A model of glomerular ultrafiltration in the rat

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Deen, W. M., C. R. Robertson, and B. M. Brenner. A model of glomerular ultrafiltration in the rat. Am. J. Physiol. 223(5): 1178-1183. 1972. A mathematical model has been developed to investigate the influence of a number of physiological variables on the net driving force for ultrafiltration \((P_{UF})\) in the rat glomerulus. The model was used to predict osmotic pressure differences as functions of distance along a glomerular capillary for a wide range of glomerular capillary plasma flow rates, membrane hydraulic permeabilities \((k)\), and axial pressure drops; these pressure profiles are consistent with recently reported experimental findings. When filtration pressure equilibrium is achieved, results obtained with the model indicate that estimates of \(P_{UF}\) at the beginning and end of the glomerular capillary bed cannot be used to infer the correct magnitudes of the mean value of \(P_{UF}\) or \(k\) in the normal rat. The results also indicate that changes in single-nephron glomerular filtration rate will vary in proportion to changes in plasma flow rate when filtration pressure equilibrium occurs.

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**THE RATE OF GLOMERULAR ULTRAФILTRATION** is governed by the same driving force that causes fluid movement across other capillary membranes, the imbalance between transmembrane hydrostatic and osmotic pressures. At any point in the glomerulus, the net driving pressure \((P_{UF})\) is given by

\[
P_{UF} = \Delta P - \Delta \pi = (P_{GC} - P_T) - (\pi_{GC} - \pi_T)
\]

where \(P_{GC}\) and \(P_T\) are the hydrostatic pressures in the glomerular capillary and Bowman’s space, respectively, and \(\pi_{GC}\) and \(\pi_T\) are the corresponding colloid osmotic pressures.

Using a strain of Wistar rats in which glomeruli are frequently present as surface structures and thus accessible to micropuncture, Brenner and co-workers (2, 3) have recently made direct measurements of \(P_{GC}\) and \(P_T\) and have estimated colloid osmotic pressures in pre- and postglomerular blood \((\pi_{AA}^1\) and \(\pi_{EA}^1\), respectively). Among their findings is the discovery that \(P_{UF}\) declines to essentially zero before glomerular capillary blood enters the efferent arteriole.

In the present study we have developed a mathematical model of glomerular filtration which allows us to predict the variation in \(P_{UF}\) with distance along the capillary under a variety of experimental conditions. This model is a useful tool for examining the effects of changes in membrane hydraulic permeability \((k)\), mean driving pressure \((<P_{UF}>)\), initial glomerular capillary plasma flow \((Q_0)\), and systemic plasma protein concentration \((C_{AA})\) on single-nephron glomerular filtration rate \((SNGFR)\).

The model finally adopted here is based primarily on conservation of mass and equation 1 and appears to provide the simplest means for predicting realistic \(P_{UF}\) profiles and of understanding variations in SNGFR. In order to justify the inclusion of certain features in this model, two simpler approaches will also be considered. The first of these involves the use of arithmetic average osmotic pressures, equivalent to assuming the \(\Delta \pi\) profile to be linear, an assumption employed earlier by Brenner et al. (2). The second approach predicts nonlinear \(\Delta \pi\) profiles, but assumes no hydrostatic pressure drop in the direction of flow in the capillary. The final model, adopted as being most useful, differs in the second approach only in that it includes a small, but finite, axial pressure drop.

**Assumption of a linear \(\Delta \pi\) profile.** Let \(x\) be the distance along a glomerular capillary measured from the point at which filtration begins. Assuming that \(P_T\) does not vary with \(x\) and neglecting \(\pi_T\), the mean ultrafiltration pressure is given by

\[
<P_{UF}> = ((P_{GC}) - P_T) - <\pi_{GC}>
\]

The most convenient way to treat the available micropuncture data is to assume that \(\pi_{GC}\) rises linearly along the capillary segment, allowing one to compute \(\langle \pi_{GC} \rangle\) as an arithmetic mean of the beginning and end-point values, as in equation 3.

\[
\langle \pi_{GC} \rangle = \frac{\pi_{EA} + \pi_{AA}}{2}
\]

The rate of production of ultrafiltrate is related to the mean driving pressure according to

\[
SNGFR = K_t \langle P_{UF} \rangle
\]

where \(K_t\) is a filtration coefficient viewed most simply as the product of the membrane hydraulic permeability \((k)\) and the available filtering surface area \((S)\). Given measurements of SNGFR and \(\langle P_{UF} \rangle\), \(K_t\) can be found readily from equation 4.

The assumption of a linear osmotic pressure profile is represented by the solid line, \(\Delta \pi\) (linear), in Fig. 1, in which it is also assumed that the axial pressure drop is small compared to \(\Delta P\), so that \(\Delta P\) is shown to be constant.

Although mathematically convenient, the assumption of
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A linear $\Delta \pi$ profile can be questioned on physical grounds. Since the local rate of filtration is proportional to $P_{UF}$, the protein in the capillary lumen should be concentrated most rapidly near $x = 0$. This in turn should produce a relatively rapid initial rise in $\Delta \pi$, with the slope of the $\Delta \pi$ curve gradually declining as $\Delta \pi$ becomes more nearly equal to $\Delta P$. According to this reasoning, the broken line in Fig. 1, $\Delta \pi$ (nonlinear), ought to be a more realistic representation of $\Delta \pi$. Since $(P_{UF})$ is proportional to the area between the AP and $\Delta \pi$ curves of Fig. 1, the linear $\Delta \pi$ profile will overestimate $(P_{UF})$ and underestimate $K_f$.

Development of model. This study was undertaken to develop a model that would provide more reasonable pressure profiles and more accurate values of $(P_{UF})$ and $K_f$ than could be obtained from the use of equation 3. For simplicity, the glomerular capillary bed has been idealized as a single tube of equivalent surface area and of length L. The tube radius ($r$) and hydraulic permeability of the membrane ($k$) are both assumed to be constant. Since glomerular capillaries are freely permeable to small solutes, the osmotic contributions of which are assumed to be negligible, the system is considered to have only two components, water and plasma protein. The tube wall is considered to be impermeable to protein (reflection coefficient, $\sigma = 1$), only the steady state is considered, and flow rates and concentrations are taken to depend only on the axial distance coordinate $x$. This idealized capillary bed is shown in Fig. 2.

The equation of Landis and Pappenheimer (4), which expresses $\pi$ as a cubic function of protein concentration, is approximated in this study by a quadratic equation:

$$\pi = a_1 C + a_2 C^2$$

where $C$ is the plasma protein concentration and $a_1$ and $a_2$ are constants found from a least-squares fit to the Landis-Pappenheimer results over the range $4 \leq C \leq 10 \text{ g/100}$ ml. Equation 5 differed from the Landis-Pappenheimer equation by less than 1% for plasma protein concentrations encountered in this study and considerably simplified the solutions to several of the equations.

Referring now to Fig. 2, a material balance over the disk bounded by $x$ and $x + \Delta x$ gives the expression for conservation of mass as

$$\frac{dQ}{dx} = \left(\frac{Sk}{L}\right) P_{UF}, \quad Q(0) = Q_0$$

where Q is the volumetric flow rate of plasma in the lumen and $S$ is the total surface area of the tube. It is more convenient to work directly with protein concentration, which is related to the volume flow rate according to

$$C = m Q, \quad \frac{dQ}{dx} = -\frac{m}{C^2} \frac{dC}{dx}$$

where $m$ is the mass flow rate of protein, a constant. Substituting equation 7 into equation 6 and nondimensionalizing with $L_n, C_{AA}$, and a reference pressure $\Delta P_{R}$ (to be defined later) gives

$$\frac{dC^*}{dx^*} = \left(\frac{kS\Delta P_R}{Q_o}\right) C_{AA}^* \frac{P_{UF}}{\Delta P_{R}}, \quad C^*(0) = 1$$

where $C^*$ and $x^*$ are dimensionless protein concentration and distance, respectively, and $Q_o$ is the initial glomerular capillary plasma flow. The product $kS$ is equivalent to the filtration coefficient, $K_f$, used in equation 4. Substituting the dimensionless expression for $P_{UF}$ into equation 8 yields

$$\frac{dC^*}{dx^*} = F C_{AA}^* \left(\frac{\Delta P}{\Delta P_{R}} - A_1 C^* - A_2 C_{AA}^*\right), \quad C^*(0) = 1$$

where

$$F = \frac{kS\Delta P_R}{Q_o}, \quad A_1 = \frac{a_1 C_{AA}}{\Delta P_{R}}, \quad A_2 = \frac{a_2 C_{AA}^2}{\Delta P_{R}}$$

A knowledge of $\Delta P(x)$ and values of the parameters $F$, $A_1$, and $A_2$ are all that are needed to obtain the concentration profile from equation 9.

Measurements of $P_{UG}$ reported by Brenner et al. (2, 3) were made at unidentified sites within the glomerular capillaries, so that it has not yet been possible to determine a complete hydrostatic pressure profile, $\Delta P(x)$. However, the use of these values of $P_{UG}$ in computing the ratio $\pi_{BA}/(P_{UG} - P_R)$ yielded an average result very close to unity, suggesting to these authors, in view of the presumably random distribution of puncture sites, that $P_{UG}$ changes little with $x$. Since flow through the capillaries requires the presence of at least a small axial pressure drop, and since $P_R$ is assumed to be independent of $x$, $\Delta P$ must decrease with $x$. We will assume here that the drop in $\Delta P$ is sufficiently small that $\Delta P$ may be approximated by a constant minus...
a small linear correction term.\footnote{Since glomerular capillary blood flow is a nonlinear function of \( x \), it is not unreasonable to expect \( P_{GC} \), and hence \( \Delta P \), also to decline in a nonlinear manner. However, given that the axial pressure drop along the glomerular capillary has been shown experimentally (7, 3) to be no more than a small fraction of \( \Delta P \), the use of a linear approximation for the pressure drop (equation 11) will have a negligible effect on calculated values of \( P_{UV} \).} Let

\[ \Delta P = \Delta P_R (1 - \epsilon(x^* - \frac{1}{2})) \quad (11) \]

where \( \epsilon \) is a small positive number. According to equation 11, the pressure drop along the length of the tube is equal to \( \epsilon \Delta P_R \). The reference pressure may now be chosen as

\[ \Delta P_R = (\Delta P) = (P_{GC}) - P_T \quad (12) \]

Substituting equation 11 for \( \Delta P \) in equation 9 yields the final form of the equation for \( C^* \),

\[ \frac{dC^*}{dx^*} = FC^*(1 - A_1 C^* - A_2 C^{*2}) - \epsilon(x^* - \frac{1}{2}), \quad C^*(0) = 1 \quad (13) \]

The parameters \( A_1 \) and \( A_2 \) can be determined directly from the available data, and in subsequent discussions these will be considered as known quantities. The pressure drop \( \epsilon \) is known only to be small and will be assumed to take on various values between 0 and 0.10. \( F \) contains the unknown filtration coefficient, \( K_f \), and given \( A_1, A_2, \epsilon \), and \( C^*_{ EA} \), \( F \) and thus \( K_f \) can, in principle, be calculated. However, as shown below, a unique value of \( K_f \) cannot be computed from presently measured quantities when filtration pressure equilibrium occurs.

Profiles for constant \( \Delta P \). As we have already discussed, \( \Delta P \) in the rat glomerulus appears to be relatively constant. It might be supposed that, if the change in \( \Delta P \) were small enough, its effect on the concentration and osmotic pressure profiles would be negligible. This turns out not to be the case, but it is still informative to solve equation 13 with \( \epsilon = 0 \) before considering the more realistic case of \( \epsilon > 0 \).

Setting \( \epsilon = 0 \) in equation 13, one obtains

\[ \frac{dC^*}{dx^*} = FC^*(1 - A_1 C^* - A_2 C^{*2}) \quad (14) \]

The quantity in parentheses in equation 14 is the dimensionless form of \( P_{UV} \), which approaches zero as \( \Delta \tau \) approaches \( \Delta P \). Inspection of the equation shows that the slope of the concentration curve will start out at a maximally positive value and gradually decrease, resulting in a \( \Delta \tau \) profile similar to the broken line in Fig. 1. An important consequence of this equation is that in a finite length of capillary, \( C^* \) can never reach a value such that \( \Delta \tau = \Delta P \); the \( \Delta \tau \) curve can closely approach the \( \Delta P \) curve, but the two cannot intersect.

The solution to equation 14 is

\[ \frac{A_1}{2} \ln \left| \frac{C^*}{1 - A_1 C^* - A_2 C^{*2}} \right| - \frac{1}{C^*} + \left( \frac{A_1^2 + 2A_2}{2 \sqrt{A_1^2 + A_2}} \right) \ln \left( \frac{\sqrt{A_1^2 + 4A_2} + A_1 + 2A_2 C^*}{\sqrt{A_1^2 + 4A_2} - A_1 - 2A_2 C^*} \right) = Fx^* + I \quad (15) \]

where \( I \) is an integration constant found from the initial condition to be equal to the left side of the equation with \( C^* = 1 \).

Profiles for small axial pressure drop. The assumption of constant \( \Delta P \) combined either with a linear or nonlinear \( \Delta \tau \) profile does not adequately simulate a capillary in which \( P_{UV} \) declines to zero. The linear \( \Delta \tau \) profile is not consistent with the expectation of more rapid filtration at the beginning of the capillary, while the \( \Delta \tau \) profile obtained from equation 15 fails to account for the observation of filtration pressure equilibrium, \( R \geq 1 \). The change in \( \Delta P \) evidently cannot be neglected.

Before solving equation 13 with \( \epsilon > 0 \) we can state with some confidence that a glomerular capillary with nonzero axial pressure drop may be expected to have certain properties: (a) If at some point along the capillary \( \Delta \tau = \Delta P \), then \( d\Delta \tau/dx = 0 \) at that point. This can be seen from equation 8, where it is clear that \( dC/dx = 0 \) when \( P_{UV} = 0 \), an equivalent statement. (b) After intersection of the \( \Delta \tau \) and \( \Delta P \) curves, \( \Delta \tau \) cannot greatly exceed \( \Delta P \), since the resultant backflow into the capillary would dilute the protein and again lower \( \Delta \tau \). (c) The \( \Delta \tau \) and \( \Delta P \) curves can intersect only once. A second intersection would require that

\[ R = \frac{\Delta \tau}{\Delta P} \quad (16) \]
The average driving pressures for ultrafiltration are proportional to the areas between the ΔP and Δτ curves in Fig. 3A, and (PUB) can be seen to decrease with increasing F. Reference to equation 10a shows that for a given ΔPR, (PUB) decreases with increasing hydraulic permeability or surface area (Ks) and increases with initial glomerular capillary plasma flow (Qp). In those cases where the system closely approaches equilibration (and the values for C*EA converge), (PUB) may vary substantially without any noticeable change in C*EA, CEA, or (ΔP).

Table 2 gives the equilibration ratio (R), the point of equilibrium (x*EQ), and the final protein concentration (C*EA and CEA) for each of the profiles shown in Fig. 3. The extent of equilibration increases with F until it reaches a plateau value of 1.002 for F = 3.0. The three lowest values of F result in distinctly different values of C*EA, but for F ≥ 1.5 the predicted values of C*EA differ by only 2%, approximately the same as the uncertainty in current techniques for measuring protein concentrations (2, 3). This convergence of concentrations makes it impossible with current techniques to distinguish, for example, between F = 1.5 and F = 6.00 (or higher), even if e, A1, and A2 were known precisely. While in principle it was possible to determine F using equation 13, small uncertainties in C*EA prevent the estimation of anything more than minimum values. The mean values of the ratio C*EA/(PUB) calculated from four sets of data in refs. 3, 4 are 0.96, 1.04, 1.02, and 1.00, indicating that equilibration is the rule rather than the exception and underlining the futility of attempting to determine values of Ks from equation 13 under these conditions.

Table 3 shows the effects of varying e from 0 to 10, the latter value corresponding to an axial pressure drop of 3.5 mm Hg. Higher values of e promote equilibration by causing ΔP to decrease more rapidly, and the inability to determine

<table>
<thead>
<tr>
<th>F</th>
<th>R</th>
<th>x*EQ</th>
<th>C*EA</th>
<th>CEA</th>
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</thead>
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<tr>
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<td>1.090</td>
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<tr>
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<td>7.09</td>
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<tr>
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<td></td>
</tr>
<tr>
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<td>1.454</td>
<td>8.43</td>
<td></td>
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<tr>
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<tr>
<td>6.00</td>
<td>1.001</td>
<td>0.48</td>
<td>1.465</td>
<td>8.49</td>
</tr>
</tbody>
</table>

* Assumes ΔPR = 35.3 mm Hg and CEA = 5.80 g/100 ml. The value of x at which ΔP = Δτ, the point of filtration pressure equilibrium. C*EA = 5.80 C*EA g/100 ml.

Table 3. Degree of equilibration as a function of e

<table>
<thead>
<tr>
<th>e</th>
<th>R</th>
<th>x*EQ</th>
<th>C*EA</th>
<th>CEA</th>
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<tbody>
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<td>1.459</td>
<td>8.46</td>
<td></td>
</tr>
<tr>
<td>0.02</td>
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<td>8.43</td>
<td></td>
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<tr>
<td>0.05</td>
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<tr>
<td>0.10</td>
<td>1.001</td>
<td>1.433</td>
<td>8.31</td>
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</tr>
</tbody>
</table>

See footnotes of Table 2.
As can be seen from Table 2 and equation I, when R is near unity (as in the normal rat), Q* will be doubled or halved (PUP), these are extremely sensitive to small errors in the uncertain magnitude of the axial pressure drop compounds this problem. Consequently, one assumes \( \Delta P \) to be constant, while the other assumes \( \Delta P \) to decrease linearly with distance.

The model with axial pressure drop is the only one of the three approaches that predicts physically reasonable pressure profiles and is fully consistent with experimental observations of filtration pressure equilibrium (2, 3). The assumption of constant \( \Delta P \) provides adequate pressure profiles only when \( \Delta P \) is always less than \( \Delta P \). Both of these models predict essentially linear \( \Delta P \) profiles when the end points are far from equilibrium, but this condition appears not to be the case for the normal rat (1-3). The model with axial pressure drop is valid for all values of R thus far observed (2, 3), whereas the model with constant \( \Delta P \) is applicable only when \( R < 1 \), and the linear \( \Delta P \) approach is valid only for R less than approximately 0.8. In the normal hyperventilating rat, it is most often the case that \( R > 0.95 \) (2, 3).

The assumption that \( \Delta \tau \) is linear provides convenient estimates of the minimum value of \( K_1 \) and the maximum value of \( P_{UR} \). While in principle the axial pressure drop model could be used to find more precise estimates of \( K_1 \) and \( P_{UR} \), these are extremely sensitive to small errors in the measurement of \( C_{EE} \) and \( C_{EA} \) when R is close to unity. The uncertain magnitude of the axial pressure drop compounds this problem.

When R is near unity, the \( \Delta \tau \) profiles for different values of F have end points that are identical within the uncertainty of available protein concentration measurements. Values of \( P_{UR} \) calculated from \( C_{AA} \) and \( C_{EA} \), for example, the linear \( \Delta \tau \) approach, would also be identical, even though the true values of \( P_{UR} \) vary markedly with F. Thus, with R close to unity, measurements of \( C_{AA} \) and \( C_{EA} \) cannot be made as evidence that \( P_{UR} \) remained constant throughout a series of experiments. It is clear that \( P_{UR} \) depends not only on \( C_{AA} \), \( C_{EA} \), and \( \Delta \tau \), but on \( K_1 \) and \( Q_0 \) as well.

The single-nephron glomerular filtration rate is related to glomerular capillary plasma flow and efferent arteriolar protein concentrations by the equation

\[
\text{SNGFR} = Q_0 \left( 1 - \frac{1}{C^{* subdivisions}} \right)
\]  

As can be seen from Table 2 and equation I, when R is near unity (as in the normal rat), \( Q_0 \) may be doubled or halved with almost no change in \( C^{* subdivisions} \). In this regime changes in SNGFR should be proportional to changes in plasma flow rate. For \( R \) not close to unity an increase in \( Q_0 \) will cause a noticeable decrease in \( C^{* subdivisions} \), and SNGFR will depend less strongly on \( Q_0 \). The same conclusion applies when \( Q_0 \) is decreased.

We have emphasized the need for including an axial pressure drop in a satisfactory model of glomerular ultrafiltration. This pressure drop was assumed to be small compared to \( \Delta \tau \) and linear in x, although properties \( \tau_1-\tau_5 \) discussed previously require only that \( \Delta \tau \) decreases monotonically. Glomerular hydrostatic pressures are known to be pulsatile (2), but the three properties should be applicable at any instant in time provided that \( \Delta \tau \) and \( \Delta \tau \) are in phase. The pressures calculated with this model should be regarded as averaged over a period of time encompassing several cardiac cycles.

GLOSSARY OF SYMBOLS

- **Values in angular parentheses are mean values.**
- **\( a_1, a_2 \)**: osmotic pressure coefficients in equation 5, mm Hg/(g/100 ml) and mm Hg/(g/100 ml), respectively
- **\( A_1, A_2 \)**: dimensionless osmotic pressure coefficients, equation 10, b and c
- **\( C \)**: plasma protein concentration, g/100 ml
- **\( C^{* subdivisions} \)**: dimensionless protein concentration, C/C&
- **\( F \)**: \( (K_1 \Delta P)/Q_0 \), permeability and plasma flow rate parameter, equation 10 a
- **\( I \)**: integration constant in equation 15
- **\( k \)**: membrane hydraulic permeability, nl/(sec-mm Hg cm²)
- **\( K_1 \)**: ultrafiltration coefficient, nl/(sec-mm Hg), equation 4
- **\( L \)**: length of capillary, cm
- **\( m \)**: mass flow rate of protein, g/sec.
- **\( P \)**: hydrostatic pressure, mm Hg
- **\( P_{UR} \)**: net ultrafiltration pressure, mm Hg, equation 1
- **\( \Delta \tau \)**: \( P_{GR} - P_T \), transmembrane hydrostatic pressure difference, mm Hg
- **\( \Delta \tau \)**: reference pressure, mm Hg, equation 12
- **\( Q \)**: volumetric flow rate in capillary lumen, nl/sec.
- **\( Q_0 \)**: glomerular capillary plasma flow rate, Q(0)
- **\( r \)**: radius of idealized capillary, cm
- **\( R \)**: ratio of osmotic to hydrostatic pressure differences at end of capillary, equation 16
- **\( S \)**: surface area available for filtration, cm²
- **\( \text{SNGFR} \)**: single-nephron glomerular filtration rate, nl/min or ml/min
- **\( \tau \)**: distance along capillary from point at which filtration begins, cm
- **\( \tau^{* subdivisions} \)**: \( x/L \), dimensionless distance along capillary
- **\( \tau^{* subdivisions} \)**: point at which \( P_{UR} = \tau \), transmembrane osmotic pressure difference, mm Hg

Greek Letters

- **\( \epsilon \)**: dimensionless axial pressure drop, equation 11
- **\( \pi \)**: colloid osmotic pressure, mm Hg
- **\( \Delta \tau \)**: \( \pi_60 - \pi_7 \), transmembrane osmotic pressure difference, mm Hg

Superscript

- **\( * \)**: dimensionless variable

Subscript

- **AA**: afferent arteriole
- **EA**: efferent arteriole
- **GC**: glomerular capillary
- **T**: Bowman’s space, or beginning or proximal tubule

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