FOURTH EDITION

MOLECULAR CELL BIOLOGY

Harvey Lodish

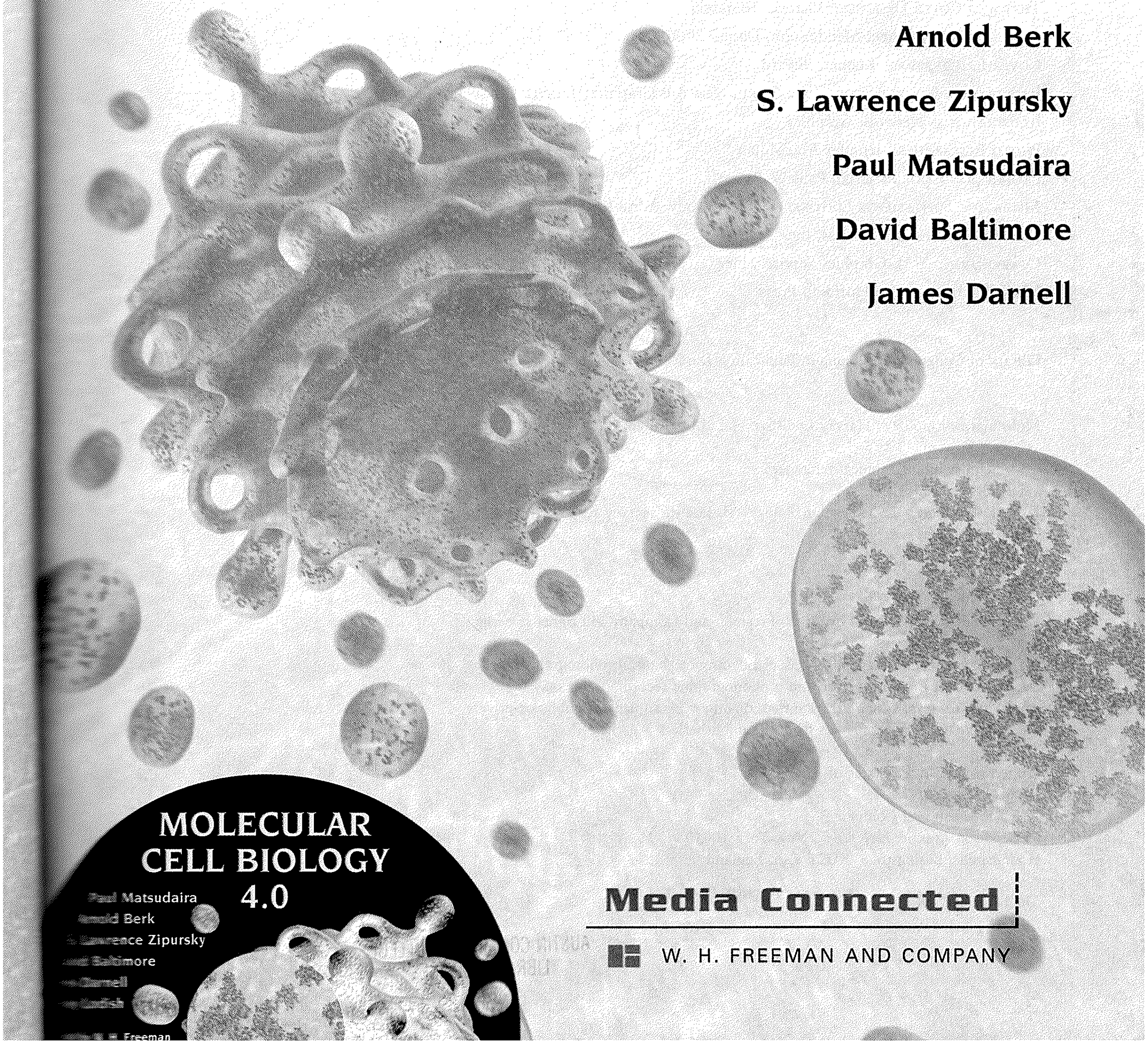
Arnold Berk

S. Lawrence Zipursky

Paul Matsudaira

David Baltimore

James Darnell



Media Connected

W. H. FREEMAN AND COMPANY

Executive Editor: Sara Tenney
Development Editors: Katherine Ahr, Ruth Steyn, Kay Ueno
Editorial Assistant: Jessica Olshen
Executive Marketing Manager: John A. Britch
Project Editor: Katherine Ahr
Text and Cover Designer: Victoria Tomaselli
Page Makeup: Michael Mendelsohn, Design 2000, Inc.
Cover Illustration: Kenneth Eward
Illustration Coordinator: John Smith, Network Graphics; Tamara Goldman, Bill Page
Illustrations: Network Graphics
Photo Researcher: Jennifer MacMillan
Production Coordinator: Paul W. Rohloff
Media and Supplements Editors: Tanya Awabdy, Adrie Kornasiewicz, Debra Siegel
Media Developers: Sumanas, Inc.
Composition: York Graphics Services, Inc.
Manufacturing: Von Hoffman Press

Library of Congress Cataloging-in-Publication Data

Molecular cell biology / Harvey Lodish p [et al.] – 4th ed.
p. cm.
Includes bibliographical references.
ISBN 0-7167-3136-3
1. Cytology. 2. Molecular biology. I. Lodish, Harvey F.
QH581.2.M655 1999
571.6–dc21 99-30831
CIP

Printed in the United States of America

W. H. Freeman and Company
41 Madison Avenue, New York, New York 10010
Houndsmills, Basingstoke RG21 6XS, England

Third Printing, 2001

Thus the overall reaction of stages 1 and 2 can be summarized as

$$2\ H_2O + 2\ NADP^+ \xrightarrow{\text{light}} 2\ H^+ + 2\ NADPH + O_2$$

Many photosynthetic bacteria do not use water as the donor of electrons. Rather, they use molecules such as hydrogen gas (H_2) or hydrogen sulfide (H_2S) as the ultimate source of electrons to reduce the ultimate electron acceptor (NAD^+ rather than $NADP^+$).

Generation of ATP Protons move down their concentration gradient from the thylakoid lumen to the stroma through the F_0F_1 complex which couples proton movement to the synthesis of ATP from ADP and P_i. This use of the proton-motive force to synthesize ATP is identical with the analogous process occurring during oxidative phosphorylation in the mitochondrion (see Figures 16-28 and 16-30).

Carbon Fixation The ATP^{4-} and NADPH generated by the second and third stages of photosynthesis provide the energy and the electrons to drive the synthesis of polymers of six-carbon sugars from CO_2 and H_2O. The overall balanced equation is written as

$$6\ CO_2 + 18\ ATP^{4-} + 12\ NADPH + 12\ H_2O \longrightarrow C_6H_{12}O_6 + 18\ ADP^{3-} + 18\ P_i^{2-} + 12\ NADP^+ + 6\ H^+$$

The reactions that generate the ATP and NADPH used in carbon fixation are *directly* dependent on light energy; thus stages 1–3 are called the *light reactions* of photosynthesis. The reactions in stage 4 are *indirectly* dependent on light energy; they are sometimes called the *dark reactions* of photosynthesis because they can occur in the dark, utilizing the supplies of ATP and NADPH generated by light energy. However, the reactions in stage 4 are not confined to the dark; in fact, they primarily occur during illumination.

Each Photon of Light Has a Defined Amount of Energy

Quantum mechanics established that light, a form of electromagnetic radiation, has properties of both waves and particles. When light interacts with matter, it behaves as discrete packets of energy *(quanta)* called *photons*. The energy of a photon, ϵ, is proportional to the frequency of the light wave: $\epsilon = h\gamma$, where h is Planck's constant (1.58×10^{-34} cal·s, or 6.63×10^{-34} J·s), and γ is the frequency of the light wave. It is customary in biology to refer to the wavelength of the light wave, λ, rather than to its frequency, γ. The two are related by the simple equation $\gamma = c \div \lambda$, where c is the velocity of light (3×10^{10} cm/s in a vacuum). Note that photons of *shorter* wavelength have *higher* energies.

Also, the energy in 1 mol of photons can be denoted by $E = N\epsilon$, where N is Avogadro's number (6.02×10^{23} molecules or photons/mol). Thus

$$E = Nh\gamma = \frac{Nhc}{\lambda}$$

The energy of light is considerable, as we can calculate for light with a wavelength of 550 nm (550×10^{-7} cm), typical of sunlight:

$$E = \frac{(6.02 \times 10^{23}\ \text{photons/mol})(1.58 \times 10^{-34}\ \text{cal·s})(3 \times 10^{10}\ \text{cm/s})}{(550 \times 10^{-7}\ \text{cm})}$$

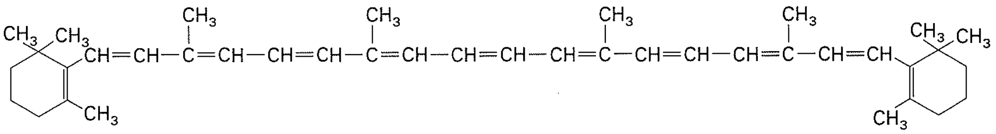
$$= 51{,}881\ \text{cal/mol}$$

or about 52 kcal/mol, enough energy to synthesize several moles of ATP from ADP and P_i if all the energy were used for this purpose.

Chlorophyll *a* Is Present in Both Components of a Photosystem

The absorption of light energy and its conversion into chemical energy occurs in multiprotein complexes, called *photosystems,* located in the thylakoid membrane. A photosystem has two closely linked components, an *antenna* containing light-absorbing pigments and a *reaction center* comprising a complex of proteins and two *chlorophyll a* molecules. Each antenna (named by analogy with radio antennas) contains one or more *light-harvesting complexes* (LHCs). The energy of the light captured by LHCs is funneled to the two chlorophylls in the reaction center, where the primary events of photosynthesis occur.

Found in all photosynthetic organisms, both eukaryotic and prokaryotic, chlorophyll *a* is the principal pigment involved in photosynthesis, being present in both antennas and reaction centers. In addition to chlorophyll *a,* antennas contain other light-absorbing pigments: *chlorophyll b* in vascular plants, and *carotenoids* in both plants and photosynthetic bacteria (Figure 16-36). The presence of various antenna



β-Carotene

▲ **FIGURE 16-36 The structure of *β*-carotene, a pigment that assists in light absorption by chloroplasts.** *β*-Carotene, which is related to the visual pigment retinal (see Figure 21-47), is one of a family of carotenoids containing long hydrocarbon chains with alternating single and double bonds.