.31 \text{ mm/d}$, respectively.

Additional materials examined: **Japan**, Kyushu, Shiiba, isolated from a baiting leaf floating in a stream running through a montane, temperate mixed forest, May 2017, T. Jung & S. Uematsu (JP055, JP418); isolated from naturally fallen leaves floating in streams running through a montane, temperate mixed forest, May 2017, T. Jung & H. Masuya (JP821, JP974); isolated from a necrotic leaf of *Pieris japonica* in a montane, mixed forest, May 2017, J. Webber & C.M. Brasier (JP425); Shikoku, Ichinomata, isolated from a baiting leaf floating in a stream running through a warm-temperate laurosilva forest, May 2017, T. Jung & K. Kageyama (JP066); isolated from a naturally fallen leaf floating in a stream running through a warm-temperate laurosilva forest, May 2017, T. Jung & M. Horta Jung (JP720).

Phytophthora facultativa T. Jung, T. Corcobado, Z.Á. Nagy & S. Raghuwinder, *sp. nov.* MB 857773. Fig. 22.

Etymology: The name refers to the facultative caducity of a low proportion of sporangia with constrictions of the sporangiophores.

Typus: **USA**, Louisiana, Dewey W. Wills, isolated from a naturally fallen leaf floating in a stream running through a subtropical forest, Mar. 2020, T. Corcobado & T. Májek [**holotype** CBS H-25671, dried culture on V8A, ex-holotype living culture CBS 153101 = LU410; GenBank accession nos. PX606965 (LSU), PX607135 (ITS), PX580970 (*βtub*), PX581632 (*hsp90*), PX581955 (*tigA*), PX581104 (*rpl10*), PX581277 (*tef-1a*), PX581455 (*enl*), PX581774 (*cox1*), PX580840 (*nadh1*), PX580669 (*rps10*)].

Morphological structures on V8A: Sporangia abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores; mostly ovoid to broad-ovoid (67.5 %; Fig. 22A–C) or obpyriform, broad-obpyriform or elongated-obpyriform (28.5 %; Fig. 22D–F), less frequently limoniform or elongated limoniform (3.5 %) or subglobose (0.5 %); sporangial apices non-papillate (Fig. 22A–F, H, I); sporangial proliferation internal in both a nested and extended way (Fig. 22H–J); sporangiophores occasionally with narrow undulating sections (Fig. 22E, H) or with constrictions (Fig. 22C) enabling rare caducity (Fig. 22I), sometimes widening towards the sporangial base (2.5 %; Fig. 22C, D); sporangial dimensions averaging $58.7 \pm 8.0 \times 41.4 \pm 4.8 \mu\text{m}$ (overall range $43.5\text{--}83.0 \times 29.5\text{--}57.9 \mu\text{m}$; range of isolate means $53.7\text{--}64.5 \times 38.9\text{--}46.4 \mu\text{m}$) with a length/breadth ratio of 1.42 ± 0.14 (overall range $1.03\text{--}2.14$); sporangial germination indirect with zoospores discharged through an exit pore $9.3\text{--}18.1 \mu\text{m}$ wide (av. $14.2 \pm 1.9 \mu\text{m}$) (Fig. 22G). Zoospores limoniform to reniform whilst motile, becoming spherical (av. diam. $14.2 \pm 1.8 \mu\text{m}$) on encystment; cysts usually germinating directly forming a hypha. Hyphal swellings rarely formed in water, subglobose, ovoid or limoniform; $34.9 \pm 8.5 \mu\text{m}$. Chlamydospores not observed. Oogonia readily produced in single culture (self-fertile 'homothallic' breeding system); borne laterally, mostly sessile or on short often curved stalks (Fig. 22K–R, T), with ornamented (57 %; Fig. 22K–M, P–R, U), flexuose (66 %; Fig. 22N, P–R, T, U) or less frequently smooth to slightly wavy (18 %; Fig. 22O, S) walls; oogonial bases predominantly short or long tapering (90 %; Fig. 22K, L, N, P–U) or less frequently round (10 %; Fig. 22M, O), often curved (44 %; Fig. 22N, O, Q–S); predominantly elongated (70 %; Fig. 22N, P–U) less frequently globose to subglobose (30 %; Fig. 22K–M, O), or excentric (30.6 %; Fig. 22N, O, Q, R, T, U) or comma-shaped (2.7 %). Oogonial diameters averaged $35.2 \pm 3.6 \mu\text{m}$ (overall range $24.1\text{--}47.8 \mu\text{m}$ and range of isolate means $34.5\text{--}36.1 \mu\text{m}$). Oospores had a mean diameter of $30.8 \pm 3.0 \mu\text{m}$ (total range $18.3\text{--}37.0 \mu\text{m}$ and range of isolate means $30.0\text{--}31.9 \mu\text{m}$), were predominantly plerotic (85.2 %), globose or frequently elongated in elongated oogonia (Fig. 22Q–S) and contained a large lipid globule (Fig. 22K–U); oospore wall thickness $1.8 \pm 0.4 \mu\text{m}$ (overall range $0.6\text{--}2.8 \mu\text{m}$); oospore wall index 0.31 ± 0.04 (overall range $0.2\text{--}0.4$); oogonial abortion rate 3.5 % (1–6 %). Antheridia were exclusively paragynous, club-shaped, ovoid or subglobose and unicellular (Fig. 22K–U), averaging $14.9 \pm 3.6 \times 11.0 \pm 2.0 \mu\text{m}$.

Culture characteristics: Colonies on V8A radiate with woolly-cottony dome-shaped centre and woolly-cottony patches at margins, on CA woolly-cottony with submerged to appressed, irregular-dendroid margins, and on PDA dense felty-cottony and uniform with irregular margins (Fig. 10).

Cardinal temperatures and growth rates: On V8A optimum 25°C with $4.6 \pm 0.8 \text{ mm/d}$ radial growth, maximum $27.5\text{--}30^\circ\text{C}$, minimum

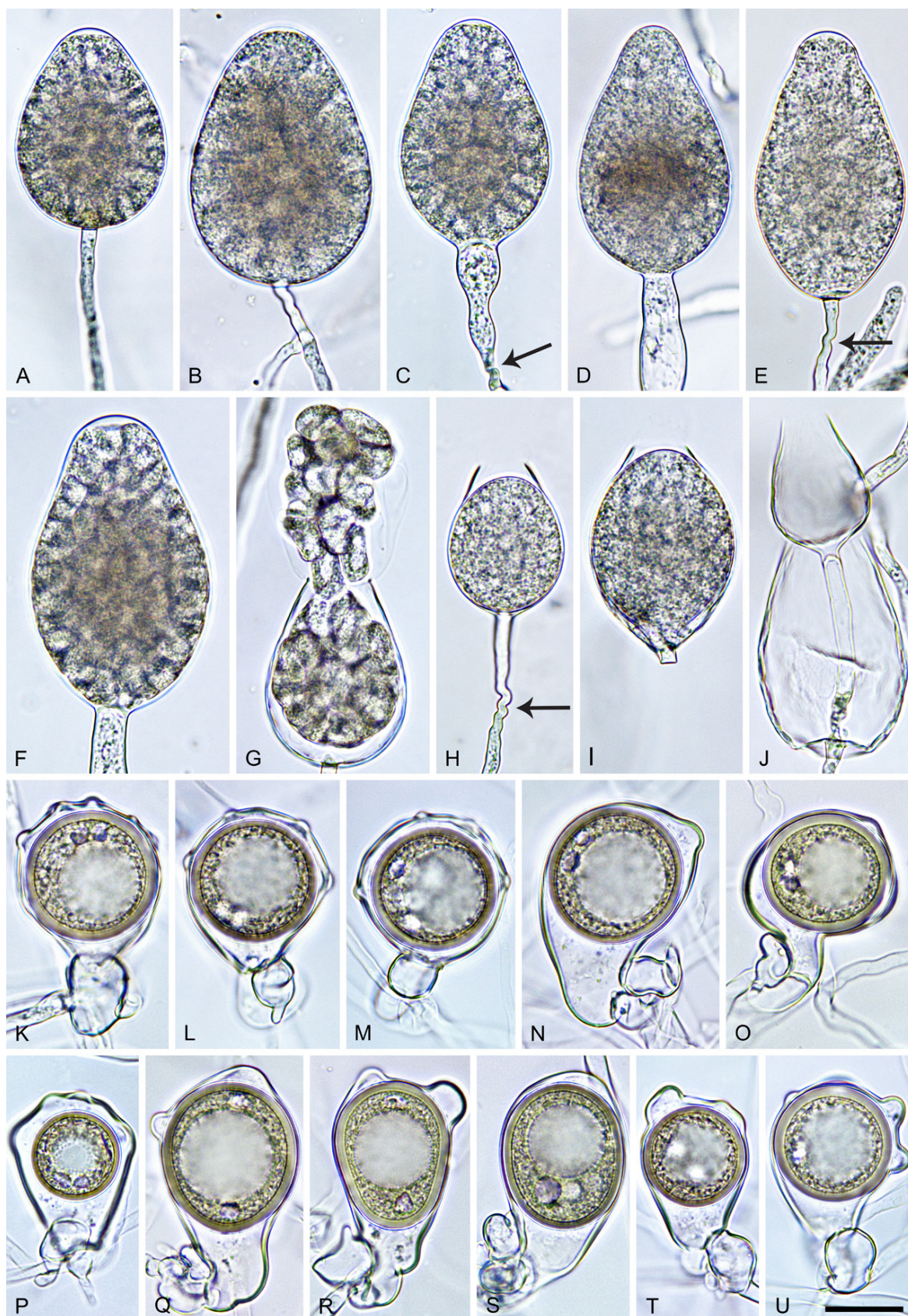


Fig. 22. *Phytophthora facultativa*. **A–J.** Sporangia formed on V8-agar (V8A) in soil extract. **A–F, H, I.** Ovoid or obpyriform sporangia with non-papillate apices. **C.** Constriction (arrow) of sporangiophore. **C, D.** Sporangiophore widening towards sporangial base. **E, H.** Sporangiophore with narrow undulating section (arrows). **F.** Sporangium shortly before the release of zoospores. **G.** Zoospore release. **H.** Internal nested proliferation. **I.** Caducous sporangium with internal nested proliferation. **J.** Internal extended proliferation. **K–U.** Oogonia with predominantly tapering, often curved bases, plerotic oospores and paragynous antheridia, sessile or on short stalks, formed in single culture in solid V8A. **K–M, P–R, U.** Ornamented oogonial walls. **N, P–R, T–U.** Flexuose oogonial walls. **O, S.** Smooth to slightly wavy oogonial walls. **N, P–U.** Elongated oogonia. **N–O, Q–R, T–U.** Excentric oogonia. **K–M, O.** Globose to subglobose oogonia. **K–M, O.** CBS 153101; **O, Q–S.** LU060; **D.** LU411; **C, E, F, H, K.** LU412. Scale bar = 20 µm; applies to A–U.



Fig. 23. *Phytophthora infundibuliformis*. **A–J.** Persistent sporangia formed on V8-agar (V8A) in soil extract. **A–F, J.** Ovoid, obpyriform or limoniform sporangia with non-papillate apices. **B.** External proliferation. **C, D.** Constriction (arrow) of sporangiophore. **F.** Hyphal swelling close to sporangial base. **G.** Zoospore release. **H, I.** Internal nested proliferation. **J.** Internal extended proliferation. **K–T.** Oogonia with predominantly tapering, often funnel-shaped bases and paragynous antheridia, sessile or on short stalks, formed in single culture in solid V8A. **K–M, R, T.** Smooth oogonial walls. **N–Q, S.** Slightly ornamented oogonial walls. **K, L, Q, R.** Elongated oogonia. **M, N, S.** Excentric oogonia. **O.** Globose to subglobose oogonium. **S.** Flexuose oogonium. **T.** Comma-shaped oogonium. **K, O.** Aplerotic oospores. **L–N, R–T.** Plerotic oospores. Images: **C, D, G, M, N, P, R, T.** CBS 153100; **A, B, F, H.** LU257; **E, I, J.** LU259; **K, L, O, Q, S.** LU260. Scale bar = 20 µm; applies to A–T.

< 10 °C (Fig. 16), lethal temperature 32.5 °C. On V8A, CA and PDA at 20 °C 4.1 ± 0.69 mm/d, 3.7 ± 0.12 mm/d and 1.3 ± 0.58 mm/d, respectively.

Additional materials examined: USA, Louisiana, Dewey W. Wills, isolated from naturally fallen leaves floating in a stream running through a subtropical forest, Mar. 2020, *T. Corcobado* & *T. Májek* (LU060, LU409, LU411).

Phytophthora infundibuliformis T. Jung, T. Májek, I. Milenković & M. Ferreira, *sp. nov.* MB 857772. Fig. 23.

Etymology: The name refers to the funnel-shaped tapering bases of the oogonia (*infundibuliformis* Latin = funnel-shaped).

Typus: USA, Louisiana, Liberty Creek, isolated from rhizosphere soil of *Acer* sp. in a subtropical forest, Mar. 2020, *T. Corcobado* & *T. Májek* [holotype CBS H-25672, dried culture on V8A, ex-holotype living culture CBS 153100 = LU258; GenBank accession nos. PX606989 (LSU), PX607156 (ITS), PX580991 (*βtub*), PX581654 (*hsp90*), PX581981 (*tigA*), PX581129 (*rpl10*), PX581302 (*tef-1a*), PX581480 (*enl*), PX581801 (*cox1*), PX580861 (*nad1*), PX580696 (*rps10*)].

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; typically borne terminally on unbranched long or short lateral sporangiophores or rarely in lax sympodia of 2 sporangia; mostly ovoid, broad-ovoid or elongated ovoid (78.5 %; Fig. 23A–D, F), less frequently limoniform to elongated-limoniform (9.5 %; Fig. 23E), obpyriform to elongated-obpyriform (7.5 %; Fig. 23J), ellipsoid to elongated-ellipsoid (2.5 %), cigar-shaped (1.0 %), obovoid (0.5 %) or ampulliform (0.5 %); apices non-papillate (Fig. 23A–F, J); sporangial proliferation internal in both a nested and extended way (Fig. 23H–J) or infrequently external (Fig. 23B); constrictions of sporangiophores enabling caducity (< 1 %; Fig. 23C, D) occasionally observed; sometimes sporangiophores widening towards sporangial base (Fig. 23F); sporangial dimensions averaging $67.9 \pm 7.6 \times 41.6 \pm 5.9$ µm (overall range 43.1–86.8 × 25.5–55.0 µm; range of isolate means $67.1\text{--}68.8 \times 39.2\text{--}44.7$ µm) with a length/breadth ratio of 1.66 ± 0.26 (overall range 1.33–3.25); sporangial germination usually indirect with zoospores discharged through an exit pore 10.1–19.5 µm wide (av. 13.6 ± 2.2 µm) (Fig. 23G). *Zoospores* limoniform to reniform whilst motile, becoming spherical (av. diam. 13.2 ± 1.1 µm) on encystment; cysts germinating directly by forming a hypha or a microsporangium or indirectly by releasing a secondary zoospore (diplanetism). *Hyphal swellings* infrequently produced in water on sporangiophores, often close to the sporangial base; globose to subglobose, limoniform or irregular (Fig. 23F). *Chlamydospores* not observed. *Oogonia* abundantly produced in single culture (self-fertile ‘homothallic’ breeding system), predominantly sessile or on short, often curved (24.6 %; Fig. 23K, M, O) stalks, with short or long, often funnel-shaped tapering bases (92.6 %; Fig. 23Q–T), smooth-walled (68.7 %; Fig. 23K–M, R, T) or slightly ornamented (31.3 %; Fig. 23N–Q, S), globose to subglobose (14.7 %; Fig. 23O), elongated (40.7 %; Fig. 23K, L, Q, R), excentric (28 %; Fig. 23M, N, S), flexuose (15.4 %; Fig. 23S) or infrequently comma-shaped (6.6 %; Fig. 23T); oogonial diam. 41.9 ± 4.1 µm (overall range 28.1–51.7 µm; range of isolate means 39.5–43.7 µm); mostly nearly plerotic to plerotic (87 %; Fig. 23L–N, P–T), less frequently slightly aplerotic to aplerotic (13 %; Fig. 23K, O). *Oospores* globose to subglobose with a large lipid globule (Fig. 23K–T); diam. 36.2 ± 3.3 µm (overall range 25.0–43.3 µm; range of

isolate means $34.7\text{--}37.5$ µm); wall thickness 2.7 ± 0.5 µm (overall range 1.4–4.0 µm); oospore wall index 0.38 ± 0.05 (overall range 0.2–0.5); low oogonial abortion rate of 2–8 % (av. 3.8 %) after 4 wk. *Antheridia* exclusively paragynous and club-shaped, ovoid or subglobose (Fig. 23K–T); dimensions $15.6 \pm 2.8 \times 11.3 \pm 1.7$ µm.

Culture characteristics: Colonies on V8A and CA uniform and woolly-cottony with submerged margins; on PDA dense felty-cottony with dendroid margins (Fig. 10).

Cardinal temperatures and growth rates: On V8A optimum at 20 °C with on average 5.47 ± 0.24 mm/d radial growth, maximum 27.5 to < 30 °C, minimum < 10 °C (Fig. 16), lethal temperature 27.5–30 °C. At 20 °C on CA and PDA 5.57 ± 0.04 mm/d and 3.37 ± 0.35 mm/d, respectively.

Additional materials examined: USA, Louisiana, Liberty Creek, isolated from rhizosphere soil of *Acer* sp. in a subtropical forest, Mar. 2020, *T. Corcobado* & *T. Májek* (LU257, LU259, LU260).

Phytophthora laevigata I. Milenković, T. Jung, Z. Tomić & Z. Stanivuković, *sp. nov.* MB 857771. Fig. 24.

Etymology: The name refers to the exclusively smooth oogonial walls (*laevigata* Latin = smooth).

Typus: Bosnia and Herzegovina, Kneževo, isolated from rhizosphere soil of *Fagus sylvatica* in a temperate forest, May 2019, I. Milenković & Z. Stanivuković [holotype CBS H-25670, dried culture on V8A, ex-holotype living culture CBS 153102 = BN333; GenBank accession nos. PX607006 (LSU), PX607170 (ITS), PX581005 (*βtub*), PX581668 (*hsp90*), PX581997 (*tigA*), PX581145 (*rpl10*), PX581319 (*tef-1a*), PX581496 (*enl*), PX581818 (*cox1*), PX580875 (*nad1*), PX580713 (*rps10*)].

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or rarely in lax sympodia of 2–3 sporangia (Fig. 24K); mostly ovoid, broad-ovoid or elongated ovoid (75.5 %; Fig. 24A–C, G, I–K), less frequently obpyriform to elongated-obpyriform (11.7 %; Fig. 24D), limoniform to elongated limoniform (8.7 %; Fig. 24E), ellipsoid to elongated ellipsoid (3.4 %; Fig. 24F), or obovoid (0.7 %); apices non-papillate (Fig. 24A–F, H–K); lateral attachment of sporangiophores (6.4 %; Fig. 24K) and constrictions of sporangiophores potentially enabling caducity (< 1 %; Fig. 24H) occasionally observed; sporangiophores rarely widening towards the sporangial base (1 %; Fig. 24E); sporangial proliferation internal in both a nested or extended way (Fig. 24H–K) or infrequently external (Fig. 24K); penetration of the lateral wall of empty sporangia by new sporangiophores in rare cases observed (Fig. 24I); sporangial dimensions averaging $61.3 \pm 6.0 \times 42.4 \pm 4.2$ µm (overall range 40.7–82.0 × 24.9–52.2 µm; range of isolate means $59.3\text{--}64.6 \times 40.5\text{--}44.4$ µm) with a length/breadth ratio of 1.45 ± 0.14 (overall range 1.18–1.92); sporangial germination indirect with zoospores discharged through an exit pore 8.8–21.3 µm wide (av. 12.6 ± 2.4 µm) (Fig. 24G). *Zoospores* limoniform to reniform whilst motile (Fig. 24G), becoming spherical (av. diam. 12.4 ± 0.8 µm) on encystment. *Hyphal swellings* not observed. *Chlamydospores* not observed. *Oogonia* readily produced in single culture (self-fertile ‘homothallic’ breeding system); borne laterally, mostly sessile or on short stalks (Fig. 24L, N–T), with smooth or rarely slightly wavy walls (Fig. 24L–T) and short or long tapering (91 %; Fig. 24L–T)

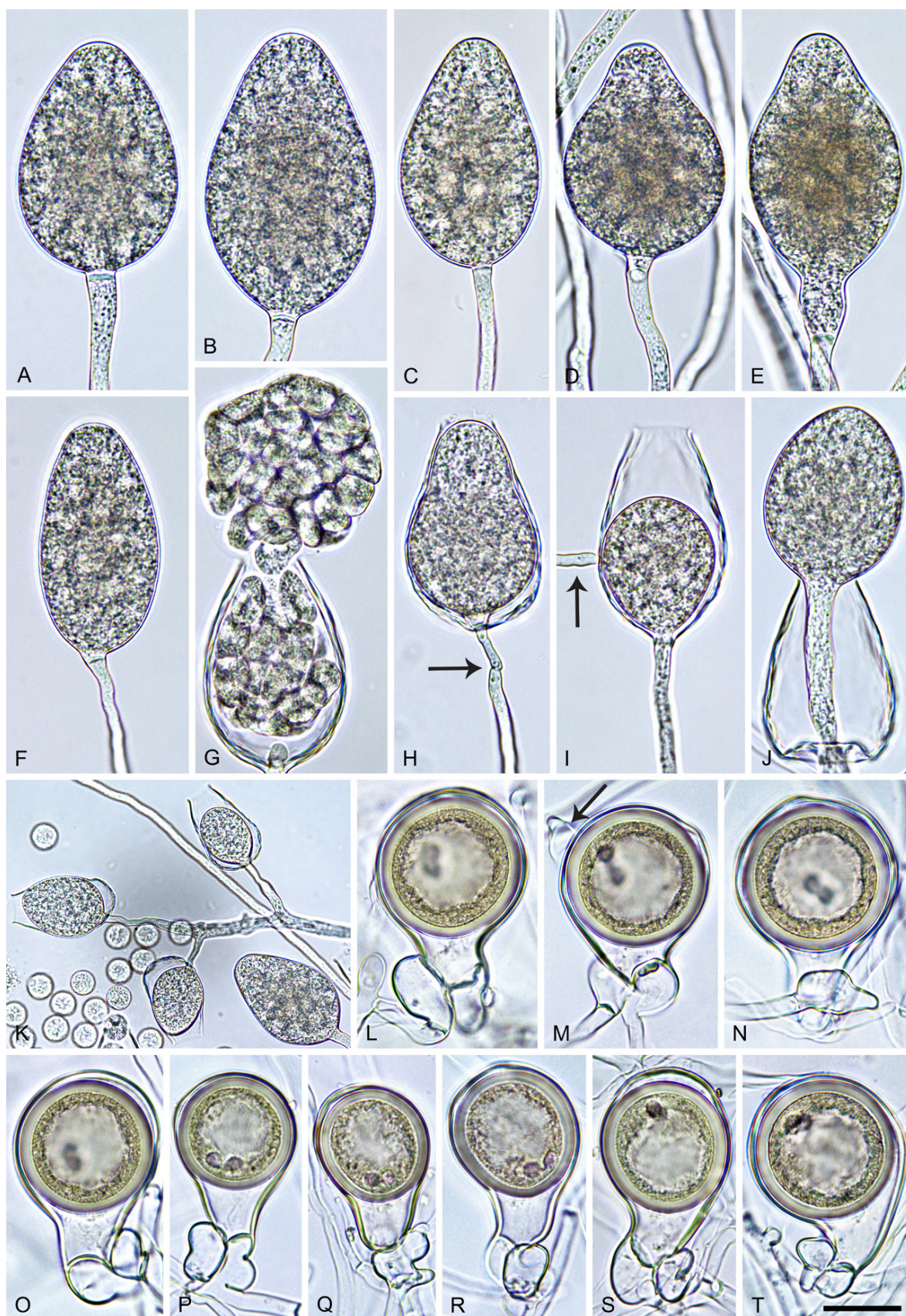


Fig. 24. *Phytophthora laevigata*. **A–K.** Persistent sporangia formed on V8-agar (V8A) in soil extract. **A–F, H–K.** Ovoid, obpyriform, limoniform or ellipsoid sporangia with non-papillate apices. **E.** Sporangiphore widening towards the sporangial base. **G.** Zoospore release. **H.** Constriction (arrow) of sporangiphore. **H, I.** Internal nested proliferation. **I.** New sporangiphore penetrating lateral sporangium wall (arrow). **J.** Internal extended proliferation. **K.** Sympodium of three sporangia with nested proliferation, one of them laterally attached; encysted zoospores. **L–T.** Oogonia with smooth or slightly wavy walls, predominantly tapering bases, plerotic oospores and paragynous antheridia, sessile or on short stalks, formed in single culture in solid V8A. **L, M.** Globose to subglobose oogonia. **N–T.** Elongated oogonia. **T.** Comma-shaped oogonium. Images: B, F, I, K, S, T. CBS 153102; C, D, J. BN301; A, E, G, N, P–R. BN321; H, L, M, O. TJ1684. Scale bar = 20 μ m in A–J, L–T, and 50 μ m in K.

and often curved (46.6 %; Fig. 24M, R–T) bases; predominantly elongated (66.8 %; Fig. 24N–T) or globose to subglobose (27.8 %; Fig. 24L, M), less frequently slightly excentric (3 %) or comma-shaped (2.4 %; Fig. 24T). Oogonial diameters averaged $36.0 \pm 3.6 \mu\text{m}$ (overall range 21.6–47.1 μm and range of isolate means 34.6–37.8 μm). Oospores had a mean diameter of $33.0 \pm 3.3 \mu\text{m}$ (overall range 19.3–40.4 μm and range of isolate means 31.0–34.7 μm), contained a large ooplast and were predominantly plerotic (92.4 %), globose (Fig. 24L–P, T) or occasionally slightly elongated in elongated oogonia (Fig. 24Q–S); oospore wall thickness $2.6 \pm 0.5 \mu\text{m}$ (overall range 0.87–3.69 μm), oospore wall index 0.4 ± 0.05 (overall range 0.2–0.5); low oogonial abortion rate of 2.5 % (1–4 %) after 4 wk. Antheridia were exclusively paragynous and club-shaped, ovoid or subglobose (Fig. 24L–T), averaging $15.6 \pm 2.9 \times 11.4 \pm 2.2 \mu\text{m}$; occasionally two antheridia attached to one oogonium (Fig. 24M).

Culture characteristics: Colonies on V8A and CA uniform or faintly striate with limited aerial mycelium; on PDA uniform and dense felty-cottony (Fig. 8).

Cardinal temperatures and growth rates: On V8A optimum 25 °C with $6.8 \pm 0.29 \text{ mm/d}$ radial growth, maximum 27.5 to < 30 °C, minimum < 10 °C (Fig. 16), lethal temperature 30 °C. At 20 °C on V8A, CA and PDA $5.65 \pm 0.31 \text{ mm/d}$, $5.2 \pm 0.23 \text{ mm/d}$ and $2.61 \pm 0.2 \text{ mm/d}$, respectively.

Additional materials examined: **Bosnia and Herzegovina**, Kneževo, isolated from rhizosphere soil of *Fagus sylvatica* in a temperate forest, May 2019, I. Milenković & Z. Stanivuković (BN300, BN301, BN321, BN332). **Croatia**, Čačinci, isolated from rhizosphere soil of a recently wilted and died *Corylus avellana* in a horticultural plantation, May 2022, Z. Tomić (TJ1684 = PLIO22).

Clade 7a4

Phytophthora algida T. Jung, N.M. Chi, I. Milenković & M. Horta Jung, *sp. nov.* MB 857767. Fig. 25.

Etymology: The name refers to the cool montane habitat of the species and its low optimum temperature for growth (*algida* Latin = cold).

Typus: **Vietnam**, Sapa, Hoang Lien National Park, isolated from rhizosphere soil of *Acer oblongum* in a montane subtropical cloud forest, Mar. 2016, T. Jung & N.M. Chi [holotype CBS H-25666, dried culture on V8A, ex-holotype living culture CBS 153095 = VN029; GenBank accession nos. PX606948 (LSU), PX607121 (ITS), PX580955 (*βtub*), PX581615 (*hsp90*), PX581935 (*tigA*), PX581088 (*rpl10*), PX581259 (*tef1α*), PX581436 (*enl*), PX581754 (*cox1*), PX580824 (*nadh1*), PX580652 (*rps10*)].

Morphological structures on V8A: Sporangia abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or rarely in dense sympodia of 2 sporangia (Fig. 25K); mostly obpyriform or elongated-obpyriform (52.4 %; Fig. 25D, E, H) or ovoid, broad-ovoid or elongated-ovoid (34.7 %; Fig. 25A–C, K), less frequently limoniform to elongated-limoniform (12.9 %; Fig. 25F); sporangial apices non-papillate (Fig. 25A–F, H, K) and sometimes pointed (0.6 %; Fig. 25B); sporangial proliferation internal in both a nested and extended way (Fig. 25H–J) and infrequently external (Fig. 25K); sporangial dimensions averaging $64.2 \pm 11.1 \times 41.2 \pm 6.3 \mu\text{m}$ (overall range 34.0–93.4 $\times$ 25.4–58.1 μm ; range of

isolate means 47.1–70.4 $\times$ 33.1–45.6 μm) with a length/breadth ratio of 1.56 ± 0.16 (overall range 1.25–1.98); sporangial germination indirect with zoospores discharged through an exit pore 8.5–19.6 μm wide (av. $14.2 \pm 2.7 \mu\text{m}$) (Fig. 25G). Zoospores limoniform to reniform whilst motile, becoming spherical (av. diam. $12.4 \pm 1.1 \mu\text{m}$) on encystment; cysts usually germinating directly forming a hypha or a microsporangium or infrequently indirectly by releasing a secondary zoospore (diplanetism). Hyphal swellings sometimes formed in water on sporangiophores close to the sporangial base, subglobose to globose (Fig. 25D). Chlamydospores not observed. Oogonia readily produced in single culture (self-fertile ‘homothallic’ breeding system); borne laterally on short stalks or sessile, or infrequently terminally, with smooth to slightly wavy (av. 52 %; Fig. 25L, M, S) or ornamented (av. 46 %; Fig. 25N–R) walls, often with tapering (av. 52.6 %; Fig. 25N–Q, S) or curved (av. 50.5 %; Fig. 25L, M, P, S) bases. They were predominantly globose to subglobose (Fig. 25L–Q), sometimes slightly elongated (av. 10.6 %; Fig. 25R), slightly excentric (av. 2.5 %), comma-shaped (av. 2.0 %; Fig. 25S) or flexuose (av. 1.6 %). Oogonial diameters averaged $38.0 \pm 2.6 \mu\text{m}$ (overall range 20.9–44.4 μm and range of isolate means 37.7–38.2 μm). Oospores had a mean diameter of $31.8 \pm 2.2 \mu\text{m}$ (total range 17.9–37.4 μm), were predominantly plerotic (96.5 %), globose and contained a large ooplast (Fig. 25L–S); oospore wall thickness $1.6 \pm 0.4 \mu\text{m}$, oospore wall index 0.28 ± 0.05 ; oogonial abortion rate 11.8 % (3–25 %). Antheridia were paragynous (av. 55.8 %; Fig. 25L, M, O, Q, S) or amphigynous (av. 44.2 %; 4 % bicellular; Fig. 25N, P, R), averaging $18.0 \pm 3.8 \times 13.9 \pm 2.0 \mu\text{m}$, with shapes ranging from subglobose to cylindrical or irregular (Fig. 25L–S).

Culture characteristics: Colonies on V8A mostly submerged with dome-shaped aerial mycelium at the centre, dendroid; on CA uniform with woolly aerial mycelium and submerged margins; on PDA uniform, dense felty-cottony (Fig. 10).

Cardinal temperatures and growth rates: On V8A optimum 15 °C with $2.76 \pm 0.23 \text{ mm/d}$ radial growth, maximum 25 to < 27.5 °C, minimum < 10 °C (Fig. 17), lethal temperature 27.5 °C. At 20 °C on V8A, CA and PDA $2.35 \pm 0.19 \text{ mm/d}$, $3.01 \pm 0.06 \text{ mm/d}$ and $2.09 \pm 0.06 \text{ mm/d}$, respectively.

Additional materials examined: **Vietnam**, Sapa, Hoang Lien National Park, isolated from rhizosphere soil of *A. oblongum* in a montane subtropical cloud forest, Mar. 2016, T. Jung & N.M. Chi (VN031, VN304); Ba Vi National Park, isolated from rhizosphere soil of *Castanopsis chinensis* in a tropical, submontane, evergreen monsoon forest, Mar. 2016, T. Jung & M. Horta Jung (VN568).

Phytophthora grandoogonia T. Jung, N.M. Chi, Z.Á. Nagy & M. Horta Jung, *sp. nov.* MB 857768. Fig. 26.

Etymology: The name refers to the large size of the oogonia (*grandis* Latin = large).

Typus: **Vietnam**, Ba Vi National Park, isolated from rhizosphere soil of *Dysoxylum juglans* and *Castanopsis chinensis* in a tropical, submontane, evergreen monsoon forest, Mar. 2016, T. Jung & N.M. Chi [holotype CBS H-25668, dried culture on V8A, ex-holotype living culture CBS 153094 = VN556; GenBank accession nos. PX606983 (LSU), PX607149 (ITS), PX580984 (*βtub*), PX581647 (*hsp90*), PX581974 (*tigA*), PX581122 (*rpl10*), PX581295 (*tef1α*), PX581473 (*enl*), PX581794 (*cox1*), PX580854 (*nadh1*), PX580689 (*rps10*)].

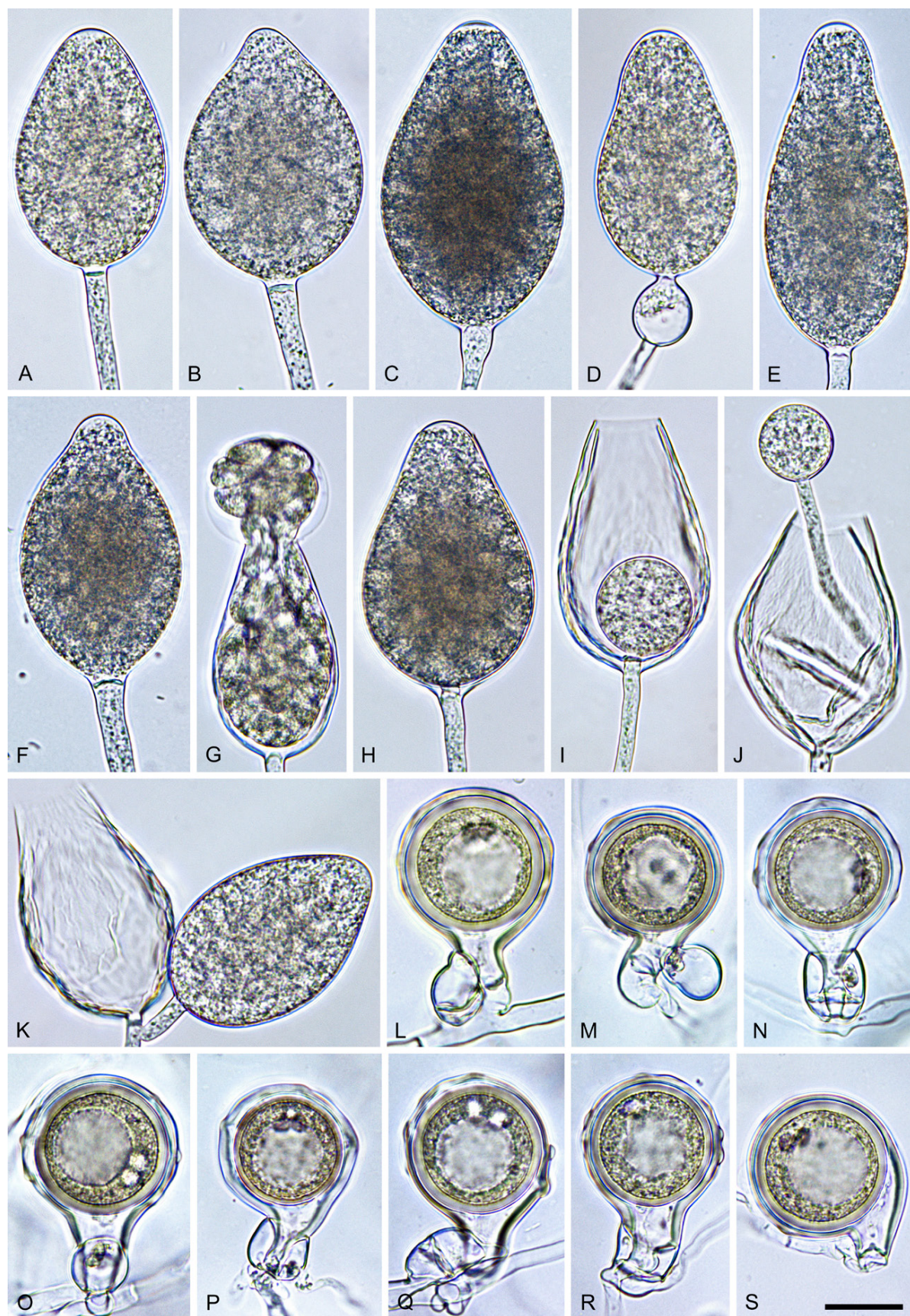


Fig. 25. *Phytophthora algida*. **A–K.** Persistent sporangia formed on V8-agar (V8A) in soil extract. **A–F, H, K.** Ovoid, obpyriform or limoniform non-papillate sporangia. **B.** Pointed apex. **D.** Hyphal swelling at sporangial base. **G.** Sporangium releasing zoospores. **H, I.** Internal nested proliferation. **J.** Internal nested and extended proliferation. **K.** Dense sympodium due to external proliferation. **L–S.** Oogonia with predominantly plerotic oospores, sessile or on short stalks, formed in single culture in solid V8A. **L, M, S.** Smooth to slightly wavy oogonial walls. **N–R.** Ornamented walls. **L, M, O, Q, S.** Paragynous antheridia. **N, P, R.** Amphigynous unicellular (P) or bicellular antheridia (N, R). **S.** Comma-shaped oogonium. Images: C, D, H, J, K, L, N. CBS 153095; B, E, F, M, O. VN031; A, G, I, Q. VN304; P, R, S. VN568. Scale bar = 20 μ m; applies to A–S.

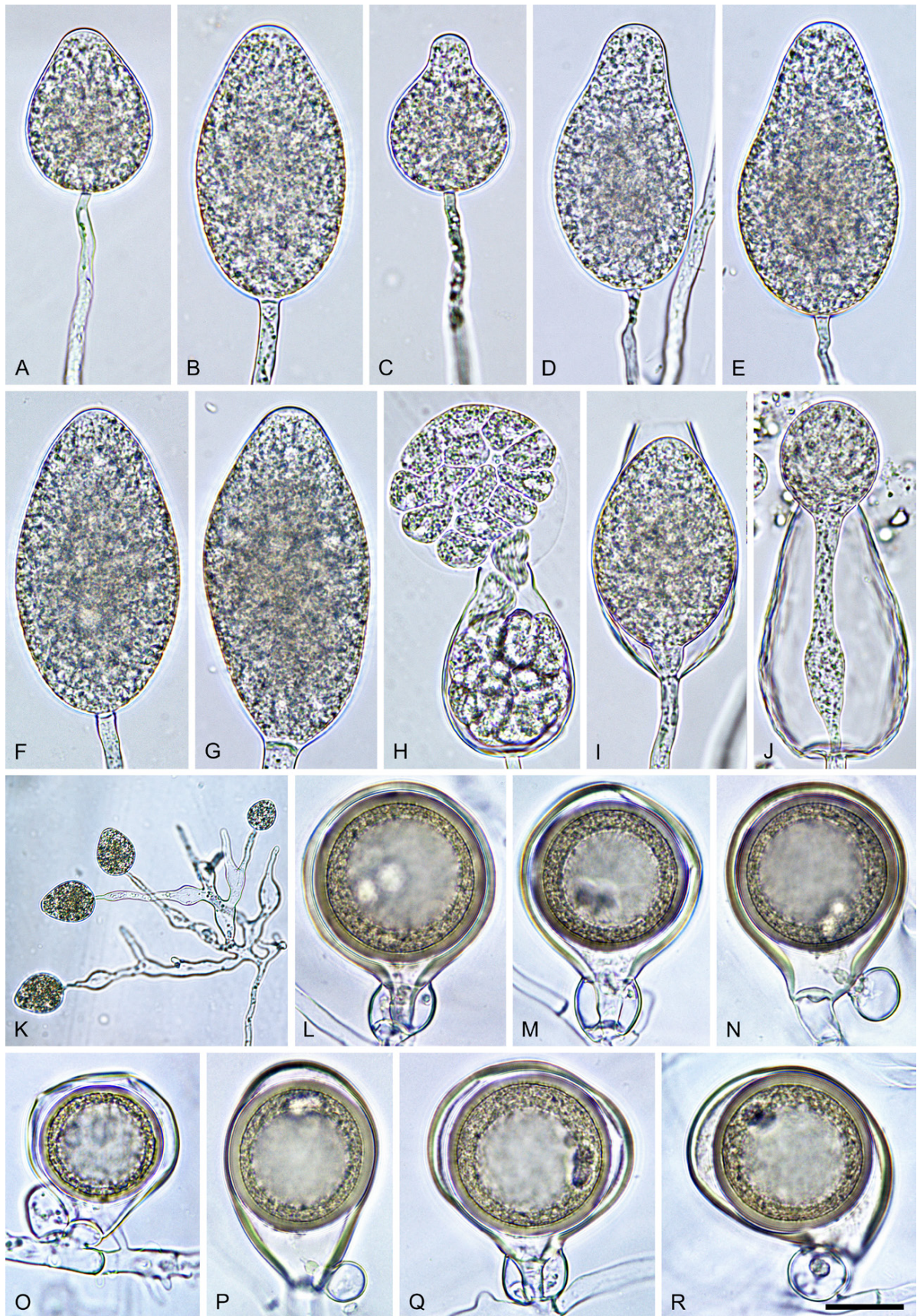


Fig. 26. *Phytophthora grandoogonia*. **A–K.** Persistent sporangia formed on V8-agar (V8A) in soil extract. **A–G, I, K.** Ovoid, obpyriform, ellipsoid or limoniform non-papillate sporangia. **D.** Slightly asymmetric sporangium. **H.** Sporangium releasing zoospores. **I.** Internal nested proliferation. **J.** Internal extended proliferation. **K.** Lax sympodium; sporangiophores with hyphal swellings. **L–R.** Oogonia with mostly tapering bases andplerotic oospores, sessile or on short stalks, formed in single culture in solid V8A. **L–N, P–R.** Smooth oogonial walls. **O.** Ornamented oogonium wall. **N, P, R.** Elongated oogonia. **N–P, R.** Paragynous antheridia. **L, M, Q.** Amphigynous bicellular (L, M) or unicellular antheridia (Q). **Q.** Excentric oogonium. **R.** Comma-shaped oogonium. Images: A, C, H, K, L, N, P, R. CBS 153094; Q. VN616; B, F, G, M. VN618; D, E, I, J, O. VN623. Scale bar = 20 μ m in A–J, L–R, and 80 μ m in K.

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; typically borne terminally on unbranched long or short lateral sporangiophores or infrequently in lax sympodia of 2–5 sporangia (Fig. 26K); apices non-papillate (Fig. 26A–G, I, K), sometimes slightly asymmetric (Fig. 26D); mostly obpyriform to elongated-obpyriform (51.9 %; Fig. 26C–E) or ovoid, broad-ovoid or elongated-ovoid (45.4 %; Fig. 26A, B, I, K), less frequently ellipsoid to elongated-ellipsoid (2 %; Fig. 26F, G) or limoniform to elongated-limoniform (0.7 %; Fig. 26F, J); sporangial proliferation internal in both a nested and extended way (Fig. 26I, J) or infrequently external; sporangial dimensions averaging $60.3 \pm 9.0 \times 38.3 \pm 5.5 \mu\text{m}$ (overall range $39.4\text{--}83.4 \times 26.4\text{--}49.9 \mu\text{m}$; range of isolate means $52.8\text{--}69.8 \times 33.1\text{--}44.0 \mu\text{m}$) with a length/breadth ratio of 1.59 ± 0.18 (overall range 1.25–2.28); sporangial germination usually indirect with zoospores discharged through an exit pore $7.5\text{--}19.9 \mu\text{m}$ wide (av. $11.1 \pm 2.0 \mu\text{m}$) (Fig. 26H). *Zoospores* limoniform to reniform whilst motile, becoming spherical (av. diam. $11.5 \pm 1.4 \mu\text{m}$) on encystment. *Hyphal swellings* infrequently produced in water on sporangiophores and hyphae; globose to subglobose, limoniform or irregular (Fig. 26K). *Chlamydospores* not observed. *Oogonia* abundantly produced in single culture (self-fertile ‘homothallic’ breeding system), predominantly sessile without stalk or less frequently on short stalks, with short or long tapering base (83.8 %; Fig. 26M–P, R) or infrequently with a round base (16.2 %; Fig. 26L, Q), almost exclusively smooth-walled (99 %; Fig. 26L–N, P–R), rarely ornamented (1 %; Fig. 26O), globose to slightly subglobose (62.1 %; Fig. 26L, M, O), elongated (20 %; Fig. 26N, P, R), excentric (18.3 %; Fig. 26Q) or rarely comma-shaped (0.6 %; Fig. 26R); oogonial diam. $47.8 \pm 3.9 \mu\text{m}$ (overall range $29.6\text{--}56.6 \mu\text{m}$; range of isolate means $45.7\text{--}49.3 \mu\text{m}$); mostly nearly plerotic to plerotic (90 %; Fig. 26L–N, P, R), less frequently slightly aplerotic (10 %; Fig. 26O, Q). *Oospores* globose with a large lipid globule (Fig. 26L–R); diam. $42.0 \pm 3.5 \mu\text{m}$ (overall range $25.0\text{--}51.1 \mu\text{m}$; range of isolate means $40.2\text{--}44.3 \mu\text{m}$); wall thickness $2.3 \pm 0.7 \mu\text{m}$ (overall range $0.5\text{--}4.6 \mu\text{m}$); oospore wall index 0.29 ± 0.08 ; abortion rate 2–43 % (av. 14.1 %) after 4 wk. *Antheridia* paragynous and club-shaped, ovoid or subglobose (76.9 %; Fig. 26N–P, R) or amphigynous, club-shaped to cylindrical and unicellular (10 %; Fig. 26Q) or bicellular, often with the basal cell being much smaller than the upper cell (13.1 %; Fig. 26L, M); dimensions $15.7 \pm 2.2 \times 13.8 \pm 1.9 \mu\text{m}$.

Culture characteristics: Colonies on V8A mostly submerged to appressed with limited aerial mycelium and a radiate pattern; on CA uniform, submerged to appressed with concentric rings of aerial mycelium; on PDA woolly-cottony and faintly petaloid (Fig. 11).

Cardinal temperatures and growth rates: On V8A each three isolates with an optimum at 20 °C and 25 °C, respectively, with an average radial growth of $3.18 \pm 0.28 \text{ mm/d}$ and $3.18 \pm 0.41 \text{ mm/d}$, respectively, maximum 27.5 to < 30 °C, minimum < 10 °C (Fig. 17), lethal temperature 27.5–30 °C. At 20 °C on V8A, CA and PDA $3.18 \pm 0.28 \text{ mm/d}$, $2.67 \pm 0.55 \text{ mm/d}$ and $3.13 \pm 0.22 \text{ mm/d}$, respectively.

Additional materials examined: **Vietnam**, Ba Vi National Park, isolated from rhizosphere soil of *C. chinensis* in a tropical, submontane, evergreen monsoon forest, Mar. 2016, *T. Jung* & *N.M. Chi* (VN574, VN581, VN616); isolated from rhizosphere soil of *Vernicia montana* and *Antidesma* sp. in a tropical, submontane, evergreen monsoon forest, Mar. 2016, *T. Jung* & *N.M. Chi* (VN618); isolated from rhizosphere soil of *Quercus glauca* and *Meliosma*

arnottiana in a tropical, submontane, evergreen monsoon forest, Mar. 2016, *T. Jung* & *N.M. Chi* (VN623).

Phytophthora sessilis *T. Jung, N.M. Chi, I. Milenković & M. Horta Jung, sp. nov.* MB 857769. Fig. 27.

Etymology: The name refers to the sessile insertion of most oogonia to the hyphae.

Typus: **Vietnam**, Sapa, Hoang Lien National Park, isolated from rhizosphere soil of *Rhododendron arboreum* in an upper-montane subtropical cloud forest, Mar. 2016, *T. Jung* & *N.M. Chi* [**holotype** CBS H-25667, dried culture on V8A, ex-holotype living culture CBS 153096 = VN059; GenBank accession nos. PX607015 (LSU), PX607173 (ITS), PX581007 (*βtub*), PX581672 (*hsp90*), PX582005 (*tigA*), PX581153 (*rpl10*), PX581326 (*tef-1a*), PX581505 (*enl*), PX581826 (*cox1*), PX580877 (*nadh1*), PX580721 (*rps10*)].

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or rarely in lax sympodia of 2 sporangia (Fig. 27K); mostly ovoid to broad-ovoid (60.8 %; Fig. 27A–C, K) or obpyriform, broad-obpyriform or elongated-obpyriform (23.6 %; Fig. 27D, E), less frequently limoniform (12.4 %; Fig. 27F, G), ellipsoid (2.8 %) or ampulliform (0.4 %); persistent; sporangial apices non-papillate (Fig. 27A–G); sporangial proliferation internal in both a nested and extended way (Fig. 27H–J); sporangial dimensions averaging $62.4 \pm 6.3 \times 41.2 \pm 4.1 \mu\text{m}$ (overall range $47.3\text{--}78.8 \times 26.9\text{--}52.4 \mu\text{m}$; range of isolate means $56.4\text{--}66.0 \times 37.6\text{--}43.7 \mu\text{m}$) with a length/breadth ratio of 1.52 ± 0.12 (overall range 1.25–2.12); sporangial germination indirect with zoospores discharged through an exit pore $8.0\text{--}19.3 \mu\text{m}$ wide (av. $13.9 \pm 2.4 \mu\text{m}$) (Fig. 27H). *Zoospores* limoniform to reniform whilst motile, becoming spherical (av. diam. $12.6 \pm 0.8 \mu\text{m}$) on encystment; cysts usually germinating directly forming a hypha or a microsporangium or infrequently indirectly by releasing a secondary zoospore (diplanetism). *Hyphal swellings* not observed. *Chlamydospores* not observed. *Oogonia* readily produced in single culture (self-fertile ‘homothallic’ breeding system); borne laterally, mostly sessile or on short stalks (Fig. 27L–P, S), with smooth to slightly wavy (91.2 %; Fig. 27L–N, Q–S) or less frequently ornamented (8.8 %; Fig. 27O, P) walls, often with short or long tapering (62.4 %; Fig. 27M, O–S) or curved (48.4 %; Fig. 27P, R, S) bases; predominantly globose to subglobose (66.3 %; Fig. 27L–N), less frequently slightly flexuose (14 %; Fig. 27O), slightly elongated (10 %; Fig. 27P–R), slightly excentric (6.5 %) or comma-shaped (3.2 %; Fig. 27S). Oogonial diameters averaged $39.8 \pm 4.5 \mu\text{m}$ (overall range $21.3\text{--}52.8 \mu\text{m}$ and range of isolate means $36.4\text{--}42.1 \mu\text{m}$). *Oospores* had a mean diameter of $33.9 \pm 3.7 \mu\text{m}$ (total range $18.9\text{--}45.1 \mu\text{m}$ and range of isolate means $32.5\text{--}35.7 \mu\text{m}$), were predominantly plerotic (92.6 %), globose and contained a large ooplast (Fig. 27L–S); oospore wall thickness $1.7 \pm 0.5 \mu\text{m}$, oospore wall index 0.28 ± 0.06 ; oogonial abortion rate 11.5 % (5–25 %). *Antheridia* were paragynous and club-shaped, ovoid or subglobose (av. 86.8 %; Fig. 27M, N, P) or amphigynous club-shaped to cylindrical and unicellular (6 %; Fig. 27L, O) or bicellular, often with the basal cell being considerably smaller than the upper cell (7.2 %; Fig. 27Q–S), averaging $17.5 \pm 3.1 \times 14.1 \pm 2.4 \mu\text{m}$; occasionally two antheridia attached to one oogonium (Fig. 27M).

Culture characteristics: Colonies on V8A mostly submerged to appressed with scanty aerial mycelium and a faint radiate pattern;

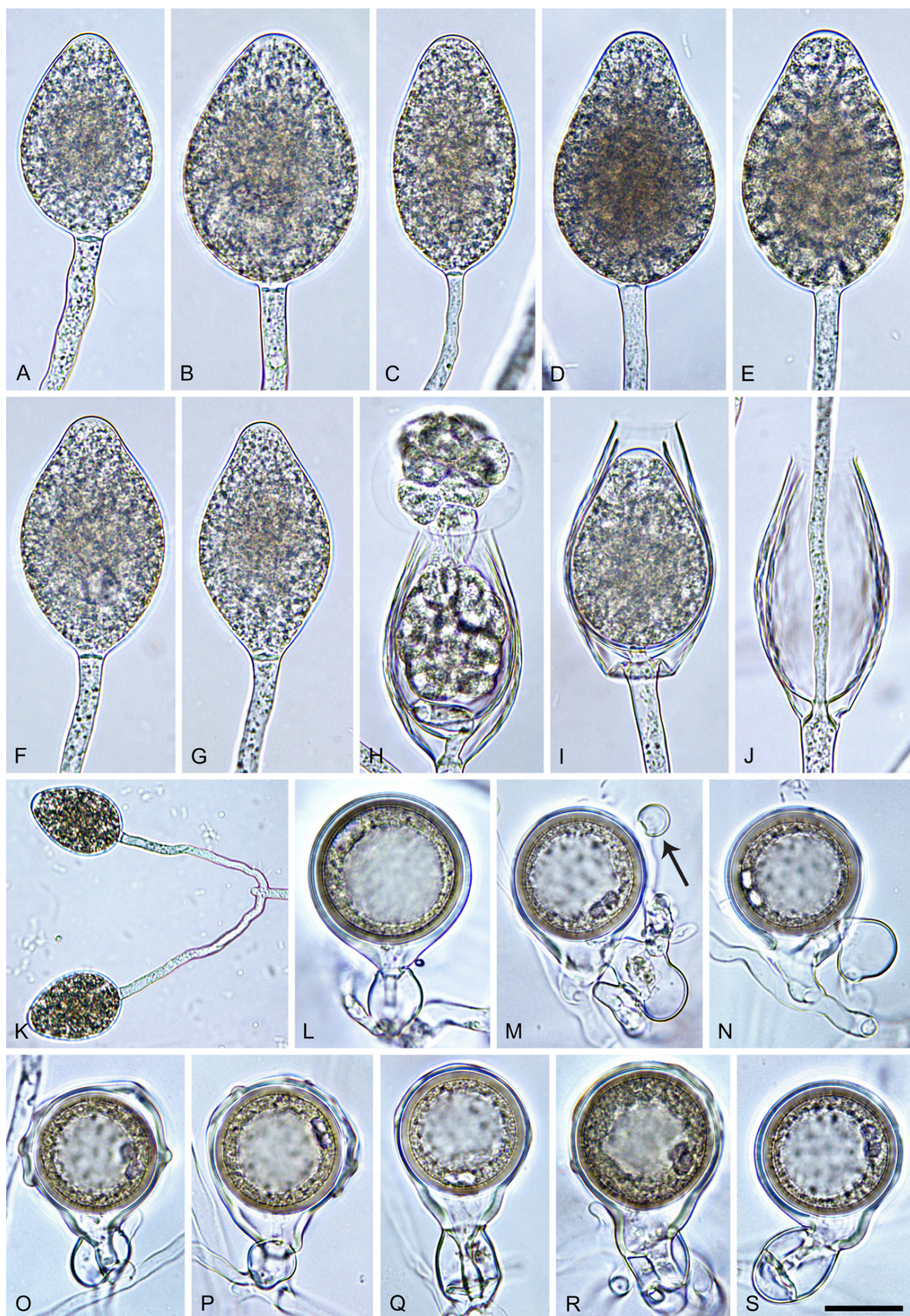


Fig. 27. *Phytophthora sessilis*. **A–K.** Persistent sporangia formed on V8-agar (V8A) in soil extract. **A–D, F, G.** Ovoid, obpyriform and limoniform non-papillate sporangia. **H.** Zoospore release. **H, I.** Internal nested proliferation. **J.** Internal extended proliferation. **K.** Lax sympodium of two ovoid sporangia. **L–S.** Oogonia with mostly tapering or curved bases and plerotic oospores, sessile or on short stalks, formed in single culture in solid V8A. **L–N, Q–S.** Smooth to slightly wavy oogonial walls. **O, P.** Ornamented oogonial walls. **O.** Slightly flexuose oogonium. **P–R.** Slightly elongated oogonia. **S.** Comma-shaped oogonium. **M, N, P.** Paragonous antheridia. **M.** Additional paragonous antheridium (arrow). **L, O, Q–S.** Amphigynous unicellular (**L, O**) or bicellular (**Q–S**) antheridia. **S.** Comma-shaped oogonium. Images: **B, E, F, K–N, Q, S.** CBS 153096; **A, C, G–J, R.** VN253; **O, P.** VN266; **D.** VN272. Scale bar = 20 µm in **A–J, L–S**, and 50 µm in **K**.



Fig. 28. *Phytophthora attenuata* from Vietnam. **A–M.** Structures formed on V8-agar (V8A) in soil extract. **A–J.** Persistent sporangia. **A–F, H.** Ovoid, obpyriform or limoniform non-papillate sporangia. **D.** External proliferation. **G.** Zoospore release. **I.** Internal nested proliferation; new sporangium before release of zoospores. **J.** Internal extended proliferation. **K.** Swollen coraloid hyphae. **L.** Empty zoospore cyst after release of a secondary zoospore (diplanetism). **M.** Dense cluster of subglobose to irregular catenulate hyphal swellings. **N–U.** Oogonia with predominantly plerotic oospores, sessile or on short stalks, formed in single culture in solid V8A. **N, O, T.** Subglobose to globose oogonia. **P–S.** Excentric oogonia. **N, U.** Smooth oogonial walls. **O–T.** Wavy or ornamented oogonial walls. **O, P, R, T, U.** Paragynous antheridia. **N, Q, S.** Amphigynous unicellular (**Q, S**) or bicellular antheridia (**N**). **U.** Comma-shaped oogonium. Images: **A–U.** VN026. Scale bar = 20 µm in **A–L** and **N–U**, and 50 µm in **M**.



Fig. 29. *Phytophthora irregularis*. **A–I.** Persistent sporangia formed on V8-agar (V8A) in soil extract. **A–C, E, H.** Non-papillate sporangial apices. **A, B, G–I.** Ovoid sporangia. **C.** Obpyriform sporangium. **D.** Zoospore release. **E, F.** Distorted sporangia with two apices, internal nested (**E**) and extended (**F**) proliferation. **G.** Internal nested and extended proliferation. **H.** Sympodium of two sporangia with nested proliferation. **I.** Empty sporangium with external proliferation and encysted zoospores, one of them (arrow) after release of a secondary zoospore (diplanetism). **J–T.** Oogonia with predominantly tapering bases and plerotic oospores, sessile or on short stalks, formed in single culture in solid V8A. **J–P, S, T.** Smooth to slightly wavy oogonial walls. **Q.** Ornamented oogonial wall. **R.** Flexuose oogonial wall. **J, K, N.** Globose to subglobose oogonia. **L, M, Q, R.** Elongated oogonia. **O, P, R, S.** Excentric oogonia. **S, T.** Comma-shaped oogonia. **J–M, O, Q, R, T.** Paragynous antheridia. **N, P, S.** Amphigynous antheridia, unicellular (**P, S**) or bicellular (**N**). Images: **E, G, K, O, R, S.** CBS 153091; **A, F, H.** JP095; **C, I, J, N, P.** JP421; **L, Q, T.** JP574; **B, D, M.** JP745. Scale bar = 20 μ m; applies to **A–T**.

on CA submerged to appressed with scanty aerial mycelium, uniform or with faint radiate pattern; on PDA dense-felty cottony with a dome-shaped centre, uniform (Fig. 11).

Cardinal temperatures and growth rates: On V8A optimum 20 °C with 2.77 ± 0.18 mm/d radial growth, maximum 27.5 °C, minimum < 10 °C (Fig. 17), lethal temperature 27.5 to < 30 °C. On CA and PDA at 20 °C 3.02 ± 0.42 mm/d and 2.48 ± 0.1 mm/d, respectively.

Additional materials examined: **Vietnam**, Sapa, Hoang Lien National Park, isolated from rhizosphere soil of *Betula alnoides* and *Elaeocarpus japonicus* in a montane subtropical cloud forest, Mar. 2016, *T. Jung* & *N.M. Chi* (VN253); isolated from rhizosphere soil of *Neolitsea poilanei* in a montane subtropical cloud forest, Mar. 2016, *T. Jung* & *N.M. Chi* (VN266); isolated from streambed soil in a swampy depression of a montane subtropical cloud forest, Mar. 2016, *T. Jung* & *N.M. Chi* (VN272, VN273).

Phytophthora irregularis *T. Jung, K. Kageyama, S. Uematsu, J.F. Webber & M. Horta Jung, sp. nov.* MB 857774. Fig. 29.

Etymology: The name refers to the high proportion of irregular-shaped oogonia.

Typus: **Japan**, Kyushu, Aya, isolated from rhizosphere soil of *Castanopsis cuspidata* in a warm-temperate laurosilva forest, May 2017, *T. Jung* & *K. Kageyama* [**holotype** CBS H-25674, dried culture on V8A, ex-holotype living culture CBS 153091 = JP1056; GenBank accession nos. PX607001 (LSU), PX607165 (ITS), PX581000 (*βtub*), PX581663 (*hsp90*), PX581992 (*tigA*), PX581140 (*rpl10*), PX581314 (*tef1a*), PX581491 (*enl*), PX581813 (*cox1*), PX580870 (*nadh1*), PX580708 (*rps10*)].

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or infrequently in dense sympodia of 2–3 sporangia (Fig. 29H) or rarely intercalary or sessile (0.6 %); ovoid, broad-ovoid or elongated-ovoid (71.1 %; Fig. 29A, B, E, G–I), obpyriform to elongated-obpyriform (19.5 %; Fig. 29C) or less frequently limoniform (3.7 %), distorted with two apices (3.1 %; Fig. 29E, F), ellipsoid (2.3 %) or obovoid (0.3 %); sporangial apices non-papillate (Fig. 29A–C, E, H); persistent; sporangial proliferation internal in both a nested and extended way (Fig. 29E–H) and less frequently external (Fig. 29H, I); sporangial dimensions averaging $55.1 \pm 6.5 \times 37.2 \pm 4.9$ µm (overall range 39.2 – 83.6×27.0 – 56.2 µm; range of isolate means 51.1 – 59.7×33.4 – 43.0 µm) with a length/breadth ratio of 1.49 ± 0.13 (overall range 1.15–1.9); sporangial germination indirect with zoospores discharged through an exit pore 6.2 – 17.7 µm wide (av. 10.9 ± 1.9 µm) (Fig. 29D). *Zoospores* limoniform to reniform whilst motile (Fig. 29D), becoming spherical (av. diam. 11.7 ± 1.0 µm) on encystment (Fig. 29I); cysts germinating directly by forming a hypha or a microsporangium or indirectly by releasing a secondary zoospore (Fig. 29I). *Hyphal swellings* not observed. *Chlamydospores* not observed. *Oogonia* abundantly produced in single culture (self-fertile ‘homothallic’ breeding system); borne laterally, mostly sessile or on short often curved stalks (Fig. 29J–M, O–T), with smooth to slightly wavy (81.2 %; Fig. 29J–P, S, T), flexuose (15.8 %; Fig. 29R) or ornamented (14 %; Fig. 29Q) walls; oogonial bases predominantly short or long tapering (81.8 %; Fig. 29J–Q) or less frequently round (18.2 %; Fig. 29R–T), often curved (42.8 %; Fig. 29L–N, S, T); predominantly globose to subglobose (41.9 %; Fig. 29J, K, N), excentric (30.2 %; Fig. 29O, P, R, S), elongated

(17.7 %; Fig. 29L, M, Q, R) or comma-shaped (13.8 %; Fig. 29S, T). Oogonial diameters averaged 32.8 ± 3.5 µm (overall range 15.9–42.7 µm and range of isolate means 31.9–34.4 µm). *Oospores* had a mean diameter of 28.2 ± 2.9 µm (total range 13.2–36.2 µm and range of isolate means 27.3–30.1 µm), were predominantly plerotic (87.5 %), globose or occasionally elongated in elongated oogonia (Fig. 29R) and contained one large (Fig. 29K–R, T) or less frequently two smaller lipid globules (Fig. 29J, S); oospore wall thickness 1.9 ± 0.4 µm (overall range 0.5–3.0 µm), oospore wall index 0.35 ± 0.06 (overall range 0.1–0.5); oogonial abortion rate 8.7 % (1–25 %) after 4 wk. *Antheridia* were predominantly paragynous, club-shaped, ovoid or subglobose and unicellular (96.1 %; Fig. 29J–M, O, Q, R, T) or infrequently amphigynous, cylindrical, subglobose or irregular and mostly unicellular (3.5 %; Fig. 29P, S) or rarely bicellular (0.4 %; Fig. 29N), averaging $12.8 \pm 2.4 \times 9.9 \pm 1.5$ µm.

Culture characteristics: Colonies on V8A submerged to appressed with scanty aerial mycelium and faint striate patterns; on CA submerged to appressed with scanty to limited aerial mycelium and radiate to striate pattern or uniform; on PDA dense-felty and uniform with dome-shaped centre (Fig. 12).

Cardinal temperatures and growth rates: On V8A optimum at 25 °C with 3.6 ± 0.21 mm/d radial growth; maximum 30 to < 32.5 °C; minimum < 10 °C (Fig. 17), lethal temperature 32.5 °C. At 20 °C on V8A, CA and PDA 3.1 ± 0.22 mm/d, 2.58 ± 0.37 mm/d and 2.23 ± 0.17 mm/d, respectively.

Additional materials examined: **Japan**, Kyushu, Takakuma, isolated from rhizosphere soil of *Castanopsis sieboldii* in a warm-temperate laurosilva forest, May 2017, *T. Jung* & *H. Masuya* (JP574, JP964); isolated from rhizosphere soil of *Zelkova serrata* in a warm-temperate laurosilva forest, May 2017, *T. Jung* & *H. Masuya* (JP745); Shikoku, Satayama, isolated from rhizosphere soil of *C. sieboldii* in a warm-temperate laurosilva forest, May 2017, *T. Jung* & *J.F. Webber* (JP095); isolated from rhizosphere soil of *C. sieboldii*, *M. thunbergii* and *Quercus acuta* in a warm-temperate laurosilva forest, May 2017, *T. Jung* & *S. Uematsu* (JP421, JP853).

Phytophthora ×grandisporangia *T. Jung, N.M. Chi, I. Milenković & M. Horta Jung, sp. nov.* MB 857775. Figs 31, 32.

Etymology: The name refers to the large sporangial sizes and the hybrid status of all known isolates (*grandis* Latin = large).

Typus: **Vietnam**, Sapa, Hoang Lien National Park, isolated from a baiting leaf floating in a stream running through an upper-montane subtropical cloud forest, Mar. 2016, *T. Jung* & *N.M. Chi* [**holotype** CBS H-25669, dried culture on V8A, ex-holotype living culture CBS 153093 = VN074; GenBank accession nos. PX607092 (LSU), PX607231 (ITS), PX581069 (*βtub*), PX581735 (*hsp90*), PX582082 (*tigA*), PX581232 (*rpl10*), PX581407 (*tef1a*), PX581586 (*enl*), PX581906 (*cox1*), PX580936 (*nadh1*), PX580797 (*rps10*)].

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or less frequently in dense or lax sympodia of 2–3 sporangia (Fig. 31O); apices non-papillate (Fig. 31A–C, E, F, H–J), sometimes slightly asymmetric or curved (6.6 %; Fig. 31G, H, J); mostly limoniform to elongated-limoniform (32.7 %; Fig. 31H–J), ellipsoid to elongated-ellipsoid (25.6 %; Fig. 31D, E, L), ovoid or elongated ovoid (24.3 %; Fig. 31B, C), or less obpyriform



Fig. 30. *Phytophthora formosa* from Japan. **A–I.** Persistent sporangia formed on V8-agar (V8A) in soil extract. **A, C.** Slightly swollen sporangial apices, shortly before releasing the already differentiated zoospores. **B, H.** Non-papillate sporangial apices. **A–F, H.** Ovoid sporangia. **A.** Laterally inserted sporangiophore. **D.** Zoospore release. **E.** Internal nested and external proliferation. **F.** Internal nested proliferation. **G.** Internal extended proliferation. **H.** Internal nested and extended (arrow) proliferation simultaneously. **I.** Sympodium of three sporangia and zoospore release. **J–R.** Oogonia with rounded (**J, M, R**) or predominantly tapering (**K, L, N–Q**) bases and plerotic oospores, sessile or on short stalks, formed in single culture in solid V8A. **J–O, S, T.** Smooth to slightly wavy oogonial walls. **P, Q.** Slightly ornamented oogonial walls. **R.** Flexuose oogonial wall. **J–N.** Globose to subglobose oogonia. **O–Q.** Elongated oogonia. **R.** Comma-shaped oogonium. **J–K, Q.** Amphigynous unicellular antheridia. **L–P, R.** Paragynous antheridia. **S.** Coralloid lateral hyphae. Scale bar = 20 µm in **A–H** and **J–S**, and 40 µm in **I**.

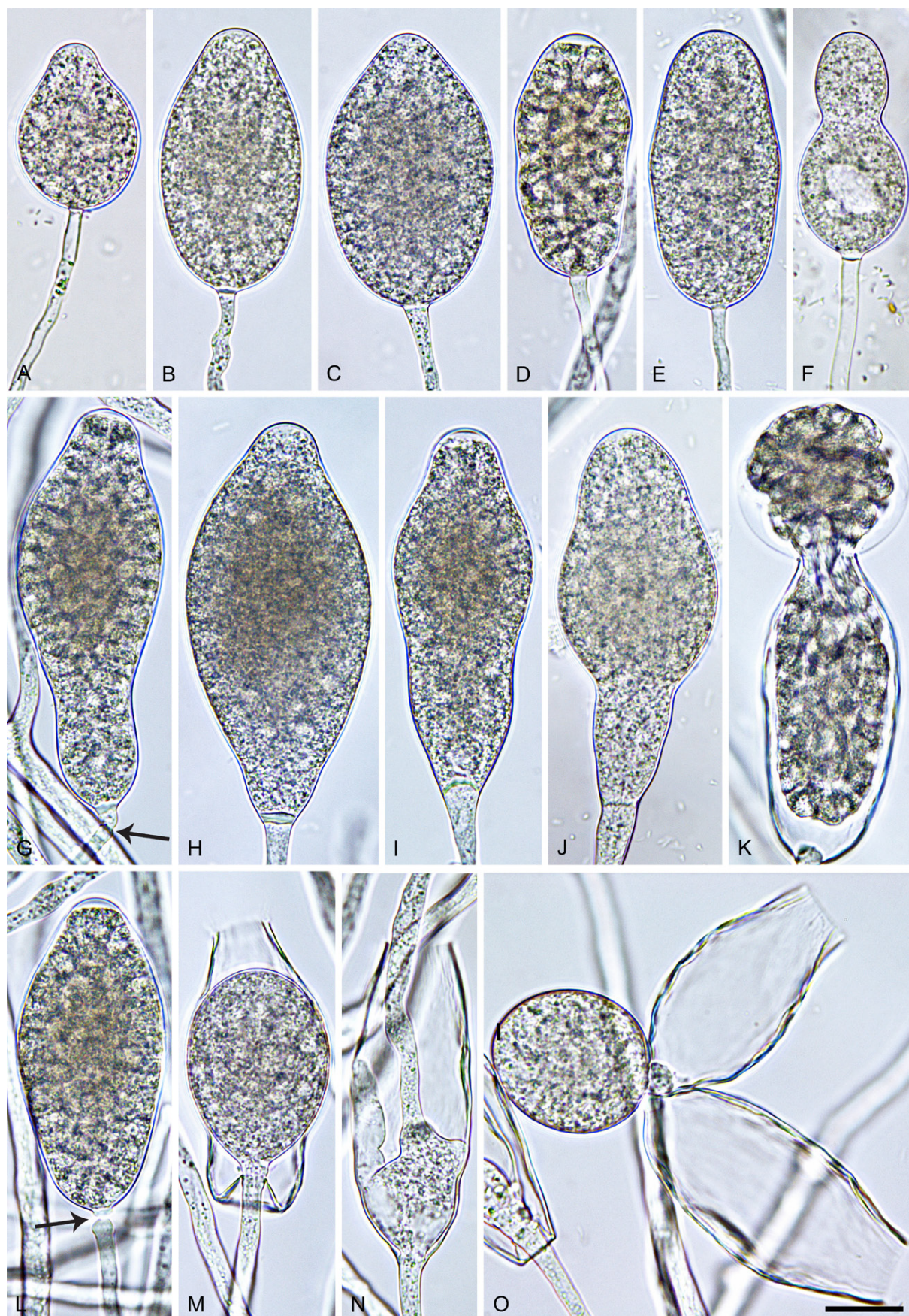


Fig. 31. *Phytophthora xgrandisporangia*. **A–O.** Persistent limoniform, ellipsoid, ovoid and ampulliform sporangia formed on V8-agar in soil extract. **A–C, E, F, H–J.** Non-papillate sporangial apices. **D, G, L.** Sporangia with swollen apices before releasing zoospores. **G, H, J.** Slightly asymmetric curved apices. **G, L.** Constrictions of the sporangiophores (arrows). **K.** Zoospore release. **M.** Internal nested proliferation. **N.** Internal extended proliferation with two sporangiophores. **O.** Sympodium of three sporangia due to external proliferation. Images: A, D–F, J, N, O. Ex-type CBS 153093; B, C, G–I, K–M. VN279. Scale bar = 20 µm; applies to A–O.

to elongated obpyriform (7.5 %; Fig. 31A, F), ampulliform (6.2 %; Fig. 31G), distorted (2.9 %), obovoid (0.4 %), or peanut-shaped (0.4 %); sporangiophores occasionally with constrictions enabling rare caducity (< 1 %; Fig. 31G, L); sporangial proliferation internal in a nested (Fig. 31M) and extended way, sometimes with 2 new sporangiophores simultaneously (Fig. 31N), and less frequently external (Fig. 31O); sporangial dimensions averaging $84.5 \pm 17.1 \times 40.1 \pm 5.2 \mu\text{m}$ (overall range $41.8\text{--}130.4 \times 24.0\text{--}53.1 \mu\text{m}$; range of isolate means $69.8\text{--}98.9 \times 38.2\text{--}42.6 \mu\text{m}$) with a length/breadth

ratio of 2.13 ± 0.48 (overall range 1.19–3.73; sporangial germination indirect with zoospores discharged through an exit pore $9.6\text{--}19.5 \mu\text{m}$ wide (av. $13.9 \pm 2.0 \mu\text{m}$) (Fig. 31K). Zoospores limoniform to reniform whilst motile, sometimes with ring-like flagella ends, becoming spherical on encystment (av. diam. $12.7 \pm 1.58 \mu\text{m}$), some zoospores larger and multinucleate (Fig. 32A). Hyphal swellings not observed on sporangiophores. Hyphae often coralloid or irregular and swollen (Fig. 32B), diam. $16.9 \pm 3.0 \mu\text{m}$. Chlamydospores not observed. Oogonia not observed in single cultures, but abundantly

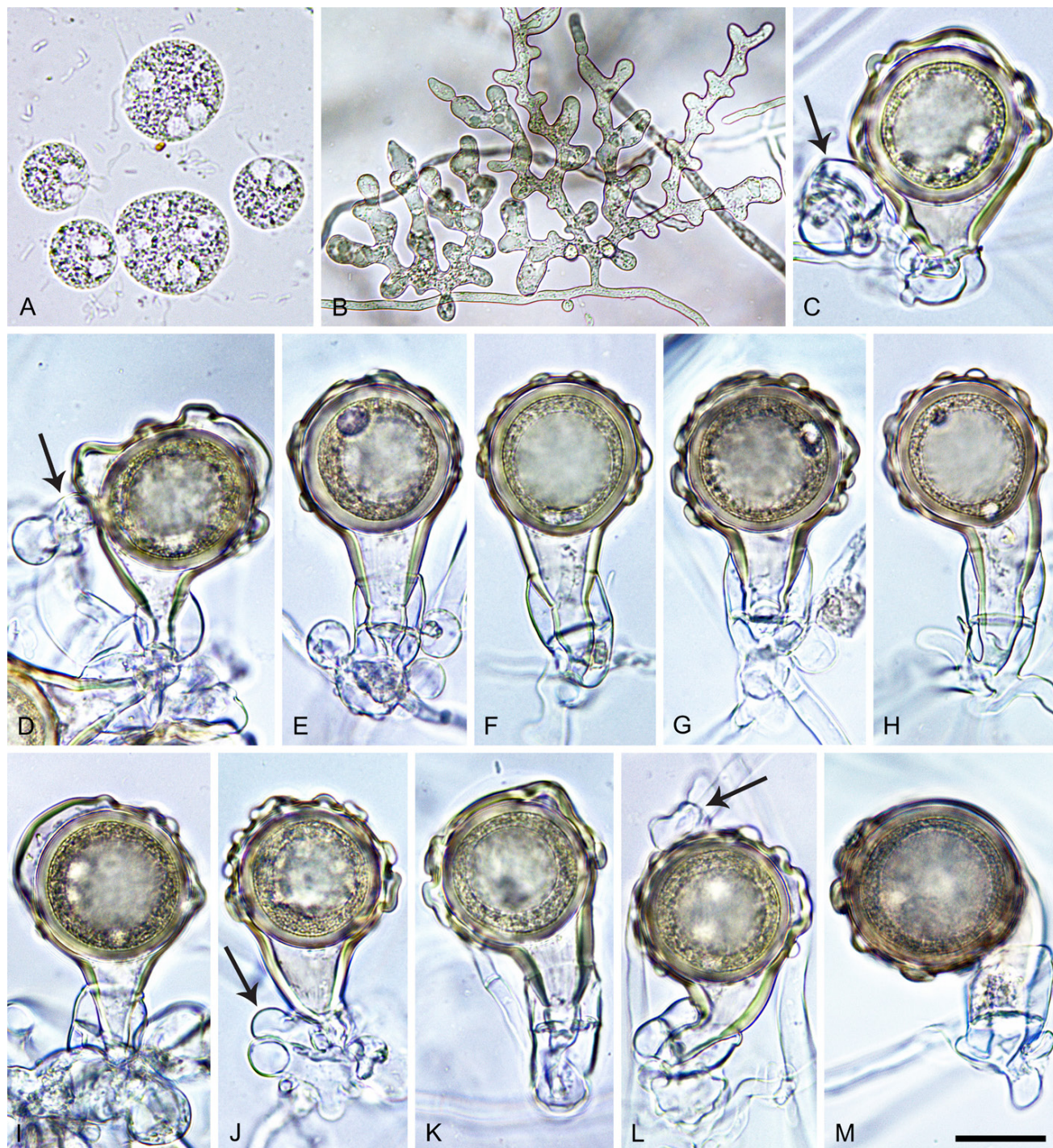


Fig. 32. *Phytophthora xgrandisporangia*. **A.** Multinucleate zoospores released from sporangium formed on V8-agar (V8A) in soil extract. **B–M.** Structures formed in solid V8A. **B.** Coralloid non-septate hyphae. **C–M.** Ornamented oogonia with near-plerotic to plerotic oospores and tapering funnel-like bases, formed in polycarbonate membrane mating tests in solid fgCA. **E–K.** Elongated oogonia. **D, I.** Excentric flexuose oogonia. **L, M.** Comma-shaped oogonia. **C, J.** Paragynous antheridia (arrows). **D–I, K–M.** Amphigynous antheridia, unicellular (D) or bicellular (E–I, K–M). **D, L.** Additional paragynous antheridia (arrows). Images: A, B, E–H, K. Ex-type CBS 153093; C, D, I. VN082; L, M. VN279. J. VN406. Scale bar = 20 μm in A, C–M and 50 μm in B.

produced by all six tested isolates in solid fgCA in polycarbonate membrane mating tests with the A2 mating type isolates MP74 and TW028 of *P. cinnamomi* and *P. ×heterohybrida*, respectively (self-sterile 'heterothallic' breeding system; all tested isolates mating type A1); sessile or terminal on short to medium-length, sometimes curved lateral hyphae (Fig. 32C, E–H, J–M); exclusively with ornamented walls; elongated (80.7 %; Fig. 32E–K), excentric (17.3 %; Fig. 32D, I), flexuose (20.3 %; Fig. 32D, I), comma-shaped (12 %; Fig. 32L, M) or globose to slightly subglobose (5 %; Fig. 32C), almost exclusively with short or long tapering bases (98.7 %; Fig. 32C–M), sometimes with curved stalks (16.7 %; Fig. 32C); oogonial diam. $45.3 \pm 4.8 \mu\text{m}$ (overall range 28.2–67.4 μm ; range of isolate means 43.8–47.0 μm); nearly plerotic to plerotic (98 %; Fig. 32C–M). Oospores globose with a large lipid globule (Fig. 32C–M); mean diam. $36.8 \pm 3.7 \mu\text{m}$ (overall range 21.3–47.1 μm ; range of isolate means 35.5–36.6 μm); wall thickness $2.3 \pm 0.9 \mu\text{m}$ (overall range 0.5–3.7 μm), oospore wall index 0.32 ± 0.09 (overall range 0.1–0.5); abortion 57–74 % (av. 64.7 %) after 4 wk. Antheridia almost exclusively amphigynous (98.7 %) and cylindrical or subglobose, bicellular (84.7 %; Fig. 32E–I, K–M) or unicellular (14 %; Fig. 32D), but a few paragynous club-shaped antheridia were rarely observed (1.3 %; Fig. 32C, J); sometimes with additional paragynous antheridia (Fig. 32D, L); dimensions of amphigynous antheridia $23.3 \pm 5.1 \times 17.4 \pm 2.3 \mu\text{m}$.

Culture characteristics: Colonies on V8A and CA uniform and submerged to appressed with limited aerial mycelium; woolly-cottony on PDA with a faint chrysanthemum-like pattern (Fig. 14).

Cardinal temperatures and growth rates: On V8A optimum 27.5 °C with $6.16 \pm 0.33 \text{ mm/d}$ radial growth, maximum 30 to < 32.5 °C, minimum < 10 °C (Fig. 18), lethal temperature 32.5–35 °C. At 20 °C on V8A, CA and PDA $4.9 \pm 0.31 \text{ mm/d}$, $6.2 \pm 0.41 \text{ mm/d}$ and $3.76 \pm 0.01 \text{ mm/d}$, respectively.

Additional materials examined: Vietnam, Sapa, Hoàng Liên National Park, isolated from baiting leaves floating in streams running through an upper-montane subtropical cloud forest, Mar. 2016, T. Jung & N.M. Chi (VN081, VN082, VN093, VN279, VN406).

Phytophthora ×leptopleura T. Jung, H. Masuya, K. Kageyama, A. Hieno & M. Horta Jung, *sp. nov.* MB 857776. Figs 33, 34.

Etymology: The name refers to the thin oospore walls (*lepto* Greek = thin, *pleura* Greek = wall).

Typus: Japan, Shikoku, Satayama, isolated from a baiting leaf floating in a stream running through a warm-temperate laurosilva forest, May 2017, T. Jung & H. Masuya [holotype CBS H-25675, dried culture on V8A, ex-holotype living culture CBS 153090 = JP859; GenBank accession nos. PX607111 (LSU), PX607242 (ITS), PX581081 (*βtub*), PX581747 (*hsp90*), PX582100 (*tigA*), PX581249 (*rpl10*), PX581425 (*tef1a*), PX581605 (*enl*), PX581924 (*cox1*), PX580949 (*nadh1*), PX580815 (*rps10*)].

Morphological structures on V8A: Sporangia abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or in dense or lax sympodia of 2–3 sporangia (Fig. 33I, N; Fig. 34A); ovoid, broad-ovoid or elongated ovoid (37.8 %; Fig. 33A, F, I), limoniform to elongated limoniform (32 %; Fig. 33D, E, G), obpyriform to elongated-obpyriform (10.6 %; Fig. 33B), ellipsoid to elongated ellipsoid (10.7 %; Fig. 33C), less

frequently distorted with often two apices (3.3 %; Fig. 33K, L), pyriform (2.0 %), peanut-shaped (1.6 %; Fig. 33H), ampulliform (1.3 %) or obovoid (0.7 %); apices non-papillate (Fig. 33A–F, H, I); pedicels occasionally observed; sporangial proliferation abundantly internal in both a nested (Fig. 33K) and extended way, sometimes with the new sporangiophore branching inside the empty sporangium (Fig. 33L, M) or less frequently external (Fig. 33I, N; Fig. 34A), sometimes with 2 or 3 sporangiophores arising from the same point (Fig. 33N); sporangial dimensions averaging $71.6 \pm 9.9 \times 39.2 \pm 5.5 \mu\text{m}$ (overall range 52.0–105.2 $\times$ 23.4–51.9 μm ; range of isolate means $69.1\text{--}77.8 \times 37.4\text{--}44.2 \mu\text{m}$) with a length/breadth ratio of 1.85 ± 0.24 (overall range 1.36–2.88); sporangial germination indirect with zoospores discharged through an exit pore 8.0–21.6 μm wide (av. $12.6 \pm 2.6 \mu\text{m}$) (Fig. 33J). Zoospores limoniform to reniform whilst motile, becoming spherical (av. diam. $12.7 \pm 1.2 \mu\text{m}$) on encystment; sometimes unusually large and multinucleate due to failure of sporangial cytoplasm to differentiate into individual zoospores (Fig. 34B); zoospore flagella occasionally with ring-like ends (Fig. 34B). Hyphal swellings elongated-irregular and catenulate (Fig. 34C). Chlamydospores not observed. Oogonia not observed in single culture, but commonly produced in mating tests between A1 and A2 mating type isolates in solid fgCA (self-sterile 'heterothallic' breeding system; isolates JP077, JP204 and JP859 belonging to the A1 mating type, isolates JP375, JP591, JP673 and JP702 to the A2 mating type); globose to subglobose (53.2 %; Fig. 34E–H), excentric (44.3 %; Fig. 34I–K) and often flexuose (22 %; Fig. 34I, K) or comma-shaped (12.5 %; Fig. 34J, K), rarely elongated (2.5 %; Fig. 34D); predominantly ornamented (82.5 %; Fig. 34F–J), less frequently smooth-walled or with a slightly wavy wall (17.5 %; Fig. 34D–E, K), sessile or with short to medium-sized stalks (Fig. 34D–K), mostly with short or long tapering bases (71 %; Fig. 34D–G, I, K), less frequently with non-tapering base (29 %; Fig. 34H, J); sometimes oogonial wall turning golden-brown during maturation (Fig. 34G, I); oogonial size very large, diam. $56.0 \pm 5.7 \mu\text{m}$ (overall range 32.5–76.3 μm ; range of means in different mating combinations 53.7–58.1 μm); plerotic or nearly plerotic (Fig. 34D–K). Oospores globose to subglobose, usually with one large lipid globule (Fig. 34F–K), occasionally with multiple smaller lipid globules (Fig. 34D, E); diam. $46.9 \pm 5.2 \mu\text{m}$ (overall range 28.2–64.5 μm ; range of means in different mating combinations 43.5–48.9 μm); walls very thin, thickness averaging $1.2 \pm 0.5 \mu\text{m}$ (overall range 0.3–4.6 μm), oospore wall index 0.14 ± 0.06 (overall range 0.1–0.4); high abortion rate of 54 % (40–63 %) after 4 wk. Antheridia almost exclusively amphigynous, cylindrical, subglobose or irregular and bicellular (84.3 %; Fig. 34D, E, G–K) or unicellular (13.9 %; Fig. 34F), rarely paragynous (1.8 %); dimensions of amphigynous antheridia $24.2 \pm 3.9 \times 18.6 \pm 2.1 \mu\text{m}$.

Culture characteristics: Colonies on V8A woolly-cottony with submerged to appressed margins, uniform or with faint stellate pattern; on CA woolly-cottony and uniform; on PDA dense woolly-cottony and uniform to faintly petaloid (Fig. 14).

Cardinal temperatures and growth rates: On V8A optimum at 25 °C with $4.4 \pm 1.12 \text{ mm/d}$ radial growth; maximum 32.5 to < 35 °C; minimum < 10 °C (Fig. 18), lethal temperature 35 °C. At 20 °C on V8A, CA and PDA $3.8 \pm 1.05 \text{ mm/d}$, $3.95 \pm 0.13 \text{ mm/d}$ and $2.64 \pm 0.26 \text{ mm/d}$, respectively.

Additional materials examined: Japan, Shikoku, Satayama, isolated from a baiting leaf floating in a stream running through warm-temperate laurosilva forest, May 2017, T. Jung & K. Kageyama

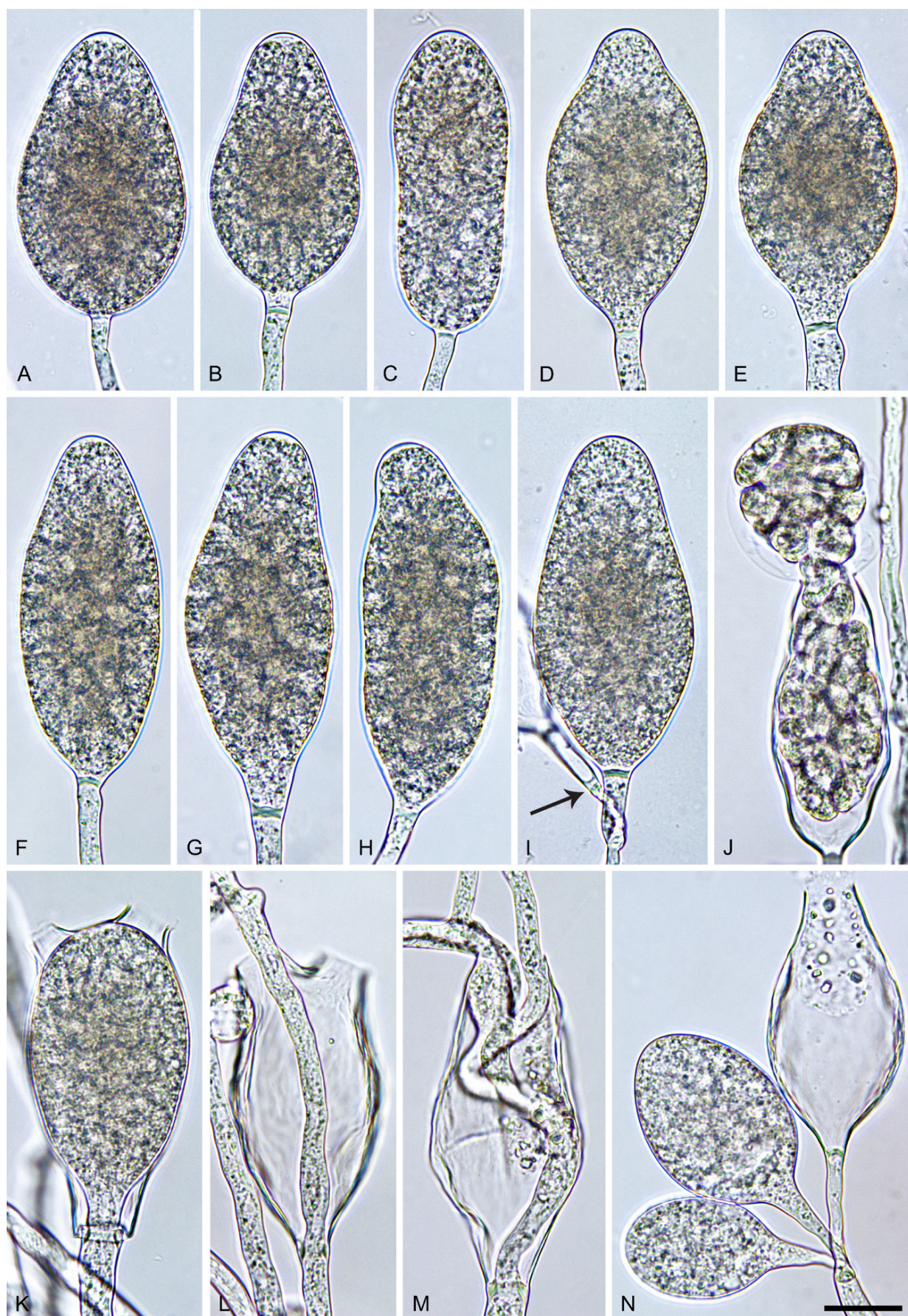


Fig. 33. *Phytophthora* *x* *leptopleura*. **A–N.** Persistent ovoid, obpyriform, limoniform, ellipsoid, distorted and peanut-shaped sporangia formed on V8-agar in soil extract. **A–F, H, I.** Non-papillate sporangial apices. **G.** Sporangium with swollen apex before releasing zoospores. **I.** External proliferation (arrow). **J.** Zoospore release. **K, L.** With two apices. **K.** Internal nested proliferation. **L, M.** Internal extended proliferation with one or more sporangiophores. **N.** Sympodium of three sporangia arising from the same point. Images: B, F–K. Ex-type CBS 153090; A, D, E, L–N. JP077; C. JP204. Scale bar = 20 μm; applies to A–N.

(JP077), T. Jung & S. Uematsu (JP204), T. Jung & M. Horta Jung (JP375), T. Jung & J.F. Webber (JP591), T. Jung & C.M. Brasier (JP673), T. Jung & A. Hieno (JP702).

Phytophthora × nodosa T. Jung, A. Hieno, H. Masuya, K. Kageyama & S. Uematsu, *sp. nov.* MB 857777. Fig. 35.

Etymology: The name refers to the nodose ornamentation of the oogonia walls (*nodosa* Latin = nodose, knobby).

Typus: **Japan**, Kyushu, Takakuma, isolated from rhizosphere soil of *Lithocarpus edulis* in a warm-temperate laurosilva forest, May 2017, T. Jung & A. Hieno [**holotype** CBS H-25677, dried culture

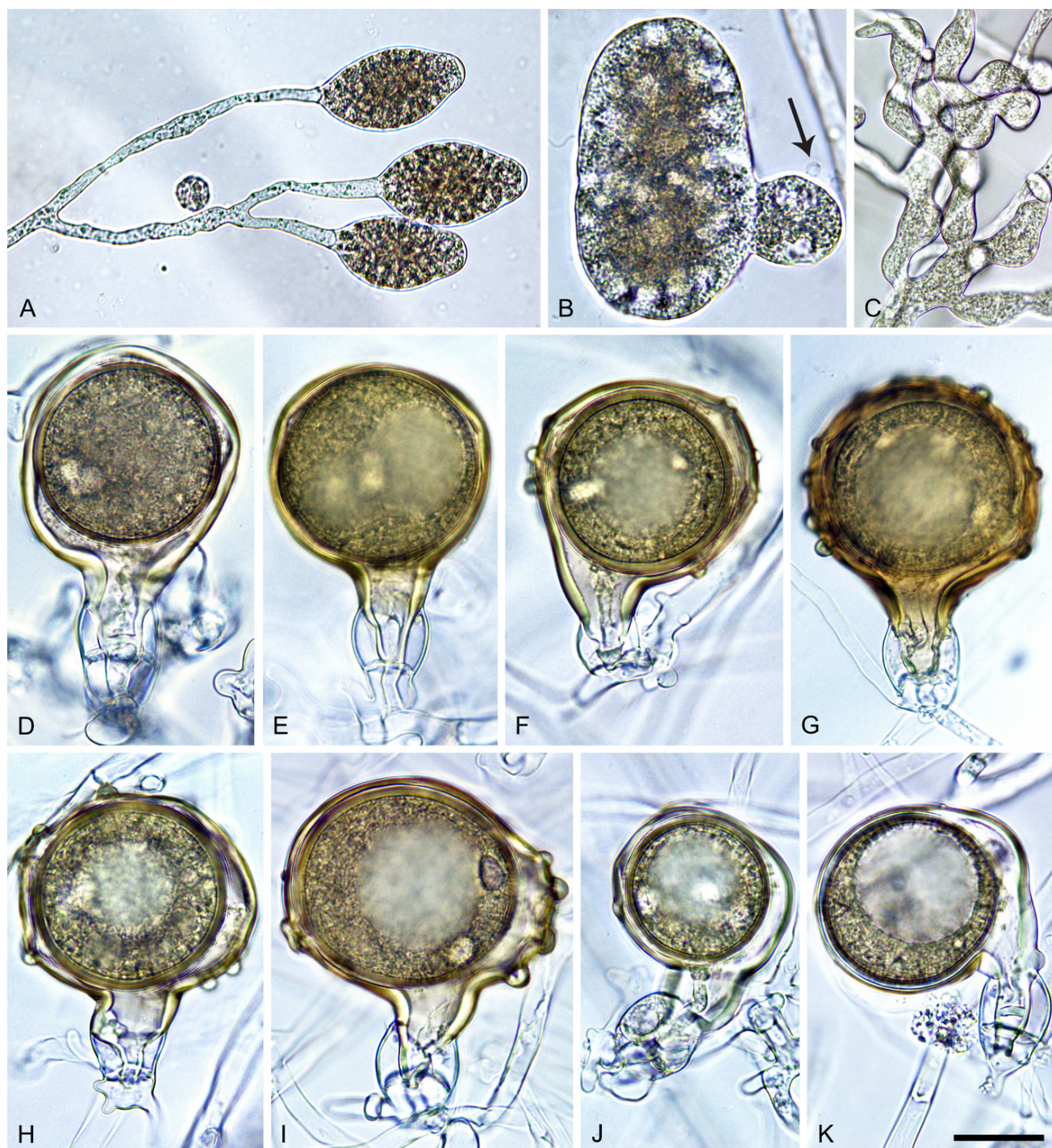


Fig. 34. *Phytophthora × leptopleura*. **A–C.** Structures formed on V8-agar in soil extract. **A.** Sympodium of three sporangia before zoospore release. **B.** Large multinucleate zoospore with ring-like flagellae ends (arrow). **C.** Elongated-irregular and catenulate hyphal swellings. **D–K.** Oögonia with mostly tapering bases, near-plerotic to plerotic thin-walled oöspores and amphigynous unicellular (F) or bicellular (D, E, G–K) antheridia, formed in mating tests in solid fgCA. **D.** Elongated oögonium. **E–H.** Globose to subglobose oögonia. **I–K.** Excentric oögonia. **I, K.** Flexuose oögonia. **J, K.** Comma-shaped oögonia. **D, E, K.** Smooth or slightly wavy oögonial walls. **F–J.** Ornamented oögonial walls. Images: **A, B.** JP077; **C.** Ex-type CBS 153090; **D, J, K.** Ex-type CBS 153090 × JP673; **E.** JP077 × JP591; **F, G.** JP077 × JP375; **H.** JP204 × JP673. Scale bar = 20 µm in B–K and 50 µm in A.



Fig. 35. *Phytophthora xnodosa*. **A–J.** Persistent ovoid, obpyriform, limoniform, ellipsoid, pyriform and obovoid sporangia formed on V8-agar in soil extract. **A–F.** Non-papillate sporangial apices. **F.** Sporangium before releasing zoospores. **G.** Zoospore release. **H, I.** Internal nested proliferation. **J.** Internal extended proliferation with branching sporangiophore. **K.** Carrot-like to tubular hyphae with pointed tips. **L–R.** Oogonia with mostly tapering bases and near-plerotic to plerotic oospores, formed in single cultures in solid fgCA. **L–N.** Globose to subglobose oogonia. **O–Q.** Excentric oogonia. **N, R.** Comma-shaped oogonia. **L, N–R.** Ornamented oogonial walls. **M.** Smooth to slightly wavy oogonial wall. **L.** Paragynous antheridium. **M–R.** Amphigynous unicellular (**M, R**) or bicellular (**N–Q**) antheridia. Images: **F, H–J, P, R.** Ex-type CBS 153088; **B, E, M, O, Q.** JP532; **D, K.** JP577; **A, C, G, L, N.** JP923. Scale bar = 20 µm in **A–J** and **L–R**, and 50 µm in **K**.

on V8A, ex-holotype living culture CBS 153088 = JP761; GenBank accession nos. PX607119 (LSU), PX607246 (ITS), PX581085 (*βtub*), PX581751 (*hsp90*), PX582107 (*tigA*), PX581257 (*rpl10*), PX581433 (*tef-1α*), PX581613 (*enl*), PX581932 (*cox1*), PX580953 (*nadh1*), PX580822 (*rps10*)).

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or rarely in lax sympodia of 2 sporangia; limoniform to elongated limoniform (32 %; Fig. 35D), ovoid, broad-ovoid or elongated ovoid (30.5 %; Fig. 35A, F), obpyriform to elongated-obpyriform (29 %; Fig. 35C), ellipsoid to elongated ellipsoid (5.5 %; Fig. 35C), less frequently pyriform (2.5 %; Fig. 35E) or obovoid (0.5 %; Fig. 35B); apices non-papillate (Fig. 35A–F); sporangial proliferation abundantly internal in both a nested (Fig. 35H, I) and extended way, sometimes with the new sporangiophore branching inside the empty sporangium (Fig. 35J) or rarely external; sporangial dimensions averaging $74.1 \pm 9.2 \times 43.5 \pm 4.9 \mu\text{m}$ (overall range $56.0\text{--}106.1 \times 29.4\text{--}53.8 \mu\text{m}$; range of isolate means $69.7\text{--}81.9 \times 41.1\text{--}46.3 \mu\text{m}$) with a length/breadth ratio of 1.72 ± 0.24 (overall range 1.16–2.43); sporangial germination indirect with zoospores discharged through an exit pore $8.6\text{--}18.6 \mu\text{m}$ wide (av. $12.1 \pm 1.9 \mu\text{m}$) (Fig. 35G). *Zoospores* limoniform to reniform whilst motile, becoming spherical (av. diam. $12.1 \pm 1.3 \mu\text{m}$) on encystment; cysts germinating directly by forming a hypha or a microsporangium or indirectly by releasing a secondary zoospore (diplanetism). *Hyphal swellings* not observed. Hyphae often carrot-like or tubular with pointed tip (Fig. 35K). *Chlamydospores* not observed. *Oogonia* abundantly produced in single culture in solid fgCA (self-fertile ‘homothallic’ breeding system); globose to subglobose (59 %; Fig. 35L–N), excentric (25.7 %; Fig. 35O–Q) and occasionally flexuose (10.5 %) or slightly bend to comma-shaped (15.3 %; Fig. 35N, R), rarely slightly elongated (4 %); predominantly slightly to strongly ornamented (88.3 %; Fig. 35L, N–R), less frequently smooth-walled or with a slightly wavy wall (11.7 %; Fig. 35M), sessile or with short stalks (Fig. 35L–R), mostly with short tapering bases (85.3 %; Fig. 35M–R), less frequently with non-tapering base (14.7 %; Fig. 35L); sometimes oogonial wall turning golden-brown during maturation (Fig. 35P); oogonial size large, diam. $51.7 \pm 6.5 \mu\text{m}$ (overall range $30.1\text{--}68.1 \mu\text{m}$; range of means $48.6\text{--}54.9 \mu\text{m}$); plerotic or nearly plerotic (77 %; Fig. 35L–N, P, R) or slightly applerotic (23 %; Fig. 35O, Q). *Oospores* globose to subglobose, with one large lipid globule (Fig. 35L–R); diam. $42.8 \pm 5.8 \mu\text{m}$ (overall range $25.5\text{--}57.5 \mu\text{m}$; range of means $40.4\text{--}45.4 \mu\text{m}$); walls thin, thickness averaging $1.6 \pm 0.5 \mu\text{m}$ (overall range $0.6\text{--}3.0 \mu\text{m}$), oospore wall index 0.20 ± 0.06 (overall range 0.1–0.4); abortion rate of 19.3 % (10–32 %) after 4 wk. *Antheridia* almost exclusively amphigynous, cylindrical, subglobose or irregular and bicellular with the basal cell being much smaller than the upper one (79.6 %; Fig. 35N–Q) or unicellular (17.1 %; Fig. 35M, R), rarely paragynous (3.3 %; Fig. 35L); dimensions of amphigynous antheridia $21.9 \pm 3.4 \times 18.0 \pm 2.5 \mu\text{m}$.

Culture characteristics: Colonies on V8A uniform to faintly radiate with limited, woolly aerial mycelium; on CA uniform and woolly-cottony or uniform with submerged dendroid margins and appressed, limited aerial mycelium in the centre; on PDA uniform and dense woolly-cottony (Fig. 14).

Cardinal temperatures and growth rates: On V8A optimum at 25 °C with $4.5 \pm 0.29 \text{ mm/d}$ radial growth; maximum 32.5 to < 35 °C; minimum < 10 °C (Fig. 18), lethal temperature 35 °C. At 20 °C on

V8A, CA and PDA $4.1 \pm 0.38 \text{ mm/d}$, $3.7 \pm 0.22 \text{ mm/d}$ and $3.36 \pm 0.05 \text{ mm/d}$, respectively.

Additional materials examined: **Japan**, Kyushu, Takakuma, isolated from baiting leaves floating in a stream running through warm-temperate laurosilva forests, May 2017, T. Jung & K. Kageyama (JP532), T. Jung & H. Masuya (JP577); isolated from rhizosphere soil of *L. edulis* in a warm-temperate laurosilva forest, T. Jung & M. Horta Jung (JP923).

Phytophthora fragariae Hickman, *J. Pomol. Hortic. Sci.* **18**: 103. 1940. MB 289688. Fig. 36.

Typus: **UK**, from roots and rootstocks of cultivated strawberries, figs 9–10 in Hickman (1940: 97, 99), showing sporangia and oospore formation (**lectotype**, designated in Abad *et al.* 2023, MBT 10008010); Scotland isolated from *Fragaria* sp. fruit, collection date and collector unknown (**epitype** CBS H-25070, designated in Abad *et al.* (2023), MBT 10008011, ex-epitype living culture CBS 309.62 = NRRL 64315 = ATCC 11107 = Hickman R-4 = CPHST BL 213; GenBank accession nos. KX251548 (LSU), HQ643230 (ITS), KX251544 (*βtub*), MWJK01001460 (*hsp90*), KX251549 (*tigA*), KX251543 (*rpl10*), KX251545 (*tef-1α*), KX251546 (*enl*), BK011985 (*cox1*), BK011985 (*nadh1*), BK011985 (*rps10*)).

Morphological structures on V8A: *Sporangia* produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores; mostly ovoid, broad-ovoid or elongated-ovoid (67 %; Fig. 36A, B, D) or limoniform to elongated-limoniform (18 %; Fig. 36C), obpyriform to elongated-obpyriform (10 %; Fig. 36E) or ellipsoid to elongated-ellipsoid (5 %); sporangial apices exclusively non-papillate; abundant internal sporangial proliferation in both a nested and an extended way (Fig. 36F), sometimes with the sporangiophore branching multiple times inside the old sporangium (Fig. 36G); sporangial dimensions averaging $65.9 \pm 8.0 \times 41.4 \pm 4.0 \mu\text{m}$ (overall range $45.6\text{--}81.4 \times 31.7\text{--}50.3 \mu\text{m}$; range of isolate means $62.3\text{--}69.5 \times 39.7\text{--}43.1 \mu\text{m}$) with a length/breadth ratio of 1.6 ± 0.25 (overall range 1.2–2.25); sporangial germination indirect with zoospores discharged through an exit pore $12.6\text{--}20 \mu\text{m}$ wide (av. $16.1 \pm 2.3 \mu\text{m}$). *Zoospores* limoniform to reniform whilst motile, becoming spherical (av. diam. $12.5 \pm 1.8 \mu\text{m}$) on encystment. *Hyphal swellings* commonly formed in water, subglobose to globose or limoniform (Fig. 36H), often catenulate; diam. $17.4 \pm 3.1 \mu\text{m}$ (range $12.8\text{--}23.2 \mu\text{m}$). *Chlamydospores* not observed. *Hyphal aggregations* commonly formed (Fig. 36S). *Oogonia* produced by both isolates in single culture (self-fertile ‘homothallic’ breeding system); mostly globose to subglobose (61 %; Fig. 36I–K, M, Q, R) or elongated (33 %; Fig. 36N, P), occasionally excentric (3 %; Fig. 36L) or slightly bend to comma-shaped (3 %; Fig. 36O); smooth-walled, turning golden-brown or dark-brown during maturation (Fig. 36I–R), sessile or with short stalks, with short tapering (69 %) or round non-tapering base (31 %); oogonial diam. $33.5 \pm 4.2 \mu\text{m}$ (overall range $25\text{--}44.8 \mu\text{m}$; range of means $31.4\text{--}35.6 \mu\text{m}$); plerotic (86 %; Fig. 36I–L, N, Q, R) or slightly applerotic (14 %; Fig. 36M, O, P). *Oospores* globose to subglobose (Fig. 36I–O, Q, R) or rarely slightly ellipsoid in elongated oogonia (Fig. 36P), usually with one medium-sized to large lipid globule (Fig. 36I–P); diam. $28.2 \pm 3.2 \mu\text{m}$ (overall range $21.4\text{--}36.0 \mu\text{m}$; range of isolate means $26.1\text{--}30.3 \mu\text{m}$); wall thickness $2.1 \pm 0.7 \mu\text{m}$ (overall range $1.2\text{--}4.8 \mu\text{m}$), oospore wall index 0.38 ± 0.08 (overall range 0.26–0.63); abortion rate of 66 % (60–72 %; Fig. 36Q, R) after 4 wk. *Antheridia*

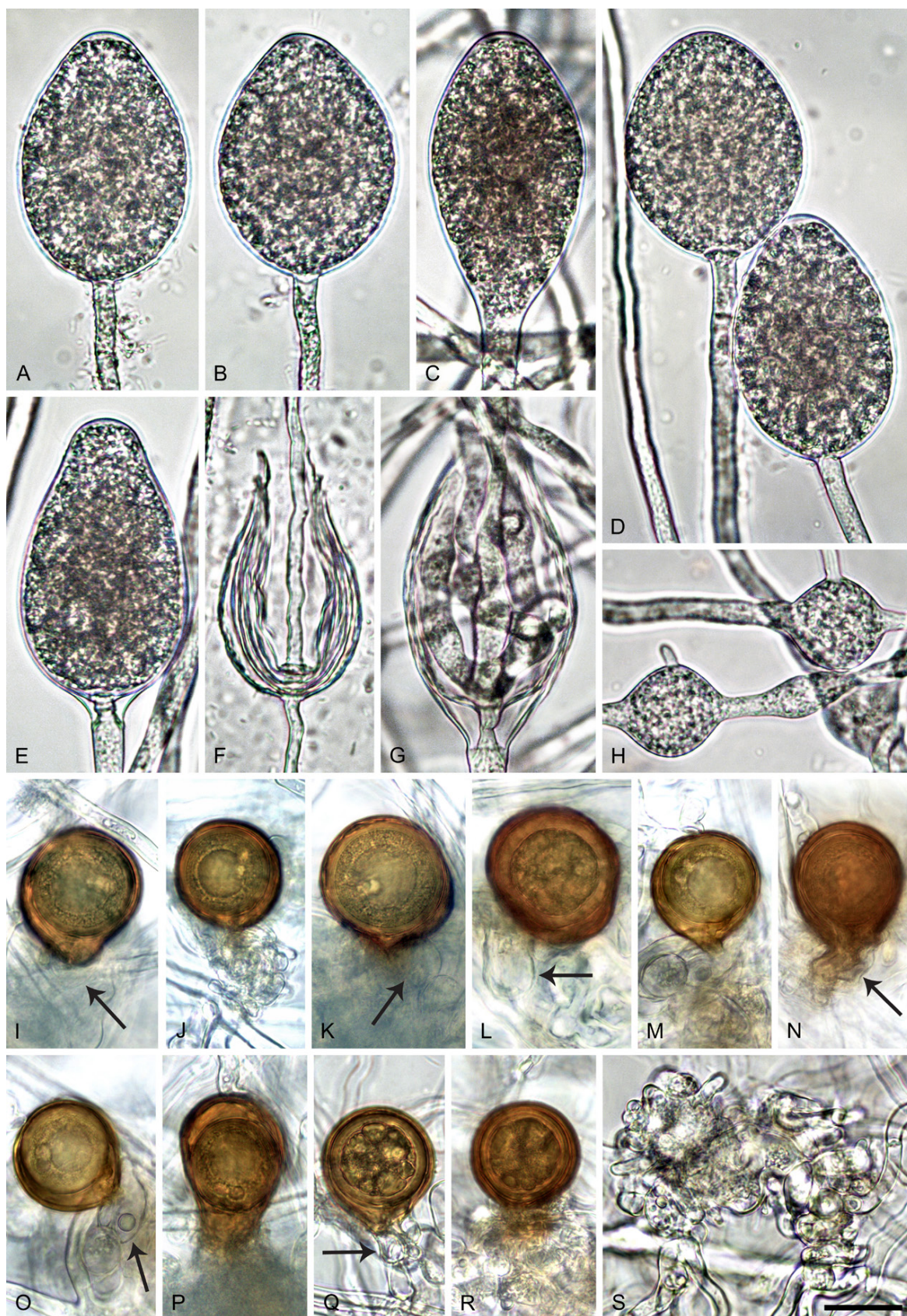


Fig. 36. *Phytophthora fragariae*. **A–H.** Structures formed on V8-agar (V8A) in soil extract. **A–G.** Persistent sporangia. **A–E.** Ovoid, limoniform or obpyriform non-papillate sporangia. **E.** Internal nested proliferation. **F.** Internal nested and extended proliferation. **G.** Internal extended proliferation with multiple sporangiophores. **H.** Subglobose to globose hyphal swellings. **I–R.** Golden- to dark-brown oogonia with smooth walls and near-plerotic to plerotic (**I–L, N, Q, R**) or slightly applerotic (**M, O, P**) oospores, formed in single culture in solid V8A. **I–K, M, Q, R.** Subglobose to globose oogonia. **N, P.** Elongated oogonia. **L.** Excentric oogonium. **O.** Comma-shaped oogonium. **I, K, L.** Paragynous antheridia (arrows). **N–O, Q.** Amphigynous antheridia (arrows). **J, M, P, R.** Antheridia almost invisible due to dense aggregations of intertwining hyphae at the oogonial base. **Q, R.** Aborted oospores. **S.** Dense hyphal aggregation in solid V8A. Images: **A–C, F–K, M, N, P, Q, S.** BBA L1; **D, E, L, O, R.** BBA 11/94. Scale bar = 20 µm; applies to **A–S**.

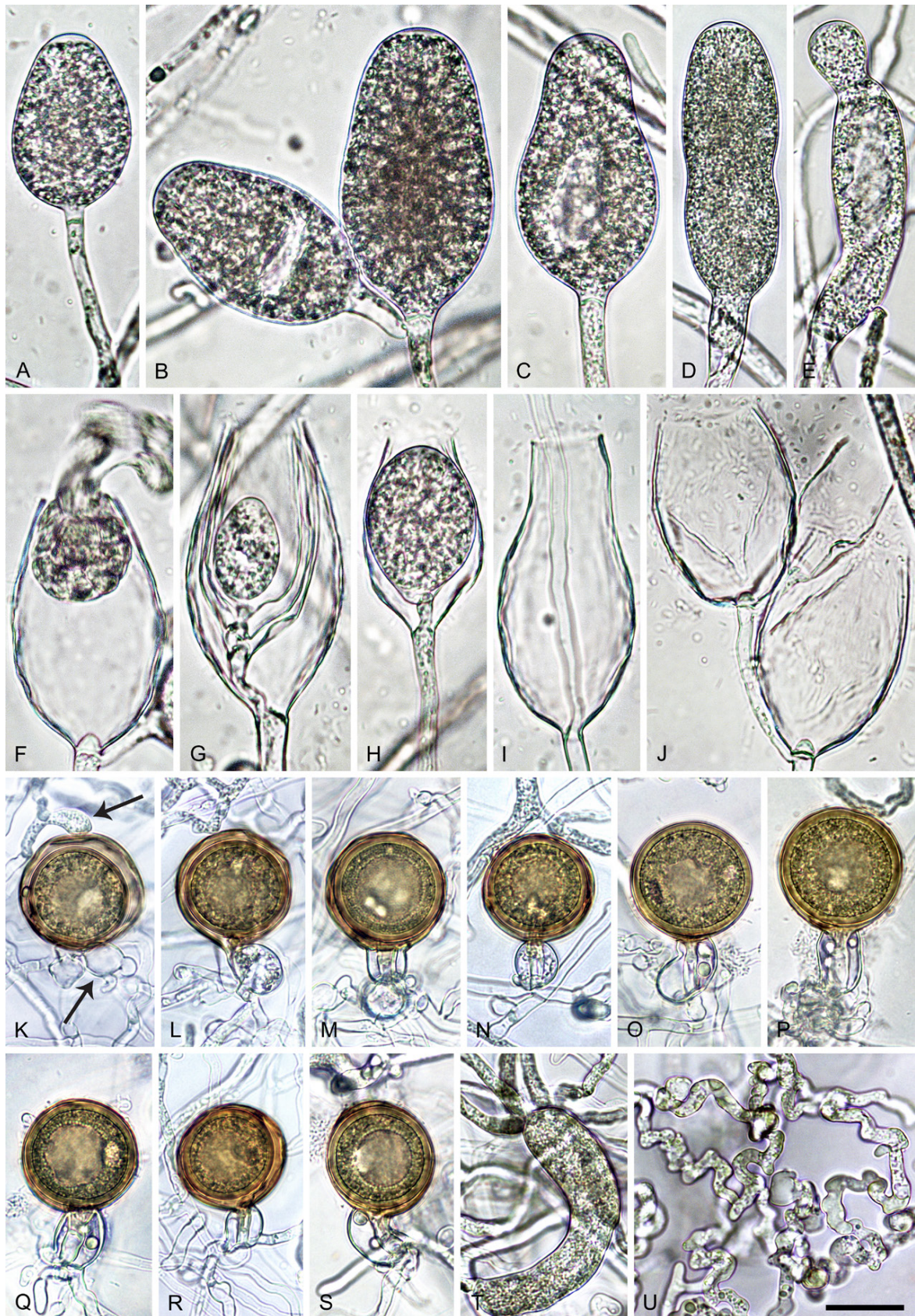


Fig. 37. *Phytophthora rubi*. **A–J.** Persistent ovoid, limoniform, ellipsoid, obpyriform, ampulliform or distorted sporangia formed on V8-agar (V8A) in soil extract. **A–D.** Non-papillate apices. **B.** External proliferation. **B, C, E.** Sporangia with irregular-shaped vacuoles. **F.** Zoospore release and external proliferation. **G, H.** Internal nested proliferation. **I.** Internal extended proliferation. **J.** Dense sympodium of three sporangia. **K–S.** Golden-brown oogonia with round bases and aplerotic (**K, L**) or plerotic (**M–S**) oospores with large lipid globules, sessile or on short stalks, formed in single culture in solid V8A. **L–Q, S.** Subglobose to globose oogonia. **K, R.** Excentric oogonia. **K, L.** Slightly wavy oogonial walls and paragynous antheridia. **M–S.** Smooth oogonial walls and amphigynous unicellular antheridia. **T, U.** Hyphal swellings formed in solid V8A. **T.** Allantoid swelling. **U.** Irregular catenulate swellings. Images: **A–H, J, M.** PHRM09; **I, O–Q, S.** CBS 109892; **L, K, N, R, T.** CH106; **U.** 230553. Scale bar = 20 µm; applies to **A–U**.

paragynous (70 %; Fig. 36I, K, L) or less frequently amphigynous, cylindrical or subglobose and usually unicellular (30 %; Fig. 36N, O, Q), often not visible due to a dense aggregation of intertwining hyphae at the oogonial base (Fig. 36J, M, P, R); dimensions $16.6 \pm 6.3 \times 12.7 \pm 2.5 \mu\text{m}$.

Culture characteristics: Colonies on V8A and CA uniform with woolly-cottony mycelium and dome-shaped centre; on PDA uniform and dense felty-cottony (Fig. 10).

Cardinal temperatures and growth rates: On V8A optimum 20°C with $1.9 \pm 0.62 \text{ mm/d}$ radial growth, maximum 25 to $< 27.5^\circ\text{C}$, minimum $< 10^\circ\text{C}$ (Fig. 17), lethal temperature 27.5°C . At 20°C on CA and PDA $1.8 \pm 0.19 \text{ mm/d}$ and $0.7 \pm 0.05 \text{ mm/d}$, respectively.

Materials examined: **Germany**, isolated from *Fragaria* × *ananassa*, 1983, Julius-Kühn Institute (BBA L1 = TJ011 = LSVM 773 = ILVO_JA06 = ILVO_SW38); isolated from *F. × ananassa* 'Elsanta', 1994, Julius-Kühn Institute (BBA 11/94 = TJ012 = K018 = ILVO_SW39).

Phytophthora rubi (W.F. Wilcox & J.M. Duncan) Man in 't Veld, *Mycologia* 99(2): 226 2007. MB 505721. Fig. 37.

Basionym: *Phytophthora fragariae* var. *rubi* W.F. Wilcox & J.M. Duncan, *Mycol. Res.* 97(7): 830. 1993. MB 360234.

Typus: **UK**, Scotland, isolated from *Rubus idaeus* cane, 1985, collector unknown [**holotype** CUP 62528, ex-type living culture CBS 967.95 = ATCC 90442 = IMI355974, WPC P15597 = WPC P16899 = CPHST BL 54 = No R49 = FVR 11 = NY 588 = SCRP 333; GenBank accession nos. KX251569 (LSU), MG865584 (ITS), KU899234 (*βtub*), QXFT01000832 (*hsp90*), KX251570 (*tigA*), KX251564 (*rpl10*), KX251566 (*tef1-α*), QXFT01000010 (*enl*), QXFT01001055 (*cox1*), KU899476 (*nadh1*), MZ365436 (*rps10*)].

Morphological structures on V8A: *Sporangia* produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or in dense sympodia of 2–3 sporangia (Fig. 37B, J); ovoid, broad-ovoid or elongated-ovoid (56.7 %; Fig. 37A, B, F–H, J), ellipsoid to elongated-ellipsoid (16.6 %; Fig. 37B), limoniform to elongated-limoniform (12.7 %; Fig. 37C), obpyriform to elongated-obpyriform (10.8 %; Fig. 37C, I) or infrequently elongated-distorted (1.9 %; Fig. 37E), pyriform (0.6 %) or ampulliform (0.6 %; Fig. 37D); occasionally with irregular-shaped vacuoles (Fig. 37B, C, E); sporangial apices exclusively non-papillate; sporangial proliferation internal in both a nested (Fig. 37G, H) or an extended way (Fig. 37I) and external close to the sporangial base (Fig. 37B, F, J); sporangial dimensions averaging $50.2 \pm 12.7 \times 29.3 \pm 8.1 \mu\text{m}$ (overall range $25.1\text{--}83 \times 11.9\text{--}46.8 \mu\text{m}$; range of isolate means $35.6\text{--}61.9 \times 18.1\text{--}37.3 \mu\text{m}$) with a length/breadth ratio of 1.75 ± 0.26 (overall range 1.25–2.69); sporangial germination indirect with zoospores discharged through an exit pore $5\text{--}30.1 \mu\text{m}$ wide (av. $16.1 \pm 4.6 \mu\text{m}$). *Zoospores* limoniform to reniform whilst motile, becoming spherical (av. diam. $13.3 \pm 1.9 \mu\text{m}$) on encystment. *Hyphal swellings* commonly formed in water, elongated-allantoid (Fig. 37T) or irregular, often catenulate (Fig. 37U). *Hyphae* sometimes undulating and contorted (Fig. 37U). *Chlamydospores* not observed. *Oogonia* produced by all isolates in single culture (self-fertile 'homothallic' breeding system); predominantly globose to subglobose (81.9 %; Fig. 37L–Q, S), less frequently elongated (9.5 %) or slightly excentric (8.6 %; Fig. 37K, R); smooth-walled, turning golden-brown during maturation (Fig. 37K–S), sessile or with short thin stalks, mostly with round non-tapering base (86.1 %; Fig. 37K–S), infrequently with short tapering

base (13.9 %); oogonial diam. $36.5 \pm 5.1 \mu\text{m}$ (overall range $23.0\text{--}47.1 \mu\text{m}$; range of isolate means $33.0\text{--}39.1 \mu\text{m}$); plerotic (64.3 %; Fig. 37M–S) or aplerotic (35.7 %; Fig. 37K, L). *Oospores* globose to subglobose with one medium-sized to large lipid globule (Fig. 37K–S); diam. $31.9 \pm 4.5 \mu\text{m}$ (overall range $29.1\text{--}35.6 \mu\text{m}$; range of isolate means $29.1\text{--}35.6 \mu\text{m}$); wall thickness $2.0 \pm 0.6 \mu\text{m}$ (overall range $0.8\text{--}4.0 \mu\text{m}$), oospore wall index 0.33 ± 0.08 (overall range 0.14–0.59); abortion rate of 65.8 % (45–82 %) after 4 wk. *Antheridia* paragynous (55.8 %; Fig. 37K, L) or amphigynous, cylindrical, subglobose or irregular and usually unicellular (44.2 %; Fig. 37M–S); dimensions $18.0 \pm 3.8 \times 13.9 \pm 2.0 \mu\text{m}$.

Culture characteristics: Colonies on V8A, CA and PDA uniform with woolly-cottony mycelium (Fig. 10).

Cardinal temperatures and growth rates: On V8A optimum 20°C with $1.5 \pm 0.43 \text{ mm/d}$ radial growth, maximum 25 to $< 27.5^\circ\text{C}$, minimum $< 10^\circ\text{C}$ (Fig. 17), lethal temperature 27.5°C . At 20°C on CA and PDA $2.2 \pm 0.03 \text{ mm/d}$ and $1.3 \pm 0.69 \text{ mm/d}$, respectively.

Materials examined: **Croatia**, isolated from *R. idaeus*, 2009, Z. Tomić (PHRM09 = P718 = TJ010). **Germany**, isolated from *R. idaeus*, collection date unknown, Julius-Kühn Institute (BBA93 = TJ013); isolated from *R. idaeus*, 1990, Julius-Kühn Institute (BBA390 = TJ014). **Netherlands**, isolated from *R. idaeus*, 2010, K. Rosendahl (5005038 = TJ322). **Norway**, isolated from *R. idaeus*, 2006, M.-L. Herrero (230 553 = TJ320). **Sweden**, isolated from *R. idaeus*, collection date unknown, C. Olsson (CH106 = TJ323). **UK**, isolated from *R. idaeus*, 1991, D. Kennedy (CBS 109892 = WPC P15596 = FVR 67 = SCRP324 = P823 = TJ015); isolated from *R. idaeus*, collection date unknown, B. Henricot (9A9 = P714 = CC947 = TJ1103).

Phytophthora uniformis (Brasier & S.A. Kirk) Abad, *Stud. Mycol.* 106: 310. 2023. MB 846427. Fig. 38.

Basionym: *Phytophthora alni* subsp. *uniformis* Brasier & S.A. Kirk, *Mycol. Res.* 108(10): 1175. 2004. MB 488624.

Synonym: '*Phytophthora uniformis*' (Brasier & S.A. Kirk) C. Husson et al., *Fungal Gen. Biol.* 77: 20. 2015. (nom. inval., Arts 41.5, F.5.1. Shenzhen). MB 631645.

Typus: **Sweden**, Gothenberg, isolated from *Alnus* bark, 1996, C. Olsson [**holotype** IMI 392315, dried culture on carrot agar, ex-type living culture CBS 149409 = NRRL 64373 = CPHST BL3 = WPC P16206 = P875; GenBank accession nos. GU259293 (ITS), MG493905 (*βtub*), MK020272 (*hsp90*), MH380053 (*rpl10*), OK267369 (*tef1-α*), MH136992 (*cox1*), JQ439158 (*rps10*)].

Morphological structures on V8A: *Sporangia* produced abundantly in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or rarely in lax sympodia of 2 sporangia; predominantly ovoid, broad-ovoid or elongated-ovoid (86.8 %; Fig. 38A–C, H, I), less frequently obpyriform to broad-obpyriform (5.6 %; Fig. 38E), ellipsoid to elongated-ellipsoid (3.2 %; Fig. 38D), limoniform to elongated-limoniform (2.8 %; Fig. 38J), ampulliform (1.2 %; Fig. 38F, G) or obturbinate (0.4 %); sporangial apices exclusively non-papillate, occasionally pointed or slightly curved (Fig. 38C); sporangial proliferation internal in both a nested (Fig. 38I) or an extended way (Fig. 38J), rarely external; sporangial dimensions averaging $58.2 \pm 7.0 \times 40.0 \pm 3.9 \mu\text{m}$ (overall range $36.8\text{--}78.3 \times 24.1\text{--}57.4 \mu\text{m}$; range of isolate means $54.1\text{--}62.1 \times 34.2\text{--}42.9 \mu\text{m}$) with a length/breadth ratio of 1.47 ± 0.19 (overall range 0.92–2.71); sporangial germination indirect with zoospores

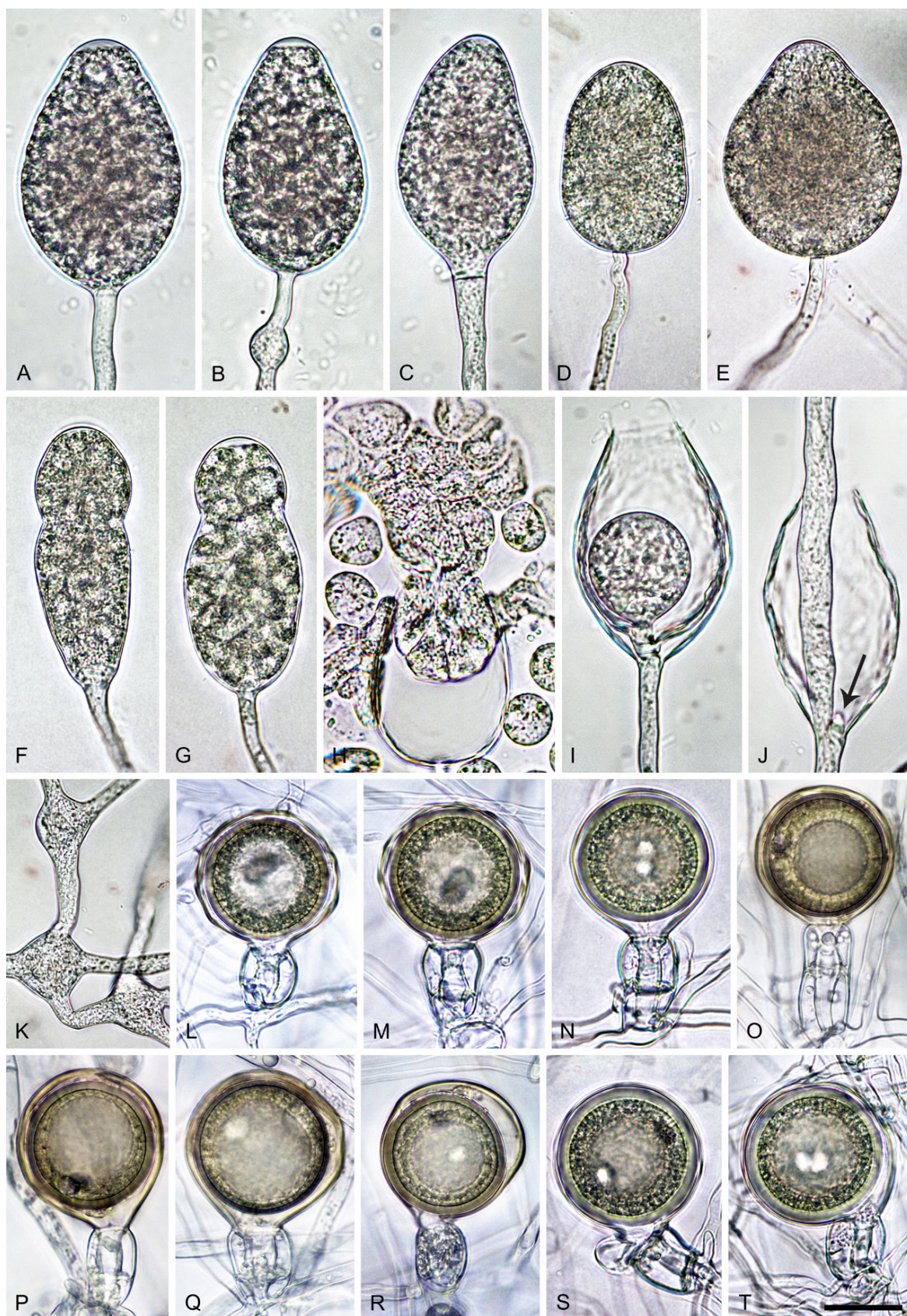


Fig. 38. *Phytophthora uniformis*. **A–K.** Structures formed on V8-agar (V8A) in soil extract. **A–J.** Persistent ovoid, limoniform, ellipsoid, obpyriform or ampulliform sporangia. **A–F.** Non-papillate apices. **B.** Limoniform hyphal swelling on sporangiophore. **G.** Sporangium with swollen apex before zoospore release. **H.** Zoospore release. **I.** Internal nested proliferation. **J.** Internal extended proliferation and protruding basal plug (arrow). **K.** Deltoid or triangular, catenulate hyphal swellings. **L–T.** Oogonia with short-tapering or round bases, apterotic (P–R) or plerotic (L–O, S, T) oospores, and amphigynous bicellular (M–Q, S) or unicellular (L, R, T) antheridia, sessile or on short stalks, formed in single culture in solid V8A. **L, M.** Wavy-edged to verrucose walls. **N–T.** Smooth walls. **L–P.** Subglobose to globose oogonia. **Q, R.** Excentric oogonia. **S, T.** Comma-shaped oogonia. Images: A, I. 250001; B, C, J. P887; D–H, K, O–R. TJ0139; L, M, T. TJ002; N, S. TJ004. Scale bar = 20 µm; applies to A–T.

discharged through an exit pore 10.3–23.9 μm wide (av. 15.5 $\pm$ 2.9 μm) (Fig. 38H). Zoospores limoniform to reniform whilst motile, becoming spherical (av. diam. 14.3 $\pm$ 2.3 μm) on encystment; cysts usually germinating directly forming a hypha or a microsporangium or infrequently indirectly by releasing a secondary zoospore (diplanetism). Hyphal swellings commonly formed in water; on sporangiophores subglobose to limoniform (Fig. 38B), on hyphae deltoid or triangular and often catenulate (Fig. 38K), av. diam. 16.7 $\pm$ 2.3 μm . Chlamydospores not observed. Oogonia produced by all isolates in single culture (self-fertile ‘homothallic’ breeding system); predominantly globose to subglobose (74.8 %; Fig. 38L–P), less frequently slightly excentric (20.5 %; Fig. 38Q, R), elongated (3.5 %) or comma-shaped (1.2 %; Fig. 38S, T); smooth-walled (87 %; 38N–T) or sometimes wavy-edged-verrucose (13 %; Fig. 38L, M), sometimes turning golden-brown during maturation (Fig. 38O, P), sessile or with short thin stalks, with short tapering (58.6 %; Fig. 38L–N, P–R) or with round non-tapering base (41.4 %; Fig. 38O, S, T); oogonial diam. 47.6 $\pm$ 3.5 μm (overall range 36.3–58.4 μm ; range of isolate means 46.6–48.6 μm); plerotic (57 %; Fig. 38L–O, S, T) or aplerotic (43 %; Fig. 38P–R). Oospores globose to subglobose with one large lipid globule (Fig. 38L–T); diam. 42.1 $\pm$ 3.1 μm (overall range 33.0–50.8 μm ; range of isolate means 41.1–42.7 μm); wall thickness 3.2 $\pm$ 0.6 μm (overall range 1.8–4.9 μm), oospore wall index 0.39 $\pm$ 0.06 (overall range 0.24–0.53); abortion rate of 13 % (1–30 %) after 4 wk. Antheridia exclusively amphigynous, cylindrical, rarely subglobose and bicellular, often with the basal cell being much smaller than the upper one (64.2 %; Fig. 38M–Q, S) or unicellular (35.8 %; Fig. 38L, R, T); dimensions 24.3 $\pm$ 4.3 $\times$ 17.7 $\pm$ 2.4 μm .

Culture characteristics: Colonies on V8A and CA uniform to faintly radiate with woolly mycelium, on PDA uniform with dense felty-cottony mycelium (Fig. 13).

Cardinal temperatures and growth rates: On V8A optimum 25 °C with 4.3 $\pm$ 0.36 mm/d radial growth, maximum 27.5 to < 30 °C, minimum < 10 °C (Fig. 18), lethal temperature 32.5 °C. At 20 °C on V8A, CA and PDA 3.9 $\pm$ 0.61 mm/d, 3.5 $\pm$ 0.45 mm/d and 1.6 $\pm$ 0.09 mm/d, respectively.

Materials examined: **Czechia**, Veverská Bítýška, Svratka River, isolated from *A. glutinosa* bark canker, 2020, T. Jung (TJ1358). **France**, isolated from *A. glutinosa* bark canker, 1999, J.C. Streito (PAU 60 = TJ017). **Germany**, Bavaria, Vilsbiburg, isolated from *Alnus glutinosa* bark canker, 1998, T. Jung (TJ002 = ALN58 = P705); Rott, isolated from *A. glutinosa* bark canker, 2001, T. Jung (ALN 222 = P706 = TJ004). **Hungary**, isolated from *A. glutinosa* bark canker, 1999, I. Szabó (WPC P10565 = PD PD_00098 = 155c = PAU 98 = TJ0139). **Norway**, isolated from *A. glutinosa* bark canker, 2012, G.M. Strømeng (250001 = P707 = TJ027). **Sweden**, Save River, isolated from *A. glutinosa* bark canker, 1997, C. Olsson (P887 = CH166 = TJ104).

Phytophthora xalni Brasier & S.A. Kirk, *Mycol. Res.* **108**(10): 1174. 2004. MB 631644. Fig. 39.

Typus: UK, Yorkshire, Doncaster isolated from *Alnus glutinosa* bark canker, 1994, G. MacAskill [holotype IMI 392314, MBT 160685, dried culture on CA; ex-type living culture IMI 403468 (old IMI 392314) = P772 = WPC P16203 = PD PD_02130 = CBS 148927 = CPHST BL 1 = 47A7; GenBank accession nos. KX251593 (LSU),

KU681013 (ITS), KU899238 (*βtub*), KU899395 (*hsp90*), PX582025 (*tigA*), PX581176 (*rpl10*), PX581350 (*tcf-1a*), PX581529 (*enl*), PX581851 (*cox1*), KU899480 (*nadh1*), JQ439156 (*rps10*)].

Morphological structures on V8A: Sporangia abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores; predominantly ovoid, broad-ovoid or elongated ovoid (90.3 %; Fig. 39A–D, G), infrequently obpyriform to elongated-obpyriform (3.7 %), limoniform to elongated limoniform (2.0 %; Fig. 39F), ellipsoid to elongated ellipsoid (2.0 %; Fig. 39E, H), obturbinate (1.7 %) or subglobose (0.3 %; Fig. 39I); apices non-papillate (Fig. 39A–E); sporangial proliferation internal in both a nested (Fig. 39H, I) or an extended way (Fig. 39J); sporangial dimensions averaging 53.6 $\pm$ 8.9 $\times$ 39.5 $\pm$ 5.4 (overall range 31.5–78.8 $\times$ 25.9–53.8 μm ; range of isolate means 50.3–59.1 $\times$ 36.7–43.9 μm) with a length/breadth ratio of 1.36 $\pm$ 0.16 (overall range 0.84–2.2); sporangial germination indirect with zoospores discharged through an exit pore 9.6–22.7 μm wide (av. 15.4 $\pm$ 2.8 μm) (Fig. 39G). Zoospores limoniform to reniform whilst motile, becoming spherical (av. diam. 14.3 $\pm$ 1.8 μm) on encystment; cysts germinating directly by forming a hypha or a microsporangium or indirectly by releasing a secondary zoospore (diplanetism); occasionally, sporangia fail to differentiate the cytoplasm into individual zoospores resulting in the release of large multinucleate and multiflagellate zoospores with uncoordinated movement. Hyphal swellings rarely formed in water, limoniform, subglobose or deltoid. Chlamydospores not observed. Oogonia produced in single culture (self-fertile ‘homothallic’ breeding system); globose to subglobose (75.5 %; Fig. 39K, L, N, Q, R), slightly bent to comma-shaped (14.6 %; Fig. 39M, O, P, S, T), rarely slightly elongated (4.3 %), slightly excentric (3.8 %) or flexuose (1.8 %); predominantly slightly to strongly ornamented (66.9 %; Fig. 39K, L, Q–T), less frequently smooth-walled or with a slightly wavy wall (33.1 %; Fig. 39M–P), sessile or with short sometimes curved stalks, often with tapering bases (45.3 %; Fig. 39L–P, R–T); sometimes oogonial wall turning golden-brown during maturation (Fig. 39Q, R); oogonial diam. 48.9 $\pm$ 7.1 μm (overall range 25.6–69.5 μm ; range of means 42.8–56.3 μm); plerotic or nearly plerotic (Fig. 39K–T). Oospores globose to subglobose, usually with one medium-sized to large lipid globule (Fig. 39K, M–S), infrequently with several small lipid globules (Fig. 39L); diam. 41.2 $\pm$ 6.0 μm (overall range 23.3–58.8 μm ; range of means 35.4–46.6 μm); wall thickness averaging 3.2 $\pm$ 0.7 μm (overall range 0.9–5.3 μm), oospore wall index 0.39 $\pm$ 0.07 (overall range 0.18–0.59); high abortion rate of 65.3 % (7–90 %; Fig. 39T) after 4 wk. Antheridia predominantly amphigynous, cylindrical, subglobose or irregular (87.6 %) and unicellular (34.9 % Fig. 39R–T) or bicellular with the basal cell being much smaller than the upper one (52.7 %; Fig. 39M–Q), less frequently paragynous (12.4 %; Fig. 39K, L); dimensions of amphigynous antheridia 22.0 $\pm$ 4.8 $\times$ 16.9 $\pm$ 2.5 μm .

Culture characteristics: Colonies on V8A uniform with increasing amounts of woolly-cottony aerial mycelium towards the margins; on CA uniform and woolly-cottony; on PDA uniform and dense felty-cottony (Fig. 13).

Cardinal temperatures and growth rates: On V8A optimum 20–25 °C with radial growth of 6.2 $\pm$ 1.35 mm/d at 20 °C and 6.3 $\pm$ 0.98 mm/d at 25 °C; maximum 27.5 to < 30 °C; minimum < 10 °C (Fig. 18), lethal temperature 30–32.5 °C. At 20 °C on CA and PDA 4.7 $\pm$ 1.22 mm/d and 2.9 $\pm$ 0.69 mm/d, respectively.



Fig. 39. *Phytophthora xalni*. **A–J.** Structures formed on V8-agar (V8A) in soil extract. **A–F, H–J.** Persistent ovoid, ellipsoid, limoniform or subglobose sporangia. **A–E.** Non-papillate apices. **F.** With slightly swollen apex before zoospore release. **G.** Ovoid sporangium releasing zoospores. **H, I.** Internal nested proliferation. **J.** Internal extended proliferation. **K–T.** Oogonia with round (K) or tapering (L–P, R–T) bases, and near plerotic or plerotic oospores, sessile or on short stalks, formed in single culture in solid V8A. **K, L, N, Q, R.** Subglobose to globose oogonia. **M, O, P, S, T.** Comma-shaped oogonia. **K, L, Q–T.** Slightly to strongly ornamented oogonial walls. **M–P.** Smooth to slightly wavy oogonial walls. **Q, R.** Golden-brown oogonial walls. **K, L.** Paragynous antheridia. **M–Q.** Bicellular (M–Q) or unicellular (R–T). **T.** Oogonium with aborted oospore. Images: A, C, K, L, Q, R. TJ001; B, E, J, O, P. TJ006; D, M, N. TJ143; F. TJ140; G. TJ1160; H, I, T. TJ023; S. TJ326. Scale bar = 20 µm; applies to A–T.



Fig. 40. *Phytophthora xmultiformis*. **A–I.** Structures formed on V8-agar (V8A) in soil extract. **A–F, H, I.** Persistent ovoid or limoniform sporangia. **A–E, I.** Non-papillate apices. **F.** Zoospore release. **G.** Large multinucleate zoospore (arrow) due to the failure of the cytoplasm to differentiate into individual zoospores. **H.** Internal nested proliferation. **I.** Internal extended proliferation. **J–R.** Oogonia with round (J, L, P, R) or tapering (K, M–O, Q) bases, sessile or on short stalks, formed in single culture in solid V8A. **K, O, P, R.** Subglobose to globose oogonia. **L, M, Q.** Comma-shaped oogonia. **N.** Excentric oogonium. **K–R.** Strongly ornamented oogonial walls. **J.** Smooth to slightly wavy oogonial wall. **N, P–R.** Golden-brown oogonial walls. **J.** Slightly aplerotic oogonium. **K–O.** Plerotic or near-plerotic oogonia. **J–O.** Oogonia with viable looking oospores. **P–R.** Oogonia aborted after (P) and before (Q, R) oospore formation. **J, K.** Paragynous antheridia. **L–R.** Amphigynous antheridia, bicellular (O–R) or unicellular (L, M). Images: A, E, G, I, J, M. PAM396; B, F, H. PHAPI 12; C, D. PH055; K, L, O. P889; N, P–R. TJ1460. Scale bar = 20 µm; applies to A–R.

Materials examined: **Belgium**, isolated from *Alnus incana* bark, 2002, *A. Chandelier* (2303 = TJ140). **Germany**, Dachau, isolated from *A. glutinosa* bark canker, 1999, *A. Schlenzig* (ALN45 = TJ001); Reischenhart, isolated from *A. glutinosa* bark canker, 2014, *T. Jung* (TJ023 = Reis2 = P691); Zolling, isolated from *A. glutinosa* bark canker, 2003, *C. Clemenz* (TJ006 = ALN402). **Hungary**, Héviz, isolated from *A. glutinosa* rhizosphere soil, 2001, *Z.Á. Nagy* (WPC P10568 = PD PD_00050 = Héviz 9 = PAA 93 = TJ326); Teskánd, isolated from *A. glutinosa* bark canker, 2002, *J. Bakonyi* (WPC P10569 = H-5/02 = TJ143). **Spain**, Galicia, Miño River, isolated from *A. glutinosa* bark canker, 2009, *T. Jung* (TJ1160 = MAL5 = P689).

Phytophthora *multiformis* (Brasier & S.A. Kirk) Abad, *Stud. Mycol.* **106**: 309. 2023. MB 846426. Fig. 40.

Basionym: *Phytophthora alni* subsp. *multiformis* Brasier & S.A. Kirk, *Mycol. Res.* **108**(10): 1177. 2004. MB 48863.

Synonym: '*Phytophthora* *multiformis*' (Brasier & S.A. Kirk) C. Husson *et al.*, *Fungal Gen. Biol.* **77**: 20. 2015. (nom. inval., Arts 41.5, F.5.1. Shenzhen). MB 631643.

Typus: **Netherlands**, isolated from *Alnus* sp. bark, 1994, *H. van Kesteren* [**holotype** IMI 392316, MBT 160683, dried culture on CA; ex-type living culture IMI 392316 = WPC P16202 = CPHST BL 2 = P770 = TJ1625; GenBank accession nos. PX607116 (LSU), AF139368 (ITS), KU899239 (*βtub*), KU899396 (*hsp90*), PX582104 (*tigA*), PX581254 (*rpl10*), PX581430 (*tef-1a*), PX581610 (*enl*), PX58192 (*cox1*), KU899481 (*nadh1*), JQ439157 (*rps10*)].

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores; predominantly ovoid, broad-ovoid or elongated ovoid (91.8 %; Fig. 40A–F, H, I), infrequently ellipsoid to elongated ellipsoid (3.2 %), limoniform to elongated limoniform (2.9 %; Fig. 40I), obpyriform to elongated-obpyriform (1.8 %) or subglobose (0.3 %); apices non-papillate (Fig. 40A–E, I); sporangial proliferation abundantly internal in both a nested and extended way (Fig. 40H, I); sporangial dimensions averaging $51.5 \pm 9.5 \times 36.5 \pm 5.6$ µm (overall range 28.3–80.3 × 22.1–49.2 µm; range of isolate means 35.8–60.4 × 29.2–41.6 µm) with a length/breadth ratio of 1.41 ± 0.17 (overall range 1.11–2.51); sporangial germination indirect with zoospores discharged through an exit pore 7.9–22.0 µm wide (av. 13.7 ± 2.9 µm) (Fig. 40F). *Zoospores* limoniform to reniform (Fig. 40F) whilst motile, becoming spherical (av. diam. = 14.4 ± 3.4 µm) on encystment; occasionally, sporangia fail to differentiate all or most of their cytoplasm into individual zoospores resulting in the release of large multinucleate and multiflagellate zoospores with uncoordinated movement (Fig. 40G). *Hyphal swellings* not observed. *Chlamydospores* not observed. *Oogonia* produced in single culture (self-fertile 'homothallic' breeding system); globose to subglobose (79.1 %; Fig. 40K, O, P, R), infrequently excentric (6.4 %; Fig. 40N) or slightly bent to comma-shaped (9.8 %; Fig. 40L, M, Q), rarely slightly elongated (2.9 %) or flexuose (1.8 %); predominantly strongly ornamented with ornamentations often forming irregular ridges rather than individual warts (78.1 %; Fig. 40K–R), less frequently smooth-walled or with a slightly wavy wall (21.9 %; Fig. 40J), sessile or with short stalks (Fig. 40J–R), with short or sometimes long tapering base (50.3 %; Fig. 40K, M–O, Q) or with non-tapering base (49.7 %; Fig. 40J, L, P, R); frequently oogonial wall turning golden-brown during maturation, in particular in aborted oogonia (Fig. 40N, P–R); oogonial size 48.0 ± 6.0 µm (overall range 27.2–66.5 µm; range of means 46.2–49.5 µm); plerotic or nearly plerotic (80.6 %; Fig. 40K–O) or slightly aplerotic (19.4 %; Fig. 40J).

Oospores globose to subglobose, with one medium-sized to large lipid globule (Fig. 40K, L, N, O) or with multiple small lipid globules (Fig. 40J, M); diam. 39.4 ± 4.6 µm (overall range 24.8–52.9 µm; range of means 37.3–41.5 µm); wall thickness 3.1 ± 0.6 µm (overall range 1.4–4.5 µm), oospore wall index 0.40 ± 0.06 (overall range 0.18–0.58); high abortion rate of 74.3 % (32–96 %; Fig. 40P–R) after 4 wk. *Antheridia* mostly amphigynous (83.1 %), cylindrical, subglobose or irregular and unicellular (48.1 %; Fig. 40L, M) or bicellular with the basal cell being much smaller than the upper one (35.0 %; Fig. 40N–R), less frequently paragynous (16.9 %; Fig. 40J, K); dimensions of amphigynous antheridia $20.4 \pm 4.5 \times 16.0 \pm 2.4$ µm.

Culture characteristics: Colonies on V8A uniform and woolly-cottony with a dome-shaped centre or uniform, appressed and dense-feltly with irregular margins; on CA uniform with irregular margins, appressed and dense-feltly, in some isolates with sparse aerial mycelium; on PDA uniform and dense woolly-cottony (Fig. 13).

Cardinal temperatures and growth rates: On V8A optimum 20–25 °C with radial growth of 5.3 ± 1.84 mm/d at 20 °C and 5.1 ± 1.47 mm/d at 25 °C; maximum 27.5 to < 30 °C; minimum < 10 °C (Fig. 18), lethal temperature 30 to < 32.5 °C. At 20 °C on CA and PDA 2.8 ± 0.76 mm/d and 3.1 ± 0.39 mm/d, respectively.

Materials examined: **Croatia**, isolated from *A. glutinosa* bark cankers, 2012, *Z. Tomić* (TJ008 = PHAKO 12 = P696; TJ009 = PHAPI 12 = P694). **France**, isolated from *A. glutinosa* bark canker, 2007, *T. Scordia* (PAM 396 = TJ022). **Germany**, Bavaria, Freising, isolated from *A. incana* bark canker, 1995, *T. Jung* (IMI 392321 = P889 = ALN 1 = TJ332). **Italy**, isolated from *A. glutinosa* bark canker, 2010, *B. Scanu* (PH055 = TJ239). **Portugal**, Lima River, isolated from *Alnus lusitanica* bark canker, 2020, *I. Gomes Marques* (TJ1460 = LI109).

Phytophthora *taxon* *alni*-like. Fig. 41.

Etymology: The informal name refers to the morphological similarity with *P. alni* and the hybrid origin of the taxon.

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores; mostly ovoid, broad-ovoid or elongated ovoid (72 %; Fig. 41A–C, F) or obpyriform to elongated-obpyriform (20 %; Fig. 41D, E), infrequently ellipsoid to elongated ellipsoid (8 %; Fig. 41H, I); apices non-papillate (Fig. 41A–E); occasionally with very narrow constrictions of the sporangiophores near the sporangial base (15 %; Fig. 41C, D, F) which nearly or completely occlude the hyphae functionally turning the hyphal section between the constrictions and the sporangial base into pedicels (27.3 ± 12.4 µm; range 11.1–44.9 µm) and potentially enabling spread of sporangia with running water and rain splash; abundant internal sporangial proliferation in both a nested and extended way (Fig. 41H, I); sporangial dimensions averaging $59.1 \pm 6.7 \times 40.9 \pm 3.0$ µm (overall range 42.4–68.9 × 34.3–46.2 µm) with a length/breadth ratio of 1.45 ± 0.13 (overall range 1.14–1.77); sporangial germination indirect with zoospores discharged through an exit pore 14.0–20.1 µm wide (av. 18.0 ± 1.8 µm) (Fig. 41F). *Zoospores* limoniform to reniform whilst motile, becoming spherical (av. diam. 14.7 ± 2.3 µm) on encystment; cysts germinating directly by forming a hypha or a microsporangium or indirectly by releasing a secondary zoospore (diplanetism; Fig. 41H); occasionally, sporangia fail to differentiate



Fig. 41. *Phytophthora* taxon *xalni*-like. **A–I.** Structures formed on V8-agar (V8A) in soil extract. **A–F, H, I.** Persistent ovoid, obpyriform or ellipsoid sporangia. **A–E.** Non-papillate apices. **C, D, F.** Constrictions of sporangiophores (arrows). **F.** Zoospore release. **G.** Large multinucleate and multiflagellate zoospore due to the failure of the cytoplasm to differentiate into individual zoospores. **H.** Internal nested proliferation and empty zoospore cyst (arrow) after release of a secondary zoospore (diplanetism). **I.** Internal extended proliferation. **J–R.** Structures formed in solid V8A. **J, K.** Catenulate, limoniform, ellipsoid and subglobose hyphal swellings. **L–Q.** Slightly to strongly ornamented oogonia with short or long tapering bases, sessile or on short stalks, formed in single culture. **L, M.** Subglobose oogonia. **N, O.** Comma-shaped oogonia. **P, Q.** Elongated aborted oogonia. **L–O.** Near plerotic to plerotic oospores. **L, M, Q.** Amphigynous bicellular antheridia. **N–P.** Amphigynous unicellular antheridia. **R.** Hyphal aggregation. Images: A–R. TJ005. Scale bar = 20 µm; applies to A–R.

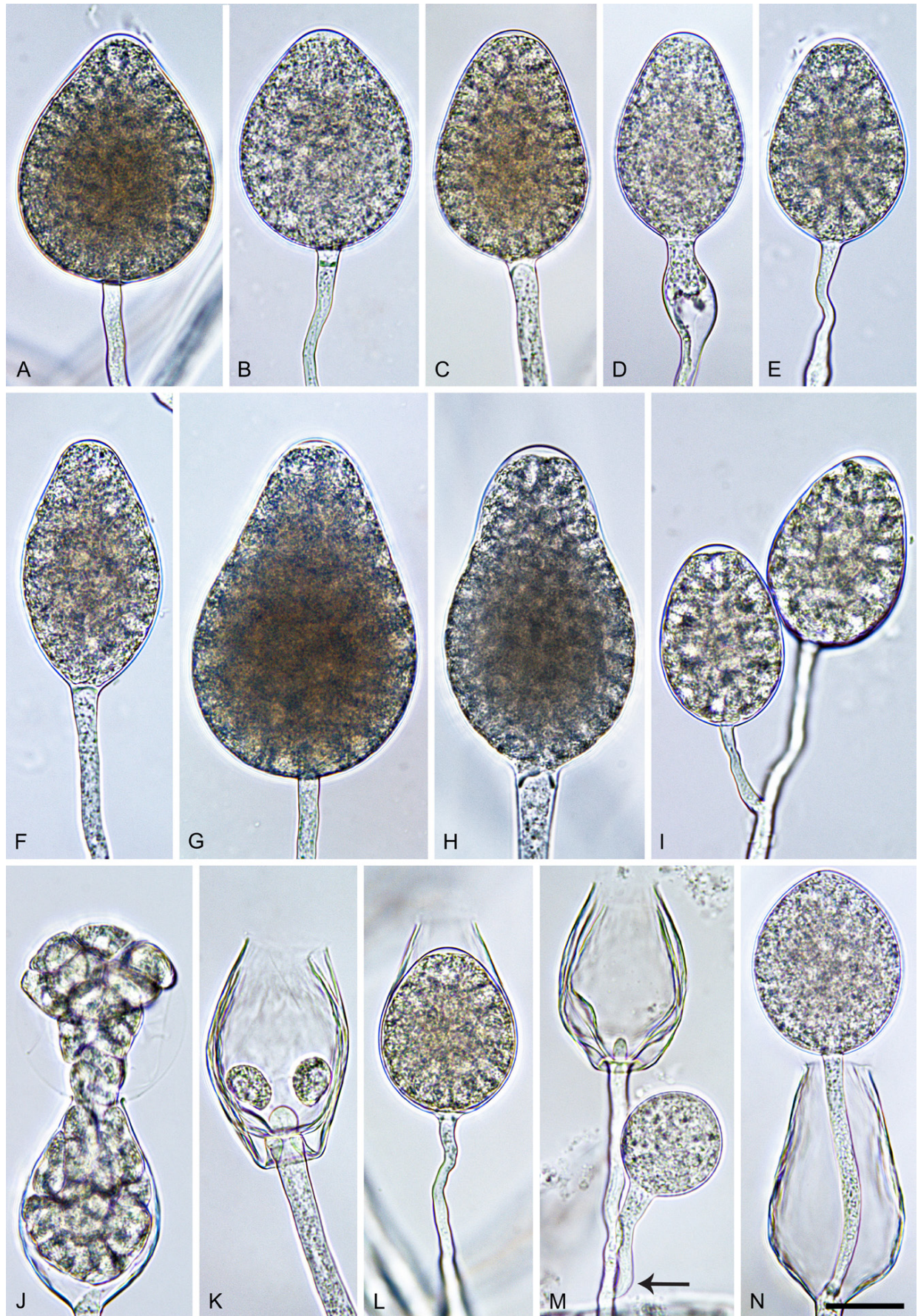


Fig. 42. *Phytophthora x cambivora* DAPC2 lineage. **A–N.** Persistent ovoid, obpyriform, limoniform or ellipsoid sporangia formed on V8-agar in soil extract. **A–F.** Non-papillate sporangial apices. **D.** Widening of sporangiophore towards the sporangial base. **G–I.** Sporangia with swollen apices before releasing zoospores. **I.** Syzygium of two sporangia. **J.** Zoospore release. **K, L.** Internal nested proliferation. **M.** Internal nested proliferation and external proliferation (arrow). **N.** Internal extended proliferation. Images: A, C, E. JP117; B, K, L, M. JP118; D, F, I, J. JP361; G, H, N. JP429. Scale bar = 20 μ m; applies to A–N.

the cytoplasm into individual zoospores resulting in the release of large multinucleate and multiflagellate zoospores with uncoordinated movement (Fig. 41G). *Hyphal swellings* commonly formed in water and in agar, limoniform, subglobose or ellipsoid, mostly catenulate (Fig. 41J, K). *Hyphal aggregations* commonly formed in agar (Fig. 41R). *Chlamydospores* not observed. *Oogonia* produced in single

culture (self-fertile 'homothallic' breeding system); globose to subglobose (61.6 %; Fig. 41L, M), comma-shaped (19.2 %; Fig. 41N, O), slightly elongated (11.5 %; Fig. 41P, Q) or slightly excentric (7.7 %); slightly to predominantly strongly ornamented (96.3 %; Fig. 41L–Q), rarely smooth-walled or with a slightly wavy wall (3.7 %); sessile or with short sometimes curved stalks (3.8 %), often with

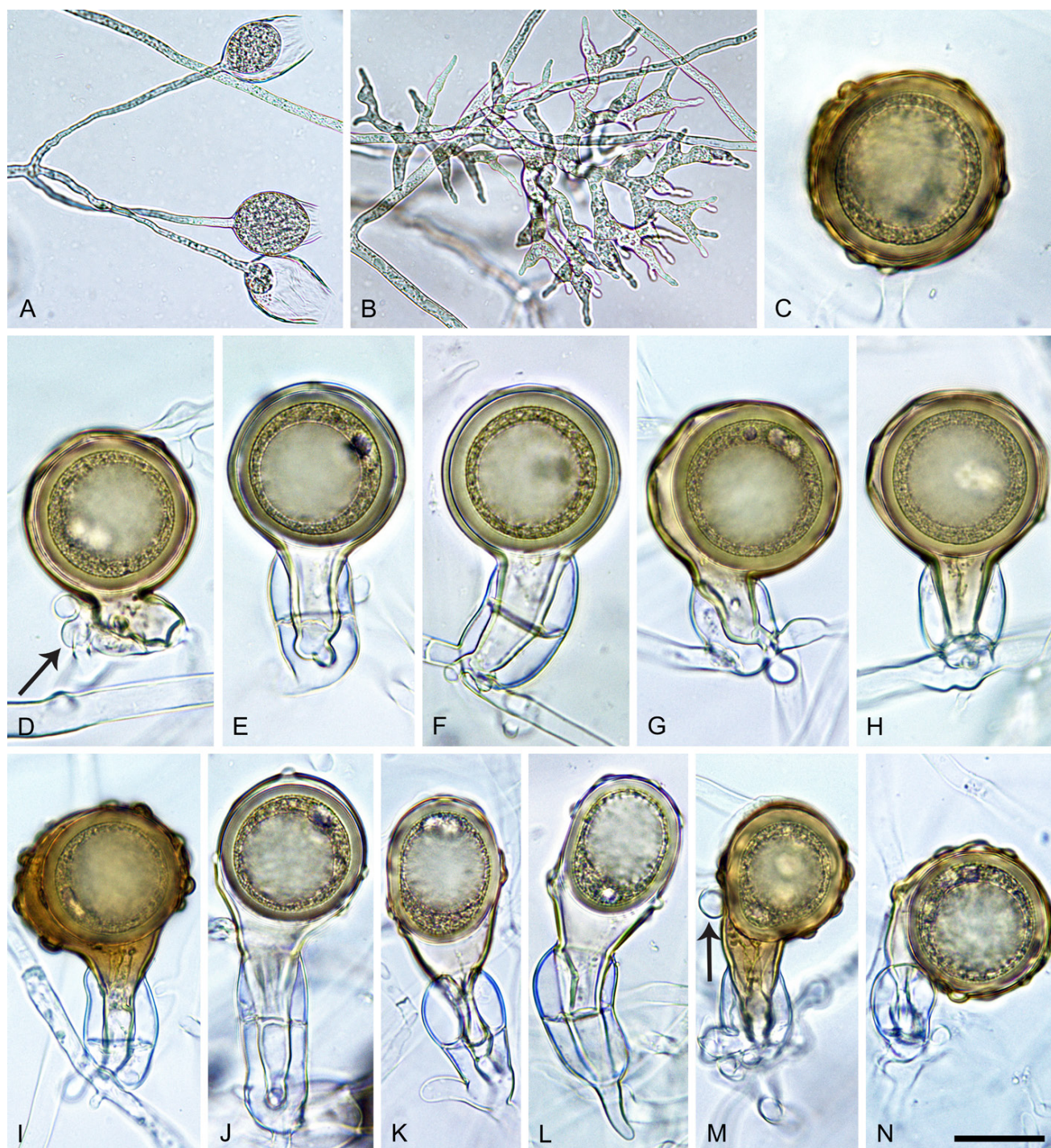


Fig. 43. *Phytophthora x cambivora* DAPC2 lineage. **A, B.** Structures formed on V8-agar in soil extract. **A.** Sympodium of three sporangia with internal nested proliferation, arising from the same point. **B.** Coralloid or stag-like, irregular lateral hyphae. **C–N.** Oogonia with mostly long-tapering funnel-like bases, near-plerotic to plerotic oospores and amphigynous unicellular (G, M) or bicellular (E, F, H–L, N) or paragynous (D) antheridia, formed in solid fgCA in mating tests. **C, E, F, H.** Globose to subglobose oogonia. **J–M.** Elongated oogonia. **G, I.** Excentric oogonia. **D, N.** Comma-shaped oogonia. **C, I–N.** Ornamented oogonial walls. **D–H.** Smooth or slightly wavy oogonial walls. **C–J.** Globose oospores. **K, L.** Ellipsoid oospores. **M.** Turbinate oospore. **M.** Additional paragynous antheridium (arrow). Images: A. JP361; B. JP927; C, I–N. JP182×JP123; D, E, G, H. JP361×JP123; F. JP361×JP429. Scale bar = 20 µm in C–N and 50 µm in A, B.

tapering bases (46.2 %; Fig. 41N–Q); oogonial diam. $44.9 \pm 6.7 \mu\text{m}$ (overall range 33.8–60.2 μm); nearly plerotic to plerotic (83.1 %; Fig. 41L–O), less frequently slightly apierotic (16.9 %). Oospores globose to subglobose, usually with one medium-sized lipid globule (Fig. 41L–O); diam. $35.4 \pm 5.4 \mu\text{m}$ (overall range 26.2–48.2 μm); wall thickness averaging $2.0 \pm 0.4 \mu\text{m}$ (overall range 1.1–2.8 μm), oospore wall index 0.30 ± 0.07 (overall range 0.17–0.45); high abortion rate of 94 % (Fig. 41P, Q) after 4 wk. *Antheridia* almost exclusively amphigynous (> 99 %), cylindrical, subglobose or irregular and unicellular (66.7 % Fig. 41N–P) or bicellular with the basal cell usually being much smaller than the upper one (33.3 %; Fig. 41L, M, Q); dimensions of amphigynous antheridia $24.5 \pm 7.1 \times 16.9 \pm 1.4 \mu\text{m}$.

Culture characteristics: Colonies on all three agar media uniform with limited aerial mycelium and submerged irregular margins due to uneven growth rates across the colonies (Fig. 13).

Cardinal temperatures and growth rates: On V8A optimum at 25 °C with 4.8 mm/d radial growth; maximum 27.5 to < 30 °C; minimum < 10 °C (Fig. 18), lethal temperature 30–32.5 °C. At 20 °C on V8A, CA and PDA 3.5 mm/d, 2.3 mm/d and 0.7 mm/d, respectively.

Material examined: **Germany**, Bavaria, Fischbachau, isolated from *A. incana* bark canker, 2001, *T. Jung* (TJ005 = ALN 268 = P692).

Phytophthora ×cambivora (Petri) Buisman, *pro sp.*, *Meded. Phytopathol. Lab. “Willie Commelin Scholten”* 11: 4, 7. 1927. MB 817284. Figs 42, 43.

Basionym: *Blepharospora cambivora* Petri, *Atti Reale Accad. Naz. Lincei, Rendiconti Cl. Sci. Fis.*, ser. 5, 26: 297. 1917. MB 146731.

Typus: **Italy**, Sicily, Mount Etna, isolated from rhizosphere soil of a declining mature *Quercus pubescens* tree, 2013, *T. Jung* [neotype CBS H-22558 designated in Jung *et al.* (2017a), MBT 371963, dried culture on V8A, ex-neotype living culture CBS 141218 = IT 5-3 = TJ197; GenBank accession nos. OK033630 (LSU), KU899179 (ITS), KU899255 (*βtub*), KU899412 (*hsp90*), PX582063 (*tigA*), OK091477 (*rpl10*), PX581388 (*tef1a*), PX581567 (*enl*), MZ736422 (*cox1*), KU899497 (*nadh1*), OK091585 (*rps10*)].

DAPC2 lineage

Morphological structures on V8A: *Sporangia* abundantly produced in non-sterile soil extract; borne terminally on unbranched long or short sporangiophores or in dense or lax sympodia of 2–3 sporangia (Fig. 42I, M; Fig. 43A); ovoid, broad-ovoid or elongated ovoid (78.4 %; Fig. 42A–E, I), obpyriform to elongated-obpyriform (10.1 %; Fig. 42G, H), limoniform to elongated limoniform (9.5 %; Fig. 42F), ellipsoid to elongated ellipsoid (2 %; Fig. 42I); apices non-papillate (Fig. 42A–F) becoming slightly swollen before release of already differentiated zoospores (Fig. 42G–I); sometimes sporangiophore widening towards sporangial base (Fig. 42D); sporangial proliferation abundantly internal in both a nested (Fig. 42K–M; Fig. 43A) and extended (Fig. 42N) way, or less frequently external (Fig. 42I, N; Fig. 43A), sometimes with 2 or 3 sporangiophores arising from the same point (Fig. 43A); sporangial dimensions averaging $68.5 \pm 11.1 \times 45.6 \pm 5.5 \mu\text{m}$ (overall range 48.3–100.1 $\times$ 29.4–60.4 μm ; range of isolate means 59.2–81.4 $\times$ 41.3–50.2 μm) with a length/breadth ratio of 1.5 ± 0.15 (overall range 1.25–2.21); sporangial germination indirect with zoospores discharged through an exit pore 9.2–25.6 μm wide (av. $15.7 \pm 3.2 \mu\text{m}$) (Fig. 42J). *Zoospores*

limoniform to reniform whilst motile, becoming spherical (av. diam. $13.2 \pm 1.5 \mu\text{m}$) on encystment. *Lateral hyphae* often coralloid or stag-like (Fig. 43B). *Chlamydospores* not observed. *Oogonia* not observed in single culture, but commonly produced in mating tests between A1 and A2 mating type isolates in solid fgCA (self-sterile ‘heterothallic’ breeding system; DAPC2 isolates JP117, JP118, JP182 and JP361 belonging to the A1 mating type, DAPC2 isolates JP123, JP429 and JP927 to the A2 mating type); globose to subglobose (35.6 %; Fig. 43C, E–F, H), elongated (34.2 %; Fig. 43J–M), excentric (12.2 %; Fig. 43G, I), comma-shaped (16.6 %; Fig. 43D, N) or rarely flexuose (1.4 %); ornamented (61.5 %; Fig. 43C, I–N) or with a smooth or slightly wavy wall (38.5 %; Fig. 43D–H), sessile or with short to medium-sized stalks (Fig. 43D–N), mostly with short or long tapering bases (86.6 %; Fig. 43E–N), less frequently with non-tapering base (13.4 %; Fig. 43D); often oogonial wall turning golden-brown during maturation (Fig. 43C, D, G–I, M); oogonial diam. $41.5 \pm 4.3 \mu\text{m}$ (overall range 23.7–51.3 μm ; range of means in different mating combinations 39.3–44.6 μm); mostly plerotic or nearly plerotic (95 %; Fig. 43C–F, H, J–N) or rarely apierotic (5 %; Fig. 43G, I). Oospores mostly globose to subglobose (Fig. 43C–J, N) or infrequently ellipsoid (Fig. 43 K, L) or turbinate (Fig. 43M), with one large lipid globule (Fig. 43C–N); diam. $35.4 \pm 3.6 \mu\text{m}$ (overall range 19.7–43.0 μm ; range of means in different mating combinations 33.9–37.7 μm); wall thickness averaging $2.2 \pm 0.5 \mu\text{m}$ (overall range 0.6–3.7 μm), oospore wall index 0.33 ± 0.07 (overall range 0.13–0.49); low abortion rate of 8.1 % (5–15 %) after 4 wk. *Antheridia* almost exclusively amphigynous (> 99 %), cylindrical, subglobose or irregular and predominantly bicellular (89.4 %; Fig. 43E, F, H–L, N) or unicellular (10.6 %; Fig. 43G, M), rarely paragynous (< 1 %; Fig. 43D); occasionally with an additional paragynous antheridium (Fig. 43M); dimensions of amphigynous antheridia $26.9 \pm 4.4 \times 18.1 \pm 1.7 \mu\text{m}$.

Culture characteristics: Colonies on V8A and CA uniform or faintly radiate, usually with dense or sometimes with sparse woolly-cottony mycelium; on PDA uniform with dense felty-cottony mycelium (Fig. 15).

Cardinal temperatures and growth rates: On V8A optimum at 25 °C with $6.3 \pm 0.59 \text{ mm/d}$ radial growth; maximum 32.5 to < 35 °C; minimum < 10 °C (Fig. 19), lethal temperature 35–36 °C. At 20 °C on V8A, CA and PDA $6.0 \pm 0.52 \text{ mm/d}$, $6.1 \pm 0.47 \text{ mm/d}$ and $3.6 \pm 0.35 \text{ mm/d}$, respectively.

Materials examined: **Japan**, Shikoku, Ichinomata, isolated from baiting leaves floating in streams running through warm-temperate laurosilva forests, May 2017, *T. Jung*, & *H. Masuya* (JP117, JP118), *T. Jung* & *K. Kageyama* (JP123, JP182, JP927); Kyushu, Aya, isolated from baiting leaves floating in a stream running through a warm-temperate laurosilva forest, *T. Jung* & *S. Uematsu* (JP361, JP429).

Notes on the taxonomy of Clade 7a taxa

Across the nuclear (LSU, ITS, *βtub*, *hsp90*, *tigA*, *rpl10*, *tef1a*, *enl*) 8205-character alignment and the mitochondrial (*cox1*, *nadh1*, *rps10*) 2 469-character alignment pairwise sequence differences between the 11 newly described and the 18 known *Phytophthora* Clade 7a species, the informally designated *P. taxon ×multiformis*-like and *P. taxon ×alni*-like were 0.1–2.7 % and 0–5.6 %, respectively. The 11 new Clade 7a species and the new informally designated *P. taxon ×alni*-like developed distinctive colony morphologies on V8A,



Table 3. Morphological characters and dimensions (µm), cardinal temperatures (°C) and temperature-growth relations (mm/d) on V8A of *Phytophthora* species in Clades 7a1–7a3. Most discriminating characters are highlighted in bold.

	<i>P. vulcanica</i>	<i>P. tyrrhenica</i>	<i>P. uliginosa</i>	<i>P. arta</i>	<i>P. flexuosa</i> (TW)	<i>P. flexuosa</i> (JP)	<i>P. europaea</i>
No. of isolates/source	5; Jung et al. (2017b) ^{1,2}	7; Jung et al. (2017b) ^{1,2}	3; Jung et al. (2017a) ^{1,3}	8 ¹	3; Jung et al. (2017a) ^{1,3}	6 ¹	7; Jung et al. (2017a) ^{1,2}
Sporangia	66 % ovoid , 32 % ellipsoid, (limoniform, obpyriform, pyriform)	56 % ellipsoid , 19 % ovoid, 18 % limoniform, 7 % obpyriform; mostly elongated	ellipsoid, ovoid, peanut-shaped, (obpyriform, limoniform)	54 % ovoid, 26 % ellipsoid, 13 % obpyriform, 4 % limoniform, (cigar-shaped, obovoid, pyriform, ampulliform)	80 % ovoid, 9 % ellipsoid, 7 % obpyriform, 4 % limoniform	47 % ovoid, 28 % obpyriform, 11 % ellipsoid, 13 % limoniform	Ovoid, obpyriform, ellipsoid, (subglobose), often pointed apex
lxb mean	57.3 ± 8.7 × 34.5 ± 4.2	68.4 ± 1.7 × 28.9 ± 1.9	67.0 ± 8.5 × 42.4 ± 6.4	67.2 ± 9.7 × 37.2 ± 4.4	56.1 ± 7.4 × 36.7 ± 5.2	66.9 ± 11.7 × 38.6 ± 5.6	63.7 ± 16.9 × 44.6 ± 8.3
range isolate means	53.6–61.0 × 31.8–36.4	66.1–70.0 × 27.5–31.9	65.7–70.3 × 30.9–44.4	55.3–77.3 × 32.5–39.3	53.3–58.6 × 33.9–39.4	57.6–76.7 × 35.3–40.4	50.0–78.9 × 36.7–51.2
total range	35.5–80.7 × 22.5–42.9	45.3–110.2 × 16.2–39.4	41.1–85.0 × 24.8–56.9	38.7–95.2 × 24.8–46.4	34.9–74.8 × 22.8–49.7	32.2–96.6 × 24.8–53.3	23.6–124.3 × 21.9–67.3
l/b ratio	1.67 ± 0.22	2.40 ± 0.18	1.60 ± 0.19	1.82 ± 0.26	1.54 ± 0.18	1.74 ± 0.24	1.42 ± 0.19
caducity	—	—	—	—	—	—	—
exitpores	17.0 ± 3.0	12.1 ± 2.4	15.4 ± 3.4	12.3 ± 2.3	19.7 ± 3.4	12.8 ± 2.1	19.3 ± 4.7
zoospore cysts	10.0 ± 1.2; diplanetism	14.6 ± 2.3; diplanetism	11.9 ± 1.8	12.0 ± 1.5; diplanetism	13.3 ± 1.3	11.9 ± 1.3; diplanetism	15.3 ± 2.0
sympodia	Lax (2–3 sporangia)	—	Rare; lax (2 sporangia)	Rare; lax (2–3 sporangia)	Rare; lax (2 sporangia) ⁴	Rare; lax (2 sporangia)	—
Breeding system	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile
Oogonia							
mean diam	35.8 ± 3.6	37.2 ± 3.3	46.2 ± 7.5	34.2 ± 3.7	36.8 ± 3.3	36.5 ± 3.2	37.3 ± 5.4
range isolate means	33.6–36.5	36.8–40.9	17.9–65.5	32.1–35.4	36.0–38.3	35.0–39.9	34.4–39.9
total range	23.0–46.0	25.0–39.3	41.6–53.3	18.1–48.3	25.7–42.8	25.9–54.3	19.2–48.4
thickwalled	—	—	—	Occurring	—	—	Occurring⁴
tapering base	37.3 % (8–60 %)	52.3 %	—	83.1 % (74–94 %)	47.9 % (32–58 %)	82.6 % (67–91 %)	60.0 % (52–81 %)
curved stalks	7.2 % (0–20 %)	29 % (26–32 %)	—	21.9 % (4–38 %)	51.5 % (20–58 %)	36.2 % (25–41 %)	—
elongated	44.8 % (8–80 %)	—	—	28.9 % (18–40 %)	19.7 % (4–36 %)	39 % (25–56 %)	21.3 % (12–34 %)
excentric	20.9 % (9–46 %)	6.7 %	—	36.7 % (14–78 %)	5.3 % (2–10 %)	41.6 % (29–65 %)	4.0 % (0–8 %)
comma-shaped	—	—	—	3 % (0–13 %)	<1 % (0–1 %)	3.8 % (0–9 %)	2.1 % (0–4 %)
ornamented	—	—	—	52.7 % (19–81 %)	65.6 % (52–81 %)	78 % (50–91 %)	—
flexuose	—	—	—	25.4 % (17–40 %)	25 % (20–28 %)	48.6 % (25–79 %)	—
Oospores	72.7 % apterotic	>99 % plerotic	70 % apterotic	83.2 % plerotic	>99 % plerotic	94.4 % plerotic	46.3 % plerotic
mean diam	30.5 ± 3.2	33.7 ± 1.3	41.3 ± 6.1	29.5 ± 3.4	32.2 ± 2.7	31.5 ± 2.2	33.2 ± 5.3
total range	19.7–38.2	24.6–39.9	12.5–55.0	14.7–37.5	22.7–37.7	20.8–36.4	16.3–45.1
wall thickness	2.4 ± 0.4	2.9 ± 1.5	4.2 ± 0.7	2.1 ± 0.5	3.1 ± 0.5	2.1 ± 0.41	2.5 ± 0.7
oospore wall index	0.40 ± 0.06	0.41 ± 0.03	0.49 ± 0.07	0.36 ± 0.06	0.47 ± 0.06	0.35 ± 0.05	0.38 ± 0.06
Abortion rate	52.8 % (0–80 %)	5 % (3–7 %)	6.2 % (3–10 %)	8.1 % (2–25 %)	1.7 % (1–2 %)	3.3 % (1–5 %)	24.9 % (18–31 %)

Table 3. (Continued).

	<i>P. vulcanica</i>	<i>P. tyrrhenica</i>	<i>P. uliginosa</i>	<i>P. arta</i>	<i>P. flexuosa</i> (TW)	<i>P. flexuosa</i> (JP)	<i>P. europaea</i>
Antheridia bicellular	95.3 % paragynous	100 % paragynous	100 % paragynous	98 % paragynous	100 % paragynous	100 % paragynous	100 % paragynous
size	16.3 ± 3.1 × 12.6 ± 2.3 In water; subglobose, irregular, catenulate	16.9 ± 4.6 × 12.8 ± 0.13 In water; subglobose, irregular, catenulate	16.9 ± 3.1 × 13.3 ± 2.5 In water; subglobose, irregular, catenulate	12.8 ± 2.6 × 9.5 ± 1.5	13.4 ± 2.1 × 10.0 ± 1.7	13.5 ± 2.1 × 10.4 ± 1.6	13.6 ± 2.6 × 10.8 ± 2.1
Hypal swellings					Coralloid		
Maximum temperature	27.5	25	25	30 to < 32.5	30 to < 32.5	30 to < 32.5	30 to < 32.5
Optimum temperature	15	20	20	27.5	25	20–25	20–25
Growth rate at 20 °C	1.3 ± 0.09	2.0 ± 0.09	1.4 ± 0.33	2.5 ± 0.64	4.1 ± 0.01	4.4 ± 0.82	4.8 ± 0.92
Growth rate at 25°C	0.6 ± 0.07	0.8 ± 0.04	0.4 ± 0.34	3.3 ± 0.88	4.6 ± 0.61	4.5 ± 0.94	5.0 ± 1.09

JP = Japan; TW = Taiwan; — = character not observed.
1 Numbers of isolates included in the temperature-growth tests: *P. vulcanica* - 2; *P. tyrrhenica* - 2; *P. uliginosa* - 2; *P. arta* - 6; *P. flexuosa* (TW) - 2; *P. flexuosa* (JP) - 6; *P. europaea* - 3.
2 Morphological and morphometric data from Jung et al. (2017b); cardinal temperatures and growth rates from this study.
3 Morphological and morphometric data from Jung et al. (2017a); cardinal temperatures and growth rates from this study.
4 Unpublished data from the study of Jung et al. (2017a).

CA and PDA at 20 °C that distinguish them from each other and from the 20 known Clade 7a species and informally designated taxa (Figs 8–15). In addition, they can be separated from each other and from known Clade 7a taxa by a combination of morphological (Figs 20–43) and temperature-growth rate characters (Figs 16–19) of which the most discriminating are highlighted in bold in Tables 3–8.

The known self-fertile species *P. vulcanica*, *P. tyrrhenica* and *P. uliginosa* from Europe (Jung et al. 2002, 2017b) are basal to Clade 7a. They are discriminated from all other Clade 7a species except *P. fragariae* and *P. rubi* by their slow growth in culture (Tables 3–8; Figs 16–19). *Phytophthora vulcanica* differs from *P. tyrrhenica* and *P. uliginosa* by its lower optimum temperature for growth (15 vs 20 °C), by producing predominantly elongated or excentric oogonia with both paragynous and amphigynous antheridia and oospores with high abortion rates (52.8 vs 5.0 and 6.2 %, respectively). *Phytophthora tyrrhenica* has sporangia with much higher l/b ratio (2.4) than *P. uliginosa* (1.6) and *P. vulcanica* (1.67) and almost exclusively plerotic oospores in contrast to the predominantly aplerotic oospores of the other two species (Table 3; Jung et al. 2002, 2017b). *Phytophthora uliginosa* differs from both *P. tyrrhenica* and *P. vulcanica* by having larger oogonia (46.2 vs 37.2 vs 35.8 µm), thicker oospore walls (4.2 vs 2.9 and 2.4 µm, respectively) and the highest oospore wall index (0.49 vs 0.41 and 0.4, respectively) (Table 3; Jung et al. 2002, 2017b).

Phytophthora intricata from Taiwan can be distinguished from all other Clade 7a species by its high frequency of intricate and intertwining oogonial and antheridial stalks (Jung et al. 2017a).

The single isolate of *P. attenuata* from Vietnam examined here concurred with the original description of the species from Taiwan (Jung et al. 2017a) with most morphometric data falling into the range of the species except for a lower proportion of oogonia with tapering bases (26 vs 46–96 %), a higher proportion of comma-shaped oogonia (18 vs 0–3 %), considerably thinner oospore walls (1.4 vs 2.9 µm) and lower oospore wall index (0.23 vs 0.41) (Table 5). In addition, the maximum temperature for growth was slightly lower in Vietnam than in Taiwan (25 to < 27.5 vs 27.5 to < 30 °C). *Phytophthora attenuata* and three new species from Vietnam, *P. algida*, *P. grandoogonia* and *P. sessilis*, form the ‘*P. attenuata* complex’. All four species have a self-fertile breeding system. Compared to the other three species, *P. attenuata* produces on average smaller sporangia which are more often ovoid (79–86 vs 35–61 %). *Phytophthora grandoogonia* differs from the other three species by forming on average considerably larger oogonia (47.8 vs 38.0–40.9 µm) which are almost exclusively smooth-walled, and sympodia with up to five sporangia. Furthermore, *P. grandoogonia* has on average higher proportions of elongated and excentric oogonia than *P. algida* and *P. sessilis* and the fastest growth above 15 °C (Table 5; Fig. 17). *Phytophthora algida* is discriminated from the other three species of the ‘*P. attenuata* complex’ by having the highest proportion of amphigynous antheridia (44.2 vs 13.2–31.9 %), the lowest optimum temperature for growth (15 vs 20 or 20–25 °C) and the slowest growth above 15 °C (Table 5; Fig. 17). In addition, oogonial walls in *P. algida* are more often ornamented (46 %) than in *P. grandoogonia* (1 %) and *P. sessilis* (8.8 %). *Phytophthora sessilis* is the only species in the ‘*P. attenuata* complex’ in which no hyphal swellings were observed (Table 5).

The morphology, cardinal temperatures and growth rates of Japanese isolates of *P. flexuosa* examined here were in accordance with the original description of the species from Taiwan (Jung et al. 2017a) except for having on average longer sporangia (66.9 vs 56.1 µm) with narrower exit pores (12.8 vs 19.7 µm), oogonia with higher proportions of tapering bases (82.6 vs 47.9 %), excentric (41.6 vs

5.3 %) or flexuose shapes (48.6 % vs 25 %) and thinner oospore walls (2.1 vs 3.1 μm) resulting in a lower oospore wall index (0.35 vs 0.47) (Table 3). *Phytophthora arta* can be distinguished from the closely related sister species *P. flexuosa* by the internal proliferation of sporangia occasionally occurring simultaneously with either two new nested sporangia or one new nested sporangium and one extended sporangiophore (Figs 20, 21). Moreover, *P. arta* has a higher optimum temperature for growth (27.5 vs 25 °C) and slower growth between 15 and 27.5 °C (Table 3; Fig. 16).

Four taxa from North America, i.e., *P. abietivora*, *P. taxon cadmea* and the new species *P. infundibuliformis* and *P. facultativa*, together with the newly described *P. laevigata* from the Balkans area in Europe, form a cluster within Clade 7a3. No morphological and physiological data are available for *P. taxon cadmea*. *Phytophthora fagacearum*, another North American species residing in Clade 7a4, shares general morphological characters with most species in Clade 7a3. *Phytophthora abietivora* and *P. fagacearum* differ from *P. facultativa*, *P. infundibuliformis* and *P. laevigata* by having on average much smaller sporangia (ca 30–33.5 $\times$ 25 μm vs ca 59–68 $\times$ 42 μm) with lower l/b ratios (1.2–1.34 vs 1.42–1.66) (Tables 4, 5; Li et al. 2019, Crous et al. 2024). However, Amemiya et al. (2011a) report for *P. abietivora* isolates from Japanese iris [see below ('Notes on properties of Clade 7a taxa')] considerably larger mean sporangial size (48 $\times$ 38 μm). In addition, *P. abietivora* has the narrowest exit pores (6–7.5 vs 12.6–14.2 μm), the thickest oospore walls (5.4 μm vs 1.8–2.7 μm) and the highest oospore wall index (0.64 vs 0.28–0.4). The original description of *P. abietivora* by Li et al. (2019) reported the production of chlamydospores but respective structures in their fig. 2 are not clearly recognisable as chlamydospores. A thorough examination of the *P. abietivora* ex-type isolate in the present study did not find chlamydospores. *Phytophthora fagacearum* differs from all Clade 7a3 species by producing, in addition to paragynous antheridia, also amphigynous antheridia (56 %) and having a much higher maximum temperature for growth (38 vs 27.5–32.5 °C) (Tables 3–5). *Phytophthora laevigata*, *P. infundibuliformis* and *P. facultativa* all show infrequently narrow constrictions of sporangiophores which may allow shedding of sporangia, as has been observed for *P. facultativa*, and potentially their aquatic or aerial spread (Figs 22–24). *Phytophthora laevigata* is discriminated from *P. infundibuliformis* and *P. facultativa* by forming sympodia with up to 3 sporangia, its lower proportion of oogonia with excentric shapes (3 vs 28–30.6 %) and the absence of ornamented or flexuose oogonia and hyphal swellings (Table 4). Further, *P. laevigata* has a higher optimum temperature for growth than *P. infundibuliformis* (25 vs 20 °C) (Fig. 16). *Phytophthora facultativa* differs from *P. infundibuliformis* by having a higher optimum temperature for growth (25 vs 20 °C) and producing sporangia which are on average shorter (58.7 vs 67.9 μm), more often obpyriform (29 vs 8 %) and never formed in sympodia. In addition, the oogonia of *P. facultativa* are on average smaller (35.2 vs 41.9 μm), more often ornamented (57 vs 31.3 %) or flexuose (66 vs 15.4 %) and contain oospores with thinner walls (1.8 vs 2.7 μm) and lower oospore wall index (0.31 vs 0.38) (Table 4; Fig. 16).

Japanese isolates of *P. formosa* examined here concurred with the original description of the species from Taiwan (Jung et al. 2017a) except for having on average considerably larger sporangia (66.7 $\times$ 44.4 vs 49.2 $\times$ 32.6 μm) which are infrequently formed in sympodia, and oospores with thinner walls (1.8 vs 3.0 μm) and lower oospore wall index (0.33 vs 0.43) (Table 4). The newly described *P. irregularis* differs from its sister species *P. formosa* by producing sporangia with occasionally two apices and narrower exitpores and oogonia which are more often excentric (30.2 vs ca 6 %) or

flexuose (15.8 vs 0–2.8 %) and less frequently ornamented (14 vs 24–32.2 %) (Tables 4, 5; Figs 29, 30).

To enable comparisons with newly described *Phytophthora* Clade 7a species, Jung et al. (2017a) included the known species *P. fragariae*, *P. rubi*, *P. uniformis*, *P. xalni*, *P. xambivora* and *P. xmultiformis* and the informally designated taxon *P. t. xmultiformis*-like in their phenotypic studies. For the same reason, these species and the informally designated taxon *P. t. xalni*-like were also included here in the temperature-growth studies and studies of colony morphologies, and their morphological structures are shown in Figs 36–43. The morphology, cardinal temperatures and growth rates of the two *P. fragariae* isolates from Germany examined by Jung et al. (2017a) were within the range presented by Ho & Jong (1988) for 21 global isolates of this species except for the slightly smaller size of the oogonia, thinner oospore walls and lower proportions of amphigynous antheridia (Table 6). Noteworthy, both studies reported high oospore abortion rates in culture. The original description of *P. rubi* did not include morphological or temperature-growth data (Man in 't Veld et al. 2007). However, extensive phenotypic studies of 18 isolates of *P. rubi*, under its previous name *P. fragariae* var. *rubi*, were performed by Wilcox et al. (1993) which can be compared with the recent studies of eight isolates by Jung et al. (2017a). Both studies showed largely congruent morphology. Exceptions were the wider range of sporangial sizes and the slight predominance of plerotic oospores and paragynous antheridia in the study of Jung et al. (2017a) (Table 6). Moreover, Jung et al. (2017a) reported high oospore abortion rates and the production of elongated, allantoid or irregular, catenulate hyphal swellings (Fig. 37), characters that were not assessed by Wilcox et al. (1993). In the present study, cardinal temperatures for growth and growth rates of *P. rubi* were similar to those presented by Wilcox et al. (1993) (Table 6).

For the three species from the '*P. xalni* complex', i.e., *P. uniformis*, *P. xmultiformis* and their interspecific hybrid *P. xalni*, the morphological characters presented by Jung et al. (2017a) were largely congruent with the original descriptions by Brasier et al. (2004) except for the occurrence of paragynous antheridia (12.4 %) in *P. xalni* (reported by both studies for *P. xmultiformis*) (Table 8; Fig. 39). For *P. xalni* and *P. xmultiformis*, the morphometric data from the original dataset of Jung et al. (2017a) were recalculated in the present study since isolate TJ005, previously designated as *P. xalni*, constitutes a new distinct taxon, *P. taxon xalni*-like, and isolate TJ008 has been transferred from *P. xalni* to *P. xmultiformis*. In addition, new morphometric data of *P. xmultiformis* isolate TJ1460 were included. For *P. xalni* those morphometric data that could be compared between Brasier et al. (2004) and Jung et al. (2017a), i.e., species ranges and ranges of isolate means, were in agreement. Unlike Brasier et al. (2004), Jung et al. (2017a) also presented morphometric data for sporangia of *P. uniformis* and *P. xmultiformis* as well as species means of all morphometric data for the three species. In addition, the occurrence of catenulate hyphal swellings was reported for the first time in *P. uniformis*. *Phytophthora t. xalni*-like differs from *P. xalni* by the occasional occurrence of sporangiophore constrictions (Fig. 41), potentially allowing aquatic and aerial spread of sporangia, by producing catenulate hyphal swellings and oogonia which are almost exclusively ornamented, have almost exclusively amphigynous antheridia and exhibit a much higher abortion rate (94 vs 65 %), and by slower growth between 10 and 27.5 °C (Tables 7, 8; Figs 18, 39, 41).

Phytophthora xheterohybrida from Taiwan and the new *P. xgrandisporangia* from Vietnam are closely related sister species which both originated from interspecific hybridisations. Both species have a functional largely self-sterile ('heterothallic') A1/A2

Table 4. Morphological characters and dimensions (µm), cardinal temperatures (°C) and temperature-growth relations (mm/d) on V8A of *Phytophthora* species in Clade 7a3 and 7a4. Most discriminating characters are highlighted in bold.

	<i>P. abietivora</i>	<i>P. facultativa</i>	<i>P. infundibuliformis</i>	<i>P. laevigata</i>	<i>P. intricata</i>	<i>P. formosa</i> (TW)	<i>P. formosa</i> (JP)
No. of isolates/source	1; Li <i>et al.</i> (2019) ^{1,2}	4 ¹	4 ¹	6 ¹	6; Jung <i>et al.</i> (2017a) ^{1,3}	6; Jung <i>et al.</i> (2017a) ^{1,3}	4 ¹
Sporangia	ovoid, ellipsoid	67 % ovoid, 29 % obpyriform , 4 % limoniform	79 % ovoid, 10 % limoniform, 8 % obpyriform, 3 % ellipsoid	76 % ovoid, 12 % obpyriform, 9 % limoniform, 3 % ellipsoid	66 % ovoid, 23 % obpyriform, 5 % limoniform, 4 % ellipsoid, (bi-/trilobed)	80 % ovoid, 8 % ellipsoid, 6 % obpyriform, 3 % limoniform, (subglobose)	55 % ovoid, 19 % limoniform, 16 % obpyriform, 8 % ellipsoid, (obovoid)
I×b mean	33.5 ± 3.7 × 25.1 ± 2.9	58.7 ± 8.0 × 41.4 ± 4.8	67.9 ± 7.6 × 41.6 ± 5.9	61.3 ± 6.0 × 42.4 ± 4.2	54.4 ± 8.0 × 34.2 ± 4.4	49.2 ± 8.1 × 32.6 ± 5.7	66.7 ± 12.7 × 44.4 ± 7.1
range isolate means	n.a.	53.7–64.5 × 38.9–46.4	67.1–68.8 × 39.2–44.7	59.3–64.6 × 40.5–44.4	51.0–58.9 × 32.1–37.5	43.7–59.6 × 29.3–40.4	62.8–73.7 × 41.4–50.6
total range	27.1–41.8 × 17.7–30.8	43.5–83.0 × 29.5–57.9	43.1–86.8 × 25.5–55.0	40.7–82.0 × 24.9–52.2	39.0–78.9 × 24.1–48.8	32.7–73.6 × 20.1–50.1	27.7–102.6 × 19.9–65.1
I/b ratio	1.34 ± 0.13	1.42 ± 0.14	1.66 ± 0.26	1.45 ± 0.14	1.60 ± 0.23	1.52 ± 0.17	1.51 ± 0.21
caducity	—	Constrictions; rare	Constrictions; infrequent	Constrictions; rare	—	—	—
exitpores	6–7.5	14.2 ± 1.9	13.6 ± 2.2	12.6 ± 2.4	15.4 ± 2.3	13.5 ± 2.7	16.1 ± 3.6
zoospore cysts	n.a.	14.2 ± 1.8	13.2 ± 1.1; diplanetism	12.4 ± 0.8	13.4 ± 1.9; diplanetism	14.3 ± 2.5; diplanetism	12.4 ± 1.8; diplanetism
sympodia	Rare; lax (2–3 sporangia)	—	Rare; lax (2 sporangia)	Rare; lax (2–3 sporangia)	Dense (2–3 sporangia)	—	Lax (2–3 sporangia)
Breeding system	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile
Oogonia							
mean diam	42.8 ± 4.7	35.2 ± 3.6	41.9 ± 4.1	36.0 ± 3.6	43.5 ± 5.1	38.5 ± 3.5	32.2 ± 3.4
range isolate means	n.a.	34.5–36.1	39.5–43.7	34.6–37.8	41.5–46.0	37.2–40.7	29.4–33.5
total range	30.6–50.5	24.1–47.8	28.1–51.7	21.6–47.1	26.3–56.7	27.1–50.0	20.2–41.9
tapering base	Infrequent	90 % (84–96 %)	92.6 % (88–96 %)	91 % (78–100 %)	28.3 % (12–50 %)	52.3 % (38–82 %)	71.5 % (62–90 %)
curved base/stalks	n.a.	44 % (26–52 %)	24.6 % (12–50 %)	46.6 % (28–56 %)	44.7 % (38–63 %) intricate	26.3 % (10–46 %) ⁺	30 % (16–48 %)
elongated	n.a.	70 % (60–80 %)	40.7 % (39–43 %)	66.8 % (50–80 %)	6.2 % (0–15 %)	1.7 % (0–6 %)	12.6 % (0–16 %)
excentric	n.a.	30.6 % (20–48 %)	28 % (10–38 %)	3 % (0–5 %)	9.4 % (4–23 %)	6.7 % (4–12 %)	5.8 % (4–8 %)
comma-shaped	n.a.	2.7 % (0–5 %)	6.6 % (2–12 %)	2.4 % (0–3 %)	—	2.7 % (0–10 %)	5.8 % (0–10 %)
ornamented	n.a.	57 % (32–80 %)	31.3 % (23–39 %)	—	1.6 % (0–2 %)	32 % (14–58 %)	24.2 % (0–74 %)
flexuose	n.a.	66 % (60–80 %)	15.4 % (5–26 %)	—	—	—	2.8 % (0–10 %)
Oospores	plerotic to slight aplerotic	85.2 % plerotic	87 % plerotic	92.4 % plerotic	100 % plerotic	>99 % plerotic	91 % plerotic
mean diam	37.5 ± 3.8	30.8 ± 3.0	36.2 ± 3.3	33.0 ± 3.3	39.9 ± 4.6	34.6 ± 3.2	28.4 ± 3.0
total range	26.5–42.5	18.3–37.0	25.0–43.3	19.3–40.4	25.1–50.3	22.4–42.5	16.5–35.7
wall thickness	5.4 ± 1.0	1.8 ± 0.4	2.7 ± 0.5	2.6 ± 0.5	3.6 ± 0.6	3.0 ± 0.5	1.8 ± 0.5
oospore wall index	0.64	0.31 ± 0.04	0.38 ± 0.05	0.4 ± 0.05	0.45 ± 0.05	0.43 ± 0.06	0.33 ± 0.07
Abortion rate	n.a.	3.5 % (1–6 %)	3.8 % (2–8 %)	2.5 % (1–4 %)	8.1 % (4–16 %)	12.7 % (7–16 %)	5.4 % (1–8 %)

Table 4. (Continued).

	<i>P. abietivora</i>	<i>P. facultativa</i>	<i>P. infundibuliformis</i>	<i>P. laevigata</i>	<i>P. intricata</i>	<i>P. formosa</i> (TW)	<i>P. formosa</i> (JP)
Antheridia	Mostly paragynous	100 % paragynous	100 % paragynous	100 % paragynous	100 % paragynous	96.7 % paragynous	91.5 % paragynous
bicellular	—	—	—	—	—	—	Rare
size	13.0 ± 2.5 × 10.7 ± 2.5	14.9 ± 3.6 × 11.0 ± 2.0	15.6 ± 2.8 × 11.3 ± 1.7	15.6 ± 2.9 × 11.4 ± 2.2	14.4 ± 2.5 × 11.4 ± 1.8	19.0 ± 3.3 × 15.3 ± 2.5	13.8 ± 2.7 × 10.8 ± 1.6
Hyphal swellings	In water; irregular, coralloid	In water; subglobose, ovoid, irregular; rare	In water near sporangium; ellipsoid, ovoid; rare	—	In water; subglobose, limoniform; rare	—	In water; subglobose, deltoid; rare
Maximum temperature	30	27.5–30	27.5 to < 30	27.5 to < 30	30 to < 32.5	30 to < 32.5	30 to < 32.5
Optimum temperature	25	25	20	25	27.5	25	25
Growth rate at 20 °C	4.8 ± 0.18	4.1 ± 0.69	5.5 ± 0.24	5.7 ± 0.31	4.9 ± 0.08	3.3 ± 0.01	3.5 ± 0.46
Growth rate at 25°C	5.4 ± 0.11	4.6 ± 0.8	4.8 ± 0.12	6.8 ± 0.29	6.5 ± 0.15	4.0 ± 0.4	4.2 ± 0.96

— = character not observed.

¹Numbers of isolates included in the temperature-growth tests: *P. abietivora* - 1; *P. facultativa* - 4; *P. infundibuliformis* - 4; *P. laevigata* - 6; *P. intricata* - 2; *P. formosa* (TW) - 4; *P. formosa* (JP) - 4.

²Morphological and morphometric data from Li et al. (2019); cardinal temperatures and growth rates from this study.

³Morphological and morphometric data from Jung et al. (2017a); cardinal temperatures and growth rates from this study.

⁴Unpublished data from the study of Jung et al. (2017a).

Table 5. Morphological characters and dimensions (µm), cardinal temperatures (°C) and temperature-growth relations (mm/d) on V8A of *Phytophthora* species in Clade 7a4. Most discriminating characters are highlighted in bold.

	<i>P. irregularis</i>	<i>P. attenuata</i> (TW)	<i>P. attenuata</i> (VN)	<i>P. aligida</i>	<i>P. grandioogonia</i>	<i>P. sessilis</i>	<i>P. fagacearum</i>
No. of isolates/source	7 ¹	6; Jung et al. (2017a) ^{1,2}	1 ¹	4 ¹	5 ¹	5 ¹	1; Crous et al. (2024)
Sporangia	71 % ovoid, 20 % obpyriform, 4 % limoniform, 3 % distort. & 2 apices (ellips.)	79 % ovoid, 17 % obpyriform, 3 % limoniform (ellipsoid, subglobose)	86 % ovoid , 13 % obpyriform (limoniform)	35 % ovoid, 52 % obpyriform, 13 % limoniform	45 % ovoid, 52 % obpyriform, 2 % ellipsoid, 1 % limoniform	61 % ovoid, 24 % obpyriform, 12 % limoniform (ellipsoid, ampulliform)	76 % ovoid, 24 % globose
lxb mean	55.1 ± 6.5 × 37.2 ± 4.9	44.7 ± 11.7 × 29.4 ± 5.3	53.5 ± 5.1 × 37.4 ± 3.0	64.2 ± 11.1 × 41.2 ± 6.3	60.3 ± 9.0 × 38.3 ± 5.5	62.4 ± 6.3 × 41.2 ± 4.1	30.2 ± 3.5 × 25.2 ± 2.4
range isolate means	51.1–59.7 × 33.4–43.0	34.5–60.3 × 24.7–35.4	n.a.	47.1–70.4 × 33.1–45.6	52.8–69.8 × 33.1–44.0	56.4–66.0 × 37.6–43.7	n.a.
total range	39.2–83.6 × 27.0–56.2	17.8–78.5 × 13.5–45.9	44.4–69.1 × 31.8–44.3	34.0–93.4 × 25.4–58.1	39.4–83.4 × 26.4–49.9	47.3–78.8 × 26.9–52.4	25.5–39.6 × 21.9–30.7
l/b ratio	1.49 ± 0.13	1.50 ± 0.2	1.43 ± 0.07	1.56 ± 0.16	1.59 ± 0.18	1.52 ± 0.12	1.2 ± 0.08
caducity	—	—	—	—	—	—	—
exitpores	10.9 ± 1.9	13.9 ± 2.7	13.2 ± 1.7	14.2 ± 2.7	11.1 ± 2.0	13.9 ± 2.4	n.a.
zoospore cysts	11.7 ± 1.0; diplanetism	12.7 ± 2.6; diplanetism	11.9 ± 0.9; diplanetism	12.4 ± 1.1; diplanetism	11.5 ± 1.4	12.6 ± 0.8; diplanetism	n.a.
sympodia	Dense (2–3 sporangia)	Rare; lax (2 sporangia)	—	Rare; dense (2 sporangia)	Rare; lax (2–5 sporangia)	Rare; lax (2 sporangia)	—
Breeding system	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile



Table 5. (Continued)

	<i>P. irregularis</i>	<i>P. attenuata</i> (TW)	<i>P. attenuata</i> (VN)	<i>P. alvida</i>	<i>P. grandooogonia</i>	<i>P. sessilis</i>	<i>P. fageacearum</i>
Oogonia							
mean diam	32.8 ± 3.5	40.9 ± 4.8	39.9 ± 3.6	38.0 ± 2.6	47.8 ± 3.9	39.8 ± 4.5	33.3 ± 4.8
range isolate means	31.9–34.4	36.8–45.2	n.a.	37.7–38.2	45.7–49.3	36.4–42.1	n.a.
total range	15.9–42.7	28.6–55.6	31.1–46.4	20.9–44.4	29.6–56.6	21.3–52.8	24.7–41.6
tapering base	81.8 % (56–98 %)	77 % (46–96 %)	26 %	52.6 % (26–64 %)	83.8 % (68–96 %)	62.4 % (56–74 %)	Occurring
curved base or stalk	42.8 % (16–72 %)	< 1 %	28 %	50.5 % (47–57 %)	28.7 % (20–48 %)	48.4 % (36–60 %)	—
elongated	17.7 % (9–32 %)	38 % (22–54 %)	24 %	10.6 % (6–20 %)	20 % (15–23 %)	10 % (2–18 %)	Occurring
excentric	30.2 % (16–70 %)	15 % (2–40 %)	18 %	2.5 % (2–3 %)	18.3 % (13–26 %)	6.5 % (2–12 %)	Occurring
comma-shaped	13.8 % (4–19 %)	2.3 % (0–3 %)	18 %	2 % (0–6 %)	0.6 % (0–2 %)	3.2 % (0–10 %)	—
ornamented	14 % (6–37 %)	18.3 % (1–43 %)	42 %	46 % (32–60 %)	1 % (0–6 %)	8.8 % (0–12 %)	Occurring
flexuose	15.8 % (8–33 %)	5.7 % (0–22 %)	24 %	1.6 % (0–6 %)	1 % (0–4 %)	14 % (2–30 %)	Occurring
Oospores	87.5 % plerotic	100 % plerotic	98 % plerotic	96.5 % plerotic	90 % plerotic	92.6 % plerotic	56 % aplerotic
mean diam	28.2 ± 2.9	36.5 ± 3.5	34.3 ± 2.8	31.8 ± 2.2	42.0 ± 3.5	33.9 ± 3.7	22.7 ± 4.2
total range	13.2–36.2	25.9–44.9	28.2–39.5	17.9–37.4	25.0–51.1	18.9–45.1	16.1–29.1
wall thickness	1.9 ± 0.4	2.9 ± 0.5	1.4 ± 0.3	1.6 ± 0.4	2.3 ± 0.7	1.7 ± 0.5	2.0 ± 0.4
oospore wall index	0.35 ± 0.06	0.41 ± 0.05	0.23 ± 0.04	0.28 ± 0.05	0.29 ± 0.08	0.28 ± 0.06	0.28
Abortion rate	8.7 % (1–25 %)	11 % (2–18 %)	15 %	11.8 % (3–25 %)	14.1 % (2–43 %)	11.5 % (5–25 %)	n.a.
Antheridia	96.1 % paragynous	68.1 % paragynous	76.2 % paragynous	44.2 % amphigynous	76.9 % paragynous	86.8 % paragynous	56 % amphigynous
bicellular	Rare	33.7 %	20 %	4 %	13.1 %	7.2 %	—
size	12.8 ± 2.4 × 9.9 ± 1.5	19.0 ± 3.3 × 15.3 ± 2.5	18.5 ± 2.4 × 13.3 ± 7.0	18.0 ± 3.8 × 13.9 ± 2.0	15.7 ± 2.2 × 13.8 ± 1.9	17.5 ± 3.1 × 14.1 ± 2.4	11.9 ± 2.2 diameter
Hyphal swellings	—	In water; limoniform	In water; subglobose, deltoid, limoniform, catenulate	In water; sub-globose, near sporangium base	In water; sub-globose, limoniform, irregular	—	In water; sub-globose limoniform, catenulate
Maximum temperature	30 to < 32.5	27.5 to < 30	25 to < 27.5	25 tot < 27.5	27.5 to < 30	27.5	38
Optimum temperature	25	20	20	15	20–25	20	25
Growth rate at 20 °C	3.1 ± 0.22	3.4 ± 0.27	2.7	2.4 ± 0.19	3.2 ± 0.28	2.8 ± 0.18	n.a.
Growth rate at 25°C	3.6 ± 0.21	3.0 ± 0.53	2.4	2.1 ± 0.15	3.2 ± 0.41	2.5 ± 0.65	3.7

JP = Japan; TW = Taiwan; VN = Vietnam; — = character not observed.

¹ Numbers of isolates included in the temperature-growth tests: *P. irregularis* - 7; *P. attenuata* (TW) - 2; *P. attenuata* (VN) - 1; *P. alvida* - 4; *P. grandooogonia* - 6; *P. sessilis* - 5.

² Morphological and morphometric data from Jung et al. (2017a); cardinal temperatures and growth rates from this study.



Table 6. Morphological characters and dimensions (µm), cardinal temperatures (°C) and temperature-growth relations (mm/d) on V8A of *Phytophthora* species in Clade 7a4. Most discriminating characters are highlighted in bold.

	<i>P. fragariae</i>	<i>P. fragariae</i>	<i>P. rubi</i>	<i>P. rubi</i>	<i>P. xgrandisporangia</i>	<i>P. xheterohybrida</i>
No. of isolates/source	21; Ho & Jong (1988)	2; Jung et al. (2017a) ^{1,2}	9; Wilcox et al. (1993)	7; Jung et al. (2017a) ^{1,2}	6 ¹	21; Jung et al. (2017a) ^{1,2}
Sporangia	Ovoid, obpyriform, elongate	67 % ovoid, 18 % limoniform, 10 % obpyriform, 5 % ellipsoid	Ovoid to obpyriform	57 % ovoid, 17 % ellipsoid, 13 % limoniform, 11 % obpyriform	33 % limoniform, 26 % ellipsoid, 24 % ovoid, 8 % obpyriform, 6 % ampulliform	63 % ovoid, 18 % limoniform, 13 % obpyriform, 4 % ellipsoid, (bi-trilobed)
l × b mean	59.2 × 33.8	65.9 ± 8.0 × 41.4 ± 4.0	59 × 40	50.2 ± 12.7 × 29.3 ± 8.1	84.5 ± 17.1 × 40.1 ± 5.2	75.3 ± 13.2 × 45.7 ± 7.6
range isolate means	43–87 × 22–56	62.3–69.5 × 39.7–43.1	n.a.	35.6–61.9 × 18.1–37.3	69.8–98.9 × 38.2–42.6	64.0–82.8 × 38.9–50.1
total range	32–90 × 22–52 ³	45.6–81.4 × 31.7–50.3	53–68 × 34–44	25.1–83 × 11.9–46.8	41.8–130.4 × 24.0–53.1	29.7–123.8 × 21.4–77.3
l/b ratio	1.8 ± 0.2	1.6 ± 0.25	1.48	1.75 ± 0.26	2.13 ± 0.48	1.66 ± 0.23
caducity	—	—	—	—	< 1 %; all isolates	< 1 %; all isolates
exitpores	n.a.	16.1 ± 2.3	n.a.	16.1 ± 4.6	13.9 ± 2.0	16.0 ± 2.6
zoospore cysts	n.a.	12.5 ± 1.8	13.0	13.3 ± 1.9	12.7 ± 1.6; diplanetism	13.4 ± 1.4; diplanetism
sympodia	Common	—	Occurring	Dense (2–3 sporangia)	Lax/dense (2–3 sporangia)	Lax (2–3 sporangia)
Breeding system	Self-fertile	Self-fertile	Self-fertile	Self-fertile	A1/A2	A1/A2
Oogonia						
mean diam	39	33.5 ± 4.2	38.2 ± 1.32	36.5 ± 5.1	45.3 ± 4.8	44.1 ± 6.7
range isolate means	34–45	31.4–35.6	36.2–40.1	33.0–39.1	43.8–47.0	37.7–50.4
total range	28–44 ³	25–44.8	30–45	23.0–47.1	28.2–67.4	25.2–61.2
thickwalled	n.a.	—	—	—	Occurring	28.7 % (8–42 %)
tapering base	Common	69 % (66–73 %)	Common	13.9 % (4–33 %)	98.7 % (95–100 %)	89.1 % (72–100 %)
curved bases/stalks	n.a.	—	—	—	16.7 % (10–21 %)	5 % (0–22 %)
elongated	Occurring	43 % (34–52 %)	n.a.	9.5 % (2–25 %)	80.7 % (63–95 %)	73.2 % (44–98 %)
excentric	n.a.	3 % (2–4 %)	n.a.	8.6 % (0–18 %)	17.3 % (15–21 %)	3.2 % (0–8 %)
comma-shaped	n.a.	3 %	n.a.	—	12 % (3–17 %)	13.3 % (6–28 %)
ornamented	—	—	—	—	100 %	97.9 % (94–100 %)
flexuose	—	—	—	—	20.3 % (8–40 %)	1.2 % (0–4 %)
Oospores	Aplerotic	86 % plerotic	Aplerotic	64.3 % plerotic	98 % plerotic	97.2 % plerotic
mean diam	32.0	28.2 ± 3.2	33.9 ± 1.68	31.9 ± 4.5	36.8 ± 3.7	36.8 ± 5.4
total range	n.a. (29–38 ⁴)	21.4–36.0	28–37	29.1–35.6	21.3–47.1	19.5–50.8
wall thickness	4.6 °	2.1 ± 0.7	2.2 ± 0.41	2.0 ± 0.6	2.3 ± 0.9	3.1 ± 0.6
oospore wall index	n.a.	0.38 ± 0.08	0.31	0.33 ± 0.08	0.32 ± 0.09	0.43 ± 0.07
Abortion rate	High	66 % (60–72 %)	n.a.	65.8 % (45–82 %)	64.7 % (57–74 %)	17.3 % (4–33 %)

Table 6. (Continued)

	<i>P. fragariae</i>	<i>P. fragariae</i>	<i>P. rubi</i>	<i>P. rubi</i>	<i>P. rubi</i>	<i>P. xgrandisporangia</i>	<i>P. xheterohybrida</i>
Antheridia bicellular	Mostly amphigynous	30 % amphigynous	70 % amphigynous	70 % amphigynous	44.2 % amphigynous	98.7 % amphigynous	100 % amphigynous
size	—	—	n.a.	n.a.	4 %	84.7 %	49.6 %
Hypal swellings	16.9 × 14.7	16.6 ± 6.3 × 12.7 ± 2.5	n.a.	n.a.	18.0 ± 3.8 × 13.9 ± 2.0	23.3 ± 5.1 × 17.4 ± 2.3	23.2 ± 4.3 × 18.0 ± 2.1
	In water; subglobose, irregular, catenulate	In water; subglobose, irregular, catenulate	n.a.	n.a.	In water; elongated, irregular, catenulate	Coralloid, catenulate	Coralloid, catenulate
Maximum temperature	25 to < 28	25 to < 27.5	25–28	25–28	25 to < 27.5	30 to < 32.5	30 to < 32.5
Optimum temperature	20	20	20	20	20	27.5	27.5
Growth rate at 20 °C	1.11–1.32 ⁵	1.9 ± 0.62	1.38–3.38	1.38–3.38	1.5 ± 0.43	4.9 ± 0.31	5.2 ± 0.92
Growth rate at 25°C	0.3–0.44 ⁵	1.4 ± 0.54	0–1.29	0–1.29	0.8 ± 0.29	6.0 ± 0.48	6.5 ± 0.86

— = character not observed.
¹ Numbers of isolates included in the temperature-growth tests: *P. fragariae* - 2; *P. rubi* - 4; *P. xgrandisporangia* - 6; *P. xheterohybrida* - 2.
² Morphological and morphometric data from Jung et al. (2017a); cardinal temperatures and growth rates from this study.
³ Ho & Jong sourced these data from Ribeiro (1978).
⁴ Range of isolate means (Erwin & Ribeiro 1996).
⁵ From Wilcox et al. (1993).

Table 7. Morphological characters and dimensions (µm), cardinal temperatures (°C) and temperature-growth relations (mm/d) on V8A of *Phytophthora* hybrid taxa in Clade 7a4. Most discriminating characters are highlighted in bold.

	<i>P. xincrassata</i>	<i>P. xleptopleura</i>	<i>P. xnodosa</i>	<i>P. xcombivora</i>	<i>P. xcombivora</i>	<i>P. t. xalni-like</i>
No. of isolates/source	7; Jung et al. (2017a) ^{1,2}	7 ¹	4 ¹	19; Jung et al. (2017a) ^{1,2}	7 ¹	1 ¹
Sporangia	85 % ovoid, 6 % ellipsoid, 6 % limoniform, 2 % pyriform, (obovoid)	37 % ovoid, 32 % limoniform, 11 % obpyriform, 11 % ellipsoid, 2 % pyriform, (ampulliform, 2 apices)	32 % limoniform, 31 % ovoid, 29 % obpyriform, 6 % ellipsoid, 2 % pyriform	74 % ovoid, 12 % obpyriform, 8 % ellipsoid, 6 % limoniform, (pyriform, cigar- or peanut-like)	78 % ovoid, 10 % obpyriform, 10 % limoniform, 2 % ellipsoid	72 % ovoid, 20 % obpyriform, 8 % ellipsoid
lxb mean	61.2 ± 8.5 × 43.7 ± 5.6	71.6 ± 9.9 × 39.2 ± 5.5	74.1 ± 9.2 × 43.5 ± 4.9	69.0 ± 11.9 × 43.5 ± 6.3	68.5 ± 11.1 × 45.6 ± 5.5	59.1 ± 6.7 × 40.9 ± 3.0
range isolate means	56.6–66.5 × 40.0–47.3	69.1–77.8 × 37.4–44.2	69.7–81.9 × 41.1–46.3	61.9–82.1 × 37.8–48.6	59.2–81.4 × 41.3–50.2	n.a.
total range	36.9–88.2 × 28.5–56.6	52.0–105.2 × 23.4–51.9	56.0–106.1 × 29.4–53.8	35.1–118.2 × 24.0–62.9	48.3–100.1 × 29.4–60.4	42.4–68.9 × 34.3–46.2
l/b ratio	1.40 ± 0.13	1.85 ± 0.24	1.72 ± 0.24	1.59 ± 0.18	1.50 ± 0.15	1.45 ± 0.13
caducity	—	—	—	—	—	Constrictions & pedicels (15 %; length 27.3 ± 12.4)
exitpores	15.0 ± 2.7	12.6 ± 2.6	12.1 ± 1.9	17.5 ± 3.4	15.7 ± 3.2	18.0 ± 1.8
zoospore cysts	14.4 ± 1.3; diplanetism	12.7 ± 1.2; often multinucleate	12.1 ± 1.3; diplanetism	13.6 ± 1.8; diplanetism	13.2 ± 1.5	14.7 ± 2.3; diplanetism
sympodia	Lax (2 sporangia)	Lax/dense (2–3 sporangia)	Lax (2 sporangia); rare	Lax, rare (2 sporangia)	Lax/dense (2–3 sporangia)	—



Table 7. (Continued)

	<i>P. xincassata</i>	<i>P. xleptopleura</i>	<i>P. xnodosa</i>	<i>P. xcambivora</i> DAPC1, 5 & 9 ³	<i>P. xcambivora</i> DAPC2 ⁴	<i>P. t. xalni-like</i>
Breeding system	A1/A2	A1/A2	Self-fertile	A1/A2	A1/A2	Self-fertile
Oogonia						
mean diam	45.2 ± 6.6	56.0 ± 5.7	51.7 ± 6.5	48.0 ± 4.5	41.5 ± 4.3	44.9 ± 6.7
range isolate means	41.4–49.1	53.7–58.1	48.6–54.9	45.7–52.9	39.3–44.6	n.a.
total range	31.8–63.6	32.5–76.3	30.1–68.1	30.4–61.8	23.7–51.3	33.8–60.2
thickwalled	77.9 % (50–100 %)	—	Occurring	1.5 % (0–15 %)	Occurring	—
tapering base	39.7 (13–68 %)	71 % (33–88 %)	85.3 % (83–89 %)	68.6 % (17–90 %)	86.6 % (60–95 %)	46.2 %
curved stalks	1.7 % (0–3 %)	22.7 % (15–36 %)	19.3 % (17–23 %)	4.5 % (0–13 %)	13.4 % (3–24 %)	3.8 %
elongated	5.1 % (0–10 %)	2.5 % (0–8 %)	4 % (2–7 %)	18.9 % (0–41 %)	34.2 % (20–48 %)	11.5 %
excentric	1.2 % (0–3 %)	44.3 % (33–55 %)	25.7 % (19–32 %)	5.0 % (0–23 %)	12.2 % (4–30 %)	7.7 %
comma-shaped	7.6 % (0–23 %)	12.5 % (1–26 %)	15.3 % (12–19 %)	6.2 % (0–15 %)	16.6 % (4–40 %)	19.2 %
ornamented	98.1 % (97–100 %)	82.5 % (41–100 %)	88.3 % (81–93 %)	67.2 % (38–93 %)	61.5 % (6–100 %)	96.3 %
flexuose	—	22 % (19–26 %)	10.5 % (2–26 %)	0.1 % (0–3 %)	1.4 % (0–5 %)	—
Oospores	100 % plerotic	Plerotic or near plerotic	77 % (near) plerotic	90.9 % (68–100 %) plerotic	95 % (88–100 %) plerotic	83.1 % plerotic
mean diam	37.7 ± 4.7	46.9 ± 5.2	42.8 ± 5.8	41.6 ± 4.0	35.4 ± 3.6	35.4 ± 5.4
total range	25.9–55.1	28.2–64.5	25.5–57.5	24.4–52.7	19.7–43.0	26.2–48.2
wall thickness	3.1 ± 0.6	1.2 ± 0.5	1.6 ± 0.5	3.3 ± 0.6	2.2 ± 0.5	2.0 ± 0.4
oospore wall index	0.41 ± 0.06	0.14 ± 0.06	0.20 ± 0.06	0.40 ± 0.06	0.33 ± 0.07	0.30 ± 0.07
Abortion rate	47.4 % (30–61 %)	54 % (40–63 %)	19.3 % (10–32 %)	38.5 % (7–90 %)	8.1 % (5–15 %)	94 %
Antheridia	100 % amphigynous	98.2 % amphigynous	96.7 % amphigynous	96.8 % amphigynous	> 99 % amphigynous	> 99 % amphigynous
bicellular	52.4 %	84.3 %	79.6 %	70.5 %	89.4 %	33.3 %
size	20.2 ± 3.4 × 16.4 ± 2.0	24.2 ± 3.9 × 18.6 ± 2.1	21.9 ± 3.4 × 18.0 ± 2.5	23.6 ± 5.0 × 18.0 ± 2.9	26.9 ± 4.4 × 18.1 ± 1.7	24.5 ± 7.1 × 16.9 ± 1.4
Hypheal swellings	Coralloid, catenulate	Elongated-irregular, catenulate	—	In water, subglobose; rare; only few isolates	Coralloid-stag-like lateral hyphae	Limoniiform, subglobose, ellipsoid; catenulate
Maximum temperature	30 to < 32.5	32.5 to < 35	32.5 to < 35	32.5 to < 35	32.5 to < 35	27.5 to < 30
Optimum temperature	25	25	25	25 ⁵	25	25
Growth rate at 20 °C	6.0 ± 0.35	3.8 ± 1.05	4.1 ± 0.38	4.7 ± 1.47	6.0 ± 0.52	3.5
Growth rate at 25°C	6.9 ± 0.37	4.4 ± 1.12	4.5 ± 0.29	5.2 ± 1.64	6.3 ± 0.59	4.8

— = character not observed.

¹ Numbers of isolates included in the temperature-growth tests: *P. xincassata* - 3; *P. xleptopleura* - 5; *P. xnodosa* - 4; *P. xcambivora* DAPC1, 5 and 9 - 14; *P. xcambivora* DAPC2 - 7; *P. t. xalni-like* - 1.

² Morphological and morphometric data from Jung et al. (2017a); cardinal temperatures and growth rates from this study.

³ DAPC groups 1, 5 and 9 within *P. xcambivora* according to the discriminant analysis of principal components (DAPC) of the population genomic study of Mullett et al. (2023). DAPC1 isolates belong to the A1 mating type; DAPC5 and 9 isolates belong to the A2 mating type; morphological and morphometric data from the original dataset of Jung et al. (2017a); cardinal temperatures and growth rates from this study.

⁴ DAPC group 2 within *P. xcambivora* according to Mullett et al. (2023). DAPC2 includes isolates from both mating types.

⁵ DAPC group 5 shows almost similar growth rates at 25, 27.5 and 30 °C (3.6, 3.7 and 3.8 mm/d, respectively).

breeding system except for one isolate of *P. ×heterohybrida* which produced gametangia in pairings with both mating types (Jung *et al.* 2017a) and two isolates of *P. ×grandisporangia* which initially produced gametangia in single culture but lost this ability gradually. *Phytophthora ×grandisporangia* differs from *P. ×heterohybrida* by producing on average larger sporangia (84.5 vs 75.3 µm) with higher l/b ratio (2.13 vs 1.66) and a higher proportion of limoniform shapes (33 vs 18 %), higher proportions of curved oogonial bases/stalks (16.7 % vs 5 %), excentric oogonia (17.3 % vs 3.2 %), flexuose oogonia (20.3 % vs 1.2 %) and bicellular antheridia (84.7 % vs 49.6 %), by the occasional occurrence of paragynous antheridia (Fig. 32) and by having oospores with thinner walls (2.3 vs 3.1 µm), lower oospore wall index (0.32 vs 0.43) and higher abortion rate (64.7 vs 17.3 %) (Table 6). *Phytophthora ×incrassata* from Taiwan and two new species from Japan, *P. ×leptopleura* and *P. ×nodosa* are closely related hybrid species. While *P. ×nodosa* has a self-fertile breeding system the other two species are self-sterile with a functional A1/A2 breeding system. *Phytophthora ×incrassata* can be distinguished from *P. ×leptopleura* and *P. ×nodosa* by producing on average shorter sporangia (61.2 vs 71.6 and 74.1 µm, respectively) with lower l/b ratio (1.4 vs 1.85 and 1.72, respectively) and a much higher proportion of ovoid shapes (85 vs 43 and 32 %, respectively), smaller oogonia (45.2 vs 56 and 51.7 µm, respectively) with thicker oospore walls (3.1 vs 1.2 and 1.6 µm, respectively), higher oospore wall index (0.41 vs 0.14 and 0.2, respectively), by the lack of paragynous antheridia, faster growth on V8A between 10 and 27.5 °C and the inability to grow at 32.5 °C (Table 6; Figs 18, 33–35; Jung *et al.* 2017a). Besides their different breeding systems, the main difference between the self-fertile *P. ×nodosa* and the self-sterile *P. ×leptopleura* is the significantly lower oospore abortion rate in *P. ×nodosa* (19.3 vs 54 %). Noteworthy, also the self-sterile *P. ×incrassata* showed high oospore abortion (47.4 %) (Table 6; Jung *et al.* 2017a).

Jung *et al.* (2017a) demonstrated the allopolyploid hybrid nature of the self-sterile A1/A2 species *P. cambivora* and provided a redescription as *P. ×cambivora* without nomenclatural act. The Discriminant Analysis of Principal components (DAPC) used in the population genomic study of Mullett *et al.* (2023) grouped a global population of 296 *P. ×cambivora* isolates into 11 DAPC lineages with the European isolates used for the redescription by Jung *et al.* (2017a) residing in three allopolyploid lineages with either A1 (DAPC1) or A2 (DAPC5 and DAPC9) mating type. Interestingly, despite their hybrid nature the Japanese lineages DAPC2 and DAPC6 have diploid genomes and both of them comprise both mating types. The seven isolates of the DAPC2 lineage examined in the present study generally showed similar morphology of sporangia and gametangia as reported for the DAPC1, 5 and 9 lineages (Jung *et al.* 2017a; Table 7). Clear differences were, however, the lower mean values and narrower ranges of oogonial and oospore sizes, thinner oospore walls (2.2 vs 3.3 µm), lower oospore wall index (0.33 vs 0.4), considerably lower oospore abortion rate (8.1 vs 38.5 %), the occurrence of coraloid or stag-like irregular lateral hyphae and the faster growth of the DAPC2 lineage as compared to the combined DAPC1, 5 and 9 lineages (Table 7; Figs 19, 42, 43; Jung *et al.* 2017a). An extensive temperature-growth test in the present study revealed considerable variability of growth rates between the 11 DAPC lineages of *P. ×cambivora* with DAPC10, 11 and 6 showing the fastest growth at 25 °C and DAPC5 growing considerably slower than all other lineages between 15 and 30 °C. Most lineages had their growth optimum at 25 °C except for DAPC8 and 11 which showed similar growth at 25 and 27.5 °C, and DAPC5 with an optimum between 27.5 and 30 °C (Fig. 19). On current evidence,

we consider differences between DAPC lineages are insufficient for splitting *P. ×cambivora* into separate species. However, this does not rule out the case for future subspecific designations in *P. ×cambivora* as already indicated as a possible approach to the lineages within *P. lateralis* (Brasier *et al.* 2012).

NOTES ON THE PROPERTIES OF CLADE 7A

Notes on geographical distribution and host and habitat associations of Clade 7a taxa

Host ranges and known diseases caused by Clade 7a taxa are presented comprehensively in Table 9. Apart from one isolate of *P. laevigata* from a dying hazelnut plant in a fruit orchard in Croatia and one isolate of *P. arta* from a necrotic attached leaf of *Pieris japonica* in Japan, all newly described Clade 7a species were isolated either (i) from forest streams (*P. arta*, *P. facultativa*, *P. ×grandisporangia*, *P. ×leptopleura*, *P. ×nodosa*) or from rhizosphere soil of forest trees (*P. algida*, *P. grandoogonia*, *P. infundibuliformis*, *P. irregularis*, *P. laevigata*, *P. sessilis*, *P. ×nodosa*). On a purely visual basis, no above-soil stem or foliar symptoms were observed in associated natural vegetation.

Clade 7a1: Phytophthora vulcanica, the only known species from Clade 7a1, was described from the rhizosphere of healthy *Fagus sylvatica* trees in a remote, natural upper-montane beech forest at Mount Etna in Sicily (Jung *et al.* 2017b). Despite extensive *Phytophthora* surveys of beech forests across Europe (Motta *et al.* 2003, Jung *et al.* 2005, 2018a, 2019, Hartmann *et al.* 2006, Brown & Brasier 2007, Munda *et al.* 2007, Vettraino *et al.* 2008, Černý *et al.* 2009, Jung 2009, Schmitz *et al.* 2009, Stępniewska & Dłuszyński 2010, Telfer *et al.* 2015, Corcobado *et al.* 2020, Horta Jung *et al.* 2025), there are only two other records of this species, both from surveys using metabarcoding approaches. One came from a submediterranean montane forest in the Sistema Central mountain range of Spain where *P. vulcanica* was detected recently in the rhizosphere of a declining *F. sylvatica* tree (Martínez-Arias *et al.* 2025). Therefore, *P. vulcanica* appears to have a cryptic, scattered natural distribution in montane beech forests of Southern Europe. The other record is from rhizosphere soil of a healthy *Castanea sativa* tree in an amenity woodland in northern Britain (Riddell *et al.* 2019). Although it cannot be ruled out that the UK is within the native origin of *P. vulcanica* it appears likely that the pathogen was introduced to this woodland via the planting of infested nursery stock.

Clade 7a2: Phytophthora uliginosa has a scattered distribution in natural and seminatural temperate and Mediterranean forests across Europe. It has been reported from the rhizosphere of declining trees of *F. sylvatica*, *Quercus petraea* and *Quercus robur* in Germany, *Q. robur* in Poland and *Quercus suber* in Portugal (Jung *et al.* 2002, Horta Jung *et al.* 2025). Using a metabarcoding approach, *P. uliginosa* was also found in the rhizosphere of dead *Fraxinus excelsior* trees in the UK (Landa *et al.* 2021). In a metabarcoding survey of nurseries across the UK, it was detected also in the rootballs of *Pseudotsuga*, *Hebe* and *Picea* plants (Green *et al.* 2025). In addition, it has been isolated from the rhizosphere of a large amenity tree of *Metasequoia glyptostroboides* in a German nursery (Jung *et al.* 2016).

Phytophthora tyrrhenica, the sister species of *P. uliginosa*, occurs endemical in natural forests of *Quercus ilex* and *Q. suber* in Sardinia and Sicily where it is associated with a chronic decline of



Table 8. Morphological characters and dimensions (µm), cardinal temperatures (°C) and temperature-growth relations (mm/d) on V8A of taxa in the ‘*Phytophthora xalni* complex’ in Clade 7a4. Most discriminating characters are highlighted in bold.

	<i>P. xalni</i> ¹	<i>P. xalni</i>	<i>P. xmultiformis</i> ²	<i>P. xmultiformis</i>	<i>P. t. xmultiformis-like</i>	<i>P. uniformis</i> ³	<i>P. uniformis</i>
No. of isolates/source	10; Brasier et al. (2004) ⁴	7; Jung et al. (2017a) ^{5,6}	7; Brasier et al. (2004) ⁴	7; Jung et al. (2017a) ^{5,7}	1; Jung et al. (2017a) ^{5,8}	2; Brasier et al. (2004) ⁴	7; Jung et al. (2017a) ^{5,8}
Sporangia	Ellipsoid, ovoid	90 % ovoid, 4 % obpyriform, 2 % limoniform, 2 % obturbinate, 2 % ellipsoid	n.a.	92 % ovoid, 3 % ellipsoid, 3 % limoniform, 2 % obpyriform, (subglobose)	98 % ovoid, (limoniform, obpyriform, ellipsoid)	Ellipsoid, ovoid	87 % ovoid, 6 % obpyriform, 3 % limoniform, 3 % ellipsoid, (ampulliform, obturbinate)
Ixb mean	n.a.	53.6 ± 8.9 × 39.5 ± 5.4	n.a.	51.5 ± 9.5 × 36.5 ± 5.6	51.8 ± 7.8 × 37.6 ± 4.7	n.a.	58.2 ± 7.0 × 40.0 ± 3.9
range isolate means	48–59.8 × 31.3–42.8	50.3–59.1 × 36.7–43.9	n.a.	35.8–60.4 × 29.2–41.6	34.6–64.3 × 29.1–46.7	n.a.	54.1–62.1 × 34.2–42.9
total range	35–70 × 27.5–50	31.5–78.8 × 25.9–53.8	n.a.	28.3–80.3 × 22.1–49.2	n.a.	n.a.	36.8–78.3 × 24.1–57.4
l/b ratio	1.32–1.62	1.36 ± 0.16	n.a.	1.41 ± 0.17	1.37 ± 0.1	n.a.	1.47 ± 0.19
caducity	—	—	—	—	—	—	—
exitpores	n.a.	15.4 ± 2.8	n.a.	13.7 ± 2.9	13.8 ± 1.6	n.a.	15.5 ± 2.9
zoospore cysts	n.a.	14.3 ± 1.8; diplanetism	n.a.	14.4 ± 3.4	13.3 ± 0.8; diplanetism	n.a.	14.3 ± 2.3; diplanetism
sympodia	—	—	n.a.	—	—	n.a.	Lax (2 sporangia); rare
Breeding system	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile	Self-fertile
Oogonia							
mean diam	n.a.	48.9 ± 7.1	n.a.	48.0 ± 6.0	46.5 ± 5.8	n.a.	47.6 ± 3.5
range isolate means	42.8–50	42.8–56.3	50–59.5	46.2–49.5	n.a.	39.8–49	46.6–48.6
total range	25–55	25.6–69.5	45–65	27.2–66.5	31.9–56.3	37.5–55	36.3–58.4
thickwalled	n.a.	1.0 % (0–6 %) ⁹	n.a.	1.7 % (0–8 %) ⁹	12 % ⁹	n.a.	— ⁱ
tapering base	Common	45.3 % (13–74 %)	Frequent	50.3 % (30–66 %)	62 %	n.a.	58.6 % (32–71 %)
curved stalks	n.a.	3.0 % (1–7 %) ⁹	n.a.	5.2 % (2–8 %) ⁹	8 % ⁹	n.a.	3.2 % (0–6 %) ⁱ
elongated	n.a.	4.3 % (0–16 %)	n.a.	3 % (0–6 %)	6 %	n.a.	3.5 % (0–14 %)
excentric	n.a.	3.8 % (0–10 %)	Frequent	6.4 % (2–14 %)	—	n.a.	20.5 % (6–30 %)
comma-shaped	Occurring	14.6 % (0–33 %)	Proportion highly variable	9.8 % (2–18 %)	2 %	—	1.2 % (0–3 %)
ornamented	Common	66.9 % (7–94 %)	Proportion highly variable	78.1 % (32–96 %)	94 %	Smooth, rarely wavy edged-verrucose	13 % (0–30 %) wavy edged-verrucose
flexuose	n.a.	1.8 % (0–5 %)	n.a.	1.8 % (0–12 %)	—	—	—
Oospores							
mean diam	n.a. (33.3–43.5 ¹⁰)	96.7 % (90–100 %) plerotic	n.a.	80.6 % (43–98 %) plerotic	96 % plerotic	n.a. (33.3–43.4 ¹⁰)	57 % (52–62 %) plerotic
total range	27.5–50	41.2 ± 6.0	n.a. (40.3–50.5 ¹⁰)	39.4 ± 4.6	38.2 ± 5.1	30–47.5	42.1 ± 3.1
wall thickness	n.a.	23.3–58.8	35–55	24.8–52.9	26.6–49.3	n.a.	33.0–50.8
oospore wall index	n.a.	3.2 ± 0.7	n.a.	3.1 ± 0.6	2.7 ± 0.4	n.a.	3.2 ± 0.6
		0.39 ± 0.07	n.a.	0.40 ± 0.06	0.37 ± 0.05	n.a.	0.39 ± 0.06



Table 8. (Continued)

	<i>P. xalni</i> ¹	<i>P. xalni</i>	<i>P. xmultiformis</i> ²	<i>P. xmultiformis</i>	<i>P. t. xmultiformis</i> -like	<i>P. uniformis</i> ³	<i>P. uniformis</i>
Abortion rate	36–70 %	65.3 % (7–90 %)	Proportion highly variable	74.3 % (32–96 %)	69.0 %	< 5 %	13 % (1–30 %)
Antheridia bicellular	Amphigynous	87.6 % amphigynous	Amphi- or paragynous	83.1 % amphigynous	78.0 % amphigynous	100 % amphigynous	100 % amphigynous
size	Predominant	52.7 %	Infrequent	35.0 %	18.0 %	100 %	64.2 %
Hyphal swellings	20–30 × 15–20	22.0 ± 4.8 × 16.9 ± 2.5	length 15–32.5	20.4 ± 4.5 × 16.0 ± 2.4	18.4 ± 2.2 × 15.9 ± 2.4	length 17.5–27.5	24.3 ± 4.3 × 17.7 ± 2.4
	n.a.	In water, rare, limoniform, subglobose, deltoid	n.a.	—	—	n.a.	In water; deltoid, triangular, some catenulate ; rare
Maximum temperature	29	27.5 to < 30	27–32	27.5 to < 30	27.5 to < 30	n.a.	27.5 to < 30
Optimum temperature	23–25	20–25	n.a.	20–25	25	n.a.	25
Growth rate at 20 °C	n.a.	6.2 ± 1.35	n.a.	5.3 ± 1.84	5.0	n.a.	3.9 ± 0.61
Growth rate at 25°C	5.9 (4.1–7.5)	6.3 ± 0.98	n.a.	5.1 ± 1.47	5.2	n.a.	4.3 ± 0.36

— = character not observed.

¹ Designated as *P. alni* subsp. *alni*.

² Designated as *P. alni* subsp. *multiformis*.

³ Designated as *P. alni* subsp. *uniformis*.

⁴ Morphological, morphometric and temperature-growth studies performed on CA.

⁵ Numbers of isolates included in the temperature-growth tests: *P. xalni* - 6; *P. xmultiformis* - 4; *P. t. xmultiformis*-like - 1; *P. uniformis* - 3.

⁶ Morphological and morphometric data recalculated from original dataset of Jung et al. (2017a) without isolates TJ005 and TJ008; cardinal temperatures and growth rates from this study.

⁷ Morphological and morphometric data recalculated from original dataset of Jung et al. (2017a) plus additional isolates TJ008 and TJ460; cardinal temperatures and growth rates from this study.

⁸ Morphological and morphometric data from Jung et al. (2017a); cardinal temperatures and growth rates from this study.

⁹ Characters not included in Jung et al. (2017a).

¹⁰ Range of isolate means.

Table 9. Breeding systems, hybrid status, natural and introduced biogeography and habitats of *Phytophthora* species from Clade 7a, their host ranges and plant diseases they cause.

<i>Phytophthora</i> taxon; breeding system; (mating types) ¹	Hybrid status; parents ²	Geographic origin	Introduced regions	Habitats	Host plants ³	Diseases ³	Main references
<i>P. abietivora</i> ⁴ ; SF	Pure	Central and Eastern North America		Christmas tree plantations, nurseries Temperate mixed forests	<i>Abies fraseri</i> , <i>A. balsamensis</i> 10 native woody species	Root rot, mortality Root rot, leafshoot blight, bark necroses of understorey plants	Li et al. (2019), Charron et al. 2024, 2025 Bily et al. (2022)
			Japan	Aquatic botanical gardens	<i>Iris ensata</i> var. <i>ensata</i>	Basal rot	Amemiya et al. (2011a, b)
<i>P. algidia</i> ⁵ ; SF	Pure	Northern Indochina	—	Subtropical cloud and lower montane forests	<i>Acer oblongum</i> , <i>Castanopsis chinensis</i> , rhizosphere soil	Not observed; most likely fine root nibbler	Jung et al. (2020), this study
<i>P. arta</i> ; SF	Pure	Japan, Kyushu and Shikoku	—	Temperate mixed forests; warm-temperate laurosilva forests	<i>Pieris japonica</i> , forest streams	Leaf necrosis, most likely fine root nibbler and decomposer of fallen leaves	This study



Table 9. (Continued).

Phytophthora taxon; breeding system; (mating types) ¹	Hybrid status; parents ²	Geographic origin	Introduced regions	Habitats	Host plants ³	Diseases ³	Main references
<i>P. attenuata</i> ; SF	Pure	Taiwan	—	Montane mixed forests	<i>Castanopsis carlesii</i> , <i>Chamaecyparis formosensis</i> , rhizosphere soil	Not observed; most likely fine root nibbler	Jung <i>et al.</i> (2017a)
<i>P. europaea</i> ; SF	Pure	Northern Indochina	—	Subtropical cloud forest	<i>A. oblongum</i> , rhizosphere soil	Not observed; most likely fine root nibbler	Jung <i>et al.</i> (2020), this study
		Europe	—	Temperate mixed broadleaved forests	<i>Fagus sylvatica</i> , <i>Quercus robur</i> , rhizosphere soil	No apparent disease or chronic decline; most likely fine root nibbler	Jung <i>et al.</i> (2002)
<i>P. facultativa</i> ; SF	Pure	USA, Louisiana	—	Subtropical mixed forest	Forest stream	Not observed; most likely fine root nibbler and decomposer of fallen leaves	This study
<i>P. fagacearum</i> ; SF	Pure	USA, Pennsylvania	—	Temperate mixed forest	<i>Fagus grandifolia</i>	Leaf blight of seedling	Crous <i>et al.</i> (2024)
<i>P. flexuosa</i> ; SF	Pure	Taiwan	—	Montane beech forest	<i>Fagus hayatae</i> , rhizosphere soil	Not observed; most likely fine root nibbler	Jung <i>et al.</i> (2017a)
		Japan, Honshu and Shikoku		Temperate montane forests	<i>Chamaecyparis pisifera</i> , <i>Chamaecyparis obtusa</i> , <i>Pterocarya rhoifolia</i> , rhizosphere soil	Not observed; most likely fine root nibbler and decomposer of fallen leaves	This study
<i>P. formosa</i> ; SF	Pure	Taiwan	—	Montane mixed forests	<i>Araucaria cunninghamii</i> , <i>Quercus glandulifera</i> , rhizosphere soil	Not observed; most likely fine root nibbler	Jung <i>et al.</i> (2017a)
		Japan, Kyushu and Shikoku		<i>Quercus-Chamaecyparis-Tsuga-Abies</i> forest	Forest streams	Not observed; most likely fine root nibbler	This study
				Warm-temperate laurosilva forests	<i>Machilus thunbergii</i> , rhizosphere soil, forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	This study
<i>P. fragariae</i> ; SF	Pure	Unknown	Europe, North America, Ecuador, India, Japan, Middle East, Egypt, New Zealand	Horticultural plantations	<i>Fragaria</i> × <i>ananassa</i> , <i>Rubus</i> × <i>loganobaccus</i>	Root rot, red stele (= red core)	Milholland 1994; Erwin & Ribeiro 1996; EPPO 2022a
<i>P. grandogonia</i> ^a ; SF	Pure	Northern Indochina	—	Subtropical lower montane forests	<i>Antidesma</i> sp., <i>C. chinensis</i> , <i>Diospyllum juglans</i> , <i>Meliosma amottiana</i> , <i>Quercus glauca</i> , <i>Vernicia montana</i> , rhizosphere soil	Not observed; most likely fine root nibbler	This study



Table 9. (Continued).

<i>Phytophthora</i> taxon; breeding system; (mating types) ¹	Hybrid status; parents ²	Geographic origin	Introduced regions	Habitats	Host plants ³	Diseases ³	Main references
<i>P. infundibuliformis</i> ; SF	Pure	USA, Louisiana	—	Subtropical mixed forest	Acer sp., rhizosphere soil	Not observed; most likely fine root nibbler	This study
<i>P. intricata</i> ; SF	Pure	Taiwan	—	Subtropical monsoon forest	<i>Quercus tarokoensis</i> , rhizosphere soil	Not observed; most likely fine root nibbler	Jung <i>et al.</i> (2017a)
<i>P. irregularis</i> ; SF	Pure	Japan, Kyushu and Shikoku	—	Warm-temperate laurosilva forests	<i>Castanopsis cuspidata</i> , <i>C. sieboldii</i> , <i>M. thunbergii</i> , <i>Quercus acuta</i> , <i>Zelkova serrata</i> , rhizosphere soil	Not observed; most likely fine root nibbler	This study
<i>P. laevigata</i> ; SF	Pure	Europe, West Balkans	—	Temperate mixed forest	<i>F. sylvatica</i> , rhizosphere soil	Not observed; most likely fine root nibbler	This study
<i>P. rubi</i> ; SF	Pure	Unknown	Australia, Chile, North America, Europe	Horticultural plantations	<i>Corylus avellana</i> , rhizosphere soil	Root rot	This study
				Horticultural plantations	<i>Rubus idaeus</i> , <i>R. × loganobaccus</i> , <i>R. fruticosus</i> × <i>R. idaeus</i>	Root and cane rot	Wilcox <i>et al.</i> (1993), Gigot <i>et al.</i> 2013, EPPO 2022b
<i>P. sessilis</i> ⁷ ; SF	Pure	Northern Indochina	—	Subtropical cloud forests	<i>Betula alnoides</i> , <i>Elaeocarpus japonicus</i> , <i>Neolitsea pollanai</i> , <i>Rhododendron arboreum</i> , rhizosphere soil	Not observed; most likely fine root nibbler	This study
<i>P. tyrrhenica</i> ; SF	Pure	Southern Europe, Sicily and Sardinia	—	Mediterranean oak forests	<i>Quercus ilex</i> , rhizosphere soil	Mild decline; most likely fine root nibbler	Jung <i>et al.</i> (2017c), Seddaiu <i>et al.</i> 2020
<i>P. uliginosa</i> ; SF	Pure	Europe		Temperate and Mediterranean forests	<i>F. sylvatica</i> , <i>Fraxinus excelsior</i> , <i>Quercus petraea</i> , <i>Q. robur</i> , <i>Q. suber</i> , rhizosphere soil	Mild decline, most likely fine root nibbler	Jung <i>et al.</i> (2002), Landa <i>et al.</i> 2021, Horta Jung <i>et al.</i> (2025)
				Nurseries	<i>Pseudotsuga</i> , <i>Hebe</i> , <i>Picea</i> , <i>Metasequoia glyptostroboides</i> , rhizosphere soil	n/a	Jung <i>et al.</i> (2016), Green <i>et al.</i> (2025)
<i>P. uniformis</i> ; SF	Pure	North America, Alaska and Oregon		Temperate to sub-boreal riparian forests	<i>Alnus incana</i> subsp. <i>tenuifolia</i> , <i>A. rubra</i>	Root rot, bark cankers (rare)	Adams <i>et al.</i> (2010), Aguayo <i>et al.</i> (2013), Sims <i>et al.</i> (2015)
			Europe	Temperate to sub-boreal riparian and swamp forests	<i>A. incana</i> , <i>A. glutinosa</i>	Root and collar rot, aerial bark cankers	Brasier <i>et al.</i> (2004), Jung & Blaschke (2004), Redondo <i>et al.</i> (2015), Jung <i>et al.</i> (2018a)
				Nurseries, forest and riparian plantings	<i>A. cordata</i> , <i>A. glutinosa</i> , <i>A. incana</i>	Root and collar rot	Santini <i>et al.</i> (2001), Jung <i>et al.</i> (2016), Bačová <i>et al.</i> (2024), Green <i>et al.</i> (2025)



Table 9. (Continued).

Phytophthora taxon; breeding system; (mating types) ¹	Hybrid status; parents ²	Geographic origin	Introduced regions	Habitats	Host plants ³	Diseases ³	Main references
<i>P. vulcanica</i> ; SF	Pure	Southern Europe (Sicily, Spain)	—	Mediterranean montane forests	<i>F. sylvatica</i> , rhizosphere soil	No apparent disease or chronic decline; most likely fine root nibbler	Jung et al. (2017c), Martínez-Arias et al. (2024)
<i>P. xalni</i> ; SF	Hybrid; <i>P. xmultiformis</i> × <i>P. uniformis</i>	United Kingdom	Europe	Amenity woodland	<i>Castanea sativa</i>	No apparent disease	Riddell et al. (2019)
		Hybrid created in Europe between two non-native species		Temperate and Mediterranean riparian and swamp forests	<i>A. glutinosa</i> , <i>A. incana</i> , <i>A. lusitanica</i>	Root and collar rot, aerial bark cankers	Brasier et al. (1999, 2004), Jung & Blaschke (2004), Husson et al. (2015), Jung et al. (2018a), Van Poucke et al. (2021), Corcobado et al. (2023); Gomes Marques et al. (2024)
<i>P. xcombivora</i> DAPC1; A1/ A2; (A1)	Hybrid; parents unknown	Unknown	Europe	Nurseries, forest and riparian plantings	<i>A. cordata</i> , <i>A. glutinosa</i> , <i>A. incana</i>	Root and collar rot, aerial bark cankers	Jung & Blaschke (2004), Schumacher et al. (2006), Jung et al. (2016, 2018a)
				Mediterranean & temperate forests, plantings, nurseries	<i>A. glutinosa</i> , <i>Castanea sativa</i> , <i>F. sylvatica</i> , <i>Quercus</i> spp., <i>Chamaecyparis</i> sp., ornamental hosts	Root and collar rot, aerial bark cankers	Jung & Blaschke (2004), Jung et al. (2017a, 2018a), Mullett et al. (2023)
<i>P. xcombivora</i> DAPC2; A1/ A2; (A1, A2)	Hybrid; parents unknown	Japan, Kyushu and Shikoku	—	Gondwana rainforest	Forest soil	n/a	Jung et al. (2017a), Van Poucke et al. (2021), Mullett et al. (2023)
				Warm-temperate laurosilva forests	Forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	Mullett et al. (2023), this study
<i>P. xcombivora</i> DAPC3; A1/ A2; (A1, A2)	Hybrid; parents unknown	Unknown	Europe, Poland	Nurseries	<i>C. sativa</i> , <i>Chamaecyparis lawsoniana</i> , <i>Cotoneaster dammeri</i> , pond water, river water	n/a	Mullett et al. (2023)
<i>P. xcombivora</i> DAPC4; A1/ A2; (A1, A2)	Hybrid; parents unknown	Japan, Honshu and Kyushu	—	Warm- & cool-temperate forests	<i>Fagus crenata</i> , forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	Mullett et al. (2023)
				Cool-temperate forests	Forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	Mullett et al. (2023)
<i>P. xcombivora</i> DAPC4 mixed; A1/A2; (A1, A2)	Hybrid; parents unknown	Japan, Honshu and Hokkaido; South Korea		Orchards	<i>Malus pumila</i>	Root and crown rot	Suzui & Hoshino (1979), Jee et al. (1997), Mullett et al. (2023)



Table 9. (Continued).

Phytophthora taxon; breeding system; (mating types) ¹	Hybrid status; parents ²	Geographic origin	Introduced regions	Habitats	Host plants ³	Diseases ³	Main references
<i>P. ×cambivora</i> DAPC5; A1/ A2; (A2)	Hybrid; DAPC1 × DAPC9	Unknown	Australia, Europe, USA	Temperate forests	<i>Abies procera</i> , <i>Chrysolepis chrysophylla</i> , <i>Pseudotsuga menziesii</i>	Root rot, bark cankers	Mircetich & Matheron (1976); Bumbleris & Wicks (1980); Wilcox & Mircetich (1985), Browne <i>et al.</i> (1995), Wicks <i>et al.</i> (1997), Saavedra <i>et al.</i> (2007), Van Poucke <i>et al.</i> (2021), Mullett <i>et al.</i> (2023), Horta Jung <i>et al.</i> (2025)
				Christmas trees	<i>Abies procera</i>		
				Orchards	<i>Malus</i> and <i>Prunus</i> spp.		
				Nurseries	Multiple forest trees & ornamentals		
<i>P. ×cambivora</i> DAPC6; A1/ A2; (A1, A2)	Hybrid; DAPC1 × DAPC9	Unknown	Europe	Mediterranean & temperate forests	<i>C. sativa</i> , <i>F. orientalis</i> , <i>F. sylvatica</i> , forest streams	Root and collar rot, aerial bark cankers	Jung <i>et al.</i> (2017a, 2018a), Mullett <i>et al.</i> (2023), Horta Jung <i>et al.</i> (2025)
				Plantings	<i>Prunus serotina</i> , <i>Thuja occidentalis</i>	Root rot	
<i>P. ×cambivora</i> DAPC7; A1/ A2; (A1)	Hybrid; parents unknown	Japan, Honshu	—	Cool-temperate forests	<i>F. crenata</i> , forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	Mullett <i>et al.</i> (2023)
<i>P. ×cambivora</i> DAPC8; A1/ A2; (A1)	Hybrid; parents unknown	Japan, Honshu and Kyushu	—	Cool-temperate & warm-temperate forests	<i>Quercus crispula</i> , rhizosphere soil, forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	Mullett <i>et al.</i> (2023)
<i>P. ×cambivora</i> DAPC9; A1/ A2; (A2)	Hybrid; parents unknown	Japan, Honshu	—	Cool-temperate forests	<i>Acer palmatum</i> , <i>Aesculus turbinata</i> , <i>Magnolia obovata</i> , rhizosphere soil, forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	Mullett <i>et al.</i> (2023)
<i>P. ×cambivora</i> DAPC10; A1/ A2; (A1)	Hybrid; parents unknown	Unknown	Europe	Mediterranean & temperate forests, plantings, nurseries	<i>Acer</i> spp., <i>A. glutinosa</i> , <i>Betula</i> spp., <i>C. sativa</i> , <i>F. sylvatica</i> , <i>Quercus</i> spp., <i>Salix caprea</i> , forest streams	Root and collar rot, aerial bark cankers, twig blight	Jung <i>et al.</i> (2017a, 2018a), Mullett <i>et al.</i> (2023), Horta Jung <i>et al.</i> (2025)
				Orchards	<i>R. idaeus</i>	Root rot	Mullett <i>et al.</i> (2023)
			Australia (SA)	Orchards	<i>Prunus avium</i>	n/a	Mullett <i>et al.</i> (2023)
			North America	Temperate forests	<i>A. procera</i> , <i>C. chrysophylla</i>	Root rot, bark cankers	Mullett <i>et al.</i> (2023)
			Chile	Amenity trees	<i>F. sylvatica</i>	Bark cankers	Jung <i>et al.</i> (2017a, 2018b), Mullett <i>et al.</i> (2023)



Table 9. (Continued).

Phytophthora taxon; breeding system; (mating types) ¹	Hybrid status; parents ²	Geographic origin	Introduced regions	Habitats	Host plants ³	Diseases ³	Main references
<i>P. ×cambivora</i> DAPC10; A1/A2; (A1)	Hybrid; parents unknown	Unknown	USA, Oregon	Temperate forests	<i>C. chrysophylla</i> , <i>Notholithocarpus densiflorus</i>	Root rot, basal cankers	Saavedra et al. (2007), Mullet et al. (2023)
<i>P. ×cambivora</i> DAPC11; A1/A2; (A1)	Hybrid; parents unknown	Unknown	Europe	Mediterranean & temperate forests	<i>C. sativa</i> , <i>F. sylvatica</i> , <i>Quercus pyrenaica</i> , <i>Q. suber</i>	Root rot, bark cankers	Mullett et al. (2023), Horta Jung et al. (2025)
<i>P. ×grandisporangia</i> ⁸ ; A1/A2; (A1+A2)	Hybrid; parents unknown	Northern Indochina	USA, Oregon	Landscape planting, soil	<i>Photinia</i> sp.	n/a	Mullett et al. (2023),
<i>P. ×grandisporangia</i> ⁸ ; A1/A2; (A1, A1ho)	Hybrid; parents unknown	—	—	Subtropical cloud forests	Forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	Jung et al. (2020), Van Poucke et al. (2021), this study
<i>P. ×heterorhybrida</i> ; A1/A2; (A1, A2, A1+A2)	Hybrid; parents unknown	Taiwan	—	Subtropical monsoon forest	Forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	Jung et al. (2017a), Van Poucke et al. (2021)
<i>P. ×incrassata</i> ; A1/A2; (A1)	Hybrid; parents unknown	Taiwan	—	Subtropical monsoon forest	Forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	Jung et al. (2017a), Van Poucke et al. (2021)
<i>P. ×leptopleura</i> ; A1/A2; (A1, A2)	Hybrid; parents unknown	Japan, Shikoku	—	Warm-temperate laurosilva forests	Forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	This study
<i>P. ×multiformis</i> ; SF	Hybrid; parents unknown	Unknown	Europe	Temperate and Mediterranean riparian and swamp forests	<i>A. glutinosa</i> , <i>A. incana</i> , <i>A. lusitanica</i>	Root and collar rot, aerial bark cankers	Brasier et al. (1999, 2004), Jung & Blaschke (2004), Husson et al. (2015), Jung et al. (2018a), Van Poucke et al. (2021), Corcobado et al. (2023)
<i>P. ×nodosa</i> , SF	Hybrid; parents unknown	Japan, Kyushu	—	Forest and riparian plantings	<i>A. glutinosa</i> , <i>A. incana</i>	Root and collar rot, aerial bark cankers	Jung & Blaschke (2004), Jung et al. (2016, 2018a)
<i>P. taxon cadmea</i> ; n/a	Pure	USA, California	—	Warm-temperate laurosilva forests	<i>Lithocarpus edulis</i> , rhizosphere soil, forest streams	Not observed; most likely fine root nibbler and decomposer of fallen leaves	This study
<i>P. taxon cadmea</i> -like; n/a	Pure	USA, West Virginia	—	Mediterranean oak woodland	<i>Juncus</i> sp., rhizosphere soil	Not observed; most likely fine root nibbler	Bourret et al. (2023), Fajardo et al. (2025)
<i>P. taxon europaea</i> -like; n/a	Pure	Europe, Poland	—	Temperate oak forest	<i>Quercus rubra</i> , rhizosphere soil	n/a	n/a
<i>P. taxon ×alni</i> -like; SF	Backcross hybrid; <i>P. ×alni</i> × <i>P. uniformis</i>	Hybrid created in Europe between two non-native species	Europe, Germany, Bavaria	Temperate beech forest	<i>F. sylvatica</i> , seedling cotyledon and stem	Seedling cotyledon and stem blight	n/a
				Temperate riparian forest	<i>A. incana</i>	Collar rot	Jung & Blaschke (2004), this study



Table 9. (Continued).

Phytophthora taxon; breeding system; (mating types) ¹	Hybrid status; parents ²	Geographic origin	Introduced regions	Habitats	Host plants ³	Diseases ³	Main references
<i>P.</i> taxon xmultiformis-like; SF	Hybrid; <i>P. uniformis</i> x <i>P. xmultiformis</i>	Hybrid created in Europe between two non-native species	Europe, Netherlands	Temperate riparian forest	<i>A. glutinosa</i>	Collar rot	Jung <i>et al.</i> (2017a), Van Poucke <i>et al.</i> (2021)
n/a = not available.							
¹ SF: self-fertile (homothallic) breeding system; A1/A2: self-sterile (heterothallic) breeding system requiring mating between A1 and A2 compatibility types; A1ho: weakly self-fertile A1 mating type (forming gametangia abundantly in pairings with A2 isolates); A1+A2: self-sterile (heterothallic) forming gametangia in pairings with both mating types.							
² Pure: taxa with mean nuclear heterozygosity level below 0.3; hybrid: taxa resulting from interspecific hybridisation with mean nuclear heterozygosity level > 0.3; also, mitochondrial genes can show high similarity to one or more other Clade 7a taxa or have multiple mitochondrial genotypes; in addition, for most hybrid taxa interspecific hybridization was confirmed by nuclear genotyping by sequencing (Van Poucke <i>et al.</i> 2021, Mullett <i>et al.</i> 2023).							
³ More detailed information on host ranges and diseases are given in the section Notes on geographical distribution and host and habitat associations.							
⁴ Includes also isolates previously designated as <i>P.</i> sp. <i>europaea</i> SW (Yang <i>et al.</i> 2017) and <i>P.</i> <i>europaea</i> (Balci <i>et al.</i> 2007).							
⁵ Previously designated as <i>P.</i> sp. <i>attenuata</i> -like 2 (Jung <i>et al.</i> 2020).							
⁶ Previously designated as <i>P.</i> sp. <i>attenuata</i> -like 3 (Jung <i>et al.</i> 2020).							
⁷ Previously designated as <i>P.</i> sp. <i>attenuata</i> -like 1 (Jung <i>et al.</i> 2020).							
⁸ Previously designated as <i>P.</i> x <i>heterohybrida</i> (Jung <i>et al.</i> 2020) and <i>P.</i> x <i>heterohybrida</i> -related (Van Poucke <i>et al.</i> 2021).							

oak trees (Jung *et al.* 2017b, Seddaiu *et al.* 2020).

Clade 7a3: Phytophthora abietivora was described in 2019 causing root rot on *Abies fraserii* trees in a christmas tree plantation in Connecticut, USA (Li *et al.* 2019). Recently, it was also found widespread in the Canadian province of Quebec as causal agent of root rot and mortality of *A. fraserii* and *Abies balsamea* christmas trees and seedlings of the latter species in one nursery (Charron *et al.* 2024, 2025). A survey in natural forests of the Appalachian mountains in Pennsylvania, USA, revealed widespread occurrence of *P. abietivora* in soil samples and foliar necroses, shoot blights and bark necroses of predominantly young understorey plants from ten native plant species: *Acer rubrum*, *Betula lenta*, *Carya* sp., *Cornus florida*, *Fagus grandifolia*, *Hamamelis virginiana*, *Ilex montana*, *Quercus alba*, *Quercus montana* and *Quercus rubra* (Bily *et al.* 2022). Isolates from oak forest soils in Minnesota, Wisconsin, Pennsylvania and West Virginia with ITS sequence (GenBank accession no. DQ313222) identity of 99.4 % to the ex-type isolate of *P. europaea* had been designated initially as *P. europaea* (Balci *et al.* 2007). However, in new BLAST searches at GenBank these isolates showed 100 % identity to numerous isolates of *P. abietivora* and, hence, should be re-assigned to this species. For one strain isolated in 2005 from oak soil in West Virginia (33F7 = p229 = BM4/6) and designated by Yang *et al.* (2017) as *P.* sp. *europaea*SW, sequences from different gene regions are identical or almost identical to the ex-type isolate of *P. abietivora* (*βtub* - KX251603 = 100 %; *enl* - KX251605 = 99.9 %; *hsp90* - KX251606 = 100 %; *tigA* - KX251608 = 99.8 %; *nadh1* - AB649211 = 99.6 %). Likewise, isolates from forest streams in Western Oregon originally assigned to *P. europaea* due to 99.7 % ITS sequence (GenBank HM004226) identity to the *P. europaea* ex-type (Reeser *et al.* 2011) exhibit 99.9 % ITS sequence identity to both *P. abietivora* and *P. t. cadmea* and most likely belong to one of these two taxa. Apparently, *P. abietivora* is widespread in and most likely native to North America and spread from natural ecosystems to neighbouring christmas tree plantations. This pathway was previously proposed for *P. cinnamomi* and cinnamon plantations in Sumatra (Rands 1922), *P. xvanyenensis* and *Acacia* plantations in Vietnam (Dang *et al.* 2021), and *P. mekongensis* and citrus plantations in Vietnam (Jung *et al.* 2024). In 2011 a previously unknown *Phytophthora* species with high ITS and *βtub* sequence similarity (99.5–100 %) to *P. europaea* was reported causing basal rot of the popular ornamental Japanese water iris (*Iris ensata* var. *ensata*) in Japan (Amemiya *et al.* 2011a, b). Assumed to have spread via infected bulbs, the disease has reached a widespread distribution in aquatic botanical gardens across Japan (Amemiya *et al.* 2011a, b). New BLAST searches at GenBank revealed 100 % identity of several Japanese isolates (e.g., SW09, YZ09; for ITS, *βtub*, *EF1a*, *cox1* and *nadh1* GenBank accession numbers see Table S1) to numerous isolates of *P. abietivora*. Although the pathway of this pathogen from North America into Japan remains unknown, the import of contaminated bulbs from overseas by private Japanese Iris collectors or by the international bulb trade seems likely.

Phytophthora laevigata, the closest relative of *P. abietivora*, is only known from the Western Balkans region where it was isolated from the rhizosphere of *F. sylvatica* trees in a natural beech forest in Bosnia-Herzegovina and from the rhizosphere of a declining hazelnut tree in a commercial orchard in Croatia.

The new species *P. facultativa* and *P. infundibuliformis* were isolated from naturally fallen *Rubus* leaves floating in a stream and from the rhizosphere of *Acer* trees, respectively, in healthy, natural, subtropical broadleaved forests of Louisiana, USA where they are most likely native to.

Phytophthora t. cadmea was isolated at two locations in California, in a restoration area in Santa Clara County from the rhizosphere of monkey flower (*Diplacus aurantiacus*) and in the Angeles National Forest from the rhizosphere of a rush species (*Juncus* sp.) growing in a riverbed of a natural Chapparral oak woodland (Bourret *et al.* 2023, Fajardo *et al.* 2025). Fajardo *et al.* (2025) reclassified two Eastern North American isolates from the original description of *P. abietivora* as *P. t. cadmea*, greatly expanding the known geographic range.

Phytophthora europaea is widespread in the rhizosphere of both declining and healthy oak forests in the UK, France, Germany, Austria and Serbia (Jung *et al.* 2002, Balci & Halmschlager 2003a, Landa *et al.* 2021; this study). It has also been isolated from rhizosphere soil of declining mature beech trees in forests of Germany (Jung 2009) and Sicily (T. Jung, S.O. Cacciola & M. Horta Jung, unpublished result). Due to its widespread distribution in Europe, its association with healthy or mildly declining trees and its comparatively low pathogenicity to *Q. robur* roots under controlled conditions (Jung *et al.* 2002), *P. europaea* is considered native to Europe. As mentioned before, early records of *P. europaea* from oak forest soils in North Central and Eastern USA (Balci *et al.* 2007) and streams in Oregon (Reeser *et al.* 2011) should be re-assigned to either *P. abietivora* or *P. t. cadmea* with which they share 99.9–100 % ITS sequence identity. However, one '*P. europaea*' isolate from the World Phytophthora Collection (WPC P15554) obtained from rhizosphere soil of *Quercus rubra* in West Virginia is closest related to *P. t. cadmea* but shows sequence identities with the latter of only 99.25–99.36 % for *cox2*, 98.47 % for *rps10* and 97.06 % for *atp9-nad9* (GenBank JF771442, JF771053 and JF771836, respectively). Most likely, isolate WPC P15554 constitutes a novel undescribed Clade 7a3 taxon informally designated here as *P. t. cadmea*-like. In an Australia-wide metabarcoding survey of forest soils molecular operational taxonomic units (MOTUs) were detected in New South Wales and Tasmania which were designated as '*P. europaea* complex' (Burgess *et al.* 2017). However, the short ITS1 fragments did not allow species identification and could belong effectively to any species from Clade 7a3 highlighting a major limitation of metabarcoding approaches. In their review of *Phytophthora* diseases in New Zealand, Scott & Williams (2014) report the occurrence of *P. europaea* in natural ecosystems without giving further details. The International Collection of Microorganisms (ICMP) includes two strains from New Zealand designated as *P. europaea*, one isolated in 2002 in South Canterbury on the South Island from a stem rot of the introduced ornamental *Iris sibirica* (ICMP 14820 = CBS 112276 = ICMP 16258) and a second one isolated in 2011 in Auckland on the North Island from a root of the native conifer species *Dacrydium cupressinum* (ICMP 19116). Since no sequence data are available for both isolates and their identification was performed prior to the description of the Clade 7a3 species *P. flexuosa* and *P. abietivora* (Jung *et al.* 2017a, Li *et al.* 2019) and the four new Clade 7a3 species described here, it remains unknown whether they belong to *P. europaea* or a related Clade 7a3 taxon. However, regardless of their exact identity, these isolates were certainly introduced to New Zealand, most likely from one of the known Northern Hemisphere Clade 7a3 centres.

Six isolates (e.g., P1385, Table 1) obtained in 2021 by a research group of the University of Agriculture in Krakow from cotyledons and stems of naturally regenerated, declining beech seedlings in four forests in Poland (Jankowiak *et al.* 2023) show almost 100 % ITS identity (e.g., GenBank OP246228) to the *P. europaea* ex-type but differ from the latter in the *cox1* gene (e.g., GenBank OP257397-OP257390 contig) at 10–11 positions (99.1 %

identity). These isolates most likely belong to a new taxon which is informally designated here as *P. taxon europaea*-like.

Phytophthora flexuosa was described from the rhizosphere of healthy *Fagus hayatae* trees in a natural montane forest in Taiwan (Jung *et al.* 2017a). In this study, it was commonly found in Honshu and Shikoku, Japan, thriving in streams and the rhizosphere of healthy trees of *Chamaecyparis obtusa*, *Chamaecyparis pisifera* and *Pterocarya rhoifolia* in natural forests.

Phytophthora arta, the sister species of *P. flexuosa*, occurs in natural forest streams on the Japanese Shikoku and Kyushu islands and was also isolated in a natural forest on Kyushu island from a necrotic attached leaf of *Pieris japonica* 1 m above ground (this study).

Clade 7a4: *Phytophthora intricata*, the basal species from Clade 7a4, is only known from a *Quercus tarokoensis* stand in Taiwan where it is most likely endemic (Jung *et al.* 2017a).

Phytophthora formosa was described from rhizosphere soil of healthy trees of *Araucaria cunninghamii* and *Quercus glandulifera* in natural, subtropical, submontane monsoon forests of Taiwan (Jung *et al.* 2017a). In this study, *P. formosa* was commonly found in streams running through natural, diverse laurosilva forests on Shikoku and Kyushu Islands. It was also isolated from the rhizosphere of healthy *Machilus thunbergii* trees in a laurosilva forest on Shikoku Island. This species is most likely native to both Taiwan and Japan.

The new species *P. irregularis* co-occurs with its sister species *P. formosa* in the laurosilva forests on Kyushu and Shikoku Islands. In contrast to *P. formosa*, *P. irregularis* has rarely been found in stream water and is commonly isolated from rhizosphere soil of a range of tree species including *Castanopsis cuspidata*, *Castanopsis sieboldii*, *M. thunbergii*, *Quercus glauca* and *Zelkova serrata*. Since it is not associated with obvious disease symptoms and has not been found elsewhere, *P. irregularis* is most likely endemic in Japan.

Phytophthora attenuata was originally described from the rhizosphere of *Castanopsis carlesii* and *Chamaecyparis formosensis* in a natural, subtropical montane monsoon forest in Taiwan (Jung *et al.* 2017a). This island appears to constitute the eastern limit of its natural distribution as *P. attenuata* was also isolated from rhizosphere soil of *Acer oblongum* in a subtropical, montane, evergreen cloud forest in northern Vietnam (Jung *et al.* 2020) but was not recovered during the extensive survey across the Japanese archipelago (this study).

Two new, closely related sister species of *P. attenuata*, *P. grandoogonia* and *P. sessilis*, are native to northern Vietnam. *Phytophthora grandoogonia* occurs in the rhizosphere of various Fagaceae tree species, including *Castanopsis chinensis* and *Q. glauca*, *Dysoxylum juglans*, *Meliosma amottiana*, *Vernicia montana* and *Antidesma* sp. in subtropical, humid, submontane to lower montane monsoon forests of Ba Vi National Park. *Phytophthora sessilis* was isolated from streambed soil and rhizosphere soil of *Betula alnoides*, *Elaeocarpus japonicus*, *Neolitsea poilanei* and *Rhododendron arboreum* in subtropical, montane evergreen cloud forests of the Hoang Lien mountain chain.

The basal species of the '*P. attenuata* complex', *P. algida*, co-occurs with *P. sessilis* in the montane cloud forests of Hoang Lien National Park and with *P. grandoogonia* in subtropical, humid, submontane to lower montane monsoon forests of Ba Vi National Park where it was isolated from the rhizosphere of *A. oblongum* and *C. chinensis*, respectively. It is most likely endemic in northern Indochina.

Phytophthora fragariae causes red stele, also known as red core, and root rot of strawberry (*Fragaria × ananassa*) and loganberry (*Rubus × loganobaccus*) (Erwin & Ribeiro 1996, EFSA

2014, EPPO 2022a). Upon artificial inoculation, it can also infect species from other genera in the *Rosaceae*, *Amaranthaceae* and *Solanaceae* families. Originally described from England by Hickman (1940), the pathogen has reached a panglobal distribution occurring on all continents except Antarctica (EPPO 2022a) and, hence, its geographical origin remains unknown.

=*Phytophthora rubi*, previously known as *P. fragariae* var. *rubi* (Duncan et al. 1991, Wilcox & Duncan 1993, Wilcox et al. 1993, Erwin & Ribeiro 1996, Man in't Veld 2007), is the main causal agent of root rot of red raspberry (*Rubus idaeus*). First reported from the UK in the 1930s, the economically most important disease of this horticultural crop species currently occurs in Western and Eastern North America, Chile, Western, Central and Northern Europe, Serbia, the Ukraine and Australia (EPPO 2022b). A survey in Washington State demonstrated the presence of *P. rubi* in 90 % of the surveyed raspberry fields (Gigot et al. 2013, Stewart et al. 2014). Natural infections by *P. rubi* have also been recorded on loganberries and tayberries (*Rubus fruticosus* × *R. idaeus*) (EPPO 2022b). Population genomic analyses of 138 isolates from across the USA and Europe using single nucleotide polymorphisms (SNPs) obtained from genotyping-by-sequencing (GBS) demonstrated predominantly clonal population structure and indicated pathogen spread from the Western to the Eastern US States and from California to Europe (Tabima et al. 2018). Despite extensive surveys, *P. rubi* has not been recovered from natural ecosystems in Western North America (Adams et al. 2010, Reeser et al. 2011, Hansen et al. 2012, Sims et al. 2015, Bourret et al. 2023, Fajardo et al. 2025) and, hence, its geographical origin remains unresolved.

Phytophthora alni, originally described as *P. alni* ssp. *alni* (Brasier et al. 2004) and later renamed by Husson et al. (2015), is an aggressive host-specific root and collar rot pathogen of alder (*Alnus*) species responsible for the epidemic mortality of *A. glutinosa*, *A. incana*, *A. lusitanica* and, rarely, *Alnus cordata* in riparian forests, alder carrs and forest stands on wet or waterlogged sites (Gibbs et al. 1999, 2003, Streito et al. 2002, Jung & Blaschke 2004, Thoirain et al. 2007, Redondo et al. 2015, Jung et al. 2018a, Corcobado et al. 2023, Gomes Marques et al. 2024). In pathogenicity trials *Alnus viridis* from the European Alps and the North American *A. rubra* were also susceptible to *P. alni* (Jung & Blaschke 2006). The pathogen was found widespread in the European nursery trade (Jung & Blaschke 2004, Schumacher et al. 2006, Jung et al. 2016). In Bavaria, a large-scale survey along 20000 kilometres of rivers and streams and in more than 3000 alder forest stands could trace back the origin of the riparian epidemic to more than 1000 alder plantings, unambiguously demonstrating that this epidemic was driven primarily by the planting of infested nursery stock (Jung & Blaschke 2004). Root and collar rot of alders by *P. alni* was first observed in 1994 in the UK and subsequently spread rapidly across Western, Central and Eastern Europe to the South of Sweden and Norway, and more recently into Iberia (Gibbs et al. 1999, 2003, Streito et al. 2002, Nagy et al. 2003, Brasier et al. 2004, Jung & Blaschke 2004, De Merlier et al. 2005, Schumacher et al. 2006, Thoirain et al. 2007, Černý & Strnadová 2010, Solla et al. 2010, Redondo et al. 2015, Trzewick et al. 2015, Jung et al. 2016, 2018a, Kanoun-Boulé et al. 2016, Corcobado et al. 2023, Gomes Marques et al. 2024, Horta Jung et al. 2025). The pathogen has not yet been reported from outside of Europe. Although *P. alni* originates from multiple hybridizations between *P. uniformis* and *P. multiformis* (Husson et al. 2015, Aguayo et al. 2016, Jung et al. 2017a, Van Poucke et al. 2021) which most likely occurred in European nurseries (Brasier et al. 1999, Brasier & Jung 2003, Jung et al. 2018a), it is considered in Europe as an exotic invasive pathogen because both parental

species were introduced from other continents.

Phytophthora uniformis, the paternal parent of *P. alni*, was originally named *P. alni* ssp. *uniformis* (Brasier et al. 2004). It is also an alder-specific pathogen causing root and collar rot on *A. glutinosa* and *A. incana* in Europe (Nagy et al. 2003, Brasier et al. 2004, Jung & Blaschke 2004, Pintos-Varela et al. 2012, Aguayo et al. 2013, Štěpánková et al. 2013, Redondo et al. 2015, Jung et al. 2018a, Landa et al. 2021, Macháčová et al. 2024) and *A. rubra* and *A. incana* subsp. *tenuifolia* in the Pacific Northwest and Alaska (Adams et al. 2010, Aguayo et al. 2013, Sims et al. 2015). Contributing to the Europe-wide epidemic alder mortality, the impact of *P. uniformis* on alders becomes prevalent in areas with very cold winters such as Southern Sweden where it outcompetes *P. alni* due to its significantly higher frost tolerance (Černý et al. 2012, Redondo et al. 2015, J. Schumacher & T. Jung unpubl. data). A microsatellite analysis demonstrated that *P. uniformis* is native to Northwestern North America and has been introduced to Europe (Aguayo et al. 2013). *Phytophthora uniformis* is also thriving in European nurseries which certainly promoted its rapid spread across Europe (Jung et al. 2016, Bačová et al. 2024, Green et al. 2025).

Phytophthora ×*multiformis*, originally described as *P. alni* ssp. *multiformis* (Brasier et al. 2004), is the maternal parent of *P. alni* (loos et al. 2006, Husson et al. 2015, Aguayo et al. 2016). This alder-specific pathogen has a wide distribution in Western and Central Europe and a scattered distribution in Central Italy, Sardinia, Portugal and Spain (Santini et al. 2001, Gibbs et al. 2003, Brasier et al. 2004, Jung & Blaschke 2004, Pintos-Varela et al. 2017, Jung et al. 2018a, Corcobado et al. 2023, Gomes Marques et al. 2025; this study). It has also been reported from a Czech nursery (Bačová et al. 2024).

In underbark inoculation trials with mature logs of *A. glutinosa*, *P. alni* showed considerably higher aggressiveness than *P. uniformis* and *P. multiformis* (Brasier & Kirk 2001). However, in underbark inoculation tests on stems of 1-year-old *A. glutinosa* seedlings lesion lengths caused by *P. alni*, *P. multiformis* and *P. uniformis* did not differ significantly (Zamora-Ballesteros et al. 2017). Also in another underbark inoculation test on stems of 6-month-old *A. glutinosa* seedlings from two different Czech provenances, no significant difference in pathogenicity was found between *P. alni* and *P. uniformis* (Macháčová et al. 2024).

Phytophthora taxon ×*multiformis*-like, a hybrid between *P. uniformis* and *P. multiformis* with reversed parental roles compared to *P. alni* (Jung et al. 2017a; this study), was isolated only once in 2011 from a bark canker of an *A. glutinosa* tree in the Netherlands.

The newly designated *P.* taxon ×*alni*-like, most likely the result of a backcross between *P. alni* and its parent *P. uniformis*, is only known from a mountain stream in Bavaria where it was isolated in 2001 from a bark canker of an *A. incana* tree (this study).

Phytophthora cambivora is an important plant pathogen with an exceptionally wide host range that includes more than 130 known plant species. Plant families with a particularly high number of susceptible species comprise the *Aceraceae* (*Acer circinatum*, *A. macrophyllum*, *A. palmatum*, *A. pennsylvanicum*, *A. pseudoplatanus*, *A. rufrum*, *A. saccharum*), *Betulaceae* (*A. glutinosa*, *A. incana*, *A. viridis*, *Betula alba*, *B. celtiberica*, *B. lenta*, *Carpinus betulus*, *Corylus colurna*), *Ericaceae* (2 *Arctostaphylos* spp., *Arbutus menziesii*, *Azalea* spp., *Erica carnea*, *Calluna vulgaris*, *Pieris japonica*, *Rhododendron* spp. and hybrids), *Fagaceae* (*Fagus crenata*, *F. grandifolia*, *F. sylvatica*, 4 *Castanea* spp., 16 *Quercus* spp., *Notholithocarpus densiflorus*, *Chrysolepis chrysophylla*), *Lauraceae* (*Laurus nobilis*, *Lindera benaoin*, *Persea americana*, *Umbellularia californica*), *Rosaceae* (11 *Prunus* spp., 3 *Malus*

spp., *Cotoneaster* sp., *Heteromeles arbutifolia*, *Photinia fraseri*, *Pyrus communis*, 2 *Rubus* spp., *Rosa* spp. and hybrids, *Sorbus aucuparia*), Asteraceae (*Bacharis pilularis*, *Chrysanthemum* sp., *Cineraria* sp., *Dahlia* sp., *Senecio* sp.), and the conifer families Pinaceae (*Abies nordmanniana*, *A. procera*, *Cedrus atlantica*, *Pinus silvestris*, *Picea abies*, *Pseudotsuga menziesii*, *Tsuga canadensis*), Cupressaceae (*Chamaecyparis lawsoniana*, *Hesperocyparis macrocarpa*, *Juniperus communis*, *Thuja occidentalis*, *Th. plicata*) and Taxodiaceae (*Sequoiadendron giganteum*). Further important host trees include *Aesculus hippocastanum*, *Ae. turbinata*, *Buxus sempervirens*, *Casuarina equisetifolia*, *F. excelsior*, *Fraxinus pennsylvanica*, *Ilex aquifolium*, *Juglans regia*, *Magnolia obovata*, *Nothofagus dombeyi*, *N. pumilio*, *Pterocarya fraxinifolia*, *Taxus baccata*, *Ta. brevifolia*, *Tilia cordata*, *Ti. × europaea*, and *Ulmus glabra* (Day 1938, Suzui & Hoshino 1979, Bumbieris & Wicks 1980, Wilcox & Mircetich 1985, Erwin & Ribeiro 1996, Jung *et al.* 1996, 2000, 2016, 2018a, b, 2019, Vettraino *et al.* 2002, 2003, 2005, Jönsson *et al.* 2003, Jung & Blaschke 2004, Greslebin *et al.* 2005, Talgø *et al.* 2006, Balci *et al.* 2007, Saavedra *et al.* 2007, Schwingle *et al.* 2007, Warfield *et al.* 2008, Jung 2009, Nechwatal *et al.* 2011, Hansen *et al.* 2012, Bienapfl & Balci 2014, Prigigallo *et al.* 2015, Milenković *et al.* 2012, 2018, Rooney-Latham *et al.* 2019, Corcobado *et al.* 2020, Frankel *et al.* 2020, Seddaiu *et al.* 2020, Vélez *et al.* 2020, Burgess *et al.* 2021, Bily *et al.* 2022, Bourret *et al.* 2023, Bačová *et al.* 2024, Green *et al.* 2025, Harkness *et al.* 2025, Horta Jung *et al.* 2025; this study). *Phytophthora ×cambivora* causes, together with *P. cinnamomi*, ink disease of chestnut (*Castanea sativa*) in Southern Europe and the UK, and is involved, together with numerous other *Phytophthora* species, in the widespread declines of oak and beech forests across Europe. These diseases are characterised by fine root losses, bleeding bark cankers on roots and stems, chlorosis, microphyllly and wilting of leaves, dieback and eventually mortality (Day 1938, Moreau & Moreau 1952, Jung *et al.* 1996, 2000, 2005, 2018a, Balci & Halmschlager 2003a, b, Vettraino *et al.* 2002, 2005, Hartmann *et al.* 2006, Jung 2009, Schmitz *et al.* 2009, Stępniewska & Dłuszyński 2010, Milenković *et al.* 2012, Telfer *et al.* 2015, Corcobado *et al.* 2020, Horta Jung *et al.* 2025). In European beech, *P. ×cambivora* is also reported causing a twig blight up to 3 m above ground (Nechwatal *et al.* 2011). The pathogen also causes bark cankers and mortality of golden chinkapin trees (*C. chrysophylla*) in Oregon (Saavedra *et al.* 2007) and is involved in the destructive dieback of the endemic shrub *Nematolepis ovatifolia* in alpine-subalpine heathlands of the Snowy Mountains in New South Wales, Australia (Green 2016). *Phytophthora ×cambivora* has a cosmopolitan distribution (Erwin & Ribeiro 1996, Scott & Williams 2014, Jung *et al.* 2017a, 2018a, b, Mullett *et al.* 2023). Some of the 11 DAPC lineages occur on more than one continent, i.e., DAPC9 in Australia, Europe, North and South America; DAPC4mixed in Europe, North America and Australia; and DAPC11 in Europe and North America. Others are restricted to one continent, i.e., DAPC2, 4 and 6–8 to East Asia; DAPC3 to Europe; and DAPC10 to North America (Mullett *et al.* 2023). The DAPC1, 5 and 9 lineages cause ink disease of chestnut and the declines of oak and beech forests in Europe whereas the declines of apple and cherry fruit trees in North America, East Asia (Japan, South Korea) and Australia (Mircetich & Matheron 1976, Suzui & Hoshino 1979, Bumbieris & Wicks 1980, Wilcox & Mircetich 1985, Browne *et al.* 1995, Jee *et al.* 1997, Wicks *et al.* 1997) appear to be associated with the DAPC4mixed lineage (Mullett *et al.* 2023). The regular association with severe disease symptoms of a wide range of forest, horticultural and ornamental plant species and the clonal population structure of *P. ×cambivora* in Australia, Europe and the Americas (Mullett *et al.* 2023) demonstrate

that it is an introduced invasive pathogen in these continents. On the contrary, the high diversity of both diploid and allopolyploid lineages with co-occurrence of both mating types and evidence of regular sexual outcrossing, and the absence of apparent disease symptoms in the associated native flora indicating a host-pathogen equilibrium resulting from long-term coevolution, strongly suggest that the *P. ×cambivora* hybrid complex originates from Japan and most likely adjacent regions in East Asia (Mullett *et al.* 2023). The apparent absence of *P. ×cambivora* from natural ecosystems in the Hainan, Yunnan and Xinjiang provinces of China and Northern Vietnam suggest that it is not native in these regions (Zeng *et al.* 2009, Huai *et al.* 2013, Xu *et al.* 2019, Jung *et al.* 2020).

Phytophthora ×heterohybrida is currently only known from Cukeng River, Ha-pen River and several tributaries of the latter in a subtropical, evergreen *Castanopsis*-dominated monsoon forest in the Fushan area of Taiwan (Jung *et al.* 2017a). Since both mating types co-occur it is most likely endemic in this region. In one of the tributaries of Ha-pen River, *P. ×incrassata* co-occurred with *P. ×heterohybrida* (Jung *et al.* 2017a). It has not been found elsewhere yet. The natural host ranges of both *P. ×incrassata* and *P. ×heterohybrida* are unknown. In soil infestation tests, however, both species demonstrated high aggressiveness to root systems and the collar region of *C. sativa* plants (Jung *et al.* 2017a).

Two new sister species, closely related to *P. ×incrassata*, show a vicariant distribution in Japan. *Phytophthora ×leptopleura* is common in multiple forest streams running through warm-temperate laurosilva forests in the Satayama region on Shikoku Island whereas *P. ×nodosa* occurs in the rhizosphere of *Lithocarpus edulis* trees and in streams of warm-temperate laurosilva forests in the Takayama region on Kyushu Island (this study). Both species have not been found anywhere else in Japan or elsewhere and are most likely endemic in Shikoku and Kyushu, respectively.

Phytophthora ×grandisporangia, the sister species of *P. ×heterohybrida*, commonly occurs in streams running through subtropical, montane cloud forests in the Hoang Lien mountain range of northern Vietnam where it is most likely endemic (Jung *et al.* 2020; this study). The natural host range of this species is unknown.

Notes on the phylogeny of Clade 7a

The phylogenetic structure of Clade 7a was studied using separate nuclear and mitochondrial (mt) DNA datasets and a concatenated nuclear-mtDNA dataset and both BI and ML analyses. In addition, both BI and ML analyses were each performed with two different programmes and different settings. All 12 phylogenetic trees shared the same deeper phylogeny and supported structuring Clade 7a into four main clusters designated here as 7a1–7a4. Expectedly, mitochondrial discordances that affected taxa with hybrid origin more than ‘pure’ (i.e., non-hybrid) taxa, and topological differences between BI and ML trees inherent to their algorithm differences were observed. Moreover, BI and ML analyses performed on the same datasets with different programmes (MrBayes vs BEAST and IQ-TREE vs RAxML, respectively) and different settings, primarily concerning evolutionary model selection and molecular clock assumptions, yielded partially different tree topologies. Naturally, due to missing data on both extinct taxa and still undiscovered extant taxa, phylogenies can be at best an approximation of reality. Since the quality of inference of BI and ML analyses is considered similar (Wertheim *et al.* 2010) and the performance of different molecular clock models in shallow phylogenies (genus level and below) is dependent on the — usually unknown — levels of evolutionary rate variations between branches



(Brown & Yang 2011, Sarver *et al.* 2019), it remains unknown which one(s) of the 12 phylogenetic trees produced in this study are the best approximation for Clade 7a. The Clade 7a trees, in particular the BI trees of the nuclear and concatenated datasets (Figs 2, 6, S1, S5), contained multiple polytomies. These could indicate true species radiations or phylogenetic conflicts caused by reticulation events, recombination events or homoplasy (Bandelt *et al.* 1999, Posada & Crandall 2001, Cassens *et al.* 2005). The polytomy of the four 'pure' North American taxa *P. abietivora*, *P. facultativa*, *P. infundibuliformis* and *P. t. cadmea* and the 'pure' European *P. laevigata* in both BI analyses of the nuclear dataset (Figs 2, S1) may likely reflect a true species radiation. In contrast, the polytomies in Clade 7a4 most likely result from phylogenetic conflicts caused by the high proportion (48 %) of taxa with confirmed or probable hybrid origin (10 of the 21 taxa). The presence of ancestors and descendants within the 11 DAPC lineages of *P. ×cambivora* is also likely to have caused phylogenetic conflicts as shown recently for the different lineages of *P. ramorum* (Jung *et al.* 2021).

Notes on the evolutionary history and biogeography of Clade 7a

The now 34 taxa in Clade 7a have a disjunct natural distribution in four biogeographic regions across the Northern Hemisphere: the Nearctic (USA, Canada), Palearctic (Europe), Sino-Japanese (Japan) and Oriental (Taiwan, Vietnam) regions (Fig. 44). Eight species are native to Japan, six to Taiwan and five to northern Vietnam. One species, *P. attenuata*, is common to both Vietnam and Taiwan, and two species, *P. flexuosa* and *P. formosa*, are shared between Taiwan and Japan. With 15 species in total believed to be native, the forests of East Asia harbour ~45 % of the known Clade 7a taxa. Europe is another centre of diversity, with six probable endemic species: *P. europaea*, *P. laevigata*, *P. tyrrhenica*, *P. uliginosa*, *P. vulcanica* and *P. t. europaea*-like. North America comprises two centres. One, ranging from Louisiana across the Eastern and Mid-Central USA to the Great Lakes, Ontario and Quebec, currently has four endemic Clade 7a taxa: *P. abietivora*, *P. facultativa*, *P. fagacearum* and *P. t. cadmea*-like. The other, ranging from California to Southeastern Alaska, currently has two, *P. uniformis* and *P. t. cadmea*.

In the updated phylogeny, Clade 7a comprises four subclusters, 7a1–7a4. Its evolutionary history is characterised by the early divergence of Clade 7a1, currently represented only by *P. vulcanica*, followed by the subsequent divergence of Clade 7a2 with *P. tyrrhenica* and *P. uliginosa*, Clade 7a3 with eight taxa and, most recently, the divergence of the largest cluster Clade 7a4 with 21 taxa (Figs 2–7, S1–S6). The two basal clusters Clades 7a1 and 7a2 are exclusive to Europe. In contrast Clade 7a3 has a disjunct holarctic distribution, with two endemic species in Europe, two in East Asia and four in North America. This indicates that the ancient ancestors of Clade 7a probably appeared in Europe after the breaking up of Laurasia and the effective separation of the North American and Eurasian Plates ~90–80 Mya; and subsequently radiated into the three clusters 7a1–7a3; and that 7a3 spread from Europe to both North America and East Asia.

The higher diversity of Clade 7a3 taxa in Eastern North America (*P. abietivora*, *P. facultativa*, *P. infundibuliformis*, *P. t. cadmea*-like) compared to Western North America (*P. t. cadmea*) suggests that the migration of Clade 7a3 to North America occurred across North Atlantic land bridges (NALBs), rather than via the Beringia land bridges. The NALBs connected Europe, Greenland and North America during the warmer climates of the late Cretaceous and Paleogene (~70–23 Mya) during which period a boreotropical vegetation thrived (Tiffney 1985, Lavin & Luckow 1993, Tiffney & Manchester 2001, Davis *et al.* 2002, 2004, Fritsch & Cruz 2012). However, both the timing and duration of NALBs are still under debate (e.g., Tiffney & Manchester 2001, Brikiatis 2014, Denk & Grimm 2009, Denk *et al.* 2010). The migration of Clade 7a3 to East Asia probably happened more recently, after the disappearance of the Turgai Strait that separated Europe from Asia between 160 and 29 Mya (Briggs 1995). That only three extant native Clade 7a3 taxa have been found so far in Europe might be a result of the greater Pleistocene extinctions there compared to Asia and North America (Huntley 1993, Latham & Ricklefs 1993, Svenning 2003).

Clade 7a4 is essentially an East Asian clade. Thus, apart from three species of cryptic origin (*P. fragariae*, *P. rubi* and *P. ×multiformis*), three taxa resulting from recent hybridisation between species introduced to Europe (*P. ×alni*, *P. t. ×alni*-like and *P. t. ×multiformis*-like) and the two native to North America

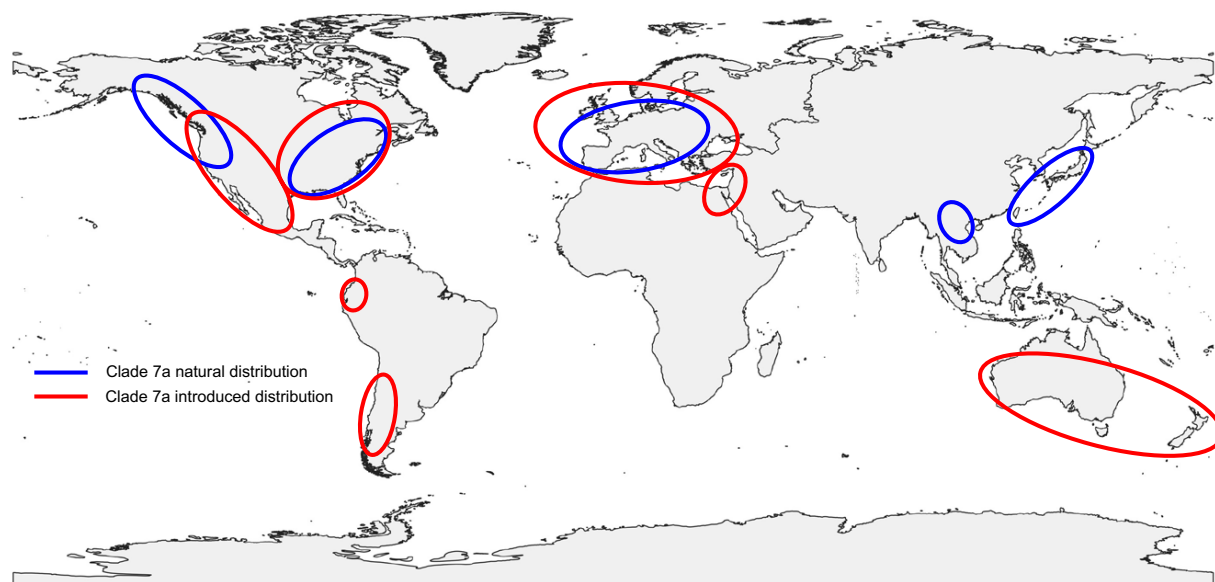


Fig. 44. Natural (blue colour) and introduced (red colour) global biogeography of *Phytophthora* Clade 7a.



(*P. fagacearum* and *P. uniformis*), all the other taxa including the basal groups are native to East Asia. It therefore seems likely that the separation of Clades 7a3 and 7a4 occurred in East Asia and that 7a4 then spread to Western and subsequently Eastern North America via the intermittent Beringia land bridges ~70–5.3 Mya (Gladenkov *et al.* 2002, Brikiatis 2016) and temporarily during the Pleistocene (Vila *et al.* 2011, Elias & Brigham-Grette 2013). These bridges enabled the intercontinental migrations responsible for the relatedness of current East Asian and North American floras (Qian 2002, Baskin & Baskin 2016, Wen 1999, Wen *et al.* 2010, 2016).

The disjunct distributions of Clades 7a1–7a4 and the often vicariant distributions of species within the different subclade centres are most likely a product of allopatric, non-adaptive radiation processes resulting from reproductive isolation imposed by geographic barriers and gradually accumulating genetic drift (Brasier 1986, Kozak *et al.* 2006, Rundell & Price 2009, Jung *et al.* 2024). Suggested examples are, within Clade 7a2 in Europe, the distributions of *P. tyrrhenica* south of the Alps and *P. uliginosa* north and west of the Alps; within Clade 7a3 its four centres in Europe, East Asia, Western and Eastern North America; within Clade 7a4 the distributions of its species-rich centre in East Asia, *P. uniformis* in Western and *P. fagacearum* in Eastern North America, and its three sub-centres in Vietnam, Taiwan and Japan. Within the Japanese archipelago, the vicarious distributions of the self-fertile *P. ×nodosa* on Kyushu Island and its self-sterile sister species *P. ×leptopleura* on Shikoku Island might also reflect allopatric speciation resulting from hybridisation of their shared paternal ancestor with unknown, local (and possibly extinct) maternal parents. Similarly, the vicarious distributions of the *P. ×cambivora* lineages DAPC6 in Northern Honshu, DAPC8 in Central Honshu and DAPC7 in Kyushu (Mullett *et al.* 2023) might result from geographically localised hybridisation events between closely related but unknown paternal parents (Figs 2, 3, S1, S2) with unknown, local maternal parents (Figs 4, 5, S3, S4).

In contrast, the co-occurrence of the sister species *P. arta*/*P. flexuosa* from Clade 7a3 and *P. formosa*/*P. irregularis* from Clade 7a4, respectively, in Japanese forests is most likely the result of sympatric adaptive radiation associated with different host plants, microclimates, soil types and microbiomes (Mayr 1942, Brasier 1986, Givnish 1997, 2015, Rundell & Price 2009, Jung *et al.* 2017b,

2022, 2024). Since the Japanese Archipelago and Taiwan were never directly connected via the Ryukyu island chain (Kimura 2000, Watanabe *et al.* 2023), the disjunct natural distributions of both *P. flexuosa* and *P. formosa* in Japan and Taiwan (Jung *et al.* 2017a, this study) are best explained by migration via the Asian mainland. These could have occurred before the opening of the Sea of Japan 20–15 Mya and/or via temporary land bridges that connected the Japanese main islands and Taiwan with the Asian mainland during periods of lowered sea levels in the Pleistocene (Hayashida & Ito 1984, Chang-Fu *et al.* 1994, Chung-Fu 1994, Maruyama *et al.* 1997, Isozaki *et al.* 2011, Gower *et al.* 2012).

The extant sympatry of all four species of the Clade 7a4 '*P. attenuata* complex' in a relatively small region of northern Vietnam is probably also the product of adaptive radiation. The two geographically isolated Clade 7a4 hotspots in Vietnam, *P. algida*, *P. attenuata*, *P. sessilis* and *P. ×grandisporangia* in upper-montane cloud forests on the Fansipan mountain and the related *P. algida* and *P. grandoogonia* in submontane monsoon forests of Ba Vi National Park are more likely to be a pleistocene relic. During glacial periods the climate in Asia was considerably cooler and drier forcing montane and hydrophilic species to retreat into isolated 'mountain island' refugia surrounded by drier savannahs or grasslands from which they could not escape when temperatures increased again, resulting in disjunct post-Pleistocene distributions (Heaney 1991, Laumonier 1997, MacKinnon *et al.* 1997, Whitten *et al.* 1997, 2002, Hope 2001, Hope *et al.* 2004, Cannon *et al.* 2009, Tian *et al.* 2010, Wurster *et al.* 2010, Ye *et al.* 2016, Jung *et al.* 2024). As with the distribution of *P. flexuosa* and *P. formosa* in Clade 7a3, the occurrence of *P. attenuata* in several mountain forests of Taiwan, almost 2000 km from northern Vietnam, may be the result of a migration via a temporary Pleistocene land bridge connecting Taiwan with the Asian mainland.

Notes on heterozygosity, breeding systems and hybridity of Clade 7a

Heterozygosity data for all taxa examined based on eight nuclear genes; and the relationship between mean heterozygosity and breeding system (self-fertile, A1/A2 outcrossing or sterile; see Terminology section) and inferred 'pure' (i.e., non-hybrid) or hybrid

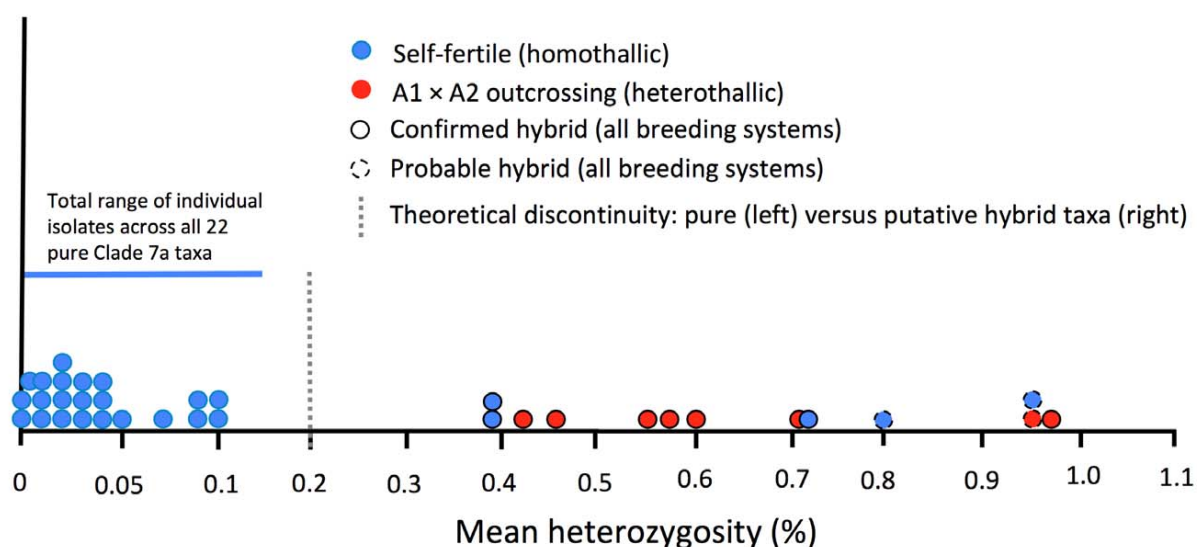


Fig. 45. Distribution of mean nuclear gene heterozygosity for the 22 'pure' (i.e., non-hybrid) and 10 hybrid taxa in *Phytophthora* Clade 7a.



status are shown in Table 2 and Fig. 45.

Ten taxa in Clade 7a (~30 %) are either confirmed or probable hybrids (Table 2). Based on nuclear genotyping by sequencing, quantification of alleles of single-copy nuclear genes and genome size estimations using flow cytometry *P. ×alni*, *P. ×cambivora*, *P. ×heterohybrida*, *P. ×incrassata*, *P. ×multiformis*, *P. t. ×multiformis*-like and the new *P. ×grandisporangia* (designated as *P. ×heterohybrida*-related) were previously identified as allopolyploid hybrids (Brasier *et al.* 1999, Husson *et al.* 2015, Jung *et al.* 2017a, Van Poucke *et al.* 2021, Mullett *et al.* 2023). Unpublished data from the GBS study of Mullett *et al.* (2023) presented here (Fig. S7) show that, similar to their close relative *P. ×incrassata*, *P. ×nodosa* and *P. ×leptopleura* exhibit high numbers of tri-allelic loci and even some tetra-allelic loci (Fig. S7), unambiguously demonstrating their allopolyploid hybrid origin. In addition, both species and the informally designated *P. t. ×alni*-like feature higher nuclear heterozygosity levels (0.95, 0.95 and 0.8 %; Table 2) than most confirmed hybrid taxa in *Phytophthora* Clades 2a, 2b and 7a (Jung *et al.* 2024), high levels of mitochondrial gene identity with another Clade 7a taxon (Figs 4, 5, S3, S4) and occasional failure to differentiate the sporangial cytoplasm into individual zoospores, resulting in large multinucleate zoospores with hampered motility (Figs 34, 41), a typical feature of interspecific *Phytophthora* hybrids (Burgess 2015, Jung *et al.* 2017a, 2024, this study). Consequently, *P. t. ×alni*-like was also considered as hybrid in this study and formally designated as such.

The proportion of confirmed or probable hybrid taxa in Clade 7a (~30 %) is nearly as high as observed in Clades 2a and 2b (each ~38 %; Jung *et al.* 2024). However, all the putative and confirmed hybrid taxa in Clades 2a and 2b have an A1/A2 compatibility system or are sexually sterile, suggesting the A1/A2 system favours interspecific hybridisation, and that sterility may be a regular product of it (Jung *et al.* 2024). In contrast, only 50 % of the Clade 7a hybrid taxa have a self-sterile A1/A2 breeding system (*P. ×cambivora*, *P. ×grandisporangia*, *P. ×heterohybrida*, *P. ×incrassata*, *P. ×leptopleura*). The others are self-fertile (*P. ×alni*, *P. ×multiformis*, *P. ×nodosa*, *P. t. ×alni*-like, and *P. t. ×multiformis*-like), similar to the Clade 1 hybrids *P. ×pelgrandis* and *P. ×serendipita* (Man in 't Veld *et al.* 2012). Since all 21 'pure' taxa in Clade 7a are self-fertile (no data available for *P. t. cadmea*, *P. t. cadmea*-like and *P. t.*

europaea-like), the A1/A2 'system' of Clade 7a taxa identified so far appears to be more a consequence than a promoter of interspecific hybridisation events, i.e., the A1/A2 species may have developed from the hybridisation between self-fertile, more inbreeding species and hence might be considered 'secondary heterothallics' (cf. Brasier 1992). This evolutionary feature of Clade 7a may apply also to other Clade 7 subclades. Based on large genome sizes (> 300 Mbp) and relatively large numbers of triallelic loci, *P. niederhauserii* and the undescribed *P. taxon niederhauserii*-related from Clade 7b, and *P. cinnamomi* and *P. parvispora* from Clade 7c, are also putative allopolyploid hybrids (Van Poucke *et al.* 2021). Failed separation of zoospores is also occasionally observed in *P. cinnamomi* (Fig. 46).

Clade 7a hybrids also differ from Clade 2a hybrids in their genome sizes, and, hence, their ploidy levels, as estimated by flow cytometry (Jung *et al.* 2017a, Van Poucke *et al.* 2021). In Clade 2a the genome sizes of hybrids with available data, *P. ×taiwanensis* (designated as *P. ×citrophthora*-related1) and the putative hybrid *P. vietnamensis* (designated as *P. ×citrophthora*-related3), range from 124–193 Mbp indicating diploidy (Van Poucke *et al.* 2021). In contrast, with the exception of *P. ×cambivora* DAPC2, 3 and 6 lineages and few isolates of the DAPC4, which have diploid genomes (Mullett *et al.* 2023), all tested Clade 7a hybrids are allopolyploid with genome sizes of 313–343 Mbp (*P. ×heterohybrida*); 285–510 Mbp (*P. ×cambivora*); 505–844 Mbp (*P. ×alni*); 518–561 Mbp (*P. ×grandisporangia* under its previous designation *P. ×heterohybrida*-related); 619–654 Mbp (*P. ×incrassata*; additional smaller nuclei with 421–426 Mbp); and 653 Mbp (*P. ×multiformis*). Yet another contrast between the presumed hybrids in Clade 7a and those in Clades 2a/2b is the exclusively aerial lifestyle of the latter (Jung *et al.* 2024); whereas the 7a taxa share a predominantly soil- and/or waterborne lifestyle with each other and with the 22 known 'pure' Clade 7a taxa.

All 21 'self-fertile pure' Clade 7a taxa for which data were available showed relatively low levels of mean nuclear heterozygosity between only 0.004 and 0.11 %. The overall range of all 67 isolates in this 'group' was 0.01 to 0.15 (Table 2 and horizontal bar in Fig. 45), i.e., nuclear heterozygosity levels were below 0.16 % in all isolates. In contrast the ten other taxa, all confirmed or probable hybrids, had mean heterozygosities ranging from 0.38 to 0.97 %, whether or not they were self-fertile or A1 × A2 outcrossing. Only a single



Fig. 46. *Phytophthora cinnamomi*. **A–D.** Structures formed on V8-agar in soil extract. **A.** Two joined zoospores failing to separate from each other. **B.** Sporangium with nested internal proliferation and constriction of the sporangiophore (arrow). **C.** Non-papillate sporangium with constriction of the sporangiophore (arrow). **D.** Caducous internally proliferating sporangium that was shed at a sporangiophore constriction. Images: A–D. TJ1244. Scale bar = 20 µm; applies to A–D.

isolate of *P. ×multiformis* isolate exhibited a nuclear heterozygosity below 0.3 % (0.26 %). There is therefore a theoretical discontinuity at around 0.2 % between the low and high heterozygosity 'groups' (Fig. 45), similar to the discontinuity, at around 0.3 %, defined between 'pure self-fertile and A1/A2' and 'hybrid A1/A2 and sterile' groups in *Phytophthora* Clades 2a and 2b (Jung *et al.* 2024).

The occurrence of several self-fertile taxa in the high heterozygosity group is expected, since most of these have either already been shown to be alloheteroploids of very recent hybrid origin, or are shown here to be recently derived from the latter via further hybridisation events. Among the A1/A2 taxa in the high heterozygosity group, the eleven previously discriminated and genetically near diploid to heteroploid *P. ×cambivora* lineages, DAPC1–11, exhibited mean heterozygosity levels ranging from 0.46 to 0.7, consistent with their previously described diversity (Mullett *et al.* 2023).

That all currently known Clade 7a hybridisation events are in Clade 7a4 probably reflects both biogeography and anthropogenic influences. All Clade 7a4 hybrids obtained from natural ecosystems in East Asia originated on islands like Taiwan (*P. ×incrassata*, *P. ×heterohybrida*) and the Japanese Archipelago (*P. ×cambivora*, *P. ×leptopleura*, *P. ×nodosa*) or on 'mountain islands' like the Fansipan (*P. ×grandisporangia*). During the Pleistocene these regions experienced episodes of migration and interchange alternating with periods of isolation facilitating, besides allopatric speciation and adaptive radiation, hybridisation between resident and newly arrived species (Chang-Fu *et al.* 1994, Chung-Fu 1994, Gower *et al.* 2012, Jung *et al.* 2017a, 2024). Modern anthropogenically-driven processes, such as the introduction to European nurseries of the non-native Clade 7a4 species, *P. uniformis* and *P. ×multiformis*, probably led to the emergence of *P. ×alni*, *P. t. ×multiformis*-like and *P. t. ×alni*-like. Owing to their assumed previous allopatric distributions *P. uniformis* and *P. ×multiformis* probably lack strong, coevolved reproductive barriers (cf. Brasier 1995, 2000). This, in combination with conducive nursery environments characterised by highly susceptible young plants, continuous moisture and recirculation systems, may have led to the emergence of *P. ×alni*, *P. t. ×multiformis*-like and *P. t. ×alni*-like. Within the overall '*P. ×alni* complex', *P. uniformis* and *P. ×multiformis* are now known to be the paternal and maternal parents of *P. ×alni*, respectively; *P. t. ×multiformis*-like has reverse parental roles compared to *P. ×alni*; and *P. t. ×alni*-like has probably resulted from a backcross between *P. ×alni* as maternal and *P. uniformis* as paternal parent (Ioos *et al.* 2006, Husson *et al.* 2015, Jung *et al.* 2017a, Van Poucke *et al.* 2021, this study).

Despite extensive surveys in natural ecosystems of Taiwan, Vietnam and Japan (Brasier *et al.* 2010, Jung *et al.* 2017a, c, 2020, this study), the parent species of the natural hybrids *P. ×cambivora*, *P. ×grandisporangia*, *P. ×heterohybrida*, *P. ×incrassata*, *P. ×leptopleura* and *P. ×nodosa* are mostly unknown. They might occupy highly cryptic niches or be extinct, possibly outcompeted and driven to extinction by their successful hybrid descendants (cf. Brasier 1995, 2000). *Phytophthora ×incrassata* differs from its sister species *P. ×leptopleura* and *P. ×nodosa* at only 1 and 1–3 positions across three mitochondrial genes, and might be the maternal parent of both these hybrid species. This possibility is further supported by *P. ×incrassata* residing in a basal position to *P. ×leptopleura* and *P. ×nodosa* in all four mitochondrial ML and BI trees (Figs 4, 5, S3, S4).

With 11 DAPC lineages and eight known mitochondrial genotypes, the '*P. ×cambivora* hybrid complex' arguably has the most intricate hybridisation history amongst all known *Phytophthora* hybrids. The DAPC1, 5 and 9 lineages, distributed mainly across

Europe, share the same maternal line and DAPC5 itself is a product of hybridisation between DAPC1 and DAPC9 (Mullett *et al.* 2023). The mitochondrial genotype of the purely North American DAPC10 lineage is identical or almost identical (0–1 bp difference) to that of DAPC1, 5 and 9, i.e., they share the same maternal line. They also share a maternal ancestor with the Japanese DAPC7 lineage, and this five-lineage cluster has a common maternal ancestor with the Japanese DAPC8 lineage (Figs 4, 5, S3, S4). Similarly, the Japanese DAPC2 and 6 lineages have an identical mitochondrial genotype which is in turn almost identical to the Japanese DAPC4 lineage (0–1 bp) and the globally distributed DAPC11 lineage (1–2 bp). This again strongly suggests these four lineages share the same maternal line (Figs 4, 5, S3, S4). DAPC3, currently known exclusively from Poland, has the most distinct of all *P. ×cambivora* maternal lines (Figs 4, 5, S3, S4). It resides separately from all other DAPC lineages, and in a sister position to *P. ×multiformis* and, hence, also *P. ×alni* and *P. t. ×alni*-like. Overall, *P. ×cambivora* comprises at least five separate maternal lines.

Notes on the morphology, physiology and lifestyles of Clade 7a

Except for a low frequency of semipapillate sporangia in *P. formosa*, *P. ×heterohybrida* and *P. ×incrassata*, all 31 taxa with available data (none available for *P. t. cadmea*, *P. t. cadmea*-like and *P. t. europaea*-like) produce non-papillate sporangia which are almost exclusively persistent and show abundant internal proliferation, consistent with a predominantly soil- and waterborne lifestyle. However, in three hybrid taxa, *P. ×grandisporangia*, *P. ×heterohybrida* and *P. t. ×alni*-like (Figs 31, 41; Jung *et al.* 2017a), and three 'pure' species, *P. facultativa*, *P. infundibuliformis* and *P. laevigata* (Figs 22–24), a small proportion of sporangia (< 1 %) exhibit narrow constrictions of sporangiophores enabling partial caducity and potentially aquatic spread or rain- and wind-splash 'aerosolling'. Similar constrictions and partial caducity also occur in soil- and waterborne species in *Phytophthora* Clades 2c (*P. obturata*, *P. platani*), 2e (*P. pseudofrigida*) and 2g (*P. inclinata*) (Jung *et al.* 2024), 7c (*P. cinnamomi*) (this study; Fig. 46), 10b (*P. pseudogallica*, *P. subarctica*, *P. ukrainensis*) (Jung *et al.* 2022) and 12 (*P. tubulina*) (Jung *et al.* 2017b). This might be an opportunistic trait, allowing species with a predominantly soil- and waterborne lifestyle to infect aerial plant tissues as a resource. Contrary to the erroneous perception that sporangial sympodia are exclusive to *Phytophthora* taxa with a predominantly aerial lifestyle, 23 of the 31 Clade 7a taxa studied here (74.2 %) produce sympodia of 2–3 sporangia (Tables 3–8).

Bullate, warty or verrucose ornamentation of oogonial walls is a scarce character in *Phytophthora*, known only from the obligate biotrophic species *P. cyperi-bulbosi* and *P. verrucosa* (Waterhouse 1970, Erwin & Ribeiro 1996), several species in Clades 5 (*P. castaneae*, *P. novae-guineae*) and 6b (*P. gibbosa*, *P. mississippiiae*, *P. ornamentata*), and Clade 7a where it occurs in numerous taxa (Brasier *et al.* 2004, Jung *et al.* 2011, 2017a, Yang *et al.* 2013, Scanu *et al.* 2015, Weir *et al.* 2015, Arentz 2023, Crous *et al.* 2024, this study). Intriguingly, ornamented oogonia are produced by both Clade 7a3 species from East Asia, *P. arta* and *P. flexuosa*; two of the three Clade 7a3 species from North America, *P. facultativa* and *P. infundibuliformis*; and within Clade 7a4 by all 13 species originating from Asia except the basal species *P. intricata*, the North American *P. fagacearum* and four of the five taxa from the '*P. ×alni* complex' introduced to or evolved subsequently in Europe (the exception being *P. uniformis*). Since none of the endemic European species in Clades 7a1–a3 form ornamented oogonia, this feature

most probably evolved after the introduction of Clade 7a3 to North America and Asia.

The vast majority of sexually self-fertile (morphologically 'homothallic') *Phytophthora* do not form chlamydospores (Wilcox *et al.* 1993, Erwin & Ribeiro 1996, Brasier *et al.* 2004, 2005, 2022, Li *et al.* 2019, Jung *et al.* 2022, 2024, Crous *et al.* 2024). This includes all 26 self-fertile taxa in Clade 7a (this study). In contrast, most A1/A2 self-sterile ('heterothallic') *Phytophthora* species do form chlamydospores, probably because of the uncertainties of encountering a genotype of the opposite compatibility group, and to ensure survival under unfavourable environmental conditions (Brasier *et al.* 2022, Jung *et al.* 2024). However, this does not apply to the five A1/A2 taxa in Clade 7a. This might again reflect the fact that these taxa have arisen exclusively from allopolyploid hybridization events between self-fertile species, most probably during the Pleistocene. Perhaps this is too recent for the evolutionary development of chlamydospore formation. Or perhaps chlamydospores would not provide a significant selective advantage in the near year-round humid conditions where these hybrids thrive (the cloud forests of Vietnam, the monsoon forests of Taiwan and the beech and laurosilva forests of the Japanese archipelago).

Intriguingly, in the sister subclades 7b to 7d, most taxa are also self-fertile, and the few taxa with A1/A2 breeding systems are also putative allopolyploid hybrids (Van Poucke *et al.* 2021). Of these, *P. niederhauserii* from Clade 7b (no data available for *P. taxon niederhauserii*-related) does not produce chlamydospores (Abad *et al.* 2014), but both *P. cinnamomi* and *P. parvispora* from Clade 7c do regularly produce chlamydospores (Jung *et al.* 2013, Scanu *et al.* 2014, EPPO 2025). This might be an adaptation to the permanently hot and seasonally dry conditions of their tropical and subtropical lowland rainforest habitats in Southeast Asia (Jung *et al.* 2017c, 2020, Shakya *et al.* 2021, Botella *et al.* 2025).

Clade 7a taxa are predominantly cool- and warm-temperate species. Only five species are found in subtropical zones, and even these occur mostly in montane, and hence temperate, forests in northern Vietnam and Taiwan. Indeed, there is a distinct absence of taxa exhibiting high maximum temperatures for growth. Amongst the 31 Clade 7a taxa with available data, only *P. leptopleura* and *P. nodosa* from warm-temperate regions in Shikoku and Kyushu and most lineages of *P. cambivora* show some growth at 32.5 °C. No Clade 7a taxa grow at 35 °C (Figs 16–19) and most die at this temperature. Within *P. cambivora*, the DAPC lineages show strong evidence of temperature adaptations to the climatic regions they inhabit. For instance, the DAPC6 lineage from cold-temperate Northern Honshu (Japan) grows much slower in tests at 32.5 °C than lineages DAPC2, 7 and 8 from warm-temperate regions, and the pan-Japanese lineage DAPC4. Most isolates of the European DAPC3 and 11 lineages, and the North American DAPC10 lineage are unable to grow at 32.5 °C (Fig. 19).

One reason why Clade 7a is currently largely restricted to temperate zones may have been strong niche competition during migration events. In particular, competition from a plethora of *Phytophthora* species from other clades and subclades which were already resident in and adapted to tropical and subtropical ecosystems. When the Isthmus of Panama began 'closing' gradually from ~12 Mya, fusing the Laurasian North American and the Gondwanan South American Plates completely at ~3.5 Mya (Woodburne 2010, Bacon *et al.* 2015, Cione *et al.* 2015, Bogarin *et al.* 2016), the latter was probably already populated by tropical *Phytophthora* species from Clades 2b, 2d, 2e, 4, 5 and 9, which subsequently spread to and radiated in Central America (Brasier & Griffin 1979, Erwin & Ribeiro 1996, Legeay *et al.* 2020, Chen *et al.*

2022, Jung *et al.* 2024). This may have impeded the migration of less-adapted temperate Clade 7a taxa to the Neotropics. Likewise, assuming Clades 7a3 arrived in Asia after the disappearance of the Turgai Strait ~29 Mya (Briggs 1995), and Clade 7a4 diverged subsequently, then the tropical regions of South and Southeast Asia, New Guinea and Queensland were probably already populated by many tropical and subtropical species, both currently extant and extinct, e.g. from Clade 2 (numerous species from subclades 2a, 2c, 2e, 2f and 2g); Clade 4 (*P. palmivora*, *P. heterospora*); Clade 5 (*P. castaneae*, *P. heveae*); Clade 7c (*P. cinnamomi*, *P. parvispora*); Clade 9 (numerous species and hybrids from high temperature clusters 9a–c), Clade 10c (*P. celebensis*, *P. gondwanensis*, *P. javanensis*, *P. multiglobulosa*) and other oomycete genera (Brasier & Griffin 1979, Arentz & Simpson 1986, Erwin & Ribeiro 1996, Brown 1999, Drenth & Guest 2004, Jung *et al.* 2017c, 2020, 2022, 2023, 2024, Dang *et al.* 2021, Scanu *et al.* 2021, Shakya *et al.* 2021, Botella *et al.* 2022, 2025).

Notes on biosecurity threats posed by Clade 7a

Clade 7a includes several species that have become seriously economically or environmentally damaging following introduction to other biogeographic regions by human activity (Fig. 44). The most notable is the wide-host range pathogen *P. cambivora*, which most probably originates from Japan, but possibly also adjacent regions in East Asia (Mullett *et al.* 2023). *Phytophthora cambivora* has become a major, panglobal pathogen, with more than 130 reported host species and involvement in several epidemic root and collar rot diseases of common fruit tree, including maple and cherry trees in North America, Asia and Australia; forest trees including *C. sativa*, *F. sylvatica* and *Quercus* spp. across Europe; and chinkapins (*C. chrysophylla*) in Oregon, (Mircetich & Matheron 1976, Suzui & Hoshino 1979, Bumbieris & Wicks 1980, Wilcox & Mircetich 1985, Erwin & Ribeiro 1996, Jee *et al.* 1997, Wicks *et al.* 1997, Jung *et al.* 2000, 2016, 2018a, b, 2019, Vettraino *et al.* 2002, 2005, Balci & Halmschlager 2003a, Saavedra *et al.* 2007, Jung 2009, Milenković *et al.* 2012, Corcobado *et al.* 2020, Burgess *et al.* 2021, Mullett *et al.* 2023, Horta Jung *et al.* 2025).

The interspecific hybrid *P. alni* (and to a lesser extent its co-taxa) is responsible for the root and collar rot epidemic that has killed millions of alder trees along rivers and in carrs and forest plantations across Europe (Gibbs *et al.* 1999, 2003, Streito *et al.* 2002, Nagy *et al.* 2003, Brasier *et al.* 2004, Jung & Blaschke 2004, Schumacher *et al.* 2006, Černý & Strnadová 2010, Redondo *et al.* 2015, Jung *et al.* 2016, 2018a, Corcobado *et al.* 2023, Gomes Marques *et al.* 2024, Horta Jung *et al.* 2025). The host-specific pathogens *P. fragariae* and *P. rubi* cause severe economic damage in strawberry and raspberry growing regions of the world. Their geographic origins are unknown, although their phylogenetic relatedness to several East Asian Clade 7a4 species might suggest an origin in this region. *P. fragariae* has spread near globally via the commercial production of strawberries (Wilcox *et al.* 1993, Erwin & Ribeiro 1996, Gigot *et al.* 2013, EFSA 2014, Stewart *et al.* 2014, EPPO 2022a). Likewise, *P. rubi* occurs in most raspberry growing regions (EPPO 2022b). *Phytophthora abietivora* is an emerging aggressive pathogen of christmas trees from the genus *Abies* in the Northeastern USA and Eastern Canada with considerable economic impact (Li *et al.* 2019, Charron *et al.* 2024, 2025).

In contrast to the above, in their native habitats most Clade 7a species appear to co-exist with the local flora without causing visually overt disease symptoms, or cause only mild symptoms. In many cases their host plants and the plant parts attacked are

unknown. *Phytophthora ×cambivora* is widespread in riparian and other broadleaved forests across the Japanese archipelago without apparent association to any disease symptoms (this study). In the Pacific Northwest, *P. uniformis* thrives in riparian habitats causing only occasional root and collar rot of native alder species. *Phytophthora abietivora* is common in Appalachian forests causing scattered leaf and shoot blights of understorey plants from multiple native coevolved tree species (Bily *et al.* 2022). In the same region, *P. fagacearum* is a rare pathogen of *F. grandifolia* seedlings (Crous *et al.* 2024). *Phytophthora tyrrhenica* and *P. vulcanica* are mild fine root pathogens of local Mediterranean Fagaceae *Q. ilex* and *Q. suber*, and *F. sylvatica* in Southern Europe. Similarly, *P. europaea* infects fine roots of otherwise often healthy-looking trees of *Q. petraea*, *Q. robur* and *F. sylvatica* across Europe. The closely related *P. t. europaea*-like causes leaf and shoot blight of natural beech regeneration. *Phytophthora uliginosa* has a similar host range and distribution to *P. europaea* and on inoculation is considerably more aggressive to *Q. robur* root systems (Jung *et al.* 2002). Nonetheless, it is rarely associated with serious disease symptoms in the field. The six Clade 7a species described previously from natural forests in Taiwan (Jung *et al.* 2017a) and the 11 Clade 7a species described here from natural forests in Japan, Vietnam, Bosnia-Herzegovina and Louisiana, were recovered mainly from the rhizosphere of visually healthy trees and sometimes adjacent forest streams, and their natural and potential host ranges remain largely unknown. Nonetheless, since several Clade 7a species have become destructive pathogens when introduced elsewhere, further introductions should, in the absence of evidence to the contrary, be considered a potential biosecurity risk to non-coevolved or otherwise susceptible hosts under the precautionary principle. The Taiwanese *P. ×heterohybrida* and *P. ×incrassata* have both proved to be highly aggressive to roots of European chestnut (*C. sativa*) in a soil infestation trial (Jung *et al.* 2017a). *Phytophthora laevigata*, naturally occurring in the rhizosphere of healthy beech forests in Bosnia and Herzegovina, is now associated with an emerging decline and mortality of European hazelnut (*Corylus avellana*) plantations in Croatia. Introductions of non-native Clade 7 taxa also pose the risk of interspecific hybridisation events comparable to that which gave rise to *P. ×alni*, leading to widespread mortality of alder trees in Europe (Brasier *et al.* 1999, 2004, Jung & Blaschke 2004, Husson *et al.* 2015, Jung *et al.* 2018a).

DISCUSSION

In their seminal monograph 'Phytophthora diseases worldwide', Erwin & Ribeiro (1996) accepted 58 *Phytophthora* species of which seven were later considered as lost or invalidly published (Brasier *et al.* 2022). The vast majority (~90 %) of the 51 'valid' taxa were described originally from diseases they cause to horticultural and agricultural crops, including tropical tree crops, and ornamental plants. Only five were from natural environments: *P. gonapodyides* from a pond in Denmark; *P. castaneae* (syn. *P. katsurae*) and *P. ×cambivora* from chestnut trees in Japan and Italy; *P. lateralis* from diseased *Chamaecyparis lawsoniana* in Oregon; and *P. mirabilis* from the wild solanaceous species *Mirabilis jalapa* in Mexico (Erwin & Ribeiro 1996).

Between 1996 and 2026, 218 new *Phytophthora* species were described (cf. Abad *et al.* 2023, Jung *et al.* 2024, Abad & Abad 2026, Bregant *et al.* 2026, Crous *et al.* 2026, Paap *et al.* 2026, Wang *et al.* 2026) (Fig. 47), consistent with a predicted 200–600 extant species (Brasier 2009, Scott *et al.* 2019). This near exponential increase is

due mainly to a new era of global *Phytophthora* surveys targeting the questions of pathogen origins and *Phytophthora* diversity in underexplored forests and natural ecosystems; and partly to the use of molecular methods to unravel morphospecies complexes. The surveys were also driven by biosecurity concerns resulting from the numerous forest and ecosystem declines involving introduced, non-native *Phytophthoras* (e.g., Rizzo *et al.* 2002, Brasier & Webber 2010, Brasier *et al.* 2012, 2022, Hansen *et al.* 2012, Jung *et al.* 2013, 2018a, 2021, Frankel *et al.* 2020, Shakya *et al.* 2021). Indeed, in contrast to pre-1996 designated taxa, around 75 % (163) of the 218 new species were from natural ecosystems and another 6 % (14) from tree plantations, often in the vicinity of natural forests. In this paper we describe 11 more new species in *Phytophthora* Clade 7a, all from natural forests. If one includes seven validly described and accepted, non-culturable biotrophic *Phytophthora* species (*P. cyperi*, *P. cyperi-bulbosi*, *P. leersiae*, *P. lepironiae*, *P. oryzo-bladis*, *P. polygoni*, *P. verrucosa*), then the number of currently known *Phytophthora* species is ~287 (Fig. 47) with the proportion of species described from natural ecosystems since 1996 remaining at ~75 % (174/229).

The discovery of so many new *Phytophthora* species is greatly enhancing our ability to interpret the origins, phylogenetic substructure and biogeographical history of the genus (e.g., Jung *et al.* 2017a, b, 2022, 2024, Bourret *et al.* 2018, Burgess *et al.* 2018, Dang *et al.* 2021, Brasier *et al.* 2022, 2025, Chen *et al.* 2022). Including the 11 new species, four informally designated taxa and 18 previously described species, subclade 7a is currently the largest subclade in the genus, with ~33 species. Based mainly on indirect evidence of endemism, it is a Northern Hemisphere subclade with strongholds in the Nearctic (USA, Canada, seven presumed endemics); Palearctic (Europe, five endemics); Sino-Japanese (Japan, eight endemics); and Oriental (Taiwan, Vietnam, 11 endemics) regions (Fig. 44, details in 'Notes on the evolutionary history and biogeography of Clade 7a'). With a total of 15 species believed to be native to the forests of East Asia, this region harbours around 40 % of Clade 7a taxa.

In our updated phylogeny, Clade 7a comprises four subclusters labelled 7a1–7a4 (Figs 2–7, S1–S6). The evolutionary history of the subclade (see 'Notes on the evolutionary history and biogeography of Clade 7a') is characterised by the early divergence of Clade 7a1 (currently only *P. vulcanica*) and subsequent divergences of Clade 7a2 (two taxa), Clade 7a3 (eight taxa) and Clade 7a4 (21 taxa). Basal clusters 7a1 and 7a2 are exclusive to Europe. In contrast, Clade 7a3 has a disjunct holarctic distribution comprising Europe, East Asia and North America. This suggests that the ancient ancestors of Clade 7a probably appeared in Europe after the breakup of Laurasia and the separation of the North American and Eurasian Plates ~90–80 Mya and radiated into the three clusters 7a1–7a3; with 7a3 then spreading from Europe to both North America, most probably via North Atlantic land bridges ~70–23 Mya (Tiffney & Manchester 2001, Brikiatis 2014), and East Asia. The migration of Clade 7a3 to East Asia probably happened more recently after the disappearance of the Turgai Strait ~29 Mya (Briggs 1995). Clade 7a4 is essentially an East Asian clade. Its separation from Clade 7a3 probably occurred in East Asia, followed by its further spread to Western and subsequently Eastern North America via the intermittent Beringia land bridges ~70–5.3 Mya (Gladenkov *et al.* 2002, Brikiatis 2016).

Different modes of speciation are probably represented in the biogeography of the Clade 7a taxa (see also 'Notes on the evolutionary history and biogeography of Clade 7a'). The disjunct distributions of Clades 7a1–7a4 and the often vicariant distributions of individual species within the subclade centres are probably a



product of allopatric, non-adaptive radiation processes resulting from physical isolation and genetic drift. Examples within Clade 7a4 are the distributions of its species-rich centre with three subcentres in East Asia, *P. uniformis* in Western and *P. fagacearum* in Eastern North America; and the two geographically isolated Clade 7a4 hotspots in Vietnam in the Hoang Lien mountain range and in Ba Vi National Park. In contrast the co-occurrence of the sister species *P. arata*/*P. flexuosa* from Clade 7a3 and *P. formosa*/*P. irregularis* from Clade 7a4, respectively, in Japanese forests may reflect sympatric adaptive radiations associated with different host plants, microclimates and soil types. Further, given the indications of some highly localized diversity hotspots associated with geographic isolation, such as with Clade 7a4 in Vietnam, there may be many more still undetected Clade 7a4 species across the isolated riverine valleys and mountains of Indochina and neighbouring Yunnan. The region is already known for its unusual plant diversity. Equally, our interpretations must be considered speculative because little is known, for example, about past extinctions, the host ranges of many current species or even the possible role of migrating birds in ancient introduction events.

A significant number of Clade 7a taxa have clearly emerged via interspecific hybridisation or introgression. Over the past 25 years numerous studies have shown that hybridisation is a major evolutionary force in both true fungi and oomycetes, generating novel variation and speciation (e.g., Brasier *et al.* 1999, 2004, 2021, Brasier 2000, 2001, Newcombe *et al.* 2000, Schardl & Craven 2003, Paoletti *et al.* 2006, Gonthier *et al.* 2007, Bertier *et al.* 2013, Burgess 2015, Stukenbrock 2016, Jung *et al.* 2017a, Van Poucke *et al.* 2021, Mullett *et al.* 2023). Hybridisation has now been demonstrated in six of the 11 major *Phytophthora* clades (e.g., Goss *et al.* 2011, Man in 't Veld *et al.* 2012, Bertier *et al.* 2013, Burgess 2015, Safaiefarahani *et al.* 2016, Dang *et al.* 2021, Van Poucke *et al.* 2021, Jung *et al.* 2024).

In Clade 7a, ten taxa (~30 %; Table 2) are confirmed or probable allopolyploid hybrids, almost as high a frequency as in Clade 2 subclades 2a and 2b (each ~38 %; Jung *et al.* 2024). All ten occur in Clade 7a4. Based on nuclear genotyping, quantification of alleles and genome sizes, *P. xalni*, *P. xcambivora*, *P. xheterohybrida*, *P. xincrassata*, *P. xmultiformis*, *P. t. xmultiformis*-like and the new *P. xgrandisporangia* (designated as *P. xheterohybrida*-related), *P. xnodosa* and *P. xleptopleura* were confirmed previously to be allopolyploid hybrids (Brasier *et al.* 1999, Husson *et al.* 2015, Jung *et al.* 2017a, Van Poucke *et al.* 2021, Mullett *et al.* 2023, Fig. S7). In the present study, the informally designated *P. t. xalni*-like was also considered a hybrid based on its high nuclear heterozygosity level, a high level of mitochondrial gene identity with *P. xalni* and *P. xmultiformis* (Figs 4, 5, S3, S4) and the occasional failure to differentiate the sporangial cytoplasm into individual zoospores (Fig. 41; see details in 'Notes on heterozygosity, breeding systems and hybridity of Clade 7a').

Not only is there a high frequency of hybridity among Clade 7a isolates and taxa, but there is also a significant level of dissonance in nuclear and mitochondrial phylogenetic placement among the hybrids but also among several pure species. This is particularly striking in the placement of the DAPC lineages of *P. xcambivora*, *P. algida*, *P. europaea*, *P. fagacearum*, *P. t. xalni*-like and *P. t. xmultiformis*-like, and in the five mitochondrial genotypes observed within the DAPC lineages of *P. xcambivora*. Often referred to as mitonuclear discordance, this is a generally well known and accepted phenomenon in the phylogenetic investigation, especially in animals (e.g., Funk & Omland 2003, Toews & Brelsford 2012, Després 2019). It has also previously been highlighted in *Phytophthora* (Kroon *et al.* 2004, Martin *et al.* 2014, Bourret *et al.* 2018). Across *Phytophthora*

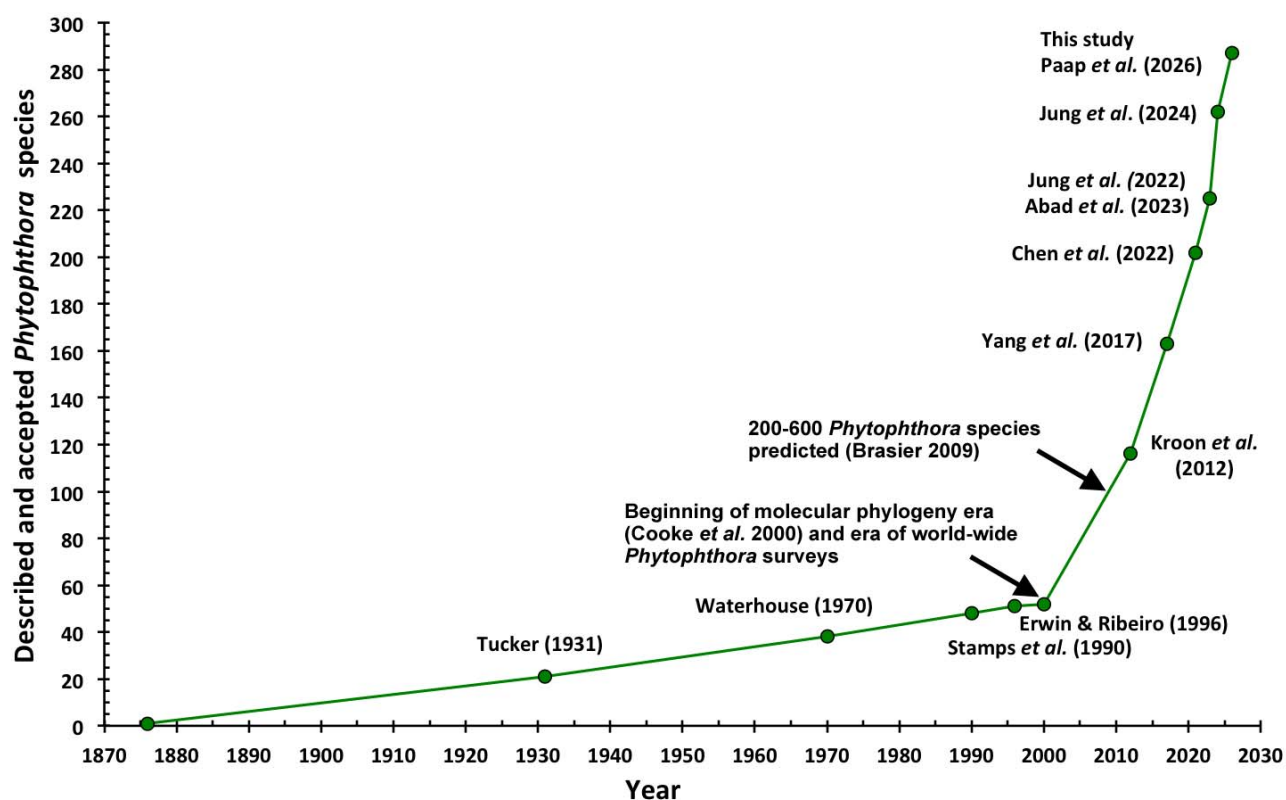


Fig. 47. Trend in the number of described and accepted *Phytophthora* species over time and selected milestones in understanding. Adapted from Brasier (2009) and Brasier *et al.* (2022). Data from pre-molecular era publications (Tucker 1931, Waterhouse 1970, Stamps *et al.* 1990, Erwin & Ribeiro 1996) include only those species currently accepted as valid species.

as a whole, further analyses, both sequencing and experimental, are needed to resolve the causes. Interpretation is currently also hampered by often very small population sample sizes. However, in the case of the Clade 7a hybrid taxa we suggest the most likely contributing factor is female-biased assortment resulting from the large amount of cytoplasm contributed by the oogonium to the oospore (and the almost zero cytoplasm contributed by the antheridium; cf. Brasier & Sansome 1975); sometimes compounded by further introgression among closely related taxa. Another factor may be the mixing of related lineages following their emergence and spread from glacial refugia.

By comparison with the many hybrids recently characterised in *Phytophthora* Clades 2a and 2b (Jung et al. 2024), the Clade 7a hybrids, with a few exceptions, tend to have a larger genome size (see details in 'Notes on heterozygosity, breeding systems and hybridity of Clade 7a'). Further, while all the Clade 2a and 2b hybrids either have an A1/A2 compatibility system or are sexually sterile, around half of the Clade 7a hybrids (*P. ×alni*, *P. ×multiformis*, *P. ×nodosa*, *P. t. ×alni*-like, and *P. t. ×multiformis*-like) are self-fertile (though with the exception of *P. ×nodosa* they are also closely interrelated). The other hybrid taxa in Clade 7a (*P. ×cambivora*, *P. ×grandisporangia*, *P. ×heterohybrida*, *P. ×incrassata*, *P. ×leptopleura*) do have an A1/A2 system. Their 'parent taxa' have not been detected in the molecular profiling. However, since the remaining 21 'pure' (non-hybrid) taxa in Clade 7a are all self-fertile, it seems likely that the five A1/A2 hybrids have actually arisen from hybridisation between self-fertile parent taxa. This would make the A1/A2 system in Clade 7a a product rather than a promoter of interspecific hybridisation events, which might be termed 'secondary self-sterility' (cf. Brasier 1992). This possibility, at face value an unusual evolutionary development, requires further investigation, including resolution of the underlying genetic mechanisms. If confirmed, it would be another example of the remarkable flexibility of *Phytophthora* breeding systems. We note that the same may also apply to *P. niederhauserii* and *P. taxon niederhauserii*-related in Clade 7b, and *P. cinnamomi* and *P. parvispora* in Clade 7c (see Van Poucke et al. 2021). We also note that the oospore formation rates and oospore viability levels of some of these inter-specific hybrids might be very low, or germings from oospores may have low fitness (cf. *P. ×alni* and *P. ×multiformis*; Brasier et al. 1999, Delcan & Brasier 2001). This possibility also needs to be investigated.

As in *Phytophthora* Clade 2 (Jung et al. 2024), there is a theoretical discontinuity of the Clade 7a taxa in estimated nuclear heterozygosity, at around 0.3 %. In Clades 2a and 2b it differentiated both the 'pure' self-fertile taxa and the pure A1/A2 taxa (overall mean heterozygosity range 0 to 0.22) from the confirmed and putative hybrid taxa (overall range 0.41 to 1.09) which had either an A1/A2 or a sterile breeding system. In the present study (in which no pure A1/A2s have been found), 0.3 % again differentiated the 'pure' self-fertile taxa from the hybrid taxa (Table 2; Fig. 45; see details in 'Notes on heterozygosity, breeding systems and hybridity of Clade 7a'), although one of two isolates of *P. ×multiformis* (mean heterozygosity 0.38 %) exhibited a nuclear heterozygosity of 0.26 %. The occurrence of this 0.3 % discontinuity in Clade 7a as well as in Clade 2 lends further support to the view (Jung et al. 2024) that eight taxa designated as putative hybrids in the Clade 2 study (*P. varipedicellata*, *P. multiplex*, *P. calidophila*, *P. pyriformis*, *P. mekongensis*, *P. pseudocitrophthora*, *P. vietnamensis* and *P. t. pseudocapsici*) are hybrids.

The high (30–40 %) rates of hybridity observed among subclades 7a, 2a and 2b taxa are unlikely to be representative of *Phytophthora* as a whole (cf. Van Poucke et al. 2021). That all Clade

7a hybridisations identified to date are found in Clade 7a4 probably reflects its biogeography, the influence of oceanic (cf. *P. ×incrassata*, *P. ×heterohybrida*, *P. ×leptopleura*, *P. ×nodosa*) and mountain (cf. *P. ×grandisporangia*) isolation processes and, in the case of the '*P. ×alni* hybrid complex', recent anthropogenic introduction events (details in 'Notes on Clade 7a properties' above). While *P. uniformis* and *P. ×multiformis* are now known to be the paternal and maternal parents of *P. ×alni* (Ioos et al. 2006, Husson et al. 2015, Jung et al. 2017a, Van Poucke et al. 2021), we show here that the reverse may be the case for *P. t. ×multiformis*-like; and that *P. t. ×alni*-like is most probably the result of a backcross between *P. ×alni* as maternal and *P. uniformis* as paternal parent. The parent species of the natural hybrids *P. ×cambivora*, *P. ×grandisporangia*, *P. ×heterohybrida*, *P. ×incrassata*, *P. ×leptopleura* and *P. ×nodosa* remain unknown. The diversity and possible interrelationship of the 11 DAPC lineages within the '*P. ×cambivora* hybrid complex' is currently the most intricate in *Phytophthora*, with eight known mitochondrial genotypes representing at least five maternal lines and sometimes distinct and widely separated geographic distributions (Figs 4, 5, S3, S4; Mullett et al. 2023).

Morphologically, the 31 Clade 7a taxa typically produce mainly non-papillate, persistent sporangia with abundant internal proliferation, consistent with a largely soil- and waterborne lifestyle. A few species produce some semipapillate sporangia but at low frequency, and some produce a low proportion (< 1 %) of sporangia with a sporangiophore constriction, which may facilitate partial caducity and, hence, a degree of aerial dispersal and greater habitat flexibility (see 'Notes on morphology, physiology and lifestyles of Clade 7a' above). Contrary to the perception that sporangial sympodia are exclusive to *Phytophthora* taxa with a predominantly aerial lifestyle, 23 of the 31 Clade 7a taxa studied (74.2 %) produce sympodia of 2–3 sporangia (Tables 3–8; no data available for *P. t. cadmea*, *P. t. cadmea*-like and *P. t. europaea*-like).

Ornamentation of oogonial walls is a rare character in *Phytophthora*, but it is found in numerous Clade 7a taxa including two Clade 7a3 species from East Asia, *P. arta* and *P. flexuosa*; two of the three Clade 7a3 species from North America, *P. facultativa* and *P. infundibuliformis*; all 13 species within Clade 7a4 originating from Asia except the basal species *P. intricata*; the North American *P. fagacearum*; and four of the five taxa in the '*P. ×alni* hybrid complex'. Since none of the endemic European species in Clades 7a1–a3 form ornamented oogonia, this property probably evolved after the spread of Clade 7a3 to North America and Asia. As it has persisted it may confer some unknown adaptive advantage. Acting as short- to medium-term survival structures, chlamydospores are a common feature of A1/A2 *Phytophthoras*, probably aiding survival under difficult conditions in the absence of the 'opposite' compatibility type. However, none of the five A1/A2 taxa in Clade 7a produce chlamydospores, possibly because they are recent (Pleistocene period) allopolyploid hybrids derived from self-fertile taxa; and exist in humid forest conditions (see details in 'Notes on morphology, physiology and lifestyles of Clade 7a').

Clade 7a comprises mostly cool- and warm-temperate species. Even the five species that inhabit subtropical regions do so in mostly cooler montane forests in northern Vietnam and Taiwan. No Clade 7a taxa are able to grow in vitro at 35 °C (Figs 16–19) and most die at this temperature. Only *P. ×leptopleura* and *P. ×nodosa* and most DAPC lineages of the '*P. ×cambivora* hybrid complex' show some growth even at 32.5 °C. Within the latter, the lineages exhibit growth-temperature responses indicating adaptation to local climatic conditions. For example, at 32.5 °C the DAPC6 lineage from cold-temperate Northern Honshu, Japan grows considerably more

slowly than DAPC2, 7 and 8 from warm-temperate regions and the pan-Japanese lineage DAPC4; and the North American DAPC10 lineage and most isolates of the European lineages DAPC3 and 11 are unable to grow at this temperature (Fig. 19). The apparent overall absence of Clade 7a taxa in tropical ecosystems may reflect a limited ability during ancient migrations to compete with already established and better adapted Phytophthoras from other clades and subclades and, hence, constitutes a textbook example of phylogenetic niche conservatism (see 'Notes on morphology, physiology and lifestyles of Clade 7a').

Several Clade 7a taxa have become seriously economically or environmentally damaging as a result of being introduced to other biogeographic regions with naïve hosts (Fig. 44; see 'Notes on Clade 7a properties'). The wide-host range tree pathogen *P. ×cambivora*, which most probably originates from Japan and possibly adjacent East Asia, is now almost panglobal (Mullett *et al.* 2023) causing root and collar rot and mortality of more than 130 plant species including many forest trees, in particular from Fagaceae genera, fruit trees and ornamentals. The host specific *P. fragariae* and *P. rubi* (origins unknown) have also spread almost globally via commercial production of strawberries and raspberries (EPPO 2022a, b). *Phytophthora uniformis* from the Pacific Northwest and *P. ×multiformis* of cryptic origin have been introduced to Europe where their novel hybrid *P. ×alni* has been highly destructive to native alder trees (Jung *et al.* 2018a). *Phytophthora abietivora* is becoming an aggressive pathogen of Christmas trees (*Abies* sp.) in the northeastern USA and eastern Canada (Li *et al.* 2019, Charron *et al.* 2024) and Japanese water iris (*Iris ensata* var. *ensata*) in Japan (Amemiya *et al.* 2011a, b).

In contrast, the above and many other Clade 7a species apparently cause little or only mild disease symptoms in their natural habitats. For example, *P. ×cambivora* is widespread in broadleaved forests across Japan but apparently causes no noticeable disease symptoms locally (this study). In the Pacific Northwest, *P. uniformis* rarely causes root and collar rot of native alder species (Sims *et al.* 2015). *Phytophthora abietivora* is common in Appalachian forests causing only scattered leaf and shoot blights of understorey plants (Bily *et al.* 2022). In Europe the endemic *P. europaea*, *P. tyrrhenica*, *P. uliginosa* and *P. vulcanica* are rarely associated with serious disease symptoms (Jung *et al.* 2002, 2017b). The natural and potential host ranges of the six Clade 7a species described previously from natural forests in Taiwan (Jung *et al.* 2017a) and the 11 Clade 7a species described here from various natural forests are unknown. They were recovered mainly from the rhizosphere of visually healthy trees, most likely subsisting as benign coevolved fine root nibblers. Nonetheless, from a perspective of global plant biosecurity, and invoking the 'precautionary principle', they must be considered to have a potential to become damaging invasives elsewhere unless shown otherwise. The relevance of this assumption is supported by experimental evidence that upon soil infestation the Taiwanese *P. ×heterohybrida* and *P. ×incrassata* are highly aggressive to roots of European chestnut (Jung *et al.* 2017a), and by emerging evidence that the novel *P. laevigata* is associated with declining hazelnut trees in Croatian orchards.

Furthermore, it is well known to many plant health practitioners and forest managers that introduced Phytophthoras are a major threat to forests and tree plantations. The number of known forest epidemics and declines associated with Phytophthoras increased from 5 to 41 between 1960 and 2022 (Brasier *et al.* 2022). The increasing discovery of previously scientifically unknown Phytophthoras in underexplored forests worldwide therefore needs to

be pro-actively addressed by world plant health agencies. Typically, current biosecurity protocols are typically heavily dependent on lists of specifically named threat organisms (cf. Brasier 2008, Jung *et al.* 2016, 2024, Brasier *et al.* 2022) rather than on regulating possible pathways of introduction, mainly via the international plant trade and plant collecting, which largely remain open. Including the 11 new Clade 7a species described here, we estimate that for around 150 of the now ~287 described *Phytophthora* species there is almost no information on natural or potential host range or parts of the host liable to be attacked. Presently, in biosecurity terms, these ~150 species barely exist. Overall, the critical absence of information on the scale and the quality of 'unknown *Phytophthora* threats' amounts to a serious, scientific evidence gap.

To begin to address this gap, we again make the following recommendations. (i) That the aggressiveness, host ranges, host organs attacked and sporulation potential of a selected sample of the many 'under the radar' Phytophthoras be tested on a standard set of well characterised, non-coevolved hosts (e.g., *Rhododendron*, *Eucalyptus*, *Fagus*, *Quercus*, *Castanea*, *Chamaecyparis* and *Larix* spp.), using well characterised *Phytophthora* species as controls. In doing so, a greater emphasis might be placed on testing A1/A2 outcrossing species which, theoretically at least, might be more evolutionarily adaptable if both mating types are introduced by the plant trade. (ii) Given that the probable geographic origins of some highly damaging *Phytophthora* species have been identified in recent surveys, including *P. cactorum*, *P. cinnamomi*, *P. kernoviae*, *P. lateralis*, *P. multivora*, *P. plurivora*, *P. ramorum* and *P. ×cambivora* (Brasier *et al.* 2010, 2012, Jung *et al.* 2018b, 2021, 2022, 2024, Shakya *et al.* 2021, Bourret *et al.* 2022, Tsykun *et al.* 2022, Mullett *et al.* 2023), research should be undertaken to understand the ecological roles these species play in their native habitats, including their natural hosts, the mechanisms of host resistance and their associated microbiomes.

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

REFERENCES

- Abad ZG, Abad JA (2026). *Phytophthora*: Timeline of taxonomy and identification from plant pathology's origin to molecular technologies. *Plant Disease* **110**: 1038–1053. <https://doi.org/10.1094/PDIS-07-25-1349-FE>.
- Abad ZG, Burgess TI, Bourret T, et al. (2023). *Phytophthora*: taxonomic and phylogenetic revision of the genus. *Studies in Mycology* **106**: 259–348. <https://doi.org/10.3114/sim.2023.106.05>.
- Abad ZG, Abad JA, Cacciola SO, et al. (2014). *Phytophthora niederhauserii* sp. nov., a polyphagous species associated with ornamentals, fruit trees and native plants in 13 countries. *Mycologia* **106**: 431–447. <https://doi.org/10.3852/12-119>
- Adams GC, Catal M, Trummer L (2010). Distribution and severity of alder *Phytophthora* in Alaska. In: *Proceedings of the Sudden Oak Death Fourth Science Symposium* (Frankel SJ, Kliejunas T, Palmieri KM, eds). USDA Forest Service, Albany, California, USA. General Technical Report PSW-GTR-229: 29–49. <https://research.fs.usda.gov/treearch/35029>
- Aguayo J, Adams GC, Halkett F, et al. (2013). Strong genetic differentiation between North American and European populations of *Phytophthora alni* subsp. *uniformis*. *Phytopathology* **103**: 190–199. <https://doi.org/10.1094/PHYTO-05-12-0116-R>
- Aguayo J, Halkett F, Husson C, et al. (2016). Genetic diversity and origins of the homoploid-type hybrid *Phytophthora ×alni*. *Applied and Environmental Microbiology* **82**: 7142–7153. <https://doi.org/10.1128/AEM.02221-16>
- Amemiya Y, Usami T, Okazaki R, Katori M, Uematsu S. (2011a). A new *Phytophthora* sp. causing basal rot on Japanese *Iris*. *Phytopathology* **101**(6): S6.
- Amemiya Y, Usami T, Okazaki R, Katori M, Uematsu S. (2011b). A new *Phytophthora* sp. causing basal rot on Japanese *Iris*. Poster presented at the APS-IPPC Joint Meeting, Honolulu, Hawaii, August 6–10, 2011.
- Arentz F (2023). Formal description of *Phytophthora novae-guineae* sp. nov., a Clade 5 species. *Forest Pathology* **53**: e12785. <https://doi.org/10.1111/efp.12785>
- Arentz F, Simpson JA (1986). Distribution of *Phytophthora cinnamomi* in Papua New Guinea and notes on its origin. *Transactions of the British Mycological Society* **87**(2): 289–295. [https://doi.org/10.1016/S0007-1536\(86\)80032-8](https://doi.org/10.1016/S0007-1536(86)80032-8)
- Atchadé YF, Roberts GO, Rosenthal JS (2011). Towards optimal scaling of metropolis-coupled Markov chain Monte Carlo. *Statistics and Computing* **21**: 555–568. <https://doi.org/10.1007/s11222-010-9192-1>
- Bacon CD, Silvestro D, Jaramillo C, et al. (2015). Biological evidence supports an early and complex emergence of the Isthmus of Panama. *Proceedings of the National Academy of Sciences USA* **112**: 6110–6115. <https://doi.org/10.1073/pnas.1423853112>
- Báčová A, Cooke DEL, Milenković I, et al. (2024). Hidden *Phytophthora* diversity unveiled in tree nurseries of the Czech Republic with traditional and metabarcoding techniques. *European Journal of Plant Pathology* **170**: 131–156. <https://doi.org/10.1007/s10658-024-02886-1>
- Bakonyi J, Nagy ZÁ, Érsek T (2006). PCR-based DNA markers for identifying hybrids within *Phytophthora alni*. *Journal of Phytopathology* **154**: 168–177. <https://doi.org/10.1111/j.1439-0434.2006.01079.x>
- Balci Y, Balci S, Eggers J, et al. (2007). *Phytophthora* spp. associated with forest soils in Eastern and North-Central U.S. oak ecosystems. *Plant Disease* **91**: 705–710. <https://doi.org/10.1094/PDIS-91-6-0705>
- Balci Y, Halmeschlager E (2003a). Incidence of *Phytophthora* species in oak forests in Austria and their possible involvement in oak decline. *Forest Pathology* **33**: 157–174. <https://doi.org/10.1046/j.1439-0329.2003.00318.x>
- Balci Y, Halmeschlager E (2003b). *Phytophthora* species in oak ecosystems in Turkey and their association with declining oak trees. *Plant Pathology* **52**: 694–702. <https://doi.org/10.1111/j.1365-3059.2003.00919.x>
- Bandelt H-J, Forster P, Röhl A (1999). Median-joining networks for inferring intraspecies phylogenies. *Molecular Biology and Evolution* **16**: 37–48. <https://doi.org/10.1093/oxfordjournals.molbev.a026036>
- Baskin JM, Baskin CC (2016). Origins and relationships of the mixed mesophytic forest of Oregon-Idaho, China, and Kentucky: Review and synthesis. *Annals of the Missouri Botanical Garden* **101**(3): 525–552. <https://annals.mobot.org/index.php/annals/article/view/466>
- Bertier L, Leus L, D'hondt L, et al. (2013). Host adaptation and speciation through hybridization and polyploidy in *Phytophthora*. *PLoS ONE* **8**: e85385. <https://doi.org/10.1371/journal.pone.0085385>
- Bienapfl JC, Balci Y (2014). Movement of *Phytophthora* spp. in Maryland's nursery trade. *Plant Disease* **98**: 134–144. <https://doi.org/10.1094/PDIS-06-13-0662-RE>
- Bily D, Nikolaeva E, Olson T, Kang S (2022). *Phytophthora* spp. associated with Appalachian oak forests and waterways in Pennsylvania, with *P. abietivora* as a pathogen of five native woody plant species. *Plant Disease* **106**: 1143–1156. <https://doi.org/10.1094/PDIS-05-21-0976-RE>
- Blair JE, Coffey MD, Park S-Y, et al. (2008). A multi-locus phylogeny for *Phytophthora* utilizing markers derived from complete genome sequences. *Fungal Genetics and Biology* **45**: 266–277. <https://doi.org/10.1016/j.fgb.2007.10.010>

- Bogarín D, Pupulin F, Smets E, *et al.* (2016). Evolutionary diversification and historical biogeography of the *Orchidaceae* in Central America with emphasis on Costa Rica and Panama. *Lankesteriana* **16**: 189–200. <https://doi.org/10.15517/lank.v16i2.26005>
- Botella L, Horta Jung M, Rost M, Jung T (2022). Natural populations from the *Phytophthora palustris* complex show a high diversity and abundance of ssRNA and dsRNA viruses. *Journal of Fungi* **8**: 1118. <https://doi.org/10.3390/jof8111118>
- Botella L, Hejna O, Kudláček T, *et al.* (2025). The virome of the panglobal, wide host-range plant pathogen *Phytophthora cinnamomi*: Phylogeography and evolutionary insights. *Virus Evolution* **11**(1): veaf020. <https://doi.org/10.1093/ve/veaf020>
- Bouckaert R, Drummond A (2017). bModelTest: Bayesian phylogenetic site model averaging and model comparison. *BMC Evolutionary Biology* **17**: 42. <https://doi.org/10.1186/s12862-017-0890-6>
- Bouckaert R, Heled J, Kühnert D, *et al.* (2014). BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* **10**: e1003537. <https://doi.org/10.1371/journal.pcbi.1003537>
- Bourret TB (2024). Common ground and shifting paradigms: How to reconcile *Phytophthora* evolution, cladistics, taxonomy, and biosecurity. Webinar presentation in: The Genus *Phytophthora* – Don't Change a Winning Concept? American Phytopathological Society Workshop, 22–25 April 2024, Session 3 - Part 1. Starting time 1:06:17. <https://www.apsnet.org/meetings/mtnetshops/Pages/APS-2024-0425-03.1.aspx>
- Bourret TB, Choudhury RA, Mehl HK, *et al.* (2018). Multiple origins of downy mildews and mito-nuclear discordance within the paraphyletic genus *Phytophthora*. *PLoS ONE* **13**: e0192502. <https://doi.org/10.1371/journal.pone.0192502>
- Bourret TB, Fajardo SN, Engert CP, Rizzo DM (2022). A barcode-based phylogenetic characterization of *Phytophthora cactorum* identifies two cosmopolitan lineages with distinct host affinities and the first report of *Phytophthora pseudotsugae* in California. *Journal of Fungi* **8**: 303. <https://doi.org/10.3390/jof8030303>
- Bourret TB, Fajardo SN, Frankel SJ, Rizzo DM (2023). Cataloging *Phytophthora* species of agriculture, forests, horticulture, and restoration outplantings in California, U.S.A.: A sequence-based meta-analysis. *Plant Disease* **107**: 67–75. <https://doi.org/10.1094/PDIS-01-22-0187-RE>
- Bourret TB, Blomquist CL, Mohan SK, *et al.* (2025). First detection of the obligate biotroph *Phytophthora cyperi* causing disease on yellow nutsedge in the United States, and establishment of molecular barcoding sequences for the species. *PhytoFrontiers* **5**: 60–66. <https://doi.org/10.1094/PHYTOFR-02-24-0013-R>
- Brasier CM (1967). *Physiology of reproduction in Phytophthora*. PhD Thesis, University of Hull, UK.
- Brasier CM (1986). The dynamics of fungal speciation. In: *Evolutionary biology of the fungi* (Rayner ADM, Brasier CM, Moore D, eds). Cambridge University Press, Cambridge, UK: 231–260.
- Brasier CM (1991). Current questions in *Phytophthora* systematics: The role of the population approach. In: *Phytophthora* (Lucas JA, Shattock RC, Shaw DS, *et al.*, eds). Cambridge University Press, Cambridge, UK: 104–128.
- Brasier CM (1992). Evolutionary biology of *Phytophthora*. Part I: Genetic system, sexuality and the generation of variation. *Annual Review of Phytopathology* **30**: 153–171. <https://doi.org/10.1146/annurev.py.30.090192.001101>
- Brasier CM (1995). Episodic selection as a force in fungal microevolution with special reference to clonal speciation and hybrid introgression. *Canadian Journal of Botany* **73**: 1213–1221. <https://doi.org/10.1139/b95-381>
- Brasier CM (2000). Rise of the hybrid fungi. *Nature* **405**: 134–135. <https://doi.org/10.1038/35012193>
- Brasier CM (2001). Rapid evolution of introduced plant pathogens via interspecific hybridization. *Bioscience* **51**: 123–133. [https://doi.org/10.1641/0006-3568\(2001\)051\[0123:REOIPP\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0123:REOIPP]2.0.CO;2)
- Brasier CM (2008). The biosecurity threat to the UK and global environment from international trade in plants. *Plant Pathology* **57**: 792–808. <https://doi.org/10.1111/j.1365-3059.2008.01886.x>
- Brasier CM (2009). *Phytophthora* biodiversity: How many *Phytophthora* species are there? In: *Phytophthoras in Forests and Natural Ecosystems: Fourth Meeting of the International Union of Forest Research Organizations (IUFRO) Working Party S07.02.09* (Goheen EM, Frankel SJ, eds). USDA Forest Service, Pacific Southwest Research Station, Albany, California. General Technical Report PSW-GTR-221: 101–115. <https://doi.org/10.2737/PSW-GTR-221>
- Brasier CM, Griffin MJ (1979). Taxonomy of *Phytophthora palmivora* on cocoa. *Transactions of the British Mycological Society* **72**: 111–143. [https://doi.org/10.1016/S0007-1536\(79\)80015-7](https://doi.org/10.1016/S0007-1536(79)80015-7)
- Brasier CM, Jung T (2003). Progress in understanding *Phytophthora* diseases of trees in Europe. In: McComb JA, Hardy GESTJ, Tommerup I (eds), *Phytophthora in Forests and Natural Ecosystems*. Murdoch University, Perth, Australia: 4–18.
- Brasier CM, Kirk SA (2001). Comparative aggressiveness of standard and variant hybrid alder *Phytophthoras*, *Phytophthora cambivora* and other *Phytophthora* species on bark of *Alnus*, *Quercus* and other woody hosts. *Plant Pathology* **50**: 218–229. <https://doi.org/10.1046/j.1365-3059.2001.00553.x>
- Brasier CM, Rayner ADM (1987). Whither terminology below the species level in the fungi? In: Rayner ADM, Brasier CM, Moore D (eds), *Evolutionary biology of the fungi*. Cambridge University Press, Cambridge, UK: 379–388.
- Brasier CM, Sansome ER (1975). Diploidy and gametangial meiosis in *Phytophthora cinnamomi*, *P. infestans* and *P. drechsleri*. *Transactions of the British Mycological Society* **65**: 49–65. [https://doi.org/10.1016/S0007-1536\(75\)80180-X](https://doi.org/10.1016/S0007-1536(75)80180-X)
- Brasier CM, Webber J (2010). Sudden larch death. *Nature* **466**: 824–825. <https://doi.org/10.1038/466824a>
- Brasier CM, Beales PA, Kirk SA, *et al.* (2005). *Phytophthora kernoviae* sp. nov. an invasive pathogen causing bleeding stem lesions on forest trees and foliar necrosis of ornamentals in Britain. *Mycological Research* **109**: 853–859. <https://doi.org/10.1017/S0953756205003357>
- Brasier CM, Cooke DEL, Duncan JM (1999). Origins of a new *Phytophthora* pathogen through interspecific hybridisation. *Proceedings of the National Academy of Sciences, USA* **96**: 5878–5883. <https://doi.org/10.1073/pnas.96.10.5878>
- Brasier CM, Cooke DEL, Duncan JM, *et al.* (2003). Multiple new phenotypic taxa from trees and riparian ecosystems in *Phytophthora gonapodyides* – *P. megasperma* ITS Clade 6, which tend to be high-temperature tolerant and either inbreeding or sterile. *Mycological Research* **107**: 277–290. <https://doi.org/10.1017/S095375620300738X>
- Brasier CM, Franceschini S, Forster J, *et al.* (2021). Enhanced outcrossing, directional selection and transgressive segregation drive evolution of novel phenotypes in hybrid swarms of the Dutch Elm Disease pathogen *Ophiostoma novo-ulmi*. *Journal of Fungi* **7**: 452. <https://doi.org/10.3390/jof7060452>
- Brasier CM, Franceschini S, Vettraino AM, *et al.* (2012). Four phenotypically and phylogenetically distinct lineages in *Phytophthora lateralis*. *Fungal Biology* **116**: 1232–1249. <https://doi.org/10.1016/j.funbio.2012.10.002>
- Brasier CM, Grünwald NJ, Bourret TB, *et al.* (2025). Preserving the biologically coherent generic concept of *Phytophthora*, ‘Plant Destroyer’. *Phytopathology* **115**: 573–586. <https://doi.org/10.1094/PHYTO-11-24-0372-LE>
- Brasier CM, Kirk SA, Delcan J, *et al.* (2004). *Phytophthora alni* sp. nov. and its variants: designation of emerging heteroploid hybrid pathogens

- spreading on *Alnus* trees. *Mycological Research* **108**: 1172–1184. <https://doi.org/10.1017/S0953756204001005>
- Brasier C, Scanu B, Cooke D, et al. (2022). *Phytophthora*: an ancient, historic, biologically and structurally cohesive and evolutionarily successful generic concept in need of preservation. *IMA Fungus* **13**: 12. <https://doi.org/10.1186/s43008-022-00097-z>
- Brasier CM, Vetraino AM, Chang TT, et al. (2010). *Phytophthora lateralis* discovered in an old growth *Chamaecyparis* forest in Taiwan. *Plant Pathology* **59**: 595–603. <https://doi.org/10.1111/j.1365-3059.2010.02278.x>
- Bregant C, Carloni F, Montecchio L, et al. (2026). *Neofusicoccum* and *Phytophthora* species: An emerging threat to fig trees (*Ficus carica*) in Italy, with the description of *Phytophthora messapica* sp. nov. *Plant Pathology* **75**: e70216. <https://doi.org/10.1111/ppa.70216>
- Briggs JC (1995). *Global Biogeography*. Amsterdam, Elsevier Science. <https://shop.elsevier.com/books/global-biogeography/briggs/978-0-444-88297-4>
- Brikiatis L (2014). The De Geer, Thulean and Beringia routes: key concepts for understanding early Cenozoic biogeography. *Journal of Biogeography* **41**: 1036–1054. <https://doi.org/10.1111/jbi.12310>
- Brikiatis L (2016). Late Mesozoic North Atlantic land bridges. *Earth-Science Reviews* **159**: 47–57. <https://doi.org/10.1016/j.earscirev.2016.05.002>
- Brown AV, Brasier CM (2007). Colonization of tree xylem by *Phytophthora ramorum*, *P. kernoviae* and other *Phytophthora* species. *Plant Pathology* **56**: 227–241. <https://doi.org/10.1111/j.1365-3059.2006.01511.x>
- Brown B (1999). Occurrence and impact of *Phytophthora cinnamomi* and other *Phytophthora* species in rainforests of the Wet Tropics World Heritage Area, and of the Mackay region, Qld. In: Gadek PA (ed), *Patch deaths in tropical Queensland rainforests: association and impact of Phytophthora cinnamomi and other soil borne organisms*. Cooperative Research Centre for Tropical Rainforest Ecology and Management, Cairns, Australia: 41–76. <https://www.wettropics.gov.au/site/user-assets/docs/Phyto.pdf>
- Brown RP, Yang Z (2011). Rate variation and estimation of divergence times using strict and relaxed clocks. *BMC Evolutionary Biology* **11**: 271. <https://doi.org/10.1186/1471-2148-11-271>
- Browne GT, Mircetich SM, Cummins JN (1995). Relative resistance of eighteen selections of *Malus* spp. to three species of *Phytophthora*. *Phytopathology* **85**: 72–76. https://www.apsnet.org/publications/phytopathology/backissues/Documents/1995Articles/Phyto85n01_72.pdf
- Bumbieris M, Wicks T (1980). *Phytophthora cambivora* associated with apple trees in South Australia. *Australasian Plant Pathology* **9**: 114. <https://doi.org/10.1071/APP9800114>
- Burgess TI (2015). Molecular characterization of natural hybrids formed between five related indigenous Clade 6 *Phytophthora* species. *PLoS ONE* **10**: e0134225. <https://doi.org/10.1371/journal.pone.0134225>
- Burgess TI, Simamora AV, White D, et al. (2018). New species from *Phytophthora* Clade 6a: evidence for recent radiation. *Persoonia* **41**: 1–17. <https://doi.org/10.3767/persoonia.2018.41.01>
- Burgess TI, White D, McDougall KM, et al. (2017). Distribution and diversity of *Phytophthora* across Australia. *Pacific Conservation Biology* **23**: 1–13. <https://doi.org/10.1071/PC16032>
- Burgess TI, Edwards J, Drenth A, et al. (2021). Current status of *Phytophthora* in Australia. *Persoonia* **47**: 151–177. <https://doi.org/10.3767/persoonia.2021.47.05>
- Cannon CH, Morley RJ, Bush AB (2009). The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. *Proceedings of the National Academy of Sciences USA* **106**: 11188–11193. <https://doi.org/10.1073/pnas.0809865106>
- Cassens I, Mardulyn P, Milinkovitch MC (2005). Evaluating intraspecific “network” construction methods using simulated sequence data: Do existing algorithms outperform the Global Maximum Parsimony approach? *Systematic Biology* **54**: 363–372. <https://doi.org/10.1080/10635150590945377>
- Černý K, Filipová N, Strnadová V (2012). Influence of low temperature and frost duration on *Phytophthora alni* subsp. *alni* viability. *Forest Systems* **21**: 337–342. <https://doi.org/10.5424/fs/2012212-02250>
- Černý K, Strnadová V (2010). *Phytophthora* alder decline: disease symptoms, causal agent and its distribution in the Czech Republic. *Plant Protection Science* **46**: 12–18. <https://doi.org/10.17221/43/2009-PPS>
- Černý K, Strnadová V, Gregorova B, et al. (2009). *Phytophthora cactorum* causing bleeding canker of common beech, horse chestnut, and white poplar in the Czech Republic. *Plant Pathology* **58**: 394. <https://doi.org/10.1111/j.1365-3059.2008.01970.x>
- Chang-Fu H, Chung-Fu S, Kuoh-Cheng Y (1994). Introduction to the flora of Taiwan, 3: floristics, phytogeography, and vegetation. In: *Flora of Taiwan*, Second Edition. Editorial Committee of the Flora of Taiwan Second Edition, Taipei, Republic of China: 7–18. <https://tai2.ntu.edu.tw/ebooks/FITaiwan2nd/1>
- Charron G, Yergeau J, Van der Heyden H, et al. (2024). Survey of *Phytophthora* diversity reveals *P. abietivora* as a potential *Phytophthora* root rot pathogen in Québec christmas tree plantations. *Plant Disease* **108**: 1445–1454. <https://doi.org/10.1094/PDIS-12-23-2670-SR>
- Charron G, Gauthier M-K, Aucoin V, Tanguay P (2025). Outbreak of *Phytophthora abietivora* in a Québec forest nursery: Emergence of a new *Phytophthora* tree pathogen? *Forest Pathology* **55**: e70041. <https://doi.org/10.1111/efp.70041>
- Chen Q, Bakhshi M, Balci Y, et al. (2022). Genera of phytopathogenic fungi: GOPHY 4. *Studies in Mycology* **101**: 417–564. <https://doi.org/10.3114/sim.2022.101.06>
- Chung-Fu S (1994). Introduction to the flora of Taiwan, 2: geotectonic evolution, paleogeography, and the origin of the flora. In: *Flora of Taiwan*, Second Edition. Editorial Committee of the Flora of Taiwan Second Edition, Taipei, Republic of China: 3–7. <https://tai2.ntu.edu.tw/ebooks/FITaiwan2nd/1>
- Cione AL, Gasparini GM, Soibelzon E, et al. (2015). *The Great American Biotic Interchange: A South American Perspective*. Springer Briefs in Earth System Sciences, South America and the Southern Hemisphere. Springer, Dordrecht, Heidelberg, New York, London.
- Cooke DEL, Drenth A, Duncan JM, et al. (2000). A molecular phylogeny of *Phytophthora* and related oomycetes. *Fungal Genetics and Biology* **30**: 17–30. <https://doi.org/10.1006/fgbi.2000.1202>
- Corcobado T, Cech TL, Brandstetter M, et al. (2020). Decline of European beech in Austria: involvement of *Phytophthora* spp. and contributing biotic and abiotic factors. *Forests* **11**: 895. <https://doi.org/10.3390/f11080895>
- Corcobado T, Cech TL, Daxer A, et al. (2023). *Phytophthora*, *Nothophytophthora* and *Halophytophthora* diversity in rivers, streams and riparian alder ecosystems of Central Europe. *Mycological Progress* **22**: 50. <https://doi.org/10.1007/s11557-023-01898-1>
- Crous PW, Akulov A, Alfenas AC, et al. (2026). New and interesting fungi. 8. *Persoonia* **56**: 457–547. <https://doi.org/10.3114/persoonia.2026.56.08>
- Crous PW, Jurjević Ž, Balashov S, et al. (2024). Fungal Planet description sheets: 1614–1696. *Fungal Systematics and Evolution* **13**: 183–440. <https://doi.org/10.3114/fuse.2024.13.11>
- Dang QN, Pham TQ, Arentz F, et al. (2021). New *Phytophthora* species in clade 2a from the Asia-Pacific region including a re-examination of *P. colocasiae* and *P. meadii*. *Mycological Progress* **20**: 111–129. <https://doi.org/10.1007/s11557-020-01656-7>
- Davis CC, Bell CD, Mathews S, et al. (2002). Laurasian migration explains Gondwanan disjunctions: Evidence from *Malpighiaceae*. *Proceedings*

- of the National Academy of Sciences USA **99**: 6833–6837. <https://doi.org/10.1073/pnas.102175899>
- Davis CC, Fritsch PW, Bell CD, Mathews S (2004). High-latitude Tertiary migrations of an exclusively tropical clade: evidence from Malpighiaceae. *International Journal of Plant Sciences* **165** (suppl.): S107–S121. <https://doi.org/10.1086/383337>
- Day WR (1938). Root-rot of sweet chestnut and beech caused by species of *Phytophthora*: 1. Cause and symptoms of disease: its relation to soil conditions. *Forestry* **12**: 101–116. <https://doi.org/10.1093/oxfordjournals.forestry.a062747>
- Delcan J, Brasier CM (2001). Oospore viability and variation in zoospore and hyphal tip derivatives of the hybrid alder *Phytophthoras*. *Forest Pathology* **31**: 65–83. <https://doi.org/10.1046/j.1439-0329.2001.00223.x>
- De Merlier D, Chandelier A, Debruxelles N, et al. (2005). Characterization of alder *Phytophthora* isolates from Wallonia and development of SCAR primers for their specific detection. *Journal of Phytopathology* **153**: 99–107. <https://doi.org/10.1111/j.1439-0434.2005.00936.x>
- Denk T, Grimm GW (2009). The biogeographic history of beech trees. *Review of Palaeobotany and Palynology* **158**: 83–100. <https://doi.org/10.1016/j.revpalbo.2009.08.007>
- Denk T, Grimsson F, Zetter R (2010). Episodic migration of oaks to Iceland: evidence for a North Atlantic 'land bridge' in the latest Miocene. *American Journal of Botany* **97**: 276–287. <https://doi.org/10.3732/ajb.0900195>
- Després L (2019). One, two or more species? Mitonuclear discordance and species delimitation. *Molecular Ecology* **28**: 3845–3847. <https://doi.org/10.1111/mec.15211>
- Dick MW (1990). *Keys to Pythium*. University of Reading Press, Reading, UK.
- Donahoo RS, Lamour KH (2008). Interspecific hybridization and apomixis between *Phytophthora capsici* and *Phytophthora tropicalis*. *Mycologia* **100**: 911–920. <https://doi.org/10.3852/08-028>
- Douglas J, Zhang R, Bouckaert R. (2021). Adaptive dating and fast proposals: revisiting the phylogenetic relaxed clock model. *PLoS Computational Biology* **17**(2): e1008322. <https://doi.org/10.1371/journal.pcbi.1008322>
- Drenth A, Guest DI (eds) (2004). *Diversity and management of Phytophthora in Southeast Asia*. Australian Centre for International Agricultural Research, Canberra, Australia. <https://www.aciar.gov.au/publication/books-and-manuals/diversity-and-management-phytophthora-southeast-asia>
- Drummond AJ, Ho SYW, Phillips MJ, et al. (2006). Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4**: 699–710. <https://doi.org/10.1371/journal.pbio.0040088>
- Duncan JM, Kennedy SM, Scott PH (1991). Relationships between non-papillate soilborne species of *Phytophthora*: Root rot of raspberry. In: Lucas JA, Shattock RC, Shaw DS, et al. (eds), *Phytophthora*. Cambridge University Press, Cambridge, UK: 129–147.
- EFSA PLH Panel (EFSA Panel on Plant Health) (2014). Scientific opinion on the risks to plant health posed by *Phytophthora fragariae* Hickman var. *fragariae* in the EU territory, with the identification and evaluation of risk reduction options. *EFSA Journal* **12**(1): 3539, 63 pp. <https://doi.org/10.2903/j.efsa.2014.3539>
- Elias S, Brigham-Grette J (2013). Late Pleistocene glacial events in Beringia. In: Elias S (ed.), *Encyclopedia of Quaternary Science*. 2nd edition, Elsevier, Amsterdam, Netherlands: 191–201. <https://doi.org/10.1016/B978-0-444-53643-3.00116-3>
- EPPO (2022a). EPPO Datasheet: *Phytophthora fragariae*. EPPO Global Database. <https://gd.eppo.int/taxon/PHYTFR/datasheet>. (accessed 29 December 2025)
- EPPO (2022b). EPPO Datasheet: *Phytophthora rubi*. EPPO Global Database. <https://gd.eppo.int/taxon/PHYTFu/datasheet>. (accessed 29 December 2025)
- EPPO (2025). PM 7/26 (2) *Phytophthora cinnamomi*. EPPO Standard on Diagnostics. *EPPO Bulletin* **55**: 183–202. <https://doi.org/10.1111/epp.13090>
- Erwin DC, Ribeiro OK (1996). *Phytophthora diseases worldwide*. APS Press, St. Paul, Minnesota, USA.
- Fajardo SN, Bourret TB, Frankel SJ, Rizzo DM (2025). *Phytophthora* species and their associations with chaparral and oak woodland vegetation in Southern California. *Journal of Fungi* **11**: 33. <https://doi.org/10.3390/jof11010033>
- Foster ZSL, Alborno FL, Fieland VJ, et al. (2022). A new oomycete metabarcoding method using the *rps10* gene. *Phytobiomes Journal* **6**: 214–226. <https://doi.org/10.1094/PBIOMES-02-22-0009-R>
- Frankel SJ, Conforti C, Hillman J, et al. (2020). *Phytophthora* introductions in restoration areas: Responding to protect California native flora from human-assisted pathogen spread. *Forests* **11**: 1291. <https://doi.org/10.3390/f11121291>
- Fritsch PW, Cruz BC (2012). Phylogeny of *Cercis* based on DNA sequences of nuclear ITS and four plastid regions: implications for transatlantic historical biogeography. *Molecular Phylogenetics and Evolution* **62**: 816–825. <https://doi.org/10.1016/j.ympev.2011.11.016>
- Funk DJ, Omland K (2003). Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology and Systematics* **34**: 397–423. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132421>
- Garbelotto MM, Lee HK, Slaughter G, et al. (1997). Heterokaryosis is not required for virulence of *Heterobasidion annosum*. *Mycologia* **89**: 92–102. <https://doi.org/10.1080/00275514.1997.12026759>
- Gibbs JN, Lipscombe MA, Peace AJ (1999). The impact of *Phytophthora* disease on riparian populations of common alder (*Alnus glutinosa*) in southern Britain. *European Journal of Forest Pathology* **29**: 39–50. <https://doi.org/10.1046/j.1439-0329.1999.00129.x>
- Gibbs JN, Van Dijk C, Webber JF (eds) (2003). *Phytophthora* disease of alder in Europe. *Forestry Commission Bulletin* **126**, Edinburgh, UK. <https://www.forestryresearch.gov.uk/publications/archive-phytophthora-disease-of-alder-in-europe>
- Gigot J, Walters TW, Zasada IA (2013). Impact and occurrence of *Phytophthora rubi* and *Pratylenchus penetrans* in commercial red raspberry (*Rubus ideaus*) fields in northwestern Washington. *International Journal of Fruit Science* **13**: 357–372. <https://doi.org/10.1080/15538362.2013.748373>
- Givnish TJ (1997). Adaptive radiation and molecular systematics: aims and conceptual issues. In: Givnish TJ, Systma KJ (eds), *Molecular evolution and adaptive radiation*. Cambridge University Press, New York, USA: 1–54.
- Givnish TJ (2015). Adaptive radiation versus 'radiation' and 'explosive diversification': why conceptual distinctions are fundamental to understanding evolution. *New Phytologist* **207**: 297–303. <https://doi.org/10.1111/nph.13482>
- Gladenkov AX, Oleinik AE, Marincovich L, et al. (2002). A refined age for the earliest opening of Bering Strait. *Palaeogeography, Palaeoclimatology, Palaeoecology* **183**: 321–328. [https://doi.org/10.1016/S0031-0182\(02\)00249-3](https://doi.org/10.1016/S0031-0182(02)00249-3)
- Gomes Marques I, Vieites-Blanco C, Barrento MJ, et al. (2025). Individual and combined effects of a simulated heatwave and the emerging *Phytophthora ×multiformis* on European alder species. *Forest Ecology and Management* **598**: 123202. <https://doi.org/10.1016/j.foreco.2025.123202>
- Gomes Marques I, Vieites-Blanco C, Rodríguez-González P, et al. (2024). The ADnet Bayesian belief network for alder decline: Integrating empirical data and expert knowledge. *Science of the Total Environment*

- 947: 173619. <https://doi.org/10.1016/j.scitotenv.2024.173619>
- Gonthier P, Nicolotti G, Linzer R, et al. (2007). Invasion of European pine stands by a North American forest pathogen and its hybridization with a native interfertile taxon. *Molecular Ecology* **16**: 1389–1400. <https://doi.org/10.1111/j.1365-294X.2007.03250.x>
- Goss EM, Cardenas ME, Myers K, et al. (2011). The plant pathogen *Phytophthora andina* emerged via hybridization of an unknown *Phytophthora* species and the Irish Potato Famine pathogen, *P. infestans*. *PLoS ONE* **6**(9): e24543. <https://doi.org/10.1371/journal.pone.0024543>
- Goss EM, Tabima JF, Cooke DEL, et al. (2014). The Irish potato famine pathogen *Phytophthora infestans* originated in central Mexico rather than the Andes. *Proceedings of the National Academy of Sciences, USA* **111**: 8791–8796. <https://doi.org/10.1073/pnas.1401884111>
- Gower DJ, Johnson KG, Richardson JE, et al. (eds) (2012). Biotic evolution and environmental change in Southeast Asia. *The Systematics Association Special Volume* **82**. Cambridge University Press, New York, USA. <https://www.cambridge.org/core/books/abs/biotic-evolution-and-environmental-change-in-southeast-asia/biotic-evolution-and-environmental-change-in-southeast-asia/207A9382E0383D1BD580EDA81CB059A7>
- Green K (2016). Dieback of *Nematolepis ovatifolia* (Rutaceae), an endemic shrub in the alpine- subalpine heaths of the Snowy Mountains, is facilitated by climate change. *Cunninghamia* **16**: 1–9. <https://doi.org/10.7751/cunninghamia.2016.16.001>
- Green S, Cooke DEL, Barwell L, et al. (2025). The prevalence of *Phytophthora* in British plant nurseries; high-risk hosts and substrates and opportunities to implement best practice. *Plant Pathology* **74**: 696–717. <https://doi.org/10.1111/ppa.14044>
- Greslebin AG, Hansen EM, Winton L, et al. (2005). *Phytophthora* species from declining *Austrocedrus chilensis* forests in Patagonia, Argentina. *Mycologia* **97**: 218–228. <https://doi.org/10.1080/15572536.2006.11832855>
- Hansen EM, Reeser PW, Sutton W (2012). *Phytophthora* beyond agriculture. *Annual Review of Phytopathology* **50**: 359–378. <https://doi.org/10.1146/annurev-phyto-081211-172946>
- Hardham AR, Blackman LM (2018). Pathogen profile update *Phytophthora cinnamomi*. *Molecular Plant Pathology* **19**: 260–285. <https://doi.org/10.1111/mp.12568>
- Harkness R, Suslow K, Sharma S, et al. (2025). Diversity and risk assessment of *Phytophthora* spp. found on plant roots in native plant nurseries and interstate shipping nurseries in California. *PhytoFrontiers* **5**: 42–51. <https://doi.org/10.1094/PHYTOFR-06-24-0064-R>
- Hartmann G, Blank R, Kunca A (2006). Collar rot of *Fagus sylvatica* caused by *Phytophthora cambivora*: damage, site relations and susceptibility of broadleaf hosts. In: Brasier CM, Jung T, Osswald W (eds), *Progress in Research on Phytophthora Diseases of Forest Trees*. Forest Research, Farnham, Hampshire, UK: 135–138.
- Hayashida A, Ito Y (1984). Paleoposition of Southwest Japan at 16 Ma: implication from paleomagnetism of the Miocene Ichishi Group. *Earth and Planetary Science Letters* **68**: 335–342. [https://doi.org/10.1016/0012-821X\(84\)90164-X](https://doi.org/10.1016/0012-821X(84)90164-X)
- Heaney LR (1991). A synopsis of climatic and vegetational change in Southeast Asia. *Climatic Change* **19**: 53–61. <https://doi.org/10.1007/BF00142213>
- Hickman CJ (1940). The red core root disease of the strawberry caused by *Phytophthora fragariae* n. sp. *Journal of Pomology and Horticultural Science* **18**: 89–118. <https://doi.org/10.1080/03683621.1941.11513556>
- Ho HH, Jong SC (1988). *Phytophthora fragariae*. *Mycotaxon* **31**: 305–322.
- Hope G (2001). Environmental change in the late Pleistocene and later Holocene at Wanda Site, Soroako, South Sulawesi, Indonesia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **171**: 129–145. [https://doi.org/10.1016/S0031-0182\(01\)00243-7](https://doi.org/10.1016/S0031-0182(01)00243-7)
- Hope G, Kershaw AP, van der Kaars S, et al. (2004). History of vegetation and habitat change in the Austral-Asian region. *Quaternary International* **118–119**: 103–126. [https://doi.org/10.1016/S1040-6182\(03\)00133-2](https://doi.org/10.1016/S1040-6182(03)00133-2)
- Hopple JS, Vilgalys R (1994). Phylogenetic relationships among coprinoid taxa and allies based on data from restriction site mapping of nuclear rDNA. *Mycologia* **86**: 96–107. <https://doi.org/10.1080/00275514.1994.12026378>
- Horta Jung M, Maia C, Mora-Sala B, et al. (2025). High diversity of *Phytophthora* species in natural ecosystems and nurseries of Portugal: Detrimental side effect of plant introductions from the age of discovery to modern globalization. *Plant Pathology* **74**: 330–362. <https://doi.org/10.1111/ppa.14022>
- Huai WX, Tian G, Hansen EM, et al. (2013). Identification of *Phytophthora* species baited and isolated from forest soil and streams in northwestern Yunnan province, China. *Forest Pathology* **43**: 87–103. <https://doi.org/10.1111/efp.12015>
- Huntley B (1993). Species-richness in north-temperate zone forests. *Journal of Biogeography* **20**: 163–180. <https://doi.org/10.2307/2845669>
- Husson C, Aguayo J, Revellin C, et al. (2015). Evidence for homoploid speciation in *Phytophthora alni* supports taxonomic reclassification in this species complex. *Fungal Genetics and Biology* **77**: 12–21. <https://doi.org/10.1016/j.fgb.2015.02.013>
- loos R, Andrieux A, Marçais B, et al. (2006). Genetic characterization of the natural hybrid species *Phytophthora alni* as inferred from nuclear and mitochondrial DNA analyses. *Fungal Genetics and Biology* **43**: 511–529. <https://doi.org/10.1016/j.fgb.2006.02.006>
- Isozaki Y, Maruyama S, Nakama T, et al. (2011). Growth and shrinkage of an active continental margin: Updated geotectonic history of the Japanese Islands. *Journal of Geography* **120**(1): 65–99. <https://doi.org/10.5026/jgeography.120.65>
- Jankowiak R, Stępniewska H, Bilański P, Taerum SJ (2023). *Phytophthora* species cause sudden and severe decline of naturally regenerated European beech (*Fagus sylvatica*) seedlings. *Plant Pathology* **72**: 774–785. <https://doi.org/10.1111/ppa.13698>
- Jee H-J, Cho W-D, Kim W-G (1997). *Phytophthora* diseases of apple in Korea: II. Occurrence of an unusual fruit rot caused by *P. cactorum* and *P. cambivora*. *Korean Journal of Plant Pathology* **13**: 145–151.
- Jönsson U, Lundberg L, Sonesson K, et al. (2003). First records of soilborne *Phytophthora* species in Swedish oak forests. *Forest Pathology* **33**: 175–179. <https://doi.org/10.1046/j.1439-0329.2003.00320.x>
- Jung T (2009). Beech decline in Central Europe driven by the interaction between *Phytophthora* infections and climatic extremes. *Forest Pathology* **39**: 73–94. <https://doi.org/10.1111/j.1439-0329.2008.00566.x>
- Jung T, Blaschke M (2004). *Phytophthora* root and collar rot of alders in Bavaria: distribution, modes of spread and possible management strategies. *Plant Pathology* **53**: 197–208. <https://doi.org/10.1111/j.0032-0862.2004.00957.x>
- Jung T, Blaschke M (2006). *Phytophthora* dieback of alders in Bavaria: distribution, pathways and management strategies. In: Brasier CM, Jung T, Osswald W (eds), *Progress in Research on Phytophthora Diseases of Forest Trees*. Forest Research, Farnham, Hampshire, UK: 61–66.
- Jung T, Balci Y, Broders KD, et al. (2023). *Synchospora* gen. nov., a new *Peronosporaceae* genus with aerial lifestyle from a natural cloud forest in Panama. *Journal of Fungi* **9**: 517. <https://doi.org/10.3390/jof9050517>
- Jung T, Blaschke H, Neumann P (1996). Isolation, identification and pathogenicity of *Phytophthora* species from declining oak stands. *European Journal of Forest Pathology* **26**: 253–272. <https://doi.org/10.1111/j.1439-0329.1996.tb00846.x>
- Jung T, Blaschke H, Oßwald W (2000). Involvement of soilborne *Phytophthora* species in Central European oak decline and the effect

- of site factors on the disease. *Plant Pathology* **49**: 706–718. <https://doi.org/10.1046/j.1365-3059.2000.00521.x>
- Jung T, Chang TT, Bakonyi J, et al. (2017c). Diversity of *Phytophthora* species in natural ecosystems of Taiwan and association with disease symptoms. *Plant Pathology* **66**: 194–211. <https://doi.org/10.1111/ppa.12564>
- Jung T, Colquhoun IJ, Hardy GESTJ (2013). New insights into the survival strategy of the invasive soilborne pathogen *Phytophthora cinnamomi* in different natural ecosystems in Western Australia. *Forest Pathology* **43**: 266–288. <https://doi.org/10.1111/efp.12025>
- Jung T, Durán A, Sanfuentes von Stowasser E, et al. (2018b). Diversity of *Phytophthora* species in Valdivian rainforests and association with severe dieback symptoms. *Forest Pathology* **48**: e12443. <https://doi.org/10.1111/efp.12443>
- Jung T, Hansen EM, Winton L, et al. (2002). Three new species of *Phytophthora* from European oak forests. *Mycological Research* **106**: 397–411. <https://doi.org/10.1017/S0953756202005622>
- Jung T, Horta Jung M, Cacciola SO, et al. (2017b). Multiple new cryptic pathogenic *Phytophthora* species from *Fagaceae* forests in Austria, Italy and Portugal. *IMA Fungus* **8**: 219–244. <https://doi.org/10.5598/imafungus.2017.08.02.02>
- Jung T, Horta Jung M, Scanu B, et al. (2017a). Six new *Phytophthora* species from ITS Clade 7a including two sexually functional heterothallic hybrid species detected in natural ecosystems in Taiwan. *Persoonia* **38**: 100–135. <https://doi.org/10.3767/003158517X693615>
- Jung T, Horta Jung M, Webber JF, et al. (2021). The destructive tree pathogen *Phytophthora ramorum* originates from the laurosilva forests of East Asia. *Journal of Fungi* **7**: 226. <https://doi.org/10.3390/jof7030226>
- Jung T, Hudler GW, Jensen-Tracy SL, et al. (2005). Involvement of *Phytophthora* spp. in the decline of European beech in Europe and the USA. *Mycologist* **19**: 159–166. [https://doi.org/10.1017/S0269-915X\(05\)00405-2](https://doi.org/10.1017/S0269-915X(05)00405-2)
- Jung T, La Spada F, Pane A, et al. (2019). Diversity and distribution of *Phytophthora* species in protected natural areas in Sicily. *Forests* **10**: 259.
- Jung T, Milenković I, Balci Y, et al. (2024). Worldwide forest surveys reveal forty-three new species in *Phytophthora* major Clade 2 with fundamental implications for the evolution and biogeography of the genus and global plant biosecurity. *Studies in Mycology* **107**: 251–388. <https://doi.org/10.3114/sim.2024.107.04>
- Jung T, Milenković I, Corcobado T, et al. (2022). Extensive morphological and behavioural diversity among fourteen new and seven described species in *Phytophthora* Clade 10 and its evolutionary implications. *Persoonia* **49**: 1–57. <https://doi.org/10.3767/persoonia.2022.49.01>
- Jung T, Orlikowski L, Henricot B, et al. (2016). Widespread *Phytophthora* infestations in European nurseries put forest, semi-natural and horticultural ecosystems at high risk of *Phytophthora* diseases. *Forest Pathology* **46**: 134–163. <https://doi.org/10.1111/efp.12239>
- Jung T, Pérez-Sierra A, Durán A, et al. (2018a). Canker and decline diseases caused by soil- and airborne *Phytophthora* species in forests and woodlands. *Persoonia* **40**: 182–220. <https://doi.org/10.3767/persoonia.2018.40.08>
- Jung T, Scanu B, Brasier CM, et al. (2020). A survey in natural forest ecosystems of Vietnam reveals high diversity of both new and described *Phytophthora* taxa including *P. ramorum*. *Forests* **11**: 93. <https://doi.org/10.3390/f11010093>
- Jung T, Stukely MJC, Hardy GESTJ, et al. (2011). Multiple new *Phytophthora* species from ITS Clade 6 associated with natural ecosystems in Australia: evolutionary and ecological implications. *Persoonia* **26**: 13–39. <https://doi.org/10.3767/003158511X557577>
- Kanoun-Boulé M, Vasconcelos T, Gaspar J, et al. (2016). *Phytophthora* × *alni* and *Phytophthora lacustris* associated with common alder decline in Central Portugal. *Forest Pathology* **46**: 174–176. <https://doi.org/10.1111/efp.12273>
- Katoh K, Standley DM (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kimura M (2000). Paleogeography of the Ryukyu Islands. *Tropics* **10**(1): 5–24. <https://doi.org/10.3759/tropics.10.5>
- Kone A, Kofke DA (2005). Selection of temperature intervals for parallel-tempering simulations. *Journal of Chemical Physics* **122**: 1–2. <https://doi.org/10.1063/1.1917749>
- Kozak KH, Weisrock DR, Larson R (2006). Rapid lineage accumulation in a non-adaptive radiation: phylogenetic analysis of diversification rates in eastern North American woodland salamanders (*Plethodontidae*: *Plethodon*). *Proceedings of the Royal Society B* **273**: 539–546. <https://doi.org/10.1098/rspb.2005.3326>
- Kozlov A, Darriba D, Flouri T, et al. (2019). RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics* **35**: 4453–4455. <https://doi.org/10.1093/bioinformatics/btz305>
- Kroon LPNM, Bakker FT, van den Bosch GBM, et al. (2004). Phylogenetic analysis of *Phytophthora* species based on mitochondrial and nuclear DNA sequences. *Fungal Genetics and Biology* **41**: 766–782. <https://doi.org/10.1016/j.fgb.2004.03.007>
- Kronmiller BA, Feau N, Shen D, et al. (2023). Comparative genomic analysis of 31 *Phytophthora* genomes reveals genome plasticity and horizontal gene transfer. *Molecular Plant-Microbe Interactions* **36**: 26–46. <https://doi.org/10.1094/MPMI-06-22-0133-R>
- Lamour K (ed) (2013). *Phytophthora a global perspective*. CABI, Wallingford, UK. <https://doi.org/10.1079/9781780640938.0000>
- Landa BB, Arias-Giraldo, LF, Henricot B, et al. (2021). Diversity of *Phytophthora* species detected in disturbed and undisturbed British soils using high-throughput sequencing targeting ITS rRNA and COI mtDNA regions. *Forests* **12**: 229. <https://doi.org/10.3390/f12020229>
- Lanfear R, Frandsen P, Wright A, et al. (2016). PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* **34**: 772–773. <https://doi.org/10.1093/molbev/msw260>
- Latham RE, Ricklefs RE (1993). Continental comparison of temperate-zone tree species richness. In: Ricklefs RE, Schluter D (eds), *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. The University of Chicago Press, Chicago: 294–314.
- Laumonier Y (1997). The vegetation and physiography of Sumatra. *Geobotany* **22**. Springer Science and Business Media, Dordrecht, Germany. <https://doi.org/10.1007/978-94-009-0031-8https://link.springer.com/book/10.1007/978-94-009-0031-8>
- Lavin M, Luckow M (1993). Origins and relationships of tropical North America in the context of the boreotropics hypothesis. *American Journal of Botany* **80**: 1–14. <https://doi.org/10.1002/j.1537-2197.1993.tb13761.x>
- Legeay J, Husson C, Boudier B, et al. (2020). Surprising low diversity of the plant pathogen *Phytophthora* in Amazonian forests. *Environmental Microbiology* **22**: 5019–5032. <https://doi.org/10.1111/1462-2920.15099>
- Lemoine F, Domelevo Entfellner J, Wilkinson E, et al. (2018). Renewing Felsenstein's phylogenetic bootstrap in the era of big data. *Nature* **556**: 452–456. <https://doi.org/10.1038/s41586-018-0043-0>
- Li D-W, Schultes NP, LaMondia JA, Cowles RS (2019). *Phytophthora abietivora*, a new species isolated from diseased christmas trees in Connecticut, U.S.A. *Plant Disease* **103**: 3057–3064. <https://doi.org/10.1094/PDIS-03-19-0583-RE>
- Macháčová M, Tomášková I, Corcobado T, et al. (2024). Response of *Alnus*

- glutinosa* to *Phytophthora* bark infections at ambient and elevated CO₂ levels. *Frontiers in Forests and Global Change* 7: 1379791. <https://doi.org/10.3389/ffgc.2024.1379791>
- MacKinnon K, Hatta G, Halim H, et al. (1997). The Ecology of Kalimantan. *Ecology of Indonesia Series Vol. III*. Oxford University Press, Oxford, UK. ISBN 978-0-9459-7173-3
- Man in 't Veld WA, Rosendahl KCHM, Hong C (2012). *Phytophthora* × *serendipita* sp. nov. and *P. ×pelgrandis*, two destructive pathogens generated by natural hybridization. *Mycologia* 104: 1390–1396. <https://doi.org/10.3852/11-272>
- Man in 't Veld WA (2007). Gene flow analysis demonstrates that *Phytophthora fragariae* var. *rubi* constitutes a distinct species, *Phytophthora rubi* comb. nov. *Mycologia* 99: 222–226. <https://doi.org/10.1080/15572536.2007.11832581>
- Martin FN, Tooley PW (2003). Phylogenetic relationships among *Phytophthora* species inferred from sequence analysis of mitochondrially encoded cytochrome oxidase I and II genes. *Mycologia* 95: 269–284. <https://doi.org/10.1080/15572536.2004.11833112>
- Martin FN, Blair JE, Coffey MD (2014). A combined mitochondrial and nuclear multilocus phylogeny of the genus *Phytophthora*. *Fungal Genetics and Biology* 66: 19–32. <https://doi.org/10.1016/j.fgb.2014.02.006>
- Martínez-Arias C, Pastor-García M, Piñeiro J, et al. (2024). Decline of beech trees in a Mediterranean forest is associated with high rhizosphere oomycete diversity. *Rhizosphere* 32: 100974. <https://doi.org/10.1016/j.rhisph.2024.100974>
- Maruyama S, Isozaki Y, Kimura G, Terabayashi M (1997). Paleogeographic maps of the Japanese Islands: Plate tectonic synthesis from 750 Ma to the present. *Island Arc* 6: 121–142. <https://doi.org/10.1111/j.1440-1738.1997.tb00043.x>
- May KJ, Drenth A, Irwin JAG (2003). Interspecific hybrids between the homothallic *Phytophthora sojae* and *Phytophthora vignae*. *Australasian Plant Pathology* 32: 353–359. <https://doi.org/10.1071/AP03037>
- Mayr E (1942). *Systematics and the origin of species*. Columbia University Press, New York.
- Milenković I, Keča N, Karadžić D, et al. (2012). Incidence of *Phytophthora* species in beech stands in Serbia. *Folia Forestalia Polonica, series A* 54: 223–232. <https://doi.org/10.5281/zenodo.30775>
- Milenković I, Keča N, Karadžić D, et al. (2018). Occurrence and pathogenicity of *Phytophthora* × *cambivora* on *Prunus laurocerasus* in Serbia. *Forest Pathology* 48: e12436. <https://doi.org/10.1111/efp.12436>
- Milholland RD (1994). *A monograph of Phytophthora fragariae and the red stele disease of strawberry*. Technical bulletin, North Carolina Agricultural Research Service, North Carolina State University, Raleigh, NC, USA.
- Minh BQ, Nguyen MAT, von Haeseler A. (2013). Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 30:1188–1195. <https://doi.org/10.1093/molbev/mst024>
- Minh BQ, Schmidt HA, Chernomor O, et al. (2020). IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37: 1530–1534. <https://doi.org/10.1093/molbev/msaa015>
- Mircetich SM, Matheron ME (1976). *Phytophthora* root and crown rot of cherry trees. *Phytopathology* 66: 549–558. https://www.apsnet.org/publications/phytopathology/backissues/Documents/1976Articles/Phyto66n05_549.PDF
- Moreau C, Moreau M (1952). Etude mycologique de la maladie de l'encre du chêne. *Revue de Pathologie Végétale* 31: 201–231.
- Motta E, Annesi T, Pane A, et al. (2003). A new *Phytophthora* causing a basal canker on beech in Italy. *Plant Disease* 87: 1005. <https://doi.org/10.1094/PDIS.2003.87.8.1005A>
- Müller N, Bouckaert R (2019). Adaptive parallel tempering for BEAST 2. *bioRxiv* [online]. <https://doi.org/10.1101/603514>.
- Mullett MS, Van Poucke K, Haegemann A, et al. (2023). Phylogeography and population structure of the global, wide host-range hybrid pathogen *Phytophthora* × *cambivora*. *IMA Fungus* 14: 4. <https://doi.org/10.1186/s43008-023-00109-6>
- Munda A, Zerjav M, Schroers H-J (2007). First report of *Phytophthora citricola* occurring on *Fagus sylvatica* in Slovenia. *Plant Disease* 91: 907. <https://doi.org/10.1094/PDIS-91-7-0907C>
- Nagel JH, Gryzenhout M, Slippers B, et al. (2013). Characterization of *Phytophthora* hybrids from ITS clade 6 associated with riparian ecosystems in South Africa and Australia. *Fungal Biology* 117: 329–347. <https://doi.org/10.1016/j.funbio.2013.03.004>
- Nagy ZÁ, Bakonyi J, Érsek T (2003). Standard and Swedish variant types of the hybrid alder *Phytophthora* attacking alder in Hungary. *Pest Management Science* 59: 484–492. <https://doi.org/10.1002/ps.681>
- Nechwatal J, Hahn J, Schönborn A, et al. (2011). A twig blight of understorey European beech (*Fagus sylvatica*) caused by soilborne *Phytophthora* spp. *Forest Pathology* 41: 493–500. <https://doi.org/10.1111/j.1439-0329.2011.00711.x>
- Newcombe G, Stirling B, McDonald S, et al. (2000). *Melampsora* × *columbiana*, a natural hybrid of *M. medusae* and *M. occidentalis*. *Mycological Research* 104: 261–274. <https://doi.org/10.1017/S0953756299001665>
- Niederhauser JS (1991). *Phytophthora infestans*: the Mexican connection. In: *Phytophthora* (Lucas JA, Shattock RC, Shaw DS, et al., eds). Cambridge University Press, Cambridge, UK: 25–45.
- Paap T, White D, Bose T, et al. (2026). Diversity and phylogeny of *Phytophthora* Clade 9, including descriptions of three novel species. *Mycological Progress* 25: 29. <https://doi.org/10.1007/s11557-026-02140-4>
- Paoletti M, Buck KW, Brasier CM (2006). Selective acquisition of novel mating type and vegetative incompatibility genes via interspecies gene transfer in the globally invading eukaryote *Ophiostoma novo-ulmi*. *Molecular Ecology* 14: 249–263. <https://doi.org/10.1111/j.1365-294X.2005.02728.x>
- Pattengale ND, Alipour M, Bininda-Emonds ORP, et al. (2010). How many bootstrap replicates are necessary? *Journal of Computational Biology* 17: 337–354. <https://doi.org/10.1089/cmb.2009.0179>
- Pérez-Sierra A, Horta Jung M, Jung T (2022). Survey and monitoring of *Phytophthora* species in natural ecosystems: Methods for sampling, isolation, purification, storage, and pathogenicity tests. In: Luchi N (ed.), *Plant Pathology. Methods in Molecular Biology* 2536: 23–49. https://doi.org/10.1007/978-1-0716-2517-0_2
- Pintos-Varela C, Rial-Martínez C, Aguin-Casal O, et al. (2012). First report of *Phytophthora alni* subsp. *uniformis* on black alder in Spain. *Plant Disease* 96: 589. <https://doi.org/10.1094/PDIS-10-11-0891-PDN>
- Pintos-Varela C, Rial-Martínez C, Aguin-Casal O, Mansilla-Vázquez JP (2017). First report of *Phytophthora* × *multiformis* on *Alnus glutinosa* in Spain. *Plant Disease* 101: 261. <https://doi.org/10.1094/PDIS-08-16-1092-PDN>
- Posada D, Crandall KA (2001). Intraspecific gene genealogies: Trees grafting into networks. *Trends in Ecology and Evolution* 16: 37–45. [https://doi.org/10.1016/S0169-5347\(00\)02026-7](https://doi.org/10.1016/S0169-5347(00)02026-7)
- Prigigallo MI, Mosca S, Cacciola SO, et al. (2015). Molecular analysis of *Phytophthora* diversity in nursery-grown ornamental and fruit plants. *Plant Pathology* 64: 1308–1319. <https://doi.org/10.1111/ppa.12362>
- Qian H (2002). Floristic relationships between Eastern Asia and North America: Test of Gray's hypothesis. *The American Naturalist* 160: 317–332. <https://doi.org/10.1086/341523>
- Rambaut A, Drummond A, Xie D, et al. (2018). Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Rands RD (1922). Streepkanker van kaneel, veroorzaakt door *Phytophthora*

- cinnamomi* n. sp. (Stripe canker of cinnamon caused by *Phytophthora cinnamomi* n. sp.). Mededeelingen van het Instituut voor Plantenziekten **54**: 1–54.
- Redondo MA, Boberg J, Olsson CHB, et al. (2015). Winter conditions correlate with *Phytophthora alni* subspecies distribution in southern Sweden. *Phytopathology* **105**: 1191–1197. <https://doi.org/10.1094/PHYTO-01-15-0020-R>
- Reeser PW, Sutton W, Hansen EM, et al. (2011). *Phytophthora* species in forest streams in Oregon and Alaska. *Mycologia* **103**: 22–35. <https://doi.org/10.3852/10-013>
- Ribeiro OK (1978). *A source book of the genus Phytophthora*. Cramer, Vaduz.
- Riddell CE, Frederickson-Matika D, Armstrong AC, et al. (2019). Metabarcoding reveals a high diversity of woody host-associated *Phytophthora* spp. in soils at public gardens and amenity woodlands in Britain. *PeerJ* **7**: e6931. <https://doi.org/10.7717/peerj.6931>
- Rizzo DM, Garbelotto M, Davidson JM, et al. (2002). *Phytophthora ramorum* as the cause of extensive mortality of *Quercus* spp. and *Lithocarpus densiflorus* in California. *Plant Disease* **86**: 205–214. <https://doi.org/10.1094/PDIS.2002.86.3.205>
- Robideau GP, De Cock AW, Coffey MD, et al. (2011). DNA barcoding of oomycetes with cytochrome c oxidase subunit I and internal transcribed spacer. *Molecular Ecology Resources* **11**: 1002–1011. <https://doi.org/10.1111/j.1755-0998.2011.03041.x>
- Ronquist F, Teslenko M, van der Mark P, et al. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Rooney-Latham S, Blomquist CL, Kosta KL, et al. (2019). *Phytophthora* species are common on nursery stock grown for restoration and revegetation purposes in California. *Plant Disease* **103**: 448–455. <https://doi.org/10.1094/PDIS-01-18-0167-RE>
- Rundell RJ, Price TD (2009). Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology and Evolution* **24**: 394–399. <https://doi.org/10.1016/j.tree.2009.02.007>
- Runge F, Telle S, Ploch S, et al. (2011). The inclusion of downy mildews in a multi-locus-dataset and its reanalysis reveals a high degree of paraphyly in *Phytophthora*. *IMA Fungus* **2**: 163–171. <https://doi.org/10.5598/imafungus.2011.02.02.07>
- Saavedra A, Hansen EM, Goheen DJ (2007). *Phytophthora cambivora* in Oregon and its pathogenicity to *Chrysopsis chrysophylla*. *Forest Pathology* **37**: 409–419. <https://doi.org/10.1111/j.1439-0329.2007.00515.x>
- Safaiefarahani B, Mostowfizadeh-Ghalefarsa R, Hardy GESTJ, Burgess TI (2016). Species from within the *Phytophthora cryptogea* complex and related species, *P. erythrosetica* and *P. sansomeana*, readily hybridize. *Fungal Biology* **120**: 975–987. <https://doi.org/10.1016/j.funbio.2016.05.002>
- Santini A, Barzanti GP, Capretti P (2001). A new *Phytophthora* root disease of alder in Italy. *Plant Disease* **85**: 560. <https://doi.org/10.1094/PDIS.2001.85.5.560A>
- Sarver BAJ, Pennell MW, Brown JW, et al. (2019). The choice of tree prior and molecular clock does not substantially affect phylogenetic inferences of diversification rates. *PeerJ* **7**: e6334. <http://dx.doi.org/10.7717/peerj.6334>
- Scanu B, Hunter GC, Linaldeddu BT, et al. (2014). A taxonomic re-evaluation reveals that *Phytophthora cinnamomi* and *P. cinnamomi* var. *parvispora* are separate species. *Forest Pathology* **44**: 1–20. <https://doi.org/10.1111/efp.12064>
- Scanu B, Jung T, Masigol H, et al. (2021). *Phytophthora heterospora* sp. nov., a new pseudoconidia-producing sister species of *P. palmivora*. *Journal of Fungi* **7**: 870. <https://doi.org/10.3390/jof7100870>
- Scanu B, Linaldeddu BT, Deidda A, et al. (2015). Diversity of *Phytophthora* species from declining Mediterranean maquis vegetation, including two new species, *Phytophthora crassamura* and *P. ornamentata* sp. nov. *PLoS ONE* **10**: e0143234. <https://doi.org/10.1371/journal.pone.0143234>
- Schardl CL, Craven KD (2003). Interspecific hybridization in plant-associated fungi and oomycetes: a review. *Molecular Ecology* **12**: 2861–2873. <https://doi.org/10.1046/j.1365-294X.2003.01965.x>
- Schmitz S, Zini J, Chandelier A (2009). Involvement of *Phytophthora* species in the decline of beech (*Fagus sylvatica*) in the southern part of Belgium. In: Goheen EM, Frankel SJ (eds), *Phytophthoras in Forests and Natural Ecosystems: Fourth Meeting of the International Union of Forest Research Organizations (IUFRO) Working Party S07.02.09*. USDA Forest Service, Pacific Southwest Research Station, Albany, California. General Technical Report PSW-GTR-221: 320–323.
- Schumacher J, Leonhard S, Grundmann BM, et al. (2006). New alder disease in Spreewald biosphere reserve – causes and incidental factors of an epidemic. *Nachrichtenblatt Deutscher Pflanzenschutzdienst* **58**: 141–147.
- Schwingle BW, Smith JA, Blanchette RA (2007). *Phytophthora* species associated with diseased woody ornamentals in Minnesota nurseries. *Plant Disease* **91**: 97–102. <https://doi.org/10.1094/PD-91-0097>
- Scott P, Williams N (2014). *Phytophthora* diseases in New Zealand forests. *New Zealand Journal of Forestry* **59**: 14–21. <https://nzif.org.nz/nzif-journal/publications/article/22799>
- Scott P, Bader MK-F, Burgess T, et al. (2019). Global biogeography and invasion risk of the plant pathogen genus *Phytophthora*. *Environmental Science & Policy* **101**: 175–182. <https://doi.org/10.1016/j.envsci.2019.08.020>
- Seddaiu S, Brandano A, Ruiu PA, et al. (2020). An overview of *Phytophthora* species inhabiting declining *Quercus suber* stands in Sardinia (Italy). *Forests* **11**: 971. <https://doi.org/10.3390/f11090971>
- Seidl MF, Bourret TB (2024). Peronosporaceae phylogenetics. Webinar presentation in: The Genus *Phytophthora* – Don't Change a Winning Concept? American Phytopathological Society Workshop, 22–25 April 2024, Session 1. Starting time 0:38:50. <https://www.apsnet.org/meetings/mtnghwshops/Pages/APS-2024-0422-01.aspx>
- Shakya SK, Grünwald NJ, Fieland VJ, et al. (2021). Phylogeography of the wide-host range panglobal plant pathogen *Phytophthora cinnamomi*. *Molecular Ecology* **30**: 5164–5178. <https://doi.org/10.1111/mec.16109>
- Sims LL, Sutton W, Reeser P, et al. (2015). The *Phytophthora* species assemblage and diversity in riparian alder ecosystems of western Oregon, USA. *Mycologia* **107**: 889–902. <https://doi.org/10.3852/14-255>
- Solla A, Pérez-Sierra A, Corcobado T, et al. (2010). *Phytophthora alni* on *Alnus glutinosa* reported for the first time in Spain. *Plant Pathology* **59**: 798. <https://doi.org/10.1111/j.1365-3059.2009.02254.x>
- Stamps DJ, Waterhouse GM, Newhook FJ, Hall GS (1990). Revised tabular key to the species of *Phytophthora*. Commonwealth Mycological Institute, Kew, UK. *Mycological Papers* **162**: 28 pp.
- Štěpánková P, Černý K, Strnadová V, et al. (2013). Identification of *Phytophthora alni* subspecies in riparian stands in the Czech Republic. *Plant Protection Science* **49**: S3–S10. <https://doi.org/10.17221/41/2013-PPS>
- Stępniewska H, Dłuszyński J (2010). Incidence of *Phytophthora cambivora* in bleeding lesions on beech stems in selected forest stands in south-eastern Poland. *Phytopathologia* **56**: 39–51.
- Stewart JE, Kroese D, Tabima JF, et al. (2014). Pathogenicity, fungicide resistance, and genetic variability of *Phytophthora rubi* isolates from raspberry (*Rubus idaeus*) in the western United States. *Plant Disease* **98**: 1702–1708. <http://dx.doi.org/10.1094/PDIS-11-13-1130-RE>
- Stöver BC, Müller KF (2010). TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics* **11**:

7. <https://doi.org/10.1186/1471-2105-11-7>
- Streito JC, Legrand P, Tabary F, et al. (2002). Phytophthora disease of alder (*Alnus glutinosa*) in France: investigations between 1995 and 1999. *Forest Pathology* **32**: 179–191. <https://doi.org/10.1046/j.1439-0329.2002.00282.x>
- Stukenbrock EH (2016). The role of hybridization in the evolution and emergence of new fungal plant pathogens. *Phytopathology* **106**: 104–112. <https://doi.org/10.1094/PHYTO-08-15-0184-RVW>
- Suzui T, Hoshino Y (1979). Collar rot of apple caused by *Phytophthora cambivora* (Petri) Buism. *Japanese Journal of Phytopathology* **45**: 344–352. <https://doi.org/10.3186/jjphytopath.45.344>
- Svenning J-C (2003). Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology Letters* **6**: 646–653. <https://doi.org/10.1046/j.1461-0248.2003.00477.x>
- Tabima JF, Coffey MD, Zazada IA, Grünwald NJ (2018). Populations of *Phytophthora rubi* show little differentiation and high rates of migration among states in the Western United States. *Molecular Plant-Microbe Interactions* **31**: 614–622. <https://doi.org/10.1094/MPMI-10-17-0258-R>
- Talgø V, Herrero M, Toppe B, et al. (2006). First report of root rot and stem canker caused by *Phytophthora cambivora* on Noble fir (*Abies procera*) for bough production in Norway. *Plant Disease* **90**: 682. <https://doi.org/10.1094/PD-90-0682B>
- Tamura K, Stecher G, Kumar S (2021). MEGA11: Molecular Evolutionary Genetics Analysis version 11. *Molecular Biology and Evolution* **38**: 3022–3027. <https://doi.org/10.1093/molbev/msab120>
- Telfer KH, Brurberg MB, Herrero M-L, et al. (2015). *Phytophthora cambivora* found on beech in Norway. *Forest Pathology* **45**: 415–425. <https://doi.org/10.1111/efp.12215>
- Tian S, López-Pujol J, Wang H-W, et al. (2010). Molecular evidence for glacial expansion and interglacial retreat during Quaternary climatic changes in a montane temperate pine (*Pinus kwangtungensis* Chun ex Tsiang) in southern China. *Plant Systematics and Evolution* **284**: 219–229. <https://doi.org/10.1007/s00606-009-0246-9>
- Thines M (2023). Nomenclatural novelties. *Index Fungorum* **548**.
- Thines M, Mishra B, Ploch S (2023). Multigene analyses with a broad sampling in *Phytophthora* and related genera provide evidence for the monophyly of downy mildews. *Mycological Progress* **22**: 82. <https://doi.org/10.1007/s11557-023-01932-2>
- Thines M, Choi Y-J (2016). Evolution, diversity and taxonomy of the *Peronosporaceae*, with focus on the genus *Peronospora*. *Phytopathology* **106**: 6–18. <https://doi.org/10.1094/PHYTO-05-15-0127-RVW>
- Thoirain B, Husson C, Marçais B (2007). Risk factors for the *Phytophthora*-induced decline of alder in north-eastern France. *Phytopathology* **97**: 99–105. <https://doi.org/10.1094/PHYTO-97-0099>
- Tiffney BH (1985). The Eocene North Atlantic land bridge: Its importance in tertiary and modern phytogeography of the northern hemisphere. *Journal of the Arnold Arboretum* **66**: 243–273. <https://www.jstor.org/stable/43782164>
- Tiffney BH, Manchester SR (2001). The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere Tertiary. *International Journal of Plant Sciences* **162** (Suppl.): S3–S17. <https://doi.org/10.1086/323880>
- Toews DPL, Brelsford A (2012). The biogeography of mitochondrial and nuclear discordance in animals. *Molecular Ecology* **21**: 3907–3930. <https://doi.org/10.1111/j.1365-294X.2012.05664.x>
- Trzewik A, Orlikowski LB, Oszako T, et al. (2015). The characterization of *Phytophthora* isolates obtained from diseased *Alnus glutinosa* in Poland. *Baltic Forestry* **21**: 44–50. ISSN 2029-9230
- Tsykun T, Prospero S, Schoebel CN, et al. (2022). Global invasion history of the emerging plant pathogen *Phytophthora multivora*. *BMC Genomics* **23**: 153. <https://doi.org/10.1186/s12864-022-08363-5>
- Tucker CM (1931). Taxonomy of the genus *Phytophthora* de Bary. *Research Bulletin of the Missouri Agricultural Experiment Station* **153**: 1–207.
- Van Poucke K, Haegeman A, Goedefroid T, et al. (2021). Unravelling hybridization in *Phytophthora* using phylogenomics and genome size estimation. *IMA Fungus* **12**: 16. <https://doi.org/10.1186/s43008-021-00068-w>
- Vélez ML, La Manna L, Tarabini N, et al. (2020). *Phytophthora austrocedri* in Argentina and co-inhabiting *Phytophthoras*: Roles of anthropogenic and abiotic factors in species distribution and diversity. *Forests* **11**: 1223. <https://doi.org/10.3390/f11111223>
- Vettraino AM, Barzanti GP, Bianco MC, et al. (2002). Occurrence of *Phytophthora* species in oak stands in Italy and their association with declining oak trees. *Forest Pathology* **32**: 19–28. <https://doi.org/10.1046/j.1439-0329.2002.00264.x>
- Vettraino AM, Belisario A, Maccaroni M, et al. (2003). Evaluation of root damage to English walnut caused by five *Phytophthora* species. *Plant Pathology* **52**: 491–495. <https://doi.org/10.1046/j.1365-3059.2003.00864.x>
- Vettraino AM, Jung T, Vannini A (2008). First report of *Phytophthora cactorum* associated with beech decline in Italy. *Plant Disease* **92**: 1708. <https://doi.org/10.1094/PDIS-92-12-1708A>
- Vettraino AM, Morel O, Perlerou C, et al. (2005). Occurrence and distribution of *Phytophthora* species associated with ink disease of chestnut in Europe. *European Journal of Plant Pathology* **111**: 169–180. <https://doi.org/10.1007/s10658-004-1882-0>
- Vila R, Bell CD, Macniven R, et al. (2011). Phylogeny and palaeoecology of *Polyommatus* blue butterflies show Beringia was a climate-regulated gateway to the New World. *Proceedings of the Royal Society B* **278**: 2737–2744. <https://doi.org/10.1098/rspb.2010.2213>
- Wang WX, Sun YJ, Chen XW, et al. (2026). Two novel species, *Phytophthora umbellata*, sp. nov., and *Phytophythium niubelliangense*, sp. nov., from a subtropical island in Japan and a warm-temperate forest in China. *Mycologia* **24**: 1–5. <https://doi.org/10.1080/00275514.2025.2592494>
- Warfield CY, Hwang J, Benson DM (2008). *Phytophthora* blight and dieback in North Carolina nurseries during a 2003 survey. *Plant Disease* **92**: 474–481. <https://doi.org/10.1094/PDIS-92-3-0474>
- Watanabe N, Arai K, Otsubo M, et al. (2023). Geological history of the land area between Okinawa Jima and Miyako Jima of the Ryukyu Islands, Japan, and its phylogeographical significance for the terrestrial organisms of these and adjacent islands. *Progress in Earth and Planetary Science* **10**: 40. <https://doi.org/10.1186/s40645-023-00567-x>
- Waterhouse GM (1970). The genus *Phytophthora* de Bary. Commonwealth Mycological Institute, Kew, UK. *Mycological Papers* **122**: 1–59. ISBN 978-0-8519-8029-4
- Weir BS, Paderes EP, Anand N, et al. (2015). A taxonomic revision of *Phytophthora* Clade 5, including two new species, *Phytophthora agathidicida* and *P. cocois*. *Phytotaxa* **205**: 21–38. <http://dx.doi.org/10.11646/phytotaxa.205.1.2>
- Wen J (1999). Evolution of Eastern Asian and Eastern North American disjunct distributions in flowering plants. *Annual Review of Ecology and Systematics* **30**: 421–455. <https://doi.org/10.1146/annurev.ecolsys.30.1.421>
- Wen J, Ickert-Bond S, Nie Z-L, et al. (2010). Timing and modes of evolution of eastern Asian-North American biogeographic disjunctions in seed plants. In: Long M, Gu H, Zhou Z (eds), *Darwin's Heritage Today: Proceedings of the Darwin 2010 Beijing International Conference*. Higher Education Press, Beijing, China: 252–269.
- Wen J, Nie Z-L, Ickert-Bond SM (2016). Intercontinental disjunctions between eastern Asia and western North America in vascular plants highlight the biogeographic importance of the Bering land bridge from late Cretaceous to Neogene. *Journal of Systematics and Evolution* **54**: 469–490. <https://doi.org/10.1111/jse.12222>

- Wertheim JO, Sanderson MJ, Worobey M, et al. (2010). Relaxed molecular clocks, the bias–variance trade-off, and the quality of phylogenetic inference. *Systematic Biology* **59**: 1–8. <https://doi.org/10.1093/sysbio/syp072>
- White TJ, Bruns T, Lee S, et al. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innes MA, Gelfand DH, Sninsky JJ, et al. (eds), *PCR Protocols: A Guide to Methods and Applications*. Academic Press, San Diego, California, USA: 315–322. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Whitten T, Damanik SJ, Anwar J, et al. (1997). The Ecology of Sumatra. *Ecology of Indonesia Series Vol. I*. Oxford University Press, Oxford, UK. ISBN 978-1-4629-0508-9
- Whitten T, Mustafa M, Henderson GS (2002). The Ecology of Sulawesi. *Ecology of Indonesia Series Vol. IV*. Oxford University Press, Oxford, UK. ISBN 978-1-4629-0507-2
- Wicks TJ, Lee TC, Scott ES (1997). Phytophthora crown rot of almonds in Australia. *EPPO Bulletin* **27**: 501–506. <https://doi.org/10.1111/j.1365-2338.1997.tb00673.x>
- Wilcox WF, Duncan JM (1993). *Phytophthora fragariae* Hickman var. *rubi* var. *nova*. *Mycological Research* **97**: 830. [https://doi.org/10.1016/S0953-7562\(09\)81157-X](https://doi.org/10.1016/S0953-7562(09)81157-X)
- Wilcox WF, Mircetich SM (1985). Pathogenicity and relative virulence of seven *Phytophthora* spp. on Mahaleb and Mazzard cherry. *Phytopathology* **75**: 221–226.
- Wilcox WF, Scott PH, Ham PB, et al. (1993). Identity of a *Phytophthora* species attacking raspberry in Europe and North America. *Mycological Research* **97**: 817–831. [https://doi.org/10.1016/S0953-7562\(09\)81157-X](https://doi.org/10.1016/S0953-7562(09)81157-X)
- Woodburne MO (2010). The Great American Biotic Interchange: Dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution* **17**: 245–264. <https://doi.org/10.1007/s10914-010-9144-8>
- Wurster CM, Bird MI, Bull ID, et al. (2010). Forest contraction in north equatorial Southeast Asia during the last glacial maximum. *Proceedings of the National Academy of Sciences USA* **107**: 15508–15511. <https://doi.org/10.1073/pnas.1005507107>
- Xu J, Yang X, Li Y, et al. (2019). *Phytophthora* species from Xinjiang Wild apple forests in China. *Forests* **10**: 927. <https://doi.org/10.3390/f10100927>
- Yang X, Copes WE, Hong CX (2013). *Phytophthora mississippiensis* sp. nov., a new species recovered from irrigation reservoirs at a plant nursery in Mississippi. *Journal of Plant Pathology and Microbiology* **4**: 180. <http://dx.doi.org/10.4172/2157-7471.1000180>
- Yang X, Tyler BM, Hong C (2017). An expanded phylogeny for the genus *Phytophthora*. *IMA Fungus* **8**: 355–384. <https://doi.org/10.5598/imafungus.2017.08.02.09>
- Ye Z, Chen P, Bu W (2016). Terrestrial mountain islands and Pleistocene climate fluctuations as motors for speciation: A case study on the genus *Pseudovelia* (Hemiptera: Veliidae). *Scientific Reports* **6**: 33625. <https://doi.org/10.1038/srep33625>
- Zamora-Ballesteros C, Haque MMU, Diez JJ, Martín-García J (2017). Pathogenicity of *Phytophthora alni* complex and *P. plurivora* in *Alnus glutinosa* seedlings. *Forest Pathology* **47**: e12299. <https://doi.org/10.1111/efp.12299>
- Zeng H-C, Ho H-H, Zheng F-C (2009). A survey of *Phytophthora* species on Hainan Island of South China. *Journal of Phytopathology* **157**: 33–39. <https://doi.org/10.1111/j.1439-0434.2008.01441.x>

Supplementary Material: <https://studiesinmycology.org/>

Fig. S1. Fifty percent majority rule consensus phylogram derived from Bayesian inference analysis of a concatenated nuclear eight-locus (LSU, ITS, *βtub*, *hsp90*, *tigA*, *rpl10*, *tef-1α*, *enl*) dataset of *Phytophthora* Clade 7a using MrBayes. Bayesian posterior probabilities are indicated but not shown below 0.5. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 expected substitutions per site per branch.

Fig. S2. ML bootstrap best tree derived from Maximum Likelihood analysis of a concatenated nuclear eight-locus (LSU, ITS, *βtub*, *hsp90*, *tigA*, *rpl10*, *tef-1α*, *enl*) dataset of *Phytophthora* Clade 7a using RAxML. Bootstrap values are indicated but not shown below 50 %. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 expected substitutions per site per branch.

Fig. S3. Fifty percent majority rule consensus phylogram derived from Bayesian inference analysis of a concatenated mitochondrial three-locus (*cox1*, *nadh1*, *rps10*) dataset of *Phytophthora* Clade 7a using MrBayes. Bayesian posterior probabilities are indicated but not shown below 0.5. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 expected changes per site per branch.

Fig. S4. ML bootstrap best tree derived from Maximum Likelihood analysis of a concatenated three-locus (*cox1*, *nadh1*, *rps10*) dataset of *Phytophthora* Clade 7a using RAxML. Bootstrap values are indicated but not shown below 50 %. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 expected substitutions per site per branch.

Fig. S5. Fifty percent majority rule consensus phylogram derived from Bayesian inference analysis of a concatenated nuclear and mitochondrial eleven-locus (LSU, ITS, *βtub*, *hsp90*, *tigA*, *rpl10*, *tef-1α*, *enl*, *cox1*, *nadh1*, *rps10*) dataset of *Phytophthora* Clade 7a using MrBayes. Bayesian posterior probabilities are indicated but not shown below 0.5. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 expected substitutions per site per branch.

Fig. S6. ML bootstrap best tree derived from Maximum Likelihood analysis of a concatenated eleven-locus (LSU, ITS, *βtub*, *hsp90*, *tigA*, *rpl10*, *tef-1α*, *enl*, *cox1*, *nadh1*, *rps10*) dataset of *Phytophthora* Clade 7a using RAxML. Bootstrap values are indicated but not shown below 50 %. *Phytophthora sojae* and *P. cinnamomi* from Clades 7b and 7c, respectively, were used as outgroup taxa (not shown). NT and T denote ex-neotype and ex-type isolates. Scale bar indicates 0.01 expected substitutions per site per branch.

Fig. S7. Number of genotyping-by-sequencing (GBS) loci with one to four alleles in isolates from 15 ‘pure’ (non-hybrid) and nine hybrid taxa in *Phytophthora* Clade 7a. For methods see Van Poucke et al. (2021) and Mullett et al. (2023). ALG = *P. alga*, ART = *P. arta*, ATT = *P. attenuata*, EUR = *P. europaea*, FLE = *P. flexuosa*, FOR = *P. formosa*, FRA = *P. fragariae*, GRA = *P. grandoogonia*, INT = *P. intricata*, IRR = *P. irregularis*,



RUB = *P. rubi*, ULI = *P. uliginosa*, UNI = *P. uniformis*, TYR = *P. tyrrhenica*, VUL = *P. vulcanica*, ×ALN = *P. ×alni*, ×CAM = *P. ×cambivora*, ×GRA = *P. ×grandisporangia*, ×HET = *P. ×heterohybrida*, ×INC = *P. ×incrassata*, ×LEP = *P. ×leptopleura*, ×MUF = *P. ×multiformis*, ×MUF-like = *P.* taxon ×multiformis-like, ×NOD = *P. ×nodosa*. DE = Germany, ES = Spain, FR = France, GB = United Kingdom, HR = Croatia, HU = Hungary, IT = Italy, JP = Japan, NL = Netherlands, NO = Norway, SE = Sweden, TW = Taiwan, VN = Vietnam. Isolates printed in bold type depict ex-type, ex-epitype or ex-neotype isolates. Isolate details and GenBank accession numbers are given in Tables 1 and S2, respectively.

File S1. Supplementary phylogenetic results.

Table S1. Overview of PCR conditions and details of primers used for amplification and sequencing of *Phytophthora* isolates.

Table S2 GenBank accession numbers of *Phytophthora* isolates included in the phylogenetic, morphological, growth-temperature and biogeography studies (sequences obtained in the present study are printed in italics: PX606948–PX607247, PX580651–PX582108, PX964341–PX964344, PX959673, PX959678, PZ326525, PZ330034–PZ330042, PZ332760).