

# JCB

THE JOURNAL OF CELL BIOLOGY

## EDITOR-IN-CHIEF

JODI NUNNARI

## EXECUTIVE EDITOR

REBECCA ALVANIA  
email: ralvania@rockefeller.edu

## EDITORS

ARSHAD DESAI  
PIER PAOLO DI FIORE  
ELAINE FUCHS  
ANNA HUTTENLOCHER  
IAN MACARA  
IRA MELLMAN  
ANA POMBO  
LOUIS F. REICHARDT  
KENNETH M. YAMADA  
RICHARD YOULE

## DEPUTY EDITOR

TIM SPENCER  
email: tspencer@rockefeller.edu

## SENIOR SCIENTIFIC EDITOR

MELINA CASADIO  
email: mcasadio@rockefeller.edu

## SCIENTIFIC EDITORS

ANDREA MARAT  
email: amarat@rockefeller.edu

MARIE ANNE O'DONNELL  
email: modonnell@rockefeller.edu

## NEWS EDITOR

BENJAMIN SHORT

## EDITORIAL BOARD

JOHN AITCHISON  
LAURA ATTARDI  
JOHAN AUWERX  
BILL BEMENT  
VANN BENNETT  
DOMINIQUE BERGMANN  
MONICA BETTENCOURT-DIAS  
MAGDALENA BEZANILLA  
SUE BIGGINS  
CÉDRIC BLANPAIN  
JULIUS BRENNECKE  
TONY BRETSCHER  
MARIANNE BRONNER  
KARLENE CIMPRICH  
DON W. CLEVELAND  
NIKA DANIAL  
TITIA DE LANGE  
RAY DESHAIES  
IVAN DIKIC  
DANIEL DUROCHER  
WILLIAM EARNSHAW  
JAN ELLENBERG  
SCOTT EMR  
JEFFREY ESKO  
MARC FREEMAN  
JUDITH FRYDMAN  
HIRONORI FUNABIKI  
MELISSA GARDNER  
LARRY GERACE  
FRANK GERTLER  
DAVID GILBERT  
YUKIKO GODA  
BRUCE GOODE  
ROGER GREENBERG  
SERGIO GRINSTEIN

ULRICH HARTL  
REBECCA HEALD  
RAMANUJAN HEGDE  
MARTIN HETZER  
NOBUTAKA HIROKAWA  
ERIKA HOLZBAUR  
MARTIN HUMPHRIES  
JAMES HURLEY  
LUISA IRUELA-ARISPE  
NANCY IP  
JOHANNA IVASKA  
SUSAN KAECH  
GERARD KARSENTY  
SCOTT KEENEY  
ALEXEY KHODJAKOV  
JÜRGEN KNOBLICH  
THOMAS LANGER  
JEANNE LAWRENCE  
DANNY LEW  
JENS LYKKE-ANDERSEN  
VIVEK MALHOTRA  
JOAN MASSAGUE  
SATYAJIT MAYOR  
JACOPO MELDOLESI  
ALEX MOGILNER  
SEAN MUNRO  
KARLA NEUGEBAUER  
EVA NOGALES  
KAREN OEGEMA  
EWA PALUCH  
ROY PARKER  
MARK PEIFER  
ELIOR PELES  
THOMAS RANDO  
SAMARA RECK-PETERSON

JEREMY REITER  
DANIEL B. RIFKIN  
DAVID RON  
MICHAEL ROUT  
CRAIG ROY  
MICHAEL RUDNICKI  
ERIK SAHAI  
TRINA SCHROER  
MARTIN SCHWARTZ  
JEAN SCHWARZBAUER  
ANDREY SHAW  
ZU-HANG SHENG  
MICHAEL SIXT  
TIM STEARNS  
JOAN STEITZ  
HARALD STENMARK  
AARON STRAIGHT  
BILLY TSAI  
RON VALE  
BAS VAN STEENSEL  
PATRIK VERSTREKEN  
MARK VON ZASTROW  
AMY WAGERS  
ERWIN WAGNER  
JOHN WALLINGFORD  
TOBIAS WALTHER  
XIAOCHEN WANG  
LOIS WEISMAN  
MATT WELCH  
TIM YEN  
TAMOTSU YOSHIMORI  
JUNYING YUAN  
MARINO ZERIAL  
HONG ZHANG  
YIXIAN ZHENG

## EDITORIAL OFFICE

Phone: 212-327-8581  
Fax: 212-319-1082  
email: jcellbiol@rockefeller.edu

## MANAGING EDITOR

LINDSEY HOLLANDER

## PREFLIGHT COORDINATOR

LAURA SMITH

## PRODUCTION OFFICE

email: jcb@rockefeller.edu

## COPY EDITORS

CASEY DALRYMPLE  
D. AARON McILHENNY

## ASSISTANT PRODUCTION EDITOR

LIBBY GOSS

## SENIOR PRODUCTION EDITOR

MARY VASQUEZ

## PRODUCTION MANAGER

CAMILLE CLOWERY

## PRODUCTION DESIGNER

ERINN A. GRADY

THE ROCKEFELLER  
UNIVERSITY  
PRESS

COPYRIGHT TO ARTICLES PUBLISHED IN THIS JOURNAL IS HELD BY THE AUTHORS. ARTICLES ARE PUBLISHED BY THE ROCKEFELLER UNIVERSITY PRESS UNDER LICENSE FROM THE AUTHORS. CONDITIONS FOR REUSE OF THE ARTICLES BY THIRD PARTIES ARE LISTED AT [HTTP://WWW.RUPRESS.ORG/TERMS](http://www.rupress.org/terms)



PRINT ISSN: 0021-9525 ONLINE ISSN: 1540-8140

WWW.JCB.ORG



# THE ROCKEFELLER UNIVERSITY PRESS

**EXECUTIVE DIRECTOR**  
SUSAN KING

**FINANCE DIRECTOR**  
RAYMOND T. FASTIGGI

**BUSINESS DEVELOPMENT DIRECTOR**  
GREGORY FLYNN MALAR

**DIRECTOR OF EDITORIAL DEVELOPMENT**  
REBECCA ALVANIA

**DIRECTOR OF PUBLISHING TECHNOLOGIES**  
ROBERT J. O'DONNELL

**DIRECTOR OF COMMUNICATIONS AND MARKETING**  
RORY WILLIAMS

**ADVERTISING SALES DIRECTOR**  
LORNA PETERSEN

**EXECUTIVE ASSISTANT TO EXECUTIVE DIRECTOR;  
OFFICE ADMINISTRATOR**  
DEMANTIE (SATI) MOTIERAM

**ASSISTANTS TO THE FINANCE DIRECTOR**  
SARAH S. KRAFT  
ANN TRAVERS

**BUSINESS DEVELOPMENT SPECIALIST**  
COLLEEN M. SMITH

**MARKETING ASSOCIATE**  
LARAINÉ KARL

---

THE JOURNAL OF CELL BIOLOGY (ISSN 0021-9525) IS PUBLISHED MONTHLY BY THE ROCKEFELLER UNIVERSITY PRESS, 950 THIRD AVENUE, NEW YORK, NY 10022. PERIODICAL POSTAGE PAID AT NEW YORK, NY AND ADDITIONAL MAILING OFFICES.

**2017 SUBSCRIPTION RATES:**

**INSTITUTIONAL RATES:**

	<b>TIER 1</b>	<b>TIER 2</b>	<b>TIER 3</b>	<b>TIER 4</b>
ONLINE	\$2,310	\$2,900	\$3,520	\$4,490
PRINT+ONLINE	\$5,220	\$5,830	\$6,320	\$8,070

FOR MORE INFORMATION, PLEASE CONTACT THE SUBSCRIPTION OFFICE:

Phone: +1 800-633-4931  
Outside the US & Canada: +1 205-955-1567  
Fax: +1 205-955-1588  
email: [rupress@subscriptionoffice.com](mailto:rupress@subscriptionoffice.com)

**ADVERTISING REQUESTS:**

Phone: 212-327-8880  
Fax: 212-319-1080  
email: [petersl@rockefeller.edu](mailto:petersl@rockefeller.edu)

**PERMISSION REQUESTS:**

email: [permissions@rockefeller.edu](mailto:permissions@rockefeller.edu)

**MEDIA REQUESTS:**

email: [news@rockefeller.edu](mailto:news@rockefeller.edu)

**POSTMASTER:**

SEND ADDRESS CHANGES TO THE JOURNAL OF CELL BIOLOGY, SUBSCRIPTION OFFICE, P.O. BOX 361, BIRMINGHAM, AL 35201-0361.