

# 微生物学

# Microbiology

---

## Lecture 8

2017.11.14

# **CHAPTER 11**

---

## **Catabolism: Energy Release and Conservation**

---

# Outline

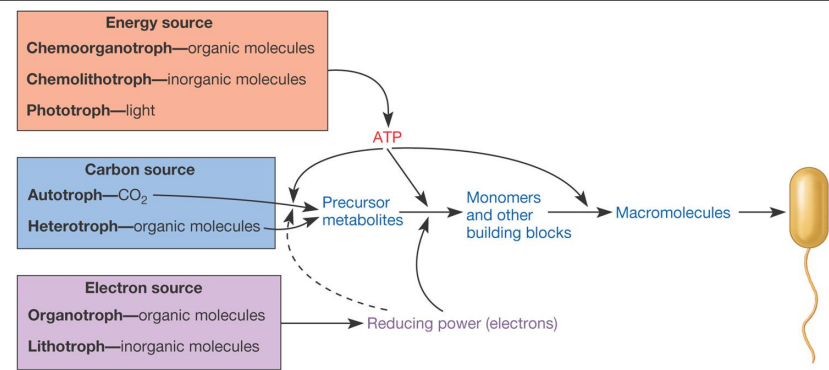
- **Chemoorganotrophic Fueling Processes**
  - **Chemolithotrophic Fueling Processes**
  - **Phototrophic Fueling Processes**
-

- *It is in the fueling reactions that bacteria display their extraordinary metabolic diversity and versatility. Bacteria have evolved to thrive in almost all natural environments, regardless of the nature of available sources of carbon, energy, and reducing power. . . .The collective metabolic capacities of bacteria allow them to metabolize virtually every organic compound on this planet. . . .*

*—F.C. Neidhardt,  
J . L. Ingraham, and M. Schaechter*

---

# Fueling Reactions



Energy, electron, and carbon sources all are used to generate **three main products:**

**ATP**, conserve the energy supplied by an energy source;

**Reducing power**, serve as a ready supply of electrons for a variety of chemical reactions;

**Precursor metabolites**, provide the carbon skeletons needed for biosynthesis of important chemical building blocks (monomers)

**The Fueling Reactions and Their Role in Metabolism.**

**Metabolism is the total of all chemical reactions in the cell and is divided into two parts**

## Catabolism

- Fueling reactions<sub>产能反应</sub>
- **energy**-conserving reactions
- provide reducing power (**electrons**)<sub>还原力</sub>
- generate **precursors**<sub>前体</sub> for biosynthesis

## Anabolism

- the synthesis of complex organic molecules from simpler ones
- requires energy from fueling reactions

**The flow of energy and the participation of enzymes make metabolism possible**

# Chemoorganotrophic fueling processes

化能有机营养型的产能代谢-能量来自有机物

## Respiration呼吸作用

**exogenous** 外源的final electron acceptor

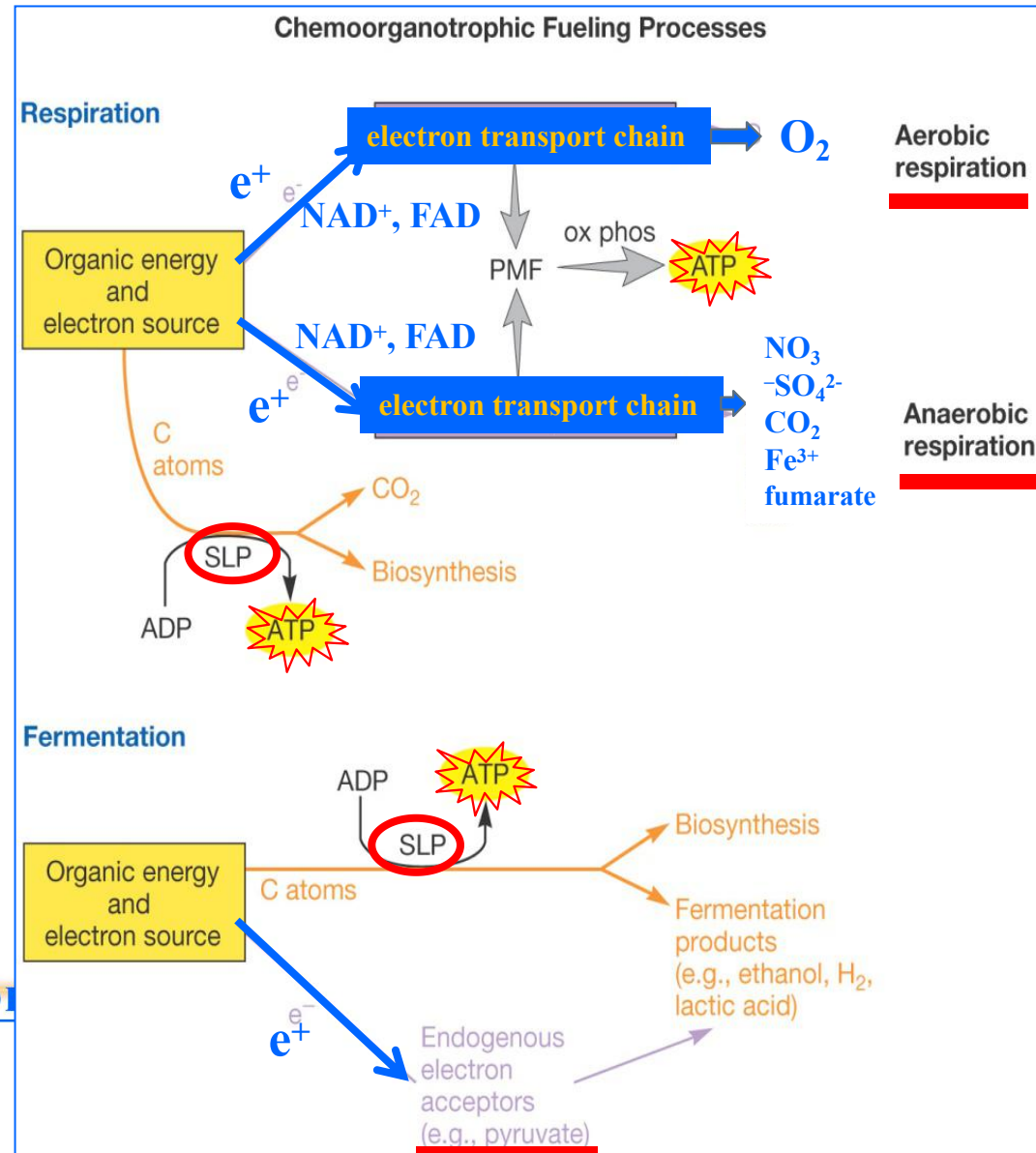
ATP made primarily by **Oxidative Phosphorylation** through ETC-PMF.

**Aerobic/Anaerobic**

## Fermentation发酵作用

**endogeneous** 内源的final electron acceptor

ATP made primarily by **Substrate-Level Phosphorylation** no ETC involved.



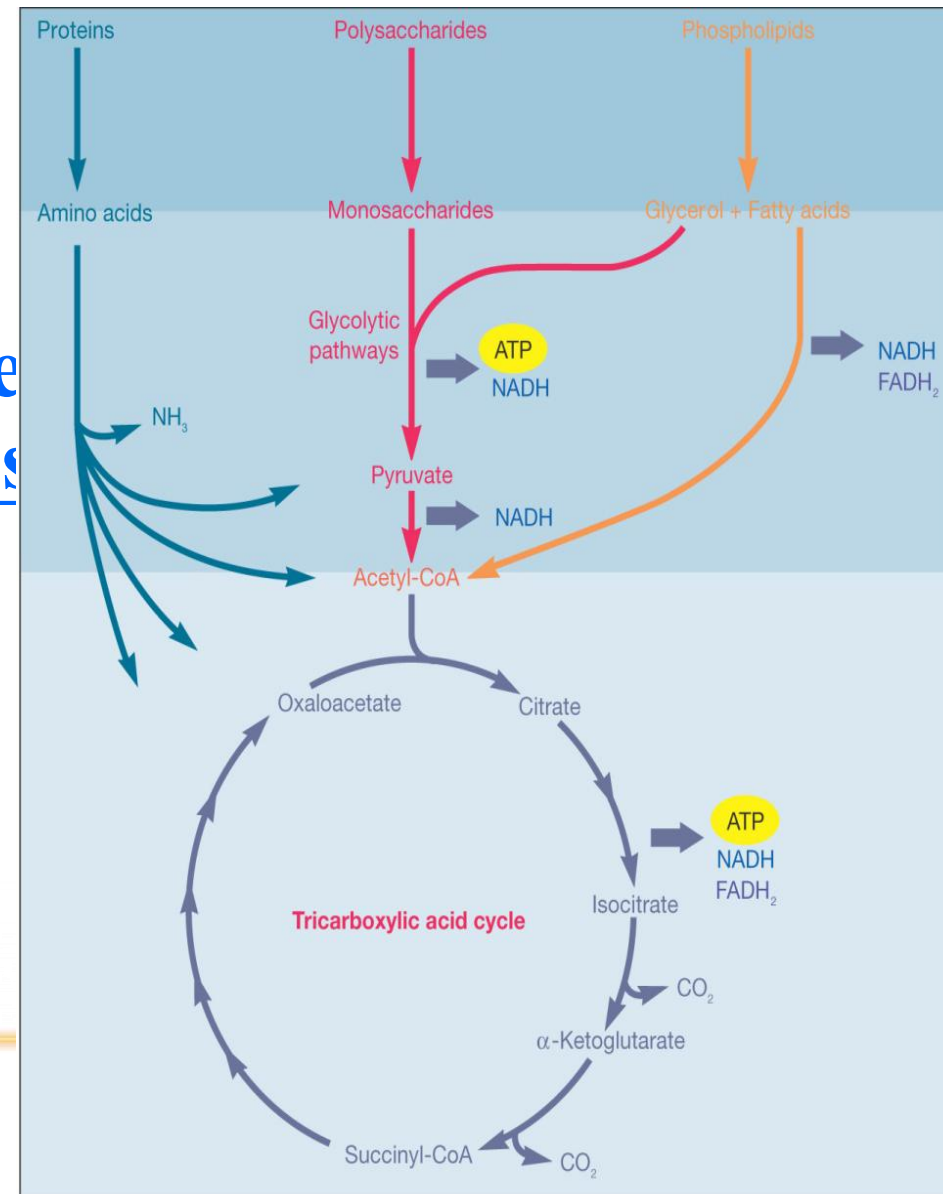
## Aerobic respiration-O<sub>2</sub>

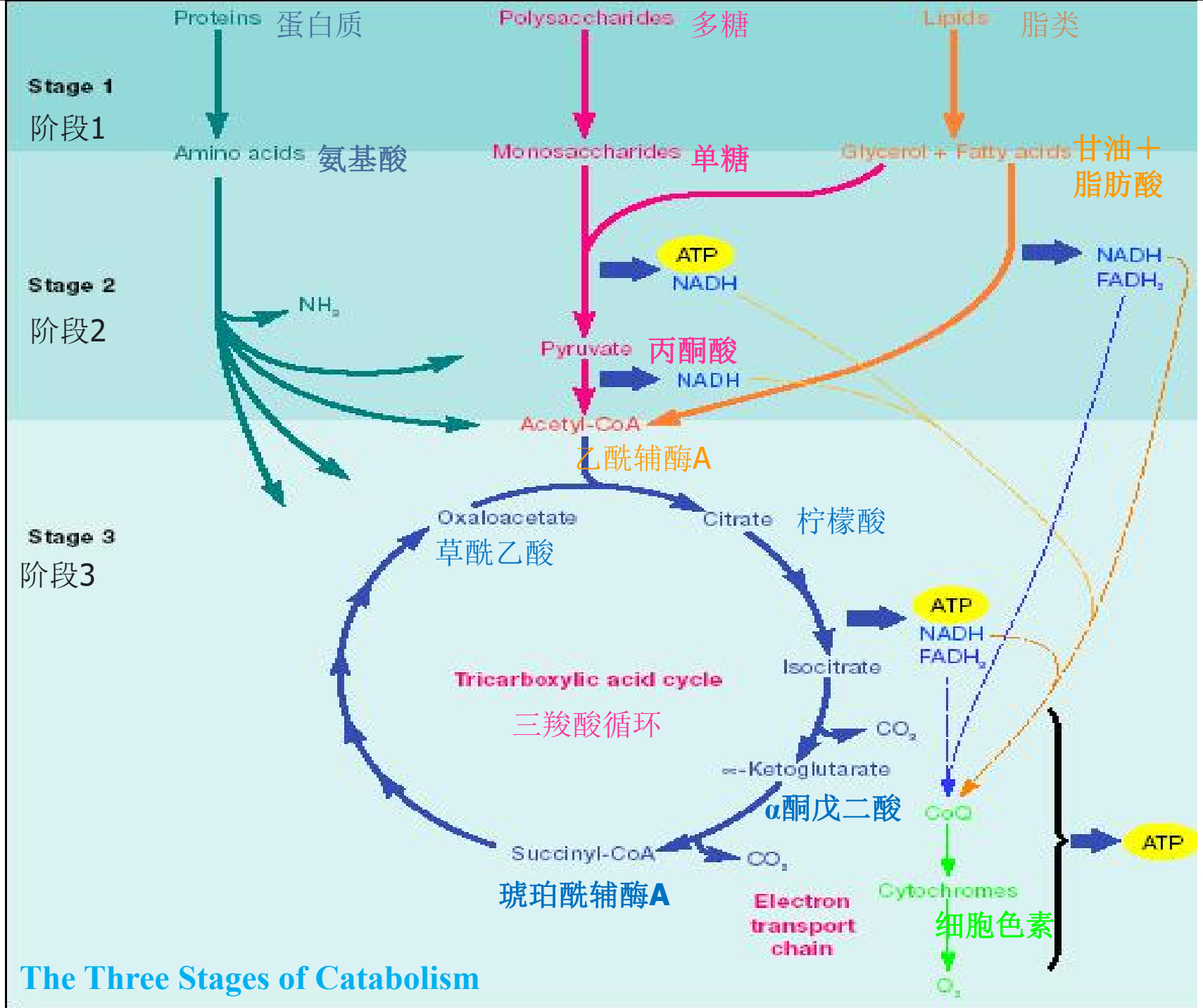
- process that can completely catabolize an organic energy source to CO<sub>2</sub> using
  - glycolytic pathways (glycolysis)糖酵解
  - TCA cycle三羧酸循环
  - ETC with oxygen as the final electron acceptor
- produces ATP, and high energy electron carriers



# Energy produce-Glucose metabolism

- many different organic molecules used as energy sources
- most pathways generate glucose or intermediates of the pathways used in glucose metabolism
- few pathways greatly increase metabolic efficiency
- Glucose metabolism





**The Three Stages of Catabolism**

# The breakdown of glucose to pyruvate

- **three common routes-glycolysis**
  - **Embden-Meyerhof pathway**
  - **Pentose phosphate pathway (Hexose monophosphate *pathway*) 戊糖磷酸途径**
  - **Entner-Duodoroff pathway (*agrobacterium, G<sup>-</sup>*)**

# The Embden-Meyerhof Pathway

- occurs in cytoplasmic matrix of most microorganisms, plants, and animals
  - the most common pathway for glucose degradation to pyruvate in stage two of aerobic respiration
  - function in presence or absence of O<sub>2</sub>
-

addition of phosphates  
 “primes the pump”

oxidation step –  
 generates **NADH**

high-energy molecules –  
 used to synthesize **ATP**  
 by substrate-level  
phosphorylation

Glucose is phosphorylated at the expense of one ATP, creating glucose 6-phosphate, a precursor metabolite and the starting molecule for the pentose phosphate pathway.

Isomerization of glucose 6-phosphate (an aldehyde) to fructose 6-phosphate (a ketone and a precursor metabolite)

ATP is consumed to phosphorylate C1 of fructose. The cell is spending some of its energy currency in order to earn more in the next part of the pathway.

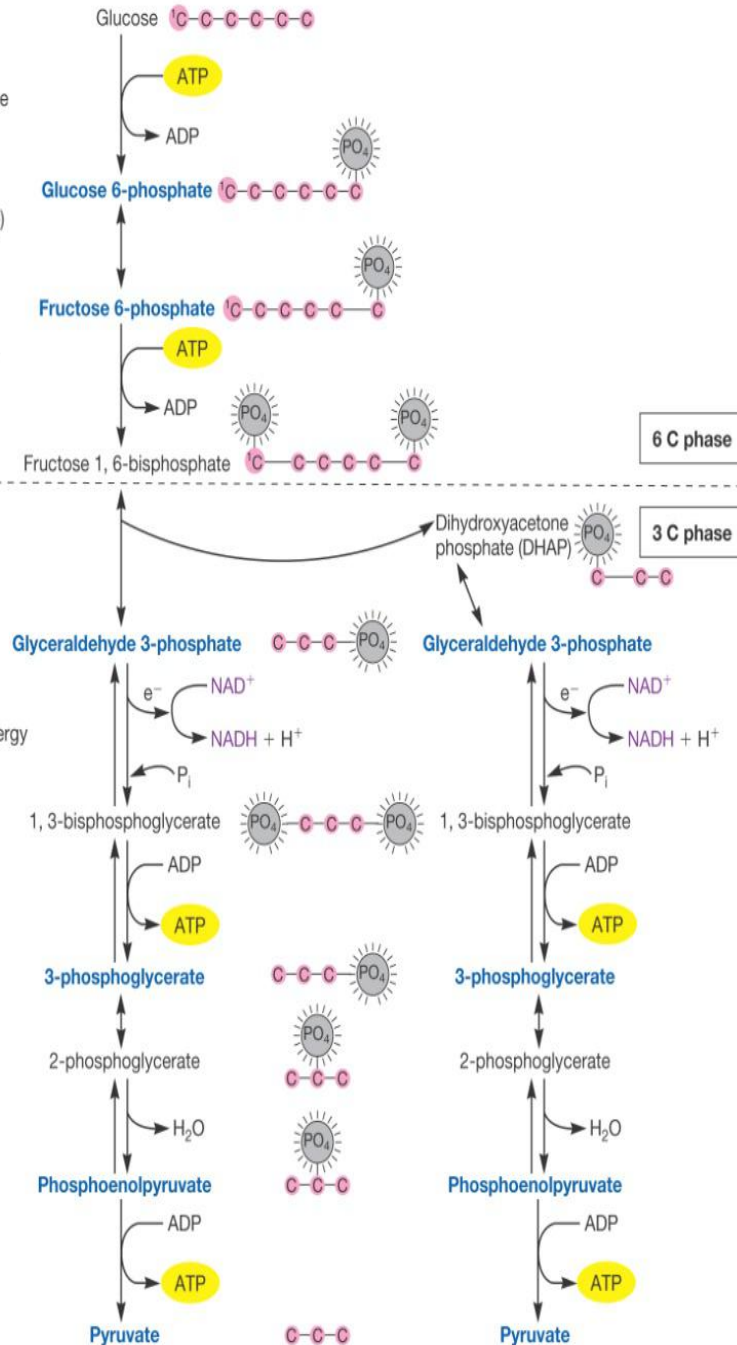
Fructose 1, 6-bisphosphate is split into two 3-carbon molecules, one of which is a precursor metabolite. DHAP is readily converted to glyceraldehyde 3-phosphate.

Glyceraldehyde 3-phosphate is oxidized and simultaneously phosphorylated, creating a high-energy molecule. The electrons released reduce  $\text{NAD}^+$  to NADH.

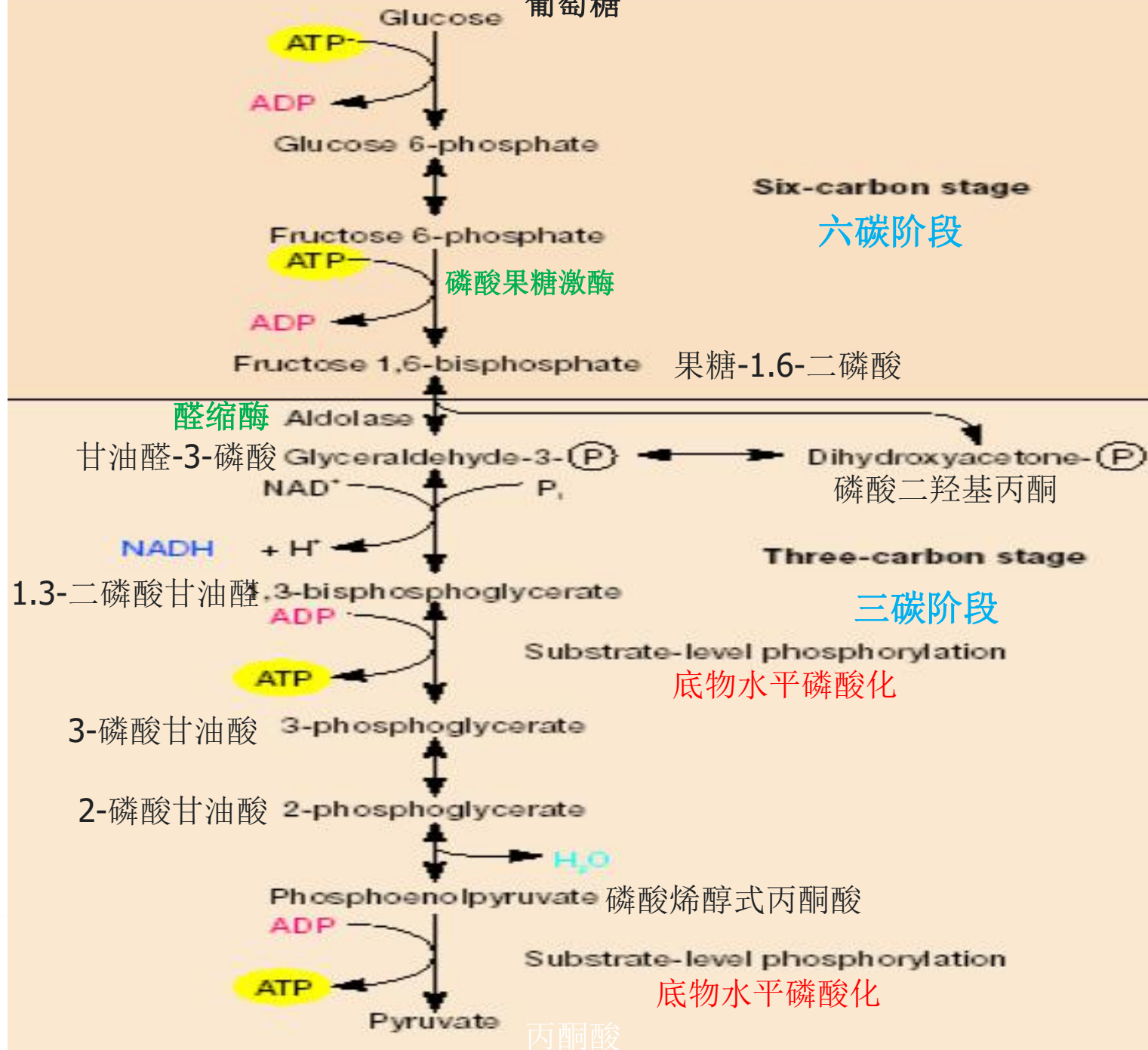
ATP is made by substrate-level phosphorylation. Another precursor metabolite is made.

Another precursor metabolite is made.

The oxidative breakdown of one glucose results in the formation of two pyruvate molecules. Pyruvate is one of the most important precursor metabolites.



# 葡萄糖



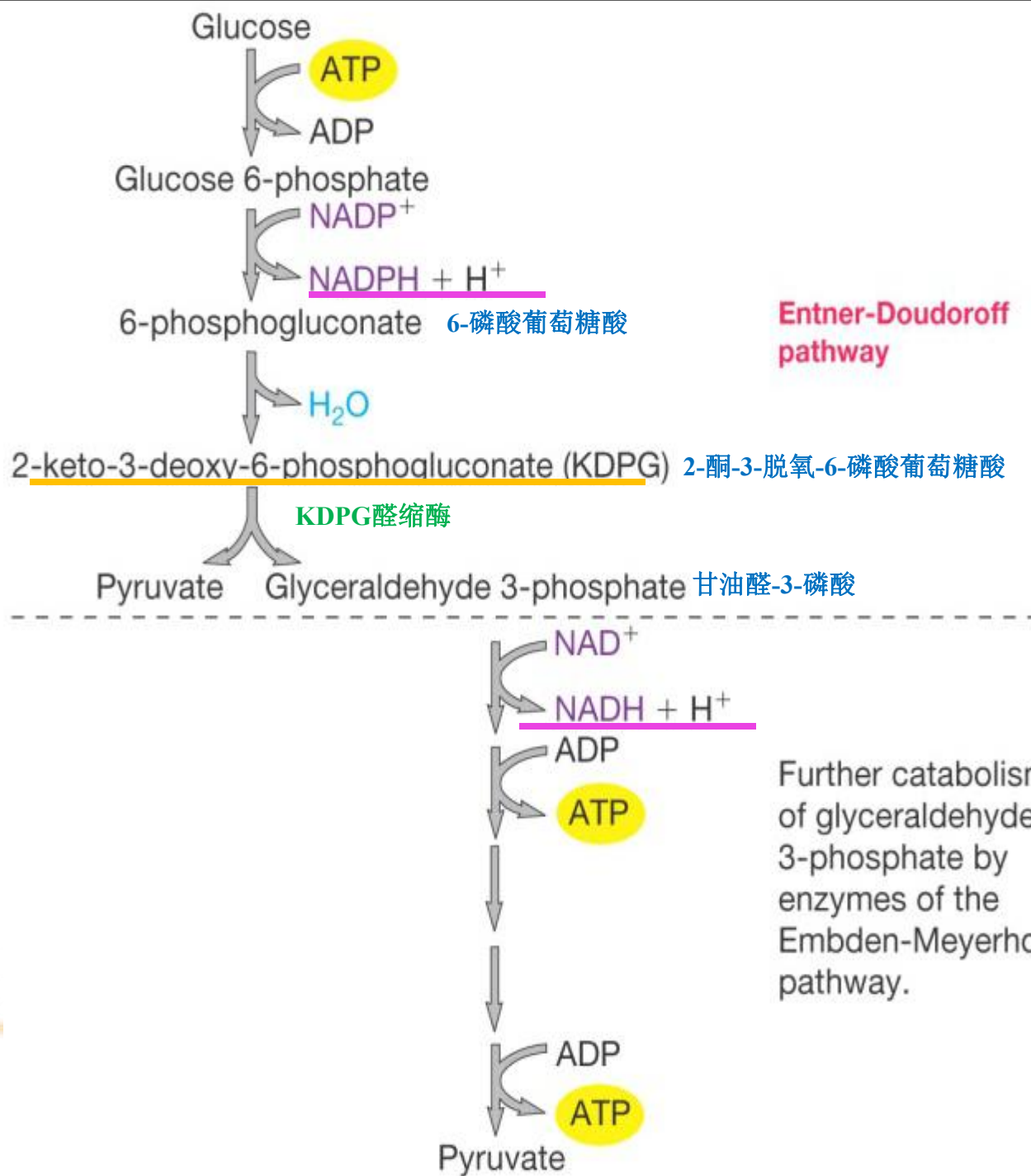
## Summary of glycolysis



# The Entner-Duodoroff pathway\*

- used by soil bacteria and a few gram-negative bacteria(G-)
  - replaces the first phase of the Embden-Meyerhof pathway
  - It is not used by eukaryotes!
-





## yield per glucose molecule:

- 1 ATP
- 1 NADPH
- 1 NADH

# The pentose phosphate pathway

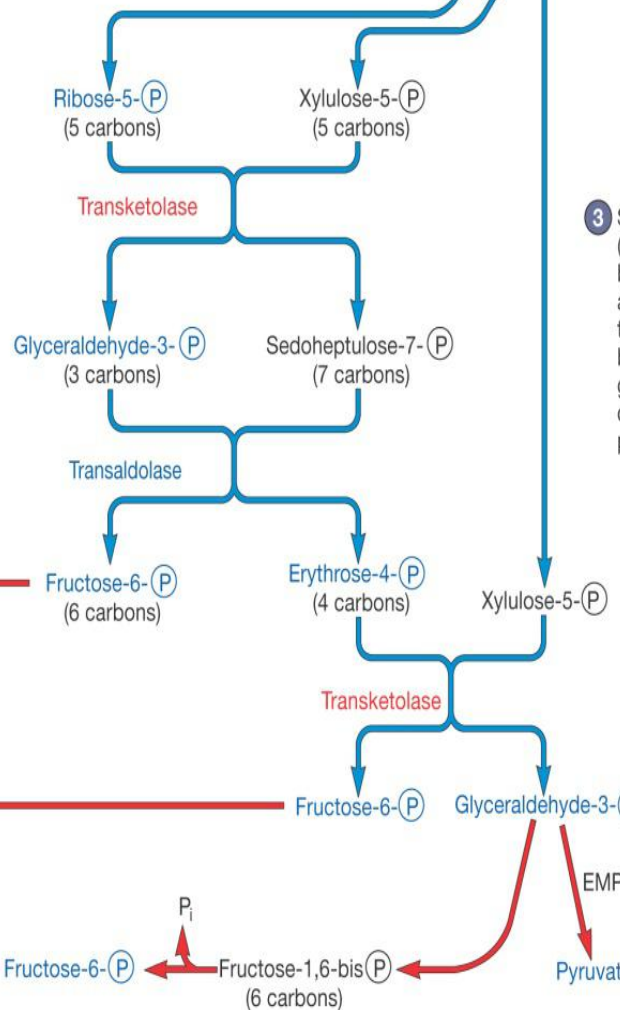
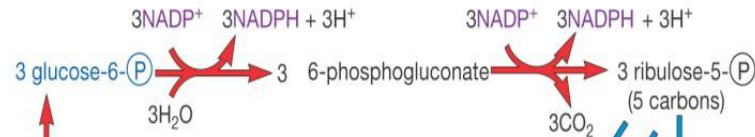
戊糖磷酸途径

- also called hexose monophosphate pathway 己糖单磷酸途径
- can operate at same time as glycolytic pathway or Entner-Duodoroff pathway
- can operate aerobically or anaerobically
- an amphibolic pathway 两用途径
- Two steps oxidative reaction(6-P-Glucose dehydrogenase and 6-P-Gluconate dehydrogenase, NADPH, CO<sub>2</sub>)

# oxidation steps

1 Glucose 6-phosphate, an intermediate of the Embden-Meyerhof pathway and a precursor metabolite, is oxidized. The reaction provides reducing power in the form of NADPH.

2 6-Phosphogluconate is oxidized and decarboxylated. This produces CO<sub>2</sub> and more reducing power in the form of NADPH.

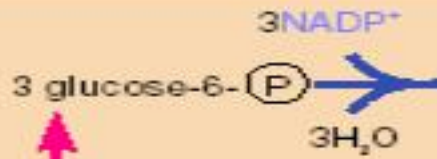


3 Sugar transformation reactions (blue arrows) are catalyzed by the enzymes transaldolase and transketolase. Some of the sugars can be used in biosynthesis or to regenerate glucose 6-phosphate. They also can be further catabolized to pyruvate.

produce sugars needed for biosynthesis

sugars can also be further degrade

produce NADPH, which is needed for biosynthesis



合成脂肪酸、类固醇  
和谷氨酸的供氢体

合成核酸、某些  
辅酶及组氨酸的  
原料

核糖-5-磷酸 Ribose-5-(P)

木酮糖-5-磷酸 Xylulose-5-(P)

转酮醇酶 Transketolase

甘油醛-3-磷酸 Glyceraldehyde-3-(P)

Sedoheptulose-7-(P)

转醛醇酶 Transaldolase

氨基苯甲酸、酪氨  
酸的前体

Fructose-6-(P)

果糖-6-磷酸

Erythrose-4-(P)

赤藓糖-4-磷酸

Xylulose-5-(P)

木酮糖-5-磷酸

转酮醇酶 Transketolase

Fructose-6-(P)

果糖-6-磷酸

Glyceraldehyde-3-(P)

果糖-6-磷酸

Fructose-6-(P)

果糖-1,6-二磷酸

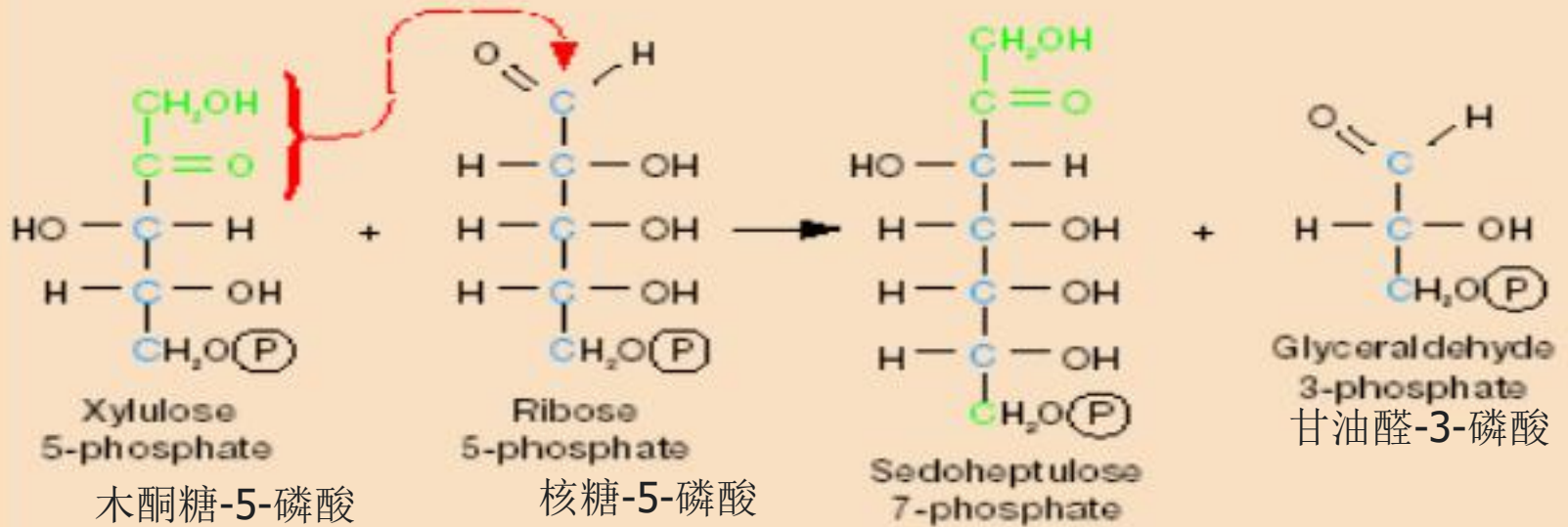
Fructose-1,6-bis(P)

丙酮酸 Pyruvate

P<sub>i</sub>

### The transketolase reaction

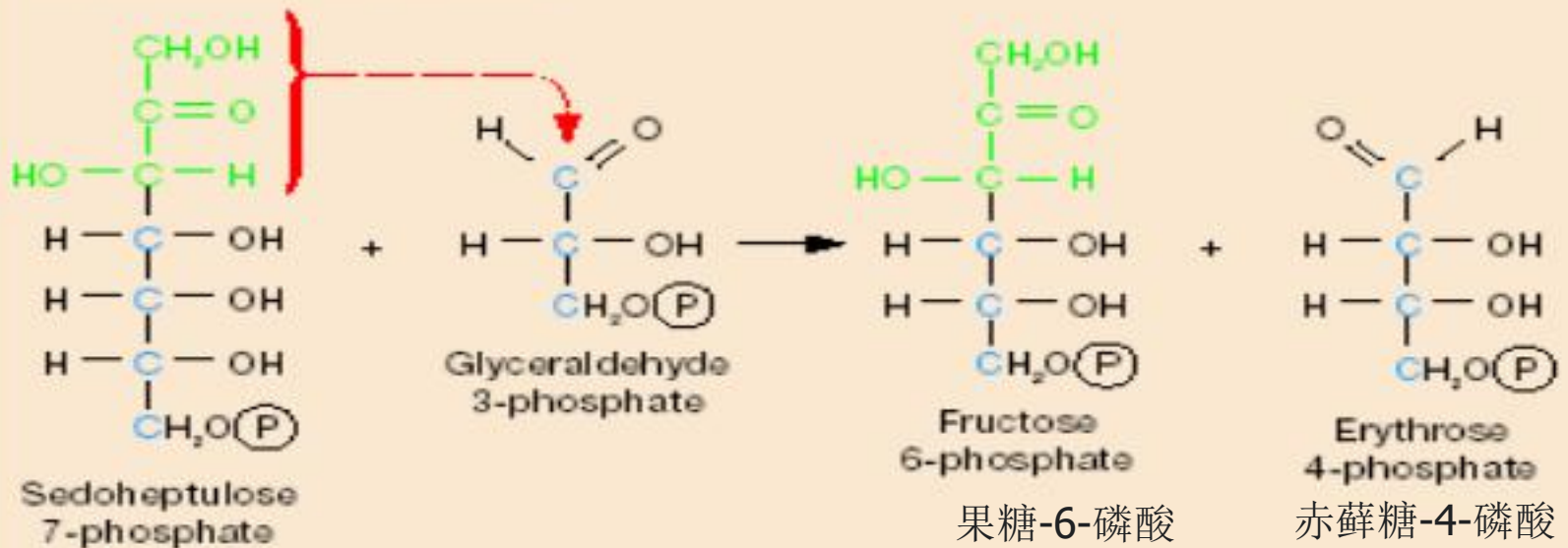
### 转酮醇酶反应



### The transaldolase reaction

### 转醛醇酶反应

景天庚酮糖-7-磷酸



**HMP**途径中转酮醇酶和转醛醇酶反应的例子

## **Discussion**

**Why might it be desirable for a microorganism with the Embden-Meyerhof pathway and the TCA cycle also to have the pentose phosphate pathway?**

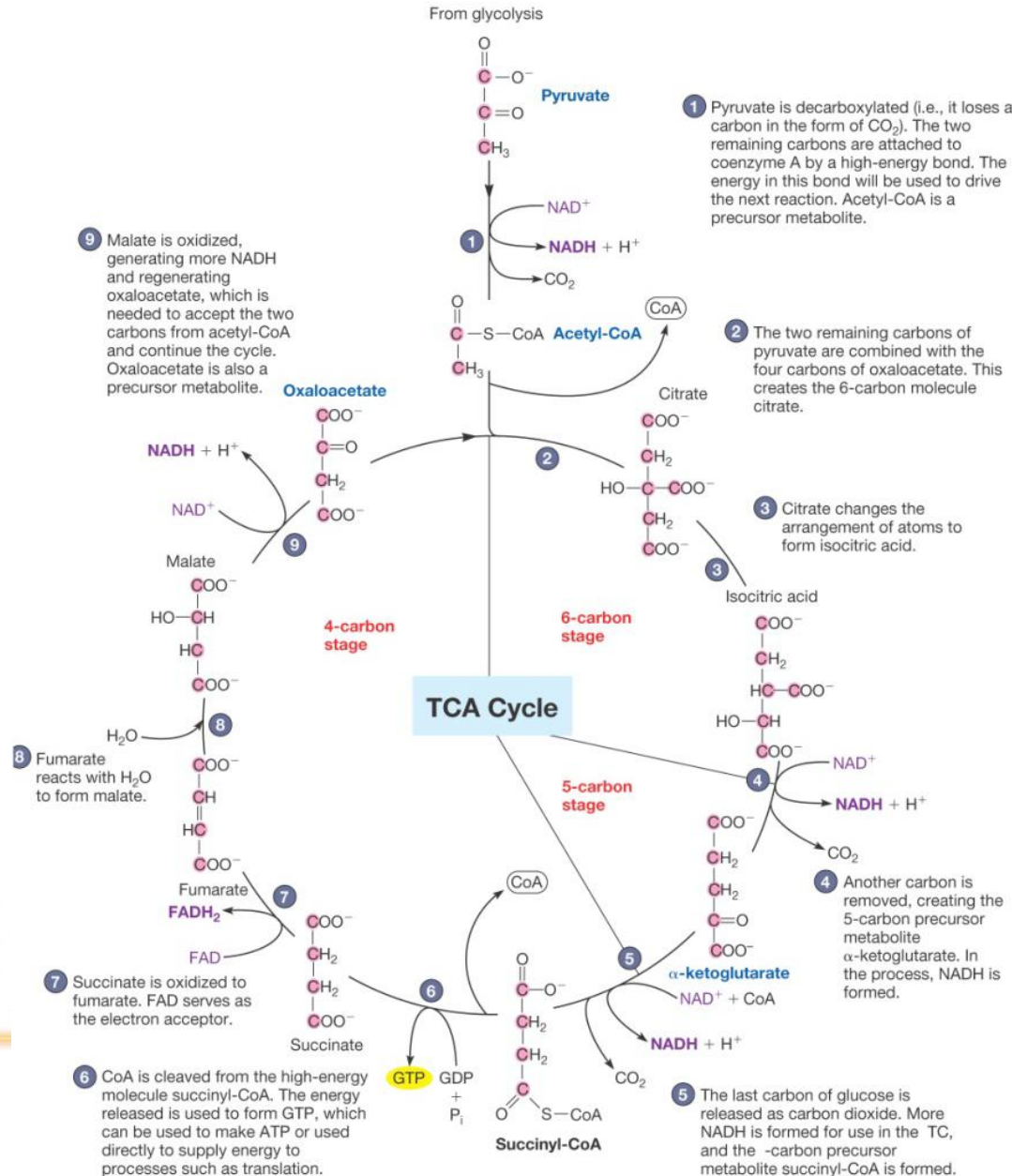
---

# The tricarboxylic acid cycle

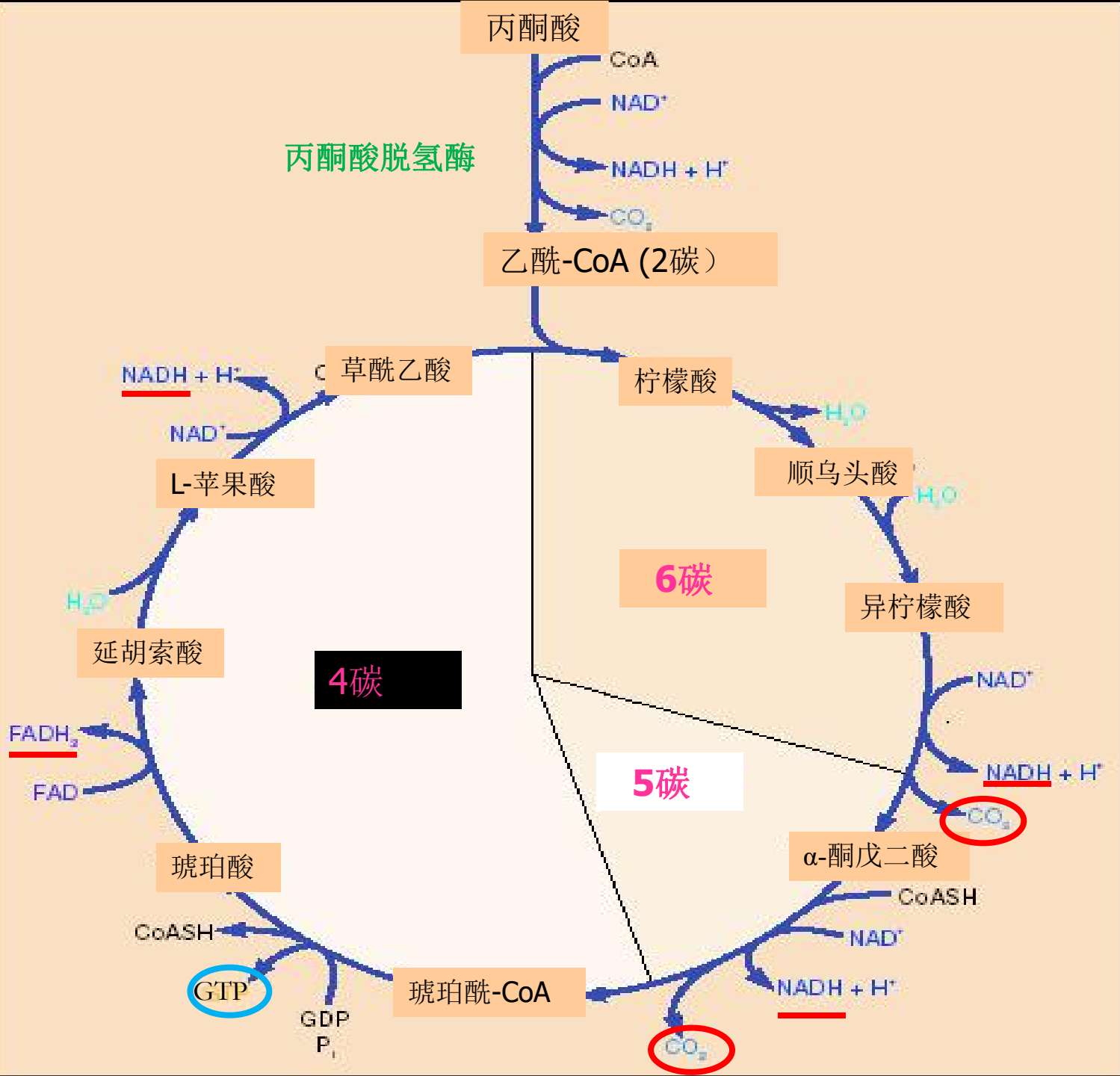
- also called citric acid cycle and Kreb's cycle

- common in aerobic bacteria, free-living protozoa, most algae, and fungi

- major role is as a source of **Carbon Skeletons** for use in biosynthesis



考察TCA循环的另一种方式是将乙酰CoA氧化成CO<sub>2</sub>的功能。





## Summary TCA cycle

- **for each acetyl-CoA molecule oxidized, TCA cycle generates:**
    - **2 molecules of CO<sub>2</sub>**
    - **3 molecules of NADH**
    - **one FADH<sub>2</sub>**
    - **one GTP**
-

# Electron transport and oxidative phosphorylation

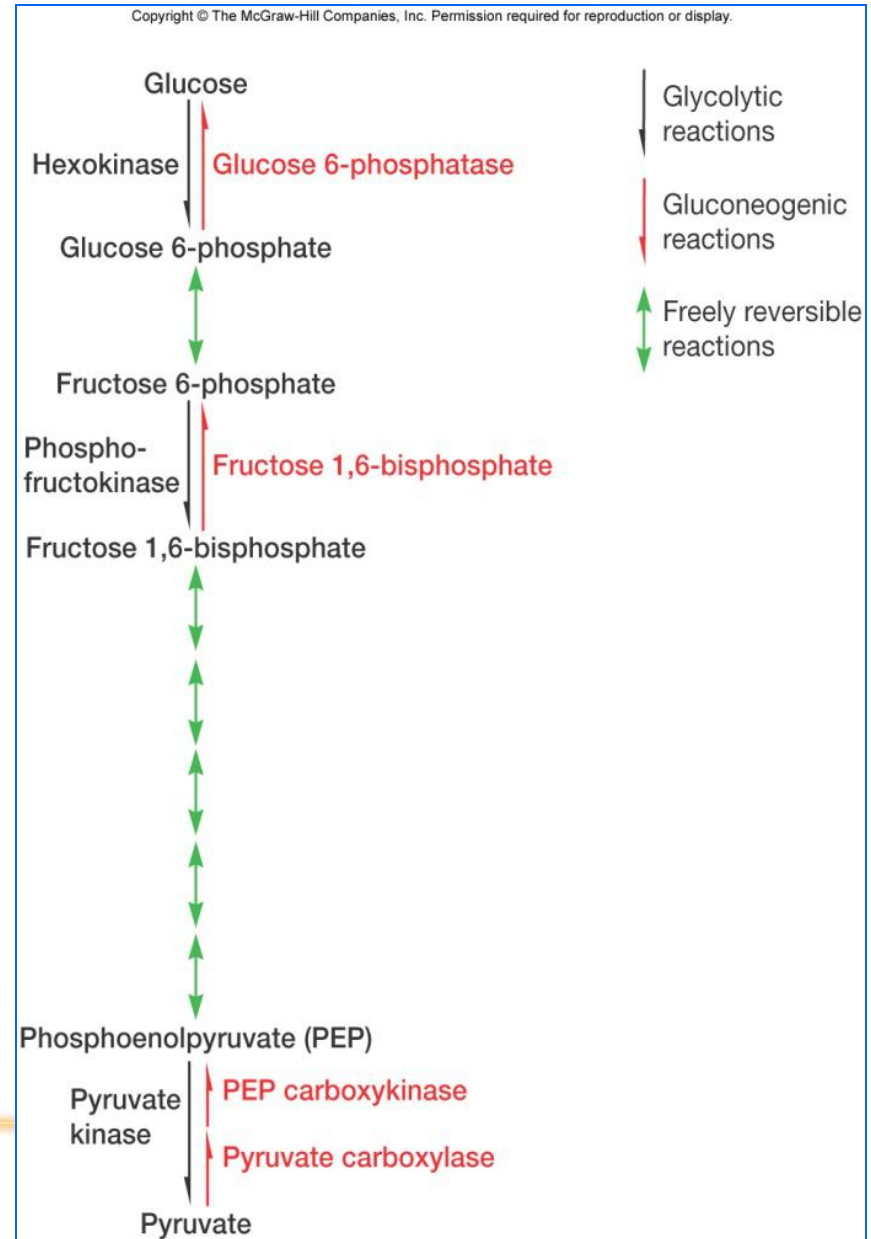
- **only 4 ATP molecules synthesized directly from oxidation of glucose to CO<sub>2</sub>**
  - **most ATP made when NADH and FADH<sub>2</sub> (formed as glucose degraded) are oxidized in ETC!**
  - **P/O ratios**  
measure of the number of ATP molecules (phosphorus) generated per oxygen (O) reduced as NADH and FADH<sub>2</sub> were oxidized.
  - **NADH P/O ratio = 2.5**
  - **FADH<sub>2</sub> P/O ratio = 1.5**
-

# Discussion

- **Calculate the ATP yield when glucose is catabolized completely to six CO<sub>2</sub> by a eukaryotic microbe. How does this value compare to the ATP yield observed for a bacterium?**
-

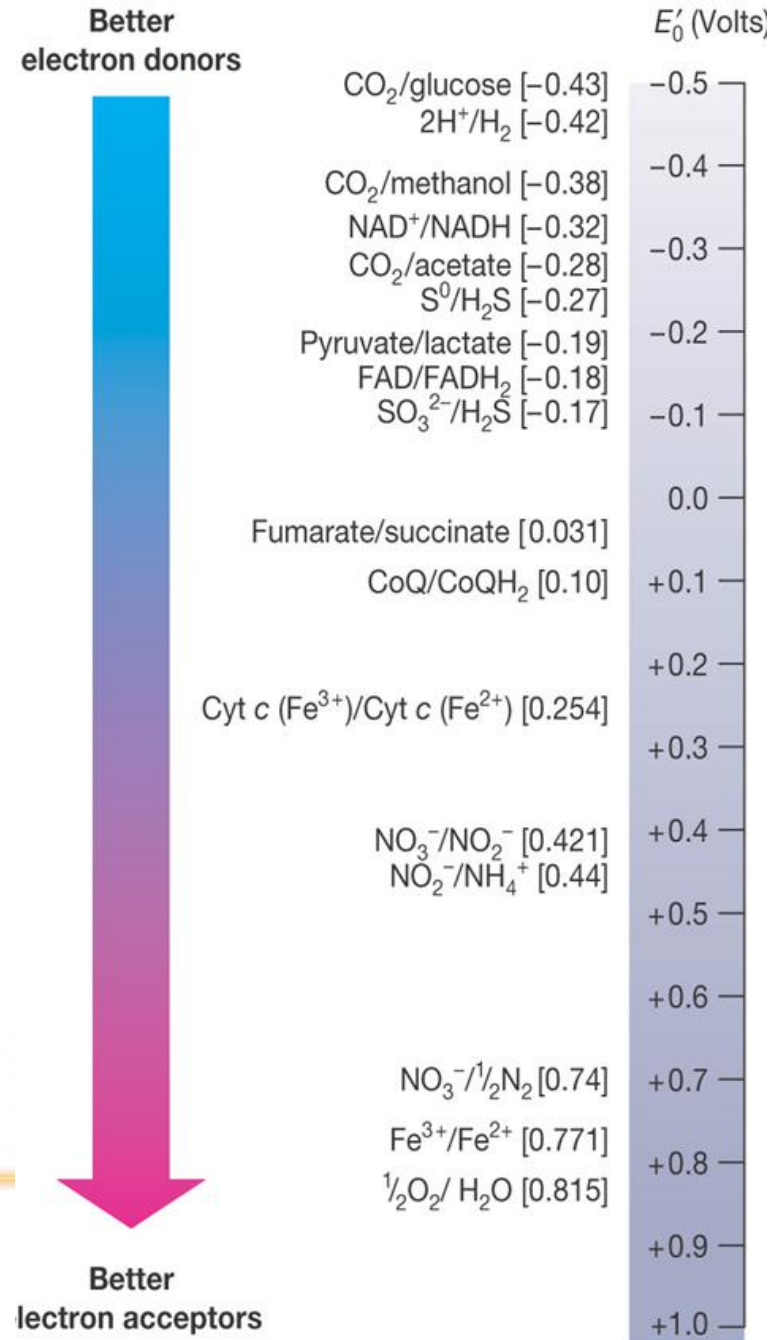
# Amphibolic pathways

- function both as catabolic and anabolic pathways
- important ones
  - Embden-Meyerhof pathway (EMP)
  - Pentose phosphate pathway
  - Tricarboxylic acid (TCA) cycle
- independent regulation



# Anaerobic respiration

- uses electron carriers other than  $O_2$
- generally yields less energy because  $E_0$  of electron acceptor is less positive than  $E_0$  of  $O_2$
- By many bacteria, archaea and some eukaryotic microbes



# Anaerobic respiration

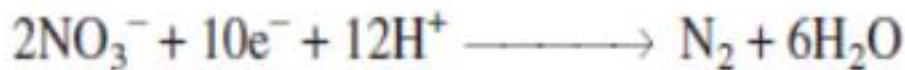
## dissimilatory nitrate reduction 硝酸盐异化还原

- use of nitrate as terminal electron acceptor



## denitrification 反硝化作用

- reduction of nitrate to nitrogen gas



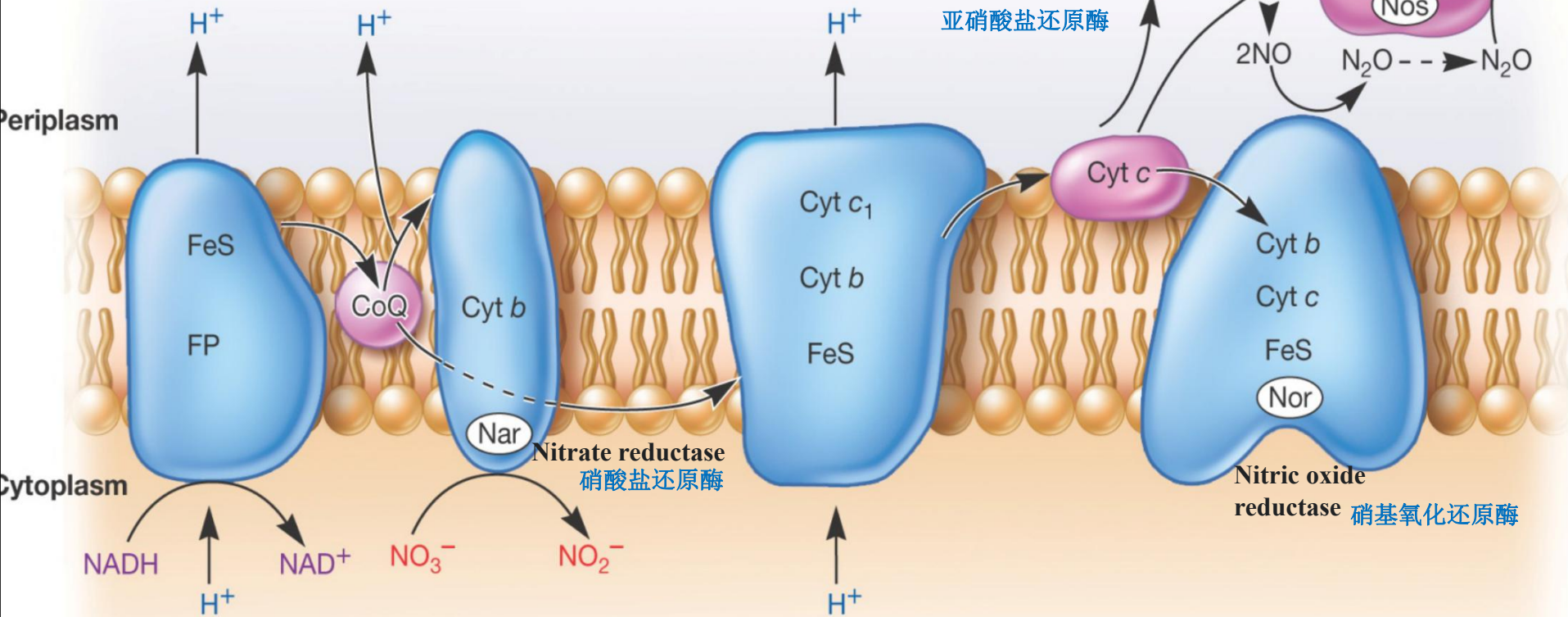
- in soil, causes loss of soil fertility

Table 10.1

Some Electron Acceptors Used in Respiration

	<i>Electron Acceptor</i>	<i>Reduced Products</i>	<i>Examples of Microorganisms</i>
Aerobic	O <sub>2</sub>	H <sub>2</sub> O	All aerobic bacteria, fungi, and protists
Anaerobic	NO <sub>3</sub> <sup>-</sup>	NO <sub>2</sub> <sup>-</sup>	Enteric bacteria
	NO <sub>3</sub> <sup>-</sup>	NO <sub>2</sub> <sup>-</sup> , N <sub>2</sub> O, N <sub>2</sub>	<i>Pseudomonas</i> , <i>Bacillus</i> , and <i>Paracoccus</i>
	SO <sub>4</sub> <sup>2-</sup>	H <sub>2</sub> S	<i>Desulfovibrio</i> and <i>Desulfotomaculum</i>
	CO <sub>2</sub>	CH <sub>4</sub>	Methanogens
	CO <sub>2</sub>	Acetate	Acetogens
	S <sup>0</sup>	H <sub>2</sub> S	<i>Desulfuromonas</i> and <i>Thermoproteus</i>
	Fe <sup>3+</sup>	Fe <sup>2+</sup>	<i>Pseudomonas</i> , <i>Bacillus</i> , and <i>Geobacter</i>
	HAsO <sub>4</sub> <sup>2-</sup>	HAsO <sub>2</sub>	<i>Bacillus</i> , <i>Desulfotomaculum</i> , <i>Sulfurospirillum</i>
	SeO <sub>4</sub> <sup>2-</sup>	Se, HSeO <sub>3</sub> <sup>-</sup>	<i>Aeromonas</i> , <i>Bacillus</i> , <i>Thauerella</i>
	Fumarate	Succinate	<i>Wolinella</i>

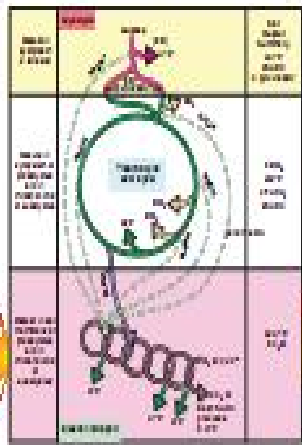
# *Paracoccus denitrificans* ETC used in anaerobic respiration 脱氮副球菌



**Denitrification causes loss of soil fertility, but has important role in ecosystem.**

**Why?**





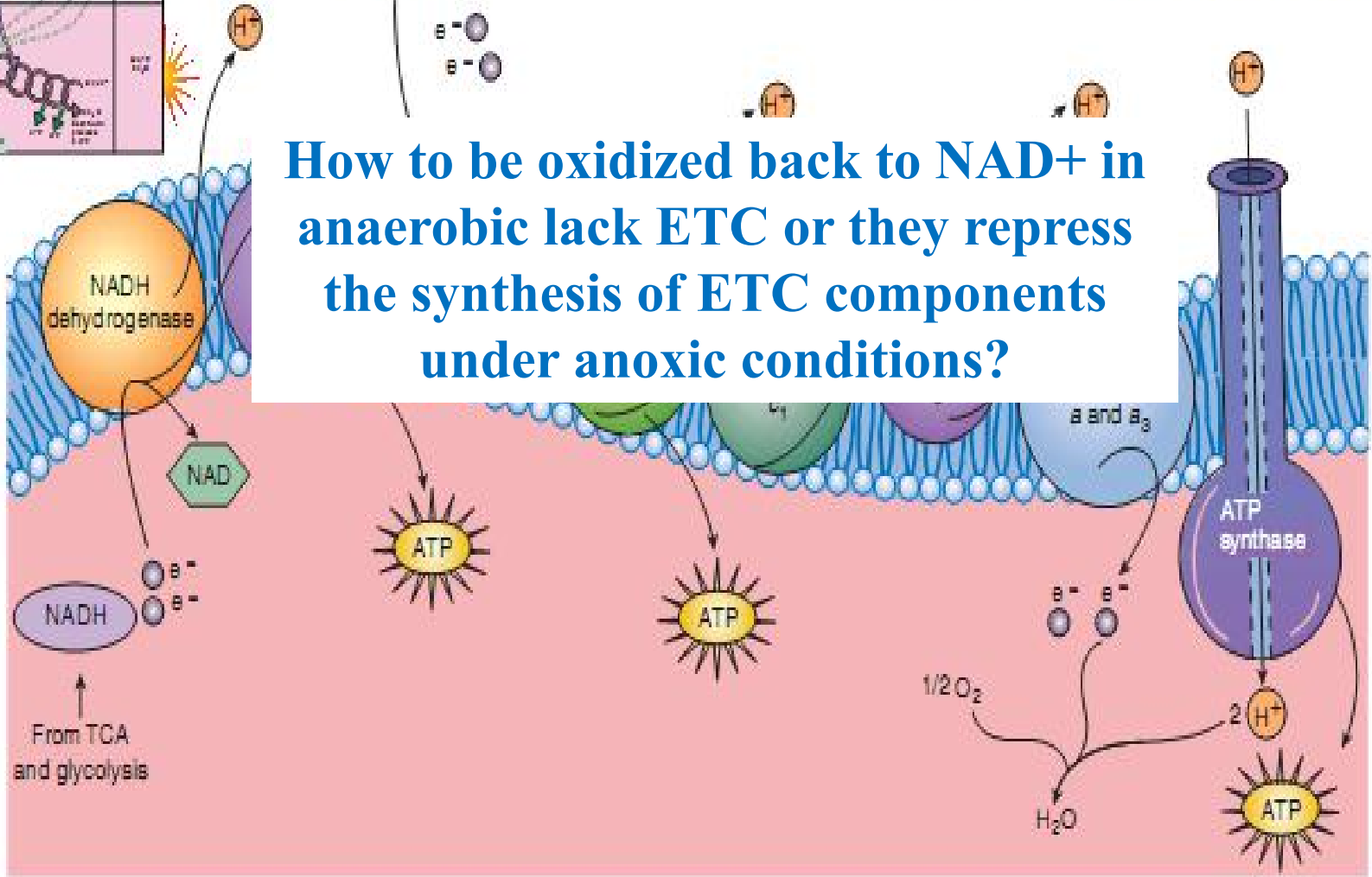
From TCA



□ Outer compartment  
 ■ Inner compartment

For each pair of electrons from NADH:  $3 \text{ ATP} + 1 \text{ H}_2\text{O}$   
 from  $\text{FADH}_2$ :  $2 \text{ ATP} + 1 \text{ H}_2\text{O}$

**How to be oxidized back to  $\text{NAD}^+$  in anaerobic lack ETC or they repress the synthesis of ETC components under anoxic conditions?**

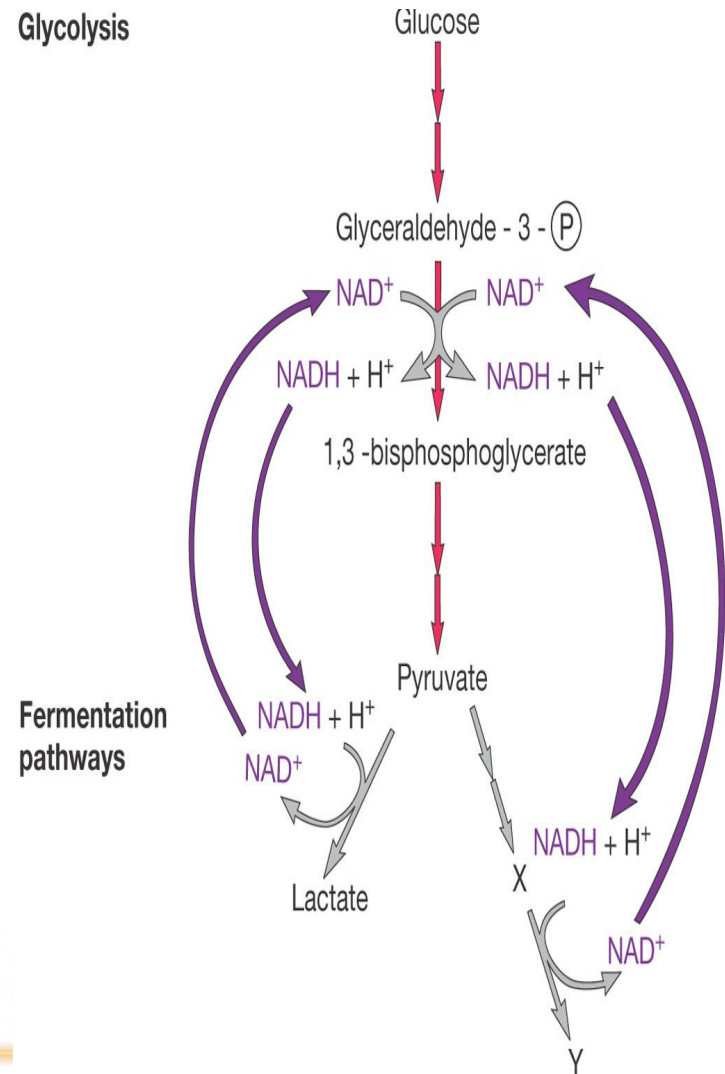


\*Note that the NADH  $\rightleftharpoons$   $\rightleftharpoons$  transfers  $\text{H}^+$  and  $\text{e}^-$  from the first 2 pathways to the 3rd.

# Fermentation

- **NADH is oxidized to NAD<sup>+</sup>**
- **electron acceptor is either pyruvate or**
- **pyruvate or**
- **Oxygen is not needed**
- **ETC not operate, ATP formed by substrate-level phosphorylation**
- **Substrate only partially oxidized**

Glycolysis



## Some common fermentation

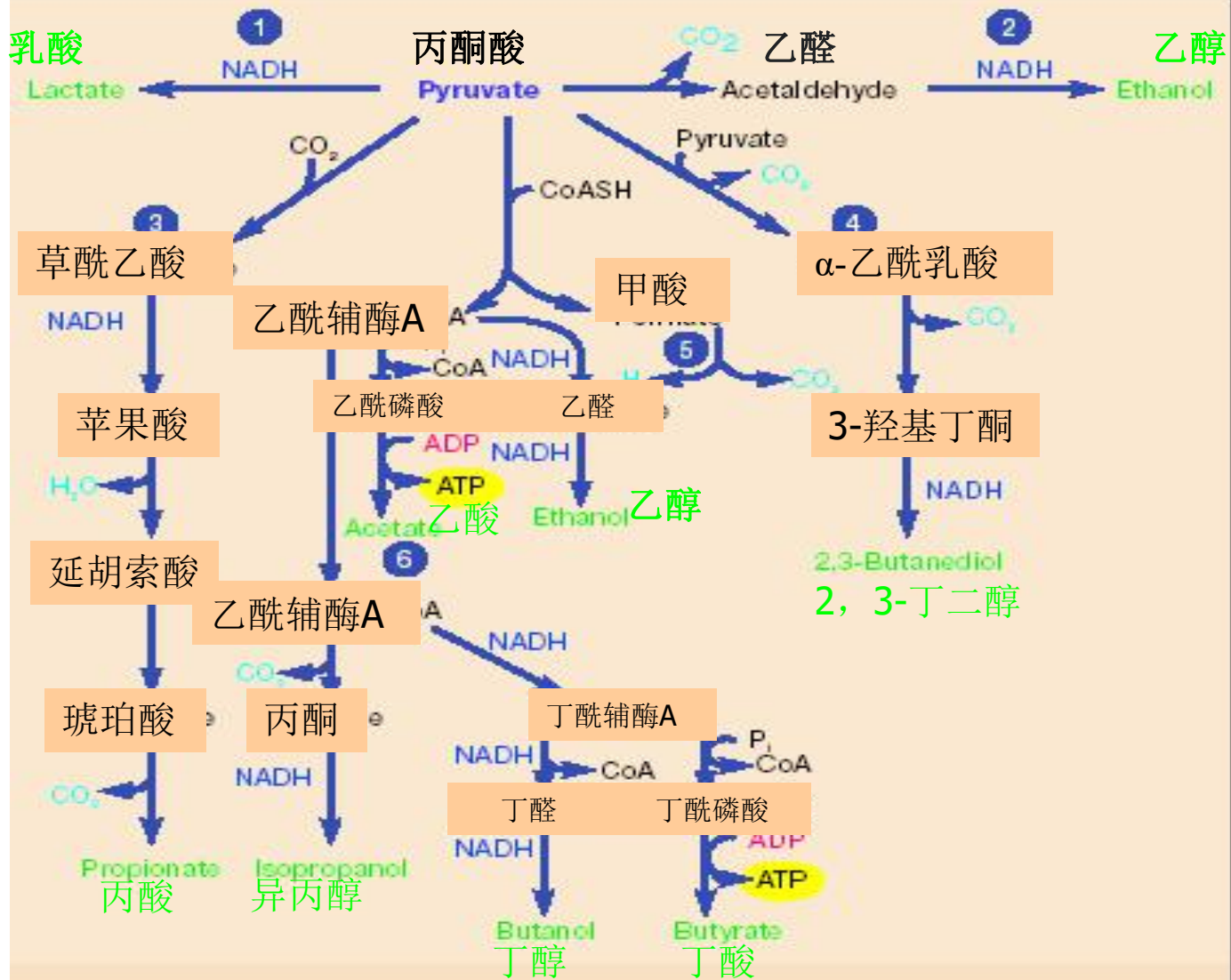
- Homolactic fermentation: Pyr  $\longrightarrow$  lactate 同型乳酸发酵
- Heterolactic fermentation: pyr  $\longrightarrow$  alcohol(yogurt)
- Alcohol fermentation: Glucose  $\longrightarrow$  alcohol+CO<sub>2</sub>
- Mixed acid fermentation: formic, acetic, lactic and succinic acid(e)+alcohol
- Butanediol fermentation: enterobacteriaceae
- Stickland reaction: *Clostridium sporogenes* 生孢梭菌

H donor: Ala; Leu, Ile, Val, Phe, Ser, His, trp

H acceptor: Gly, Pro, Ori, OH-Pro, Arg, trp.

# 发酵类型

一些常见的微生物发酵作用



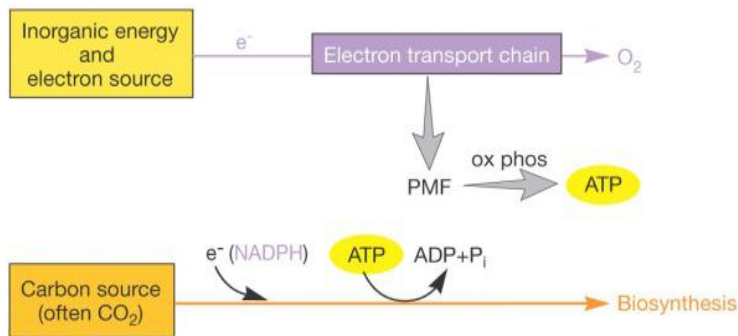
- 1. Lactic acid bacteria (*Streptococcus*, *Lactobacillus*), *Bacillus* 乳酸细菌, 芽孢杆菌
- 2. Yeast, *Zymomonas* 酵母, 发酵单孢菌
- 3. Propionic acid bacteria (*Propionibacterium*) 丙酸细菌 (丙酸杆菌)
- 4. *Enterobacter*, *Serratia*, *Bacillus* 肠杆菌, 赛氏杆菌, 芽孢杆菌
- 5. Enteric bacteria (*Escherichia*, *Enterobacter*, *Salmonella*, *Proteus*) 肠道杆菌
- 6. *Clostridium* 梭菌

How about of the  
chemolithotrophy?

---

# Chemolithotrophic fueling processes

- **Electrons source - an inorganic molecule**
  - transferred to terminal electron acceptor (usually  $O_2$ ) by ETC
- **ATP synthesized by oxidative phosphorylation**
- **Carbon source- $CO_2$**



Reaction	$\Delta G^{\circ\prime}$ (kcal/mole) <sup>a</sup>
$H_2 + 1/2 O_2 \rightarrow H_2O$	-56.6
$NO_2^- + 1/2 O_2 \rightarrow NO_3^-$	-17.4
$NH_4^+ + 1 1/2 O_2 \rightarrow NO_2^- + H_2O + 2H^+$	-65.0
$S^0 + 1 1/2 O_2 + H_2O \rightarrow H_2SO_4$	-118.5
$S_2O_3^{2-} + 2O_2 + H_2O \rightarrow 2SO_4^{2-} + 2H^+$	-223.7
$2Fe^{2+} + 2H^+ + 1/2 O_2 \rightarrow 2Fe^{3+} + H_2O$	-11.2

<sup>a</sup> The  $\Delta G^{\circ\prime}$  for complete oxidation of glucose to  $CO_2$  is -686 kcal/mole. A kcal is equivalent to 4.184 kJ.

**Much less energy is available from oxidation of inorganic molecules than glucose oxidation due to more positive redox potentials.**

$$P/O \approx 1.0$$

# Three major groups of chemolithotrophs

- oxidize hydrogen (several bacteria and archaea)



- sulfur-oxidizing microbes

- hydrogen sulfide ( $\text{H}_2\text{S}$ ), sulfur ( $\text{S}^0$ ), thiosulfate ( $\text{S}_2\text{O}_3^{2-}$ ) 硫代亚硫酸盐

- oxidize ammonia 氨 to nitrate nitrifying bacteria 硝化细菌  
bacterial and archaeal species

- have ecological importance

Bacteria	Electron Donor	Electron Acceptor	Products
<i>Alcaligenes</i> , <i>Hydrogenophaga</i> , and <i>Pseudomonas</i> spp.	$\text{H}_2$	$\text{O}_2$	$\text{H}_2\text{O}$
<i>Nitrobacter</i>	$\text{NO}_2^-$	$\text{O}_2$	$\text{NO}_3^-$ , $\text{H}_2\text{O}$
<i>Nitrosomonas</i>	$\text{NH}_4^+$	$\text{O}_2$	$\text{NO}_2^-$ , $\text{H}_2\text{O}$
<i>Thiobacillus denitrificans</i>	$\text{S}^0$ , $\text{H}_2\text{S}$	$\text{NO}_3^-$	$\text{SO}_4^{2-}$ , $\text{N}_2$
<i>Acidithiobacillus ferrooxidans</i>	$\text{Fe}^{2+}$ , $\text{S}^0$ , $\text{H}_2\text{S}$	$\text{O}_2$	$\text{Fe}^{3+}$ , $\text{H}_2\text{O}$ , $\text{H}_2\text{SO}_4$

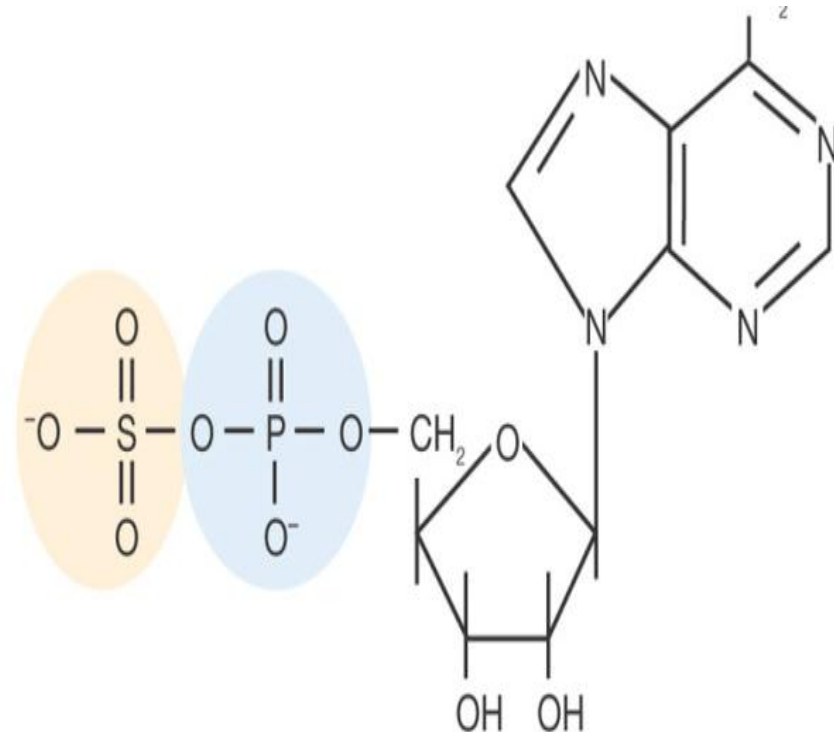
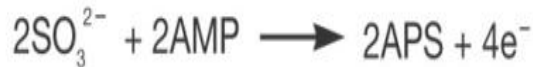
# Sulfur-oxidizing bacteria

ATP can be synthesized by both oxidative phosphorylation and substrate-level phosphorylation

## (a) Direct oxidation of sulfite



## (b) Formation of adenosine 5'-phosphosulfate 腺苷酰硫酸的形成



(c) Adenosine 5'-phosphosulfate





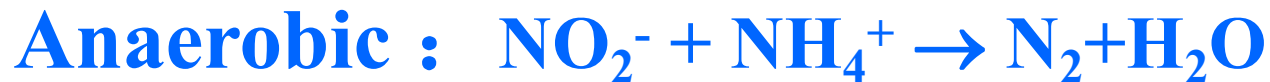
# Nitrifying bacteria example

oxidize ammonia to nitrate  
requires 2 different genera



*Nitrobacte*

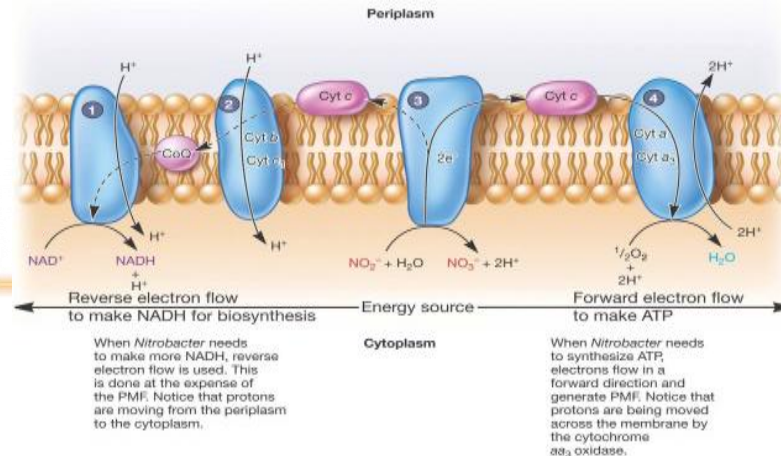
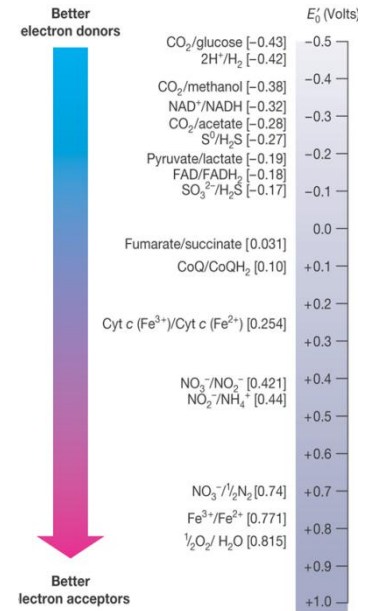
*Planctomycetes* 浮霉状菌



Anaerobic ammoniooxidation-anammoxosome

# \*Reverse electron flow by chemolithotrophs

- Calvin cycle requires NAD(P)H as electron source for fixing CO<sub>2</sub>
- many energy sources used by chemolithotrophs have E<sub>0</sub> more positive than NAD<sup>+</sup>(P)/NAD(P)H
- use reverse electron flow to generate NAD(P)H



## **\*Metabolic flexibility of chemolithotrophs**

- **many switch from chemolithotrophic metabolism to chemoorganotrophic metabolism**
- **many switch from autotrophic metabolism (via Calvin cycle) to heterotrophic metabolism**

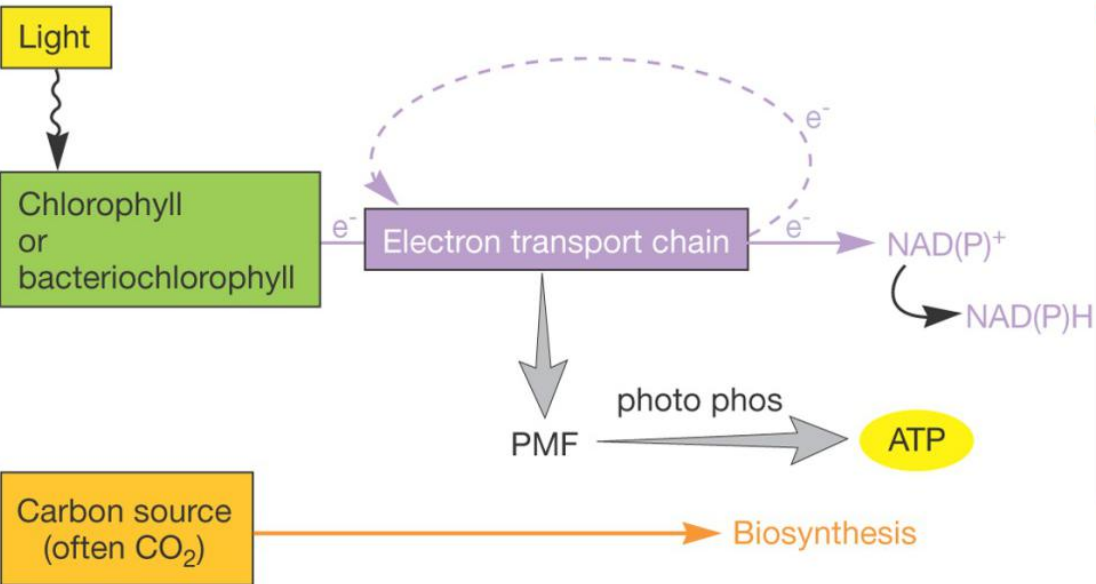
**How about**

**the fueling reactions of phototrophs?**

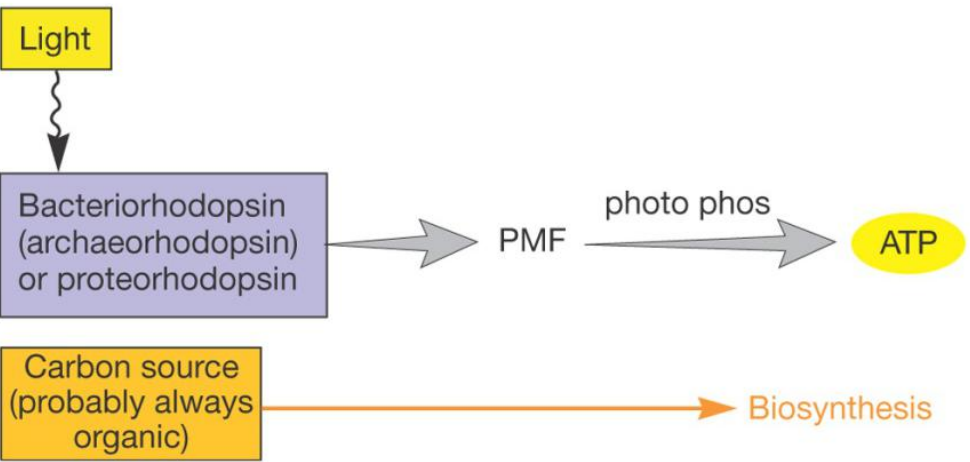
# Phototrophy

- **photosynthesis**
    - energy from light trapped and converted to chemical energy
    - a two-part process
      - light reactions in which light energy is trapped and converted to chemical energy
      - dark reactions in which the energy produced in the light reactions is used to reduce  $\text{CO}_2$  and synthesize cell constituents(see 12.3)
-

**Chlorophyll-based phototrophy**



**Rhodopsin-based phototrophy** 视紫质



**Table 10.5** Diversity of Phototrophic Organisms

<i>Eukaryotes</i>	Plants; multicellular green, brown and red algae; unicellular protists (e.g., euglenoids, dinoflagellates, diatoms)
<i>Bacteria</i>	Cyanobacteria, green sulfur bacteria, green nonsulfur bacteria, purple sulfur bacteria, purple nonsulfur bacteria, heliobacteria, acidobacteria
<i>Archaea</i>	Halophiles

**Over half the photosynthesis on Earth is carried out by microorganisms!**

# Oxygenic photosynthesis 生氧光合作用

- photosynthetic eukaryotes and cyanobacteria 蓝细菌
- oxygen is generated and released into the environment
- most important pigments are chlorophylls 叶绿素

**Table 10.6** Properties of Chlorophyll-Based Photosynthetic Systems

Property	Eukaryotes	Cyanobacteria	Green Bacteria, Purple Bacteria, Heliobacteria, and Acidobacteria
Photosynthetic pigment	Chlorophyll <i>a</i>	Chlorophyll <i>a</i>	Bacteriochlorophyll
Number of photosystems	2	2 <sup>a</sup>	1
Photosynthetic electron donors	H <sub>2</sub> O	H <sub>2</sub> O	H <sub>2</sub> , H <sub>2</sub> S, S, organic matter
O <sub>2</sub> production pattern	Oxygenic	Oxygenic <sup>b</sup>	Anoxygenic
Primary products of energy conversion	ATP + NADPH	ATP + NADPH	ATP
Carbon source	CO <sub>2</sub>	CO <sub>2</sub>	Organic or CO <sub>2</sub>

<sup>a</sup> A recently discovered cyanobacterium lacks photosystem II.

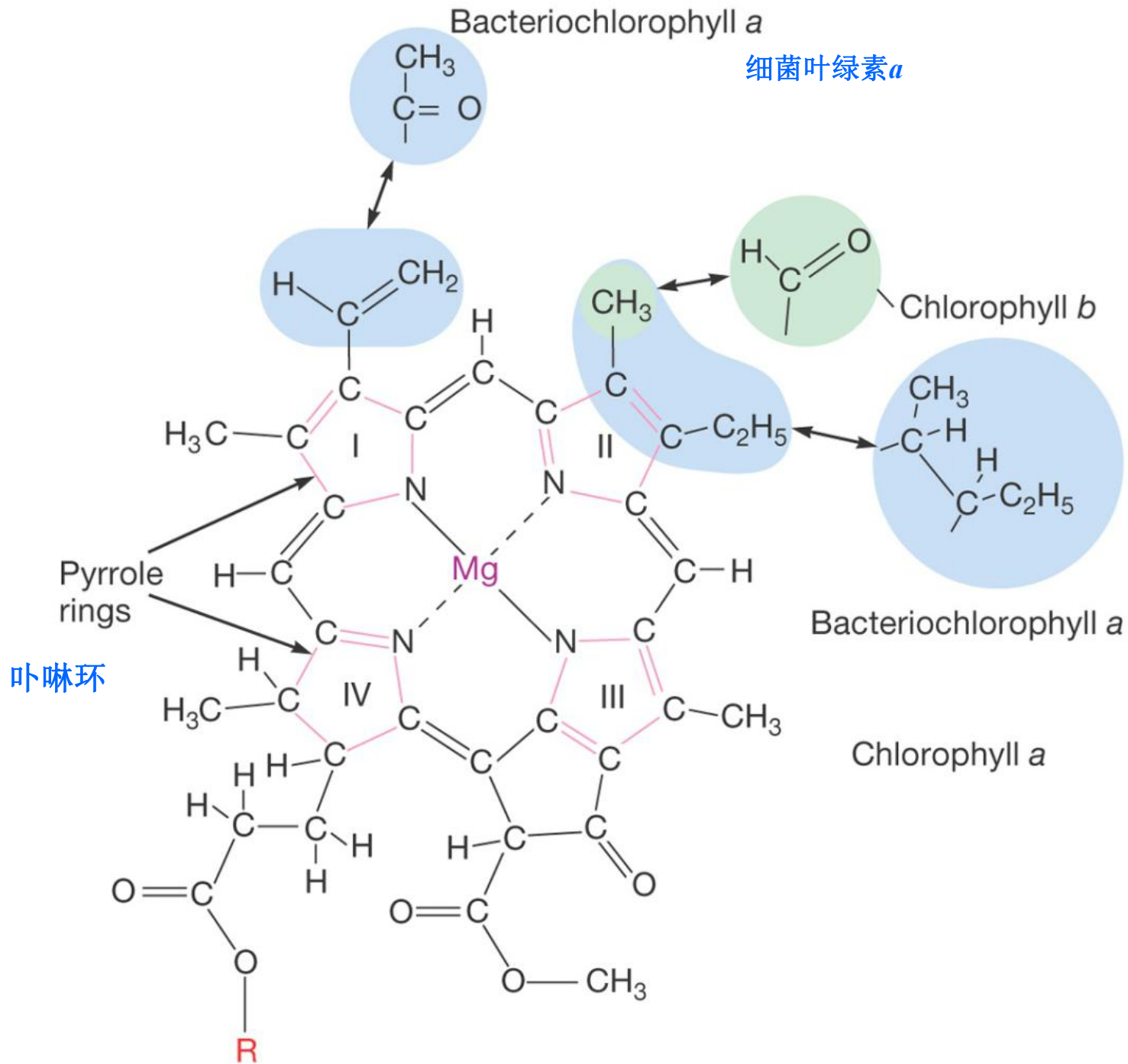
<sup>b</sup> Some cyanobacteria can function anoxygenically under certain conditions. For example, *Oscillatoria* can use H<sub>2</sub>S as an electron donor instead of H<sub>2</sub>O.

# Oxygenic photosynthesis 生氧光合作用

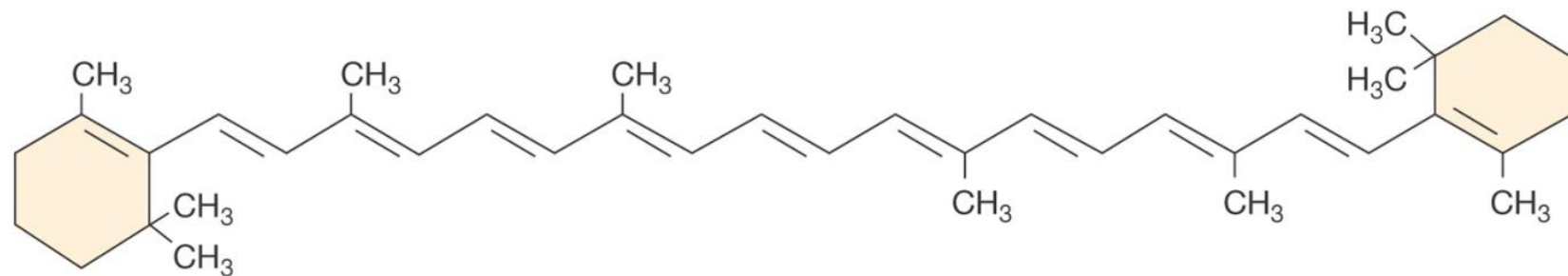
- **Chlorophylls 叶绿素**
  - major light-absorbing pigments
  - different chlorophylls have different absorption peaks
- **accessory pigments 辅助色素**
  - transfer light energy to chlorophylls
  - e.g., carotenoids (类胡萝卜素) and  
phycobiliproteins 藻胆 (色素) 蛋白
  - accessory pigments absorb different wavelengths of light than chlorophylls

Bacteriochlorophyll a

细菌叶绿素a

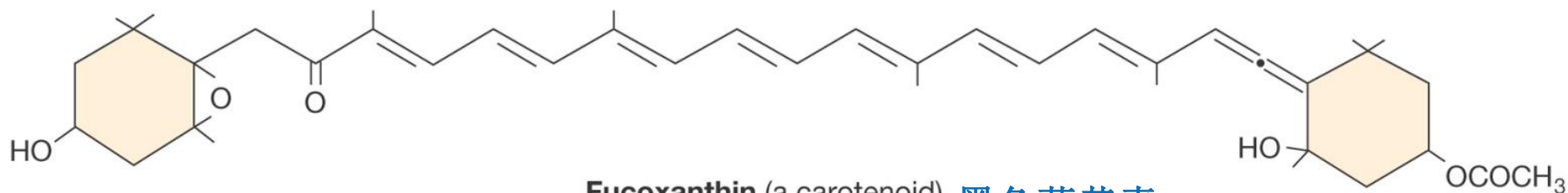






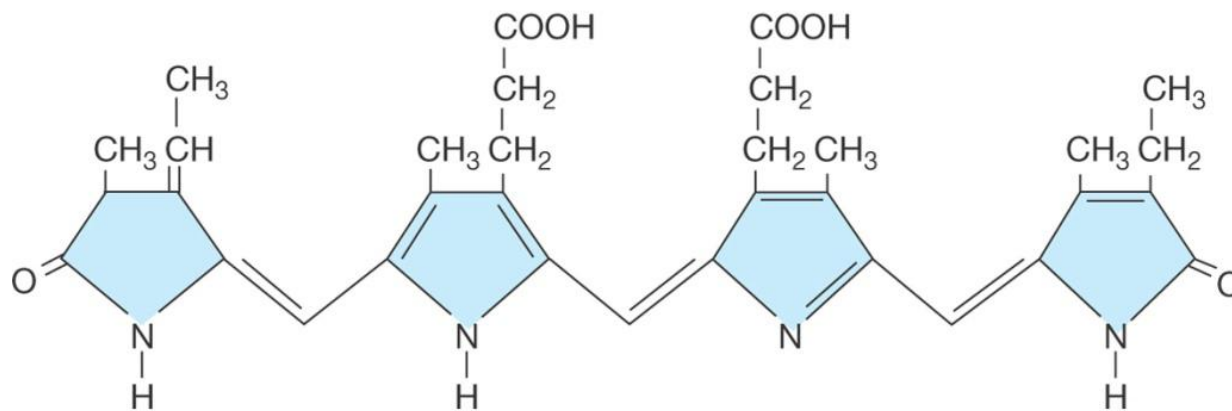
**β-Carotene** (a carotenoid)

**β-胡萝卜素**



**Fucoxanthin** (a carotenoid)

**墨角藻黄素**



**Phycocyanobilin**

**藻蓝素**

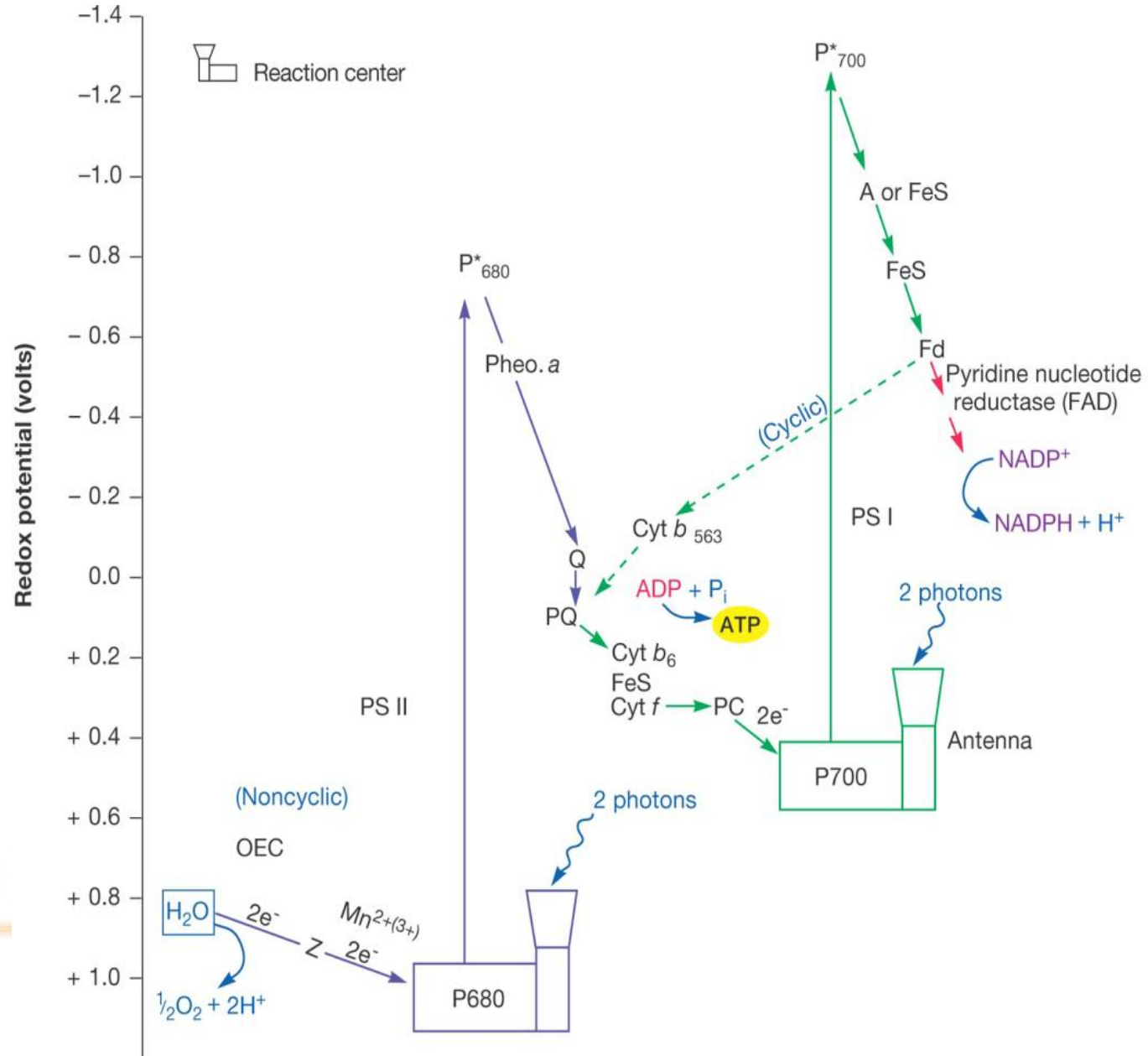
# Organization of pigments

- **Antennas** 天线色素
  - highly organized arrays of chlorophylls and accessory pigments
  - captured light transferred to special reaction-center chlorophyll
    - directly involved in photosynthetic electron transport
- **photosystems**
  - antenna and its associated reaction-center chlorophyll
  - **PS-P700** 光合系统I/ **PSII-P680** 光合系统II
- **electron flow → PMF → ATP**

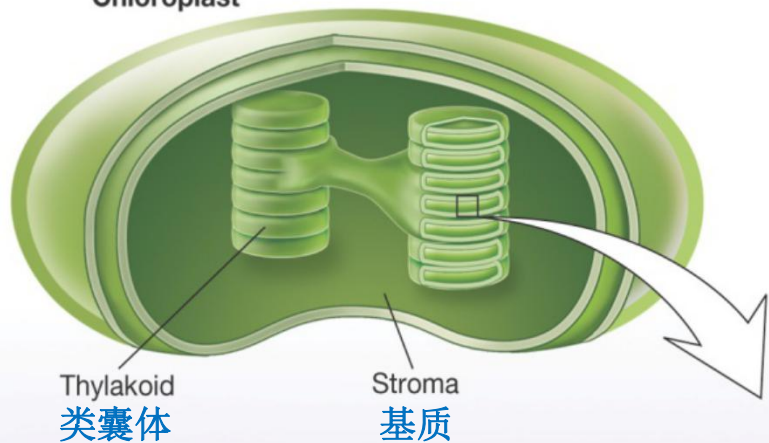
# Oxygenic photosynthesis

Cyclic electron flow – ATP made (cyclic photophosphorylation 环式光合磷酸化)

Noncyclic electron flow – ATP + NADPH made (noncyclic photophosphorylation)



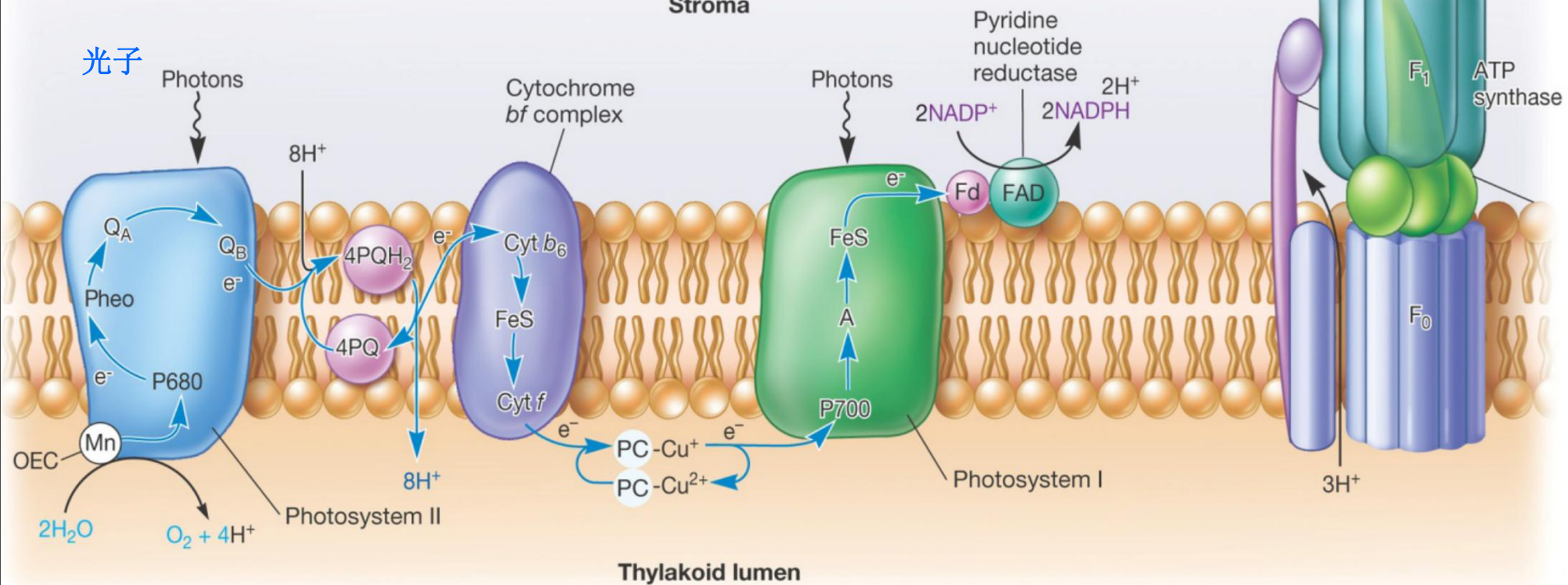
# Chloroplast



## Stroma

光子

Photons



Thylakoid lumen

Thylakoid lumen

2H<sub>2</sub>O

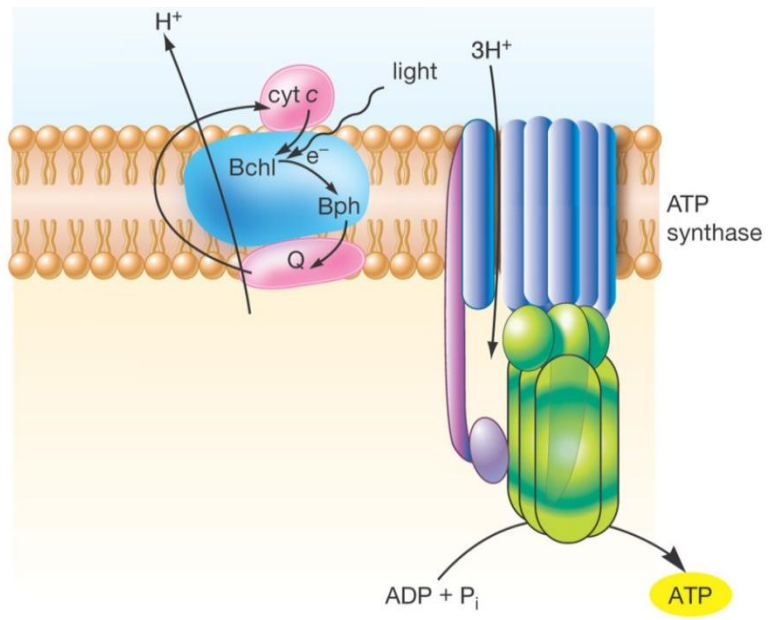
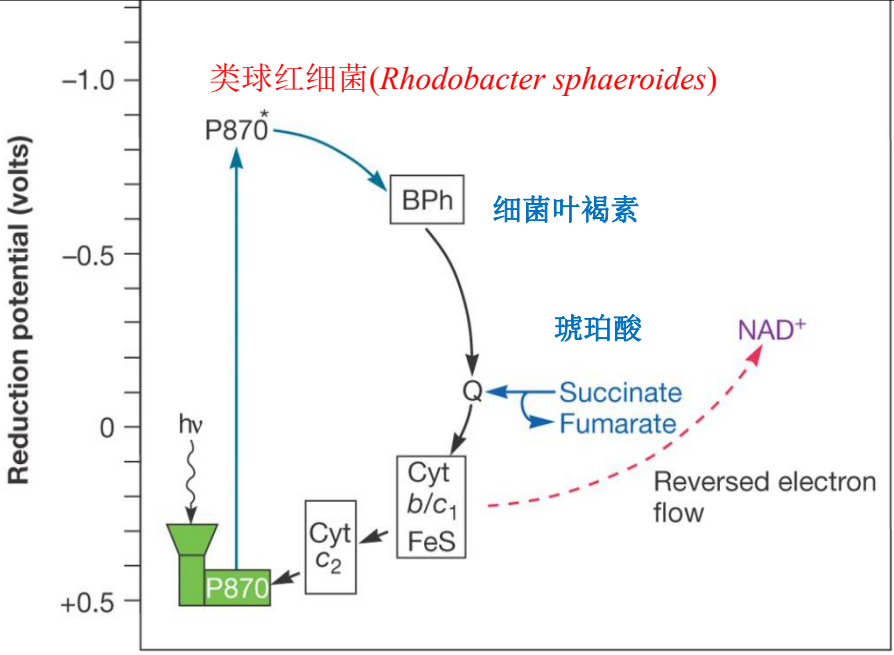
O<sub>2</sub> + 4H<sup>+</sup>

Photosystem II

# Anoxygenic photosynthesis

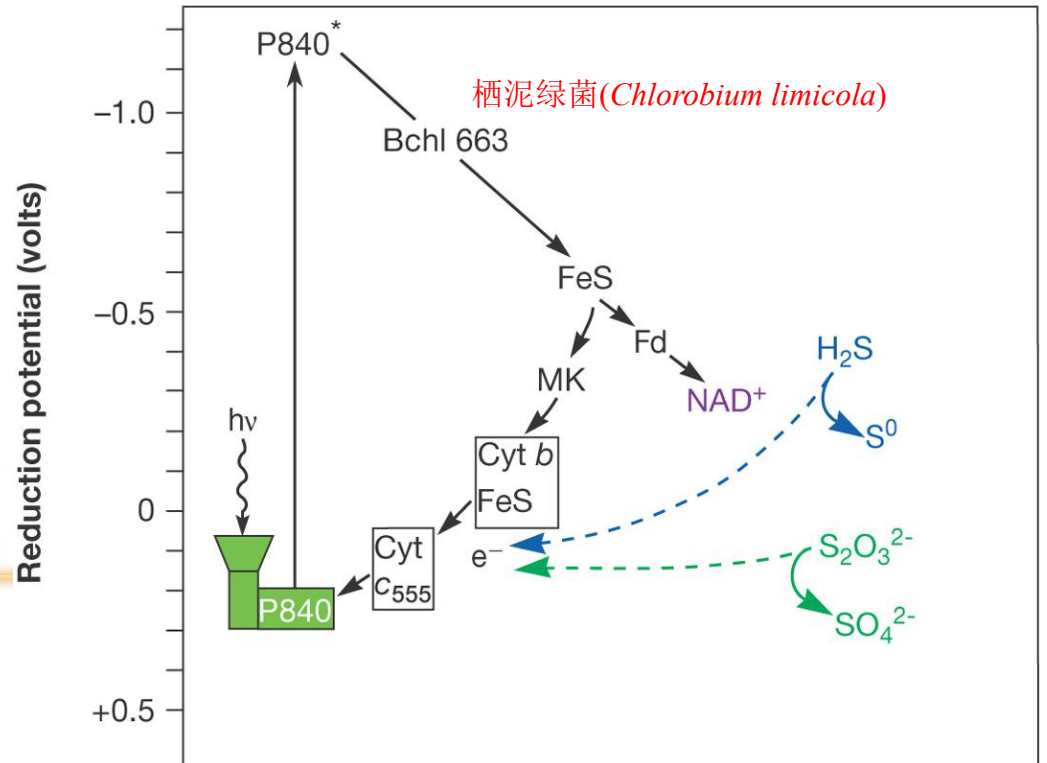
非产氧光合作用

- **H<sub>2</sub>O not used as an electron source; therefore O<sub>2</sub> is not produced**
  - **only one photosystem involved(anaerobe)**
  - **uses bacteriochlorophylls细菌叶绿素 and mechanisms to generate reducing power**
  - **carried out by phototrophic green bacteria, phototrophic purple bacteria, and heliobacteria**
-



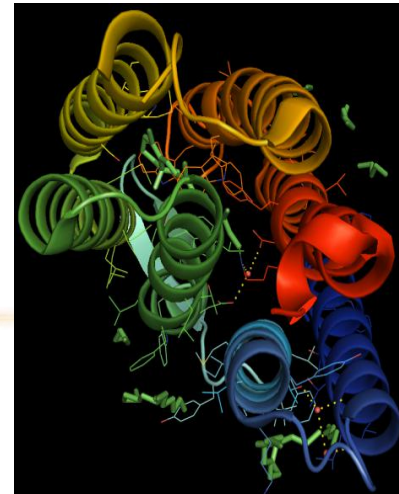
**How to produce reducing power?**

1. Hydrogenase
2. Reverse electron
3. Electron draw off (noncyclic-)



# Bacteriorhodopsin 细菌视紫红质 -based phototrophy (Halophilie)

- some archaea use a type of phototrophy that involves bacteriorhodopsin, a membrane protein which functions as a light-driven proton pump 光驱动质子泵
- a proton motive force is generated
- an electron transport chain is not involved



# • Summary

- Catabolism is a fueling process which included in respiration and fermentation. A big difference of R and F is energy production and electron acceptor.
  - three common routes-glycolysis
    - Embden-Meyerhof pathway
    - pentose phosphate pathway
    - Entner-Duodoroff pathway(*agrobacterium, G<sup>-</sup>*)
  - TCA cycle oxidizes acetyl-CoA to CO<sub>2</sub> and forms one GTP or ATP, three NADH, and one FADH<sub>2</sub> per acetyl-CoA. It also generates several precursor metabolites.
-



# Discussion

1. Why might it be desirable for a microorganism with the Embden-Meyerhof pathway and the TCA cycle also to have the pentose phosphate pathway?
2. Calculate the ATP yield when glucose is catabolized completely to six  $\text{CO}_2$  by a eukaryotic microbe. How does this value compare to the ATP yield observed for a bacterium?
3. What is denitrification? Why do farmers dislike this process? but it has important role in ecosystem. Why?
4. When bacteria carry out fermentation, only a few reactions of the TCA cycle operate. What purpose do you think these reactions might serve? Why are some parts of the cycle shut down?
5. Why can hydrogen-oxidizing bacteria and archaea donate electrons to  $\text{NAD}^+$ , whereas sulfur- and ammonia-oxidizing bacteria and archaea cannot? How do they get NADH?
6. Compare and contrast anoxygenic phototrophy and oxygenic photosynthesis. How do these two types of phototrophy differ from rhodopsin-based phototrophy?