support the earlier proposal that contraction is spontaneous but that relaxation requires the energy involved in the binding of ATP to the protein.

A mechanism can be proposed to account for the increase in axial ratio by the nucleotides and particularly by pH 11 buffer. All active compounds would tend to increase the net negative charge on the sheath. Since the subunits are arranged helically the increase in charge would cause repulsion and an increase in the distance between subunits or a lengthening of the molecule. Although it cannot be concluded that this is the only factor involved in the relaxation of this protein (especially since the addition of various substances to the isolated sheath only increased the axial ratio from 1.4 to 1.6 while the completely relaxed protein has a ratio of 4.8), it should be emphasized that the addition of ATP to phage after interaction with cell walls (Kozloff and Lute, 1959) was much more effective and caused an increase in the axial ratio of the sheath protein from 1.4 to 2.8.

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Tail Components of T2 Bacteriophage. II. Properties of the Isolated Tail Cores*

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Highly purified and homogeneous preparations of tail cores of T2L bacteriophage have been obtained by centrifugation of proteolytic digests of denatured virus protein coats. The cores do not neutralize anti-T2 serum nor do they clump host cells. The isolated tail cores have sedimentation and diffusion coefficients of 11.6 S and 21.8 $\times 10^{-8}$ cm^2/sec, respectively. The molecular weight of the individual cores is 487,000, all of which can be accounted for as amino acids. A model for the structure of the tail core has been proposed based upon the amino acid analysis and the fact that cores are stiff, long, hollow rods. Each core appears to be a hollow five-stranded cable made up of five identical polypeptide chains or subunits.

Bacteriophage T2 has a complex tail structure with a number of distinct components (Kellenberger and Arber, 1955; Williams and Fraser, 1956). The main component of the tail is a contractile protein (Kozloff and Lute, 1959) which has been termed the *contractile-sheath protein* (Brenner *et al.*, 1959) because it surrounds an inner component known as the *tail core*.

Some observations on the formation of tail cores in the infected cell have been reported by Kellenberger and Séchaud (1957) which indicated that they are formed independently of the whole phage. Brenner and his colleagues (1959) in their investigation of the structural components of bacteriophage obtained electron micrographs showing the cores to be stiff hollow

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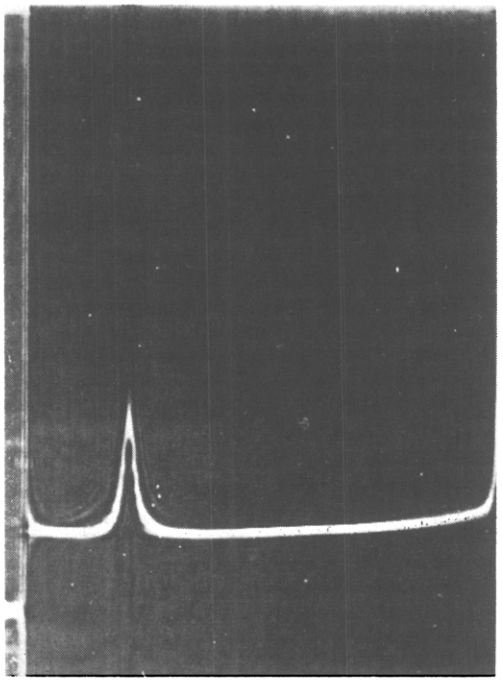

FIG. 1.—Sedimentation pattern of T2L tail cores, 2.5 mg/ml in 0.13 M ammonium acetate, *p*H 7.0. Temperature 5°, bar angle of 65°. Picture is taken 30 minutes after reaching 59,780 rpm.

rods. The function of the tail core is unknown. Finally, the distal ends of the tail core and sheath are joined to a hexagonal tail plate to which in turn six tail fibers are attached (Brenner *et al.*, 1959).

In the course of the isolation of sufficient amount of T2L contractile tail sheaths for chemical characterization (Sarkar *et al.*, 1964), it proved possible also to isolate highly purified tail cores. This paper describes some of the physicochemical properties of purified T2L tail cores such as molecular weight, sedimentation and diffusion coefficients, and amino acid composition. A model for the structure of the tail core is also presented.

EXPERIMENTAL PROCEDURE

Preparation of Phage Stock.—Methods for the preparation, purification, and assay of T2L phage and T2L ghosts have been described in the preceding paper (Sarkar *et al.*, 1964).

Preparation of Tail Cores.—With some modifications the method of Brenner *et al.* (1959) was used for disrupting T2. The conditions for the enzymatic digestion of the disrupted T2 with trypsin and chymotrypsin have been described previously (Sarkar *et al.*, 1964). The supernatant solution obtained after sedimenting the contractile-sheath protein was found to contain the T2L tail cores, tail fibers, and digested head protein. This solution was centrifuged in the Spinco Model L preparative ultracentrifuge at 4° for 16 hours at 100,000 × *g*. The tail fibers, which would be expected to have a much lower sedimentation rate than the tail cores because of their lower mass and greater asymmetry, were not sedimented. The small and almost transparent pellet was slowly suspended in 1 ml of 0.13 M ammonium acetate, *p*H 7.0. This crude preparation of tail cores was then purified by two cycles of centrifugation. After centrifugation at 100,000 × *g* for 90 minutes in the preparative ultracentrifuge, most of the contaminating tail sheaths were removed. The supernatant solution was then centrifuged at 100,000 × *g* for 16 hours to again sediment the tail cores. The cores were further purified by one more centrifugation at 100,000 × *g* for 90 minutes. Starting with 50–60 ml of about 5×10^{12} ghosts/ml, the final recovery of cores was about 50% of that expected from its molecular weight. It was also possible to prepare tail cores using whole T2 instead of ghosts as the starting material.

Ultracentrifugation Studies.—Sedimentation-velocity studies of the purified tail cores were made with the Spinco Model E analytical ultracentrifuge operating at 59,780 rpm and 5° using schlieren optics and the standard aluminum centerpiece. The solvent used was 0.13 M ammonium acetate, *p*H 7.0. The calculated sedimentation coefficients were corrected to the standard state of water at 20°. Densities and viscosities needed for corrections to 20° were measured for the 0.13 M ammonium acetate buffer using a 5-ml pycnometer and an Ostwald-type viscometer, respectively. The partial specific volume of the tail cores, as calculated from its amino acid composition, was 0.725 ml/g.

Determination of Molecular Weight and Diffusion Coefficient.—Since the quantities of tail cores isolatcd were too small for a direct measurement of the diffusion coefficient, the procedure of Ehrenberg (1957) for obtaining the diffusion coefficient and the molecular weight in the ultracentrifuge by using a 12-mm synthetic-boundary cell at low speeds was used. Tail core solutions, 2–3 mg/ml, were equilibrated by dialysis with 0.13 M ammonium acetate, *p*H 7.0. The speed and temperature used were 12,590 rpm and 15°, respectively. Care was taken to maintain the different variables such as acceleration time, rotational speed, temperature, bar angle, exposure times, and exposure intervals exactly the same in the two runs with and without layering of the equilibrated buffer. From the slope of the line obtained by plotting $(\text{area})^2/(\text{maximum height})^2$ versus time, i.e., "the maximum ordinate-area method" (Ehrenberg, 1957), the diffusion coefficient was measured and corrected to water at 20° ($D_{20,w}$). The molecular weight of the cores was calculated from the sedimentation coefficient and diffusion in the standard manner. The value of the molecular weight was also calculated by an independent estimate of the ratio s/D, calculated at the meniscus by Ehrenberg's procedure (1957).

Amino Acid Analysis.—The amino acid composition of tail cores was determined on a microcolumn with a Technicon automatic amino acid analyzer according to the procedure of Moore and Stein (1954). The core solutions were equilibrated by dialysis against 0.1 M NaCl containing 10^{-3} M Mg^{2+}, *p*H 7.0. For hydrolysis, 1 ml of concentrated HCl was added to 1.0 ml of the core solution containing 0.5–0.6 mg protein. Duplicate samples were heated at 110° for 24 and 70 hours in evacuated sealed tubes. The tryptophan content was determined from the ultraviolet-absorption spectrum of intact tail cores in 0.1 N NaOH according to the method of Goodwin and Morton (1946) using a 1-cm cell in a Perkin-Elmer Model 202 recording spectrophotometer.

Electron Microscopy of Tail Cores.—Electron micrographs were taken with an RCA EMU-3 electron microscope. Samples of tail cores in 0.13 M ammonium acetate were diluted with water to a concentration of 10^{12} cores/ml. To this were added polystyrene latex balls 88 mμ in diameter. The solution was dropped on Formvar-coated copper grids, air dried, and shadowed with palladium at an angle of 5/1.

Clumping of Escherichia coli by Tail-Core Preparation.—For the assay of host-cell clumping (Anderson, 1963) 2 ml of logarithmically growing *E. coli* suspension

TABLE I
PHYSICAL CONSTANTS OF T2L TAIL CORES[a]

$s^\circ_{20,w}$ (S)	$D_{20,w}$ (10^{-8} cm²/sec)	s/D at the Meniscus (10^{-6} cm² sec²)	Molecular Weight From $s^\circ_{20,w}$ and $D_{20,w}$	Molecular Weight From s/D at the Meniscus	Dimensions from Electron Microscopy
11.6 ± 0.1	21.8 ± 0.4	5.44 ± 0.1	481,000 ± 6,000	487,000 ± 9,000	1000 A × 100 A

[a] All values are expressed as the mean deviation from the average. The value for $s^\circ_{20,w}$ was the computed average of four sedimentation velocity runs at 0.3, 0.2, 0.1, and 0.06% of tail cores. The value of $D_{20,w}$ was calculated as the average of three different samples from the slope of the plot of (area)²/(maximum height)² versus time using the synthetic-boundary cell. The value of s/D was independently calculated at the meniscus in the three runs used for the evaluation of $D_{20,w}$. The dimensions are those observed with metal-shadowed cores and are probably high.

in tryptone broth at a concentration of 5×10^8 cells/ml was dispensed in a series of tubes. Small aliquots (0.2 ml or less) of a purified tail-core suspension in 0.13 M ammonium acetate, *p*H 7.0, were added to these tubes. The final tail-core concentrations ranged from 4×10^{12}/ml to 7×10^{13}/ml. Control tubes received corresponding amounts of ammonium acetate solution. The tubes were incubated at 25° for 6 hours and then examined for flocculation and precipitation.

Serum-blocking Power of Tail-Core Preparation.—A modification of the method of Hershey (1946) for testing the depletion of the neutralizing capacity of serum was used. A small volume (0.05 ml) of a suitably diluted antiserum in tryptone broth having an inactivation K value of 6.4 min^{-1} was added to 1 ml of broth or a suspension of known quantities of T2 or tail cores in broth as test material. After incubation at 37° for 2 hours the residual K values of the serum were measured. The number of cores used was calculated from the protein content of the solution using a molecular weight of 487,000.

RESULTS

Analytical Ultracentrifugation.—A single sharp symmetrical peak is observed in the sedimentation pattern of tail cores (Fig. 1). Sedimentation coefficients for tail cores were determined at concentrations of 0.3, 0.2, 0.1, and 0.06% in 0.13 M ammonium acetate, *p*H 7.0 (ionic strength 0.13). The sedimentation coefficients were found to be independent of concentration. The average sedimentation coefficient ($s^\circ_{20,w}$) was 11.6 S.

Diffusion and Molecular Weight.—From synthetic-boundary runs with three different samples, a mean diffusion coefficient of 21.8×10^{-8} cm²/sec was calculated for tail cores (Table I). The value of s/D at the meniscus showed a very good agreement with the ratio of $s_{20,w}/D_{20,w}$. It seems reasonable to assume from the sedimentation analyses, which are independent of concentration, that the dependence of diffusion coefficient on concentration would be quite small. The mean molecular weight of tail cores calculated from $s^\circ_{20,w}/D_{20,w}$ and s/D are 481,000 and 487,000, respectively. The values of s/D remained essentially constant with respect to time during the ultracentrifugal runs indicating that the tail core solution behaved like a monodisperse homogenous system. Since the precise value of $D^\circ_{20,w}$ at infinite dilution is not known, more weight is assigned to the molecular weight obtained from the direct determination of s/D at the meniscus. However, the two values showed very good agreement.

Amino Acid Composition.—The absorption spectrum of T2L cores showed a maximum of 280 mμ and a minimum in the region of 255 mμ. This indicated that the preparations were typical proteins, essentially free of any nucleic acid contaminant. The results of quantitative amino acid analysis of T2L tail cores are summarized in Table II. Two different preparations were analyzed, one of them in duplicate. The corrections for destruction of serine and threonine during hydrolysis were calculated from the difference in the values of 24- and 70-hour duplicate samples assuming first-order kinetics for decomposition (Hirs *et al.*, 1954), and amounted to 11.4 and 8.7%, respectively. The increase in the values of valine, isoleucine, and leucine after 70 hours of hydrolysis were 5.5, 10.8, and 6.3%, respectively. No significant change was observed in the values of the other amino acids. The

TABLE II
AMINO ACID COMPOSITION OF T2L TAIL CORES

Amino Acid	No. of Residues to Nearest Integer/ 487,000 mw	Grams of Amino Acid Residues/100 g Protein: T2L Tail Cores	Grams of Amino Acid Residues/100 g Protein: T2L Contractile Sheath (Sarkar *et al.*, 1964)
Aspartic acid	630 ± 8[a]	14.8	12.2
Threonine[b]	429 ± 11	8.90	7.47
Serine[b]	373 ± 9	6.66	5.50
Glutamic acid	429 ± 6	11.38	9.76
Proline	324 ± 5	6.47	3.50
Glycine	503 ± 10	5.88	3.91
Alanine	343 ± 9	5.01	6.53
Phenylalanine	180 ± 4	5.45	4.77
Lysine	183 ± 5	4.81	4.21
Histidine	35 ± 1.5	1.06	0.265
Arginine	189 ± 4	6.07	7.31
Valine[c]	285 ± 6	5.81	5.54
Isoleucine[c]	282 ± 7	6.54	6.32
Leucine	222 ± 6	5.16	6.11
Tyrosine	129 ± 5	4.31	5.58
Half-cystine	5 ± 0.2	0.105	0.371
Methionine	65 ± 2	1.75	0.945
Tryptophan[d]	30 ± 1.5	1.15	2.68
Amide NH_3[e]	(557 ± 29)	(1.82)	1.30
Total[f]	4630	101.3	93.0

[a] The variation is expressed as the average of the deviations from the mean from all analyses. Two different preparations of cores were analyzed; one of the preparations was analyzed twice. [b] Extrapolated values corrected for losses during hydrolysis. [c] Values calculated from the data of 70-hour hydrolysate to correct for incomplete hydrolysis. [d] The concentration of tryptophan is calculated from the ultraviolet spectra (Goodwin and Morton, 1946). Tyrosine calculated from the spectra gave a value of 125 ± 4 residues/mole. [e] Values calculated from the chromatographic results. [f] The amide groups are not included in the summation of the amino acid residues. The molecular weight of tail cores calculated on the basis of the integral numbers of residues is 493,000, including the terminal molecule of water and the amide groups.

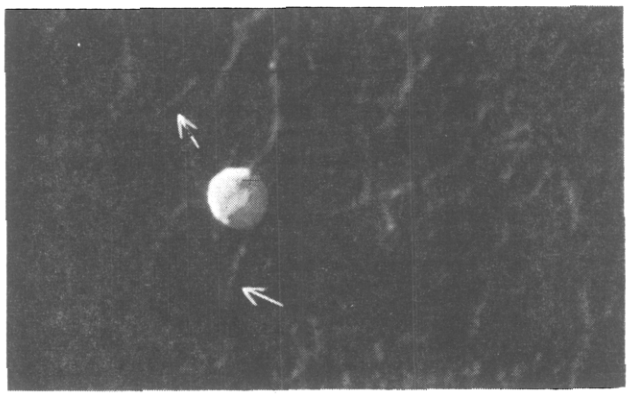

FIG. 2.—Electron micrograph of purified tail cores from T2 bacteriophage. The individual rods can be seen (arrows) but many of them have aggregated into bundles. The large round white object is a polystyrene latex ball 88 mμ in diameter. The magnification is 115,000 × and the rods are approximately 100 × 10 mμ.

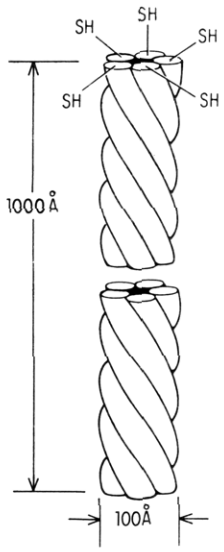

FIG. 3.—Model for structure of T2 tail cores. The dimensions are given from metal-shadowed electron micrograph; true dimensions are somewhat lower. The -SH groups are thought to be at the distal end of the phage particle and to link the tail core to the tail plate.

recovery calculated on the basis of amino acid residues varied from 99 to 101%.

The tryptophan content of tail cores was derived from the absorption spectrum. Tyrosine values, similarly obtained from the spectrum, showed good agreement with those found from the chromatographic results. The presence of tryptophan in tail cores was also confirmed by the appearance of a characteristic 340-mμ fluorescence peak when the core solutions were examined in an Amìnco spectrophotofluorometer (Teale, 1960).

The amino acid composition of tail cores, calculated on a molecular weight of 487,000, is given in Table II. The histidine, methionine, tryptophan and half-cystine contents are low, while aspartic acid, threonine, serine, glutamic acid, glycine, alanine, valine, isoleucine and leucine are present in large quantities. Of special interest is the unusually high proline content of tail cores which amounts to 1 proline for every 14 residues. A comparison of the amino acid composition of tail cores with that of the contractile tail sheath, the major protein component of the tail of T2 bacteriophage, shows certain interesting similarities and dissimilarities (Table II). The tail cores and sheaths contain similar amounts of aspartic acid, threonine, serine, glutamic acid, phenylalanine, lysine, valine, and isoleucine, but sheaths contain about twice the amount of tryptophan and four times the amount of half-cystine. In contrast, cores have about four times more histidine and twice as much proline than are present in sheaths.

An estimate of the net charge of tail cores was made from the amino acid composition. At *p*H 7 tail cores have about 130 negative charges and at higher *p*H values the number should increase. Experiments with electrophoresis on cellulose acetate "Oxoid" using Veronal-acetate buffer, *p*H 8.6 and ionic strength 0.028, have shown that cores do migrate toward the anode and therefore are negatively charged.

Electron-Microscopic Appearance of Tail Cores.—Preparations of tail cores were suitably diluted and observed in the electron microscope after metal shadowing (Fig. 2). The cores appear as short stiff rods approximately 100 mμ by 10 mμ; these dimensions are very similar to those previously reported in 1957 by Kellenberger and Séchaud (100 × 8–12 mμ) for metal-shadowed cores. The cores tended to aggregate in thick bundles. No tail fibers or other contaminants were visible but this does not eliminate the possibility that there may be 1–2% tail fibers by weight. This quantity of tail fibers would not cause an extra peak in the ultracentrifuge or alter the molecular weight determination or the amino acid composition.

Host-Cell Clumping and Serum-blocking Power of Purified Tail-Core Preparations.—Two biological properties of tail cores were investigated. Kellenberger and Séchaud (1957) found that tail cores from T2 which still have tail plates and tail fibers attached to them can still adsorb to host-cell walls. Recently Anderson (1963) showed that tail fibers clump bacterial cells. It was found that the addition of aliquots of tail-core solution did clump some cells but that complete precipitation of the cells required 14,000 cores per cell. However, the presence of only 1 or 2% contaminating tail fibers would be expected to clump the cells and it seems most unlikely that the isolated tail cores, which have no attached tail fibers, can clump host cells.

Kellenberger and Séchaud (1957) also studied the serum-blocking power of cores and concluded that cores have at most 0.1 unit of serum-blocking power as compared to whole phage. The serum-blocking power of tail cores isolated in this work was compared to that of whole T2. It was found that 2.5×10^{12} T2 particles reduced the neutralizing capacity of anti-T2-serum to 4% of its original value. In a parallel series of experiments it was found that an aliquot of the core preparation containing 6.8×10^{13} tail cores reduced the neutralizing capacity of an identical aliquot of anti-T2 serum to 19% of its original value. It appears that cores isolated by these procedures have less than 4% of the neutralizing capacity of whole phage particles. In view of the fact that there might also be present in the tail-core preparation 1–2% of tail fibers which in the free form have an increased ability to neutralize serum (as compared to fibers on whole phage, Franklin, 1961), it can be concluded that the cores isolated by these procedures have little or no serum-blocking power.

DISCUSSION

Three lines of evidence indicate that the material isolated from T2L ghosts by the procedure described

is a highly purified preparation of tail cores: (1) the homogeneity of the preparation in the sedimentation-velocity runs and the behavior of cores as a homogenous system in synthetic-boundary runs; (2) the appearance of the cores in the electron micrographs; and (3) the absence of significant ability either to clump host bacteria or to neutralize antiphage serum, which are properties of tail fibers but not of tail cores. While the presence of trace amounts of contaminants, particularly tail fibers, cannot be ruled out, the amino acid composition shows that the material is not a fragment of the contractile-sheath protein.

The molecular weight of the isolated tail cores using Ehrenberg's ultracentrifugal method is 487,000 ± 9,000. Based upon the relatively rare five half-cystine residues found in the cores there appear to be five subunits with a minimum molecular weight of 97,400 for each subunit. The number of residues of the three other rare amino acid residues, histidine, methionine, and tryptophan, are also multiples of five. Various models of a stiff rod containing five subunits can be constructed using the detailed morphology as shown in the electron micrographs. Although metal-shadowed cores are readily recognizable, unique structures approximately 100 × 10 mμ, considerably more detail can be seen in negatively stained micrographs of Brenner *et al.* (1959). These workers have clearly shown that tail cores are long hollow rods approximately 80 mμ long, 7 mμ in total diameter, and having a central hole 2.5 mμ in diameter. (Metal shadowing tends to give high values for the dimensions while negative staining gives low values.) Since a helical arrangement of five polypeptide chains (a 5-stranded cable) to give a rod requires a central hole while no other model requires such a central hole, such a model seems most likely and is illustrated in Figure 3. The diameter of the individual subunits would be about 25 A, suggesting that the subunits themselves are probably helical since the diameter of a typical α helix including side chains is 20–25 A. It should also be noted that this structure composed of 5 helically arranged subunits, each of which also is probably helical, would account for both the stiffness of the rod and its complete resistance to enzymatic attack.

Since there are only five half-cystine residues in each tail core, it is apparent that these half-cystine residues cannot form symmetrical disulfide bonds between the subunits (Fig. 3). One might expect then that each tail core might have five-SH groups. It has not been possible to analyze cores for their -SH contents because of the small amounts available. However, the lack of effect of -SH reagents such as Zn^{2+} or Cu^{2+} on T2 viability (Kozloff and Lute, 1957), indicates that there are probably no free -SH groups which are necessary for virus activity. It seems more likely that the single -SH group of each polypeptide chain may be involved in binding the cores to the tail plate. On the basis of the effect of reagents such as *N*-ethyl maleimide and *p*-mercuribenzoate, which removes the tail plate from the tail core upon prolonged incubation, it was suggested that bonds involving sulfur, possibly thiolester bonds, link together protein components in the tail (Kozloff, 1959). The sulfhydryl groups in the tail core are attractive candidates for one component of these bonds.

While the tail core is thought to aid the injection of the viral DNA into the host cell its exact role is not clear. It has been proposed that the tail core is a plug which falls out after the sheath protein contracts (Kozloff and Lute, 1959) leaving a relatively large opening for the viral DNA. Alternatively with the observation that the tail core has a central channel possibly wide enough for the passage of the viral DNA (diameter about 24 A) this possibility also deserves consideration. The apparent tight fit and the net negative charges on both DNA and tail core would not necessarily prohibit the passage of the DNA especially if there were an internal groove or channel through which the DNA were to travel. However, if the DNA were to travel through the core in a short time this would seem to require that one end of the DNA fiber be prethreaded into the central hole of the core.

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