Neth. J. Pl. Path. 75 (1969) 96–99

The virion, an outdated conception?

J. P. H. VAN DER WANT

Laboratorium voor Virologie, Wageningen

Accepted 1 August, 1968

Abstract

The use of the term virion, proposed in 1962, is discussed. From new views on the nature of certain viruses, it is concluded that this term may lead to confusion. The auth orpoints out that the expression "virus particle" may be maintained, if it is defined more precisely.

Caspar et al. (1962) proposed the term "virion" for "the ultimate phase of viral development, the mature virus". Their paper dealt with the structure of virus particles and consequently they did not include infectivity in the definition of the virion as they indicated.

After its introduction this term has been used with increasing frequency as an equivalent of the more common designation virus particle. As a result the term has attained a wider implication than Caspar et al. had in mind. Perhaps these authors suggested this development by using the expression "mature virus". According to the Concise Oxford Dictionary, 4th Edition, one meaning of mature is: "complete in natural development" Applied to virus this may include the development of all properties which makes the virus particle capable of starting the infection process when introduced in the host.

For instance, Jawetz et al. (1962, p. 243) state: "... the term "virion" has been proposed for an infective virus particle...", and Wildy et al. (1967), in a less precise manner, call the virion "the effective virus particle". Luria and Darnell (1967, p. 3) mention the term in their definition of viruses: "Viruses are entities whose genome is an element of nucleic acid, either DNA or RNA, which reproduces inside living cells and uses their synthetic machinery to direct the synthesis of specialized particles, the virions, which contain the viral genome and transfer it to other cells". In their following paragraph these authors extend the definition of the virion by indicating one of the qualities of a virus: "the possession of an extra-cellular infective state, represented by specialized objects, the virions, which are produced in the cell under the genetic control of the virus itself and serve as vehicles for introducing the viral genome into other cells". Evidently, the viral genome, being responsible for the infective nature of the virus, forms an integral part of the virion in the conception of these authors.

With certain plant viruses, e.g. turnip yellow mosaic virus (Markham and Smith, 1949) two types of particles are formed, both identical in shape and dimensions. One type of particle which is capable of initiating infection, contains nucleic acid; the other type consists only of protein, i.e. the empty capsid after the terminology of Caspar et al. (1962). The former particle is the virion according to the definition of Luria and

Darnell. The empty protein shell can be referred to only as incomplete virion, as its protein shares all chemical and structural features of the protein from the infective particle but lacks the nucleic acid. Luria and Darnell (1962, p. 88) devote a special section to the occurrence of incomplete virions associated with various virus infections. It confirms that they consider infectivity as an essential characteristic of the virion.

For some viruses the virion can be readily defined in terms of physical and chemical characteristics. The virion of tobacco mosaic is a rod-shaped particle of 300 mμ length, having a particle weight of 39×10^6, containing about 2200 protein subunits, having 5% ribonucleic acid comprised of about 6400 nucleotides with a nucleotide composition of 28% adenylic acid, 24% guanylic acid, 20% cytidylic acid and 28% uridylic acid (Knight, 1963).

Recently, data on certain viruses have become available which make it questionable whether the term "virion" in its developed sense can be generally applied. The viruses involved are sometimes called multicomponent viruses. Their purified preparations are not homogeneous but they contain a number of components. Each component consists of nucleoprotein particles which can be characterized by chemical and/or physical means. The interrelationships between components may differ from one multicomponent virus to the other. To elucidate the matter three such viruses are briefly considered here, viz. tobacco rattle virus, cowpea mosaic virus, and alfalfa mosaic virus[1]. Data in the literature suggest that more viruses exist which show the phenomenon of being multicomponent.

In dip preparations as well as purified nucleoprotein suspensions of *tobacco rattle virus* short and long rod-shaped particles occur (Harrison and Nixon, 1959). Both types of particles can be separated by density gradient centrifugation. The long rods are infectious, but the short ones are not. The infective long rods give rise to the reproduction of their nucleic acid. However, no viral coat protein is produced and, hence, the viral nucleic acid of the long rods remains naked (Frost et al., 1967). For production of coat protein it is necessary to introduce the short particles into the host in combination with the long ones. Then short particles also are formed. The short particles alone do not induce either the production of their RNA or the viral coat protein. Thus, the long particles carry the information for the synthesis of their own RNA and that of the short particles if the latter have been introduced at the same time; the short particles carry the information for the production of coat protein for both particle types but are unable to multiply in the absence of the genome of the long particles.

Can we apply the term virion to both types of rattle virus particles? The short particles by themselves are unable to initiate the infection process, hence they are not virions as defined by Luria and Darnell. The long particles are infectious but they are unable to induce information of coat protein. They may be considered as virions as far as their infectivity is concerned but upon reproduction they do not induce the reproduction of nucleoprotein particles but only of viral nucleic acid. By using an extracting procedure based on phenol, the naked viral nucleic acid can be transmitted mechanically. However, it would seem inappropriate to refer to these naked nucleic acid particles as virions. The same question could be raised regarding certain mutants of tobacco mosaic virus which are unable to induce the production of coat protein or of protein suitable to coat the viral nucleic acid (Siegel et al., 1962).

[1] The author has not aimed to cite all the relevant literature concerning these viruses.

Purified preparations of *cowpea mosaic virus* contain a number of components, all having the same polyhedral shape. They are designated top component (consisting of capsids exempt of viral nucleic acid), and bottom and middle components both consisting of nucleoprotein particles (van Kammen, 1967). Extremely purified preparations of bottom and middle components are non-infectious; the infectivity is obtained only when both are present in the inoculum (van Kammen, 1968).
Purified preparations of *alfalfa mosaic virus* contain a number of nucleoprotein components from sausage-shaped to spherical particles; the coat protein of the components is considered to be the same (Gibbs et al., 1963; Jaspars and Moed, 1966). There is evidence that the nucleic acid from the top component *a* carries the information for the coat protein (van Ravenswaay Claasen et al., 1967). The infectivity of the combined nucleic acids obtained from purified top component *a* and bottom component is strongly enhanced as compared to the infectivity of the same nucleic acids separately (van Vloten-Doting and Jaspars, 1967). This result indicates that the inoculum has to contain at least top component *a* and bottom component to start the infection process resulting in the production of the components specific for alfalfa mosaic virus, i.e. these components together carry the necessary genetic information for infection and reproduction. Inoculated separately, they are active, although this does not necessarily mean that they could not undergo some of the initial basic steps of the infection process.
This brief summary shows that in certain cases the viral genetic material is distributed over more than one nucleoprotein particle. Evidently the genetic viral material is distributed not at random over the mutually complementory components but in a regular fashion. This means that the distinct distribution of the viral nucleic acid over the components is genetically controlled. Thus the particles of each component are not incomplete in themselves; therefore they cannot be designated as incomplete virions. According to the definition by Luria and Darnell they cannot be called virions either as they carry only part of the necessary genetic information. It is only when particles of one component are complemented by those of the other that the conditions for viral activity leading to the production of new nucleoprotein particles are fulfilled.
In this connection attention should be also paid to satellite virus. In association with tobacco necrosis virus a satellite virus may occur which is capable of reproducing only in the presence of the former (Kassanis, 1965). There is evidence that the satellite virus genome carries information for the production of satellite viral coat protein (Clark et al., 1965) but that it lacks the information for the replication of its nucleic acid for which it depends on the tobacco necrosis virus. The tobacco necrosis virus is not dependent upon the presence of the satellite virus since the former is capable of initiating infection and multiplying without the latter.
In view of the quoted definition by Luria and Darnell the particles of the satellite virus cannot be called virions since their activity can only be triggered by the tobacco necrosis virus.
From the facts mentioned here it can be concluded that the term "virion" as defined by common usage is inadequate to cover all the "ultimate phases of viral development" as a consequence of the manyfold specific qualities virus particles may have according to recent findings. To avoid further confusion it is necessary to abandon the term "virion". The less precise designation "virus particle" is still useful, and gains value if additional information about the characteristics of the type of particle is given.

Samenvatting

Het virion, een achterhaald begrip?

Een bespreking wordt gegeven van het gebruik van de term virion sedert 1962 toen hij werd voorgesteld. Naar aanleiding van nieuwe inzichten in de aard van bepaalde virussen wordt geconcludeerd dat deze term tot verwarring kan leiden. De schrijver stelt dat de uitdrukking "virusdeeltje", mits nader omschreven, kan worden gehandhaafd.

References

Caspar, D. L. C., Dulbecco, R., Klug, A., Lwoff, A., Stoker, M. G. P., Tournier, P., and Wildy, P., 1962. Proposals. Cold Spring Harbor Symposia on Quantitative Biology 27: 49–50.

Clark Jr., J. M., Chang, A. Y., Spiegelman, S., and Reichmann, M. E., 1965. The in vitro translation of a monocistronic message. Proc. natn. Acad. Sci. U.S.A. 54: 1193–1197.

Frost, R. R., Harrison, B. D., and Woods, R. D., 1967. Apparent symbiotic interaction between particles of tobacco rattle virus. J. gen. Virol. 1: 57–70.

Gibbs, A. J., Nixon, H. L., and Woods, R. D., 1963. Properties of purified preparations of lucerne mosaic virus. Virology 19: 441–449.

Harrison, B. D., and Nixon, H. L., 1959. Separation and properties of particles of tobacco rattle virus with different lengths. J. gen. Microbiol. 21: 569–581.

Jaspars, E. M. J. and Moed, J. R., 1966. The complexity of alfalfa mosaic virus. In: A. B. R. Beemster and J. Dijkstra (Editors), Viruses of plants, pp. 188–195. North-Holland Publishing Company, Amsterdam.

Jawetz, E., Melnick, J. L., and Adelberg, E. A., 1962. Review of medical microbiology. Lange Medical Publications, Los Altos, California, 400 pp.

Kammen, A. van, 1967. Purification and properties of the components of cowpea mosaic virus. Virology 31: 633–642.

Kammen, A. van, 1968. The relationship between the components of cowpea mosaic virus. I. Two ribonucleoprotein particles necessary for the infectivity of CPMV. Virology 34: 312–318.

Kassanis, B., 1965. Properties of tobacco necrosis virus and its association with satellite virus. Annls Inst. phytopath. Benaki 6: 7–26.

Knight, C. A., 1963. Chemistry of viruses. Protoplasmatologia IV, 2. Springer-Verlag, Wien. 177 pp.

Luria, S. E., and Darnell Jr., J. E., 1967. General virology. 2nd ed. Wiley, Inc. New York, 512 pp.

Markham, R., and Smith, K. M., 1949. Studies on the virus of turnip yellow mosaic. Parasitology 39: 330–342.

Ravenswaay Claasen, J. C. van, Leeuwen, A. B. J. van, Duijts, G. A. H., and Bosch, L., 1967. In vitro translation of alfalfa mosaic virus RNA. J. molec. Biol. 23: 535–544.

Siegel, A., Zaitlin, M., and Sehgal, O. P., 1962. The isolation of defective tobacco mosaic virus strains. Proc. natn. Acad. Sci. U.S.A. 48: 1845–1851.

Vloten-Doting, L. van and Jaspars, E. M. J., 1967. Enhancement of infectivity by combination of two ribonucleic acid components from alfalfa mosaic virus. Virology 33: 684–693.

Wildy, P., Ginsberg, H. S., Brandes, J., and Maurin, J., 1967. Virus-classification, nomenclature and the International Committee on Nomenclature of Viruses. Prog. med. Virol. 9: 476–482.