Seeking Agriculture's Ancient Roots

As they pinpoint when and where many crops were first domesticated, researchers are painting a new picture of how—and perhaps why—humans began to change their relationship to plants

JALÈS, FRANCE—In his lab in a 12th century fortress that now houses the Archéorient research center here, archaeobotanist George Willcox pops the top off a plastic capsule filled with tiny black particles, spills them out into a petri dish, and puts the dish under a binocular microscope. Magnified 50 times, the particles leap into focus. They are charred fragments of wheat spikelets from a 10,500-year-old archaeological site in Turkey called Nevali Çori. Wheat spikelets are attached to the central stalk of the wheat ear and carry the seeds, or grain, that humans grind into flour. "Look at the scar at the lower end of the spikelet, where it has broken off," Willcox says. The scar is jagged—a hallmark of domesticated wheat. It's a sign that the spikelet did not come off easily but detached only when harvested, so the plant probably needed human help to disperse its seeds. "This is the earliest evidence for domesticated wheat in the world."

Willcox spills the contents of a second capsule into another dish. The scars are round and smooth, showing that these spikelets easily detached and dispersed their stores of grain. "This is wild wheat, also from Nevali Çori," he says. So in the earliest cultivated fields, wild and domesticated wheat grew in close proximity.

The scarred spikelets under Willcox's microscope represent one simple, physical sign of a very complicated process: the rise of agriculture. Farming was revolutionary in its implications for humanity, providing the food surpluses that later fueled full-blown civilization, with all of its blessings and curses. Domestication—defined as the physical changes plants undergo as they adapt to human cultivation—was key to this transformation. It allowed former foragers to increasingly control when, where, and in what quantities food plants were grown rather than simply depending upon the vagaries of nature. And unlike other aspects of early agriculture, such as whether a seed was planted or simply gathered by human hands, "domestication is visible" in the archaeological record, says archaeologist Timothy Denham of Monash University in Clayton, Australia.

Over the past decade, a string of high-profile papers has pinpointed the time and place of the first domestication of crops, ranging from wheat and maize to figs and chili peppers. Now researchers are beginning to fit all of these into a larger story of worldwide plant domestication.

Research field. George Willcox grows cereals for science at Jalès.

At Nevali Çori, where wild and domesticated plants grew in the same fields and perhaps even exchanged genes, Willcox and colleagues conclude that full domestication might have taken thousands of years rather than the 200 years or fewer that some archaeobotanists had predicted. "They could not have gone from one kind of economy to another in just a few generations," Willcox says of the early cultivators. "These things happened gradually."

A decade or so ago, most archaeologists saw the advent of agriculture as an abrupt break with the hunting-and-gathering lifestyle on which hominids had relied for millions of years. Researchers thought that domesticated crops appeared very soon after people began to cultivate fields, first in the Near East as early as 13,000 years ago, then somewhat later in a handful of other regions.

But the new data suggest that the road from gathering wild plants to cultivating them and finally domesticating them was long and winding (see chart on p. 1835), unfolding over many millennia. "If the agricultural revolution is supposed to be evidence for a punctuated change in human cultural evolution, it seems to have taken quite a long time to get to the punctuation point," says archaeobiologist Melinda

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Wheat's-eye view. Crop plants adapted slowly to human cultivation, evolving on a time scale of millennia rather than centuries.

Zeder of the Smithsonian Institution in Washington, D.C. Douglas Kennett of the University of Oregon, Eugene, agrees. "Agriculture was not a revolution," he says. "People were messing about with plants for a very long time."

Clues to how this slow transition took place are accumulating rapidly. An alliance of archaeologists and geneticists armed with new techniques for probing plant genomes and analyzing microscopic plant remains (see sidebar on p. 1834) has been tracing the route to farming in much closer detail. In the Near East, for example, researchers are finding that domestication itself happened a bit later than had been thought, although humans apparently cultivated wild cereals for thousands of years before plants showed physical changes. Meanwhile, new research in the Americas has pushed the dates for the first domestication of squash and other crops back to about 10,000 years ago, making the roots of farming in the New World almost as deep as those in the Old World.

Moreover, new archaeological work shows that plants were domesticated independently in many parts of the globe. There is now convincing evidence for at least 10 such "centers of origin," including Africa, southern India, and even New Guinea (see map on p. 1833). "All around the world, people took this very new step and started cultivating plants," which led to their domestication, says Smithsonian archaeobotanist Dolores Piperno. The rush of new data could help eventually solve the puzzle of why agriculture arose in the first place—a riddle archaeologists have been trying to solve for nearly a century.

Wild plants: The long goodbye

In his writings about evolution, Charles Darwin argued that domestication was a clear example of selection in action. By cultivating plants—growing them deliberately—humans intentionally or unintentionally select certain traits. Today, researchers define domestication as the genetically determined physical and physiological changes a plant has undergone in response to human behavior. "Domestication is the result of genetic changes that have evolved because of cultivation," explains archaeologist Dorian Fuller of the Institute of Archaeology at University College London (UCL).

These alterations make up what botanists call the "domestication syndrome": signs that plants have adapted to humans and that researchers eagerly seek at archaeological sites. In cereals such as wheat and barley, the syndrome includes the tendency for spikelets to stay on the stalk until they are harvested, as seen in the jaggedly scarred specimens found at Nevali Çori, plus larger seeds and a thinner seed coat that allows easier germination. (It also includes less visible traits, such as simultaneous flowering times.)

Once humans began to cultivate plants, how long did domestication take? In 1990, the pendulum swung toward a rapid scenario after archaeobotanist Gordon Hillman of UCL and plant biologist Stuart Davies of Cardiff University in Wales plugged data from cultivation experiments into a computer model. They concluded that domestication might have occurred within 200 years and perhaps in as few as 20 to 30 years, assuming, as many archaeologists have, that early farmers used sickles to harvest their crops. Sickles presumably would have strongly selected for spikelets that stayed on the stalk until harvest, because those that dropped earlier would be lost and not replanted. "It was possible to put together a nice story, that agriculture appeared fairly abruptly," says botanist Mark Nesbitt of the Royal Botanic Gardens, Kew, in Richmond, U.K.

Before long, however, new data began to raise doubts about this story. For example, at Jalès, Willcox and colleagues conducted experiments in a nearby field, cultivating wild varieties of wheat, barley, and rye to deduce how quickly domesticated forms might evolve. The answer: not very fast. No matter how researchers harvested the grains, a good portion of the easy-to-detach wild spikelets fell to the ground and germinated to sprout a new generation of wild wheat.

Meanwhile, a remarkable discovery in Israel also suggested a long run-up to domestication. In 1989, a team led by Dani Nadel of the University of Haifa in Israel began excavating a site called Ohalo II on the southwest shore of the Sea of Galilee. The site was radiocarbon-dated to 23,000 years ago, when the last Ice Age was still in full frost and at least 10,000 years before the earliest domesticated plants. Excavators found the remains of huts, plus a burial and several hearths. More than 90,000 individual plant remains were recovered, including acorns, pistachios, wild olives, and lots of wild wheat and barley. But "there is not a single domesticated species at this site," says team member Ehud Weiss of Bar-Ilan University in Ramat Gan, Israel, nor any evidence that the people of Ohalo II were cultivating the cereals rather than just gathering them.

To their surprise, however, the researchers, in collaboration with Piperno, found microscopic remains of barley and possibly wheat on a large stone implement. They concluded that the inhabitants of Ohalo II had ground the grains to make flour and possibly also baked dough in one of the ovenlike hearths.

"Ohalo II is an important warning to archaeologists," Fuller says. "We need to abandon some of our long-held assumptions that as soon as people began to use cereals, they would begin to [cultivate and] domesticate them."

More recently, some researchers have begun taking a second look at just when domesticated plants first showed up in the Near East. For decades, excavators had pegged this transformation to an archaeological period that began about 11,800 years ago and is marked by the first permanently settled villages. There were a few claims for even earlier dates, such as a few relatively large seeds of rye at Abu Hureyra in Syria, dated to about 13,000 years ago, and which Hillman argued were domesticated. But in a 2002 survey, Nesbitt found that the earliest Near Eastern villages lacked definitive evidence of domesticated cereals, although wild plants were plentiful. Unambiguous signs of domestication didn't turn up until about 10,500 years ago, in larger settlements with different architecture and a much more complex social organization, he concluded.

All in the family. Maize and its wild ancestor teosinte (*left*) are closely related despite their differences.

"There is no current evidence for domesticated plants in the [first settled villages]," Weiss agrees. "But it was probably a very energetic period, when people all across the region were playing with cultivation of wild plants." And once plants were domesticated, making farming more efficient and intensive, this way of life apparently exploded across the Near East, as large farming villages sprung up like mushrooms and people quickly formed trade and communication networks over the entire region.

The notion of a long run-up to domestication also gets support from new findings by Willcox and archaeobotanist Ken-ichi Tanno of the Research Institute for Humanity and Nature in Kyoto, Japan. They examined charred wheat spikelets from four sites of different ages in Syria and Turkey. There was a clear trend over nearly 3000 years: Earlier sites had fewer domesticated spikelets and later sites had more. At 10,500-year-old Nevali Çori, only about 10% of the spikelets were clearly domesticated, whereas 36% were domesticated at 8500-year-old el-Kerkh in Syria and 64% at 7500-year-old Kosak Shamali, also in Syria, Willcox and Tanno reported last year in *Science* (31 March 2006, p. 1886). These results suggest that wild varieties were only gradually replaced by domesticated ones, they say.

"Domestication was the culmination of a lengthy process in which plants were cultivated but retained their wild phenotypes," says geneticist Terry Brown of the University of Manchester in the U.K. "Early farmers were receiving the benefits of agriculture long before domestication evolved." Even Hillman says that he is "very impressed" with the analysis, although it contradicts his previous work: "[Domestication] probably did take this long."

But why? Fuller, in an article earlier this year in the *Annals of Botany*, suggests that humans may have exerted weak rather than strong selection pressure on their crops. "Weaker selection means domestication would take longer, while stronger selection means it would happen more quickly," he explains.

And there are many ways that early farmers' behavior might have weakened selection. For example, Fuller questioned whether sickles were actually used in early harvesting. Other methods, such as picking already-fallen spikelets from the ground, would not have selected for spikelets that stay on the stalk. Although sickles date as far back as 15,000 years ago, no domesticated plants show up before 10,500 years ago. So the first sickles may have been used for other tasks, such as cutting reeds for floor matting, rather than harvesting grains, Fuller argued.

Willcox favors an alternative explanation: During hard years, early farmers replenished their seed stocks with wild varieties, thus slowing domestication. Only when farmers began planting domesticated plants farther from the wild stands—

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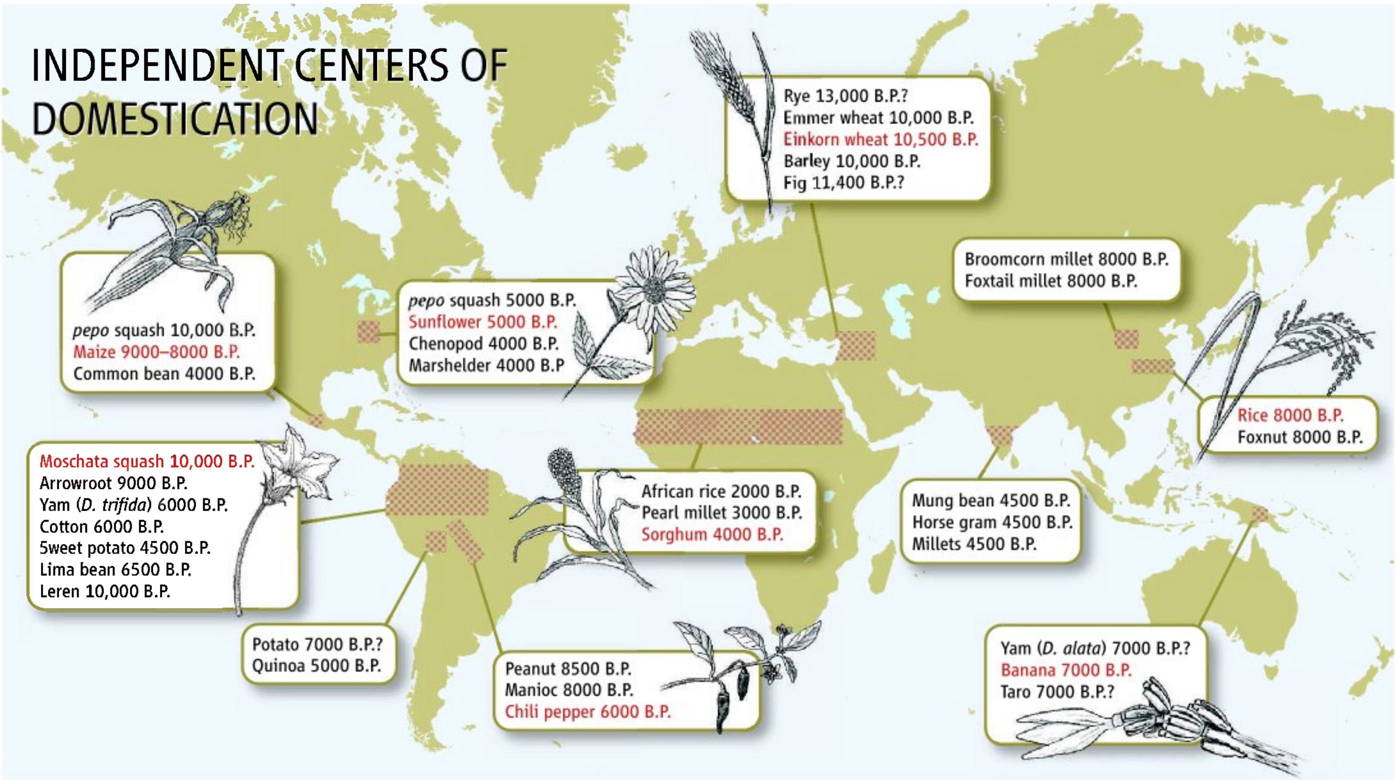


Multiple birth. People in many different parts of the world independently began to cultivate and eventually domesticate plants.

physically and genetically isolating them from their wild ancestors—did the process speed up, he says. Reproductive isolation of domesticated and wild plants could have acted as a "trigger," agrees Manchester's Brown, spurring increasing proportions of domesticates as farming spread across the Near East. Eventually, says Weiss, sowing, tilling, and harvesting "create[d] these artificial environments that lead to domestication. … It meant totally new ideas and a totally new way of life."

New World, new paradigm

At the same time that archaeologists are concluding that Old World crops were fully domesticated a little later than once thought, recent discoveries are pushing domestication in the New World back, way back. Not so long ago, researchers saw little evidence for farming of crops such as squash, maize, and manioc before about 5000 years ago. "Some archaeologists thought little of importance had taken place in these tropical forests," Piperno says. "We didn't have the data." Researchers now have new methods to identify microscopic bits of poorly preserved tropical plants, and genetic studies can date when domesticated lineages split from wild ancestors.

"We were misled by what was not preserved and what we could not see," says anthropologist Tom Dillehay of Vanderbilt University in Nashville, Tennessee. "These people had a very sophisticated knowledge of the plants that were out there."

Archaeologists began to see more clearly back in 1997, when the Smithsonian's Bruce Smith radiocarbon-dated domesticated seeds and other fragments of pepo squash seeds from a cave near Oaxaca, Mexico, to nearly 10,000 years ago (*Science*, 9 May 1997, pp. 894 and 932). The signs of domestication were clear: The seeds were larger and the stems and rinds thicker than those of closely related wild squash that still grows in the region; indeed the fragments found were identical to today's domesticated pepo squash. Since then, earlier dates have steadily accumulated for the domestication of nearly every New World crop. Piperno's team has dated starch grains from domesticated manioc, arrowroot, and maize on milling stones in Panama to up to 7800 years old, and other Panamanian sites have yielded dates for these crops that are nearly as early.

Wild. A 23,000-year-old wheat fragment from Ohalo II.

This week, on page 1890 of this issue of *Science*, a team led by Dillehay reports 10,000-year-old squash and 8500-year-old peanuts on the floors and hearths of houses made of stone and reeds in the Andes Mountains of Peru. Genetic studies and the distribution of possible wild ancestors suggest that these crops were probably domesticated elsewhere, in South America's lowland tropical forests. So these very ancient dates show how quickly domesticated crops spread from their original centers of origin, the team concludes. But identifying domestication is not always easy: Smith questions whether Dillehay's evidence proves that squash, peanuts, and other plants had actually undergone "any of the genetic or morphological markers of domestication."

All the same, the flurry of early dates in the New World is "remarkable," says ethnobotanist Eve Emshwiller of the University of Wisconsin, Madison, because the first domesticates appear not too long after humans colonized the Americas, at least 13,000 years ago. That's a contrast to the Old World, where people lived for tens of thousands of years before domesticating plants. Dillehay agrees: "People between 13,000 and 10,000 years ago were adapting

CREDITS (TOP TO BOTTOM): J. NEWFIELD AND K. SUTLIFF/*SCIENCE*; SOURCE: B. SMITH AND D. PIPERNO/SMITHSONIAN; COURTESY OF EHUD WEISS to [changing climatic conditions] more favorably than we had thought before."

Genetic data support the early dates, too. For example, John Doebley of the University of Wisconsin, Madison, genotyped numerous specimens of that New World staple, maize, and its wild ancestor, teosinte. From the number of genetic changes between teosinte and maize, and the likely speed of the "molecular clock," Doebley's team concluded in a paper published in the *Proceedings of the National Academy of Sciences* (*PNAS*) in 2002 that maize was domesticated about 9000 years ago. And they found that maize was probably domesticated only once, in the Balsas River Valley of southern Mexico.

In an astonishing stream of studies, Doebley and other researchers have also taken a detailed look at the genetic changes underpinning maize domestication. The transformation of teosinte to maize was dramatic, as these plants look so different that researchers once doubted their relationship. Ears of teosinte are multistalked and have only five to 12 kernels, whereas single-stalk maize ears have 500 or more. A tough casing also protects teosinte kernels, whereas maize kernels are "naked" and accessible to humans. Indeed, some archaeologists have suggested that the unappetizing teosinte was first domesticated to make alcoholic drinks from its sugary stalks rather than for the dinner table.

Maize domestication genes include *tb1*, which controls the number of stalks, *pbf*, which controls protein storage in the kernel, and *su1*, which affects starch storage. Recently, Doebley teamed up with ancient DNA specialists to track changes in these genes in ancient maize, using 11 maize cobs from Mexico and New Mexico dated from 5000 to about 600 years ago. The domesticated variants of *tb1* and *pbf* were present in all the ancient DNA samples, and all the Mexican cobs had the domesticated variant of the *su1* gene. But 1900-year-old cobs from New Mexico showed a mix of wild and domesticated variants, the team reported in *Science* (14 November 2003, p. 1158).

If the domesticated variant of *su1*—which may give corn the properties necessary for making good tortillas—was not widespread in maize populations until much later, then domestication might have taken place over an extended period, the team concluded. "There must be several stages to genetic domestication of plants," says Manchester's Brown.

Doebley's work has spurred the archaeologists to try to keep up. His finding that maize was domesticated 9000 years ago in Mexico's Balsa River region inspired Piperno's international team to comb the valleys in search of confirmation, for example. In the 30 May online edition of *PNAS*, they reported preliminary evidence that domesticated squash and maize were grown on ancient lakesides probably by 8500 years ago, although the dates are not yet confirmed. "We think that before long we will be able to push the archaeological dates back to match the genetic data," says Piperno.

Yet even if people in the New World were domesticating plants early, they did not necessarily become full-fledged farmers right away, some archaeologists argue. "The first plant domestication was 10,000 years ago, but the development of village-based agricultural economies did not happen until more than 5000 years later," says Smith. In a 2001 paper in the *Journal of Archaeological Research*, Smith argued that in many parts of the world initial plant domestication was followed by a long period of "low-level food production," during which prehistoric peoples continued to hunt and gather while slowly adding already domesticated crops to their diet.

"Domestication of a plant is one thing, and fully adopting it is another," agrees Dillehay. But he argues that his new evidence from the Peruvian Andes, which includes houses, may indicate that both settled village life and farming economies arose earlier than researchers thought, at least in some parts of the Americas. Piperno agrees that the work of Dillehay and others may now be providing the "missing evidence" to fill at least some of that 5000-year gap.

Tell me why

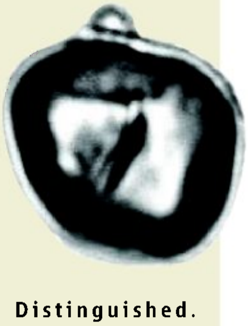
Back in the 1950s, many archaeologists thought agriculture was born in only two places: the Near East and the Americas. From these two fountainheads of farming, the story went, agriculture spread throughout the world. Yet archaeologists now recognize at least 10 independent centers, and even regions once thought to be agricultural backwaters have taken on a new importance. In 2003, a team led by Monash's Denham clinched the case that bananas, taro, and yams were independently domesticated in New Guinea nearly 7000 years ago (*Science*, 11 July 2003, p. 180).

So if domestication happened repeatedly, what sparked this new relationship between people and plants? Researchers have pondered the question since the 1920s, when Australian prehistorian V. Gordon Childe

STARCH REVEALS CROP IDENTITIES

Until very recently, archaeologists searching for the first domesticated forms of tropical plants such as yams, manioc, and bananas just kept on looking. The humid tropical environments in which these plants grow destroyed evidence of their existence, leaving archaeologists with "patchy and speculative" accounts of their domestication, says archaeobotanist Andrew Fairbairn of the University of Queensland in Brisbane, Australia.

Then in the mid-1990s, archaeologists realized the potential of starch grain analysis, a technique used for more than a century by botanists to identify modern plants. Plants manufacture and store starches in microscopic organelles called amyloplasts. Both the size of the amyloplasts and the pattern of starch deposition vary from plant to plant, often making it possible to distinguish species. "This methodology makes things visible that were previously invisible," says archaeobotanist Linda Perry of the Smithsonian Institution in Washington, D.C. That new visibility has pushed back the dates of domestication for a number of tropical crops, including squash, manioc, and chili peppers (see main text). When Perry and her colleagues went looking for chili pepper starch grains in Central and South America, for example, they found them seemingly everywhere: in sediments, on milling stones and stone tools, and on pottery shards. The oldest date back to 6100 years ago.



Distinguished. Starch grains identify manioc (*top*) and maize (*bottom*).

What's more, in some plants—although not all—starch grains of wild and domesticated strains are distinct. For example, starch grains of wild chili peppers are 5 to 6 micrometers long, whereas the domesticated versions are a whopping 20 micrometers. The method is now used to identify everything from bananas to maize to wild barley and has "breathed new life into the investigation of early agriculture," says Timothy Denham of Monash University in Clayton, Australia.

–M.B.

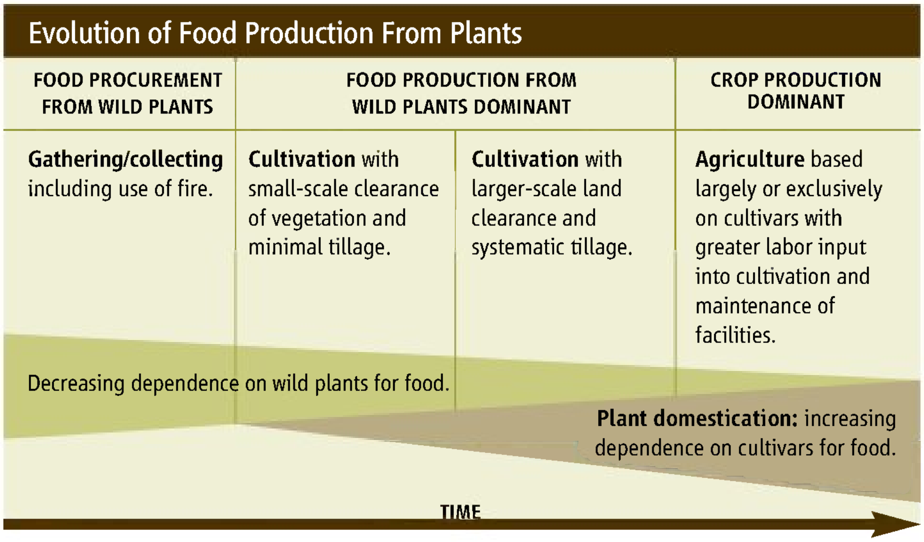
CREDIT: COURTESY OF DOLORES PIPERNO AND LINDA PERRY pegged the rise of farming to dramatic climatic changes now known to have taken place around 11,500 years ago. That's when the last Ice Age ended and the Pleistocene period gave way to the much milder Holocene—the geological epoch in which we live today, with a warmer, wetter, and more stable climate.

Childe's hypothesis sparked a lot of research. But since his day researchers have swung back and forth between environmental explanations and those that focus more on social changes within increasingly sedentary communities of hunters and gatherers. All the same, most archaeologists agree that the origins of agriculture have something to do with the broader transition from the Pleistocene to the Holocene. "I am comfortable seeing this climate change as a precondition for agriculture," says the Smithsonian's Smith. But he points out that it can't be the sole explanation for the rise of farming in regions such as eastern North America, where squash and several other crops were domesticated only about 5000 years ago.

Some researchers correlate the origins of farming not with the early Holocene but with a late Pleistocene global cold snap called the Younger Dryas, which hit about 13,000 years ago and sharply reversed warming trends for more than a millennium. This hypothesis was prompted by excavations at Abu Hureyra in Syria's Euphrates Valley, led by British archaeologist Andrew Moore, now at the Rochester Institute of Technology in New York. Abu Hureyra was first occupied by hunter-gatherers about 13,500 years ago and later by early farmers, providing a rare window on the transition to agriculture. UCL's Hillman, who analyzed the plant remains, suggested that the Younger Dryas had a devastating effect on the availability of the wild cereals and other plants at the site. Hunter-gatherers eventually disappeared, and a short time later possible first evidence of farming—larger grains of rye—show up. Hillman and Moore proposed that the region's hunter-gatherers invented agriculture to solve food shortages brought on by the cold climate.

"Hillman's evidence is convincing," at least for the Near East, says Piperno. "The Younger Dryas may have been some kind of trigger." The worldwide invention of agriculture, Piperno adds, suggests "that there must have been a common set of underlying factors."

But not everyone is persuaded by Hillman's case for rye domestication. And after its possible appearance at Abu Hureyra, domesticated rye doesn't show up for thousands of years anywhere in the Near East. Even if the Younger Dryas can explain the sequence of events at Abu Hureyra, it hasn't been shown to spur farming in other regions, says David Harris of the Institute of Archaeology in London. Willcox, in a 2005 review of Near East farming in the journal *Vegetation History and Archaeobotany*, argued that agriculture did not really catch on until after the Younger Dryas was over and the Holocene, with its more stable climatic conditions, had begun.



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Indeed, the agricultural lifestyle might have been "impossible" during the glacial conditions of the Pleistocene but "mandatory" during the Holocene, argued ecologist Peter Richerson of the University of California, Davis, and his colleagues in a 2001 paper in *American Antiquity*. One explanation: Dramatically lower carbon dioxide levels during the Pleistocene might have made farming untenable, a hypothesis first proposed back in 1995 by botanist Rowan Sage of the University of Toronto. Crops grow more in higher ambient CO_2 levels. As the Holocene began, CO_2 levels rose by roughly 50%, from 180 parts per million to 280 ppm in just a few thousand years, according to polar ice-core records. "This would have had a big effect on photosynthesis and plant productivity," Richerson says.

The Pleistocene-Holocene transition might also have affected decisions about what to eat. Recently, Piperno, Denham, Kennett, and others have been studying the choices humans make, borrowing methods from optimal foraging theory, a Darwinian approach that assumes humans and other animals pursue the most advantageous strategy for getting food. In a recent study, Piperno looked at the lowland tropics of the New World, as forests expanded into once-open areas. Based on the changing availability of both plants and animals, she calculated that farming would have been more advantageous than foraging right around the time that the first domesticated crops appear, about 10,000 years ago.

But some archaeologists think that too much emphasis on environmental explanations gives short shrift to the less easily testable social and symbolic aspects of human behavior. "We have tended to leave these aspects out and focused on an economic paradigm," says archaeologist Joy McCorriston of Ohio State University in Columbus.

In the 1980s, for example, the late French prehistorian Jacques Cauvin, who founded the Jalès center, proposed that in the Near East a rise of religious symbolism changed the relationship between people and nature and made farming possible. More recently, archaeologist Brian Hayden of Simon Fraser University in Burnaby, Canada, argued that farming had been invented by ambitious hunter-gatherers seeking greater prestige and wealth within their communities.

As ideas are batted back and forth, some doubt that a global explanation for agriculture will be found. "We are all thrashing around, trying to find an explanation for something that is worldwide," says archaeologist Graeme Barker of the University of Cambridge in the U.K. "It is far too simplistic." But that won't stop researchers from trying. Says Kennett: "The transition to agriculture is one of the central questions in archaeology. We need to understand it."

–MICHAEL BALTER

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