

Plant Development



Edited by
Marja Timmerman



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Plant Development

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Edited by

MARJA C. P. TIMMERMANS
Cold Spring Harbor Laboratory
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30 Corporate Drive, Suite 400, Burlington, MA 01803, USA
32, Jamestown Road, London NW1 7BY, UK
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First edition 2010

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ISBN: 978-0-12-380910-0
ISSN: 0070-2153

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CONTENTS

<i>Contributors</i>	<i>xi</i>
<i>Preface</i>	<i>xv</i>
1. Green Beginnings – Pattern Formation in the Early Plant Embryo	1
Cristina I. Llavata Peris, Eike H. Rademacher, and Dolf Weijers	
1. Introduction–Seeds and Embryos	2
2. Landmarks of Embryo Pattern Formation	5
3. Regulation of Embryo Pattern Formation	8
4. Evolutionary Aspects of Plant Embryogenesis	20
5. Concluding Remarks	22
Acknowledgments	22
References	23
2. Light-Regulated Plant Growth and Development	29
Chitose Kami, Séverine Lorrain, Patricia Hornitschek, and Christian Fankhauser	
1. Multiple Photoreceptors to Sense a Variety of Light Colors and Intensities	30
2. Physiological Responses Mediated by Plant Photoreceptors	41
3. Photomorphogenesis in a Changing Environment	47
4. Sites of Perception and Action of a Light Signal	50
5. Signal Transduction	52
6. Concluding Remarks	58
References	58
3. Root Development–Two Meristems for the Price of One?	67
Tom Bennett and Ben Scheres	
1. Introduction	68
2. Structure of the Root	68
3. Ontogeny of Roots	70
4. The Root Stem Cell Niche	76
5. The Meristematic Zone	87
6. Elongation	93

7. Differentiation	95
8. Concluding Remarks	96
References	96
4. Shoot Apical Meristem Form and function	103
Chan Man Ha, Ji Hyung Jun, and Jennifer C. Fletcher	
1. Introduction	104
2. Shoot Apical Meristem Organization	104
3. Shoot Apical Meristem Maintenance	107
4. Lateral Organ Initiation	116
5. Phyllotaxis	119
6. Communication Between the SAM and Differentiated Tissues	122
7. Floral Meristem Termination	124
8. Live Imaging and Computational Modeling Technology	127
9. Concluding Remarks	129
References	129
5. Signaling Sides: Adaxial–Abaxial Patterning in Leaves	141
Catherine A. Kidner and Marja C. P. Timmermans	
1. Leaves Evolved Late in Land Plant History	142
2. Leaves Develop from a Patterned Meristem	142
3. Maintaining Polarity beyond the Meristem	143
4. Determinants of Adaxial Fate— <i>PHANTASTICA</i>	145
5. Determinants of Adaxial Fate—The HD-ZIPIII Genes	147
6. Regulation of HD-ZIPIII Activity	148
7. Determinants of Abaxial Fate—The KAN Genes	150
8. Determinants of Abaxial Fate—The AUXIN RESPONSE FACTORS	152
9. Regulation of <i>ARF3</i> and <i>ARF4</i> by the <i>TAS3</i> ta-siRNA Pathway	152
10. How Are These Polarized Gene Expression Domains Established?	155
11. Maintenance of Organ Polarity—Cross-Talk between Polarity Determinants	157
12. Downstream Genes Regulating Medio-Lateral Blade Outgrowth	158
13. Why So Complicated?	160
Acknowledgments	162
References	162
6. Evolution Of Leaf Shape: A Pattern Emerges	169
Daniel Koenig and Neelima Sinha	
1. Introduction	170
2. Determinacy and Leaf Dissection	170

3. The Patterning of Growth During Leaf Development	172
4. The Role of Auxin in Leaf Patterning	174
5. What Distinguishes Lobes, Leaflets, and Blade?	175
6. The Perception of Auxin Maxima and Specification of Differential Growth	178
7. Homologies in Leaf Development	179
Acknowledgments	181
References	181
7. Control of Tissue and Organ Growth in Plants	185
Holger Breuninger and Michael Lenhard	
1. Introduction	186
2. Description of Organ Growth	187
3. Proliferative Growth Control	190
4. Growth by Cell Elongation	202
5. Compensation	205
6. Coordination of Growth Across and Within Tissue Layers	207
7. Modulation of Growth by Environmental Signals	210
8. Modeling Plant Growth	211
9. Concluding Remarks	213
References	214
8. Vascular Pattern Formation in Plants	221
Enrico Scarpella and Ykä Helariutta	
1. Introduction	222
2. The Plant Vascular System	223
3. Origin of Vascular Tissues	225
4. Levels of Vascular Organization	225
5. Control of Longitudinal Vascular Patterning and Integration with Organ Formation	227
6. Regulation of Radial Vascular Patterning	244
7. Concluding Remarks	251
Acknowledgments	253
Note Added in Proof	253
References	253
9. Stomatal Patterning and Development	267
Juan Dong and Dominique C. Bergmann	
1. Introduction	268
2. The Signaling Cascade: From Extracellular Signals to Nuclear Factors	270

3. Signaling through a MAP Kinase Module	278
4. Transcription Factors	282
5. Regulation of Stomatal Asymmetric Cell Division	288
6. Concluding Remarks	293
7. Key Conclusions	293
References	293
10. Trichome Patterning in <i>Arabidopsis thaliana</i>: From Genetic to Molecular Models	299
Rachappa Balkunde, Martina Pesch, and Martin Hülskamp	
1. Introduction	300
2. Trichome Form and Function in Plants	300
3. Trichome Development in <i>Arabidopsis thaliana</i>	301
4. Random Versus Regulated Trichome Pattern	302
5. Genetic Analysis of the Core Patterning Machinery	302
6. Genetic Interactions Between the Trichome Initiation Genes	305
7. Expression Patterns of Patterning Genes: An Apparent Paradox	306
8. Protein–Protein Interactions Between Patterning Components	307
9. Transcriptional Cross-Regulation Between Patterning Genes	308
10. Cellular Interactions are Mediated by Intercellular Protein Movement	310
11. Immediate Downstream Genes—or Additional Patterning Components?	311
12. The Role of Chromatin Structure in Patterning	313
13. Modeling the Patterning System—Starting With Two Components	314
14. Modeling the Patterning System: Global Interaction Models versus Solution of Discrete Problems	316
15. Perspective	317
References	317
11. Comparative Analysis of Flowering in Annual and Perennial Plants	323
Maria C. Albani and George Coupland	
1. Introduction	324
2. Control of Flowering in the Annual Model <i>Arabidopsis Thaliana</i>	325
3. Flowering in Perennials	333
4. The Evolution of Plant Life Strategies	340
5. Concluding Remarks	341
References	341

12. Sculpting the Flower; the Role of microRNAs in Flower Development	349
Anwasha Nag and Thomas Jack	
1. miRNAs in Plant Development	350
2. miR172 Functions to Control Genes that Function in both Flowering Time Control and Floral Organ Identity in Arabidopsis	354
3. miR172 Functions to Regulate Inflorescence Development in Maize	361
4. miR156 Regulates Phase Change and Floral Induction	363
5. miR164 Regulates Genes that Function in Organ Boundary Formation	365
6. miR169 Represses C Class Activity in the Perianth in Antirrhinum and Petunia	367
7. <i>miR319a</i> Controls Floral Organ Size and Shape in Arabidopsis	368
8. miR159 Regulates Genes with Broad Roles in Flower Development	369
9. miR167 is Critical for Male and Female Fertility	370
10. Regulation of Floral Organ Polarity by miR166	371
11. Perspective and Future Challenges	371
Acknowledgments	373
References	373
13. Development of Flowering Plant Gametophytes	379
Hong Ma and Venkatesan Sundaresan	
1. Introduction	380
2. Development of the Male Gametophyte or Pollen Grain	380
3. Development of the Female Gametophyte or Embryo SAC	391
4. Double Fertilization: Signaling and Reception between Male and Female	400
5. Concluding Remarks	403
References	404
<i>Subject Index</i>	413
<i>Contents of Previous Volumes</i>	423

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PREFACE

This book captures many of the major advances made in the field of plant developmental biology. Over the past 20 years, genetic screens in *Arabidopsis* and other species have yielded a wide array of developmental mutants whose analyses have greatly enhanced our understanding of plant morphogenesis. Perhaps because of an initial focus on mutants with clearly defined, non-pleiotropic phenotypes, transcription factors were prominently represented among the first genes isolated from these screens. The field has matured to a point, however, that complex networks comprising signal transduction pathways, transcription factors, and downstream target genes are becoming clear for an ever-increasing number of developmental processes. Significant progress has been made on analysis of the mobile positional signals critical to plant development, which has long remained a main challenge in contemporary plant development. Moreover, by utilizing real-time analyses and computer modeling developmental principles are being elucidated in the context of the whole organ or organism.

Given the wealth of tools and resources available in *Arabidopsis*, the analysis of development has progressed most substantially in this model species. Comparative studies at the molecular and genetic level are beginning to illuminate the history of morphogenesis in plants, revealing evolutionary changes in key molecular players that form the basis for the enormous morphological diversity present within the plant kingdom. Moreover, with the tremendous advances in genomics, more complex systems are becoming accessible. This will allow new insights to be tested in the context of incisive classical experiments that have been the cornerstone of developmental biology, and can provide new interpretations of such formative experiments at the molecular and cellular level. Several of the reviews provide an insight into this new trend.

The chapters presented in this book describe our current knowledge, prospective insights, and key outstanding questions of multiple fundamental facets of plant development. Chapter 1 outlines the formative events that sculpt the organization of the plant body during embryogenesis and discusses the molecular mechanisms that regulate these patterning processes. It emerges that auxin has a profound coordinating role in embryogenesis. One example of this is in the formation of the embryonic root (Chapter 3), where an auxin reflux loop specifies the stem cell niche. This chapter also presents the progress in our understanding of root meristem function, outlining the distinctive properties of stem cells within the root meristem

and the network that controls root growth through the coordinate regulation of cell division and elongation. Germination as well as numerous other developmental transitions and adaptive growth responses are regulated through the perception of light. How plants sense light and coordinate the molecular events underlying photomorphogenesis is presented in Chapter 2. The signaling networks that maintain the position and activity of stem cells within the shoot apical meristem and that organize the initiation of lateral organs on the meristem periphery are discussed in Chapter 4. The complexity of these networks is remarkable, but with the development of live imaging approaches and computational tools, our understanding of the central principles of shoot apical meristem function has rapidly advanced.

The next three chapters focus on patterning, growth, and the morphological diversification of lateral organs in plants. Chapter 5 describes the evolutionary distinct contributions of three highly conserved interlocking pathways to leaf polarity and outlines the unique contributions of mobile small RNAs as positional signals that refine the boundary between the upper and lower sides of the leaf. Chapter 6 compares the mechanisms that regulate leaf shape in simple and compound leafed model species. Auxin is recognized as a key player also in this aspect of development. The emergent picture is one in which developmental pathways that modulate determinacy within the leaf can vary auxin-signaling outputs to generate diverse compound and simple leaf forms. Recent insights into how plant organs reach their characteristic final shape and size are presented in Chapter 7. In addition to the genetic networks that affect organ size at the cellular level by regulating cell proliferation and expansion, insights into the systems that coordinate such cellular processes across the entire organ or modulate them in response to environmental stimuli are discussed.

New insights into the patterning processes that give rise to the precise arrangements of vasculature, stomatal complexes, and trichomes are outlined in Chapters 8 through 10. Interestingly, these tissue or cell patterns are generated through entirely distinct mechanisms. Chapter 8 describes the role of polarized auxin transport in generating the distinctive arrangements of vascular strands within leaves, stems, and roots. In contrast, stereotyped asymmetric cell divisions are at the center of stomatal patterning and, as outlined in Chapter 9, the spacing of such instructive divisions is regulated by signaling pathways involving secreted peptide ligands and receptor-like kinases. Finally, Chapter 10 discusses current models for trichome patterning, presenting evidence for the involvement of two parallel spacing mechanisms; a lateral inhibition mechanism that relies in part on plasmodesmatal movement of trichome inhibitor proteins and an activator-depletion mechanism in which inducers of trichome differentiation are depleted around incipient trichome cells.

Chapter 11 reviews our understanding of the networks that regulate the switch from vegetative growth to flowering in response to intrinsic signals and environmental stimuli in *Arabidopsis thaliana*, and then broadens the discussion to the control of flowering in perennial species. The contribution of miRNAs in regulating the transition to flowering is described in Chapter 12. This chapter also outlines the varied contributions of small regulatory RNAs to the specification of floral organ identity and the control of floral organ shape and size. The final chapter of the book focuses on the progress in understanding the development of the male and the female gametophytes, and their interactions during the process of double fertilization. Signaling molecules and downstream genetic pathways that direct the differentiation of distinct cell types within the developing gametophytes, pollen tube attraction, or fertilization are beginning to emerge. An exciting example is the recent finding that auxin acts as a morphogenic determinant in the patterning of the female gametophyte.

Besides providing timely reviews of new advances in many fundamental aspects of plant development, the chapters presented in this book illustrate clearly the diversity of patterning mechanisms that drive plant morphogenesis. Mobile transcription factors, secreted peptides, hormones, and small regulatory RNAs function as instructive signals feeding into a wide array of signaling pathways and gene regulatory networks. This wealth of new data also allows us to draw parallels with animal development. It is now probably safe to state, rather than speculate, that many of the individual molecular components are either different or wired differently, but that the logic of developmental circuitry is conceptually quite similar between plants and animals. This book is testimony to the progress in our understanding of plant development that has been made in a surprisingly short time.

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GREEN BEGINNINGS – PATTERN FORMATION IN THE EARLY PLANT EMBRYO

Cristina I. Llavata Peris,* Eike H. Rademacher,* and Dolf Weijers

Contents

1. Introduction—Seeds and Embryos	2
2. Landmarks of Embryo Pattern Formation	5
2.1. Formation of the apico-basal axis	5
2.2. Outside versus inside—radial pattern establishment	7
2.3. Stem cell niches—sources of all other cells	7
2.4. Initiation of cotyledons	7
3. Regulation of Embryo Pattern Formation	8
3.1. Auxin biosynthesis, transport, and response	8
3.2. Specification of the apico-basal axis	10
3.3. Establishment of the radial pattern	13
3.4. Initiation of meristems	16
3.5. Cotyledon initiation	18
4. Evolutionary Aspects of Plant Embryogenesis	20
5. Concluding Remarks	22
Acknowledgments	22
References	23

Abstract

Embryogenesis in plants transforms the zygote into a relatively simple structure, the seedling, which contains all tissues and organs that later form the mature plant body. Despite a profound diversity in cell division patterns among plant species, embryogenesis yields remarkably homologous seedling architectures. In this review, we describe the formative events during plant embryogenesis and discuss the molecular mechanisms that regulate these processes, focusing on *Arabidopsis*. Even though only a relatively small number of factors are known that regulate each patterning step, a picture emerges where locally acting transcription factors and intercellular signaling contribute to the specification and spatio-temporal coordination of the various cell types in the embryo.

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Current Topics in Developmental Biology, Volume 91
ISSN 0070-2153, DOI 10.1016/S0070-2153(10)91001-6

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Notably, several patterning processes are controlled by the plant hormone auxin. Most regulators that were identified in *Arabidopsis* have orthologs in other sequenced plant genomes, and several of these are expressed in similar patterns. Therefore, it appears that robust conserved mechanisms may underlie pattern formation in plant embryos.

1. INTRODUCTION—SEEDS AND EMBRYOS

During evolution, plants as largely immobile organisms have developed sophisticated mechanisms to disperse their offspring and explore new habitats. One way to expand the populated area is to grow into the surrounding by means of vegetative propagation via specialized structures such as rhizomes or stolons. However, these mechanisms do not reach over great distances and fail to overcome relatively small obstacles.

The innovation that surpassed such restrictions and allowed plants to use wind, water, animals, gravity, and even ballistic mechanisms as means of dispersal is the seed. Furthermore, seeds permit the enclosed embryo to remain in a dormant state and survive long periods of harsh environmental conditions, thereby mastering not only spatial but also temporal restrictions to its habitat. Finally, when conditions are beneficial for germination, the seed provides the embryo with the nutrients that support the first steps of post-embryonic development. To fulfill all of these different requirements, seeds develop in very different shapes and sizes. Adaptations in seed morphology have enabled plants to occupy new ecological niches with the result that plants now dominate habitats on all different kinds of land, in both hot and cold climates (Kessler and Stuppy, 2006).

Seed-bearing plants (spermatophytes) can be subdivided into two major groups: gymnosperms and angiosperms. The name-giving difference between these lies in the organization of the reproductive organs. Gymnosperms bear ovules on scales, which are usually in cone-like structures as, for example, in pine. Angiosperms instead have their reproductive organs arranged in flowers. Another important difference is that flowering plants feature a double fertilization step to produce the (typically) diploid embryo and the triploid extra-embryonic endosperm (Lersten, 2004). Despite these differences in seed anatomy and function, the development and basic body organization of the embryo are very similar among most higher plants (Cairney and Pullman, 2007; Johri *et al.*, 1992). Accordingly, embryogenesis in both groups undergoes three common phases. Initially the fertilized egg cell (zygote) undergoes elongation and after a few cell division rounds develops an apico-basal and radial axis. During the next phase, further cell divisions occur and the primordia of the fundamental organs for post-embryonic growth are established. A final phase of desiccation prepares the mature

embryo for dormancy and equips the seed with storage products that aid the seedling in the process of germination (Bewley and Black, 1994).

Typically, seeds carry a single embryo that emerges as the product of fertilization of the egg cell (Fig. 1.1, box 1). However, the formation of poly-embryonic seeds has been observed in many taxa (e.g., *Rutacea* (Citrus) or *Pinacea* (Pinus); Batygina and Vinogradova, 2007; Lakshmanan and Ambegaokar, 1984). Interestingly, the additional embryos within seeds do not always originate from cells that are derived from the zygote. More importantly, this is not even obligatory in mono-embryonic seeds. Hence, also unfertilized cells possess the potential to form embryos within a seed. Such asexual reproductive mechanisms of embryo formation have been summarized under the term *apomixis* (Fig. 1.1, box 2). We refer the reader to another review (Koltunow and Grossniklaus, 2003) that covers the various developmental origins of apomictic embryos. In addition to the naturally occurring origins of embryogenesis, male gametes (pollen grains) can give rise to viable but haploid embryos when cultured under certain

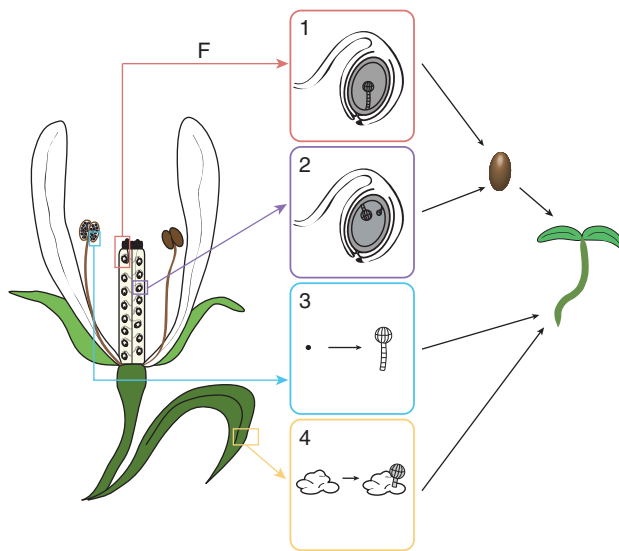


Figure 1.1 Origins of plant embryos. Embryogenesis normally occurs in the reproductive tissues within the flower. Shown here is a flower with subtending leaf. Zygotic embryogenesis (box 1) occurs when a pollen grain lands on the stigma of the carpel and fertilizes the egg cell in an ovule contained within the gynoecium. This ovule develops into a seed (brown oval) which, upon germination, generates the seedling (here dicotyledonous). Alternative modes of embryogenesis include the initiation of apomictic embryos within the ovule (box 2), microspore-derived embryos developing from pollen grains (box 3), and somatic embryos that are initiated from callus tissue derived from somatic cells (box 4). While only zygotic and apomictic embryogenesis pass through a seed stage, all these different modes of embryogenesis finally give rise to seedlings with the same body plan.

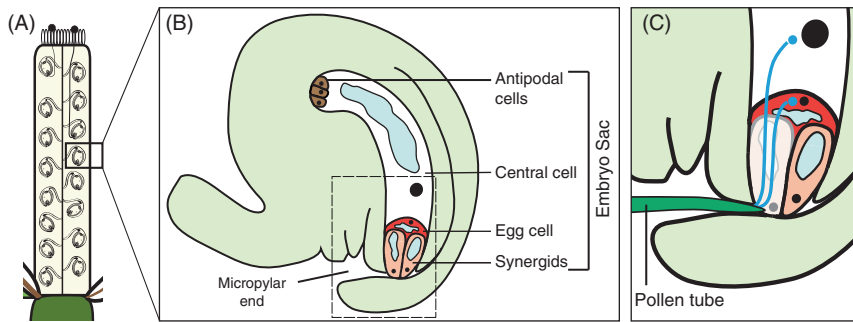


Figure 1.2 Fertilization in *Arabidopsis*. Fertilization occurs within the gynoecium (A), where ovules (B) are attached to the placental tissues. The *Arabidopsis* ovule consists of a gametophyte (embryo sac) covered with somatic integument cell layers. The egg cell, surrounded by two synergid cells, is localized at the micropylar end. Additionally, the embryo sac houses a central cell nucleus and three antipodal cells. (C) Upon germination and growth, the pollen tube is attracted to the ovule by the synergid cells. The pollen tube then releases its generative nuclei in the degenerating synergid, upon which the nuclei fuse with the egg cell and central cell nuclei. (B, C) Drawn after Sundaresan and Alandete-Saez (2010).

conditions (Seguí-Simarro and Nuez, 2008; Fig. 1.1, box 3). Finally, somatic cells can be forced into an embryogenic pathway by treatment of cultured explants with auxin (2,4-D) (Toonen and de Vries, 1996; Fig. 1.1, box 4).

As transpires from the above, a wide variety of cells can generate embryos either naturally or after experimental treatment. However, despite the distinct origins of embryos and the often different patterns of cell divisions within the embryo, the outcome is always a seedling that consists of an apico-basal axis with apical shoot and root meristems, a radial axis that defines the respective tissues, and one or two cotyledons positioned in the immediate surrounding of the shoot apical meristem (SAM). It is therefore likely that a robust set of conserved genetically encoded instructions underlies pattern formation during embryogenesis in all species.

Molecular processes underlying pattern formation and development are best described in *Arabidopsis thaliana*. Due to the regular pattern of cell divisions during embryogenesis (Jürgens and Mayer, 1994), this species has also become the model for studying zygotic embryogenesis. In this review we will discuss embryogenesis in *Arabidopsis* to exemplify basic mechanisms that sculpt the organization of the plant body during embryogenesis. In the following sections, we will first describe the developmental landmarks during embryogenesis, and then discuss the molecular mechanisms that control pattern formation, followed by a perspective on the evolutionary conservation of the regulatory mechanisms that have been found in *Arabidopsis*.

2. LANDMARKS OF EMBRYO PATTERN FORMATION

In angiosperms such as *Arabidopsis*, the female gamete (egg cell) is positioned within the embryo sac, which in turn is embedded in the protective maternal tissue of the ovule inside the carpel (Fig. 1.2A, B). After deposition of a male microgametophyte (pollen grain) on the stigma of the carpel, a pollen tube extends toward the ovule. This tube eventually enters the ovule via its micropylar end and facilitates the delivery of two haploid sperm nuclei. One of these nuclei fertilizes the egg cell while the other fuses with the two nuclei of the central cell to give rise to the triploid endosperm (Lersten, 2004; Fig. 1.2C). Embryo and endosperm develop simultaneously, and several mutant studies suggest that their growth patterns are interdependent (reviewed in Berger *et al.*, 2006). So far, however, there is no conclusive evidence that embryo pattern formation depends on the presence of the endosperm. Hence, consistent with the flexible origin of embryos, pattern formation in the embryo is driven by intrinsic factors rather than by environmental cues.

Embryo patterning follows a series of “landmarks” that each establishes part of the final organization. In the following, we briefly describe each such landmark.

2.1. Formation of the apico-basal axis

Embryo development occurs within the highly polarized environment of the ovule. Both the ovule and the embryo sac have a distinct polarized axis, and also the egg cell is intrinsically polar as judged from the localization of its organelles on the basal (e.g. vacuole) or apical end (e.g. nucleus) (Fig. 1.2C; Lersten, 2004). Fertilization induces stretching of the zygote, which is followed by an asymmetric division that gives rise to two daughter cells with different composition, shape, and developmental fate. The apical cell is small with a dense cytoplasm, while the basal cell is large and vacuolated. With three rounds of cell divisions, the apical cell generates a spherical proembryo consisting of a total of eight cells, while the basal cell only divides transversally and gives rise to a transient filamentous structure called the suspensor. This extra-embryonic suspensor connects the proembryo to maternal tissue and pushes it into the lumen of the ovule. Later during embryogenesis, only the uppermost suspensor cell, the hypophysis, becomes incorporated in the embryonic root meristem, as precursor of the quiescent center (QC) and central root cap cells (see below) (Fig. 1.3A).

At the eight-cell (octant) stage, four different domains can be distinguished along the apico-basal axis of the embryo; the proembryo consists of an upper and a lower tier of four cells each and is positioned on top of hypophysis and suspensor (Fig. 1.3A, B).

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