Current Topics in Developmental Biology

Volume 45

Edited by

Roger A. Pedersen Gerald P. Schatten

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Volume 45

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Front cover photograph: Longitudinal sections through mature (stage 12) wild-type carpels. (For more details see Chapter 4, Figure 2.)

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Preface

Plant developmental biologists will be particularly interested in this volume of *Current Topics in Developmental Biology*. Three chapters are devoted to exciting breakthroughs in plant development. Chapter 1, by Philip W. Becraft, discusses the development of the leaf epidermis. John L. Bowman, Stuart F. Baum, Yuval Eshed, Joanna Putterill, and John Alvarez contributed Chapter 4, which considers the molecular genetics of gynoecium development in *Arabidopsis*. Ben Scheres and Renze Heidstra discuss pattern formation, cell division, and morphogenesis in plants in their cleverly titled chapter "Digging out Roots."

This volume also continues the custom of this series in addressing developmental mechanisms in a variety of experimental systems. In Chapter 2, Giovanni Giudice provides a comprehensive treatment of one of the powerful experimental systems of development—the sea urchin—which had been the subject of some concerns regarding genetic investigations. Anne Camus and Patrick P. L. Tam discuss the organizer of the gastrulating mouse embryo, an essential aspect of mammalian development.

Together with the other volumes in this series, this volume provides a comprehensive survey of major issues in the forefront of modern developmental biology. These chapters should be valuable to researchers in the fields of plant and animal development, as well as to students and other professionals who want an introduction to current topics in cellular, molecular, and genetic approaches to both developmental and plant biology. This volume in particular will be essential reading for anyone interested in plant development and plant biology, morphogenesis and embryo formation, gene regulation of development, development in invertebrates, and molecular basis of mammalian embryogenesis.

This volume has benefited from the ongoing cooperation of a team of participants who are jointly responsible for the content and quality of its material. The authors deserve full credit for their success in covering their subjects in depth, yet with clarity, and for challenging the reader to think about these topics in new ways. We thank the members of the Editorial Board for their suggestions of topics and authors and Liana Hartanto and Michelle Emme for their exemplary administrative and editorial support. We are grateful for the unwavering support of Craig Panner and Hilary Rowe in the editorial office at Academic Press in San Diego. We

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are also grateful to the scientists who prepared chapters for this volume and to their funding agencies for supporting their research.

Gerald P. Schatten Roger A. Pedersen

Development of the Leaf Epidermis

Philip W. Becraft

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I. Introduction

The epidermis is the cell layer which forms the interface between a plant and its environment. As such, the epidermis is crucial for protecting the plant against environmental insults and for regulating the exchange of materials between a plant and its environment. Leaves constitute the majority of the surface area of aerial portions in most plants. Leaves are the major site of gas exchange, transpiration, and attack by insects and pathogens. Thus the leaf epidermis is of particular importance for plant protection. Plant epidermises have evolved various features to allow the performance of this protective role. The epidermis consists of epidermal ground cells interspersed with specialized structures such as stomates, trichomes, or fibers which enable the epidermis to perform its various functions. The waxy cuticle forms a barrier to moisture loss and has been implicated in resistance to insects, pathogens, frost, and UV radiation. The epidermis is also a physically tough tissue, providing mechanical support and protection. In addition, the epidermis plays key roles in development. Evidence suggests that patterns of surface reinforcement are a critical element in organogenesis and shape determination. Likewise epidermal properties are important in controlling whether leaves or floral organs remain as individual organs or fuse into compound structures.

Because of the functional significance of various epidermal components, there is potential practical application in understanding their development. In addition, the epidermis has emerged as a powerful system for studying fundamental processes of development. Questions of cell fate specification, cellular pattern formation, and cellular morphogenesis are readily addressable. Epidermal markers have allowed excellent fate-mapping experiments, interpretation of homeotic transformations, and analysis of cell interactions. The purpose of this review is to provide a broad framework in which to consider these various aspects of epidermal development. The focus will be on angiosperms and particular attention will be paid to model systems where the most information is available.

II. Morphology

General descriptions of epidermal morphology can be found in most plant anatomy texts (Fahn, 1990). Epidermal morphology is extremely variable, reflecting the vast array of environments in which plants grow. The epidermis is most commonly a single-cell layer (uniseriate) although some plants such as *Pepperomia* and *Ficus* contain a multiple, or multiseriate, epidermis (more than one cell thick). The internal cells of a multiple epidermis are commonly large unspecialized cells with no or few chloroplasts and often function in water storage. Some plants form an anatomically similar tissue called the hypodermis or subepidermis, the difference being one of ontogeny; a multiple epidermis is derived by periclinal divisions (new cell wall parallel to the organ surface) of the developing epidermis whereas the hypodermis descends from internal tissues.

The epidermis is covered by a waterproof layer of complex lipid polymers called the cuticle, which will be discussed in detail later. The cuticle has a layered structure and the surface can be variously textured. The cuticle is bound to the cellulosic cell wall by a layer of pectin. Cell wall thickness varies among plants and among cell types within an epidermis although the outer cell wall is frequently