

# 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

*B. Brüne, Frankfurt/Main*

## EXECUTIVE EDITORS

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

## EDITORIAL BOARD

*P. Agostinis, Leuven  
L. Banks, Trieste  
A.G. Beck-Sickinger, Leipzig  
L. Bosca, Madrid  
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  
M. Lamkanfi, Ghent  
V. Magdolen, Munich  
G. Mugesh, Bangalore  
M. Müschen, San Francisco  
C.M. Overall, Vancouver  
G. Pejler, Uppsala  
N. Pfanner, Freiburg  
R. Pike, Melbourne  
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  
C. Hunte, Freiburg  
I. Koch, Frankfurt/Main  
T. Proikas-Cezanne, Tübingen  
L. Randau, Marburg  
J. Riemer, Cologne  
C. Seidel, Düsseldorf  
R. Sterner, Regensburg  
C. Villmann, Würzburg*

**DE GRUYTER**

**ABSTRACTED/INDEXED IN** Academic OneFile (Gale/Cengage Learning), ASFA1: Biological Sciences & Living Resources, Biochemistry & Biophysics Citation Index, Biological Abstracts, BIOSIS Previews, CAB Abstracts, Calcium and Calcified Tissue Abstracts, Chemical Abstracts and the CAS databases, CSA Illustrata - Natural Sciences, CSA Neurosciences Abstracts, Current Contents/Life Sciences, Elsevier BIOBASE/Current Awareness in Biological Sciences (CABS), EMBASE - the Excerpta Medica database, EMBiology, Index Medicus/MEDLINE, Journal Citation Reports/Science Edition, Reaction Citation Index, Reference Update, Science Citation Index, Science Citation Index Expanded (SciSearch), Scopus, SIIC Data Bases, Zoological Record.

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](http://www.degruyter.com/bc).

**RESPONSIBLE EDITOR(S)** Professor Dr. Bernhard Brüne, Goethe-University Frankfurt, Faculty of Medicine, Biochemistry I, Theodor-Stern-Kai 7, D-60590 Frankfurt/Main, Germany, Tel.: +49-69-6301 7424, Email: [B.Bruene@biochem.uni-frankfurt.de](mailto:B.Bruene@biochem.uni-frankfurt.de)

**JOURNAL MANAGER** Dr. Torsten Krüger, De Gruyter, Genthiner Straße 13, 10785 Berlin, Germany, Tel.: +49 (0)30 260 05-176, Fax: +49 (0)30 260 05-298, Email: [biol.chem.editorial@degruyter.com](mailto:biol.chem.editorial@degruyter.com)

**RESPONSIBLE FOR ADVERTISEMENTS** Jana Kuchta, De Gruyter, Genthiner Straße 13, 10785 Berlin, Germany. Email: [anzeigen@degruyter.com](mailto:anzeigen@degruyter.com)

© 2020 Walter de Gruyter GmbH, Berlin/Boston

**TYPESETTING** TNQ Technologies, Chennai, India

**PRINTING** Franz X. Stücker Druck und Verlag e.K., Ettenheim

#### COVER ILLUSTRATION

On the front cover a biofilm formed by the undomesticated *Bacillus subtilis* strain NCIB3610 is shown. *Bacillus subtilis* is the model organism for Gram-positive bacteria. Through complex signal-perception and signal-transduction mechanisms it can develop into different cell types that can co-exist in a self-produced extracellular matrix that encases the constituent cells. These multi-cellular assemblages of *B. subtilis* cells, referred to as biofilms, can form complex structured macro-colonies on solid surfaces and plant roots [Vlamakis et al., Nat. Rev. Microbiol. 11 (2013), pp. 157–168]. The picture shows such a macro-colony of the *B. subtilis* strain NCIB3610 grown for two days at 30 °C on biofilm-inducing MSgg agar plates containing Congo Red (40 µg/ml) and Coomassie Brilliant Blue (20 µg/ml) to stain the colony [Brada et al., Proc. Natl. Acad. Sci. USA 98 (2001), pp. 11621–11626; Assaly et al., Proc. Natl. Acad. Sci. USA 109 (2012), pp. 18891–18896]. The diameter of the shown macro-colony is approximately 1 cm. See also the article by Bange and Bedrunka on pp. 1307–1322 in this issue.

Image courtesy of Dr. Patricia Bedrunka [Center for Synthetic Microbiology (SYNMIKRO), Philipps-University Marburg, Germany].



## Contents

### Highlight: How Microorganisms View and Respond to Their World

#### Guest Editorial — 1305

Gert Bange and Patricia Bedrunka

**Physiology of guanosine-based second messenger signaling in *Bacillus subtilis* — 1307**

Sandra Kunz and Peter L. Graumann

**Spatial organization enhances versatility and specificity in cyclic di-GMP signaling — 1323**

Elizaveta Krol, Simon Schäper and Anke Becker

**Cyclic di-GMP signaling controlling the free-living lifestyle of alpha-proteobacterial rhizobia — 1335**

Muriel C. F. van Teeseling and Martin Thanbichler

**Generating asymmetry in a changing environment: cell cycle regulation in dimorphic alphaproteobacteria — 1349**

Daniel K.H. Rode, Praveen K. Singh and Knut Drescher

**Multicellular and unicellular responses of microbial biofilms to stress — 1365**

María Pérez-Burgos and Lotte Søgaard-Andersen

**Biosynthesis and function of cell-surface polysaccharides in the social bacterium *Myxococcus xanthus* — 1375**

Lars-Oliver Essen, Marian Samuel Vogt and Hans-Ulrich Mösch

**Diversity of GPI-anchored fungal adhesins — 1389**

Ulrich Mühlenhoff, Joseph J. Braymer, Stefan Christ, Nicole Rietzschel, Marta A. Uzarska, Benjamin D. Weiler and Roland Lill

**Glutaredoxins and iron-sulfur protein biogenesis at the interface of redox biology and iron metabolism — 1407**

Lennart Schada von Borzyskowski, Iria Bernhardsgrütter and Tobias J. Erb

**Biochemical unity revisited: microbial central carbon metabolism holds new discoveries, multi-tasking pathways, and redundancies with a reason — 1429**

Lucas Hermann, Christopher-Nils Mais, Laura Czech, Sander H.J. Smits, Gert Bange and Erhard Bremer

**The ups and downs of ectoine: structural enzymology of a major microbial stress protectant and versatile nutrient — 1443**

Anna Hakobyan and Werner Liesack

**Unexpected metabolic versatility among type II methanotrophs in the Alphaproteobacteria — 1469**

Martin Lempp, Paul Lubrano, Gert Bange and Hannes Link

**Metabolism of non-growing bacteria — 1479**

Stephan Kiontke, Tanja Göbel, Annika Brych and Alfred Batschauer

**DASH-type cryptochromes – solved and open questions — 1487**

Gianluca Dell'Aquila and Uwe G. Maier

**Specific acclimations to phosphorus limitation in the marine diatom *Phaeodactylum tricornutum* — 1495**