Minireview

The proton-pumping respiratory complex I of bacteria and mitochondria and its homologue in chloroplasts

Thorsten Friedrich[a,*], Klaus Steinmüller[b], Hanns Weiss[a]

[a]*Institut für Biochemie and* [b]*Institut für Entwicklungs- und Molekularbiologie der Pflanzen, Heinrich-Heine-Universität Düsseldorf, Universitätsstraße1, D-40225 Düsseldorf, Germany*

Received 28 April 1995

Abstract The proton-pumping NADH:ubiquinone oxidoreductase, also called complex I, is the first of the respiratory complexes providing the proton motive force which is essential for the synthesis of ATP. Closely related forms of this complex exist in the mitochondria of eucaryotes and in the plasma membranes of purple bacteria. The minimal structural framework common to the mitochondrial and the bacterial complex is composed of 14 polypeptides with 1 FMN and 6–8 iron-sulfur clusters as prosthetic groups. The mitochondrial complex contains many accessory subunits for which no homologous counterparts exist in the bacterial complex. Genes for 11 of the 14 minimal subunits are also found in the plastidial DNA of plants and in the genome of cyanobacteria. However, genes encoding the 3 subunits of the NADH dehydrogenase part of complex I are apparently missing in these species. The possibility is discussed that chloroplasts and cyanobacteria contain a complex I equipped with a different electron input device. This complex may work as a NAD(P)H: or a ferredoxin:plastoquinone oxidoreductase participating in cyclic electron transport during photosynthesis.

Key words: NADH:ubiquinone oxidoreductase; NAD(P)H:plastoquinone oxidoreductase; Ferredoxin:plastoquinone oxidoreductase; Complex I; Iron-sulfur cluster; Respiratory chain

1. Introduction

The proton-pumping NADH:ubiquinone oxidoreductase catalyzes the electron transfer from NADH to ubiquinone linked with a proton translocation according to the overall equation

$$NADH + Q + 5\ H^+_n \rightarrow NAD^+ + QH_2 + 4\ H^+_p$$

where Q refers to ubiquinone, and H^+_n and H^+_p to the protons taken up from the negative inner and delivered to the positive outer side of the membrane [1–3]. Thus, a proton-motive force is generated which is utilized mainly for ATP synthesis. Characteristic features of the enzyme are its prosthetic groups, namely 1 FMN and 6–8 iron-sulfur (FeS) clusters, and its sensitivity to a number of naturally occurring compounds, e.g. the insectizide rotenone or the antibiotic piericidin A [1,3,4]. The enzyme present in mitochondria is traditionally called complex I, while its counterpart in many bacteria is referred to as NADH dehydrogenase 1 [5]. For simplicity, we will use the term complex I for both the mitochondrial and the bacterial complex throughout this review.

The structure of complex I is extraordinarily complex. The mitochondrial complex comprises about 40 different polypeptides, that are of both nuclear and mitochondrial genetic origin [1,3,6]. Bacteria contain a minimal form of complex I with fewer subunits but including homologues of all subunits of the mitochondrial complex presumed to bind subtrates or prosthetic groups, and of all subunits encoded by mitochondrial genes [5,7,8]. In the genome of chloroplasts and cyanobacteria most genes encoding the subunits of this minimal complex I have been found [9–12]. All efforts, however, to demonstrate the existence of the genes encoding the NADH dehydrogenase part of complex I failed. It might turn out that chloroplasts and cyanobacteria contain a complex I equipped with a different electron input device. This complex may work as a NAD(P)H: or ferredoxin:plastoquinone oxidoreductase during the cyclic electron transfer of photosynthesis.

No evidence exists for the presence of a complex I in Archaea [G. Schäfer, pers. comm.], the third domain of organisms [13]. The recently isolated $F_{420}H_2$:quinone oxidoreductase from *Archeoglobus fulgidus* (of the kingdom of Euryarchaeota) may, however, represent a proton-pumping enzyme related to complex I. The $F_{420}H_2$:quinone oxidoreductase is made up of several polypeptides with 1 or 2 FAD and several FeS clusters as prosthetic groups [14].

This minireview compares the different forms of complex I occuring in the domains of bacteria and eucarya focussing on the complex of purple bacteria, mitochondria, and chloroplasts. For a more comprehensive discussion of complex I the reader is referred to other recent reviews [1–3,15,16].

2. The *minimal* complex I of bacteria

Within the domain of bacteria, complex I has been demonstrated to occur at least in 3 of the 4 subgroups of the purple bacteria. For example, *Zymomonas mobilis* (α-subgroup) shows a piericidin A-sensitive NADH oxidase activity [17]. Typical EPR signals characteristic for complex I have been measured in membranes of *Alcaligenes eutrophus* (β-subgroup) [18]. The complex I genes have been sequenced and the complex isolated from *Escherichia coli* (γ-subgroup) [7,19]. There are no clear evidences for a complex I containing member of the δ-subgroup. Genes homologous to the mitochondrially encoded ND1 and ND5 genes have been sequenced in *Bacillus stearothermophilus* and *B. subtilis*, indicating that gram positive bacteria might also contain a complex I [20,21]. A

*Corresponding author. Fax: (49) (211) 311 3085.

SSDI 0014-5793(95)00548-X

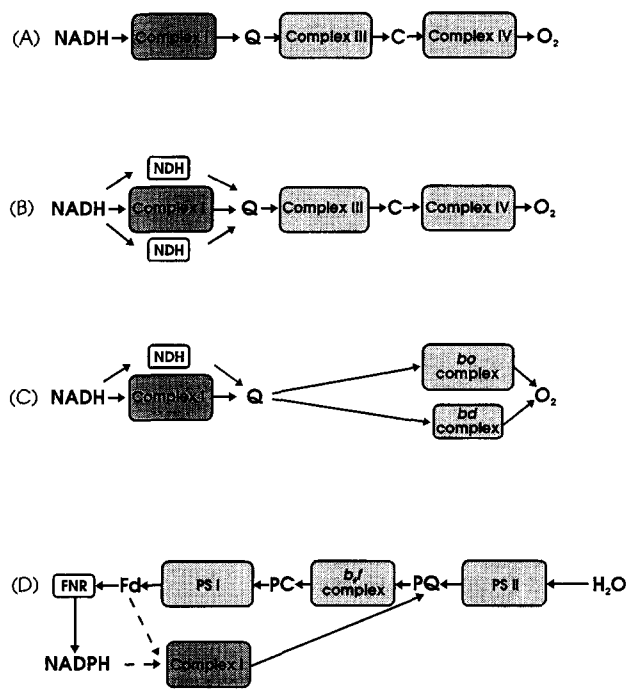

Fig. 1. Scheme of electron transfer chains of (A) mammalian mitochondria, (B) plant and fungal mitochondria, (C) *E. coli* cytoplasmic membrane and (D) plant chloroplast and cyanobacterial membrane. Dashed lines in (D) indicate hypothetical electron transfer steps. White boxes represent non energy conserving complexes, hatched boxes represent energy transducing complexes. The complex I is drawn as a dark hatched box. The following abbreviations are used: Complex I, NADH:ubiquinone oxidoreductase; complex III, ubiquinol:cytochrome *c* oxidoreductase; complex IV, cytochrome *c* oxidoreductase; NDH, non-proton-pumping NADH:ubiquinone oxidoreductase; *bo*, cytochrome *bo* ubiquinol oxidase; *bd*, cytochrome *bd* ubiquinol oxidase; PSI, photosystem I; PSII, photosystem II; b_6f, cytochrome b_6f plastoquinol:plastocyanine oxidoreductase; FNR, ferredoxin:NADPH oxidoreductase; Q, ubiquinone; C, cytochrome *c*; PQ, plastoquinone; PC, plastocyanine; Fd, ferredoxin. See text for details.

NADH:menaquinone oxidoreductase which is considered to be a proton pump and which contains at least 10 different subunits with 1 FMN and several FeS clusters has been isolated from the thermophilic (eu)bacterium *Thermus thermophilus* [22]. Since *T. thermophilus* and the Gram-positive bacteria contain only menaquinone as a pool component it might be possible that these bacteria contain a complex I with a different electron output segment or a different energy efficiency. The presence of a complex I in cyanobacteria is discussed below.

Much more frequently occurring in bacteria is the non proton-pumping NADH:quinone oxidoreductase, called NADH dehydrogenase 2 (Fig. 1). It is a single polypeptide enzyme with FAD as the only redox group [5].

Based on sequence comparisons including the mitochondrial complex I, the (putative) plastidial complex I, and bacterial electron transfer enzymes related to parts of complex I, a minimal structural framework of 14 different subunits was deduced [3]. These were found to be encoded by the *nuo* locus (from NADH:ubiquinone oxidoreductase) of the *E. coli* chromosome [7]. The locus contains a cluster of 14 genes, and all the derived proteins are related to subunits of the mitochondrial complex I. Among them are the homologues of all subunits presumed to bind substrates and to harbour the redox groups. The counterparts of all mitochochondrially encoded subunits of the eucaryotic complex I are present as well [7]. Based on the *nuo* genes, a molecular mass of 525 kDa was derived for the *E. coli* complex I.

According to secondary structure prediction, 7 subunits were classified as membrane intrinsic in agreement with their mitochondrially encoded counterparts in animals and fungi. The other 7 subunits are predicted to be peripheral or predominantly peripheral proteins (Table 1).

A highly conserved peripheral 50 kDa subunit of complex I contains the motifs for binding NADH, FMN and 1 tetranuclear FeS cluster. Binding sites for the other FeS clusters are predicted to be located at four other peripheral subunits (Table 1). In this respect, complex I differs from the other proton-pumping respiratory complexes which carry their prosthetic groups at membrane intrinsic subunits. The binding site for ubiquinone is suggested to be located at one of the 7 membrane intrinsic subunits [23]. The function of the remaining 6 subunits is obscure.

P. denitrificans, if grown aerobically, expresses a mitochondrion-type respiratory chain with a complex I that, in terms of

Table 1
Nomenclature and properties of homologous complex I subunits of *E. coli* (*E.c.*) [7], *B. taurus* (*B.t.*) [3], and the plastidial complex of *O. sativa* (*O.s.*) [9]

Designation of the subunit			Molecular mass (kDa)			Membrane helices			Predicted function
E.c.	*B.t.*	*O.s.*	*E.c.*	*B.t.*	*O.s.*	*E.c.*	*B.t.*	*O.s.*	
NuoA	ND3	NDH-C	16.3	13.1	13.9	3	3	3	
NuoB	PSST	NDH-K	25.1	20.1	27.7	1	0	0	1 × [4Fe-4S]
NuoC	30(IP)	NDH-J	21.5	26.4	18.6	0	0	0	
NuoD	49(IP)	NDH-H	45.9	48.9	45.7	0	0	0	
NuoE	24(FP)	not found	18.6	23.7	–	0	0	–	1 × [2Fe-2S]
NuoF	51(FP)	not found	49.6	48.4	–	0	0	–	NADH-binding; FMN; 1 × [4Fe-4S]
NuoG	75(IP)	not found	91.2	77.1	–	0	0	–	1 × [4Fe-4S]; 1 (2*) × [2Fe-2S]
NuoH	ND1	NDH-A	36.3	35.7	40.4	8	8	8	Ubiquinone-binding
NuoI	TYKY	NDH-I	20.4	20.2	21.1	1	0	0	2 × [4Fe-4S]
NuoJ	ND6	NDH-G	19.9	19.1	19.4	5	5	5	
NuoK	ND4L	NDH-E	11.2	10.8	11.3	3	3	3	
NuoL	ND5	NDH-F	66.3	68.3	82.6	13	11	13	
NuoM	ND4	NDH-D	56.5	52.1	56.5	12	12	12	
NuoN	ND2	NDH-B	45.9	39.7	56.8	10	8	9	

The additional FeS cluster of the *E. coli* complex on subunit G is indicated by an asterix.

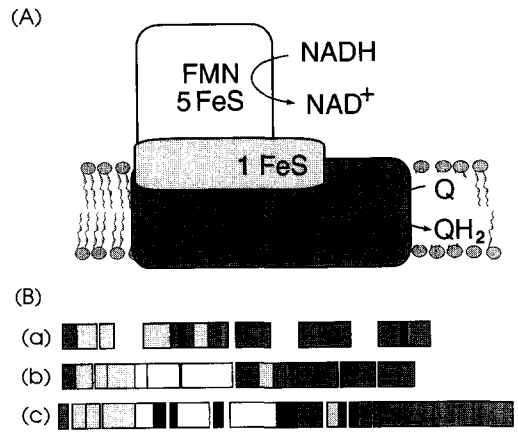

Fig. 2. (A) Arrangement of the *E. coli* complex I fragments and (B) order of the corresponding genes in (a) *Oryza sativa*, (b) *E. coli* and (c) *P. denitrificans*. The NADH dehydrogenase fragment and the genes encoding the subunits of this fragment are shown in white, the connecting fragment and its genes in light grey and the membrane fragment and its genes in dark grey. The homologues in (a) and (c) are depicted in the same manner. The black boxes denote introns in (a) and URFs in (c). The clustered genes in (a) depict the transcriptional units.

EPR spectroscopic properties of FeS clusters, is very similar to the mitochondrial complex I. The group of Yagi sequenced the gene cluster encoding the *P. denitrificans* complex I [5]. Besides the 14 genes corresponding to the *E. coli nuo* genes, 6 unidentified reading frames (URFs) were found. Whether these are accessory subunits specific for *P. denitrificans* cannot yet be decided because the intact complex has not been isolated from this bacterium. A complex I gene cluster has also been characterized for *Rhodobacter capsulatus* [24]. The cluster contains the 14 complex I genes and 6 URFs which, however, are not related to the *P. denitrificans* URFs. Disruption of these URFs in *R. capsulatus* has no effect on complex I activity indicating that their products are not necessary for the assembly of complex I [24].

Attempts to isolate complex I from purple bacteria failed for some time due to the fragility of the complex in detergent solution. However, the *E. coli* complex was recently isolated by chromatographic steps performed in the presence of an alkylglucoside detergent at pH 6.0 [19]. The complex is obtained in a monodisperse state with a molecular mass of ~550 kDa and contains the expected 14 subunits which could be assigned to the *nuo* genes, partly by their N-terminal sequences and partly by their apparent molecular masses in SDS-PAGE. One non-covalently bound FMN, 3 binuclear (N1a, N1b and N1c) and 3 tetranuclear (N2, N3 and N4) FeS clusters were found in the preparation. No counterpart of the binuclear cluster N1c has so far been found in the mitochondrial complex I (Table 1) [19].

The isolated *E. coli* complex I readily falls into three fragments at neutral pH [19]. An NADH dehydrogenase fragment made up of 3 subunits (Nuo E–G; Table 1) and bearing the FMN and 4 FeS clusters is obtained in water soluble form. The second, amphipathic fragment which is presumed to connect the NADH dehydrogenase fragment with the membrane contains 4 subunits (Nuo B–D and I) and 1 FeS cluster whose EPR spectral properties are similar to the mitochondrial cluster N2. The third, membrane fragment is composed of the 7 homologues of the mitochondrially encoded subunits of the eucaryotic complex I (Nuo A, H, and J–N). This subunit arrangement coincidences to some extent with the order of the genes in the *E. coli nuo* locus (Fig. 2).

3. The *de luxe* complex I of mitochondria

The mitochondrial complex I is found in most eucaryotic organisms. Known exceptions are the fermentative yeasts *Saccharomyces cerevisae, Schizosaccharomyces pombe* and *Kluyveromyces lactis* which do not contain a complex I [25]. Whereas complex I is the only NADH : ubiquinone oxidoreductase in animals, lower eukaryotes and plants contain in their mitochondria in addition two non proton-pumping alternative NADH : ubiquinone oxidoreductases, one facing the matrix, the other the intermembrane space of mitochondria (Fig. 1) [26]. The internal enzyme is a single polypeptide FAD enzyme related to the NADH dehydrogenase 2 of bacteria. The enzyme has lower affinity for NADH than complex I and possibly operates as an overflow outlet for an excess of reducing equivalents [27]. The above mentioned yeasts which do not contain a complex I oxidize mitochondrial NADH only by means of this enzyme.

Preparations of the mitochondrial complex I exist for several animals (e.g. bovine, rat, pigeon), for the fungi *Neursopora crassa* and *Aspergillus niger* [1,3], and for the higher plants *Vicia faba, Beta vulgaris* and *Solanum tuberosum* [28–30]. SDS gel electrophoresis resolves the preparations in a large number of polypeptides rendering non specialists suspicious of the purity of the preparations.

The sequences of all 42 subunits of the bovine complex I and of 27 subunits of the *Neurospora crassa* complex I are now known [6, 31]. The 14 minimal subunits whose homologues make up the bacterial complex I can be subdivided according to their predicted secondary structure as mentioned above. Seven are peripheral or predominantly peripheral proteins (Table 1), and among them are all subunits predicted to bind the known redox groups. These subunits are nuclear-encoded in animals and fungi. Mitochondrially encoded are the 49 kDa and 30 kDa subunit of plants [32], the 49 kDa, 30 kDa and 20 kDa subunit of the ciliate *Paramecium aurelia* [33], and the 75 kDa subunit of the slime mold *Dictyostelium discoideum* [34]. In the flagellate *Trypanosoma brucei*, the 49 kDa, 30 kDa and 23 kDa subunits are encoded on the maxi-circle DNA [35]. The remaining 7 minimal subunits are membrane intrinsic proteins. They are mitochondrially encoded in all above mentioned species.

The additional group of subunits appear to be a specific feature of the mitochondrial complex I. They are all nuclear-encoded. Most of them show no relationship to other proteins, and several even show no sequence similarity between bovine and *N. crassa*. This could mean that many of these 'accessory' complex I subunits emerged late in evolution when animals and fungi had been already divided. It may be speculated that these subunits form an insulation around complex I preventing the high energy electrons from escaping the complex and forming reactive oxygen species.

Two accessory subunits, however, are exceptional. A 10 kDa subunit was found to be an acyl carrier protein (ACP) with a phosphopantetheine as prosthetic group [36,37]. This mitochondrial ACP most closely resembles the bacterial or plastidial ACPs that participate in fatty acid synthesis. In a *N. crassa*

mutant lacking the ACP, complex I is not assembled and the mitochondrial lysophospholipid content is increased fourfold (R. Schneider and H. Weiss, unpub. data). A 40 kDa 'accessory' subunit contains an NAD(P) binding motif and is weakly related to several dehydrogenases and reductases ([15] and R. Schneider, Th. Friedrich and H. Weiss, unpub. data). It is an attractive idea that these two subunits may participate in a synthetic pathway which delivers an unknown redox group for complex I, but this remains speculative until the products of the putative pathway are identified.

4. The *alien* complex I of cyanobacteria and chloroplasts

The genes for 11 of the 14 minimal subunits of complex I have been found in the plastidial genomes of *Marchantia polymorpha*, *Nicotiana tabacum* and *Oryza sativa*, [9], and in the genome of the cyanobacterium *Synechocystis sp.* PCC6803 [10, 12]. They are organized in 4 transcriptional units (Fig. 2). All efforts failed to demonstrate the existence of the genes encoding the remaining 3 minimal subunits (K. Steinmüller, unpub. results). Remarkably, these 3 subunits make up the NADH dehydrogenase part, a highly conserved structural and functional unit of complex I containing the FMN and at least 4 FeS clusters. This unit is found in the NAD^+-reducing hydrogenase of the purple bacterium *Alcaligenes eutrophus* [38,39]. The genes encoding the subunits of this unit are clustered in exactly the same order in *E. coli*, *P. denitrificans*, *R. capsulatus*, and *A. eutrophus* (Fig. 2). Therefore, this unit is believed to represent a NADH dehydrogenase (diaphorase) module conserved during evolution.

A gene for the NADH-binding subunit has been identified in the nuclear genome of *Arabidopsis thaliana* and *S. tuberosum* [32]. The gene, however, specifies a subunit with a typical mitochondrial import sequence and therefore represents the gene of the corresponding subunit in the mitochondrial complex I of the plants (L. Grohmann, pers. comm.).

We therefore propose that the complex I in cyanobacteria and plastides should be equipped with a different electron input device which does not receive electrons from NADH. Since it has been shown that the plastidial complex is located on the stroma thylakoids in close connection to photosystem I [40], ferredoxin might be the electron donor. In this case, the complex would work as a ferredoxin:plastoquinone oxidoreductase (Fig. 1). Alternatively, NADPH provided by the ferredoxin:NADPH oxidoreductase might be the electron donor (Fig. 1), and the complex would operate as a NADPH:plastoquinone oxidoreductase. Both possibilities imply that the complex participates in a cyclic electron flow passing the electrons from photosystem I back to the plastoquinone pool. This has been shown to occur in cyanobacteria [41]. In this respect, it is noteworthy that a photosystem I gene is included in one of the 4 transcriptional units encoding the plastidial complex I [9].

There is a higher degree of sequence identity between the mitochondrial complex I of animals and plants than between the mitochondrial and plastidial complex I in the same plant. Furthermore, the cyanobacterial and the plastidial complex I are more closely related to each other than the cyanobacterial and the purple bacterial complex. Therefore, it appears that the mitochondrial and the plastidial complex I have been brought into plants by separate endosymbiotic events.

Acknowledgements: We would like to thank Dr. L. Grohmann, IGF Berlin for sharing unpublished data and helpful discussions. This work was supported by the Deutsche Forschungsgemeinschaft and the Fonds der Chemischen Industrie.

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