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On the osmotically induced convective-diffusion transfer of non-electrolytes within two long narrow compartments separated by the semipermeable membrane of a general rheological nature

A boundary value problem modelling the passive water transfer through plane epithelial tissues

by

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A plane free boundary value problem is formulated describing the osmotically induced convective-diffusion transfer of non-electrolytes along two narrow compartments separated by a deformable semipermeable membrane of a fairly general linear rheology. The concrete model under consideration is chosen with the aim to imitate the process of the passive water transfer through plane epithelial tissues taking into account data reported in papers [19], [23], [25].

1. Introduction

There exist in biology a broad class of transport phenomena characterized by the presence of volume fluxes along narrow compartments, induced by strong discontinuities in the concentration fields, located on the boundaries of membranes, separating these compartments. This class of phenomena includes the process of osmotically induced mass transfer through rigid membranes, diffusion mass transfer, accompanied by volume fluxes induced by jumps of concentrations on boundaries of deformable membranes not resisting deformations, and the intermediate class of processes of mass transfer through deformable membranes, appreciably resisting deformations. This latter class of processes is the most important in biology, but its mathematical aspects apparently remain almost untackled. In such slow convective-diffusion problems the main interest consists in determining volume fluxes and their dependence of the changes of the shape and location of the deformable membrane. This relates, in particular, to the process of a passive water transfer through plane epithelial tissues where the main passway for water is the lateral membrane, separating cells of these tissues from the intercellular space, and where the transfer of hyper/hypo tonicity from the serosal to the mucosal side of the tissue implies drastic changes of volume fluxes [10], [19, [25]. Although the rheological nature of plasmatic membranes remains unknown in its quanitative details, one may assert that they are liquids, possessing appreciate elasticity [11]. This means that water transfer through epithelial tissues has to be put to the aforementioned intermediate class of transport phenomena.

In what follows we formulate a boundary value problem, modelling water and low-molecular non-electrolyte transfer trough epithelial tissue. Our model is chosen with the aim to perform in the future numerical computations, roughly repreducing conditions described in papers by Wright et al [25], Smuglers et al [19] and Van Os [23]. These experiments seemingly are the most informative among others, mentioned for example in Krolenko's monograph [9] or Stefenson's review [21].

We mainly use the same approach as in the previous author's papers [15], [16], [18]. The theory presented there is oriented towards description of non-electrolyte transfer through deformable membranes not resisting deformations. In such a case the whole system of equations and boundary conditions of the problem is proved to be decomposed into two groups of conditions. The first one (we call it "kinematic") serves for determining the concentration distribution and the membrane shape, whereas the second group of "dynamical" equations serves for determining the hydrostatic pressure and deformation stresses in the system under consideration. The main peculiarity of that theory is that the kinematic equations and boundary conditions are independent of dynamical variables and may therefore be solved prior to the solution of the group of dynamical equations. Such a split of the problem into the "kinematic" and "dynamical" parts is evidently unphysical and wrong when one deals with the mass transfer through membranes resisting deformations. One has, therefore, to reconsider the main assumptions of the theory in order to exclude the very possibility of the mentioned split, making the kinematic part of the problem independent of the dynamical one.

Let us recall the basic assumptions of the theory we are refrerring to.

1. The system was considered, consisting of two solutions filling narrow compartments separated by a deformable semipermeable membrane. These solutions were supposed to be perfect mixture*) of $n+1$ incompressible liquid components a_j, of which a_0 was an impermeant with respect to the membrane, and the rest of them were involved into a convective-diffusion transfer through the membrane and along the compartments.

2. The membrane was considered as a diluted solution of all a_j, $j=1, 2, \dots, n$, in the main membrane constituent a_{n+1}.

3. Conditions of a local thermodynamic equilibrium, expressed in the form of the Nernst distribution theorem [13] were assumed to be valid on the membrane boundaries. Coefficients of distribution were taken constant, which is admissible

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*) We use Prigogine's terminology, according to which the solution is called "perfect" if the coefficients of activity of all components of the solution are equal to 1 in a whole range of the possible changes of concentrations [13].

if the molar fraction of every penetrating component remains practically constant as well as the jump of pressure on the membrane boundaries.

4. Since the membrane boundaries are surfaces of concentration discontinuity conditions of dynamical compatibility for the convective-diffusion mass transfer, velocity of solution motion and momentum transfer had to be valid on these boundaries. The process was assumed to be isothermal so that condition of dynamical compatibility for energy transfer could be omitted.

5. All diffusion fluxes defined in the system of the average volume velocity [5], [15] were described by the simple Fick's law with constant coefficients of diffusion and with neglect of all cross-effects, including that of barodiffusion*)

Besides these basic assumptions the theory employed the following ones:

5. Two points p_1 and p_2 are called congruent if they belong to the same normal to one of the membrane boundaries. The difference between directions of normals to the membrane boundaries in their congruent points were assumed to be negligible, as well as the change of the membrane thickness due to its shrinking or swelling.

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*) Let μ_k be the chemical potential of a_k, μ_k^0 its standard value, c_k — the molar concentration of a_k, γ_k its coefficient of activity, Ω_k — the partial molar volume of a_k, p — pressure, $\bar{v}_k$ — the local average velocity of a_k in the laboratory coordinate system, $\bar{w}$ — the average volume velocity of the solution under consideration and $\bar{J}_k$ the diffusion flux of a_k in the system of the average volume velocity. According to the thermodynamics of irreversible processes

$$\mu_k = \mu_k^0 + \Omega_k p + \mathrm{RT} \ln x_k \tag{o}$$

and the flux of a_k in the laboratory system of coordinates is equal to

$$c_k \bar{v}_k = \sum_0^n L_{km} \operatorname{grad} \mu_m \tag{oo}$$

Here x_k is the molar fracture of the a_k activity, i.e.

$$x_k = \gamma_k c_k / X; \quad X = \sum_0^n \gamma_m c_m, \tag{ooo}$$

and L_{km} are so called reversed phenomenological coefficients [7].

Note that γ_k are functions of all c_m, p and of the temperature T which is now considered to be constant.

By the definition

$$\bar{w} = \sum_0^n \Omega_k c_k \bar{v}_k; \quad \bar{J}_k = c_k (\bar{v}_k - \bar{w}) \tag{0}$$

we find, comparing (o), (oo) and (0) that

$$\bar{J}_j = -D_j \operatorname{grad} c_j + \sum_{m \neq j} D_{jm} \operatorname{grad} c_m - L_j \operatorname{grad} p \tag{00}$$

Here the first term of the right hand side describes the simple Fick's diffusion, the second — all diffusion cross-effects and the third one — barodiffusion. If all coefficients of activity are equal to 1, then

$$\begin{gathered} L_k = -\sum_0^n \Omega_m \Big(L_{km} - c_k \sum_0^n L_{sm} \Omega_s \Big); \quad D_k = -D_{kk}; \\ D_{km} = (\mathrm{RT}/c_m) \Big(L_{km} - c_k \sum_0^n L_{sm} \Omega_s \Big) - (\mathrm{RT}/X) \sum_0^n \Big(L_{kq} - c_k \sum_0^n L_{sq} \Omega_s \Big); \end{gathered} \tag{000}$$

6. Diffusion fluxes and the average volume velocity within the membrane were regarded as quasistationary. Tangential components of diffusion fluxes within the membrane were regarded as negligible.

A careful consideration of the basic assumptions of the theory we are referring to shows that two of its positions need reconsideration:

1. The use of the approximate values of the coefficients of distribution taken constant.
2. The neglect of the effect of barodiffusion.

The relinquish of both these inaccuracies would imply the abolishment of the aforementioned split of the problem into kinematic and dynamical parts with the former independent of the latter. At the same time one cannot expect that in conditions imitating those reported in the experimental papers [19], [23], [25] the use of the approximately constant coefficients of distribution may yield an essential quantitative inaccuracy. Indeed, computations performed in [4] with the aim of modelling the process of swelling and shrinking of the single muscle fibres accompanied by the change of the shape of tubulus of the *T*-system have withstood the comparison with experiments. These computations have used the aforementioned approximation and the input data were there similar to those in the papers we are referring to. On the other hand barodiffusion in bulk flows, as well as all diffusion cross-effects are known to be of smaller importance compared with that of the simple Fick's diffusion in solutions having no elastic properties. However within the membrane, exhibiting an appreciable elasticity the effect of barodiffusion may appear to be large enough in order to motivate taking it into account. Taking into account the contribution of barodiffusion through the membranes into volume fluxes and determining the membrane shape and location, affected by baro-diffusion, is the main goal of this paper. Besides, in contrast to [15], [16], [18] we now consider not only the swelling and shrinking of the whole cell due to the motion of the apical membrane, but also the change of the lateral membrane thickness due to its swelling or shrinking and its curving.

The material presentation is as follows. First (section 2) we introduce the geometrical model we deal with and the equations of the general theory. The rest of the paper is devoted to derivation of equations of the one-dimensional formalism of the theory, appropriate for describing transport phenomena in narrow channels (section 3) and to derivation of the equations of the membrane approximation, where all values, defined within the membranes, are eliminated (section 4). Conclusive remarks are made in section 5. Appendices 1 and 2 contain the table of notations, numerical data and scaling. Appendix 3 contains the collection of all normalized equations of the one-dimensional membrane approximation of the theory, describing the process in the case of a bicomponent solutions: water+an impermeant.

2. Geometrical model, basic assumptions and equations

As it is pointed out in the introduction we formulate the problem in a version allowing to imitate the water transfer through epithelial tissues. The latter may be considered as a periodic structure, consisting of cells, bounded by basal, apical and lateral membranes, intercellular space and unstirred layers, washing the basal and apical sides of the tissue. At the apical side of the intercellular space there are tight junctions, connecting every two adjacent cells, but permeable for low-molecular nonelectrolytes and water. For the sake of simplicity we restrict our consideration with a plane model whose schematic structure is presented in Fig. 1.

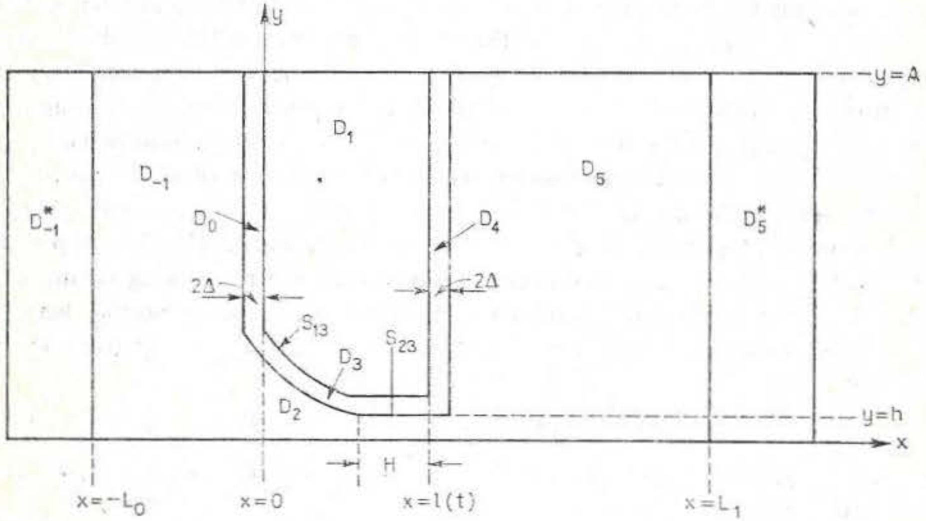

Fig. 1.

Here

$$
\begin{aligned}
&D_1=(x, y: 0<x<l(t);\ y_1(x, t)<y<A),\\
&D_2=(x, y: 0<x<l(t);\ 0<y<y_2(x, t)),\\
&D_0=(x, y: -2\Delta<x<0;\ y_2(0, t)<y<A)),\\
&D_3=(x, y: 0<x<l(t);\ y_2(x, t)<y<y_1(x, t)),\\
&D_4=(x, y: l(t)<x<l(t)+2\Delta;\ y_2(l(t), t)<y<A)
\end{aligned}
\tag{2.1}
$$

represent the cell, the intercellular space, the basal, lateral and respectively apical membrane. Regions

$$
\begin{aligned}
&D_{-1}=(x, y: -L_0<x<0;\ 0<y<A)\setminus\bar{D}_0,\\
&D_5=(x, y: l(t)<x<L_1;\ 0<y<A)\setminus\bar{D}_4
\end{aligned}
\tag{2.2}
$$

imitate unstirred layers and regions D^*_{-1} and $D^{\cdot}_5$ represent reservoirs of infinitely large volume where the prescribed concentrations are maintained. Finally the subregion

$$D_2^*=(x, y: l(t)-H\leqslant x\leqslant l(t);\ 0<y<h) \tag{2.3}$$

of D_2 represents the tight junction. Here

$$h=y_2(x,t)\ \forall x\in\big(l(t)-H,\,l(t)\big) \tag{2.4}$$

In what follows we assume that all the regions D_k, $k=-1,1,2,5$, are filled with a perfect mixture of $n+1$ liquid non-electrolyte components a_j of molar concentration c_j^k, coefficient of activity γ_j^k, molar weight M_j, partial molar volume Ω_j and partial density ρ_j^k All the components a_j, $j=1,2,\dots,n$, are involved in convective-diffusion along D_k, $k=-1,1,2,5$, and in the convective-diffusion transfer through the membranes D_m, $m=0,3,4$. Every solution D_k, $k=-1,1,2,5$, is assumed to be a viscous liquid of a constant viscosity μ_k and negligible body viscosity.

Concerning the membranes D_k, $k=0,3,4$, we use the following approach. First we describe them as porous media of the porosity m^k, where fictitious volume forces of the resistance act on the solution moving through the porous space. The solid skeleton is identified with the osmotically inactive part of the main membrane constituent a_{n+1}, and the forces of the resistance are defined proportional to the difference between the average volume velocity of the motion of all the membrane constituents and the average local velocity of the component a_{n+1}. After this the usual process of "homogenizing" of the "heterogeneous media" [2], [3], [14] permits to consider the membranes as diluted solutions of all the penetrating components a_j, $j=1,2,\dots,n$, in the main membrane constituent a_{n+1}. The connection between the porosity m^k and the coefficient γ_{n+1}^k of activity of a_{n+1} is evidently given by the equality

$$m^k=1-\Omega_{n+1}\,c_{n+1}^k\,(1-\gamma_{n+1}^k);\ k=0,3,4. \tag{2.5}$$

Coefficients γ_j^k of activity of all other components a_j, $j=0,1,\dots,n$, $k=-1,0.,\dots,5$, are taken below equal to 1.

Rheological properties of the membranes D_k, $k=0,3,4$, are assumed to be the following:

A. The basal and the apical membranes ($k=0;4$) are supposed to be of the constant thickness 2Δ in x-direction and such that the change of the length $A-y_2(0,t)$ of the basal membrane, induced by the motion and deformation of the lateral membrane, is considered as resistance free*).

On the opposite the length $A-y_2\big(1(t),t\big)$ of the apical membrane remains constant because of the existence of the tight junction in the apical side of the intercellular space.

As usual in the theory of slow motion of liquids through porous media the forces of the inner tension within solutions, percolating through the porous space of those media are assumed to be negligible compared with forces $\bar{R}^k$ of the resistance.

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*) This singular property of the basal membrane is supposed in order to avoid difficulties created by the roughness of the geometrical model we deal with. It would be much better for the general description to consider the basal membrane as a smooth prolongation of the lateral membrane. However, such a more realistic description would imply unreasonable complications for introduction of the one-dimensional formalism of the theory.

B. Let $\tilde{\Pi}^3$, $\tilde{e}^3$ and $\tilde{\varepsilon}^3$ be two-dimensional stress, strain velocity and strain tensors within D_3. Assuming the motion of D_3 and motion of all the penetrating components $a_j, j=1, 2, \ldots, n$, to be small we neglect the difference between the local and material derivatives. Hence for a fairly general linear rheology

$$\begin{aligned}
&\tilde{\varepsilon}^3(x, y, t)=\tilde{\varepsilon}^3(x, y, 0)+\int_0^t \tilde{e}^3(x, y, s)\, ds \\
&\tilde{\tau}^3(x, y, t)=\tilde{\tau}^3(x, y, 0) \exp(-at)+be^3(x, y, t)+ \\
&\qquad\qquad +\int_0^t \exp(-a(t-s))\left(c\tilde{e}^3(x, y, s)+d\varepsilon^3(x, y, s)\right) ds
\end{aligned} \tag{2.6}$$

with constant coefficients a, b, c and d. Here $\tilde{\tau}^3(x, y, t)$ is the deviator of the stress tensor $\tilde{\Pi}^3(x, y, t)$.

Note that with

$$a=c=d=0;\ b\neq 0 \tag{2.7}$$

the lateral membrane is a viscous liquid with a negligible impact of the bulk viscosity. With

$$a=b=d=0;\ c\neq 0 \tag{2.8}$$

D_3 is a linearly elastic body. With

$$b=d=0;\ a\neq 0;\ c\neq 0 \tag{2.9}$$

D_3 is the Maxwell visco-elastic liquid. With, finally,

$$b=c=0;\ a\neq 0;\ d\neq 0 \tag{2.10}$$

D_3 is the Kelvin solid.*)

Let $\bar{v}_j^k$ be the vector of the local average velocity of the motion of a_j in a laboratory coordinate system. The average volume velocity $\bar{w}^k$, the velocity of the center of mass $\bar{v}^k$ and diffusion fluxes $\bar{J}_j^k$ and $\bar{J}_j^{*k}$ in the system of the average volume velocity and respectively in the center of mass system are connected by the equalities:

$$\bar{w}^k=\sum_{m_k}^{n_k} \Omega_j c_j^k \bar{v}_j^k; \qquad \sum_{m_k}^{n_k} \Omega_j c_j^k=1, \tag{2.11}$$

$$\bar{v}^k=(1/\rho^k) \sum_{m_k}^{n_k} \rho_j^k \bar{v}_j^k; \quad \rho^k=\sum_{m_k}^{n_k} \rho_j^k, \tag{2.12}$$

$$\bar{J}_j^k=c_j^k(\bar{v}_j^k-\bar{w}^k); \tag{2.13}$$

$$\bar{J}_j^{*k}=\rho_j^k(\bar{v}_j^k-\bar{v}^k) \tag{2.14}$$

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*) We preserve the above freedom to vary rheological properties of the lateral membrane due to the lack of clear experimental data on this subject. One only may state that plasmatic membranes are liquids possessing an appreciable elasticity [11]. Therefore the numerical modelling of the respective biological experiments has to be performed with a variation of the accepted assumptions concerning the rheological nature of the membranes. Such a variation may, apparently, help one to understand better the mechanical properties of plasmatic membranes.

Here

$$m_k=0;\ n_k=n \text{ for } k=-1, 1, 2, 5;\ m_k=1;\ n_k=n+1 \text{ for } k=0, 3, 4 \tag{2.15}$$

Note that (2.11)–(2.14) imply the identities

$$\sum_{m_k}^{n_k} \Omega_j \bar{J}_j^k=0; \qquad \sum_{m_k}^{n_k} \bar{J}_j^{*k}=0;\ k=-1, 0, \ldots, 5 \tag{2.16}$$

and

$$\bar{v}^k=\bar{w}^k+\sum_{m_k}^{n_k} \eta_j^k \bar{J}_j^k;\ \eta_j^k=(1/\rho^k)(M_j-M_s\,\Omega_j/\Omega_s)$$

$$(s=0 \quad \text{for } k=-1, 1, 2, 5;\ s=n+1 \quad \text{for } k=0, 3, 4) \tag{2.17}$$

Besides, definitions (2.11), (2.12) yield

$$\operatorname{div} \bar{w}^k=0;\ k=-1, 0, \ldots, 5 \tag{2.18$_1$}$$

$$\rho_t^k+\operatorname{div}(\rho^k \bar{v}^k)=0;\ k=-1, 0, \ldots, 5. \tag{2.18$_2$}$$

Thus every solution behaves as an incompressible liquid in the system of the average volume velocity, whereas in the center of mass system it behaves as commpressible one. Therefore it is convenient to write equations of convective diffusion in the system of the average volume velocity. In contrast to this equations of the solution motion have to be written in the center of mass system because only in this system forces of the inter-component interaction appear to be eliminated [24].

Bearing in mind the purpose of introduction of the one-dimensional formalism we write equations of the convective diffusion, continuity and momentum transfer in their integral form, assuming that no external forces act on the system and that there are no chemical reactions, neither volume nor surface.

Taking into account conditions of biological experiments quoted in [9], [21], [23], i.e. the smallness of the motion of solutions in a whole system under consideration, and also the diluteness of the membrane composing solutions, we neglect all the inertial terms in the equations of motion, and disregard the difference between the average volume velocites and those of the center of mass when we consider the motion within membranes.

Thus the integral equations of the convective-diffusion, continuity and momentum transfer are

$$\int_D c_{jt}^k\, d\sigma+\int_\Gamma c_j^k w_n^k\, ds=-\int_\Gamma J_{jn}^k\, ds;\ m_k\leqslant j\leqslant n_k;\ k=-1, 0, \ldots, 5 \tag{2.19}$$

$$\int_\Gamma w_n^k\, ds=0,\ k=-1, 0, \ldots, 5 \tag{2.20}$$

$$\begin{gathered} \int_\Gamma \bar{\Pi}_n^k\, ds=0;\ k=-1, 1, 2, 5 \\ \int_\Gamma \bar{\Pi}_n^k\, ds+\int_D \bar{R}^k\, ds=0;\ k=0, 3, 4 \end{gathered} \tag{2.21}$$

Here D is an arbitrary simple-connected region belonging to $\bar{D}_k$ and bounded by a piecewise smooth contour Γ. The subscript n denotes the outward normals of any vectors. Finally $\bar{\Pi}_n^k$ is the stress density at Γ and

$$\bar{R}^k = \lambda^k (\bar{v}_{n+1}^k - \bar{w}^k); \quad k=0, 3, 4 \tag{2.22}$$

is the fictitious volume force of the resistance of the main membrane constituent a_{n+1} to the percolation of solutions through the membrane.

Note that equation (2.19) is valid whatever the definition of diffusion fluxes is. We define them by the equalities

$$J_j^k = \begin{cases} -D_j^k \operatorname{grad} c_j^k \text{ for } j=0, 1, ..., n;\ k=-1, 1, 2, 5 \\ -D_j^k \operatorname{grad} c_j^k - L_j^k \operatorname{grad} p^k \ \text{ for } j=1, 2, ..., n+1;\ k=0, 3, 4 \end{cases} \tag{2.23}$$

All diffusion coefficients D_j^k are assumed to be constant. As it is seen from the definition of the coefficients of barodiffusion (see the footnote in page 51) they are linear functions of concentrations c_j^k if all the activity coefficients γ^k are constant. In our case only $\gamma_{n+1}^k \neq 1$. Since, however, in cases of our interest the concentrations of all the penetrating components are small and vary little in the course of the process evolution (see Appendix 2 and [4]) we may assume γ_{n+1}^k to be constant and together with this to assume $L_j^k = \text{const}$ for all j and k, entering (2.23).

We now have to add the conditions for a local thermodynamic equilibrium and those of dynamical compatibility at the boundaries of all membranes. The first ones may be written in the form of the Nernst distribution theorem

$$c_j^m = \kappa_j^{km} c_j^k \text{ at } S_{km}; \quad m = \begin{cases} 0 \text{ for } k=-1; 1 \\ 4 \text{ for } k=1, 5; \\ 3 \text{ for } k=1; 2 \end{cases} \quad S_{km} = \bar{D}_k \cap \bar{D}_m \tag{2.24}$$

The exact expression for the distribution coefficients is

$$\kappa_j^{km} = (X^m/X^k) \exp\left(\Omega_j (p^k - p^m)/RT\right) \quad \text{at } S_{km} \tag{2.25}$$

which is the corollary of the continuity of the chemical potentials of all penetrating components (see the footnote in page 51). Note that only dynamical conditions, which have to be valid on the membrane boundaries, are those of the continuity of tangential stresses and of the dynamical compatibility of normal stresses. Hence the membrane boundaries are, generally speaking, surfaces of the pressure discontinuity. As it is seen from (2.25) κ_j^{km} vary in the course of the process evolution. However for values of our interest (see Appendix 2) all κ_j^{km} are approximately constant. Therefore, and exceptionally for the sake of simplicity of the material presentation, we take them constant:

$$\kappa_j^{km} = \kappa_j = \text{const}; \quad j=1, 2, ..., n \tag{2.25*}$$

for all k and m entering (2.25).

Conditions of dynamical compatibility for diffusion fluxes at the boundaries of the lateral membrane are

$$(1-\kappa_j)\, c_j^i\, (n_{it}-w_n^i)=J_{jn}^i-J_{jn}^3; \quad j=1, 2, \ldots, n \quad \text{on } S_{13}; \quad i=1, 2 \tag{2.26}$$

$$c_0^i\, (n_{it}-w_n^i)=J_{0n}^i \tag{2.27}$$

Conditions of dynamical compatibility for the average volume velocity and for momentum transfer are

$$w_n^i=w_n^3 \quad \text{on } S_{13}; \quad i=1, 2 \tag{2.28}$$

and

$$\overline{\Pi}_n^i=\overline{\Pi}_n^3+(-1)^{i+1}\, \sigma_i\, K_i \quad \text{on } S_{i3}; \quad K=1, 2 \tag{2.29}$$

Here subscript n denotes the normal components of all respective vectors, σ_i is the surface tension on S_{i3} and

$$n_{it}=y_{it}/(S_{i3})_x; \quad K_i=y_{ixx}/(S_{i3})_x^3; \quad (S_{i3})_x=(1+y_{ix}^2)^{\frac{1}{2}}; \quad i=1, 2 \tag{2.30}$$

are the velocity of the motion of the surface S_{i3} in direction of its normal $\bar{n}^0$, and respectively the curvature of S_{i3}. $\bar{n}^0$ is assumed to be directed toward D_1.

On the boundaries of the basal membrane conditions (2.26)–(2.29) turn into*)

$$\begin{aligned} &J_{jx}^k+(1-\kappa_j)\, c_j^k\, w_x^k=J_{jx}^0; \\ &J_{0x}^k+c_0^k\, w_x^k=0 \end{aligned} \qquad j=1, 2, \ldots, n; \quad k=\begin{cases} 1 & \text{for } x=0 \\ -1 & \text{for } x=-2\Delta \end{cases} \tag{2.31}$$

$$w_x^k=w_k^0; \quad k=1 \quad \text{for } x=0; \quad k=-1 \quad \text{for } x=-2\Delta \tag{2.32}$$

$$P^0=p^k-\tau_{xx}^k; \quad k=1 \quad \text{for } x=0; \quad k=-1 \quad \text{for } x=-2\Delta \tag{2.33}$$

On the boundaries of the apical membrane these conditions become*)

$$\begin{aligned} &(1-\kappa_j)\, c_j^k\, (\dot{l}\,(t)-w_x^k)=J_{jx}^k-J_{jx}^4; \quad j=1, 2, \ldots, n \\ &c_0^k\, (\dot{l}\,(t)-w_x^k)=J_{0x}^k. \quad k=1 \quad \text{for } x=l\,(t); \quad k=5 \quad \text{for } x=l\,(t)+2\Delta \end{aligned} \tag{2.34}$$

$$w_x^k=w_x^4; \quad k=1 \quad \text{for } x=i\,(t); \quad k=5 \quad \text{for } x=l\,(t)+2\Delta \tag{2.35}$$

$$p^4=p^k-\tau_{xx}^k \quad k=1 \quad \text{for } x=l\,(t); \quad k=5 \quad \text{for } x=l\,(t)+2\Delta \tag{2.36}$$

All fluxes are continuous at common boundaries of the unstirred layers and the intercellular space, so that

$$J_{jx}^k=J_{jx}^2, \quad j=0, 1, \ldots, n; \quad w_x^k=w_x^2; \quad \overline{\Pi}_x^k=\overline{\Pi}_x^2; \quad x=\begin{cases} 0 & \text{for } k=-1 \\ l\,(t) & \text{for } k=5 \end{cases} \tag{2.37}$$

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*) Conditions of continuity of normal components of stresses (i.e. conditions of dynamical compatibility for momentum transfer in the quasistationary approximation we deal with) have to be valid on every subset of the boundary S_{km} of the membrane D_m and the solution D_k. It is obvious that on the boundary of a heterogeneous medium the stress on the solid skeleton coincides with that on the boundary of a percolating liquid. Since, by the agreement above, stresses within solutions percolating through membranes D_m, $m=0.4$; are considered as negligible compared with the fictitious volume forces of the resistance we see the correctness of conditions (2.33) and (2.36).

Conditions of symmetry on lines $y=A$ and $y=0$ are

$$c^k_{jy}=0;\quad m_k\leqslant j\leqslant n_k;\quad (w^k_x)_y=0;\quad p^k_y=0;\quad (\Pi^k_{xx})_y=0;\quad \Pi^k_{yy}=0 \text{ at } y=y^k$$
$$y^k=\begin{cases} A & \text{for } k=-1,1,5,0,4 \\ 0 & \text{for } k=-1,2,5,0,4 \end{cases} \tag{2.38}$$

Finally, tangential components of $\bar{v}^k, \bar{w}^k, \bar{J}^k_j$ and $\bar{\tau}^k_s$ on lines S_{k3} must satisfy the conditions*)

$$\left.\begin{aligned} &v^k_s=v^3_s; && (2.39)\\ &w^k_s=w^3_s; && (2.40)\\ &\kappa_j J^k_{js}=J^3_{js};\quad j=1,2,\dots,n; && (2.41)\\ &\tau^k_{ss}=\tau^3_{ss} && (2.42) \end{aligned}\right\} \text{ on } S_{k3};\quad k=1,2$$

Possible conditions on the external boundaries of the unstirred layers accepted in this paper are

$$\begin{gathered} p^k=p^{ko}(t);\quad c^k_j=c^{ko}_j(t),\quad j=0,1,\dots,n; \\ x=-L_0 \quad \text{for } k=-1;\quad x=L_1 \quad \text{for } k=5;\quad t\geqslant 0 \end{gathered} \tag{2.43}$$

We assume that c^{ko}_j satisfy the identity

$$\sum_0^n \Omega_k\, c^{io}_k(t)=1;\quad i=-1;5 \tag{2.44}$$

As the initial conditions we take

$$\begin{gathered} c^k_j(x,0)=c^k_{jo}(x);\quad y_i(x,0)=y_{io}(x);\quad i=1,2;\quad l(0)=l_o \\ m_k\leqslant j\leqslant n_k;\quad k=-1,0,\dots,5 \end{gathered} \tag{2.45}$$

assuming that

$$\begin{gathered} 0<y_{20}(x)<y_{10}(x)<A;\quad 0\leqslant x\leqslant l_o \\ y_{20}(x)=h;\quad l_o-H\leqslant x\leqslant l_o \end{gathered} \tag{2.46}$$

and that c^k_{jo} satisfy all the conditions (2.24).

---

*) Equalities (2.39), (2.40) are the corollaries of the adhesion conditions:

$$v^k_{js}=v^3_{n+1,s};\quad j=0,1,\dots,n;\quad v^3_{js}=v^k_0;\quad j=1,2,\dots,n+1, \tag{f1}$$

implying

$$v^k_{js}=v^k_{0s};\quad v^3_{js}=v^3_{n+1,s};\quad j=1,2,\dots,n;\quad k=1,2 \tag{f2}$$

We have

$$\rho^k v^k_s=\sum_0^n \rho^k_j v^k_{js}=v^k_{ms}\sum_0^n \rho^k_j=\rho^k v^k_{ms};\quad m=0,1,\dots,n. \tag{f3}$$

Analogously

$$w^3_s=w^3_{ms};\quad m=1,2,\dots,n+1 \tag{f4}$$

Hence (f1)—(f4) imply (2.39). Quite analogously, using (2.11) and (2.12) we see the validity of (2.40). Further, definitions (2.13), equality (2.40) and conditions (2.24) imply (2.41). Finally the second of equalities (2.42) is a corollary of the first one and of conditions (2.29).

This terminates the formulation of the problem in its general form. Here we treat membranes as thick shells and to not employ the assumption of narrowness of compartments D_1 and D_2.

3. One-dimensional formalism

Define regions D, entering equations (2.19), (2.20) and (2.21) as

$$D=\{s, y: x<s<x+dx;\ z_1(s, t)<y<z_2(x, t)\}\subset D_k; \qquad k=-1, 0, \dots, 5 \tag{3.1}$$

where

$$z_1=\begin{cases} 0 & \text{for } k=-1, 2, 5 \\ y_2(s, t) & \text{for } k=0, 3, 4 \\ y_1(s, t) & \text{for } k=1 \end{cases} \qquad z_2=\begin{cases} A & \text{for } k=-1, 0, 1, 4, 5 \\ y_1(s, t) & \text{for } k=3 \\ y_2(s, t) & \text{for } k=2 \end{cases} \tag{3.2}$$

and introduce averages

$$\hat{F}(s, t)=\big(1/(z_2(s, t)-z_1(s, t))\big)\int\limits_{z_1(s, t)}^{z_2(s, t)} F(s, y, t)\, dy \tag{3.3}$$

whatever the function $F(s, y, t)$ defined within D_k is. In what follows we only deal with functions whose deviations from their averages are small. For such functions we use the approximation

$$\widehat{F_1 F_2}=\hat{F}_1 \hat{F}_2 \tag{3.4}$$

Divide now equations (2.19), (2.20) and (2.21) by dx and pass to a limit $dx\to 0$. We obtain

$$\begin{aligned}(z_2-z_1)\, c^k_{jt}+(c^k_j-c^k_j|_{y=z_2})\, z_{2t}-(c^k_j-c^k_j|_{y=z_1})\, z_{1t}+\\ +((z_2-z_1)\, c^k_j\, w^k_x)_x+c^k_j\, w^k_n\, S_x|_{y=z_2}-c^k_j\, w^k_n\, S_x|_{y=z_1}=\\ =-((z_2-z_1)\, J^k_{jx})_x-J^k_{jn}\, S_x|_{y=z_2}+J^k_{jn}\, S_x|_{y=z_1}; \qquad j=1, 2, \dots, n\end{aligned} \tag{3.5}$$

instead of (2.19),

$$((z_2-z_1)\, w^k_x)_x+w^k_n\, S_x|_{y=z_2}-w^k_n\, S_x|_{y=z_1}=0 \tag{3.6}$$

instead of (2.20) and

$$((z_2-z_1)\, \bar{\Pi}^k_x)_x+\bar{\Pi}^k_n\, S_x|_{y=z_2}-\bar{\Pi}^k_n\, S_x|_{y=z_1}=\begin{cases} 0 & \text{for } k=-1, 1, 2, 5 \\ \lambda^k(\bar{w}^k-\bar{v}^k_{n+1}) & \text{for } k=0, 3, 4 \end{cases} \tag{3.7}$$

instead of (2.21). Here F_q, $q=x, y, n, s$, means the q-th component of any vector $\bar{F}$, n and s are notes of the normal and respectively the tangential direction to the line $y=z(x, t)$, and

$$S_x=(1+z_x^2)^{\frac{1}{2}} \tag{3.8}$$

Let us now specify equalities (3.5)–(3.7) using the basic inequalities*)

$$h \leqslant y_2(x, 0) < y_1(x, 0) = y_2(x, 0) + 2\Delta \ll A \ll l(t) \ll \min(L_0, L_1); \ \forall t \geqslant 0 \tag{3.9}$$

and the following simplifying approximations:

1. Due to the smallness of motion, diffusion fluxes and stresses all the terms, quadratic with respect to derivatives in x-direction, of all the functions of interest, are disregarded, if this neglect does not lead to any observable contradiction.

2. Since the basal and the apical membranes are assumed to be rigid, so that the possible swelling or shrinking of them are disregarded, the distribution of concentration there is considered as quasistationary.

3. The specific (i.e. per unit of crossection) resistance of membranes to mass transfer is incomparably greater than that of the cell and intercellular space (see Appendix 2). Therefore we neglect the mass transfer within the basal and the apical membranes in y direction compared with that in the transversal x-direction, as well as the mass exchange between the unstirred layers and the lateral membrane through their common boundaries.

4. Inequalities (3.9) show that the time of relaxation of concentration fields in y-direction within the unstirred layers D_{-1} and D_5, the cell D_1 and intercellular space D_2 may be assumed negligible compared with that in x-direction. Since, by the assumption c_j^{ko}, $j=0, 1, \ldots, n$, are independent of y we may presuppose that

$$\begin{aligned} &c_{jy}^k = 0; \quad j = 0, 1, \ldots, n; \quad k = -1; 5 \\ &c_j^k|_{y=y_k(x,t)} = \hat{c}_j^k; \quad j = 1, 2, \ldots, n; \quad k = 1, 2 \end{aligned} \tag{3.10}$$

5. Tangential components J_{js}^3 of diffusion fluxes $\bar{J}_j^3$, $j=1, 2, \ldots, n$, on the boundaries S_{k3}, $k=1, 2$, of the lateral membrane are considered as negligible compared with their normal components.

6. In addition to the approximation above we use, if necessary, the simplest approximation of functions of the interest compatible with conditions of symmetry and dynamical compatibility. This yields, in particular the approximation

$$w_x^k(x, y, t) = w_x^k(x, t); \quad k = 0, 1, 2, 4 \tag{3.11}$$

$$p^k(x, y, t) = p^k(x, t); \quad k = -1, 0, 1, 2, 4, 5 \tag{3.12}$$

Note that the the approximation (3.11) is inapplicable to w_x^{-1} and w_x^5. Indeed, conditions of dynamical compatibility (2.32) and (2.35) show that

$$\begin{aligned} &w_x^{-1}(-2\Delta, t) = (1/A)\big((A - y_2(0, t)\, w^0(-2\Delta, t) + y_2(0, t)\, w_x^2(-2\Delta, t)\big) \\ &w_x^5\big(l(t) + 2\Delta, t\big) = (1/A)\big(\big(A - y_2\big(l(t), t\big)\big)\, w^4\big(l(t) + 2\Delta, t\big) + \\ &\qquad\qquad + y_2\big(l(t), t\big)\, w^2\big(l(t) + 2\Delta, t\big)\big) \end{aligned} \tag{3.13}$$

---

*) For the magnitude of values, entering (3.9), see Appendix 2.

which is clearly incompatible with the assumption of the independency of w_x^k, $k=-1; 5$, of y, since w^0 and w_x^2, as well as w^5 and w_x^2 are essentially different.

7. We accept, for any function f defined within the lateral membrane the approximation

$$f(x, t)=\tfrac{1}{2}\big(f(x, y_1(x, t), t)+f(x, y_2(x, t), t)\big) \tag{3.14}$$

and approximations

$$\begin{aligned} J_{jy}^3|_{S_{13}}&=-2\,(D_j^3\,(c_j^3|_{S_{13}}-c_j)+L_j^3\,(p^3|_{S_{13}}-p))/(y_1(x, t)-y_2(x, t))\\ J_{jy}^3|_{S_{23}}&=-2\,(D_j^3\,(c_j-c_j^3|_{S_{23}})+L_j^3\,(p-p^3|_{S_{23}}))/(y_1(x, t)-y_2(x, t)) \end{aligned} \tag{3.15}$$

with unknown

$$Q_j^3=2\,(D_j^3\,c_j+L_j^3\,p)/(y_1(x, t)-y_2(x, t)) \tag{3.16}$$

8. Dealing with the cell and intercellular space, note, first of all, that

$$\begin{aligned} \tau_{nn}^k&=\mu_k\,\big(2\,(v_n^k)_n-(2/3)\,((v_n^k)_n+(v_s^k)_s-K_k\,v_n^k)\big)\\ \tau_{ns}^k&=\mu_k\,((v_n^k)_s+(v_s^k)_n+K_k\,v_s^k); \qquad k=1; 2\\ \tau_{ss}^k&=\mu_k\,\big(2\,(v_s^k)_s-2v_n^k\,K_k-(2/3)\,((v_n^k)_n+(v_s^k)_s-K_k\,v_n^k)\big) \end{aligned} \tag{3.17}$$

and that

$$v_y^k(x, y^k, t)=0; \qquad v_n^k=\alpha_{k3}\,v_x^k+\beta_{k3}\,v_y^k; \qquad v_s^k=\beta_{k3}\,v_x^k-\alpha_{k3}\,v_y^k \tag{3.18}$$

Here α_{k3} nad β_{k3} are direction cosines of a normal to S_{k3} and K_k is defined by (2.30). Further $y^1=A$ and $y^2=0$.

We use the approximations

$$(v_r^k(x, y, t))_y=(v_r^k(x, y^k, t)-v_r^k(x, y_k, t))/(y^k-y_k); \qquad r=y, n, s; \; k=1; 2. \tag{3.19}$$

Hence we approximately have

$$\left.\begin{aligned} (v_n^k)_n&=\alpha_{k3}\,(v_n^k)_x+\beta_{k3}\,(\alpha_{k3}\,v_x^k-v_n^k)/(y^k-y_k)\\ (v_s^k)_n&=\alpha_{k3}\,(v_s^k)_x+\beta_{k3}\,(\beta_{k3}\,v_x^k-v_s^k)/(y^k-y_k) \end{aligned}\right\} \text{ on } S_{k3}; \qquad k=1, 2 \tag{3.20}$$

Note that by virtue of conditions of symmetry

$$J_{jn}^k(x, y^k, t)=\alpha_{k3}\,J_{jx}^k(x, t); \qquad j=0, 1, 2, \ldots, n; \qquad k=1, 2 \tag{3.21}$$

and that the adhesion conditions and the equality

$$J_{js}^3(x, y_k, t)=0 \tag{3.22}$$

imply

$$J_{js}^k(x, y_k, t)=0; \qquad j=0, 1, \ldots, n; \qquad k=1, 2 \tag{3.23}$$

Using all these assumptions and approximations we easily conclude that equations (3.5)–(3.7) yield:

A. Equations of transfer through the basal and apical unstirred layers

Assuming that w^k_x, $k=-1;5$, are continuous functions of y we find that*)

$$w^k_x(x,t)=w^k_x(x_k,t); \quad x\in D^k; \quad k=-1;5 \tag{3.24}$$

where

$$D^{-1}=(x: -L_0<x<-2\Delta); \quad D^5=(x: l(t)+2\Delta<x<L_1), \tag{3.25}$$

and $w^k_x(x_k,t)$ are defined by (3.13). Further

$$\left.\begin{aligned}&(c^k_j)_t+w^k_x(c^k_j)_x=D^k_j(c^k_j)_{xx}; \quad j=0,1,\ldots,n,\\&(\hat{p}^k-\hat{\tau}^k_{xx})_x=0\end{aligned}\right. \qquad x\in D^k, \quad k=-1;5 \tag{3.26}$$

and by virtue of (3.24)

$$\hat{\tau}^k_{xx}=-2(\mu_k/\rho^k)\sum_1^n(M_j-M_0\,\Omega_j/\Omega_0)\,D^k_j(c^k_j)_{xx} \tag{3.26*}$$

B. Equations of transfer trough the basal and apical membranes

$$\begin{aligned}&(J^k_j)_x+w^k_x(c^k_j)_x=0; \quad j=1,2,\ldots,n+1;\\&(w^k_x)_x=0 \quad x\in D^k; \quad k=0;4\\&(p^k)_x-\lambda^k(w^k-v^k_{n+1})=0\end{aligned} \tag{3.27}$$

---

*) It is obvious that points $(x_k, y_2(x_k,t))$, $k=-1;5$, $x_{-1}=-2\Delta$, $x_5=1(t)+2\Delta$ are points of discontinuity of the average volume velocity $w^k(x,y,t)$ since the specific (i.e. per unit of length of the crossection $x=\text{const}$) resistance of membranes to the solutions motion are incomparably greater than that of the intercellular space. Denote $y=z_k(x,t)$ the streamline of the field of the average volume velocity, entering the point $(x_k, y_2(x_k,t))$ and belonging to D_k. We have

$$w^k_x=(1/A)\int_0^A w^k_x\,dy=(1/A)\left((A-z_k)\,w^k_{x1}+z_k\,w^k_{x2}\right) \tag{o}$$

where

$$w^k_{x1}=(1/(A-z_k))\int_{z_k}^A w^k_x\,dy; \quad w^k_{x2}=\int_0^{z_k} w^k_x\,dy \tag{oo}$$

Hence

$$((w^k_x)_x)=(1/A)\,(w^k_x)_x+(1/A)\,[w^k_x]\,(z_k)_x \tag{ooo}$$

where [f] means a jump of f on the line $y=z_k$ whatever the function f is. Thus (3.24) may be valid if and only if

$$[w^k_x]\,(z_k)_x=0; \quad x\in D^k. \tag{iv}$$

Since $w^k_x\neq 0$ at points $(x_k, y_2(x_k,t))$ it perhaps is rather more natural to suppose that the streamline $y=z_k$ has a zero slope everywhere in D_k than to assume that the points $(x_k, y_2(x_k,t))$ are the only points of discontinuity of $w^k_x(x,y,t)$; $k=-1;5$.

Here

$$D^0=(x\colon -2\Delta<x<0); \qquad D^4=(x\colon l\,(t)<x<l\,(t)+2\Delta) \tag{3.28}$$

Note that

$$v_{n+1}^k\,(x,t)=\begin{cases} 0\ ; & x=-2\Delta \text{ or } x=0 \qquad \text{for } k=0 \\ \dot{l}\,(t); & x=l\,(t) \quad \text{or } x-l\,(t)+2 \text{ for } k=4 \end{cases} \tag{3.29}$$

C. Equations of transfer through the cell and intercellular space

$$\begin{aligned} &(y^k-y_k)\,(c_j^k)_t+((y^k-y_k)\,w_x^k\,c_j^k)_x-c_j^k\,w_n^k\,(S_{k3})_x|_{S_{k3}}= \\ &\qquad =-((y^k-y_k)\,J_{jx}^k)_x-J_{jn}^k\,(S_{k3})_x|_{S_{k3}}=0; \qquad j=0,1,2,\ldots,n \\ &((y^k-y_k)\,w_x^k)_x-w_n^k\,(S_{k3})_x|_{S_{k3}}=0; \qquad k=1,2; \qquad x\in D^k \end{aligned} \tag{3.30}$$

Note that

$$\begin{aligned} &\tau_{zz}^k=-(2/3)\,\mu_k\operatorname{div}\bar{v}^k+2\mu_k\,(\bar{v}_z^k)_z; \qquad z=x;\,y, \\ &\tau_{xy}=\mu_k\,((v_y^k)_x+(v_x^k)_y); \qquad \bar{v}^k=\bar{w}^k+\sum_1^n \eta_j^k\,J_j^k; \qquad k=1;\,2, \\ &\operatorname{div}\bar{w}^k=0; \quad \bar{J}_j^k=-D_j^k\operatorname{grad}c_j^k; \quad \eta_j^k=(\mu_k/\rho^k)\,(M_j-M_0\,\Omega_j/\Omega_0) \end{aligned} \tag{3.31}$$

Using (3.10), conditions of symmetry and the first of assumptions above, we conclude that

$$\begin{aligned} \hat{\tau}_{xx}^k=&\sum_1^n (2/3)\,\eta_j^k\,(-\hat{J}_{jx}^k)_x+(1/(y^k-y_k))\,(J_{jn}^k|_{S_{k3}}+(y_{kx}\,J_{jx}^k))+ \\ &\qquad\qquad +2\left(\mu_k\,\hat{w}_x^k+\sum_1^n \eta_j^k\,\hat{J}_{jx}^k\right); \\ \hat{\tau}_{xy}^k=&-1/2\left(\mu_k\,w_n^k+\sum_1^n \eta_j^k\,J_{jn}^k|_{S_{k3}}\right)_x+ \\ &\qquad +1/2\left(\mu_k\,w_x^k+\sum_1^n \eta_j^k\,\hat{J}_{jx}^k\right)(y_{kxx}+y_{kx}/(y^k-y_k)); \\ \hat{\tau}_{yy}^k=&-(2/3)\sum_1^n \eta_j^k\,(\hat{J}_{jx}^k)_x-(1/(y^k-y_k))\left(\sum_1^n (4/3)\,\eta_j^k\,J_{jn}^k+2\mu_k\,w_n^k\right)\Bigg|_{S_{k3}}+ \\ &\qquad +\left(\sum_1^n (4/3)\,\eta_j^k\,J_{jx}^k+(2\mu_k\,w_x^k)\,y_{kxx}\right). \end{aligned} \tag{3.32}$$

D. Equations of transfer through the lateral membrane

$$\begin{aligned} &1/2\,((y_1-y_2)\,(c_j^3|_{S_{13}}+c_j^3|_{S_{23}})_t-c_j^3|_{S_{13}}\,y_{1t}+c_j^3|_{S_{23}}\,y_{2t}+ \\ &\qquad +1/2\,((y_1-y_2)\,(c_j^3\,w_x^3|_{S_{13}}+c_j^3\,w_x^3|_{S_{23}}))_x+c_j^3\,w_n^3\,(S_{13})_x|_{S_{13}}- \\ &\qquad -c_j^3\,w_n^3\,(S_{23})_x|_{S_{23}}=J_{jn}^3\,(S_{13})_x|_{S_{13}}-J_{jn}^3\,(S_{23})_x|_{S_{23}} \qquad j=1,2,\ldots,n \end{aligned} \tag{3.33}$$

where the term

$$((y_1-y_2)\,\hat{J}^3_{jx})=1/2\,((y_1-y_2)\,(\alpha_{13}\,J^3_{jn}|_{S_{13}}+\alpha_{23}\,J^3_{jn}|_{S_{23}}) \tag{3.34}$$

is omitted*).

Further

$$1/2\,((y_1-y_2)\,(w^3_x|_{S_{13}}+w^3_x|_{S_{23}}))_x+w^3_n\,(S_{13})_x|_{S_{13}}-w^3_n\,(S_{23})_x|_{S_{23}}=0 \tag{3.35}$$

and**)

$$1/2\,((y_1-y_2)\,(\overline{\Pi}^3_x|_{S_{13}}+\overline{\Pi}^3_x|_{S_{23}}))_x+1/2\,(y_1-y_2)\,(\bar{R}^3|_{S_{13}}+\bar{R}^3|_{S_{23}})+$$
$$+\overline{\Pi}^3_n\,(S_{13})_x|_{S_{13}}-\overline{\Pi}^3_n\,(S_{23})_x|_{S_{23}}=0 \tag{3.36}$$

Note that the fictitious volume forces $\bar{R}^3$ of the resistance have no tangential components at points of the membrane boundaries S_{13} and S_{23}. Indeed

$$R^3_s|_{S_{k3}}=\lambda^3\,(v^3_{n+1,s}-w^3_s)|_{S_{k3}}=(1/c^3_{n+1})\,J^3_{n+1,s}|_{S_{k3}}=0 \tag{3.37}$$

(see point 5 in page 61). Thus (3.36) may be rewritten as

$$1/2\,((y_1-y_2)\,(\overline{\Pi}^3_x|_{S_{13}}+\overline{\Pi}^3_x|_{S_{23}}))_x+1/2\,\lambda^3\,(y_1-y_2)\,(n_{1t}-w^3_n|_{S_{13}})\,\bar{n}^0_{13}+$$
$$+(n_{2t}-w^3_n|_{S_{23}})\,\bar{n}^0_{23}+\overline{\Pi}^3_n\,(S_{13})_x|_{S_{13}}-\overline{\Pi}^3_n\,(S_{23})_x|_{S_{23}}=0 \tag{3.38}$$

which is valid since

$$v^3_{n+1,n}|_{S_{k3}}=n_{kt}=y_{kt}/(S_{k3})_x;\qquad k=1,2\,. \tag{3.39}$$

Here $\bar{n}^0_{k3}$ are the unit vectors of the normals to S_{k3}, $k=1;2$.

E. Conditions of conjugation. Boundary and initial conditions

Recall that by virtue of conditions of symmetry the average volume velocity is independent of x in both the unstirred layers, which justifies equating w^k, $k=-1;5$, to values defined by (3.13), as well as definitions of τ^k_{xx} by (3.26). This shows that conditions (2.24) and conditions of dynamical compatibility are satisfied by the average concentrations, average volume velocities and everywhere except for boundaries of the unstirred layers. On these boundaries they take the forms of:

$$\hat{J}^{-1}_{jx}+\hat{c}^{-1}_j\,\hat{w}^{-1}_x=(1/A)\,((A-y_1)\,(\hat{J}^0_{jx}+\hat{c}^0_j\,\hat{w}^0_x)+y_2\,(\hat{J}^2_{jx}+\hat{c}^2_j\,\hat{w}^2_x)$$
$$j=1,2,\ldots,n;\qquad x=-2\Delta \tag{3.40$_1$}$$

$$\hat{J}^{-1}_{0x}+\hat{c}^{-1}_0\,\hat{w}^{-1}_x=(y_2/A)\,(\hat{J}^2_{0x}+\hat{c}^2_0\,\hat{w}^2_x);\qquad x=-2\Delta$$

$$\hat{p}^{-1}-\hat{\tau}^{-1}_{xx}=(1/A)\,(\hat{p}^0+y_2\,(\hat{p}^2-\hat{\tau}^2_{xx})+(y_1-y_2)\,\hat{p}^3);\qquad x=-2\Delta \tag{3.40$_2$}$$

$$\hat{w}^{-1}_x=(1/A)\,((A-y_1)\,\hat{w}^0_x+y_2\,\hat{w}^2_x);\qquad x=-2\Delta \tag{3.40$_3$}$$

---

*) This term is of the first order with respect to derivatives in x-direction, so that we cannot refer to the assumption 1 above. However, comparing its magnitude with that of the terms in the right hand side of (3.33) we see that it is negligible (See Appendix 2).

**) For computation of stresses $\overline{\Pi}^3_n$ and $\overline{\Pi}^3_x$ on boundaries S_{k3} see the next section.

$$\hat{J}^5_{jx}+\hat{c}^5_j\,(\hat{w}^5_x-\dot{l}\,(t))=(1/A)\,\big((A-y)\,(\hat{J}^4_{jx}+c^4_j\,(\hat{w}^4_x-\dot{l}\,(t))\big)+$$
$$+y_2\,(\hat{J}^2_{jx}+\hat{c}^2_j\,(\hat{w}^2_x-\dot{l}\,(t)))\big)\quad j=1,2,\ldots,n;\quad x=l\,(t)+2 \tag{3.41$_1$}$$

$$\hat{J}^5_{0x}+\hat{c}^5_0\,(\hat{w}^5_x-\dot{l}\,(t))=(y_2/A)\,(\hat{J}^2_{0x}+\hat{c}^2_0\,(\hat{w}^2_x-\dot{l}\,(t)));\quad x=1\,(t)+2 \tag{3.41$_2$}$$

$$\hat{p}^5-\hat{\tau}^5_{xx}=(1/A)\,((A-y_1)\,\hat{p}^4+y_2\,(\hat{p}^2-\hat{\tau}^2_{xx})+(y_1-y_2)\,\hat{p}^3);\quad x=l\,(t)+2\Delta \tag{3.41$_3$}$$

$$\hat{w}^5_x-\dot{l}\,(t)=(1/A)\,((A-y_1)\,(\hat{w}^4_x-\dot{l}\,(t))+y_2\,(\hat{w}^2_x-\dot{l}\,(t)))\,, \tag{3.41$_4$}$$

Recall that the conditions of dynamical compatibility (2.31)–(2.36), which remain unchanged on the boundaries of the cell, are

$$\left.\begin{array}{l}\hat{J}^0_{jx}+\hat{c}^0_j\,\hat{w}^0_x=\hat{J}^1_{jx}+\hat{c}^1_j\,\hat{w}^1_x;\quad \hat{J}^1_{0x}+\hat{c}^1_0\,\hat{w}^1_x=0;\quad j=1,2,\ldots,n\\ \hat{w}^0_x=\hat{w}^1_x;\\ \hat{p}^0=\hat{p}^1-\hat{\tau}^1_{xx}\end{array}\right\}\quad x=0 \tag{3.42$_1$}$$

$$\left.\begin{array}{l}\hat{J}^4_{jx}+\hat{c}^4_j\,(\hat{w}^4_x-\dot{l}\,(t))=\hat{J}^1_{jx}+\hat{c}^1_j\,(\hat{w}^1_x-\dot{l}\,(t));\quad j=1,2,\ldots,n\\ \hat{J}^1_{0x}+\hat{c}^1_0\,(\hat{w}^1_x-\dot{l}\,(t))=0\\ \hat{w}^4_x=\hat{w}^1_x\\ \hat{p}^4=\hat{p}^1-\hat{\tau}^1_{xx}\end{array}\right\}\quad x=l\,(t) \tag{3.42$_2$}$$

Further

$$\begin{array}{l}c^k_j=((A-y_1)/\kappa_j\,A)\,c^1_j+(y_2/A)\,c^2_j+((y_1-y_2)/\kappa_j\,A)\,c^3_j;\ x=x_k;\ k=-1;5\\ x_{-1}=-2\Delta;\ x_5=l\,(t)+2\Delta;\ j=1,2,\ldots,n\end{array} \tag{3.43}$$

Note that terms $(y_1-y_2)\,\hat{p}^3$ and $(y_1-y_2)\,c^3_j/\kappa_j$, entering (3.40$_2$), (3.31$_3$) and respectively (3.43) are negligible since p^1, p^2, p^3 and respectively c^1_j/κ_j, c^3_j/κ_j and c^2_j are of the same order, and y_1-y_2 is two order smaller than A (see Appendix 2).

4. Equations of the membrane approximation

Equations by the membrane approximation are corollaries of the one-dimensional formalism of the theory (section 3) and conditions of conjugation (sections 2, 3). Using equations of transfer through the membranes and conditions of conjugation we may find an explicit relationship between diffusion fluxes, velocities and stresses on the cell boundaries and those on the boundaries of the intercellular space and unstirred layers. As the result of this all the values determined within membranes appear to be eliminated. Remembering that 2Δ is incomparably smaller than L_0 and L_1 we may, after such an elimination, consider lines $x=0$ and $x=l\,(t)$ as the only representative of the basal and apical membranes, and consider them as the boundaries of unstirred layers. It is also convenient to introduce

$$z\,(x,t)=y_1\,(x,t)-y_2\,(x,t) \tag{4.1}$$

as a new unknown, and consider the boundary S_{23} of the intercellular space as the only representative of the lateral membrane, and therefore as the boundary of the cell. It appears, due to the magnitude of values we deal with, (see Appendix 2) that the distribution of concentrations, velocities and stresses interior to the lateral membrane are not noticeably affected when z varies. This means that the boundary $y=y_2(x,t)$ may be determined in the approximation

$$2\Delta=\text{const.} \tag{4.2}$$

where 2Δ is the thickness of the lateral membrane measured along the normal to its boundary S_{23}. In such an approximation $y_2(x,t)$ has to be determined from the simplified system of equations, where the swelling and shrinking of the lateral membrane, as well as the change of its thickness due to bending are disregarded, whereas $z(x,t)$ may be found after obtaining the solution of this simplified system*)

A. Elimination of the basal membrane

Equations (3.27) yield

$$\begin{aligned} &J_{jx}^0(-2\Delta,t)+\hat{c}_j^0(-2\Delta,t)\,w_x^0(t)=J_j^0(0,t)+c_j^0(0,t)\,w_x^0(t); \quad j=1,2,\ldots,n \\ &p^0(-2\Delta,t)+2\Delta\lambda^0\,w_x^0(t)=\hat{p}^0(0,t); \quad w_x^0(x,t)_x=0 \end{aligned} \tag{4.3}$$

Comparing (4.3) and (3.40), and replacing -2Δ by 0 we obtain**)

$$\begin{aligned} &\hat{J}_{jx}^{-1}+\hat{c}_j^{-1}\,\hat{w}_x^{-1}=(1/A)\left((A-y_1)\,(\hat{J}_{jx}^1+\hat{c}_j^1\,\hat{w}_x^1)+y_2\,(\hat{J}_{jx}^2+\hat{c}_j^2\,\hat{w}_x^2)\right) \\ &\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad j=1,2,\ldots,n; \\ &\hat{p}^{-1}-\hat{\tau}_{xx}^{-1}=(1/A)\left((A-y_1)\,(\hat{p}^1-\hat{\tau}_{xx}^1+2\Delta\lambda^0\,\hat{w}_x^1)+y_2\,(\hat{p}^2-\hat{\tau}_{xx}^2\right); \quad x=0 \\ &\hat{w}_x^{-1}=(1/A)\left((A-y_1)\,\hat{w}_x^1+y_2\,\hat{w}_x^2\right) \end{aligned} \tag{4.4}$$

Besides

$$\hat{J}_{0x}^{-1}+\hat{c}_0^{-1}\,\hat{w}_x^{-1}=(y_2/A)\,(\hat{J}_x^2+\hat{c}_0^2\,\hat{w}_x^2) \text{ at } x=0 \tag{4.5}$$

On the other hand we find, using (4.3), definition (2.23) and conditions (2.24) of conjugation, that

$$\begin{aligned} &\hat{c}_{jx}^0-(\hat{w}_x^1/D_j^0)\,c_j^0=-(1/D_j^0)\,(\hat{J}_j^1+\hat{c}_j^1\,\hat{w}_x^1+L_j^0\,\lambda^0\,\hat{w}_x^1)|_{x=0} \\ &\hat{c}_j^0=\kappa_j\,\hat{c}_j^1; \quad j=1,2,\ldots,n; \quad x=0 \end{aligned} \tag{4.6}$$

---

*) The width of the tight junction is of order $2h=10$ Å whereas $2\Delta=100$ Å and $A-y_1(x,0)$ is of the order 3μ (see Appendix 2). This shows that the shift of the boundary $y=y(x,t)$ of the cell to the line $y=y_2(x,t)$ cannot become essentially influential, at least at the initial stage of the process evolution, when the cell is by far from the possible collapse.

**) Here and below we disregard terms $(y_1-y_2)\,p^3$ and $(y_1-y_2)\,c_j^3/\kappa_j$ in the accordance with what is said at the end of page 22.

Equations (4.4) and (4.9) are written taking into account the assumption concerning negligibility of the mass transfer through the regions

$$\begin{aligned} &D^{k*}=((x,y\colon x_k<x<x_k+2\Delta),\ y_2(x,t)<y<y_1(x,t)); \\ &k=-1;5;x_{-1}=-2\Delta;\ x_5=l(t) \end{aligned}$$

This and the approximation

$$\exp\left(-2\Delta\, \hat{w}_x^1(0,t)/D_j^0\right)=1-2\Delta\, \hat{w}_x^1(0,t)/D_j^0 \tag{4.7}$$

yield (see the table of notations)

$$\hat{c}_j^0(-2\Delta,t)=(\kappa_j/p_j^0)\left(\left(\hat{c}_j^1\left(\hat{p}_j^0+\hat{w}_x^1(1-\kappa_j)\right)+\hat{J}_j^1+L_j^0\,\lambda^0\,\hat{w}_x^1\right)\right|_{x=0} \qquad j=1,2,\dots,n \tag{4.8}$$

Inserting (4.8) into (3.43) and replacing -2Δ by 0 we accomplish the elimination of the basal membrane.

B. Elimination of the apical membrane

Quite analogously we have

$$\left.\begin{aligned}
&\hat{J}_j^5+\hat{c}_j^5\left(\hat{w}_x^5-\dot{l}(t)\right)=(1/A)\left((A-y_1)\left(\hat{J}_{jx}^1+\hat{c}_j^1\left(\hat{w}_x^1-\dot{l}(t)\right)\right)+\right.\\
&\qquad\qquad\left.+y_2\left(\hat{J}_{jx}^2+\hat{c}_j^2\left(\hat{w}_x^2-\dot{l}(t)\right)\right)\right); \quad j=1,2,\dots,n;\\
&\hat{p}^5-\hat{\tau}_{xx}^5=(1/A)\left((A-y_1)\left(\hat{p}^1-\hat{\tau}_{xx}^1+2\Delta\lambda^4\,\hat{w}_x^1\right)+y_2\left(\hat{p}^2-\hat{\tau}_{xx}^2\right)\right); \quad x=l(t)\\
&\hat{w}_x^5-\dot{l}(t)=(1/A)\left(\left(\hat{w}_x^1-\dot{l}(t)\right)+y_2\left(\hat{w}_x^2-\dot{l}(t)\right)\right)
\end{aligned}\right\} \tag{4.9}$$

$$\hat{J}_{0x}^5+\hat{c}_0^5\left(\hat{w}_x^5-\dot{l}(t)\right)=(y_2/A)\left(\hat{J}_{0x}^2+\hat{c}_0^2\left(\hat{w}_x^2-\dot{l}(t)\right)\right) \quad \text{at } x=l(t) \tag{4.10}$$

and

$$\begin{aligned}c_j^4\left(l(t)+2\Delta,t\right)=-(\kappa_j/p_j^4)\left(\hat{J}_j^1-\hat{c}_{jx}^1\left(p_j^4-\left(w_x^1-\dot{l}(t)\right)(1-\kappa_j)\right)+\right.\\
\left.+L_j^4\,\lambda^4\left(\hat{w}_x^1-\dot{l}(t)\right)\right|_{x=l(t)}; \quad j=1,2,\dots,n.\end{aligned} \tag{4.11}$$

Again, inserting (4.11) into (3.43) and replacing 2Δ by 0 we accomplish elimination of the apical membrane.

C. Elimination of the lateral membrane

Note, first of all, that (3.35), (2.28) and (2.40) yield

$$w_n^1(S_{13})_x|_{S_{13}}-w_n^2(S_{23})_x|_{S_{23}}+1/2\left((y_1-y_2)\left(w_x^1|_{S_{13}}+w_x^2|_{S_{23}}\right)\right)=0 \tag{4.12}$$

Consider (3.36). Note that

$$\bar{\Pi}_x^3|_{S_{k3}}=\left(-p^3\,\bar{i}+\bar{\tau}_x^3\right)|_{S_{k3}}=\left(\Pi_{nn}^3-\tau_{nn}^3\right)\bar{i}\,|_{S_{k3}}+\bar{\tau}_x^3|_{S_{k3}}; \quad k=1;2 \tag{4.13}$$

Using now (2.29), (2.30) and (2.42) we obtain, after some simple computations,

$$\bar{F}=\bar{F}^3 \tag{4.14}$$

where*)

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*) Below we use these equalities omitting all terms quadratic with respect to derivatives in x-direction if, naturally, they are not divided by a small value of the order of y_1-y_2.

$$\begin{aligned}\bar{F}=&\left((A-y_1)\,\bar{\Pi}^1_x|_{S_{13}}+y_2\,\bar{\Pi}^2_x|_{S_{23}}\right)_x+\sigma_1\,K_1\,(S_{13})_x\,\bar{n}^0_{13}-\sigma_2\,K_2\,(S_{23})_x\,\bar{n}^0_{23}+\\ &+1/2\left((y_1-y_2)\,\sum_1^2\alpha_{k3}\,\tau^k_{ns}\,\bar{n}^0_{k3}\right)_x+\bar{i}\;1/2\,(y_1-y_2)\,\left((1/(S_{13})_x)\times\right.\\ &\times\left((A-y_1)\,\Pi^1_{xn}|_{S_{13}}\right)_x-\left(1/(S_{23})_x\,(y_2\,\Pi^2_{xn})_x|_{S_{23}}-\right.\\ &-(A-y_1)\,K_1\,\Pi^1_{xs}|_{S_{13}}+y_2\,K_2\,\Pi^2_{xs}|_{S_{23}}-\sigma_1\,K_1+\sigma_2\,K_2)\big)_x\\ \bar{F}^3=&\,1/2\,(y_1-y_2)\,(R^3|_{S_{13}}\,\bar{n}^0_{13}+R^3|_{S_{23}}\,\bar{n}^0_{23})-\bar{i}\;1/2\,\left((y_1-y_2)\,(\tau^3_{nn}|_{S_{13}}+\right.\\ &\left.+\tau^3_{nn}|_{S_{23}})\right)_x+1/2\,\left((y_1-y_2)\,(\alpha_{13}\,\tau^3_{nn}|_{S_{13}}\,\bar{n}^0_{13}+\alpha_{23}\,\tau^3_{nn}|_{S_{23}}\,\bar{n}^0_{23})\right)_x\end{aligned}\tag{4.15}$$

Thus in order to eliminate the lateral membrane from the equation of the momentum transfer we must do this with the expression of $\bar{F}^3$.

By the definition (2.22) and conditions (2.40) we have

$$R^3|_{S_{k3}}=\lambda^3\,\left((n^3_{n3})_t-w_n\right)|_{S_{k3}}\tag{4.16}$$

Further, remembering the assumption of the smalness of motion, we may neglect the difference between the local and material derivatives at points of the lateral membrane boundaries. This means that instead of equations (2.6) we may write**)

$$\begin{aligned}&\tilde{\varepsilon}^3\left(x,y_k(x,t),t\right)=\tilde{\varepsilon}^3\left(x,y_k(0),0\right)+\int_0^t\tilde{e}^3\left(x,y_k(x,s),s\right)ds\\ &\tilde{\tau}^3\left(x,y_k(x,t),t\right)=\tilde{\tau}^3\left(x,y_k(x,0),0\right)\exp(-\mathrm{at})+be^3\left(x,y_k(x,t),t\right)+\\ &\qquad+\int_0^t\exp\left(-a\,(t-s)\left(c\tilde{e}^3\left(x,y_k(x,s),s\right)+d\tilde{\varepsilon}^3\left(x,y_k(x,s),s\right)\right)\right)ds.\end{aligned}\tag{4.17}$$

Recall that

$$\begin{aligned}&e^3_{nn}=(w^3_n)_n;\qquad e^3_{ns}=1/2\,\left((w^3_n)_s+(w^3_s)_n+K_k\,w^3_s\right);\\ &e^3_{ss}=(4/3)\,\left((w^3_n)_s-K_k\,w^3_n\right)-(2/3)\,(w^3_n)_n;\qquad k=1;2\end{aligned}\tag{4.18}$$

Compute values $(w^3_s)_n|_{S_{k3}}$ and $(w^3_n)_n|_{S_{k3}}$ by the following way. We have

$$\operatorname{div}\bar{w}^3=0\quad\text{in }D_3\tag{4.19}$$

Hence

$$\operatorname{div}\left((\bar{w}^3)_y\right)=0\quad\text{in }D_3\tag{4.20}$$

so that

$$\int_\Gamma\left((\bar{w}^3)_y\right)d\bar{s}=0;\;\Gamma=\partial D;\;D=\left(\xi,\eta\colon x<\xi<x+dx;\;y_2(\xi,t)<\eta<y_1(\xi,t)\right)\tag{4.21}$$

Since α_{k3} and β_{k3} are independent of y by their definition, we have

$$(\bar{w}^3)_y\bar{n}_{k3}=(w^3_n)_y\quad\text{on }S_{k3};\;k=1;2\tag{4.22}$$

**) Really this means that we consider the membrane surfaces as possessing specific rheological properties whereas inside that membrane only the body forces $\bar{R}^3$ of the resistance act.

Hence (4.21) yields

$$(w_n^3)_y)\, S_{13})_x|_{S_{13}} - (w_n^3)_y\, (S_{23})_x|_{S_{23}} = -(\hat{w}_x^1 - \hat{w}_x^2)_x \tag{4.23}$$

Here the equalities

$$w_x^3|_{S_{k3}} = w_x^k|_{S_{k3}} = \hat{w}_x^k; \qquad k=1, 2 \tag{4.24}$$

following from (2.28), (2.40) and (3.11) are taken into account.

Use now the approximations

$$(w_n^3)_y|_{S_{13}} = 2\, (w_n^1|_{S_{13}} - w)/(y_1 - y_2); \quad (w_n^3)_y|_{S_{23}} = 2\, (w - w_n^2|_{S_{23}})/(y_1 - y_2) \tag{4.25}$$

with an unknown w. By solving the system (4.23), (4.25) we get

$$\begin{aligned} (w_n^3)_n|_{S_{13}} &= \alpha_{13}\, (w_n^1)_x|_{S_{13}} + \beta_{13}\, ((S_{23})_x\, (f_2+f_3)+f_1)/((S_{13})_x+(S_{23})_x) \\ (w_n^3)_n|_{S_{23}} &= \alpha_{23}\, (w_n^2)_x|_{S_{23}} + \beta_{23}\, ((S_{13})_x\, (f_2+f_3)-f_1)/((S_{13})_x+(S_{23})_x) \end{aligned} \tag{4.26}$$

where

$$f_1 = (w_x^2 - w_x^1)_x; \quad f_2 = 2\, (w_n^1|_{S_{13}})/(y_1 - y_2); \quad f_3 = -2\, (w_n^2|_{S_{23}})/(y_1 - y_2) \tag{4.27}$$

We further have

$$\operatorname{div} \bar{w}^3|_{S_{k3}} = (\hat{w}_x^k)_x + (\beta_{k3}\, w_n^3 - \alpha_{k3}\, w_s^3)_y|_{S_{k3}} = 0 \tag{4.28}$$

which yields

$$(w_s^3)_y|_{S_{k3}} = (1/\alpha_{k3})\, (\hat{w}_x^k)_x + (\beta_{k3}/\alpha_{k3})\, (w_n^k)_y|_{S_{k3}} \tag{4.29}$$

Using this, conditions (2.28) of dynamical compatibility and (2.38) of symmetry, as approximations (3.20), which are valid not only for $\bar{v}^k$ but also for $\bar{w}^k$, we obtain, after some manipulations:

$$\begin{aligned} (w_s^3)_n|_{S_{k3}} = {} & (1/\alpha_{k3}\, \beta_{k3})\, (\hat{w}_x^k)_x + (1/\alpha_{k3})\, (w_n^3)_y|_{S_{k3}} + (\alpha_{k3}/\beta_{k3})\, \big(\beta_{k3}\, (\hat{w}_x^k/\beta_{k3} - \\ & - (\alpha_{k3}/\beta_{k3})\, w_n^k|_{S_{k3}})_x + (\alpha_{k3}/\beta_{k3})\, \big(\alpha_{k3}\, (\alpha_{k3}\, \hat{w}_x^k - w_n^k|_{S_{k3}})/(\beta_{k3}\, (y^k - y_k)\big)\big) \end{aligned} \tag{4.30}$$

Besides

$$(w_n^3)_s|_{S_{k3}} = (w_n^k)_s|_{S_{k3}} = \beta_{k3}\, (w_n^k)_x|_{S_{k3}} - \alpha_{k3}\, (\alpha_{k3}\, w_x^k - w_n^k|_{S_{k3}})/(y^k - y_k) \tag{4.31}$$

and

$$w_s^3|_{S_{k3}} = w_s^k|_{S_{k3}} = (1/\beta_{k3})\, w_x^k - (\alpha_{k3}/\beta_{k3})\, w_n^k|_{S_{k3}}\,. \tag{4.32}$$

Inserting (4.25), (4.26), (4.31) and (4.32) into (4.18) we express deformations e_{qr}^3, $q, r=n, s$, on S_{k3}, $k=1; 2$, through values determined within the cell and the intercellular space. Together with this we get the desired elimination of the lateral membrane from the equation of momentum transfer.

Consider, finally, equation (3.33) of the convective-diffusion mass transfer through the lateral membrane. Using approximation (3.15) and the assumption 5 in the page 61 we obtain

$$\begin{aligned} J_{jn}^3|_{S_{12}} &= ((S_{23})_x\, (f_{1j}+f_{2j}) + \beta_{23}\, f_{3j})/(\beta_{13}\, (S_{23})_x + \beta_{23}\, (S_{13})_x) \\ J_{jn}^3|_{S_{23}} &= ((S_{13})_x\, (f_{1j}+f_{2j}) - \beta_{13}\, f_{3j})/(\beta_{13}\, (S_{23})_x + \beta_{23}\, (S_{13})_x) \end{aligned} \tag{4.33}$$

where

$$\begin{aligned} f_{1j}&=-2\,(\kappa_j\,D_j^3\,\hat{c}_j^1+L_j^3\,p^3|_{S_{13}})/(y_1-y_2)\\ f_{2j}&=2\,(\kappa_j\,D_j^3\,\hat{c}_j^2+L_j^3\,p^3|_{S_{23}})/(y_1-y_2)\end{aligned}\qquad j=1,2,\ldots,n \tag{4.34}$$

and

$$\begin{aligned} f_{3j}&=(S_{13})_x\,J_{jn}^3|_{S_{13}}-(S_{23})_x\,J_{jn}^3|_{S_{23}}=\sum_1^3 f_{3j}^k;\quad j=1,2,\ldots,n;\\ f_{3j}^1&=(\kappa_j/2)\,((y_1-y_2)\,(\hat{c}_j^1+\hat{c}_j^2)_t)-\kappa_j\,(\hat{c}_j^1\,y_{1t}+\hat{c}_j^2\,y_{2t});\\ f_{3j}^2&=(\kappa_j/2)\,((y_1-y_2)\,(\hat{c}_j^1\,\hat{w}_x^1+\hat{c}_j^2\,\hat{w}_x^2)_x;\\ f_{3j}^3&=\kappa_j\,(c_j^1\,w_n^1|_{S_{13}}\,(S_{13})_x-c_j^2\,w_n^2|_{S_{23}}\,(S_{23})_x)\,.\end{aligned} \tag{4.35}$$

Recall that

$$-p^3|_{S_{k3}}=\Pi_{nn}^k|_{S_{k3}}+(-1)^{k+1}\,\sigma_k\,K_k-\tau_{nn}^3|_{S_{k3}};\quad k=1;2 \tag{4.36}$$

where $\tau_{nn}^3|_{S_{k3}}$ are determined by (4.17), (4.18), (4.26) and (4.30)–(4.32).

Note that equations (2.27) and (2.11)–(2.14) yield

$$\left(1-\sum_1^n \Omega_j\,\kappa_j\,\hat{c}_n^k\right)((n_{k3})_t-w_n^k|_{S_{k3}})=-\sum_1^n \Omega_j\,J_{jn}^k|_{S_{k3}};\quad k=1;2 \tag{4.37}$$

These equations serve for determinig the boundaries S_{k3}, $k=1;2$, of the lateral membrane.

Rather lengthy computations show that (4.32), (3.20) and (2.27)–(2.30) imply

$$\begin{aligned} &z_t+1/2\,(\hat{w}_x^1+\hat{w}_x^2)\,z_x+1/2\,(\hat{w}_x^1+\hat{w}_x^2)_x\,z+\\ &\qquad+\sum_1^n \Omega_j\,\kappa_j\,(\hat{c}_j^2-\hat{c}_j^1)\,(y_{2t}+((A-y_2)\,\hat{w}_x^1)_x)=0\,.\end{aligned} \tag{4.38}$$

At the same time equation (4.37) may be rewritten for $k=2$ as

$$y_{2t}+(y_2\,w_x^2)_x=-\sum_1^n \Omega_j\,J_{jn}^3\,(S_{23})_x\,. \tag{4.39}$$

Let us now simplify this equation using data on the magnitude of values we deal with (see Appendix 2). Note, first of all, that f_{3j}, entering expressions $J_{jn}^3|_{S_{23}}$, are at least three order smaller than f_{1j} and f_{fj}, so that (4.33_2) may be replaced by

$$J_{jn}^3|_{S_{23}}=A\,(f_{1j}+f_{2j}) \tag{4.10}$$

where

$$A=\beta_{23}\,(S_{13})_x/(\beta_{13}\,(S_{23})_x+\beta_{23}\,(S_{13})_x) \tag{4.41}$$

It is easy to see that up to the terms of the higher order of smallness

$$A=1/2\,(1-2\Delta\,(x,t)\,K_2\,(x,t)) \tag{4.42}$$

This gives (see (4.27))

$$y_{2t}+(w_x^2\, y_2)_x=(1/2\, \Delta\,(x,t))\,(1+2\Delta\,(x,t)\,K_2\,(x,t))\times$$
$$\times\sum_1^n (\kappa_j\, D_j^3\,(\hat{c}_j^2-\hat{c}_j^1)+(L_j^3\, p^3|_{S_{23}}-L_j^3\, p^3|_{S_{13}}))\,\Omega_j \qquad (4.43)$$

Bending, shrinking or swelling imply the change of permeability of membranes, as it seen from the usual definition

$$p_j^k=(1/2\Delta)\,\kappa_j\,\Omega_j\,D_j^k;\quad j=1,2,\ldots,n;\ k=0,3,4. \qquad (4.44)$$

We, however, disregard this effect since it is seen from (4.43) that the small changes of Δ (and these changes are definitely small) yield a small contribution into the shape and location of the boundary S_{23} and therefore into the concentrations, velocities and stresses within the system under consideration*). Thus we approximately take in (4.43)

$$\Delta\,(x,t)=\Delta=\text{const}. \qquad (4.45)$$

Denote**)

$$q^k=(1/2\Delta)\sum_1^n \Omega_j\, L_j^k \qquad (4.46)$$

and use the approximation

$$K_2=y_{2xx} \qquad (4.47)$$

Then (4.38) turns into

$$y_{2t}+(w_x^2\, y_2)_x=(1+2\Delta y_{2xx})\Bigg(\sum_1^n p_j^3\,(c_j^2-c_j^1)+q^3\,(p^3|_{S_{23}}-p^3|_{S_{13}}) \qquad (4.48)$$

from where the mathematical nature of the problem becomes more lucid***).

5. Concluding remarks

We have to make the following remarks.

1. The one-dimensional formalism of the theory above is essentially based on the use of equalities

$$\hat{c}_j^k=c_j^k|_{S_{k3}};\quad \hat{w}_x^k=w_x^k|_{S_{k3}};\quad j=1,2,\ldots,n;\ k=1,2. \qquad (5.1)$$

---

*) It is true if the state of the system is far from the — possible in principle — collapse of the cell or the intercellular space. We, however, do not deal with such a situation, requiring a special consideration.

**) Strictly speaking L_j^k are linear functions of concentrations c_j^k (see the footnote in page 51). Hence q^k are different at different boundaries of the membranes D_k, $k=0,3,4$. Recall that we agree to disregard this effect, considering coefficients of barodiffusion as constant (see page 57)

***) This question is shortly discussed in the next section.

These equalities are motivated by the narrowness of regions D_1 and D_2. In doing this we ignore the existence of boundary layers separating the bulk of these regions from the membrane boundaries. Such an ignorance seems to be quite reasonable, when one deals with concentration fields, since the time of relaxation of these fields in y direction is at least two order smaller than that in x direction. However it is not so clear when we deal with the field of the average volume velocity. The more rigorous theory has to take this into account.

2. Evidently

$$\left|p^3|_{S_{23}} - p^3|_{S_{13}}\right| < |p^{-1,0} - p^{5,0}| \tag{5.2}$$

Assume that

$$\sum_1^n p_j^3 \left(c_j^2(x,0) - c_j^1(x,0)\right) + q^3 (p^{-1,0} - p^{5,0})(-1)^s \tag{5.3}$$

changes its sign within the region $0<x<l(0)$ for $s=0$ or $s=1$. Then equation (4.43) is of the parabolic type with the time reversed in some subregion of the region $0<x<l(t)$ bounded by a free line along which that equation degenerates. Such a situation had been studied earlier for a model problem, formulated for a pure diffusion approximation of the theory*) [17]. One has to observe, however, that the coefficient at y_{2xx} in this equation has to be considered as a small functional parameter. This means that, perhaps, the approach based on the use of methods of the theory of singular perturbations would be more appropriate than that used in the mentioned paper.

Appendix 1

A. Table of notations

D_{-1}, D_5 — the basal and apical unstirred layers.
D_0, D_3, D_4 — the basal, lateral and apical membranes.
D_1, D_2 — the cell and the intercellular space.
2Δ — the thickness of the membranes.
x, y — Cartesian coordinates, t — the time.
$l(t)$ the length of the cell. $x=l(t)$ — the common boundary of the cell and of the apical membrane.
$L_0, L_1-l(t)$ — the basal and apical lengths.
A — the with of the system (that of the unstirred layers).
h — the thickness of the tight junction.
H — the length of the tight junction.

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*) This approximation consists in the neglect of convection, induced by a jump of diffusion fluxes through deformable membrane.

$S_{k3}=\{x, y: 0\leqslant x\leqslant l(t);\ y=y_k(x, t)\}$; $k=1; 2$, — the boundaries of the lateral membrane common with those of the cell ($k=1$) and of the intercellular space ($k=2$)

a_j, $j=1, 2, \ldots, n$ — liquid incompressible components penetrating trough all the membrane.

a_0 — the impermeant of solutions D_k, $k=-1, 1, 2, 5$.

a_{n+1} — the main membrane constituent, nonpenetrating into solutions D_k, $k=-1, 1, 2, 5$.

c_j^k — molar concentration of a_j in D_k; $m_k\leqslant j\leqslant n_k$;

$m_k=0$ for $k=-1, 1, 2, 5$; $m_k=1$ for $k=0, 3, 4$;

$n_k=n$ for $k=-1, 1, 2, 5$; $n_k=n+1$ for $k=0, 3, 4$.

Ω_j — the partial molar volume of a_j, $j=0, 1, \ldots, n+1$.

ρ_j^k — the density of a_j within the solution D_k; $k=-1, 0, \ldots, 5$.

ρ^k — the density of the solution D_k; $k=-1, \ldots, 5$.

κ_j — the coefficient of distribution of a_j between solution D_k and membranes D_m; $k=-1, 1, 2, 5$; $m=0, 3, 4$; $j=1, 2, \ldots, n$.

$\bar{v}_j^k$ — the vector of velocity of motion of a_j within D_k in a laboratory coordinate system; $m_k\leqslant j\leqslant n_k$; $k=-1, 0, \ldots, 5$.

$\bar{w}^k$ — the average volume velocity in D_k.

$\bar{v}^k$ — the center of mass velocity in D_k.

$\bar{J}_j^k$ — the diffusion flux of a_j within D_k in the system of the average volume velocity.

$\bar{J}_j^{k*}$ — the diffusion flux of a_j in the center of mass system.

L_j^k — the coefficient of barodiffusion of a_j within D_k; $k=0, 3, 4$.

D_j^k — the coefficient of diffusion of a_j within D_k; $k=-1, 0, \ldots, 5$.

p^k — the pressure within D_k; $k=-1, 0, \ldots, 5$.

$\tilde{\Pi}^k$ — the stress tensor within D_k; $k=-1, 0, \ldots, 5$.

$\tilde{\tau}^k$ — the deviator of $\tilde{\Pi}^k$.

$\tilde{e}^k$ — the strain velocity tensor within D_k.

$\tilde{\varepsilon}^k$ — the strain tensor within D_k.

a, b, c, d — coefficients of the equation of the rheological state of the lateral membrane.

λ^k — the frictional coefficient within D_k; $k=0, 3, 4$.

$\hat{f}^k$ — the average value of any function f defined within D_k, the averaging being made over crossection $x=\text{const.}$ of D_k; $k=-1, 0, \ldots, 5$.

p_j^k — the coefficient of permeability of a_j through the membrane D_k; $k=0, 3, 4$, $j=1, 2, \ldots, n$.

q^3 — the coefficient at the right hand side of the equation (4.43).

σ_k — the surface tension on the interface S_{k3} of the lateral membrane and solutions D_k; $k=1; 2$.

K_k — the curvature of S_{k3}, $k=1; 2$.

μ_k — the coefficient of dynamical viscosity of solutions D_k, $k=-1, 1, 2, 5$.

$\bar{n}_{k3}^0, \bar{s}_{k3}^0$ — the unit normal and tangential vectors at S_{k3}; $k=1; 2$.

$\bar{i}, \bar{j}$ — the basis vectors of the Cartesian coordinate system (x, y).

α_{k3}, β_{k3} — the direction cosines of $\bar{n}^0_{k3}$ ($\bar{n}^0_{k3}$ are directed toward D_1).

f_r — the r-th component of any vector $\bar{f}$; $r=x, y, n, s$.

$(f)_{,r}, f_{kr}$ — the partial derivative of any f in r-th direction; $r=x, y, n, s$; $k=-1, 0, \ldots, 5$.

$\dot{f}$ — the ordinary derivative of any f.

B. Scaling

All values enumerated in the table of notations are dimensional ones. Let us mark them by the superscript * and introduce, after this, dimensionless values by setting

$$\begin{aligned}
&x=x^*/L^*; \quad y=y^*/L^*; \quad t=t^*/T^*;\\
&A=A^*/L^*; \quad y_k(x,t)=y_k^*(x^*,t^*)/L^*, k=1;2; \quad l(t)=l^*(t^*);\\
&\Delta=\Delta^*/L^*; \quad h=h^*/L^*; \quad H=H^*/L^*; \quad L_k=L_k^*/L^*, \quad k=0;1;\\
&c_j^k=c_j^{k*}/C^*; \quad m_k \leqslant j \leqslant n_k; \quad k=-1, 0, \ldots, 5;\\
&\bar{v}_j^k=\bar{v}_j^{k*}/W^*; \quad \text{—,,—,,—,,—,,—,,—,,—,,—}\\
&\rho_j^k=\rho_j^{k*}/\rho^*; \quad \text{—,,—,,—,,—,,—,,—,,—,,—}\\
&\bar{J}_j^k=\bar{J}_j^{k*}/J^*; \quad \bar{J}_j^{k*}=\bar{J}_j^{k**}/J^{**} \ \text{—,,—,,—,,—}\\
&\bar{v}^k=\bar{v}^{k*}/W^*; \quad \bar{w}^k=\bar{w}^k/W^*; \quad \rho^k=\rho^{k*}/\rho^*; \quad M_j=M_j^*/M^*;\\
&\tilde{\Pi}^k=\tilde{\Pi}^k/P^*; \quad \overline{\Pi}_n^k=\overline{\Pi}_n^{k*}/P^*; \quad \overline{\Pi}_s^{k*}=\overline{\Pi}_s^{k*}/P^*; \quad p^k=p^{k*}/P^*; \quad \sigma_k=\sigma_k^*/\sigma^*\\
&\tilde{e}^k=\tilde{e}^{k*}/e^*; \quad \tilde{\varepsilon}^k=\tilde{\varepsilon}^{k*}/\tilde{\varepsilon}^*; \quad \bar{R}^k=\bar{R}^{k*}/R^*, \quad \Omega_j=\Omega_j^*/\Omega^*
\end{aligned} \tag{A1.1}$$

where*)

$$\begin{aligned}
&L^*=L_0^*+L_1^*; \quad T^*=L^{*2}/D^*; \quad D^*=\max_k \max_j D_j^k;\\
&\qquad\qquad\qquad\qquad\qquad k=-1, 0, \ldots, 5; \quad m_k \leqslant j \leqslant n_k.\\
&C^*=\max \max (c_{j0}^{k*}, c_j^{m0*}); \ m_k \leqslant j \leqslant n_k; \ k=-1, 0, \ldots, 5; \ m=-1; 5.\\
&W^*=L^*/T^*; \ P^*=\max(p^{-10*}, p^{50*}); \ R^*=P^*/L^*; \ \sigma^*=P^* L^*;\\
&e^*=1/T^*; \ \varepsilon^*=1; \ J^*=C^* W^*; \ J^{**}=\rho^* W^*; \ \rho^*=1^*;\\
&\qquad\qquad\qquad\qquad\qquad M^*=1^*; \ \Omega^*=1^*.
\end{aligned} \tag{A1.2}$$

Then all the equations of the main text remain unchanged, if there are introduced dimensionless coefficients, defined by the following quantities

$$\begin{aligned}
&D_j^k=D_j^{k*}/D^*; \quad L_j^k=L_j^{k*} P^*/(L^* J^*); \quad \mu_k=\mu_k^* W^*/(P^* L^*);\\
&a=a^* T^*; \quad b=b^* e^*/P^*; \quad c=c^* e^* T^*/P^*; \quad d=d^* T^*/P^*.
\end{aligned} \tag{A1.3}$$

---

*) We refer to the subscript n for water — the solvent of all the solutions D_k. One of p^{k0}, $k=-1; 5$, may be equal to zero. Hence the characteristic pressure P^* is really taken equal to the maximum of the pressure drop.

Appendix 2

Numerical data

The range of parameters and input data, accepted below, is chosen as follows.

1. Geometrical values (A2.1) are taken accordingly to data of [19] except for the length H^* of the tight junction, not indicated there. As it is seen from the electron micrographs shown in [10] H^* may exceed half of the cell length. The accepted value $H^* = l_0/3$ may therefore be considered as representative.

2. Non-electrolytes a_j, $j = 1, 2, \ldots, n$ may be characterized, for example, by the Table 1 of [4].

3. The characteristic value C^* of molar concentrations is taken in accordance with the ones used in experiments reported in [19], [23], [25].

4. The characteristic pressure drop P^* is taken in the accordance with the respective experiments, described in [23].

5. Coefficients of diffusion, distribution and permeability are estimated as in [4] where the motivation of the respective choice is given.

6. Coefficients of barodiffusion are taken with the use of the chosen values of concentrations with the reference to the footnote in page 51.

7. Dynamical viscosity of solutions, filling regions D_k, $k = -1, 1, 2, 5$; are taken in the interval including the most representative values of the reference [22] and those mentioned in [12].

8. Rheological parameters $a^*, \ldots, c^*$ of the lateral membrane are unknown. They were estimated from above as those which may be taken for high-elastic polymers with the reference to [1] and for b^* — to [22] *)

9. Values k^*, $k = 0, 3, 4$, of the coefficients of filtration are taken of the order, found in [12], of the characteristic surface tension as in [22] p. 482.

Thus we accept the following ranges of numerical data:

$$\left.\begin{array}{l} L_0^* \cong 100\ \mu;\ L_1 \cong 800\ \mu;\ l_0^* \cong 30\ \mu;\ A \cong 3\ \mu; \\ \varDelta^* \cong 50\ \text{Å};\ h^* = 5\ \text{Å};\ H^* \cong 10\ \mu;\ 5\ \text{Å} \leqslant y_2(x, 0) \leqslant 300\ \text{Å}; \end{array}\right\} \tag{A2.1}$$

$$\left.\begin{array}{l} C^* = 400\ \text{mMol}/L;\ \Omega_j = 18\text{–}200\ \text{cm}^3/\text{Mol};\ \rho^* = 1\ \text{g/cm}^3; \\ M_j^* = 18\text{–}150\ \text{g/Mol}; \end{array}\right\} \tag{A2.2}$$

$$P^* = 30\,\text{cmH}_{20};\ \lambda^{k*} = 10^9 - 10^{10}\,\text{g/cm}^3\,\text{sec};\ L_j^{k*} = 10^{-19} - 10^{-18}\,\text{Mol.sec/g} \tag{A2.3}$$

$$a^* = 10^6 - 2 \cdot 10^7\ 1/\text{sec};\ b^* = 1\text{–}10\ \text{P};\ c^* = 10^6 - 2 \cdot 10^7\ \text{g/cm sec}^2. \tag{A2.4}$$

$$p_j^{k*} = 10^{-4} - 10^{-6}\ \text{cm/sec};\ D^* = 10^{-5}\ \text{cm}^2/\text{sec};\ \kappa_j = 10^{-4} - 10^{-5}. \tag{A2.5}$$

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*) We restrict ourself with estimation of rheological parameters of the lateral membrane D_3, considering it as a Maxwell fluid.

Thus parameters (A1.2) and (A1.3) are chosen in the range

$$\begin{gathered} L^*\cong 10^{-1}\ \text{cm};\quad T^*\cong 10^3\ \text{sec};\quad W^*\cong 10^{-4}\ \text{cm/sec}; \\ P^*\cong 3\cdot 10^4\ \text{g/cm}\cdot\text{sec}^2;\quad R^*\cong 3\cdot 10^5\ \text{g/cm}^2\text{sec}^2;\quad \sigma^*\cong 1\ \text{g/sec}^2 \\ e^*\cong 10^{-3}\ 1/\text{sec};\quad J^*\cong 10^{-8}\ \text{Mol/cm}^2\text{sec};\quad J^{**}\cong 10^{-4}\ \text{g}\cdot\text{cm/sec} \end{gathered} \tag{A2.6}$$

and respectively

$$\begin{gathered} D_j^k\sim 1;\quad L_j^k\sim 10^{-5};\quad \mu_k\sim 10^{-7};\quad \lambda^k\sim 3 \\ p_j^k\sim 10^{-2}-10^{-3};\quad q^k\sim 10^{-3}-10^{-4} \end{gathered} \tag{A2.7}$$

Besides that, all values subject to determination are of the order of one.

Appendix 3

Collection of all equations corresponding to the case of bicomponent solutions: water+an impermeant.

It is more convenient, dealing with bicomponent solutions, to introduce the impermeant concentrations into all the equations instead of that of water.

Below we use the following simplified notations:

$$\begin{aligned} &u_k=\hat{c}_0^k;\quad k=-1,1,2,5. \\ &p_k=\hat{p}^k;\quad k=-1,1,2,5. \\ &p^k=p^3|_{S_{k3}};\quad k=1;2. \\ &y=y_2(x,t); \\ &v_k=\hat{w}_x^k;\quad k=-1,1,2,5. \\ &w_k=w_n^k|_{S_{k3}};\quad k=1;2. \\ &J_k=J_{0x}^k;\quad k=-1,1,2,5. \\ &J^k=J_{0n}^k|_{S_{k3}};\quad k=1;2. \\ &p_k^0=p_1^k;\quad k=0,3,4. \\ &q_k=q_1^k;\quad k=0,3,4. \end{aligned} \tag{A3.1}$$

All other notations coincide with those of Appendix 1. All values, entering the right hand side of (A3.1) are defined in Appendix 1.

Equations below are written in approximations accepted in the main text. In particular we take everywhere

$$(S_{k3})_x=1;\quad \alpha_{k3}=-y_x;\quad \beta_{k3}=1;\quad K_k=y_{xx};\quad y_1-y_2=2\Delta=\text{const}^{*)} \tag{A3.2}$$

The collection of all governing equations is as follows:

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*) We recall that $z(x,t)=y_1(x,t)-y_2(x,t)$ has te be calculated after $y(x,t)$ and all the fields of the interest are found with the use of these approximations.

A. Equation of the convective-diffusion transfer in D_k; $k=-1.1,\ 2.5$

$$u_{kt}=u_{kxx}+F_k\,(x,\,t:v_k,\,y,\,y_x,\,u_{kx},\,J^k);\qquad k=-1,\,1,\,2,\,5 \tag{A3.3}$$

where

$$F_1=-u_{1x}\,(v_1+y_x/(A-y))-J^1/(A-y);\qquad F_2=u_{2x}\,(y_x/y-v_2)+J^2/y;$$
$$0<x<l\,(t), \tag{A3.4}$$
$$F_k=-v_k\,u_{kx};\qquad -L_0<x<0\quad \text{for } k=-1;\ l\,(t)<x<L_1\quad \text{for } k=5,$$

and

$$\begin{aligned}&J_{-1}+u_{-1}\,v_{-1}=(y/A)\,(J_2+u_2\,v_2);\quad J_1+u_1\,v_1=0 \text{ at } x=0\\ &J_5+u_5\,V_5=(y/A)\,(J_2+V_2);\ J_1+u_1\,V_1=0;\ V_1=v_1-\dot{l}\,(t);\ \text{at } x=l\,(t)\end{aligned} \tag{A3.5$_1$}$$

$$\begin{aligned}u_{-1}=(1/A)\,\big((A-y)\,&\big(u_1\,(1-\kappa_1\,v_1/p_1^0)+yu_2\big)+\\ &+(A-y)\,(1-\kappa_1+L_1^0\,\lambda^0\,\Omega_1)\,v_1/(\Omega_0\,p_1^0)\big) \text{ at } x=0\\ u_5=(1/A)\,\big((A-y)\,&\big(u_1\,(1-\kappa_1\,V_1/p_1^4)+yu_2\big)+\\ &+(A-y)\,(1-\kappa_1+L_1^4\,\lambda^4\,\Omega_1)\,V_1/\Omega_0\,p_1^4\big) \text{ at } x=l\,(t)\end{aligned} \tag{A3.5$_2$}$$

$$u_{-1}=u^0_{-1}\,(t) \text{ at } x=-L_0;\qquad u_5=u_5^0\,(t) \text{ at } x=L_1; \tag{A3.6}$$

$$u_k\,(x,\,0)=u_{k0}\,(x);\qquad k=-1,\,1,\,2,\,5 \tag{A3.7}$$

Equations (A3.3) and (A3.5) are corollaries of equations (3.30) of the convective-diffusion transfer and continuity as well as identities (2.11), (2.16).

B. Equations of continuity

$$\begin{aligned}&v_k\,(x,\,t)=(1/A)\,\big((A-y)\,v_1\,(x_k,\,t)+yv_2\,(x_k,\,t)\big);\qquad x\in D^k;\ k=-1;\,5.\\ &D^{-1}=(x:\ -L_0<x<0);\qquad D^5=\big(x:\,l\,(t)<x<L_1\big).\end{aligned} \tag{A3.8}$$

$$\left.\begin{aligned}&((A-y)\,v_1)_x-w_1=0\\ &(yv_2)_x+w_2=0\qquad 0<x<l\,(t)\\ &w_1-w_2+\Delta\,(v_1-v_2)=0\end{aligned}\right\} \tag{A3.9}$$

C. Equations of momentum transfer solved with respect to p_k; $k=-1,\ 1.2$

Equations of momentum transfer are written below in the form solved with respect to pressures p_k, which may be obtained by means of simple but rather lengthy computations. We have

$$p_1=\hat{\tau}^1_{xx}+X_0+\int\limits_0^x h_1\,(s,\,t)\,ds;\qquad p_2=\hat{\tau}^2_{xx}+Y_0+\int\limits_0^x h_2\,(s,\,t)\,ds \tag{A3.10$_1$}$$

or

$$p_1=\hat{\tau}^1_{xx}+X_1-\int_x^{l(t)} h_1(s,t)\,ds; \qquad p_2=\hat{\tau}^2_{xx}+Y_1-\int_x^{l(t)} h_2(s,t)\,ds \qquad (\mathrm{A}3.10_2)$$

$$\left.\begin{aligned}
&X_0=\big(b_0\,(a_1 H_1+b_1 H_2)+c_0 b_1-c_1 b_0\big)/\rho; && x=0;\\
&X_1=\big(b_1\,(a_0 H_1+b_0 H_2)+c_0 b_1-c_1 b_0\big)/\rho; && x=l(t);\\
&Y_0=(c_0 a_0+c_1 a_1)-a_0\,(a_1 H_1+b_1 H_2)/\rho; && x=0;\\
&Y_1=(c_1 a_0-c_0 a_1)-a_1\,(a_0 H_1+b_0 H_2)/\rho; && x=l(t);
\end{aligned}\right\} \qquad (\mathrm{A}3.11_1)$$

$$\left.\begin{aligned}
&H_k=\int_0^{l(t)} h_k(s,t)\,ds; \quad k=1;2;\\
&h_1=\big(1/(A-y)\big)\big(y_x\,(\tau^1_{xx}-\tau^1_{nn})+\tau^1_{ns}\big);\\
&h_2=(1/y)\big(y_x\,(\tau^2_{xx}-\tau^2_{nn})+\tau^2_{ns}\big);
\end{aligned}\right\} \qquad (\mathrm{A}3.11_2)$$

$$\left.\begin{aligned}
&c_0=p_{-1}-\tau^{-1}_{xx}-(2/A)\,\Delta\lambda^0\,v_1(0,t);\\
&c_1=p_5-\tau^5_{xx}-(2/A)\,\Delta\lambda^4\,v_1\big(l(t),t\big);
\end{aligned}\right\} \qquad (\mathrm{A}3.11_3)$$

$$\left.\begin{aligned}
&a_0=1-y(0,t)/A; \quad a_1=1-y\big(l(t),t\big)/A;\\
&b_0=y(0,t)/A; \quad b_1=y\big(l(t),t\big)/A;\\
&\rho=a_0 b_1-a_1 b_0=(1/\mathrm{A})\big(y\big(l(t),t\big)-y(0,t)\big)
\end{aligned}\right\} \qquad (\mathrm{A}3.11_4)$$

and

$$\left.\begin{aligned}
&\hat{\tau}^k_{xx}=(2/3)\,\eta_k\big(-J_k+(y^k-y)^{-1}(J^k+y_x J_{kx})\big)+2\,(\mu_k v_k+\eta_k J_k)_x;\\
&\hat{\tau}^k_{xy}=1/2\,(\mu_k w_k+\eta_k J^k)_x+1/2\,(\mu_k v_k+\eta_k J_k)\big(y_{xx}+y_x/(y^k-y)\big);\\
&\hat{\tau}^k_{yy}=-(2/3)\,\eta_k J_{kx}-(y^k-y)^{-1}\big((4/3)\,\eta_k J^k+2\mu_k w_k+\\
&\qquad\qquad\qquad\qquad +\big((4/3)\,\eta_k J_k+2\mu_k v_k\big)\,y_x\big);
\end{aligned}\right\} \qquad (\mathrm{A}3.12_1)$$

$$\left.\begin{aligned}
&\tau^k_{nn}=\mu_k\big(2\,(w_k)_n-(2/3)\,(w^k)_s\big);\\
&\tau^k_{ns}=\mu_k\big(2\,(w^k)_s+(w^k)_n+y_{xx}\,w^k\big); \quad k=1;2.\\
&\tau^k_{ss}=\mu_k\Big(2\,(w^k)_s+2y_{xx}\,w_k-\big(2/3\,\big((w_k)_n+(w^k)_s+y_{xx}\,w_k\big)\big)\Big);
\end{aligned}\right\} \qquad (\mathrm{A}3.12_2)$$

$$\begin{aligned}
&(w_k)_n=(v_k-w_k)/(y^k-y); \quad (w^k)_n=(v_k-w^k)/(y^k-y);\\
&w^k=v_k+y_x\,w_k; \quad (w^k)_s=(w^k)_n+y_x\,(w^k)_x; \quad k=1;2.
\end{aligned} \qquad (\mathrm{A}3.12_3)$$

$$\begin{aligned}
&(p^k-\tau^k_{xx})_x=0; \quad x\in D^k\\
&\hat{\tau}^k_{xx}=2\mu_k J_{kx}; \quad k=-1;5
\end{aligned} \qquad (\mathrm{A}3.12_4)$$

$$\eta_k=(\mu_k/\rho^k)\,(M_0-\mathrm{M}_1\,\Omega_0/\Omega_1); \quad J_k=-u_{kx}; \quad k=-1,1,2,5. \qquad (\mathrm{A}3.12_5)$$

D. Equation determining the length $l(t)$ of the cell*)

$$\dot{l}(t)=v_1-(1/u_1)\,u_{1x} \quad \text{at } x=l(t) \tag{A3.13$_1$}$$

$$l(0)=l_0>0 \tag{A3.13$_2$}$$

E. Equation determing the lateral boundary $y=y(x,t)$ of the intercellular space

$$\begin{aligned} &y_t+(v_2\,y)_x=(1\leqslant 2\Delta y_{xx})\,(p\,(u_1-u_2)+q\,(p^2-p^1)); \quad 0<x<l(t)-H;\\ &y(x,0)=y_0(x); \quad 0<x<l_0; \quad y(x,t)=h \quad \text{for } l(t)-H<x<l(t) \end{aligned} \tag{A3.14}$$

where

$$p=\kappa_1\,\Omega_0\,D_1^3/2\Delta; \qquad q=\Omega_1\,L_1^3/2 \tag{A3.15}$$

$$p^k=p_k-\tau_{nn}^k+\tau_{nn}^3|_{S_{k3}}+(-1)^k\,\sigma_k\,y_{xx} \tag{A3.16}$$

and $\tau_{nn}^3|_{S_{k3}}$ are determined by (A3.19)–(A3.21).

F. Equations determining the thickness of the lateral membrane

$$z_t+1/2\,(v_1+v_2)\,z_x+1/2\,(v_1+v_2)_x z+\omega\,(u_1-u_2)\,(y_t+((A-y)\,v_1)_x)=0 \tag{A3.17}$$

where

$$\omega=\Omega_0\,\kappa_1; \quad 0\leqslant x<l(t). \tag{A3.17*}$$

and

$$z(x,0)=2\Delta \tag{A3.18}$$

G. Equations determining stresses within the lateral membrane

$$\begin{aligned} &\tau_{pq}^3(x,t)|_{S_{k3}}=\tau_{pq}^3(x,0)|_{S_{k3}}\exp(-at)+be_{pq}^3(x,t)|_{S_{k3}}+\\ &\quad+\int_0^t \exp(-a\,(t-s))\,(ce_{pq}^3(x,s)|_{S_{k3}}+d\varepsilon^3(x,s)|_{S_{k3}})\,ds; \quad k=1;2;\\ &\varepsilon_{pq}^3(x,t)|_{S_{k3}}=\varepsilon_{pq}^3(x,0)|_{S_{k3}}+\int_0^t e_{pq}^3(x,s)|_{S_{k3}}\,ds; \quad p,q=n,s. \end{aligned} \tag{A3.19}$$

Here

$$\begin{aligned} &(w_n^3)_n|_{S_{k3}}=1/2\,(f_3+f_2+(-1)^{k+1}f_1); \quad k=1;2;\\ &f_1=(v_2-v_1)_x; \quad f_2=w_1/\Delta; \quad f_3=-w_2/\Delta; \end{aligned} \tag{A3.20}$$

$$\begin{aligned} &w_s^3|_{S_{k3}}=v_k+y_x\,w_k;\\ &(w_n^3)_s|_{S_{k3}}=w_{kx}-y_x\,w_k/(y^k-y);\\ &(w_s^3)_n|_{S_{k3}}=(1/y_x)\,(-v_{kx}-1/2\,(f_2+f_3+(-1)^{k+1}f_1))-y_x v_k+y_x w_k/(y^k-y);\\ &y^1=A; \quad y^2=0. \end{aligned} \tag{A3.21}$$

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*) Equation (A3.13$_1$) is written for the second time in order to emphasize its role.

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O osmotycznym przepływie konwekcyjno-dyfuzyjnym nieelektrolitów o dwóch długich komorach przedzielonych półprzepuszczalną błoną reologiczną

Zadanie brzegowe modelowania pasywnego przepływu wody przez płaską tkankę nabłonkową

W pracy sformułowano dwuwymiarowe zadanie brzegowe opisujące osmotyczny przepływ nieelektrolitów wzdłuż dwóch wąskich komór oddzielonych odkształcalną półprzepuszczalną błoną o dosyć ogólnych właściwościach reologicznych. Rozważania są prowadzone na konkretnym zadaniu, które powstało przy modelowaniu pasywnego przepływu wody przez płaską tkankę nabłonkową na podstawie danych z prac [19, 23, 25].

Об осмотическом диффузионном потоке двух неэлектролитов во внутри двух длинних камер разделенных мембраной диализатора

В работе рассмотрена двумерная краевая задача описывающая осмотический поток двух неэлектролитов вдоль двух длинних камер пределенных деформировальной мембраной диализатора. Представлен конкретный пример пассивного потока воды через плоскую элителейную ткань.