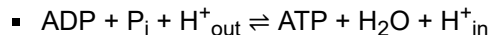


ATP synthase

ATP synthase is an enzyme that creates the energy storage molecule adenosine triphosphate (ATP). ATP is the most commonly used "energy currency" of cells for all organisms. It is formed from adenosine diphosphate (ADP) and inorganic phosphate (P_i). The overall reaction catalyzed by ATP synthase is:



The formation of ATP from ADP and P_i is energetically unfavorable and would normally proceed in the reverse direction. In order to drive this reaction forward, ATP synthase couples ATP synthesis during cellular respiration to an electrochemical gradient created by the difference in proton (H⁺) concentration across the mitochondrial membrane in eukaryotes or the plasma membrane in bacteria. During photosynthesis in plants, ATP is synthesized by ATP synthase using a proton gradient created in the thylakoid lumen through the thylakoid membrane and into the chloroplast stroma.

ATP synthase consists of two main subunits, F_O and F₁, which has a rotational motor mechanism allowing for ATP production.^{[1][2]} Because of its rotating subunit ATP Synthase is a molecular machine.

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F₁ region

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E. coli

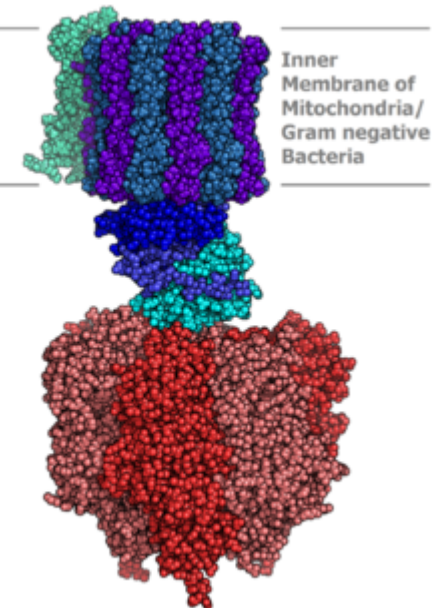
Yeast

Plant

Bovine

Human

ATP Synthase



Molecular model of ATP synthase determined by X-ray crystallography. Stator is not shown here.

Identifiers

EC number 3.6.3.14 (<http://www.chem.qmul.ac.uk/iubmb/enzyme/EC3/6/3/14.html>)

CAS number 9000-83-3 (<http://www.commonchemistry.org/ChemicalDetail.aspx?ref=9000-83-3&title=>)

Databases

See also

References

Further reading

External links

Nomenclature

The F_1 fraction derives its name from the term "Fraction 1" and F_O (written as a subscript letter "o", not "zero") derives its name from being the binding fraction for *oligomycin*, a type of naturally-derived antibiotic that is able to inhibit the F_O unit of ATP synthase.^{[3][4]} These functional regions consist of different protein subunits — refer to tables. This enzyme is used in synthesis of ATP through aerobic respiration.

Structure and function

Located within the *thylakoid membrane* and the *inner mitochondrial membrane*, ATP synthase consists of two regions F_O and F_1 . F_O causes rotation of F_1 and is made of c-ring and subunits a, b, d, F6. F_1 is made of α , β , γ , δ subunits. F_1 has a water-soluble part that can hydrolyze ATP. F_O on the other hand has mainly hydrophobic regions. $F_O F_1$ creates a pathway for protons movement across the membrane.^[7]

F_1 region

The F_1 portion of ATP synthase is hydrophilic and responsible for hydrolyzing ATP. This portion is located through the intermembrane space between the inter membrane space of the mitochondria. Subunits α and β make a hexamer with 6 binding sites. Three of them are catalytically inactive and they bind ADP.

Other three subunits catalyze the ATP synthesis. The other F_1 subunits γ , δ , ϵ are a part of a rotational motor mechanism. γ subunit allows β to go through conformational changes, i.e. closed, half open and open states allows for ATP to be bound and released once synthesized. The F_1 particle is large and can be seen in the transmission electron microscope by negative staining.^[8] These are particles of 9 nm diameter that pepper the inner mitochondrial membrane.

IntEnz	IntEnz view (https://www.ebi.ac.uk/intenz/query?cmd=SearchEC&ec=3.6.3.14)
BRENDA	BRENDA entry (http://www.brenda-enzymes.org/enzyme.php?ecno=3.6.3.14)
ExpPASy	NiceZyme view (http://www.expasy.org/enzyme/3.6.3.14)
KEGG	KEGG entry (http://www.genome.ad.jp/dbget-bin/www_bget?enzyme+3.6.3.14)
MetaCyc	metabolic pathway (https://biocyc.org/META/substring-search?type=NIL&object=3.6.3.14)
PRIAM	profile (http://priam.prabi.fr/cgi-bin/PRIAM_profiles_CurrentRelease.pl?EC=3.6.3.14)
PDB structures	RCSB PDB (http://www.rcsb.org/pdb/search/smartSubquery.do?smartSearchSubtype=EnzymeClassificationQuery&EnzymeClassification=3.6.3.14) PDBe (https://www.ebi.ac.uk/pdbe/entry/search/index?ec_number:3.6.3.14) PDBsum (https://www.ebi.ac.uk/thornton-srv/databases/cgi-bin/enzymes/GetPage.pl?ec_number=3.6.3.14)
Gene	AmiGO (http://amigo.geneontology.org)

F₁ - Subunits

Subunit	Human Gene
<u>alpha</u>	<u>ATP5A1</u> , <u>ATPAF2</u>
<u>beta</u>	<u>ATP5B</u> , <u>ATPAF1</u> , <u>C16orf7</u>
<u>gamma</u>	<u>ATP5C1</u>
<u>delta</u>	<u>ATP5D</u>
<u>epsilon</u>	<u>ATP5E</u>

F_O region

F_O is a water insoluble protein with eight subunits and a transmembrane ring. The ring has a tetramer shape with a helix loop helix protein that goes through conformational changes when protonated and deprotonated, pushing neighboring subunits to rotate, causing the spinning of F_O which then also affects conformation of F₁, resulting in switching of states of alpha and beta subunits. The F_O region of ATP synthase is a proton pore that is embedded in the mitochondrial membrane. It consists of three main subunits a, b, and c, and (in humans) six additional subunits, d, e, f, g, F6, and 8 (or A6L). An atomic model for the dimeric yeast F_O region was determined by cryo-EM at an overall resolution of 3.6 Å^[10] This part of the enzyme is located inside the inter membrane space and is actually the portion that catalyzes the reaction between ADP and the inorganic phosphate.

F_O-Main subunits

Subunit	Human Gene
<u>a</u>	<u>ATP6</u>
<u>b</u>	<u>ATP5F1</u>
<u>c</u>	<u>ATP5G1</u> , <u>ATP5G2</u> , <u>ATP5G3</u>

Binding model

In the 1960s through the 1970s, Paul Boyer, a UCLA Professor, developed the binding change, or flip-flop, mechanism theory, which postulated that ATP synthesis is dependent on a conformational change in ATP synthase generated by rotation of the gamma subunit. The research group of John E. Walker, then at the

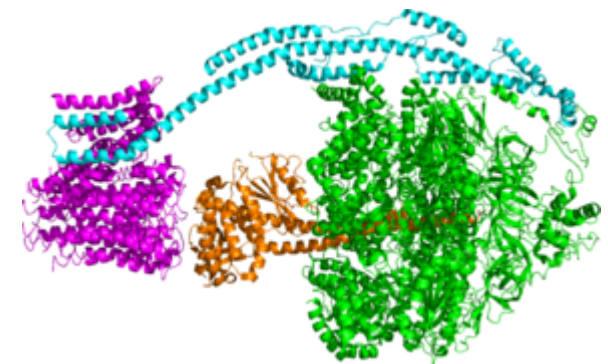
Ontology [ogy.org/cgi-bin/amigo/go.cgi?query=0046961&view=details](https://www.ebi.ac.uk/QuickGO/term/GO:0046961) / QuickGO (<https://www.ebi.ac.uk/QuickGO/term/GO:0046961>)

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PubMed articles (<https://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=pubmed&term=3.6.3.14%5BEC/RN%20Number%5D>)

NCBI proteins (<https://www.ncbi.nlm.nih.gov/protein?term=3.6.3.14%5BEC/RN%20Number%5D>)



Bovine mitochondrial ATP synthase. The F_O, F₁, axle, and stator regions are color coded magenta, green, orange, and cyan respectively.^{[5][6]}

MRC Laboratory of Molecular Biology in Cambridge, crystallized the F_1 catalytic-domain of ATP synthase. The structure, at the time the largest asymmetric protein structure known, indicated that Boyer's rotary-catalysis model was, in essence, correct. For elucidating this, Boyer and Walker shared half of the 1997 [Nobel Prize in Chemistry](#).

The crystal structure of the F_1 showed alternating alpha and beta [subunits](#) (3 of each), arranged like segments of an orange around a rotating asymmetrical gamma subunit. According to the current model of ATP synthesis (known as the alternating catalytic model), the transmembrane potential created by (H^+) proton cations supplied by the electron transport chain, drives the (H^+) proton cations from the intermembrane space through the membrane via the F_O region of ATP synthase. A portion of the F_O (the ring of [c-subunits](#)) [rotates](#) as the protons pass through the membrane. The [c-ring](#) is tightly attached to the asymmetric central stalk (consisting primarily of the gamma subunit), causing it to rotate within the $\alpha_3\beta_3$ of F_1 causing the 3 catalytic nucleotide binding sites to go through a series of conformational changes that lead to ATP synthesis. The major F_1 subunits are prevented from rotating in sympathy with the central stalk rotor by a peripheral stalk that joins the $\alpha_3\beta_3$ to the non-rotating portion of F_O . The structure of the intact ATP synthase is currently known at low-resolution from [electron cryo-microscopy](#) (cryo-EM) studies of the complex. The cryo-EM model of ATP synthase suggests that the peripheral stalk is a flexible structure that wraps around the complex as it joins F_1 to F_O . Under the right conditions, the enzyme reaction can also be carried out in reverse, with ATP hydrolysis driving proton pumping across the membrane.

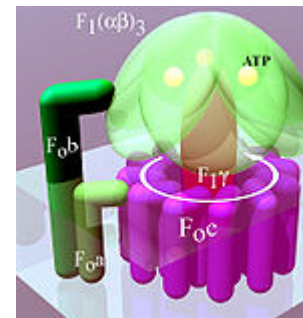
The binding change mechanism involves the active site of a β subunit's cycling between three states.^[11] In the "loose" state, ADP and phosphate enter the active site; in the adjacent diagram, this is shown in pink. The enzyme then undergoes a change in shape and forces these molecules together, with the active site in the resulting "tight" state (shown in red) binding the newly produced ATP molecule with very high [affinity](#). Finally, the active site cycles back to the open state (orange), releasing ATP and binding more ADP and phosphate, ready for the next cycle of ATP production.^[12]

Physiological role

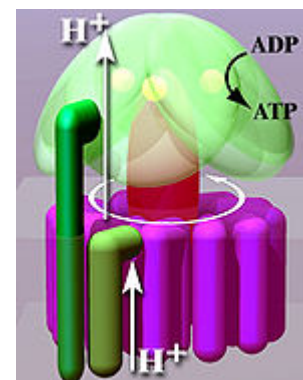
Like other enzymes, the activity of F_1F_O ATP synthase is reversible. Large-enough quantities of ATP cause it to create a transmembrane [proton gradient](#), this is used by fermenting bacteria that do not have an electron transport chain, but rather hydrolyze ATP to make a proton gradient, which they use to drive [flagella](#) and the transport of nutrients into the cell.

In respiring [bacteria](#) under physiological conditions, ATP synthase, in general, runs in the opposite direction, creating ATP while using the [proton motive force](#) created by the [electron transport chain](#) as a source of energy. The overall process of creating energy in this fashion is termed [oxidative phosphorylation](#). The same process takes place in the [mitochondria](#), where ATP synthase is located in the inner mitochondrial membrane and the F_1 -part projects into mitochondrial matrix. The consumption of ATP by ATP-synthase pumps proton cations into the matrix.

Evolution



Simplified model of F_0F_1 -ATPase alias ATP synthase of *E. coli*. Subunits of the enzyme are labeled accordingly.



Rotation engine of ATP synthase.

The evolution of ATP synthase is thought to have been modular whereby two functionally independent subunits became associated and gained new functionality.^{[13][14]} This association appears to have occurred early in evolutionary history, because essentially the same structure and activity of ATP synthase enzymes are present in all kingdoms of life.^[13] The F-ATP synthase displays high functional and mechanistic similarity to the V-ATPase.^[15] However, whereas the F-ATP synthase generates ATP by utilising a proton gradient, the V-ATPase generates a proton gradient at the expense of ATP, generating pH values of as low as 1.^[16]

The F₁ region also shows significant similarity to hexameric DNA helicases, and the F_O region shows some similarity to H⁺-powered flagellar motor complexes.^[15] The α₃β₃ hexamer of the F₁ region shows significant structural similarity to hexameric DNA helicases; both form a ring with 3-fold rotational symmetry with a central pore. Both have roles dependent on the relative rotation of a macromolecule within the pore; the DNA helicases use the helical shape of DNA to drive their motion along the DNA molecule and to detect supercoiling, whereas the α₃β₃ hexamer uses the conformational changes through the rotation of the γ subunit to drive an enzymatic reaction.^[17]

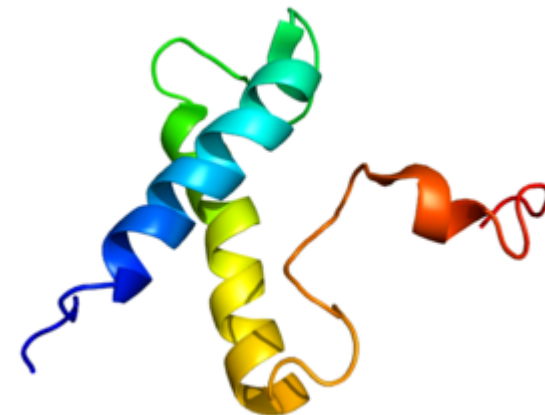
The H⁺ motor of the F_O particle shows great functional similarity to the H⁺ motors that drive flagella.^[15] Both feature a ring of many small alpha-helical proteins that rotate relative to nearby stationary proteins, using a H⁺ potential gradient as an energy source. This link is tenuous, however, as the overall structure of flagellar motors is far more complex than that of the F_O particle and the ring with about 30 rotating proteins is far larger than the 10, 11, or 14 helical proteins in the F_O complex.

The modular evolution theory for the origin of ATP synthase suggests that two subunits with independent function, a DNA helicase with ATPase activity and a H⁺ motor, were able to bind, and the rotation of the motor drove the ATPase activity of the helicase in reverse.^{[13][17]} This complex then evolved greater efficiency and eventually developed into today's intricate ATP synthases. Alternatively, the DNA helicase/H⁺ motor complex may have had H⁺ pump activity with the ATPase activity of the helicase driving the H⁺ motor in reverse.^[13] This may have evolved to carry out the reverse reaction and act as an ATP synthase.^{[14][18][19]}

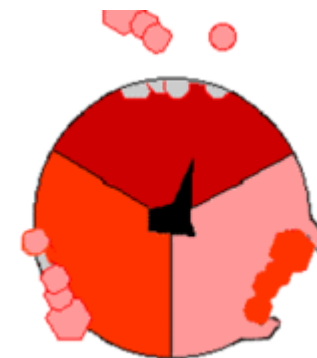
In different species

E. coli

E. coli ATP synthase is the simplest known form of ATP synthase, with 8 different subunit types.^[20]



F_O subunit F6 from the peripheral stalk region of ATP synthase.^[9]



Mechanism of ATP synthase. ADP and P_i (pink) shown being combined into ATP (red), and the rotating γ (gamma) subunit in black causing conformation.

Yeast

Yeast ATP synthase is one of the best-studied eukaryotic ATP synthases; and five F_1 , eight F_0 subunits, and seven associated proteins have been identified.^[7] Most of these proteins have homologues in other eukaryotes.^{[21][22][23]}

Plant

In plants, ATP synthase is also present in chloroplasts (CF_1F_0 -ATP synthase). The enzyme is integrated into thylakoid membrane; the CF_1 -part sticks into stroma, where dark reactions of photosynthesis (also called the light-independent reactions or the Calvin cycle) and ATP synthesis take place. The overall structure and the catalytic mechanism of the chloroplast ATP synthase are almost the same as those of the mitochondrial enzyme. However, in chloroplasts, the proton motive force is generated not by respiratory electron transport chain but by primary photosynthetic proteins.

Bovine

The ATP synthase isolated from bovine heart mitochondria (*Bos taurus*) is, in terms of biochemistry and structure, the best-characterized ATP synthase. Beef heart is used as a source for the enzyme because of the high concentration of mitochondria in cardiac muscle.^{[24][25][26]}

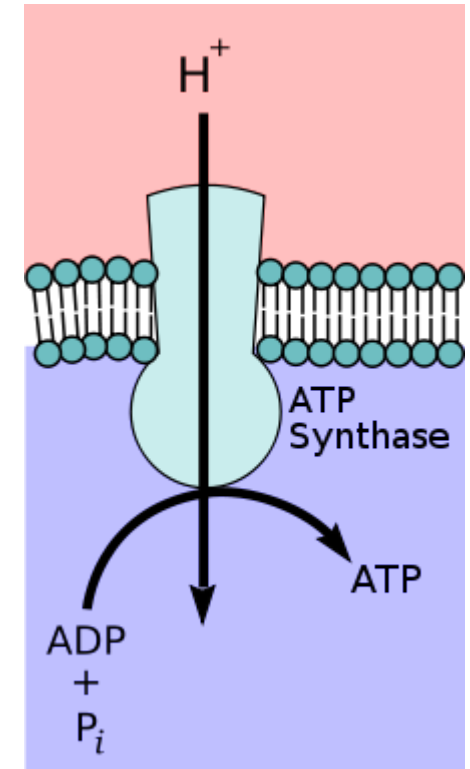
Human

The following is a list of humans genes that encode components of ATP synthases:

- ATP5A1, ATP5AL1
- ATP5B, ATP5BL1
- ATP5C2, ATP5D, ATP5E, ATP5F1, ATP5G1, ATP5G2, ATP5G3, ATP5H, ATP5HP1, ATP5I, ATP5J, ATP5J2, ATP5L, ATP5L2, ATP5O, ATP5S
- ATP6, ATP6AP1, ATP6AP2
- ATPSBL1, ATPSBL2
- MT-ATP6, MT-ATP8

See also

- ATP10 protein required for the assembly of the F_0 sector of the mitochondrial ATPase complex.
- Chloroplast
- Electron transfer chain
- Flavoprotein
- Mitochondrion
- Oxidative phosphorylation
- P-ATPase
- Proton pump





Depiction of ATP synthase using the chemiosmotic proton gradient to power ATP synthesis through oxidative phosphorylation.

- [Rotating locomotion in living systems](#)
- [Transmembrane ATPase](#)

- [V-ATPase](#)

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Further reading

- Nick Lane: *The Vital Question - Energy, Evolution, and the Origins of Complex Life* (https://books.google.com/books?id=IfJYBQAAQBAJ&pg=PT77&lpg=PT77&dq=nick+lane+the+vital+question+f0+f1+atp+synthase&source=bl&ots=wZ1vmiXh7z&sig=DAn9E_5fw8XGQ8nmsGom1_R4Vll&hl=de&sa=X&ved=0ahUKEwjKnLWhtuPVAhWLPxQKHxK3B1sQ6AEIIDA#v=onepage&q=nick%20lane%20the%20vital%20question%20f0%20f1%20atp%20synthase&f=false), Ww Norton, 2015-07-20, ISBN 978-0393088816 (Link points to Figure 10 showing model of ATP synthase)

External links

- Boris A. Feniouk: "ATP synthase — a splendid molecular machine" (<http://www.atpsynthase.info/>)
- Well illustrated ATP synthase lecture (<http://www.life.uiuc.edu/crofts/bioph354/lect10.html>) by Antony Crofts of the University of Illinois at Urbana-Champaign.
- Proton and Sodium translocating F-type, V-type and A-type ATPases in OPM database (<http://opm.phar.umich.edu/families.php?superfamily=5>)
- The Nobel Prize in Chemistry 1997 (http://nobelprize.org/nobel_prizes/chemistry/laureates/1997/illpres/index.html) to Paul D. Boyer and John E. Walker for the enzymatic mechanism of synthesis of ATP; and to Jens C. Skou, for discovery of an ion-transporting enzyme, Na⁺, K⁺-ATPase.
- Harvard Multimedia Production Site — Videos (<https://web.archive.org/web/20080422024412/http://multimedia.mcb.harvard.edu/media.html>) — ATP synthesis animation
- David Goodsell: "ATP Synthase- Molecule of the Month" (<http://www.rcsb.org/pdb/101/motm.do?momID=72>)

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