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Review Article

Mycovirome: biology, diversity, structures, advantages, and applications in plant protection

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ABSTRACT

The mycovirome comprises viruses that interact with fungi. These viruses are transmitted intracellularly during cell division, sporogenesis, or hyphal anastomosis, typically lacking an extracellular phase in their life cycle. Mycoviruses have been identified in a wide variety of fungal species, but their host range is restricted to compatible vegetative groups. While many mycoviruses exhibit no apparent effects on their hosts, others induce phenotypic changes, including uneven growth, abnormal pigmentation, and, in some cases, alterations in sexual reproduction. Notably, many virus-infected fungi display reduced virulence toward plants, a phenomenon termed hypovirulence. Such viruses often possess broad infectivity across multiple fungal species, making them valuable tools for the biological control of plant fungal diseases. Most known mycoviruses possess RNA genomes, either single-stranded or double-stranded, with only a few having single-stranded DNA genomes. To date, no mycoviruses with double-stranded DNA genomes have been identified, possibly due to technological limitations. However, advances in nucleic acid sequencing technologies hold significant promise for advancing mycovirus research. This review explores the biology, diversity, structural features, and applications of mycoviruses, with a focus on their potential in plant protection.

KEYWORDS
Biocontrol, dsRNA, Hypovirulence, Mycovirus, ssRNA.

INTRODUCTION

Eukaryotic organisms exist in a microbial world dominated by viruses, bacteria, archaea, and protozoa. Mounting evidence demonstrates that nearly every ecological niche on Earth, including the external and internal tissues of higher organisms (such as fungi), as well as marine, arid, and polar environments, is colonized by diverse microbial communities (Soltani 2017, 2020). Recent studies have revealed extensive communities of endosymbiotic viruses, bacteria, and archaea within the internal tissues of humans, insects, and plants. These microorganisms actively interact with their hosts, often inducing phenotypic changes (Moran et al. 2008, Soltani 2017, 2020).

Current evidence suggests that all major fungal taxa may harbor endogenous viruses, collectively termed mycoviruses (Ghabrial 1998). By definition, any viral genome (RNA or DNA) detected within fungal hosts constitutes a mycovirus. These fungal viruses (or the mycovirome) are ubiquitous across both filamentous fungi and yeasts (Buck 1986, Hollings 1962). Most mycoviruses exist as cryptic infections, typically causing no observable phenotypic changes or symptoms in their fungal hosts (Hollings 1962, Buck 1986, Wickner et al. 2012). However, certain mycoviruses can significantly alter fungal biology, affecting growth patterns, reproductive capacity, and/or pathogenic potential (Kotta-Loizou and Coutts 2017, Wickner et al. 2012).

The foundational discovery of fungal viruses traces back to 1948, when a pathogenic condition severely affected *Agaricus bisporus* cultivation at the La France brothers' mushroom farm in Pennsylvania. This economically devastating disease, subsequently termed La France disease, was characterized by malformed sporophores and dramatic yield reductions. Within years, similar disease reports emerged globally, with documented cases in Australia, Japan, and throughout Europe (Ghabrial et al 2015). These observations marked the first conclusive evidence of viral infections in fungi.

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The field of mycovirology experienced transformative advances in the 1970s through two pivotal discoveries, i.e., the demonstration that hypovirulence in *Cryphonectria parasitica* (the chestnut blight pathogen) correlated with mycovirus infection (Van Alfen et al 1975) and characterization of a mycovirus-induced killer phenotype in *Saccharomyces cerevisiae* strains (Berry and Bevan 1972). The *C. parasitica* findings revealed mycoviruses' capacity to modulate fungal virulence, while the *S. cerevisiae* system demonstrated their industrial applicability in fermentation technologies. Together, these breakthroughs established agents mycoviruses as both potential biocontrol against phytopathogens and valuable biotechnological tools (Nuss 2005), stimulating sustained research interest in mycovirology.

Emerging evidence indicates widespread colonization of endophytic fungi by symptomless mycoviruses (Bao and Roossinck 2013). A seminal study demonstrated that the thermal tolerance conferred to panic grass (*Dichanthelium lanuginosum*) by its fungal endophyte *Curvularia protuberata* depends entirely on a symbiotic mycovirus (Redman et al 2002). Subsequent research has revealed similar mutualistic mycovirus-fungus relationships in mycorrhizal systems, where these viral partners significantly influence symbiotic function (Ikeda et al 2012). Notably, diverse dsRNA viruses populate mycorrhizal fungi, with their presence first documented in *Glomus* species (arbuscular mycorrhizal fungi). Intriguingly, fungal colonies harboring these dsRNA elements exhibit enhanced plant growth promotion capabilities (Ikeda et al 2012). Current surveys demonstrate mycovirus ubiquity across fungal phyla, with infections reported in over eighty distinct fungal species (Diana et al 2023), highlighting their extensive host range and ecological significance.

Current mycovirus inventories reveal a pronounced bias toward the phyla *Ascomycota* and *Basidiomycota*, reflecting their status as the most extensively studied fungal groups. To date, researchers have documented 224 viral species infecting *Ascomycetes* and 37 species in *Basidiomycetes* (Myers et al 2020). The remaining fungal phyla show substantially lower mycovirus diversity, with only three species reported in *Mucoromycota* and a single species identified in both *Monoblepharidomycota* and *Blastocladiomycota* (Picarelli et al 2019). At the family level, *Botourmiaviridae* represents the most prevalent mycoviral group, comprising 14% (38 species) of characterized fungal viruses. This is followed by *Mymonaviridae* (11%; 29 species) and *Partitiviridae* (10%; 27 species) (Picarelli et al 2019). These distribution patterns highlight both the current research focus on particular fungal taxa and the potential for undiscovered viral diversity in understudied phyla.

GENOMIC FEATURES OF MYCOVIRUSES

As shown in Table 1, most known mycoviruses have either double-stranded RNA (dsRNA) or single-stranded RNA (ssRNA) genomes, which can be positive- or negative-sense. So far, only one circular single-stranded DNA (ssDNA) mycovirus has been discovered (Yu et al 2010), and no double-stranded DNA (dsDNA) mycovirus has been found (Jan et al., 2018). The tables also include several unclassified mycoviruses with dsRNA, (+) ssRNA, and (-) ssRNA genomes.

Table1. Genome structure percentages of mycoviruses.

dsRNA(37.8%)	(+)ssRNA (33.6%)	(-)ssRNA (12.6%)	RNA-RT(4.2%)	*ssDNA(1.9%)
Amalgaviridae	*Alphaflexiviridae*	*Mymonaviridae*	*Metaviridae*	*Genomoviridae*
Chrysoviridae	*Barnaviridae*	*Phenuiviridae*	*Pseudoviridae*	
Curvulaviridae	*Botourmiaviridae*			
Megabirnaviridae	*Deltaflexiviridae*			
partitiviridae	*Endornaviridae*			
polymycoviridae	*Gamaflexiviridae*			
quadriviridae	*Hypoviridae*			
Reoviridae	*Mitoviridae*			
Totiviridae	*Narnaviridae*			

*9.9% is related to unclassified mycoviruses.

The relative abundance and distribution of mycoviruses among plant-pathogenic fungi remain a subject of ongoing research. The majority of these mycoviruses occur in *Ascomycota*, where they are distributed across eight taxonomic classes. *Basidiomycota* represents the second most populated phylum, with mycoviruses identified in six classes. Additional phyla hosting mycoviruses in plant-pathogenic fungi include, in descending order of viral abundance: *Blastocladiomycota*. *Chytridiomycota*, *Mucoromycota*. *Neocallimastigomycota*, *Zoopagomycota*. For complete taxonomic details and quantitative distributions, refer to Table 2.

MYCOVIRUSES WITH DOUBLE-STRANDED RNA (dsRNA)

Several dsRNA viral families are classified as mycoviruses within Baltimore Class III, including: *Amalgaviridae, Chrysoviridae, Curvulaviridae, Megabirnaviridae, Partitiviridae, Polymycoviridae, Quadriviridae, Reoviridae, Totiviridae.* (Refer to Table 3 for complete taxonomic details and distribution data).

Mycoviruses with dsRNA genome exhibit substantial variation in genome size, ranging from compact 3.0 kb genomes to more extensive 29 kb genomes across different families (Vainio et al. 2018, Yang et al. 2020). Beyond size differences, these viruses display distinct genomic architectures. While all dsRNA mycoviruses possess an RNA-dependent RNA polymerase (RdRp) domain, its genomic position varies significantly among families (Myers et al. 2020). For instance, in unsegmented *Amalgaviridae* viruses, the RdRp domain resides in the 3'-proximal open reading frame (ORF), in segmented *Chrysoviridae* viruses, it is encoded in the 5' region of the genome (Krupovic et al. 2015, Kotta-Loizou et al. 2020). A key observation is that nearly all known dsRNA mycoviruses produce a coat protein (CP), except for those classified under the *Botybirnavirus* genus (Ghabrial et al. 2015, Krupovic et al. 2015, Chiba et al. 2018, Vainio et al. 2018, Sato et al. 2019, Kotta-Loizou et al. 2020, Yang et al. 2020).

Table 2. The frequency (%) of mycovirus genomic structures in fungi.

Phylum	Class	dsRNA	(+)ssR NA	(-)ssRNA	RT ssRNA	ssDNA
Ascomycota	*Arthoniomycetes*	100	0	0	0	0
	Dothideomycetes	52.6	33.33	10.5	1.75	1.75
	Eurotiomycetes	60	30	10	0	0
	Lecanoromycetes	100	0	0	0	0
	Sordariomycetes	55.6	36.1	6.9	0	1.4
	Leotiomycetes	40	44	8	0	8
	Pezizomycetes	57.1	35.7	0	7.1	0
	Saccharomycetes	78.9	10.5	0	10.5	0
Basidiomycota	*Agaricomycetes*	42	48	10	0	0
	Exobasidiomycetes	100	0	0	0	0
	Malasseziomycetes	100	0	0	0	0
	Microbotryomycetes	75	25	0	0	0
	Tremellomycetes	100	0	0	0	0
	Wallemiomycetes	100	0	0	0	0
Blastocladiomycota	*Blastocladiomycetes*	100	0	0	0	0
Chytridiomycota	*Chytridiomycetes*	66.7	33.3	0	0	0
Mucoromycota	*Glomeromycetes*	33.3	55.5	0	0	11.1
	Mortierellomycetes	60	20	20	0	0
	Mucoromycetes	57.1	14.3	14.3	0	14.3
	Umbelopsidomycetes	100	0	0	0	0
Neocallimastigomycota	*Neocallimastigomycetes*	33.3	33.3	0	0	33.3
Zoopagomycota	*Entomophthoromycetes*	50	50	0	0	0
	Kickxellomycetes	50	50	0	0	0
	Zoopagomycetes	0	100	0	0	0

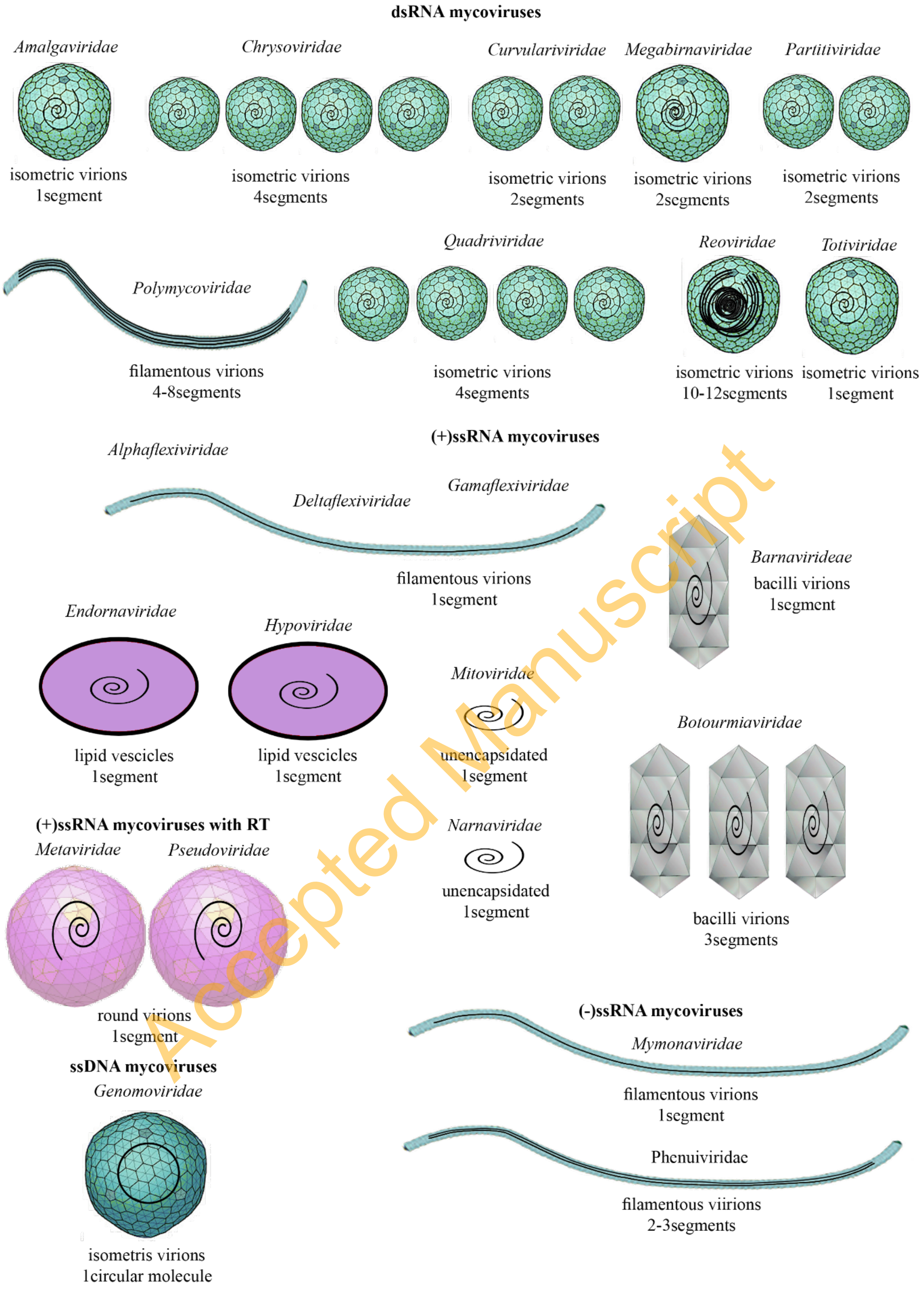

Fig. 1. Schematic diagram of mycovirus families that infect fungi (reviewed in this paper).

Current research has identified dsRNA viruses in diverse fungal lineages. Within Ascomycota, eight classes harbor these viruses: *Arthoniomycetes, Dothideomycetes, Eurotiomycetes, Lecanoromycetes, Leotiomycetes, Pezizomycetes, Saccharomycetes, and Sordariomycetes* (Myers et al 2020). The phylum *Basidiomycota* contains six virus-hosting classes: *Agaricomycetes*, *Exobasidiomycetes*, *Malasseziomycetes*, *Microbotryomycetes*, *Tremellomycetes*, and *Wallemiomycetes* (Myers et al. 2020). Additionally, dsRNA viruses have been detected in nine other fungal classes spanning multiple phyla: *Blastocladiomycetes*, *Chytridiomycetes*, *Glomeromycetes*, *Mortierellomycetes*, *Mucoromycetes*, *Umbelopsidomycetes*, *Neocallimastigomycetes*, *Kickxellomycetes*, and *Zoopagomycetes* (Kartali et al. 2022, Hough et al. 2023). Table 3 provides a comprehensive overview of these dsRNA viral families and their characteristics.

Amalgaviridae

The *Amalgaviridae* family comprises two genera: *Amalgavirus* and *Zybavirus*, with only the latter having been identified in fungal hosts. Members of this family possess double-stranded RNA genomes (~3.4 kb), single-segment genomic organization, icosahedral virion morphology (Fig. 1), and two overlapping open reading frames encoding a CP, an RdRp (Debate et al. 2019). Phylogenetic analyses reveal that *Amalgaviridae* share characteristic features with both *Partitiviridae* and *Totiviridae* families (Sabanadzovic et al. 2009, Martin et al. 2011). The type species, Zybavirus Z (ZbV-Z), was isolated from the yeast *Zygosaccharomyces bailii* (Depierreux et al. 2016).

Chrysoviridae

The *Chrysoviridae* family comprises two genera of dsRNA viruses infecting fungi: *Alphachrysovirus* and *Betachrysovirus* (Kotta-Loizou et al. 2020). The type species, *Penicillium chrysogenum virus* (PcV), represents the first characterized member of this family (Ghabrial and Castón 2011, Kotta-Loizou et al. 2020). PcV possesses four monocistronic dsRNA segments (2.4-3.6 kbp), each encapsidated in separate virions (Fig. 1). These segments encode: dsRNA1: RdRp, dsRNA2: major CP, dsRNA3: P3 protein (unknown function; contains conserved *phytoreovirus* S7 domain motifs), dsRNA4: P4 protein (unknown function). Notably, the P3 protein sequence exhibits a *phytoreovirus* S7 domain with structural motifs resembling those of the P4 protein core, suggesting potential functional conservation among viral proteins (Ghabrial and Castón 2011).

Curvulaviridae

The *Orthocurvulavirus* genus (family *Curvulaviridae*) comprises dsRNA viruses characterized by bipartite genome organization, isometric virion morphology (Fig. 1), and a CP encoded by two distinct ORFs, conserved 5' and 3' untranslated regions (Yan et al. 2023). Molecular analyses revealed significant sequence homology between two viral segments from *Agrocybe praecox* (strain MV011) and RdRP and CP genes of *Rhizoctonia solani bipartite virus 1*, now classified within the *Orthocurvulavirus* genus (Yan et al. 2023).

Megabirnaviridae

The *Megabirnaviridae* family comprises dsRNA viruses belonging to the genus *Megabirnavirus*, which are specific fungal pathogens (Sato et al. 2019). Currently, this genus includes only one identified species, *Rosellinia necatrix megabirnavirus 1* (RnMBV1). This virus features two genomic segments enclosed in non-enveloped, isometric particles (~50 nm in diameter; Fig. 1), dsRNA1 (8.9 kbp), which contains two overlapping ORFs on a single strand: ORF1 encodes the CP, and ORF2 encodes the RdRp. The CP-RdRp fusion product is likely produced via a ribosomal frameshift strategy (Chiba et al. 2009, Salipath et al. 2014). The dsRNA2 (7.2 kbp) contains two non-overlapping, in-frame ORFs. ORF3 produces a protein that undergoes proteolytic processing into smaller products in infected mycelia, ORF4 (for which no protein product has been detected) (Kanematsu et al. 2014). Both genomic segments feature exceptionally long untranslated regions (UTRs; 1.6 kb) that function as an internal ribosome entry site (IRES) for translation initiation. Transfection experiments with purified virions have demonstrated that while dsRNA2 is essential for viral replication, efficient replication requires both low viral induction levels and culture-free maintenance conditions (Kanematsu et al. 2014).

Partitiviridae

The *Partitiviridae* family comprises three genera of dsRNA viruses: The genera *Alphapartitivirus, Betapartitivirus,* and *Gammapartitivirus* (Nibert et al. 2014, Jaccard et al. 2023), which exhibit distinct host ranges. While *Gammapartitivirus* species infect only filamentous fungi, those in *Alphapartitivirus* and *Betapartitivirus* can infect both plants and filamentous fungi. *Partitivirus* infections are typically asymptomatic in their hosts. A notable member of this family is *P. stoloniferum virus S* (PsV-S), classified within *Gammapartitivirus*, which was isolated from its fungal host *P. stoloniferum* (Buck and Gillian 1970). Members of this family possess bipartite genomes (1.4-2.4 kbp segments) packaged in separate isometric particles (Vainio et al. 2018) (Fig. 1), each genomic segment containing a single large ORF, dsRNA1 (larger segment) encodes the RdRp, dsRNA2 (smaller segment) encodes the CP (Nibert et al. 2014).

Polymycoviridae

The *Polymycoviridae* family comprises small viruses with unconventional, segmented dsRNA genomes that are encapsidated within viral proteins (Kanhayuwa et al. 2015, Kotta-Loizou and Coutts 2017). These viruses belong to the genus *Polymycovirus* and typically possess four-segmented genomes, although some members contain up to eight segments (Kotta-Loizou et al. 2022). Each genomic segment features long non-coding regions (NCRs) with conserved terminal sequences.

The polymycovirus genome (7.5–12.5 kb) encodes several functional proteins. DsRNA1: RdRp for viral replication, dsRNA2: a putative scaffolding protein involved in virion assembly and replication (function currently unknown), dsRNA3: methyltransferase responsible for 5' capping of positive-sense viral RNA strands (Kanhayuwa et al. 2015, Kotta-Loizou and Coutts 2017), dsRNA4: PASrp protein, dsRNAs5-8 (when present): proteins of unknown function. Polymycoviruses infect diverse hosts including *Ascomycetes*, *Basidiomycetes*, and *Oomycetes*, often altering host morphology, sporulation, growth, and pathogenicity. Notably, filamentous capsids (10-12 nm wide × >1000 nm long) have been observed in only one member of this family: *Colletotrichum camelliae filamentous virus 1* (CcFV1) (Fig. 1) (Jia et al. 2017). Another representative member, *Aspergillus fumigatus polymycovirus 1* (AfuTmV1), possesses the characteristic unconventional four-segmented genome (Kotta-Loizou et al. 2022).

Quadriviridae

The genus *Quadrivirus* belongs to the family *Quadriviridae* of dsRNA viruses. Currently, this genus contains a single recognized species, *Rosellinia necatrix quadrivirus 1*, which exists as two distinct strains: W1075 and W1118 (Lin et al. 2012). The viral genome consists of four monocistronic segments, each independently packaged within densely packed, isometric virions approximately 45 nm in diameter (Fig. 1). The genomic segments of these viruses vary in size from 3.7 to 4.9 kb. Each segment encodes proteins with distinct functions: DsRNA1 produces a translation product whose function remains unknown; dsRNA2 and dsRNA4 both encode CPs that participate in viral assembly; and dsRNA3 encodes the RNA-dependent RNA polymerase (RdRp) (Wu et al. 2012).

Reoviridae

The possible presence of Reoviridae-like viral particles in fungi was first suggested in 1994 (Enebak et al. 1994). In this family, all members of the genus Mycoreovirus are known to infect fungi. Currently, three species have been identified: Mycoreovirus 1, Mycoreovirus 2, and Mycoreovirus 3, which correspond to isolates MyRV1, MyRV2, and MyRV3, respectively. While MyRV1 and MyRV2 were isolated from *Cryphonectria parasitica*, MyRV3 was obtained from *Rosellinia necatrix* (Hillman and Suzuki 2004, Wei et al. 2004). These mycoreoviruses exhibit distinct genomic organizations: MyRV1 and MyRV2 have 11 genomic segments ranging in size from 0.7 to 4.1 kilobases, while MyRV3 consists of 12 genomic segments (Kanematsu et al. 2004, Supyani et al. 2007) (Fig. 1).

Orthototiviridae

The family *Orthototiviridae* was registered in the ICTV in 2024. This new taxonomic group includes viruses that were previously classified under the obsolete family *Totiviridae*. The family *Orthototiviridae* consists of viruses that contain dsRNA genomes. Currently, the family includes one fungal infecting genus, *Totivirus*. (ICTV 2024). These viruses have the following: unsegmented bicistronic genomes (Fig. 1), single RNA fragments ranging from 4.6 to 7.0 kbps in length, two major and partially overlapping open reading frames (ORFs) on a single strand (Stielow and Menzel 2010, Baeza et al. 2012, Taylor et al. 2013). Genomic organization features: 5'-proximal ORF, CP, and 3'-proximal ORF, RdRp. *Totiviruses* have been identified in a wide range of fungal hosts and are the first mycoviruses to be recorded in ectomycorrhizal fungi. Notable examples include infection in the yeasts *Saccharomyces cerevisiae*, *Scheffersomyces segobiensis*, and *Xanthophyllomyces dendrorhous* (*Ascomycetes*), the black fungus *Ustilago maydis* (*Basidiomycetes*), and the subterranean fungus Tuber aestivum (summer black fungus) (Stielow and Menzel 2010, Baeza et al. 2012, Taylor et al. 2013). Table 3 summarizes the major examples of dsRNA mycoviruses and their host-related effects.

MYCOVIRUSES WITH SINGLE-STRANDED RNA (ssRNA)

Single-stranded RNA (ssRNA) mycoviruses comprise three major categories: positive-sense single-stranded RNA viruses (+) ssRNA, negative-sense ssRNA viruses (-) ssRNA and single-stranded RNA-RT (ssRNA-Reverse Transcriptase) viruses (Buck 1996, Dreher 1999, Gale et al. 2000). Positive-sense ssRNA viruses, classified as Class IV viruses, have genomes that act directly as messenger RNA (mRNA) and can be instantly translated into viral proteins by the host's ribosomes. Conversely, negative-sense single-stranded RNA (-) ssRNA viruses (Class V) possess genomes that function as complementary strands, necessitating initial mRNA synthesis by the viral RdRp before translation. During replication, the RdRp produces a positive-sense antigenome that subsequently serves as a template for generating genomic negative-sense RNA (Buck 1996, Dreher 1999, Gale et al. 2000). The ssRNA-RT viruses belong to Class VI.

Positive-sense single-stranded RNA (+)ssRNA mycoviruses

The positive-sense ssRNA (+) ssRNA mycoviruses encompass multiple viral families, including: *Alphaflexiviridae*, *Barnaviridae*, *Botourmiaviridae*, *Deltaflexiviridae*, *Endornaviridae*, *Gamaflexiviridae*, *Hypoviridae*, *Mitoviridae*, *Narnaviridae*. (Table 1). These mycoviruses utilize a distinctive replication strategy involving: synthesis of a negative-sense antigenome during replication, subsequent use of this antigenome as a template to generate new positive-sense viral genome (+) ssRNA viruses utilize a distinctive replication strategy involving synthesis of a negative-sense antigenome during replication, subsequent use of this antigenome as a template to generate new positive-sense viral genomes (Valverde et al. 2019, Ma et al. 2022).

Table 3. List of mycovirus families identified in *Ascomycota* with dsRNA genomes and their effects on their host.

Fungi Class	Fungi Family	Mycovirus Family	Genus	Sample member	Effect of the virus on its host
Dothideomycetes	*Botryosphaeriaceae*	*Chrysoviridae*	*Betachrysovirus*	*Botryosphaeria dothidea chrysovirus* (BdCV1)	hypovirulence
	Massarinaceae	*Totiviridae*	*Victorivirus*	*Helminthosporium victoriae* 190SV(Hv190SV)	hypovirulence
	Pleosporaceae	*Curvulaviridae*	*Orthocurvulavirus*	*Curvularia orthocurvulavirus* 1 (CThTV)	temperature tolerance
		Unassigned	Unassigned	*Alternaria alternata* virus 1 (AaV-1)	hypovirulence
Eurotiomycetes	*Aspergillaceae*	*Chrysoviridae*	*Alphachrysovirus*	*Penicillium chrysogenum* virus (PcV)	hypovirulence
		Partitiviridae	*Gammapartitivirus*	*Penicillium stoloniferum* virus S (PsV-S)	hypovirulence
		Polymycoviridae	*Polymycovirus*	*Aspergillus fumigatus polymycovirus* 1 (AfuTmV1)	No significant effect
Saccharomycetes	*Saccharomycetaceae*	*Amalgaviridae*	*Zybavirus*	*Zygosaccharomyces bailii* virus Z (ZbV-Z)	Killing the host by producing zygosine toxin
		Totiviridae	*Totivirus*	*Saccharomyces cerevisiae* virus L-A (ScV-L-)A	hypervirulence
Sordariomycetes	*Clavicipitaceae*	*Partitiviridae*	*Betapartitivirus*	*Atkinsonella hypoxylon* virus (AhV)	unkhnown
		Unassigned	Unassigned	*Ustilaginoidea virens* RNA virus M (UvRVM)	hypovirulence
	Cryphonectriaceae	*Reoviridae*	*Mycoreovirus*	*Cryphonectria parasitica Mycoreovirus* 1 (MyRV1)	hypovirulence
	Hypocreaceae	Unassigned	Unassigned	*Fusarium virguiliforme* dsRNA *mycovirus* 1 (FvV1)	hypovirulence
	Xylariaceae	*Megabirnaviridae*	*Megabirnavirus*	*Rosellinia necatrix megabirnavirus* 1 (RnMBV1)	hypovirulence
		Partitiviridae	*Alphapartitivirus*	*Rosellinia necatrix partitivirus* 2 (RnPV2)	No effect on pathogenicity
		Quadriviridae	*Quadrivirus*	*Rosellinia necatrix quadrivirus* 1 (RnQV1)	hypervirulence
		Unassigned	Unassigned	*Rosellinia necatrix* Yado-nushi virus (YnV1)	growth defect
		Unassigned	Unassigned	*Rosellinia necatrix megatotivirus* 1 (RnMTV1)	hypovirulence

The positive-sense ssRNA mycoviruses predominantly possess unsegmented genomes, with the notable exception of hadakaviruses—unclassified viral members identified in *Fusarium oxysporum* that exhibit 10–11 genomic segments (Sato et al. 2023). While most (+) ssRNA mycoviruses replicate in the host cytoplasm, members of the *Mitoviridae* family demonstrate unique mitochondrial localization for their replication (Ma et al. 2022). All (+) ssRNA mycoviruses share the defining characteristic of encoding an RdRp domain. The taxonomic distribution of these viruses reveals: The taxonomic distribution of these mycoviruses across fungal lineages, as summarized by Bianca et al. (2023), is as follows: they have been identified in *Ascomycota* across all its classes except *Saccharomyces*, whereas in *Basidiomycota*, their presence is currently documented only within the class *Agaricomycetes*. These viruses are absent in the phyla *Blastocladiomycota* and *Chytridiomycota*. However, they are present in several lineages of mycorrhizal and other fungi, including *Glomeromycetes*, *Neocalymastigomycetes*, *Entomophthoromycetes*, *Kickxellomycetes*, and *Zoopagomycetes*. The +ssRNA families (Table 2) are further described below:

Alphaflexiviridae

The *Alphaflexiviridae* family comprises viruses with (+) ssRNA genomes. To date, only one genus within this family, *Botrexvirus*, has been identified as a mycovirus. The sole characterized member of this genus is *Botrytis virus X*, which infects the plant pathogenic fungus *Botrytis cinerea* (Howitt et al. 2001, Pearson and Bailey 2013). This virus possesses several distinctive genomic features including: 7.0 kb positive-sense, linear RNA genome without capsid coverage (Fig. 1) and: five ORFs with the following functions: ORF1: encodes a large multifunctional protein containing methyltransferase, helicase, and RdRp domains, ORF3 encodes the sole structural protein (capsid protein, CP), ORF2, ORF4, and ORF5: encode proteins of unknown function (Howitt et al. 2001).

Barnaviridae

The *Barnaviridae* family consists of viruses with (+) ssRNA genomes. Currently, only one genus (*Barnavirus*) is recognized within this family, containing a single known species: *Mushroom bacilliform virus* (MBV). This virus infects the common button mushroom (*Agaricus bisporus*) and has been associated with La France disease (Revill 2011). Key features of MBV include: bacilliform-shaped virions containing a single linear 4.0 kbp (+) ssRNA molecule (Fig. 1). A genomic organization comprising: four major and three minor ORFs, ORF2: contains putative serine protease motifs with chymotrypsin-like activity, ORF3: encodes a putative RdRp, ORF4: encodes the CP, ORFs 1, 5, 6, and 7: encode hypothetical polypeptides with no known homologs. The virus is transmitted horizontally via mycelial contact and may be transmitted vertically through basidiospores (Revill 2011).

Botourmiaviridae

The *Botourmiaviridae* family comprises viruses with (+) ssRNA genomes. This family includes five genera: *Botoulivirus*, *Magoulivirus*, *Ourmiavirus*, *Rhizoulivirus*, and *Scleroulivirus*. These viruses possess several distinctive features: small genomes ranging from 2,900 to 4,800 nucleotides and bacilliform-shaped virions containing three genomic segments (Fig. 1). Segments encoding: CP, Movement protein (MP), RdRp (Silva et al. 2022). Notably, these genomes encode only one RdRp and lack structural proteins. A representative member of this family, *Magnaporthe oryzae botourmiavirus 2* (MOBV2), was isolated from the fungus *Magnaporthe grisea* (Liu et al. 2020).

Deltaflexiviridae

The *Deltaflexiviridae* family is defined by its possession of linear, (+) ssRNA genomes, with filamentous virions ranging from 6 to 9 kb in size (Fig. 1). Currently, this family contains a single genus, *Deltaflexivirus*. A representative member, *Sclerotinia sclerotiorum deltaflexivirus 1* (SsDFV1), was identified from the fungal host *Sclerotinia sclerotiorum* (Li et al. 2015). Key genomic features include: 4-5 ORFs encoding RdRP, CP, multiple proteins involved in viral cell-to-cell movement, likely 5' cap structure, 3’ terminus (Li et al. 2015).

Endornaviridae

The *Endornaviridae* family comprises viruses with a linear, (+) ssRNA genome. This family contains two genera: *Alphaendornavirus* infects plants and *oomycetes* (including *Phytophthora* species), *Betaendornavirus*: infects *ascomycete* fungi (including *Sclerotinia* species) (Valverde et al. 2019). Key genomic features include: large genome size ranging from ~14 kb to 17.6 kb, lack of a CP gene, resulting in: absence of true virions, encapsulation within host-derived lipid vesicles (Fig. 1). A single ORF encoding a polyprotein (3217–5825 amino acids), potential proteinase(s) for polyprotein cleavage into functional units (Gibbs et al. 2011, Stielow et al. 2011, Fukuhara and Gibbs 2012).

Gammaflexiviridae

The *Gammaflexiviridae* family consists of viruses characterized by flexible, filamentous particles and a single-segment, linear (+) ssRNA genome of 6.8 kb (Fig. 1). The family includes three genera, *Gammaflexivirus*, *Xylavirus*, and *Mycoflexivirus*, which infect fungi (ICTV, 2025). The index species, *Botrytis* virus F (BVF), serves as the prototype of this genus (Howitt et al. 2001, Pearson and Bailey 2013). The genomic organization includes two ORFs: ORF1 encodes a replicase and ORF2: encodes a CP (Howitt et al. 2001, Svanella-Dumas et al. 2018).

Hypoviridae

The *Hypoviridae* family represents one of the viral families containing (+) ssRNA genome. The family *Hypoviridae* includes eight genera (*Alphahypovirus*, *Betahypovirus*, *Gammahypovirus*, *Deltahypovirus*, *Epsilonhypovirus*, *Zetahypovirus*, *Tetahypovirus*, *Atahypovirus*) and 39 species (Chiba et al. 2023). *Cryphonectria hypoviruses* 1 to 4 (CHV1-CHV4) (Nuss and Hillman 2011). Key characteristics of *hypoviruses* include: absence of a CP gene, resulting in lack of true virion formation, and encapsulation within polymorphic host-derived lipid vesicles (Fig. 1). Relatively large genomes ranging from 9 to 13 kb in length. Two ORFs, each containing an autocleaving papain-like protease domain (Suzuki et al. 2018).

Mitoviridae

The *Mitoviridae* family possesses a linear, unsegmented (+) ssRNA genome. This family contains a single genus, *Mitovirus*, whose members exclusively inhabit host mitochondria (Ghabrial and Suzuki 2009, Hillman and Esteban 2011). Key features of *mitoviruses* include: absence of true virions, lack of structural proteins or CP (Fig. 1). Unencapsidated genomes consisting of: the genetic structure contains one ORF that produces RdRp essential for replication (Hillman and Esteban 2011). *Mitoviruses* are recognized as the most basic independently replicating viruses currently identified. (Hillman and Esteban 2011).

Narnaviridae

Members of the *Narnaviridae* family possess the simplest known viral genomes among independently replicating RNAs. These viruses exhibit several distinctive characteristics: lack of true virions, absence of structural proteins or CP (Dolja and Koonin 2012). (Fig. 1) small linear RNA genomes (2.3–3.6 kbp) containing a single ORF encoding RdRp (Hillman and Cai 2013, Wickner et al. 2013). The family includes the genus *Narnavirus*, whose members are exclusively found in the cytosol of their hosts, including species inhabiting the yeast *Saccharomyces cerevisiae* (ICTV, 2021). For significant examples of (+) ssRNA mycoviruses and their host-related effects, see Table 4.

Table 4. List of mycovirus families identified in *Ascomycota* with +ssRNA genomes and their effects on their host.

Fungi Class	Fungi Family	Mycovirus Family	Genus	Sample member	Effect of the virus on its host
Leotiomycetes	*Sclerotiniaceae*	*Alphaflexiviridae*	*Botrexvirus*	*Botrytis virus* X (BotVX)	hypovirulence
		Botourmiaviridae	*Botoulivirus*	*Botrytis botoulivirus* (BOLV)	No significant effect
			Scleroulivirus	*Sclerotinia scleroulivirus* 1 (SsOLV1)	hypovirulence
		Deltaflexiviridae	*Deltaffexivirus*	*Sclerotinia sclerotiorum deltaffexivirus* 1 (SsDFV1)	hypovirulence
		Endornaviridae	*Betaendornavirus*	*Sclerotinia sclerotiorum betaendornavirus* 1 (SsEV1)	No significant effect
		Gammaflexiviridae	*Mycoflexivirus*	*Botrytis* virus F (BVF)	hypovirulence
		Narnaviridae	*Sclerodarnavirus*	*Sclerotinia sclerotiorum* RNA virus (SsDRV)	hypovirulence
Saccharomycetes	*Saccharomycetaceae*	*Narnaviridae*	*Narnavirus*	*Saccharomyces 20S narnavirus* (ScNV-20S)	Reduced sporulation
Sordariomycetes	*Cryphonectriaceae*	*Hypoviridae*	*Hypovirus*	*Cryphonectria hypovirus* 1 (CHV1)	hypovirulence
		Mitoviridae	*Mitovirus*	*Cryphonectria mitovirus* 1 (CpMV1)	hypovirulence
	Diaporthaceae	Unassigned	Unassigned	*Diaporthe* RNA virus (DRV)	hypovirulence
	Hypocreaceae	*Mitoviridae*	*Mitovirus*	*Fusarium circinatum*	Reducing the probability of survival of seedlings
		Unassigned	Unassigned	*Fusarium graminearum* virus DK21 (FgV/ DK21)	hypovirulence
		Unassigned	Unassigned	*Fusarium oxysporum* Hadaka virus 1 (HadV1)	no effect
	Magnaporthaceae	*Botourmiaviridae*	*Magoulivirus*	*Magnaporthe magoulivirus* 1 (MOLV1)	unknown
	Togniniaceae	*Botourmiaviridae*	*Penoulivirus*	*Phaeoacremonium penoulivirus* (PmOLV1)	unknown
Agaricomycetes	*Ceratobasidiaceae*	*Botourmiaviridae*	*Rhizoulivirus*	*Rhizoctonia rhizoulivirus* (RsOLV1)	unknown
		Barnaviridae	*Barnavirus*	Mushroom bacilliform virus (MBV)	unknown
		Unassigned	Unassigned	Oyster mushroom spherical virus (OMSV)	Decreased mycelial growth, abnormality in the fruiting organ, and reduced yield

Single-stranded RNA (-) mycoviruses with negative sense

Negative-sense single-stranded RNA viruses represent a distinct class of viruses whose genomes function as complementary strands. During replication, the viral RdRp produces a positive-sense antigenome, which serves as a template for generating genomic negative-sense RNA. These viruses exhibit several characteristic features: Filamentous, enveloped virions, linear genomes encoding multiple proteins, including RdRp and nucleoprotein (NP) (Hao et al. 2018, Jiang et al. 2019, Linnakoski et al. 2021, Wang et al. 2022). The taxonomic distribution of (-)ssRNA mycoviruses includes: *Ascomycetes*: *Dothideomycetes*, *Eurotiomycetes*, *Sordariomycetes*, *Leotiomycetes*. *Basidiomycetes*: *Agaricomycetes*. Other fungal groups: *Mortierellomycetes*, *Mucoromycetes* (Bianca Hough et al. 2023). The two known families of negative-sense ssRNA mycoviruses are as follows:

Mymonaviridae

The *Mymonaviridae* family comprises viruses generating filamentous, enveloped virions that encapsulate a single linear negative-sense RNA molecule measuring roughly 10 kbp. (Fig. 1). These virions range from 200 to 2000 nm in size. Key features of this family include: nine genera (*Auricularimonavirus*, *Botrytimonavirus*, *Hubramonavirus*, *Lentimonavirus*, *Penicillimonavirus*, *Phyllomonavirus*, *Plasmopamonavirus*, *Rhizomonavirus* and *Sclerotimonavirus*) and 61 species. (Jiāng et al. 2022, Biana et al. 2023). Primary hosts are filamentous fungi. Genomic organization contains 1-7 ORFs. All members encode an RdRp near the 3' end, some encode a nucleoprotein (NP) near the 5' end, and may include additional ORFs encoding putative proteins of unknown function (Biana et al. 2023). Current evidence suggests that *Mymonaviridae* replicate in the host cell's cytoplasm (Jiang et al. 2019).

Phenuiviridae

The *Phenuiviridae* family represents a group of (-) ssRNA viruses with genomes ranging from 8.1 to 25.1 kb in length (Sasaya et al. 2023). These viruses exhibit diverse virion morphologies: The viral particles are enveloped and exhibit spherical or pleomorphic morphology (80-120 nm in diameter), containing a helical nucleocapsid and a lipid bilayer envelope. Additionally, non-enveloped filamentous variants have been documented. (Yu-Hsin et al. 2019). Among the 22 genera in this family, two infect fungi: *Entovirus*: virion morphology unknown (predicted to be filamentous and uncoated; Fig. 1), genome organization: RNA1: encodes large (L) protein (putative RdRp), RNA2: encodes nucleocapsid (N) protein and putative eMPe, three total genes encoding: two structural proteins (L and N), one non-structural protein (likely MP for cell-to-cell movement in plants)(Sasaya et al. 2023). *Lentinuvirus*: Includes *Lentinula edodes negative-strand RNA virus 2* (LeNSRV-2). First reported (-) ssRNA virus infecting mushrooms (*Lentinula edodes*)(Lin et al. 2019). For significant examples of (-) ssRNA mycoviruses and their host-related effects, see Table 5.

Reverse transcription single-stranded RNA (ssRNA-RT) mycoviruses

In addition to conventional ssRNA and dsRNA mycoviruses, fungal genomes also harbor reverse-transcribing RNA elements historically classified as *Pseudoviruses*. These elements are now recognized as retrotransposons rather than true viruses (Bianca et al. 2023). Current research has identified these viral-like retrotransposons primarily in *Ascomycota*, including members of the *Saccharomycetes* class (Bianca et al. 2023). The retrotranscribing elements comprise two main families: *Metaviridae* and *Pseudoviridae* (Boeke et al. 2011, Eickbush et al. 2011).

These families exhibit distinct genomic features: genome size: *Metaviridae*: 3-15 kb, *Pseudoviridae*: typically shorter (4-9 kb) (Llorens et al. 2020, 2021). Genomic structure: both families possess circular, single-segmented genomes (Figure 1), long terminal repeat (LTR) sequences flanking an intergenic region, likely encoding two core genes (gag and pol). Key difference: *Metaviridae*: single ORF encoding both Gag and Pol proteins, *Pseudoviridae*: may encode Gag and Pol in separate ORFs (Llorens et al. 2020, 2021). Replication mechanism: reverse transcription occurs within intracellular virus-like particles (VLPs), produces complementary DNA (cDNA), and integrase-mediated insertion into host chromosomes (Llorens et al. 2020, 2021). A representative example is *Saccharomyces* spp., which harbor single-stranded RNA-RT (ssRNA-RT) genomes. Notable examples of single-stranded RNA reverse-transcribing (ssRNA-RT) mycoviruses and their associated host effects are presented in Table 6.

Table 5. List of mycovirus families with (-)ssRNA genomes and their effects on their host.

Fungi phylum	Fungi Class	Fungi Family	Mycovirus Family	Genus	Sample member	Effect of the virus on its host
Ascomycota	*Eurotiomycetes*	*Aspergillaceae*	*Mymonaviridae*	*Penicillimonavirus*	*Penicillimonavirus alphapenicillii* (PdNSRV-1)	unknown
	Leotiomycetes	*Sclerotiniaceae*	*Mymonaviridae*	*Botrytimonavirus*	*Botrytimonavirus botrytidis* (BcNSRV-7)	unknown
				Sclerotimonavirus	*Sclerotinia sclerotiorum* 1 (SsNSRV-1)	hypovirulence
	Sordariomycetes	*Hypocreaceae*	Unassigned	Unassigned	*Fusarium poae* negativestranded RNA virus 1 (FpNSV-1)	hypovirulence
		Xylariaceae	*Phenuiviridae*	*Entovirus*	*Entoleuca entovirus* (EnPLV-1)	unknown
Basidiomycota	*Agaricomycetes*	*Auriculariaceae*	*Mymonaviridae*	*Auricularimonavirus*	*Auricularimonavirus auriculariae* (AhNSRV-1)	unknown
		Omphalotaceae	*Mymonaviridae*	*Lentimonavirus*	*Lentinula lentmonavirus* (LeNSRV-1)	unknown
			Phenuiviridae	*Lentinuvirus*	*Lentinula lentinuvirus* (LeNSRV-2)	unknown

Table 6. Two mycovirus families identified in *Ascomycota* with (ssRNA-RT) genomes.

Fungi Class	Fungi Family	Mycovirus Family	Genus	Sample member	Effect of virus on its host	Accession number
Saccharomycetes	*Saccharomycetaceae*	*Metaviridae*	*Metavirus*	*Saccharomyces cerevisiae* Ty3 virus (SceTy3V)	unknown	M34549
		Pseudoviridae	*Pseudovirus*	*Saccharomyces cerevisiae* Ty1 virus (SceTy1V)	unknown	M18706
			Hemivirus	*Saccharomyces cerevisiae* Ty5 virus (SceTy5V)	unknown	U19263

SINGLE-STRANDED DNA (ssDNA) VIRUSES

The DNA mycoviruses possess small genomes, with initial discoveries limited to plant and vertebrate hosts prior to the isolation of mycoviral DNA from *Sclerotinia sclerotiorum*. Currently, *Genomoviridae* represents the sole recognized family of ssDNA mycoviruses (Yu et al. 2010).

Genomoviridae

Currently, *Genomoviridae* represents the sole recognized family of ssDNA mycoviruses. Members of this family are characterized by icosahedral virions and small circular ssDNA genomes (1.8–2.4 kb; Figure 1) (Krupovic et al. 2016). The family comprises two genera that infect plant-pathogenic fungi: *Gemytripvirus*: includes *Fusarium graminearum gemytripvirus 1* (FgGMTV1) and *Gemycircularvirus*: includes *Sclerotinia sclerotiorum hypovirulence-associated DNA virus 1* (SsHADV-1) (Li et al. 2010, Yu et al. 2010).

The *Gemycircularvirus* genome consists of a single circular ssDNA segment (~1.8-2.4 kb), two genes arranged in ambisense orientation: rolling circle replication initiation protein (REP), CP, (Li et al 2020, Varsani and Krupovic 2021). In contrast, the *Gemytripvirus* genome comprises three distinct segments (~1.3 kb each): DNA-A encodes REP protein, DNA-B encodes CP, DNA-C encodes p26 (protein of unknown function) (Li et al 2020, Varsani and Krupovic 2021). Evolutionary analyses reveal: REP proteins show homology with other eukaryotic ssDNA viruses, plant-infecting *Geminiviridae* (constituting a sister clade in phylogenetic analyses), and CP sequences are distinct from other known viral CPs (Kazlauskas et al. 2017, 2018). These ssDNA viruses have been identified in: *Ascomycota: Dothideomycetes*, *Leotiomycetes*, *Sordariomycetes*. Mycorrhizal fungi: *Glomeromycetes*, *Mucoromycetes* (Bianca et al. 2023). Table 7 provides a comprehensive summary of significant single-stranded DNA (ssDNA) mycoviruses.

Table 7. Mycovirus families identified in *Ascomycota* with ssDNA genomes and their effects on their host (Bianca et al. 2023).

Fungi Class	Fungi Family	Mycovirus Family	Genus	Sample member	Effect of the virus on its host	Accession number
Leotiomycetes	*Sclerotiniaceae*	*Genomoviridae*	*Gemicirculavirus*	*Sclerotinia sclerotiorum* hypovirulence -associated DNA virus 1 (SsHDV1)	hypovirulence	GQ365709
Sordariomycetes	*Hypocreaceae*		*Gemytripvirus*	*Fusarium graminearum Gemytripvirus* fungal (FgGMTV1)	hypovirulence	MK430076

FEATURES OF MYCOVIRUSES

Mycoviruses, or fungal viruses, predominantly possess genomes composed of ribonucleic acid (RNA). These RNA genomes are categorized into three main types based on their structure: double-stranded RNA (dsRNA), positive-sense single-stranded RNA (+ssRNA), and negative-sense single-stranded RNA (–ssRNA), each associated with distinct replication mechanisms within the fungal cell. While this RNA-based genomic architecture is typical for intracellular fungal pathogens, the known diversity has recently broadened with the identification of mycoviruses containing circular, single-stranded DNA (ssDNA) genomes. Phylogenetic analysis places these novel ssDNA mycoviruses within the same evolutionary clade as plant viruses from the *Geminiviridae* family. This genetic relationship points toward possible historical events of viral transmission across kingdom boundaries, potentially mediated by close ecological interactions between fungi and plants, such as endophytic colonization or pathogenic relationships (Kazlauskas et al. 2017, 2018).

In the field of mycovirology, the detection and analysis of dsRNA molecules serve as a fundamental, non-targeted discovery method. For many RNA mycoviruses, dsRNA forms a stable, double-stranded replication intermediate. This structural stability confers resistance against degradation by host cellular enzymes, facilitating its extraction and identification from even small quantities of fungal material. Consequently, dsRNA profiling continues to be a powerful initial approach for uncovering previously unknown viruses (Dodds et al. 1984, Mu et al. 2018). From a structural virology perspective, mycoviruses frequently display conserved organizational principles. Notably, the capsid designs and core replication complexes of dsRNA mycoviruses show significant similarities to those found in dsRNA viruses that infect a wide range of other eukaryotic hosts. These shared features suggest ancient evolutionary links and possible common origins among these virus groups (Cheng et al. 1994, Kotta-Loizou 2021).

A key ecological trait of mycoviruses is the absence of a free, extracellular phase in their life cycle. Their spread is primarily dependent on the growth and reproductive mechanisms of their fungal host. Horizontal transmission occurs through hyphal anastomosis, the cytoplasmic fusion of compatible fungal filaments, allowing the virus to spread within a colony or between individuals. Vertical transmission takes place when the virus is incorporated into fungal spores, both sexual and asexual, thereby passing the infection to subsequent generations (Pearson et al. 2009, Xie and Jiang 2014). Importantly, no natural biological vectors, such as insects or nematodes, are known to transmit mycoviruses, limiting their dissemination to host-mediated processes.

Recent advances in genomics have illuminated the sophisticated molecular strategies mycoviruses employ to adapt to their fungal hosts. One significant adaptation involves organelle-specific localization. Certain mycoviruses, exemplified by many in the family *Mitoviridae*, have evolved to replicate exclusively within the host's mitochondria. To achieve this, they utilize the mitochondrial genetic code and often encode mitochondrial targeting signals, demonstrating a high degree of specialization to this cellular compartment (Nibert 2017, Larios et al. 2023). Furthermore, to optimize the expression of their proteins from often compact genomes, mycoviruses deploy complex genetic coding strategies. These include ribosomal frameshifting, leaky scanning during translation initiation, and the generation of subgenomic messenger RNAs, all of which allow for the production of multiple proteins from overlapping reading frames (Ghabrial et al. 2015, Larios et al. 2023). Collectively, these genomic adaptations increase viral fitness by enabling efficient replication, avoiding host immune recognition, and ensuring persistent, long-term infection.

Reflecting their transmission modes, the entire replication cycle of most mycoviruses is completed within the host cell's cytoplasm, without any requirement for entry into the nucleus (Luque et al. 2018, Bian et al. 2020, Hantula et al. 2020). This strictly intracellular, non-lytic lifestyle, combined with direct cell-to-cell spread, characterizes a symbiotic-like association between the virus and its fungal host. The phenotypic consequences of this association exist on a broad spectrum. Many infections are latent, causing no observable change to the host. Others can be mutualistic, potentially enhancing the host's virulence (hypervirulence) or tolerance to environmental stresses. Conversely, some mycoviruses have a parasitic effect, reducing host growth, sporulation, or pathogenic ability—a phenomenon termed hypovirulence (Nuss 2005, Vainio et al. 2017, Ninomiya et al. 2020). Deciphering the molecular basis of these diverse outcomes is a central research objective, particularly for harnessing mycoviruses as biocontrol agents against economically damaging plant-pathogenic fungi.

Mycoviruses as hypervirulence agents with increased pathogenicity

The relationship between mycoviruses and their fungal hosts extends beyond mere persistence, significantly influencing the pathogenic profile of the fungus. While viral infection often attenuates fungal virulence, a state termed hypovirulence that is valuable for biological control, a compelling body of evidence reveals that mycoviruses can also act as hypervirulence factors, enhancing the aggressiveness and ecological success of their hosts (Chiba et al. 2013). This duality underscores the complex, context-dependent nature of fungal-viral symbioses.

A seminal example of hypervirulence is illustrated by the "killer" phenotype in *Saccharomyces cerevisiae*. This trait is facilitated by a persistent infection with the dsRNA virus ScV-L-A and associated satellite M dsRNAs. The viral machinery orchestrates the production and secretion of potent proteinaceous toxins that are lethal to competing, virus-free microbial strains. Crucially, the infected host yeast is immune to its own toxin. This viral-endowed capability provides a direct competitive advantage in mixed microbial communities, fundamentally altering the ecological dynamics in favor of the infected fungus (Lukša et al. 2017).

In phytopathogenic fungi, mycovirus-induced hypervirulence can involve sophisticated manipulation of the host's metabolic pathways. Research on the rice blast fungus *Magnaporthe oryzae* has shown that infection by a specific *totivirus* can trigger host epigenetic reprogramming. This leads to the increased expression of genes responsible for synthesizing tenuazonic acid, a major virulence-associated mycotoxin. The virus, therefore, acts as an epigenetic regulator, enhancing the fungus's destructive potential (Ninomiya et al. 2020). Similarly, infection by *Rosellinia necatrix quadrivirus* 1 in the white root rot fungus correlates with markedly accelerated mycelial growth and altered morphology, traits that likely promote more rapid host colonization and disease progression (Shah et al. 2018, Picarelli et al. 2019).

The phenomenon also extends to fungi used for biological control. In the entomopathogenic fungus *Beauveria bassiana*, infection by certain viruses, such as BbPmV-1 and BbVV-1, has been associated with increased virulence against insect pests. This suggests that resident mycoviruses can be intrinsic components of a biocontrol agent's efficacy, potentially augmenting its killing power (Filippou et al. 2018). Recent studies in other systems, like the human pathogen *Aspergillus fumigatus*, have identified mycoviruses that upregulate host genes involved in stress response and secondary metabolism, further supporting a model where viral infection fine-tunes host physiology for increased robustness and pathogenicity (Khan et al. 2023).

The evolutionary drivers for hypervirulence are thought to be aligned with viral persistence. A virus that enhances its host's fitness—whether through improved competition, resource acquisition, or survival under stress—secures its own replicative niche and long-term propagation.

In conclusion, mycoviruses are potent, though often overlooked, modulators of fungal ecology and pathogenicity. Their capacity to induce hypervirulence adds a critical layer of complexity to understanding fungal diseases in agriculture, medicine, and natural ecosystems. Recognizing this potential is essential for risk assessment in biocontrol applications and opens novel avenues for research into leveraging viral-fungal partnerships for industrial or therapeutic purposes.

Mycoviruses as biocontrol agents

The capacity of mycoviruses to attenuate the virulence of their fungal hosts, a phenomenon termed hypovirulence, has established them as promising candidates for biological control of plant and forest diseases. This approach leverages natural viral-fungal interactions to manage pathogens in an environmentally sustainable manner (Pandey et al. 2018).

The foundational success story in this field is the management of chestnut blight in Europe. The disease, caused by the ascomycete *Cryphonectria parasitica*, was mitigated by the spread of a hypovirulence-conferring mycovirus (CHV1, family *Hypoviridae*). This virus reduces fungal sporulation, canker formation, and overall pathogenicity. Its successful application demonstrated the principle that mycoviruses could be harnessed for natural disease suppression (Heiniger and Rigling 1994). Subsequent research has identified other potent hypovirulence agents. A groundbreaking example is *Sclerotinia sclerotiorum* hypovirulence-associated DNA virus 1 (SsHADV-1), a single-stranded DNA mycovirus. It not only severely attenuates the virulence of *S. sclerotiorum*, a devastating necrotrophic pathogen, but also converts it into a beneficial endophyte. Mechanistically, SsHADV-1 silences key fungal pathogenicity genes. Field trials have shown that application of the virus-infected fungal strain during canola flowering can enhance plant defense responses, improve growth, and significantly reduce stem rot incidence while increasing yield (Wang et al. 2016, Lyu et al. 2018, Qu et al. 2020). A similar strategy using a hypovirulent strain of *Fusarium graminearum*, infected with the mycovirus FgV1, achieved substantial reductions in *Fusarium* head blight severity and mycotoxin contamination in wheat, accompanied by a measurable yield increase (Tian et al. 2020).

In forest pathology, mycoviruses offer hope for managing root rot diseases. For instance, diverse *partitiviruses* (family *Partitiviridae*) have been found to induce hypovirulence in various species of *Heterobasidion*, major pathogens of conifers. These viruses reduce mycelial growth and decay capacity in infected fungi, showing potential for in-situ biological control (Vainio et al. 2017, Kashif et al. 2019). Similarly, *Rosellinia necatrix* partitivirus 2 has been shown to diminish the virulence of the white root rot fungus, offering another model system (Zheng et al. 2014).

Beyond plant pathogens, mycoviruses are also being studied in medically relevant fungi. In the human pathogen *Aspergillus fumigatus*, infections with various mycoviruses (e.g., *chrysoviruses*, *partitiviruses*) can lead to significant phenotypic alterations, including reduced growth and altered stress responses, suggesting a broader applicability of hypovirulence concepts (Özkan et al. 2017).

Despite these successes, the deployment of mycoviruses as biocontrol agents faces challenges. Their transmission relies on hyphal contact, limiting spread. Host range is often narrow, and the stability of the hypovirulent trait must be ensured. Current research focuses on overcoming these hurdles through novel delivery systems, such as engineered fungal strains or lipid-based transfection of purified viral particles, and on deepening our understanding of the molecular mechanisms behind hypovirulence to design more robust strategies (Ghabrial et al. 2015, García-Pedrajas et al. 2019).

Mycoviruses as beneficial agents

A significant and emerging paradigm in fungal virology recognizes that many fungi, particularly those living as endophytes within plant tissues, harbor diverse mycoviruses that establish persistent, often latent infections. Far from being mere passengers, these viruses actively shape the biology of their fungal hosts. Through vertical transmission via spores, they become heritable genetic elements that can modulate key fungal phenotypes. These modifications include alterations in growth patterns, reproduction, stress tolerance, and critically, their pathogenic or mutualistic potential toward plant hosts (Roossinck 2011a, 2011b).

This viral-fungal symbiosis is especially prominent and ecologically significant in endophytic fungi. These fungi reside within plant tissues without causing immediate disease and are classified into functional groups (Classes I-IV) based on their life history, transmission mode, and ecological effects (Rodriguez et al. 2009). Research indicates that mycoviruses are common inhabitants of these endophytes, suggesting a stable, co-evolved relationship where the virus contributes to fungal fitness within the plant environment (Bao and Roossinck 2013, Roossinck 2014).

The presence of a mycovirus transforms a simple plant-fungus association into a complex tripartite interaction between the plant, the endophytic fungus, and the virus. The biology and evolutionary trajectory of all three partners are profoundly interconnected in this system (Márquez et al. 2007, Roossinck 2015). For instance, a mycovirus may attenuate the fungus's virulence, effectively converting a potential pathogen into a benign or even beneficial endophyte from the plant's perspective. Conversely, a virus might enhance fungal production of metabolites that boost plant growth or induce systemic resistance against other pathogens.

The functional roles these resident viruses play are diverse and are increasingly being uncovered (see Table 7 for specific examples). Documented effects include:

Enhanced Stress Tolerance: Some mycoviruses can increase the host fungus's resistance to abiotic stresses like heat or drought, which indirectly benefits the plant during environmental challenges.

Modulation of Secondary Metabolism: Viral infection can upregulate or downregulate the production of fungal alkaloids, hormones, or antimicrobial compounds, directly influencing the nature of the plant-fungal interaction. Regulation of Symbiotic Stability: By fine-tuning fungal growth and aggression, mycoviruses can help maintain the delicate balance of endophytism, preventing the fungal symbiont from tipping into a pathogenic state (Márquez et al. 2007).

The persistence of diverse viral genomes within fungal endophytes strongly implies they provide selective advantages, acting as malleable genetic elements that expand the functional repertoire of the fungal host. This interplay underscores that to fully understand plant health, microbiome ecology, and symbiotic evolution, one must consider the often-hidden yet influential role of the fungal virome (Márquez et al. 2007).

CONCLUSION

Two principal theories have been proposed to explain the genesis of mycoviruses (Pearson et al., 2009): the ancient coevolutionary hypothesis: proposes long-term coevolution between mycoviruses and fungal hosts, suggests mycoviruses originated through gradual adaptation, acknowledges their precise origins remain unknown and the plant virus hypothesis: posits relatively recent divergence from plant viruses, proposes initial mycoviruses were plant viruses that: crossed kingdom boundaries and Transmitted from plants to cohabitating fungi (Max et al. 2014).

Mycoviruses exhibit fascinating interactions when multiple viruses co-infect the same fungal host. Two notable examples demonstrate these complex relationships: in *Rosellinia necatrix*, certain viruses display mutual dependence, requiring each other's presence for successful replication in the fungal cytoplasm (Zhang et al. 2016). In *Cryphonectria parasitica*, co-infection by *Totivirus* and *Hypovirus* leads to activation of RNA silencing by the *Hypovirus* and *s*ubsequent disruption of *Totivirus* replication (Chiba and Suzuki 2015).

The study of mycoviruses presents unique challenges due to their frequent asymptomatic nature in fungal hosts (Abbas 2016). Despite this difficulty, research into mycovirus identification has gained momentum primarily because of their potential as biological control agents against fungal diseases through hypovirulence induction (García-Pedrajas et al. 2019). Key findings and applications include: mycoviruses represent a valuable resource for developing protection strategies for economically important plants, as demonstrated by multiple species capable of attenuating fungal phytopathogen virulence (Marzano et al. 2016). The first successful mycovirus-based fungal disease control method was developed in the 1980s using *Cryphonectria parasitica* spores, engineered hypovirulence-causing viruses for seedling protection (Dawe et al. 2004).

Transcriptomic comparisons between virus-free and virus-infected fungal strains have revealed fundamental aspects of fungal-viral interactions. Hypovirulent mycoviruses frequently alter fungal development by disrupting host signaling pathways (Dawe et al. 2004). Key findings include: in *Cryphonectria parasitica*, the CHV1 virus modifies expression of approximately 50% of affected genes, like deletions in G protein α or β subunits, and alters transcription factor (TF) gene expression, particularly targets of MAPK signaling that are crucial for development and mating (Drew et al. 2004), In addition, CHV1 induces epigenetic modifications by increasing DNA methylation in *C. parasitica*, exhibiting strain-specific effects on cytosine methylation across different fungal isolates, and correlating methylation levels with phenotypic severity (Nuskern et al. 2018). These findings suggest that CHV1-induced hypovirulence results from complex interactions between viral components and multiple host regulatory systems. Despite being ubiquitous in nature alongside their fungal hosts, mycoviruses present significant research challenges: single fungal isolates often harbor multiple asymptomatic viruses and ecological and biological roles remain largely enigmatic (Marzano et al. 2016, Zhang et al. 2016).

Vegetative incompatibility serves as a critical determinant of mycovirus transmission and natural dissemination. The availability of genomic sequences from various important plant-pathogenic fungi now enables the identification and characterization of vegetative incompatibility genes and potential manipulation of adaptive responses through these genetic factors. This approach has been successfully demonstrated in the chestnut blight fungus (*Cryphonectria parasitica*), where researchers have identified six distinct vegetative incompatibility loci (Choi et al. 2012, Zhang et al. 2014b).

The ssDNA mycovirus *SsHADV1*, which is phylogenetically related to *Geminiviruses*, shows promise as a novel biological fungicide. Its purified viral particles can directly infect fungal hyphae, inducing hypovirulence and reducing pathogenicity (Lyu et al. 2018, Zhang et al. 2020).

Vegetative compatibility groups (VCGs) exhibit remarkable diversity, reflecting how the fungal host's genetic composition primarily governs natural mycovirus transmission pathways (Jiang et al. 2013, Pearson and Bailey 2013). Key observations from CHV1, *Heterobasidion partitivirus 2, 3,* and *13* studies reveal enhanced transmission efficiency: higher rates occur in natural environments compared to laboratory conditions, more frequent transmission between conspecific isolates and environmental significance: external ecological factors substantially influence transmission dynamics (García-Pedrajas et al. 2019).

Comparative analyses reveal significant differences in gene expression between virus-free and mycovirus-infected fungal isolates (Abbas 2016). Key findings include: expression variation patterns distinct between virus-infected and uninfected fungi, differ among viruses from various taxonomic groups; host dependency mechanisms: mycoviruses utilize multiple cellular pathways, including cell migration processes, metabolic pathways, RNA processing systems, RNA-mediated signaling cascades, dependence on diverse host factors for replication and persistence (Abbas 2016).

FUTURE DIRECTIONS

Future studies should prioritize investigating the molecular mechanisms governing host-mycovirus interactions, with particular emphasis on: viral-mediated modifications of fungal host biology and the dual role of dsRNA viral genomes as both targets of antiviral RNA silencing pathways and activators of host defense systems. Additionally, insights from other host-pathogen systems suggest the importance of protein-protein interactions between viral and host components and viral manipulation of critical host cellular pathways.

Emerging bioinformatics approaches offer powerful tools to enhance mycovirus studies, including simulation of RdRp-Targeting Compounds**,** i.e., computational modeling of substances that modulate mycovirus proliferation by affecting RNA-dependent RNA polymerase (RdRP) activity, and design of vegetative incompatibility (VIC) gene suppressors, i.e., *in silico* strategies to develop inhibitors of VIC genes that facilitate cross-host mycovirus transmission studies. These methods can significantly advance research on mycovirus-host interactions across diverse fungal systems.

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AUTHOR CONTRIBUTION

J.S. conceived and designed the analyses. S.G collected the data, performed the analyses and wrote the first draft of the paper. A. P. contributed to data analyses and writing the paper. J.S. supervised the team, and proofread, revised and confirmed the paper editions.

DATA AVAILABILITY

All data used in the current study are available from the corresponding authors upon request.

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DECLARATION

The authors declare that there is no conflicts of interest.

ETHICAL APPROVAL

Not applicable.

REFERENCES

Abbas A. 2016. A review paper on mycoviruses. Journal of Plant Pathology and Microbiology. 7: 2157–7471. https://doi.org/10.4172/2157-7471.1000390.

Abbas A, Mustansar M, Qaiser Sh, … et al. 2022. History, taxonomy, scope, and challenges of research on mycoviruses in Pakistan. Journal of Phytopathology. 34(02): 361–368. https://doi.org/10.33866/phytopathol.034.02.0832.

Araldi-Brondolo SJ, Spraker J, Shaffer JP, … et al. 2017. Bacterial endosymbionts: master modulators of fungal phenotypes. Microbiology Spectrum. 5(5): FUNK-0056-2016. https://doi.org/10.1128/microbiolspec.FUNK-0056-2016.

Arora P, Riyaz-Ul-Hassan S. 2019. Endohyphal bacteria: the prokaryotic modulators of host fungal biology. Fungal Biology Reviews. 33: 72–81. https://doi.org/10.1016/j.fbr.2018.08.003.

Assenberg R, Delmas O, Morin B, … et al. 2010. Genomics and structure/function studies of *Rhabdoviridae* proteins involved in replication and transcription. Antiviral Research. 87: 149–161. https://doi.org/10.1016/j.antiviral.2010.02.322.

Baeza M, Bravo N, Sanhueza M, … et al. 2012. Molecular characterization of *Totiviruses* in *Xanthophyllomyces dendrorhous*. Journal of Virology. 9: 140. https://doi.org/10.1186/1743-422X-9-140.

Bao X, Roossinck MJ. 2013. Multiplexed interactions: viruses of endophytic fungi. Advances in Virus Research. 86: 37–57. https://doi.org/10.1016/B978-0-12-394315-6.00002-7.

Bekal S, Domier LL, Niblack TL, … et al. 2011. Discovery and initial analysis of novel viral genomes in the soybean cyst nematode. Journal of General Virology. 92: 1870–1879. https://doi.org/10.1099/vir.0.030585-0.

Berry E, Bevan EA. 1972. New species of double-stranded RNA from yeast. Nature. 239: 279–280. https://doi.org/10.1038/239279a0.

Bian R, Andika IB, Pang T, … et al. 2020. Facilitative and Synergistic Interactions between Fungal and Plant Viruses. Proceedings of the National Academy of Sciences of the United States of America. 117(7): 3779–3788. https://doi.org/10.1073/pnas.1915996117.

Bianca H, Emma S, Brenda W, … et al. 2023. Fungal Viruses Unveiled: A Comprehensive Review of Mycoviruses. Viruses. 15(5): 1202. https://doi.org/10.3390/v15051202.

Boeke JD, Eickbush T, Sandmeyer SB, … et al. 2011. Family *Pseudoviridae*. In: Virus Taxonomy (King AMQ, Adams MJ, Carstens EB, … et al., eds.): Ninth Report of the International Committee for the Taxonomy of Viruses. Elsevier Academic Press, USA. p. 467–476.

Brusini J, Robin C. 2013. Mycovirus transmission revisited by in situ pairings of vegetatively incompatible isolates of *Cryphonectria parasitica*. Journal of Virological Methods. 187(2): 435–442. https://doi.org/10.1016/j.jviromet.2012.11.025.

Buck KW, Kempson-Jones GF. 1970. Three Types of Virus Particles in *Penicillium stoloniferum*. Nature. 225: 945–946. https://doi.org/10.1038/225945a0.

Buck KW. 1986. Fungal virology: an overview. In: Fungal Virology. (Buck KW, ed): 1–84. CRC Press, USA.

Cheng RH, Castón JR, Wang GJ, … et al. 1994. Fungal virus capsids, cytoplasmic compartments for the replication of double-stranded RNA, formed as icosahedral shells of asymmetric Gag dimers. Journal of Molecular Biology. 244(3): 255–258. https://doi.org/10.1006/jmbi.1994.1726.

Chiba S, Lin YH, Kondo H, … et al. 2013a. Effects of Defective Interfering RNA on Symptom Induction by, and Replication of, a Novel *Partitivirus* from a Phytopathogenic Fungus, *Rosellinia necatrix*. Journal of Virology. 87(4): 2330–2341. https://doi.org/10.1128/JVI.02835-12.

Chiba S, Lin YH, Kondo H, … et al. 2013b. A novel *Victorivirus* from a phytopathogenic fungus, *Rosellinia necatrix*, is infectious as particles and targeted by RNA silencing. Journal of Virology. 87(12): 6727–6738. https://doi.org/10.1128/JVI.00323-13.

Chiba S, Castón JR, Ghabrial SA, … et al. 2018. ICTV Virus Taxonomy Profile: *Quadriviridae*. Journal of General Virology. 99(11): 1480–1481. https://doi.org/10.1099/jgv.0.001127.

Chiba S, Suzuki N. 2015. Highly activated RNA silencing via strong induction of dicer by one virus can interfere with the replication of an unrelated virus. Proceedings of the National Academy of Sciences of the United States of America. 112(33): E4911–E4918. https://doi.org/10.1073/pnas.1508098112.

Chiba S, Salaipeth L, Lin YH, … et al. 2009. A novel bipartite dsRNA mycovirus from the white root rot fungus *Rosellinia necatrix*: molecular and biological characterization, taxonomic considerations, and potential for biological control. Journal of Virology. 83(24): 12801–12812. https://doi.org/10.1128/JVI.01830-09.

Chiba S, Bai C, Xie J, … et al. 2023. ICTV Virus Taxonomy Profile: *Hypoviridae*. Journal of General Virology. 104(4): 001848. https://doi.org/10.1099/jgv.0.001848.

Choi GH, Dawe AL, Churbanov A, … et al. 2012. Molecular characterization of vegetative incompatibility genes that restrict hypovirus transmission in the chestnut blight fungus *Cryphonectria parasitica*. Genetics. 190(1): 113–127. https://doi.org/10.1534/genetics.111.133983.

Jiang D, Ayllón MA, Marzano SYL. 2019. ICTV Virus Taxonomy Profile: *Mymonaviridae*. Journal of General Virology. 100(10): 1343–1344. https://doi.org/10.1099/jgv.0.001301.

Das S, Falloon RE, Stewart A, … et al. 2016. Novel Mitoviruses in *Rhizoctonia solani* AG-3PT infecting potato. Fungal Biology. 120(3): 338–350. https://doi.org/10.1016/j.funbio.2015.12.009.

Dawe AL, Segers GC, Allen TD, … et al. 2004. Microarray analysis of *Cryphonectria parasitica* Galpha- and Gbeta-gamma-signalling pathways reveals extensive modulation by *hypovirus* infection. Microbiology. 150(12): 4033–4043. https://doi.org/10.1099/mic.0.27424-0.

Debat HJ, Iaffaldano BJ, Zhang X, … et al. 2019. Molecular Identification and Characterization of Two Rubber Dandelion *Amalgaviruses*. BioRXiv. https://doi.org/10.1101/614123.

Depierreux D, Vong M, Nibert ML. 2016. Nucleotide sequence of *Zygosaccharomyces bailii* virus Z: Evidence for +1 programmed ribosomal frameshifting and for assignment to family *Amalgaviridae*. Virus Research. 217: 115–124. https://doi.org/10.1016/j.virusres.2016.02.003.

Dodds JA, Morris TJ, Jordan RL. 1984. Plant viral double-stranded RNA. Annual Review of Phytopathology. 22: 151–168. https://doi.org/10.1146/annurev.py.22.090184.001103.

Doehlemann G, Ökmen B, Zhu W, … et al. 2016. Plant pathogenic fungi. Microbiology Spectrum. 5(1): FUNK-0023-2016. https://doi.org/10.1128/microbiolspec.FUNK-0023-2016.

Dolja VV, Koonin EV. 2012. Capsid-Less RNA viruses. In: Encyclopedia of Life Sciences. (eLS). John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470015902.a0024163.

Eickbush T, Boeke JD, Sandmeyer SB, … et al. 2011. Family *Metaviridae*. In: Virus Taxonomy: Ninth Report of the International Committee for the Taxonomy of Viruses. (King AMQ, Adams MJ, Carstens EB, et al., eds): 457–466. Elsevier Academic Press, USA.

Enebak SA, Hillman BI, Macdonald WL. 1994. A hypovirulent isolate of *Cryphonectria parasitica* with multiple, genetically unique dsRNA segments. Molecular Plant-Microbe Interactions. 7(5): 590–595. https://doi.org/10.1094/MPMI-7-0590.

Egerton-Warburton LM, Querejeta JI, Allen MF, … et al. 2005. Mycorrhizal fungi. In: Encyclopedia of Soils in the Environment. (Hillel D, ed) 4: 533–542. Elsevier, UK.

Feldman TS, Morsy MR, Roossinck MJ. 2012. Are communities of microbial symbionts more diverse than communities of macrobial hosts? Fungal Biology. 116(2): 465–477. https://doi.org/10.1016/j.funbio.2012.01.005.

Filippou C, Garrido-Jurado I, Meyling NV, … et al. 2018. Mycoviral population dynamics in Spanish isolates of the entomopathogenic fungus *Beauveria bassiana*. Viruses. 10(12): 665. https://doi.org/10.3390/v10120665.

Fukuhara T, Gibbs MJ. 2012. Family *Endornaviridae*. In: Virus Taxonomy: Ninth Report of the International Committee for the Taxonomy of Viruses. (King AMQ, Adams MJ, Carstens EB, et al., eds): 519–521. Elsevier Academic Press, USA.

García-Pedrajas MD, Cañizares MC, Sarmiento-Villamil JL, … et al. 2019. Mycoviruses in biological control: from basic research to field implementation. Phytopathology. 109(12): 1828–1839. https://doi.org/10.1094/PHYTO-05-19-0168-RVW.

Ghabrial SA, Castón JR, Jiang D, … et al. 2015. 50-plus years of fungal viruses. Virology. 479-480: 356–368. https://doi.org/10.1016/j.virol.2015.02.034.

Ghabrial SA. 2008. *Totiviruses*. In: Encyclopedia of Virology. (Mahy BWJ, Van Regenmortel MHV, eds) 3: 163–174. Academic Press, USA.

Ghabrial SA, Nibert ML. 2009. *Victorivirus*, a new genus of fungal viruses in the family *Totiviridae*. Archives of Virology. 154(2): 373–379. https://doi.org/10.1007/s00705-008-0299-1.

Ghabrial SA, Suzuki N. 2009. Viruses of plant pathogenic fungi. Annual Review of Phytopathology. 47: 353–384. https://doi.org/10.1146/annurev-phyto-080508-081932.

Ghabrial SA, Castón JR. 2011. Family *Chrysoviridae*. In: Virus Taxonomy: Ninth Report of the International Committee for the Taxonomy of Viruses. (King AMQ, Adams MJ, Carstens EB, et al., eds): 509–513. Elsevier Academic Press, USA.

Gibbs MJ, Koga R, Moriyama H, … et al. 2000. Phylogenetic analysis of some large double-stranded RNA replicons from plants suggests they evolved from a defective single-stranded RNA virus. Journal of General Virology. 81(1): 227–233. https://doi.org/10.1099/0022-1317-81-1-227.

Gil H, Choi GH, Dawe AL, … et al. 2012. Molecular characterization of vegetative incompatibility genes that restrict *Hypovirus* transmission in the chestnut blight fungus *Cryphonectria parasitica*. Genetics. 190(1): 113–127. https://doi.org/10.1534/genetics.111.133983.

Hacker CV, Brasier CM, Buck KW. 2005. A double-stranded RNA from a P*hytophthora* species is related to the plant *Endornaviruses* and contains a putative UDP glycosyltransferase gene. Journal of General Virology. 86(5): 1561–1570. https://doi.org/10.1099/vir.0.80808-0.

Hantula J, Mäkelä S, Xu P, … et al. 2020. Multiple virus infections on *Heterobasidion* sp. Fungal Biology. 124(2): 102–109. https://doi.org/10.1016/j.funbio.2019.12.004.

Hao F, Wu M, Li G. 2018. Molecular characterization and geographic distribution of a *Mymonavirus* in the population of *Botrytis cinerea*. Viruses. 10(8): 432. https://doi.org/10.3390/v10080432.

Heiniger U, Rigling D. 1994. Biological control of chestnut blight in Europe. Annual Review of Phytopathology. 32: 581–599. https://doi.org/10.1146/annurev.py.32.090194.003053.

Hillman BI, Cai G. 2013. The family *Narnaviridae*: simplest of RNA viruses. Advances in Virus Research. 86: 149–176. https://doi.org/10.1016/B978-0-12-394315-6.00006-4.

Hillman BI, Suzuki N. 2004. Viruses of the chestnut blight fungus, *Cryphonectria parasitica*. Advances in Virus Research. 63: 423–472. https://doi.org/10.1016/S0065-3527(04)63014-0.

Hillman BI, Esteban R. 2011. *Narnaviridae*. In: Virus Taxonomy: Ninth Report of the International Committee for the Taxonomy of Viruses. (King AMQ, Adams MJ, Lefkowitz EJ, eds): 1055–1060. Elsevier, USA.

Hollings M. 1962. Viruses associated with a die-back disease of cultivated mushroom. Nature. 196: 962–965. https://doi.org/10.1038/196962a0.

Hongsanan S, Li YM, Liu JK, … et al. 2014. Revision of genera in *Asterinales*. Fungal Diversity. 68: 1–68. https://doi.org/10.1007/s13225-014-0292-7.

Hongsanan S, Tian Q, Peršoh D, … et al. 2015a. *Meliolales*. Fungal Diversity. 74: 1–51. https://doi.org/10.1007/s13225-015-0344-7.

Hongsanan S, Tian Q, Bahkali AH, … et al. 2015b. *Zeloasperisporiales* ord. nov., and two new species of *Zeloasperisporium*. Cryptogamie, Mycologie. 36(3): 301–317. https://doi.org/10.7872/crym/v36.iss3.2015.301.

Howitt RLJ, Beever RE, Pearson MN, … et al. 2001. Genome characterization of *Botrytis* virus F, a flexuous rod-shaped mycovirus resembling plant 'potex-like' viruses. Journal of General Virology. 82(1): 67–78. https://doi.org/10.1099/0022-1317-82-1-67.

Hyde KD, Xu JC, Rapior S, … et al. 2019. The amazing potential of fungi: 50 ways we can exploit fungi industrially. Fungal Diversity. 97: 1–136. https://doi.org/10.1007/s13225-019-00430-9.

International Committee on Taxonomy of Viruses. 2025. Family: *Gammaflexiviridae* (Interim Report) [Internet]. ICTV Report; 2025 Feb [cited 2025 Apr 9]. Available from: https://ictv.global/report/chapter/gammaflexiviridae/gammaflexiviridae.

International Committee on Taxonomy of Viruses. 2024. Family: *Orthototiviridae* (Interim Report) [Internet]. ICTV Report; 2024 Nov [updated 2024 Dec; cited 2025 Apr 10]. Available from: https://ictv.global/report/chapter/orthototiviridae/orthototiviridae.

Ikeda Y, Shimura H, Kitahara R, … et al. 2012. A novel virus-like double-stranded RNA in an obligate biotroph arbuscular mycorrhizal fungus: a hidden player in mycorrhizal symbiosis. Molecular Plant-Microbe Interactions. 25(7): 1004–1012. https://doi.org/10.1094/MPMI-11-11-0291.

Jaccard A, Dubuis N, Kellenberger I, Brodard J, Schnee S, Gindro K, Schumpp O. 2023. New viruses of *Cladosporium* sp. expand considerably the taxonomic structure of *Gammapartitivirus* genus. Journal of General Virology. 104(8):001879. https://doi.org/10.1099/jgv.0.001879.

Jackson AO, Francki RIB, Zuidema D. 1987. Biology, Structure, and replication of plant *Rhabdoviruses*. In: The Rhabdoviruses. (Wagner RR, ed): 427-508. Plenum Press, USA.

Jiang D, Fu Y, Li G, … et al. 2013. Viruses of the Plant Pathogenic Fungus *Sclerotinia sclerotiorum*. Advances in Virus Research. 86: 215–248. https://doi.org/10.1016/B978-0-12-394315-6.00008-8.

Jiāng D, Ghabrial SA, Liú H, … et al. 2022. ICTV Virus Taxonomy Profile: *Mymonaviridae*. Journal of General Virology. 103(12): 001787. https://doi.org/10.1099/jgv.0.001787.

Kanematsu S, Shimizu T, Salaipeth L, … et al. 2014. Genome rearrangement of a mycovirus *Rosellinia necatrix megabirnavirus* 1 affecting its ability to attenuate virulence of the host fungus. Virology. 450-451: 308–315. https://doi.org/10.1016/j.virol.2013.12.002.

Kanhayuwa L, Kotta-Loizou I, Özkan S, … et al. 2015. A novel mycovirus from *Aspergillus fumigatus* contains four unique dsRNAs as its genome and is infectious as dsRNA. Proceedings of the National Academy of Sciences of the United States of America. 112(29): 9100–9105. https://doi.org/10.1073/pnas.1419225112.

Kartali T, Zsindely N, Nyilasi I, … et al. 2022. Molecular Characterization of Novel Mycoviruses in Seven *Umbelopsis* Strains. Viruses. 14(11): 2343. https://doi.org/10.3390/v14112343.

Kashif M, Hyder R, De Vega Perez D, … et al. 2015. *Heterobasidion* Wood Decay Fungi Host Diverse and Globally Distributed Viruses Related to *Helicobasidium mompa Partitivirus* V70. Virus Research. 195: 119–123. https://doi.org/10.1016/j.virusres.2014.10.005.

Kazlauskas D, Dayaram A, Kraberger S, … et al. 2017. Evolutionary history of ssDNA *bacilladnaviruses* features horizontal acquisition of the capsid gene from ssRNA *Nodaviruses*. Virology. 504: 114–121. https://doi.org/10.1016/j.virol.2017.01.019.

Kazlauskas D, Varsani A, Krupovic M. 2018. Pervasive chimerism in the replication-associated proteins of uncultured single-stranded DNA viruses. Viruses. 10(4): 187. https://doi.org/10.3390/v10040187.

Kazlauskas D, Varsani A, Koonin EV, … et al. 2019. Multiple origins of prokaryotic and eukaryotic single-stranded DNA viruses from bacterial and archaeal plasmids. Nature Communications. 10: 3425. https://doi.org/10.1038/s41467-019-11433-0.

Khalifa ME, Pearson MN. 2014. Characterization of a novel *Hypovirus* from *Sclerotinia sclerotiorum* potentially representing a new genus within the *Hypoviridae*. Virology. 464-465: 441–449. https://doi.org/10.1016/j.virol.2014.07.005.

Khan HA, Noguchi M, Kondo H, … et al. 2023. Two novel *partitiviruses* that accumulate differentially in *Rosellinia necatrix* and *Entoleuca* sp. infected with a hypovirulence-conferring virus. Nature Communications. 14: 5268. https://doi.org/10.1038/s41467-023-41010-3.

King, A. M. Q., Adams, Michael, Carstens, E. B. and Lefkowitz, E. J. (eds.). 2012. Virus taxonomy: classification and nomenclature of viruses. Ninth report of the International Committee on Taxonomy of Viruses. UNSPECIFIED, 1327pp.

Koloniuk I, El-Habbak MH, Petrzik K, … et al. 2014. Complete genome sequence of a novel *Hypovirus* infecting *Phomopsis longicolla*. Archives of Virology. 159: 1861–1863. https://doi.org/10.1007/s00705-014-2007-5.

Kondo H, Chiba S, Toyoda K, … et al. 2013. Evidence for negative-strand RNA virus infection in fungi. Virology. 435(1): 201–209. https://doi.org/10.1016/j.virol.2012.09.008.

Kotta-Loizou I, Coutts RHA. 2022. ICTV Virus Taxonomy Profile: *Polymycoviridae*. Journal of General Virology. 103(6): 001747. https://doi.org/10.1099/jgv.0.001747.

Kotta-Loizou I. 2021. Mycoviruses and their role in fungal pathogenesis. Current Opinion in Microbiology. 63: 10–18. https://doi.org/10.1016/j.mib.2021.05.007.

Kotta-Loizou I, Castón JR, Coutts RHA, … et al. 2020. ICTV Virus Taxonomy Profile: *Chrysoviridae*. Journal of General Virology. 101(2): 143–144. https://doi.org/10.1099/jgv.0.001383.

Kotta-Loizou I, Coutts RHA. 2017. Studies on the virome of the entomopathogenic fungus *Beauveria bassiana* reveal novel dsRNA elements and mild hypervirulence. PLoS Pathogens. 13(1): e1006183. https://doi.org/10.1371/journal.ppat.1006183.

Krupovic M, Ghabrial SA, Jiang D, … et al. 2016. *Genomoviridae*: a new family of widespread single-stranded DNA viruses. Archives of Virology. 161(9): 2633–2643. https://doi.org/10.1007/s00705-016-2943-3.

Krupovic M, Dolja VV, Koonin EV. 2015. Plant viruses of the *Amalgaviridae* family evolved via recombination between viruses with double-stranded and negative-strand RNA genomes. Biology Direct. 10: 12. https://doi.org/10.1186/s13062-015-0050-0.

Larios BMC, Pirovani CP, Loguercio LL, … et al. 2023. Exploring the mycovirus universe: identification, diversity, and biotechnological applications. Journal of Fungi. 9(3): 361. https://doi.org/10.3390/jof9030361.

Linnakoski R, Sutela S, Coetzee MP, … et al. 2021. *Armillaria* root rot fungi host single-stranded RNA viruses. Scientific Reports. 11: 7336. https://doi.org/10.1038/s41598-021-86326-2.

Llorens C, Soriano B, Krupovic M. 2020. ICTV Virus Taxonomy Profile: *Metaviridae*. Journal of General Virology. 101(11): 1131–1132. https://doi.org/10.1099/jgv.0.001509.

Llorens C, Soriano B, Krupovic M. 2021. ICTV Virus Taxonomy Profile: *Pseudoviridae*. Journal of General Virology. 102(12): 001563. https://doi.org/10.1099/jgv.0.001563.

Li P, Wang S, Zhang L, … et al. 2020. A tripartite ssDNA mycovirus from a plant pathogenic fungus is infectious as cloned DNA and purified virions. Science Advances. 6(14): eaay9634. https://doi.org/10.1126/sciadv.aay9634.

Liu C, Lakshman DK, Tavantzis SM. 2003. Quinic acid induces hypovirulence and expression of a hypovirulence-associated double-strand RNA in *Rhizoctonia solani*. Current Genetics. 43: 103–111. https://doi.org/10.1007/s00294-003-0375-6.

Liu L, Xie J, Cheng J, … et al. 2014. Fungal negative-stranded RNA virus that is related to *Bornaviruses* and Nyaviruses. Proceedings of the National Academy of Sciences of the United States of America. 11(33): 12205–12210. https://doi.org/10.1073/pnas.1401786111.

Liu S, Xie J, Cheng J, … et al. 2016. Fungal DNA virus infects a mycophagous insect and utilizes it as a transmission vector. Proceedings of the National Academy of Sciences of the United States of America. 113(45): 12803–12808. https://doi.org/10.1073/pnas.1608013113.

Liu Y, Zhang LY, Esmael A, … et al. 2020. Four novel *Botourmiaviruses* co-infecting an isolate of the rice blast fungus *Magnaporthe oryzae*. Viruses. 12(12): 138. https://doi.org/10.3390/v12121388.

Lin YH, Fujita M, Chiba S, … et al. 2019. Two novel fungal negative-strand RNA viruses related to *Mymonaviruses* and *Phenuivirids* in the shiitake mushroom (*Lentinula edodes*). Virology. 533: 125–136. https://doi.org/10.1016/j.virol.2019.05.008.

Lyu R, Zhang Y, Tang Q, … et al. 2018. Two *Alphapartitiviruses* co-infecting a single isolate of the plant pathogenic fungus *Rhizoctonia solani*. Archives of Virology. 163: 515–520. https://doi.org/10.1007/s00705-017-3618-6.

Lukša J, Ravoitytė B, Konovalovas A, … et al. 2017. Different metabolic pathways are involved in response of *Saccharomyces Cerevisiae* to L-A and M Viruses. Toxins. 9(8): 233. https://doi.org/10.3390/toxins9080233.

Luque D, Mata CP, Suzuki N, … et al. 2018. Capsid Structure of DsRNA Fungal Viruses. Viruses. 10(9): 481. https://doi.org/10.3390/v10090481.

Ma G, Zhang B, Qi K, … et al. 2022. Characterization of a novel *Mitovirus* isolated from the phytopathogenic fungus *Fusarium pseudograminearum*. Archives of Virology. 167(6): 1369–1373. https://doi.org/10.1007/s00705-022-05452-8.

Márquez LM, Redman RS, Rodriguez RJ, … et al. 2007. A virus in a fungus in a plant: three-way symbiosis required for thermal tolerance. Science. 315(5811): 513–515. https://doi.org/10.1126/science.1136237.

Martin RR, Zhou J, Tzanetakis IE. 2011. Blueberry latent virus: An amalgam of the *Partitiviridae* and *Totiviridae*. Virus Research. 155(1): 175–180. https://doi.org/10.1016/j.virusres.2010.09.020.

Marzano SYL, Nelson BD, Ajayi-Oyetunde O, … et al. 2016. Identification of Diverse Mycoviruses through Metatranscriptomics Characterization of the Viromes of Five Major Fungal Plant Pathogens. Journal of Virology. 90(15): 6846–6863. https://doi.org/10.1128/JVI.00357-16.

Moran NA, McCutcheon JP, Nakabachi A. 2008. Genomics and evolution of heritable bacterial symbionts. Annual Review of Genetics. 42: 165–190. https://doi.org/10.1146/annurev.genet.41.110306.130119.

Mu F, Xie J, Cheng S, … et al. 2018. Virome characterization of a collection of *S. sclerotiorum* from Australia. Frontiers in Microbiology. 12: 757330. https://doi.org/10.3389/fmicb.2021.757330.

Myers JM, Bonds AE, Clemons RA, … et al. 2020. Survey of Early-Diverging Lineages of Fungi Reveals Abundant and Diverse Mycoviruses. mBio. 11(5): e02027-20. https://doi.org/10.1128/mBio.02027-20.

Nibert ML, Ghabrial SA, Maiss E, … et al. 2014. Taxonomic reorganization of family *Partitiviridae* and other recent progress in *Partitivirus* research. Virus Research. 188: 128–141. https://doi.org/10.1016/j.virusres.2014.04.005.

Nibert ML. 2017. *Mitoviruses*: fungal viruses that infect mitochondria. In: Kielian M, Maramorosch K, Mettenleiter TC (eds), Advances in Virus Research, vol 98. Academic Press, pp 119–148. https://doi.org/10.1016/bs.aivir.2017.02.002.

Ninomiya A, Urayama S, Suo R, … et al. 2020. Mycovirus-Induced Tenuazonic Acid Production in a Rice Blast Fungus *Magnaporthe oryzae*. Frontiers in Microbiology. 11: 1641. https://doi.org/10.3389/fmicb.2020.01641.

Nuskern L, Ježić M, Liber Z, … et al. 2018. *Cryphonectria* hypovirus 1-Induced Epigenetic Changes in Infected Phytopathogenic Fungus *Cryphonectria parasitica*. Microbial Ecology. 75: 790–798. https://doi.org/10.1007/s00248-017-1074-8.

Nuss DL, Hillman BI. 2011. Family *Hypoviridae*. In: Virus Taxonomy: Ninth Report of the International Committee for the Taxonomy of Viruses. (King AMQ, Adams MJ, Carstens EB, et al., eds): 1029–1033. Elsevier Academic Press, USA.

Nuss DL. 2005. Hypovirulence: mycoviruses at the fungal-plant interface. Nature Reviews Microbiology. 3(8): 632–642. https://doi.org/10.1038/nrmicro1206.

Olsthoorn RCL, Owen CA, Livieratos IC. 2022. Role of an RNA pseudoknot involving the polyA tail in replication of Pepino mosaic *Potexvirus* and related plant viruses. Nature Communications. 12: 11532. https://doi.org/10.1038/s41467-021-26891-0.

Özkan S, Mohorianu I, Xu P, … et al. 2017. Profile and Functional Analysis of Small RNAs Derived from *Aspergillus Fumigatus* Infected with Double-Stranded RNA Mycoviruses. BMC Genomics. 18: 416. https://doi.org/10.1186/s12864-017-3773-6.

Pandey B, Naidu RA, Grove GG. 2018. Detection and analysis of mycovirus related RNA viruses from grape powdery mildew fungus *Erysiphe necator*. Archives of Virology. 163: 1019–1030. https://doi.org/10.1007/s00705-017-3690-y.

Patchett A, Newman JA. 2021. Comparison of Plant Metabolites in Root Exudates of *Lolium perenne* Infected with Different Strains of the Fungal Endophyte *Epichloë festucae* var. *lolii*. Journal of Fungi. 7(2): 148. https://doi.org/10.3390/jof7020148.

Pearson MN, Bailey AM. 2013. Viruses of *Botrytis*. Advances in Virus Research. 86: 249–272. https://doi.org/10.1016/B978-0-12-394315-6.00009-X.

Pearson MN, Beever RE, Boine B, … et al. 2009. Mycoviruses of filamentous fungi and their relevance to plant pathology. Molecular Plant Pathology. 10(1): 115–128. https://doi.org/10.1111/j.1364-3703.2008.00503.x.

Picarelli MASC, Forgia M, Rivas EB, … et al. 2019. Extreme Diversity of Mycoviruses Present in Isolates of *Rhizoctonia Solani* AG2-2 LP From *Zoysia Japonica* from Brazil. Frontiers in Cellular and Infection Microbiology. 9: 244. https://doi.org/10.3389/fcimb.2019.00244.

Qu Z, Zhao H, Zhang H, … et al. 2020. Bio-priming with a hypovirulent phytopathogenic fungus enhances the connection and strength of microbial interaction network in rapeseed. Biofilms and Microbiomes. 6: 1–13. https://doi.org/10.1038/s41522-020-00142-2.

Redman RS, Sheehan KB, Stout RG, … et al. 2002. Thermotolerance conferred to plant host and fungal endophyte during mutualistic symbiosis. Science. 298(5598): 1581. https://doi.org/10.1126/science.1078051.

Revill PA. 2011. Family Barnaviridae. In: Virus Taxonomy: Ninth Report of the International Committee for the Taxonomy of Viruses. (King AMQ, Adams MJ, Carstens EB, et al., eds): 961–964. Elsevier Academic Press, USA.

Rodriguez R, White J, Arnold AE, et al. 2009. Fungal endophytes: diversity and ecological roles. New Phytologist. 182(2): 314–330. https://doi.org/10.1111/j.1469-8137.2008.02773.x.

Roossinck MJ. 2011a. Changes in population dynamics in mutualistic versus pathogenic viruses. Viruses. 3(1): 12–19. https://doi.org/10.3390/v3010012.

Roossinck MJ. 2011b. The good viruses: viral mutualistic symbioses. Nature Reviews Microbiology. 9(2): 99–108. https://doi.org/10.1038/nrmicro2491.

Roossinck MJ. 2014. Metagenomics of plant and fungal viruses reveals an abundance of persistent lifestyles. Frontiers in Microbiology. 5: 767. https://doi.org/10.3389/fmicb.2014.00767.

Roossinck MJ. 2015. A new look at plant viruses and their potential beneficial roles in crops. Molecular Plant Pathology. 16(4): 331–333. https://doi.org/10.1111/mpp.12241.

Sabanadzovic S, Valverde RA, Brown JK, … et al. 2009. Southern tomato virus: The link between the families *Totiviridae* and *Partitiviridae*. Virus Research. 140(1–2): 130–137. https://doi.org/10.1016/j.virusres.2008.11.018.

Salaipeth L, Eusebio-Cope A, Chiba S, … et al. 2014. Biological properties and expression strategy of *Rosellinia necatrix megabirnavirus* 1 in an experimental host *Cryphonectria parasitica*. Journal of General Virology. 95(Pt 4): 740-750. https://doi.org/10.1099/vir.0.058164-0.

Sato Y, Turina M, Chiba S, … et al. 2023. ICTV Virus Taxonomy Profile: *Hadakaviridae*. Journal of General Virology. 104(4): 001820. https://doi.org/10.1099/jgv.0.001820.

Sato Y, Miyazaki N, Kanematsu S, … et al. 2019. ICTV Virus Taxonomy Profile: *Megabirnaviridae*. Journal of General Virology. 100(9): 1269–1270. https://doi.org/10.1099/jgv.0.001300.

Shah UA, Kotta-Loizou I, Fitt BDL, … et al. 2018. Identification, Molecular Characterization, and Biology of a Novel *Quadrivirus* Infecting the Phytopathogenic Fungus *Leptosphaeria biglobosa*. Viruses. 11(1): 9. https://doi.org/10.3390/v11010009.

Silva JM, Pratas D, Caetano T, … et al. 2022. The complexity landscape of viral genomes. Giga Science. 11: giac005. https://doi.org/10.1093/gigascience/giac005.

Soltani J. 2017. Endophytism in Cupressoideae (Coniferae): a model in endophyte biology and biotechnology. In: Maheshwari DK (ed) Endophytes: Biology and Biotechnology, Sustainable Development and Biodiversity, vol 15. Springer, Cham, pp 127-144. https://doi.org/10.1007/978-3-319-66544-3_7.

Stielow B, Menzel W. 2010. Complete nucleotide sequence of TaV1, a novel *Totivirus* isolated from a black truffle ascocarp (*Tuber aestivum* Vittad.). Archives of Virology. 155(12): 2075–2078. https://doi.org/10.1007/s00705-010-0794-8.

Stielow B, Klenk HP, Menzel W. 2011. Complete genome sequence of the first Endornavirus from the ascocarp of the ectomycorrhizal fungus *Tuber aestivum* Vittad. Archives of Virology. 156(2): 343–345. https://doi.org/10.1007/s00705-010-0861-3.

Supyani S, Hillman BI, Suzuki N. 2007. Baculovirus expression of the 11 mycoreovirus-1 genome segments and identification of the guanylyltransferase-encoding segment. Journal of General Virology. 88(5): 190–198. https://doi.org/10.1099/vir.0.82318-0.

Suzuki N, Ghabrial SA, Kim KH, … et al. 2018. ICTV Virus Taxonomy Profile: *Hypoviridae*. Journal of General Virology. 99(5): 615–616. https://doi.org/10.1099/jgv.0.001049.

Svanella-Dumas L, Marais A, Faure C, … et al. 2018. Genome characterization of a divergent isolate of the mycovirus *Botrytis* virus F from a grapevine metagenome. Archives of Virology. 163(11): 3181–3183. https://doi.org/10.1007/s00705-018-3958-8.

Taylor DJ, Ballinger MJ, Bowman SM, … et al. 2013. Virus–host co-evolution under a modified nuclear genetic code. PeerJ. 1: e50. https://doi.org/10.7717/peerj.50.

Tercero B, Terasaki K, Nakagawa K, … et al. 2019. A strand-specific real-time quantitative RT-PCR assay for distinguishing the genomic and antigenomic RNAs of Rift Valley fever *Phlebovirus*. Journal of Virological Methods. 272: 113701. https://doi.org/10.1016/j.jviromet.2019.113701.

Tian B, Xie J, Fu Y, … et al. 2020. A cosmopolitan fungal pathogen of dicots adopts an endophytic lifestyle on cereal crops and protects them from major fungal diseases. The ISME Journal. 14(12): 3120–3135. https://doi.org/10.1038/s41396-020-00744-6.

Vainio EJ, Jurvansuu J, Hyder R, … et al. 2017. The *Partitivirus HetPV13-An1* Mediates Severe Growth Debilitation and Major Alterations in the Gene Expression of a Fungal Forest Pathogen. Journal of Virology. 91(17): e01744-17. https://doi.org/10.1128/JVI.01744-17.

Vainio EJ, Chiba S, Ghabrial SA, … et al. 2018. ICTV Virus Taxonomy Profile: *Partitiviridae*. Journal of General Virology. 99(1): 17–18. https://doi.org/10.1099/jgv.0.000985.

Valverde RA, Khalifa ME, Okada R, … et al. 2019. ICTV Virus Taxonomy Profile: *Endornaviridae*. Journal of General Virology. 100(8): 1204–1205. https://doi.org/10.1099/jgv.0.001277.

Van Alfen NK, Jaynes RA, Anagnostakis SL, … et al. 1975. Chestnut blight: Biological control by transmissible hypovirulence in *Endothia parasitica*. Science. 189(4206): 890–891. https://doi.org/10.1126/science.189.4206.890.

Varsani A, Krupovic M. 2021. Family *Genomoviridae*: taxonomy update. Archives of Virology. 166(10): 2911–2926. https://doi.org/10.1007/s00705-021-05192-x.

Villan Larios DC, Reyes BMD, Pirovani CP, … et al. 2024. Exploring the Mycovirus Universe: Identification, Diversity, and Biotechnological Applications. Journal of Fungi. 10(3): 195. https://doi.org/10.3390/jof10030195.

Wang Y, Zhao H, Cao J, … et al. 2022. Characterization of a Novel Mycovirus from the Phytopathogenic Fungus *Botryosphaeria dothidea*. Viruses. 14(2): 331. https://doi.org/10.3390/v14020331.

Wang L, Zhang J, Zhang H, … et al. 2016. Two novel relative double-stranded RNA mycoviruses infecting *Fusarium poae* strain SX63. International Journal of Molecular Sciences. 17(5): 641. https://doi.org/10.3390/ijms17050641.

Wang S, Kondo H, Liu L, … et al. 2013. A novel virus in the family *Hypoviridae* from the plant pathogenic fungus *Fusarium graminearum*. Virus Research. 174(1-2): 69–77. https://doi.org/10.1016/j.virusres.2013.03.002.

Wei CZ, Osaki H, Iwanami T, et al. 2004. Complete nucleotide sequences of genome segments 1 and 3 of *Rosellinia* anti-rot virus in the family *Reoviridae*. Archives of Virology. 149(4): 773–777. https://doi.org/10.1007/s00705-003-0254-9.

Wickner RB, Ghabrial SA, Nibert ML, … et al. 2011. Family *Totiviridae*. In: Virus Taxonomy: Ninth Report of the International Committee for the Taxonomy of Viruses. (King AMQ, Adams MJ, Carstens EB, et al., eds): 639–650. Elsevier Academic Press, USA.

Wickner RB, Fujimura T, Esteban R. 2013. Viruses and prions of *Saccharomyces cerevisiae*. Advances in Virus Research. 86: 1–36. https://doi.org/10.1016/B978-0-12-394315-6.00001-5.

Wu M, Jin F, Zhang J, … et al. 2012. Characterization of a novel bipartite double stranded RNA mycovirus conferring hypovirulence in the phytopathogenic fungus *Botrytis porri*. Journal of Virology. 86(12): 6605–6619. https://doi.org/10.1128/JVI.00292-12.

Xie J, Jiang D. 2014. New insights into mycoviruses and exploration for the biological control of crop fungal diseases. Annual Review of Phytopathology. 52: 45–68. https://doi.org/10.1146/annurev-phyto-102313-050222.

Xie J, Xiao X, Fu Y, … et al. 2011. A novel mycovirus closely related to *Hypoviruses* that infects the plant pathogenic fungus *Sclerotinia sclerotiorum*. Virology. 418(1): 49–56. https://doi.org/10.1016/j.virol.2011.07.008.

Xie J, Ghabrial SA. 2012. Molecular characterizations of two *Mitoviruses* co-infecting a hyovirulent isolate of the plant pathogenic fungus *Sclerotinia sclerotiorum*. Virology. 428(2): 77–85. https://doi.org/10.1016/j.virol.2012.03.015.

Yaegashi H, Kanematsu S, Ito T. 2012. Molecular characterization of a new *hypovirus* infecting a phytopathogenic fungus, *Valsa ceratosperma*. Virus Research. 165(2): 143–150. https://doi.org/10.1016/j.virusres.2012.02.008.

Yang Y, Gaspard G, McMullen N, … et al. 2020. Polycistronic Genome segment evolution and gain and loss of fast protein function during Fusogenic Orthoreovirus Speciation. Viruses. 12(7): 702. https://doi.org/10.3390/v12070702.

Yu X, Li B, Fu Y, … et al. 2010. A *Geminivirus*-related DNA mycovirus that confers hypovirulence to a plant pathogenic fungus. Proceedings of the National Academy of Sciences of the United States of America. 107(18): 8387–8392. https://doi.org/10.1073/pnas.0914439107.

Zhang R, Hisano S, Tani A, … et al. 2016. A capsidless ssRNA virus hosted by an unrelated dsRNA virus. Nature Microbiology. 1: 15001. https://doi.org/10.1038/nmicrobiol.2015.1.

Zhang DX, Spiering MJ, Dawe AL, … et al. 2014. Vegetative incompatibility loci with dedicated roles in allorecognition restrict mycovirus transmission in chestnut blight fungus. Genetics. 197(2): 701–714. https://doi.org/10.1534/genetics.114.164574.

Zhang H, Xie J, Fu Y, … et al. 2020. A 2-kb mycovirus converts a pathogenic fungus into a beneficial endophyte for Brassica protection and yield enhancement. Molecular Plant. 13(10): 1420–1433. https://doi.org/10.1016/j.molp.2020.08.016.

Zhao YJ, Shirouzu T, Chiba Y, … et al. 2023. Identification of novel RNA mycoviruses from wild mushroom isolates in Japan. Virus Research. 325: 199045. https://doi.org/10.1016/j.virusres.2022.199045.

Zheng L, Liu H, Zhang M, … et al. 2013. The complete genomic sequence of a novel mycovirus from *Rhizoctonia solani* AG-1 IA strain B275. Archives of Virology. 158(7): 1609–1612. https://doi.org/10.1007/s00705-013-1626-6.

Zoll J, Verweij PE, Melchers WJG. 2018. Discovery and characterization of novel *Aspergillus fumigatus* mycoviruses. PLOS ONE. 13(6): e0200511. https://doi.org/10.1371/journal.pone.0200511.

Zhong J, Chen CY, Gao BD. 2015. Genome sequence of a novel mycovirus of *Rhizoctonia solani*, a plant pathogenic fungus. Virus Genes. 51(1): 167–170. https://doi.org/10.1007/s11262-015-1195-8.

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مقاله مروری

مایکوویروم: زیست‌شناسی، تنوع، ساختارها، مزایا و کاربردها در حفاظت از گیاهان

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چکیده

مایکوویروم شامل ویروس‌هایی است که با قارچ‌ها برهمکنش دارند. این ویروس‌ها در طول تقسیم سلولی، اسپورزایی یا آناستوموز هیفی به صورت درون‌سلولی منتقل می‌شوند و معمولاً فاقد مرحله برون‌سلولی در چرخه زندگی خود هستند. مایکوویروس‌ها در گستره‌ی وسیعی از گونه‌های قارچی شناسایی شده‌اند، اما دامنه میزبانی آنها به گروه‌های رویشی سازگار محدود شده است. در حالی که بسیاری از مایکوویروس‌ها هیچ اثر آشکاری بر میزبان خود نشان نمی‌دهند، برخی دیگر تغییرات فنوتیپی، از جمله رشد ناهمگون، تولید رنگدانه غیرطبیعی و در برخی موارد، تغییرات در تولید مثل جنسی را القا می‌کنند. نکته مهم این است که بسیاری از قارچ‌های آلوده به ویروس، قدرت بیماری‌زایی کمتری (هیپوویرولانس) در گیاهان میزبان دارند. چنین ویروس‌هایی اغلب شیوع گسترده‌ای در گونه‌های قارچی میزبان دارند که همین موضوع آنها را به ابزار ارزشمندی برای مدیریت‌زیستی بیماری‌های قارچی گیاهان بدل می‌کند. اکثر مایکوویروس‌های شناخته شده دارای ژنوم *RNA*، چه تک رشته‌ای و چه دو رشته‌ای، هستند و تنها تعداد کمی از آنها ژنوم *DNA* تک رشته‌ای دارند. تا به امروز، هیچ مایکوویروس با ژنوم *DNA* دو رشته‌ای شناسایی نشده است، که احتمالاً به دلیل محدودیت‌های فنی است. با این حال، پیشرفت در فناوری‌های تعیین توالی اسید نوکلئیک، نویدبخش پیشرفت در تحقیقات مربوط به مایکوویروس‌ها است. مرور حاضر، زیست‌شناسی، تنوع، ویژگی‌های ساختاری و کاربردهای مایکوویروس‌ها را با تمرکز بر پتانسیل آنها در حفاظت از گیاهان بررسی می‌کند.

واژگان کلیدی: کنترل زیستی، مایکوویروس، هیپوویرولانس، dsRNA، ssRNA.

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