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The Chloroplast ATP Synthase: Structural Changes During Catalysis

Mark L. Richter[1] and Fei Gao[1]

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This article summarizes some of the evidence for the existence of light-driven structural changes in the ε and γ subunits of the chlorplast ATP synthase. Formation of a transmembrane proton gradient results in: (1) a change in the position of the ε subunit such that it becomes exposed to polyclonal antibodies and to reagents which selectively modify εLys109; (2) enhanced solvent accessibility of several sulfhydryl residues on the γ subunit; and (3) release/exchange of tightly bound ADP from the enzyme. These and related experimental observations can, at least partially, be explained in terms of two different bound conformational states of the ε subunit. Evidence for structural changes in the enzyme which are driven by light or nucleotide binding is discussed with special reference to the popular rotational model for catalysis.

KEY WORDS: Chloroplast F_1 epsilon and gamma subunit; nucleotide/proton-driven conformation.

INTRODUCTION

The chloroplast ATP synthase, like its closely related counterparts in bacteria and mitochondria, is made up of two physically separable parts, CF_0 (chloroplast coupling factor 0) which is an integral membrane-spanning proton channel, and CF_1 (chloroplast coupling factor 1) which is peripheral to the membrane and contains the catalytic site(s) for reversible ATP synthesis. CF_0 has four different subunit types, labeled I to IV, whereas CF_1 has five different subunit types labeled α to ε in order of decreasing molecular weight. The probable subunit stoichiometry is $I_1II_1III_{12}I-V_1\alpha_3\beta_3\gamma_1\delta_1\varepsilon_1$ (reviewed in Richter and Mills, 1995). The chloroplast F_1-F_0 very closely resembles the bacterial enzyme in its subunit composition (reviewed in Hatefi, 1985). There is, however, substantial overall structural similarity among all of the ATP synthases, as well as a very high degree of amino acid sequence homology within structurally and functionally important regions of the different F_1-F_0 subunits (Walker *et al.*, 1985). These are compelling reasons to assume that all of the ATP synthases share a common ancestry and almost certainly use the same basic catalytic mechanism for ATP synthesis/hydrolysis.

The reader is referred to several recent reviews which have dealt with various aspects of the structure and function of the chloroplast ATP synthase (McCarty and Nalin, 1986; Nalin and Nelson, 1987; Ort, 1992; Richter and Mills, 1995). This article will summarize studies of the chloroplast enzyme which have demonstrated the occurrence of significant structural changes in the enzyme during activation and catalysis. These studies will be discussed with special reference to the controversial rotational model for catalysis, which has gained considerable support recently as a possible general catalytic feature of the ATP synthase enzymes. The most pertinent details of this model are discussed briefly in the following section.

ROTATIONAL CATALYSIS

The idea that subunits of the F_1 portion of the ATP synthase may rotate relative to other subunits

[1] Department of Biochemistry, The University of Kansas, Lawrence, Kansas 66045.

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of the enzyme during the catalytic cycle is a natural extension of the binding change hypothesis proposed some years ago by Paul Boyer and colleagues (reviewed in Boyer, 1993). In order to achieve a sequential change in the conformations of three participating catalytic sites, as predicted by this model, it was proposed that the hexameric ring formed by alternating α and β subunits of F_1 rotates relative to the smaller, single copy subunits. Changing interactions between the αβ ring and the small subunits would provide the necessary structural asymmetry to allow all three catalytic sites to be structurally inequivalent at any given time in the catalytic cycle. The published structure of part of the mitochondrial F_1 has renewed interest in the rotational model, as it identified three potential catalytic sites, one on each of the three β subunits, existing in three different conformational states. The three conformational states loosely corresponded to those predicted by the binding change hypothesis (Abrahams *et al.*, 1994).

Included in the crystal structure were three helical segments of the γ subunit. A very long α helix comprised of the 64 C-terminal γ residues 209 to 272 was shown to extend all the way from the base to the top of the hexamer. The last seven or eight residues of the helix extended through a sleeve of hydrophobic residues formed from the N-terminal domains of all six αβ subunits. The γ helix was proposed to act as a spindle about which the αβ hexamer rotates, the hydrophobic sleeve providing a greasy bearing to facilitate rotation. The γ subunit contacted the hexamer in two other places, a catch between the C-terminal helix and one of the three β subunits, and another catch between a small helical stretch of γ located at the very bottom of the molecule which interacts with a helical "foot" of another β subunit. The different interactions between the αβ subunits and different parts of the γ subunit introduced a significant amount of asymmetry into the αβ hexamer. It was suggested that, as the αβ hexamer rotated relative to the γ subunit, the γ contacts would sequentially impart the necessary conformational information to the three catalytic sites (Abrahams *et al.*, 1994).

LIGHT-INDUCED STRUCTURAL CHANGES IN THE γ AND ε SUBUNITS OF CF_1

That CF_1 undergoes some kind of conformational change during energization of thylakoid membranes was first observed by Ryrie and Jagendorf (1971) who noted a light-dependent exchange of tritiated water from the medium into CF_1. Indeed, the crystal structure of the mitochondrial enzyme revealed a sizable aqueous pocket within the central portion of the hexameric structure of the enzyme (Abrahams *et al.*, 1994).

Extensive analysis centered around the four cysteine residues of the 36 kDa γ subunit of CF_1 by McCarty and coworkers (reviewed in McCarty and Moroney, 1985; McCarty and Richter, 1987), has identified an integral role of the γ subunit in regulating the catalytic activity of the enzyme. Figure 1 shows a cartoon of the chloroplast γ subunit illustrating the location of the four sulfhydryl residues, two of which (cysteines 199 and 205) form a disulfide bond, the only one present in CF_1. The cartoon also shows the corresponding positions of the three helical segments of the mitochondrial γ (hatched areas) which were identified in the crystal structure.

In contrast to the bacterial and mitochondrial enzymes, the chloroplast ATP synthase is a latent ATPase requiring some form of activation for expression of significant rates of ATP hydrolysis. Activation of CF_1 from dark-adapted membranes can be achieved artificially in two ways; (1) reduction of the γ disulfide bond (Fig. 1) using thiol reducing agents such as dithi-

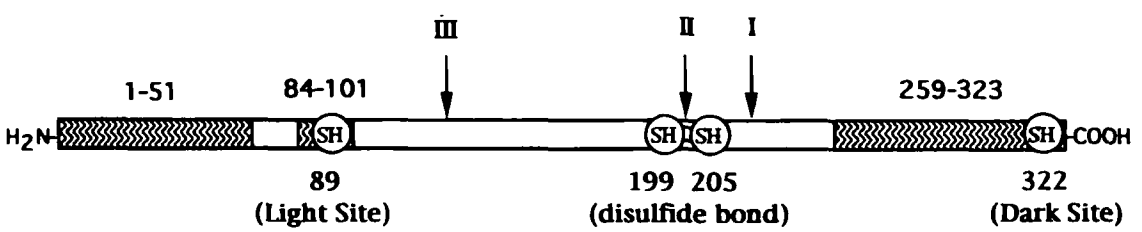

Fig. 1. Structural features of the chloroplast γ subunit. The positions of the four cysteine residues of the spinach chloroplast γ subunit are indicated. The hatched areas are the regions corresponding to the three α helical segments of the mitochondrial F_1 which were identified in the 2.8 Å crystal structure (Abrahams *et al.*, 1994). The Roman numerals indicate three tryptic cleavage sites which are cleaved during limited trypsin digestion of either CF_1 lacking the ε subunit or CF_1 reduced by exposure to dithiothreitol (Schumann *et al.*, 1985).

othreitol (Arana and Vallejos, 1982; Nalin and McCarty, 1984), or (2) removal of the inhibitory ε subunit from CF_1 (Richter *et al.*, 1984, 1985). These two activation mechanisms are interrelated. Reduction of the γ disulfide bond decreases the affinity of CF_1 for the ε subunit by about twentyfold (Soteropoulos *et al.*, 1992a). On the other hand, removal of ε from CF_1 exposes trypsin-sensitive sites on the γ subunit (sites I and II in Fig. 1) and significantly enhances the accessibility of the γ disulfide bond to thiol reagents (Richter *et al.*, 1985; Schumann *et al.*, 1985). The activations resulting from reduction of the γ disulfide and from ε removal are additive. For example, removal of the ε subunit increases the specific ATPase activity from ca. 0.6 to ca. 14 μmol per min per mg of protein at 37°C, a decrease in activation energy of about 12 kcal per mole. Subsequent reduction of the γ disulfide by dithiothreitol doubles the specific activity of the ε-deficient CF_1 at 37°C, an additional decrease of ca. 5 kcal per mole in activation energy for ATP hydrolysis (Richter and McCarty, 1987b).

Activation of the latent ATPase activity of CF_1 on the membrane is also achieved by reducing the γ disulfide either artificially by dithiothreitol, or under physiological conditions by the enzyme thioredoxin (Mills and Mitchell, 1982; Dann and McCarty, 1992). Efficient reduction of the γ disulfide, as well as induction and maintenance of the activated state of the enzyme, both require the presence of a small transmembrane potential gradient (reviewed by McCarty and Moroney, 1985 and Ort and Oxborough, 1992). A close relationship between the γ and ε subunits for activation of the membrane-bound enzyme has also been observed. Induction of the activated state of the enzyme by formation of a light-driven transmembrane potential gradient coincides with formation of an activated state in CF_1 which is essentially identical to the ε-deficient state of the isolated enzyme (Richter *et al.*, 1985; Schumann *et al.*, 1985). In the light, accessibility of the γ disulfide is significantly enhanced, and the same trypsin-sensitive sites on γ that were exposed by ε removal in isolated CF_1 (sites I and II in Fig. 1) become exposed (Nalin and McCarty, 1984; Ketcham *et al.*, 1984; Schumann *et al.*, 1985).

Further evidence for light-induced structural change in the γ subunit has been indicated by the differential reactivity toward sulfhydryl reagents of the remaining two cysteinyl residues of the γ subunit, Cys89 and Cys322 (Fig. 1). Cysteine 322 is readily labeled by sulfhydryl reagents under all conditions on or off the membrane with no observable effect on catalytic activity. This residue has been called the "dark" site to distinguish it from Cys89 which is only accessible to sulfhydryl reagents in the light and is thus termed the "light" site. Modification of Cys89 by maleimides strongly inhibits ATP synthesis and hydrolysis by CF_1 (Moroney *et al.*, 1980; Nalin *et al.*, 1983). Treatment of CF_1–CF_0 in the light with bifunctional maleimides resulted in an internal crosslink within the γ subunit between Cys89 and one of the other three γ sulfhydryls. The other sulfhydryl was assumed to be Cys322 since crosslinking occurred regardless of the oxidation state of the γ disulfide bond. Formation of the crosslink resulted in inhibition of ATP synthesis and hydrolysis as well as a pronounced increase in the proton permeability of the membranes (Moroney and McCarty, 1979). The close proximity between Cys89 and Cys322 was confirmed by fluorescence resonance energy transfer distance measurements (Richter *et al.*, 1985). This is, however, at extreme odds with the crystal structure of mitochondrial F_1 which places the equivalent residues on mitochondrial F_1 ca. 70 Å apart (Abrahams *et al.*, 1994).

Formation of a reversible disulfide crosslink between the segment of *E. coli* γ which contains the residue equivalent to Cys89 of $CF_1\gamma$, and a conserved region of one of the three β subunits, resulted in essentially complete inhibition of the ATPase activity of the enzyme (Duncan *et al.*, 1995a). This confirms that the region of γ in the vicinity of Cys89 is important for catalysis, possibly by forming an essential and reversible contact with the β subunit during the catalytic cycle. Further studies (Duncan *et al.*, 1995b) have suggested that this region of γ may reversibly interact with each of the three β subunits in *E. coli* F_1 under conditions of catalytic turnover, strongly supporting the rotational model. This is consistent with the observation that Cys89 on CF_1 becomes exposed to sulfhydryl reagents in response to light, indicating that it may change position during catalysis on CF_1 also. However, we have tried exhaustively, without success, to label Cys89 on isolated CF_1 under many different conditions including slow and rapid turnover. The fact that Cys89 remains totally inaccessible in the isolated form of the enzyme suggests to us that the conformation of CF_1 during turnover on the membrane is significantly different from that during turnover off the membrane.

Attempts to crosslink different subunits of CF_1 to each other to test the rotational hypothesis have provided mixed results. In one study, the γ subunit was crosslinked to the αβ hexamer using bifunctional

reagents attached to the dark and disulfide sulfhydryls of γ (Musier and Hammes, 1987). Although crosslinking appeared to be extensive (ca. 70%) the enzyme was scarcely inhibited (<10%), thus arguing against rotation. On the other hand, studies using photoaffinity azido nucleotide analogs (Melese and Boyer, 1985) suggested that all three β subunits are capable of switching properties with each other during catalytic turnover. Similarly, forming a reversible disulfide crosslink introduced between the γ subunit (the region corresponding to the Cys89 in $CF_1\gamma$, see Fig. 1) and one of the three β subunits of *E. coli* F_1 reversibly inhibited catalytic activity (Duncan *et al.*, 1995a). These observations clearly show that flexibility of the γ subunit is critical for function, but suggest that complete rotation of the γ subunit within the αβ hexamer is not necessary. A similar conclusion was reached from crosslinking studies involving the ε subunit of the *E. coli* F_1 (Mendel-Hartvig and Capaldi, 1991).

Changes in the conformation of the ε subunit on CF_1–CF_0 have also been observed using polyclonal antibodies (Richter and McCarty, 1987b). Access of the antibodies to their targets on the ε subunit was light-dependent. Once bound, the antibodies stripped the ε subunit from the complex and uncoupled the membranes. Similarly, formation of a light-induced change in the conformation of the ε subunit resulted in a significant increase in accessibility of εLys109 to modifying reagents (Komatsu-Takaki, 1989). These experiments have pioneered the idea that the γ and ε subunits are involved in responding to the transmembrane potential gradient, and may indeed be responsible, at least in part, for gating the flow of protons across the membrane.

CF_1 will bind specifically to thylakoid membranes in the absence of the ε subunit, but the membranes remain proton permeable. Addition of isolated ε subunit to the membranes containing the bound ε-deficient enzyme blocked proton permeation and restored coupled enzyme activity (Richter *et al.*, 1984). It is not likely, therefore, that the ε subunit dissociates completely from the enzyme during activation and catalysis of the membrane-bound enzyme, but rather it probably shifts between different conformational states in a proton-dependent manner (Richter and McCarty, 1987b). This change is indicated by the cartoon shown in Fig. 2 which suggests that the ε subunit moves between two conformational states, a light-driven state in which it associates more closely with CF_0 and an alternate state in which it associates more closely with CF_1. A direct interaction between ε and subunit III of CF_0 has been indicated from crosslinking studies (Süss, 1986). The model also speculates that as ε moves toward the membrane it drags part of γ with it thus exposing Cys89 to the medium.

One of the key questions to be answered in connection with the movement of the ε and γ subunits is whether the change in conformation is part of an

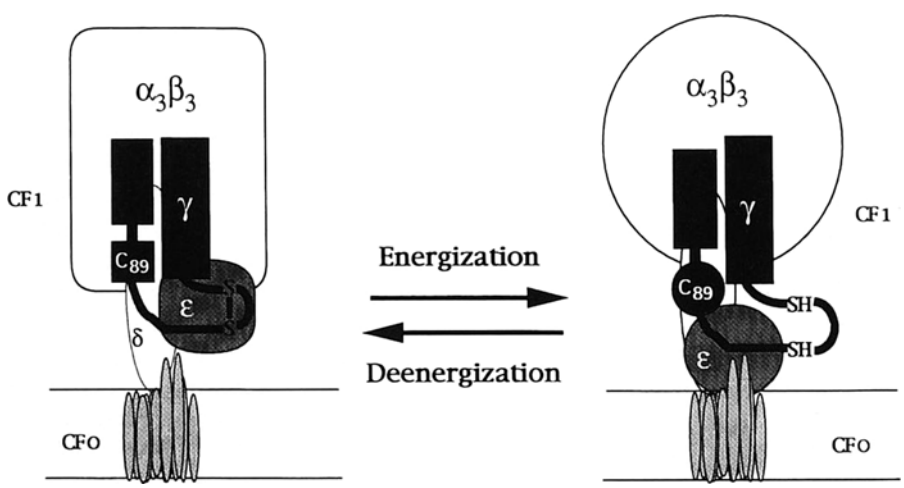

Fig. 2. Model showing light-induced movement of the ε subunit of CF_1. The model suggests that light induces a change in the position of the ε subunit such that it associates primarily with components of the proton channel portion of the ATP synthase. Light-induced movement of ε toward the membrane would expose the γ disulfide bond to the medium. As ε moves it may pull part of the γ subunit along with it, exposing γCys89 to the medium. Tight binding of ADP and phosphate would favor the alternate conformation in which ε binds primarily to CF_1.

activation process, an integral part of the catalytic cycle, or both. A hint that the changes may be part of the catalytic cycle is provided by the observation that addition of the substrates ADP and phosphate significantly lowers the extent of labeling of the *light* site on γ (Moroney *et al.*, 1980) and decreases the accessibility of ε Lys109 (Komatsu-Takaki, 1989) in the light. These observations suggest that the light-induced state of CF_1 in which the conformations of ε and γ are altered, reflects a conformational state that is only transiently present while the enzyme is actively turning over.

Numerous studies (for example, Strotmann *et al.*, 1976; Bickel-Sandkotter, 1983; Schumann, 1984; Feldman and Boyer, 1985; Fromme and Gräber, 1990; Groth and Junge, 1993) have documented the presence of light-induced changes in the enzyme which result in release of tightly bound nucleotides and enhanced rates of exchange of nucleotides from the enzyme. Recent studies of isolated CF_1 have suggested that removal of ε from the enzyme promotes the exchange of the tightly bound ADP (Richter, unpublished observation). Since a form of F_1 containing tightly bound ADP may be an essential intermediate catalytic state of the enzyme (Strotmann, 1986; Boyer, 1989; Schumann, 1990), reversible association of ε may be the means of achieving this intermediate state. Soteropoulis *et al.* (1992b) showed that light-dependent alkylation of γCys89 did not alter ε binding to CF_1 but led to a significant enhancement of cooperative nucleotide exchange on the enzyme. Thus alkylation blocked the effect of ε binding, supporting the idea that a direct interaction between ε and γ mediates proton-driven changes in the properties of nucleotide binding sites on the enzyme (Fig. 2).

AN INTACT γ SUBUNIT IS NOT REQUIRED FOR ATPASE ACTIVITY

Tryptic cleavage of the γ subunit of isolated or membrane-bound CF_1 at the sites which are exposed upon ε removal (sites I and II in Fig. 1) results in release from the enzyme of the small segment of the γ subunit in-between the two cleavage sites. In isolated CF_1, tryptic cleavage in this region of γ is accompanied by a substantial further activation of the ATPase activity of CF_1 (Moroney and McCarty, 1982a; Richter *et al.*, 1985; Nalin and McCarty, 1984). It also results in a complete loss of the inhibitory response to ε binding, indicating that ε inhibition requires connectivity between the C-terminal and N-terminal parts of the γ subunit (Richter *et al.*, 1985). The γ subunit can be further cleaved by trypsin, at least at the site III, without significant loss of ATPase activity (Moroney and McCarty, 1982a; Schumann *et al.*, 1985). Interestingly, tryptic cleavage at sites I and II of γ (Fig. 1) on the membrane-bound enzyme results in a dramatic activation of the ATPase activity, but the membranes become uncoupled (Moroney and McCarty, 1982b).

Gao *et al.* (1995) recently described methods for purifying and reconstituting the γ subunit with an αβ complex purified from CF_1 to form a fully active core enzyme complex. The same methods have been successfully used to reconstitute the active core enzyme using cloned, overexpressed γ subunit which was solubilized from inclusion bodies and folded during dialysis (Gao and Richter, unpublished experiments). This system was used to examine the ability of two fragments of the γ subunit to reconstitute with the native α and β subunits, an N-terminal fragment consisting of residues 1–196, and a C-terminal fragment consisting of residues 206–323. The nine residues missing between residues 196 and 206 includes the γ disulfide sulfhydryls (Fig. 1). The two fragments were independently over-expressed, solubilized from inclusion bodies and folded. Together, but not individually, the two fragments could reconstitute with the αβ subunits to form an enzyme complex which exhibited more than 50% of wild type ATPase activity and normal sensitivity to inhibitors of CF_1. This nicely confirms the results obtained with trypsin in indicating that the γ subunit need not be intact for high rates of catalysis by CF_1 *in vitro*.

Comparison of the sequence of spinach γ with sequences of γ subunits from other organisms (Mikki *et al.*, 1988), taken together with the known position of two introns in the spinach γ gene (Mason and Whitfeld, 1990), suggests that there are three domains in the γ subunit, an N-terminal domain consisting of residues 1–138, a central domain consisting of residues 139–220, and a C-terminal domain consisting of residues 221–323. The major sites of tryptic cleavage during limited tryptic digestion (Fig. 1) fall nicely into the regions likely to connect the three domains (Schumann *et al.*, 1985). The tryptic cleavage experiments have clearly demonstrated that direct sequence connectivity between these domains of the γ subunit is not required for uncoupled ATP hydrolysis, but is absolutely necessary for all coupled processes as well as for effective regulation by the ε subunit. Any model for rotational catalysis which requires the coincident movement of

different parts of the γ subunit relative to other parts of the enzyme, must take these observations into account.

EVIDENCE FOR PERMANENT STRUCTURAL ASYMMETRY WITHIN CF_1

Treatment of CF_1 with the vinyl-sulfone derivative of the fluorophore Lucifer Yellow resulted in selective labeling of a single lysine residue at position 385 on one of the three α subunits (Nalin *et al.*, 1985). The labeled lysine was mapped to several other sites on the enzyme using fluorescence resonance energy transfer. Repeated exposure of CF_1 to Lucifer Yellow under turnover conditions would be expected to increase the stoichiometry of labeling to three if the asymmetry were changing as a result of rotational catalysis. The stoichiometry, however, saturated at one and did not further increase significantly during turnover (Nalin *et al.*, 1985). This observation has been confirmed in several laboratories including our own, and has indicated the presence of permanent asymmetry among the different α subunits of CF_1.

Since labeling of CF_1 with Lucifer Yellow did not significantly affect catalytic activity (less than 10%; Nalin *et al.*, 1985) it was possible to use this site as a reference point to follow changes in the relative positions of nucleotide binding sites on the enzyme (Shapiro *et al.*, 1988, 1990). This was done by following changes in fluorescence resonance energy transfer between Lucifer Yellow and the fluorescent nucleotide analog trinitrophenyl-ADP (TNP-ADP) or TNP-ATP bound at previously characterized nucleotide binding sites (Snyder and Hammes, 1984, 1985). These experiments demonstrated that two putative catalytic sites on CF_1 (sites 1 and 2 using the notation of Snyder and Hammes, 1985) switched properties with each other during ATP hydrolysis. The same conformational change could be elicited by binding of the poorly hydrolyzable nucleotide analog, adenyl-β,γ-imidodiphosphate (AMP-PNP) to the enzyme (Shapiro and McCarty, 1990). The conformation induced by catalysis or AMP-PNP binding slowly decayed to the former asymmetric state after removal of medium nucleotides (Shapiro and McCarty, 1988). The presence of site switching is predicted by the binding change hypothesis, but the results fit best to a model in which two pairs of catalytic sites switch properties with each other during catalysis, rather than three alternating sites (Shapiro and McCarty, 1988). Taken together with the existence of permanent asymmetry among the larger subunits of the enzyme, these experiments argue against a rotational model.

CONCLUDING REMARKS

It has been possible to detect substantial structural changes in CF_1 which occur during activation and catalysis of the enzyme both *in vitro* and *in situ*. A number of independent studies have shown that the ε and γ subunits respond to the formation of a transmembrane potential gradient. These two subunits may assume the primary responsibility for gating the flow of protons across the thylakoid membrane in a manner that induces structural change at the catalytic sites.

The crystal structure of parts of the mitochondrial F_1 has offered some interesting insight into how structural changes in the γ subunit might affect alterations in the nucleotide binding sites during the catalytic cycle, and has spawned a new generation of experiments aimed at testing current models for catalysis in all of the F_1 enzymes. Unfortunately, only a limited amount (ca. 45%) of the structure of the γ subunit was solved, leaving still unsolved the structures of several functionally important regions of this subunit. There may also be some important differences between the chloroplast and mitochondrial enzymes, most notably a significant difference in the structure/orientation of the C-terminus of the γ subunit. Thus the structure of the mitochondrial F_1 may not be fully representative of the structures of all of the F_1 enzymes, and it may not be possible to ascertain general mechanistic features until significantly more structural information is available for enzymes from different sources. Furthermore, and perhaps even more importantly, there are significant differences between the conformation of CF_1 on and off the membrane, further warranting care in interpreting structural data obtained with the isolated enzyme.

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