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REVIEW

The Genus *Phytophthora* Anno 2012

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ABSTRACT

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Plant diseases caused by *Phytophthora* species will remain an ever increasing threat to agriculture and natural ecosystems. *Phytophthora* literally means plant destroyer, a name coined in the 19th century by Anton de Bary when he investigated the potato disease that set the stage for the Great Irish Famine. *Phytophthora infestans*, the causal agent of potato late blight, was the first species in a genus that at present has over 100 recognized members. In the last decade, the number of recognized *Phytophthora* species has nearly doubled and new species are added almost on a monthly basis. Here we present an overview of the 10 clades that are currently distinguished within the genus *Phytophthora* with special emphasis on new species that have been described since 1996 when Erwin and Ribeiro published the valuable monograph '*Phytophthora* diseases worldwide' (35).

In the 120 years separating the studies of Heinrich Anton de Bary (24) and the reference monograph '*Phytophthora* diseases worldwide' by Erwin and Ribeiro (35), approximately 100 species of *Phytophthora* have been described in the literature of which 58 were officially recognized (34). In the last decade, the number of validly described *Phytophthora* species has nearly doubled (Fig. 1) and new species are added almost on a monthly basis. This enormous increase is, on the one hand, due to the availability of more sophisticated tools for species delimitation and, on the other hand, large-scale surveys for the presence of novel *Phytophthora* species in natural and agricultural settings. In this review we first briefly introduce the basics of classification and identification of *Phytophthora* species. We then present the 10 clades that currently constitute the genus *Phytophthora* and particularly mention the new *Phytophthora* species that have been described in the scientific literature since the release of the reference monograph in 1996 (35).

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SPECIES IDENTIFICATION AND DELIMITATION

For a long time identification and classification of species within the genus *Phytophthora* were based on the key developed by Waterhouse (104), which was later revised and adjusted by Stamps et al. (100). Waterhouse divided the genus into six groups, based on the three sporangium types and two antheridium types. Further criteria used to distinguish species in the pre-molecular era were host range, sporangium morphology, presence or absence of chlamydospores and hyphal swellings, optimal growth temperature, colony and oogonium morphology, and some other criteria. The allocation of an isolate to a particular species was arduous work and required trained experts with a good eye and attention to detail.

The description of a new species was even more challenging, requiring the researcher to be a skilled mycologist able to distinguish the potential new species from all other species, an artist to draw morphological structures by hand, and a classicist to phrase the findings in Latin. Researchers often found discrepancies within a species, for example groups of isolates with much higher optimal growth temperature or aberrant oogonium size. Since the Waterhouse key could often not handle these discrepancies, footnotes were made to justify why the deviating isolates were kept within the species.

Besides morphology, physiological characters have also been used to distinguish species, e.g., temperature-growth relations (100), growth in the presence of malachite green (71), or isozyme patterns (89). When DNA-based identification became common practice, molecular markers were combined with morphological data sets.

For *Phytophthora*, a variety of DNA-based identification methods has been explored. Amplified fragment length polymorphism fingerprinting, for example, was first used to construct a molecular-genetic linkage map of *P. infestans* (102). Later on AFLP markers as well as microsatellite markers were used as

high-resolution markers for characterizing *Phytophthora* isolates and for tracking clonal lineages within populations (36,38, 43,66,93). These studies provided invaluable new insights into both population structure within species and variation between species. The exploitation of DNA sequencing provided another big leap forward in knowledge on *Phytophthora* species. If the sequences for particular genes or DNA regions are identical or nearly identical, the isolates supposedly belong to the same species. If DNA sequences of the same region are available for dozens of species, a phylogeny can be made. Species can then be grouped in clades, consisting of a single common ancestor and all its descendants. The variation revealed by DNA sequencing can also be used for coalescent analysis; a method to trace all alleles of a region of DNA to the most recent common ancestor. In combination with phylogenetic trees, coalescent analysis is particularly useful for delineating species complexes (41,46).

The tendency towards a more phylogenetic species concept based on DNA sequences is most obvious from the *Phytophthora* Database (http://www.Phytophthoradb.org) in which isolates that form a distinct cluster are considered as representing new species. These species have been labeled as *Phytophthora* sp. xxxx, e.g., *Phytophthora* sp. "niederhauserii" or *Phytophthora* sp. 2-04B. The decision whether or not to consider a group of isolates as a new species is arbitrary: new species cannot be distinguished solely based on a defined number of different nucleotides. A multilocus approach as used by Blair et al. (13) is useful for phylogenetic analysis, but not necessarily for species delimitations. Crucially, sequences should be consistently similar within species and distinct between species, thus pointing to reproductive isolation of the species (biological species concept). Host specificity and geographic isolation may well play an important role in this respect. A complicating factor with *Phytophthora*, however, is that the species that we know are often introduced pathogens and thus may only represent a single or a few clones of a species that is indigenous in other parts of the world. Such a single clonal lineage may therefore appear to be distinct from other species but if the overall intraspecific variation were known, it may well show significant overlap with character traits from existing species. In the pre-molecular era several species were presented in the literature as new species but, as a result of DNA-based identification, turned out to be synonymous to existing species. Examples of species that were listed as a distinct species in Erwin and Ribeiro (35) but were synonymized are *P. arecae* (synonym of *P. palmivora*), *P. mexicana* (synonym of *P. capsici*), and *P. sinensis* (synonym of *P. melonis*) (35,82). We anticipate that the decrease in costs for (whole genome) sequencing, combined with intensified sampling will greatly support and accelerate species identification and delimitation in the genus *Phytophthora* in the coming years.

In biology, the value of proper and accurate species descriptions and a consistent nomenclature is obvious. Therefore the use of provisional names should be discouraged. In the *Phytophthora* literature many provisional names have been used without being formally described according to the International Code of Nomenclature for algae, fungi, and plants (the former International Code of Botanical Nomenclature). Since no type isolates have been assigned for these provisional species, it is not possible to verify whether or not newly collected isolates belong to a species with a provisional name. If these newly collected isolates are then described under a different name it may be difficult to link the provisional name to the later, validly published name.

INTERSPECIFIC HYBRIDS

There is increasing evidence that interspecific hybridization is not uncommon between *Phytophthora* species. Interspecific hybrids have been successfully created in the laboratory by sexual crossing of *P. mirabilis* with *P. infestans* (40,68), *P. sojae* with *P. vignae* (81), and *P. capsici* with *P. tropicalis* (29), or by fusion of zoospores of *P. capsici* and *P. nicotianae* (32). More importantly, naturally generated hybrids have also been found. Man in 't Veld et al. (77) described hybrids between *P. cactorum* and *P. nicotianae* occurring in greenhouses. Later hybrids between the same two species were found in Taiwan and Peru on loquat trees (56). Brasier et al. (17) described three variants of the new species *P. alni*; *P. alni* subsp. *alni*, *P. alni* subsp. *uniformis*, and *P. alni* subsp. *multiformis*. They were originally described as hybrids between *P. cambivora* and a species close to *P. fragariae* (15,17) but according to Ioos et al. (58) these subspecies are a group of emergent heteroploid hybrids between two phylogenetically close *Phytophthora* species. A combination of nuclear and mitochondrial DNA analyses suggests that *P. alni* subsp. *alni* may have

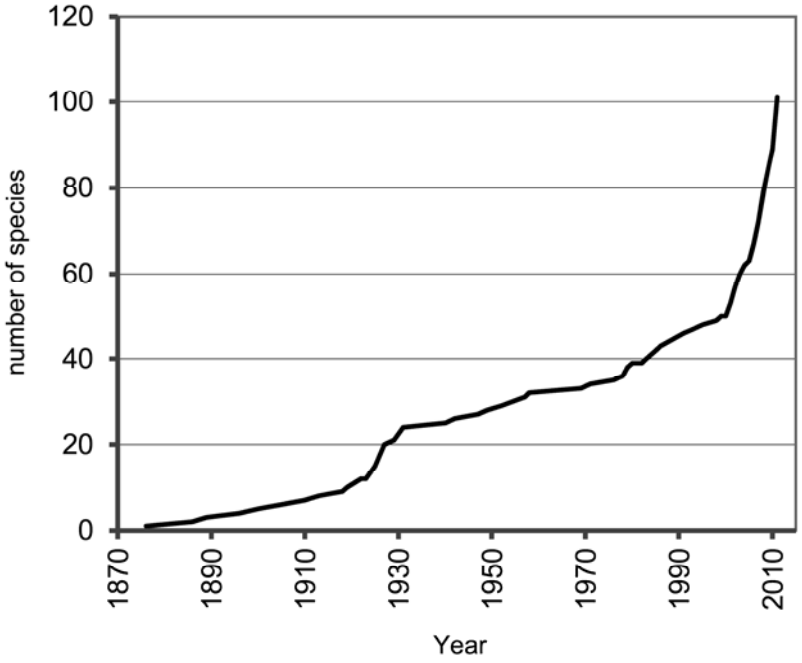

FIGURE 1

Increase in the number of described *Phytophthora* species over time. The first species, *P. infestans,* was described in 1876. By October 2011, the number of validly described and recognized species has risen to 101. These taxa are listed in Tables 1 through 10. In this graph, lost species or species that cannot be cultured have been excluded.

been generated on several occasions by hybridization between *P. alni* subsp. *uniformis* and *P. alni* subsp. *multiformis*, or their respective ancestors. *P. alni* subsp. *uniformis* might have *P. cambivora* as a species ancestor, whereas *P. alni* subsp. *multiformis* seems to have been generated either by an ancient reticulation or by autopolyploidization (58). Interestingly, the hybrid variant *P. alni* subsp. *alni* seems far more destructive and aggressive on alder when compared with its parents. Evidence for altered host ranges and aggressiveness through hybridization has also been found in lab-induced hybrids (32). Another example is *P. andina* that has recently been shown to have emerged via hybridization of *P. infestans* and another unknown clade 1c hybrid *Phytophthora* parent (42).

The occurrence of hybridization in *Phytophthora* is important since hybridization may be responsible for rapid generation of new pathogens. Evidence for rapid evolution or genetic recombination in hybrids was presented by Man in 't Veld et al. (75). In the Netherlands they found several hybrid isolates derived from *P. hedraiandra* and *P. cactorum* which showed characteristics that may be explained by backcrossing between hybrids and parental species, or from further evolution. These interspecific hybrids appeared to be more virulent; in recent years they have been found far more often on *Rhododendron* than their parent species (75). Chamnanpunt et al. (21) observed high frequency mitotic gene conversion in intraspecific hybrids of *P. sojae*, resulting in heterokaryotic mycelium. This means that a single hybridization event may lead to a wide variety of genotypes through vegetative propagation by means of uninucleate zoospores.

Genetic (in-)stability and divergence in interspecific hybrids may play a major role in the rapid evolution of *Phytophthora* and its ability to explore new host plants. Epidemiological aspects of hybrids are comparable to those associated with the introduction of a new pathogen in a given environment. However, in contrast to new pathogens, which often represent a single genome of a single population (as in the case of *P. ramorum* for example), hybrids may well have increased genome plasticity.

Hardly anything is known about the way hybrids are generated in nature. One might speculate that the international plant trade and the current hydroponic culture system brings different, geographically isolated *Phytophthora* species close together, allowing hybrids to form by zoospore fusion (somatic hybrids) or through interspecific mating (sexual hybrids). A review in which these issues were addressed was published by Érsek and Nagy (33). Nirenberg et al. (87) described hybrids of *P. cactorum* and *P. nicotianae* pathogenic to cultivars of *Pelargonium grandiflorum* as a new (notho-)species, *Phytophthora* × *pelgrandis*, leaving other hybrids of these species unassigned. Assigning a species status to hybrids requires, in our opinion, a much better understanding of the formation mechanisms, the stability and the origin of hybrids. Also in this respect (whole genome) sequencing will be instrumental and should be exploited.

LARGE-SCALE SURVEYS

In the last decades, several plant-pathogenic *Phytophthora* species have caused huge damage to crops, landscape plants, forests, and ecosystems, for instance *P. cinnamomi* in Australia, *P. alni* in European forests and riparian vegetation, and *P. ramorum* in North America and Europe (19). The impact of *Phytophthora* diseases on plant species diversity in the affected ecosystems, or economic damage on wood stands, triggered several large-scale surveys to monitor the presence and diversity of *Phytophthora* populations (9–11,14,20,59,60,65,85,101). In addition, isolates from earlier surveys were reexamined with modern identification techniques. These efforts not only increased our knowledge of host range of *Phytophthora* species or the habitats in which these species thrived, but also resulted in the discovery of a fair number of new *Phytophthora* species. For most of these species, a connection could be made between the presence of the species and disease symptoms on a nearby host. However, several new species were discovered that were distinct from all other prevailing *Phytophthora* species based on morphology and DNA sequence, but for which no apparent host plant was found (9,62,85).

PHYTOPHTHORA PHYLOGENIES BASED ON DNA SEQUENCES

One of the first DNA regions to be used in phylogenetic analysis was the 5.8S ribosomal RNA gene and the flanking internal transcribed spacers 1 and 2 (ITS1 and ITS2) (70). The flanking genes of this region contain stretches of high homology that were used to design primers for polymerase chain reaction (PCR) amplification. For almost all *Phytophthora* species, the same primers can be used. The first extensive phylogenetic study of the genus *Phytophthora* based on ITS1 and ITS2 sequences was described by Cooke et al. (22). This study, which included 234 isolates from 50 distinct *Phytophthora* species, provided the basis for the clade nomenclature currently used to group *Phytophthora* species and replaced the Waterhouse classification which was found wanting and was never intended to reflect phylogenetic relationships in the first place.

The advantage of the ITS approach is that the sequence of ITS1, 5.8S, and ITS2 can be readily obtained and as a result the ITS sequences of a large number of *Phytophthora* species are currently available in GenBank. A disadvantage, however, is the low or in some cases even lack of variation in ITS sequences between closely related species raising doubts about the applicability of ITS regions for phylogenetic inference (6,8). This led to a new approach for generating appropriate sequences for phylogenetic analysis of *Phytophthora* species. This approach involves the sequencing of "housekeeping" genes, i.e., genes, either mitochondrial or nuclear, encoding proteins with known functions in the metabolism of the organism. These genes also possess highly conserved regions that are suited for universal primer design, but the nucleotide variation within the genes is higher. This approach results in better resolved phylogenies when compared to ITS-based analyses (6). Introns often have a higher level of polymorphism when compared with exons and this higher level of polymorphism makes intron sequences more useful for phylogenetic studies. However, many *Phytophthora* genes lack introns and hence, larger stretches of exon sequences are needed to create a well-resolved phylogenetic tree.

The first significant example of a study using *Phytophthora* "housekeeping" genes was published by Martin and Tooley (78) who sequenced two mitochondrial genes, cytochrome oxidase I and II (*cox*1 and *cox*2) from 51 isolates representing 27 *Phytophthora* species. However, it covered only a subset of the known *Phytophthora* species with clades that were less resolved when compared with the study by Cooke et al. (22) and the study used only mitochondrial genes, which are uniparentally inherited. As a result, the novel clade nomenclature that Martin and Tooley (78) introduced in their study for the genus *Phytophthora* did not prevail. In another study, the same authors (79) combined mitochondrial and ITS sequences. This study, however, was not aimed at resolving the overall *Phytophthora* phylogeny but at establishing the phylogenetic position of a few new *Phytophthora* species found in California in areas with sudden oak death.

In 2004, Kroon et al. (69) presented the first overall phylogenetic analysis of the genus based on sequences of multiple nuclear and mitochondrial genes. That study covered 113 isolates from 48 *Phytophthora* species and expanded on the firm basis of the clade nomenclature introduced by Cooke et al. (22). Separate analyses were carried out for both nuclear and mitochondrial regions, and for all regions combined. This revealed discrepancies

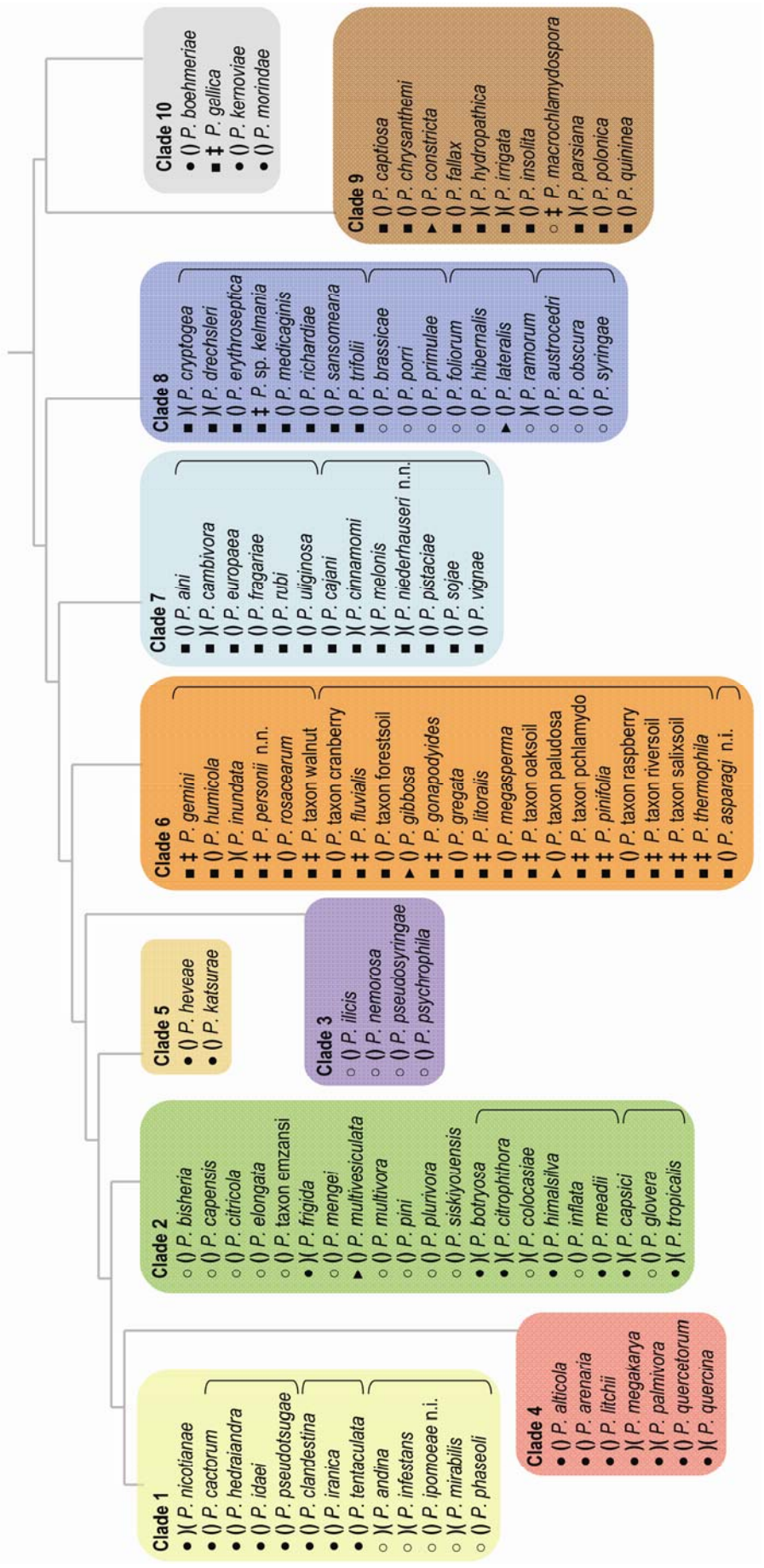

FIGURE 2

Overview of the species and clades that are currently distinguished within the genus *Phytophthora*. The topology of the relationships between clades is depicted according to Blair et al. (13). The open nd closed circles, boxes, and arrowheads reflect whether the sporangia of the species are papillate (●), semi-papillate (○), nonpapillate (■), non- to semipapillate (▶), or a mixture of nonpapillate and semipapillate (▶). Heterothallic species are marked as)(, homothallic species as (), and sterile species (i.e., oogonia unknown or rarely produced) as ‡. The brackets shown in clades 1, 2, 6, 7, and 8 group the species known to be members of a subclade. Within each clade and/or subclade, species are ordered alphabetically. Further details on the species and their distribution in subclades are listed in Tables 1 to 10. n.i. = nomen invalidum; n.n. = nomen nudum.

in the phylogenetic position of a number of *Phytophthora* isolates, hinting at interspecific mating or somatic hybridization events. Phenotypic traits from the Waterhouse key were interpolated on the phylogenetic tree, in order to speculate on the ancestry of traits like mating type, sporangium morphology and attachment of the antheridia to the oogonia. Four years later, Blair et al. (13) published an even more expanded multi-gene phylogeny based on seven nuclear genes, the sequences of which are available in the online *Phytophthora* database (90). For the analysis they included 8,700 nucleotides from seven loci in 234 isolates that represented 82 species, including many new *Phytophthora* species from recent surveys and this resulted in the most detailed and complete *Phytophthora* phylogeny available to date. That study as well as the online *Phytophthora* database (http://www.phytophthoradb.org/) (90) and the online *Phytophthora* identification tool (http://www.phytophthora-ID.org) (47) are extremely valuable resources for plant pathologists. Importantly, Blair et al. (13) defined the currently accepted clade and subclade structure.

THE TEN CLADES IN THE GENUS *PHYTOPHTHORA*

In this review we combined the data presented in the *Phytophthora* phylogeny by Blair et al. (13) with data on a large number of new *Phytophthora* species that have been described in the scientific literature since the release of the monograph in 1996 by Erwin and Ribeiro entitled '*Phytophthora* diseases worldwide' (35). We consulted publications that appeared or were known to be in press before mid-October 2011. We give an overview of the 10 clades that are currently distinguished within the genus *Phytophthora* (Fig. 2). Some of the new species names have not been validly published. They are included with the species name followed by the abbreviation 'nom. nud.' or 'nom. inval.'; 'nom. nud.' (nomen nudum) is used when no description has been published (e.g., *P. niederhauseri* nom. nud.) and 'nom. inval.' (nomen invalidum) when the description is not valid because the type assignment or the Latin species description required prior to January 2012 was missing (e.g., *P. asparagi* nom. inval.). In the literature, the expression '*Phytophthora* taxon host/substrate' or

TABLE 1
Clade 1 *Phytophthora* species

	Group								Origin
***Phytophthora* sp.**[a]	Clade	WH[b]	Study[c]	Host[d]	Infected tissue[e]	Sex[f]	A/P[g]	Papil.[h]	Author(s) and year[i]
P. nicotianae	1	II	ECKB	Multiple	Roots/foliage	He	A	P	Breda de Haan, 1896
P. cactorum	1a	I	ECKB	Multiple	Roots/foliage	Ho	P	P	(Lebert & Cohn) J. Schröter, 1886
P. hedraiandra	1a	I	B	Multiple	Foliage	Ho	P	P	De Cock & Man in 't Veld, 2004
P. idaei	1a	I	ECKB	*Rubus idaeus*	Roots	Ho	P	P	D.M. Kennedy, 1995
P. pseudotsugae	1a	I	ECKB	*Pseudotsuga menziesii*	Roots	Ho	P	P	Hamm & E.M. Hansen, 1983
P. clandestina	1b	I	ECKB	*Trifolium subterraneum*	Roots	Ho	P	P	P.A. Taylor et al., 1985
P. iranica	1b	I	ECKB	Multiple	Roots	Ho	P	P	Ershad, 1971
P. tentaculata[j]	1b	I	ECKB	Multiple	Roots	Ho	P	P	Kröber & Marwitz, 1993
P. andina	1c	IV	KB	Multiple	Foliage/fruits	He	A	SP	Adler & Flier, 2010
P. infestans	1c	IV	ECKB	Multiple	Foliage	He	A	SP	(Montagne) de Bary, 1876
***P. ipomoeae* nom. inval.**[k]	1c	IV	KB	*Ipomoea longipedunculata*	Foliage	Ho	A	SP	Flier & Grünwald, 2002
P. mirabilis	1c	IV	ECKB	*Mirabilis jalapa*	Foliage	He	A	SP	Galindo & H.R. Hohl, 1986
P. phaseoli	1c	IV	ECKB	*Phaseolus lunatus*	Foliage/fruits	Ho	A	SP	Thaxter, 1889

[a] Bold indicates a 'new' species not described in the monograph "*Phytophthora* species worldwide" (35).
[b] Group according to the key of Waterhouse (104).
[c] Study in which the species was included: E = Erwin and Ribeiro, 1996 (35), C = Cooke et al., 2000 (22), K = Kroon et al., 2004 (69), B = Blair et al., 2008 (13).
[d] Host on which the pathogen occurs.
[e] Most prominent tissue infected on the majority of host plants, or niche (rhizosphere, soil).
[f] He = heterothallic species; Ho = homothallic species.
[g] A = amphigynous, P = paragynous attachment of antheridia.
[h] P = papillate; SP = semipapillate.
[i] Refers to the author(s) and year listed in the original species description for which literature references can be found in MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/).
[j] This species was previously included in clade 2 due to wrong data or a misidentified isolate (69).
[k] nom. inval. = nomen invalidum; is a well-characterized species that has a Latin species description but lacks a type designation.

'*Phytophthora* sp. *epithet*' has been used to informally circumscribe phylogenetically distinct lineages that still need a formal description (e.g., *P.* taxon salixsoil). In this review we use the same expressions as in the literature. Per clade, the most notable characteristics for each new species are covered. The description is accompanied by a table listing all the species in the clade with the author(s) and year of publication as listed in the official species name database MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/). In those databases the original literature references can be found. For species still lacking an official species description, the tables refer to the publication in which the name first appeared. These are marked with prefix 'Ref.' and included in the section with references (literature cited). For most species the Waterhouse groups are

TABLE 2
Clade 2 *Phytophthora* species

	Group								Origin
***Phytophthora* sp.**[a]	**Clade**	**WH**[b]	**Study**[c]	**Host**[d]	**Infected tissue**[e]	**Sex**[f]	**A/P**[g]	**Papil.**[h]	**Author(s) and year**[i]
P. bisheria	2	III	B	Multiple	Roots	Ho	P	SP	Z.G. Abad et al., 2008
P. capensis	2	III	–	Multiple	Roots	Ho	P	SP	Bezuidenhout et al., 2010
P. citricola	2	III	ECKB	Multiple	Foliage/fruits/roots	Ho	P	SP	Sawada, 1927
P. elongata	2	III	–	Multiple	Roots	Ho	P	SP	Rea et al., 2010
***P.* taxon emzansi**	2	IV	–	Unknown	Soil	Ho	A	SP	Bezuidenhout et al, 2010
P. frigida	2	II	–	*Eucalyptus smithii*	Roots	He	A	P	Maseko et al., 2007
P. mengei	2	III	–	*Persea americana*	Roots	Ho	P	SP	G.T. Browne et al., 2009
P. multivesiculata	2	IV	CKB	*Cymbidium*	Foliage	Ho	A	NP/SP	Ilieva et al., 1998
P. multivora	2	III	–	Multiple	Rhizosphere/foliage	Ho	P	SP	P.M. Scott & T. Jung, 2009
P. pini	2	III	–	Multiple	Roots	Ho	P	SP	Leonian, 1925
P. plurivora	2	III	–	Multiple	Rhizosphere/foliage	Ho	P	SP	T. Jung & T.I. Burgess, 2009
P. siskiyouensis	2	III	–	*Umbellularia californica*	Rhizosphere	Ho	P	SP	Reeser & E.M. Hansen, 2008
P. botryosa[j]	2a	II	ECKB	*Hevea brasiliensis*	Foliage	He	A	P	Chee, 1969
P. citrophthora	2a	II	ECKB	Multiple	Foliage/fruits/roots	He[k]	A	P	(R.E. Smith & E.H. Smith) Leonian, 1925
P. colocasiae	2a	IV	ECKB	*Colocasia esculenta*	Foliage	He	A	SP	Raciborski, 1900
P. himalsilva	2a	I/II	–	Unknown	Soil	Ho	AP	P	Vettraino, Brasier & Vannini, 2011
P. inflata	2a	III	ECKB	*Ulmus americana*	Foliage	Ho	P	SP	Caroselli & Tucker, 1949
P. meadii	2a	II	EKB	*Hevea brasiliensis*	Fruits/foliage	Ho	A	P	McRae, 1918
P. capsici[l]	2b	II	ECB	Multiple	Foliage/fruits/roots	He	A	P	Leonian, 1922
P. glovera	2b	III	B	*Nicotiana* spp.	Roots	Ho	A	SP	Z.G. Abad & Shew, 2011
P. tropicalis	2b	II	KB	Multiple	Foliage	He	A	P	Aragaki & J.Y. Uchida, 2001

[a] Bold indicates a 'new' species not described in the monograph "*Phytophthora* species worldwide" (35).
[b] Group according to the key of Waterhouse (104).
[c] Study in which the species was included: E = Erwin and Ribeiro, 1996 (35), C = Cooke et al., 2000 (22), K = Kroon et al., 2004 (69), B = Blair et al., 2008 (13).
[d] Host on which the pathogen occurs.
[e] Most prominent tissue infected on the majority of host plants, or niche (rhizosphere, soil).
[f] He = heterothallic species; Ho = homothallic species.
[g] A = amphigynous, P = paragynous attachment of antheridia.
[h] P = papillate; SP = semipapillate; NP = nonpapillate.
[i] Refers to the author(s) and year listed in the original species description for which literature references can be found in MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/).
[j] This species was previously included in clade 4 due to wrong data or a misidentified isolate (69).
[k] There is ambiguity on the mating type of this species (35).
[l] *P. mexicana* is a species described in Erwin and Ribeiro (35) that is synonymous to *P. capsici* (http://www.phytophthoradb.org/) and is not included in this table.

included, linking the molecular data to phenotypic data. Also listed are their hosts, target tissues for infection, mating system, and morphology of sexual and asexual reproductive structures.

Clade 1. Clade 1 is a well-studied clade. It comprises 13 species including the most widely known species of *Phytophthora, P. infestans* (Table 1). Since 1996 (35) three new species have been added to this clade, one of which is *P. andina* in clade 1c, a close relative of *P. infestans* and described recently by Oliva et al. (88). More recently, *P. andina* was shown to be a hybrid between *P. infestans* and an unknown clade 1c hybrid parent (42). Another new species that is a close associate of *P. infestans* is *P. ipomoeae* (37), which was found in the Toluca valley in central Mexico, a center of diversity of *P. infestans* and *P. mirabilis* (45). The third new species is *P. hedraiandra*, a pathogen that is provisionally positioned in clade 1a (25). Recently interspecific hybrids were found that seem to be the offspring of *P. hedraiandra* and *P. cactorum* (75), and *P. nicotianae* and *P. cactorum* (77). These hybrids can be confused with their parent species if only mitochondrial sequences are considered as these are uniparentally inherited.

Clade 1 contains *Phytophthora* species that are papillate or semipapillate, with only one type present in each subclade. For species in clades 1a and 1b, the zoosporangia are papillate, the attachment of antheridia to the oogonia is paragynous, and the pathogens mainly infect roots. Clade 1c species have amphigynous antheridia and semipapillate zoosporangia, which develop on distinctly differentiated sporangiophores. The sporangia are deciduous and spread by aerial dispersal. The species are foliar pathogens. *P. nicotianae* is singular in this clade; it could not be placed in one of the subclades of clade 1 based on sequence analysis, and it has amphigynous antheridia and papillate sporangia.

Clade 2. With the addition of 14 new species since 1996 (35), clade 2 has become one of the largest clades in the *Phytophthora* phylogeny with 21 species in total (Table 2). Isolates of five new clade 2 species, *P. mengei*, *P. capensis*, *P. elongata*, *P. multivora*, and *P. plurivora*, were previously considered as distinct subgroups within the *P. citricola* complex. One group of isolates was pathogenic on avocado trees, where they infected feeder roots and trunks. The pathogen responsible for this disease is now named *P. mengei*. It can be classified in clade 2 based on sequence homology with *P. capsici* and *P. tropicalis*, but its morphological traits place it just outside clade 2b (52). *P. multivora* was found in the rhizosphere of declining Eucalyptus trees in Australia (99). In Europe, large-scale surveys for soilborne *Phytophthora* species were conducted in more than a thousand forests, nurseries, and seminatural stands showing devastating declines and diebacks of major forest tree species (60). Based on morphological and physiological characters and the similarity of ITS DNA sequences, the species causing the decline were routinely identified as *P. citricola.* In a more detailed characterization based on additional DNA sequence data, it was however concluded that the decline should be attributed to a new species that was named *P. plurivora* (60). *P. capensis*, a species from South Africa, has also recently been separated from *P. citricola sensu stricto* (12). The same study also describes isolates of a related new taxon provisionally named *P.* taxon emzansi, which has not yet been formally described as a new species. *P.* taxon emzansi can be distinguished from other members of the citricola complex by the production of amphigynous antheridia. *P. pini* was long considered to be a synonym of *P. citricola* but has recently been shown to be a valid species (53).

Another new species in clade 2, *P. bisheria*, causes root rot on strawberry in the United States, roses in The Netherlands, and raspberry in Australia (2). It is related to several other new species in this clade: the homothallic species *P. multivesiculata* (57) and *P. elongata* (95) and the heterothallic, papillate species *P. frigida*. This species is found on infected roots and collars of Eucalyptus trees in South Africa (80).

Soil and water stream monitoring experiments revealed the presence of a homothallic species in Oregon, *P. siskiyouensis* (96). Positioning in clade 2 was only based on ITS sequencing; additional sequence information should resolve its exact position in this clade. Another species, related to *P. citrophthora*, but with a homothallic instead of heterothallic mating system was found in Nepal. *P. himalsilva* was isolated from soil using baits; its host range is unknown (103). *P. tropicalis* is a species that is pathogenic on several hosts including Macadamia trees. Isolates of this species were initially described as *P. capsici*, but based on more detailed morphological analysis they were reclassified as *P. tropicalis* (7). In the early 1990s, a root rot disease of cultivated tobacco was observed in burley production areas in Brazil. The disease, called yellow stunt, is caused by the semipapillate, homothallic species *P. glovera* (4).

TABLE 3
Clade 3 *Phytophthora* species

	Group								Origin
***Phytophthora* sp.**[a]	**Clade**	**WH**[b]	**Study**[c]	**Host**[d]	**Infected tissue**[e]	**Sex**[f]	**A/P**[g]	**Papil.**[h]	**Author(s) and year**[i]
P. ilicis	3	IV	ECKB	Multiple	Foliage	Ho	A	SP	Buddenhagen & Roy A. Young, 1957
P. nemorosa	3	IV	B	Multiple	Foliage	Ho	A	SP	E.M. Hansen et al., 2003
P. pseudosyringae	3	III	B	*Quercus* spp.	Rhizosphere	Ho	P	SP	T. Jung & Delatour, 2003
P. psychrophila	3	IV	B	Multiple	Rhizosphere	Ho	A	SP	T. Jung & E.M. Hansen, 2002

[a] Bold indicates a 'new' species not described in the monograph "*Phytophthora* species worldwide" (35).
[b] Group according to the key of Waterhouse (104).
[c] Study in which the species was included: E = Erwin and Ribeiro, 1996 (35), C = Cooke et al., 2000 (22), K = Kroon et al., 2004 (69), B = Blair et al., 2008 (13).
[d] Host on which the pathogen occurs.
[e] Most prominent tissue infected on the majority of host plants, or niche (rhizosphere, soil).
[f] Ho = homothallic species.
[g] A = amphigynous, P = paragynous attachment of antheridia.
[h] SP = semipapillate.
[i] Refers to the author(s) and year listed in the original species description for which literature references can be found in MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/).

Species in clade 2 all have papillate or semipapillate zoosporangia, and the majority (15 out of 21) are homothallic.

Clade 3. Previously *P. ilicis* was the only species in clade 3 but in the last decade three new species have been added (Table 3). *P. pseudosyringae* was found in Europe in rhizosphere samples collected in declining oak stands and is associated with fine root and stem necrosis of beech (*Fagus sylvatica*) and alder (*Alnus glutinosa*) (64). *P. pseudosyringae* has also been found in the same regions and ecosystems in the United States as *P. ramorum*, together with another new species, *P. nemorosa*. *P. nemorosa* was isolated from myrtlewood and California bay laurel and causes lethal bole cankers on tanoak and coast live oak (49). *P. psychrophila* was isolated from rhizosphere samples from oak in Europe (*Quercus robur*) although no clear host could be found that was affected by this species (62).

All species in clade 3 have semipapillate sporangia, are homothallic, and are associated with trees.

Clade 4. Clade 4 is another small clade that expanded rapidly. The number of species has more than tripled compared to that in 1996 (35) (Table 4). During a large survey in the United States in 2004, isolates of the species *P. quercetorum* were frequently found with an oak leaf baiting method from soil samples (9). Although the pathogen has the ability to cause infection on oak, it has never been found to be associated with oak decline. A species that is responsible for oak decline is *P. quercina*, found on *Quercus* spp. throughout Europe (61). In South Africa, a new clade 4 species, *P. alticola*, was found on Eucalyptus trees, causing root and collar rot (80). Recently, Rea et al. (94) described *P. arenaria*, a new species associated with dieback of indigenous vegetation in Western Australia and pathogenic on *Banksia* species. *Peronophythora litchii* was formally transferred to *Phytophthora* by Göker et al. (39), based on multi-gene sequencing.

Species in clade 4 have papillate sporangia and are mainly pathogenic on roots. The homothallism/heterothallism distribution in this clade is about equal.

Clade 5. Clade 5 is the smallest distinct clade comprising only two species, *P. heveae* and *P. katsurae* (Table 5). These two species were already known in 1996 when Erwin and Ribeiro (35) published their inventory of the genus *Phytophthora*.

The two clade 5 species have papillate sporangia and are both homothallic with small amphigynous antheridia. *P. katsurae* is characterized by its distinctly ornamented oogonia.

Clade 6. This is another clade that has expanded enormously. Since 1996, 20 new or putative new species have been added resulting in a total of 23 divided over three subclades (Table 6). Clade 6 includes a lot of taxa that have not yet been formally described.

P. asparagi nom. inval. is a well characterized species but lacks a formal Latin diagnosis and type designation. It infects the spears and crown of asparagus plants and can cause significant damage in asparagus production areas (98). The same pathogen has also been isolated from infected agave plants in Australia (98). Another new species, *P.* taxon cranberry, is pathogenic on cranberry (92) and is closely related to *P. gregata*. *P. rosacearum* was previously classified as a subgroup of *P. megasperma*. Based on host range and ITS sequences, however, the group of isolates now forming the new species differed sufficiently to warrant a classification as a new species (50).

During large-scale surveys of dying vegetation in natural ecosystems and associated waterways in Western Australia many clade 6 isolates were found that could not be assigned to known species (20). This has by now resulted in the description of five

TABLE 4
Clade 4 *Phytophthora* species

	Group								Origin
***Phytophthora* sp.**[a]	**Clade**	**WH**[b]	**Study**[c]	**Host**[d]	**Infected tissue**[e]	**Sex**[f]	**A/P**[g]	**Papil.**[h]	**Author(s) and year**[i]
P. alticola	4	II	B	*Eucalyptus dunnii*	Roots	Ho	A	P	Maseko et al., 2007
P. arenaria	4	I	–	*Banksia* spp.	Rhizosphere	Ho	P	P	A. Rea, M. Stukely & T. Jung, 2011
P. litchii[j]	4	I	–	*Litchi chinensis*	Fruits	Ho	P	P	(C.C. Chen ex W.H. Ko et al.) Voglmayr et al., 2007
P. megakarya	4	II	ECKB	*Theobroma cacao*	Foliage/fruits/roots	He	A	P	Brasier & M.J. Griffin, 1979
P. palmivora[k]	4	II	ECKB	Multiple	Foliage/fruits/roots	He	A	P	(E.J. Butler) E.J. Butler, 1910
P. quercetorum	4	I	B	*Quercus robur*	Rhizosphere	Ho	P	P	Y. Balci & S. Balci, 2008
P. quercina[l]	4	I	CB	*Quercus* spp.	Roots	He	P	P	T. Jung, 1999

[a] Bold indicates a 'new' species not described in the monograph "*Phytophthora* species worldwide" (35).
[b] Group according to the key of Waterhouse (104).
[c] Study in which the species was included: E = Erwin and Ribeiro, 1996 (35), C = Cooke et al., 2000 (22), K = Kroon et al., 2004 (69), B = Blair et al., 2008 (13).
[d] Host on which the pathogen occurs.
[e] Most prominent tissue infected on the majority of host plants, or niche (rhizosphere, soil).
[f] He = heterothallic species; Ho = homothallic species.
[g] A = amphigynous, P = paragynous attachment of antheridia.
[h] P = papillate.
[i] Refers to the author(s) and year listed in the original species description for which literature references can be found in MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/).
[j] This species was previously described as *Peronophytora litchii* by Ko et al. (67), but was transferred to the genus *Phytophthora* by Göker et al. (39).
[k] *P. arecae* is a species described in Erwin and Ribeiro (35) that is synonymous to *P. palmivora* (35), and is not included in this table.
[l] This species was previously included in clade 3 by Cooke et al. (22).

new clade 6 species, one described by Crous et al. (23) and four by Jung et al. (65) who also included an informally described clade 6 taxon. The latter, *P.* taxon paludosa, and two of the five new species, *P. gregata* and *P. gibbosa*, are homothallic (65). The other three, *P. litoralis*, *P. thermophila*, and *P. fluvialis*, are sexually sterile (23,65). Some of *P. litoralis* isolates, though, could induce formation of gametangia in *P. cinnamomi* isolates and one of five tested isolates of *P. thermophila* produced oogonia when flooded with nonsterile soil extract (65). *P. gibbosa* can be easily distinguished from other clade 6 species by its ornamented oogonia. Also, its semi- to nonpapillate sporangia are rather unique for clade 6 species and so far shared only by *P.* taxon paludosa. All other clade 6 members produce nonpapillate sporangia.

In 2003, Brasier et al. (16) described a number of new clade 6 species that still await formal publication. These include *P.* taxon pgchlamydo, *P.* taxon oaksoil, *P.* taxon riversoil, *P.* taxon walnut, *P*. taxon raspberry, *P.* taxon forestsoil, and *P.* taxon salixsoil. The latter was also found by Nechwatal and Mengden (85) in the rhizosphere of reed stands (*Phragmites australis*) of Lake Constance, Germany. So far, no apparent disease symptoms have been found associated with *P*. taxon salixsoil but in disease assays it is pathogenic on leaves of *Salix alba*. Like many other clade 6 species, it is widely occurring in flooded habitats. Species of *Phytophthora* that are widely spread in ecosystems, but are not causing an apparent disease on available hosts may play a role in the breakdown of plant litter. It cannot be excluded, however, that they are pathogens of considerable significance (16).

Most species in clade 6 are infectious on roots or present in the rhizosphere. There are a few notable exceptions to this rule. In 2008, *P. pinifolia* was described as the cause of a new disease on pine trees in Chile (30,31). Despite its placement in clade 6 it is a foliar pathogen that infects needles and shoots resulting in defoliation of trees in winter that can even lead to plant death. Another species found in an unexpected habitat is *P. gemini*; it was isolated from rotting *Zostera marina* leaves from saline water in the Netherlands (76). The same study also found several isolates of *P. inundata* in the same habitat. This clade 6 species was previously described on horse chestnut (*Aesculus hippocastanum*) and willow (*Salix matsudana*) in the UK and on flooded olive trees in Spain (18) but was not known to occur in salt water. Hardly anything is known about the occurrence of *Phytophthora* spp. in marine environments, mostly due to the lack of large scale surveys. A large number of unknown species may hide in this unexplored habitat.

All species in clade 6 have nonpapillate sporangia. Two species, however, produce not only nonpapillate but also semi-papillate sporangia. Over half of the species in this clade (12 out of 23) is sexually sterile or partially sterile, one species is clearly heterothallic, and the remaining 10 are homothallic.

Clade 7. Clade 7 comprises 13 species of which six have first been described after 1996 (35). One of the new species is *P. alni,* the causal agent of a destructive disease on alder that first emerged in the UK in 1993 and in subsequent years was found to be widely spread in Europe (17). As described above in the section on hybrids, *P. alni* is a species hybrid complex with three known subspecies. Two other new clade 7 species found in central Europe are *P. europaea* and *P. uliginosa* (62). Both were present in the rhizosphere of oak (*Quercus robur*), but only *P. uliginosa* appears to be a true pathogen on oak. The group of isolates known as the *P. megasperma* complex houses a number of putative new species that can be distinguished based on sequence analysis. One of these is a new clade 7 species named *P. pistaciae* that is found on pistachio trees (82) (Table 7).

For *P. fragariae* Erwin and Ribeiro (35) listed three varieties, var. *fragariae,* var. *rubi*, and var. *oryzobladis*. Man in 't Veld (73) provided evidence that strains isolated from strawberry (*Fragaria* × *ananassa*) are distinct from strains isolated from raspberry (*Rubus idaeus*). The two pathogenic varieties var. *fragariae* and var. *rubi* are reproductively isolated and hence *P. fragariae* var. *rubi* was raised to the species level and renamed *P. rubi*. Based on morphological characteristics Ho (51) proposed to also raise *P. fragariae* var. *oryzobladis* to the species level. The isolates, however, could not be cultured and the species was not maintained in any culture collection. Hence, we consider *P. oryzo-bladis* as a lost species.

All species in clade 7 are nonpapillate and mostly pathogenic on roots. There is a random distribution of homothallism and heterothallism in clade 7b while in clade 7a homothallism is more pronounced.

Clade 8. At present, clade 8 approaches the number of species in clades 2 and 6, making these three the largest clades in the *Phytophthora* phylogeny (Table 8). Since 1996 (35) seven species have been added.

Isolates that are now classified as *P. sansomeana* were previously grouped in the *P. megasperma* complex (50). All the isolates in the *P. megasperma* complex shared morphological traits, but other characteristics, like host range and optimal growth temperature, differed significantly. *P. sansomeana* was isolated from infected soybean plots. Soybean crops with resistance or tolerance to *P. sojae* suffered great damage from this new disease and the pathogen isolated from infected plants differed from *P. sojae* based on sequence analyses. Man in 't Veld et al. (74) used

TABLE 5
Clade 5 *Phytophthora* species

	Group								Origin
***Phytophthora* sp.**	**Clade**	**WH[a]**	**Study[b]**	**Host[c]**	**Infected tissue[d]**	**Sex[e]**	**A/P[f]**	**Papil.[g]**	**Author(s) and year[h]**
P. heveae	5	II	ECKB	Multiple	Fruits/roots	Ho	A	P	A.W. Thompson, 1929
P. katsurae	5	II	ECKB	*Castanea crenata*	Trunk	Ho	A	P	W.H. Ko & H.S. Chang, 1979

[a] Group according to the key of Waterhouse (104).
[b] Study in which the species was included: E = Erwin and Ribeiro, 1996 (35), C = Cooke et al., 2000 (22), K = Kroon et al., 2004 (69), B = Blair et al., 2008 (13).
[c] Host on which the pathogen occurs.
[d] Most prominent tissue infected on the majority of host plants, or niche (rhizosphere, soil).
[e] Ho = homothallic species.
[f] A = amphigynous attachment of antheridia.
[g] P = papillate.
[h] Refers to the author(s) and year listed in the original species description for which literature references can be found in MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/).

isozyme analysis and ITS sequence data to show that a group of isolates placed in the species *P. porri* in clade 8b, in fact represent a different species. This pathogen was named *P. brassicae*; it infects roots and collars of cabbage and can cause massive postharvest damage (74).

With the identification of a new species that is closely related to *P. syringae*, Grünwald et al. (48) recently revisited the subclade structure in this clade. Based on phylogenetic analyses of eight nuclear genes and one mitochondrial gene, they provided significant support for the introduction of a fourth subclade, 8d, that comprises two new species in addition to *P. syringae*. *P. austrocedri*, which was described incorrectly as *P. austrocedrae* (and should be corrected according to Art. 32.7 of the International Code of Botanical Nomenclature), causes damage on the conifer

TABLE 6
Clade 6 *Phytophthora* species

Phytophthora sp.[a]	Group			Host[d]	Infected tissue[e]	Sex[f]	A/P[g]	Papil.[h]	Origin
	Clade	WH[b]	Study[c]						Author(s) and year[i]
P. gemini	6a[j]	V/VI	–	*Zostera marina*	Rotten leaves	–	–	NP	Man in 't Veld et al., 2011
P. humicola	6a	V	ECKB	*Citrus* spp.	Soil	Ho	P	NP	W.H. Ko & Ann, 1985
P. inundata	6a	VI	B	Multiple	Roots	He	A	NP	Brasier et al., 2003
P.* sp. *personii	6a	V/VI	B	*Grevillea mccutcheonii*	Soil	–	–	NP	Ref. 5
P. rosacearum	6a	V	–	*Malus domestica*	Rhizosphere	Ho	P	NP	E.M. Hansen & Wilcox, 2009
***P.* taxon walnut**	6a	V/VI	–	*Juglans hindsii*		–	–	NP	Ref. 16
***P.* taxon cranberry**	6b	VI	–	*Vaccinium macrocarpon*	Roots	Ho	A	NP	Ref. 92
P. fluvialis	6b	V/VI	–	Unknown	Water	–	–	NP	T. Jung & T.I. Burgess, 2011
***P.* taxon forestsoil**	6b	V	–	Unknown	Soil	Ho	A	NP	Ref. 16
P. gibbosa	6b	VI	–	Unknown	Soil	Ho	A	SP/NP	T. Jung et al., 2011
P. gonapodyides	6b	V/VI	ECKB	Saprophyte	Roots	–	–	NP	(H.E. Petersen) Buisman, 1927
P. gregata	6b	V/VI	–	Unknown	Soil/roots	Ho	AP	NP	T. Jung et al., 2011
P. litoralis	6b	V/VI	–	Unknown	Soil	–	–	NP	T. Jung et al., 2011
P. megasperma	6b	V	ECKB	Multiple	Roots	Ho	P	NP	Drechsler, 1931
***P.* taxon oaksoil**	6b	V/VI	–	Unknown	Soil	–	–	NP	Ref. 16
***P.* taxon paludosa**	6b	V/VI	–	Unknown	Water	Ho	AP	SP/NP	Ref. 65
***P.* taxon pgchlamydo**	6b	V/VI	–	Unknown	Roots	–	–	NP	Ref. 16
P. pinifolia	6b	V/VI	–	*Pinus radiata*	Foliage	–	–	NP	Alv. Durán et al., 2008
***P.* taxon raspberry**	6b	V/VI	–	Raspberry	Soil/roots	Ho	AP	NP	Ref. 16
***P.* taxon riversoil**	6b	V/VI	–	Unknown	Soil	–	–	NP	Ref. 16
***P.* taxon salixsoil**	6b	V/VI	–	*Salix alba*	Soil	–	–	NP	Ref. 16
P. thermophila	6b	V/VI	–	Unknown	Soil/roots	–[k]	P	NP	T. Jung et al., 2011
***P. asparagi* nom. inval.**[l]	6c	VI	CB	*Asparagus officinalis*	Spear/crown	Ho	A	NP	Saude & Hausbeck, 2008

[a] Bold indicates a 'new' species not described in the monograph "*Phytophthora* species worldwide" (35).
[b] Group according to the key of Waterhouse (104).
[c] Study in which the species was included: E = Erwin and Ribeiro, 1996 (35), C = Cooke et al., 2000 (22), K = Kroon et al., 2004 (69), B = Blair et al., 2008 (13).
[d] Host on which the pathogen occurs.
[e] Most prominent tissue infected on the majority of host plants, or niche (rhizosphere, soil).
[f] He = heterothallic species; Ho = homothallic species; – = oogonia unknown or rarely produced.
[g] A = amphigynous, P = paragynous attachment of antheridia; – = unknown.
[h] SP = semipapillate; NP = nonpapillate.
[i] Refers to the author(s) and year listed in the original species description for which literature references can be found in MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/). For species still lacking an official species description, the publication in which the name first appeared is given, marked with prefix 'Ref.' and followed by the reference number.
[j] For consistency among clades the subclades have the lower case letters a, b, and c, instead of the Roman numbers I, II and III, as in Brasier et al. (16) and Jung et al. (65).
[k] One of five isolates tested produced oogonia when flooded with non sterile soil filtrate (65).
[l] nom. inval. = nomen invalidum; is a well characterized species but lacks a formal Latin diagnosis and type designation.

Austrocedrus chilensis in Patagonia (44). *P. obscura* was detected in the United States infecting foliage of *Kalmia latifolia* and in Germany in soil samples (48).

The most notorious new species in clade 8 is *P. ramorum*, the causal agent of sudden oak death (SOD), responsible for widespread mortality of oaks in the United States (97,105). Infections in Europe seemed to be mainly limited to *Rhododendron* and *Viburnum.* Recently, however, it was found to cause widespread defoliation and dieback of Japanese larch (*Larix kaempferi*) in the UK (19). Since the late 1990s, it has had major impact on ecosystems in the United States. During the SOD surveys in the United States, a new pathogen of Azalea was found that was sufficiently different to define it as a new species, *P. foliorum* (28).

All species in clade 8a are nonpapillate and those in clade 8b, 8c, and 8d are semipapillate. The one exception is *P. lateralis*, which was typed as nonpapillate in the original description by Tucker and Milbrath (cited in 35). However, recent examination of several isolates, including the type isolate, indicated that *P. lateralis* isolates produce both nonpapillate and semipapillate sporangia (106, A. W. A. M. de Cock, *personal communication*). The majority of the clade 8 species (15 out of 18) are homothallic.

Clade 9. Clade 9 was one of the less-resolved clades in the phylogeny published by Kroon et al. (69) but has expanded enormously since 1996 (35) (Table 9).

One of the new species is *P. parsiana*, a pathogen of pistachio, almond, and fig (83). Isolates described as *P. parsiana* formed a heterogeneous group and should be considered a species complex. Recently, a group of distinct isolates belonging to this complex was described as the new species named *P. hydropathica* by Hong et al. (55). It was recovered from necrotic leaves and blighted shoots of *Rhododendron* and *Kalmia*. Another related species, *P. chrysanthemi*, was isolated from *Chrysanthemum*. It can be distinguished from *P. parsiana* by its homothallic mating behavior and paragynous antheridia (84).

P. irrigata was isolated from irrigation reservoirs and natural waterways (54). It was found to be pathogenic on Azalea. *P. polonica* was isolated from the rhizosphere of infected alder trees in Poland. Belbahri et al. (11) placed the species in clade 8c sensu Kroon (69), but in the phylogeny by Blair et al. (13) that has a

TABLE 7
Clade 7 *Phytophthora* species

Phytophthora sp.[a]	Group			Host[d]	Infected tissue[e]	Sex[f]	A/P[g]	Papil.[h]	Origin
	Clade	WH[b]	Study[c]						Author(s) and year[i]
P. alni[j]	7a	VI	KB	*Alnus* spp.	Stem/roots	Ho	A	NP	Brasier & S.A. Kirk, 2004
P. cambivora	7a	VI	ECB	Multiple	Roots	He	A	NP	(Petri) Buisman, 1927
P. europaea	7a	V	B	*Quercus* spp.	Rhizosphere	Ho	P	NP	E.M. Hansen & T. Jung, 2002
P. fragariae	7a	V	ECKB	*Fragaria* x *ananassa*	Roots	Ho	P	NP	Hickman, 1940
P. rubi[k]	7a	V	ECK	*Rubus idaeus*	Roots	Ho	P	NP	(W.F. Wilcox & J.M. Duncan) Man in 't Veld, 2007
P. uliginosa	7a	V	B	*Quercus robur*	Rhizosphere	Ho	P	NP	T. Jung & E.M. Hansen, 2002
P. cajani	7b	VI	ECB	*Cajanus cajan*	Stem	Ho	A	NP	K.S. Amin et al., 1978
P. cinnamomi	7b	VI	ECKB	Multiple	Roots/foliage	He	A	NP	Rands, 1922
P. melonis[l]	7b	VI	ECB	Multiple	Roots	He	A	NP	Katsura, 1976
***P. niederhauseri* nom. nud.**[m]	7b	VI	B	Multiple	–	He	A	NP	Ref. 1 (as *P. niederhauseria*)
P. pistaciae	7b	V	B	*Pistachia vera*	Trunk/roots	Ho	P	NP	Mirabolfathy, 2001
P. sojae	7b	V	ECKB	*Glycine max*	Roots/stem	Ho	P	NP	Kaufmann & Gerdemann, 1958
P. vignae	7b	VI	ECKB	*Vigna unguiculata*	Roots/stem	Ho	A	NP	Purss, 1957

[a] Bold indicates a 'new' species not described in the monograph "*Phytophthora* species worldwide" (35).
[b] Group according to the key of Waterhouse (104).
[c] Study in which the species was included: E = Erwin and Ribeiro, 1996 (35), C = Cooke et al., 2000 (22), K = Kroon et al., 2004 (69), B = Blair et al., 2008 (13).
[d] Host on which the pathogen occurs.
[e] Most prominent tissue infected on the majority of host plants, or niche (rhizosphere, soil).
[f] He = heterothallic species; Ho = homothallic species.
[g] A = amphigynous, P = paragynous attachment of antheridia.
[h] NP = nonpapillate.
[i] Refers to the author(s) and year listed in the original species description for which literature references can be found in MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/). For species still lacking an official species description, the publication in which the name first appeared is given, marked with prefix 'Ref.' and followed by the reference number.
[j] This species was included as *P.* hybrid-Dutch variant in the study of Kroon et al. (69).
[k] This species was known as *P. fragariae* var. *rubi* (35).
[l] *P. sinesis* is a species described in Erwin and Ribeiro (35) that is synonymous to *P. melonis* (82), and is not included in this table.
[m] This species has also been cited as "*P. niederhauserii*" and "*P. niederhauseria*"; nom. nud. = nomen nudum; no description published.

better resolution, *P. polonica* could be assigned to clade 9. Several new pathogens of Eucalyptus trees have been described in recent years. Two of these, *P. captiosa* and *P. fallax* that are associated with a crown disease in Eucalyptus plantations in New Zealand, were also added as new species to clade 9 (26). *P. constricta* is another new species found in association with dieback of indigenous vegetation in Western Australia, together with the clade 4 species *P. arenaria.* Similar to *P. arenaria*, *P. constricta* was found to be pathogenic on *Banksia* species (94).

Species in clade 9 are nonpapillate (except for *P. macrochlamydospora*) and mainly found in the soil. Most species in this clade are homothallic.

Clade 10. Like clade 3, clade 10 was previously represented by only one species and now comprises four (Table 10). One new species is *P. gallica* (63), which was isolated from soil and responsible for a decline in stands of oak and reed in Germany and France. Another recently described species in clade 10 is *P. kernoviae*, a pathogen of beech found in Cornwall in the UK (14). The third new species is *P. morindae*, which caused a severe foliar blight and fruit rot disease of noni (*Morinda citrifolia* L. var. *citrifolia*) on the island of Hawaii in 1999 (86).

Species in clade 10 are papillate and pathogenic on foliage and stem with the exception of *P. gallica*. New phylogenetic analyses on the complete set of *Phytophthora* species may shift *P. gallica* from clade 10 to clade 9.

Lost species. In the reference work of Erwin and Ribeiro (35), nine species are described that are not included in Tables 1 to 10 in this review or in Figure 1. They were also not included in the

TABLE 8
Clade 8 *Phytophthora* species

Phytophthora sp.[a]	Group			Host[d]	Infected tissue[e]	Sex[f]	A/P[g]	Papil.[h]	Origin
	Clade	WH[b]	Study[c]						Author(s) and year[i]
P. cryptogea	8a	VI	ECKB	Multiple	Roots/foliage	He	A	NP	Pethybridge & Lafferty, 1919
P. drechsleri	8a	VI	ECKB	Multiple	Roots	He	A	NP	Tucker, 1931
P. erythroseptica	8a	VI	ECKB	Multiple	Roots	Ho	A	NP	Pethybridge, 1913
P.* sp. *kelmania	8a	V/VI	B	*Gerbera* spp.	–	–	–	NP	Ref. 3
P. medicaginis	8a	V	ECB	*Medicago sativa*	Roots	Ho	PA	NP	E.M. Hansen & D.P. Maxwell, 1991
P. richardiae[j]	8a	VI	ECKB	*Zantedeschia aethiopica*	Roots	Ho	A	NP	Buisman, 1927
P. sansomeana	8a	V	B	*Glycine max*	Rhizosphere	Ho	P	NP	E.M. Hansen & Reeser, 2009
P. trifolii	8a	V	ECB	*Trifolium* spp.	Roots	Ho	P	NP	E.M. Hansen & D.P. Maxwell, 1991
P. brassicae	8b	IV	KB	*Brassica oleracea*	Head (storage)	Ho	A	SP	De Cock & Man in 't Veld, 2002
P. porri	8b	III	ECB	*Allium porrum*	Foliage	Ho	PA	SP	Foister, 1931
P. primulae	8b	III	ECB	*Primula* spp.	Roots	Ho	PA	SP	J.A. Tomlinson, 1952
P. foliorum	8c	III	B	*Azalea* spp.	Foliage	Ho	PA	SP	Donahoo & Lamour, 2006
P. hibernalis	8c	IV	EKB	Multiple	Foliage/fruits	Ho	A	SP	Carne, 1925
P. lateralis	8c	V	ECKB	*Chamaecyparis lawsoniana*	Roots	Ho	P	SP/NP	Tucker & Milbrath, 1942
P. ramorum	8c	IV	KB	Multiple	Trunk/foliage	He	A	SP	Werres et al., 2001
P. austrocedri	8d	IV	–	*Austrocedrus chilensis*	Roots/stem	Ho	A	SP	Greslebin & E.M. Hansen, 2007 (as *P. austrocedrae*[k])
P. obscura	8d	III	–	*Kalmia latifolia*	Foliage/soil	Ho	P	SP	Grunwald & Werres, 2011
P. syringae	8d	III	ECKB	Multiple	Foliage	Ho	P	SP	(Klebahn) Klebahn, 1905

[a] Bold indicates a 'new' species not described in the monograph "*Phytophthora* species worldwide" (35).
[b] Group according to the key of Waterhouse (104).
[c] Study in which the species was included: E = Erwin and Ribeiro, 1996 (35), C = Cooke et al., 2000 (22), K = Kroon et al., 2004 (69), B = Blair et al., 2008 (13).
[d] Host on which the pathogen occurs.
[e] Most prominent tissue infected on the majority of host plants, or niche (rhizosphere, soil).
[f] He = heterothallic species; Ho = homothallic species; – = oogonia unknown or rarely produced.
[g] A = amphigynous, P = paragynous attachment of antheridia; – = unknown.
[h] SP = semipapillate; NP = nonpapillate.
[i] Refers to the author(s) and year listed in the original species description for which literature references can be found in MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/). For species still lacking an official species description, the publication in which the name first appeared is given, marked with prefix 'Ref.' and followed by the reference number.
[j] This species was previously included in clade 10 by Cooke et al. (22).
[k] Improper Latin termination; see Art. 32.7 of the International Code of Botanical Nomenclature.

TABLE 9
Clade 9 *Phytophthora* species

Phytophthora sp.[a]	Group			Host[d]	Infected tissue[e]	Sex[f]	A/P[g]	Papil.[h]	Origin
	Clade	WH[b]	Study[c]						Author(s) and year[i]
P. captiosa	9	VI	B	*Eucalyptus* spp.	Crown	Ho	A	NP	M.A. Dick & Dobbie, 2006
P. chrysanthemi	9	V	–	*Chrysanthemum* × *morifolium*	Roots	Ho	P	NP	Naher et al., 2011
P. constricta	9	V	–	*Banksia* spp.	Rhizosphere	Ho	P	NSP	A. Rea, M. Stukely & T. Jung, 2011
P. fallax	9	V	B	*Eucalyptus* spp.	Crown	Ho	PA	NP	Dobbie & M.A. Dick, 2006
P. hydropathica	9	VI	–	*Rhododendron catawbiense*	Foliage	He	A	NP	Hong et al., 2010
P. irrigata	9	VI	–	*Azalea* spp.	Irrigation water	He	A	NP	C. Hong & M. Gallegly, 2008
P. insolita	9	V/VI	ECKB	*Citrus* spp.	Soil	Ho	–	NP	Ann & W.H. Ko, 1981
P. macrochlamydospora[j]	9	III/IV	ECB	*Glycine max*	Roots	–	–	SP	J.A.G. Irwin, 1991
P. parsiana	9	VI	–	Multiple	Trunk	He	A	NP	Mostowfizadeh et al., 2008
P. polonica	9	V	B	*Alnus glutinosa*	Rhizosphere	Ho	P	NP	Belbahri et al., 2006
P. quininea	9	V	EKB	*Cinchona officinalis*	Roots	Ho	P	NP	Crandall, 1947

[a] Bold indicates a 'new' species not described in the monograph "*Phytophthora* species worldwide" (35).
[b] Group according to the key of Waterhouse (104).
[c] Study in which the species was included: E = Erwin and Ribeiro, 1996 (35), C = Cooke et al., 2000 (22), K = Kroon et al., 2004 (69), B = Blair et al., 2008 (13).
[d] Host on which the pathogen occurs.
[e] Most prominent tissue infected on the majority of host plants, or niche (rhizosphere, soil).
[f] He = heterothallic species; Ho = homothallic species; – = oogonia unknown or rarely produced.
[g] A = amphigynous, P = paragynous attachment of antheridia; – = unknown.
[h] SP = semipapillate; NP = nonpapillate; NSP non- to semipapillate.
[i] Refers to the author(s) and year listed in the original species description for which literature references can be found in MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/).
[j] This species was previously included in clade 10 by Cooke et al. (22).

TABLE 10
Clade 10 *Phytophthora* species

Phytophthora sp.[a]	Group			Host[d]	Infected tissue[e]	Sex[f]	A/P[g]	Papil.[h]	Origin
	Clade	WH[b]	Study[c]						Author(s) and year[i]
P. boehmeriae	10	II	EKB	Multiple	Foliage	Ho	A	P	Sawada, 1927
P. gallica	10	V/VI	–	*Quercus robur*	Rhizosphere	–	–	NP	T. Jung & J. Nechwatal, 2008
P. kernoviae	10	II	B	Multiple	Stem/foliage	Ho	A	P	Brasier, Beales & S.A. Kirk, 2005
P. morindae	10	II	–	*Morinda citrifolia*	Foliage/fruit	Ho	A	P	Z.G. Abad & S.C. Nelson, 2010

[a] Bold indicates a 'new' species not described in the monograph "*Phytophthora* species worldwide" (35).
[b] Group according to the key of Waterhouse (104).
[c] Study in which the species was included: E = Erwin and Ribeiro, 1996 (35), C = Cooke et al., 2000 (22), K = Kroon et al., 2004 (69), B = Blair et al., 2008 (13).
[d] Host on which the pathogen occurs.
[e] Most prominent tissue infected on the majority of host plants, or niche (rhizosphere, soil).
[f] Ho = homothallic species; – = oogonia unknown or rarely produced.
[g] A = amphigynous attachment of antheridia; – = unknown.
[h] P = papillate; NP = nonpapillate.
[i] Refers to the author(s) and year listed in the original species description for which literature references can be found in MycoBank (http://www.mycobank.org/) or Index Fungorum (http://www.indexfungorum.org/).

phylogenies presented by Kroon et al. (69) and Blair et al. (13). The isolates on which these species descriptions are based were no longer available either because they could not be properly cultured or were not properly stored for long term preservation. Since no sequence data are available for these species, they can never be inincluded in the current phylogenies. It is even possible that new isolates from these "lost" species have been put forward as new species. For many new species the Waterhouse criteria were included in the description but a comparison to check if such a new species coincides with another previously described "lost" species is usually lacking. Since the Waterhouse grouping largely coincides with particular clades or subclades, and species within a (sub)clade share habitat or host type, it should be feasible to deduce the position of "lost" species in the *Phytophthora* phylogeny and here we made an attempt to do so. Over the years several species have been described in the literature that were lost afterwards; this section, however, is limited to the nine "lost" species that were included in the Erwin and Ribeiro monograph (35).

P. cyperi and *P. cyperi-bulbosi* are semipapillate species that are pathogenic on *Cyperus* spp. and may belong in clade 2, 3, 8b, or 8c. However, the latter species has thick-walled, verrucose oogonium walls and could not be cultivated; it could also belong to the Sclerosporales.

P. eriugena causes necrosis on leaves and stems of Cypres (*Chamaecyparis lawsoniana*) and although it has papillate sporangia, it was placed in Waterhouse group IV. This exceptional status makes it hard to find a suitable clade for this species.

P. fragariae var. *oryzobladis* is a pathogen on rice. Ho (51) observed that this variety differs significantly from *P. fragariae* and suggested to name it *P. oryzo-bladis.* Unlike *P. fragariae* it produces only amphigynous antheridia and the oogonia are shaped differently. With its nonpapillate sporangia it may still fall in clade 7 like *P. fragariae*, but could also belong to clade 6, 8, or 9.

P. italica is a root pathogen of myrtle (*Myrtus communis*) in Italy. Since it has papillate sporangia and is a root pathogen, it could fall in clade 1, 2, 4, 5, or 10, which all contain papillate species. Of these only clade 1 and clade 4 contain species with paragynous antheridia. Since *P. italica* has strictly paragynous antheridia and is very similar to *P. iranica*, it likely belongs to clade 1.

P. japonica is pathogenic on rice (*Oryza sativa*) and has nonpapillate sporangia. It could belong in either clade 6, 7, 8, or 9.

P. lepironiae is a pathogen of the reed *Lepironia mucronata* that most likely belongs to clade 2, 3, 8b, or 8c.

P. undulata is a peculiar species. The species was originally described as *Pythium undulatum* (91) but transferred to *Phytophthora* by Dick (27). Several sequences are available in GenBank and some indeed cluster with sequences from *Phytophthora* species and some with *Pythium* sequences. According to the phylogenetic study of Lévesque and De Cock (72), this species clearly belongs in the genus *Pythium* and should be referred to as *Pythium undulatum*. To clarify this discrepancy the morphological characteristics of isolates of which the sequences cluster with *Phytophthora* species should be reanalysed.

P. verrucosa was described as a pathogen causing foot rot on tomato and having nonpapillate sporangia. It could be a member of clade 8a, which consists of other species that are pathogenic on roots of solanaceous host, are nonpapillate, and have both paragynous and amphigynous antheridia. However, the very thick, predominantly verrucose oogonium wall and the fact that the species could not be cultured suggest that it does not belong to *Phytophthora*. It might well belong to the Sclerosporales.

CONCLUSION

Plant diseases caused by *Phytophthora* species will remain an ever increasing threat to agriculture and natural ecosystems. This overview includes 116 species, 15 of which await valid publication, but for sure, this is an underrepresentation of the number of species existing in nature. New species, or new variants of known species, emerge continuously. The intensive international trade increases the risk that plants infected with *Phytophthora* are brought into new areas where the indigenous flora can become the victim of these potential new pathogens. Moreover, when crops or ornamentals are grown in areas different from their center of origin, there is always a chance that endemic *Phytophthora* species discover these new potential hosts. This may result in new diseases and likely in the expansion of the pathogen population. The means to control *Phytophthora* diseases are limited, but the technologies to detect and identify these plant pathogens are rapidly improving. Molecular diagnostics for faster and more precise identification of species is instrumental for tracking unintended spread of *Phytophthora* species and as such, supportive of integrated disease management strategies to control *Phytophthora* diseases.

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