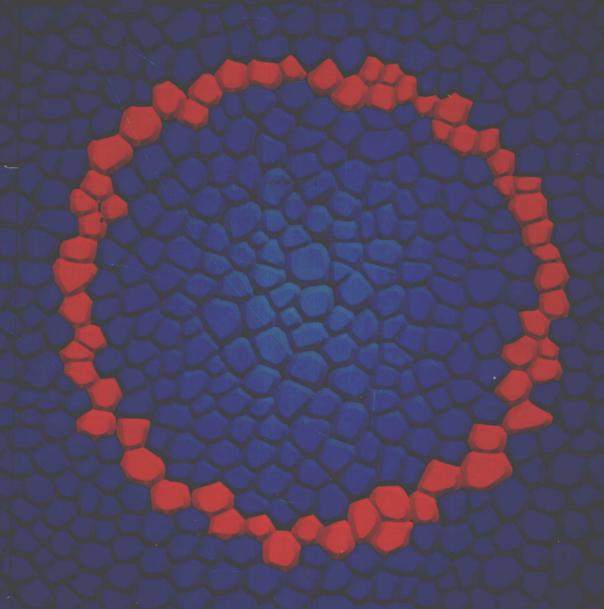
# PRINCIPLES OF DEVELOPMENT



### Lewis Wolpert

Rosa Beddington • Jeremy Brockes • Thomas Jessell
Peter Lawrence • Elliot Meyerowitz

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The cover represents cells communicating positional information and cell identity by production of a diffusion gradient in a signaling molecule. At a threshold concentration, cells are triggered to differentiate, thus expressing a new phenotype. Design by Matthew McClements.

### **Preface**

Developmental biology is at the core of all biology. It deals with the process by which the genes in the fertilized egg control cell behavior in the embryo and so determine its pattern, its form, and much of its behavior. The progress in developmental biology in recent years with the applications of advances in cell and molecular biology, has been remarkable and an enormous amount of information is now available.

Principles of Development is designed for undergraduates as well as graduates, and the emphasis is on principles and key concepts. Central to our approach is that development can be best understood by understanding how genes control cell behavior. We have assumed that the students have some very basic familiarity with cell biology and genetics, but all key concepts, like the control of gene activity, are explained in the text.

Conscious of the pressures on students, we have tried to make the principles as clear as possible and to provide numerous summaries, both in words and in pictures. The illustrations in the book are a special feature and have been carefully designed and chosen to illuminate both experiments and mechanisms.

We have resisted the temptation to cover every aspect of development and have, instead, focused on those systems that best illuminate common principles. Indeed a theme that runs throughout the book is that universal principles govern the process of development. At all stages, what we included has been guided by what we believe undergraduates should know about development.

We have thus concentrated our attention on vertebrates and *Drosophila*, but not to the exclusion of the other systems, such as nematodes and sea urchins, where they best illustrate a concept. An important feature of our book is the inclusion of the development of plants, which is usually neglected in text books. There have been striking advances in plant developmental biology in recent times, and some unique and important features have emerged. As knowing the basic features of the embryology of the main organisms used to study development is essential for an understanding of molecular mechanisms, we have introduced embryology at an early stage.

Whereas our emphasis has been on the laying down of the body plans and organ systems, such as limbs and the nervous system, we have also included later aspects of development, including growth and regeneration. The book concludes with a consideration of evolution and development.

In providing references, our prime concern has been to guide the students to helpful papers rather than giving credit to the scientists who have made major contributions: to those whom we have neglected, we apologize.

The way the book was written was rather special. Although I was in continual consultation with my co-authors, I did all the writing—and I mean writing, which was skillfully typed by Maureen Moloney. Each chapter was also reviewed by a number of experts (see page xv), to whom we give thanks. The text was initially edited, and often re-written, by Eleanor Lawrence, whose expertise and influence pervades the book. Further critical editing was carried out by Hazel Richardson. And Huw Woodman magically turned the whole text into finished pages.

Central to the book are the illustrations, which were brilliantly created or adapted by Matthew McClements. The whole complex project was masterfully managed by Giles Montier. Particularly to Giles and Matthew, I offer my thanks for their patient dealing with my impatience and incompetence. The complete team was a pleasure, even fun, to work with.

Finally my thanks to Peter Newmark, the head of Current Biology Ltd., and to Vitek Tracz, the head of the Current Science Group; without them, the book would never have been started, let alone completed.

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- Fig. 2.24, illustration after Hogan, B., Beddington, R., Costantini, F., Lacy, E.: *Manipulating the Mouse Embryo: A Laboratory Manual, 2nd edition.* New York: Cold Spring Harbor Laboratory Press, 1994.
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- Fig. 2.38, illustration after Sulston, J.E., Schierenberg, E., White, J.G., Thomson, J.N.: The embryonic cell lineage of the nematode *Caenorhabditis elegans. Dev. Biol.* 1983, **100**:64–119.
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### Chapter 3

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### Chapter 4

- Fig. 4.6, illustration after Johnson, R.L., Laufer, E., Riddle, R.D., Tabin, C.: Ectopic expression of *Sonic hedgehog* alters dorsal-ventral patterning of somites. *Cell* 1994, **79**:1165–1173.
- Box 4A, illustration after Coletta, P.L., Shimeld, S.M., Sharpe, P.T.: The molecular anatomy of Hox gene expression. *J. Anat.* 1994, **184**:15–22.
- Fig. 4.10, illustration after Burke, A.C., Nelson, C.E., Morgan, B.A., Tabin, C.: Hox genes and the evolution of vertebrate axial morphology. *Development* 1995, **121**: 333–346.
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- Fig. 4.17, illustration after Kelly, O.G., Melton, D.A.: Induction and patterning of the vertebrate nervous system. *Tr. Genet.* 1995, 11:273–278.
- Fig. 4.18, illustration after Kintner, C.R., Dodd, J.: Hensen's node induces neural tissue in *Xenopus* ectoderm. Implications for the action of the organizer in neural induction. *Development* 1991, 113:1495–1505.

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- Fig. 4.20, illustration after Doniach, T., Phillips, C.R., Gerhart, J.C.: Planar induction of antero-posterior pattern in the developing central nervous system of *Xenopus laevis*. *Science* 1992, **257**: 542–545.
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- Fig. 5.12, illustration after González-Reyes, A., Elliott, H., St. Johnston, D.: Polarization of both major body axes in *Drosophila* by *gurken-torpedo* signalling. *Nature* 1995, **375**:654–658.
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### Chapter 6

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- Fig. 6.11, illustration after Wilmer, P. *Invertebrate Relationships*. Cambridge: Cambridge University Press, 1990.
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- Fig. 6.15, illustration after Bissen, S.T., Smith, C.M.: Unequal cleavage in leech embryos: zygotic transcription is required for correct spindle orientation in a subset of early blastomeres. *Development* 1996, 122:599–606.
- Fig. 6.17, illustration after Wedeen, C.J., Weisblat, D.A.: Segmental expression of an engrailed-class gene during early development and neurogenesis in an annelid. *Development* 1991, 113:805–814.
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- Fig. 6.29, illustration after Nakatani, Y., Yasuo, H., Satoh, N., Nishida, H.: Basic fibroblast growth factor induces notochord formation and the expression of *As-T*, a *Brachyury* homolog, during ascidian embryogenesis. *Development* 1996, **122**:2023–2031.
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### Chapter 7

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- Fig. 7.8, illustration after Alberts, B., Bray, D., Lewis, J., Raff, M., Roberts, K., Watson, J.D.: *Molecular Biology of the Cell, 2nd edition.* New York: Garland Publishing, 1989.
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- Fig. 7.25, illustration after Coen, E.S., Meyerowitz, E.M.: The war of the whorls: genetic interactions controlling flower development. *Nature* 1991, 353:31–37.

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- Fig. 8.38, illustration after Alberts, B., Bray, D., Lewis, J., Raff, M., Roberts, K., Watson, J.D.: *Molecular Biology of the Cell, 2nd edition*. New York: Garland Publishing, 1989.
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### Chapter 9

- Fig. 9.1, illustration after Friederich, E., Prignault, E., Arpin, M., Louvard, D.: From the structure to the function of villin, an actin-binding protein of the brush border. *BioEssays* 1990, **12**:403–408.
- Fig. 9.5, illustration after Okada, T.S.: *Transdifferentiation*. Oxford: Clarendon Press, 1992.
- Fig. 9.6, illustration after Doupe, A.J., Landis, S.C., Patterson, P.H.: Environmental influences in the development of neural crest derivatives: glucocorticoids, growth factors, and chromaffin cell plasticity. *J. Neurosci.* 1985, 5:2119–2142.
- Fig. 9.7, illustration after Janeway, C.A., Travers, P.: Immunobiology: The Immune System in Health and Disease, 3rd edition. London: Current Biology/Garland, 1997.
- Fig. 9.8, illustration after Janeway, C.A., Travers, P.: Immunobiology: The Immune System in Health and Disease, 3rd edition. London: Current Biology/Garland Publishing, 1997.
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- Fig. 9.11, illustration after Alberts, B., Bray, D., Lewis, J., Raff, M., Roberts, K., Watson, J.D.: Molecular Biology of the Cell, 2nd edition. New York: Garland Publishing, 1989.
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- Fig. 9.29, illustration after Doupe, A.J., Landis, S.C., Patterson, P.H.: Environmental influences in the development of neural crest derivatives: glucocorticoids, growth factors, and chromaffin cell plasticity. *J. Neurosci.* 1985, 5:2119–2142.

### Chapter 10

- Box 10A, top illustration after Meinhardt, H., Gierer, A.: **Applications** of a theory of biological pattern formation based on lateral inhibition. *J. Cell Sci.* 1974, **15**:321–346.
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- Fig. 10.42, illustration after Horvitz, H.R., Sternberg, P.W.: Multiple intercellular signalling systems control the development of the *Caenorhabditis elegans* vulva. *Nature* 1991, **351**:535–541.

### Chapter 11

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- Fig. 11.5, illustration after Campuzano, S., Modolell, J.: Patterning of the *Drosophila* nervous system: the achaete-scute gene complex. *Trends Genet.* 1992, 8:202–208.
- Fig. 11.6, illustration after Jan, Y.N., Jan, L.Y.: Genes required for specifying cell fates in Drosophila embryonic sensory nervous system. *Trends Neurosci.* 1990, **13**:493–498.
- Fig. 11.8, illustration after Guo, M., Jan, L.Y., Jan, Y.N.: Control of daughter cell fates during asymmetric division: interaction of Numb and Notch. *Neuron* 1996, 17:27–41.
- Fig. 11.15, illustration after Rakic, P.: Mode of cell migration to the superficial layers of fetal monkey neocortex. *J. Comp. Neurol.* 1972, 145:61–83.
- Fig. 11.18, illustration after Alberts, B., Bray, D., Lewis, J., Raff, M., Roberts, K., Watson, J.D.: *Molecular Biology of the Cell, 2nd edition.* New York: Garland Publishing, 1989.
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- Fig. 11.32, illustration after Davies, A.M.: Neurotrophic factors: switching neurotrophin dependence. *Curr. Biol.* 1994, 4:273–276.
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- Fig. 11.37, illustration after Goodman, C.S., Shatz, C.J.: Developmental mechanisms that generate precise patterns of neuronal connectivity. *Cell Suppl.* 1993, **72**:77–98
- Fig. 11.38, illustration after Goodman, C.S., Shatz, C.J.: Developmental mechanisms that generate precise patterns of neuronal connectivity. *Cell Suppl.* 1993, **72**:77–98

Fig. 11.39 illustration after Kandell, E.R., Schwartz, J.H., Jessell, T.M.: Essentials of Neural Science and Behavior. Norwalk, Connecticut: Appleton & Lange, 1991.

Fig. 11.40, illustration after Goodman, C.S., Shatz, C.J.: Developmental mechanisms that generate precise patterns of neuronal connectivity. *Cell Suppl.* 1993, **72**:77–98

### Chapter 12

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Fig. 12.3, illustration after Higgins, S.J., Young, P., Cunha, G.R.: Induction of functional cytodifferentiation in the epithelium of tissue recombinants II. Instructive induction of Wolffian duct epithelia by neonatal seminal vesicle mesenchyme. *Development* 1989, 106:235–250.

Fig. 12.7, illustration after Cline, T.W.: The *Drosophila* sex determination signal: how do flies count to two? *Trends Genet.* 1993 9:385–390.

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Fig. 12.22, illustration after Alberts, B., Bray, D., Lewis, J., Raff, M., Roberts, K., Watson, J.D.: *Molecular Biology of the Cell, 2nd edition.* New York: Garland Publishing, 1989.

### Chapter 13

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Fig. 13.20, illustration after French, V., Bryant, P.J., Bryant, S.V.: Pattern regulation in epimorphic fields. *Science* 1976, 193:969–981.

Fig. 13.21 illustration after French, V., Bryant, P.J., Bryant, S.V.: Pattern regulation in epimorphic fields. *Science* 1976, 193:969–981.

### Chapter 14

Fig. 14.3, illustration after Edgar, B.A., Lehman, D.A., O'Farrell, P.H.: Transcriptional regulation of *string* (*cdc25*): a link between developmental programming and the cell cycle. *Development* 1994, 120:3131–3143.

Fig. 14.5, illustration after Gray, H.: *Gray's Anatomy*. Edinburgh: Churchill-Livingstone, 1995.

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Fig. 14.12, illustration after Alberts, B., Bray, D., Lewis, J., Raff, M., Roberts, K., Watson, J.D.: *Molecular Biology of the Cell, 2nd edition*. New York: Garland Publishing, 1989.

Fig. 14.18, illustration after Tata, J.R.: Gene expression during metamorphosis: an ideal model for post-embryonic development. *BioEssays* 1993, **15**: 239–248.

Fig. 14.19, illustration after Tata, J.R.: Gene expression during metamorphosis: an ideal model for post-embryonic development. *BioEssays* 1993, 15: 239–248.

### Chapter 15

Fig. 15.2, illustration after Larsen, W.J.: *Human Embryology*. New York: Churchill Livingstone, 1993.

Fig. 15.3, illustration after Romer, A.S.: *The Vertebrate Body*. Philadelphia: W.B. Saunders, 1949.

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Fig. 15.6, illustration after Coates, M.L.: Limb evolution: fish fins or tetrapod limbs—a simple twist of fate? *Curr. Biol.* 1995, 5:844–848.

Fig. 15.9, illustration after Garcia-Fernández, J., Holland, P.W.: Archetypal organization of the amphioxus Hox gene cluster. *Nature* 1994 370: 563–566.

Fig. 15.10, illustration after Akam, M.: Hox genes and the evolution of diverse body plans. *Phil. Trans. Roy. Soc. Lond. B* 1995, **349**:313–319.

Fig. 15.11, illustration after Ferguson, E.L.: Conservation of dorsal-ventral patterning in arthropods and chordates. *Curr. Opin. Genet. Dev.* 1996, **6**:424–431.

Fig. 15.12, illustration after Gregory, W.K.: *Evolution Emerging*. New York: Macmillan, 1957.

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