第25章 戊糖磷酸途径和糖的其他代谢途径

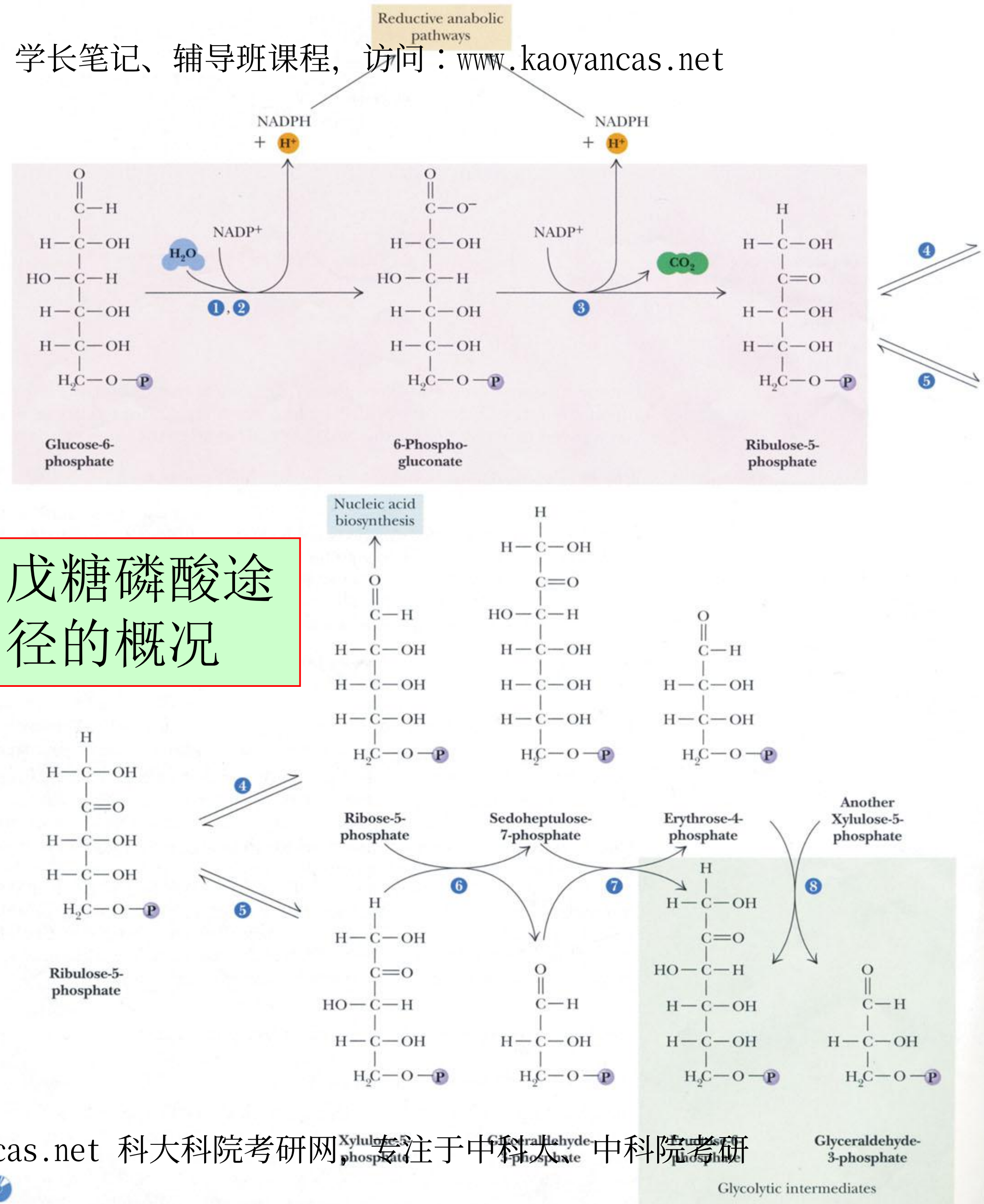
一、戊糖磷酸途径

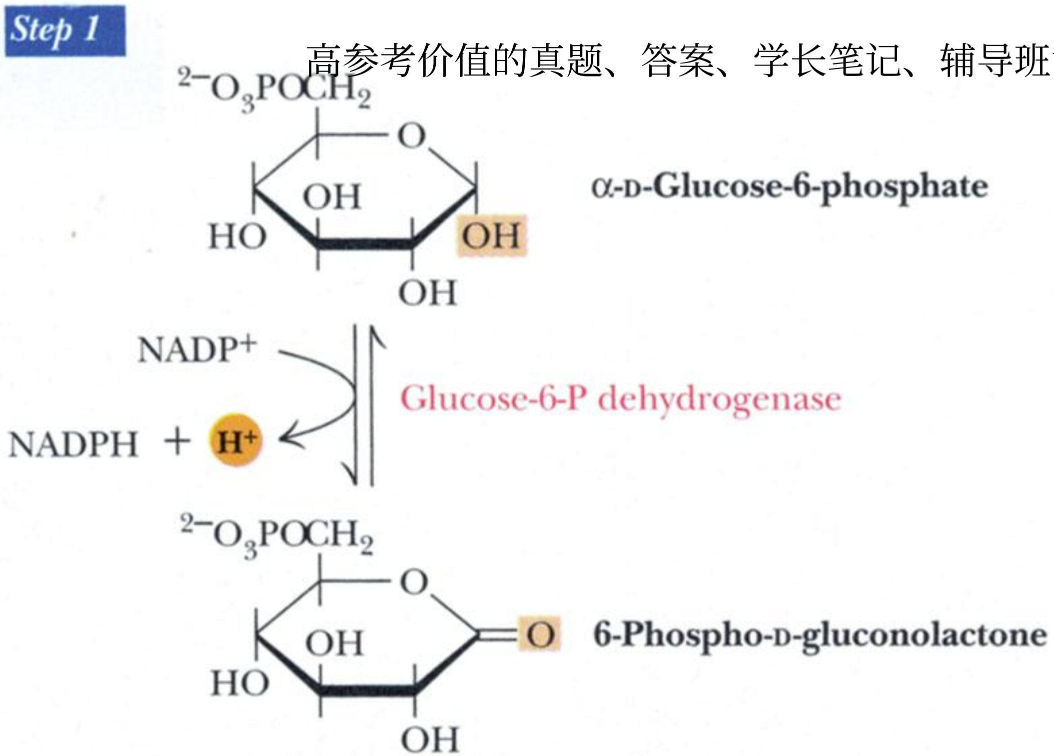
（一）戊糖磷酸途径的发现

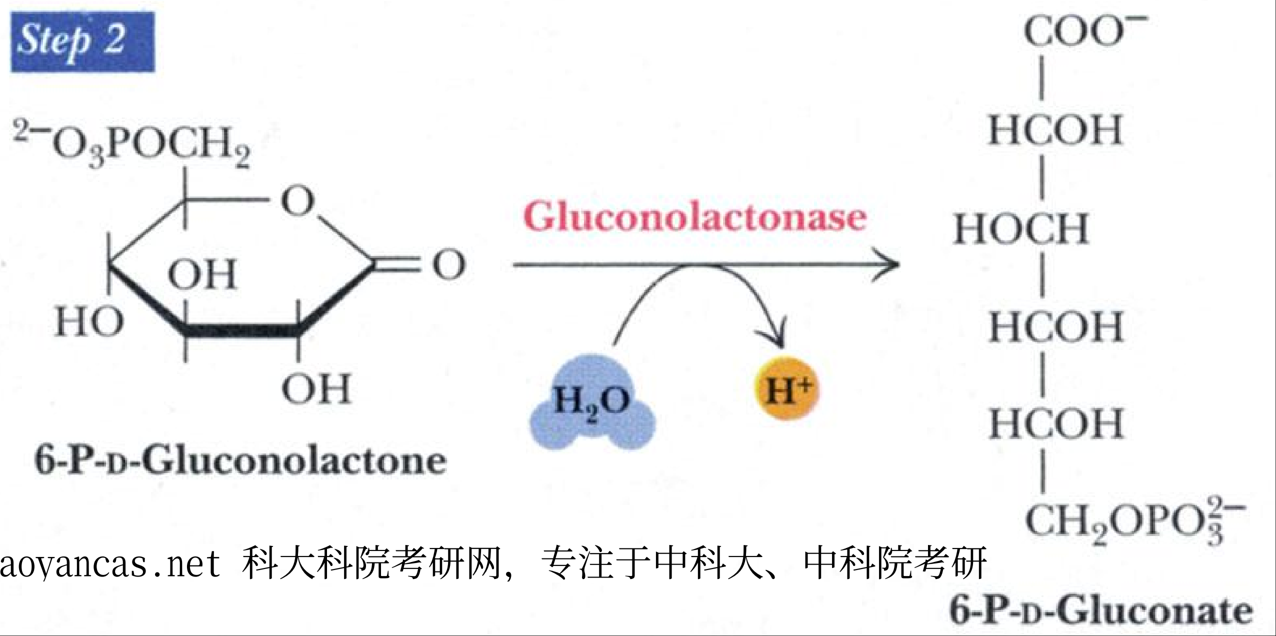
1931年Otto Warburg 等发现G-6-p脱氢酶和葡萄糖酸-6-p脱氢酶可以使葡萄糖进入未知的代谢途径，$NADP^+$是两种酶的辅酶； Frank Dickens分离了戊糖磷酸途径的不少中间物，于1953年在总结前人工作的基础上提出了戊糖磷酸途径，随后证明这一途径普遍存在。

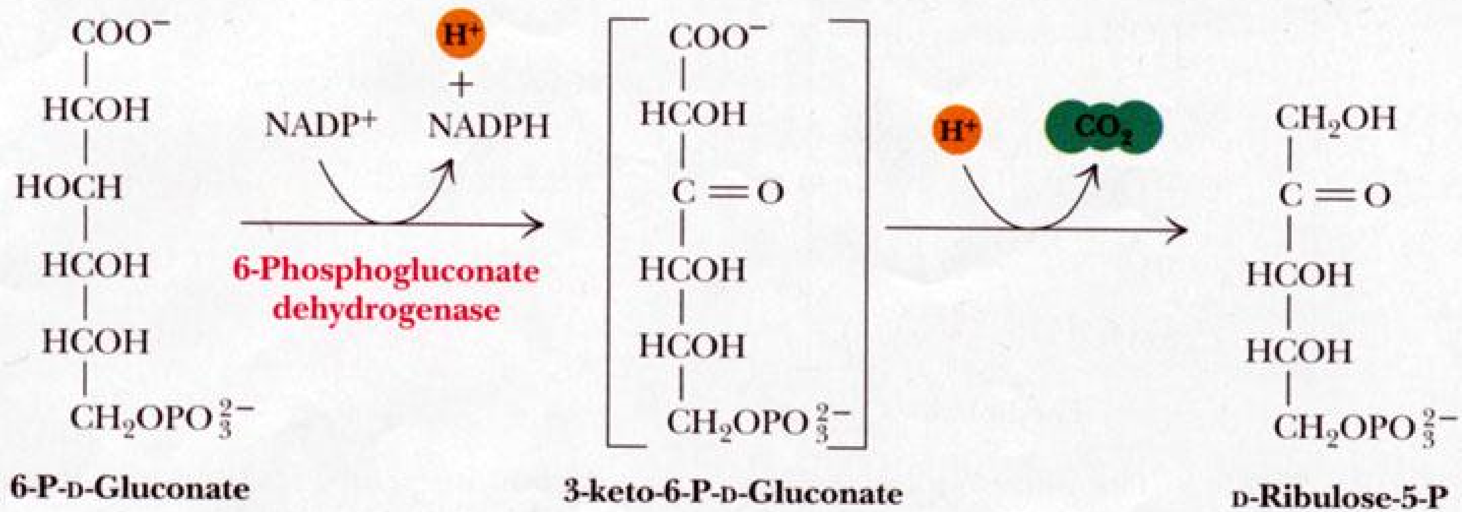
Otto Warburg
1883–1970

戊糖磷酸途径的概况

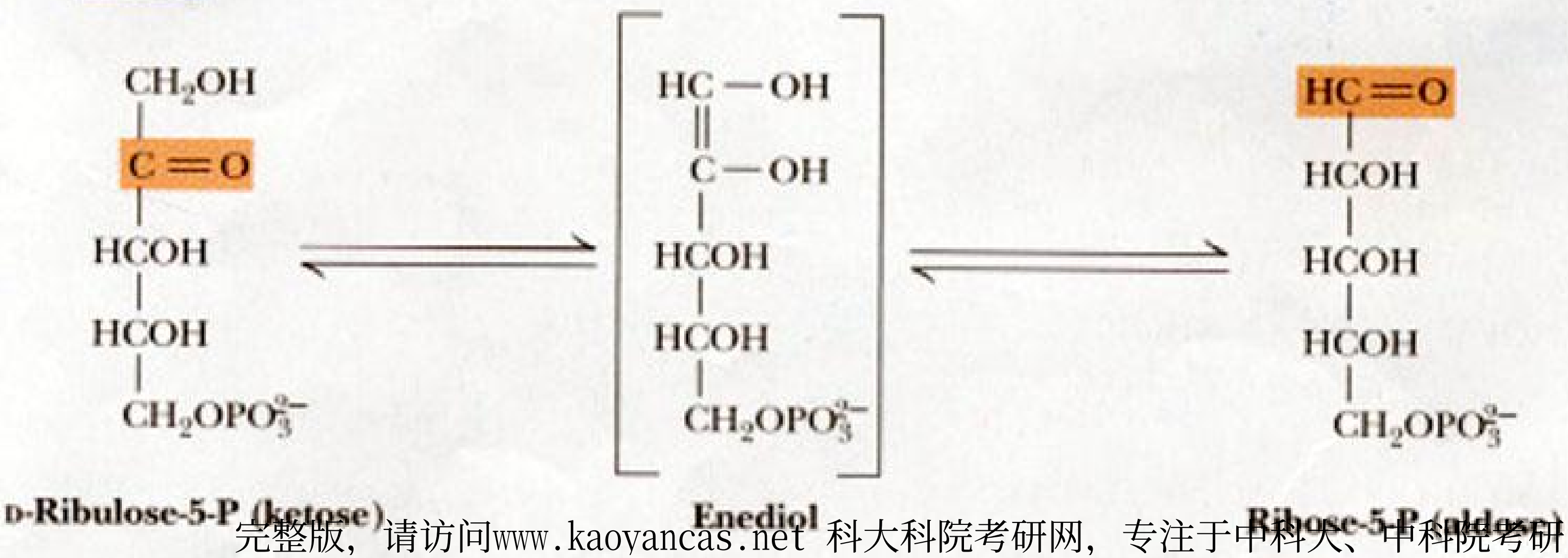


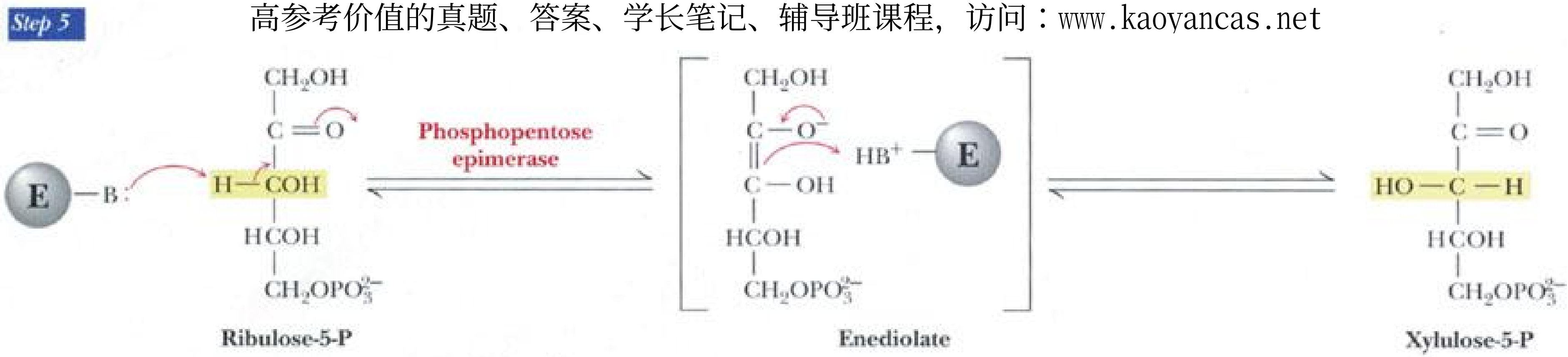

Step 1
α-D-Glucose-6-phosphate
NADP+
NADPH + H+
Glucose-6-P dehydrogenase
6-Phospho-D-gluconolactone

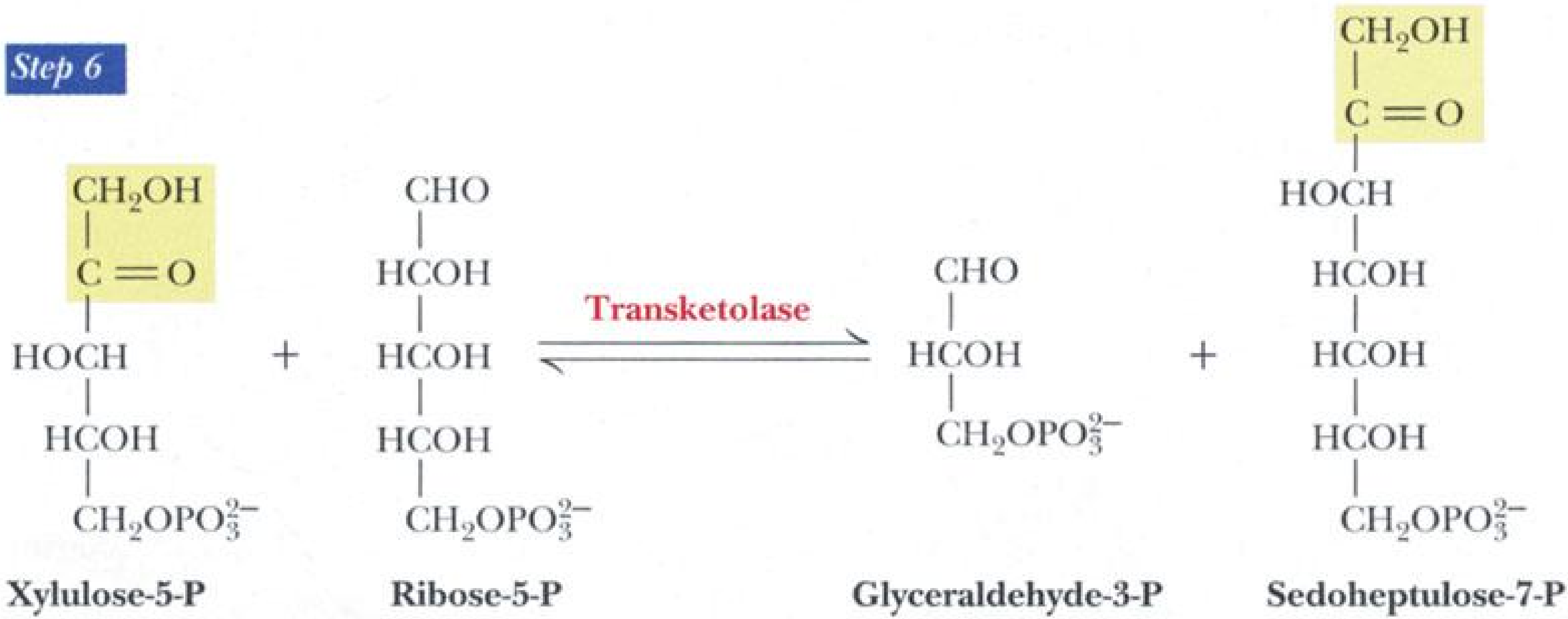

Step 2
6-P-D-Gluconolactone
Gluconolactonase
H2O
H+
6-P-D-Gluconate


COO⁻
HCOH
HOCH
HCOH
HCOH
$CH_2OPO_3^{2-}$
6-P-D-Gluconate
H^+
+
$NADP^+$
NADPH
6-Phosphogluconate
dehydrogenase
COO⁻
HCOH
C=O
HCOH
HCOH
$CH_2OPO_3^{2-}$
3-keto-6-P-D-Gluconate
H^+
CO_2
CH_2OH
C=O
HCOH
HCOH
$CH_2OPO_3^{2-}$
D-Ribulose-5-P

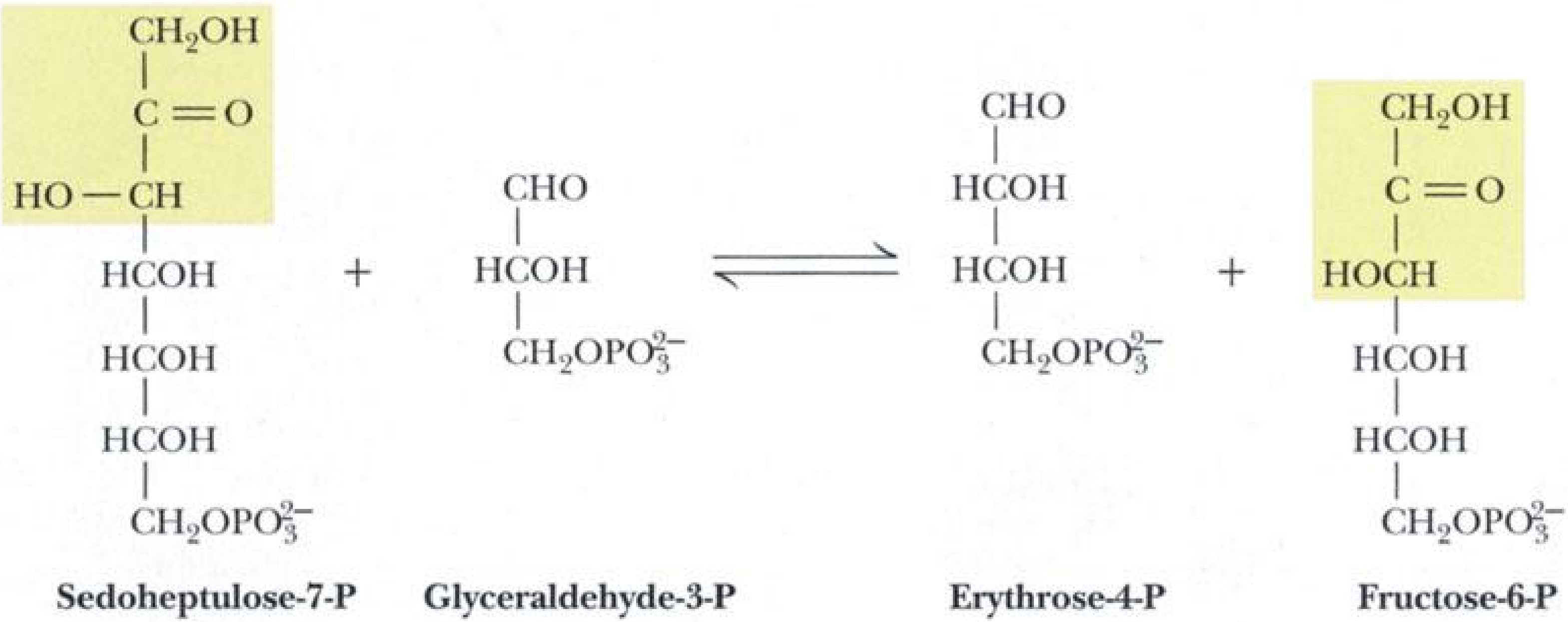
Step 4


CH_2OH
C=O
HCOH
HCOH
$CH_2OPO_3^{2-}$
D-Ribulose-5-P (ketose)
HC—OH
C—OH
HCOH
HCOH
$CH_2OPO_3^{2-}$
Enediol
HC=O
HCOH
HCOH
HCOH
$CH_2OPO_3^{2-}$

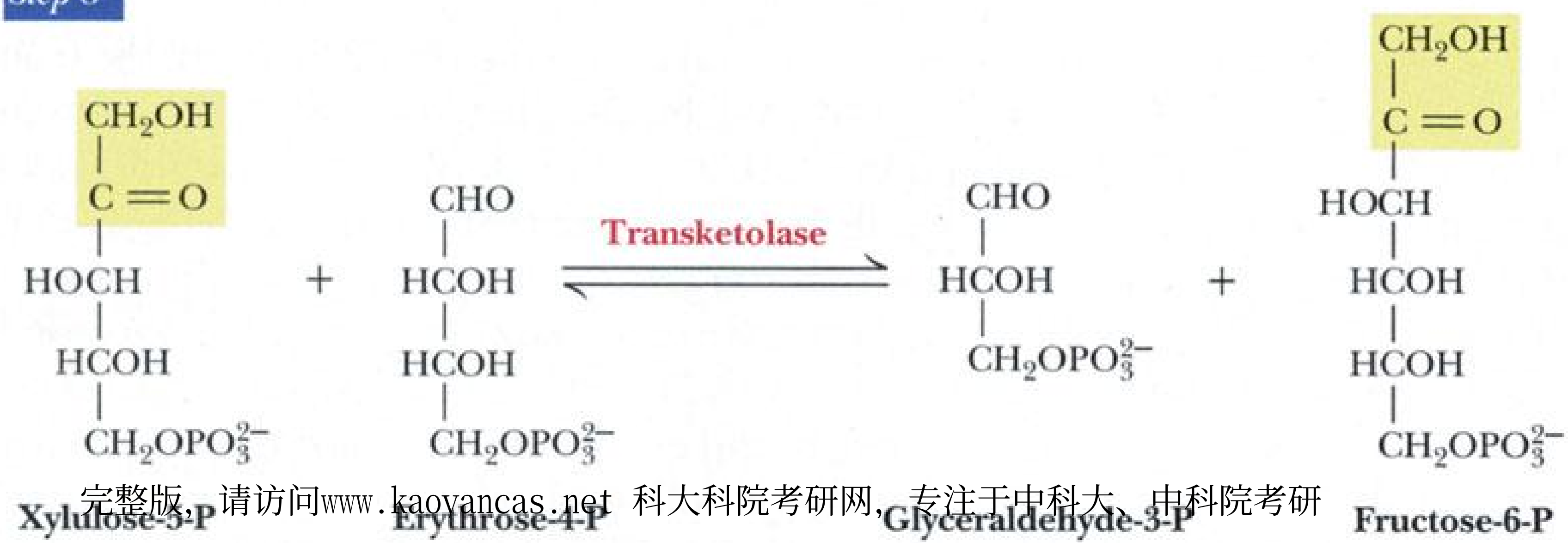

Step 5
CH_2OH
C=O
E
B:
H—COH
HCOH
$CH_2OPO_3^{2-}$
Phosphopentose epimerase
C—O⁻
C—OH
HB⁺
HO—C—H
Ribulose-5-P
Enediolate
Xylulose-5-P


Step 6
CH_2OH
C=O
HOCH
HCOH
$CH_2OPO_3^{2-}$
CHO
Transketolase
Xylulose-5-P
Ribose-5-P
Glyceraldehyde-3-P
Sedoheptulose-7-P

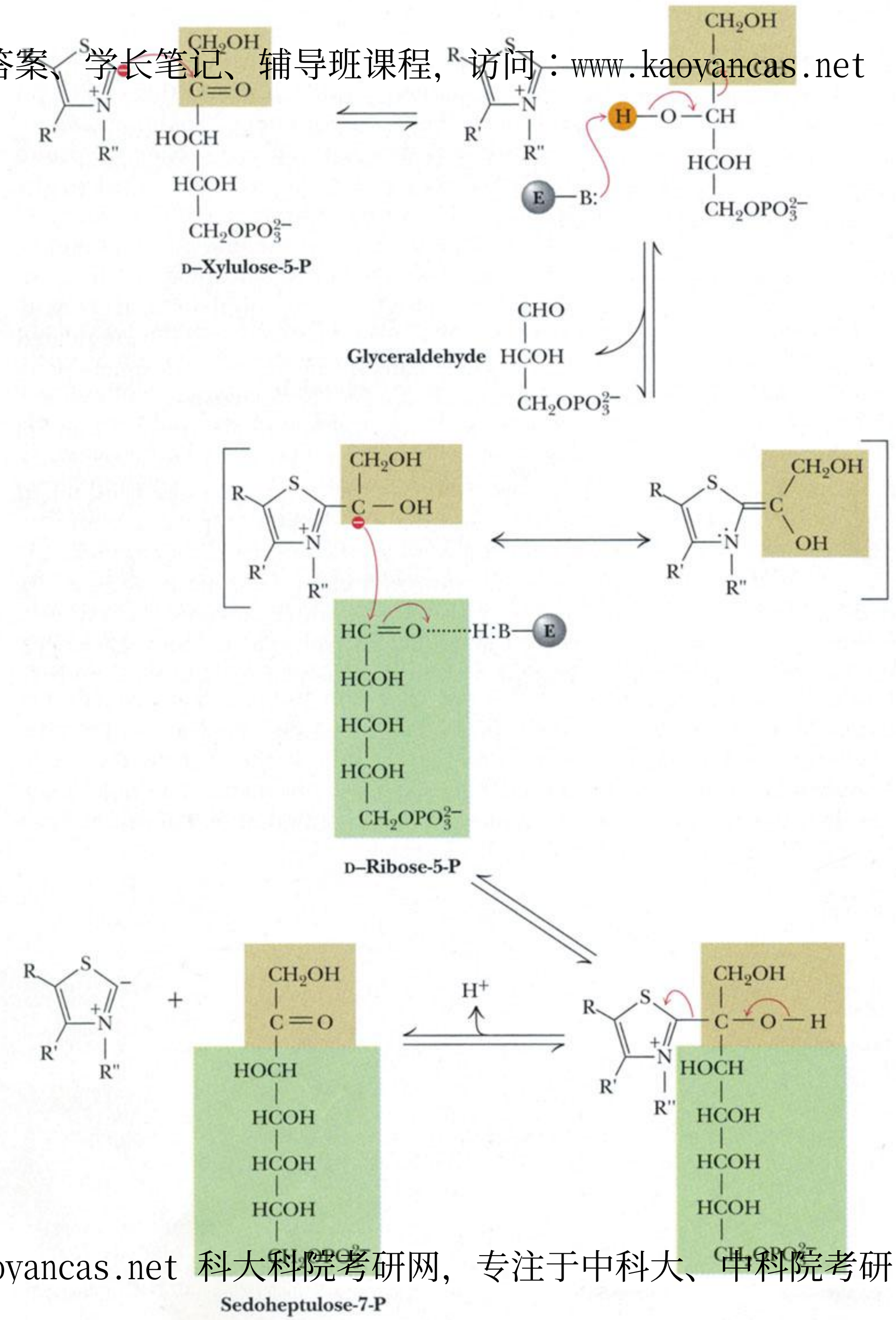
Step 7

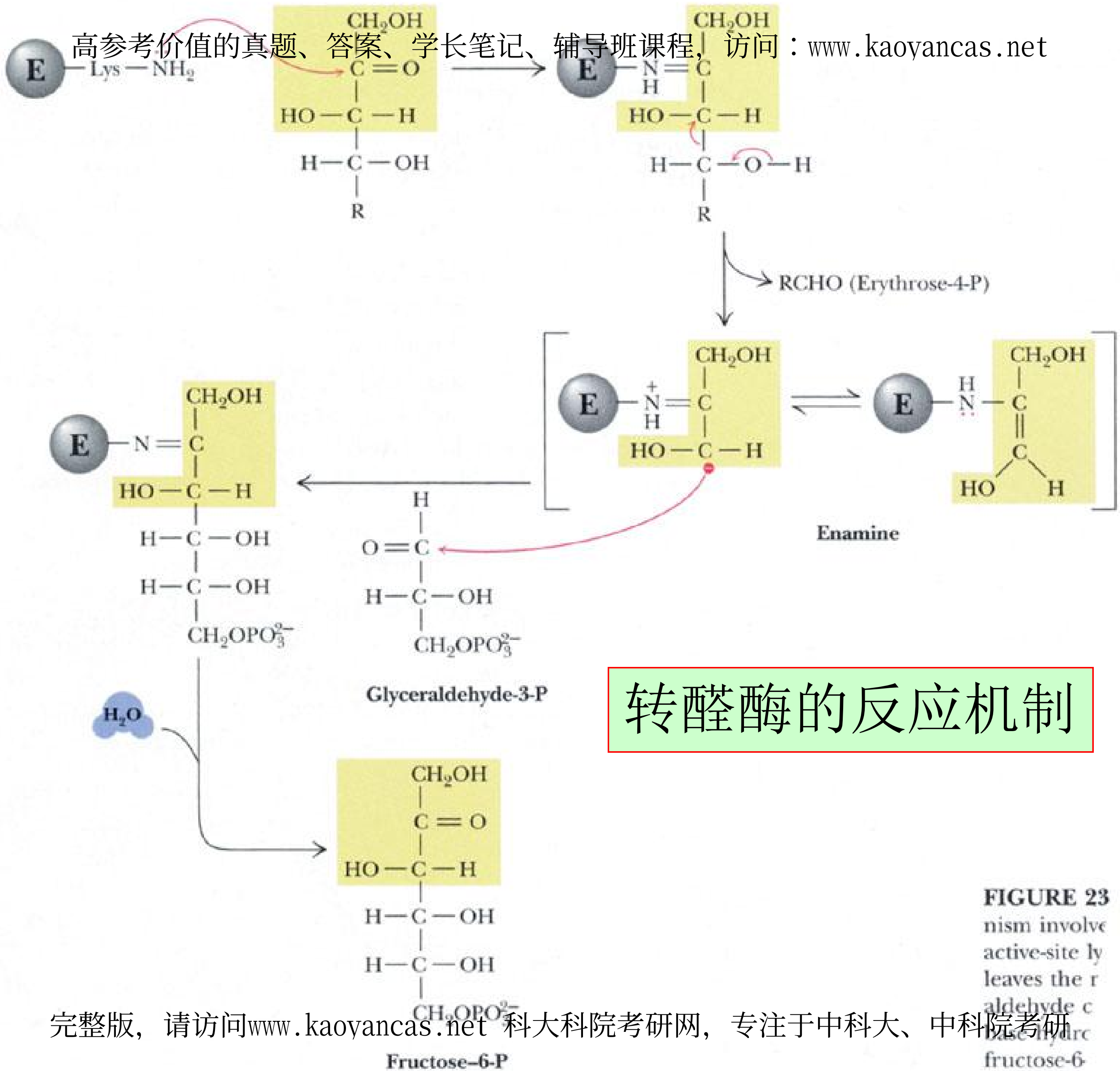

Sedoheptulose-7-P
Glyceraldehyde-3-P
Erythrose-4-P
Fructose-6-P

Step 8


Transketolase
Xylulose-5-P
Erythrose-4-P
Glyceraldehyde-3-P
Fructose-6-P

依赖TPP的转酮酶反应机制

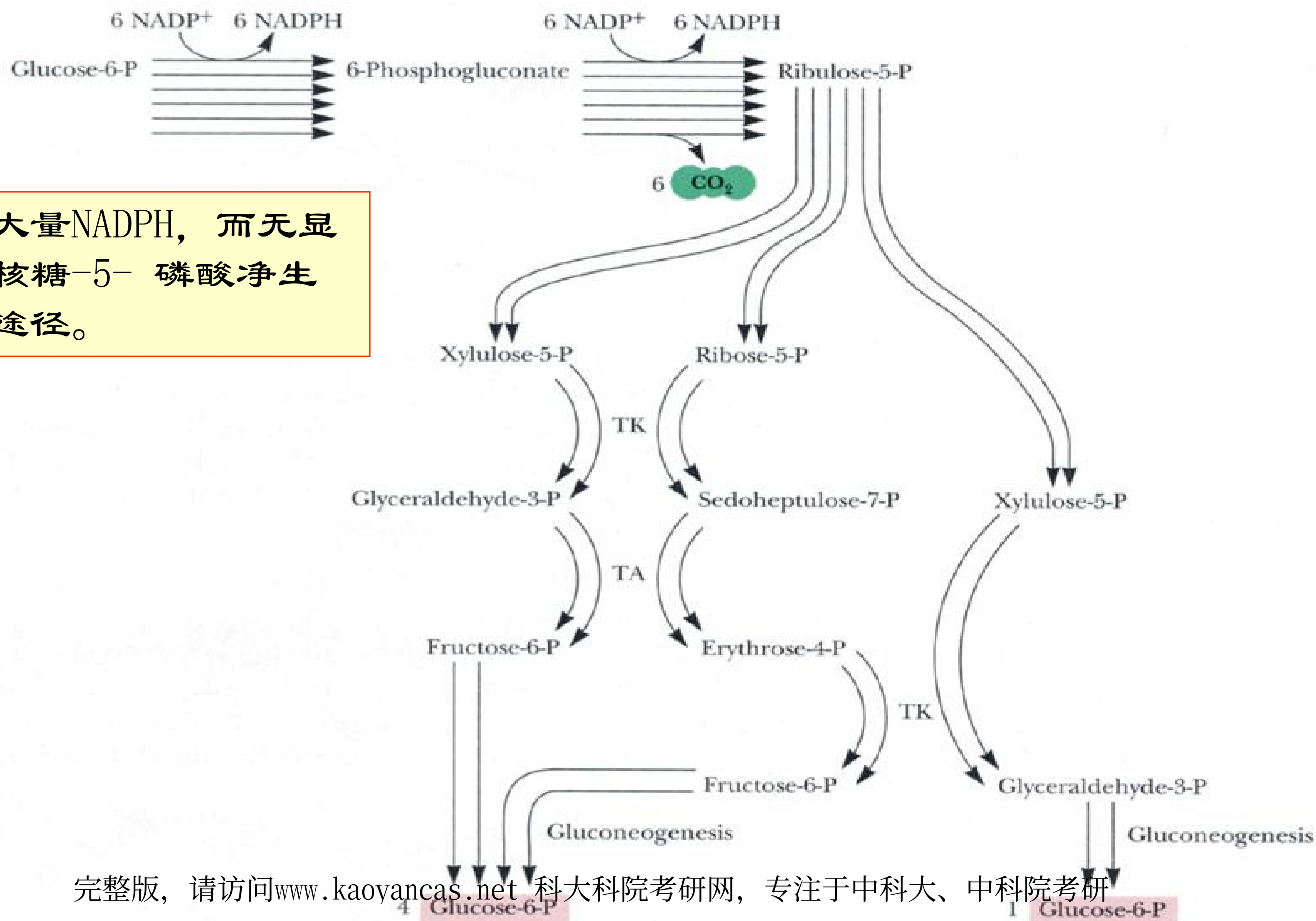


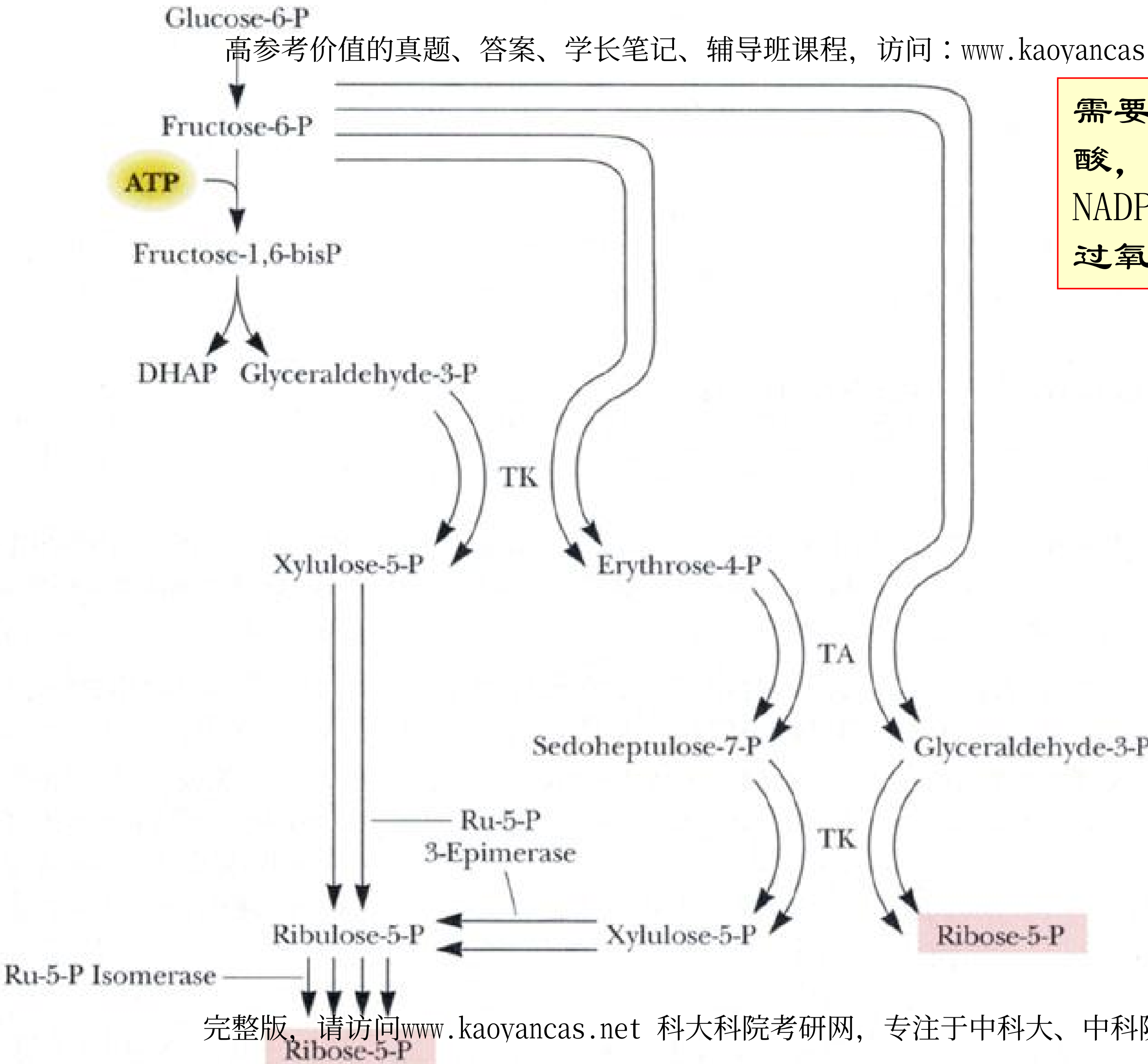


转醛酶的反应机制

FIGURE 23
nism involve
active-site ly
leaves the r
aldehyde c
base hydro
fructose-6

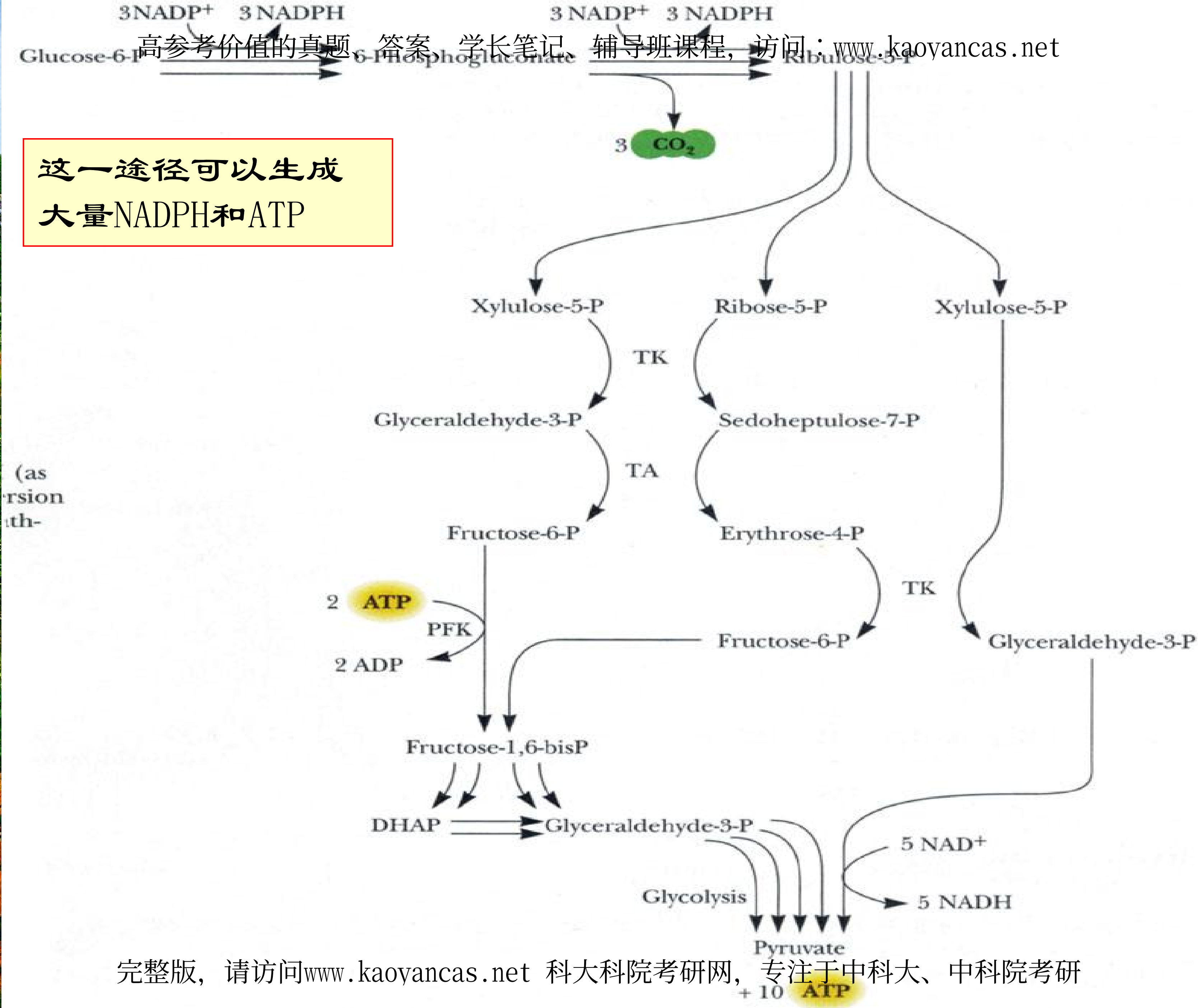
生成大量NADPH，而无显著的核糖-5-磷酸净生成的途径。





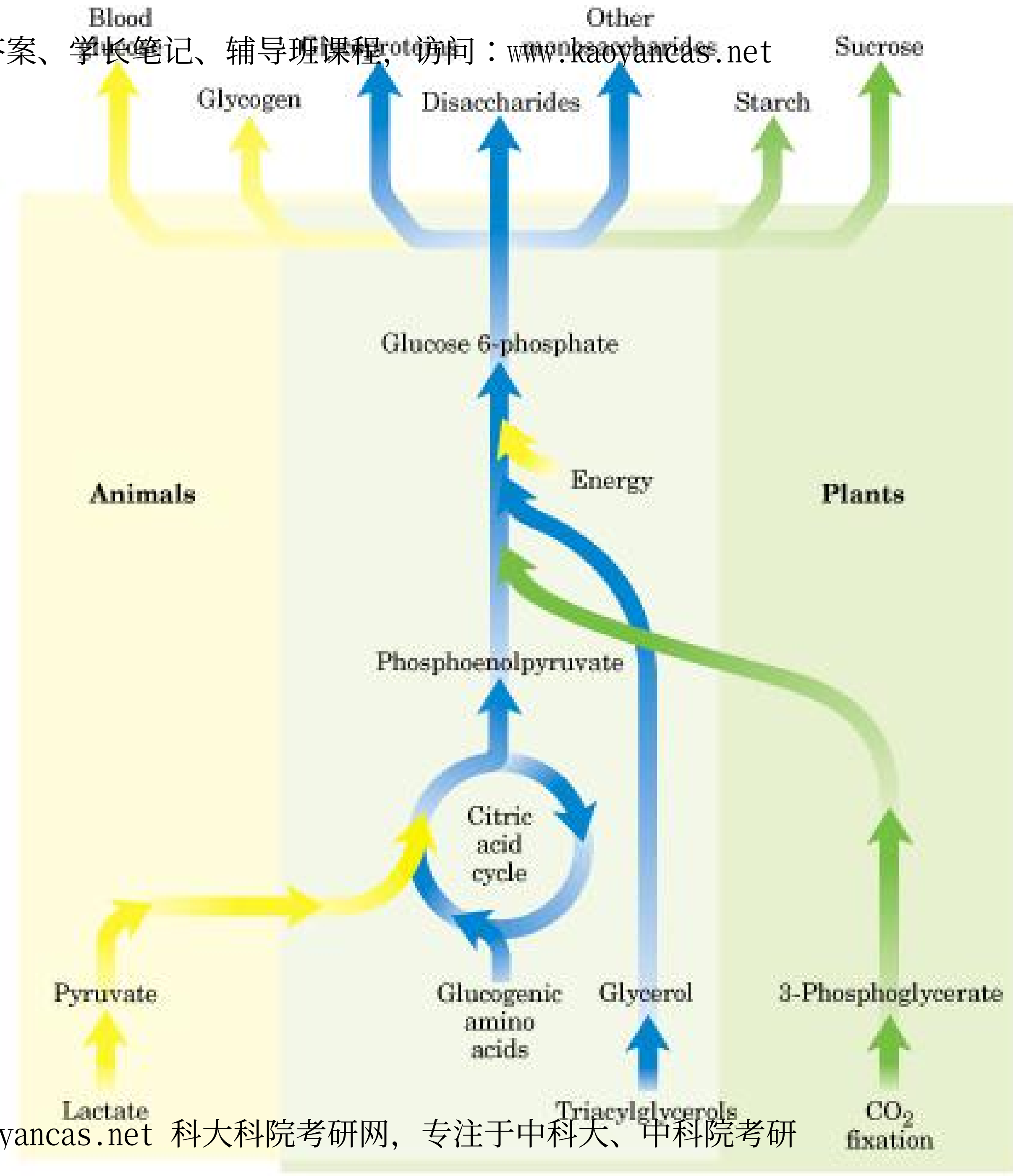
需要核糖-5- 磷酸，而不需要NADPH时，可以绕过氧化步骤。

这一途径可以生成
大量NADPH和ATP



二、糖的其他代谢途径

（一）葡糖异生作用



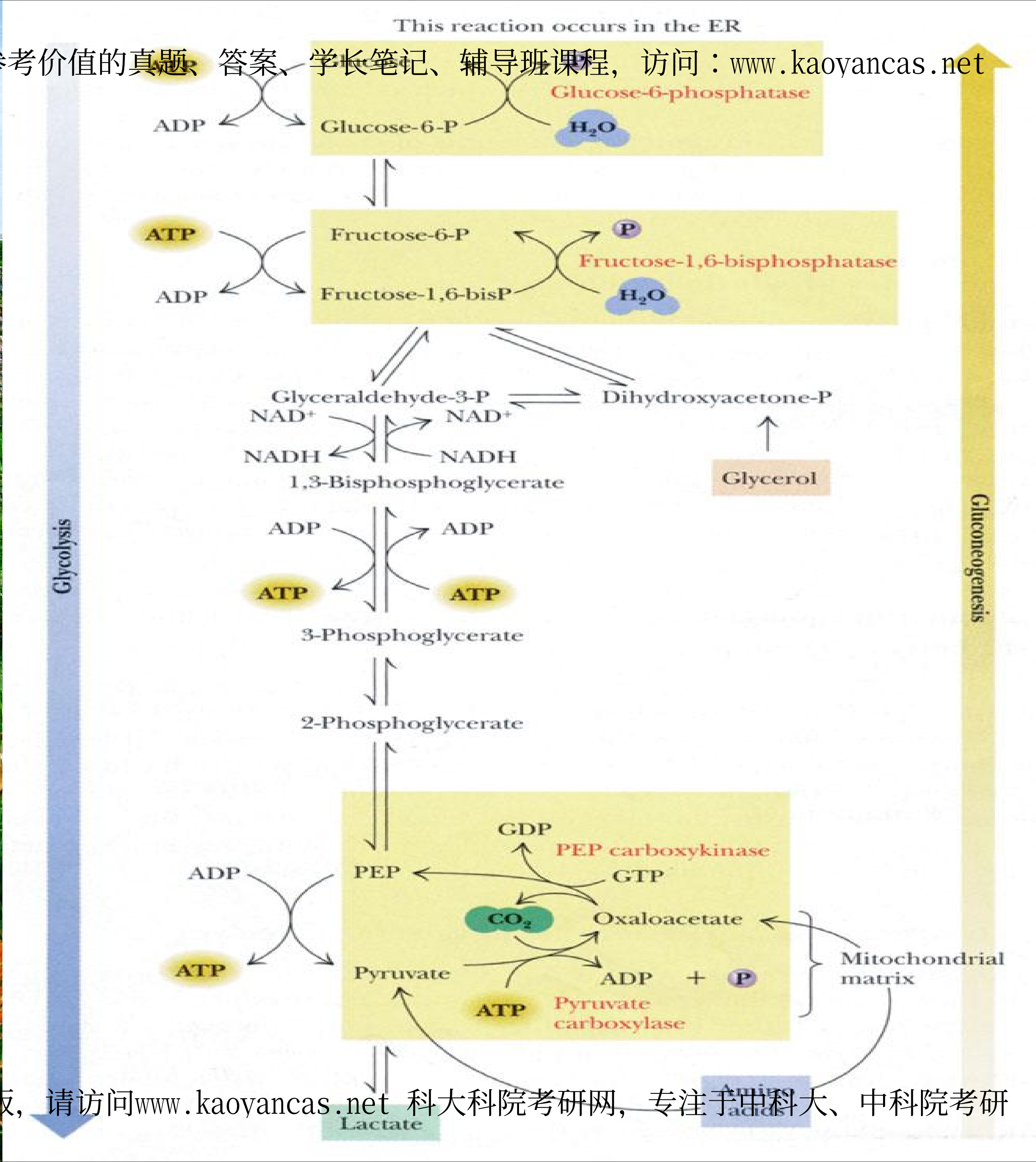
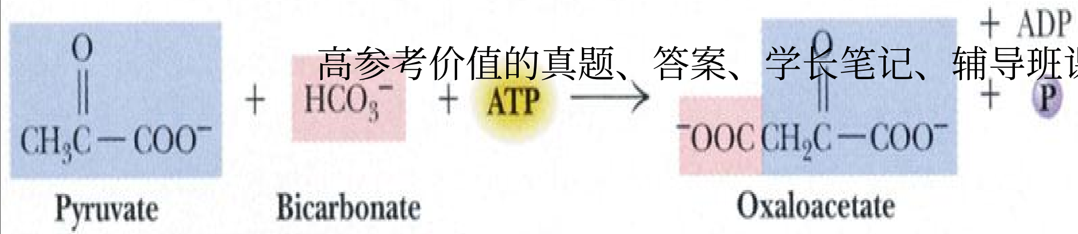

This reaction occurs in the ER
ADP
Glucose-6-P
Glucose-6-phosphatase
H_2O
ATP
ADP
Fructose-6-P
Fructose-1,6-bisP
P
Fructose-1,6-bisphosphatase
H_2O
Glyceraldehyde-3-P
Dihydroxyacetone-P
NAD^+
NAD^+
NADH
NADH
1,3-Bisphosphoglycerate
Glycerol
ADP
ADP
ATP
ATP
3-Phosphoglycerate
2-Phosphoglycerate
GDP
PEP carboxykinase
ADP
PEP
GTP
CO_2
Oxaloacetate
Mitochondrial
matrix
ATP
Pyruvate
ADP + P
ATP
Pyruvate
carboxylase
Lactate
Glycolysis
Gluconeogenesis

table 20–1

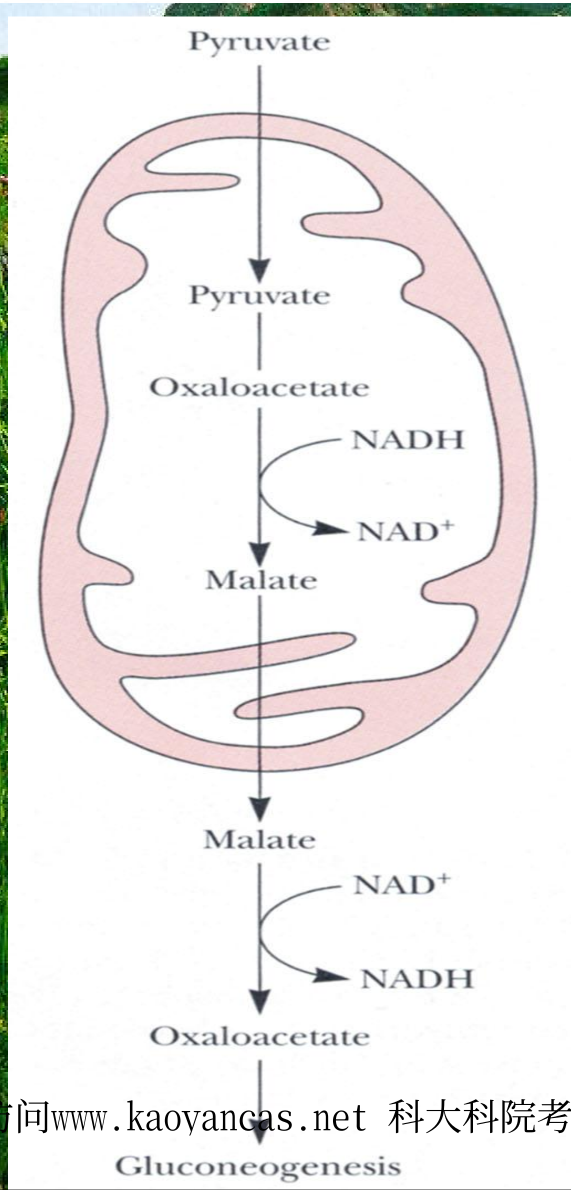
Free-Energy Changes of Glycolytic Reactions in Erythrocytes*

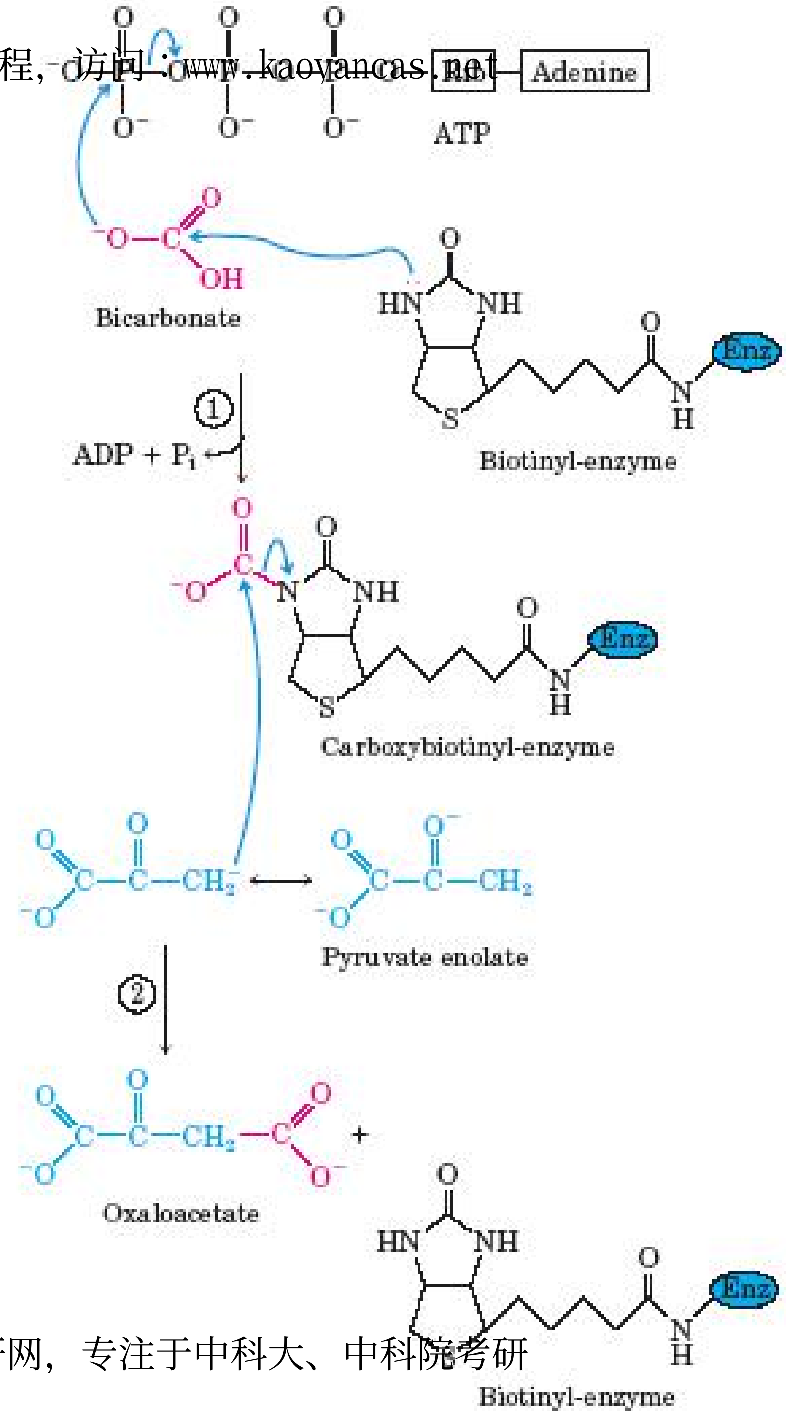
Glycolytic reaction step	$\Delta G'^\circ$ (kJ/mol)	ΔG (kJ/mol)
① Glucose + ATP ⟶ glucose 6-phosphate + ADP + H^+	−16.7	−33.4
② Glucose 6-phosphate ⇌ fructose 6-phosphate	1.7	−2.5
③ Fructose 6-phosphate + ATP ⟶ fructose 1,6-bisphosphate + ADP + H^+	−14.2	−22.2
④ Fructose 1,6-bisphosphate ⇌ dihydroxyacetone phosphate + glyceraldehyde 3-phosphate	23.8	−1.25
⑤ Dihydroxyacetone phosphate ⇌ glyceraldehyde 3-phosphate	7.5	2.5
⑥ Glyceraldehyde 3-phosphate + P_i + NAD^+ ⇌ 1,3-bisphosphoglycerate + NADH + H^+	6.3	−1.7
⑦ 1,3-Bisphosphoglycerate + ADP ⇌ 3-phosphoglycerate + ATP	−18.8	1.25
⑧ 3-Phosphoglycerate ⇌ 2-phosphoglycerate	4.4	0.8
⑨ 2-Phosphoglycerate ⇌ phosphoenolpyruvate + H_2O	7.5	−3.3
⑩ Phosphoenolpyruvate + ADP + H^+ ⟶ pyruvate + ATP	−31.4	−16.7

*$\Delta G'^\circ$ is the standard free-energy change, as defined in Chapter 14 (see p. 494). At pH 7.0, ΔG is the free-energy change calculated from the actual concentrations of glycolytic intermediates present under physiological conditions in erythrocytes. The glycolytic reactions bypassed in gluconeogenesis are shown in red.

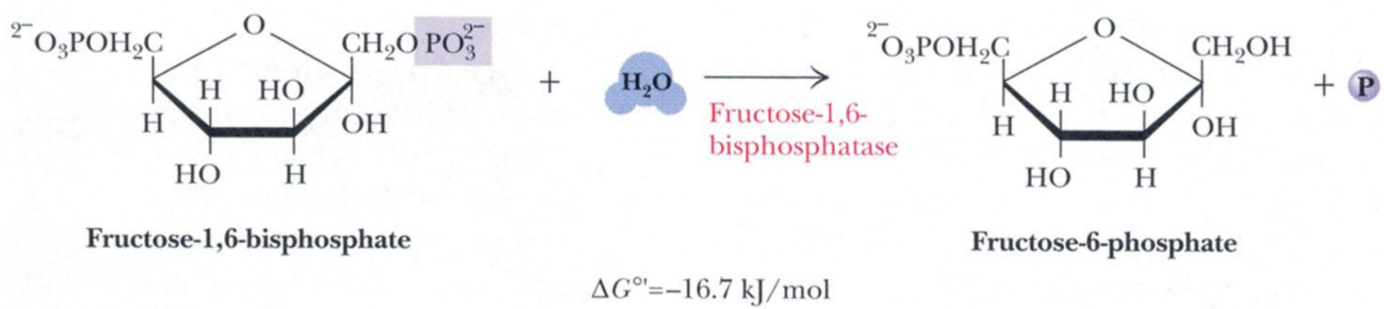

Pyruvate
Bicarbonate
ATP
ADP
P
Oxaloacetate

丙酮酸羧化反应的机制

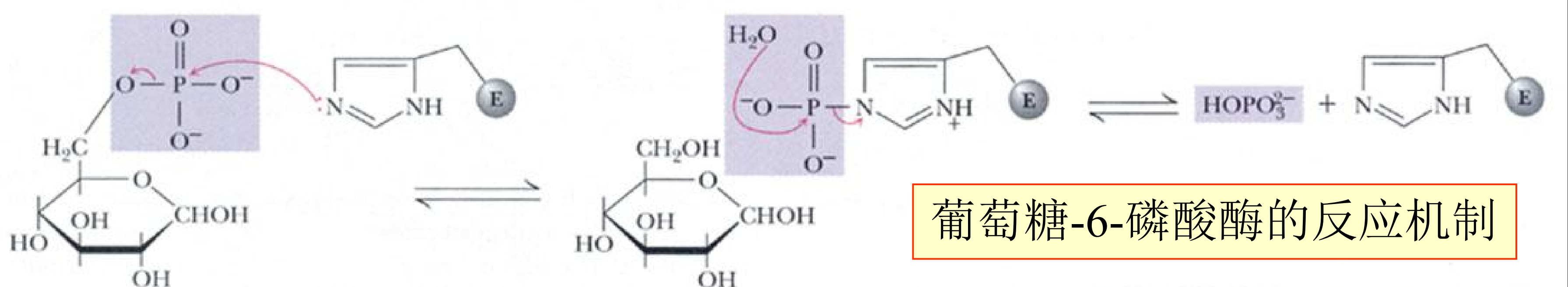

Pyruvate
Pyruvate
Oxaloacetate
NADH
NAD+
Malate
Malate
NAD+
NADH
Oxaloacetate
Gluconeogenesis


Adenine
ATP
Bicarbonate
Biotinyl-enzyme
Enz
ADP + Pi
①
Carboxybiotinyl-enzyme
Pyruvate enolate
②
Oxaloacetate
Biotinyl-enzyme

PEP羧化激酶催化的反应



果糖二磷酸磷酸酶催化的反应



葡萄糖-6-磷酸酶的反应机制

FIGURE 23.9 • The glucose-6-phosphat

葡萄糖-6-磷酸酶定位内在内质网膜

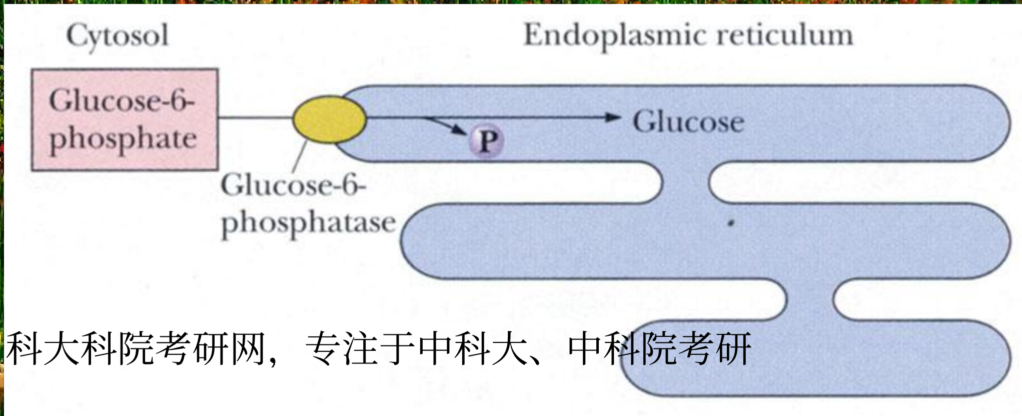


table 20–2

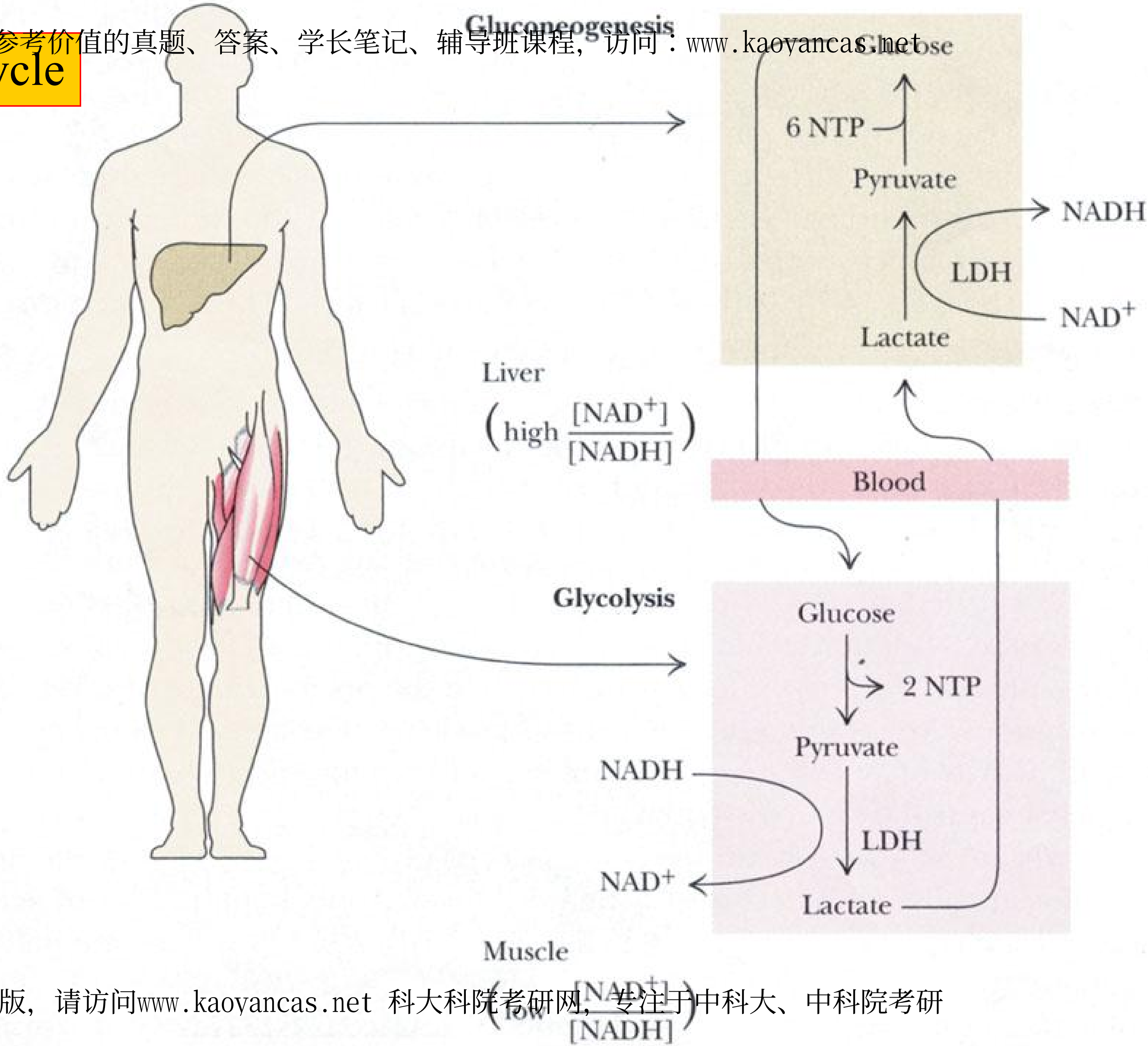
Sequential Reactions in Gluconeogenesis Starting from Pyruvate*

Pyruvate + HCO_3^- + ATP $\longrightarrow$ oxaloacetate + ADP + P_i + H^+	×2
Oxaloacetate + GTP $\rightleftharpoons$ phosphoenolpyruvate + CO_2 + GDP	×2
Phosphoenolpyruvate + H_2O $\rightleftharpoons$ 2-phosphoglycerate	×2
2-Phosphoglycerate $\rightleftharpoons$ 3-phosphoglycerate	×2
3-Phosphoglycerate + ATP $\rightleftharpoons$ 1,3-bisphosphoglycerate + ADP + H^+	×2
1,3-Bisphosphoglycerate + NADH + H^+ $\rightleftharpoons$ glyceraldehyde 3-phosphate + NAD^+ + P_i	×2
Glyceraldehyde 3-phosphate $\rightleftharpoons$ dihydroxyacetone phosphate	
Glyceraldehyde 3-phosphate + dihydroxyacetone phosphate $\rightleftharpoons$ fructose 1,6-bisphosphate	
Fructose 1,6-bisphosphate + H_2O $\longrightarrow$ fructose 6-phosphate + P_i	
Fructose 6-phosphate $\rightleftharpoons$ glucose 6-phosphate	
Glucose 6-phosphate + H_2O $\longrightarrow$ glucose + P_i	

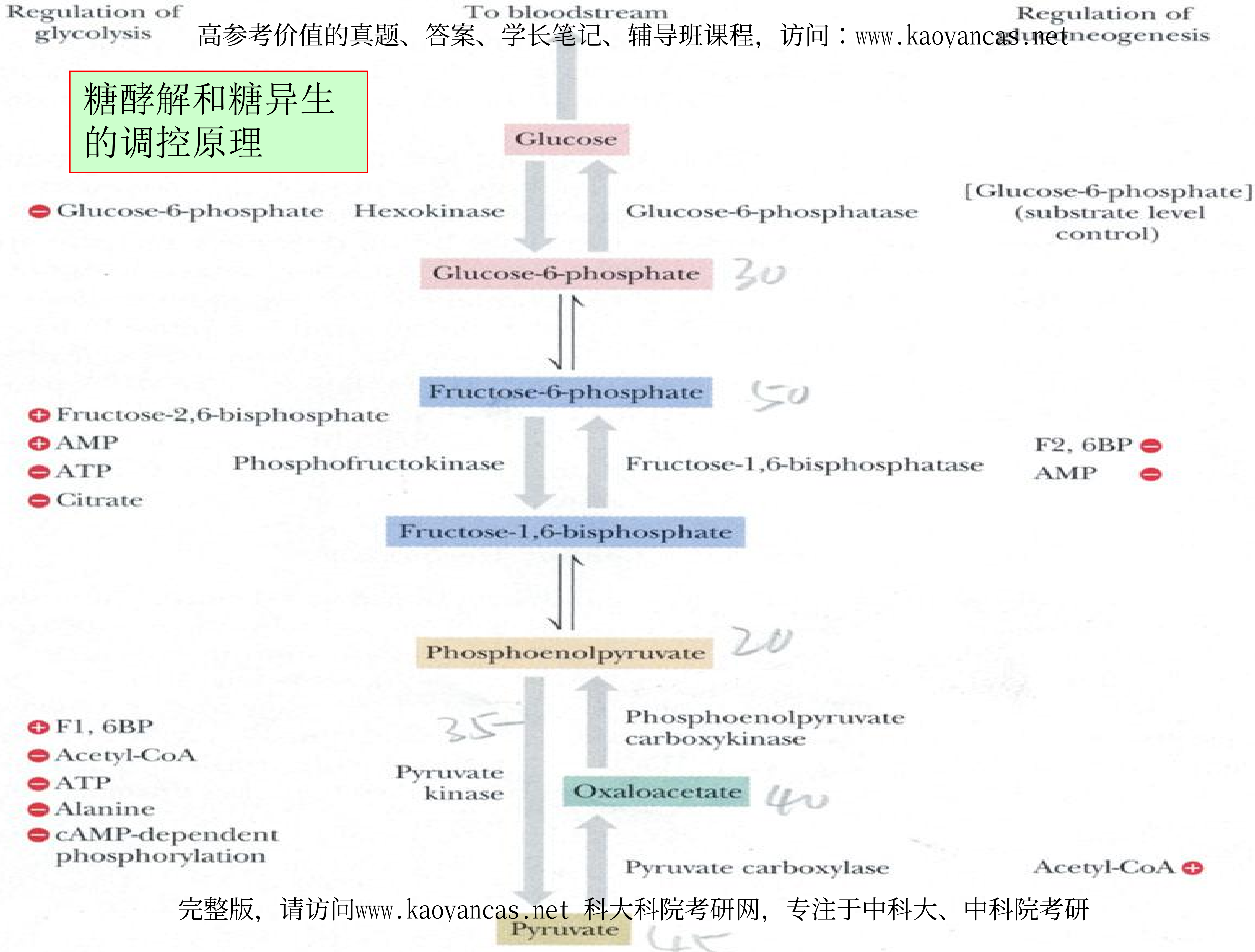
Sum: 2 Pyruvate + 4ATP + 2GTP + 2NADH + $4H_2O$ $\longrightarrow$ glucose + 4ADP + 2GDP + $6P_i$ + $2NAD^+$ + $2H^+$

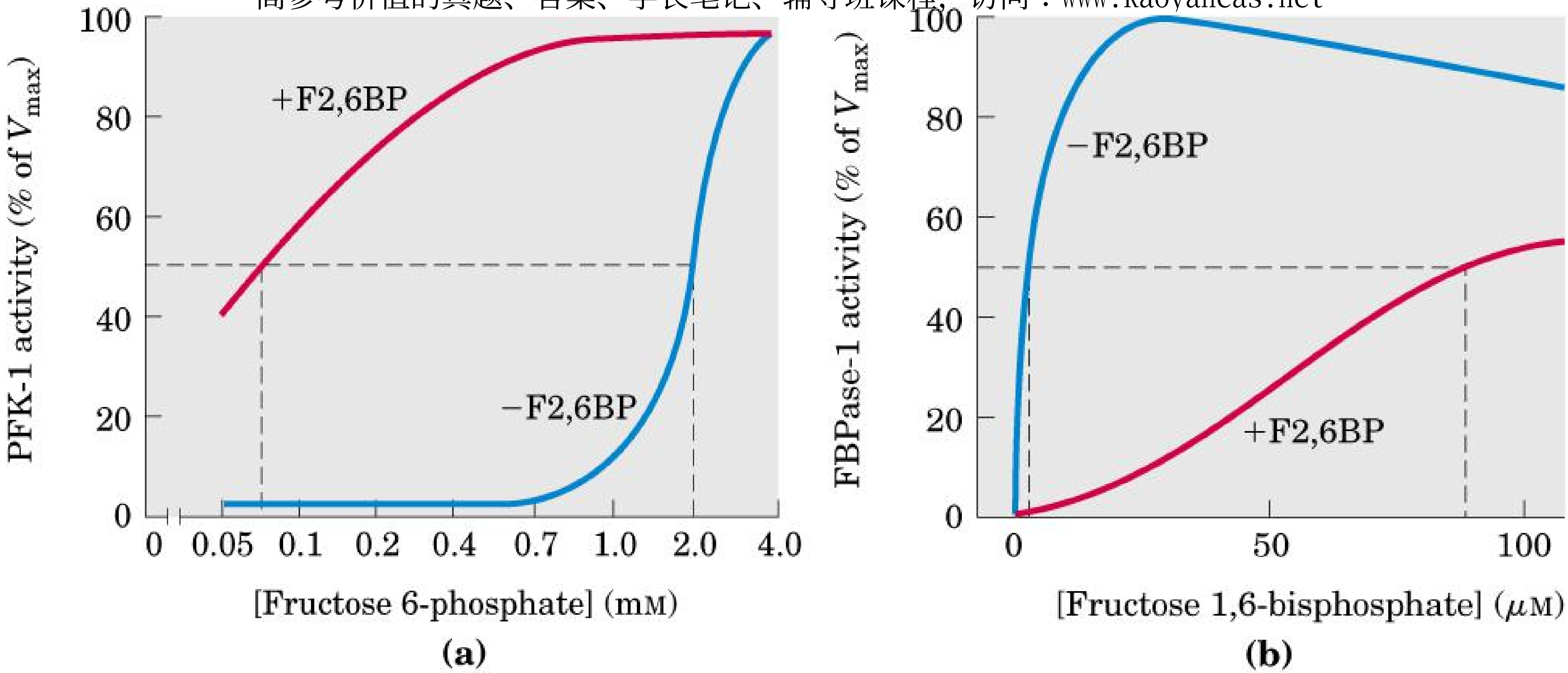
*The bypass reactions are in red; all other reactions are reversible steps of glycolysis. The figures at the right indicate that the reaction is to be counted twice, because two three-carbon precursors are required to make a molecule of glucose. Note that the reactions required to replace the cytosolic NADH consumed in the glyceraldehyde 3-phosphate dehydrogenase reaction (the conversion of lactate to pyruvate in the cytosol or the transport of reducing equivalents from mitochondria to the cytosol in the form of malate) are not considered in this summary.

The Cori cycle



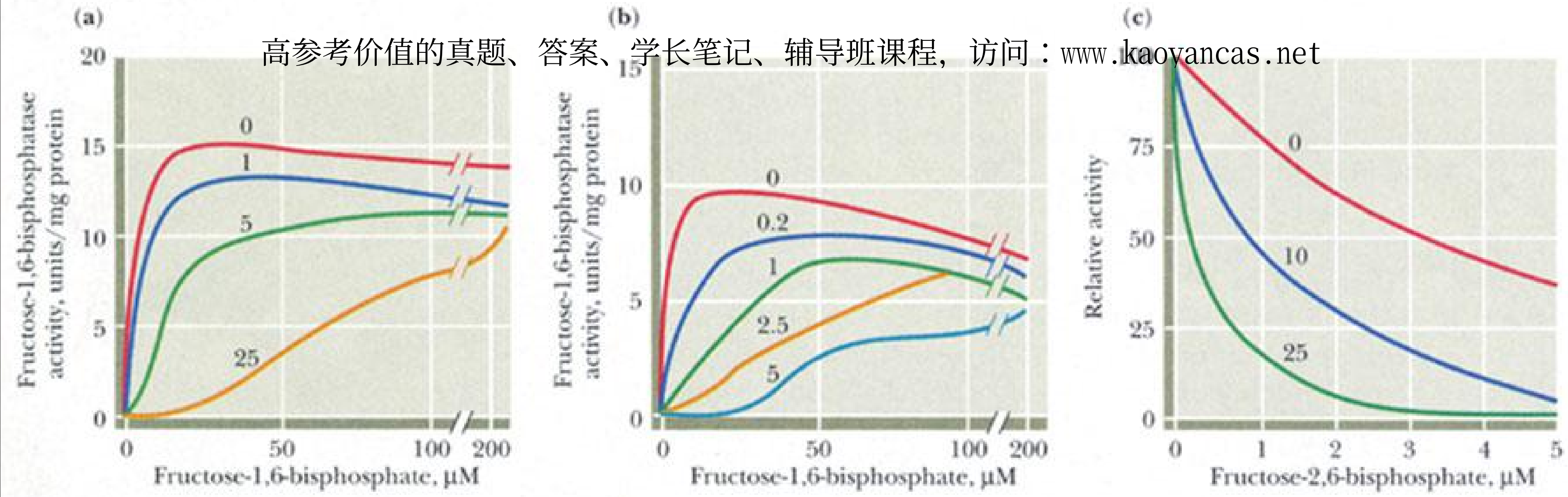
糖酵解和糖异生的调控原理





F2,6BP对磷酸果糖激酶的调控

F2,6BP对磷酸果糖二磷酸酶的调控

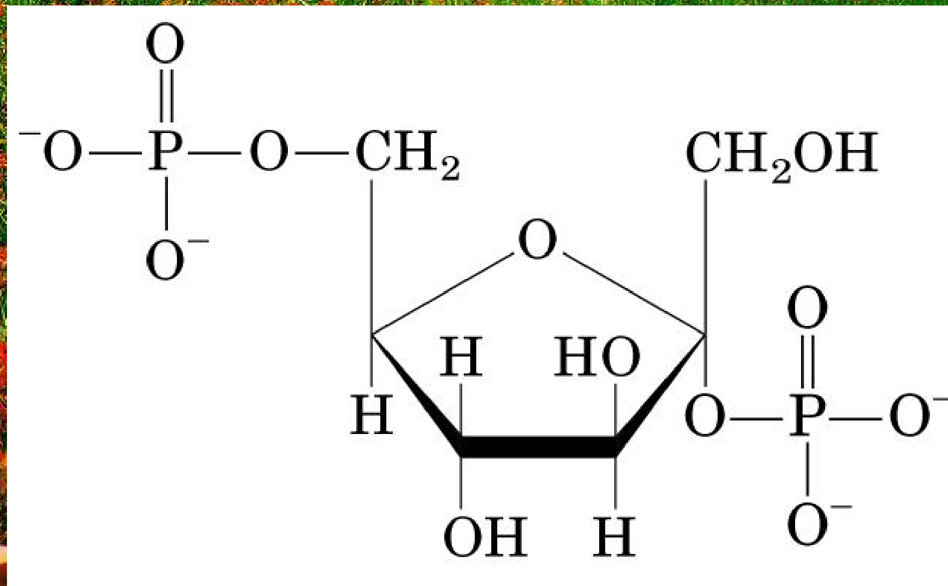


果糖-1,6-二磷酸酶被果糖-2,6-二磷酸和AMP抑制:

(a) 不存在AMP;

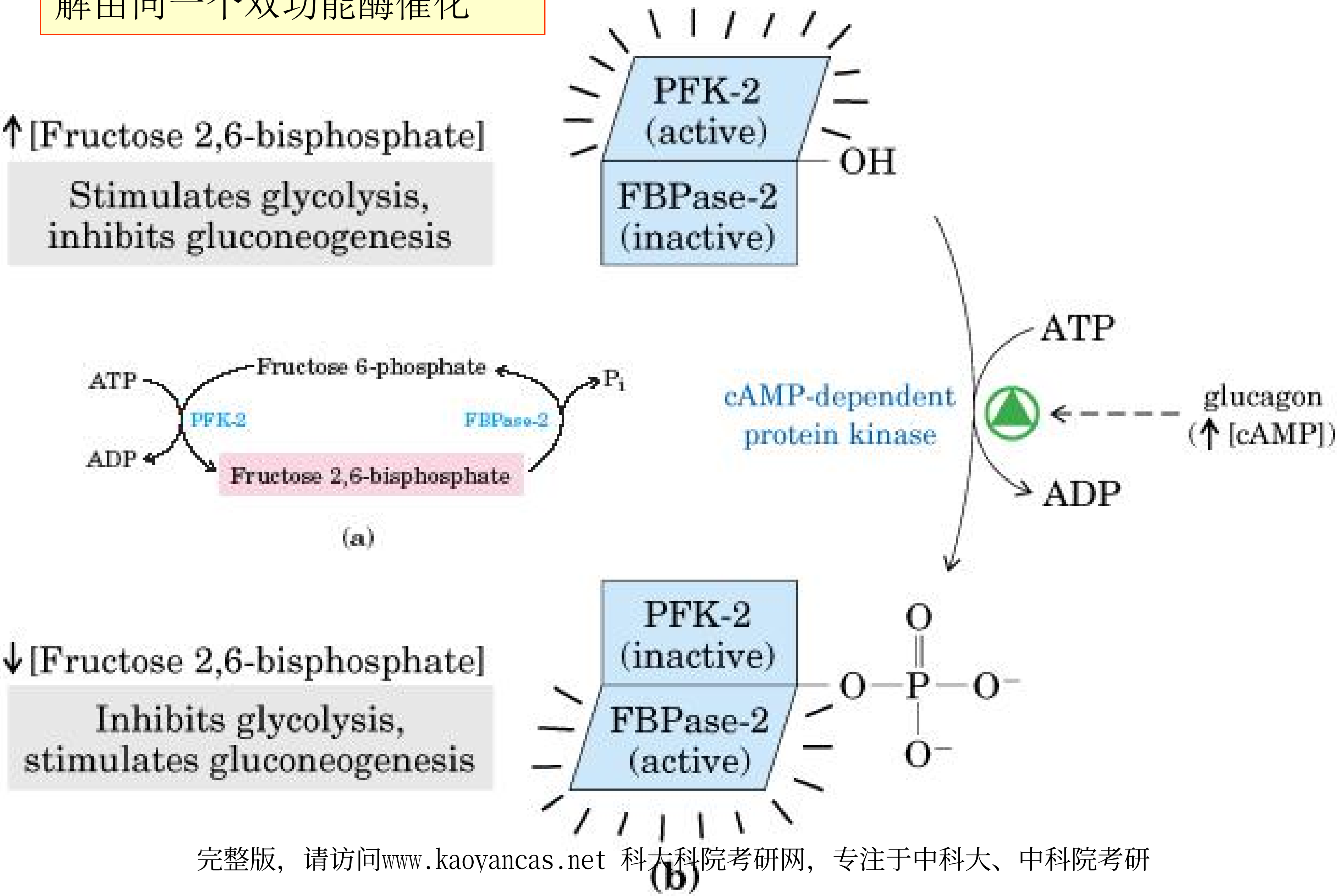
(b) 存在0.25　mol/L AMP;

(c) 0,10,25　mol/L AMP对果糖-2,6-二磷酸抑制果糖-1,6-二磷酸酶的影响。



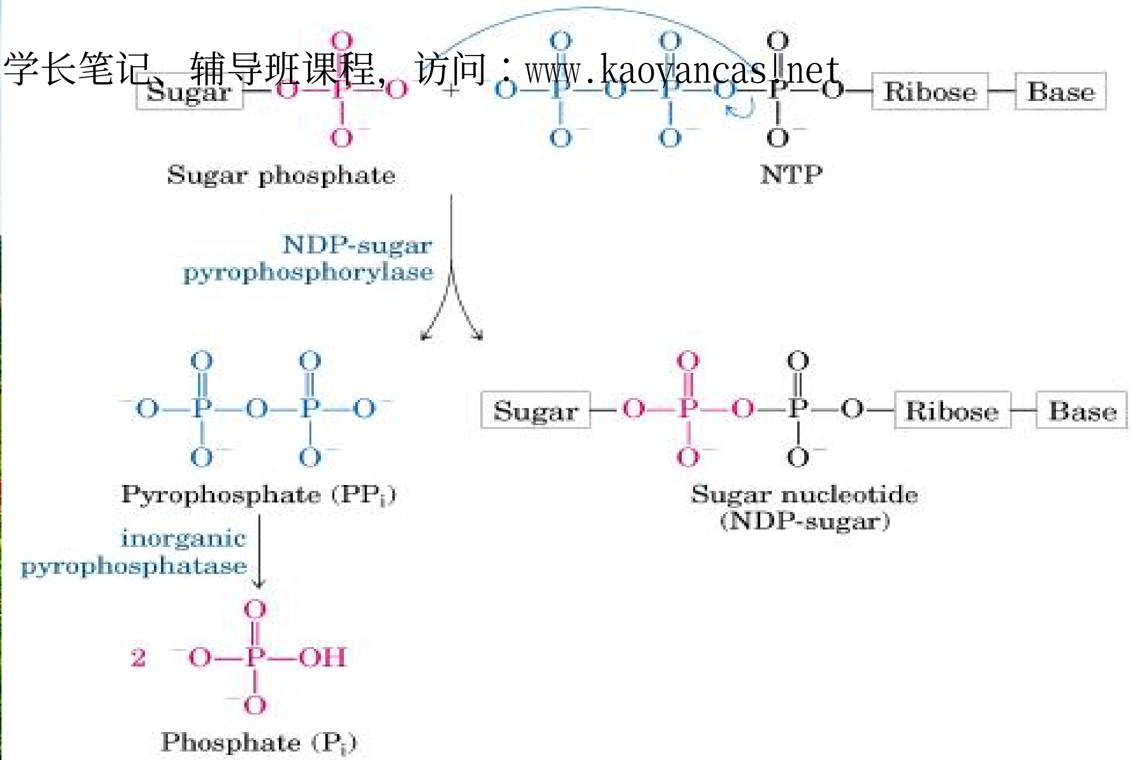
Fructose 2,6 -bisphosphate

果糖-2,6-二磷酸的合成和分解由同一个双功能酶催化



五、寡糖类的生物合成和分解

(一) 概论



Net reaction: Sugar phosphate + NTP ⟶ NDP-sugar + $2P_i$

表 25－2　糖基转移反应中与单糖相应的核苷酸

UDP	GDP	CMP
N－乙酰半乳糖胺(N－acetyl galactosamine)	岩藻糖(fucose)	唾液酸(sialic acid)
(N－乙酰葡糖胺)(N－acetyl glucosamine)	甘露糖(mannose)	
N－乙酰胞壁酸(N－acetyl muramic acid)		
半乳糖(galactose)		
葡糖醛酸(glucuronic acid)		
木糖(xylose)		

(二) 乳糖的生物合成和分解

乳糖的分解由乳糖酶或β-半乳糖酶(微生物)催化，不少成人的乳糖酶活力下降，出现乳糖不耐症。

细菌的β-半乳糖酶为诱导酶，天然诱导物为1,6-别乳糖，常用的人工诱导物为IPTG(异丙基硫代半乳糖苷)。

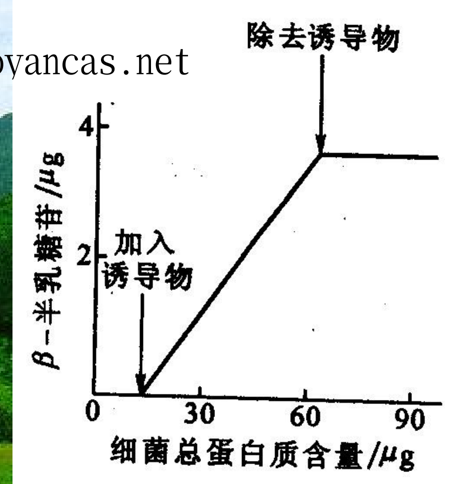
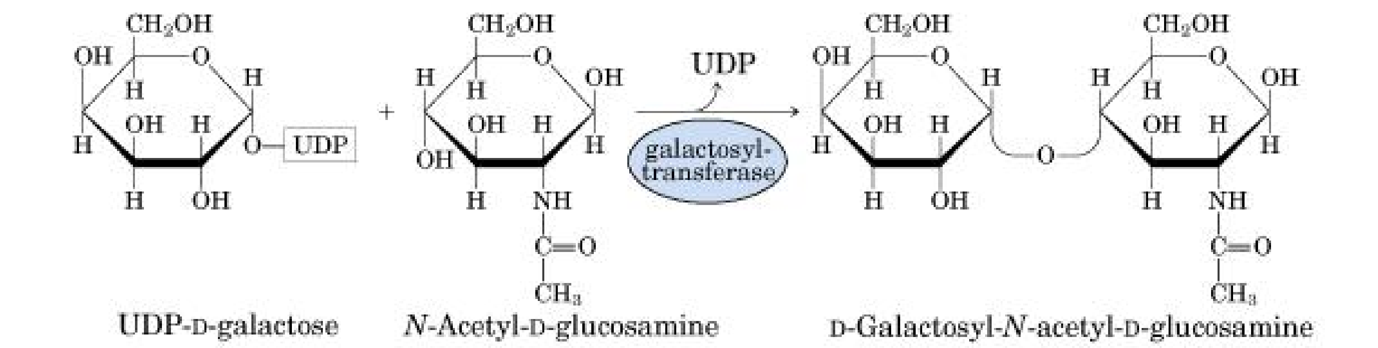


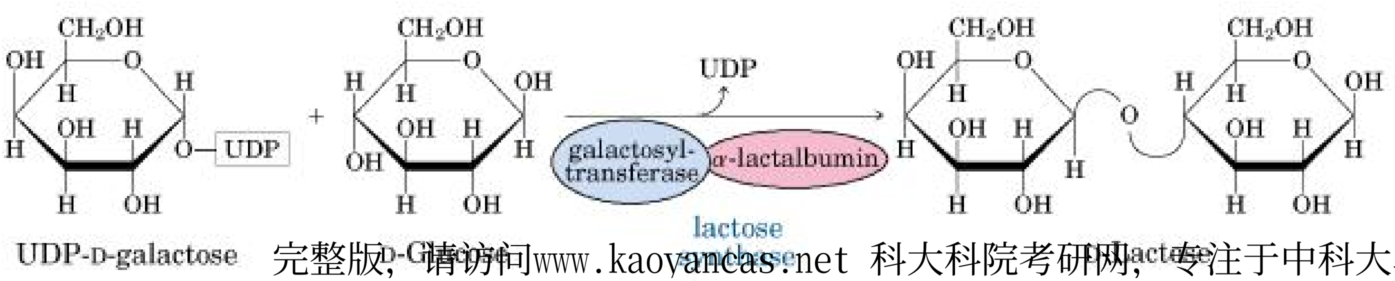
图 25-8 β-半乳糖苷酶量的增加和生长在培养基上 *E. coli* 细胞的增加成平行关系

图中的斜率表明，6.6%的蛋白质是合成的β-半乳糖苷酶



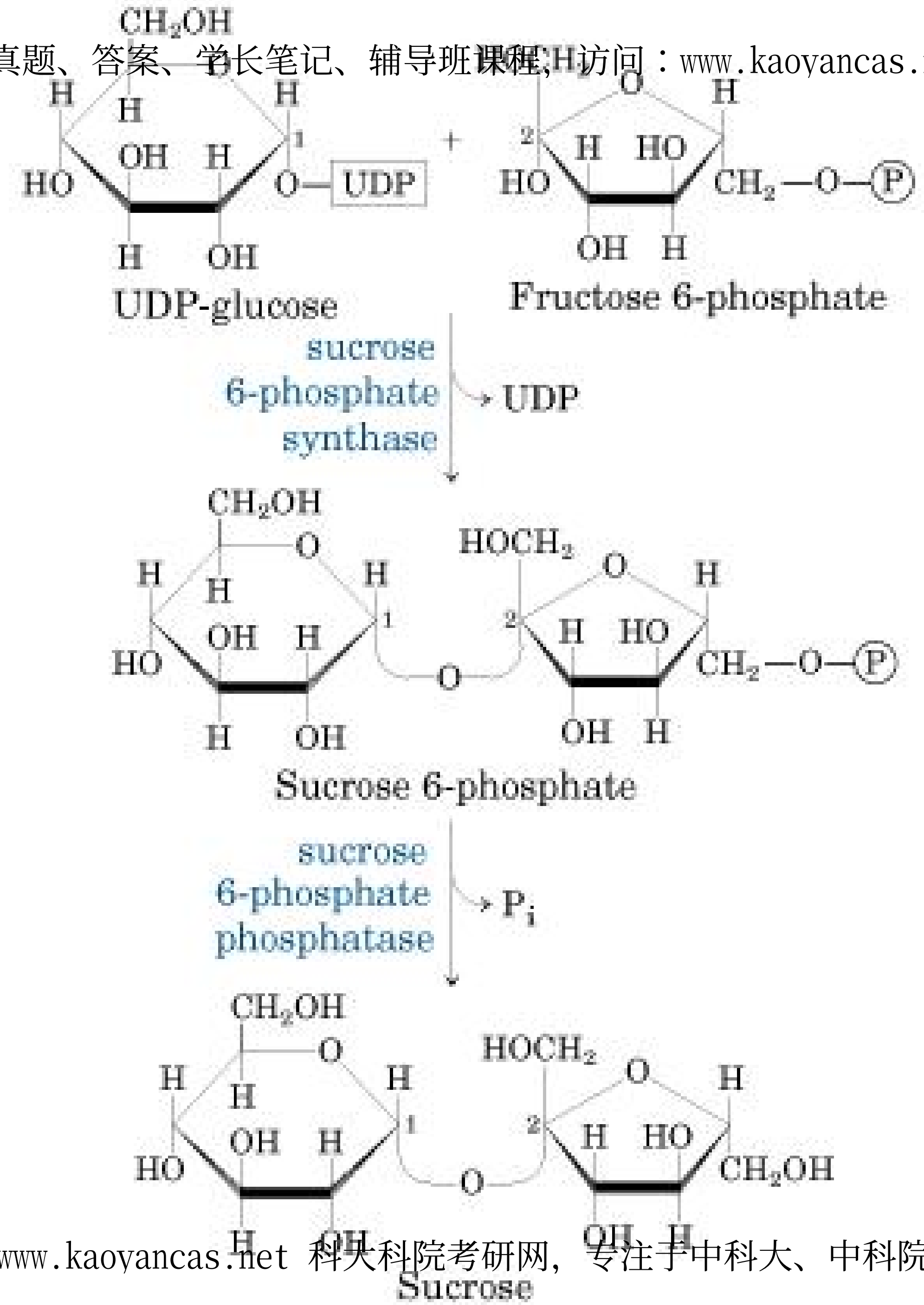
(a) Nonlactating tissues

乳糖的生物合成



(b) Lactating mammary gland

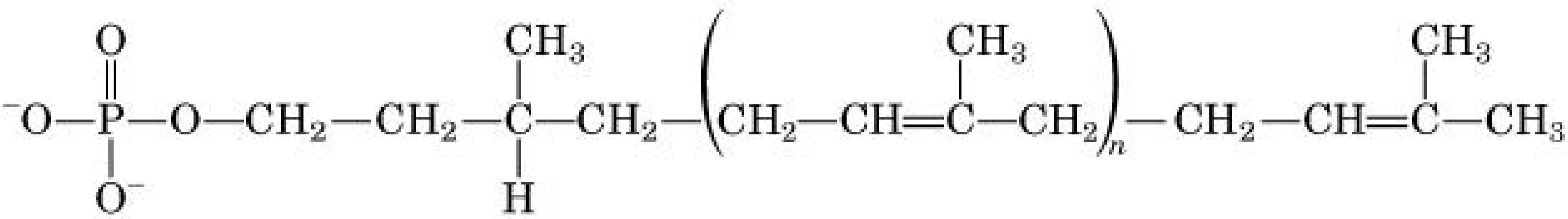
蔗糖的合成


UDP-glucose
Fructose 6-phosphate
sucrose 6-phosphate synthase
UDP
Sucrose 6-phosphate
sucrose 6-phosphate phosphatase
P_i
Sucrose

(三) 糖蛋白的生物合成

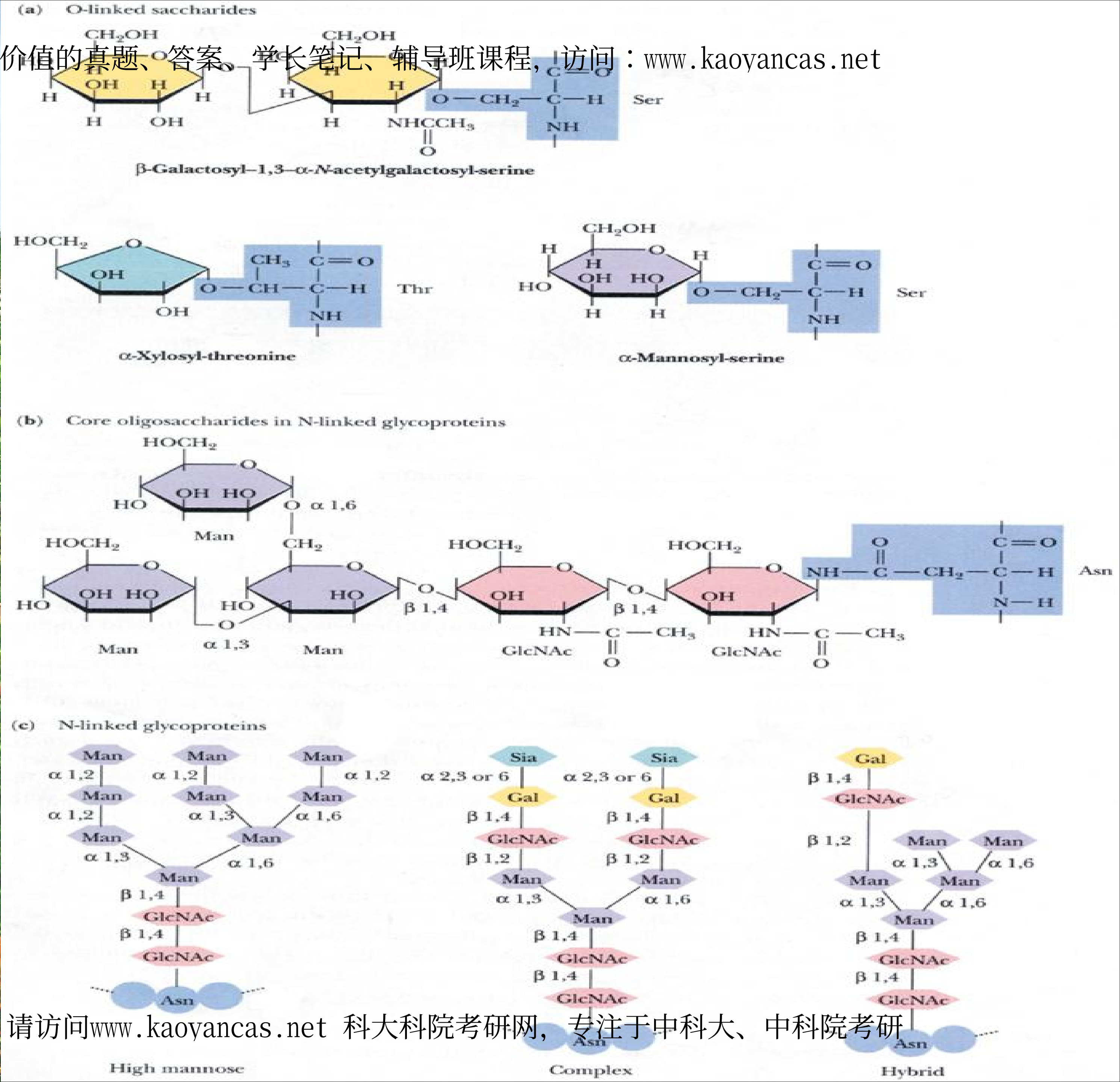
1.糖蛋白糖链生物合成的特点

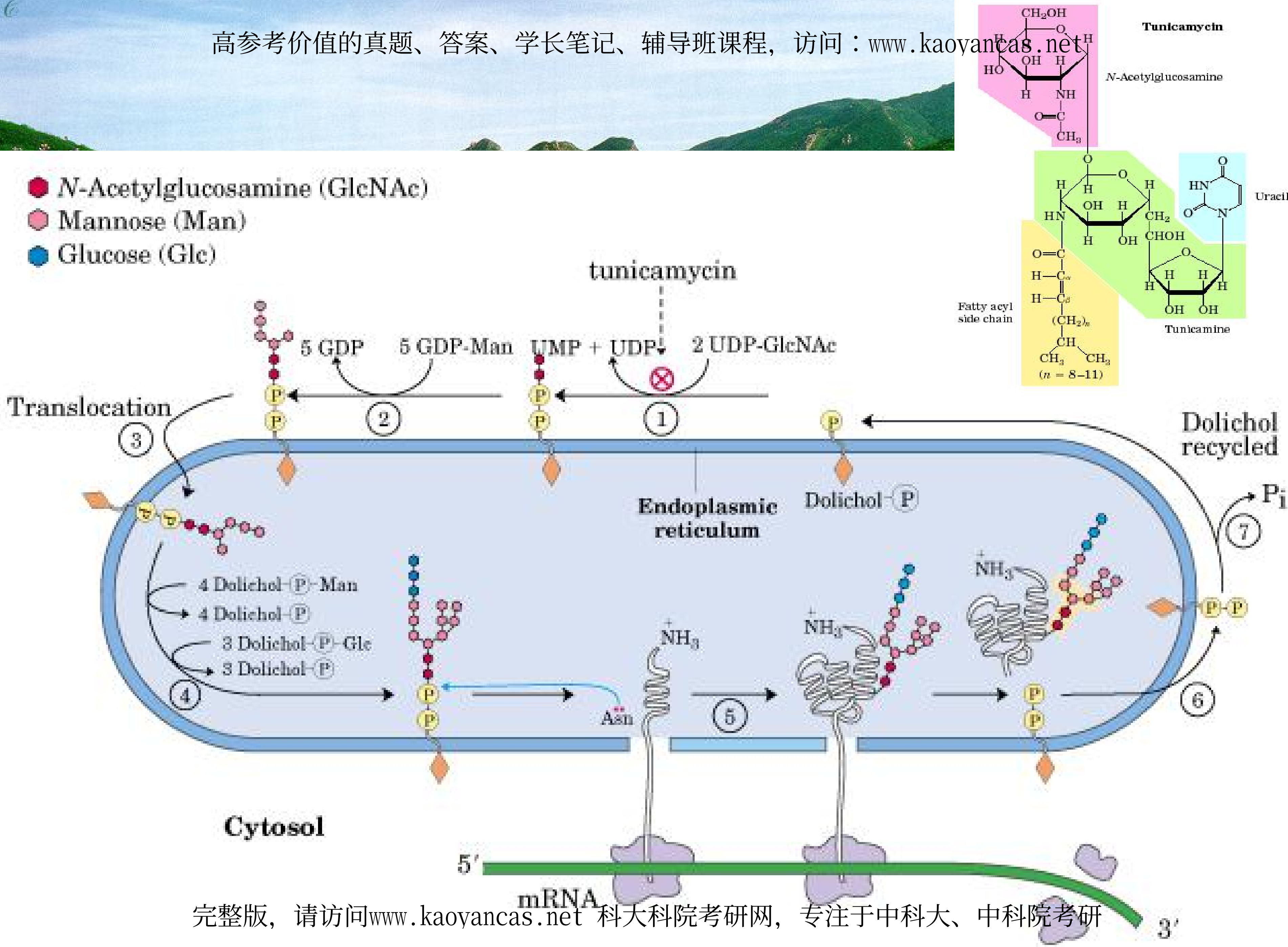
糖基的供体是单糖的核苷二磷酸；在长醇焦磷酸上合成核心寡糖链，整体转移到肽链上，在进行进一步加工。

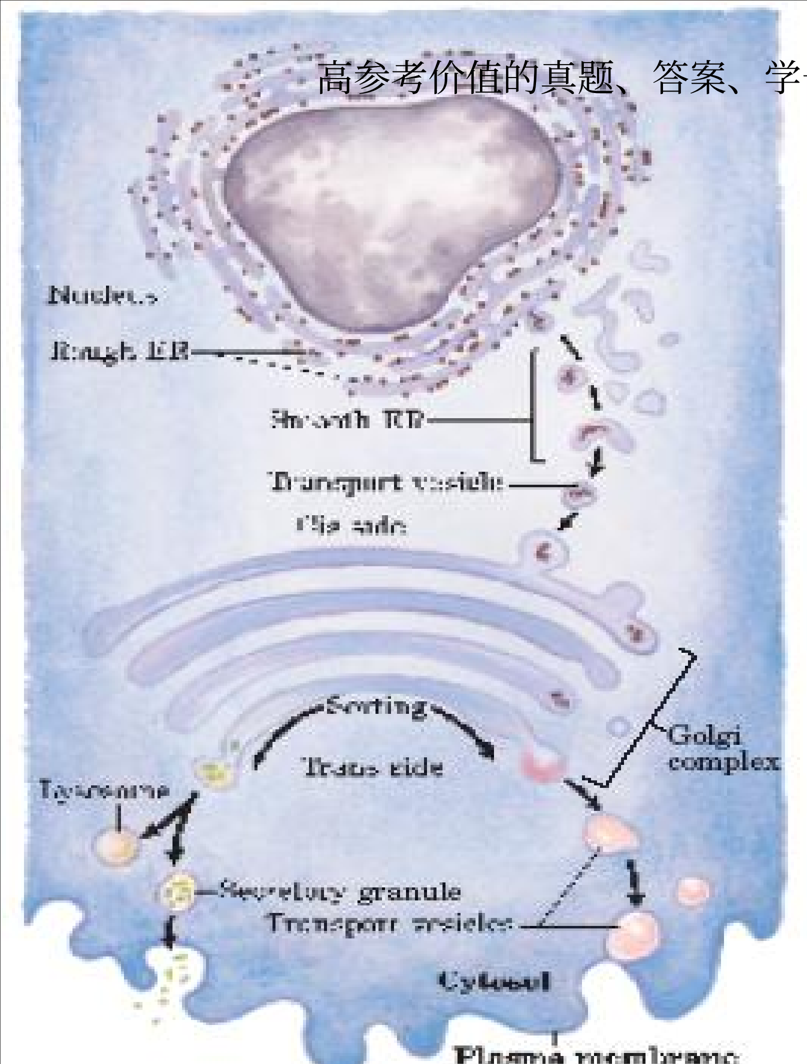


Dolichol phosphate
(n = 9–22)

2.寡糖与多肽链连接的类型




Tunicamycin
CH₂OH
HO
OH
NH
O=C
CH₃
N-Acetylglucosamine
HN
CH₂
CHOH
OH
Uracil
Fatty acyl side chain
(n = 8–11)
Tunicamine
N-Acetylglucosamine (GlcNAc)
Mannose (Man)
Glucose (Glc)
tunicamycin
5 GDP
5 GDP-Man
UMP + UDP
2 UDP-GlcNAc
Translocation
Dolichol recycled
Endoplasmic reticulum
Dolichol-P
Pi
4 Dolichol-P-Man
4 Dolichol-P
3 Dolichol-P-Glc
3 Dolichol-P
Asn
Cytosol
5′
3′
mRNA



N-连接寡糖链在高尔基体经过复杂的加工和修饰，被分选到细胞的有关部位。

FIGURE 27-35 Pathway taken by proteins destined for lysosomes, the plasma membrane, or secretion. Proteins are moved from the ER to the cis side of the Golgi complex in transport vesicles. Sorting occurs primarily in the trans side of the Golgi complex.

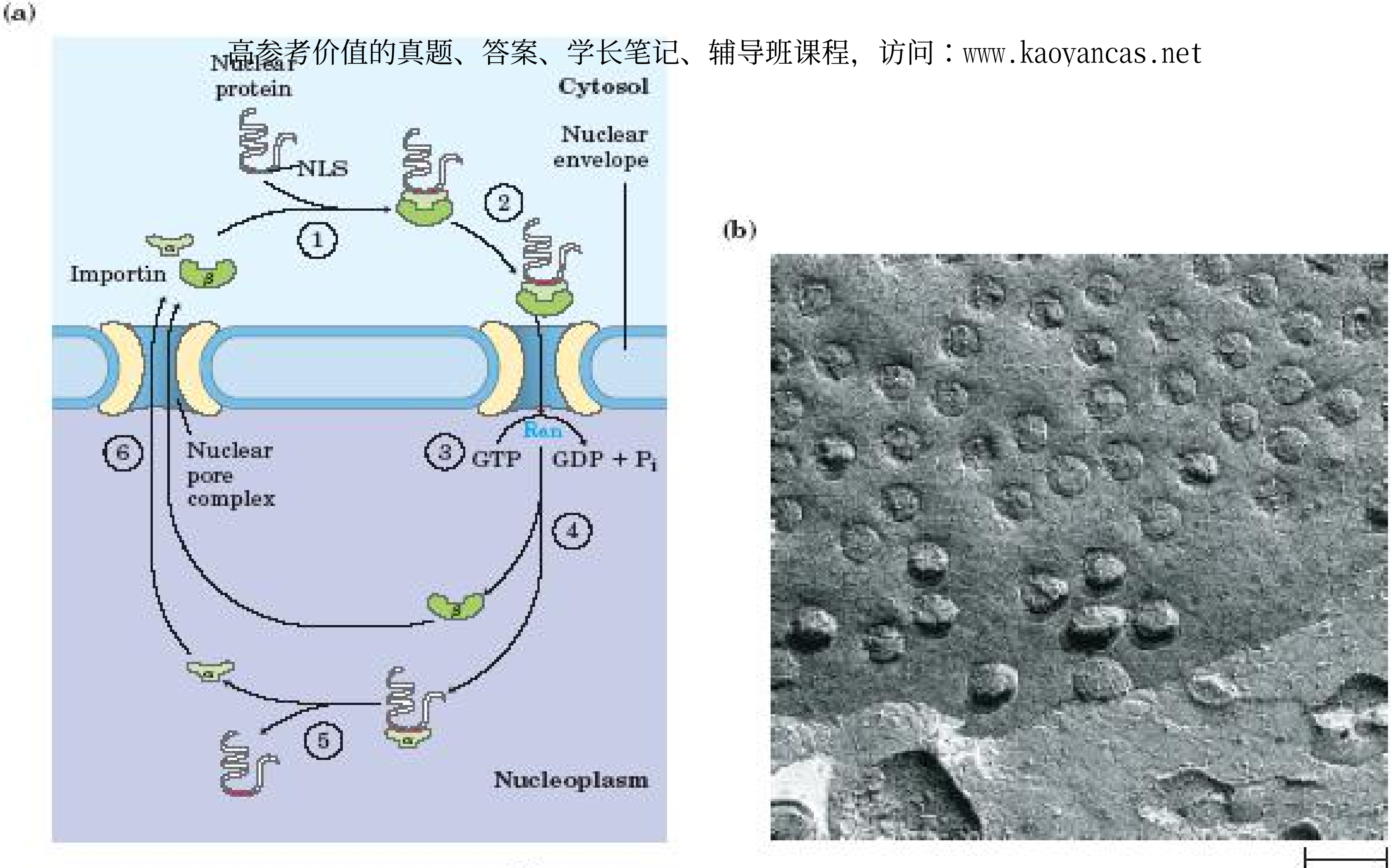


FIGURE 27–37 Targeting of nuclear proteins. (a) ① A protein with an appropriate nuclear localization signal (NLS) is bound by a complex of importin α and β. ② The resulting complex binds to a nuclear pore, and ③ translocation is mediated by the Ran GTPase. ④ Inside the nucleus, importin β dissociates from importin α, and ⑤ importin α then releases the nuclear protein. ⑥ Importin α and β are transported out of the nucleus and recycled. (b) Scanning electron micrograph of the surface of the nuclear envelope, showing numerous nuclear pores.

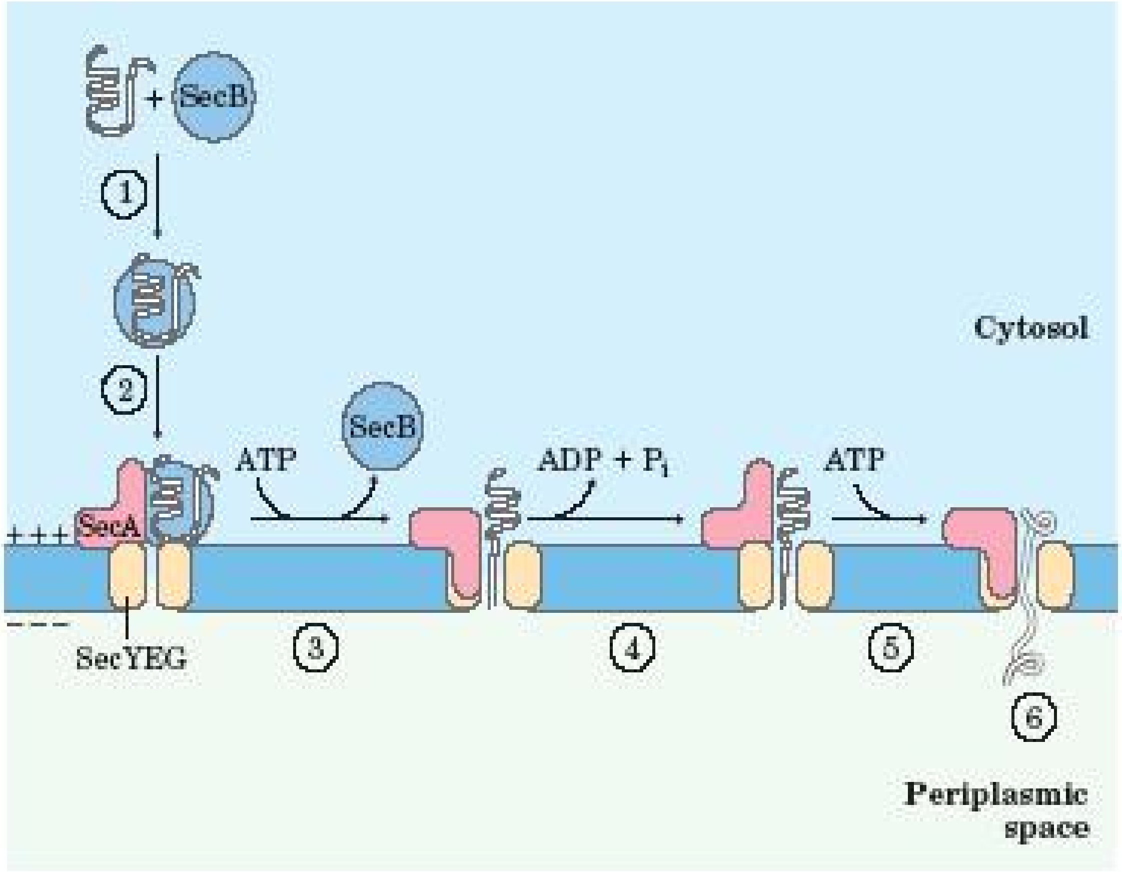


FIGURE 27-39 Model for protein export in bacteria. (1) A newly translated polypeptide binds to the cytosolic chaperone protein SecB, which (2) delivers it to SecA, a protein associated with the translocation complex (SecYEG) in the bacterial cell membrane. (3) SecB is released, and SecA inserts itself into the membrane, forcing about 20 amino acid residues of the protein to be exported through the translocation complex. (4) Hydrolysis of an ATP by SecA provides the energy for a conformational change that causes SecA to withdraw from the membrane, releasing the polypeptide. (5) SecA binds another ATP, and the next stretch of 20 amino acid residues is pushed across the membrane through the translocation complex. Steps (4) and (5) are repeated until (6) the entire protein has passed through and is released to the periplasm. The electrochemical potential across the membrane (denoted by + and −) also provides some of the driving force required for protein translocation.

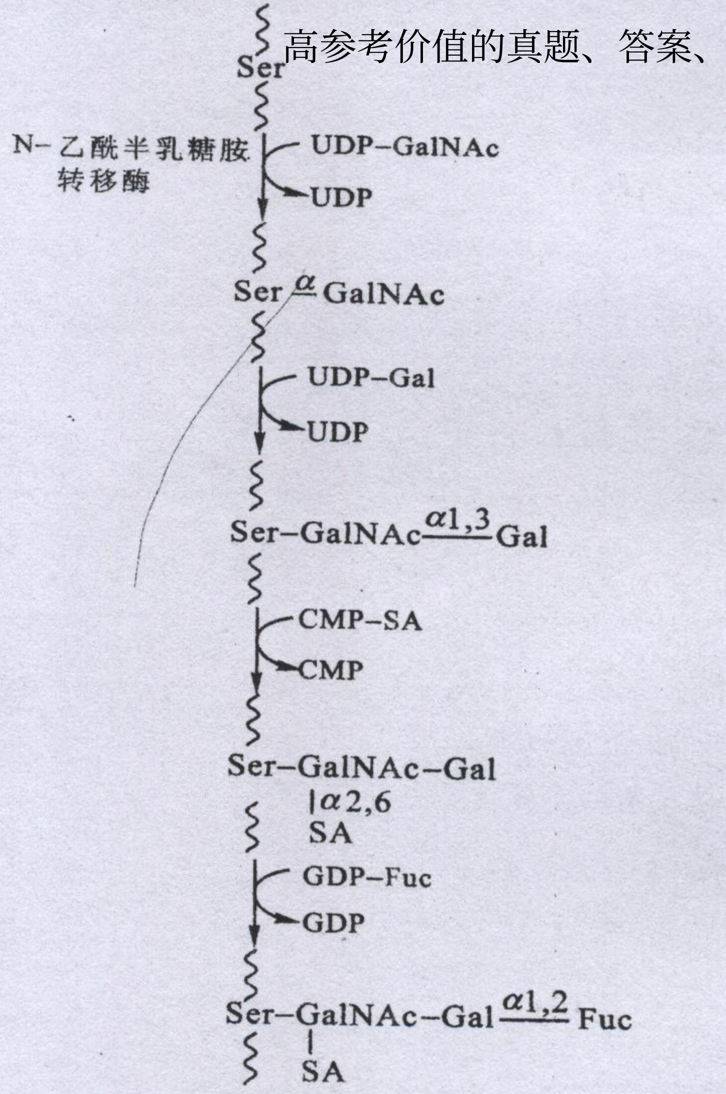


图 25－18 狗颌下唾液腺 O－连寡糖链糖单位的合成途径示意

GalNAc：N－乙酰－D－半乳糖胺，Gal：半乳糖，SA：唾液[illegible]

O-连接寡糖链是通过翻译后加工合成的

基本要求

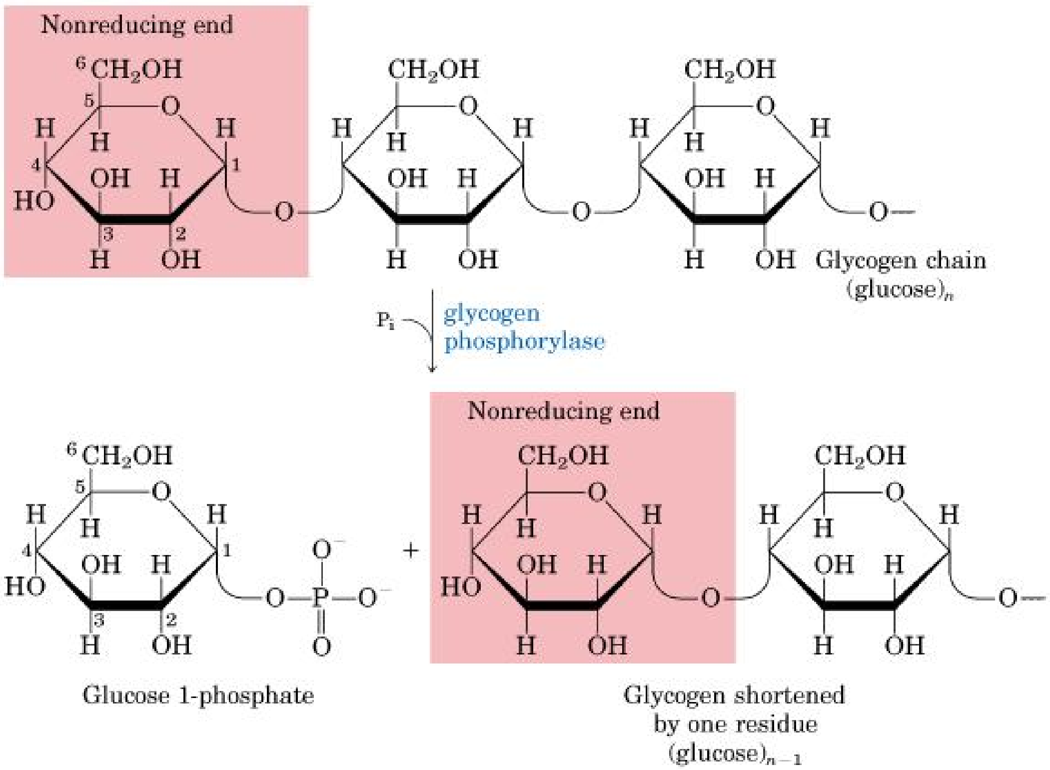
1. 掌握戊糖磷酸途径的基本途径和生物学意义。 （重点）
2. 掌握糖异生作用的过程、意义和调控。 （重点）
3. 掌握乙醛酸途径的过程和意义。 （重点）
4. 熟悉寡糖的生物合成和分解途径。

第26章

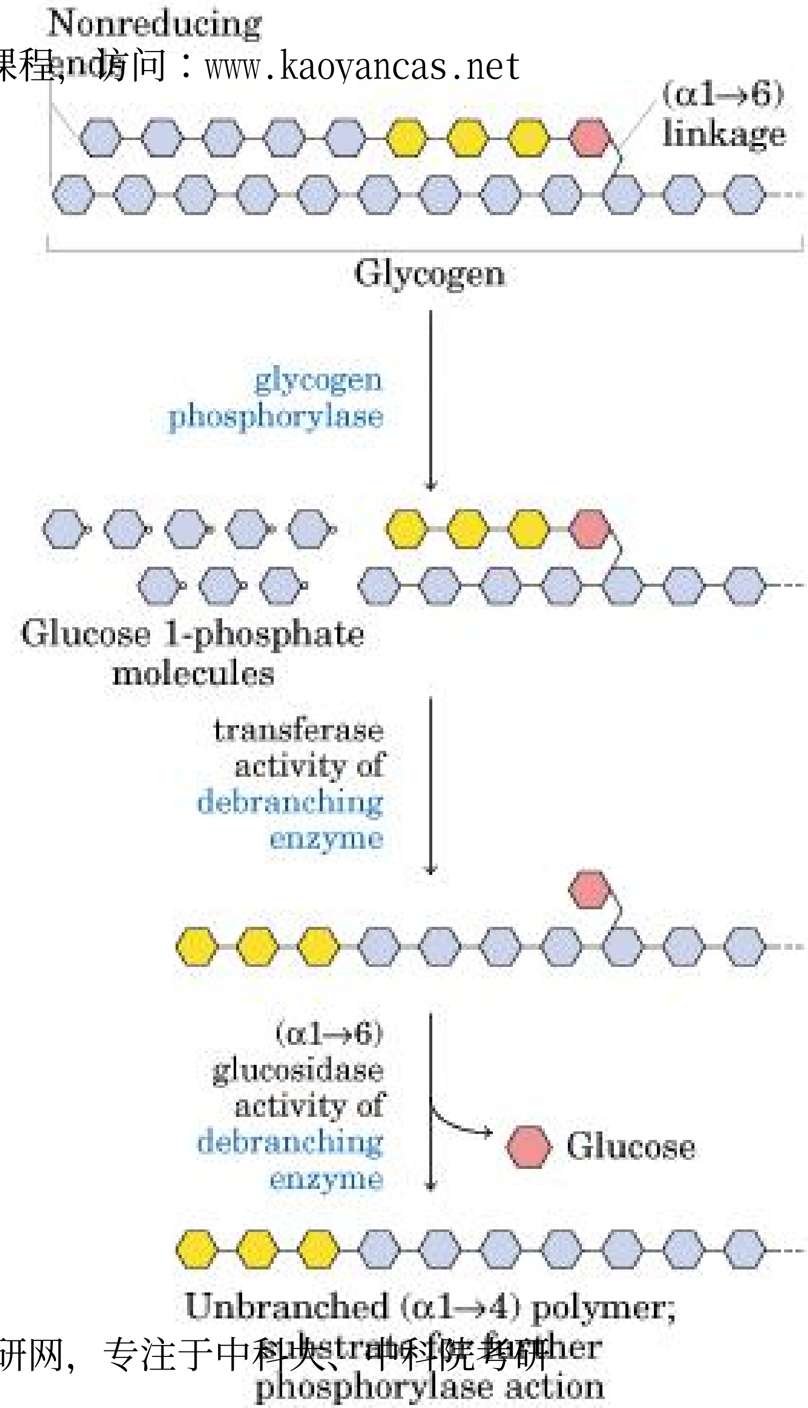
糖原的分解和生物合成

一、糖原的降解(glycogen breakdown)

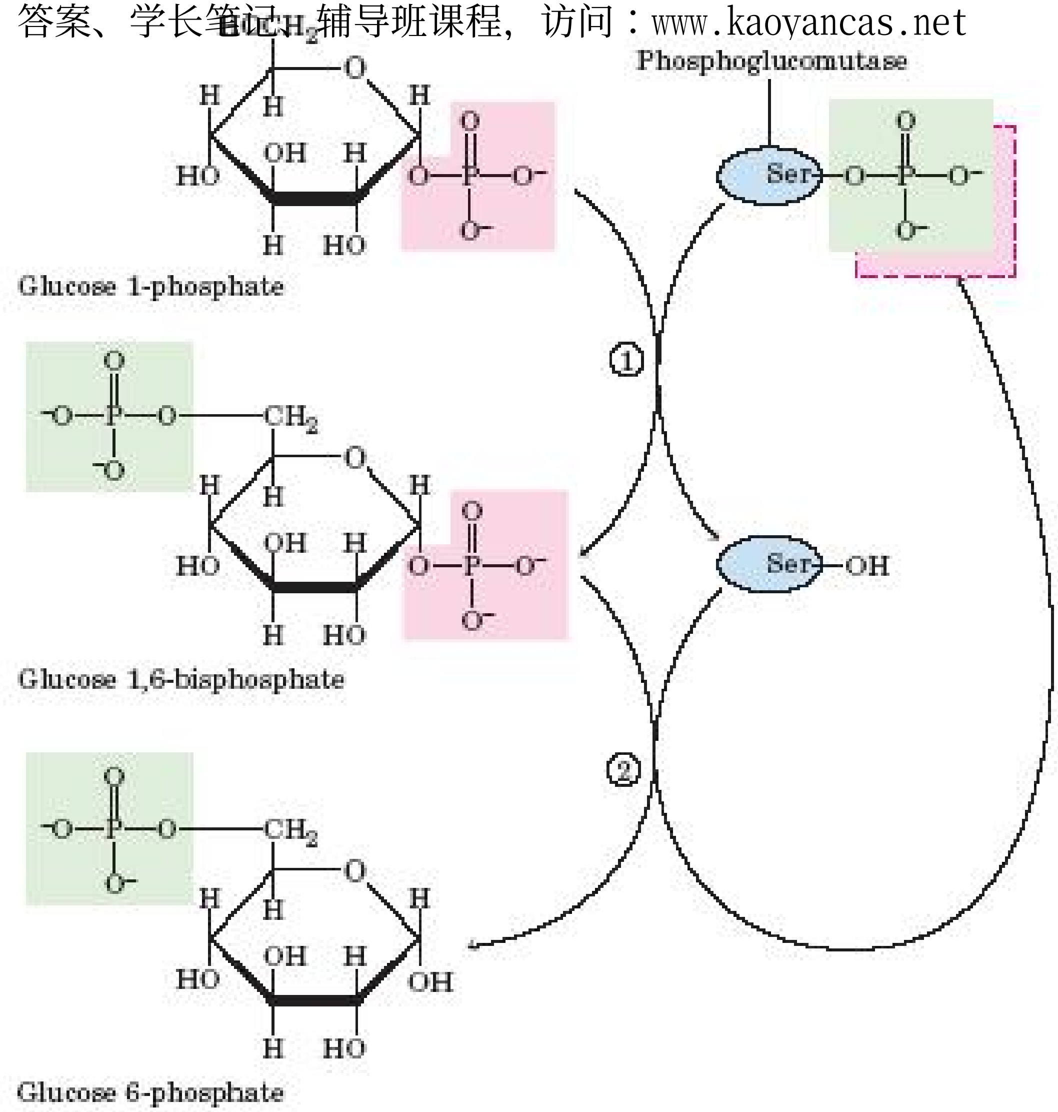
1.糖原磷酸化酶催化的反应



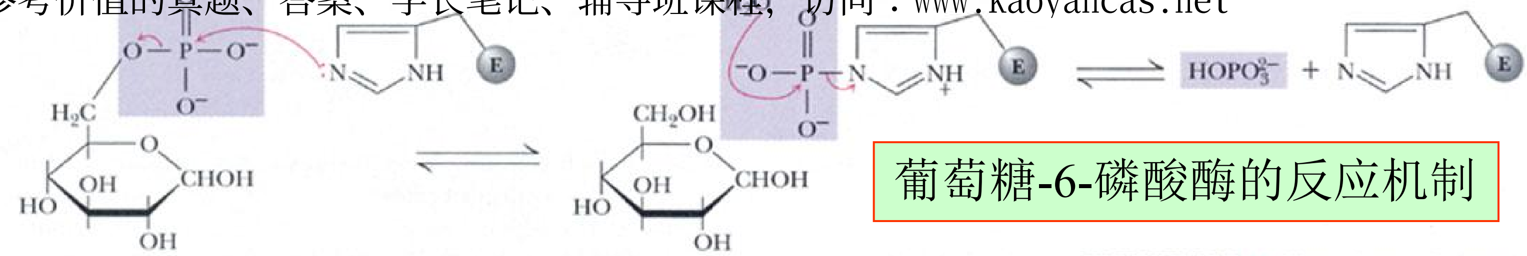
2.糖原脱支酶(glycogen debranching enzyme，包括糖基转移酶)催化的反应



3.磷酸葡萄糖变位酶(phosphoglucomutase)的作用

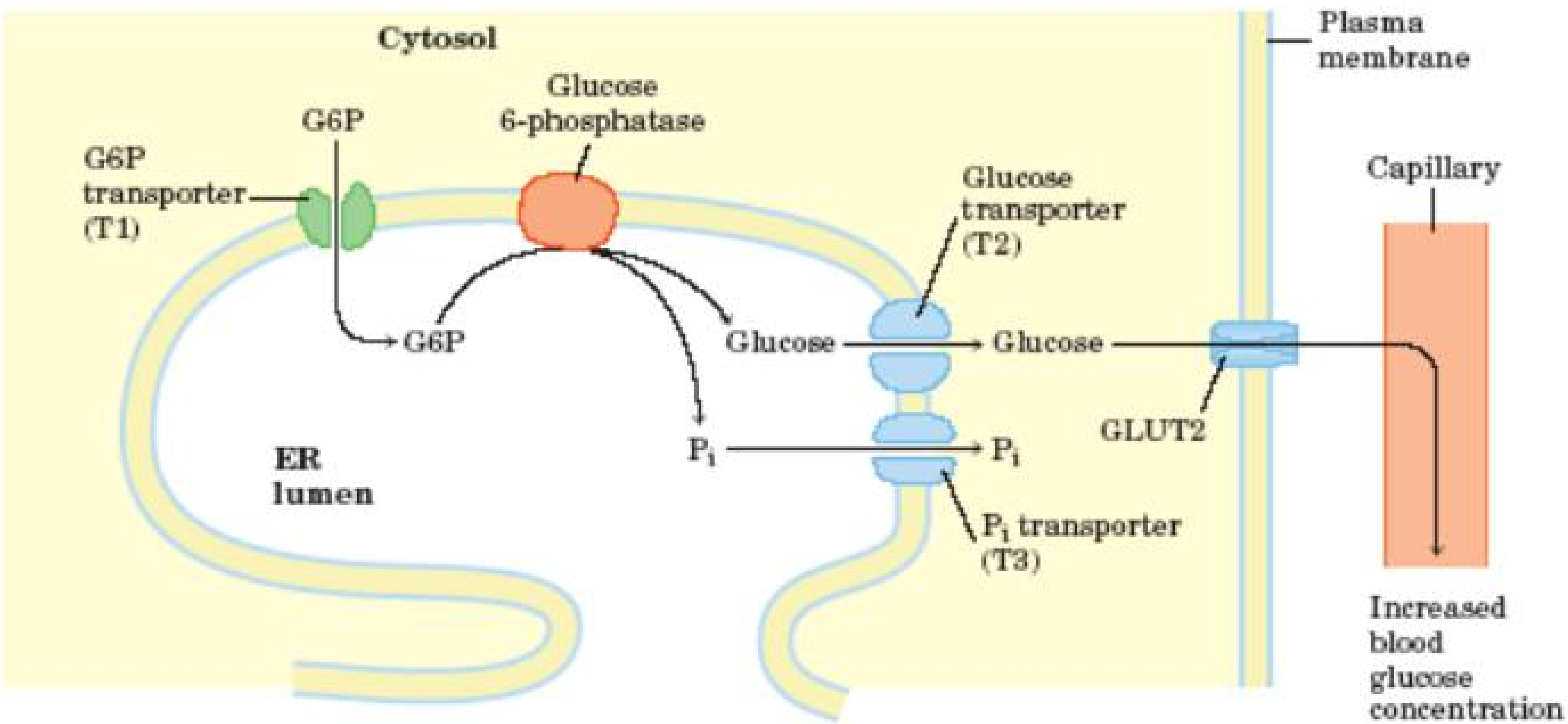


4.葡萄糖-6-磷酸酶



葡萄糖-6-磷酸酶的反应机制

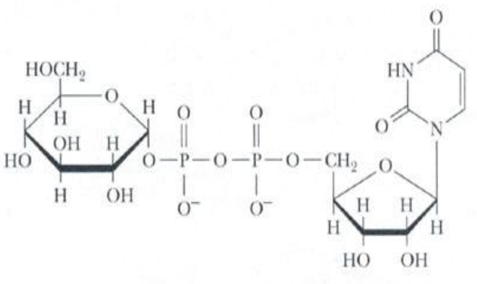
FIGURE 23.9 • The glucose-6-phosphat



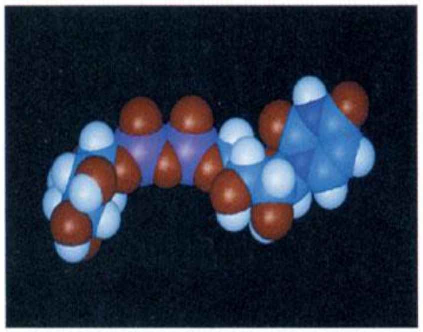
葡萄糖-6-磷酸酶定位内在内质网膜

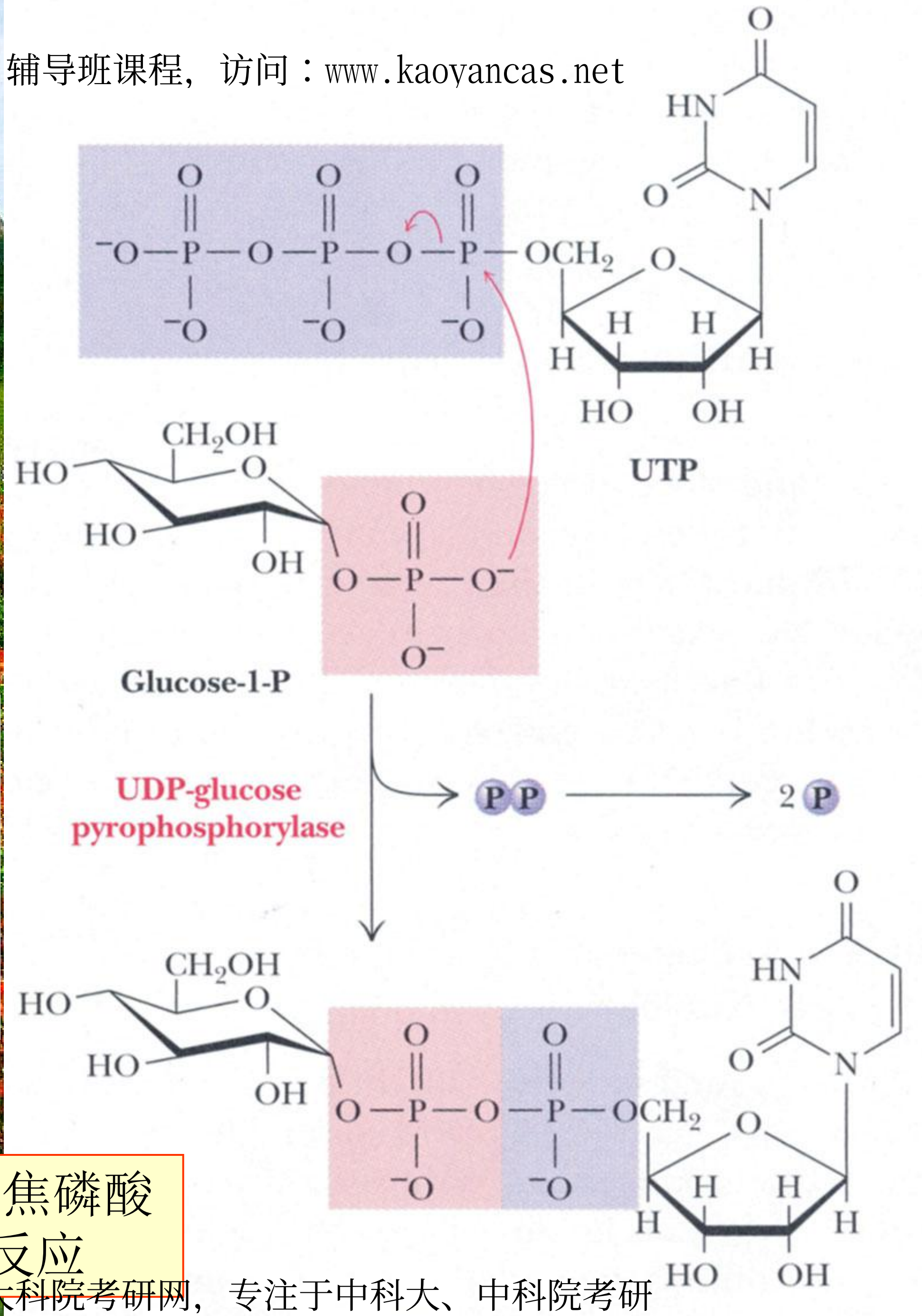
三、糖原的生物合成

糖原生物合成的研究经历了缓慢的历程，直到1957年，才发现糖原生物合成中，糖基的供体是 UDPG。



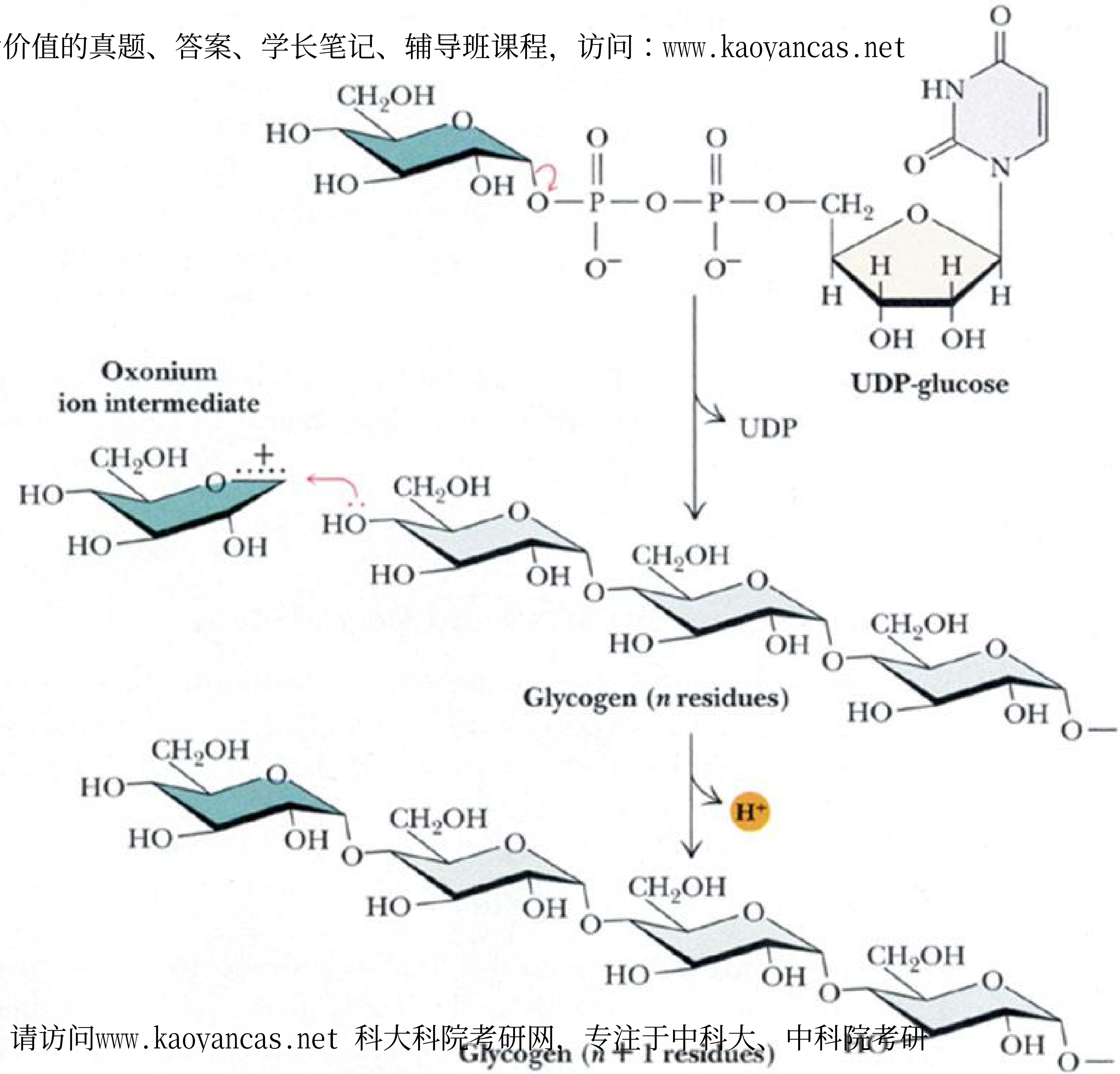
Uridine diphosphate glucose
(UDPG)



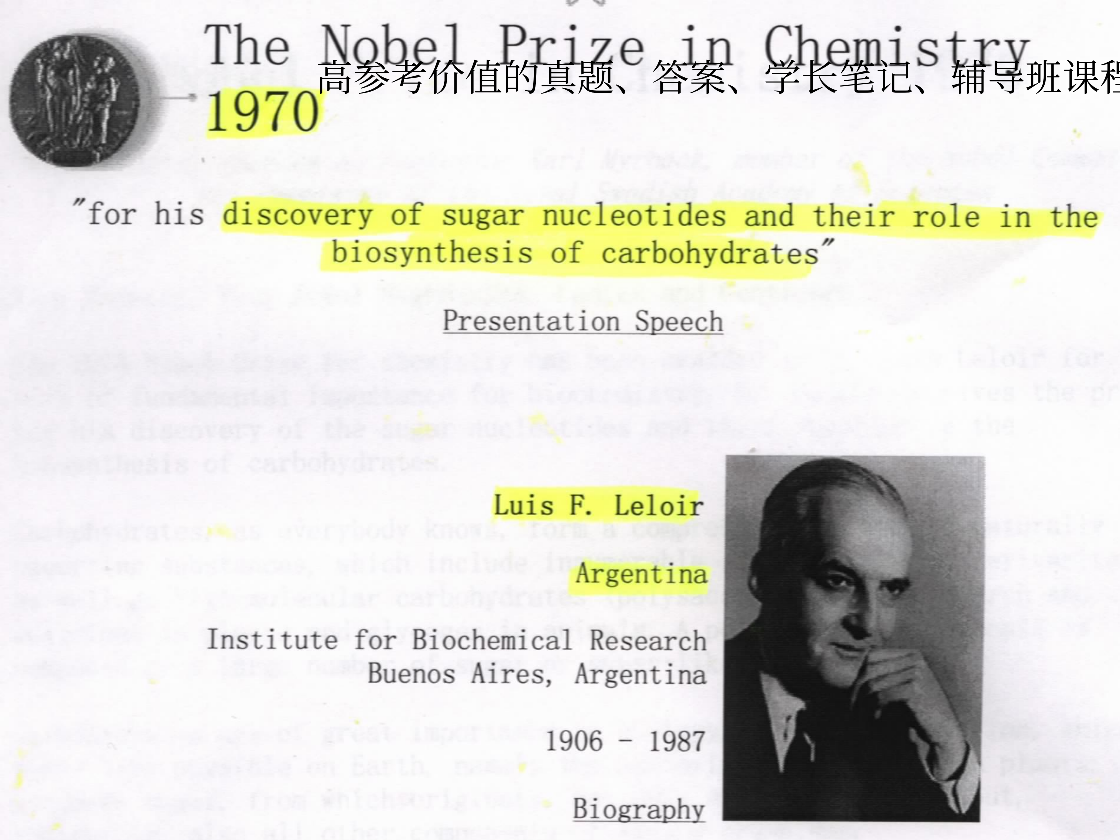


UDP-葡萄糖焦磷酸化酶催化的反应

糖原合成酶催化的反应



CH₂OH
HO
O
OH
O
P
O⁻
CH₂
H
OH
HN
N
UDP-glucose
UDP
Oxonium
ion intermediate
+
Glycogen (n residues)
H⁺
Glycogen (n + 1 residues)



The Nobel Prize in Chemistry 1970

"for his discovery of sugar nucleotides and their role in the biosynthesis of carbohydrates"

Presentation Speech

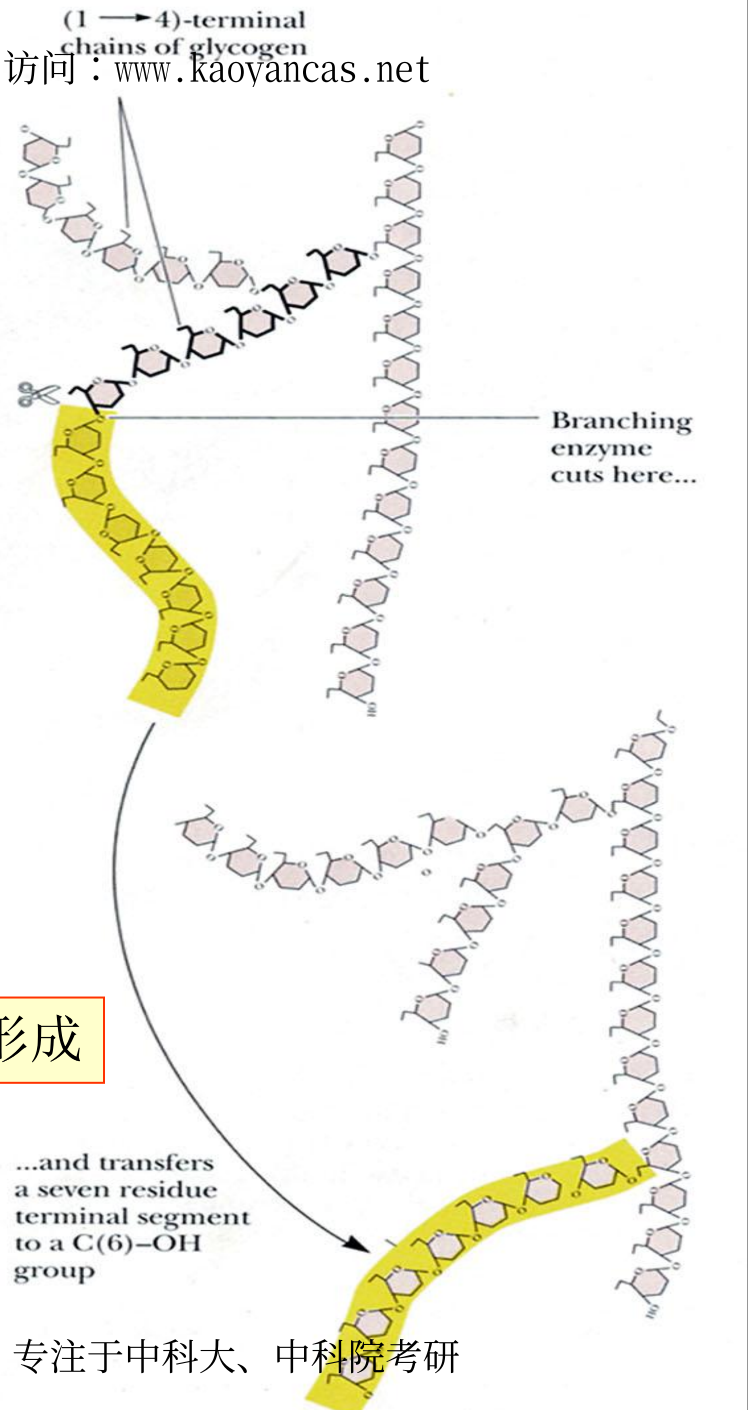
Luis F. Leloir

Argentina

Institute for Biochemical Research
Buenos Aires, Argentina

1906 - 1987

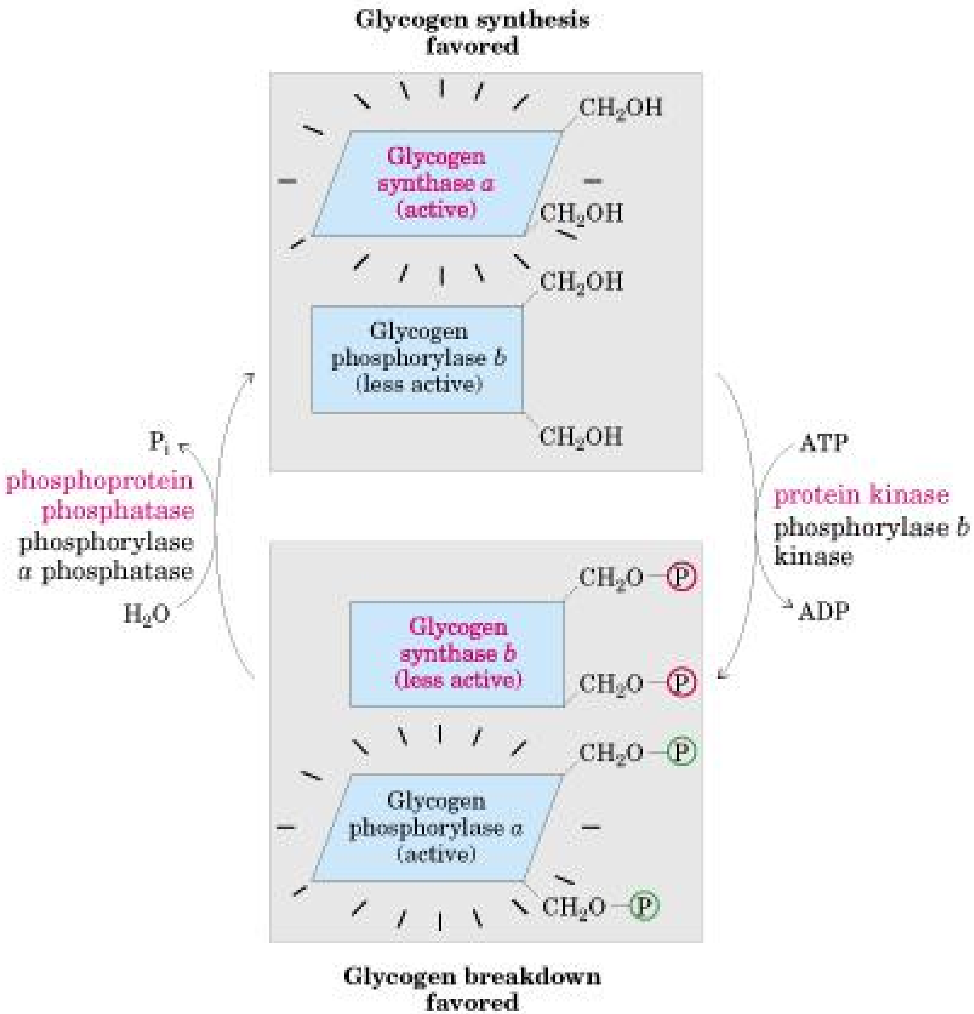
Biography



糖原新分支的形成

四、糖原代谢的调控

（一）糖原磷酸化酶的调控机制



The Nobel Prize in Physiology or Medicine 1992

"for their discoveries concerning reversible protein phosphorylation as a biological regulatory mechanism"

Press release
Illustrated presentation

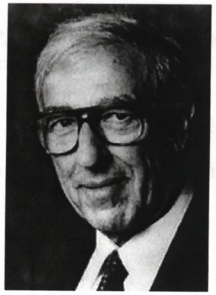
Edmond H. Fischer

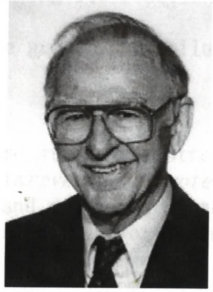
USA

University of Washington
Seattle, WA, USA

1920 -

Autobiography





Edwin G. Krebs

USA

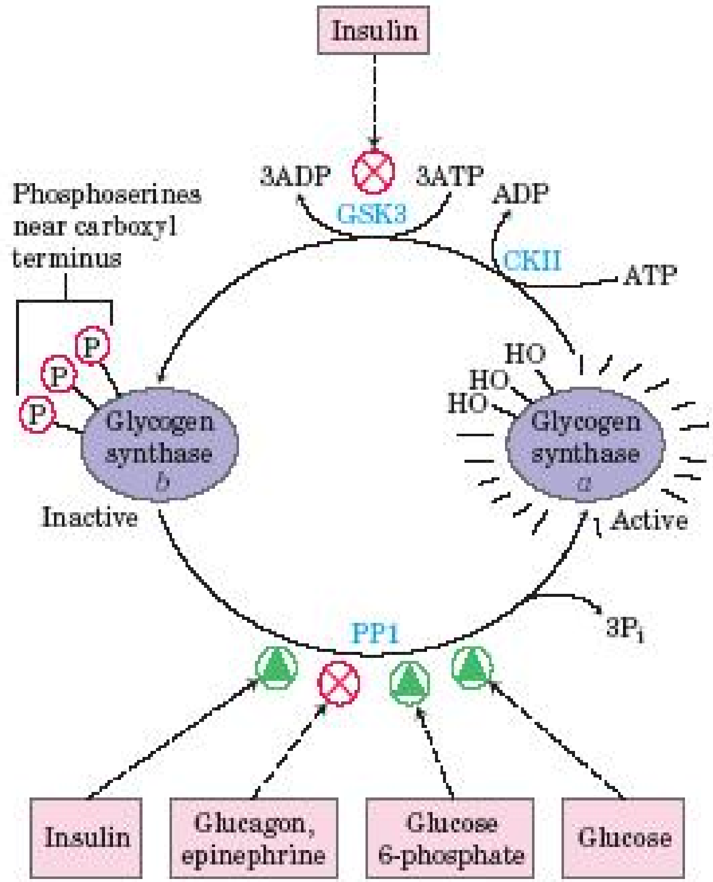
University of Washington
Seattle, WA, USA

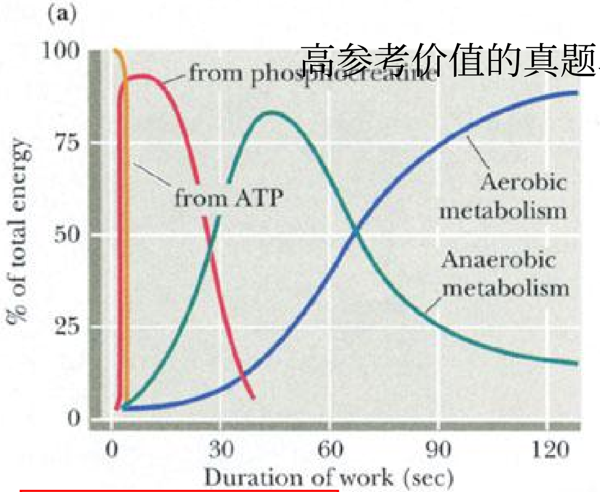
1918 -

Autobiography

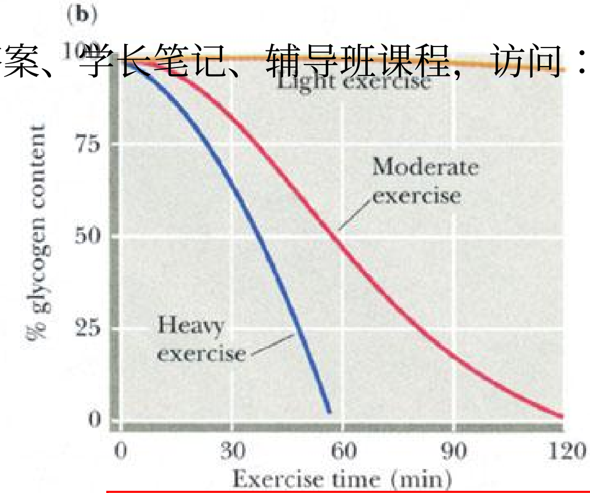
（二）对糖原合酶的调控

FIGURE 15–27 **Effects of GSK3 on glycogen synthase activity.** Glycogen synthase a, the active form, has three Ser residues near its carboxyl terminus, which are phosphorylated by glycogen synthase kinase 3 (GSK3). This converts glycogen synthase to the inactive (*b*) form (GS*b*). GSK3 action requires prior phosphorylation (priming) by casein kinase (CKII). Insulin triggers activation of glycogen synthase *b* by blocking the activity of GSK3 (see the pathway for this action in Fig. 12–8) and activating a phosphoprotein phosphatase (PP1 in muscle, another phosphatase in liver). In muscle, epinephrine activates PKA, which phosphorylates the glycogen-targeting protein G_M (see Fig. 15–30) on a site that causes dissociation of PP1 from glycogen. Glucose 6-phosphate favors dephosphorylation of glycogen synthase by binding to it and promoting a conformation that is a good substrate for PP1. Glucose also promotes dephosphorylation; the binding of glucose to glycogen phosphorylase a forces a conformational change that favors dephosphorylation to glycogen phosphorylase *b*, thus relieving its inhibition of PP1 (see Fig. 15–29).

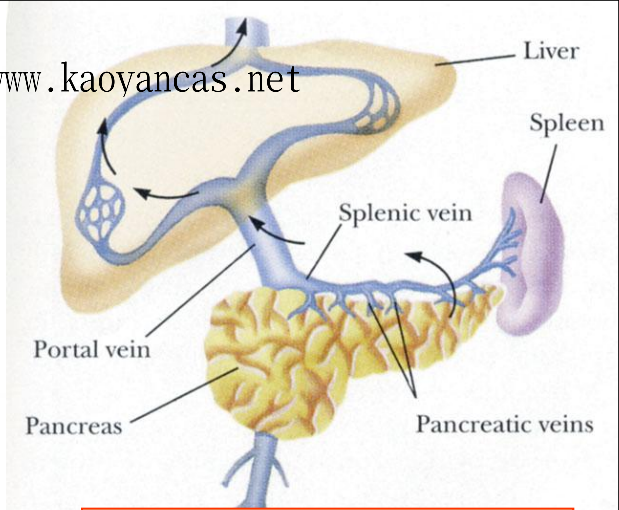




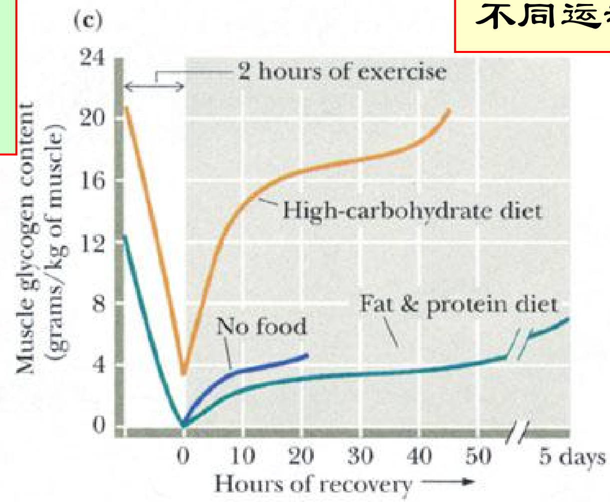
温和运动对肌肉几种能源物质的影响



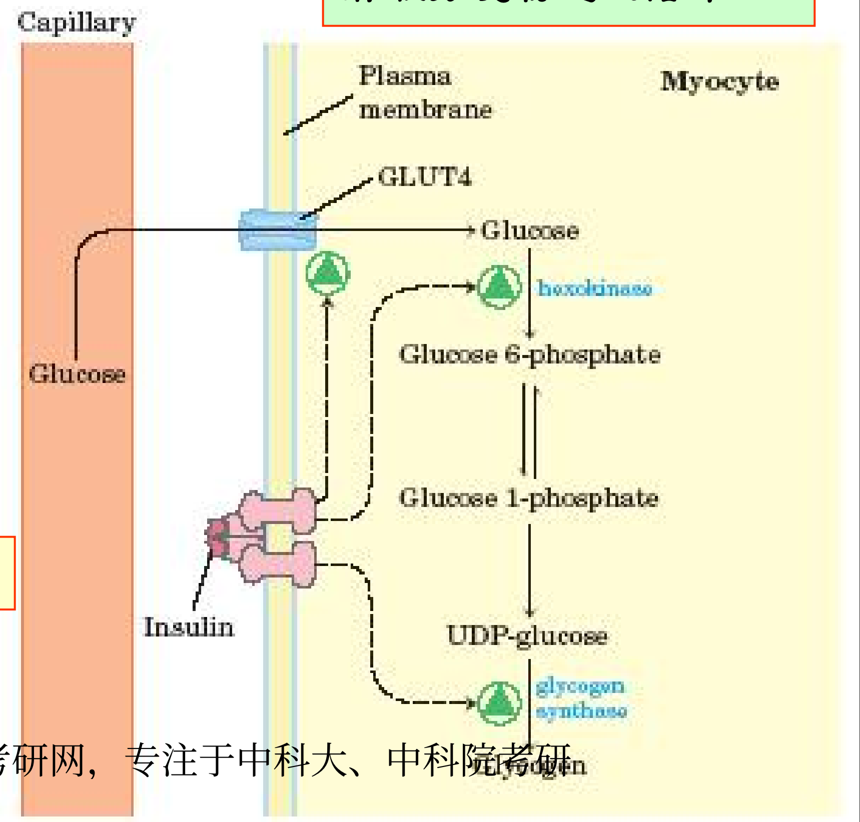
不同运动对糖原的消耗



门静脉系统携带胰脏和肝脏分泌物进入循环

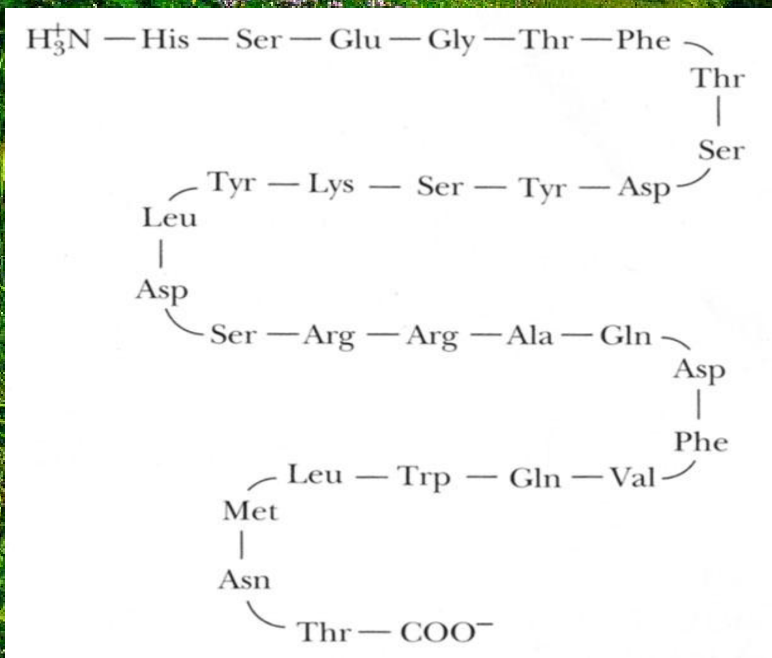


力竭运动后糖原的恢复

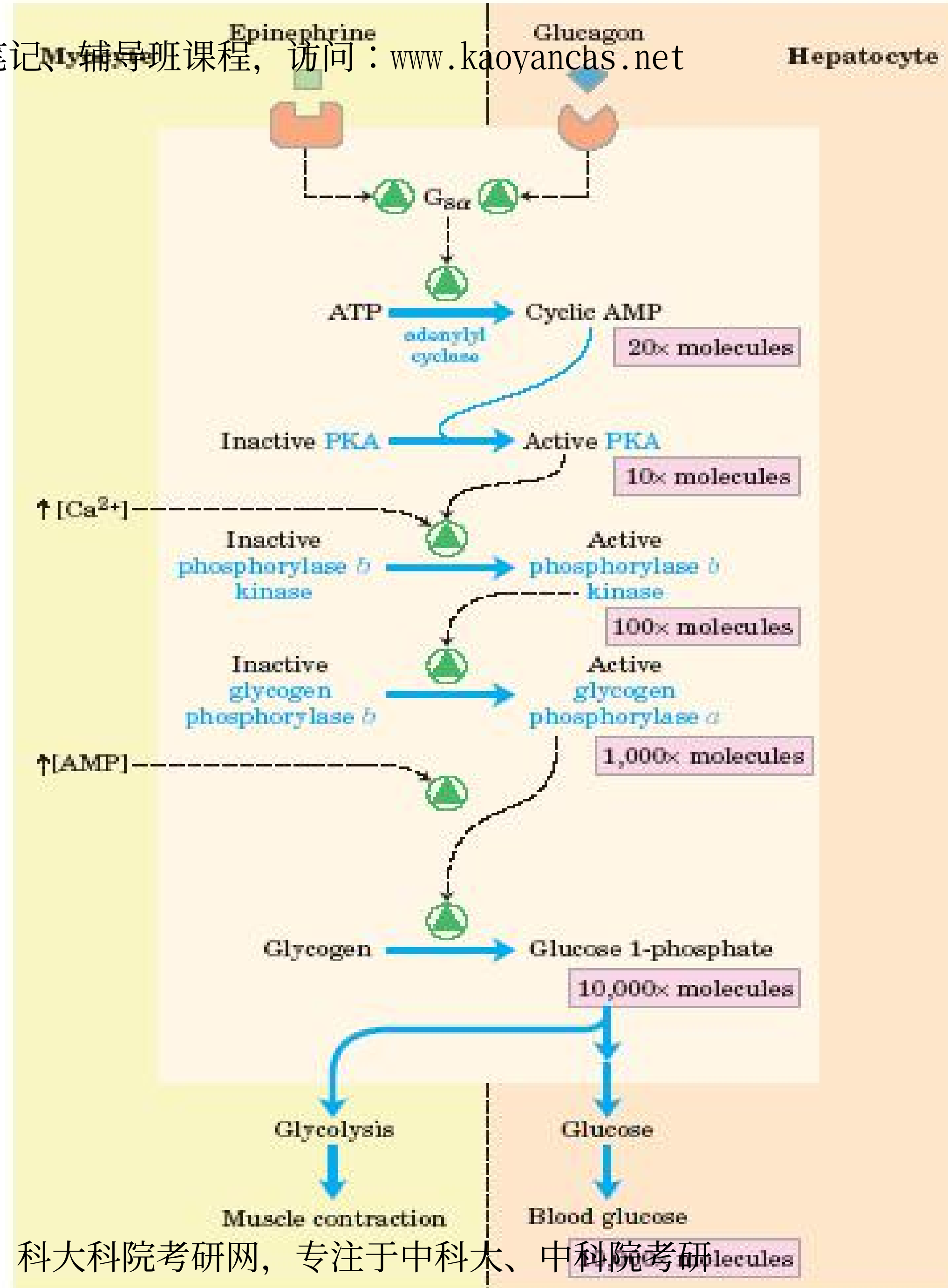


肌糖原的合成

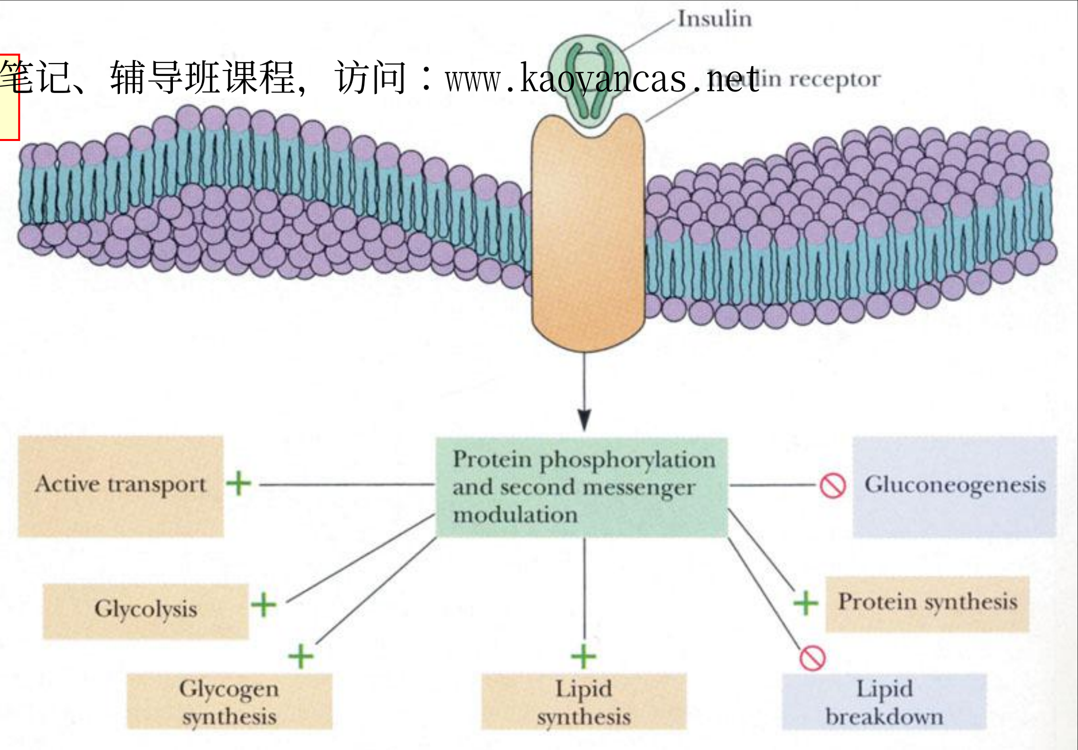
（四）激素对糖原代谢的调节和激素效应的级联放大系统



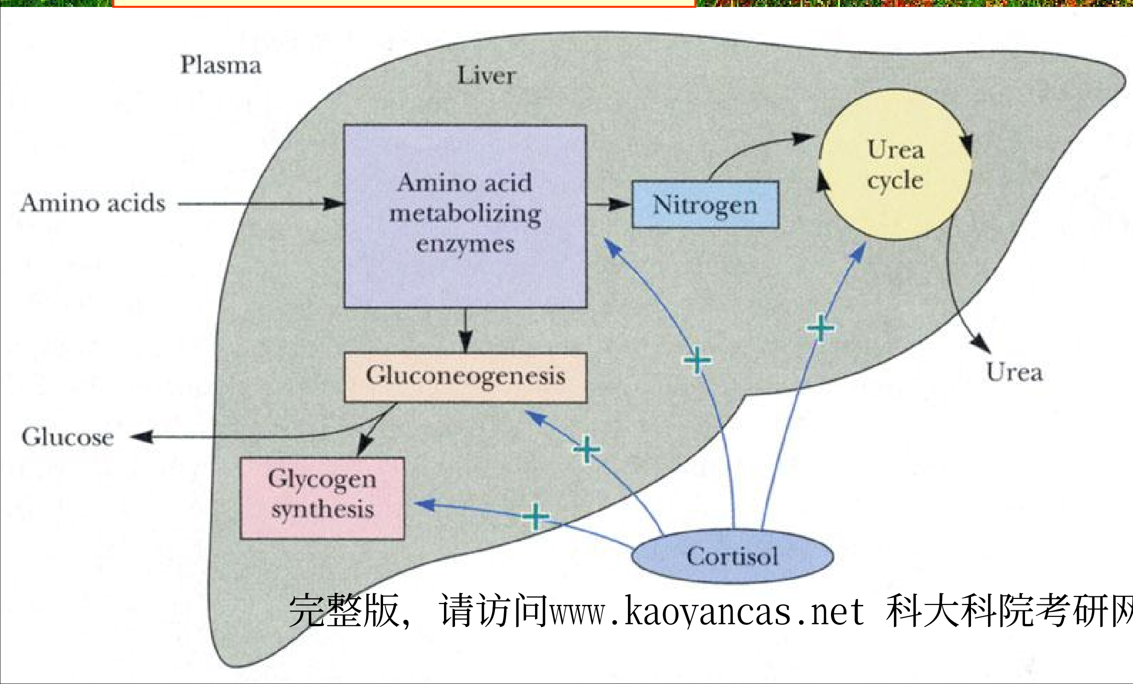
胰高血糖素的氨基酸序列



胰岛素对代谢的作用



皮质醇在肝脏糖代谢和蛋白质代谢中的作用



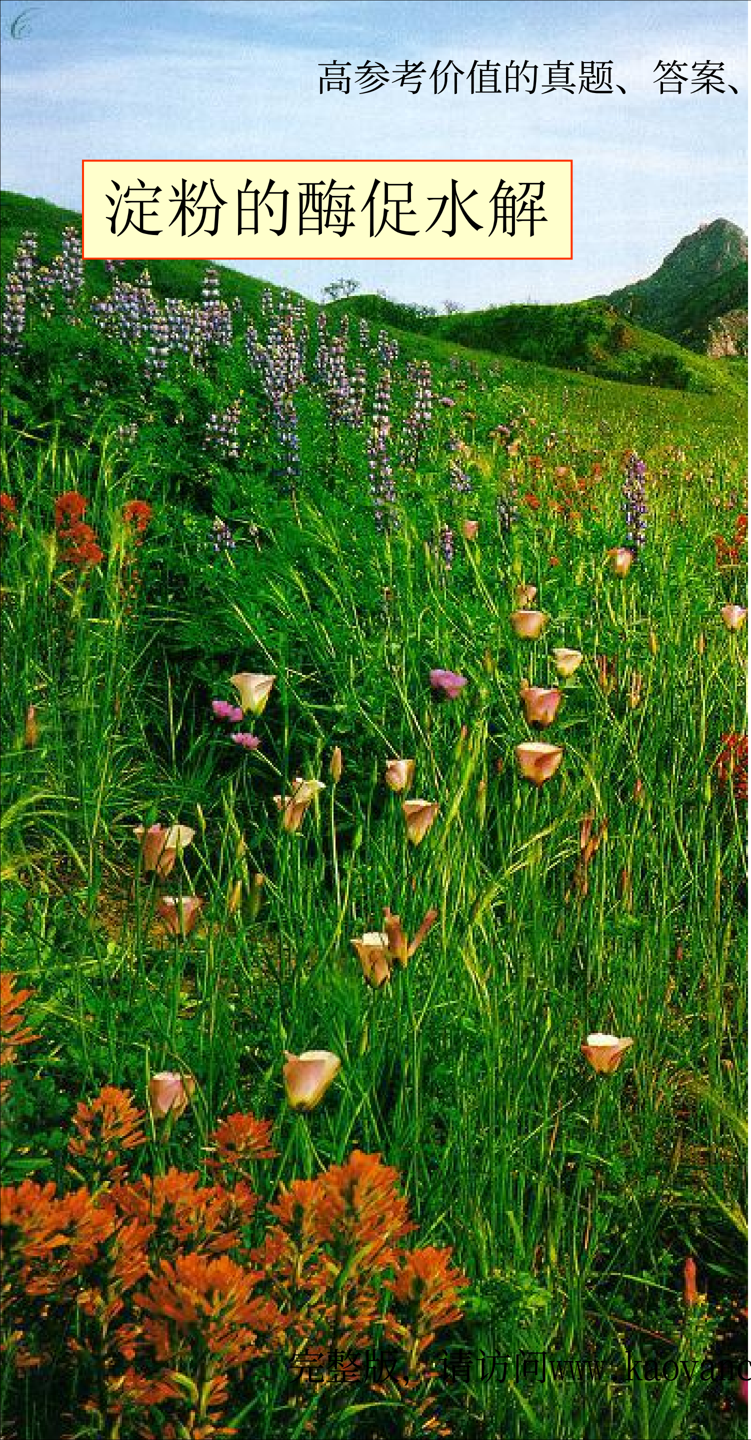
（五）G蛋白及其对激素信号的传递作用

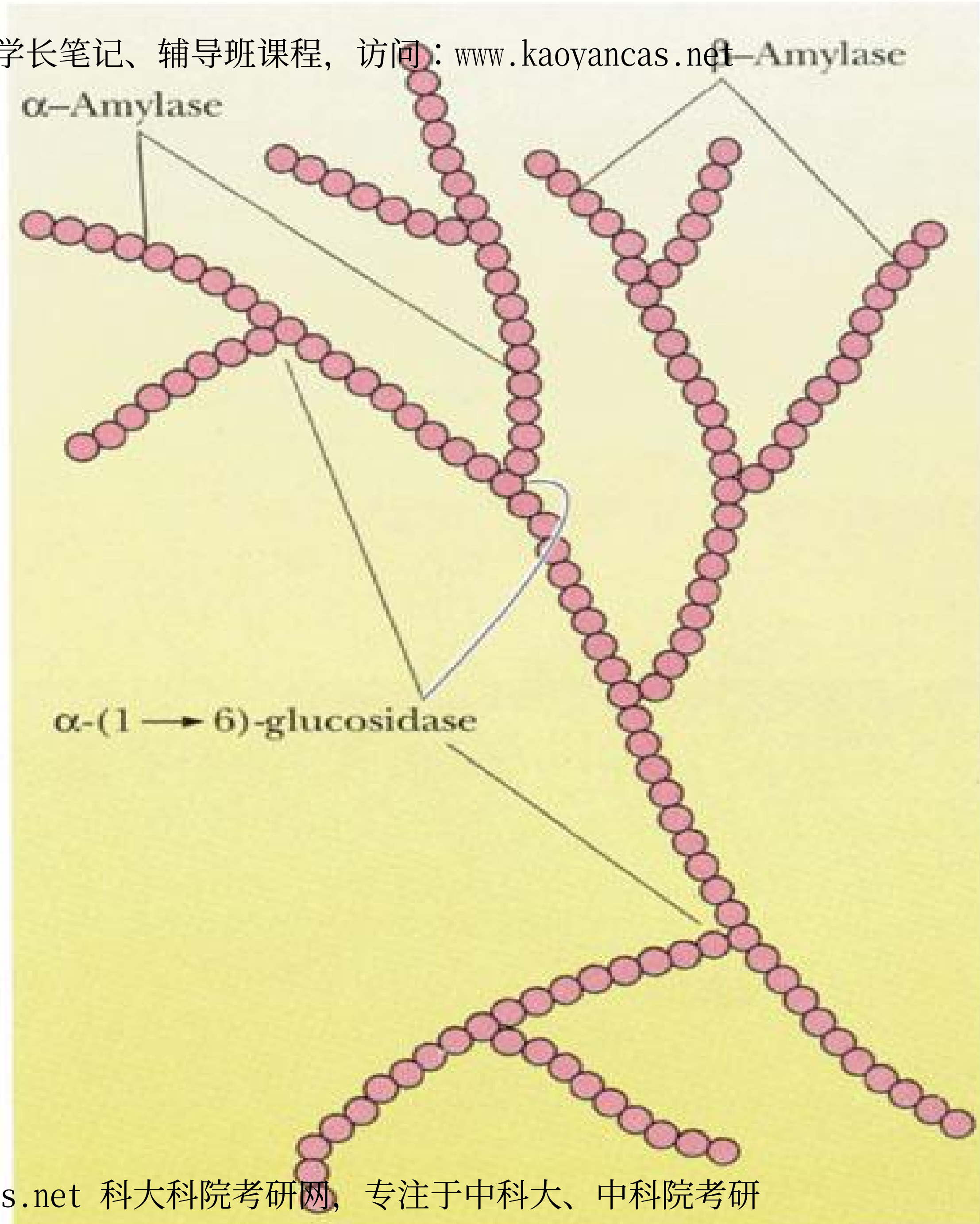
参见激素的作用机制

（六）糖原累积症

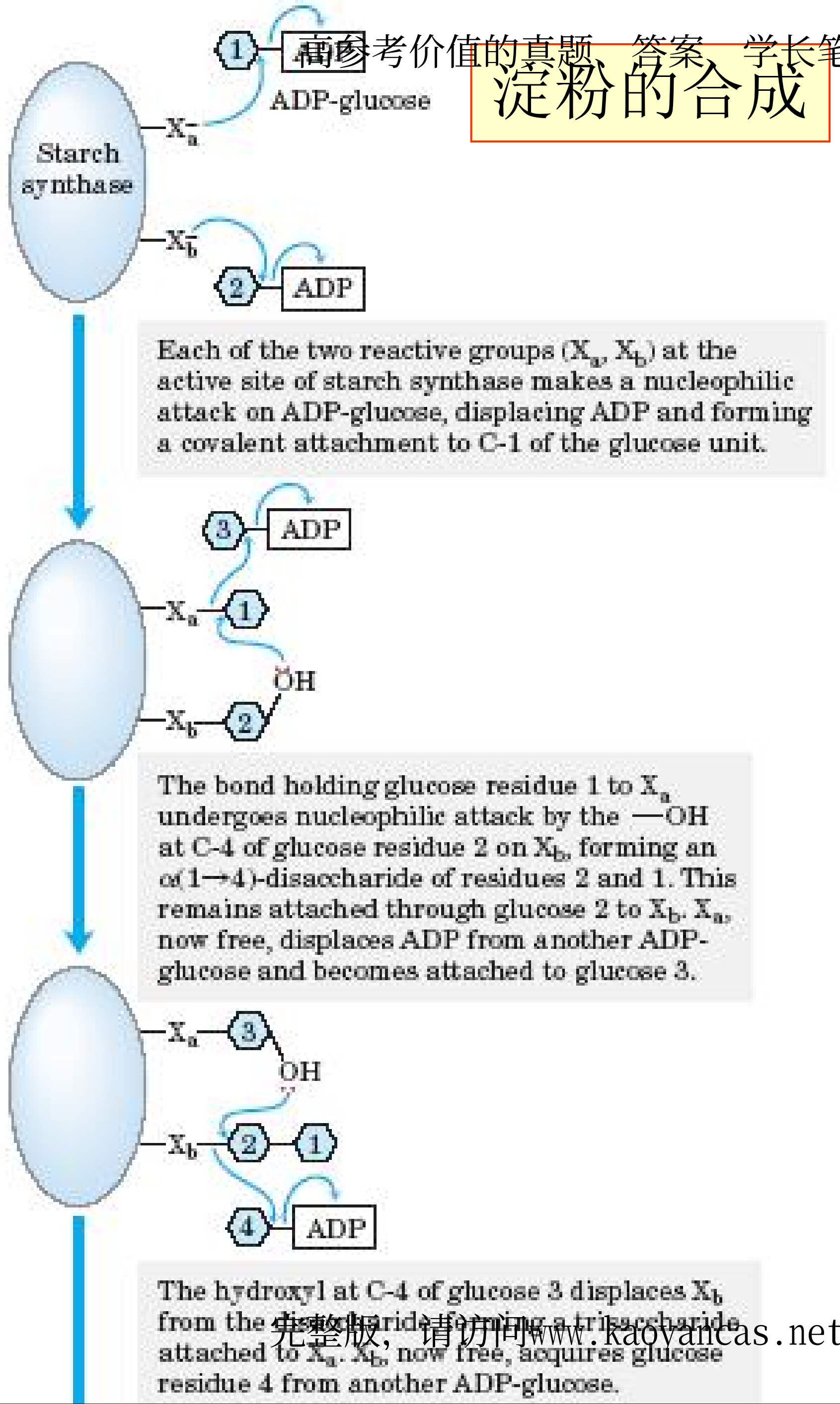
参见表26-1

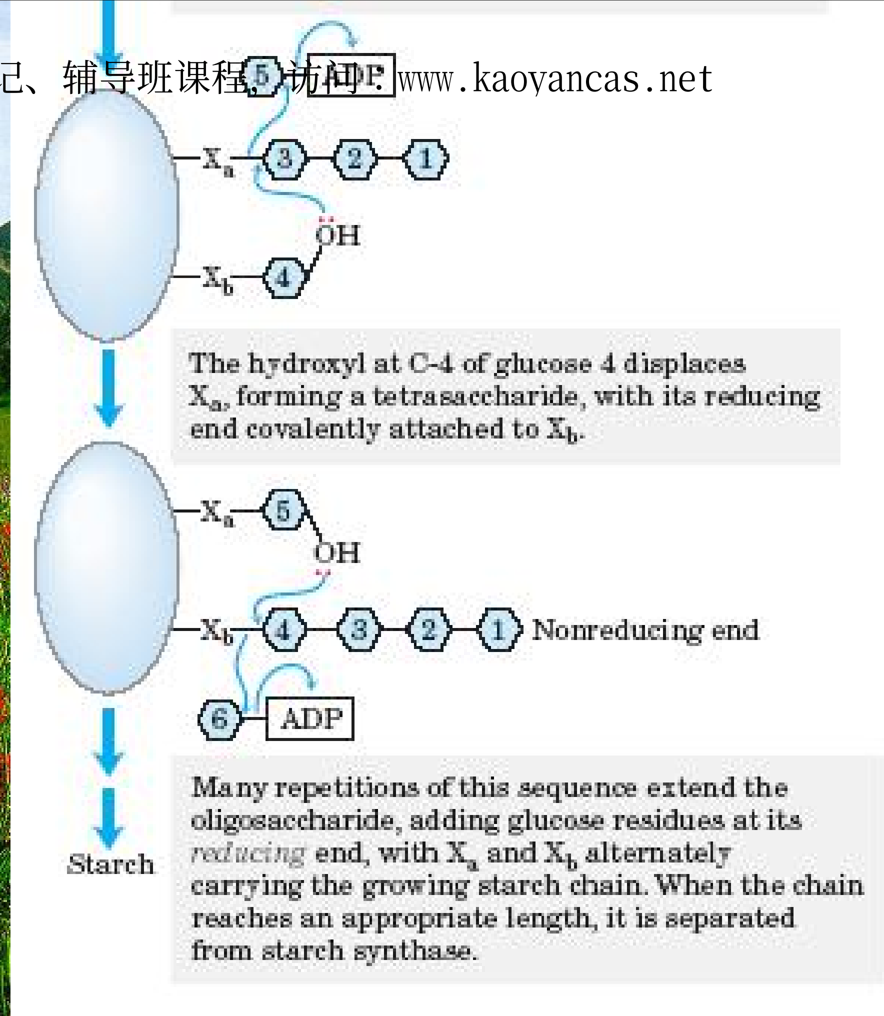
淀粉的酶促水解





淀粉的合成





基本要求

1. 掌握糖原降解和生物合成的过程。（重点）
2. 掌握糖原代谢的调控及生理意义。（重点）

第27章

光合作用

一、光合作用的概况
1.光合作用的总过程

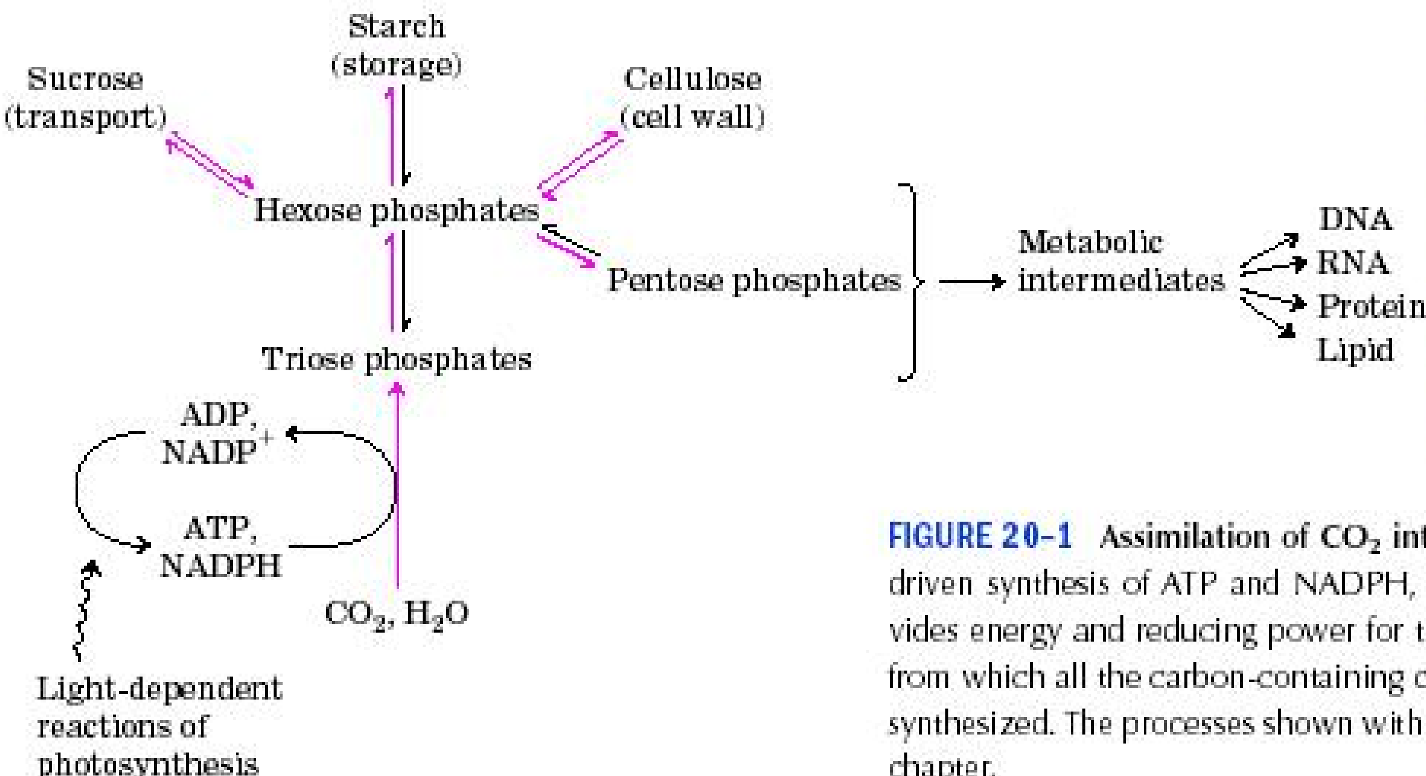
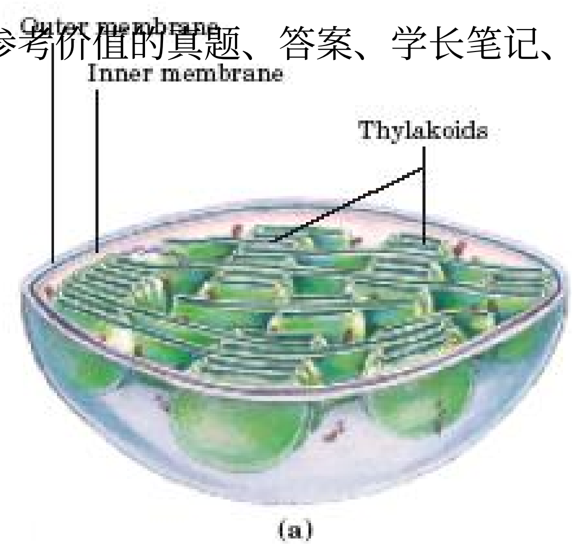


FIGURE 20-1 **Assimilation of CO_2 into biomass in plants.** The light-driven synthesis of ATP and NADPH, described in Chapter 19, provides energy and reducing power for the fixation of CO_2 into trioses, from which all the carbon-containing compounds of the plant cell are synthesized. The processes shown with red arrows are the focus of this chapter.

2.光合作用的场所—叶绿体



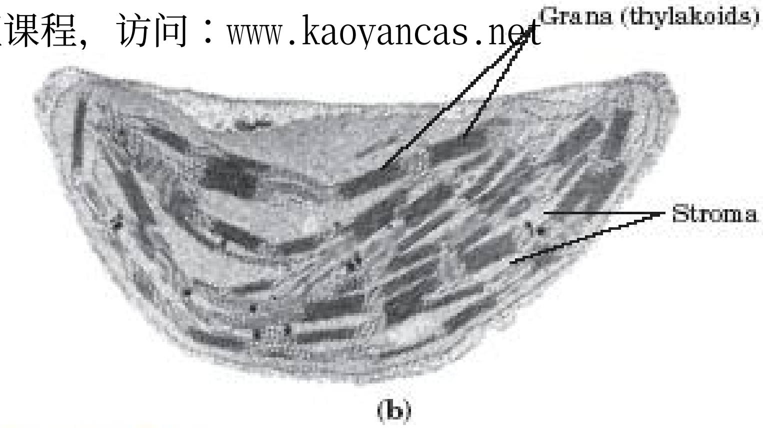
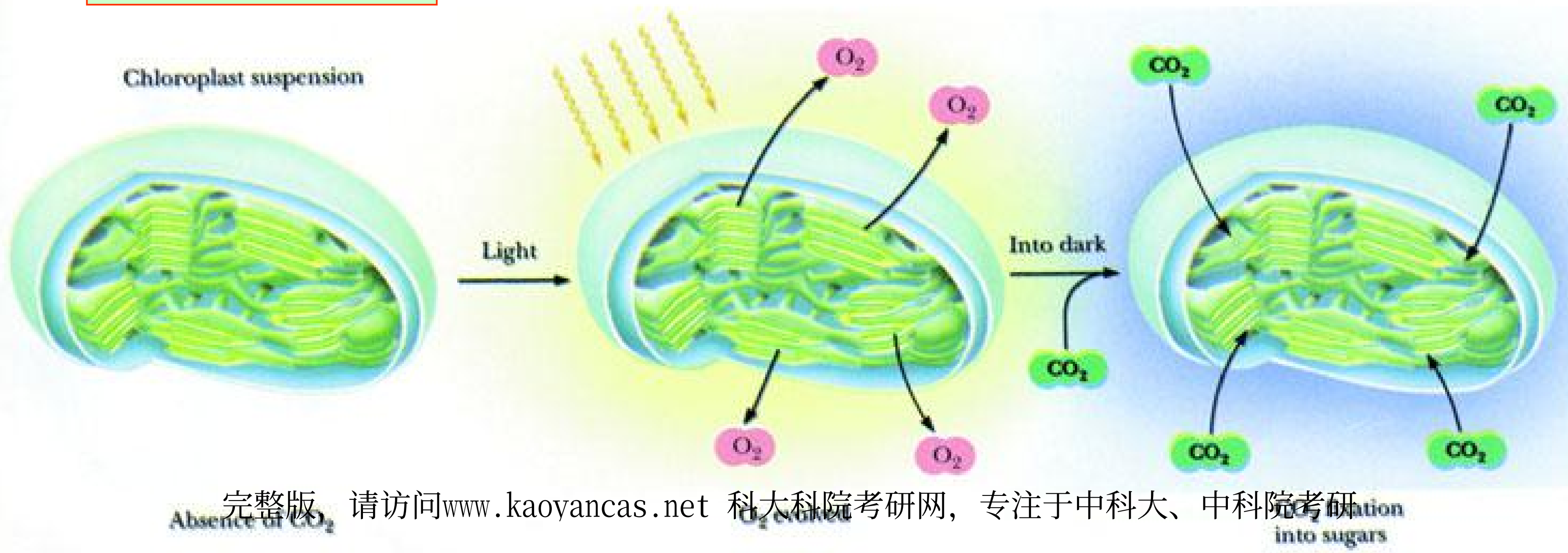
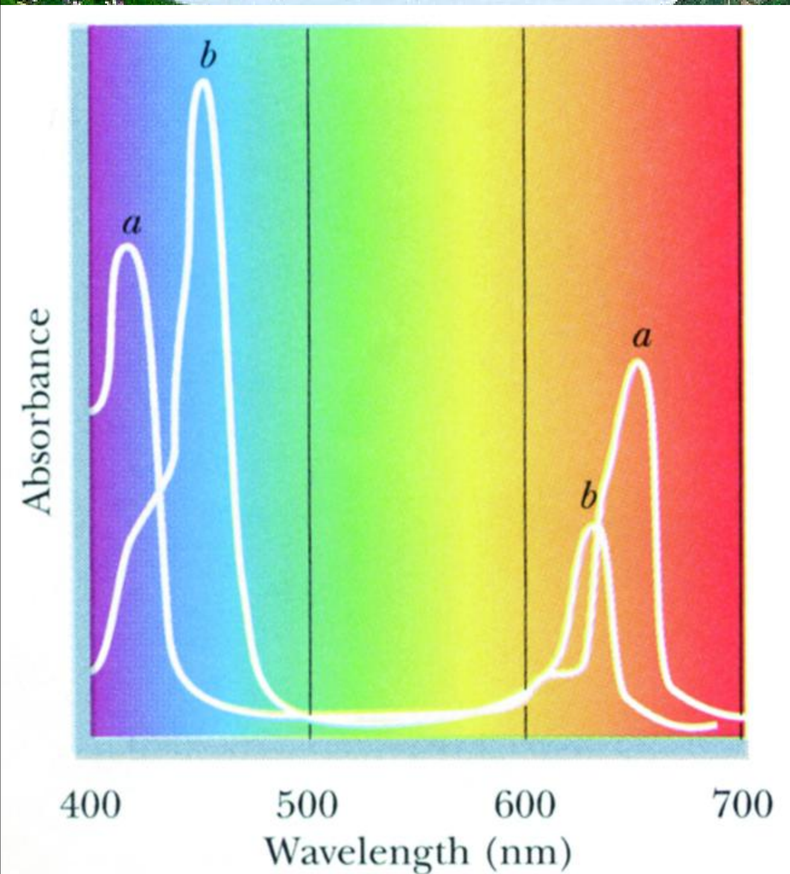


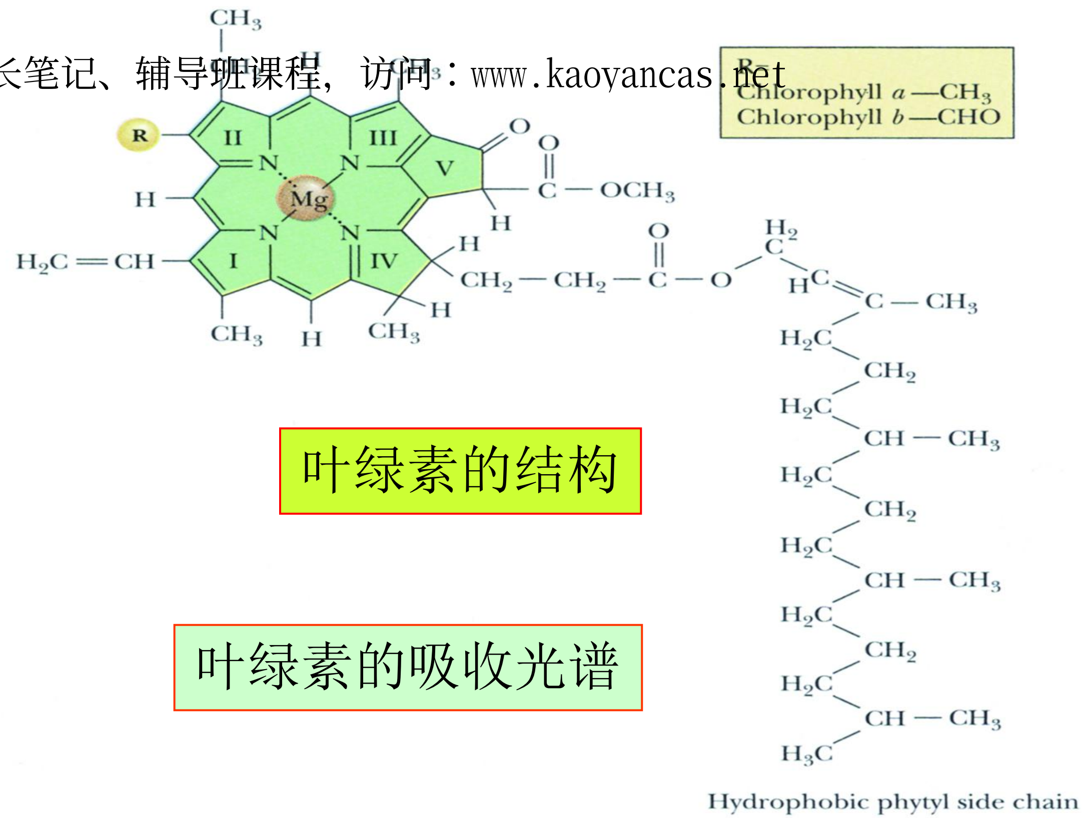
FIGURE 19–38 Chloroplast. (a) Schematic diagram. (b) Electron micrograph at high magnification showing grana, stacks of thylakoid membranes.

光反应和暗反应



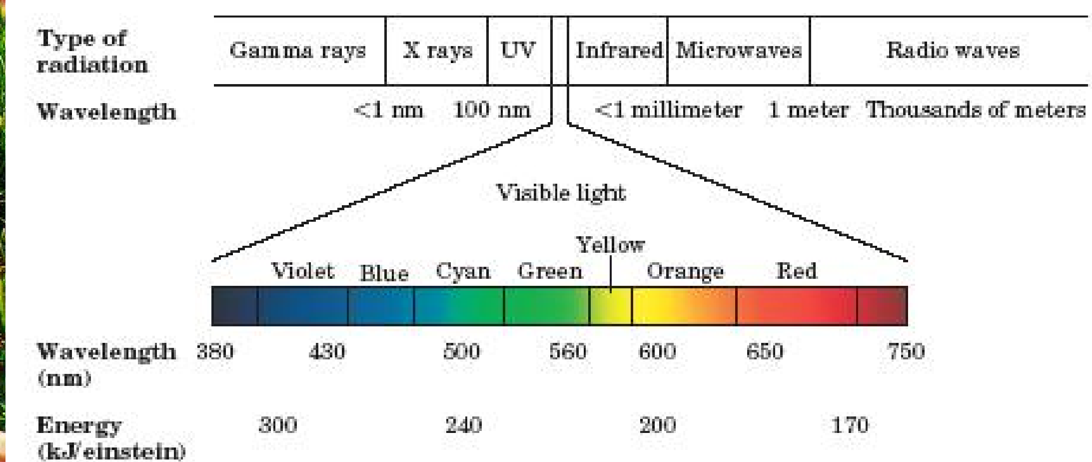
3.叶绿素的光学特性





叶绿素的结构

叶绿素的吸收光谱



... radiation, and the energy of photons in the visible range of the spectrum. One einstein is 6×10^{23} photons.

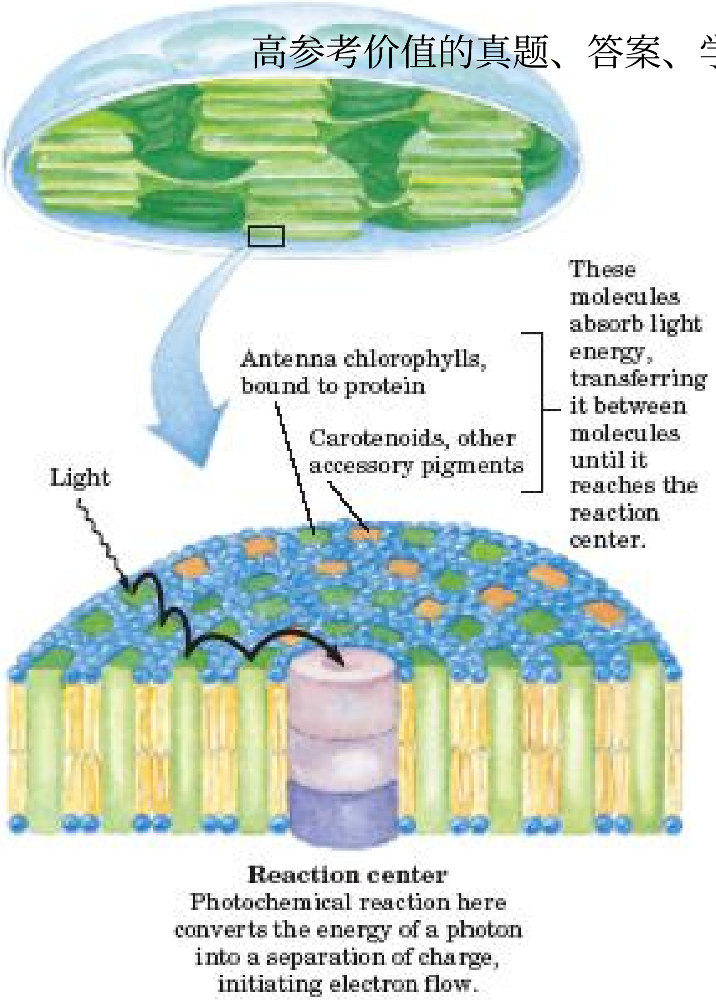
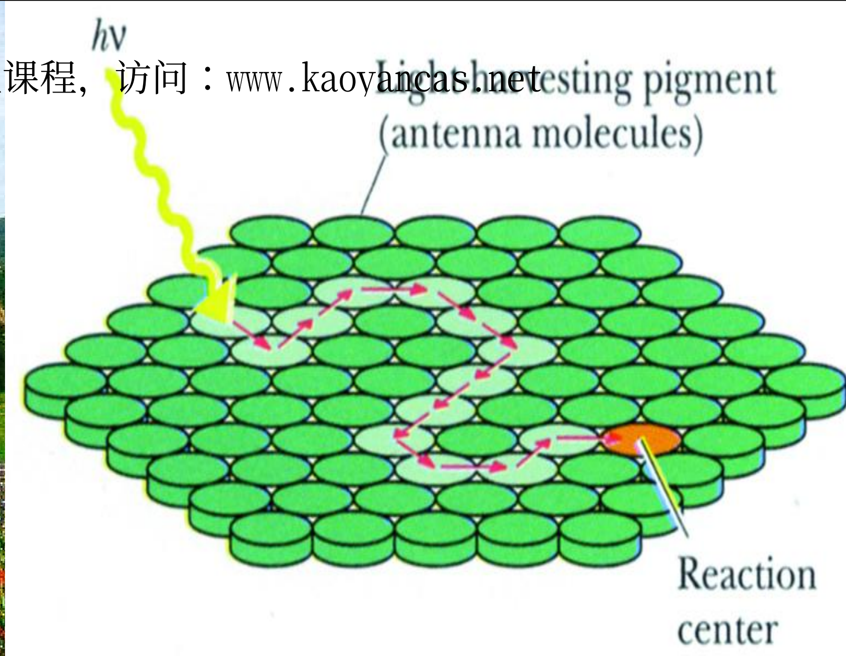
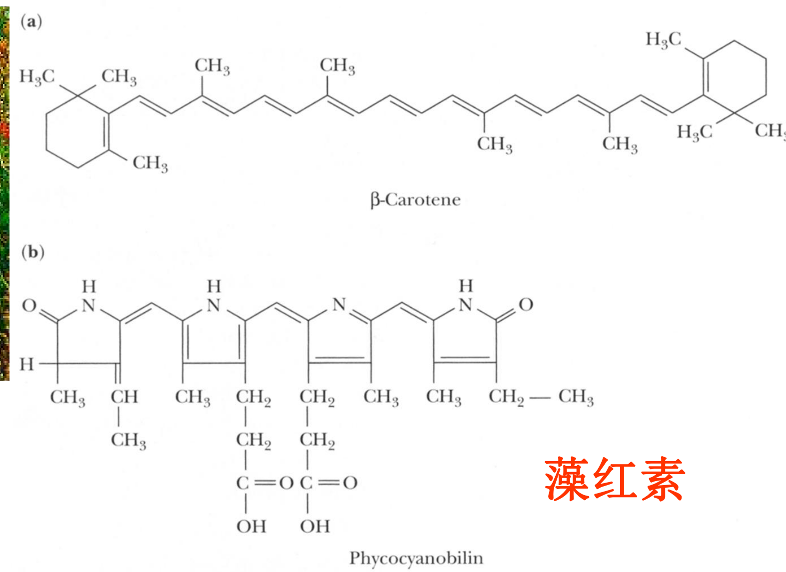


FIGURE 19–45 Organization of photosystems in the thylakoid membrane. Photosystems are tightly packed in the thylakoid membrane, with several hundred antenna chlorophylls and accessory pigments surrounding a photoreaction center. Absorption of a photon by any of the antenna chlorophylls leads to excitation of the reaction center by exciton transfer (black arrow). Also embedded in the thylakoid membrane are the cytochrome b_6f complex and ATP synthase (see Fig. 19–52).

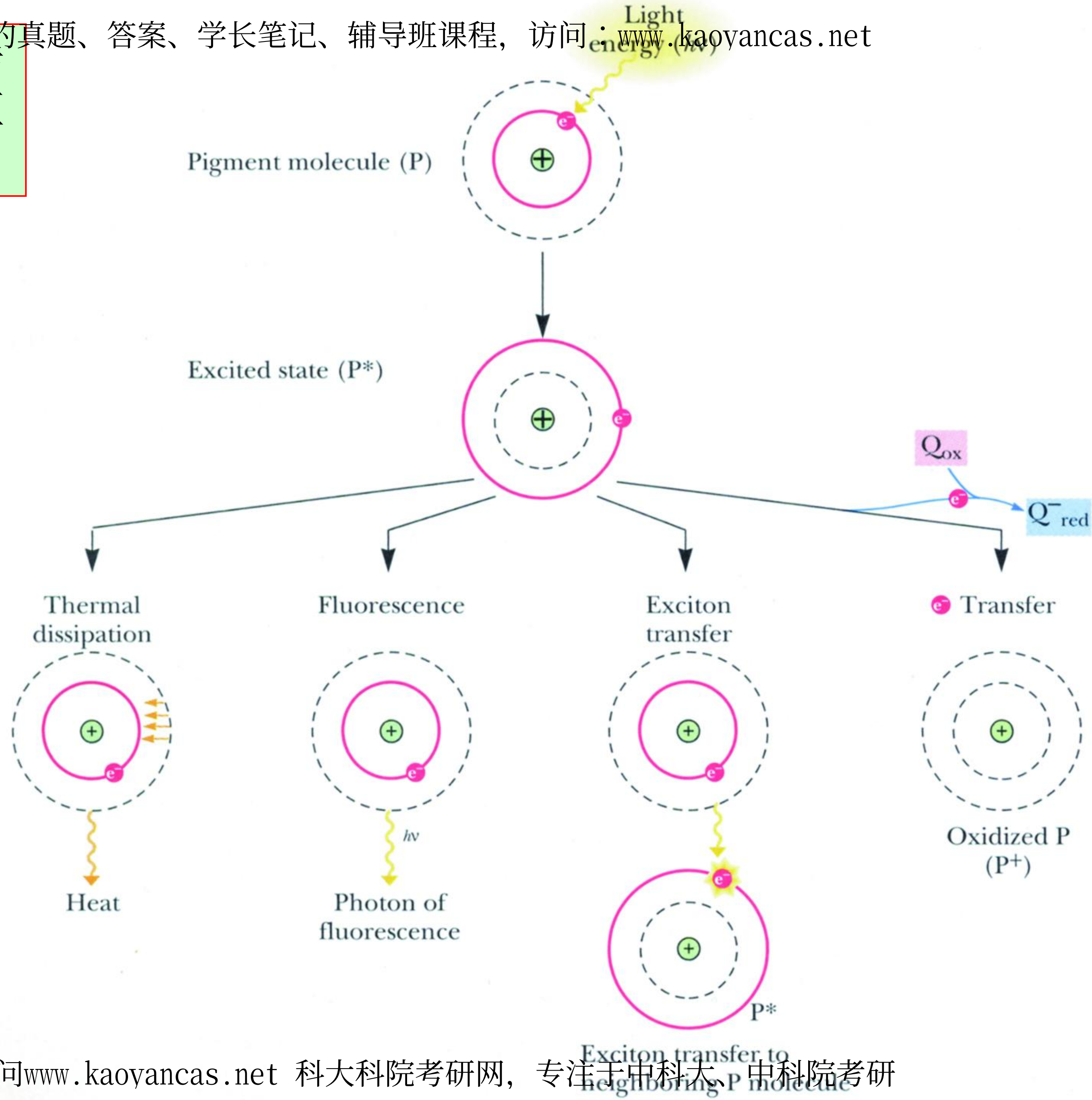
4.叶绿素在膜上被组织成光合单位

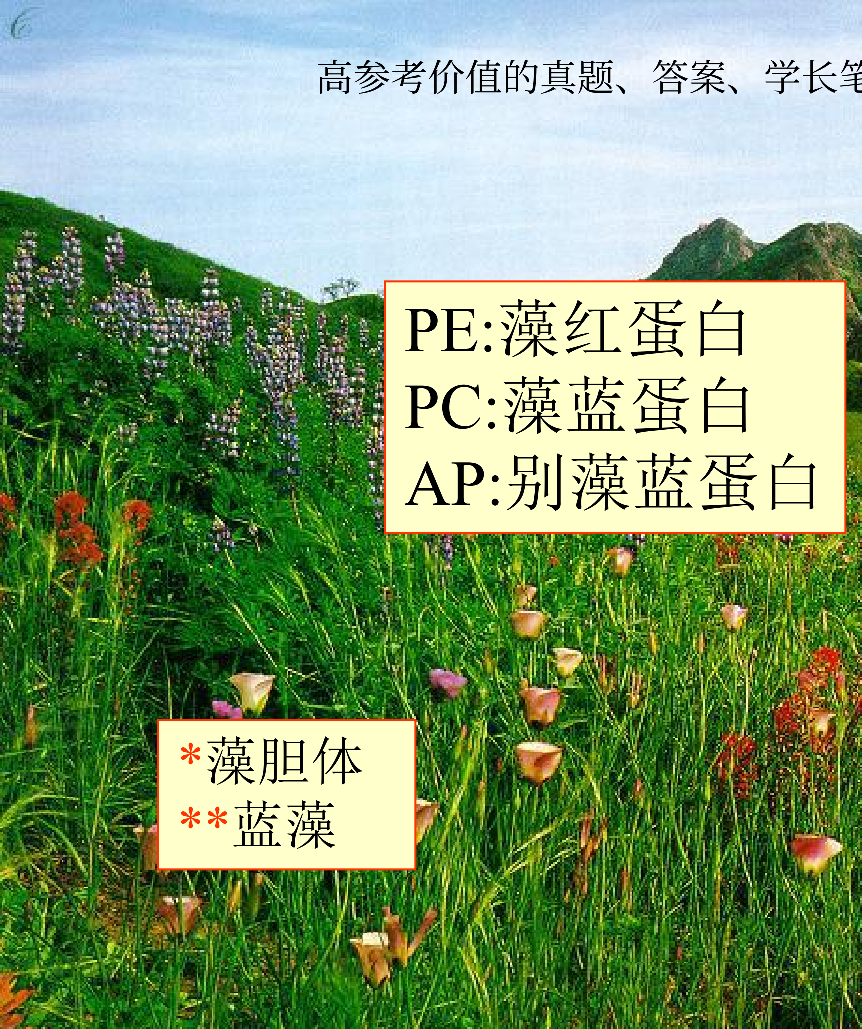




藻红素

叶绿素通过激子传递把吸收的能量汇集到作用中心





PE:藻红蛋白
PC:藻蓝蛋白
AP:别藻蓝蛋白

*藻胆体
**蓝藻

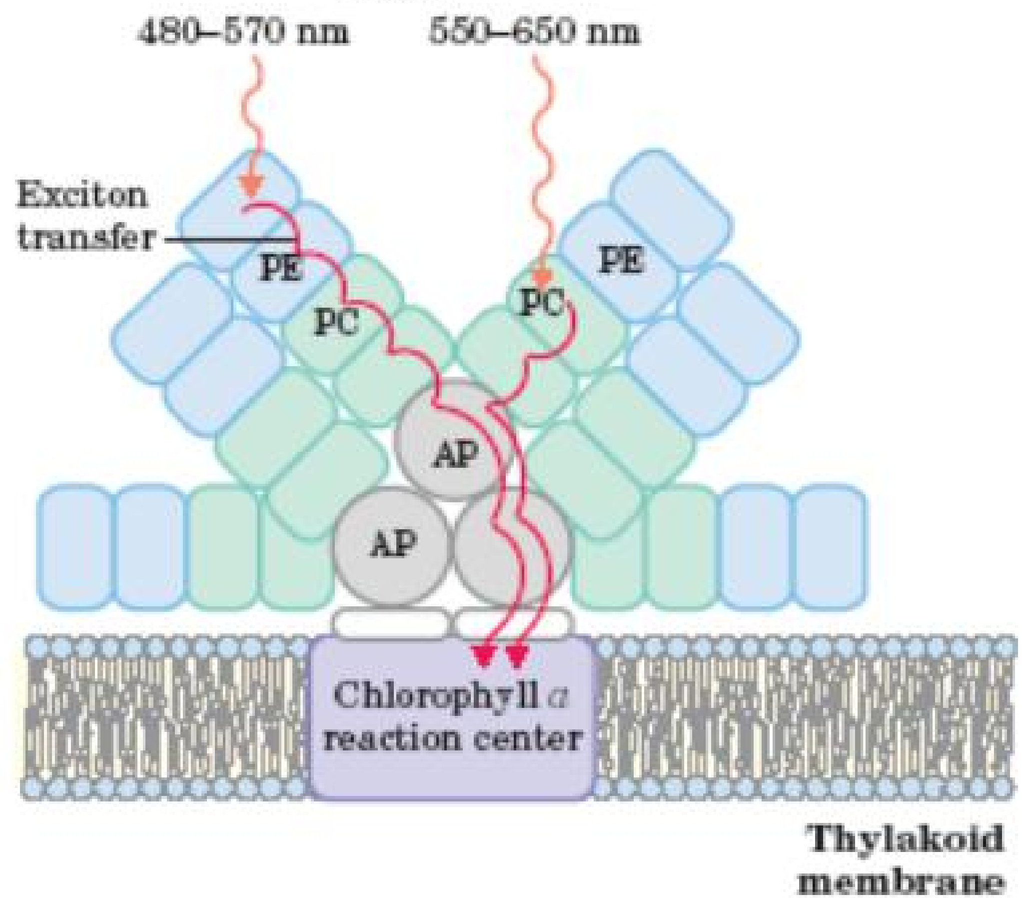


FIGURE 19–43 A phycobilisome.* In these highly structured assemblies found in cyanobacteria** and red algae, phycobilin* pigments bound to specific proteins form complexes called phycoerythrin (PE), phycocyanin (PC), and allophycocyanin (AP). The energy of photons absorbed by PE or PC is conveyed through AP (a phycocyanobilin-binding protein) to chlorophyll a of the reaction center by exciton transfer, a process discussed in the text.

*藻胆素

二、光合作用的光反应

1.光合细菌只有一个光化学作用中心

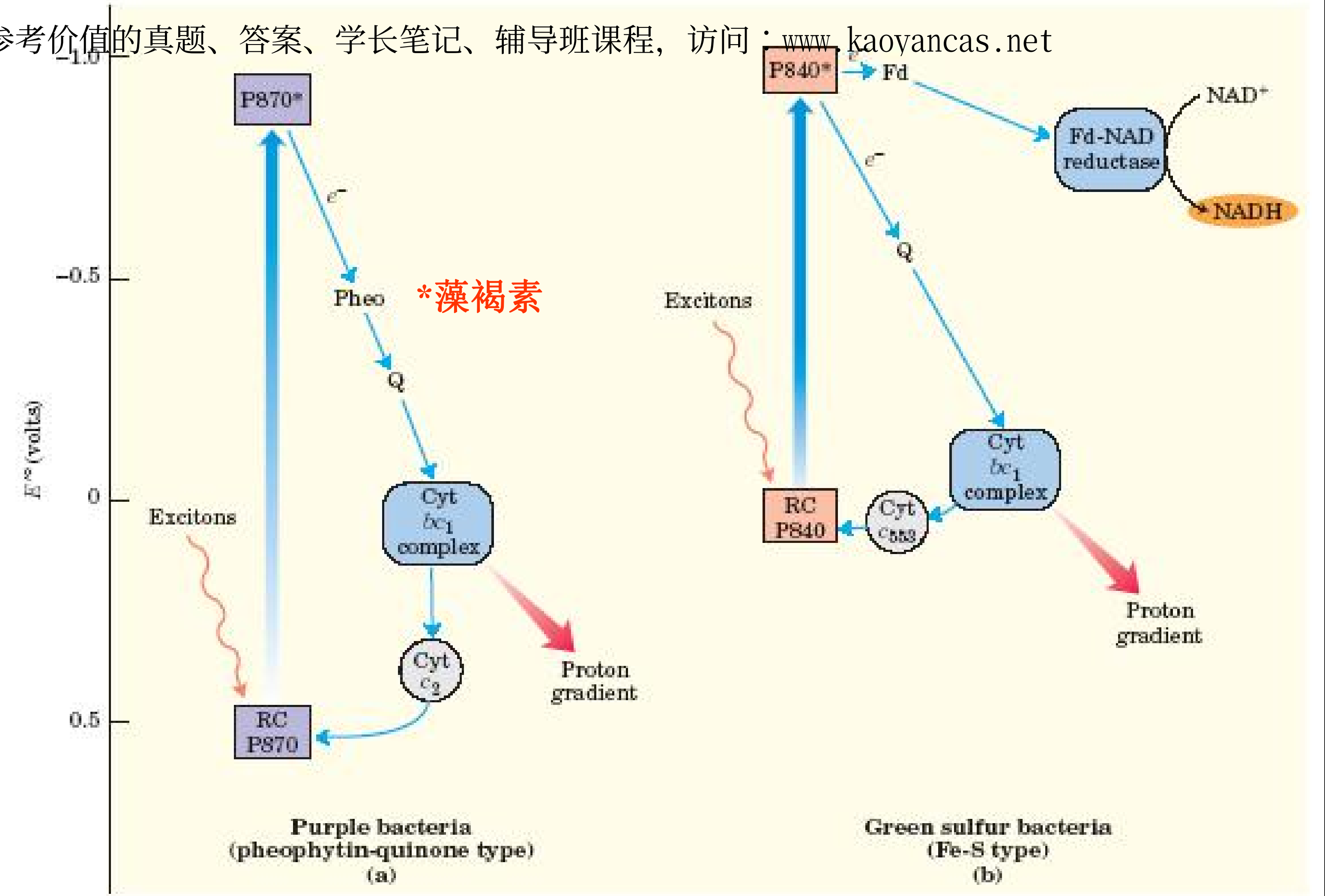
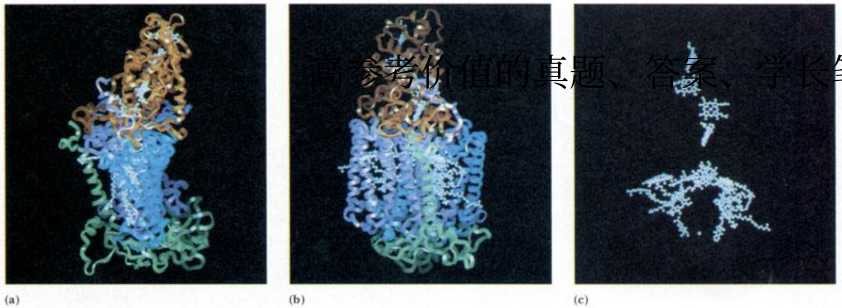


FIGURE 19–47 Functional modules of photosynthetic machinery in purple bacteria and green sulfur bacteria. (a) In purple bacteria, light energy drives electrons from the reaction center P870 through pheophytin (Pheo)*, a quinone (Q), and the cytochrome bc_1 complex, then through cytochrome c_2 back to the reaction center. Electron flow through the cytochrome bc_1 complex causes proton pumping, creating an electrochemical potential that powers ATP synthesis. (b) Green sulfur bacteria have two routes for electrons driven by excitation of P840: a cyclic route passes through a quinone to the cytochrome bc_1 complex and back to the reaction center via cytochrome c, and a noncyclic route from the reaction center through the iron-sulfur protein ferredoxin (Fd), then to NAD+ in a reaction catalyzed by ferredoxin:NAD reductase.

紫细菌光反应中心的模型。M亚基为金色，L亚基为蓝色，H亚基为绿色。c表示不同基团之间的特定关系。



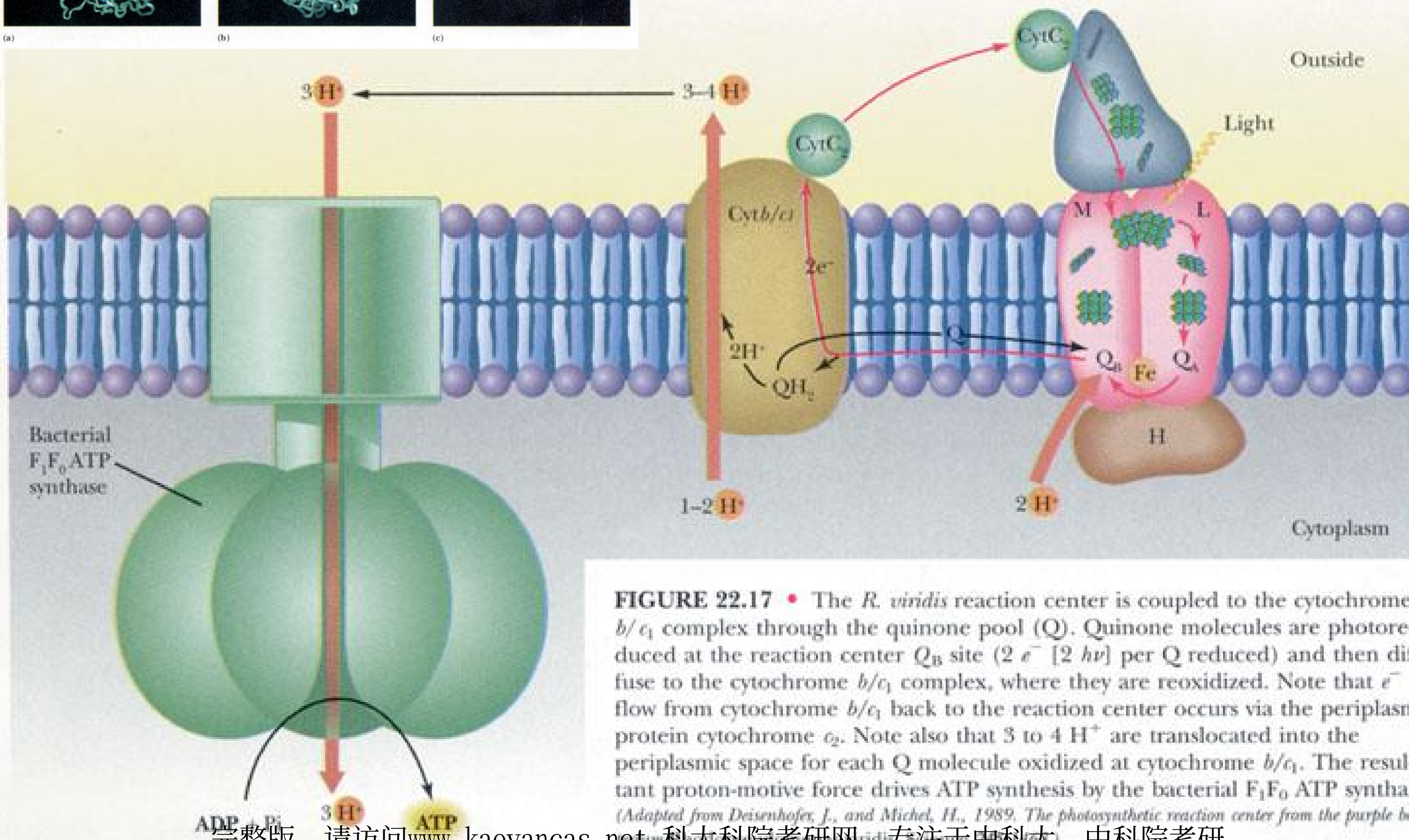
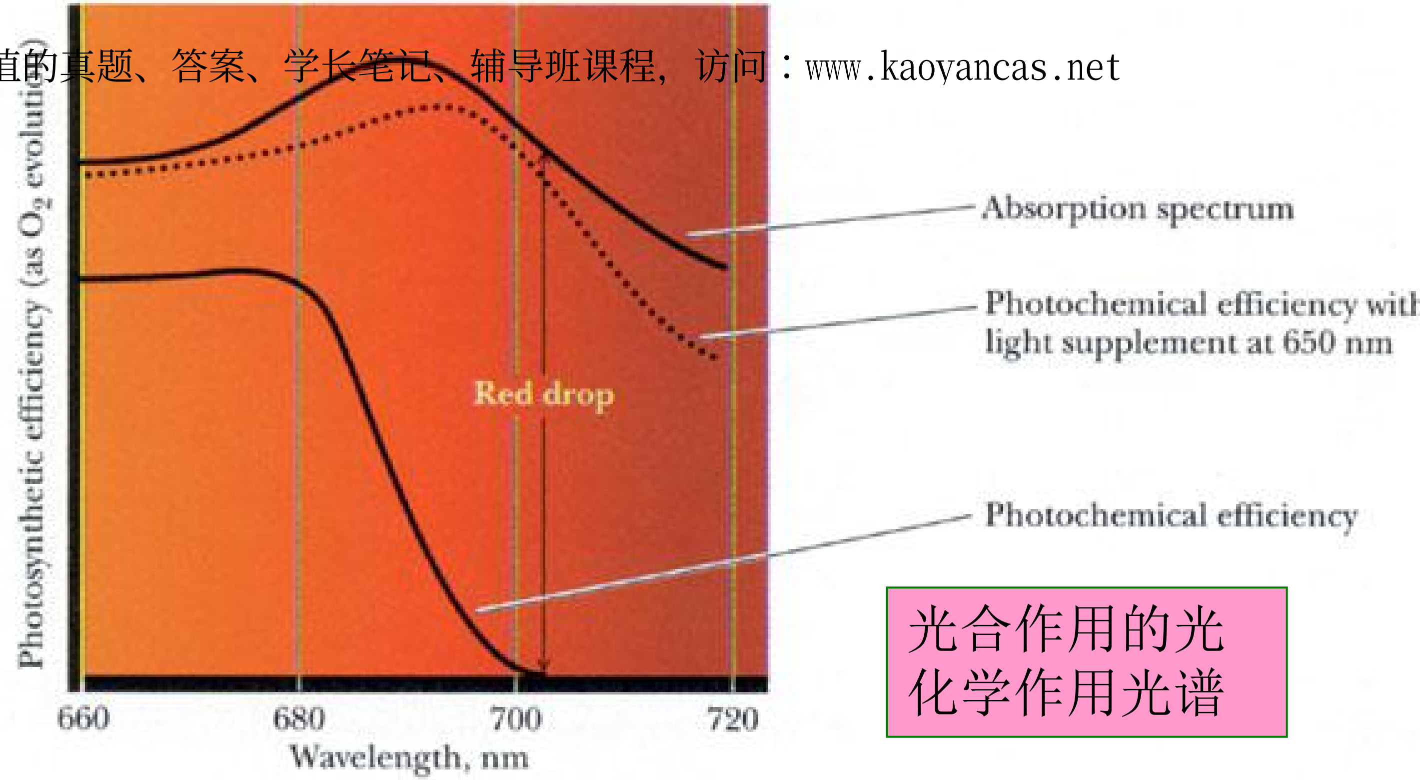


FIGURE 22.17 • The *R. viridis* reaction center is coupled to the cytochrome b/c_1 complex through the quinone pool (Q). Quinone molecules are photoreduced at the reaction center Q_B site ($2\ e^-$ [$2\ h\nu$] per Q reduced) and then diffuse to the cytochrome b/c_1 complex, where they are reoxidized. Note that e^- flow from cytochrome b/c_1 back to the reaction center occurs via the periplasmic protein cytochrome c_2. Note also that 3 to 4 H^+ are translocated into the periplasmic space for each Q molecule oxidized at cytochrome b/c_1. The resultant proton-motive force drives ATP synthesis by the bacterial F_1F_0 ATP synthase. *(Adapted from Deisenhofer, J., and Michel, H., 1989. The photosynthetic reaction center from the purple bac-*

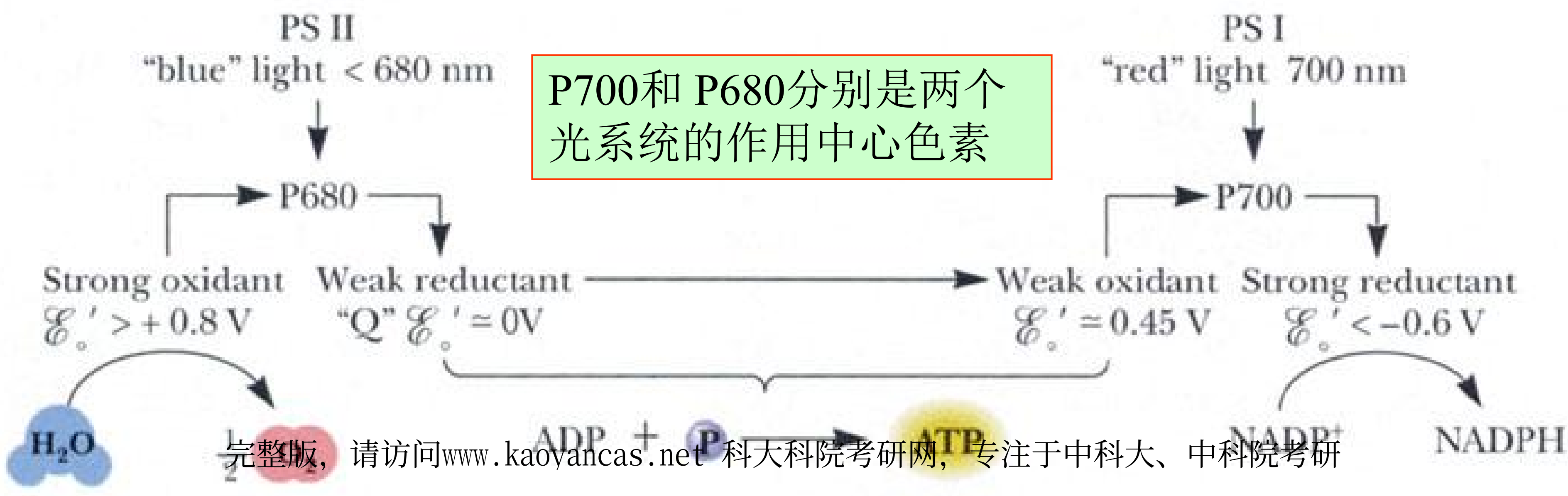
2.高等植物和藻类具有两个光系统

红降现象说明光合细胞有两个光反应系统



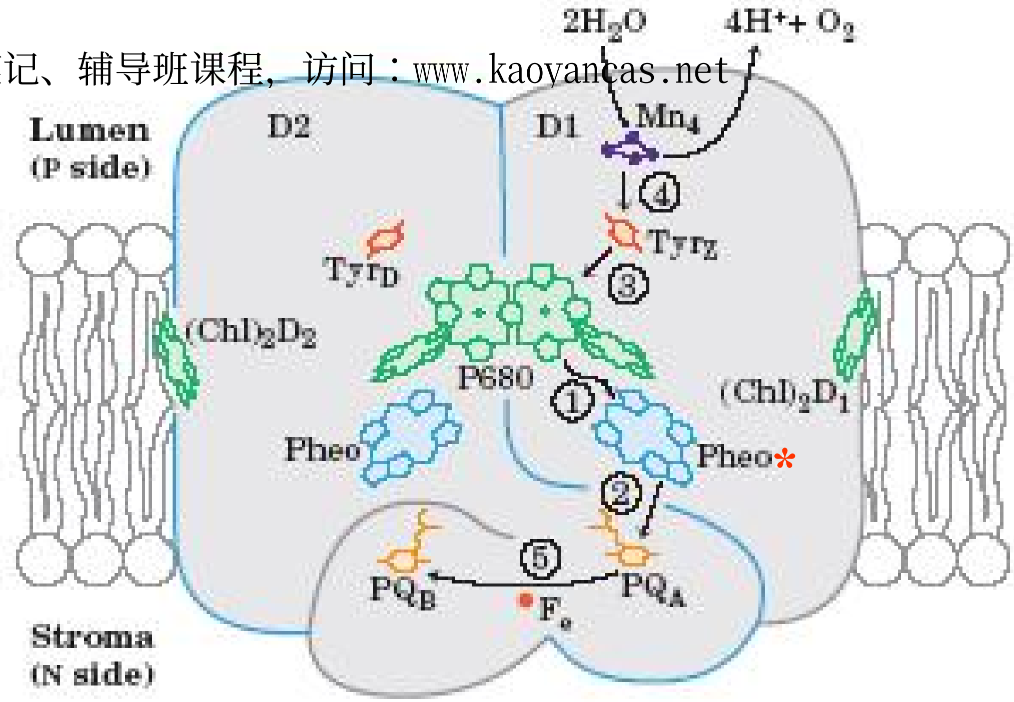
光合作用的光化学作用光谱

P700和 P680分别是两个光系统的作用中心色素



3. 放氧光合生物光作用中心的结构

光系统 II 的结构



*藻褐素

FIGURE 19–50 Photosystem II of the cyanobacterium *Synechococcus elongates*. The monomeric form of the complex shown here has two major transmembrane proteins, D1 and D2, each with its set of cofactors. Although the two subunits are nearly symmetric, electron flow occurs through only one of the two branches of cofactors, that on the right (on D1). The arrows show the path of electron flow from the Mn ion cluster (Mn_4, purple) of the water-splitting enzyme to the quinone PQ_B (orange). The photochemical events occur in the sequence indicated by the step numbers. Notice the close similarity between the positions of cofactors here and the positions in the bacterial photoreaction center shown in Figure 19–48. The role of the Tyr residues is discussed later in the text.

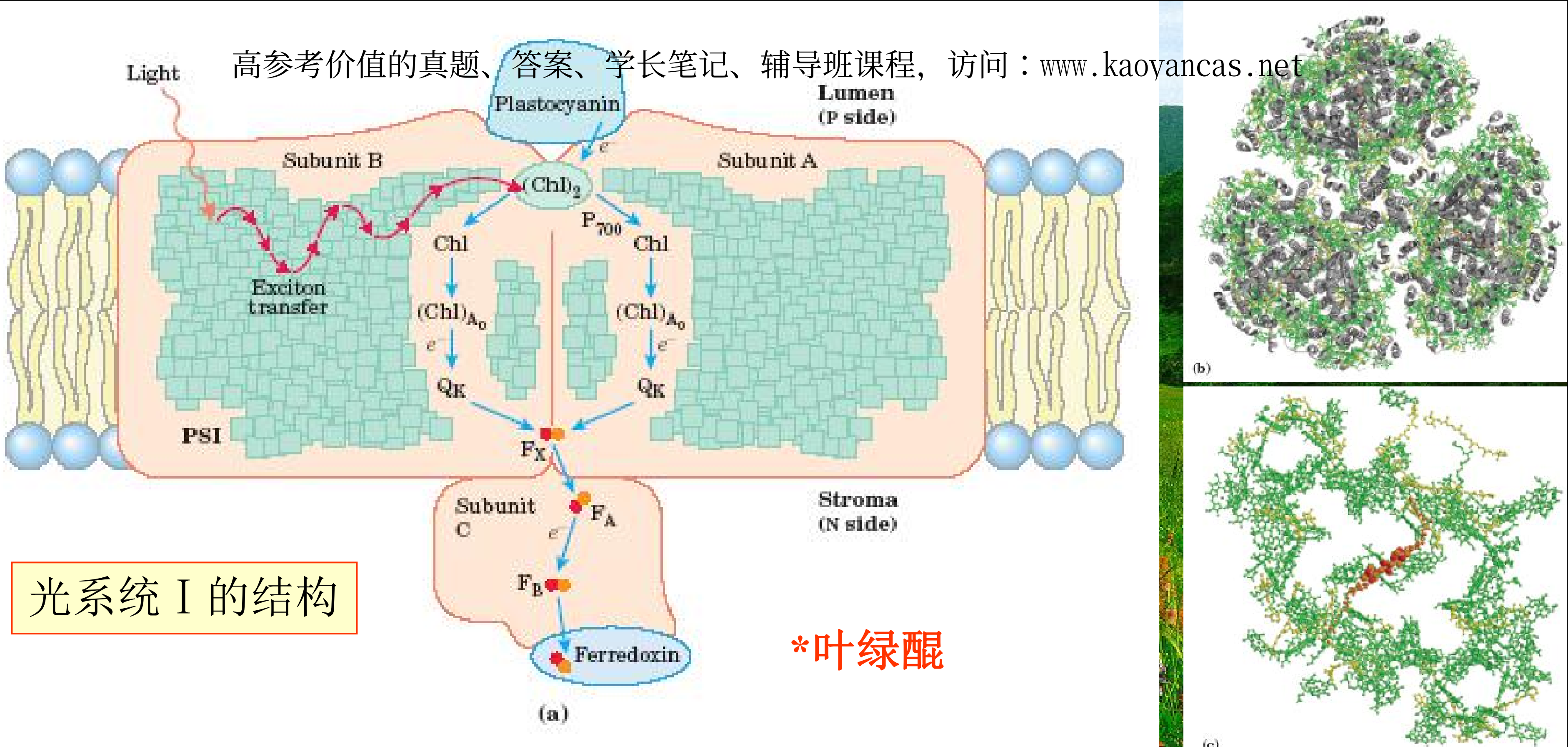
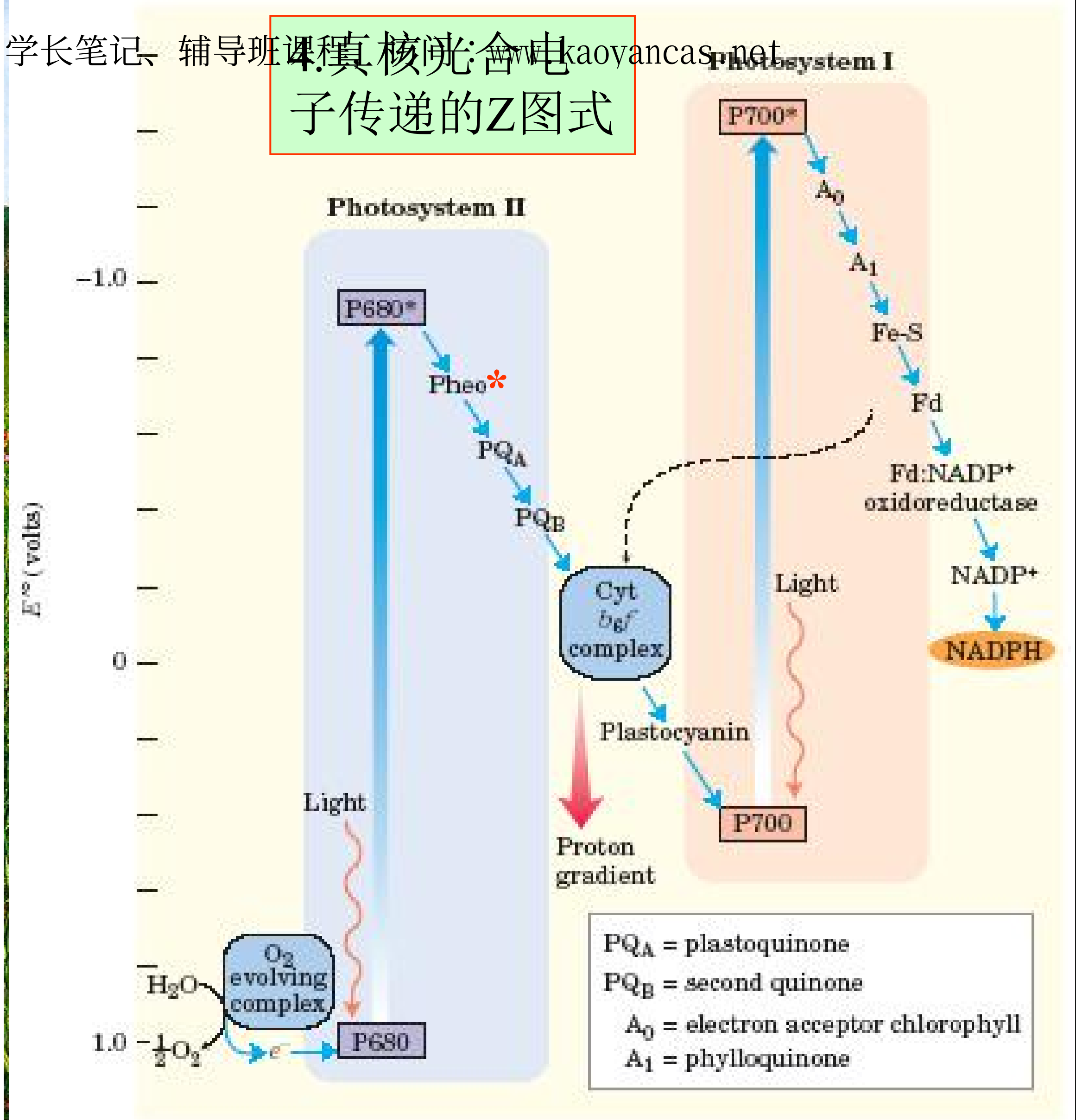


FIGURE 19–51 **The supramolecular complex of PSI and its associated antenna chlorophylls.** (a) Schematic drawing of the essential proteins and cofactors in a single unit of PSI. A large number of antenna chlorophylls surround the reaction center and convey to it (red arrows) the energy of photons they have absorbed. The result is excitation of the pair of chlorophyll molecules that constitute P700. Excitation of P700 greatly decreases its reduction potential, and it passes an electron through two nearby chlorophylls to phylloquinone*(Q_K; also called A_1). Reduced phylloquinone is reoxidized as it passes two electrons, one at a time, to an Fe-S protein (F_X) near the N side of the membrane. From F_X, electrons move through two more Fe-S centers (F_A and F_B), then to the Fe-S protein ferredoxin in the stroma. Ferredoxin then donates electrons to $NADP^+$(not shown), reducing it to NADPH, one of the forms in which the energy of photons is trapped in chloroplasts. (b) The trimeric structure (derived from PDB ID 1JB0), viewed from the thylakoid lumen perpendicular to the membrane, showing all protein subunits (gray) and cofactors (described in (c)). (c) A monomer of PSI with all the proteins omitted, revealing the antenna and reaction center chlorophylls (green with dark green Mg^{2+} ions in the center), carotenoids (yellow), and Fe-S centers of the reaction center (space-filling red and orange structures). The proteins in the complex hold the components rigidly in orientations that maximize excitation transfer between antenna molecules and the reaction center.

4.真核光合电子传递的Z图式

FIGURE 19–49 Integration of photosystems I and II in chloroplasts. This "Z scheme" shows the pathway of electron transfer from H_2O (lower left) to $NADP^+$ (far right) in noncyclic photosynthesis. The position on the vertical scale of each electron carrier reflects its standard reduction potential. To raise the energy of electrons derived from H_2O to the energy level required to reduce $NADP^+$ to NADPH, each electron must be "lifted" twice (heavy arrows) by photons absorbed in PSII and PSI. One photon is required per electron in each photosystem. After excitation, the high-energy electrons flow "downhill" through the carrier chains shown. Protons move across the thylakoid membrane during the water-splitting reaction and during electron transfer through the cytochrome b_6f complex, producing the proton gradient that is central to ATP formation. The dashed arrow is the path of cyclic electron transfer (discussed later in the text), which involves only PSI; electrons return via the cyclic pathway to PSI, instead of reducing $NADP^+$ to NADPH.



*藻褐素

5.水的光解与放氧

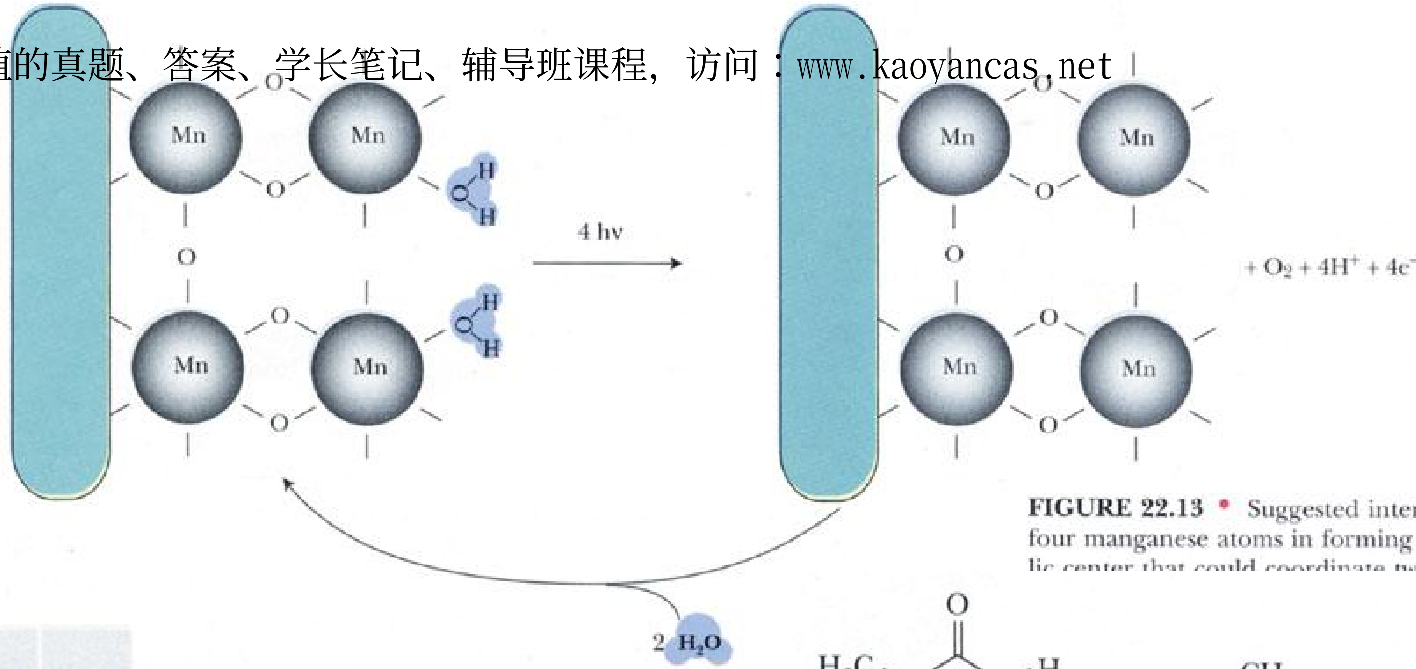
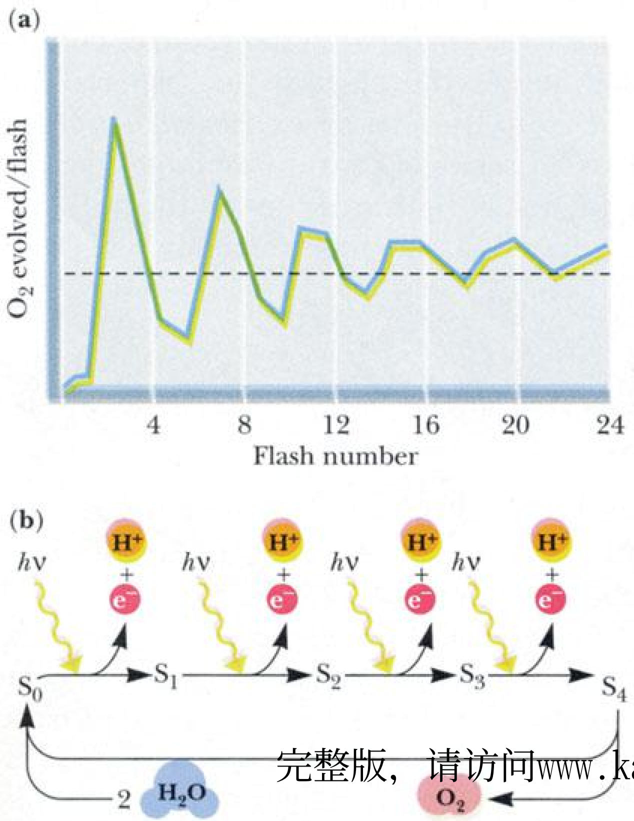
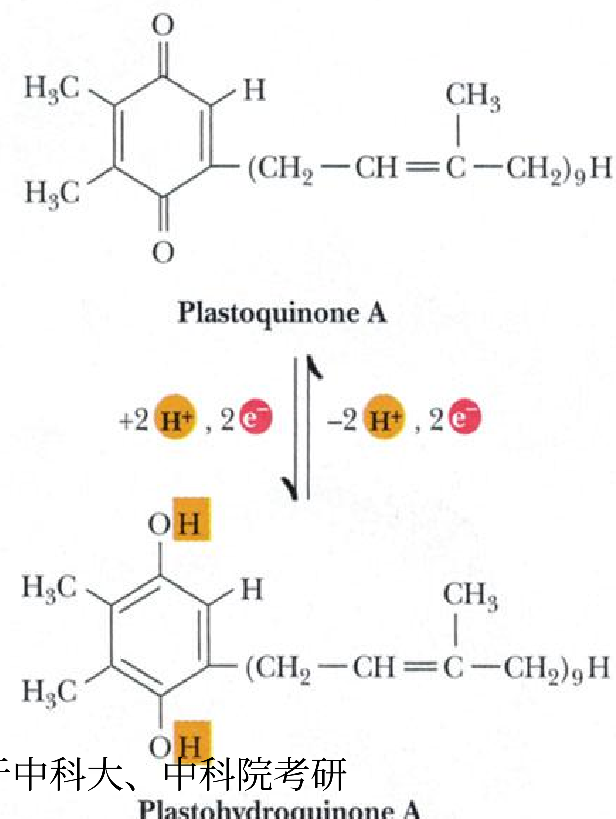


FIGURE 22.13 • Suggested intera
four manganese atoms in forming a
lic center that could coordinate two



质体醌的结构和氧化还原



6.PSI和PSⅡ在类囊体膜上的定位

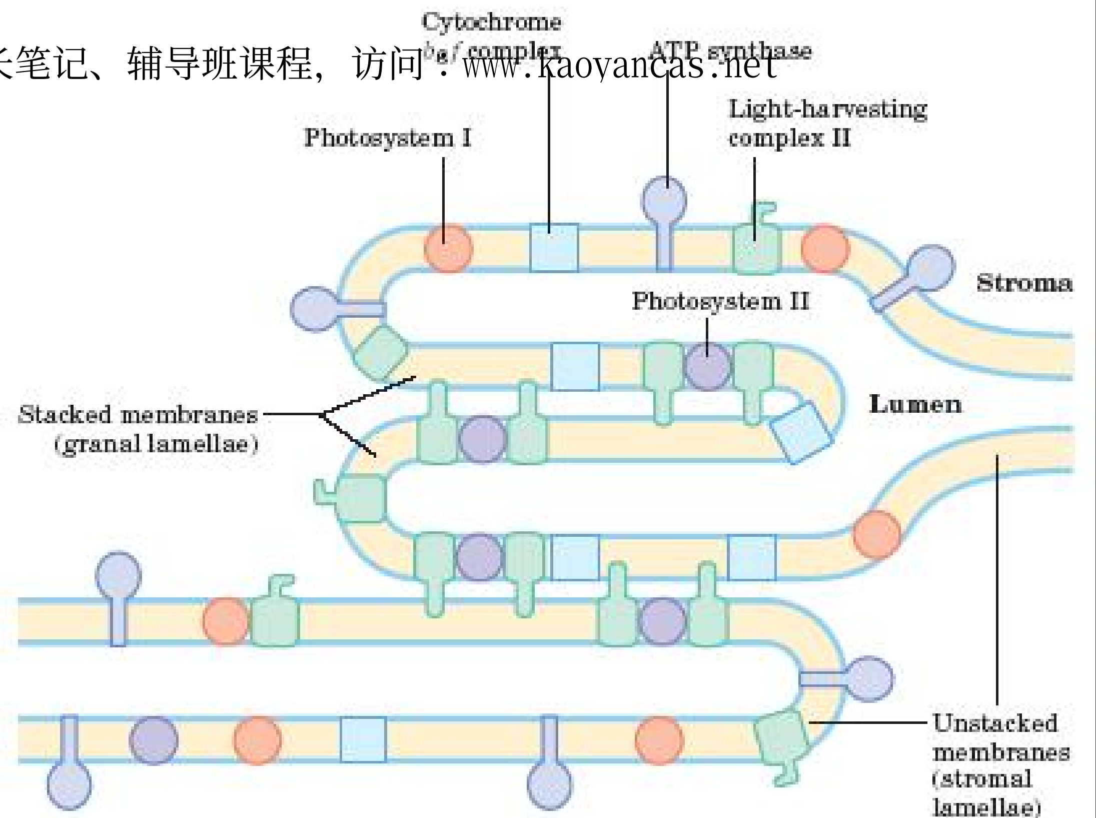


FIGURE 19–52 Localization of PSI and PSII in thylakoid membranes. Light-harvesting complex LHCII and ATP synthase are located in regions of the thylakoid membrane that are appressed (granal lamellae, in which several membranes are in contact) and in regions that are not appressed (stromal lamellae) and have ready access to ADP and $NADP^+$ in the stroma. Photosystem II is present almost exclusively in the appressed regions, and photosystem I almost exclusively in nonappressed regions exposed to the stroma. LHCII is the "adhesive" that holds appressed lamellae together (see Fig. 19–53).

7.细胞色素b_6f复合体的结构

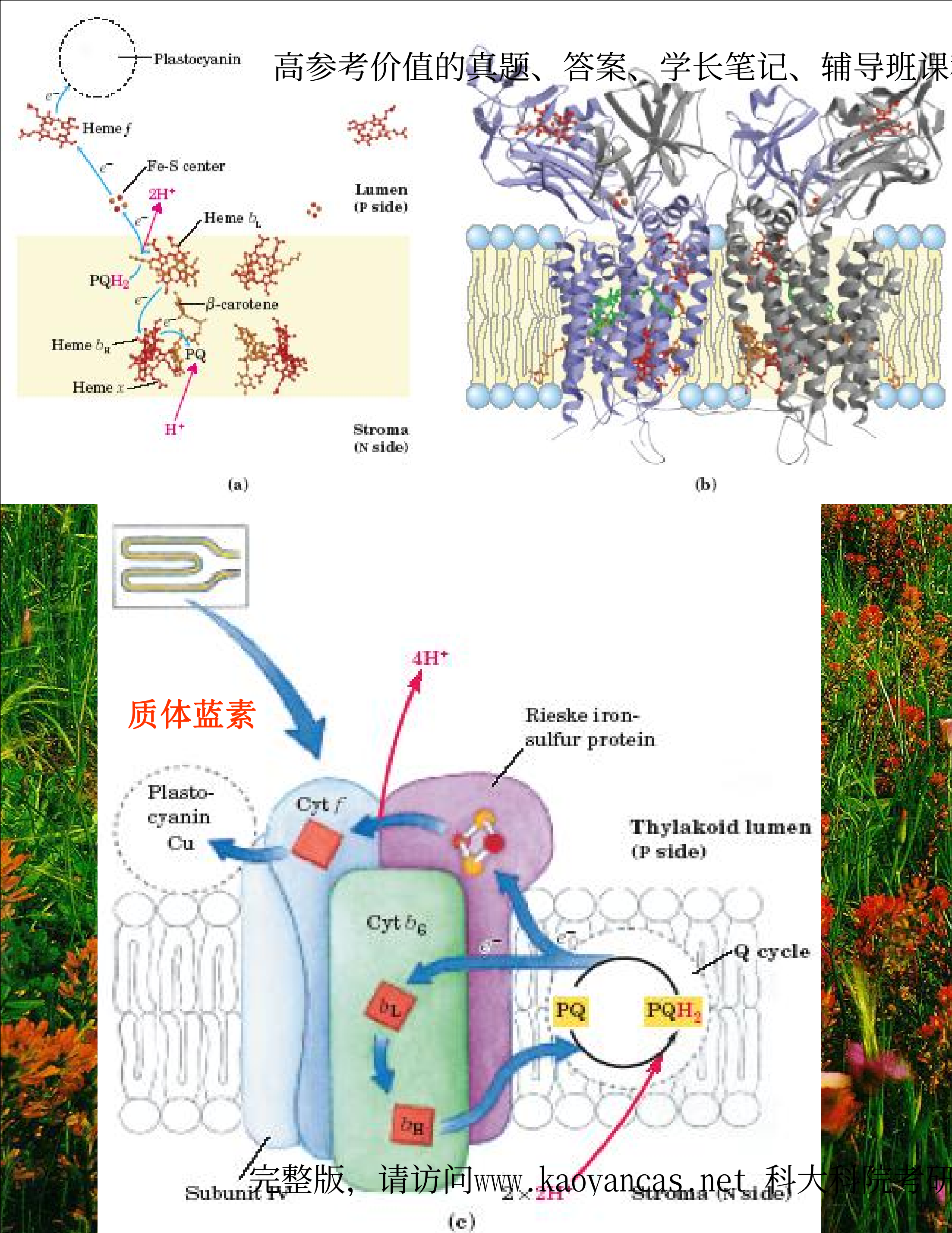


FIGURE 19-54 Electron and proton flow through the cytochrome b_6f complex. (a) The crystal structure of the complex (PDB ID 1UM3) reveals the positions of the cofactors involved in electron transfers. In addition to the hemes of cytochrome b (heme b_H and b_L; also called heme b_N and b_P, respectively, because of their proximity to the N and P sides of the bilayer) and that of cytochrome f (heme f), there is a fourth (heme x) near heme b_H, and there is a β-carotene of unknown function. Two sites bind plastoquinone: the PQH_2 site near the P side of the bilayer, and the PQ site near the N side. The Fe-S center of the Rieske protein lies just outside the bilayer on the P side, and the heme f site is on a protein domain that extends well into the thylakoid lumen. (b) The complex is a homodimer arranged to create a cavern connecting the PQH_2 and PQ sites (compare with the structure of mitochondrial Complex III in Fig. 19–12). This cavern allows plastoquinone movement between the sites of its oxidation and reduction.

(c) Plastoquinol (PQH_2) formed in PSII is oxidized by the cytochrome b_6f complex in a series of steps like those of the Q cycle in the cytochrome bc_1 complex (Complex III) of mitochondria (see Fig. 19–11). One electron from PQH_2 passes to the Fe-S center of the Rieske protein (purple), the other to heme b_L of cytochrome b_6 (green). The net effect is passage of electrons from PQH_2 to the soluble protein plastocyanin, which carries them to PSI.

8.细胞色素b_6f复合体的双重作用

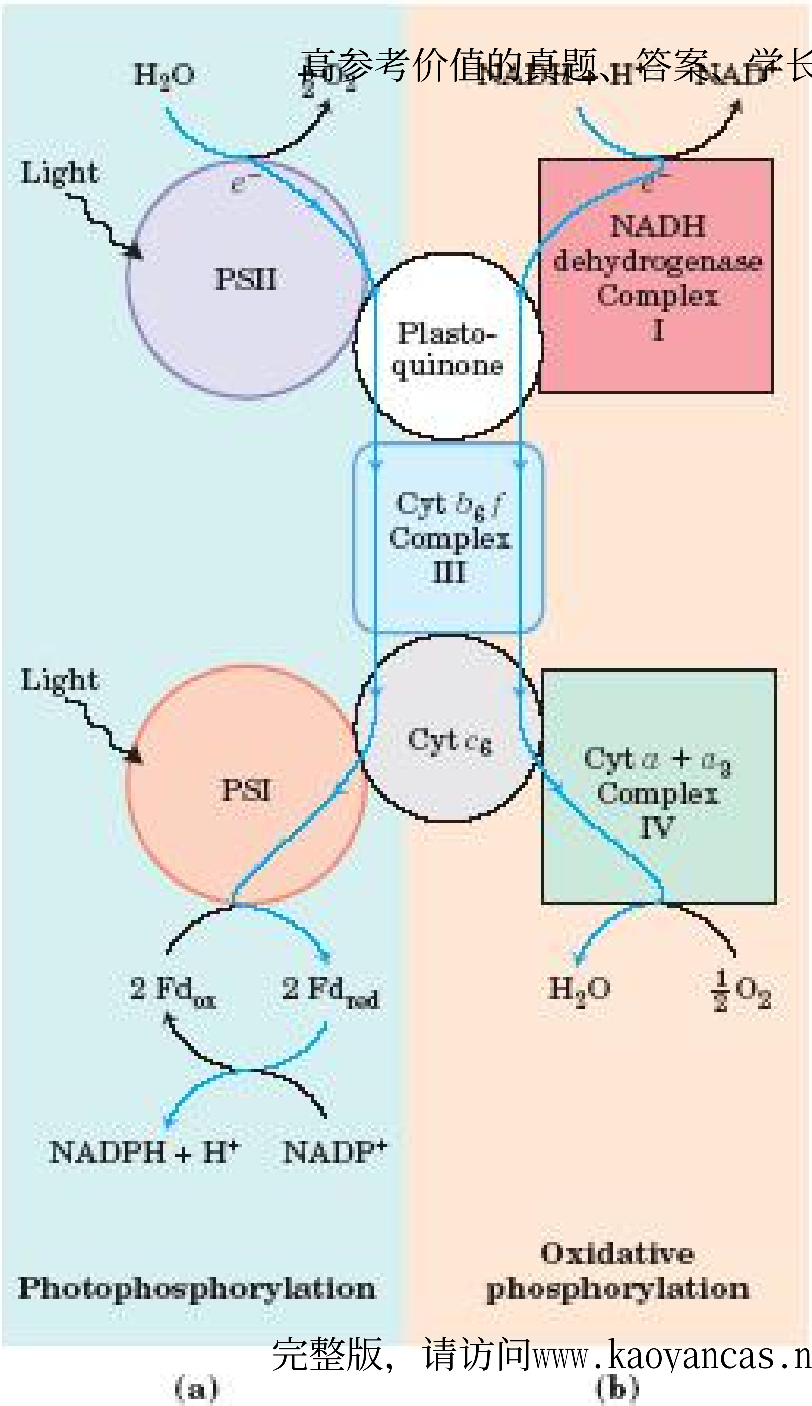


FIGURE 19–55 Dual roles of cytochrome b_6f and cytochrome c_6 in cyanobacteria. Cyanobacteria use cytochrome b_6f, cytochrome c_6, and plastoquinone for both oxidative phosphorylation and photophosphorylation. (a) In photophosphorylation, electrons flow (top to bottom) from water to NADP⁺. (b) In oxidative phosphorylation, electrons flow from NADH to O_2. Both processes are accompanied by proton movement across the membrane, accomplished by a Q cycle.

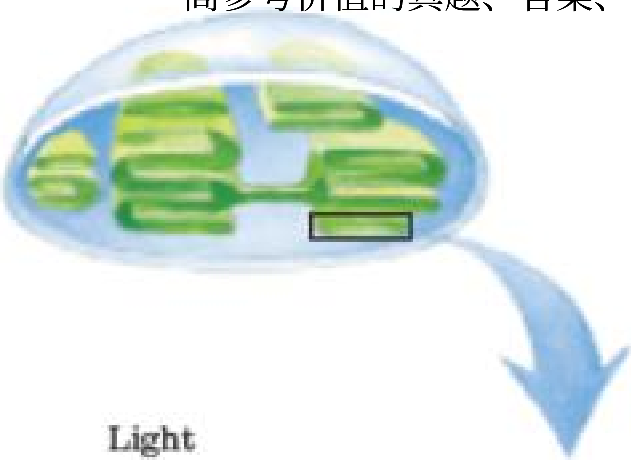
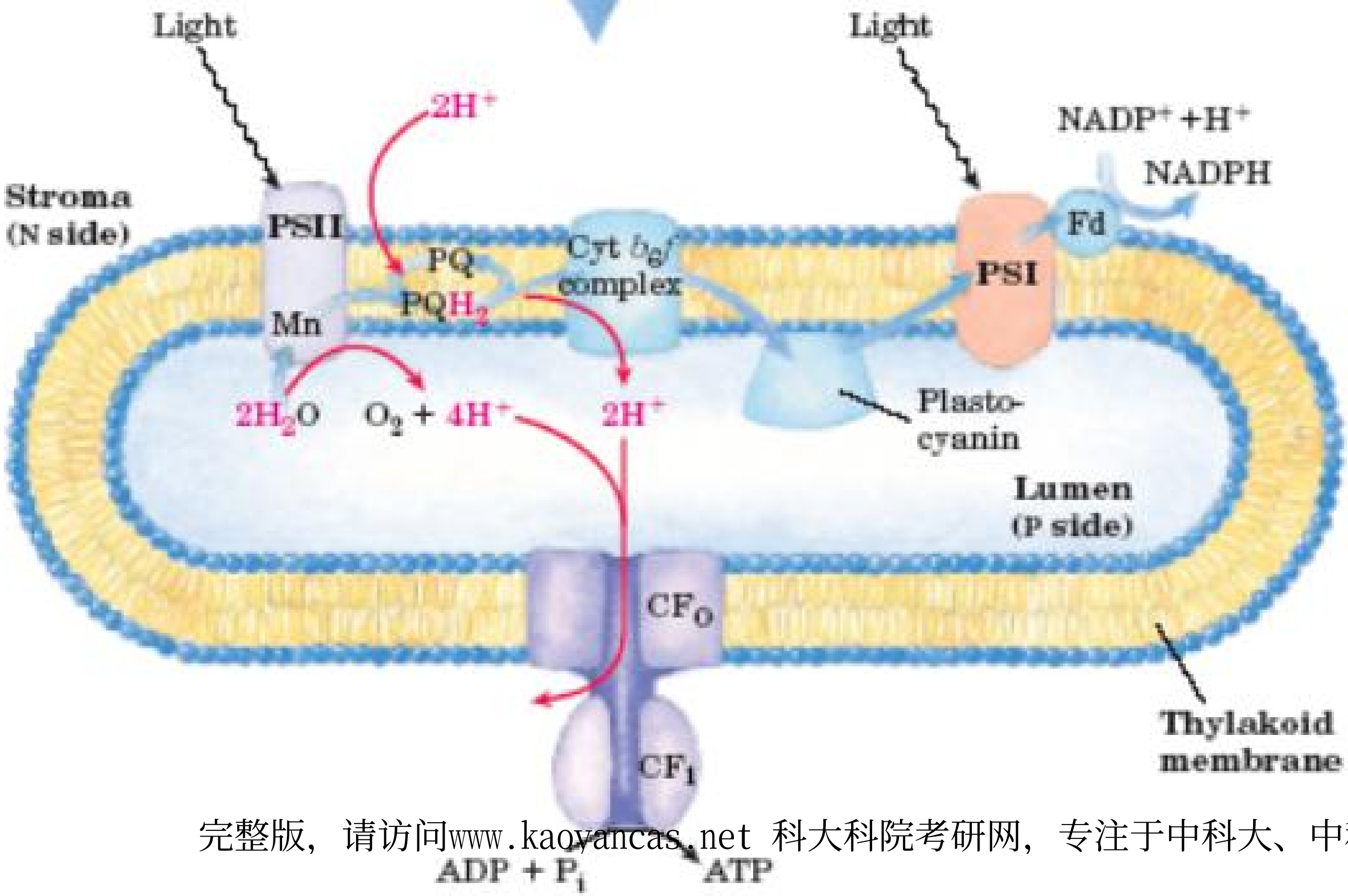
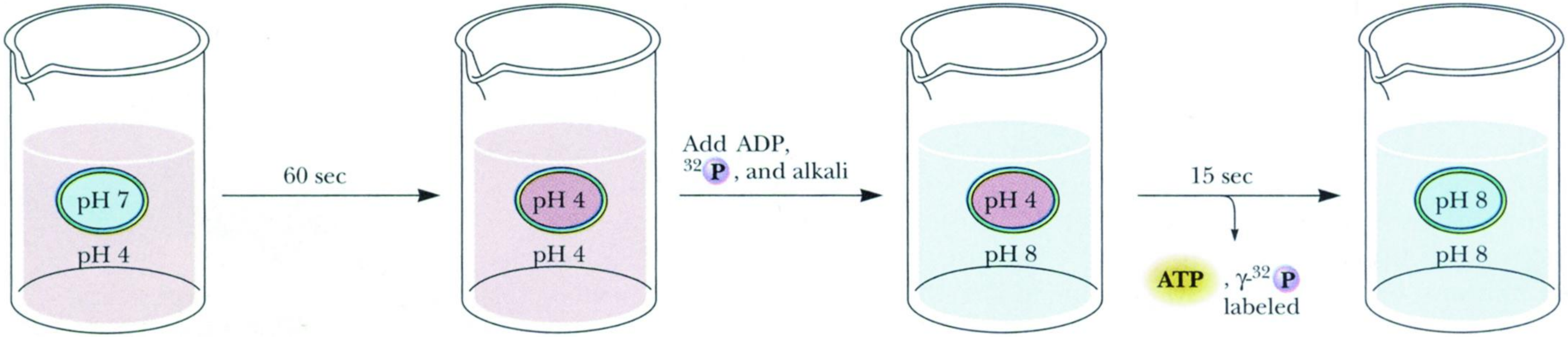


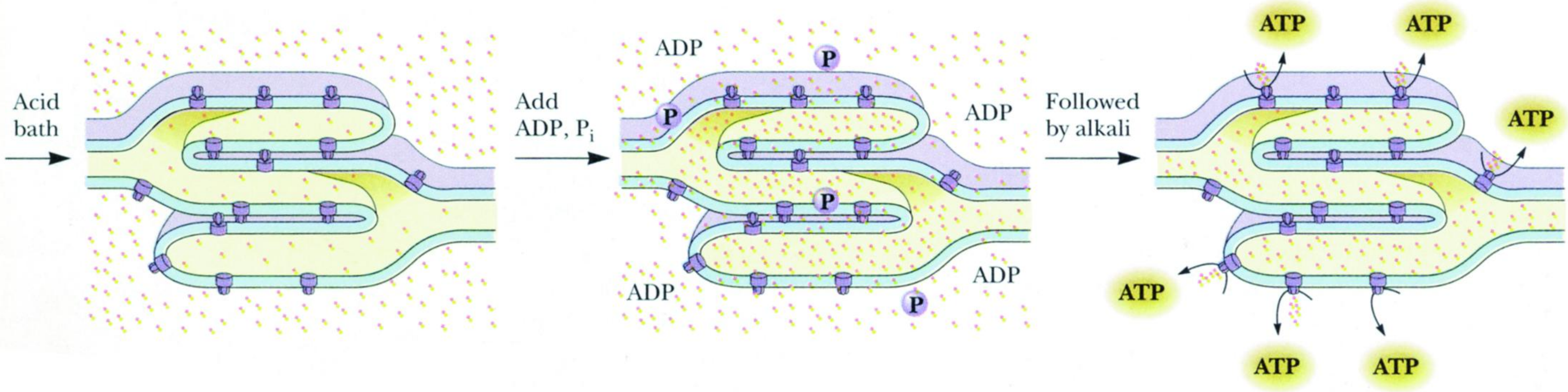
FIGURE 19-57 Proton and electron circuits in thylakoids. Electrons (blue arrows) move from H_2O through PSII, through the intermediate chain of carriers, through PSI, and finally to $NADP^+$. Protons (red arrows) are pumped into the thylakoid lumen by the flow of electrons through the carriers linking PSII and PSI, and reenter the stroma through proton channels formed by the F_o (designated CF_o) of ATP synthase. The F_1 subunit (CF_1) catalyzes synthesis of ATP.

9.光驱动的ATP合成：光合磷酸化



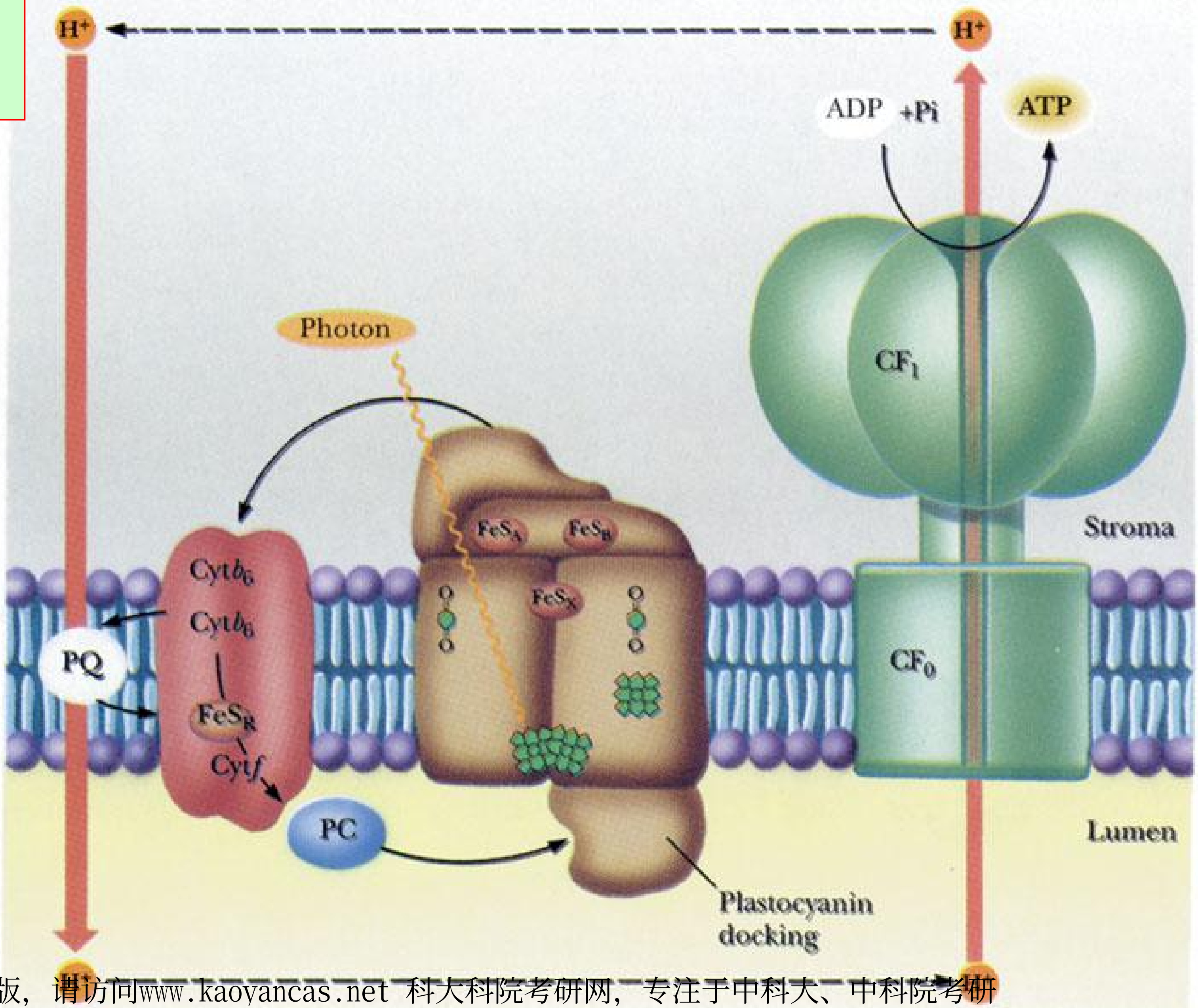


pH 7
pH 4
60 sec
pH 4
pH 4
Add ADP,
32 P, and alkali
pH 4
pH 8
15 sec
ATP, γ-32 P
labeled
pH 8
pH 8



Acid
bath
Add
ADP, Pi
ADP
P
ADP
ADP
ADP
Followed
by alkali
ATP
ATP
ATP
ATP
ATP
ATP

10.光系统I的循环磷酸化作用



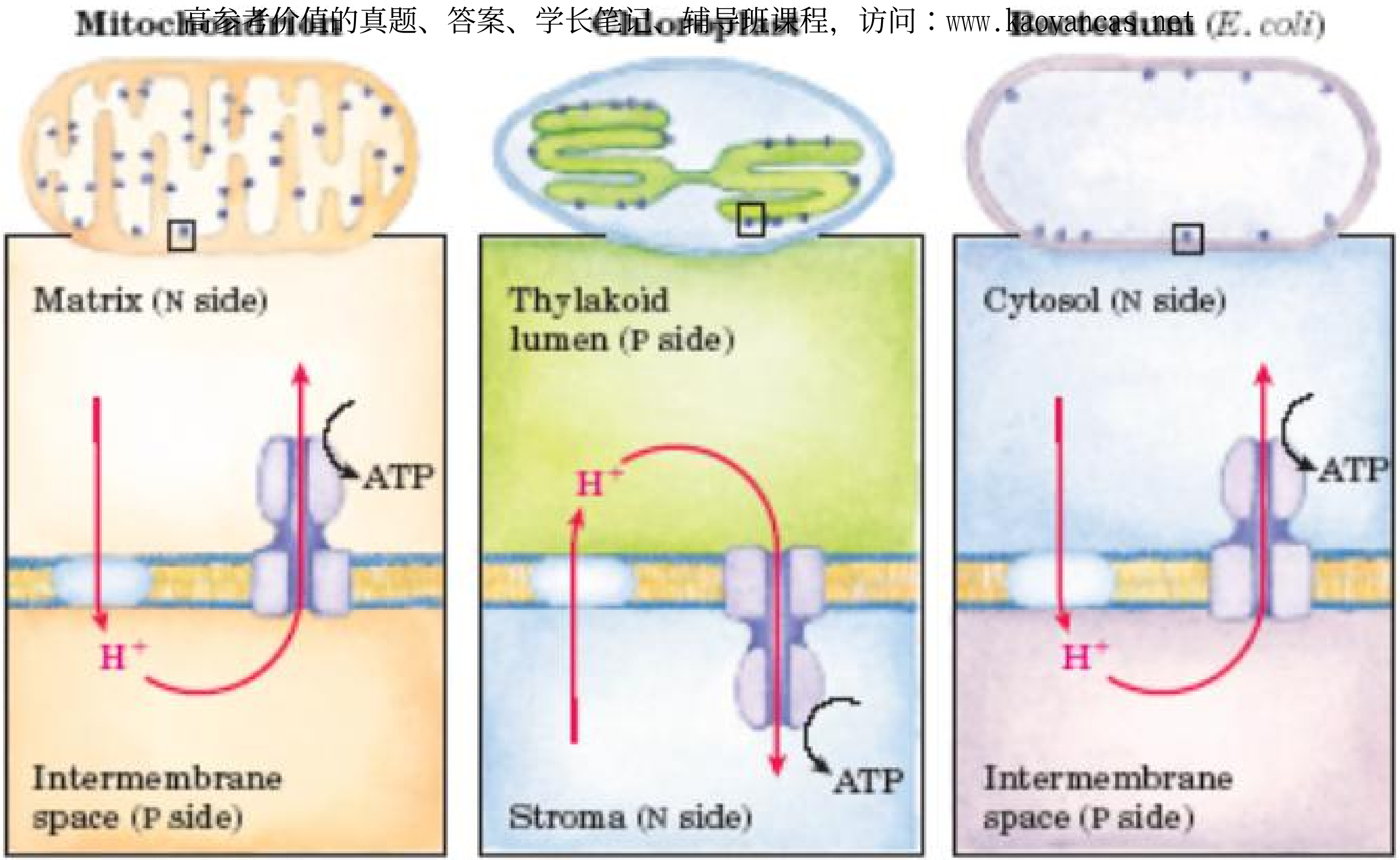


FIGURE 19–58 Comparison of the topology of proton movement and ATP synthase orientation in the membranes of mitochondria, chloroplasts, and the bacterium *E. coli*. In each case, orientation of the proton gradient relative to ATP synthase activity is the same.

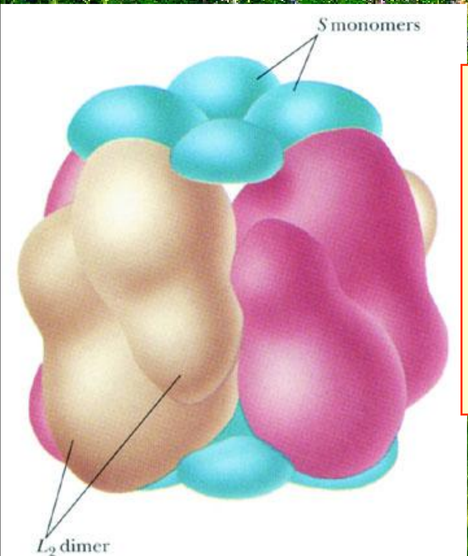
三、暗反应：Calvin循环

1.第一阶段：CO_2固定

The Nobel Prize in Chemistry 1961

"for his research on the carbon dioxide assimilation in plants"

Presentation Speech



核酮糖-1,5-二磷酸羧化酶由8个大亚基和8个小亚基组成，约占绿叶蛋白质的50%。

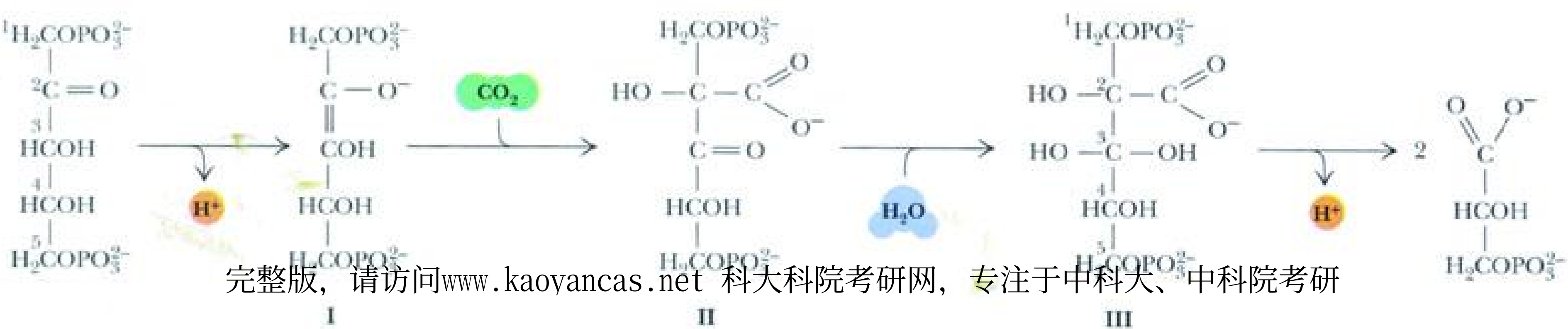
Melvin Calvin

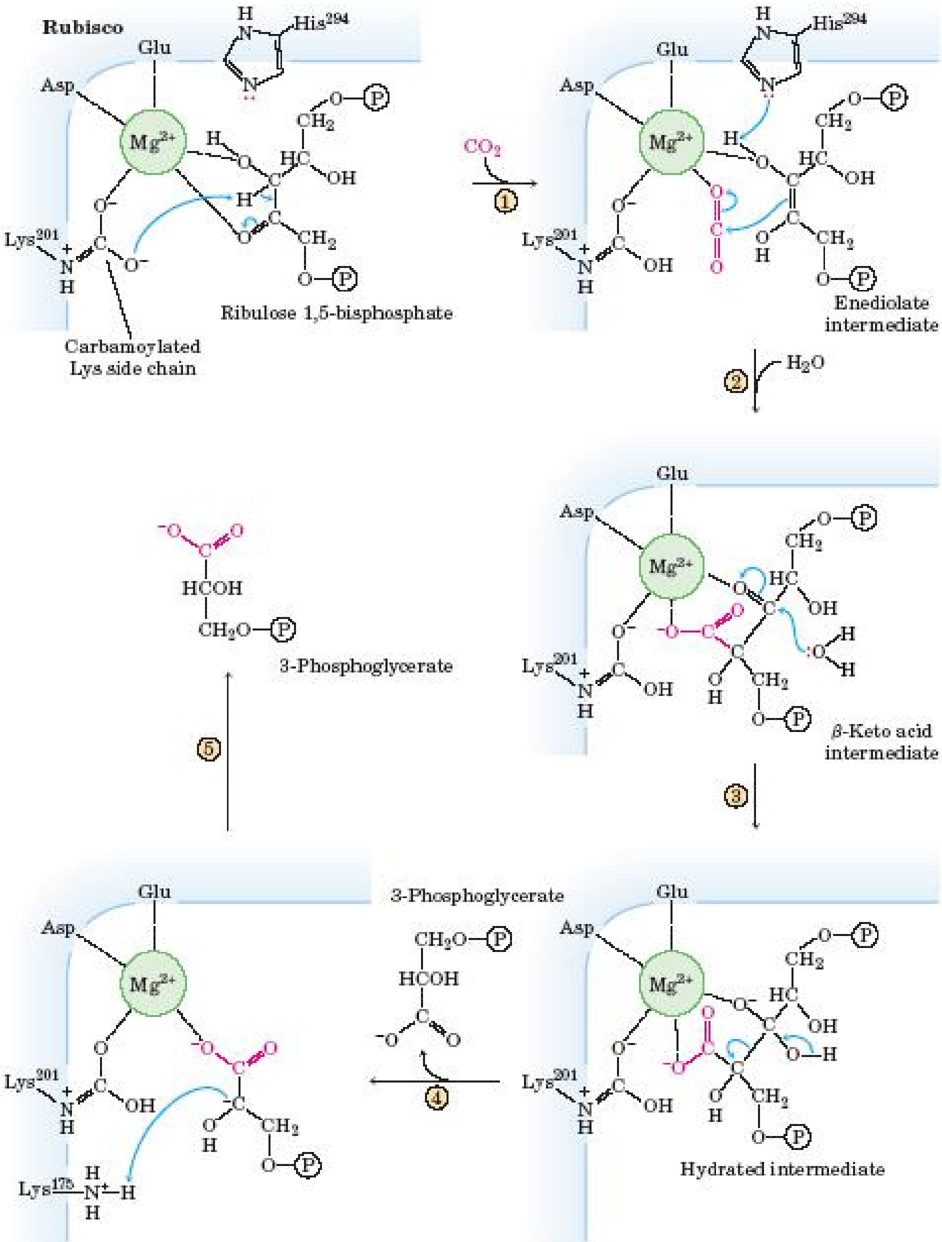
USA

University of California
Berkeley, CA, USA

1911 - 1997

Biography





MECHANISM FIGURE 20–7 First stage of CO_2 assimilation: rubisco's carboxylase activity. The CO_2-fixation reaction is catalyzed by ribulose 1,5-bisphosphate carboxylase/oxygenase (rubisco). (1) Ribulose 1,5-bisphosphate forms an enediolate at the active site. (2) CO_2, polarized by the proximity of the Mg^{2+} ion, undergoes nucleophilic attack by the enediolate, producing a branched six-carbon sugar. (3) Hydroxylation at C-3 of this sugar, followed by aldol cleavage (4), forms one molecule of 3-phosphoglycerate, which leaves the enzyme active site. (5) The carbanion of the remaining three-carbon fragment is protonated by the nearby side chain of Lys[175], generating a second molecule of 3-phosphoglycerate. The overall reaction therefore accomplishes the combination of one CO_2 and one ribulose 1,5-bisphosphate to form two molecules of 3-phosphoglycerate, one of which contains the carbon atom from CO_2 (red). Rubisco Mechanism; Rubisco Tutorial

2.第二阶段：生成三磷酸甘油醛

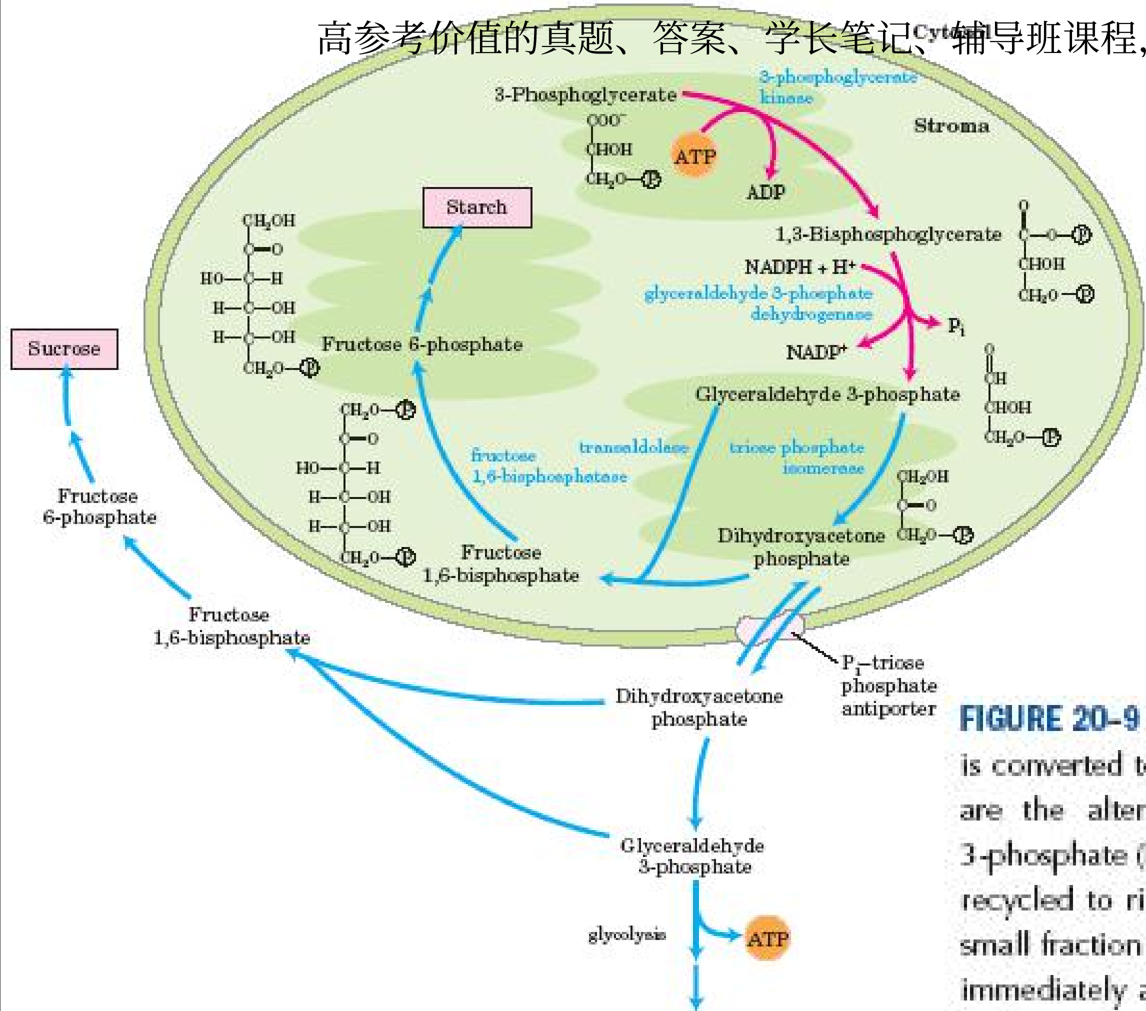
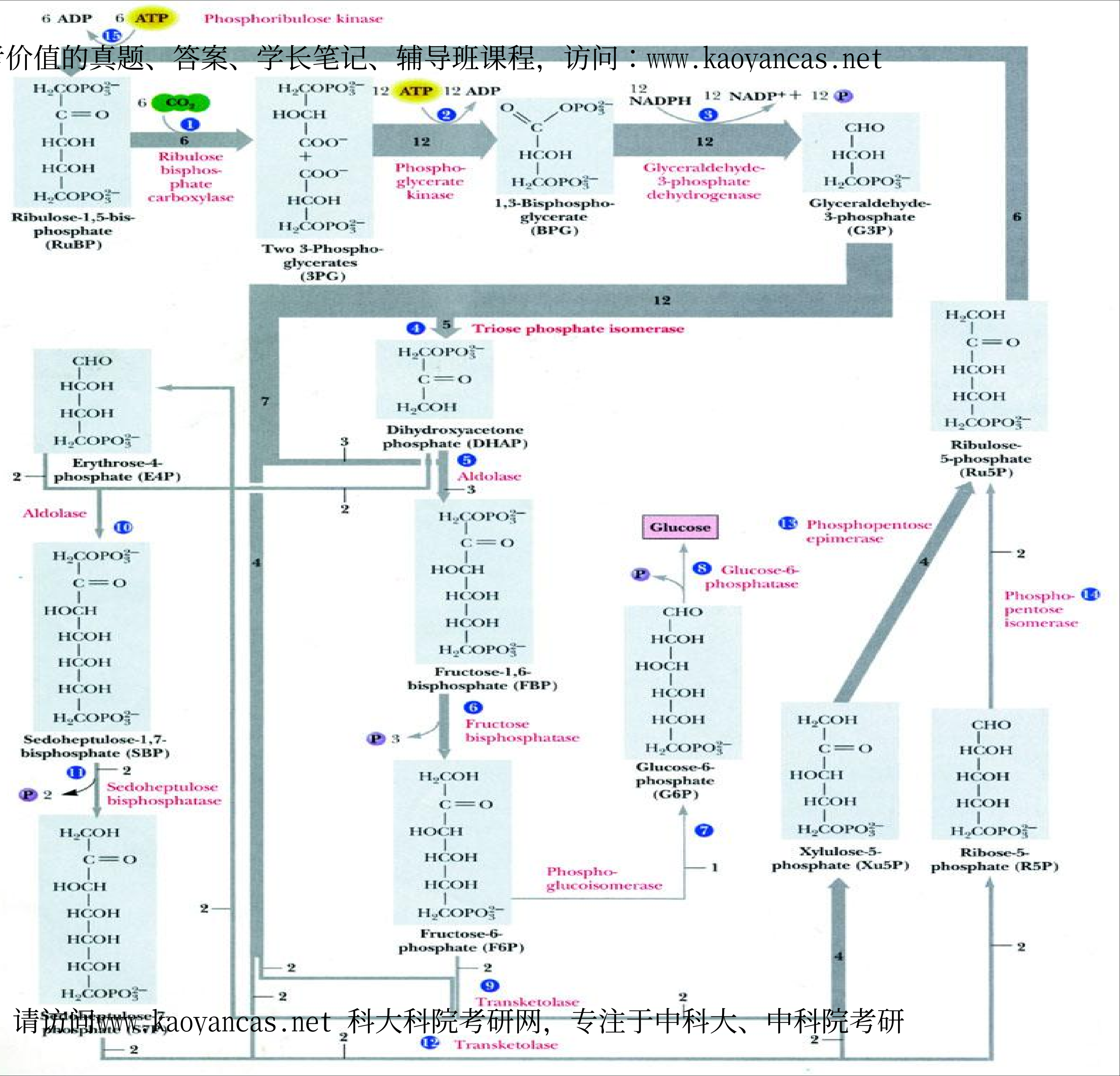


FIGURE 20-9 Second stage of CO_2 assimilation. 3-Phosphoglycerate is converted to glyceraldehyde 3-phosphate (red arrows). Also shown are the alternative fates of the fixed carbon of glyceraldehyde 3-phosphate (blue arrows). Most of the glyceraldehyde 3-phosphate is recycled to ribulose 1,5-bisphosphate as shown in Figure 20–10. A small fraction of the "extra" glyceraldehyde 3-phosphate may be used immediately as a source of energy, but most is converted to sucrose for transport or is stored in the chloroplast as starch. In the latter case, glyceraldehyde 3-phosphate condenses with dihydroxyacetone phosphate in the stroma to form fructose 1,6-bisphosphate, a precursor of starch. In other situations the glyceraldehyde 3-phosphate is converted to dihydroxyacetone phosphate, which leaves the chloroplast via a specific transporter (see Fig. 20–15) and, in the cytosol, can be degraded glycolytically to provide energy or used to form fructose 6-phosphate and hence sucrose.

3.第三阶段：核酮糖-1，5-二磷酸的再生



4.Calvin循环的化学计量

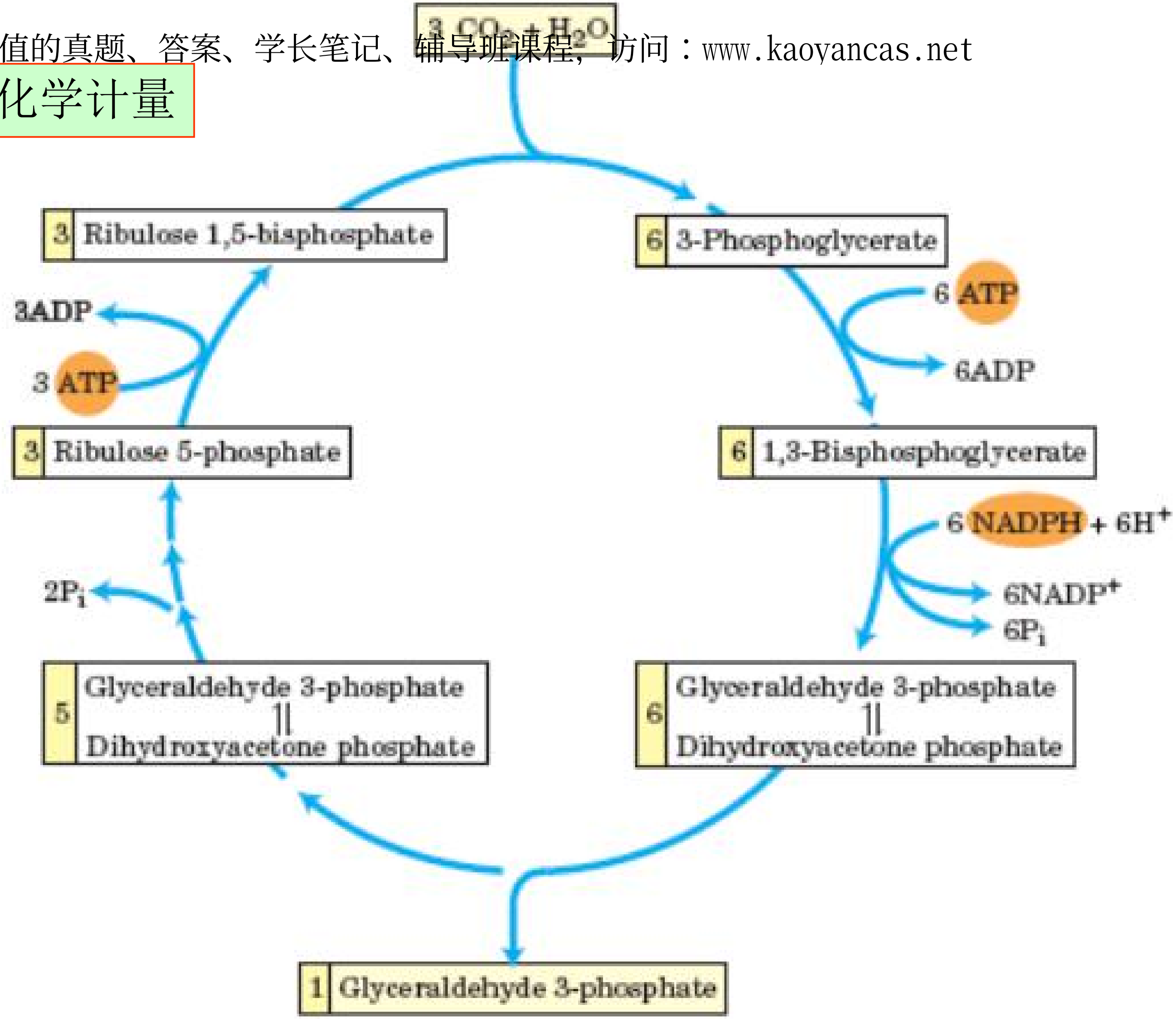
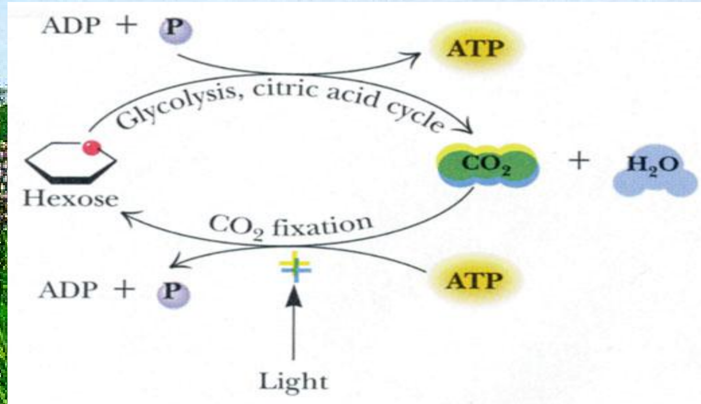


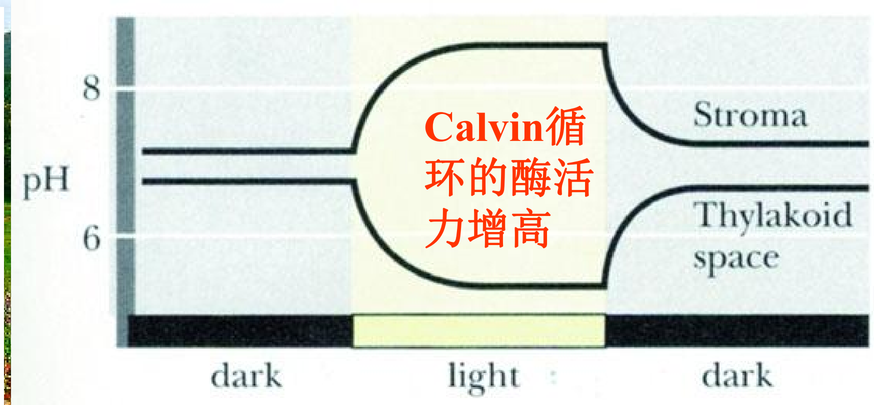
FIGURE 20-14 Stoichiometry of CO_2 assimilation in the Calvin cycle. For every three CO_2 molecules fixed, one molecule of triose phosphate (glyceraldehyde 3-phosphate) is produced

5.Calvin循环的调节

光调控叶绿体小室的pH变化

光调控二氧化碳固定，防止细胞呼吸和己糖合成的循环。





光调控Calvin循环 的途径

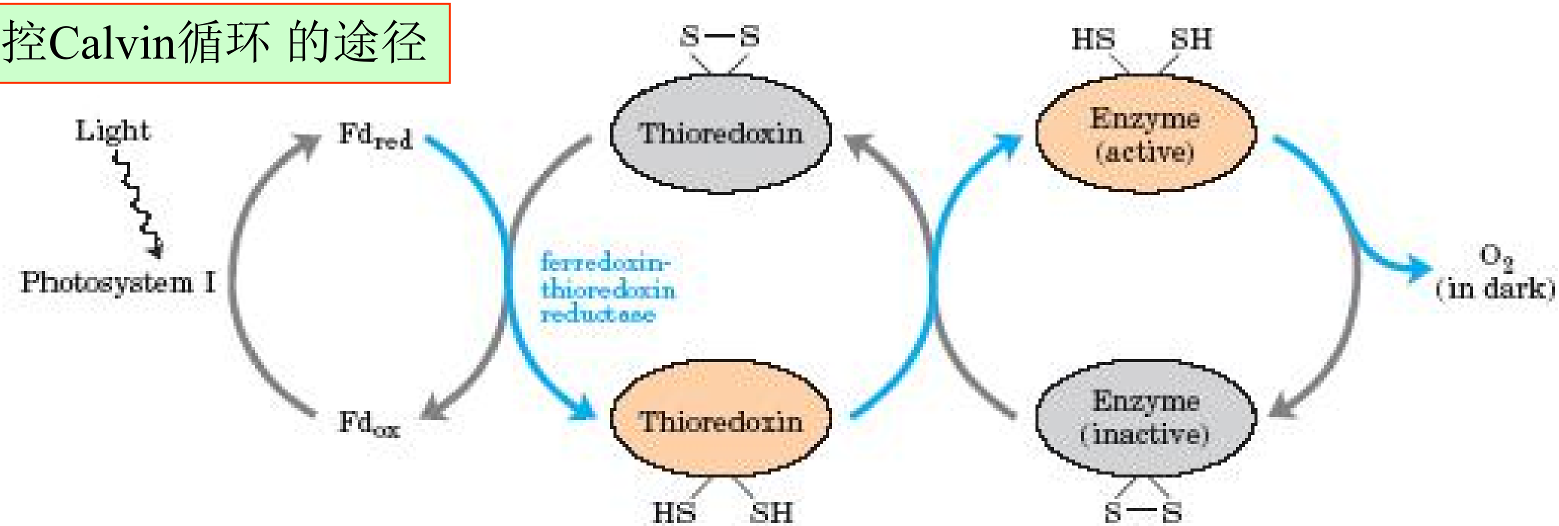
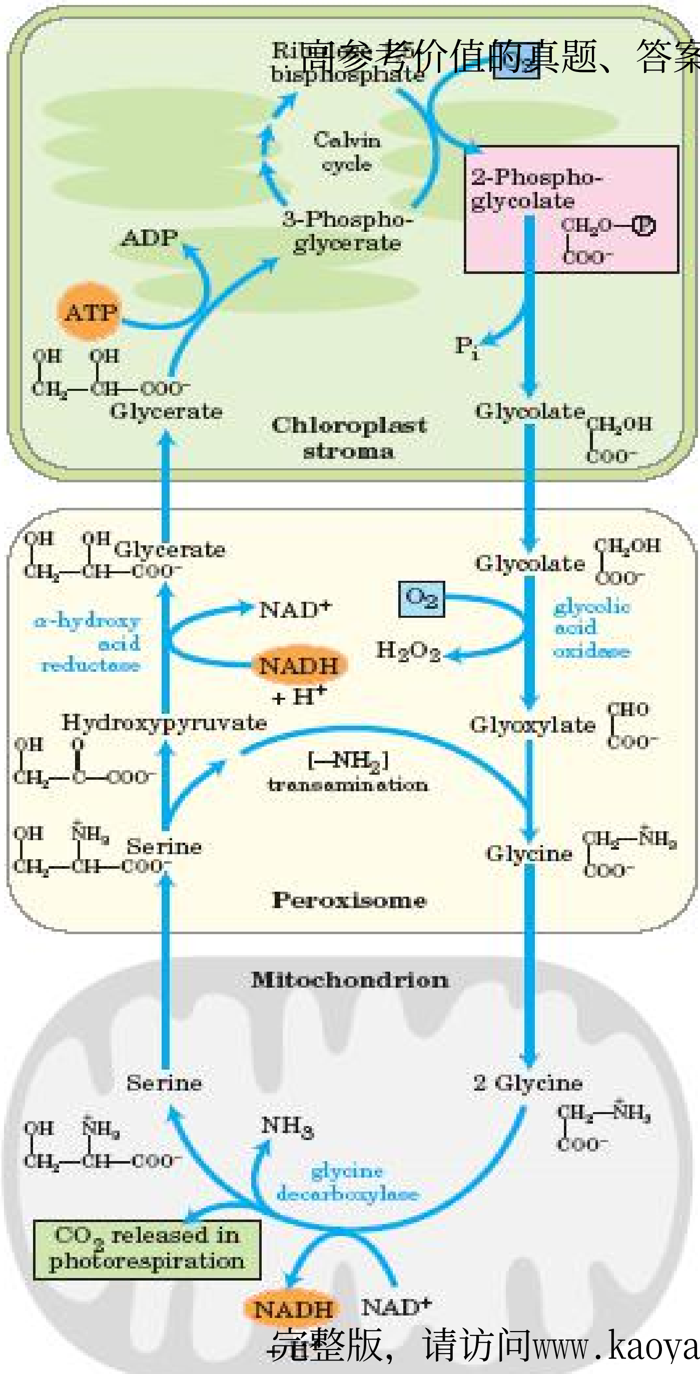


FIGURE 20–19 Light activation of several enzymes of the Calvin cycle. The light activation is mediated by thioredoxin, a small, disulfide-containing protein. In the light, thioredoxin is reduced by electrons moving from photosystem I through ferredoxin (Fd) (blue arrows), then thioredoxin reduces critical disulfide bonds in each of the enzymes sedoheptulose 1,7-bisphosphatase, fructose 1,6-bisphosphatase, ribulose 5-phosphate kinase, and glyceraldehye 3-phosphate dehydrogenase, activating these enzymes. In the dark, the —SH groups undergo reoxidation to disulfides, inactivating the enzymes.

6.核酮糖二磷酸加氧酶反应:光呼吸



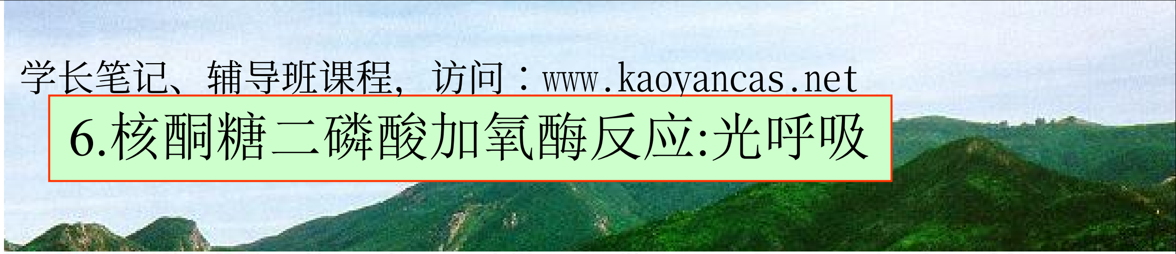
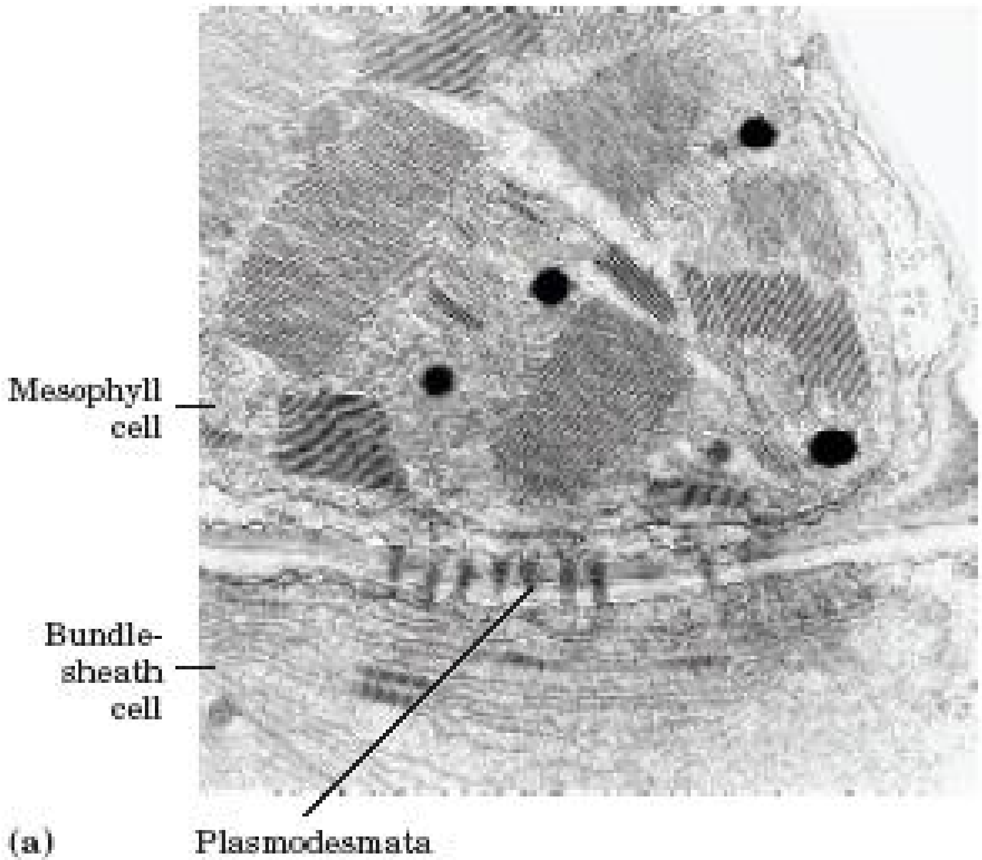


FIGURE 20–21 Glycolate pathway. This pathway, which salvages 2-phosphoglycolate (shaded pink) by its conversion to serine and eventually 3-phosphoglycerate, involves three cellular compartments. Glycolate formed by dephosphorylation of 2-phosphoglycolate in chloroplasts is oxidized to glyoxylate in peroxisomes and then transaminated to glycine. In mitochondria, two glycine molecules condense to form serine and the CO_2 released during photorespiration (shaded green). This reaction is catalyzed by glycine decarboxylase, an enzyme present at very high levels in the mitochondria of C_3 plants (see text). The serine is converted to hydroxypyruvate and then to glycerate in peroxisomes; glycerate reenters the chloroplasts to be phosphorylated, rejoining the Calvin cycle. Oxygen (shaded blue) is consumed at two steps during photorespiration.

7.CO_2固定的C_4途径



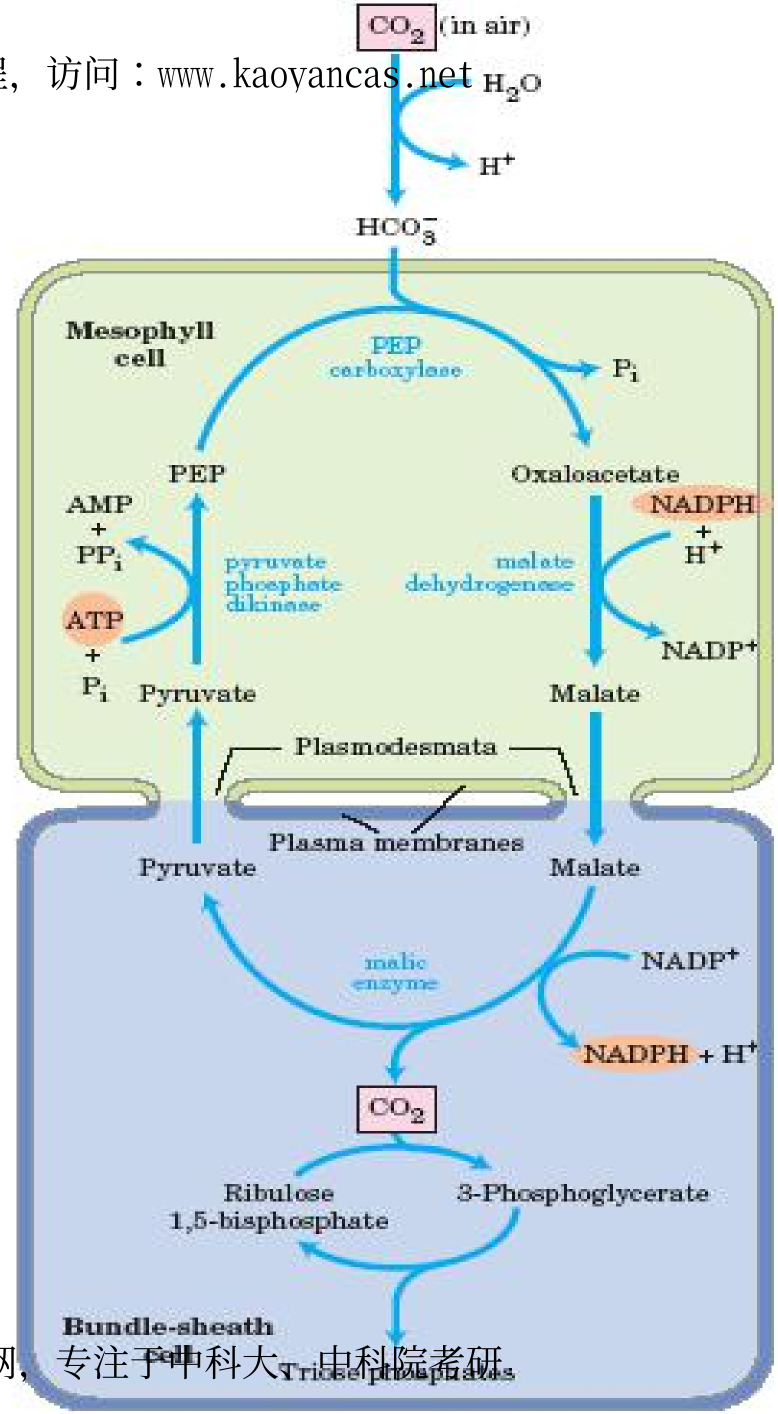


FIGURE 20–23 Carbon assimilation in C_4 plants. The C_4 pathway, involving mesophyll cells and bundle-sheath cells, predominates in plants of tropical origin. (a) Electron micrograph showing chloroplasts of adjacent mesophyll and bundle-sheath cells. The bundle-sheath cell contains starch granules. Plasmodesmata connecting the two cells are visible. (b) The C_4 pathway of CO_2 assimilation, which occurs through a four-carbon intermediate.

8.景天酸代谢

景天科植物白天炎热时气孔不开，以防水分散失。夜间气孔开放，吸收CO_2。在PEP羧化酶作用下，CO_2与PEP结合生成草酰乙酸，随后被苹果酸脱氢酶还原成苹果酸，贮存于液泡中直到天亮，白天苹果酸从液泡中释放出来，脱羧生成CO_2和丙酮酸，CO_2进入Calvin循环。

基本要求

1. 与呼吸链和氧化磷酸化对比，了解光合作用的光反应。
2. 与戊糖磷酸途径对比，了解光合作用的暗反应。