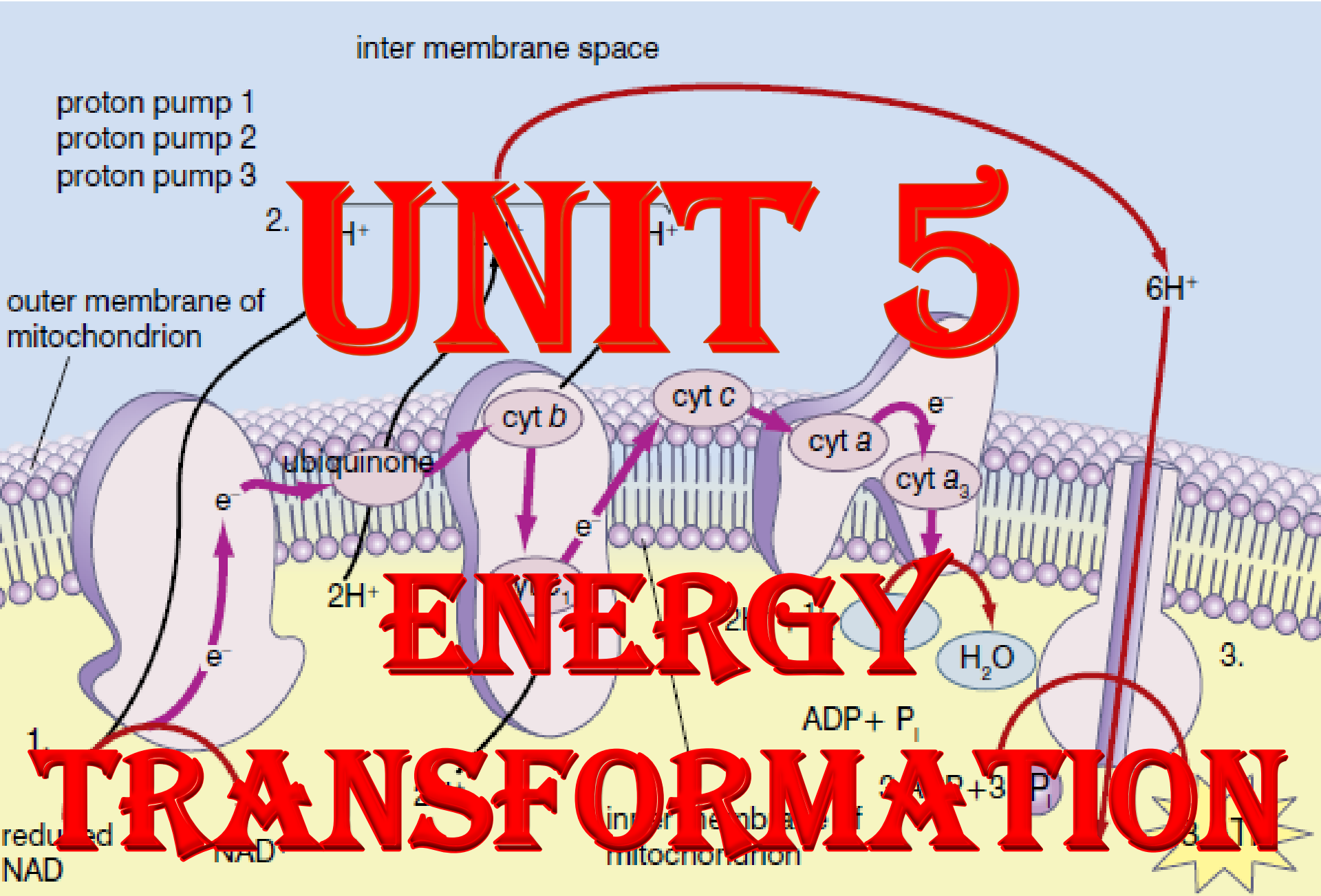


UNIT 5 ENERGY TRANSFORMATION

5.1 Respiration

- **The process of releasing energy(ATP) from the food.**

What is the ATP molecule like?

- ATP is **A**denosine **T**ri-**P**hosphate.
- All nucleotides contain:

I. a nitrogenous base (this one contains adenine)

II. a pentose sugar

III. a phosphate group

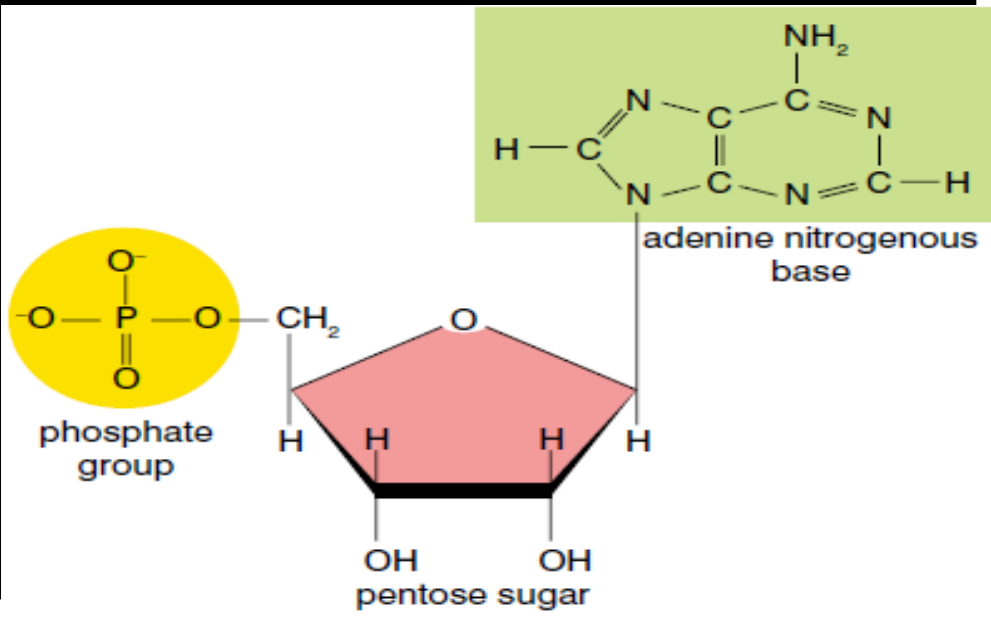


Figure 5.1 A nucleotide containing the nitrogenous base adenine

- The ATP molecule is based on this nucleotide.
- ATP is some times described as a **phosphorylated nucleotide.**
- When you 'phosphorylate' a molecule, you add one or more phosphate groups to it.
- ATP is essentially the adenine nucleotide with two extra phosphate groups added on - making three in all.
- Adding the extra phosphates requires energy, particularly when the third phosphate is added.

- As a result, energy is stored in the ATP molecule and when the bonds that hold this third phosphate in place are broken, the energy is released again.
- When the third phosphate is removed from ATP, we are still left with a phosphorylated nucleotide, but this one only has two nucleotides.
- It is Adenosine Di-Phosphate - or ADP.

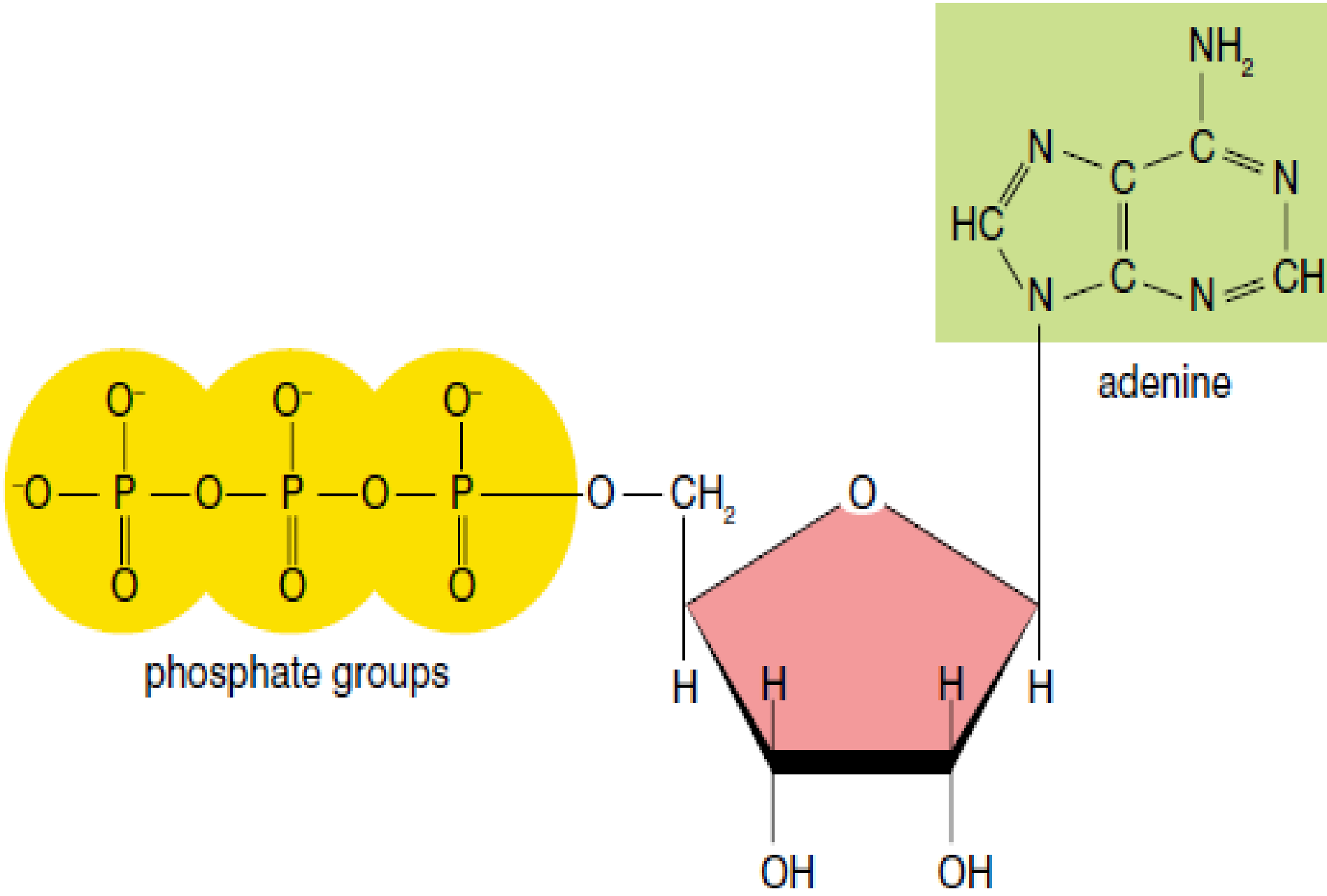


Figure 5.2 The structure of the ATP molecule

- The phosphate group that is split off is usually written as P_i.
- The energy to form ATP can come from 'sunlight or from food'.
- This is because ATP is formed in both photosynthesis and in cellular respiration.

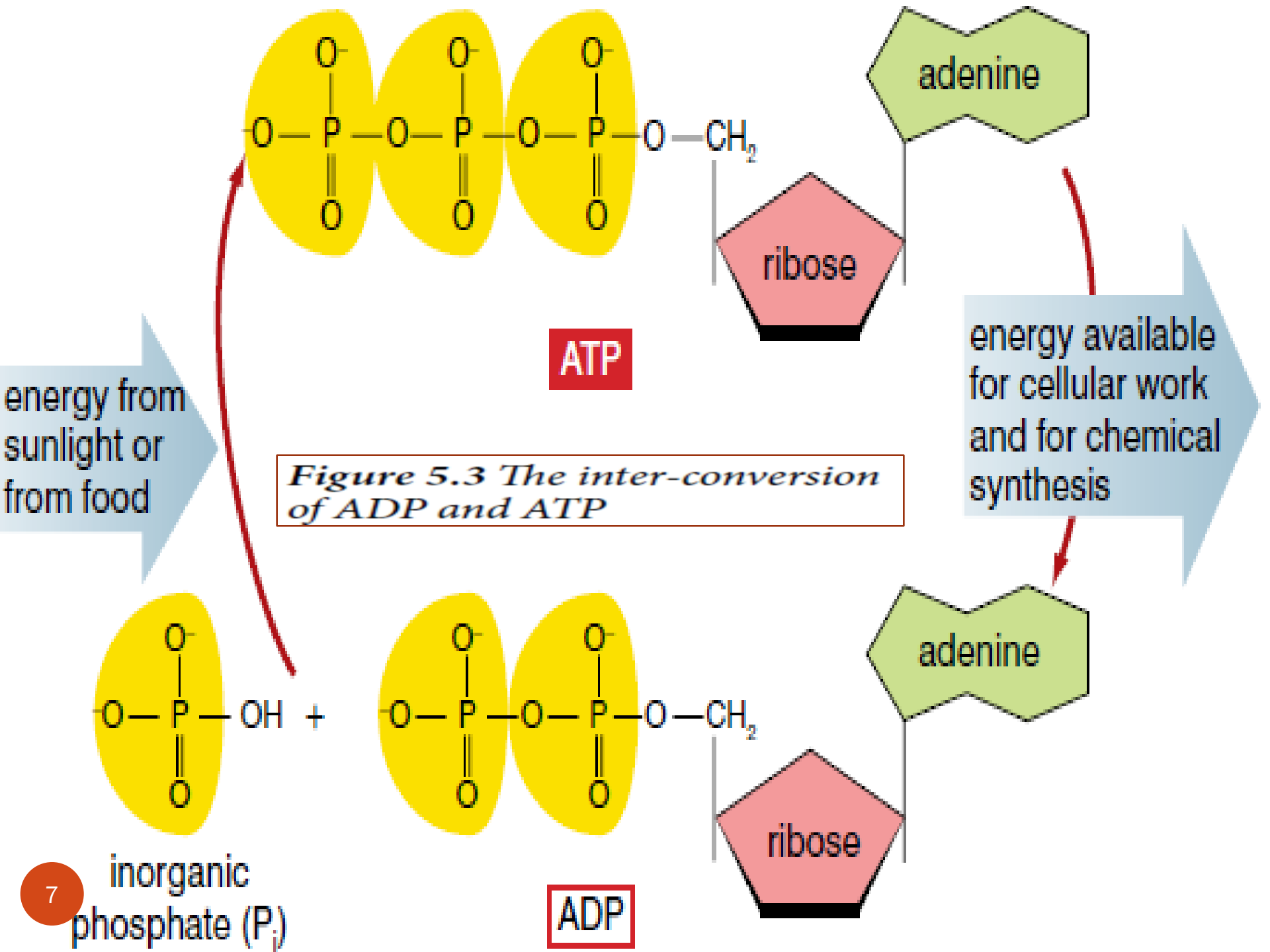


Figure 5.3 The inter-conversion of ADP and ATP

How is ATP adapted to its role as an energy transfer molecule in cells?

- Sunlight energy cannot be used directly by plants to 'drive' the synthesis of proteins - or any other molecules.
- The same applies to the energy held in a glucose molecule.
- These two energy sources must be used to produce ATP, which is used to transfer the energy to the relevant cellular process.
- We say that it is **coupled** to these processes.

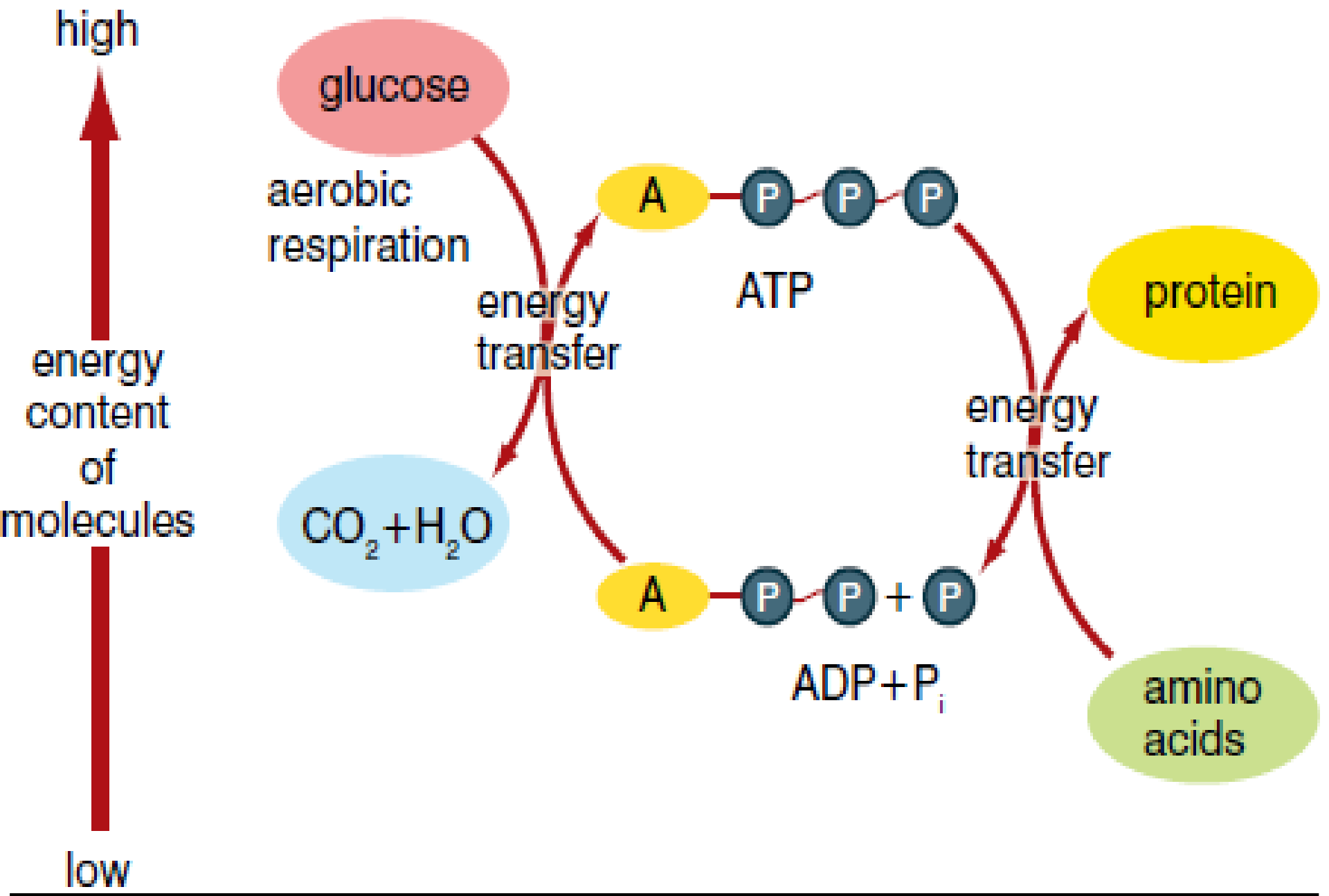


Figure 5.4 Coupled reactions transfer energy in cells

- **phosphorylated nucleotide** the adding of one or more phosphate groups to a molecule
- **adenosine di-phosphate** removing the third phosphate from ATP leaves a phosphorylated nucleotide with two nucleotides
- ATP is adapted to this role because it:

a. **releases energy in relatively small amounts** that are closely matched to the amounts of energy required in many biological processes occurring inside cells
b. **releases energy in a single-step hydrolysis reaction**, so the energy can be released quickly
c. **is able to move around the cell easily**, but cannot escape from the cell

- The following processes are examples of processes that require energy from ATP:

1. the synthesis of macromolecules - such as proteins
2. active transport across a plasma membrane
3. muscle contraction
4. conduction of nerve impulses
5. the initial reactions of respiration (the later reactions release energy from glucose to form more ATP)

- *ATP synthase* is the enzyme involved in the formation of ATP

How is ATP produced in a cell?

- It involves ADP and P_i joining to form ATP and this requires an input of energy.
- The formation of ATP involves an enzyme called ***ATP synthase***.
- The ATP synthase is in one of the membranes of a mitochondrion and it could be in a membrane in a chloroplast.

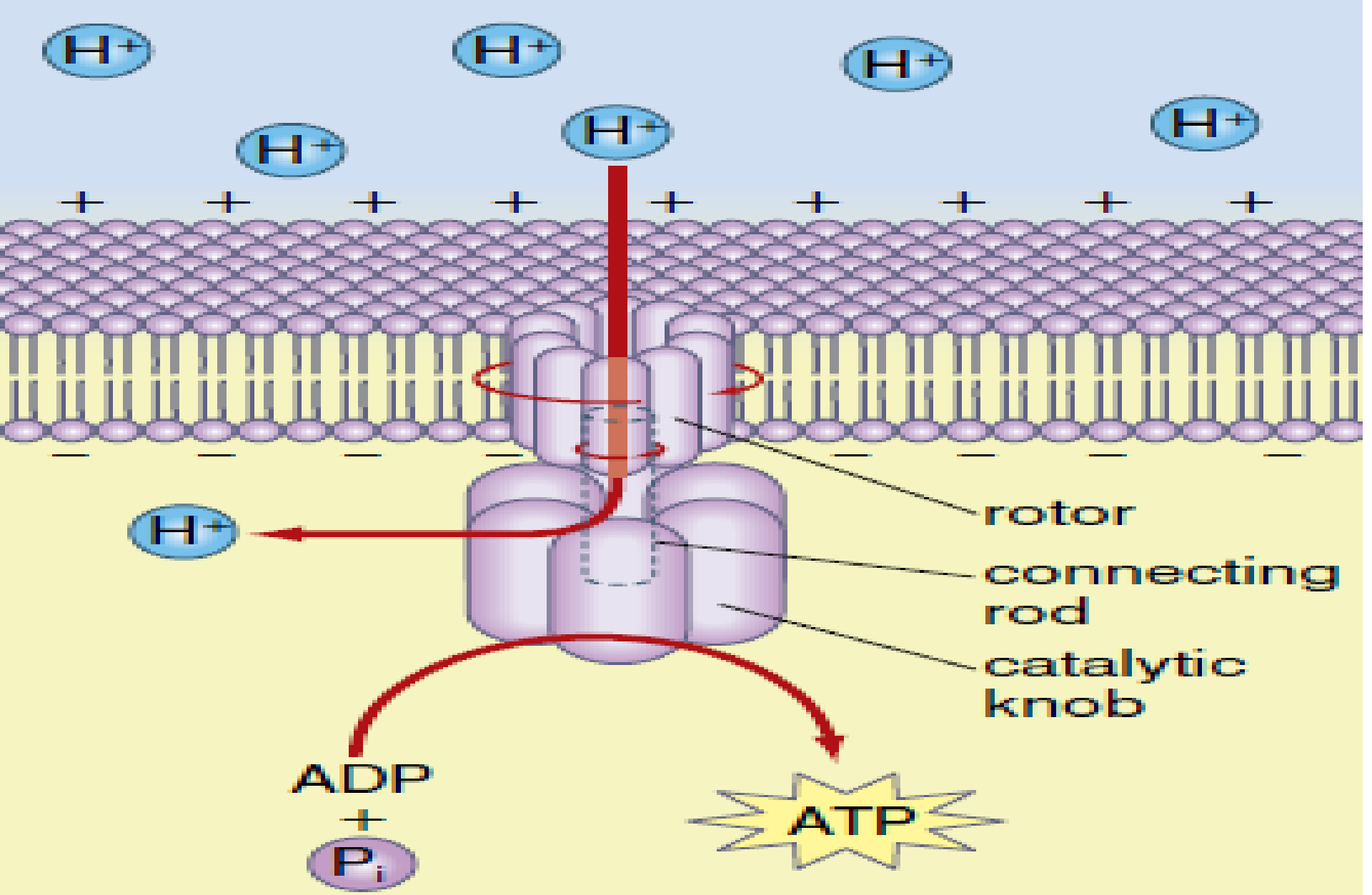


Figure 5.5 The structure of ATP synthase

- When the rotor is made to spin by hydrogen ions passing through it, the energy of the spinning is used to activate sites in the catalytic knob that convert ADP and P_i to ATP.
- In both photosynthesis and aerobic respiration, many of the reactions generate the hydrogen ions that will pass through the ATP synthase to produce ATP.

How is ATP produced in respiration?

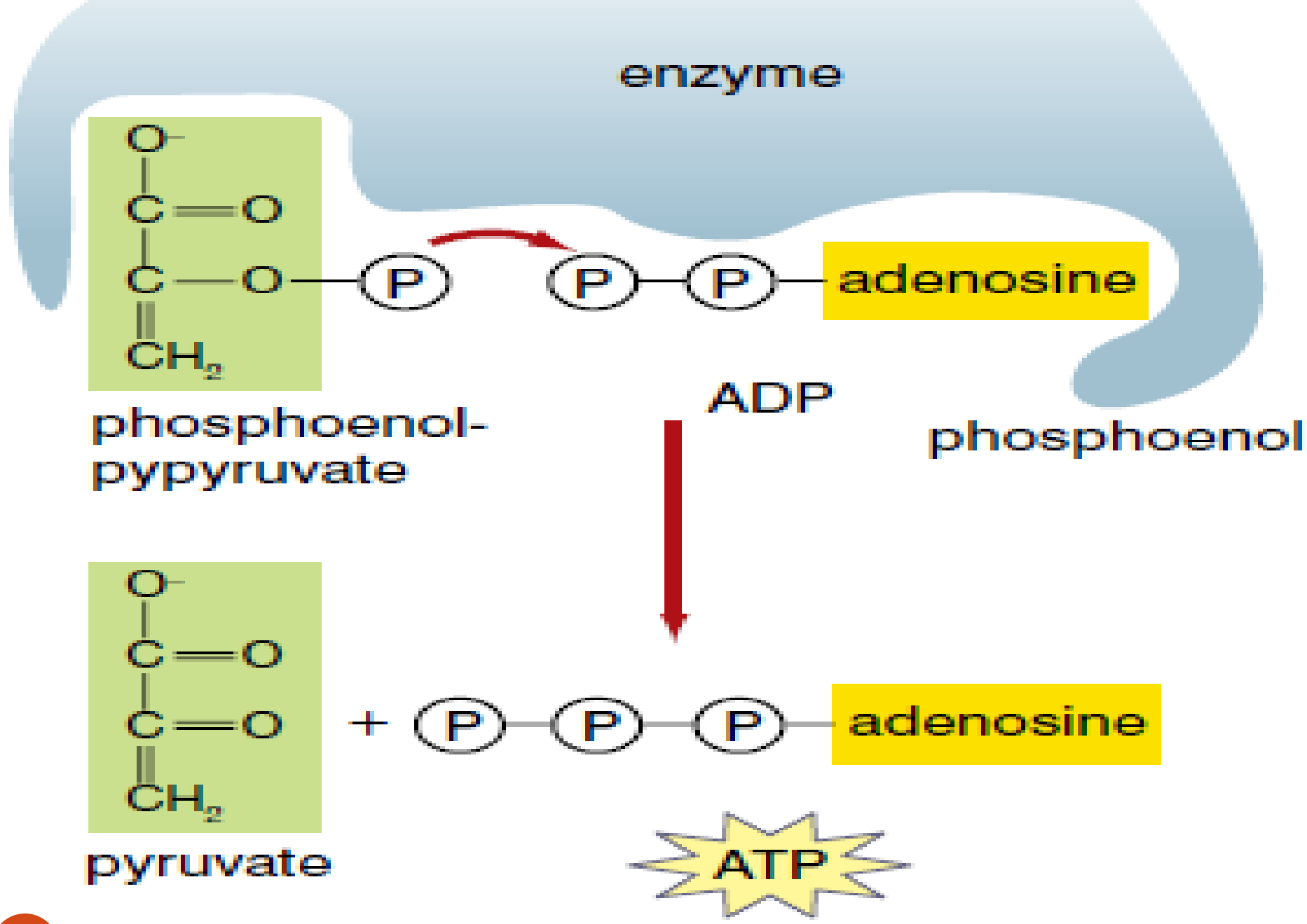
- There are two main pathways by which respiration can produce ATP:

a. the **aerobic pathway** (aerobic respiration) - this requires the presence of oxygen, and

b. the **anaerobic pathway** (anaerobic respiration and fermentation)– this can take place in the absence of oxygen.

How is ATP produced in aerobic respiration?

- A small amount of ATP is produced in a way that does not involve the ATP synthase molecule; this method is called substrate level phosphorylation.
- In this process, another molecule such as phosphoenol pyruvate is able to transfer a phosphate group directly to ADP.
- There is *no ATP synthase* involved and *no Pi*.



gure 5.6 Substrate level
phosphorylation

- This process only produces a relatively small amount of the ATP produced in aerobic respiration – about 10% of the total ATP produced in aerobic respiration.
- As about 90% of the ATP produced in aerobic respiration is produced by *ATP synthase*, many of the reactions of this process are geared to producing the hydrogen ions that will spin the rotor of the ATP synthase molecule.
- Many different organic molecules can be respired - they are called **respiratory substrates**.
- However, glucose is the most commonly respired substrate.

- *substrate level phosphorylation* when another molecule (substrate) is able to transfer a phosphate group directly to ADP
- *respiratory substrates* organic molecules that can be respired
- *reduce* decrease the oxidation state of a substance
- *oxidise* increase the oxidation state of a substance

How are hydrogen ions transferred from glucose to ATP synthase?

- Two molecules are important in this transfer process:

A. Nicotinamide Adenine Dinucleotide (**NAD**)

B. Flavine Adenine Dinucleotide (**FAD**)

- Both are coenzymes and are capable of accepting hydrogen ions (reduced).
- We write the reduced forms of the molecules as NAD**H** and FAD**H** or NAD(reduced) and FAD(reduced).
- These molecules can release their hydrogen ions and become oxidised again.
- The hydrogen ions can then be used to turn the rotor of ATP synthase.

What are the stages of aerobic respiration of glucose?

- There are **four** stages in the aerobic respiration of glucose.
- These are:

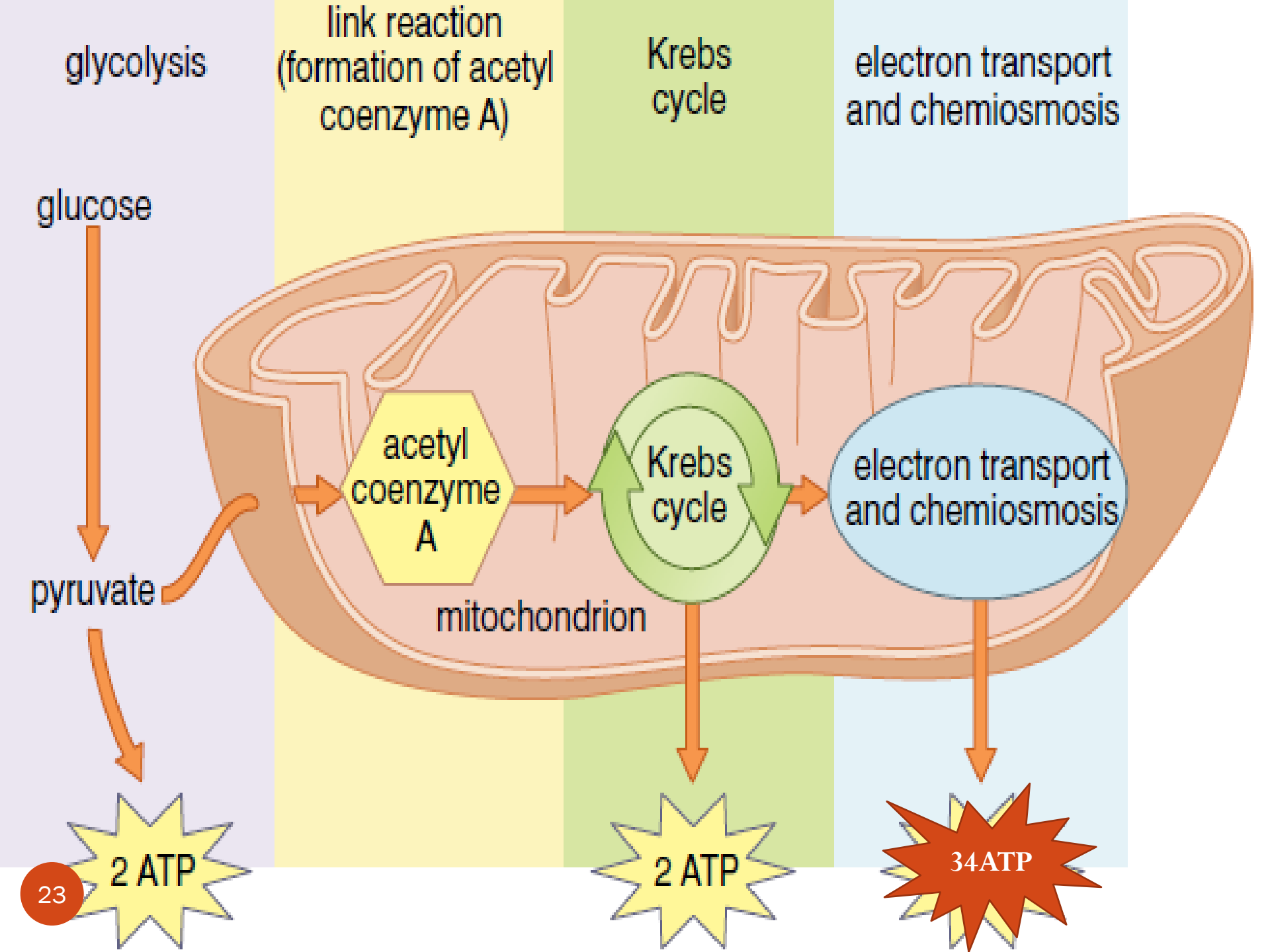
a. Glycolysis
b. the link reaction
c. Krebs cycle
d. electron transport and chemiosmosis.

- The first stage, glycolysis, takes place in the cytoplasm. It does not take place inside the mitochondria because:

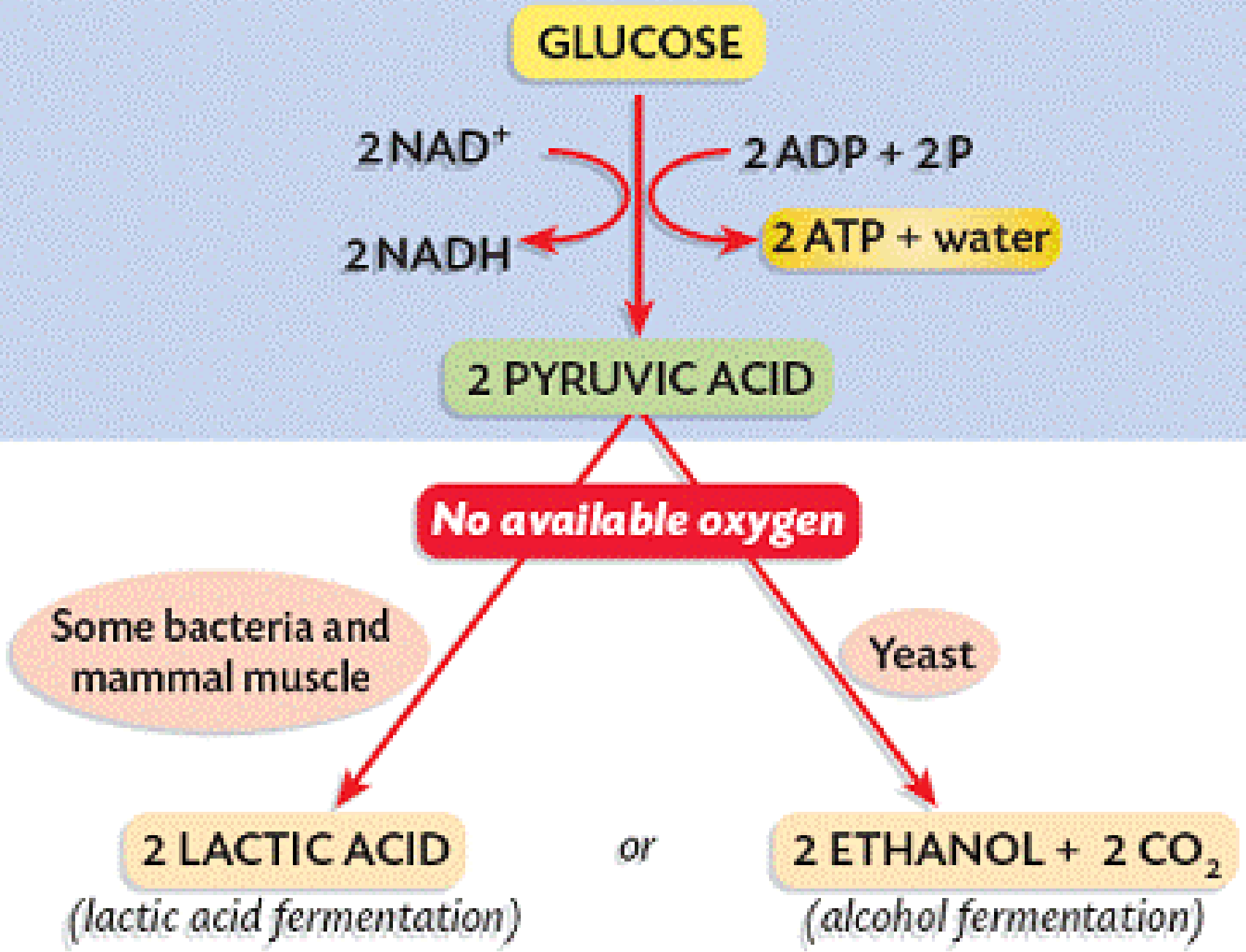
a. the glucose molecule cannot diffuse through the mitochondrial membranes (it is a medium-sized molecule and is not lipid soluble), and

b. there are no carrier proteins to transport the glucose molecule across the membranes.

- Glycolysis results in glucose being converted into a smaller molecule containing only three carbon atoms - ***pyruvate***.
- Pyruvate can enter the mitochondria and so all the other stages take place inside the mitochondrion.


glycolysis
link reaction (formation of acetyl coenzyme A)
Krebs cycle
electron transport and chemiosmosis
glucose
pyruvate
acetyl coenzyme A
Krebs cycle
electron transport and chemiosmosis
mitochondrion
2 ATP
2 ATP
34ATP

GLYCOLYSIS


GLUCOSE
2 NAD+
2 NADH
2 ADP + 2 P
2 ATP + water
2 PYRUVIC ACID
No available oxygen
Some bacteria and mammal muscle
Yeast
2 LACTIC ACID
(lactic acid fermentation)
or
2 ETHANOL + 2 CO2
(alcohol fermentation)

- In the link reaction, pyruvate is then converted into a two-carbon compound that enters into a cycle of reactions - the Krebs cycle
- Both these stages take place in the fluid matrix of a mitochondrion.
- In all three stages (glycolysis, the link reaction and Krebs cycle),hydrogen atoms are transferred to NAD to produce **reduced NAD**.
- The Krebs cycle also produces reduced FAD.
- These molecules later release their hydrogen atoms as protons (hydrogen ions) and electrons in the final stage of aerobic respiration.

- The electrons pass along a series of molecules called **an electron transport chain**.
- The protons are used in the chemiosmotic synthesis of ATP as they spin the rotor of the ATP synthase enzyme located in the inner membrane of the mitochondrion.
- Eventually, the protons (hydrogen ions) and electrons will combine with oxygen to form water.
- Without the oxygen, this cannot happen as there is nothing at the end of the electron transport chain to accept the electrons.

- The electron transport chain grinds to a halt and so does the production of ATP by ATP synthase. Because it is oxygen-dependent, this method of production of ATP is called **oxidative phosphorylation**

- The link reaction, Krebs cycle and the reactions of the electron transport chain all depend on the presence of oxygen.
- None of these occurs in anaerobic respiration.
- Glycolysis can take place in the absence of oxygen and is the only energy-releasing process in anaerobic respiration.

✓ **matrix** fluid in the mitochondrion in which the reactions of the Krebs cycle take place

✓ **electron transport chain** a series of molecules along which electrons travel

✓ **oxidative phosphorylation** oxygen-dependent production of ATP

What happens in glycolysis?

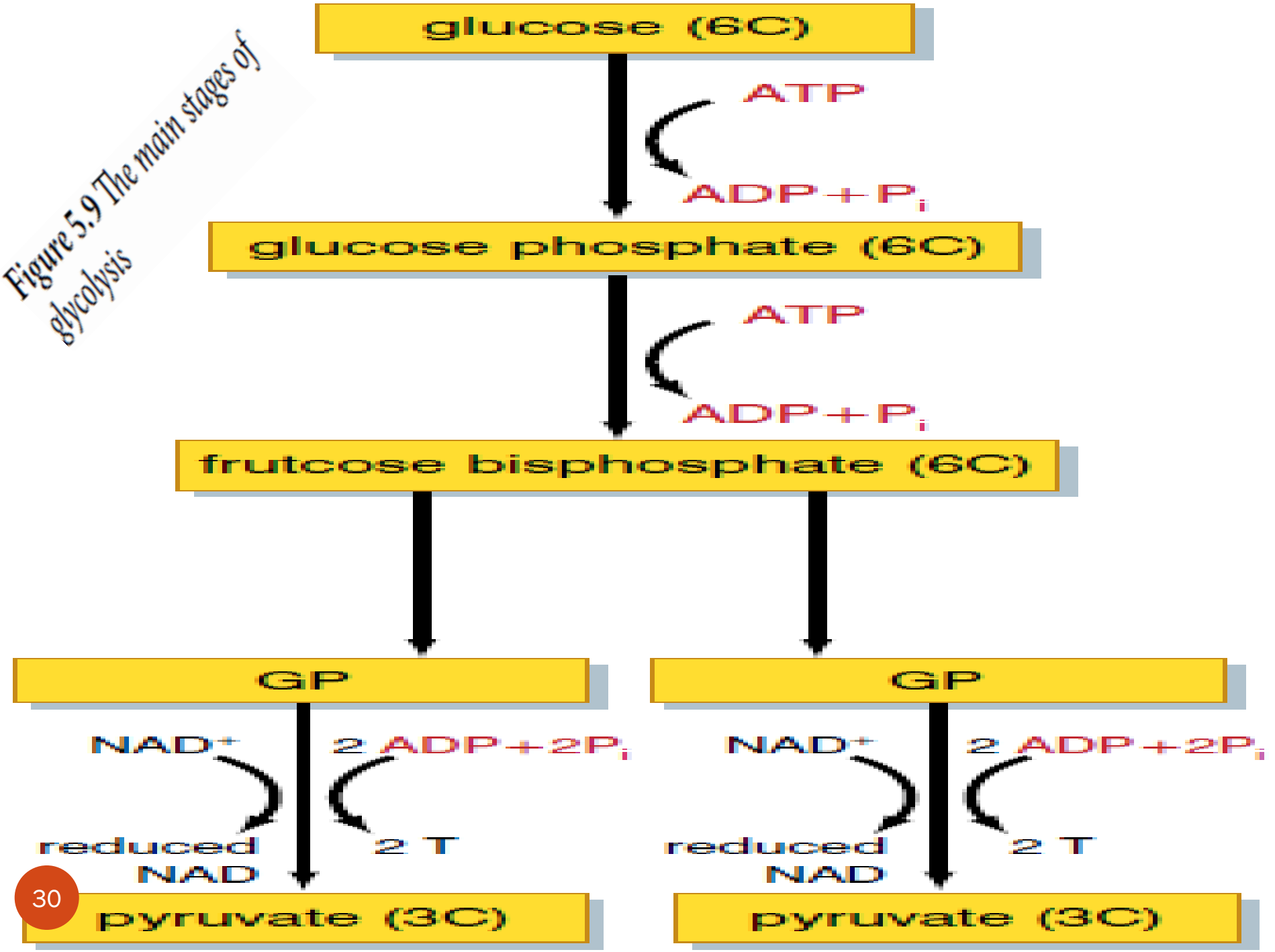
- The reactions of glycolysis take place in the cytoplasm.
- The following reactions take place in glycolosis:

a. two molecules of ATP are used to 'phosphorylate' each molecule of glucose. This makes the glucose more reactive

b. in the phosphorylation process, it is converted to another six-carbon sugar (fructose 1,6-bisphosphate)

c. the fructose **1,6-bisphosphate** is split into two molecules of the three-carbon sugar glyceraldehyde-3 phosphate (GP)

Figure 5.9 The main stages of glycolysis



d. each molecule of GP is then converted into pyruvate, with the production of two molecules of ATP by substrate level phosphorylation and one molecule of reduced NAD

- At the end of glycolysis, there is a net gain of two ATP molecules per molecule of glucose (two molecules are used initially and then four are produced).
- Two molecules of reduced NAD are also produced per molecule of glucose.
- The molecules of pyruvate pass into the mitochondria through carrier molecules in the mitochondrial membrane.

✓ $C_6H_{12}0_6 + 2ATP + 4ADP + 2P_i + 2NAD \rightarrow 2C_3H_40_3 +$ 2ADP + 4ATP +2NAD reduced + $2H^+$ +2H2O

What happens in the link reaction?

- Both of these stages of respiration take place in the fluid matrix of the mitochondrion.
- In the link reaction, a molecule of pyruvate reacts with a molecule of coenzyme A (CoA) to form a molecule of acetyl coenzyme A (acetyl CoA).
- In the reaction:

a. hydrogen is lost and reduced NAD is formed (dehydrogenation)

b. a carbon atom is lost to form carbon dioxide (decarboxylation).

- The acetyl coenzyme A then reacts with a C4 molecule called *oxaloacetate.*
- In the reaction, acetyl CoA breaks down into:

a. a two-carbon 'acetyl' group, which reacts with the C4 compound oxaloacetate to form a C6 compound, and

b. the original coenzyme A molecule, which is reused in further reactions with other molecules of pyruvate.

- This is the first reaction of the Krebs cycle.

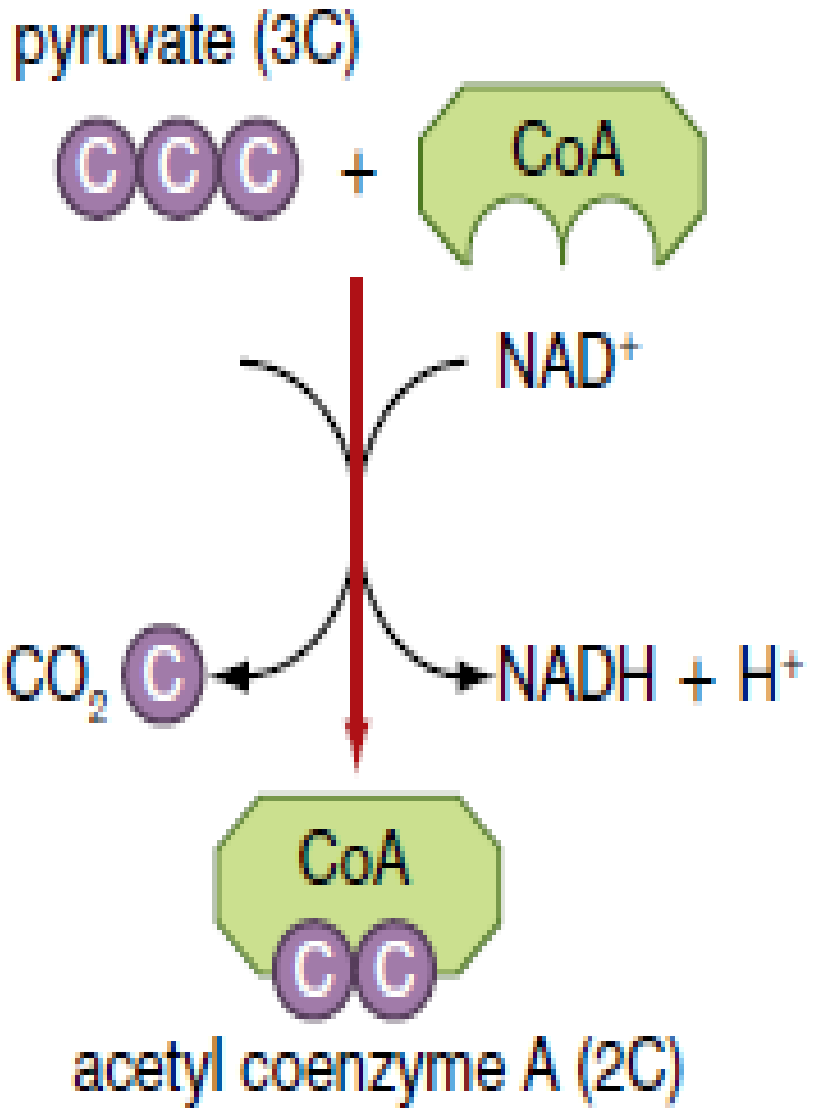


Figure 5.10 The link reaction

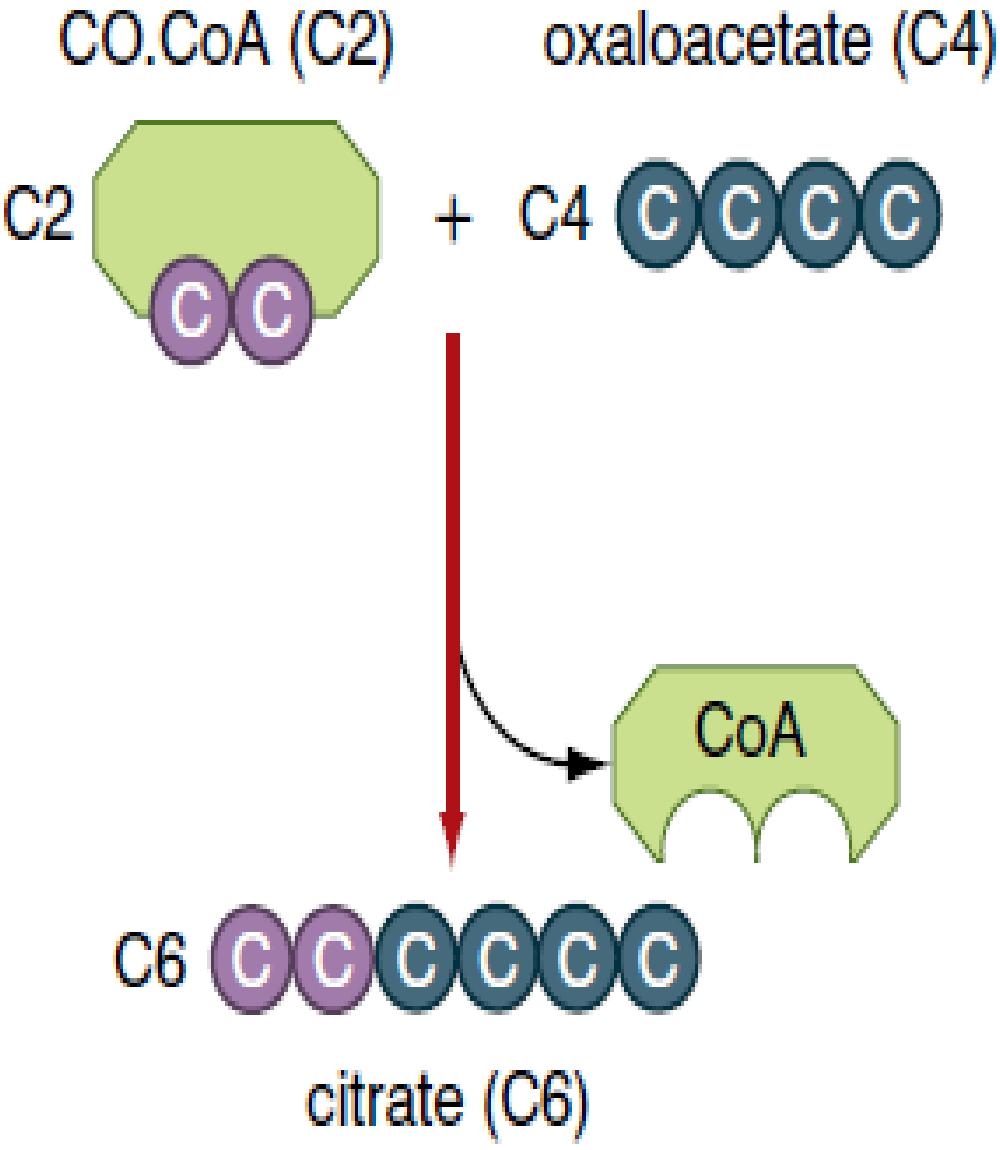


Figure 5.11 The first reaction of the Krebs cycle

What happens in the Krebs cycle?

a. the two-carbon group from acetyl coenzyme A reacts with the four-carbon compound oxaloacetate to form a six-carbon compound called ***citrate***

b. citrate then loses a carbon atom (decarboxylated) to form a five-carbon compound and CO_2 is produced

c. the five-carbon compound is then further decarboxylated to form a four-carbon compound and CO_2 is again produced; a molecule of ATP is also produced by substrate level phosphorylation

d. the four-carbon compound undergoes several molecular transformations to regenerate the original four-carbon compound (oxaloacetate) and the cycle is complete and can begin again with oxaloacetate reacting with another molecule of acetyl CoA .

e. in several reactions in the cycle, reduced NAD is produced and, in just one reaction, reduced FAD is produced

A summary of the overall reaction of the Krebs cycle:

$$CH_3CO.CoA + 3NAD + FAD + C_4H_2O_5^{2-} \rightarrow 2CO_2 + 3NAD$$

reduced + FAD reduced + CoA + $C_4H_2O_5^{2-}$

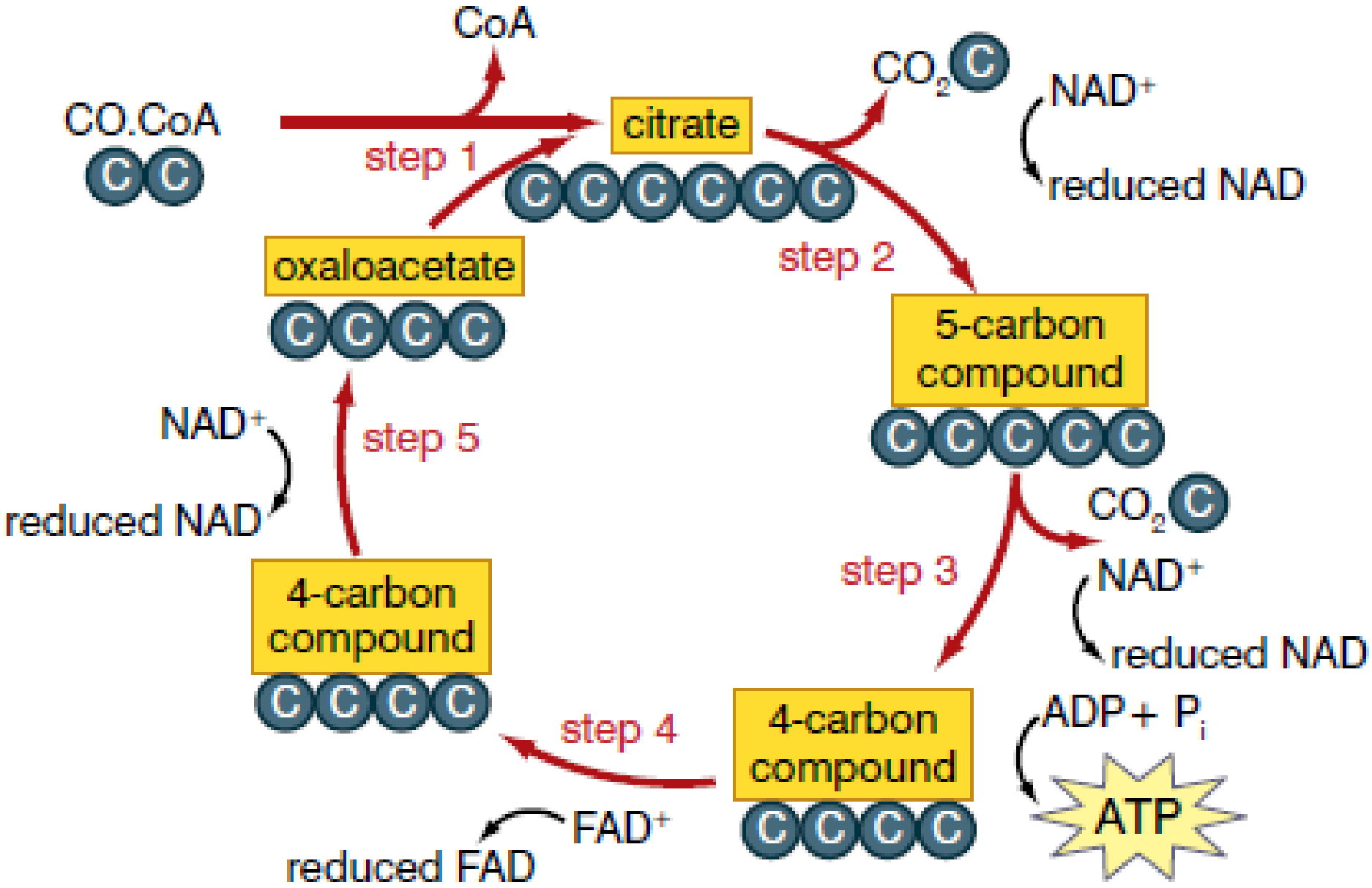


Figure 5.12 The main stages of the Krebs cycle

1. **coenzyme A** coenzyme derived from pantothenic acid needed for respiration
2. **acetyl coenzyme A** produced by the reaction of coenzyme A with a molecule of pyruvate
3. **dehydrogenation** removing hydrogen from a molecule
4. **decarboxylation** removing carbon from a molecule
5. **oxaloacetate** an ester of oxaloacetic acid
6. **citrate** an ester of citric acid

What happens in the electron transport chain and chemiosmosis?

- The electron transport chain and chemiosmosis together make up the process of **oxidative phosphorylation.**
- The reactions of the *link reaction* and *Krebs cycle* take place in the *fluid matrix of the mitochondrion*, whereas the reactions of the **electron transport chain** and **chemiosmosis** take place on the **inner mitochondrial membrane.**

- On the cristae, the following events take place

1. the hydrogen atoms carried by reduced NAD and reduced FAD are released and split into protons (hydrogen ions) and electrons.
2. the electrons pass along a series of electron carriers that form the transport chain; they lose energy as they pass from one carrier to the next.
3. three of the electron carriers are proton pumps that move protons from the matrix of the mitochondrion to the inter-membrane space.

4. as the electrons are transferred through these three proton pumps, the energy they lose powers the pumps which move the protons into the inter-membrane space.
5. electrons from reduced NAD make this happen at all three pumps.

- The molecules that act as electron carriers in the electron transport chain are:

a) **reduced NAD** dehydrogenase (also a proton pump)

b) **ubiquinone** (also a proton pump), and

c) a number of carriers called **cytochromes** (these are proteins that contain iron); two of them form a complex that acts as the third proton.

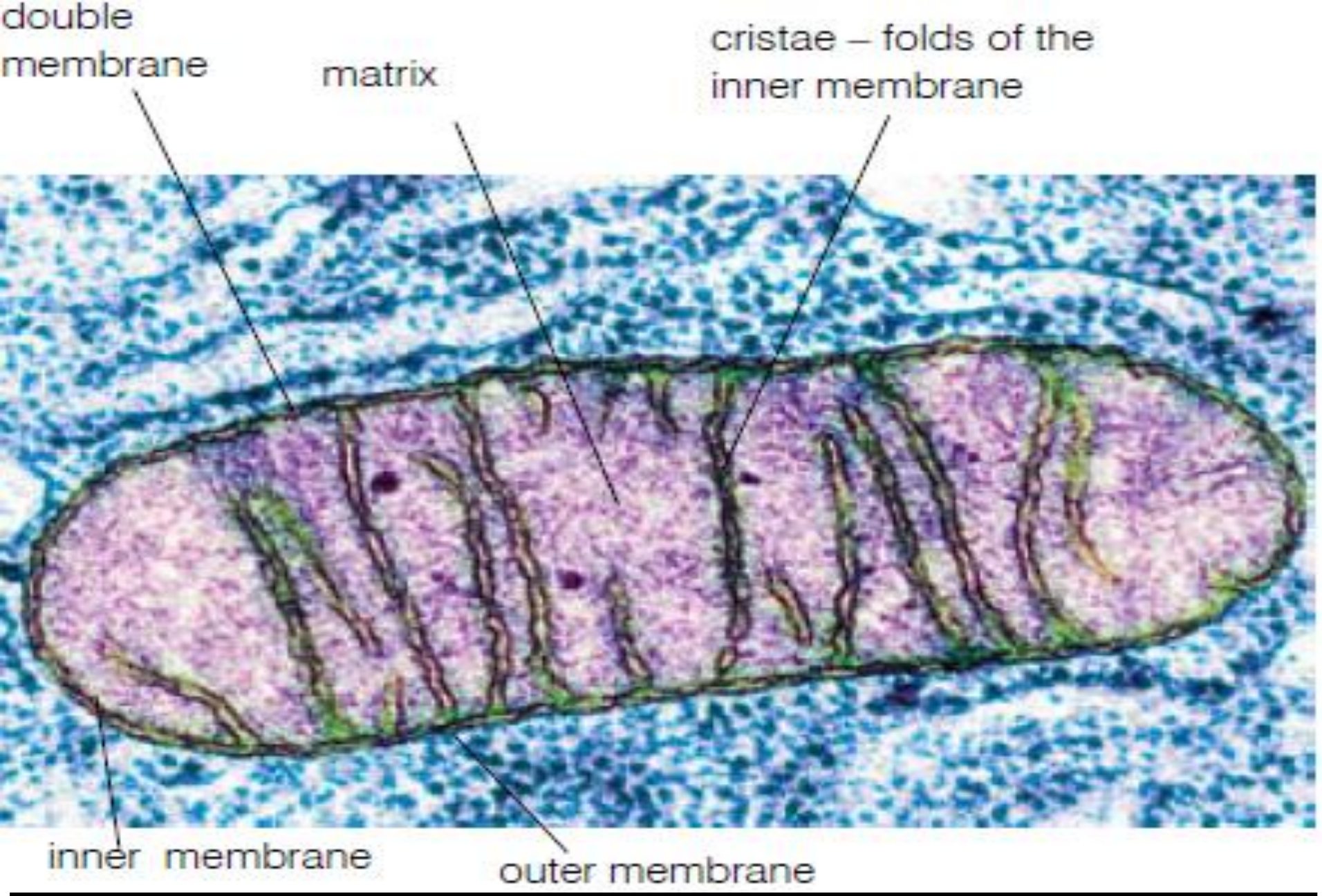


Figure 5.13 An electron-micrograph of a mitochondrion

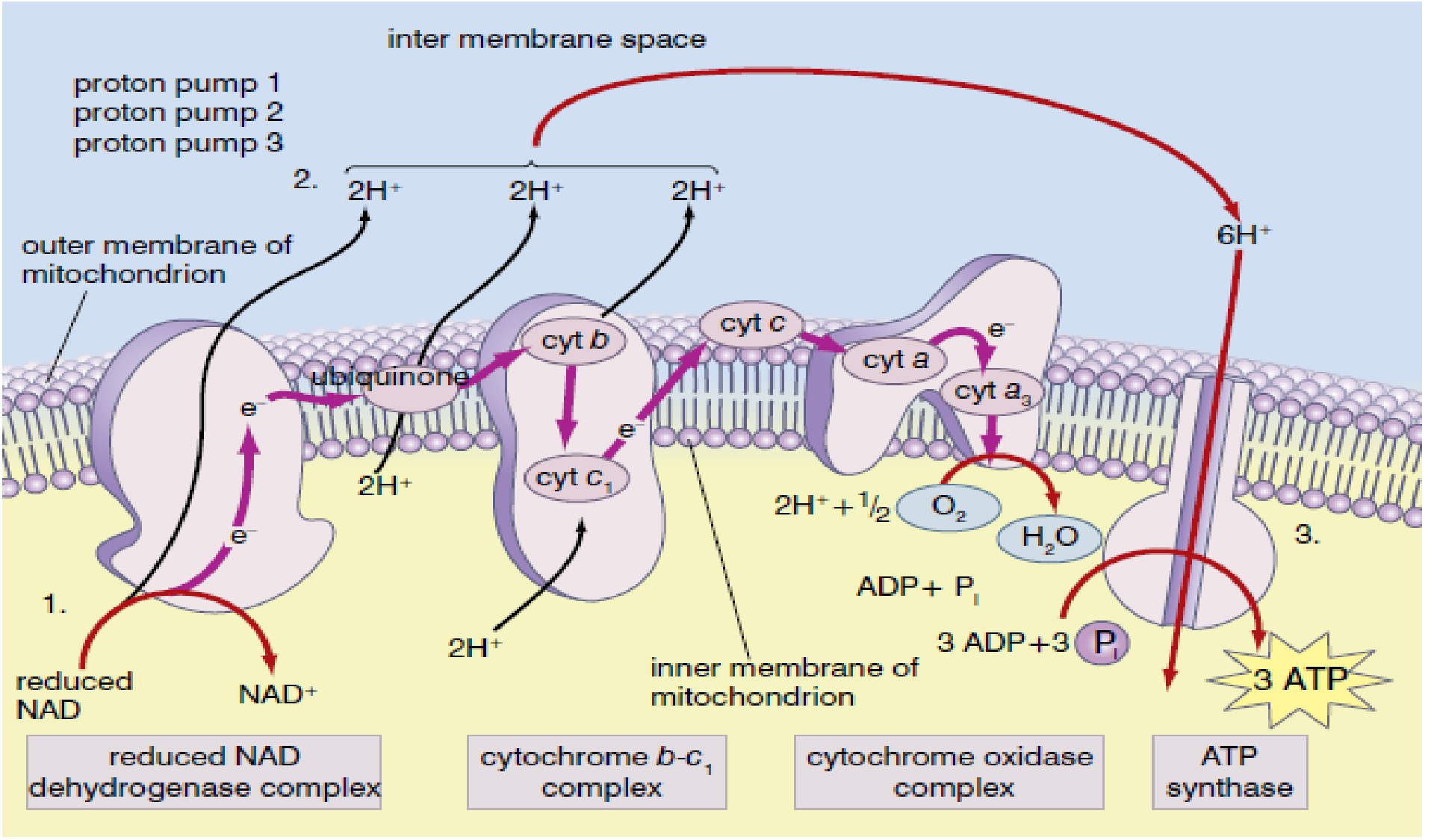


Figure 5.14 The carrier molecules in the electron transport chain in the inner membrane of a mitochondrion

- At the end of the electron transport chain, the electrons combine with protons and with oxygen to form molecules of water.
- Because of this, oxygen is known as the **terminal electron acceptor.**
- Whereas *reduced NAD is dehydrogenated by the NAD dehydrogenase complex*, reduced FAD is dehydrogenated by ubiquinone.
- So electrons from reduced FAD only operate two of the three proton pumps.
- Because of the action of the proton pumps, protons accumulate in the inter-membrane space creating a higher concentration there than in the matrix

- This proton gradient results in protons diffusing through the ATP synthase molecule (down the concentration gradient) making the synthase rotor 'spin' and produce ATP from ADP and P_i.
- The diffusion of hydrogen ions through the ATP synthase is chemiosmosis.
- The oxidation of one molecule of reduced NAD results in six protons passing through ATP synthase and so leads to the synthesis of three molecules of ATP.

- The oxidation of one molecule of reduced FAD results in four protons passing through ATP synthase and so leads to the synthesis of just two molecules of ATP.
- By adding up the number of molecules of ATP produced, the model of aerobic respiration we have discussed predicts that there will be a net yield of 36 molecules of ATP per molecule of glucose.
- ***terminal electron acceptor:-*** the final molecule at the end of the electron transport chain to accept an electron

- In practice, this is not achieved because some energy (the equivalentof just over two molecules of ATP) is used to drive the proton pumps.
- The actual yield is about 36 molecules of ATP per molecule of glucose.

A summary of the overall reaction of the electron transport system:

6 reduced NAD (from Krebs' cycle) + 2 reduced NAD (from glycolysis) + 2 reduced FAD (from Krebs' cycle) + 30 ADP + 30 Pi - 2ATP (used in proton pumps) → 36 ATP + 8 NAD + 2FAD

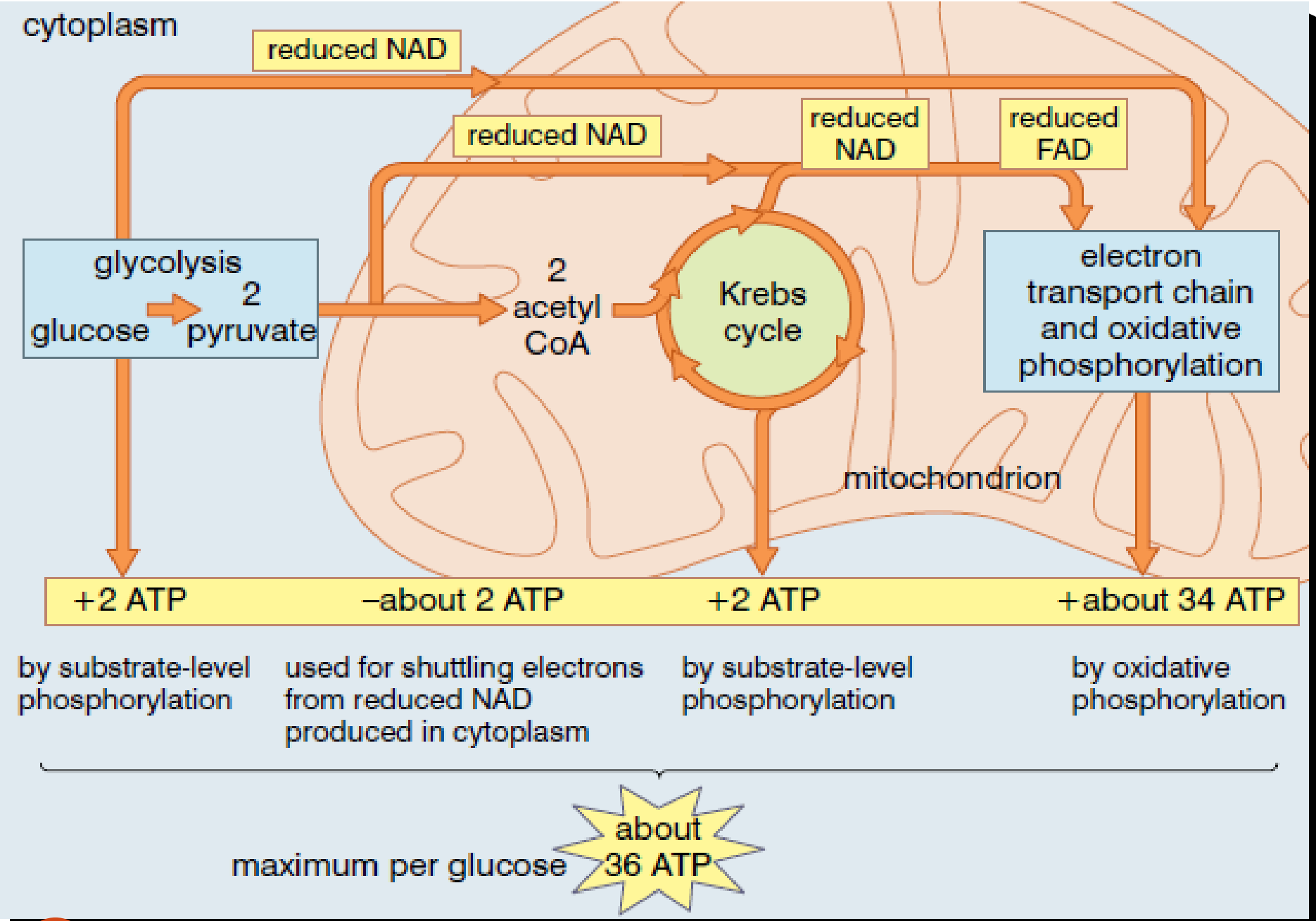


Figure 5.15 The production of ATP during the aerobic respiration of glucose

- The summary equation for aerobic respiration is:

$C_6H_{12}O_6 + 6O_2 \rightarrow 6H_2O + 6CO_2 +$ energy released

- The overall summary equation for the aerobic respiration of glucose is:

$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + 36ATP$

1. Glycolysis

2ATP + 2NAD = 2+6=8ATP

2. Link rxn

1NAD=3ATP

3. Kreb cycle

2x3NADx3=18ATP

2X2FAD= 4ATP

2ATP

} = 24ATP

4. Chemiosmosis

3ATP

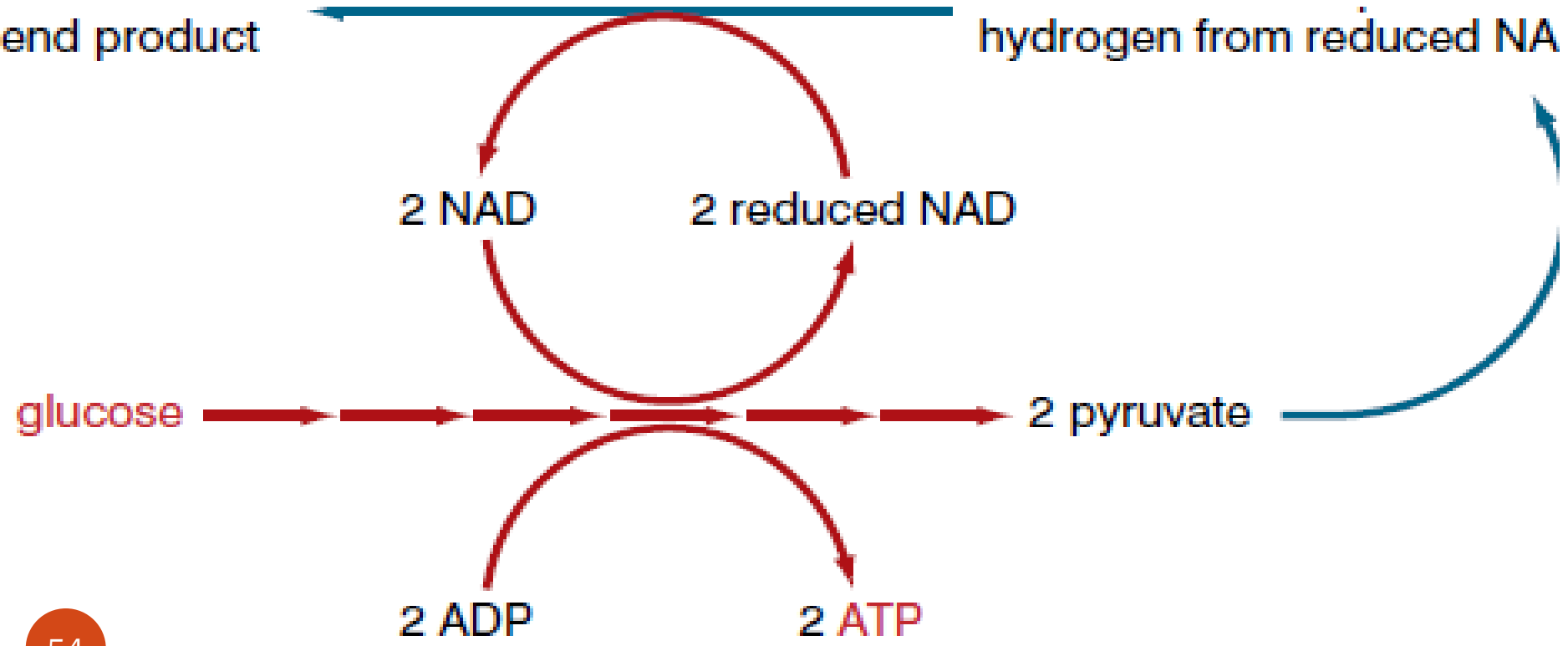
Total 8ATP+3ATP+24ATP+3ATP=38ATP

What happens in the anaerobic pathway?

- If there is no oxygen present, the final reaction of oxidative phosphorylation, where electrons and protons react with oxygen to form water, cannot take place.
- As a result, the electron transport chain comes to a halt.
- No protons are pumped and the action of ATP synthase also stops.
- If the electron transport chain does not function, NAD is not regenerated from reduced NAD and FAD is not regenerated from reduced FAD.

- Very quickly, the Krebs cycle and the link reaction come to a halt as both NAD and FAD are required in their oxidised forms for the Krebs cycle to function.
- NAD is also required in the link reaction and so this comes to a halt also.
- However, glycolysis can continue even though it also requires NAD.
- This is because the reduced NAD formed during glycolysis can be regenerated under anaerobic conditions by converting the pyruvate into another product in a reduction reaction.

- Reduced NAD supplies the hydrogen for this reduction and becomes oxidised itself.
- It is therefore regenerated and can be used again in glycolysis



- Different organisms produce different fermentation end products.
- Animal cells produce lactate (lactic acid) when they ferment glucose.
- Yeast cells produce ethanol (ethyl alcohol).
- But both only produce two molecules of ATP per molecule of glucose.

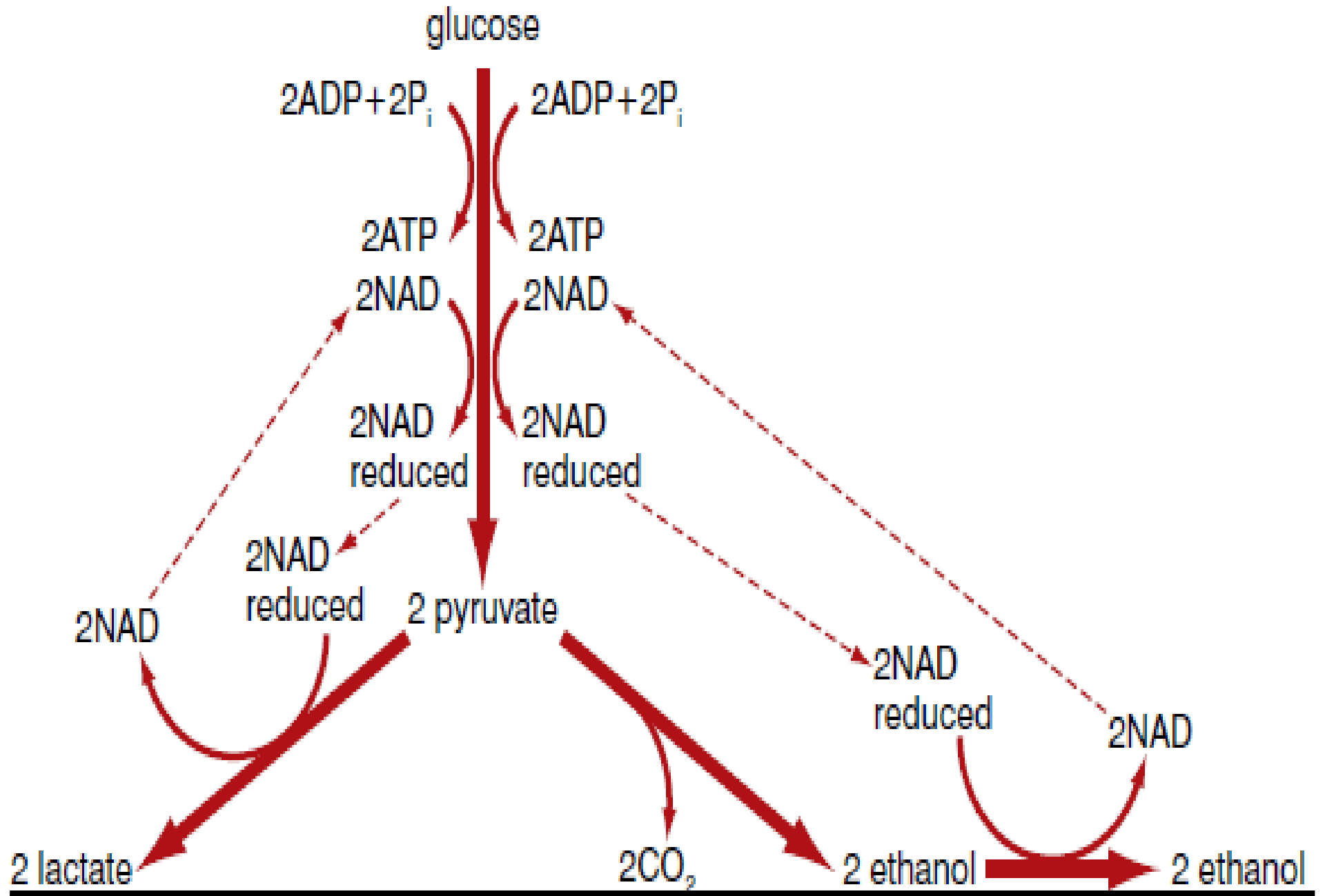


Figure 5.22 The fermentation processes in animal cells and yeast

A summary of anaerobic respiration in yeast cells

$C_6H_{12}O_6 \longrightarrow 2C_2H_5OH + 2CO_2 + 2ATP$

Glucose — Ethanol (alcohol) — carbon dioxide

A summary of anaerobic respiration in animal cells

$C_6H_{12}O_6 \longrightarrow 2C_3H_6O_3 + 2ATP$

Glucose — Lactate (lactic acid)

Lactate formation during exercise

- During exercise, the energy demand of muscle cells increases greatly.
- More glucose is respired to meet the demand. However, sometimes, aerobic respiration is insufficient to meet this energy demand.
- Fermentation of glucose supplies the extra energy. But it also forms lactate and as this accumulates, it leads to muscle fatigue.
- Also, fermentation only yields 2 molecules of ATP per molecule of glucose whereas aerobic respiration yields 38.
- However, fermentation is a much faster process and can produce a lot of ATP quickly, over a short period of time.

- The ATP used in sprints and short-distance runs is nearly all generated anaerobically.
- But, due to muscle fatigue, this cannot be sustained. Longer races must be run slower to allow aerobic respiration to produce the ATP at its slower rate.
- Lactate, once formed, can be used to regenerate glucose or be metabolised as an energy source by the liver.

5.2 How do plants harness light energy in photosynthesis?

Harness :-to control the energy of something in order to produce power or to achieve something

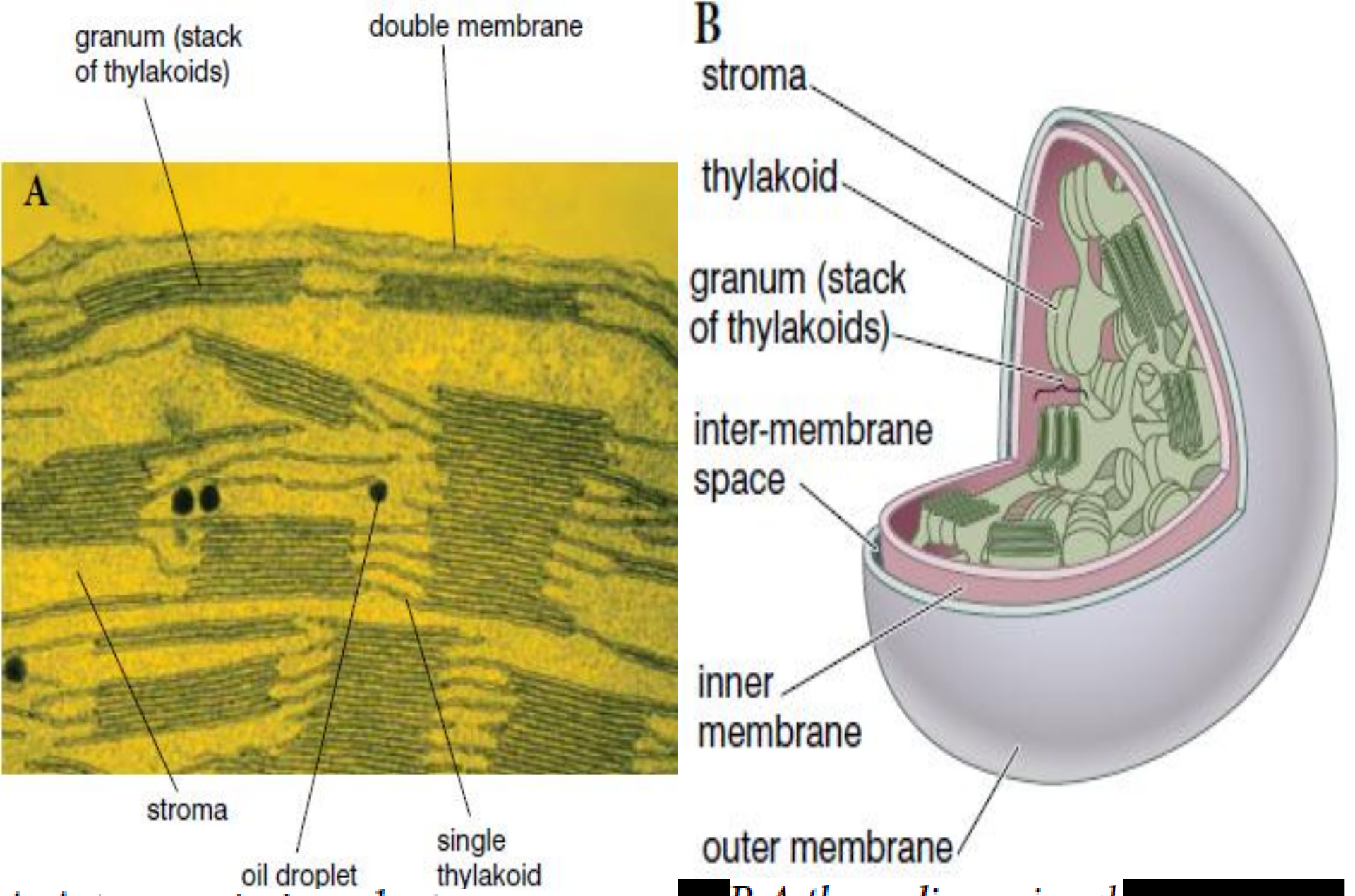
A. Photosynthesis

- In photosynthesis, light energy is used in a series of reactions that lead to the synthesis of a range of organic molecules.
- The energy that entered the system as light is now held in the organic molecules produced.
- It is now chemical energy.
- When energy is changed from one form to another, we say it has been **transduced.**
- This takes place in a series of reactions called the **light-dependent reactions.**

- Light energy is absorbed by special photosensitive pigments such as chlorophyll in the chloroplasts.
- The light-dependent reactions take place in the **membranes of the thylakoids** in the chloroplasts.
- The **liquid stroma** is the site of the **light-independent reactions**, in which carbohydrates are synthesised.
- Chemical reactions like these take place most effectively in solution, rather than if some were fixed in membranes.

How is the structure of a chloroplast suited to its function?

- The chlorophyll and other photosensitive pigment molecules are arranged in special photosystems that are linked to electron transport chains (ETCs).
- The molecules of the photosystems and the electron transport chains are fixed in the membranes of the thylakoids.
- There are two different photosystems, each sensitive to light of a different wavelength and linked to a different electron transport chain.
- These are called *photosystem I* and *photosystem II*



A A transmission electron m raph of a section through a chloroplast

B A three-dimensional representation of the structure of a chloroplast

What is the structure of a photosystem?

- A photosystem consists of a number of pigment molecules all clustered around one particular chlorophyll molecule called the **reaction centre molecule.**
- This cluster of pigment molecules is called **an antenna complex**.
- Only the reaction centre molecule is positioned next to the electron transport chain.
- Energy absorbed by other molecules in the photosystem is transferred to the reaction centre molecule, where the light-dependent reactions begin.

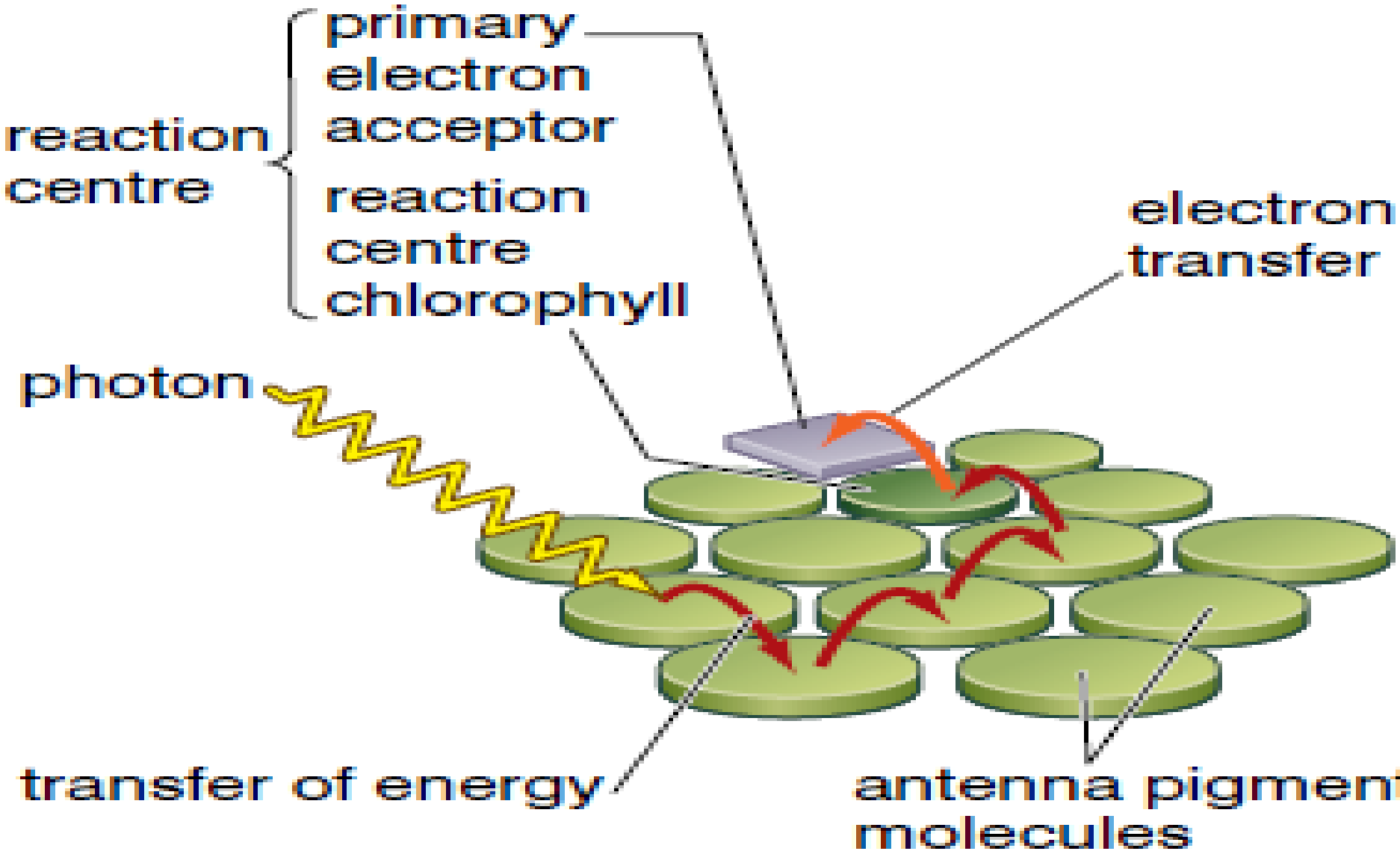
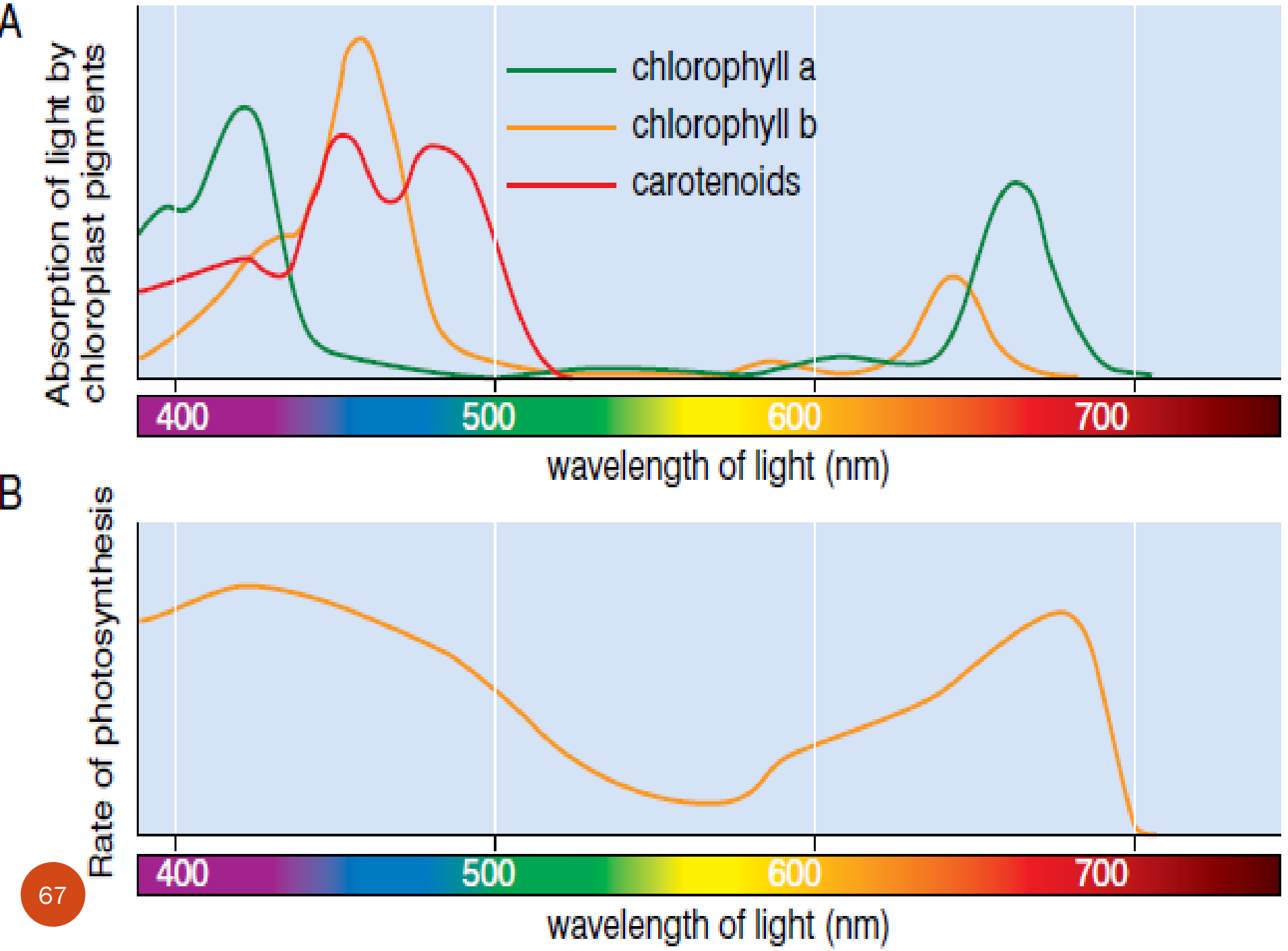


Figure 5.30 The structure of a photosystem

- Different pigment molecules in the antenna complex can absorb different wavelengths of light, making the whole system more efficient.
- The pigments in the antenna complex include **chlorophyll a**, **chlorophyll b** and **carotenoids.**
- The reaction centre molecule is always **chlorophyll a.**
- The range of wavelengths each molecule absorbs is its absorption spectrum.


A
Absorption of light by chloroplast pigments
chlorophyll a
chlorophyll b
carotenoids
400
500
600
700
wavelength of light (nm)
B
Rate of photosynthesis
400
500
600
700
wavelength of light (nm)

1. *reaction centre molecule* is where light-dependent reactions begin.
2. *antenna complex* an array of protein and chlorophyll light-harvesting molecules embedded in the thylakoid membrane.
3. *absorption spectrum* the range of wavelengths a molecule absorbs.
4. *action spectrum* the photosynthesis effectiveness of each wavelength.
5. *photosystems* biochemical mechanism by which chlorophyll absorbs light energy
6. *photosystem I* photosystem in photosynthetic light reactions. Discovered before photosystem II

What happens in the light-dependent reactions?

- The light-dependent reactions use light energy to 'drive' the synthesis of two molecules that will, in turn, drive the light-independent reactions.
- These two molecules are:

1. **ATP** - this provides the energy for the reactions, and
2. **reduced NADP** - this provides the hydrogen ions for a key reduction reaction.

- NADP is very similar to NAD that is used in respiration and it has the same function - transporting hydrogen ions.

Photosystem I and photosystem II

1. Electrons (e^-) in chlorophyll molecules in photosystem II are excited by the energy in photons of light - they become more energetic. Because of the extra energy, they escape from the chlorophyll and pass to an electron acceptor (the primary electron acceptor).
2. The conditions created in the chloroplast cause the following reaction to occur:

$$2H_2O \rightarrow O_2 + 4H^+ + 4e^-$$

- This light-dependent splitting of water is called *photolysis.*
- The electrons replace those lost from the chlorophyll molecule

3. The primary electron acceptor passes the electrons to the next molecule in an electron transport chain (**plastoquinone** or 'Pq'). The electrons then pass along a series of **cytochromes** (similar to those in the mitochondrial electron transport chain) and finally to **plastocyanin** (Pc) - the last carrier in the chain. The electrons lose energy as they are passed from one carrier to the next.
4. One of the molecules in the cytochromes complex is a proton (hydrogen ion) pump. As electrons are transferred to and then transferred from this molecule, the energy they lose powers the pump which moves protons from the stroma of the chloroplast to the space inside the thylakoid. This leads to an accumulation of protons inside the thylakoid, which drives the chemiosmotic synthesis of ATP.

5. Electrons in chlorophyll molecules in photosystem I are excited (as this photosystem absorbs photons of light) and escape from the molecule. They are replaced by the electrons that have passed down the electron transport chain from photosystem II.
6. The electrons then pass along a second electron transport chain involving **ferredoxin** (Fd) and NADP reductase. At the end of this electron transport chain, they can react with protons (hydrogen ions) and NADP in the stroma of the chloroplast to form reduced NADP.

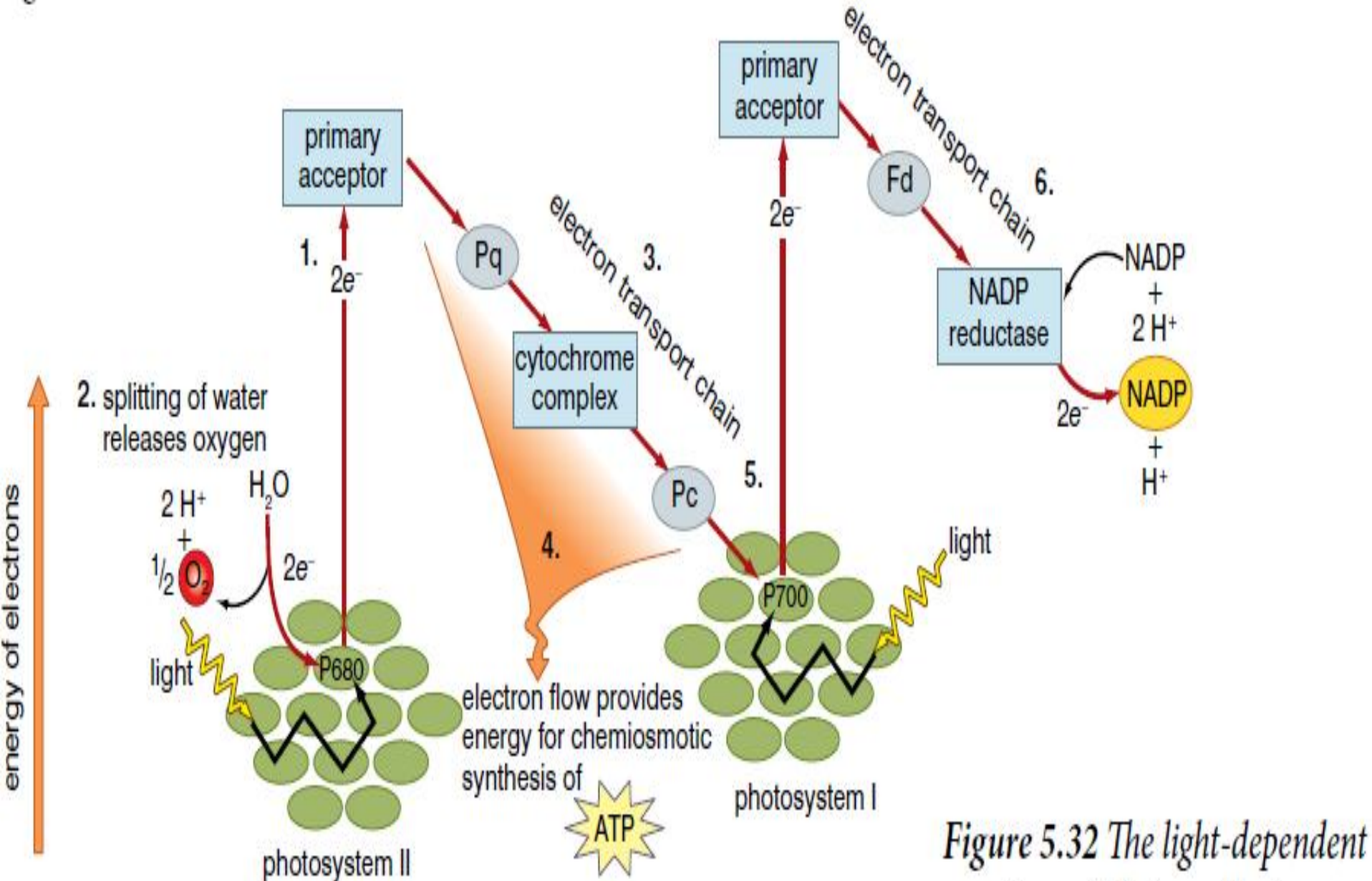


Figure 5.32 The light-dependent reactions of photosynthesis

- *primary electron acceptor* the first molecule to accept the excited electron displaced from a chlorophyll molecule.
- *photolysis* light-dependent splitting of water.

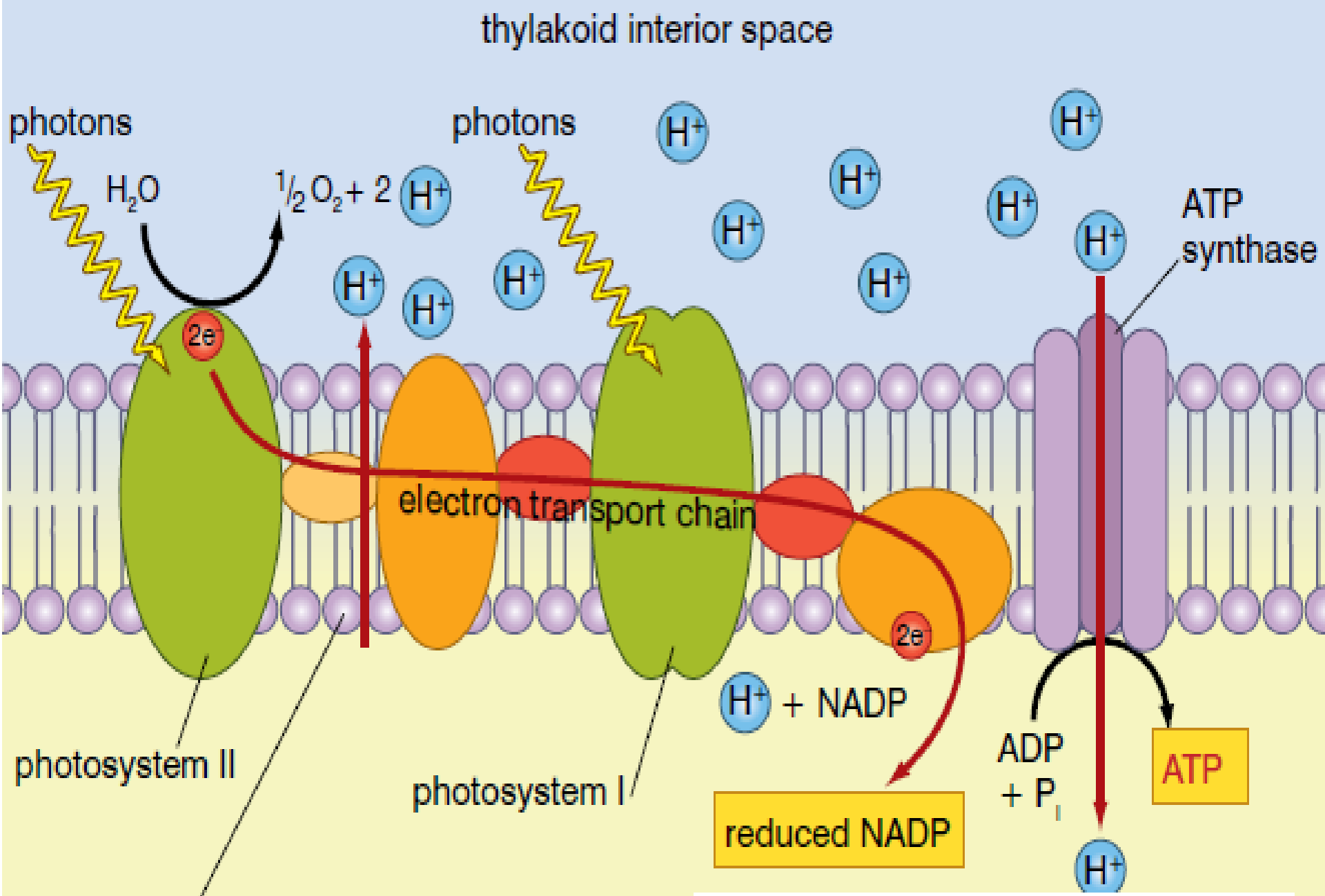


Figure 5.33 How the molecules are arranged in a photosynthetic unit

- A photosynthetic unit is a **unit of pigments**, **electron carriers and ATP synthase** that is capable of carrying out all the reactions in the light-dependent stage of photosynthesis.
- The formation of ATP in the way described above is called **non-cyclic photophosphorylation.**
- This is because:

a. the phosphorylation (formation of ATP) is light-dependent
b. the electrons lost from the chlorophyll are not recycled in any way

- Plants sometimes generate ATP by cyclic photophosphorylation.
- In cyclic photophosphorylation, only photosystem I is used.
- No oxygen and no reduced NADP are formed.
- Electrons lost from the chlorophyll molecule are returned to it. Hence the name **'cyclic'.**
- This process usually only happens when sugars cannot be synthesised for some reason - such as lack of carbon dioxide.
- In cyclic and non-cyclic photophosphorylation, ATP is produced because:

a. there is an accumulation of protons (hydrogen ions) in the interior of a thylakoid.
b. this creates a concentration gradient between the thylakoid interior and the stroma of the chloroplast.
c. protons move down this concentration gradient, through ATP synthase, causing the rotor to spin, just as in mitochondria during respiration.

- **photosynthetic unit** an arrangement of molecules capable of carrying out all the reactions in the light-dependent stage of photosynthesis.
- **non-cyclic photophosphorylation** the formation of ATP via photosystem II
- **cyclic photophosphorylation** use of only photosystem I to generate ATP

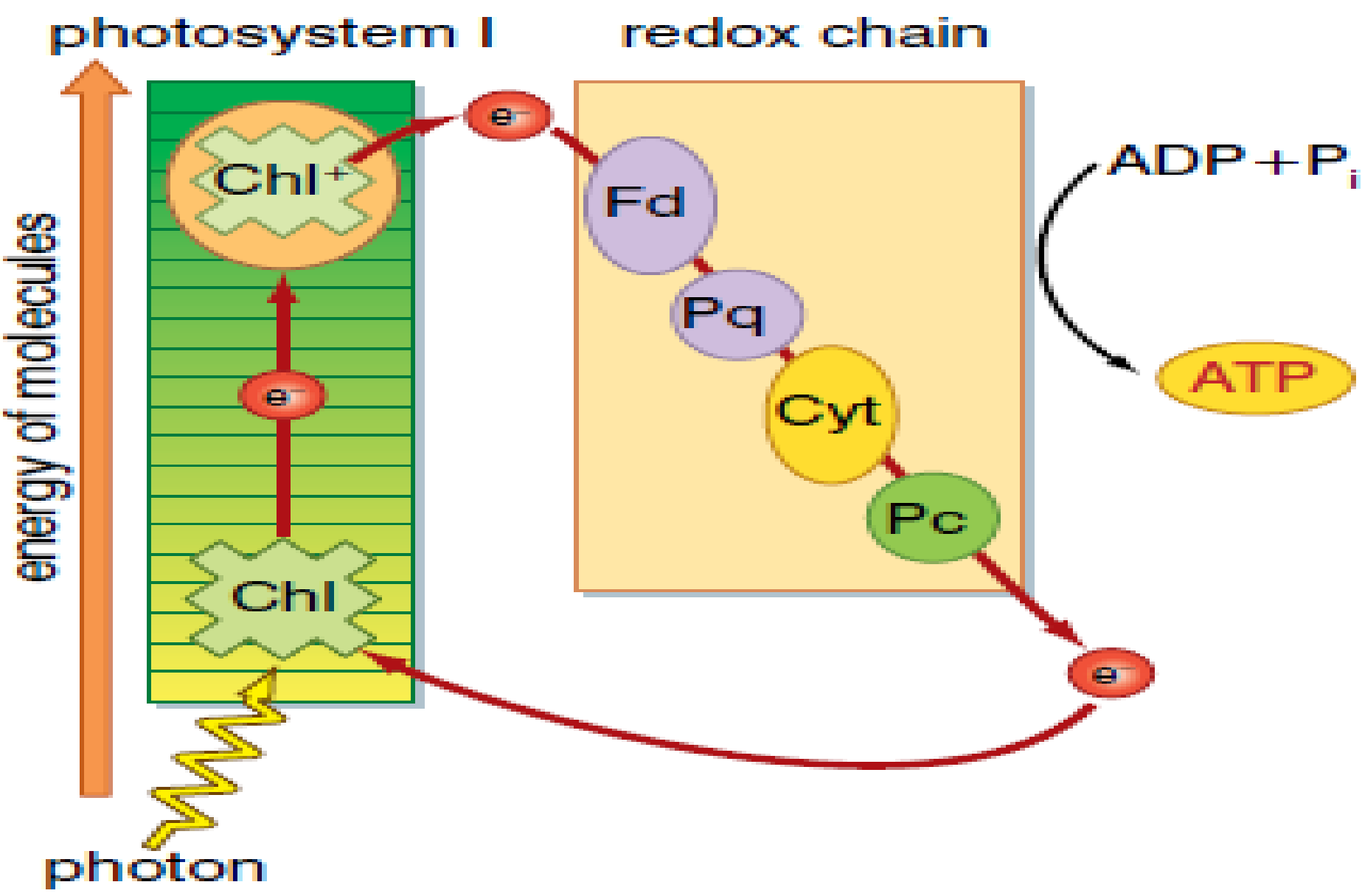


Figure 5.34 Cyclic photophosphorylation

A summary of the light-dependent reactions

- Light energy is used to excite electrons which then:

a. cause the transfer of protons to the inside of the thylakoid membrane as they pass along the first electron transport chain; this eventually leads to the formation of ATP, and

b. react with hydrogen ions and NADP at the end of the second electron transport chain to form **reduced NADP**; this reaction could only happen because of the extra energy possessed by the electrons.

- The ATP and reduced NADP are used to drive the synthesis of carbohydrates in the light-independent reactions of photosynthesis

How is carbohydrate synthesised in the light-independent reactions?

- The light-independent reactions of photosynthesis occur in the **stroma** of the chloroplasts.
- They comprise a complex cycle of reactions that involves the addition of **carbon dioxide** to a pre-existing **five-carbon molecule** (ribulose bisphosphate) within the chloroplast.
- The resulting molecules are modified to regenerate the original molecule whilst, at the same time, synthesising glucose.

- The sequence of reactions was discovered by **Melvin Calvin**, an American biologist. Because of his work, the light-independent reactions are also referred to as the Calvin cycle.
- The main stages of the light-independent reactions are:

a. carbon dioxide reacts with ribulose bisphosphate (RuBP) – a five-carbon compound in the stroma; the reaction is catalysed by the enzyme **Rubisco** (ribulosebisphosphate carboxylase oxygenase)
b. two molecules of the three-carbon compound GP are formed from this reaction.
c. each molecule of GP is converted to TP (triose phosphate -another three-carbon compound; this is a reduction reaction using hydrogen ions from reduced NADP and energy from ATP.

d. some of the TP formed is used to regenerate the RuBP (ATP is again required) whilst some is used to form glucose and other useful organic compounds

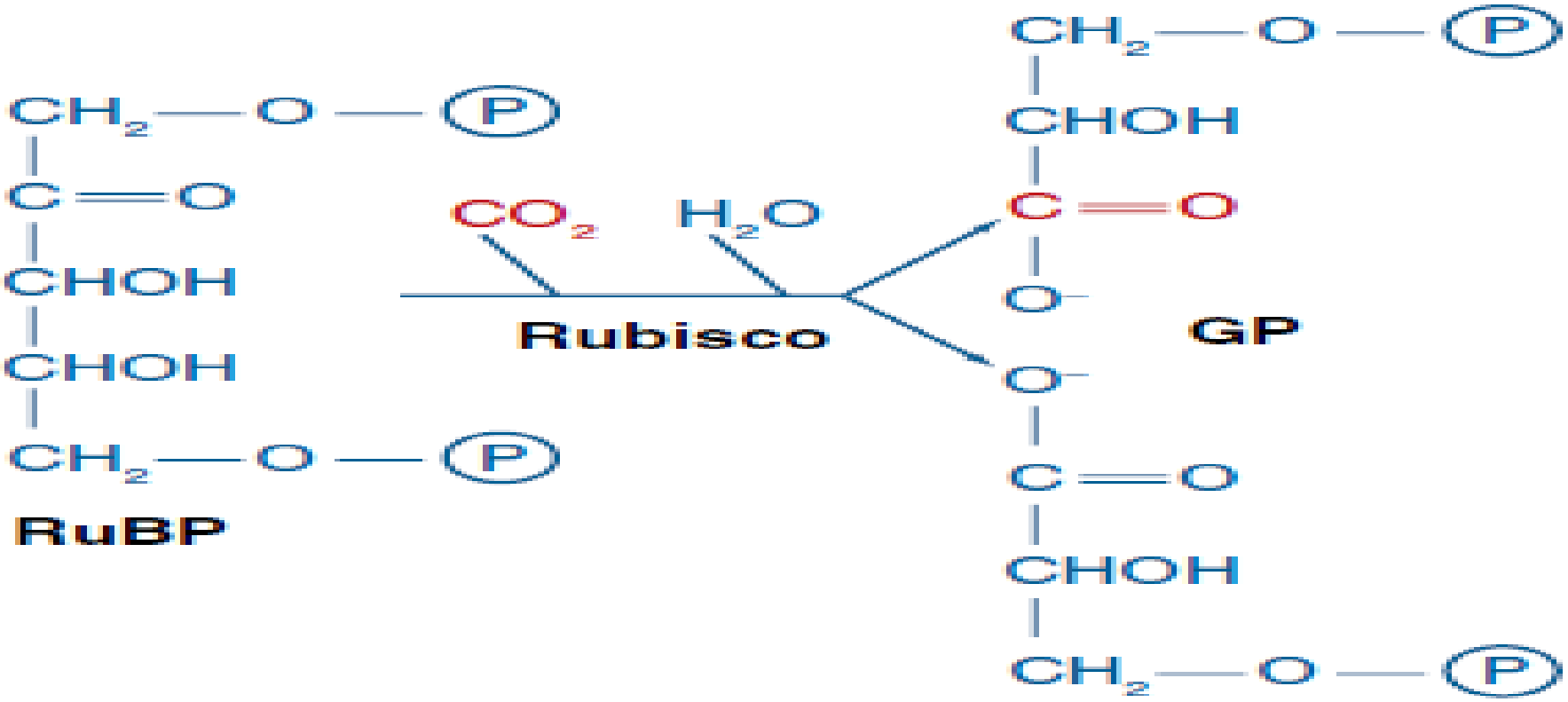
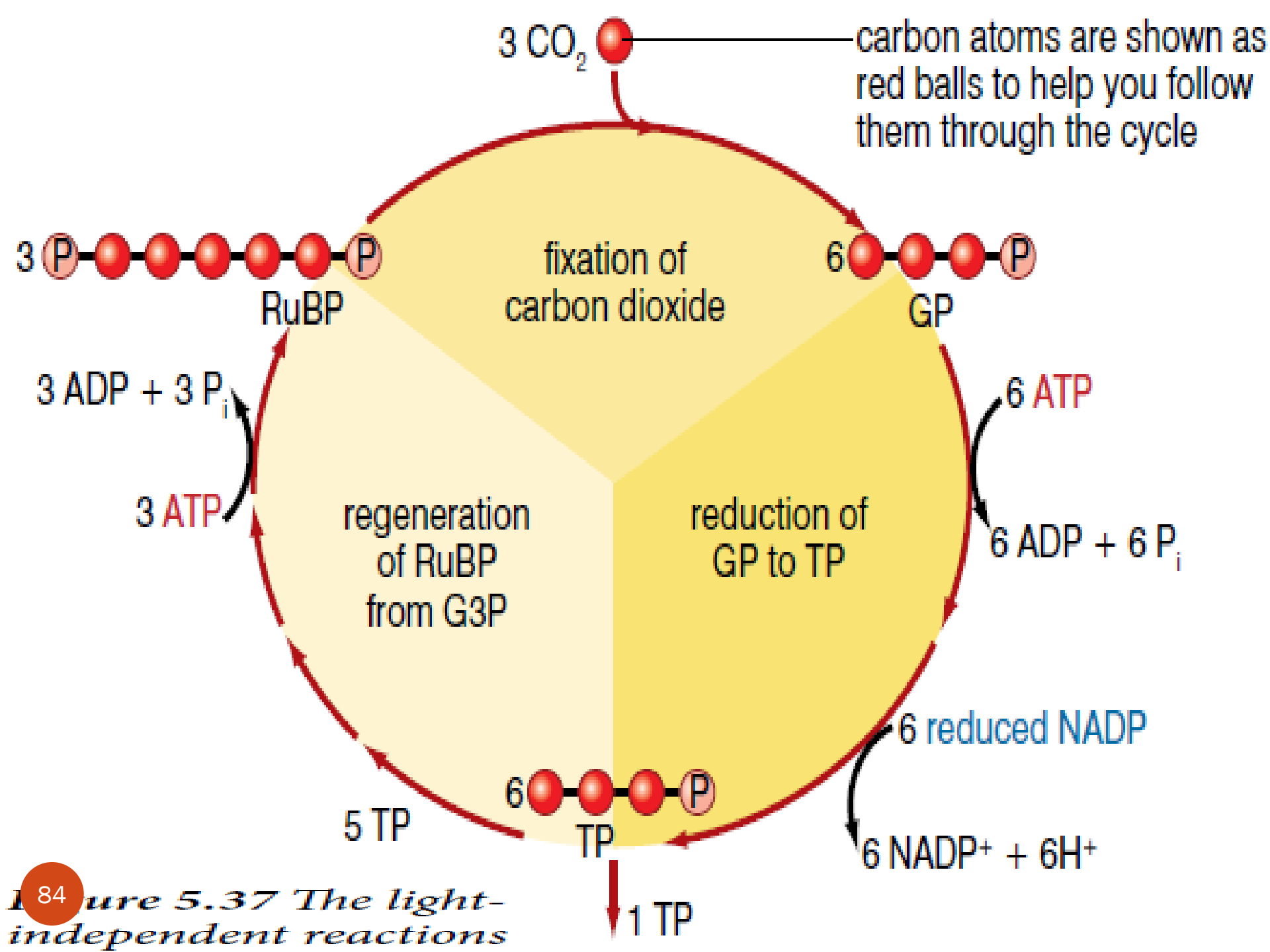


Figure 5.36 The action of Rubisco



ure 5.37 The light-independent reactions

What factors affect the rate of photosynthesis?

- Photosynthesis is dependent on a number of factors.

Factor	Effect on photosynthesis
Light intensity	Low light intensity can limit the light-dependent reactions by reducing the number of electrons in chlorophyll molecules that are photo-excited.
Carbon dioxide concentration	Can limit the light-independent reactions by influencing the rate of the initial reaction with RuBP.
Temperature	Can limit the rate of enzyme action, for example, ATP synthase (light-dependent reactions) and Rubisco (light-independent reactions).

Table 5.1 Factors affecting the rate of photosynthesis

What is the effect of light intensity on the rate of photosynthesis?

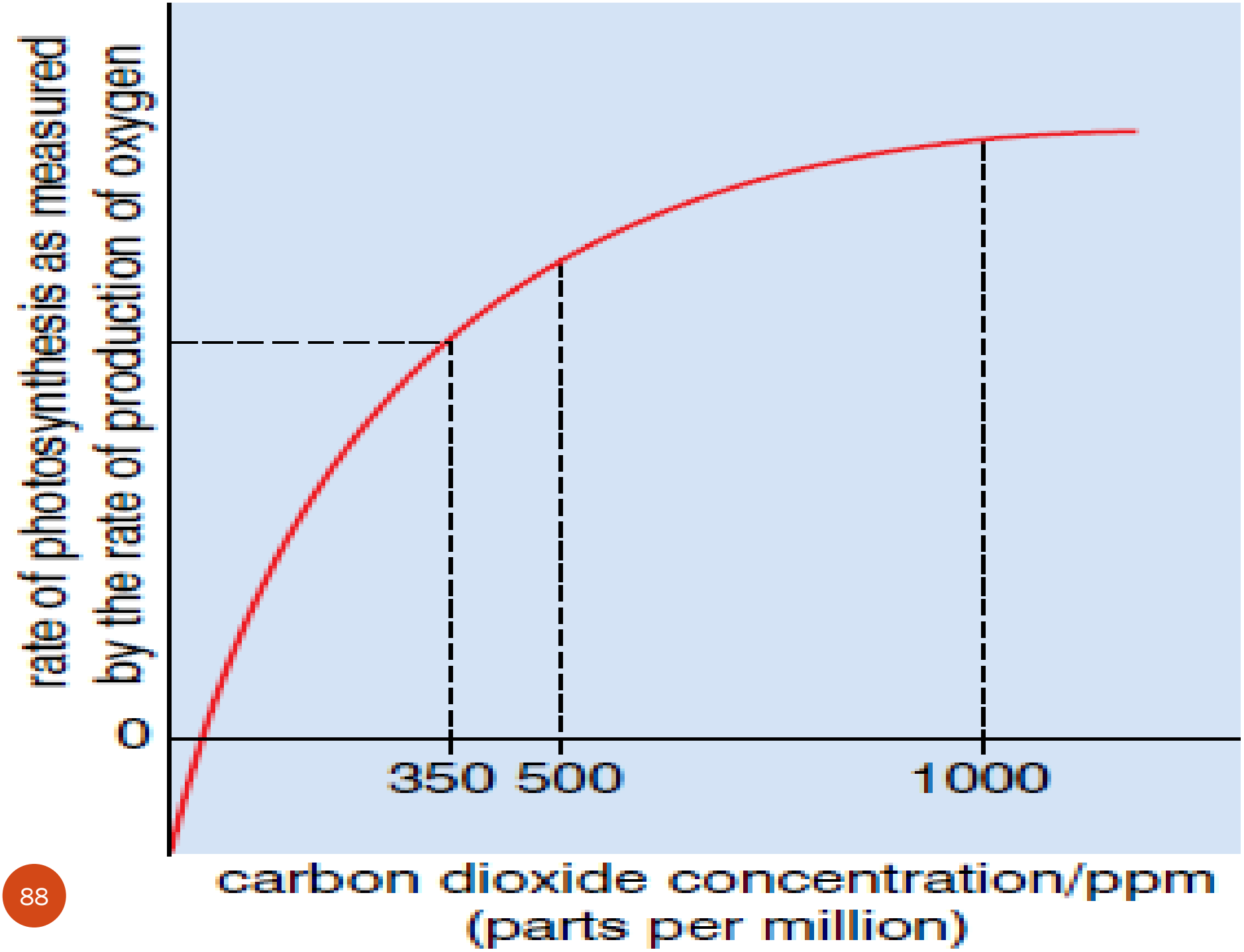
a) *very low light intensities* - respiration is still occurring and is taking in oxygen faster than photosynthesis is producing it

b) *medium light intensities* - photosynthesis is producing more oxygen than respiration uses, the rate of photosynthesis increases with increasing light intensity

c) *very high light intensities* - the rate of photosynthesis is beginning to level out, even though the light intensity is still increasing; some other factor is probably limiting the rate.

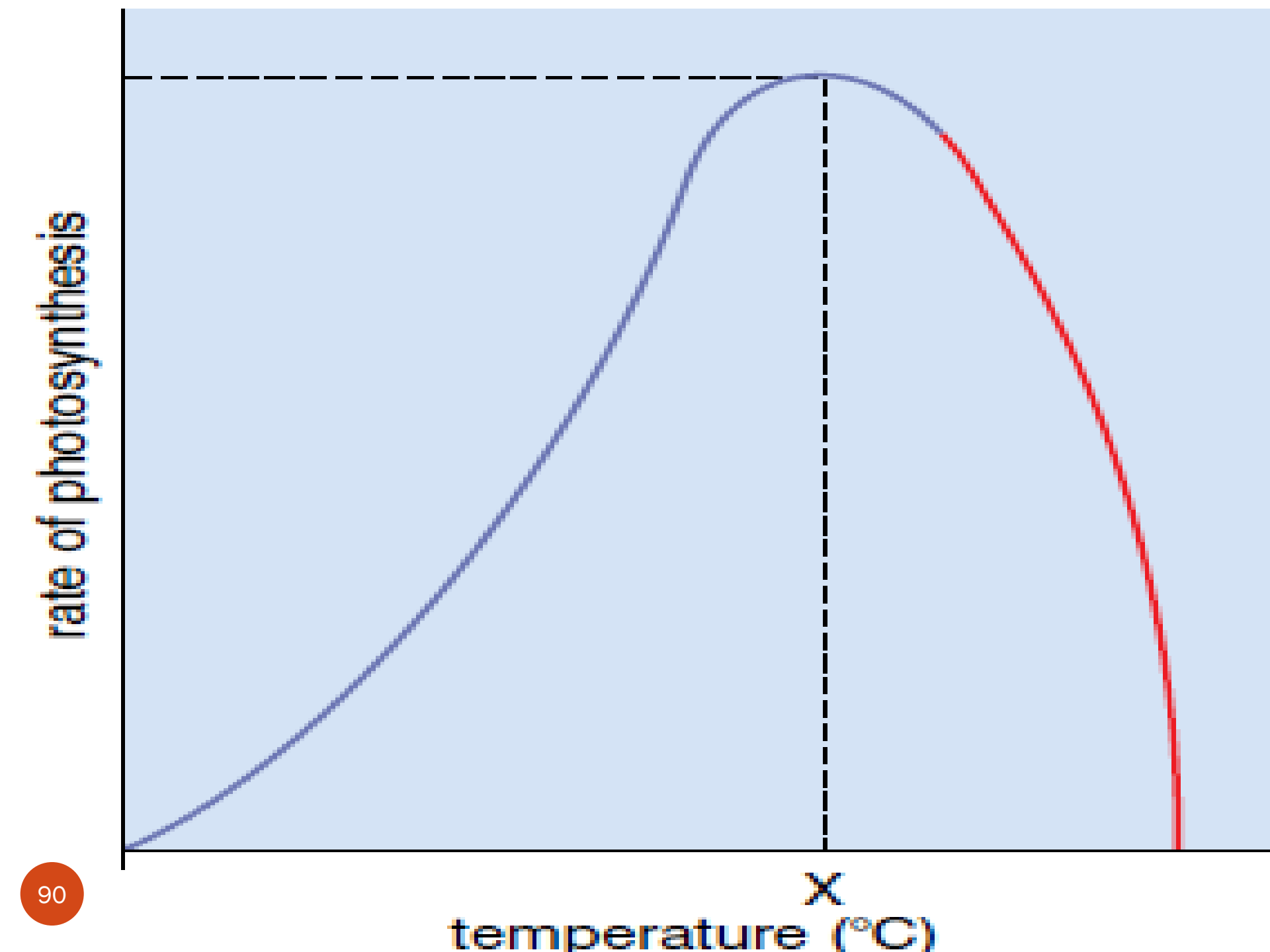
What is the effect of the concentration of carbon dioxide on the rate of photosynthesis?

- At very low concentrations of carbon dioxide, little photosynthesis takes place, although respiration is still using up oxygen.
- As the carbon dioxide concentration increases, so does the rate of photosynthesis.
- Again, however, it begins to level off at higher concentrations.
- This may be due to some other factor, or it could be due to the saturation of Rubisco.


rate of photosynthesis as measured by the rate of production of oxygen
0
350
500
1000
carbon dioxide concentration/ppm (parts per million)

How does temperature affect the rate of photosynthesis?

- Many of the reactions in both the light-dependent stage and the light-independent stage are controlled by enzymes, which are affected by temperature.
- Once the temperature exceeds the optimum, the enzyme denatures and the rate of photosynthesis decreases rapidly.


rate of photosynthesis
X
temperature (°C)

How can all the factors interact to influence the rate of photosynthesis?

- Increasing the light intensity should increase the rate at which ATP and reduced NADP are produced in the light-dependent reactions and, as a result, increase the rate at which the Calvin cycle can take place.
- However, the rate at which the Calvin cycle can 'turn' could be limited by:

a. a low temperature (limiting the rate at which enzymes such as Rubisco can operate)
b. a low concentration of carbon dioxide.

- This limits the rate at which reduced NADP and ATP can be used, which, in turn, limits the amount of NADP and ADP + P_i that can be reused by the light-dependent reactions.
- The whole process is therefore limited, even though the light intensity continues to increase.
- There are number of other factors influence the rate of photosynthesis. These include:

a. the wavelength of the light; photosynthesis takes place faster in '**red**' and '**blue**' wavelengths than in other wavelengths because these wavelengths are absorbed more efficiently than others; leaves are green because green wavelengths are reflected

b. the amount of chlorophyll present

C3 photosynthesis and photorespiration

- The method of photosynthesis that takes place in plants living in temperate environments, such as those found in Europe is called *C3 photosynthesis* - because the first compound formed in the light-independent reactions of the Calvin cycle is GP, which contains three carbon atoms.
- C3 plants have leaves that are adapted to this method of photosynthesis.
- These leaves are generally **broad**, to catch as much sunlight as possible.
- The cells that contain most chloroplasts (the palisade cells) are nearest to the upper surface of the leaf (to absorb as much light as possible).

- The stomata are mainly on the lower surface, to minimise water loss.
- During the day, the stomata are open for most of the time to allow the entry of carbon dioxide, but they can be closed if the water loss is too great on a hot day.
- The spongy mesophyll has air spaces that allow easy diffusion of carbon dioxide and oxygen between the palisade layer and the stomata.
- However, plants in the tropics have a problem. Here, it can be very hot and the leaves close their stomata to minimise water loss.

- When C3 plants do this, the concentration of carbon dioxide in the leaves falls and the enzyme Rubisco starts to behave in an unusual way.
- In the low concentrations of carbon dioxide, Rubisco binds with oxygen, not carbon dioxide.
- This means that RuBP which is a five-carbon compound in the stroma is oxidised to one molecule of GP and a molecule of phosphoglycolate.

$$\text{Ribulose bisphosphate} + \text{oxygen} \xrightarrow{\text{Rubisco}} \text{GP} + \text{phosphoglycolate}$$

- In addition, carbon dioxide is produced in the process.
- The process is called **photorespiration** because it involves oxidation of carbon.

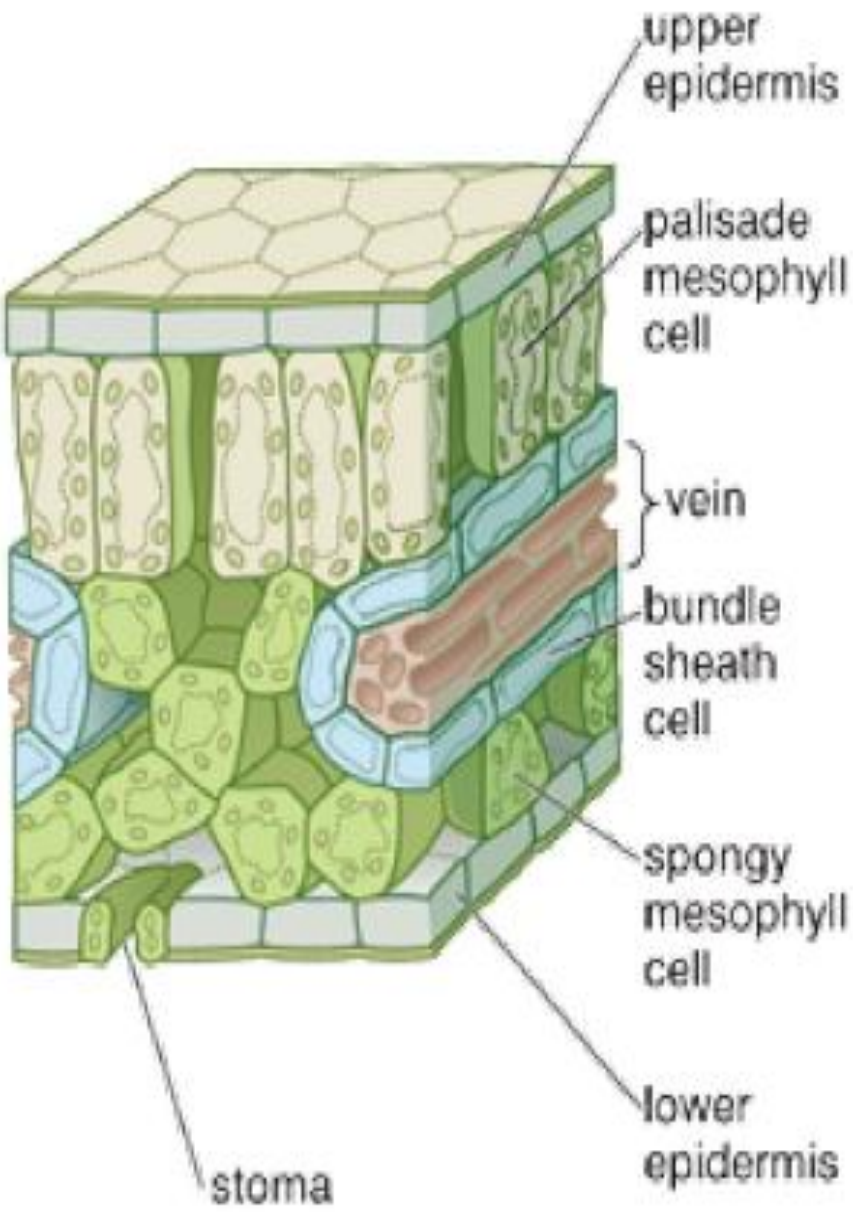


Figure 5.45 A leaf from a C3 plant

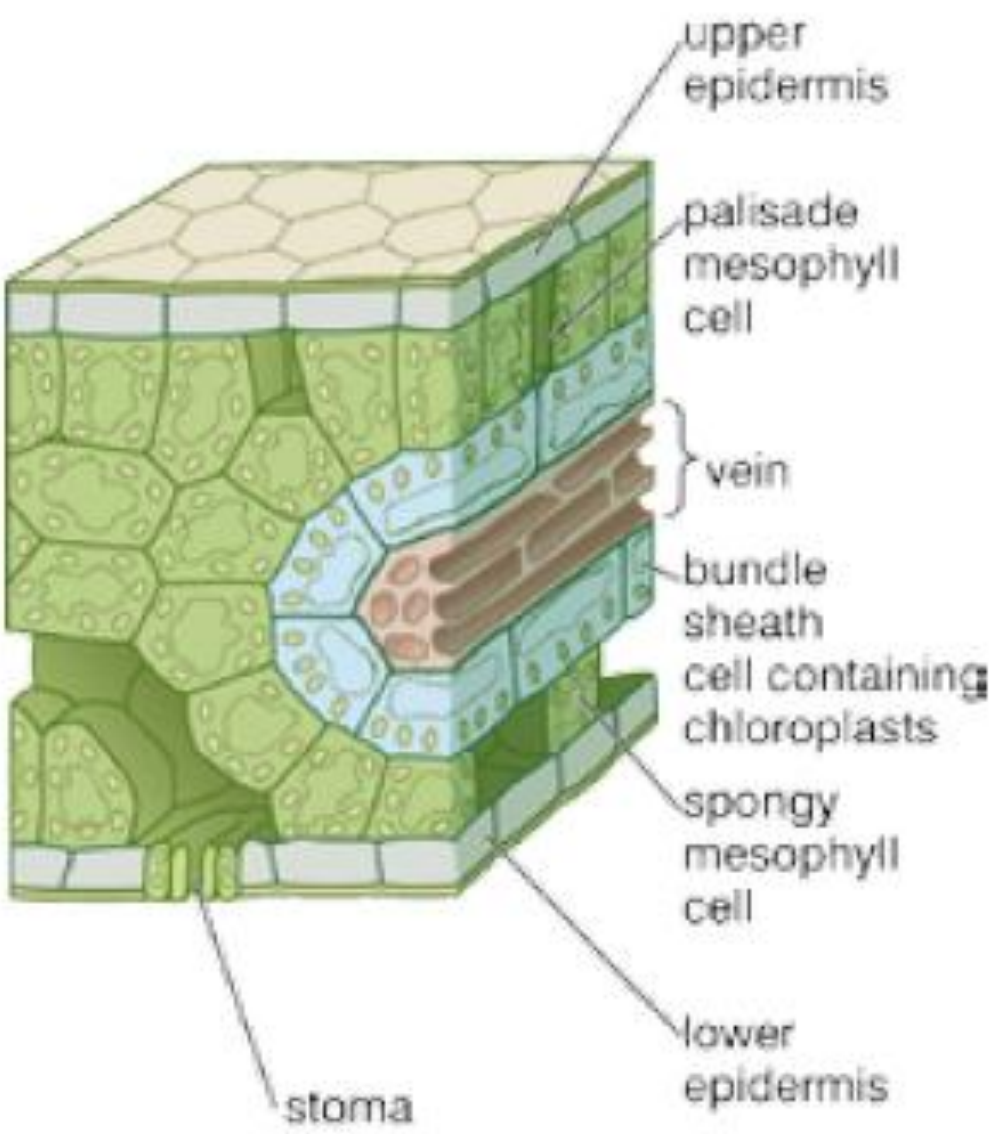


Figure 5.47 The structure of a leaf from a C4 plant

- The one molecule of GP formed in photorespiration can re-enter the Calvin cycle, but the phosphoglycolate must be converted into GP for use in the Calvin cycle by a complex series of reactions.
- These reaction involves a chloroplast, a peroxisome and a mitochondrion

- The two phases of photorespiration:

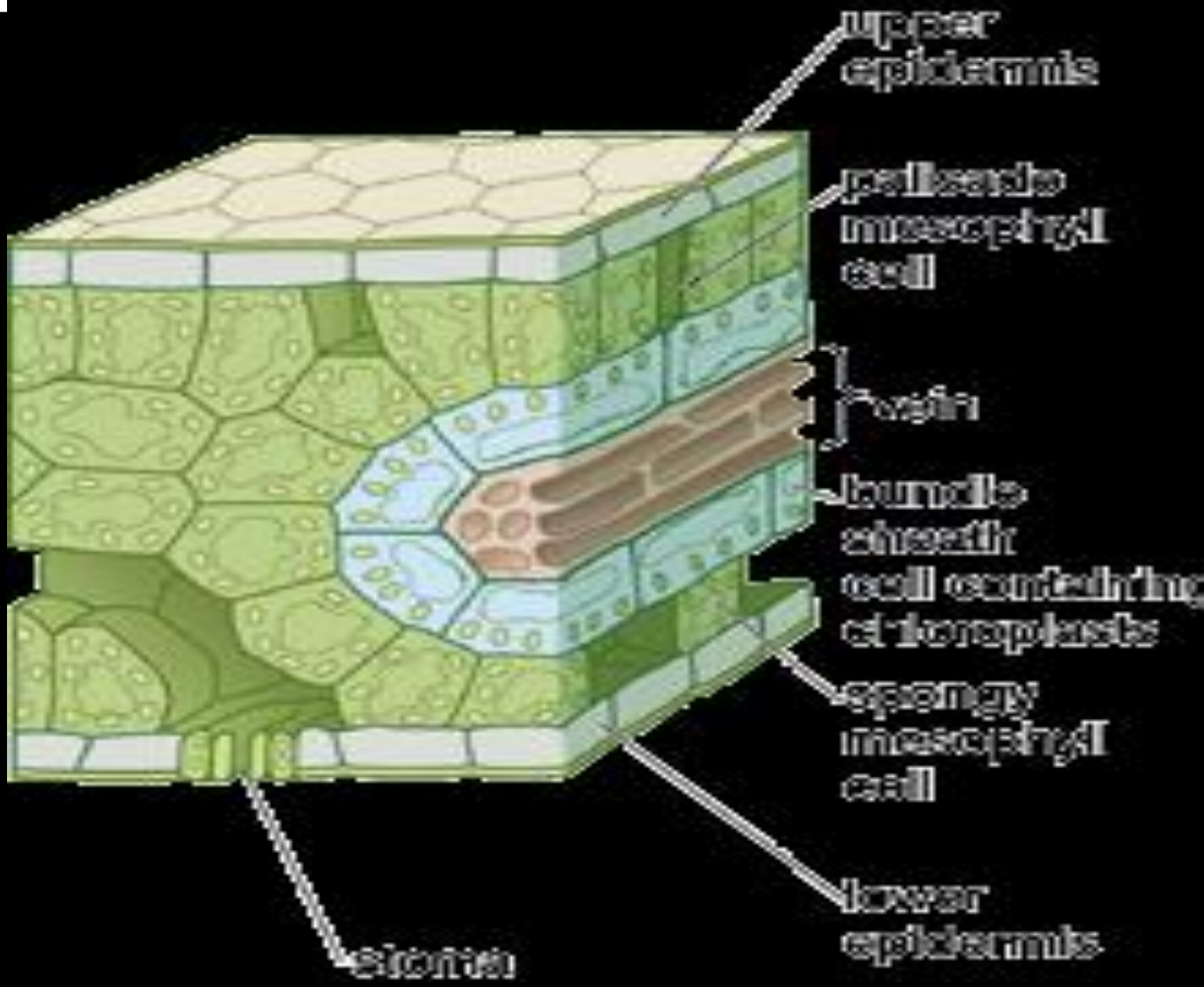
1. Rubisco catalyses a reaction between oxygen and RuBP to form one molecule of GP and one molecule of phosphoglycolate.
2. The phosphoglycolate is converted to GP in reactions in the chloroplast, peroxisome and mitochondrion

- **Photorespiration reduces the efficiency of photosynthesis for several reasons, including:**

a. **the carbon is oxidised, which is the reverse of photosynthesis**
b. **the ribulose bisphosphate must be re synthesised and the phosphoglycolate removed**
c. **ATP is used in the resynthesis of RuBP.**

C4 photosynthesis

- To get round the problem of photorespiration reducing the efficiency of photosynthesis, plants that grow in tropical areas like Ethiopia (such as maize, crabgrass, sorghum and sugarcane) have evolved a different photosynthetic pathway called C4 photosynthesis.
- As the name suggests, the first compound formed in the light-independent reactions is a **C4 compound** **not GP** .
- The light-dependent reactions are the same as in the C3 plants, but there is a difference in how glucose is synthesised in the light-independent reactions.


upper epidermis
palisade mesophyll cell
vein
bundle sheath cell containing chloroplasts
spongy mesophyll cell
lower epidermis
stoma

- The structure is essentially similar to that of a C3 plant, but there is one important difference.
- The cells of the **bundle sheath contain chloroplasts**, which they do not in C3 plants.
- Having no thylakoids means that the light-dependent reactions cannot occur here and so oxygen is not produced in these chloroplasts.
- This helps to prevent photorespiration and allows the Calvin cycle to take place in these cells.
- The light-dependent reactions in the C4 pathway also involve a set of reactions not found in C3 plants.

- These reactions take place in the mesophyll cells, which have chloroplasts with thylakoids and so can carry out the light-dependent reactions
- However, they do not have the enzymes to catalyse the reactions of the Calvin cycle.
- Instead, the following reactions take place:

1. Carbon dioxide reacts with a C3 compound called PEP to form the C4 compound oxaloacetate.

✓ This is catalysed by the enzyme PEP carboxylase.

2. Oxaloacetate is converted into another C4 compound (malate), which then passes from the mesophyll cell into a bundle sheath cell.

3. In the bundle sheath cell, malate is converted to pyruvate with the release of a molecule of carbon dioxide, which starts the reactions of the Calvin cycle by binding with RuBP.
4. The pyruvate is converted back to PEP; this reaction requires ATP.

- Overall, the C4 cycle uses two more molecules of ATP to deliver a molecule of carbon dioxide to Rubisco than does the C3 cycle.
- During active photosynthesis in the tropics, this is not a problem, as the high light intensity generates much ATP from the light-dependent reactions.

- C4 photosynthesis is most efficient in conditions of:

a. low carbon dioxide concentration
b. high light intensity
c. high temperature

DID YOU KNOW?

Cacti do it yet another way!

In the extreme heat of deserts, having stomata open during the day is a sure path to desiccation and death for the plants. But if they don't open their stomata, how will they get the carbon dioxide they need for photosynthesis? The answer is obvious really – open them at night when temperatures fall.

Cacti use what is essentially the same set of reactions as C4 plants, but they separate the two stages not by carrying them out in different cells, but by carrying them out at different times. The CAM photosynthesis cycle is as follows:

1. At night, the plants open their stomata to allow in CO_2, which then reacts with PEP in mesophyll cells to form oxaloacetate, and then malate just as in the C4 pathway.
2. The malate is then stored in the vacuoles of these cells overnight.
3. During the day, the light-dependent reactions generate ATP and reduced NADP so that the Calvin cycle can continue.
4. Malate is released from the vacuoles and is broken down to glycerate, releasing carbon dioxide for the reactions of the Calvin cycle.





sugar cane

pineapple

C_4

CAM

mesophyll cell

bundle sheath cell

CO_2

malate

Calvin cycle

sugar

1. CO_2 incorporated into four-carbon organic acids (carbon fixation)

2. malate releases CO_2 to Calvin cycle

night

day

(a) spatial separation of steps

(b) temporal separation of steps

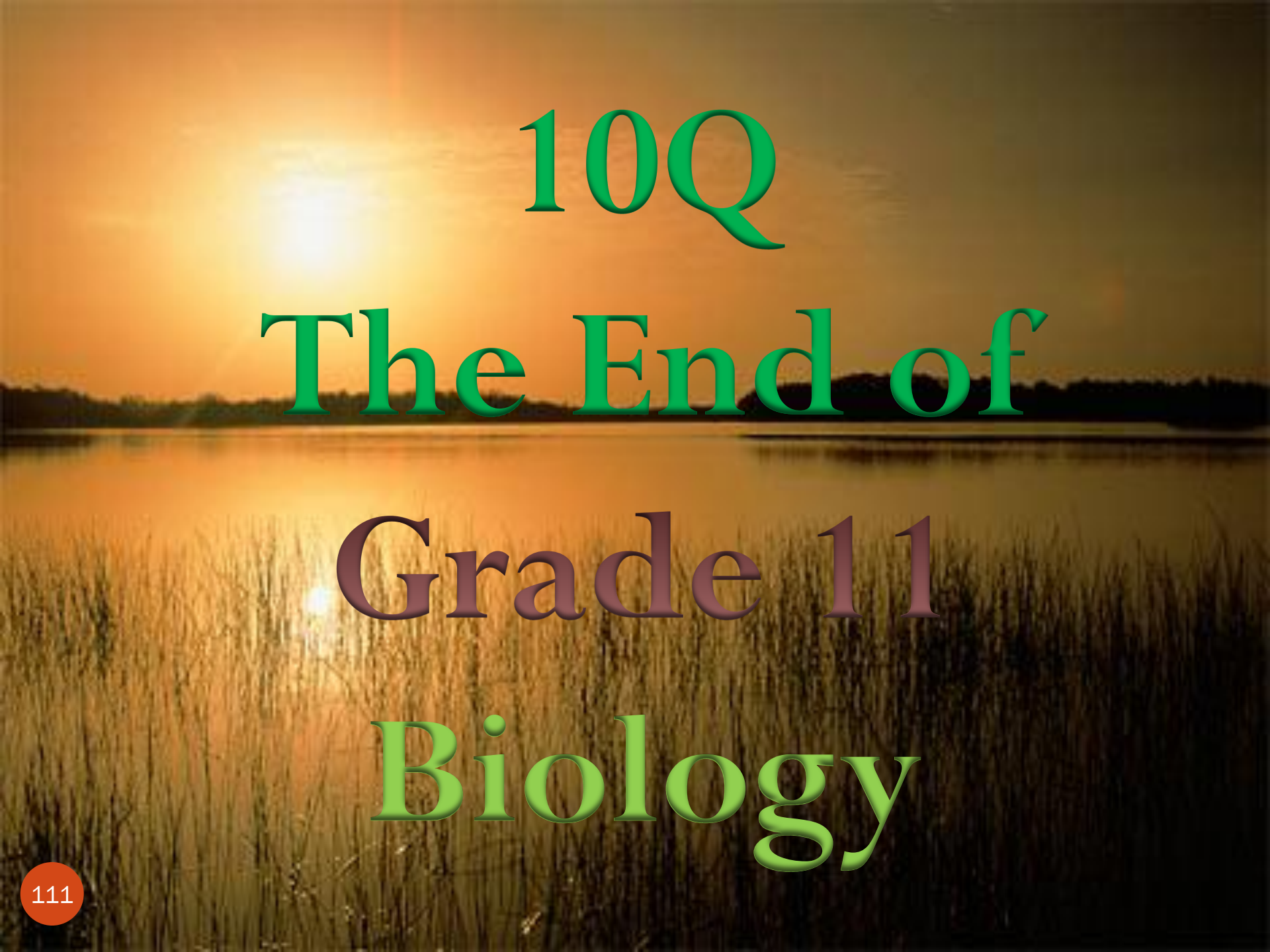
Figure 5.50 The C4 and CAM photosynthetic pathways

Feature	C3	C4
Bundle sheath cells	Lack chloroplasts	Have chloroplasts with no thylakoids
Enzyme used to fix CO_2	Rubisco	Pepco (PEP carboxylase)
Optimum temperature	15–25 °C	30–40 °C
Optimum CO_2 concentration	700 ppm	400 ppm
Fixation of CO_2	Mesophyll cells	Mesophyll cells
Calvin cycle	Mesophyll cells	Bundle sheath cells



Figure 5.43 Crop plants being grown in a polytunnel

- The crop plants that are grown in Ethiopia (such as sorghum and wheat) are all C4 plants and are, therefore, well adapted to photosynthesise efficiently in the hot, bright days found in this country.
- Crop plants that are grown in temperate areas (such as peas and carrots) would not photosynthesise as efficiently, because they are C3 plants. They would, therefore, not produce high yields.
- CAM= crassulucian acid metabolism


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