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# Plant pararetroviruses: interactions of cauliflower mosaic virus with plants and insects

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Virion associated protein (VAP) binds to the icosahedral capsid of cauliflower mosaic virus (CaMV) — a plant pararetrovirus. The interactive coiled-coil domains of this protein can interact with the coiled-coils of either the movement protein or the aphid transmission factor, thereby mediating both cell-to-cell movement and aphid transmission. The host counters CaMV infection with two lines of defense: innate immunity and silencing. The viral protein 'transactivator/viroplasmin' (TAV) is recognized as an effector and either initiates the innate immunity reaction in a non-permissive host or interferes with it in a permissive host. As a silencing suppressor, TAV interferes with dicing of dsRNAs.

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## Cell-to-cell movement and insect transmission

Plant cells are surrounded not only by cell membranes but also cell walls, which are difficult to penetrate. Therefore the plant pararetroviruses (and other plant viruses) have acquired special functions for plant entry and cell-to-cell movement. Unlike mammalian retroviruses, which enter a host cell via membrane fusion, plant viruses usually do not have membranes; rather, about 80% of them employ insects and others, i.e. nematodes or fungi as helpers to enter and leave their plant hosts. They make use of, and widen, plasmodesmata — connections between plant cells that usually allow passage only of ions and small molecules — for cell-to-cell movement. All these functions require that plant viruses encode transmission factors and movement proteins. Both transmission and movement factors can be autonomous proteins or can be domains of the capsid protein.

Caulimoviruses, and perhaps other plant pararetroviruses, have three types of proteins involved in cell-to-cell movement and insect transmission: a 15-kDa virion-associated-protein (VAP), a movement protein (MOV) and an insect transmission factor (ITF), or, more precisely for the icosahedral pararetroviruses, an aphid transmission factor (ATF). An exception is RTBV, which is insect-transmitted by the ITF of a helper virus. CaMV MOV, ATF and VAP are not required for production and accumulation of virus particles in single cells [1], but MOV is required for systemic spread, ATF for insect transmission and VAP for both these processes.

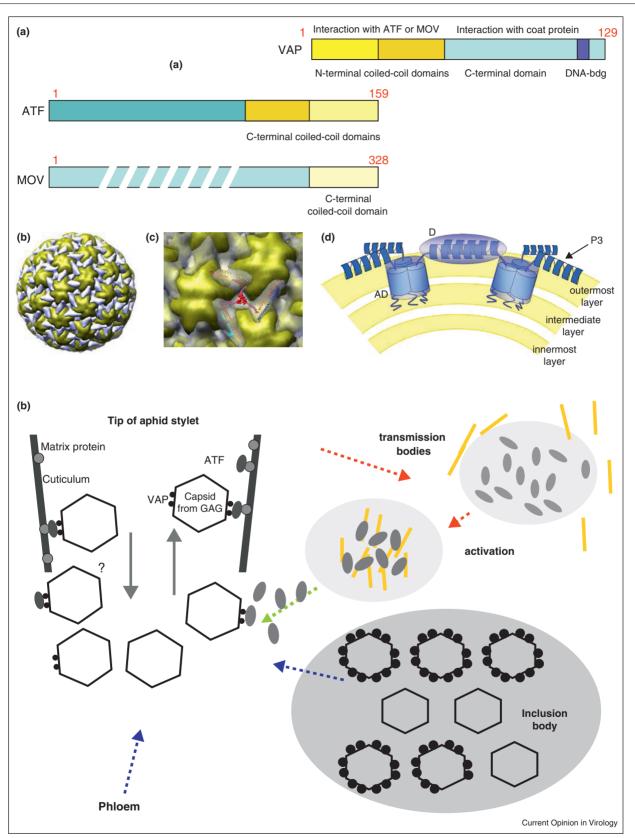
VAP has a proline-rich C-terminal domain, which interacts with the capsid protein [2] and an N-terminal domain consisting of two coiled-coil domains with opposite super coiling handedness (Figure 1a) [3,4°,5,10] — a feature conserved in plant pararetroviruses. Un-liganded VAP accumulates as a tetramer via parallel coiled-coil interactions [3,6]. Virus-liganded VAP decorates virions with the VAP Cterminal domains anchored within the icosahedral capsid [5], probably also interacting with the genome via a nucleic acid binding site [7]. The N-terminal extremities reach out from the capsid surface, dimerize and fold into an antiparallel coiled-coil network coating the virus surface. MOV [11] and ATF [12,13] also contain (C-terminal) coiled-coiled domains and in both cases these domains are involved in self-aggregation as well as in binding the coiled-coiled structure of VAP; MOV forms trimers [11] and ATF forms large aggregates via these coiled-coil regions [13].

Two different mechanisms of plant virus cell-to-cell movement have been recognized. In one, MP is associated with viral RNA in a nucleoprotein complex that is transported through plasmodesmata to neighboring cells [8]; in the other, the protein modifies plasmodesmata by inserting itself as tubules, allowing entire virus particles to pass [9°]. CaMV MP (MOV) belongs to the second class. MOV complexes migrate to the cellular plasmodesmata, where they assemble and form tubular structures spanning the membrane and cell wall. Virus particles then accumulate in the interior of the tubules [11]. Transport is effected either by virus particles moving through the tubules, or by tubules plus virus particles moving through the plasmodesmata together in a treadmill-type mechanism, that is, assembling at the donor side and disassembling at the receiver side.

#### Insect transmission

Three types of insects are involved in plant pararetrovirus transmission: icosahedral plant pararetroviruses are transmitted by aphids [14], badnaviruses by mealy bugs [15]

Figure 1



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