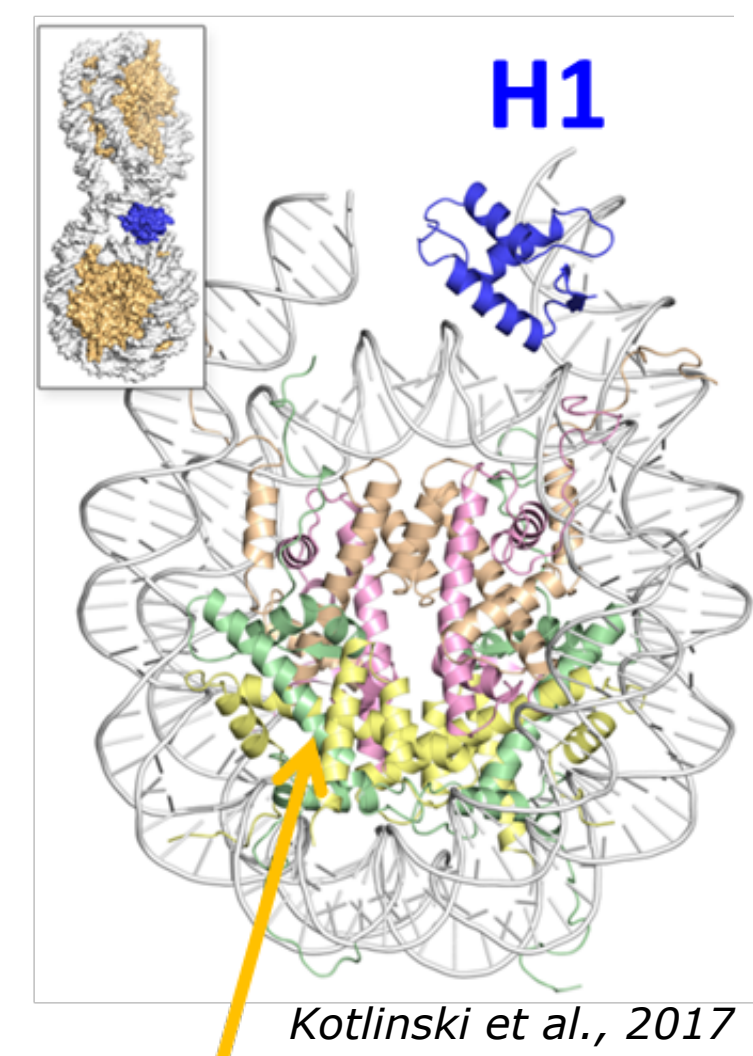


Linker histones - their roles beyond the chromatin architecture

Kinga Rutowicz^{1,#}, Maciej Lirski^{2,#}, Benoît Mermaz^{1,3}, Gianluca Teano⁴, Jasmin Schubert¹, Imen Mestiri⁴, Magdalena A. Kroteń⁵, Tohnyui Ndinyanka Fabrice¹, Simon Fritz¹, Stefan Grob¹, Christoph Ringli¹, Lusik Cherkezyan⁶, Fredy Barneche⁴, Andrzej Jerzmanowski^{2,7} and Célia Baroux¹

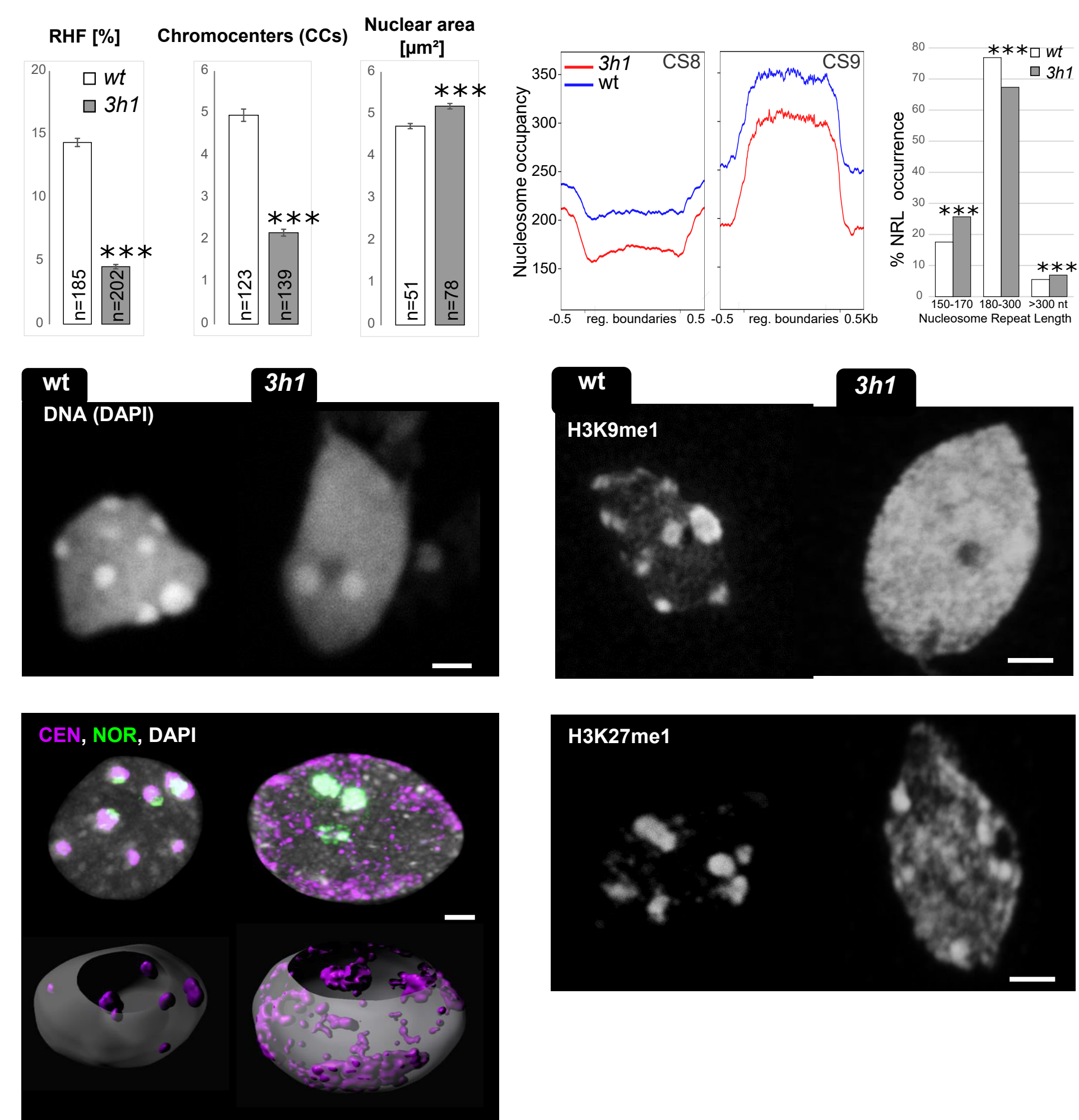
1. Institute of Plant and Microbial Biology, UZH, Zürich, Switzerland; 2. Institute of Biochemistry and Biophysics, PAS, Warsaw, Poland; 3. Imperial College London, UK; 4. Département de Biologie, PSL Research University, Paris, France; 5. CIFISMNS, University of Warsaw, Poland; 6. Department of Biomedical Engineering, Northwestern University, Evanston, USA; 7. Faculty of Biology, University of Warsaw, Poland, # equal contribution to the work



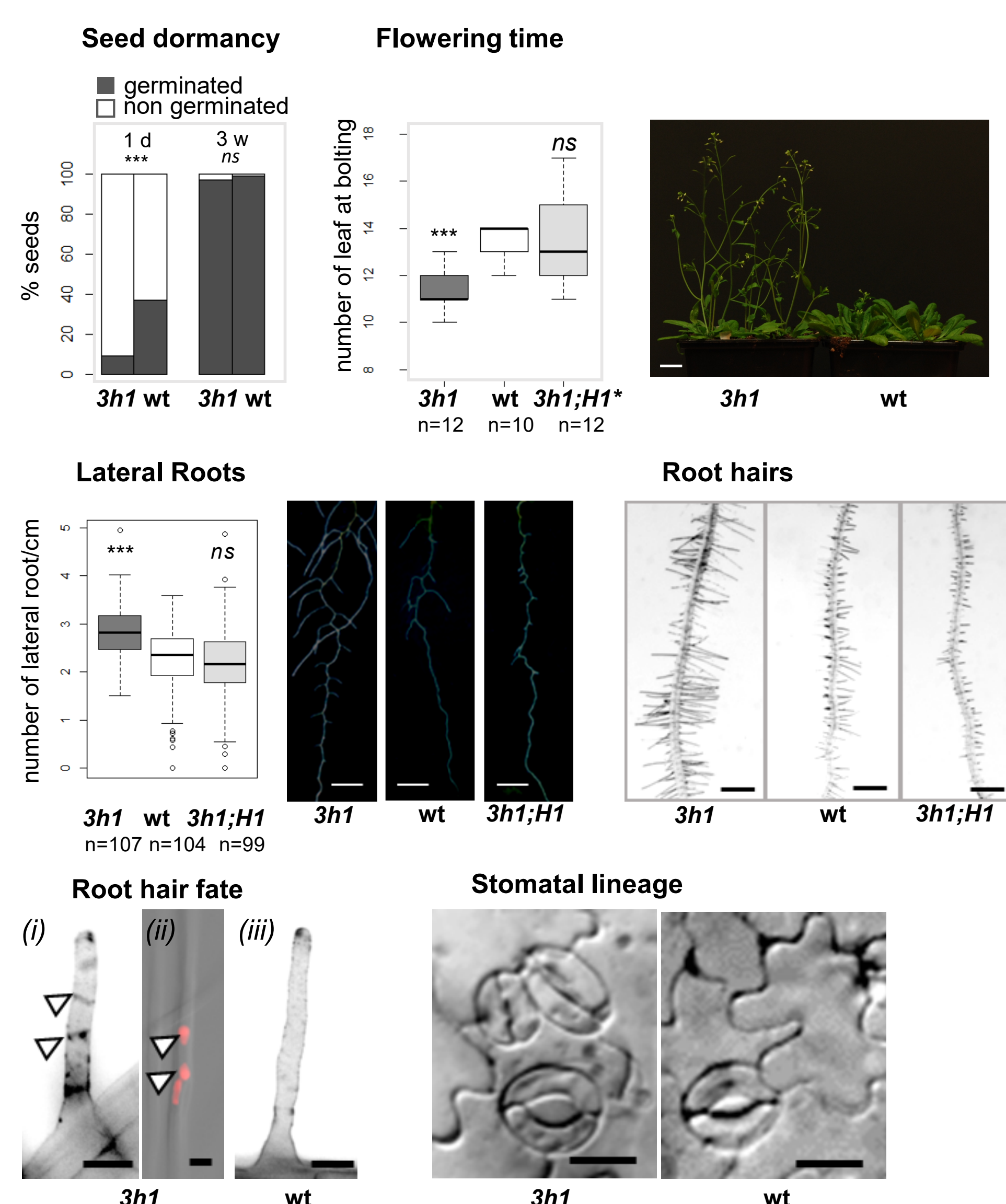
Core histones
H2A, H2B, H3, H4

Linker histones (H1) belong to major constituents of plant and animal chromatin besides the core nucleosomal histones. H1 variants appeared early during evolution as lysine-rich, proto-linker histones found in the ancestral eukaryotes such as protists but not Archaea (Kasinsky, Lewis et al. 2001). In contrast to core nucleosomal constituents H1 form a highly divergent class of histones (Kasinsky, Lewis et al. 2001).

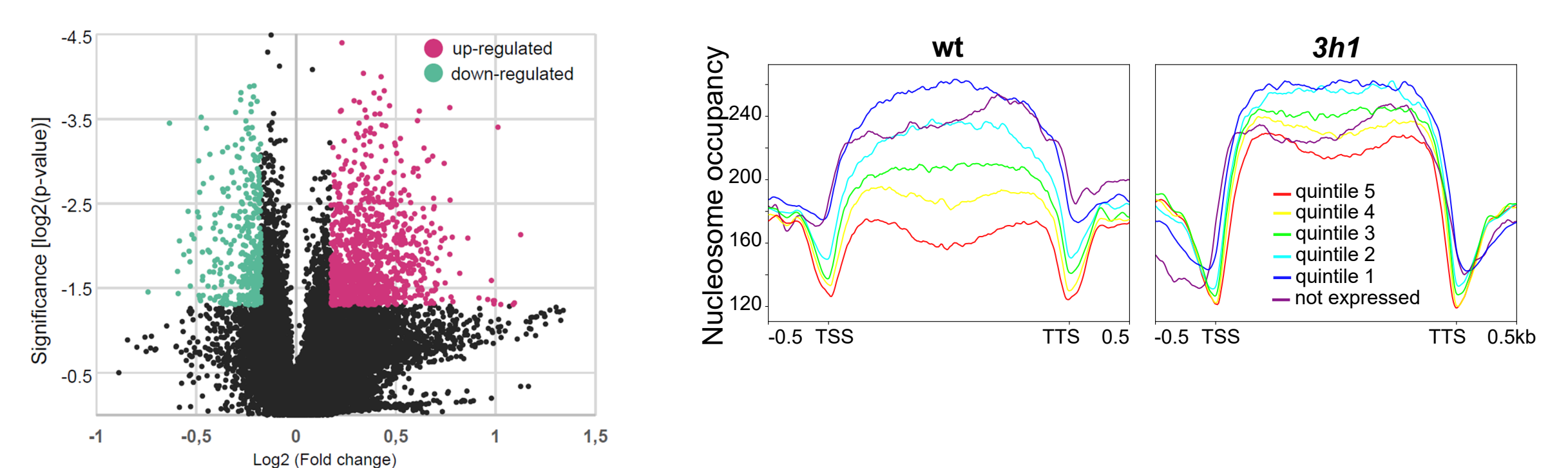
H1 variants are necessary to form compact heterochromatin domains but are dispensable for TE silencing and peripheral positioning of chromocenters



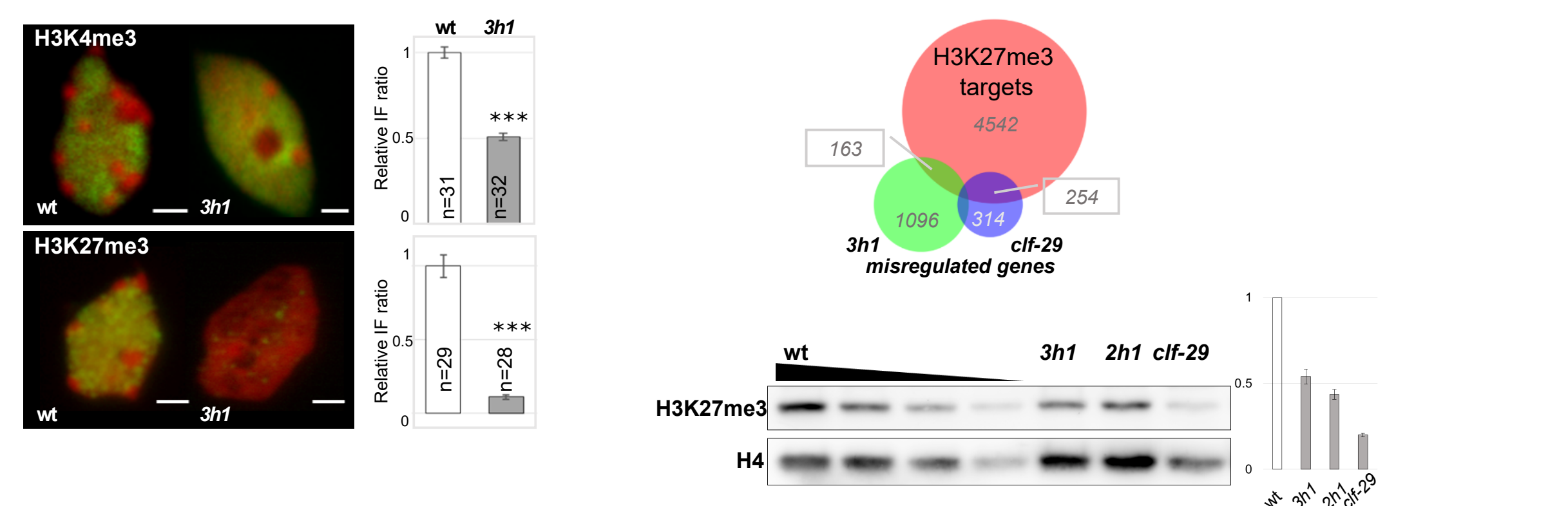
H1-deficient plants are viable yet show mild phenotypes.



H1 loss-of-function allows identifying both H1-sensitive and H1-independent genes



H1 depletion impairs the distribution of H3K27me3 and to a lesser extent of H3K4me3



Conclusion

H1 variants have a profound impact on the molecular and spatial (nuclear) chromatin organization in Arabidopsis with distinct roles in euchromatin and heterochromatin and a dual causality on gene expression. Phenotypical analyses further suggest the novel possibility that H1-mediated chromatin organization may contribute to the epigenetic control of developmental and cellular transitions.

Acknowledgments

We are indebted to Ueli Grossniklaus (UG; University of Zurich) for valuable advice and insightful discussions, for sharing laboratory facilities and for financial support; to Chris Bowler and Vincent Collet (Ecole Normale Supérieure Paris) for constant support and helpful discussions; to Valeria Gagliardini, Christof Eichenberger, Arturo Bolanos, Daniela Guthori, and Peter Kopf (University of Zurich) for general lab support; to Daniel Prata (University of Zurich) for assistance in plant growth and selection; to Stefan Wyder (University Research Priority Program - Evolution in Action; University of Zurich) for advice on statistical tests; to Dominique Bergman (Stanford University) for advice on stomata analysis; to Matthieu Inqouff (IRD Montpellier) for sharing the DynaME1 lines; to Alexis Matzel and Daniel von Wangenheim (University of Heidelberg) for the PUBQ10:H2B-RFP line; to Mariamawit Ashenafi (University of Zurich) for technical assistance in FISH and immunostaining; and to Marek Kalinowski for scripts to analyze chromatin state distributions. We thank Urs Ziegler, Jana Dohner, Andres Kaech, Claudia Dumrese, and Moritz Kirschman (University of Zurich) for service and support at the Cytometry Facility and the Center for Microscopy and Image Analysis for nuclei sorting, STED and GSD imaging, TEM preparation, FRAP imaging, and advice on data analysis. We also thank Marta Kobylowska (Institute of Biochemistry and Biophysics PAS) for sharing the facilities of Laboratory of Microarray Analysis for RNA-seq and MNase-seq experiments and Maciej Kotlinski (University of Warsaw) for conceptual support in designing and analyzing for RNA-seq and MNase-seq experiments.