Comparative analyses of complete Oomycete mitochondrial genome sequences — insights into structural evolution

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Abstract

The oomycetes, or “water molds”, are fungi-like in appearance but more closely related to algae and diatoms. This large, widespread group of pathogens infects a wide range of plant and animal hosts across habitats ranging from marine, to freshwater and terestrial. Previous studies of oomycete mitogenomes suggest that large invert repeats are common as are structural rearrangements. However, sampling has been heavily biased towards Peronosporaceae with only limited representation of the other families.

This study presents comparative and phylogenetic analyses of 135 mitogenomes, including 74 newly assembled sequences, from representatives of six families in the oomycete crown group. Gene content is strongly conserved across the sampled genomes, but synteny is only weakly conserved. The present analyses identified 68 distinct synteny types and within these 26 synteny blocks ranging in size from one to 23 genes. Patterns of diversity differed between the two major crown clades, one containing Saprolegniaceae and the other the remaining families. Several types of structural change appear to have occurred with the frequency of change varying across individual genomes (e.g., conserved and variable regions). Combined with the well resolved and supported phylogenetic tree recovered from analyses of the concatenated 32 mitochondrial gene matrix these results provide insights into the structural evolution of oomycete mitocohondrial genomes. In particular, suggesting associations between the loss of the large inverted repeat and duplications of *tRNA-Met* and between the compactness of these genome and the relative importance of different types of structural change in specific groups (e.g., early and late diverging Peronosporaceae).

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List of Abbreviations

BWA	Burrows-Wheeler Aligner
CR-A	Conserved Region A
CR-B	Conserved Region B
CR-C	Conserved Region C
CR-D	Conserved Region D
CREx	Common interval Rearrangement Explorer
DNA	deoxyribonucleic acid
IDBA-UD	Iterative de Bruijn assembler - uneven depth
NCBI	National Centre for Biotechnology Information
SRA	sequence read archive
V1	Variable Region 1
V2	Variable Region 2
V3	Variable Region 3
V4	Variable Region 4
atp1	adenosine 5' - triphosphate (ATP) synthase F0 subunit 1
atp6	adenosine 5' - triphosphate (ATP) synthase F0 subunit 6
atp8	adenosine 5' - triphosphate (ATP) synthase F0 subunit 8
atp9	adenosine 5' - triphosphate (ATP) synthase F0 subunit 9
bp	base pairs
cob	apocytochrome b
cox1	cytochrome c oxidase 1
cox2	cytochrome c oxidase 2
cox3	cytochrome c oxidase 3
gCF	gene concordance factor
LECA	last eukaryotic common ancestor
lsRNA	large subunit ribosomal ribonucleic acid
nad1	nicotinamide adenine dinucleotide + hydrogen (NADH) dehydrogenase subunit 1
nad2	nicotinamide adenine dinucleotide + hydrogen (NADH) dehydrogenase subunit 2
nad3	nicotinamide adenine dinucleotide + hydrogen (NADH) dehydrogenase subunit 3
nad4	nicotinamide adenine dinucleotide + hydrogen (NADH) dehydrogenase subunit 4
nad4L	nicotinamide adenine dinucleotide + hydrogen (NADH) dehydrogenase subunit 4L
nad5	nicotinamide adenine dinucleotide + hydrogen (NADH) dehydrogenase subunit 5
nad6	nicotinamide adenine dinucleotide + hydrogen (NADH) dehydrogenase subunit 6
nad7	nicotinamide adenine dinucleotide + hydrogen (NADH)

	dehydrogenase subunit 7
nad9	nicotinamide adenine dinucleotide + hydrogen (NADH) dehydrogenase subunit 9
nad11	nicotinamide adenine dinucleotide + hydrogen (NADH) dehydrogenase subunit 11
nt	nucleotides
orf176	open reading frame 176
orf217	open reading frame 217
rRNA	ribosomal ribonucleic acid
rpl2	ribosomal protein L2
rpl5	ribosomal protein L5
rpl6	ribosomal protein L6
rpl14	ribosomal protein L14
rpl16	ribosomal protein L16
rps2	ribosomal protein S2
rps3	ribosomal protein S3
rps4	ribosomal protein S4
rps7	ribosomal protein S7
rps8	ribosomal protein S8
rps10	ribosomal protein S10
rps11	ribosomal protein S11
rps12	ribosomal protein S12
rps13	ribosomal protein S13
rps14	ribosomal protein S14
rps19	ribosomal protein S19
sCF	site concordance factor
secY	sec-independent transporter protein
ssRNA	small subunit ribosomal ribonucleic acid
tRNA	transfer ribonucleic acid
tRNA-Ala	transfer ribonucleic acid for alanine
tRNA-Arg	transfer ribonucleic acid for arginine
tRNA-Asn	transfer ribonucleic acid for asparagine
tRNA-Asp	transfer ribonucleic acid for aspartic Acid
tRNA-Cys	transfer ribonucleic acid for cysteine
tRNA-Gln	transfer ribonucleic acid for glutamine
tRNA-Glu	transfer ribonucleic acid for glutamic Acid
tRNA-Gly	transfer ribonucleic acid for glycine
tRNA-His	transfer ribonucleic acid for ghistidine
tRNA-Ile	transfer ribonucleic acid for isoleucine
tRNA-Leu	transfer ribonucleic acid for leucine
tRNA-Lys	transfer ribonucleic acid for lysine
tRNA-Met	transfer ribonucleic acid for methionine
tRNA-Phe	transfer ribonucleic acid for phenylalanine
tRNA-Pro	transfer ribonucleic acid for proline

tRNA-Ser	transfer ribonucleic acid for serine
tRNA-Trp	transfer ribonucleic acid for tryptophan
tRNA-Tyr	transfer ribonucleic acid for tyrosine
tRNA-Val	transfer ribonucleic acid for valine
ymf98	hypothetical protein 98
ymf99	hypothetical protein 99
ymf100	hypothetical protein 100
ymf101	hypothetical protein 101

CHAPTER 1

Introduction

1.1 Oomycetes

Oomycetes, or “water molds”, are a widespread group of heterotrophic eukaryotes. Based on features such as filamentous growth and the production of spores it had been assumed that oomycetes were closely related to fungi. However, unlike fungi oomycete cell walls contain cellulose (Bartnicki-Garcia, 1968) and they produce biflagellate zoospores (Burki et al., 2007). This latter feature, together with the results of molecular phylogenetic analyses, places oomycetes firmly within the Bikonta. Oomycetes are, therefore, more closely related to diatoms and algae than fungi.

1.1.1 Distribution and diversity

Oomycetes are geographically widespread. They have been found at the poles (e.g., Bridge et al., 2008), in the tropics (e.g., Tan and Pek, 1997), and in the temperate zone (Schubert et al., 1999). They also occupy a number of habitat types and have been found in marine, freshwater and terrestrial environments (Dick, 2001).

The Oomycota currently comprises approximately 100 genera and 1,700 described species (Beakes and Thines, 2017; Wijayawardene et al., 2020). Lévesque (2011) provided an overview of species numbers for the largest genera (Figure 1.1). For some of these groups species numbers have increased

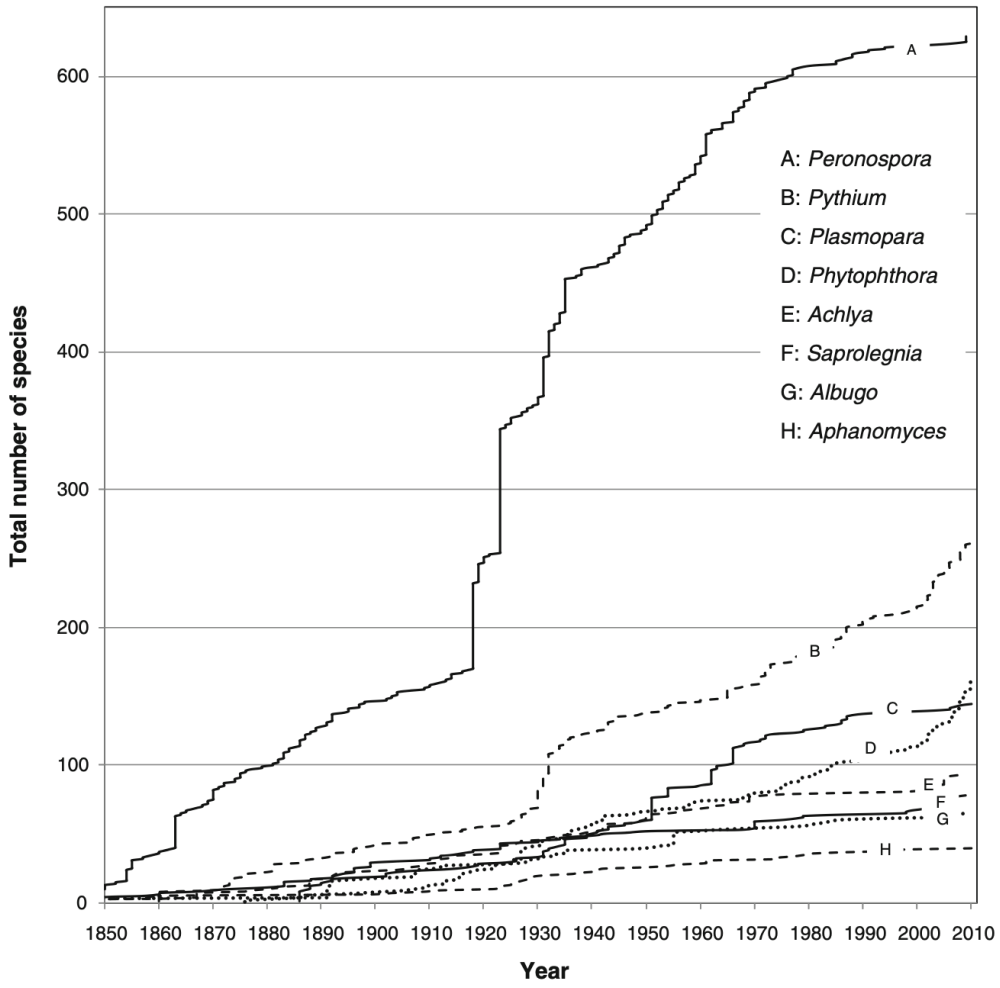


Figure 1.1 Total number of species over the years for different genera of oomycetes. Species names and years based on data in Mycobank (from Lévesque, 2011 [with permission]).

only slowly (e.g., *Achlya*, *Saprolegnia*). Whereas for others they have increased much more dramatically. With over 600 species, *Peronospora* is the largest genus of the oomycetes. In this case species number increased rapidly between the 1920s and 1980s, but have since plateaued (Lévesque, 2011). In contrast, the numbers of *Pythium* and *Phytophthora* have increased more rapidly since the 1990s (Lévesque, 2011). For example, the number of

recognised taxa within *Phytophthora* has almost trebled in the last 25 years (c.f., Erwin and Ribeiro, 1996; Yang et al., 2017).

Current estimates of oomycete diversity are limited by biases in discovery. Even in groups that have received considerable attention (e.g., *Pythium* and *Phytophthora*) new species are still being reported on a regular basis (e.g., Dobbie et al., 2022; Weir et al., 2015). There are habitats and lineages that are yet to be thoroughly surveyed leaving open the possibility that there are many species yet to be discovered.

1.1.2 Lifestyles

Oomycetes exhibit a wide range of lifestyles including free-living saprophytes to above ground endophytes, to hemibiotrophic and obligate biotrophic parasites of algae, plants, fungi, and animals.

Saprophytes are free-living organisms, that use dead and decaying matter for nutrition (Lewis, 1973). Saprotrophy has been suggested to be ancestral in oomycetes (Martin et al., 2016) and the saprotrophic species are thought to be important colonisers and decomposers of organic matter (Marano et al., 2016). Additionally, it has been suggested that many of the saprotrophic oomycetes may be facultative necrotrophic pathogens. Necrotrophs kill the host tissue that they colonise and gain nutrition from the dead or dying cells (Stone, 2001). At least some members of Pythiaceae are facultative necrotrophs. Members of the oomycetes exhibit two forms of parasitism, hemibiotrophy and obligate biotrophy. In hemibiotrophic species there is an initial biotrophic phase during which the pathogen gains nutrition without killing the host. This is followed by a necrotrophic phase, after death of the host, or part of it, the

pathogen feeds on the dead material (Fawke et al., 2015). Both the Verrucalvaceae and Peronosporaceae contain hemibiotrophic species. Obligate biotrophs obtain nutrition exclusively from living hosts (Spanu and Kämper, 2010). In oomycetes both the Albuginaceae and Peronosporaceae include representatives that are obligate biotrophs.

1.1.3 Hosts

Oomycetes infect various hosts across a wide array of both natural and managed ecosystems. The group is perhaps best known as plant pathogens, Indeed several of the most diverse oomycete taxa (e.g., *Peronospora*, *Phytophthora*) are comprised exclusively of plant pathogens. The host range of the plant pathogenic oomycetes ranges from very narrow, with perhaps one or a few potential hosts (e.g., *Phytophthora infestans*), to those with hundreds of potential hosts (e.g., *Phytophthora cinnamomi*).

Oomycetes cause significant damage to agricultural crops and are, increasingly, threatening species from natural ecosystems (e.g., kauri dieback, sudden oak death). Perhaps the best known of the plant pathogenic oomycetes is *Phytophthora infestans*, the pathogen responsible for late blight of potatoes and tomatoes. Symptoms of the disease include spotting on the surface of leaves and stems as well as stunted, corky tubers. Late blight first appeared in the United States during the early 1840's and was responsible for several potato famines across Europe during the mid to late 1840's. Perhaps most infamous was the 1845-1852 Irish potato famine (Bourke, 1964). In Ireland where potato was an important subsistence crop, late blight was devastating. More than 1.5 million people are thought to have died with a similar number

emigrating from Ireland (Bourke, 1964). Late blight continues to represent a serious threat causing approximately $US6 billion of damage to crops each year (Nowicki et al., 2012). In part the ongoing issues reflect how difficult the pathogen is to control (Nowicki et al., 2013).

Members of the oomycetes also infect a wide range of animals. Hosts include mammals (e.g., *Pythium insidiosum*), amphibians (e.g., *Saprolegnia ferax*) and insects (e.g., *Lagenidium giganteum*). As with the plant pathogenic species, the animal pathogens have the potential to be devastating. For example, crayfish plague is caused by *Aphanomyces astaci*. This highly specialised parasite occurs naturally on North American freshwater crayfish and it was unintentionally introduced into Italy during the 1860's (Alderman, 1997). Unlike there North American relatives European and Asian freshwater crayfish have no resistance to *Aphanomyces astaci*, and the pathogen is responsible for declines throughout Europe (Keller and Lodge, 2022; Makkonen et al., 2016). This pathogen, now considered one of the world's 100 worst invasive species (Lowe et al., 2001), has altered the balance of European freshwater ecosystems (Makkonen et al., 2016; Martín-Torrijos et al., 2021).

Marine oomycetes remain more poorly known. There are several recognised pathogens of algae (e.g., *Pythium porphyrae*) and recent studies suggest there are perhaps many oomycetes pathogenic of phytoplankton that remain to be described (Massana et al., 2004; Massana et al., 2006; Richards et al., 2012).

1.1.4 Taxonomy and phylogeny

The phylogeny and taxonomy of oomycetes remains uncertain. In part this is because new species and lineages continue to be recognised. Given that for many oomycete groups diversity is poorly documented it seems likely that aspects of the phylogeny and taxonomy will remain uncertain for some time.

Phylogenetic analyses of the oomycetes have focused on several of the larger plant pathogenic groups (e.g., *Phytophthora*) with broader relationships having received less attention. Studies to date suggest the oomycetes are split between several early diverging clades and a crown clade (Buaya and Thines, 2022; Sekimoto et al., 2008). The earliest diverging oomycetes almost exclusively occupy marine habitats and as a result these remain very poorly understood (Beakes et al., 2012). The crown oomycetes fall into two broad groups. The Saprolegnians, which mainly occupy aquatic habitats, and the Peronosporaleans, which are found mainly in terrestrial habitats. This latter clade contains the best-known of the oomycete taxa, *Phytophthora* and *Pythium* (Beakes et al., 2012; Thines, 2014) (Figure 1.2).

The phylogeny and taxonomy of groups such as *Phytophthora* and *Pythium* has received much more attention. In the case of *Phytophthora* molecular phylogenetic analyses over the last 20 years (e.g., Blair et al., 2008; Cooke et al., 2000; Martin et al., 2014) have fairly consistently recovered the same ten phylogenetic groups (i.e., Clades 1-10). However, in recent studies (e.g., Bourret et al., 2018; Jung et al., 2017) increased sampling has identified additional clades (e.g., Clades 11-16). Two of these clades (i.e., 15 and 16) contain members from several genera of downy mildews (Bourret et al., 2018). This latter finding suggests that as traditionally defined the genus *Phytophthora*

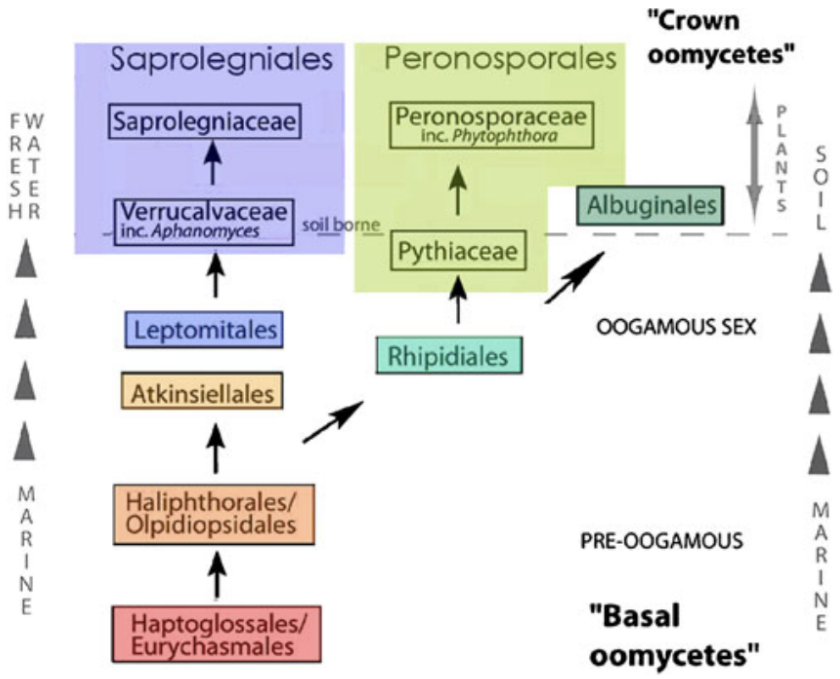


Figure 1.2 A schematic summary of the possible phylogenetic relationships between the main oomycete orders and families, based on current molecular data (from Beakes et al., 2011 [with permission]).

is not monophyletic. There have also been studies addressing the phylogeny of *Pythium* (e.g., Lévesque and De Cock, 2004; Nguyen et al., 2022). As in *Phytophthora* these studies have identified several clades (i.e., Clades A-K) and again it appears that, as traditionally defined, *Pythium* is not monophyletic. For example, Clade K is more closely related to *Phytophthora* than to the remainder of the traditional *Pythium* (Uzuhashi et al., 2010). In this case it has been suggested that the limits of *Pythium* should be revised and four new genera recognised (Uzuhashi et al., 2010).

Despite the headway that has been made towards understanding the phylogeny and taxonomy of oomycetes it is clear that work is still needed. This involves both increased sampling of currently underrepresented groups and

ensuring that taxonomy provides a robust framework within which to understand oomycete biology.

1.2 Mitochondria and their genomes

Mitochondria are double-membrane-bound organelles that occur in the cells of almost all eukaryotes. As result of its double-membrane mitochondria are comprised of five distinct zones; these include the outer membrane, intermembrane space, inner membrane, cristae and the matrix. Referred to as “the powerhouse of the cell”, mitochondria use aerobic respiration to supply adenosine triphosphate (ATP) to cells where is it used an energy source (Roger et al., 2017). Mitochondria vary considerably in size, shape, and number. For example, the number of mitochondria per cell varies widely by organism, tissue, and cell type (Friedman and Nunnari, 2014).

1.2.1 The origins of mitochondria

The endosymbiotic hypothesis (Sagan, 1967) is widely accepted as explaining the origins of mitochondria and plastids. This hypothesis suggests that these organelles were originally free-living prokaryotic cells that were endocytosed for parasitism or predation but have gone on to form a mutualism with the host cell. In the case of mitochondria an aerobic, heterotrophic bacterium closely related to α-proteobacteria was endocytosed. The combination of the host and the internalized bacterium is recognised as the last eukaryotic common ancestor or LECA (Zimorski et al., 2014).

Several lines of evidence support the endosymbiotic hypothesis. The double membrane structure provides a couple of key pieces of evidence. For

example, consistent with the hypothesis the molecular structure of the inner membrane is prokaryote-like whereas the outer membrane is eukaryote-like. Ribosomes also provide evidence. Specifically, mitochondria possess their own ribosomes and these are more similar to 70S bacterial ribosomes than to 80S eukaryotic ribosomes. Perhaps most importantly mitochondria have their own genomes and these share key features with bacterial genomes. In both cases the genomes are haploid and circular, with naked DNA and in neither case is there a nucleus. Mitochondrial genes tend to be clustered into operon-like arrangements and the genes themselves are more similar to those in prokaryotes. Finally, phylogenetic analyses have indicated evolutionary links between mitochondrial DNA and the genomes of prokaryotes, in particular α-proteobacteria.

1.2.2 Diversity of mitochondrial genomes

Although mitochondria, and hence their genomes, likely have a single origin there is considerable variation in the size and structure of mitochondrial genomes across eukaryotes. These differences are the result of the evolutionarily separate trajectories of the mitochondrial genomes following divergence of the lineages that contain them. Therefore, differences in the size and structure of mitochondrial genomes typically occur between major groups of eukaryotes, whereas within any particular group mitochondrial genomes tend to be relatively similar.

The mitochondrial genomes of animals are very small and compact. Typically, around 16,500 bp in size, animal mitogenomes lack introns and contain little non-coding DNA (Morley and Nielsen, 2017; Zhang, 1995).

Additionally, gene content and order is largely stable in animal mitogenomes. Typically, there are 12 protein-coding, two rRNA and 22 tRNA genes (Boore, 1999) with differences in gene order only occurring between phyla (Aguileta et al., 2014). There are few examples of recombination amongst animal mitogenomes (Aguileta et al., 2014).

At the other end of the spectrum, plant mitochondrial genomes range from 86,000 bp to 2,400,000 bp in size (Zhang, 1995). However, despite being much larger plant and animal mitogenomes have similar gene contents. Inflated plant mitogenome sizes are the result of long introns and large amounts non-coding, including repetitive, DNA. It has also been shown that the non-coding DNA of plant mitogenomes contains DNA derived from the nuclear and chloroplast genomes. Occurring in relatively short segments these sequences make a substantial contribution to overall genome size and appear to have been integrated at various times during plant evolution (Morley and Nielsen, 2017). Structural rearrangements are common in plant mitogenomes and studies suggest that recombination is an important mechanism (Aguileta et al., 2014).

The mitochondrial genomes of other groups fall somewhere between these two extremes. For example, fungal mitogenomes range from 12,000 to 272,000 bp in size (Fonseca et al., 2021). Even the smallest fungal mitogenomes contain introns (Zhang, 1995) and these are responsible for much of the observed size variation with both the number and the length of introns varying between taxa (Aguileta et al., 2014). Repetitive DNA is also a feature of non-coding sequences in fungi, in this case increasing the size of intergenic spacers (Zhang, 1995). Unlike non-coding DNA content, mitochondrial gene

content is fairly constant in fungi. Typically, fungal mitogenomes contain 14 protein-coding, two rRNA, and 20-31 tRNA genes (Fonseca et al., 2021). Although gene content is strongly conserved, gene order varies both within and between the major groups of fungi (Aguileta et al., 2014).

1.2.3 Evolution of mitochondrial genomes

Mitochondrial genomes exhibit a general trend towards genome downsizing. It is difficult to predict the exact gene content of the free-living predecessor of mitochondria, however it is likely that it was closer in size and gene content to free-living modern relatives. The subsequent reduction in the gene content and size of the mitocgenome could therefore reflect the loss of genes not required for an endosymbiotic lifestyle or the transfer of necessary gene to the nuclear genome of the host cell (Lang and Gray, 1999). Despite this overall trend, the mitogenomes of animals and plants are evolving in distinct ways with those of plants having accumulated considerable amounts of non-coding DNA (Lang and Gray, 1999).

Although mitochondrial genome structure is broadly conserved within many groups there is evidence of structural changes. Indeed several studies have suggested that tRNA genes have an important role in mitogenome rearrangement. For example, comparisons of several metazoan mitogenomes found that the positions of the tRNA genes varied more so than other mitochondrial genes (Saccone et al., 2002). It suggested that tRNA genes could be viewed as mobile elements and that when tRNA genes flank another mitochondrial gene this grouping it might be expected to behave much like a transposable element (Saccone et al., 2002). The movement of transposon-like

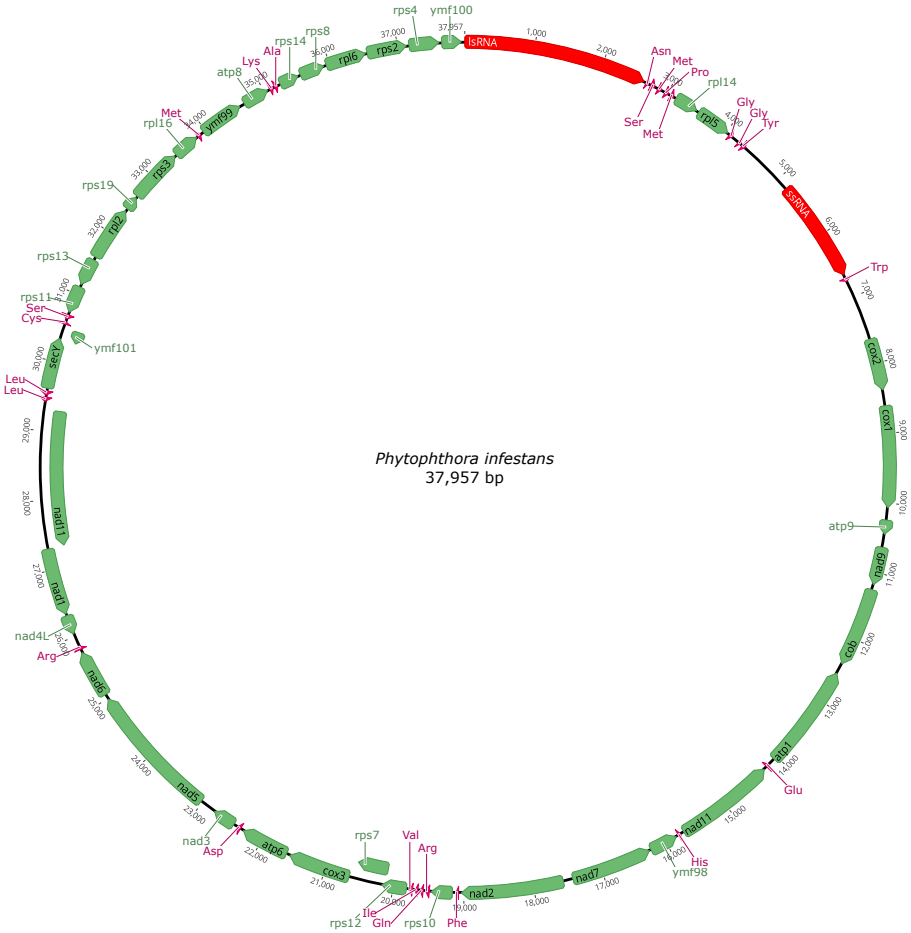
groupings of genes has also been suggested for fungi (Pantou et al., 2006). Observations, again in fungi, further support a link between tRNA gene distribution and the structural diversity of mitogenomes. Specifically, in groups where mitogenomes were structurally diverse tRNA genes tend to be scattered across the genome whereas in groups where there is little structurally diversity, tRNA genes were clustered together into distinct blocks (Aguileta et al., 2014).

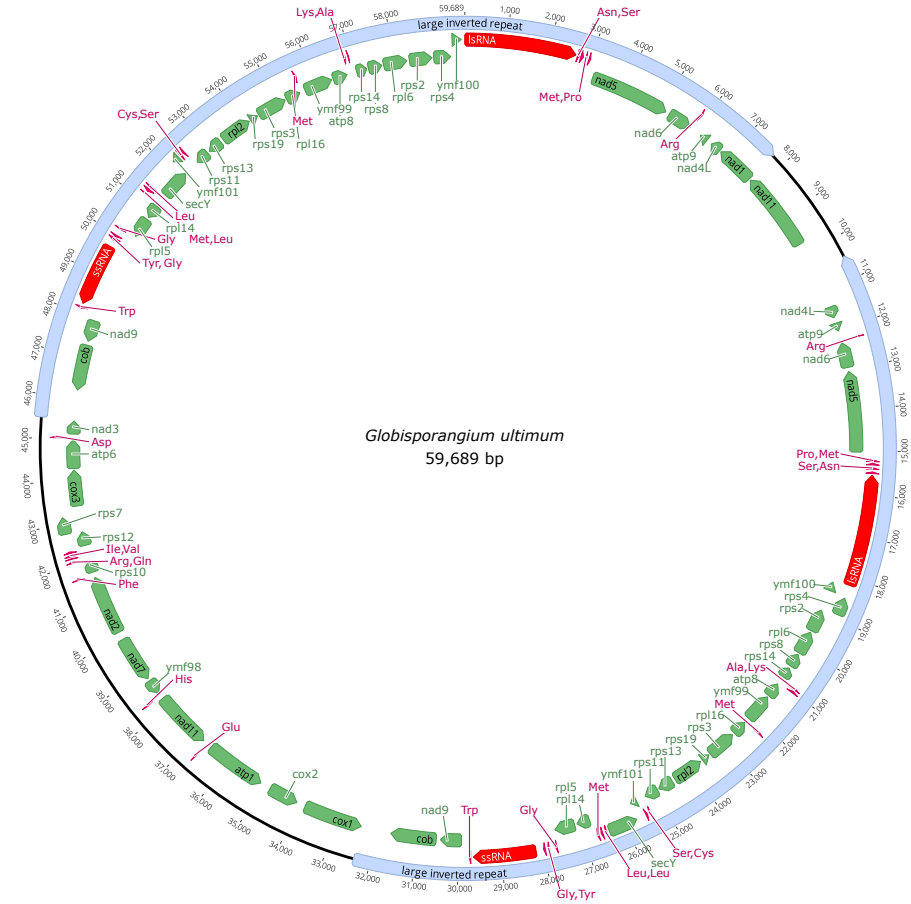
Ultimately, the mechanisms that underpin the structural evolution of mitogenomes remain uncertain. However, it appears likely that a combination of mechanisms, some lineage specific and some acting across many groups, are responsible for the observed patterns of structural rearrangement.

1.3 The mitogenomes of oomycetes

Oomycete mitochondrial genomes are intermediate in size, the currently available sequences range in length from 36,826 to 61,242 bp (Winkworth et al., 2022). These genomes are also relatively compact with little non-coding sequence and no introns (Martin et al., 2007; Winkworth et al., 2022) (Figure 1.3). Instead, this size range largely reflects the presence of duplicated sequences. Unusually for mitochondrial genomes, those of many oomycetes possess a large inverted repeat (Figure 1.3). Such repeats have been reported from *Phytopythium* (Winkworth et al., 2022), *Pythium* (Lévesque et al., 2010;

Figure 1.3 The mitogenomes of *Phytophthora infestans* (upper) and *Pythium ultimum* (lower). Coloured blocks represent mitochondrial genes (red, rRNA genes; green, protein coding genes; pink, tRNA genes). For genes the direction of transcription is indicated by the direction of the arrowhead. Pictures were generated in Geneious R9 (Kearse et al., 2012). Light blue blocks indicate large inverted repeats.


Phytophthora infestans
37,957 bp
lsRNA
ssRNA
rps4
ymf100
rps8
rps14
Lys
Ala
atp8
rpl6
rps2
Asn
Met
Pro
rpl14
Ser
Met
rpl5
Gly
Gly
Tyr
Trp
cox2
cox1
atp9
nad9
cob
atp1
Glu
nad7
His
ymf98
nad2
rps7
Val
Arg
Ile
Gln
rps12
rps10
Phe
cox3
atp6
Asp
nad3
nad5
nad6
Arg
nad4L
nad1
nad11
Leu
Leu
ymf101
secY
Ser
Cys
rps11
rps13
rps19
rpl2
rps3
rpl16
Met
ymf99


Globisporangium ultimum
59,689 bp
large inverted repeat
large inverted repeat
lsRNA
ssRNA
Lys,Ala
rps14
rps8
rps2
rpl6
ymf100
rps4
Asn,Ser
Met,Pro
nad5
nad6
Arg
atp9
nad4L
nad1
nad11
Cys,Ser
rps2
rps3
rps19
rpl16
Met
ymf99
atp8
rps13
rps11
ymf101
secY
Leu
rpl14
Gly
Met,Leu
rpl5
Tyr, Gly
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
rpl2
nad7
ymf98
His
nad11
Glu
atp1
cox2
cox1
nad9
Trp
cob
Gly
rpl5
rpl14
Met
ymf101
rps11
rps13
rps19
rps3
rpl16
Met
ymf99
atp8
Ala,Lys
rps14
rps8
rpl6
rps2
ymf100
rps4
lsRNA
Pro,Met
Ser,Asn
nad5
nad4L
atp9
Arg
nad6
Leu,Leu
secY
Ser,Cys
Gly,Tyr

Tangphatsornruang et al., 2016), *Saprolegnia* (Grayburn et al., 2004), *Aphanomyces* (Makkonen et al., 2016) *Achlya* and *Thraustotheca* (O'Brien et al., 2014). In these taxa the inverted repeat ranges from 8,289 to 24,164 bp in length. Given that large inverted repeats occur are a common feature of oomycete mitogenomes it has been suggested to be an ancestral characteristic of oomycetes (McNabb and Klassen, 1988). That said, large inverted repeats have not been identified within the mitogenomes of the sampled members of Peronosporaceae. More work is needed but current results suggest that this feature was lost early in the evolution of this family (Winkworth et al., 2022).

The large inverted repeat of oomycete mitogenomes is broadly similar to those of chloroplast genomes (McNabb and Klassen, 1988). In chloroplast genomes, the inverted repeat is thought to be stabilising the genome against structural rearrangements (Mohanta et al., 2020). A similar role has been proposed for the inverted repeat in oomycete mitogenomes (Boyd et al., 1984; Makkonen et al., 2016; Martin et al., 2007; O'Brien et al., 2014). Analyses of restriction fragment length polymorphisms have found that copies of the large inverted repeat tend to be more stable than the single copy regions (Boyd et al., 1984; McNabb et al., 1987; Shumard et al., 1986). Several ideas have been proposed to this apparent stability. One suggestion is that stability is not a function of the repeat but is limited to the portion of the repeat that contains the rRNA genes (Boyd et al., 1984; Shumard et al., 1986,). Alternatively, in some taxa (e.g., *Pythium*) a portion of the repeat between the rRNA genes also appears to be relatively stable. Perhaps this contains genes that act to stabilise the repeat (Boyd et al., 1984). Finally, it has been suggested that repeat stability

is not related to the repeat itself but is instead a reflection of overall genome organisation (Boyd et al., 1984).

Oomycete mitogenomes encode a much larger set of genes than those of many other groups. Members of the Peronosporaceae lack a large inverted repeat and in this group the core gene set consists of 66 genes, including 39 protein-coding, two rRNA and 25 tRNA genes (Martin et al., 2007; Winkworth et al., 2022). Amongst the currently available oomycete mitogenomes possession of an inverted repeat increases the size of the gene set by between 11 and 45 genes. The two rRNA genes are always contained within the inverted repeat, with the remainder of the repeat made up of various protein coding and tRNA genes. Although the mitogenomes of Peronosporaceae lack a large inverted repeat, several taxa have smaller repeats. Some of these are gene-containing and add between one and six genes to the gene set (Martin et al., 2007; Winkworth et al., 2022).

For most of the oomycetes there are few if any complete mitogenome sequences available. In contrast the sampling of Peronosporaceae is more extensive with mitogenomes currently reported for 52 taxa. In this group structural rearrangements of the mitogenome have been found to be relatively common, with 28 syntenies currently recognised (Winkworth et al., 2022). Comparisons of these mitogenomes suggest that the rearrangements responsible for the different syntenies are not uniformly distributed across the genome (Winkworth et al., 2022). One reason for this may be the non-uniform distribution of non-coding DNA across the genome. In this case certain regions may be more accepting of changes than others (Martin et al., 2007).

1.4 Focus of the investigation

The currently available sampling of mitogenomes is heavily biased towards *Phytophthora*. Mitogenomes are available for approximately 50 representatives of *Phytophthora* whereas for the remainder of the groups there are, at best, two or three sequences. Although comparisons of the mitogenomes of Peronsporaceae (Winkworth et al., 2022) have provided some insights, the limited sampling hampers a broader understanding of diversity and of the processes responsible for it. To address this, I assembled mitogenome sequences for 74 oomycete species. This more than doubles the number of species for which a complete mitogenome sequence is available.

Comparative and phylogenetic analyses of a combined data set of 135 mitogenome sequences representing six families were aimed at addressing three hypotheses. First, that outside the Peronsporaceae, large inverted repeats will be a common feature of oomycete mitogenomes. In previous studies (e.g., Grayburn et al., 2004; Winkworth et al., 2022) large inverted repeats have consistently been identified in representatives of the other oomycete clades. However, sampling of these groups remains limited and it is yet to be seen how widespread this feature is. Second, that levels of mitogenome structural diversity will vary within and between the major groups of oomycetes. The recent study of Peronosporaceae of Winkworth et al. (2022) suggests that mitogenome diversity is high in that group. It remains unclear what levels of diversity may exist in other families. For example, one possibility is that the structural diversity of mitogenomes will be lower elsewhere in oomycetes due to the presence of large inverted repeats in these families. Finally, that there will be a relationship between average genome size and the structural diversity of

oomycete mitogenomes. A possible role for genome size in determining the frequency with which structural changes occur has previously been suggested (e.g., Martin et al., 2007; Winkworth et al., 2022).

The following chapters describe the assembly of the genomes and analyses of the dataset.

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CHAPTER 2

Materials and Methods

2.1 Taxon sampling

Oomycete taxonomy remains somewhat uncertain in part because published taxonomic treatments (e.g., Dick, 2001) only partially reflect the evolutionary relationships (e.g., Bourett et. al, 2018; Nguyen et al., 2022). For example, as traditionally delimited neither *Phytophthora* nor *Pythium* are monophyletic (Runge et al., 2011; Uzuhashi et al., 2010). Given that these issues remain controversial (e.g., Brasier et al., 2022; Nguyen et al., 2022) the framework provided by the NCBI taxonomy browser (Schoch et al., 2020) was used as a basis for taxon sampling and subsequent analyses. This treatment addresses some (e.g., *Pythium* is subdivided into five smaller genera) but not all (e.g., *Phytophthora* is still treated as monophyletic) of the taxonomic uncertainty. Taxon selection within specific genera was further informed by recent molecular phylogenetic analyses (e.g., Nguyen et al., 2022; Winkworth et al., 2022). Sampling for the present project included six of ca. 20 families and 20 of ca. 83 genera currently recognised within the NCBI taxonomy browser.

2.1.1 Publicly available mitogenomes

Publicly available mitogenome sequences for oomycetes were retrieved from the NCBI GenBank nucleotide (https://www.ncbi.nlm.nih.gov/nuccore) and RefSeq databases (https://www.ncbi.nlm.nih.gov/refseq) (Appendix I). Database

searches used the GenBank taxon identifier for Oomycota (i.e.,txid4762) with search results filtered to include only mitochondrial sequences, sorted by sequence length.

2.1.2 Sequence Read Archives

To expand taxon sampling, mitogenome sequences were also assembled from publicly available whole genome sequencing data. These data were retrieved from the NCBI Read Sequence Archive (SRA) database (https://www.ncbi.nlm.nih.gov/sra) (Appendix I). Database searches again used the GenBank taxon identifier for Oomycota, but in this case search results filtered to include only Illumina paired-end sequencing of DNA.

2.2 Mitogenome assembly

Genome skimming is used to recover sequences that are highly represented in whole genome sequencing of total cellular DNA (Straub et al., 2012; Twyford and Ness, 2017). Typically, the approach is used when nuclear genome coverage is low but is not limited to such situations. Specific sequences can be “skimmed” from whole genome sequencing even when nuclear genome coverage is high. In the present project a custom bioinformatics pipeline, described below, was used to skim mitogenome sequences from publicly available whole genome sequencing data.

2.2.1 Retrieving and extracting read archives

Read archives were retrieved and extracted using tools contained within the NCBI SRA toolkit (https://www.ncbi.nlm.nih.gov/sra). Specifically, the

prefetch tool for retrieval of SRAs and fastq-dump tool for extraction of the sequence reads in fastQ format. Reads were extracted using the “--split-files” option that results in the members of each read pair being split between two files.

2.2.2 Read trimming

In some cases SRAs retrieved from NCBI contained paired-end reads more than 250 bp in length. To enable subsequent processing these were trimmed with Trimmomatic V0.39 using the “CROP 250” option (Bolger et al., 2014).

2.2.3 Contig assembly

Paired-end sequence reads were assembled into contigs using IBDA_UD, an iterative de Bruijn graph assembler that is robust to uneven coverage of the genome (Peng et al., 2012). Sequence read files were first converted from fastQ to fastA format using a custom perl script and then assembled with IDBA_UD using default parameters.

2.2.4 Genome skimming

Contigs assembled by IDBA_UD were first filtered to remove those shorter than 150 nt. Standalone BLAST (Altschul et al., 1997) searches against a reference collection of publicly available, complete oomycete mitogenome sequences (Appendix II) to remove sequences with low similarity to these references.

2.2.5 Genome assembly

Filtered contigs were assembled into larger scaffolds and, ultimately, into draft mitogenome sequences using the *de novo* assembly tools in Geneious R9 (Kearse et al., 2012). Mitogenome drafts were considered complete when the ends of linear drafts could be circularised.

If a circular mitogenome draft was not immediately recovered, the Geneious R9 Repeat Finder plugin was used to identify sequence repeats within those linear scaffolds that had been recovered. Typically, large repeat structures were not identified using this procedure but were inferred based on a characteristic pattern of distribution for two pairs of smaller repeats (i.e., 25-100 bp in length). In this case, the smaller repeats were assumed to mark the boundaries of a larger repeat structure. The putative inverted repeat sequence was extracted, reverse complemented, and then spliced back into the draft mitogenome in order to circularise it (Figure 2.1).

2.2.6 Assembly evaluation

To evaluate the completeness of mitogenome sequence drafts, the original sequence reads were mapped directly onto linearised drafts using BWA (Li and Durbin, 2009). The resulting read maps were visualised in Tablet (Milne et al., 2010) with inconsistency in read coverage assumed to reflect assembly errors. In such cases, drafts were modified and the mapping procedure repeated until all errors were resolved.

Following error correction mitogenome drafts were subjected to a final round of read mapping. For this the sequence start position was first offset by

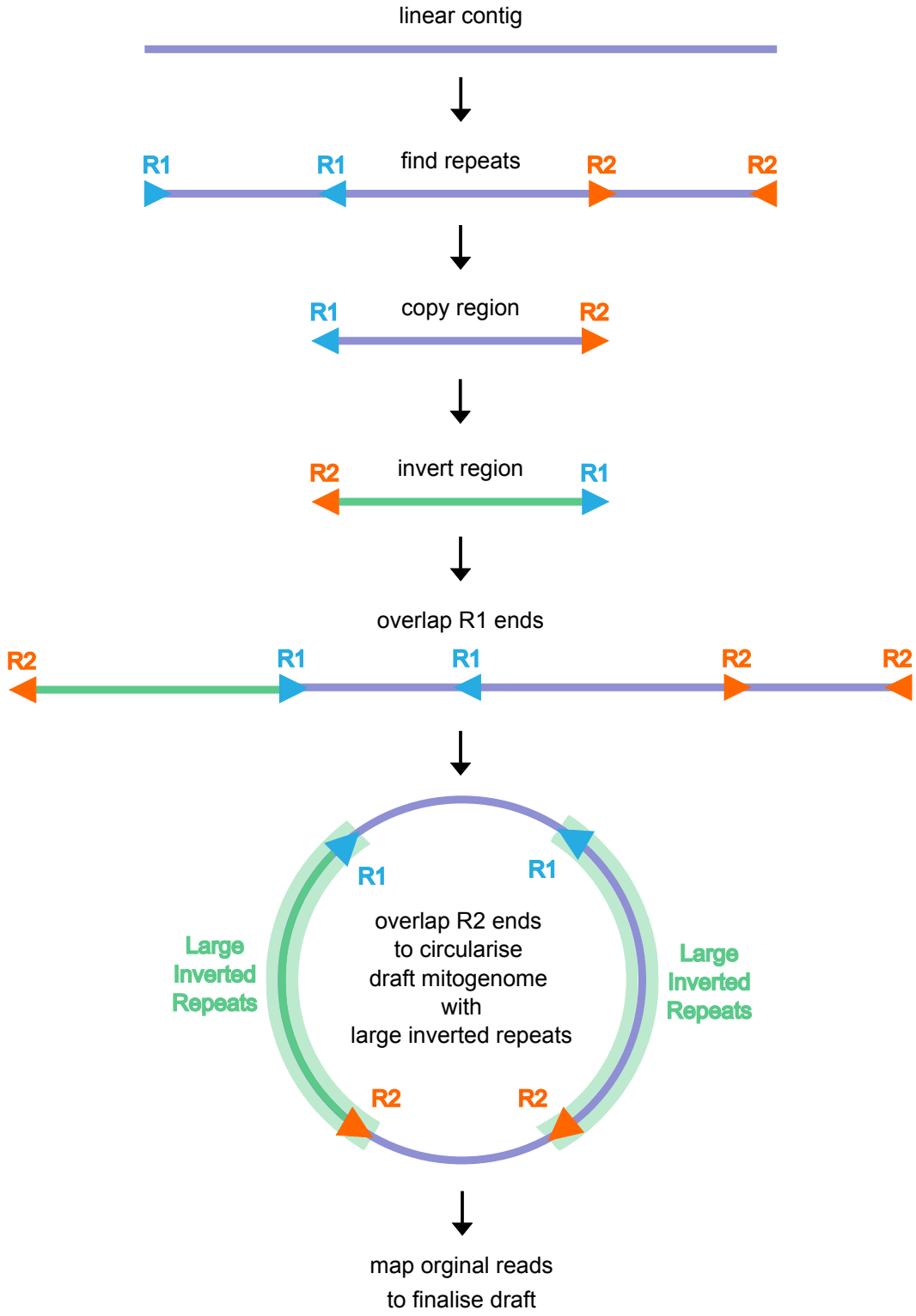

Figure 2.1 Flow diagram illustrating the identification of a region corresponding to the large inverted repeat structures in a linear contig and circularisation of the draft mitogenome.

1,000-10,000 bp. The mitogenome sequence was considered finalised if read coverage on the modified draft was also complete.

2.3 Mitogenome annotation

2.3.1 Gene annotations

Previous studies (e.g., Winkworth et al., 2022) have identified a core gene set of 39 protein coding, 25 tRNA, and two rRNA genes for oomycetes. In publicly available mitogenomes, departures from this core set include duplications of one or more of the genes (e.g., duplication of *cox2* in *Phytophthora* × *alni*), the inclusion of open reading frames (e.g., *orf217* in *Phytophthora infestans*, *orf176* in *Phytophthora ramorum*), or gene losses (e.g., loss of *ymf101* from *Phytophthora andina* and several closely related species).

Annotations for both the publicly available mitogenomes and those sequences assembled in this thesis were standardised to this core gene set. For the publicly available mitogenome sequences, duplicated core genes (e.g., the *cox2* gene in *Phytophthora* × *alni*) were retained, as were open reading frames that shared high identity with one of the core genes (e.g., *orf217* in *Phytophthora infestans* shared identity with *ymf99* in *Phytophthora cactorum*). Open reading frames with low similarity to the genes in the set were removed (e.g., *orf176* in *Phytophthora ramorum*). Where an annotation for one or more of the core genes was missing from a publicly available mitogenome sequence, a search using the live annotate and predict tool in Geneious R9 was conducted to confirm gene absence. A gene annotation was added where this procedure identified sequences with high similarity to supposedly missing genes (e.g., an *rps7* gene annotation was added to *Thraustotheca clavata*).

For mitogenome sequences assembled in this thesis, final sequences were annotated on the basis of sequence similarity to the core gene set using a combination of Geneious R9 and tRNAScan-SE 2.0 (Lowe and Chan, 2016). Protein coding genes and rRNAs were identified using the live annotate and predict tool in Geneious R9; selection of the reference mitogenome for the annotation was based on evolutionary relatedness. Initial searches used a similarity criterion of 65%, with lower thresholds used if core genes were not recovered by the first search. Annotations for the protein coding genes were checked manually and, where necessary, adjusted to ensure appropriate start and stop codons as well as that the sequence remained in frame throughout. Transfer RNAs were identified using the default parameters of tRNAScan-SE 2.0, with the resulting annotation transferred onto mitogenome sequences in Geneious R9. As for publicly available mitogenomes, duplicate annotations for genes belonging to the core set were retained.

2.3.2 Repeats

The Repeat Finder tool in Geneious R9 was used to find perfect (i.e., sharing 100% identity) repeats of >150 bp in length. In a few cases shorter repeats (i.e., <150 bp in length) were also recognised. These were recognised primarily because these repeats contained a duplicated tRNA gene (e.g., in *Phytophthora podocarpi* direct repeats 80 bp in length contained copies of *tRNA-Lys*). Annotations of publicly available mitogenomes were adjusted to only include perfect repeats >150 bp in length (e.g., *Achlya hypogyna* and *Thraustotheca clavata* had imperfect repeats annotated).

2.3.3 Genome orientation

Typically, mitogenomes assembled in this thesis were oriented such that the *lsRNA* gene was in the forward orientation with the first residue of the genome corresponding to the first residue the *lsRNA* gene. Where a mitogenome sequence contained two copies of this gene, the genome was orientated such that the *atp1* gene was in the reverse direction with the first position of the genome set corresponding to the first residue of whichever *lsRNA* gene copy was in the forward orientation.

2.4 Comparative analyses

2.4.1 Genome statistics

For each mitogenome sequence total genome size, the numbers of each gene type (i.e., protein coding, rRNA and tRNA genes), as well as the proportions of coding (i.e., the proportion of the genome occupied by protein coding, rRNA and tRNA genes) and non-coding DNA were recorded from Geneious R9. For species that contained repeats, the lengths of the repeats were also recorded.

2.4.2 Overall synteny

Previous analyses have identified large inverted repeats for members of the Pythiaceae (including *Phytopythium*) and Saprolegniaceae. Mitogenomes for the members of these two groups included in this thesis also appear to be characterised by inverted repeats. Available methods for evaluating synteny (e.g., CREx, Bernt et al., 2007) are confounded by the presence of repeats and

given the prevalence of repeats in the present dataset it was necessary to visually assess synteny.

For each of the mitogenome sequences assembled in this thesis, synteny was evaluated by comparing the gene order of newly assembled to those of publicly available mitogenomes. Where an identical gene order was identified, the newly assembled mitogenome was assigned to the same synteny group; see Winkworth et al. (2022) for a list of previously identified synteny groups. If the newly assembled gene order was unique, a new synteny group was established.

2.4.3 Synteny blocks and their arrangement

To evaluate the role of changes in gene order in the evolution of oomycete mitogenomes, conserved gene blocks – or “synteny blocks” – were first identified and their arrangements compared within and between the families of oomycetes.

First an iterative process was used to identify synteny blocks for each of the family-level taxa. A gene was selected at random from the core set and for all the representatives of the family under consideration the two immediately adjacent genes, one on either side of the selected gene, were identified. Three situations were possible,

(i) the same two genes were adjacent to the selected gene in all the mitogenomes. In this case the synteny block was expanded to include the two genes (one on either side of the initially selected gene). At one end of the synteny block adjacent genes were identified and compared until an adjacent gene was not shared by all the mitogenomes; the last shared gene was

assumed to represent the corresponding end of the synteny block. The process was then repeated from the other end of the block.

(ii) only one of the adjacent genes was the same for all the mitogenomes. If so, the selected gene was assumed to represent one end of the synteny block. The block was expanded to include the shared gene with further adjacent gene comparisons conducted from that same end of the block until an adjacent gene was not shared.

(iii) neither of the initially adjacent genes was shared by all the mitogenomes. In this case the initially selected gene was assumed to be a single gene synteny block.

This process was repeated for other randomly selected genes until all genes had been assigned to a synteny block. Initial synteny block sets for each family were then assessed to ensure that block ends were recognised on the basis of genome rearrangements rather than gene duplications or losses. In several cases the duplications or losses involved individual genes. For example, the loss of the *ymf101* gene from four of the ten representatives of *Phytophthora* Clade 1 resulted in a pair of smaller synteny blocks being recognised at the family-level, despite these comprising a single block in the remaining representatives of Peronosporaceae. Since these subdivisions were not the result of a gene rearrangement, the larger gene blocks were retained in the final family-level synteny block sets. Other cases involved duplications of several genes as a part of a repeat structure in members of Peronosporaceae, Pythiaceae, and Saprolegniaceae. In each case the duplicated sequence represented a partial copy of a larger synteny block. For example, the large inverted repeat in *Globisporangium barbulae*, a member of Pythiaceae, contains

a partial copy of the *nad9*, *cob* synteny block. Since these partial copies did not otherwise disrupt the corresponding synteny block and complete copies of the synteny block were retained in all the representative mitogenomes, the partial copies were not considered further.

An oomycete synteny block set was constructed by comparing synteny blocks between the family-level taxa. Where synteny blocks were identical across all the families they were retained in the oomycete synteny block set. Where synteny blocks differed, they were sub-divided such that the resulting blocks were representative of the oomycetes as a whole. For example, the genes *nad4L*, *nad1*, and *nad11* form a synteny block in both Peronosporaceae and Pythiaceae whereas in Saprolegniaceae *nad5*, *nad4L*, and *nad1* form a synteny block with *nad11* forming a single gene synteny block. To reflect this difference, three synteny blocks were included in the oomycete synteny block set. Specifically, two single gene blocks, one containing *nad5* and the other *nad11* with a third containing *nad4L* and *nad1.*

2.4.4 Analysis of synteny block order

The oomycete synteny block set was used to evaluate broad patterns in mitogenome arrangement across the group. First, for each mitogenome the neighbours of each of the oomycete synteny blocks was determined. Next, the neighbours of each oomycete synteny block were compared within and between families.

2.4.5 Synteny and gene duplication

Large inverted repeats have previously been reported from members of the Pythiaceae and Saprolegniaceae (e.g., Grayburn et al., 2004; Lévesque et al., 2010; Makkonen et al., 2016; Tangphatsornruang et al., 2016). These were also identified in many of the mitogenomes assembled in this thesis. To evaluate the effect of inverted repeats on synteny the gene content of the inverted repeats was compared across the oomycetes.

2.5 Phylogenetic analyses

2.5.1 Data matrices

For phylogenetic analyses, multiple sequence alignments were assembled for each of the protein-coding, rRNA and tRNA gene loci in the core gene set. If, for genes represented more than once in oomycete mitogenomes, the sequence copies were identical then one copy was excluded (e.g., the protein coding gene, *cob,* in *Lagenidium giganteum*). If gene copies were nonidentical, the sequence from the gene copy in what was considered to be the "standard" position was included (e.g., *tRNA-Glu* in *Pythium porphyrae*, *tRNA-Met* in *Pythium monospermum*).

Initial multiple sequence alignments were performed in Geneious R9. Protein coding gene alignments used the transitional alignment tool and alignments of rRNA and tRNA sequences used MUSCLE (Edgar, 2004) as implemented within Geneious R9. Initial alignments were inspected in Mesquite v3 (Maddison and Maddison, 2021) with minor modifications to resolve potential misalignments; in particular, portions of sequence where less than 50% of the sequences were represented or where alignments were otherwise ambiguous

were removed. Consistent with Winkworth et al. (2022) the levels of length and sequence variation for several genes resulted in alignments being reliable. Alignments for the four hypothetical proteins (i.e., *ymf98*, *ymf99*, *ymf100*, and *ymf100*), the sec-independent transporter protein (i.e., *secY*), four ribosomal protein genes (i.e., *rpl6, rps3*, *rps7* and *rps10*) and the large rRNA subunit (i.e., *lsRNA*) were excluded from further analyses.

2.5.2 Partition and model selection

For phylogenetic analyses, a concatenated matrix containing 32 loci was compiled. The best-fit partition scheme and, subsequently, the best-fit substitution models for each of these partitions were identified using ModelFinder (Kalyaanamoorthy et al., 2017), as implemented in IQ-TREE v2.2.0 (Minh et al., 2020b).

The initial data matrix included partitions representing each of the 32 loci and ModelFinder used a greedy strategy of progressive merging of partitions until there was no further improvement in model fit. To reduce the computational time the TESTMERGEONLY flag was used; this results in an analysis equivalent to that of PartitionFinder2 (Lanfear et al., 2017).

2.5.3 Maximum likelihood analysis

A partitioned maximum likelihood search using IQ-TREE v2.2.0 (Chernomor et al., 2016; Minh et al., 2020b). For this search, the best-fit substitution models were applied to the corresponding sequence partitions and support for inferred relationships was evaluated using 1,000 bootstrap replicates.

2.5.4 Bayesian analysis

Bayesian searches were performed using MrBayes 3.2 (Ronquist et al., 2012) with the best-fit substitution models applied to the corresponding sequence partitions. Two identical searches, each 2.0×10^7 generations in length and sampled every 1.0×10^3 generations, were conducted. For each run, burn-in was determined using convergence diagnostics with samples drawn prior to stationarity discarded. Posterior distributions of parameters were examined using Tracer v1.7 (Rambaut et al., 2018) and consensus trees visualized with FigTree v1.4 (http://tree.bio.ed.ac.uk/software/figtree/).

2.5.5 Concordance between data partitions

To examine conflict within the data set, a pair of concordance factors implemented in IQ-TREE 2.2.0 (Minh et al., 2020a) were calculated. For a given branch in a reference topology, the site concordance factor (sCF) is the percentage of alignment positions from a concatenated matrix that are informative with respect to the branch and that support the branch. Again for a given branch in a reference topology, the gene concordance factor (gCF) is the percentage of sequence partitions for which an analysis of that partition recovers the branch.

These analyses made use of the topology from the partitioned maximum likelihood search as well as those from similar searches for each of the 32 gene partitions. Kendall's τ, as implemented in R (R Core Team, 2021), was used to evaluate correlation between the two concordance factors as well as whether there were correlations with the length of and support values for the corresponding branches.

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CHAPTER 3

Results

3.1 Taxon sampling

For the present study a dataset of 135 complete oomycete mitogenome sequences was compiled (Table 3.1; Appendix III). Of these, 61 were publicly available, including 53 representatives of Peronosporaceae (e.g., *Phytophthora*), three of Pythiaceae (e.g., *Globisporangium*) and five of Saprolegniaceae (e.g., *Aphanomyces).* The remaining 74 were newly assembled from publicly available data. These included 54 representatives of Pythiaceae, 10 of Peronosporaceae and six of Saprolegniaceae. The remaining four sequences represented three groups for which mitogenome sequences had not previously been reported. Specifically, Salisapiliaceae (i.e., *Salisapilia*), Lagenidiaceae (i.e., *Lagenidium*) and Albuginaceae (i.e., *Albugo*).

3.2 Mitogenomes

3.2.1 Genome size

The included oomycete mitogenomes ranged in size from 36,826 bp (i.e., *Phytophthora agathidicida*) to 79,790 bp (i.e., *Pythium oligandrum*) (Table 3.1). Genome size also varied within families. For example, for representatives of Peronosporaceae, mitogenome size ranged from 36,826 bp (i.e., *Phytophthora agathidicida*) to 51,184 bp (i.e., *Phytophthora*

Table 3.1 Summary statistics for the included oomycete mitochondrial genomes						
Species	**Genome Size (bp)**	**Proportion of genome**		**Gene numbers**		
		Coding	**Non-coding**	**Protein**	**rRNA**	**tRNA**
Peronosporaceae						
Clade 1						
Phytophthora mirabilis	37,779	0.9	0.1	38	2	25
Phytophthora andina	37,874	0.9	0.1	38	2	25
Phytophthora ipomoeae	37,872	0.9	0.1	38	2	25
Phytophthora betacei	37,948	0.9	0.1	39	2	25
Phytophthora infestans	37,957	0.9	0.1	39	2	25
Phytophthora phaseoli	37,914	0.9	0.1	38	2	25
Phytophthora nicotianae	37,749	0.9	0.1	39	2	25
Phytophthora aleatoria	38,936	0.88	0.12	39	2	25
Phytophthora idaei	38,165	0.89	0.11	39	2	25
Phytophthora cactorum	38,068	0.9	0.1	39	2	25
Clade 16						
Plasmopara muralis	43,946	0.79	0.21	39	2	27
Plasmopara viticola	42,644	0.81	0.19	39	2	27
Plasmopara nivea	40,571	0.87	0.13	39	2	27
Plasmopara halstedii	38,944	0.88	0.12	39	2	27
Bremia lactucae	39,302	0.87	0.13	39	2	26
Clade 4						
Phytophthora megakarya	39,277	0.87	0.13	39	2	25
Phytophthora palmivora	38,741	0.88	0.12	39	2	25
Phytophthora litchii	37,950	0.9	0.1	39	2	25

Clade 3						
Phytophthora pseudosyringae	39,143	0.87	0.13	39	2	25
Phytophthora pluvialis	39,327	0.87	0.13	39	2	25
Clade 12						
Phytophthora castanetorum	38,326	0.89	0.11	39	2	25
Phytophthora quercina	38,471	0.89	0.11	39	2	25
Phytophthora sp. ohioensis	38,145	0.89	0.11	39	2	25
Phytophthora tubulina	38,065	0.9	0.1	39	2	25
Phytophthora versiformis	38,011	0.9	0.1	39	2	25
Clade 5						
Phytophthora agathidicida	36,826	0.93	0.07	39	2	25
Phytophthora cocois	37,078	0.92	0.08	39	2	25
Phytophthora castaneae	37,083	0.92	0.08	39	2	25
Phytophthora heveae	37,150	0.92	0.08	39	2	25
Phytophthora sp. novaeguineae	37,072	0.92	0.08	39	2	25
Clade 2						
Phytophthora tropicalis	37,047	0.92	0.08	39	2	25
Phytophthora capsici	38,427	0.89	0.11	39	2	25
Phytophthora sp. subnubulis	37,854	0.9	0.1	39	2	25
Phytophthora colocasiae	41,367	0.82	0.18	39	2	25
Phytophthora multivora	38,032	0.9	0.1	39	2	25
Phytophthora plurivora	38,082	0.9	0.1	39	2	25
Clade 15						
Peronospora tabacina	43,225	0.79	0.21	39	2	25
Peronospora effusa	41,318	0.83	0.17	39	2	25

Peronospora belbahrii	40,063	0.85	0.15	39	2	25
Pseudoperonospora cubensis	38,561	0.88	0.12	39	2	25
Pseudoperonospora humuli	39,087	0.87	0.13	39	2	25
Hyaloperonospora arabidopsidis	38,797	0.88	0.12	39	2	25
Sclerospora graminicola	41,470	0.83	0.17	39	2	25
Phytophthora podocarpi	38,130	0.9	0.1	39	2	26
Clade 6						
Phytophthora gonapodyides	43,974	0.78	0.22	39	2	25
Phytophthora pinifolia	43,061	0.88	0.12	43	2	27
Phytophthora chlamydospora	38,329	0.89	0.11	39	2	25
Clade 7						
Phytophthora × alni	45,343	0.77	0.23	40	2	25
Phytophthora × cambivora	51,184	0.67	0.33	39	2	25
Phytophthora fragariae	44,706	0.76	0.24	39	2	25
Phytophthora rubi	45,523	0.76	0.24	40	2	25
Phytophthora sojae	42,977	0.8	0.2	40	2	25
Phytophthora cinnamomi	39,225	0.87	0.13	39	2	25
Clade 8						
Phytophthora ramorum	39,494	0.9	0.1	40	2	26
Phytophthora lateralis	38,507	0.89	0.11	39	2	26
Phytophthora sansomeana	39,618	0.87	0.13	40	2	25
Phytophthora cryptogea	38,163	0.89	0.11	39	2	25
Clade 9						
Phytophthora fallax	43,681	0.78	0.22	39	2	25
Phytophthora captiosa	44,662	0.76	0.24	39	2	25

Phytophthora polonica	40,467	0.84	0.16	39	2	25
Clade 10						
Phytophthora boehmeriae	38,001	0.9	0.1	39	2	26
Phytophthora kernoviae	37,467	0.91	0.09	39	2	27
Nothophytophthora						
Nothophytophthora sp.	38,518	0.89	0.11	39	2	27
Pythiaceae						
Halophytophthora						
Halophytophthora batemanensis	62,824	0.9	0.1	65	4	42
Halophytophthora polymorphica	64,467	0.88	0.12	65	4	44
Clade K (*Phytopythium*)						
Phytopythium aichiense	63,645	0.88	0.12	65	4	42
Phytopythium boreale	63,093	0.89	0.11	65	4	42
Phytopythium chamaehyphon	62,839	0.89	0.11	65	4	42
Phytopythium helicoides	63,571	0.88	0.12	65	4	42
Phytopythium sp. cucurbitacearum	61,254	0.91	0.09	65	4	42
Phytopythium vexans	61,242	0.91	0.09	65	4	42
Globisporangium						
Clade G						
Globisporangium barbulae	60,138	0.86	0.14	62	4	42
Globisporangium cederbergense	70,988	0.75	0.25	63	4	42
Globisporangium iwayamai	64,039	0.87	0.13	65	4	42
Globisporangium okanoganense	69,322	0.78	0.22	64	4	42
Globisporangium nagaii	57,646	0.91	0.09	62	4	42

Clade F						
Globisporangium cylindrosporum	60,681	0.92	0.08	65	4	42
Globisporangium irregulare	60,610	0.92	0.08	65	4	42
Globisporangium mamillatum	60,953	0.92	0.08	65	4	42
Globisporangium debaryanum	67,010	0.79	0.21	62	4	42
Globisporangium emineosum	57,491	0.92	0.08	62	4	42
Clade E						
Globisporangium erinaceum	60,764	0.92	0.08	65	4	42
Globisporangium radiosum	60,766	0.92	0.08	65	4	42
Globisporangium camurandrum	60,088	0.93	0.07	65	4	42
Globisporangium middletonii	60,714	0.87	0.13	62	4	42
Globisporangium rhizosaccharum	58,038	0.91	0.09	62	4	42
Clade J						
Globisporangium nunn	61,099	0.86	0.14	62	4	42
Globisporangium orthogonon	61,053	0.86	0.14	62	4	42
Globisporangium acanthophoron	58,427	0.9	0.1	62	4	42
Globisporangium perplexum	59,403	0.91	0.09	64	4	42
Clade I						
Globisporangium ultimum	59,689	0.89	0.11	63	4	42
Globisporangium solare	60,675	0.89	0.11	64	4	42
Globisporangium splendens	59,351	0.89	0.11	62	4	42
Globisporangium heterothallicum	57,919	0.91	0.09	62	4	42
Clade H (*Elongisporangium*)						
Elongisporangium dimorphum	63,637	0.88	0.12	65	4	42
Elongisporangium senticosum	64,314	0.87	0.13	65	4	42

Elongisporangium anandrum	64,825	0.83	0.17	64	4	42
Elongisporangium prolatum	59,450	0.91	0.09	63	4	42
Pilasporangium						
Pilasporangium apinafurcum	57,022	0.92	0.08	60	4	42
Salisapiliaceae						
Salisapilia						
Salisapilia sapeloensis	56,039	0.88	0.12	59	4	42
Pythiaceae cont.						
Pythium						
Clade B						
Pythium aristosporum	71,953	0.81	0.19	67	4	42
Pythium arrhenomanes	71,876	0.81	0.19	66	4	42
Pythium phragmiticola	71,721	0.82	0.18	67	4	44
Pythium vanterpoolii	65,996	0.8	0.2	62	4	42
Pythium graminicola	67,595	0.78	0.22	62	4	41
Pythium plurisporium	66,356	0.79	0.21	62	4	42
Pythium rishiriense	68,188	0.83	0.17	66	4	43
Pythium torulosum	72,024	0.8	0.2	66	4	42
Pythium myriotylum	71,327	0.79	0.21	65	4	42
Pythium pyrilobum	69,302	0.81	0.19	65	4	42
Pythium dissotocum	68,007	0.83	0.17	66	4	42
Pythium sukuiense	67,243	0.84	0.16	66	4	42
Pythium brachiatum	75,884	0.77	0.23	67	4	44
Clade A						
Pythium monospermum	76,333	0.77	0.23	67	4	44

Pythium porphyrae	77,813	0.72	0.28	65	4	46
Pythium aphanidermatum	62,533	0.78	0.22	58	4	41
Clade C						
Pythium insidiosum	54,989	0.91	0.09	59	4	41
Clade D						
Pythium lycopersicum	70,765	0.84	0.16	69	4	43
Pythium oligandrum	79,790	0.74	0.26	69	4	43
Pythium amasculinum	70,791	0.84	0.16	69	4	43
Pythium grandisporangium	72,477	0.8	0.2	67	4	42
Lagenidiaceae						
Lagenidium						
Lagenidium giganteum	60,537	0.91	0.09	63	4	42
Albuginaceae						
Albugo						
Albugo candida	61,303	0.95	0.05	67	4	42
Albugo laibachii	62,278	0.94	0.06	67	4	42
Saprolegniaceae						
Aphanomyces						
Aphanomyces frigidophilus	51,130	0.92	0.08	47	4	33
Aphanomyces invadans	49,061	0.93	0.07	46	4	33
Aphanomyces astaci	49,489	0.92	0.08	46	4	33
Aphanomyces cochlioides	47,983	0.8	0.2	38	4	25
Aphanomyces euteiches	46,015	0.83	0.17	38	4	25
Aphanomyces sp. NJM 9510	48,926	0.93	0.07	46	4	33

Saprolegnia						
Saprolegnia diclina	46,595	0.89	0.11	42	4	30
Saprolegnia parasitica	46,802	0.88	0.12	42	4	30
Saprolegnia ferax	46,930	0.92	0.08	43	4	30
Achlya						
Achlya hypogyna	46,840	0.83	0.17	39	4	29
Thraustotheca						
Thraustotheca clavata	47,382	0.81	0.19	38	4	30

cambivora). Despite this, average mitogenome size differed between families. At 39,694 bp, Peronosporaceae has the smallest average mitogenome size (range 36,826-51,184 bp), with Saprolegniaceae averaging 47,923 bp (range 46,015-51,130 bp) and the combination of Pythiaceae, Salisapiliaceae, Lagenidiaceae, and Albuginaceae having the largest average mitogenome size at 64,462 bp (range 54,989-79,790 bp) (Table 3.1; Table 3.2).

Repeats are a key feature of many oomycete mitogenomes. The mitogenome sequences for all the included Pythiaceae, Salisapiliaceae, Lagenidiaceae, Albuginaceae and Saprolegniaceae contained a large inverted repeat structure. The inverted repeats of Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae ranged in size from 18,227 bp (i.e., *Salisapilia sapeloensis*) to 32,635 bp (i.e., *Pythium monospermum*) (Table 3.3). Those of Saprolegniaceae were smaller, ranging in size from 6,175 bp (i.e., *Aphanomyces euteiches*) to 14,548 bp (i.e., *Aphanomyces frigidophilus*). Repeat structures are less common in the mitogenomes of Peronosporaceae, being present in 33% of the included taxa. These were a combination of direct and inverted repeats, ranging from 80 bp (i.e., *Phytophthora podocarpi*) to 5,442 bp (i.e., *Phytophthora* × *cambivora*). In some cases more than one repeat type was present (e.g., repeats 185 and 394 bp long were present in *Bremia lactucae*) (Table 3.4).

3.2.2 Coding and non-coding DNA content

The included mitogenomes differed in terms of coding and non-coding DNA content. Across the full dataset the proportions of coding and non-

Table 3.2 Summary statistics for the included oomycete mitochondrial genomes averaged by family, genus and clade					
Species	**Number of species**	**Average Genome size (bp)**	**Average NC**	**No of Syntenies**	**Syntenies/Species**
Peronosporaceae	63	39,694	0.13	29/63	0.46
Clade 1	10	38,026	0.10	3/10	0.30
Clade 16	5	41,081	0.16	3/5	0.60
Clade 4	3	38,656	0.12	3/3	1.00
Clade 3	2	39,235	0.13	1/2	0.50
Clade 12	5	38,204	0.11	1/5	0.20
Clade 5	5	37,042	0.08	1/5	0.20
Clade 2	6	38,468	0.11	2/6	0.33
Clade 15	8	40,081	0.15	5/8	0.63
Clade 6	3	41,788	0.15	2/3	0.67
Clade 7	6	44,826	0.23	6/6	1.00
Clade 8	4	38,946	0.11	2/4	0.50
Clade 9	3	42,937	0.21	2/3	0.67
Clade 10	2	37,734	0.10	2/2	1.00
Nothophytophthora	1	38,518	0.11	1/1	1.00
Pythiaceae	57	64,772	0.14	29/57	0.51
Halophytophthora	2	63,646	0.11	2/2	1.00
Clade K (*Phytopythium)*	6	62,607	0.11	2/6	0.33
Globisporangium	23	61,168	0.12	8/23	0.35
Clade G	5	64,427	0.17	5/5	1.00
Clade F	5	61,349	0.11	3/5	0.60
Clade E	5	60,074	0.09	3/5	0.60
Clade J	4	59,996	0.12	3/4	0.75
Clade I	4	59,409	0.11	4/4	1.00

Clade H *(Elongisporangium)*	4	63,057	0.13	3/4	0.75
Pilasporangium	1	57,022	0.08	1/1	1.00
Salisapiliaceae	1	56,039	0.12	1/1	1.00
Salisapilia	1	56,039	0.12	1/1	1.00
Pythiaceae *cont.*					
Pythium	21	70,141	0.20	17/21	0.81
Clade B	13	69,806	0.19	11/13	0.85
Clade A	3	72,226	0.24	3/3	1.00
Clade C	1	54,989	0.09	1/1	1.00
Clade D	4	73,456	0.19	2/4	0.50
Lagenidiaceae	1	60,537	0.09	1/1	1.00
Lagenidium	1	60,537	0.09	1/1	1.00
Albuginaceae	2	61,791	0.06	1/2	0.50
Albugo	2	61,791	0.06	1/2	0.50
Saprolegniaceae	11	47,923	0.12	7/11	0.64
Aphanomyces	6	48,767	0.11	4/6	0.67
Saprolegnia	3	46,776	0.10	1/3	0.33
Achlya	1	46,840	0.17	1/1	1.00
Thraustotheca	1	47,382	0.19	1/1	1.00

coding DNA were 0.67-0.95 and 0.05-0.33, respectively; *Albugo candida* and *Phytophthora* × *cambivora* represent the extremes of each of these ranges (Table 3.1).

Average values for the proportions of coding and non-coding DNA were similar for the families of oomycetes. Specifically, average values for the Peronosporaceae, Pythiaceae, and Saprolegniaceae were 0.87-0.88 for coding and 0.12-0.13 for non-coding DNA (Table 3.2). In contrast, average proportions often differed between groups within families. For example, within Peronosporaceae average proportions of coding and non-coding DNA are 0.92 and 0.08, respectively, for the included members of Clade 5, but 0.77 and 0.23, respectively, for the members of Clade 7 (Table 3.2).

3.2.3 Gene content

Consistent with previous reports (e.g., Martin et al. 2007; Winkworth et al., 2022), all the newly assembled oomycete mitogenomes shared the same core set of 39 protein coding, 25 tRNA, and two rRNA genes. However, total gene numbers for the 135 included mitogenomes ranged from 65 (e.g., *Phytophthora andina*, *Phytophthora mirabilis*) to 116 (e.g., *Pythium lycopersicum*, *Pythium oligandrum*). Differences in total gene numbers reflected a combination of individual gene losses and gene duplications associated with sequence repeats (Table 3.1).

Of the included Peronosporaceae mitogenomes, 70% (44/63) contained the 66 genes of the core set. The remaining 30% (19/63) had either lost the *ymf101* gene (e.g., *Phytophthora andina*, *Phytophthora mirabilis*) and therefore contained 65 genes or had gained one to six genes

Table 3.3 Summary statistics for the large inverted repeat of the included members of Pythiaceae, Salisapiliaceae, Lagenidiaceae, Albuginaceae and Saprolegniaceae

Species	Repeat Length (bp)	Inverted/Direct	No of Genes	Single Copy Region (V1)
Pythiaceae				
Halophytophthora				
Halophytophthora batemanensis	24,239	Inverted	45	1,188 bp
Halophytophthora polymorphica	25,292	Inverted	46	197 bp
Clade K (*Phytopythium*)				
Phytopythium aichiense	25,188	Inverted	45	24 bp
Phytopythium boreale	25,046	Inverted	45	33 bp
Phytopythium chamaehyphon	25,050	Inverted	45	34 bp
Phytopythium helicoides	25,257	Inverted	45	110 bp
Phytopythium sp. cucurbitacearum	24,152	Inverted	45	30 bp
Phytopythium vexans	24,164[a]	Inverted	45	Overlapping (48,328 bp)
Globisporangium				
Clade G				
Globisporangium barbulae	21,379	Inverted	42	*nad1, nad11*
Globisporangium cederbergense	27,168	Inverted	43	*nad11, nad1*
Globisporangium iwayamai	25,239	Inverted	45	518 bp
Globisporangium okanoganense	26,886	Inverted	44	*nad11*
Globisporangium nagaii	20,167	Inverted	42	*nad11, nad1, nad4L*
Clade F				
Globisporangium cylindrosporum	23,801[a]	Inverted	45	Overlapping (47,602 bp)
Globisporangium irregulare	23,778[a]	Inverted	45	Overlapping (47,556 bp)
Globisporangium mamillatum	23,904	Inverted	45	48 bp
Globisporangium debaryanum	24,136	Inverted	42	*nad11, nad1, nad4L*

Globisporangium emineosum	20,526	Inverted	42	*nad4L, nad1, nad11*
Clade E				
Globisporangium erinaceum	23,612	Inverted	45	494 bp
Globisporangium radiosum	23,613	Inverted	45	495 bp
Globisporangium camurandrum	23,473	Inverted	45	79 bp
Globisporangium middletonii	22,288	Inverted	42	*nad4L, nad1, nad11*
Globisporangium rhizosaccharum	20,917	Inverted	42	*nad11, nad1, nad4L*
Clade J				
Globisporangium nunn	22,348	Inverted	42	*nad4L, nad1, nad11*
Globisporangium orthogonon	22,313	Inverted	42	*nad4L, nad1, nad11*
Globisporangium acanthophoron	20,782	Inverted	42	*nad11, nad1, nad4L*
Globisporangium perplexum	22,677	Inverted	44	*nad11*
Clade I				
Globisporangium ultimum	21,950	Inverted	43	*nad11, nad1*
Globisporangium solare	23,309	Inverted	44	*nad11*
Globisporangium splendens	21,657	Inverted	42	*nad4L, nad1, nad11*
Globisporangium heterothallicum	20,747	Inverted	42	*nad11, nad1, nad4L*
Clade H (*Elongisporangium*)				
Elongisporangium dimorphum	25,285	Inverted	45	93 bp
Elongisporangium senticosum	25,697[a]	Inverted	45	Overlapping (51,374 bp)
Elongisporangium anandrum	24,968	Inverted	44	*nad11*
Elongisporangium prolatum	22,247[a]	Inverted	43	Overlapping (44,494 bp)
Pilasporangium				
Pilasporangium apinafurcum	20,287	Inverted	42	*nad11, nad1, nad4L*
Salisapiliaceae				
Salisapilia				

Salisapilia sapeloensis	18,227	Inverted	39	*nad11, nad1, nad4L, nad5*
Pythiaceae cont.				
Pythium				
Clade B				
Pythium aristosporum	30,864	Inverted	47	21 bp
Pythium arrhenomanes	30,823	Inverted	47	32 bp
Pythium phragmiticola	30,697	Inverted	48	119 bp
Pythium vanterpoolii	24,949	Inverted	42	*cox1, cox2, nad11, nad1, nad4L*
Pythium graminicola	23,500	Inverted	41	*tRNA-Trp, cox1, cox2, nad11, nad1, nad4L*
Pythium plurisporium	24,277	Inverted	42	*nad4L, nad1, nad11, cox1, cox2*
Pythium rishiriense	27,159	Inverted	47	*cox1, cox2*
Pythium torulosum	28,469	Inverted	46	*cox2*
Pythium myriotylum	29,554	Inverted	45	64 bp
Pythium pyrilobum	28,297	Inverted	45	*cox2, cox1*
Pythium dissotocum	27,803	Inverted	46	*nad5*
Pythium sukuiense	26,279	Inverted	46	*nad5*
Pythium brachiatum	31,280	Inverted	48	2,158 bp
Clade A				
Pythium monospermum	32,635	Inverted	48	401 bp
Pythium porphyrae	31,860	Inverted	47	*cox1, cox2*
Pythium aphanidermatum	18,894	Inverted	37	*cox2, cox1, tRNA-Trp, nad11, nad1, nad4L, atp9, nad5*
Clade C				
Pythium insidiosum	18,266	Inverted	40	*nad4L, nad1, nad11, cox2, cox1, tRNA-Trp, nad5*
Clade D				
Pythium lycopersicum	30,146	Inverted	50	182 bp

Pythium oligandrum	30,666	Inverted	50	8,169 bp
Pythium amasculinum	30,140	Inverted	50	213 bp
Pythium grandisporangium	30,703	Inverted	50	838 bp
Lagenidiaceae				
Lagenidium				
Lagenidium giganteum	24,096	Inverted	46	5 bp
Albuginaceae				
Albugo				
Albugo candida	25,625[a]	Inverted	47	Overlapping (51,250 bp)
Albugo laibachii	26,015[a]	Inverted	47	Overlapping (52,030 bp)
Saprolegniaceae				
Aphanomyces				
Aphanomyces frigidophilus	14,548[a]	Inverted	19	Overlapping (29,096 bp)
Aphanomyces invadans	12,367	Inverted	18	*nad11*
Aphanomyces astaci	12,570	Inverted	18	*nad11*
Aphanomyces cochlioides	7,304	Inverted	2	17 genes
Aphanomyces euteiches	6,175	Inverted	2	17 genes
Aphanomyces sp. NJM 9510	12,431	Inverted	18	*nad11*
Saprolegnia				
Saprolegnia diclina	8,353	Inverted	11	17 genes
Saprolegnia parasitica	8,370	Inverted	11	17 genes
Saprolegnia ferax	8,618	Inverted	11	17 genes
Achlya				
Achlya hypogyna	8,289[b]	Inverted	11(8)[c]	17 genes
Thraustotheca				
Thraustotheca clavata	9,302[b]	Inverted	11(8)[c]	17 genes

[a] Half of the duplicated material in a overlapping repeat

[b] Overall size of degraded repeat structure

[c] Total genes in a repeat copy (total genes in a repeat copy excluding degraded genes)

Table 3.4 Summary statistics for duplicated sequences in Peronosporaceae

Species	Repeat(s) Length (bp)	Inverted/Direct	No of Genes	Genes
Peronosporaceae				
Clade 16				
Plasmopara muralis	98	Inverted	1	*tRNA-Lys*
Plasmopara viticola	299	Inverted	2	*tRNA-Ala, tRNA-Lys*
Plasmopara nivea	456	Inverted	2	*tRNA-Ala, tRNA-Lys*
Plasmopara halstedii	341	Inverted	2	*tRNA-Lys, tRNA-Ala*
Bremia lactucae	394, 185	Direct, Inverted	1	*tRNA-Lys*
Clade 15				
Peronospora tabacina	298, 286	Inverted, Direct	0	Non-coding
Peronospora effusa	464, 205, 204	Inverted	0	Non-coding
Sclerospora graminicola	2,500	Inverted	0	Non-coding
Phytophthora podocarpi	80	Direct	1	*tRNA-Lys*
Clade 6				
Phytophthora pinifolia	4,588	Inverted	6	*atp6, tRNA-Asp, nad3, nad5, nad6, tRNA-Arg*
Clade 7				
Phytophthora × alni	1,109	Inverted	1	*cox2*
Phytophthora × cambivora	5,442, 170	Direct, Inverted	0	Non-coding
Phytophthora fragariae	2,385	Inverted	0	Non-coding
Phytophthora rubi	2,986	Inverted	1	*nad4L*

Clade 8				
Phytophthora ramorum	1150, 192	Inverted, Direct	1	*tRNA-Arg*
Phytophthora lateralis	1,038	Inverted	1	*tRNA-Arg*
Clade 9				
Phytophthora fallax	814	Inverted	0	Non-coding
Phytophthora captiosa	984	Inverted	0	Non-coding
Clade 10				
Phytophthora boehmeriae	91	Direct	1	*tRNA-Met*
Phytophthora kernoviae	180	Inverted	2	*tRNA-Lys, tRNA-Ala*
Nothophytophthora				
Nothophytophthora sp.	130, 81	Direct, Inverted	2	*tRNA-Met; tRNA-Met*

as the result of sequence repeats (e.g., *Phytophthora boehmeriae*, *Phytophthora pinifolia*) (Table 3.4). In 67% (14/21) of the repeat containing mitogenomes, the repeats contained one or more genes. Of these, 79% (11/14) contained one or two tRNA genes (e.g., *Plasmopara muralis*) with the remaining 21% containing either protein-coding genes (e.g., *Phytophthora rubi*) or a combination of protein-coding and tRNA genes (e.g., *Phytophthora pinifolia*) (Table 3.4).

For the other oomycete groups, the gene content of the included mitogenome sequences was expanded as the result of the inverted repeats. In the Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae the inverted repeats are broadly comparable in terms of gene content; typically 37-50 genes, including protein coding, tRNA, and rRNA genes (Table 3.3). In Pythiaceae, the large inverted repeats of several taxa contain additional copies of particular tRNA genes; these appear to be the result of additional duplication events. For example, duplicate copies of genes for *tRNA-Met* and *tRNA-Glu* are present in the inverted repeats of *Halophytophthora polymorphica* and *Pythium porphyrae*, respectively. In Saprolegniaceae, the inverted repeats contain between two and 19 genes (Table 3.3). Minimally, repeats included the two rRNA genes, with various protein-coding and tRNA genes included when gene contents were larger. The mitogenomes of all the included Saprolegniaceae genomes had lost the *ymf100* gene while degradation of parts of the inverted repeat in both *Achlya* and *Thraustotheca* appear to have resulted in genes being lost from one repeat copy (e.g., *rps10*, *nad2*).

3.3 Phylogenetic analyses

3.3.1 Data matrix

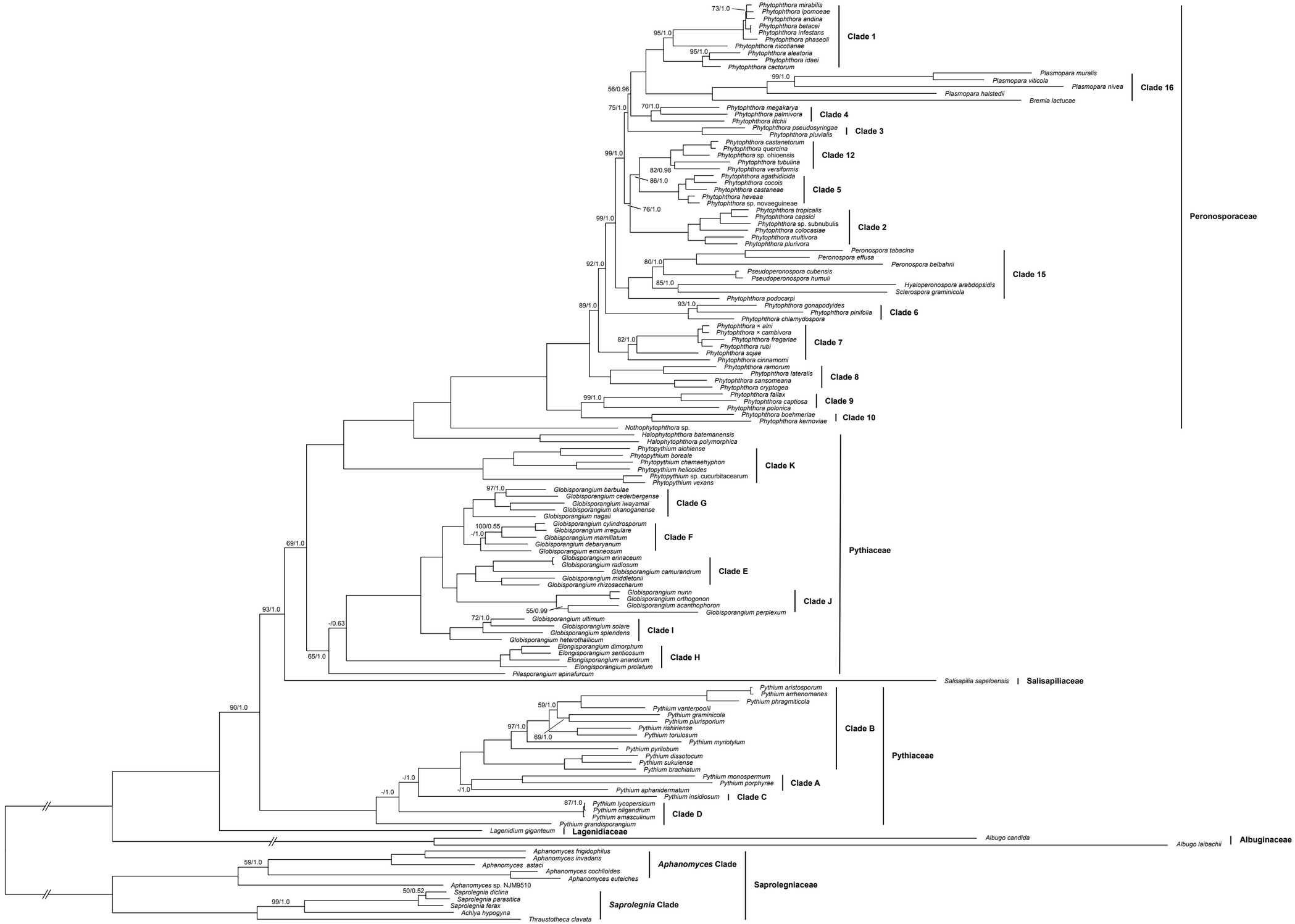
The final data matrix contained 32 gene partitions. The final matrix was 24,584 aligned nucleotide positions in length, of which 13,555 (55.1%) were variable and 11,029 (44.9%) invariant. Gapped characters composed 0.03% of the matrix (978/3,318,840 characters); 15 of the 32 gene partitions (46.9%) contained gaps, with 70.2% of the gaps (687/978) fell within four partitions (i.e., *atp1*, *nad2*, *ssRNA* and tRNA).

Using ModelFinder the 32 gene partitions were aggregated into 11 data partitions for phylogenetic analysis. The largest of these partitions included eight gene partitions and the two smallest a single gene each (Appendix IV).

3.3.2 Bayesian analysis

The sampled pool for each of the replicate Bayesian runs included 60,002 trees with the 95% credible tree set for each including 51-53 trees. The majority-rule consensus of the combined pool of sampled Bayesian trees was a well-resolved and generally well-supported topology (Figure 3.1). Posterior probabilities for 94.7% (124/131) of the inferred relationships were

Figure 3.1 Phylogenetic relationships within oomycetes based on analyses of the combined 32-gene mitochondrial sequence matrix. The topology is that recovered by Bayesian analyses with branch lengths proportional to the mean of the corresponding posterior probability density. Values associated with branches are maximum likelihood bootstrap support (left) and Bayesian posterior probabilities (right); values are only reported where bootstrap support was <100%. Previously recognised clades (e.g., Bourret et al., 2018; Lévesque and De Cock, 2004) and family-level taxa, as defined by the NCBI taxonomy browser (Schoch et al., 2020), are indicated on the right.


Phytophthora mirabilis
Phytophthora ipomoeae
Phytophthora andina
Phytophthora betacei
Phytophthora infestans
Phytophthora phaseoli
Phytophthora nicotianae
Phytophthora aleatoria
Phytophthora idaei
Phytophthora cactorum
Clade 1
Plasmopara muralis
Plasmopara viticola
Plasmopara nivea
Plasmopara halstedii
Bremia lactucae
Clade 16
Phytophthora megakarya
Phytophthora palmivora
Phytophthora litchii
Clade 4
Phytophthora pseudosyringae
Phytophthora pluvialis
Clade 3
Phytophthora castanetorum
Phytophthora quercina
Phytophthora sp. ohioensis
Phytophthora tubulina
Phytophthora versiformis
Clade 12
Phytophthora agathidicida
Phytophthora cocois
Phytophthora castaneae
Phytophthora heveae
Phytophthora sp. novaeguineae
Clade 5
Phytophthora tropicalis
Phytophthora capsici
Phytophthora sp. subnubulis
Phytophthora colocasiae
Phytophthora multivora
Phytophthora plurivora
Clade 2
Peronospora tabacina
Peronospora effusa
Peronospora belbahrii
Pseudoperonospora cubensis
Pseudoperonospora humuli
Hyaloperonospora arabdopsidis
Sclerospora graminicola
Clade 15
Phytophthora podocarpi
Phytophthora gonapodyides
Phytophthora pinifolia
Phytophthora chlamydospora
Clade 6
Phytophthora × alni
Phytophthora × cambivora
Phytophthora fragariae
Phytophthora rubi
Phytophthora sojae
Phytophthora cinnamomi
Clade 7
Phytophthora ramorum
Phytophthora lateralis
Phytophthora sansomeana
Phytophthora cryptogea
Clade 8
Phytophthora fallax
Phytophthora captiosa
Phytophthora polonica
Clade 9
Phytophthora boehmeriae
Phytophthora kernoviae
Clade 10
Peronosporaceae
Nothophytophthora sp.
Halophytophthora batemanensis
Halophytophthora polymorphica
Phytopythium aichiense
Phytopythium boreale
Phytopythium chamaehyphon
Phytopythium helicoides
Phytopythium sp. cucurbitacearum
Phytopythium vexans
Clade K
Globisporangium barbulae
Globisporangium cederbergense
Globisporangium iwayamai
Globisporangium okanoganense
Globisporangium nagaii
Clade G
Globisporangium cylindrosporum
Globisporangium irregulare
Globisporangium mamillatum
Globisporangium debaryanum
Globisporangium emineosum
Clade F
Globisporangium erinaceum
Globisporangium radiosum
Globisporangium camurandrum
Globisporangium middletonii
Globisporangium rhizosaccharum
Clade E
Globisporangium nunn
Globisporangium orthogonon
Globisporangium acanthophoron
Globisporangium perplexum
Clade J
Globisporangium ultimum
Globisporangium solare
Globisporangium splendens
Globisporangium heterothallicum
Clade I
Elongisporangium dimorphum
Elongisporangium senticosum
Elongisporangium anandrum
Elongisporangium prolatum
Clade H
Pilasporangium apinafurcum
Pythiaceae
Salisapilia sapeloensis
Salisapiliaceae
Pythium aristosporum
Pythium arrhenomanes
Pythium phragmiticola
Pythium vanterpoolii
Pythium graminicola
Pythium plurisporium
Pythium rishiriense
Pythium torulosum
Pythium myriotylum
Pythium pyrilobum
Pythium dissotocum
Pythium sukuiense
Pythium brachiatum
Clade B
Pythium monospermum
Pythium porphyrae
Pythium aphanidermatum
Clade A
Pythium insidiosum
Clade C
Pythium lycopersicum
Pythium oligandrum
Pythium amasculinum
Pythium grandisporangium
Clade D
Pythiaceae
Lagenidium giganteum
Lagenidiaceae
Albugo candida
Albugo laibachii
Albuginaceae
Aphanomyces frigidophilus
Aphanomyces invadans
Aphanomyces astaci
Aphanomyces cochlioides
Aphanomyces euteiches
Aphanomyces Clade
Aphanomyces sp. NJM9510
Saprolegnia diclina
Saprolegnia parasitica
Saprolegnia ferax
Achlya hypogyna
Saprolegnia Clade
Thraustotheca clavata
Saprolegniaceae

1.0 and for only 2.3% (3/131) did support fall below 0.95. Nodes with posterior probabilities were distributed across the phylogeny. For example, the node uniting *Saprolegnia diclina* and *Saprolegnia parasitica* received a posterior probability of 0.52 while that uniting *Elongisporangium* and *Globisporangium* was 0.63 (Figure 3.1).

All of the numbered Peronosporaceae clades represented in the data set were recovered as monophyletic in this analysis (i.e., Clades 1-10, 12, 15 and 16) as were all but one of the named clades within Pythiaceae (i.e., Clades A-C, E-K). All of these clades were supported by posterior probabilities of 1.0 (Figure 3.1). The one exception was Pythium Clade D. In this analysis one member of this clade, *Pythium grandisporangium*, fell sister to a larger clade containing Pythiaceae Clades A, B, and C, as well as the remaining members of Clade D. This arrangement was well supported (posterior probability = 1.0). Previously recognised generic-level groups were also recovered with strong support in the Bayesian analysis. For example, clades corresponding to *Phytopythium* and *Globisporangium* both received posterior probabilities of 1.0. Likewise relationships amongst the named and numbered clades were generally strongly supported (Figure 3.1). In only two cases were support for these relationships not 1.0. Specifically, for the *Elongisporangium*-*Globisporangium* pairing (posterior probability = 0.63) and the grouping of *Phytophthora* Clade 1, 16 and 4 (posterior probability = 0.96). Similarly within the named and numbered clades most relationships were supported by posterior probabilities of 1.0. There were just five exceptions. For example, the pairings of *Phytophthora tubulina* and *Phytophthora versiformis* (posterior probability = 0.98) and *Globisporangium*

acanthophoron and *Globisporangium perplexum* (posterior probability = 0.99).

3.3.3 Maximum likelihood analysis

The IQTREE analysis also resulted in a well-resolved and generally well-supported topology. This topology was very similar to that recovered by the Bayesian analysis. The one exception involved Pythiaceae Clade D. In the maximum likelihood tree this clade was resolved as monophyletic, albeit with relatively weak support (bootstrap support = 55%).

As in the Bayesian analysis there was very strong support for almost all of the relationships suggested by the maximum likelihood analysis. All of the numbered clades within Peronosporaceae as well as all the named clades within Pythiaceae (i.e., Clades A-K plus the generic-level clades) were recovered as monophyletic. Support of these clades was typically strong (bootstrap support = 99-100%) (Figure 3.1). Relationships amongst these groups were generally well supported (bootstrap support = 80-100%) and in just two cases did bootstrap support fall below 70%. The exceptions were again the pairing of *Elongisporangium* and *Globisporangium* (bootstrap support = <50%) and the grouping of *Phytophthora* Clade 1, 16 and 4 (bootstrap support = 56%) (Figure 3.1). Likewise, relationships within the named or numbered clades were also well supported. There were just six cases were bootstrap support fell below 70%. These included the pairings of *Globisporangium acanthophoron* and *Globisporangium perplexum* (bootstrap support = 53%) and *Phytophthora ipomoeae* and *Phytophthora mirabilis* (bootstrap support = 54%) (Figure 3.1).

3.3.4 Concordance factor analysis

Concordance factor values (i.e., gCF and sCF) estimated using IQTREE were typically lower than the bootstrap value for the corresponding branches. The range of values for gCF and sCF were 9.09–100.0 and 27.73–99.28, respectively. However, in both cases more than half of the values were 50.0 or above; specifically, 73.5% (97/132) for gCF and 58.0% (40/69) for sCF. Moreover, the values of gCF and sCF appear to be strongly correlated (Kendall's $\tau = 0.644$, $P = 2.2 \times 10^{-16}$). Both gCF and sCF are also strongly correlated with both branch length and bootstrap values (Kendall's $\tau = 0.4181–0.5923$, $P = 1.15 \times 10^{-12}–2.2 \times 10^{-16}$) and moderately correlated with posterior probabilities (Kendall's $\tau = 0.147–0.169$, $P = 0.0166–0.0480$).

3.4 Genome structure

3.4.1 Syntenies

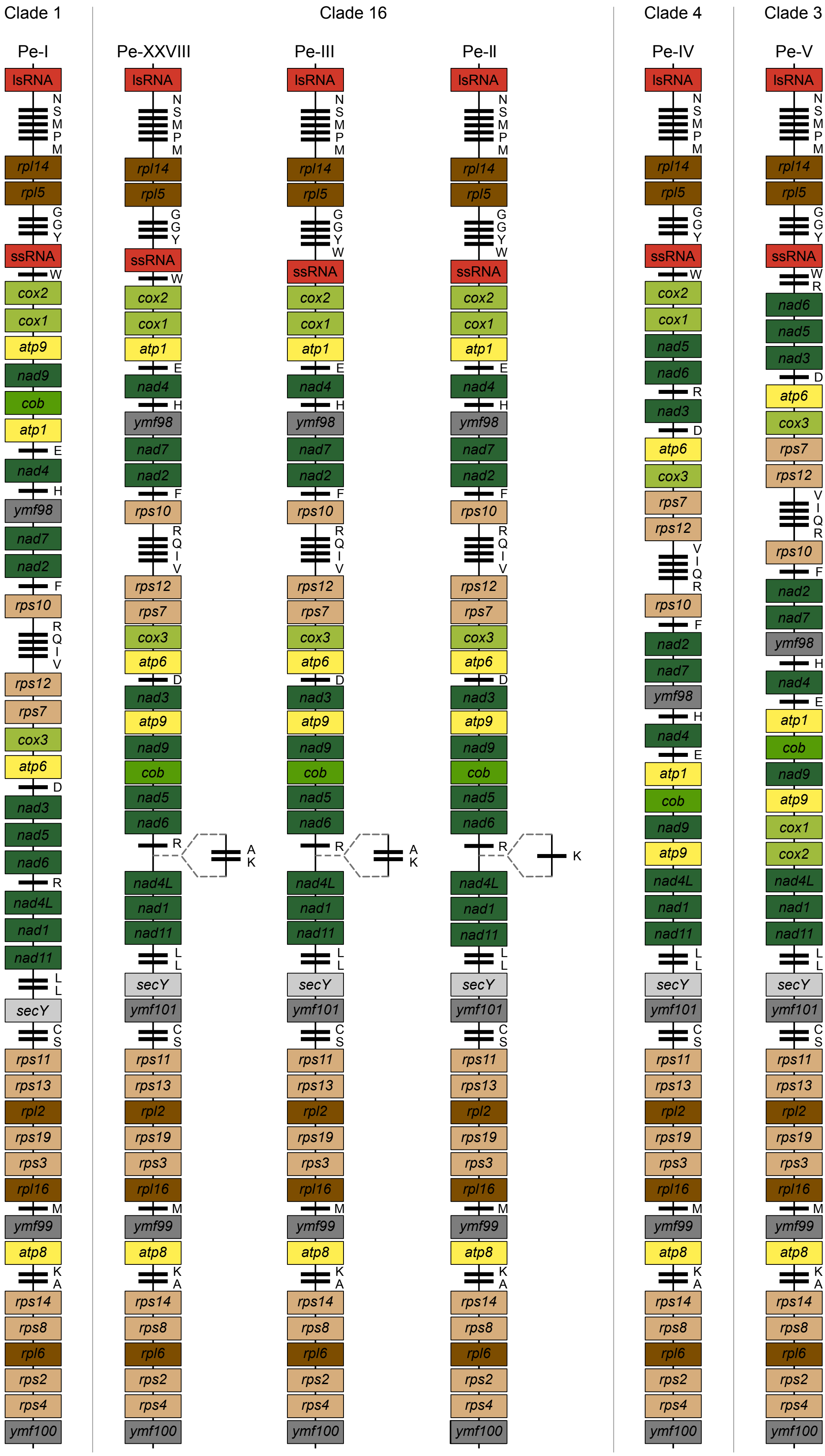
Gene order often differed between the included oomycete mitogenomes. A total of 68 distinct syntenies were identified from the 135 taxa (Figure 3.2). Of these, 59% (40/68) were unique to a single included accession. For example, synteny Pe-XXIX from *Phytophthora boehmeriae* and La-I from *Lagenidium giganteum* (Table 3.5). The remaining 41% (28/68) were shared by multiple accessions. For example, synteny Py-XXVII was shared by *Pythium amasculinum*, *Pythium lycopersicum*, and *Pythium oligandrum*, with synteny Sa-III shared by *Aphanomyces cochlioides* and *Aphanomyces euteiches* (Table 3.5). As in these examples, syntenies were typically shared by members of the same genus. However, in some cases syntenies were shared between genera. For example, *Phytophthora sojae*

and *Peronospora effusa* share synteny Pe-XXII, and *Halophytophthora batemanensis* and *Globisporangium iwayamai* sharing synteny Py-I.

The numbers of syntenies per species were calculated for oomycete families represented by more than two taxa. For Peronosporaceae, Pythiaceae and Saprolegniaceae syntenies per species were 0.46 (29/63), 0.51 (29/57) and 0.64 (7/11), respectively (Table 3.2). This value also varied amongst genera and clades. For example, there were 0.35 (8/23) syntenies per species in *Globisporangium* but 0.81 (17/21) in *Pythium,* and in Peronosporaceae Clade 5 the number of syntenies per species was 0.2 (1/5) but it was 1.0 (6/6) for Clade 7 (Table 3.2).

Figure 3.2 Schematic diagrams illustrating the 68 identified oomycete mitogenome syntenies. Genomes are oriented relative to the large ribosomal subunit with protein encoding and rRNA genes represented by colored rectangles labeled with standard gene abbreviations. Thick black lines represent tRNA genes and these are labeled with the one-letter code for the corresponding amino acid. Transparent gene boxes indicate that a gene copy was identified as partitially degraded the original authors of the sequence. Each synteny is labeled with a two letter abbreviation indicating the family from which it was recovered with Roman numerals used differentiate between syntenies. Order of mitogenomes reflects their relative phylogenetic positions (Figure 3.1). **Peronosporaceae:** Pe-I *Phytophthora mirabilis, Phytophthora andina, Phytophthora ipomoeae, Phytophthora phaseoli*; Pe-XXVIII *Plasmopara muralis, Plasmopara viticola, Plasmopara nivea*; Pe-III *Plasmopara halstedii*; Pe-II *Bremia lactucae*; Pe-IV *Phytophthora megakarya*; Pe-V *Phytophthora pseudosyringae, Phytophthora pluvialis*; Pe-VIII *Phytophthora agathidicida, Phytophthora cocois, Phytophthora castaneae, Phytophthora heveae, Phytophthora* sp. novaeguineae; Pe-VI *Phytophthora tropicalis, Phytophthora capsici, Phytophthora multivora, Phytophthora plurivora*; Pe-VII *Phytophthora* sp. subnubulis*, Phytophthora colocasiae*; Pe-X *Peronospora belbahrii*; Pe-XII *Pseudoperonospora humuli, Pseudoperonospora cubensis*; Pe-IX *Hyaloperonospora arabidopsidis*; Pe-XI *Phytophthora podocarpi*; Pe-XIII *Phytophthora gonapodyides, Phytophthora chlamydospora*; Pe-XIV *Phytophthora pinifolia*; Pe-XV *Phytophthora × alni*; Pe-XVI *Phytophthora × cambivora*; Pe-XVIII *Phytophthora fragariae*; Pe-XIX *Phytophthora rubi*; Pe-XVII *Phytophthora cinnamomi*; Pe-XXIV *Phytophthora ramorum, Phytophthora lateralis*; Pe-XXV *Phytophthora fallax, Phytophthora capitosa*; Pe-XXIX *Phytophthora boehmeriae*; Pe-XXVI *Phytophthora kernoviae*; Pe-XXVII

Nothophytophthora sp.; Pe-XX *Phytophthora betacei, Phytophthora infestans, Phytophthora palmivora*; Pe-XXI *Phytophthora nicotianae, Phytophthora aleatoria, Phytophthora idaei, Phytophthora cactorum, Phytophthora litchii*; Pe-XXII *Phytophthora castanetorum, Phytophthora quercina, Phytophthora* sp. ohioensis*, Phytophthora tubulina, Phytophthora versiformis, Peronospora tabacina, Peronospora effusa, Phytophthora sojae, Phytophthora polonica*; Pe-XXIII *Sclerospora graminicola, Phytophthora sansomeana, Phytophthora cryptogea.* **Pythiaceae:** Py-II *Halophytophthora polymorphica*; Py-III *Phytopythium aichuiense, Phytopythium boreale, Phytopythium chamaehyphon, Phytopythium* sp. cucurbitacearum*, Phytopythium vexans*; Py-IV *Phytopythium helicoides*; Py-V *Globisporangium barbulae*; Py-VI *Globisporangium cederbergense;* Py-XXIX *Globisporangium ultimum*; Py-XI *Elongisporangium prolatum*; Py-I *Halophytophthora batemanensis, Globisporangium iwayamai*; Py-VIII *Globisporangium nagaii, Globisporangium debaryanum, Globisporangium rhizosaccharum, Globisporangium acanthophoron, Globisporangium heterothallicum*; Py-VII *Globisporangium okanoganense, Globisporangium perplexum, Globisporangium solare, Elongisporangium anandrum*; Py-X *Globisporangium emineosum, Globisporangium middletonii, Globisporangium nunn, Globisporangium orthogonon, Globisporangium splendens, Pilasporangium apinafurcum*; Py-IX *Globisporangium cylindrosporum, Globisporangium irregulare, Globisporangium mamillatum, Globisporangium erinaceum, Globisporangium radiosum, Globisporangium camurandrum, Elongisporangium dimorphum, Elongisporangium senticosum.* **Salisapiliaceae:** *Ss-I Salisapilia sapeloensis.* **Pythiaceae:** Py-XII *Pythium aristosporum, Pythium arrhenomanes*; Py-XIII *Pythium phragmiticola*; Py-XIV *Pythium vanterpoolii*; Py-XIX *Pythium myriotylum*; Py-XV *Pythium graminicola*; Py-XVI *Pythium plurisporium*; Py-XVII *Pythium rishiriense*; Py-XVIII *Pythium torulosum*; Py-XX *Pythium pyrilobum*; Py-XXI *Pythium dissotocum, Pythium sukuiense*; Py-XXII *Pythium brachiatum*; Py-XXIII *Pythium monospermum*; Py-XXIV *Pythium porphyrae*; Py-XXV *Pythium aphanidermatum*; Py-XXVI *Pythium insidiosum*; Py-XXVII *Pythium lycopersicum, Pythium oligandrum, Pythium amasculinum*; Py-XXVIII *Pythium grandisporangium*. **Lagenidiaceae:** La-I *Lagenidium giganteum*. **Albuginaceae:** Al-I *Albugo candida, Albugo laibachii*. **Saprolegniaceae:** Sa-I *Aphanomyces frigidophilus*; Sa-II *Aphanomyces invadans, Aphanomyces astaci*; Sa-III *Aphanomyces cochlioides, Aphanomyces euteiches*; Sa-IV *Aphanomyces* sp. NJM 9510; Sa-V *Saprolegnia diclina, Saprolegnia parasitica, Saprolegnia ferax*; Sa-VI *Achlya hypogyna*; Sa-VII *Thraustotheca clavata.*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Clade 16
Clade 4
Clade 3
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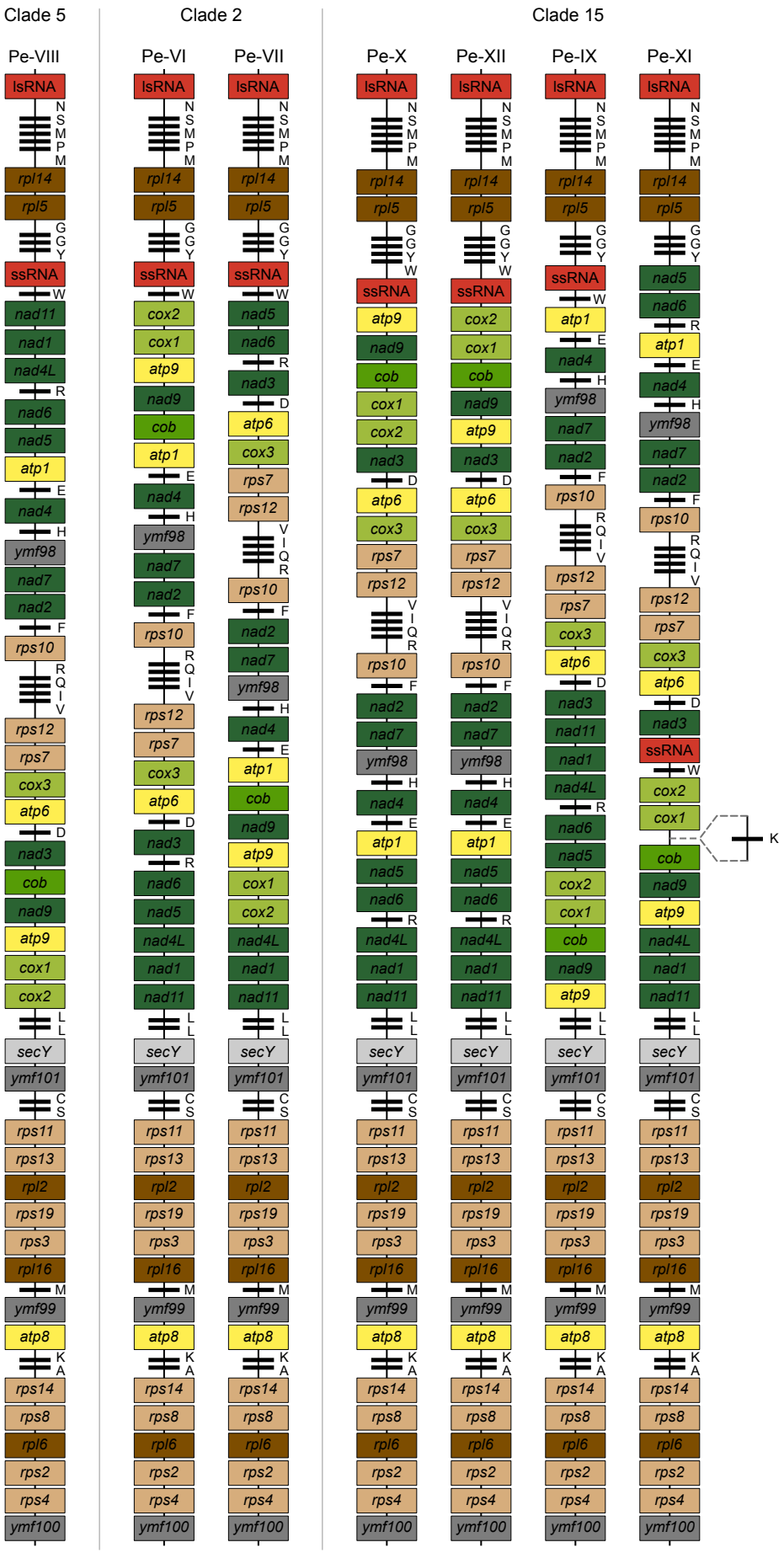
Pe-XXVIII: lsRNA N S M P M rpl14 rpl5 G G Y ssRNA W cox2 cox1 atp1 E nad4 H ymf98 nad7 nad2 F rps10 R Q I V rps12 rps7 cox3 atp6 D nad3 atp9 nad9 cob nad5 nad6 R A K nad4L nad1 nad11 L L secY ymf101 C S rps11 rps13 rpl2 rps19 rps3 rpl16 M ymf99 atp8 K A rps14 rps8 rpl6 rps2 rps4 ymf100
Pe-III: lsRNA N S M P M rpl14 rpl5 G G Y W ssRNA cox2 cox1 atp1 E nad4 H ymf98 nad7 nad2 F rps10 R Q I V rps12 rps7 cox3 atp6 D nad3 atp9 nad9 cob nad5 nad6 R A K nad4L nad1 nad11 L L secY ymf101 C S rps11 rps13 rpl2 rps19 rps3 rpl16 M ymf99 atp8 K A rps14 rps8 rpl6 rps2 rps4 ymf100
Pe-II: lsRNA N S M P M rpl14 rpl5 G G Y W ssRNA cox2 cox1 atp1 E nad4 H ymf98 nad7 nad2 F rps10 R Q I V rps12 rps7 cox3 atp6 D nad3 atp9 nad9 cob nad5 nad6 R K nad4L nad1 nad11 L L secY ymf101 C S rps11 rps13 rpl2 rps19 rps3 rpl16 M ymf99 atp8 K A rps14 rps8 rpl6 rps2 rps4 ymf100
Pe-IV: lsRNA N S M P M rpl14 rpl5 G G Y ssRNA W cox2 cox1 nad5 nad6 R nad3 D atp6 cox3 rps7 rps12 V I Q R rps10 F nad2 nad7 ymf98 H nad4 E atp1 cob nad9 atp9 nad4L nad1 nad11 L L secY ymf101 C S rps11 rps13 rpl2 rps19 rps3 rpl16 M ymf99 atp8 K A rps14 rps8 rpl6 rps2 rps4 ymf100
Pe-V: lsRNA N S M P M rpl14 rpl5 G G Y ssRNA W R nad6 nad5 nad3 D atp6 cox3 rps7 rps12 V I Q R rps10 F nad2 nad7 ymf98 H nad4 E atp1 cob nad9 atp9 cox1 cox2 nad4L nad1 nad11 L L secY ymf101 C S rps11 rps13 rpl2 rps19 rps3 rpl16 M ymf99 atp8 K A rps14 rps8 rpl6 rps2 rps4 ymf100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Clade 2
Clade 15
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Pe-VI
Pe-VII
Pe-X
Pe-XII
Pe-IX
Pe-XI
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GGY
VIQR
RQIV
LL
CS
KA
rpl14
rpl5
nad11
nad1
nad4L
nad6
nad5
atp1
nad4
ymf98
nad7
nad2
rps10
rps12
rps7
cox3
atp6
nad3
cob
nad9
atp9
cox1
cox2
secY
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
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E
H
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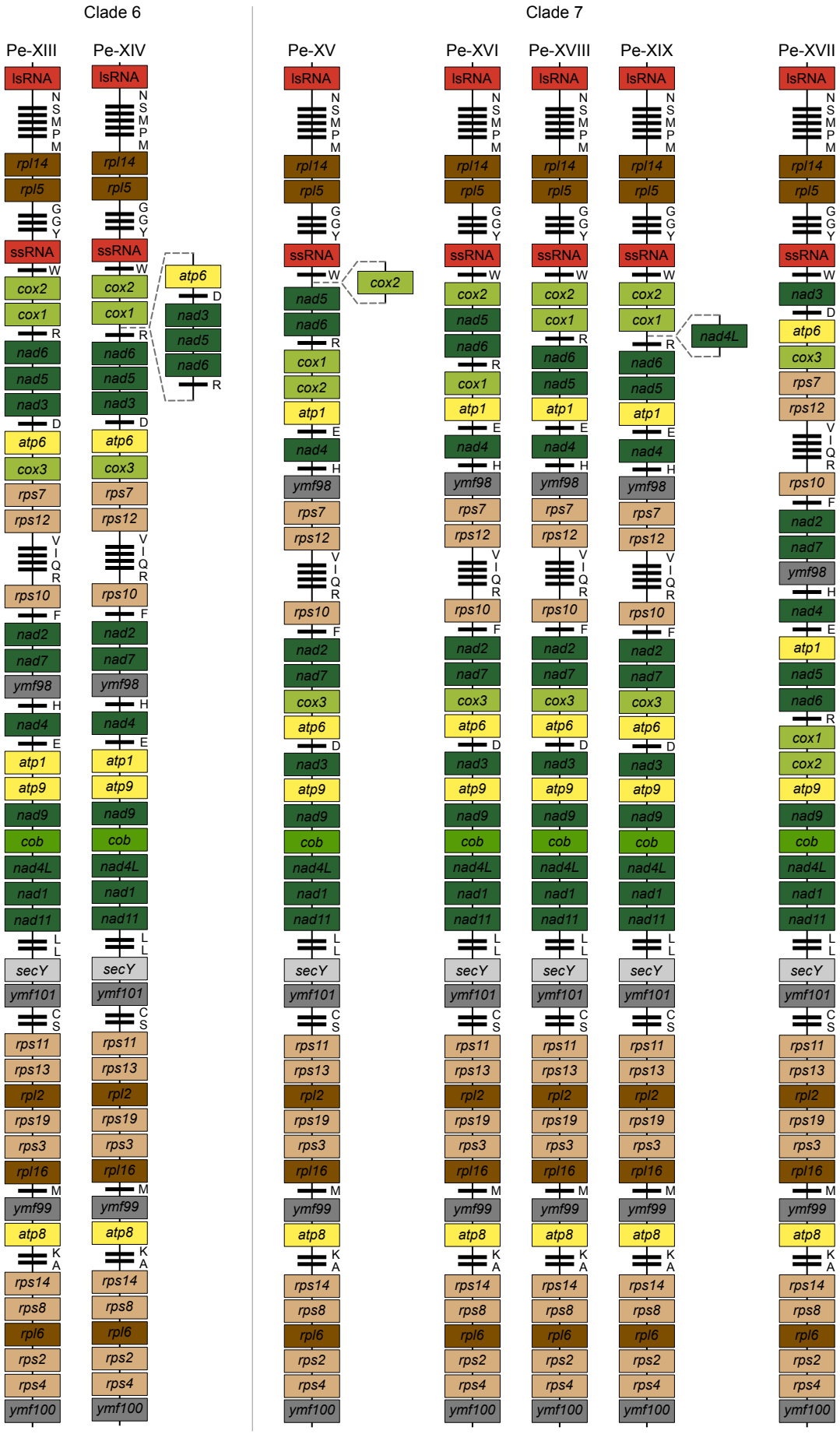
D
R
M
K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Clade 7
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Pe-XIV
Pe-XV
Pe-XVI
Pe-XVIII
Pe-XIX
Pe-XVII
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rpl5
cox2
cox1
nad6
nad5
nad3
atp6
cox3
rps7
rps12
rps10
nad2
nad7
ymf98
nad4
atp1
atp9
nad9
cob
nad4L
nad1
nad11
secY
ymf101
rps11
rps13
rpl2
rps19
rps3
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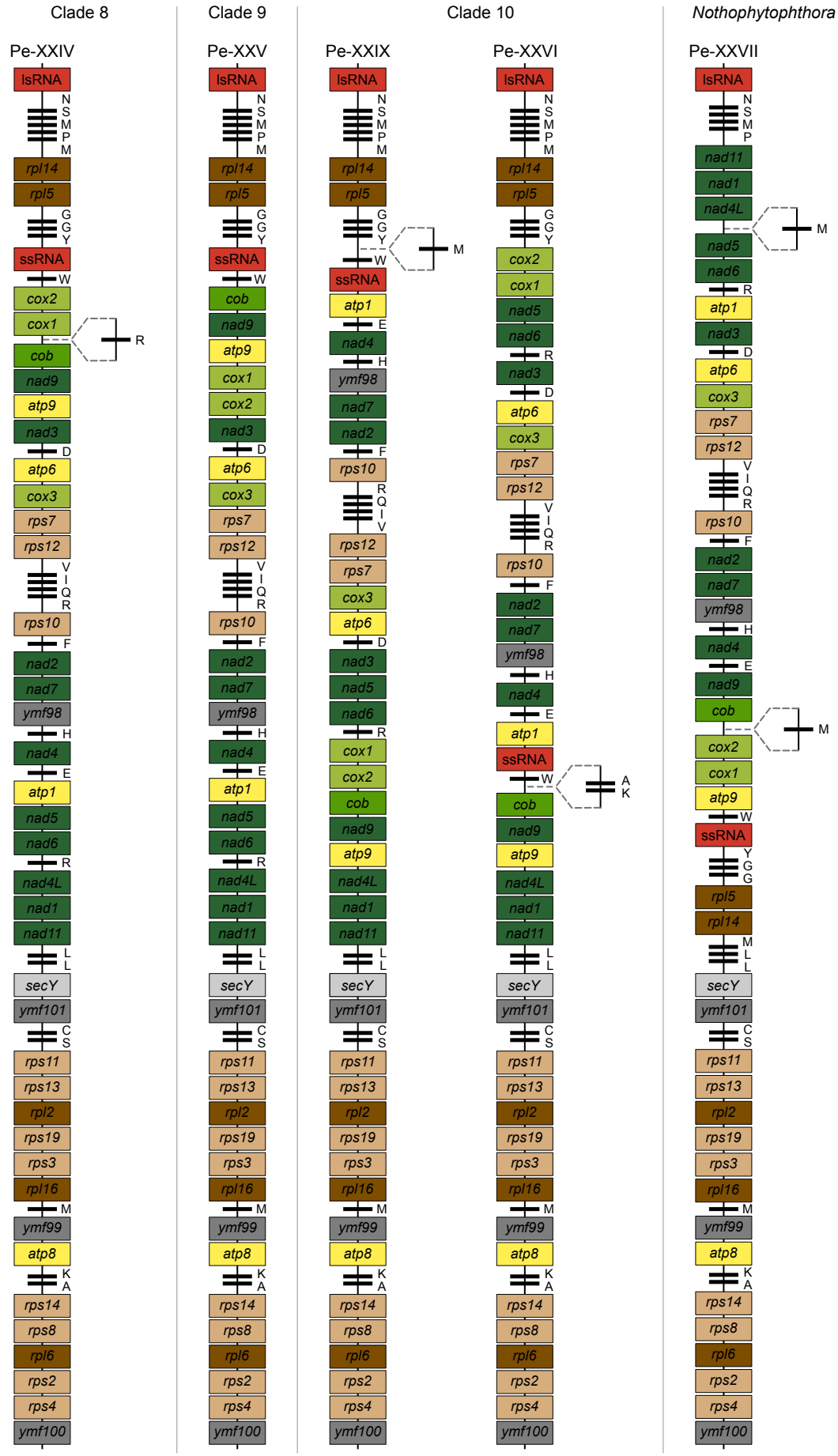
nad4L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Clade 9
Clade 10
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Pe-XXV
Pe-XXIX
Pe-XXVI
Pe-XXVII
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ssRNA
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rpl5
cox2
cox1
cob
nad9
atp9
nad3
atp6
cox3
rps7
rps12
rps10
nad2
nad7
ymf98
nad4
atp1
nad5
nad6
nad4L
nad1
nad11
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ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
atp8
rps14
rps8
rpl6
rps2
rps4
ymf100
nad11
nad1
nad4L
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nad6
atp1
nad3
atp6
cox3
rps7
rps12
rps10
nad2
nad7
ymf98
nad4
nad9
cob
cox2
cox1
atp9
ssRNA
rpl5
rpl14
secY
ymf101
rps11
rps13
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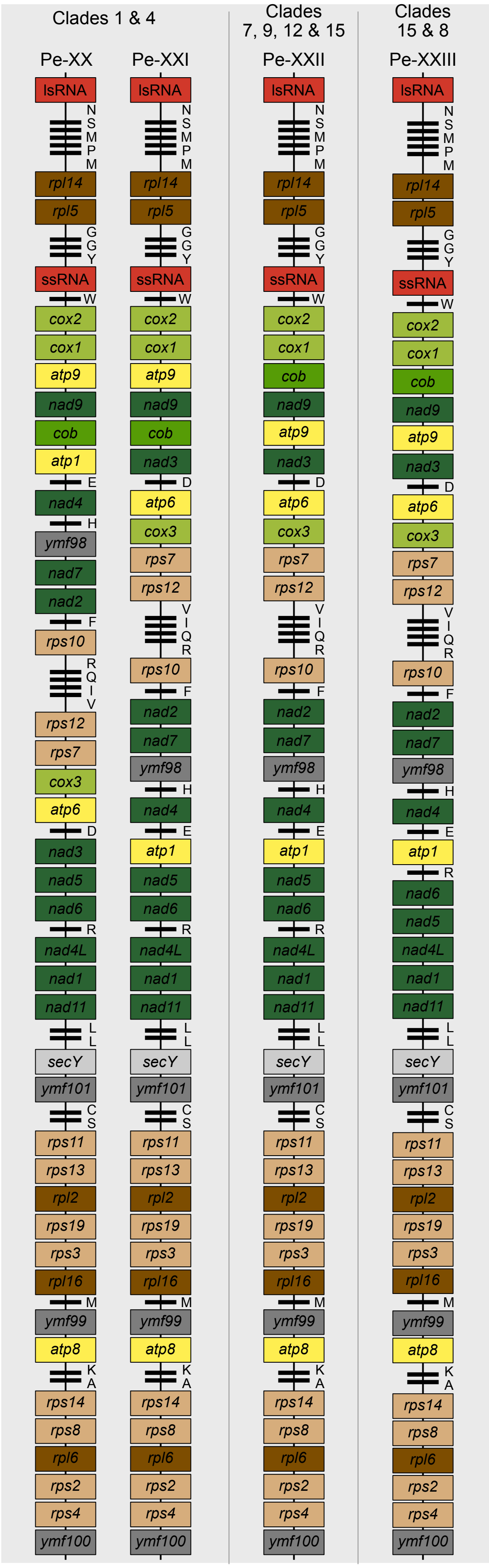
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Clades 7, 9, 12 & 15
Clades 15 & 8
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G
G
Y
ssRNA
W
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cox1
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nad9
cob
atp1
E
nad4
H
ymf98
nad7
nad2
F
rps10
R
Q
I
V
rps12
rps7
cox3
atp6
D
nad3
nad5
nad6
R
nad4L
nad1
nad11
L
L
secY
ymf101
C
S
rps11
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rpl2
rps19
rps3
rpl16
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ymf99
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rps2
rps4
ymf100
Pe-XXI
lsRNA
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S
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P
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rpl14
rpl5
G
G
Y
ssRNA
W
cox2
cox1
atp9
nad9
cob
nad3
D
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cox3
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V
I
Q
R
rps10
F
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nad7
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nad4
E
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nad1
nad11
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C
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Pe-XXII
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nad4
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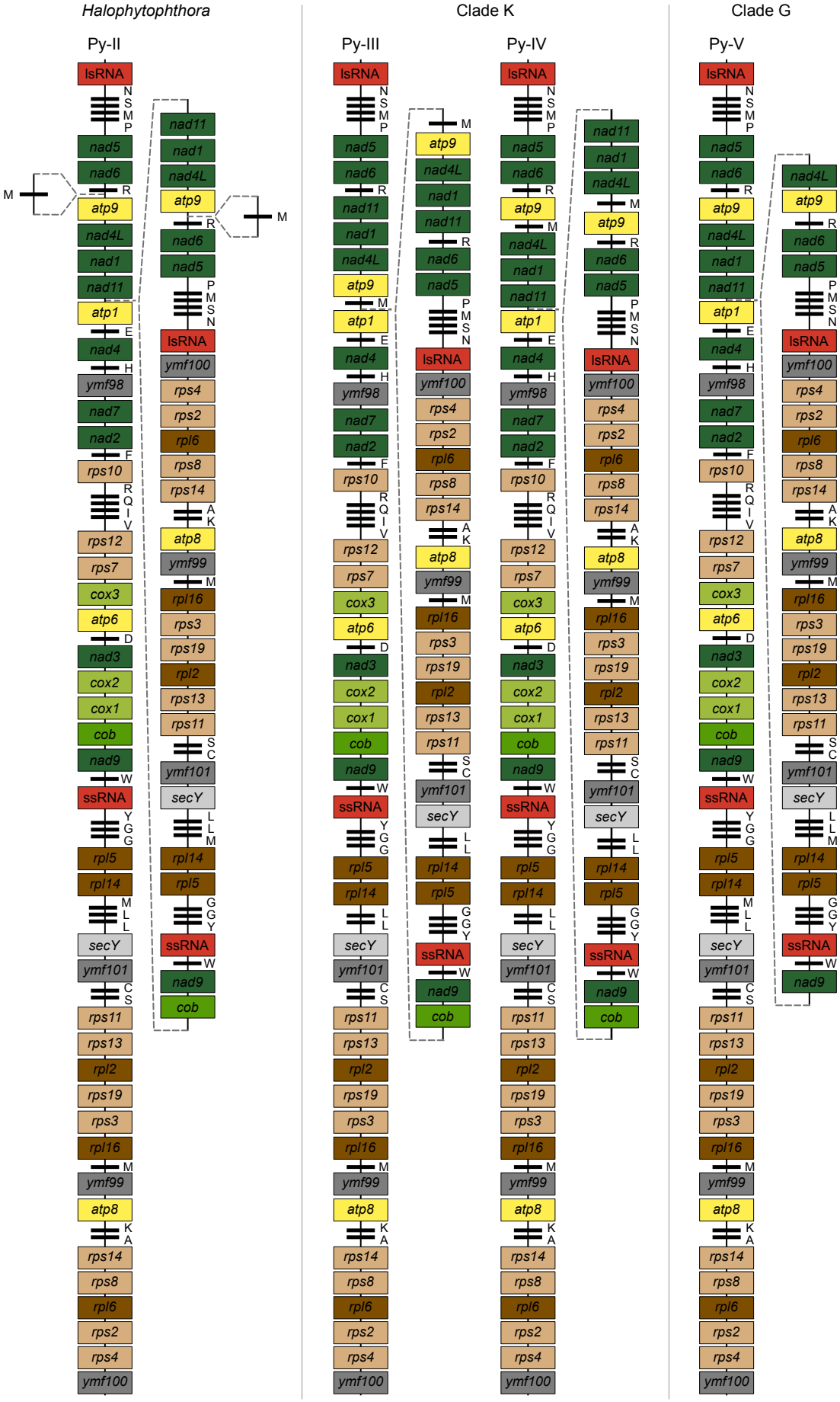
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Clade G
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Py-III
Py-IV
Py-V
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cob
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ymf99
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rps4
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nad6
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ymf99
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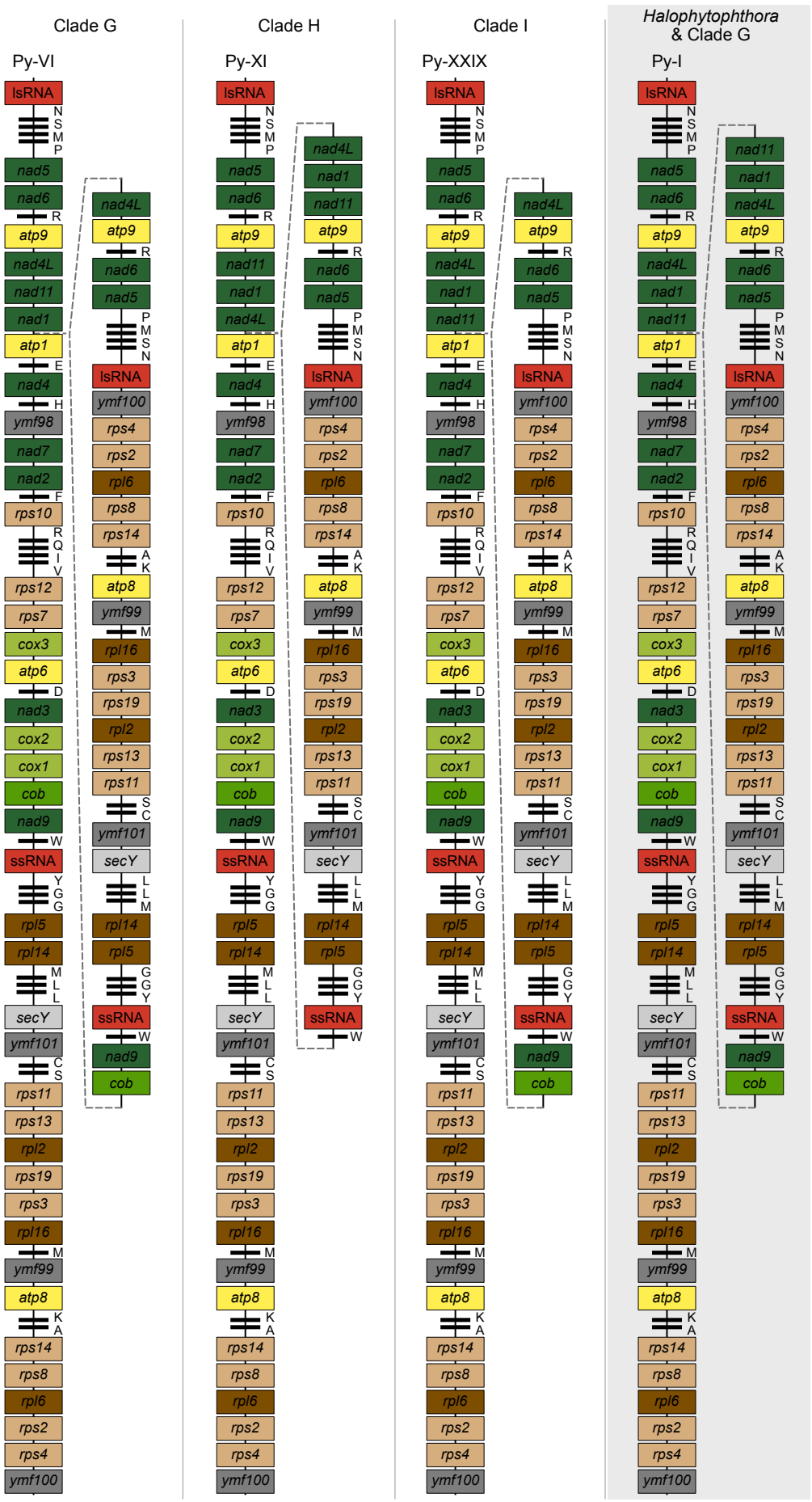
Clade G
Py-VI
Clade H
Py-XI
Clade I
Py-XXIX
Halophytophthora & Clade G
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nad4L
nad11
nad1
atp1
nad4
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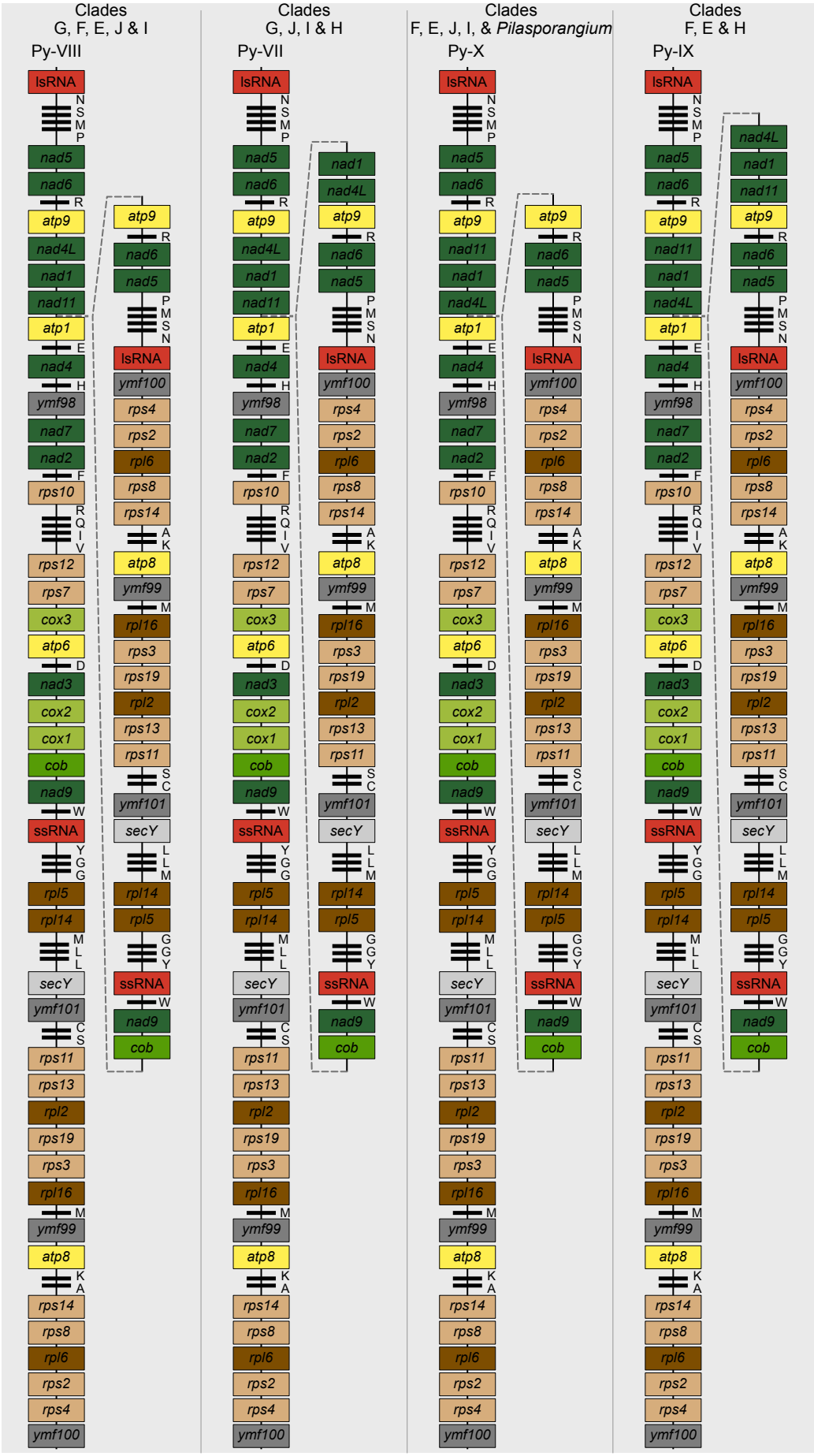
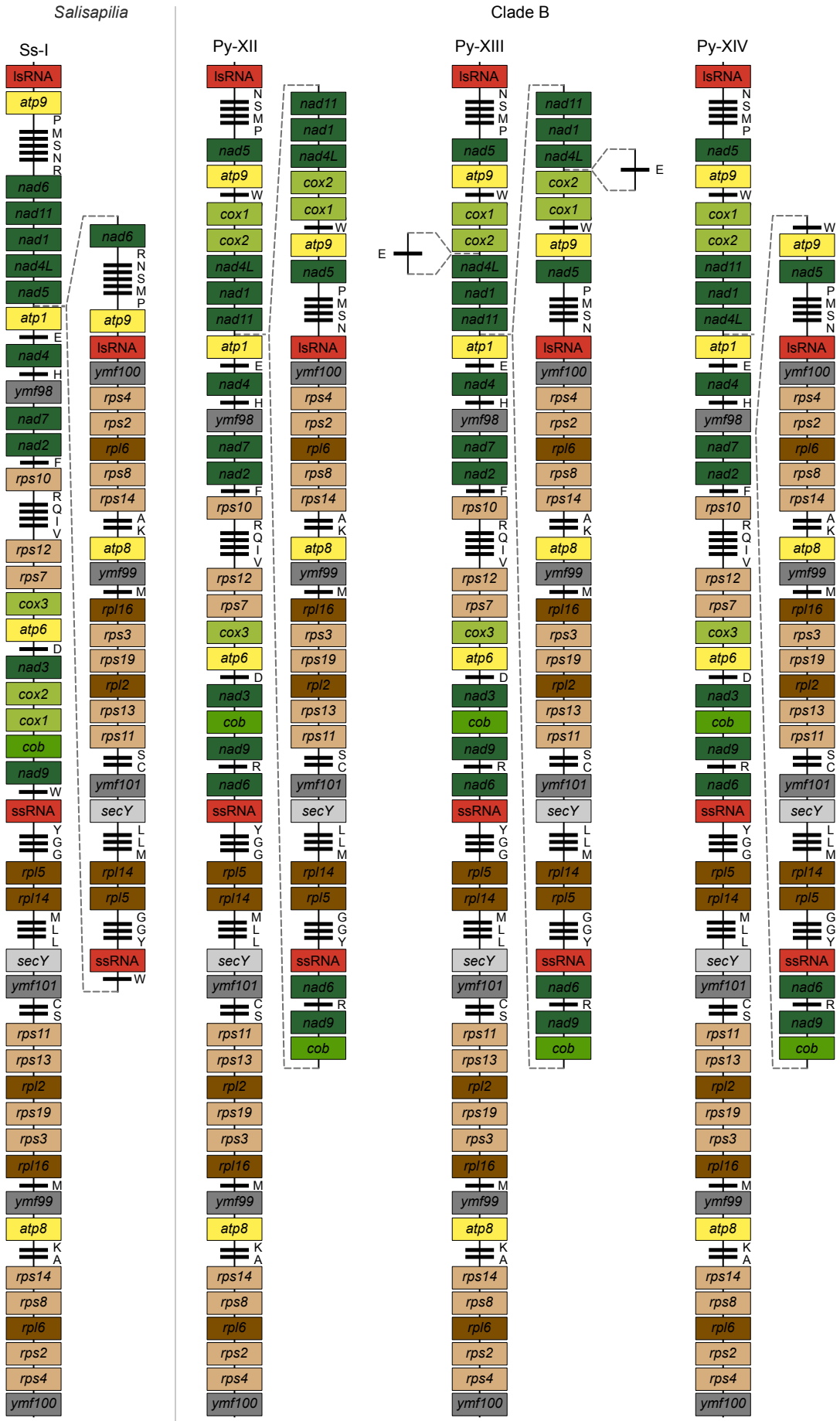
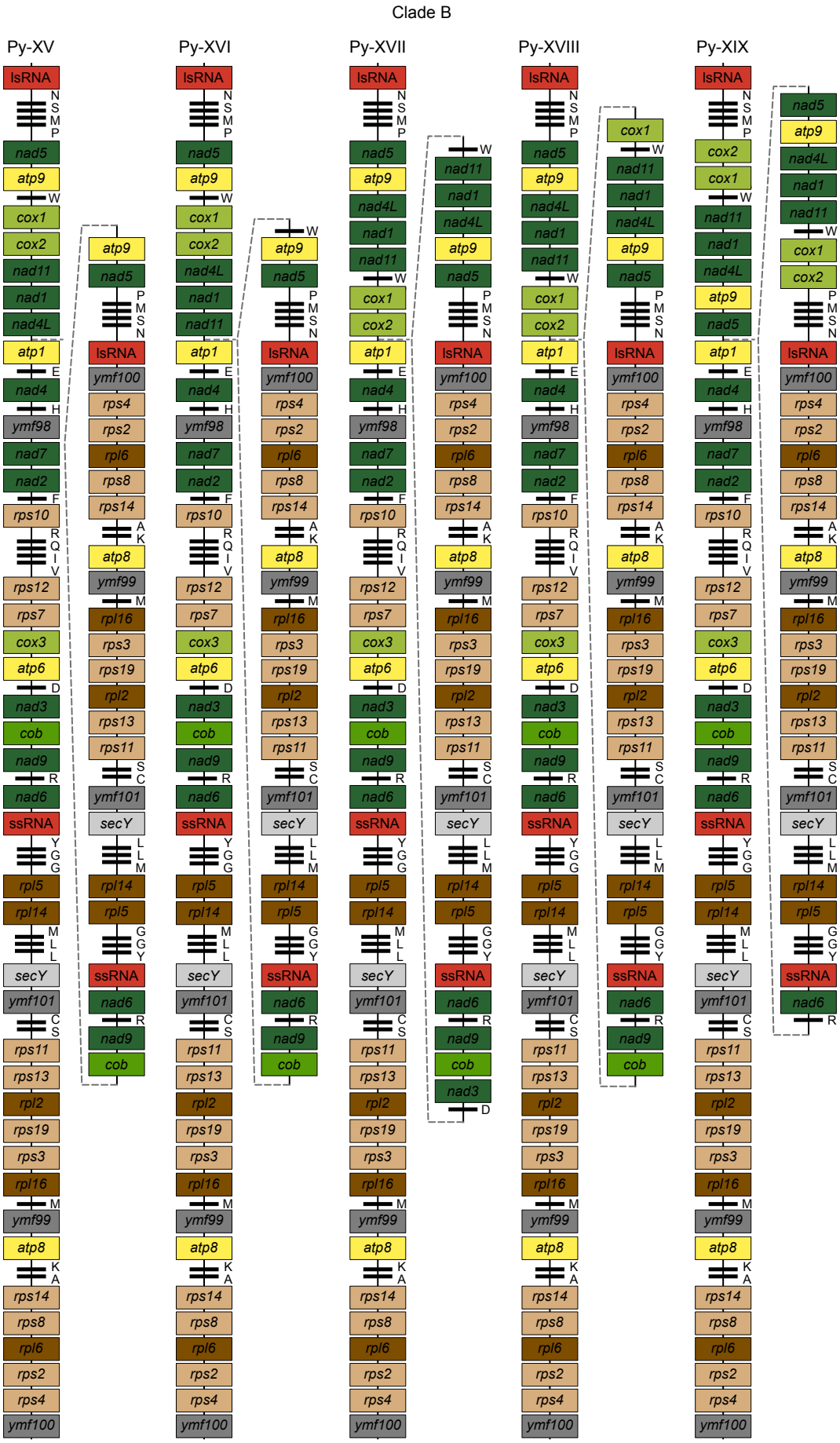
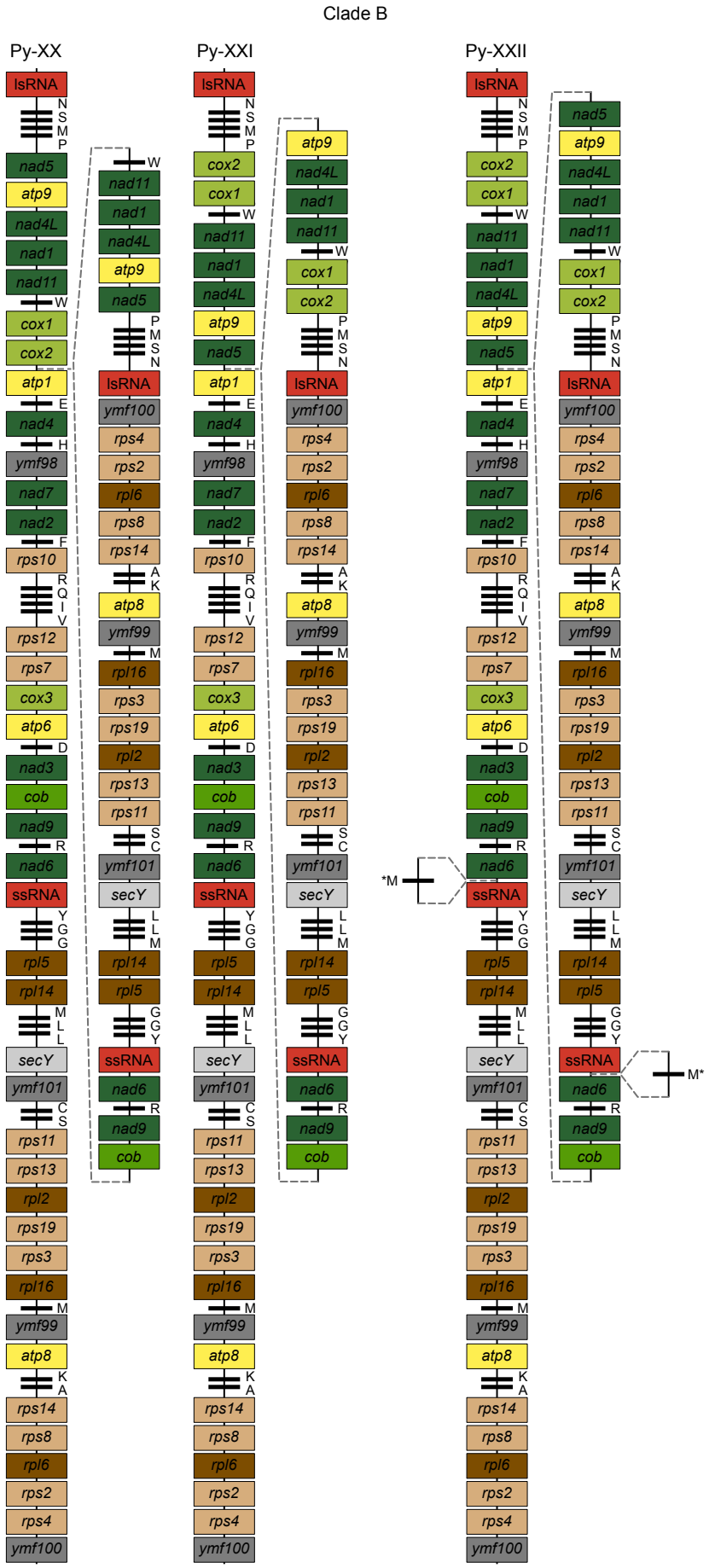
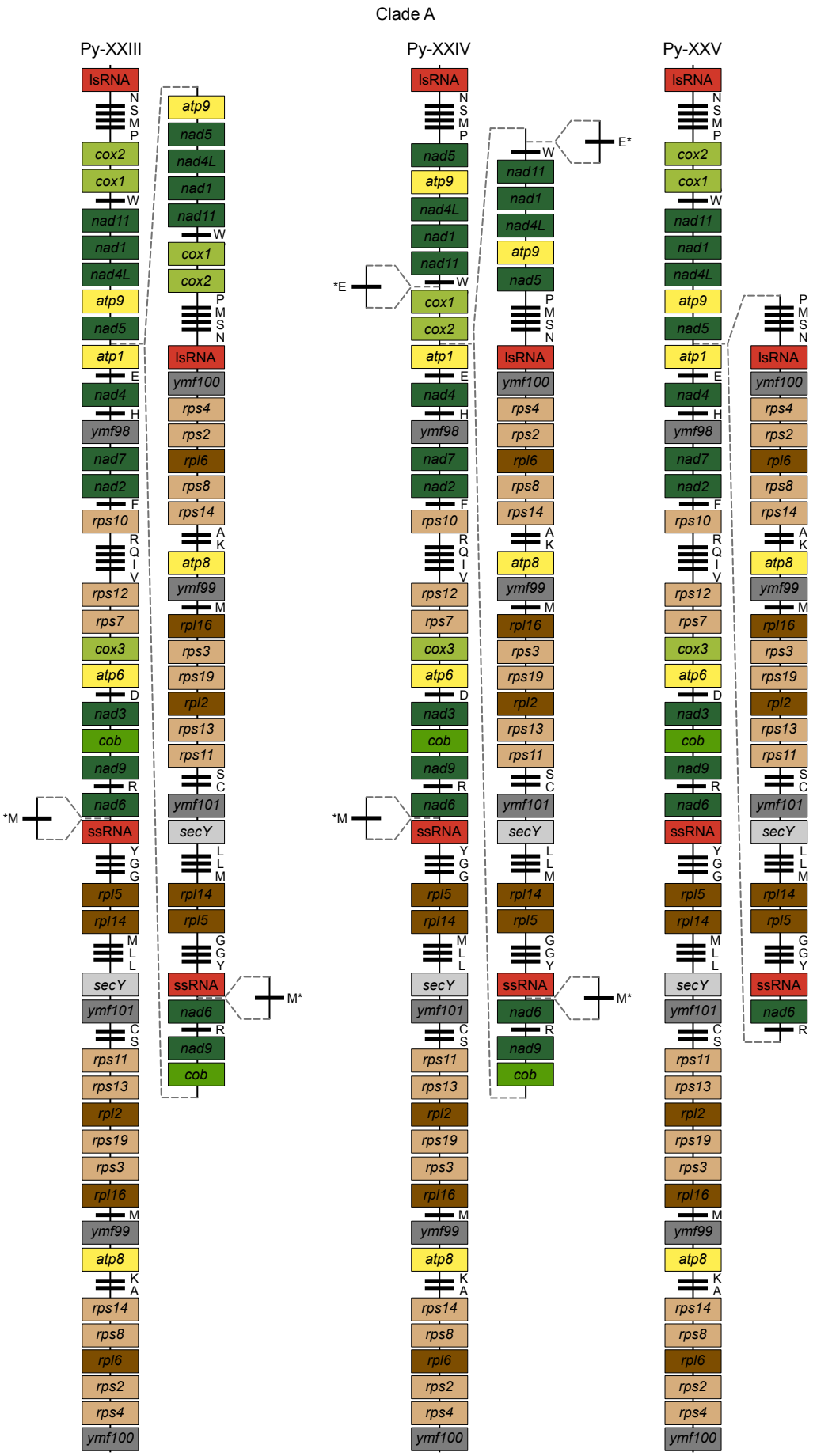
rpl2
rps13
rps11
ymf101
secY
rpl14
rpl5
ssRNA
nad9
cob
nad1
rps12
rps7
cox3
atp6
nad3
cox2
cox1
cob
nad9
ssRNA
rpl5
rpl14
secY
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
atp8
rps14
rps8
rpl6
rps2
rps4
ymf100
rps4
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps3
rps19
rpl2
rps13
rps11
ymf101
secY
rpl14
rpl5
ssRNA
nad9
cob
nad11
nad1
nad4L
atp9
nad6
nad5
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps3
rps19
rpl2
rps13
rps11
ymf101
secY
rpl14
rpl5
ssRNA
nad9
cob

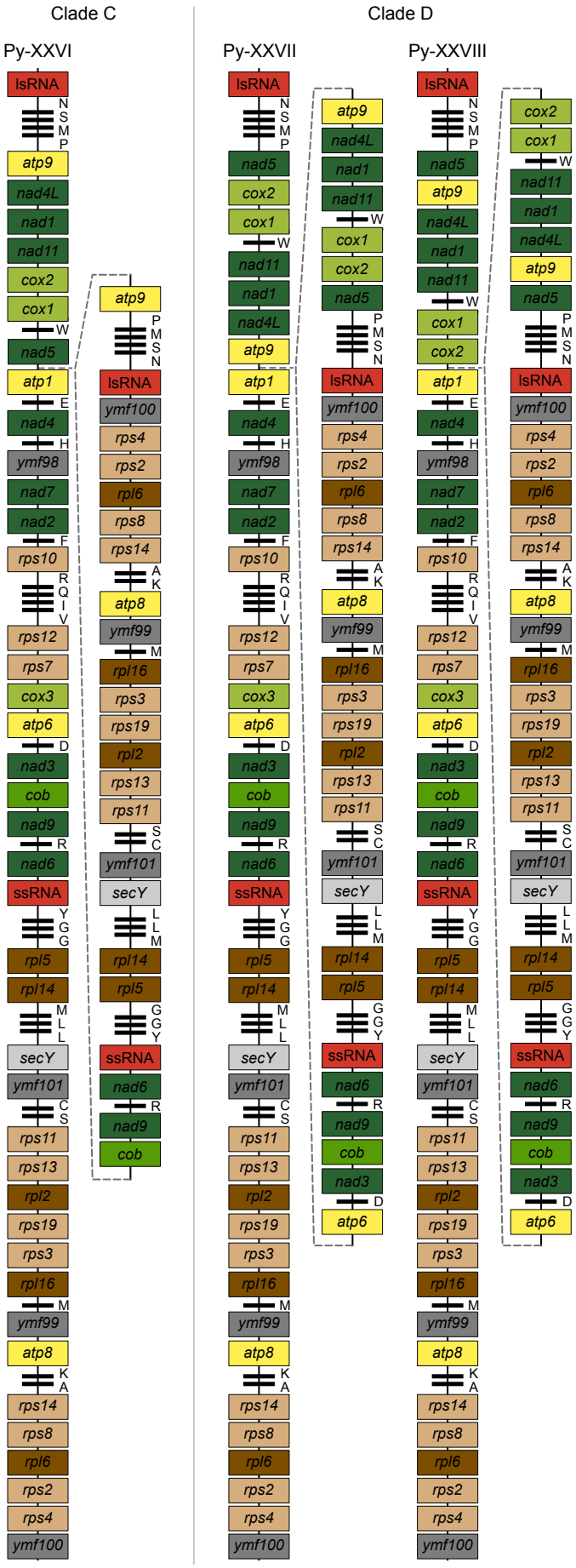

Clades
G, F, E, J & I
Py-VIII
lsRNA
N S M P
nad5
nad6
R
atp9
nad4L
nad1
nad11
atp1
E
nad4
H
ymf98
nad7
nad2
F
rps10
R Q I V
rps12
rps7
cox3
atp6
D
nad3
cox2
cox1
cob
nad9
W
ssRNA
Y G G
rpl5
rpl14
M L L
secY
ymf101
C S
rps11
rps13
rpl2
rps19
rps3
rpl16
M
ymf99
atp8
K A
rps14
rps8
rpl6
rps2
rps4
ymf100
atp9
R
nad6
nad5
P M S N
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
A K
atp8
ymf99
M
rpl16
rps3
rps19
rpl2
rps13
rps11
S C
ymf101
secY
L L M
rpl14
rpl5
G G Y
ssRNA
W
nad9
cob
Clades
G, J, I & H
Py-VII
lsRNA
N S M P
nad5
nad6
R
atp9
nad4L
nad1
nad11
atp1
E
nad4
H
ymf98
nad7
nad2
F
rps10
R Q I V
rps12
rps7
cox3
atp6
D
nad3
cox2
cox1
cob
nad9
W
ssRNA
Y G G
rpl5
rpl14
M L L
secY
ymf101
C S
rps11
rps13
rpl2
rps19
rps3
rpl16
M
ymf99
atp8
K A
rps14
rps8
rpl6
rps2
rps4
ymf100
nad1
nad4L
atp9
R
nad6
nad5
P M S N
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
A K
atp8
ymf99
M
rpl16
rps3
rps19
rpl2
rps13
rps11
S C
ymf101
secY
L L M
rpl14
rpl5
G G Y
ssRNA
W
nad9
cob
Clades
F, E, J, I, & *Pilasporangium*
Py-X
lsRNA
N S M P
nad5
nad6
R
atp9
nad11
nad1
nad4L
atp1
E
nad4
H
ymf98
nad7
nad2
F
rps10
R Q I V
rps12
rps7
cox3
atp6
D
nad3
cox2
cox1
cob
nad9
W
ssRNA
Y G G
rpl5
rpl14
M L L
secY
ymf101
C S
rps11
rps13
rpl2
rps19
rps3
rpl16
M
ymf99
atp8
K A
rps14
rps8
rpl6
rps2
rps4
ymf100
atp9
R
nad6
nad5
P M S N
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
A K
atp8
ymf99
M
rpl16
rps3
rps19
rpl2
rps13
rps11
S C
ymf101
secY
L L M
rpl14
rpl5
G G Y
ssRNA
W
nad9
cob
Clades
F, E & H
Py-IX
lsRNA
N S M P
nad5
nad6
R
atp9
nad11
nad1
nad4L
atp1
E
nad4
H
ymf98
nad7
nad2
F
rps10
R Q I V
rps12
rps7
cox3
atp6
D
nad3
cox2
cox1
cob
nad9
W
ssRNA
Y G G
rpl5
rpl14
M L L
secY
ymf101
C S
rps11
rps13
rpl2
rps19
rps3
rpl16
M
ymf99
atp8
K A
rps14
rps8
rpl6
rps2
rps4
ymf100
nad4L
nad1
nad11
atp9
R
nad6
nad5
P M S N
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
A K
atp8
ymf99
M
rpl16
rps3
rps19
rpl2
rps13
rps11
S C
ymf101
secY
L L M
rpl14
rpl5
G G Y
ssRNA
W
nad9
cob

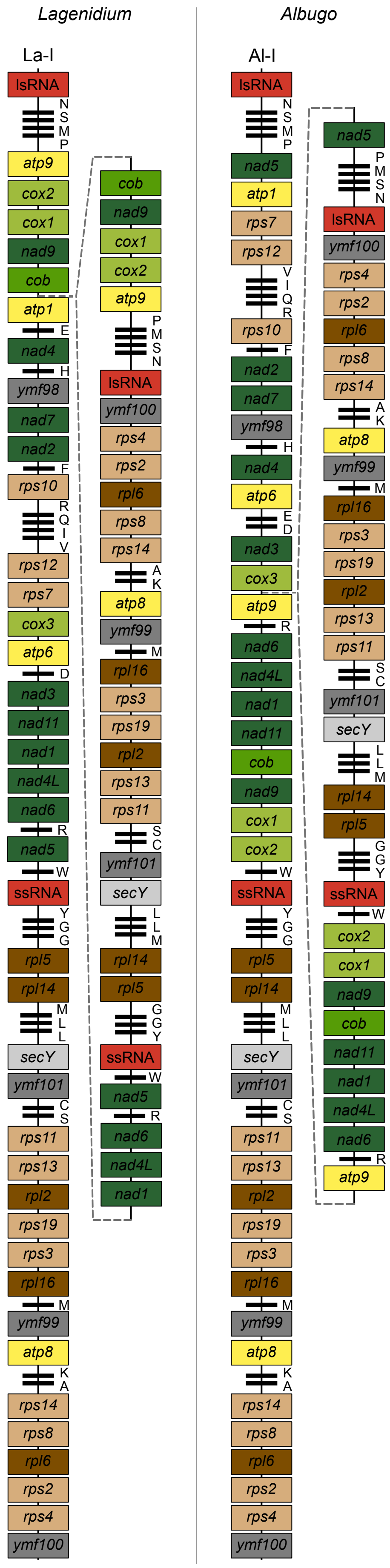

Salisapilia
Clade B
Ss-I
Py-XII
Py-XIII
Py-XIV
lsRNA
atp9
nad6
nad11
nad1
nad4L
nad5
atp1
nad4
ymf98
nad7
nad2
rps10
rps12
rps7
cox3
atp6
nad3
cox2
cox1
cob
nad9
ssRNA
rpl5
rpl14
secY
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
atp8
rps14
rps8
rpl6
rps2
rps4
ymf100
nad11
nad1
nad4L
cox2
cox1
atp9
nad5
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps3
rps19
rpl2
rps13
rps11
ymf101
secY
rpl14
rpl5
ssRNA
nad6
nad9
cob
E


Clade B
Py-XV
Py-XVI
Py-XVII
Py-XVIII
Py-XIX

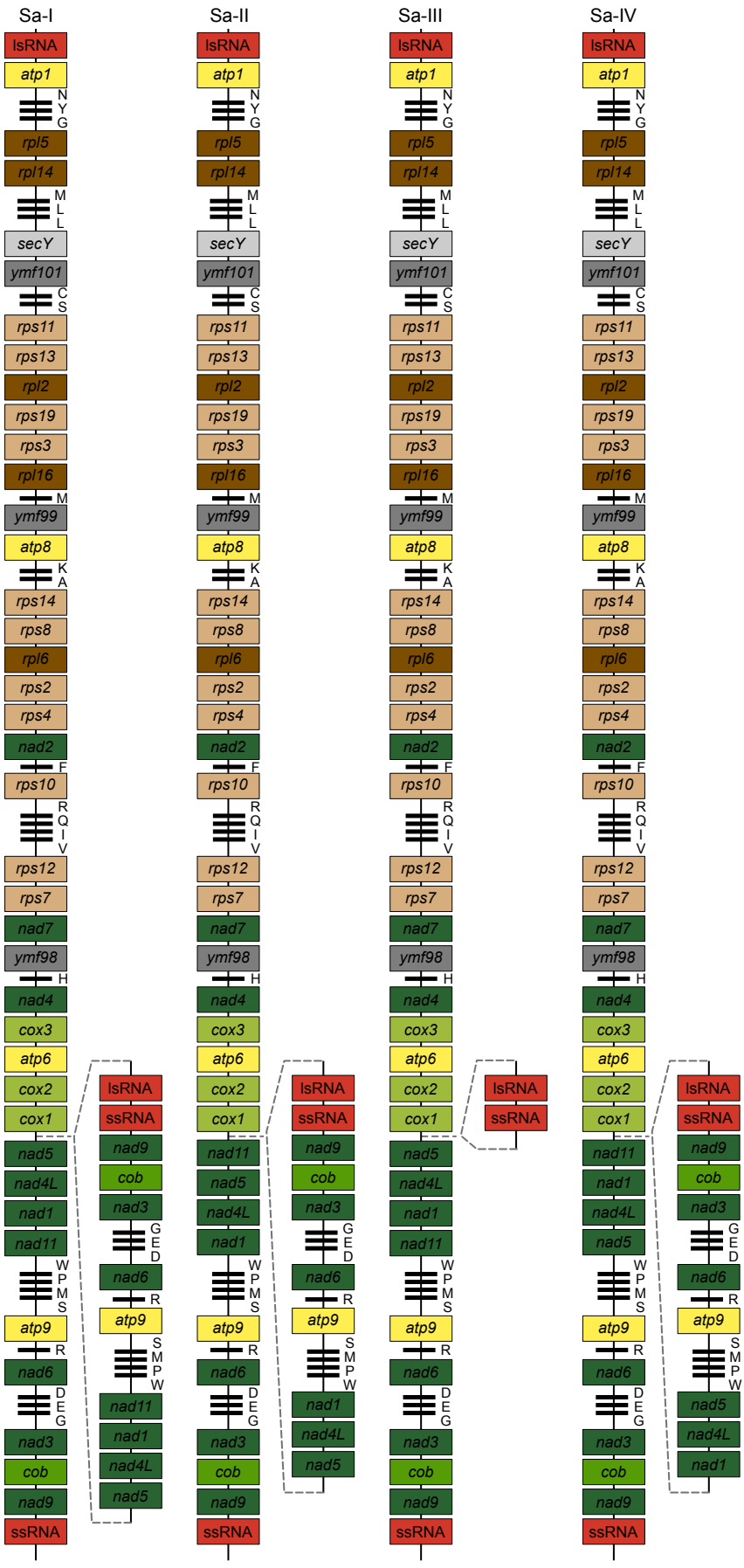

Clade B
Py-XX
Py-XXI
Py-XXII
lsRNA
nad5
atp9
nad4L
nad1
nad11
cox1
cox2
atp1
nad4
ymf98
nad7
nad2
rps10
rps12
rps7
cox3
atp6
nad3
cob
nad9
nad6
ssRNA
rpl5
rpl14
secY
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
atp8
rps14
rps8
rpl6
rps2
rps4
ymf100
ymf102
ymf103
*M
M*


Clade A
Py-XXIII
Py-XXIV
Py-XXV
lsRNA
ssRNA
*M
M*
*E
E*


Clade C
Clade D
Py-XXVI
Py-XXVII
Py-XXVIII
lsRNA
N S M P
atp9
nad4L
nad1
nad11
cox2
cox1
W
nad5
atp1
E
nad4
H
ymf98
nad7
nad2
F
rps10
R Q I V
rps12
rps7
cox3
atp6
D
nad3
cob
nad9
R
nad6
ssRNA
Y G G
rpl5
rpl14
M L L
secY
ymf101
C S
rps11
rps13
rpl2
rps19
rps3
rpl16
M
ymf99
atp8
K A
rps14
rps8
rpl6
rps2
rps4
ymf100
P M S N
ymf100
rps4
rps2
rpl6
rps8
rps14
A K
atp8
ymf99
M
rpl16
rps3
rps19
rpl2
rps13
rps11
S C
ymf101
secY
L L M
rpl14
rpl5
G G Y
ssRNA
nad6
R
nad9
cob
nad3
D
atp6
cox2
cox1
W
nad11
nad1
nad4L
atp9
nad5


Lagenidium
Albugo
La-I
lsRNA
N S M P
atp9
cox2
cox1
nad9
cob
atp1
E
nad4
H
ymf98
nad7
nad2
F
rps10
R Q I V
rps12
rps7
cox3
atp6
D
nad3
nad11
nad1
nad4L
nad6
R
nad5
W
ssRNA
Y G G
rpl5
rpl14
M L L
secY
ymf101
C S
rps11
rps13
rpl2
rps19
rps3
rpl16
M
ymf99
atp8
K A
rps14
rps8
rpl6
rps2
rps4
ymf100
cob
nad9
cox1
cox2
atp9
P M S N
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
A K
atp8
ymf99
M
rpl16
rps3
rps19
rpl2
rps13
rps11
S C
ymf101
secY
L L M
rpl14
rpl5
G G Y
ssRNA
W
nad5
R
nad6
nad4L
nad1
Al-I
lsRNA
N S M P
nad5
atp1
rps7
rps12
V I Q R
rps10
F
nad2
nad7
ymf98
H
nad4
atp6
E D
nad3
cox3
atp9
R
nad6
nad4L
nad1
nad11
cob
nad9
cox1
cox2
W
ssRNA
Y G G
rpl5
rpl14
M L L
secY
ymf101
C S
rps11
rps13
rpl2
rps19
rps3
rpl16
M
ymf99
atp8
K A
rps14
rps8
rpl6
rps2
rps4
ymf100
nad5
P M S N
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
A K
atp8
ymf99
M
rpl16
rps3
rps19
rpl2
rps13
rps11
S C
ymf101
secY
L L M
rpl14
rpl5
G G Y
ssRNA
W
cox2
cox1
nad9
cob
nad11
nad1
nad4L
nad6
R
atp9

Aphanomyces Clade



Saprolegnia Clade

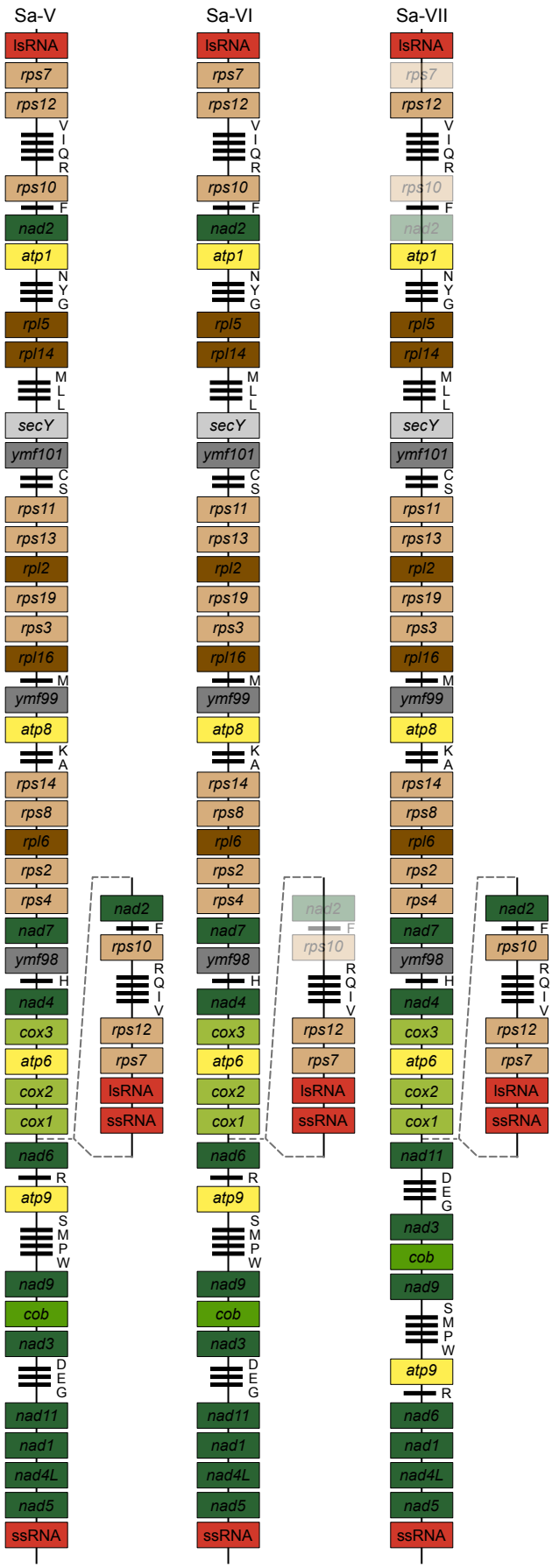


Table 3.5 Syntenies of the included oomycete mitogenomes	
Species	**Synteny**
Peronosporaceae	
Clade 1	
Phytophthora mirabilis	Pe-I
Phytophthora andina	Pe-I
Phytophthora ipomoeae	Pe-I
Phytophthora betacei	Pe-XX
Phytophthora infestans	Pe-XX
Phytophthora phaseoli	Pe-I
Phytophthora nicotianae	Pe-XXI
Phytophthora aleatoria	Pe-XXI
Phytophthora idaei	Pe-XXI
Phytophthora cactorum	Pe-XXI
Clade 16	
Plasmopara muralis	Pe-XXVIII
Plasmopara viticola	Pe-XXVIII
Plasmopara nivea	Pe-XXVIII
Plasmopara halstedii	Pe-III
Bremia lactucae	Pe-II
Clade 4	
Phytophthora megakarya	Pe-IV
Phytophthora palmivora	Pe-XX
Phytophthora litchii	Pe-XXI
Clade 3	
Phytophthora pseudosyringae	Pe-V
Phytophthora pluvialis	Pe-V
Clade 12	
Phytophthora castanetorum	Pe-XXII
Phytophthora quercina	Pe-XXII
Phytophthora sp. ohioensis	Pe-XXII
Phytophthora tubulina	Pe-XXII
Phytophthora versiformis	Pe-XXII
Clade 5	
Phytophthora agathidicida	Pe-VIII
Phytophthora cocois	Pe-VIII
Phytophthora castaneae	Pe-VIII
Phytophthora heveae	Pe-VIII
Phytophthora sp. novaeguineae	Pe-VIII
Clade 2	
Phytophthora tropicalis	Pe-VI
Phytophthora capsici	Pe-VI

Phytophthora sp. subnubulis	Pe-VII
Phytophthora colocasiae	Pe-VII
Phytophthora multivora	Pe-VI
Phytophthora plurivora	Pe-VI
Clade 15	
Peronospora tabacina	Pe-XXII
Peronospora effusa	Pe-XXII
Peronospora belbahrii	Pe-X
Pseudoperonospora cubensis	Pe-XII
Pseudoperonospora humuli	Pe-XII
Hyaloperonospora arabidopsidis	Pe-IX
Sclerospora graminicola	Pe-XXIII
Phytophthora podocarpi	Pe-XI
Clade 6	
Phytophthora gonapodyides	Pe-XIII
Phytophthora pinifolia	Pe-XIV
Phytophthora chlamydospora	Pe-XIII
Clade 7	
Phytophthora × alni	Pe-XV
Phytophthora × cambivora	Pe-XVI
Phytophthora fragariae	Pe-XVIII
Phytophthora rubi	Pe-XIX
Phytophthora sojae	Pe-XXII
Phytophthora cinnamomi	Pe-XVII
Clade 8	
Phytophthora ramorum	Pe-XXIV
Phytophthora lateralis	Pe-XXIV
Phytophthora sansomeana	Pe-XXIII
Phytophthora cryptogea	Pe-XXIII
Clade 9	
Phytophthora fallax	Pe-XXV
Phytophthora captiosa	Pe-XXV
Phytophthora polonica	Pe-XXII
Clade 10	
Phytophthora boehmeriae	Pe-XXIX
Phytophthora kernoviae	Pe-XXVI
Nothophytophthora	
Nothophytophthora sp.	Pe-XXVII
Pythiaceae	
Halophytophthora	
Halophytophthora batemanensis	Py-I
Halophytophthora polymorphica	Py-II
Clade K (*Phytopythium*)	

Phytopythium aichiense	Py-III
Phytopythium boreale	Py-III
Phytopythium chamaehyphon	Py-III
Phytopythium helicoides	Py-IV
Phytopythium sp. cucurbitacearum	Py-III
Phytopythium vexans	Py-III
Globisporangium	
Clade G	
Globisporangium barbulae	Py-V
Globisporangium cederbergense	Py-VI
Globisporangium iwayamai	Py-I
Globisporangium okanoganense	Py-VII
Globisporangium nagaii	Py-VIII
Clade F	
Globisporangium cylindrosporum	Py-IX
Globisporangium irregulare	Py-IX
Globisporangium mamillatum	Py-IX
Globisporangium debaryanum	Py-VIII
Globisporangium emineosum	Py-X
Clade E	
Globisporangium erinaceum	Py-IX
Globisporangium radiosum	Py-IX
Globisporangium camurandrum	Py-IX
Globisporangium middletonii	Py-X
Globisporangium rhizosaccharum	Py-VIII
Clade J	
Globisporangium nunn	Py-X
Globisporangium orthogonon	Py-X
Globisporangium acanthophoron	Py-VIII
Globisporangium perplexum	Py-VII
Clade I	
Globisporangium ultimum	Py-XXIX
Globisporangium solare	Py-VII
Globisporangium splendens	Py-X
Globisporangium heterothallicum	Py-VIII
Clade H (*Elongisporangium*)	
Elongisporangium dimorphum	Py-IX
Elongisporangium senticosum	Py-IX
Elongisporangium anandrum	Py-VII
Elongisporangium prolatum	Py-XI
Pilasporangium	
Pilasporangium apinafurcum	Py-X
Salisapiliaceae	

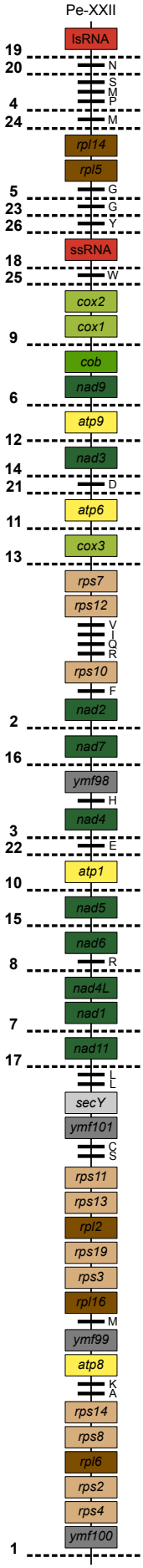
Salisapilia	
Salisapilia sapeloensis	Ss-I
Pythiaceae cont.	
Pythium	
Clade B	
Pythium aristosporum	Py-XII
Pythium arrhenomanes	Py-XII
Pythium phragmiticola	Py-XIII
Pythium vanterpoolii	Py-XIV
Pythium graminicola	Py-XV
Pythium plurisporium	Py-XVI
Pythium rishiriense	Py-XVII
Pythium torulosum	Py-XVIII
Pythium myriotylum	Py-XIX
Pythium pyrilobum	Py-XX
Pythium dissotocum	Py-XXI
Pythium sukuiense	Py-XXI
Pythium brachiatum	Py-XXII
Clade A	
Pythium monospermum	Py-XXIII
Pythium porphyrae	Py-XXIV
Pythium aphanidermatum	Py-XXV
Clade C	
Pythium insidiosum	Py-XXVI
Clade D	
Pythium lycopersicum	Py-XXVII
Pythium oligandrum	Py-XXVII
Pythium amasculinum	Py-XXVII
Pythium grandisporangium	Py-XXVIII
Lagenidiaceae	
Lagenidium	
Lagenidium giganteum	La-I
Albuginaceae	
Albugo	
Albugo candida	Al-I
Albugo laibachii	Al-I
Saprolegniaceae	
Aphanomyces	
Aphanomyces frigidophilus	Sa-I
Aphanomyces invadans	Sa-II
Aphanomyces astaci	Sa-II
Aphanomyces cochlioides	Sa-III
Aphanomyces euteiches	Sa-III

Aphanomyces sp. NJM 9510	Sa-IV
Saprolegnia	
Saprolegnia diclina	Sa-V
Saprolegnia parasitica	Sa-V
Saprolegnia ferax	Sa-V
Achlya	
Achlya hypogyna	Sa-VI
Thraustotheca	
Thraustotheca clavata	Sa-VII

3.4.2 Synteny blocks

For the included oomycetes, 26 synteny blocks were identified (Figure 3.3). These blocks ranged in size from one to 23 genes. Most (17) of these blocks contained just one gene. Each of the rRNA genes formed a single gene synteny block as did eight protein-coding (e.g., *atp6*, *nad7*) and seven tRNA (e.g., *tRNA-Gly*, *tRNA-Tyr*). Gene content also varied for the nine synteny blocks containing more than one gene. Some contained solely tRNA or protein-coding genes, with others a combination of both. For example, the largest synteny block, block 1, contained 16 protein-coding and seven tRNA genes. Although 26 synteny blocks were recognised, in related taxa

Figure 3.3 Oomycete synteny blocks identified based on comparisons of the 68 oomycete mitogenome syntenies. 1. Schematic diagram illustrating the distribution of the synteny blocks on Pe-XXII. Genomes are oriented relative to the large ribosomal subunit with protein encoding and rRNA genes represented by colored rectangles labeled with standard gene abbreviations. Thick black lines represent tRNA genes and these are labeled with the one-letter code for the corresponding amino acid. Bold dashed lines indicate synteny block boundaries, bold numbers denoted the different synteny blocks. **2.** List of the 26 synteny blocks and the genes that each contains.



1

2

Block	Genes
1	*tRNA-Leu, tRNA-Leu, secY, ymf101, tRNA-Cys, tRNA-Ser, rps11, rps13, rpl2, rps19, rps3, rpl16, tRNA-Met, ymf99, atp8, tRNA-Lys, tRNA-Ala, rps14, rps8, rpl6, rps2, rps4, ymf100*
2	*nad2, tRNA-Phe, rps10, tRNA-Arg, tRNA-Gln, tRNA-Ile, tRNA-Val, rps12, rps7*
3	*ymf98, tRNA-His, nad4*
4	*tRNA-Ser, tRNA-Met, tRNA-Pro*
5	*tRNA-Gly, rpl5, rpl14*
6	*cob, nad9*
7	*nad1, nad4L*
8	*nad6, tRNA-Arg*
9	*cox1, cox2*
10	*atp1*
11	*atp6*
12	*atp9*
13	*cox3*
14	*nad3*
15	*nad5*
16	*nad7*
17	*nad11*
18	*sRNA*
19	*lsRNA*
20	*tRNA-Asn*
21	*tRNA-Asp*
22	*tRNA-Glu*
23	*tRNA-Gly*
24	*tRNA-Met*
25	*tRNA-Trp*
26	*tRNA-Tyr*

particular blocks were often consistently grouped together. For example, in representatives of Peronosporaceae block 8 (*tRNA-Arg, nad6*) and block 15 (*nad5*) were always paired, with *nad5* and *nad6* always side-by-side.

3.5 Conserved and variable regions

3.5.1 Definition of regions

Oomycete mitogenomes appear to be composed of distinct conserved and variable regions. These regions were recognised based on the extent to which the content and arrangement of synteny blocks was maintained when compared across taxa.

Conserved regions were recognised on the basis of two criteria. First, that any given synteny block from within a conserved region shared the same neighbours in >90% of the genomes being compared. For example, synteny blocks 3 (*ymf98*, *tRNA-His*, *nad4*) and 16 (*nad7*) were neighbouring synteny blocks in >90% of the mitogenomes, with *ymf98* and *nad7* side-by-side. The exceptions being that blocks terminating a conserved region only shared one neighbour. Second, that changes in synteny block order were rare but where they occurred the region remained in intact (i.e., the synteny blocks of the region were grouped together >90% of the time).

Based on these criteria, two conserved regions were identified in the mitogenomes of Peronosporaceae, Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae. Referred to as Conserved Region A (CR-A) and Conserved Region B (CR-B) these regions each contained the same set of synteny blocks in all five of these families. Two conserved regions were also identified in Saprolegniaceae. However, in this case the gene

contents were different and these have therefore been denoted Conserved Region C (CR-C) and Conserved Region D (CR-D).

Synteny blocks not included within one of the conserved regions fell within one on the variable regions. As for the conserved regions, two variable regions were identified per mitogenome. For Peronosporaceae, Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae, these regions were denoted Variable Region 1 (V1) and Variable Region 2 (V2). In Saprolegniaceae, the two variable regions were denoted Variable Region 3 (V3) and Variable Region 4 (V4). These regions were recognised on the basis of their relative positions within the mitogenome rather than their synteny block content.

3.5.2 Arrangement of the regions

The arrangement of conserved and variable regions was comparable across all the mitogenomes in the dataset. Specifically, conserved and variable regions were interspersed; that is, conserved regions were followed by variable regions and *vice versa*. In Peronosporaceae, each mitogenome contained a single copy of each region (Figure 3.4). However, in Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae there are two copies of CR-A and two of V2, the latter differing in synteny block content in some cases (Figure 3.4). In these groups the entire CR-A as well as portions of V1 and V2 always fell within the large inverted repeat. In contrast, CR-B was part of the single copy region. In Saprolegniaceae, most of the included mitogenomes contained a single copy of each conserved and variable region (Figure 3.4). The exceptions were several members of *Aphanomyces* (e.g.,

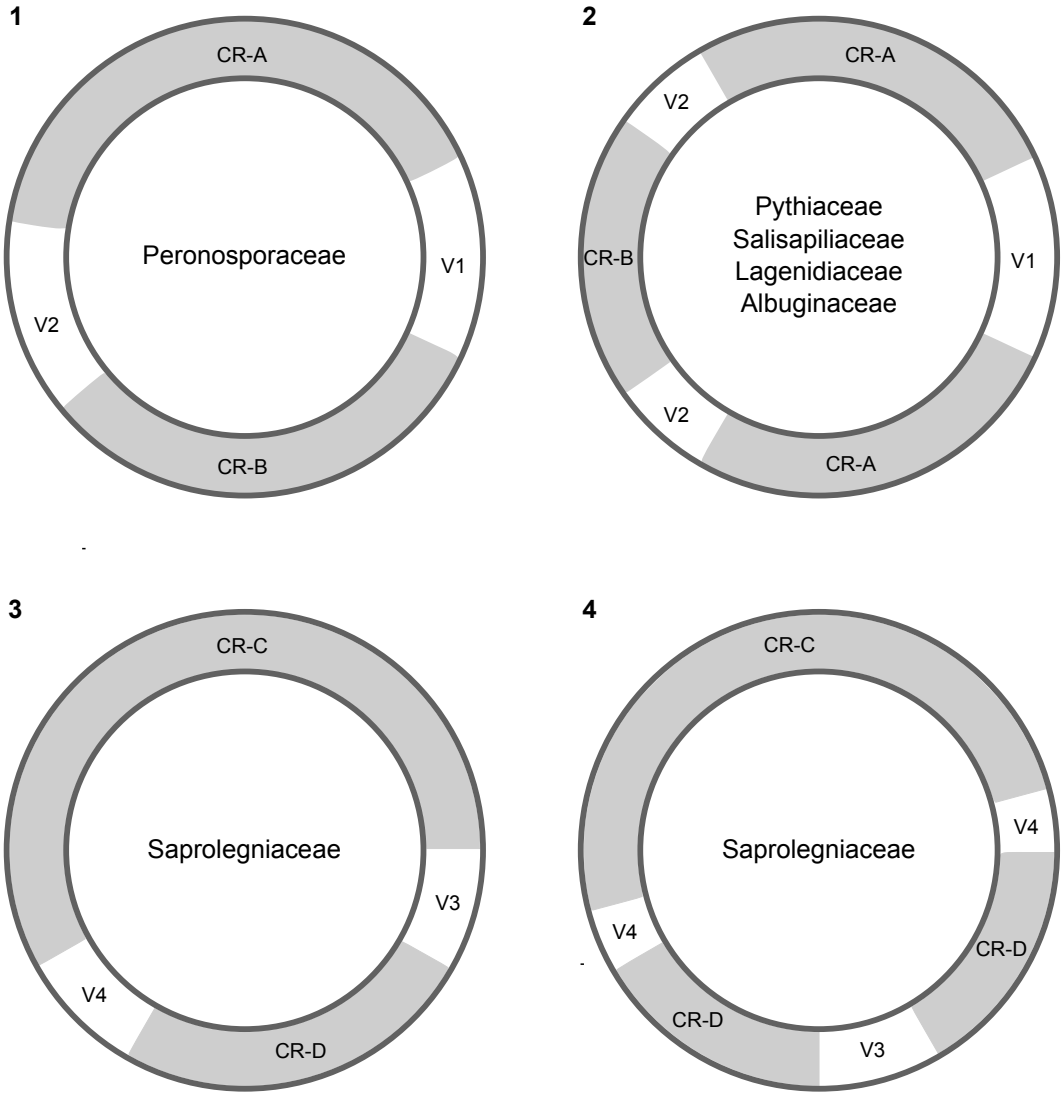


Figure 3.4 Schematic diagrams illustrating the arrangement of conserved and variable regions in oomycete mitogenomes. 1. Arrangement of conserved and variable regions in Peronosporaceae. 2. Arrangement of conserved and variable regions in Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae. 3. Typical arrangement of conserved and variable regions in Saprolegniaceae. 4. Arrangement of conserved and variable regions in *Aphanomyces frigidophilus*, *Aphanomyces invadans*, *Aphanomyces astaci* and *Aphanomyces* sp. NJM 9510.

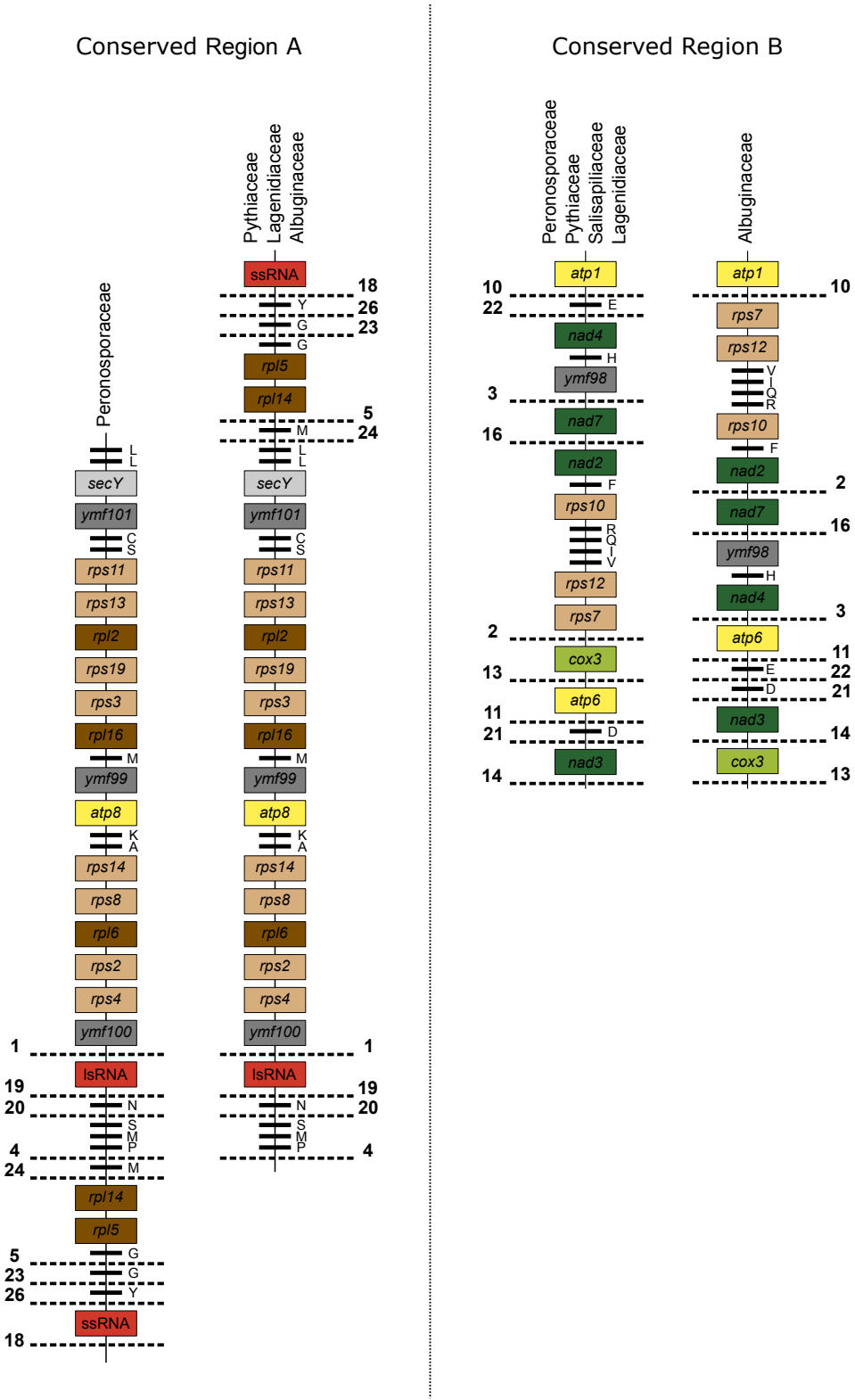
Aphanomyces frigidophilus, Aphanomyces astaci) where CR-D and V4 were duplicated due to their inclusion within the inverted repeat (Figure 3.4).

3.5.3 Gene content of the conserved regions

Conserved region A - In Peronosporaceae, Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae CR-A typically included blocks 1, 4, 5, 18, 19, 20, 23, 24 and 26. Therefore, CR-A usually contained 18 protein coding, two rRNA and 15 tRNA genes. The synteny blocks in CR-A had two standard orders, one typical of most Peronosporaceae and the other of *Nothophytophthora* sp. (Peronosporaceae), Pythiaceae, Lagenidiaceae, and Albuginaceae (Figure 3.5). Although typical of the included taxa, there were departures from the conserved orders. These always involved one or more of the synteny blocks typical of CR-A instead falling within one of the variable regions. In several cases these blocks fell within V1. Specifically, in Peronosporaceae synteny block 18 in syntenies Pe-III and Pe-XXIX and in *Phytopythium* synteny block 24 in syntenies Py-III and Py-IV. In two Peronosporaceae syntenies the synteny blocks fell within V2 (i.e., Pe-XI, Pe-XXVI). Salisapiliaceae has a Pythiaceae-type CR-A, except in *Salisapilia* CR-A synteny blocks 4 and 20 fall within V1 (synteny Ss-I).

Conserved Region B - In Peronosporaceae, Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae CR-B consists of synteny blocks 2, 3, 7, 10, 11, 13, 14, 21 and 22. Therefore, CR-B contained 11 protein-coding and eight tRNA genes. There is one standard order for CR-B in

Figure 3.5 Schematic diagrams illustrating the standard gene and synteny block orders for Conserved Region A and Conserved Region B. Protein encoding and rRNA genes represented by colored rectangles labeled with standard gene abbreviations. Thick black lines represent tRNA genes and these are labeled with the one-letter code for the corresponding amino acid. Bold dashed lines indicate synteny block boundaries, bold numbers denoted the different synteny blocks.

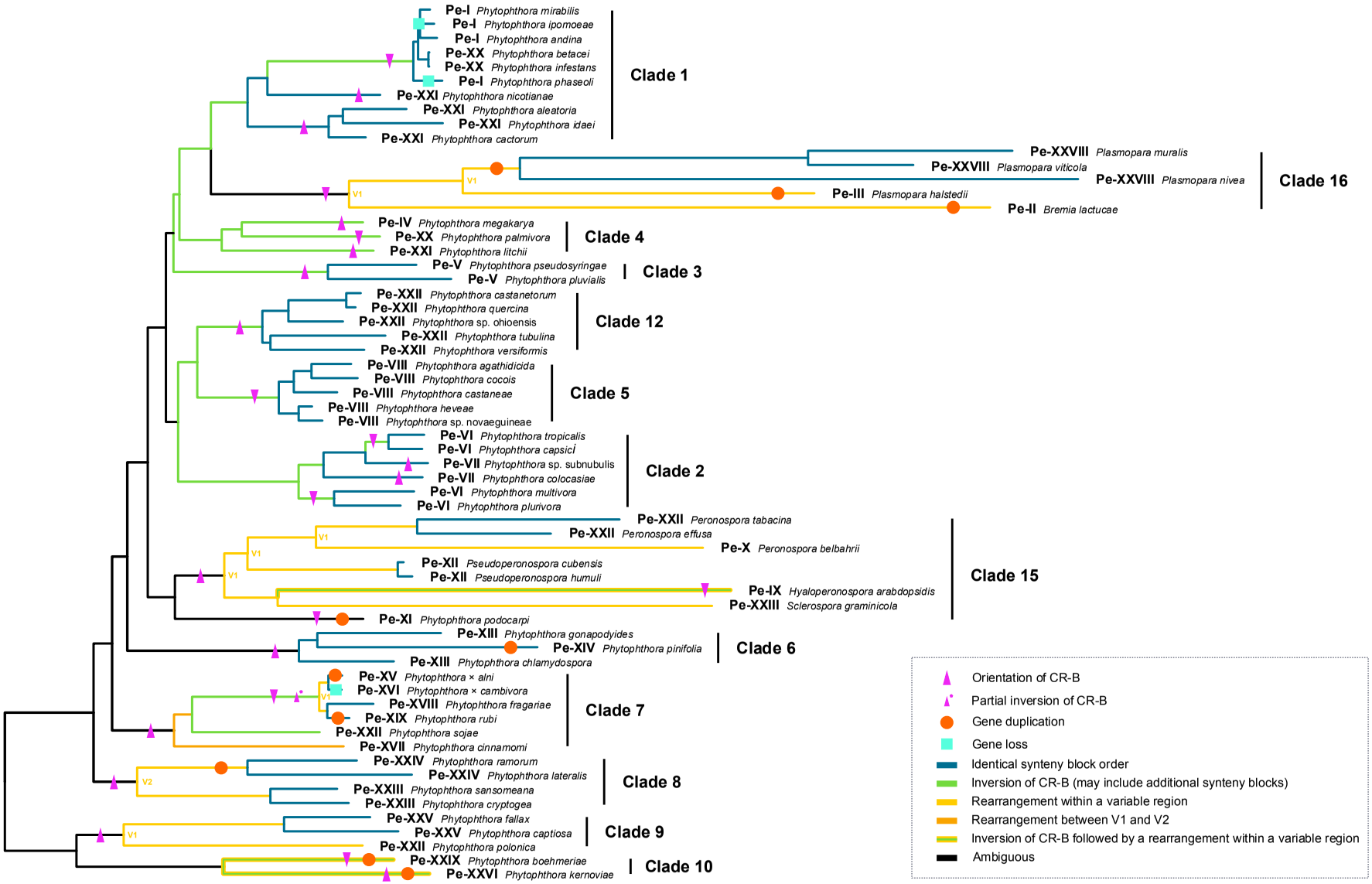

Conserved Region A
Conserved Region B
Peronosporaceae
Pythiaceae
Lagenidiaceae
Albuginaceae
Salisapiliaceae
secY
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
atp8
rps14
rps8
rpl6
rps2
rps4
ymf100
lsRNA
rpl14
rpl5
ssRNA
atp1
nad4
ymf98
nad7
nad2
rps10
rps12
rps7
cox3
atp6
nad3

Peronosporaceae, Pythiaceae, Salisapiliaceae, and Lagenidiaceae (Figure 3.5). Minor departures from this standard order were observed. One example involved syntenies from four *Phytophthora* Clade 7 species (i.e., Pe-XV, Pe-XVI, Pe-XVIII, Pe-XIX) in which blocks 16 and 2 were inverted relative to other Peronosporaceae (Figure 3.6). Another example was .*Nothophytophthora sp.* (i.e., Pe-XXVII). In this case block 10 fell next to synteny block 14 rather than block 22 as in other members of these families. The CR-B synteny block order in Albuginaceae differs markedly from that of the other four families; in this case there is a general reshuffling of the blocks (Figure 3.5).

Although synteny block order is typically maintained in Peronosporaceae, the orientation of the CR-B region differs between syntenies (Figure 3.6) For example, in syntenies Pe-VIII and Pe-XXIX the synteny block 10 end of CR-B and *ssRNA* end of CR-A are at opposing ends of V1 whereas in other Peronosporaceae syntenies (e.g., synteny Pe-IV or Pe-XXV) it is the block 14 end of CR-B that is closest to V1.

Conserved Region C – In Saprolegniaceae, CR-C contains synteny blocks 1, 2, 3, 5, 9, 10, 11, 13, 16, 18, 19, 20, 24 and 26. The gene content of CR-C is 29 protein-coding, two rRNA and 17 tRNA genes. With one exception the synteny block order for CR-C was the same for all the examined members of Saprolegniaceae. The exception involved the position

Figure 3.6 The phylogenetic distribution of structural rearrangements in the mitogenomes of **the included members of Peronosporaceae.**


Pe-I Phytophthora mirabilis
Pe-I Phytophthora ipomoeae
Pe-I Phytophthora andina
Pe-XX Phytophthora betacei
Pe-XX Phytophthora infestans
Pe-I Phytophthora phaseoli
Pe-XXI Phytophthora nicotianae
Pe-XXI Phytophthora aleatoria
Pe-XXI Phytophthora idaei
Pe-XXI Phytophthora cactorum
Clade 1
Pe-XXVIII Plasmopara muralis
Pe-XXVIII Plasmopara viticola
Pe-XXVIII Plasmopara nivea
Pe-III Plasmopara halstedii
Pe-II Bremia lactucae
Clade 16
V1
Pe-IV Phytophthora megakarya
Pe-XX Phytophthora palmivora
Pe-XXI Phytophthora litchii
Clade 4
Pe-V Phytophthora pseudosyringae
Pe-V Phytophthora pluvialis
Clade 3
Pe-XXII Phytophthora castanetorum
Pe-XXII Phytophthora quercina
Pe-XXII Phytophthora sp. ohioensis
Pe-XXII Phytophthora tubulina
Pe-XXII Phytophthora versiformis
Clade 12
Pe-VIII Phytophthora agathidicida
Pe-VIII Phytophthora cocois
Pe-VIII Phytophthora castaneae
Pe-VIII Phytophthora heveae
Pe-VIII Phytophthora sp. novaeguineae
Clade 5
Pe-VI Phytophthora tropicalis
Pe-VI Phytophthora capsici
Pe-VII Phytophthora sp. subnubulis
Pe-VII Phytophthora colocasiae
Pe-VI Phytophthora multivora
Pe-VI Phytophthora plurivora
Clade 2
Pe-XXII Peronospora tabacina
Pe-XXII Peronospora effusa
Pe-X Peronospora belbahrii
Pe-XII Pseudoperonospora cubensis
Pe-XII Pseudoperonospora humuli
Pe-IX Hyaloperonospora arabdopsidis
Pe-XXIII Sclerospora graminicola
Clade 15
V1
Pe-XI Phytophthora podocarpi
Pe-XIII Phytophthora gonapodyides
Pe-XIV Phytophthora pinifolia
Pe-XIII Phytophthora chlamydospora
Clade 6
Pe-XV Phytophthora × alni
Pe-XVI Phytophthora × cambivora
Pe-XVIII Phytophthora fragariae
Pe-XIX Phytophthora rubi
Pe-XXII Phytophthora sojae
Pe-XVII Phytophthora cinnamomi
Clade 7
Pe-XXIV Phytophthora ramorum
Pe-XXIV Phytophthora lateralis
Pe-XXIII Phytophthora sansomeana
Pe-XXIII Phytophthora cryptogea
Clade 8
V2
Pe-XXV Phytophthora fallax
Pe-XXV Phytophthora captiosa
Pe-XXII Phytophthora polonica
Clade 9
Pe-XXIX Phytophthora boehmeriae
Pe-XXVI Phytophthora kernoviae
Clade 10
Orientation of CR-B
Partial inversion of CR-B
Gene duplication
Gene loss
Identical synteny block order
Inversion of CR-B (may include additional synteny blocks)
Rearrangement within a variable region
Rearrangement between V1 and V2
Inversion of CR-B followed by a rearrangement within a variable region
Ambiguous

of synteny block 2, which differs between the *Aphanomyces* and *Saprolegnia* Clades (Figure 3.7).

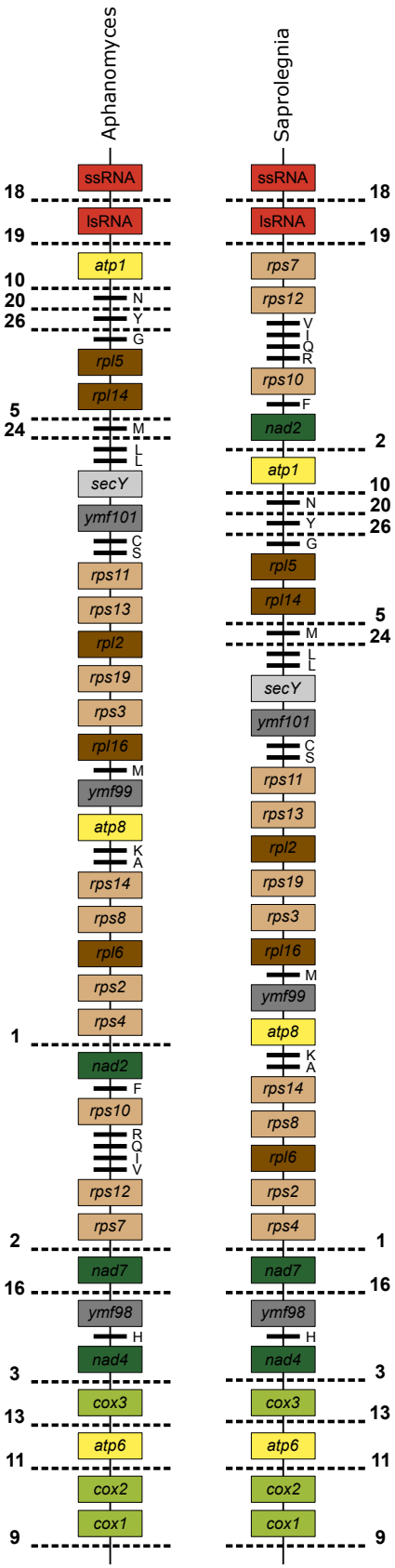
Conserved Region D – In Saprolegniaceae, CR-D consists of synteny blocks 4, 6, 8, 12, 14, 21, 22 and 23. The gene content of CR-D is five protein-coding and eight tRNA genes. The synteny block order of CR-D differs between the *Aphanomyces* and *Saprolegnia* Clades; two groups of blocks were recognised one containing the blocks 25, 4, 12 and 8, the other blocks 21, 22, 23, 14 and 6. Members of the *Aphanomyces* and *Saprolegnia* Clades differ in terms of the orientation of the two groups of blocks (Figure 3.7).

3.5.4 Gene content of the variable regions

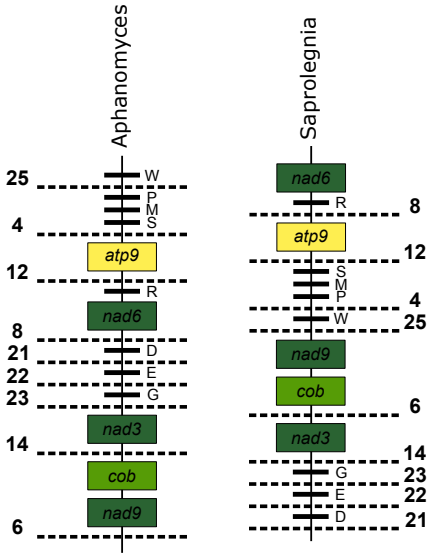
Variable Regions 1 and 2 – In Peronosporaceae, Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae, together the variable regions contained the synteny blocks 6, 7, 8, 9, 12, 15, 17 and 25. In combination these eight blocks contained 10 protein-coding and 2 tRNA genes. Although the same synteny blocks consistently fell within the variable regions, individual syntenies differed in the distribution of blocks between V1 and V2, as well as block order within each of these regions. Both these different types were observed when comparing syntenies between families.

Figure 3.7 Schematic diagrams illustrating the standard gene and synteny block orders for Conserved Region C and Conserved Region D. Protein encoding and rRNA genes represented by colored rectangles labeled with standard gene abbreviations. Thick black lines represent tRNA genes and these are labeled with the one-letter code for the corresponding amino acid. Bold dashed lines indicate synteny block boundaries, bold numbers denoted the different synteny blocks.

Conserved Region C



Conserved Region D



Differences in the distribution of blocks within and between each of the two variable regions were also observed for comparisons within families. In Peronosporaceae both types were observed for comparisons between and within genera (Table 3.6). The pattern was similar for Pythiaceae, although in this case block order differences were not observed in V2 for comparisons within genera. Instead, differences in the content of V2 were due to changes in repeat boundaries rather than rearrangements of the synteny blocks.

Table 3.6 Distribution of genes across the variable regions

Taxa	Number of taxa	V1	V2
Peronosporaceae[a]	10/28 35.7%	*cox1, cox2* *tRNA-Trp* ***atp9, nad9, cob***	*nad4L, nad1, nad11* ***nad5, nad6, tRNA-Arg***
	7/28 25.0%	*cox1, cox2* *tRNA-Trp* ***nad5, nad6, tRNA-Arg***	*nad4L, nad1, nad11* ***atp9, nad9, cob***
Phytopythium	6/6 100%	*nad5* ***nad6, tRNA-Arg*** *nad4L, nad1, nad11* *atp9* ***tRNA-Met***[b]	***tRNA-Trp*** *nad9, cob* ***cox1, cox2***
Globisporangium *Elongisporangium* *Pilasporangium*	28/28 100%	*nad5* ***nad6, tRNA-Arg*** *atp9* *nad4L, nad1, nad11*	***tRNA-Trp*** *nad9, cob* ***cox1, cox2***
Pythium	21/21 100%	*nad5* *atp9* *nad4L, nad1, nad11* ***tRNA-Trp*** ***cox1, cox2***	***nad6, tRNA-Arg*** *nad9, cob*

[a] Excluding *Nothophytophthora* [b] From CR-A

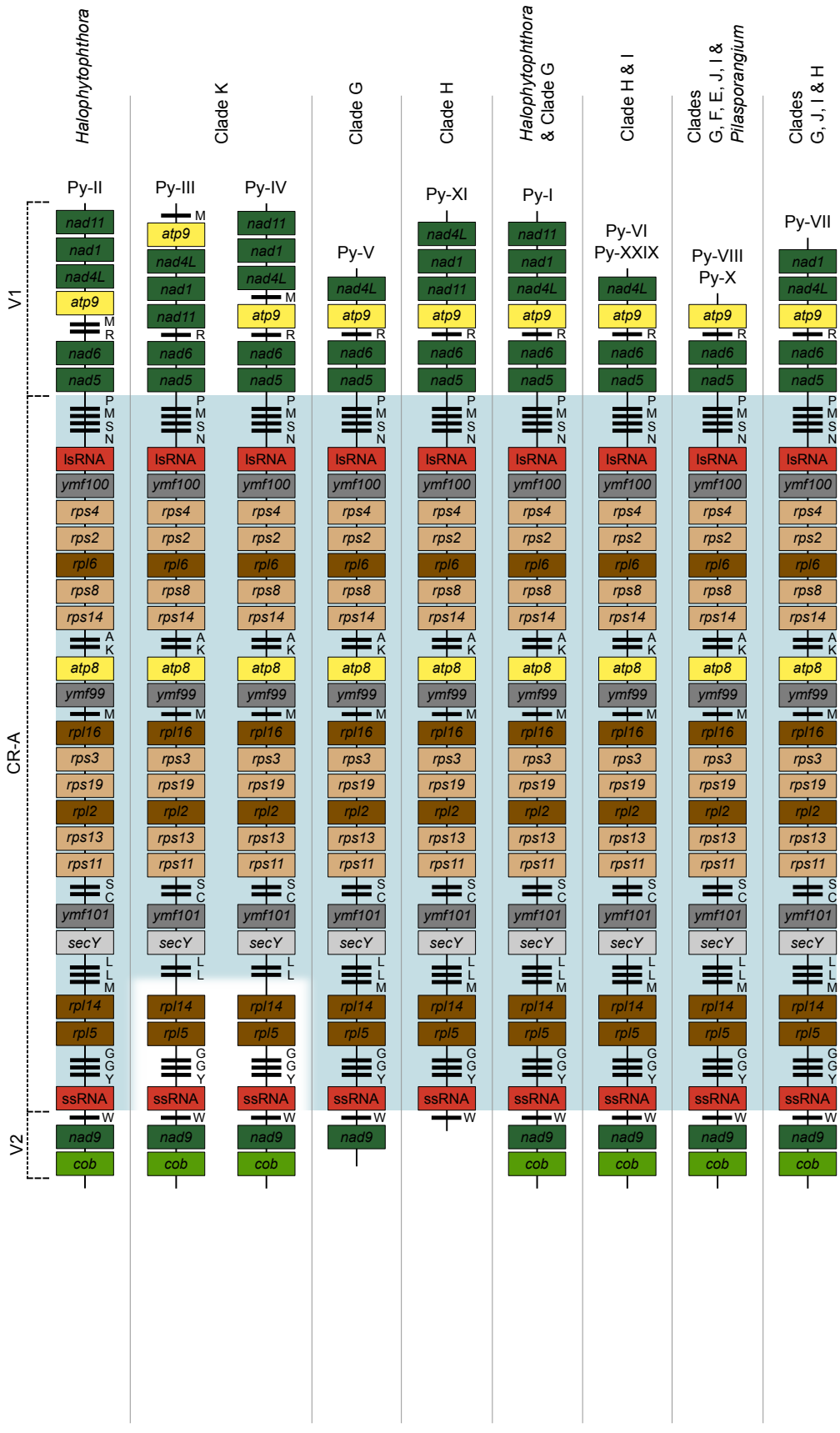
Variable Regions 3 and 4 – In Saprolegniaceae, V3 and V4 together contains three synteny blocks. Specifically, blocks 7, 15 and 17. Together these blocks contained four protein-coding genes. As in the other oomycetes *Thraustotheca clavata* has two obvious variable regions; V3 containing block 17 and V4 containing blocks 7 and 15. In the other Saprolegniaceae mitogenomes all three synteny blocks are grouped into one of the corresponding regions. In the *Aphanomyces* Clade, all three synteny blocks are grouped together in V3, whereas in the *Saprolegnia* Clade they all fall within V4.

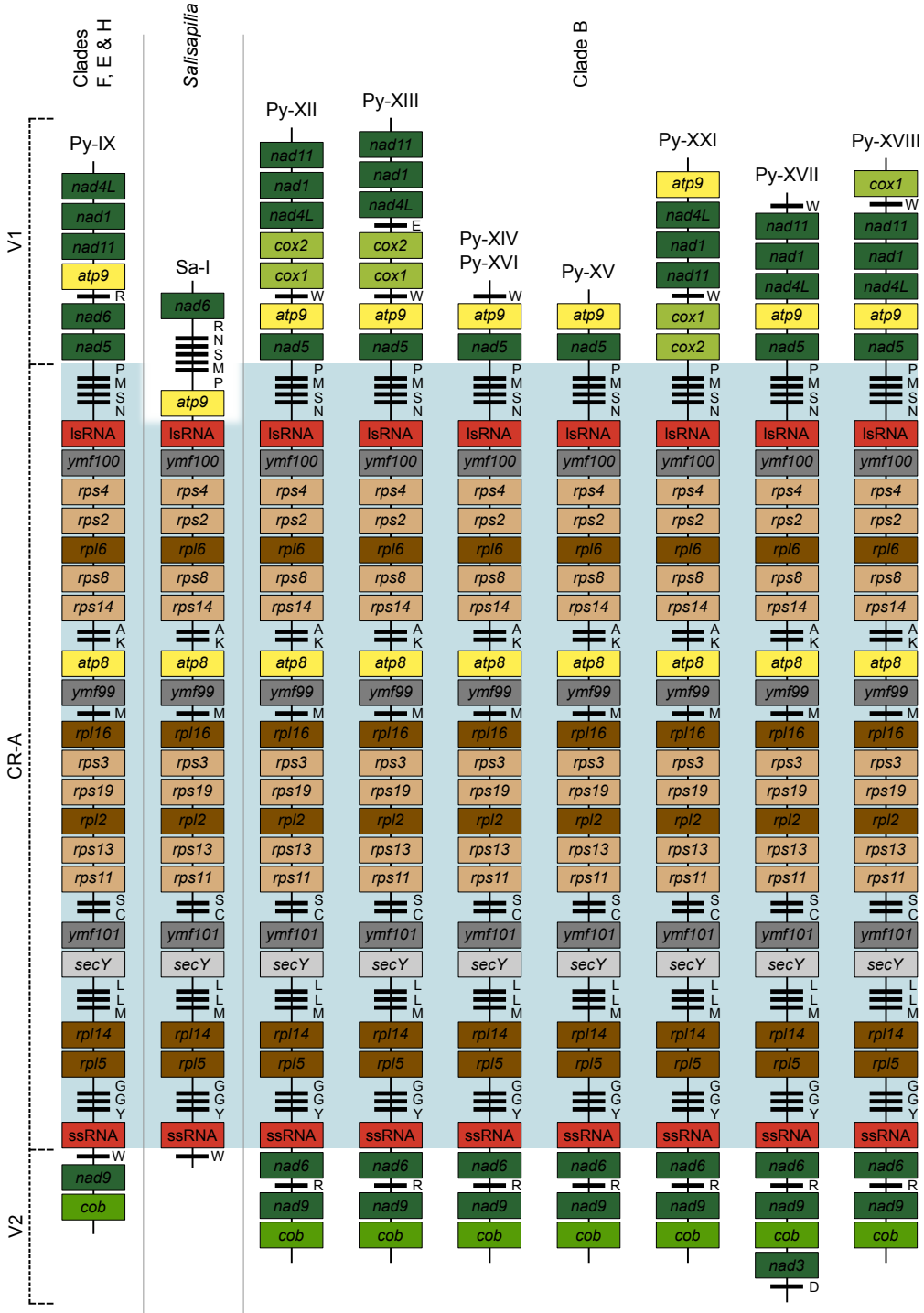
3.6 Inverted repeats and single copy regions

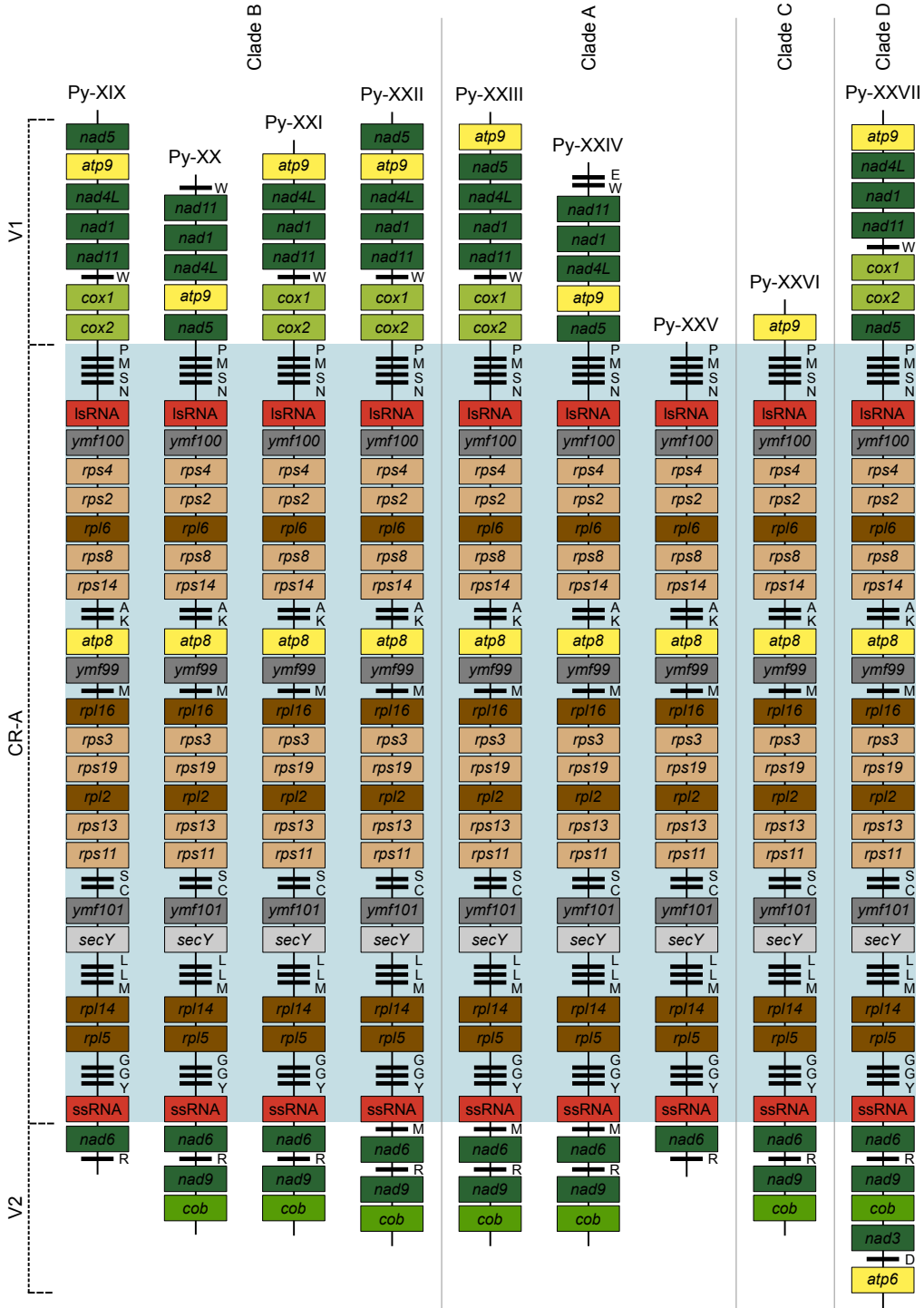
3.6.1 Large inverted repeats

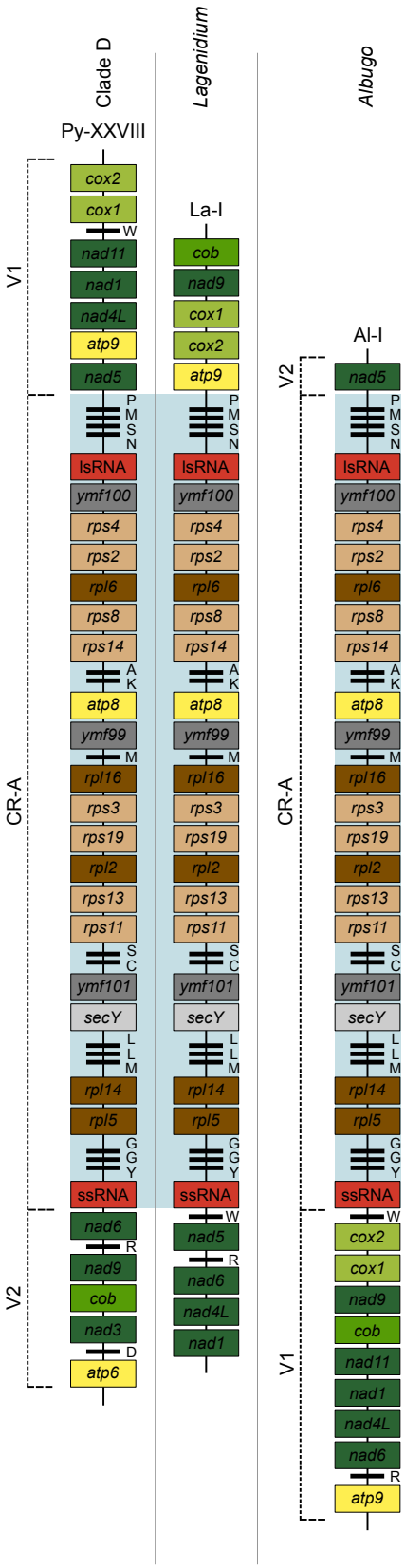
Large inverted repeats were identified in the families Pythiaceae, Salisapiliaceae, Lagenidiaceae, Albuginaceae and Saprolegniaceae. In Pythiaceae, Salisapiliaceae, Lagenidiaceae, and Albuginaceae the large inverted repeat always includes the entirety of CR-A as well as portions of V1 and V2 at the repeat ends (Figure 3.8). In Pythiaceae, Salisapiliaceae and Lagenidiaceae the *ssRNA* end of the repeat extended into V2. Of the

Figure 3.8 Schematic diagrams illustrating the large inverted repeats from members of Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae. Repeats are oriented such that CR-A is consistently aligned. Protein encoding and rRNA genes represented by colored rectangles labeled with standard gene abbreviations. Thick black lines represent tRNA genes and these are labeled with the one-letter code for the corresponding amino acid. Bold dashed lines indicate synteny block boundaries, bold numbers denoted the different synteny blocks. Repeats are labeled with the synteny code for the synteny that it corresponds to. Order of the repeats reflects their relative phylogenetic positions.


Halophytophthora
Clade K
Clade G
Clade H
Halophytophthora & Clade G
Clade H & I
Clades G, F, E, J, I & Pilasporangium
Clades G, J, I & H
Py-II
Py-III
Py-IV
Py-V
Py-XI
Py-I
Py-VI Py-XXIX
Py-VIII Py-X
Py-VII
V1
CR-A
V2
nad11
nad1
nad4L
atp9
nad6
nad5
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps3
rps19
rpl2
rps13
rps11
ymf101
secY
rpl14
rpl5
ssRNA
nad9
cob


Clades F, E & H
Salisapilia
Clade B
Py-IX
Sa-I
Py-XII
Py-XIII
Py-XIV Py-XVI
Py-XV
Py-XXI
Py-XVII
Py-XVIII
V1
CR-A
V2
nad4L
nad1
nad11
atp9
R
nad6
nad5
P M S N
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
A K
atp8
ymf99
M
rpl16
rps3
rps19
rpl2
rps13
rps11
S C
ymf101
secY
L L M
rpl14
rpl5
G G Y
ssRNA
W
nad9
cob
R N S M P
nad11
nad1
nad4L
cox2
cox1
W
E
cox1
cox2
nad3
D


Clade B
Clade A
Clade C
Clade D
Py-XIX
Py-XX
Py-XXI
Py-XXII
Py-XXIII
Py-XXIV
Py-XXV
Py-XXVI
Py-XXVII
V1
CR-A
V2
nad5
atp9
nad4L
nad1
nad11
W
cox1
cox2
nad4
P M S N
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
A K
atp8
ymf99
M
rpl16
rps3
rps19
rpl2
rps13
rps11
S C
ymf101
secY
L L M
rpl14
rpl5
G G Y
ssRNA
nad6
R
nad9
cob
E W
nad3
D
atp6


Clade D
Lagenidium
Albugo
Py-XXVIII
La-I
Al-I
V1
V2
CR-A
cox2
cox1
W
nad11
nad1
nad4L
atp9
nad5
P
M
S
N
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
A
K
atp8
ymf99
M
rpl16
rps3
rps19
rpl2
rps13
rps11
S
C
ymf101
secY
L
L
M
rpl14
rpl5
G
G
Y
ssRNA
nad6
R
nad9
cob
nad3
D
atp6
cob
nad9
cox1
cox2
atp9
nad5
W
nad6
R
nad4L
nad1

syntenies identified for these groups, 68% (19/28) had the repeat boundary after the *cob* gene (e.g., syntenies Py-VI and Py-XXII), 18% (5/28) had the repeat boundary before the *cob* gene (e.g., syntenies Ss-I and Py-XIX) and in 11% (3/28) repeat extended beyond V2 into CR-B (i.e., syntenies Py-VII, Py-XXVII, Py-XXVIII). In the final synteny, La-I, the *cob* gene fell within V1 not V2; at the *ssRNA* end of the repeat in this synteny the boundary fell within V2. The *lsRNA* end of the repeat was less consistent in terms of the boundary position. With the exception of synteny Py-XXV where the repeat did not extend beyond CR-A, in all other cases the repeat boundary fell within V1. In Albuginaceae the orientation of CR-A was reversed, such that the *lsRNA* end of the repeat extended into V2 and the *ssRNA* end extended into V1. In synteny Al-I the entirety of V1 and V2 is included in the repeat.

In Saprolegniaceae, the large inverted repeats always incorporated both the *ssRNA* and *lsRNA* genes, with extensions beyond these genes occurring from only from one side (Figure 3.9). In the *Aphanomyces* Clade extensions of the repeat, where they occur, do so only from the *ssRNA* end. This creates additional copies of V4, CR-D and parts of V3 (e.g., synteny Sa-IV). In the *Saprolegnia* Clade, extensions of the repeat only occur from the *lsRNA* end into CR-C (e.g., synteny Sa-V). In syntenies Sa-VI and Sa-VII, one copy of the inverted repeat contain degraded copies for several genes (e.g., *nad2* and *rps10*).

3.6.2 Single copy regions

There are two single copy regions in the large inverted repeat containing mitogenomes. In Pythiaceae, Salisapiliaceae, Lagenidiaceae and

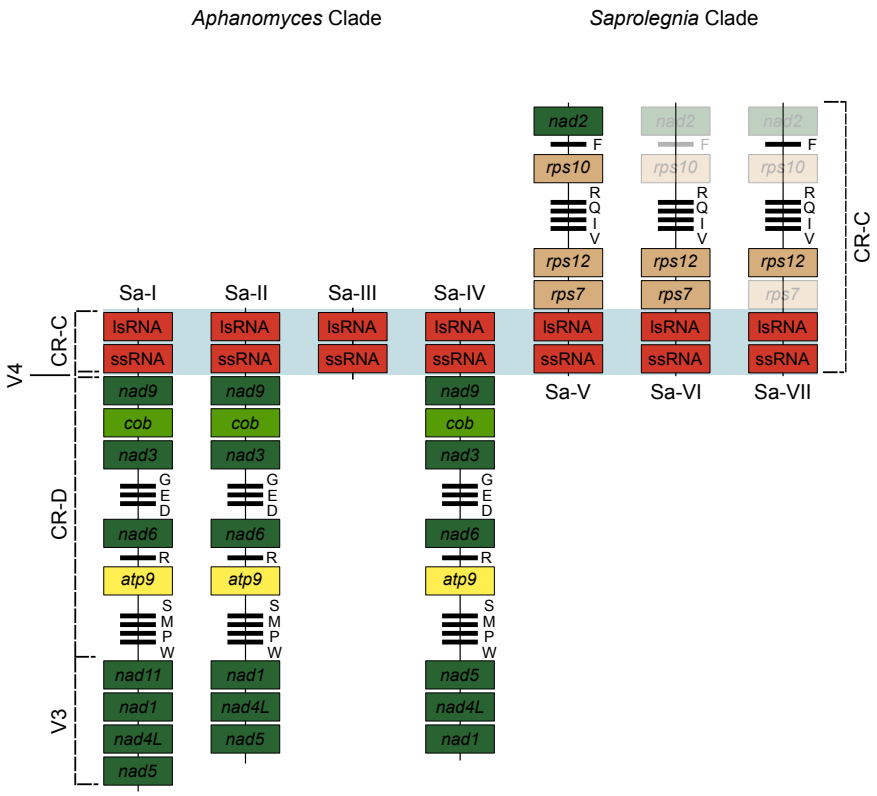


Figure 3.9 Schematic diagrams illustrating the large inverted repeats from members of Saprolegniaceae. Repeats are oriented such that CR-C is consistently aligned. Protein encoding and rRNA genes represented by colored rectangles labeled with standard gene abbreviations. Thick black lines represent tRNA genes and these are labeled with the one-letter code for the corresponding amino acid. Bold dashed lines indicate synteny block boundaries, bold numbers denoted the different synteny blocks. Repeats are labeled with the synteny code for the synteny that it corresponds to. Order of the reats reflects their relative phylogenetic positions.

Albuginaceae one of the single copy regions is always CR-B with the other being a portion of V1. In Saprolegniaceae the single copy regions are variable, but generally most of CR-C falls within one single copy region and parts/all of CR-D, V3 and V4 in the other. In some mitogenomes there is only one single copy region (CR-B or CR-C) with the other ends of the repeat (V1

or V3) overlapping (Table 3.3). This is seen in taxa from *Phytopythium, Globisporangium, Elongisporangium, Albugo* and *Aphanomyces*. Some single copy regions only contain non-coding sequence, ranging from 5 bp (i.e., *Lagenidium giganteum*) to 8,169 bp in length (i.e., *Pythium oligandrum*) (Table 3.3). Sometimes the single copy region contains varying number of genes. In *Globisporangium, Pilasporangium* and *Elongisporangium* the gene content varies from one to three genes, made up of a combination of *nad11, nad1,* and *nad4L,* in different orientations. *Salisapilia* contains 4 genes. In *Pythium* species, the gene content varies from one to eight genes, that differ in order and orientation (Table 3.3). The single copy region in Saprolegniaceae taxa had either one or 17 genes (Table 3.3).

3.7 Distribution of the tRNA genes

The number and distribution of tRNA genes was first evaluated for each synteny block. These data were then used to examine patterns in the distribution of these genes across the conserved and variable regions (Table 3.8). For these comparisons only one copy of the inverted repeat was considered.

The majority of tRNA genes were located within the conserved regions (i.e., 23/25 in CR-A and CR-B, and 25/25 in CR-C and CR-D). Moreover, within conserved regions the tRNA genes were typically clustered into groups. For example, (e.g., *tRNA-Ala* & *tRNA-Lys* in CR-A, or *tRNA-Ser, tRNA-Met, tRNA-Pro* & *tRNA-Trp* in CR-D). In contrast, few tRNA genes fell within variable regions; specifically, two fell within V1 and V2 with none

located in either V3 or V4. The two tRNA genes found in V1 and V2 are not grouped; they occur individually.

Table 3.7 Distribution of tRNA genes across the conserved and variable regions

Region	Number of tRNA	Grouped	Group Size
CR-A	15	Yes	1-5
CR-B	8	Yes	1-4
V1 & V2	2	No	1
CR-C	17	Yes	1-4
CR-D	8	Yes	1-4
V3 & V4	0	-	-

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CHAPTER 4

Discussion

A dataset consisting of 135 complete oomycete mitochondrial genome sequences including 74 newly assembled sequences, representing six oomycete families has been complied. This sampling improves dramatically upon that of previous studies (e.g., Winkworth et al., 2022). Several previously unrepresented groups (e.g., *Elongisporangium*, *Halophytophthora*) have been included and for others (e.g., *Globisporangium*, *Pythium*) the number of taxa for which mitogenome sequences are available has been increased. Comparisons across this dataset have provided new insights into the diversity and evolution of oomycete mitogenomes.

4.1 General structure of oomycete mitochondrial genomes

The sampled oomycete mitogenomes were broadly similar in overall size with an approximately two-fold difference between the largest and smallest. Despite the overall similarity, mitogenome size differs between oomycete families. Specifically, on average the mitogenomes of Peronosporaceae are smaller (i.e., 39,694 bp) than those of Saprolegniaceae (i.e., 47,923 bp), which are in turn smaller than those of Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae (i.e., 64,462 bp). The larger average sizes of Pythiaceae, Salisapiliaceae, Lagenidiaceae, Albuginaceae and Saprolegniaceae is attributable to the presence of large, gene-containing inverted repeat. The

average length of this repeat is 24,996 bp in Pythiaceae, Salisapiliaceae, Lagenidiaceae and Albuginaceae, and 9,848 bp in Saprolegniaceae. Removing one copy of the repeat from these mitogenomes would leave them comparable in size to Peronosporaceae, the members of which lack a large, gene-containing inverted repeats.

Unsurprisingly, mitochondrial gene content in oomycetes is strongly linked to overall genome size. In Peronosporace 68% (43/63) of the sampled mitogenomes contained 66 genes, including 39 protein-coding, two rRNA and 25 tRNA genes. The remainder have either lost a single protein coding gene (e.g., *Phytophthora andina* and *Phytophthora mirabilis*) or have gained between one and six genes due to small duplications (e.g., *Phytophthora* × *alni* and *Phytophthora pinifolia*). Mitogenomes from the remaining families contain the same 66 genes but total gene number varies due to differences in the size of the large inverted repeat. The smallest large inverted repeat containing mitogenomes, those of *Aphanomyces cochlioides* and *Aphanomyces euteiches*, only the rRNA genes are duplicated, whereas in Pythiaceae Clade D, which had the largest repeats, both rRNA genes plus 30 protein-coding and 18 tRNA genes are duplicated. Across the sampled oomycetes total gene number therefore ranges from 65-116 but is broadly similar for members of any given family.

The large inverted repeats vary in gene content both within and between the families of oomycetes. However, inverted repeats contain a core region that is more or less conserved for any given group. This core region is delimited by the two rRNA genes. In Saprolegniaceae, only the two rRNA are included in the core region (Figure 3.9), but in Albuginaceae, Lagenidiaceae, Salisapiliaceae

and Pythiaceae the core region is typically made up an additional 33 genes (Figure 3.8). Beyond this core region, additional genes were often incorporated into each end of the inverted repeat. These terminal arms varied in gene content but typically involved similar sets of genes, especially at the genus level. For example, *atp9* (synteny block 12) was always included within the same repeat arm in *Globisporangium.*

Oomycete mitochondrial genomes exhibit high levels of structural diversity. In the present study 68 distinct mitochondrial gene orders were identified among the 135 sampled taxa. Each family has a characteristic set of syntenies and in turn each of the named and numbered clades was also characterised by one or more arrangements. For example, all five representatives of *Phytophthora* Clade 5 shared the same synteny (i.e., arrangement Pe-VIII), whereas each of the five included members of *Globisporangium* Clade G had a different synteny (i.e., arrangements Py-I, Py-V–Py-VIII). While some syntenies were only identified in a single clade, others were shared between clades (i.e., nine shared arrangements were identified). For example, in Pythiaceae synteny Py-X was shared by members of *Pilasporangium* and *Globisporangium* whereas synteny Py-VII was shared by members of Clades G, J, I and H (Table 3.5).

4.2 Conserved and variable regions

Although there are high levels of structural diversity in oomycete mitogenomes, the changes that underpin this diversity appear not to be uniformly distributed across oomycete mitogenomes. Instead, pairs of conserved and variable regions are distinguished based on the frequency that

syntenies differed within these sections. These regions were broadly similar across Albuginaceae, Lagenidiaceae, Salisapiliaceae, Pythiaceae and Peronosporaceae (i.e., CR-A, CR-B, V1 and V2) but those of Saprolegniaceae were distinct (i.e., CR-C, CR-D, V3 and V4).

4.2.1 Conserved regions

There are two main types of CR-A, differing by an inversion and movement of five synteny blocks from one end of the region to the other. One of these types is typical of Albuginaceae, Lagenidiaceae, Pythiaceae and *Nothophytophthora* sp., the earliest diverging member of Peronosporaceae. The other type occurs in the remaining Peronosporaceae (Figure 3.5). In addition, there are variations on these two types involving the movement of synteny blocks from CR-A into one of the variable regions. Such variations arise in several genera (e.g., members of *Salisapilia*, *Phytopythium*, and *Plasmopara*). Examples of the variations include a small inversion at the end of the Pythiaceae-type CR-A that shifts several synteny blocks into V1 (e.g., *Salisapilia* sapeloensis) or a larger inversion, again at the end of the Peronosporaceae type CR-A, that moves several synteny blocks into V2 (e.g., *Phytophthora podocarpi*). In Albuginaceae, Lagenidiaceae, Salisapiliaceae and Pythiaceae CR-A falls within the large inverted repeat and there are, as a result, two copies of this region. There is just a single copy of CR-A in Peronosporaceae, which lack the large inverted repeat structure.

There are also two main types of CR-B. The sampled members of Lagenidiaceae, Salisapiliaceae, Pythiaceae and Peronosporaceae all share one type, while the two included species of Albuginaceae have a different

arrangement (Figure 3.5). The difference between the two versions is complex and the mechanism by which it arose is unclear. There are two variations on the typical CR-B arrangement. In *Nothophytophthora* sp. synteny block 10 falls at the opposite end of CR-B and in four *Phytophthora* Clade 7 species (e.g., *Phytophthora fragariae* and *Phytophthora rubi*) synteny blocks 2 and 7 have been inverted. All the sampled mitogenomes contained a single copy of CR-B. However, in some species of *Pythium* the large inverted repeat extends into a portion of CR-B (e.g., *Pythium grandisporangium*). Interestingly in members of the Peronosporaceae the orientation of CR-B varied. Such rearrangements are possible in the remaining families, but they are difficult to identify due to the large inverted repeats.

The conserved regions in Saprolegniaceae (i.e., CR-C, CR-D) share the same synteny blocks as CR-A and CR-B, but differ in block order and contain additional blocks that otherwise fall within V1 or V2 (e.g., synteny blocks 6 and 9). Synteny block arrangements within both CR-C and CR-D differed between the *Saprolegnia* and *Aphanomyces* Clades. In CR-C the difference involves a change in the position and orientation of synteny block 2 and in CR-D the synteny blocks form two groups that are inverted relative to one another (Figure 3.7). In all the sampled members of Saprolegniaceae a portion of CR-C fall within the large inverted repeat and in four representatives of *Aphanomyces* (e.g., *Aphanomyces frigidophilus* and *Aphanomyces* sp. NJM 9510) CR-D fell entirely within the large inverted repeat (Figure 3.9).

4.2.2 Variable regions

In variable regions, the orientation of the synteny blocks often differs between syntenies as does the relative positions of the blocks within and between the regions. As a result the same variable region (e.g., V1) in different syntenies may differ both in gene order and gene content. The variable regions are therefore identified on a positional basis.

Members of the Peronosporaceae have single copies of both V1 and V2. However, in Albuginaceae, Lagenidiaceae, Salisapiliaceae and Pythiaceae the variable regions are, at least partially, duplicated due to their inclusion within the large inverted repeat (Figure 3.4). There are always two copies of V2. However, in some cases one of the copies of V2 was incomplete because the terminal arm of the inverted repeat did not incorporate all of V2. For example, in *Pythium torulosum* (i.e., Py-XVIII) there are two full copies of V2 but in *Pythium myriotylum* (i.e., Py-XIX) the two V2 regions differ in length by two genes. The large inverted repeat also extends into V1 (Figure 3.8). This extension does not result in an additional copy of V1, instead the gene content of this region is expanded by the inclusion of additional gene copies.

In Saprolegniaceae variable regions V3 and V4 were also identified based on comparisons of the included mitogenomes. However, only in *Thraustotheca clavata* (i.e., Sa-VII) do synteny blocks fall into both regions. In the sampled *Aphanomyces* (i.e., Sa-I – Sa-IV), only V3 contained synteny blocks whereas only V4 contained synteny blocks in *Saprolegnia* and *Achlya* (i.e., Sa-V and Sa-VI). This pattern is perhaps unsurprising given that only three synteny blocks (i.e., blocks 7, 15 and 17) were associated with the variable regions in Saprolegniaceae and that two of the blocks, 7 and 15, were

consistently grouped. In this case there are four possible arrangements, three of which appear amongst the sampled mitogenome sequences (i.e., all in V3, all in V4, and one block in V3 and two grouped blocks in V4). Sampling of Saprolegniaceae is limited so it is unclear whether the distribution of the arrangements is significant. That said, in the other groups that possess large inverted repeats synteny blocks only rarely shift between variable regions V1 and V2. When this does occur it does so between genera, not within them.

4.2.3 A role for the tRNA genes

The structural differences that distinguish syntenies more commonly fell in variable than conserved regions. However, there was also a marked difference in the distribution of tRNA genes between these regions. Specifically, for mitogenomes with either the Pythiaceae- or Peronosporaceae-type CR-A 92.0% (23/25) of the tRNA genes fell within one of the conserved regions. Only the *tRNA-Arg* and *tRNA-Trp* genes fell within one of the variable regions. In Saprolegniaceae all 25 of the tRNA genes fell within the conserved regions. Additionally, in the conserved regions the tRNA genes were often grouped together. These tRNA gene groups ranged from two to five genes in size. For example, CR-B contained a group of four tRNA genes consisting of *tRNA-Val*, *tRNA-Ile*, *tRNA-Gln*, and *tRNA-Arg.* The two tRNA genes that occur in variable regions always occur singly.

One possibility is that the tRNA genes act to stabilize the conserved regions. This possibility is consistent within observations from fungal mitochondrial genomes where structural diversity is lower for groups in which tRNA genes are clustered (Aguileta et al., 2014).

4.3 Types of structural evolution

The present study has identified high levels of structural diversity in oomycete mitogenomes but, also suggests that the structural changes responsible for this diversity are not uniformly distributed across these genomes. Comparisons of the sampled mitogenomes identified three types of structural change.

4.3.1 Changes in gene order

Changes in gene order commonly distinguish oomycete mitochondrial syntenies. Such changes may be relatively simple and involve a single synteny block or be far more complex involving changes in both the relative positions and orientations of multiple gene blocks spread over a substantial portion of the genome.

Changes in gene order often appear to be the result of inversions. These vary in complexity ranging in size from just one or two synteny blocks (e.g., an inversion of synteny blocks 17 and 7 differentiates syntenies Py-VIII and Py-X) to much larger numbers of synteny blocks (e.g., CR-A is inverted in Albuginaceae relative to Lagenidiaceae, Salisapiliaceae and Pythiaceae). Inversions may also be responsible for seemingly more complex changes involving shuffling of synteny block order (e.g., rearrangement of synteny blocks 6, 9 and 12 between syntenies Pe-XXII and Pe-XXV). In this case repeated inversions, each involving different gene sets would be needed to explain differences in gene orders. Importantly, the impact of this mechanism need not

be limited to just one or a few neighbouring synteny blocks and may instead result in changes to large section of a mitogenome and involve many genes.

4.3.2 Gene losses and gains

Comparisons of the sampled mitogenome sequences indicate that the loss and gain, via gene duplication, of genes has contributed to the structural diversity of oomycete mitochondrial genomes. Gene losses are rare although these characterise a group of four taxa from Peronosporaceae Clade 1 (e.g., *Phytophthora andina*, *Phytophthora ipomoeae*) and members of the Saprolegniaceae.

Large, gene-containing inverted repeats are absent from Peronosporaceae mitogenomes. However, in the present study, 25.4% (16/63) of the mitogenomes from this family had small (i.e., 81 to 4,588 bp), gene-containing inverted repeats. These contained one to six genes including both tRNA (e.g., *tRNA-Arg* or *tRNA-Ala*) and protein-coding (e.g., *nad4L*) genes. Direct repeats were also identified in several taxa (e.g., *Phytophthora podocarpi*, *Phytophthora boehmeriae*) (Table 3.4). Unlike the large inverted repeats of the other oomycete families, the repeats in Peronosporaceae vary markedly in gene content and position within the mitogenome. These results are consistent with the suggestion that small inverted repeats have arisen on multiple occasions in Peronosporaceae (Winkworth et al., 2022).

In addition to large inverted repeats, the mitogenomes of several Pythiaceae contain additional tRNA gene copies (e.g., *tRNA-Met* in *Halophytophthora polymorphica* and *tRNA-Glu* in *Pythium phragmiticola*). The additional copies were readily identified based on their atypical locations within

the mitogenome. Although exact positions usually differed between taxa, the exceptions involved closely related taxa (e.g., *tRNA-Met* in *Pythium brachiatum*, *Pythium monospermum* and *Pythium porphyrae*). The additional copies always fell within one of the variable regions. For example, in Pythiaceae the standard location for *tRNA-Glu* is between the *atp1* and *nad4* genes in CR-B but an additional copy fell within V1 between the *nad4L* and *cox2* genes in *Pythium phragmiticola* (Py-XIII). The mechanism that generated these duplications remains uncertain but may be similar to that responsible for gene duplication in Peronosporaceae. One difference between these situations is that the additional tRNA gene copies are always perfect in Peronosporaceae but are not always so in Pythiaceae (e.g., there is one substitution in the duplicated copy of *tRNA-Met* in *Pythium brachiatum*).

Typically, structural changes involving gene loss or gain were simple. That is, the loss of a single gene or gain of a single block of one or more genes as the result of a duplication. However, in one case the explanation appears to be a combination of gene gain and loss. The *cox1* and *cox2* genes form a synteny block in all sampled mitogenomes except that of *Phytophthora* × *cambivora* (Pe-XVI). This synteny is highly similar to that of *Phytophthora* × *alni* (Pe-XV), which often falls sister to *Phytophthora* × *cambivora* in phylogenetic analyses (e.g., Bourret et al., 2018; Winkworth et al., 2022). In Pe-XV an additional copy of *cox2* falls between synteny blocks 25 (*tRNA-Trp*) and 15 (*nad5*), the position occupied by the single *cox2* gene copy in Pe-XVI. Additionally, in Pe-XVI there is 170 bp long section of the *cox2* gene sequence in this genes standard position (i.e., alongside *cox1*; Appendix III). It seems plausible that the common ancestor of *Phytophthora* × *cambivora* and

Phytophthora × *alni* possessed a *cox2* gene duplication and that in *Phytophthora* × *cambivora* the original copy of *cox2*, which typically sits next to *cox1*, was lost. Despite this block being disrupted in *Phytophthora* × *cambivora* it has been retained in the oomycete synteny block set because this change is due to gene gain and loss not a structural rearrangement.

4.3.3 Shifts in the inverted repeat boundaries

The chloroplast genomes of most photosynthetic angiosperms possess a large inverted repeat. These are widely assumed to confer structural stability on chloroplast genomes (Boyd et al., 1984; Mohanta et al., 2020). Large inverted repeats may also confer some degree of stability on the mitochondrial genomes of oomycetes. For example, although the same set of conserved and variable regions are recognised both Pythiaceae and Peronosporaceae, synteny block order in CR-A and V2 is more stable in Pythiaceae, which have inverted repeat containing mitogenomes, than in Peronosporaceae. Despite this, changes in inverted repeat length are an important source of structural diversity in those oomycete mitogenomes that contain them. Indeed, differences in repeat length may fully explain the differences between syntenies for some closely related taxa (e.g., Py-XIV, *Pythium vanterpoolii* and Py-XV, *Pythium graminicola*).

In Pythiaceae and Lagenidiaceae the large inverted repeat has a common core of genes that corresponds to CR-A. In addition to this core region these repeats typically also include terminal arms that extend into V1 at the *lsRNA* gene end of the repeat and into V2 at the *ssRNA* gene end. The genes located within these terminal arms, and which are therefore duplicated, differed between syntenies. At its smallest the l*sRNA*-V1 arm was absent (i.e., Py-XXV,

Pythium aphanidermatum) and at its largest contained nine genes (i.e., Py-XIII, *Pythium phragmiticola*). In some taxa, the V1 terminal arms overlapped and the single copy region was absent (e.g., *Albugo laibachii*, *Phytopythium vexans*; Appendix III). The *ssRNA*-V2 arm ranged in size from one (e.g., Py-XI, *Elongisporangium prolatum*) to seven genes, extending into CR-B (i.e., *Pythium* Clade D) (Figure 3.8).

Patterns for the two other families are similar. In Salisapiliaceae and Albuginaceae, the inverted repeats are again composed of a core region and terminal arms. In the representatives of Albuginaceae the core of the inverted repeat is the same as in Pythiaceae and Lagenidiaceae but it has been inverted relative to V1 and V2 (e.g., Al-I, *Albugo candida*). In Salisapiliaceae the core region is truncated at the lsRNA gene end (i.e., Sa-I, *Salisapilia sapeloensis*) (Figure 3.8).

4.3.4 Impact of overall size and non-coding DNA content

Overall size and non-coding DNA content do not, in themselves, lead to synteny changes. However, the present analyses suggest that these features may influence the frequency at which changes that do result in the generation of new syntenies occur.

Average numbers of syntenies per species differ between groups of oomycetes. For example, for *Globisporangium* the average number of syntenies per species is 0.35 (8/23) whereas for *Pythium* it is 0.81 (17/21). These differences are broadly consistent with differences in the average size and non-coding DNA content. Specifically for *Globisporangium* average mitogenome size and proportion of non-coding DNA content were 61,168 bp and 0.12. For

Pythium they were 70,141 bp and 0.20, respectively. There are similar patterns within groups. Within Peronosporaceae the syntenies per species for Clades 2 and 7 were 0.33 (2/6) and 1.0 (6/6), respectively. For Clade 2 the average mitogenome size (38,468 bp) and average proportion of non-coding DNA (0.11) were both below the Peronosporaceae averages (39,694 bp and 0.13) whereas for Clade 7 taxa both were above the family average mitogenome size (44,826 bp and 0.23, respectively). These observations suggest that larger mitogenomes with larger proportions of non-coding DNA are more accepting of structural change. One possibility is that the average distance between genes increases together with the proportion of non-coding DNA, and that this reduces the likelihood that structural changes result in gene disruption. Conversely, in smaller, more compact mitogenomes the genes are more closely packed and the likelihood that a structural change would disrupt a gene higher (Martin et al., 2007; Winkworth et al., 2022).

Non-coding DNA may help to explain the non-uniform distribution of structural changes within oomycete mitogenomes. Specifically, non-coding DNA is not evenly distributed within a mitogenome. In some cases there is no non-coding DNA between genes as their coding sequences overlap (e.g., *rps12* and *rps7* in *Phytophthora castanetorum*; Appendix III) whereas in others there are thousands of nucleotides between genes (e.g., *cox2* and *nad11* in *Pythium graminicola*; Appendix III). The uneven distribution of non-coding DNA within a mitogenome may predispose portions to accept structural changes while limiting the likelihood of such changes in others. In some *Phytophthora*, *Globisporangium* and *Pythium* mitogenomes structural variation in the V1 region appears to coincide with higher non-coding DNA content (e.g., *Phytophthora*

gonapodyides, *Pythium dissotocum*; Appendix III) whereas lower non-coding DNA content in the V2 region of large inverted repeat containing mitogenomes (e.g., *Globisporangium perplexum*, *Globisporangium solare*; Appendix III) may explain more infrequent changes in this region.

One interesting observation is that oomycete mitogenomes may be accepting large insertions of non-coding DNA. For example, *Pythium lycopersicum*, *Pythium oligandrum* and *Pythium amasculinum* are closely related in the phylogeny, share the same synteny and gene content (i.e., 116 genes), and have comparably sized inverted repeats (i.e., 30,140–30,666 bp). However, the *Pythium oligandrum* mitogenome is markedly larger due to the incorporation of a ~9,000 bp long segment of non-coding DNA into the single copy region (Appendix III). Such events have the potential to change the likelihood of structural changes within a mitogenome over time.

4.4 Explaining the structural evolution of oomycete mitogenomes

The mitogenomes of oomycetes have undergone substantial amounts of structural evolution. The present study provides a number of insights and these provide the basis for beginning to explain patterns of structural evolution in oomycete mitogenomes.

4.4.1 Loss of the large inverted repeat in Peronosporaceae

The loss of the large inverted repeat in Peronosporaceae is arguably the single most important event in the structural evolution of oomycete mitogenomes. Large inverted repeats are common to the mitogenomes of Saprolegniaceae, Albuginaceae, Lagenidiaceae, Salisapiliaceae, Pythiaceae

(including *Phytopythium* and *Halophytophthora*). In these groups these vary considerably in length and in several members of the Albuginaceae, Pythiaceae and Saprolegniaceae the inverted repeats overlap. Inverted repeats are absent from all the sampled members of Peronosporaceae. The mechanism behind such a large-scale change is not well understood although IR losses have also been reported from the chloroplast genomes of several chloroplast possessing lineages (Maréchal and Brisson, 2010; Mohanta et al., 2020; Wolfe et al., 1987).

Comparison of mitochondrial gene order across the transition from Pythiaceae to Peronosporaceae suggests *tRNA-Met* may play a role. In most of the Pythiaceae mitogenomes *tRNA-Met* (i.e., synteny block 24) fell within CR-A and formed part of the core portion of the inverted repeat. However, in *Phytopythium* this gene fell within V1. For example, in synteny Py-III, which was shared by five of the six *Phytopythium* representatives, *tRNA-Met* was at the repeat boundary. A copy of *tRNA-Met* also fell within V1 in *Halophytophthora polymorphica* (Py-II). In this species a second copy of *tRNA-Met* was present in CR-A, the standard position for this gene in Pythiaceae. In the other included representative of *Halophytophthora*, *Halophytophthora batemanensis*, *tRNA-Met* has been lost from V1 and only the CR-A copy remained. Loss of the V1 copy of *tRNA-Met* appears to be associated with a series of deletions in this section of the genome.

The data set contained one representative of *Nothophytophthora*. In this mitogenome one of the inverted repeats has been lost but the CR-A gene order typical of Pythiaceae retained. In this genome there were three identical copies of *tRNA-Met*. One in the standard position within CR-A, one within V1 at a position comparable to that in *Halophytophthora polymorphica*, and the last in

V2. This final copy fell at the most common location for the inverted repeat boundary at the V2 end of inverted repeat and the one found in all the included *Halophytophthora* and *Phytopythium* mitogenomes. Although all three copies are identical that the V1 and V2 copies of *tRNA-Met* sit within a larger 130 bp long repeats suggests a closer link between these copies (Appendix III). Perhaps the V2 copy of *tRNA-Met* and the surrounding repeat are a remnant of the inverted repeat or, alternatively, the duplication of the V1 *tRNA-Met* into V2 acted to stabilise the genome following loss of the inverted repeat.

The organisation of CR-A differs between Pythiaceae and Peronosporaceae. The difference in Peronosporaceae being that several synteny blocks, including that containing *tRNA-Met*, are at the opposite end of CR-A. Additionally, these blocks are inverted such that *tRNA-Met* is nested well within the CR-A boundary, which in this group was marked by the ssRNA gene. With just a few exceptions this arrangement is common to all Peronosporaceae. For example, syntenies from the included Clade 10 representatives. In both *Phytophthora boehmeriae* (Pe-XXIX) and *Phytophthora kernoviae* (Pe-XXVI) synteny block 18, which contains the *ssRNA* gene is located within one of the variable regions. The remainder of CR-A is typical of Peronosporaceae in both cases. Interestingly *Phytophthora boehmeriae* is the only member of Peronosporaceae, apart from the included *Nothophytophthora*, to have a duplication of *tRNA-Met*. In this mitogenome the duplicated *tRNA-Met* occupies the position usually held by the *ssRNA* gene.

As yet there is no mechanism to explain inverted repeat loss or the role that duplications of *tRNA-Met* may play. However, given that tRNA gene duplications are uncommon in oomycete mitogenomes it seems more than

coincidental that *tRNA-Met* is duplicated in several groups (i.e., *Phytopythium*, *Halophytophthora*, *Nothophytophthora* and Peronosporaceae Clade 10) and that the additional copies often occupy the same or similar locations. If *tRNA-Met* has played a role it remains unclear whether this was to destabilise the repeat or to stabilise the genome following repeat loss. A better understanding of inverted repeat loss will require further sampling of *Phytopythium*, *Halophytophthora*, *Nothophytophthora* and Peronosporaceae Clades 9 and 10. Additional sampling will also be needed to understand the role of tRNA gene duplications in the structural evolution of oomycete mitogenomes. For example, *tRNA-Met* duplications in three *Pythium* species (e.g., Py-XXII, *Pythium brachiatum* and Py-XXIII, *Pythium monospermum*) are not associated with inverted repeat loss and based on the presence of nucleotide substitutions, may be being degraded.

4.4.2 Structural rearrangements

Since the mitogenomes of Peronosporaceae lack a large inverted repeat, mechanisms for structural evolution in these mitogenomes are limited to gene losses, gene gains, and changes in gene order. However, there are differences between two broad subgroups of Peronosporaceae (Figure 3.6). One including several early diverging clades (i.e., Clades 15, 6, 7, 8, 9 and 10) and the other several later diverging clades (i.e., Clades 1, 4, 3, 12, 5 and 2).

The early diverging clades tended to have larger mitogenomes, higher proportions of non-coding DNA and more syntenies per species than the later diverging ones. Considering only clades represented by five or more mitogenomes, average sizes were 40,081-44,826 bp, average proportions of

non-coding DNA were 0.15-0.23, and the numbers of syntenies per species were 0.63-1.0 for early diverging clades. In contrast, for the later diverging clades the values were 37,042-38,468 bp, 0.08-0.11, and 0.2-0.33, respectively (Table 3.2). The smaller, more compact genomes of the later diverging species exhibit less structural diversity, presumably because they have less non-coding DNA and therefore the spaces within which structural changes could occur are more limited. The opposite applies to the early diverging clades. In addition to this apparent difference in the frequency with which rearrangements have occurred, the types of changes that underpin these rearrangements also differed.

Rearrangements that have shifted synteny blocks between V1 and V2 have occurred in both early and later diverging Peronosporaceae. In the sampled representatives of this family there were two common arrangements of the eight blocks that fall within the variable regions. These arrangements differed with respect to four blocks. In 35.7% (10/28) of the syntenies, blocks 12 (*atp9*) and 6 (*nad9* and *cob*) were in V1, with blocks 15 (*nad5*) and 8 (*nad6* and *tRNA-Arg*) in V2. In a further 25.0% (7/28) of the syntenies the positions of these two synteny block pairs were exchanged. The other four blocks remain in the same variable region in both arrangements (Table 3.6). Rearrangement of the remaining four synteny blocks between the variable regions also occur, although are less frequent in the syntenies.

In later diverging Peronosporaceae, the shifting of synteny blocks between V1 and V2 appears to be linked to inversion of CR-B. Inversions of the entire CR-B appear to have occurred within (e.g., within Clades 1, 4 and 2) and between clades (e.g., between Clades 12 and 5) (Figure 3.6). In most cases,

synteny blocks associated with one of the neighbouring variable regions were inverted together with CR-B. For example, the difference between syntenies Pe-VIII and Pe-XXII is the inversion of CR-B plus seven variable region synteny blocks. Only rarely has CR-B inverted without impacting neighbouring synteny blocks (e.g., the different between syntenies Pe-XX and Pe-XXI). In early diverging Peronosporaceae inversions of CR-B, with or without additional variable region synteny blocks, were also identified. However, these appear to have been less important as they only observed for Clades 15, 7 and 10. In a group of four closely related members of Clade 7 (e.g., *Phytophthora rubi*, *Phytophthora fragariae*), there has been a second partial inversion of CR-B (Figure 3.6). In this case the initial inversion of CR-B was not associated with movements of variable region synteny blocks and the second inversion involved a pair of synteny blocks (i.e., synteny blocks 2 and 16) in the middle of this region.

Several other types of change were identified. However, these were restricted to either the early and later diverging Peronosporaceae (Figure 3.6). For the later diverging Peronosporaceae, the only other type of structural change observed was gene loss. Loss of a gene occurred in four members of Clade 1 that all shared synteny Pe-I. In the early diverging Peronosporaceae several other types of structural change were identified. Small gene containing repeats contribute to structural diversity in Clades 15, 6, 7, 8 and 10. For example, the difference between syntenies Pe-XVIII and Pe-XIX is a duplication of *nad4L* in Pe-XIX. Rearrangement of the synteny blocks within variable regions was observed in Clades 16, 15, 7, 8 and 9. For example, the difference between syntenies Pe-XXV and Pe-XXII is the rearrangement of synteny blocks

6 (*cob*, *nad9*), 12 (*atp9*) and 9 (*cox1*, *cox2*) in V1. There have also been rearrangements of the synteny blocks between the variable regions, that do not appear to be linked to the inversion of CR-B. For example, the difference between syntenies Pe-XXII and Pe-XVII. In Clades 15 and 10 synteny blocks that typically fell within CR-A also appear to have shifted into one of the neighbouring variable regions. For example, in synteny Pe-X block 18 (*ssRNA*) has shifted from CR-A into V1.

Mitogenome diversity patterns in Peronosporaceae Clade 16, which contains several representatives of the downy mildews, are consistent with those of the early diverging Peronosporaceae (Figure 3.6). Specifically, average mitogenome size (41,081 bp), proportion of non-coding sequence (0.16) and number of syntenies per species (0.6, 3/5) for Clade 16 are comparable to those of the early diverging clades (Table 3.2). However, Clade 16 is nested within a clade that otherwise contained only later diverging Peronosporaceae. Structural diversity in Clade 16 appears to have arisen as a result of synteny blocks rearrangements within V1, shifting of synteny blocks into V1 from CR-A, inversions of CR-B and gene duplication. Again, that a larger number of mechanisms have been identified is consistent with observations for the early diverging Peronosporaceae clades.

All members of the Pythiaceae possess a large inverted repeat. Therefore in addition to the types of change identified for Peronosporaceae, shifts in the inverted repeat boundary also contribute to structural diversity in Pythiaceae. As in Peronosporaceae diversity patterns in Pythiaceae differed between two broad subgroups, corresponding to *Pythium* and *Globisporangium*. Sampled members of *Pythium* had the largest average mitogenome size

(70,141 bp) and highest number of syntenies per species (0.81, 17/21) for a genus-level group. Their average proportion of non-coding DNA was also high (0.20). In contrast, the included *Globisporangium* mitogenomes were smaller, had less non-coding DNA and fewer syntenies per species. Specifically, these were 61,168 bp, 0.12 and 0.35 (8/23), respectively (Table 3.2). The similarities between these two groups and those identified within Peronosporaceae are perhaps more apparent when one copy of the inverted repeat removed from consideration. In this case the average size of *Pythium* genomes was 42,176 bp, which falls within the range of sizes for early diverging Peronosporaceae, and for *Globisporangium* it was 38,269 bp, comparable in size to the mitogenomes of the later diverging clades.

Mitogenome size and structural diversity metrics for *Pythium* were also consistent with several types of mechanisms being involved. In this group shifts in the length of the large inverted repeat terminal arms were often responsible for structural diversity. Extensions at the *lsRNA*-V1 end of the repeat were particularly frequent. For example, in synteny Py-XXV no V1 genes fell within the repeat arm whereas all eight of them were included within the repeat in synteny Py-XXVIII. Across the remaining syntenies varying numbers of V1 synteny blocks were included in this terminal arm. At the *ssRNA*-V2 end of the repeat the terminal arm also changed length, albeit less frequently. In some cases (e.g., Py-XXVIII) the *ssRNA*-V2 terminal arm extended into CR-B. Within V1 synteny block order has been variously rearranged in *Pythium*. It is not clear at this stage whether any or all of these rearrangements are related to changes in the extent of the large inverted repeat. In contrast, synteny block order is fixed in V2. This is perhaps a reflection of differences in the distribution of non-

coding DNA across the variable regions. Specifically, there is a large amount of non-coding DNA in V1 but comparatively little in V2. Several *Pythium* mitogenomes also contain duplicated, not always perfectly, tRNA gene copies (e.g., *Pythium monospermum*, Py-XXIII; *Pythium porphyrae*, Py-XXIV).

In *Globisporangium*, consistent with the mitogenome size and structural diversity metrics, just two mechanisms for structural change were identified. Specifically, shifts in the length of the large inverted repeat terminal arms and rearrangement of synteny block order in V1. Changes in the length of terminal arms were more common at the *lsRNA*-V1 end of repeat with only one synteny (i.e., Py-V) exhibiting changes at the *ssRNA*-V2 end. Although changes at the lsRNA-V1 end of the repeat were more common in *lsRNA*-V1, these changes were more limited in extent than in *Pythium*. Amongst the sampled mitogenomes the *lsRNA*-V1 terminal arm differed by the inclusion of, at most, two V1 synteny blocks. At its longest *lsRNA*-V1 contained all the synteny blocks included in V1 and at its shortest only synteny blocks 17 (*nad11*) and 7 (*nad1*, *nad4L*) were excluded from this arm. In *Globisporangium* rearrangements within V1 were also limited. The only observed change involved synteny blocks 17 and 7. Together as a pair, the orientation of these blocks appears to have been inverted multiple times in *Globisporangium*. The order and orientation of all the remaining V1 synteny blocks remained the same. With one exception *Elongisporangium* (Clade H) and *Pilasporangium* share the same syntenies as *Globisporangium* suggesting that there may be similar constraints on their mitogenomes arrangement.

Based on the current sampling mitogenome diversity was 0.81 (17/21) syntenies per species for *Pythium*. Only four syntenies were shared and then

only by closely related taxa (e.g., Py-XII shared by *Pythium aristosporum* and *Pythium arrhenomanes*). This is in stark contrast to *Globisporangium* where there were 0.35 (8/23) syntenies per species. Yet when clades within these two groups were compared their syntenies per species were more similar. Specifically, syntenies per species for the four included clades of *Pythium* (i.e., Clades A-D) were 0.5-1.0 and for the five *Globisporangium* clades (i.e., Clades E-G, I, J) were 0.6-1.0 (Table 3.2). This contrast arises because syntenies were shared both within and between clades in *Globisporangium*. As a result, the syntenies per species were higher at the clade-level than the genus level. Ultimately this pattern likely reflects the repeated evolution of the same syntenies due to the limited range of structural changes that appear to be possible in *Globisporangium* mitogenomes.

4.5 Evolutionary and taxonomic implications

Maximum likelihood and Bayesian analyses of the combined mitochondrial gene sequences resulted in highly similar topologies both of which were well resolved and supported (Figure 3.1). The relationships suggested by these analyses were broadly consistent with those reported previously. For example, relationships within the Peronosporaceae are consistent with those reported by Bourret et al. (2018) and those of the traditional *Pythium* reported by Nguyen et al. (2022). In particular, all 13 of the numbered clades of Peronosporaceae (i.e., Clades 1-10, 12, 15 and 16) included in the data set plus nine of the 10 named clades of Pythiaceae represented by more than one species (i.e., Clades A, B, and D-K) were recovered as monophyletic in both analyses. Within these clades inferred

relationships were also consistent with those previously reported (e.g., Bourret et al., 2018; Nguyen et al., 2022).

Previous analyses have often focused on specific groups of oomycetes (e.g., Lévesque and De Cock, 2004; Martin et al., 2007; Winkworth et al., 2022). The present analyses combined a broad sample of oomycete lineages with substantial sampling of several of the larger generic-level groups. These analyses therefore provide an overview of the broad-level relationships within the crown oomycetes. For example, those at the transition between Pythiaceae and Peronosporaceae, a portion of the tree that has not received the same level of attention *Phytophthora* or *Pythium*, as more traditionally defined. In this analysis *Phytopythium* is first branch on the lineage leading to *Phytophthora* and the downy mildews, this is followed by *Halophytophthora*, with *Nothophytophthora* sister to the crown group including *Phytophthora* and the downy mildews. This arrangment is the same as reported by Uzuhashi et al. (2010) based on sequences from two genes, although support for these relationships is stronger in the present analyses.

Previous phylogenetic studies have highlighted issues with the traditional view of oomycete taxonomy. Amongst the key issues are delimitation of *Phytophthora* and *Pythium*. Phylogenetic analyses clearly indicate that neither of these groups are monophyletic (Bourret et al., 2018; Runge et al., 2011; Uzuhashi et al., 2010). However, there is little consensus about how to address these issues. For example, Brasier et al. (2022) have argued for the conservation of *Phytophthora* and the continued recognition of downy mildews as distinct despite this leaving *Phytophthora* paraphyletic. In contrast Nguyen et al. (2022) urged that clades within the traditional *Pythium* be recognised at the

generic-level. These authors recognised a total of five genera including *Pythium*, *Elongisporangium*, and *Phytopythium*. Phylogenetic analyses also point to issues at other taxonomic levels. For example, questions about the assignment of genera to families (e.g., *Halophytophthora* and *Salisapilia*) as well as the status of several families (e.g., Pythiaceae and Salisapiliaceae). Resolving these issues is important if there is to be a stable, robust taxonomic framework for oomycetes.

A number of factors are likely to have contributed to ongoing taxonomic uncertainty. Over the last two decades much of the taxonomic effort has been focused on the discovery, delimitation, and description of new species. Solving issues with the higher-level taxonomy has not recieved the same attention (c.f., Thomson et al., 2018). In addition, phylogenetic analyses have typically treated groups within the oomycetes in isolation. For example, several studies have addressed *Phytophthora* phylogeny with one of the most recent having included some 200 taxa (Yang et al., 2017). In contrast, not more than a handful of the 600 plus species of *Peronospora* have been included in evolutionary analyses (e.g., Bourret et al., 2018). The data needed to resolve the remaining uncertainty at higher taxonomic levels has simply not been available.

There is increasing interest in resolving taxonomic uncertainty in the oomycetes (e.g., Brasier et al., 2022; Nguyen et al., 2022). In part this will require a robust phylogenetic framework. Although headway has been made, because previous studies have tended to treat groups in isolation there is still uncertainty about several lineages (e.g., *Halophytophthora*, *Nothophytophthora*, *Salisapilia*). Even with this framework there is likely to be continued tension between conservation of traditional taxonomic concepts and changing the

existing taxonomy to better reflect evolutionary patterns (e.g., Brasier et al., 2022; Nguyen et al., 2022). Yet as important as any decision to conserve or to change the taxonomy may be, perhaps more important is the need to apply the selected approach consistently. Even with a robust phylogeny, making taxonomic decisions without considering oomycetes more widely is unlikely to fully resolve taxonomic uncertainty.

4.6 Future prospects

One area for further work is growing the data set. Although there is now a broad sample of the crown oomycetes for which a complete mitogenome sequence is available, several groups remain under-sampled (e.g., *Halophytophthora*, *Nothophytophthora*). Adding further representatives of these groups will be important both for resolving taxonomic uncertainty and for better understanding patterns of structural evolution (e.g., loss of the inverted repeat in Peronosporaceae). Adding representatives of earlier diverging oomycete groups will also be important. This will help to develop hypotheses for the origin of the large inverted repeat and refine existing ideas about the structural evolution of oomycete mitogenomes and the roles that tRNA genes may have played.

4.7 References

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Appendix I Taxa, authorities, isolate, GenBank accession numbers and references for the accessions included in this study

Species and authority	Isolate	GenBank accession	Mitogenome assembly reference
Achlya hypogyna Coker & Pemberton	–	KF226724[a]	O'Brien et al. (2013)
Albugo candida (Persoon) Roussel	Ac 2V	SRR1811471[b]	This thesis
Albugo laibachii Thines & Y.J. Choi	went1	ERR3606874[b]	This thesis
Aphanomyces astaci Schikora	–	KX405004[a]	Makkonen et al. (2016)
Aphanomyces cochlioides Drechsler	103-1	SRR14253067[b]	This thesis
Aphanomyces euteiches Drechsler	MC2B	SRR18327313[b]	This thesis
Aphanomyces frigidophilus Kitancharoen & Hatai	RP2	SRR11671126[b]	This thesis
Aphanomyces invadans Willoughby, R.J. Roberts & Chinabut	–	KX405005[a]	Makkonen et al. (2016)
Aphanomyces sp. NJM 9510	NJM 9510	SRR11713508[b]	This thesis
Bremia lactucae Regel	–	NC_040179[a]	Martin et al. (2018)[c]
Elongisporangium anandrum (Drechsler) Uzuhashi, Tojo & Kakishima	CBS 285.31	SRR15309486[b]	This thesis
Elongisporangium dimorphum (F. F. Hendrix & W. A. Campbell) Uzuhashi, Tojo & Kakishima	CBS 406.72	SRR15309494[b]	This thesis
Elongisporangium prolatum (W. A. Campbell & F. F. Hendrix) Uzuhashi, Tojo & Kakishima	CBS 845.68	SRR15309551[b]	This thesis
Elongisporangium senticosum (Senda & Kageyama) H.D.T. Nguyen & C.F.J. Spies	CBS 122490	SRR15309535[b]	This thesis
Globisporangium acanthophoron (Sideris) Uzuhashi, Tojo & Kakishima	CBS 337.29	SRR15309491[b]	This thesis
Globisporangium barbulae (S. Ueta & M. Tojo) H.D.T. Nguyen & C.F.J. Spies	CBS 139569	SRR15309473[b]	This thesis
Globisporangium camurandrum (Bala, de Cock & Lévesque) Uzuhashi	CBS 124059	SRR15309539[b]	This thesis
Globisporangium cederbergense (Bahramisharif, Botha & Lamprecht) H.D.T. Nguyen & C.F.J. Spies	CBS 133716	SRR15309541[b]	This thesis
Globisporangium cylindrosporum (B. Paul) Uzuhashi, Tojo & Kakishima	CBS 133716	SRR15309541[b]	This thesis

Globisporangium debaryanum (R. Hesse) Uzuhashi, Tojo & Kakishima	CBS 752.96	SRR15309502[b]	This thesis
Globisporangium emineosum (Bala, de Cock & Lévesque) H.D.T. Nguyen & C.F.J. Spies	CBS 124057	SRR15309538[b]	This thesis
Globisporangium erinaceum (J. A. Robertson) Uzuhashi, Tojo & Kakishima	CBS 505.80	SRR15309570[b]	This thesis
Globisporangium heterothallicum (W. A. Campbell & F. F. Hendrix) Uzuhashi, Tojo & Kakishima	CBS 450.67	SRR15309492[b]	This thesis
Globisporangium irregulare (Buisman) Uzuhashi, Tojo & Kakishima	CBS 494.86	SRR5241067[b]	This thesis
Globisporangium iwayamai (S. Ito) Uzuhashi, Tojo & Kakishima	P174	SRR235482[b]	This thesis
Globisporangium mamillatum (Meurs) Uzuhashi, Tojo & Kakishima	CBS 251.28	SRR15309576[b]	This thesis
*Globisporangium middletonii (*Sparrow) Uzuhashi, Tojo & Kakishima	CBS 528.74	SRR15309496[b]	This thesis
Globisporangium nagaii (S. Ito & Tokunaga) Uzuhashi, Tojo & Kakishima	CBS 779.96	SRR15309550[b]	This thesis
Globisporangium nunn (Lifshitz, Stanghellini & R.E.D. Baker) Uzuhashi, Tojo & Kakishima	CBS 808.96	SRR15309527[b]	This thesis
Globisporangium okanoganense (P. E. Lipps) Uzuhashi, Tojo & Kakishima	CBS 315.81	SRR15309490[b]	This thesis
Globisporangium orthogonon (Ahrens) Uzuhashi, Tojo & Kakishima	CBS 376.72	SRR15309493[b]	This thesis
Globisporangium perplexum (H. Kouyeas & Theohari) Uzuhashi, Tojo & Kakishima	CBS 674.85	SRR15309497[b]	This thesis
Globisporangium radiosum (B. Paul) Uzuhashi, Tojo & Kakishima	CBS 217.94	SRR15309546[b]	This thesis
Globisporangium rhizosaccharum (K. K. Singh, R. Mathew, Masih & Paul) Uzuhashi, Tojo & Kakishima	CBS 112356	SRR15309523[b]	This thesis
Globisporangium solare (De Cock, Melero-Vara,Y. Serrano & Julio Gomez) Uzuhashi, Tojo & Kakishima	CBS 119359	SRR15309509[b]	This thesis
Globisporangium splendens (Sawada) Uzuhashi, Tojo & Kakishima	rgcb-1	SRR9305779[b]	This thesis
Globisporangium ultimum (Trow) Uzuhashi, Tojo & Kakishima	–	NC_014280[a]	Levesque et al. (2010)

Halophytophthora batemanensis (Gerrettson-Cornell & J.A. Simpson) H.H. Ho & S.C. Jong	CBS 680.84	SRR15309500[b]	This thesis
Halophytophthora polymorphica (Gerrettson-Cornell & J.A. Simpson) H.H. Ho & S.C. Jong	CBS 679.84	SRR15309499[b]	This thesis
Hyaloperonospora arabidopsidis (Gäum.) Göker, Riethm., Voglmayr, Weifl & Oberw.	–	BK011976[a]	Winkworth et al. (2022)
Lagenidium giganteum Couch ex Redhead	K1	SRR10201514[b]	This thesis
Nothophytophthora sp. T. Jung, Scanu, Bakonyi & M. Horta Jung	–	MW648547[a]	Winkworth et al. (2022)
Peronospora belbahrii Thines	–	BK011978[a]	Winkworth et al. (2022)
Peronospora effusa (Grev.) Rabenh.	–	MH142315[a]	Fletcher et al. (2018)
Peronospora tabacina Adam	–	KT893455[a]	Derevnina et al. (2015)
Phytophthora × *alni* Brasier & S.A.Kirk	–	BK059194[a]	Winkworth et al. (2022)
Phytophthora × *cambivora* (Petri) Buisman	–	BK059195[a]	Winkworth et al. (2022)
Phytophthora agathidicida B.S. Weir, Beever, Pennycook & Bellgard	–	MN883601[a]	Winkworth et al. (2021)
Phytophthora aleatoria P.M.Scott, R.McDougal & P.M.Taylor	–	BK059193[a]	Winkworth et al. (2022)
Phytophthora andina Adler & Flier	–	NC_015619[a]	Lassiter et al. (2015)
Phytophthora betacei Mideros, L.E. Lagos & S. Restrepo	P8084	SRR14352918[b]	This thesis
Phytophthora boehmeriae Sawada	SCRP23	SRR13717515[b]	This thesis
Phytophthora cactorum (Lebert & Cohn) J. Schröt.	–	BK011979[a]	Winkworth et al. (2022)
Phytophthora capsici Leonian	–	BK012087[a]	Winkworth et al. (2022)
Phytophthora captiosa M.A. Dick & Dobbie	–	MN883606[a]	Winkworth et al. (2022)
Phytophthora castaneae Katsura & K. Uchida	–	MN883602[a]	Winkworth et al. (2021)
Phytophthora castanetorum T. Jung, M. Horta Jung, J. Bakonyi & B. Scanu	ST_20191112	SRR12192202[b]	This thesis
Phytophthora chlamydospora Brasier & Hansen	–	CM022726[a]	McGowan et al. (2020)

Phytophthora cinnamomi Rands	–	BK012089[a]	Winkworth et al. (2022)
Phytophthora cocois B.S. Weir, Beever, Pennycook, Bellgard & J.Y. Uchida	–	MN883603[a]	Winkworth et al. (2021)
Phytophthora colocasiae Racib.	–	BK012090[a]	Winkworth et al. (2022)
Phytophthora cryptogea Pethybr. & Laff.	–	BK011984[a]	Winkworth et al. (2022)
Phytophthora fallax Dobbie & M. A. Dick	–	MN883608[a]	Winkworth et al. (2022)
Phytophthora fragariae Hickman	–	BK011985[a]	Winkworth et al. (2022)
*Phytophthora gonapodyides (*H. E. Petersen) Buisman	–	CM022728[a]	McGowan et al. (2020)
Phytophthora heveae A.W. Thomps.	–	MN883604[a]	Winkworth et al. (2021)
Phytophthora idaei D.M. Kennedy	SCRP371	SRR7007147[b]	This thesis
Phytophthora infestans (Mont.) de Bary	–	NC_002387[a]	Lang & Forget (1992)
Phytophthora ipomoeae Flier & Grünwald	–	NC_015622[a]	Lassiter et al. (2015)
Phytophthora kernoviae Brasier	–	BK012091[a]	Winkworth et al. (2022)
Phytophthora lateralis Tucker & Milbrath	–	BK011987[a]	Winkworth et al. (2022)
Phytophthora litchii (C.C. Chen ex W.H. Ko, H.S. Chang, H.J. Su, C.C. Chen & L.S. Leu) Voglmayr, Göker, Riethm. & Oberw.	–	BK011980[a]	Winkworth et al. (2022)
Phytophthora megakarya Brasier & Griffin	–	BK059191[a]	Winkworth et al. (2022)
Phytophthora mirabilis Galindo & H.R. Hohl	–	NC_015606[a]	Lassiter et al. (2015)
Phytophthora multivora P.M. Scott & T. Jung	–	BK012093[a]	Winkworth et al. (2022)
Phytophthora nicotianae Breda de Haan	–	BK012094[a]	Winkworth et al. (2022)
Phytophthora palmivora (E.J. Butler) E.J. Butler	–	MT032128[a]	Winkworth et al. (2022)
Phytophthora phaseoli Thaxter	–	NC_015616[a]	Lassiter et al. (2015)
Phytophthora pinifolia Alv. Dur·n, Gryzenh. & M.J. Wingf.	–	BK011991[a]	Winkworth et al. (2022)
Phytophthora plurivora Jung & Burgess	–	BK059192[a]	Winkworth et al. (2022)
Phytophthora pluvialis Reeser, Sutton & Hansen	–	BK012095[a]	Winkworth et al. (2022)

*Phytophthora podocarp*i K. Dobbie, R.L. McDougal & P.M. Scott	–	BK011993[a]	Winkworth et al. (2022)
Phytophthora polonica Belbahri et al.	–	NC_029397[a]	Jastrzebski et al. (2015)[c]
Phytophthora pseudosyringae T. Jung and T.I. Burgess	–	CM022727[a]	McGowan et al. (2020)
Phytophthora quercina T. Jung and T.I. Burgess	–	BK014412[a]	Winkworth et al. (2022)
Phytophthora ramorum Werres, De Cock & Man in 't Veld	–	EU427470[a]	Martin (2008)
Phytophthora rubi (W.F. Wilcox & J.M. Duncan) W.A. Man in 't Veld	–	BK014413[a]	Winkworth et al. (2022)
Phytophthora sansomeana E.M. Hansen & Reeser	–	NC_045089[a]	Cai & Scofield (2019)
Phytophthora sojae Kaufm. & Gerd.	–	NC_009385[a]	Martin et al. (2007)
Phytophthora sp. novaeguinee	–	MN883605[a]	Winkworth et al. (2021)
Phytophthora sp. ohioensis	ST_20191016	SRR12192204[b]	This thesis
Phytophthora sp. subnubulis	–	BK012096[a]	Winkworth et al. (2022)
Phytophthora tropicalis Aragaki & J. Y. Uchida	–	BK011981[a]	Winkworth et al. (2022)
Phytophthora tubulina Jung, Cech, Horta Jung & Bakonyi	–	BK014414[a]	Winkworth et al. (2022)
Phytophthora versiformis Paap and Burgess	–	BK014415[a]	Winkworth et al. (2022)
Phytopythium aichiense M.A. Baten & Koji Kageyama	CBS 137195	SRR15309481[b]	This thesis
Phytopythium boreale (R.L. Duan) Abad, de Cock, Bala, Robideau, A.M. Lodhi & Lévesque	CBS 551.88	SRR15309572[b]	This thesis
Phytopythium chamaehyphon (Sideris) Abad, de Cock, Bala, Robideau, A.M. Lodhi & Lévesque	CBS 259.30	SRR15309479[b]	This thesis
Phytopythium helicoides (Drechsler) Abad, De Cock, Bala, Robideau, Lodhi & Lévesque	CBS 286.31	SRR15309565[b]	This thesis
Phytopythium sp. cucurbitacearum	CBS 748.96	SRR15309574[b]	This thesis

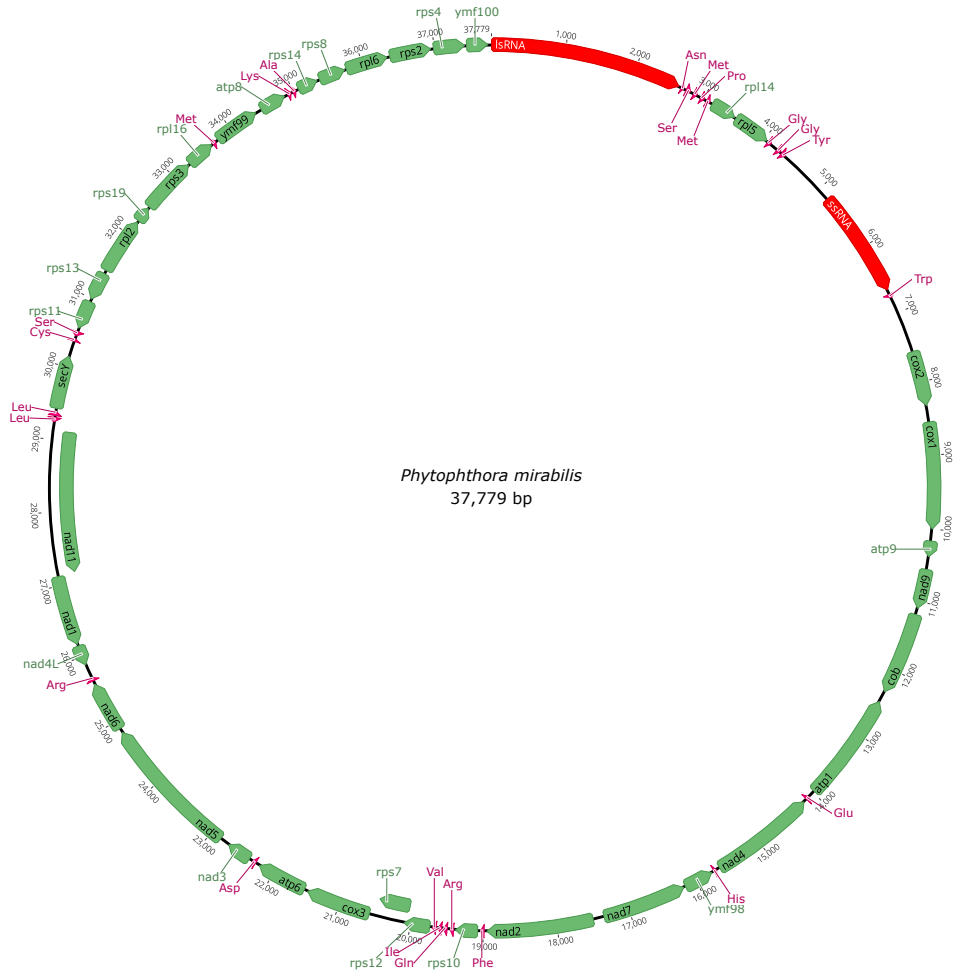
Phytopythium vexans (de Bary) Abad, De Cock, Bala, Robideau, Lodhi & Levesque	–	BK059196[a]	Winkworth et al. (2022)
Pilasporangium apinafurcum Uzuhashi, Tojo & Kakishima	JCM 30514	DRR032581[b]	This thesis
Plasmopara halstedii (Farl.) Berl. & De Toni	–	BK012098a	Winkworth et al. (2022)
Plasmopara muralis Thines	INRA-PM001	SRR8346067[b]	This thesis
Plasmopara nivea (Unger) J. Schröter	DMS-9317092	SRR12518654[b]	This thesis
Plasmopara viticola (Berkeley & Curtis) Berlese & de Toni	INRA-PV330-E1	SRR12603176[b]	This thesis
Pseudoperonospora cubensis (Berkeley & Curtis) Rostovtsev	MSU-1	SRR412825[b]	This thesis
Pseudoperonospora humuli (Miyabe & Takah.) G.W. Wilson	–	NC_042478[a]	Rahman et al. (2019)
Pythium amasculinum Y. N. Yu	CBS 552.88	SRR15309525[b]	This thesis
Pythium aphanidermatum (Edson) Fitzpatrick	CBS 118.80	SRR15309532[b]	This thesis
Pythium aristosporum Vanterpool	CBS 263.38	SRR15309564[b]	This thesis
Pythium arrhenomanes Drechsler	PAR_AA	SRR234857[b]	This thesis
Pythium brachiatum Uzuhashi & G. Okada	JCM 30210	SRR15309552[b]	This thesis
Pythium dissotocum Drechsler	CBS 166.68	SRR15309517[b]	This thesis
Pythium graminicola Subramanian	CBS 327.62	SRR15309567[b]	This thesis
Pythium grandisporangium Fell & Master	CBS 286.79	SRR15309566[b]	This thesis
Pythium insidiosum de Cock, Mendoza, Padhye, Ajello & Kaufman	–	NC_027966[a]	Tangphatsornruang et al. (2016)
Pythium lycopersicum G. Karaca, G. Tepedelen, & B. Paul	CBS 122909	SRR15309537[b]	This thesis
Pythium monospermum Pringsh.	CBS 158.73	SRR15309544[b]	This thesis
Pythium myriotylum Drechsler	SL2	SRR13960211[b]	This thesis
Pythium oligandrum Drechsler	Po37	SRR3130739[b]	This thesis
Pythium phragmiticola J. Nechwatal & R. Lebecka	CBS 135511	SRR15309480[b]	This thesis

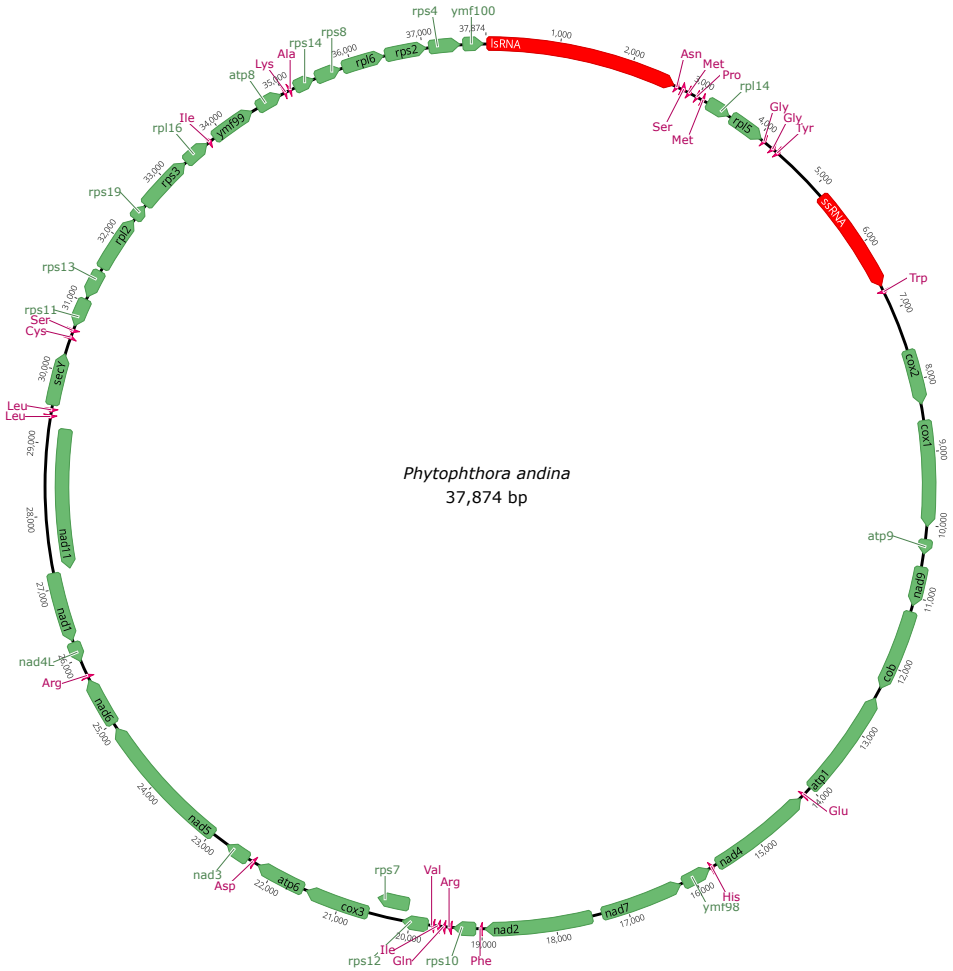
Pythium plurisporium Abad, Shew, Grand & L.T. Lucas	CBS 100530	SRR15309553[b]	This thesis
Pythium porphyrae M. Takah. & M. Sasaki	CBS 369.79	SRR15309568[b]	This thesis
Pythium pyrilobum Vaartaja	CBS 158.64	SRR15309560[b]	This thesis
Pythium rishiriense M.Z. Rahman, Abdelz. & Kageyama	CBS 139278	SRR15309482[b]	This thesis
Pythium sukuiense W. H. Ko, Shin Y. Wang & Ann	CBS 110030	SRR15309507[b]	This thesis
Pythium torulosum Coker & P. Patterson	CBS 316.33	SRR15309521[b]	This thesis
Pythium vanterpoolii V. Kouyeas & H. Kouyeas	CBS 295.37	SRR15309520[b]	This thesis
Salisapilia sapeloensis Hulvey, Nigrelli, Telle, Lamour & Thines	CBS 127946	SRR15309556[b]	This thesis
Saprolegnia diclina Humphrey	VS20	SRR576639[b]	This thesis
Saprolegnia ferax (Gruith) Thuret	–	AY534144[a]	Grayburn et al. (2004)
Saprolegnia parasitica Coker	N12	SRR515950[b]	This thesis
Sclerospora graminicola (Saccardo) J.Schröter	Sg-4	DRR097254[b]	This thesis
Thraustotheca clavata (de Bary) Humphrey	–	KF226725[a]	O'Brien et al. (2013)

[a] Complete mitogenome sequence accession [b] Sequence reads accession [c] Direct submission to GenBank

Appendix II Accessions included in the BLAST library used to identify contigs with similarity to oomycete mitochondrial genome sequences	
Species	**GenBank accession**
Achlya hypogyna	KF226724
Aphanomyces astaci	KX405004
Aphanomyces invadans	KX405005
Bremia lactucae	NC_040179
Peronospora effusa	MH142315
Peronospora tabacina	KT893455
Phytophthora agathidicida	MN883601
Phytophthora andina	NC_015619
Phytophthora chlamydospora	CM022726
Phytophthora gonapodyides	CM022728
Phytophthora infestans	NC_002387
Phytophthora ipomoeae	NC_015622
Phytophthora mirabilis	NC_015606
Phytophthora phaseoli	NC_015616
Phytophthora polonica	NC_029397
Phytophthora pseudosyringae	CM022727
Phytophthora ramorum	EU427470
Phytophthora sansomeana	NC_045089
Phytophthora sojae	NC_009385
Pseudoperonospora humuli	NC_042478
Pythium insidiosum	NC_027966
Pythium ultimum	NC_014280
Saprolegnia ferax	AY534144
Thraustotheca clavata	KF226725

Appendix III The mitogenomes of the oomycetes included in this study. Coloured blocks represent mitochondrial genes (red, rRNA genes; green, protein coding genes; pink, tRNA genes). For genes the direction of transcription is indicated by the direction of the arrowhead. Pictures were generated in Geneious R9 (Kearse et al., 2012). Light blue blocks indicate repeats; where present large inverted repeats are labelled, smaller repeats are numbered.

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Gly
Gly
Tyr
rpl5
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6,000
Trp
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cox2
8,000
cox1
9,000
10,000
atp9
atp8
11,000
cob
12,000
13,000
atp1
Glu
15,000
nad4
His
ymf98
17,000
nad7
18,000
19,000
nad2
Phe
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Arg
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rps12
Ile
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cox3
21,000
atp6
22,000
nad3
Asp
23,000
nad5
24,000
25,000
nad6
nad4L
Arg
27,000
nad1
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nad11
29,000
Leu
Leu
secY
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Ser
Cys
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rps13
rpl2
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rps19
rps3
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Gly
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ssRNA
6,000
Trp
7,000
cox2
8,000
cox1
9,000
10,000
atp9
atp8
11,000
cob
12,000
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atp1
Glu
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nad7
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nad2
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rps12
Val
Gln,Ile
20,000
cox3
21,000
atp6
22,000
nad3
Asp
23,000
nad5
24,000
25,000
nad6
nad4L
Arg
27,000
nad1
28,000
nad11
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Leu
secY
30,000
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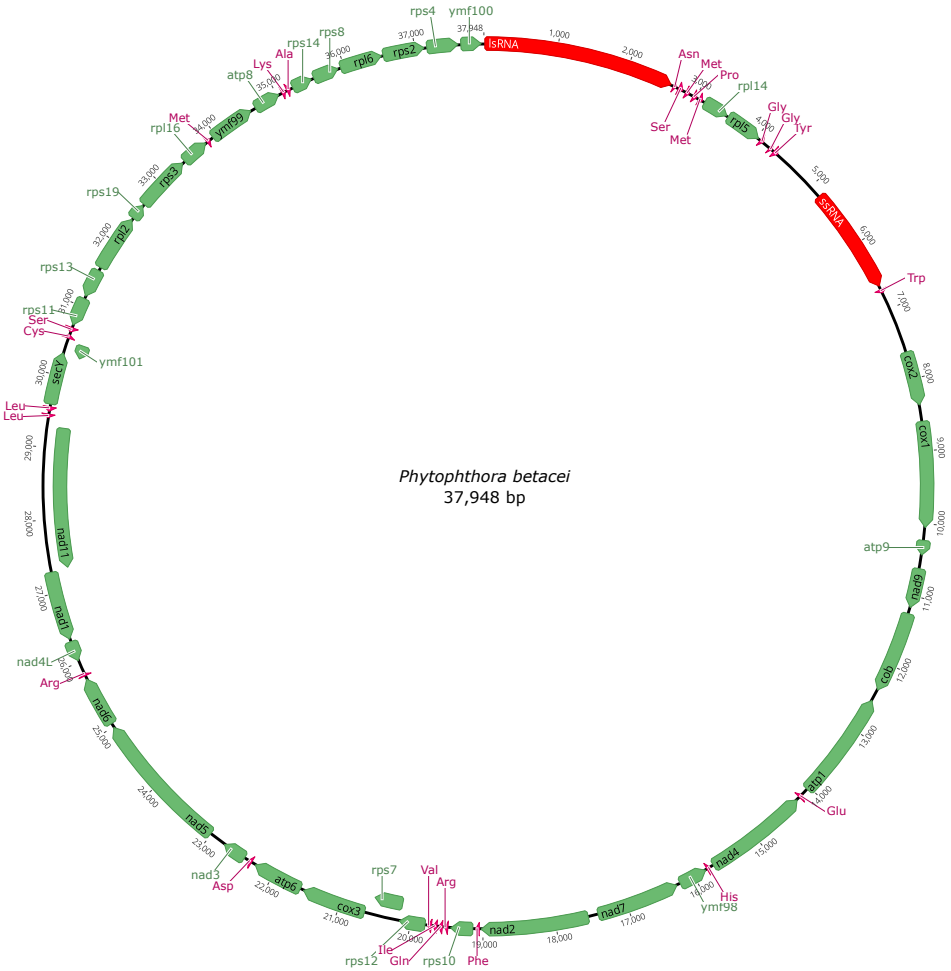
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Trp
7,000
cox2
8,000
cox1
9,000
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nad9
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cob
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Glu
nad4
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nad7
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nad2
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Ser
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Trp
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cox1
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nad3
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nad11
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Leu
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ymf101
rps11
Ser
Cys
rps13
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rpl2
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ymf99
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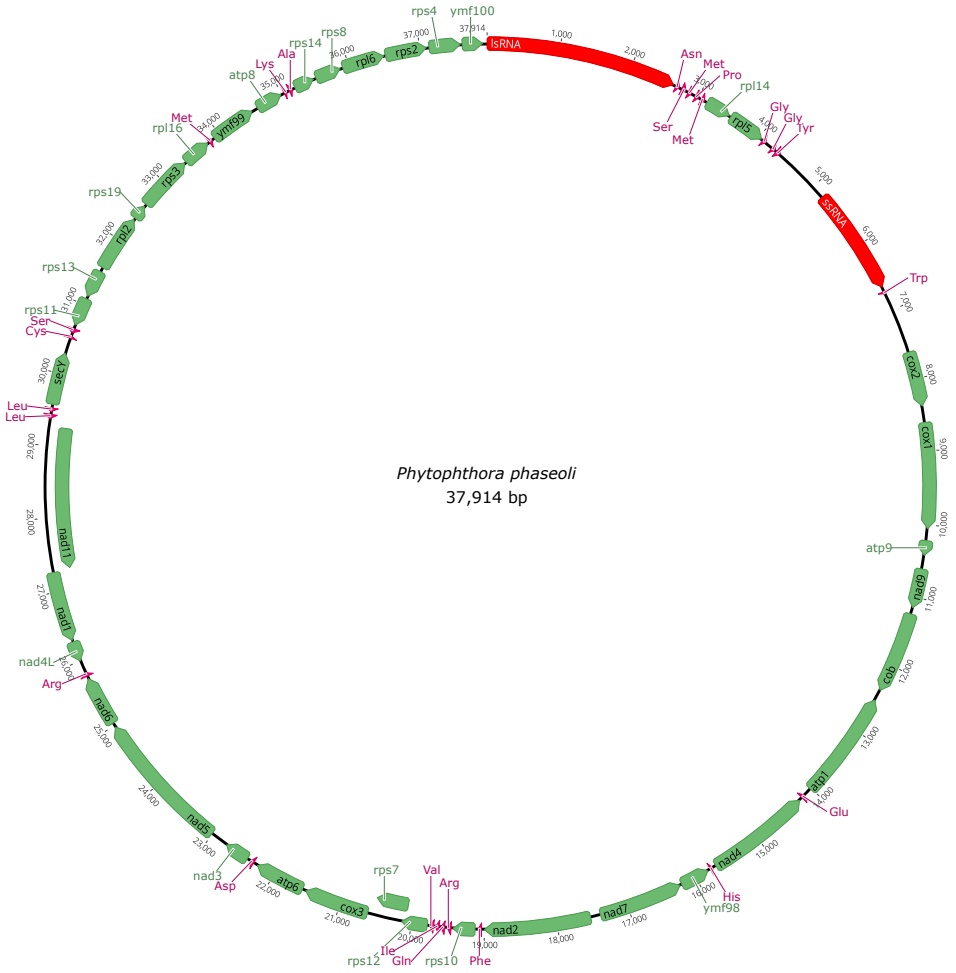
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Trp
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cox1
atp9
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nad4
atp1
Glu
nad7
His
ymf98
nad2
Phe
rps10
Arg
Gln
Ile
rps12
Val
rps7
cox3
atp6
Asp
nad3
nad5
nad6
nad4L
Arg
nad1
nad11
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Leu
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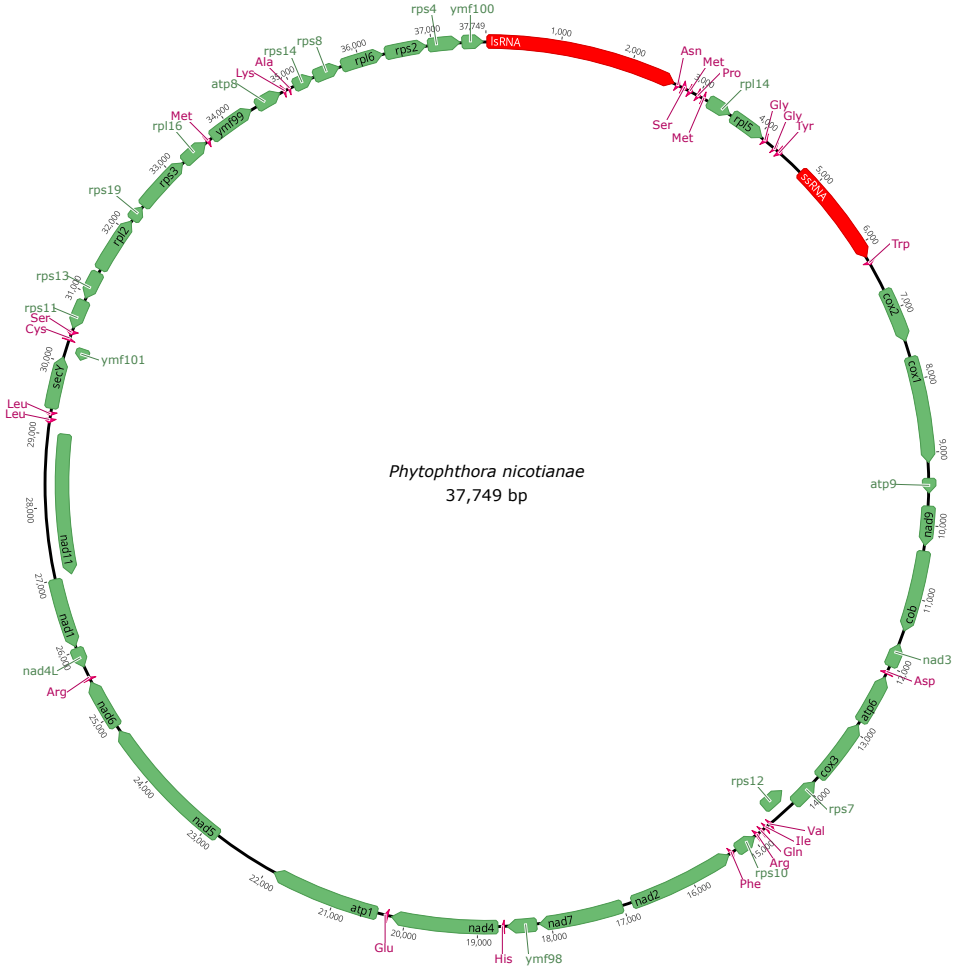
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nad4
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atp1
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nad4L
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nad1
nad11
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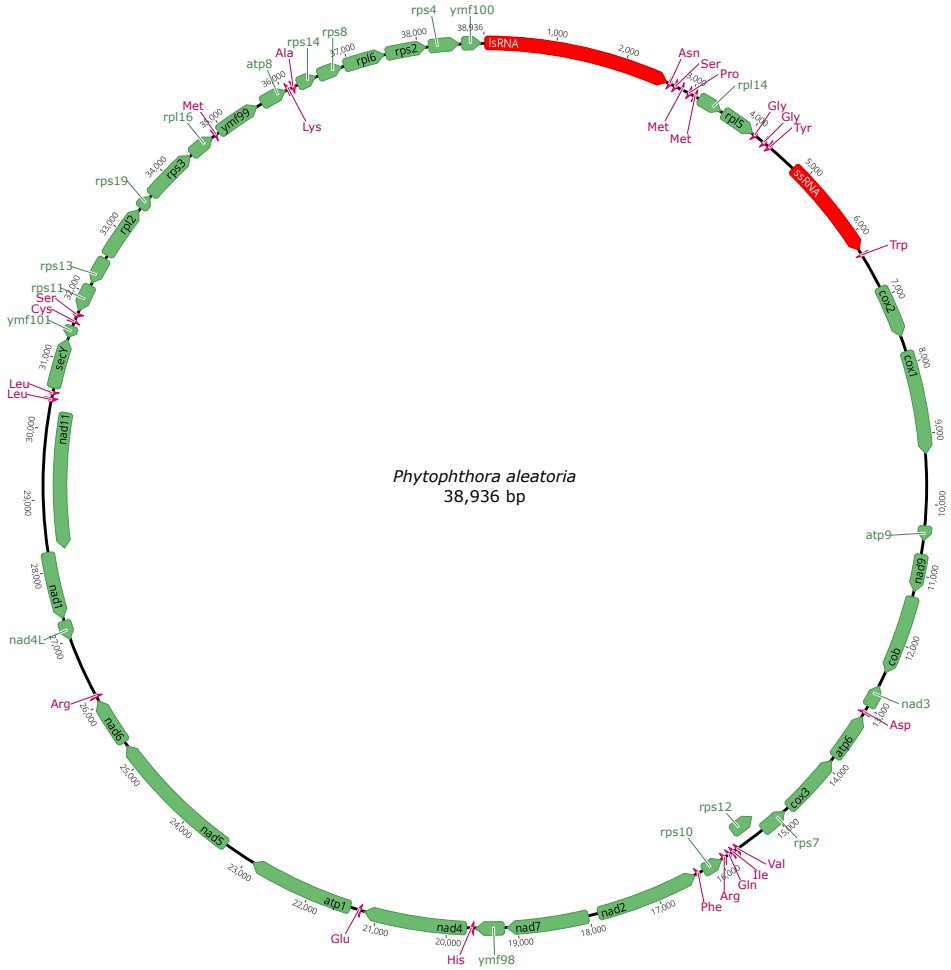
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rpl2
rps13
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Ser
Cys
ymf101
sdh3
Leu
Leu
nad11
nad1
nad4L
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nad6
nad5
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nad2
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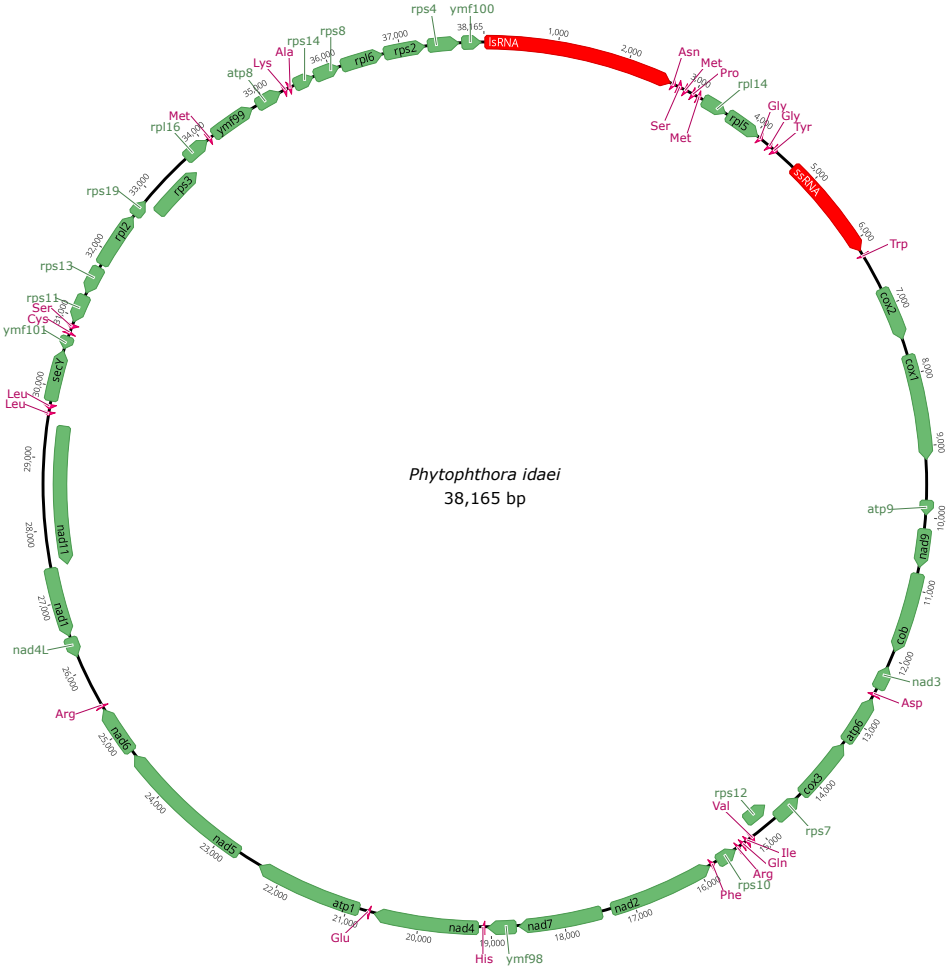
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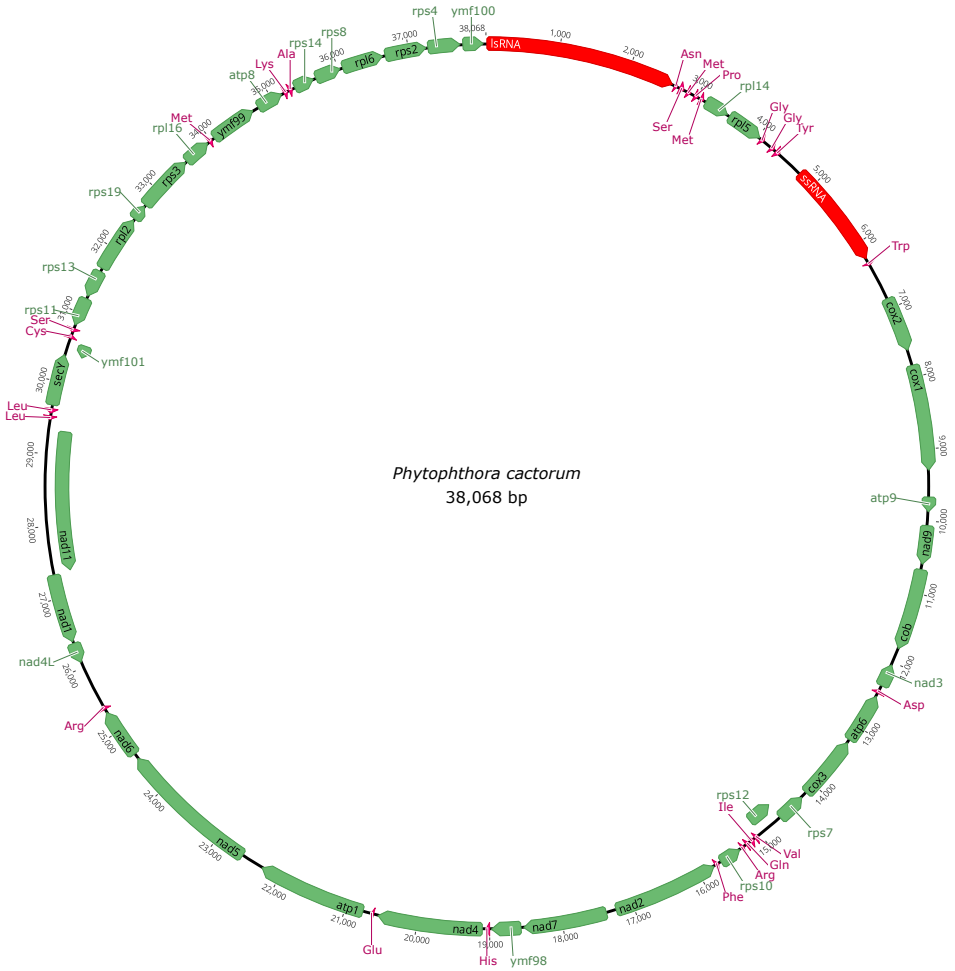
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Leu
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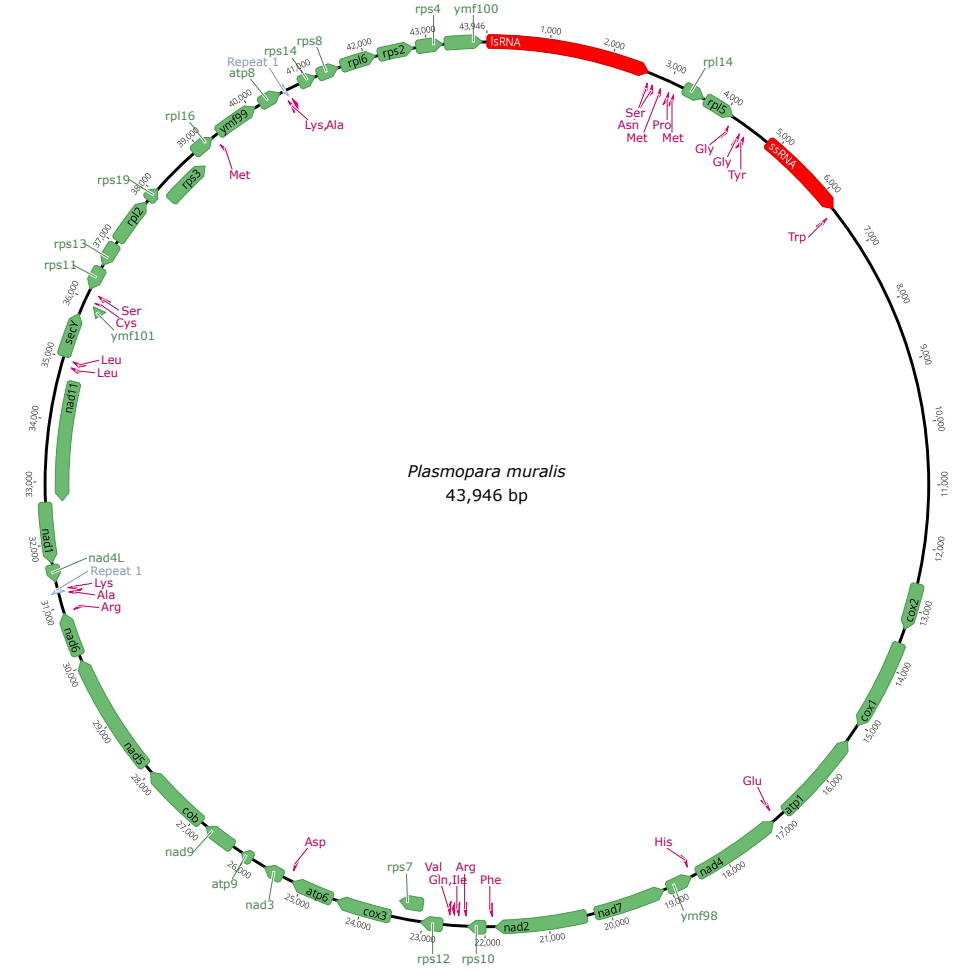
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rps11
Ser
Cys
ymf101
sec7
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Leu
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nad1
nad4L
Repeat 1
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cob
nad9
Asp
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nad4
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cox1
cox2


Plasmopara viticola
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Gly
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ymf100
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Ala
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atp8
ymf99
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rps3
rps19
rpl2
rps13
rps11
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ymf101
sdh4
Leu
Leu
nad11
nad1
nad4L
Lys
Ala
Arg
nad6
nad5
cob
nad9
atp9
nad3
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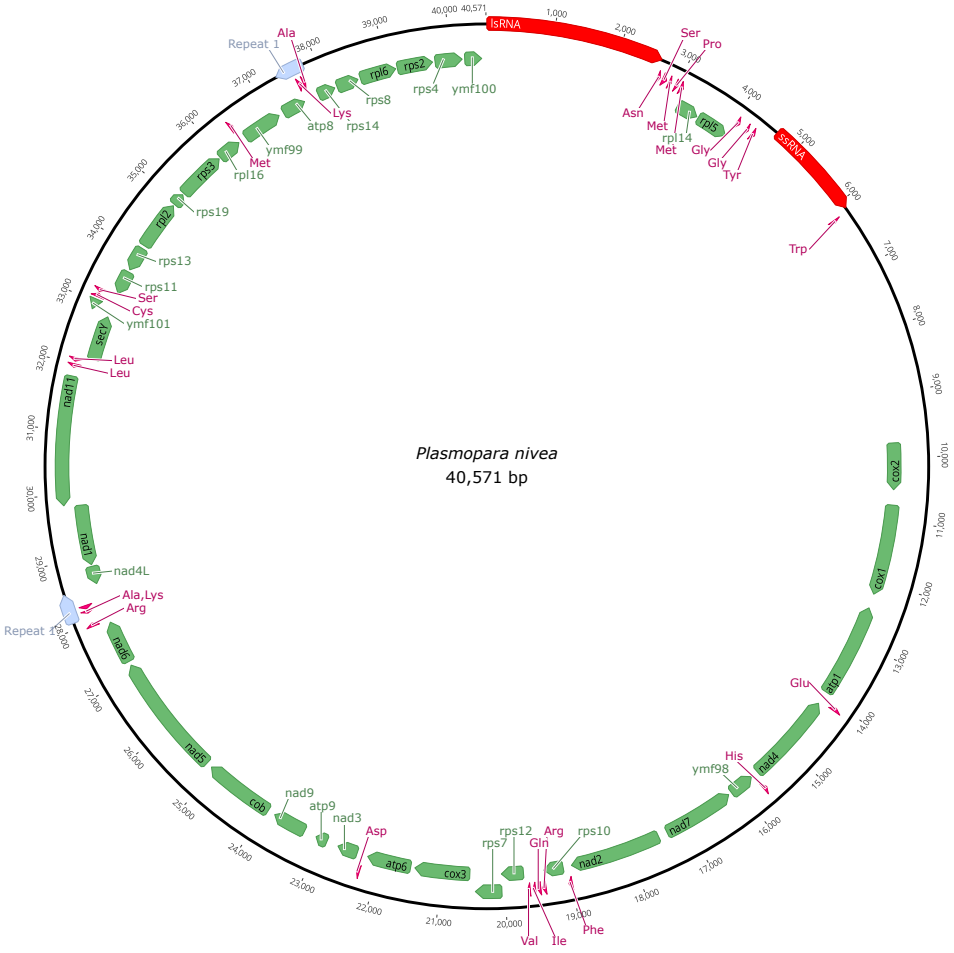
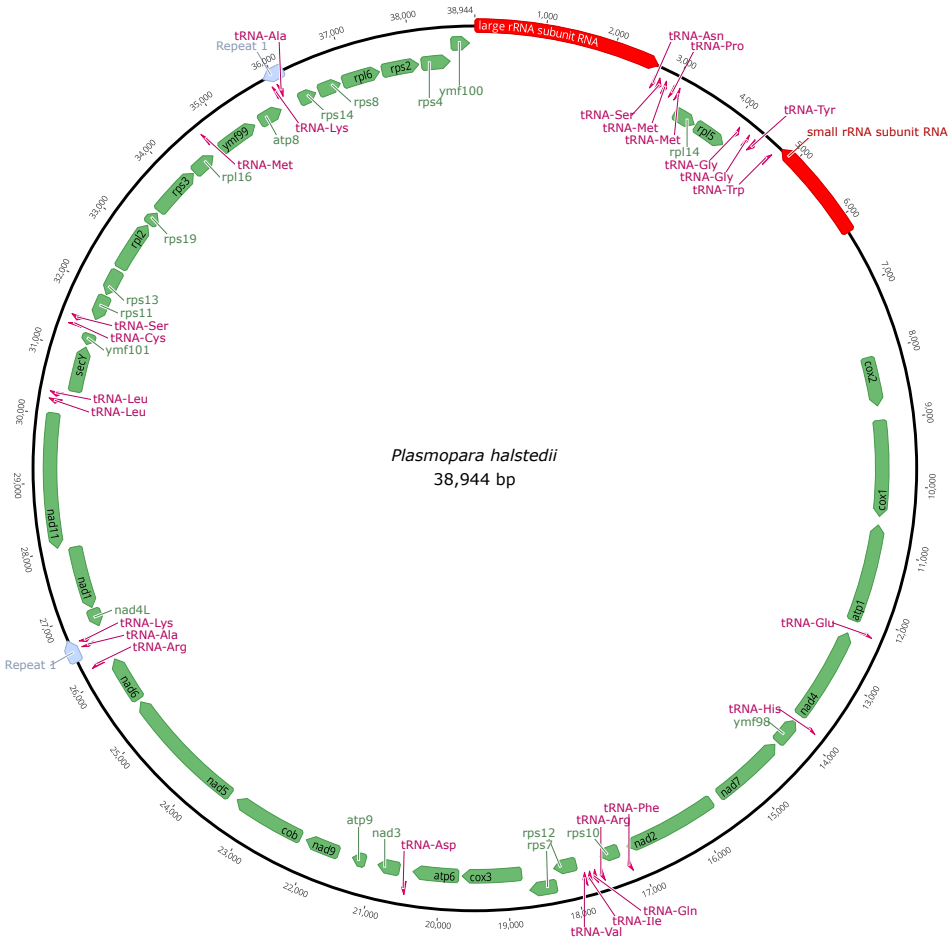
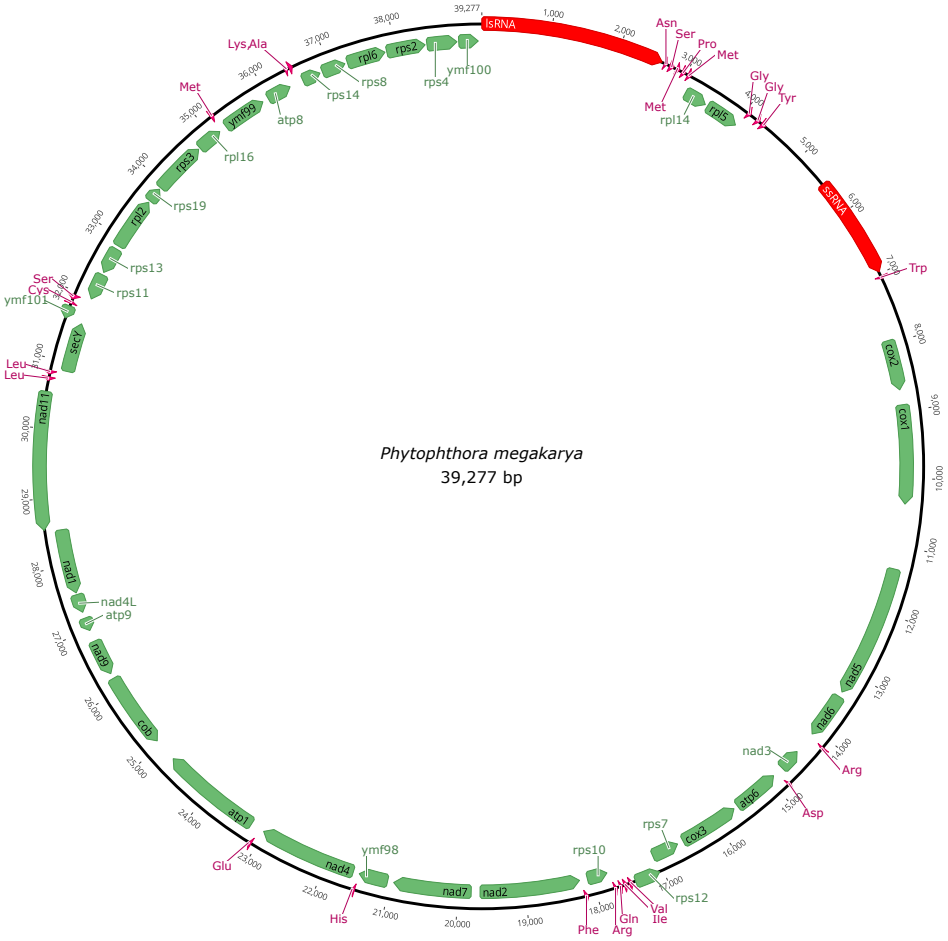
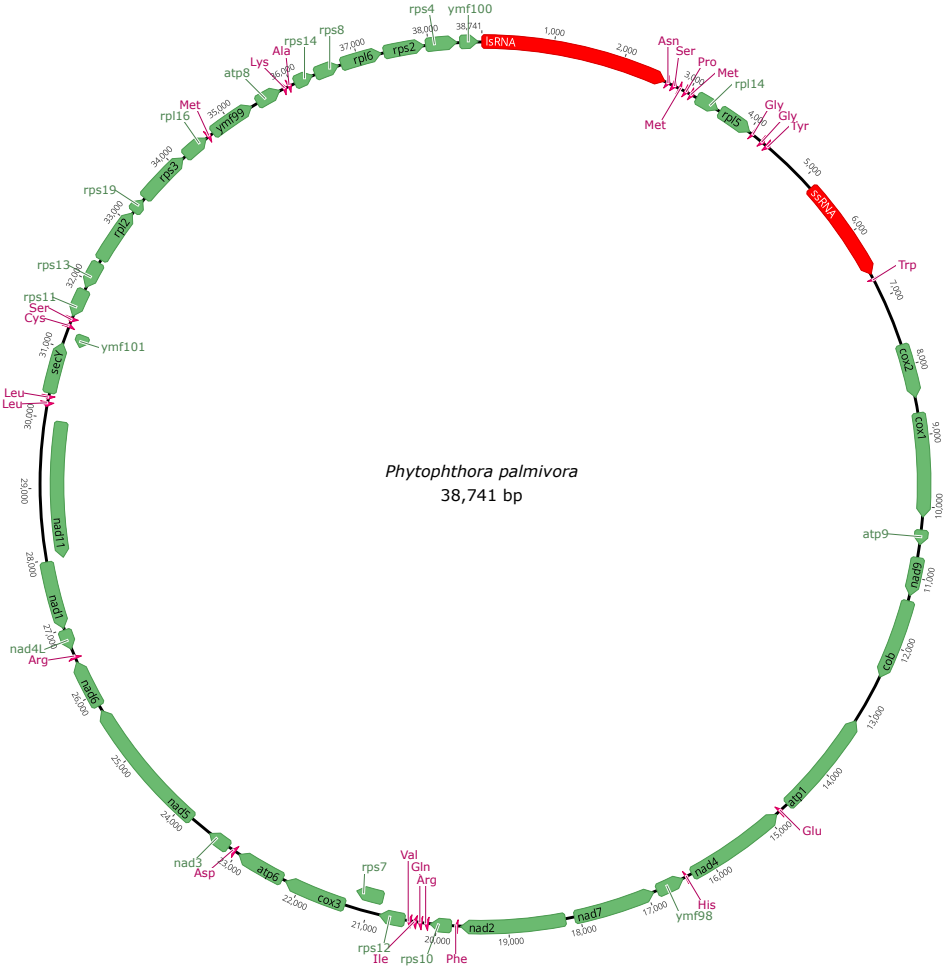
ymf98
His
nad4
Glu
atp1
cox1
cox2
rps7
Val
Arg
Phe

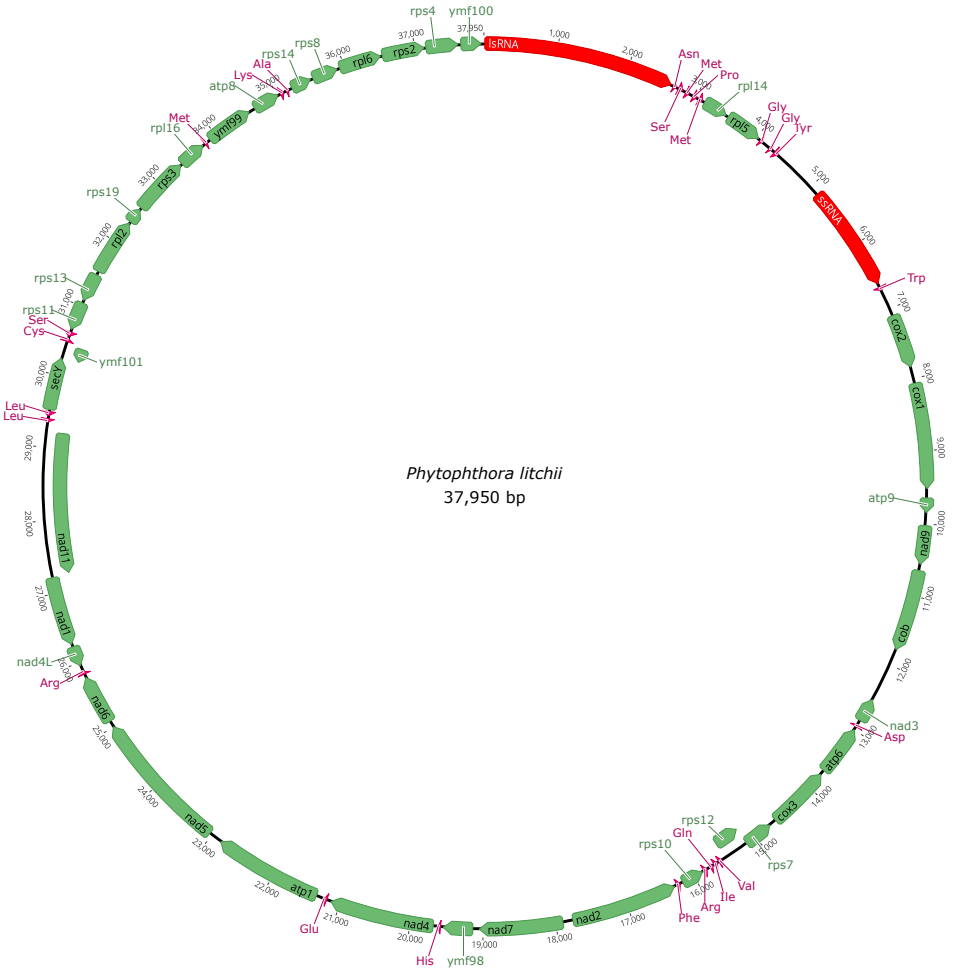

Plasmopara nivea
40,571 bp
lsRNA
ssRNA
Repeat 1
Repeat 1
Ala
Ser
Pro
Asn
Met
rpl14
Met
rpl5
Gly
Gly
Tyr
Trp
rps4
ymf100
rps2
rpl6
rps8
rps14
Lys
atp8
ymf99
Met
rpl16
rps3
rps19
rpl2
rps13
rps11
Ser
Cys
ymf101
sdh4
Leu
Leu
nad11
nad1
nad4L
Ala,Lys
Arg
nad6
nad5
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
rps12
Gln
Arg
rps10
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox1
cox2
Val
Ile
Phe

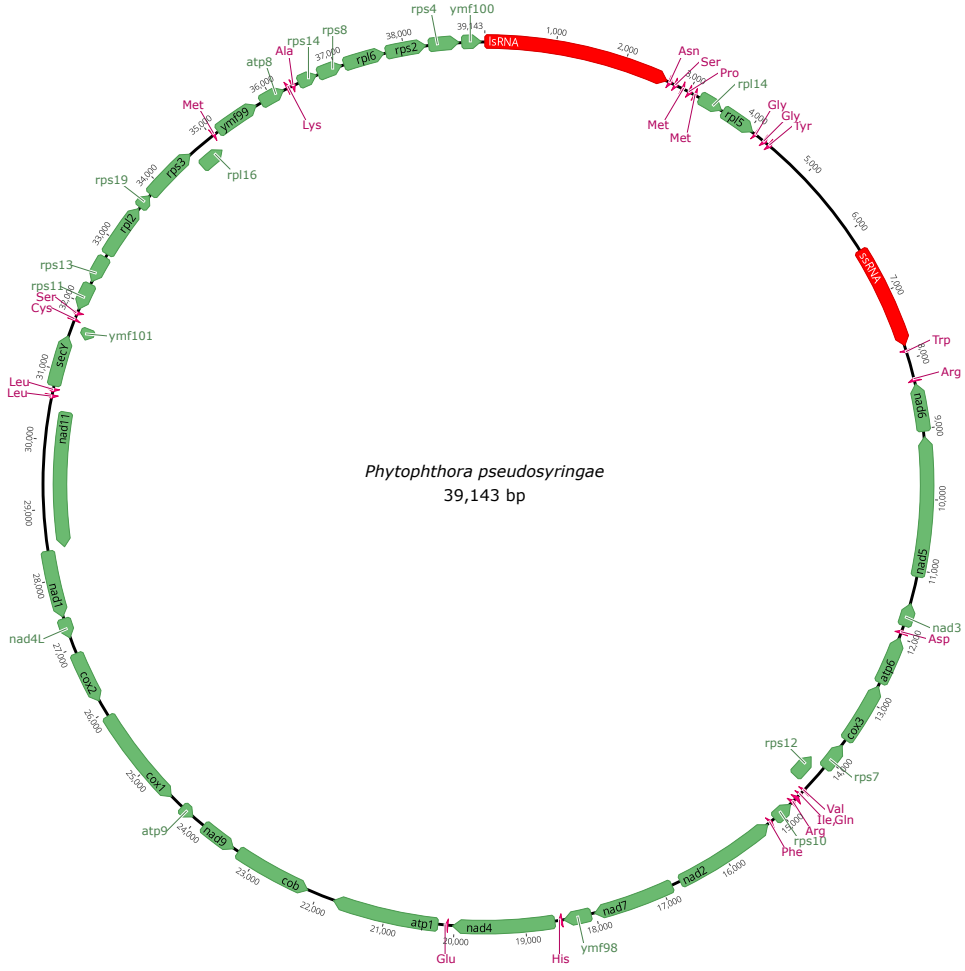

large rRNA subunit RNA
small rRNA subunit RNA
tRNA-Ala
Repeat 1
tRNA-Asn
tRNA-Pro
tRNA-Ser
tRNA-Met
tRNA-Met
tRNA-Tyr
tRNA-Gly
tRNA-Gly
tRNA-Trp
rpl6
rps2
rps4
ymf100
rps14
rps8
tRNA-Lys
atp8
ymf99
tRNA-Met
rpl16
rps3
rpl2
rps19
rps13
rps11
tRNA-Ser
tRNA-Cys
ymf101
secY
tRNA-Leu
tRNA-Leu
nad11
nad1
nad4L
tRNA-Lys
tRNA-Ala
tRNA-Arg
Repeat 1
nad6
nad5
cob
nad9
atp9
nad3
tRNA-Asp
atp6
cox3
rps12
rps7
tRNA-Phe
tRNA-Arg
rps10
nad2
tRNA-Gln
tRNA-Ile
tRNA-Val
nad7
tRNA-His
ymf98
nad4
tRNA-Glu
atp1
cox1
cox2
Plasmopara halstedii
38,944 bp

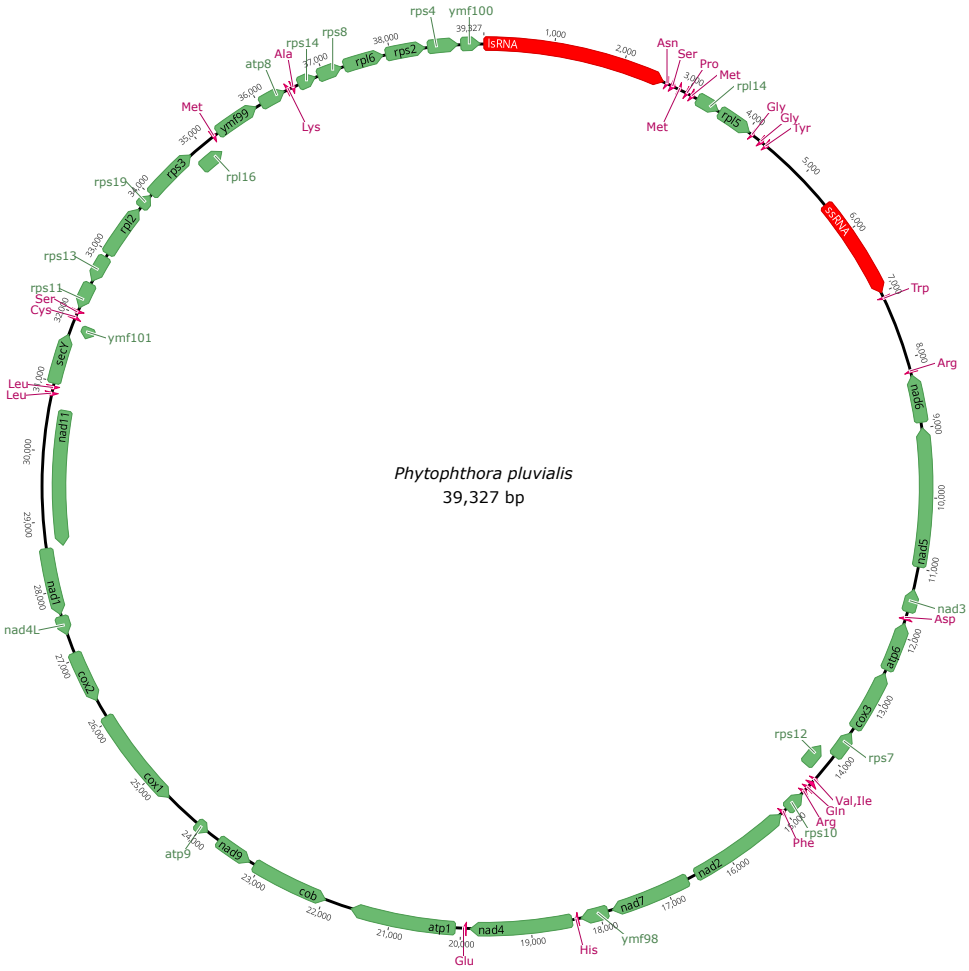

lsRNA
ssRNA
Repeat 2
Asn
Met
Ser
Pro
rpl5
rpl14
Met
Gly
Tyr
Gly
Trp
rpl6
rps2
rps4
ymf100
rps14
rps8
Lys
Ala
atp8
ymf99
Met
rpl16
rps3
rpP
rps19
rps13
rps11
ymf101
Ser
Cys
secY
Leu
Leu
nad11
nad1
nad4L
Lys
Arg
Repeat 2
nad6
nad5
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps12
Ile
Val
rps7
Gln
rps10
Phe
Arg
nad2
nad7
His
ymf98
nad4
Glu
atp1
cox1
cox2
Repeat 1
Repeat 1
Bremia lactucae
39,302 bp

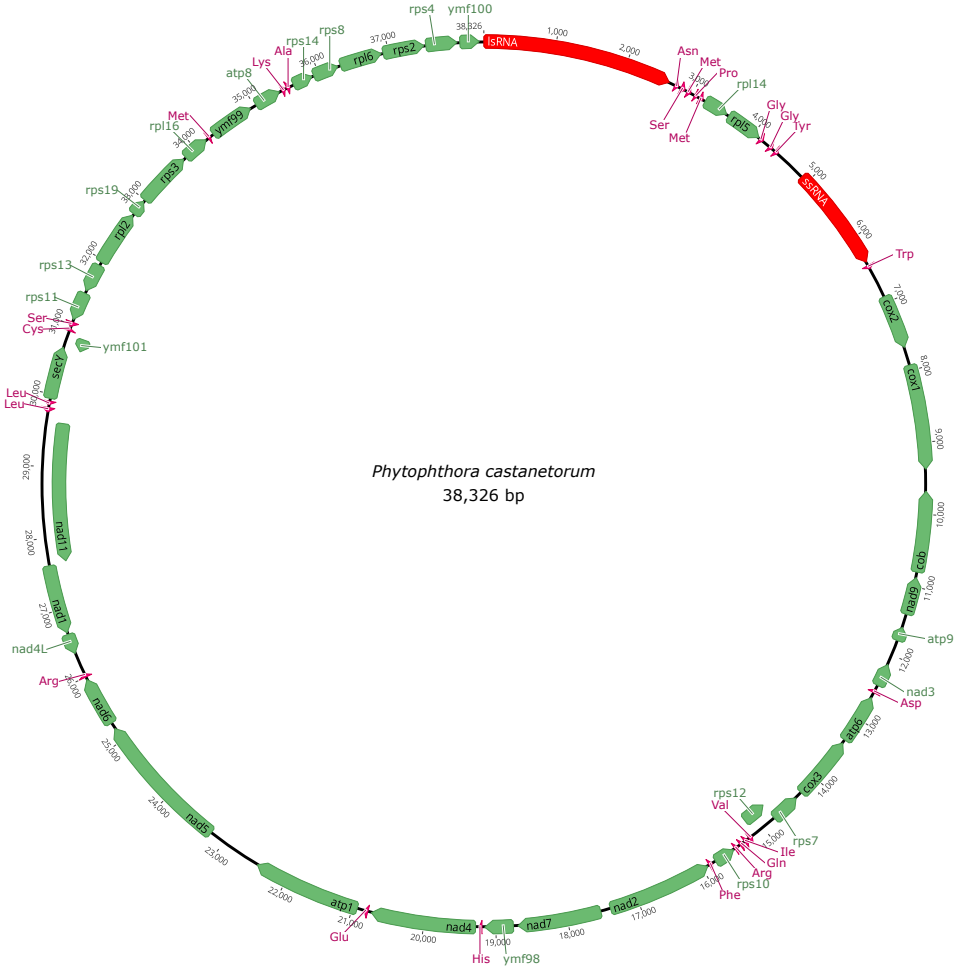

Phytophthora megakarya
39,277 bp
lsRNA
ssRNA
rps2
rps4
ymf100
rps8
rps14
rpl6
atp8
ymf99
rpl16
rps3
rpl2
rps19
rps13
rps11
ymf101
sec7
nad11
nad1
nad4L
atp9
nad9
cob
atp1
nad4
ymf98
nad7
nad2
rps10
rps12
rps7
cox3
atp6
nad3
nad6
nad5
cox1
cox2
rpl5
rpl14
Asn
Ser
Pro
Met
Gly
Tyr
Trp
Lys
Ala
Glu
His
Phe
Gln
Arg
Val
Ile
Asp
Leu
Cys

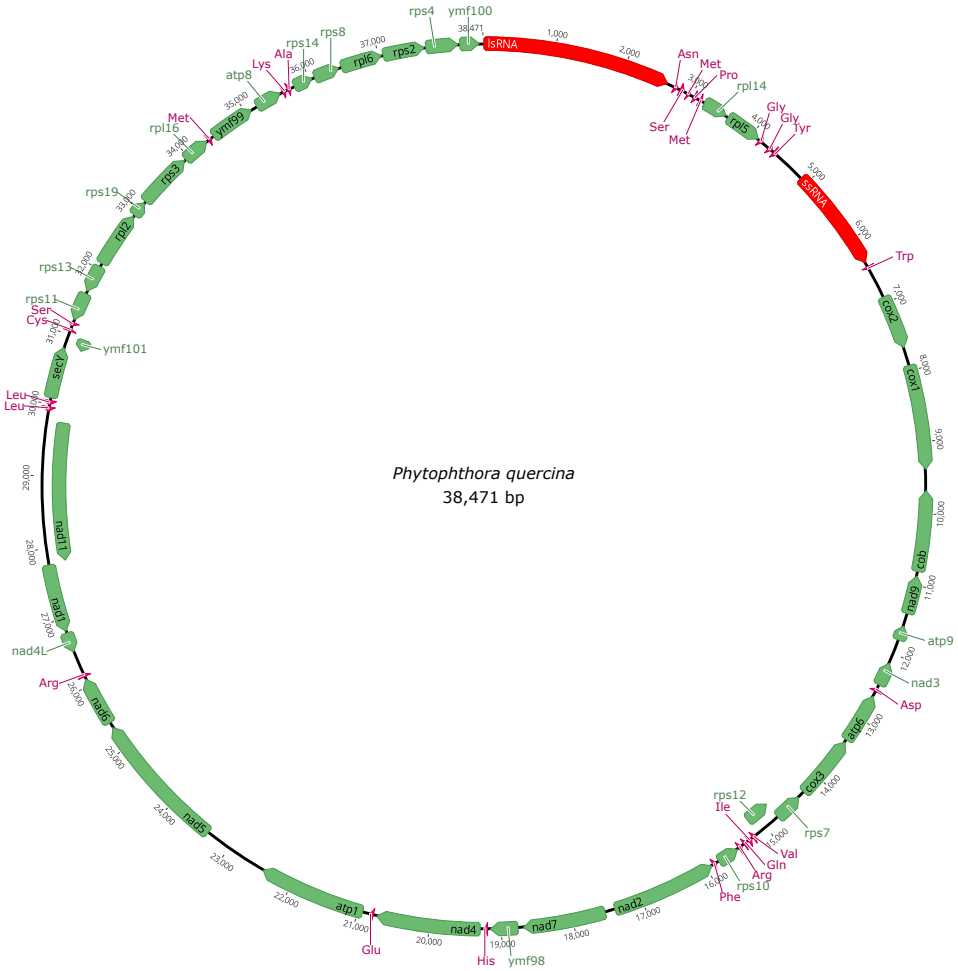

Phytophthora palmivora
38,741 bp
lsRNA
ssRNA
rps4
ymf100
rps8
rps14
rpl6
rps2
atp8
ymf99
rpl16
rps3
rpl2
rps19
rps13
rps11
ymf101
sec7
nad11
nad1
nad4L
nad9
cob
atp9
atp1
nad4
ymf98
nad7
nad2
rps10
rps12
rps7
cox3
atp6
nad3
nad5
cox1
cox2
rpl5
rpl14
Asn
Ser
Pro
Met
Gly
Tyr
Trp
Lys
Ala
Glu
His
Phe
Gln
Arg
Val
Ile
Asp
Leu
Cys


Phytophthora litchii
37,950 bp
rps4
ymf100
lsRNA
Asn
Met
Pro
rpl14
Ser
Met
rpl5
Gly
Gly
Tyr
sRNA
Trp
cox2
cox1
atp9
nad9
cob
nad3
Asp
atp6
cox3
rps12
Gln
rps7
rps10
Val
Ile
Arg
Phe
nad2
nad7
ymf98
His
nad4
atp1
Glu
nad5
nad6
nad1
nad4L
Arg
nad11
Leu
Leu
sec1
ymf101
Ser
Cys
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys
Ala
rps14
rps8
rpl6
rps2

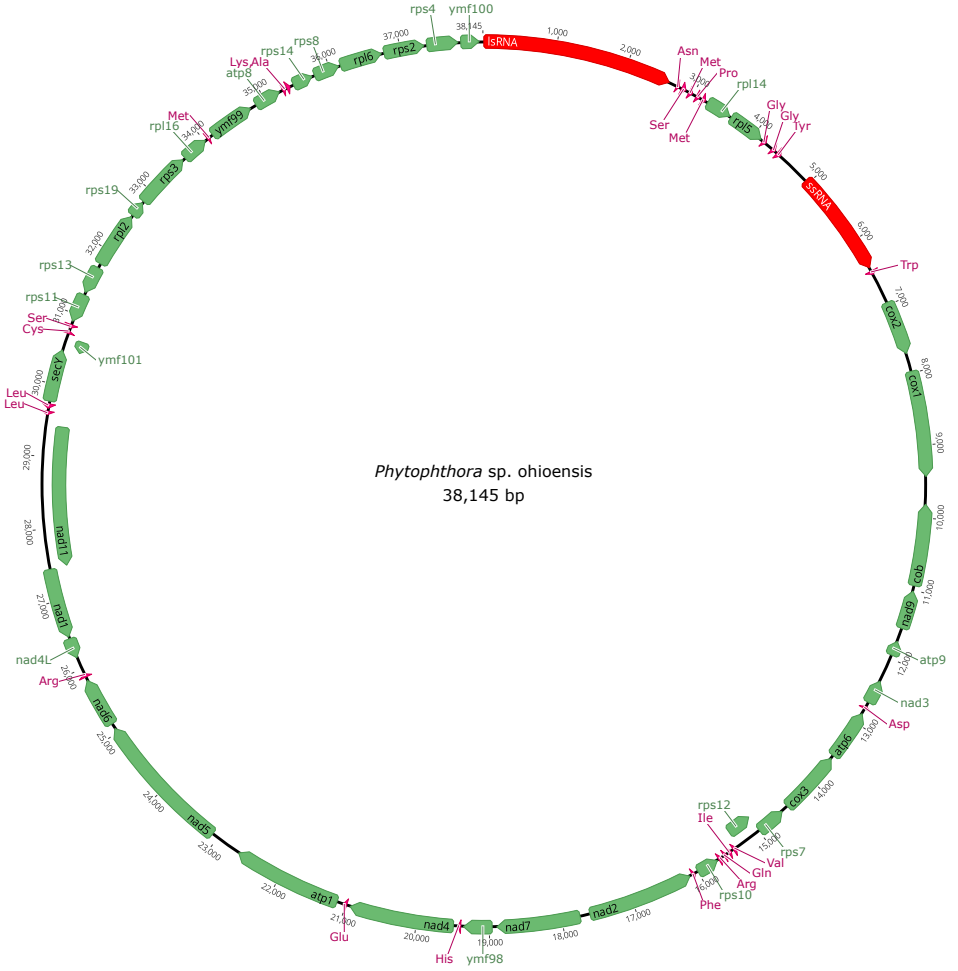

Phytophthora pseudosyringae
39,143 bp
rps4
ymf100
lsRNA
Asn
Ser
Pro
rpl14
Met
Met
rpl5
Gly
Gly
Tyr
sRNA
Trp
Arg
nad6
nad5
nad3
Asp
atp6
cox3
rps12
rps7
Val
Ile
Gln
Arg
rps10
Phe
nad2
nad7
ymf98
His
nad4
atp1
Glu
cob
nad9
atp9
cox1
cox2
nad4L
nad1
nad11
Leu
Leu
sec1
ymf101
Ser
Cys
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
Met
Lys
atp8
Ala
rps14
rps8
rpl6
rps2


Phytophthora pluvialis
39,327 bp
rps4
ymf100
lsRNA
Asn
Ser
Pro
Met
rpl14
rpl5
Gly
Gly
Tyr
ssRNA
Trp
Arg
nad6
nad5
nad3
Asp
atp6
cox3
rps7
rps12
Val,Ile
Gln
Arg
rps10
Phe
nad2
nad7
ymf98
His
nad4
atp1
Glu
cob
atp9
nad9
rps3
rpl16
Met
ymf99
Lys
atp8
Ala
rps14
rps8
rpl6
rps2
rps19
rpl2
rps13
rps11
Ser
Cys
ymf101
sec4
Leu
Leu
nad11
nad1
nad4L

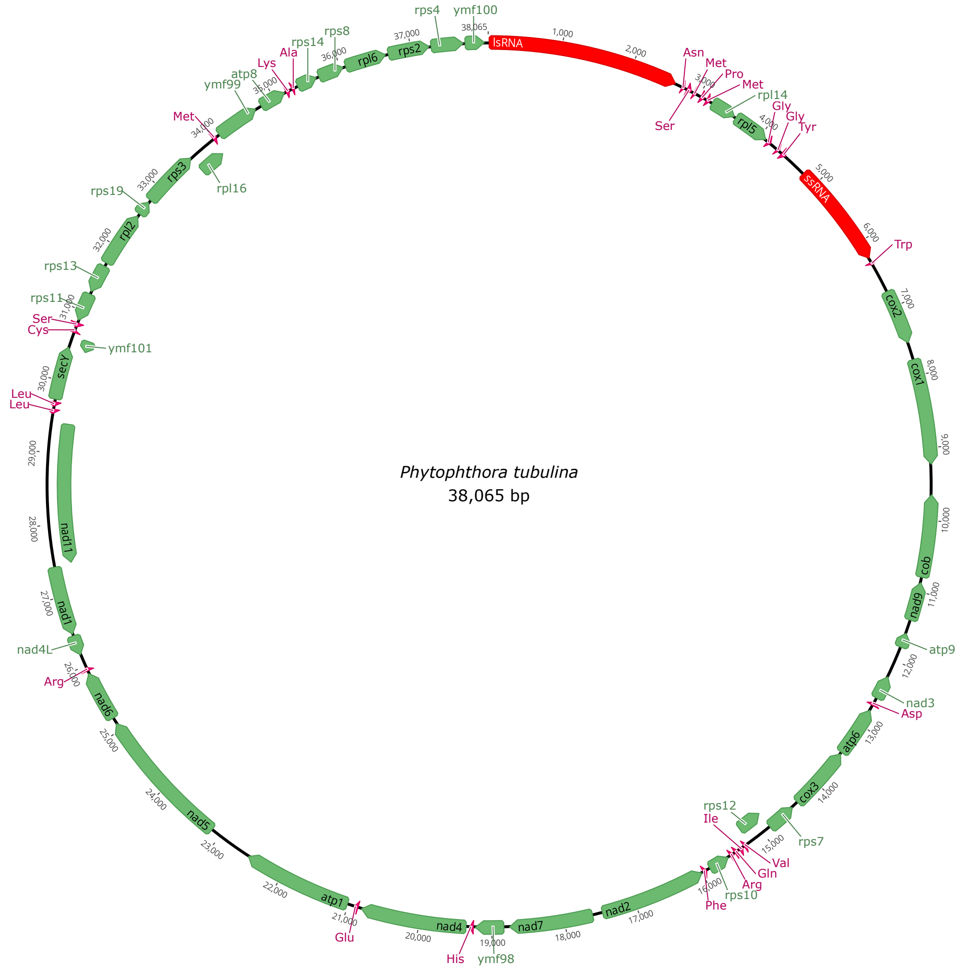

Phytophthora castanetorum
38,326 bp
rps4
ymf100
lsRNA
Asn
Met
Pro
rpl14
rpl5
Gly
Gly
Tyr
ssRNA
Trp
cox2
cox1
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
rps12
Val
Ile
Gln
Arg
rps10
Phe
nad2
nad7
ymf98
His
nad4
atp1
Glu
nad5
nad6
Arg
nad4L
nad1
nad11
sec4
Leu
Leu
ymf101
Ser
Cys
rps11
rps13
rpl2
rps19
rps3
Met
rpl16
ymf99
Lys
atp8
Ala
rps14
rps8
rpl6
rps2

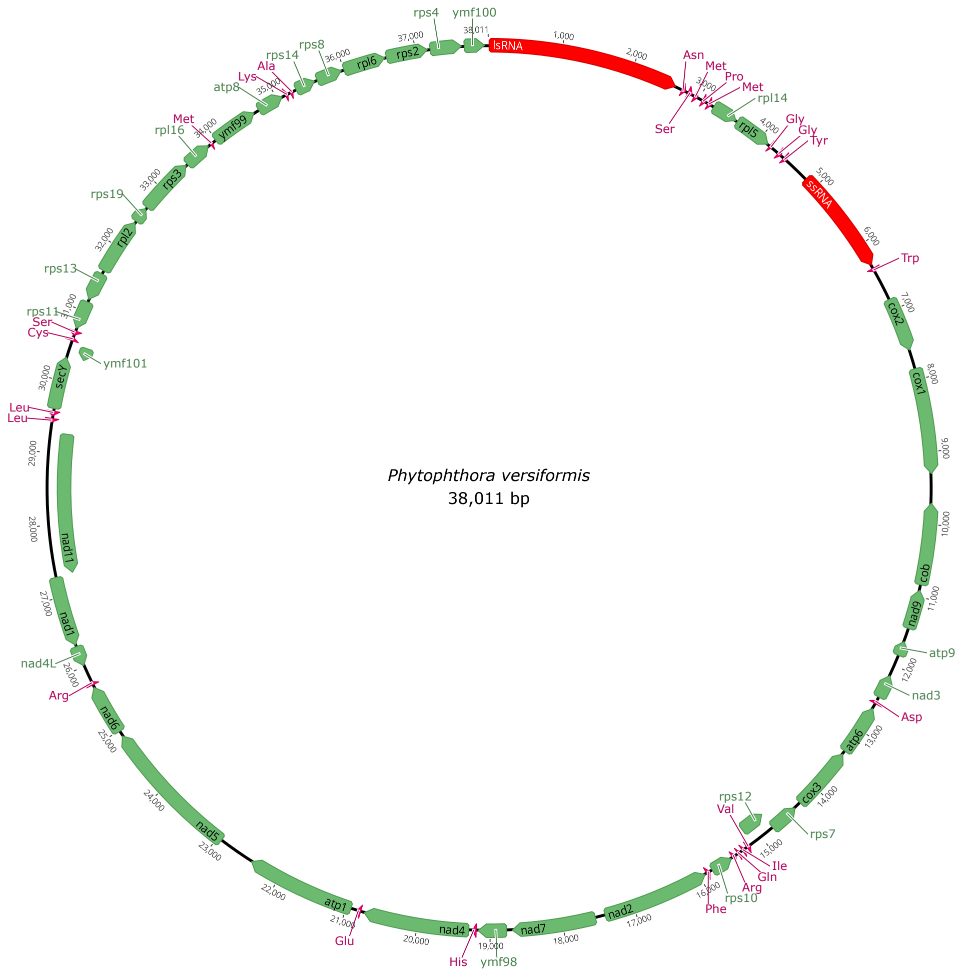


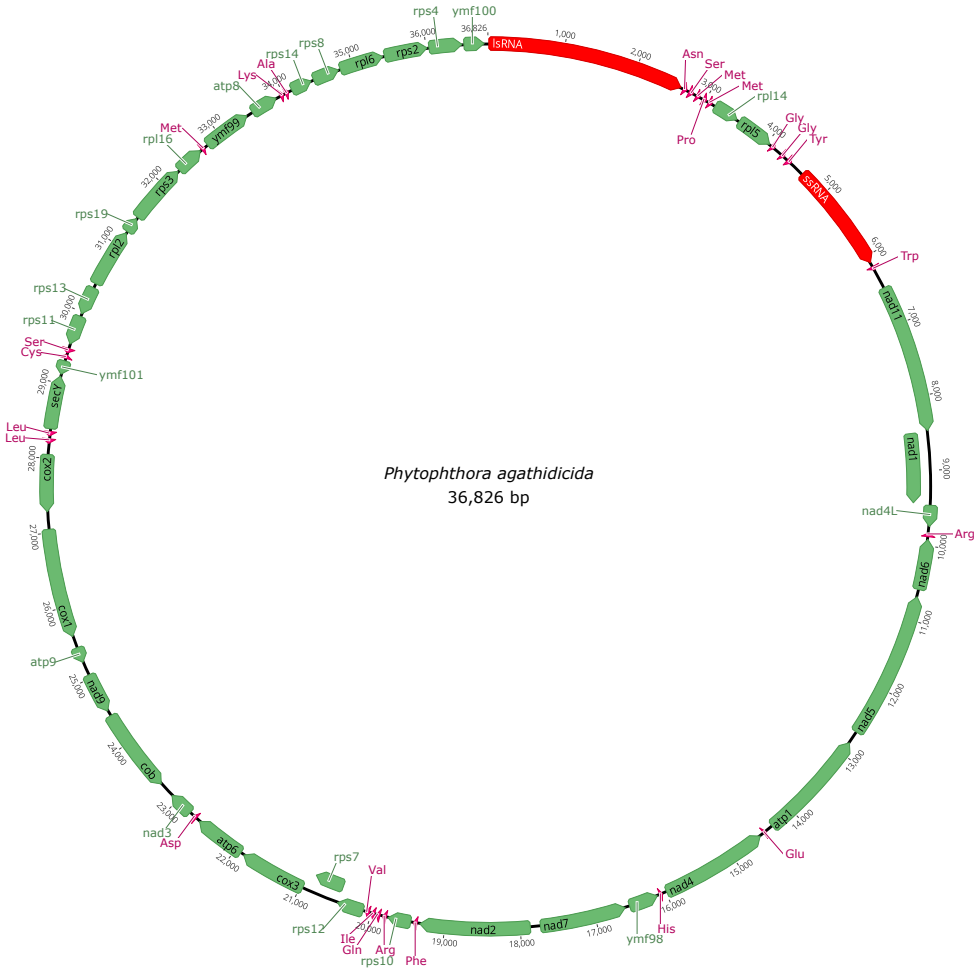
Phytophthora quercina
38,471 bp



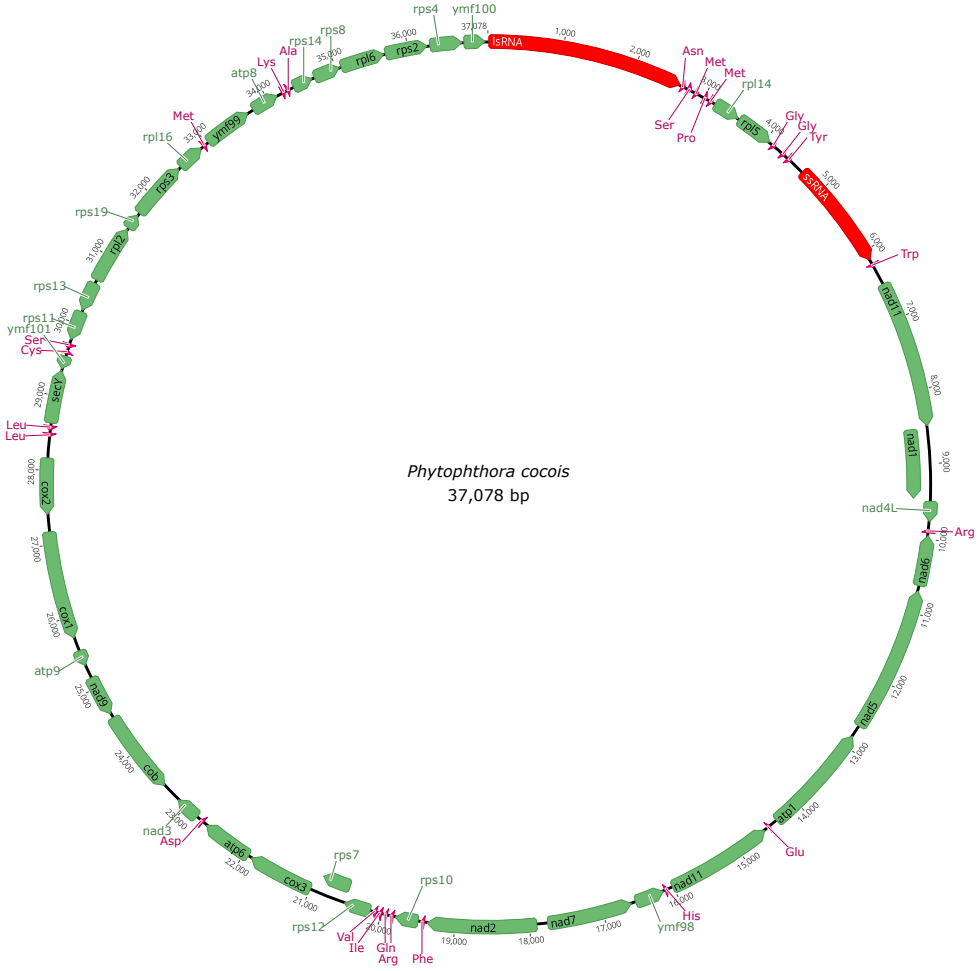
Phytophthora sp. ohioensis
38,145 bp


Phytophthora tubulina
38,065 bp
lsRNA
ssRNA
Asn
Met
Pro
Met
Ser
rpl14
rpl5
Gly
Gly
Tyr
Trp
cox2
cox1
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
rps12
Ile
Val
Gln
Arg
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
nad5
nad6
Arg
nad4L
nad1
nad11
Leu
Leu
secY
ymf101
Ser
Cys
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys
Ala
rps14
rps8
rpl6
rps2
rps4
ymf100

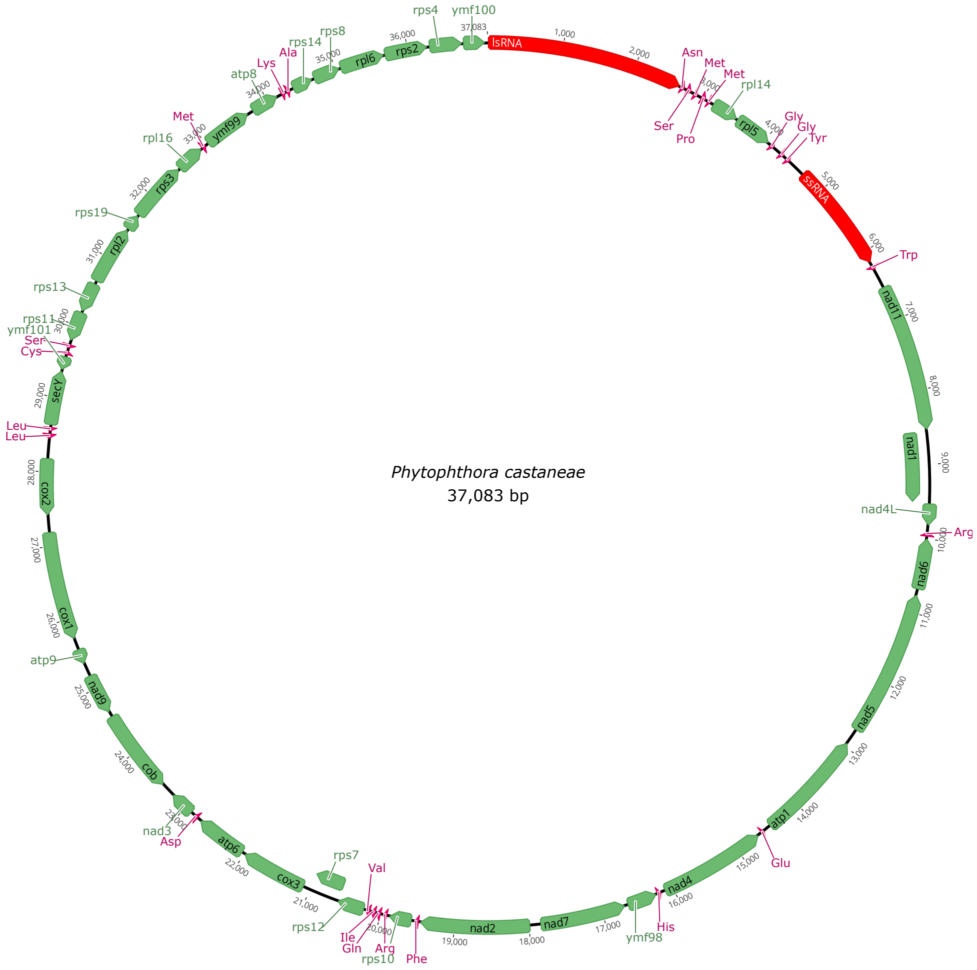

Phytophthora versiformis
38,011 bp
lsRNA
ssRNA
Asn
Met
Pro
Met
Ser
rpl14
rpl5
Gly
Gly
Tyr
Trp
cox2
cox1
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
rps12
Val
Ile
Gln
Arg
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
nad5
nad6
Arg
nad4L
nad1
nad11
Leu
Leu
secY
ymf101
rps11
Ser
Cys
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys
Ala
rps14
rps8
rpl6
rps2
rps4
ymf100



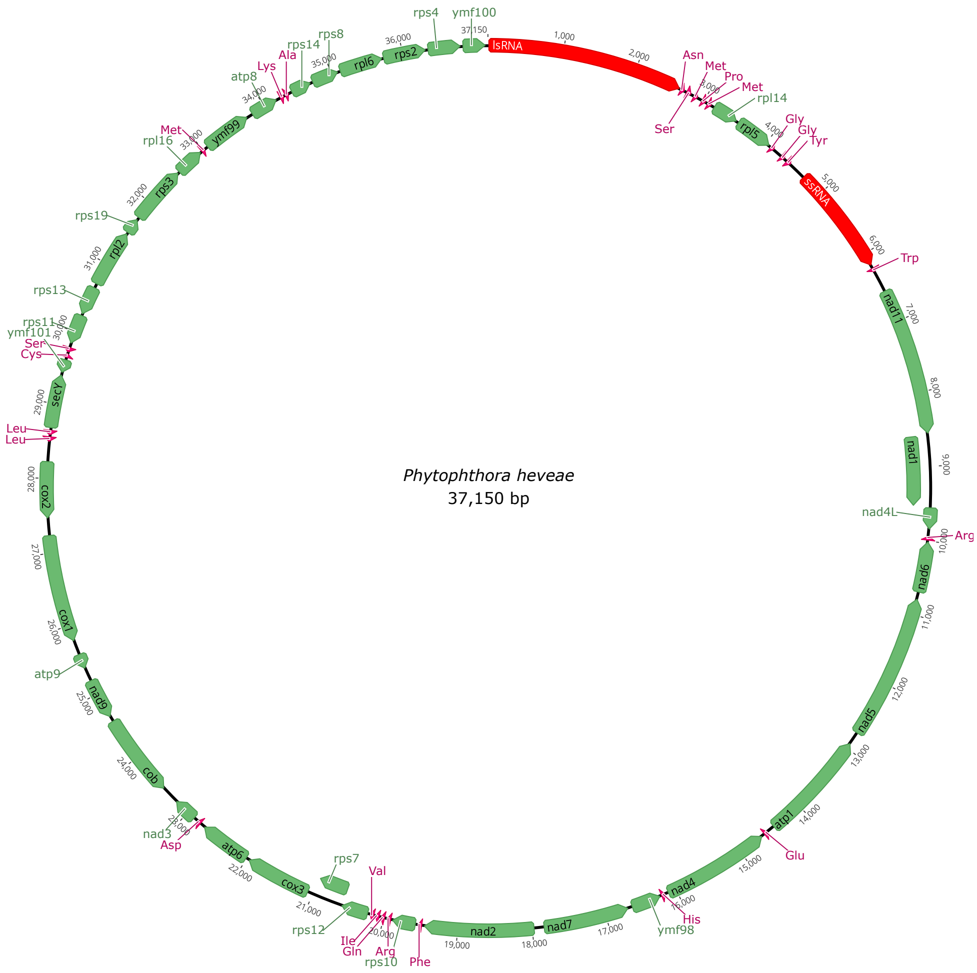
Phytophthora agathidicida
36,826 bp



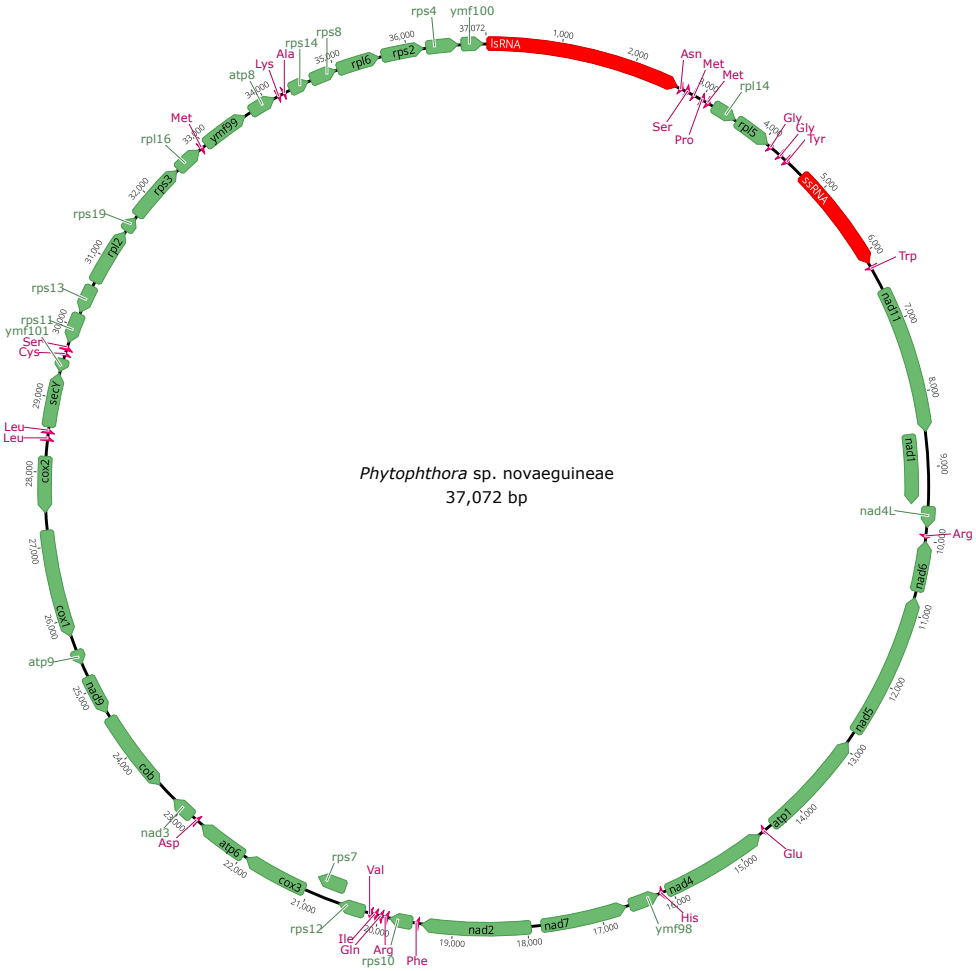
Phytophthora cocois
37,078 bp

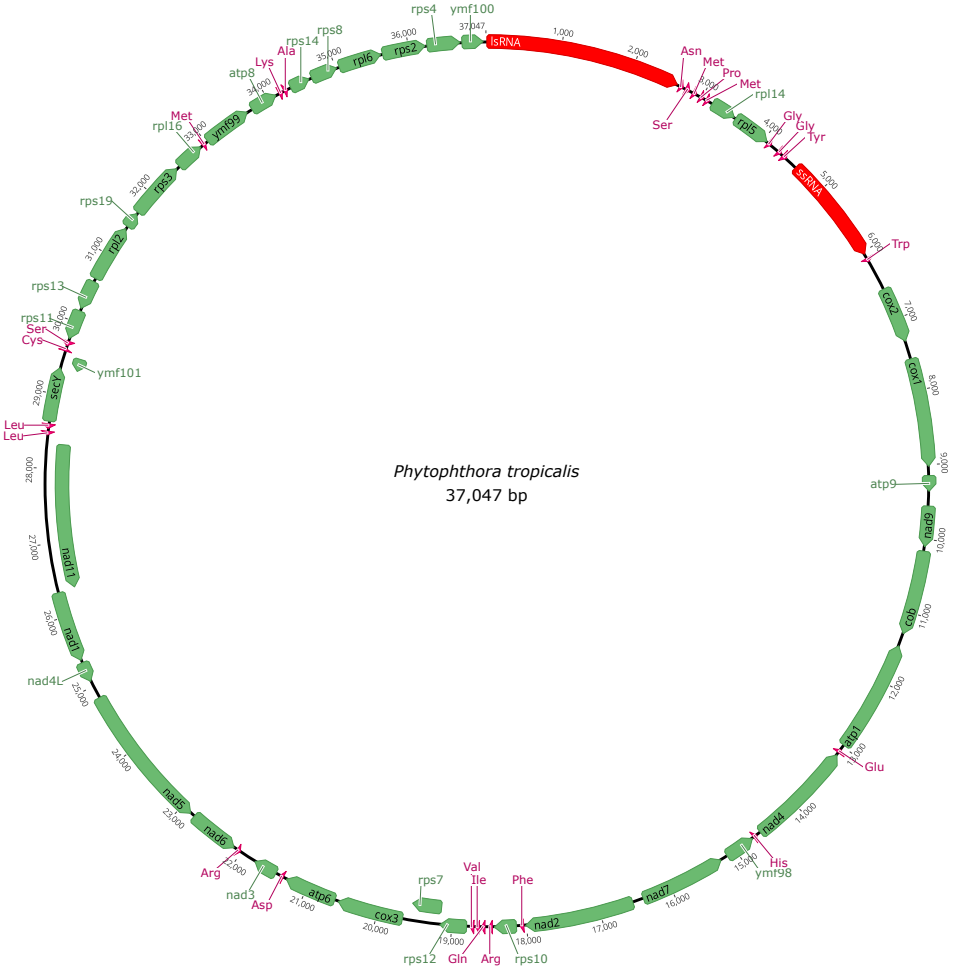


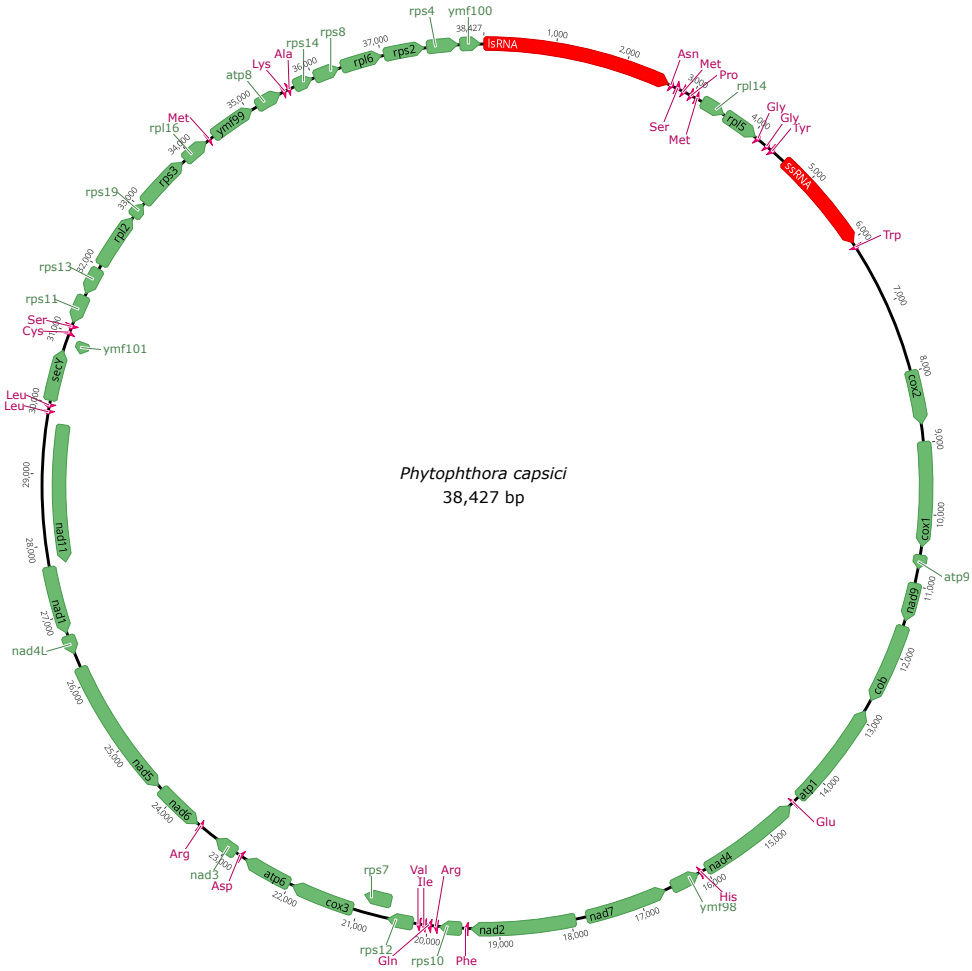
Phytophthora castaneae
37,083 bp
rps4
ymf100
lsRNA
Asn
Met
Met
Ser
Pro
rpl14
rpl5
Gly
Gly
Tyr
ssRNA
Trp
nad11
nad1
nad4L
Arg
nad6
nad5
atp1
Glu
nad4
His
ymf98
nad7
nad2
Phe
rps10
Arg
Gln
Ile
Val
rps12
rps7
cox3
atp6
Asp
nad3
cob
nad9
atp9
cox1
cox2
Leu
Leu
secY
Cys
Ser
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys
Ala
rps14
rps8
rpl6
rps2

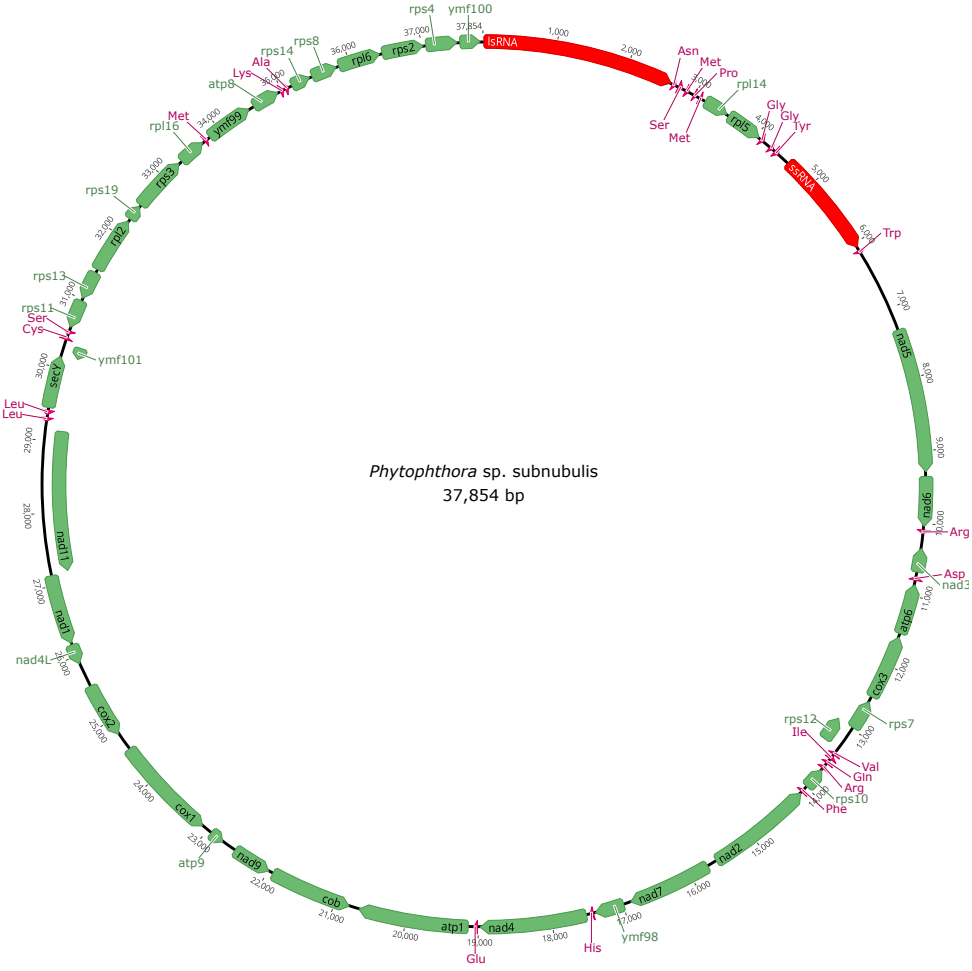


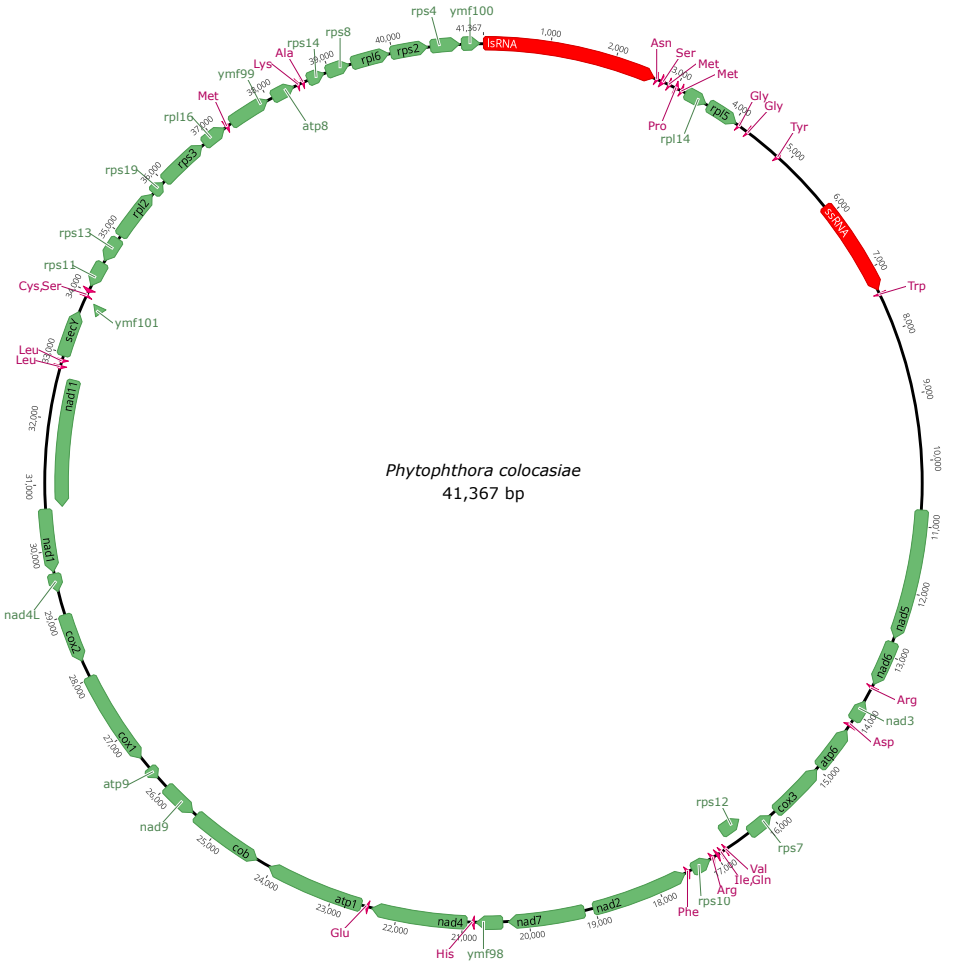
Phytophthora heveae
37,150 bp
rps4
ymf100
lsRNA
Asn
Met
Pro
Met
Ser
rpl14
rpl5
Gly
Gly
Tyr
ssRNA
Trp
nad11
nad1
nad4L
Arg
nad6
nad5
atp1
Glu
nad4
His
ymf98
nad7
nad2
Phe
rps10
Arg
Gln
Ile
Val
rps12
rps7
cox3
atp6
Asp
nad3
cob
nad9
atp9
cox1
cox2
Leu
Leu
secY
Cys
Ser
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys
Ala
rps14
rps8
rpl6
rps2

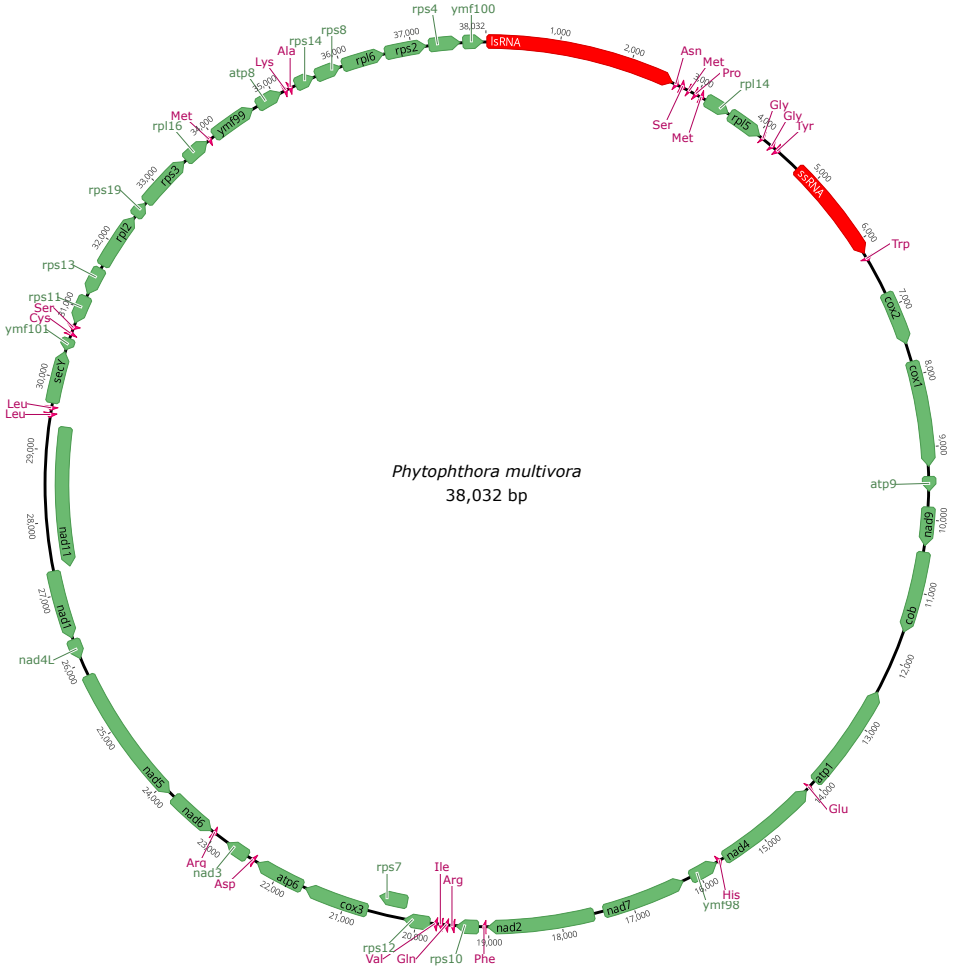

Phytophthora sp. novaeguineae
37,072 bp
rps4
ymf100
lsRNA
Asn
Met
Met
rpl14
Ser
Pro
rpl5
Gly
Gly
Tyr
ssRNA
Trp
nad11
nad1
nad4L
Arg
nad6
nad5
atp1
Glu
His
ymf98
nad4
nad7
nad2
Phe
Arg
Gln
Ile
rps12
rps10
Val
rps7
cox3
atp6
Asp
nad3
cob
atp9
cox1
cox2
Leu
Leu
sec7
Cys
Ser
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
Lys
Ala
atp8
rps14
rps8
rpl6
rps2

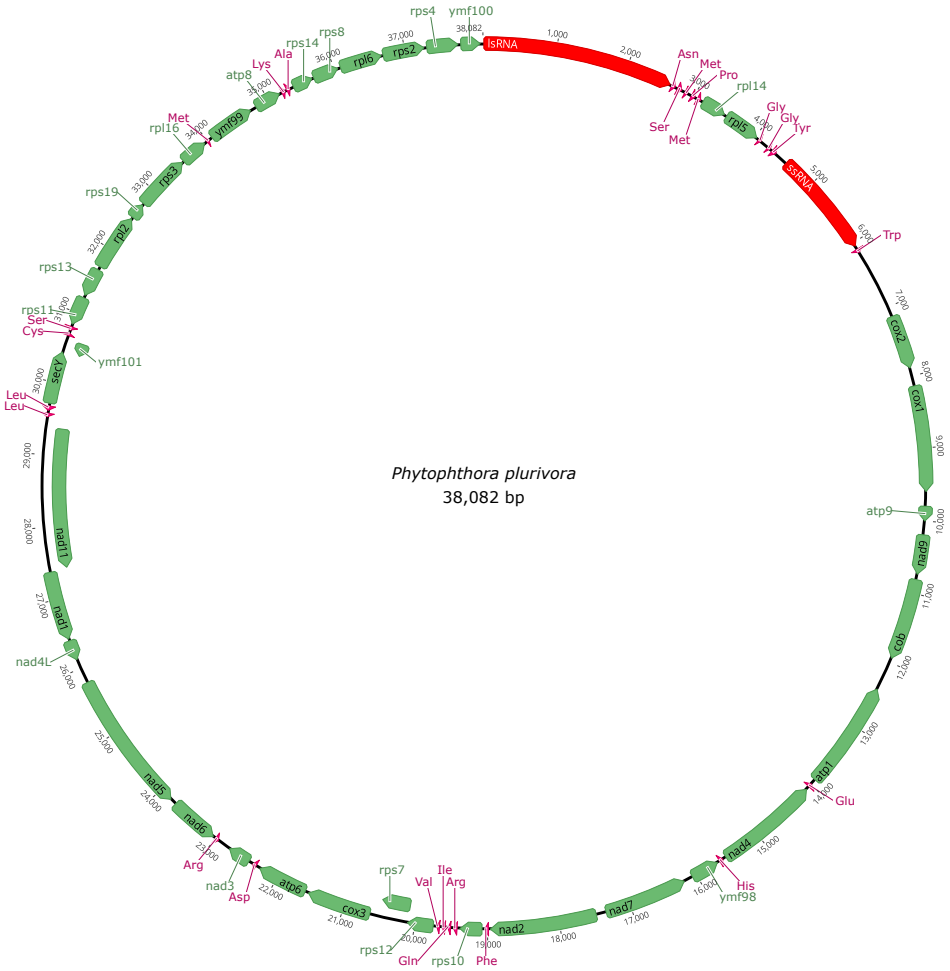

Phytophthora tropicalis
37,047 bp
rps4
ymf100
lsRNA
Asn
Met
Pro
Met
rpl14
Ser
rpl5
Gly
Gly
Tyr
ssRNA
Trp
cox2
cox1
atp9
nad6
cob
atp1
Glu
nad4
His
ymf98
nad7
nad2
Phe
Val
Ile
Arg
Gln
rps12
rps10
rps7
cox3
atp6
Asp
nad3
Arg
nad5
nad1
nad4L
nad11
Leu
Leu
sec7
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
Lys
Ala
atp8
rps14
rps8
rpl6
rps2

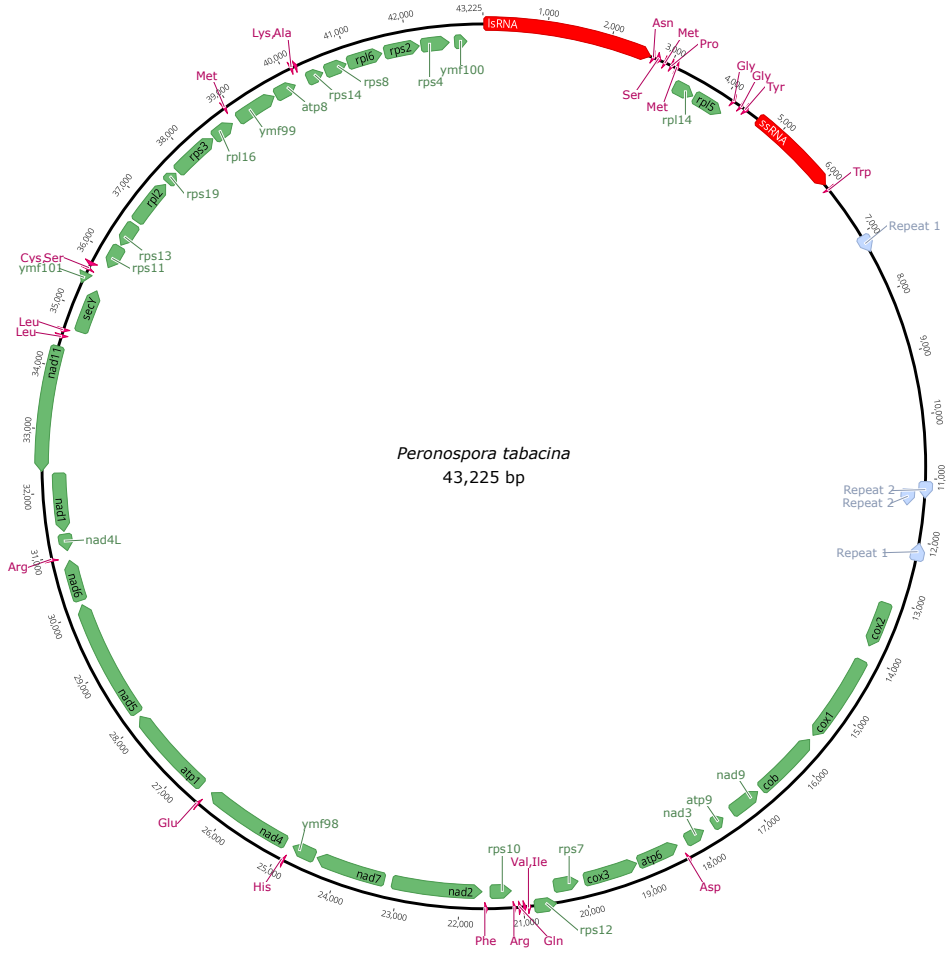

Phytophthora capsici
38,427 bp

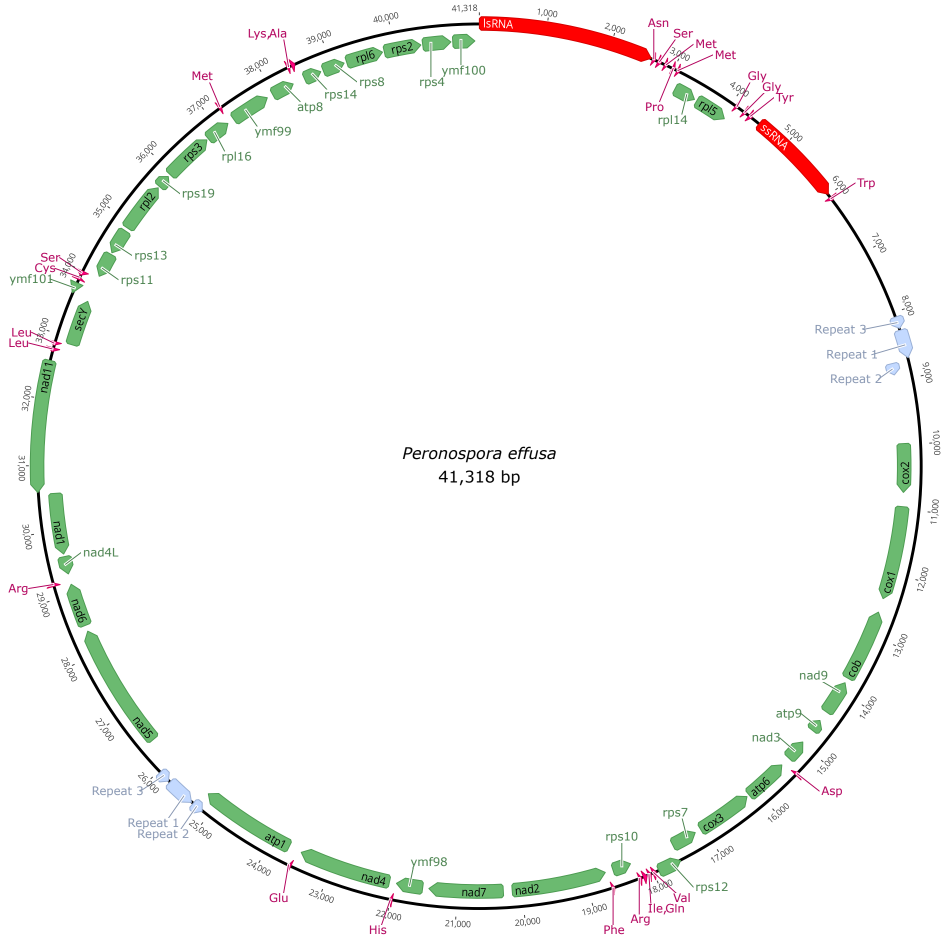

Phytophthora sp. subnubulis
37,854 bp

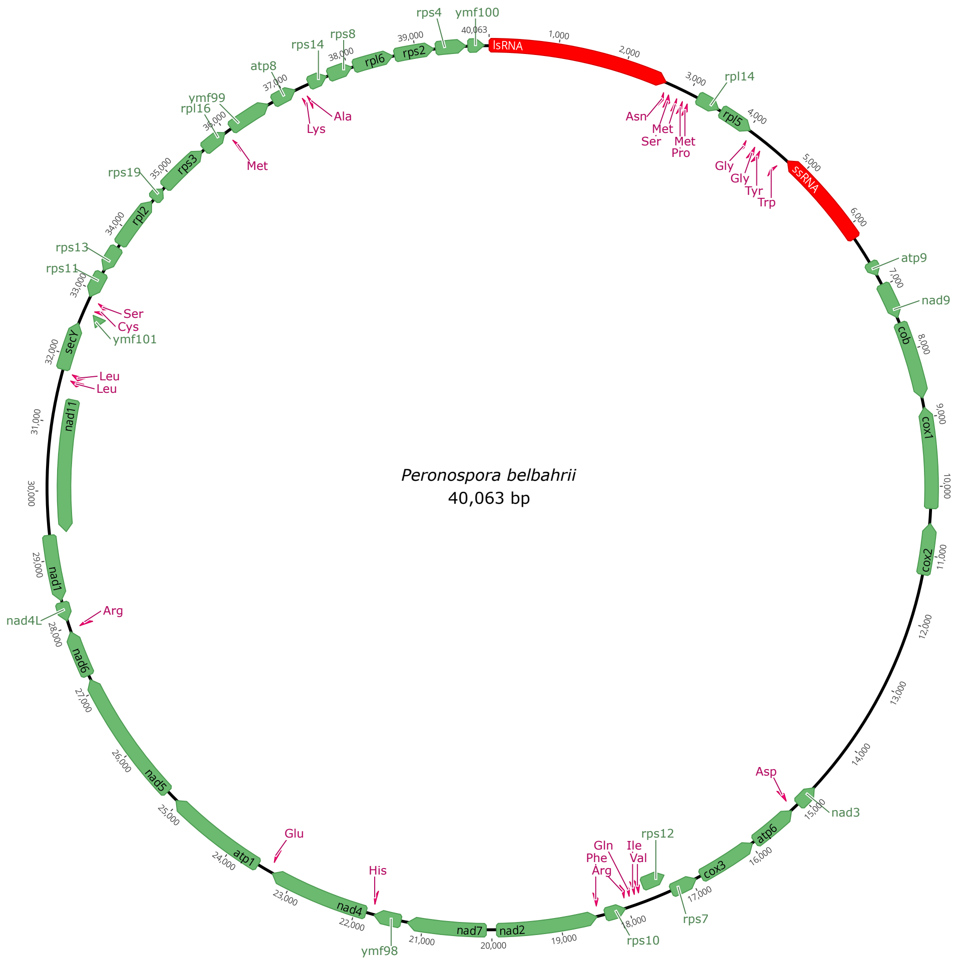

Phytophthora colocasiae
41,367 bp
rps4
ymf100
lsRNA
Asn
Ser
Met
Met
Pro
rpl14
rpl5
Gly
Gly
Tyr
ssRNA
Trp
nad5
nad6
Arg
nad3
Asp
atp6
cox3
rps7
rps12
Val
Ile
Gln
Arg
rps10
Phe
nad2
nad7
nad4
His
ymf98
atp1
Glu
cob
nad9
atp9
cox1
cox2
nad4L
nad1
nad1
Leu
Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
Lys
Ala
rps14
rps8
rpl6
rps2
atp8

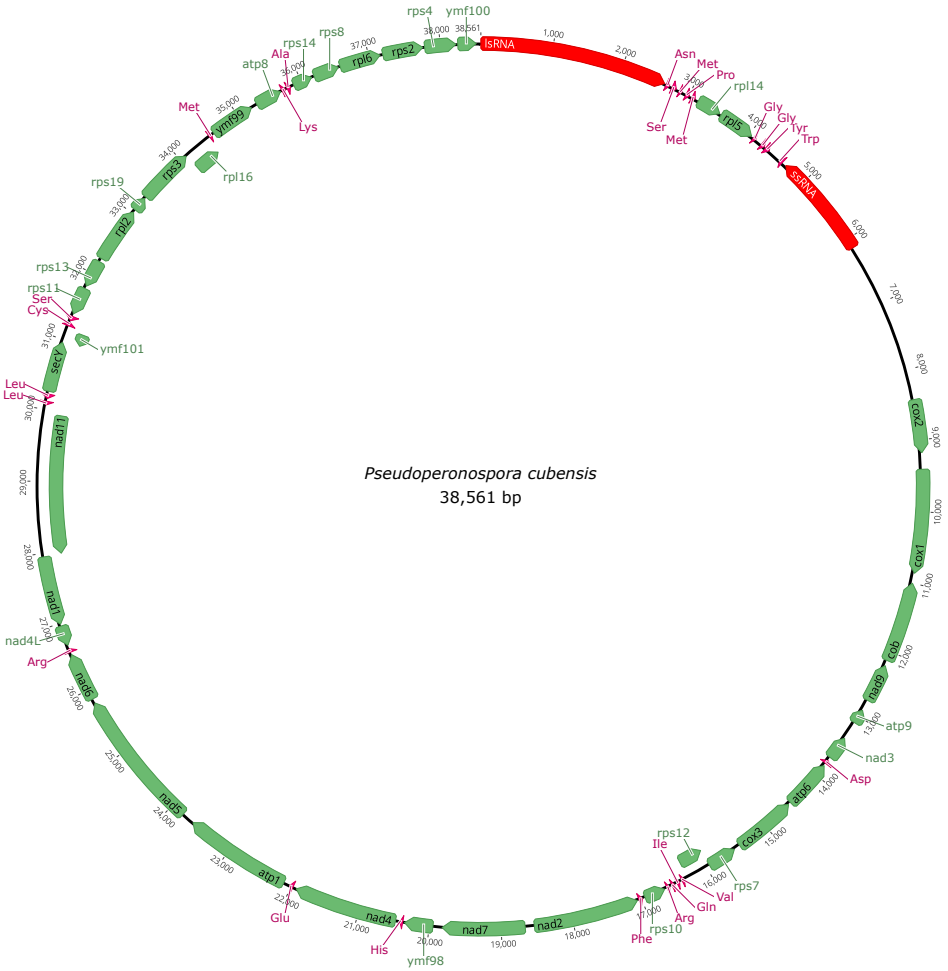

Phytophthora multivora
38,032 bp
rps4
ymf100
lsRNA
Asn
Met
Pro
rpl14
Gly
Gly
Tyr
rpl5
Ser
Met
ssRNA
Trp
cox2
cox1
atp9
nad9
cob
atp1
Glu
nad4
His
ymf98
nad7
nad2
Phe
rps10
Arg
Ile
rps7
cox3
atp6
Asp
nad3
Arg
nad6
nad5
nad4L
nad1
nad1
Leu
Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys
Ala
rps14
rps8
rpl6
rps2


Phytophthora plurivora
38,082 bp
rps4
ymf100
lsRNA
rps14
rps8
Lys
Ala
atp8
rpl6
rps2
Asn
Met
Pro
rpl14
Ser
Met
rpl5
Gly
Gly
Tyr
ssRNA
Trp
rps19
rpl16
Met
ymf99
rps3
rpl2
rps13
rps11
Ser
Cys
ymf101
sec1
Leu
Leu
cox2
cox1
atp9
nad9
cob
atp1
Glu
nad4
His
ymf98
nad7
nad2
rps7
Val
Ile
Arg
rps12
Gln
rps10
Phe
cox3
atp6
nad3
Asp
Arg
nad6
nad5
nad4L
nad1


Peronospora tabacina
43,225 bp
lsRNA
Lys
Ala
rps14
rps8
rpl6
rps2
ymf100
rps4
Asn
Met
Pro
Ser
Met
rpl14
rpl5
Gly
Gly
Tyr
ssRNA
Trp
Repeat 1
Repeat 2
Repeat 2
Repeat 1
Met
atp8
ymf99
rps3
rpl16
rps19
rpl2
rps13
rps11
Cys
Ser
ymf101
sec1
Leu
Leu
nad1
nad4L
Arg
nad6
nad5
atp1
Glu
nad4
ymf98
His
nad7
nad2
rps10
Phe
Val
Ile
Arg
rps12
Gln
cox3
rps7
atp6
Asp
nad3
atp9
nad9
cob
cox1
cox2

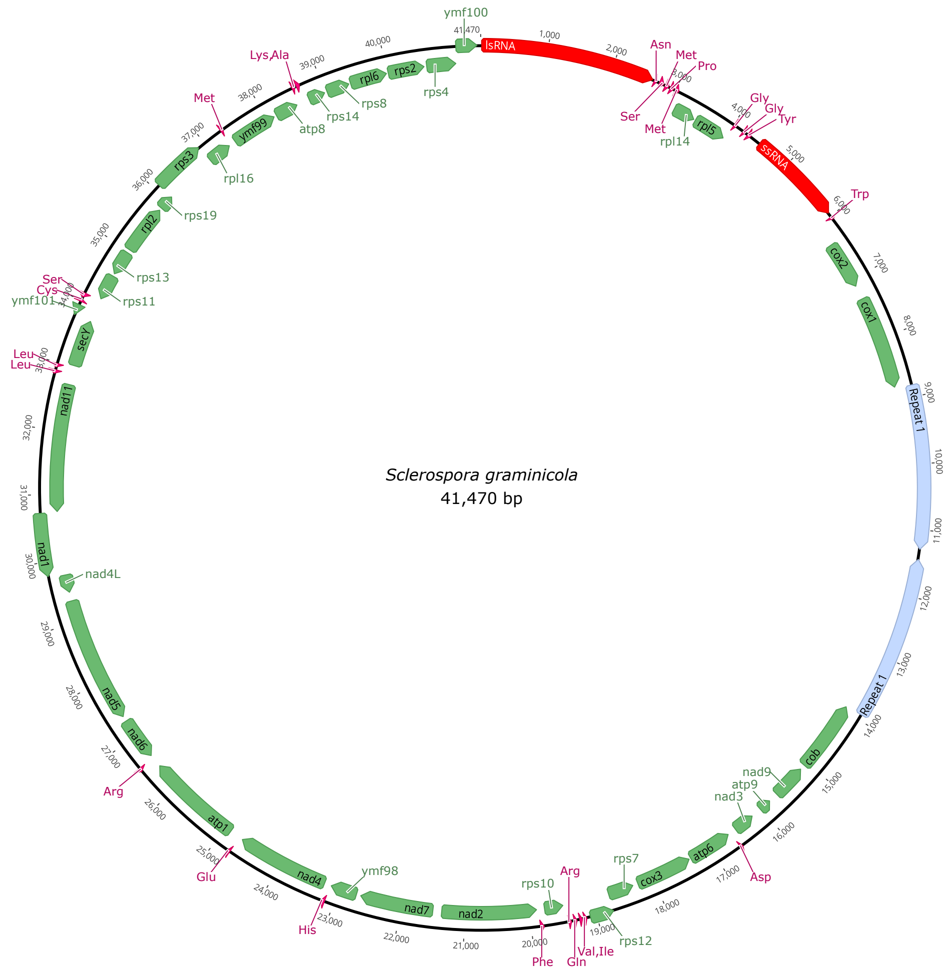

Peronospora effusa
41,318 bp
lsRNA
ssRNA
Asn
Ser
Met
Met
Pro
Gly
Gly
Tyr
Trp
rpl14
rpl5
Repeat 3
Repeat 1
Repeat 2
cox2
cox1
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
rps12
rps10
Val
Ile,Gln
Arg
Phe
nad2
nad7
ymf98
His
nad4
atp1
Glu
nad5
nad6
Arg
nad4L
nad1
nad11
Leu
Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
Met
atp8
rps14
rps8
rpl6
Lys,Ala
rps2
rps4
ymf100

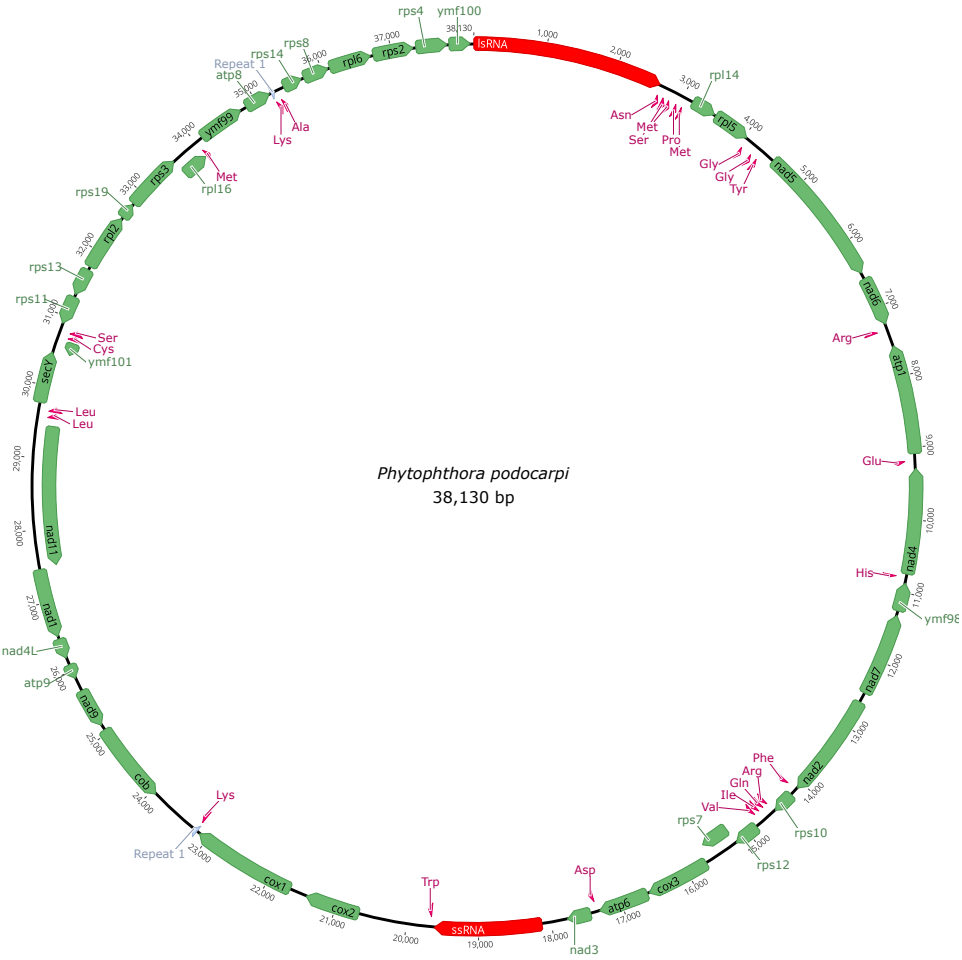

Peronospora belbahrii
40,063 bp
lsRNA
ssRNA
rpl14
rpl5
Asn
Met
Ser
Met
Pro
Gly
Gly
Tyr
Trp
atp9
nad9
cob
cox1
cox2
Asp
nad3
atp6
cox3
rps7
rps12
Gln
Phe
Arg
Ile
Val
rps10
nad2
nad7
ymf98
His
nad4
Glu
atp1
nad5
nad6
nad4L
Arg
nad1
nad11
Leu
Leu
secY
Ser
Cys
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
Met
atp8
Lys
Ala
rps14
rps8
rpl6
rps2
rps4
ymf100

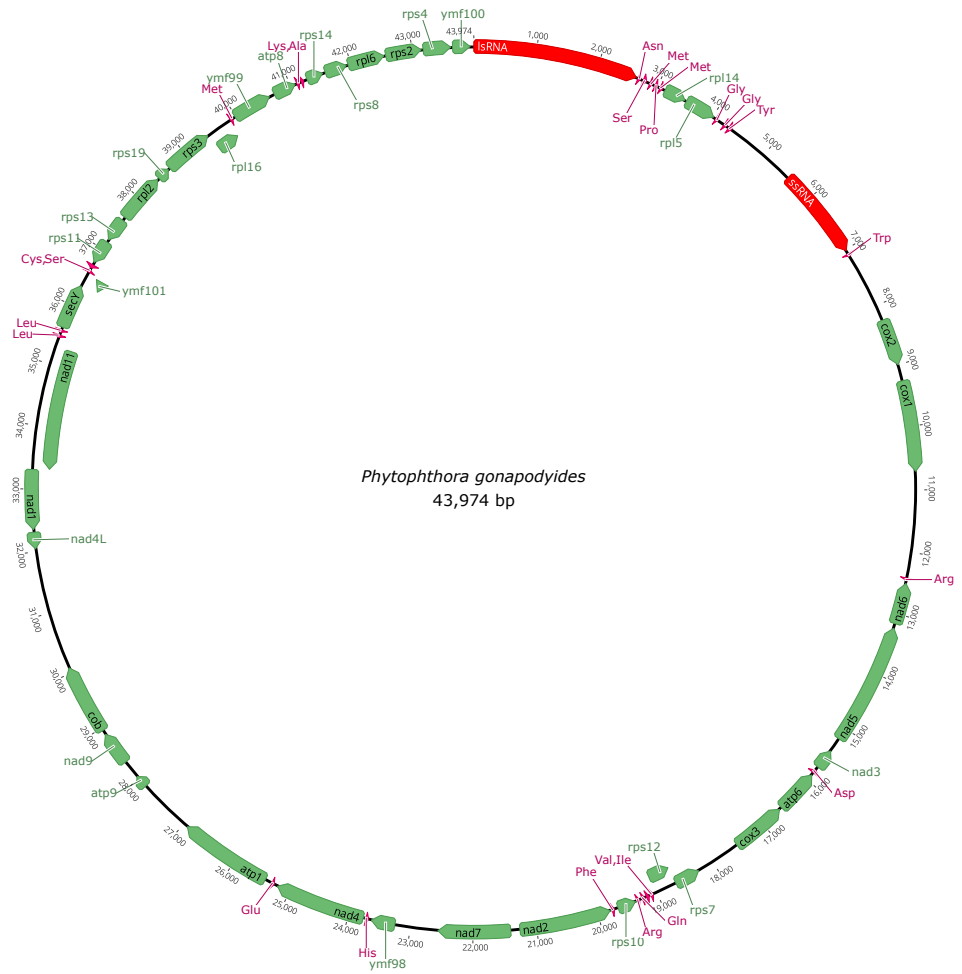

Pseudoperonospora cubensis
38,561 bp
rps4
ymf100
lsRNA
Asn
Met
Pro
rpl14
rpl5
Gly
Gly
Tyr
Trp
ssRNA
cox2
cox1
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
Val
Gln
Arg
rps10
Phe
rps12
Ile
nad2
nad7
ymf98
His
nad4
Glu
atp1
nad5
Arg
nad6
nad4L
nad1
Leu
Leu
nad1
sec1
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
Lys
atp8
Ala
rps14
rps8
rpl6
rps2


Pseudoperonospora humuli
39,087 bp
lsRNA
Asn
Met
Pro
Ser
Met
rpl14
rpl5
Repeat 4
Gly
Gly
Tyr
Trp
ssRNA
Repeat 2
Repeat 2
cox2
cox1
Repeat 1
Repeat
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
Val
Gln
Arg
rps10
Phe
rps12
Ile
nad2
nad7
ymf98
His
Repeat 4
nad4
Glu
atp1
Repeat 3
Repeat 3
nad5
Arg
nad6
nad4L
nad1
Leu
Leu
nad1
sec1
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
Lys
atp8
Ala
rps14
rps8
rpl6
rps2
rps4
ymf100

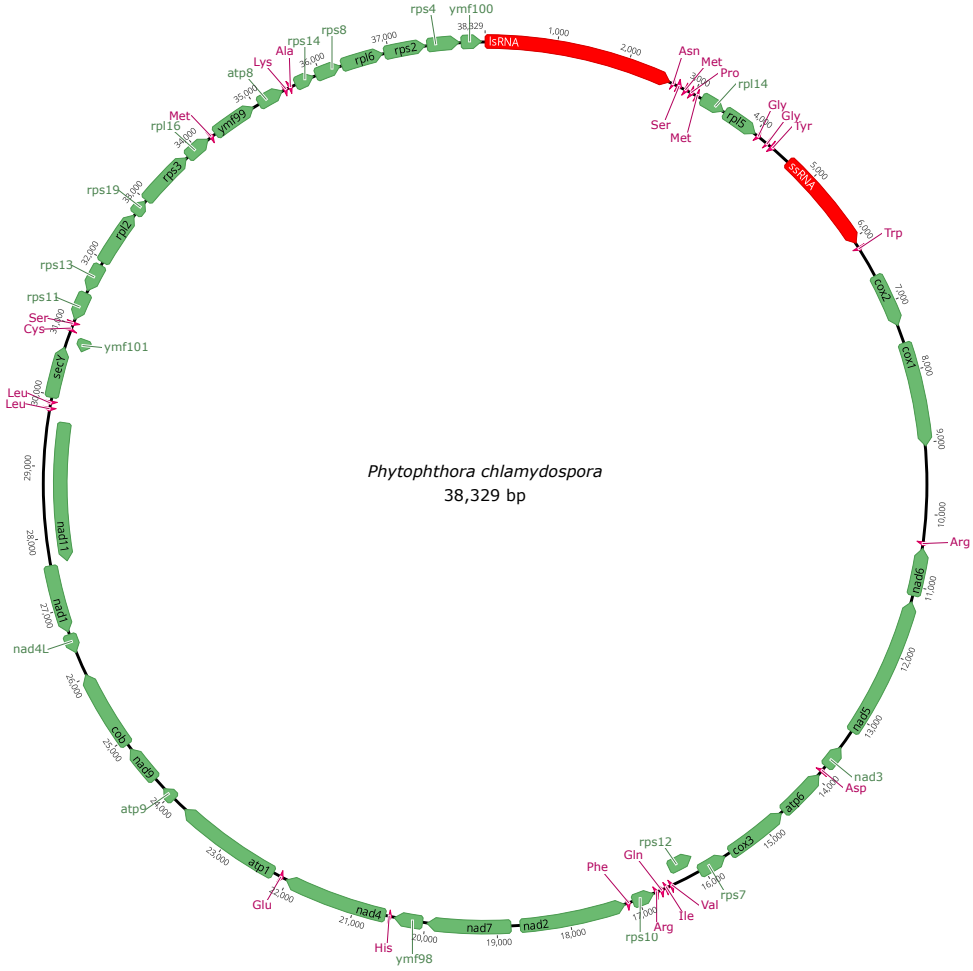

Hyaloperonospora arabidopsidis
38,797 bp
lsRNA
ssRNA
Asn
Met
Met
Ser
Pro
rpl14
rpl5
Gly
Gly
Tyr
Trp
atp1
Glu
nad4
His
ymf98
nad7
nad2
rps10
Gln
Phe
rps12
Arg
Ile
Val
rps7
cox3
atp6
nad3
Asp
nad11
nad1
nad4L
Arg
nad6
nad5
Repeat 1
Repeat 1
cox2
cox1
cob
nad9
atp9
Leu
Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
Met
atp8
rps14
Lys
Ala
rps8
rpl6
rps2
rps4
ymf100

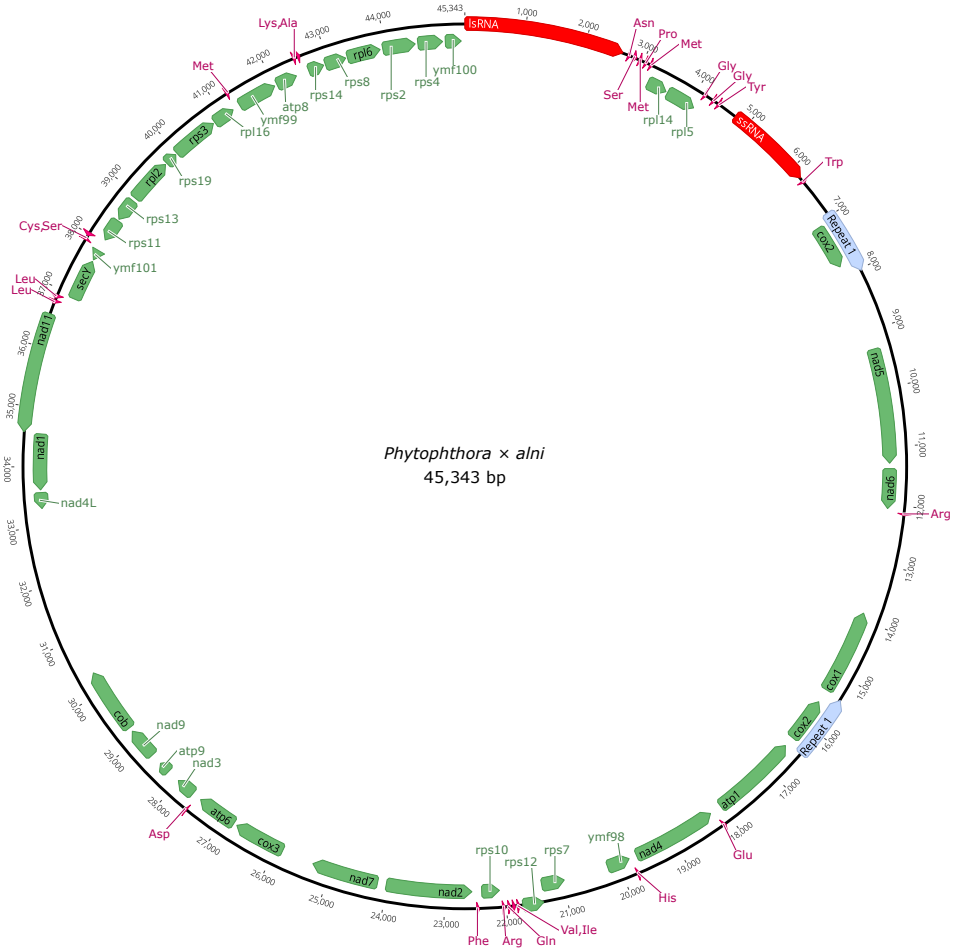

Sclerospora graminicola
41,470 bp
ymf100
lsRNA
ssRNA
Asn
Met
Pro
Ser
Met
rpl14
rpl5
Gly
Gly
Tyr
Trp
cox2
cox1
Repeat 1
Repeat 1
cob
nad9
atp9
nad3
atp6
Asp
cox3
rps7
rps12
Arg
rps10
Val,Ile
Gln
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
Arg
nad6
nad5
nad4L
nad1
nad11
Leu
Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
Met
atp8
rps14
Lys,Ala
rps8
rpl6
rps2
rps4


Phytophthora podocarpi
38,130 bp
lsRNA
ssRNA
rps4
ymf100
rps2
rpl6
rps8
rps14
atp8
Repeat 1
ymf99
rps3
rps19
rpl2
rps13
rps11
sec1
ymf101
nad11
nad1
nad4L
atp9
nad9
cob
cox1
cox2
trnW
nad3
atp6
cox3
rps7
rps12
nad2
rps10
nad7
nad4
ymf98
atp1
nad5
rpl5
rpl14
rpl16
Asn
Met
Ser
Pro
Met
Gly
Gly
Tyr
Arg
Glu
His
Phe
Arg
Gln
Ile
Val
Lys
Repeat 1
Trp
Asp
Ser
Cys
Leu
Leu
Met
Ala
Lys

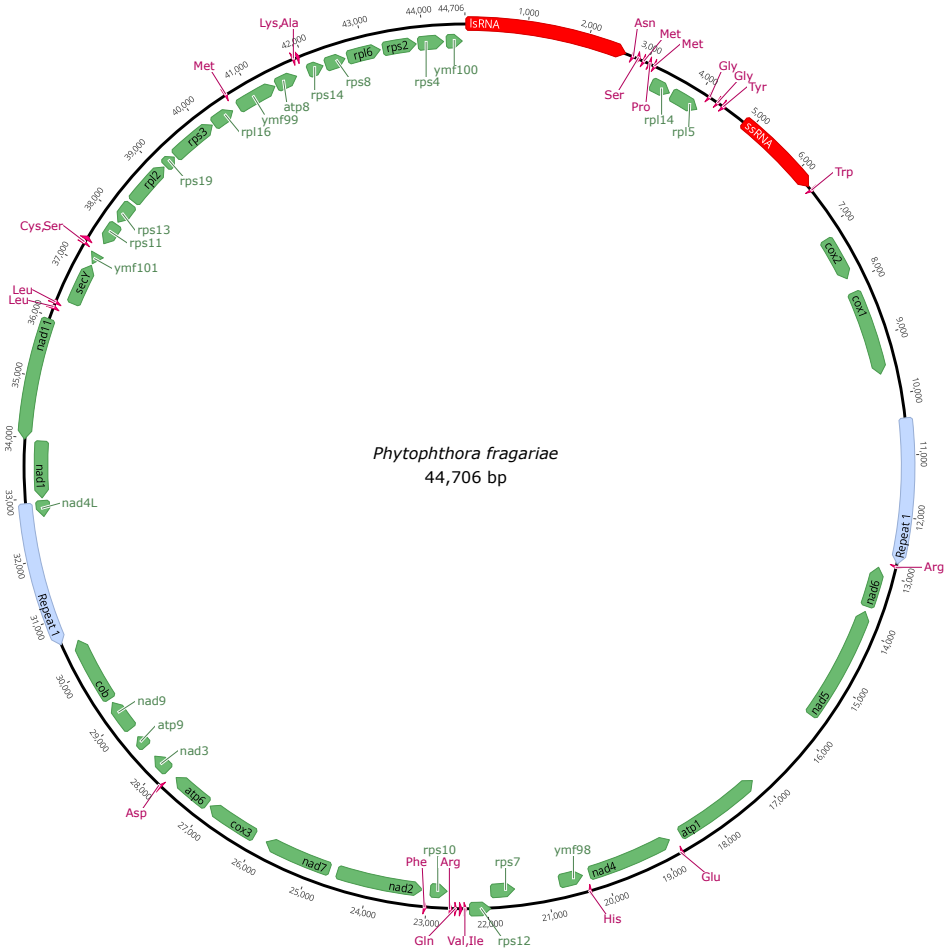

Phytophthora gonapodyides
43,974 bp
lsRNA
ssRNA
rps4
ymf100
rps2
rpl6
rps14
atp8
Lys,Ala
ymf99
Met
rps8
rps3
rps19
rpl16
rpl2
rps13
rps11
Cys,Ser
sec1
ymf101
Leu
Leu
nad11
nad1
nad4L
nad9
cob
atp9
atp1
Glu
nad4
His
ymf98
nad7
nad2
rps10
Arg
Gln
Phe
Val,Ile
rps12
rps7
cox3
atp6
nad3
Asp
nad5
cox1
cox2
Trp
Arg
Asn
Met
Met
rpl14
Gly
Gly
Tyr
Ser
Pro
rpl5

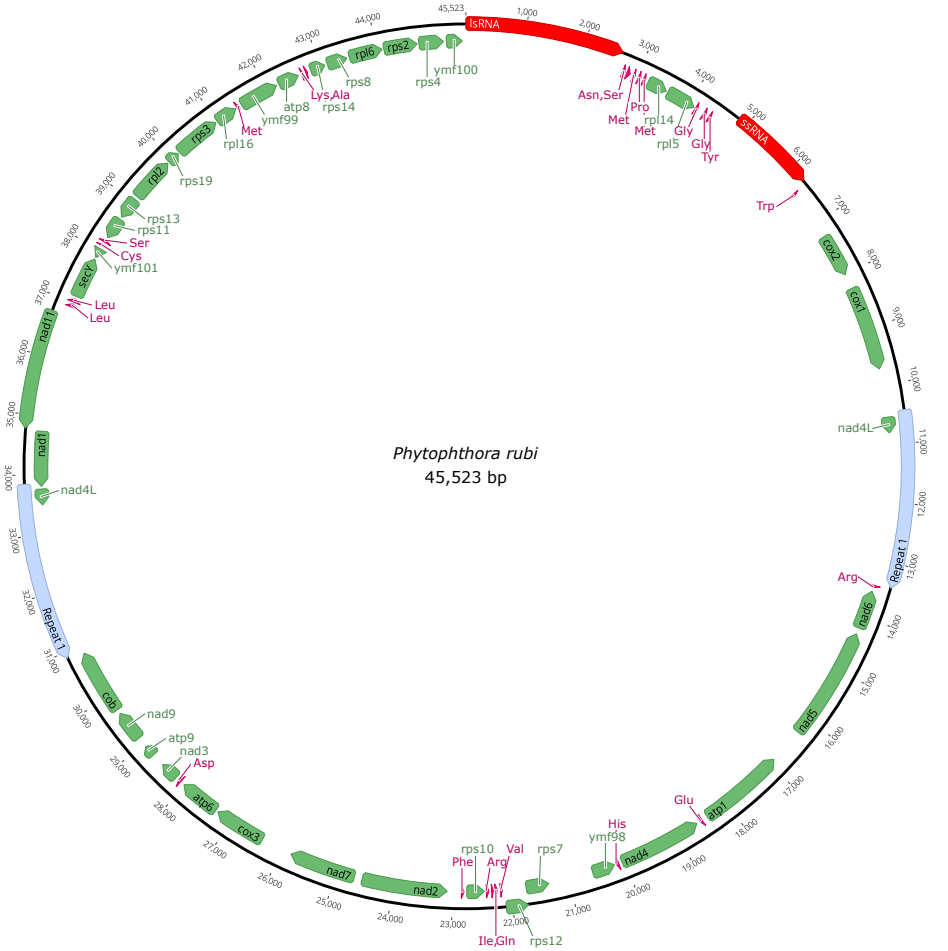

Phytophthora pinifolia
43,061 bp
lsRNA
ssRNA
rps12
Repeat 1

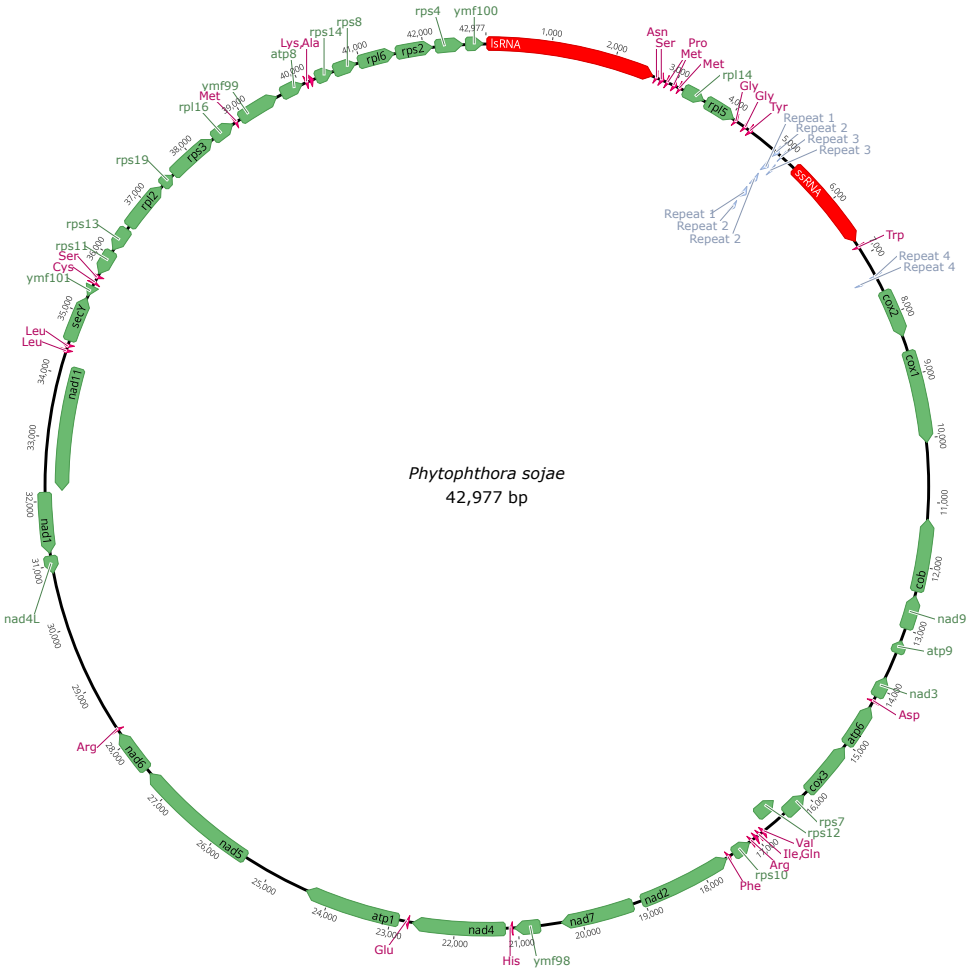

Phytophthora chlamydospora
38,329 bp
lsRNA
ssRNA
Repeat 1

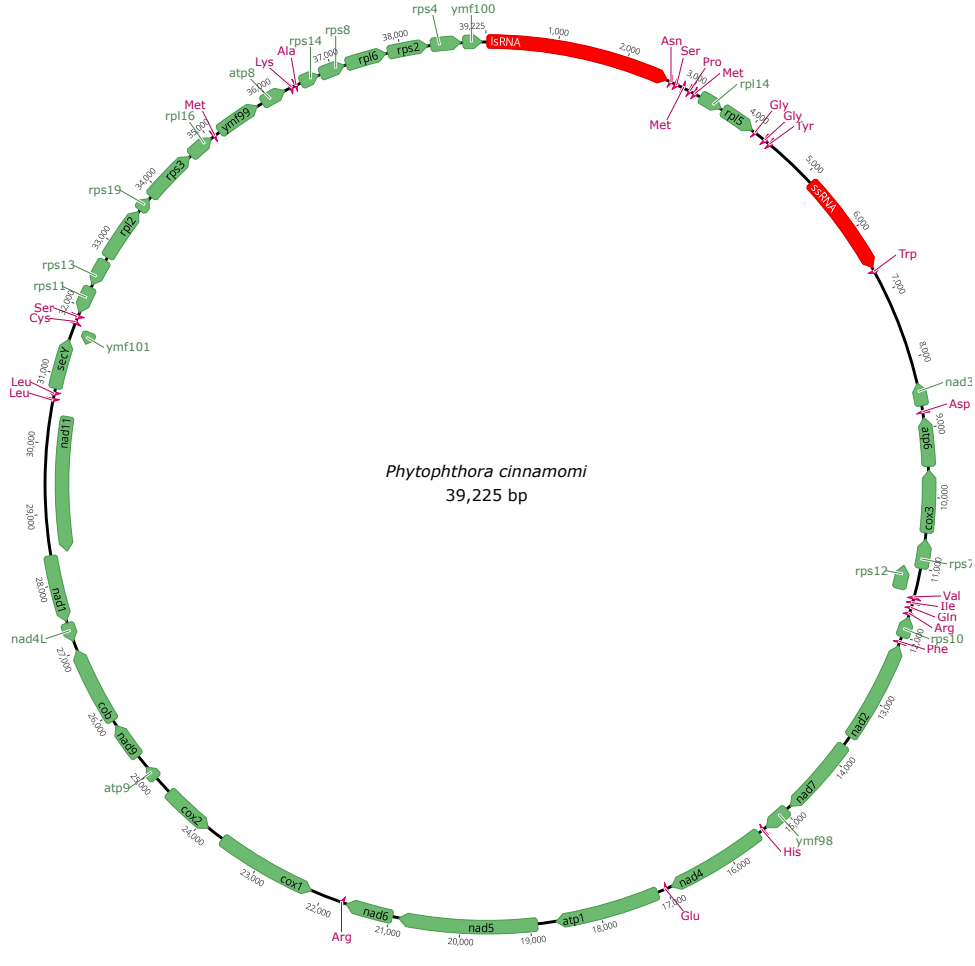

Phytophthora × alni
45,343 bp
lsRNA
ssRNA
Repeat 1
Repeat 2
cox2
nad5
nad6
cox1
cox2
atp1
nad4
nad2
nad7
cox3
atp6
nad3
nad9
cob
sec4
nad11
nad1
nad4L
rps3
rpl2
rps19
rps13
rps11
ymf101
rpl16
ymf99
atp8
rps14
rps8
rpl6
rps2
rps4
ymf100
rpl14
rpl5
rps10
rps12
rps7
ymf98
Trp
Arg
Glu
His
Phe
Val,Ile
Gln
Asp
Cys,Ser
Leu
Leu,Leu
Met
Lys,Ala
Asn
Pro
Gly
Tyr
Ser
Pro,Met
Ser,Met

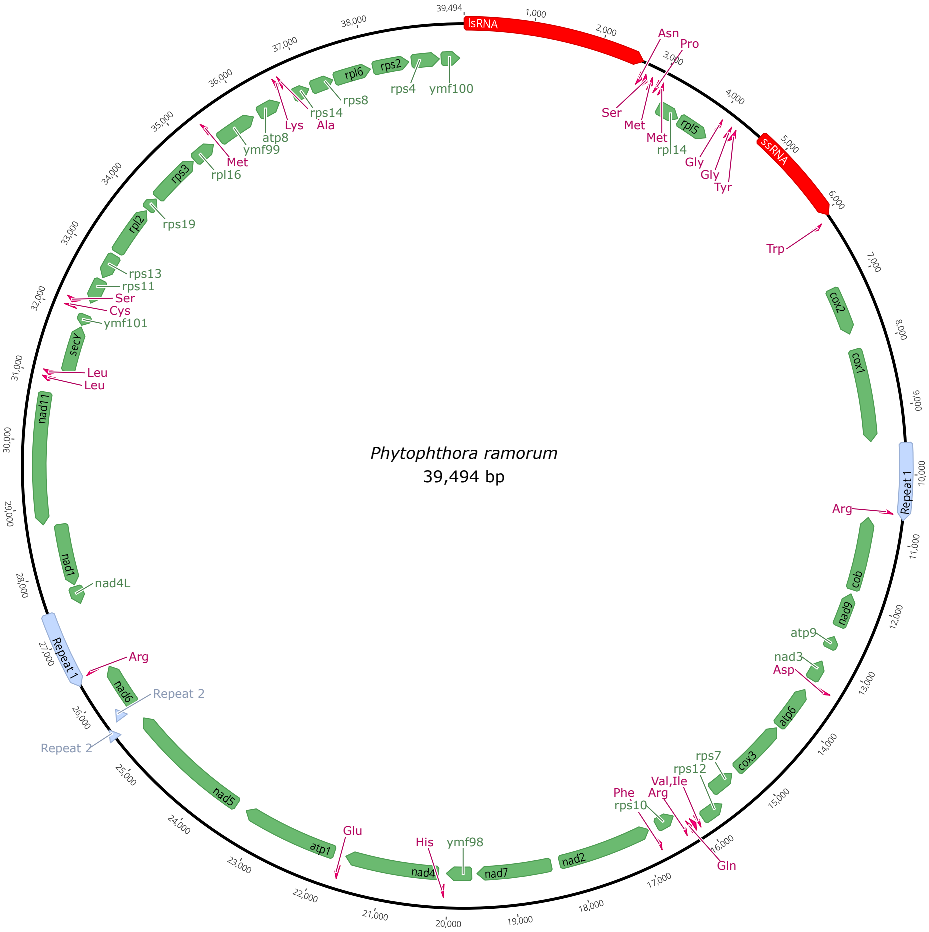

Phytophthora × cambivora
51,184 bp
lsRNA
ssRNA
Repeat 1
Repeat 2
cox2
nad5
nad6
cox1
cox2
atp1
nad4
nad2
nad7
cox3
atp6
nad3
nad9
cob
sec4
nad11
nad1
nad4L
rps3
rpl2
rps19
rps13
rps11
ymf101
rpl16
ymf99
atp8
rps14
rps8
rpl6
rps2
rps4
ymf100
rpl14
rpl5
rps10
rps12
rps7
ymf98
Trp
Arg
Glu
His
Phe
Val,Ile
Gln
Asp
Cys,Ser
Leu,Leu
Met
Lys,Ala
Asn
Pro,Met
Gly
Tyr
Ser,Met

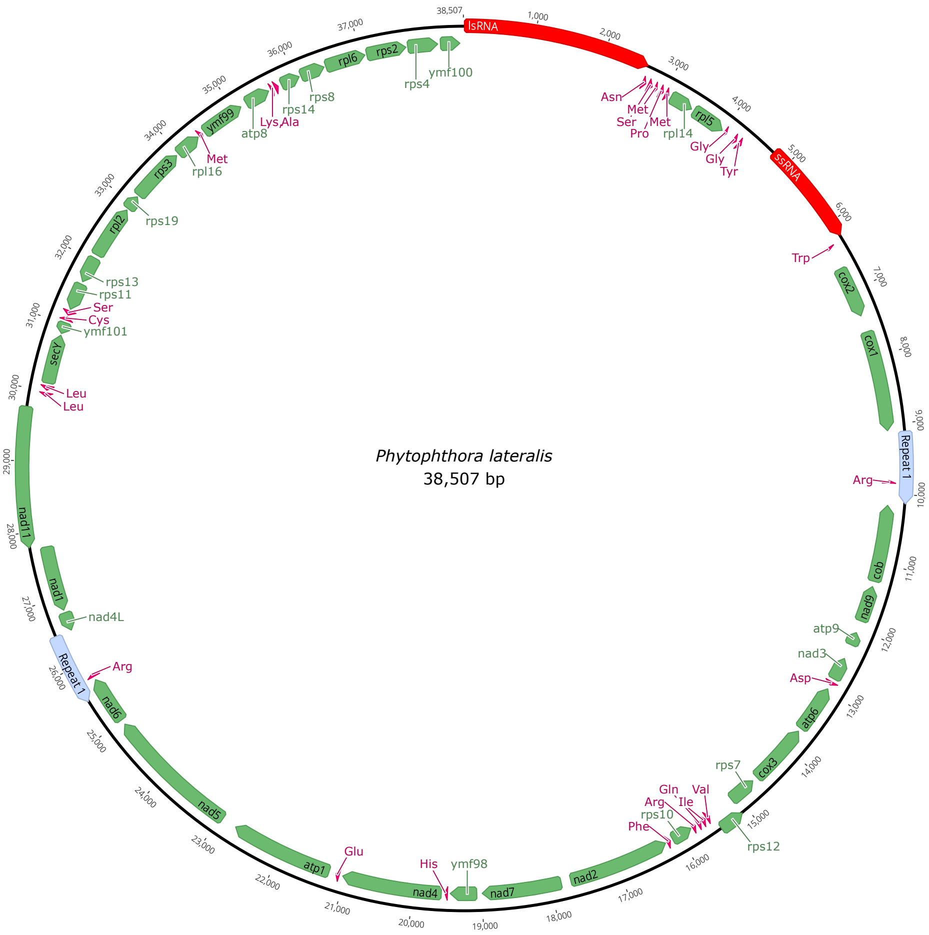

Phytophthora fragariae
44,706 bp
lsRNA
ssRNA
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps3
rpP
rps19
rps13
rps11
ymf101
secY
nad11
nad1
nad4L
Repeat 1
cob
nad9
atp9
nad3
atp6
cox3
nad7
nad2
rps10
rps7
ymf98
nad4
atp1
nad5
nad6
cox1
cox2
Lys,Ala
Met
Cys,Ser
Leu
Leu
Asp
Phe
Arg
Gln
Val,Ile
rps12
His
Glu
Ser
Pro
rpl14
rpl5
Asn
Met
Met
Gly
Gly
Tyr
Trp
Arg


Phytophthora rubi
45,523 bp
lsRNA
ssRNA
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps3
rpP
rps19
rps13
rps11
ymf101
secY
nad11
nad1
nad4L
Repeat 1
cob
nad9
atp9
nad3
atp6
cox3
nad7
nad2
rps10
rps7
ymf98
nad4
atp1
nad5
nad6
cox1
cox2
Lys,Ala
Met
Ser
Cys
Leu
Leu
Asp
Phe
Arg
Ile,Gln
rps12
His
Glu
Asn,Ser
Pro
rpl14
rpl5
Met
Met
Gly
Gly
Tyr
Trp
Arg

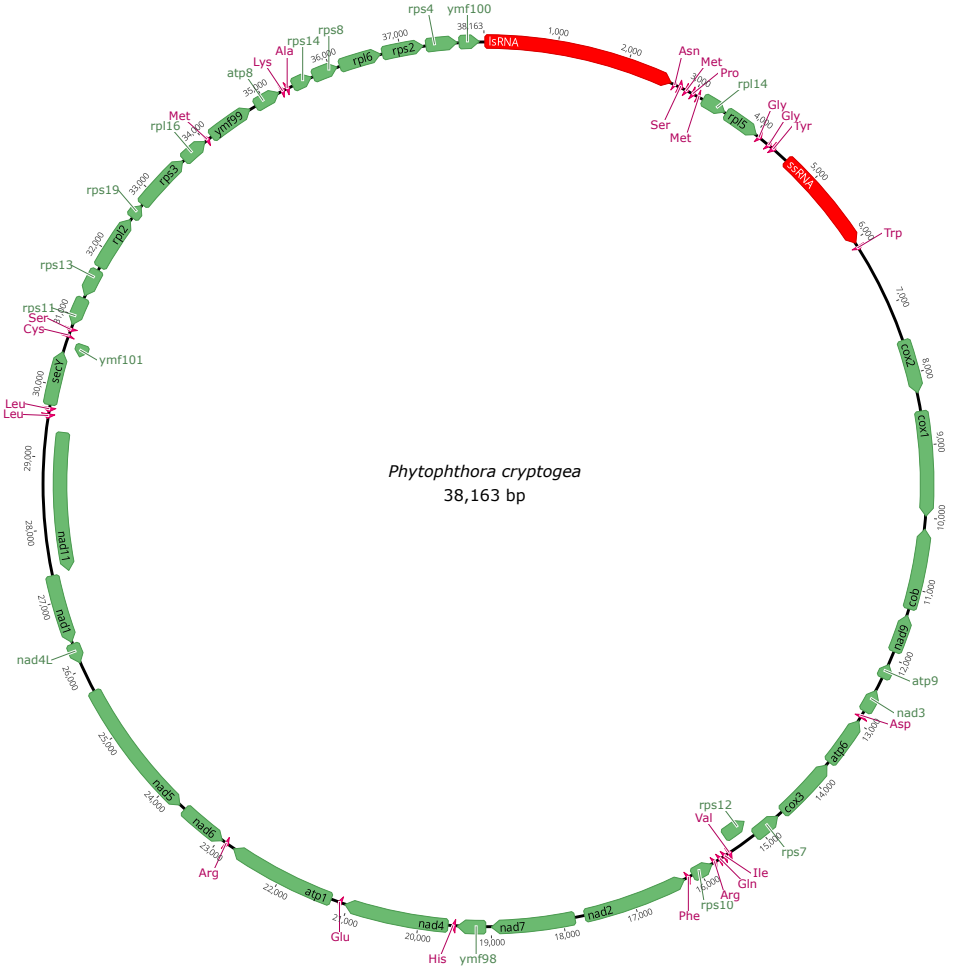

Phytophthora sojae
42,977 bp
rps4
ymf100
lsRNA
Asn
Ser
Pro
Met
Met
rpl14
Gly
Gly
Tyr
rpl5
Repeat 1
Repeat 2
Repeat 3
Repeat 3
Repeat 1
Repeat 2
Repeat 2
ssRNA
Trp
Repeat 4
Repeat 4
cox2
cox1
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
rps12
Val
Ile
Gln
Arg
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
nad5
nad6
Arg
nad1
nad4L
nad1
Leu
Leu
secY
ymf101
Ser
Cys
rps11
rps13
rpl2
rps19
rps3
ymf99
Met
rpl16
Lys
Ala
atp8
rps14
rps8
rpl6
rps2

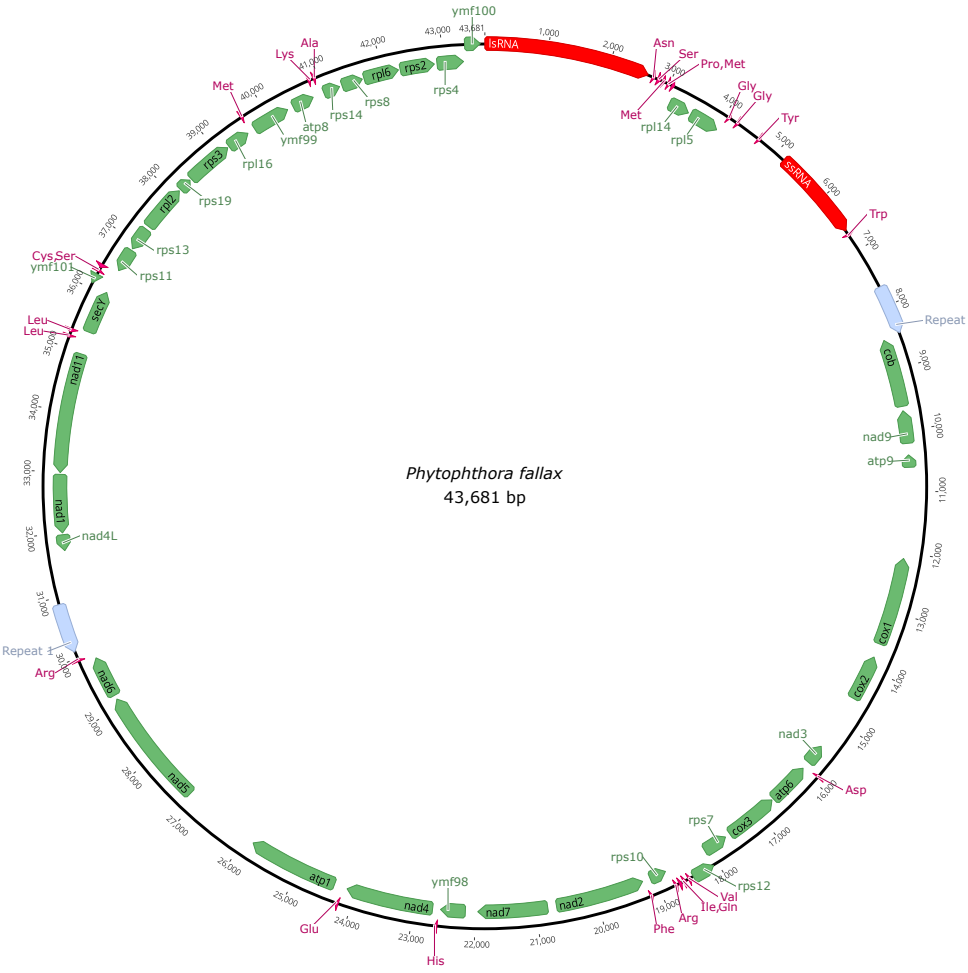

Phytophthora cinnamomi
39,225 bp
rps4
ymf100
lsRNA
Asn
Ser
Pro
Met
Met
rpl14
Gly
Gly
Tyr
rpl5
ssRNA
Trp
nad3
Asp
atp6
cox3
rps12
rps7
Val
Ile
Gln
Arg
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
nad5
nad6
Arg
cox1
cox2
nad9
atp9
cob
nad1
nad4L
nad1
Leu
Leu
secY
ymf101
Ser
Cys
rps11
rps13
rpl2
rps19
rps3
ymf99
Met
rpl16
Lys
Ala
atp8
rps14
rps8
rpl6
rps2


Phytophthora ramorum
39,494 bp
lsRNA
ssRNA
Repeat 1
Repeat 2
Repeat 2
cox2
cox1
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
rps12
Val,Ile
Arg
Phe
rps10
Gln
nad2
nad7
ymf98
His
nad4
Glu
atp1
nad5
nad6
Arg
nad4L
nad1
nad11
Leu
Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys
Ala
rps14
rps8
rpl6
rps2
rps4
ymf100
Asn
Pro
Ser
Met
Met
rpl14
rpl5
Gly
Gly
Tyr
Trp
Arg


Phytophthora lateralis
38,507 bp
lsRNA
ssRNA
Repeat 1
Repeat 1
cox2
cox1
Arg
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
Gln
Val
Ile
Arg
rps10
Phe
rps12
nad2
nad7
ymf98
His
nad4
Glu
atp1
nad5
nad6
Arg
nad4L
nad1
nad11
Leu
Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys,Ala
rps14
rps8
rpl6
rps2
rps4
ymf100
Asn
Met
Ser
Met
Pro
rpl14
rpl5
Gly
Gly
Tyr
Trp

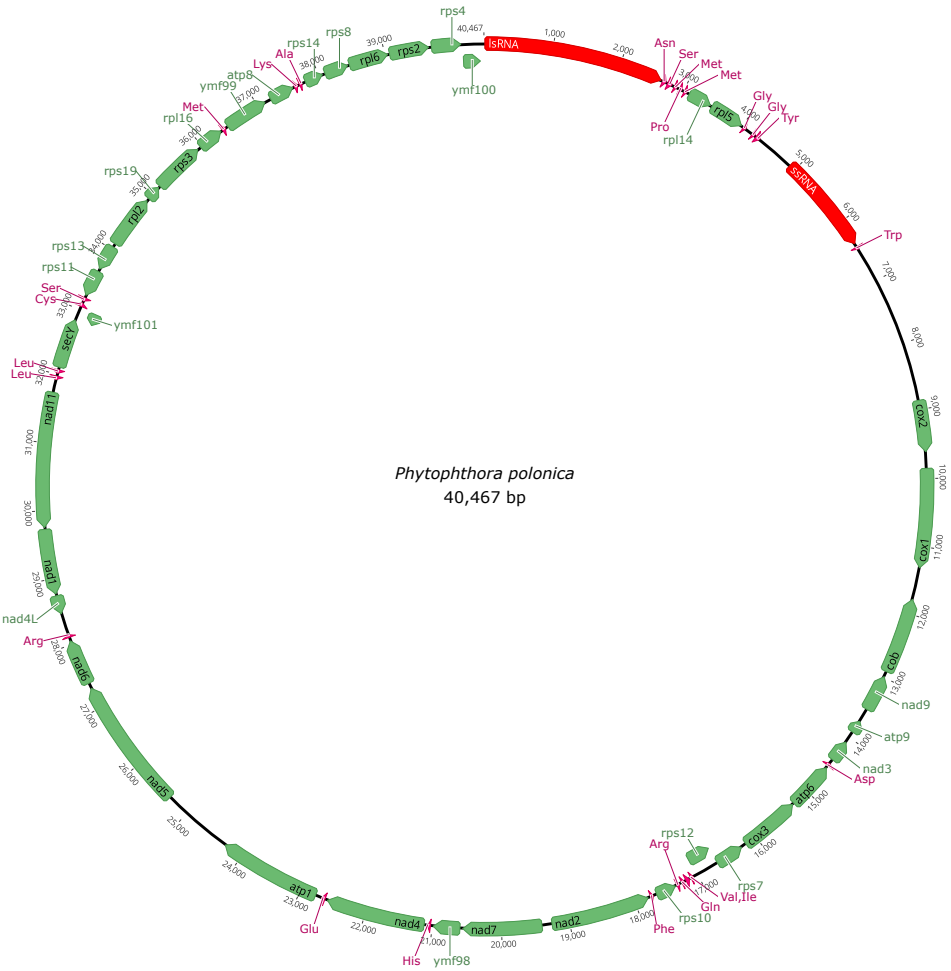

rps4
ymf100
39,618
lsRNA
Asn
Ser
Pro
Met
Met
rpl14
Gly
Gly
Tyr
rpl5
5SRNA
Trp
Repeat 2
Repeat 2
Repeat
Repeat 1
cox2
cox1
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
rps12
Val
Gln
Ile
Arg
rps10
Phe
nad2
nad7
ymf98
His
nad4
atp1
Glu
Arg
nad6
nad5
nad4L
nad1
Leu
Leu
sec1
ymf101
Ser
Cys
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
Ile
atp8
Lys
Ala
rps14
rps8
rpl6
rps2
Phytophthora sansomeana
39,618 bp

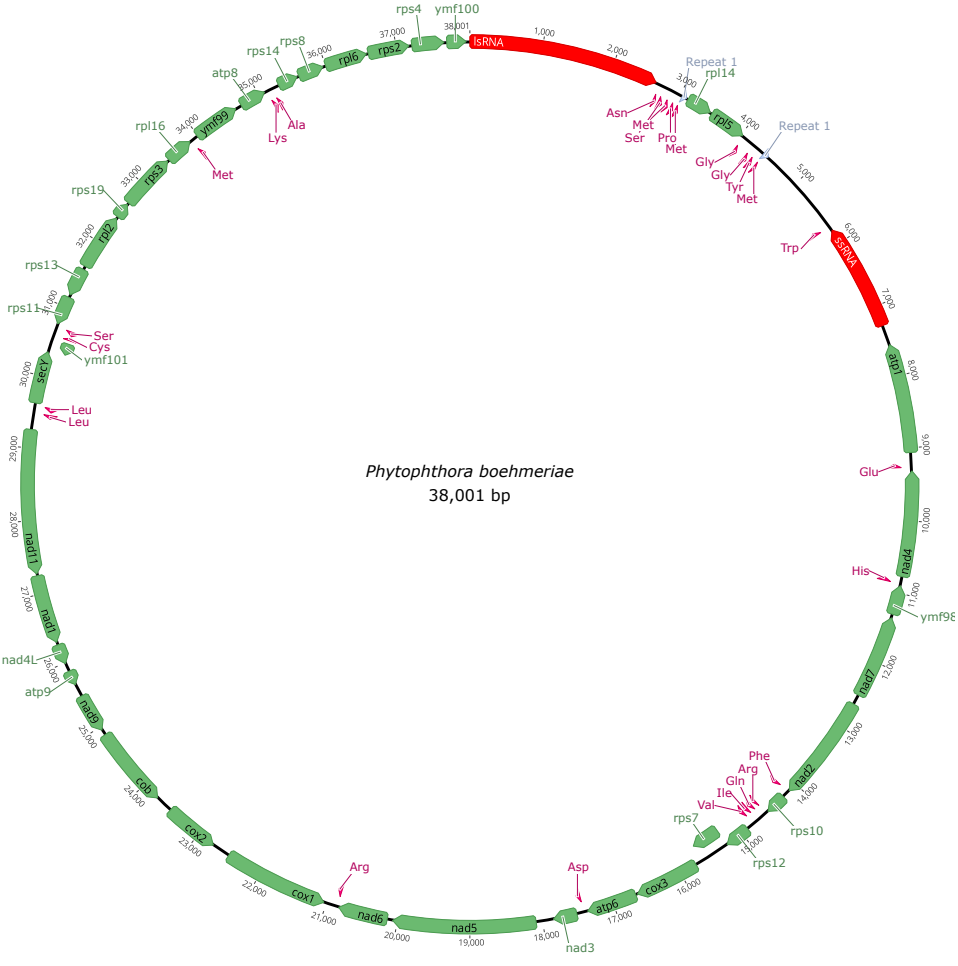

rps4
ymf100
38,163
lsRNA
Asn
Met
Pro
rpl14
Gly
Gly
Tyr
rpl5
Ser
Met
5SRNA
Trp
cox2
cox1
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps7
rps12
Val
Ile
Gln
Arg
rps10
Phe
nad2
nad7
ymf98
His
nad4
atp1
Glu
Arg
nad6
nad5
nad4L
nad1
nad11
Leu
Leu
sec1
ymf101
Ser
Cys
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys
Ala
rps14
rps8
rpl6
rps2
Phytophthora cryptogea
38,163 bp

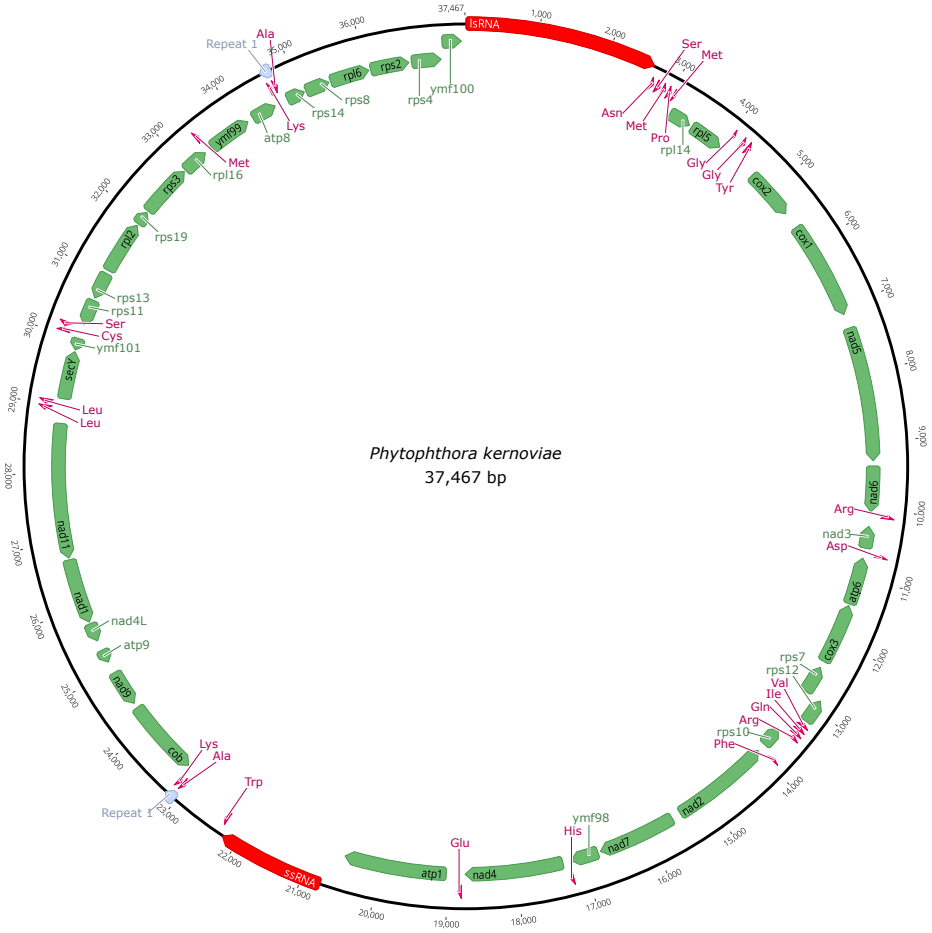


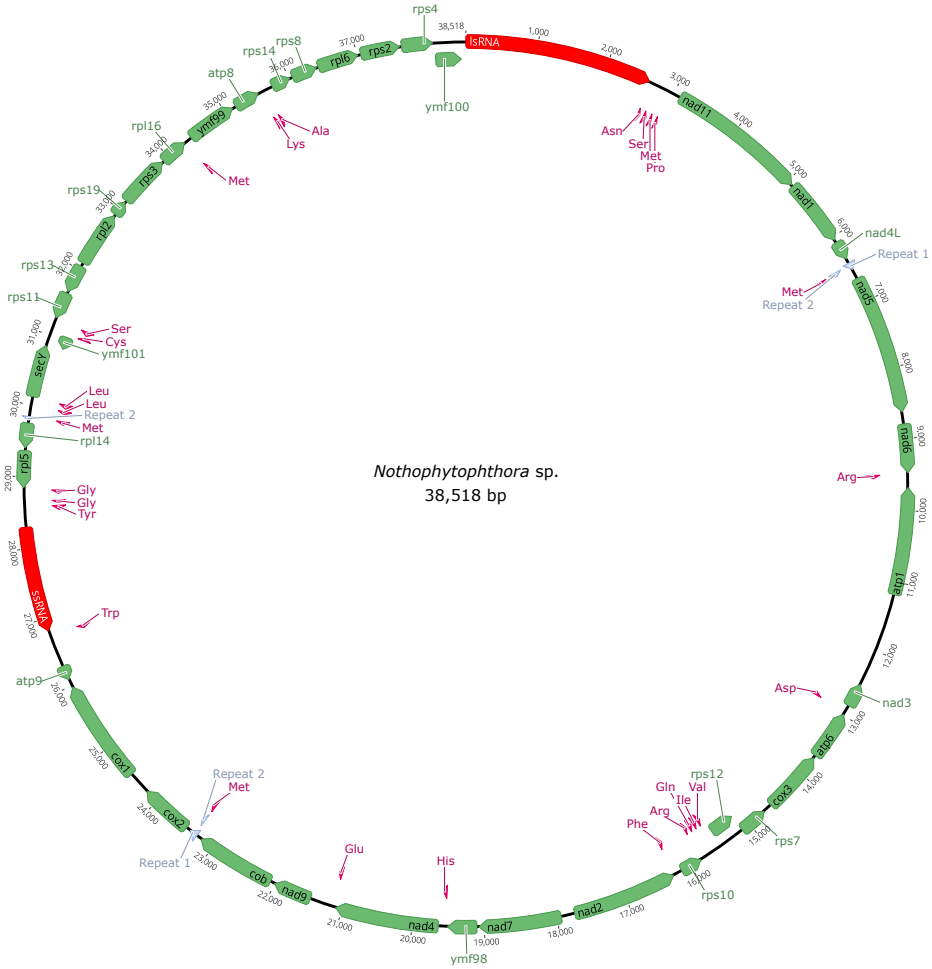
Phytophthora fallax
43,681 bp

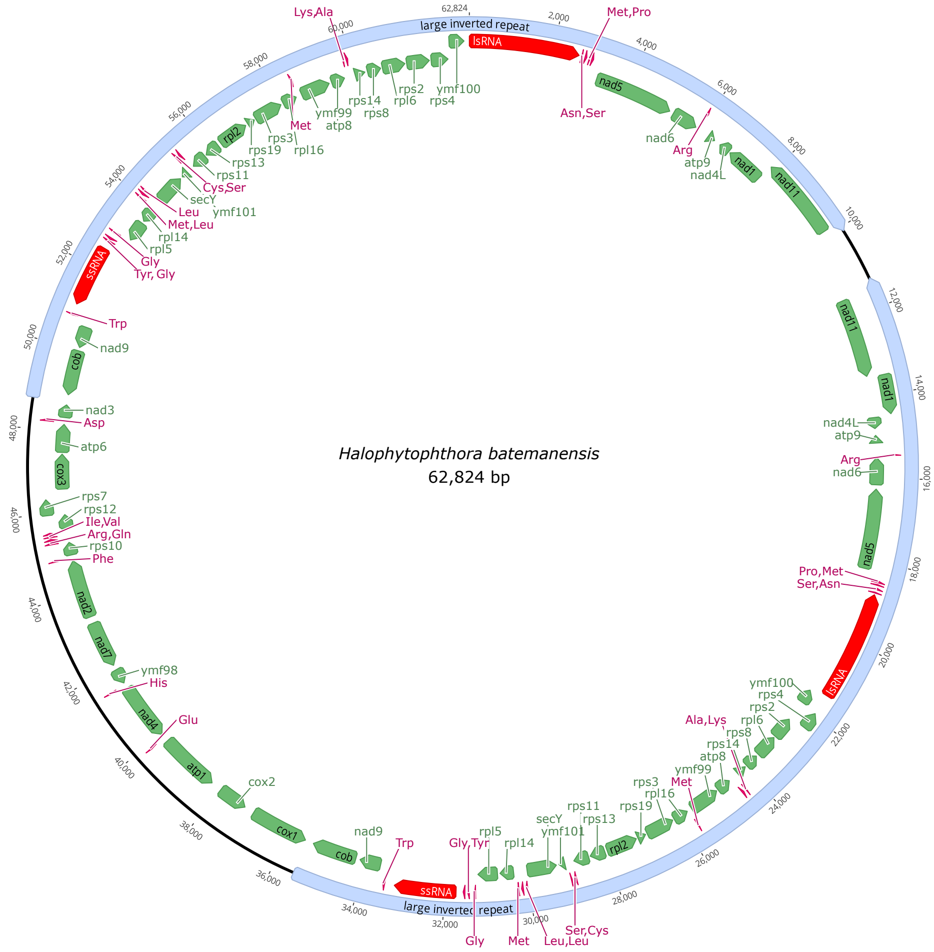
Phytophthora capitosa
44,662 bp


Phytophthora polonica
40,467 bp
rps4
lsRNA
ymf100
Asn
Ser
Met
Met
Pro
rpl14
rpl5
Gly
Gly
Tyr
ssRNA
Trp
cox2
cox1
cob
nad9
atp9
nad3
Asp
atp6
cox3
rps12
Arg
rps7
Val,Ile
Gln
rps10
Phe
nad2
nad7
nad4
His
ymf98
atp1
Glu
nad5
nad6
Arg
nad4L
nad1
Leu
Leu
secY
ymf101
Ser
Cys
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys
Ala
rps14
rps8
rpl6
rps2


Phytophthora boehmeriae
38,001 bp
rps4
ymf100
lsRNA
Repeat 1
rpl14
Asn
Met
Ser
Pro
Met
rpl5
Repeat 1
Gly
Gly
Tyr
Met
Trp
ssRNA
atp1
Glu
nad4
His
ymf98
nad7
Phe
Arg
Gln
Ile
Val
nad2
rps7
rps10
rps12
cox3
atp6
Asp
nad3
nad5
nad6
Arg
cox1
cox2
cob
nad9
atp9
nad4L
nad1
Leu
Leu
secY
ymf101
Ser
Cys
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
Met
atp8
Lys
Ala
rps14
rps8
rpl6
rps2

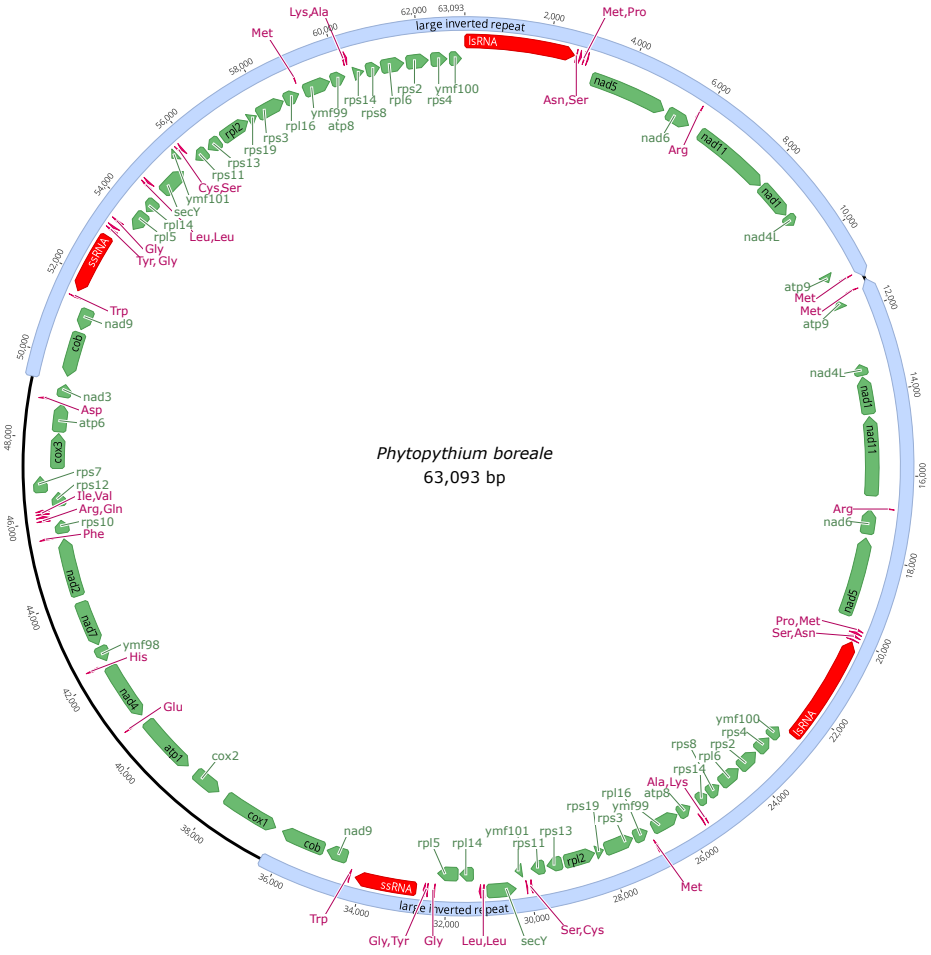

Phytophthora kernoviae
37,467 bp
lsRNA
ssRNA
cox1
cox2
cox3
nad1
nad2
nad3
nad4
nad4L
nad5
nad6
nad7
nad9
cob
atp1
atp5
atp6
atp8
atp9
rps2
rps3
rps4
rps7
rps8
rps10
rps12
rps13
rps14
rps19
rpl2
rpl5
rpl6
rpl14
rpl16
secY
ymf98
ymf99
ymf100
ymf101
Repeat 1
Ala
Lys
Met
Asn
Pro
Ser
Gly
Tyr
Arg
Asp
Val
Ile
Gln
Phe
Leu
Cys
Trp
His
Glu

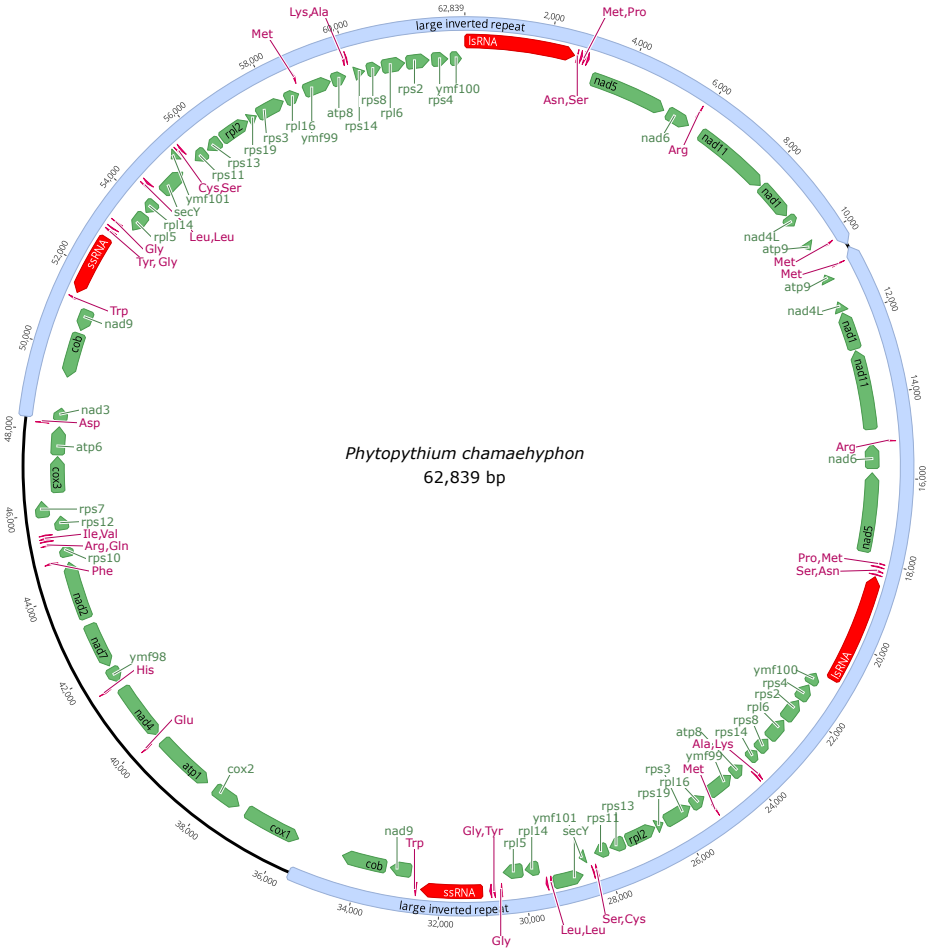

Nothophytophthora sp.
38,518 bp
lsRNA
ssRNA
cox1
cox2
cox3
nad1
nad2
nad3
nad4
nad4L
nad5
nad6
nad7
nad9
cob
atp1
atp5
atp6
atp8
atp9
rps2
rps3
rps4
rps7
rps8
rps10
rps12
rps13
rps14
rps19
rpl2
rpl5
rpl6
rpl14
rpl16
secY
ymf99
ymf100
ymf101
Repeat 1
Repeat 2
Met
Asn
Ser
Pro
Ala
Lys
Gln
Ile
Val
Arg
Phe
Asp
Gly
Tyr
Leu
Cys
Trp
His
Glu


Halophytophthora batemanensis
62,824 bp
large inverted repeat
lsRNA
ssRNA
Lys,Ala
Met,Pro
Asn,Ser
nad5
nad6
Arg
atp9
nad4L
nad1
nad11
ymf100
rps4
rps2
rpl6
rps8
rps14
atp8
ymf99
Met
rpl16
rps3
rps19
rps13
rpl2
rps11
Cys,Ser
secY
ymf101
Leu
Met,Leu
rpl14
rpl5
Gly
Tyr, Gly
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox2
cox1
Pro,Met
Ser,Asn
Ala,Lys
Gly,Tyr
Ser,Cys
Leu,Leu


Halophytophthora polymorphica
64,467 bp
large inverted repeat
lsRNA
ssRNA
Lys,Ala
Met,Pro
Asn,Ser
nad5
nad6
Arg
Met
atp9
nad4L
nad1
nad11
ymf100
rps4
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps3
rps19
rps13
rpl2
rps11
Cys,Ser
Leu
ymf101
secY
rpl14
rpl5
Met,Leu
Gly
Tyr
Trp
nad9
cob
nad3
Asp
atp6
cox3
nad7
nad2
Phe
rps10
Gln,Arg
Val,Ile
rps12
rps7
ymf98
His
nad4
Glu
atp1
cox2
cox1
Pro,Met
Ser,Asn
Ala,Lys
Ser,Cys
Leu,Leu


Phytopythium aichiense
63,546 bp
large inverted repeat
lsRNA
ssRNA
Lys,Ala
Met
Met,Pro
Asn,Ser
nad5
nad6
Arg
nad1
nad4L
atp9
Met
Met
atp9
nad4L
nad1
rnl11
Arg
nad6
nad5
Pro,Met
Ser,Asn
lsRNA
ymf100
rps4
rps2
rps14
rpl6
atp8
rps8
Ala,Lys
ymf99
rps19
rpl16
rps3
rps11
rps13
ymf101
Ser,Cys
rpl5
rpl14
rpl2
Met
Gly,Tyr
Gly
Leu,Leu
secY
Trp
ssRNA
nad9
cob
cox1
cox2
atp1
Glu
nad4
ymf98
His
nad7
nad2
Phe
rps10
Arg,Gln
Ile,Val
rps12
rps7
cox3
atp6
Asp
nad3
Trp
ssRNA
Tyr, Gly
Gly
rpl5
rpl14
Leu,Leu
secY
Cys,Ser
rps11
rps13
rps19
rps3
rpl2
rpl16
ymf99
atp8
rps14
rps8
rpl6
rps2
ymf100
rps4
lsRNA


Phytopythium boreale
63,093 bp
large inverted repeat
lsRNA
ssRNA
Lys,Ala
Met
Met,Pro
Asn,Ser
nad5
nad6
Arg
nad1
nad4L
atp9
Met
Met
atp9
nad4L
nad1
rnl11
Arg
nad6
nad5
Pro,Met
Ser,Asn
lsRNA
ymf100
rps4
rps2
rps8
rpl6
rps14
Ala,Lys
atp8
rpl16
rps19
ymf99
rps3
rps11
rps13
ymf101
Ser,Cys
rpl5
rpl14
rpl2
Met
Gly,Tyr
Gly
Leu,Leu
secY
Trp
ssRNA
nad9
cob
cox1
cox2
atp1
Glu
nad4
ymf98
His
nad7
nad2
Phe
rps10
Arg,Gln
Ile,Val
rps12
rps7
cox3
atp6
Asp
nad3
Trp
ssRNA
Tyr, Gly
Gly
rpl5
rpl14
Leu,Leu
secY
Cys,Ser
rps11
rps13
rps19
rps3
rpl2
rpl16
ymf99
atp8
rps14
rps8
rpl6
rps2
ymf100
rps4
lsRNA

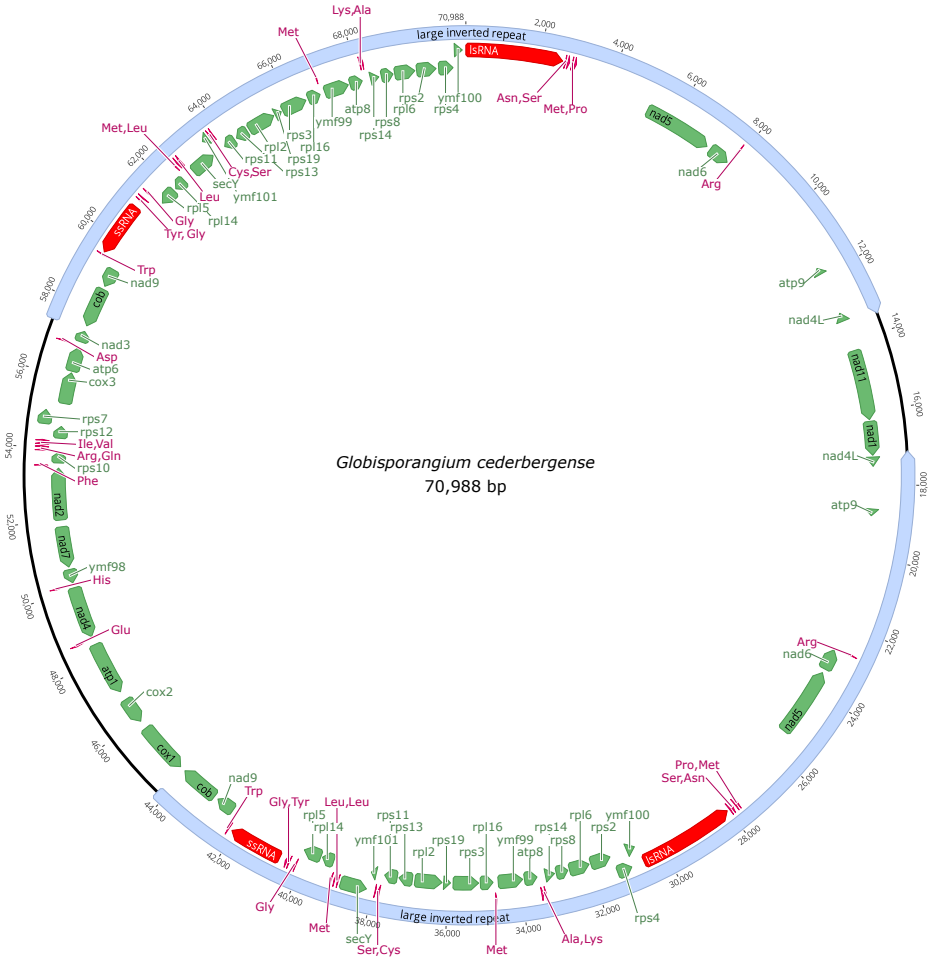

Phytopythium chamaehyphon
62,839 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat
Lys,Ala
Met
Met,Pro
Asn,Ser
Arg
Trp
Asp
Ile,Val
Arg,Gln
Phe
His
Glu
Gly
Tyr, Gly
Leu,Leu
Cys,Ser
Ser,Cys
Pro,Met
Ser,Asn
Ala,Lys
nad5
nad6
nad1
nad11
nad4L
atp9
nad9
cob
nad3
atp6
cox3
rps7
rps12
rps10
nad2
nad7
ymf98
nad4
atp1
cox2
cox1
rps4
ymf100
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps3
rps19
rps13
rps11
rpl2
ymf101
secY
rpl14
rpl5


Phytopythium helicoides
63,571 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat
Lys,Ala
Met
Met,Pro
Asn,Ser
Arg
Trp
Asp
Ile,Val
Arg,Gln
Phe
His
Glu
Gly
Tyr, Gly
Leu,Leu
Cys,Ser
Ser,Cys
Pro,Met
Ser,Asn
Ala,Lys
nad5
nad6
nad1
nad11
nad4L
atp9
nad9
cob
nad3
atp6
cox3
rps7
rps12
rps10
nad2
nad7
ymf98
nad4
atp1
cox2
cox1
rps4
ymf100
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps3
rps19
rps13
rps11
rpl2
ymf101
secY
rpl14
rpl5


Phytopythium sp. cucurbitacearum
61,254 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat


Phytopythium vexans
61,242 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat


large inverted repeat
lsRNA
ssRNA
large inverted repeat
Globisporangium barbulae
60,138 bp


large inverted repeat
lsRNA
ssRNA
large inverted repeat
Globisporangium cederbergense
70,988 bp


large inverted repeat
lsRNA
ssRNA
Globisporangium iwayamai
64,039 bp

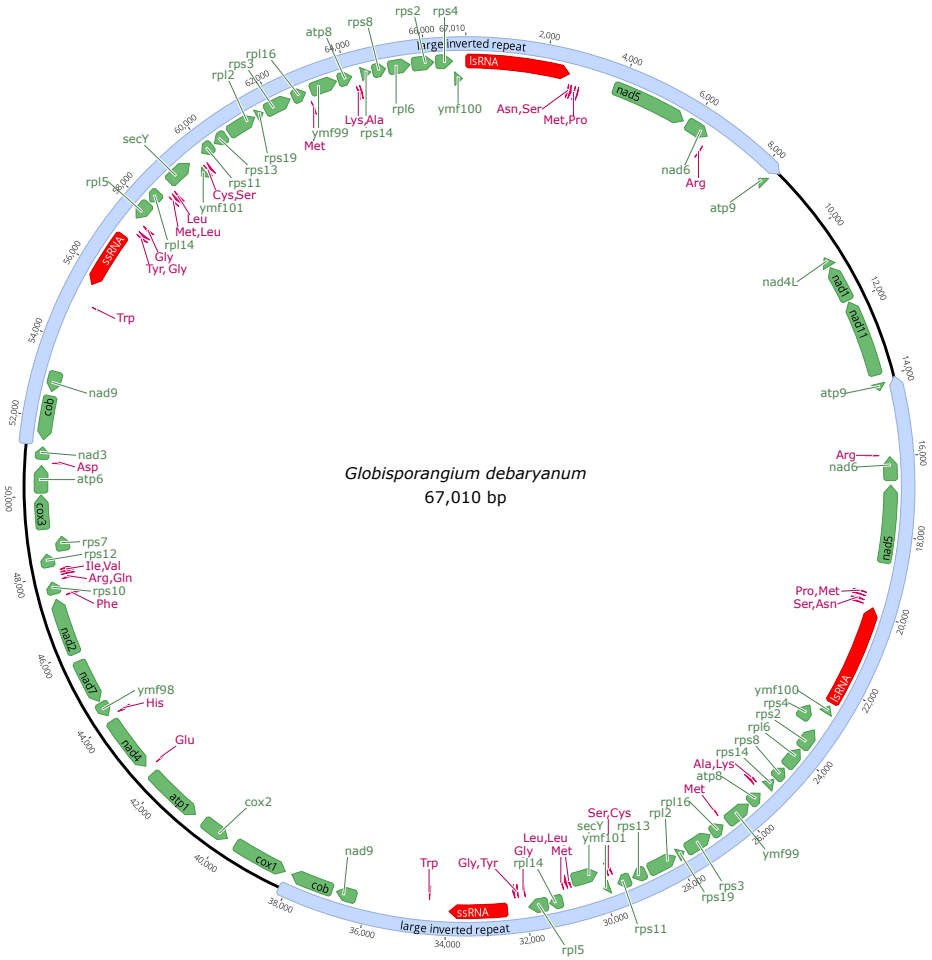

large inverted repeat
lsRNA
ssRNA
Globisporangium okanoganense
69,322 bp


large inverted repeat
lsRNA
ssRNA
large inverted repeat
Globisporangium nagaii
57,646 bp

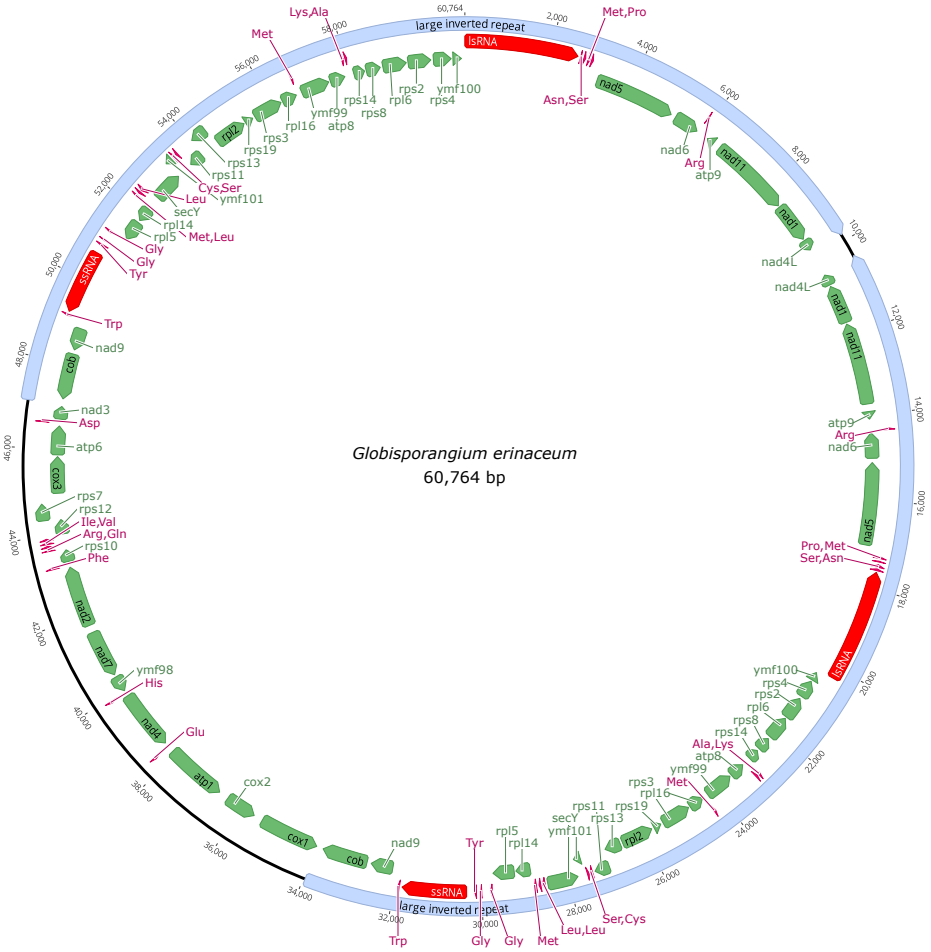

large inverted repeat
lsRNA
ssRNA
large inverted repeat
Globisporangium cylindrosporum
60,681 bp

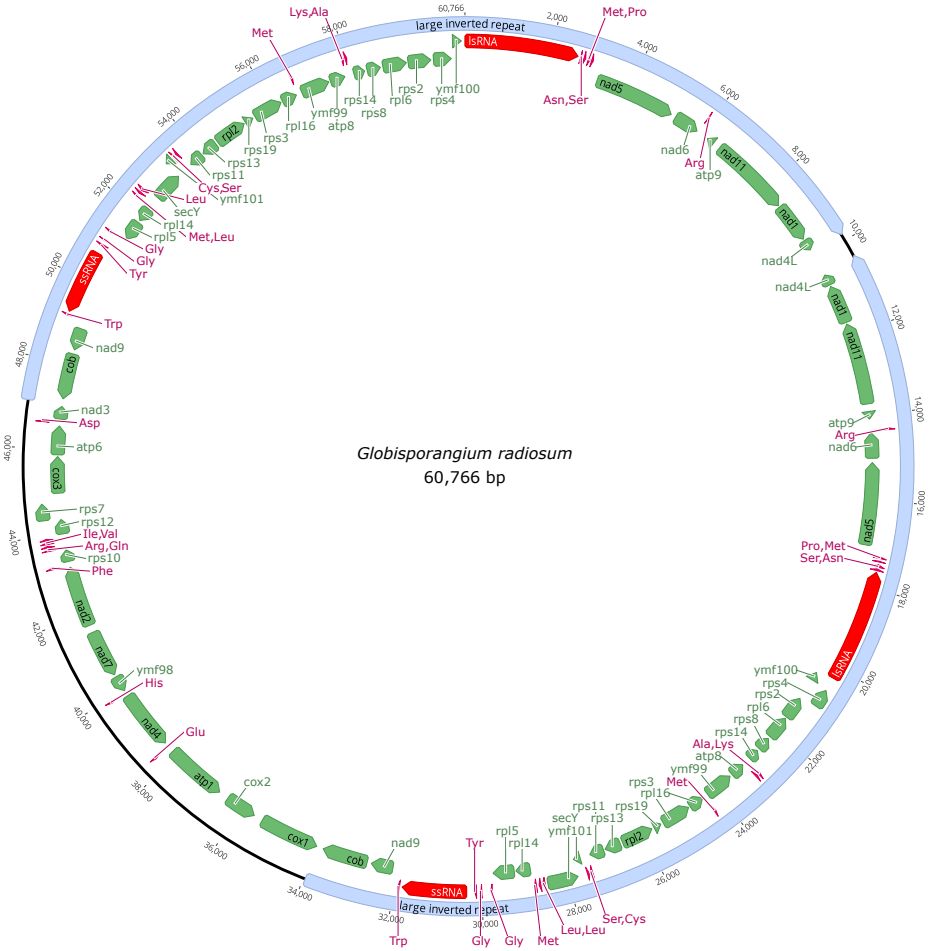

Globisporangium irregulare
60,610 bp
lsRNA
ssRNA
large inverted repeat
large inverted repeat
nad5
nad6
nad11
nad1
nad4L
nad4L
nad1
nad1
atp9
Arg
nad6
nad5
Pro,Met
Ser,Asn
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
Ala,Lys
atp8
Met
ymf99
rps19
rpl16
rps3
rpl2
rps11
rps13
Ser,Cys
Leu,Leu
rpl14
rpl5
Gly,Tyr
Gly
ymf101
secY
Met
Asn,Ser
Met,Pro
Trp
nad9
cob
cox1
cox2
atp1
nad4
Glu
nad7
ymf98
His
nad2
Phe
rps10
Arg,Gln
Ile,Val
rps12
rps7
cox3
atp6
Asp
nad3
Cys,Ser
rps11
rps13
rps19
rps3
rpl16
Met
ymf99
rps14
rps8
rpl6
rps2
rps4
ymf100
Lys,Ala
atp8
rpl2
secY
Leu
Met,Leu
rpl14
rpl5
Gly
Tyr, Gly
ssRNA

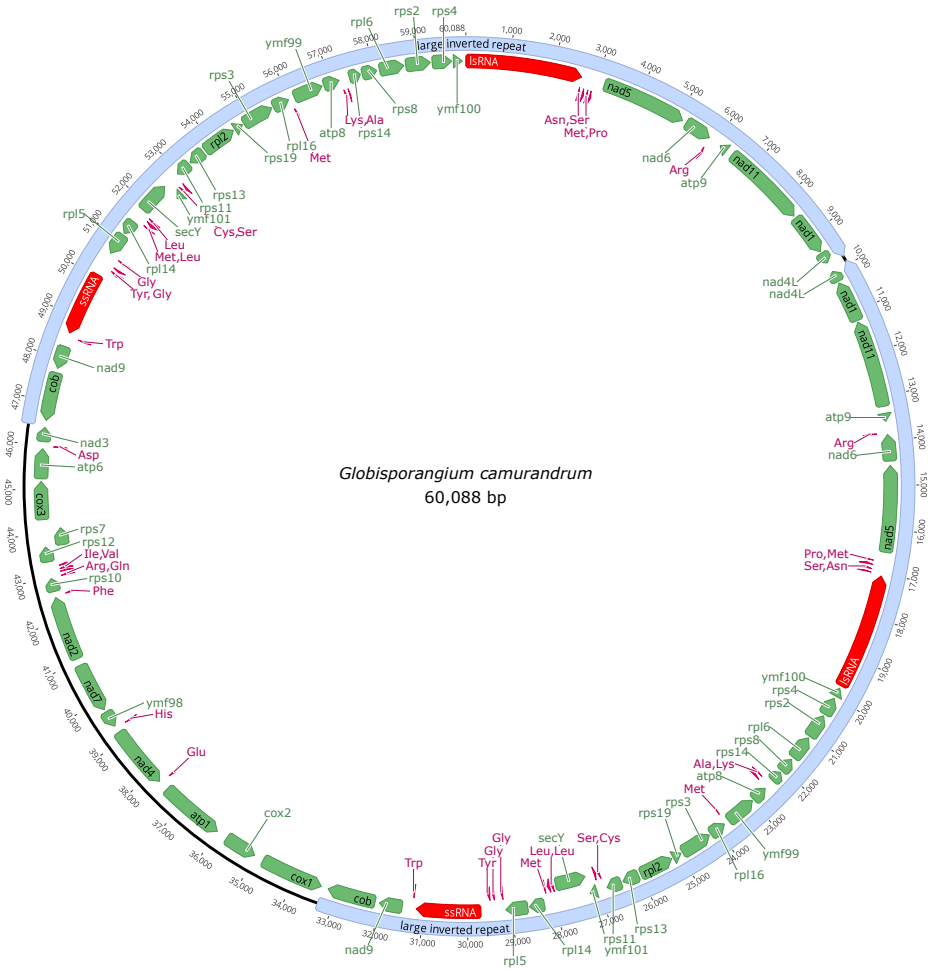

Globisporangium mamillatum
60,953 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat
nad5
nad6
nad11
nad1
nad4L
nad4L
nad1
nad1
atp9
Arg
nad6
nad5
Pro,Met
Ser,Asn
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
Ala,Lys
atp8
Met
rpl16
rps3
ymf99
rps19
rpl2
rps13
Ser,Cys
Leu,Leu
secY
Met
Gly
Gly,Tyr
ymf101
rps11
rpl14
rpl5
Asn,Ser
Met,Pro
Trp
nad9
cob
cox1
cox2
atp1
nad4
Glu
nad7
ymf98
His
nad2
Phe
rps10
Arg,Gln
Ile,Val
rps12
rps7
cox3
atp6
Asp
nad3
Cys,Ser
rps11
rps13
rps19
rps3
rpl16
Met
ymf99
rps14
rps8
rpl6
rps2
rps4
ymf100
Lys,Ala
atp8
rpl2
secY
Leu
Met,Leu
rpl14
rpl5
Gly
Tyr, Gly
ssRNA

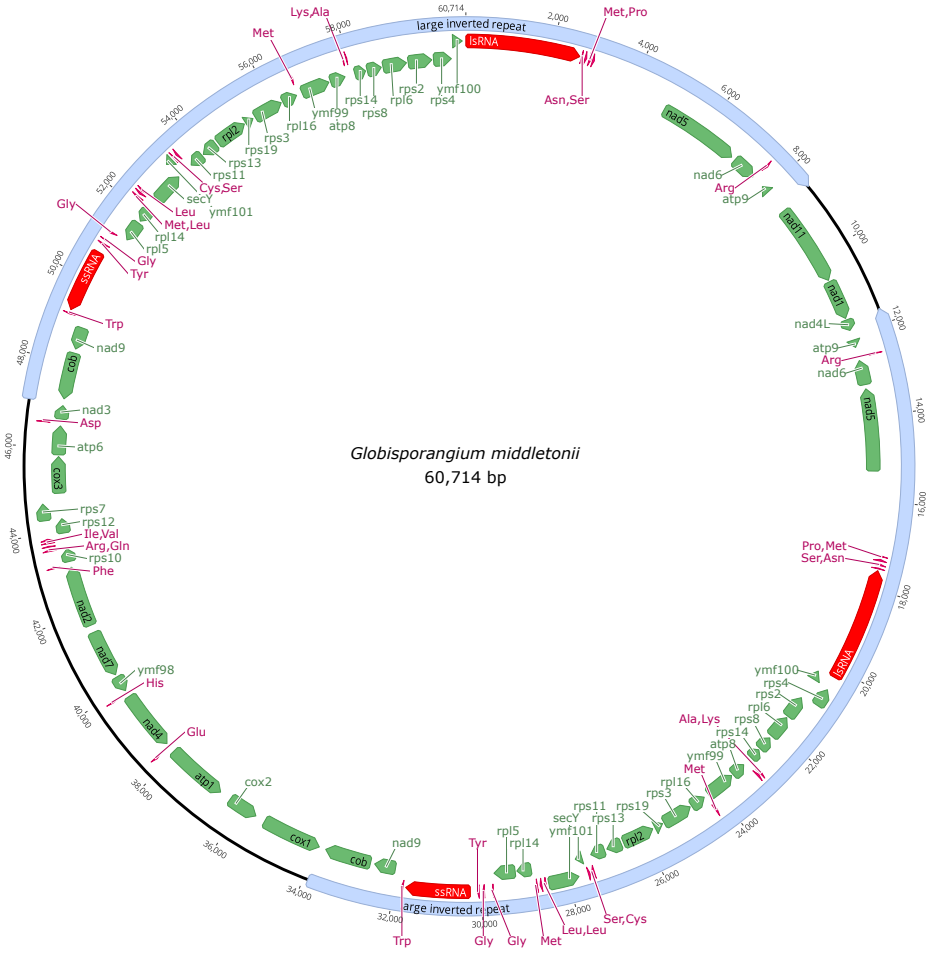

Globisporangium debaryanum
67,010 bp
large inverted repeat
lsRNA
ssRNA
rps2
rps4
rps8
atp8
rpl16
rps3
rpl2
rps19
rps14
rpl6
ymf100
ymf99
Met
Lys,Ala
Asn,Ser
Met,Pro
nad5
nad6
Arg
atp9
nad4L
nad1
nad11
secY
rpl5
rps13
rps11
Cys,Ser
ymf101
Leu
Met,Leu
rpl14
Gly
Tyr, Gly
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox2
cox1
Pro,Met
Ser,Asn
Ala,Lys
Ser,Cys
Leu,Leu
Gly,Tyr


Globisporangium emineosum
57,491 bp
large inverted repeat
lsRNA
ssRNA
rpl6
rps2
rps4
ymf99
rpl16
rps8
atp8
rps14
Lys,Ala
Met
rps3
rps19
ymf100
Asn,Ser
Met,Pro
nad5
nad6
Arg
atp9
nad11
nad1
nad4L
secY
rps13
rps11
Cys,Ser
ymf101
Leu
Met,Leu
rpl14
rpl5
Gly
Tyr, Gly
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox2
cox1
Pro,Met
Ser,Asn
Ala,Lys
Ser,Cys
Leu,Leu
Gly,Tyr
rpl2
rps19
rps3

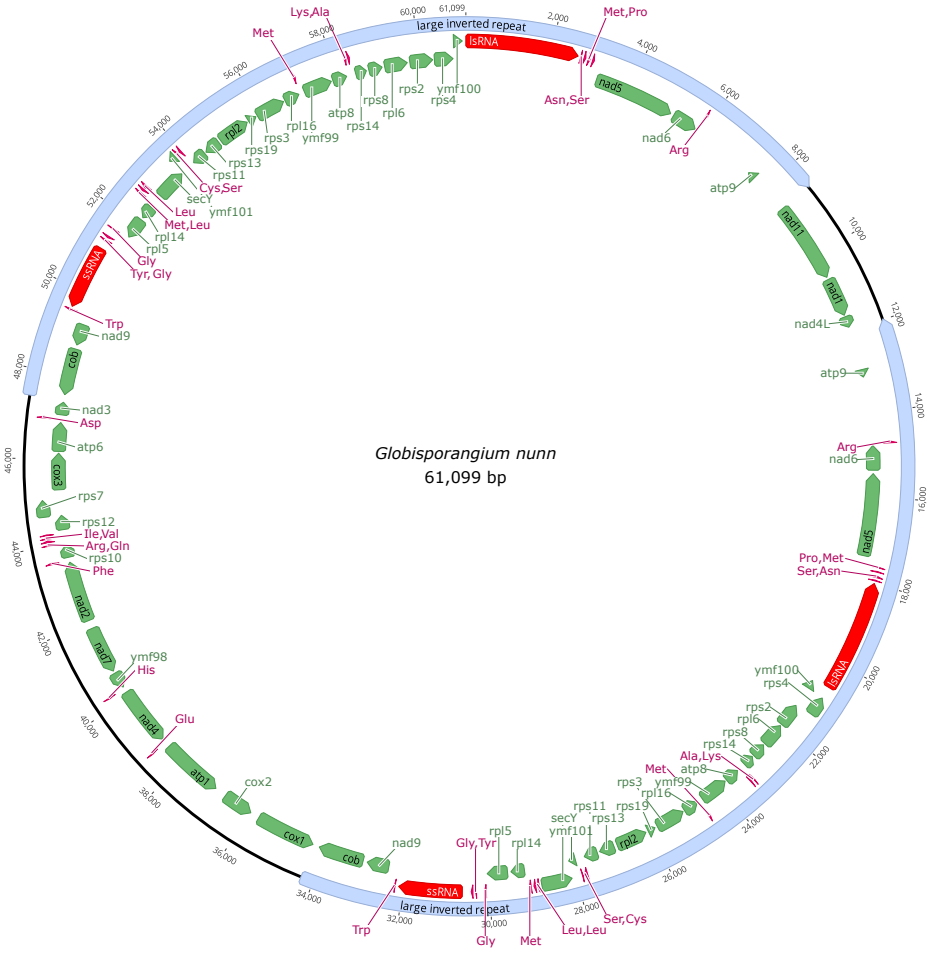

Globisporangium erinaceum
60,764 bp
large inverted repeat
lsRNA
ssRNA
nad5
nad6
nad11
nad1
nad4L
atp9
Arg
Asn,Ser
Met,Pro
Pro,Met
Ser,Asn
rps4
ymf100
rps2
rpl6
rps8
rps14
Ala,Lys
atp8
ymf99
Met
rps3
rpl16
rps19
rps13
rps11
secY
ymf101
rpl2
Cys,Ser
Leu
rpl14
rpl5
Met,Leu
Gly
Tyr
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox2
cox1
Ser,Cys

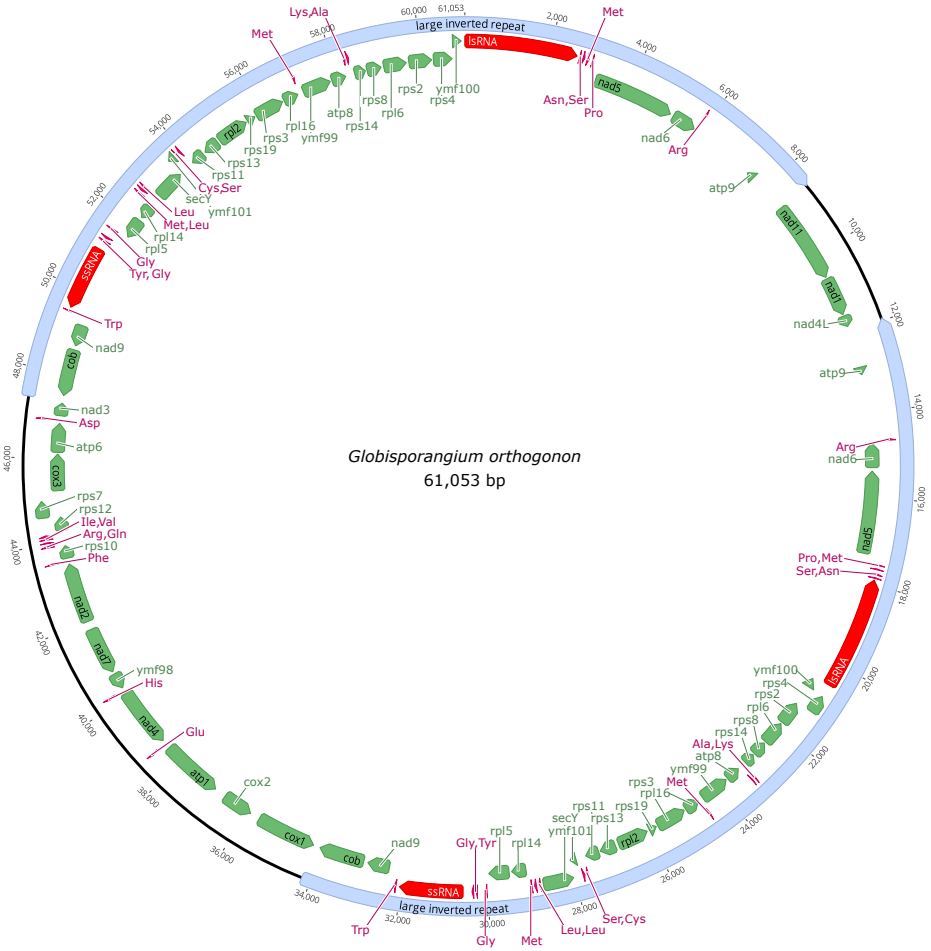

Globisporangium radiosum
60,766 bp
large inverted repeat
lsRNA
ssRNA
nad5
nad6
nad11
nad1
nad4L
atp9
Arg
Asn,Ser
Met,Pro
Pro,Met
Ser,Asn
rps4
ymf100
rps2
rpl6
rps8
rps14
Ala,Lys
atp8
ymf99
Met
rps3
rpl16
rps19
rps13
rps11
secY
ymf101
rpl2
Cys,Ser
Leu
rpl14
rpl5
Met,Leu
Gly
Tyr
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox2
cox1
Ser,Cys


large inverted repeat
lsRNA
ssRNA
Globisporangium camurandrum
60,088 bp

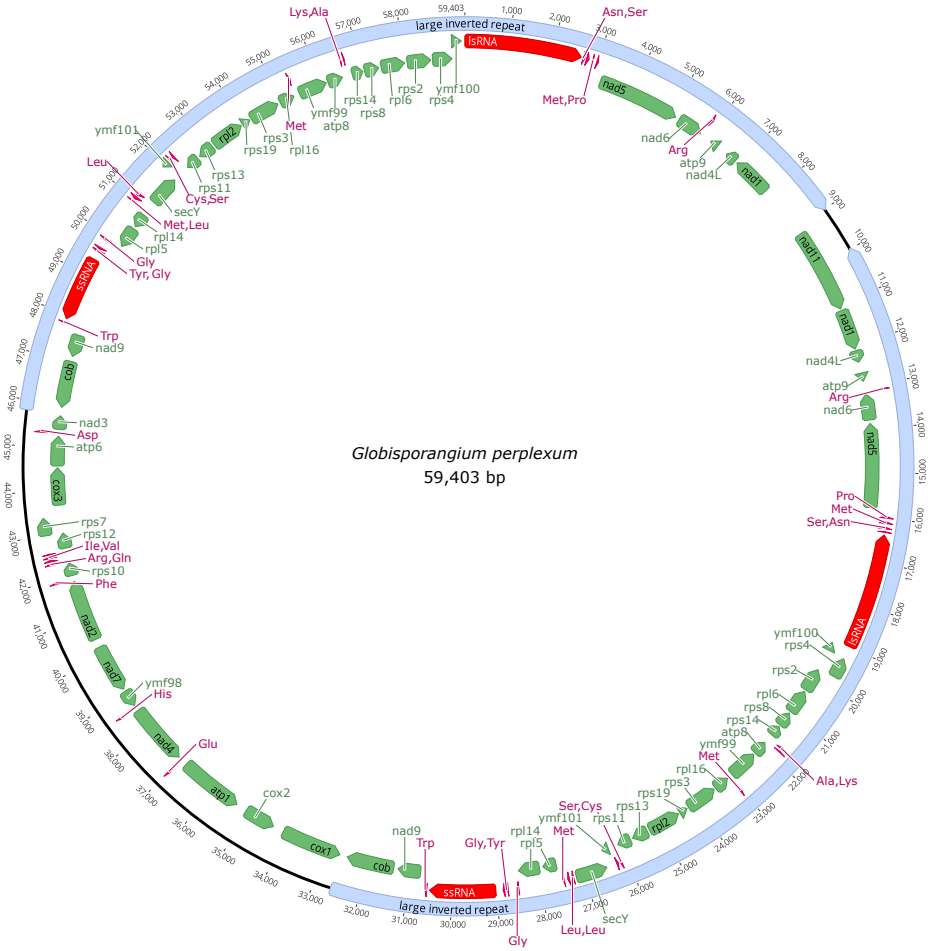

large inverted repeat
lsRNA
ssRNA
Globisporangium middletonii
60,714 bp


Globisporangium rhizosaccharum
58,038 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat
rps4
rps14
rpl6
ymf99
rpl16
rps3
rps2
ymf100
atp8
rps8
Lys,Ala
Met
Asn,Ser
Met,Pro
nad5
nad6
Arg
atp9
nad4L
nad1
nad11
rpl2
rps19
rps13
rps11
secY
Cys,Ser
ymf101
Leu
Met,Leu
rpl14
rpl5
Gly
Gly
Tyr
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox2
cox1
Pro,Met
Ser,Asn
Ser,Cys
Leu,Leu

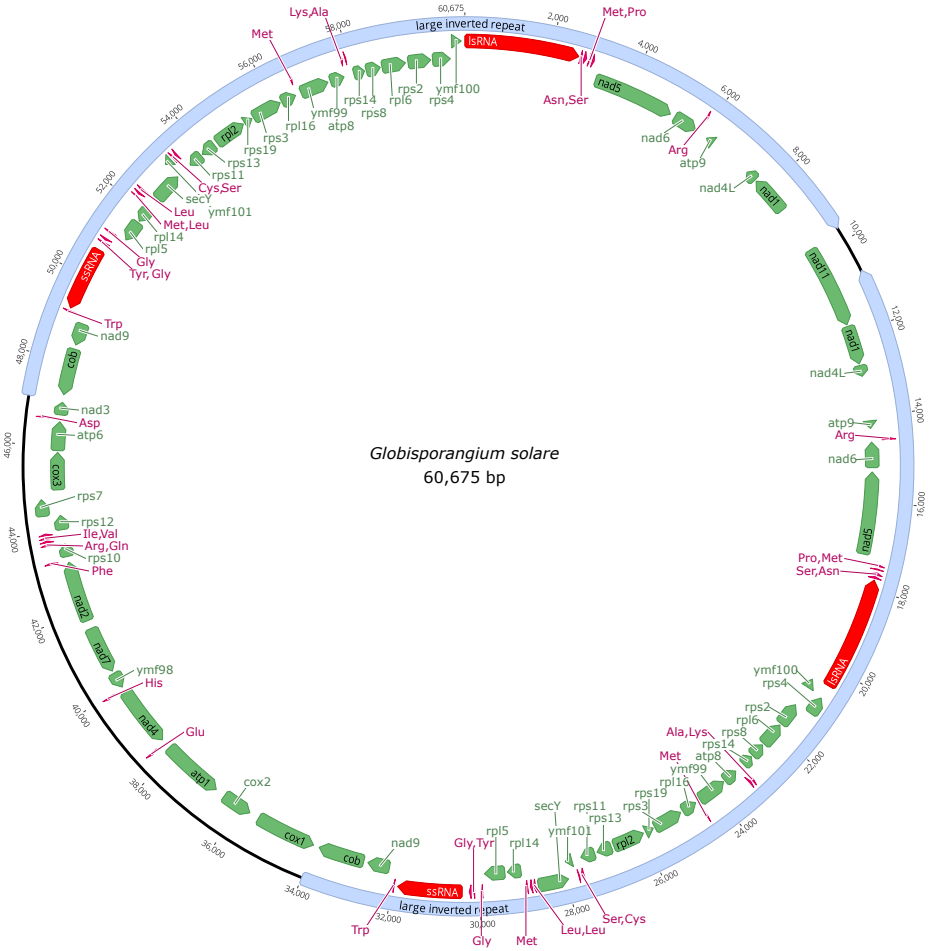

Globisporangium nunn
61,099 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat
Lys,Ala
Met
Met,Pro
rps8
rps2
ymf100
rps4
rpl6
atp8
rps14
rpl16
ymf99
rps3
rps19
rps13
rps11
secY
Cys,Ser
ymf101
Leu
Met,Leu
rpl14
rpl5
Gly
Tyr, Gly
Asn,Ser
nad5
nad6
Arg
atp9
nad1
nad11
nad4L
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox2
cox1
Pro,Met
Ser,Asn
rpl2
rpl5
Gly,Tyr
rpl14
Ser,Cys
Leu,Leu
Met
Gly
Trp


large inverted repeat
lsRNA
ssRNA
Globisporangium orthogonon
61,053 bp


large inverted repeat
lsRNA
ssRNA
Globisporangium acanthophoron
58,427 bp

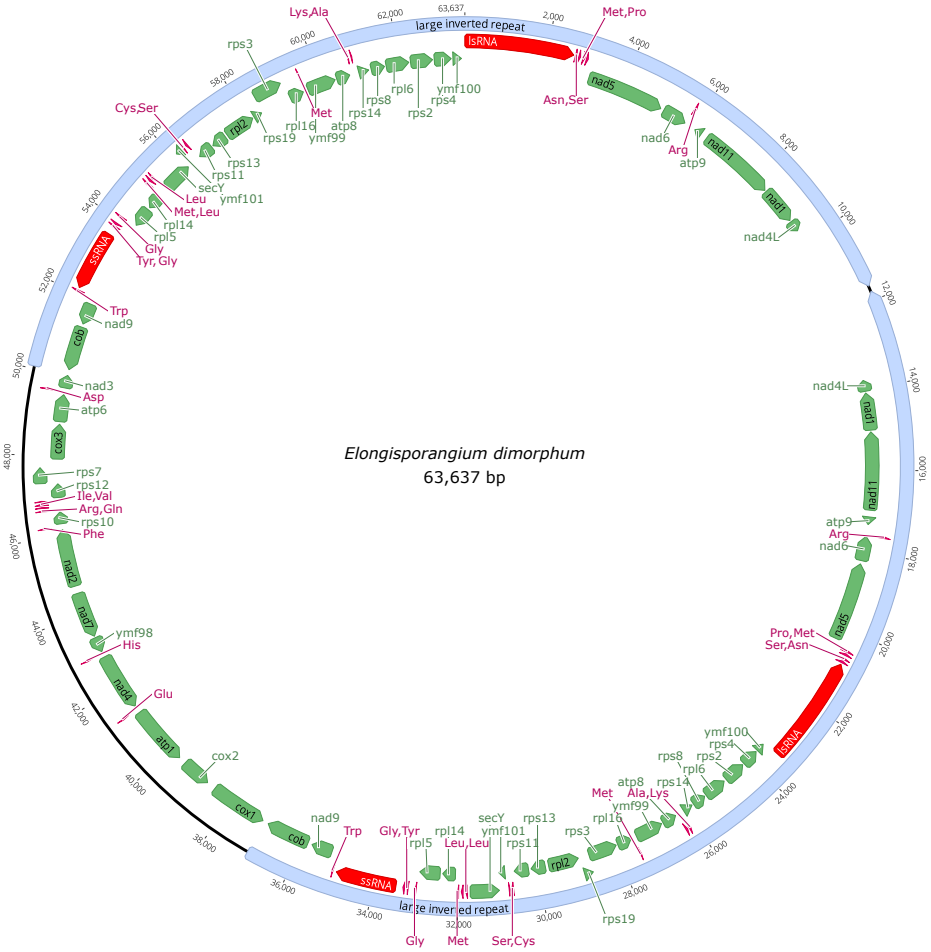

large inverted repeat
lsRNA
ssRNA
Globisporangium perplexum
59,403 bp

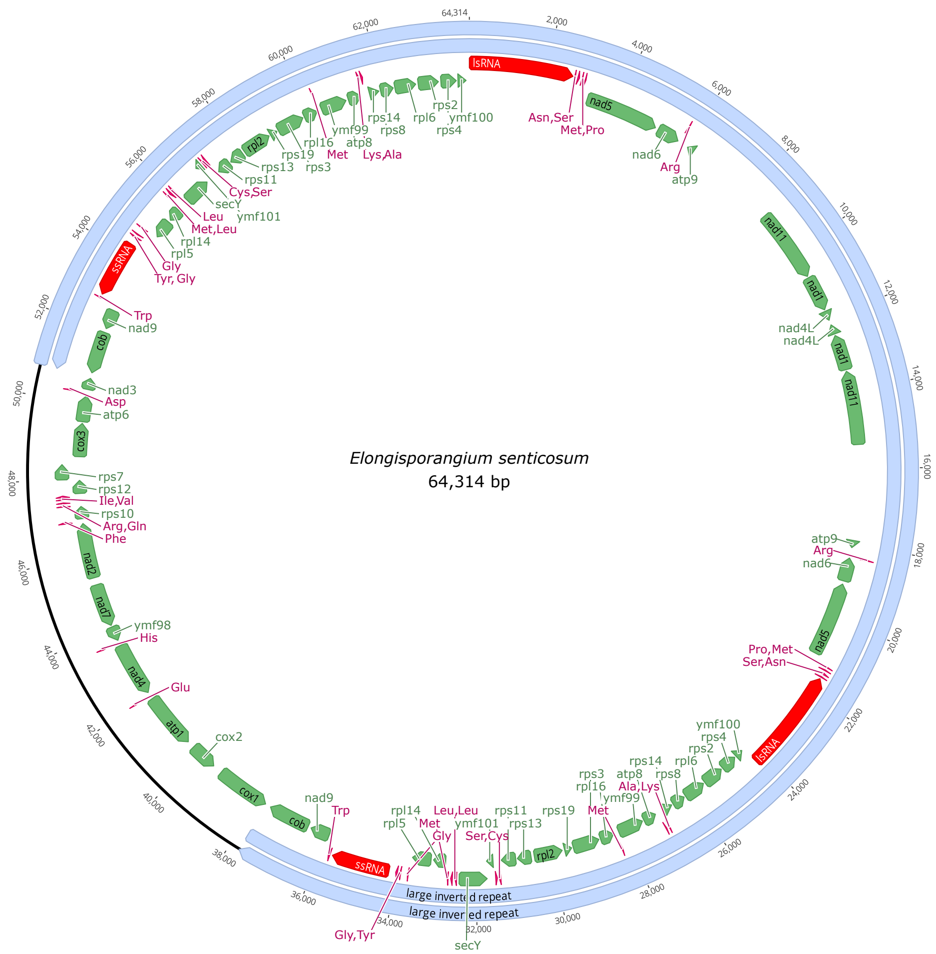

large inverted repeat
lsRNA
ssRNA
Globisporangium ultimum
59,689 bp

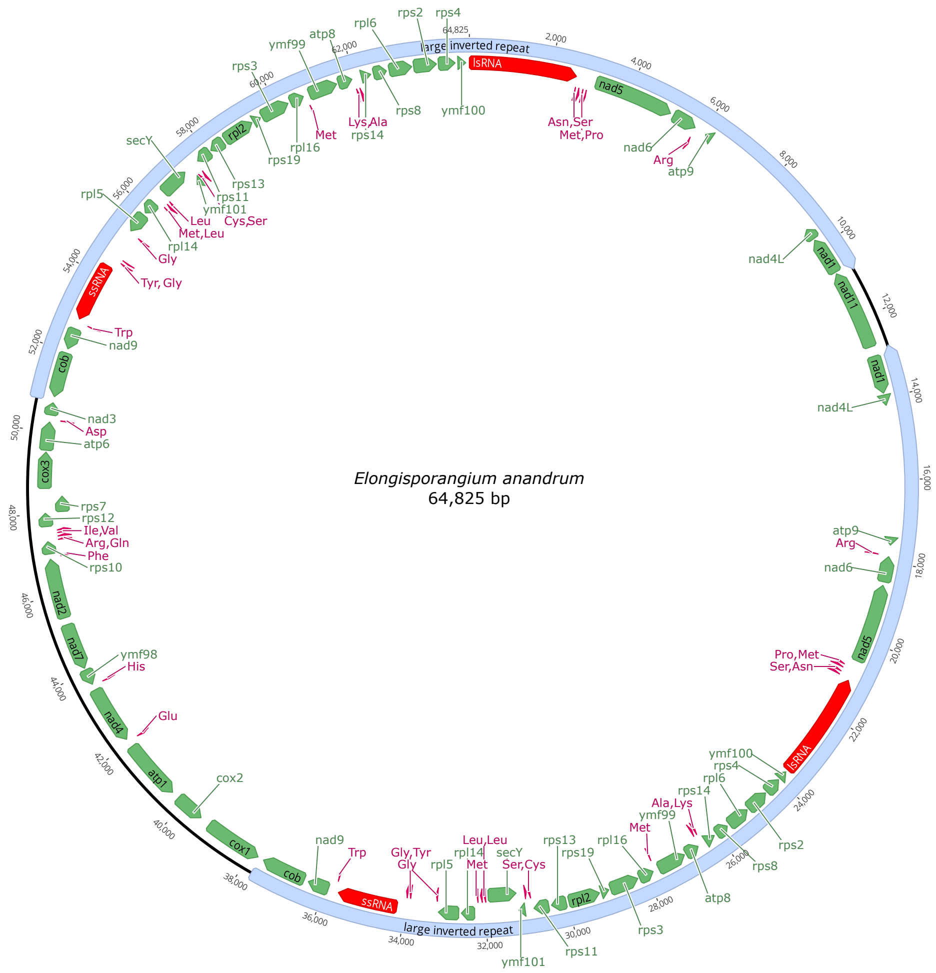

large inverted repeat
lsRNA
ssRNA
large inverted repeat
Globisporangium solare
60,675 bp
Lys,Ala
Met
Met,Pro
Asn,Ser
Arg
Cys,Ser
Leu
Met,Leu
Gly
Tyr, Gly
Trp
Asp
Ile,Val
Arg,Gln
Phe
His
Glu
Gly,Tyr
Ser,Cys
Leu,Leu
Pro,Met
Ser,Asn
Ala,Lys
nad9
nad3
atp6
rps7
rps12
rps10
nad2
nad7
nad4
atp1
cox2
cox1
cob
cox3
nad5
nad6
atp9
nad4L
nad1
nad11
rps4
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps19
rps3
rpl2
rps13
rps11
secY
ymf101
rpl14
rpl5
ymf100
ymf98

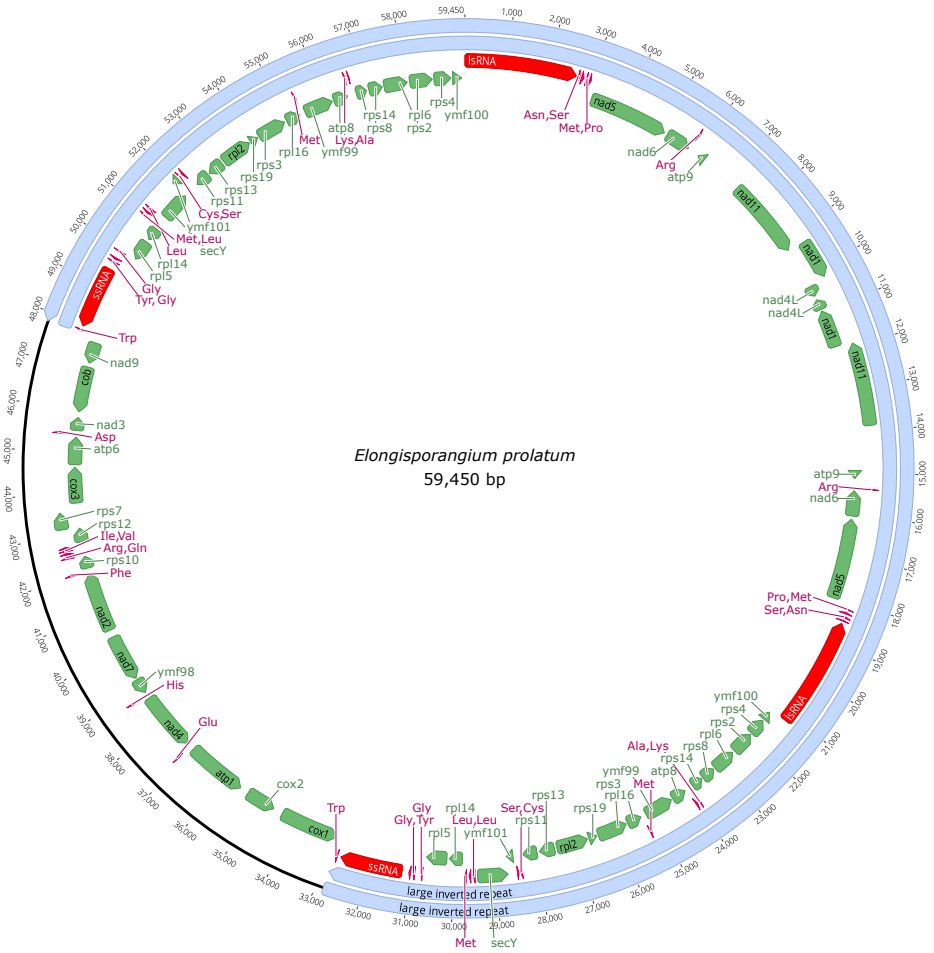

large inverted repeat
lsRNA
ssRNA
large inverted repeat
Globisporangium splendens
59,351 bp
Lys,Ala
Asn,Ser
Met,Pro
Cys,Ser
Met
Arg
Leu
Met,Leu
Gly
Tyr, Gly
Trp
Asp
Ile,Val
Arg,Gln
Phe
His
Glu
Gly,Tyr
Leu,Leu
Ser,Cys
Pro,Met
Ser,Asn
Ala,Lys
nad9
nad3
atp6
rps7
rps12
rps10
nad2
nad7
nad4
atp1
cox2
cox1
cob
cox3
nad5
nad6
atp9
nad4L
nad1
nad11
rps4
rps2
rpl6
rps8
rps14
atp8
ymf99
rpl16
rps19
rps3
rpl2
rps13
secY
ymf101
rpl14
rpl5
ymf100
ymf98

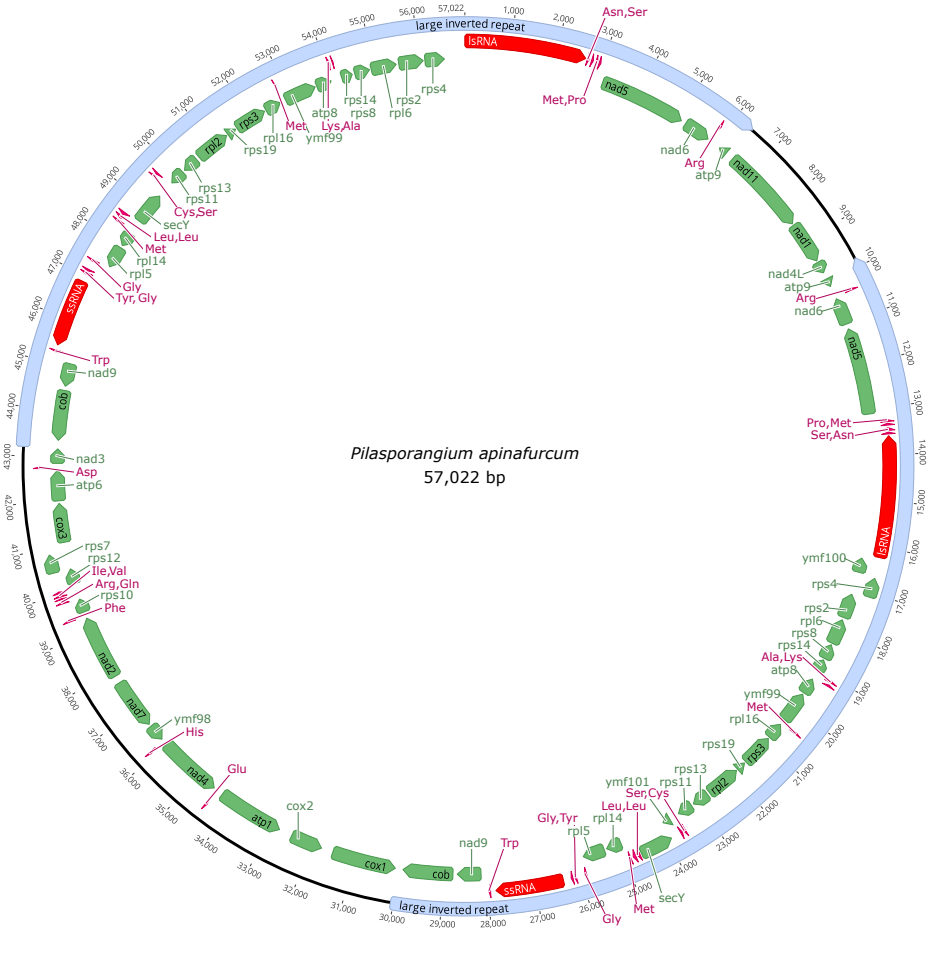

large inverted repeat
lsRNA
ssRNA
large inverted repeat
Lys,Ala
Asn,Ser
Met,Pro
rps3
rpl2
rps19
rpl16
Met
atp8
rps14
rps8
rpl6
rps2
ymf100
rps4
ymf99
rps13
rps11
Cys,Ser
ymf101
Leu,Leu
secY
Met
rpl14
rpl5
Gly
Tyr, Gly
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad7
nad2
ymf98
His
nad4
Glu
atp1
cox2
cox1
nad9
Trp
Gly,Tyr
rpl5
rpl14
Leu,Leu
ymf101
rps13
rps11
rpl2
rps3
rpl16
Met
ymf99
atp8
Ala,Lys
rps14
rps8
rpl6
rps2
ymf100
rps4
rps19
Ser,Cys
secY
Met
Gly
nad5
nad6
Arg
atp9
nad4L
nad1
nad11
atp9
Arg
nad6
nad5
Pro,Met
Ser,Asn
lsRNA
Globisporangium heterothallicum
57,919 bp

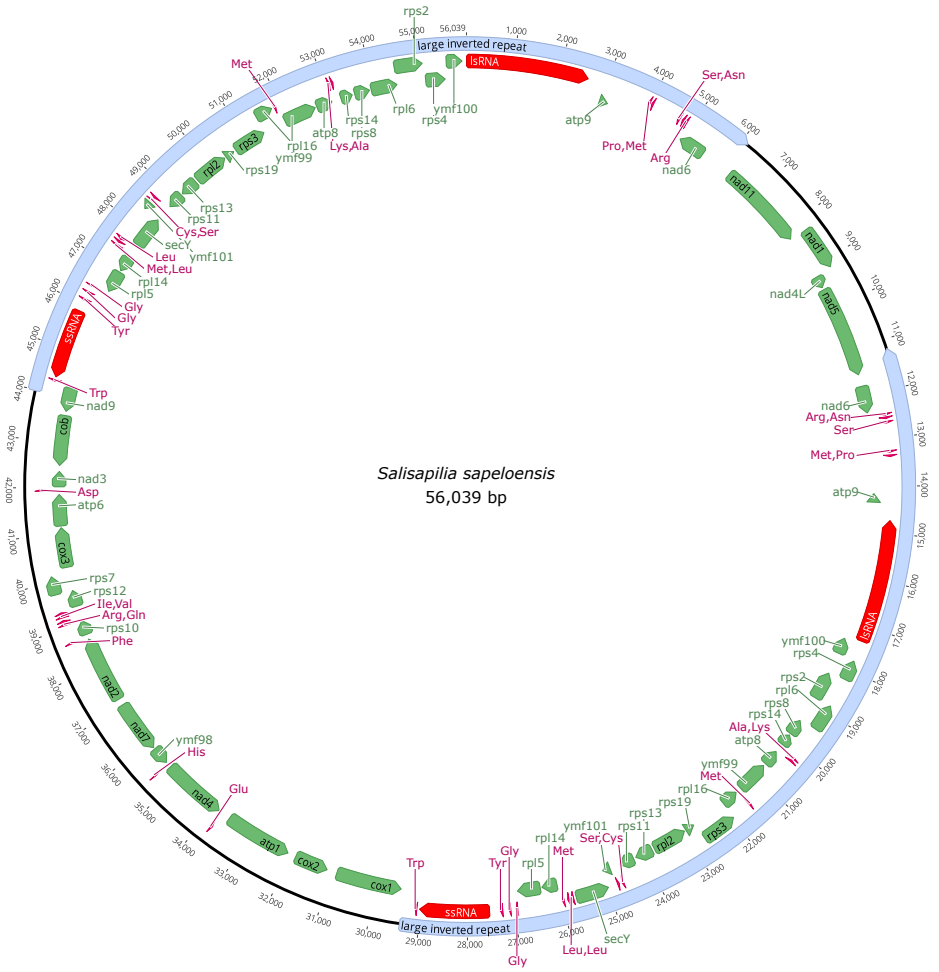

large inverted repeat
lsRNA
ssRNA
large inverted repeat
Lys,Ala
Met,Pro
Asn,Ser
rps3
rpl2
rps19
rpl16
Met
atp8
rps14
rps8
rpl6
rps2
ymf100
rps4
ymf99
Cys,Ser
rps13
rps11
secY
Leu
ymf101
Met,Leu
rpl14
rpl5
Gly
Tyr, Gly
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox2
cox1
nad9
Trp
Gly,Tyr
rpl5
rpl14
Leu,Leu
secY
ymf101
rps13
rps11
rpl2
rps3
rpl16
Met
ymf99
atp8
Ala,Lys
rps14
rps8
rpl6
rps2
ymf100
rps4
rps19
Ser,Cys
Met
Gly
nad5
nad6
Arg
atp9
nad4L
nad1
nad11
atp9
Arg
nad6
nad5
Pro,Met
Ser,Asn
lsRNA
Elongisporangium dimorphum
63,637 bp

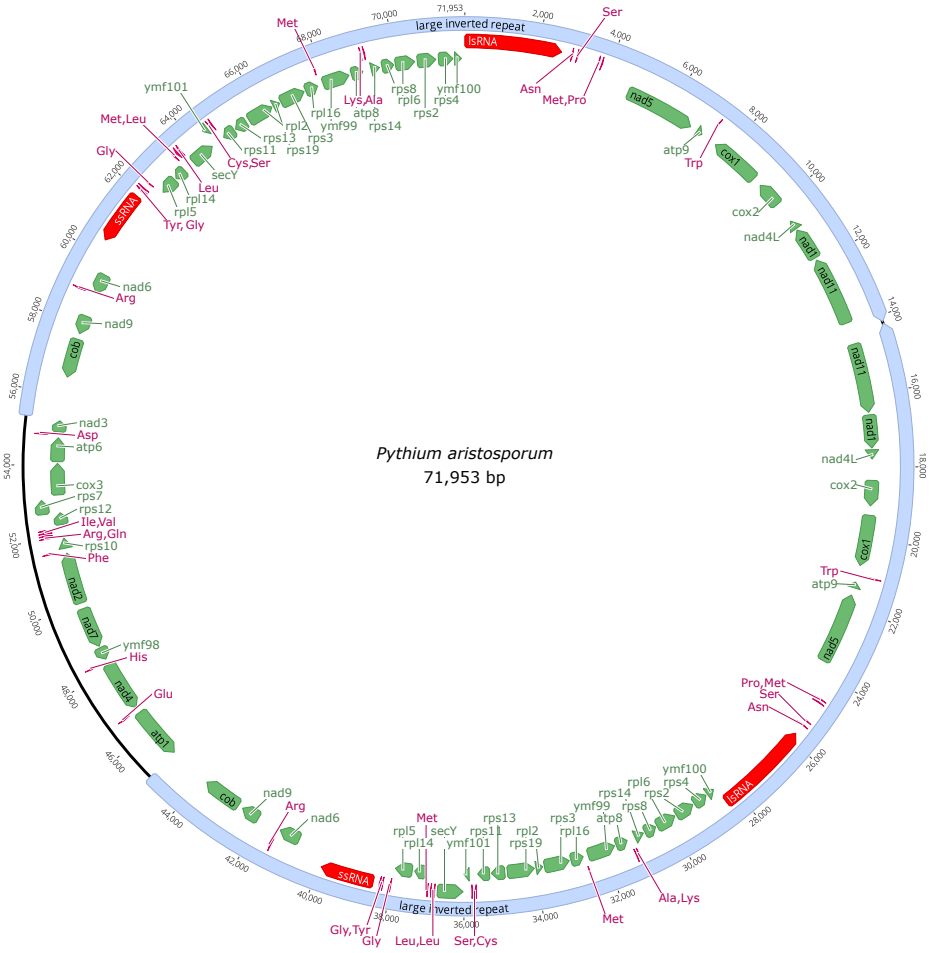

Elongisporangium senticosum
64,314 bp
large inverted repeat
lsRNA
ssRNA
nad5
nad6
atp9
nad11
nad1
nad4L
nad3
atp6
cox3
rps7
rps12
rps10
nad2
nad7
ymf98
nad4
atp1
cox2
cox1
cob
nad9
rpl14
rpl5
rpl2
rpl16
rpl6
rps3
rps19
rps13
rps11
rps14
rps8
rps2
rps4
ymf99
ymf100
ymf101
secY
atp8

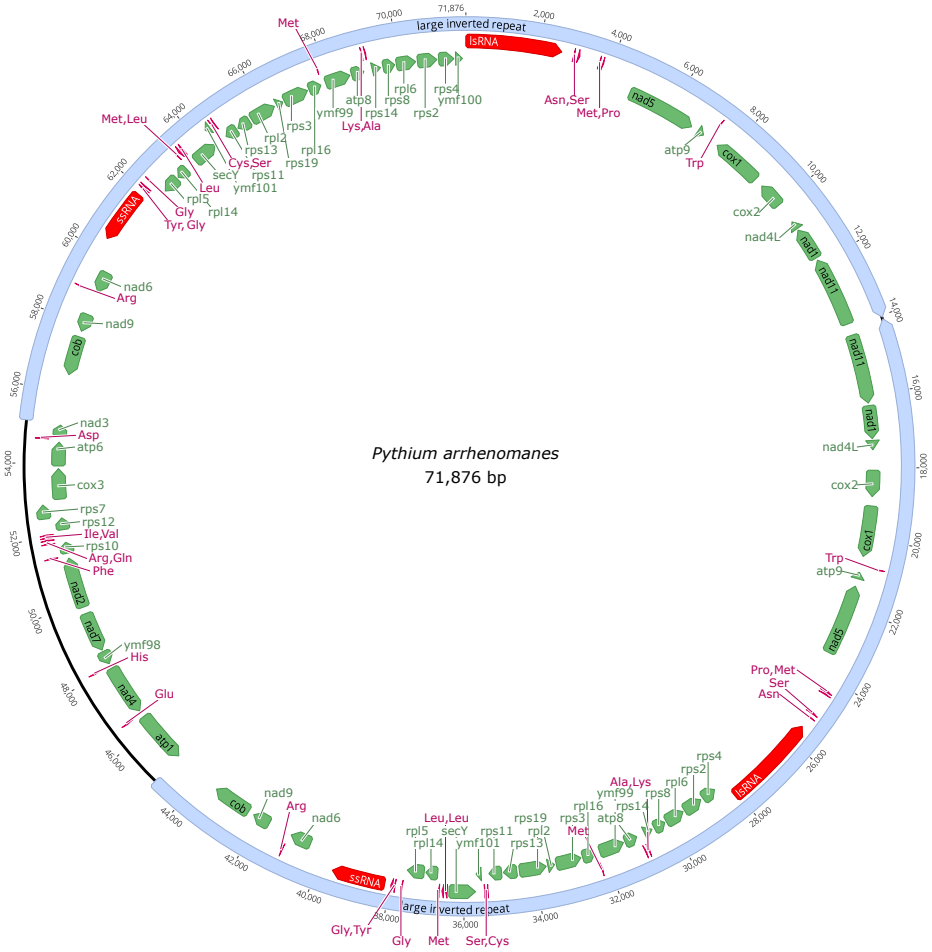

Elongisporangium anandrum
64,825 bp
large inverted repeat
lsRNA
ssRNA
nad5
nad6
atp9
nad11
nad1
nad4L
nad3
atp6
cox3
rps7
rps12
rps10
nad2
nad7
ymf98
nad4
atp1
cox2
cox1
cob
nad9
rpl14
rpl5
rpl2
rpl16
rpl6
rps3
rps19
rps13
rps11
rps14
rps8
rps2
rps4
ymf99
ymf100
ymf101
secY
atp8

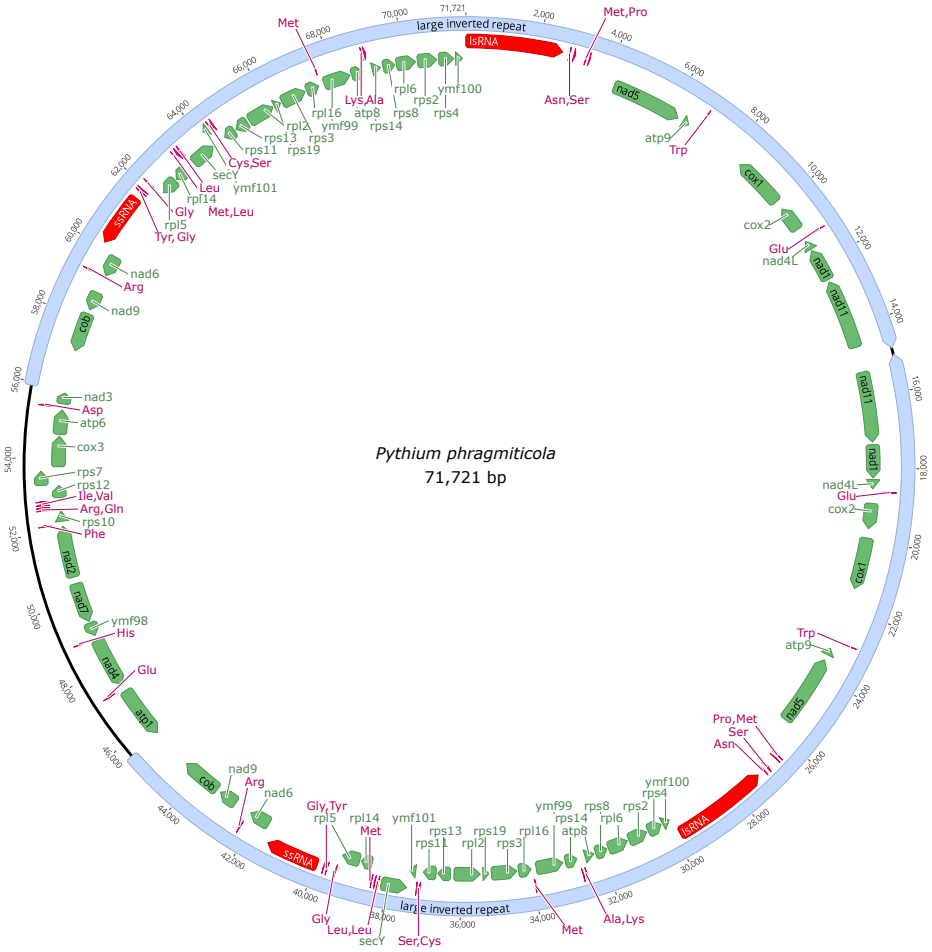

lsRNA
Asn,Ser
Met,Pro
nad5
nad6
Arg
atp9
nad1
nad4L
rps4
rpl6
rps2
ymf100
rps14
rps8
atp8
Lys,Ala
ymf99
Met
rpl16
rps3
rpl2
rps19
rps13
rps11
Cys,Ser
ymf101
Met,Leu
Leu
secY
rpl14
rpl5
Gly
Tyr,Gly
ssRNA
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox2
cox1
Pro,Met
Ser,Asn
Ala,Lys
Gly,Tyr
Ser,Cys
Leu,Leu
large inverted repeat
Elongisporangium prolatum
59,450 bp

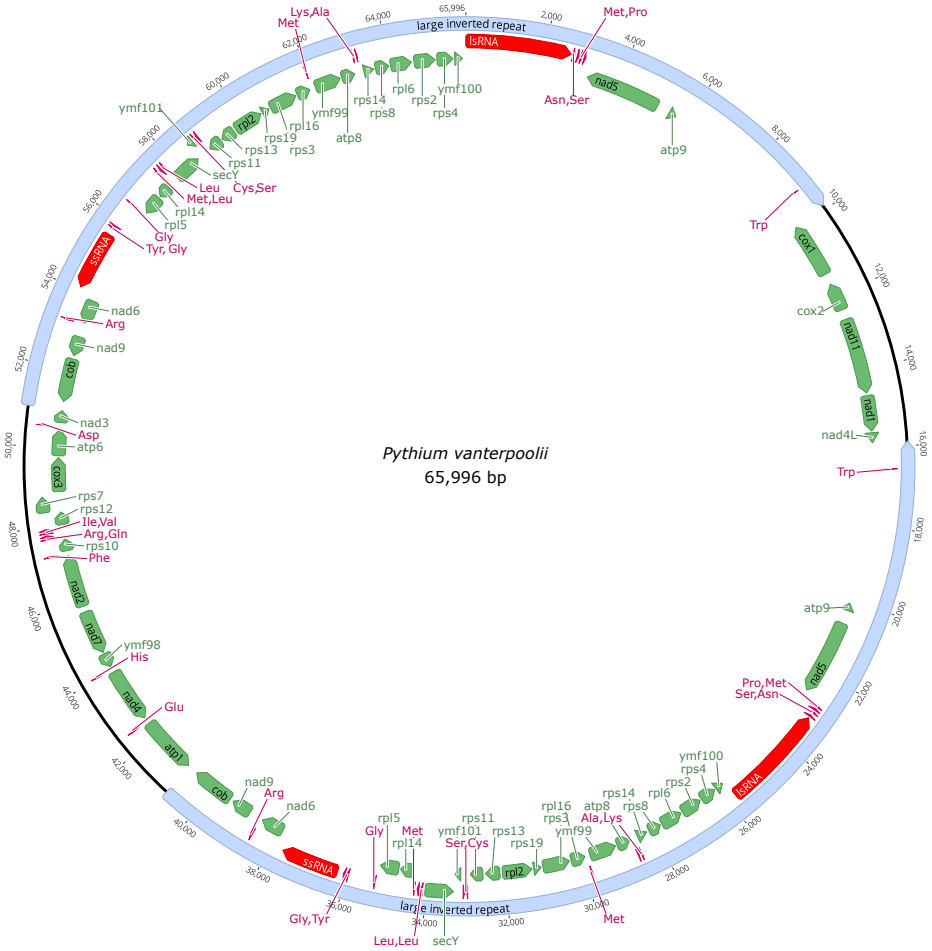

large inverted repeat
lsRNA
Asn,Ser
Met,Pro
nad5
nad6
Arg
atp9
nad1
nad4L
rps4
rps2
rpl6
rps14
rps8
atp8
Lys,Ala
ymf99
Met
rpl16
rps3
rpl2
rps19
rps13
rps11
Cys,Ser
secY
Leu,Leu
Met
rpl14
rpl5
Gly
Tyr,Gly
ssRNA
Trp
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cox2
cox1
Pro,Met
Ser,Asn
ymf100
Ala,Lys
Gly,Tyr
Ser,Cys
Leu,Leu
secY
Pilasporangium apinafurcum
57,022 bp

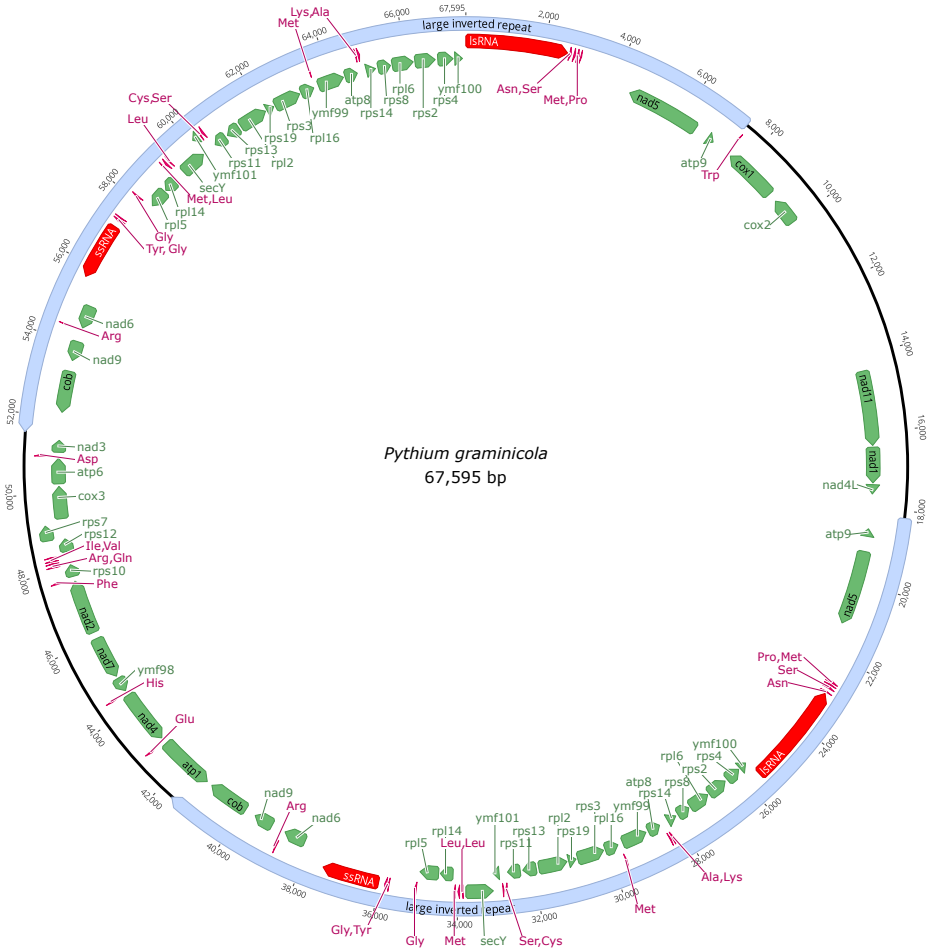

Salisapilia sapeloensis
56,039 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat

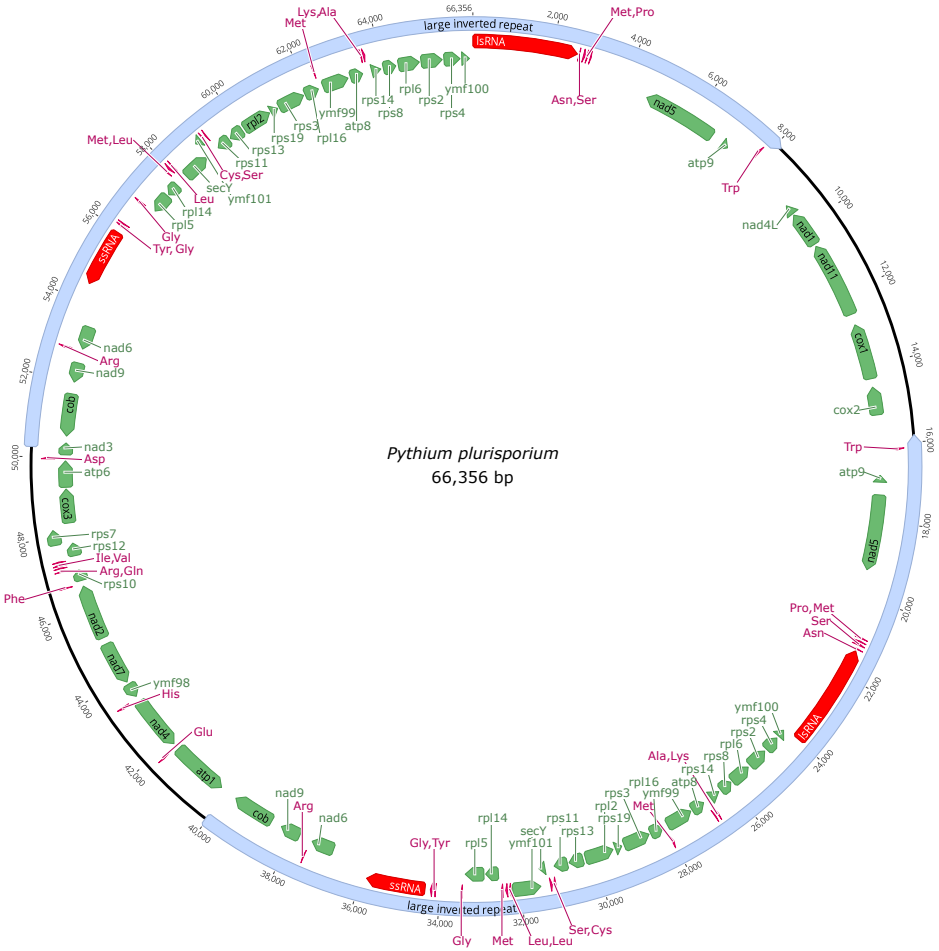

Pythium aristosporum
71,953 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat

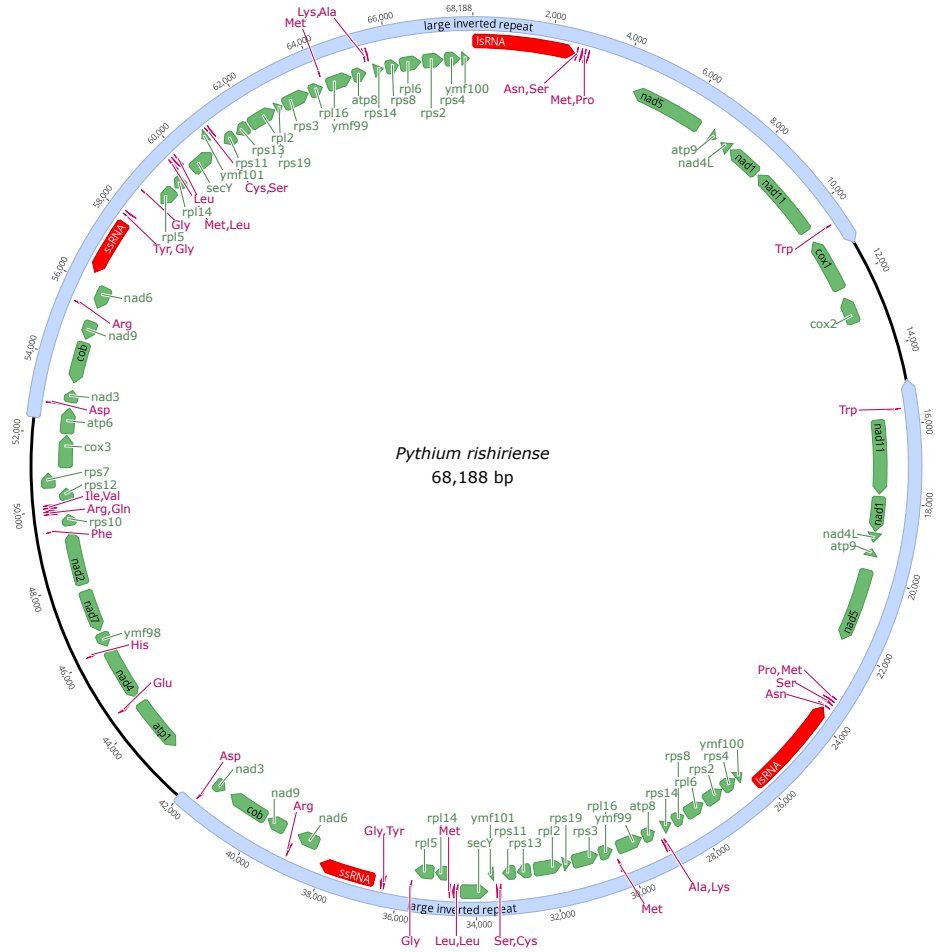

large inverted repeat
lsRNA
ssRNA
large inverted repeat
Pythium arrhenomanes
71,876 bp


large inverted repeat
lsRNA
ssRNA
large inverted repeat
Pythium phragmiticola
71,721 bp

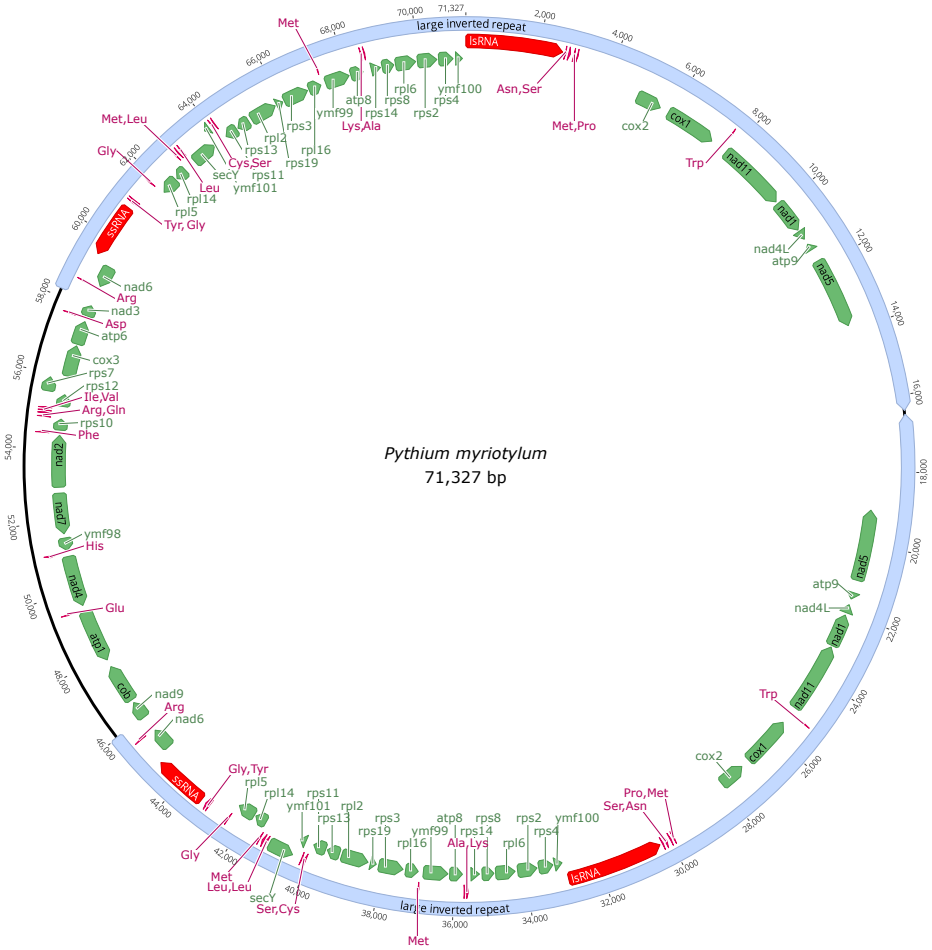

large inverted repeat
lsRNA
ssRNA
Lys,Ala
Met
Met,Pro
Asn,Ser
nad5
atp9
Trp
cox1
cox2
nad1
nad4L
rps14
rpl6
rps2
ymf100
rps4
rps8
ymf99
atp8
rps19
rps13
rps3
rpl16
rpl2
rps11
ymf101
secY
Leu
Cys,Ser
Met,Leu
rpl14
rpl5
Gly
Tyr, Gly
nad6
Arg
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
Pro,Met
Ser,Asn
Gly,Tyr
Leu,Leu
Ala,Lys
Ser,Cys
Pythium vanterpoolii
65,996 bp

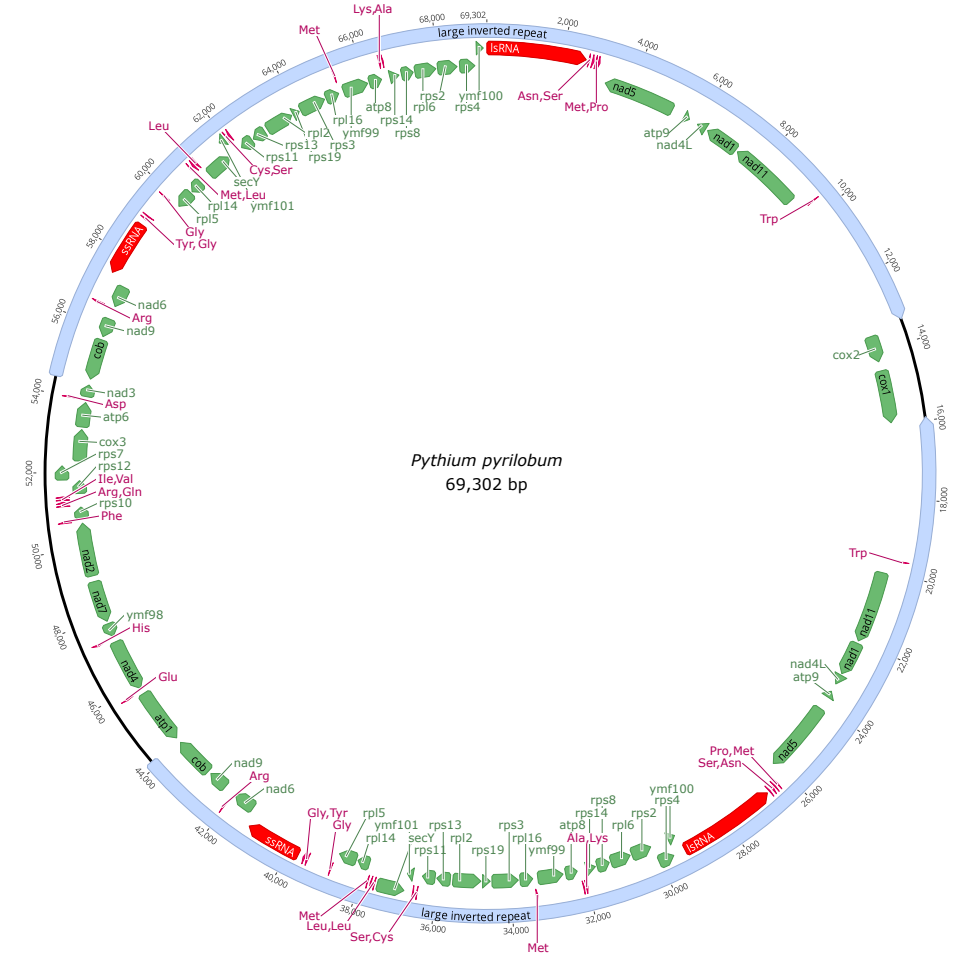

large inverted repeat
lsRNA
ssRNA
Lys,Ala
Met
Asn,Ser
Met,Pro
nad5
atp9
Trp
cox1
cox2
nad1
nad4L
rps14
rpl6
rps2
ymf100
rps4
rps8
ymf99
atp8
rps3
rps19
rps13
rpl16
rpl2
rps11
ymf101
secY
Leu
Cys,Ser
Met,Leu
rpl14
rpl5
Gly
Tyr, Gly
nad6
Arg
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
Pro,Met
Ser
Asn
Gly,Tyr
Gly
Met
secY
Ser,Cys
Ala,Lys
Pythium graminicola
67,595 bp

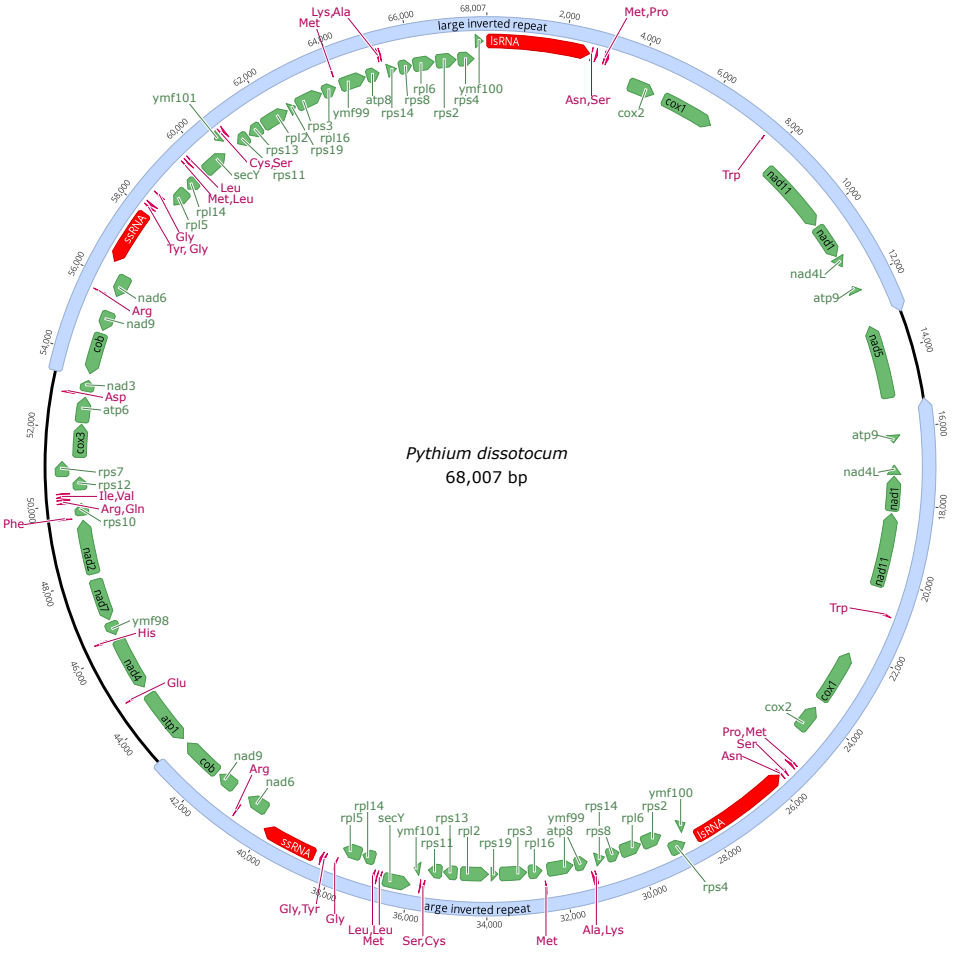

Pythium plurisporium
66,356 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat
Lys,Ala
Met
Met,Pro
Asn,Ser
nad5
atp9
Trp
nad4L
nad1
nad11
cox1
cox2
Trp
atp9
nad5
Pro,Met
Ser
Asn
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
Ala,Lys
atp8
rpl16
ymf99
rps3
rpl2
rps19
Met
rpl14
rps11
rps13
secY
ymf101
rpl5
Gly,Tyr
ssRNA
Gly
Met
Leu,Leu
Ser,Cys
nad9
Arg
nad6
cob
Glu
atp1
nad4
ymf98
His
nad7
nad2
Phe
rps10
Arg,Gln
Ile,Val
rps12
rps7
cox3
atp6
Asp
nad3
cob
nad6
Arg
nad9
ssRNA
Met,Leu
Cys,Ser
secY
Leu
ymf101
rpl14
rpl5
Gly
Tyr, Gly
rps13
rps11
rps19
rps3
rpl2
ymf99
rpl16
atp8
rps8
rpl6
rps2
rps4
ymf100

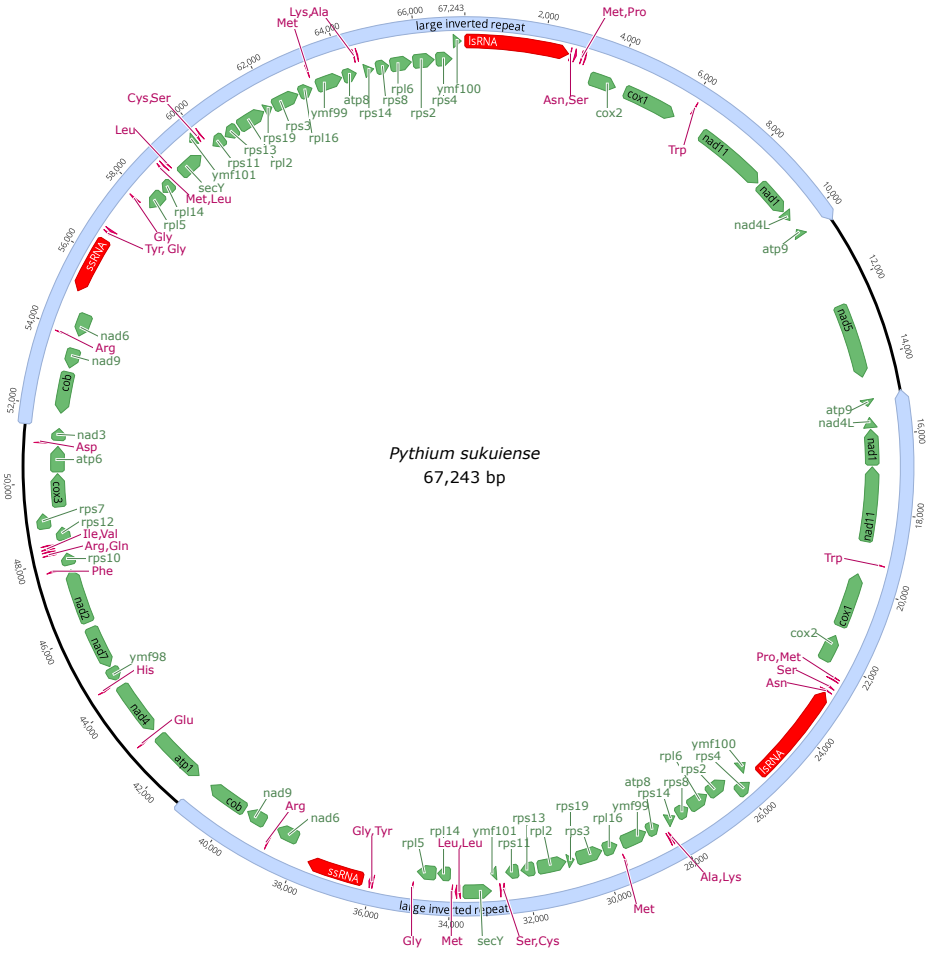

Pythium rishiriense
68,188 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat
Lys,Ala
Met
Asn,Ser
Met,Pro
nad5
atp9
nad4L
nad1
nad11
Trp
cox1
cox2
Trp
nad11
nad1
nad4L
atp9
nad5
Pro,Met
Ser
Asn
lsRNA
ymf100
rps4
rps2
rpl6
rps8
rps14
atp8
rpl16
ymf99
rps3
rpl2
rps19
rps11
rps13
secY
ymf101
rpl5
rpl14
Met
Gly,Tyr
ssRNA
Gly
Leu,Leu
Ser,Cys
Ala,Lys
Met
Asp
nad3
cob
nad9
Arg
nad6
Glu
atp1
nad4
ymf98
His
nad7
nad2
Phe
rps10
Arg,Gln
Ile,Val
rps12
rps7
cox3
atp6
nad6
Arg
nad9
cob
ssRNA
Met,Leu
Cys,Ser
secY
Leu
ymf101
rpl14
Gly
rpl5
Tyr, Gly
rps19
rps11
rps13
rps3
rpl2
ymf99
rpl16
atp8
rps14
rps8
rpl6
rps2
rps4
ymf100

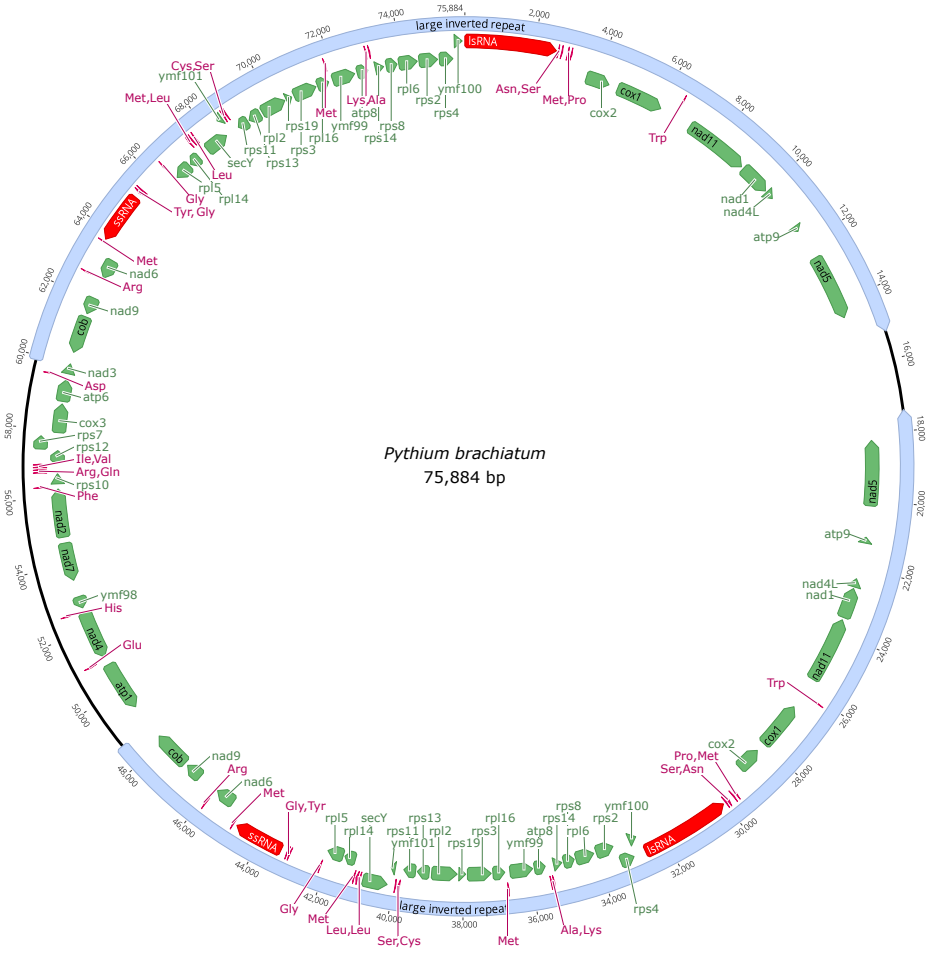

large inverted repeat
lsRNA
ssRNA
Pythium torulosum
72,024 bp

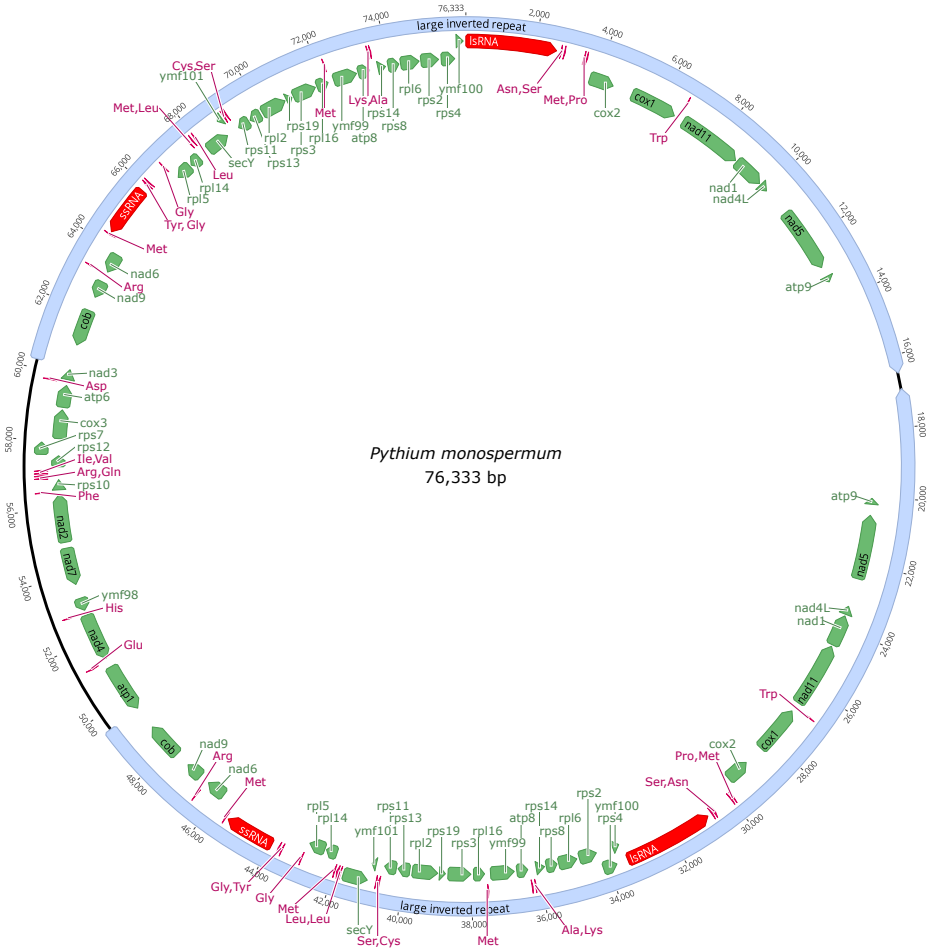

large inverted repeat
lsRNA
ssRNA
Pythium myriotylum
71,327 bp

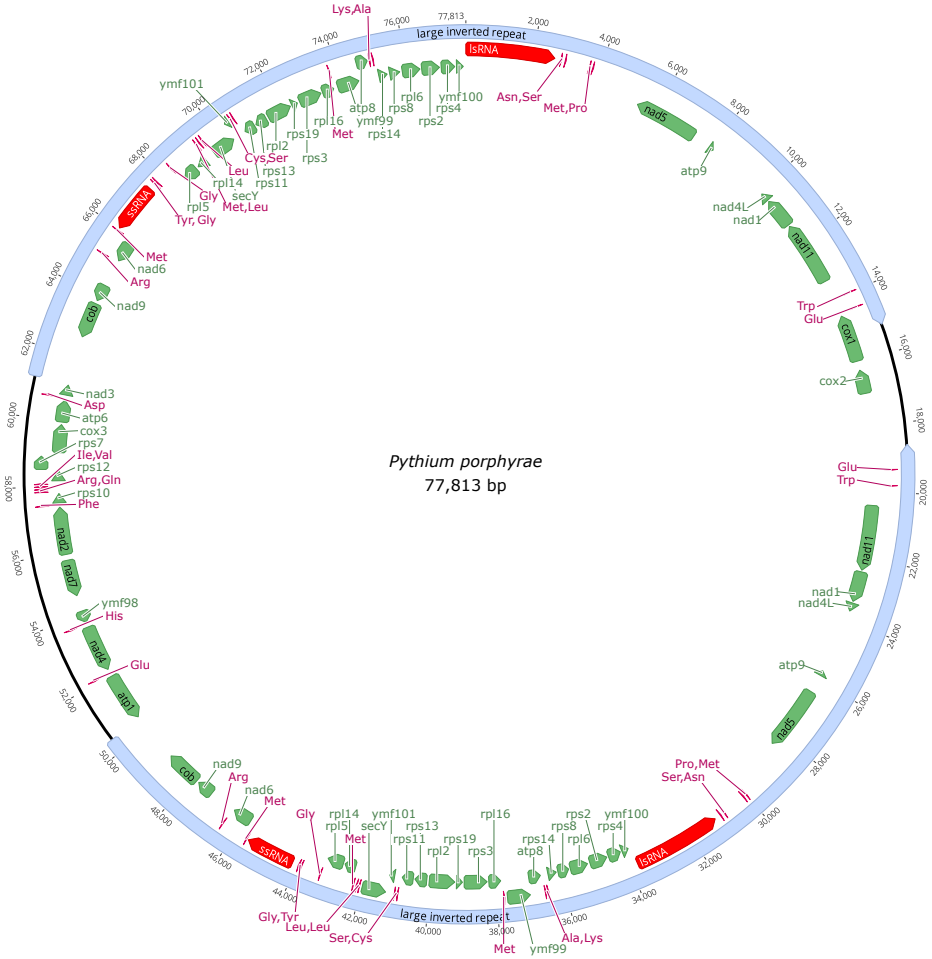

Pythium pyrilobum
69,302 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat

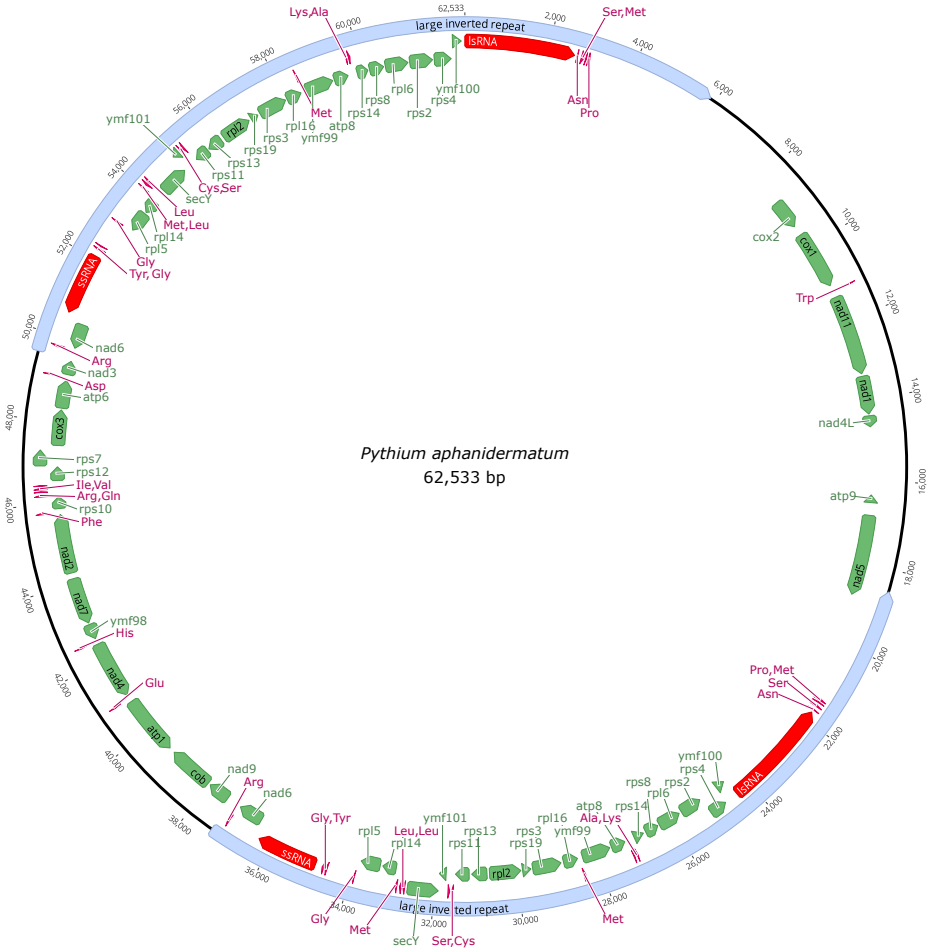

Pythium dissotocum
68,007 bp
large inverted repeat
lsRNA
ssRNA
large inverted repeat

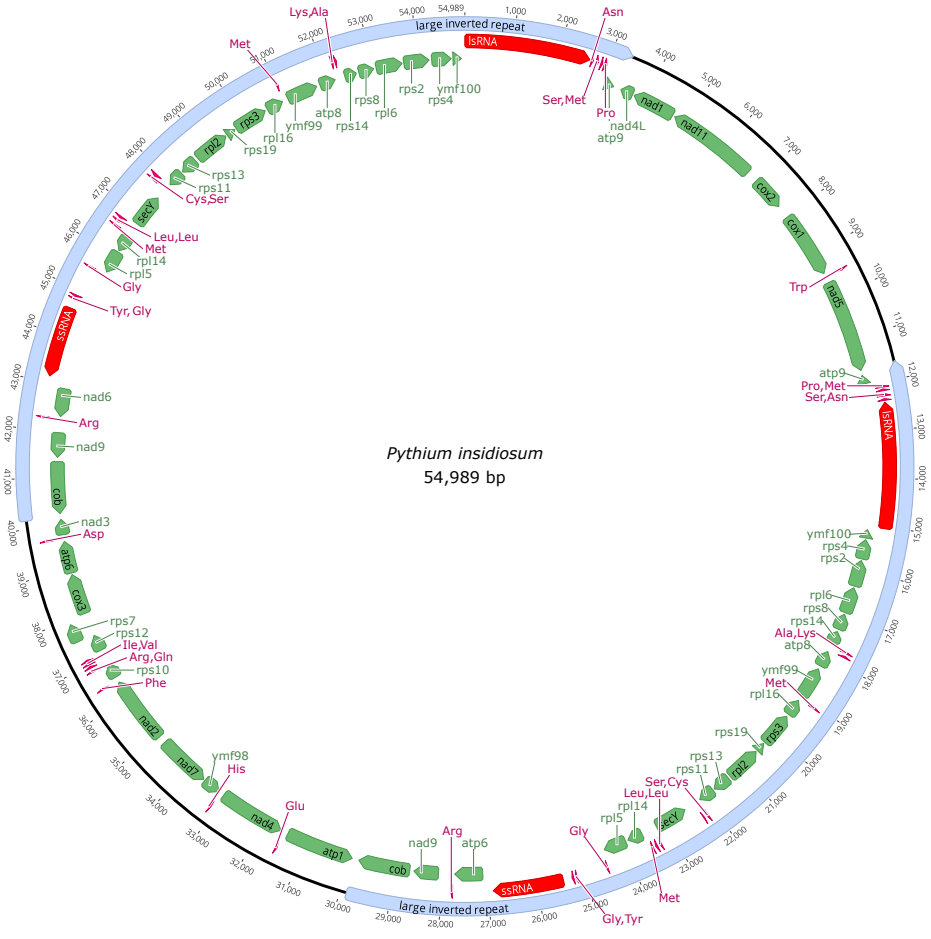

Pythium sukuiense
67,243 bp
large inverted repeat
lsRNA
ssRNA
Lys,Ala
Met
Met,Pro
Asn,Ser
cox1
cox2
Trp
nad11
nad1
nad4L
atp9
nad5
atp9
nad4L
nad1
nad11
Trp
cox1
cox2
Pro,Met
Ser
Asn
lsRNA
ymf100
rpl6
rps4
rps2
atp8
rps8
rps14
rps19
ymf99
rpl16
rps13
rpl2
rps3
ymf101
rps11
rpl5
rpl14
Leu,Leu
Gly,Tyr
Ala,Lys
Met
Gly
Met
secY
Ser,Cys
ssRNA
Cys,Ser
Leu
Met,Leu
Gly
Tyr, Gly
nad6
Arg
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1

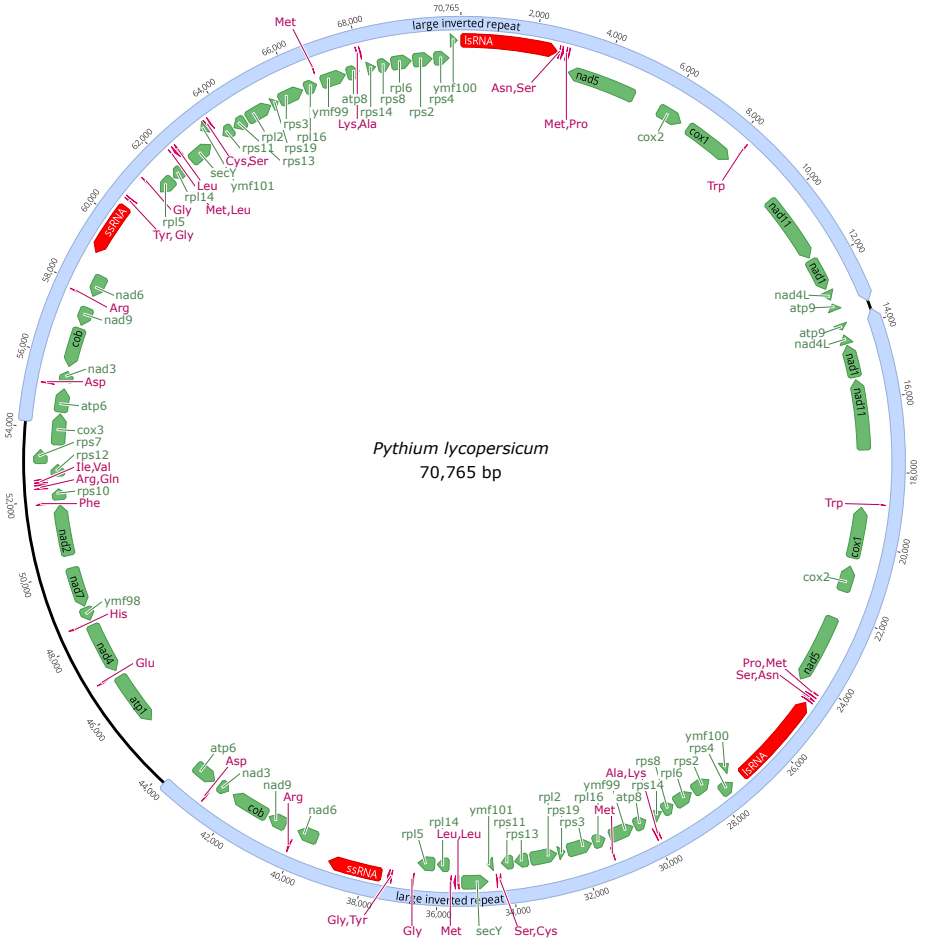

Pythium brachiatum
75,884 bp
large inverted repeat
lsRNA
ssRNA
Asn,Ser
Met,Pro
cox2
Trp
nad11
nad1
nad4L
atp9
nad5
atp9
nad4L
nad1
nad11
Trp
cox1
cox2
Pro,Met
Ser,Asn
lsRNA
ymf100
rps8
rps14
rps2
rpl6
atp8
rps3
rpl16
ymf99
rps19
rpl2
rps13
ymf101
rps11
rpl14
rpl5
secY
Gly,Tyr
Met
Leu,Leu
Gly
Ser,Cys
Met
Ala,Lys
rps4
ssRNA
Cys,Ser
ymf101
Met,Leu
Leu
Gly
Tyr, Gly
Met
nad6
Arg
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1

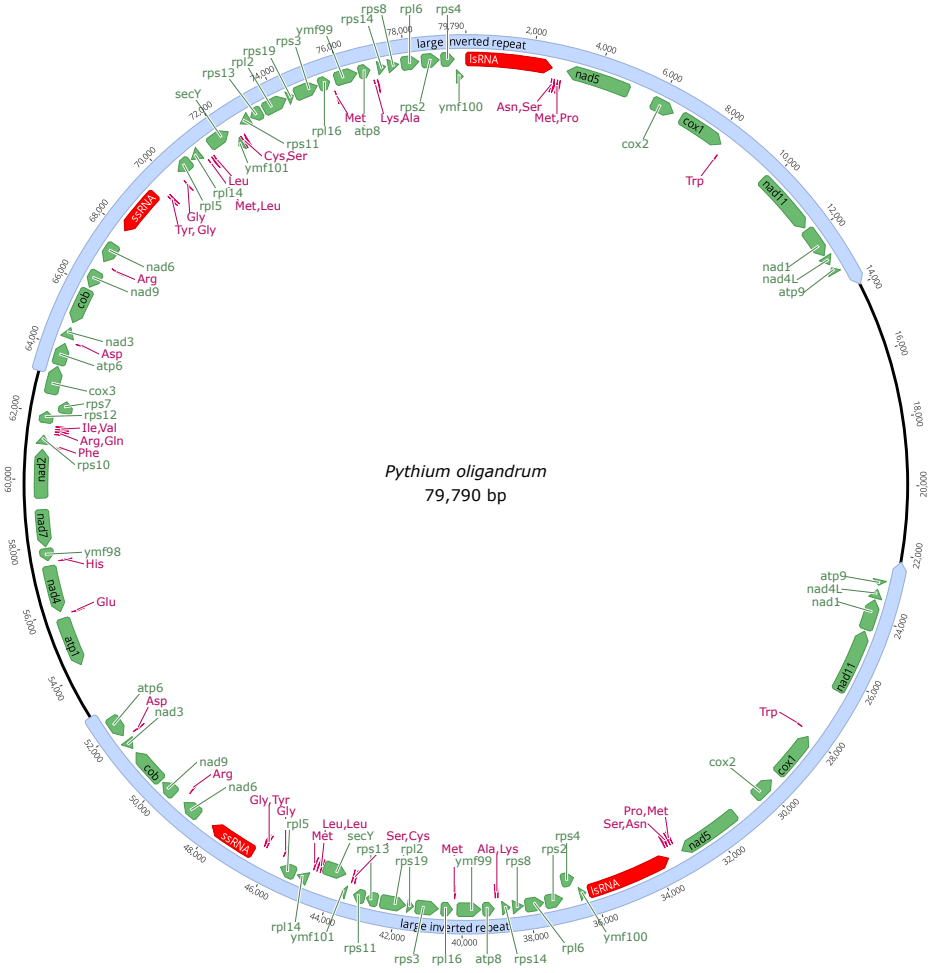

large inverted repeat
lsRNA
ssRNA
Pythium monospermum
76,333 bp
large inverted repeat
lsRNA
ssRNA

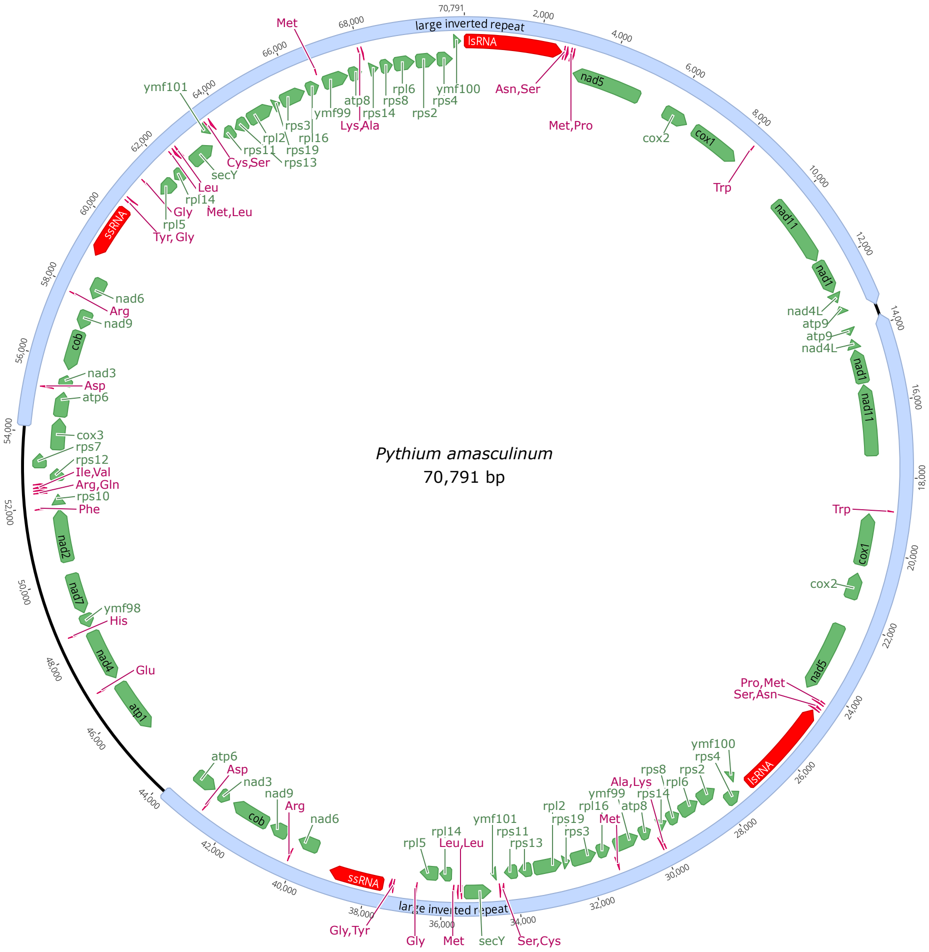

large inverted repeat
lsRNA
ssRNA
Pythium porphyrae
77,813 bp
large inverted repeat
lsRNA
ssRNA

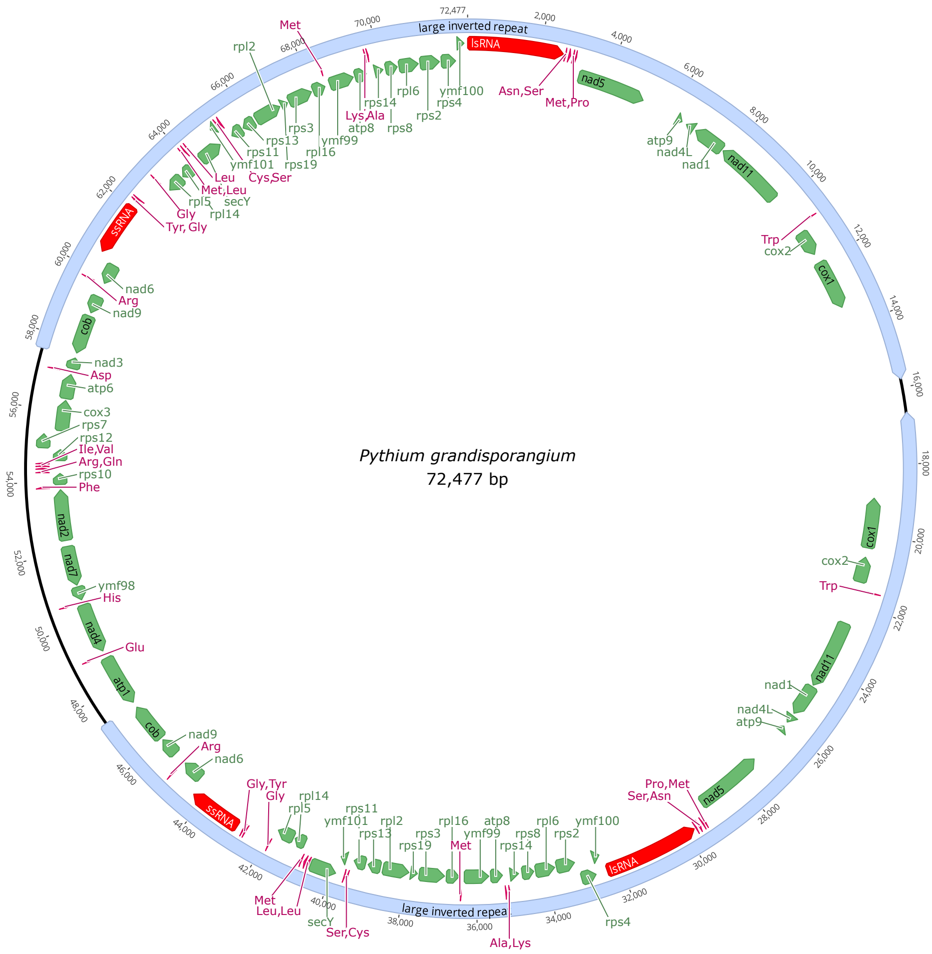

large inverted repeat
lsRNA
ssRNA
large inverted repeat
Pythium aphanidermatum
62,533 bp
Lys,Ala
Met
Asn
Pro
Ser,Met
rps8
rpl6
rps2
rps4
ymf100
rps14
atp8
rpl16
rps3
ymf99
rpl2
rps19
rps13
rps11
ymf101
secY
Cys,Ser
Leu
Met,Leu
rpl14
rpl5
Gly
Tyr, Gly
nad6
Arg
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cob
nad9
Arg
nad6
Gly,Tyr
rpl5
Leu,Leu
rpl14
rps11
rps13
rps3
rps19
rpl16
ymf99
atp8
Ala,Lys
rps14
rps8
rpl6
rps2
ymf100
rps4
Pro,Met
Ser
Asn
cox2
cox1
Trp
nad11
nad1
nad4L
atp9
nad5


large inverted repeat
lsRNA
ssRNA
large inverted repeat
Pythium insidiosum
54,989 bp
Lys,Ala
Met
Asn
Ser,Met
Pro
nad4L
atp9
nad1
nad11
cox2
cox1
Trp
nad5
Pro,Met
Ser,Asn
rps8
rpl6
rps2
rps4
ymf100
rps14
atp8
rpl16
rps3
ymf99
rpl2
rps19
rps13
rps11
Cys,Ser
secY
Leu,Leu
Met
rpl14
rpl5
Gly
Tyr, Gly
nad6
Arg
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
cob
nad9
Arg
atp6
ssRNA
Gly
rpl5
rpl14
Leu,Leu
Ser,Cys
secY
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
Met
Ala,Lys
atp8
rps14
rps8
rpl6
rps2
ymf100
rps4
Gly,Tyr


Pythium lycopersicum
70,765 bp
large inverted repeat
lsRNA
ssRNA
nad5
cox2
cox1
nad11
nad1
nad4L
atp9
nad7
nad2
nad4
atp1
cob
nad3
atp6
cox3
rps7
rps12
rps10
nad6
nad9
Met
Asn,Ser
Met,Pro
Trp
Lys,Ala
Cys,Ser
Leu
Met,Leu
Tyr,Gly
Gly
Arg
Asp
Ile,Val
Arg,Gln
Phe
His
Glu
Pro,Met
Ser,Asn
Gly,Tyr
Ser,Cys
Leu,Leu

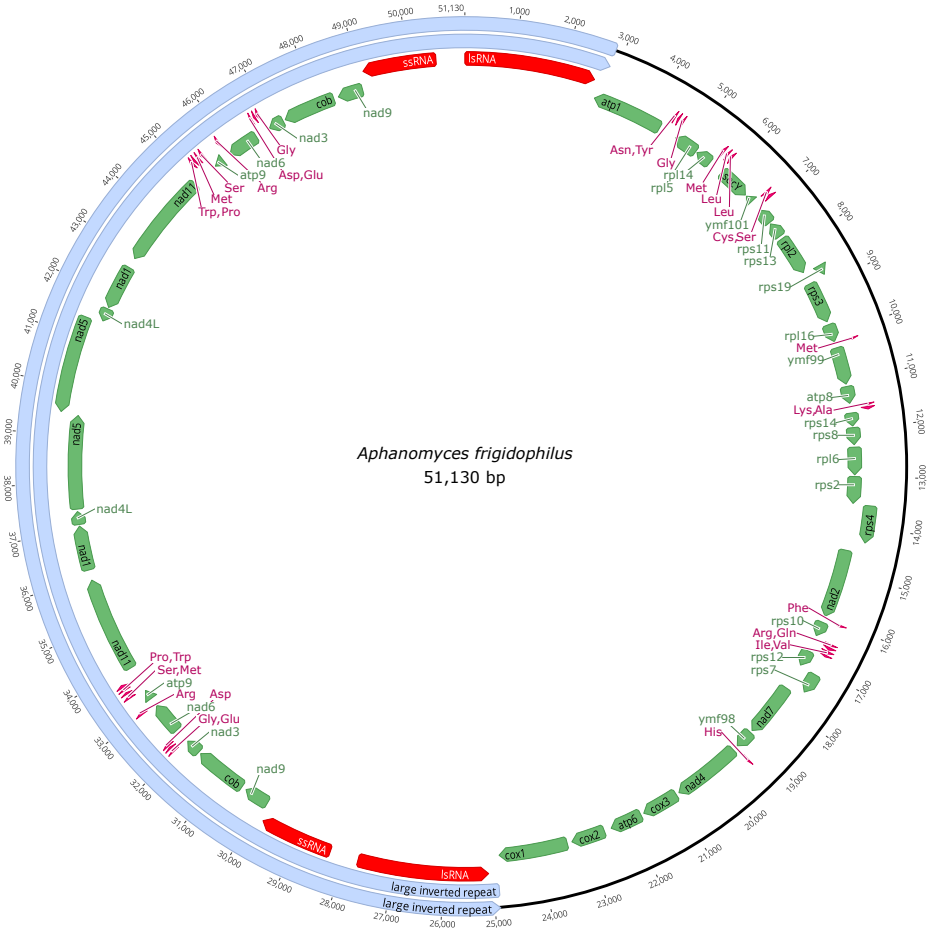

Pythium oligandrum
79,790 bp
large inverted repeat
lsRNA
ssRNA
nad5
cox2
cox1
nad11
nad1
nad4L
atp9
nad7
nad2
nad4
atp1
cob
nad3
atp6
cox3
rps7
rps12
rps10
nad6
nad9
Met
Asn,Ser
Met,Pro
Trp
Lys,Ala
Cys,Ser
Leu
Met,Leu
Tyr,Gly
Gly
Arg
Asp
Ile,Val
Arg,Gln
Phe
His
Glu
Pro,Met
Ser,Asn
Gly,Tyr
Ser,Cys
Leu,Leu

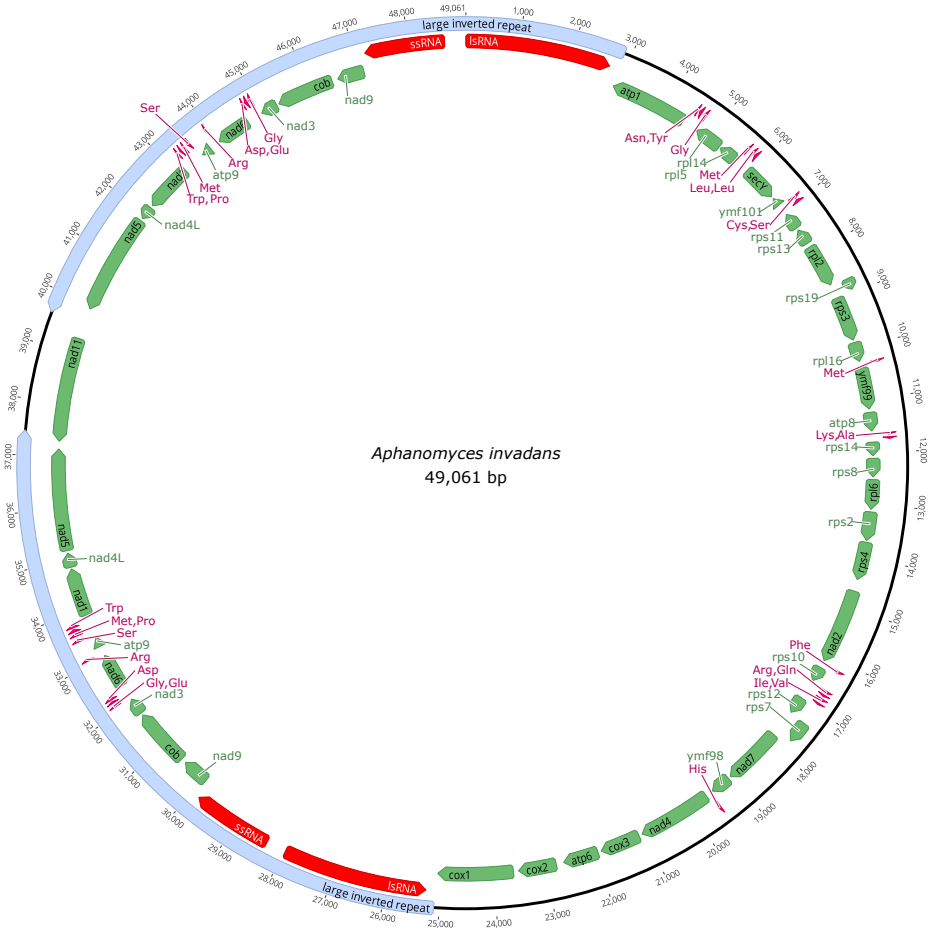

Pythium amasculinum
70,791 bp
large inverted repeat
lsRNA
ssRNA
nad5
cox2
cox1
Trp
nad11
nad1
nad4L
atp9
cob
nad3
Asp
atp6
nad6
Arg
nad9
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
Met
ymf101
ymf99
atp8
rps14
rps8
rpl6
ymf100
rps4
rps2
Lys,Ala
rps3
rpl16
rpl2
rps11
rps19
rps13
Cys,Ser
secY
Leu
rpl14
Met,Leu
Gly
rpl5
Tyr, Gly
Asn,Ser
Met,Pro
Pro,Met
Ser,Asn
Ala,Lys
Leu,Leu
Gly,Tyr
Ser,Cys

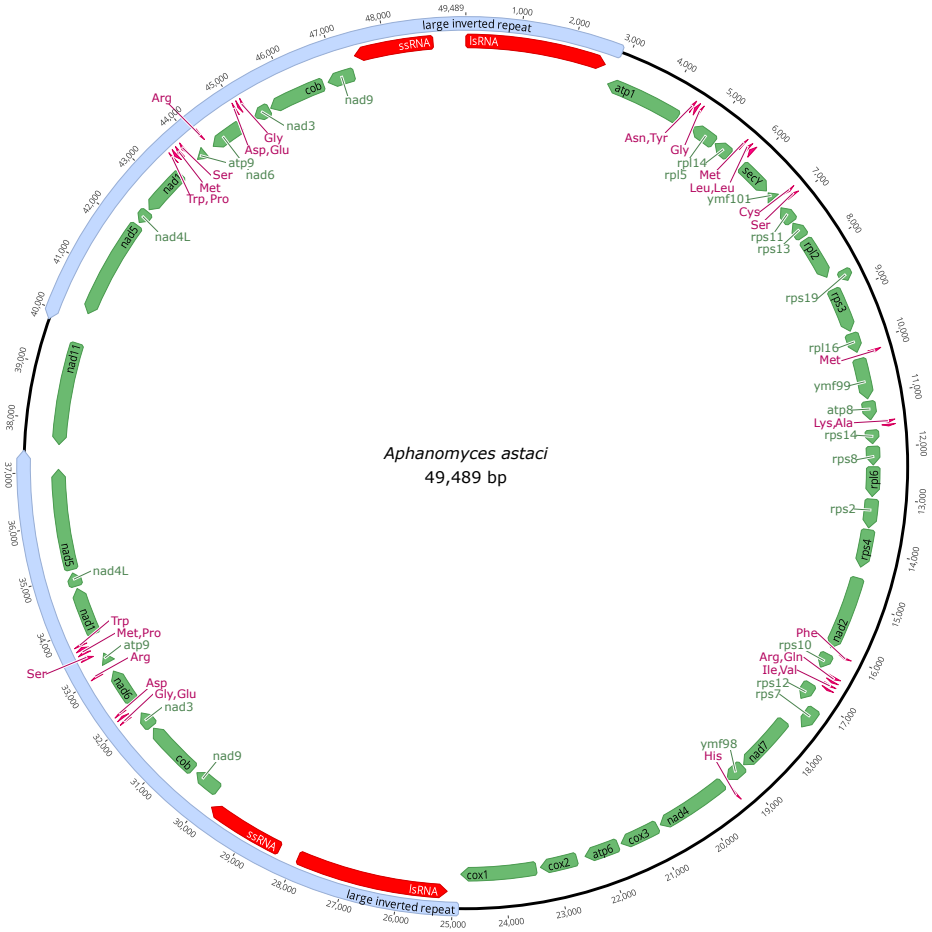

Pythium grandisporangium
72,477 bp
large inverted repeat
lsRNA
ssRNA
nad5
atp9
nad4L
nad1
nad11
Trp
cox2
cox1
Met
rpl2
ymf100
rps4
rps2
rps8
atp8
rps14
Lys,Ala
ymf99
rpl16
rps19
rps3
rps13
rps11
ymf101
Cys,Ser
secY
Leu
Met,Leu
rpl5
rpl14
Gly
Tyr, Gly
Asn,Ser
Met,Pro
nad6
Arg
nad9
cob
nad3
Asp
atp6
cox3
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
nad7
ymf98
His
nad4
Glu
atp1
Gly,Tyr
Pro,Met
Ser,Asn
Leu,Leu
Ser,Cys
Ala,Lys

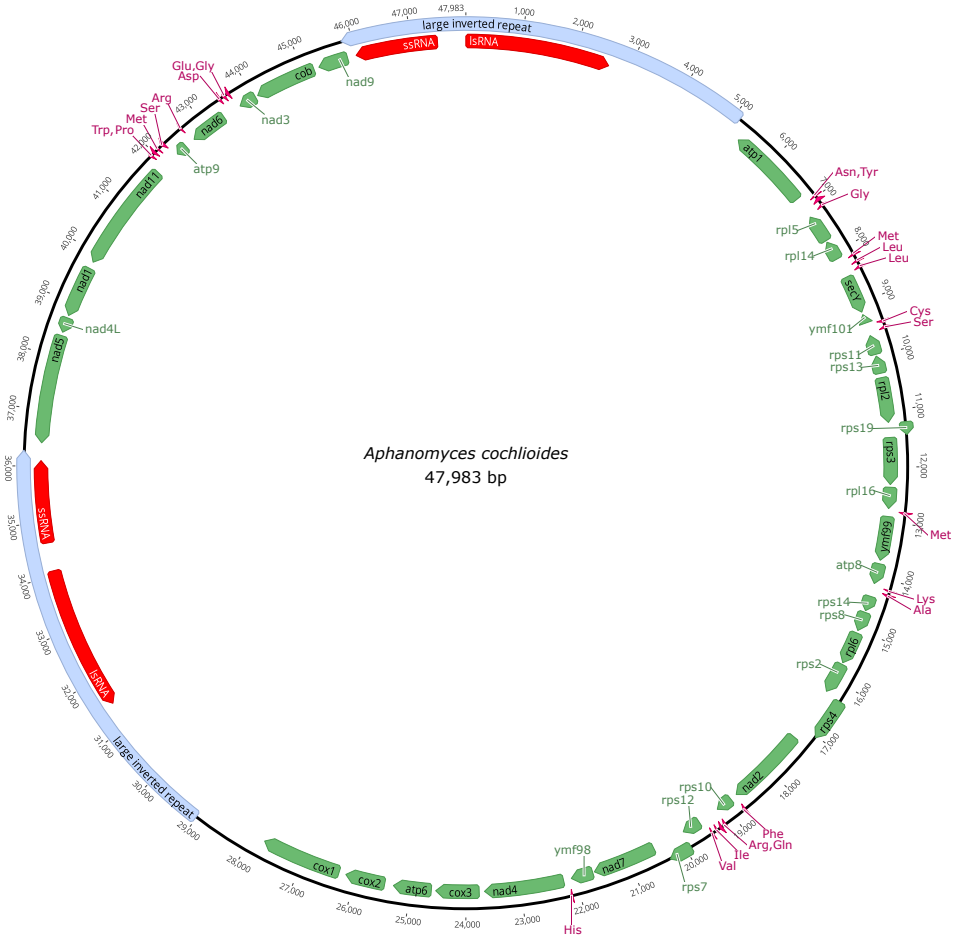

Lagenidium giganteum
60,537 bp
large inverted repeat
large inverted repeat
lsRNA
ssRNA
rps4
rpl6
rps8
rps14
atp8
rpl16
rps3
rps19
rpl2
rps11
rps13
secY
ymf101
rpl14
rpl5
nad5
nad4L
nad6
nad1
nad3
atp6
nad2
rps7
rps12
nad7
ymf98
nad4
atp1
cox3
cox1
nad9
cob
cox2
atp9
ymf100
ymf99
Met
Lys,Ala
Asn,Ser
Met,Pro
Cys,Ser
Leu
Met,Leu
Gly
Tyr, Gly
Trp
Arg
Arg,Gln
Phe
Ile,Val
Asp
His
Glu
Pro,Met
Ser,Asn
Ala,Lys
Ser,Cys
Leu,Leu
Gly,Tyr
Val,Ile
Gln,Arg
Glu,Asp
Albugo candida
61,303 bp

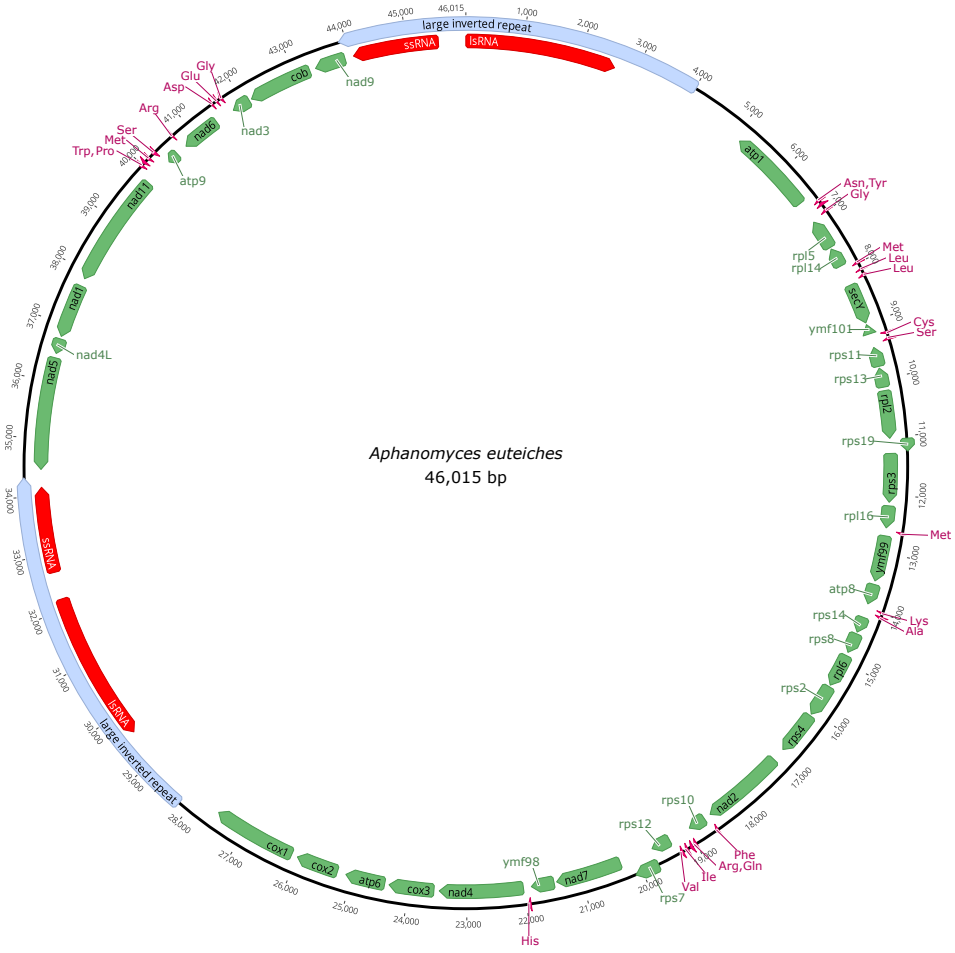

large inverted repeat
large inverted repeat
lsRNA
ssRNA
Albugo laibachii
62,278 bp


ssRNA
lsRNA
large inverted repeat
large inverted repeat
Aphanomyces frigidophilus
51,130 bp


large inverted repeat
ssRNA
lsRNA
atp1
Asn,Tyr
Gly
rpl14
rpl5
Met
Leu,Leu
secY
ymf101
Cys,Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys,Ala
rps14
rps8
rpl6
rps2
rps4
nad2
Phe
rps10
Arg,Gln
Ile,Val
rps12
rps7
nad7
ymf98
His
nad4
cox3
atp6
cox2
cox1
lsRNA
large inverted repeat
ssRNA
nad9
cob
nad3
Gly
Asp,Glu
Arg
atp9
Met
Trp,Pro
Ser
nad6
nad4L
nad5
nad1
Trp
Met,Pro
Ser
atp9
Arg
Asp
Gly,Glu
nad3
Aphanomyces invadans
49,061 bp

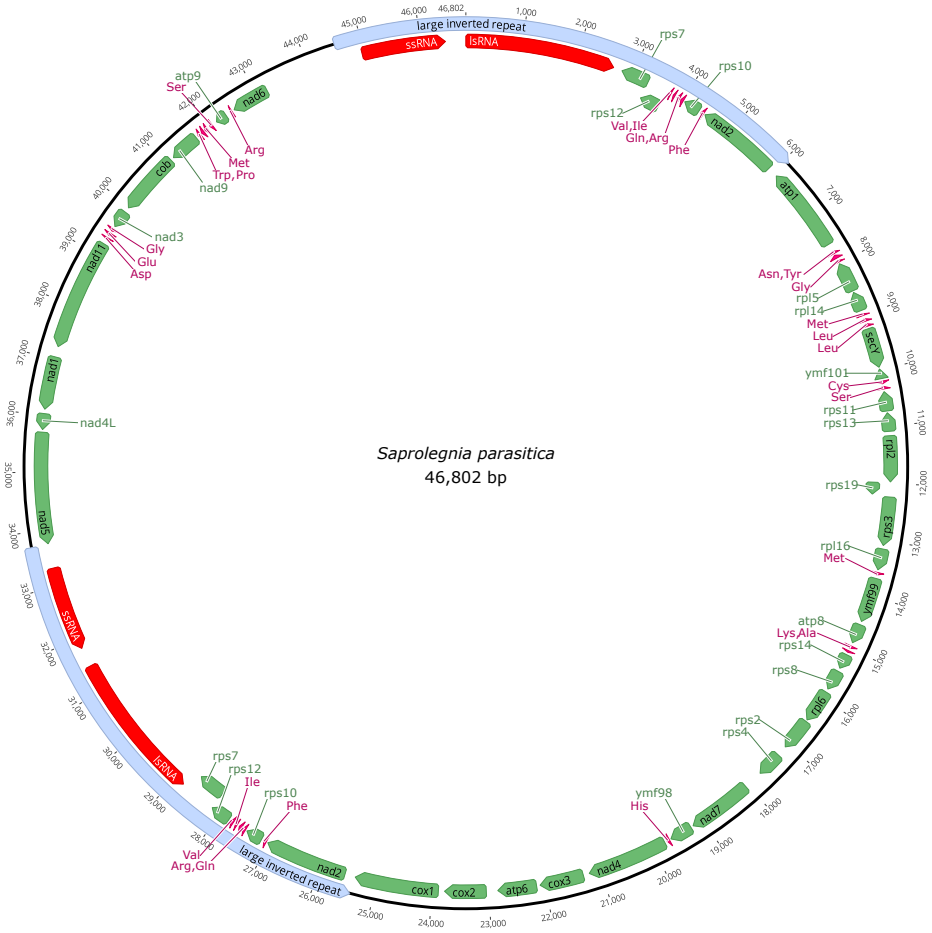

large inverted repeat
ssRNA
lsRNA
atp1
Asn,Tyr
Gly
rpl14
rpl5
Met
Leu,Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys,Ala
rps14
rps8
rpl6
rps2
rps4
nad2
Phe
rps10
Arg,Gln
Ile,Val
rps12
rps7
nad7
ymf98
His
nad4
cox3
atp6
cox2
cox1
lsRNA
large inverted repeat
ssRNA
nad9
cob
nad3
Gly
Asp,Glu
atp9
nad6
Ser
Met
Trp,Pro
Arg
nad4L
nad5
nad1
Trp
Met,Pro
atp9
Arg
Ser
Asp
Gly,Glu
nad3
Aphanomyces astaci
49,489 bp


Aphanomyces cochlioides
47,983 bp
large inverted repeat
ssRNA
lsRNA
cob
nad9
nad3
nad6
atp9
nad1
nad4L
nad5
atp1
Asn,Tyr
Gly
rpl5
rpl14
Met
Leu
Leu
secY
Cys
Ser
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
Met
atp8
rps14
rps8
Lys
Ala
rpl6
rps2
rps4
nad2
rps10
rps12
Phe
Arg,Gln
Ile
Val
rps7
ymf98
nad7
cox1
cox2
atp6
cox3
nad4
His
Glu,Gly
Asp
Arg
Ser
Met
Trp,Pro

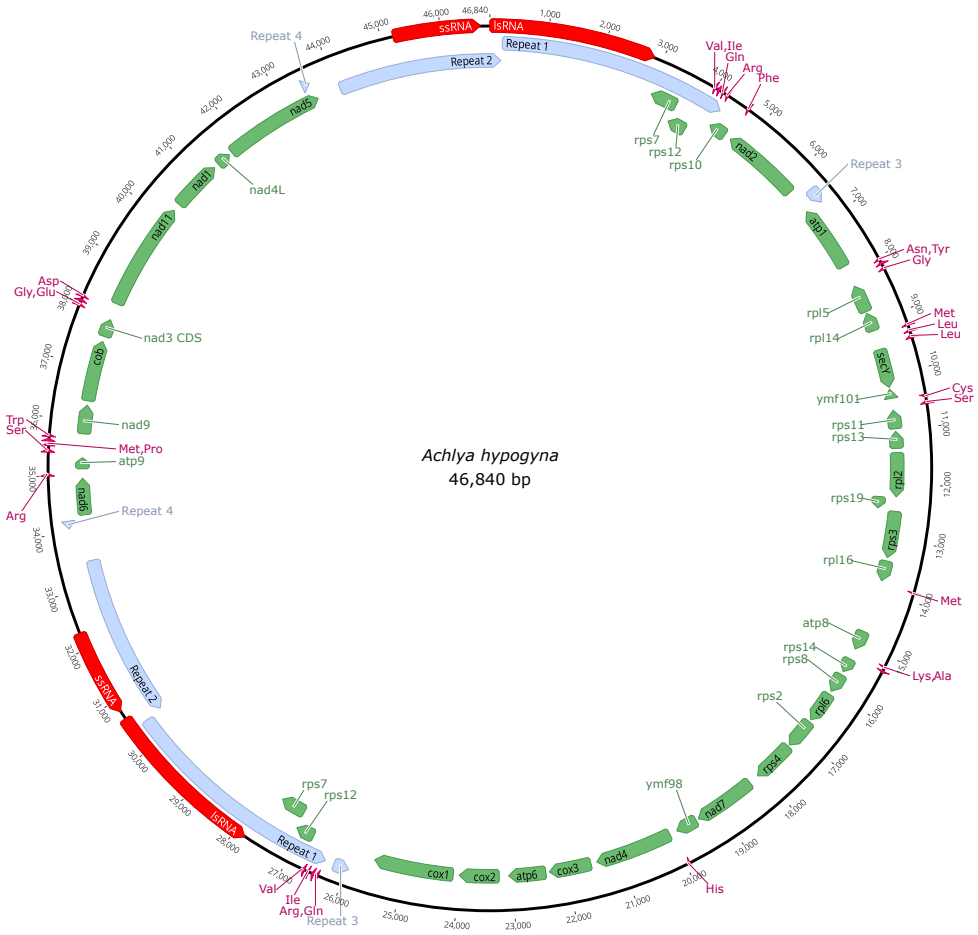

Aphanomyces euteiches
46,015 bp
large inverted repeat
ssRNA
lsRNA
cob
nad9
nad3
nad6
atp9
nad1
nad4L
nad5
atp1
Asn,Tyr
Gly
rpl5
rpl14
Met
Leu
Leu
secY
Cys
Ser
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
ymf99
Met
atp8
rps14
rps8
Lys
Ala
rpl6
rps2
rps4
nad2
rps10
rps12
Phe
Arg,Gln
Ile
Val
rps7
ymf98
nad7
cox1
cox2
atp6
cox3
nad4
His
Gly
Glu
Asp
Arg
Ser
Met
Trp,Pro

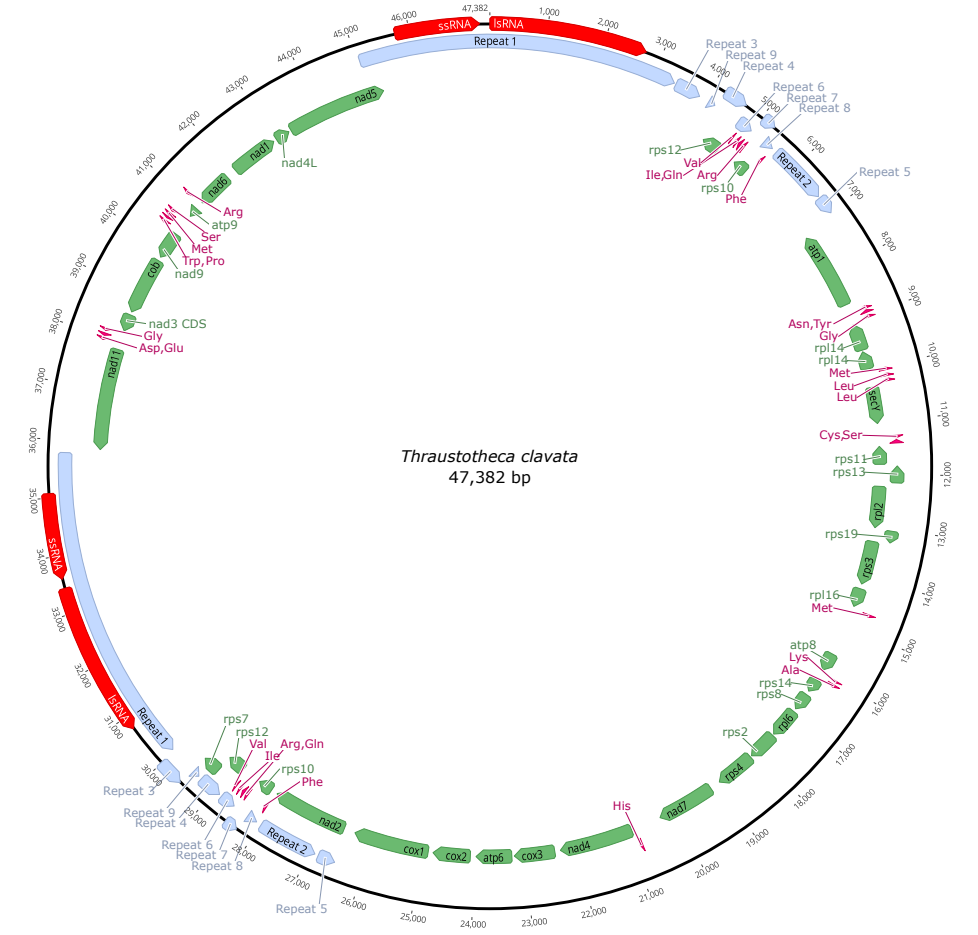

large inverted repeat
ssRNA
lsRNA
cob
nad9
nad3
nad5
Gly
Asp,Glu
Arg
atp9
Met,Ser
Trp,Pro
nad6
nad1
nad4L
nad1
nad1
nad4L
nad5
Trp
Pro
Ser,Met
atp9
Arg
nad6
Glu,Asp
Gly
nad3
cob
nad9
ssRNA
lsRNA
large inverted repeat
cox1
cox2
atp6
cox3
nad4
nad7
ymf98
His
rps7
rps12
Ile,Val
Arg,Gln
rps10
Phe
nad2
Phe
rps10
Arg,Gln
Ile,Val
rps12
rps7
nad2
atp1
Asn,Tyr
Gly
rpl14
rpl5
Met
Leu
Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys,Ala
rps14
rps8
rpl6
rps2
rps4
Aphanomyces sp. NJM 9510
48,926 bp


large inverted repeat
ssRNA
lsRNA
rps7
Ile,Gln
rps12
Val
Arg
rps10
Phe
nad2
nad5
nad1
nad4L
nad1
nad1
Asp
Glu
Gly
nad3
cob
nad9
Trp
Met,Pro
Ser
atp9
Arg
nad6
ssRNA
lsRNA
rps7
Ile,Val
Arg,Gln
rps10
Phe
rps12
large inverted repeat
nad2
cox1
cox2
atp6
cox3
nad4
nad7
ymf98
His
rps4
rps6
rps2
rps8
rps14
ymf66
atp8
Lys
Ala
rpl16
Met
rps3
rpl2
rps19
rps11
rps13
secY
ymf101
Cys
Ser
rpl5
rpl14
Met
Leu
Leu
atp1
Asn
Tyr, Gly
Saprolegnia diclina
46,595 bp


large inverted repeat
ssRNA
lsRNA
rps7
rps10
rps12
Val,Ile
Gln,Arg
Phe
nad2
atp1
Asn,Tyr
Gly
rpl5
rpl14
Met
Leu
Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
ymf99
atp8
Lys,Ala
rps14
rps8
rpl6
rps2
rps4
nad7
ymf98
His
nad4
cox3
atp6
cox2
cox1
nad2
large inverted repeat
Val
Arg,Gln
rps7
rps12
Ile
rps10
Phe
lsRNA
ssRNA
nad5
nad4L
nad1
nad11
Asp
Glu
Gly
nad3
cob
nad9
Trp,Pro
Met
Arg
atp9
Ser
nad6
Saprolegnia parasitica
46,802 bp


large inverted repeat
ssRNA
lsRNA
rps7
Val
Arg
rps10
rps12
Ile,Gln
Phe
nad2
atp1
Asn,Tyr
Gly
rpl14
rpl14
Met
Leu
Leu
secY
ymf101
Cys
Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Ile
ymf99
atp8
Lys,Ala
rps14
rps8
rpl6
rps2
rps4
nad7
ymf98
His
nad4
cox3
atp6
cox2
cox1
nad2
large inverted repeat
rps12
rps7
Ile,Val
Arg,Gln
rps10
Phe
lsRNA
ssRNA
nad6
nad9
Trp
Met,Pro
Ser
atp9
Arg
cob
nad3
Asp
Glu
Gly
nad11
nad1
nad4L
nad5
Saprolegnia ferax
46,930 bp


Achlya hypogyna
46,840 bp
lsRNA
ssRNA
Repeat 1
Repeat 2
Repeat 3
Repeat 4
nad5
nad4L
nad1
nad1
nad3 CDS
cob
nad9
atp9
nad6
Repeat 4
Repeat 2
ssRNA
lsRNA
Repeat 1
Repeat 3
rps7
rps12
rps10
nad2
atp1
rpl5
rpl14
sec1
ymf101
rps11
rps13
rpl2
rps19
rps3
rpl16
atp8
rps14
rps8
rps6
rps2
rps4
ymf98
nad7
cox1
cox2
atp6
cox3
nad4
Val,Ile
Gln
Arg
Phe
Asn,Tyr
Gly
Met
Leu
Leu
Cys
Ser
Met
Lys,Ala
His
Ile
Arg,Gln
Val
Asp
Gly,Glu
Trp
Ser
Met,Pro
Arg


Thraustotheca clavata
47,382 bp
lsRNA
ssRNA
Repeat 1
Repeat 2
Repeat 3
Repeat 4
Repeat 5
Repeat 6
Repeat 7
Repeat 8
Repeat 9
nad5
nad4L
nad1
nad6
atp9
Ser
Met
Trp,Pro
nad9
cob
nad3 CDS
Gly
Asp,Glu
nad1
rps12
Val
Ile,Gln
Arg
rps10
Phe
atp1
Asn,Tyr
Gly
rpl14
rpl14
Met
Leu
Leu
sec1
Cys,Ser
rps11
rps13
rpl2
rps19
rps3
rpl16
Met
atp8
Lys
Ala
rps14
rps8
rps6
rps2
rps4
nad7
His
cox1
cox2
atp6
cox3
nad4
nad2
rps7
rps12
Val
Ile
Arg,Gln
rps10
Phe

Appendix IV Statistics for the nine sequence partitions included in the phylogenetic analyses

Gene partitions	Aligned length	Best-fit substitution models	
		IQ-TREE	MrBayes
atp1, cox2	2,235	GTR+I+G	GTR+I+G
atp6, cob, cox3, nad1, nad4, nad4L, nad5, nad6	7,671	GTR+I+G	GTR+I+G
atp8, rps19	552	TPM3u	GTR+I+G
atp9, cox1	1,674	GTR+I+G	GTR+I+G
nad2	1,494	GTR+I+G	GTR+I+G
nad3	354	GTR+I+G	GTR+I+G
nad7, nad11	2,589	GTR+I+G	GTR+I+G
nad9, rpl14, rps8, rps13	1,614	GTR+I+G	GTR+I+G
rpl2, rpl16, rps12, rps14	1,722	GTR+I+G	GTR+I+G
rpl5, rps2, rps4, rps11	1,518	TPM3u	GTR+I+G
srRNA, tRNA	3,161	GTR+I+G	GTR+I+G

References

Cai, G. & Scofield, S.R. (2020) Mitochondrial genome sequence of *Phytophthora sansomeana* and comparative analysis of *Phytophthora* mitochondrial genomes. PLoS ONE. 15: e0231296

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