

The Journal of Biochemistry

第148巻 第3号 2010年9月1日発行(毎月1回1日発行) 昭和32年7月9日 第三種郵便物認可

ISSN 0021-924X (PRINT)

ISSN 1756-2651 (ONLINE)



THE JOURNAL OF BIOCHEMISTRY

Published Monthly by THE JAPANESE BIOCHEMICAL SOCIETY

VOL. 148 NO. 3 SEP. 2010

JOBIAO 148 (3) 263–370



OXFORD JOURNALS
OXFORD UNIVERSITY PRESS

EDITORIAL BOARD

Editor-in-Chief

Kohei MIYAZONO (Tokyo)

Editors

JB Reviews
Biochemistry

Molecular Biology
Cell
Biotechnology

Keiji MIYAZAWA (Chuo)
Koichi HONKE (Nankoku)
Katsuyuki TANIZAWA (Ibaraki)
Yukio FUJIKI (Fukuoka)
Akira KIKUCHI (Suita)
Takuya UEDA (Kashiwa)

Managing Editors

Kensaku MIZUNO (Sendai) Kazumitsu UEDA (Kyoto)

Associate Editors

JB Reviews

Biochemistry

Molecular Biology

Cell

Biotechnology

Junken AOKI (Sendai)
Shigeaki KATO (Tokyo)
Hiroshi OHNO (Yokohama)
Fumio ARISAKA (Yokohama)
Hiroko BABA (Hachioji)
Kiyoshi FUKUI (Tokushima)
Jules Mitchell GUSS (Sydney)
Hideyuki HAYASHI (Takatsuki)
Michael A. HOLLINGSWORTH (Omaha)
Hiroshi ICHINOSE (Yokohama)
Shoichi ISHIURA (Tokyo)
Hiroyuki ITABE (Tokyo)
Makoto ITO (Fukuoka)
Kazuhiro IWAI (Suita)
Koichi FURUKAWA (Nagoya)
Fuyuki ISHIKAWA (Kyoto)
Thomas LANGER (Köln)
Kazutoshi MORI (Kyoto)
Matthias MULLER (Freiburg)
Juergen BEHRENS (Erlangen)
Kang-Yell CHOI (Seoul)
Kazuhiko IGARASHI (Sendai)
Takeshi IWATSUBO (Tokyo)
Peter S. KLEIN (Philadelphia)
Munehito ARAI (Tokyo)
Dominique FOURMY (Gif-sur-Yvette)
Itaru HAMACHI (Kyoto)
Yo KIKUCHI (Toyohashi)

Arne ÖSTMAN (Stockholm)
Hiroyuki SORIMACHI (Tokyo)
Kaoru SUGASAWA (Kobe)
Kenji KADOMATSU (Nagoya)
Yasushi KAWATA (Tottori)
Ken KITAJIMA (Nagoya)
Atsushi NAKAGAWA (Suita)
Toru NAKAYAMA (Sendai)
Ryuichiro SATO (Tokyo)
Hideki SUMIMOTO (Fukuoka)
Natsuo UEDA (Kagawa)
Takehiko YOKOMIZO (Fukuoka)
Tohru YOSHIMURA (Nagoya)

Masao SAKAGUCHI (Hyogo)
Takashi SUDA (Kanazawa)
Takeshi TODO (Suita)
Toshiki TSURIMOTO (Fukuoka)
Tamotsu YOSHIMORI (Suita)
Yasuhiro MINAMI (Kobe)
Patricia C. SALINAS (London)
Toshiyuki TAKAI (Sendai)
Kazuma TANAKA (Sapporo)

Ken-ichi NISHIYAMA (Morioka)
Hiroschi UEDA (Tokyo)
Kazuo YAMAMOTO (Kashiwa)

Editorial Assistants

Daizo KOINUMA (Tokyo) Tetsuro WATABE (Tokyo)

Advisory Board

Biochemistry

Vytas A. BANKAITIS (Chapel Hill)
Jin Won CHO (Seoul)
Jeffrey D. ESKO (La Jolla)
Junichi FUJII (Yamagata)
Jianguo GU (Sendai)
Yann GUÉRARDEL (Villeneuve d'Ascq)
Robert S. HALTIWANGER (Stony Brook)
Gerald W. HART (Baltimore)
Toshiharu HASE (Suita)
Yasuhiro HASHIMOTO (Fukushima)
Kihachiro HORIIKE (Otsu)
Tatsuro IRIMURA (Tokyo)
Yoshizumi ISHINO (Fukuoka)
Johannis P. KAMERLING (Utrecht)

Molecular Biology

Masato ENARI (Tokyo)
Toshiya ENDO (Nagoya)
Masatoshi FUJITA (Tokyo)
Kenji KOHNO (Ikoma)
Tetsuro KOKUBO (Yokohama)
Bok Luel LEE (Busan)
Won-Jae LEE (Seoul)
Roland LILL (Marburg)

Reiji KANNAGI (Nagoya)
Shun-ichi KAWABATA (Fukuoka)
Ikuro KAWAGISHI (Koganei)
Gota KAWAI (Narashino)
Makoto KIMURA (Fukuoka)
Hiroshi KITAGAWA (Kobe)
Masayasu KOJIMA (Kurume)
Hiroki KONDO (Iizuka)
Michiko KONNO (Tokyo)
Yasunori KOZUTSUMI (Kyoto)
Seiki KURAMITSU (Toyonaka)
Bettie Sue MASTERS (San Antonio)
Ryoji MASUI (Toyonaka)
Catharina Taiko MIGITA (Yamaguchi)

Hisao MASAI (Tokyo)
Katsuyoshi MIHARA (Fukuoka)
Masayuki MIURA (Tokyo)
Masamichi MURAMATSU (Kanazawa)
Kazuhiro NAGATA (Kyoto)
Walter NEUPERT (München)
Shoko NISHIHARA (Hachioji)
Kunihiro OHTA (Tokyo)

Hisashi NARIMATSU (Tsukuba)
Takeshi NIKAWA (Tokushima)
Haruko OGAWA (Tokyo)
Toshihisa OHSHIMA (Fukuoka)
Yoshihiro SAMBONGI (Higashi-Hiroshima)
Ryo TAGUCHI (Tokyo)
Masato UMEDA (Uji)
Yoshinao WADA (Izumi)
Keisuke WAKASUGI (Tokyo)
Yuriko YAMAGATA (Kumamoto)
Junn YANAGISAWA (Tsukuba)
Akihiko YOSHIMURA (Tokyo)

Takashi OSUMI (Hyogo)
Pradman K. QASBA (Frederick)
Kazuhiro SAKAMAKI (Kyoto)
Shigeomi SHIMIZU (Tokyo)
Minoru TAKATA (Kyoto)
Yoshihide TSUJIMOTO (Suita)
Tohru YOSHIHISA (Nagoya)

Cell

Tomoichiro ASANO (Hiroshima)
Suk-Chul BAE (Gaesindong)
Frank D. BÖHMER (Jena)
Nils BROSE (Göttingen)
Mitsunori FUKUDA (Sendai)
Masato HASEGAWA (Tokyo)
Yutaka HATA (Tokyo)
Thorsten HEINZEL (Jena)
Shigeki HIGASHIYAMA (Toon)
Hidenori ICHUO (Tokyo)

Yasuki ISHIZAKI (Maebashi)
Bong-Kiun KAANG (Seoul)
Dimitris KARDASSIS (Heraklion)
Eunjoon KIM (Daejeon)
Tohru KOZASA (Chicago)
Hitoshi KUROSE (Fukuoka)
Atsushi MIYAJIMA (Tokyo)
Noboru MIZUSHIMA (Tokyo)
Aristidis MOUSTAKAS (Uppsala)
Tatsushi MUTA (Sendai)

Hideaki NAGASE (London)
Koh-ichi NAGATA (Kasugai)
Kazuhisa NAKAYAMA (Kyoto)
Hitoshi OHMORI (Okayama)
Chie SAKANAKA (South San Francisco)
Takuya SASAKI (Tokushima)
Kiyotoshi SEKIGUCHI (Suita)
Roger K. SUNAHARA (Ann Arbor)
Keiko UDAKA (Nankoku)

Biotechnology

Toshihiko EKI (Toyohashi)
Yoshihisa HAGIHARA (Ikeda)
Jun HIRABAYASHI (Tsukuba)
Mitsuhiro ITAYA (Tsuruoka)

Sunghoon KIM (Seoul)
Włodzimierz J. KRZYŻOSIAK (Poznań)
Katsumi MAENAKA (Fukuoka)
Makoto MAKISHIMA (Tokyo)

Tomoaki MATSUURA (Suita)
Chris Y. H. TAN (Vancouver, Canada)
Kouhei TSUMOTO (Kashiwa)

This JOURNAL, devoted to publication of original papers in the fields of biochemistry, molecular biology, cell, and biotechnology, was founded in 1922.

The JOURNAL is published monthly, with two volumes per annum.

All correspondences concerning this JOURNAL should be addressed to: The Japanese Biochemical Society, Ishikawa Building-3f, 25-16, Hongo 5-chome, Bunkyo-ku, Tokyo 113-0033, Japan. Tel. +81-3-3815-1913, Fax. +81-3-3815-1934

Subscription

Annual subscription rate (Volume 147 and Volume 148, 2010)

Corporate Subscribers

Print and Online £361.00/ \$722.00/ €542.00

Online Only £301.00/ \$602.00/ €452.00

Print Only £331.00/ \$662.00/ €497.00

Institutional Subscribers

Print and Online £289.00/ \$578.00/ €434.00

Online Only £241.00/ \$482.00/ €362.00

Print Only £265.00/ \$530.00/ €398.00

Methods of Payment

- (1) By cheque in £ sterling drawn on a UK bank, € Euro drawn on a European bank, or in \$ US drawn on a US bank. Cheques should be made payable to Oxford Journals. All orders should be accompanied by full payment and sent to your nearest Oxford Journals office.
- (2) By bank transfer to Barclays Bank Plc, Oxford Group Office, Oxford (bank sort code: 20-65-18) (UK). Overseas only: SWIFT BARC GB 22.

– GB £ Sterling to a/c no 70299332 – IBAN GB89BARC20651870299332

– US \$ Dollars to a/c no 66014600 – IBAN GB27BARC20651866014600

– EU € Euros to a/c no 78923655 – IBAN GB16BARC20651878923655

Please quote our renewal/invoice number and subscriber (if known) when making payment.

- (3) By MasterCard, Switch/Maestro, Visa, or American Express.

- (4) By charge card: automatic annual charge to either Visa or MasterCard is available. Please contact us for further details.

Periodicals postage paid at Rahway, NJ and at additional entry points.

US Postmaster: send address changes to The Journal of Biochemistry (ISSN 0021-924X), c/o Mercury International, 365 Blair Road, Avenel, NJ 07001, USA.

Agencies

Oxford University Press
Journals Subscription Department
Great Clarendon Street
Oxford, OX2 6DP, UK

Japan Publications Trading Co., Ltd.
P.O. Box 5030, Tokyo International,
2-1, Sarugaku-cho 1-chome, Chiyoda-ku,
Tokyo 101-0064, Japan

Maruzen Co., Ltd.
P.O. Box 5050, Tokyo International,
100-3199, Japan

All back issues of the *Journal of Biochemistry* from Volume 1, 1922, are available from our agency: TOA BOOK EXPORTS, INC., Ikebukuro 4-13-4, Toshima-ku, Tokyo 171-0014, Japan. Tel. +81-3-3985-4701, Fax. +81-3-3985-4703

Copyright © 2010, by the Japanese Biochemical Society

Published in association with Oxford University Press

Notice on photocopying With the exception of cases permitted by the Copyrights Law, such as the photocopying services provided by the libraries duly designated by government ordinance and photocopying for lectures by teachers at educational institutions, the photocopying of any part of this publication without explicit consent of the relevant author is a violation of the law. To legally photocopy any part of this publication, the person wishing to photocopy, or the corporation or organization employing such person, is recommended to enter into a comprehensive copyright approval agreement with the following trustee of copyrights from the authors:

(Except in the U.S.A.) The Copyright Council of the Academic Societies, 41-6, Akasaka 9-chome, Minato-ku, Tokyo 107-0052, Japan. Phone: 3-3475-4621, Fax: 3-3403-1738

(In the U.S.A.) Copyright Clearance Center, Inc., 222 Rosewood Drive, Danvers, MA 01923, U.S.A. Phone: 978-750-8400, Fax: 978-646-8600

NOTES TO CONTRIBUTORS

The JOURNAL OF BIOCHEMISTRY publishes contributions written in English and submitted in the form of (1) Regular paper or (2) Rapid communication, covering materials requiring prompt publication.

The submission of a manuscript implies that the work has not been published previously, that it is not under consideration for publication elsewhere, and that if it is accepted for publication, the author(s) will grant an exclusive license to publish to the Japanese Biochemical Society.

Manuscripts should be succinct. No length limit is set for a Regular paper, whereas a Rapid communication must not exceed 3.5 printed pages. Author charges consist of Color Charge and Offprint Charge, but there are no Page Charges.

Submission should be made through the online submission system at <<http://mc.manuscriptcentral.com/jb>>. We no longer handle submission by post. For further information on online submission, please see: Instructions for Online Submission <http://www.oxfordjournals.org/jbchem/for_authors/auth1.html>.

Reprints can be purchased, in lots of 50 copies, at cost prices. The orders should be submitted with the returned proof.

When submitting manuscripts, authors are asked to select one of the following four fields and its topic under which the submission should be reviewed. Please indicate this selection on the title page of the manuscript. Authors may suggest names and addresses of persons suitable for reviewing their submitted works.

Fields and topics to be selected:

Fields: Topics

Biochemistry: Biochemistry General

- Protein Structure
- Protein Interaction and Recognition
- Biomolecular Structures
- Nucleic Acid and Peptide Biochemistry
- Glycobiology and Carbohydrate Biochemistry
- Lipid Biochemistry
- Enzymology
- Enzyme Inhibitors
- Biochemistry of Proteolysis
- Metabolism and Bioenergetics
- Reactive Oxygen and Nitrogen Species
- Biochemistry in Cell Membranes
- Biochemistry in Diseases and Aging
- Neurochemistry
- Immunochemistry
- Physiological Chemistry
- Biochemical Pharmacology
- Analytical Biochemistry

Molecular Biology: Molecular Biology General

- Genes and Other Genetic Materials
- Replication and Recombination
- Gene Expression
- Protein Synthesis
- DNA-Protein Interaction
- RNA Processing
- Genetic Engineering
- Genetic Diseases
- Molecular Genetics
- Molecular Evolution
- Bioinformatics

Fields: Topics

Cell: Cell General

Biomembranes, Organelles, and Protein Sorting
Muscles
Cytoskeleton, Cell Motility, and Cell Shape
Extracellular Matrices and Cell Adhesion Molecules
Cell Cycle
Receptors and Signal Transduction
Stress Proteins and Molecular Chaperones
Cell Death
Differentiation, Development, and Aging
Neurobiology
Tumor and Immunology

Biotechnology: Biotechnology General

Biomimetic Chemistry
Biomaterials
Bioactive Substances
Synthetic Peptides and Oligonucleotides
Gene and Protein Engineering
RNA Technology
Glycotechnology
Immunological Engineering
Cell and Tissue Engineering
Transgenic Technology
Gene Delivery Systems
Drug Delivery Systems
Biosensor and Bioelectronics
New Devices in Biotechnology
Environmental Technology

“Instructions to Authors” are printed in the January and July issues of this JOURNAL every year. Please conform to these instructions when submitting manuscripts. Reprint of “Instructions to Authors” is available.

New Announcement (Limited Publication)

JOURNAL OF BIOCHEMISTRY, GENERAL CONTENTS

Volume 37–66 (1950–1969) Cloth Bound 700
page, including Author and Subject Index US
\$90.00

Volume 67–98 (1970–1985) Cloth Bound 1000
page, including Author and Subject Index US
\$120.00

Now available through: TOA BOOK EXPORTS, INC.,
Ikebukuro 4-13-4, Toshima-ku, Tokyo 171-0014, Japan.

Author Index

- | | | | |
|-----------------------|------------------------|-----------------------|-------------------|
| Beauregard M., 299 | Huang X., 341 | Nakamura A., 289 | Tsai M.-Y., 349 |
| Cai Y.-C., 319 | Huang Y.-J., 319 | Nakamura S., 335 | Wei Y., 263, 273 |
| Chang G.-G., 349 | Iwahashi H., 289 | Niki E., 289 | Wu G., 263, 273 |
| Chang H.-P., 349 | Jiang J., 263, 273 | Nishio K., 289 | Wu M.-W., 319 |
| Chang W.-H., 349 | Kato H., 289 | Ochiya T., 281 | Xian L.-J., 319 |
| Charbonneau D.M., 299 | Katsuda T., 281 | Ota F., 359 | Xu H.-M., 341 |
| Chen H., 263, 273 | Kinugasa S., 289 | Pongkitwitoon B., 335 | Yamaguchi W., 327 |
| Chen K., 273 | Kojima S., 309 | Sakai Y., 281 | Yamamoto K., 289 |
| Cui C., 263, 273 | Korekane H., 359 | Sakamoto S., 335 | Yamamoto O., 289 |
| Endoh S., 289 | Li Q., 273 | Shen J., 263 | Yang Z., 263, 273 |
| Fujimoto E., 327 | Liang J.-Y., 349 | Shida K., 359 | Yoshida Y., 289 |
| Fujita K., 289 | Lin L.-L., 349 | Shinohara N., 289 | Zeng Z.-L., 319 |
| Ge Y., 263, 273 | Liu D., 263 | Sun J., 319 | Zhang F., 341 |
| Gu J., 263, 273 | Maenaka K., 335 | Sun S., 273 | Zhao L., 341 |
| Hasegawa T., 359 | Matsumoto A., 359 | Sun Y.-L., 319 | Zhou F., 263, 273 |
| Higuchi M., 327 | Meddeb-Mouelhi F., 299 | Tabata I., 327 | Zhu B., 341 |
| Hizukuri Y., 309 | Misonou Y., 359 | Tanaka H., 335 | |
| Homma M., 309 | Miyamoto Y., 359 | Taniguchi N., 359 | |
| Horie M., 289 | Morimoto S., 335 | Teratani T., 281 | |

COVER:

Discovery in Japan

Single particle reconstruction using electron microscope revealed that Keap1 has a forked-stem dimer structure with two large spheres, which resembles a cherry bob (1). Picture is courtesy of Drs. Chikara Sato and Anne Kohtz (AIST, Japan).

A group led by Dr. Masayuki Yamamoto (Tohoku University) has identified the Nrf2-Keap1 system that regulates gene induction in response to electrophilic and oxidative stresses (2). Illustrated analysis provides a molecular basis for the Keap1 function as a stress sensor. Nrf2 is the master transcription factor that activates detoxifying and antioxidant enzyme genes, while Keap1 is a component of ubiquitin E3 ligase (3). Under unstressed conditions Keap1 ubiquitinates Nrf2 and renders it rapid degradation. Upon exposure to the stresses Keap1 loses the ubiquitin ligase activity, which results in the Nrf2 stabilization and accumulation in the nucleus. Nrf2 coordinately activates transcription of cytoprotective enzyme genes. Recent studies revealed that cancer cells hijack Nrf2 and protect themselves from the challenge of stresses (4, 5).

References

- Ogura, T., Tong, K.I., Mio, K., Maruyama, Y., Kurokawa, H., Sato, C., and Yamamoto, M. (2010) Keap1 is a forked-stem dimer structure with two large spheres enclosing the intervening, double glycine repeat, and C-terminal domains. *Proc. Natl. Acad. Sci. USA* **107**, 2842–2847.
- Itoh, K., Wakabayashi, N., Katoh, Y., Ishii, T., Igarashi, K., Engel, J.D., and Yamamoto, M. (1999) Keap1 represses nuclear activation of antioxidant responsive elements by Nrf2 through binding to the amino-terminal Neh2 domain. *Genes Dev.* **13**, 76–86.
- Motohashi, H., and Yamamoto, M. (2004) Nrf2-Keap1 defines a physiologically important stress response mechanism. *Trends Mol. Med.* **10**, 549–557.
- Padmanabhan, B., Tong, K.I., Ohta, T., Nakamura, Y., Scharlock, M., Ohtsuji, M., Kang, M.I., Kobayashi, A., Yokoyama, S., and Yamamoto, M. (2006) Structural basis for defects of Keap1 activity provoked by its point mutations in lung cancer. *Mol. Cell* **21**, 689–700.
- Komatsu, M., Kurokawa, H., Waguri, S., Taguchi, K., Kobayashi, A., Ichimura, Y., Sou, Y.-S., Ueno, I., Sakamoto, A., Tong, K.I., Kim, M., Iemura, S., Natsume, T., Ueno, T., Kominami, E., Motohashi, H., Tanaka, K., and Yamamoto, M. (2010) The selective autophagy substrate p62 activates the stress responsive transcription factor Nrf2 through inactivation of Keap1. *Nat. Cell Biol.* **12**, 213–223.