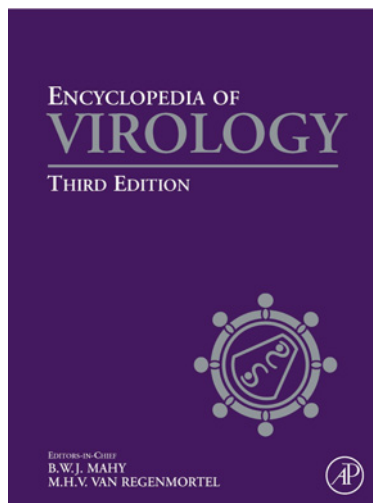


Provided for non-commercial research and educational use.  
Not for reproduction, distribution or commercial use.

This article was originally published in the *Encyclopedia of Virology, Volumes 1–5* published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who you know, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

<http://www.elsevier.com/locate/permissionusematerial>

Ghabrial S A, Ochoa W F, Baker T S and Nibert M L. Partitiviruses: General Features. *Encyclopedia of Virology*, 5 vols. (B.W.J. Mahy and M.H.V. Van Regenmortel, Editors), pp. 68-75 Oxford: Elsevier.

multiply mainly in areas of the fungal mycelium that are less involved in fungal growth might be one of the reasons that partitiviruses, although they replicate to relatively high levels, are usually associated with a symptomless infection of their respective fungal hosts. Recently, the latency of a partitivirus infection was demonstrated by direct experimental evidence in the case of ascomycete *Rosellinia necatrix* and the RnV-1-W8 partitivirus. Protoplasts of *R. necatrix* were transfected with purified particles of RnV-1-W8. The resulting mycelium contained transmissible RnV-1-W8 virions but showed no observable symptoms associated with the presence and replication of this virus. In contrast, in the *H. annosum* study (see previous section), germination frequency of basidiospores was significantly reduced ( $P < 0.05$ ) by the presence of partitivirus dsRNA in the parental fruit bodies. Use of isogenic fungal lines may be needed to verify these results.

See also: Fungal Viruses; Chrysovirus; Partitiviruses: General Features; Totiviruses.

## Further Reading

- Bruenn JA (1993) A closely related group of RNA-dependent RNA polymerases from double-stranded RNA viruses. *Nucleic Acids Research* 21: 5667–5669.
- Ghabrial SA (1998) Origin, adaptation and evolutionary pathways of fungal viruses. *Virus Genes* 16: 119–131.
- Ghabrial SA, Buck KW, Hillman BI, and Milne RG (2005) *Partitiviridae*. In: Fauquet CM, Mayo MA, Maniloff J, Desselberger U, and Ball LA (eds.) *Virus Taxonomy: Eighth Report of the International Committee on Taxonomy of Viruses*, pp. 581–590. San Diego, CA: Elsevier Academic Press.
- ICTVdB Management (2006) 00.049.0.01. Partitivirus. In: Büchen-Osmond C (ed.) *ICTVdB – The Universal Virus Database, version 4*, New York: Columbia University.
- Kim JW, Choi EY, and Kim YT (2006) Intergeneric relationship between the aspergillus ochraceous virus F and the penicillium stoloniferum virus S. *Virus Research* 120: 212–215.
- Strauss EE, Lakshman DK, and Tavantzis SM (2000) Molecular characterization of the genome of a partitivirus from the basidiomycete *Rhizoctonia solani*. *Journal of General Virology* 81: 549–555.
- Tavantzis SM and Bandy BP (1988) Properties of a mycovirus from *Rhizoctonia solani* and its virion-associated RNA polymerase. *Journal of General Virology* 69: 1465–1477.

## Partitiviruses: General Features

**S A Ghabrial**, University of Kentucky, Lexington, KY, USA

**W F Ochoa** and **T S Baker**, University of California, San Diego, La Jolla, CA, USA

**M L Nibert**, Harvard Medical School, Boston, MA, USA

© 2008 Elsevier Ltd. All rights reserved.

### Glossary

#### Cryo-transmission electron microscopy

Transmission electron microscopy of unstained, unfixed, frozen-hydrated (vitrified) specimens, preserved as close as possible to their native state.

**Hyphal anastomosis** The union of a hypha with another resulting in cytoplasmic exchange.

**Icosahedral symmetry** Arrangement of 60 identical objects or asymmetric units adopted by many isometric (spherical) viruses, with a combination of two-, three-, and fivefold rotations equivalently relating the units about a point in space.

**Mycoviruses** Viruses that infect and multiply in fungi.

**'T = 2' symmetry** The so-called 'forbidden' triangulation symmetry, in which 120 chemically identical protein monomers, form 60 identical, asymmetric dimers arranged with icosahedral symmetry. Monomers in a 'T = 2' structure occupy two distinct, nonequivalent positions and therefore

differ from the 'allowed' symmetries where monomers are either equivalently or quasi-equivalently related.

**Virus capsid** Generally a protective shell, composed of multiple copies each of one or more distinct protein subunits, that encapsidate the viral genome.

### Introduction

In the early 1960s, interest in the antiviral activities associated with cultural filtrates of *Penicillium* spp. led to the discovery of double-stranded RNA (dsRNA) isometric viruses in these and other filamentous fungi. Fungal viruses, or mycoviruses, are now known to be of common occurrence. The isometric dsRNA viruses isolated from *Penicillium* spp. were among the first to be molecularly characterized and were shown to have segmented genomes. Those with bipartite genomes are currently classified in the genus *Partitivirus* in the family *Partitiviridae*. Interestingly, plant viruses (also called cryptoviruses) with

bipartite dsRNA genomes and very similar properties to the fungal partitiviruses were discovered in the late 1970s and are presently classified in the genera *Alphacryptovirus* and *Betacryptovirus* in the family *Partitiviridae*. The fungal partitiviruses and plant partitiviruses are discussed elsewhere in this encyclopedia. The goals of this article are to examine the similarities and differences between these two groups of viruses and to discuss future perspectives of partitivirus research.

## Biological Properties

Fungal and plant partitiviruses are both associated with latent infections of their respective hosts. There are no known natural vectors for any partitivirus. Fungal partitiviruses are transmitted intracellularly during cell division and sporogenesis (vertical transmission) as well as following hyphal anastomosis, that is, cell fusion, between compatible fungal strains (horizontal transmission). In some ascomycetes (e.g., *Gaeumannomyces graminis*), virus is usually eliminated during ascospore formation. Experimental transmission of fungal partitiviruses has been reported by transfecting fungal protoplasts with purified virions. The plant cryptoviruses, on the other hand, are not horizontally transmitted by grafting or other mechanical means, but are vertically transmitted by ovule and/or pollen to the seed embryo. Thus, whereas sexual reproduction of the host is required for the survival of plant partitiviruses, it is detrimental to the continued existence of the fungal partitiviruses that infect some ascomycetes. Transmission of fungal partitiviruses through asexual spores, however, can be highly efficient, with 90–100% of single conidial isolates having received the virus. In summary, transmission of fungal partitiviruses by asexual spores and plant partitiviruses by seed provide the primary or only means for disseminating these viruses.

Both fungal and plant partitiviruses are generally associated with symptomless infections of their hosts. While cryptoviruses are present in very low concentrations in plants (e.g., 200 µg of virions per kg of tissue for white clover cryptic virus), fungal partitiviruses can accumulate to very high concentrations (at least 1 mg of virions per g of mycelial tissue for penicillium stoloniferum virus F (PsV-F)). Mixed infections of fungal or plants hosts with two distinct partitiviruses are not rare. PsV-S and PsV-F represent one example in which two partitiviruses infect the same fungus, *Penicillium stoloniferum*. Interestingly, a significant increase in cryptovirus concentration has been observed in mixed infections with unrelated viruses belonging to other plant virus families.

## Virion Properties

The buoyant densities of virions of members of the partitivirus family range from 1.34 to 1.39 gm cm<sup>-3</sup>, and the

sedimentation coefficients of these virions range from 101S to 145S (S<sub>20w</sub> in Svedberg units). Generally, each virion contains only one of the two genomic dsRNA segments. However, with some viruses like the fungal partitivirus PsV-S, purified preparations can contain other distinctly sedimenting forms that include empty particles and replication intermediates (see the next section).

All fungal and plant partitiviruses examined to date have been shown to possess virion-associated RNA-dependent RNA polymerase (RdRp) activity, which catalyzes the synthesis of single-stranded RNA (ssRNA) copies of the positive strand of each of the genomic dsRNA molecules. The *in vitro* transcription reaction occurs by a semi-conservative mechanism, whereby the released ssRNA represents the displaced positive strand of the parental dsRNA molecule and the newly synthesized positive strand is retained as part of the duplex.

## Genome Organization and Replication

Virions of members of the partitivirus family contain two unrelated segments of dsRNA, in the size range of 1.4–2.3 kbp, one encoding the capsid protein (CP) and the other encoding the RdRp. The two segments are usually of similar size and are encapsidated separately, that is, each particle generally contains only one dsRNA segment. The genomes of at least 16 members of the genus *Partitivirus* have recently been completely sequenced (Table 1). In contrast, the complete genome sequences of only three alphacryptoviruses and no betacryptoviruses have yet been determined (Table 1). The genomic structure of *Atkinsonella hypoxylon* virus (AhV-1), the type species of the genus *Partitivirus*, comprising segment 1 (2180 bp, encoding the RdRp) and segment 2 (2135 bp, encoding the CP), is schematically represented in Figure 1.

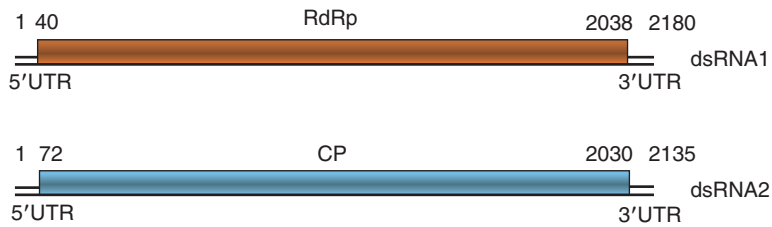
The presence of one or more additional dsRNA segments is common among members of the family *Partitiviridae*. For example, in addition to the two genomic segments, preparations of AhV-1 contain a third dsRNA segment of 1790 bp. With the exception of the termini, this third segment is also unrelated to the other two. The absence of any long open reading frame (ORF) on either strand of segment 3 of AhV-1 suggests that it is a satellite segment, not required for replication. Satellite dsRNAs are often associated with infections by members of the family *Partitiviridae* (Table 1).

Limited information on how fungal viruses in the genus *Partitivirus* replicate their dsRNAs is derived from *in vitro* studies of virion-associated RdRp and the isolation from naturally infected mycelium of particles that represent various stages in the replication cycle. The RdRp is believed to function as both a transcriptase and a replicase. The transcriptase activity within an assembled virion catalyzes the synthesis of progeny positive-strand

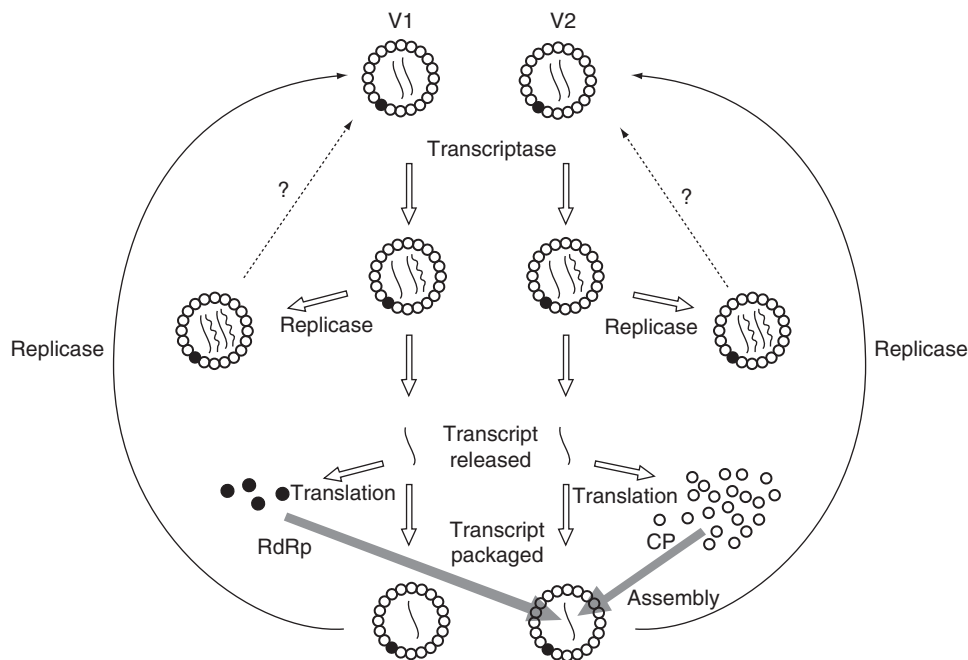
**Table 1** List of viruses in the family *Partitiviridae* with sequenced genomic dsRNAs

<i>Virus</i> <sup>a</sup>	<i>Abbreviation</i>	<i>dsRNA segment no. (size in bp; encoded protein, size in kDa)</i>	<i>GenBank accession no.</i>
Genus: <i>Partitivirus</i>			
<i>Atkinsonella hypoxylon virus</i> *	AhV	1 (2180; RdRp, 78) 2 (2135; CP, 74) 3 (1790; satellite)	L39125 L39126 L39127
<i>Ceratocystis resinifera virus</i>	CrV	1 (2207; RdRp, 77) 2 (2305; CP, 73)	AY603052 AY603051
<i>Discula destructiva virus 1</i> *	DdV1	1 (1787; RdRp, 62) 2 (1585; CP, 48) 3 (1181; satellite) 4 (308; satellite)	NC_002797 NC_002800 NC_002801 NC_002802
<i>Discula destructiva virus 2</i> *	DdV2	1 (1781; RdRp, 62) 2 (1611; CP, 50)	NC_003710 NC_003711
<i>Fusarium poae virus 1</i> *	FpV-1	1 (2203; RdRp, 78) 2 (2185; CP, 70)	NC_003884 NC_003883
<i>Fusarium solani virus 1</i> *	FsV-1	1 (1645; RdRp, 60) 2 (1445; CP, 44)	D55668 D55669
<i>Gremmeniella abietina virus MS1</i> *	GaV-MS1	1 (1782; RdRp, 61) 2 (1586; CP, 47) 3 (1186; satellite)	NC_004018 NC_004019 NC_004020
<i>Helicobasidium mompa virus</i> *	HmV	V1-1 (2247; RdRp, 83) V1-2 (1776; RdRp, 63) V-70 (1928; RdRp, 70)	AB110979 AB110980 AB025903
<i>Heterobasidion annosum virus</i> *	HaV	1 (2325; RdRp, 87)	AF473549
<i>Ophiostoma partitivirus 1</i>	OPV-1	1 (1744; RdRp, 63) 2 (1567; CP, 46)	AM087202 AM087203
Oyster mushroom virus	OMV	1 (2038; RdRp, 70)	AY308801
<i>Penicillium stoloniferum virus F</i> *	PsV-F	1 (1677; RdRp, 62) 2 (1500; CP, 47) 3 (677; satellite)	NC_007221 NC_007222 NC_007223
<i>Penicillium stoloniferum virus S</i> *	PsV-S	1 (1754; RdRp, 62) 2 (1582; CP, 47)	NC_005976 NC_005977
<i>Pleurotus ostreatus virus</i>	PoV	1 (2296; RdRp, 82) 2 (2223; CP, 71)	NC_006961 NC_006960
<i>Rhizoctonia solani virus 717</i> *	RhsV-717	1 (2363; RdRp, 86) 2 (2206; CP, 76)	NC_003801 NC_003802
<i>Rosellinia necatrix virus 1</i>	RnV-1	1 (2299; RdRp, 84) 2 (2279; CP, 77)	NC_007537 NC_007538
Genus: <i>Alphacryptovirus</i>			
<i>Beet cryptic virus 3</i> *	BCV-3	2 (1607; RdRp, 55)	S63913
<i>Vicia cryptic virus</i> *	VCV	1 (2012; RdRp, 73) 2 (1779; CP, 54)	NC_007241 NC_007242
<i>White clover cryptic virus 1</i> *	WCCV-1	1 (1955; RdRp, 73) 2 (1708; CP, 54)	NC_006275 NC_006276
Unclassified viruses in the family <i>Partitiviridae</i>			
Cherry chlorotic rusty spot associated partitivirus	CCRSAPV	1 (2021; RdRp, 73) 2 (1841; CP, 55)	NC_006442 NC_006443
<i>Fragaria chiloensis cryptic virus</i>	FCCV	1 (1743; RdRp, 56)	DQ093961
<i>Pyrus pyrifolia cryptic virus</i>	PpV	1 (1592; RdRp, 55)	AB012616
<i>Raphanus sativus cryptic virus 1</i> (or Radish yellow edge virus*)	RasV-1 (RYEV)	1 (1866; RdRp, 67) 2 (1791; CP, 56)	NC_008191 NC_008190
<i>Raphanus sativus cryptic virus 2</i>	RasV-2	1 (1717; RdRp, 55) 2 (1521; unknown) 3 (1485; unknown)	DQ218036 DQ218037 DQ218038

<sup>a</sup>An asterisk next to the virus name indicates it is presently recognized by ICTV as a member or a tentative member in the family *Partitiviridae*. Family members or tentative members that have not been sequenced to date are not included.



**Figure 1** Genome organization of *atkinsonella hypxylon* virus (AhV), the type species of the genus *Partitivirus*. dsRNA1 contains the RdRp ORF (nt positions 40–2038) and dsRNA2 codes for the CP ORF (nt positions of 72–2030). The RdRp and CP ORFs are represented by rectangular boxes. Reproduced from Ghabrial SA, Buck KW, Hillman BI, and Milne RG (2005) *Partitiviridae*. In: Fauquet CM, Mayo MA, Maniloff J, Desselberger U, and Ball LA (eds.) *Virus Taxonomy: Eighth Report of the International Committee on Taxonomy of Viruses*, pp. 581–590. San Diego, CA: Elsevier Academic Press, with permission from Elsevier.



**Figure 2** Model for replication of *penicillium stoloniferum* virus S (PsV-S). The open circles represent capsid protein (CP) subunits and the closed circles represent RNA-dependent RNA polymerase (RdRp) subunits. Solid lines represent parental RNA strands whereas wavy lines represent newly synthesized progeny RNA strands. Reproduced from Ghabrial SA and Hillman BI (1999) *Partitiviruses-fungal (Partitiviridae)*. In: Granoff A and Webster RG (eds.) *Encyclopedia of Virology*, 2nd edn., pp. 1477–1151. San Diego: Academic Press, with permission from Elsevier.

RNA from the parental dsRNA template, accompanied by the displacement of the parental positive strand and its release from the virion. This can presumably occur through repeated rounds, giving rise to multiple positive-strand copies. Each released positive strand can then be consecutively or alternatively (1) used as a template for protein (CP or RdRp) translation by the host machinery or (2) packaged by CP and RdRp into an assembling progeny virion. The replicase activity within this assembling virion then catalyzes the synthesis of negative-strand RNA on the positive-strand template, reconstituting a genomic dsRNA segment. The replication of plant

partitiviruses is presumed to mimic that described for the fungal viruses.

Partially purified virion preparations are known to include a small proportion of particles that contain only one ssRNA molecule corresponding to the genomic positive strand. These may be particles in which the replicase reaction is defective or has not yet occurred. In addition, partially purified virion preparations are known to contain a relatively large proportion of a heterogeneous population of particles more dense than the mature virions. These dense particles may represent various stages in the replication cycle including particles containing

the individual genomic dsRNAs with ssRNA tails of varying lengths, particles with one molecule of dsRNA and one molecule of its ssRNA transcript and particles with two molecules of dsRNA (Figure 2).

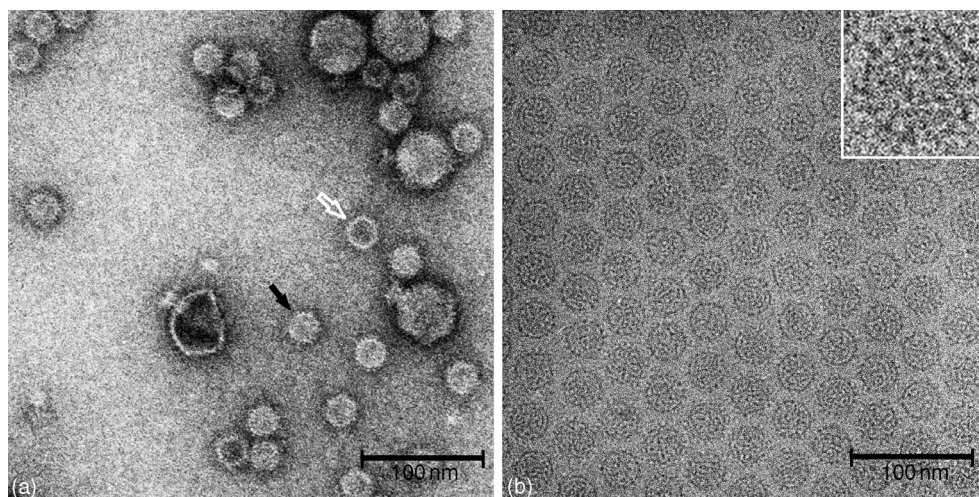
### Structures of Partitivirus Virions

The isometric dsRNA mycoviruses are classified within the families *Totiviridae*, *Chrysoviridae*, and *Partitiviridae*. The capsid structures of representative members of each of the first two families have been determined, at least one at near atomic resolution using X-ray crystallography, and the others at low to moderate resolutions ( $\sim 1.5\text{--}2.5$  nm) using cryo-transmission electron microscopy (cryo-TEM) combined with three-dimensional (3D) image reconstruction. We have recently initiated systematic cryo-TEM and image reconstruction studies of three viruses, PsV-S, PsV-F, and FpV-1, within the genus *Partitivirus*. Based on phylogenetic analysis of partitivirus CPs or RdRps, PsV-S, and PsV-F form sister clades in the same cluster, whereas FpV-1 is placed in a separate and distinct cluster within this genus (see section on 'Taxonomic and phylogenetic considerations'). These viruses are structurally distinguished primarily on the basis of significant differences in the sizes of the respective CPs and percent nucleotide and amino acid sequence identity of their RdRps and CPs. Structures of partitiviruses from the

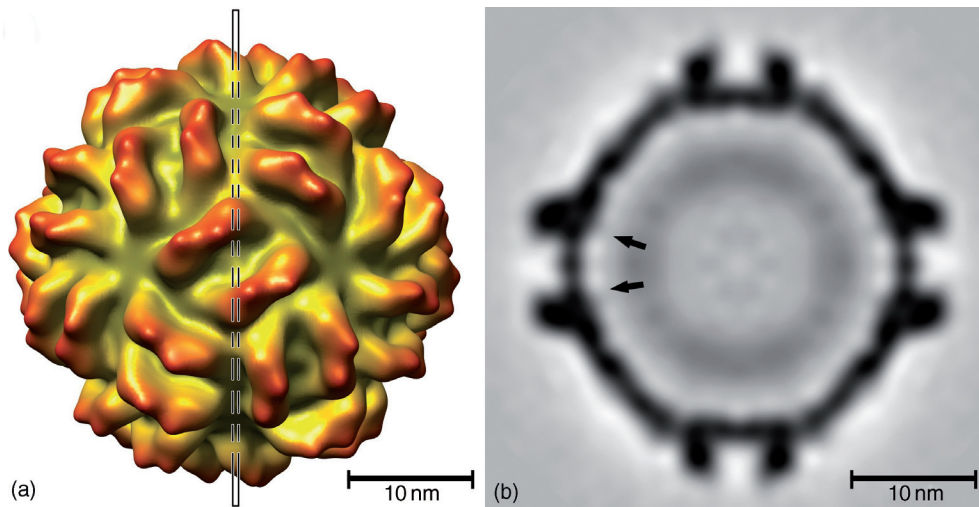
genera *Alphacrypto-* and *Betacryptovirus*, all of which are plant viruses, have yet to be reported.

Preliminary studies of PsV-S, PsV-F, and FpV-1 strongly suggest that all members of the genus *Partitivirus* share a number of common features. The structure of PsV-S is used to highlight these features, and significant differences are identified below.

PsV-S represents one of the simplest of the dsRNA viruses. Each virion comprises of one of the two genome segments (S1, 1754 bp and S2, 1582 bp), one or two copies of the 62 kDa RdRp, and 120 copies of the 47 kDa CP. Virions exhibit an overall spherical morphology in negative stain or in vitrified solution (Figure 3). Reports of virion diameters based on measurements from stained specimens likely underestimate the true virion size, owing to distortions and other potential artifacts associated with the imaging of negatively stained specimens. Based on cryo-TEM images, the maximum diameter of fully hydrated PsV-S virions is 35 nm. 3D reconstruction of the PsV-S structure at  $\sim 21$  Å resolution demonstrates that the capsid is a contiguous shell (average thickness  $\sim 2$  nm) of subunits arranged with icosahedral symmetry (Figure 4(a)). The external surface of PsV-S displays 60 prominent protrusions that rise approximately 3 nm above an otherwise relatively featureless, spherical shell. Each protrusion and a portion of the underlying shell, constitutes one asymmetric unit (1/60th) of the capsid. The dimeric morphology of each protrusion is



**Figure 3** Electron micrographs of penicillium stoloniferum virus S (PsV-S). Samples were negatively stained in 2% uranyl acetate (a) or prepared unstained and vitrified (b). Micrographs were recorded on a CCD detector in an FEI Polara transmission electron microscope operated at 200 keV with samples at (a) room or (b) liquid nitrogen temperatures. In (a) bacteriophage P22 (five largest particles) was mixed with PsV-S to serve as a calibration reference. Heavy metal stain surrounds virions (e.g., black arrow) and contrasts their surfaces against the background carbon support film. Stain penetrates into the interior of 'empty' capsids (e.g., white arrow), resulting in particle images in which only a thin, annular shell of stain-excluding material (capsid) is seen. In (b) the unstained PsV-S sample was vitrified in liquid ethane. Here particles appear dark (higher density) against a lighter background of surrounding water (lower density). The inset shows a three-times enlarged view of an individual particle, in which several knobby surface features are clearly visible.



**Figure 4** Three-dimensional (3D) structure of PsV-S. (a) Shaded, surface representation of PsV-S 3D reconstruction viewed along an icosahedral twofold axes. The 3D map is color-coded to emphasize the radial extent of different features (yellows and greens highlight features closest to the particle center, and oranges and reds those farthest from the center). A total of 60 prominent protrusions extend radially outward from the capsid surface. Each protrusion exhibits an approximate dyad symmetry, which is consistent with the expectation that the partitivirus capsid consists of 120 capsid protein monomers, organized as 60 asymmetric dimers in a so-called ‘ $T=2$ ’ lattice. (b) Density projection image of a central, planar section through the PsV-S 3D reconstruction (from region marked by dashed box in (a)). Darker shades of gray correspond to higher electron densities in the map section and lighter shades represent low-density features such as water outside as well as inside the particles. The capsid shell appears darkest because it contains a closely packed, highly ordered (icosahedral) arrangement of capsid subunits. The genomic dsRNA on the inside appears at lower density, in part because the RNA is not as densely packed and in part because the RNA adopts a less ordered arrangement. The protrusions seen in (a) appear as large ‘bumps’ in the central section view that decorate the outside of a contiguous, ~2 nm thick, shell. Arrows point to faint density features that appear to form contacts between the inner surface of the protein capsid and the underlying RNA. These contacts occur close to the fivefold axes of the icosahedral shell.

consistent with an asymmetric unit being composed of two CP monomers. Hence, there are 120 protein subunits arranged as 60 asymmetric dimers packed in a so-called ‘ $T=2$ ’ (‘forbidden’) lattice, which requires that the monomers do not interact equivalently or quasiequivalently as often occurs, especially in smaller, simpler virus capsids (e.g., with triangulation symmetries such as  $T=1, 3, 4$ ).

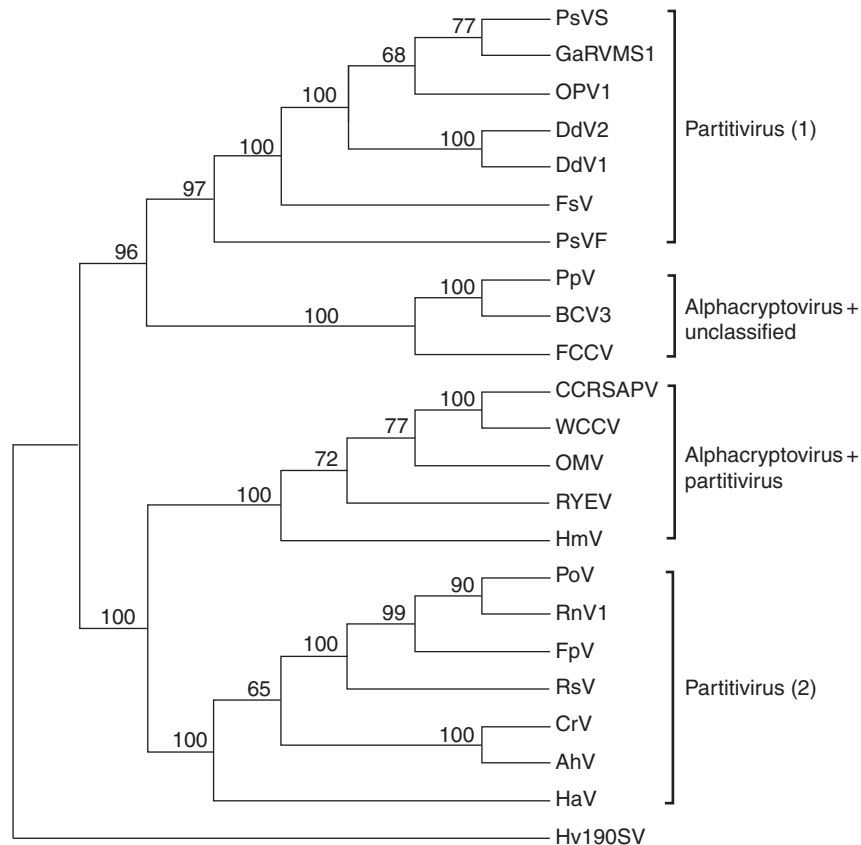
An additional, symmetric ball of weak density within the capsid is attributed to the genomic dsRNA, and does not appear to adopt any regular structure at the limited resolution of this initial 3D reconstruction (Figure 4(b)). Lack of detectable genome organization may, in part, be attributed to averaging effects that occur when images of both PsV-S particle types are combined to produce the reconstructed 3D density map. Potential interactions between the genome and the inner wall of the capsid are suggested by faint lines of density observed in thin, planar sections through the density map (arrows; Figure 4(b)).

PsV-F and PsV-S co-infect and are co-purified from the fungal host, *Penicillium stoloniferum*. The coat protein of PsV-F (420 aa; 47 kDa) is very similar in size to that of PsV-S, but they only share 17% sequence identity. PsV-F virions are ~37 nm in diameter and the gross morphology and  $T=2$  organization of the capsid is remarkably similar to that of PsV-S (not shown). However, the 60 protrusions

in PsV-F are narrower, they extend further above the shell (~6.5 nm), and their long axes are rotationally aligned ~18° in a more anti-clockwise orientation compared to those in PsV-S.

*Fusarium poae* virus (FpV-1) also exhibits a ‘ $T=2$ ’ arrangement of its more massive coat protein subunits (637 aa; 70 kDa) (not shown). These subunits assemble to form ~42 nm diameter virions, significantly larger than both PsV-S and PsV-F. The average thickness of the FpV-1 shell varies considerably and is much less uniform than the shells of the smaller partitiviruses. The dimeric protrusions in FpV-1 extend ~3 nm above the capsid shell and have a wide base that appears to form more extensive interactions or connections to the underlying shell compared with the other two partitiviruses. Central sections through a low-resolution density map of FpV-1 exhibit three concentric layers of weak density, with a 3 nm spacing consistent with a relative close packing of nucleic acid as found in other dsRNA virus capsids.

Current studies are aimed at obtaining higher-resolution 3D reconstructions for each of the fungal partitiviruses mentioned above. In the absence of any crystallographic structure determinations, higher-resolution cryo-TEM reconstructions should enable more detailed comparisons to be made, and potentially provide a means to locate the



**Figure 5** Phylogenetic analysis of the RdRp conserved motifs and flanking sequences derived from aligned, deduced amino acid sequences of members of the family *Partitiviridae* using the program CLUSTAL X. Motifs 3 through 8 and the sequences between the motifs, as previously designated by Jiang and Ghabrial (*Journal of General Virology* 85, 2111–2121, 2004) were used. See [Table 1](#) for virus name abbreviations. Bootstrap numbers out of 1000 replicates are indicated at the nodes. The tree was rooted with the RdRp of *Helminthosporium victoriae* 190S virus (Hv190SV), a member of the genus *Totivirus* in the family *Totiviridae* (GenBank accession no. NC\_003607), which was included as an outgroup.

RdRps that are presumed to be fixed inside the capsid shell and possibly associated with a specific recognition site on each of the separately encapsidated genomic dsRNA segments. Such studies will also allow evolutionary links to the ‘ $T=2$ ’ cores of other well-studied dsRNA viruses that infect both fungal and nonfungal hosts to be explored. Structural studies expanded to include members of the genera *Alphacrypto-* and *Betacryptovirus* also have the potential to systematically characterize the similarities as well as differences in the life cycles of fungal and plant partitiviruses.

### Taxonomic and Phylogenetic Considerations

Recent phylogenetic analyses based on amino acid sequences of RdRps (conserved motifs) of members of the family *Partitiviridae* led to the identification of four clusters, two of which are large and comprise only members of the genus *Partitivirus* ([Figure 5](#)). One large

cluster with strong bootstrap support includes the partitiviruses DdV1, DdV2, FsV, GaV-MS1, OPV, and PsV-S (see [Table 1](#) for virus abbreviations). The CPs of these viruses share significant amino acid sequence identities (34–62%), but less than the RdRps (55–70% identity), suggesting that the CPs have evolved at a faster rate. The second partitivirus RdRp cluster consists of AhV, CrV, FpV, PoV, RhsV, and RnV1. These two large clusters were proposed to comprise two subgroups (subgroups 1 and 2) of the genus *Partitivirus* ([Figure 5](#)). Interestingly, the CPs of these two subgroups differ significantly in size with average sizes of 47 and 74 kDa for subgroups 1 and 2, respectively. Of the remaining two RdRp clusters ([Figure 5](#)), one consists of BCV (genus *Alphacryptovirus*) and two other, unclassified plant cryptoviruses (FCCV and PpV). The fourth cluster consists of a mixture of plant viruses (WCCV and RYEV, genus *Alphacryptovirus*) and fungal viruses (OMV and HmV, genus *Partitivirus*), together with CCRSAV, which may be either a fungal or a plant virus, as yet to be determined. This raises the interesting possibility of horizontal transfer of members of the



family *Partitiviridae* between fungi and plants. This is a reasonable possibility because some of the viruses in these clusters have fungal hosts that are pathogenic to plants. Based on our current knowledge of partitiviruses, the taxonomy of the family *Partitiviridae* will probably need to be reconsidered. As additional molecular and structural information from a wider range of plant and fungal partitiviruses is gathered, the need for new or revised taxonomic classifications may become even more apparent.

## Future Perspectives

### Development of Infectivity Assays for Fungal Partitiviruses

The recent success of using purified RnV-1 virions to infect virus-free isolates of the fungal host *Rosellinia necatrix* is very promising since there is considerable need to advance our knowledge of the biology of fungal partitiviruses (e.g., host-range, virus–host interaction, and molecular basis of latent infection). The natural host range of partitiviruses is restricted to the same or closely related vegetative compatibility groups that allow lateral transmission. At present, there are no known experimental host ranges for fungal partitiviruses because suitable infectivity assays have yet to be developed. With the success of the *Rosellinia necatrix*-RnV-1 infectivity assays, it is expected that future research would explore the potential experimental host range of RnV-1 including other fungal species in the genus *Rosellinia* and related genera. It is also anticipated that comparable infectivity assays using purified virions would be developed for other fungal partitiviruses. Because of the possibility alluded to earlier, of horizontal transfer of partitiviruses between fungi and plants, it is interesting to test the infectivity, using fungal protoplasts, of plant partitiviruses such as the alphacryptoviruses WCCV-1 and RYEV, which are known to be more closely related to certain fungal partitiviruses (e.g., OMV, HaV, and HmV) than to other plant partitiviruses. Alternatively, it would likewise be interesting to explore the infectivity of fungal partitiviruses such as OMV, HaV, and HmV to appropriate plant protoplasts.

Fungal partitiviruses are known to be associated with latent infections of their natural hosts. But, conceivably, some partitiviruses may induce phenotypic changes and/or virulence attenuation in one or more of their experimental host fungi. If true, this would provide excellent opportunities for exploiting fungal partitiviruses for biological control and for basic studies on host–pathogen interactions. Furthermore, transfection assays using fungal protoplasts electroporated with full-length, *in vitro* transcripts of cloned cDNA to viral dsRNAs should also be applicable to partitiviruses. This would allow for the

development of partivirus-based vectors for expressing heterologous proteins in fungi. Because many partitiviruses are known to support the replication and encapsidation of satellite dsRNA, this property would facilitate the construction of recombinant vectors. Genes of interest could be inserted into the satellite molecule between the conserved termini that are presumed to be required for replication and encapsidation. Considering the high level of partivirus accumulation in their fungal hosts, the use of partiviral vectors provides an attractive and cost-effective means for the overproduction of valuable proteins in filamentous fungi.

### Reconsideration of the Taxonomy of the Family *Partitiviridae*

There is an urgent need to characterize at the molecular level, a broad range of plant partitiviruses that should include representatives of the genus *Betacryptovirus*. Taxonomic considerations of partitiviruses may benefit greatly from elucidating the capsid structure of representative members of each of the four clusters delineated by phylogenetic analysis. It may, however, require concerted efforts to generate purified virions of alphacryptoviruses and betacryptoviruses in quantities needed for structural studies since they generally occur at very low concentrations in their hosts.

*See also:* *Alphacryptovirus* and *Betacryptovirus*; Fungal Viruses; Partitiviruses of Fungi.

## Further Reading

- Antoniw JF (2002) *Alphacryptovirus (Partitiviridae)*. In: Tidona CA and Darai G (eds.) *The Springer Index of Viruses*, pp. 676–679. New York: Springer.
- Antoniw JF (2002) *Betacryptovirus (Partitiviridae)*. In: Tidona CA and Darai G (eds.) *The Springer Index of Viruses*, pp. 680–681. New York: Springer.
- Crawford LJ, Osman TAM, Booy FP, *et al.* (2006) Molecular characterization of a partivirus from ophiostoma himal-ulmi. *Virus Genes* 33: 33–39.
- Ghabrial SA (2001) Fungal viruses. In: Maloy O and Murray T (eds.) *Encyclopedia of Plant Pathology*, pp. 478–483. New York: Wiley.
- Ghabrial SA (2002) *Partivirus (Partitiviridae)*. In: Tidona CA and Darai G (eds.) *The Springer Index of Viruses*, pp. 685–688. New York: Springer.
- Ghabrial SA and Hillman BI (1999) Partitiviruses-fungal (*Partitiviridae*). In: Granoff A and Webster RG (eds.) *Encyclopedia of Virology*, 2nd edn., pp. 1477–1481. San Diego: Academic Press.
- Ghabrial SA, Buck KW, Hillman BI, and Milne RG (2005) *Partitiviridae*. In: Fauquet CM, Mayo MA, Maniloff J, Desselberger U, and Ball LA (eds.) *Virus Taxonomy: Eighth Report of the International Committee on Taxonomy of Viruses*, pp. 581–590. San Diego, CA: Elsevier Academic Press.
- Sasaki A, Kanematsu S, Onoue M, Oyama Y, and Yoshida K (2006) Infection of *Rosellinia necatrix* with purified viral particles of a member of *Partitiviridae* (RnPV1-W8). *Archives of Virology* 151: 697–707.