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ICTV Virus Taxonomy Profile: *Pseudoviridae*

Carlos Llorens^{1,*}, Beatriz Soriano¹, Mart Krupovic^{2,*} and ICTV Report Consortium

Abstract

Pseudoviridae is a family of reverse-transcribing viruses with long terminal repeats (LTRs) belonging to the order *Ortervirales*. Pseudoviruses are commonly found integrated in the genomes of diverse plants, fungi and animals and are broadly known as Ty1/Copia LTR retrotransposons. Inside the cell, they form icosahedral virus particles, but unlike most other viruses, do not have an extracellular phase. This is a summary of the ICTV Report on the family *Pseudoviridae*, which is available at ictp.global/report/pseudoviridae.

Table 1. Characteristics of members of the family *Pseudoviridae*

| Example: | <i>Saccharomyces cerevisiae</i> Ty1 virus (M18706), species <i>Saccharomyces cerevisiae</i> Ty1 virus, genus <i>Pseudovirus</i> |
|-------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Virion | Virions are icosahedral ($T=3$ or 4) and might be enveloped |
| Genome | Two identical copies of linear single-stranded RNA |
| Replication | Replication by reverse transcription primed with a host-encoded tRNA |
| Translation | Genomic RNA is translated into one or more polyproteins |
| Host range | Fungi, plants and animals |
| Taxonomy | Realm <i>Riboviria</i> , kingdom <i>Pararnavirae</i> , phylum <i>Artverviricota</i> , class <i>Revtraviricetes</i> , order <i>Ortervirales</i> , family <i>Pseudoviridae</i> ; the genera <i>Pseudovirus</i> , <i>Hemivirus</i> and <i>Sirevirus</i> include >30 species |

VIRION

Pseudoviruses form intracellular, somewhat irregularly shaped virus-like particles (VLPs) 30–40 nm in diameter, which do not display infectivity and remain intracellular (Table 1). VLPs are formed by self-assembly of proteins encoded by the *gag* gene, namely the capsid (CP) and nucleocapsid (NC) proteins, which are homologous to the equivalent proteins of retroviruses and other members of the order *Ortervirales* [1]. Expression of truncated Gag protein variants yields icosahedral VLPs of different diameters but with a mean radius of 20 nm built on the $T=3$ or $T=4$ lattice (Fig. 1) [2, 3].

GENOME

The genome of pseudovirids ranges from 4 kb to >9 kb and has an internal region flanked by two identical non-coding

sequences called long terminal repeats (LTRs) (Fig. 2). LTRs are variable in size and contain three regions, named U3-R-U5 in analogy to retroviral LTRs. U3 contains promoters, R is repeated on each end of the transcript, and U5 constitutes the first portion of the reverse-transcribed genome. The internal region is delimited by two short motifs: the primer binding site (PBS), which is located downstream of the 5'-LTR and is usually complementary to the initiator tRNA^{Met}, and the polypurine tract (PPT), which is upstream of the 3'-LTR. The internal region may contain one (*gag-pol*), two (*gag* and *pol*) or three (*gag*, *pol* and *env*) ORFs. The Gag polyprotein includes domains for the CP and NC proteins, while Pol includes domains for the protease (PR), integrase (INT) and reverse transcriptase-ribonuclease H (RT-RH). Members of the genus *Sirevirus* carry a third ORF downstream of *gag-pol* encoding a putative envelope protein [4].

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Abbreviations: CP, capsid; INT, integrase; LTR, long terminal repeat; NC, nucleocapsid; PBS, primer binding site; PPT, polypurine tract; PR, protease; RH, ribonuclease H; RT, reverse transcriptase; VLP, virus-like particles.

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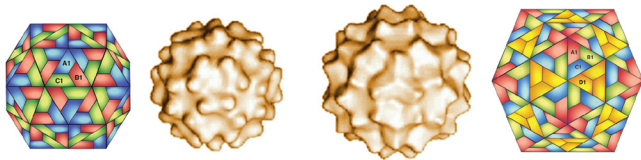


Fig. 1. *Saccharomyces cerevisiae* Ty1 virus particles formed from truncated capsid protein (aa 1–381). The surface structures of two forms ($T=3$, left; $T=4$, right) of around 30–40 nm determined by cryo-electron microscopy, are flanked by the corresponding schematic models. (Courtesy of H. Saibil, adapted from [3] with permission from American Society for Microbiology.)

REPLICATION

The replication of pseudovirids resembles that of retroviruses and occurs via reverse transcription in the VLP. The cellular tRNA molecule, typically initiator tRNA^{Met}, which is packaged into the VLP, anneals to the viral RNA genome at the PBS complementary to the 3'-end of that tRNA and is used by RT as a primer to start reverse transcription. Once the full-length proviral cDNA is synthesized, it is imported into the nucleus, where it is integrated into a chromosomal target site by INT. The integrated form (equivalent to the retroviral provirus) is transcribed by the host RNA polymerase II to generate a new viral RNA molecule, which is translated to produce the Gag and Pol polyproteins and is packaged into the VLPs to reinitiate the replication cycle.

TAXONOMY

Current taxonomy: ictv.global/taxonomy. The family *Pseudoviridae* belongs to the order *Ortervirales* [5] and includes the genera *Pseudovirus*, *Hemivirus* and *Sirevirus*. Current classification is based on host tropism, gene content and the length of the tail of the tRNA used as a primer to initiate reverse transcription. Hemiviruses differ from members of the genus *Pseudovirus* in that they use only a short segment of the tRNA. By contrast, sireviruses are restricted to plants and mostly encode a protein equivalent to retroviral Env downstream of the *gag-pol* gene [4]. Further updates and revisions in the genus demarcation of pseudovirids are expected to be based on phylogenetic criteria as described in the full ICTV Report (see Resources).

RESOURCES

Full ICTV Report on the family *Pseudoviridae*: ictv.global/report/pseudoviridae.

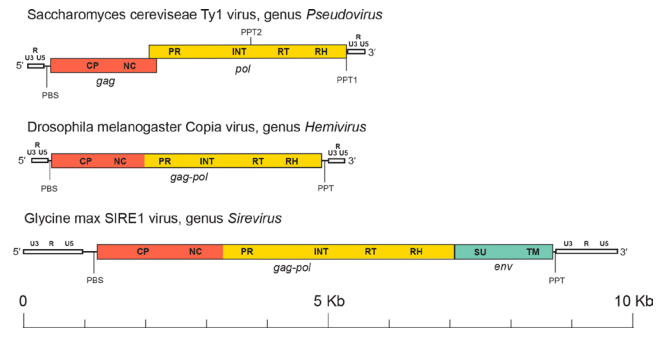


Fig. 2. Pseudovirid genome organization. LTRs are white and show labels for the U3, R and U5 regions. Other labels are: capsid (CP); integrase (INT); long terminal repeat (LTR); nucleocapsid (NC); polypurine tract (PPT); primer binding site (PBS); protease (PR); reverse transcriptase (RT); ribonuclease H (RH); surface (SU); transmembrane (TM).

Gypsy Database (GyDB) devoted to viruses and mobile genetic elements: <http://gydb.org>.

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Conflicts of interest

The authors declare that there are no conflicts of interest.

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