A STUDY OF PURIFIED VIRUSES WITH THE ELECTRON MICROSCOPE

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PLATES 1 TO 4

(Received for publication, January 31, 1941)

Viruses were discovered in 1892 when Iwanowski (1) observed that the agent causing the mosaic disease of tobacco passed through a filter which retained all of the bacteria then known. During the ensuing years many viruses causing diseases in plants, animals, and bacteria have been discovered, and in general these agents have also been found to pass filters which retain ordinary bacteria. It has been necessary, therefore, to devise special means for determining the sizes of these very small infectious agents. For some years the method of ultrafiltration analysis with graded collodion membranes was widely and successfully used (2). Ultraviolet light photography (3), fluorescent microscopy (4), and special staining techniques (5) were also used for some of the larger viruses. By means of such methods it was established that the sizes of viruses ranged from about 250 mμ down to about 10 mμ. Although objects as small as 5 mμ may be rendered visible by dark-field illumination, nothing may be gleaned as to their detailed structure; hence, it is obvious that ordinary microscopy cannot, in general, be used successfully for the viruses, since the limit of resolution for visual light is about 250 mμ.

During the past 5 years, several viruses have been obtained in highly concentrated and presumably essentially pure form, and it has been possible to learn something of the size and shape of the particles in these preparations by means of sedimentation, diffusion, double refraction of flow, viscosity, and x-ray studies (6).

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One of the outstanding developments was the finding that, in confirmation of an earlier indication (7), some of the viruses depart markedly from a spherical form. For example, by means of data obtained in the studies mentioned above, tobacco mosaic virus was estimated by indirect methods to be about 12 m\(\mu\) in diameter and about 400 m\(\mu\) in length and to have a molecular weight of about 40 millions (8). Although the theory of the physico-chemical behavior of spherical particles has been worked out fairly thoroughly and appears to rest on a firm foundation, that of particles which depart markedly from a spherical form assuredly is on a much less firm basis. Frampton, for example, considers that in the case of tobacco mosaic virus the asymmetry and molecular weight values calculated from physicochemical data are wholly ambiguous and has shown that by his method of calculation a molecular weight value of infinity on the one hand and of zero on the other hand may be obtained (9). For reasons which have already been discussed (6), there appears to be little justification for the assumption of such an extreme viewpoint. Nevertheless, the indirect methods provide at best only approximations of the true sizes and shapes of asymmetrical particles and a means for the direct mensuration of such particles has been lacking.

In recent years electron microscopes having resolving powers extending down to about 5 m\(\mu\) have been developed. Complete descriptions of the different instruments and of the mode of operation and preparation of specimens may be found elsewhere (10–13). Although excellent micrographs of bacteria have been obtained by means of this apparatus and have proved of value in supplementing information already available (11, 14), it would appear that the electron microscope will be of greatest value in the microscopy of objects having sizes between about 5 and 250 m\(\mu\), a range not covered by the light microscope and one in which practically all viruses have been found to fall. The electron microscope offers the possibility of securing micrographs of individual virus particles and thus of establishing their sizes and shapes with some precision. It should also be possible to determine the extent of the variation in the size and shape of a given virus and even perhaps learn something of the mechanism by means of which a virus particle is duplicated within the host and of the
nature of the difference between strains of a given virus. In this paper are presented the results of preliminary electron microscopic studies of five plant viruses.

EXPERIMENTAL

*Tobacco Mosaic Virus*—Tobacco mosaic is the only one of the viruses used in the present study which has been investigated previously by means of an electron microscope (15–18). Most of the virus preparations used in the earlier studies were purified by chemical treatment and such treatment has been found to cause inactivation and aggregation of this virus. Tobacco mosaic virus purified by means of differential centrifugation has been found to be essentially the same as the virus in the untreated infectious juice with respect to biological activity and physicochemical properties (19); hence it appeared desirable to repeat and extend the electron microscope studies with virus purified by differential centrifugation. In preliminary work a small drop of a solution containing 0.2 mg. of four times ultracentrifuged tobacco mosaic virus per cc. in distilled water was applied by means of a capillary pipette to a collodion film about 15 μm thick supported on a copper gauze. An attempt was made to secure as thin a film of liquid as possible on the mount. The film was allowed to dry, the mount was placed in the microscope, and the chamber was evacuated. When an area near the center of the mount was brought into focus, the field shown in Fig. 1 (Plate 1) was obtained. It is obvious that the concentration of virus was too great to give a good definition of the individual particles. Fig. 2 presents the appearance of a field nearer the edge of the same mount, in which the individual particles may be seen. Still greater separation of the particles was obtained in an area near the edge, which is shown in Fig. 3. A similar area of another virus preparation which was applied in the same way but at a concentration of 0.01 mg. per cc. is given in Fig. 4 (Plate 2).

The virus shown in Figs. 1 to 3 was used about 3 weeks after preparation. It seemed possible that the granular background and the suggestion of a granular structure for the rods might result from some aging process. Freshly prepared samples of tobacco mosaic virus were applied at a concentration of 0.01 mg. per cc. and examined by means of the electron microscope. Some
of the results which were obtained are shown in Figs. 5 to 7 (Plates 2 and 3), and it may be seen that the granular appearance is absent in these micrographs. However, when a drop of dilute ammonia was added to 1 cc. of an aqueous solution containing 0.01 mg. of tobacco mosaic virus and the preparation immediately observed, the results shown in Figs. 8 and 9 were obtained. The rod-like particles begin to disintegrate with the formation of material which has a granular appearance. It is known from previous chemical work that an excess of alkali causes the denaturation and disintegration of tobacco mosaic virus (20). In Fig. 8 some of the rods may still be seen, whereas in Fig. 9 the field is free of rods and only a granular material remains. However, it is known from previous studies (11) that the film obtained from a dilute solution of an inorganic salt also has a granular appearance. The induced or the spontaneous disintegration of a virus preparation or the presence of a small amount of inorganic material may, therefore, be responsible for the presence of granules. Later micrographs of virus aged for a period of some weeks were similar to those shown in Figs. 5 to 7; hence a granular appearance does not appear to be an invariable result of aging.

Figs. 2 to 7 demonstrate unequivocally the existence of discrete rod-like units in purified preparations of tobacco mosaic virus. The fact that the bulk of the material exists in this form, together with the fact that a great mass of evidence has been accumulated which indicates that the virus activity is associated with such a unit (6), makes it reasonable to assume that the predominating unit shown in Figs. 3 to 6 represents a single particle of tobacco mosaic virus. During the past few years, indirect evidence was obtained which indicated that under certain conditions there occurred an end-to-end as well as a side-to-side aggregation of tobacco mosaic virus (21). Figs. 3 to 6 provide convincing evidence for the existence of elongated aggregates presumably formed by the end-to-end combination of two or more units. Side-to-side aggregation, as well as a combination of this with end-to-end aggregation, is shown in Figs. 5 to 7. The type of aggregation shown in Fig. 7 appears to be that which obtains in the structures which have been referred to as crystals of tobacco mosaic virus (20). There is little indication of a regular structure and, in accordance with earlier results (16), the mass has more
nearly the appearance of a fiber. However, x-ray data have been obtained which indicate that in such aggregates the rods are arranged laterally in two-dimensional, hexagonal close packing (22).

The nature of the forces involved in the end-to-end type of aggregation is of some interest. There is evidence that the ultimate unit of tobacco mosaic virus possesses a dipole moment in the direction of the long axis or that such a moment is induced by an electrical field (23, 24). However, an unsymmetrical distribution of specific charges may be responsible for the marked tendency of the particles to aggregate. The aggregates do not appear to represent the natural form of the virus, for when carefully prepared samples of virus or virus in the freshly expressed untreated infectious juice are examined by means of the analytical ultracentrifuge no evidence for the existence of the aggregates is obtained, whereas following treatment with salt the same samples show either a second sedimenting boundary, presumably due to a component formed by the end-to-end aggregation of two particles, or a more rapidly sedimenting diffuse boundary indicative of even more extensive aggregation. Furthermore, recent micrographs show clearly the unaggregated rods in the freshly expressed untreated juice from mosaic-diseased plants (18). It seems likely that much of the aggregation shown in Figs. 5 to 7 takes place at the time of the drying of the films, when a marked concentration of the virus occurs. As the final stages of the drying occur, a violent whipping motion has been observed by means of an ordinary light microscope. This may be responsible for the formation near the edge of the collodion film of such great masses as those shown in Figs. 5 and 6. The possibility of avoiding aggregation due to such causes through the use of more dilute solutions of virus is being investigated. However, the micrographs already obtained provide good evidence for the existence of a predominating unit having a fairly uniform size and shape. Many measurements of the dimensions of the unit seen in these micrographs have been made and the particle appearing in greatest preponderance is about 15 m\(\mu\) in diameter and about 280 m\(\mu\) in length. The precision in the measurements of particle lengths in this work is of the order of 5 m\(\mu\), while the absolute error in magnification may be as great as 10 per cent. As may be seen from Fig. 10, measure-
measurements of the lengths of all of the 58 particles in two selected fields indicate that a unit having a length of 280 mμ predominates. It may be calculated that on a weight basis over 50 per cent of the material exists in the form of particles having a length of 280 mμ and over 70 per cent in the form of particles having lengths within 7 per cent of this value. The values for the dimensions of this unit do not conflict with estimates based on x-ray data (22) of a particle diameter of 15 mμ and a particle length of some value greater than 150 mμ. It seems likely that the value of 15 mμ estimated from x-ray data and that of 280 mμ estimated from the present micrographs represent the best values for the dimensions of the virus used in the present work. The density of tobacco mosaic virus has been found to be 1.33 (23, 25). The molecular weight of a particle having a circular cross-section 15 mμ in diameter, a length of 280 mμ, and a density of 1.33 would be 39.8 × 10⁶. This value is in unusually good agreement with the value of 42.6 × 10⁶ which was estimated by indirect methods and used tentatively in earlier calculations (21). It has been suggested

![Graph showing distribution of lengths of particles in an ultracentrifugally prepared sample of tobacco mosaic virus.](http://www.jbc.org/)

**Fig. 10.** Distribution of lengths of particles in an ultracentrifugally prepared sample of tobacco mosaic virus.
that the molecule collapses on drying so that the cross-section is elliptical rather than circular and that the molecular weight is actually slightly lower than the above. However, x-ray data on dried films indicate that there is no extensive collapse of the particles, for there is no distortion of the intramolecular structure and the interparticle distance in such films is 150 mμ (22). In addition, it may be possible to secure further evidence by refined techniques designed to determine the molecular weight from the total electron scattering produced by the molecule. However, it is apparent from the present micrographs that tobacco mosaic virus has a definite size, shape, and molecular weight and that the dimensions indicated by the electron microscope studies are of the same order of magnitude as those indicated previously by indirect methods (21). This finding is of importance in connection with the theories of the physicochemical behavior of asymmetrical particles, for it indicates that the indirect methods based on physicochemical data are reasonably valid when correctly used. Tobacco mosaic virus has therefore been of considerable value in demonstrating the usefulness of different methods of approach in the estimation of the size and shape of colloidal particles.

The particle length of about 280 mμ indicated by the micrographs of the ultracentrifugally purified tobacco mosaic virus used in the present work is significantly larger than the values of about 140 and 190 mμ which were estimated by Melchers and coworkers (18) from electron micrographs of two strains of tobacco mosaic virus, one of which is referred to as tomato mosaic virus since it was first noted in tomato plants. These results indicate that the strains of a virus have different particle lengths. Some years ago it was found in this laboratory that the sedimentation constants of different samples of the same strain of tobacco mosaic virus prepared from different lots of the same as well as different species of diseased plants were the same, whereas preparations of strains of tobacco mosaic virus even when obtained from the same type of host plant were found to have different sedimentation constants (26, 27). For example, when determined under the same conditions the sedimentation constant of the strain known as aucuba mosaic virus was found to be about 6 per cent larger than that of ordinary tobacco mosaic virus. Although at that time it was impossible to assign a definite reason for this difference, it was inferred that the difference was due either to a difference in
weight or to a difference in asymmetry. Because of the electron micrographs and the x-ray data which are now available, it seems likely that the particles of strains of tobacco mosaic virus differ both in weight and in asymmetry. The best estimate of particle thickness is probably provided by the x-ray data which indicate that the three strains, ordinary tobacco mosaic, aucuba mosaic, and enation mosaic viruses, all have the same diameter; namely, 15 μm. The electron micrographs show the two strains of virus used by Melchers and coworkers (18) to have particle lengths of about 140 and 190 μm, respectively, and the strain used in the present work to have a particle length of about 280 μm. It is of interest to correlate these dimensions with the sedimentation constants of these preparations. Unfortunately, it is not known whether the sedimentation constant values reported by Melchers and coworkers represent true and reproducible values, since there was no indication of repeated determinations. However, assuming these values to be correct, it follows from Lauffler's work (28) that the values which were each reported to be 180 × 10^{-13} cannot in fact be identical, for one constant was determined at a virus concentration of 2 mg. per cc., whereas a concentration of 3 mg. per cc. was used for the other. If it be assumed that the variation in sedimentation constant with concentration is similar to that which Lauffler found to obtain with his preparations of tobacco mosaic virus, it may be calculated that the sedimentation constant of 180 × 10^{-13} at a concentration of 3 mg. per cc. corresponds to a constant of 183 × 10^{-13} at a concentration of 2 mg. per cc. It may or may not be significant that the corrected value of 183 × 10^{-13} belongs to the strain having the longer particle length of 190 μm. Although the values which Melchers and coworkers reported for the sedimentation constants may be fortuitous, the results now available for strains of virus at a concentration of 2 mg. per cc. would indicate a correlation between the length of particle and sedimentation constant, for preparations having particle lengths of 140, 190, and 280 μm have sedimentation constants of 180, 183, and 187 × 10^{-13}, respectively. If these results are treated in the manner described by Lauffler and Stanley (21), it may be seen that there is a good correlation and that it is in accord with theory. Similar calculations show that the sedimentation constant reported for the dimer formed by the end-to-end aggregation of two particles of length 190 μm is in good
agreement with the theoretical value. If the considerations just discussed are valid, it may be predicted that aucuba mosaic virus, which has been reported to have a sedimentation constant about 6 per cent larger than that of the virus used in the present work, should have a particle length of about 330 \( \mu \). It is obvious, however, that, although the results already obtained indicate that strains of a virus have the same thickness but differ in both weight and particle length, many more experimental data must be obtained before the full significance of the differences between strains may be realized.

More extended observations must be made in connection with the electron microscope studies in order to establish the nature of any artifacts which may result from the drying of the film of a virus preparation or the exposure to the electron beam. The fact that a micrograph taken with the first flow of electrons through a given specimen does not appear to differ from subsequent micrographs taken after longer exposure to the electron beam makes it seem unlikely that gross changes are caused by the electrons. However, the violent motion which takes place as the film dries or the extreme desiccation which occurs on evacuation of the chamber containing the mount may cause some alteration of the specimen. Although it seems very unlikely that these could cause any gross changes in the size and shape of the particles, it is to be hoped that more exact information concerning the nature and extent of any change will become available as the work progresses. It has already been pointed out that on intensive drying of films of tobacco mosaic virus the interparticle distance decreases only from 152 to 150 \( \AA \). (22), thus indicating but little shrinkage.

In Figs. 3 to 6 of the present paper, a number of particles are in evidence which are definitely shorter than the predominating unit. It is not known whether these short particles occur regularly in preparations of tobacco mosaic virus or are produced at the time the specimen is mounted. It seems unlikely that they are due to an image produced by a particle of ordinary length which is not lying flat, since surface forces would tend to flatten all the molecules. Furthermore, the particles shown in the micrographs have about the same density, a condition which could obtain only if the particles were lying flat so that uniform thicknesses would be traversed by the electrons. There is at present
no evidence either from activity measurements on the supernatant fluids obtained on ultracentrifugation or from measurements by means of the analytical ultracentrifuge for the existence of these particles. They may, however, possess no virus activity or represent but a small fraction of a preparation and hence not be demonstrable by these methods. The true nature and significance of these short particles is not known at present. If it can be proved that they are not an artifact, that they regularly occur in mosaic-diseased cells and do not represent a degradation product, it is conceivable that they may represent partially synthesized virus particles or viable as well as non-viable virus variants. Nothing is known of the mechanism by means of which a virus particle is duplicated, but it is possible that these particles may provide a clue. The evidence at hand provides no definite indication as to whether duplication is preceded by longitudinal growth and lateral division, lateral growth and longitudinal division, growth from a point, or by some cataclysmic event, although the first possibility might appear most reasonable. It is to be hoped, however, that future work will provide some evidence regarding the course of events during the process of duplication of a virus particle.

Cucumber Mosaic Virus 3—Cucumber mosaic virus 3 may be regarded as being rather unusual, since it has not been found transmissible to any plants except members of the Cucurbitaceae (29). Most plant viruses do not have such a narrow host range; tobacco mosaic virus, for example, has been transmitted to forty-six different species of plants representing fourteen widely separated families (30, 31). Despite the fact that cucumber mosaic virus 3 will not multiply in plants susceptible to tobacco mosaic virus and the latter cannot be transmitted to cucumber plants, the two viruses have been found to have very similar physical, chemical, and immunological properties (32). Although the x-ray data indicate a particle thickness of 14.6 mμ, a value which is considered to be significantly smaller than the value of 15 mμ for tobacco mosaic virus (22), it seems possible that cucumber mosaic virus may have arisen from tobacco mosaic virus through some fortuitous event. It was therefore of interest to determine whether the micrographs of the particles of the cucumber mosaic virus obtained with the electron microscope would

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*Knight, C. A., unpublished work.*
be similar to those of tobacco mosaic virus. The samples of cucumber mosaic virus 3 used were prepared by means of differential centrifugation by Dr. C. A. Knight. It is a pleasure to thank Dr. Knight for making these preparations and those described in the following section available to us.

An aqueous solution containing 0.1 mg. of the virus per cc. was mounted as previously described and the micrograph reproduced in Fig. 11 (Plate 3) was obtained. It is obvious that the virus solution was too concentrated, so it was diluted with 99 volumes of water. The micrograph obtained with the dilute solution is shown in Fig. 12 (Plate 1). It may be seen that this virus has a rod-like form and that the diameter is about the same as that of tobacco mosaic virus but that the end-to-end aggregation appears to be somewhat more marked than in the case of tobacco mosaic virus. It is possible that the latter may be due to the use of a solution at a slightly more acid reaction and this point is now under investigation. It may be seen from Fig. 13 (Plate 3) that the rod-like particles of cucumber mosaic virus form fibrous aggregates similar in appearance to those formed by tobacco mosaic virus. Although more extensive studies will be required to establish definitely the length of the particle, measurements on the micrographs already available indicate that cucumber mosaic virus 3 has a particle length of about 300 μμ. The micrographs show, therefore, that, in accordance with previously obtained chemical, physical, and serological data, the ultimate unit of cucumber mosaic virus 3 is similar in size and shape to that of tobacco mosaic virus.

Tomato Bushy Stunt Virus—Tomato bushy stunt virus has been
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purified by chemical means (33) and by differential centrifugation (34) and obtained in the form of large rhombic dodecahedral crystals. During the course of these studies, evidence was obtained that the virus particles were essentially spherical in shape and had a diameter of about 26 μm (35). An aqueous solution containing 0.01 mg. of ultracentrifugally isolated bushy stunt virus per cc. was mounted and studied by means of the electron microscope. It may be seen from Fig. 16 (Plate 4) that the particles which are shown have essentially the size and shape indicated by other methods. The tendency of the particles to collect along a fold in the collodion membrane may be noted. Since the size of bushy stunt virus has been well established by different independent methods (34-36), the good agreement of the size of the virus estimated from the electron micrograph with that estimated previously by other methods is significant, for it may be regarded as an indication that no gross change in size occurs during the preparation of the mount.

Tobacco Necrosis Virus—Pirie and coworkers (37) purified tobacco necrosis virus by chemical methods and reported that crystalline and amorphous preparations having the same specific virus activity had sedimentation constants of $130 \times 10^{-13}$ and $58 \times 10^{-13}$, respectively. However, Price and Wyckoff (38) found a sedimentation constant of $112 \times 10^{-13}$ for tobacco necrosis virus purified by differential centrifugation. The size of this virus was estimated to be between 13 and 20 μm by ultrafiltration measurements (39) and by means of radiation studies (40). Since the two extreme values for the sedimentation constant might be considered to indicate a size between about 10 and 30 μm, it is obvious that only the order of the magnitude of the size of tobacco necrosis virus is known. In the present study an aqueous solution containing 1 mg. of ultracentrifugally isolated tobacco necrosis virus per cc. was used and the electron micrograph reproduced as Fig. 17 (Plate 4) was obtained. It may be seen that the particles appear to be spherical in shape and have diameters of about 20 μm.

The writers desire to thank Dr. V. K. Zworykin for his interest and encouragement during the course of the work. It is also a pleasure to thank Dr. L. Marton and Mr. J. Hillier for assistance and advice during the preparation of the micrographs shown in the present paper.
SUMMARY

Purified preparations of five viruses have been studied by means of the electron microscope. The electron micrographs of the ultracentrifugally isolated tobacco mosaic virus used in the present work showed a predominating unit about 15 mμ in width and 280 mμ in length and presumably representing single particles of this virus, together with aggregates formed by the end-to-end as well as side-to-side aggregation of this unit and a small amount of rods having shorter although variable lengths. The fact that the dimensions of this unit were of the same order of magnitude as those estimated previously by indirect methods based on physico-chemical data indicates that the latter procedures are useful and essentially valid even for asymmetrical particles when correctly used. Since the particle length of the virus used in the present work was significantly greater than those of two strains studied by other workers, it seems likely that strains of a virus may have different particle lengths. The electron micrographs of cucumber mosaic virus 3 and of its related strain cucumber mosaic virus 4 were very similar, showed a marked amount of end-to-end aggregation, and indicated that the ultimate units were similar in size and shape to that of tobacco mosaic virus. In the case of tomato bushy stunt virus, the micrographs showed spherical particles about 26 mμ in diameter, whereas with tobacco necrosis virus the results indicated that the particles were essentially spherical and about 20 mμ in diameter.

BIBLIOGRAPHY

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EXPLANATION OF PLATES

PLATE 1

FIG. 1. Area near center of mount prepared with an aqueous solution containing 0.2 mg. of ultracentrifugally isolated tobacco mosaic virus per cc. \( \times 55,000 \).
FIG. 2. Area nearer edge of mount used for Fig. 1. \( \times 54,000 \).
FIG. 3. Area near edge of mount used for Fig. 1. \( \times 55,000 \).
FIG. 12. Ultracentrifugally isolated cucumber mosaic virus 3 applied at a concentration of 0.001 mg. per cc., showing single particles and characteristic aggregation. \( \times 30,000 \).
PLATE 2

FIG. 4. Tobacco mosaic virus applied to a collodion film at a concentration of 0.01 mg. per cc.  × 24,600.

FIG. 5. Tobacco mosaic virus applied at a concentration of 0.01 mg. per cc. Aggregation of particles near the fold in the collodion film may be noted. × 19,500.
PLATE 3

FIG. 6. Aggregation of tobacco mosaic virus near a fold in the collodion film as in Fig. 5. × 17,500.

FIG. 7. Fiber-like aggregation of tobacco mosaic virus. × 22,500. (Micrograph by Dr. L. Marton.)

FIG. 8. Partial disintegration of tobacco mosaic virus by dilute ammonia. × 11,250.

FIG. 9. Complete disintegration of tobacco mosaic virus by dilute ammonia. × 17,500.

FIG. 11. Ultracentrifugally isolated cucumber mosaic virus 3 applied at a concentration of 0.1 mg. per cc. A thick mat of virus and holes in the collodion film may be noted. × 25,800.

PLATE 4

Fig. 14. Cucumber mosaic virus 4 applied at a concentration of 0.01 mg. per cc. End-to-end aggregation of particles is especially noteworthy. × 39,000.

Fig. 15. Cucumber mosaic virus 4. Several particles about 300 µm in length are shown. × 20,000.

Fig. 16. Ultracentrifugally isolated bushy stunt virus applied at a concentration of 0.01 mg. per cc. It may be noted that there is a tendency for the particles to collect at folds in the collodion membrane. × 31,600.

Fig. 17. Ultracentrifugally isolated tobacco necrosis virus applied at a concentration of 1 mg. per cc. × 30,500. (Micrograph by Dr. L. Marton.)
(Stanley and Anderson: Electron microscopy of viruses)
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J. Biol. Chem. 1941, 139:325-338.

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