niques developed by the daguerreotypists to improve the images. Of particular interest is the detailed discussion of attempts to produce daguerreotypes recreating natural colors (probably the least known aspect of its history), based on the Becquerel effect. One chapter deals with the use of the daguerreotype as a scientific tool, particularly in astronomy but also in conjunction with geological and archeological expeditions and in anthropology and medicine.

The second section, chapters 8 and 9, deals with the scientific explanation for the daguerreotype and summarizes the extraordinary analytic work undertaken by the authors at the Materials Research Laboratory of Pennsylvania State University. Of special interest is their detailed analysis of the image formation, which is not a photographic development in the strictest sense of the term. We can now appreciate the good fortune and doggedness the pioneer daguerreotypists needed to create their remarkable images.

This laboratory work on the part of the authors was indispensable for tackling the problems of conservation and preservation of daguerreotypes, the subject of the third section. The limitations of early conservation techniques are described and modern ones reported on, in particular reactive sputtering and electrocleaning. One of the first American daguerreotype portraits from life, made by John William Draper, would not have been lost through zealous cleaning



Daguerreotype of Robert Cornelius "demonstrating the proper way to use a syringe-bottle to wash a precipitate out of a beaker onto a filter." Engravings based on daguerreotypes produced by Cornelius were used by James C. Booth to illustrate his book *The Encyclopedia of Chemistry* (1850), "the first chemistry textbook published in the United States." [From *The Daguerreotype*; International Museum of Photography at George Eastman House] if these new techniques had been known in the 1930s. The final chapter of the book is a homily on the value of interdisciplinary studies as applied to problems in the history of science and technology. This book attests to the success of this approach. What makes it especially interesting is seeing the problems through the eyes of material scientists.

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## **Processes in Development**

**Developmental Patterning of the Vertebrate Limb**. J. RICHARD HINCHLIFFE, JUAN M. HURLE, and DENNIS SUMMERBELL, Eds. Plenum, New York, 1991. xii, 452 pp., illus. \$115. NATO Advanced Science Institute Series A, vol. 205. From a workshop, Santander, Spain, Sept. 1990.

The development of the vertebrate limb was first investigated in depth by Ross Harrison in urodele embryos. This volume reflects the growing trend toward molecular studies of limb development and is one of a few volumes to cover the role of development in limb evolution. It will serve as a reference point from which to gauge how fast the field of limb development is advancing when compared to research presented at the Fourth International Conference on Limb Development and Regeneration, which took place recently at Asilomar, California.

The book appropriately begins with an overview chapter by Wolpert that enumerates the major questions about mechanisms of limb development that everyone wants answered. These are (i) how the relative positions of skeletal and soft tissues are specified in the limb; (ii) how the basic blueprint of the segmentation and branching pattern of the limb skeleton is generated; (iii) how specific axial identity arises in each of the skeletal and soft tissue elements; (iv) how the differentiation of skeletal cells and the migration and differentiation of myogenic cells are initiated and maintained; (v) how the form of each limb element is attained; and (vi) what changes in developmental mechanisms are responsible for the evolutionary transformation of appendages.

These questions are addressed in the book's three main sections (on the molecular basis of patterning, on the extracellular matrix in limb development, and on the developmental basis of limb evolution),

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which in all contain nearly 50 chapters. Many of the chapters are simply abstracts of posters, but there are enough long chapters to give an extended and thoughtful view of the various problems in research on limb development. Overview and summary chapters at the beginning and end of each section summarize the broader themes emerging, and they can be read as a group to get a good sense of where the field stands at the moment.

As might be expected, retinoic acid (RA) is a major topic in the first section. The most interesting results, presented by Summerbell and Waterson and by Bryant *et al.*, call into question the idea that RA is the morphogen that specifies the anteroposterior axis of the chick limb bud. They instead affirm that exogenous RA simply posteriorizes the positional identity of anterior cells and turns them into zone-ofpolarizing-activity cells. Maden *et al.* provide the interesting observation that RA is present in the regeneration blastema, suggesting that it plays some important role in limb regeneration.

A major new direction in the molecular analysis of limb patterning is the study of homeobox (Hox) gene expression. In addition to information about the asymmetric spatial and temporal patterns of Hox gene expression in different limb tissues, or within the same tissue, two interesting studies by Lyons et al. and Blundell et al. demonstrate, using the mutants limbless and limb deformity, how interactions between the apical ectodermal Mal ridge (AER) and mesenchyme define patterns of gene expression in these tissues. These studies emphasize the analytical power of combining the experimental manipulation of normal and mutant tissues with the use of molecular probes to study the relationship between tissue interactions and the expression of specific genes. On the molecular level, Tabin et al. describe an interesting set of retroviral gene transfer and tissue culture techniques to directly analyze the developmental functions of cloned genes in limb growth and development.

The section on extracellular matrix contains several notable chapters describing interactions between extracellular matrix (ECM) molecules, cell surface molecules, and growth factors that are involved in initiating prechondrogenic condensation and the role of ECM in the migration of myoblasts from the somites into the limb buds. It is now clear that condensation of precartilage cells is mediated by interactions between several matrix molecules, including heparan sulfate proteoglycans, mesenchymal chondroitin sulfate proteoglycan, fibronectin, and tenascin, as well as syndecan, an integral membrane proteoglycan that links the cytoskeleton to ECM

components. Kosher *et al.* describe interesting experiments implicating several growth factors of the TGF- $\beta$  family, including TGF- $\beta$ 3 and BMP-2A, in the expression of most of these ECM molecules. The unraveling of the relationships of matrix molecules with one another and with growth factors is a growing industry and should provide interesting insights into the molecular mechanisms of limb development.

Christ et al. and Brand-Saberi and Krenn present fascinating evidence that limb myoblasts are derived from the lateroventral edge of the dermamyotome and migrate first out of the anterior half of the somites into the limb bud. This migration appears to be promoted by the ECM-rich environment around the anterior halves of the somites. Migration of myoblasts distally within the limb bud continues as long as there is a high concentration of hyaluronic acid in the undifferentiated subapical mesenchyme of the limb bud. The role of hyaluronic acid is apparently to open up intercellular spaces into which the myoblasts can move.

I particularly enjoyed the section on the role of developmental processes in limb evolution. Alberch and Hinchliffe point out in their chapter that the motor of limb evolution is the regulation of developmental processes, not the accumulation of mutations. Hinchliffe and Coates describe the modern and paleontological evidence that the blueprints for modern tetrapod limbs are species-specific; there is no recapitulation of an archetypal developmental pattern. What is shared by these species-specific blueprints is an asymmetrical branching pattern of cartilage condensations that unfolds in a posteroproximal to anterodistal direction and a set of developmental processes that create this pattern. An example of these shared developmental processes is the interaction between the AER and the mesenchyme that is essential for the outgrowth and patterning of the limb bud. The basic molecular mechanism of this interaction is evolutionarily conserved, as shown in cross-species grafting experiments by Fallon et al.

Muller argues effectively that the most plausible mechanism of limb transformation is pedomorphic heterochrony, that is, the evolutionary modification of rates and timing of developmental processes. The primary developmental modification in the evolution of limbs is the progressive reduction in the number of distal skeletal condensations by suppressing the formation of the anterior structures that are the last ones to form in the developmental sequence. A secondary mechanism of reduction, after the primary pattern is laid down, is the fusion of cartilage condensations.

On the basis of homology considerations

and secondary reductions in limb elements, the evolutionary biologists favor mechanochemical models of skeletal patterning over positional-information models. In a mechanochemical model, patterning is a result of the skeletal condensation process itself, whereas positional-information models require graded chemical signals to specify the primary pattern. Branching per se is viewed as a physical property of growing condensations that is sensitive to a small set of developmental parameters such as the size and shape of the limb bud and the mechanical properties of the extracellular matrix. Unlike positional information models, mechanochemical models can account for the secondary fusion of skeletal condensations and for the fact that extra digits can be induced from interdigital mesoderm at a late stage of development, when positional signals are presumably no longer operating (Hurle). On the other hand, positional signaling models are better able to account for the formation of two humeri in double anterior half limb constructs that are made well before the stage of cartilage condensations (Wolpert). Further experiments clearly will be required to resolve the difficult and complex issue of the types of mechanisms that operate to specify limb pattern.

Overall, this is a book that is well worth reading, and judging from the research it represents, we can expect to see some major advances emerge in our understanding of limb development and evolution in the not too distant future.

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## **Maize Models**

The Origins of Southwestern Agriculture. R. G. MATSON. University of Arizona Press, Tucson, 1991. xvi, 356 pp., illus. \$55.

One of the problems that has fascinated archeologists in the southwestern United States for at least 70 years is how and when agriculture reached this region. Several explanations have been presented over the years, but none has ever been completely accepted and few have been completed rejected. For those actively involved in researching this problem, or for those who need an up-to-date treatment of the current status of knowledge and the history of research on this problem, R. G. Matson has written a valuable book.

Matson's objective is to examine, in both empirical and explanatory fashion, the

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spread of agriculture from the United States-Mexico boundary northward across the Colorado Plateau. His principal focus is the origin of the pre-ceramic Basketmaker II culture of the Colorado Plateau, the earliest group in that region to successfully-and apparently intensively-cultivate maize and other crops. He approaches the problem by evaluating the predictions of two existing explanatory models against an extensive, up-to-date empirical data base and by offering a new model of his own. The first of the two existing models, the in situ development of Basketmaker II from indigenous Archaic hunting-gathering populations who acquired agriculture, has been deeply rooted in the southwestern literature since the 1920s. The second model, dating to the 1950s, invokes a "migration" of agricultural, pre-ceramic, San Pedro Stage, Cochise Culture populations from southern Arizona and New Mexico onto the Colorado Plateau to become Basketmaker II. Matson presents a new "maize evolutionary model," which posits a three-stage sequence of agricultural spread and development dependent upon perceived changes in maize cultivation practices and in maize itself.

To evaluate the current status of the two older models, Matson devotes the first three chapters (better than half the book) to an intensive and thorough examination of the state of empirical knowledge about Basketmaker II and the Colorado Plateau Archaic. Chapter 2 discusses Basketmaker II archeology. Organized along historical lines, it provides a good perspective on the development of knowledge about this cultural group, and effectively demonstrates the range of variability that has been subsumed under this cultural label. Using attributes of architecture and material culture, Matson identifies distinctive western and eastern geographic variants of Basketmaker II and three temporal variants spanning the period between approximately 500 B.C. and A.D. 400. This synthesis alone represents a tremendous collation of information, including Matson's own research at Cedar Mesa, Utah. Chapter 3 discusses the pre-agricultural Archaic period for the Colorado Plateau as well as the Basin and Range Province to the south and west, providing an excellent foundation for examining settlement, subsistence, and culture history of the Southwest prior to Basketmaker II. It too is guite comprehensive and like chapter 2 includes a great deal of often obscure or unpublished contract work.

However, much detailed information in these chapters is presented in the form of "sidebars," which appear in smaller type in columns along the outer half of the page. These sidebars treat selected sites in greater detail, but it is sometimes unclear why a