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# ICTV Virus Taxonomy Profile: *Pseudoviridae*

Carlos Llorens<sup>1,\*</sup>, Beatriz Soriano<sup>1</sup>, Mart Krupovic<sup>2,\*</sup> 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 [ictv.global/report/pseudoviridae](https://www.ictv.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 polypeptides
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<sup>Met</sup>, 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 polypeptide 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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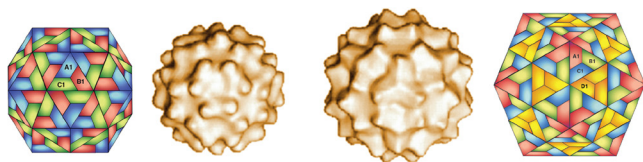
**Keywords:** *Pseudoviridae*; ICTV Report; taxonomy.

**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

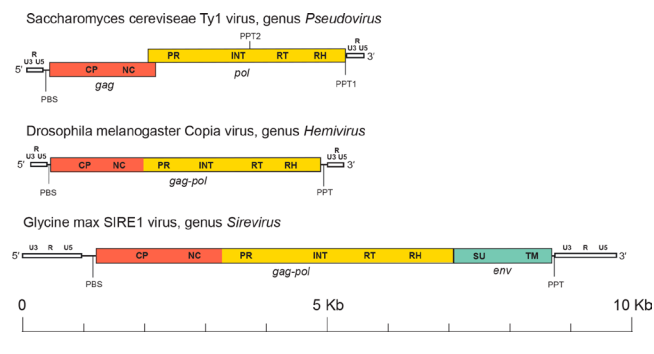
The replication of pseudovirids resembles that of retroviruses and occurs via reverse transcription in the VLP. The cellular tRNA molecule, typically initiator tRNA<sup>Met</sup>, which is packaged into the VLP, anneals to the viral RNA genome at the PBS complementary to the 3'-end of that tRNA and is 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](http://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](http://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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