

BIOLOGICAL CHEMISTRY

*Founded in 1877 by Felix Hoppe-Seyler as
Zeitschrift für Physiologische Chemie*

Felix Hoppe-Seyler (1825–1895) was a pioneer of biochemistry, remembered not only for his discovery of hemoglobin and his contributions to the chemical characterization of many other biological compounds and processes but also for having been the mentor of Friedrich Miescher and Albrecht Kossel. In his preface to the first issue of *Zeitschrift für Physiologische Chemie*, Felix Hoppe-Seyler coined the term *Biochemistry* ('Biochemie') for the then newly emerging discipline.



Biological Chemistry is associated
with the Gesellschaft für Biochemie und
Molekularbiologie e.V. (GBM)

EDITOR-IN-CHIEF

D. Thomas, Chicago

EXECUTIVE EDITORS

*J. Buchner, Munich
J. Herrmann, Kaiserslautern
M. Lei, Shanghai
S. Ludwig, Münster
B. Turk, Ljubljana
A. Wittinghofer, Dortmund*

EDITORIAL BOARD

*P. Agostinis, Leuven
L. Banks, Trieste
A.G. Beck-Sickinger, Leipzig
L. Bosca, Madrid
B. Brüne, Frankfurt/Main
E. Cadenas, Los Angeles
I. Dikic, Frankfurt/Main
W.-X. Ding, Kansas City
C. Hammann, Bremen
F.U. Hartl, Martinsried
D. Häussinger, Düsseldorf
J. Hiscott, Rome
L.-O. Klotz, Jena
V. Magdolen, Munich
G. Mugesh, Bangalore
M. Müschen, San Francisco
G. Pejler, Uppsala
N. Pfanner, Freiburg
J. Potempa, Krakow
K. Sandhoff, Bonn
J. Scheller, Düsseldorf
H. Sies, Düsseldorf
G. Tiegs, Hamburg
J.M. Valpuesta, Madrid*

ASSOCIATE EDITORS (GBM STUDY GROUPS)

*J.W. Bartsch, Marburg
S. Clemens, Bayreuth
A. Ebert, Göttingen
R. Erdmann, Bochum
K. Giehl, Giessen
S. Hiller, Basel
B. Höcker, Bayreuth
I. Koch, Frankfurt/Main
T. Proikas-Cezanne, Tübingen
J. Riemer, Cologne
C. Seidel, Düsseldorf
C. Villmann, Würzburg
J. Weigand, Marburg
V. Zickermann, Frankfurt/Main*

DE GRUYTER

ABSTRACTED/INDEXED IN AGRICOLA (National Agricultural Library) · Baidu Scholar · Biobase · Cabells Journalytics · CABI (over 50 subsections) · Case · Chemical Abstracts Service (CAS): CAPLUS; SciFinder · CNKI Scholar (China National Knowledge Infrastructure) · CNPIEC: cnpLINKer · Dimensions · EBSCO (relevant databases) · EBSCO Discovery Service · EMBASE · Genamics JournalSeek · Google Scholar · ICAP Alcohol Information Databases · Japan Science and Technology Agency (JST) · J-Gate · Journal Citation Reports/Science Edition · JournalGuide · JournalTOCs · KESLI-NDSL (Korean National Discovery for Science Leaders) · Medline · Meta · MyScienceWork · Naver Academic · Naviga (Softweco) · Norwegian Register for Scientific Journals, Series and Publishers · Pathway Studio · Primo Central (ExLibris) · ProQuest (relevant databases) · Publons · PubMed · QOAM (Quality Open Access Market) · ReadCube · Reaxys · SCImago (SJR) · SCOPUS · Semantic Scholar · Sherpa/RoMEO · SIIC Data Bases · Summon (ProQuest) · TDNet · Text Mining · Ulrich's Periodicals Directory/ulrichsweb · WanFang Data · Web of Science: Biological Abstracts; BIOSIS Previews; Current Contents/Life Sciences; Prous Science Integrity; Reaction Citation Index; Science Citation Index; Science Citation Index Expanded · WorldCat (OCLC) · X-MOL · Yewno Discover

The Journal is associated with the Gesellschaft für Biochemie und Molekularbiologie e.V. 

The publisher, together with the authors and editors, has taken great pains to ensure that all information presented in this work (programs, applications, amounts, dosages, etc.) reflects the standard of knowledge at the time of publication. Despite careful manuscript preparation and proof correction, errors can nevertheless occur. Authors, editors and publisher disclaim all responsibility for any errors or omissions or liability for the results obtained from use of the information, or parts thereof, contained in this work.

The citation of registered names, trade names, trademarks, etc. in this work does not imply, even in the absence of a specific statement, that such names are exempt from laws and regulations protecting trademarks etc. and therefore free for general use.

ISSN 1431-6730 · e-ISSN 1437-4315 · CODEN BICHF3

All information regarding notes for contributors, subscriptions, Open access, back volumes and orders is available online at www.degruyter.com/bc.

RESPONSIBLE EDITOR(S) Douglas D. Thomas, Department of Medicinal Chemistry and Pharmacognosy, University of Illinois at Chicago, College of Pharmacy, 900 S. Ashland Avenue (M/C 870), Chicago, IL 60607, USA, e-mail: ddthomas@uic.edu.

JOURNAL COORDINATOR Dr. Torsten Krüger, De Gruyter, Genthiner Straße 13, 10785 Berlin, Germany, Tel.: +49 (0)30 260 05-176, Fax: +49 (0)30 260 05-352, e-mail: biol.chem.editorial@degruyter.com

RESPONSIBLE FOR ADVERTISEMENTS Markus Kügel, De Gruyter, Rosenheimer Str. 143, 81671 München, Germany. Tel.: +49 89 76 902-424, e-mail: anzeigen@degruyter.com

© 2022 Walter de Gruyter GmbH, Berlin/Boston

TYPESETTING TNQ Technologies, Chennai, India

PRINTING Franz X. Stückle Druck und Verlag e.K., Ettenheim



Contents

Highlight: Heme research – the past, the present and the future

Guest Editorial — 983

Harry A. Dailey and Amy E. Medlock

A primer on heme biosynthesis — 985

Dennis J. Stuehr, Yue Dai, Pranjal Biswas,
Elizabeth A. Sweeny and Arnab Ghosh

New roles for GAPDH, Hsp90, and NO in regulating heme allocation and hemeprotein function in mammals — 1005

Rebecca K. Donegan

The role of host heme in bacterial infection — 1017

Jakub Vávra, Artur Sergunin, Petr Jeřábek,
Toru Shimizu and Markéta Martínková

Signal transduction mechanisms in heme-based globin-coupled oxygen sensors with a focus on a histidine kinase (*AfGCHK*) and a diguanylate cyclase (*YddV* or *EcDosC*) — 1031

Yue Dai, Angela S. Fleischhacker, Liu Liu, Sara Fayad,
Amanda L. Gunawan, Dennis J. Stuehr and
Stephen W. Ragsdale

Heme delivery to heme oxygenase-2 involves glyceraldehyde-3-phosphate dehydrogenase — 1043

Marie-Therese Hopp, Dhruv Chetanbhai Rathod,
Kristina Helena Winn, Shubhi Ambast and Diana Imhof

Novel insights into heme binding to hemoglobin — 1055

Guido Gessner, Mahdi Jamili, Pascal Tomczyk,
Dirk Menche, Roland Schönherr, Toshinori Hoshi and
Stefan H. Heinemann

Extracellular heme is a reverse use-dependent gating modifier of cardiac voltage-gated Na⁺ channels — 1067

Lubka T. Roumenina and Jordan D. Dimitrov

Assessment of the breadth of binding promiscuity of heme towards human proteins — 1083

Vijith Vijayan, Robert Greite, Sebastian Schott,
Julian Dorcic, Kuku Madyaningrana, Pooja Pradhan,
Jörg Martens, Rainer Blasczyk, Sabina Janciauskiene
and Stephan Immenschuh

Determination of free heme in stored red blood cells with an apo-horseradish peroxidase-based assay — 1091

Joey Lukas, Ivona Družeta and Toni Kühl

Comparative studies of soluble and immobilized Fe(III) heme-peptide complexes as alternative heterogeneous biocatalysts — 1099