

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 (Hurler). 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 completely 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

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 quite comprehensive and like chapter 2 includes a great deal of often obscure or unpublished contract work.

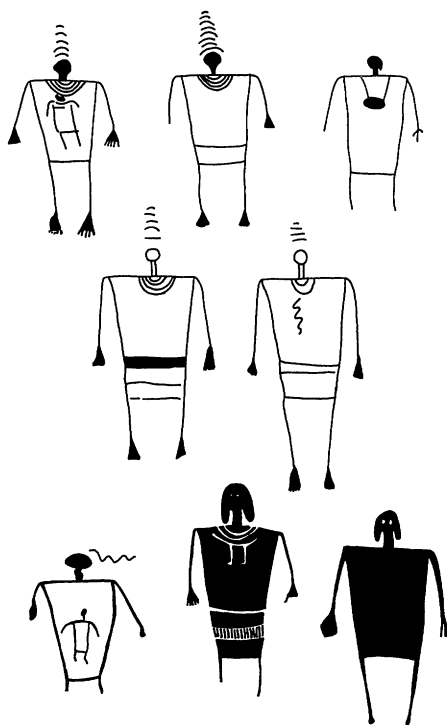
However, much detailed information in these chapters is presented in the form of "sidebars," which appear in smaller type in columns along the outer half of the page. These sidebars treat selected sites in greater detail, but it is sometimes unclear why a

particular site is discussed in a sidebar instead of in the regular text. The sidebars, some of which extend for two or three pages, also lack headings to permit quick assessment of their subjects.

In chapter 4 Matson presents his evolutionary model of maize use, which in my judgment is the least successful aspect of the book. This model is derived from the integration of data in the evolutionary history of maize; morphology and ecology of "Chapalote, the earliest corn race found in the Southwest"; and changes in cultivation practices over time and space. Matson proposes that the earliest agriculture in the Southwest was floodwater farming of arid-adapted Chapalote maize in the lowland Basin and Range Province at about 1000 B.C. It was succeeded, by approximately 500 B.C., on the Colorado Plateau by floodwater farming involving cultivars more tolerant of colder, shorter growing seasons and deep planting to utilize stored soil moisture. This coincided with the initial appearance of Basketmaker II culture. The third stage, highland dry farming, necessitated maize with greater tolerance of colder and still briefer growing seasons, and perhaps greater drought resistance as well; it appeared by approximately A.D. 200 to 400.

The maize model treats several issues common to earlier discussions of the origins of southwestern agriculture, and it could actually be viewed as a reformulation of Emil Haury's seminal model on the subject. Somewhat inexplicably, Matson never compares his maize model to Haury's model, of which it is almost the antithesis. Matson posits that the earliest maize was grown in the lowland Basin and Range Province instead of the highlands above 6000 feet; that agriculture spread from the lowlands to the highlands instead of vice versa; that the earliest cultivation was by floodwater farming instead of dry farming; and that early maize was adapted to arid rather than mesic environments. Both models require that maize undergo genetic change before it spreads outward from its initial, optimal areas of cultivation.

In my view the maize model suffers from two principal flaws: an explanatory focus on cultivation practices, and reliance on the ecology of the modern Chapalote maize race to reconstruct that of pre-ceramic southwestern maize. With regard to the first point, Matson assumes that floodwater farming and dry farming are distinct forms of cultivation and that the former is the more ancient. Interestingly, he conceives of early agriculturalists in southeastern Arizona's river basins as practicing floodwater farming, despite the fact that the known early agricultural sites are located along perennial or semipermanent streams where water-table farming or even simple forms of "pot" (perhaps better described as "gourd" for the pre-ceramic



"Basket maker II rock art human figures." Adapted from P. Schaafsma's *The Rock Art of Utah*, Peabody Museum Papers, vol. 65, 1971.

period) or canal irrigation would be possible. Regardless, the problem is that we remain ignorant of what cultivation techniques were in use prior to the Christian era, and we will be hard pressed to identify them archeologically. There is no particular reason to suppose that floodwater farming was the earliest or the only cultivation method known at that time, nor is there any obvious explanatory value in focusing so closely on cultivation techniques. Second, the use of modern Chapalote as a morphological and ecological analog for pre-ceramic maize may be questioned. This practice has a long history in the Southwest, ultimately being rooted in the work of Mangelsdorf and his now nearly discredited theory of maize evolution. Chapalote was seen as "primitive" on the basis of its grain color and cupule structure, but recent morphological and isozyme studies have challenged this view. It seems inadvisable to uncritically accept modern Chapalote, the product of at least 3000 years of additional human and natural selection, as wholly representative of early Southwestern maize for modeling purposes.

Finally, the evidence to contradict the maize model may already be on hand. As Matson notes in chapter 5, which discusses the age of maize in the Southwest, maize directly dated to approximately 2800 to 3100 years ago has been found from sites in the Basin and Range of southeastern Arizona and southwestern New Mexico up into the Mogollon Highlands at Bat Cave and on the Colorado Plateau near Chaco Canyon, per-

haps even at Three Fir Shelter on Black Mesa. One might reasonably conclude from this distribution that early maize could be successfully cultivated across this full range of environments and that no evolutionary sequence of changes in cultivation practices or maize itself was necessary for its apparently rapid spread across the Southwest. That improved cultivars and new cultivation practices did appear later is not an issue; the archeological and ethnographic records demonstrate both. Maize has been shown to be remarkably plastic in its ability to grow in a wide range of habitats, and there is no reason to suspect that early maize was any less able to adapt to a broad range of growing conditions through repeated exposure to both human and natural selective pressures.

In chapters 6 through 8, Matson evaluates the fit between the available data on early agriculture and the expectations of all three models. Although he finds neither of the two older models to be decisively supported or discredited by the available archeological data, he does conclude that the maize model appears to be supported as a developmental sequence independent of either the *in situ* development or migration models. However, in my view the maize model rests largely on an inferred sequence of changes that treats cultivation techniques and maize ecology as the sole explanatory factors in the complex issue of how maize agriculture was able to spread across the Southwest. As a model, it is therefore difficult to assess from empirical data and may be extremely hard to either verify or falsify.

Despite my reservations about his maize model, Matson's book is one that any student of the transition from hunting and gathering to agriculture in the southwestern United States will find informative and thought-provoking. It represents the only up-to-date synthesis of the Archaic and early agricultural periods that considers the entire Southwest, and it should provide researchers with a much fuller picture of this complex issue than has been available before.

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## Other Books of Interest

**Geology of Japan.** MITSUO HASHIMOTO, Ed. Terra Scientific, Tokyo, and Kluwer, Boston, 1991. x, 249 pp., illus. \$125. *Developments in Earth and Planetary Sciences*, 8. Translated, with revisions, from the Japanese edition (1980).

Japan played such an important role in the development of plate tectonic theory that it