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# Pomovirus

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## Glossary

g0005 **Spore balls** Resting spores (cystosori) of *Spongospora subterranea* found in lesions or pustules (powdery scabs) on potato tubers; a single cystosorus comprises 500–1000 resting spores aggregated together in a ball that is partially hollow, traversed by irregular channels.

g0010 **Spraing** Virus disease symptoms of internal brown lines and arcs in potato tuber flesh.

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## Introduction

p0005 Pomoviruses have tubular rod-shaped particles and tripartite genomes; they are transmitted by soil-borne zoosporic organisms belonging to two genera (*Polymyxa* and *Spongospora*) in the family Plasmodiophoraceae. Pomoviruses have limited host ranges, infecting species in a few families of dicotyledenous plants. Agriculturally important hosts include potato and sugar beet. There are four member species: *Potato mop-top virus*, *Beet soil-borne virus*, *Beet virus Q*, and *Broad bean necrosis virus*. Beet virus Q (BVQ) and beet soil-borne virus (BSBV) often occur in mixed infections with the benyvirus beet necrotic yellow vein virus (BNYVV).

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## Taxonomy and Classification

p0010 The classification of tubular rod-shaped viruses transmitted by soil-borne plasmodiophorid vectors was revised in 1998 to establish four genera: *Furovirus*, *Pomovirus*, *Benyvirus*, and *Pecluvirus*. The revision was prompted by new virus sequence information that revealed major differences in genome properties (number of RNA species, sequence, and genome organization). The genera are not assigned currently to any family. Pomovirus is a siglum from *Potato mop-top virus*, the type species.

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## Physical Properties of Particles

p0015 Pomovirus particles are hollow, helical rods, 18–20 nm in diameter, comprising multiple copies of a single major coat protein (CP; *c.* 19–20 kDa). The CP gene is terminated by a UAG (or UAA in broad bean necrosis virus (BBNV)) stop codon that is thought to be suppressible, readthrough (RT) of which would produce a fusion protein of variable mass (54–104 kDa). One or a few copies of the RT fusion protein are present at the extremity of potato mop-top virus (PMTV) particles thought to contain the 5′ end of the virus RNA. Pomovirus particles are fragile and particle size distribution measurements are variable; PMTV particles have predominant lengths of 125, 137, and 283 nm. PMTV particles sediment as three components with sedimentation coefficients ($S_{20,\mathrm{W}}$) of 126, 171, and 236 S.

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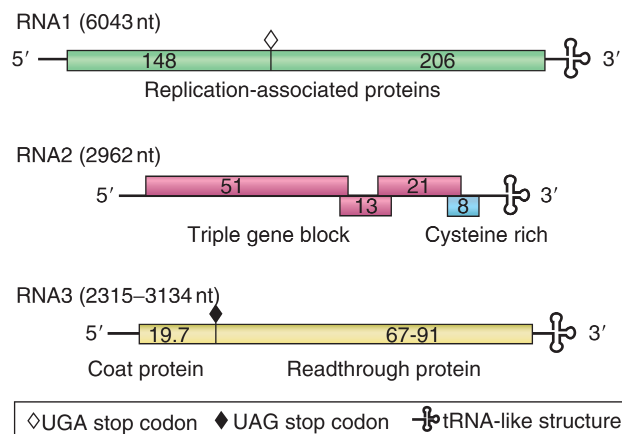
## Genome Properties

p0020 Complete genome sequences are available for three member species and an almost complete sequence (without the 5′ and 3′ untranslated regions (UTRs)) is available for BBNV. Pomovirus genomes comprise three species of positive-sense single-stranded RNA of *c.* 5.8–6, 2.8–3.4, and 2.3–3.1 kbp (**Figure 1**). RNA1 encodes the replicase proteins. It contains a large open reading frame (ORF) that is interrupted by a UGA stop codon (ORF1) (or UAA in BVQ and BSBV); the sequence continues in-phase to encode an RT protein (204–207 kDa). The ORF1 protein (145–149 kDa) contains methyltransferase and helicase motifs while the RT domain contains the GDD RNA-dependent RNA polymerase (RdRp) motif. Phylogenetic analysis reveals that the RdRp's of the pomoviruses and soil-borne wheat mosaic furovirus share between 50% and 60% sequence identity.

p0025 The 5′ UTR of pomovirus RNAs contains the starting sequence $\mathrm{GU(A)_{1\text{–}4}(U)}_n$ (except BVQ RNA1 which begins with AUA). The RNAs are probably capped at the 5′ end since the RNA1 ORF contains methyltransferase motifs associated with capping activity. The terminal 80 nucleotides of the 3′ UTR can be folded into a tRNA-like structure that contains an anticodon for valine. Both BSBV and PMTV RNAs were shown to be valylated experimentally.

p0030 The virus movement proteins are encoded on RNA2 of PMTV (RNA3 in BSBV, BVQ, and BBNV). Three 5′ overlapping ORFs encode a conserved module of movement proteins known as the triple gene block (TGB). TGB movement proteins are found in the genomes of other rod-shaped viruses (hordei-, beny, pecluviruses) and in monopartite filamentous viruses in the genera *Potexvirus* and *Carlavirus*. The TGB proteins (TGB1, TGB2, and TGB3) are named according to their position on the RNA and have molecular masses of 48–53, 13, and




f0005 **Figure 1** Diagram of the PMTV genome organisation; boxes indicate open reading frames with the molecular masses of predicted protein products (kDa) indicated within.

20–22 kDa, respectively. The TGB1 contains a deoxyribonucleotide triphosphate (dNTP) binding site and helicase motifs in the C-terminal half typical of all TGB1sequences and an extended N-terminal domain found in hordei-like TGB1's that do not share obvious sequence identities. TGB1 binds RNA and is thought to interact with genomic RNAs to facilitate movement. The sequence of the second TGB protein is the most conserved with BSBV, BVQ, and PMTV sharing 63–75% sequence identity and 49% identity with that of BBNV; there is little sequence identity among the TGB3 sequences. Analysis shows that TGB2 and TGB3 proteins contain two hydrophobic regions (predicted transmembrane domains) separated by a hydrophilic domain and these proteins are associated with intracellular membranes in infected plants.

p0035 In PMTV and BBNV, a fourth small ORF is predicted that encodes an 8 kDa cysteine-rich or 6 kDa glycine-rich protein, respectively, of unknown function whereas no such ORF is present in BSBV or BVQ. The 8 kDa cysteine-rich protein of PMTV is not needed for virus movement or infection of *Nicotiana benthamiana* and is not thought to function as silencing suppressor. Although a subgenomic RNA (sgRNA) that could encode the 8 kDa protein was detected in infected *N. benthamiana*, the protein is not readily detectable in extracts of infected leaves.

p0040 The CP and RT proteins are encoded on RNA3 of PMTV (RNA2 in BSBV, BVQ, and BBNV). The PMTV RNA3 is of variable size, from 2315 to 3134 nt. Analysis of naturally occurring and glasshouse-propagated isolates revealed that deletions of *c.* 500–1000 nucleotides occur in both field and laboratory isolates and that they occur predominantly in the RT domain, particularly in the region toward the C-terminus. Deletions in this region are correlated with loss of transmission by the natural vector *Spongospora subterranea*. The first PMTV sequence to be published contained a shorter form of the CP–RT-encoding RNA and was designated as RNA3, whereas in BSBV, BVQ, and BBNV the corresponding RNA is RNA2. The RT domain of BVQ is shorter than the others and the RT coding sequence is followed by two additional ORFs for proteins of predicted mass of 9 and 18 kDa. Amino acid sequence comparisons reveal conserved motifs between these two proteins and domains in the C-terminal portions of BSBV and PMTV RT proteins which may indicate that they have arisen by degeneration of a larger ORF.

p0045 The occurrence of encapsidated deleted forms of RNA2 and RNA3 in natural and laboratory isolates of PMTV has been described and sequence analysis suggests that these PMTV RNAs contain sites that are susceptible to recombination possibly through a template switching mechanism. Variable base composition is found in natural isolates of BSBV in the sequence at the 3′ end of RNA3 between the stop codon of the third TGB and the terminal tRNA-like structure.

## Virus–Host Interactions and Movement

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p0050 Cytoplasmic inclusions of enlarged endoplasmic reticulum (ER) and the accumulation of distorted membranes and small virion bundles can be seen by electron microscope examination of thin sections of BSBV- and BVQ-infected leaves. In PMTV-infected potato leaves, abnormal chloroplasts with cytoplasmic invaginations were seen in thin sections as well as tubular structures in the cytoplasm associated with the ER and tonoplast and in the vacuole.

p0055 PMTV does not require CP for movement and it is thought that TGB1 interacts with viral RNA forming a movement competent ribonucleoprotein (RNP) complex. Studies of transiently expressed PMTV TGB proteins fused to marker proteins such as green fluorescent protein or monomeric red fluorescent protein in epidermal cells of *N. benthamiana* have helped to elucidate events in intracellular trafficking and indicate that PMTV interacts with the cellular membrane recycling system. PMTV

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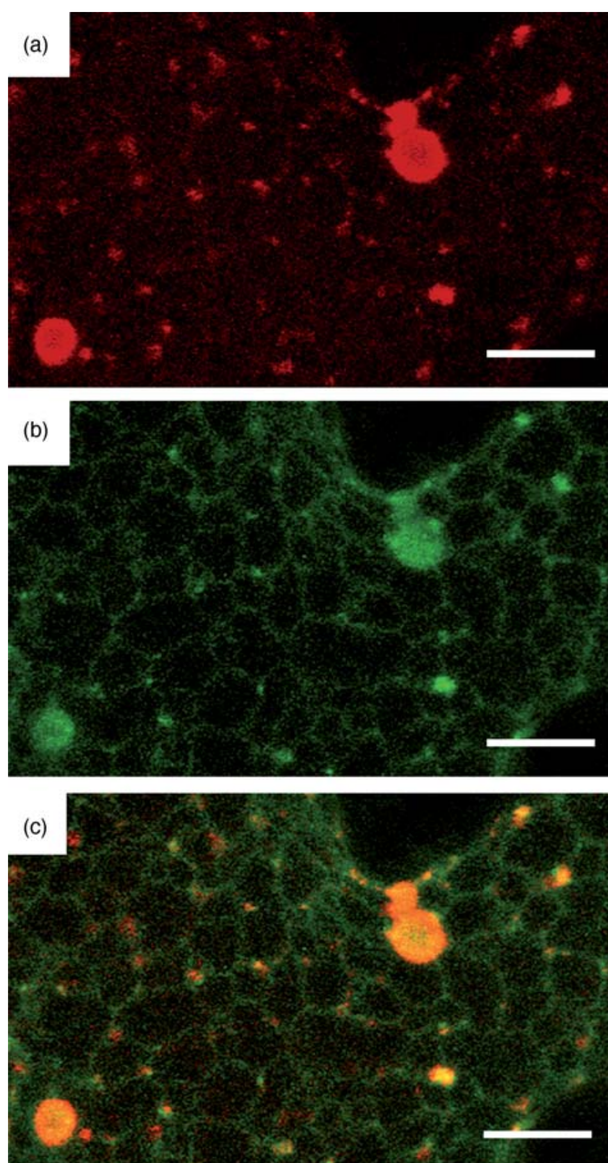


f0010 **Figure 2** Confocal laser scanning microscope images of PMTV TGB2 and TGB3 fluorescent fusion proteins in epidermal cells of *Nicotiana benthamiana*. Monomeric red fluorescent protein (mRFP) tagged PMTV-TGB2 was transiently expressed with green fluorescent protein (GFP) tagged PMTV-TGB3, the proteins co-localized on membranes of the ER and in motile granules seen moving on the ER network. (a) Expression of mRFP-TGB2 (red channel); (b) expression of GFP-TGB3 (green channel); (c) merged image. Scale = 10 nm.

TGB2 and TGB3 were shown to co-localize on the ER (**Figure 2**) and in small motile granules that utilize the actin–ER network to reach the cell periphery and plasmodesmata (PD) and TGB3 contains a putative tyrosine sorting signal (Y-Q-D-L-N), mutation of which inhibits PD localization. TGB2 and TGB3 act together to transport GFP-TGB1 to the PD for movement into neighboring cells and TGB2 and TGB3 have the capacity to gate the PD pore. TGB2 co-localizes in endocytic vesicles with the Rab 5 ortholog Ara 7 (AtRabF2b) that marks the early endosomal compartment. Also, protein-interaction analysis revealed that recombinant TGB2 interacted with a tobacco protein belonging to the highly conserved RME-8 (receptor mediated endocytosis-8) family of J-domain chaperones, essential for endocytic trafficking.

## Host Range, Geographical Distribution, and Transmission by Vector

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p0060 Pomoviruses have a limited host range and are transmitted in soil by zoosporic plasmodiophorid vectors that have been classified as protists (**Figure 3**). Viruses that are transmitted by plasmodiophorid vectors include pomo-, peclu-, furo-, beny-, and bymoviruses and they are thought to be carried within the zoospores. The vector life cycle includes production of environmentally resistant thick-walled resting spores and viruliferous resting spores can survive in soil for many years.

p0065 BBNV has been reported only from Japan; it causes necrosis and stunting in broad beans and peas. It is mechanically transmitted by inoculation of sap to a few species including *Vicia faba*, *Pisum sativum*, and *Chenopodium quinoa*.

p0070 BVQ and BSBV are often found associated with BNYVV; BVQ is reported only from Europe whereas BSBV is found in sugar-beet-growing areas worldwide. No symptoms have been attributed to BSBV or BVQ alone in sugar beet. The viruses are thought to be transmitted in soil by *Polymyxa betae*. BVQ is mechanically transmissible only to *C. quinoa* and BSBV to members of the Chenopodiaceae.

p0075 PMTV is found in potato-growing regions of Europe, North and South America, and Asia; virus incidence is favored by cool, wet growing conditions. It is transmitted in soil by *S. subterranea*, also a potato pathogen which causes the tuber blemish disease powdery scab. PMTV can be transmitted mechanically to members of the Solanaceae and Chenopodiaceae.

## Serological Relationships, Diagnosis, and Control

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p0080 The viruses are serologically distinct. Distant relationships have been reported between BSBV and BVQ; PMTV and soil-borne wheat mosaic furovirus; and PMTV, BBNV, and tobamoviruses. PMTV, BSBV, and BVQ CPs contain a conserved sequence (SALNVAHQL) that reacts in Western blots with a monoclonal antibody, SCR70, produced against PMTV but which is not exposed on intact particles. PMTV particles contain an immunodominant epitope at the N-terminus of the CP

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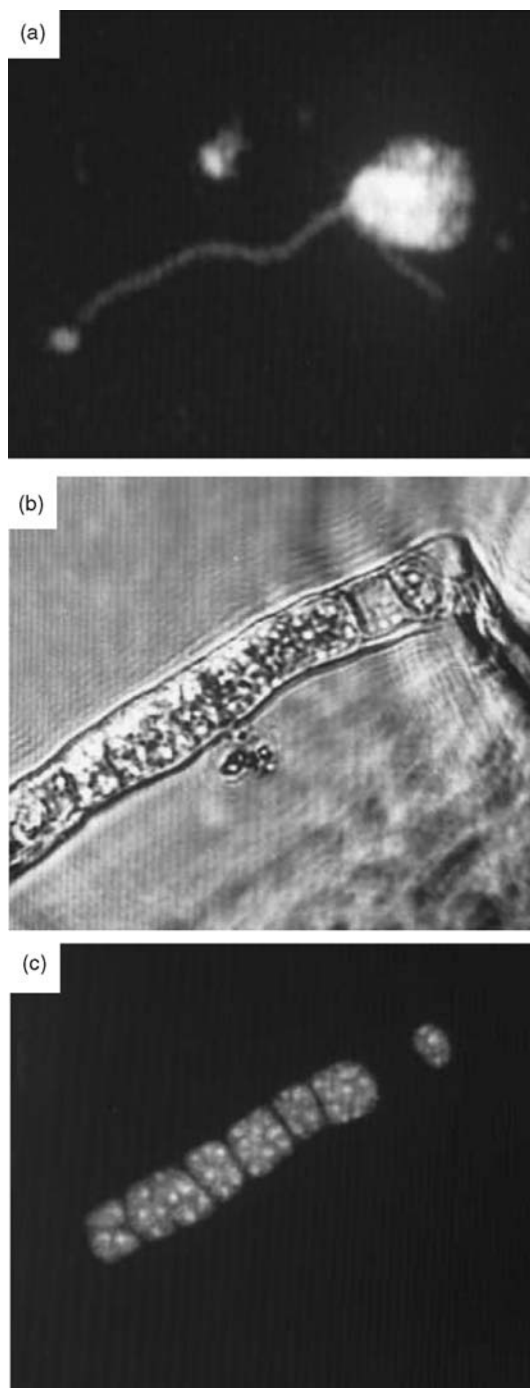


f0015 **Figure 3** (a) Biflagellate zoopore of *Spongospora subterranea*. (b) Bright field and (c) fluorescence microscope images of zoosporangia in tomato root hair.

that is exposed at the surface along the sides of the particles and can be detected by monoclonal antibody SCR69 (**Figure 4**).

p0085 The viruses can be detected by serological tests (immunosorbent electron microscopy, enzyme-linked immunosorbent assay) and by assays based on the reverse transcriptase-polymerase chain reaction (RT-PCR) in

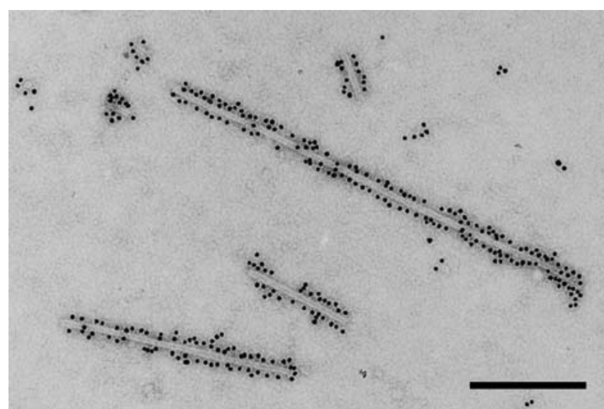

**Figure 4** Electron micrograph of PMTV particles labeled with monoclonal antibody SCR69/gold conjugate. f0020

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leaves, roots, or tubers from naturally infected plants. PMTV is known to be erratically distributed in potato leaves and tubers and can move systemically in the absence of CP in potato leaves which raises a risk of false negative results. In addition, test plants grown in soil that has been previously air-dried can be used as indicators either by observing visual symptoms such as the PMTV-induced necrotic 'thistle-leaf'-shaped line patterns on leaves of *Nicotiana debneyi* or by conducting serological or RT-PCR analysis on the test plant roots or leaves.

p0090 PMTV causes an economically important disease affecting the quality of tubers grown for the fresh and processing markets. Tubers of sensitive potato cultivars that are infected from soil during the growing season develop spraing symptoms that include unsightly brown lines, arcs, or marks in the flesh sometimes accompanied by slightly raised external lines and rings (**Figure 5**). Potato plants grown from infected tubers display yellow markings or chevrons on the leaves and may have shortened internodes (mop-top) producing cracked or malformed tubers, both tuber quality and yield can be affected. However, the virus does not infect all plants grown from infected tubers. Haulm and tuber symptoms vary markedly with cultivar, and some cultivars are symptomlessly infected. Environmental conditions also affect disease incidence and severity, and PMTV incidence was shown to increase with annual rainfall. Soil temperatures of 12–17 °C and high soil moisture at tuber initiation favor powdery scab incidence.

p0095 PMTV can be established at new sites by planting infected tubers and once established, PMTV is a persistent problem, as the resting spore balls of the vector *S. subterranea* are long-lived and resistant to drought and agrochemicals. Viruliferous spore balls are spread readily to new sites by farm vehicles, contaminated seed tubers, wind-blown surface soil; motile zoospores can be spread through contaminated irrigation or drainage water. In certain areas, potatoes have become infected by PMTV

f0025 **Figure 5** Symptoms of PMTV in potato tubers cv. Nicola.

18 years after potatoes were last grown (the longest period recorded). There is no effective practicable means to control *S. subterranea* but decreased severity of powdery scab can be achieved by application of fluazinam to soil. In addition, various chemicals for disinfection of tubers such as formaldehyde have decreased incidence, but their efficacy depends on the level of soil infestation where the tubers are planted and a combination of tuber and soil treatments may be more effective.

p0100 The best prospect for virus disease control is development of resistant cultivars but there are no known sources of PMTV resistance in commercial potato cultivars and most of the commercially grown cultivars are also susceptible to *S. subterranea*. However, plants transformed with virus transgenes (CP and a mutated form of TGB2) have exhibited resistance to PMTV with decreased virus accumulation and incidence in tubers of plants grown in infested soil.

*See also:* Benyvirus (00541); Furovirus (00408); Hordeivirus (00426); Pecluvirus (00542); Tobamovirus (00514).

## Further Reading


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