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Processing of precursors of mitochondrial proteins

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More than 95% of mitochondrial proteins are coded for by nuclear genes (Schatz & Mason, 1974). These proteins are translated on cytoplasmic ribosomes (Sabatini *et al.*, 1982) and have to be selectively transported to their sites of function within the mitochondrion. Transfer into mitochondria is a multistep process comprising at least four different steps that can be resolved up to now (Zimmermann, 1984): (i) recognition and binding, (ii) translocation, (iii) processing, (iv) assembly.

Mitochondrial proteins are synthesized as water-soluble precursors. They are released into an extramitochondrial pool (Hallermayer *et al.*, 1977). Many of the precursors carry *N*-terminal peptide extensions (Teintze & Neupert, 1984) of essentially unknown function. These precursor proteins bind to the mitochondrial surface via specific receptor sites (Hennig *et al.*, 1983; Zwizinski *et al.*, 1983). The putative receptor for apocytochrome *c*, the precursor to cytochrome *c*, was purified to homogeneity (H. Köhler, B. Henning & W. Neupert, unpublished work). The next step after binding is the translocation of the precursor from the binding site into the mitochondria. This step requires energy for a large number of mitochondrial proteins (Schleyer *et al.*, 1982). During or shortly after the transfer into mitochondria, the precursor peptides are processed by proteolytic removal of peptide extensions and/or by other covalent modifications. The proteolytic processing of many precursors takes place in the mitochondrial matrix and is catalysed by a water-soluble enzyme (Böhni *et al.*, 1983; B. Schmidt, E. Wachter, W. Sebald & W. Neupert, unpublished work). Some purification of the yeast enzyme has been achieved (Böhni *et al.*, 1983). The last step in protein import into mitochondria is the assembly of newly transferred proteins. This step is less well understood due to the experimental difficulties of inhibiting assembly and distinguishing between assembled and non-assembled peptides.

In this report we will focus on the role of processing in the transport pathway of *Neurospora* ATPase subunit 9 (proteolipid, dicyclohexylcarbodi-imide-binding protein Su9). We characterize the processing activity referred to as processing peptidase that cleaves pre-Su9 and other precursor proteins. It is a water-soluble enzyme, located in the mitochondrial matrix, which can be inhibited by chelating agents. Based on these observations, it was possible to transport *in vitro* pre-Su9 into mitochondria in the absence of processing. Another interesting result is that pre-Su9 is processed in two steps. The two cleavage sites are very similar in their amino acid sequence. The data presented led us to propose a more detailed mechanism of how the precursor to Su9 is transported into mitochondria.

Characterization of processing peptidase

Processing peptidase activity can be assayed using membrane-free mitochondrial extracts as a source for the enzyme and precursor proteins synthesized *in vitro* as a substrate. The enzyme assay is carried out in the presence of Mn^{2+} and Triton X-100. The products are then analysed by immunoprecipitation and sodium dodecyl sulphate/polyacrylamide-gel electrophoresis. Processing peptidase cleaves the precursors to ATPase subunit 2 ($F_1\beta$), and Su9 to the mature-sized peptides. The precursor to cytochrome c_1 is processed to an intermediate-sized peptide described by Teintze *et al.* (1982). The unexpected feature of the peptidase was that pre-Su9 was processed in two steps via an intermediate-sized band, which was not observed before (see Schmidt *et al.*, 1983 for comparison). Because of this finding we were interested to see whether both the processing steps occurred in the same subcompartment of mitochondria. It was shown in yeast that the two-step processing of the precursors to cytochrome c_1 and b_2 was catalysed by two enzymes: one is located in the matrix (Böhni *et al.*, 1980), the other one catalysing the second step is supposed to reside on the outer side of the inner membrane. This second protease is not inhibited by chelating agents (Daum *et al.*, 1982) in intact mitichondria. We worked out a procedure to subfractionate mitochondria under conditions which preserved processing peptidase activity. In these experiments the processing activity producing intermediate as well as mature Su9, fractionated with the matrix markers fumarase and citrate synthase.

To make sure that we were looking at the right reaction in the processing assay, we carried out radio-sequencing experiments with the intermediate- and mature-sized Su9. The sequence of the precursor was revealed by molecular cloning (Viebrock *et al.*, 1982). Sequencing the mature-sized peptide after processing *in vitro* it was found that it displayed the same *N*-terminus as the mature protein. The first cleavage site is in the middle of the additional sequence between Thr-32 and Ile-31 (Table 1).

The sequence of amino acids around the cleavage sites seems to follow the common rule: -hydrophobic-polar-Lys-Arg-small-bulky hydrophobic-polar-polar. Together with the fact that both cleaving reactions can be inhibited by chelating agents, we assume that it is the same catalysing both reactions.

Table 1. *Cleavage sites of ATPase subunit 9 precursor*

The cleavage sites are indicated by the arrow. A, second cleavage site; B, first cleavage site.

```
                                        -1 ↓ +1
A    -Gln-Ala-Phe-Gln-Lys-Arg-Ala-Tyr-Ser-Ser-Glu-
                                       -32↓-31
B    -Ala-Gln-Val-Ser-Lys-Arg-Thr-Ile-Gln-Thr-Gly-
```

Transfer in the absence of processing

Based on the finding that processing peptidase is inhibited by chelating agents we were able to prevent processing in intact mitochondria *in vitro* (Zwizinski & Neupert 1983). The system used *in vitro* included precursor proteins synthesized in reticulocyte lysates and isolated mitochondria. We demonstrated that precursor proteins are transported into mitochondria in the presence of chelating agents. The transported precursors were resistant to proteolytic digestion. They were associated with the membrane fraction of mitochrondia. In the case of Su9 the intermediate-sized band was observed. Upon re-addition of excess metal ion, the precursors were processed to mature-sized polypeptides in the absence of a membrane potential. The conclusion drawn from these experiments is that processing occurs after translocation of precursor proteins into mitochondria. Energy is required only for translocation, not for processing.

Concluding remarks

The data presented in this report give some detailed insight into the mechanism of how proteins are imported into mitochondria. Further studies are in progress to get access to the components involved in protein transfer. Although it will be a considerable effort to purify all the proteins constituting the transport machinery, this seems to us to be the way to define the components involved and to understand how they work on a molecular basis.

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