Mitochondrial respiration in algae : from mitochondrial genome to regulation of photosynthesis.

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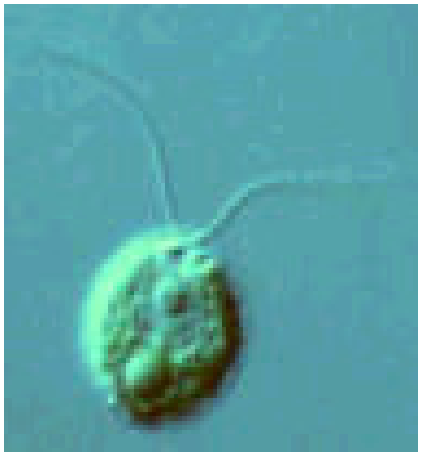

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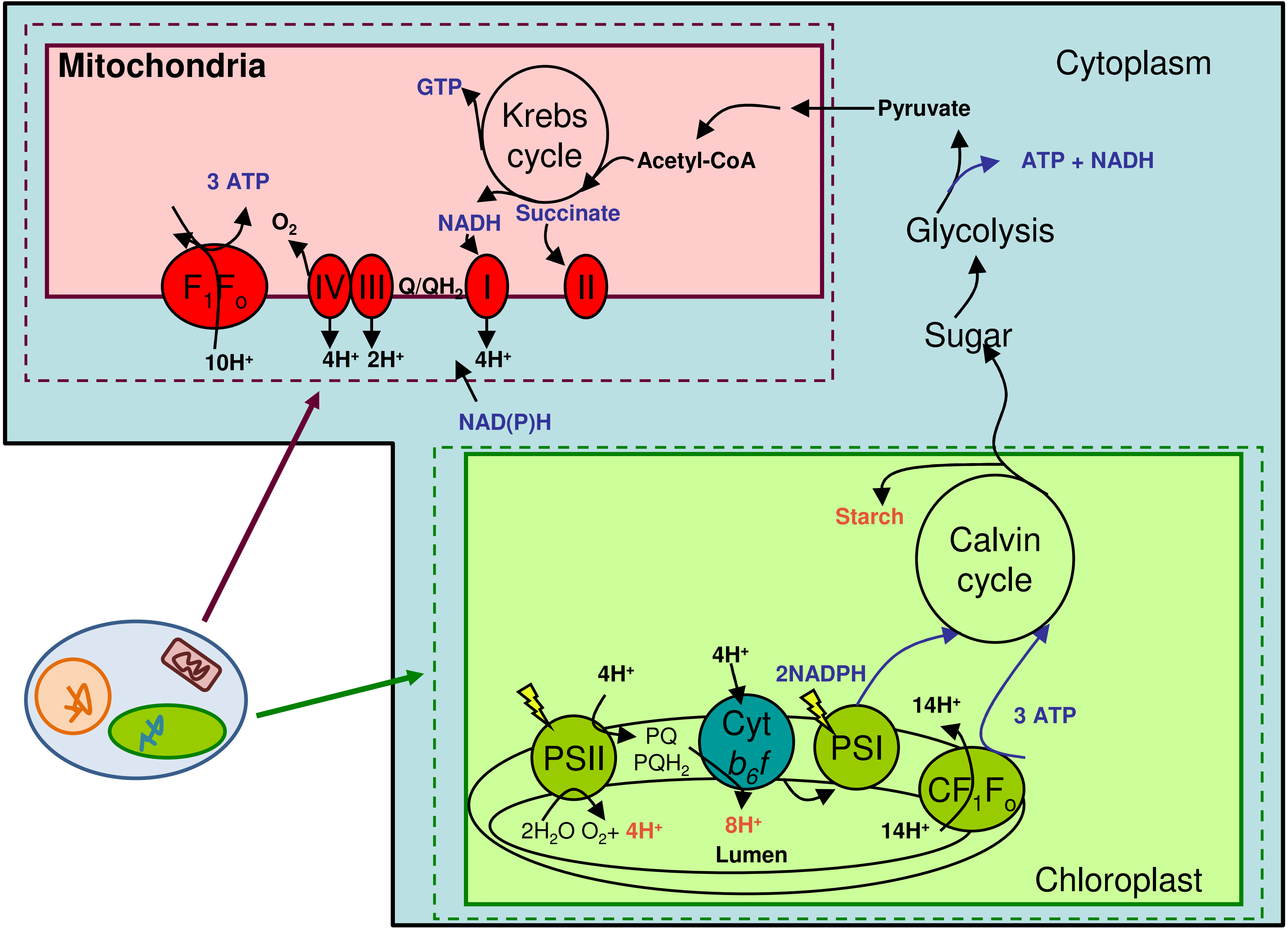
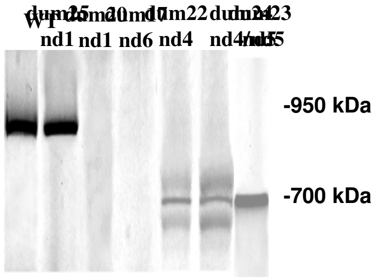
Münster 11/06/2013

Energy production Respiration and Photosynthesis

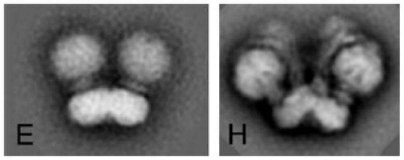


Summary

Part I :
Chlamydomonas as a model organism to study Complex I

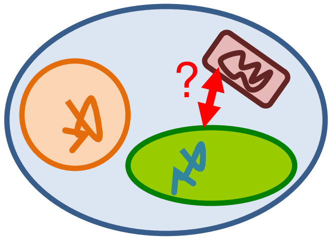


Part II :
ATP synthase evolution in eukaryotes :
Relation structure / function

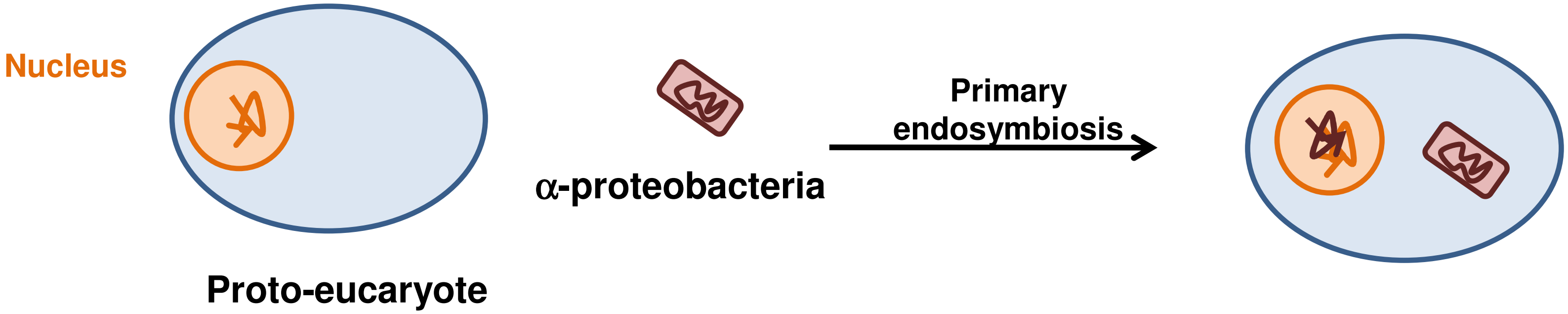


N.V. Dudkina et al. / FEBS Letters xxx (2006) xxx–xxx

Part III :
Interaction between respiration and photosynthesis



Mitochondria : a common feature in eukaryotes

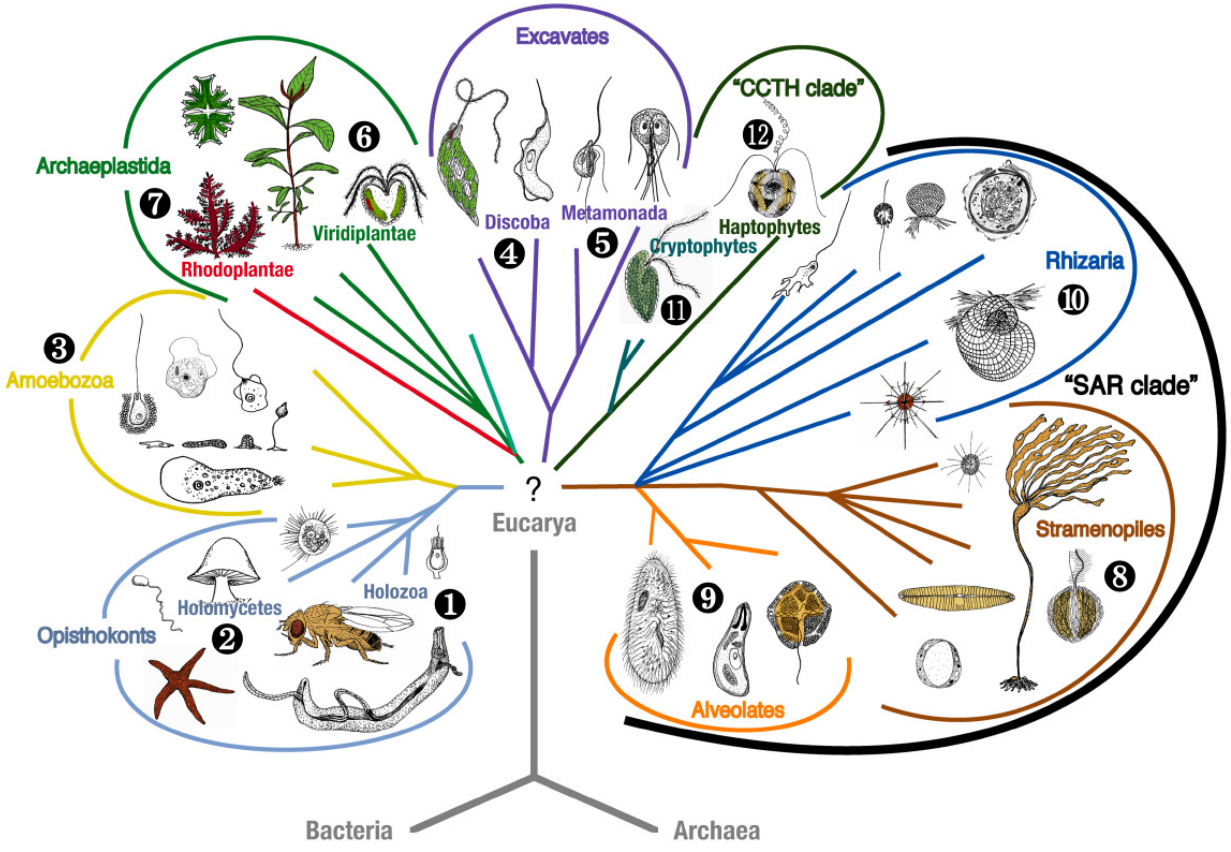


Nucleus

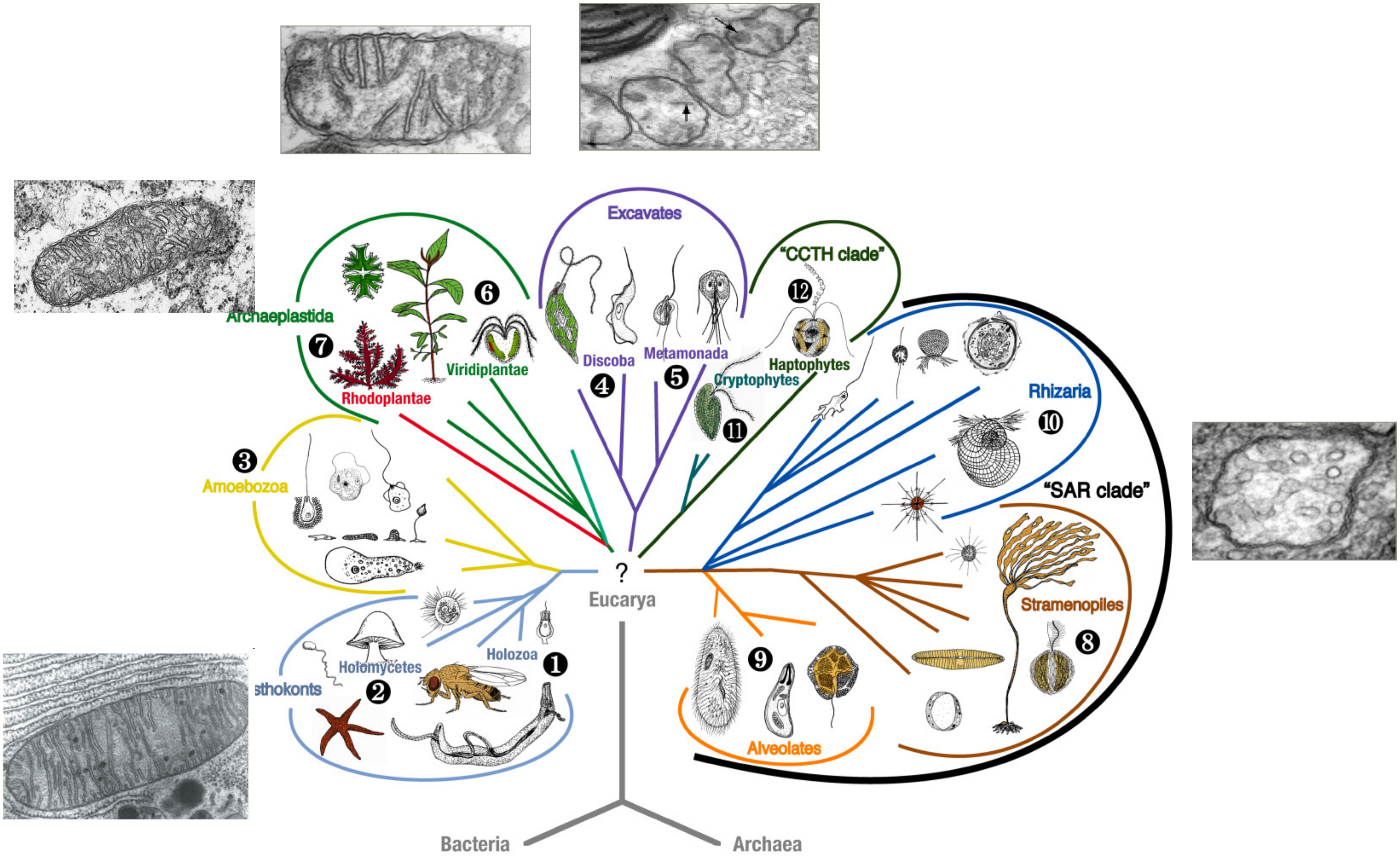
α-proteobacteria

Primary endosymbiosis

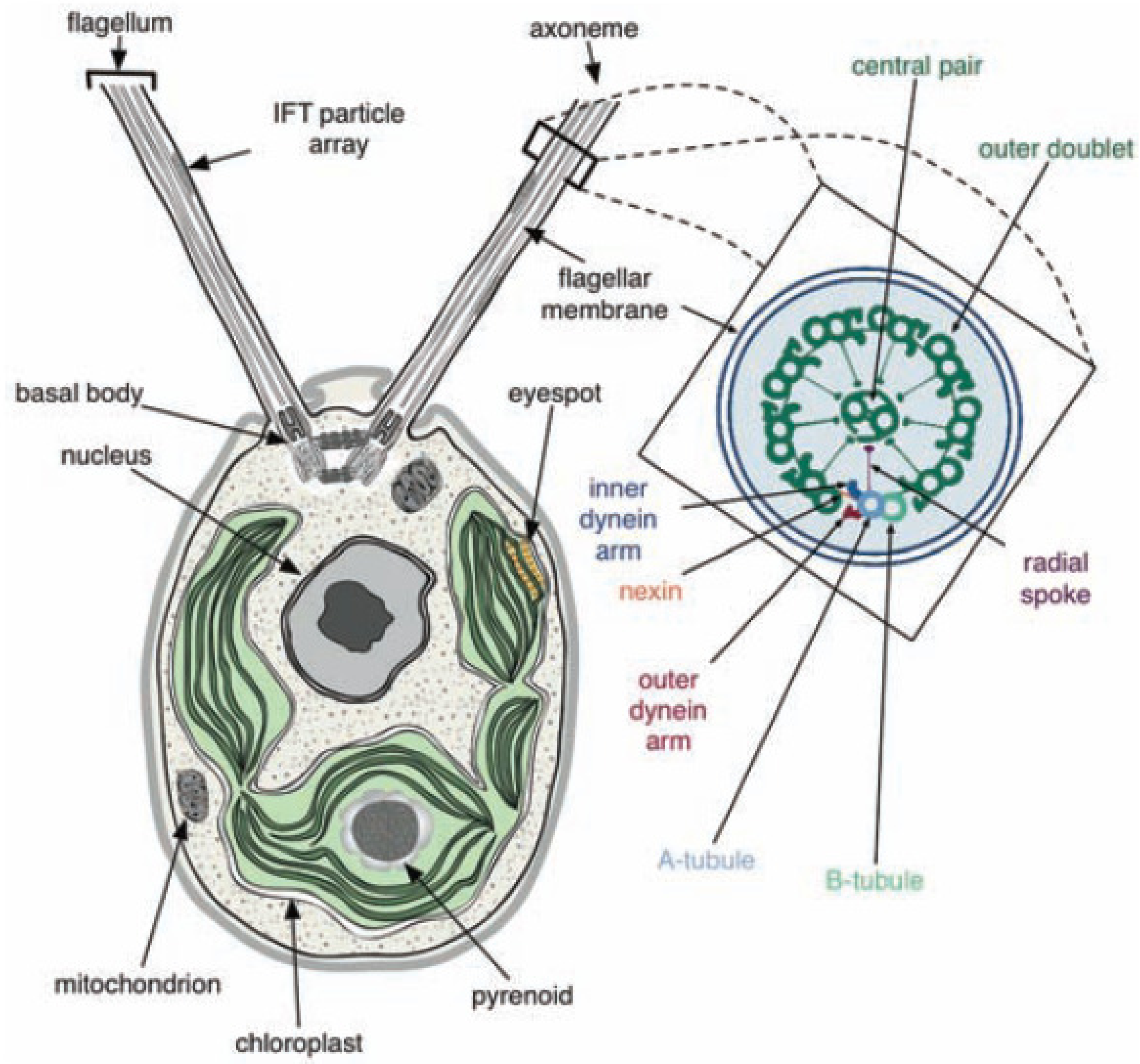
Proto-eucaryote



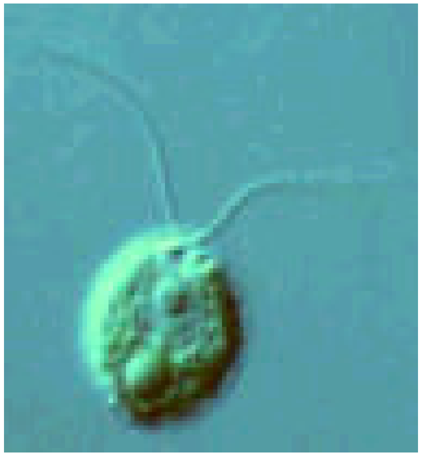
Mitochondria : a common feature in eukaryotes

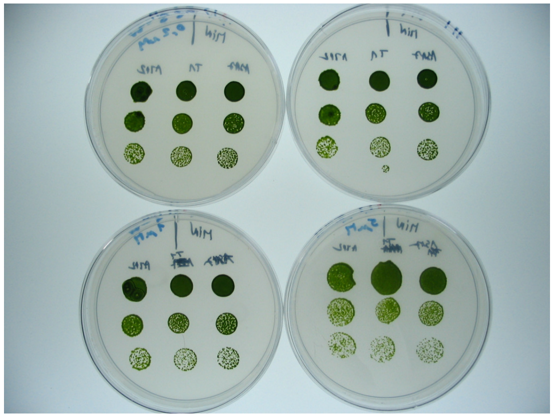


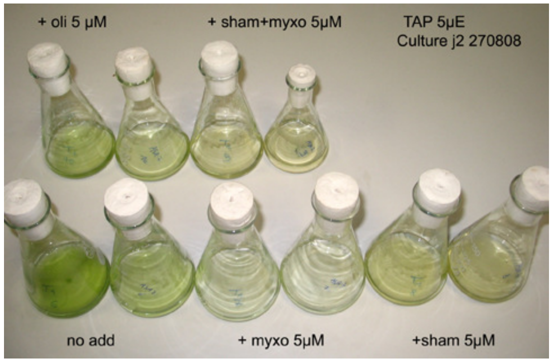
Chlamydomonas reinhardtii



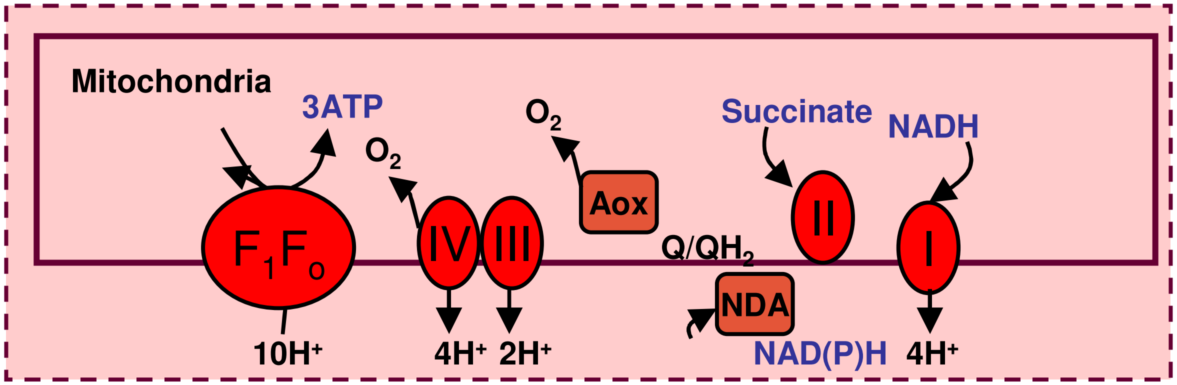
Merchant et al., 2007, Sciences





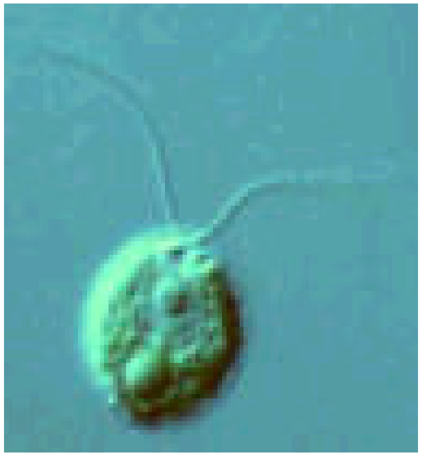


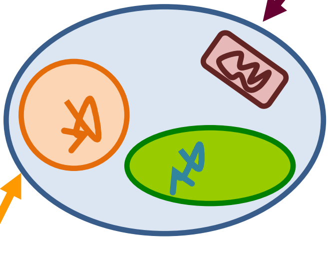
Chlamydomonas : mitochondrial respiratory-chain



	Subunits	Mt-encoded	Mw (kDa)	H+/e
I	>40	5	>1000	4
II	4	0	~200	0
III	10	1	~500 (III_2)	6
IV	>14	1	~200	
F_1F_o	>17	0	~1700 (V_2)	10H+ / 3ATP (?)
Aox	1(*2)	0	100 ($_2$)	0
NDA	1(*3)	0	50-70	0

Chlamydomonas reinhardtii : genetic tools





Mitochondrion

Random mutagenesis (Ra)
Site-directed mutagenesis (SD)

Matagne et al., 1989
Remacle et al., 2006, PNAS

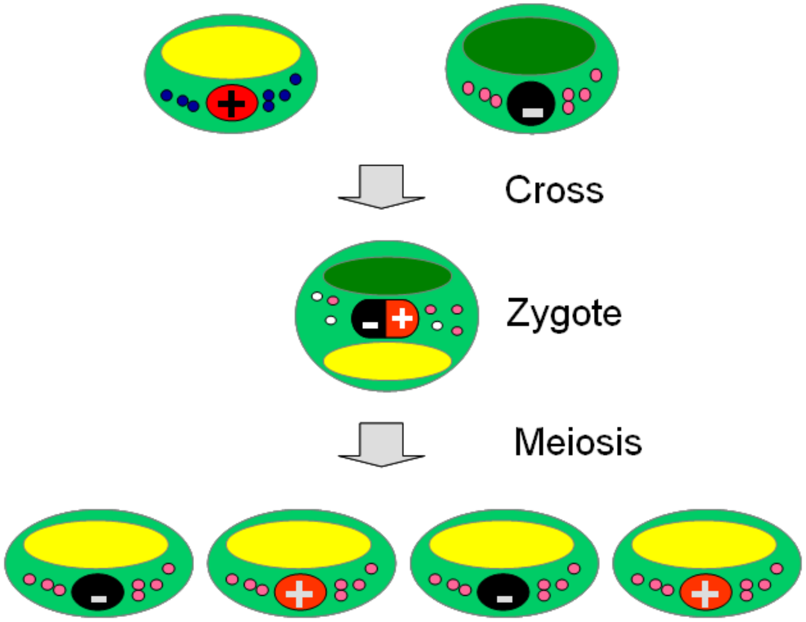
Nucleus

Random insertional mutagenesis (KO) : resistance to hygromycin
RNA interference strategy (KD)

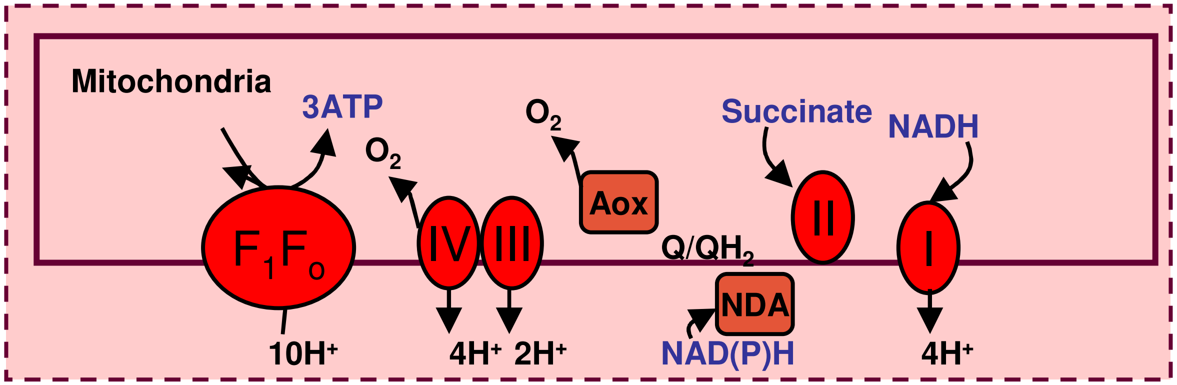
Berthold et al., 2002, Protist
Fuhrmann et al., 2001, J. Cell. Sc.

Chlamydomonas mitochondrial/nuclear/chlorplastic genome : Transmission mode

Boynton et al., 1987
Matagne et al., 1993

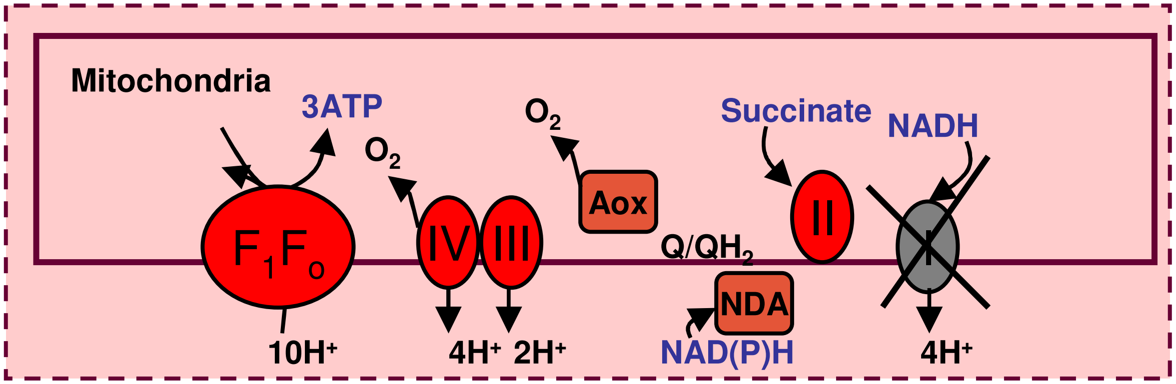


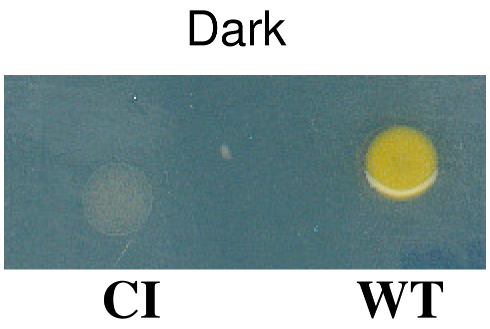
Chlamydomonas : mitochondrial respiratory-chain



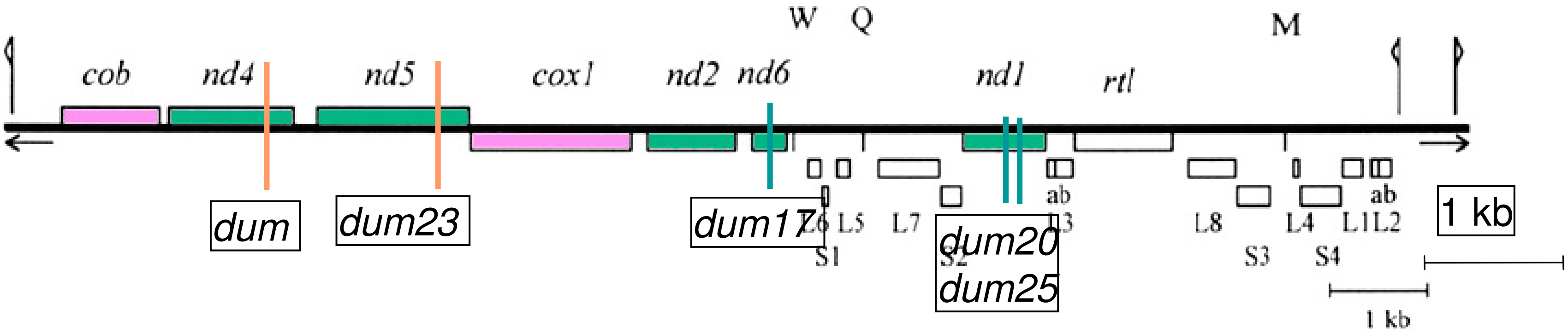
	Subunits	Mt-encoded	Mw (kDa)	H^+/e	Mutants	
I	>40	5	>1000	4	Mt^{sd,ra} Nu^{ko,kd}	Remacle et al., 2001(a,b), 2006; Cardol et al., 2002, 2004, 2006, 2008, 2011
II	4	0	~200	0		Cardol et al., 2005
III	10	1	~500 (III$_2$)	6	Mt^{ra}	Dorthu et al, 1992, Matagne et al., 1989, Duby et al, 1999
IV	>14	1	~200		Mt^{ra} Nu$^{kd, ko}$	Matagne et al., 1989, Remacle et al., 2010
F_1F_o	17	0	~1700 (V$_2$)	$\frac{3ATP}{10H^+}$	Nu^{kd}	Vazquez-Acevedo et al, 2006; Lapaile et al., 2010 (a,b)
Aox	2*	0	100 ($_2$)	0	Nu^{kd}	Mathy et al., 2010
NDA	1-3*	0	50-70	0	Nu^{kd}	Jans et al., 2008; Lecler et al., 2013

Isolation of mitochondrial complex I mutants





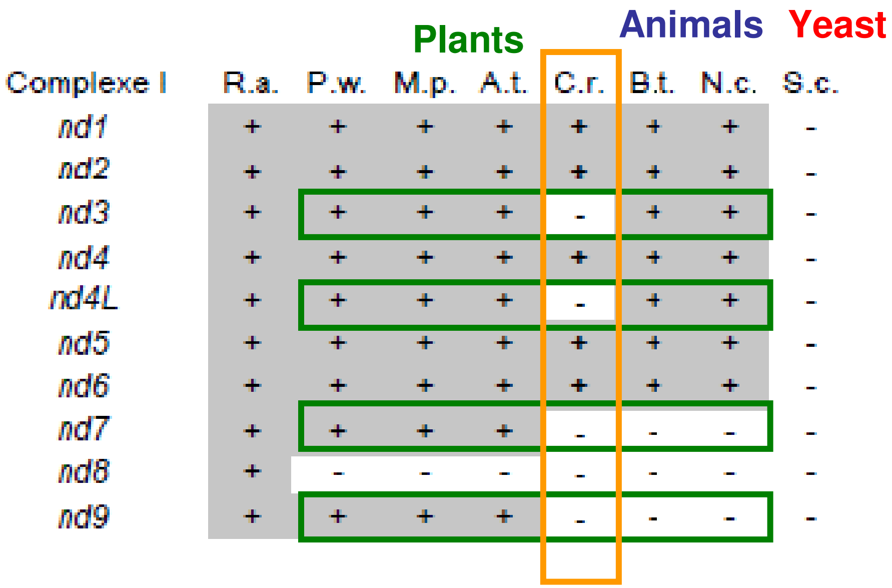
	Chlamy	Animals		Yeast
Complexe I	C.r.	B.t.	N.c.	S.c.
nd1	+	+	+	-
nd2	+	+	+	-
nd3	-	+	+	-
nd4	+	+	+	-
nd4L	-	+	+	-
nd5	+	+	+	-
nd6	+	+	+	-



Study of complex I nucleus-encoded subunits

The Chlamydomonas Genome Reveals the Evolution of Key Animal and Plant Functions
Sabeeha S. Merchant, *et al.*
Science **318**, 245 (2007);
DOI: 10.1126/science.1143609

→ ND3, ND4L, ND7 and ND9 are encoded in the nucleus



		Plants				Animals		Yeast
Complexe I	R.a.	P.w.	M.p.	A.t.	C.r.	B.t.	N.c.	S.c.
nd1	+	+	+	+	+	+	+	-
nd2	+	+	+	+	+	+	+	-
nd3	+	+	+	+	-	+	+	-
nd4	+	+	+	+	+	+	+	-
nd4L	+	+	+	+	-	+	+	-
nd5	+	+	+	+	+	+	+	-
nd6	+	+	+	+	+	+	+	-
nd7	+	+	+	+	-	-	-	-
nd8	+	-	-	-	-	-	-	-
nd9	+	+	+	+	-	-	-	-

Strategy : RNA interference

Principle Expression of double-stranded RNA
Specific degradation of endogenous RNA

Study of nucleus-encoded subunits : RNA interference

Construction of an inactivation vector

801 pb gene fragment *480 pb* cDNA fragment

Co-transformation :Arginine auxotrophy (*ARG7*)

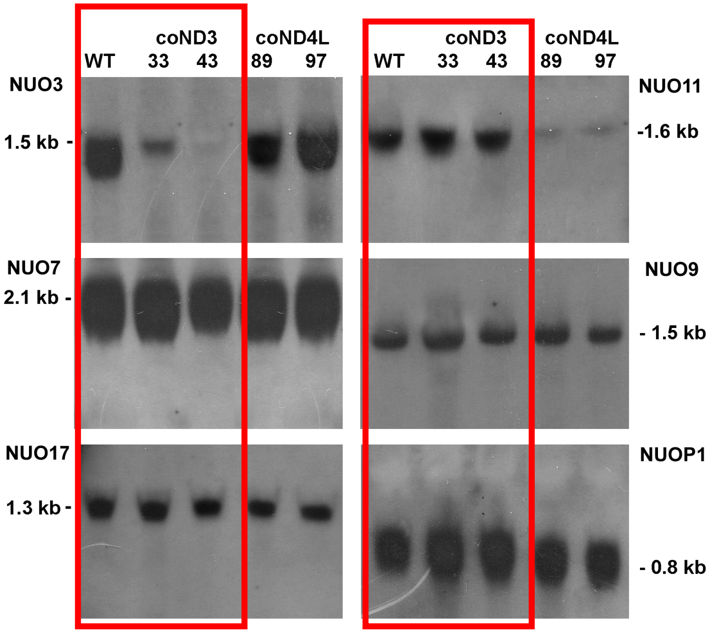
Selection of Arg+

Analysis of 100 Arg+ transformants by PCR

- Rate of Co-transformation is ~50 %

Complex I activity and assembly

- ~5% clones defectives



Assembly of complex I in the mutants

Mitochondrial mutants		CI activity
dum5	**-1T 3' UTR** ***nd5***	12%
dum17	**-1T** ***nd6*** (codons 143-144)	0
*dum23**	**-1T** ***nd5*** (codons 145-146)	0
dum20	**-1T** ***nd1*** (codon 243)	0
dum25	**-6 NT** ***nd1*** (codons 199-200)	0
dum22	**délétion** *cob +* **3'** ***nd4***	0
dum24	**délétion** *cob +* ***nd4*** **+ 3'** ***nd5***	0
dum28	**-69 NT** ***nd4***	0

Nuclear mutants		
Co-Nd3	Inactivation of ***Nd3*** expression	0
Co-Nd4L	Inactivation of ***Nd4L*** expression	0
Co-Nd7	Inactivation de ***Nd7*** expression	0
Co-Nd9	Inactivation of ***Nd9*** expression	0
nuo9	Insertion of HygR. Loss of **Nd9**	0
nuob10	Insertion of HygR (**Nuob10**/**PSSW**)	0
nuop4	Insertion of HygR in **NUOP4** gene	50%

Complex I assembly in mutants

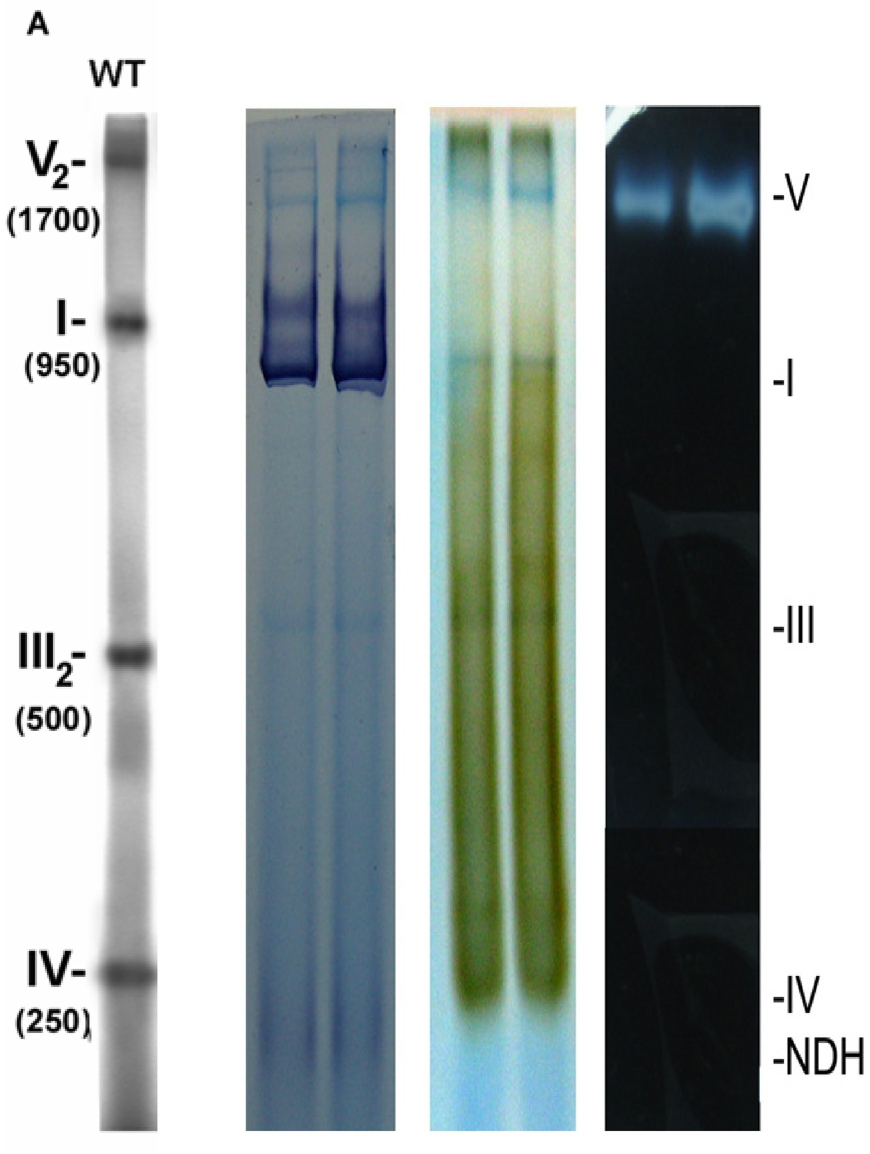
Generation of wall-less strain

Purification of mitochondria

Solubilization by mild-detergent

Blue-Native PAGE

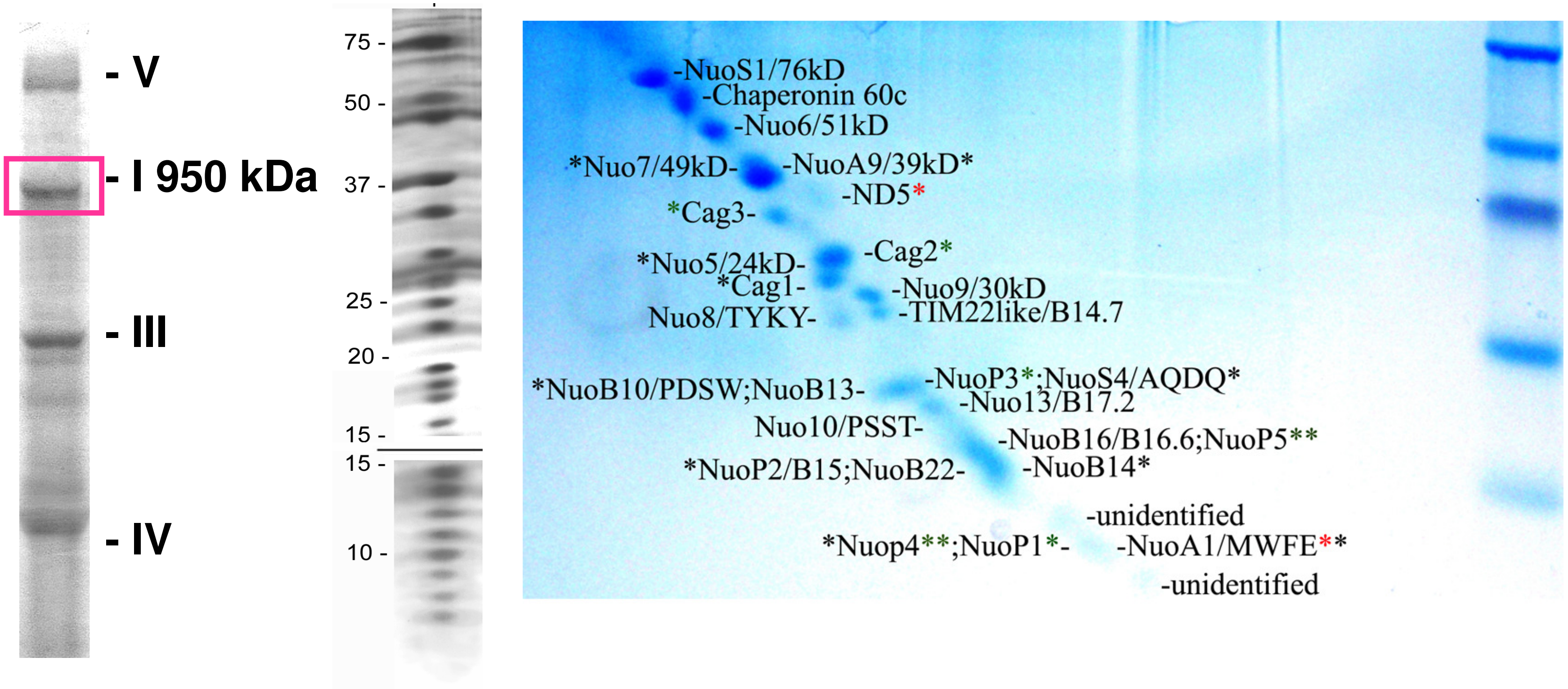
Complex enzyme detection



Chlamydomonas : mitochondrial respiratory-chain

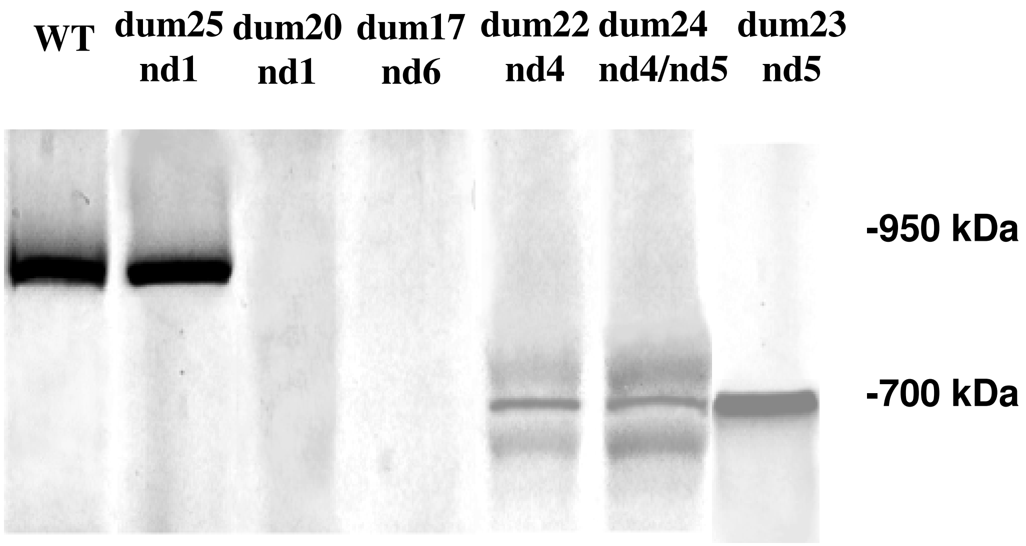
Genomic and proteomic characterization of complexI

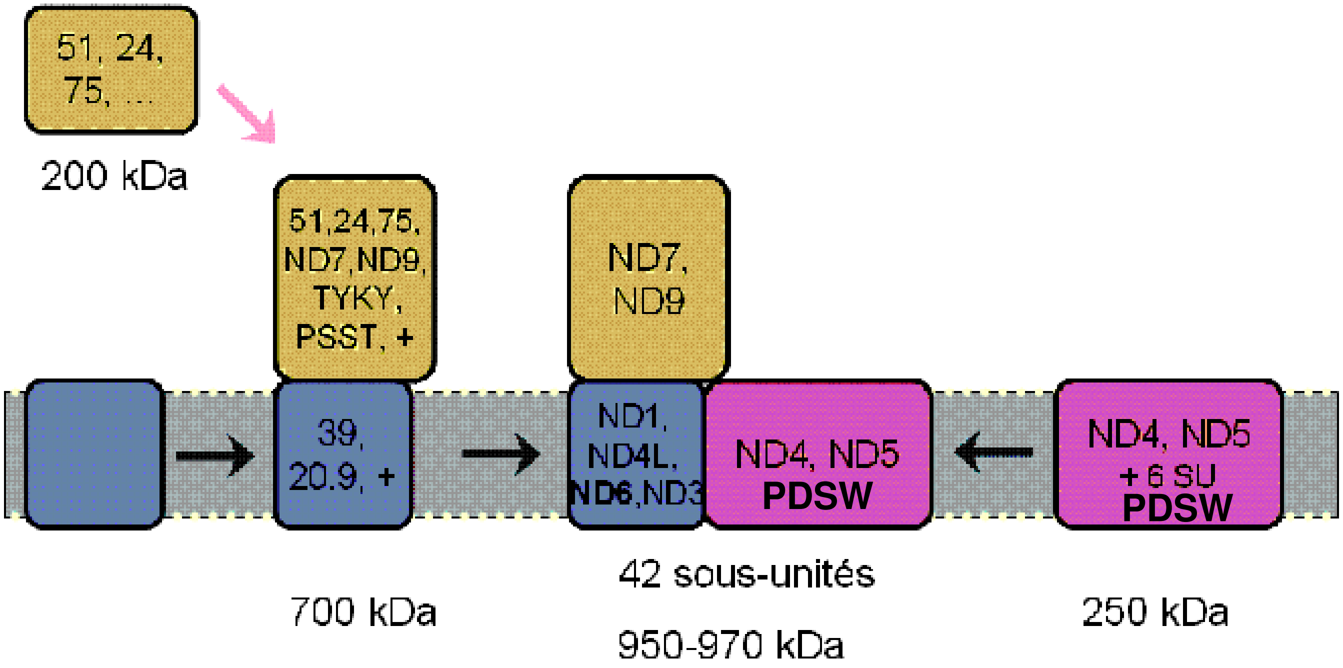
Purification of mitochondria from wall-less cells
Separation of solubilized mitochondrial complexes by BN-PAGE
Separation of complex components by 2D SDS-PAGE
Identification of proteins by mass spectrometry



Van Lis et al., 2003 Plant physiol. 132:318-30
Cardol et al 2004 BBA Bioenergetics 1658:212-24
Cardol et al 2005 Plant Physiol 137: 447-459

Complex I modular assembly deduced from mutant analysis





51, 24, 75, ...

200 kDa

51,24,75, ND7,ND9, TYKY, PSST, +

39, 20.9, +

700 kDa

ND7, ND9

ND1, ND4L, ND6,ND3

ND4, ND5
PDSW

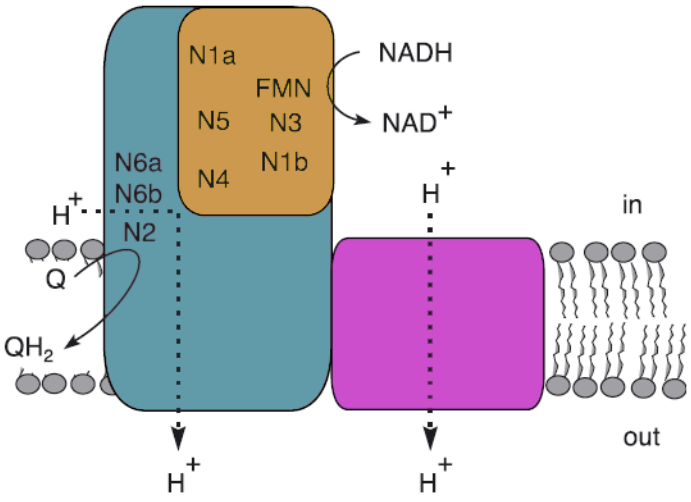
42 sous-unités

950-970 kDa

ND4, ND5 + 6 SU
PDSW

250 kDa

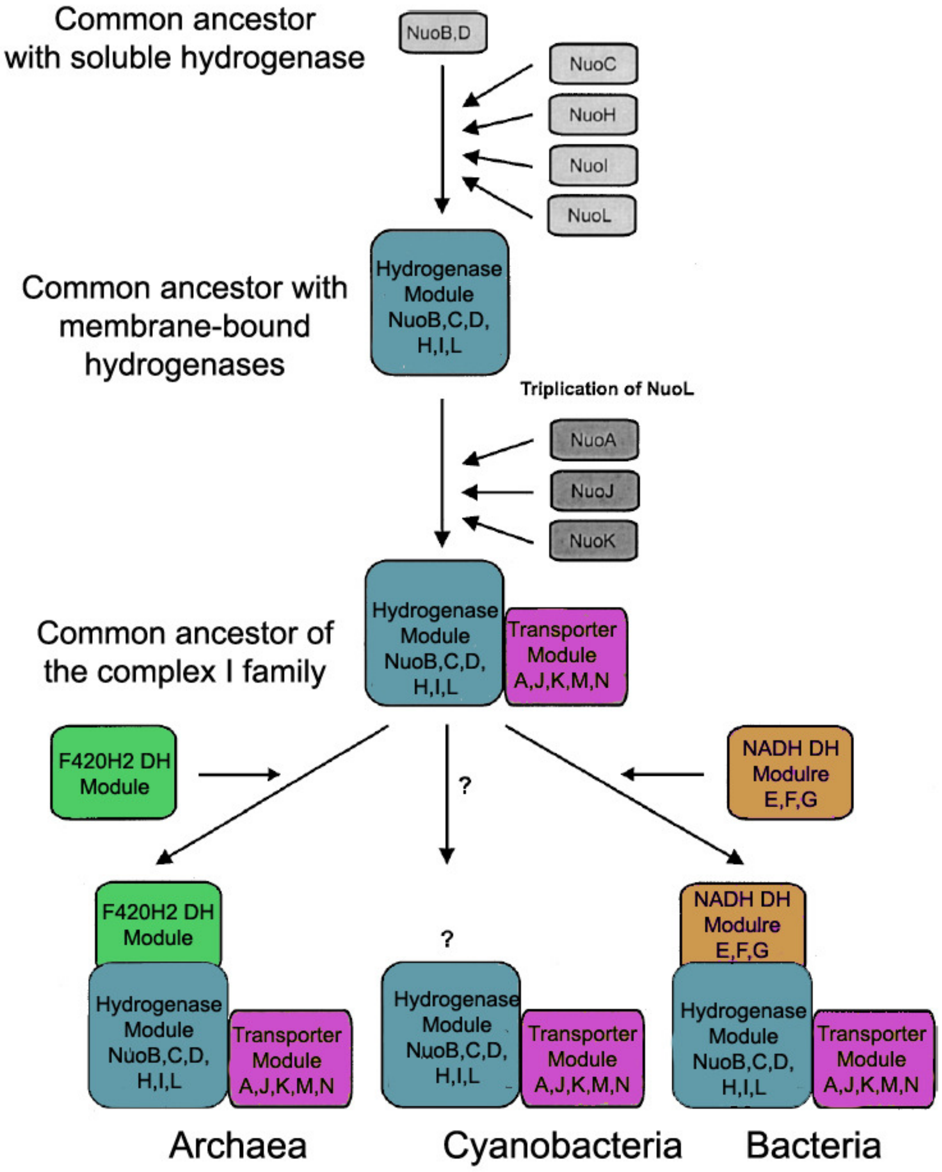
Modular Evolution of Complex I - part I : to prokaryote



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

Fig. 2. Cartoon of complex I, showing the three modules. The NADH dehydrogenase module is drawn in yellow, the hydrogenase module in blu and the transporter module in red . The Fe/S clusters are denoted as N1a, N1b, N2, N3, N4, N5, N6a, and N6b. The two proposed coupling sites are indicated, see text for details.

Fig. 1. Hypothetical scheme of the modular evolution of complex I. A ancestral hydrogenase made up by the progenitors of NuoB and D (uppe block) evolved by addition of a ferredoxin (NuoI), a transport protein (th progenitor of NuoL, M, and N), a quinone-binding protein (NuoH), and protein of yet unknown function (NuoC). This led to the formation of th common ancestor of complex I and the membrane-bound hydrogenases This enzyme was equipped with further proteins by triplication of th transporter protein NuoL and addition of NuoA, J, and K leading to th common ancestor of complex I of bacteria, cyanobacteria, and archaea The bacterial and the archaeal complex I emerged by acquisition of th NADH dehydrogenase module (NuoE, F, and G) and the $F_{420}H_2$ de hydrogenase module, respectively. The nature of the module adapted t build the cyanobacterial complex is not yet known. It cannot be exclude



Common ancestor with soluble hydrogenase

Common ancestor with membrane-bound hydrogenases

Common ancestor of the complex I family

Archaea

Cyanobacteria

Bacteria

Modular Evolution of Complex I - Role of core subunits

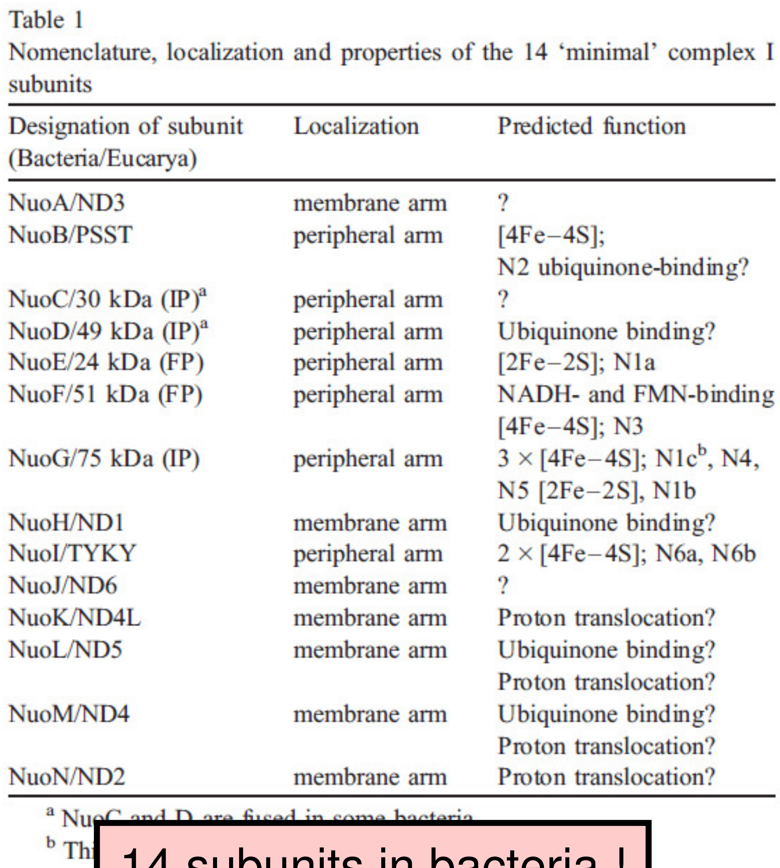


Table 1

Nomenclature, localization and properties of the 14 'minimal' complex I subunits

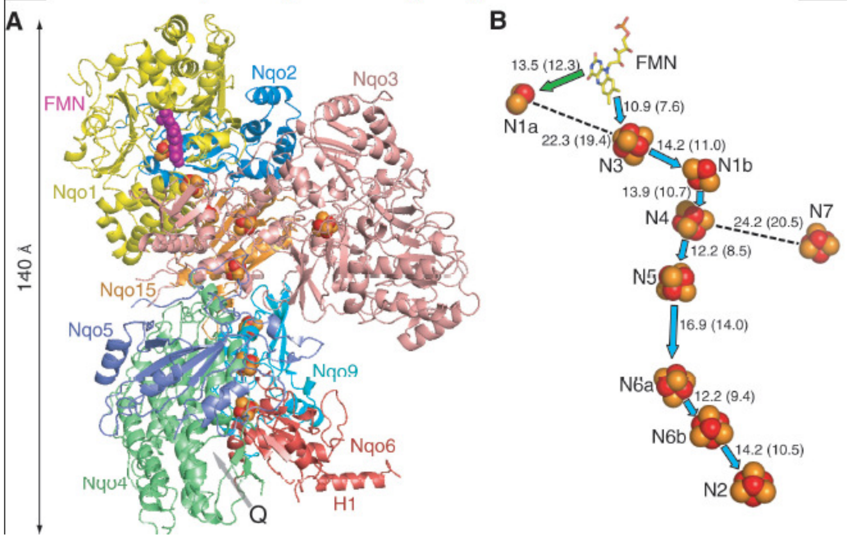
Designation of subunit (Bacteria/Eucarya)	Localization	Predicted function
NuoA/ND3	membrane arm	?
NuoB/PSST	peripheral arm	[4Fe–4S]; N2 ubiquinone-binding?
NuoC/30 kDa (IP)[a]	peripheral arm	?
NuoD/49 kDa (IP)[a]	peripheral arm	Ubiquinone binding?
NuoE/24 kDa (FP)	peripheral arm	[2Fe–2S]; N1a
NuoF/51 kDa (FP)	peripheral arm	NADH- and FMN-binding [4Fe–4S]; N3
NuoG/75 kDa (IP)	peripheral arm	3 × [4Fe–4S]; N1c[b], N4, N5 [2Fe–2S], N1b
NuoH/ND1	membrane arm	Ubiquinone binding?
NuoI/TYKY	peripheral arm	2 × [4Fe–4S]; N6a, N6b
NuoJ/ND6	membrane arm	?
NuoK/ND4L	membrane arm	Proton translocation?
NuoL/ND5	membrane arm	Ubiquinone binding? Proton translocation?
NuoM/ND4	membrane arm	Ubiquinone binding? Proton translocation?
NuoN/ND2	membrane arm	Proton translocation?

[a] NuoC and D are fused in some bacteria.

[b] Thi

14 subunits in bacteria !

www.sciencexpress.org / 9 February / Page 8/ 10.1126/science.1123809



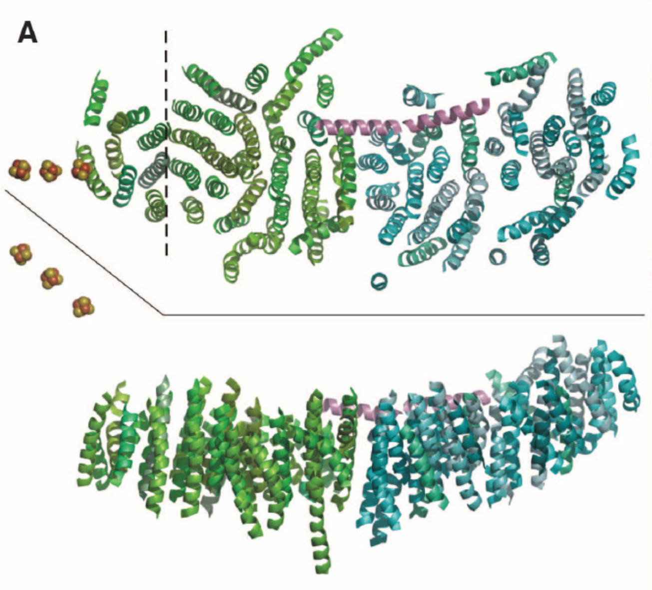


Fig. 2. Transmembrane segments and interface of the membrane arm and the peripheral arm. (**A**) Top view from matrix side and side view of the α-helical model of the transmembrane segments (upper and lower panel, respectively) fitted with helices arranged in a proximal (green) and a distal (cyan) domain. The border of the docking area with the peripheral arm is indicated by a dashed line (top). The three iron-sulfur clusters of the Q module are shown in space-filled representation. An extended helical element (magenta) may be critical for energy transmission within the membrane arm.

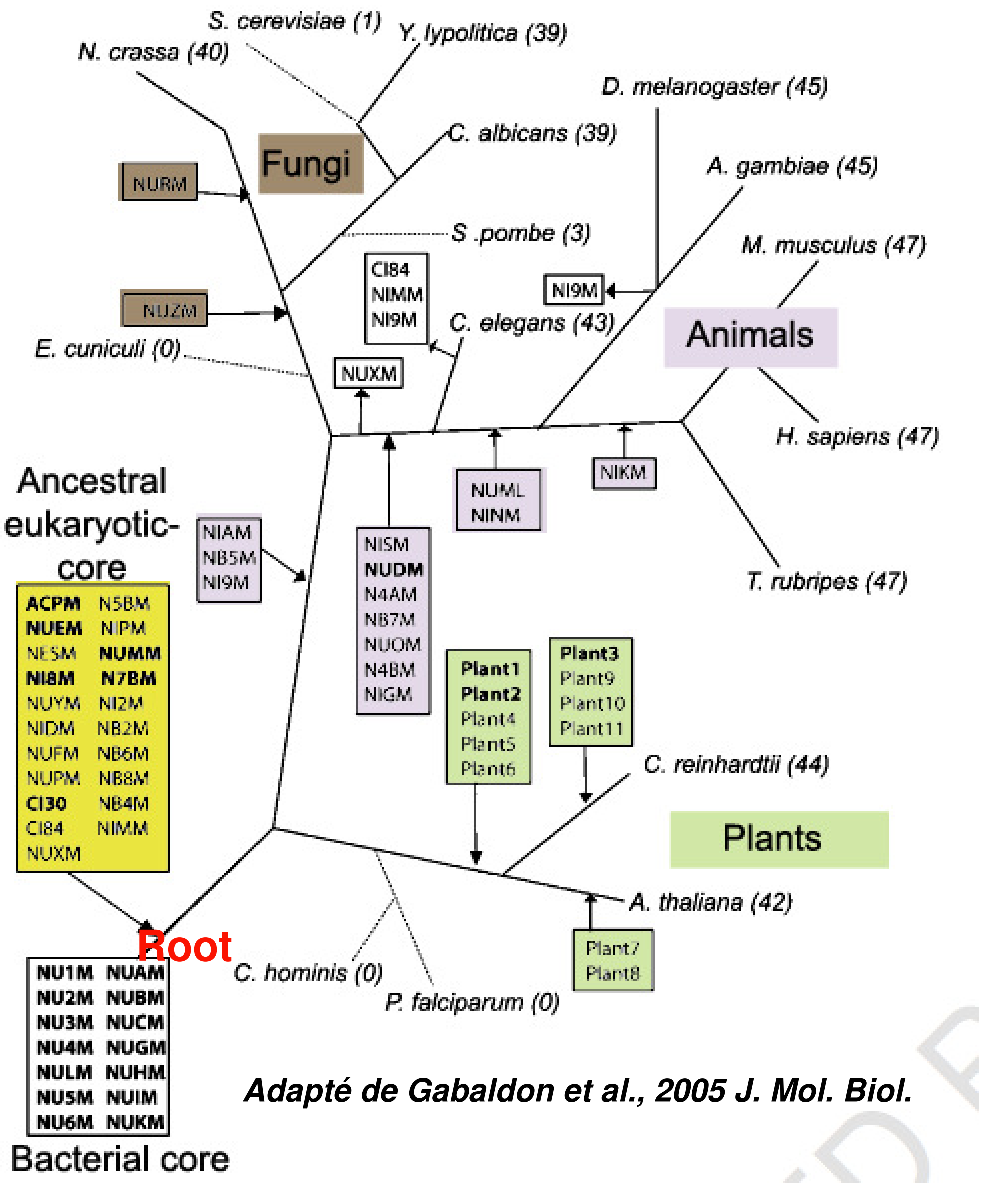
Hunte et al, 2010, Hinchcliffe and Sazanov., 2006, Science; Efremov and Sazanov, 2011, Nature

Modular Evolution of Complex I - part II : to eukaryotes

2005 :

Conserved subunits :
32 Mammals/Fungi/Plants

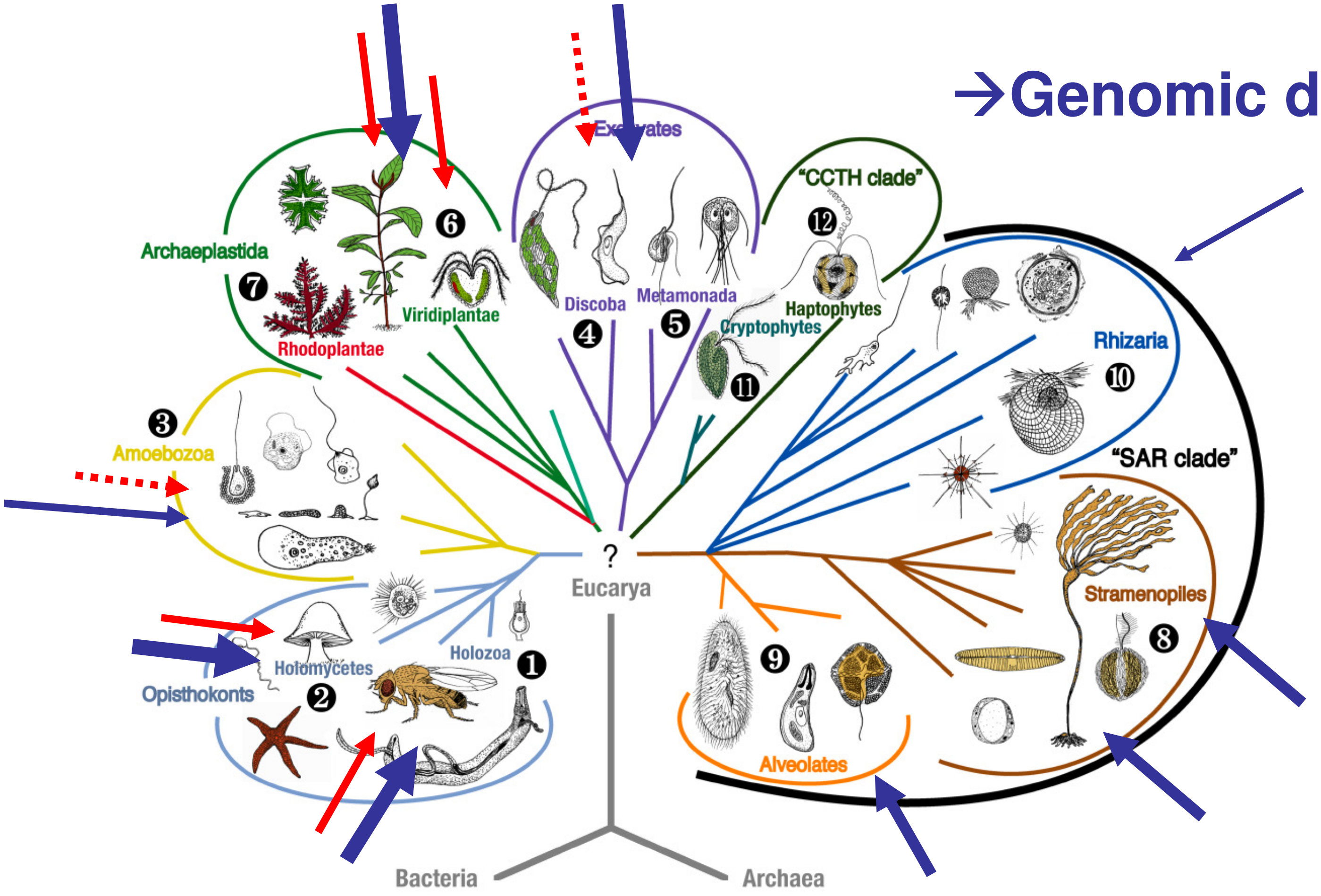
→More than 10 lineages specific subunits ?



Adapté de Gabaldon et al., 2005 J. Mol. Biol.

**(Cardol et al. 2005 Plant Phys
Gabaldon et al 2005 J. Mol Biol)**

Modular Evolution of Complex I - part II : to eukaryotes



→Genomic data

Klodmann et al., 2010
Bridges et al., 2010
Gawryluk and Gray, 2010

→Proteic data

Identification of orthologs to lineage-specific subunits

1/ % of amino acid identities/similarities

Psi (Position specific iterative) BLAST ***(Altschul et al., 1997)***

- -profile on initial multiple alignement
- -position specific scoring matrix
- -iterative BLAST search
- -the results of each "iteration" is used to refine

2/ protein size (+/- 50%)

3/Hydropathy profiles (Kite and Doolittle scale, Protscale)

4/ Putative transmembrane helices ?

5/ Structural motifs ?

Identification of orthologs to lineage-specific subunits

		NCBI	Mw	pI	Gravy	TMHH
35	**B14.5b / NDUFC2**					
Mammals	*Homo sapiens* NDUFC2	AAD20958	14,2	9,0	-0,39	(25-45),54-75
Fungi	*Neurospora crassa* Nuo10.4	XP_956744	10,5	10,8	-0,39	(5-20),31-50
Amoebozoa	*Dictyostelium discoideum*	XP_645303	13,0	9,6	-0,45	31-50,60-80
Viridiplantae	*Arabidopsis thaliana* NDU9	CAA18240	11,8	9,8	0,36	0-21,(29-49),75-95
Chromalveolates	*Ectocarpus siliculosus*	CBN76703	9,4	9,6	-0,03	(0-18,21-39,41-60)
Excavates	*Naegleria gruberi*	XP_002678500	12,5	9,8	-0,48	11-32,41-59

```
Mammals   Hs  1 --MIARRNPEPLRFLPDEARSLPPPKLTDPRLLYIGFLGYCSGLIDNVIRRRPIATAG--
Amoebozoa Dd  1 MTQEIIRPTNTENYISNETNPF-KKISRTKRVIMGVGLGISCGVITNGFYKRPMGSNP--
Fungi     Nc  1 ---------------------------MVHRMIFWAGFGLATRAWSLGIERRPILGRNTL
Excavates Ng  1 -------------------MPLDFKFEIGNPFLLGNAIGFLGYAGACKLQRVHFVRRP--
Chlorophy Cr  1 -------------------MGW------AYSGEWGMLAGFCFGTLKNVQEGKAWFRRP--
Streptoph At  1 -------------------MPI-------SATMVGALLGLGTQMYSNALRKLPYMRHP--
Stramenop Es  1 -------------------MGI-------TAMTVGGAFGIVAKGTVNRLMKVSLRRAP--
consensus     1                    . .         .......*.      . . .... ...

Hs           57 LHRQLLYITAFFFAGYYLVKREDYLYAVRDREMFGYMKLHPEDFPEEDKKTYG------E
Dd           58 HVHA----LWAVALGTLMYKSYDFNDYIVKREIFTLSIHQQRVREQELLKQ--------E
Nc           34 WGYP-VFAAIGASFGYWVQGVDERQQAILQERKQAILDKRARRAARQQEQAHG------E
Ng           40 WHLITTMLLTGTGFQAYSGAHESFTDDLVRKRRLYVQRRRKRFNSSD------------D
Cr           34 YIHG-----AGMIAGYYLFKAAADWEDEALKRIITRYERKGYAIPEDRKELFA-------
At           33 WEHV-----VGMGLGAVFANQLVKWDVKLKEDL---DVMLAKARAANERRYFGIYYPLLV
Es           33 WEYV-----LGAGIGAYVGNKIPQWEATLISDI---NEMRADRNMPPATRVGG-----YE
consensus    61 . .       . . . ..       . .. ...     ....    .  .  .      .
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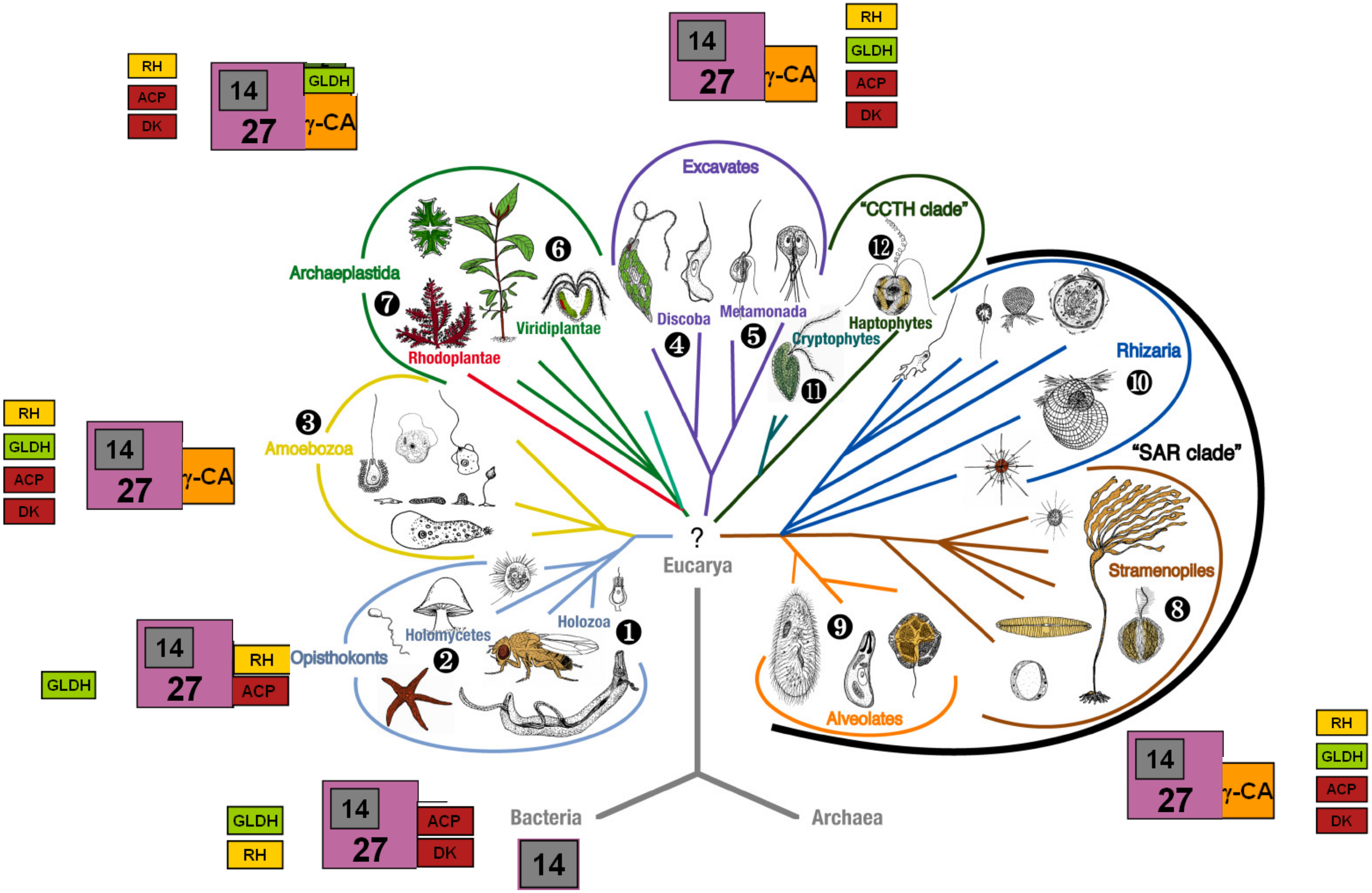
Cardol et al., 2011, BBA

Modular Evolution of Complex I - part II : to eukaryotes



Cardol et al., 2011, BBA

Part I : conclusions

1) Use of non mammalian model systems to study human diseases caused by complex I deficiency

2) newly-identified conserved components (e.g. SGDH, AGGG, KFYI)
probably play yet to elucidate conserved functions

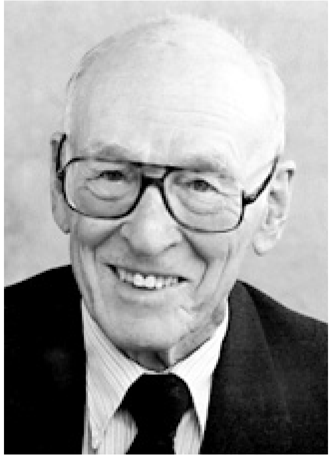
3) x-ray cartography performed on Yarrowia complex I ***(Hunte et al. 2010)***
highly relevant for understanding complex I from other sources.

4) machinery required for its assembly is well conserved among eukaryotes
→Could be elucidated in non mammalian model systems

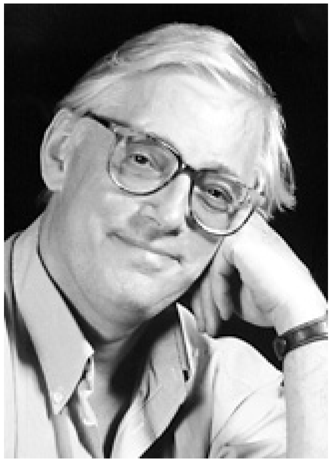
5) complexification of mitochondrial complex I did not occur progressively during speciation of eukaryotic lineages

Part II : Structure and function of Complex V

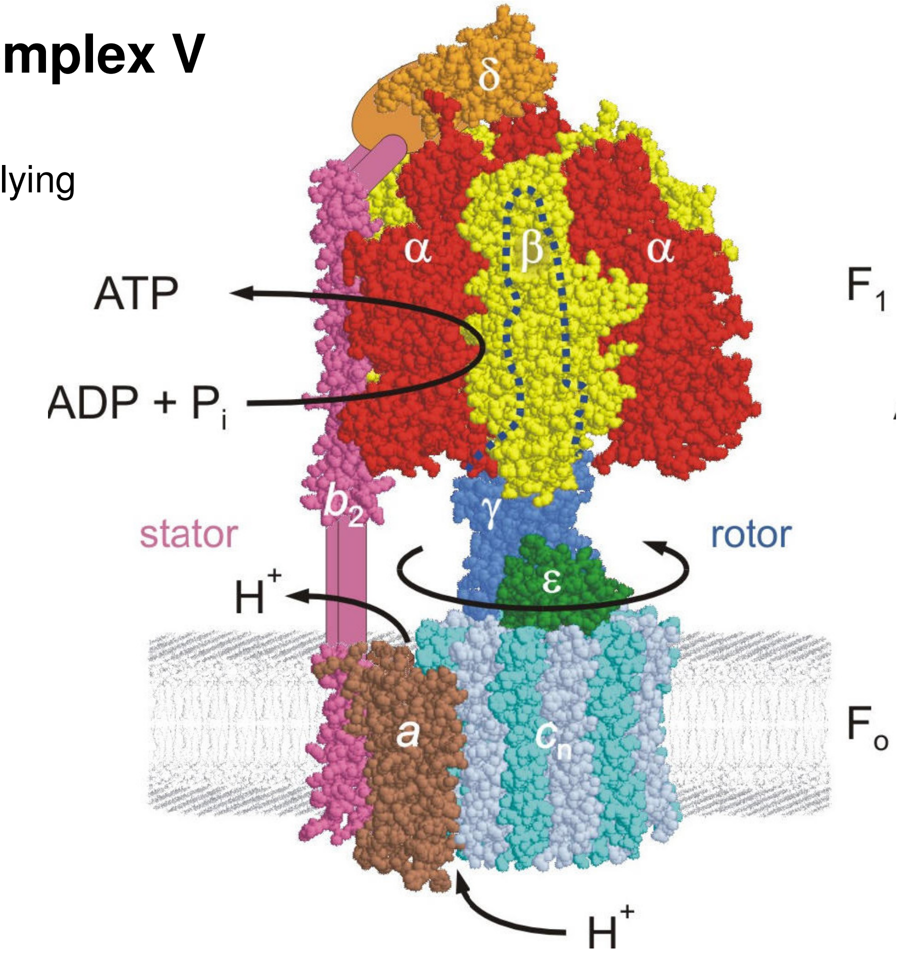
The Nobel Prize in Chemistry 1997
"for their elucidation of the enzymatic mechanism underlying
the synthesis of adenosine triphosphate (ATP)"

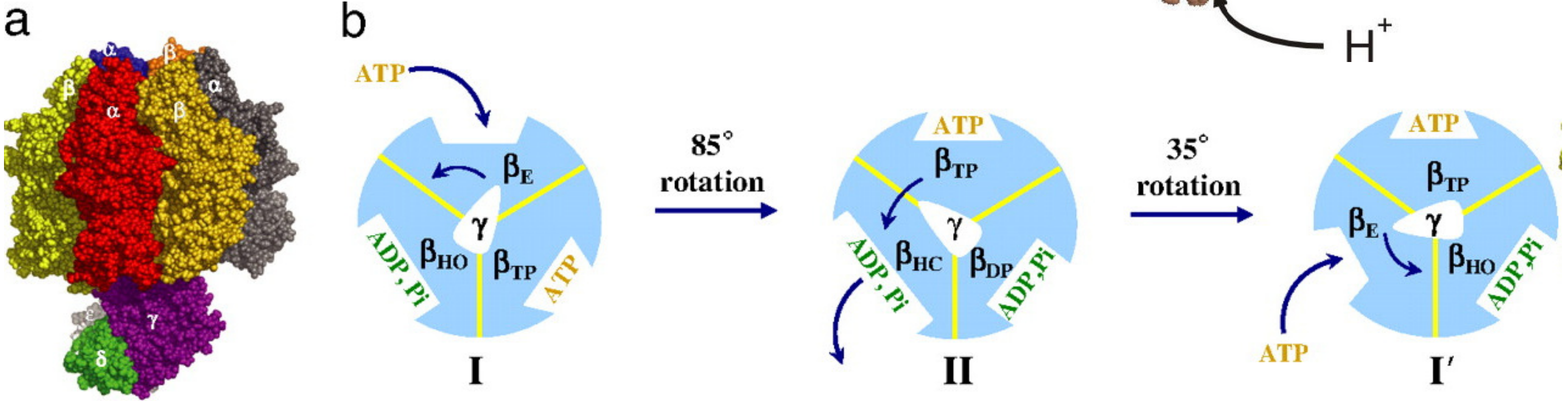


Paul D. Boyer



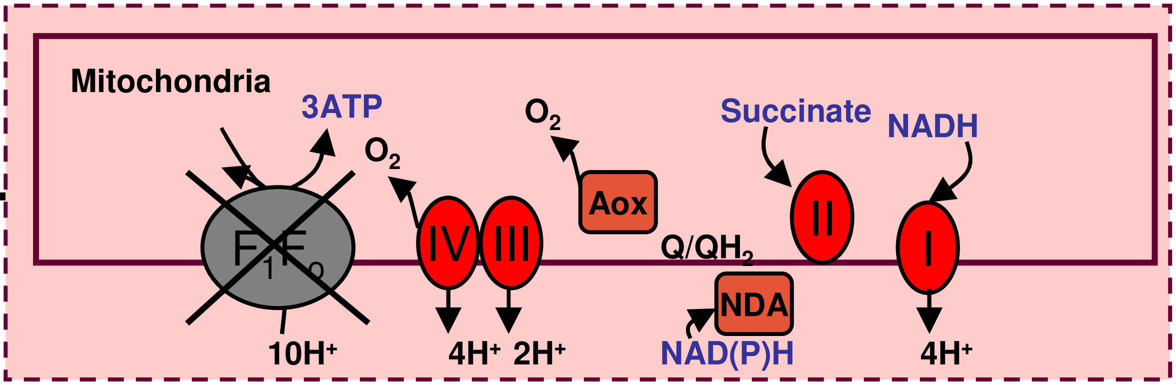
John E. Walker



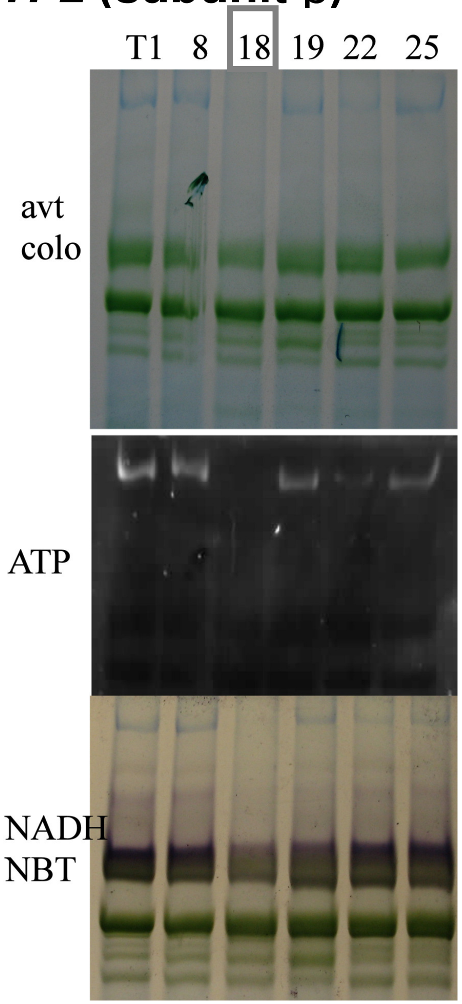


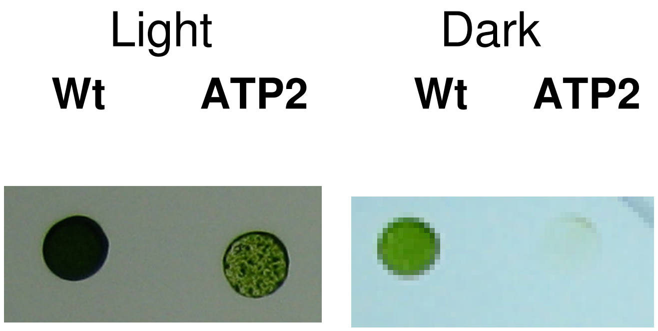
Pu J, Karplus M PNAS 2008;105:1192-1197

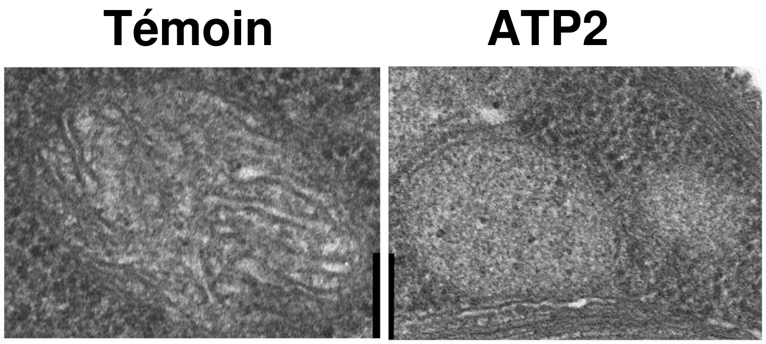
Chlamydomonas



<u>RNA interference</u> : *ATP2* (subunit β)

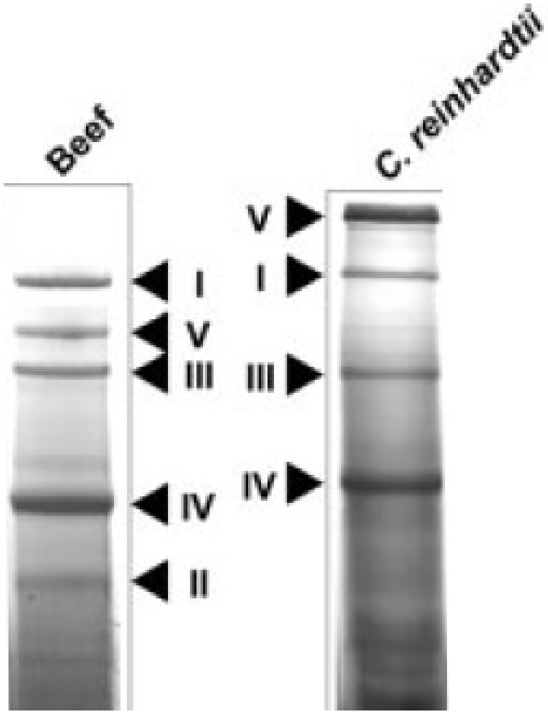






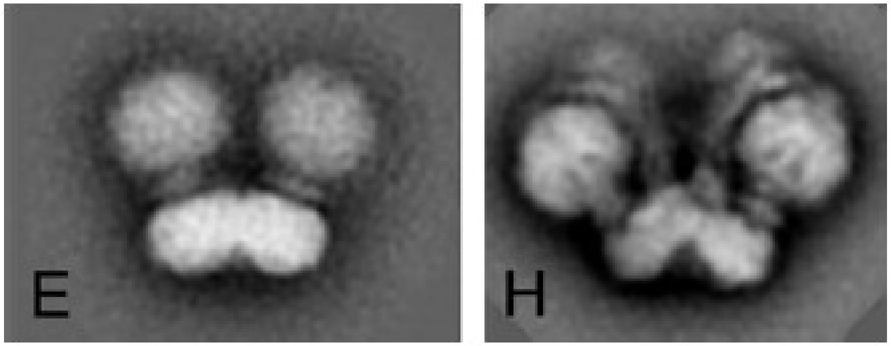
Lapaille et al., 2010, BBA

Evolution of Complex V : Chlorophyceae

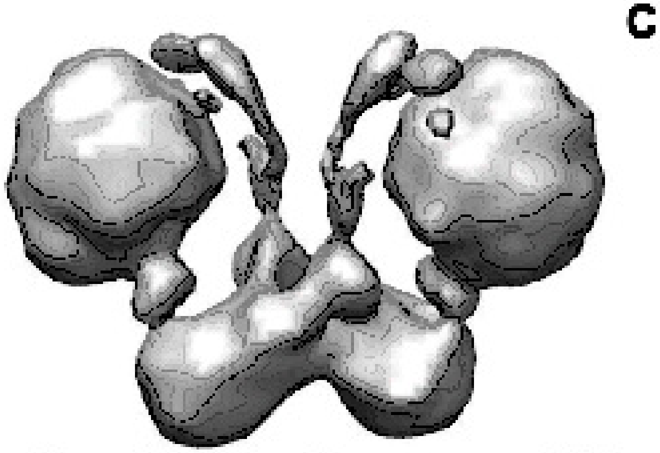


Plant Physiology, May 2003, Vol. 132, pp. 318–330,

N. V. Dudkina et al. / FEBS Letters xxx (2006) xxx–xxx



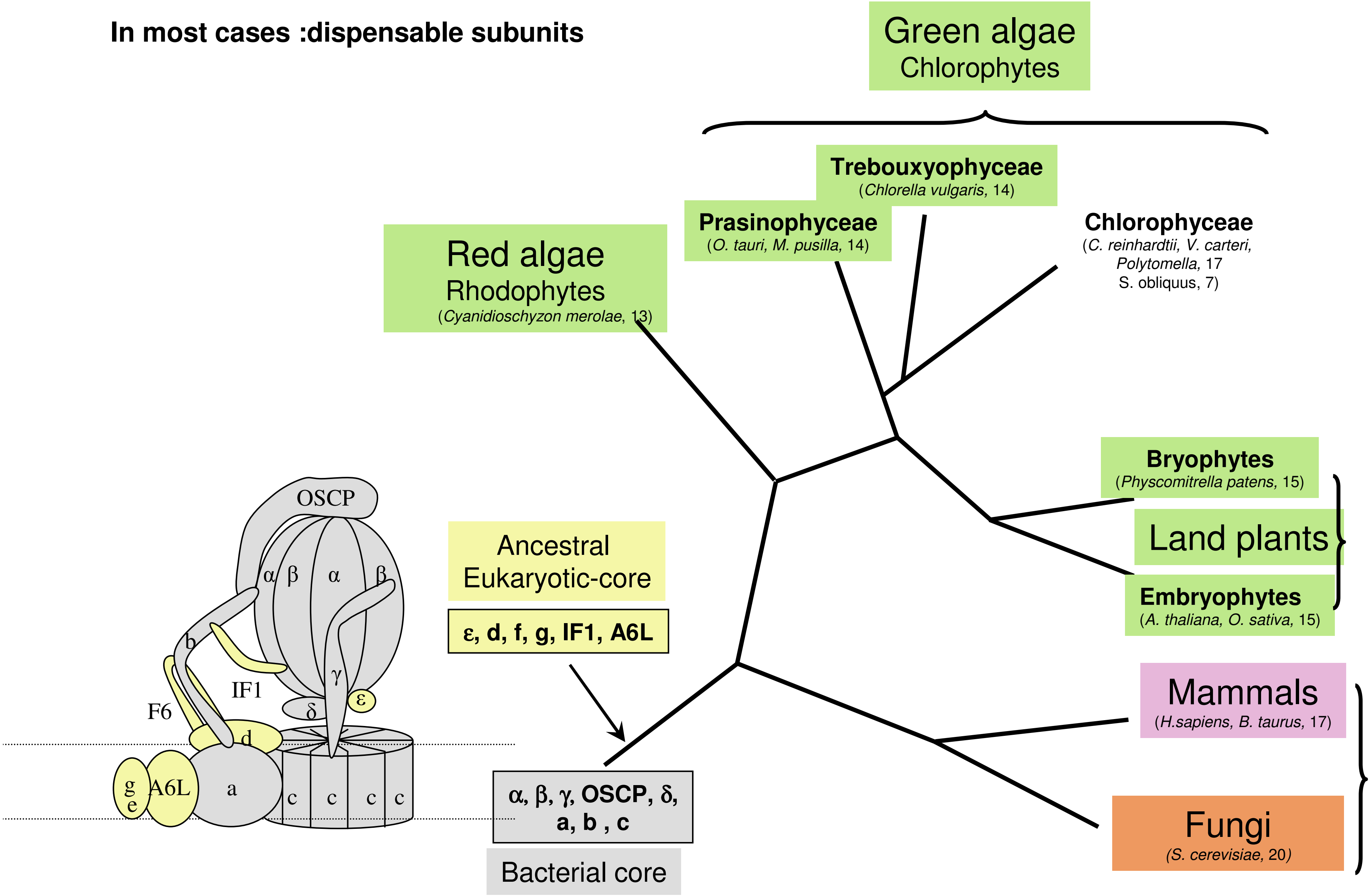
Yeast (~mammal)) Polytomella (~Chlamydomonas)



Gonzalez-Halphen D., pers. comm. 2009

Complex V : Complexification in eukaryotes

In most cases :dispensable subunits



Green algae
Chlorophytes

Trebouxyophyceae
(*Chlorella vulgaris,* 14)

Prasinophyceae
(*O. tauri, M. pusilla,* 14)

Chlorophyceae
(*C. reinhardtii, V. carteri,*
Polytomella, 17
S. obliquus, 7)

Red algae
Rhodophytes
(*Cyanidioschyzon merolae,* 13)

Bryophytes
(*Physcomitrella patens,* 15)

Land plants

Embryophytes
(*A. thaliana, O. sativa,* 15)

Ancestral
Eukaryotic-core

ε, d, f, g, IF1, A6L

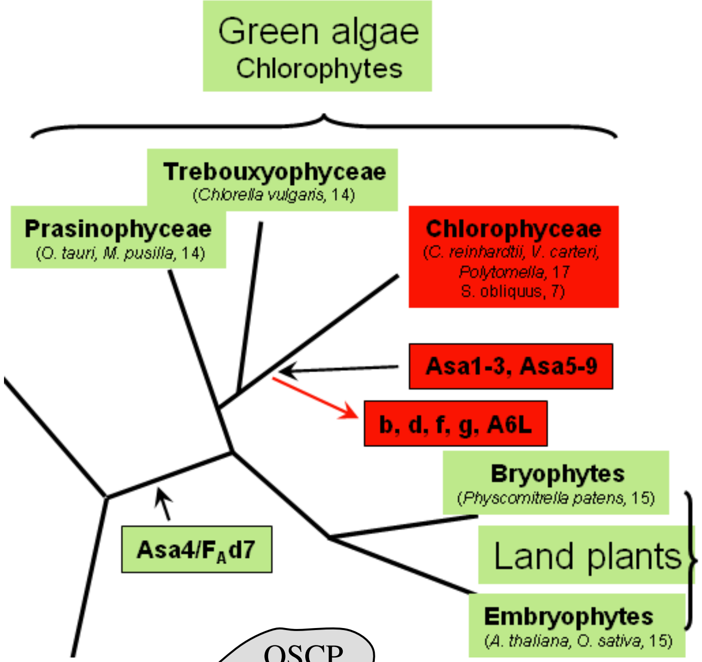
α, β, γ, OSCP, δ,
a, b , c

Bacterial core

Mammals
(*H.sapiens, B. taurus,* 17)

Fungi
(*S. cerevisiae,* 20)

Evolution of Complex V : Chlorophyceae



Green algae
Chlorophytes

Trebouxyophyceae
(*Chlorella vulgaris*, 14)

Prasinophyceae
(*O. tauri*, *M. pusilla*, 14)

Chlorophyceae
(*C. reinhardtii*, *V. carteri*, *Polytomella*, 17
S. obliquus, 7)

Asa1-3, Asa5-9

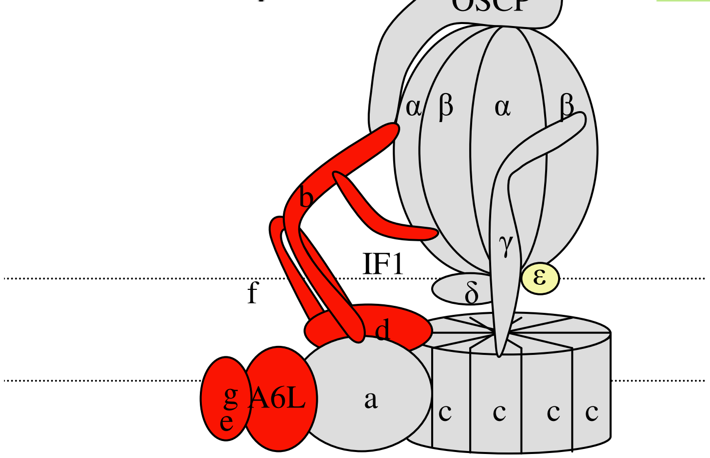
b, d, f, g, A6L

Bryophytes
(*Physcomitrella patens*, 15)

Land plants

Embryophytes
(*A. thaliana*, *O. sativa*, 15)

Asa4/F$_A$d7



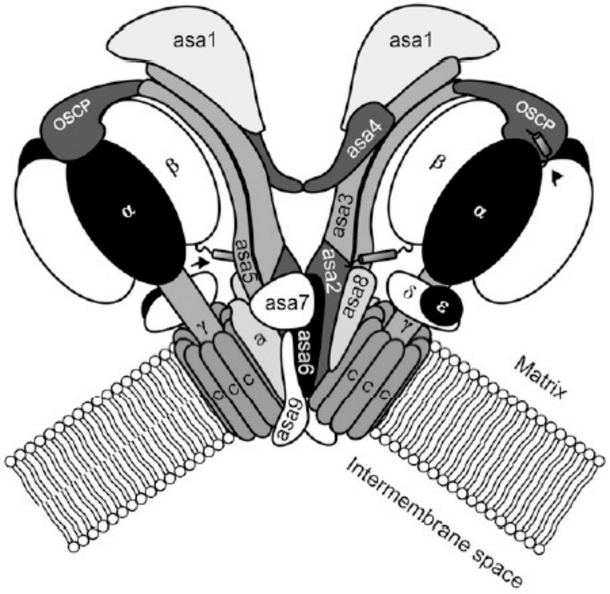
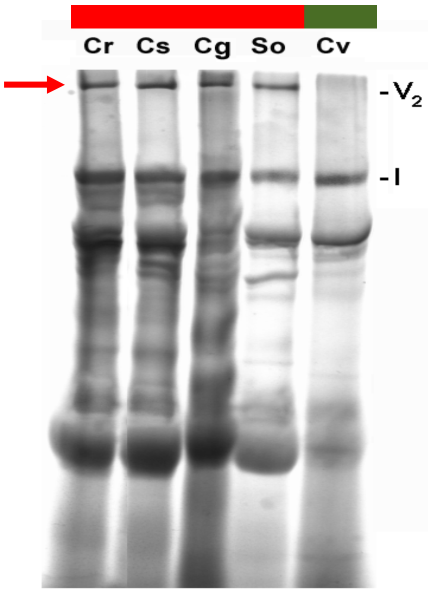
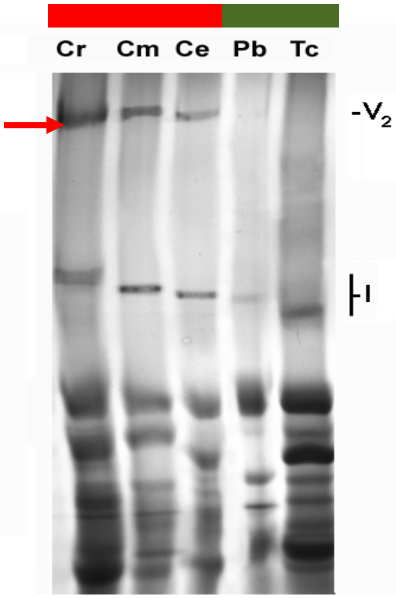
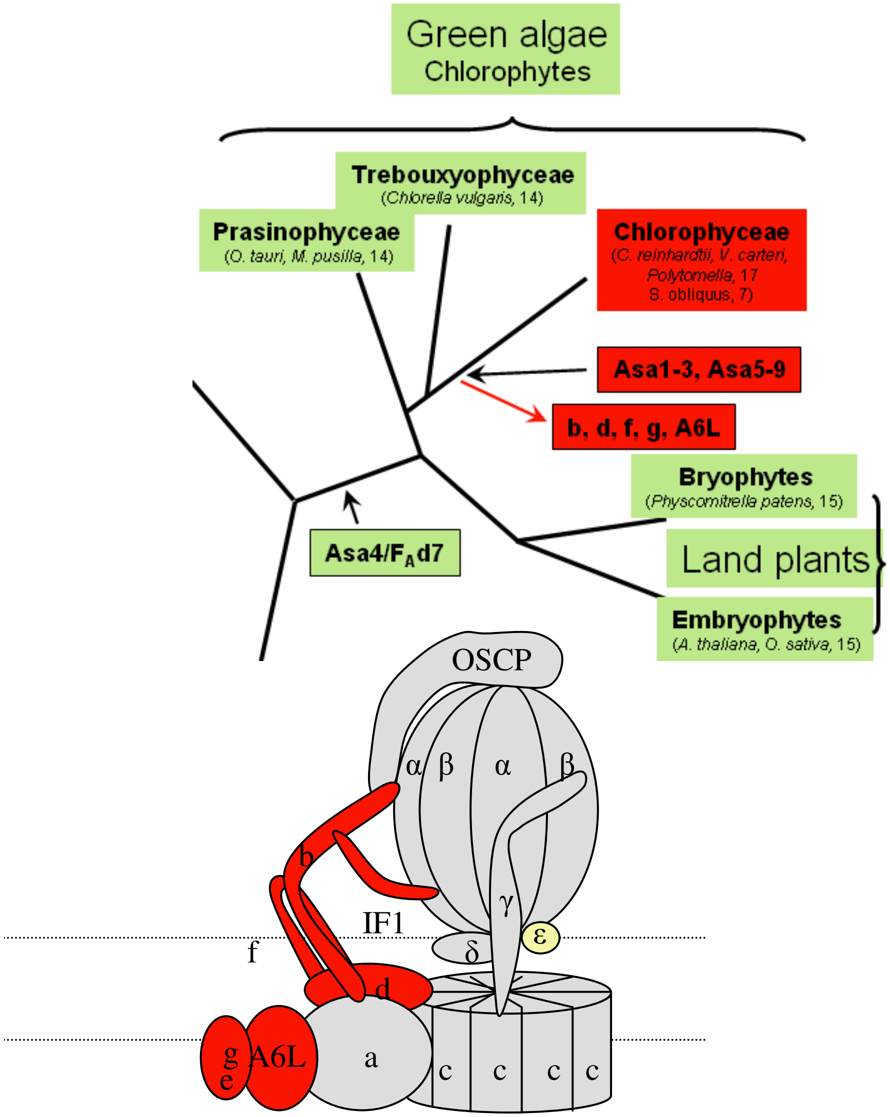


Figure 6. Working model of dimeric mitochondrial ATP synthase in Chlamydomonad algae, based on our current knowledge of the enzyme from both *C. reinhardtii* and *Polytomella* sp. The monomers are shown rotated 180° one from another (around a vertical axis), as proposed previously for the yeast enzyme (Paumard et al., 2002).





Evolution of Complex V : Chlorophyceae



Green algae
Chlorophytes

Trebouxyphyceae
(*Chlorella vulgaris*, 14)

Prasinophyceae
(*O. tauri, M. pusilla*, 14)

Chlorophyceae
(*C. reinhardtii, V. carteri, Polytomella*, 17
S. obliquus, 7)

Asa1-3, Asa5-9

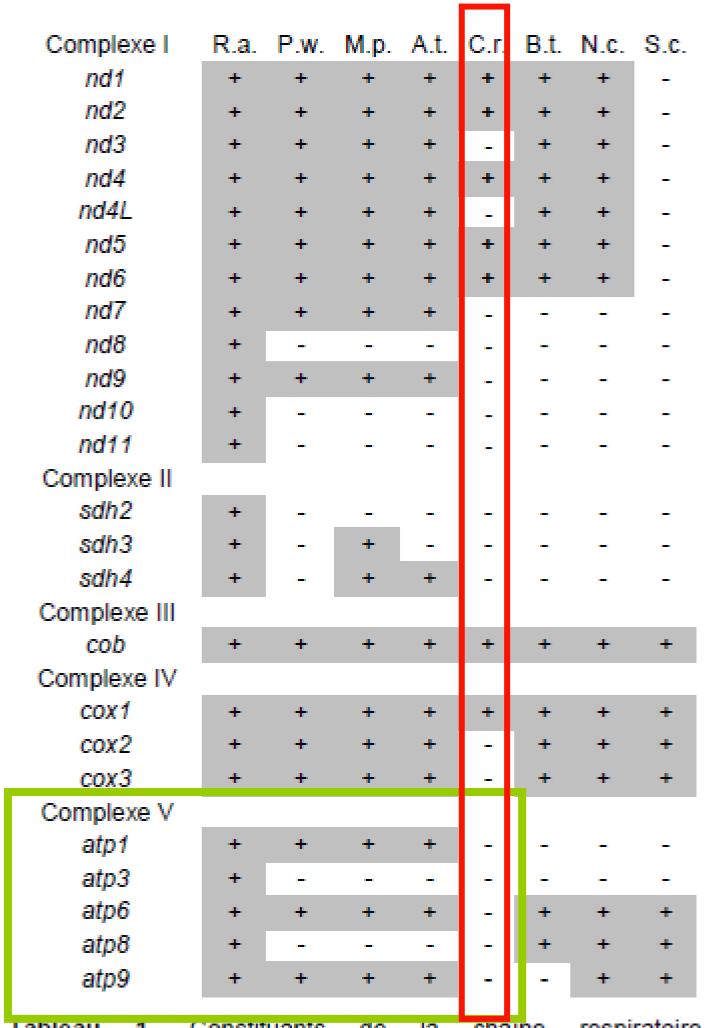
b, d, f, g, A6L

Bryophytes
(*Physcomitrella patens*, 15)

Land plants

Asa4/F$_A$d7

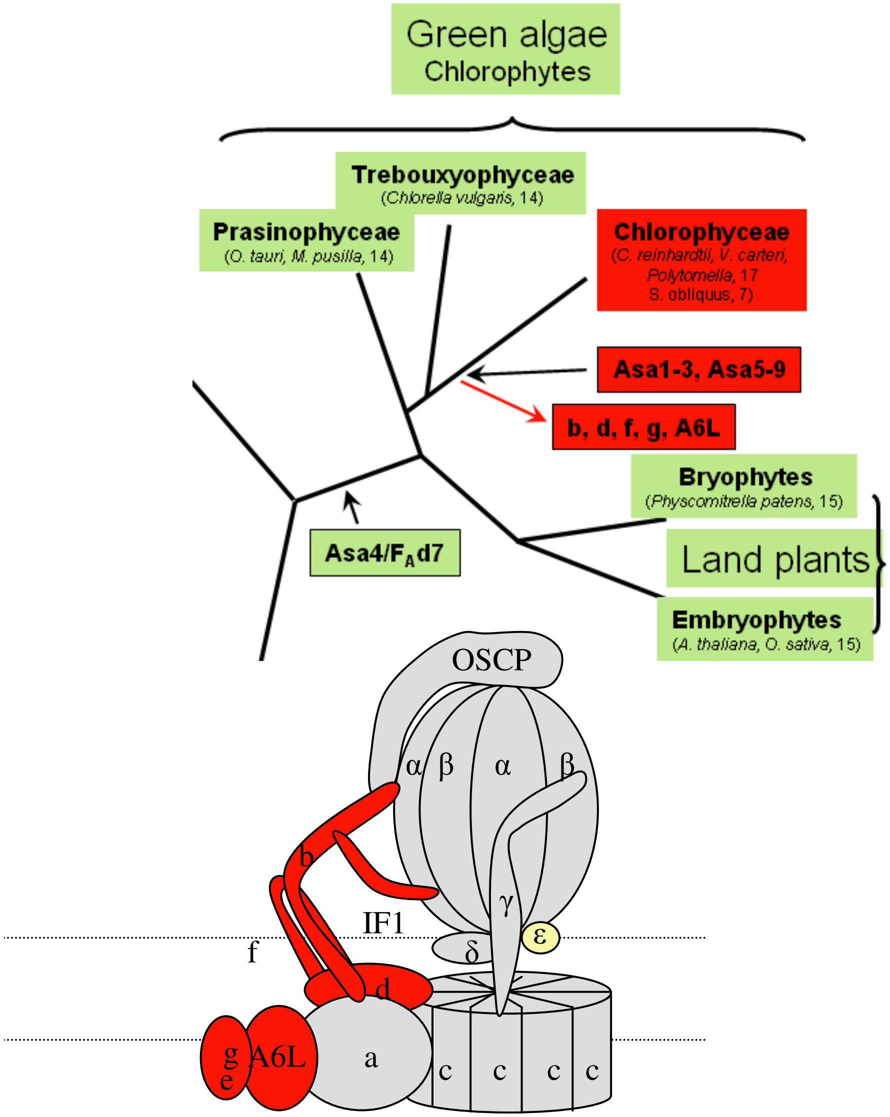
Embryophytes
(*A. thaliana, O. sativa*, 15)



Complexe I	R.a.	P.w.	M.p.	A.t.	C.r.	B.t.	N.c.	S.c.
nd1	+	+	+	+	+	+	+	-
nd2	+	+	+	+	+	+	+	-
nd3	+	+	+	+	-	+	+	-
nd4	+	+	+	+	+	+	+	-
nd4L	+	+	+	+	-	+	+	-
nd5	+	+	+	+	+	+	+	-
nd6	+	+	+	+	+	+	+	-
nd7	+	+	+	+	-	-	-	-
nd8	+	-	-	-	-	-	-	-
nd9	+	+	+	+	-	-	-	-
nd10	+	-	-	-	-	-	-	-
nd11	+	-	-	-	-	-	-	-
Complexe II								
sdh2	+	-	-	-	-	-	-	-
sdh3	+	-	+	-	-	-	-	-
sdh4	+	-	+	+	-	-	-	-
Complexe III								
cob	+	+	+	+	+	+	+	+
Complexe IV								
cox1	+	+	+	+	+	+	+	+
cox2	+	+	+	+	-	+	+	+
cox3	+	+	+	+	-	+	+	+
Complexe V								
atp1	+	+	+	+	-	-	-	-
atp3	+	-	-	-	-	-	-	-
atp6	+	+	+	+	-	+	+	+
atp8	+	-	-	-	-	+	+	+
atp9	+	+	+	+	-	-	+	+

Tableau 1. Constituants de la chaîne respiratoire mitochondriale encodés par le génome mitochondrial chez divers organismes (adapté de Vedel *et al.*, 1999). R.a., *Reclinomonas americana* ; P.w., *Prototheca wickerhamii* ; M.p., *Marchantia polymorpha* ; A.t., *Arabidopsis thaliana* ; C.r., *Chlamydomonas reinhardtii*; B.t., *Bos taurus* ; N.c., *Neurospora crassa* ; S.c., *Saccharomyces cerevisiae* . + ou – indique la présence ou l'absence du gènes mitochondrial.

Evolution of Complex V : Chlorophyceae



Transfer of Mitochondrial genes to the nucleus

Loss of conserved subunits

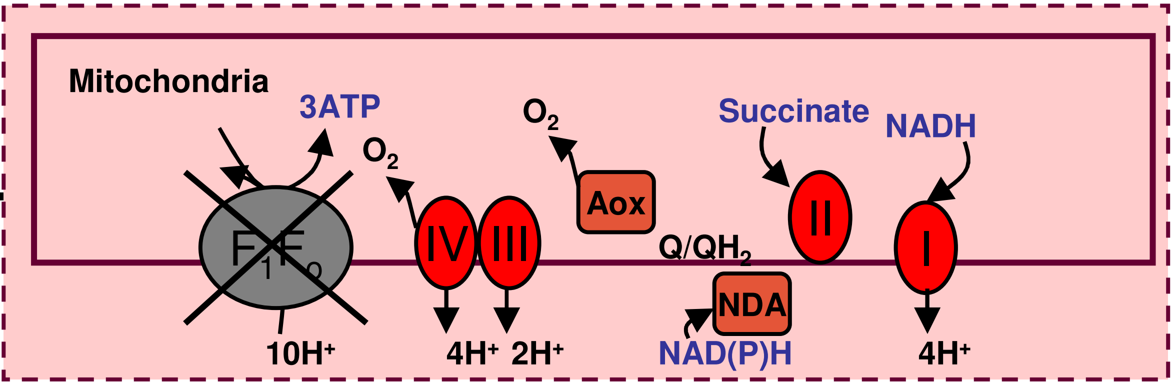
Recruitement of ASAs

i) relocation of previously extant proteins to the mitochondria,

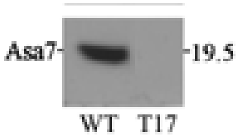
ii) acquisition of novel genes by lateral gene transfer

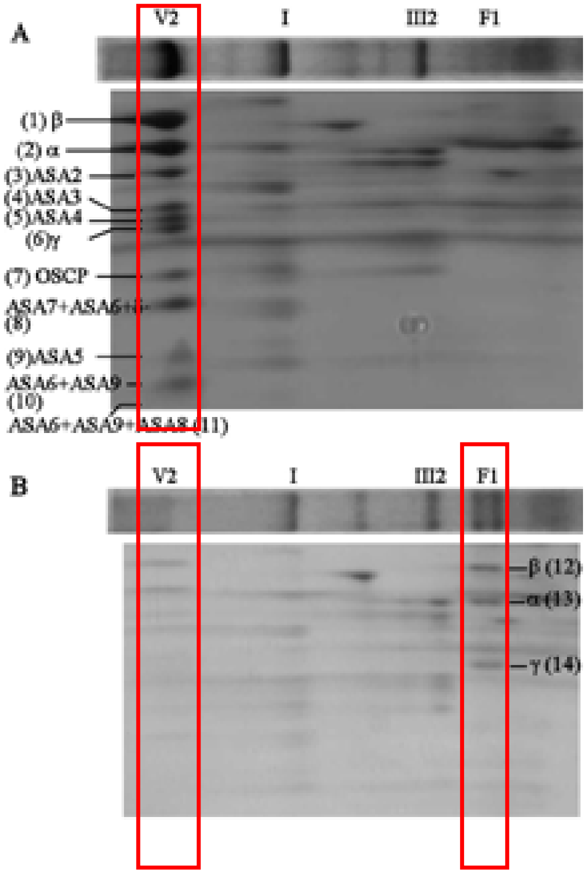
No sequence or pattern similarities in existing DB

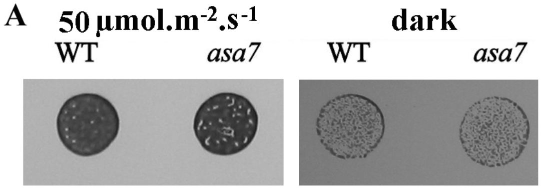
Chlamydomonas

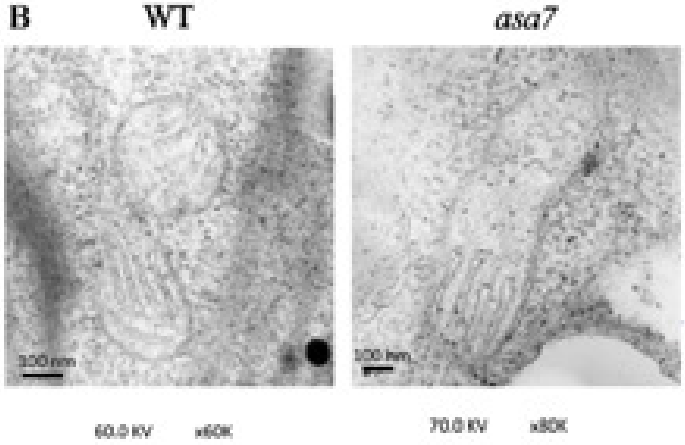


<u>RNA interference</u> : *ASA7*





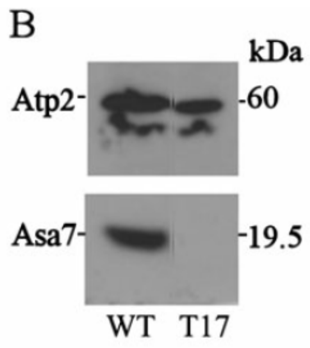


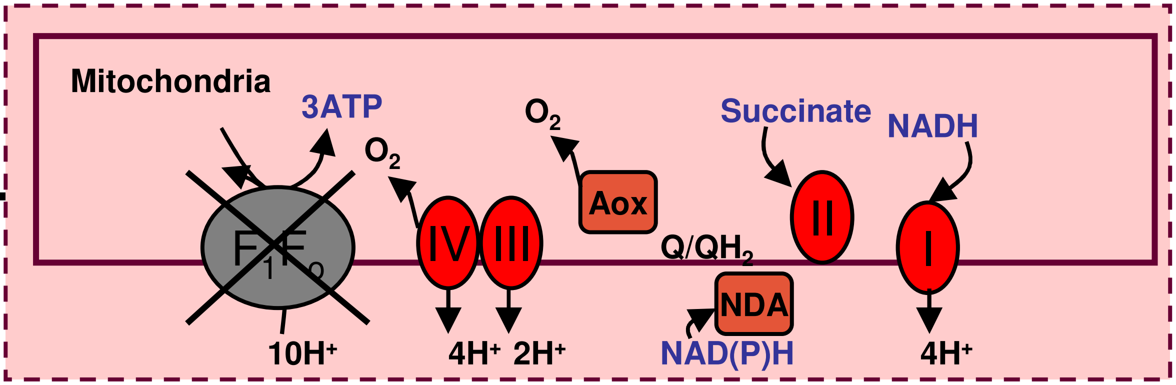


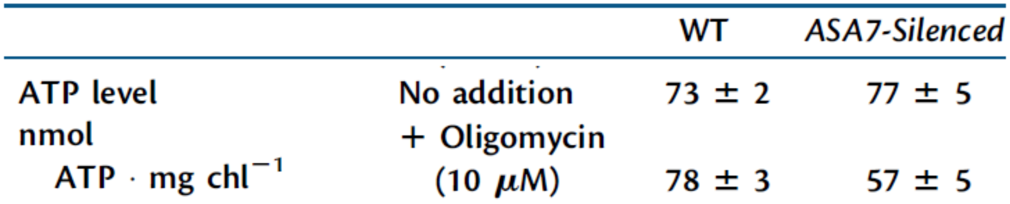
Lapaille et al., 2010, Mol. Biol. Evol.

Chlamydomonas

<u>RNA interference</u> : *ASA7*

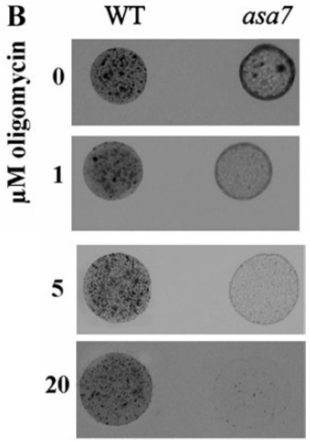






		WT	*ASA7-Silenced*
ATP level nmol ATP · mg chl^{-1}	No addition	73 ± 2	77 ± 5
	+ Oligomycin (10 µM)	78 ± 3	57 ± 5

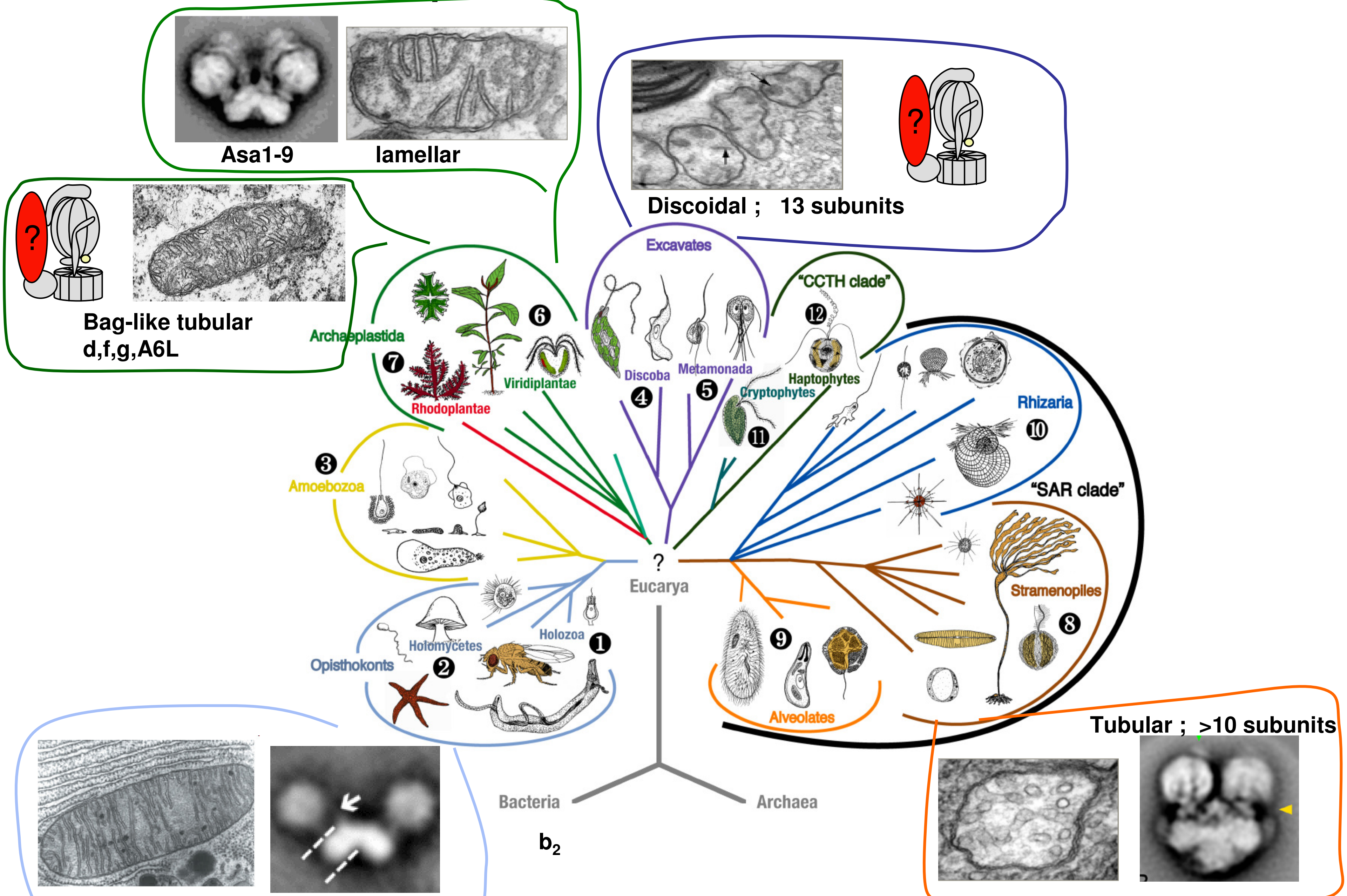
→ ASA7 subunit stabilizes the dimeric form



→ASA7 confer resistance to natural inhibitor present in soil-environment

Lapaille et al., 2010, Mol. Biol. Evol.

stator composition and mitochondrial structure



Asa1-9 **lamellar**

Bag-like tubular
d,f,g,A6L

Discoidal ; 13 subunits

Tubular ; >10 subunits

b_2

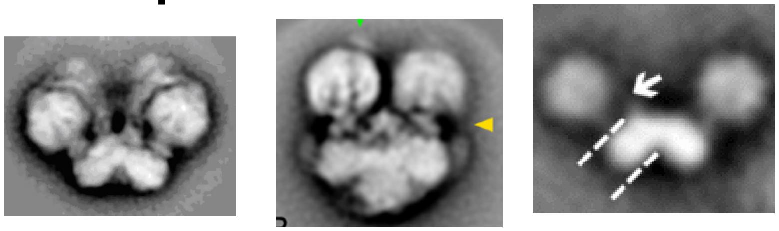
Crêtes lamellaires ; b, d, f, e, g

Balabaskaran Nina, PloS Biology
2010, 8(7), e1000418

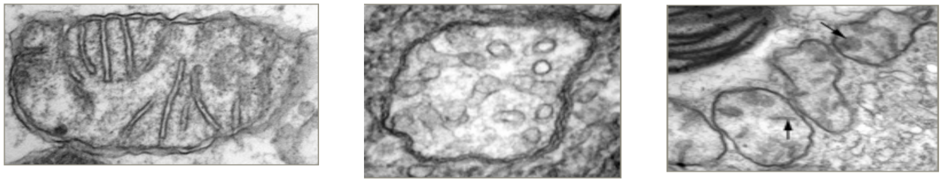
Part II : Conclusions and perspectives

Transfer of mt genes coding for stator subunits to nucleus has led to recruitment of new subunit in various lineages

New subunits are responsible for the various dimeric structure of ATP synthase

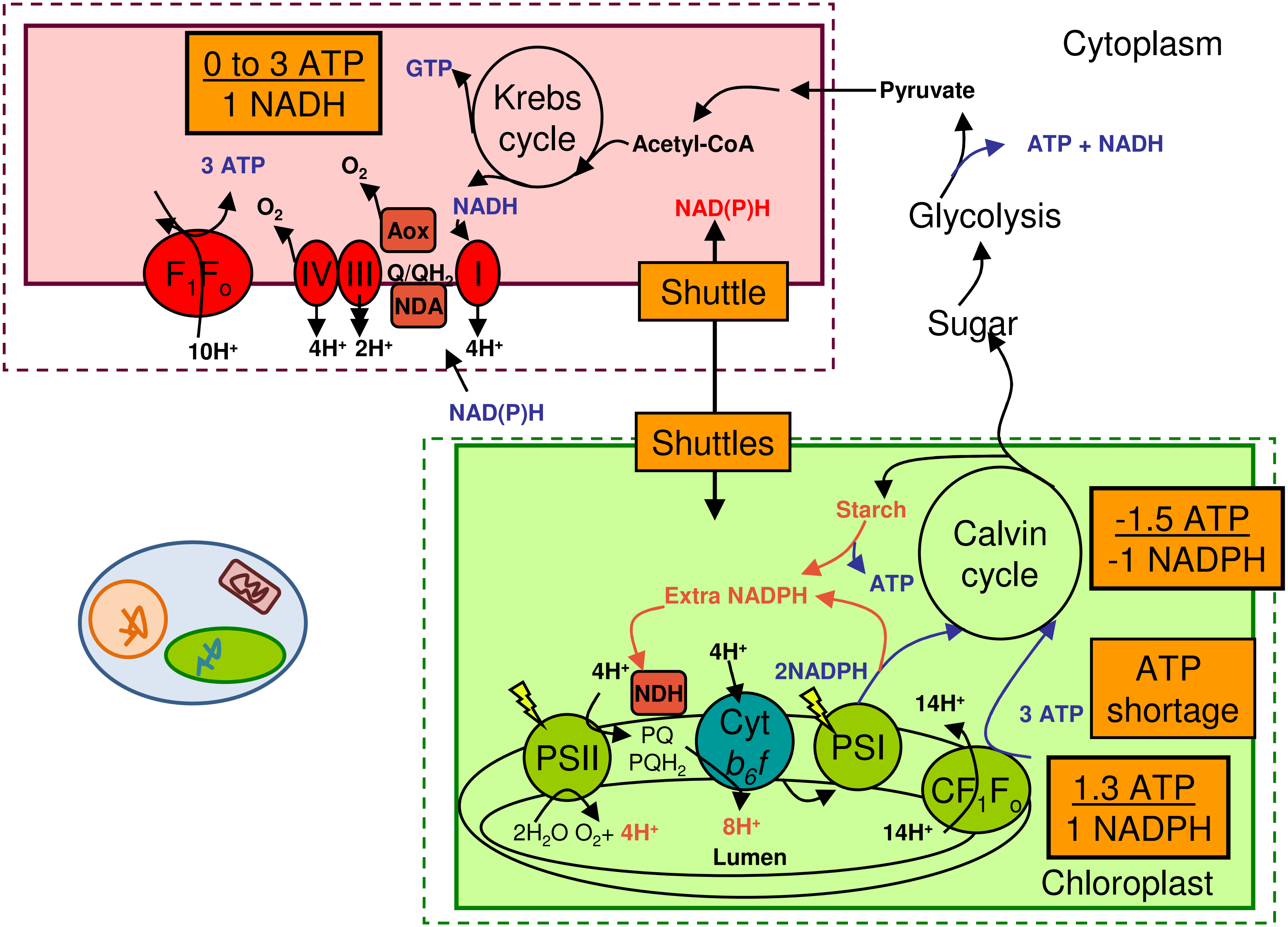


Dimeric enzyme bends the inner membrane and are maybe responsible for cristae structure

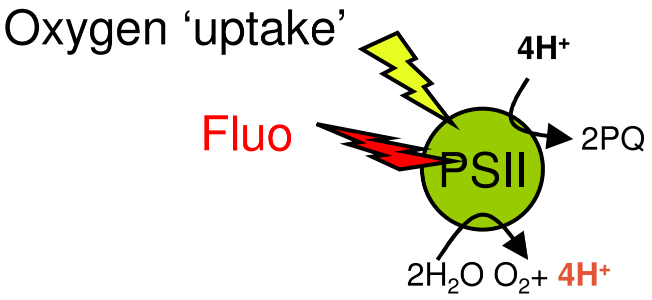


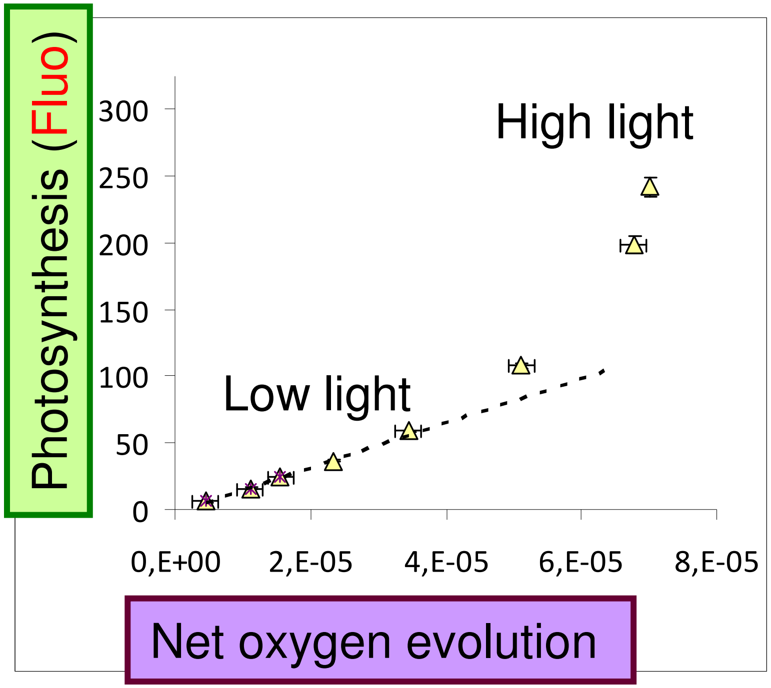
Cristae structure imposes physical constraints (electric field) for the activity of ATP synthase

Part III. Energy production : Respiration and Photosynthesis

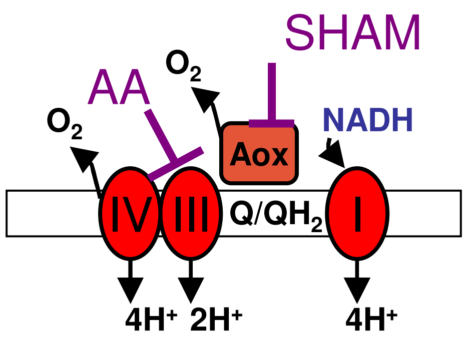


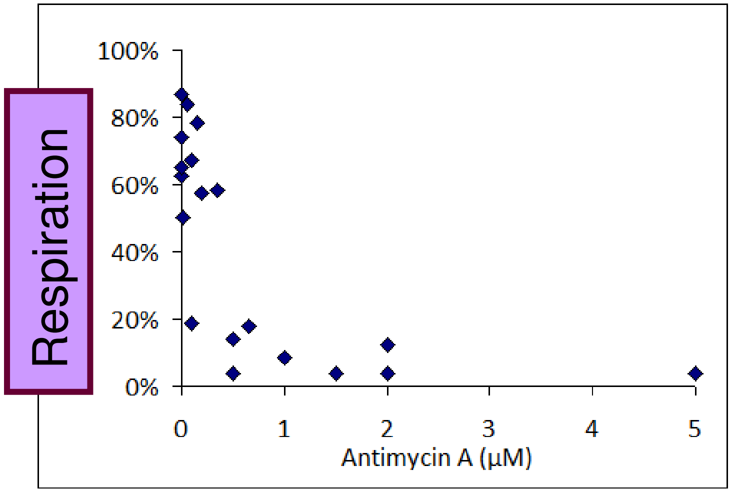
Involvement of respiration in the light

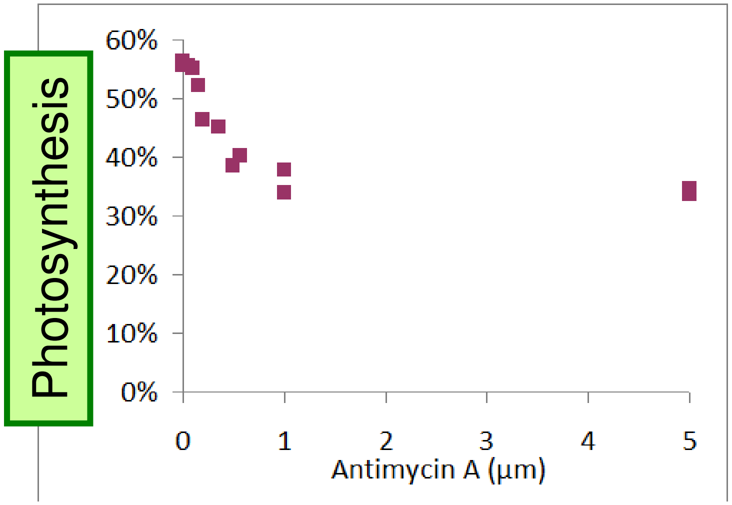




Inhibition studies

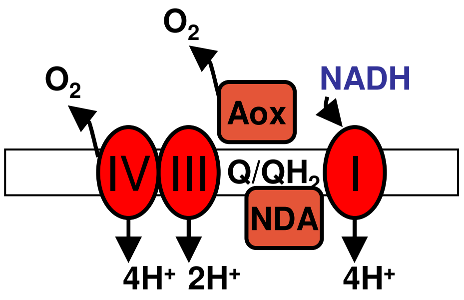


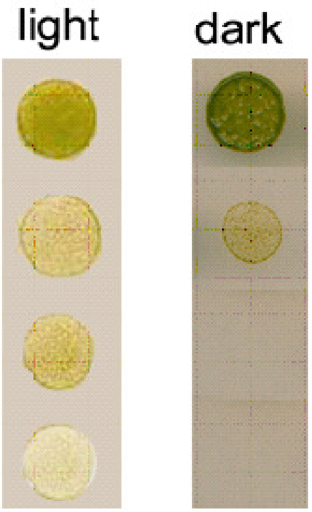




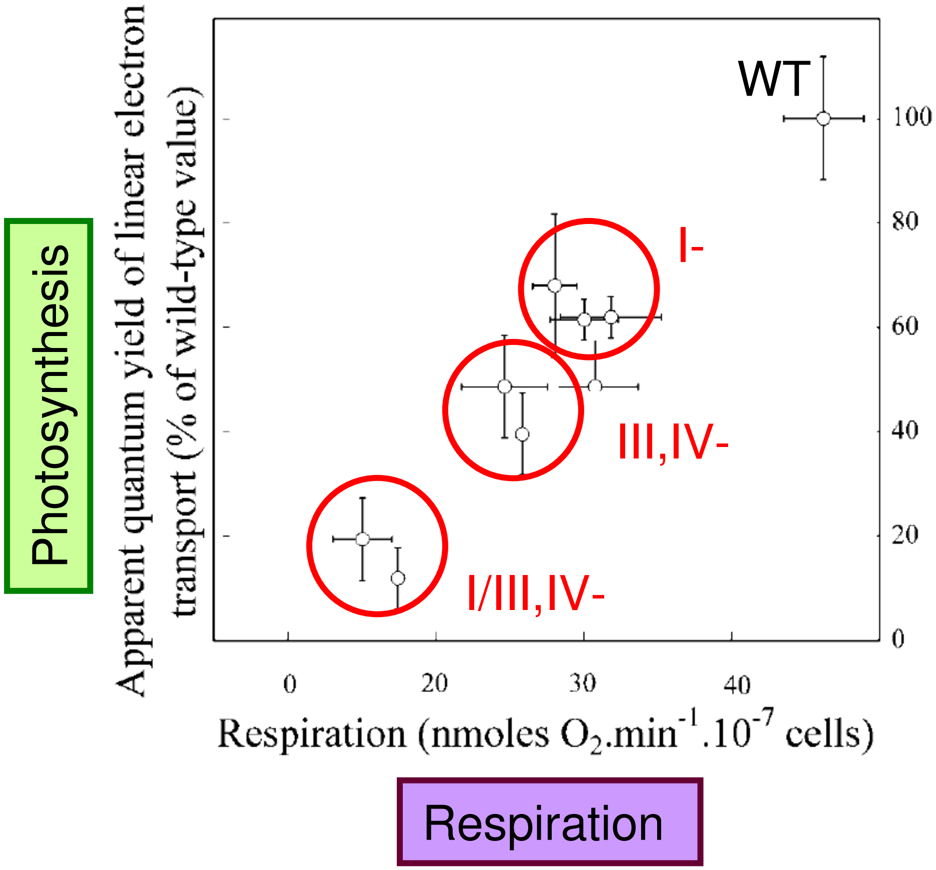
Involvement of respiration in the light

Use of mutants



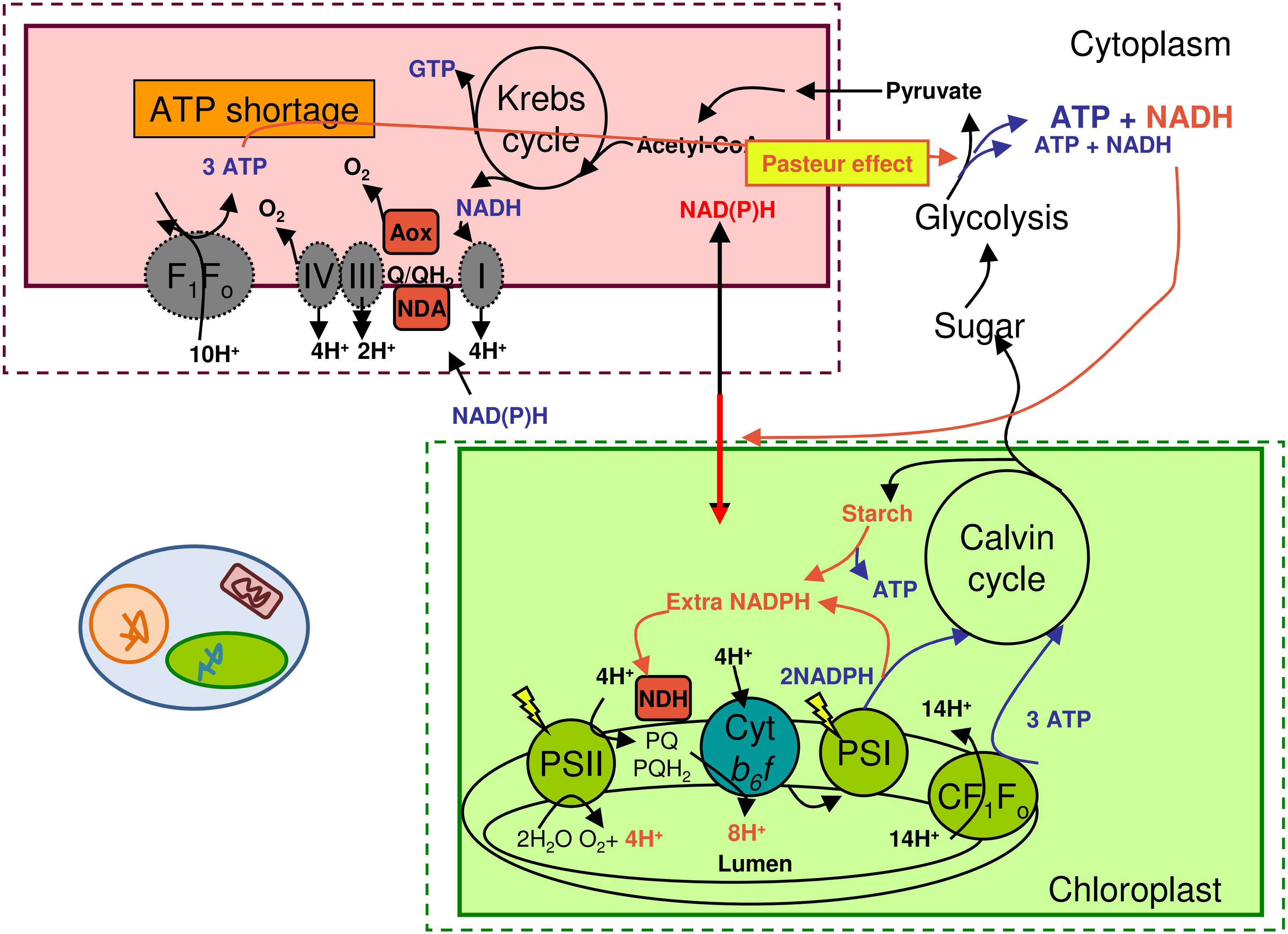


	ATP/NADH max
WT	3
I-	1.8
III-	1.2
I+III-	0

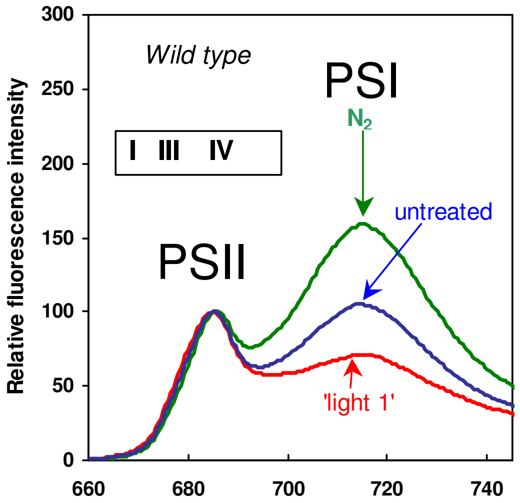


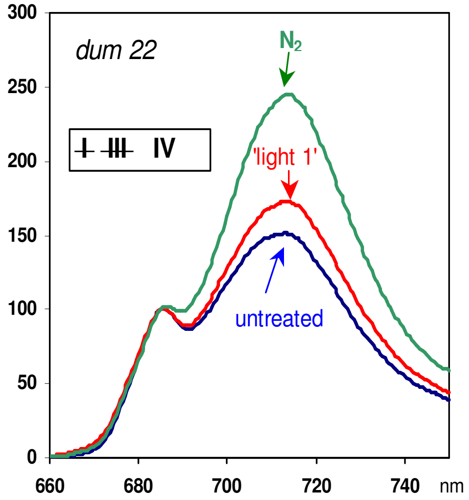
Cardol et al., 2003, Plant Physol.

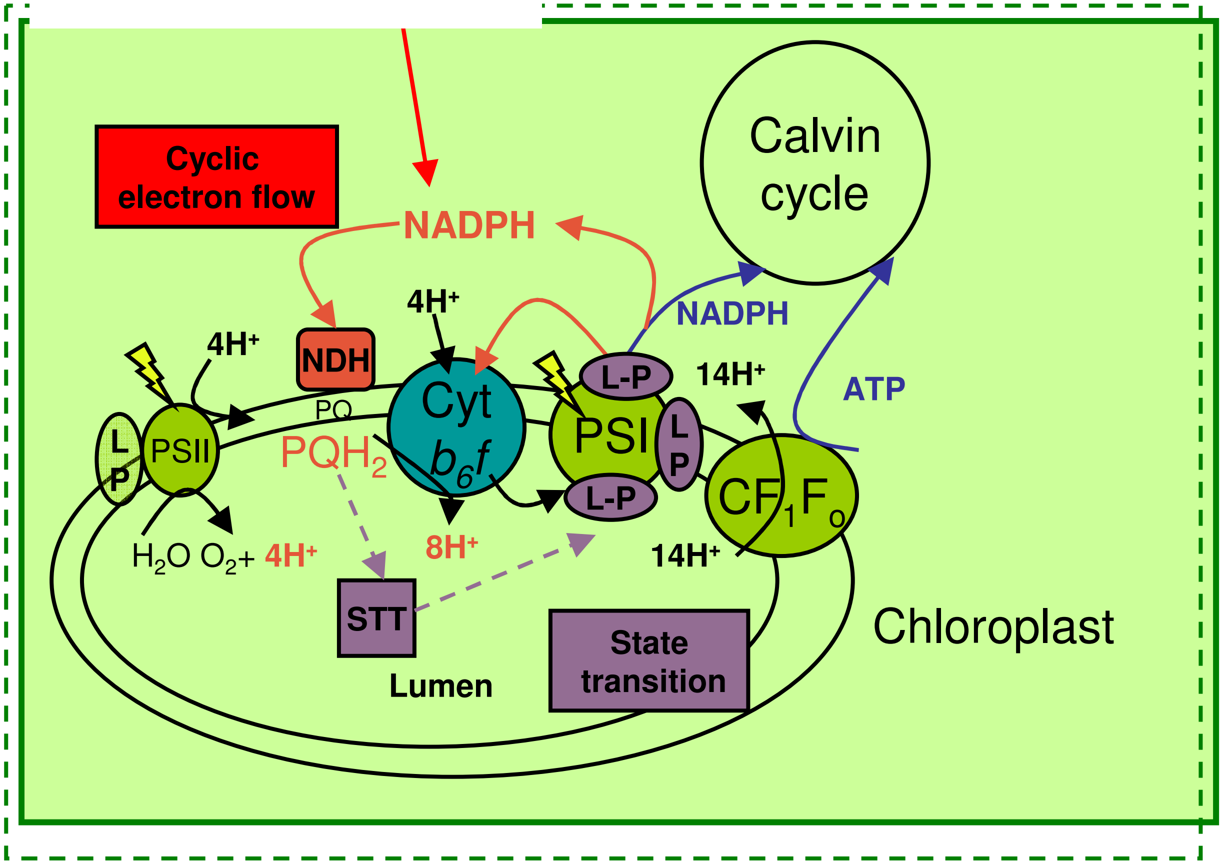
Part III. Energy production : Respiration and Photosynthesis



Mitochondrial deficiency compensated by chloroplastic state transition

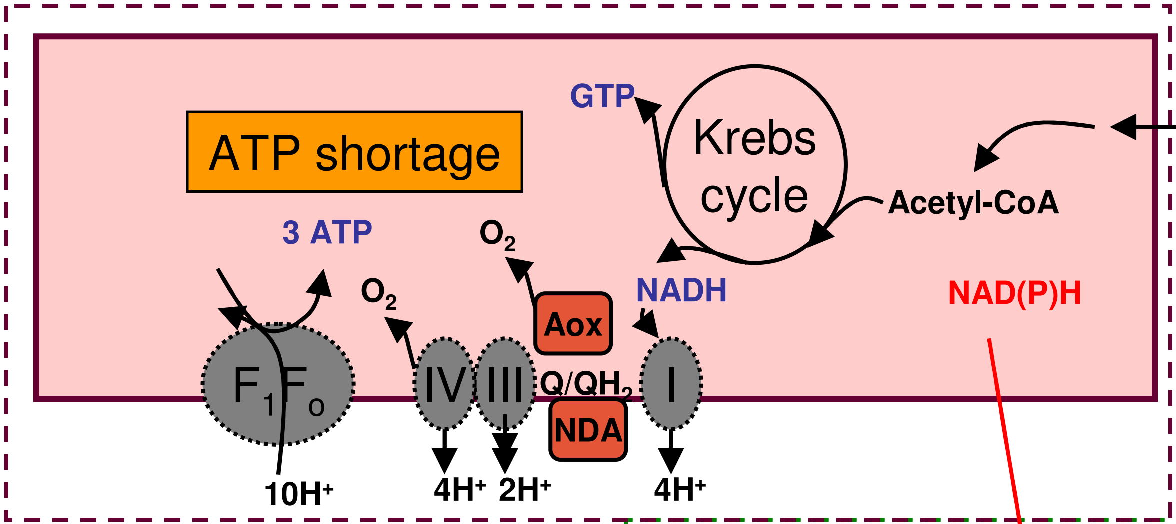


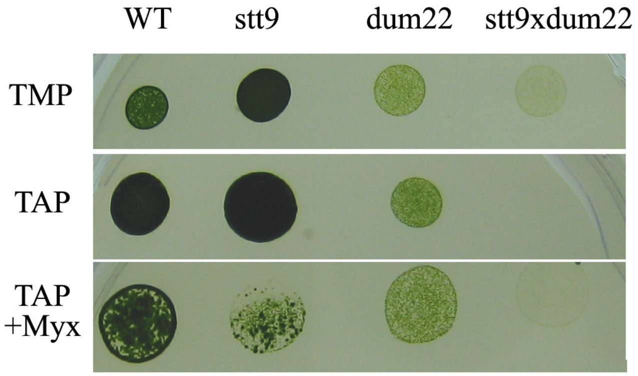


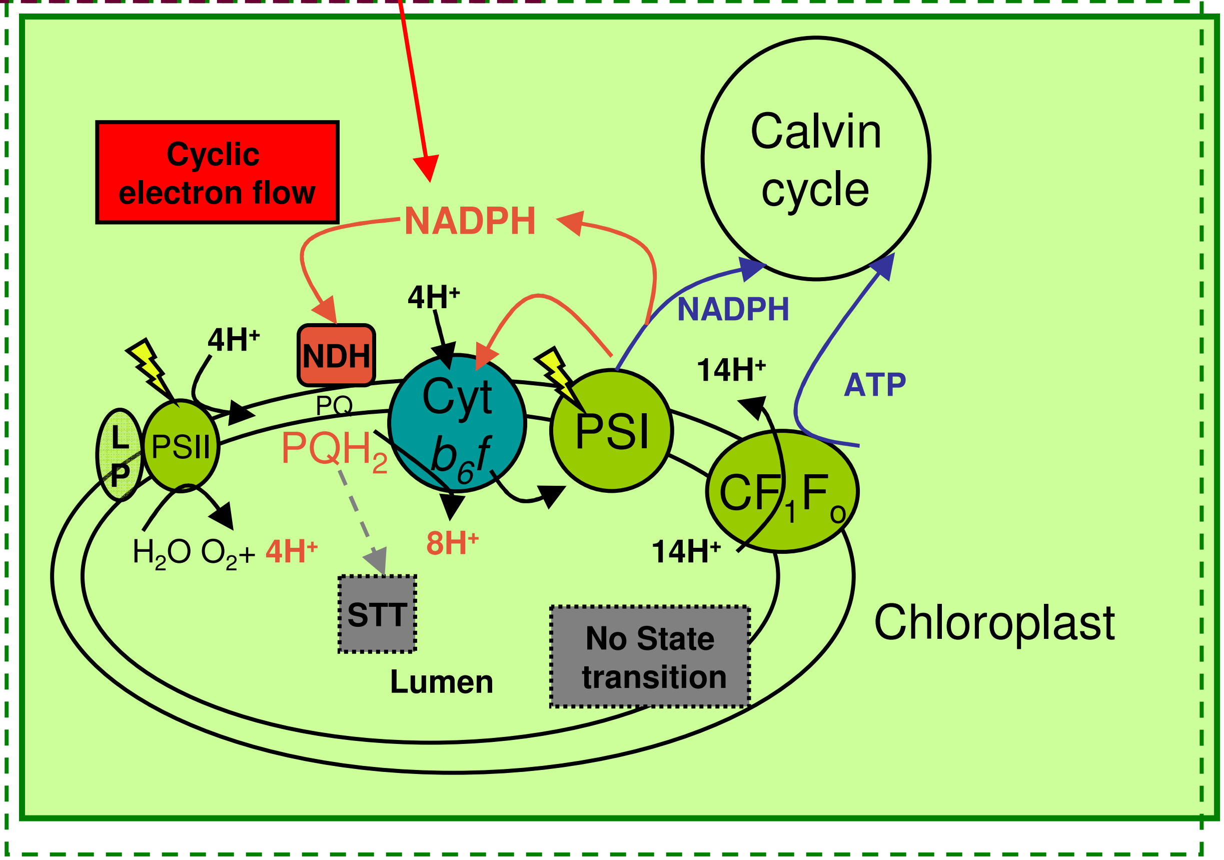


Wolman, 2001, Embo reports,
Cardol et al., 2003, Plant Physol.,
Iwai et al. 2010, Nature

Mitochondrial deficiency compensated by chloroplastic state transition







Depege et al., 2005, Sciences
Cardol et al., 2009, Plant Physol.
Lapaille et al., 2010, BBA bioenergetics

Conclusion part III

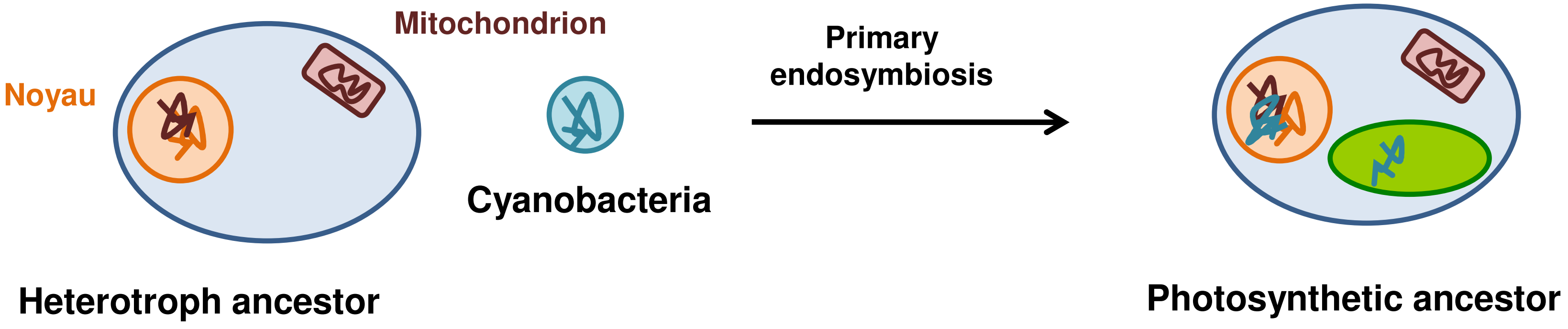
Respiration can be an effective electron sink for photosynthetic electrons

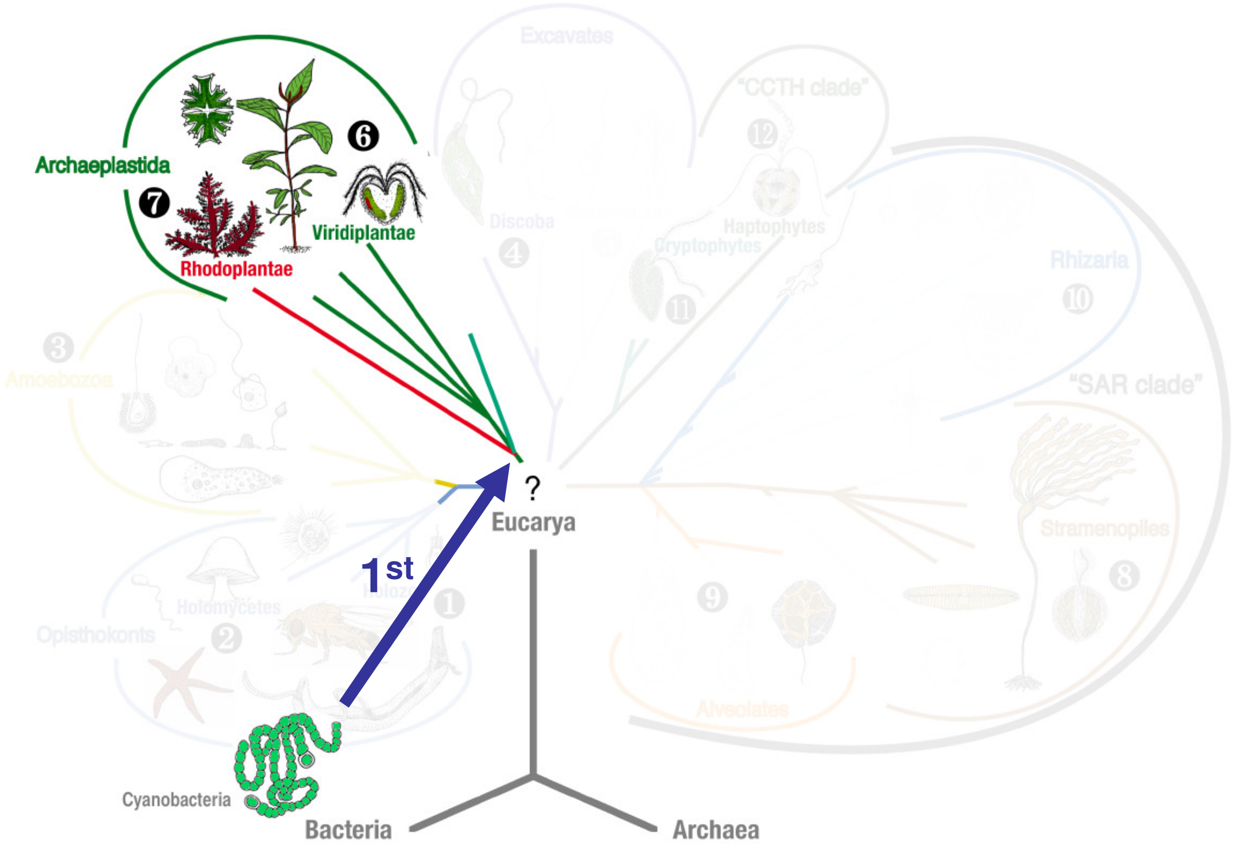
State transition/cyclic electron flow are critical when mitochondrial respiration is impaired

Photosynthetic cyclic electron flow and respiration sustain ATP for carbon fixation

Future work…

Chloroplast acquired through primary endosymbiosis





Chloroplast acquired through secondary endosymbiosis