

**TABLE 3.5. Permeability of Phospholipid ( $\pm$  Sterol) Bilayers to Various Solutes and to Water, Corrected (Where the Permeability Coefficient P is High) for Effects of Unstirred Layers [see Stein, 1967]<sup>a</sup>**

Permeability coefficient ( $P/\text{ms}^{-1}$ ) of lipid bilayers to the undissociated form (HA) and the dissociated form ( $A^-$ ) of organic acids (N.D. = not determined)

Solute	$P_{HA}$	$P_{A^-}$	References
Formic acid	$1.0-1.1 \cdot 10^{-4}$	N.D.	Walter et al. [1982], Walter and Gutknecht [1984]
Acetic acid	$0.24-6.6 \cdot 10^{-5}$	N.D.	Deuticke et al. [1982], Walter and Gutknecht [1984]
Propionic acid	$2.6 \cdot 10^{-4}$	N.D.	Walter and Gutknecht [1984]
Butyric acid	$6.4-9.5 \cdot 10^{-4}$	N.D.	Deuticke et al. [1982], Walter et al. [1982], Walter and Gutknecht [1984]
Hexanoic acid	$1.1 \cdot 10^{-2}$	N.D.	Walter and Gutknecht [1984]
Lactic acid	$5.0 \cdot 10^{-7}$	N.D.	Deuticke et al. [1982]
Maleic acid	$4.0 \cdot 10^{-7}$	$4.0 \cdot 10^{-11}$	Prestegaard et al. [1979]
Benzoic acid	$5.5 \cdot 10^{-9}$	N.D.	Walter and Gutknecht [1984]
Salicylic acid	$1.0-7.7 \cdot 10^{-3}$	$1.0 \cdot 10^{-9}$	Gutknecht and Tosteson [1973], Walter and Gutknecht [1984]
Indoleacetic Acid	$3.4 \cdot 10^{-5}$	$1.0 \cdot 10^{-11}$	Gutknecht and Walter [1980]

Permeability coefficient ( $P/\text{m s}^{-1}$ ) of lipid bilayers to the unassociated form (B) and the associated form ( $BH^+$ ) of organic bases

Solute	$P_B$	$P_{BH^+}$	References
Histamine	$3.5 \cdot 10^{-7}$	very low	Gutknecht and Walter [1981a]
Theophylline	$2.9 \cdot 10^{-6}$	very low	Gutknecht and Walter [1981a]
Tryptamine	$1.8 \cdot 10^{-3}$	very low	Gutknecht and Walter [1981a]

Permeability coefficients ( $P/m\ s^{-1}$ ) of lipid bilayers to organic nonelectrolytes

Solute	P	Reference
Formamide	$7.8 \cdot 10^{-7}$	Poznansky et al. [1976]
Acetamide	$2.4 \cdot 10^{-7}$	Poznansky et al. [1976]
Propionamide	$6.1 \cdot 10^{-7}$	Poznansky et al. [1976]
Valeramide	$18.3 \cdot 10^{-7}$	Poznansky et al. [1976]
Urea	$0.6-4.0 \cdot 10^{-8}$	Vreeman [1966], Finkelstein [1976], Poznansky et al. [1976], Orbach and Finkelstein [1980]
Glycerol	$4.5-5.4 \cdot 10^{-8}$	Vreeman [1966], Orbach and Finkelstein [1980], Brown et al. [1982]
Glucose, sorbitol, mannitol	$10^{-12}$	Vreeman [1966], Wood et al. [1968]

Permeability coefficients ( $P/m\ s^{-1}$ ) of lipid bilayers to inorganic nonelectrolytes and weak acids

Solute	P	References
HOH, DOH, TOH	$0.57-2.2 \cdot 10^{-5}$	Finkelstein [1976], Orbach and Finkelstein [1980]
HCl, HSCN	$3 \cdot 10^{-2}$	Gutknecht and Walter [1981b, 1982]
HF, HNO <sub>3</sub>	$0.1-1.0 \cdot 10^{-6}$	Gutknecht and Walter [1981c]
B(OH) <sub>3</sub>	$1-4 \cdot 10^{-8}$	Raven [1980c], JAC Smith [personal communication]
Si(OH) <sub>4</sub>	$10^{-10}$	Raven [1983b]
CO <sub>2</sub>	$3.5 \cdot 10^{-3}$	Gutknecht et al. [1977]
HgCl <sub>2</sub>	$1.3 \cdot 10^{-4}$	Gutknecht [1981]

**TABLE 3.5. (Continued)**

Permeability coefficient ( $P/m\ s^{-1}$ ) of lipid bilayers to inorganic ions		
Solute	P	References
$H^+/OH^-$	0.3– $20 \cdot 10^{-6}$	Nichols and Deamer [1980], Nichols et al. [1980], Gould and Bell [1981], Pohl [1982], Elamrani and Blume [1983], Deamer and Nichols [1983]
$H^+$	0.5– $10 \cdot 10^{-11}$	Gutknecht and Walter [1981b], Cafiso and Hubbell [1981, 1983], Nozaki and Tanford [1981]
$OH^-$	$1.8 \cdot 10^{-11}$	Gutknecht and Walter [1981d]
$Li^+, Na^+, K^+, Rb^+,$ $Cs^+$	$2 \cdot 10^{-12}$	Pagano and Thompson [1968], Thompson and Henn [1970]
$F^-, Cl^-, NO_3^-,$ $HCO_3^-, SCN^-$	$1-5 \cdot 10^{-12}$	Pagano and Thompson [1968], Thompson and Henn [1970], Gutknecht and Walter [1981b,c, 1982], Gutknecht et al. [1977], Kaethner and Bangham [1977]

The disparities in the values for  $P_{H^+}$  ( $P_{OH^-}$ ) in the table may, in part, be related to transfer of  $H^+$  across the membrane as HCl [Gutknecht and Walter, 1981b]: However, this cannot explain all of the "high" values [Deamer and Nichols, 1983]. Deamer and Nicholls [1983] suggest that the low values of  $P_{H^+}$  obtained by Nozaki and Tanford [1981] are a result of the development of large diffusion potentials which decreased the driving force on  $H^+$  to a value substantially below the  $H^+$  activity difference which was used to compute  $P_{H^+}$ . Cafiso and Hubbell [1983] point out that the high values reported by Biege and Gould [1981] and Clement and Gould [1981] are probably a result of the presence of  $CHCl_3$  in their membranes.

<sup>a</sup>P is defined for a nonelectrolyte n by the equation

$$J_n = P_n \cdot (C_{n1} - C_{n2})$$

where  $J_n$  = flux of n ( $\text{mol m}^{-2} \text{s}^{-1}$ ) from phase 1 to phase 2.

$C_{n1}, C_{n2}$  = concentration of n ( $\text{mol m}^{-3}$ ) in phases 1, 2.

$P_n$  = permeability coefficient to n ( $\text{m s}^{-1}$ ).

P is defined for an electrolyte  $j^\pm$  by the equation

$$J_{j^\pm} = -P_{j^\pm} \cdot \frac{zF\psi_{12}/RT}{1 - \exp(zF\psi_{12}/RT)} (C_{j^\pm 1} - C_{j^\pm 2} \exp(zF\psi_{12}/RT))$$

where  $J_{j^\pm}$  = flux of  $j^\pm$  from phase 1 to phase 2 ( $\text{mol m}^{-2} \text{s}^{-1}$ ).

$z$  = algebraic charge on  $j^\pm$ .

$F$  = Faraday's constant ( $\text{J V}^{-1} \text{mol}^{-1}$ ).

$R$  = gas constant ( $\text{J mol}^{-1} \text{K}^{-1}$ ).

$T$  = temperature (K).

$\psi_{12}$  = electrical potential of phase 1 relative to phase 2 (V).

$C_{j^\pm 1}, C_{j^\pm 2}$  = concentration of  $j^\pm$  ( $\text{mol m}^{-3}$ ) in phases 1, 2.

$P_{j^\pm}$  = permeability coefficient to  $j^\pm$  ( $\text{m s}^{-1}$ ).