Dependence of the Shape of the Plasma Fibronectin Molecule on Solvent Composition

IONIC STRENGTH AND GLYCEROL CONTENT*

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Fibronectin has been purified to apparent homogeneity according to measurements of molecular weight and diffusion constant from light scattering and sedimentation in the analytical ultracentrifuge. This gives two estimates of molecular weight close to 500,000. (The difference with the gel electrophoretic value of 440,000 may indicate the presence of some material of molecular weight higher than that of the monomer.) The (corrected) diffusion constant is found to decrease with ionic strength, much more rapidly in 30% glycerol than in water. A corresponding change occurs when the glycerol content is varied from 0 to 30% at moderate ionic strength, but at very low ionic strength the diffusion constant does not depend on glycerol content. It is concluded that fibronectin can occur in two extreme conformations: the open form, in 30% glycerol at moderate ionic strength, should correspond to the extended shapes visualized by others in electron microscopy of samples prepared from solutions containing glycerol, while the closed form occurs under more physiological conditions. The Stokes radii of these forms, 14.5 and 9.6 nm, respectively, have been compared with calculated Stokes radii of chains of beads of overall length 140 nm having varying stiffness, simulated by a Monte Carlo procedure. These have a Stokes radius of 14.5 nm when made relatively extended to where the distance between chain ends averages 90 nm, as observed in the electron micrographs. When these chains are made very flexible, the Stokes radius reaches a limit of about 10 nm, apparently a lower limit to which a randomly coiled molecule of this size and volume may collapse in a disordered fashion. These results and electron micrographs obtained at low ionic strength suggest a tangled model of the compact form, rather than the ordered model recently proposed by others (17) and confirmed by us. The quality of the preparation and in buffered glycerol/water mixtures that support the above conclusion. Furthermore, we report calculated properties of hypothetical but reasonable models of the fibronectin molecule, which are shown to agree, both with the observed electron microscopic dimensions and with the measured frictional coefficients.

It is thought that fibronectin, a protein having a dimeric structure, can act as a fastener, holding together different components for which it has affinity, but it is not clear what circumstances are required for the requisite double attachment to occur in vivo (1–4). This cohesive role would be facilitated if fibronectin were to have an extended and flexible conformation. Such a molecular shape has been observed in electron micrographs of plasma fibronectin obtained in different laboratories (5, 6), which show irregularly bent, elongated particles, having a width of roughly 2 nm and an average contour length of roughly 140 nm and end to end distance of roughly 90 nm.

However, other hands have obtained electron micrographs showing fibronectin as a more compact particle (7–10). In a recent study the observation of either the extended or the compact form was found to depend on the nature of the supporting medium (11). The observed sedimentation constant of 12–14 S (7, 12, 13) for a molecular weight of ~450,000 was noted to be incompatible with the observed extended shape. Comparison of the experimental conditions under which samples for electron microscopic viewing were prepared revealed that the elongated specimens were obtained from solutions that either contained a high concentration of glycerol, or else had low pH. This suggested that the extended molecular form had been obtained from a more compact form as the result of a conformation change caused by changes of solvent composition; the observed dependence of the sedimentation constant on pH (12, 14), temperature (15), and ionic strength (16) further favored this possibility.

In this paper we report measurements of molecular weight and sedimentation and diffusion constants in aqueous buffer and in buffered glycerol/water mixtures that support the above conclusion. Furthermore, we report calculated properties of hypothetical but reasonable models of the fibronectin molecule, which are shown to agree, both with the observed electron microscopic dimensions and with the measured frictional coefficients.

MATERIALS AND METHODS

Fibronectin was obtained from human plasma Cohn fraction I by successive adsorption on a gelatin affinity column, elution with 4 M urea, adsorption of contaminating material on a fibrin monomer affinity column, recombination, and gel filtration chromatography (Sepharose 4B) to remove larger molecules. The protein was assumed to have an extinction coefficient of 1.28 ml/g at 280 nm, as published by others (17) and confirmed by us. The quality of the preparation was monitored by electrophoresis in the presence of sodium dodecyl sulfate on gels of 3% agarose (nonreduced) and in buffered glycerol/water mixtures that either contained a high concentration of glycerol, or else had low pH. This suggested that the extended molecular form had been obtained from a more compact form as the result of a conformation change caused by changes of solvent composition; the observed dependence of the sedimentation constant on pH (12, 14), temperature (15), and ionic strength (16) further favored this possibility.

In this paper we report measurements of molecular weight and sedimentation and diffusion constants in aqueous buffer and in buffered glycerol/water mixtures that support the above conclusion. Furthermore, we report calculated properties of hypothetical but reasonable models of the fibronectin molecule, which are shown to agree, both with the observed electron microscopic dimensions and with the measured frictional coefficients.

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unreduced fibronectin of 440,000 and of the reduced, half-molecule of 220,000. Bovine serum albumin, Pentex fraction V, reagent grade, sulphydryl modified, was purchased from Miles. For this protein, we used an extinction coefficient of 0.666 ml/g (18). Except for the experiments of which the ionic strength was varied, solutions contained the following buffer: 0.1 M sodium phosphate, 0.15 M NaCl, 0.001 M EDTA, 4-10 units of porcine pancreatic trypsin inhibitor (Trasylol, Mobay Chemical) at pH 7.2. As required, solutions contained in addition glycerol (Fisher, certified ACS grade).

Light scattering measurements were performed at 633 nm with an instrument having a 5 mW HeNe laser and a photomultiplier detector equipped for photon counting and photocurrent measurement (19). The photon count signal was supplied to a Langley-Ford 64-channel autocorrelator. Measured intensities were converted to Rayleigh ratios, R, in the usual way (20), with use of benzene as a standard and R (90, benzene) = 1.184 × 10−6 (21). Solutions were clarified by filtration through a 0.22 μm filter (Millex GY, Millipore). Intensity fluctuation measurements were performed on samples thermostatted at 20 °C.

Specific index increments, dn/dc, were measured with a Brice-Phoenix differential refractometer (20). Protein solutions were equilibrated with buffered water or buffered glycerol/water mixtures by one of two methods: by equilibrium dialysis or by passage over a gel chromagramphy column (Sephadex G-25) previously equilibrated with the solvent. Procedures were tested with bovine serum albumin, before application to fibronectin. The following results were obtained: for serum albumin, dn/dc (λ = 546 nm, water) = 0.183 and dn/dc (λ = 546 nm, 30% glycerol) = 0.133; for fibronectin, dn/dc (λ = 633 nm, water) = 0.174 and dn/dc (λ = 633 nm, 30% glycerol) = 0.145 ml/g.

Sedimentation coefficients were determined at 20 °C in a Beckman-Spinco model E analytical ultracentrifuge, using schlieren optics. For a value of the partial specific volume of fibronectin we used 0.72 ml/g (12).

The angular dependence of the light scattering intensity of fibronectin solutions was found to be insignificant for scattering angles between 30 and 135°; thus, molecular weights, M, could be calculated from the intensities (Rayleigh ratios) measured at 90°, with the well known formula (20):

\[ \frac{Kc}{R} = 1/M \]

where \( c \) is the protein concentration and

\[ K = 4\pi^2n^2(dn/dc)/N_A \lambda^4 \]

\( n \) being the refractive index, \( c \) the concentration of protein, \( N_A \) Avogadro’s number, and \( \lambda \) the wavelength in vacuo. The observation that \( R \) is proportional to \( c \) for \( c < 7 \) mg/ml, rendered extrapolation to \( c = 0 \) unnecessary.

The net scattering intensity of fibronectin was found to decrease with increasing glycerol concentration, in an approximately linear fashion; in 30% glycerol the intensity was 61% of that in water. According to Equation 2, the scattering is proportional to \( (dn/dc)^2 \), which in 30% glycerol is 69% of that in water; this is sufficiently close to the ratio of the net scatter in these two solvents to demonstrate the absence of an appreciable change in molecular weight.

Diffusion constants were calculated from the measured autocorrelation functions with the assumption that the scatter was that of a single macromolecular component, according to (22, 23)

\[ A(q, t) = A(q)(1 + \exp(-2q^2D_t)) \]

where

\[ q = (4\pi/\lambda) \sin(\theta/2) \]

# being the scattering angle and \( t \) the time. For a typical measurement, a signal at \( \sim 5 \times 10^8 \) s−1 was sampled by the autocorrelator for 100 s; measurements were fit according to Equation 2 via a linear least squares fit of ln[\( A - A_0 \)] versus time (23), with each point weighted in proportion to \( (A - A_0)^2 \); measurements for which the "polydispersity index," defined as the normalized variance of the linear fit, were above 10% were rejected; reported values were obtained as averages over a series of successive measurements of the same solution.

Measured sedimentation and diffusion constants were corrected in the usual way for differences of solvent viscosity and solvent density.

The accuracy of the correction when applied to the diffusion constant in 30% glycerol was confirmed by measurement of the diffusion constant of latex spheres (Polysciences 8691) in water and 30% glycerol, respectively.

Frictional coefficients of molecular models were calculated as follows. Each model consisted of a string of beads in which each bead, except the first and the last, just touched two other beads; the chain’s contour length was as suggested by the electron micrographs of the extended form of fibronectin, and its volume was that of the unreduced protein. Thus, if \( m \) is the number of beads per molecule and \( b \) the radius of a bead, then the contour length, \( L \), is given by

\[ L = 2mb = 140 \text{ nm} \]

and the volume, \( V \), by

\[ V = (4/3)\pi b^3 = 590 \text{ nm}^3 \]

from which one gets \( m = 49 \) and \( b = 1.42 \text{ nm} \) as best estimates.

Odermatt et al. (24) did similar calculations for rigid models and for models that were given the exact size and shape of extended fibronectin molecules and fragments observed in their electron micrographs.

Randomness of the chain was produced by imposing no conditions on the internal rotation of the chain, except those demanded by steric exclusion of the beads, and by restraining the bond angle, i.e. the angle defined by three successive beads, by imposing what amounts to a Boltzmann distribution according to a harmonic potential for strain of the bond angle away from its equilibrium value of \( \pi \). This gives for the probability of finding \( \alpha \) in the range from \( \alpha \) to \( \alpha + d\alpha \):

\[ P(\alpha)d\alpha = \text{constant} \cdot (\pi - \alpha) \exp[-\beta(\pi - \alpha)]d\alpha \]

The parameter \( \beta \) determines the stiffness of the chain: one-half of the values of \( \pi - \alpha \) will be below \( 1/2\beta \). (In addition, values of \( \alpha < \pi/3 = 60° \) are never used, since these invariably give bead overlap.)

The set of different conformations that correspond to a particular angular restraint was sampled by a Monte Carlo procedure, the Stokes radius, \( R_s \), was calculated for each member of the sample by the method of Garcia de la Torre and Bloomfield (25) and finally averaged over the sample. (Averaging according to \( R_{\text{ave}} = 1/(1/R_s) \) or to \( R_{\text{ave}} = (R_s) \) gave essentially the same results.)

An alternative set of models was obtained by taking successive randomly generated chains and bringing together one or two pairs of beads located at different points of the chain by application of internal rotations of the model in a Monte Carlo procedure.

RESULTS

Molecular Characterization and Homogeneity—Concentration dependence of sedimentation and diffusion coefficients of fibronectin is shown in Fig. 1. Extrapolated values of \( s \) and \( D \) are given in Table I, which also includes two values of \( M \), that calculated from the light scattering intensity and that calculated from the ratio of \( s \) and \( D \) with

\[ M = (s/D)RT/(1 - \vartheta \rho) \]

where \( R \) is the gas constant, \( T \) the absolute temperature, \( \vartheta \) the partial specific volume of the protein, and \( \rho \) the solvent density. The two values of \( M \) are in good agreement, as should be the case for a homogeneous preparation. A second check of homogeneity is provided by a comparison of observed and calculated boundary spreading during ultracentrifugation; the agreement is seen to be good (Fig. 2). A third confirmation of sample homogeneity is obtained from the goodness of fit of a

FIG. 1. Concentration dependence of corrected sedimentation and diffusion coefficients of human plasma fibronectin.

Phosphate buffer, pH 7.2, ionic strength 0.35 M.
single exponential to the autocorrelation function (cf. Equation 3). The polydispersity index (see above) was found to be less than 1% in many cases, i.e. within random experimental error.

The molecular weights obtained here by two techniques exceed by approximately 10% that obtained from sedimentation equilibrium (13) and by some 15% that estimated from mobility in sodium dodecyl sulfate-gel electrophoresis, by us and others. Causes for this difference may include a slightly anamolous mobility of fibronectin and the presence of fibronectin oligomers, in spite of our efforts to remove these by gel filtration and lack of success in detecting these by sodium dodecyl sulfate-gel electrophoresis.

Studied in Glycerol/Water Mixtures—Measured diffusion constants in solutions of moderate ionic strength (0.35 M) containing increasing amounts of glycerol are shown in Fig. 3. The observed change of D with solvent composition was shown to be reversed when a sample was first exposed to 30% glycerol and then returned to aqueous solution by dialysis. In Fig. 4 are shown results of a series of measurements in a solvent containing 30% glycerol, 1.2 mM phosphate buffer, pH 7.2 and a varying concentration of NaCl. Values from Ref. 16 are included for comparison (0).

To check that fibronectin did not aggregate in 30% glycerol, the sedimentation constant at 1 mg/ml was determined to be 7.4 S (corrected value). With the value of D measured for the same solution, this gave a molecular weight of 424,000 (Equation 8), which was on the low side. The discrepancy may reflect a slightly different value of \( \phi \).

**Fitting Molecular Models to the Observations**—The following analysis will proceed on the basis of the values of the frictional coefficients, \( f \), of fibronectin, that may be calculated from the observed diffusion constants, with the equation

\[
D = kT/f \tag{9}
\]

where \( k \) is Boltzmann’s constant. It is convenient to convert \( f \) to an equivalent Stokes radius, \( R_s \), with

\[
I = 6\pi \eta R_s \tag{10}
\]

\( \eta \) being the solvent viscosity; the Stokes radius is the radius of a spherical particle with the same frictional coefficient. The Stokes radius of plasma fibronectin is then found to be equal to 9.6 nm at very low salt concentration, both in water and in 30% glycerol, and to 14.5 nm in 30% glycerol at high ionic strength, in phosphate buffer. The problem will be to rationalize these two extreme values in terms of the structures observed by electron microscopy.

The most likely model of fibronectin suggested by the electron micrographs is that of a long and thin, flexible particle, which is largely extended in 30% glycerol at moderate ionic strength (5, 6), but which occurs in a considerably more compact form at low ionic strength at neutral pH (7-10). Qualitatively, the variation of the size of the images with ionic strength appears to agree with the variation of the Stokes radius.

A quantitative analysis can be given by use of a method developed by García de la Torre and Bloomfield (25), according to which one may calculate the Stokes radius of any particle that consists of a set of rigidly connected spheres. In order to apply this method here, two problems must be solved, i.e. one must select a representation of the fibronectin molecule as a set of spheres, and one must take into account the (limited) randomness of the conformation of a flexible model.

As a simple, and by no means unique, model, we have selected a string of beads of identical radius. The models differed in that some were rigid and either linear or folded.
and others were flexible as a result of free internal rotation and a varying extent of bending at each bead along the chain. We stress that the fine details of the models are meant to correspond only in a most general way to details of the molecular structure of fibronectin, but also that the conclusions drawn below are insensitive to changes in these same details.

Fig. 5 shows average Stokes radii for the flexible model, plotted versus the root mean square end to end distance, which both increase as the angle is restrained to be closer to 180°. The completely extended, rodlike model is seen to have a Stokes radius slightly larger than observed at high ionic strength in 30% glycerol; the observed Stokes radius of 14.5 nm corresponds to a root mean square end to end distance of ~80 nm, in reasonable agreement with a value of 90 nm estimated from the electron micrographs. On the other hand, the Stokes radius of the model approaches that observed for fibronectin at low ionic strength only when the model is made highly flexible, and the root mean square end to end distance is less than 40 nm. It is interesting to note that as the flexibility is increased beyond a certain point, the vast majority of the randomly generated model chains is rejected because of intrachain overlap, and that the few acceptable chains do not have a particularly low Stokes radius; a value for $R_s$ of about 10 nm appears to be the lower limit that can be reached by this method of model generation. Fig. 6 shows projections of some of the generated model chain conformations. The model labeled $a$ belongs to the set having Stokes radius as observed in 30% glycerol at high ionic strength; the flexibility of the models increases from $a$ through $b$ and $c$ to $d$; the model labeled $d$ belongs to the set having a Stokes radius nearly that observed at low ionic strength.

Some calculations were done in order to show that the results of the modeling procedure are quite insensitive to exact specifications such as the value of $V$ in Equation 6, or to the presence of a permanent kink of 70° in the center of the chain, as suggested by the electron micrographs (6).

An alternative method of decreasing the effective size of the models consisted of requiring closure of the chain into a (near) loop as an additional condition. Both singly and doubly connected models were examined. Stokes radii of models obtained in this manner were 12.1 and 11.3 nm, respectively, when these were obtained by internal rotation of what were originally relatively extended models of type $a$ of Fig. 6 (for which the parameter $\beta$ of Equation 7 equals 2). If the loop condition is applied to inherently somewhat more flexible chains, the values of $R_s$ were found to be lower. In Fig. 7 are shown doubly looped models in which each chain end was forced to be close to a unit near the middle of the chain ("pretzels"). The average Stokes radius of these particular models was ~11.3 nm, for the few models that could be obtained from originally relatively extended models ($\beta = 2$), and 9.7 nm when an inherently more flexible open chain was used to generate the looped model ($\beta = 1$).

A model in which the two halves of the chain are folded back on themselves, as proposed by Hormann (24, 26) for the compact form of fibronectin (see also Ref. 16), was found to have a Stokes radius of 10.8 nm when extended and 10.3 nm when given a V-shape with an angle of 70°.

The Stokes radii of similar random models, but only half as long, were found to be 9.1 and 7.0 nm, if the flexibility was that which, respectively, gave $R_s = 14.5$ and $R_s = 10.5$ for the whole chain; a doubled-up rodlike model of 25 beads was found to have $R_s = 6.9$ nm. Fully extended chains had $R_s = 9.6$ nm for $m = 25$ beads and $R_s = 15.9$ nm for $m = 49$ beads.

**DISCUSSION**

Implications for Structure and Function of Fibronectin—

The fibronectin molecule is known to consist of two polypep-
tide chains linked by two disulfide bonds near their carboxyl ends, the two chains having similar, but probably not identical, amino acid sequence. A (partial) amino acid sequence and disulfide bonding pattern suggests that this molecule consists of "modules" of from 45 to 90 amino acids; these modules can be classed as belonging to only a few different types (27, 28).

A modular structure is also suggested by the observation of multiple thermal transitions for fibronectin and fragments (12, 14, 24, 25, 26). Different modules supposedly have different functions; for many, this function is the ability to bind to a specific type of macromolecule. It is easy to imagine the connections between some of the modules to be flexible, but it is not immediately obvious what feature of the structure is responsible for the existence of different conformations which are stable under different circumstances. It would be reasonable to assume that some intermodule bond exists in one of the extreme forms, and not in the other. The question then is in which form does the bond exist.

Intuition favors assigning the bond to the compact form, since interactions between distant parts of the chain could easily turn a long and flexible particle into a compact shape. These interactions could well be similar to the ones that lead to fibronectin self-association at low temperatures in the presence of small amounts of impurities (31), except that in that case the bonds are intermolecular, rather than intramolecular. The interactions could be attractions between negatively and positively charged segments of the molecule; the observation of the compact form at low ionic strength and of the dependence of molecular shape on ionic strength indicates that such interactions contribute to the stability of this form. This has also been suggested by Hörmann (24, 26), who proposed a model in which each of the two halves of the fibronectin molecule folds back on itself as a result of this kind of an interaction. However, we believe that the electron micrographs favor a more disordered model of the compact form of fibronectin (Fig. 7). We have found a limit to the compactness of simulated chains of increasing flexibility; the most compact non-self-overlapping models that can be obtained in this way have Stokes radius close to that observed experimentally for the compact form. The observed size of the compact form would thus be a natural lower limit if a structure. It should be noted that glycerol favors microtubule assembly; also, from work of Gekko and Timasheff (32, 33), it appears that glycerol has a stabilizing effect on the tertiary structure of proteins. These results suggest that the open form of fibronectin may be the more structured one. However, this would not be incompatible with stabilization of the compact form by long range electrostatic forces.

Results of experiments with half-molecules of fibronectin and smaller molecular fragments are relevant to this question. Erickson and Carrell (10) report an ionic strength dependence of the sedimentation rate of half-molecules and fragments in a glycerol/water mixture. This indicates that the half-molecule and fragments can exist in compact conformations and that attraction between domains with opposite charge contributes to the stability of the compact forms.

Finally, it may be pointed out that the existence of a compact, circulating, and somewhat inert form of fibronectin may have physiological advantages. It is possible for such a molecule to have some affinity for a number of different ligands which it frequently encounters, but for no or little binding to occur, as long as an opening-up of the fibronectin molecule is a prerequisite for binding. In addition, there would be a set of primary, high affinity ligands, such as perhaps collagen, which are infrequently encountered, to which the protein can bind. Upon binding, the protein will change to the open form (16). Following this first binding step, the open molecule will be able to bind a low affinity ligand at another site, and thus perform its cohesive role cooperatively, and only when required by the presence of one of the primary ligands.

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