On the linkage of exoplasmatic freeze-fracture particles to phycobilisomes*

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Abstract. The thylakoids of the thermophilic cyanobacterium *Mastigocladus laminosus* were examined by freeze-fracture analysis. The exoplasmatic (EF)-freeze-fracture particles are organized in rows, separated by 45 nm or more with a 12-nm center-to-center spacing of neighboring particles. Phycobilisomes, associated to the outer thylakoid surfaces show a similar spacing pattern. Fractures exposing simultaneously phycobilisomes and EF-freeze-fracture particles on the same thylakoid show a direct alignment of both systems. Consequently the phycobilisomes are concluded to be associated peripherally on top of the EF-freeze-fracture particles in a 1:1 assembly pattern. The periodicity of the EF-freeze-fracture particles determines the arrangement of the phycobilisomes in the rows. The planar phycobilisome model of Mörschel et al. (1977) easily allows a successive arrangement of the phycobilisomes in a row, whereas with the staggered model developed by Bryant et al. (1979), only a cогged arrangement of neighboring phycobilisomes is possible.

Key words: Cyanobacteria – *Mastigocladus* (cyanobacterium) – Photosystem II (freeze fracture) – Phycobilisome – Thylakoid (freeze fracture).

Introduction

The light-harvesting systems of higher plants and green algae with a chlorophyll a/b pigmentation are integral components of the thylakoid membranes. In cyanobacteria and red algae, the major light-harvesting pigments are the biliproteins. They are organized into high-molecular-weight complexes called phycobilisomes, which are regularly ordered on the outer surface of the thylakoids. The phycobilisomes are composed of a morphologically distinct core from which rods of stacked biliprotein aggregates radiate in a semicircular pattern. The assembly of phycobilisomes is mediated by special polypeptides. Some of these polypeptides may also link the phycobilisome core to integral protein complexes within the membranes. However, it is uncertain, to which membrane particles the phycobilisomes are coupled. The aim of this study was to determine those integral complexes as freeze-fracture particles to which phycobilisomes are linked peripherally. Models for phycobilisome arrangement on the thylakoids are constructed which are influenced by the spatial pattern of the intramembrane particles and the supramolecular structure of the phycobilisomes.

Material and methods

Strains and culture conditions. The thermophilic cyanobacterium *Mastigocladus laminosus* (Cohn) was obtained from Professor Dr. H. Zuber (ETH Zürich, Switzerland). It was cultured in medium D of Castenholz (1970) as described by Nies and Wehrmeyer (1980).

Preparation of phycobilisomes and biliproteins. Phycobilisomes were isolated by methods developed by Nies and Wehrmeyer (1980). Phycobilisomes dissociates were obtained by diluting the phycobilisome suspensions 10 times.

Isolation of phycoerythrocyanin and phycoerythrocyanin. C-phycoerythrocyanin was prepared as described by Binder et al. (1972). Phycoerythrocyanin was purified after Fueglistaller et al. (1981), omitting chromatography on Bio Gel P 60, or by ion-exchange chromatography on DEAE-Sephael from dissociated phycobilisomes as developed by Morisset (personal communication).

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* This study is dedicated to Professor Dr. H.-A. von Stosch on the occasion of his 75th birthday

Abbreviation: EF-face = exoplasmatic fracture face
Fig. 1. Longitudinal fracture of *Mastigocladius laminosus*. Bar = 1 \( \mu \)m; \( \times 26,000 \)

Fig. 2. a Cross fracture through thylakoid membranes exposing the closely associated phycobilisomes from the side. Bar = 100 nm; \( \times 153,000 \). b Exoplasmatic fracture face of a thylakoid illustrating well-aligned rows of homogeneously sized particles. Bar = 100 nm; \( \times 131,000 \)