

immunoblot relies on the availability of a good antibody against the target protein. Alternatives are available; for example, one can use in vitro translation systems or RNAs that contain the target sequence and encode an epitope-tagged version of the protein (see Zhang et al., 2006). Conversely, if RNA splice-blocking morpholinos are used, RT-PCR analysis is straightforward. Finally, the method for generating transgenic *X. laevis* embryos described by Bryan Allen and Daniel Weeks (Chapter 9) is clearly exciting, but it is worth noting that since it was first described in 2005 (Allen and Weeks, 2005) no other lab has (apparently) published using the technique. In this light, a general review of other transgenic methods (Ogino et al., 2006; Waldner et al., 2006; L'Hostis-Guidet et al., 2009), as well as a discussion of the application of these methods to *X. tropicalis*, a diploid relative with a shorter generation time and a sequenced genome, would seem to be both appropriate and useful.

All of which is to say that, while this book provides a useful guide to experimental design, the savvy investigator should take the time to explore the various ancillary technical issues associated with their specific project.

References

- Allen, B. G. and Weeks, D. L. (2005). Transgenic *Xenopus laevis* embryos can be generated using phiC31 integrase. *Nat. Methods* **2**, 975-979.
- Briggs, R. and King, T. J. (1952). Transplantation of living nuclei from blastula cells into enucleated frogs' eggs. *Proc. Natl. Acad. Sci. USA* **38**, 455-463.
- Chambers, R. (1918). The microvivisection method. *Biol. Bull.* **34**, 121-136.
- Chambers, R. (1922). New apparatus and methods for the dissection and injection of living cells. *Anat. Rec.* **24**, 1-19.
- Goldstein, L. and Prescott, D. M. (1967). Proteins in nucleocytoplasmic interactions. I. The fundamental characteristics of the rapidly migrating proteins and the slow turnover proteins of the Amoeba proteus nucleus. *J. Cell Biol.* **33**, 637-644.
- Gurdon, J. B. (1960). Factors responsible for the abnormal development of embryos obtained by nuclear transplantation in *Xenopus laevis*. *J. Embryol. Exp. Morphol.* **8**, 327-340.
- Gurdon, J. B. and Byrne, J. A. (2003). The first half-century of nuclear transplantation. *Proc. Natl. Acad. Sci. USA* **100**, 8048-8052.
- Hollenberg, S. M., Cheng, P. F. and Weintraub, H. (1993). Use of a conditional MyoD transcription factor in studies of MyoD trans-activation and muscle determination. *Proc. Natl. Acad. Sci. USA* **90**, 8028-8032.
- Klymkowsky, M. W. (1981). Intermediate filaments in 3T3 cells collapse after intracellular injection of a monoclonal anti-intermediate filament antibody. *Nature* **291**, 249-251.
- Klymkowsky, M. W. (1982). Vimentin and keratin intermediate filament systems in cultured Ptk2 epithelial cells are interrelated. *EMBO J.* **1**, 161-165.
- Kolm, P. J. and Sive, H. L. (1995). Efficient hormone-inducible protein function in *Xenopus laevis*. *Dev. Biol.* **171**, 267-272.

- L'Hostis-Guidet, A., Recher, G., Guillet, B., Al-Mohammad, A., Coumilleau, P., Tiaho, F., Boujard, D. and Madigou, T. (2009). Generation of stable *Xenopus laevis* transgenic lines expressing a transgene controlled by weak promoters. *Transgenic Res.* **18**, 815-827.
- Lin, J. J. and Feramisco, J. R. (1981). Disruption of the in vivo distribution of the intermediate filaments in fibroblasts through the microinjection of a specific monoclonal antibody. *Cell* **24**, 185-193.
- Mabuchi, I. and Okuno, M. (1977). The effect of myosin antibody on the division of starfish blastomeres. *J. Cell Biol.* **74**, 251-263.
- Nicklas, R. B. (1967). Chromosome micromanipulation. II. Induced reorientation and the experimental control of segregation in meiosis. *Chromosoma* **21**, 17-50.
- Nicklas, R. B. and Staehly, C. A. (1967). Chromosome micromanipulation. I. The mechanics of chromosome attachment to the spindle. *Chromosoma* **21**, 1-16.

- Ogino, H., McConnell, W. B. and Grainger, R. M. (2006). Highly efficient transgenesis in *Xenopus tropicalis* using I-SceI meganuclease. *Mech. Dev.* **123**, 103-113.
- Paine, P. L. and Feldherr, C. M. (1972). Nucleocytoplasmic exchange of macromolecules. *Exp. Cell Res.* **74**, 81-98.
- Qiu, S., Adema, C. M. and Lane, T. (2005). A computational study of off-target effects of RNA interference. *Nucleic Acid Res.* **33**, 1834-1847.
- Taylor, D. L. and Wang, Y. L. (1978). Molecular cytochemistry: incorporation of fluorescently labeled actin into living cells. *Proc. Natl. Acad. Sci. USA* **75**, 857-861.
- Waldner, C., Sakamaki, K., Ueno, N., Turan, G. and Ryffel, G. U. (2006). Transgenic *Xenopus laevis* strain expressing cre recombinase in muscle cells. *Dev. Dyn.* **235**, 2220-2228.
- Zhang, C., Carl, T. F., Trudeau, E. D., Simmet, T. and Klymkowsky, M. W. (2006). An NF-kappaB and slug regulatory loop active in early vertebrate mesoderm. *PLoS ONE* **1**, e106.

An essential glycobiology resource for developmental biologists

Xinhua Lin

State key Laboratory of Biomembrane and Membrane Biotechnology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China.
Xinhua.lin@ioz.ac.cn

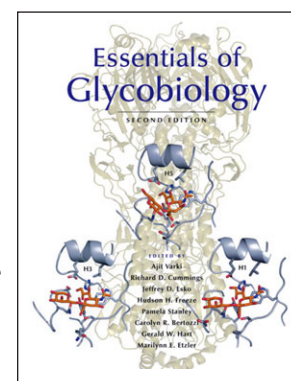
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Essentials of Glycobiology, Second Edition

Edited by Ajit Varki, Richard D. Cummings, Jeffrey D. Esko, Hudson H. Freeze, Pamela Stanley, Carolyn R. Bertozzi, Gerald W. Hart and Marilynn E. Etzler

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During the development of multicellular organisms, the formation of complex organs and tissues requires cell-cell and cell-matrix interactions. Cells in a developing embryo carry large quantities of carbohydrates known collectively as glycans that can serve as signaling effectors, recognition markers and structural components. Understanding the functions and regulation of glycans in growth and development is therefore a key issue in developmental biology. The second edition of the book *Essentials of Glycobiology*, written and edited by glycobiology experts, provides a comprehensive and updated overview of glycan structures, biosynthesis and functions. This book is an invaluable resource for both students and established investigators who are interested in glycan-related processes in development, as well as in many other areas of basic research.



The book consists of 51 chapters, which are divided into six sections: (1) General Principles, (2) Structure and Biosynthesis, (3) Organismal Diversity, (4) Glycan-Binding Proteins, (5) Glycans in Physiology and Disease, and (6) Methods and Applications. Together, the editors attempt to provide extensive coverage of glycobiology-related subjects using up-to-date information derived from a variety of research fields.

So, what's new in the second edition? The first edition of this book provides basic information needed to understand the fundamentals of glycobiology along with a summary of the state of the field of glycobiology in the 1990s. While the overall organization of the book has not changed, the second edition includes several new chapters, in which significant advances in the glycobiology field, which have occurred since the publication of the first edition, are presented. These chapters are integrated into three sections: a genomic view of glycobiology; the section on organismal diversity, which contains several new chapters; and the last section, which contains a new chapter on glycomics, which is analogous to genomics and proteomics, and which aims to

systematically study all the glycan structures of a given cell type or organism. These additions are mainly due to the availability of the complete genomic sequence of more model systems and to the rapid progress in our understanding of the functions of glycans in model systems, such as *Drosophila*, *C. elegans* and mouse. When the first edition of this book was published in 1999, only a few completely sequenced genomes were available, but now many genomes have been published, allowing the comprehensive comparison of various glycosyltransferase, glycosidase and glycan-binding proteins among various organisms.

The book begins with a historical account of the glycobiology research field, which is followed by an introduction to the fundamentals of glycan chemistry and the general principles of glycan biosynthesis, cellular organization and the biological functions of glycans. Specific terms and unified symbol nomenclature are introduced. In the first section, Chapter 5 focuses on the general characteristics of the enzymes involved in glycan biosynthesis and modifications. Chapter 6 then attempts to introduce some of general principles of glycan functions in various biological settings. Finally, Chapter 7 introduces the concept of the 'glycome' and provides an updated genomic view of glycobiology. Most of the contents in this section are well synthesized and easy to follow. Understanding the contents of this first section will greatly help readers to follow the remaining sections of the book.

Sections two to four constitute the main body of this book. A total of 11 chapters in section two describe the detailed and up-to-date knowledge of the structure and biosynthesis of various glycans and glycoproteins. Topics include the biosynthesis and functions of N-glycosylated proteins and of the O-glycans, which are linked with mucin and mucin-like glycoproteins. The biosynthesis of glycolipids and other novel classes of endoplasmic reticulum/Golgi-derived glycans are further introduced in several other chapters in this section. It is worth mentioning that the specific function of the O- α -fucose modification was initially discovered in developmental studies of *Drosophila*. Fringe, a molecule well known to developmental biologists, encodes an essential enzyme involved in the O-fucose glycosylation pathway that is required for Notch signaling in both *Drosophila* and mammals. The study of Fringe as a glycosyltransferase that modifies O-fucose residues on Notch provides one of the best examples of the importance of glycans in development. The detailed structure, biosynthesis and biological functions of proteoglycans are also covered in Chapter 16 of this section.

The book then shifts to section three on 'Organismal Diversity'. A total of seven chapters are provided in this section to describe the diversity and complexity of glycans and glycoproteins in various organisms, ranging from Eubacteria and yeast, to multicellular organisms such as *C. elegans* and *Drosophila*, as well as mammalian cells, fungi and plant cells. Much of the information presented in this section comes from recent progress in the genomic studies of various model systems. Specific functions of glycans and glycoproteins are also integrated and discussed in these chapters. Of particular relevance to developmental studies are the roles of O-linked glycosylation in Notch signaling and the functions of proteoglycans in morphogen gradient formation and axon guidance, which are discussed in Chapter 24 of this section.

The breadth and depth of the coverage of this book is the main strength of this new edition

Sections four and five focus mainly on the biological functions of glycans. A total of 10 chapters in section four introduce the structure and functions of glycan-binding proteins (GBPs). GBPs can interact with discrete glycans, thereby mediating specific biological functions of glycans. Two major classes of GBPs are lectins and glycosaminoglycan-binding proteins. From Chapters 28 to 34, various types of lectins and their biochemical properties and biological functions are introduced in great detail. Chapter 35 describes the proteins that bind sulfated glycosaminoglycans. Morphogens, such as Wnt, Bmp and Hh, are glycosaminoglycan-binding proteins that are essential for patterning during development. In Section 5, eight chapters introduce examples of the specific functions of glycans in physiology and human disease. Glycans have very diverse physiological roles, ranging from protein quality control to controlling bacterial and viral infections, while mutations in glycans-encoding genes can cause various human developmental defects and diseases, such as multiple hereditary exostoses.

The last section focuses on unique methods used in glycan analysis, as well as on their applications in biotechnology and the pharmaceutical industry. This section introduces some of the essential methods used in glycobiology research, such as the use of specific glycan antibodies and glycan

inhibitors. These reagents can be very useful for functional studies of glycan in development.

What are the strengths of this book? There are many to list. In my view, the breadth and depth of the coverage of this book is the main strength of this new edition. A number of new editors have been recruited in the second edition to expand its coverage across a broader range of the glycobiology field. Glycobiology covers a large spectrum of subjects due to the diversity of the structures and the functions of glycans; therefore, it is not an easy task to cover so many topics in a single book. I found there to be little or no redundancy between related chapters, while each chapter refers well to other related chapters.

Overall, the contents of book are well organized and clearly articulated. Each chapter contains a brief introduction to the subjects being discussed. The color figures will also be particularly useful to readers who are unfamiliar with the glycobiology field, as simplified symbols of sugar units help readers to understand various sulfation patterns, as well as the differences between heparan sulfate and chondroitin sulfate. Although 'glycobiology' is not traditionally a course that is taught to graduate students (unlike Cell Biology and Molecular Biology), the *Essentials of Glycobiology* could serve as an excellent textbook for selected course studies that focus on glycobiology. In fact, the book was originally created from the teaching materials created for a short course on glycobiology for graduate students at the University of San Diego. As indicated by the Executive Editor Ajit Varki, graduate students have provided critiques of each chapter. The 'study questions' listed on page 739 are an invaluable source for students' self-evaluation of their understanding of the contents of each chapter. In addition, the Glossary and Index listed at the back of the book are a very useful resource for those who are unfamiliar with glycobiology and would like to know more about this field.

In summary, I found the second edition of *Essentials of Glycobiology* to be an excellent resource book for many of us who are interested in developmental biology studies. Unbiased screens by traditional genetic strategies and by RNAi techniques will no doubt identify other important genes involved in glycan-mediated processes, while analyses of the functions of glycan-related genes in the context of development will further uncover the important functions of glycans in development; advances that might perhaps, one day, necessitate the publication of a third edition.