1 Composition and architecture of viruses

1.1 Composition of viruses

Each virus consist of nucleic acid (***RNA or DNA genome***) wrapped up in a protein coat (***capsid***) consisting of viral ***coat proteins*** (also called ***nucleocapsid proteins***) and these capsids are sometimes surrounded by a lipid membrane (***envelope***). In this envelope one or more virus-encoded glycoproteins are present. The proteins that make part of the virus particle (coat proteins and glycoproteins) are called ***structural proteins***, as opposed to the ***non-structural proteins***, which are viral proteins (e.g. polymerase) that are formed during infection but do not take part in the structure of the mature virus particle (***virion***).
Among the plant viruses, only few have an envelope; examples are viruses from the genera *Tospovirus* and *Rhabdovirus*. For example the composition of a rhabdovirus is: 2% RNA, 75% protein, 15% lipids and 5-10% carbohydrates. Most (plant) viruses are not enveloped and consist only of nucleic acid and protein. The content of each of these components varies strongly between different viruses, e.g. *Tobacco mosaic virus* (TMV) contains 5% RNA and 95% protein, while *Cowpea mosaic virus* (CPMV) contains 35% RNA and 65% protein. Some viruses additionally contain poly-amines that neutralise the phosphate groups in the nucleic acid.

At the simplest level, the function of the capsid of a virus particle is to protect the fragile nucleic acid genome from:
- Physical damage (e.g. shearing by mechanical forces).
- Chemical damage (e.g. UV irradiation (sunlight) leading to chemical modification).
- Enzymatic damage (e.g. nucleases that breakdown the nucleic acids).

1.2 Architecture of viruses

Most viruses possess a capsid that is assembled from ***subunits***, the coat proteins. There are several reasons for a particle architecture that is based on the assembly of small subunits:
1. **Structural necessity**: although proteins can have a regular secondary structure (e.g. in form of a α-helix) the tertiary structure is never symmetrical. The symmetry of a virus particle, therefor, comes from a regular arrangement of asymmetrical components (the proteins).
2. **Economy of space**: Besides the coat proteins, the viral genome encodes for other non-structural proteins that are essential for its existence. If a large virus particle can be assembled from relatively small protein subunits, this means that the size of the genome can be restricted.
3. **Allowing self-assembly**: a particle composition of (nearly) identical proteins allows a simple mechanism of self-assembly (no requirement for a complicated intracellular mechanism for virus assembly).
4. **Genetic stability**: a small coat protein gene makes the target for detrimental mutations also smaller.

There are two ways to form symmetrical virus particles from asymmetrical proteins:
a. Rotational arrangement of the proteins into a helix: this leads to particles with a ***helical symmetry***, i.e. ***rod-shaped*** and ***filamentous*** virus particles.
b. Arrangement of the proteins in isometric polygons: this leads to particles with an ***isometric symmetry,*** i.e. *spherical* (round-shaped) virus particles.

Besides these symmetrical viruses, also viruses exist with a more complex architecture (e.g. the enveloped viruses).

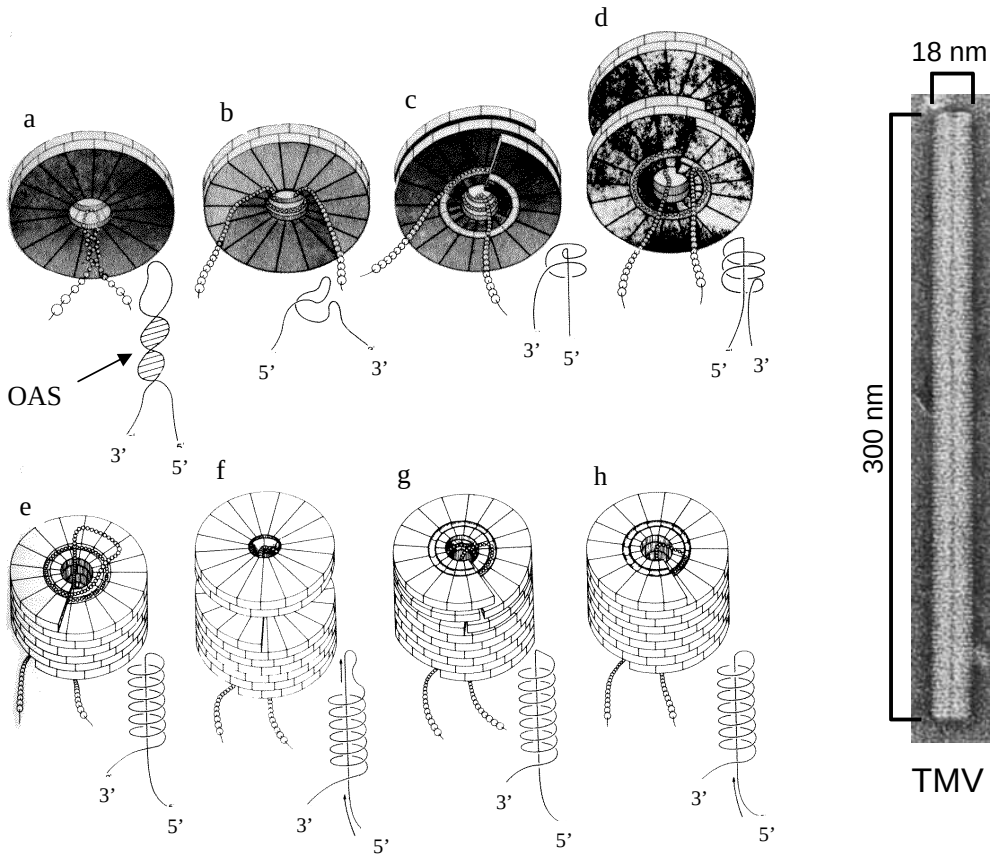

Fig. 1.1 Assembly of a TMV particle. Discs of coat proteins are the building stones in this process. The Origin of Assembly (OAS) on the RNA forms a short hairpin, which binds to the coat protein. On the right an electron micrograph of a TMV particle (length = 300nm; diameter = 18nm.

1.2.1 Viruses with a helical symmetry

Tobacco mosaic virus (TMV) is representative of viruses with a **helical symmetry**. The simplest way to arrange multiple, identical protein subunits is to use rotational symmetry and to arrange the irregularly shaped proteins around the circumference of a circle to form a disc. Multiple discs can then be stacked on top of one another to form a cylinder, with the virus genome coated by the protein shell or contained in the hollow centre of the cylinder. Closer examination of the TMV particle reveals, however, that the structure of the capsid actually consists of a helix rather than a pile of stacked disks (Fig. 1.1).

TMV particles are rigid, rod-like structures, but some helical viruses demonstrate considerable flexibility and longer helical virus particles are often seen to be curved or bent (see **Fout! Verwijzingsbron niet gevonden.** and **Fout! Verwijzingsbron niet gevonden.**) e.g. viruses from the genera *Potyvirus* (750 nm length) and *Closterovirus* (>2000 nm length). Flexibility is important attribute since long helical particles are subject to damage from shear forces and the ability to bend reduces the chance of breakage.

The fact that helical symmetry is a useful way of arranging a single protein subunit to form a particle is confirmed by the large number of different types of viruses that have evolved with this capsid arrangement.

1.2.2 Viruses with an icosahedral (isometric) capsid

Another way of building a virus capsid is to arrange protein subunits in the form of a hollow quasi-spherical structure, enclosing the genome within. The criteria for arranging subunits on the surface of a solid, are more complex than those for building a helix. In order to construct a capsid from repeated subunits, a virus must 'know the rules' which dictate how these are arranged. For an icosahedron (surface of 20 equilateral triangles), the rules are based on the rotational symmetry of the solid, which is known as **2-3-5 symmetry** (Fig. 1.2A). In an icosahedron, 60 asymmetrical proteins can be arranged in 12 groups of 5 protein subunits (***pentamers***; one subunit in each corner of a triangular face) in such a way, that they take up identical (equivalent) positions in relation to the neighbouring subunits and thus form a symmetrical particle (Fig. 1.2B). With plant viruses only the satellite of *Tobacco necrosis virus* (STNV) has such a basic (T=1) icosahedral capsid structure. Other viruses, with larger genomes require larger capsids. To retain the particle symmetry and at the same time enlarge the spherical structure, the triangular faces of the icosahedron can be subdivided into smaller equilateral triangles, a process which is called ***triangulation*** (Fig. 1.2C). In such particles the protein subunits, positioned in the corner of each triangle, form both ***pentamers*** as well as ***hexamers*** (arrangements of 6 subunits) (Fig. 1.2D).

1.2.3 Enveloped viruses

Enveloped viruses use cellular (lipid) membranes to enwrap their genome. With plant viruses these include the rhabdo- and tospoviruses. The site of assembly of the virus particle varies for different viruses, e.g. tospoviruses obtain their membrane at the Golgi complex (see **Fout! Verwijzingsbron niet gevonden.**) and nucleorhabdoviruses at the nuclear membrane (see **Fout! Verwijzingsbron niet gevonden.**).

Viruses modify their lipid envelopes by the synthesis of several classes of proteins, which are associated in different ways with the envelope

1. **Matrix Proteins** (only rhabdoviruses; see also **Fout! Verwijzingsbron niet gevonden.**): These are internal virion proteins whose function is effectively to link the internal nucleocapsid assembly.
2. **Glycoproteins** (rhabdo- and tospoviruses; see also **Fout! Verwijzingsbron niet gevonden.**): These are transmembrane proteins, anchored to the membrane by a hydrophobic domain.

1.2.4 Viruses with a complex structure

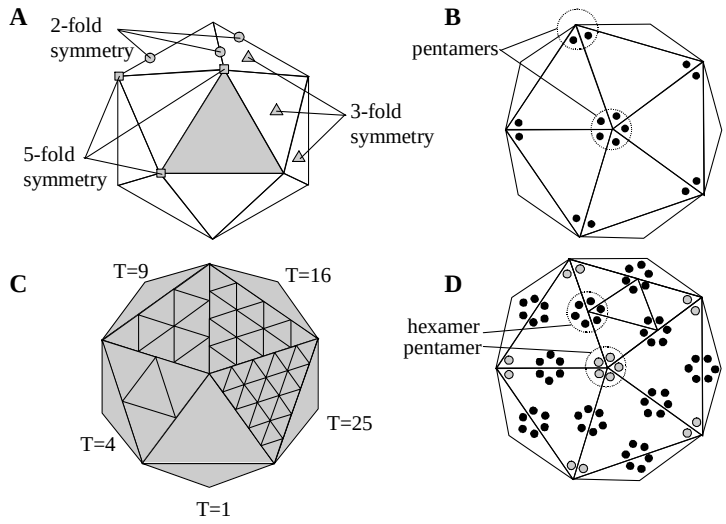

Fig. 1.2 **A)** Symmetry-axes (2, 3 and 5 fold) of an icosahedron. **B)** In each corner of the 20 triangles a coat protein subunit is positioned. This way a capsid is formed consisting of 60 proteins arranged in 12 pentamers (groups of 5 protein subunits). Such a particle is called a T=1 particle. **C)** Further division of the basic triangle in multiple triangles ("Triangulation"), e.g. to enlarge the size of the particle, generates the T=4, T=9 etc. particle. **D)** a T=4 particle with 240 subunits arranged in 12 pentamers (group of 5 subunits) and 40 hexamers (group of 6 subunits).

The majority of viruses can be fitted into one of the three structural classes outlined above, i.e. those with **helical** symmetry, **icosahedral** symmetry or **enveloped** viruses. However, there are many animal-infecting viruses whose structure is more complex, often showing a mixture of the aforementioned architectures.