STRUCTURE OF BACTERIOPHAGE T7

Small-Angle X-ray and Neutron Scattering Study

G. RONTÓ
Institute of Biophysics, Medical University, Budapest, Hungary

M. M. AGAMALYAN AND G. M. DRABKIN
Leningrad Institute of Nuclear Physics, Academy of Science, Leningrad, Union of Soviet Socialist Republics

L. A. FEIGIN AND Y. M. LVOV
Institute of Crystallography, Academy of Science, Moscow, Union of Soviet Socialist Republics

ABSTRACT Small-angle x-ray and neutron scattering techniques were applied to bacteriophage T7 solutions at different scattering densities. Scattering curves determined under a variety of experimental conditions were used to derive a set of parameters characterizing the shape, size, and weight of the whole phage particle and of its DNA and protein components. The T7 head has an icosahedral shape with an edge of 37.7 ± 0.5 nm, a volume of (12.0 ± 1.0) × 10^4 nm^3, and a small tail amounting to 6–7% of the head volume. The intraphage DNA region is most probably a hollow sphere. The best fit to the data was obtained with a model in which the hollow sphere filled with a protein core with a diameter of 24 nm. The average degree of swelling (i.e., the ratio of the hydrated to the dry volume) of the particle is 2.3; the degree of swelling of the DNA component is higher, 3.2, and that of the protein part is lower, 1.2.

INTRODUCTION

Though the bacteriophage T7 of *Escherichia coli* (*E. coli*) was described in the early 1940's, it is still the object of rather intense research work because it provides an excellent biological substance, whose structure may serve in several aspects as a model system of the chromosomes. The problem of the intraphage packaging of the DNA accomplished during the phage maturation process by nucleic acid-protein interaction is of special interest (1, 2).

There is already considerable information available on the physical and morphological properties of the whole T7 particle (3–11), but the values of the parameters characterizing it have several inaccuracies, perhaps due to the wide variety of the methods used for their determination. Inside the phage particle T7 (50 × 10^6 daltons) a double stranded DNA of molecular mass 26 × 10^6 daltons (3–6, 12–15) was found. The phage has an isometric polyhedral head with a small tail attached to it with an average diameter of 58–65 nm according to Davison and Freifelder (16). Permogorov et al., on the other hand, found a diameter of 47–52 nm (17). Serwer found a significant variation in the phage volume depending on the method of determination and on the state of hydration of the particle (18, 19).

The aim of the present work is to report on the phage T7 structure in solution as obtained by small-angle x-ray and neutron scattering. Using these two different radiations, which have different types of interactions with matter (x rays are scattered by the electrons, neutrons by the atomic nuclei), and interpreting the diffraction curves in terms of the same models resulted in a set of parameters characterizing the whole phage particle, namely, the size, shape, and weight of the phage. The dimensions and shape of the area occupied by intraphage DNA and the character of DNA ordering inside the phage head were also obtained.

The method of small-angle thermal neutron scattering gives information on two- and multicomponent biological structures by means of the so-called contrast variation technique (20). The considerable difference between the scattering length of hydrogen (-0.37×10^{-12}cm) and that of deuterium ($+0.67 \times 10^{-12}$cm) enables one to select scattering densities of the solvent that are equal to one of the phage components by changing the ratio H_2O/D_2O of the solution. The possibilities offered by this method were extensively applied in our investigations.

MATERIALS

Phage T7 was grown using *E. coli B* (wild type) as host cells making use of our earlier experience with the optimalization of phage production (21) in a chemostat. The concentration and purification of the lysate were carried out by sedimentation according to Strauss and Sinsheimer (22). The final centrifugation was accomplished in a CsCl density gradient. CsCl was then removed by ultrafiltration in an Amicon cell (Amicon

Corp., Scientific Sys. Div., Lexington, MA) on an XM-300 filter. Finally the process was completed by a resuspension of the phage in a solution containing 0.04M Tris buffer, pH 7, and 0.1 M NaCl.

For x-ray scattering measurements phage concentrations of 6–52 mg/ml were used in a thin-walled glass capillary 0.08 cm in diameter. For neutron-scattering experiments four types of preparation were used. Phage T7 in a Tris buffer containing either 100% D_2O or 100% H_2O and a Tris buffer with a D_2O content of 41 or 63%. In all cases 0.1 M NaCl was present. The biological activity of the phage, pH 7.0–7.3, did not change after the D_2O treatment.

METHODS

The detailed methods were published earlier (23). The intensity of the x ray scattered by the samples of the phage was recorded with two types of automatic small-angle diffractometer equipped with a Kratky (A. Paar, Graz, Austria) or a Rigaku Denki (Rigaku Denki, Inc., Tokyo, Japan) camera. Unfiltered copper radiation with a 0.154-nm wavelength (λ) was used; the range of the scattering angles (θ) was 0.1–20°, which corresponds to $Q = 0.07–14\ nm^{-1}$ ($Q = 4\pi \sin\theta/\lambda$) at a temperature of 12°C. Both the sample and solvent curves were smoothed by a computer program. Proper collimation corrections for the slit height and width were made (24, 25). The small-angle scattering curves of the phage were taken as the difference between the sample and the solvent scattering curves.

The first four maxima of the small-angle x-ray scattering curve of phage T7 are shown in Fig. 1. The drop of intensity in the measured range of Q is 6 orders of magnitude, and there are 20 maxima. In this case the contrast ($\Delta\rho$) is 4.3×10^{10} cm/cm^3, where $\Delta\rho$ is the difference between the scattering density of the particle (ρ) and that of the solvent (ρ_s).

Neutron measurements were carried out on the small-angle scattering instrument "Membrane" utilizing the horizontal channel of the VVR-M reactor (Leningrad Institute of Nuclear Physics, Leningrad, Union of Soviet Socialist Republics). The neutron beam is selected by a magnetic monochromator; the specimen is placed in a cell with quartz windows (volume of ~0.5 cm^3). The scattered radiation was recorded with a multichannel detector on line with the computer. The wavelength of the incident radiation in these experiments was $\lambda = 0.303$ nm, the wavelength

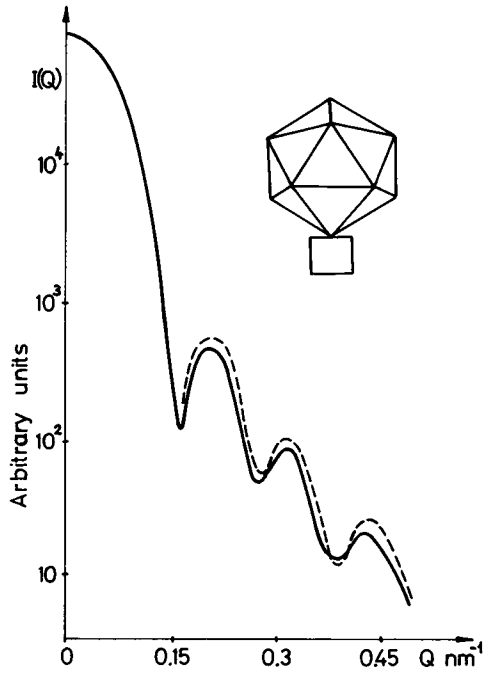

FIGURE 1 Small-angle x-ray scattering on bacteriophage T7. ———, experimental curve. ---, theoretical curve from the model shown in inset.

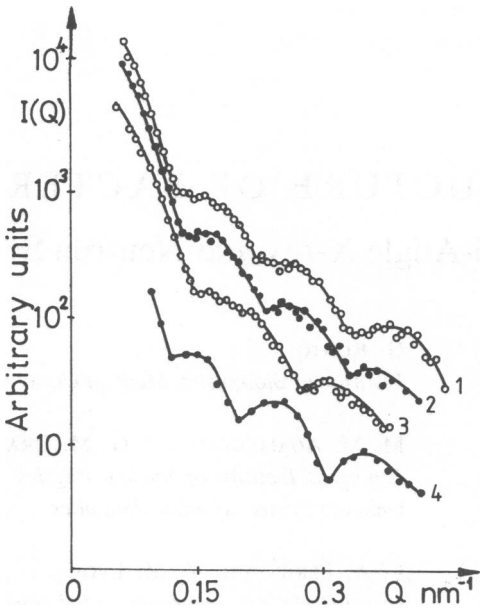

FIGURE 2 Small-angle neutron scattering on bacteriophage T7. In curve *1* the solvent is H_2O, in *2* D_2O, in *3* 41% D_2O/59% H_2O, and in *4* 63% D_2O/37% H_2O.

resolution was $\Delta\lambda/\lambda = 4.5\%$; the vertical resolution was 0.2° and the horizontal, 0.04°. The scattering curve was only slightly changed because of the collimation correction for the height of slits.

The measurements carried out with the four solvents resulted in the scattering curves presented in Fig. 2. Curves 1 and 2 correspond to the scattering by the phage particle as a whole, curve 3 represents the DNA region, and curve 4 the protein part of the particle. In the case of curves 1 and 2 the scattering densities of both the protein part and of the phage DNA were different from that of the solvent. In the case of curve 3 the solvent containing 41% of D_2O provides a contrast only for the DNA region of the phage, i.e., the scattering curve gives information on the DNA only because the scattering density of the solvents is the same as that of the protein and, consequently, the protein shell as well as the tail are contrast matched. With a D_2O content of 63% the DNA component is matched and curve 4 gives information on the protein component. The scattering densities at the different experimental conditions are summarized in Table I.

RESULTS AND DISCUSSION

The small-angle x-ray (Fig. 1) and neutron (Fig. 2) scattering curves show many common characteristics, but in the case of the neutron scattering the maxima are more spread out due to perhaps the smaller wavelength resolution of neutron radiation than x rays.

Radius of Gyration

The radius of gyration (R_g) of the phage T7 was determined from the Guinier region as well as from the positions of the maxima and minima of the scattering curves in Fig. 1 and 2. In Fig. 3 the R_g^2 values are presented as a function of $\Delta\rho^{-1}$. Note that the values of the radius of gyration as shown in Fig. 3 and listed in Table II depend on the type of radiation and the contrast of the sample. Varying the scattering density of the solvent and the type of radiation allows one to shade or illuminate particular components of

TABLE I
VALUES OF SCATTERING DENSITIES*

Material	Radiation	
	Neutron ($\times 10^{10}$)	X rays ($\times 10^{10}$)
	cm^{-2}	cm^{-2}
DNA	+3.7	+15.4
Protein	+1.9 ± 0.1	+12.0 ± 0.2
H_2O	−0.56	+9.4
D_2O	+6.34	+9.4
41% D_2O	+2.27 protein matching	+9.4
63% D_2O	+3.79 DNA matching	+9.4

*See reference 19.

the phage particle, i.e., their partial contribution to the scattering changes. On the basis of the above-mentioned dependence (for an analytical formula see reference 26) two types of results can be obtained.

The first is obtained by interpolating the data to $\Delta\rho^{-1} = 0$. The dimensions of the whole particle (of uniform density corresponding to its average value) characterizing the form of the phage are derived from these data. This interpolation was performed for neutron experiments. In the case of x-ray data the contrast is high ($\Delta\rho = 4.3 \times 10^{10}$ cm/cm^3; $\Delta\rho^{-1} = 0.24 \times 10^{-10}$ cm^2) and the dimensions of phage obtained in buffer solution and those obtained by interpolation to $\Delta\rho^{-1} = 0$ coincide within an error of 3–5% (Fig. 3). The second is obtained when the scattering of one of the other components is matched by an appropriate solvent composition. These results yield the radius of gyration, and other structural characteristics of phage DNA, and the radius of the protein shell, respectively.

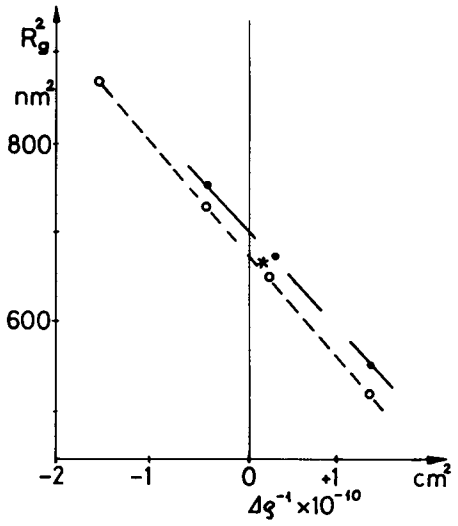

FIGURE 3 The reciprocal contrast dependence of the radius of gyration of phage T7. ⋆ indicates R_g determined from the x-ray data of the Guinier region (phage concentration: 16 mg/ml); ○, R_g determined from the neutron data of the Guinier region (phage concentration: 16 mg/ml); ●, R_g determined from the neutron data of the positions of maxima and minima (independent of the concentration).

Shape and Size of Phage T7

The geometric characteristics of the bacteriophage are determined from the x-ray scattering data. The phage volume was calculated by Porod's invariant (27, 28). In the range of the 2–5 subsidiary maxima the decrease of the scattered intensity follows the relation $I \sim Q^{-4}$. The value $V = (124 \pm 10) \times 10^3$ nm^3 was found for the volume. Since the small phage tail influences the scattering curve only in the range of the main maximum and minimum, the positions of the subsidiary maxima are unaffected (29), the radius of gyration of the phage head was derived from the positions of the first five subsidiary maxima; its value was $R_g = 23.6 \pm 0.5$ nm. The dimensions of the phage obtained from the x-ray data are necessarily smaller (~3%) than those obtained from neutron scattering, since in the latter case no interpolation was carried out to $\Delta\rho^{-1} = 0$, namely, infinite contrast (see Fig. 3). The scattering curve shown in Fig. 1 is consistent with a polyhedral nucleocapsid, the structure derived from electron microscopic data (2, 10, 19).

A more precise determination of the shape of the phage

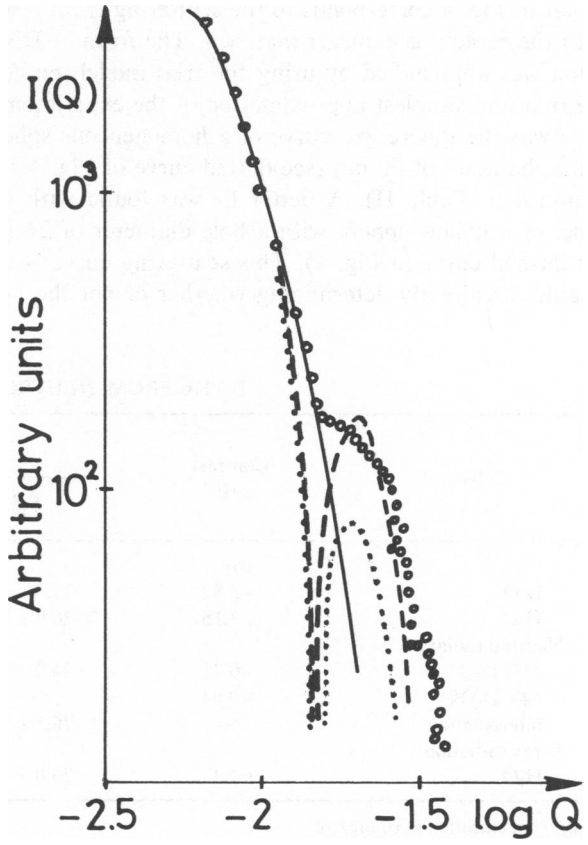

FIGURE 4 Small-angle neutron scattering curves of phage T7. The solvent is 41% D_2O/59% H_2O. ○○○ indicates experimental data; ———, theoretical curve of a rotational ellipsoid with an anisometry of 0.5; ---, hollow sphere $d/D = 0.4$; ●●●, solid sphere.

particle has also been carried out. Of a series of possible forms (sphere, ellipsoid, icosahedron) the best fit of the theoretical scattering curve to the experimental data in the range of the first five maxima was found in the case of the model presented in Fig. 1 (30). Thus phage T7 has an icosahedral shape with an edge of 37.7 ± 0.5 nm, a volume of (120 ± 10) × 10^3 nm^3, and a small tail that is 6–7% of the head volume.

Weight of Bacteriophage T7

The weight determination of a biological macromolecule is based on the fact that the scattered intensity at angle zero is proportional to the square of the number of electrons in the scattering particles, and does not depend on their shape. Thus the knowledge of the chemical composition of the macromolecule or particle enables one to calculate their mass (28). From earlier results (31) the value of 0.669 cm^3/g was used for the specific volume, and with this value the mass of the phage was found to be (58 ± 8) × 10^6 daltons. This is somewhat higher than the values obtained by other methods (4, 6, 12, 13).

Structural Characteristics of Intraphage DNA

The small-angle neutron scattering curve 3 in Fig. 2 as well as that in Fig. 4 corresponds to the scattering from DNA when the protein is contrast matched. The form of DNA region was approached by using the trial model method. The first and simplest approximation of the experimental curve was the theoretical curve of a homogeneous sphere with a diameter of 60 nm (see dotted curve of Fig. 4 and column 4 in Table II). A better fit was found with the model of a hollow sphere with a hole diameter of 24 nm (see dashed curve in Fig. 4). This scattering curve is not suitable for directly determining whether or not the hole contains protein because the scattering density of the solvent is the same as that of the protein.

A comparison of the R_g values for the whole phage (at infinite contrast, i.e., R_g of the shape), its DNA and protein part, has been carried out. The experimental values used for the analysis are listed in Table II. For the case of DNA matching (curve 4 in Fig. 2), where there are only two density levels, 0 and 1 (solvent and protein, respectively), from the results of the central symmetric approximation (i.e., approximation without taking into account the phage tail) it is possible to select one of the following two models: (*a*) a model of protein shell with a protein core, and (*b*) a model of protein shell without any core.

The radius of gyration for model *a* is given by

$$R_g^2 = 3/5\left(\frac{r_3^5 - r_2^5 + r_1^5}{r_3^3 - r_2^3 + r_1^3}\right),$$

and for model *b*

$$R_g^2 = 3/5\left(\frac{r_3^5 - r_2^5}{r_3^3 - r_2^3}\right),$$

where r_1, r_2, and r_3 denote the radii of the hole (or that of the protein core) of the invisible DNA part and the outer radius of the phage head, respectively. For model *a* we calculated an R_g value of 30.3 nm using 12 nm, 30 nm, and 34 nm (experimental value 33.9 nm) for the radii (see Table II). For model *b* the calculation yielded R_g = 32.5 nm. The experimental value obtained with contrast-matched DNA was R_g = (29.5 ± 1) nm. Consequently a protein core exists inside the phage T7. Electron microscopy of negatively stained phage T7 has revealed a cylindrical protein core with dimension of 10–25 nm (32, 33) surrounded by DNA. The form of the protein core deduced from our measurements may be approximated by a sphere with a diameter of 24 nm (the accuracy of the data is 10%).

TABLE II
DATA FROM NEUTRON* AND X-RAY‡ SCATTERING

Solvent	Contrast ×10^{10}	Radius of gyration		Radius by spherical approximation	
		R_g§	R_g‖	R§	R‖
	cm^{-2}	*nm*		*nm*	
D_2O	−2.82	27.5 ± 0.5	27.1 ± 0.5	35.5 ± 0.7	35.2 ± 0.6
H_2O	+3.16	26.0 ± 0.6	25.6 ± 0.5	33.5 ± 0.6	32.8 ± 0.6
Neutron radiation					
41% D_2O	+0.71	24.0 ± 1	23.0 ± 1.0	30.0 ± 1.3	28.8 ± 1.3
64% D_2O¶	−0.64	—	29.5 ± 1.0	—	36.0 ± 1.3
interpolation	—	26.3 ± 0.6	25.9 ± 0.5	33.9 ± 0.7	33.2 ± 0.6
X-ray radiation					
H_2O	+4.3	26.0 ± 0.3	23.6 ± 0.5	33.6 ± 0.4	30.4 ± 0.7

*Phage concentration is 16 mg/ml.
‡Extrapolated to infinite dilution.
§Calculated from Guinier approximation.
‖Calculated from the positions of the subsidiary maxima, and consequently the values are independent of the phage concentration.
¶Phage concentration is 70 mg/ml.

Note that our method has the advantage of yielding data about the native phage in solution.

According to the comparison of the experimental and theoretical (34) x-ray scattering curves in the range of 5–20° (the corresponding Q values are 3.5–14 nm^{-1}) the intraphage DNA has a conformation similar to the B form. The reflection in the range of 3.5° (Q = 2.45 nm^{-1}) corresponds to the Bragg distance of 2.4 nm produced by the parallel packing of the DNA chains. This reflection was obtained in x-ray scattering experiments on the intact phage particles. A distinct modulation of this maximum was obtained earlier by Earnshaw and Harrison (35) with the help of a point camera and interpreted as resulting from DNA packing into concentric layers.

Hydration of the Phage

The weight of the phage obtained by the absolute determination of the scattered x-ray intensity is the dry weight of the particle but its hydration can be deduced by geometric data. From the x-ray scattering data the average hydration is 0.7 g/g of dry weight and the degree of swelling (i.e., the ratio of the hydrated to the dry volume) is 2.3.

The size of the DNA region as well as that of the protein core was determined from neutron measurements. From the diameter of the phage head the volumes of its components were calculated as follows: $V_{protein} = 4.7 \times 10^4$ nm^3 and $V_{DNA} = 10.6 \times 10^4$ nm^3. Both values obtained in Tris buffer are ~15–20% higher than those found by Serwer (18) with the iothalamate buoyant density sedimentation method. Taking into account the identical masses of the components in our case (2, 4, 12, 16) the calculation of the average swelling of the phage gives a value of 2.2, which is in agreement with the x-ray data. Based on the different specific volumes of DNA and protein the swelling values for the DNA and protein components are 3.2 and 1.2, respectively. The corresponding hydrations are 1.2 g H_2O per gram of DNA and 0.25 g/g of protein; thus the DNA is highly hydrated. Practically the same value (0.693 g H_2O/1 g dry material) was found by Serwer (18). The slight differences in the values for DNA hydration: 1.12 g H_2O/1 g DNA (18) and 1.2 g H_2O/1 g DNA in our case may be due to differences in techniques and to differences in media used.

Since the submission of this paper a publication appeared dealing with the dimensions of phage T7 determined by small-angle x-ray scattering (36). The value of 30.1 ± 0.2 nm for the radius of the phage head found in a spherical approximation is in good agreement with our value (30.4 ± 0.7 nm) listed in Table II. The total phage volume ([114 ± 5] × 10^3 nm^3 in their case and [120 ± 10] × 10^3 nm^3 in our case) also agree. The volumes of the components ($V_{protein}$ and V_{DNA}) are not directly comparable because of the different techniques used for their determination: x-ray scattering and contrast matching by neutron scattering.

The authors thank Professors B. K. Vainshtein and I. Tarján for their continued interest in this work.

Received for publication 25 February 1981 and in final form 10 December 1982.

REFERENCES

1. Roeder, G. S., and P. D. Sadowski. 1977. Bacteriophage T7 morphogenesis. Phage-related particles in cells infected with wild-type and mutant T7 phage. *Virology.* 76:263–285.
2. Serwer, P. 1980. A metrizamide-impermeable capsid in the DNA packaging pathway of bacteriophage T7. *J. Mol. Biol.* 138:65–91.
3. Studier, F. W. 1972. Bacteriophage T7 (genetic and biochemical analysis of this simple phage gives information about genetic processes). *Science (Wash. DC).* 176:367–375.
4. Freifelder, D. 1970. Molecular weights of coliphages and coliphage DNA. IV. Molecular weights of DNA from bacteriophages T4, T5 and T7 and general problem of determination of M. *J. Mol. Biol.* 54:567–577.
5. Bancroft, F. C., and D. Freifelder. 1970. Molecular weights of coliphages DNA. I. Measurements of the molecular weight of bacteriophage T7 by high-speed equilibrium centrifugation. *J. Mol. Biol.* 54:537–546.
6. Camerini-Otrero, R. D., P. N. Pusey, D. E. Koppel, D. W. Schaefer, and R. M. Franklin. 1974. Intensity fluctuation spectroscopy of laser light scattered by solution of spherical viruses: R17, Qβ, BSV, PM2 and T7. II. Diffusion coefficients, molecular weights, solvation and particle dimensions. *Biochemistry.* 13:960–970.
7. de Groot, G., J. Greve, and J. Blok. 1977. Transient electric birefringence of the bacteriophages T3 and T7. *Biopolymers.* 16:639–654.
8. Serwer, P. 1978. A Technique for observing extended DNA in negatively stained specimens. Observation of bacteriophage T7 capsid–DNA complexes. *J. Ultrastruct. Res.* 65:112–118.
9. Kosturko, L. D., M. Hogan, and N. Dattagupta. 1979. Structure of DNA within three isometric bacteriophages. *Cell.* 16:515–522.
10. Panessa-Warren, B. J. 1979. High resolution SEM of bacterial viruses T7. *Ultramicroscopy.* 4:317–322.
11. Monaselidze, D. R., D. I. Chanchalashvili, G. N. Mgeladze, G. V. Madjagaladze, A. Fekete, and G. Rontó. 1978. Thermodynamical properties of phages T7. *Stud. Biophys.* 70:213–220.
12. Bahr, G. F., W. F. Engler, and H. M. Mazzone. 1976. Determination of the mass of viruses by quantitative electron microscopy. *Q. Rev. Biophys.* 9:459–489.
13. Murialdo, H., and A. Becker. 1978. Head morphogenesis of complex double-stranded DNA bacteriophages. *Microbiol. Rev.* 42:529–540.
14. Clark, R. W., G. H. Wever, and J. S. Wiberg. 1980. High-molecular weight DNA and the sedimentation coefficient: a new perspective based on DNA from T7 bacteriophage and two novel forms of T4 bacteriophage. *J. Virol.* 33:438–448.
15. Harpst, J. A. 1980. Analysis of low angle light scattering results from T7 DNA. *Biophys. Chem.* 11:295–302.
16. Davison, P., and D. Freifelder. 1962. Physical properties of the DNA from T7 bacteriophage. *J. Mol. Biol.* 5:643–650.
17. Permogorov, V. I., B. V. Taglov, V. G. Bogush, and V. E. Minaev. 1977. Light scattering of T7 and S_d phages in process of melting. *Soviet Mol. Biol.* 11:134–139.
18. Serwer, P. 1975. Buoyant density sedimentation of macromolecules in sodium iothalamate density gradients. *J. Mol. Biol.* 92:433–448.
19. Serwer, P. 1977. Flattening and shrinkage of bacteriophage T7 after preparation for electron microscopy by negative staining. *J. Ultrastruct. Res.* 58:235–243.
20. Jacrot, B. 1976. The study of biological structures by neutron scattering from solution. *Rep. Progr. Phys.* 39:911–953.

21. Gaspar, S., G. Rontó, and G. Müller. 1979. Determination of the biological parameters of bacterium-phage complexes. *Z. Allg. Mikrobiol.* 19:163–169.
22. Strauss, I., and R. L. Sinsheimer. 1963. Purification and properties of bacteriophage MS2 and of its ribonucleic acid. *J. Mol. Biol.* 7:43–48.
23. Feigin, L. A., A. T. Dembo, and A. K. Boyarintseva. 1974. X-ray small-angle studies of dimensions and weight parameters of T2, S_d and DD2 bacteriophages. *J. Appl. Crystall.* 7:164–167.
24. Shchedrin, B. M., and L. A. Feigin. 1965. Collimation correction for x-ray small-angle scattering curves. *Sov. Phys. Crystallogr.* 11:159–163.
25. Kiste, R. G., and H. B. Stuhrmann. 1967. Eliminierung der intrapartikulären Untergrundstreuung bei der Röntgenkleinwinkelstreuung an kompakten Teilchen. III. Verifizierung in Lösungen von Myoglobin. *Z. Phys. Chem. (Frankfurt).* 56:338–342.
26. Agamalian, M. M., J. Shweizer, Y. M. Otchik, and V. R. Khawronin. 1979. Optimization of the Drabkin monochromator. *Nucl. Instr. Methods.* 158:395–399.
27. Kayushina, R. L., Y. A. Rolbin, and L. A. Feigin. 1974. Determination of the volume of biological macromolecule by mean of small-angle x-ray scattering. *Sov. Phys. Crystallogr.* 19:1161–1165.
28. Kratky, O., and I. Pilz. 1972. Recent advances and applications of diffuse x-ray small-angle scattering on biopolymers in dilute solutions. *Q. Rev. Biophys.* 5:481–537.
29. Boyarintseva, A. K., A. T. Dembo, Y. A. Rolbin, and L. A. Feigin. 1975. Small-angle x-ray scattering of unoriented polyhedrons. *Sov. Phys. Crystallogr.* 20:149–152.
30. Rolbin, Y., A. D. I. Svergun, L. A. Feigin, S. Gaspar, and D. Ronto. 1980. Small angle x-ray scattering data on the structure of phage T7. *Rep. Acad. Sci. USSR.* 255:1497–1500.
31. Boyarintseva, A. K., A. T. Dembo, T. I. Tikhonenko, and L. A. Feigin. 1973. Small-angle x-ray scattering determination of weight and hydration of bacteriophage S_d. *Rep. Acad. Sci. USSR.* 212:487–489.
32. Serwer, P. 1976. Internal proteins of bacteriophages T7. *J. Mol. Biol.* 107:271–291.
33. Serwer, P. 1979. Fibrous projections from the core of a bacteriophage T7 procapsid. *J. Supramol. Struct.* 11:321–326.
34. Bram, S. 1971. The secondary structure of DNA in solution and in nucleohistone. *J. Mol. Biol.* 58:277–288.
35. Earnshaw, W. C., and S. C. Harrison. 1977. DNA arrangement in isometric phage heads. *Nature (Lond.).* 268:598–602.
36. Stroud, R. M., P. Serwer, and M. J. Ross. 1981. Assembly of bacteriophage T7. Dimensions of the bacteriophage and its capsids. *Biophys. J.* 36:743–757.