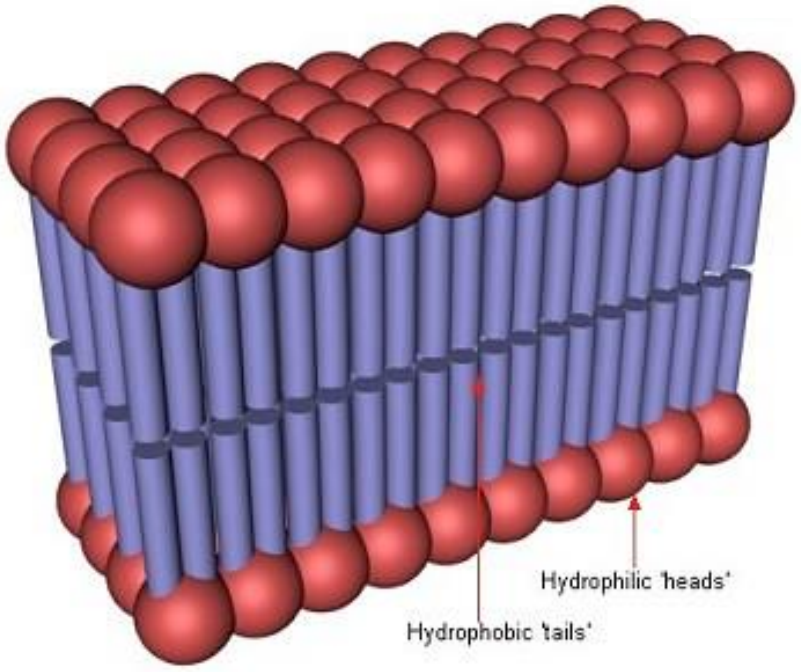
Struktura in dinamika bioloških membran

Stryer (9th), 12. poglavje
Voet (4th), 12. poglavje
Lodish (8th), 7. poglavje

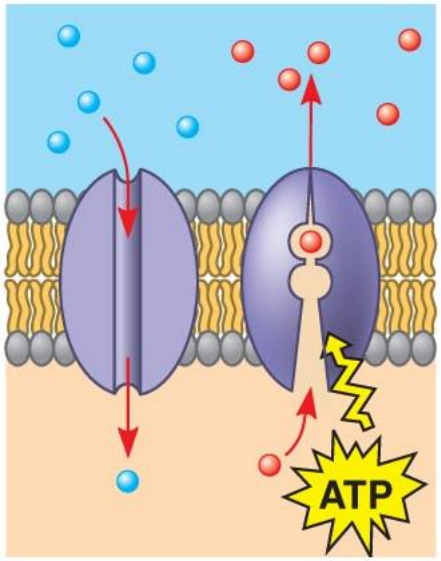


Pregled

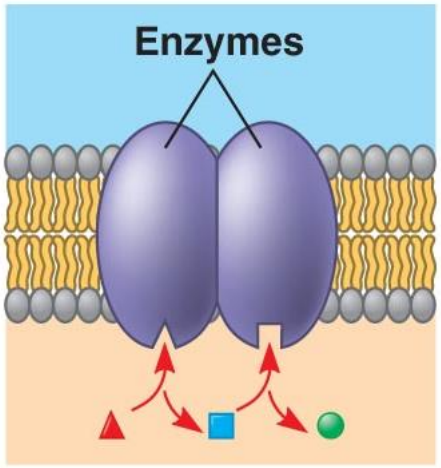
- Funkcije bioloških membran
- Lastnosti bioloških membran
- Sestava bioloških membran
- Membranski lipidi
- Membranski proteini

Funkcije bioloških membran

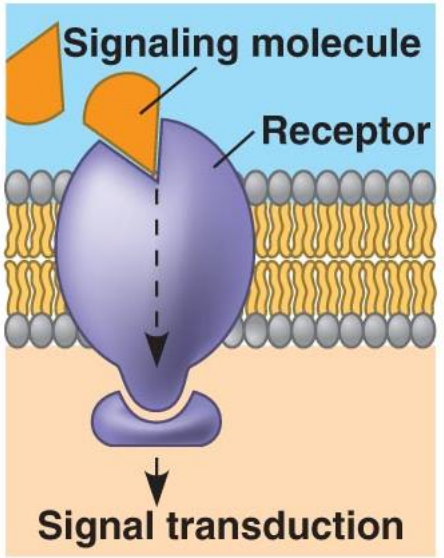
- (Selektivna) bariera za molekule.
- Energijska zaloga in pretvorbe.
- Prenos in modulacija signalov.
- Celični transport.
- Kompartimentizacija in akumulacija metabolitov.
- Posredovanje pri medceličnih interakcijah.
- Pomoč pri pomnoževanju celic (delitev).



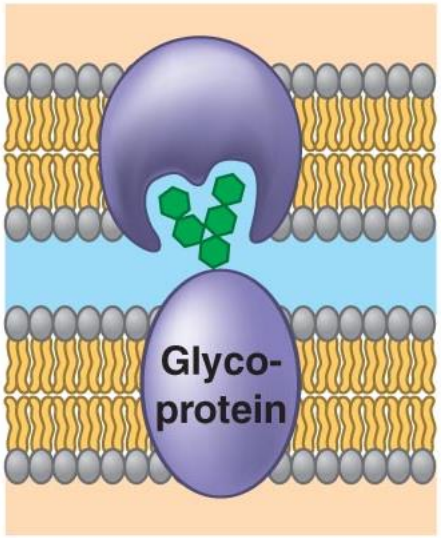
(a) Transport



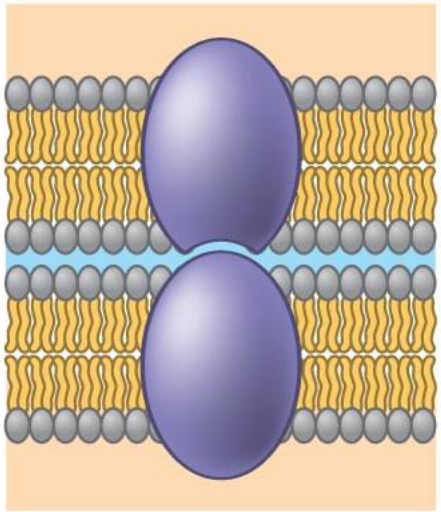
(b) Enzymatic activity



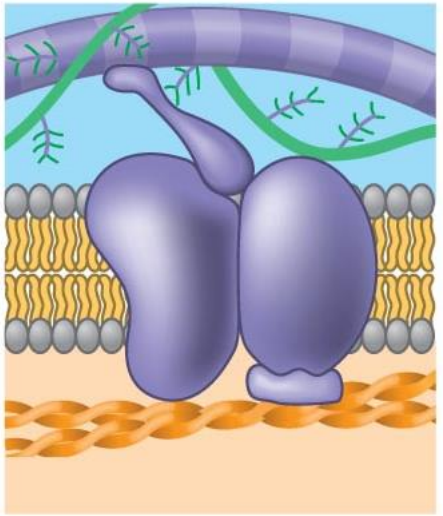
(c) Signal transduction



(d) Cell-cell recognition



(e) Intercellular joining



(f) Attachment to the cytoskeleton and extracellular matrix (ECM)

Lastnosti bioloških membran

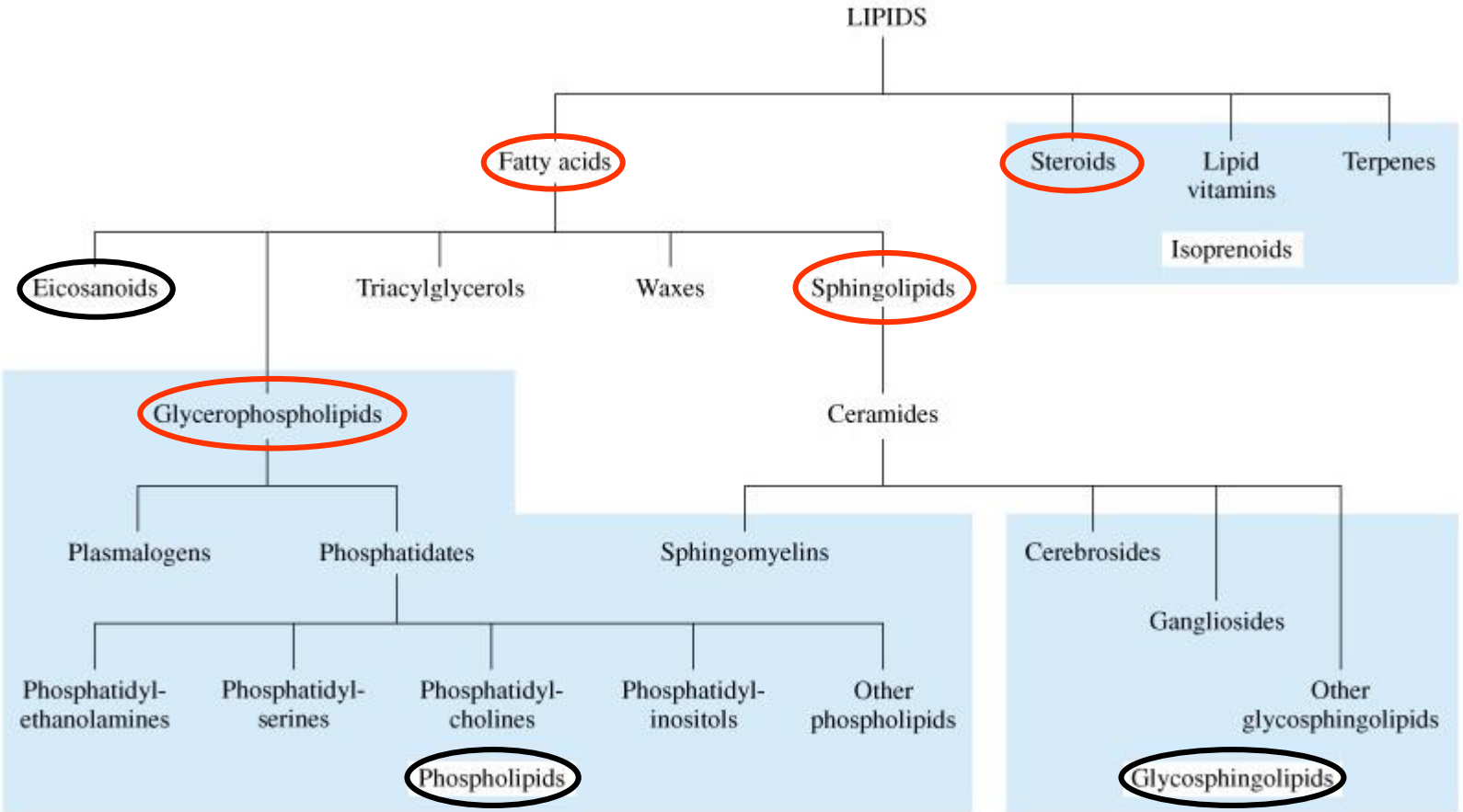
- Debelina 6-10 nm (2 molekuli).
- Sestavljene predvsem iz lipidov in proteinov.
- Lipidi predstavljajo hidrofobno bariero.
- Različnost funkcij predvsem zaradi proteinov.
- Asimetričnost.
- Tekoča (fluidna) struktura.
- Večina električno polarizirana.

Sestava bioloških membran (utež.%)

MEMBRANA	PROT.	LIP.	O.H.	P/L
Mielin	18	79	3.0	0.23
Trombocit (p.m.)	33-42	51-58	7.5	0.70
Miš. jetra (p.m.)	46	54	2-4	0.85
Človeški eritrocit	49	43	8	1.10
Ameba	54	42	4	1.30
Podg.jetra (p.m.)	58	42	5-10	1.40
Podg.jetra (j.m.)	59	35	2.9	1.60
Gov.retina (palč.)	51	49	4	1.00
Mitohondrij (z.m.)	52	48	2-4	1.10
SER	67	33	-	2.00
Kloroplast (lam.)	70	30	6	2.30
Mitohondrij (n.m.)	76	24	1-2	3.20
Halobacterium sp.	75	25	-	3.00
Mycoplasma sp.	58	37	1.6	1.60

LIPIDI

- **gradniki bioloških membran**
- **signalne molekule**
- **visoko-koncentrirana zaloga energije**



Membranski lipidi
(vsi so amfipatični oz. amfifilni)

- Maščobne kisline
- Sestavljeni lipidi (mašč. kisline + alkohol)
  - Glicerofosfatidi
  - Sfingolipidi
- Enostavni lipidi (derivati izoprena)
  - Steroidi (holesterol)

Maščobne kisline

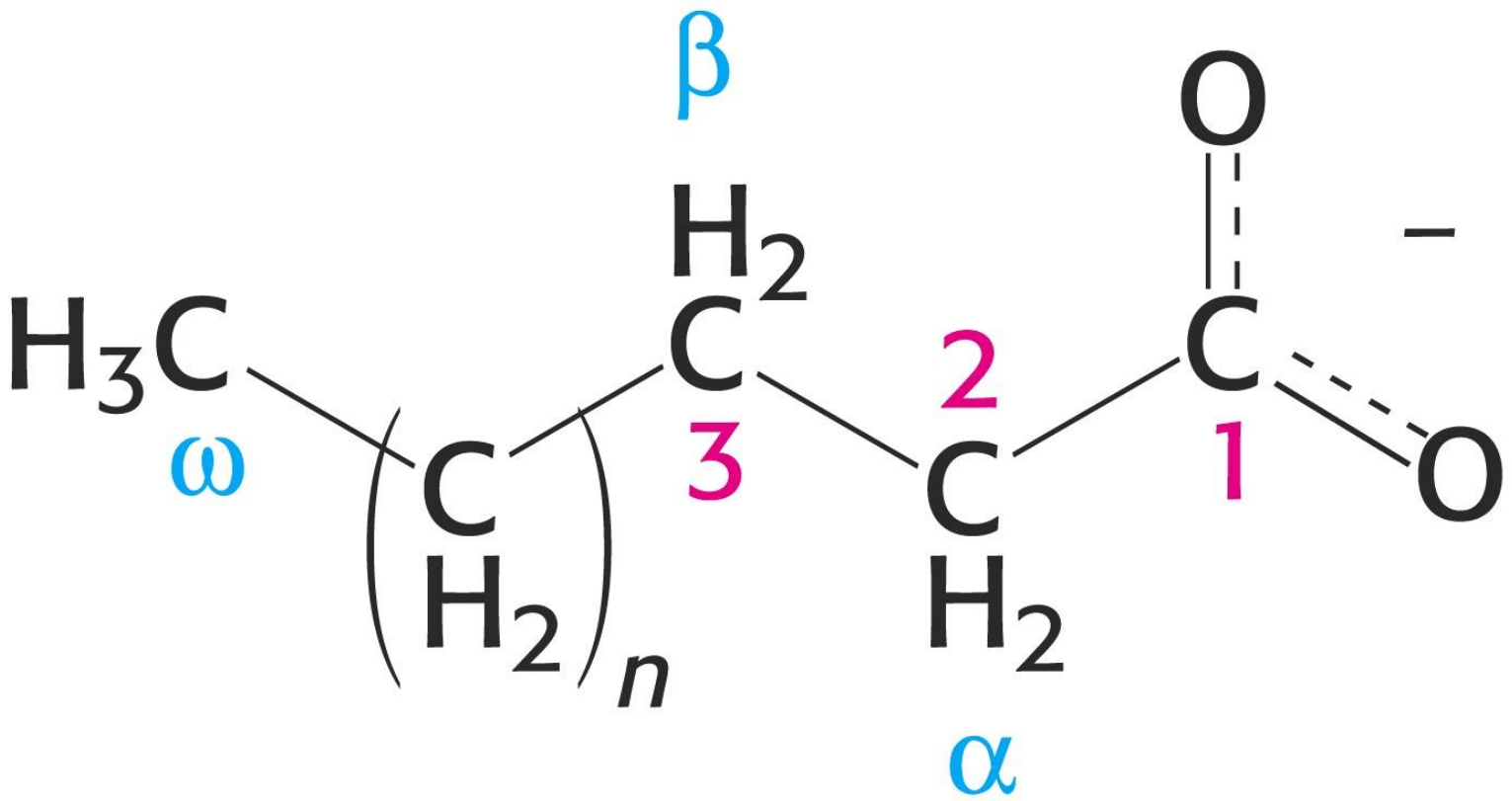
Maščobne kisline v bioloških membranah 14–24 C; najpogosteje 16 in 18 C atomov.

- Nasičene R-COOH
  - Laurinska kisl. $C_{12:0}$ – dodekanojska k.
  - Miristinska kisl. $C_{14:0}$ – tetradekanojska k.
  - Palmitinska kisl. $C_{16:0}$ – heksadekanojska k.
  - Stearinska kisl. $C_{18:0}$ – oktadekanojska k.
  - Arahidinska kisl. $C_{20:0}$ – eikozanojska k.

Maščobne kisline

- Nenasičene — $R\text{-}CH{=}CH\text{-}(CH_2)_n\text{-}COOH$
  - Palmitoleinska kisl. — *cis*-Δ^9-$C_{16:1}$ (heksa<u>dekeno</u>jska k.)
  - Oleinska kisl. — *cis*-Δ^9-$C_{18:1}$ (okta<u>dekeno</u>sjka k.)
  - Linolna kisl. — *cis*-$\Delta^{9,12}$-$C_{18:2}$ (okta<u>dekadieno</u>jska k.)
  - α-Linolenska kisl. — *cis*-$\Delta^{9,12,15}$-$C_{18:3}$ (okta<u>dekatrieno</u>jska k.)
  - γ-Linolenska kisl. — *cis*-$\Delta^{6,9,12}$-$C_{18:3}$ (okta<u>dekatrieno</u>jska k.)
  - Arahidonska kisl. — *cis*-$\Delta^{5,8,11,14}$-$C_{20:4}$ (eikoza<u>tetraeno</u>jska k.)

- Dvojne vezi v naravnih m. k. so ***cis*** konfiguracije!


β
O
H2
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H3C
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2
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3
1
O
C
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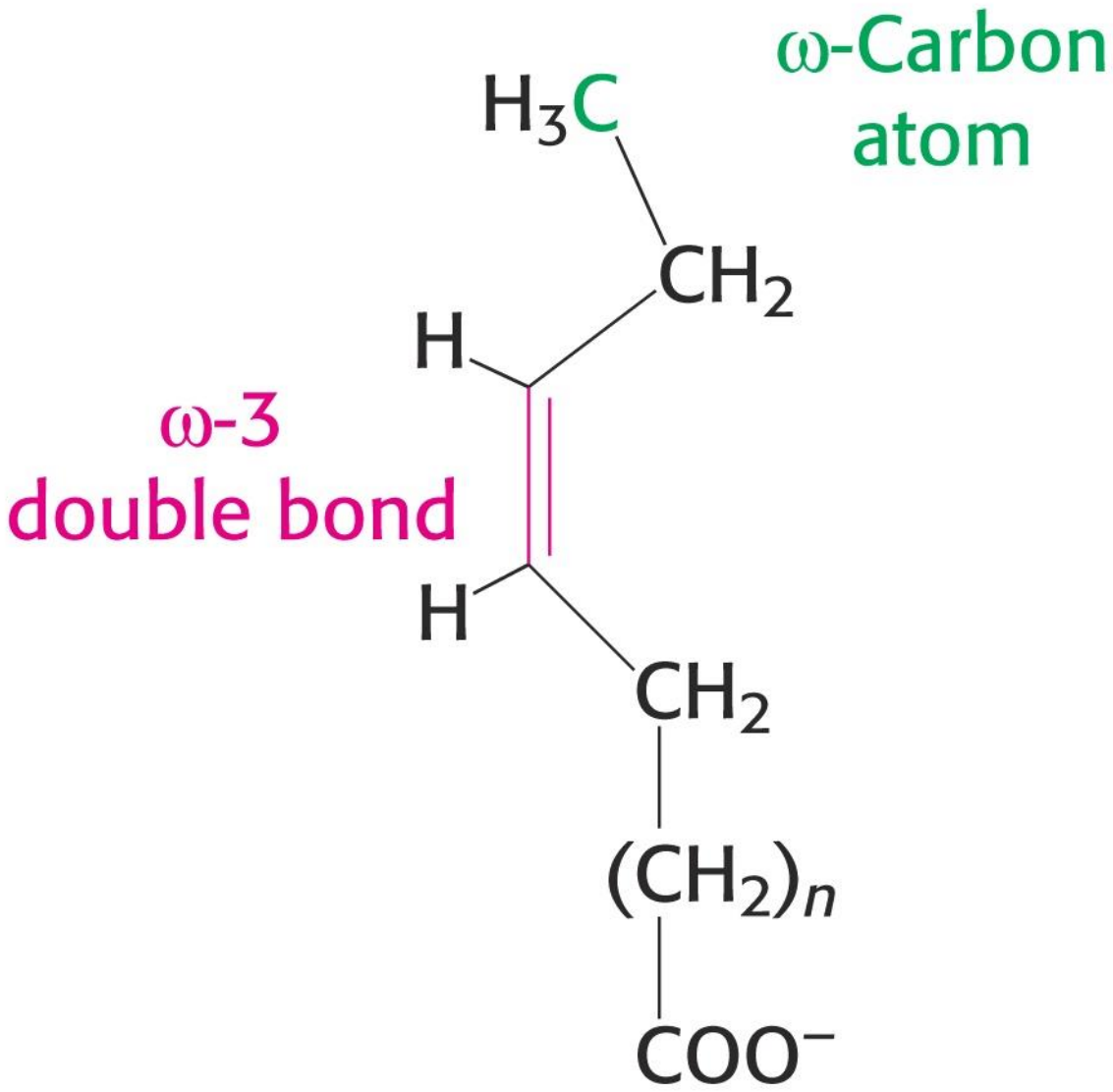
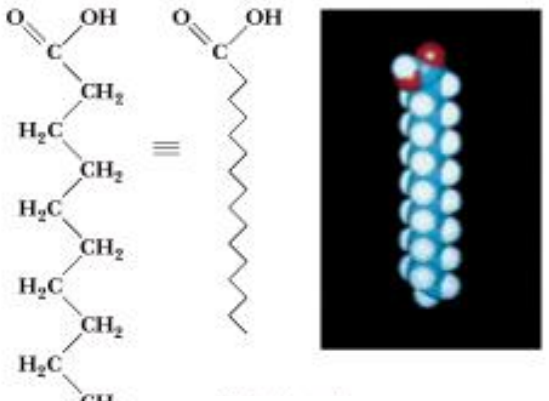
H2
n
α

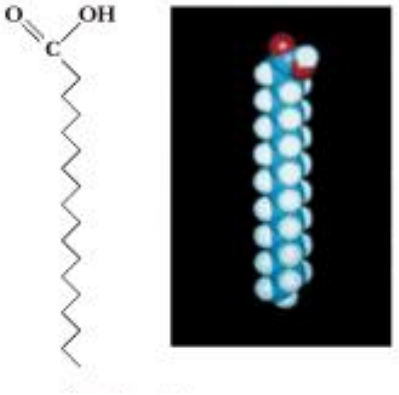


An ω-3 fatty acid

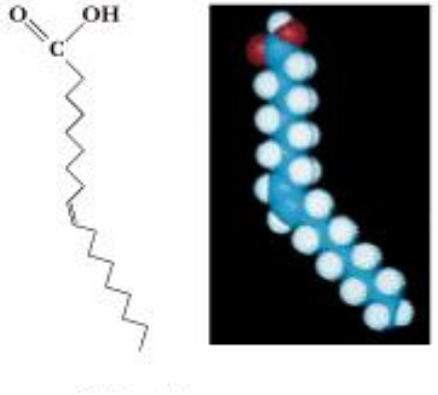
Zgradba maščobnih kislin



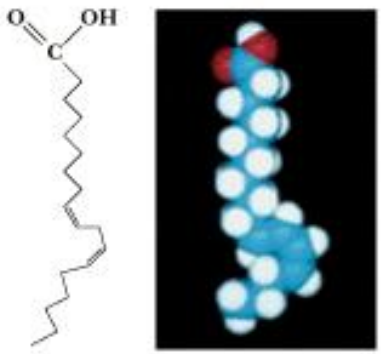
Palmitinska k.



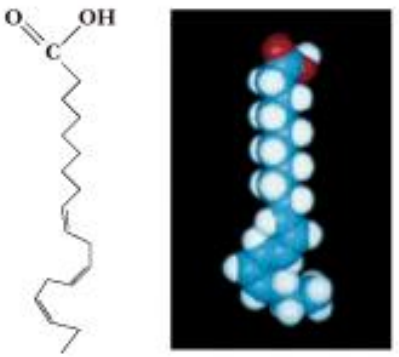
Stearinska k.



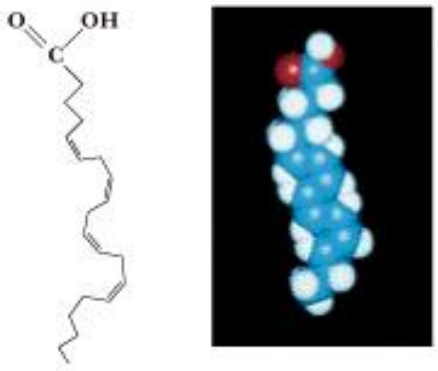
Oleinska k.



Linolna k.



α-linolenska k.



arahidonska k.

Lastnosti maščobnih kislin

Funkcija velikosti, stopnje nasičenosti in naboja.

- Nasičene verige: tesno zlaganje, višje tališče, urejene in rigidne v membranah.
- Nenasičene verige: ukrivljene, manj tesno zlaganje, nižje tališče, bolj gibljive v membranah.
- Pri fiziološkem pH vse v obliki $R\text{-}COO^-$.
- Lastnosti detergentov (tvorijo kroglaste micele).

Tališče maščobnih kislin

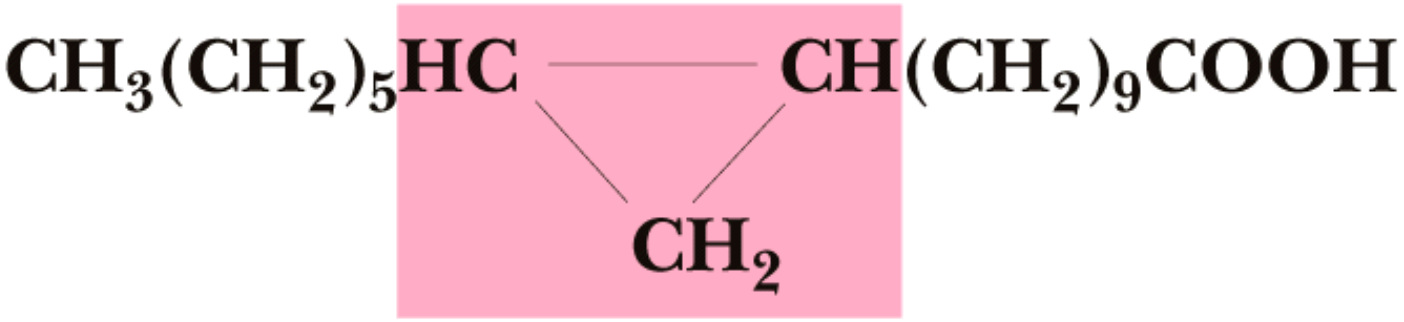
Oznaka	Trivialno ime	Sistematsko ime	Tališče (°C)
Nasičene			
12:0	**Lavrinska**	**Dodekanojska**	**44.2**
14:0	**Miristinska**	**Tetradekanojska**	**52.0**
16:0	**Palmitinska**	**Heksadekanojska**	**63.1**
18:0	**Stearinska**	**Oktadekanojska**	**69.6**
20:0	**Arahidinska**	**Eikozanojska**	**75.4**
22:0	**Behenska**	**Dokozanojska**	**81.0**
24:0	**Lignocerinska**	**Tetrakozanojska**	**84.2**

Tališče maščobnih kislin

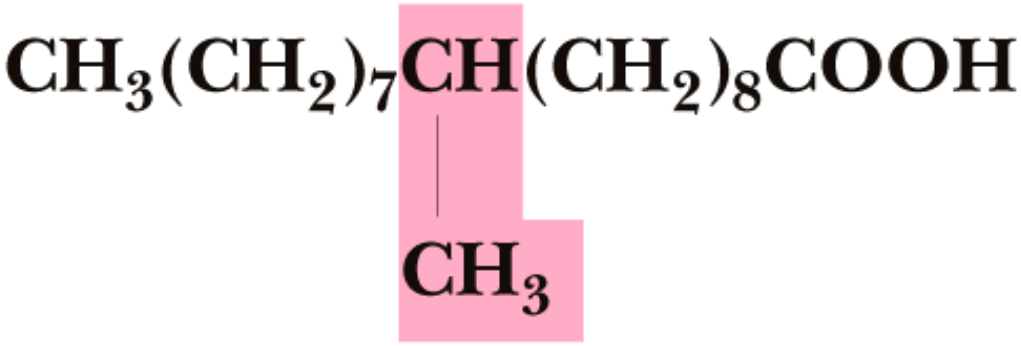
Oznaka	Trivialno ime	Sistematsko ime	Tališče (°C)
Nenasičene			
16:1	**Palmitoleinska**	**9-heksadekenojska**	**-0.5**
18:1	**Oleinska**	**9-oktadekenojska**	**13.4**
18:2	**Linolna**	**9,12-oktadekendienojska**	**-9.0**
18:3	**α-Linolenska**	**9,12,15-oktadekentrienojska**	**-17.0**
18:3	**γ-Linolenska**	**6,9,12-oktadekentrienojska**	**-11.0**
20:4	**Arahidonska**	**5,8,11,14-eikozatetraenojska**	**-49.5**
20:5	**EPA**	**5,8,11,14,17-eikozapentaenojska**	**-54.0**
24:1	**Nervonska**	**15-tetrakozaenojska**	**39.0**

Neobičajne maščobne kisline

Laktobacilna kislina (rastlinska olja, mikroorganizmi)
(aliciklična k.)



Tuberkulostearinska kislina (bakterije)

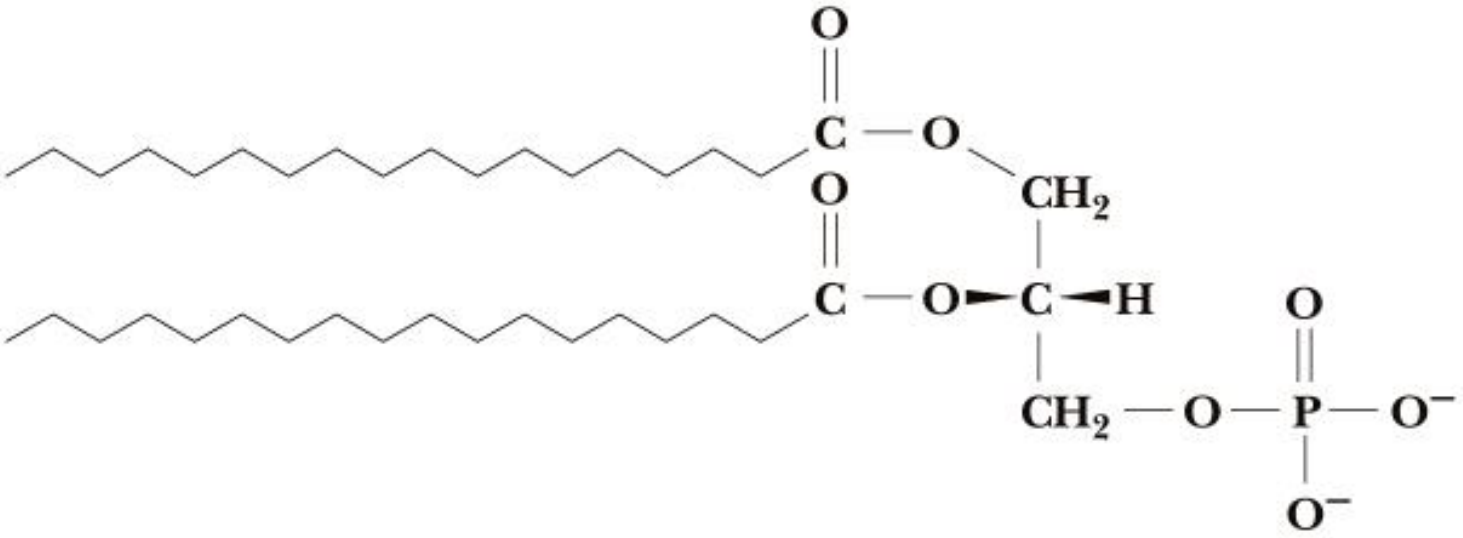


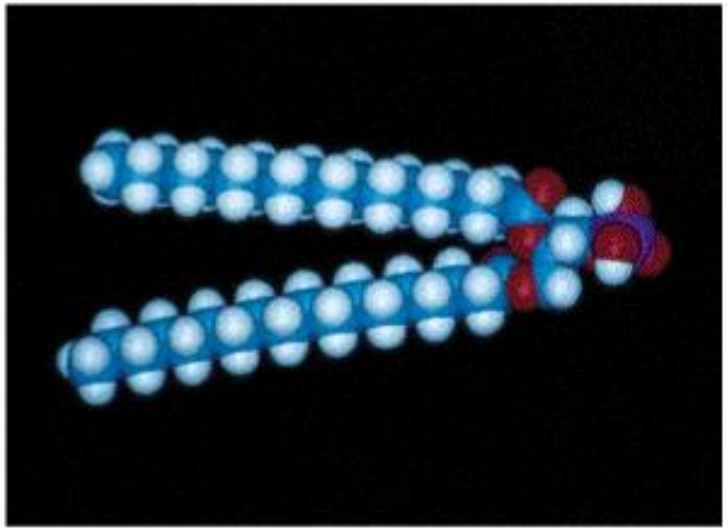
Glicerofosfatidi

Glicerofosfatidi so fosfolipidi.

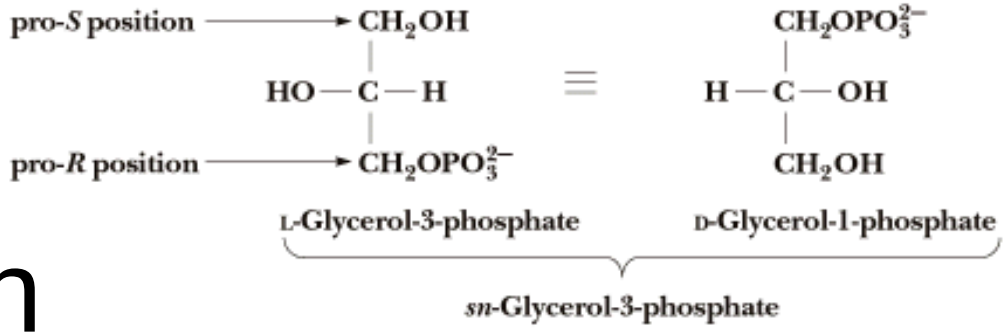
- Osnova glicerol (alkohol).
- Glicerol zaestren na mestih 1 in 2 z maščobno kislino (če nenasičena, je običajno na mestu 2).
- Mesto 3 zaestreno s fosforno kislino.
- Fosfatidna kisl. + alkoholna komponenta = fosfatid:
  - Fosfatidilholin
  - Fosfatidiletanolamin
  - Fosfatidilserin
  - Fosfatidilinozitol
  - Fosfatidilglicerol in kardiolipin itd.

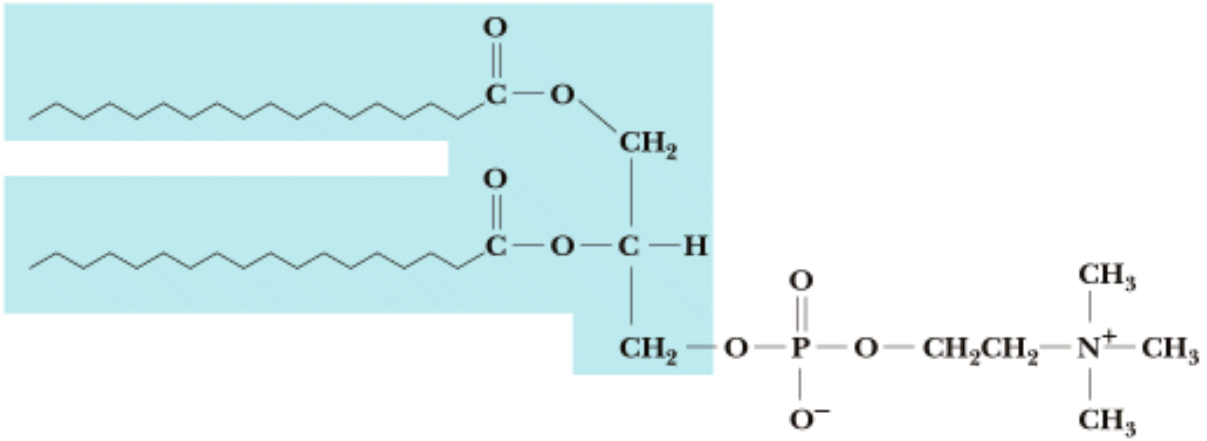
Fosfatidna kislina

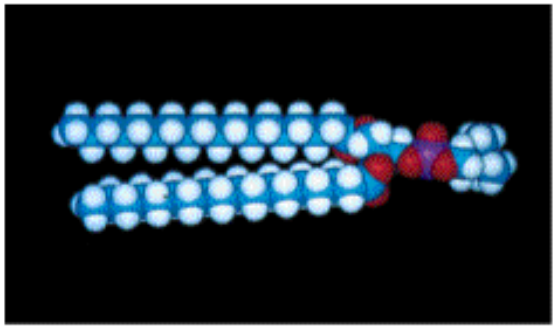




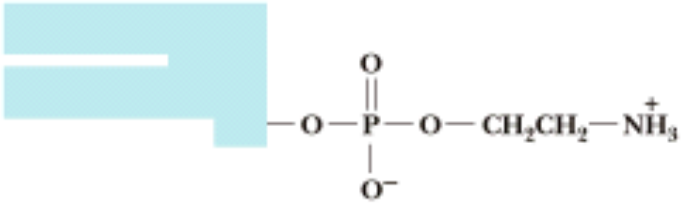
Fosfatidilholin



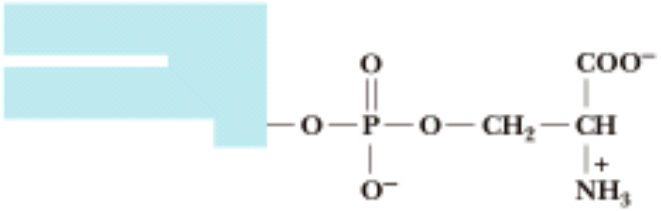




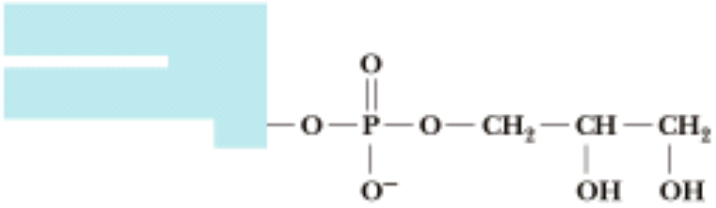
Drugi pogosti glicerofosfatidi



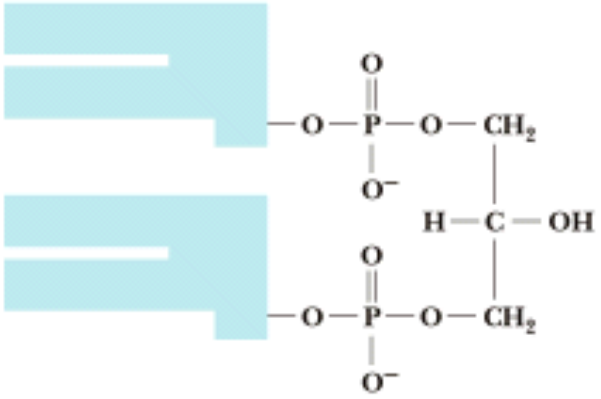
Fosfatidiletanolamin



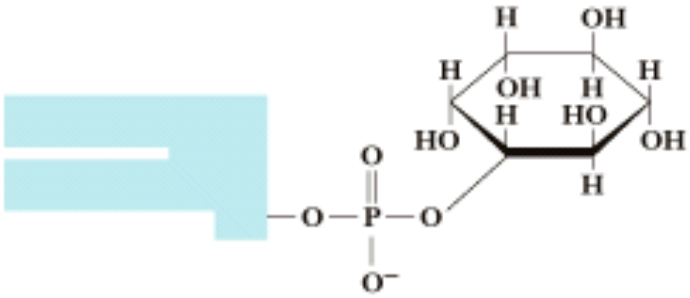
Fosfatidilserin



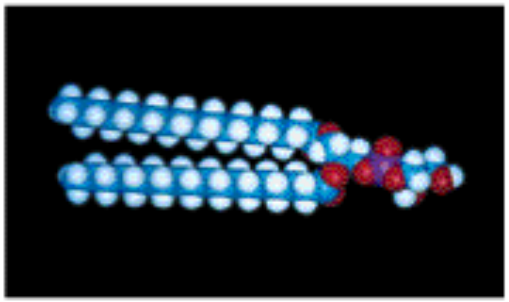
Fosfatidilglicerol

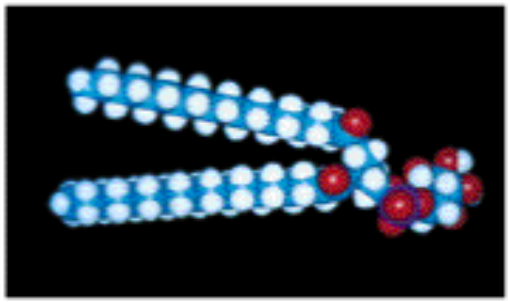


Kardiolipin

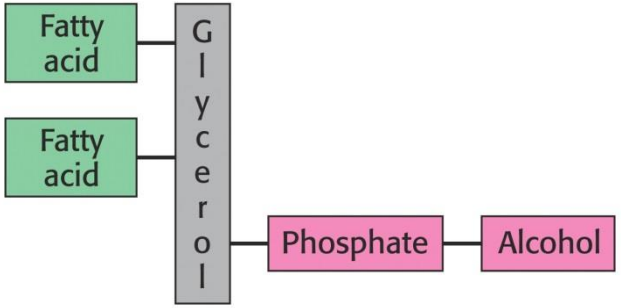


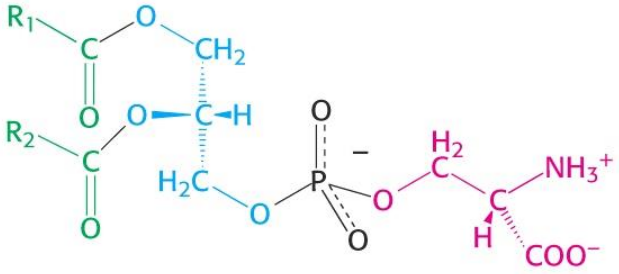
Fosfatidilinozitol



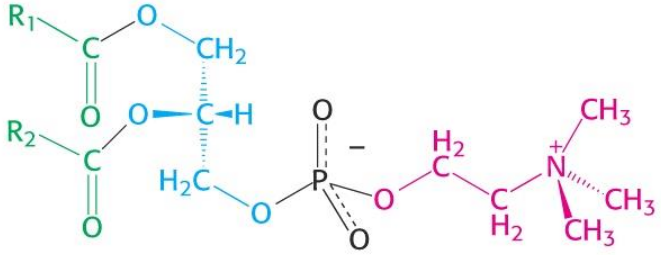


Konfiguracija na *sn*-2 glicerola je pri naravnih glicerofosfatidih **vedno R (D)**

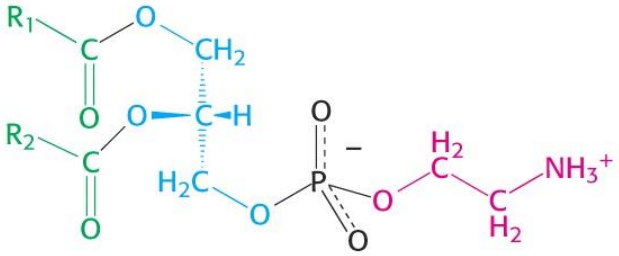




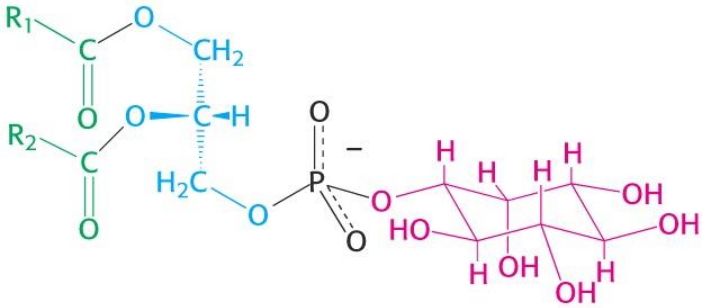
Phosphatidyl serine



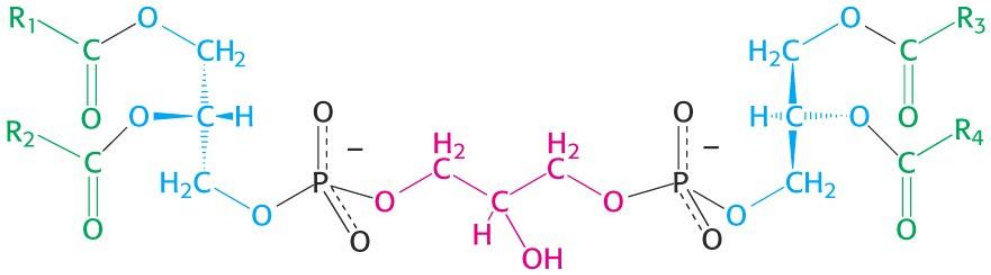
Phosphatidyl choline



Phosphatidyl ethanolamine

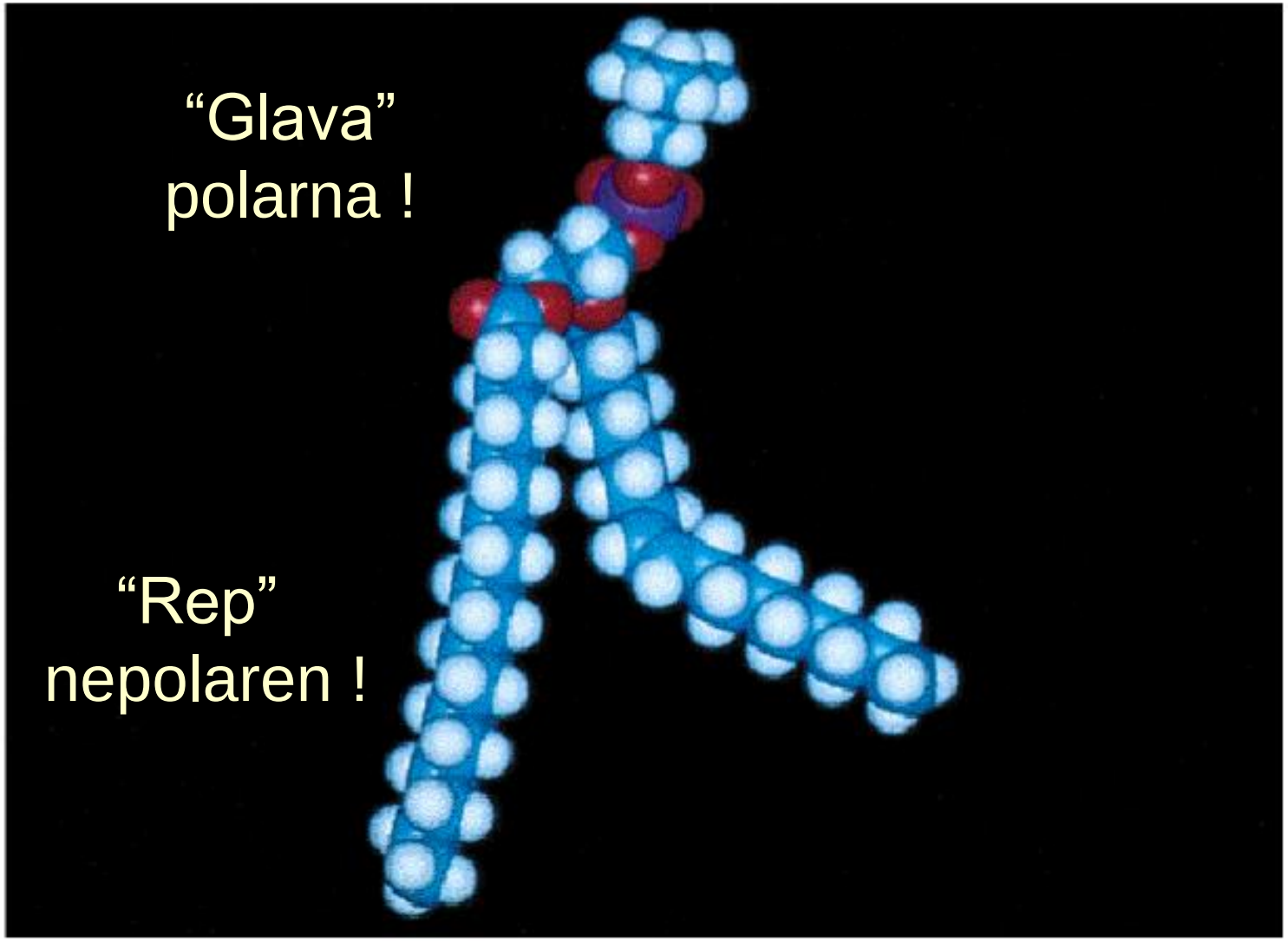


Phosphatidyl inositol



Diphosphatidyl glycerol (cardiolipin)

Glicerofosfatid – model



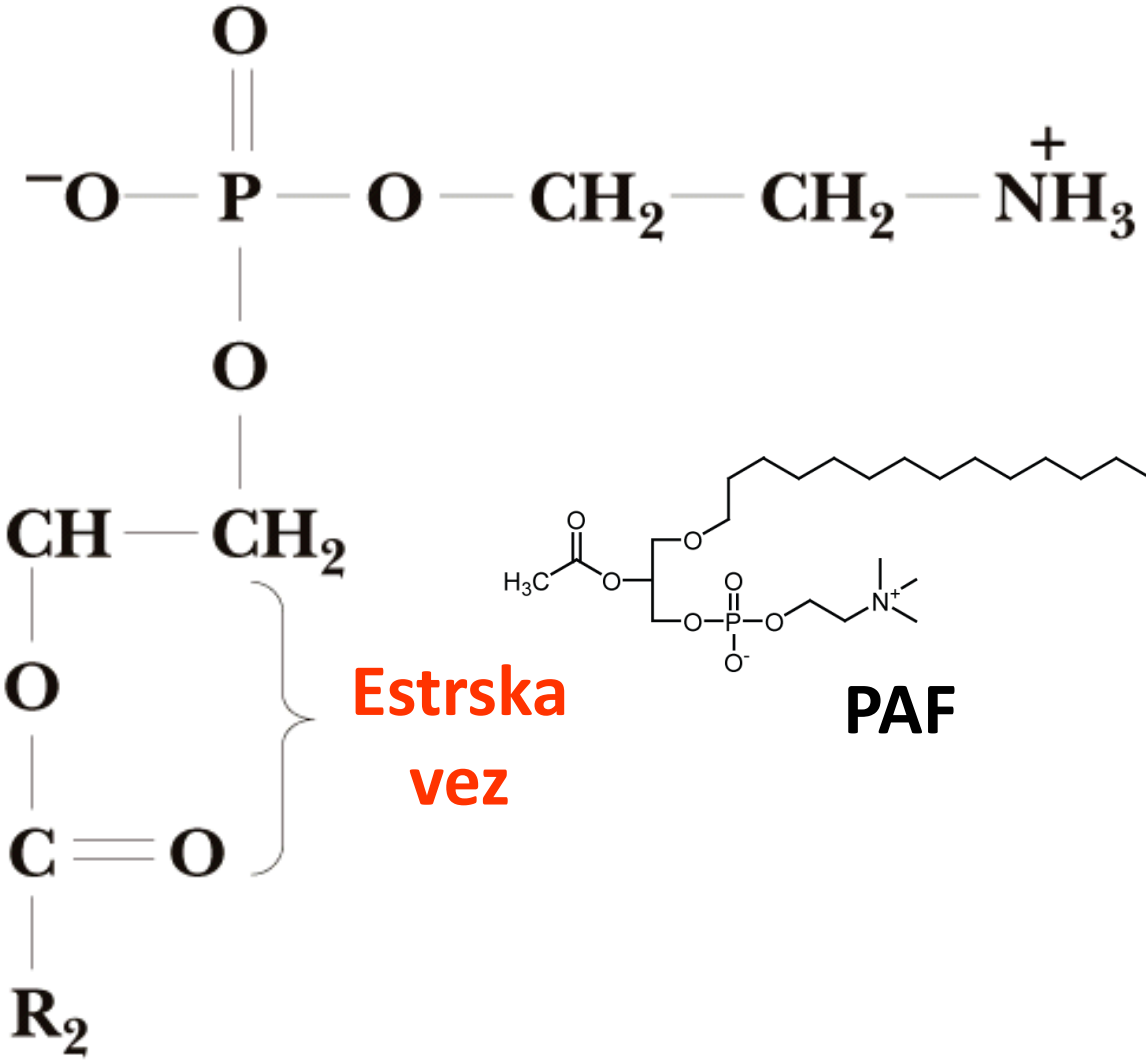
Etrski glicerofosfatidi

Na C-1 etrska vez namesto estrske!

- **Plasmalogeni**:

  etrski glicerofosfolipidi z nenasičeno alkilno verigo (vinilni ostanek na *sn*-1 ► dvojna vez takoj ob etrski vezi)
- Zalsti v membr. srca, živcev, ledvic in testisov
- PAF (platelet activating factor) – signalna molekula

Etrska vez na C-1 glicerola

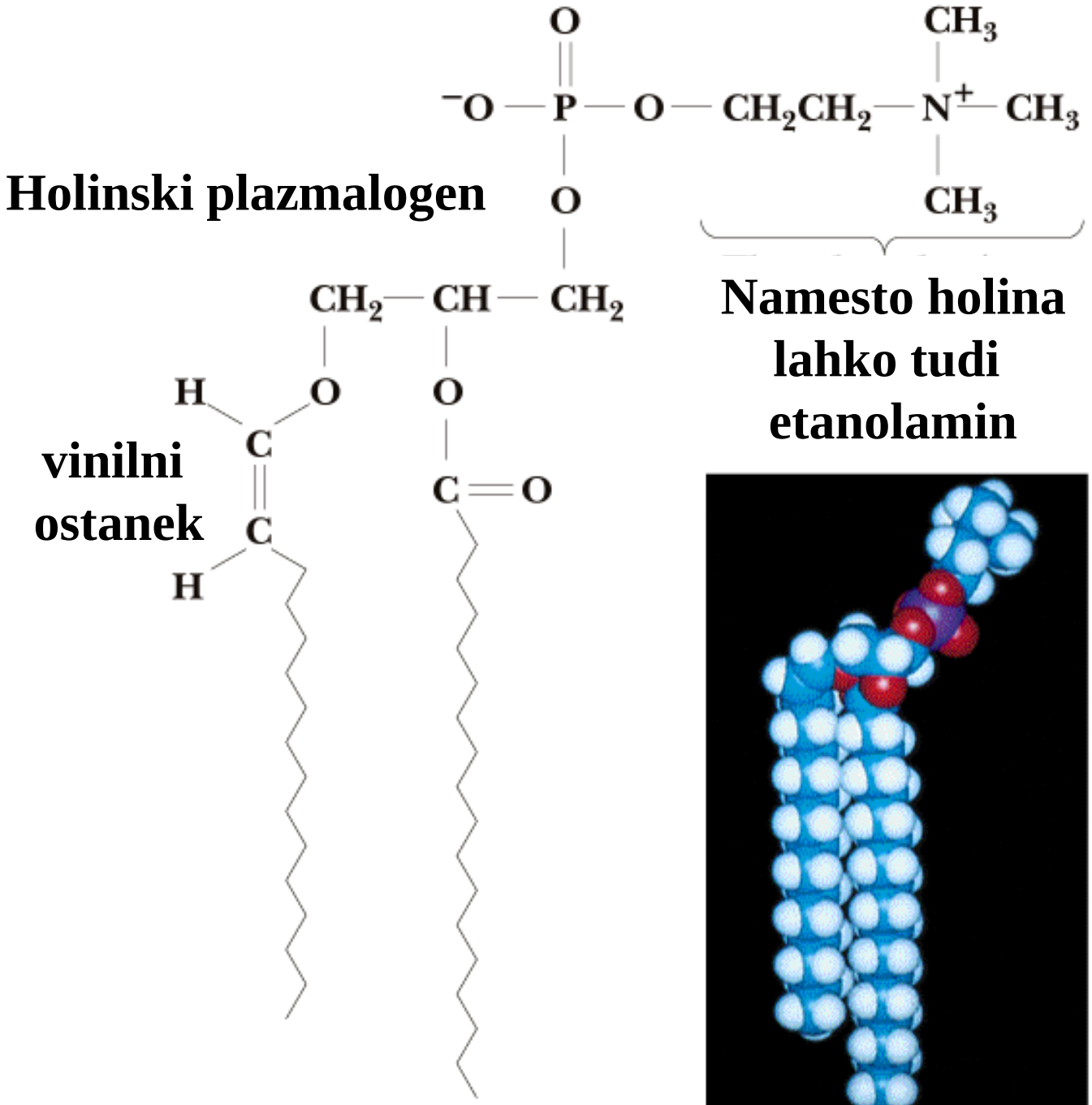


Etrska vez

Estrska vez

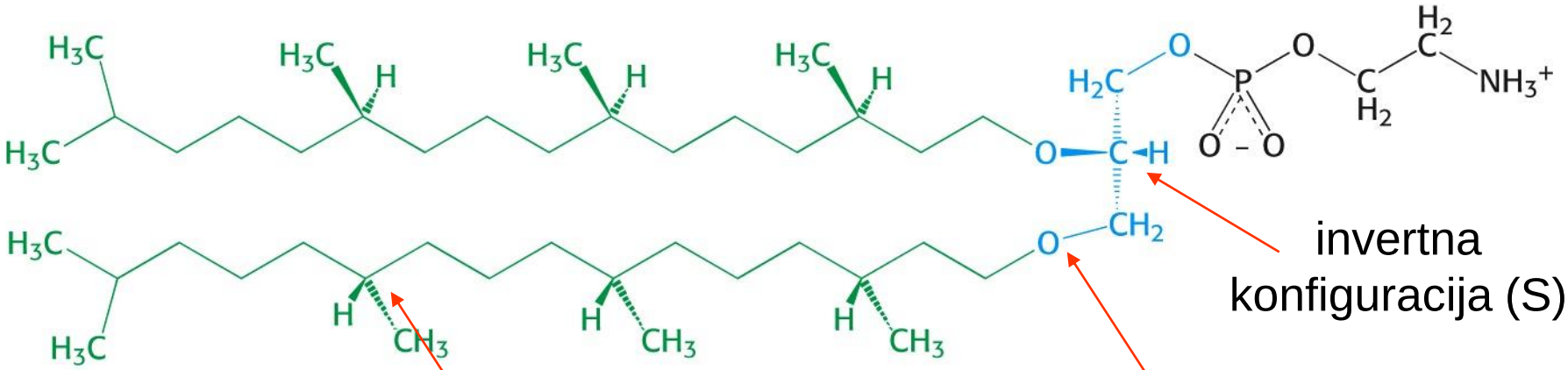
PAF

Membranski plazmalogen
1-alkil-2-acil-glicerofosfoholin



Etrski fosfolipidi v arhejah, ki se tudi sicer razlikujejo od tistih pri evkariontih in bakterijah

fosfolipid iz membrane *Methanococcus jannaschii*



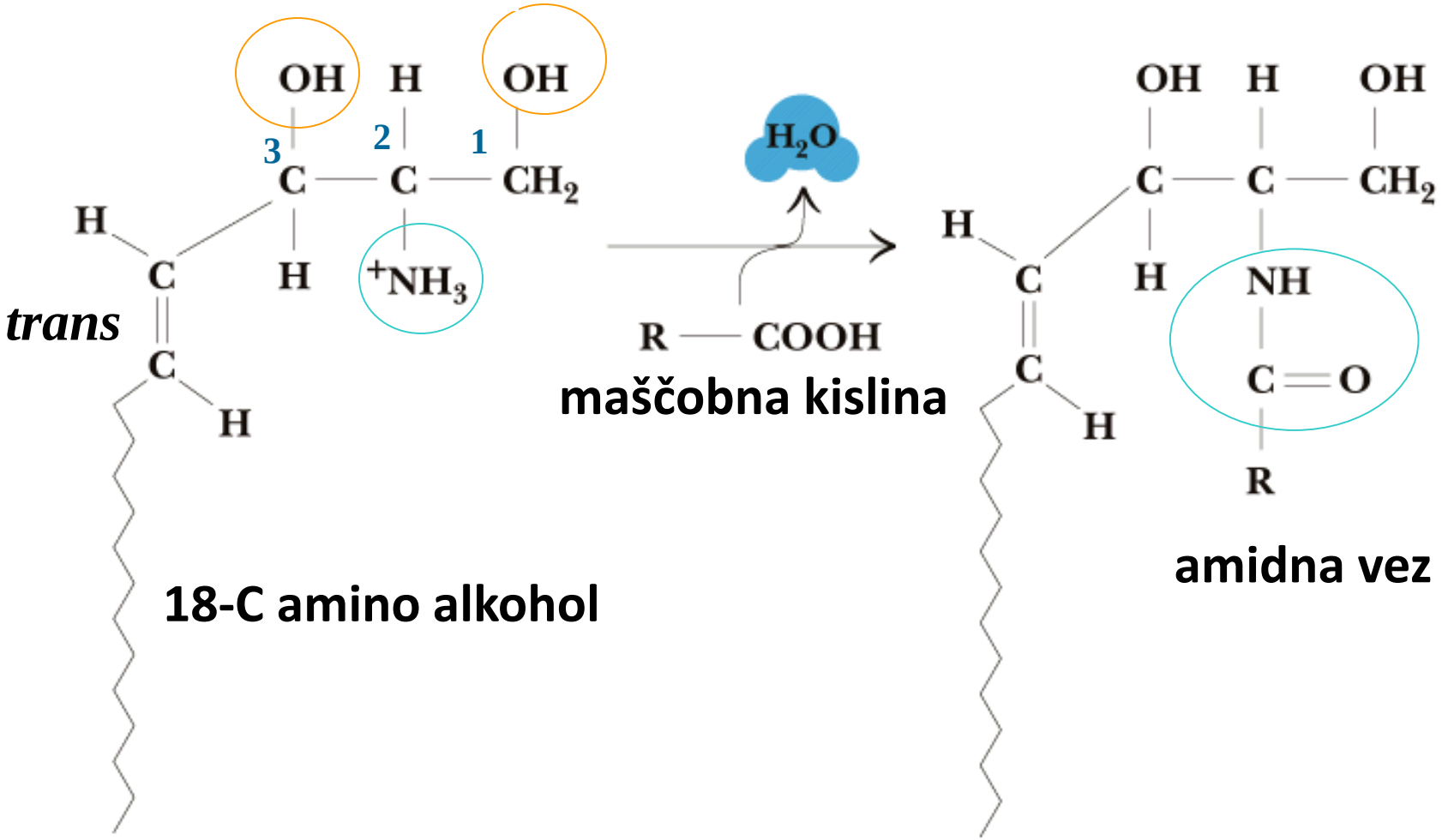
Sfingolipidi

- Osnova je **sfingozin**, 18-C amino alkohol (2-OH).
- **Ceramidi**: sfingozin + amidno vezana maščobna kislina.
- **Fosfosfingolipidi** : ceramidi + fosfoholin = SM.
- **Glikosfingolipidi**: ceramidi + β-glikozidno vezan monosaharid (**cerebrozidi**) ali oligosaharid (**gangliozidi**) na 1-OH skupino sfingozina.

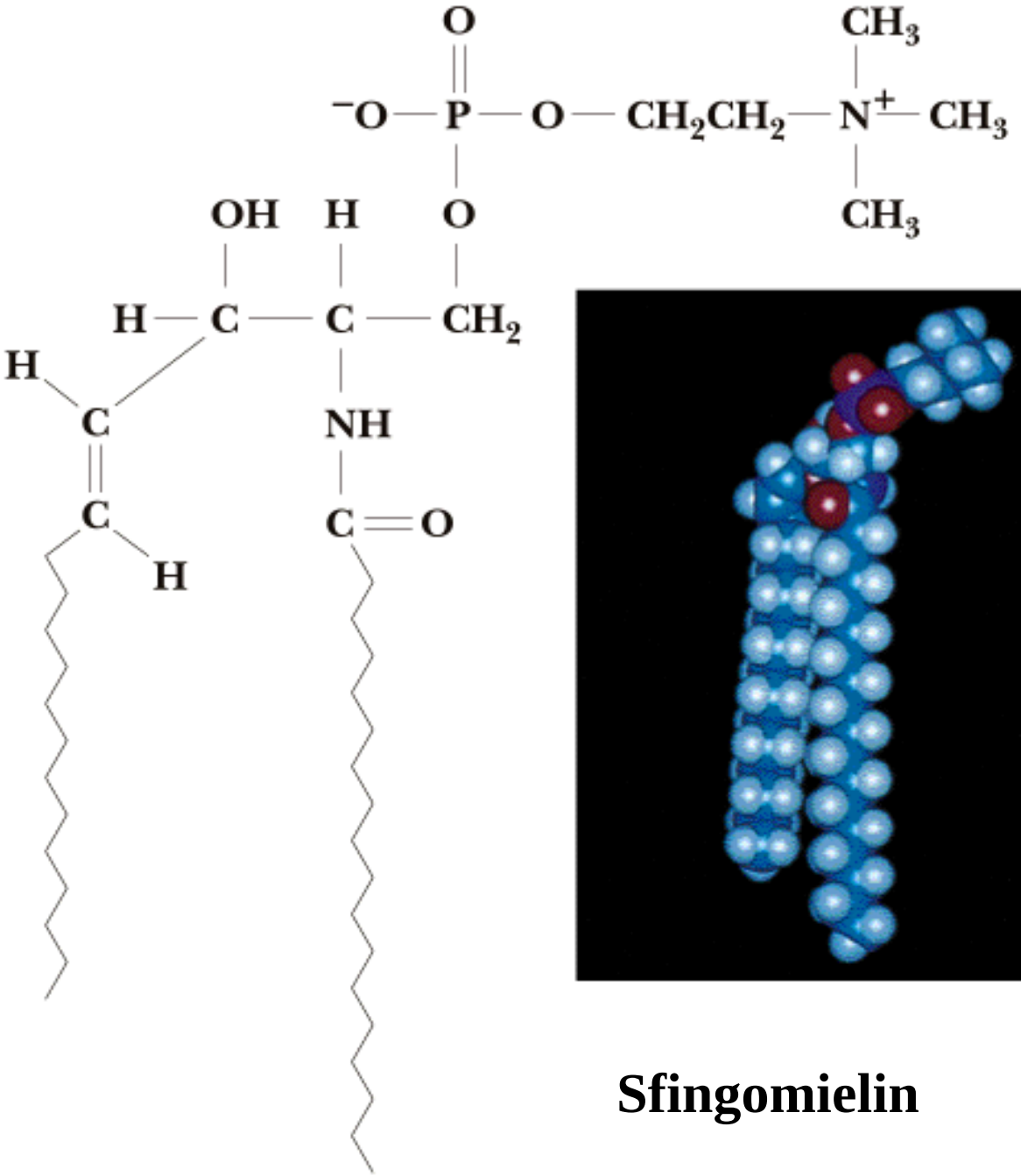
  Vedno na ekstracelularni strani p.m.

  Gangliozidi vsebujejo vsaj en ostanek sialične kisline (npr. NANA).

Zgradbi sfingozina in ceramida



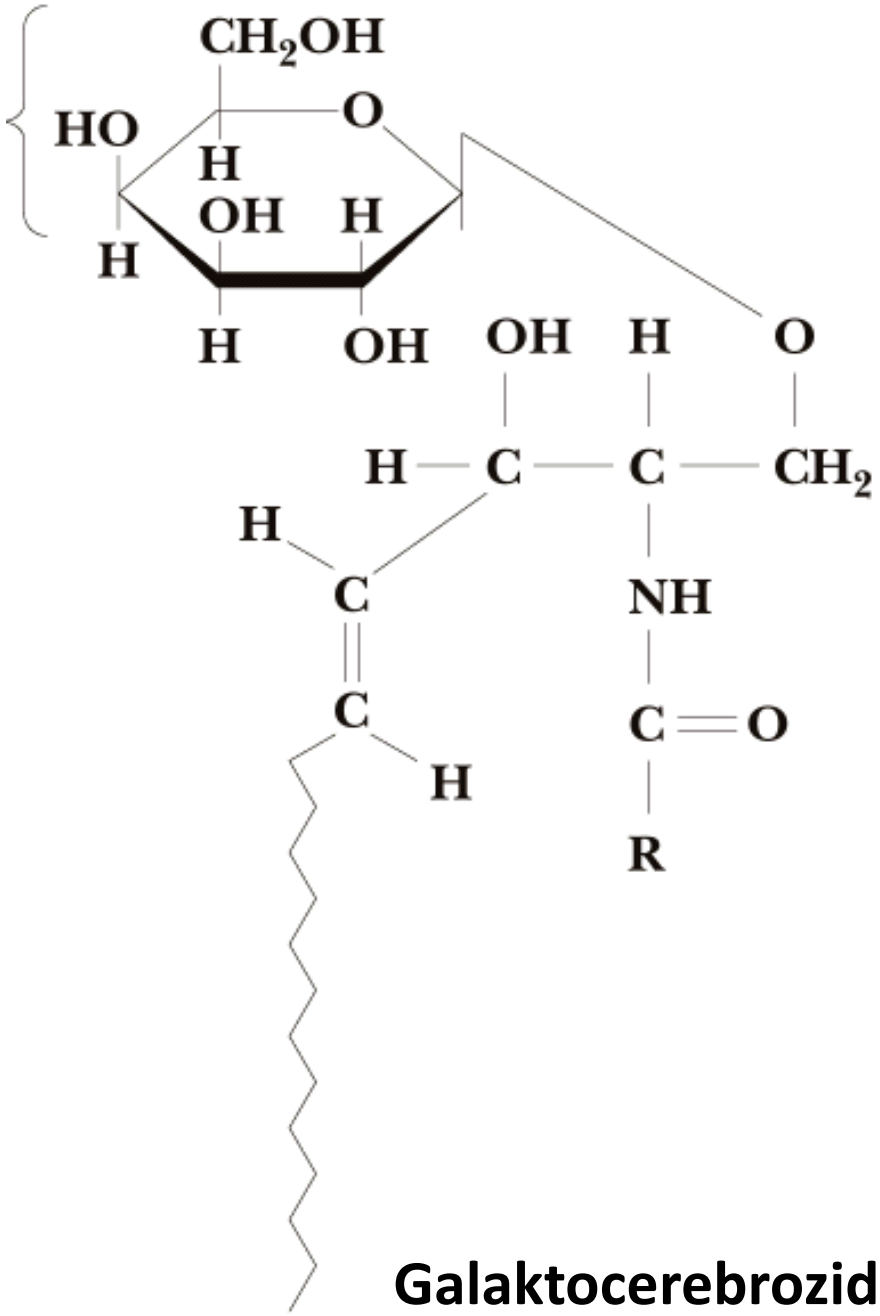
Zgradba sfingomielina (SM)



Sfingomielin

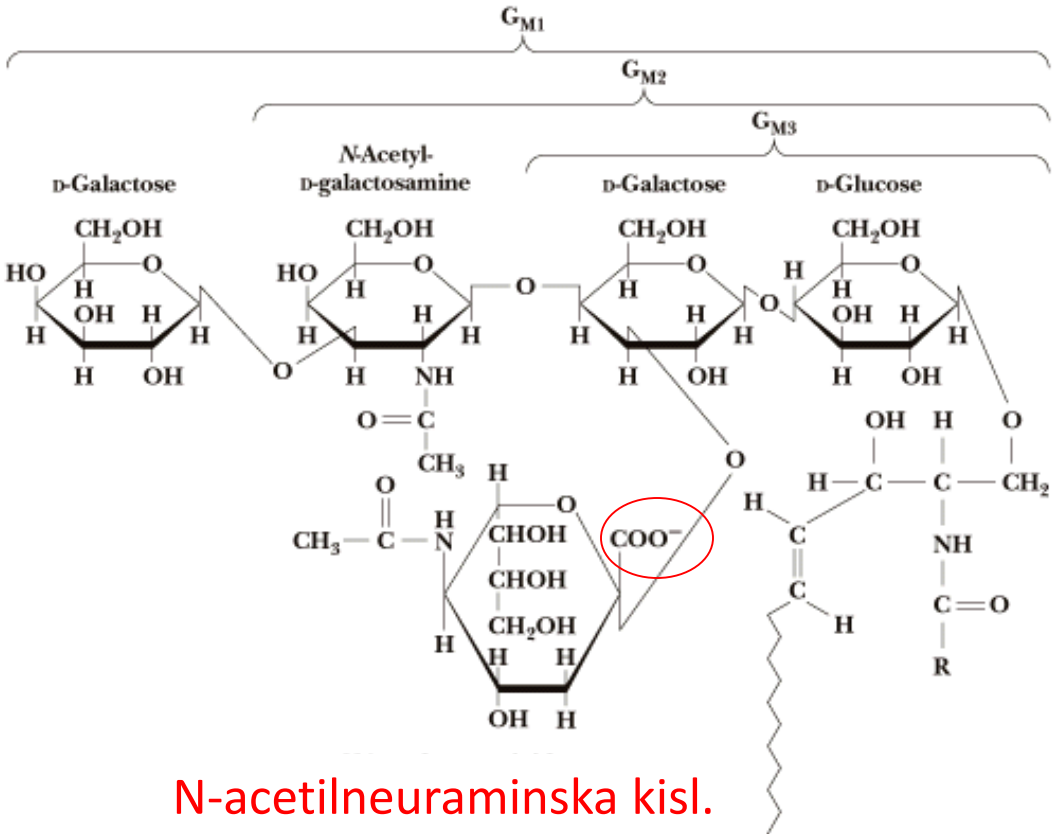
Zgradba cerebrozida

β-D-galaktoza



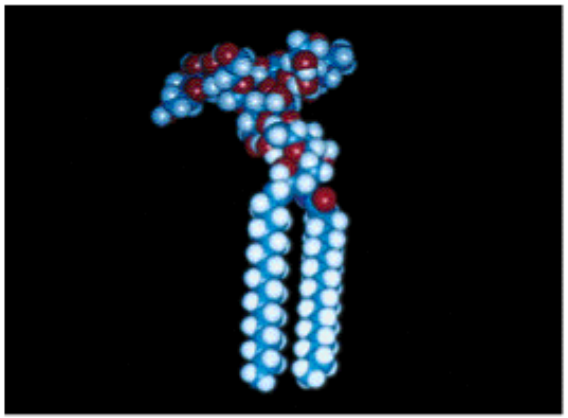
Galaktocerebrozid

Gangliozidi

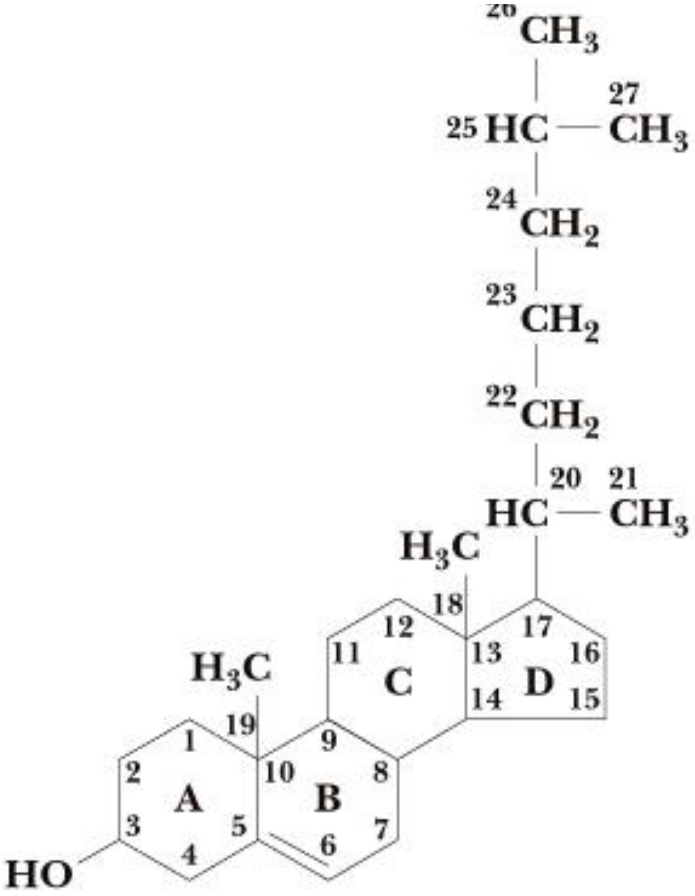


N-acetilneuraminska kisl.

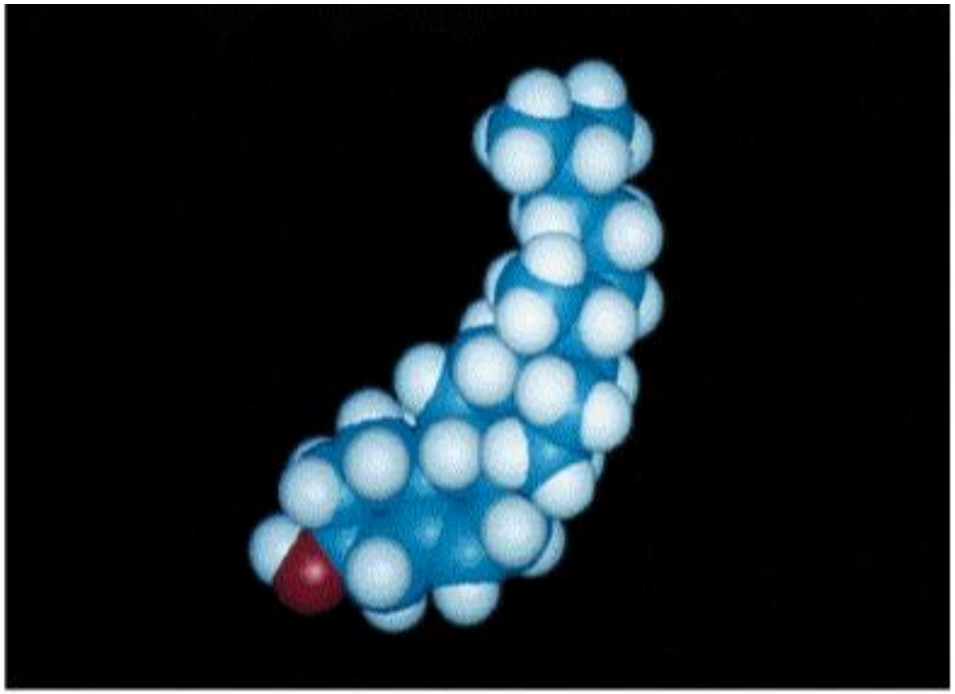
Gangliozidi G_{M1}, G_{M2}, G_{M3} … (60+)



Enostavni membranski lipid: holesterol



Holesterol (27-C)
(steroid, triterpenski derivat)



Holesterola naj ne bi bilo v prokariontih!

Lipidna sestava b.m. (utež.%)

LIPID	ERITROCIT (Človek)	MIELIN (Človek)	MITOH. (Gov. srce)	*E. coli*
Fosfatidna k.	1.5	0.5	0	0
Fosfatidilholin	19	10	39	0
Fosfatidiletanolamin	18	20	27	65
Fosfatidilglicerol	0	0	0	18
Fosfatidilinozitol	1	1	7	0
Fosfatidilserin	8.5	8.5	0.5	0
Kardiolipin	0	0	22.5	12
Sfingomielin	17.5	8.5	0	0
Glikolipidi	10	26	0	0
Holesterol	25	26	3	0

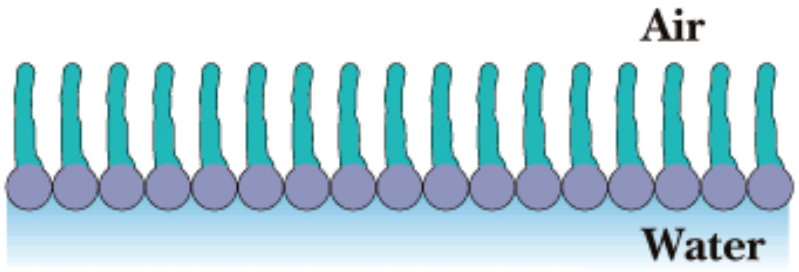
Lipidne strukture se spontano tvorijo

hidrofobne interakcije + van der Waalsove sile

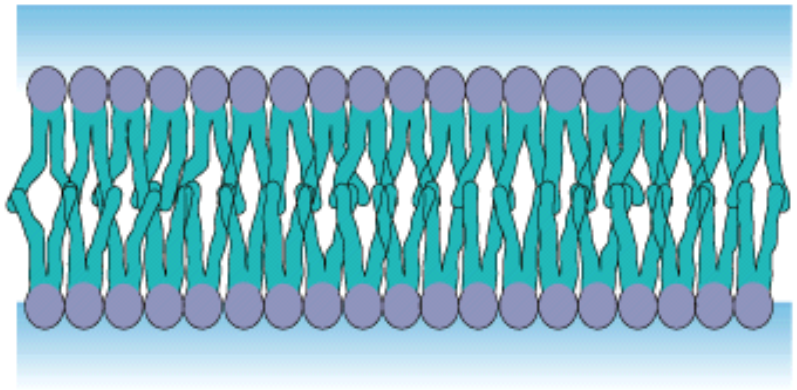
- Malo lipidov monomernih v vodi.
- Lipidni monosloji - nepolarni lipidni repi v zraku.
- Lipidni dvosloji:
  - unilamelarni vezikli (liposomi)
  - multilamelarni vezikli.
- Miceli - lipidni repki zaprti v kroglaste ali cilindrične strukture v polarnih topilih.
- Obrnjeni (reverzni) miceli v nepolarnih topilih.

Lipidne tvorbe v vodi

Sloji

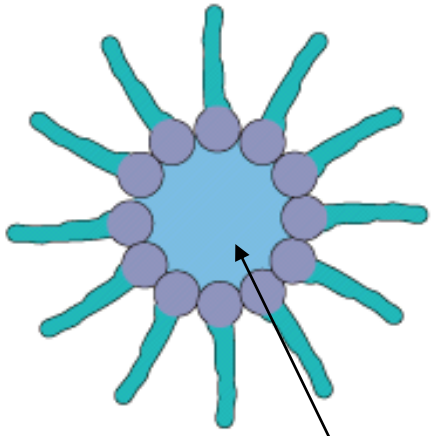


Monomolekulski sloj

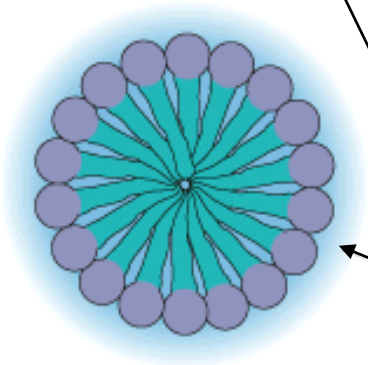


Bimolekulski sloj
= lipidni dvosloj

Miceli



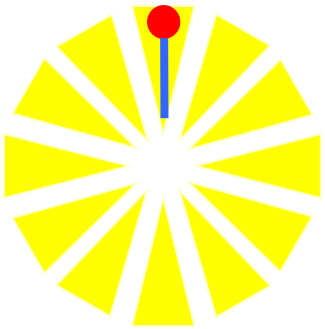
Obrnjen

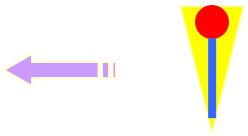


Običajen

Voda

Kritični Parameter Pakiranja - KPP





⅓ – ½

inverzni konus

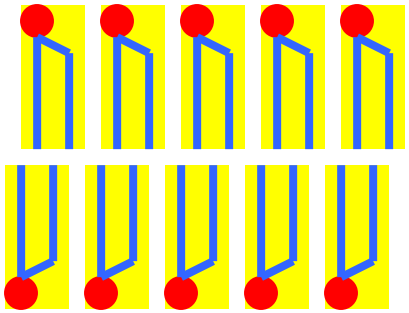
lizofosfatidi, detergenti

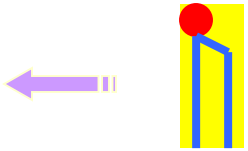
KPP = V/(L×S)

V = volumen monomera

L = dolžina verige

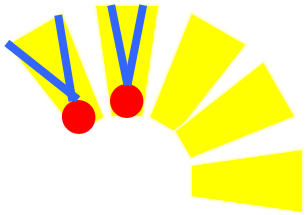
S = površina polarne glave monomera

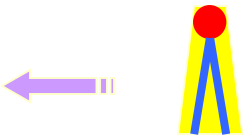




½ – 1

PC, SM, PS, PI …





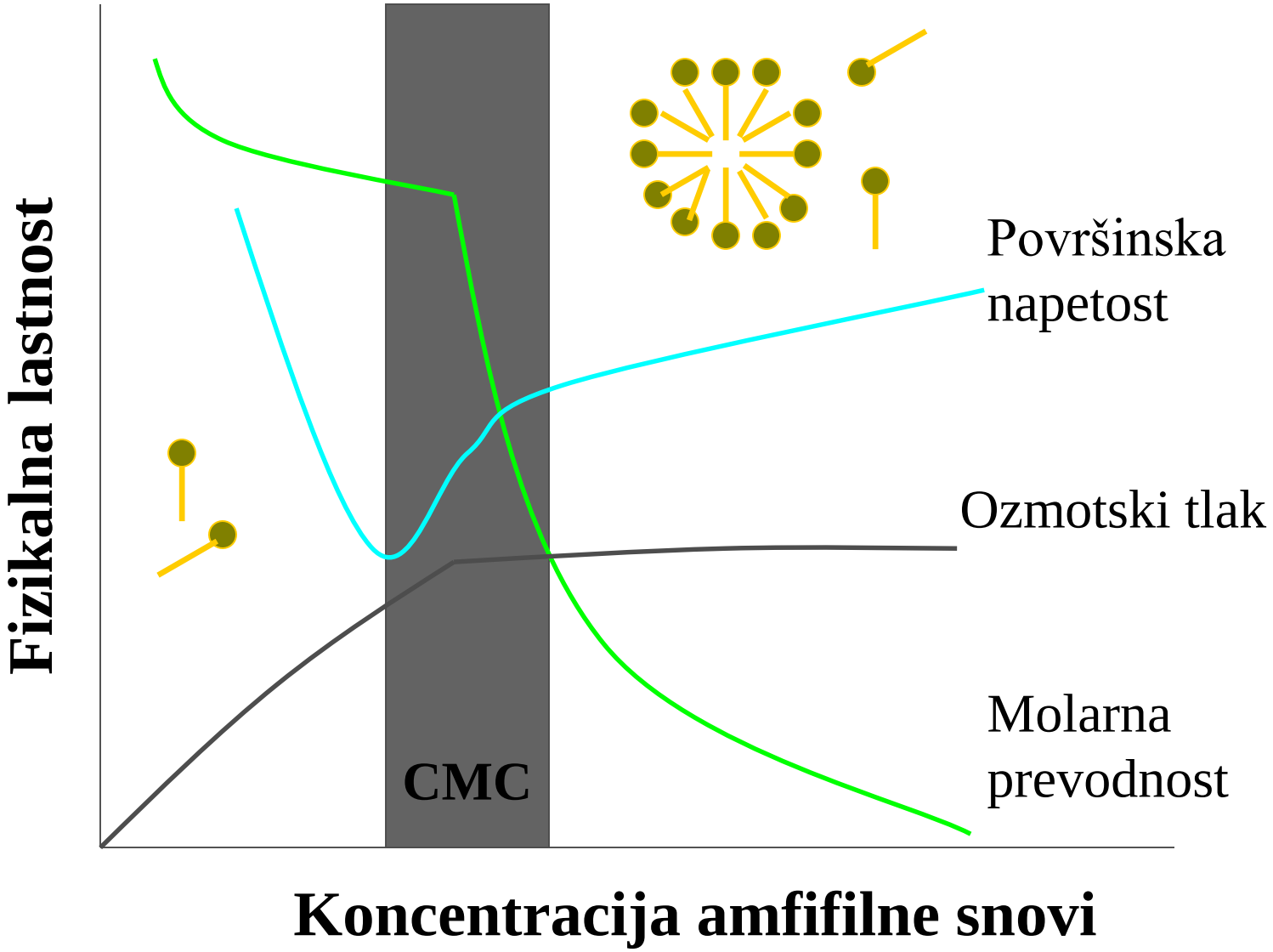
> 1

konus

Heksagonalna faza (H_{II})

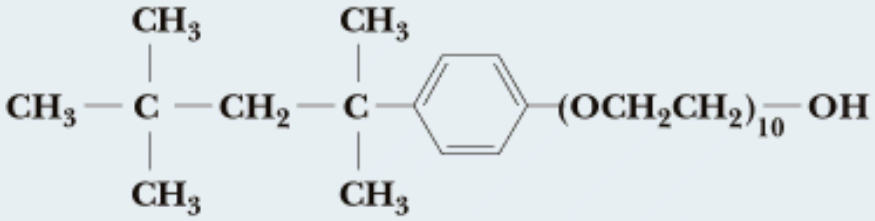
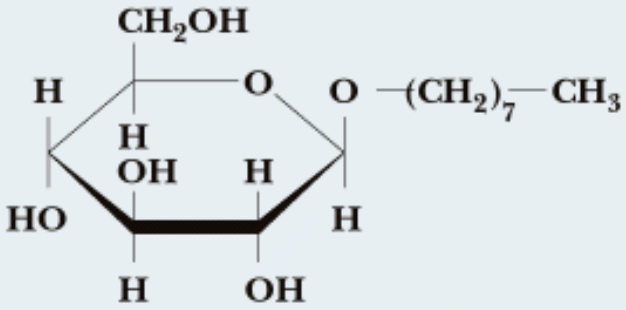
PE, kardiolipin-Ca^{2+}, PA-Ca^{2+}

Kritična micelna koncentracija (CMC)



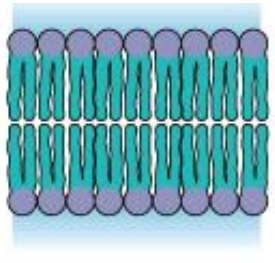
Detergenti - CMC

Figure 9.3

Structure	M_r	CMC	Micelle M_r
Triton X-100 	625	0.24 mM	90–95,000
Octyl glucoside 	292	25 mM	
$C_{12}E_8$ (Dodecyl octaoxyethylene ether) 	538	0.071 mM	

Lipidni dvosloji

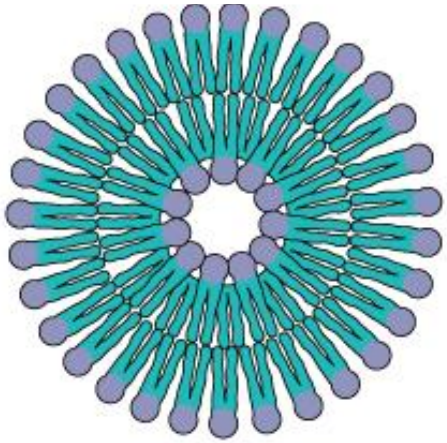
Planarni dvosloj



(a)

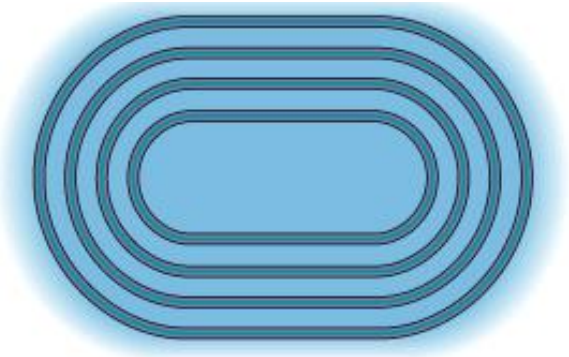
Unilamelarni vezikli → SUV

Unilamelarni vezikli → LUV



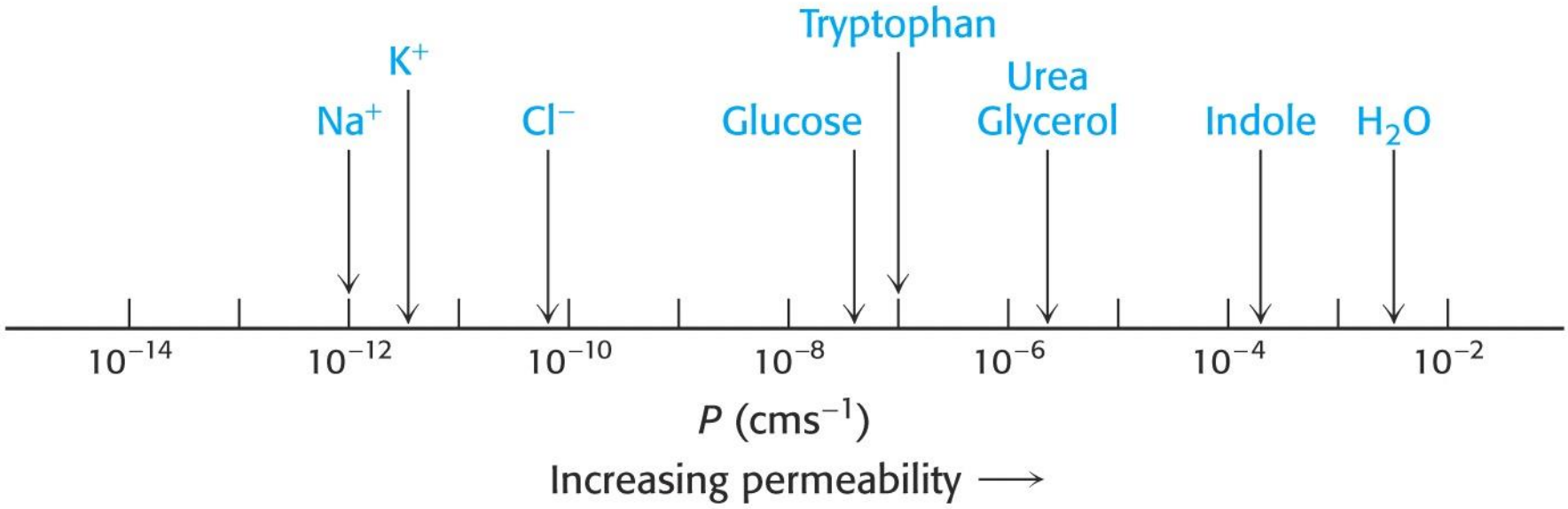
(b)

Multilamelarni vezikli

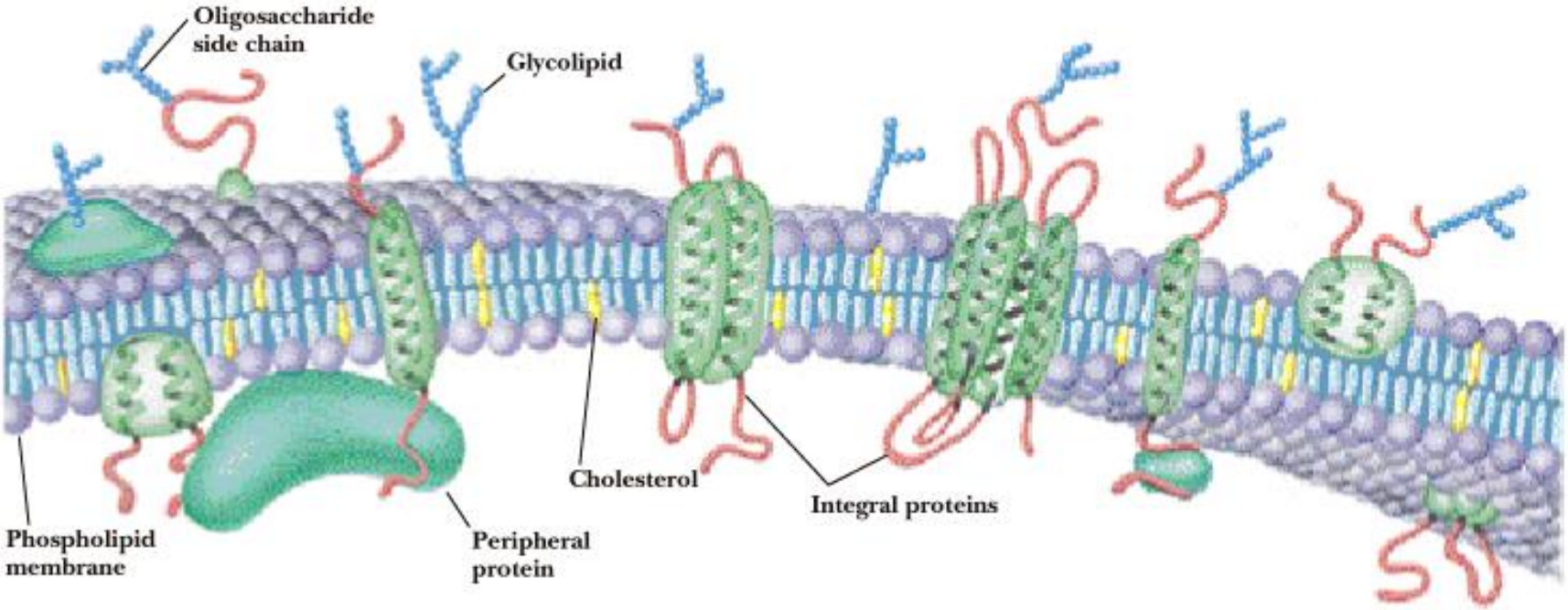


(c)

Prepustnostni koeficienti nekaterih ionov in molekul čez lipidni dvosloj



Modela biološke membrane



Model tekočega mozaika

„Fluid mosaic model of BM“

Singer & Nicolson, 1972

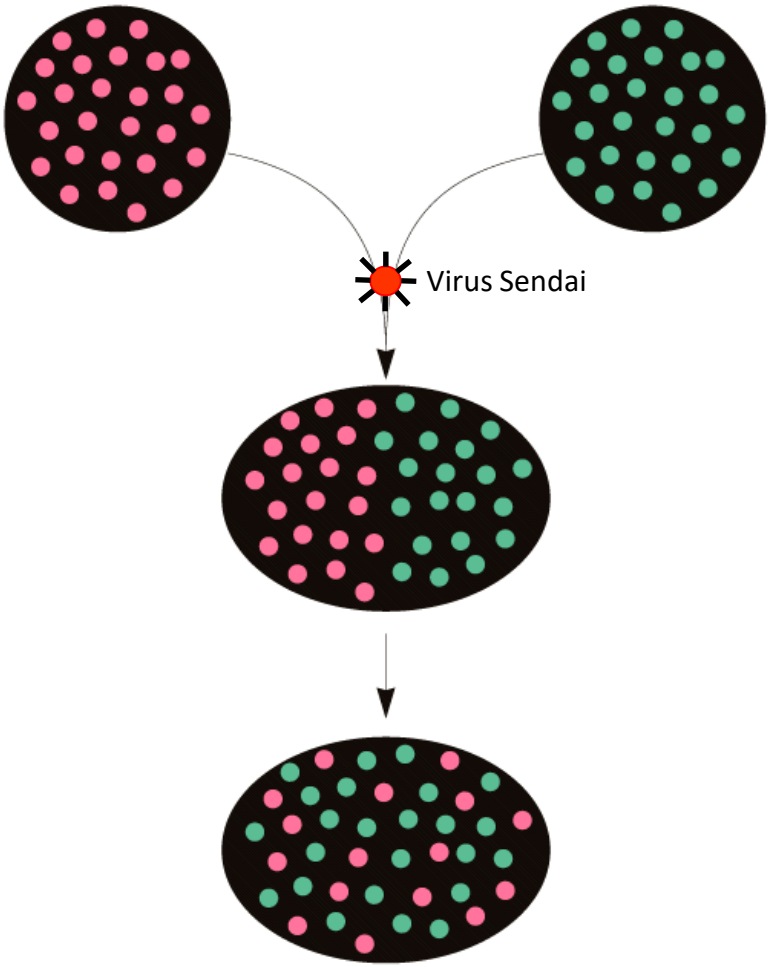
- Fosfolipidni dvosloj je dvodimenzionalno topilo.
- Lipidi in proteini - gibljivost:
  - lateralna difuzija,
  - rotacijska difuzija,
  - transferzalna difuzija (“flip-flop”).
- Dva razreda membranskih proteinov:
  - periferni (zunanji),
  - integralni (notranji).

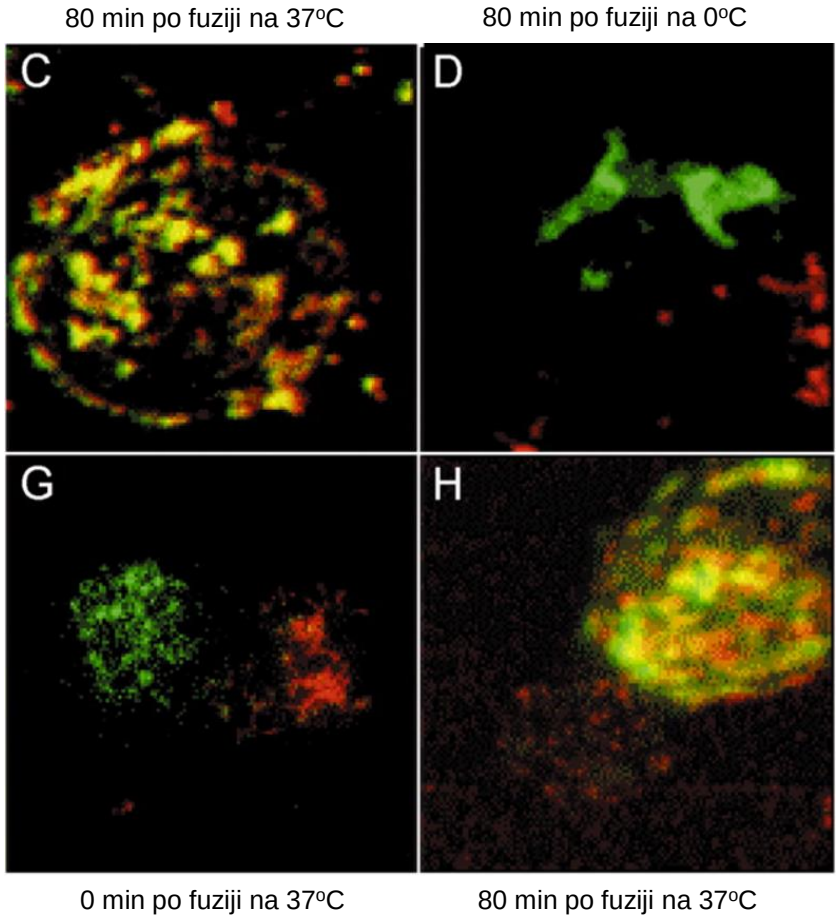
Gibanja molekul v lipidnem dvosloju

- Lipidne verige: upogibanje, nagib glede na normalo in rotacija.
- Lipidi in proteini – lateralna, rotacijska in transferzalna difuzija v dvosloju.
- Metode za spremljanje gibanja molekul:
  - fluorescenčna mikroskopija
  - FRET in FRAP
  - EPR
  - NMR

Frye – Edidinova demonstracija lateralne mobilnosti molekul v BM

Scanning near-field optical (C-D) and confocal microscopical (G-H) images of fused cells

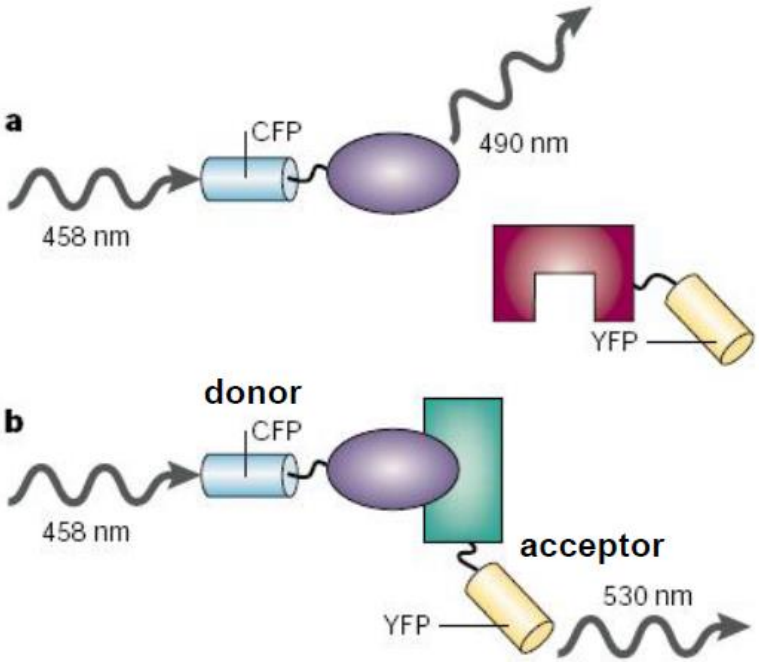


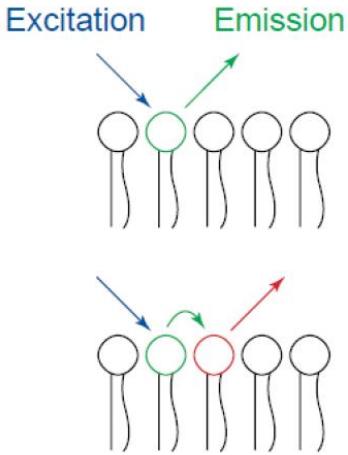


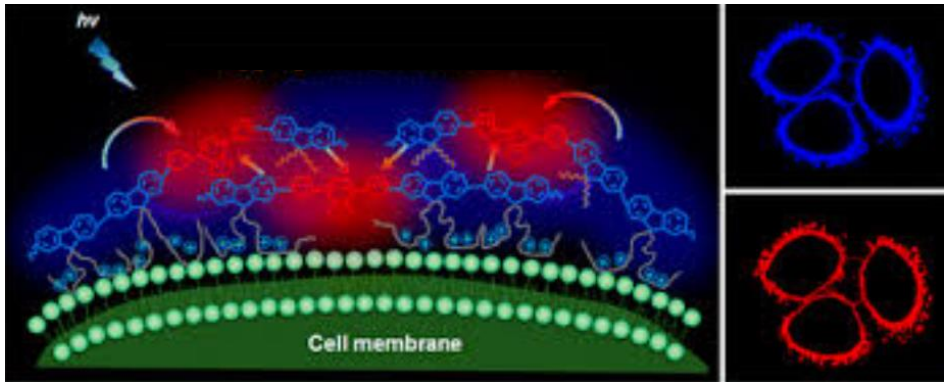
Nagy, P. et al. (2001) J. Cell Sci. 114, 4063-4071.

FRET

Fluorescence Resonance Energy Transfer

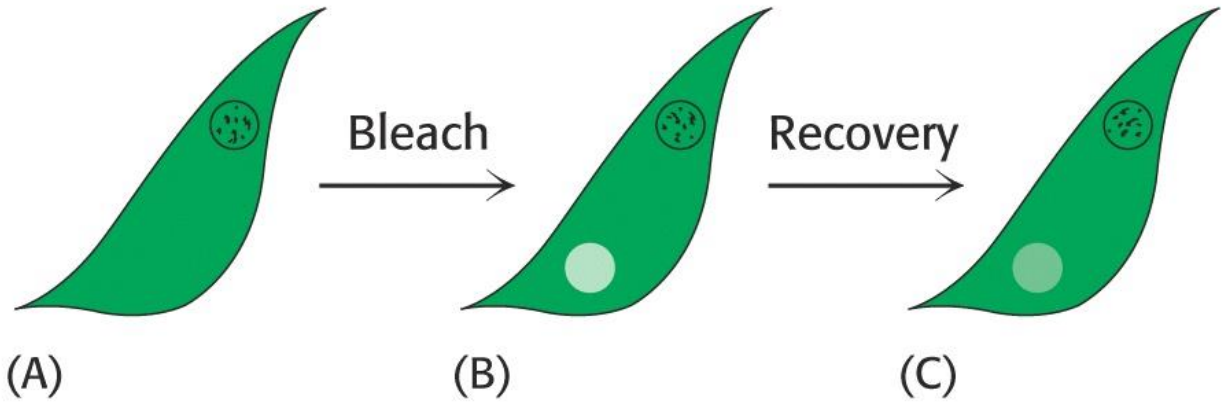


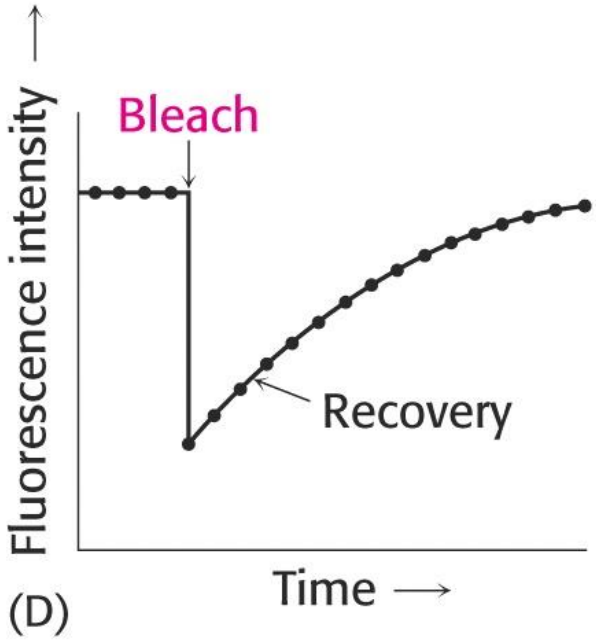




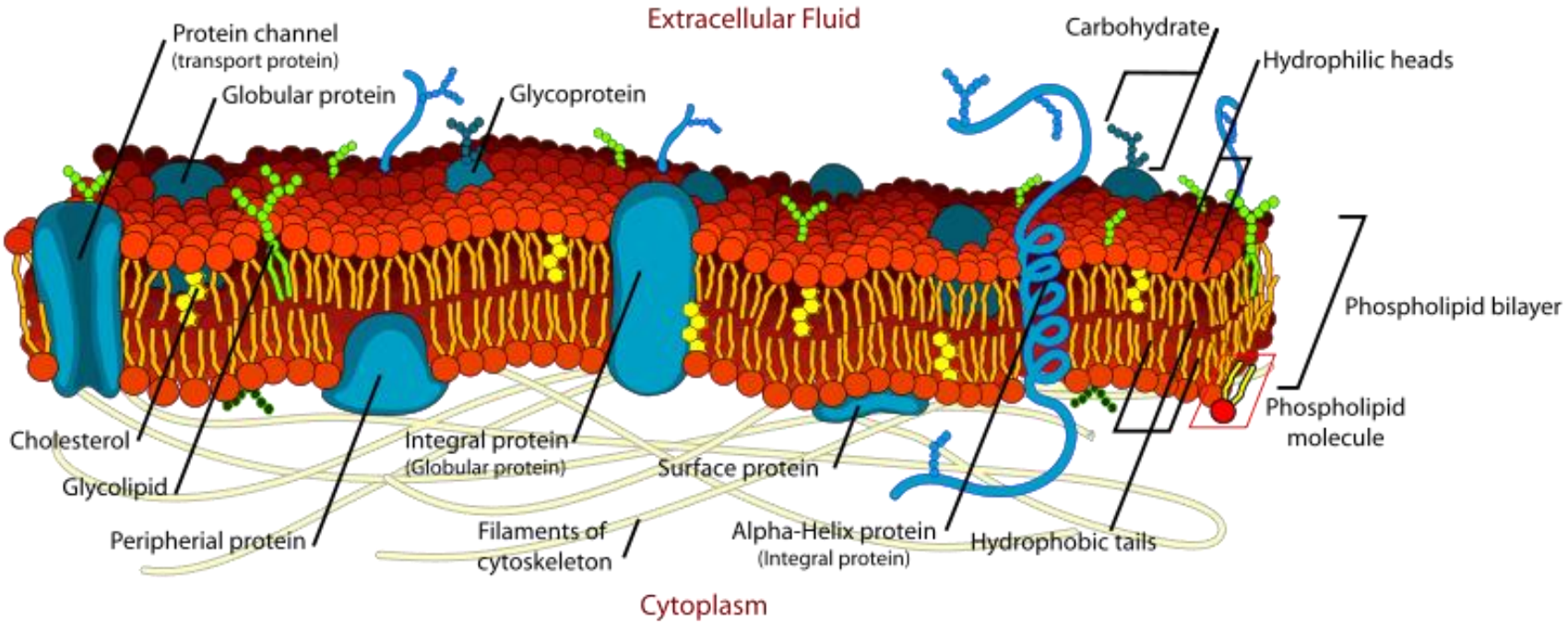
FRAP
Fluorescence Recovery After Photobleaching

$s = (4Dt)^{1/2}$ ⇨ PL ~ 2 µm v 1s





Biološke membrane so asimetrične

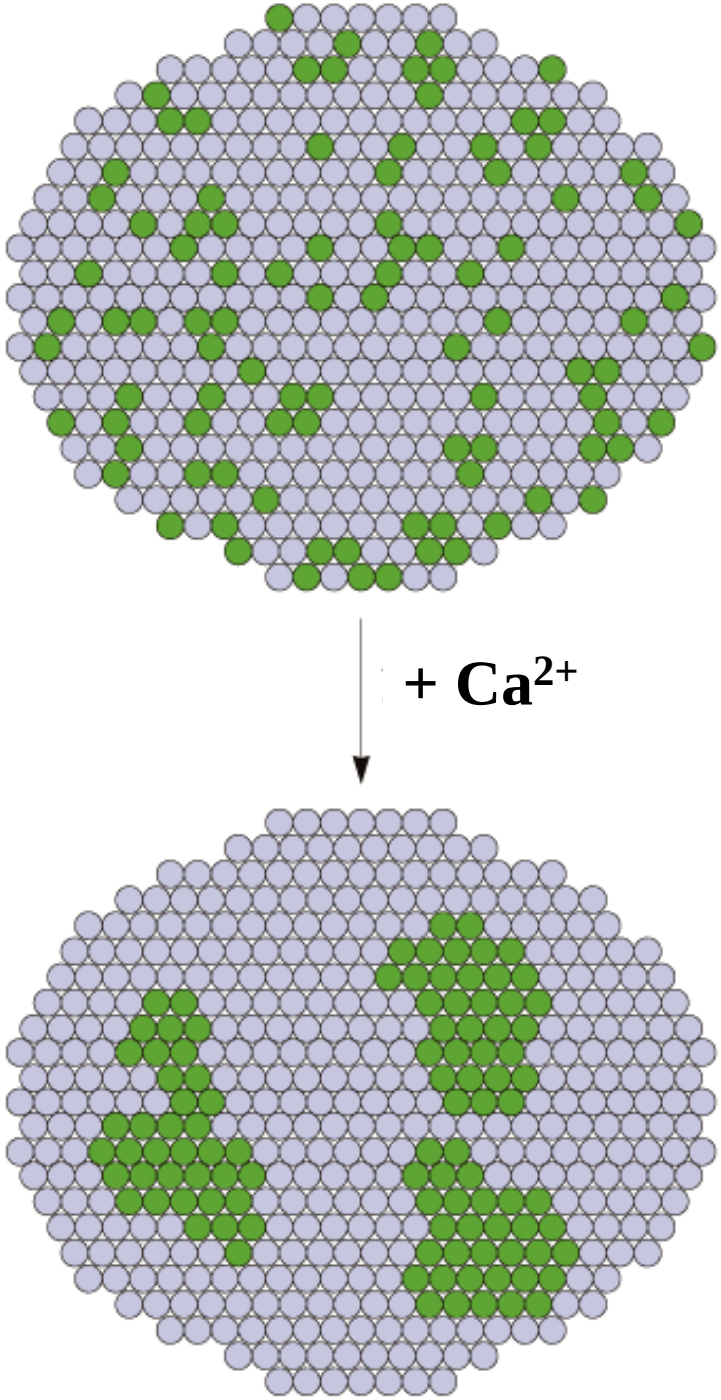


Lateralna asimetričnost BM

- Lateralna asimetrija proteinov:
  - Proteini se lahko oligomerizirajo v ravnini membrane - večinoma ni enakomerne porazdelitve.
- Lateralna asimetrija lipidov:
  - Lipidi se združujejo v ravnini membrane - fazna separacija - “**lipidne mikrodomene** ali **rafti**”.

Fazna separacija lipidov

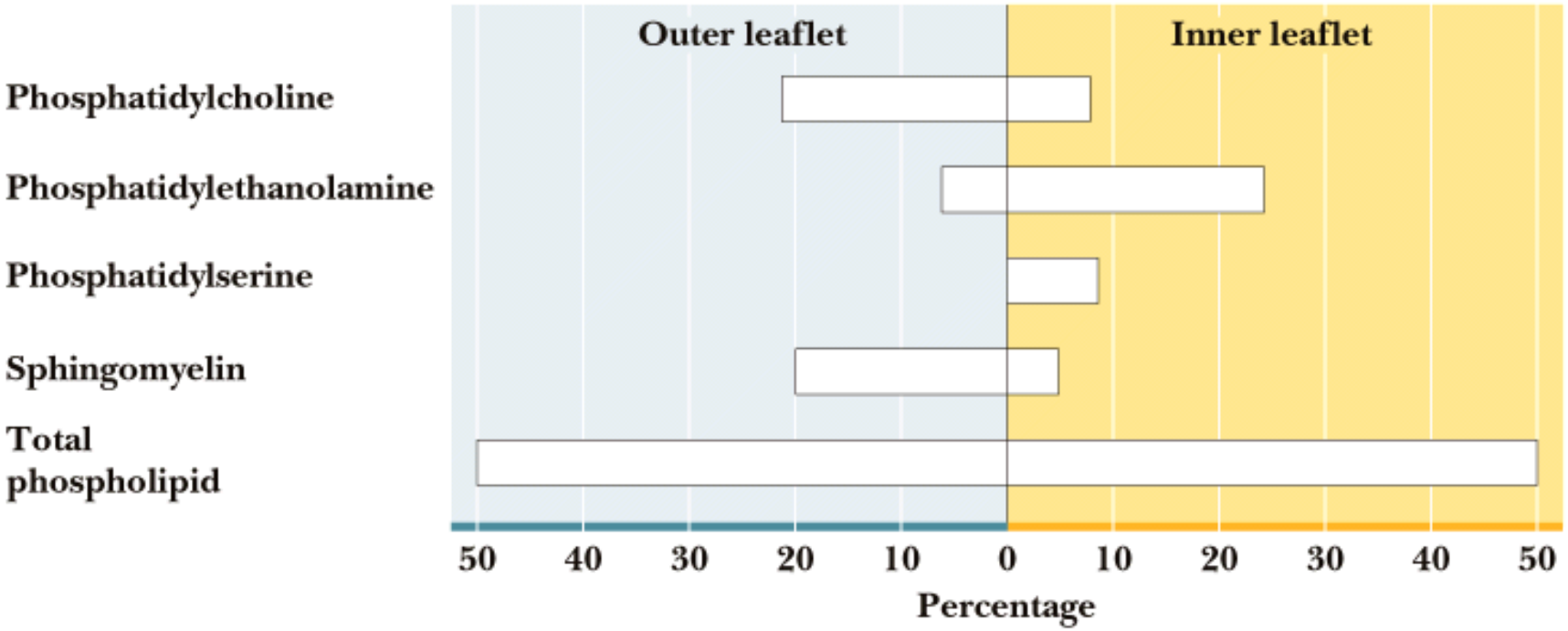
Raftni model BM



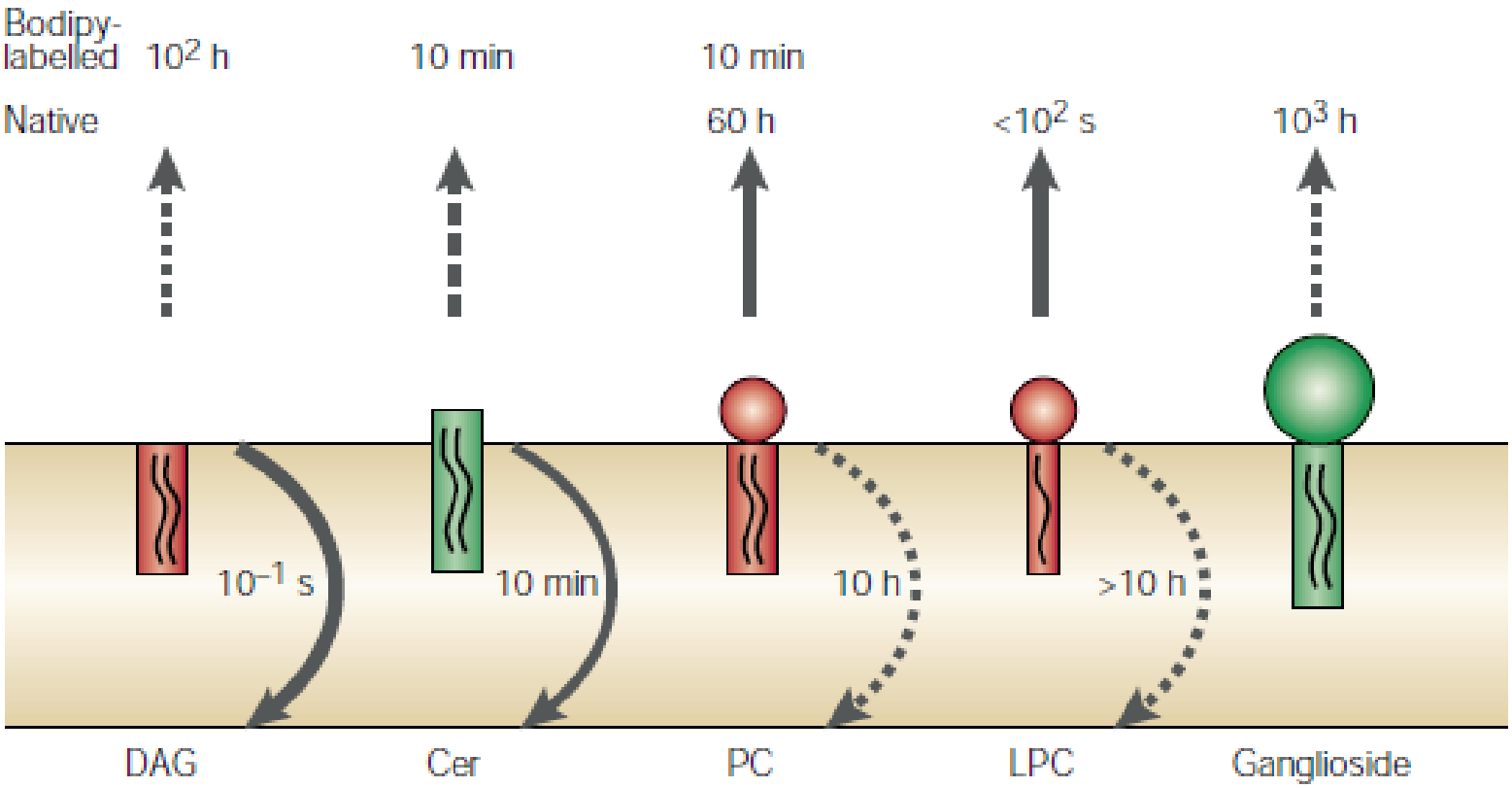
Transverzalna asimetričnost BM

- Transverzalna asimetrija proteinov
  - Primer: N-konec glikoforina je ekstracelularen, C-konec intracelularen.
- Transverzalna asimetrija lipidov
  - Sestava zunanjega monosloja je drugačna od notranjega.

Eritrocitna membrana: razlike v lipidni sestavi obeh slojev

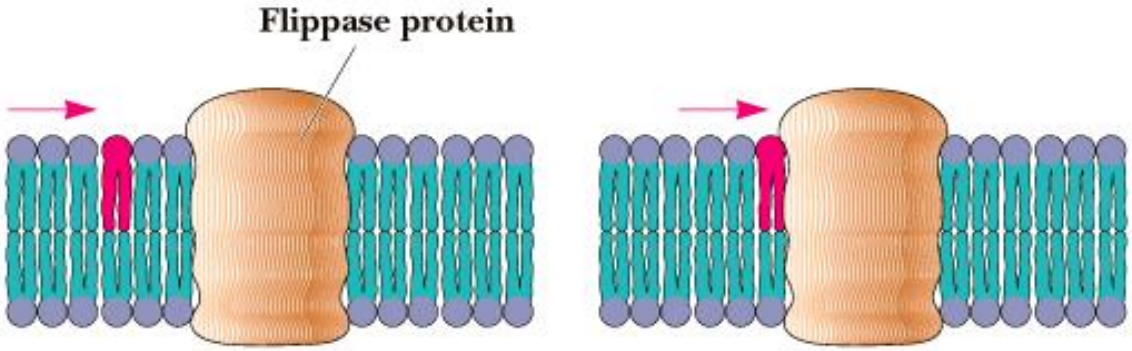


Čas potreben za spontan prehod lipida čez membranski dvosloj in za difuzijo v vodno fazo

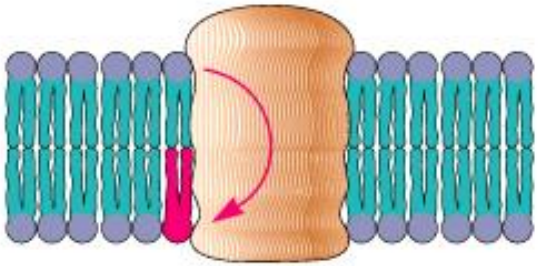


Flipaze

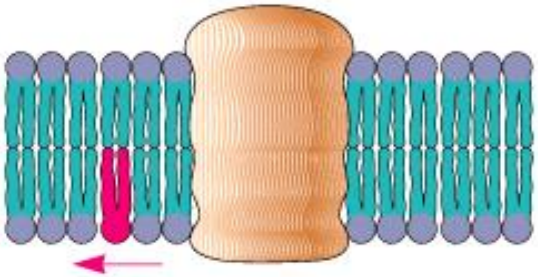
- Flipaze, proteini, katalizirajo transverzalno gibanje lipidov (“flip-flop”).
- Flipaze
  - pasivni transport
  - aktivni transport (poraba energije v obliki ATP).
- Aktivne flipaze (ABC transporterji) generirajo asimetrijo lipidov v membranah.



1 Lipid molecule diffuses to flippase protein



2 Flippase flips lipid to opposite side of bilayer



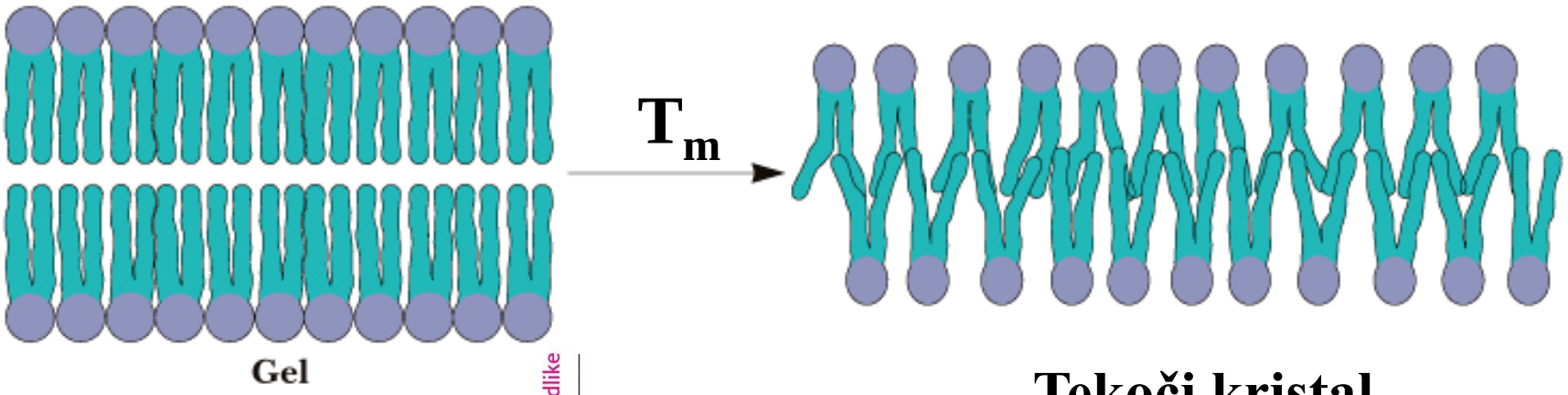
3 Lipid diffuses away from flippase

Fluidnost BM je odvisna od njene lipidne sestave

”Taljenje" membranskih lipidov - temperatura prehoda oz. „taljenja“ (“melting T”; T_m)

- Pod T_m - membranski lipidi togi, tesno zloženi.
- Nad T_m - lipidi fleksibilni, živahna lateralna difuzija.
- T_m - je posledica lastnosti lipidov v membrani.
- Samo čisti lipidni sistemi – fazni prehod v ozkem temperaturnem intervalu.

Fazni prehod



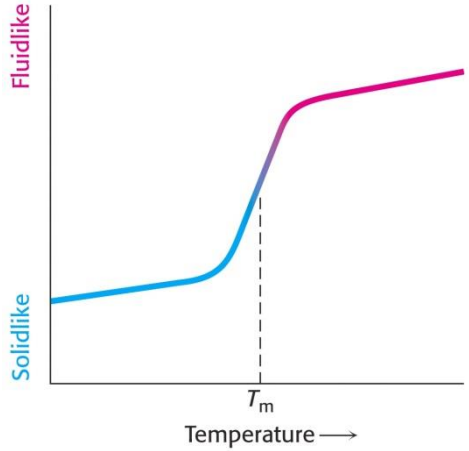
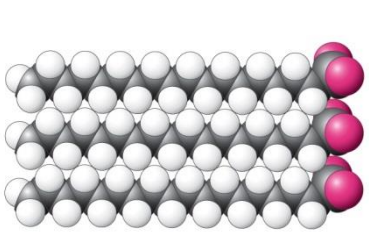
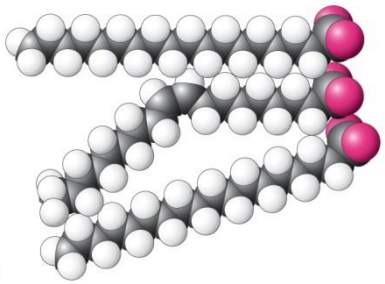


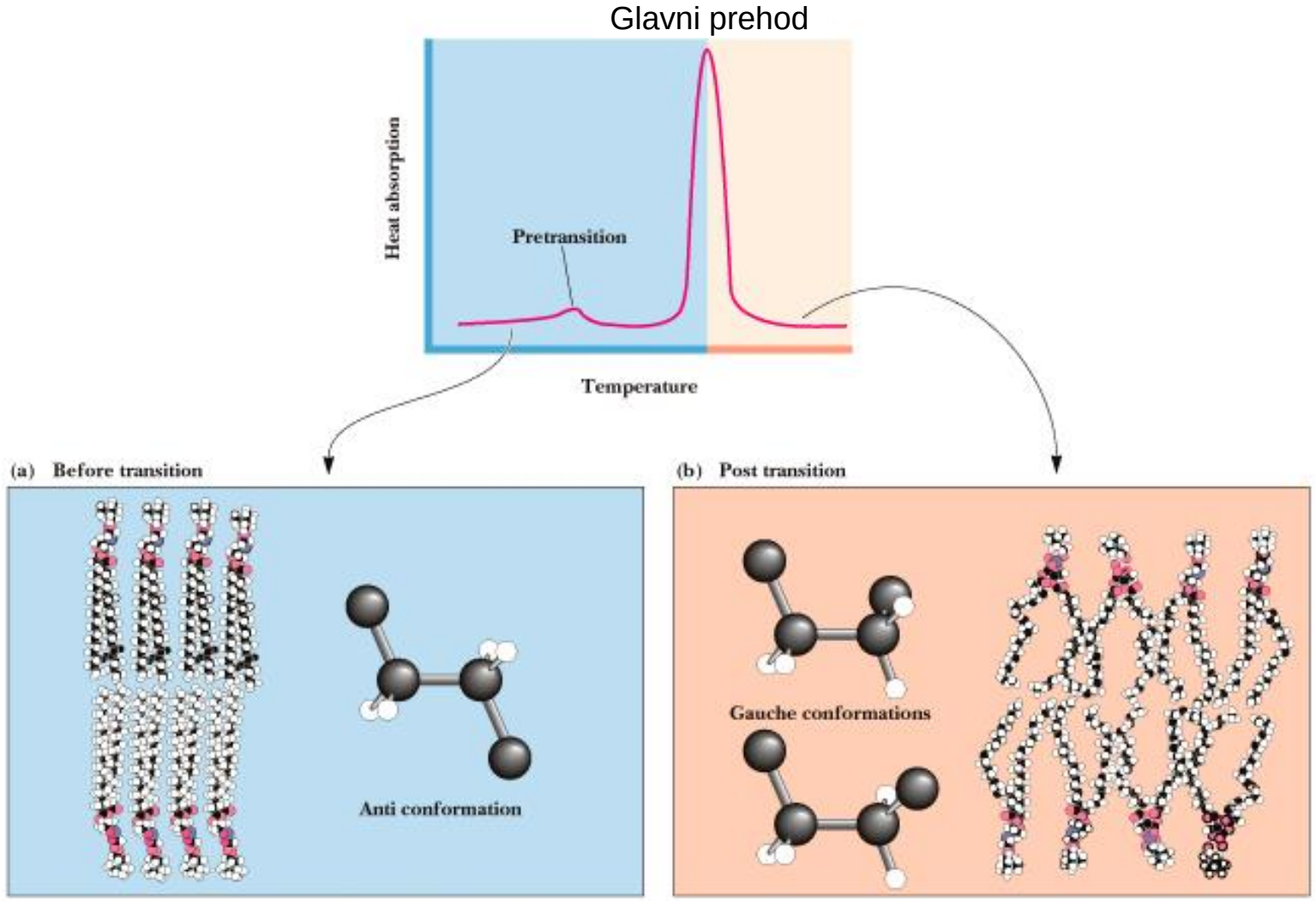
TABLE 12.3 **The melting temperature of phosphatidyl choline containing different pairs of identical fatty acid chains**

Number of carbons	Number of double bonds	Fatty acid		T_m (°C)
		Common name	Systematic name	
22	0	Behenate	*n*-Docosanote	75
18	0	Stearate	*n*-Octadecanoate	58
16	0	Palmitate	*n*-Hexadecanoate	41
14	0	Myristate	*n*-Tetradecanoate	24
18	1	Oleate	*cis*-Δ^9-Octadecenoate	−22





Določanje faznega prehoda s kalorimetrijo

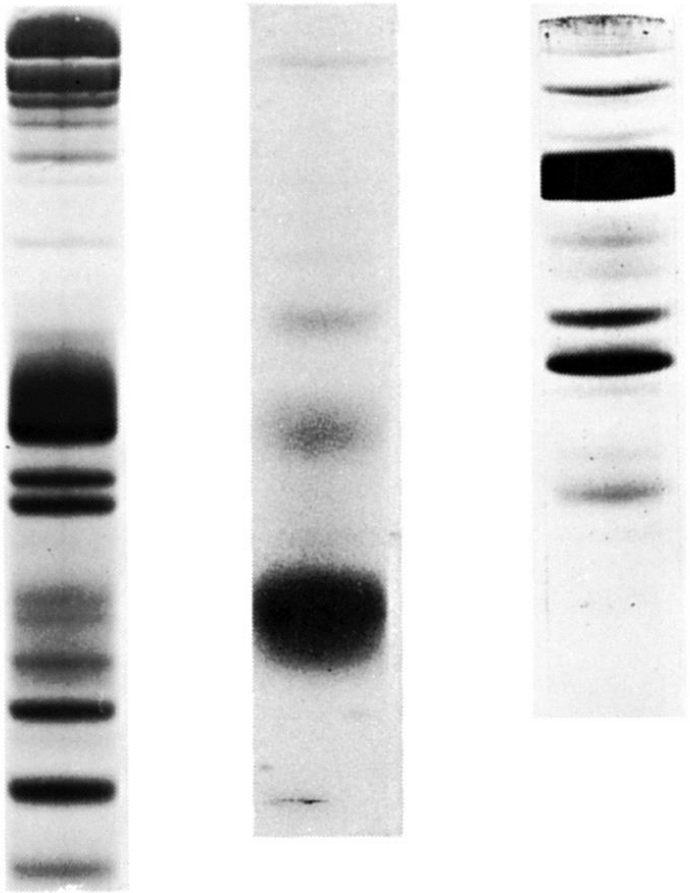


Membranski proteini

- Periferni membranski proteini.
- Integralni membranski proteini.
- Proteini, zasidrani v membrani z lipidnimi “sidri”.

Vsebnost proteina v b.m. je lahko zelo različna

- mielin (oligodendrociti) 18%
- notranja m. MT 75%
- povprečno v PM 50%



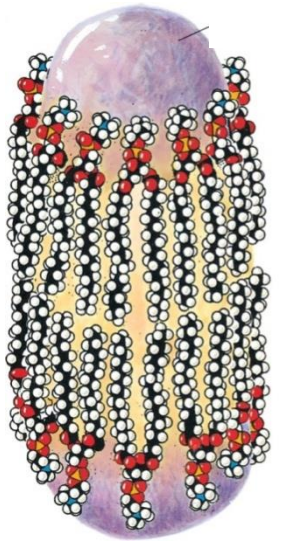
eritrocit fotoreceptor sarkopl. ret.

Periferni proteini

- Periferni proteini šibko vezani na površino membran.
- Se ločijo (oddisociirajo) od membrane z detergenti ali povišano ionsko jakostjo raztopine (npr. 1M KCl, 1M NaCl).

Integralni membranski proteini

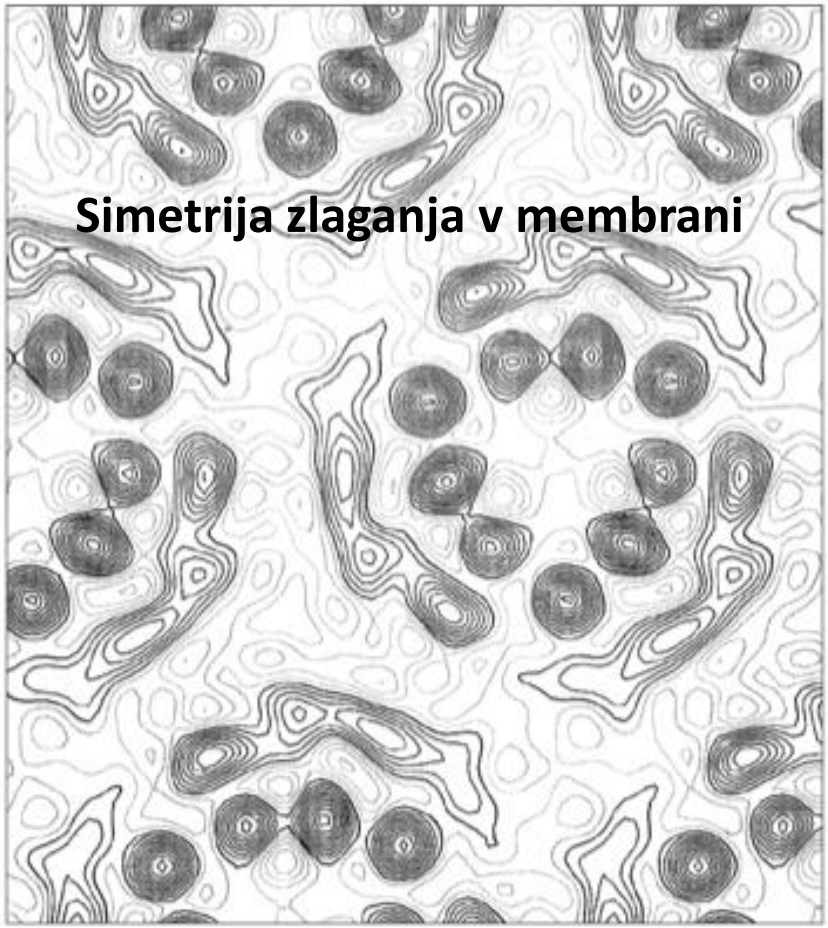
- Močno zasidrani v lipidni dvosloj.
- Ekstrakcija le z “raztapljanjem” lipidnega dvosloja:
  - organska topila
  - detergenti
- Pogosto transmembranski, ni pa nujno.
- Primeri: bakteriorodopsin, glikoforin, porini.

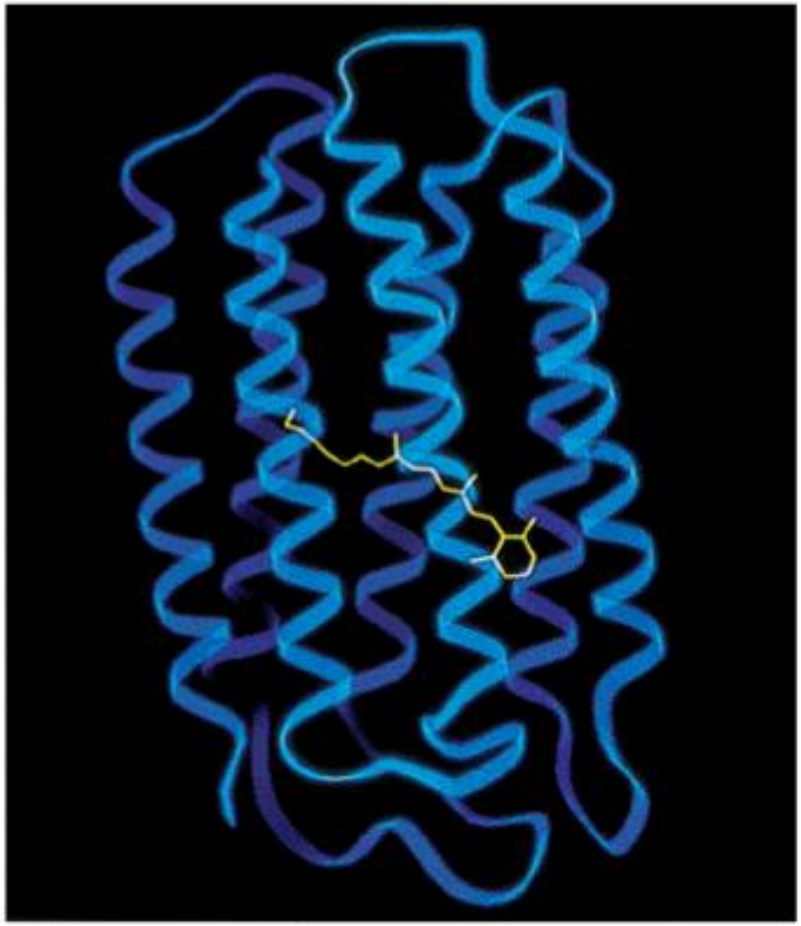


Bakteriorodopsin

- Ima 7 transmembranskih α-vijačnih predelov s kratkimi vmesnimi zankami.
- Vir: *Halobacterium halobium* (škrlatna bakterija - arhea).
- Funkcija: sodeluje pri pretvarjanju svetlobne energije v kemijsko (ATP) - je svetlobno-gnana protonska črpalka! Nastali pH gradient poganja sintezo ATP.

Struktura bakteriorodopsina





α-vijačnico tvorijo pretežno nepolarni aminokislinski ostanki.
Je najbolj pogost strukturni element za prehajanje membrane pri m. proteinih.

Glikoforin

- Transmembranski protein v PM eritrocitov.
- En transmembranski segment + globularni domeni, na N- in C-koncu.
- Transmembranski segment je α-vijačnica, sestavljna iz 19 hidrofobnih ak ostankov.
- Zunajcelični del je močno glikoziliran (60%): sladkorji tvorijo hidrofilen plašč eritrocitov in določajo krvno skupino.

Struktura glikoforina

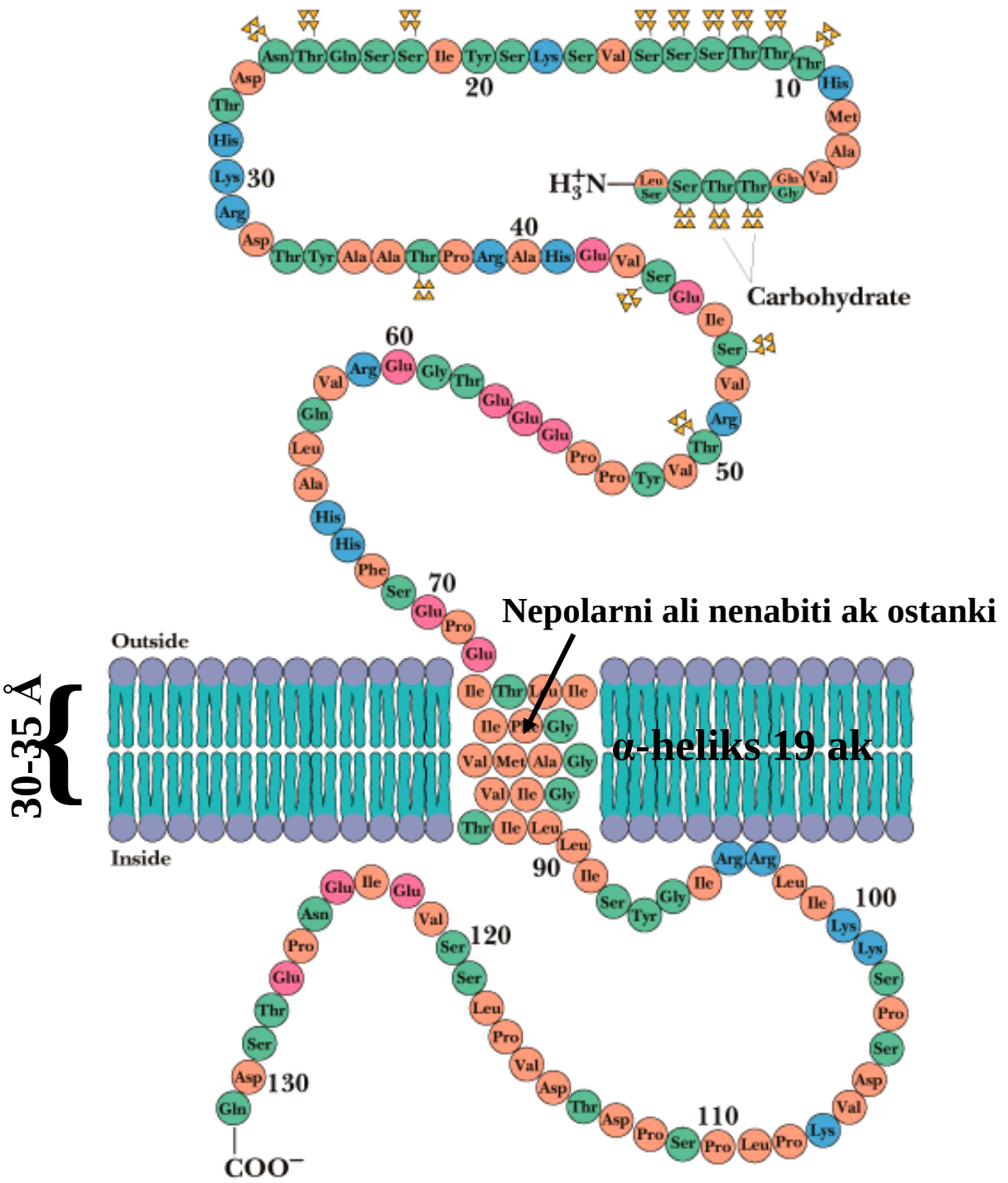
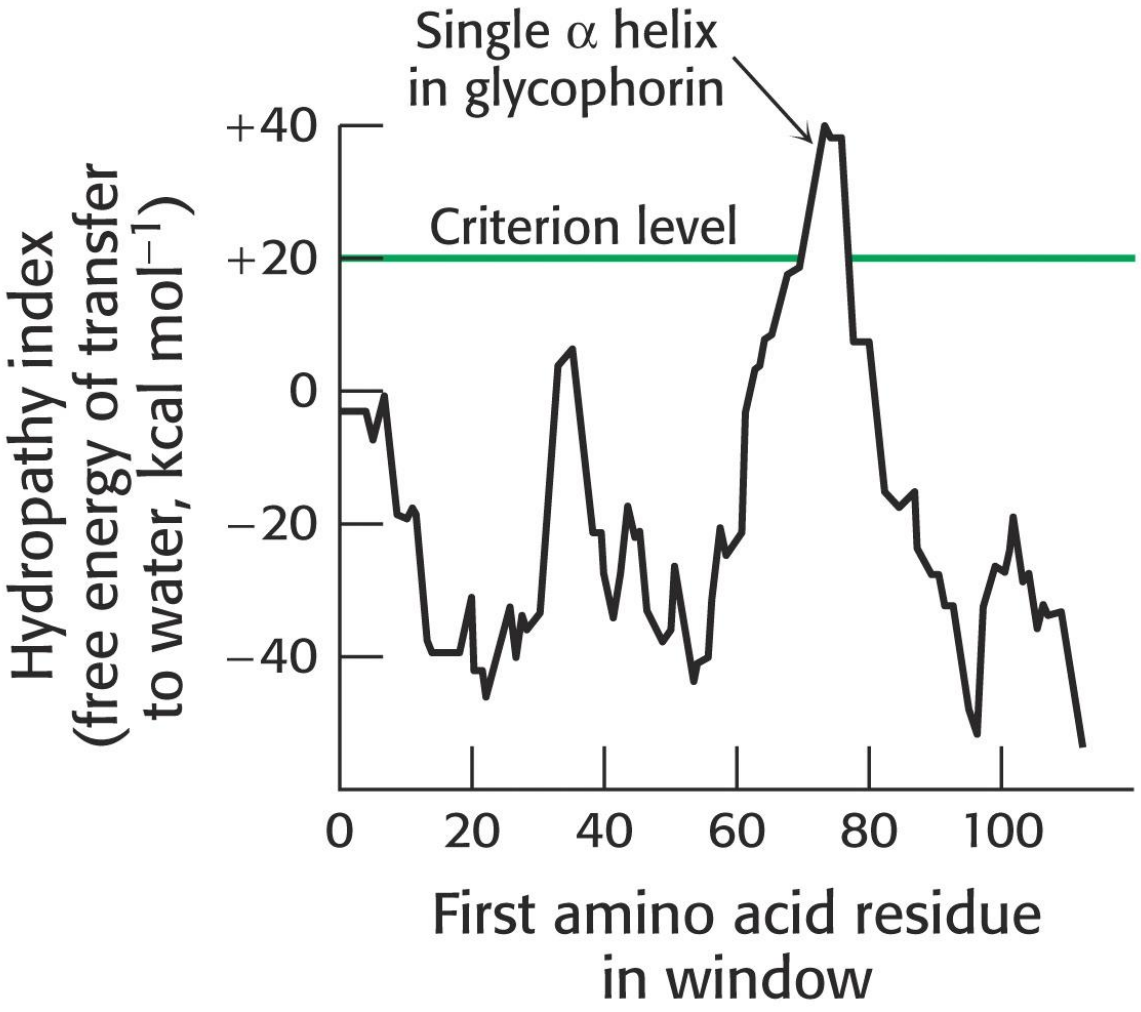


TABLE 12.2 Polarity scale for identifying transmembrane helices

Amino acid residue	Transfer free energy kcal mol^{-1} (kJ mol^{-1})
Phe	3.7 (15.5)
Met	3.4 (14.3)
Ile	3.1 (13.0)
Leu	2.8 (11.8)
Val	2.6 (10.9)
Cys	2.0 (8.4)
Trp	1.9 (8.0)
Ala	1.6 (6.7)
Thr	1.2 (5.0)
Gly	1.0 (4.2)
Ser	0.6 (2.5)
Pro	−0.2 (−0.8)
Tyr	−0.7 (−2.9)
His	−3.0 (−12.6)
Gln	−4.1 (−17.2)
Asn	−4.8 (−20.2)
Glu	−8.2 (−34.4)
Lys	−8.8 (−37.0)
Asp	−9.2 (−38.6)
Arg	−12.3 (−51.7)

Source: After D. M. Engelman, T. A. Steitz, and A. Goldman. *Annu. Rev. Biophys. Biophys. Chem.* 15(1986):330.
Note: The free energies are for the transfer of an amino acid residue in an α helix from the membrane interior (assumed to have a dielectric constant of 2) to water.

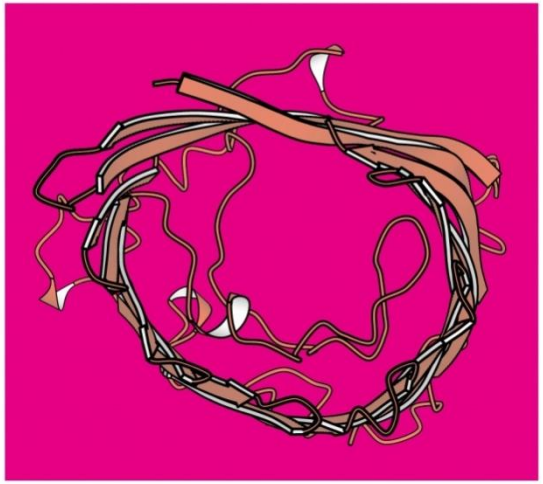
Hidropatski profil glikoforina A

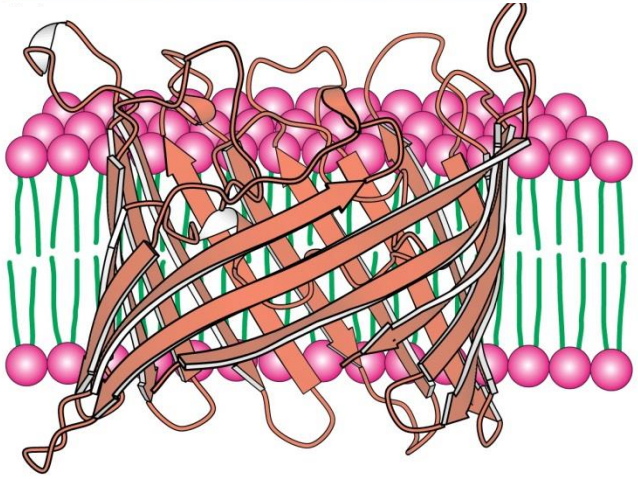


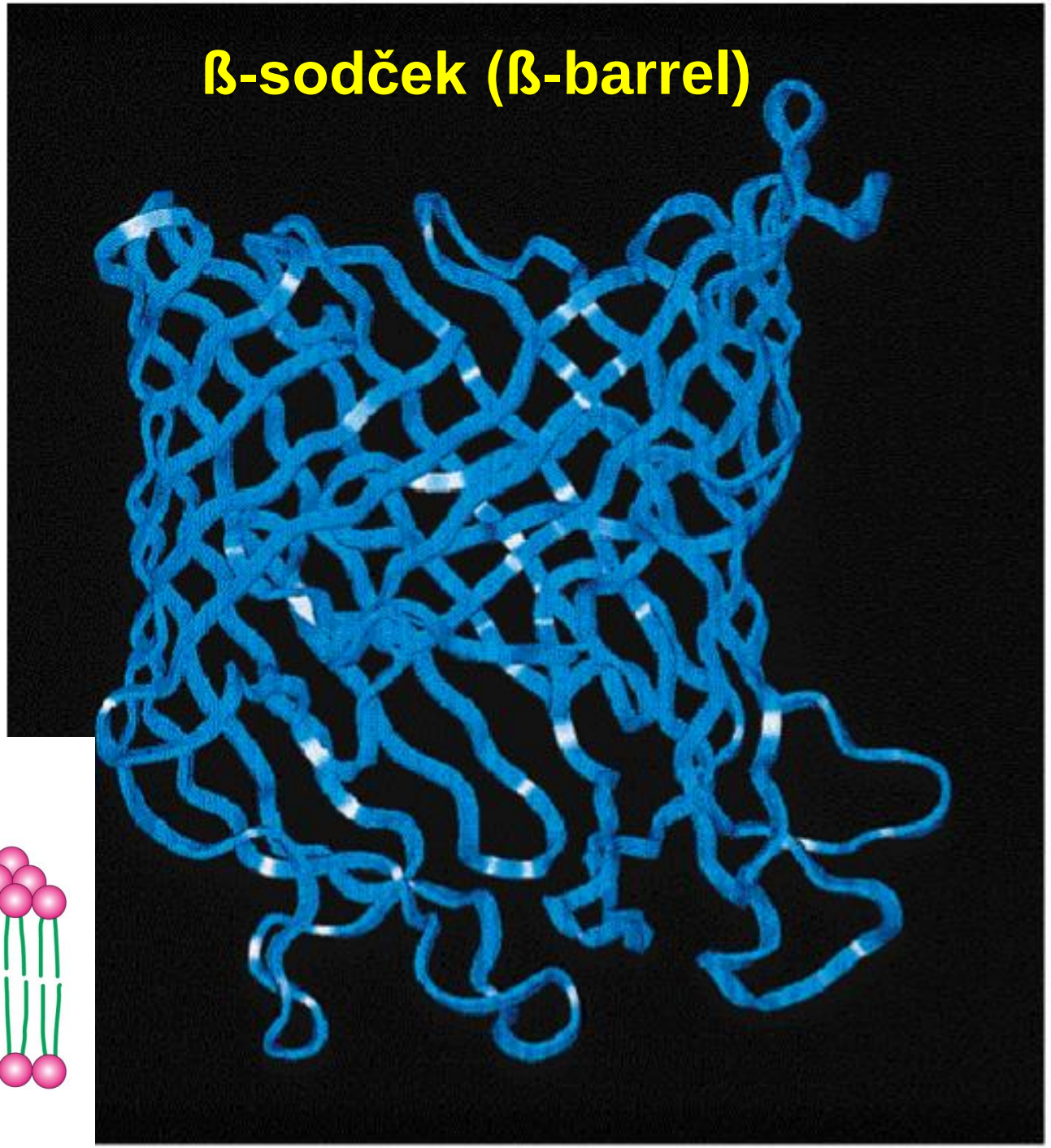
Porini

- Transmembranski protein v zunanji m. G^- in nekaterih G^+ bakterij, MT in kloroplastih.
- Transmembranski proteini s strukturo ß-sodčka.
- Tvorijo kanalčke, ki omogočajo pasivno difuzijo različnih vrst molekul.

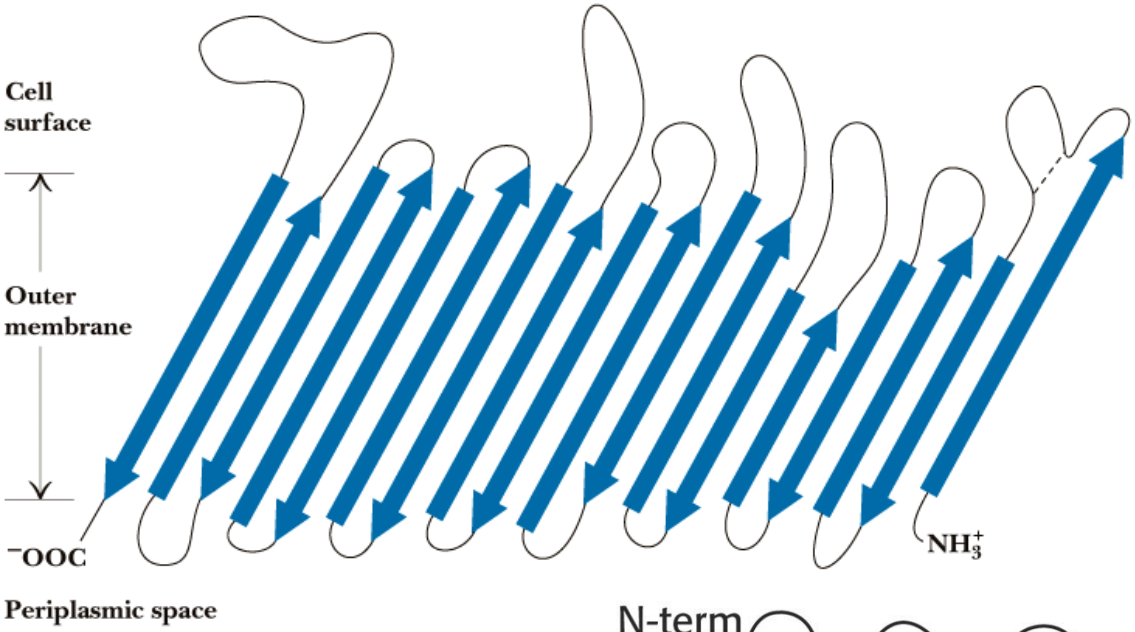
Bakterijski porin

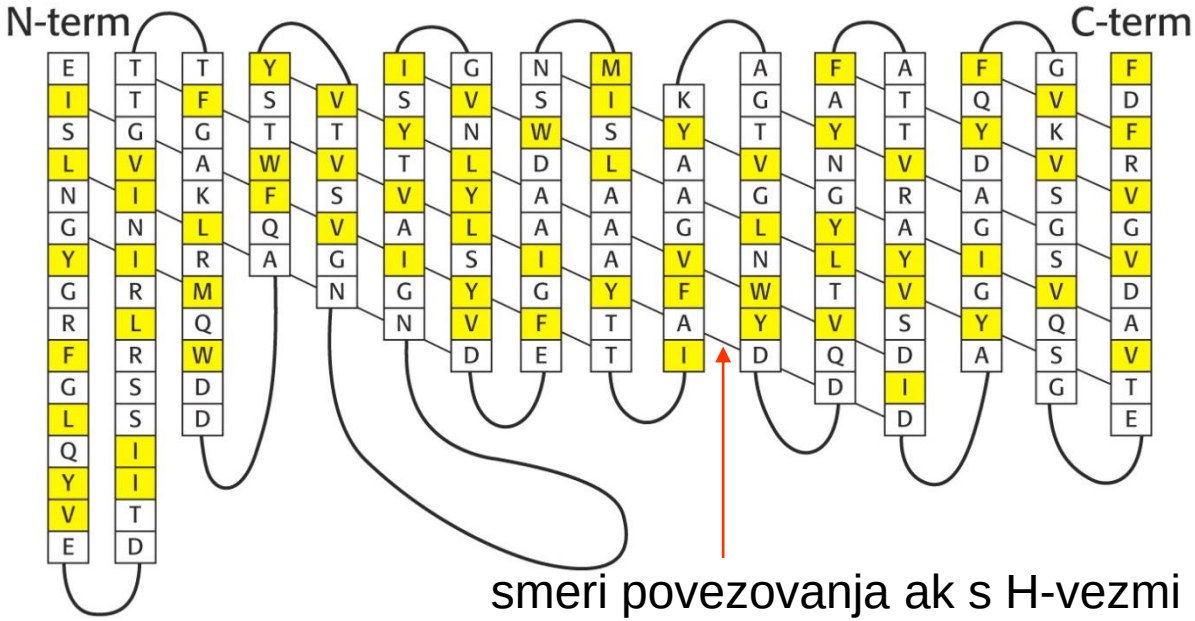




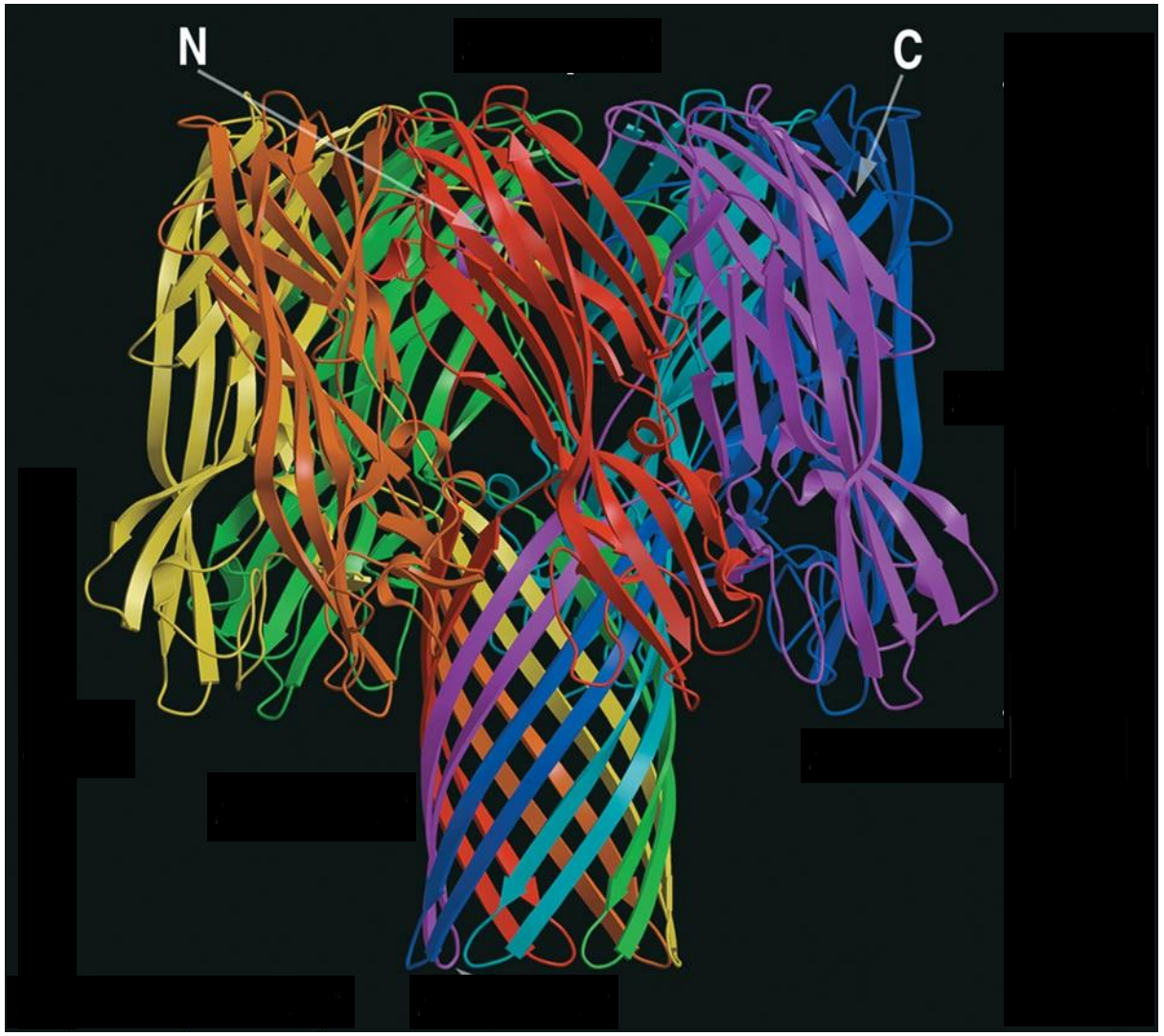


Bakterijski porin

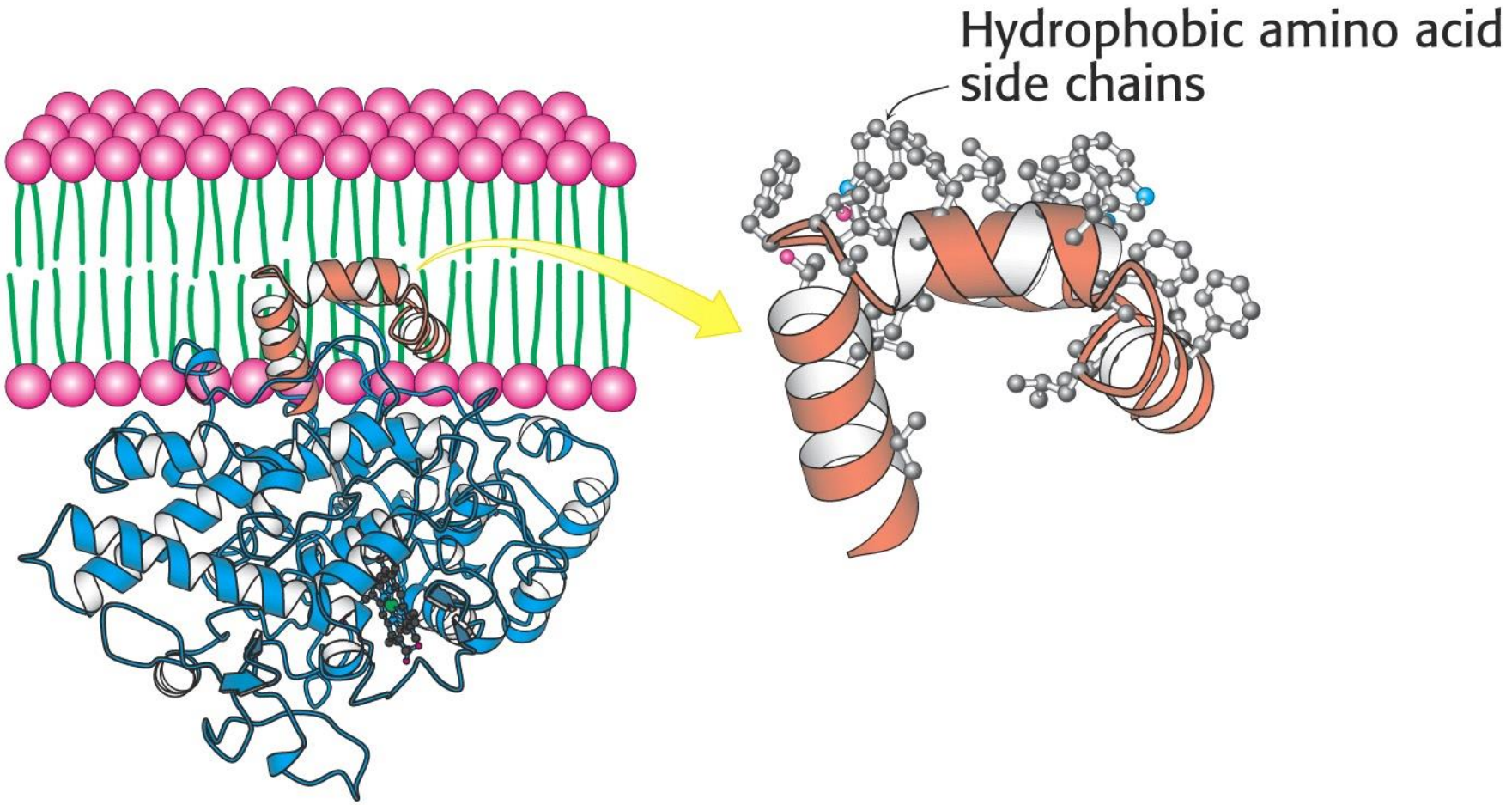


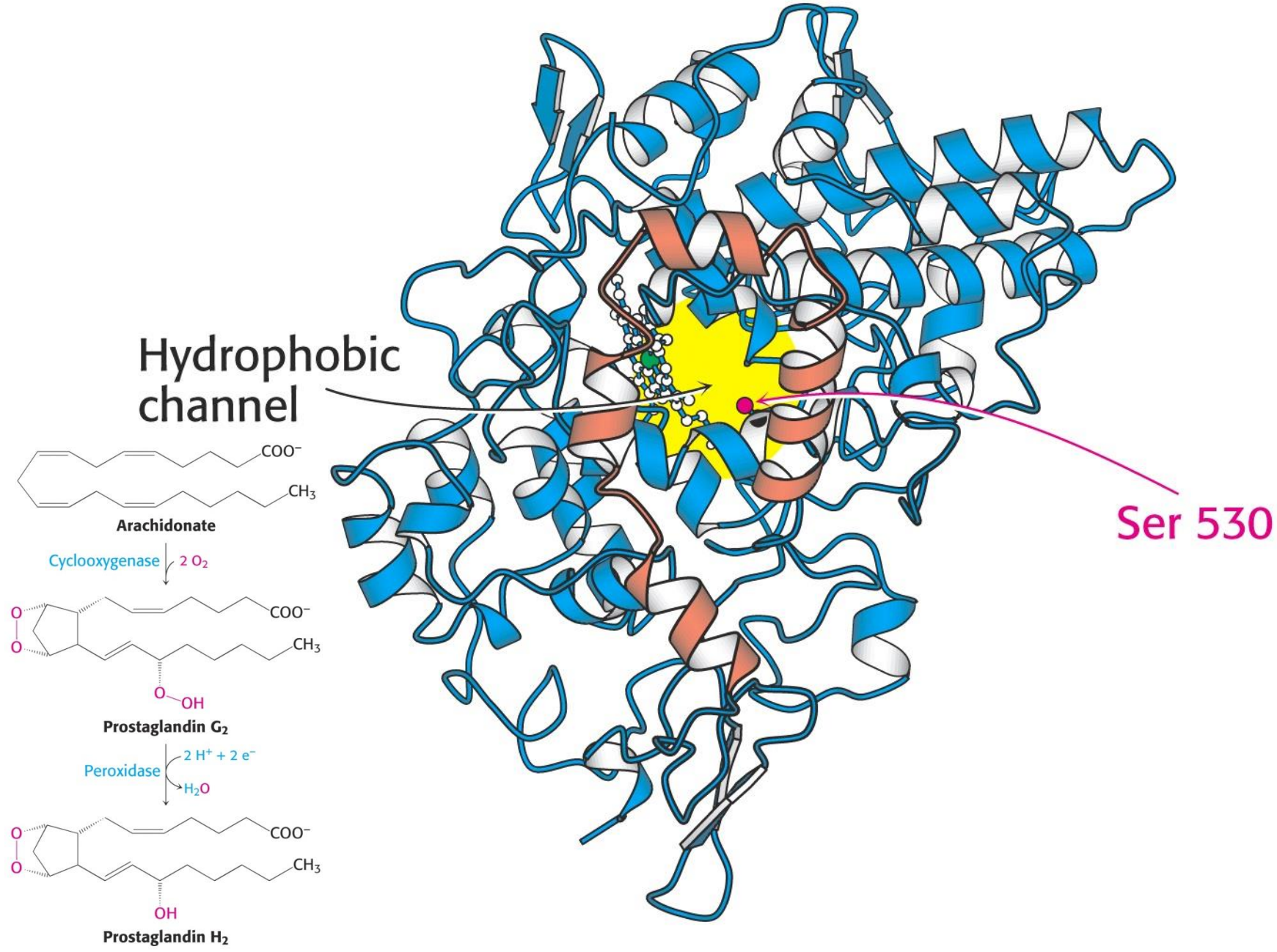


Kristalna struktura α-hemolizina (*Staphylococcus aureus*)



Prostaglandin-sintaza: ne-transmembranski integralni m.p.




Hydrophobic channel
Ser 530
COO⁻
CH3
Arachidonate
Cyclooxygenase
2 O2
O
O
OH
Prostaglandin G2
Peroxidase
2 H+ + 2 e⁻
H2O
Prostaglandin H2

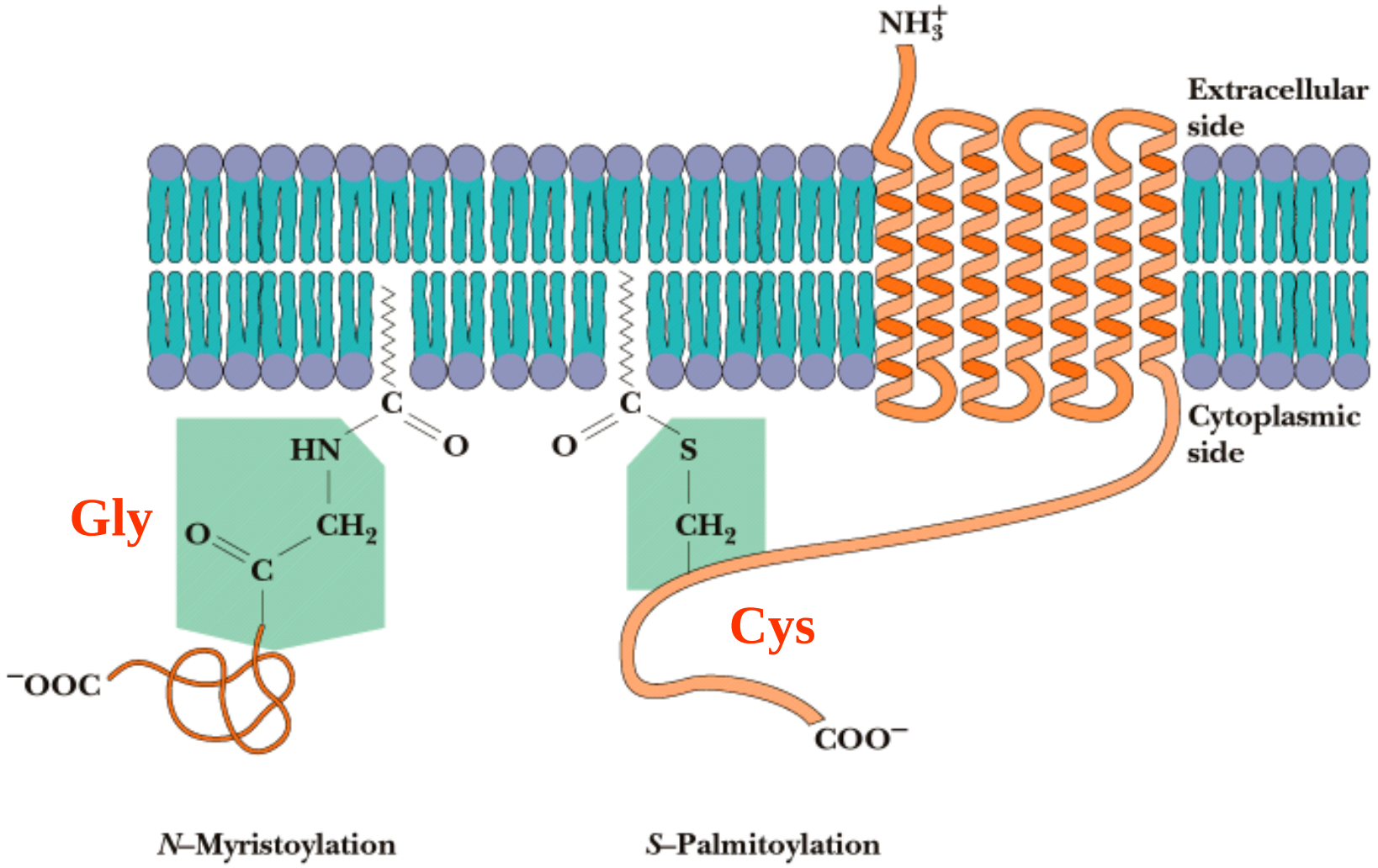
Membranski proteini, sidrani v BM s kovalentno-vezanimi lipidi

- 4 tipi vezav v lipidno plast:
  - Acilno sidro - amidna vez z N-koncem proteina (miristoilno sidro).
  - Acilno sidro - tioestrska vez s proteinom (Cys).
  - Prenilno sidro - tioetrska vez.
  - Glikozil-fosfatidilinozitolno (GPI) sidro.

Miristoilno sidro

- Miristinska kislina ($C_{14:0}$) vezana na α-NH_2-skupino proteina z amidno vezjo.
- Vezava izključno na N-terminalni Gly v proteinih.
- Primeri: cAMP-odvisna proteinska kinaza, $pp60^{src}$ tirozinska kinaza, kalcineurin B, α-podenota G-proteina, gag-protein HIV-1.

Miristoilno in druga acilna sidra



Acilno sidro

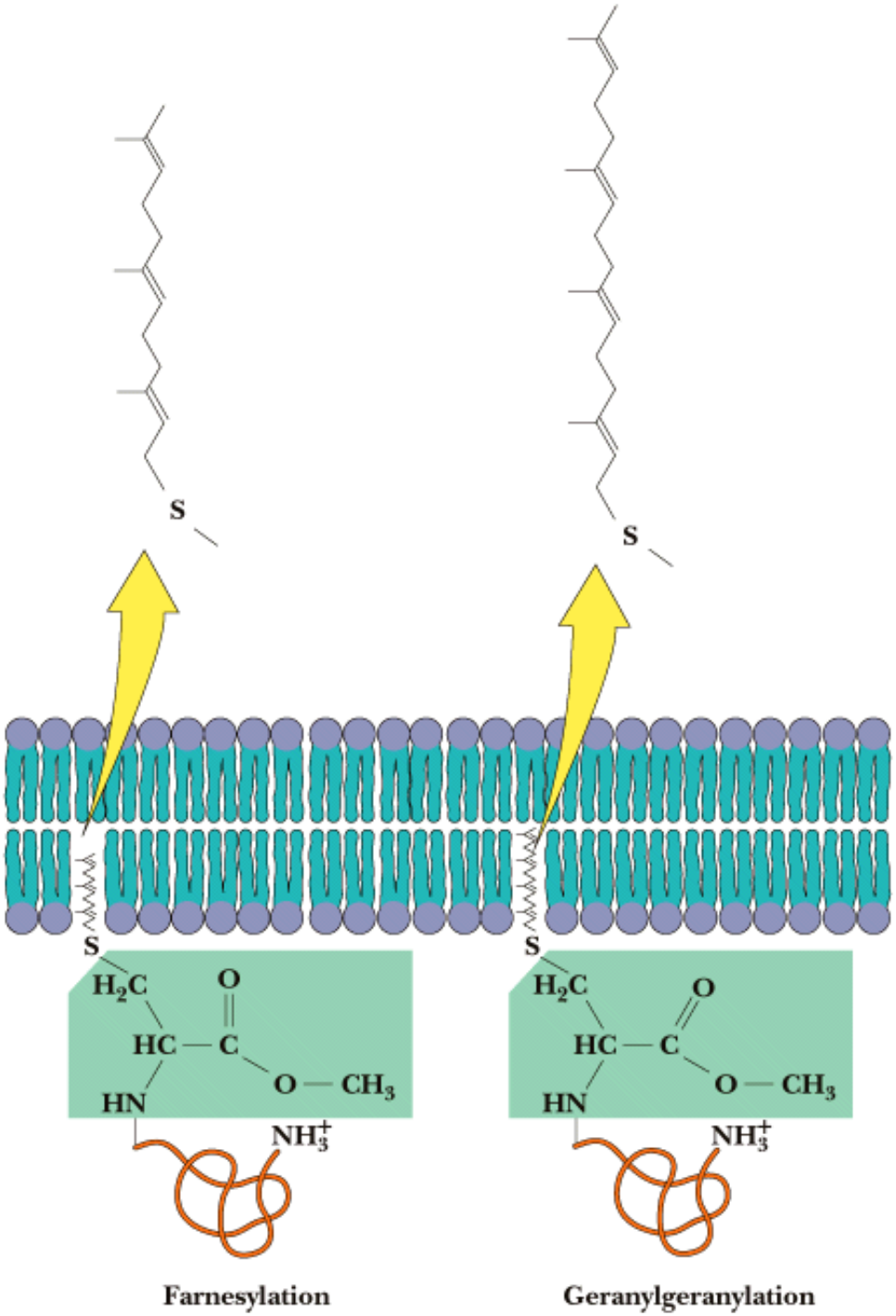
- Acilno sidro je lahko miristat, palmitat, stearat ali oleat.
- Vezano s (tio)estrsko vezjo na Cys, Ser ali Thr ostanek v proteinu.
- Primeri: G-protein-sklopljeni receptorji, površinski glikoproteini nekaterih virusov, transferinski receptor, SNAP-25, kaveolini ...

Prenilno sidro

- Prenilacija: vezava “izoprenskih derivatov”.
- Vezano s tioetersko vezjo na Cys v zaporedju CAAX na C-koncu proteina (C=Cys, A=alifatski ostanek, X=poljubni ostanek).
- Izoprenske skupine (C_5):
  - farnezilni ostanek (C_{15}, 3 dvojne vezi) - seskviterpen
  - geranilgeranilni ostanek (C_{20}, 4 dvojne vezi) - diterpen
- Primeri: Ras in Rab proteini, jedrni lamini ...

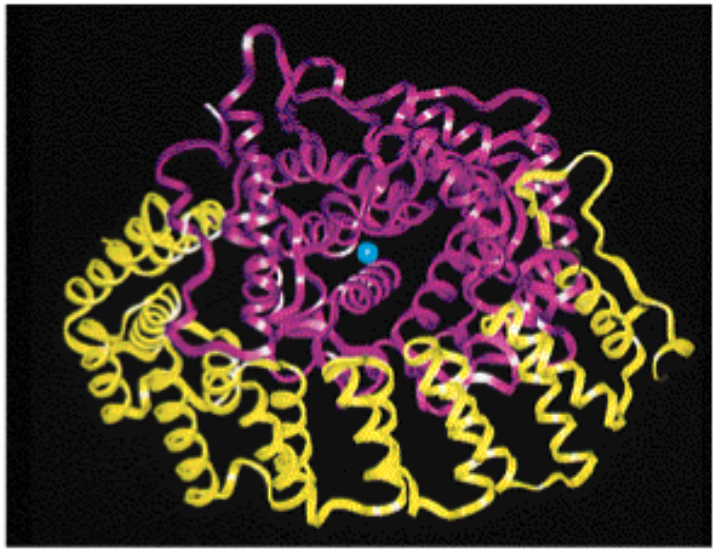
Prenilni sidri:

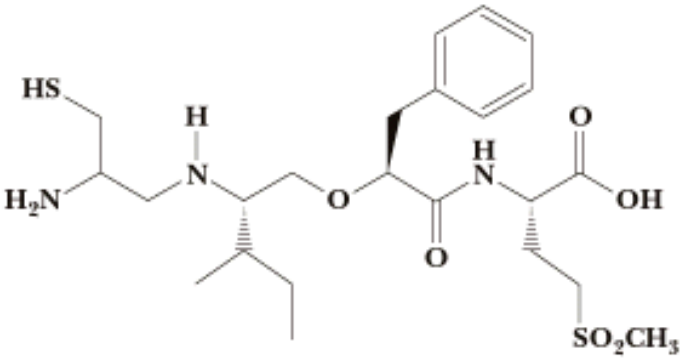
- farnezilno
- geranil-geranilno



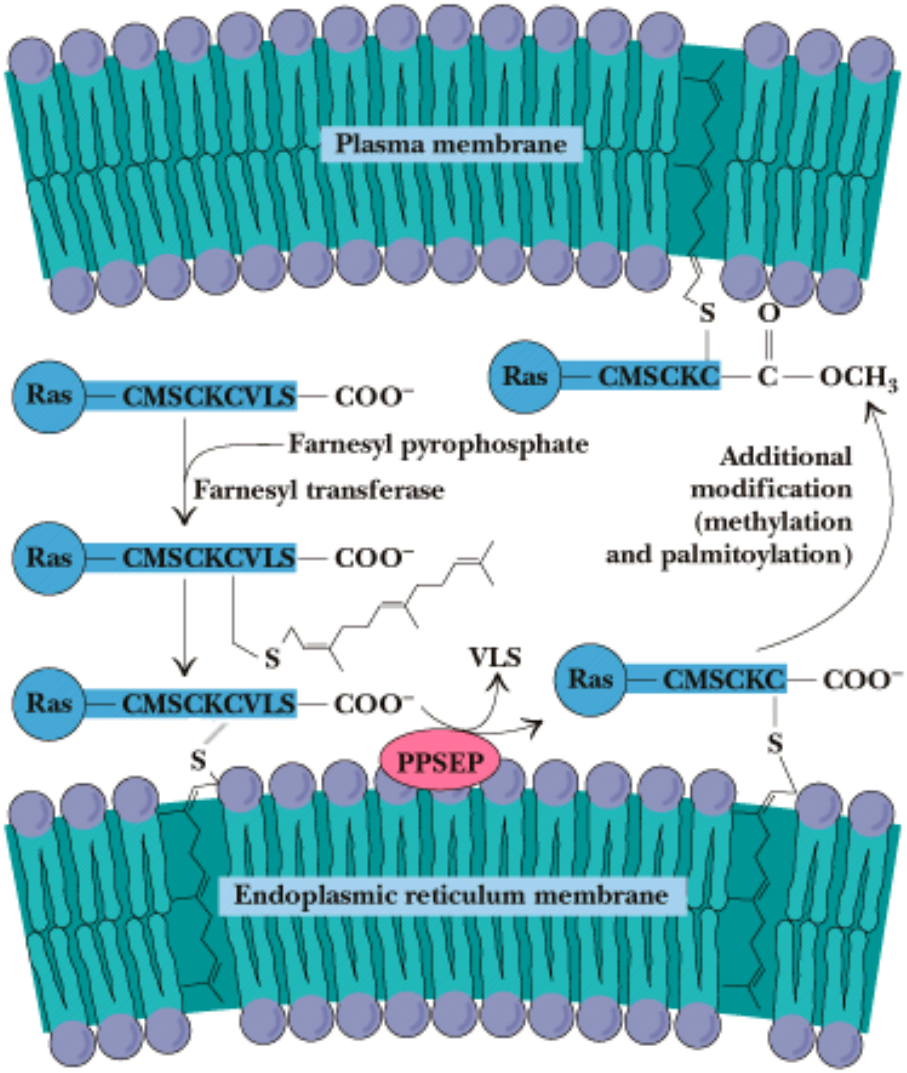
Farnezilacija Ras-proteina

Farnezil transferaza





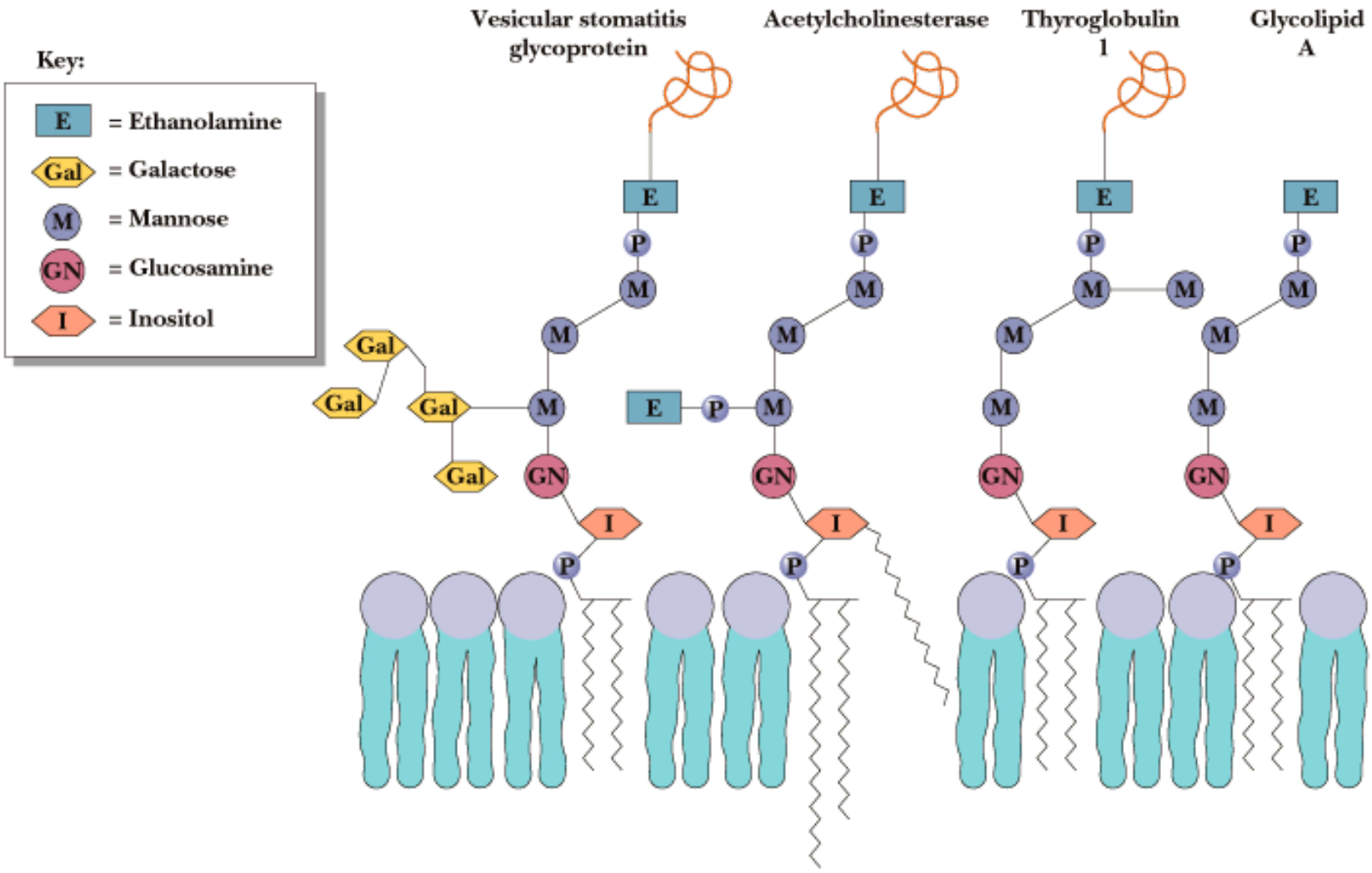
Inhibitor farnezil transferaze



Glikozil-fosfatidilinozitolno sidro (GPI sidro)

- Vedno vezava na C-terminalni ostanek.
- Fosfoetanolamin povezuje C-konec proteina preko oligosaharidne enote na fosfatidilinozitol (PI).
- Primeri: adhezijske molekule, hidrolaze na površini celic, PrP^{C}, PLAP, Thy-1 ...
- Pogosto v lipidnih “raftih”.

Različna GPI sidra



Lipidna sidra – vloga pri signaliziranju

- Reverzibilna vezava sidra - kontrolna funkcija/modulacija v signalnih poteh (alternativno razmeščanje proteina).
- Podobnost s fosforilacijo/defosforilacijo, vezavo/disociacijo substrata, proženjem s proteolitičnim razcepom, itd …