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Review

Taxonomic reorganization of family *Partitiviridae* and other recent progress in partitivirus research

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ABSTRACT

Phylogenetic analyses have prompted a taxonomic reorganization of family *Partitiviridae* (encapsidated, bisegmented dsRNA viruses that infect plants, fungi, or protozoa), the focus of this review. After a brief introduction to partitiviruses, the taxonomic changes are discussed, including replacement of former genera *Partitivirus*, *Alphacryptovirus*, and *Betacryptovirus*, with new genera *Alphapartitivirus*, *Betapartitivirus*, *Gammapartitivirus*, and *Deltapartitivirus*, as well as redistribution of species among these new genera. To round out the review, other recent progress of note in partitivirus research is summarized, including discoveries of novel partitivirus sequences by metagenomic approaches and mining of sequence databases, determinations of fungal partitivirus particle structures, demonstrations of fungal partitivirus transmission to new fungal host species, evidence for other aspects of partitivirus–host interactions and host effects, and identification of other fungal or plant viruses with some similarities to partitiviruses. Some outstanding questions are also discussed.

Contents

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1. Introduction to partitiviruses

Viruses in taxonomic family *Partitiviridae* have been shown to infect plants (mostly angiosperms to date), fungi (asco- and basidiomycetes), and protozoa (*Cryptosporidium* spp.), and possible evidence for even broader host range is described below. Partitiviruses possess two essential dsRNA genome segments, dsRNA1 (or S1) and dsRNA2 (or S2), each 1300–2500 bp in length and containing one long open reading frame (ORF) on one of the RNA strands, i.e., the plus strand (Fig. 1). The segment encoding the RNA-dependent RNA polymerase (RdRp) protein is designated dsRNA1 (the longer segment in almost all strains), and that encoding the capsid/coat protein (CP) is designated dsRNA2 (Fig. 1). For other recent reviews on these viruses, see Ghabrial et al. (2008, 2011), Nibert et al. (2009, 2013), Roossinck (2010), and Tavantzis (2011).

Partitivirus particles are isometric, with diameters of different strains ranging from 25 to 40 nm by negative-stain electron microscopy (EM). Recent structures determined by cryo-EM and three-dimensional (3D) image reconstruction (Ochoa et al., 2008; Pan et al., 2009; Tang et al., 2010a, 2010b), as well as one by X-ray crystallography (Pan et al., 2009), have shown partitivirus capsids to have a so-called "$T=2$" organization (Hill et al., 1999) comprising sixty CP dimers arranged on a $T=1$ icosahedral lattice, as described more below. The one or two molecules of RdRp packaged inside each particle are presumably anchored noncovalently to the interior capsid surface (Fig. 1), as demonstrated for several other dsRNA viruses (Estrozi et al., 2013; Sen et al., 2008; Zhang et al., 2003). As originally suggested by Buck and Kempson-Jones (1973), each of the two genome segments is thought to be individually encapsidated, inside a separate particle, making partitiviruses not only bisegmented but also biparticulate (Fig. 1).

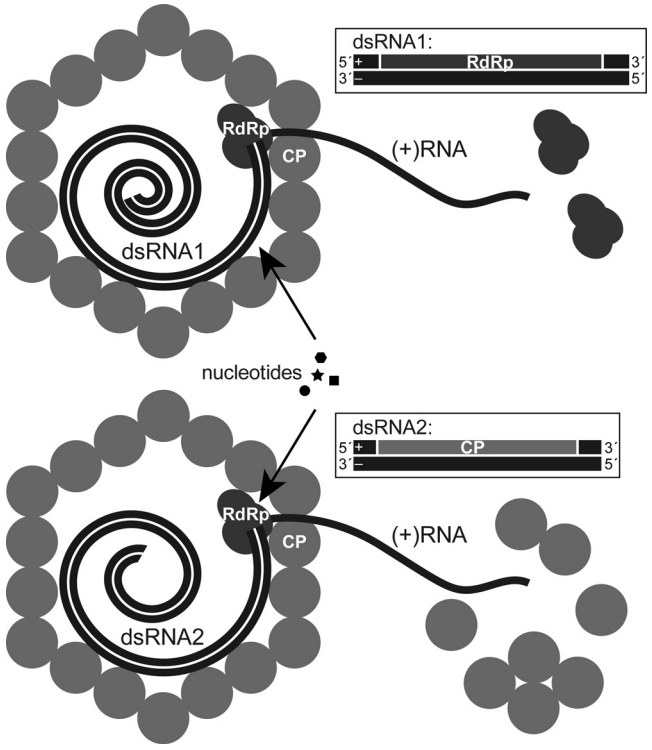

Fig. 1. Schematic diagrams of partitivirus particles and genome segments. The genome segments encoding RdRp (dsRNA1) and CP (dsRNA2) are packaged inside separate capsids formed by multiple (120 total) copies of CP (lighter gray). One or two copies of RdRp (darker gray) are also packaged inside each capsid, presumably noncovalently bound to the inner capsid surface and also associating with one end of the genome segment (end including the 3′ terminus of the minus-strand RNA, which serves as template for transcription initiation). The function of each particle type as a transcriptase machine is also illustrated, including uptake of nucleotides and release of plus-strand (+)RNA transcripts encoding RdRp and CP, respectively. Transcription occurs via a semiconservative mechanism, not illustrated here. Association of CP monomers into dimeric and tetrameric assembly intermediates is suggested at bottom. Insets: the duplex nature of each genome segment is indicated by parallel bars, with the large plus-strand ORF labeled and colored according to the encoded protein.

Like those of other dsRNA viruses, the partitivirus particle is a transcriptase machine in which at least one of the copies of RdRp mediates plus-strand RNA synthesis (transcription) using the minus strand of the genome dsRNA as template (Fig. 1). In the case of partitiviruses, the transcriptase appears to be semiconservative (Buck, 1978), meaning that the newly synthesized plus strand is retained inside the particle as part of the dsRNA while the previous genomic plus strand is extruded for use in translation by cellular ribosomes and/or in packaging into a new partitivirus particle. The 3D structure of a partitivirus RdRp remains to be reported.

Partitivirus particles are thought not to possess capsid-associated protein machinery for mediating efficient entry of uninfected cells from the extracellular environment. Rather, they are regularly transmitted by direct cell-to-cell means, either vertically during cell division, including gamete or spore formation in some cases, or horizontally during intimate cell–cell contacts such as anastomoses between fungal hyphae. Dispersal from host individuals is then by pollen or seeds in the case of plant partitiviruses, asexual or sexual spores in the case of fungal partitiviruses (conidio- and basidiospores, but perhaps not ascospores), and oocysts in the case of *Cryptosporidium* partitiviruses (Boccardo et al., 1985; Ihrmark et al., 2002, 2004; Kniel et al., 2004; Valverde and Gutierrez, 2008). Because the two genome segments are separately encapsidated, at least two partitivirus particles must be transmitted into any new cell to launch a productive infection. Unlike many types of plant viruses that encode movement proteins, partitiviruses show little or no evidence for cell-to-cell spread within plants via plasmodesmata, and indeed spread of partitiviruses to other parts of a plant after grafting does not regularly occur (Boccardo et al., 1985; Valverde and Gutierrez, 2008).

Partitiviruses consistently mediate persistent infections of their hosts and are classically considered to have few, if any, deleterious effects on host cells. They have hence sometimes been called cryptic viruses, or cryptoviruses, especially in the case of plant partitiviruses. In more recent years, however, several examples have emerged in which host effects are seen, as described in more detail below.

2. Taxonomic reorganization of family *Partitiviridae*

2.1. Taxonomic history, phylogenetic findings, and approved changes

The International Committee on Taxonomy of Viruses (ICTV) publishes an encyclopedic report every several years to maintain a regularly updated, authoritative record of its decisions. Family *Partitiviridae* was first recognized in the fifth report and contained the single genus *Partitivirus*, comprising fungal dsRNA viruses with bisegmented genomes (Buck and Ghabrial, 1991) (Table 1). By the sixth report, family *Partitiviridae* had expanded to include genus *Chrysovirus*, comprising fungal dsRNA viruses with tri- or tetrasegmented genomes, as well as genera *Alphacryptovirus* and *Betacryptovirus*, comprising plant dsRNA viruses with bisegmented genomes, but separated into the two different "cryptovirus" genera based on serologic and morphologic properties (Ghabrial et al., 1995). This status quo remained in the ICTV's seventh report (Ghabrial et al., 2000), but by the eighth report, chrysoviruses had been moved into their own family, *Chrysoviridae*, reflecting their larger number of genome segments and other distinctive