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The biological attributes, genome architecture and packaging of diverse multi-component fungal viruses

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Many fungal viruses or mycoviruses have multi-segmented, rather than single-segmented, genomes. This multi-segment nature is frequently possessed by double-stranded RNA viruses, which include members of the *Chrysoviridae*, *Quadriviridae*, *Megabirnaviridae*, *Partitiviridae*, and *Reoviridae* families, and unassigned groups. Their genome segments are often packaged separately with the exception of mycoreoviruses, which are multi-segmented but mono-particulate viruses. These multi-segmented fungal dsRNA viruses, as exemplified by reoviruses, have been extensively studied among structural biologists, and contributed to discoveries of novel virion structures. Multi-component systems, interactions of viruses with subviral agents such as satellite and defective RNAs as typified by the yeast killer, and the rule-breaking neo-virus lifestyle exhibited by a capsidless single-stranded RNA virus hosted in an unrelated double-stranded RNA virus are also discussed. Fungal multi-segmented viruses and multicomponent virus systems would continue to provide virologists with interesting future challenges.

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Introduction

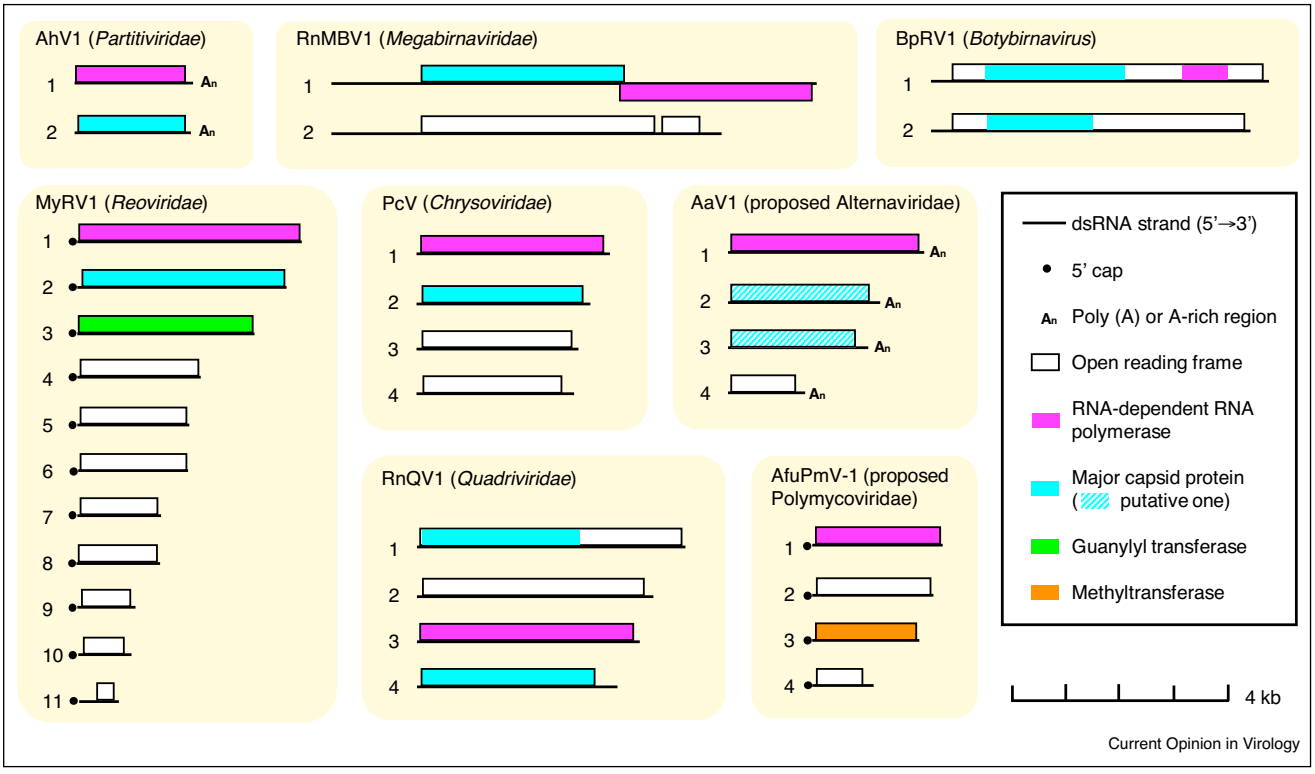
Fungal viruses or mycoviruses are omnipresent and detected in major groups of fungi such as members of the divisions Ascomycota, Basidiomycota, and Glomeromycota. Although few DNA viruses were reported, viruses with negative-sense (−), and positive-sense (+), single-stranded (ss) RNA genomes, or double-stranded RNA genomes, have increasingly been reported [1••,2]. Among them are several multi-segmented dsRNA fungal viruses exemplified by partitiviruses, chrysoviruses, megabirnaviruses, and mycoreoviruses (see below for details). The (−)ssRNA mycoviruses characterized so far largely have undivided genomes, and different genome organization from viruses infecting plants or animals. Although there are a few putative fungal (−)ssRNA viruses with genome sequences similar to multi-segmented plant (−)RNA viruses such as ophioviruses and bunyaviruses [3], they await thorough characterization as infectious entities of a multi-segmented genomic nature. There are a few documented multi-segmented (+)ssRNA mycoviruses, and these are described below.

As in plant and animal hosts, many interesting multi-component interactions involve virus/host virus/virus and virus/subviral nucleic acids in fungi [4]. Recent examples include peculiar virus/virus interplays: a neo-virus lifestyle exhibited by a capsidless (+)ssRNA virus hosted by an unrelated dsRNA virus [4,5•]. They also demonstrate a variety of interactions with their respective fungal hosts, and the majority show asymptomatic infections [1••]. This article focuses on multi-segmented dsRNA fungal viruses, but also touches on interesting partnerships among multiple viral components in which virus/virus and virus/satellite interplays are featured. We provide an overview of the taxonomy, genome organization, structures, and biological attributes of fungal multi-segmented viruses. Interesting interactions involving multi-component virus systems that include satellite and defective molecules are also considered. Experimental systems using *Saccharomyces cerevisiae* have been developed as a surrogate host for plant and animal viruses, including the tripartite brome mosaic virus and influenza A virus, for which many host factors were identified [6,7]. The main focus of this article, however, is *bona fide* fungal viruses naturally occurring in fungi.

Diverse multi-segmented RNA viruses in fungi

There are at least five established virus families, and one established genus, whose members have multi-segmented dsRNA genomes: families *Reoviridae*, *Partitiviridae*, *Chrysoviridae*, *Quadriviridae*, and *Megabirnaviridae*, and genus *Botybirnavirus* (Figure 1). In addition, there are two proposed families Alternaviridae and Polymycoviridae [8,9]. Although polymycoviruses appear to be infectious as naked dsRNA, they show greater phylogenetic affinity to eukaryotic (+)ssRNA viruses [10,11]. There are many unclassified fungal viruses with multi-segmented

Figure 1



Genome organization of multi-segmented RNA mycoviruses. Genome segments of multi-segmented RNA mycoviruses are illustrated. Symbols and diagrams for RNA sequence features and protein domains are explained in the box.

genomes, as exemplified by the newly identified reovirus [12]. Table 1 shows a comparison of some properties for those viruses. Except for mycoreoviruses, which are multisegmented but mono-particulate, all listed viruses appear to be multi-particulate: genomic segments are encapsidated separately (see below). Metaviromic analysis of several fungi showed sequences related to multi-segmented RNA viruses infecting plants and animals, such as ophioviruses and bunyaviruses [3], however, only one multi-segmented (+)ssRNA virus has been reported as an infectious entity from fungi, the cucumber mosaic virus, isolated from a natural isolate of a phytopathogenic fungus, *Rhizoctonia solani* [13]. Andika and others suggested that plant viruses can be replicated in, and transmitted by, fungi.

Few multi-segmented mycoviruses have been thoroughly examined for their phenotypic effects on host fungi, possibly because of the technical difficulty with virus curing or introduction, and/or unavailability of their reverse genetics. Tested cases, however, suggest that like many other fungal viruses, many multi-segmented dsRNA viruses cause no phenotypic alterations, as exemplified by quadriviruses [14•,15]. Most partitiviruses and possibly chrysoviruses belonging to Cluster I also show asymptomatic infections [16,17]. Exceptions to this include many members of Cluster II of the family *Chrysoviridae*, and *Megabirnaviridae*, and genus *Mycoreovirus* [18••,19•,20]. Partitiviruses were believed to cause no symptoms until recently. There are an increasing number of examples showing symptomatic infections such as *Sclerotinia sclerotiorum* partitivirus 1 and Rhizoctonia solani partitivirus 2, which induce hypovirulence to their hosts, phytopathogenic fungi [21,22]. Viral etiology was established for these examples by comparing isogenic virus-free and virus-infected strains. It may be possible to obtain virus-free strains by hyphal tipping and protoplasting, and virus-infected strains may be obtained by transfection with infectious particles, lateral transfer between vegetatively compatible or incompatible groups. Due to the lack of reverse genetics for any of fungal dsRNA viruses, however, functional information on virus protein or RNA elements is very limited, other than that expected from sequence motifs. An exploration of some virus mutants with genome rearrangements revealed viral factors necessary or dispensable for the normal symptom expression of Rosellinia necatrix megabirnavirus 1 (RnMBV1) and mycoreovirus 1 (MyRV1) [23–26]. This contrasts the situation for one of the best studied mycoviruses, CHV1 with a (+)ssRNA virus genome, for which reverse genetics is available [27,28].