# Persistence of the Mitochondrial Lineage Responsible for the Irish Potato Famine in Extant New World *Phytophthora infestans*

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## Abstract

**The plant pathogen *Phytophthora infestans* emerged in Europe in 1845, triggering the Irish potato famine and massive European potato crop losses that continued until effective fungicides were widely employed in the 20th century. Today the pathogen is ubiquitous, with more aggressive and virulent strains surfacing in recent decades. Recently, complete *P. infestans* mitogenome sequences from 19th-century herbarium specimens were shown to belong to a unique lineage (HERB-1) predicted to be rare or extinct in modern times. We report 44 additional *P. infestans* mitogenomes: four from 19th-century Europe, three from 1950s UK, and 37 from modern populations across the New World. We use phylogenetic analyses to identify the HERB-1 lineage in modern populations from both Mexico and South America, and to demonstrate distinct mitochondrial haplotypes were present in 19th-century Europe, with this lineage initially diversifying 75 years before the first reports of potato late blight.**

***Key words:*** **mitogenomics, ancient DNA, evolutionary biology, molecular evolution, pathogens, potato.**

Letter

*Phytophthora infestans* (Mont.) de Bary is an oomycete pathogen of potatoes and tomatoes that causes late potato blight (Haas et al. 2009). Known to exist as two mating types (A1 and A2), it can reproduce sexually in regions where they both coexist and clonally when only one type is present (Fry 2008). Although it is clear that the pathogen originated somewhere in the New World, both the species' center of origin and the source of the 19th-century inoculum are debated. Deeply divergent nuclear and mitochondrial lineages are found in South America, but to date, there have been very few observations of the A2 mating type, suggesting sexual reproduction rarely occurs there (Grünwald and Flier 2005; Goméz-Alpizar et al. 2007; Vargas et al. 2009; Cárdenas et al. 2011). In contrast, Mexican populations maintain substantial genetic diversity and are known to harbor both mating types, implying that the origin may be in this region (Fry 2008).

The introduction of *P. infestans* to domestic potato crops in Europe in 1845 triggered massive crop losses, resulting in the Irish potato famine and its associated social and economic destruction (Stevens 1933; Bourke 1964). Initially, a single clonal lineage named US-1, which was globally distributed in the late 20th century, was suspected to be the cause of the "famine-era" outbreaks of *P. infestans* (Goodwin et al. 1994). However, subsequent direct polymerase chain reaction amplification of mitochondrial genes from 19th-century herbarium samples of blight-afflicted potato leaves led to the conclusion that these early historical *P. infestans* all possessed mitochondrial DNA (mtDNA) haplotype Ia, whereas US-1 lineage isolates possessed haplotype Ib (Ristaino et al. 2001; May and Ristaino 2004). It was then concluded that another migration must have led to the introduction of the US-1 clonal lineage to the United States and Europe in the 20th century (Ristaino et al. 2013). The US-1 clonal lineage has now been mostly displaced by aggressive and genetically diverse new strains, along with the A2 mating type, introduced from the New World since the mid-1980s (Fry and Goodwin 1997; Fry 2008; Cooke et al. 2012).

Recently, two independent studies reported genomic sequence data from both modern and historical *P. infestans* samples (Martin et al. 2013; Yoshida et al. 2013). These historical samples were derived from leaves of infected herbarium potato samples from Western and Northern Europe, collected between 1845 (the initial outbreak of late potato blight in Europe) and 1889. Both studies concluded that the historical samples were distinct from modern populations at avirulence loci. Furthermore, one of the studies used a reference-guided iterative assembly strategy to produce the first historical-era mitogenome sequences (Yoshida et al. 2013). Using this data set of 13 19th-century mitogenomes, the authors described a new mitochondrial lineage that they named "HERB-1" and made the key observation that this lineage was distinct from the modern Ia lineage and from all other

lineages (that previously had been characterized using a smaller number of standard mtDNA polymorphisms). As a consequence, the authors hypothesized that today HERB-1 is rare or possibly even extinct. Furthermore, based on the limited number of within-lineage polymorphisms that were observed, Yoshida et al. (2013) argued that HERB-1 was a rapidly evolving clonal genotype stemming from a single introduction into Europe. In contrast, Martin et al. (2013) analyzed nuclear genome data and found several distinct, rapidly evolving lineages of *P. infestans* in the 19th-century samples studied, which suggested multiple early introductions of the pathogen into Europe.

Herein, we report mitogenome sequences of a larger sample of *P. infestans* isolates from across its New World range, including Mexico and South America, as well as four additional 19th-century mitogenomes from Europe, and three mitogenomes from US-1 lineage samples collected in the United Kingdom during the 1950s. Through phylogenetic analyses of these and previously reported mitogenome sequences, we survey the global diversity of *P. infestans*, especially in the context of the historical outbreaks of the 19th and 20th centuries. We conclude by offering insights into the origin of both the species and the 1845 outbreak.

## Results

### Phylogenetic Analyses of Mitogenomes

A maximum-likelihood phylogeny of all well-assembled (table 1, supplementary tables S1 and S2, Supplementary Material online) *P. infestans* mitogenome sequences was consistent with previous mitogenomic estimates (Avila-Adame et al. 2006; Yoshida et al. 2013) and contained members from lineages already identified (fig. 1). Many of these lineages were well supported, with 100% bootstrap support at the common node of the IIb lineage, 97% support for the IIa lineage, and 94% support for the Ib lineage. In addition, our extended data set enabled identification of two novel lineages. One of these lineages principally contains isolates from central Mexico (with the single exception being Ecuador isolate P13346), and the other is a Peruvian lineage closely related to the reference genome IIa that includes isolates PCO038, PCZ033, and PCZ098. Support for the Ia and HERB-1 lineages were somewhat lower than for other lineages (65% and 73%, respectively), and the node representing a common ancestor of these two sister lineages received only 34% support, indicating a relatively close phylogenetic relationship at this resolution.

Consistent with our expectation based on the observations of Yoshida et al. (2013), the HERB-1 lineage contains all additional 19th-century European specimens sequenced in this study (Pi1845A, Pi176, Pi1882, and Pi1889). Of these, Pi1845A, which is the oldest known sample and is believed to have been collected extremely close (both temporally and geographically) to the probable site of initial introduction (Bourke 1964), is basal to all others within the lineage. The HERB-1 lineage was distinct from the lineages containing the reference genomes for modern mtDNA haplotypes Ia and Ib, which were previously implicated as the first and later introductions to Europe, respectively. Although both phylogenies indicate the HERB-1 lineage shares a more recent common ancestor with the Ia lineage, this relationship is only well supported in the Bayesian phylogeny. Isolates 8140 (Mexico), P7036 (Mexico), and P13346 (Ecuador) were placed within the HERB-1 lineage, thus demonstrating that this lineage is not extinct today and is likely found across the native range of *P. infestans* in the New World.

The samples Kew122, Kew123, and Kew126, derived from infected herbarium leaves collected in the United Kingdom in the 1950s, belong to the US-1 lineage, which contains the reference genome of mtDNA haplotype Ib. Similar findings of Ib haplotypes in early- and mid-20th century herbarium specimens screened for mtDNA SNPs have been reported (Ristaino 2002; May and Ristaino 2004). Interestingly, two more recent 20th-century samples from Mexico (P1362 and P8141) also grouped with the US-1 lineage.

### Bayesian Phylogenetic Analyses and Estimation of Evolutionary Timescale

Using the sample ages as calibrations for the molecular clock, we estimated the evolutionary timescale based on the mitogenome sequences. We confirmed that the sample ages were sufficient for this purpose using a date-randomization analysis (supplementary fig. S1, Supplementary Material online). The estimated coalescence time of all *P. infestans* mitogenomes is 638 years (95% credibility interval: 313–1,022 years), somewhat older than about 460-year estimate of Yoshida et al. (2013), although the 95% credibility intervals overlap (fig. 2). Similarly, the estimated coalescence time of all members of the HERB-1 lineage is 257 years (95% CI: 193–357 years), also older than the estimate of Yoshida et al. (2013). In this analysis, the Ia mtDNA lineage is a well-supported sister group to the HERB-1 lineage.

Overall, the Bayesian and maximum-likelihood analyses produced compatible estimates of the phylogeny. As relationships within the HERB-1 lineage are not well supported, the position of the modern New World isolates differed between the two estimates of the phylogeny. In the maximum-likelihood phylogeny, these isolates were basal to all other HERB-1 samples other than Pi1845A, whereas these samples are nested in the lineage in the Bayesian phylogeny. Although support values were higher for many nodes within the maximum-likelihood phylogeny, the clustering of these New World HERB-1 samples is only supported in the Bayesian phylogeny.

## Discussion

The principal finding of this study is that the *P. infestans* HERB-1 lineage is neither extinct nor likely to be particularly rare or geographically limited, given its presence in two Mexican isolates and one from Ecuador. Furthermore, our observation from the Bayesian (and not the maximum likelihood) phylogenetic analysis that these three modern-day New World isolates cluster with most of the more recent 19th-century historical European samples, with Pi1845A

**Table 1.** Provenance and Sampling Dates of *Phytophthora infestans* Samples for Which Novel mtDNA Genomes Were Assembled and Analyzed in This Study.

| Isolate ID | Alternative IDs or Species | Host | Location | Date of Isolation or Collection | Tissue Source | Sequence Reads, Sample Source | Genotype and/or mtDNA Lineage |
|---|---|---|---|---|---|---|---|
| Pi1845A | K91 | *Solanum tuberosum* | Audenarde, Belgium | 1845 | Herbarium | Martin et al. (2013) | HERB-1 |
| Pi1876 | UPS 1 | *S. tuberosum* | Skårop, Denmark | 1876 | Herbarium | Martin et al. (2013) | HERB-1 |
| Pi1882 | UPS 2 | *S. tuberosum* | Stockholm, Sweden | 1882 | Herbarium | Martin et al. (2013) | HERB-1 |
| Pi1889 | K 79 | *S. tuberosum* | Germany | 1889 | Herbarium | Martin et al. (2013) | HERB-1 |
| Kew126 | | *S. tuberosum* | Britain | 1952 | Herbarium | This report | Ib |
| Kew122 | | *S. tuberosum* | Britain | 1955 | Herbarium | This report | Ib |
| Kew123 | | *S. tuberosum* | Ireland | 1955 | Herbarium | This report | Ib |
| P6636 | PD_01096, Spelman 618 | | Toluca, MX | 1980s | Mycelium | This report | Ia |
| P8844 | Hohl, Pineda 151 | *S. tuberosum* | Peru | 1982 | Mycelium | This report | Ib |
| P3681 | Tooley 529 | *S. tuberosum* | Mexico | 1983 | Mycelium | This report | Ia |
| P3683 | Tooley 550 | *S. stoloniferum* | Mexico | 1983 | Mycelium | This report | Ia |
| P3685 | Tooley 533 | *S. tuberosum* | Mexico | 1983 | Mycelium | This report | Ia |
| P6629 | Tooley 511 | *S. tuberosum* | Mexico | 1983 | Mycelium | This report; Peter Tooley | Ia |
| P6634 | PD_02383, Speil543 | | Mexico | 1983 | Mycelium | This report; Linda Speilman | Ia |
| P7036 | Goodwin 575 | *S. tuberosum* | Central Mexico | 1986 | Mycelium | This report; Steve Goodwin | HERB-1 |
| P8140 | PD_01946 , P15103, Fry 572 | | Central Mexico | 1986 | Mycelium | This report | HERB-1 |
| P6635 | PD_02388, Fry 580 | | Toluca, MX | 1986 | Mycelium | This report | Ia |
| P8141 | Fry 616 | | Central Mexico | 1987 | Mycelium | This report | Ib |
| P8143 | PD_01949, P15154, Fry 619 | | Central Mexico | 1987 | Mycelium | This report | Ia |
| P8144 | Fry 622 | | Central Mexico | 1987 | Mycelium | This report | Ia |
| T30-4 | | *S. tuberosum* | Netherlands | 1988 | Mycelium | Raffaele et al. (2010) | Ia |
| P6570 | Davidse 89018, P570 | | Netherlands | 1989 | Mycelium | This report; Davidse | Ia |
| P6515 | CIP 27, PD_00883, Fry 543 | *S. tuberosum* | Peru | 1989 | Mycelium | This report; Greg Forbes | Ib |
| P6750 | Goodwin 586 | *S. tuberosum* | Saltillo, Mexico | 1989 | Mycelium | This report | IIa |
| P6752 | Goodwin 606 | *S. tuberosum* | Saltillo, Mexico | 1989 | Mycelium | This report | IIa |
| 90128 | | *S. tuberosum* | Netherlands | 1990 | Mycelium | Raffaele et al. (2010) | Ia |
| PHU006 | | *S. tuberosum* | Peru | 1996 | Mycelium | This report | EC-1, IIa |
| PIC97207 | | *S. tuberosum* | Mexico | 1997 | Mycelium | This report | Ia |
| PIC97605 | | *S. tuberosum* | Mexico | 1997 | Mycelium | This report | Ia |
| PIC97630 | | *S. tuberosum* | Mexico | 1997 | Mycelium | This report | Ia |
| PCO038 | | *S. tuberosum* | Peru | 1997 | Mycelium | This report; Greg Forbes | EC-1, IIa |
| PCZ026 | | *S. tuberosum* | Peru | 1997 | Mycelium | This report | PE-6, IIa |
| PCZ033 | | *S. tuberosum* | Peru | 1997 | Mycelium | This report; Greg Forbes | EC1.2, IIa |
| PCZ050 | | *S. tuberosum* | Peru | 1997 | Mycelium | This report; Greg Forbes | PE-3, Ia |
| PCZ098 | | *S. tuberosum* | Peru | 1997 | Mycelium | This report; Greg Forbes | EC1.3, IIa |
| PIC98372 | | | Mexico | 1998 | Mycelium | This report | Ia |
| P13198 | CIP3198 tuq | *S. tuquerrense* | Napo, Ecuador | 1998 | Mycelium | This report | EC-1, IIa |
| P10650 | MX980099 | *S. tuberosum* | Toluca, Mexico | 1998 | Mycelium | This report | Ia |
| PIC99189 | | *S. stoloniferum* | Mexico | 1999 | Mycelium | Raffaele et al. (2010) | Ia |
| P13346 | CIP3346 col | *S. colombianum* | Napo, Ecuador | 2001 | Mycelium | This report; David Cooke | HERB-1 |
| P13873 | CIP 3873 | *S. tuberosum* | Cañar, Ecuador | 2005 | Mycelium | This report | IIa |
| BL2009P4 | PA112 | *S. tuberosum* | PA | 2009 | Mycelium | Martin et al. (2013) | US-23. Ia |
| IN2009T1 | PA114 | *S. tuberosum* | PA | 2009 | Mycelium | Martin et al. (2013) | US-22, Ia |
| RS2009P1 | PA117 | *S. tuberosum* | PA | 2009 | Mycelium | Martin et al. (2013) | US-8, Ia |

NOTE.—PA, Pennsylvania.

and Pi1876 (dating to 1845 and 1876, respectively) basal to all other HERB-1 isolates, provides some evidence that the HERB-1 mitogenomes had diverged prior to their introduction to Europe. Two further sources of evidence support this conclusion. First, the estimated age of the most recent common ancestor of the HERB-1 lineage is 257 years (95% CI: 193–357 years), thus prior to the first reports of late blight in both the United States (1843; Stevens 1933) and Europe (1845; Bourke 1964) and 75 years prior to the 182-year best estimate of Yoshida et al. (2013). This difference is probably due to our inclusion of more divergent and older samples from 19th-century Europe. Moreover, our estimate of the

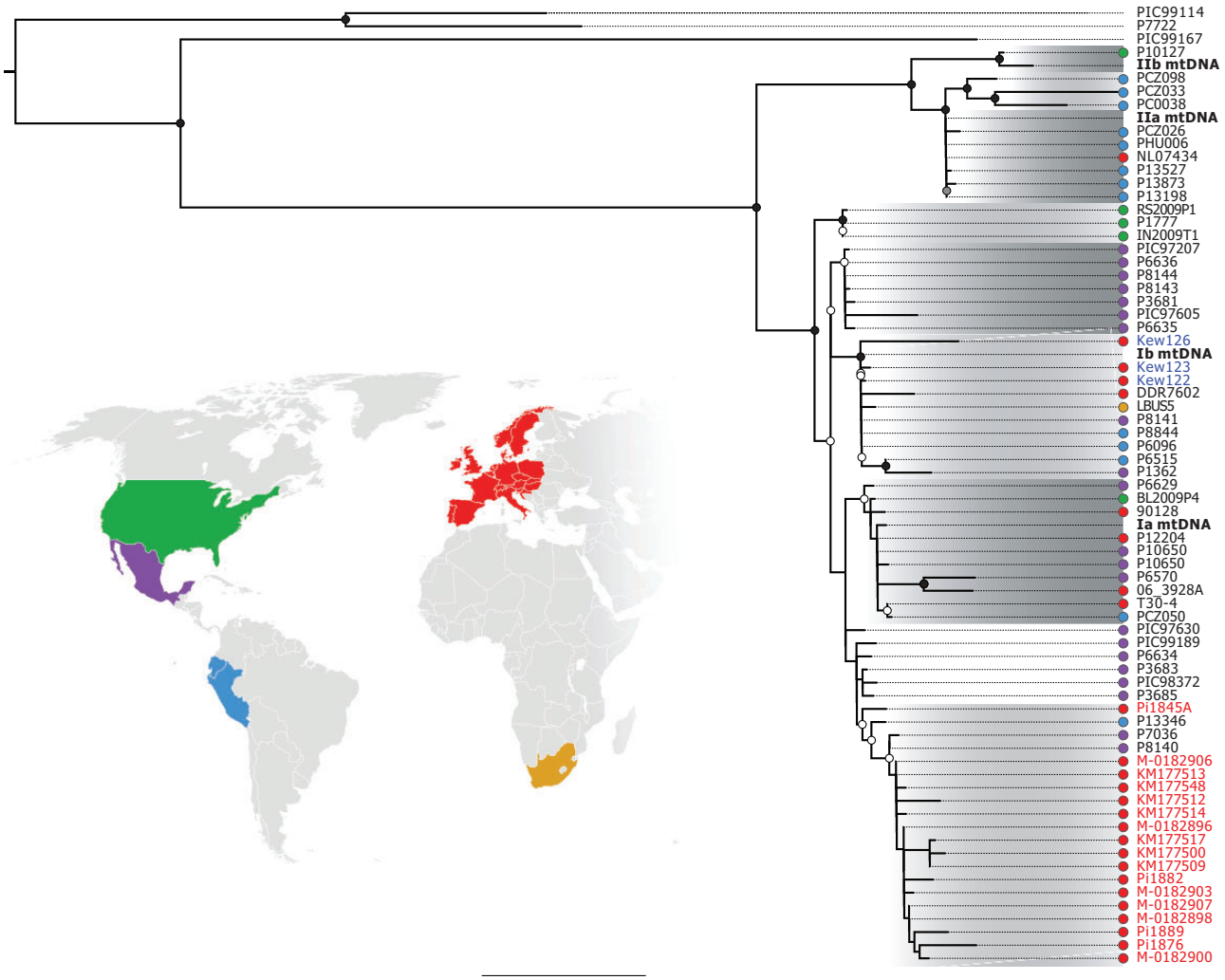


**Fig. 1.** Maximum-likelihood estimate of the mitogenome phylogeny of *Phytophthora infestans* and close relatives from *Phytophthora* clade 1c. *Phytophthora infestans* reference genomes (Ia, Ib, IIa, and IIb) were included in the alignment for illustrative purposes (bold sample labels). Shaded circles at nodes indicate the support from 100 bootstrap replicates: black, 90–100%; gray, 80–90%; white, 50–80%. Colored circles on the right indicate sampling location and correspond to the world map (inset). Sample labels in red for 19th-century samples, blue for 1950s samples, and black for modern isolates and reference genomes. The tree is rooted using the two *P. mirabilis* isolates PIC99114 and P7722 as outgroups. Gray shading highlights major clades that are well supported in this analysis. Scale bar indicates a branch length of 0.0009 substitutions per site.

evolutionary rate is conservatively high because there are various factors that can cause the elevation of rates when they are calibrated using sample ages (Gibbs et al. 2010; Ho et al. 2011). If the actual evolutionary rate is lower than that estimated in our analysis, then the most recent common ancestor of the HERB-1 lineage would be even older. Second, Pi1845A, which is recognized as deriving from the very first outbreak in 19th-century Europe and is likely the oldest sample analyzed in this study, is clearly basal (as opposed to ancestral) to the other members of HERB-1 in both phylogenetic analyses.

Highly supported structure within the HERB-1 lineage indicates that multiple distinct mitogenome haplotypes were present in 19th-century Europe, a situation compatible with either multiple introductions of different haplotypes or a single introduction containing multiple haplotypes. These observations are consistent with the hypothesis of Martin et al. (2013), based on nuclear genome polymorphisms differentiating 19th-century *P. infestans* strains, and do not support the conclusions drawn by Yoshida et al. (2013) from a more limited data set.

Whether multiple HERB-1 mitogenomes were present in 19th-century Europe as a result of multiple introduction events, as opposed to a single introduction containing multiple HERB-1 haplotypes, remains uncertain. We note, however, that the Ia and HERB-1 mtDNA lineages (both formerly type Ia) show some phylogenetic resolution at the sublineage level and appear to have radiated several times. Mexican samples are basal to the Ia lineage in both phylogenetic analyses, suggesting migration of Ia out of Mexico in recent times. However, given the lack of robust, relevant phylogeographic structure within the tree, we believe our data demonstrate that further work is needed to resolve the long-debated question (Grünwald and Flier 2005; Fry 2008; Gómez-Alpizar et al. 2007; Birch and Cooke 2013) as to whether the 19th century *P. infestans* outbreaks were derived from introductions sourced in Mexico versus South America. Although historical evidence of movement of potatoes supports the latter

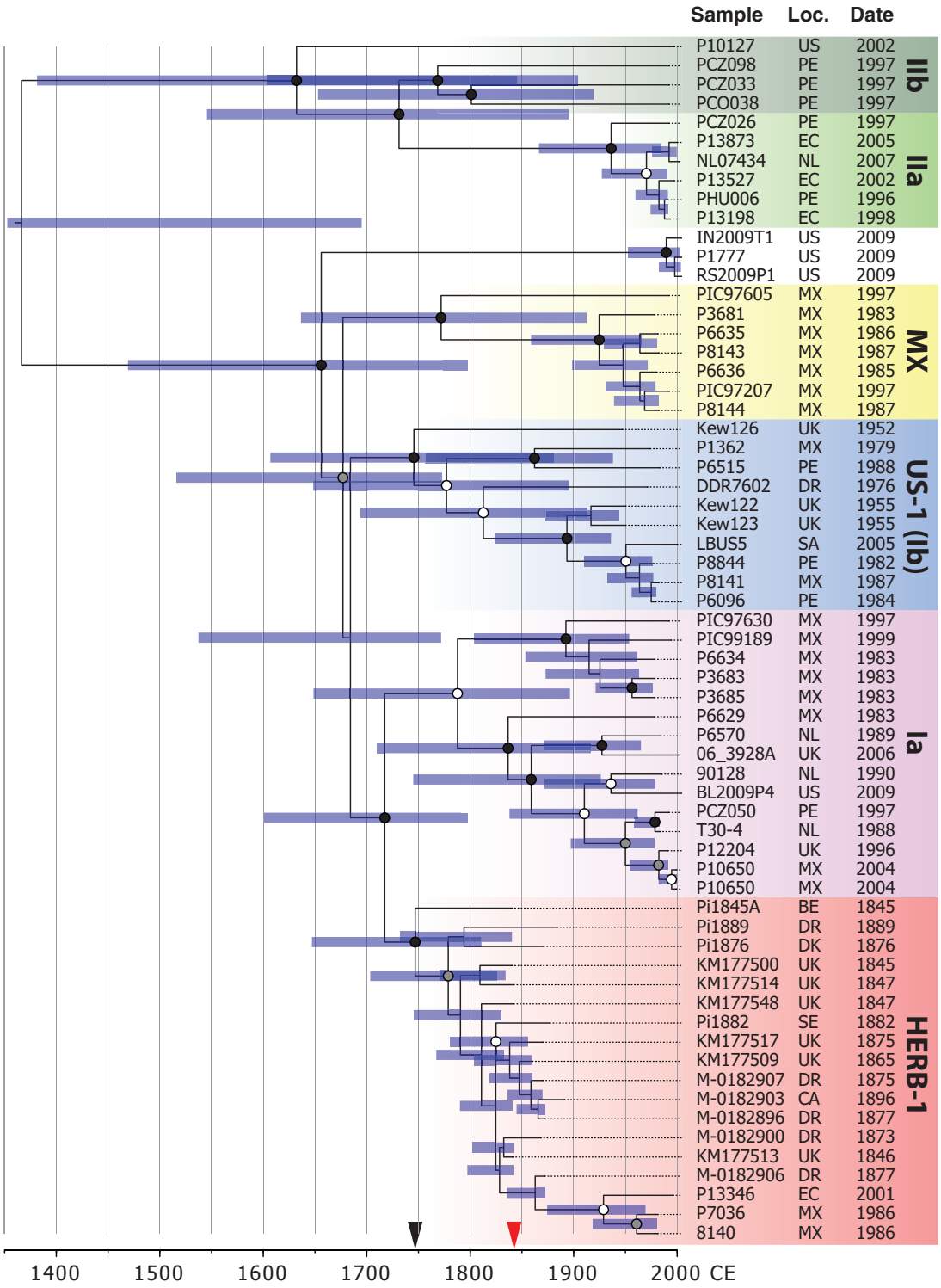


**Fig. 2.** Bayesian phylogeny of assembled *Phytophthora infestans* mitogenome sequences from dated collections. Major mtDNA clades are highlighted and labeled. Node bars represent 95% credibility intervals for estimates of node ages. Note that the 95% CI of the root node bar extends to 987 AD, but the bar is truncated. Shaded circles at nodes indicate the node posterior probabilities: black, 90–100%; gray, 80–90%; and white, 50–80%. The red arrow indicates the first report of late blight in Europe in 1845, whereas the black arrow indicates the median estimated age for the HERB-1 lineage. BE, Belgium; CA, Canada; DK, Denmark; DR, Germany; EC, Ecuador; MX, Mexico; NL, Netherlands; PE, Peru; SA, South Africa; SE, Sweden.

possibility (Bourke 1964), a paucity of South American isolates in mtDNA lineages closely related to HERB-1 points to an introduction from Mexico.

Our study further sheds light onto the origins of the US-1 lineage (containing the reference genome for mtDNA haplotype Ib), represented in our data by nine samples, including three derived from infected herbarium leaves collected in the United Kingdom in the 1950s (Kew122, Kew123, and Kew126). Although this lineage originally was proposed as the causative agent of the 19th-century potato

blight outbreaks (Goodwin et al. 1994), this hypothesis was subsequently disproven (Ristaino et al. 2001). Our analysis shows that the introduction of this lineage to Europe must have occurred before 1952, and is consistent with the identification of the US-1 lineage in Southeast Asia and China from herbarium samples collected in the early part of the 20th century (Ristaino and Hu 2009). We also note that this lineage existed in Europe with considerable substructure. In the Bayesian phylogeny, Kew126 (collected 1952) clusters with one group of more modern Mexican and South American isolates, whereas Kew122 and Kew123 (both collected 1955) cluster with another group of New World and introduced isolates. Although both Mexican and Peruvian isolates belong to the US-1 lineage, the lineage has been found more commonly in South America than in Mexico (Grünwald and Flier 2005). Neither the Bayesian nor the maximum likelihood analyses support an emergence of the US-1 mtDNA lineage from the HERB-1 lineage as suggested in a recent review (Birch and Cooke 2013). In our BEAST analysis, the Ia mtDNA lineage is a well-supported sister group to the HERB-1 lineage, suggesting that they shared a common ancestor more recently than did HERB-1 and the Ib lineage (fig. 2).

Indeed, we report the presence of most of the identified lineages in South American and Mexican populations. Thus, lacking any clear phylogeographic structure, we cannot contribute substantially to the open question of whether the *P. infestans* species complex originated in Mexico or South America and conclude that this question is unlikely to be resolved using mitochondrial data alone. Interestingly, the most divergent mtDNA lineages (type II), basal to all others, are from South America, further supporting previous observations that the earliest measurable evolutionary divergence within this species (separating the type I and II mtDNA lineages) occurred in South America (Avilia-Adame et al. 2006; Goméz-Alpizar et al. 2007). It should be noted that this deepest divergence in the *P. infestans* mitogenome tree is dated at 638 years (95% CI: 313–1,022 years), which, as implied by Yoshida et al. (2013), is recent enough that human-mediated movement of potato tubers from South America to Mexico is a possible factor (Salaman 1949). Increased resolution of the phylogeny through detailed sampling of the *P. infestans* lineages of the South American Andes could answer this open question.

## Supplementary Material

Supplementary tables S1 and S2 and figure S1 are available at *Molecular Biology and Evolution* online (http://www.mbe.oxfordjournals.org/).

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