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THE SIGNIFICANCE OF VISCOUS FLOW PROPERTIES IN THE THEORY OF OPERATION OF A NEPHRON

by

H. M. Lieberstein

March 1968

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ABSTRACT

The salient feature of a nephron is its tiny size, six to ten microns radius, since the forth power law requires a tiny flow rate even from a large pressure gradient. Along closely folded hairpin loops, present in the nephrons of birds and mammals and called loops of Henle, a salt concentration gra[illegible] forms in the ambient medullary tissue. Urine collects in this tissue in ducts, equilibrates with it osmotically, and produces a final product hypertonic to blood. Other authors explain the mechanism of this loop in terms of an hypothesis of active extrusion of a small amount of sodium from one branch of the loop and operation of a countercurrent multiplication principle. By close attention to real-

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istic physical principles we construct a model that does not use this hypothesis but produces in numerical studies the observed concentration gradient and an amplification of this effect with length. A much weaker assumption than similar ones made in other models, that two salt concentrations take on stationary values, causes a linear initial value problem for a (2x2) first order ordinary differential equation system to replace a (4x4) first order partial differential equation system. Basic mechanisms used such as back diffusion were of no importance in previous square law models.

1. Introduction. A kidney can to some extent be characterized as an aglomeration of nephrons, the nephron being a tiny tubular unit responsible for chemical processing of the blood. It forms from the blood a cell-free filtrate and concentrates it to a urine while at the same time collecting the residual for excretion. One feature of the nephron in highly developed organisms is that to a very large extent the blood components which are essential to life are first passed into the filtrate (being prepared for excretion) and then retrieved or reabsorbed by the organism. It was contended by the late Homer W. Smith [7],

dean of renal authorities, that to understand why this should be one must undertake a study of the evolution of the kidney. We will not here pursue the subject in this manner but rather only try to understand the gross properties of the nephron mechanism as it now operates in mammals and birds. Really we take the much more limited purpose, to correct certain assumptions formerly made in the analysis of the nephron mechanism so that they conform closely to realistic physical principals. We then undertake a somewhat detailed analysis of the function of one particularly interesting portion of the nephron, the loop of Henle.

Among the many blood components first filtered and then retrieved (some in minute amounts) the principal ones by volume and weight are simply water and salt (sodium chloride) [7], [9], [5]. Transport of these two most common of materials so dominate the picture of operation of the nephron that many authors have felt one could adequately represent the gross properties of nephron function in an analysis which does not acknowledge the presence of other participating components. In our treatment we operate under this viewpoint, although we are well aware that some other authors have chosen to treat a three or more

component system [2]. One human kidney would be composed of perhaps 10^6 nephrons [7], [1], this being approximately one half the number available for processing the blood volume. The blood is processed several times in one day [7] and a liter or two only of concentrated waste products are thus produced. Since the task is of Herculean proportions and a single nephron is so very tiny, we could not say without study how many more nephrons are available to the body than are needed, but since people very often live normal lives with only one kidney, we may regard the system as overdesigned in capacity by at least a factor of two. Of course, to regard the kidney exclusively as an excretory device without recognizing that the discarding of non-reusable materials is a secondary phase of its role in processing the blood and maintaining a workable blood chemistry environment for the body, would be grossly to underestimate the importance of the kidney. Even if we are not of sufficiently poetic nature to espouse the tenet of Homer Smith that "the kidneys are that of which philosophy is made", still we cannot fail to acknowledge that the kidneys are an absolutely basic unit in maintaining the homeostatic condition of blood necessary

for the survival of advanced organisms. The kidneys have been regarded as basic units in modern physiology since its founding in the spirit of Claude Bernard, "a constant internal environment is a necessary condition for an unfettered life".†

There is perhaps a possibility to obtain an insight into the physiology of advanced organisms by noting the difference in the nephron as a unit of renal physiology and the neuron as a unit of neurophysiology. The neuron, just as the nephron, is the smallest functioning unit of a large structure, but unlike the kidney, a nerve structure may involve such complex relations between its units that its overall function appears to be entirely unrelated to the functions of its constituent parts. The function of the kidney structure, on the other hand, seems to arise largely as a massive superposition, or adding, of functions of nephrons where, of course, we regard the tissue matrix of nephric tubules to be an integral part of the nephron. We will find that in birds and mammals the last stage of urine concentration (on which we intend to focus our attention) is accomplished by creating

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†very loose translation.

a concentration gradient in the medullary tissue of the kidney in which parts of nephrons are embedded, and then allowing the urine to be concentrated by osmotic equilibration in collecting ducts located deep in this tissue. Thus the concentration gradient in part of the kidney tissue which is outside the nephric tubule does play a role, and this might be a little difficult to understand in terms of an isolated analysis of one nephron. Moreover, some devices exterior to the nephric tubule (distributed capillary beds [2, p.232]) seem to be partly responsible that concentration gradients can be maintained in the medullary tissue at stationary values (see Stationary concentrations functions conditions in this paper). We will see, however, that as long as we are clearly aware of these features, an intelligible analysis of the mechanism of one isolated nephron is possible.

The salient property of the nephron, considering that it is a fluid device, is its extremely small size, and we propose here for the first time that this accounts almost entirely for its efficiency as a concentrating and refining unit. In previous analyses this small size was tacitly ignored by treating flow through nephric

tubules to be essentially inviscid. Here we propose that there are sound technical reasons why the kidney has evolved as a large mass of tiny nephric units and not as a collection of a few large units. In the final analysis this observation will be found to depend on the very simple fact that for large N,

$$Nr^4 \ll (Nr)^4.$$

2. Gross properties of flow in the proximal tubule.

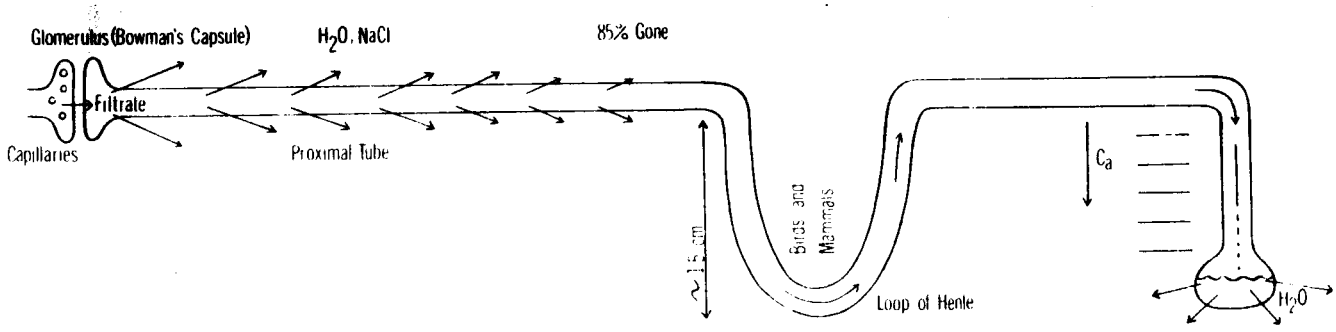

Fig. 1. Schematic of gross properties of a nephron

The nephron begins in the glomerulus located in the Bowman's capsule where pressure differences across the membrane structures from capillaries to an adjacent nephron (aided by osmotic transport) cause the passage of a filtrate of blood plasma into the nephron, and a pressure

is built sufficient to push the fluid through a long tiny tubule to its destination in the collecting duct. As we see it, a pressure which is sufficient to this task also ought to be sufficient to complete the entire refinement or concentration of the urine whereas in former analyses it was deemed necessary (for a part of this passage) to hypothesize an extra expenditure of extraneous energy in performance of a small active extrusion of sodium from the nephric tubule to its ambient tissue. In at least one analysis [2, p.233] the effects of transmural pressure in moving solutes and solvent through the walls was ignored whereas this mechanism appears to us to be the principal, or at least the key or triggering, factor involved. If the glomerular pressure head is, indeed, not large enough for the purpose of refinement of the urine (it was so claimed by the principal author in this area, Werner Kuhn, see [1]) then we contend that it probably also cannot be large enough to drive the fluid to its destination; one would thus have to hypothesize still another mechanism for pumping urine through the nephric tubule in order to explain the observed volume flow rate to the collecting

On page 9, line 8, after the word "osmosis" place a reference to the following footnote:

* Osmosis, of course, is simply diffusion which is taking place through a permeable membrane. If different salt concentrations are generated on two sides of a membrane (due say, to a pressure difference), then water will tend to move toward the regime of higher concentration and sodium ions will tend to move in the direction of lower concentrations, both thus moving so as to bring concentrations on the two sides to a common value and ~~thus to~~ destroy the concentration difference. Some membranes are so constructed that the size of pour blocks the passage of ions as large as sodium ions. That many such membranes exist has given rise to a tacit assumption which is often made that water travels toward the higher concentration and no sodium moves back. Here we assume that in the proximal tubule, the walls are permeable to sodium and these ions travel across the walls driven either by a pressure difference across the walls or by a concentration difference ("osmosis" or "diffusion"). If active transport is involved in the proximal tubule then the concentration at the end of the tubule would not nearly agree with that of the general blood plasma. Even then it is still quite likely that some sodium passes through passively. We believe, actually, that it will turn out that the walls of the thin segment in the loop of Henle where we work are impermeable to sodium while the walls of the proximal tubule are not. If the thin segment walls are impermeable to sodium ions, this will not at all affect our final results since we will simply replace our parameter combination $\ell + \beta$ in equations (8) and (9) with the single parameter β.

ducts.† The nephric tubule is so small that it would almost seem problematical whether a given pressure head would drive the fluid principally down the channel course or principally through lateral pores in the epithelial layer which is semipermeable to water. Actually, in the segment of the tubule proximal to the glomerulus a good deal of water is driven through the walls by the pressure head, and the sodium ions follow by osmosis, serving to carry along the chloride ions, again by osmosis. In this manner, in the course of the travel of the proximal segment of the tubule alone, 80-85% by volume of the water and salt [2, p.228], [7, p.143], [1, p.553] passed into the filtrate at the glomerulus is reabsorbed again into the ambient tissue, while the urine in the channel retains the same osmotic concentration as the general blood plasma. This is essentially the total picture of the mechanism of a primitive nephron, but it is not for the nephron of a bird or mammal which is capable of forming a urine that is

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†Kuhn feels that electromotive forces, not yet understood [1, p.555], are involved in forming the observed glomerular pressure head which he says is somewhat larger than can be accounted for on the basis of blood pressure effects alone.

hypertonic to the blood plasma. Were it not for the large percentage, by volume, of water pumped through the walls in the proximal segment, we could quickly compute approximately what transmural pressures are responsible for pumping the water through the walls. From an observed, or surmised, volume flow rate in the tubule, the average radius of the tubule, and the well-known Poiseuille law, we could compute the pressure gradient responsible for the flow rate (see Physically realistic flow considerations in this paper). But the Poiseuille law says that the volume flow rate is proportional to the pressure gradient times the fourth power of the radius, and the radius is so small that a large pressure gradient would be necessary to achieve even a very very low volume flow rate down the channel. Now if the walls of the proximal segment of the tube were rigid and approximately impermeable, and the fluid incompressible, the pressure would vary approximately linearly with distance down the tube from its value at the glomerulus to its value at the far end of the proximal segment. Knowledge of one of these two pressures, of course, and the pressure gradient, would give an approximate value of the

other, and this linearly varying pressure in the tubule minus the pressure in the ambient tissue would be the transmural pressure available for pumping water laterally. Progressively less water would be pumped through the walls as the urine approached the far end of the proximal segment. Actually, of course, the large amount of water pumped laterally in the proximal segment is a clue to a significant pressure release in the channel so the amount of pressure available for lateral pumping is diminished greatly from what would seem to be available in this discussion as the fluid procedes down the channel. Nevertheless, the simple mechanism for lateral pumping should now be entirely clear. We repeat for emphasis that whatever pressure is available for pumping fluid down the channel is also available for pumping it through semipermeable walls if a lower pressure obtains on the other side of the wall. If it does not, the tubule will probably collapse, block the flow, and build up a larger pressure inside the channel to reopen flow both down the channel and through the channel walls. The small channel size shows that lateral pumping in response to pressure gradients across the walls cannot fail to be a major

factor in urine refinement.

3. Gross properties in the loop of Henle and the collecting duct. In birds and mammals, that small part of the original filtrate which emerges from the proximal tubule enters a closely folded hairpin shaped segment called the loop of Henle and thence passes through the distal segment and into the collecting duct. It has long been known [1], [5], [7], [9] that the occurence of a loop so constructed in birds and mammals is closely associate with the fact that these animals can form a urine which is hypertonic to the general blood plasma. Such a urine, however, is certainly not hypertonic to the tissue surrounding the place in the body where it is collected. Rather it is collected in ducts or basins with semipermeable epithelial layers to allow for osmotic equilibration with the ambient tissue. These ducts are buried deep in the medullary tissue (the "deep" part of the kidney) where the operation of the many loops of Henle cause a large concentration gradient to be maintained; the osmotic concentration in the tissue surrounding the collecting ducts being large, the collecting ducts (and distal

tubules leading to them) give up large quantities of water to the surrounding tissue, thus conserving this item so essential (and, therefore, necessarily comparitively rare) to mammals and birds and producing a highly concentrated urine. Micropuncture studies have shown [5, p.105] that the concentration of the urine leaving through the distal end of the loop of Henle is not significantly different from that entering through the proximal end, and this is the evidence that the sight of concentration must be, as indicated, in the collecting ducts. Moreover, micropuncture studies also show an increasing osmotic concentration inside the loop tubule, down the length of the loop, and a similar one in the tissue surrounding it. By what mechanism such a concentration gradient is created by flow in the loop and diffusion with the surrounding tissue will be the subject of this study. The reader may already notice that there is probably no need for considering a significant change in total volume pumped in the channel due to lateral pumping in the loop (as there was for the proximal segment), and this simplifies our treatment of channel flow properties in the loop.

Our model will differ from former ones (see [1], [5], [9], [2]) in four important respects: (i) We utilize viscous flow properties because of the compelling necessity produced by the existence of a very small radius of the nephric tubule. (ii) We do not assume (as, for example, in [1]) a pressure which remains the same with distance down the tubule (either on each branch of the loop, as in [1], or on the whole loop, as in [5]) because the pressure must vary at least linearly with distance (even in a rigid tube filled with an incompressible fluid). (iii) We find no need to assume that the walls of the ascending branch of the loop are less permeable to water than those of the descending branch since the pressure downstream is anyway much smaller than upstream and it thus simply gives rise to less pumping of water through the walls downstream than upstream. Also the ascending branch contains a larger channel pressure than the distal tubules and collecting ducts. (iv) We include effects of diffusion in the channel and in the ambient tissue. (v) We do not find it necessary to assume any active extrusion of sodium. Though it has often been necessary in biological considerations to

assume some sort of active transport (and sodium is very often convenient to so involve), still active transport is an assumption to be avoided if possible since it indicates lack of knowledge of the fundamental mechanism.

That sodium passes out of the nephric tubule is not under contention. We assume, in fact, that it follows osmotically the water which must be pushed out by pressure differences across the walls. Even if sodium is "actively extruded," we find that such an extrusion is not required in order to explain observed effects and that there is no reason to believe in such an extrusion taking place at an isolated point exclusively as has previously been hypothesized.

J. Sperber [8] showed in an intensive comparitive study of various mammals that there is a strong relation between the level of urine concentration possible for an animal to produce and the lengths of loops of Henle in the animal's kidneys. Some desert animals that live almost exclusively on water of metabolism, ingesting almost no preformed water, possess extremely long loops and produce urine which is virtually crystalline [6]. We obtain here a much stronger "concentration versus

loop length" relation than it has been possible to obtain from other models except those that hypothesize an active transport. Such models are said to operate on a countercurrent multiplication principal, and a major concern in such models is their efficiency [1, p.546]. In our model no such concern will be manifest since we do not utilize any extraneous energy.†

4. Loop mechanisms operating on a countercurrent multiplication principle. Some remarkable differences in loop models described in the literature may be unconscious insertions on the part of the author. These could perhaps arise out of differences in style of exposition. The discourse given in Pitts [5] is largely intended for an introductory pedagogical purpose and emphasizes the understanding of basic concepts in current thought rather than a critical examination of them. It is, perhaps necessarily, not altogether compatible with the largely encyclopedic discussion given in [9] by Wesson. Moreover, any author with only qualitative tools of discussion at his disposal cannot reach for the precision of statement obtainable in a detailed

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†Unless, as suggested as a possibility in the footnote above, the pressure gradient in the nephron does come from sources at present unkown.

mathematical analysis of the loop mechanism. An exhaustive analysis of this type was attempted by B. Hartigay and Werner Kuhn in [1]. Also, a suggestive but incomplete mathematical analysis of the loop mechanism as one element in modeling the entire renal cortex and medulla was given by Jacques, Carnahan, and Abbrecht in [2].

The Kuhn model. The treatise [1] (already cited) by B. Hartigay and Werner Kuhn, expounding the details of operation and the empirical findings which lent support to the countercurrent multiplication principle and sodium extrusion hypothesis appeared at the culmination of an extended period of activity of Werner Kuhn in this area. All other modern works available to us would seem either to be extensions of his ideas or to be gross descriptions of them. We will find that in order to give a physically realistic treatment of flow and diffusion processes in the loop it will be necessary to depart from the Kuhn model in ways which are so serious as to cause us to abandon the countercurrent multiplication principle altogether as a mechanism. However, the geometry of the loop will still be fundamental in the formation of a concentration gradient in the medullary tissue.

In its construction the Kuhn model would seem to reveal the strong influence of laboratory (and, perhaps, industrial) apparatus since the role of the ambient tissue as the common intermediate reservoir between branches of the loop is deleted. Materials such as water and salt are simply passed directly from one loop branch to the other through the interstitial material regarded as a somewhat thick semipermeable membrane. The velocity is tacitly assumed to be constant across the channel by assigning

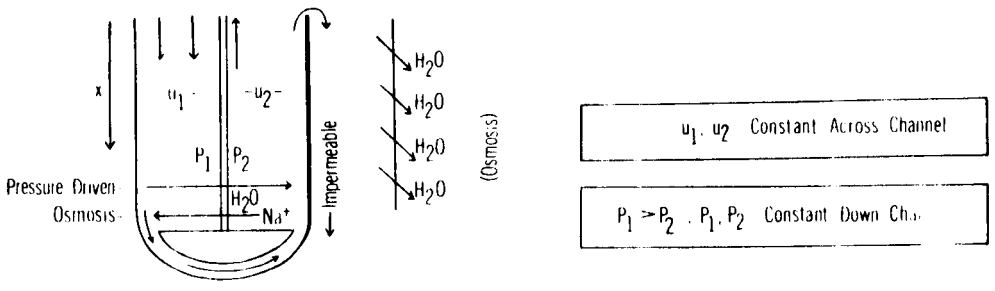

Fig. 2. Kuhn model

values of u_1, velocity in the descending branch, and u_2, velocity in the ascending branch, at various values of x measured from the loop entrance. The pressure p_1 in the descending branch and p_2 in the ascending branch are assumed constant down the channels (as well as across) with a large positive difference, $p_1 - p_2$, occuring because

a narrow connecting tube at the bottom of the two channels is assumed to provide a large drag. The narrow connecting tube does not occur in a nephron and is not intended to exist physically; it is introduced as a mathematical device for absorbing all change in pressure from the proximal to the distal end of the loop at one point, thus allowing the difference, $p_1 - p_2$, between pressures in the two channels to be treated as a constant and materially simplifying the analysis.

Water is forced through the semipermeable membrane separating the two branches of the loop by the constant difference of pressure, $p_1 - p_2$. A rate of flow through the membrane is assigned proportional to this pressure difference and Darcy's (empirical) law is thus invoked. A concept of osmotic pressure, whereby the effects of diffusion across a membrane are attributed to an equivalent pressure difference, is introduced to account for the movement of solute mass in the direction of a concentration difference across the membrance, and through this artifice the process of osmosis is also treated by Darcy's law. This treatment of osmosis allows all differential equations to be solved by quadratures, and the assumption that $p_1 - p_2$

is constant (not varying with distance x) makes these quadratures yield exceptionally simple linear results. It then becomes possible to handle the mathematics of the model with extremely elementary manipulative tools, and to obtain such an end would seem to be the purpose of the highly simplified nature of the assumptions. They have the advantage of giving explicit results in terms of parameters so that the effects of varying some of the parameters can be seen without extensive numerical studies. In particular, limiting values of parameters are readily obtainable.

The simple differential equations used in [1] are obtained by reasoning that the transfer of water across the membrane separating the two channels causes an increase in velocity in the channel it is transfered to (and a decrease, in the channel it is transfered from). Back diffusion in the channels is ignored, as is the effect of channel flow in bringing material down the channel of a different concentration. We call the latter the Pitt effect for, as we will soon see, the Pitt model operates on this effect and active sodium extrusion only. The assumptions in the Kuhn model are all consistent with the use of inviscid properties to describe channel flow.

In [1] it is found that the pressure difference, $p_1 - p_2$, across the membrane required to produce empirically realistic concentration gradients in the loop is fifty atmospheres, an absurd figure which would give p_1 a value that would burst a kidney. Therefore, an hypothesis is made that a small active transport of sodium ions from the ascending to the descending branch takes place. This causes a virtual short-circuit of salt across the top of the loop and results in the repeated recirculation of some salt through the bottom of the loop. Thus the "single effect" of a small transport of sodium is multiplied several times and in [1] a demonstration is presented which is intended to show that only a very small amount of sodium transport is necessary to produce realistic concentration gradients in the loop channel. The ambient tissue concentration plays no role, of course, in this model; it is simply assumed that the ambient tissue takes on immediately the same concentration as that inside the channel. The role of the distal tubules and the collecting duct is modeled by the insertion of another tube running along side the ascending branch but with a water impermeable wall separating them. How this impermeable wall can be managed

in the nephron without destroying other essential functions such as water communication between loop branches or the ascending branch with ambient tissue seems to us to be problematical.

We are told that some chemical industries utilize an apparatus which operates on a countercurrent multiplication principle. If these devices employ large Reynold's number flows, say because of the use of extremely large channels, and a mechanism for pumping a chemical component of the flow from one channel to another, then it would appear that the Kuhn analysis may be essentially correct, but due to the tiny channel size occuring in a nephron, it cannot be expected to give even a grossly correct picture of kidney function. The current literature, then should be materially revised in this particular respect.

The Pitt model. In the Pitt model [5] the ascending limb

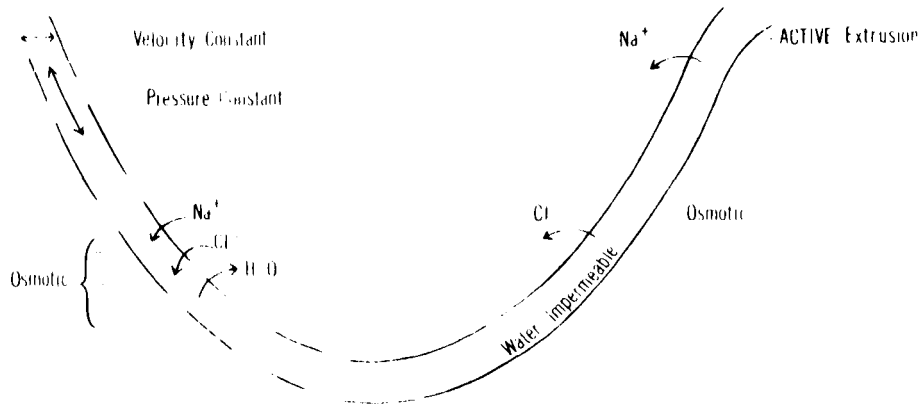

Fig. 3. Pitt model

is assumed impermeable to water, but the interstitium (ambient tissue) is recognized, as it was not by Kuhn, to form a reservoir for salt and water. Thus sodium ions, followed by chloride ions, are actively transported from the ascending branch to the interstitium, increasing salt concentration there and causing both a passive movement of salt from the interstitium to the descending branch and a passive movement of water from the descending branch to the interstitium. No pressure differences across walls occur in this model, back osmosis is ignored in both channel branches as well as in the interstitium, and the principal effect used by Kuhn, of the water volume transfer on channel velocity, is ignored. The only effect acknowledged in the model other than active transport and osmosis, is the effect of channel flow bringing material of a different concentration into a given cross section. Vivid picturizations of this effect are given by Pitts [5, p.106], and, in fact, one may well feel that he does not understand the importance of this effect until he studies these pictures. Apparently Kuhn left out this effect; to include it in his mathematical analysis would require the inclusion of gradients of concentration in his simple differential equations and greatly complicate them.

Pitt gives no mathematical analysis in [5], but his picturizations are convincing as to the efficient operation of a multiplier principle.

The Jacques, Carnahan, and Abbrecht model. The formulation of a loop model in [2] is quite incomplete since it is only to be regarded as one small portion of the formulation of a differential equation system which models the function of the entire cortex and medulla tissue, and, also, numerical and analytical studies of this system are not included.

The model treats of four quantities, water volume and salt concentration in the channel and in the ambient tissue. Four differential equations are then written for time flux of water volumes and salt masses. We found this treatment suggestive and have adopted it in our formulation below. Almost all other facets of our formulation are different. In [2], because the channel size is small, it is argued that the velocity may be treated as constant across the channel, thus essentially utilizing an inviscid model. All pressure gradients are ignored, and it is said that "the flow is assumed to be bulk displacement type". Back diffusion and the Pitt effect of the channel flow bringing

material of another concentration down the channel is ignored. In fact, all factors are ignored except active extrusion of sodium ions and osmosis of a number of filtrate compounds. It is assumed that all quantities, the two volumes as well as the two concentrations, reach stationary values. We believe this is too much to assume; in our model only the concentrations (channel and ambient) are assumed stationary, and these assumptions alone give us the existence of a unique solution in our model. In our model, the other assumptions would yield sets of inconsistent results.

Actually, the equations given in [2] allow for a multicomponent system, in which case the number of unknowns and equations are appropriately increased.

5. Physically realistic fluid considerations. Continuum model flows of incompressible fluids in tubes with rigid walls depend (in the sense of the Buckingham Pi Theorems) on two dimensionless parameters only,

$$Re = \frac{vr}{\nu} \qquad \text{and} \qquad \alpha^2 = \frac{r^2\sigma}{\nu} ,$$

the first, the Reynold's number, being the one that is best known and most generally held responsible for fluid dynamic phenomena. Here v is point velocity, r is radius

of channel, and $\nu = \mu/d$ is the kinematic viscosity coefficient where d is density and μ is the viscosity coefficient, and $\mathcal{F}$ is frequency of a periodic pressure gradient (or possibly a Fourier component of a pressure gradient function varying with time in a more complicated fashion). Of course, if the flow can be treated as stationary (time independent), then it will depend on the Reynold's number only. If the walls of the tube are compliant, then a number of other dimensionless parameters actually become involved, but for a very small radius and even moderately small variations of radius, these need not be seriously considered (see [4]).

In the case of a flow through a nephric tubule, because of the effects of both small $\mathcal{F}$ and r, the effects of the dimensionless parameter α^2 can clearly be ignored. We see then from the Reynold's number that effects of small radius can be identified with effects of large viscosity. Thus the occurence of a tiny radius clearly demands treatment of the flow as viscous (i.e., that any treatment of the flow does not delete the effects of viscosity). That this should be the case can be understood intuitively without knowledge of the Reynold's number by noting that the viscosity is a shear

stress between layers of fluid (and does not allow layers to slip by each other). Since the walls are fixed, the fluid next to the walls cannot move and this effect must feed from one layer to the next through the fluid. Thus only at a large distance from the walls could one possibly conceive to treat flow as inviscid. But in the case of a small radius, the flow inside a tube never can get far from the walls, and, thus, only viscous flow treatments can be justified in channels of small radius.

Since for viscous flow, the flow velocity must vanish at the walls, it cannot be constant across the channel for it would then vanish everywhere and no flow could occur. For time-independent flows of incompressible fluids in rigid wall channels, the velocity rigorously takes on a parabolic profile across the channel, rising from zero at the walls to its maximum in the center, and this profile is asymptotically approached for small channel radius even for time dependent flows in moderately compliant channels. This gives a far different picture from the constant velocity radial profile assumed in inviscid flow. For a constant velocity profile the volume flow rate, which is the integral of velocity over a cross section, is obviously proportional

to the cross section area, or to r^2 while the volume flow rate for a parabolic profile turns out to be proportional to r^4. In our loop considerations, the much smaller volume flow rate associated with viscous flow causes the transport of fluids down the channel by flow to become small and allow the back diffusion of the solute in the channel, a factor that was ignored in previous studies, to become of relative importance. Also, relative to the balance of these two opposing effects, the much smaller effect of diffusion in the ambient tissue becomes important. Furthermore, because of the large potential of the tube to resist a change in volume flow rate due to a change in pressure, the change of velocity in the tubule due to volume transport across the walls is very much smaller than before. In fact, this effect, which was a major factor in the Kuhn model, is now to be ignored.

In [4] and [5] it was shown that, ignoring short-lived transients, the volume flow rate for even a time dependent flow of an incompressible fluid in a channel of small radius is given simply by

$$\frac{\pi r^4}{8\mu} f(t)$$

where $f(t)$ is the time dependent pressure gradient[†], and for an extremely tiny radius this is also true if the tube has compliant walls. This is simply the time dependent Poiseuille law which is valid for small channels.

One comment of definitive interest here must now be made. The above forth power law is valid for flows in channels of even moderately small radius and of moderately small compliance -- probably even for blood flow in the brachial or femoral arteries of man (but not in the aorta). In the extreme case, however, of flows in channels with tiny radii, we have noticed that even a very very small volume flow rate can be maintained only by an extremely large difference in pressure at the two ends of the channel whenever the above forth power law is valid. Fortunately, for blood flow in the extreme case of a tiny arterial radius, (such as in arteriols or capillaries) such a law is not valid since continuum models are not valid for that case; the blood cell to channel size ratio is large for tiny

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[†] for flows in rigid tubes of length L,

$$f(t) = \frac{p_i - p_o}{L} ,$$

where p_o is the outlet pressure and p_i the inlet pressure.

channels (approximately one or even more in some cases). Actually, blood exhibits much less resistance to flow in small channels than indicated by the forth power law. We may speculate that, were it not so, evolution would have provided us with much larger minimum size blood flow channels since the present ones would provide a resistance that would require an excessive blood pressure in order to maintain volume flow at a minimum required rate; organisms that had a blood for which the forth power law was valid (even in small channels) would thus probably have perished long since from this sphere.

However, the glomerular filtrate, being filtered blood, is cell free. It contains at best a few large molecules and these are still small compared to a nephric tubule radius. The general practitioner (physician) tests for the presence of certain large molecules -- for example, albumin molecules -- in the urine as evidence of the effects of high blood pressure having forced large particles through the glomerulus membranes, but even the presence of these molecules, which is to be considered a somewhat pathologic condition, does not affect our conclusion: <u>A continuum model is justified for flow in the nephric tubule and the</u>

forth power law for volume flow rate must apply there. Moreover, this changes the nature of the dominant effects operating in the loop.

Since nephric tubule radii have been estimated to be between six and ten microns (.006 - .010mm) we can see, as noted earlier, that a truly phenomenal difference between inlet and outlet pressure must be built up to send a fluid through a long section of such a tubule at even a small flow rate. As we have pointed out earlier this same pressure can be used as well to drive fluid through permeable walls. It should be noted also that while the velocity can never be treated as constant across the channel for flows in small channels, the pressure can and should be so treated unless non-zero cross components of velocity are thought to be present. A non-zero pressure gradient in a radial direction would give rise to a radial component of velocity. For flows in such tiny channels we take it here to be intuitively evident that no significant radial components of velocity occur even under the large curvature conditions in the lower end of the loop. We thus treat the pressure as constant across the channel and, ignoring effects of compliance (for such small channels) and the channel pressure release

due to lateral transport across walls (for small amounts), let the pressure vary linearly from one end of the loop to the other.

6. A pressure driven loop mechanism. As it will turn out, it seems unlikely that the actual details of flow (such as velocity profile) are of any real importance in the operation of the loop mechanism. One may thus be led to conclude erroneously that it is of little importance whether one assumes viscous or inviscid flow in the nephric tubule. That this is not the case is because of the factors pointed out above: to obtain even a small volume flow rate, a large pressure difference is required, the pressure varies at least linearly down the tube (with distance) giving rise to a larger transmural pressure on the ascending than the descending branch, and, because of the slow rate of flow (compared to the rate of flow that such a pressure difference would produce in an inviscid fluid), the mechanism of back diffusion, both within the tubule and outside it, become inportant while, because of large drag, the change of fluid velocity in the tube due to fluid being pumped into and out of the tube (the "Kuhn" effect) becomes negligible.

Much more water is pumped laterally out of the walls at the top of the descending branch of the loop than out of the bottom of the descending branch, and this would seem to create a higher concentration of salt in the top than in the bottom of this branch, exactly the opposite of what is observed in nature. However, several other processes are at work here. The channel, which after all should account for a good deal more movement of fluid than lateral pumping accounts for, is constantly moving the higher concentration material downstream (Pitt effect), tending to reverse the salt concentration gradient in the channel. However, back diffusion is then working in the channel against the flow to try to decrease the magnitude of the concentration gradient, and, finally, osmosis across the epithelial layer to the ambient tissue is acting to move toward equilibration with the ambient tissue which, in turn, "communicates" with the other branch and in which back diffusion is also taking place.

Since more water is driven out of the descending than the ascending branch into the common reservoir of ambient tissue, to attain equilibrium with the ambient tissue more sodium ions (followed by chloride ions) pass out of the

ascending branch than would pass just to balance the water loss out of the ascending branch. This then would seem to cause the sodium concentration at the top of the branch to be smaller than at the bottom (as we would like to see it), but the other factors -- for example, back diffusion, and the effect of channel flow as mentioned above -- could either destroy or reverse or enhance this gradient.

There is already so complicated a play of one effect against another that it is hopeless with discussion alone to try to understand whether or not the mechanism we have described can produce the observed effects; i.e., whether they can produce an increasing concentration down the length of the loop and amplification of this effect with increased length. Also, we must clearly acknowledge that a salt concentration gradient in the right directions inside the channel branches will not affect a hypertonic concentration in the final urine unless a concentration gradient is produced in the ambient tissue in the right direction. Obviously, we need some analysis in precise terms.

After laying down, to the best of our ability, the model described above in the desired precise terms and

saying what kind of steady state (stationary concentrations) is assumed, we will provide detailed numerical studies showing that it is possible, by making a sensitive adjustment of parameters, for this mechanism to operate and produce the observed results. At least this is true within the range of our very incomplete knowledge of parameters. We invoke a special prejudice to the observed results in only one way; we assume, based on observations that concentrations at the top of the two loop branches are nearly equal, that they are actually equal throughout the length of these branches. To do otherwise would lead us to study a system of difference-differential equations, rather than the simple system of ordinary differential equations we end up with, and thus immensely complicate the model. The more complicated model may be of interest for future studies, but just now we wish clearly to establish feasibility. We invoke, as described above, only those properties that are generally recognized to be physically reasonable for the phenomena of flow in small tubules and for diffusion, osmosis, and flow through porous material (without knowingly rejecting any assumptions either except on the basis of such criteria), and then discover, without making any ad hoc assumptions

other than the single exception just mentioned, that the model so acquired can produce the observed results.

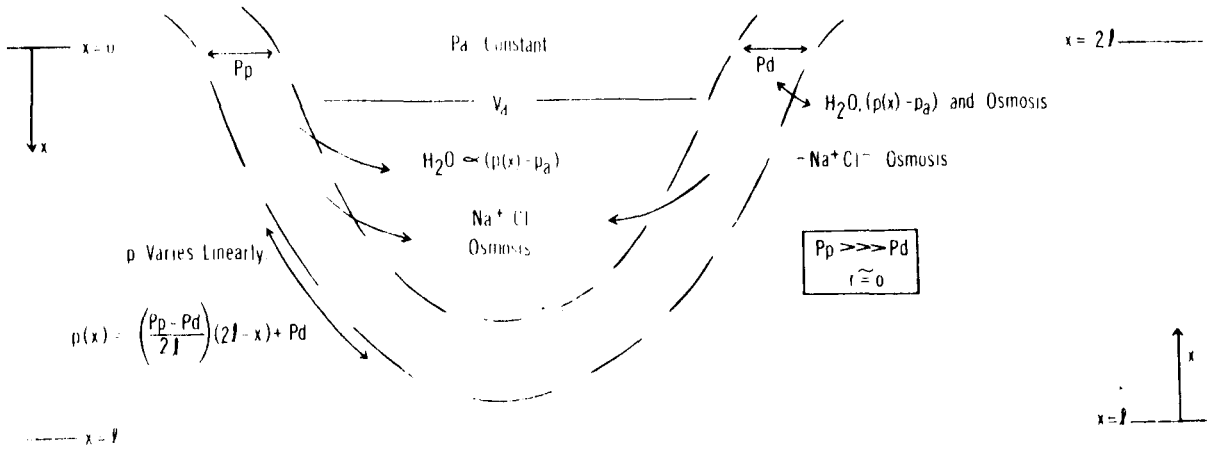

Fig. 4. <u>A pressure driven loop mechanism</u>

We assume all walls are equally permeable to water, but, for example, the pressure difference available for pumping water laterally at the top of the ascending branch is very small compared to that at the top of the descending branch, and, likewise, the transmural pressure available in the distal tubules and collecting ducts are small compared to any of those in the loop.

We treat the pressure as constant radially across the channel, varying down the length linearly from its proximal

value p_p at entrance to its distal value p_d at exit. We assume there is no volume flow in the ambient tissue although there is longitudinal diffusion there, and thus the ambient pressure p_a is taken to be constant. The ambient tissue is treated as though it were contained in a small radius tubule. This was also a feature of the Jacques, Carnahan, and Abbrecht model [2]. Immediate mixing radially is assumed both in the channel and in the ambient tissue.† This was assumed in all previous works. It is assumed that mass rate of change of sodium in response to a concentration gradient, either across the walls or down the channel or longitudinally in the ambient tissue, is simply proportional to this gradient (or difference). This is the usual linearizing assumption for reasonably small changes of concentration (see Handbook of Chemistry and Physics, 48th edition, The Chemical Rubber Co., 1967, p. F-45). Water is assumed to pass through the epithelial layer of the loop branches in proportion to a pressure difference across this layer (Darcy's law) and in proportion to the relative change of

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†Thus there is no concentration gradient perpedicular to the walls either in the tubules or in the ambient tissue though there is a concentration difference across the walls. This simplifies our formulation of osmosis.

sodium concentration. The relative change in sodium concentration is introduced here so that the osmotic coefficient used for water would be dimensionally consistent with that used for sodium, the transport of water across a membrane by osmosis in one direction being physically equivalent in this model to the transport of sodium in the other direction.†

We consider the variation of two quantities in the tubes: volume V, which is taken to be the volume of essentially water in a unit length (i.e., a cross section) of tube at position x and time t, and C, concentration of sodium in the tube at position x and time t, and the two similar quantities in the ambient tissue denoted by V_a and C_a. We thus write partial differential equations for

$$V(x, t),\ C(x, t) \quad \text{and} \quad V_a(x, t),\ C_a(x, t) \quad ,$$

the tube fluid volume and salt concentration, and ambient tissue fluid volume and salt concentration:

$$(1) \qquad \partial V/\partial t = -\alpha\left[f\cdot(\ell - \frac{x}{2}) + (p_d - p_a)\right] + \beta(C - C_a)/C$$

$$(2) \qquad \partial(CV)/\partial t = -\gamma(C - C_a) - (F - \gamma_1)\partial C/\partial x$$

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† In our model the two effects (if both can be said to operate) are eventually included as the effect of one parameter.

(3) $\partial(C_a V_a)/\partial t = 2\gamma(C - C_a) + \gamma_2 \partial C_a/\partial x$

(4) $\partial V_a/\partial t = \alpha\left[f\cdot\ell + 2(p_d - p_a)\right] - 2\beta(C - C_a)/C_a$

(5) $C(x, t) = C(2\ell - x, t), \quad C_a(x, t) = C_a(2\ell - x, t)$

for every t and for $0 \leq x \leq 2\ell$. Here

ℓ is length of loop,

F is volume flow rate,

f is $(p_p - p_d)/(2\ell) = ((8\mu)/(\pi r^4))\,F$, the total pressure gradient in the loop,

α is the permeability of the epithelial layer to water,

γ is the osmotic coefficient of the epithelial layer to salt,

β is the osmotic coefficient of the epithelial layer for water in response to a relative gradient of salt concentration (see discussion immediately above),

γ_1 is the diffusion (or osmotic) coefficient for salt (in the channel),

and γ_2 is the diffusion (or osmotic) coefficient for the ambient tissue to salt.

As we have pointed out, while the volume flow is bringing salt into a cross section (or unit length) of tube, the salt is fighting the stream by diffusion (osmosis). Thus occurence

of the rather remarkable factor $(F - \gamma_1)$ of $\partial C/\partial x$ in equation (2). It turns out to be important that this factor is small but positive. It would be negative if r^2 appeared in place of r^4 in the expression for getting the flow rate F from the pressure gradient f (which is that

which is supplied by the other physiological conditions of the body). In spite of the fact that we are aware, for example, that in the presence of a high titer of antidiuretic harmone (ADH), α will change quite appreciably, and that all the tissue parameters would be (and, in the future, should be) better treated as intricate functions determined from empirical data, we treat them here as constants in order simply to attain our goal to give an explanation of the gross properties of the loop mechanism.

7. <u>Stationary concentration functions conditions</u>. We seek to determine the concentrations C and C_a only (i.e., not V and V_a) such that they are stationary,

$$(6) \qquad \partial C/\partial t = \partial C_a/\partial t = 0$$

for every t and for $0 \leq x \leq 2\ell$, and such that

$$(7) \qquad C(0, t) = C_a(0, t) = C_o$$

where C_o is the salt concentration in the general blood

plasma. Condition (5) requires that C be symmetric in x. The ambient tissue, of course, is conceived of as being contained in a single tube of length ℓ being fed by the two branches of the loop simultaneously so that what may appear to be a symmetry condition on C_a in (5) is only a condition to assure uniform lateral mixing, and both equations in (5) are partially by way of explanation of some of the details in the derivation of equations (3) and (4). Without assuming symmetry for C our equations (1) through (4) would be quite considerably more complicated since they would involve differences as well as derivatives. It does not seem to be possible to attain smooth symmetry of C; i.e., such that $\partial C/\partial x(\ell/2, t) = 0$. In the more complicated (and more complete) difference-differential equations model which would delete the symmetry requirement on C, first order smoothness of C at $x = \ell/2$ is probably attainable but not here.

It will turn out that conditions (6) (7) guarantee the existence and uniqueness of functions C and C_a. We emphasize that it is not assumed here the V and V_a are stationary. From the uniqueness contention, (which will be clear in the equations below on the basis of elementary

theory) it is evident that this would be too much to assume; we feel, then, that the avoidance of these assumptions is a salient feature of this work. The question arises, do the stationary functions C and C_a obtained here evolve as steady states from the model (1) through (5); i.e., with any given initial values would the C and C_a parts of the solutions of (1) through (5) (with some appropriately chosen boundary conditions) asymptotically approach stationary values? Probably not. It seems apparent that other "devices" will have to be present to wash away an excess of water or salt, expecially in light of our knowledge of the large flow of water from nearby collecting ducts which acts specifically in response to the concentration gradient near the loop and tends to destroy it. In the past it has been hypothesized that certain "countercurrent exchangers" [5, p.110] were responsible for a drainage of the tissue, but it would now seem reasonable to believe that "distributed capillary beds" [2, p.232] are really responsible for keeping the tissue drained. We propose here that they cause the salt concentrations to reach and maintain a stationary level, as demanded in (6), while this would not necessarily happen in our model other-

wise.[†] We believe, then, that equation (6) is an assumption of our model extraneous to (1) through (5). We make it because it seems biologically cogent. It is quite considerably weaker than similar assumptions used elsewhere in the literature. For example, as noted earlier, in [2] V and V_a are also assumed to reach stationary values, and the Kuhn analysis in [1] is static throughout. Note that the volume of water can change radically here as long as the masses of sodium change appropriately to maintain constant concentrations.

Utilizing (6), multiplying (1) by C, and subtracting it from (2), gives

$$(8) \quad \frac{dC}{dx} = \frac{1}{(F-\gamma_1)}\left\{-(\gamma+\beta)(C-C_a) + \alpha C\left[f\cdot(\ell - \frac{x}{2}) + (p_d - p_a)\right]\right\},$$

while multiplying (4) by C_a, and subtracting it from (3), gives

$$(9) \quad \frac{dC_a}{dx} = \frac{2}{\gamma_2}\left\{-(\gamma+\beta)(C-C_a) + \alpha C_a\left[f\cdot\frac{\ell}{2} + (p_d - p_a)\right]\right\}.$$

We thus need only to solve the ordinary differential equations (8) (9) with standard initial conditions (7).

[†]Of course, while such devices can affect the concentration in the ambient tissue directly, they cannot affect directly the concentrations in the channels. By what indirect means such devices (say through an effect on the ambient tissue volume) can affect the salt concentration interior to the channel will not be investigated here.

This can be accomplished numerically in a straightforward manner using Runge-Kutta, proceding from $x = 0$ to $x = \ell$. Because of the linearity of the equations (8) (9), since they satisfy certain theorems on Fuchsian type, we could solve the equations by power series (or perhaps by other elementary means). This has seemed to be ponderous and not worth the effort in view of our belief that future investigations will show that some of the laws used above should be replaced by ones that are highly nonlinear.

Remark. The fact that γ_1, γ_2, and $F = (\pi r^4/(8\mu))\cdot f$ are small would not justify dropping them from equations (8) and (9) (or equations (1) through (4)) because they multiply $\partial C/\partial x$ and $\partial C_a/\partial x$ which are observed to be large. Also these are the highest order derivatives appearing in our differential equations and certainly cannot be dropped without careful study. We note from (8) and (9) that smallness of γ_2 and $(F - \gamma_1)$ give our sought for effects on concentration gradients.

8. Parameter selections. We find that very few of the values of the parameters we need are readily available to us. However, some are known, and reasonably intelligent, order of magnitude, guesses can be made for the values of

others so that in the end only two remain to be determined. Of these, one is length of loop, which is highly variable and a rational guess at the range is known; specifically we wish to compute the variation of concentration patterns within this range of lengths. The last parameter, γ_2, is selected so that the salient features observed in loop operation -- an increase of salt concentration down the length of the loop both inside the loop channel and in the ambient tissue, and an amplification of this effect with loop length -- are obtained. These seem to be determined with surprising sensitivity which gives some confidence in the manner of determination of parameters and in the validity of the model.

Whenever variations of our parameters occur with temperature we have taken $T = 25°C$ to be standard. Then the following values are quoted with an accuracy that is quite sufficient for our purposes. From the Handbook Of Chemistry and Physics, 48th edition, The Chemical Rubber Co., 1967, p. F-45, we have

$$\gamma_1 = 1.5 \times 10^{-5} \quad \text{in cgs units.}$$

From the Handbook of Chemistry by N. A. Lange, McGraw-Hill, 1961,

$$\mu = .01 \quad \text{in cgs units.}$$

From the Biochemists' Handbook, D. van Nostrand Co., Inc., 1961, p.879, for man

$$C_o = .3 \quad \text{in cgs units.}$$

We have taken for the radius

$$r = .001 \text{ cm}$$

which is twice the value given by Kuhn [1, p.555] but which seems more realistic according to the current literature. We start with ℓ given by

$$\ell = 1.5 \text{ cm}$$

as used by Kuhn [1, p.555], but we feel free to regard a lower value, say 1.1 cm, as standard since among the nephrons found even in the same kidney this value is highly variable [8], and sometimes, at least, it is only crudely intended as an average value in a whole kidney, being estimated from measurements of the thickness of the medullary tissue. We use

$$F = 1.6 \times 10^{-5} \quad \text{in cgs units}$$

in order to give a reasonable determination of the pressure gradient f. When based on this value of F, the pressure gradient comes out to be

$$f = .4142 \times 10^{6} \quad \text{in cgs units,}$$

which is well below half an atmosphere and is altogether reasonable considering either the reported observed pressures in the nephron or those that, according to Kuhn, could be due to blood pressure effects alone. The value of F we use is consistent with various values quoted in Kuhn [1, p.555], but these seem to have been crudely determined from daily values for the whole kidney and knowledge of what percentage water is reabsorbed in the distal segment and collecting ducts. The parameter α is chosen to be

$$\alpha = .4 \times 10^{-11} \quad \text{in cgs units}$$

to keep the effect of f in lateral pumping down to reasonable limits. The value was "obtained" by reasoning that at the end of the loop C would have a derivative which is "close" to zero. Assuming it is zero in equation (8), one obtains a relation between C and C_a at the end of the loop in terms of α, f and ℓ. Then, knowing f and ℓ, a value of α is taken so that at the end of the loop C_a will not be too much smaller than C. Our value of α cannot be compared with the permeability figures given variously by Kuhn as 3×10^{-6} and 3×10^{-10} because Kuhn's values were obtained by

some computations from the model, not from observations, and, moreover, the Kuhn value of α applies to the entire interstitial medium regarded as a somewhat thick wall. It is, by the artifice of introducing an osmotic pressure, made to account for the movement of masses of solute in response to a concentration gradient as well as to the movement of water in response to a pressure difference across the wall.

We imagine that γ is somewhat smaller than γ_1, although it must be admitted that they are not of comparable dimensions, and, therefore, choose

$$\gamma + \beta = .2 \times 10^{-5} \quad \text{in cgs units.}$$

We choose

$$p_d - p_a = 0 ,$$

a value that is to be regarded as really positive but not available to us in any better accuracy than this. It is surely accurate enough for our purpose but not accurate enough to describe conditions in the distal segment or the collecting ducts.

All these values are now frozen in order to determine from calculations a value of γ_2 (diffusion coefficient in the ambient tissue) which will give a con-

centration profile in the ambient tissue (and in the loop channels) that corresponds to the known gross properties. When this appears to have been chosen, ℓ will be allowed to vary, and, on the basis of this result, a slightly different value of γ_2 will be chosen.

In order to start our search for γ_2 we select the dimensionless parameter $\gamma_2/(F-\gamma_1)$ to be one, thus obtaining our starting value

$$\gamma_2 = 1 \times 10^{-6} \quad \text{in cgs units.}$$

It will be seen from Table 1 that this is really a surprisingly good guess, but it gives somewhat overdramatic results. It will be seen from Table 1 that our concentrationtion profiles are really extremely sensitive to the value of γ_2. The value $\gamma_2 = 1.3 \times 10^{-6}$ would seem to be a possible best choice. It is the largest value of γ_2 listed that does not yield impossible (negative) values of salt concentration, and it also gives smooth symmetry for C at the end of the loop.

However, in Table 2 it can be seen that the variation of loop length gives some impossible (negative) results (at $\gamma_2 = 1.3 \times 10^{-6}$) and exactly the opposite of the observed effect of length.

Table 3 shows variation of ℓ with $\gamma_2 = 1.27 \times 10^{-6}$. The results are somewhat more acceptable in that no impossible (negative) values for concentrations are obtained, but the effect of varying ℓ is small and in the wrong direction.

Table 4 shows remarkably good results with respect to varying the loop length ℓ through the values

$$\ell = 1.7,\ 1.6,\ 1.5,\ 1.4,\ 1.3,\ 1.2,\ 1.1 \text{ cm}$$

at

$$\gamma_2 = 1.2 \times 10^{-6} \quad \text{in cgs units.}$$

This, of course, corresponds to the value of our dimensionless parameter

$$\gamma_2/(F-\gamma_1) = 1.2.$$

Apparently the operation of our loop mechanism is very sensitive to its parameters, and, when presented with other parameters fixed, there is a critical value of γ_2. Then, if success is to be obtained with respect to the varying of loop length, the value of γ_2 must be moved away from the critical value -- not too far, however, or overly dramatic results quickly develope.

9. <u>Computational results</u>. Our computational results are thus contained in Table 4 with $\gamma_2 = 1.2 \times 10^{-6}$ (in cgs

units). We obtain

at $\ell = 1.1$ cm a salt concentration in the ambient tissue at the bottom end of the loop which is about $4\frac{1}{2}$ times that at the top end of the loop

from $\ell = 1.1$ to 1.7 a 400% increase in salt concentration at the bottom end of the loop in the ambient tissue is obtained for about a 50% increase in length of loop.

In truncation error checks all answers agreed to at least the three digits quoted. Actually, machine printouts seemed to be good to eight digits.

In Figure 5 the result with $\ell = 1.1$ cm is pictured while in Figure 6, the salt concentration at the end of the loop in the ambient tissue is plotted versus length of loop.

We repeat for emphasis that there is no question that sodium does leave the channel through the epithelial layers, but, in the context of our model, no active transport of sodium is required to explain the observed effects and there is no evidence of extrusion at an isolated location as required for the operation of a countercurrent multiplication principle. For the truly viscous flow

that we have here, it is even not certain that the countercurrent principle would operate effectively.

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The Wichita State University computing machine IBM 1620 was utilized here throughout and both time for its use and programming services were donated by Wichita State University.

References.

[1] Hagitay, B. and Kuhn, Werner, "Das Multiplikationsprinzip als Grundlage der Harnskonzentrierung in der Niere", Zeitschrift fur Electrochemie u. angewandte physik. chem., Bd. 55, Nr. 6, August 1951.

[2] Jacques, John A., Carnahan, Bruce, and Abbrecht, Peter, "A Model of the Renal Cortex And Medulla", Mathematical Biosciences, vol. 1, no. 2, June 1967.

[3] Elcrat, A. R., and Lieberstein, H. M., "Asymptotic Uniqueness for Elastic Tube Flows Satisfying a Windkessel Condition", Journal of the Mathematical Biosciences, vol. 1, no. 3, September 1967.

[4] Lieberstein, H. M., "Determination of the tension-stretch relation for a point in the aorta from measurement in vivo of pressure at three equally spaced points", Acta Biotheoretica, Leiden, vol. XVII, Pars II, 1965, 50-94.

[5] Pitts, Robert F., Physiology of the Kidneys and Body Fluids, Yearbook Medical Publishers, 1966.

[6] Schmidt-Nielsen, Knut, Desert Animals, Physiology Problems of Heat And Water, Oxford University Press, 1964.

[7] Smith, Homer W., From Fish To Philosophers, The American Museum of Natural History, 1961, Doubleday and Co..

[8] Sperber, J., "Studies on the mammalian kidney", Zoologiska bidrag fran Uppsala, 22, 249-431 (1944).

[9] Wesson, Lawrence G., Jr., Physiology Of The Kidney appearing in Physiology and Pathological Physiology of Handbuch der Urology, Springer-Verlag, 1955. Library of Congress Cat. No. 58-4788.

TABLE 1. Salt Concentration Profiles For ℓ = 1.5cm And Various γ_2 Values

γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.00×10^{-6}	.00	.30	.30
	.03	.33	.33
	.07	.36	.36
	.11	.39	.39
	.15	.43	.43
	.18	.47	.47
	.22	.51	.52
	.26	.56	.57
	.30	.61	.63
	.33	.66	.69
	.37	.72	.76
	.41	.78	.84
	.45	.85	.93
	.48	.93	1.02
	.52	1.01	1.13
	.56	1.10	1.26
	.60	1.20	1.40
	.63	1.30	1.56
	.67	1.42	1.74
	.71	1.55	1.94
	.75	1.70	2.18
	.78	1.86	2.45
	.82	2.04	2.76
	.86	2.24	3.12
	.90	2.47	3.53
	.93	2.72	4.01
	.97	3.01	4.56
	1.01	3.33	5.20
	1.05	3.70	5.95
	1.08	4.11	6.82
	1.12	4.59	7.83
	1.16	5.13	9.01
	1.20	5.75	10.38
1.00×10^{-6} (cont.)	1.23	6.47	11.99
	1.27	7.29	13.88
	1.31	8.23	16.08
	1.35	9.33	18.67
	1.38	10.59	21.70
	1.42	12.06	25.26
	1.46	13.76	29.44
	1.50	15.73	34.35
1.10×10^{-6}	.00	.30	.30
	.03	.33	.33
	.07	.36	.35
	.11	.39	.39
	.15	.43	.42
	.18	.47	.45
	.22	.51	.49
	.26	.55	.53
	.30	.59	.58
	.33	.64	.62
	.37	.70	.68
	.41	.75	.73
	.45	.81	.79
	.48	.88	.86
	.52	.94	.93
	.56	1.02	1.01
	.60	1.09	1.09
	.63	1.18	1.18
	.67	1.27	1.29
	.71	1.36	1.40
	.75	1.46	1.52
	.78	1.57	1.66
	.82	1.69	1.82
	.86	1.82	1.99

γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.10×10^{-6} (cont.)	.90	1.95	2.18
	.93	2.10	2.39
	.97	2.26	2.63
	1.01	2.44	2.90
	1.05	2.63	3.21
	1.08	2.84	3.55
	1.12	3.07	3.94
	1.16	3.32	4.39
	1.20	3.60	4.89
	1.23	3.91	5.47
	1.27	4.26	6.13
	1.31	4.65	6.89
	1.35	5.08	7.76
	1.38	5.57	8.75
	1.42	6.11	9.90
	1.46	6.73	11.21
	1.50	7.42	12.73
1.20×10^{-6}	.00	.30	.30
	.03	.33	.32
	.07	.36	.35
	.11	.39	.38
	.15	.43	.41
	.18	.46	.44
	.22	.50	.47
	.26	.54	.50
	.30	.59	.54
	.33	.63	.57
	.37	.68	.61
	.41	.73	.65
	.45	.78	.70
	.48	.84	.74
	.52	.90	.79
	.56	.96	.84
	.60	1.02	.89

γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue
1.20×10^{-6} (cont.)	.63	1.09	.95
	.67	1.16	1.01
	.71	1.23	1.07
	.75	1.31	1.13
	.78	1.39	1.20
	.82	1.47	1.27
	.86	1.55	1.35
	.90	1.64	1.43
	.93	1.73	1.52
	.97	1.83	1.61
	1.01	1.93	1.71
	1.05	2.03	1.82
	1.08	2.14	1.94
	1.12	2.25	2.06
	1.16	2.37	2.20
	1.20	2.49	2.35
	1.23	2.62	2.52
	1.27	2.76	2.70
	1.31	2.90	2.90
	1.35	3.06	3.12
	1.38	3.22	3.37
	1.42	3.40	3.64
	1.46	3.59	3.95
	1.50	3.79	4.30
1.25×10^{-6}	.00	.30	.30
	.03	.33	.32
	.07	.36	.35
	.11	.39	.37
	.15	.43	.40
	.18	.46	.43
	.22	.50	.46
	.26	.54	.49
	.30	.58	.52
	.33	.63	.55

γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.25×10^{-6} (cont.)	.37	.67	.59
	.41	.72	.62
	.45	.77	.66
	.48	.83	.70
	.52	.88	.74
	.56	.94	.78
	.60	1.00	.82
	.63	1.06	.86
	.67	1.12	.91
	.71	1.18	.95
	.75	1.25	1.00
	.78	1.32	1.04
	.82	1.39	1.09
	.86	1.46	1.14
	.90	1.53	1.19
	.93	1.60	1.24
	.97	1.68	1.29
	1.01	1.75	1.34
	1.05	1.83	1.39
	1.08	1.90	1.45
	1.12	1.98	1.50
	1.16	2.06	1.56
	1.20	2.14	1.62
	1.23	2.22	1.68
	1.27	2.29	1.74
	1.31	2.37	1.81
	1.35	2.45	1.87
	1.38	2.53	1.94
	1.42	2.62	2.02
	1.46	2.70	2.10
	1.50	2.78	2.18

γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.27×10^{-6}	.00	.30	.30
	.03	.33	.32
	.07	.36	.35
	.11	.39	.37
	.15	.42	.40
	.18	.46	.43
	.22	.50	.45
	.26	.54	.48

γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)	γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.27×10^{-6} (cont.)	.30	.58	.52	1.28×10^{-6}	.00	.30	.30
	.33	.62	.55		.03	.33	.32
	.37	.67	.58		.07	.36	.35
	.41	.72	.61		.11	.39	.37
	.45	.77	.65		.15	.42	.40
	.48	.82	.68		.18	.46	.42
	.52	.87	.72		.22	.50	.45
	.56	.93	.76		.26	.54	.48
	.60	.99	.79		.30	.58	.51
	.63	1.05	.83		.33	.62	.54
	.67	1.11	.87		.37	.67	.58
	.71	1.17	.91		.41	.72	.61
	.75	1.23	.95		.45	.77	.64
	.78	1.29	.99		.48	.82	.68
	.82	1.36	1.03		.52	.87	.71
	.86	1.42	1.07		.56	.93	.75
	.90	1.49	1.10		.60	.98	.78
	.93	1.56	1.14		.63	1.04	.82
	.97	1.62	1.18		.67	1.10	.85
	1.01	1.69	1.22		.71	1.16	.89
	1.05	1.76	1.25		.75	1.22	.93
	1.08	1.83	1.29		.78	1.28	.96
	1.12	1.89	1.32		.82	1.35	1.00
	1.16	1.96	1.36		.86	1.41	1.03
	1.20	2.02	1.39		.90	1.47	1.07
	1.23	2.08	1.42		.93	1.54	1.10
	1.27	2.15	1.44		.97	1.60	1.13
	1.31	2.20	1.47		1.01	1.66	1.16
	1.35	2.26	1.49		1.05	1.73	1.19
	1.38	2.32	1.51		1.08	1.79	1.22
	1.42	2.37	1.53		1.12	1.85	1.24
	1.46	2.42	1.55		1.16	1.91	1.26
	1.50	2.47	1.56		1.20	1.97	1.28

γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.28×10^{-6} (cont.)	1.23	2.02	1.30
	1.27	2.08	1.31
	1.31	2.13	1.32
	1.35	2.18	1.32
	1.38	2.22	1.32
	1.42	2.26	1.32
	1.46	2.30	1.31
	1.50	2.33	1.29
1.29×10^{-6}	.00	.30	.30
	.03	.33	.32
	.07	.36	.35
	.11	.39	.37
	.15	.42	.40
	.18	.46	.42
	.22	.50	.45
	.26	.54	.48
	.30	.58	.51
	.33	.62	.54
	.37	.67	.57
	.41	.72	.60
	.45	.76	.64
	.48	.82	.67
	.52	.87	.70
	.56	.92	.74
	.60	.98	.77
	.63	1.03	.80
	.67	1.09	.84
	.71	1.15	.87
	.75	1.21	.91
	.78	1.27	.94
	.82	1.33	.97
	.86	1.39	1.00
	.90	1.46	1.03
	.93	1.52	1.06

γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.29×10^{-6} (cont.)	.97	1.58	1.08
	1.01	1.64	1.11
	1.05	1.70	1.13
	1.08	1.76	1.15
	1.12	1.81	1.17
	1.16	1.87	1.18
	1.20	1.92	1.19
	1.23	1.97	1.19
	1.27	2.01	1.19
	1.31	2.05	1.18
	1.35	2.09	1.17
	1.38	2.13	1.15
	1.42	2.16	1.12
	1.46	2.18	1.08
	1.50	2.20	1.04
1.3×10^{-6}	.00	.30	.30
	.03	.33	.32
	.07	.36	.35
	.11	.39	.37
	.15	.42	.40
	.18	.46	.42
	.22	.50	.45
	.26	.54	.48
	.30	.58	.51
	.33	.62	.54
	.37	.67	.57
	.41	.71	.60
	.45	.76	.63
	.48	.81	.66
	.52	.86	.69
	.56	.92	.73
	.60	.97	.76
	.63	1.03	.79
	.67	1.09	.82

γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.3×10^{-6} (cont.)	.71	1.14	.85
	.75	1.20	.89
	.78	1.26	.92
	.82	1.32	.94
	.86	1.38	.97
	.90	1.44	1.00
	.93	1.50	1.02
	.97	1.56	1.04
	1.01	1.61	1.06
	1.05	1.67	1.07
	1.08	1.72	1.09
	1.12	1.77	1.09
	1.16	1.82	1.10
	1.20	1.87	1.09
	1.23	1.91	1.09
	1.27	1.95	1.07
	1.31	1.99	1.05
	1.35	2.02	1.02
	1.38	2.04	.98
	1.42	2.06	.94
	1.46	2.07	.88
	1.50	2.07	.81
1.4×10^{-6}	.00	.30	.30
	.03	.33	.32
	.07	.36	.34
	.11	.39	.36
	.15	.42	.39
	.18	.46	.41
	.22	.50	.43
	.26	.53	.46
	.30	.57	.48
	.33	.61	.51
	.37	.66	.53
	.41	.70	.56

γ_2(cgs)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
$1.4\times10^{-}$ (cont.)	.45	.75	.58
	.48	.79	.60
	.52	.84	.62
	.56	.89	.64
	.60	.93	.66
	.63	.98	.68
	.67	1.03	.70
	.71	1.08	.71
	.75	1.13	.72
	.78	1.17	.73
	.82	1.22	.73
	.86	1.26	.73
	.90	1.30	.73
	.93	1.34	.72
	.97	1.38	.70
	1.01	1.41	.68
	1.05	1.44	.65
	1.08	1.47	.62
	1.12	1.48	.57
	1.16	1.50	.51
	1.20	1.50	.45
	1.23	1.50	.37
	1.27	1.50	.27
	1.31	1.48	.16
	1.35	1.45	.04
	1.38	1.41	-.11
	1.42	1.36	-.27
	1.46	1.30	-.46
	1.50	1.22	-.67

TABLE 2. Salt Concentration Profiles For γ_2 = 1.3x10^{-} (cgs) And Various ℓ Values

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)	ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.4	.00	.30	.30	1.4 (cont.)	1.19	1.62	1.07
	.03	.32	.32		1.22	1.65	1.08
	.07	.35	.34		1.26	1.69	1.09
	.10	.38	.36		1.29	1.72	1.10
	.14	.41	.38		1.33	1.75	1.10
	.17	.44	.40		1.36	1.77	1.10
	.21	.47	.43		1.40	1.80	1.10
	.24	.50	.45	1.45	.00	.30	.30
	.28	.53	.47		.03	.33	.32
	.31	.57	.50		.07	.35	.34
	.35	.60	.52		.10	.38	.37
	.38	.64	.55		.14	.42	.39
	.42	.68	.58		.18	.45	.41
	.45	.72	.60		.21	.48	.44
	.49	.76	.63		.25	.52	.46
	.52	.80	.65		.29	.55	.49
	.56	.84	.68		.32	.59	.52
	.59	.88	.71		.36	.63	.54
	.63	.93	.73		.39	.68	.57
	.66	.97	.76		.43	.72	.60
	.70	1.02	.79		.47	.76	.63
	.73	1.06	.81		.50	.81	.66
	.77	1.11	.84		.54	.86	.69
	.80	1.15	.86		.58	.90	.72
	.84	1.20	.89		.61	.95	.75
	.87	1.24	.91		.65	1.00	.78
	.91	1.29	.93		.68	1.05	.81
	.94	1.33	.96		.72	1.10	.83
	.98	1.38	.98		.76	1.16	.86
	1.01	1.42	1.00		.79	1.21	.89
	1.05	1.46	1.02		.83	1.26	.92
	1.08	1.50	1.03		.87	1.31	.94
	1.12	1.54	1.05		.90	1.36	.97
	1.15	1.58	1.06		.94	1.41	.99

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.45 (cont.)	.97	1.46	1.00
	1.01	1.51	1.03
	1.05	1.56	1.04
	1.08	1.61	1.06
	1.12	1.65	1.07
	1.16	1.70	1.08
	1.19	1.74	1.09
	1.23	1.78	1.09
	1.26	1.81	1.09
	1.30	1.85	1.08
	1.34	1.88	1.07
	1.37	1.90	1.05
	1.41	1.92	1.03
	1.45	1.94	1.00
1.5	.00	.30	.30
	.03	.33	.32
	.07	.36	.35
	.11	.39	.37
	.15	.42	.40
	.18	.46	.42
	.22	.50	.45
	.26	.54	.48
	.30	.58	.51
	.33	.62	.54
	.37	.67	.57
	.41	.71	.60
	.45	.76	.63
	.48	.81	.66
	.52	.86	.69
	.56	.92	.73
	.60	.97	.76
	.63	1.03	.79
	.67	1.09	.82
	.71	1.14	.85
	.75	1.20	.89

ℓ(cm) (length)	x(cm) (distance	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.5 (cont.)	.78	1.26	.92
	.82	1.32	.94
	.86	1.38	.97
	.90	1.44	1.00
	.93	1.50	1.02
	.97	1.56	1.04
	1.01	1.61	1.06
	1.05	1.67	1.07
	1.08	1.72	1.09
	1.12	1.77	1.09
	1.16	1.82	1.10
	1.20	1.87	1.09
	1.23	1.91	1.09
	1.27	1.95	1.07
	1.31	1.99	1.05
	1.35	2.02	1.02
	1.38	2.04	.98
	1.42	2.06	.94
	1.46	2.07	.88
	1.50	2.07	.81
1.55	.00	.30	.30
	.03	.33	.32
	.07	.36	.35
	.11	.40	.38
	.15	.43	.40
	.19	.47	.43
	.23	.51	.46
	.27	.56	.49
	.31	.60	.53
	.34	.65	.56
	.38	.70	.59
	.42	.76	.63
	.46	.81	.66
	.50	.87	.70
	.54	.93	.73

ℓ (cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)	ℓ (cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.55 (cont.)	.58	.99	.77	1.6 (cont.)	.36	.69	.58
	.62	1.05	.80		.40	.74	.62
	.65	1.11	.84		.44	.80	.66
	.69	1.18	.87		.48	.86	.69
	.73	1.24	.91		.52	.93	.73
	.77	1.31	.94		.56	.99	.77
	.81	1.38	.97		.60	1.06	.81
	.85	1.45	1.00		.64	1.13	.85
	.89	1.51	1.03		.68	1.21	.89
	.93	1.58	1.05		.72	1.28	.93
	.96	1.65	1.07		.76	1.36	.96
	1.00	1.72	1.09		.80	1.43	1.00
	1.04	1.78	1.11		.84	1.51	1.03
	1.08	1.84	1.11		.88	1.59	1.06
	1.12	1.90	1.12		.92	1.67	1.09
	1.16	1.96	1.11		.96	1.74	1.11
	1.20	2.01	1.10		1.00	1.82	1.13
	1.24	2.06	1.08		1.04	1.89	1.14
	1.27	2.10	1.06		1.08	1.97	1.15
	1.31	2.14	1.02		1.12	2.03	1.15
	1.35	2.17	.97		1.16	2.10	1.14
	1.39	2.19	.90		1.20	2.16	1.12
	1.43	2.20	.83		1.24	2.21	1.08
	1.47	2.21	.73		1.28	2.26	1.04
	1.51	2.20	.61		1.32	2.30	.98
	1.55	2.18	.48		1.36	2.33	.91
1.6	.00	.30	.30		1.40	2.35	.81
	.04	.33	.33		1.44	2.36	.70
	.08	.37	.35		1.48	2.35	.56
	.12	.40	.38		1.52	2.33	.39
	.16	.44	.41		1.56	2.30	.19
	.20	.49	.44		1.60	2.24	-.05
	.24	.53	.48				
	.28	.58	.51				
	.32	.63	.54				

TABLE 3. Salt Concentration Profiles For $\gamma_2 = 1.27 \times 10^{-6}$ (cgs) And Various ℓ Values

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)	ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.4	.00	.30	.30	1.4 (cont.)	1.15	1.69	1.28
	.03	.32	.32		1.19	1.74	1.32
	.07	.35	.34		1.22	1.79	1.35
	.10	.38	.36		1.26	1.84	1.39
	.14	.41	.38		1.29	1.89	1.43
	.17	.44	.41		1.33	1.94	1.48
	.21	.47	.43		1.36	1.99	1.52
	.24	.50	.46		1.40	2.04	1.57
	.28	.53	.48	1.45	.00	.30	.30
	.31	.57	.51		.03	.33	.32
	.35	.61	.53		.07	.35	.34
	.38	.64	.56		.10	.38	.37
	.42	.68	.59		.14	.42	.39
	.45	.72	.62		.18	.45	.42
	.49	.77	.65		.21	.48	.44
	.52	.81	.68		.25	.52	.47
	.56	.85	.71		.29	.56	.50
	.59	.90	.74		.32	.60	.53
	.63	.94	.77		.36	.64	.56
	.66	.99	.80		.39	.68	.59
	.70	1.04	.83		.43	.72	.62
	.73	1.08	.87		.47	.77	.65
	.77	1.13	.90		.50	.82	.68
	.80	1.18	.93		.54	.87	.72
	.84	1.23	.96		.58	.92	.75
	.87	1.28	1.00		.61	.97	.78
	.91	1.33	1.03		.65	1.02	.82
	.94	1.38	1.07		.68	1.07	.85
	.98	1.44	1.10		.72	1.13	.89
	1.01	1.49	1.14		.76	1.18	.92
	1.05	1.54	1.17		.79	1.24	.96
	1.08	1.59	1.21		.83	1.30	1.00
	1.12	1.64	1.24		.87	1.35	1.03

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)	ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.45 (cont.)	.90	1.41	1.07	1.5 (cont.)	.67	1.11	.87
	.94	1.47	1.10		.71	1.17	.91
	.97	1.53	1.14		.75	1.23	.95
	1.01	1.59	1.18		.78	1.29	.99
	1.05	1.65	1.21		.82	1.36	1.03
	1.08	1.70	1.25		.86	1.42	1.07
	1.12	1.76	1.28		.90	1.49	1.10
	1.16	1.82	1.32		.93	1.56	1.14
	1.19	1.88	1.35		.97	1.62	1.18
	1.23	1.93	1.39		1.01	1.69	1.22
	1.26	1.99	1.42		1.05	1.76	1.25
	1.30	2.04	1.46		1.08	1.83	1.29
	1.34	2.09	1.49		1.12	1.89	1.32
	1.37	2.15	1.52		1.16	1.96	1.36
	1.41	2.20	1.56		1.20	2.02	1.39
	1.45	2.25	1.59		1.23	2.08	1.42
1.5	.00	.30	.30		1.27	2.15	1.44
	.03	.33	.32		1.31	2.20	1.47
	.07	.36	.35		1.35	2.26	1.49
	.11	.39	.37		1.38	2.32	1.51
	.15	.42	.40		1.42	2.37	1.53
	.18	.46	.43		1.46	2.42	1.55
	.22	.50	.45		1.50	2.47	1.56
	.26	.54	.48	1.55	.00	.30	.30
	.30	.58	.52		.03	.33	.32
	.33	.62	.55		.07	.36	.35
	.37	.67	.58		.11	.40	.38
	.41	.72	.61		.15	.43	.41
	.45	.77	.65		.19	.47	.44
	.48	.82	.68		.23	.52	.47
	.52	.87	.72		.27	.56	.50
	.56	.93	.76		.31	.61	.53
	.60	.99	.79		.34	.66	.57
	.63	1.05	.83		.38	.71	.61

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)	ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.55 (cont.)	.42	.76	.64	1.6 (cont.)	.16	.45	.41
	.46	.82	.68		.20	.49	.45
	.50	.88	.72		.24	.53	.48
	.54	.94	.76		.28	.58	.52
	.58	1.00	.80		.32	.63	.55
	.62	1.07	.84		.36	.69	.59
	.65	1.13	.89		.40	.75	.63
	.69	1.20	.93		.44	.81	.67
	.73	1.27	.97		.48	.87	.72
	.77	1.34	1.01		.52	.94	.76
	.81	1.42	1.06		.56	1.01	.81
	.85	1.49	1.10		.60	1.08	.85
	.89	1.57	1.14		.64	1.15	.90
	.93	1.65	1.18		.68	1.23	.94
	.96	1.72	1.22		.72	1.31	.99
	1.00	1.80	1.26		.76	1.39	1.04
	1.04	1.88	1.30		.80	1.47	1.09
	1.08	1.95	1.33		.84	1.56	1.13
	1.12	2.03	1.37		.88	1.65	1.18
	1.16	2.10	1.40		.92	1.73	1.22
	1.20	2.18	1.42		.96	1.82	1.26
	1.24	2.25	1.45		1.00	1.91	1.31
	1.27	2.32	1.46		1.04	2.00	1.34
	1.31	2.38	1.48		1.08	2.09	1.38
	1.35	2.44	1.49		1.12	2.17	1.41
	1.39	2.50	1.49		1.16	2.26	1.44
	1.43	2.56	1.49		1.20	2.34	1.46
	1.47	2.61	1.48		1.24	2.42	1.48
	1.51	2.65	1.47		1.28	2.50	1.48
	1.55	2.69	1.44		1.32	2.57	1.49
1.6	.00	.30	.30		1.36	2.64	1.48
	.04	.33	.33		1.40	2.70	1.46
	.08	.37	.35		1.44	2.76	1.44
	.12	.41	.38		1.48	2.81	1.39

(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)	(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.6 (cont.)	1.52	2.85	1.34				
	1.56	2.88	1.27				
	1.60	2.89	1.18				

TABLE 4. Salt Concentration Profiles For $\gamma_2 = 1.2 \times 10^{-6}$ (cgs) And Various ℓ Values

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)	ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.10	.00	.30	.30	1.10 (cont.)	.93	1.04	1.06
	.02	.31	.31		.96	1.07	1.10
	.05	.33	.33		.99	1.10	1.15
	.08	.35	.34		1.01	1.13	1.21
	.11	.36	.35		1.04	1.17	1.26
	.13	.38	.37		1.07	1.20	1.32
	.16	.40	.38		1.10	1.24	1.39
	.19	.41	.40	1.20	.00	.30	.30
	.22	.43	.41		.03	.32	.32
	.24	.45	.43		.06	.34	.33
	.27	.47	.44		.09	.36	.35
	.30	.49	.46		.12	.38	.36
	.33	.51	.48		.15	.40	.38
	.35	.53	.49		.18	.42	.40
	.38	.55	.51		.21	.44	.42
	.41	.57	.53		.24	.46	.44
	.44	.59	.55		.27	.49	.46
	.46	.61	.57		.30	.51	.48
	.49	.63	.59		.33	.53	.50
	.52	.65	.61		.36	.56	.52
	.55	.67	.63		.39	.58	.54
	.57	.70	.65		.42	.61	.56
	.60	.72	.68		.45	.64	.59
	.63	.74	.70		.48	.67	.61
	.66	.77	.72		.51	.69	.64
	.68	.79	.75		.54	.72	.66
	.71	.82	.78		.57	.75	.69
	.74	.84	.81		.60	.78	.72
	.77	.87	.84		.63	.81	.75
	.79	.89	.87		.66	.85	.78
	.82	.92	.90		.69	.88	.81
	.85	.95	.94		.72	.91	.85
	.88	.98	.98		.75	.94	.88
	.90	1.01	1.02		.78	.98	.92

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.20 (cont.)	.81	1.02	.96
	.84	1.05	1.00
	.87	1.09	1.05
	.90	1.13	1.09
	.93	1.17	1.14
	.96	1.21	1.20
	.99	1.25	1.25
	1.02	1.30	1.32
	1.05	1.34	1.38
	1.08	1.39	1.45
	1.11	1.44	1.53
	1.14	1.49	1.62
	1.17	1.55	1.71
	1.20	1.60	1.81
1.30	.00	.30	.30
	.03	.32	.32
	.06	.34	.34
	.09	.37	.36
	.13	.39	.38
	.16	.42	.40
	.19	.44	.42
	.22	.47	.44
	.26	.50	.47
	.29	.53	.49
	.32	.56	.52
	.35	.59	.54
	.39	.62	.57
	.42	.65	.60
	.45	.69	.63
	.48	.72	.66
	.52	.76	.69
	.55	.80	.72
	.58	.84	.76
	.61	.88	.79

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.30 (cont.)	.65	.92	.83
	.68	.96	.87
	.71	1.00	.91
	.74	1.05	.95
	.78	1.09	1.00
	.81	1.14	1.05
	.84	1.19	1.10
	.87	1.24	1.15
	.91	1.29	1.21
	.94	1.35	1.27
	.97	1.40	1.34
	1.00	1.46	1.41
	1.04	1.52	1.48
	1.07	1.58	1.57
	1.10	1.64	1.66
	1.13	1.71	1.75
	1.17	1.78	1.86
	1.20	1.86	1.97
	1.23	1.93	2.10
	1.26	2.02	2.24
	1.30	2.11	2.39
1.40	.00	.30	.30
	.03	.32	.32
	.07	.35	.34
	.10	.38	.37
	.14	.41	.39
	.17	.44	.42
	.21	.47	.44
	.24	.50	.47
	.28	.54	.50
	.31	.57	.53
	.35	.61	.56
	.38	.65	.59
	.42	.69	.63

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.40 (cont.)	.45	.74	.66
	.49	.78	.70
	.52	.83	.74
	.56	.88	.78
	.59	.93	.82
	.63	.98	.87
	.66	1.03	.92
	.70	1.09	.96
	.73	1.15	1.02
	.77	1.21	1.07
	.80	1.27	1.13
	.84	1.33	1.19
	.87	1.40	1.25
	.91	1.46	1.32
	.94	1.54	1.40
	.98	1.61	1.48
	1.01	1.68	1.56
	1.05	1.76	1.65
	1.08	1.84	1.75
	1.12	1.93	1.86
	1.15	2.02	1.98
	1.19	2.11	2.10
	1.22	2.21	2.24
	1.26	2.32	2.40
	1.29	2.43	2.57
	1.33	2.55	2.75
	1.36	2.67	2.96
	1.40	2.81	3.19
1.50	.00	.30	.30
	.03	.33	.32
	.07	.36	.35
	.11	.39	.38
	.15	.43	.41
	.18	.46	.44

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.50 (cont.)	.22	.50	.47
	.26	.54	.50
	.30	.59	.54
	.33	.63	.57
	.37	.68	.61
	.41	.73	.65
	.45	.78	.70
	.48	.84	.74
	.52	.90	.79
	.56	.96	.84
	.60	1.02	.89
	.63	1.09	.95
	.67	1.16	1.01
	.71	1.23	1.07
	.75	1.31	1.13
	.78	1.39	1.20
	.82	1.47	1.27
	.86	1.55	1.35
	.90	1.64	1.43
	.93	1.73	1.52
	.97	1.83	1.61
	1.01	1.93	1.71
	1.05	2.03	1.82
	1.08	2.14	1.94
	1.12	2.25	2.06
	1.16	2.37	2.20
	1.20	2.49	2.35
	1.23	2.62	2.52
	1.27	2.76	2.70
	1.31	2.90	2.90
	1.35	3.06	3.12
	1.38	3.22	3.36
	1.42	3.40	3.64
	1.46	3.59	3.95
	1.50	3.79	4.30

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)	ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.60	.00	.30	.30	1.60 (cont.)	1.36	3.64	3.48
	.04	.33	.33		1.40	3.85	3.77
	.08	.37	.36		1.44	4.08	4.09
	.12	.41	.39		1.48	4.32	4.45
	.16	.45	.42		1.52	4.59	4.85
	.20	.49	.46		1.56	4.87	5.31
	.24	.54	.50		1.60	5.18	5.83
	.28	.59	.54	1.70	.00	.30	.30
	.32	.64	.58		.04	.34	.33
	.36	.70	.63		.08	.38	.37
	.40	.76	.68		.12	.42	.40
	.44	.82	.73		.17	.47	.44
	.48	.89	.78		.21	.52	.49
	.52	.96	.84		.25	.58	.53
	.56	1.04	.90		.29	.64	.58
	.60	1.12	.96		.34	.71	.63
	.64	1.21	1.03		.38	.78	.69
	.68	1.29	1.10		.42	.85	.75
	.72	1.39	1.18		.46	.94	.81
	.76	1.48	1.26		.51	1.02	.88
	.80	1.59	1.34		.55	1.12	.95
	.84	1.69	1.43		.59	1.22	1.03
	.88	1.81	1.53		.63	1.32	1.11
	.92	1.92	1.63		.68	1.43	1.20
	.96	2.04	1.74		.72	1.55	1.29
	1.00	2.17	1.86		.76	1.68	1.39
	1.04	2.31	1.98		.80	1.81	1.50
	1.08	2.45	2.12		.85	1.95	1.61
	1.12	2.59	2.26		.89	2.10	1.73
	1.16	2.74	2.42		.93	2.25	1.85
	1.20	2.91	2.60		.97	2.41	1.99
	1.24	3.07	2.79		1.02	2.58	2.13
	1.28	3.25	3.00		1.06	2.76	2.29
	1.32	3.44	3.23				

ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)	ℓ(cm) (length)	x(cm) (distance)	C(gr/cm^3) (channel)	C_a(gr/cm^3) (tissue)
1.70 (cont.)	1.10	2.95	2.46				
	1.14	3.15	2.64				
	1.19	3.35	2.84				
	1.23	3.57	3.06				
	1.27	3.80	3.29				
	1.31	4.05	3.55				
	1.36	4.30	3.84				
	1.40	4.58	4.17				
	1.44	4.87	4.53				
	1.48	5.18	4.93				
	1.53	5.51	5.39				
	1.57	5.87	5.90				
	1.61	6.26	6.49				
	1.65	6.69	7.16				
	1.70	7.16	7.93				

FIGURE 5.
SALT CONCENTRATION IN THE AMBIENT TISSUE AT L = 1.1 cm (SEE TABLE 4)

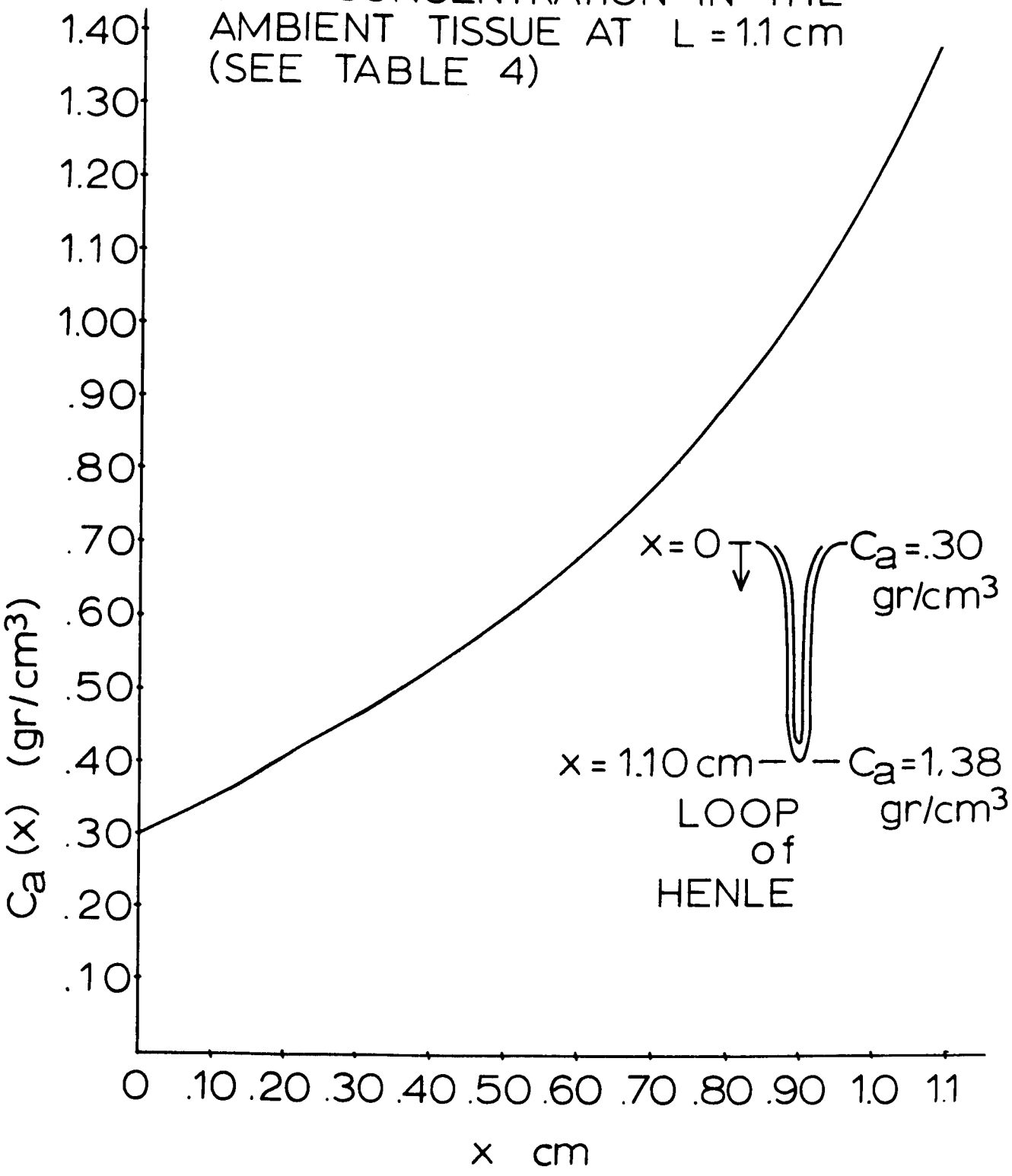
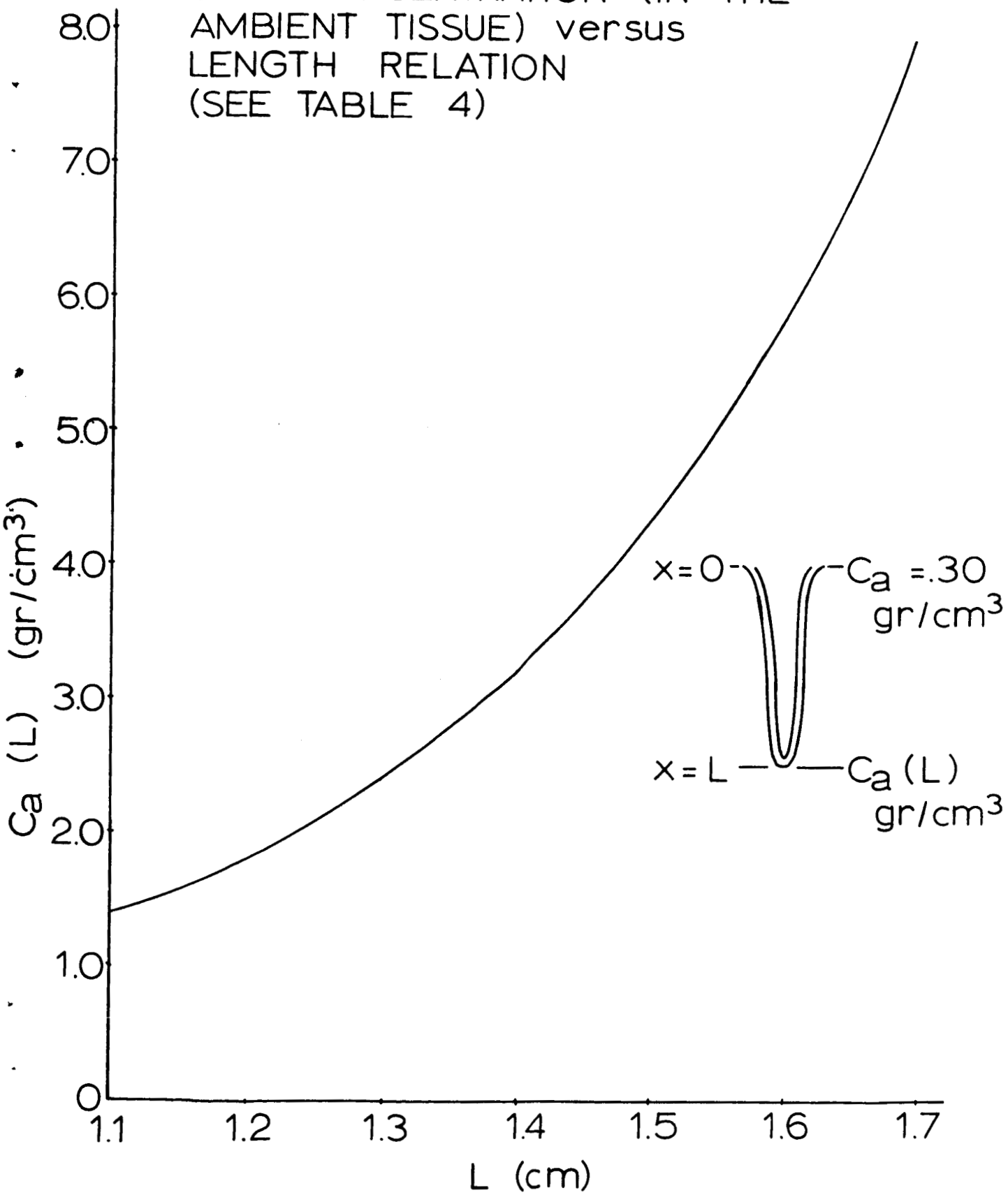
FIGURE 6.
SALT CONCENTRATION (IN THE AMBIENT TISSUE) versus LENGTH RELATION (SEE TABLE 4)