

Curriculum Vitae Walter Jakob Gehring

Date and place of birth March 20, 1939 in Zürich, Switzerland

Citizenship Swiss

Civil status married to Elisabeth Lott

Children Stephan (1965), Thomas (1970)

Present position Professor

Institute address Dept. of Cell Biology
Biozentrum, University of Basel
Klingelbergstr. 70
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Home address Hochfeldweg 32
CH-4106 Therwil, Switzerland
Tel.: +41 61 721 35 93
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Education

1952-1958 Realgymnasium Zürich

1958 Matura

1958-1965 Studies in Zoology
University of Zürich

1963 Diploma in Zoology
Title: Radar Studies on Bird Migration

1965 Ph.D. (summa cum laude)
Dept. of Zoology (Prof. E. Hadorn)
Title: Transdetermination of Antennal Discs in *Drosophila*

Professional Experience

1963-1967 Research Associate
University of Zürich (Prof. E. Hadorn)

1967-1968	Postdoctoral fellowship of the Swiss National Science Foundation Yale University (Prof. Alan Garen)
1968-1969	Postdoctoral fellowship from the Jane Coffin Childs Fund Yale University (Prof. Alan Garen)
1967-1969	Visiting Assistant Professor Dept. of Molecular Biophysics, Yale University
1969-1972	Associate Professor Dept. of Anatomy and Dept. of Molecular Biophysics Yale University
1972-2009	Full Professor Dept. of Cell Biology, Biozentrum, University of Basel
2009	Professor emeritus

Academies

National Academy of Sciences USA (Foreign Associate)
 Royal Society London (Foreign Member)
 Académie des Sciences (Foreign Member)
 Royal Swedish Academy of Sciences
 Deutsche Akademie der Naturforscher Leopoldina
 Academia Europaea

Professional Societies

Member of

- EMBO (European Molecular Biology Organization)
- EDBO (European Developmental Biology Organization)
- American Association for the Advancement of Science
- The Genetics Society of America
- ISDB (International Society of Developmental Biologists)
- Sigma XI The Scientific Research Society
- Swiss Society for Cell Biology, Molecular Biology and Genetics (ZMG)

American Society for Developmental Biology
 HUGO (The Human Genome Organization)

Editorial Activities

Associate Editor of

- The Journal of Experimental Zoology
- Mechanisms of Development
- Trends in Genetics
- Development, Growth & Differentiation

The International Journal of Developmental Biology

Advisory Boards

Institute of Medical Radiobiology, University of Zürich & Paul Scherrer
Institute
Schlumberger Stiftung, Fondation Les Treilles
National Institute of Genetics, Mishima, Japan

Research Interests

Genetic Control of Development: Homeotic Genes, Cell Determination
and Differentiation, Eye Morphogenesis and Evolution

Special Lectures

1979 Jenkinson Memorial Lecture, Oxford
1985 Ernst Hadorn Lecture, Heidelberg
1985 Sigma Xi Lecture, Yale
1985 Friday Evening Lecture, Woods Hole
1986 Theodor Boveri Lecture, Würzburg
1986 Harvey Lecture, New York
1987 Feulgen Lecture, Basel
1988 Bernard Cohen Lecture, Philadelphia
1990 From DNA to Body Plan, Lectures at the Collège de France
1990 Jean Brachet Lecture, Bruxelles
1992 Nirenberg Symposium "Genes and Development: 25 years after
deciphering the genetic code", Bethesda/Maryland
1993 Terry Lectures at Yale University
1994 Werner Heisenberg Vorlesung der Siemens Stiftung München
1994 Darwin Prize Lecture Series, University of Edinburgh
1995 Runnström Lecture, University of Stockholm
1995 International Institute of Advanced Studies, Kyoto
1996 10. Hartmann Müller-Gedächtnisvorlesung, Zürich
1997 Viktor Hamburger Lecture, Washington University, St. Louis/Missouri
1998 Wolfgang Pauli Lecture, ETH Zürich
1998 The Bourke Lecture, Boston University
1998 Marker Lectures, Pennsylvania State University
1999 Keynote Lecture, European Developmental Biology Conference, Oslo,
Norway
1999 Keynote Lecture, Howard Hughes Meeting, Washington D.C.
1999 Stadtler Lecture, M.D. Anderson Cancer Center, University of Texas
2000 Warner-Lambert Lecture, Society for Neuroscience, Florida
2001 Jeanne Mitchell Watson Lecture, University of Chicago
2002 Keynote Lecture, Combio Conference, Canberra

2002	Dupont Lecture, Research Laboratories, Division of Neurobiology,
2003	Arizona
2004	Rachford Lecture, Children's Hospital Research Foundation, Cincinnati
2004	Inaugural Lecture for the Academic Year 2003, University of Costa Rica
2004	Edds Lecture, Brown University, Providence, Rhode Island
2005	Norman Giles Lecture, Athens, Georgia
2005	Keynote Lecture, Genomes and Evolution 2004, Pennsylvania State
2006	University
	Les Rencontres d'ISIS, Strasbourg
2007	Peter-Hemmerich-Vorlesung, Konstanz
2007	Woolsey Lecture, Center for Neuroscience Lecture Series, University of
	Wisconsin
	Vienna, Darwin Lecture Series, University of Vienna, Austria
	Mendel Lectures, Augustinian Abbey, Academy of Sciences, Brno, Czech
	Republic

Honors

1985	Frank Lillie Fellow, Marine Biological Laboratory, Woods Hole
1986	Election to the US National Academy of Sciences
1987	Election to the American Academy of Arts and Sciences
1987	Election to the Leopoldina (Deutsche Akademie der Naturforscher)
1989	Election to the Academia Europaea
1989	Election to the Royal Swedish Academy of Sciences
1991	Election to the Fellow of the American Assoc. Adv. Sciences (AAAS)
1994	Orden pour le Mérite für Wissenschaften und Künste,
	Bundesministerium des Inneren, Deutschland
1997	Election to Foreign Member of The Royal Society of London for
	Improving Natural Knowledge
1998	Election to the French "Académie des Sciences"
2003	Dr. med. honoris causa, University of Torino, Italy
2003	Dr. med. honoris causa, Universität Nuevo León, Mexico
2007	Ehrenmitgliedschaft Naturforschende Gesellschaft, Basel
2007	Dr. honoris causa de l'Université Pierre et Marie Curie (UPMC) en
2008	Sorbonne
2009	Dr. honoris causa of the University of Salento, Italy
2010	Dr. honoris causa of the University of Barcelona
	Grosses Bundesverdienstkreuz mit Stern der Bundesrepublik
	Deutschland

Prizes

1982	Otto Naegeli-Prize
1986	Warren Triennial Prize (Harvard Medical School)
1986	Dr. Albert Wander Preis (Wander AG. Bern)
1986	Prix Charles-Léopold Mayer (Institut de France, Paris)

1987	Prix Louis Jeantet de Médecine (Fondation Jeantet Genève)
1987	Gairdner Foundation International Award (Canada)
1993	Prix d'Honneur Science pour l'Art, Moët Hennessy-Louis Vuitton, Paris
1995	Runnström Medal, Stockholm
1996	1994-95 AAAS Newcomb Cleveland Prize for outstanding research article
1996	in <i>Science</i>
1996	Otto Warburg-Medaille 1996, Gesellschaft für biologische Chemie (GBCh) Munich
1997	Prix Paul Wintrebert, Université Pierre & Marie Curie, Laboratoire Arago,
1997	Banyuls-sur-Mer, France
	Mendel-Medal, Deutsche Akademie der Naturforscher Leopoldina
2000	March of Dimes Prize in Developmental Biology, awarded by March of
2000	Dimes Birth Defects Foundation, White Plains, NY
2000	Karl Ritter Von Frisch-Medaille 2000, Deutsche Zoologische Gesellschaft,
2001	Bonn
2002	Kyoto Prize, The Inamori Foundation, Japan
	Preis der Alfred Vogt Stiftung zur Förderung der Augenheilkunde, Zürich
2004	Premio Balzan, Fondazione Internazionale Premio E. Balzan for
	Developmental Biology
	Alexander Kowalevsky Medal, St. Petersburg Society of Naturalists, St.
	Petersburg, Russia

Publikationen

Suga, H., Tschopp, P., Graziussi, D.F., Stierwald, M., Schmid, V. & Gehring, W.J. (2010). Flexibly deployed Pax genes in eye development at the early evolution of animals demonstrated by studies on a hydrozoan jellyfish. *Proc. Natl. Acad. Sci. USA* **107**: 14263-14268.

Vukojevic, V., Papadopoulos, D.K., Terenius, L., Gehring, W.J. & Rigler, R. (2010). Quantitative study of synthetic Hox transcription factor-DNA interactions in live cells. *Proc. Natl. Acad. Sci. USA* **107**: 4093-4098.

Papadopoulos, D.K., Vukojevic, V., Adachi, Y., Terenius, L., Rigler, R. & Gehring W.J. (2010). Function and specificity of synthetic Hox transcription factors in vivo. *Proc. Natl. Acad. Sci. USA* **107**: 4087-4092.

Gehring, W.J. and Seimiya, M. (2010). Eye Evolution and the Origin of Darwin's Eye Prototype. *Italian Journal of Zoology* **77**: 124-136.

Walter J. Gehring (2009). Neue Perspektiven über die Entwicklung und Evolution der Augen. *Mitt. Naturforsch. Ges. Basel* **11**, 215-230.

Grieder, N.C., Morata, G., Affolter, M. and Gehring, W.J. (2009). *spalt major* controls the development of the notum and of wing hinge primordia of the *Drosophila melanogaster* wing imaginal disc. *Dev Biol.* **329**: 315-326.

Walter J. Gehring (2009). Neue Perspektiven über die Entwicklung und Evolution der Augen. *Mitt. Naturforsch. Ges. Basel* **11**, 215-230.

Grieder, N.C., Morata, G., Affolter, M. and Gehring, W.J. (2009). *spalt major* controls the development of the notum and of wing hinge primordia of the *Drosophila melanogaster* wing imaginal disc. *Dev Biol.* **329**: 315-326

Blanco, J., Seimiya, M., Pauli, T., Reichert, H., and Gehring, W.J. (2009). Wingless and Hedgehog signaling pathways regulate orthodenticle and eyes absent during ocelli development in *Drosophila*. *Dev Biol.* **329**: 104-115.

Gehring, W.J., Kloter, U., and Suga, H. (2009). Evolution of the Hox Gene Complex from an Evolutionary Ground State. A contribution of HOX GENES, a volume of Current Topics in Developmental Biology, edited by Olivier Pourquie. Vol. **88**: 35-61.

Plaza, S., Prince, F., Adachi, Y., Punzo, C., Cribbs, D. and Gehring, W.J. (2008). Cross-regulatory Protein-Protein Interactions between Hox and Pax Transcription factors. *Proc. Natl. Acad. Sci. USA* **105**: 13439-13444.

Blanco, J. and Gehring, W.J. (2008). Analysis of twin of eyeless during early embryogenesis in *Drosophila melanogaster*. *Gene Expr Pattern* **8**: 523-527.

Clements, J., Lu, Z., Gehring, W.J., Meinertzhagen, I.A., and Callaerts, P. (2008). Central projections of photoreceptor axons originating from ectopic eyes in *Drosophila*. *Proc. Natl. Acad. Sci. USA* **105**: 8968 – 8973.

Prince, F., Katsuyama, T., Oshima, Y., Plaza, S., Resendez-Perez, D., Berry, M., Kurata, S. and Gehring, W.J. (2008). The YPWM-motif links Antennapedia to the basal transcriptional machinery. *Development*, **135**: 1669-1679.

Suga, H., Schmid, V., Gehring, W.J. (2008). Evolution and functional diversity of jellyfish opsins. *Curr Biol*, **18**: 51-55.

Wehner, R. und Gehring, W.J. (2007). *Zoologie*, 24. Auflage, Georg Thieme Verlag KG, Stuttgart.

Vuilleumier, R., Boeuf, G., Fuentes, M., Gehring, W.J. and Falcón, J. (2007). Cloning and early expression pattern of two melatonin biosynthesis enzymes in the turbot (*Scophthalmus maximus*). *Eur J Neurosci*, **25**: 3047-3057.

Grieder, N.C., Charlafti, I., Kloter, U., Jäckle, H., Schäfer, U. and Gehring, W.J. (2007). Misexpression screen in *Drosophila melanogaster* aiming to reveal novel factors involved in formation of body parts identifies abrupt. *Genetics*, **175**: 1707-1718.

Gehring, W.J. (2007). The Homeobox as a key for understanding the principles of the genetic control of development. Chapter in book: *Hox Gene Expression* by Dr. S. Papageorgiou. Chapter 1. Landes Bioscience and Springer Science + Business Media.

Vuilleumier, R., Besseau, L., Boeuf, G., Piparelli, A., Gothilf, Y., Gehring, W.J., Klein, D.C. and Falcón, J. (2006). Starting the Zebrafish Pineal Circadian Clock with a Single Photic Transition. *Endocrinology*, **147**: 2273-2279.

Kobayashi, M., Michaut, L., Ino, A., Ghangrekar, I., Nakajima, T., Takahashi, K., Ueda, R., Saigo, K., Gehring, W.J. and Furukubo-Tokunaga, K. (2006). A Genome-Wide Survey of *Drosophila* Mushroom Body Transcripts with Chemical Ablation. *Proc Natl Acad USA*, **103, 14417-14422.**

Cottet, S., Michaut, L., Boisset, G., Arsenijevic, Y., Schlecht, U., Munier, F.L., Gehring, W.J. and Schorderet D.F. (2005). Biological characterization of gene response in *Rpe65*^{-/-} mouse model of Leber's congenital amaurosis during progression of the disease. *FASEB J*, **20**, 2036-2049.

Katsuyama, T., Sugawara, T., Tatsumi, M., Oshima, Y., Gehring, W.J., Aigaki, T., Kurata, S. (2005). Involvement of *winged eye* encoding a chromatin-associated bromo-adjacent homology domain protein in disc specification. *Proc. Natl. Acad. Sci. USA*, **102, 15918-15923.**

Grieder, N.C., Kloter, U. and Gehring, W.J. (2005). Expression of COPI components during development of *Drosophila melanogaster*. *Gene Expr Patterns*, **6**, 11-21.

Pauli, T., Seimiya, M., Blanco, J., Gehring, W.J. (2005). Identification of functional sine oculis motifs in the autoregulatory element of its own gene, in the eyeless enhancer and in the signaling gene hedgehog. *Development*, **132**, 2771-2782.

Blanco, J., Girard, F., Kamachi, Y., Kondoh, H. and Gehring, W.J. (2005). Functional analysis of the chicken $\delta 1$ -*crystallin* enhancer activity in *Drosophila* reveals remarkable evolutionary conservation between chicken and fly. *Development*, **132**, 1895-1905.

Gehring, W.J. (2005). New Perspectives on Eye Development and the Evolution of Eyes and Photoreceptors. *Journal of Heredity*, 96, 171-184.

Gehring, W.J. (2004). Historical Perspective on the Development and Evolution of Eyes and Photoreceptors. *Int. J. Dev. Biol.* **48**, 707-717.

Punzo, C., Plaza, S., Seimiya, M., Schnupf, P., Kurata, S., Jaeger, J. and Gehring W.J. (2004). Functional divergence between eyeless and twin of eyeless in *Drosophila melanogaster*. *Development* **131**, 3943-3953.

Gehring, W.J. (2004). Precis of Edwin G. Conklin's JEZ Article, "Mosaic Development in Ascidian eggs". *J. Exp. Zool.* **301A**: 461-463.

Gehring, W.J. and Rosbash, M. (2003). The Coevolution of Blue-Light Photoreception and Circadian Rhythms. *J. Mol. Evol.* **57**, 286-289.

González-Estévez, C., Momose, T., Gehring, W.J., Saló, E. (2003). Planarian transgenic lines obtained by electroporation using transposon-derived vectors and an eye-specific GFP marker. *Proc. Natl. Acad. Sci. USA* **100**, 14046-14051.

Plaza, S., De Jong, D.M., Gehring, W.J. and Miller, D.J. (2003). DNA-Binding Characteristics of Cnidarian Pax-C and Pax-B Proteins In Vivo and In Vivo: No Simple Relationship With the Pax-6 and Pax-2/5/8 Classes. *J. Exp. Zool. (Mol Dev Evol)* **299 B**, 26-35.

Michaut, L., Flister, S., Neeb, M., White, K., Certa, U. and Gehring, W.J. (2003). Analysis of the eye developmental pathway in *Drosophila* using DNA microarrays. *Proc. Natl. Acad. Sci. USA* **100**, 4024-4029.

Benassayag, C., Plaza, S., Callaerts, P., Clements, J., Romeo, Y., Gehring W.J. and Cribbs, D.L. (2003). Evidence for a direct functional antagonism of the selector genes *proboscipedia* and *eyeless* in *Drosophila* head development. *Development* **130**, 575-586.

Niimi, T., Clements, J., Gehring, W.J., Callaerts, P. (2002). Dominant-Negative Form of the Pax6 Homolog *eyeless* for Tissue-Specific Loss-of-Function Studies in the Developing Eye and Brain in *Drosophila*. *Genesis* **34**, 74-75.

Gehring, W.J., Michaut L. (2002). Deciphering the eye morphogenetic pathway. Uehara Memorial Foundation Symposium 2002. *International Congress Series* **1246**, 83-89.

Tarpin, M., Gehring, W.J., Bièrne, J. (2002). Conversion of a postocellar into an ocellar region as a transdetermination event occurring in adult ribbonworms. *Mech. Dev.* **118**, 39-44.

Walter, N. (2002). From Transdetermination to the Homeodomain at Atomic Resolution. An interview with Walter J. Gehring by Niklaus Walter. *Int. J. Dev. Biol.* **46**, 29-37.

Gehring, W.J. (2002). The genetic control of eye development and its implications for the evolution of the various eye-types. *Int. J. Dev. Biol.* **46**, 65-73.

Onuma, Y., Takahashi, S., Asashima, M., Kurata, S. and Gehring, W.J. (2002). Conservation of Pax 6 function and upstream activation by *Notch* signaling in eye development of frogs and flies. Proc. Natl. Acad. Sci. USA **99**, 2020-2025.

Punzo, C., Seimiya, M., Flister, S., Gehring, W.J. and Plaza S. (2002). Differential interactions of *eyeless* and *twin of eyeless* with the *sine oculis* enhancer. Development **129**, 625-634.

Callaerts, P., Lee, P.N., Hartmann, B., Farfan, C.B., Choy, D.W., Fischbach, K.-F., Gehring, W.J. and de Couet, H.G. (2002). HOX genes in the sepiolid squid *Euprymna scolopes*: implications for the evolution of complex body plans. Proc. Natl. Acad. Sci. USA **99**, 2088 – 2093.

Gehring, W.J. (2000). Ein tiefer Blick in die Entwicklung und Evolution der Augen. Eine besondere Dankesrede. Zoologie, Mitt. DZG.

Gehring, W.J. (2001). The genetic control of eye development and its implications for the evolution of the various eye-types. Zoology 104, 171-183.

Kammermeier, L., Leemans, R., Hirth, F., Flister, S., Wenger, U., Walldorf, U., Gehring, W.J., Reichert, H. (2001). Differential expression and function of the *Drosophila Pax 6* genes *eyeless* and *twin of eyeless* in embryonic central nervous system development. Mechanisms of Development **103**, 71-78.

Punzo, C., Kurata, S., and Gehring, W.J. (2001). The *eyeless* homeodomain is dispensable for eye development in *Drosophila*. Genes & Development **15**, 1716-1723.

Plaza, S., Prince, F., Jaeger, J., Kloter, U., Flister, S., Benassayag, C., Cribbs, D. and Gehring W.J. (2001). Molecular basis for the inhibition of *Drosophila* eye development by *Antennapedia*. EMBO J. **20**, 802-811.

W. Gehring (2001). Wie Gene die Entwicklung steuern. Birkhäuser, Basel, 275 pp.

Gröger, H., Callaerts, P., Gehring, W.J., Schmid, V., (2000). Characterization and expression analysis of an ancestor-type *Pax* gene in the hydrozoan jellyfish *Podocoryne carnea*. Mechanisms of Development **94**, 157-169.

Berry, M. and Gehring, W.J. (2000). Phosphorylation status of the SCR homeodomain determines its functional activity: essential role for protein phosphatase 2A,B'. EMBO J. **19**, 2946-2957.

Pineda, D, Gonzalez, J., Callaerts, P., Ikeo, K., Gehring, W.J. and Salo, E. (2000). Searching for the prototypic eye genetic network: *sine oculis* is essential for eye regeneration in planarians. Proc. Natl. Acad. Sci. USA **97**, 4525-4529.

Miller, D.J., Hayward, D.C., Reece-Hoyes, J., Scholten, I., Catmull, J., Gehring, W.J., Callaerts, P., Larsen, J.E. and Ball, E. (2000). Pax gene diversity in the basal cnidarian *Acropora millepora* (Cnidaria; Anthozoa): Implications for the evolution of the Pax gene family. Proc. Natl. Acad. Sci. USA **97**, 4475-4480.

Seimiya, M. and Gehring, W. (2000). The *Drosophila* homeobox gene *optix* is capable of inducing ectopic eyes by an *eyeless*-independent mechanism. Development **127**, 1879-1886.

Engels, A., Reichert, H., Gehring, W.J. and Gärtner, W. (2000). Functional expression of a locust visual pigment in transgenic *Drosophila melanogaster*. Eur. J. Biochem. **267**, 1917-1922.

- Kurusu, M., Nagao, T., Walldorf, U., Flister, S., Gehring, W.J. and, Furukubo-Tokunaga, K. (2000). Genetic control of development of the mushroom bodies, the associative learning centers in the *Drosophila* brain, by the *eyeless*, *twin of eyeless*, and *dachshund* Genes. Proc. Natl. Acad. Sci. USA **97**, 2140-2144.
- Kurata, S., Go, M.J., Artavanis-Tsakonas, S. and Gehring, W.J. (2000). *Notch* signalling and the determination of appendage identity. Proc. Natl. Acad. Sci. USA **97**, 2117-2122.
- Gröger, H., Callaerts, P., Gehring, W.J., Schmid, V. (1999). Gene Duplication and Recruitment of a Specific Tropomyosin into Striated Muscle Cells in the Jellyfish *Podocoryne carnea*. Journal of Experimental Zoology (Mol Dev Evol) **285**, 378-386.
- Tarpin, M., Gehring W.J. and Biérne J. (1999). Reverse homeosis in homeotically reconstructed ribbonworms. Proc. Natl. Acad. Sci. USA **96**, 11900-11903.
- Gehring, W.J. and Ikeo, K. (1999). *Pax 6*. Mastering eye morphogenesis and eye evolution. Trends in Genetics **15**, 371-377.
- Niimi, T., Seimiya, M., Kloter, U., Flister, S. and Gehring, W.J. (1999). Direct regulatory interaction of the *eyeless* protein with an eye-specific enhancer in the *sine oculis* gene during eye induction in *Drosophila*. Development **126**, 2253-2260.
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- Janssens, H. and Gehring, W.J. (1999). Isolation and Characterization of *drosocrystallin*, a Lens Crystallin Gene of *Drosophila melanogaster*. Dev. Biol. **207**, 204-214.
- Hauck, B., Gehring, W. J. and Walldorf, U. (1999). Functional analysis of an eye specific enhancer of the *eyeless* gene in *Drosophila*. Proc. Natl. Acad. Sci USA **96**, 564-569.
- Callaerts, P., Munoz-Marmol, A.M., Glardon, S., Castillo, E., Sun, H., Li, W.-H., Gehring, W.J. and Salo, E. (1999). Isolation and expression of a *Pax-6* gene in the regenerating and intact Planarian *Dugesia(G)tigrina*. Proc. Natl. Acad. Sci. USA **96**, 558-563.
- Gehring, W.J. (1998). Master Control Genes in Development and Evolution: The Homeobox Story. Yale University Press New Haven, USA, pp. 236.
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- Glardon, S., Holland, L.Z., Gehring, W.J. and Holland N.D. (1998). Isolation and developmental expression of the amphioxus *Pax-6* gene (*AmphiPax-6*): insights into eye and photoreceptor evolution. Development **125**, 2701-2710.
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- Kmita-Cunisse, M., Loosli, F., Bièrne, J. and Gehring, W.J. (1998). Homeobox genes in the ribbonworm *Lineus sanguineus*: Evolutionary implications. *Proc. Natl. Acad. Sci. USA* **95**, 3030-3035.
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- Gehring, W.J. (1997). The discovery of the homeobox in retrospective. IX Taniguchi Symposium on Developmental Biology "Developmental Biology in Half a Century", Kyoto/Japan
- Yamamoto, Y., Girard, F., Bello, B., Affolter, M. and Gehring, W.J. (1997). The *cramped* gene of *Drosophila* is a member of the *Polycomb*-group, and interacts with *mus209*, the gene encoding proliferating cell nuclear antigen. *Development* **124**, 3385-3394.
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